CYMINDINE LEBIINI OF AUTHORS: REDEFINITION AND RECLASSIFICATION OF GENERA (CLEOPTERA: CARABIDAE)

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ABSTRACT

Based on examination of character states of adults (in particular, sclerites of the ovipositor) of a limited sample of taxa, heretofore included in the lebiine subtribe Cymindina (= Tribes Cymindina and Pseudomasoreini, or Subfamily Cyminditae of authors), the following tribes and subtribes were found to be represented: Tribe Pterostichini, subtribe Platynina; Tribe Lachnophorini; Tribe Lebiini, Subtribes Pericalina, Apenina, Cymindina, Calleidina, and Dromiina; and Tribe Zuphiini. The South African Anarmosta *Péringuey, 1896 (= Euplynes Schmidt-Goebel, 1846) is confirmed as a platynine. The New World tropical and subtropical* Eucaerus *LeConte, 1853 and* Lachnaces *Bates, 1872, are included in the* Eucaerus *complex, and transferred to the Lachnophorini.* Eucaerus *and* Lachnaces *are regarded as congeneric subgenera (new rank). Also included in the* Eucaerus *complex are the Neotropical genera* Asklepia *Liebke, 1938, and* Phaedrusium *Liebke, 1951. Transferred to the subtribe Pericalina are the Afrotropical (South African)* Leptosarcus *Péringuey, 1896, and (East African montane)* Selenoritus *Alluaud, 1917, the latter included as a subgenus of* Thyreopterus *Dejean, 1831 (new rank). Transferred to the subtribe Apenina are three genera: the New World* Apenes *LeConte, 1851, with subgenera* Apenes sensu stricto *(=* Malisus *Motschulsky, 1864), and* Sphalera *Chaudoir, 1875 (=* Didymochaeta *Chaudoir, 1875, new synonymy); Palaearctic* Trymosternus *Chaudoir, 1873; and the Old World Tropical* Cymindoidea *Castelnau, 1832. The latter genus includes as subgenera* Cymindoidea (sensu stricto), Platytarus *Fairmaire, 1850 (new rank), and* Habutarus *new subgenus (generitype* Nototarus papua *Darlington, 1968). The subtribe Cymindina includes the new Oriental genus* Ceylonitarus *(generitype* C. ceylonicus, *new species, with type locality vicinity of Mannar, Sri Lanka), the Megagean* Cymindis *Latreille, 1806, and the Afrotropical-western Palaearctic* Hystrichopus *Boheman, 1848. The genus* Cymindis *includes four subgenera (new rank): Oriental* Taridius *Chaudoir, 1875; Nearctic-Neotropical* Pinacodera *Schaum, 1857; Afrotropical-Oriental* Afrotarus *Jeannel, 1949; and Holarctic* Cymindis sensu stricto. Hystrichopus *includes four subgenera (new rank): Madagascan* Assadecma *Basilewsky, 1982; Afrotropical-Palaearctic* Pseudomasoreus *Desbrochers des Loges, 1904; Afrotropical* Hystrichopus sensu stricto*; and Afrotropical* Plagiopyga *Boheman, 1848. Transferred to the* *subtribe Calleidina are the Palaearctic- Old World Tropical- Australian* Anomotarus *Chaudoir, 1875, and the Australian* Trigonothops *MacLeay, 1864. Transfer of* Anomotarus *renders the names Calleidina and Anomotarina synonyms; the latter name is junior.* Anomotarus *includes three subgenera: Palaearctic- Old World Tropical- Australian* Anomotarus sensu stricto*; Australian* Nototarus *Chaudoir, 1875, new rank (=* Lithostrotus *Blackburn, 1894, new synonymy); and Afrotropical* Dromiotes *Jeannel, 1949 (=* Cephalotarus *Mateu, 1973).* Trigonothops *includes five subgenera (new rank):* Trigonothops sensu stricto; Phloeocarabus *MacLeay, 1871;* Diabaticus *Bates, 1878;* Abaditicus *new subgenus (generitype* Diabaticus collaris *Blackburn, 1901); and* Speotarus *Moore, 1964. Transferred to the Dromiina is the Afrotropical (South African) genus* Metaxymorphus *Chaudoir, 1873, including as subgenera (new rank):* Metaxymorphus sensu stricto; Periphobus *Pêringuey, 1896; and* Callidomorphus *Pêringuey, 1896. Inclusion of the South African* Syndetus *Pêringuey, 1896 (=* Coptoptera *Chaudoir, 1837) in the Dromiina is comfirmed. The Old World* Agastus *Schmidt-Goebel, 1846 is transferred to the tribe Zuphiini. Also included in the Dromiina are the tribes Lichnasthenini and Singilini.*

The Madagascan genera Thysanotus *Chaudoir, 1837,* Antimerina *Alluaud, 1897, and* Madecassina *Jeannel, 1949 (formally tribe Thysanotini, subfamily Calleiditae) are placed in the subtribe Pericalina, with the name Thysanotini becoming thereby a junior synonym of the name Pericalina.*

The name Lachnaces sericeus *Bates, 1872 is changed to* Eucaerus *(*Lachnaces*)* sericeus, *thereby becoming a junior secondary homonym of* Eucaerus *(*sensu stricto*)* sericeus *Bates, 1871.* Eucaerus sericatus *is proposed as a name for the junior homonym.*

The nominal species Cymindis (Taridius) stevensi *(Andrewes, 1923) is expanded to include as subspecies* C. s. nilgirica *(Andrewes, 1935),* C. s. andrewesi *(van Emden, 1937), and* C. s. stevensi sensu stricto. Taridius niger *Andrewes, 1935 is transferred to subgenus* Afrotarus *Jeannel. New species of* Hystrichopus *(subgenus* Pseudomasoreus) *are described, based on material from the Union of South Africa:* H. (P) reticulatus *(type locality– Cape Province, Clanwilliam District, Sederburg);* H. (P.) basilewskyi *(type locality– Cape Province, Swellendam Distr., Grootvaderbos);* H. (P.) thoracicus *(type locality– Grahamstown); and* H. (P.) mateui *(type locality Natal, Malvern). A new species of* Trigonothops *is described:* T. (Abaditicus) meyeri *(type locality– AUSTRALIA, Victoria, Nunniong Plateau, Woodhouse Creek).*

RÉSUMÉ

L'examen des caractères des adultes (en particulier des sclérites de l'ovipositeur), réalisé sur un échantillon limité de taxons jusqu'ici inclus dans la sous-tribu lêbiienne des Cymindina (= tribus des Cymindina et des Pseudomasoreini, ou sous-famille des Cyminditae de certains auteurs), rêvèle que les tribus et sous-tribus suivantes y sont représentées: tribu des Platynina; tribu des Lachnophorini; tribu des Lebiini, sous-tribus des Pericalina, Apenina, Cynindina, Calleidina et Dromiina; et tribu des Zuphiini. Cette étude confirme en outre que le genre sud-african Anarmosta *Pêringuey, 1896 (=* Euplynes *Schmidt-Goebel, 1846) est bien platyninien. Les genres* Eucaerus *LeConte, 1853 et* Lachnaces *Bates, 1872, des tégions tropicales et subtropicales du Nouveau Monde, sont inclus dans le complexe des* Eucaerus, *et transférés dans les Lachnophorini.* Eucaerus *et* Lachnaces *sont considêrês comme des sous-genres congênêriques (nouveau rang). Les genres néotropicaux* Asklepia *Liebke, 1938 et* Phaedrusium *Liebke, 1951 sont êgalement inclus dans le complexe* Eucaerus. Leptosarcus *Pêringuey, 1896, du sud de l'Afrique, et* Selenoritus *Alluaud, 1917, des montagnes est-africaines [ce dernier étant considêrê comme un sous-genre de* Thyreopterus *Dejean, 1831 (nouveau rang)], sont transférés dans la sous-tribu des Pericalina. Trois genres sont transfêrês dans la sous tribu des Apenina:* Apenes *LeConte, 1851, du Nouveau Monde, comprenant les sous-genres* Apenes sensu stricto *(=* Malisus *Motschulsky, 1864), et* Sphalera *Chaudoir, 1875 (=* Didymochaeta *Chaudoir, 1875, synonyme nouveau);* Trymosternus *Chaudoir, 1873, de ;'Eurasie; et* Cymindoidea *Castelnau, 1832, des tropiques de l'Ancien Monde. Ce dernier genre comprend les souis-genres* Cymindoides (sensu stricto, Platytarus *Fairmaire, 1850 (nouveau rang), et* Habutarus, *nouveau genre (gênotype* Nototarus papua *Darlington, 1968). La sous-tribu des Cymindina comprend un nouveau genre de la région orientale,* Ceylonitarus (génotype C. ceylonicus, *nouvelle espèce, localité du type située dans les environs de Mannar, Sri Lanka),* Cymindis *Latrielle, 1806, réparti en Amérique du Nord, Eurasie et Afrique, et* Hysteichopus *Boheman, 1848, de l'Afrique tropicale et de la partie occidentale de l'Eurasie. Le genre* Cymindis inclut quatre sous-genres (nouveau rang): Taridius *Chaudoir, 1875, de la région orientale;* Pinacodera *Schaum, 1857, des régions néarctique et néotropicale;* Afrotarus *Jeannel, 1949, des régions orientale et afrotropicale; et* Cymindis sensu stricto *de la région holarctique.* Hystrichopus *comprend quatre sous-genres (nouveau rang):* Assadecma *Basilewsky, 1982, de Madagascar;* Pseudomasoreus *Desbrochers des Loges, 1904, des régions paléarctique et afrootropicale;* Hystrichopus sensu stricto, *de la région afrotropicale; et* Plagiopyga *Boheman, 1848, aussi de l'Afrique tropicale.* Anomotarus *Chaudoir, 1875, des régions paléarctique et australienne ainsi que des tropiques de l'Ancien Monde, et* Trignothops *MacLeay, 1864, d'Australie, sont transférés dans la sous-tribu des Calleidina. Calleidina et Anomotarina deviennent synonymes à la suite du transfert d'*Anomotarus, *Anomotarina étant le plus récent des deux.* Anomotarus sensu stricto, *réparti en Eirasie, dans les tropiques de l'Ancien Monde et dans la région australienne;* Nototarus *Chaudoir, 1875, nouveau rang (=* Lithostrotus *Blackburn, 1894, nouveau synonyme), d'Australie; et* Dromiotes *Jeannel, 1949 (=* Cephalotarus *Mateu, 1973), de lAfrique tropicale.* Trigonothops *comprend cinq sous-genres (nouveau rang):* Trigonothops sensu stricto; Phloeocarabus *MacLeay, 1871;* Diabaticus *Bates, 1878;* Abaditicus *nouveau genre (gênotype* Diabaticus collaris *Blackburn, 1901); et* Speotarus *Moore, 1964.* Metaxymorphus *Chaudoir, 1873, de l'Afrique tropicale (sud de l'Afrique) est transféré dans les Dromiina et inclut les sous-genres (nouveau rang)* Metaxymorphus sensu stricto, Periphobus *Péringuey, 1896, et* Callidomorphys *Péringuey, 1896. Cette étude confirme en outre l'inclusion du genre sud-africain* Syndetus *Péringuey, 1896 (=* Coptoptera *Chaudoir, 1837) dans les Dromiina.* Agastus *Schmidt-Goebel, 1846, de l'Ancien Monde, est transféré dans la tribu des Zuphiini. Les tribus des Lichnasthenini et des Singilini sont aussi incluses dans les Dromiina.*

Les genres malgaches Thysanotus *Chaudoir, 1837,* Antimerina *Alluaud, 1897, et* Madecassina *Jeannel, 1949 (formellement, de la tribu des Thysanotini, sous-famille des Calleiditae) sont inclus dans la sous-tribu des Pericalina, rendant ainsi le nom Thysanotini synonyme récent du mom Pericalina.*

Le binome Lachnaces sericeus *Bates, 1872 est changé en* Eucaerus (Lachnaces) sericeus, *et devient ainsi homonyme secondaire récent d'*Eucaerus (sensu stricto) sericeus *Bates, 1871. L'auteur propose* Eucaerus sericatus *comme remplacement de l'homonyme récent.*

La signification de l'espèce nominale Cymindis (Taridius) stevensi *Andrewes, 1923) est élargie piur inclure les sous-espèces* C. s. nilgirica *(Andrewes, 1935),* C. s. andrewesi *van Emden, 1937), et* C. s. stevensi sensu stricto. Taridius niger *Andrewew, 1935 est transféré dans le sous-genre* Afrotarus *Jeannel. De nouvelles espèces d'*Hystrichopus *(sous-genre* Pseudomasoreus) *sont décrites à partir de spécimens provenant de l'Union Sud-Africaine; ce sont:* H. (P.) reticulatus *(localité du type: province du Cap, district de Clanwilliam, Sederburg);* H. (P.) basilewskyi *(localité dy type: province du Cap, district de Swellendam, Grootvaderbos);* H. (P.) thoracicus *(localité du type: Grahamstown; et* H. (P.) mateui *(localité du type: Natal, Malvern). Une nouvelle espèce de* Trigonothops *est décrite; il s'agit de* T. (Abaditicus) meyeri *(localité du type: Australie, Victoria, plateau du Nunniong, Woodhouse Creek).*

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INTRODUCTION

During preparation of a revision of the species of the New World taxon *Pinacodera* Schaum, we wished to identify its sister group, and so undertook what was hoped to be a brief review of the genera that René Jeannel and other previous workers had included in the subtribe Cymindina. That outstanding Japanese student of Carabidae, Akinobu Habu (1967), showed that details of the ovipositor of adult lebiines were of substantial value in classification. We also knew that mandibles offered useful and previously unused character states.

Preliminary examination of these structures of adults of a few supposedly cymindine genera showed striking heterogeneity, so much so that it became evident that the cymindine assemblage was very likely to be unsatisfactory, at least from a phylogenetic viewpoint. This realization left us with three choices: to abandon the original goal, and to proceed with an analysis of *Pinacodera* without knowing the sister group; or to attempt to locate close relatives of *Pinacodera* and leave the rest of the cymindines for another time; or to attempt to sort out the group by assigning all genera to their proper subtribes, and at the same time, to identify the sister group of *Pinacodera*. We chose the last course, and this paper is the result.

At first, we thought that reclassification of the cymindine Lebiini would form the introductory part of a treatment of *Pinacodera,* but the introduction grew in volume and complexity, until it became obvious that inclusion of a detailed treatment of that genus would appear almost as an appendage. Therefore, revision of the species of *Pinacodera* will be published separately.

In the present paper, genera of the Cymindina of authors are briefly characterized on the basis of features of adults, and assigned to their proper groups. Several subtribes of Lebiini are characterized. Most genera are treated in cursory fashion, but for some, material was available for partial revision, and we took advantange of the opportunities thus offered.

This paper is not a revision of the higher classification of the Lebiini. It is more a collection of notes that ought to be useful for such a revision. Habu (1967) provided the basis for such a treatment, but structures of many more taxa must be examined in detail, to assess character systems thought to be of value, and to identify evolutionary trends.

MATERIALS AND METHODS

Materials

Several hundred lebiine adults were examined, representing described cymindine genera. A few taxa were represented in the Strickland Museum, University of Alberta (UASM), but most specimens were borrowed. Listed below, with abbreviations used in the text, are names and addresses of the lending institutions.

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.

CSIRO	Commonwealth Scientific and Industrial Research Organization, Division of Entomology, Black Mountain, Canberra City, ACT 2601, Australia
IRSB	Section d'Entomologie, Institut Royal des Sciences Naturelles du Belgique, Bruxelles 4, Rue Vautier 31, Belgium.
MACT	Musée Royal de l'Afrique Centrale, B- 1980, Tervuren, Belgique.
MCZ	Museum of Comparative Zoology, Harvard University Cambridge, Massachusetts, U.S.A. 02138.
MNHP	Entomologie, Muséum National d'Histoire Naturelle, Paris (Ve), France.
SAMC	South African Museum, P.O. Box 61, Cape Town, South Africa.
USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560.
ZSIC	Zoological Survey of India, 34 Chittaranjan Avenue, Calcutta, 700 012 India.

Methods

Because of the nature of this study, most taxa were represented by few specimens. Therefore, no attempt was made to assess range of variation of character states studied, and few specimens of each taxon were dissected or measured. In general, however, characters used tend to be stable intraspecifically.

Taxonomic principles, criteria for ranking taxa, and general working methods were the same as those previously described (Ball, 1975 and 1978, and Allen and Ball, 1980), and are not repeated here. However, if we have erred in taxonomic judgement, it is in the direction of lumping rather than splitting, by emphasis of similarities that we felt are likely to represent close phylogenetic relationship, rather than emphasis of differences that, although they might be numerous, seem the sort of features that might change rapidly.

Genitalia and other small structures were preserved in glycerine, in microvials, pinned beneath the specimens from which they were removed.

Measurements made with a Wild M5 stereobinocular microscope, at 25X or 50X, are as follows, and are expressed in the text by these abbreviations:

Hl-	length of head, measured on left side, from base of left mandible to posterior margin of compound eye;
Hw-	maximum transverse distance across head, including eyes;
Vwm-	minimum transverse distance across vertex (used for specimens with markedly constricted head, posteriorly);
Pl-	length of pronotum, measured along mid-line, from base to apex;
PwB-	width of pronotum, at base;
Pwm-	maximum width of pronotum;
MES l (and w)-	length of metepisternum, measured along lateral margin; (width of metepisternum, measured along basal margin);
El-	length of longer elytron (if elytra of a single specimen were unequal) from basal ridge to apex.

Size was expressed in the text as the sum of Hl, Pl, and El, and referred to as Standardized Body Length, or SBL. Other measurements were used to form ratios which seemed to provide adequate diagnostic features for differentiation among members of some taxa.

For photographs of some structures, a Stereo Electron Microsope was used, Cambridge Model S150. Specimens were cleaned, using a sonicator, and were gold-coated.

STRUCTURES USED IN CLASSIFICATION

All of the features used are standard for carabids, especially lebiines. Nonetheless, attention is drawn here to terms that have yet to be stabilized in the carabid literature for various structures.

For micro-units of surface sculpture bounded by lines of microsculpture, we use "sculpticell" (Allen and Ball, 1980: 486); for elytral stria, "interneur" (Erwin, 1974: 3-5). For abdominal sterna, Roman numerals are used, with first visible sternum being II, and the last one that is not normally retracted, VII.

The median lobe of the male genitalia is classified depending upon position of the apical orifice: anopic, if dorsal; catopic, if ventral (Jeannel, 1949: 878). For a discussion of the significance of catopy see Jeannel (1955: 82-86). The word "hemiopic" is used for median lobes in which the apical orifice is more lateral than it is dorsal or ventral (Ball and Shpeley, in press).

Sclerites of the ovipositor are named according to Tanner (1927), with modifications proposed by Noonan (1973), and Ball and Shpeley (in press). Thus, the terminal sclerite of the ovipositor is "stylomere 2", abbreviated S2. Terms used for surfaces are those proposed by Ball and Shpeley (in press), based on orientation of surfaces in the extended position.

CLASSIFICATION

The cymindine genera of authors represent one subtribe of Pterostichini, the Lachnophorini, five subtribes of Lebiini, and the Zuphiini. As a guide to the text, we list by name these supraspecific taxa, as well as two that are new, and several not included in the Cymindina of authors, but related more or less directly to the general subject matter of this study.

Tribe PTEROSTICHINI
    Subtribe PLATYNINA
        Anarmosta Péringuey, 1896 (junior subjective synonym of *Euplynes* Schmidt-Goebel, 1846)
Tribe LACHNOPHORINI
        Eucaerus LeConte, 1853
        Lachnaces Bates, 1872
        Asklepia Liebke, 1938
        Phaedrusium Liebke, 1951
Tribe LEBIINI
    Subtribe PERICALINA (including THYSANOTINI)
        Thysanotus Chaudoir, 1837
        Antimerina Alluaud, 1897
        Madecassina Jeannel, 1949
        Selenoritus Alluaud, 1917
        Thyreopterinus Alluaud, 1932
        Thyreopterus Dejean, 1831

- *Leptosarcus* Péringuey, 1896
- Subtribe APENINA
  - *Apenes* LeConte, 1851
  - *Malisus* Motschulsky, 1864
  - *Sphalera* Chaudoir, 1875
  - *Didymochaeta* Chaudoir, 1875
  - *Trymosternus* Chaudoir, 1873
  - *Cymindoidea* Castelanu, 1832
  - *Platytarus* Fairmaire, 1850
  - *Habutarus*, new subgenus
- Subtribe CYMINDINA
  - *Ceylonitarus*, new genus
  - *Taridius* Chaudoir, 1875
  - *Pinacodera* Schaum, 1857
  - *Afrotarus* Jeannel, 1949
  - *Cymindis* Latreille, 1806
  - *Assadecma* Basilewsky, 1982
  - *Pseudomasoreus* Desbrochers des Loges, 1904
  - *Hystrichopus* Boheman, 1848
  - *Plagiopyga* Boheman, 1848
- Subtribe CALLEIDINA
  - *Trigonothops* Macleay, 1864
  - *Phloeocarabus* Macleay, 1871
  - *Diabaticus* Bates, 1878
  - *Abaditicus*, new subgenus
  - *Speotarus* Moore, 1964
- Subtribe DROMIINA (including LICHNASTHENINI and SINGILINI
  - *Metaxymorphus* Chaudoir, 1873
  - *Periphobus* Péringuey, 1896
  - *Callidomorphus* Péringuey, 1896
  - *Syndetus* Péringuey, 1896 (junior subjective synonym of *Coptoptera* Chaudoir, 1837)

Tribe ZUPHIINI
- *Agastus* Schmidt-Goebel, 1846

Details about these subtribes and genus-group taxa are provided below.

TRIBE PTEROSTICHINI, SUBTRIBE PLATYNINA

Genus *Euplynes* Schmidt-Goebel
Figs. 1 and 2

Euplynes Schmidt-Goebel, 1846: 52. GENERITYPE: *Euplynes cyanipennis* Schmidt-Goebel, 1846: 52 (monotypy).– Burgeon, 1937: 397.– Jeannel, 1949: 611.– Mateu, 1974: 487-506.– Habu, 1978: 292.

Euplenes Darlington, 1952: 122.

Xatis Fairmaire, 1901: 125. GENERITYPE: *Xatis nigripes* Fairmaire, 1901: 125 (monotypy).– Jeannel, 1949: 611.– Habu, 1978: 294.

Anarmosta Péringuey, 1896: 221. GENERITYPE: *Anarmosta dispar* Péringuey, 1896: 222. (=*Euplynes callidoides* Chaudoir, 1878) (monotypy).– Mateu, 1974: 487.

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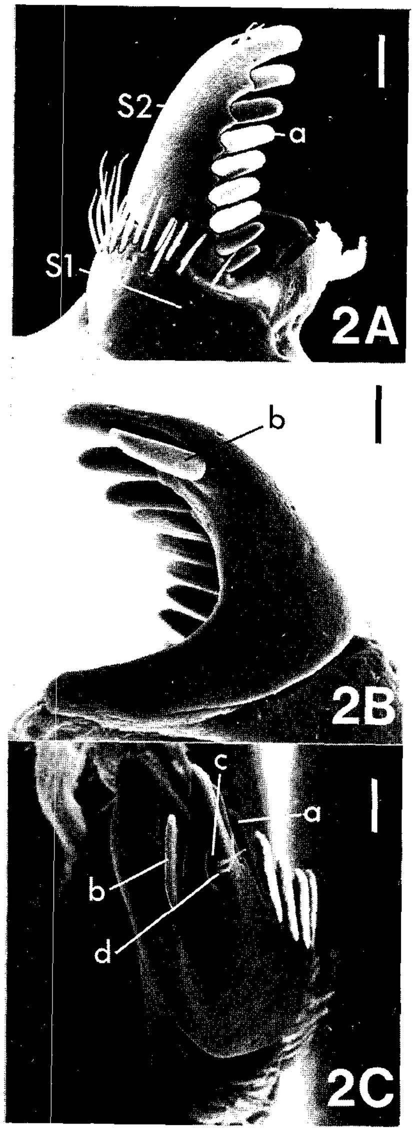


Figs. 1 and 2. Photographs of Platynina, *Euplynes callidoides* Chaudoir (= *Anarmosta dispar* Péringuey).—Fig. 1: habitus, dorsal aspect (SBL –9.79 mm). Fig. 2: SEM photograph of ovipositor, right stylomeres—A, lateral aspect; B, medial aspect; C, apico-ventral aspect. Scale bars = 50 μm. Legend: a, lateral ensiform seta; b, medial ensiform seta; c, sensory furrow peg; d, nematoid seta; Sl, stylomere 1; S2, stylomere 2.

Notes about types and synonymy.— Although we have not seen type material, we have studied three specimens from the Péringuey collection (SAMC) from the type locality of Salisbury, and labelled as follows: male, Salisbury, Rhodesia, 17.1.11, J.A. O'Neill; female, Salisbury, 11.2.18; female, Salisbury, 3.11.1914, J. O'Neil. Additionally, each specimen bears: two determination labels (*Anarmosta dispar* Per.; and *Euplynes dispar* Pering. det. Ball, '80); and a museum label (SAMC). Mr. V. Whitehead, of the South African Museum, advised us that these were the only specimens available of this species in the Péringuey collection. The features of these specimens fit those provided in the original description. Fig. 1 illustrates the habitus of *E. callidoides* Chaudoir.

It seems difficult to believe that Péringuey would have placed a typical platynine among the Lebiini. However, there are some clues about how such an error could be made. First, his diagnosis of the "Lebiides" does not exclude specimens with approximately normal elytral apices ("...or very deeply sinuate behind..."). Second, in the key to genera of "Cymindidae" (included in the "Lebiides"), Péringuey gave the name "*Haplopeza*" following the singlet in which *Anarmosta* runs out, and the former name is not listed again. It seems likely that he originally regarded the specimen of *A. dispar* as belonging to *Haplopeza,* realizing at a later date (possibly when the manuscript was in press) that this was incorrect. *Haplopeza,* however, is a platynine. From this, we infer that *A. dispar,* although not a species of *Haplopeza,* is a platynine. We feel confident that the specimens labelled *Anarmosta dispar* Péringuey are indeed members of that nominal species. This is the same conclusion that Straneo (1943: 58) reached.

The above comments are not made to criticize Péringuey. Rather, they illustrate the difficulties that our predecessors had in distinguishing among lebiines and platynines, and especially some of the tropical members of these groups. As a further example of the problem, Bates (1883:158) suggested that *Euplynes* might be related to *Leptotrachelus* .

Figs. 2A-C illustrate the highly distinctive stylomere 2 of the ovipositor of *E. dispar,* with its dorso-lateral row of thick spines, and the well developed basal lobe. We think that it might be a generic character state for *Euplynes*. Habu's illustrations (1978: 293-295, Figs. 590-592a) of Oriental- eastern Palaearctic females are about the same as our Fig. 2. Jeannel (1949: 611) suggests that the African genus *Haplopeza* Boheman is related to *Euplynes.*

Mateu (1974) revised the African species of *Euplynes.*

Tribe LACHNOPHORINI

To this tribe, four genus-group taxa are assigned: *Eucaerus* LeConte, *Lachnaces* Bates, *Asklepia* Liebke, and *Phaedrusium* Liebke. We have seen representatives of only the first two groups. T. L. Erwin (personal communcation) suggested that the latter two groups should be included, also. Figures provided by Reichardt (1974: 178, Figs. 1, and 3-7) confirm that *Asklepia* is indeed like *Eucaerus,* and the original description of *Phaedrusium* (Liebke, 1951: 240-241) includes mention of character states that are *Eucaerus*- like.

The marked similarity of adults of *Lachnaces* and *Eucaerus* in several features is taken as evidence of very close relationship of these taxa. Therefore, we combine them as subgenera of a single genus. We believe that re-examination of specimens of *Asklepia* and *Phaedrusium* will show that these groups should be included in *Eucaerus,* as well.

Reichardt (1974: 178) transferred *Asklepia* Liebke from the Colliurini to the Lachnophorini, and *Phaedrusium* was compared with lachnophorines (*Lachnophorus* and

Calybe by Liebke (1951: 241), though he included the genus in the Lebiini. Bates (1871: 77) noted both lachnophorine and lebiine affinities of *Eucaerus*. Horn (1881: 155) commented about the lachnophorine affinities of *Eucaerus,* referring to it as "an osculant form" between that group and the Lebiini. He decided, nonetheless, that *Eucaerus* was a lebiine, a view that was accepted by subsequent cataloguers and American workers (see Ball, 1960: 162, and Reichardt, 1977: 444).

Terry L. Erwin (personal communication) suggested that this complex belonged in the Lachnophorini, and we place it there on the basis of: terminal palpomeres with acuminate tips (Figs. 10 and 12); mandibles of same form (details provided in description of *Eucaerus*); elytral apices subtruncate; wings with oblongum cell reduced (stalked), wedge cell absent; stylomere 1 of ovipositor with terminal row of setae, stylomere 2 of plesiotypic form and setation (Figs. 17 and 18). Form of palpomeres is autapotypic. Details of wing venation are also apotypic, but could have been independently acquired by reduction. Mandibles are probably a mixture of symplesiotypic and autapotypic features. We cannot sort out the details at this time. All antennomeres of *Eucaerus* (*sensu stricto*) and *Asklepia* adults have a vestiture of short setae, like antennomeres 4-11. Antennomeres 1-3 of *Phaedrusium* adults and antennomere 1 of subgenus *Lachnaces* adults are without such vestiture, contrasting with antennomeres 4-11.

According to Reichardt (1977: 413), the Lachnophorini (excluding *Anchonoderus* Reiche) is "A weakly characterized tribe of still uncertain position and constitution". He provided an account of the taxonomic history of the group (1977: 406 and 413), which has been treated as an independent tribe near the Perigonini (with or without *Anchonoderus*), or as a subtribe of the Pterostichini. Liebherr (MS) presents evidence based on structural features of larvae and adults, showing clear lebiomorph affinities of lachnophorines, and this is our basis for ranking this group (including *Anchonoderus*) as a tribe apart from the Pterostichini, and placing it in the lebiomorph assemblage. Further work might require including in a single tribe the lachnophorines and lebiines, but this possibility remains to be investigated.

Geographical distribution.— This complex is confined to the tropics and warm temperate areas of the New World: all four genera are known from South America, but only *Eucaerus* ranges north to Middle America and to southeastern Unites States.

Description of the Eucaerus complex.— The following describes range of variation of selected features useful in recognizing lachnophorine taxa, and for determining their relationships.

Color. Various, from somber to pale; dorsum all black to combinations of rufous and testaceous, elytra spotted or not; legs and palpi testaceous; antennae uniformly testaceous, or tricolored, antennomeres 1-3 rufous or piceous, 4-6 black, and 7-11 white.

Microsculpture. Various, but generally transverse: some members of *Eucaerus* with dorsum of head and/or pronotum with isodiametric meshes and sculpticells convex, surface thus beaded.

Luster. Generally iridescent, or dorsum of head and pronotum dull.

Macrosculpture. Dorsum generally smooth, without constant depressions or swellings, but frontal impressions with transverse rugulae; ventral surface rather coarsely but sparsely punctate.

Vestiture. Dorsal surface generally glabrous; all antennomeres setose; or antennomeres 1 or antennomeres 1-3 glabrous except for normal preapical setae; terminal palpomeres densely setose; maxillary palpomere 3 densely setose, palpomere 2 sparsely setose; ventral surface sparsely setose.

Fixed setae. Average for lachnophorine adults: labrum with six long apical setae; head and pronotum with two pairs; elytron with three setae on interval 3, or in *Asklepia strandi* adults, with two rows of setae on disc; umbilical series of about 10-12 setigerous punctures laterally, broadly interrupted medially, penultimate lateral seta in straight line with antepenultimate and ultimate setae.

Head. Clypeus transverse, anterior margin truncate. Frontal impressions broad and shallow or deep and linear. Sub-antennal ridge average. Eyes orbicular, convex, prominent. Antennae average for lachnophorine adults: filiform, flagellar antennomeres sub-cylindrical distinctly longer than wide; antennomere 2 short, 3 longer than 4.

Mouthparts. Labrum with anterior margin truncate. Left and right mandibles about same in overall shape. Scrobes less than 0.50 total length of mandibles, ventral edge of scrobe curved upward. Left mandible (Figs. 3A, C, 4A, C, 5A, C) with terebral ridge distinct, extended more than half length of terebra; terebral tooth absent; retinacular ridge cutting edge; retinacular tooth prominent, cleft, ventral ridge well developed; premolar tooth blunt, small, set off from posterior part of retinacular ridge by indentation; ventral premolar ridge not developed. Right mandible (Figs. 3B, D, 4B, D, 5B, D) cutting edge terebral ridge anteriorly, retinacular ridge posteriorly: terebral tooth blunt; retinacular ridge well developed; anterior retinacular tooth prominent in *Eucaerus*, small in *Asklepia*; (Reichardt, 1974: Fig.6); premolar tooth blunt, small, continuous with retinacular ridge; ventral premolar ridge indistinct. Ventral grooves long, setose, extended more than 0.5 length of mandibles. Maxilla (Figs. 6-7) with sclerites generally elongate; lacinia with long setae on dorsal surface; galeomere 2 distinctly shorter than 1; palpomere 4 slightly swollen, subulate apically. Labium with mentum bisetose, median tooth developed (some members of *Lachnaces*), or not, or very slightly developed; lateral lobes pointed apically; epilobes expanded apically; glossal sclerite narrow, bisetose, keeled ventrally; paraglossae membranous, glabrous either shorter (Fig. 10) or longer (Fig. 12) than glossal sclerite; palpus with palpomeres 1 and 2 slender, 3 swollen, subulate apically.

Thorax. Pronotum various: subcordate (Fig 13) to pronouncedly transverse; base lobed or not; anterior angles broadly rounded, posterior angles sharp or rounded; disc slightly convex, median longitudinal impression sharp, well developed; anterior and posterior lateral impressions well developed. Metepisternum distinctly longer than wide.

Elytra. Average in form; humeri broadly rounded; basal ridge marginal, prominent, extended to scutellum; apical margin obliquely subtruncte. Interneurs average or effaced, impunctate.

Wings. Well developed; wedge cell absent, oblongum cell stalked, well developed. Venation otherwise normal for carabids.

Legs. Generally average for Lachnophorini. Tarsomere 4 with apical margin sub-truncate, tarsomere 5 with row of ventro-lateral setae, each side. Male anterior tarsus ventrally (Figs. 14-16) with reduced adhesive vestiture, on tarsomeres 2 and 3; present or not on tarsomere 1; tarsomere 4 with pair of flattened, expanded sense organs apicoventrally (Fig.14B).

Abdominal sterna. Average for Carabidae, in form; surface generally setose, or glabrous.

Male genitalia. Median lobe relatively broad in cross section, dorsal surface mostly membranous; apical orifice dorsal. Internal sac with microtrichial fields only, or with latter and varied number and groups of spines. Parameres average for Lachnophorini.

Ovipositor and associated abdominal sclerites. Tergum VIII completely sclerotized basally, not divided into two parts by median membranous area; apodemes with apices curved laterad. Sternum VIII extensively unsclerotized medially. Tergum X transverse, narrow. Valvifers average. Stylomeres 1 and 2 subequal in length, stylomere 1 with row of setae apically, stylomere 2 (Figs.17A, 18A) falcate, blade slender, with preapical sensory furrow and long nematoid setae on ventral surface, with two or three long spines on dorso-lateral margin, one on dorso-medial margin; row of sensory pits on lateral and ventral surfaces.

Key to Genera of the Eucaerine Complex

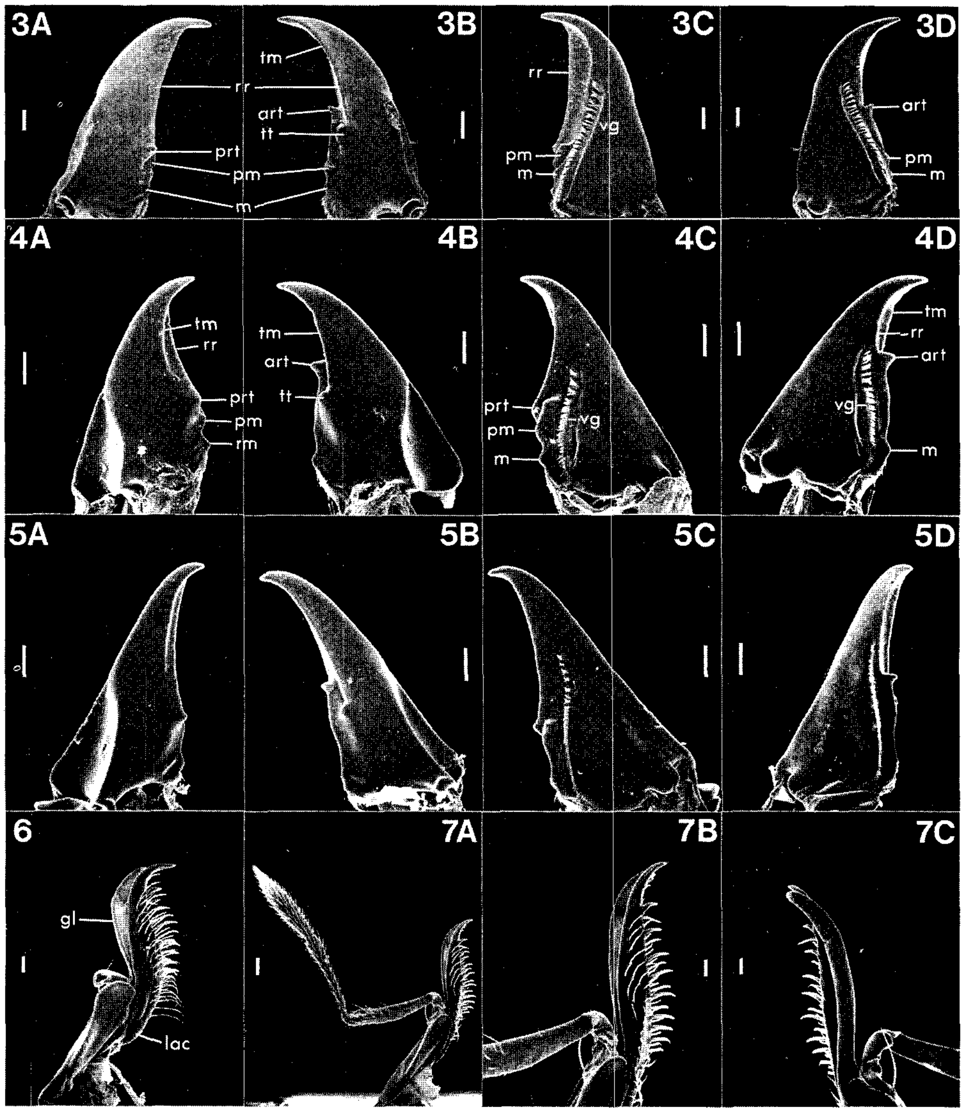
1 (0) Pronotum with base truncate, not lobed medially. Disc of elytron with two rows of setigerous punctures; interneurs effaced, intervals flat; bicolored; microsulpture not evident at ordinary magnifications (to 50X) .... *Asklepia* Liebke.

1′ Pronotum with base lobed medially (Fig. 13). Elytral disc with single row of setigerous punctures (on interval 3); interneurs effaced or evident; concolorous or bicolored; microsculpture not evident, or meshes transverse .... 2.

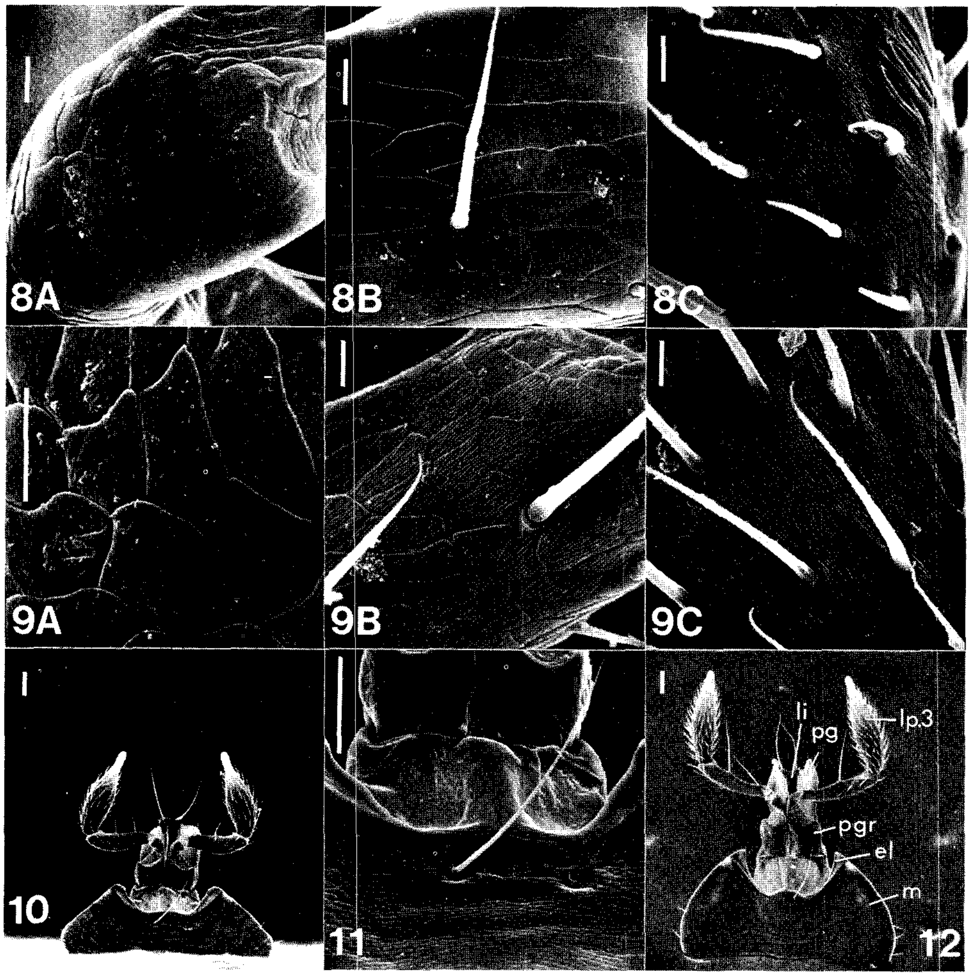
2 (1′) Antennomeres 1-3 without vestiture of short setae, glabrous except for few, normal (long) preapical setae. Male anterior tarsomeres ventrally without adhesive vestiture .... *Phaedrusium* Liebke.

2′ Antennomeres 1-3 (or 2-3) with vestiture of short setae, like antennomeres 4-11. Male anterior tarsomeres 2 and 3, or 2-4 ventrally with adhesive vestiture (Figs. 14A, 15, and 16) .... *Eucaerus* LeConte, p. 107

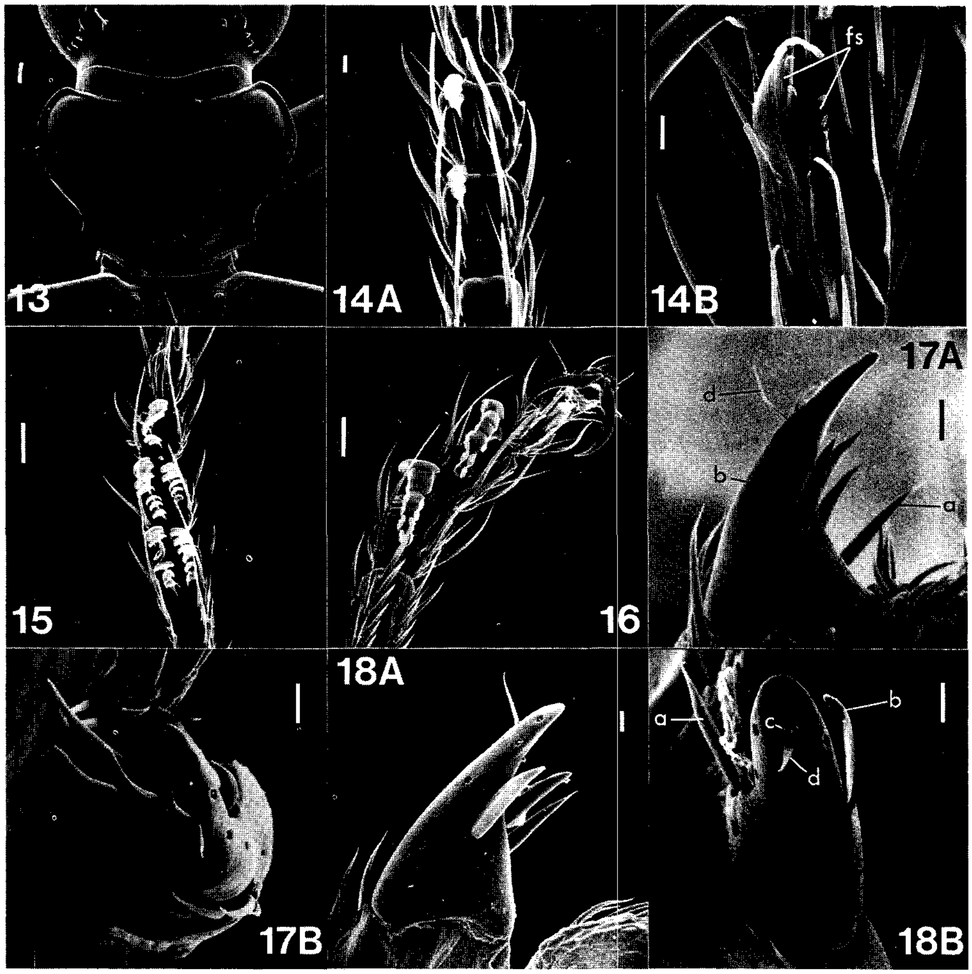
The genus *Asklepia* includes the single species *A. strandi* Liebke, 1938. *Phaedrusium* Liebke, 1951 includes *P. suturalis* Liebke, 1951 (generitype), and *P. titschacki* Liebke, 1951. We have nothing further to add about these genera.



Figs. 3–7. SEM photographs of structures of Lachnophorini.— Figs. 3–5: mandibles, A and C, left, dorsal and ventral aspects, respectively, B and D, right, dorsal and ventral aspects, respectively, of: 3, *Lachnophorus guttulatus* Bates; 4, *Eucaerus (sensu stricto)* species; 5, *E. (Lachnaces) olisthopoides (Bates)*. *Figs. 6–7: right maxilla of—6, Eucaerus (sensu stricto)* species, ventral aspect; 7, *E. (Lachnaces) olisthopoides* (Bates), A, entire structure, ventral aspect, B, lacinia and galea, ventral aspect, C, galea and lacinia, dorsal aspect. Scale bars = 50 μm. Legend, mandibles: art, anterior retinacular tooth; m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin; vg, ventral groove. Legend, maxilla: gl, galea; lac, lacinia



Figs. 8–12. SEM photographs of Lachnophorini.—Structures of the labium. Figs. 8 and 9, palpomeres, microsculpture, A, palpomere 1, B, palpomere 2, and C, palpomere 3, of: 8, *Eucaerus (sensu stricto)* species; 9, *E. (Lachnaces) olisthopoides* (Bates). Scale bars = 5 um, Fig. 10: labium, ventral aspect, of *Eucaerus (sensu stricto)* species. Fig. 11: mentum and palpigers, ventral aspect, of *Eucaerus (sensu stricto)* species. Fig. 12: labium, ventral aspect, of *E. (Lachnaces) olisthopoides* (Bates). Scale bars = 50 μm. Legend: el, epilobe; li, glossal (or ligular) sclerite; lp3, labial palpomere 3; m, mentum; pg, paraglossae; pgr, palpiger.



Figs. 13–18. SEM photographs of structures of Lachnophorini.—Fig. 13: bases of head and elytra, and pronotum, dorsal aspect, of *Eucaerus (sensu stricto) hilaris* Bates. Figs. 14–16, front tarsomeres of males, ventral aspect, showing adhesive vestiture: 14, *Eucaerus (sensu stricto) hilaris* Bates, A–tarsomeres 1–4, B–tarsomere 4; 15, *Eucaerus (sensu stricto)* species, tarsomeres 1–4; 16 *E. (Lachnaces) olisthopoides* (Bates), tarsomeres 1–5. Figs. 17–18: ovipositor, left stylomeres, A–medial aspect, B–apico-ventral aspect, of: 17, *Eucaerus (sensu stricto)* species; 18, *E. (Lachnaces) olisthopoides*. Scale bars, Figs. 13, 15, 16 = 50 μm; Figs. 14, 17, 18 = 10 μm. Legend, for tarsi: fs–foliose seta. Legend, for stylomeres: a, lateral ensiform seta; b, medial ensiform seta; c, furrow pegs; d, nematoid seta.

Eucaerus LeConte
Figs. 4-18

Eucaerus LeConte, 1853: 386. GENERITYPE: *E. varicornis* LeConte, 1853 (monotypy).– 1862: 22.– Chaudoir, 1871: 285.– Horn, 1881: 157, 159.– 1882: 158.– LeConte and Horn, 1883: 45.– Csiki, 1932: 1497.– Leng, 1920: 67.– Blackwelder, 1944: 63.– Ball, 1960: 162.– Erwin *et al*, 1977: 4: 60.

Lachnaces Bates, 1872: 201. GENERITYPE: *L. sericeus* Bates, 1872: 201 (here designated). Csiki, 1932: 1497.– Blackwelder, 1944: 63. NEW SYNONYMY.

Note about nomenclature.— The name *Lachnaces sericeus*, 1872 becomes *Eucaerus sericeus* by virtue of combining *Eucaerus* and *Lachnaces*. However, in 1871, Bates had already proposed the name *E. sericeus* for another species. Thus, the Bates name of 1872 becomes a junior secondary homonym. For the species to which that name applied, we propose *E. sericatus*, new name.

Classification.— The species of *Eucaerus* are arranged in two subgenera and two species groups, as indicated in the following key.

Key to Subgenera and Species Groups of *Eucaerus* LeConte

1 (0) Antennomere 1 without vestiture of short setae. Pronotum subquadrate, sides rounded, not sinuate; disc smooth, without pair of shallow depressions; surface iridescent, microsculpture meshes transverse, in form of diffraction grating. Elytron with inteneurs average, intervals convex. Maxillary palpomere 3 longer than antennal scape. Labium with mentum as long as wide; paraglossa (Fig. 12) narrow apically, longer than glossal sclerite. Male front tarsomere 1 without adhesive vestiture ventrally, tarsomeres 2 and 3 with single row, only (Fig. 16). Median lobe of male genitalia with apical portion very short and broad; internal sac without spines .... subgenus *Lachnaces* Bates.

1′ Antennomere 1 with vestiture. Pronotum (Fig. 13) cordate, sides markedly sinuate posteriorly, posterior angles sharp; disc with pair of paramedian shallow depressions; pronotum with surface iridescent, microsculpture meshes grated, not visible at 50X, or surface dull, meshes isodiametric, microlines visible at 50X. Elytron with interneurs average or effaced, intervals convex or flat. Maxillary palpomere 3 shorter than antennal scape. Labium (Fig. 10) with mentum wider than long; paraglossa broad apically, shorter than glossal sclerite. Male front tarsomere 1 with or without adhesive vestiture; tarsomeres 2 and 3 with vestiture uniseriate (Fig. 14A) or biseriate (Fig. 15). Median lobe of male genitalia with apical portion very short, or longer; internal sac with or without spines ...... *Eucaerus (sensu stricto)* 2

2 (1′) Pronotum with sides narrow, proepisternum visible from dorsal aspect. Elytra bicolored. Head and pronotum smooth, microlines absent. Elytra with interneurs impressed or not, meshes transverse, surface iridescent, or microlines obsolete, surface shining. Male front tarsomere 1 without adhesive vestiture, tarsomere 2 and 3 with vestiture uniseriate. Median lobe with apical portion short .... *E. hilaris* Group.

2′ Pronotum (Fig.13) with sides average, proepisternum not visible from dorsal aspect. Elytra concolorous. Head and pronotum with surface dull, microsculpture meshes isodiametric; elytra with surface iridescent, microlines in form of diffraction grating. Elytra with interneurs normally developed. Male front tarsomeres 1-3 with biseriate adhesive vestiture. Median lobe with apical portion larger . . . . *E. varicornis* Group.

List of species.— The senior author has studied representatives of all described species of *Eucaerus* . Names are listed here, and the species are assigned to their respective groups.

- Subgenus *Eucaerus*
    - *E. varicornis* Group
        - *E. sulcatus* Bates
        - *E. striatus* Bates
        - *E. sericeus* Bates
        - *E. opacicollis* Bates
        - *E. insularis* Darlington
        - *E. haitianus* Darlington
        - (additionally, three undescribed species from Mexico).
    - *E. hilaris* Group
        - *E. geminatus* Bates
        - *E. hilaris* Bates
        - *E. lebioides* Bates
        - *E. pulchripennis* Bates
- Subgenus *Lachnaces* Bates
    - *E. sericatus, new name (=E. sericeus* Bates, 1872, not 1871).
    - *E. badestrinus* Bates
    - *E. olisthopoides* Bates

Notes about habitat.— Members of this genus live in leaf litter, in swamp forest, or in flood zones along tropical rivers. Adults of the *E. hilaris* Group are in litter in areas with more light, close to river edges, whereas adults of the *E. varicornis* Group and *Lachnaces* are in more densely shaded places. On the Rio Negro, in northern Brazil, adults of the latter two groups are microsympatric.

Geographical distribution.— Species of subgenus *Lachnaces* and of the *E. hilaris* Group are known only from the Amazon Basin, in Brazil. Range of the *E. varicornis* Group extends from the Amazon Basin northward to southeastern United States, and eastward to the Greater Antilles. However, no species are shared between South America and areas further north, nor between the West Indies and the adjoining continents.

Tribe LEBIINI

As background for more detailed consideration of cymindines, we need to comment about the tribe Lebiini, which includes the subtribe Cymindina. Collectively, lebiine adults are strikingly divergent in form, color, and in more detailed external features, making it difficult to provide a simple diagnosis for recognition of the tribe. Some adults (cymindines) look much like platynines, others (*Nemotarsus* members) have the long pectinate tibial spurs of masoreines, others (some *Lebia* members) are hardly different from pentagonicines in form and color, and still others (members of *Agra*) are colliurine- like. Internal features and mouthparts offer a similar range of attributes. While it seems unlikely that the Lebiini is a polyphyletic taxon, it could very well be paraphyletic. It is polythetic, for most character states used for recognition of the group are not shared by all member taxa, and those states that seem to be almost universal (biperforate anterior coxal cavities, two pairs of supraorbital setae, for example) are shared with members of non-lebiine taxa.

We are not, however, prepared to pursue this subject further. These comments are words of caution for those who use the following list of features for identification of adults, or those who wish to pursue phylogentic studies of carabids.

Recognition.— Most lebiine adults exhibit most of these character states: apical margins of elytra truncate or subtruncate; tergum VIII more or less extensively membranous medially, laterally exposed, each side posteriorly with a projection that bears the openings of ducts of defensive glands; head with two pairs of supraorbital setigerous punctures; tibial spurs of middle and posterior legs of equal length, smooth, not serrate (if unequal and serrate, head sharply constricted posteriorly); terminal palpomeres more or less pubescent, apical margins subtruncate or truncate (not swollen medially and tapered to narrow apex); antennomeres 4-11 setose; front tarsomeres 1-3 of males with biseriate adhesive vestiture; anterior coxal cavities biperforate; abdomen with sternum X principally membranous; median lobe of male genitalia with dorsal surface extensively sclerotized, membranous area relatively small; right paramere smaller than left paramere; ovipositor with stylomere 1 setose or spinose.

Some pericaline and gallerucoid calleidine adults have virtually complete elytra, with apices extended to the apex of tergum VII. However, pericalines are recognized by a combination of well developed suborbital setae, displaced penultimate umbilical setigerous puncture, and long, slender labrum. Gallerucoid calleidines are chrysomelid-like in appearance, with well developed suborbital setae on the head.

Notes about classification.— The tribe Lebiini, as generally accepted by carabid specialists (for example, LeConte and Horn (1883), Sloane (1923), Andrewes (1929), Ball (1960), Lindroth (1969), and Erwin (1979)) was assembled by Horn (1881: 154), who combined the Lebiides and Pericalides of Lacordaire (1854), but excluded the genera *Mormolyce* Hagenbach and *Agra* Fabricius. Subsequently, these genera were returned to the Lebiini (*Mormolyce,* by Ball, 1975: 147, and *Agra,* by Erwin, 1978: 263). Erwin (1979: 590) also returned the eucheiline genera *Eucheila* Dejean and *Inna* Putzeys to the Lebiini.

Grouping the numerous lebiine genera has been a problem since it was first attempted by Lacordaire (1854: 102). In addition to the Pericalides, he recognized three basic forms centering on *Cymindis* Latreille, *Dromius* Bonelli, and *Lebia* Latreille. Lacordaire wrote that he was unable to find diagnostic characters for such groups.

Chaudoir gave tribal ranking to these groups, as well as to several others, based on slight differences in structure of the labium, as well as on other features. Horn (1881) undertook a detailed study of maxillae and labia of carabids, and one of his conclusions was that the differences among lebiine tribes were too slight and inconstant to be valid as taxonomic characters at the tribal level. Horn's lead was followed by European workers of the late 19th and early 20th centuries. For example, Csiki (1932: 1305-1500) included in the Lebiini most of the groups that Horn had included. He recognized seven subtribes, four of which were groups proposed by Lacordaire: Lebii, Catascopi (equivalent to Pericalides), Dromii, and Cymindina. Three other subtribes were established for genera included by Lacordaire in one or the other of his groups of Lebiides: Physoderi, Lebidii, and Callidi. Nemotarsines, agrines, and masoreines were excluded, each being assigned to a tribe of its own.

Jeannel (1949: 876-1039) used a system similar to that of Lacordaire, for organizing the lebiine fauna of Madagascar, but he excluded nemotarsines and masoreines. He recognized three families (Lebiidae, Thyreopteridae, and Lionychidae), the second including many of the genera that Lacordaire included in the Pericalides. Jeannel included physoderines and lebidiines in the Lebiidae. Genera of Lebiidae were arranged in five subfamilies: Cyminditae, Lebiitae (including also physoderines), Coptoderitae, Calleiditae (including Lebidii), and Dromiitae. Genera of Thyreopteridae were arranged in two subfamilies: Thyreopteritae and Pericalitae. Lionychidae, a new family, included four genera regarded as dromiines by most authors.

Jedlička (1963: 295-464) recognized the same seven subtribes into which Csiki arranged the genera of Lebiini.

Habu (1967: 60) recognized eight subtribes: Cymindina, Catascopina, Pericalina, Anomotarina, Calleidina, Lebiina, Demetriina, and Dromiina. The Cymindina and Lebiina are each about the same as proposed by Csiki; catascopines and pericalines are the equivalent of Catascopi; demetriines (proposed first by Bates (1886: 207)) and dromiines are the equivalent of Dromii; and calleidines (including Lebidiina and Physoderina) and anomotarines (new subtribe) are the equivalent of Callidi.

It is evident that central to these more or less divergent arrangements is the system proposed by Lacordaire, with various assemblages of his four basic groups (three of Lebiides plus Pericalides) shifted about on the basis of detailed study and weighting of various character systems. Authors previous to Habu relied principally on details of structure of: labium (particularly of the ligula); pronotum; and tarsi, particularly form of tarsomere 4 and pectination of the claws. Habu used these features, and also form of mandibles and details of structure and armature of the ovipositor sclerites.

Although Habu's treatment is restricted to the fauna of Japan and adjacent islands, most of the major groups of lebiines are represented there. His illustrations of structures are profuse, well-chosen, and well executed, his descriptions are detailed and accurate, and he has exhibited a good sense of proportion in ranking. It seems to us that Habu has provided a firm basis for resolving the long-standing problem of recognition of natural (i.e., phylogenetically valid) groups of lebiines.

To work out a phylogentically valid classification, it is necesary to reconstruct the phylogeny of the Lebiini. Clues are provided by association of many groups of lebiines with vegetation, and at least some character states of adults (particularly those of the tarsi) seem to be associated with life above the surface of the ground (Erwin,1979: 552). Which way has evolution of lebiines proceeded: from occupation of terrestrial to arboreal habitats; or from arboreal to terrestrial; or from terrestrial to arboreal and back to terrestrial? The same sorts of questions are applicable to arboreal habitats. Some lebiines live principally on tree trunks, others hunt on small branches and twigs, still others on leaf surfaces (Erwin, 1979: 559-560, Table 1). What has been the direction of evolution within arboreal habitats?

If these questions could be answered for all comparisons of taxa thought to be related, it would be possible to work out a classification consonant with direction of habitat change. Probably the arboreal zone has been invaded by terrestrial- based ancestors (Erwin, 1979: 509, Fig. 13), but it also seems likely that some ancestral stocks have given rise to terrestrial inhabitants, as well. Movements in both directions may have taken place several times.

Structure of the ovipositor may be associated with different modes of egg-laying, and if these modes were known they might offer another basis for inferring evolutionary sequences. Mode of oviposition is known for some terrestrial calleidines: females of *Tecnophilus* and *Philophuga* climb on low plants, carrying on the stylomeres of the ovipositor a small ball of mud. An egg is laid in the mud ball, and the latter is suspended from a twig by a silken thread produced by the female (Larson, 1969: 64).

Females of most groups of carabids are believed to oviposit in the ground, in chambers scooped out by the ovipositor. Compared to the latter, calleidines seem to be apotypic in oviposition. The ovipositor of *Tecnophilus* and many other calleidines is characterized by absence of ensiform setae from stylomere 2 and narrow form, whereas females of ground-ovipositing carabids have broader second stylomeres and ensiform setae.

Erwin (1982: 40), referring to the remarkable telescopic ovipositor that charcterizes females of the genus *Agra,* inferred that such structures are used to lay eggs "deep in existing burrows in wood or in other deep fissures". Stylomeres of *Agra* females also seem apotypic in their elongate form and reduced number of spine-like ensiform setae.

Among lebiines, pericalines (most taxa are arboreal) and apenines (all known taxa are terrestrial) have the more plesiotypic form of ovipositor. However, almost nothing is known about where eggs are laid or how they are laid by members of these groups. (An exception is the genus *Eurycoleus,* females of one species of which lay eggs on the surfaces of wood, near endomychid pupae which the developing *Eurycoleus* larvae eat [Erwin and Erwin, 1976]). We are satisfied that evidence from structure of the ovipositor offers sufficient grounds to infer that apenines and pericalines are relatively primitive lebiines, that cymindines, with moderately modified ovipositors, occupy an evolutionarily intermediate position, and that the other subtribes whose females have highly modified ovipositors, represent more highly evolved groups. Details of relationships among genera and subtribes remain to be worked out.

In lieu of a definitive treatment of classification of the Lebiini, we offer a key to the subtribes, based on features of adults.

Key to Subtribes of Lebiini

1 (0) Head ventrally with at least one pair of suborbital setigerous punctures . . . . . . 2.

1′ Head ventrally without suborbital setigerous punctures . . . . 4.

2 (1) Labrum narrow, as long or longer than wide. Penultimate setigerous puncture of umbilical series of elytron displaced laterally (as in Fig. 27B) . . . . Subtribe Pericalina, p. 116

2′ Labrum normal, wider than long. Penultimate setigerous punctures of elytra not displaced laterally . . . . 3.

3 (2′) Elytron smooth, without striae. Pronotum with sides curved, widest near base, narrowed evenly anteriorly, apical margin much narrower than basal margin. Head sharply constricted posteriorly, pedunculate. Stylomere 2 of ovipositor with broad apex, without ensiform setae . . . . gallerucoid Calleidina.[1]

3′ Elytron striate. Pronotum with sides sinuate posteriorly, widest at or anterior to middle. Head gradually constricted posteriorly. Stylomere 2 of ovipositor with narrowed apex, ensiform setae two, one dorsal, one ventral . . . . genus *Euproctinus* Leng and Mutchler, 1927.[2] p.

4 (1′) Penultimate setigerous puncture of elytron displaced laterally. Stylomere 2 of ovipositor with ensiform setae, and stylomere 1 with prominent ventral projection extended beyond base of stylomere 2 (Figs. 38 and 39) . . . .

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[1] Adults of *Lebidia* Morawitz and *Gallerucidia* Chaudoir (Lebidii or Gallerucidiini, of authors) key out here although in all other respects they seem to be calleidine.

[2] This Neotropical and southern Nearctic genus seems to be of uncertain position. It has been included with calleidines, based on general appearance and structure of tarsi, but Larson (1969: 23) suggested *Euproctinus* should be placed in a subtribe of its own.

. . . . Subtribe Apenina, p. 120

4′ Penultimate setigerous puncture of elytron not displaced laterally, thus in line with rest of series, or displaced toward stria 8. Stylomere 1 of ovipositor without projection; stylomere 2 with (Fig. 62A) or without (Fig. 96B) ensiform setae . 5.

5 (4′) Posterior tibial spurs markedly unequal, margins serrate, inner spur almost as long as tarsomere 1. Head sharply constricted posteriorly, pedunculate . . . . Subtribe Nemotarsina.

5′ Posterior tibial spurs subequal, margins smooth, not markedly serrate. Head sharply constricted or not . . . . 6.

6 (5′) Mandible widened near base, scrobe wide, lateral margins markedly rounded . 7.

6′ Mandible not conspicuously widened basally, scrobe narrowed, lateral margins not markedly rounded . . . . 8.

7 (6) Head markedly narrowed and prolonged behind eyes. Pronotum longer than wide, markedly narrowed anteriorly, without lateral flange. Ovipositor strikingly telescopic, stylomere 2 elongate . . . . Subtribe Agrina.

7′ Head average, not markedly prolonged behind eyes (Fig. 101). Pronotum wider than long, or as wide as long, not markedly narrowed anteriorly, basal and apical margins subequal in width, with lateral flange. Ovipositor not strikingly telescopic, stylomere 2 not especially lengthened . . . . Subtribe Calleidina, p. 173

8 (6′) Tarsomeres broad, tarsomere 4 with apex subtruncate, not bilobed. Female with stylomere 2 with one or two ensiform setae (Fig. 55A) . . . . Subtribe Cymindina, p. 129

8′ Tarsomeres broad, with tarsomere 4 bilobed, OR tarsomeres slender and tarsomere 4 with apical margin sub-truncate. Stylomere 2 of ovipositor without ensiform setae . . . . 9.

9 (8′) Tarsomeres slender, tarsomere 4 with apical margin sub-truncate. Stylomere 2 of ovipositor glabrous or setose apically . . . . Subtribe Dromiina[3] p. 196

9′ Tarsomeres stout, dilated, tarsomere 4 bilobed. Ovipositor with stylomere 2 glabrous . . . . 10.

10 (9′) Tarsomere 4 with lobes almost half length of tarsomere 5. Ovipositor with stylomere 1 fully sclerotized, stylomere 2 narrow, tapered apically . . . . Subtribe Demetriina.

10′ Tarsomere 4 with lobes short, less than half length of tarsomere 5. Stylomere 1 partially desclerotized, stylomere 2 broad, short, broadly rounded apically . . . . Subtribe Lebiina.

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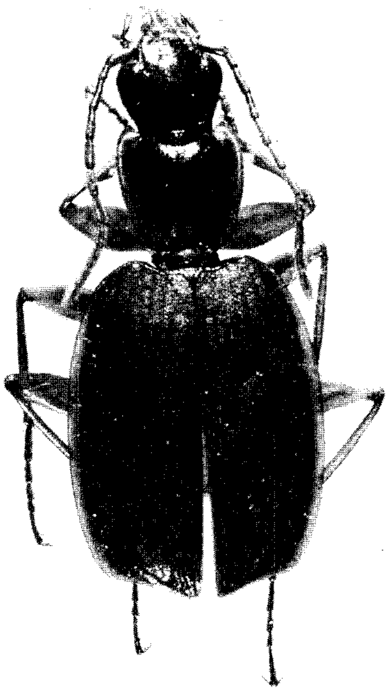
[3] Habu (1967: 250) expressed doubt about including *Celaenephes* Schmidt-Goebel in the Dromiina because of the setose stylomeres 1 and 2 of its females. Thus it would not key out above. Bates (1892: 156) included this genus among the cymindines, along with several other genera that were subsequently assigned to the Dromiina (Csiki, 1932). *Celaenephes* is clearly not a dromiine, and we believe that the stylomeres of its females are too plesiotypic for the genus to be included in the Cymindina. It may be a platynine, or it may represent a separate lineage of Lebiini that will require establishment of another subtribe.

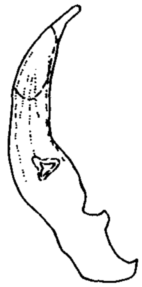
19



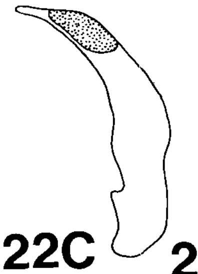
20

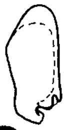
21

Figs. 19-21. Photographs of Pericalina, genus *Thyreopterus*.—Habitus, dorsal aspect. 19, *T. (Thyreopterinus)* species? (SBL = 5.38 mm); 20, *T. (sensu stricto) kivuanus* Basilewsky. (SBL = 6.30 mm); 21, *(Selenoritus) ptolemaei* (Alluaud) (SBL = 5.32 mm).

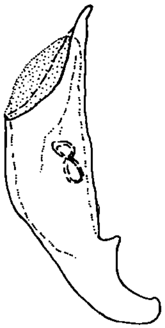

22A


22B


22C


22D


22E

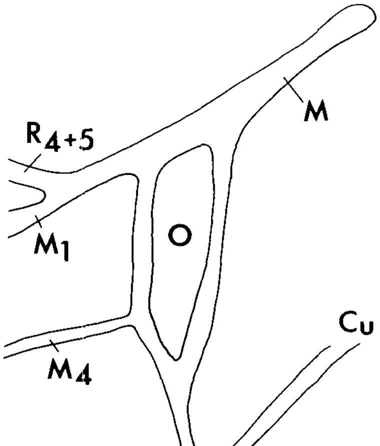

23A


23B


23C

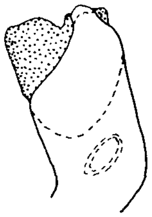

23D

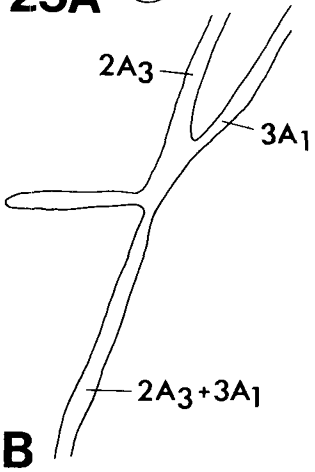
1mm



25A


24A


24B



25B


24C


24D

Figs. 22–24. Line drawings of structures of Pericalina, genus *Thyreopterus*.—Male genitalia. Fig. 22: *T. (Thyreopterinus)* species, A, B, C—median lobe, left lateral, ventral, and right lateral aspects, respectively, D and E, parameres, left and right, respectively, ventral aspect. Fig. 23: *T. (sensu stricto) kivuanus* Basilewsky–A and B, median lobe, left lateral, and ventral aspects, respectively; C and D, parameres, left and right, respectively, ventral aspect. Fig. 24: *T. (Selenoritus) ptolemaei* (Alluaud)–A and B, median lobe, left lateral and ventral aspects, respectively; C and D parameres, left and right, respectively, ventral aspect. Fig. 25. Line drawings of structures of Apenina.—Wing cells and surrounding veins of *Cymindoidea (sensu stricto) indica* Schmidt-Goebel, left wing: A, oblongum cell; B, wedge cell. Legend: cells–O, oblongum, W, wedge; veins—A, Anal; Cu, Cubital; M, Median; R, Radial.

Tribe LEBIINI, Subtribe PERICALINA

Two genera (*Selenoritus* Alluaud, 1917, and *Leptosarcus* Péringuey, 1896), described originally as cymindines, are more appropriately assigned to the Pericalina because adults of each genus exhibit the diagnostic features of this subtribe: extended mouthparts (including elongate labrum), pair of suborbital setae, laterally displaced penultimate umbilical setigerous puncture of an elytron (Fig. 27B), stylomere 2 relatively small, falcate, with three large dorsal setae, and without a ventral preapical sensory furrow or nematoid setae (Figs. 28A-C).

Within the Pericalina, we place both of these genera in the thyreopteroid assemblage: *Selenoritus,* because it is actually a member of *Thyreopterus*; and *Leptosarcus* because stylomere 2 of the ovipositor lacks nematoid setae.

Jeannel (1949: 975) included *Selenoritus* in the tribe Thysanotini, subfamily Calleiditae, along with the Madagascan endemic genera *Antimerina* Alluaud, *Thysanotus* Chaudoir, and *Madecassina* Jeannel. External features of adults of these genera (seen in the MCZ) confirm that they are pericalines, and absence of nematoid setae from stylomere 2 of females of *Antimerina elegans* Alluaud, and *Thysanotus alluaudi* (Jeannel) provide the basis for assigning this geographical complex of genera to the thyreopteroid assemblage. Basilewsky (l953a: 10) suggested that Thysanotini should be included in the Thyreopteridae, but Ball (1975:147), on the basis of study of descriptions and illustrations, suggested that such a grouping would be incorrect. This group could be near the base of the stock that gave rise to the thyreopteroid radiation on Madagascar.

Selenoritus Alluaud, 1917
Figs. 21-22

Selenoritus Alluaud, 1917: 103. GENERITYPE: *Selenoritus ptolemaei* Alluaud, 1917: 104 (monotypy). LECTOTYPE male (here selected), labelled: MUSEUM PARIS MONTS ROUWENZORI zone des forêts Makitawa (2660 m) Ch. Alluaud 1909 [blue paper]; TYPE [red paper]; Museum Paris coll. Ch. Alluaud [blue paper]; Selenoritus ptolemaei Alluaud Type [white paper, with blue strip across top]. [MNHP]. PARALECTOTYPE male, similarly labelled in Museé d'Afrique Centrale, Tervuren.– Burgeon, 1937: 356.

Selenorites (misspelling) Jeannel, 1949: 975.– Basilewsky,1962: 300 and 321.

Notes about type material.— The type locality of *S. ptolemaei* is more fully specified, as follows: ZAIRE, Mount Ruwenzori, east versant, in forest above the shelter, beneath peak of Makitawa, between 2600 and 2800 meters (Alluaud, 1917). Alluaud (1917: 103-104) provided a detailed description of external features of type specimens. His basis for claiming a relationship of this species to the cymindines is a combination of these features: truncate elytra, not covering apex of abdomen; broad paraglossae, clearly extended beyond apex of ligula; and denticulte tarsal claws.

Alluaud lists the following features as diagnostic of *Selenoritus*: disc of elytra more covex; elytra more ovoid with humeri more rounded, and basal groove not sinuate between humeri and scutellum; posterior pair of supraorbital setigerous punctures far removed posteriorly on occiput; antennomere 3 with more than apical setae; lateral margins of pronotum without setigerous punctures; and posterior tarsi with tarsomeres 1-5 filiform, not dilated nor grooved dorsally, elongate and subequal to one another. Most of these character states, however, appear in the pericaline genus *Thyreopterus (sensu lato)* as pointed out in conversation by Dr. P. Basilewsky, who had previously recognized the similarities between members of these two taxa.

Pectinate tarsal claws and small size place *Selenoritus* near the subgenus *Thyreopterinus* Alluaud.

Character states that distinguish adults of *Selenoritus* from those of *Thyreopterinus* are: small eyes (Fig. 21; cf. Fig. 19); posterior pair of supraorbital setigerous punctures clearly behind posterior margins of compound eyes; pronotum without posterior pair of setigerous punctures (members of both groups lack the anterior pair); basal ridge of elytron not extended to sutural margin, but terminated near base of interneur 4; metathorax and hind wings reduced. Small eyes, loss of setae, and reduced metathorax and hind wings seem to be adaptations associated with life in montane environments, and the position of the posterior pair of supraorbital setigerous punctures is probably the result of reduction of eyes, rather than posterior migration of the setigerous punctures. These differences might have evolved relatively recently, and thus do not constitute evidence that *S. ptolemaei* is phylogenetically old. Instead, this species may be only a moderately specialized member of *Thyreopterinus.*

On the other hand, many montane-adapted stocks seem to be relics of older stocks that have been replaced in the lowlands by later evolving relatives. Until the relationships of *Thyreopterinus* and *Selenoritus* can be more fully resolved, it seems as well to treat the two groups as separate subgenera of *Thyreopterus*. Evidence supporting this decision is provided by details of stylomere 2 of the ovipositor, for a combination of number and length of ensiform seta and form of these sclerites themselves distinguish females of these groups from one another. See Table 1 for details.

Male genitalia of *Selenoritus ptolemaei* are also markedly different from those of the one species of *Thyreopterus* examined (Fig. 24; cf. Fig. 23). In males of both *S. ptolemaei* and *T.*

TABLE 1.
COMPARISON :OF FEATURES OF STYLOMERE 2 OF :THE OVIPOSITOR OF FEMALES OF SUBGENERA OF *THYREOPTERUS* DEJEAN

	STYLOMERE 2			
	Ensiform Setae			Apical Portion
NAME OF SUBGENUS	No.	L. dorso-medial seta	Form	Width
Thyreoterus (sensu stricto)	2	long	slightly falcate	markedly narrowed
Thyreopterinus Alluaud	3	long	markedly falcate	markedly narrowed
Selenoritus Alluaud	2	short	slightly falcate	wide

(sensu stricto) kivuanus, the apical orifice of the median lobe is slightly left of the mid-line; in males of *Thyreopterinus* species, it is to the right. However, such differences are common among pericalines, and their evaluation must be made in terms of additional species of subgenus *Thyreopterinus.*

Thyreopterus (Selenoritus) ptolemaei Alluaud, 1917, new combination

Figs. 21-22A, C

Description.— Habitus as in Fig 21. Standarized body length 6.20 mm. (lectotype; other specimens of similar size). Form pterostichoid or agonoid, slender.

Color generally rufo-piceous dorsally, more rufous ventrally, palpi, antennae and legs flavous. Elytra each with three groups of rufo-flavous marks: one group in basal 0.20 on intervals 2, 3, 6, 7, and 8; one group medially on intervals 7 and 8; and one group in apical 0.80 on intervals 2-8.

Microsculpture of dorsum. Head and elytra, with meshes isodiametric, those of elytra slightly shingled; pronotum with meshes transverse.

Luster. Surface generally shining.

Head. Clypeus longer than average; anterior margin concave; bipunctate, each puncture in longitudinal groove extended to posterior margin. Frons with impressions broad and shallow, each side with single longitudinal ridge; vertex slightly convex. Posterior pair of supraorbital setigerous punctures well posterad of posterior margin of compound eyes. Temples not extended.

Eyes. Reduced. Paragenae at narrowest less than width of antennal scape.

Antennae. Length average: scape slightly longer than antennomere 3, and slightly broader; outer antennomeres longer than wide (ant. 9 l/w– 3.00). Scape with single seta; pedicel with terminal ring of setae; antennomere 3 generally sparsely setose; remaining antennomeres setose.

Mouthparts. Labrum longer than average, tapered anteriorly. Mandibles elongate, slender (not studied in detail). Maxilla: stipes with several setae; palpus slender, palpomere 4 distinctly longer than 3; apical margin truncate, narrow. Labium: mentum with well developed tooth; ligula narrow, bisetose apically; paraglossae broad, extended clearly beyond apex of ligula; palpi slender, palpomere 2 bisetose; palpomere 3 with apical margin truncate.

Pronotum. Without lateral setae. Dorsal surface generally sparsely setose, setae short. Form slender, elongate, sides markedly sinuate posteriorly; anterior margin concave, angles short but distinctly set off; basal margin truncate. Sides moderately elevated, lateral grooves narrow, indistinctly isolated from posterior lateral impressions by convexity; median longitudinal impression shallow; anterior and posterior transverse impressions evident, but broad.

Prosternum. With few setae at apex of intercoxal projection.

Metepisternum. Short, almost quadrate.

Elytra. Slightly explanate, widest point evidently behind middle; humerus broadly rounded; basal ridge terminated near base of interneur 4, not extended to suture; apical margin sinuately truncate. Surface sparsely punctate, setae short. Parascutellar setigerous punctures present. Interneurs teminated before apex, shallow; intervals slightly convex. Umbilicate punctures l6, penultimate puncture slightly displaced laterally. (Lectotype with right elytron broken and detached).

Hind wings. Markedly reduced.

Legs. Average, generally. Tibial spines reduced, as usual for pericalines. Anterior femur with numerous setae ventrally. Anterior tibia with terminal spur thickened. Claws long, each with 4-5 pectinations. Anterior tarsomeres without adhesive vestiture.

Abdomen. Sterna average, sternum 6 with four setae near posterior margin.

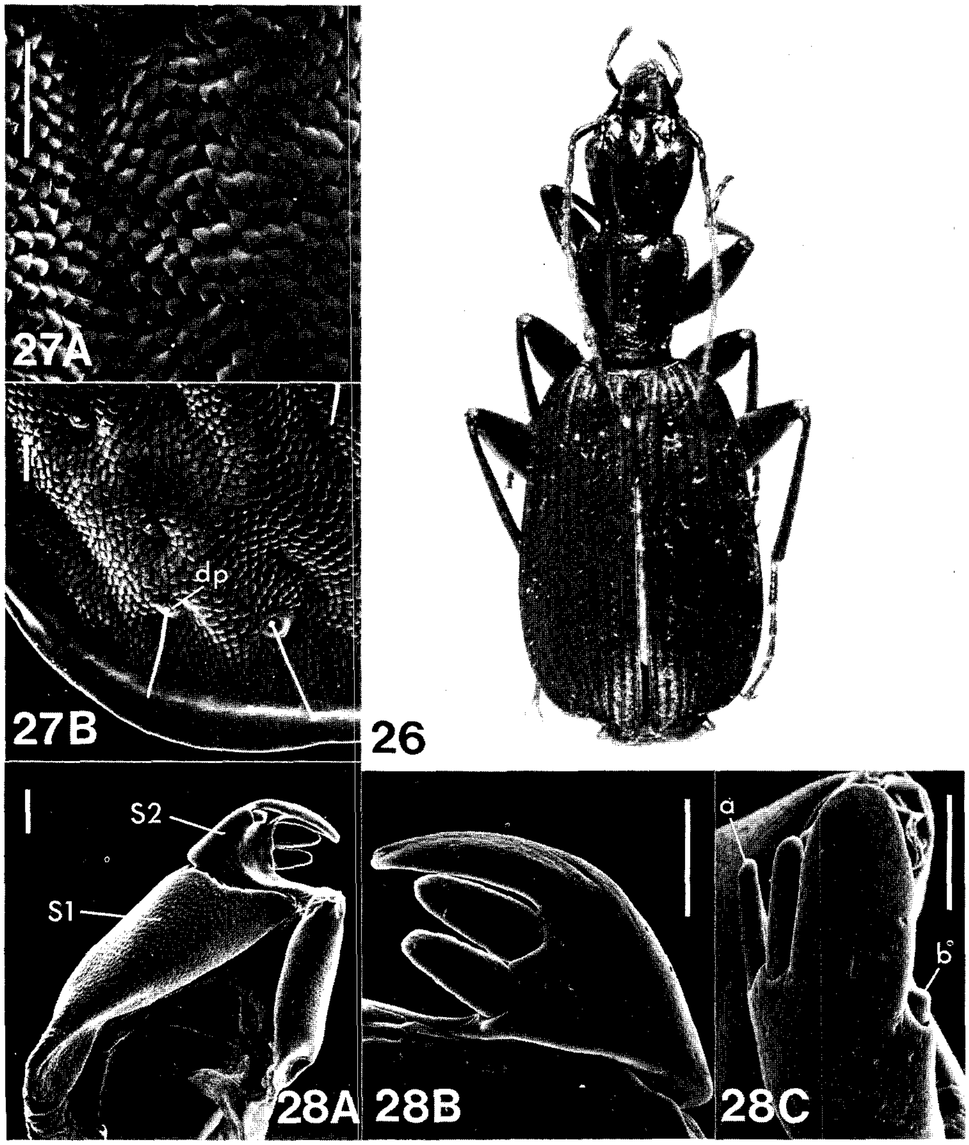
Male genitalia. Median lobe (Figs. 22A-C) short, broad; apical portion in ventral aspect short, rounded; dorsal surface extensively sclerotized; apical orifice long, inclined to left. Internal sac with narrow sclerotized rim apically, otherwise unarmored. Left paramere with apical margin sinuate- truncate. Right paramere with apex acute. (Cf. Figs. 23A-C and 24A-C)

Ovipositor. Stylomeres 1 and 2 subequal in length. Stylomere 2 elongate, hardly curved, dorsally with two broad ensiform setae; without nematoid setae.

Geographical distribution and habitat.— This species is known from the higher slopes of Mt. Ruwenzori, Zaire. Two specimens were collected in dead bamboo.

Material examined.— We have seen the types and three additional specimens, as follows: Two males– Kilindera, north face of Ruwenzori, 2750 m., VII- VIII. 1974 R. P. M. Lejeune (MACT). Female.– Vallee Mont Mulungu, Massif Ruwenzori, 2600 m., 29.11.1957, P. Vanschuytbroeck (MACT).

We also examined superficially material representing five additional species of *Thyreopterus (sensu stricto)* and four additional species of subgenus *Thyreopterinus,* from



Figs. 26–28. Photographs of Pericalina, genus *Leptosarcus*.—Fig. 26: *L. hessei* Basilewsky, habitus, dorsal aspect (SBL = 12.86mm). Figs. 27–28. SEM photographs of elytra and stylomeres of *L. porrectus* Péringuey. Fig. 27: Left elytron, microsculpture, dorsal aspect–A, discal area; B, preapical area. Fig. 28 ovipositor, left stylomeres; A, stylomeres 1 and 2, medial aspect; B, stylomere 2, lateral aspect; C, stylomere 2, apico-ventral aspect. Scale bars, Figs. 27–28 = 50 μm. Legend, elytra: dp, penultimate umbilical puncture, displaced toward lateral margin. Legend, stylomeres: a, lateral ensiform seta; b–medial ensiform seta; S1, stylomere 1; S2, stylomere 2.

collections of CAS. Fig. 20 illustrates the habitus of *T.* (*sensu stricto*) *kivuanus* Basilewsky.

Leptosarcus Péringuey, 1896

Leptosarcus Péringuey, 1896: 218. GENERITYPE: *Leptosarcus porrectus* Péringuey, 1896: 219 (monotypy).– Basilewsky, 1954a: 83.

Basilewsky (1954a) studied the few specimens of *Leptosarcus* that were available, including type material of *L. porrectus* Péringuey (type locality– Vonstantia, Cape Province, South Africa). He provided a description of adult features generally satisfactory for recognition of specimens, and figured heads, labra, labia, and male genitalia. He also described a second species, *L. hessei* (type locality– Zululand). To Basilewsky's characterizations, we add the following observations.

Microsculpture of the elytra is shingled (Figs. 27A, B), like that of some of the more highly derived members of the New World genus *Phloeoxena* (see Ball, 1975), and is quite unlike the smoother microsculpture characteristic of the elytra of cymindine adults. The penultinate umbilical setigerous punctures of the elytra are displaced laterally (Fig. 27B). Stylomeres 1 and 2 (Figs. 28A-C) are typical of the thyreopteroid Pericalina. Probably adults of *Leptosarcus* should be sought in the types of habitats occupied by *Phloeoxena* adults; *i.e.,* in association with fallen logs, or standing trees with loose or scaly bark, in wet forests.

We conclude that general similarity in form and size between adults of *Leptosarcus* and of *Hystrichopus (sensu stricto)* is convergent. Males of *Leptosarcus* have anopic median lobes as have males of *Cymindis,* but this feature is plesiotypic, and is thus not of use in establishing relationships.

This genus seems to be relict for several reasons: low diversity; seemingly without close relatives among pericalines; adults brachypterous, and metathorax reduced; and geographical distribution peripheral to the main area (tropics) of the Pericalina.

Material examined.— We have seen seven specimens representing both known species, all from the collections of the South African Museum, and all collected at localities in the Union of South Africa, as follows.

Leptosarcus porrectus Péringuey
Figs. 27-28

Male, holotype, labelled: C.T. 8.26 type; HOLOTYPUS [red paper]; Leptosarcus porrectus P; Leptosarcus porrectus Per Basilewsky vid 1953. Male, paratype, from same locality as holotype, and also seen by Basilewsky. Female, same locality, det. by Basilewsky, 1953. Female, Hott- Holl Mts. 4000 f., Caledon C.C., Bernard 1916; det. by Basilewsky, 1953.

Leptosarcus hessei Basilewsky
Fig. 26

Female HOLOTYPUS [red paper]; Mt. Kendhla forest Zululand; Leptosarcus hessei n.sp. P. Basilewsky det. 1953.

Tribe LEBIINI, Subtribe APENINA

This subtribe was erected by Ball (1982). Diagnostic character states are: head without suborbital setigerous punctures; elytron with penultimate umbilical puncture laterad of antepenultimate and ultimate umbilical punctures; tibiae and tarsi relatively slender;

ovipositor, (Figs. 38, 39A, B) with stylomere 1 much longer than 2, asetose; stylomere 2 markedly curved, apex of blade pointed; two large ensiform setae on dorsal margins; preapical sensory furrow and associated setae absent.

Description.— The following statements indicate range of variation of selected features useful for recognizing apenine adults, and for determining relationships of taxa.

Color. Various, but mostly somber: dorsum dark rufous to black, elytra with or without paler spots; venter piceous to testaceous; legs and palpi of most specimens pale– rufous to testaceous, though femora of some specimens as dark as ventral surface.

Microsculpture. Labrum and clypeus with meshes isodiametric. Dorsum of head with meshes isodiametric, or microlines effaced; venter with meshes transverse. Pronotum with meshes isodiametric, or transverse, or microlines effaced. Lateral and ventral thoracic sclerites with meshes transverse (characteristic of most groups) or isodiametric. Scutellum with meshes isodiametric (characteristic of most groups) or transverse. Elytra with meshes isodiametric, transverse, or effaced. Abdominal sterna with meshes transverse, or transverse medially, and isodiametric laterally.

Luster. Surface of head and thorax shining to dull; surface of elytra and abdominal sterna iridescent, shining, or dull.

Macrosculpture. Surface generally smooth, except as noted. Head (frons and vertex), pronotum, and elytral intervals smooth, or variously transversely ridged and grooved. Surface impunctate, or covered with coarse punctures.

Vestiture. Surfaces of adults of most taxa glabrous, but *Trymosternus* adults generally setose. Antennomeres 1 and 2 with setae confined to apex, or generally setose; antennomere 3 with setae confined to apical 0.50, or generally setose; antennomeres 4–11 generally setose. Tarsomeres dorsally setose.

Fixed setae. Average for lebiine adults: labrum with six long marginal setae, clypeus with one pair; head and pronotum each with two pairs; elytra each with two discal setae in interval 3, parascutellar and preapical setae, and 15 umbilical setae along lateral margin; penultimate umbilical seta displaced laterally of an imaginary line extended between antepenultimate and ultimate umbilical punctures. Legs (anterior, middle, and posterior) with number of setae as follows: coxae– 0–1, 2–5, 2; trochanters– 1, 1, 1; femora– 2 (posterior face), 3–5 (anterior face), 2 (anterior face). Sternum VII with two setae in males, and two or four setae in females.

Head. Clypeus transverse, anterior margin of each truncate or slightly concave. Frontal impressions shallow, indistinct. Sub-antennal ridge average or prominent. Eyes: orbicular, convex, visible in ventral aspect; or reduced, longer than wide, flattened, ventral margin obliquely truncate, and not visible in ventral aspect. Insertion of antennal scape close to or remote from anterior margin of adjacent eye.

Antennae. Average for lebiine adults: filiform, flagellar antennomeres sub-cylindrical, distinctly longer than wide, antennomere 2 short, antennomere 3 longer than 4.

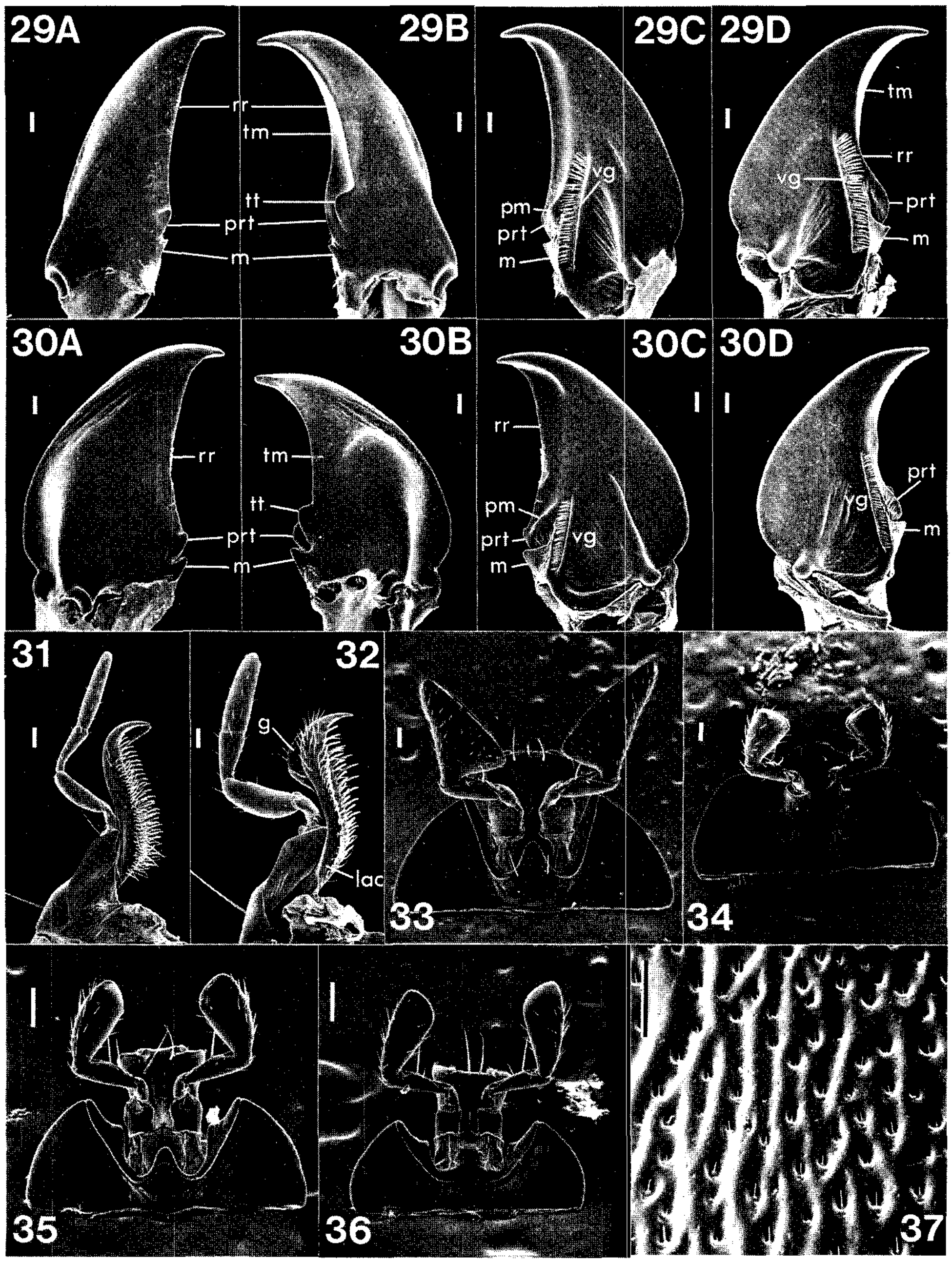
Mouthparts. Labrum transverse, anterior margin truncate or slightly concave. Mandibles. Left and right mandible about same shape, overall. Left mandible (Figs. 29A, C,- 30A, C) with terebral margin reduced, no terebral tooth. Cutting edge retinacular ridge; posterior retinacular tooth small, not divided; ventral retinacular ridge blunt; premolar triangular; premolar ridge well developed, sharp. Right mandible (Figs. 29B, D - 30B, D) with terebral margin cutting edge, terebral tooth blunt, large; retinacular ridge well developed, anterior and posterior teeth blunt; ventral ridge not developed; premolar tooth triangular, sharp at apex; ventral groove extended basad, to premolar area. Maxillae, average for lebiine adults: lacinia with (Fig. 32), or without (Fig. 31) apico-lateral setae; palpomeres slender, 4 with apical margin truncate, slightly longer than 3, markedly longer than 2. Labium: mentum (Figs. 33-36) bisetose, with lateral lobes pointed apically (Fig 33) or broadly rounded (Fig. 34), tooth well developed, pointed apically (Figs. 33-35), or absent (Fig. 36); glossal sclerite with apical margin broad, sub-truncate, bisetose (or quadrisetose, median two setae close together, much shorter than lateral pair); paraglossae fused to glossal sclerite, apical margins finely setose, hardly extended beyond apex of glossal sclerite; palpomeres 1 and 2 slender, palpomere 3 more (Fig. 33) or less (Fig. 36) broadly securiform, more so in males than in females.

Thorax. Pronotum with sides rounded, more constricted basally than apically (or markedly cordate, constricted basally, sides strikingly sinuate basally); base lobate medially (or almost truncate); anterior angles broadly rounded, posterior angles sharp, prominent; disc slightly convex, median longitudinal impression sharply defined, anterior and posterior transverse impressions hardly evident; posterior lateral impressions shallow, indistinct. Prosternum with intercoxal process immarginate. Metepisternum distinctly longer than wide, lateral margin 1.5 times longer than anterior margin (or almost as long as wide, anterior and lateral margins subequal).

Elytra. Average in form; humeri prominent, extended slightly forward, basal ridge marginal, extended to edge of scutellum. Apical margin obliquely subtruncate. Interneurs average for carabids (or broader than average), punctate; scutellar interneur well developed. Intervals slightly convex (or alternate odd-numbered intervals sub-carinate to carinate, raised above even-numbered intervals).

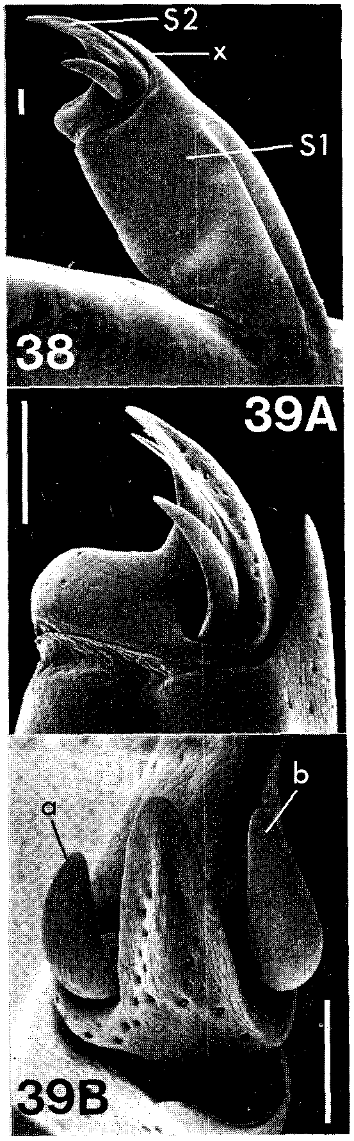
Wings. Well developed (or short stubs); wedge cell absent (Fig. 25B), oblongum cell average (Fig. 25A) (or reduced, or absent). Venation otherwise normal for lebiines.

Legs. Average for carabids. Middle tibia with spines of outer row numerous, extended length of margin (or spines few, located in apical 0.25). Tarsal claws pectinate. Tarsomere 4 notched, but not bilobed. Male with front tarsomeres 1–3 ventrally with biseriate adhesive vestiture.



Figs. 29–37. SEM photographs of structures of Apenina.—Figs. 29–30, mandibles–A and C, left, dorsal and ventral aspects, respectively, B and D–right, dorsal and ventral aspects, respectively, of: 29, *Cymindoidea (sensu stricto) indica* Schmidt–Goebel; 30, *Apenes (sensu stricto) lucidula* Dejean. Figs. 31 and 32, right maxilla, ventral aspect of: 31, *C. indica*; 32, *A. lucidula*. Figs. 33–36, labium, ventral aspect of: 33, *C. indica*; 34, *A. lucidula*; 35, *A. (Sphalera)* species; and 36, *A. (Sphalera) postica* (Dejean). Fig. 37, *C. indica*: head, microsculpture, dorsal aspect. Scale bars = 100 μm. Legend, mandibles: m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin; tt, terebral tooth; vg, ventral groove.

40



Figs. 38–40. Photographs of Apenina.—Figs. 38–39: SEM photographs of ovipositor, left stylomeres. Fig. 38: *Cymindoidea (sensu stricto) indica* Schmidt-Goebel, stylomeres 1 and 2, lateral aspect, Fig. 39: *Apenes (sensu stricto) lucidula* Dejean: A and B, lateral and apico-ventral aspects, respectively,. Scale bars = 50 μm. Fig. 40: *Cymindoidea (Habutarus) papua* (Darlington), habitus, dorsal aspect (SBL = 4.81 mm.). Legend, stylomeres: a, lateral ensiform seta; S1, stylomere 1; S2, stylomere 2; x, projection of stylomere 1.

Abdomen. Sterna II–VII average. Female: tergum VIII broadly membranous medially; sternum VIII broadly membranous medially, lateral apodemes short; tergum X completely sclerotized.

Male genitalia. Median lobe cylindrical, elongate, slightly curved ventrally. Apical portion slender, without projections, quite short, but varied in length; anopic, orifice either dorsal, or dorso-lateral, toward left side. Internal sac with vestiture of smaller (or larger) microtrichia; with or without long, coiled, flagellum. Left paramere average for lebiomorph males; right paramere, though reduced, large for lebiomorphs.

Ovipositor (Figs. 38 - 39A, B). Valvifer markedly transverse, narrow. Stylomere 1 about twice length of stylomere 2, ventral apical angle markedly produced beyond base of stylomere 2, asetose; stylomere 2 with base extended dorsally as lobe; apical portion sword-like, apex pointed; two very large ensiform setae dorsally; ventral surface with two rows of sensory pits; without ventral preapical sensory furrow and associated setae.

Classification.— Included in the Apenina are three genera: *Apenes* LeConte (subgenus *Apenes* and *Sphalera* Chaudoir); *Cymindoidea* Castelnau (subgenus *Cymindoidea, Platytarus* Fairmaire, and *Habutarus,* new subgenus); and *Trymosternus* Chaudoir. Reduction of the oblongum cell of the hind wing is an autapotypic feature establishing monophyly of the New World genus *Apenes.* Monophyly for the Old World assemblage of *Trymosternus* and *Cymindoidea sensu lato* is established by an autapotypic feature of the interal sac of male genitalia: possession of a moderately to very long and coiled flagellum. In the Old World assemblage, monophyly of *Trymosternus* is established by a combination of: integument generally setose, and labial palpomere 2 plurisetose.

We have not been able to establish monophyly of *Cymindoidea,* for we have not identified synapotypic features for all three subgenera. *Cymindoidea* and *Platytarus* are linked by a quadripunctate glossal sclerite, broadened pronotum, and rugose dorsum. We could make *Cymindoidea* monophyletic by including in it *Trymosternus,* but we suspect this decision would not be acceptable to our European colleagues, who seem generally to prefer retention of traditionally recognized taxa, in spite of phylogenetic considerations. We could also achieve the desired result by exluding *Habutarus,* but this would require establishment of a monobasic genus, and we are reluctant to do this. The compromise (which yields a cladisitcally unacceptable genus) is to include *Habutarus* in *Cymindoidea* on the basis of a symplesiotypic feature: the glabrous integument.

Geographical distribution.— This subtribe has a Gondwanian distribution pattern, with a sister group on each side of the Atlantic Ocean, mainly in the Southern Hemisphere and tropics.

Key to Genera and Subgenera of Subtribe Apenina

1 (0) Dorsum setose. Eyes reduced, not visible in ventral aspect. Antennal fossa remote from anterior margin of eye. Elytron with humerus sloped. Metepisternum quadrate, wings represented by short stubs. Metasternum with deep pit near middle coxae . . . . *Trymosternus* Chaudoir, p. 128

1′ Dorsum glabrous, except for normal fixed setae. Eyes various. Antennal fossa close to or remote from anterior margin of eye. Elytron with humerus broadly rounded. Metepisternum and wings various. Metasternum without pit near middle coxae . . . . 2.

2 (1′) Glossal sclerite with four setae. Dorsal surface modified, either coarsely and irregularly sculptured and punctate, or microsculpture with lines deep, sculpticells convex, luster dull, and discal elytral intervals keeled . . . . 3.

2′ Glossal sclerite with two setae. Dorsal surface unmodified, smooth, elytral intervals more or less flat . . . . 4.

3 (2) Microsculpture of thoracic pleura and sterna with meshes isodiametric.

Antennomeres 1 and 2 generally setose. Elytron with odd-numbered intervals carinate. Fossa of antenna and anterior margin of adjacent eye separated by wide gap .... *C. (Platytarus)* Fairmaire.

3′ Microsculpture meshes of thoracic pleura and sterna transverse. Antennomeres 1 and 2 with setae near apices, only. All elytral intervals non-carinate. Antennal fossa and anterior margin of adjacent eye close together .... *C. (Cymindoidea)* Castelnau p. 126

4 (2′) Metepisternum quadrate, wing represented by short stub. Dorsum of head with irregular shallow grooves and irregular ridges. Range– New Guinea .... *C. (Habutarus)* new subgenus, p. 127

4′ Metepisternum elongate, wing long, normally developed. Head with dorsum smooth or ridged. Range– Neotropical and southern Nearctic Regions ...... 5.

5 (4′) Head with dorsum ridged or coarsely punctate .... *A. (Apenes)* LeConte, p. 125

5′ Head with dorsum smooth, not punctate or ridged .... *A. (Sphalera)* Chaudoir.

Apenes LeConte

Figs. 30, 32, 34-36, and 39

Apenes LeConte, 1851: 174. GENERITYPE: *Cymindis lucidula* Dejean, 1831:320 (subsequent designation, by Motschulsky, 1864: 240, table).– LeConte, 1861: 24.– Chaudoir, 1875: 21, 35.– Horn, 1881: 156.– 1882: 156.– Bates, 1883: 188.– Blatchley, 1910: 147, 154.– Ball, 1960: 161.– Lindroth, 1969a: 1087.– Reichardt, 1977: 443

Sphenopalpus Blanchard, 1853: 32. GENERITYPE: *Sphenopalpus parallelus* Blanchard, 1853: 32 (=*Cymindis aenea* Dejean, 1831: 319) (monotypy):– Chaudoir, 1871: 385.

Sphenopselaphus Gemminger and Harold, 1868: 299. Unjustified emendation of *Sphenopalpus*.

Nominus Motschulsky, 1864: 240 (table). GENERITYPE: *Cymindis punctulata* Dejean, 1831: 316 (=*Cymindis sinuata* Say, 1823: 8) (original designation by Motschulsky, 1864: 240, table).– Chaudoir, 1875: 42.

Malisus Motschulsky, 1864: 240 (table). GENERITYPE: *Cymindis variegata* Dejean, 1825: 217 (original designation).

Didymochaeta Chaudoir, 1875: 50. GENERITYPE: *Didymochaeta hamigera* Chaudoir, 1875: 53 (here designated).

Sphalera Chaudoir, 1875: 54. GENERITYPE: *Cymindis postica* Dejean, 1831:317 (monotypy). NEW SYNONYMY.

Notes about synonymy.— Chaudoir (1875) recognized four genus-group taxa that we include in *Apenes: Apenes (sensu stricto); A. (Malisus* Motschulsky); *Didymochaeta* Chaudoir, 1875; and *Sphalera* Chaudoir, 1875. Bates (1883: 189) synonymized the first three names because the taxa were based on "slight characters (*Malisus*) on general form and facies, (*Didymochaeta*) on the narrow ligula and tooth of mentum". To these names, we add *Sphalera* Chaudoir, this taxon being based on absence of a mental tooth (Fig. 36). This feature involves a minor desclerotization. Otherwise, adults are strikingly like those included in *Didymochaeta*.

For the atypical subgenus, we choose the name *Sphalera* (rather than *Didymochaeta*) because the former has fewer letters, and is thus easier to write, if not to remember.

Recognition.— Adults of this genus are distinguished from other apenines by the following combination of character states: glossal sclerite with a single pair of setae, dorsum glabrous, metepisternum longer than wide, hind wings normally developed, metasternum smooth, without a pit near the middle coxae. Additionally, males are distinguished by lack of a flagellum of the internal sac.

Description.— Character states mostly as for subtribe, with restrictions or exceptions as follows.

Microsculpture. Dorsum of head with meshes isodiametric. Pronotum and elytra with meshes isodiametric or transverse.

Vestiture. Surface generally glabrous. Antennomeres 1 and 2 with setae confined to apex, antennomere 3 with setae confined to apical 0.50.

Head. Sub-antennal ridge average. Eyes orbicular, prominent, ventral margin rounded. Antennal fossa close to antero-ventral margin of eye. Flagellar antennomeres distally longer than wide or length and width subequal, and antenna short.

Mouthparts. Labium: mentum with lateral lobes broadly rounded or pointed apically; tooth absent or present and bluntly or sharply pointed; glossal sclerite bisetose; palpomere 2 bisetose; palpomere 3 slightly to markedly securiform.

Thorax. Pronotum with sides rounded, or sinuate posteriorly; base lobate medially. Metepisternum distinctly longer than wide.

Elytra. Interneurs average. Intervals slightly convex.

Wings. Well developed: oblongum cell shortened (stalked) or absent.

Male genitalia. Internal sac without coiled flagellum.

Classification.— The species of *Apenes* are here grouped into two subgenera: *Apenes (sensu stricto),* including the species of *Malisus*), adults larger, body thicker, more terete, with head grooved or coarsely punctate, and oblongum cell of wing stalked; and *Sphalera* (including *Didymochaeta*), adults smaller, flatter, with head smooth (frontal impressions extended diagonally to anterior supraorbital setigerous punctures), and wings without oblongum cell.

Phylogenetic considerations.— External features of adults of subgenus *Sphalera* seem more plesiotypic, but absence of the oblongum cell from the wing, and absence of a mental tooth are apotypic features. Conversely, adults of *Apenes (sensu stricto)* seem more derived in body form, but retain the oblongum cell. The more sculptured integument characteristic of *Apenes (sensu stricto)* adults is shared with adults of the Old World *Cymindoidea (sensu stricto)* and subgenus *Platytarus*. This similarity is probably convergent.

Geographical distribution.— The range of *Apenes* extends from northern Argentina in South America, to southern Ontario in eastern North America.

Cymindoidea Castelnau
Figs. 29, 31, 33, 37, 38, and 40

Cymindoidea Castelnau, 1832: 390. GENERITYPE: *Cymindis bisignata* Dejean, 1831: 322 (monotypy).– Andrewes, 1930: 140-141.– Basilewsky, 1961a: 154.– Csiki, 1932: 1490.– Jedlička, 1963: 462.

Philotecnus Mannerheim, 1837: 42. GENERITYPE: *Philotecnus stigma* Mannerheim, 1837: 42 (=*Cymindis bisignata* Dejean) (monotypy).

Platytarus Fairmaire, 1850, XVII (Bull.), XVII. GENERITYPE: *Cymindis famini* Dejean 1826: 447. (original designation).– Basilewsky, 1961a: 165.– Antoine, 1962: 554.– Jedlička, 1963: 463.

Notes about synonymy.— Basilewsky (1961a: 154 and 165-166) provided relatively recent listings of references to the above genus-group names. Reasons for including *Cymindoidea (sensu stricto)* and *Platytarus* in the same genus are given under "Classification".

Recognition.— Adults of this genus are distinguished from those of *Trymosternus* by the glabrous dorsum and unmodified metasternum. Additionally, adults of subgenus *Platytarus* (the only group partially sympatric with *Trymosternus*) have four glossal setae, and flatter eyes. Adults of the Papuan subgenus *Habutarus* are like those of the New World subgenus *Apenes,* but the two groups are distinguished not only on the basis of wing development (see key) and geographical distribution, but males of *Habutarus* have a long flagellum in the internal sac that is characteristic of *Cymindoidea.*

Description.— Character states mostly as described for subtribe, with restrictions and exceptions as follows.

Head. Frons and vertex with longitudinal ridges and grooves, irregularly rugose (Fig. 37); with or without prominent supraocular ridges. Subantennal ridge prominent. Eyes orbicular or flattened, and longitudinally oriented; ventral margin straight or curved. Temples well developed. Antennal fossa close to or remote from anteroventral margin of eye. Flagellar antennomeres longer than wide.

Mouthparts. Maxilla: lacinia (Fig. 31) without setae on lateral preapical margin, few setae on ventral surface; mentum (Fig. 33) with lateral lobes pointed apically, tooth well developed, pointed apically. Glossal sclerite (Fig 33) with two or four setae, for latter condition, median pair very close together basally; palpomere 3 markedly securiform, maximally so in males.

Thorax. Metathorax normal, or reduced, with metepisternum quadrate.

Wings. Well developed, with oblongum cell not reduced (Figs. 25A, B), or brachypterous.

Legs. Spines of tibiae reduced.

Male genitalia. Internal sac with long coiled flagellum.

Classification.— Although Jeannel (1949: 947) included *Platytarus* in the subfamily Calleiditae on the basis of reduced tibial spines of adults, other character states show that the group is correctly placed near *Cymindoidea* – where it was placed by previous authors. In fact, the only character states separating the two groups seem neither sufficiently numerous nor sufficiently important (they involve form and surface sculpture only) to accord generic rank to these groups. On the other hand, with antennae shifted forward, eyes flatter and seemingly more protected by the rest of the head, the body generally narrower and deeper, we believe that the species of *Platytarus* occupy an ecological zone rather different from that occupied by the species of *Cymindoidea* (*sensu stricto*). On this basis, we accord subgeneric rank to these groups.

Adults of the new taxon *Habutarus,* described below, are superficially strikingly different from those of *Cymindoidea* and *Platytarus.* Nonetheless, they have the basic attributes of *Cymindoidea,* and we prefer to emphasize similarities rather than differences. We do this by including *Habutarus* in *Cymindoidea (sensu lato).*

Identification of species.— Andrewes (1935: 202-204) provides keys to adults of the species of *Cymindoidea* (*sensu stricto*) and the subgenus *Platytarus.* Basilewsky (196la) provides keys to adults of the African species of *Cymindoidea* (pp. 155-158) and *Platytarus* (pp. 166-168).

Material examined.— We have seen adults of the following: *Cymindoidea (sensu stricto)*– 19 specimens (two dissected; CAS), representing four Afrotropical and four Oriental species; *Platytarus* – 41 specimens (two dissected, CAS), representing four species; and *Habutarus* – 17 specimens (three dissected, MCZ), representing *C. papua* (Darlington), all paratypes, from Dobodura, Papua, New Guinea.

Geographical distribution.— The range of this genus is discontinuous: *Cymindoidea (sensu stricto)* and *Platytarus* are widespread in Africa and the Oriental Region, with the range of *Platytarus* extended eastward to Indo-China and northward to Hong Kong, and that of *Cymindoidea* only as far as Burma (Jedlička, 1963: 462-463); *Habutarus* is known only from New Guinea, that is, the northern part of the Australian Region. Species of *Cymindoidea (sensu lato)* have not previously been recorded from the Indo-Australian Archipelago.

Habutarus, new subgenus
Fig. 40

GENERITYPE: *Nototarus papua* Darlington, 1968: 186 (monotypy; here designated).

Derivation of name.— From the surname of Dr. Akinobu Habu; and "*tarus*", one of the junior synonyms of *Cymindis,* and a name used in various combinations for cymindine-like forms. Features of the ovipositor provide the principal clue to determining the correct location of this taxon. Dr. Habu emphasized the importance of features of this structure in classification of Lebiini, and so we are pleased to dedicate this subgenus to him, in recognition of his contribution.

Recognition.— Adults of the single species included here resemble those of the Australian calleidine subgenus *Nototarus* Chaudoir (see below), but as indicated above, they have the basic attributes of the Apenina in general, and of *Cymindoidea* in particular.

Description.— Darlington (1968: 185-186) provides a good description of the type species of *Habutarus.* We draw attention here to certain features that are useful in comparing this group with other members of *Cymindoidea sensu lato.*

Habitus as in Fig. 40. Body size small (SBL ca. 5.5-6.0 mm.). Dorsal surface shining, lines of microsculpture fine, meshes of elytra irregular, from isodiametric to slightly transverse. Eyes and temples like those of *Cymindoidea (sensu stricto)*, antennal fossae near anterior margins of eyes. Pronotum with base markedly narrower than maximum width, hind angles acute; median longitudinal impression rather wide and deep. Metathorax reduced, metepisternum subquadrate; brachypterous. Male genitalia and ovipositor average for *Cymindoidea sensu lato*.

Habitat.— Darlington (1968: 186) stated that adults of *C. papua* were collected from flood debris on rain forest floor.

Phylogenetic relationships.— Because of its plesiotypic character states (relatively unmodified dorsal integument, glossal sclerite with single pair of setae, and pronotum cordate), we believe that *Habutarus* must be closely related to the ancestral stock of *Cymindoidea sensu lato*, and thus remote from the other extant species of this genus. Geographical remoteness from the main range of the genus and reduced hind wings are also features suggesting a relict status for this subgenus.

Trymosternus Chaudoir

Trymosternus Chaudoir, 1873: 106. GENERITYPE: *Cymindis onychina* Dejean, 1825: 217 (subsequent designation, by Antoine, 1962: 559). Seidlitz, 1887: 8.– 1888: 8.– Bedel, 1906: 242.– Iakobson, 1907: 396.– Csiki, 1932: 1486.– Jeannel, 1942a: 1057.– 1949: 396.– Mateu, 1952: 109-141. 1958: 1-6.– Antoine, 1962: 559.

Recognition.— Adults of this genus are distinguished from other apenines by combination of a markedly cordate pronotum, metasternum with a deep pit near middle coxae, short (reduced) metepisternum, and generally setose integument.

Description.— Character states mostly as for subtribe, with restrictions and exceptions as follows. See Mateu (1952: 111-113) or Antoine (1962: 559) for a more detailed description.

Color. Body piceous to rufo-piceous; elytra concolorous.

Vestiture. Surface generally coarsely punctate, setose, including mandibular scrobes and antennomeres 1-3.

Head. Frons laterally with pronounced ridge each side. Sub-antennal ridge prominent. Eyes oblong, flattened. Temples prominent. Antennal fossa well in front of antero-ventral margin of eye. Flagellar antennomeres longer than wide.

Mouthparts. Labium: mentum with lateral lobes pointed apically; tooth acute at apex; glossal sclerite bisetose; palpomere 3 distinctly securiform.

Thorax. Pronotum cordate, sides markedly sinuate posteriorly; base subtruncate, not lobed medially. Metepisternum short. Metasternum with deep pit anteriorly, near middle coxae.

Elytra. Humeri distinctly narrowed. Interneurs average, though coarsely punctate. Intervals slightly convex.

Wings. Reduced to short stubs.

Legs. Middle and posterior tibiae with reduced spines, latter absent from lateral margins.

Male genitalia. Internal sac with coiled flagellum.

Notes about identification of species.— See Mateu (1952).

Material examined.— Three specimens (CAS): *Trymosternus onychinus* (Dejean), male; and *T. cordatus* Rambur, male and female.

Geographical distribution.— The range of the 10 species of this genus is confined to the mountains of the Iberian Peninsula and to North Africa north of Morocco and Oran (Mateu, 1952, 1958; Antoine, 1962). Only one polytypic species (*T. truncatus* Rambur) occurs in North Africa, and in that part of Spain immediately adjacent to Gibraltar. The other nine species are on the mainland, most of them in southern Spain, and most with markedly restricted geographical ranges. *Trymosternus onychinus* is wide-ranging (see Mateu, 1952: Fig. 4).

Phylogenetic considerations.— Antoine (1962: 560) regards this genus as highly evolved and isolated. Certainly, body form resulting in part from wing loss and in part from the striking lateral lobes of the pronotum exhibited by adults of some species, give this impression. However, the bisetose glossal sclerite, relatively unmodified elytral intervals, and restricted geographical range suggest that this genus is the survivor of an old stock. It was probably isolated for an extended period on the Miocene betico-rifian massif (Antoine, 1962: 560), where it differentiated. In post-Miocene time, it dispersed northward, attaining its present range (Mateu, 1952: 117).

Evolution of the Apenina: preliminary considerations.— We are not in position to address this topic in detail, but some aspects of a general pattern seem clear enough to formulate a preliminary hypothesis in the form of a scenario.

The ancestral stock of the extant taxa, whose adults were like those of *Sphalera* and *Habutarus*, was widespread in Gondwana. Following the split which led to formation of South America and Africa, and thus to division of the ancestral stock of Apenina, the New World group differentiated as *Apenes*. In the Tertiary, various stocks dispersed northward, differentiating to produce the complex of extant species that presently inhabit Middle and North America and the West Indies.

In the Old World, events seem to have been more complex, for the distribution of extant taxa seems to suggest at least two major episodes of evolution: an early one, represented by taxa with limited ranges– *Trymosternus* (centered in the Iberian Peninsula), and *Habutarus* (known only from New Guinea); and a later episode, represented by centrant groups *Cymindoidea* and *Platytarus*. We believe that the present centrant groups overran the ranges of the early-evolved taxa, displacing the latter from the central areas, and leaving only peripheral remnants. This does not explain absence of species of *Cymindoidea (sensu lato)* from the Indo-Australian Archipelago, but we expect that the group is represented there, though specimens have not yet been collected.

If our hypothesis is correct, the main islands of the Indo-Australian Archipelago will be populated by stocks of *Cymindoidea (sensu stricto)* or *Platytarus*, and the peripheral islands (near New Guinea) by *Habutarus*. We also anticipate that the pattern we presently perceive will not be altered by subsequent discoveries. However, if it is altered by discovery of additional remnants of early-evolved groups in Africa or on the mainland of southeastern Asia, they will be residents of high altitude forests, and their adults will be brachypterous.

Subtribe CYMINDINA

We have seen specimens representing seven taxa of this group that are currently ranked as genera: *Cymindis* Latreille, 1806; *Hystrichopus* Boheman, 1848; *Plagiopyga* Boheman, 1848; *Pinacodera* Schaum, 1857; *Taridius* Chaudoir, 1875; *Pseudomasoreus* Desbrochers des Loges, 1904; and *Afrotarus* Jeannel, 1949. We have not seen material of *Assadecma* Basilewsky, 1982, so our comments about it are based on study of the description and illustrations. In spite of the rank accorded them, these taxa are not easily characterized on the basis of adult features. In our opinion, they are over-ranked. Accordingly, we make in the following pages adjustments in ranking that seem required by the evidence available.

We add to this subtribe a new monobasic genus, *Ceylonitarus*. Reasons for assigning this rank are presented below.

Recognition.— Diagnostic features of the subtribe are: head without suborbital setigerous punctures; elytron with penultimate umbilical puncture not laterad of antepenultimate and ultimate punctures; scutellar interneur separate from interneur 1, base of latter evident; tibiae average, spined laterally; tarsomeres slender, glabrous or setose dorsally, male front tarsomeres moderately expanded, articles 1-3 with biseriate adhesive vestiture ventrally; tarsal claws pectinate; ovipositor with stylomeres 1 and 2 subequal in length, stylomere 1 asetose; stylomere 2 without baso-dorsal projection, with one or two ensiform setae dorsally; preapical sensory furrow reduced, with one or two nematoid setae, or without these, and without furrow pegs;

projection; ensiform setae one or two, longer (Fig. 55A) or shorter (Fig. 56A); trichoid setae few, ventral in position, or absent; preapical sensory furrow narrow, with one or two short nematoid setae or without these, and without furrow-peg setae; microsculpture (Figs. 62-65) almost isodiametric, more or less extensive; sculpticells with (Fig. 65) or without microspines.

Classification.— Eight genus-group taxa are arranged in two genera: *Cymindis* Latreille, and *Hystrichopus* Boheman. Taxa recognized by previous authors as subgenera of *Cymindis* are thus accorded lesser rank. Jeannel (1942a: 1039) also recognized within his subfamily Cyminditae two groups that correspond to the genera that we recognize: tribes Pseudomasoreini and Cymindini. At the time, however, he did not realize the close affinity between *Psuedomasoreus, Hystrichopus,* and *Plagiopyga,* and thus did not include the latter two groups in the Pseudomasoreini. A third genus is *Ceylonitarus.*

Geographical distribution.– This subtribe is basically Megagean in distribution, with one subgenus extending into the northern part of the Neotropical Region (*Pinacodera*; to Honduras, in Central America). Table 2 provides a summary. Details are presented below.

Key to Genera and Subgenera of Cymindina

1 (0) Elytron with lateral umbilicate punctures not distinguishable from other serial setigerous punctures of intervals. Dorsum generally punctate and setose, serial setae of elytral intervals each more than half length of antennal scape. Head with three pairs of supraorbital setigerous punctures. Tarsal claws smooth, not pectinate. Elytra bicolored: flavous with black basal, medial, and apical fasciae (Fig. 40.1). Specimen from Oriental Region ... *Ceylonitarus,* new genus, p. 135

1′ Elytron with lateral umbilicate punctures distinctly larger than serial punctures of discal intervals. Dorsum various, glabrous or more or less setose. Head with two pairs of supraorbital setigerous punctures. Tarsal claws smooth or pectinate. Elytral color various. Specimen from Megagaea, or from the northern Neotropical Region .... 2.

2 (1′) Specimen from locality in Nearctic or Neotropical Region .... 3.

2′ Specimen from locality in Palaearctic, Oriental, or Afrotropical Region ..... 4.

3 (2) Dorsum glabrous or more or less densely setose. Male with tarsomeres 1-4 of both front and middle legs slightly widened, ventrally with adhesive vestiture *C. (Pinacodera)* Schaum, p. 149

3′ Dorsum densely setose. Male with tarsomeres 1-3 of front legs only slightly widened, ventrally with adhesive vestiture ....
.... *C. (Cymindis)* Latreille(part), p. 156

4 (3′) Dorsum with vestiture of short setae, more or less densely punctate, or at least intervals 4-7 each with several irregular rows of punctures; dorsal surfaces of tarsomeres sparsely to densely setose .... 5.

4′ Dorsal surface glabrous, elytral intervals impunctate, dorsal surfaces of tarsomeres sparsely setose or glabrous .... 6.

5 (4) Frons with two sharply defined longitudinal ridges each side. Integument piceous; lateral margins of pronotum and eltyra rufo-flavous. Pronotum with broad lateral margins. Range– Indian sub-continent, south of the Himalaya ...
.... *C. (Afrotarus)* Jeannel (part), p. 154

5′ Frons laterally smooth, or with indistinct ridges. Integument various, of most specimens rufous or rufo-piceous, and elytra with or without pale marks.

Pronotum with lateral margins various. Range– Atlantic Islands, Africa north of Atlas Mountains, Palaearctic Region, including upper slopes of the Himalayan system .... *C. (Cymindis)* Latreille[4] (part) p. 156

6 (4′) Frons laterally smooth or irregularly, sparsely punctate; without two or more regular ridges. Median lobe of male catopic (Fig. 86A). Stylomere 2 with single ensiform seta (Figs. 55A-57), in basal half .... 7.

6′ Frons each side with two or more regular ridges (Fig. 50). Median lobe of male anopic (Fig. 69A). Stylomere 2 of ovipositor with two ensiform setae, located in posterior half .... 10.

7 (6) Mentum with pair of setae on tooth. Paraglossae glabrous. Antennomere 3 pubescent toward apex; internal sac of male genitalia with rows of small spines .... *H. (Assadecma)* Basilewsky, p. 170

7′ Mentum with setae on lateral lobes, only; paraglossae setose. Antennomere 3 pubescent toward apex, or nearly glabrous. Internal sac with or without spines 8.

8 (7′) Antennomere 3 sparsely pubescent toward apex; denticles of tarsal claws sharp (Fig. 52); interval 3 of elytron with two or three setigerous punctures; stylomere 2 of ovipositor with moderate to long ensiform seta (Fig. 55A) .... *H. (Pseudomasoreus)* Desbrochers des Loges, p. 158

8′ Antennomere 3 not pubescent, with few long setae apically and preapically; tarsal claws smooth, or with sharp or blunt denticles; interval 3 of elytron with three or more setigerous punctures; stylomere 2 of ovipositor with ensiform seta very short (Figs. 56A and 57) .... 9.

9 (8′) Interval 3 of elytron with four or more setigerous punctures; tarsal claws with denticles sharp (as in Fig. 52) .... *H. (Hystrichopus)* Boheman, p. 171

9′ Interval 3 of elytron with two or three setigerous punctures; tarsal claws smooth, or with denticles blunt (Fig. 54) .... *H. (Plagiopyga) Boheman*, p. 172

10 (6′) Vertex and frons with isodiametric meshes; metepisternum with lateral margin distinctly longer than basal width, macropterous; pronotum with sides explanate; antennomeres 4-10 each distinctly longer than wide; internal sac of male genitalia (Fig. 69A) without large sclerite .... *C. (Taridius)* Chaudoir, p. 145

10′ Vertex and frons smooth medially, microlines effaced; metepisternum with lateral and basal margins subequal, brachypterous; sides of pronotum narrow; antennomeres 4-10 each 2.0 longer than wide, or shorter, not more than 1.5 longer than wide; internal sac of male genitala (Figs. 70A, 71A) with large

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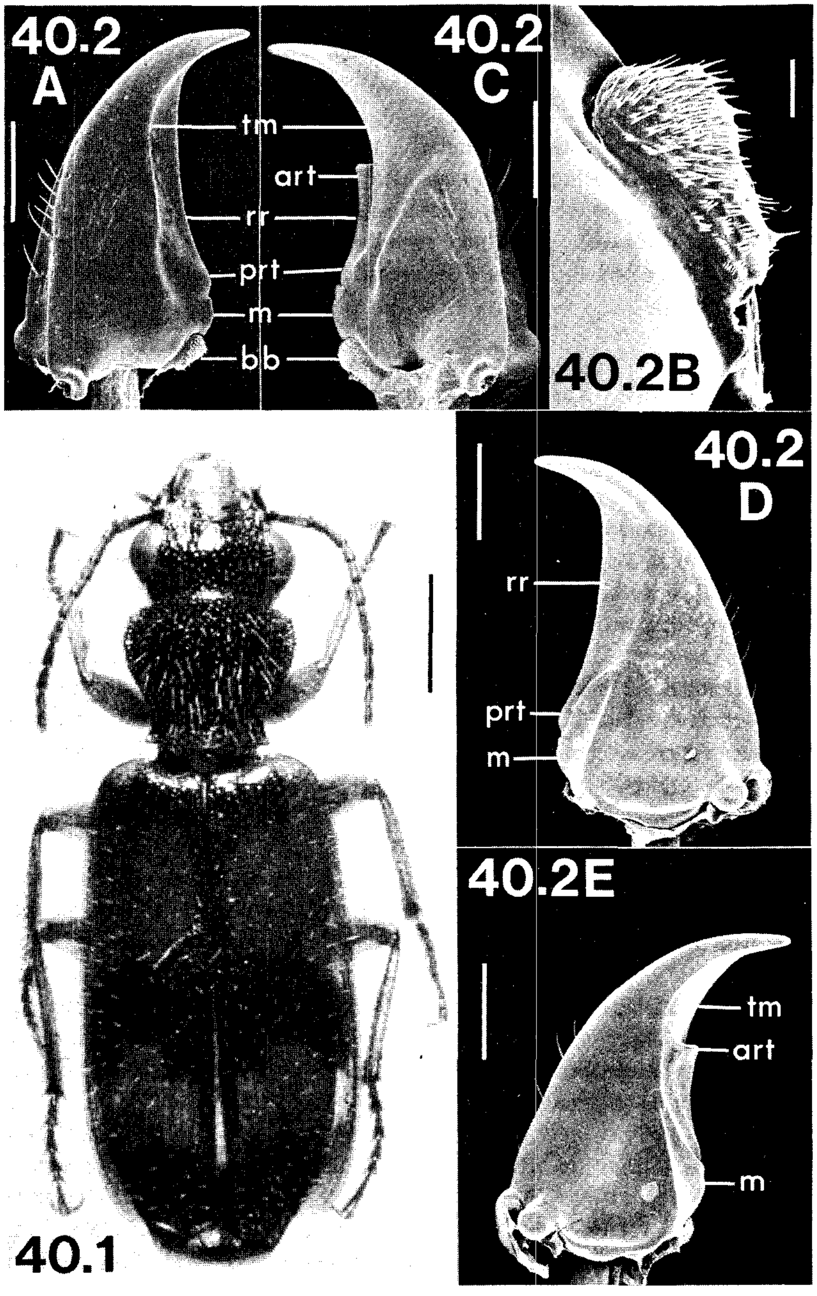
[4] According to Antoine 1962: 567), adults of all species of subgenus *Cymindis* (as delimited here) have setose elytra, although in some species the setae are very short and sparse. In any event, glabrous- appearing specimens of subtribe Cymindina occurring to the north of the Pyrenees Mountains in Western Europe are members of subgenus *Cymindis*



Figs. 40.1-40.2. Photographs of Cymindina, *Ceylonitarus ceylonicus*, new species. Fig. 40.1: habitus, dorsal aspect (SBL= 5.92 mm.). ; Figs. 40.2A-E: SEM photographs of mandibles, A and D, left, dorsal and ventral aspects, respectively, B and E, right, ditto; C, basal brush of left mandible, dorsal aspect. Legend, mandibles: art, anterior retinacular tooth; bb, basal brush; m, molar; part, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin. Scale bars= Figs. 40.1 = 1.0 mm.; Figs. 40.2A, C, D, and E = 200 μm; Fig. 40.2B = 20 μm.

sclerite ....
.... *C. (Afrotarus)* Jeannel (part), p. 154

Ceylonitarus new genus

Figs. 40.1-40.6

GENERITYPE: *Ceylonitarus ceylonicus*, new species (here designated).

Derivation of name.— From the former name of the type area ("Ceylon"), and "*tarus*", a name used in various combinations for *Cymindis*- like forms.

Recognition.— Diagnostic features of this taxon are: habitus *Cymindis*- like: color of elytra flavous, with three black fasciae (Fig. 40.1); body generally setose, setae long (Figs. 40.5A and B), head with three pairs of supraorbital setae; serial setigerous punctures of discal intervals of elytron as large as lateral umbilicate punctures, latter not readily distinguishable by eye; frons laterally shallowly and irregularly grooved; mandibles without ventral grooves (Figs. 40.2E and D), with large basal brushes (Fig. 40.2B); left mandible with well developed terebral margin (Fig. 40.2A); right mandible without premolar tooth (Figs. 40.2C and E); tarsal claws smooth; stylomere 2 of ovipositor narrow at base, falcate, with single long ensiform seta, dorso-lateral in position (Fig. 40.6A), ventral sensory furrow well removed from apex (Fig. 40.6B), without nematoid or furrow-peg setae, and microsculpture meshes of blade transverse, most sculpticells terminated apically with a microspine (Fig. 40.6C).

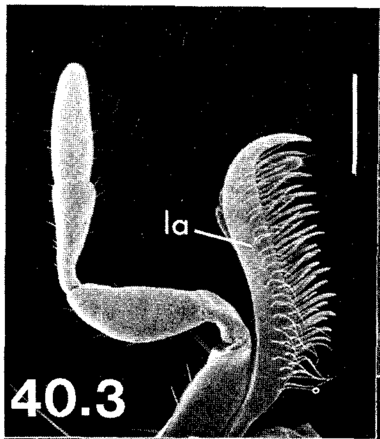
Classification.— Consideration in evolutionary terms of character states of *Ceylonitarus* compel us to rank this taxon as a genus, though we are reluctant to recognize monobasic genera. The following character states suggest that this group is more primitive that either *Cymindis* or *Hystrichopus*: left mandible with well developed terebral margin (Fig. 40.2A); maxilla with lacinia sparsely setose ventro-apically (Fig. 40.3; cf. Fig. 45); mental tooth not ridged (Fig. 40.4; cf. Figs. 46-49); terminal palpomeres narrow apically (Fig. 40.3; cf. Fig. 46); and stylomere 2 narrow and falcate. The extensive wedge cell of the wing is symplesiotypic for *Ceylonitarus* and *Hystrichopus*.

The following autapotypic features testify to the distinctness of the group: gains– an extra pair of supraorbital setae, additional antero-lateral marginal setae of pronotum, and the generally setose body; large basal brushes of the mandibles (Fig. 40.2B), and acute apices of lateral lobes of the mentum (Fig. 40.4); losses– ventral grooves, from mandibles; medial ensiform seta, nematoid setae, and furrow-peg setae, from stylomere 2.

The following apotypic features are shared with other cymindine taxa, but we believe they were acquired independently in each lineage: color pattern of elytra (shared with some members of subgenus *Taridius*); absence of microsculpture from most of dorsal surface, setose condition of body, and reduced basal ridge of elytron (shared with some members of *Cymindis sensu stricto*); stylomere 2 with single ensiform seta, dorso-lateral in position (shared with females of *Hystrichopus sensu lato*), and ensiform seta longer than usual (shared with females of subgenus *Pseudomasoreus*).

The smooth tarsal claws are difficult to interpret, for they may be primitively smooth, and thus plesiotypic, or secondarily smooth, and thus apotyic. In any event, this character state is shared with some members of the subgenus *Plagiopyga*.

The pattern of shared features suggests that they are examples of convergence, rather than of close relationship. Further, the plesiotypic features plus probably restricted geographical range that is peripheral to that of other cymindine groups, suggest to us that *Ceylonitarus* is a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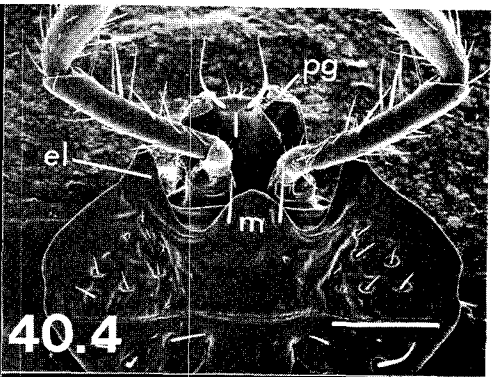
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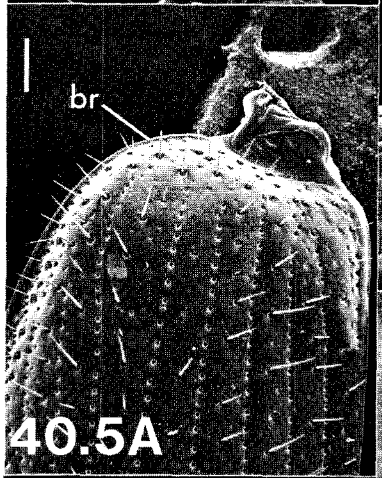
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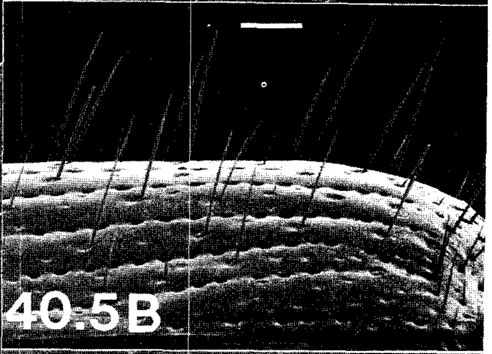
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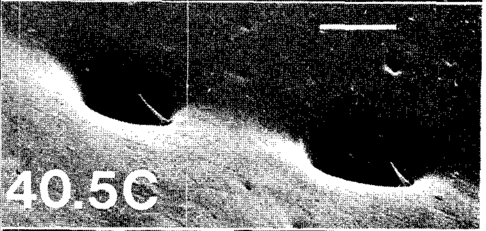
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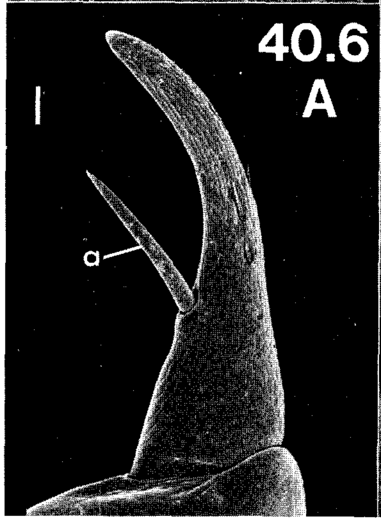
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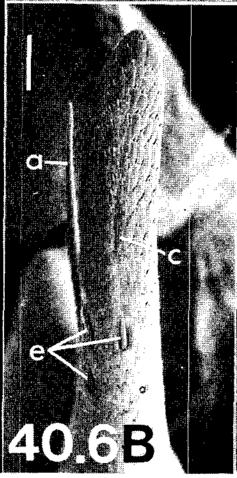
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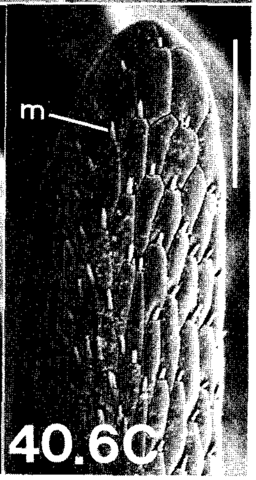
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Figs. 40.3-40.6. SEM photographs of structures of Cymindina, *Ceylonitarus ceylonicus,* new species.-- Fig. 40.3: Right Maxilla, lacinia, palpifer, and palpus, ventral aspect. Fig. 40.4: Labium, ventral aspect, mentum and parts of prementum. Fig. 40.5: Left elytron--A, basal portion, dorsal aspect, B, basal portion dorso-medial aspect, c, two interneural punctures, dorso-medial aspect. Fig. 40.6: ovipositor, left stylomere 2--A, lateral aspect; B, ventral aspect; C, apical portion, ventral aspect. Legend, maxilla: la, lacinia. Legend, labium: el, epilobe; l, glossal sclerite; m, mental tooth; pg, paraglossa. Legend, elytra: br, basal ridge. Legend, ovipositor, stylomere 2: a. lateral ensiform seta; c, sensory furrow; e, trichoid setae; m, microspine of sculpticell. Scale bars= Figs. 40.3-40.5B = 200 μm; Figs. 40.5C-40.6C = 20 μm.

phylogenetic relic, closer to the ancestral stock of the Cymindina than are the other two genera of this subtribe. The several and striking autapotypic features suggest the possibility of an extended period of isolation and probably of ethological (as well as structural) divergence from the other groups of cymindines.

Males are unknown. Features of the male genitalia might shed light on relationships of *Ceylonitarus*: if catopic, this would suggest close relationship with *Hystichopus*; if anopic, and with an elaborate apical sclerite on the internal sac, this would suggest close relationship with *Cymindis*. We believe that the median lobe will prove to be anopic, and the internal sac either devoid of armature, or with armature that is strikingly different from that of the taxa of *Cymindis*.

We think it possible that *Ceylonitarus* may include additional species. If so, the character states of such taxa might provide clues that will make possible a better assessment of the phylogenetic relationships of this group, and thus provide a better basis for its classification.

Description.— Size small (SBL less that 7.0 mm.), body slender, habitus as in Fig. 40.1. Color fuscous to flavous, with elytra markedly bicolored.

Microsculpture. Labrum with meshes isodiametric, sculpticells slightly convex. Rest of body surface without microlines (at least not visible at 50X; very faint vestiges on dorsum seen at 1000X), surface essentially smooth.

Fixed setae. Standard, except: head with three pairs of supraorbital setae; pronotum with several pairs of marginal setae in anterior 0.5. Abdominal sternum VII with four setae apically.

Punctation and vestiture. Scape and antennomeres 2-4 generally setose, antennomeres 5-11 more densely so. Eyes glabrous. Head, prothorax, and lateral and ventral sclerites of pterothorax densely and moderately coarsely punctate, abdominal sterna more sparsely and finely so. Elytral interneurs more finely punctate than intervals; latter uniseriately punctate, setae flavous, many more than 0.5 length of antennal scape; serial punctures of discal intervals as large as umbilicate punctures, latter not readily distinguished by eye.

Head. Frons each side with two or three rather indistinct and irregular ridges. Frontal impressions shallow, indistinct. Eyes moderately prominent (Fig. 40.1). Antennae with antennomere 3 slightly longer than 4, but shorter than scape.

Mouthparts. Labrum larger than average (l/w 0.59-0.68, $\bar{x}>=0.62$). Mandibles as in Figs. 40.2A-E, both without premolar and ventral groove (Figs. 40.2D-E), and with large basal brush (Fig. 40.2B); left mandible with well developed terebral margin (Fig. 40.2A); right mandible with prominent retinacular ridge and small retinacular teeth (Figs. 40.2C and E). Maxillae average, lacinia ventrally with setae near medial margin, not extended to lateral margin pre-apically (Fig. 40.3), terminal palpomere fusiform, apex narrow. Labium (Fig. 40.4): mentum with lateral lobes acute apically; epilobes slender throughout, not toothed medially, and terminated at base of mental tooth; latter prominent, broadly rounded and immarginate apically; glossal sclerite broad, rounded apically; paraglossae membranous apically, setose, with apices extended slightly beyond plane of apex of glossal sclerite.

Thorax. Pronotum as in Fig. 40.1 (for details, see description of generitype). Ventral and lateral thoracic sclerites without notable features. Metepisternum with lateral margin clearly longer than basal margin.

Elytra. Dorsal surface deplanate. Base with humerus broadly rounded (Fig. 40.5A). Apical margin truncate and markedly sinuate. Basal ridge close to anterior margin, terminated near base of interval 5. Interneurs shallow, punctate. Epipleuron average.

Wings. Fully developed, veins rather pale and probably slightly sclerotized. Oblongum with short stalk (cf. Figs. 73A, 74A, and 84A), wedge cell more extensive than in *Cymindis* (cf. Figs. 73B and 74B).

Legs. Average for Cymindina, except tarsal claws smooth.

Ovipositor. Stylomere 1 glabrous, stylomeres 1 and 2 subequal in length. Stylomere 2 falcate in lateral aspect (Fig. 40.6A), slender, parallel-sided in ventral aspect, apex narrowly pointed. Lateral ensiform seta (Fig. 40.6A) longer than average, about half length of stylomere; several trichoid setae medio-ventrally. Following setae lacking: medial ensiform, nematoid, and furrow-peg. Sensory furrow (Fig. 40.6B) very narrow, about half way between apex and plane of insertion point of ensiform seta. Microsculpture: meshes generally transverse, broadly so basally (Fig. 40.6A), more narrowly so preapically (Figs. 40.6B and C); sculpticells flat basally, convex preapically, though not keeled, most terminated with single microspine (Fig. 40.6C).

Relationships of genus.— We believe that *Ceylonitarus* is more primitive than *Cymindis* or *Hystrichopus*, and is the sister group of the ancestral stock of these two genera. See "Classification", above, for a discussion of the basis for this hypothesis.

Included species.— Only one, *C. ceylonicus*, new species, described below.

Ceylonitarus ceylonicus, new species

Type material.— HOLOTYPE female, labelled: SRI LANKA Man Dist. 8 mi. SE Mannar black light 15 feet, 6 Nov. 1976; Collected by G. F. Hevel, R. E. Dietz IV, S. Karunaratne, D. W. Balasooriya (USNM). Seven paratypes, females, labelled: SRI LANKA Man. Dist. 4 mi. NW Mannar black light, 100 ft. 3 November 1976; collector label same as for holotype (USNM). TYPE LOCALITY: vicinity of Mannar, Sri Lanka.

Derivation of specific epithet.— From the former name of the type area, Ceylon.

Recognition.— Color pattern (Fig. 40.1) of adults of this species is like that of the mainland species *Cymindis (Taridius) stevensi*, known from the Nilgiri Hills of India. The two are easily distinguished, however, by differences in: setation (adults of *C. stevensi* with dorsal integument glabrous except for normal fixed setae; adults of *C. ceylonicus* with dorsal integument generally setose); microsculpture (pronotum and elytra of *C. stevensi* with meshes distinct; these surfaces smooth in *C. ceylonicus*); details of color pattern of elytra (cf. Figs. 40.1 and 75B); pronotum (sides explanate in *C. stevensi* adults, not so in members of *C. ceylonicus*); tarsal claws (pectinate in *C. stevensi*; smooth in *C. ceylonicus*); and in setae of stylomere 2 (*C. stevensi* females with median and lateral ensiforms, nematoids, and furrow-pegs; *C. ceylonicus* females with only lateral ensiform).

Description.— Habitus as in Fig. 40.1, *Cymindis*- like. Standardized Body Length 5.36-6.64 mm. ($\bar{x}$=6.02 mm).

Color. Head and pronotom dorsally rufo-piceous to piceous, rufous ventrally. Elytra with disc predominantly flavous, with suture dark, and three black fasciae (Fig. 40.1); epipleura flavous. Metepisterna and abdominal sterna rufo-piceous, other sclerites of pterothorax rufous; antennae, palpi, and legs flavous.

Microsculpture, setation, form of head, details of mouthparts, thorax (except pronotum), elytra, legs, abdominal sterna and ovipositor sclerites as described for genus, above.

Pronotum. As wide as or slightly wider than head (Hw/Pwm 0.93-1.00, $\bar{x}$=0.96), slightly wider than long (Pl/Pwm 0.83-0.91, $\bar{x}$=0.87), width near mid-line greater than width at base (PwB/Pwm 0.67-0.73, $\bar{x}$=0.71). Sides narrrow, not explanate, sharply beaded, markedly sinuate. Anterior lateral angles broadly rounded; posterior-lateral angles rectangular or acute, distinctly anterior to medial part of basal margin Basal margin not beaded, laterally with short, marked sinuation. Disc markedly convex medially, sloped downward laterally. Marginal grooves narrow, continuous with narrow posterior-lateral impressions. Median longitudinal impression shallow; anterior transverse impression indistinct; posterior transverse impression broad, shallow, continuous with posterior-lateral impressions.

Geographical distribution.— Known only from low altitude localities, in the vicinity of Mannar, Sri Lanka, where the specimens were taken at light.

Material examined.— Type series, only. We owe a special note of thanks to Terry Erwin, who drew these specimens to our attention, and made them available for our study.

Cymindis Latreille

Figs. 41-43,45-51, 53, 59-63, 65, and 67-76

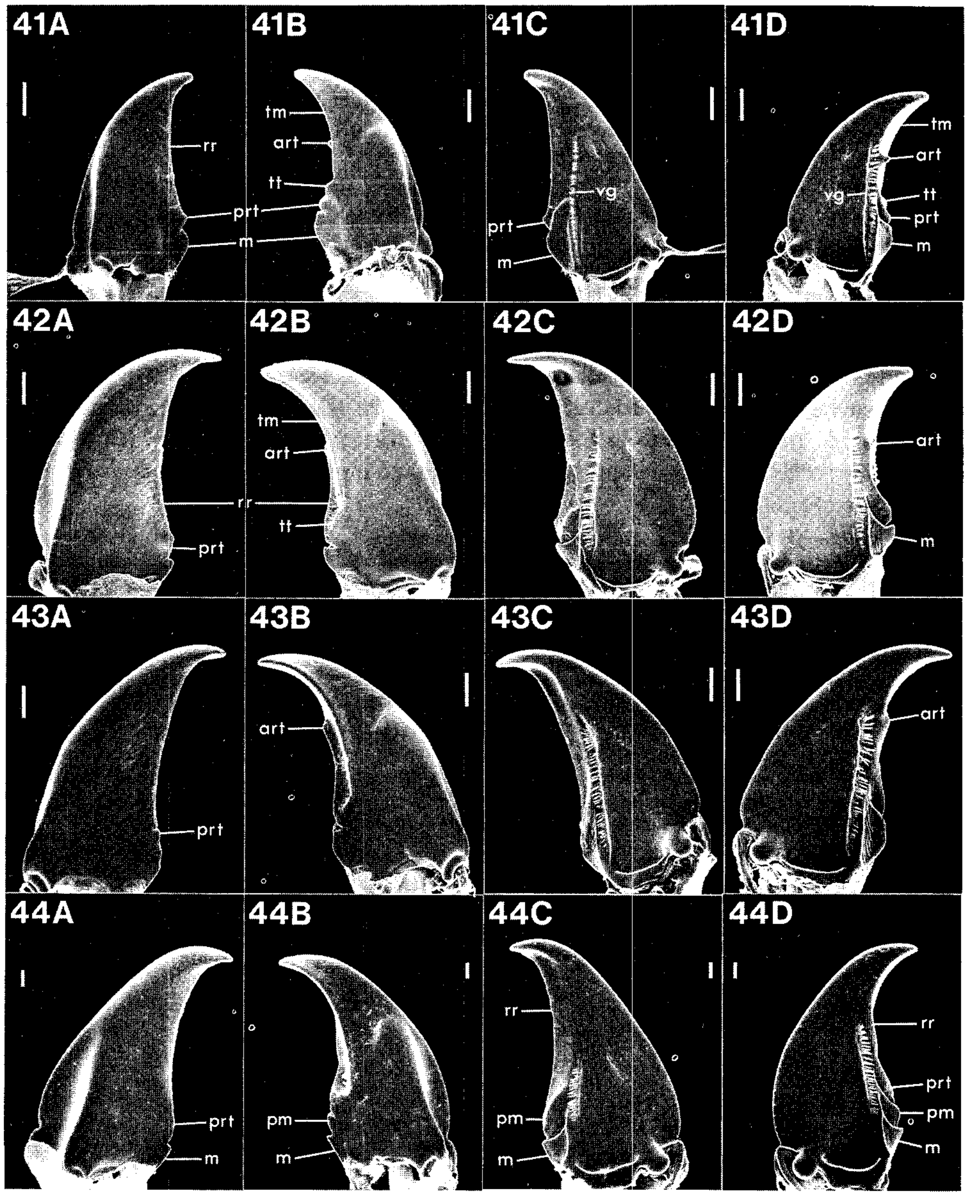
Cymindis Latreille, 1806: 190: GENERITYPE: *Buprestis humeralis* Fourcroy, 1785:57 (monotypy).– Chaudoir, 1873: 53-120.– Csiki, 1932: .– Jeannel, 1942a: 1041-1056.– Antoine, 1962: 564-587.– Jedlička, 1963: 452-461.– Habu, 1967: 57-74.– Lindroth, 1969: 1070-1086.– Ball, 1982:——.

Pinacodera Schaum, 1857: 294. GENERITYPE: *Cymindis limbata* Dejean, 1831:320 (designated by Lindroth, 1969: 1067).– LeConte, 1861: 24.– Chaudoir, 1875: 2.– Horn, 1881: 156.– 1882: 146.– LeConte and Horn 1883: 45.– Bates, 1883: 187-188.– 1884: 296.– Blatchley, 1910: 142, 152.– Leng, 1920: 67.– Casey, 1920: 279.– Csiki, 1932: 1487.– Blackwelder, 1944: 62.– Jeannel, 1949: 878.– Ball, 1960: 161.– Lindroth, 1969: 1067-1070. Erwin *et al.*, 1977: 4.58.– Ball, 1982: ——. NEW SYNONYMY.

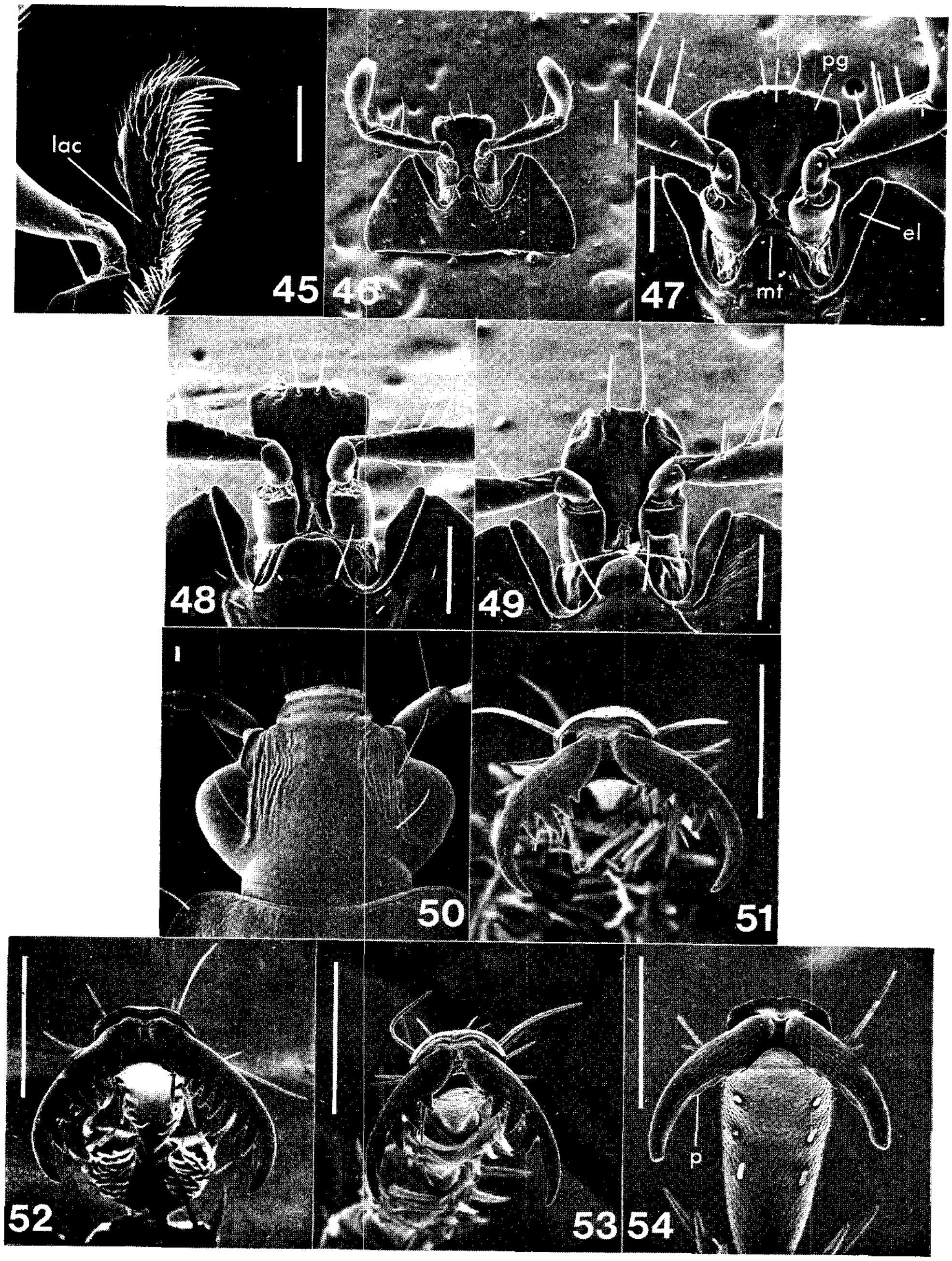
Planesus Motschulsky, 1864: 240(table). GENERITYPE: *Cymindis fuscata* Dejean, 1831:321 (=*Cymindis platicollis* Say, 1823) (original designation by Motschulsky, 1864: 240 (table)).

Taridius Chaudoir, 1875: 71. GENERITYPE: *Taridius opaculus* Chaudoir, 1875: 7 (monotypy).– Bates, 1892: 416).– Andrewes, 1930: 342-343.– Csiki, 1932: 1489.– Andrewes, 1935: 204-205.– van Emden, 1937: 123-125.– Jedlička, 1963: 461.– Ball, 1982:---. NEW SYNONYMY.

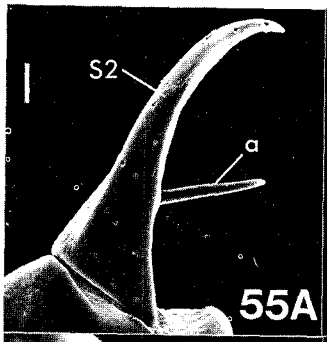
Afrotarus Jeannel, 1949: 878. GENERITYPE: *Cymindis kilimana* Kolbe, 1898: 51 (original designation).– Basilewsky, 1962: 252.– 1968a: 360.– Ball, 1982:----. NEW SYNONYMY



Figs. 41–44. SEM photographs of structures of Cymindina.—Mandibles –A and C, left, dorsal and ventral aspects, respectively, B and D, right, dorsal and ventral aspects, respectively.— 41, *Cymindis (sensu stricto) suturalis* Dejean; 42, *C. (Taridius) opacula* (Chaudoir); 43, *C. (Pinacodera)* new species no. 1; 44, *Hystrichopus (sensu stricto)* near *dorsalis* Thunberg. Scale bars = 100 μm. Legend: art, anterior retinacular tooth; m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin; tt, terebral tooth; vg, ventral groove.



Figs. 45–54. SEM photographs of structures of Cymindina.-Mouthparts and tarsal claws. Fig. 45: *C. (Pinacodera) limbata* Dejean, right maxilla, ventral aspect. Figs. 46–49, labium, ventral aspect: 46, *C. (P.) limbata*; 47, C. (P.) new species no 2; 48, C. (P.) new species no. 1: 49, *C. (Taridius) opacula*. Fig. 50: *C. (Taridius) opacula*, head, dorsal aspect. Figs. 51–54, tarsal claws, terminal aspect: 51, *C. (T.) opacula*; 52, *Hystrichopus (sensu stricto)* nr. *dorsalis*; 53, *C. (Afrotarus) kilimana* Kolbe; 54, *H. (Plagiopyga) cymindoides* (Péringuey). Scale bars = 200 μm. Legend, labium: el, epilobe of mentum; l, glossal (or ligular) sclerite; m, tooth of mentum; pg, paraglossa. Legend, tarsus: p, denticle of tarsal claw.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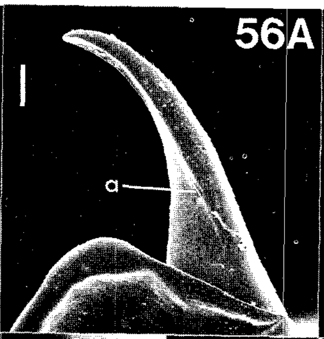
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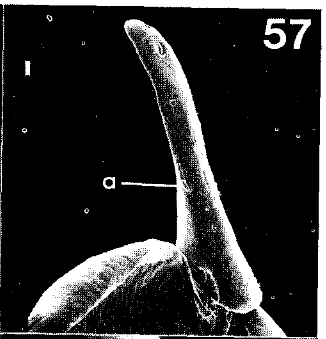
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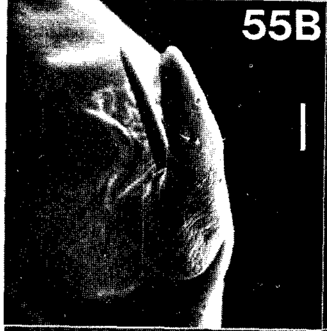
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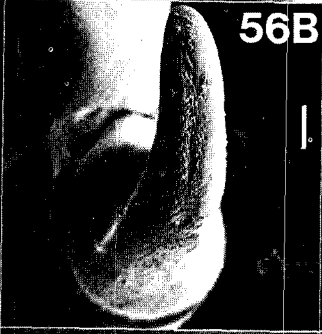
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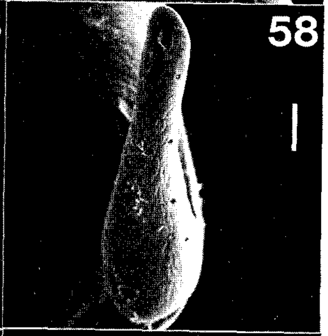
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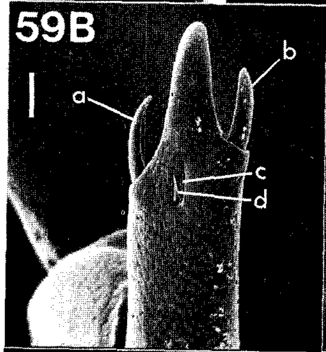
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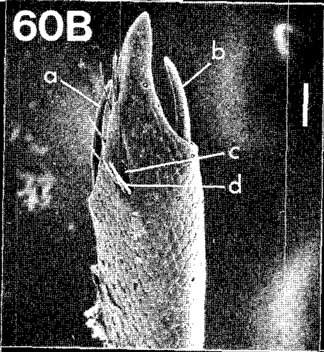
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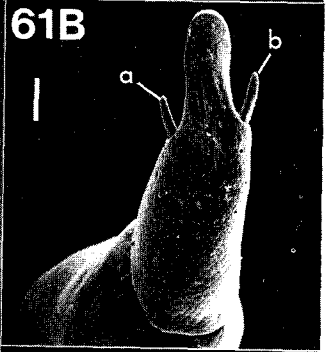
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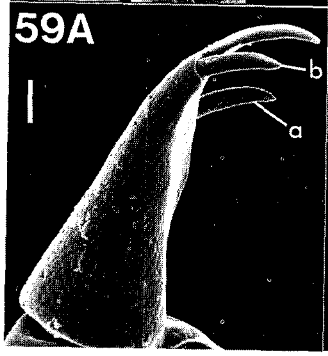
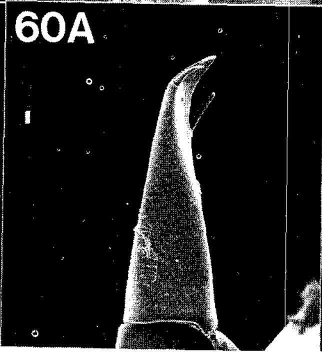
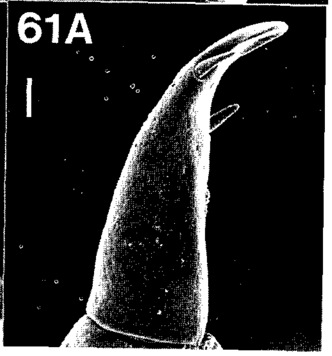
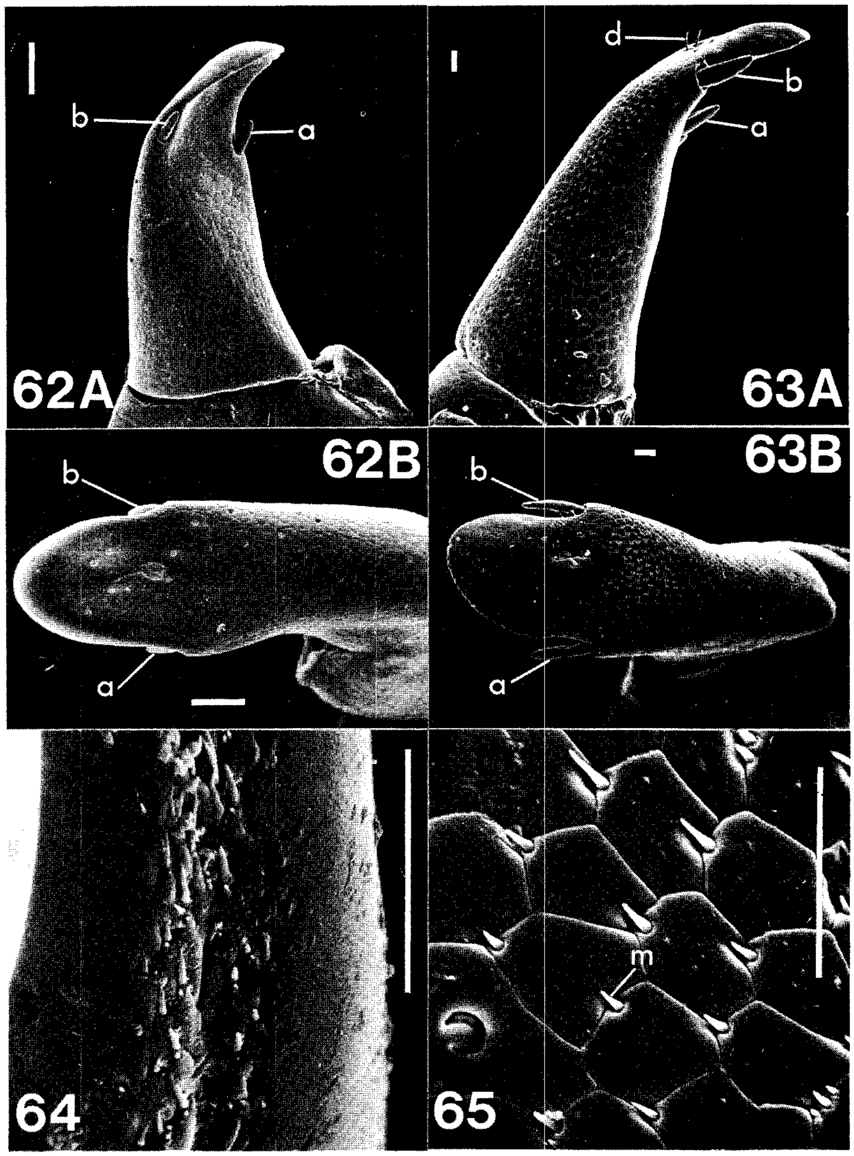

59A


60A


61A

Figs. 55–61. SEM photographs of structures of Cymindina.—Left stylomeres of ovipositor. Fig. 55: *Hystrichopus (Pseudomasoreus) capicola* Basilewsky, A and B, medial and ventral aspects, respectively. Fig. 56: *H. (sensu stricto)* nr. *dorsalis* Thunberg, A and B, lateral and ventral aspects, respectively. Figs. 57, 58: *H. (Plagiopyga) cymindoides* (Péringuey), lateral and ventral aspects, respectively. Figs. 59–61, A and B, medial and ventral aspects, respectively: 59, *Cymindis (Afrotarus) kilimana* Kolbe; 60, *C. (Taridius) opacula* (Chaudoir); 61, *C. (sensu stricto) hieronticus* (Reiche). Scale bars = 20 μm. Legend: a, lateral ensiform seta; b, medial ensiform seta; c, sensory furrow; d, nematoid seta; S2, stylomere 2.



Figs. 62–65. SEM photographs of structures of Cymindina.—Ovipositor, left stylomere 2. Figs. 62–63, A and B, medial and ventral aspects, respectively: 62 *Cymindis (sensu stricto) suturalis* Dejean; 63, *C. (Pinacodera)* new species no. 1. Figs. 64 and 65, microsculpture: 64, *Hystrichopus (sensu stricto)* nr. *dorsalis* Thunberg; 65, *C. (P.)* new species no. 1. Scale bars = 20 um.

Recognition.— Diagnostic features of this genus are the following: head with two pairs of supraorbital punctures; frons with (most members) or without longitudinal ridges and grooves laterally; elytron with lateral umbilicate punctures larger than, and thus clearly distinguishable from, setigerous punctures of discal intervals; right mandible without premolar tooth; median lobe of male genitalia anopic, internal sac with or without sclerites; stylomere 2 of ovipositor broad at base, with two ensiform setae on dorsal margins.

Classification.— Although the four groups ranked as subgenera are not easy to diagnose for recognition of individual specimens, we are satisfied that each is monophyletic, and is reasonably distinctive in combinations of structural features, and in patterns of geographical distribution. The sequence of subgenera in the text is based on our concept of sister-group relations, as discussed in more detail, below.

The characteristic form of stylomere 2 of the ovipositor (relatively straight, broad at least preapically in ventral aspect), with ensiform setae relatively close to the apex (Figs. 59-62) seems to be apotypic, and is the only such feature for delimiting *Cymindis (sensu lato)* in relation to *Hystrichopus (sensu lato)*. It is sufficient, however, to suggest that *Cymindis* is monophyletic.

Features interpreted as synapotypic for *Cymindis (sensu lato)* and *Hystrichopus (sensu lato)* and that thus support inference of a sister group relationship for these two taxa are the ridged mental tooth (Figs. 46-49), and pectinate tarsal claws (Figs. 51-54; denticles reduced in some members of subgenus *Plagiopyga*, and interpreted as lost from other members).

Subgenus *Taridius* Chaudoir, new status

Figs. 42, 49-51, 60, 69, 73, and 75

Diagnostic description.— Size small (SBL ca. 5.5-7.4 mm.) to average (ca. 10 mm.). Color: uniformly rufo-piceous to piceous, or elytra bicolored piceous and flavous (Figs. 75A, B) appendages paler (rufous or flavous) than dorsum. Microsculpture: head– vertex and frons with meshes isodiametric, lines clearly developed; pronotum with meshes transverse; elytra– dorsal surface with meshes isodiametric. Vestiture: dorsum glabrous, except for standard setae, dorsal surfaces of tarsomeres each with single pair of setae near apex, or very sparsely setose (*i.e.*, one or two additional short setae). Head: frons each side with from two to seven (Fig 50) sharply defined ridges. Antennae: scape and antennomeres 2 and 3 with ring of setae near apex, otherwise glabrous; antennomeres 4-11 generally setose; antennomeres 3 and 4 subequal in length. Mandibles as in Figs. 42A - D. Labium as in Fig. 49. Metepisternum with lateral margin clearly longer than anterior margin. Wings fully developed, oblongum and wedge cells as in Figs. 73A and B. Tarsal claws as in Fig. 51. Median lobe of male genitalia (Figs. 69A, B) with apex simple; internal sac without sclerotized plate. Stylomere 2 of ovipositor average for cymindoids, though more slender apically than in *Pinacodera* (Fig. 60A; cf Fig. 63A); microspines on ventral surface.

Relationships of subgenus.— Compared to other subgenera of *Cymindis, Taridius* seems more primitive, and thus likely to be the sister group of *Pinacodera - Afrotarus - Cymindis.* Adults share with those of *Pinacodera* and some adults of *Cymindis* similar body form and fully developed wings–but these features are correlated functionally and symplesiotypic. Females of *Taridius* and *Pinacodera* share microspines on stylomere 2 (Figs. 60B and 65). However, females of *Ceylonitarus* and *Hystrichopus (sensu stricto)* also exhibit this feature (Fig. 64), and so we are disinclined to weight it heavily, for the similarity might be symplesiotypic or homoplasious. In fact, *Taridius* seems to be without autapotypic character states, and thus may be paraphyletic.

The distribution pattern is consistent with a relict status for *Taridius:* populations of this structurally plesiotypic group occupy montane areas which are marginal relative to lowland tropical forests. This suggests displacement from the surrounding lowland tropics. However, it is also possible that the species are persisting in those areas where forest is still able to persist;

TABLE 3

DATA ABOUT VARIATION IN STANDARDIZED BODY LENGTH (MM) AND IN VALUES FOR THE RATIO Hw/Pmw AMONG SAMPLES OF *CYMINDIS STEVENSI* (ANDREWES)

SUPSPECIES AND LOCALITY	N	SBL RANGE	MEAN	Hw/Pmw RANGE	MEAN
C. s. nilgirica					
Palni Hills	1 ♀	7.32		0.74	
Nilgiri Hills	3 ♀	5.84–6.90	6.22	0.79–0.80	0.79
C. s. stevensi					
Sikkim	1 ♀	6.42		0.77	
Gopaldhara	2 ♀	6.40–6.90	6.65	0.73–0.78	0.76
	1 ♂	5.80		0.76	
C. s. andrewesi					
Karen Hills, Burma	1 ♀	6.78		0.82	
Java	1 ♂	6.48		0.83	
	1 ♀	5.80		0.86	

Cymindis s. andrewesi occupies areas to the east of the Irawaddy River, with samples known from as far north and west as the Karen Hills of Burma and as far south and east as the Indo-Australian island of Java.

Chorological affinities.— The range of *C. s. stevensi* is overlapped by that of *C. opacula,* though the two species have not been recorded from the same locality. The range of *C. s. andrewesi* overlaps that of *C. birmanica* in the Karen Hills. Locality data are not sufficiently precise to indicate if the two taxa are microsympatric, or if their life cycles are synchronic. Nonetheless, these geographical contacts are reasonable evidence for reproductive isolation between *C. stevensi* and the other two species. Specific distinctness of *C. opacula* and *C. birmanica* is not tested by chorological data.

Material examined.— In addition to type material recorded above, we have seen nine specimens, as follows.

C. s. nilgirica. Three females: Nilgiri Hills, H. E. Andrewes (BMNH); same locality, collected by G. F. Hampson (BMNH); and Palni Hills, Kodaikanal, 6900-7200 ft., IZ. 22, S. Kemp (ZSIC).

C. s. stevensi. Male and three females (including one paratype) Gopaldhara, Darjeeling, Sikkim, H. Stevens (BMNH).

C. s. andrewesi. Male, female, paratypes, O. Java Tengger Nonkodjadjan 1300 m. Wegner (BMNH). Female, Burma Karen Hills; Taridius sp. H. E. Andrewes det. (BMNH).

Subgenus *Pinacodera* Schaum, new status
Figs. 43, 46-48, 63, 65, and 76

Diagnostic description.— Body moderately flattened, generally elongate. Size about average for carabids, SBL ca. 5.50-10.50 mm. Color: somber, with dorsum of most specimens darker than venter, and appendages paler than body integument; head rufous, piceous or black; pronotum rufous, piceous, or black, lateral areas paler or not, than disc; elytra with dorsal surface rufo-flavous, rufous, piceous, or black, or various combinations of these, epipleura of most specimens paler than dorsal surface; venter rufous, piceous, or black; antennae rufo-flavous, or rufo-piceous, with scape of most specimens paler than remaining antennomeres; legs rufo-flavous to black, with femora of most specimens paler than other articles. Microsculpture: meshes in general, isodiametric, or transverse, but comparatively wide; head– frons and clypeus with meshes isodiametric, microlines distinct or indistinct, or meshes partially or wholly effaced, ventral surface with meshes transverse, microlines clear, or partially or wholly effaced; pronotum with meshes uniformly transverse, or isodiametric postero-laterally, lines clear or partially or wholly effaced; scutellum and elytra with meshes uniformly isodiametric; prosternum and pterothorax ventrally with meshes transverse, microlines clear, or partially or wholly effaced, proepisternum with meshes oblique, microlines partially or wholly effaced; abdominal sterna with meshes transverse, microlines clear or partially or wholly effaced. Vestiture: glabrous (except fixed setae), or sparsely to densely setose and punctate; elytral intervals impunctate, or with one or more irregular rows of setigerous punctures. Head: frons each side with two to five irregular longitudinal ridges and grooves more or less distinctly developed. Antennomeres 1-3 either glabrous (except normal preapical setae) or sparsely setose, setae short; antennomeres 3 and 4 subequal in length. Mandibles as in Figs. 43A-D. Lacinia as in Fig. 45. Labium as in Figs. 46-48. Metepisternum either distinctly longer than wide, or width at base and length of lateral margin subequal. Wings fully developed, or reduced to short stubs. Median lobe of male genitalia with apical portion in lateral aspect straight and narrow, or expanded slightly into knob, internal sac with sclerotized plate, as in subgenus *Cymindis* (cf. Fig. 72C), or without armature. Stylomere 2 of ovipositor average for *Cymindis* (Figs. 63A, B; cf. Figs. 62A, B); microspines on ventral surface (Fig. 65).

Included species.— Twenty seven species are known of which nine are described. The group is presently under study by us.

Way of life.— Data about life histories are available for two species, *C. platicollis* Say, and *C. limbata* Dejean (Mahar, 1978). Adults of both species are crepuscular or nocturnal, living on ground in leaf litter, and in trees. Larvae are terrestrial. *C. platicollis* is a spring breeder, while *C. limbata* breeds during summer. Site of oviposition has not been determined.

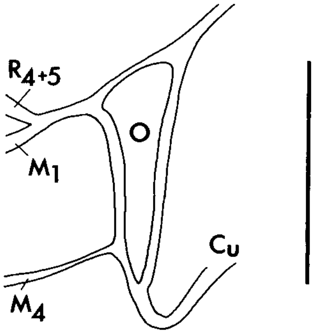
Notes about habitat.— Taxa are associated with arboresecent vegetation, from desert, tropical thorn scrub and thorn forest, to dry oak forests, wet conifer forests and cloud forests in the mountains of northern Middle America. Altitudinal range of the subgenus extends from sea level to 2900 meters above sea level.

Geographical distribution.— The range of this subgenus extends from Honduras in Middle America, to southern Nova Scotia and Ontario, in eastern North America.

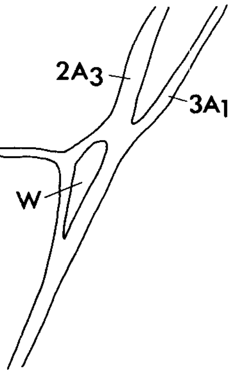
Classification.— The species are arrayed in two groups: a more northern group, males of which have armature in the internal sac, and a more southern group whose males have unarmored internal sacs.

Phylogenetic relationships.— We believe that *Pinacodera* is the sister group of the ancestor of *Afrotarus* + *Cymindis* (sensu stricto), based on the inference that males of the common ancestor of subgenera *Pinacodera* + *Afrotarus* + *Cymindis* exhibited the autapotypic feature of the complex apical sclerite in the internal sac, as preserved in the descendant stocks. This requires loss of this sclerite from at least one descendant lineage of *Pinacodera*

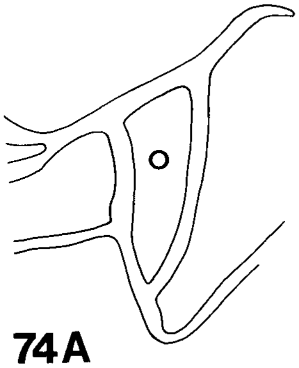
A second hypothesis, based on the pattern of geographical distribution of Cymindis sensu lato (Pinacodera confined to the New World, two of the other three subgenera confined to the Old World, and one with most of its species there), is that *Pinacodera* is the sister group of the ancestral stock of the other three subgenera. Such an hypothesis requires either independent gains of the genital sclerite (once in *Pinacodera* and once in the *Afrotarus* + *Cymindis* stock), or at least two losses of this sclerite (once from *Taridius*, and once from *Pinacodera*). Neither hypothesis is very well supported, but we think the first is rather stronger, requiring one less



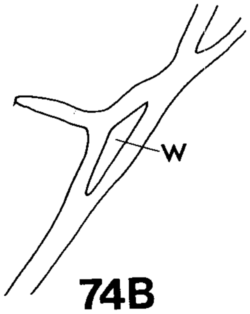
73A



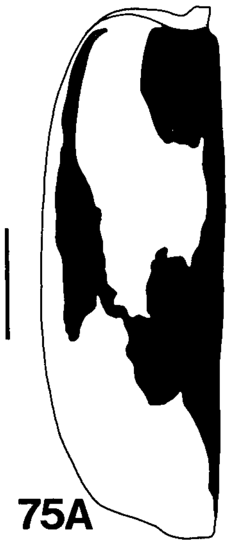
73B



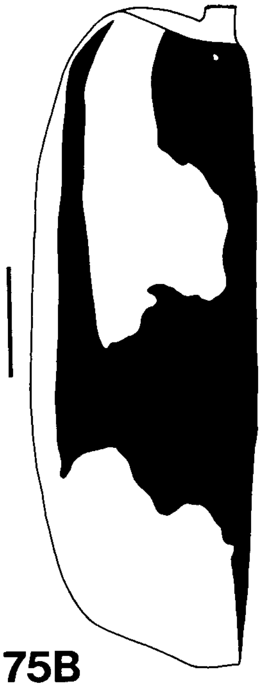
74A



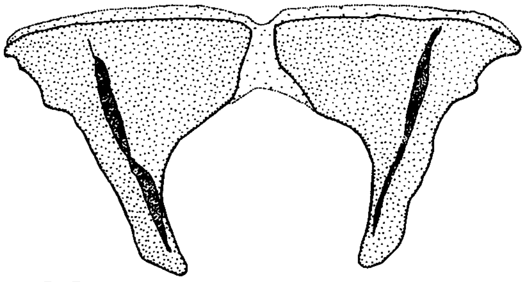
74B



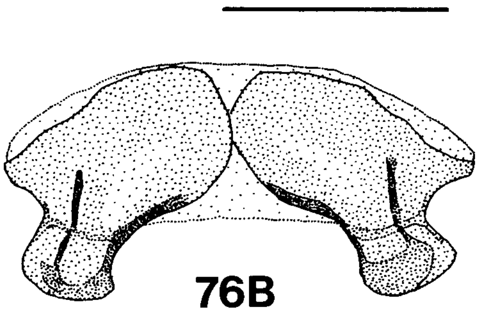
75A



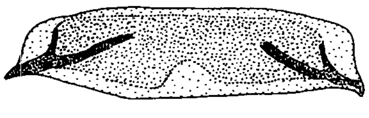
75B



76A



76B



76C

Figs. 73–76. Line drawings of structures of Cymindina.—Figs. 73–74. Wing veins and cells of *Cymindis* species, A and B, oblongum and wedge cells, respectively: 73, *C. (Taridius) opacula* (Chaudoir); 74, *C. (sensu stricto) suturalis* Dejean. Fig. 75. Color pattern of left elytron of *Cymindis (Taridius) stevensi* (Andrewes): A, *C. s. andrewesi* (van Emden); B, *C. s. nilgirica* (Andrewes). Fig. 76. Terminal abdominal sclerites of *C. (Pinacodera)* new species no. 1: A, Tergum VIII, dorsal aspect; B, Sternum VIII, ventral aspect; Tergum X, dorsal aspect. Legend. Wing cells: O, oblongum; W, wedge. Veins: A, anals; Cu, cubitus; M. media; R, radius.

loss of a complex structure, and not requiring its independent development in two lineages.

Subgenus *Afrotarus* Jeannel, new status

Figs. 53, 59, 66-68, and 70-71

Diagnostic description.— Size small SBL ca. 5.0-7.0 mm. Color: body rufo-piceous to almost black, appendages somewhat paler. Microsculpture: head– vertex with meshes isodiametric, frons with meshes transverse or absent; pronotum with meshes transverse; elytra with meshes transverse or isodiametric; ventral surface with meshes generally transverse. Luster: head shining; pronotum and elytra shining to slightly iridescent; ventral surface generally slightly iridescent. Vestiture: dorsal surface of body glabrous (adults of most species) or sparsely setose (adults of one species), and dorsal surfaces of tarsomeres glabrous or setose. Head: frons each side with two or three sharply defined ridges extended longitudinally. Antennae various: antennomeres 4-10 each either average in proportions (l/w ca. 2.00) or shortened (l/w ca. 1.50). Pronotum (Figs. 66-68) transverse or only slightly wider than long, sides sinuate, lateral margins slightly elevated posteriorly. Metathorax reduced, metepisternum with lateral and basal margins subequal in length, or lateral margin distinctly longer than basal margin. Wings reduced to short stubs. Median lobe of male genitalia with apex hooked or straight; internal sac with sclerotized plate, as in subgenus *Cymindis* (Figs. 70A, 71A). Stylomere 2 of ovipositor with dorsal ensiform setae longer (Figs. 59A, B) or average.

Included species.— This subgenus includes five species: four African; one Arabian; and one Indian. The African species are: *C. kilimana* Kolbe; *C. leleupi* (Basilewsky); *C. meruana* (Basilewsky); and *C. raffrayi* Fairmaire. The Arabian species is *C. scotti* Basilewsky, and the Indian species is *C. nigra* (Andrewes).

Notes about habitat.— The species are known from mountain forests and their environs.

Geographical distribution.— The range of this subgenus includes the high mountains of east Africa (Kilimanjaro and Meru, in Tanzania), Ethiopia, the southern mountains in the Arabian Peninsula, and the hills in southern India. Two species (*C. kilimana* and *C. leleupi*) are known from a single massif (Kilimanjaro). The remaining species are allopatric relative to one another. However, all of these taxa are known from very few specimens.

Phylogenetic considerations.— Basilewsky (1962: 205-207) suggested that the extant species of *Afrotarus* (known to him only from Africa and Arabia) represented a Palaearctic lineage derived from *Cymindis* stock. Presence of the group in southern India suggests that it probably occupied lands farther north, an inference that could also be derived from Basilewsky's hypothesis. However, the evidence at hand does not require that *Afrotarus* be a southern derivative of a northern group. We think it likely that *Afrotarus* is relict, and is the sister group of subgenus *Cymindis*.

Key to Species of Subgenus *Afrotarus* Jeannel

1 (0) Dorsal surface and eyes sparsely setose; median lobe of male genitalia with apical hook (Fig. 71). . . . . *C. (Afrotarus) nigra* (Andrewes), p. 155

1′ Dorsal surface and eyes glabrous; apex of median lobe hooked or not . . . . 2.

2 (1′) Pronotum about as long as wide, impunctate, marginal grooves each broad throughout length, lateral margins elevated. Elytra subovoid, disc markedly flattened, marginal grooves deep, lateral margins elevated, microlines of intervals distinct. Head elongate, smooth, eyes small, hardly prominent, temples long. Antenna long, slender, three articles extended past base of pronotum. Labial tooth broad, rounded apically. Head and pronotum rufo-testaceous, elytra castaneous medially, testaceous marginally, and with large humeral mark testaceous. Length 8.00 mm. or more. . . . .

TABLE 4
DATA ABOUT VARIATION IN STANDARDIZED BODY LENGTH (SBL) AND IN VALUES FOR THE RATIO Pl/PwB AMONG SPECIMENS OF *CYMINDIS NIGRA* (ANDREWES)

LOCALITY AND SEX	SBL (mm.)	Pl/PwB
Palni Hills ♀	5.46	0.94
Cardomon Hills ♂	5.02	1.03
Maharashtra ♂	6.54	1.02

. . . . *C. (Afrotarus) scotti* Basilewsky.

2′ Pronotum transverse, wider than long, disc punctate or not, lateral margins not elevated. Head broad, eyes large and prominent, temples shorter. Antennomeres 4-10 short and wide, extended past base of pronotum only slightly more than two articles. Mentum with apex of tooth acute. Elytron with lateral margin plane, not elevated. Length 7.00 mm. or less . . . . 3.

3 (2′) Elytral intervals with microlines indistinct, meshes transverse, surface slightly iridescent. Pronotum 1.40 times wider than long, sides markedly constricted posteriorly, but not sinuate; posterior angles slightly projected. Elytra castaneous, with vague testaceous humeral markings in basal 0.25 of intervals 5 and 6 . . . . *C. (Afrotarus) raffrayi* Fairmaire.

3′ Elytral intervals with microlines less well developed, meshes isodiametric, dull 4.

4 (3′) Elytra generally castaneous, each with testaceous mark on interval 3 anterior to middle, and another short one preapically . *C. (Afrotarus) leleupi* (Basilewsky).

4′ Elytron with interneurs shallow, impunctate, uniformly piceous or bicolored with well developed humeral marks. Median lobe without apical hook . . . .
. . . . *C. (Afrotarus) kilimana* Kolbe.

Cymindis (Afrotarus) nigra (Andrewes), NEW COMBINATION
Figs. 66-68, and 71

We record a few observations about the limited material that we have seen of this species: three specimens from the proximally located Palni (type locality) and Cardomon Hills, and one specimen from Maharashtra, some 500 km. to the north. The male from Maharashtra differs rather strikingly from the more southern specimens: dorsal integument and eyes of the former are more evidently setose, lateral margins of the pronotum (Fig. 68 cf. Figs. 66 and 67) are more reflexed, elytral humeri are less constricted, the metepisternum is distinctly longer than wide, and body size is larger (Table 4). These differences suggest specific distinctness. On the other hand, the adult of *C. nigra* from the Cardomon Hills differs from specimens in the Palni Hills in form and proportions of pronotum (pronotum longer than wide, Table 4), and in color, though the localities are close together. This suggests that *C. nigra* is inherently variable, so that one could imagine that populations that are far apart geographically could differ strikingly. Further, the apex of the median lobe of the northern male is identical in form to that of a male paratype. For now, we prefer to include all of these specimens in a single species, with the expectation that additional material will eventually be accumulated and will serve as the basis for a revision of this interesting complex.

One might expect that the Indian species of *Afrotarus* would exhibit a combination of features that would set it apart from the more western species which are geographically close to one another. In fact, this expectation is not realized, and the Indian species seems to differ no more from the African species than the latter differ from one another.

Material examined.— We have studied specimens of subgenus *Afrotarus*, labelled as follows.

C. kilimana Kolbe. Male and female, TANZANIA, Kilimanj. Sjostedt; Kiboscho 3000 m Mus Paris coll. Ch. Alluaud (MNHP).

C. nigra (Andrewes). Male, INDIA Madero Ind. Or.; Staudinger and Bang-Haas, 1933; H. E. Andrewes Coll. BM 1945-97 (BMNH). Female, Shores of Kodaikanal Lake, 6550 ft Palni Hills S. India VII.22 (under stones), S. Kemp (ZSIC). Female, S. INDIA 8 mi. NE Munnar, 6200′ III.20.62; E. S. Ross, D. Q. Cavagnaro (CAS). Note: this locality is in the Cardomon Hills of the Western Ghats, and is also known as Pallivasal. Male, INDIA, Maharashtra Mahableshwar 1250 m. II.13.62; E. S. Ross, D. Q. Cavagnaro (CAS).

C. raffrayi Fairmaire. Male, ETHIOPIA Simien Derasghie c. 9800 ft. 22.XII.1952; from grove of tall juniper trees north of town; N. Ethiopia 1952-1953, Hugh Scott, 3 m, 1953-335; Afrotarus raffrayi Fairmaire, det. Basilewsky 1953 (BMNH).

Subgenus *Cymindis* Latreille, NEW STATUS

Figs. 41A-D, 61A-B, 62A-B, 72A-B, 74A-B

Major recent faunal treatments of *Cymindis* are for: France, by Jeannel (1942a); Morocco, by Antoine (1962); eastern Asia, by Jedlička (1963); Japan, by Habu (1967); and the Nearctic Region, by Lindroth (1969a). V. M. Emetz is actively studying the eastern Palaearctic species. Perhaps in the near future, he will be able to write a general revision of the subgenus on a world-wide basis, and thus establish a general system.

Diagnostic description.— The faunal treatments listed above offer detailed characterizations of adults. Especially useful are the descriptions by Antoine and Lindroth. Here, we record only those features that serve to differentiate *Cymindis* adults from those of other subgenera, and that offer promise for establishing phylogenetic relationships.

Size average for carabids (length 7.0 - 12.0 mm.). Color various, dorsum varied from nearly black to rufous, or bicolored, with head and prothorax rufous, elytra darker (black or metallic blue); venter generally paler than dorsum; legs and mouthparts piceous to testaceous, generally paler than dorsum; elytra concolorous, or dark with pale humeral marks. Microsculpture developed or not, but if developed: meshes isodiametric on head and elytra, slightly transverse on pronotum. Luster: dorsal surface generally dull, pronotum more shiny than head or elytra, metallic in members of few species (group designated *Menas* Motschulsky). Vestiture: surface generally setose, though markedly reduced in members of some species (for example, *C. suturalis* Dejean, and *C. hieronticus* Reiche) to very sparse and very short setae, visible only in lateral aspect at high magnification; tarsomeres dorsally and antennomeres 1-3 setose. Surface generally punctate, though punctures reduced in specimens with reduced setation. Fixed setae average, though members of some species with additional lateral setae on pronotum; elytron with three or four setigerous punctures in interval 3. Head: frons each side with or without longitudinally extended ridges and grooves, frontal impressions indistinct. Antennae average for carabids, antennomere 3 distinctly longer than 4; antennomeres 4-10 each longer than wide. Mouthparts: mandibles as in Figs. 41A-D, right mandible with well developed anterior terebral tooth (Fig. 41A); terminal palpomeres similar in form, or labial of males of some species broader than maxillary; labial palpomeres of females unmodified. Pronotum slightly or markedly transverse, sides slightly sinuate or incurved evenly posteriorly; disc slightly convex; posterior angles rectangular or more or less rounded; base arcuate; metepisternum with lateral margin longer than anterior margin (*i.e.*, longer than wide). Elytra average for lebiines. Macropterous or brachypterous. Tarsal claws with denticles well developed, three or more (adults of most species), or very small, one or two. Median lobe of male genitalia with apical portion short, either straight or curved, apical orifice on left side (Figs. 72A-E); internal sac with fields of microtrichia, with apical sclerite (Fig. 72C). Stylomere 2 of ovipositor average for *Cymindis* (Figs. 62A-B).

Included species.— This subgenus is moderately diverse, including more than 150 species, but it is not very divergent (Antoine, 1962: 566). Thus it seems to be, in terms of its state of evolution, in full flower.

As Chaudoir (1873: 53) noted, *Cymindis* became a dumping ground ("une espèce de magazin"), including a collection of unrelated lebiines that shared in common terminal securiform palpomeres. He traced development of the concept of the genus that he had, which is essentially the one we use for the nominotypical subgenus. Csiki (1932: 1464) listed *Iscariotes* Reiche and *Psammoxenus* Chaudoir as subgenera of *Cymindis* (Chaudoir treated these groups as genera close to *Cymindis*). The subgenus *Tarulus* Bedel, 1906 was accepted as such by Csiki (1932: 1464). Jeannel (1942a) excluded *C. canigoulensis* (placed in the subgenus *Pseudomasoreus* by Desbrochers des Loges (1904), and similarly ranked by Csiki (1932: 1464)). Additionally, subgenera have been added to those listed by Csiki (1932: 1464-1465): *Pseudocymindis* Habu, 1967; *Paracymindis* Jedlička, 1968; *Assadera* Mandl, 1973; *Pteroritziella* Mandl, 1973; *Neopsammoxenus* Emetz, 1973; and *Pseudomastes* Emetz, 1972. We believe that all of these groups should be subordinate to the rank of subgenus, but that remains to be determined.

Notes about habitat.— According to Lindroth (1969a: 1071), and from our experience with the Nearctic fauna, the species are xerophilous, individuals living in open country with sparse vegetation. In forested regions, adults are found in open meadows, or along edges of forests. Populations of some species (for example, *C. arizonensis* Horn) inhabit deserts, while those of other species (for example, *C. borealis* LeConte) occur on dry arctic tundra.

Geographical distribution.— This subgenus is widespread in the Holarctic Region. In the Old World, it ranges from the Atlas Mountains in the west and Himalaya in the east northward to the Arctic. The range in the New World is similar: from northern Chihuahua, Mexico, to the Arctic Islands of Canada. Most species, however, are concentrated in the middle latitudes of the Northern Hemisphere.

Phylogeny and zoogeography.— We have three points to make. Judging from the numerous species identified by means of few characters, and wide continuous range of the subgenus, we believe its differentiation to be relatively recent. Because the group is much more diverse and divergent in the Old World than the New (all Nearctic species probably belong to a single Holarctic species group), and because its seemingly closest relatives are also in the Old World, we believe that *Cymindis (sensu stricto)* is of Old World origin. We also believe that the xerophily of the species is a derived feature that enabled the group to spread and diversify with the later Tertiary development of dry temperate habitats.

Material examined.— We have seen specimens of most Nearctic species, but we have studied and dissected only the following Old World forms.

Cymindis suturalis Dejean. Male and female, labelled: ALGERIA Biskra, Van Dyke Coll. (CAS).

Cymindis hieronticus Reiche. Four males labelled: W. PAKISTAN 10 mi. SW Kohat 650 m. XII.19.1961; E. S. Ross and D. Q. Cavagnaro. Four females, labelled: W. PAKISTAN, 2 mi. w. Cherat, 1200 m., XII.20.1961; E. S. Ross and D. Q. Cavagnaro.

Hystrichopus Boheman
Figs. 44A-D, 52, 54, 58, 64, 77-88C

Hystrichopus Boheman, 1848: 42. GENERITYPE: *Hystrichopus angusticollis* Boheman, 1848 (subsequent designation by Basilewsky, 1954b: 15).– Péringuey, 1896: 212-218.– Basilewsky, 1954b: 7-80.– 1958: 297-302.– 1960: 85-86.– 1961b: 122-126.– 1962: 207-212.– 1976: 717.

Plagiopyga Boheman, 1848: 75. GENERITYPE: *Plagiopyga ferruginea* Boheman, 1848: 76 (monotypy). NEW SYNONYMY.– Péringuey, 1896: 212-221.– Basilewsky, 1945b: 80-94.– 1958: 302.

Pseudomasoreus Desbrochers des Loges, 1904: 140, 143, 163. GENERITYPE: *Cymindis canigoulensis* Fairmaire and Laboulbène, 1854: 32 (monotypy).– Bedel, 1906: 241.– Porta, 1923: 227.– Antoine, 1938: 171.– Jeannel, 1941: 62.– 1942a: 1039-1041.– 1949: 878-881.– Basilewsky, 1953b: 57-58.– 1954c: 89-96.– 1958a: 296-297.– 1962: 212-216.– Antoine, 1962: 562.– Mateu, 1970a: 173-175.– Basilewsky, 1976: 717.– Mateu, 1980: 16-23.

Assadecma Basilewsky, 1982: 20. GENERITYPE: *Assadecma madagascariensis* Basilewsky, 1982: 22 (original designation and monotypy). NEW SYNONYMY.

Data about synonymy are provided in conjunction with treatments of subgenera.

The following features of adults characterize this genus: head with two pairs of supraorbital setigerous punctures; frons without ridges and grooves laterally; elytron with lateral umbilicate punctures larger and thus clearly distinguishable from other setigerous punctures; right mandible with well developed premolar (Figs. 44B and D); median lobe of male catopic, internal sac without sclerites (Figs. 86C-88C); valvifer of ovipositor with extra lobe, stylomere 2 elongate, slender, with single ensiform seta (Figs. 55-57).

Jeannel (1942a) established the tribe Pseudomasoreini for *Pseudomasoreus* Desbrochers des Loges, adding to it (1949) *Hystrichopus* Boheman. Subsequently, Basilewsky (1954b), who treated this group as a tribe of Lebiinae equivalent to the Cymindini and other lebiine tribes, added *Plagiopyga* Boheman. Three years later, Basilewsky (1957: 240) noted that male dromiines of *Klepturus* and *Klepteromimus* also had catopic median lobes, and concluded that it would be necessary to re-evaluate this character state as a basis for ranking the pseudomasoreine group as a tribe of Lebiinae. With Mateu (1980: 17) we believe that this feature does not constitute a sufficient basis for giving pseudomasoreines a high rank, though in contrast to him, we believe that catopy was evolved only once in the Cymindina, and thus delimits a monophyletic group.

Subgenus *Pseudomasoreus* Desbrochers des Loges, 1904, NEW STATUS

Characteristics.— This subgenus is adequately characterized by Jeannel (1942a and 1949), Basilewsky (1954a), and Antoine (1962). To the features noted by these authors, we add: stylomere 2 of ovipositor slender throughout length, more or less tubular, with dorso-lateral ensiform setae moderate to long (Fig. 55A).

Included species.— This subgenus includes 13 previously described species, and four more from localities in the Union of South Africa, are described below.

Geographical distribution.— The range of *Pseudomasoreus* extends from the Cape Region of the Union of South Africa to the Pyrenees Mountains of Spain and France, and includes Madagascar. However, the range is discontinuous: five species are known only from South Africa (see below); nine species are known only from Madagascar (Mateu, 1980); two species are known only from the high mountains of East Africa (Basilewsky, 1962); and *P. canigoulensis* is known only from localities in and to the north of the Atlas Mountains.

Notes about phylogeny and zoogeography.— Mateu (1980: 15), in conjunction with his useful revision of the Madagascan species, notes that they seem to be montane- adapted and possibly xerophilous, but that little is known about their way of life. Most species (including those in Africa) are known from single localities, only. Mateu also noted the relative abundance of species of Madagascar compared with those on the African continent, and suggested that additional species may be discovered. He stated that the subgenus, though truly old, seems to have been revitalized on Madagascar, for its species there are very similar to one another, and thus seem to have evolved recently.

Jeannel (1942b: 316-317), when species were known only from Madagascar and north of the Atlas Moutains, suggested that *Pseudomasoreus* had arisen in eastern Africa during the

Cretaceous, had reached the two areas listed above, and survived there, but had become extinct on mainland Africa, to the south of the Sahara. Subsequent discovery of *H. capicola, H. kivuanus,* and *H. uluguruanus* confirmed Jeannel's prediction that the group had been in Afrotropical mainland Africa. Basilewsky (1954c: 91), when he described *H. capicola,* predicted that the group would also be represented on the mountains of East Africa. Thus, his more detailed prediction was confirmed with discovery of *H. kilimanus hkb,f>and H. uluguruanus.*

Both Jeannel and Basilewsky stated that *Pseudomasoreus* had arisen in Cretaceous time, and had once been continuously distributed. Thus, the present discontinuous range is interpreted as relict, and these authors suggested that *Pseudomasoreus* is on the way to extinction. This may be true, but it is interesting to note that the northern periphery of the range of the group is occupied by a species whose adults are macropterous. It thus seems possible that this lineage may be a recent arrival in the north. However, until phylogeny can be reconstructed and used as a basis for interpreting the distribution pattern, it seems best to avoid making additional inferences.

The Species of *Pseudomasoreus* of East and South Africa

We have had the opportunity to study 16 specimens of *Pseudomasoreus* from Afrotropical localities. These represent material of three described species and four undescribed species. We describe the latter and provide a key to these and to the previously described mainland Afrotropical species.

Description.— We list here features shared by adults of all of the species.

Color. Generally somber, dorsal surface various, lateral margins of pronotum and elytra generally a bit paler than medial areas; ventral surface constantly dark (rufo-piceous to piceous); appendages flavous.

Microsculpture. Dorsum of head (including clypeus) and labrum with meshes isodiametric; pronotum with meshes various; meshes of pro- and pterothoracic sterna and metepisterna transverse; meshes of pro- and mesepisterna elongate; meshes of abdominal sterna transverse. Luster of dorsal surface various; of ventral surface, iridescent.

Eyes. Moderate in size, flattened, not prominent.

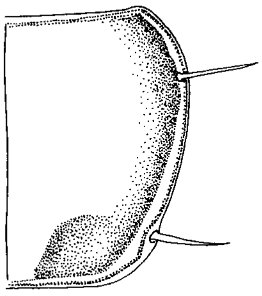
Pronotum (Figs. 77-82). Subcordate to cordate, sides incurved posteriorly; posterior angles obtuse; disc with median longitudinal impression and laterally with irregular shallow impressions, without transverse impressions; surface slightly convex, laterally slightly sloped; lateral grooves well developed, posterior lateral impressions irregular shallow basins, more or less continuous with lateral grooves. Two pairs of lateral setae.

Elytra flat; posterior margins subtruncate. Interneurs average, impunctate; scutellar interneur developed. Intervals slightly convex, sparsely punctate. Parascutellar setigerous puncture developed. Disc with two setigerous punctures in interval 3; umbilical series including about 14 setigerous punctures.

Relationships.— The data are not available to do more than arrange the species in order of increasing apotypy, based on inferred morphoclines of changes in microsculpture (from isodiametric to transverse meshes) and structural changes associated with loss of wings (reduction of metathorax, and change in form of elytral humeri). We also assume that these species are more closely related to one another than they are to the Madagascan species of *Pseudomasoreus* or to the Mediterranean *P. canigoulensis.*

Key to Eastern and Southern African Species of the Subgenus *Pseudomasoreus* Desbrochers des Loges

1 (0) Elytron with microsculpture meshes isodiametric 2
1′ Elytron with microsculpture meshes transverse, surface iridescent or not ..... 3.
2 (1) Metepisternum elongate (w/l=ca. 1.50); size smaller (SBL ca. 5.00 mm) ....
.... *H. (Pseudomasoreus) reticulatus* new species, p. 164
2′ Metepisternum short (w/l ca. 1.00); size larger (SBL more than 6.00 mm) ....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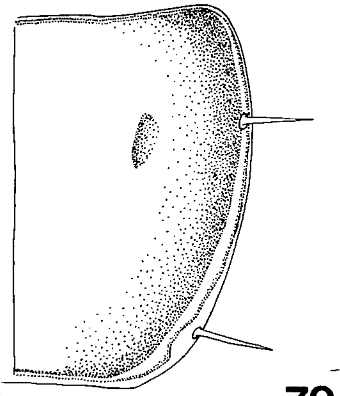
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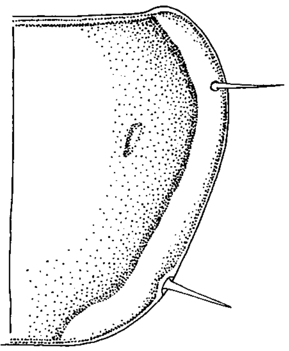
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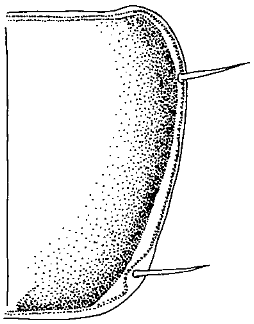
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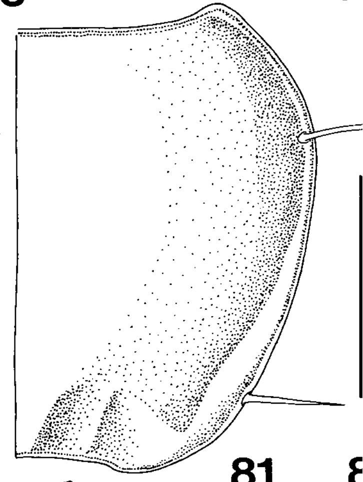
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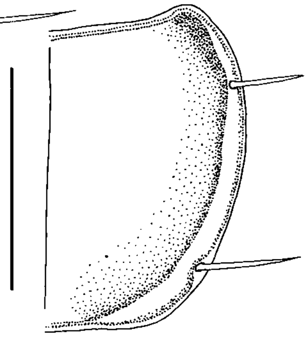
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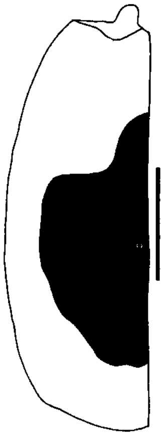
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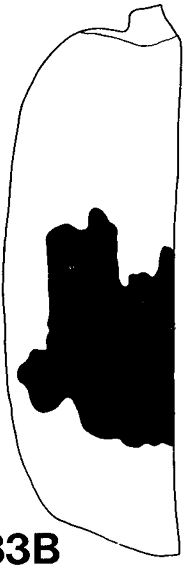
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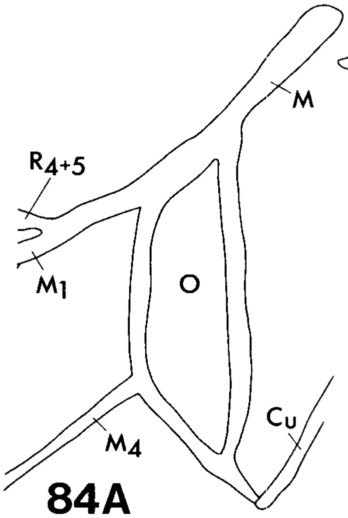

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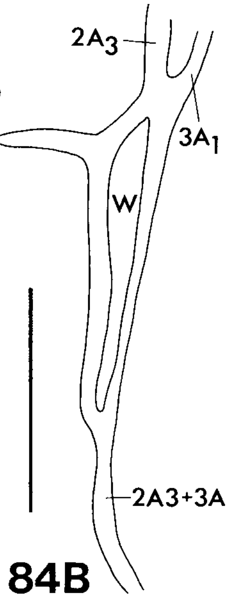
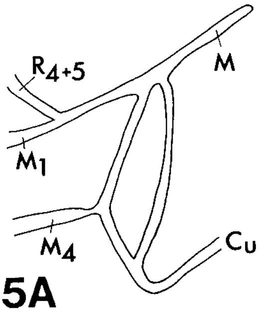


84B

Figs. 77–84. Line drawings of structures of Cymindina.—Figs. 77–82. Pronota, dorsal aspect, of *Hystrichopus (Pseudomasoreus)* species: 77, *H. reticulatus,* new species; 78, *H. capicola* (Basilewsky); 79, *H. uluguruanus* (Basilewsky); 80, *H. basilewskyi,* new species; 81, *H. thoracicus,* new species; 82, *H. mateui,* new species. 83A, *H. kivuanus* (Basilewsky); 83B, *H. mateui,* new species. Fig. 84. Wing cells and associated veins of *Hystrichopus (sensu stricto) massaicus* Basilewsky: A. oblongum cell; B, wedge cell. Legend. Wing cells: O, oblongum; W, wedge. Veins: A, anals; Cu, cubitus; M, median; R, radius.



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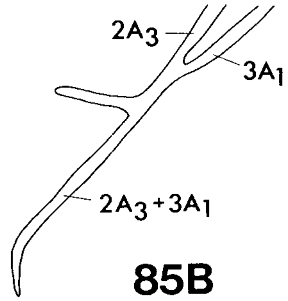

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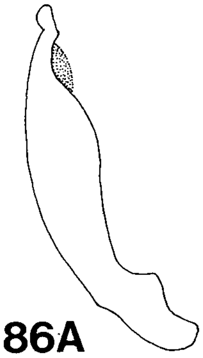

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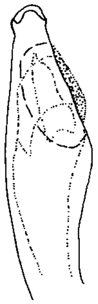

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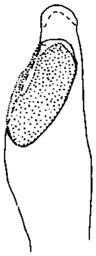

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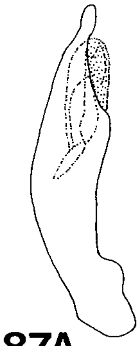
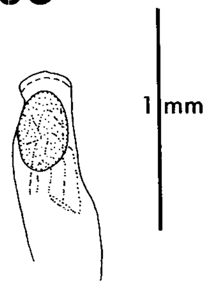


87A

87B



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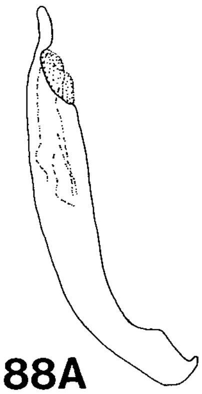

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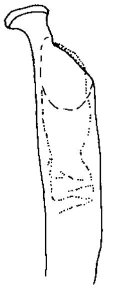

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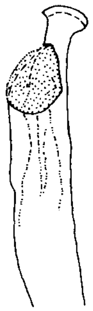


88C

Figs 85–88. Line drawings of structures of Cymindina.—Fig. 85. Wing cells and associated veins of *Hystrichopus (Plagiopyga) chaudoiri* Péringuey: A, oblongum cell; B, wedge cell. Figs. 86–88. Male genitalia, median lobe of *Hystrichopus (Pseudomasoreus)* species. A, B, C, left lateral, dorsal, and ventral aspects (basal lobe excluded), respectively, of: 86, *H. uluguruanus* (Basilewsky); 87, *H. basilewskyi,* new species and 88, *H. mateui,* new species. Legend. Wing cells: O, oblongum; W, wedge. Veins: A, anals; Cu, cubitus; M, media; R, radius.

.... *H. (Pseudomasoreus) capicola* Basilewsky, p. 167

3 (1′) Metepisternum long and slender (w/l more than 1.50); microsculpture meshes of elytron wide, surface not iridescent; elytron with dark mark behind middle (Fig. 83A) .... *H. (Pseudomasoreus) kivuanus* Basilewsky, p. 167

3′ Metepisternum short (w/l less than 1.50); elytra iridescent, bicolored or not .. 4.

4 (3′) Elytron with distinct dark mark near suture, rest of surface rufo-flavous ..... 5.

4′ Elytron concolorous, rufo-piceous to piceous .... 6.

5 (4) Specimen from locality in South Africa; pronotum less markedly constricted posteriorly; dark mark of elytron extended more anterad (Fig. 83B); male with apical portion of median lobe long, inclined to left (Figs. 88B, C) .... *H. (Pseudomasoreus) mateui*, new species, p. 170

5′ Specimen from Tanzania; pronotum markedly narrowed posteriorly; dark mark of elytron not extended anterad; male with apical portion of median lobe straight .... *H. (Pseudomasoreus) uluguruanus* Basilewsky, p. 168

6 (4′) Metepisternum slightly longer than wide (w/l 1.25- 1.38); smaller (SBL ca. 5.00 mm.) .... *H. (Pseudomasoreus) basilewskyi* new species, p. 168

6′ Metepisternum about quadrate, length less than width; larger (SBL ca. 7.00 mm) .... *H. (Pseudomasoreus) thoracicus*, new species, p. 169

Hystrichopus (Pseudomasoreus) reticulatus, new species

Fig. 77

HOLOTYPE female, labelled: COLL MUS TERVUREN Cape Prn: Clanwilliam distr., Sederberg VII.1958 1500m J. Smith (MACT).

ion of specific epithet.— A Latin adjective, meaning net-like, in allusion to appearance of the isodiametric microsculpture of the elytra.

Recognition.— In addition to features cited in the key, the single female of this species differs from females of *H. capicola* having a wider pronotum in relation to length (see Table 7). From females of other species, this one differs in having the pronotum narrow in relation to head width (see Table 6).

Description.— Values for SBL and for ratios Hw/Pmw, Pl/Pmw and MES: l/w are presented in Tables 5-8.

Color. Dorsum piceous; epipleura of elytra rufous.

Microsculpture. Dorsum of head and elytra with isodiametric meshes, pronotum with wide, transverse meshes.

Luster. Surface generally dull.

Pronotum. As in Fig. 77. Sides not markedly constricted posteriorly.

Elytra. Humerus rounded, not projected anteriorly. Basal ridge not markedly sinuate.

Ovipositor. Stylomere 2 longer and straighter, and with ensiform setae shorter than in *H. mateui*.

Geographical distribution.— This species is known only from the type locality in the Union of South Africa.

Relationships.— The long metepisternum, rounded elytral humeri, and isodiametric microsculpture of the elytra indicate that this is the most primitive species of *Pseudomasoreus* on mainland Africa.

Material examined.— Known only from the holotype.

TABLE 5
DATA ABOUT VARIATION IN STANDARDIZED BODY LENGTH (MM) AMONG EAST AND SOUTH AFRICAN SPECIES OF *PSEUDOMASOREUS*

	MALES		FEMALES	
SPECIES	N	RANGE	N	RANGE
H. reticulatis			1	4.92
H. capicola			3	6.12–6.24
H. kivuanus			1	6.28
H. uluguruanus	2	5.20–5.56	1	5.32
H. basilewskyi	2	5.00–5.36	2	5.04–5.20
H. thoracicus			3	6.84–7.12
H. mateui	1	5.00	2	5.40–5.68

TABLE 6
DATA ABOUT VARIATION IN VALUES FOR THE RATIO Hw/Pmw AMONG EAST AND SOUTH AFRICAN SPECIES OF *PSEUDOMASOREUS*

	MALES		FEMALES	
SPECIES	N	RANGE	N	RANGE
H. reticulatus			1	0.78
H. capicola			3	0.78–0.80
H. kivuanus			1	0.69
H. uluguruanus	2	0.73	1	0.76
H. basilewskyi	2	0.75–0.77	2	0.78
H. thoracicus			3	0.68–0.72
H. mateui	1	0.77	2	0.72

TABLE 7
DATA ABOUT VARIATION IN VALUES FOR THE RATIO Pl/Pmw AMONG EAST AND SOUTH AFRICAN SPECIES OF *PSEUDOMASOREUS*

	MALES		FEMALES	
SPECIES	N	RANGE	N	RANGE
H. reticulatis			1	0.78
H. capicola			3	0.82–0.85
H. kivuanus			1	0.69
H. uluguruanus	2	0.75	1	0.75
H. basilewskyi	2	0.85–0.86	2	0.83–0.84
H. thoracicus			3	0.76–0.78
H. mateui	1	0.77	2	0.72

TABLE 8
DATA ABOUT VARIATION IN VALUES FOR THE RATIO MES: 1/w AMONG EAST AND SOUTH AFRICAN SPECIES OF *PSEUDOMASOREUS*

	MALES		FEMALES	
SPECIES	N	RANGE	N	RANGE
H. reticulatus			1	1.52
H. capicola			1	1.00
H. kivuanus			1	1.80
H. uluguruanus	2	1.00	1	1.00
H. basilewskyi	2	1.25–1.38	2	1.28–1.32
H. thoracicus			3	0.86–0.97
H. mateui	1	0.76	2	0.72–0.96

Hystrichopus (Pseudomasoreus) capicola (Basilewsky), NEW COMBINATION
Figs. 55A-B, and 78.

Pseudomasoreus capicola Basilewsky 1954c: 93. HOLOTYPE female, labelled: HOLOTYPUS [orange paper]; COL.MUS. CONGO. Cape Colony Dunbrody Co. P. Basilewsky; Pseudomasoreus capicola n. sp. P. Basilewsky det. 1954. (MACT). TYPE LOCALITY.– Dunbrody Cape Colony, South Africa.– Basilewsky, 1958a: 296-297, Fig. 40.

Recognition.— Large size, slender pronotum in relation to length and width of head, short metepisterna, isodiametric microsculpture of elytra, and slightly transverse microsculpture meshes of pronotum distinguish this species from others of *Pseudomasoreus.*

Description.— Tables 5-8 provide data about variation in SBL, and in values for ratios Hw/Pmw; Pl/Pmw and MES: l/w.

Color. Dorsum piceous, epipleura of elytra rufous.

Microsculpture. Head and elytra with meshes isodiametric, pronotum with meshes slightly transverse.

Luster. Dull.

Pronotum (Fig. 78) Narrow, sides slightly constricted posteriorly.

Elytra. Humeri projected forward, basal ridge markedly sinuate.

Geographical distribution.— This species is known only from the Union of South Africa, in Cape Province and Basutoland.

Relationships.— These have not been determined. The predominantly isodiametric microsculpture of the dorsum suggests that this species is primitive. However, the metathorax is appreciably shortened, suggesting some derivativeness.

Material examined.— In addition to the holotype, we have seen two females labelled: S. Afr. Basutoland Makhere Mts. 15 miles ENE Mokhotlong 8.IV.51 No. 268 Swedish South Africa expedition 1950-51 Brinck Rudebeck 9500 ft; COLL MUS CONGO (ex Lund Mus) Coll. P. Basilewsky (MACT). Six more specimens are known from this locality (Basilewsky, 1958a: 297), but we have not seen them.

Hystrichopus (Pseudomasoreus) kivuanus (Basilewsky), NEW COMBINATION
Fig. 83A

Pseudomasoreus kivuanus Basilewsky, 1962: 215. HOLOTYPE, female, labelled: HOLOTYPUS [orange paper]; COLL MUS CONGO Tanganyika Terr: Kilimanjaro Marangu Versant S.E. 1800-2200 m 20/27.VII.57; Resideu de foret transition [blue paper]; Mission Zoologiq. IRSAC en Afrique orientale P. Basilewsky et N. Leleup; *Pseudomasoreus kivuanus* n.sp. P. Basilewsky det. 1960 (MACT).

Recognition.— In addition to character states listed in the key, the female of *H. kivuanus* is distinguished by moderate size (SBL- 6.28 mm.) (smaller than the type of *H. thoracicus,* about same as females of *H. capicola,*), and the pronotum very broad in relation to both head width (Table 6) and pronotum length (Table 7).

Description.— Data about Standardized Body Length, and ratios Hw/Pmw, Pl/Pmw, and MES: w/l are presented in Tables 5 to 8.

Color. Head and pronotum piceous, elytra generally rufous with broad, irregular, transverse dark mark in posterior half (Fig. 83A); elytral epipleura rufous.

Microsculpture. Meshes of head and pronotum isodiametric; meshes of elytra transverse.

Luster. Head and pronotum dull. Elytra shining, but not iridescent.

Pronotum. Very broad, sides rounded, moderately constricted posteriorly.

Elytra. Humeri average, not extended anteriorly as prominent lobes; basal ridge not markedly sinuate. Hind wing with cells as in Figs. 84A, B.

Basilewsky (1962: 215) stated that adults of this species were apterous. However, wing rudiments are about half the length of the elytra.

Geographical distribution and habitat.— The single known female was collected in Tanzania, on Mount Kilimanjaro, in forest, between 1800 and 2200 meters above sea level.

Relationships.— Color pattern and geographical proximity suggest that *H. kivuanus* and *H. uluguruanus* are more closely related to one another than to other species of

Pseudomasoreus. Their immediate common ancestor was probably from a primitive stock, for *H. kivuanus* has very slightly derived microsculpture of the dorsal surface, has retained long wing rudiments and features associated with wing reduction are not well developed; that is, the metathorax is large (as shown by long metepisterna), and the elytral humeri are not projected forward.

Hystrichopus (Pseudomasoreus) uluguruanus Basilewsky, NEW COMBINATION
Figs. 79 and 86

Pseudomasoreus uluguruanus Basilewsky, 1962: 213. HOLOTYPE male, labelled: HOLOTYPUS [orange paper] ; vert foret/ombrophile dans l'humus [blue paper] ; COLL MUS CONGO Tanganyika Terr: Bunduki, Uluguru Mts., 1300 m. 2.5.1957; Mission Zoologique IRSAC en Afrique Orientale (P. Basilewsky and N. Leleup); Pseudomasoreus uluguruanus n. sp. P. Basilewsky det. 1960. (MACT). PARATYPE male, similarly labelled to holotype, but collected on summit of Mt. Kidunda, 1800-1950 m., 3.V.1957. (MACT). PARATYPE female, similarly labelled to holotype, but collected on Mgeta, 1300 m., 30.IV- 2.V. 1957. (MACT).

Recognition.— In addition to character states listed in the key, members of this species are recognized by a combination of small size (SBL less than 6.00 mm.), and cordate pronotum (Fig. 79).

Description.— Data about variation in Standardized Body Length, and in ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

Color. Head piceous; pronotum with disc piceous, broad lateral area rufous; elytra generally rufo-flavous, with broad irregular transverse dark mark in posterior half, less distinct in similarly marked female of *H. kivuanus*. Elytral epipleura flavous.

Microsculpture. Head with meshes isodiametric; pronotum with meshes isodiametric to transverse; elytra, with meshes transverse, narrow.

Pronotum. Form as in Fig. 79, cordate, sides constricted posteriorly.

Elytra. Humeri produced anteriorly as lobes, basal ridge of elytron markedly sinuate.

Male genitalia.– Median lobe as in Figs. 86A-C: apical portion in dorsal aspect short and broad; internal sac with basal microtrichial fields short, concentrated near apical orifice of median lobe (two males dissected).

Basilewsky (1962: 213) stated that specimens of this species are winged. However, each wing comprises a small stub only, no longer than the combined lengths of two abdominal terga.

Geographical distribution and habitat.— This species is known only from the type locality– The Uluguru Mountains in Tanzania, at elevation of 1800-1900 m. Adults were collected in mountain forest, in leaf litter.

Relationships.— Color pattern and geographical distribution indicate that *H. uluguruanus* and *H. kivuanus* are sister species. However, *H. uluguruanus* shares with the more derived species of *Pseudomasoreus* transverse microsculpture and iridescent luster of the elytra, reduction of wings, marked reduction of the metathorax (indicated by short metepisterna), and produced elytral humeri. Evidently, these states were developed convergently with the same states in other members of the subgenus.

Hystrichopus (Pseudomasoreus) basilewskyi, new species
Figs. 80 and 87

HOLOTYPE male, labelled: COLL MUS TERVUREN Cape prov. Swellendam distr., Grootvadersbos J. Smith VII.1958. (MACT). ALLOTYPE female, same label as holotype. Holotype and female paratypes returned to MACT; male paratype deposited in CAS.

Derivation of specific epithet.— We take pleasure in naming this species for Pierre Basilewsky, distinguished specialist of the African carabid fauna and of African biogeography.

Recognition.— In addition to key character states, small size, concolorous elytra, and metepisternum slightly longer than wide, distinguish members of this species from all others.

Males are further distinguished by the very short and broad apical portion of the median lobe (Fig. 87B, C).

Description.— Data about variation in Standardized Body Length, and in ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

Color. Head, rufo-testaceous; pronotum rufous; elytra rufo-piceous to piceous.

Microsculpture. Head with meshes isodiametric. Pronotum with meshes transverse, but not especially narrow; elytra with meshes transverse, very narrow.

Luster. Dorsum of head dull; pronotum with surface shining, not iridescent. Elytra with surface iridescent.

Pronotum. Form as in Fig. 80, moderately broad in relation to head, sides not markedly constricted posteriorly.

Elytra. Humeri projected anteriorly, basal ridge markedly sinuate.

Male genitalia. Median lobe (Fig. 87A-C) with apical portion very short and broad. Internal sac with basal microtrichial fields long, extended anteriorly in inverted position.

Geographical distribution.— This species is known only from the type locality, in South Africa.

Relationships.— This is a markedly derived species, adults having iridescent elytra and humeri projected. However, the metathorax is only partially reduced, and microsculpture of the pronotum is not modified enough to provide iridescence. Iridescence of the elytra is an apotypic character state shared with *P. thoracicus* and *P. mateui,* and on this basis we locate *P. basilewskyi* in an informal group with these species.

Material examined.— This species is known only from the type series.

Hystrichopus (Pseudomasoreus) thoracicus, new species

Fig. 81

HOLOTYPE female, labelled Grahamstown 14.1.1904 (J. O'N) [handwritten]; Platynus sp. nov. [handwritten]; Pseudomasoreus sp. ign. [handwritten] South African Museum. PARATYPES, two females, labelled: [G or A]? T, 15.V,12; S. Africa Cle Deux acc. 67769. (USNM). And as above, except "Cle Doux" (USNM).

Derivation of specific epithet.— This is an adjectival form of "thorax", and draws attention to the large pronotum that is characteristic of specimens included in this species.

Recognition.— Large size (SBL about 7.00 mm.), iridescent pronotum and elytra, and broad pronotum with wide lateral grooves distinguish adults of this species from other known Afrotropical species of *Pseudomasoreus.*

Description.— Data about variation in Standardized Body Length and in values for ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

Color. Dorsum of head, pronotum and elytra piceous, elytral epipleura rufous.

Microsculpture.– Head with meshes isodiametric; pronotum and elytra with meshes transverse, narrow.

Luster. Dorsum of head dull; pronotum and elytra with surfaces iridescent.

Pronotum. As in Fig. 81, cordate, lateral grooves wider than usual.

Elytra. Humeri projected anteriorly, basal ridge markedly sinuate.

Ovipositor. Stylomere 2 average for subgenus *Pseudomasoreus.*

Geographical distribution.— This species is known from the Union of South Africa, only.

Relationships.— This is a derived species in that its adults are characterized by iridescent pronotum and elytra, markedly reduced metathorax, and produced elytral humeri. These character states are shared with adults of *H. mateui,* new species, which we regard as the sister species of *H. thoracicus.*

Hystrichopus (Pseudomasoreus) mateui, new species
Figs. 82, 83B and 88A-C

HOLOTYPE male, labelled: Malvern, Natal; G. A. K. Marshall 1917-55 [blue line in middle of label]; Cymindide gen et sp nova? Per. [handwritten] (BMNH). ALLOTYPE female, labelled: NATAL Ekombe For. 39 mi. N. of Kranskop 1520 m. IV.10.58; E.S. Ross and R.E. Leech, collectors (CAS). PARATYPE female, labelled: Mbabang Swaziland [handwritten] ; Pseudomasoreus n. sp. (ap. capicola Basilw) P. Basilewsky det. 1962 other specimens are necessary [Note: the left mandible missing]. (SAMC).

Derivation of specific epithet.— This is based on the surname of Dr. Joaquin Mateu, who has published extensively about carabids of the tropics of the world, especially about lebiines.

Recognition.— In addition to the key character states, specimens of this species are distinguished by small size (SBL less than 6.00 mm.) and cordate pronotum (Fig. 82). Males have a long apical portion of the median lobe, with apex spatulate (Figs. 88B, C).

Description.— Data about variation in Standardized Body Length, and in ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

Color. Head rufo-piceous; pronotum piceous to disc rufo-piceous, with lateral areas rufo-flavous (specimen may be slightly teneral); elytra with dorsal surface generally rufous to rufo-flavous, medially with dark mark extended along suture into basal half.

Pronotum. As in Fig. 82, cordate, sides markedly constricted posteriorly.

Elytra. Humeri projected anteriorly, basal ridge markedly sinuate. Hind wing with cells as in Fig. 84B.

Male genitalia. Median lobe (Figs. 88A-C) long, with apical portion long, spatulate. Internal sac with microtrichial fields long, extended basally.

Ovipositor. Stylomere 2 average for *Pseudomasoreus.*

Geographical distribution.— This species is known only from two localities in the Union of South Africa.

Relationships.— This species seems to be the sister species of *H. thoracicus,* new species.

Subgenus *Assadecma* Basilewsky, NEW STATUS

Characteristics.– The most striking features of this subgenus are: size of specimens (overall length 14 to 15 mm., estimated SBL 12 to 13 mm.), relative size of pronotum (almost half the length of elytra), its form (parallel-sided, base and apex about equal in width), very short and broad tarsomere 4, armature of the male internal sac (several rows of spines), and long, slender apical portion of the median lobe. Mandibles are markedly different from those of other cymindines, but we judge from the illustration (Basilewsky, 1982: Fig. 2c) of the ventral surface of the right mandible that it is worn. If so, the features exhibited are not of taxonomic value.

Other character states are shared with members of other subgenera of *Hystrichopus.* Even though females of *Assadecma* are not available, we believe that they will be found to have stylomeres characteristic of *Hystrichopus (sensu lato),* and probably characteristic of subgenus *Pseudomasoreus.*

Included species.— The single known species of this *subgenus, H. madagascariensis* (Basilewsky), is based on two males, collect at different localities in eastern Madagascar. The type locality is Hiaraka (1000 meters), on the Masoala Peninsula. The holotype is in MNHP, the paratype in MACT.

Notes about phylogeny.— Relatively large size of its members, a markedly distinctive combination of other character states, and seeming isolation of the single known species on Madagascar suggest that *Assadecma* is a phylogenetic relic, rather than representing a recently evolved descendant of one of the other extant subgenera. Thus, this taxon is likely to be of substantial importance in reconstructing the evolutionary history of *Hystrichopus (sensu lato).*

Subgenus *Hystrichopus (sensu stricto)* Boheman, new status

Figs. 44A-D, 52, 56A-B, 64, and 84A-B

Notes about synonymy.— Basilewsky (1954b: 13) listed the following genus-group names as junior synonyms: *Ctenoncus* Chaudoir, 1850; and *Assotatus, Assoterus, Astus,* and *Aspastus* Péringuey, 1896. He discussed the nomenclatural history of *Hystrichopus* and its junior synonyms (1954a: 15-16). Details are not reviewed here.

Characteristics.— This subgenus was adequately characterized by Basilewsky (1954b: 13-14), for purposes of identification. He did not, however, examine the mandibles (Figs. 44A-D), hind wings (oblongum cell large, Fig. 84A, wedge cell small, Fig. 84B) or stylomere 2 of the ovipositor (Fig. 56A): note the very short ensiform seta).

Notes about classification.— This subgenus includes 58 described, and two undescribed species. In spite of this diversity, *Hystrichopus* seems quite homogeneous, so .uch so that Basilewsky (1954b: 16) chose not to recognize formal subgenera, but instead arranged the species in two sections and 11 groups, to which he also assigned those species that he described subsequently.

Although many of the most closely related taxa are allopatric, Basilewsky elected not to use the subspecies category. He argued that more information was required to establish subspecies than species, and that he did not have the requisite information because of a shortage of specimens. He also argued that the brachypterous montane vicariads had been isolated long enough to have differentiated to the species level.

The two sections of *Hystrichopus* are distinguished by differences in development of the metathorax, which are in turn associated with wing development: adults of Section I have long metepisterna, dehiscent elytra, and are either macropterous or brachypterous; those of Section II have reduced metepisterna, elytra more or less fused together along the suture, and wings absent.

Although wing loss is characteristic of both groups, Basilewsky stated that processes of change were probably different: reduction of the flight function in Section II he recognized as an orthogenetic process, whereas wing loss by members of Section I was adaptive. The important point to note here is that he conceived the sections (as well as "Groups") as phylogenetically valid assemblages.

Nonetheless, in our view, wing loss in both sections is the result of the same process, that of adaptation. Furthermore, in the absence of additional evidence that Section II is monophyletic, this taxon must be suspect in a phylogenetic system: reduction of the metathorax could have taken place in a number of lineages independently. Section I is based on a symplesiotypy, and may not be monophyletic, either.

Habitat.— Basilewsky (1954b: 18) classified the species as "lapidicoles" or "humicoles". Lapidicoles are found under stones at lower elevations in savanna land, mainly in South Africa, but also at high altitudes in East Africa. Humicoles are residents of mountain forests, and are found in damp humus (leaf litter, *et al.* Adults do not show a tendency for reduction of pigment or eye size, so it seems certain that they are not associated with deep litter, nor are they troglophiles.

Altitudinal range extends from near sea level in the south to between 3000 to 4000 meters on Mount Kilimanjaro, in Tanzania. Generally, the more northern taxa live at elevations above 1800 meters.

Geographical distribution.— The range of this subgenus extends from southernmost South Africa northward to the southeastern mountains of the Arabian Peninsula, and with an isolated species (*H. nimbanus* Basilewsky) on the massif of Nimba, in French Guinea, West Africa. The range is discontinuous, because the East African species occur on mountains, at high elevations.

The species of Section II seem to be restricted to South Africa and Zimbabwe. The range of the species of Section I is co-extensive with range of the subgenus as a whole.

Notes about phylogeny and zoogeography.— Basilewsky did not attempt to reconstruct the phylogeny of subgenus *Hystrichopus* in detail. However, he considered the topic in a general way (1954b: 21-23; see also 1962: 207-212). The distribution pattern (especially the marked isolation of *H. nimbanus* in the mountains of French Guinea), suggested to him that the group is ancient, at least earlier in origin than development of the Red Sea. The group was formerly widespread in Africa, and had wider ecological tolerances than have the extant stocks. Thus, the latter are relics– that is, they do not represent a temperate-adapted stock that recently spread north from South Africa.

On the contrary, it seems to us that the distribution pattern could be subject to a very different interpretation. However, what must come first is a phylogenetic analysis of the species, so that relationships can be hypothesized, and thus sense can be made of the different distributions of macropterous and brachypterous taxa, especially those of Section I. Basilewsky (1954a: 22) suggested that occurrence of brachypterous forms of Section I at high altitude is a function of "stenohygrothermy", for adults of such species live in damp humus in mountains forests. This may be so, but it is no help in understanding phylogenetic relationships of taxa with macropterous and brachypterous adults.

Material examined.— Our observations are based on the following material, from collections of the California Academy of Sciences.

Hystrichopus dorsalis Thunberg. Three males, three females– South Africa Cape Province George X.28.49 B. Malkin.

Hystrichopus massaicus Basilewsky. Two females, from Kenya. Nairobi XII.31.1959, E. S. Ross. 17 mi. SE Nakuru 1900 m; E. S. Ross, R. E. Leech.

Hystrichopus rufipes Dejean. Male– South Africa 6mi. NW Port Beaufort 70 m 14.I.1967; E. S. Ross, K. Lorenza.

Subgenus *Plagiopyga* Boheman, NEW STATUS

Figs. 50, 57, 58, and 85A-B

Notes about synonymy.— Basilewsky (1954b: 80) listed *Diaphoroncus* Chaudoir, 1850 as a junior synonym of *Plagiopyga,* and cites as well earlier references to this subgenus.

Characteristics.— Basilewsky (1954b: 80-81) provided a useful characterization of adults of this subgenus, contrasting their character states with those of *Hystrichopus* (*sensu stricto*). To these we add: stylomore 2 of ovipositor with very short ensiform seta (Fig. 57), and hind wing with oblongum cell larger (Fig. 85A), wedge cell absent (Fig. 85B).

Notes about classification.— Ten species are included in this subgenus. Basilewsky (1954a) characterized them, but did not provide an infrageneric arrangement: the species are treated in the sequence in which their names appear in the key (pp. 83-85).

Notes about habitat.— Little information is available about this topic. As Basilewsky (1954a: 82) noted, testaceous body color and tendency for reduction in eye size exhibited by adults indicates that they avoid light. In fact, adults of some species have been collected from caves, rodents' nests, and from under larger rocks. However, the winged condition of adults indicates that dispersal by flight is normal, so that the species are not confined to subterranean situations.

Geographical distribution.— This subgenus is predominantly South African, with one species (*H. cyclogonus* Chaudoir) ranging as far north as Tanzania, and four species being known from Zaire, only.

Notes about phylogeny and zoogeography.— These topics have not been addressed previously, with reference to this subgenus. Without representative material of all species, we can only make suggestions about a line of investigation to pursue. Because of many shared similarities with members of the surface-dwelling *Pseudomasoreus* and *Hystrichopus,* one can assume that the ancestor of *Plagiopyga* must have been a surface-dweller, also, with average eyes, pectinate tarsal claws (Figs. 52 and 54), and darker color. Extant species whose adults are thus characterized are near the ancestral stock. Reduction of these features probably occurred in more derived stocks that had developed a more apotypic mode of existence. These considerations plus vicariant distribution patterns of species thought to be closely related should provide the clues necessary to reconstruct the phylogeny of the extant species of *Plagiopyga.*

Material examined.— Our observations are based on the following material, collected in South Africa.

H. (Plagiopyga) cymindoides Péringuey. Three females, - E. Cape Province, Congo Caves X.30.49 B. Malkin (CAS). Three males, female; Stormsriver, W. Humansdorp, 2403415, 4-10.XII. 1981, 525 Peck (from a cave).

H. (*Plagiopyga*) *chaudoiri* Basilewsky. Female, Queenstown E. T. Wells 1902-19 (BMNH). Female, Natal Estcourt G. A. K. Marshall 1917-55 (BMNH).

Subtribe CALLEIDINA

We include here two groups of nominal genera that were originally assigned to the Cymindina: *Anomotarus* assemblage– *Anomotarus* Chaudoir, *Lithostrotus* Blackburn, *Dromiotes* Jeannel, and *Cephalotarus* Mateu; and the *Trigonothops* assemblage– *Trigonothops* Macleay, *Phloeocarabus* Macleay, and *Diabaticus* Bates. We add to the latter assemblage *Speotarus* Moore.

By including *Anomotarus* in the Calleidina, we declare the latter name and Anomotarina synonymous. Calleidina is the older name, and is thus valid for this group.

Habu (1967: 117), who established the subtribe Anomotarina, recognized a close relationship of the single included genus with the calleidines, citing as evidence similarity in form of mandibles and female genitalia. Terrestrial modifications of tarsi of adult *Anomotarus* satisfied Habu that this genus should not be included in the Calleidina. However, adults of some calleidine taxa are basically terrestrial, and do not have structurally generalized tarsi that one might expect. We conclude that either tarsi modified for climbing were part of the ground plan of the Calleidina, and were relatively recently lost from some (but not all) groups that became terrestrial secondarily, or that arboreal modifications occurred after calleidines had evolved, and thus were not part of the ground plan. This argument is basic for combining anomotarines and calleidines in a single subtribe.

Recognition.— The following features are diagnostic: labrum transverse; without suborbital setae; right mandible with broad, edentate retinacular ridge; maxilla with lacinia and galea sparsely setose; mentum toothed; elytron with umbilical setigerous punctures in continuous line, penultimate puncture not displaced laterally; tarsomeres broad, apical margin of tarsomere 4

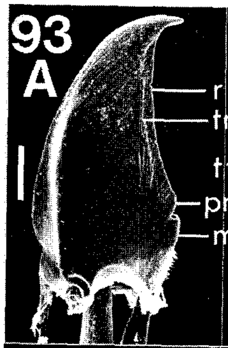
89

90

91

92

Figs. 89–92. Photographs of Calleidina.—Habitus, dorsal aspect, of specimens of *Trigonothops*: 89, *T. (Diabaticus) australis* (Erichson) (SBL=10.29 mm); 90, *T. (Diabaticus) pauper* (Blackburn) (SBL=6.89 mm); 91, *T. (Abaditicus) collaris* (Blackburn) (SBL=7.88 mm); 92, *T. (Abaditicus) meyeri*, new species (SBL=7.88 mm).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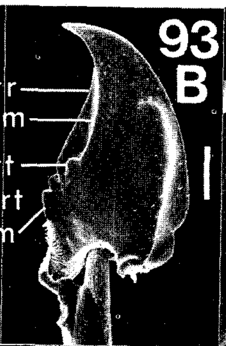
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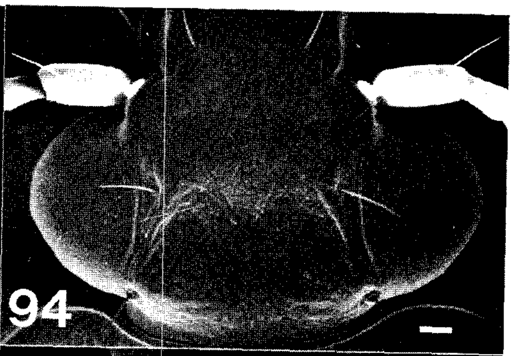
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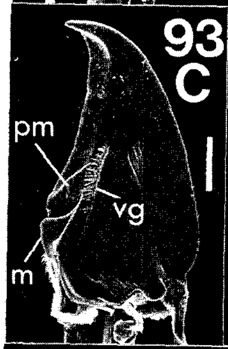
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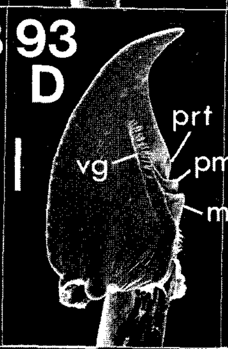
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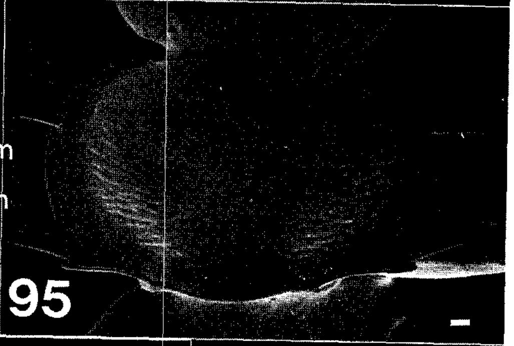
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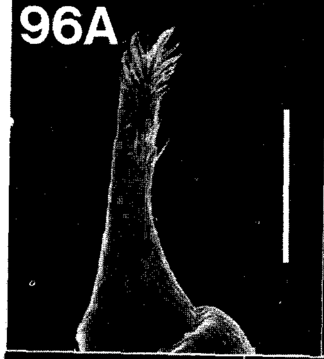
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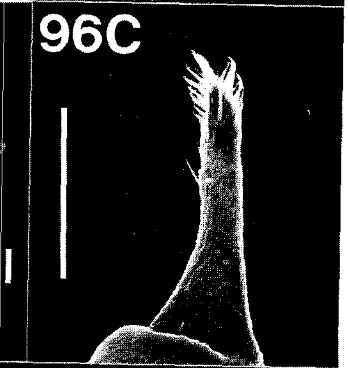
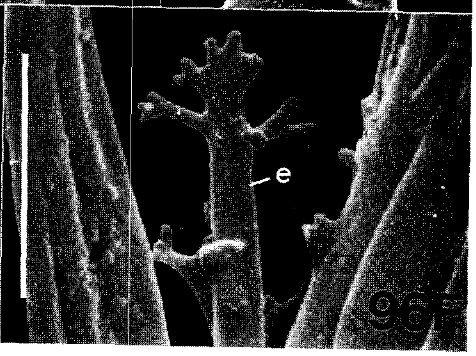
96B

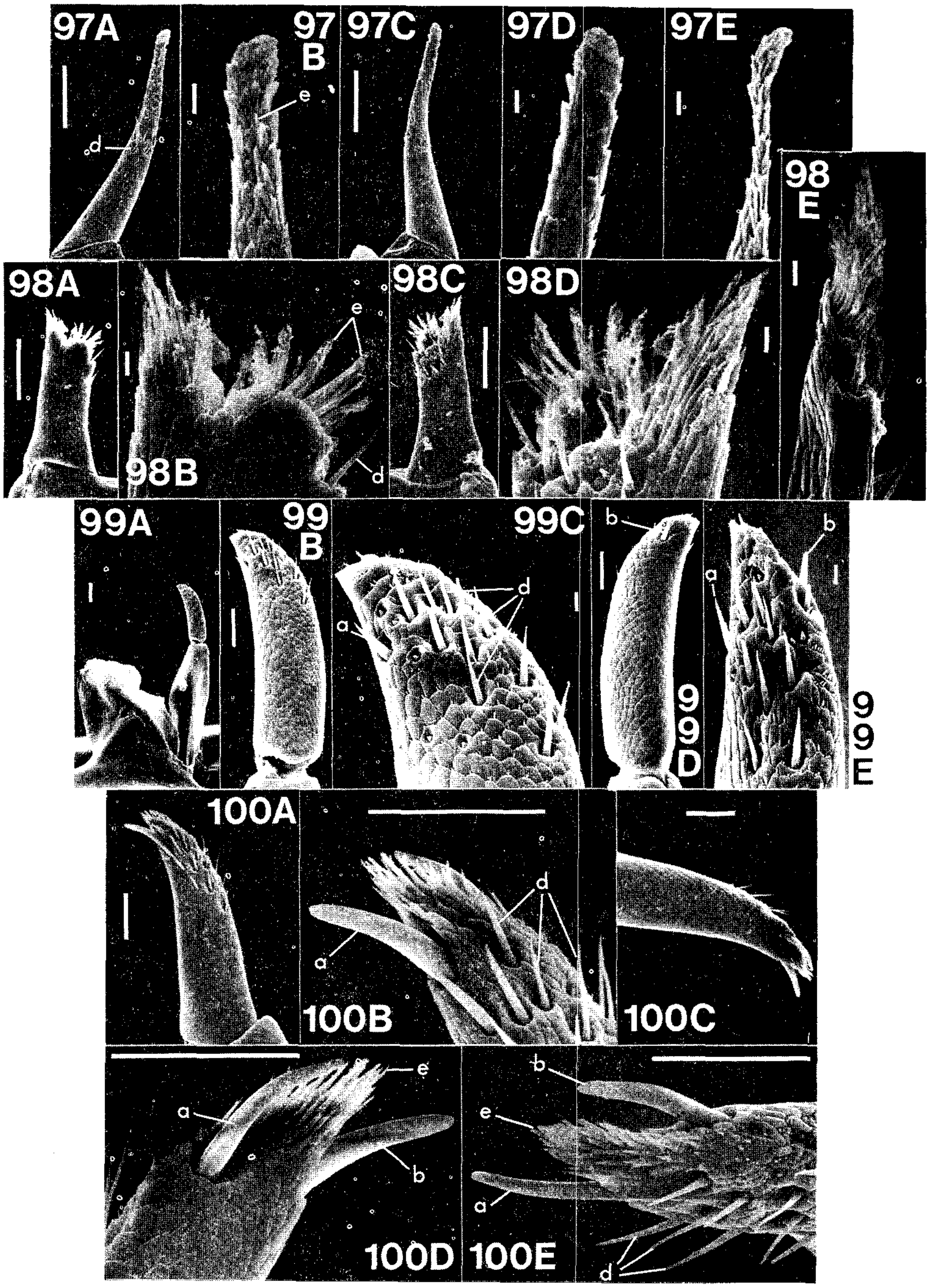

96C


96 D

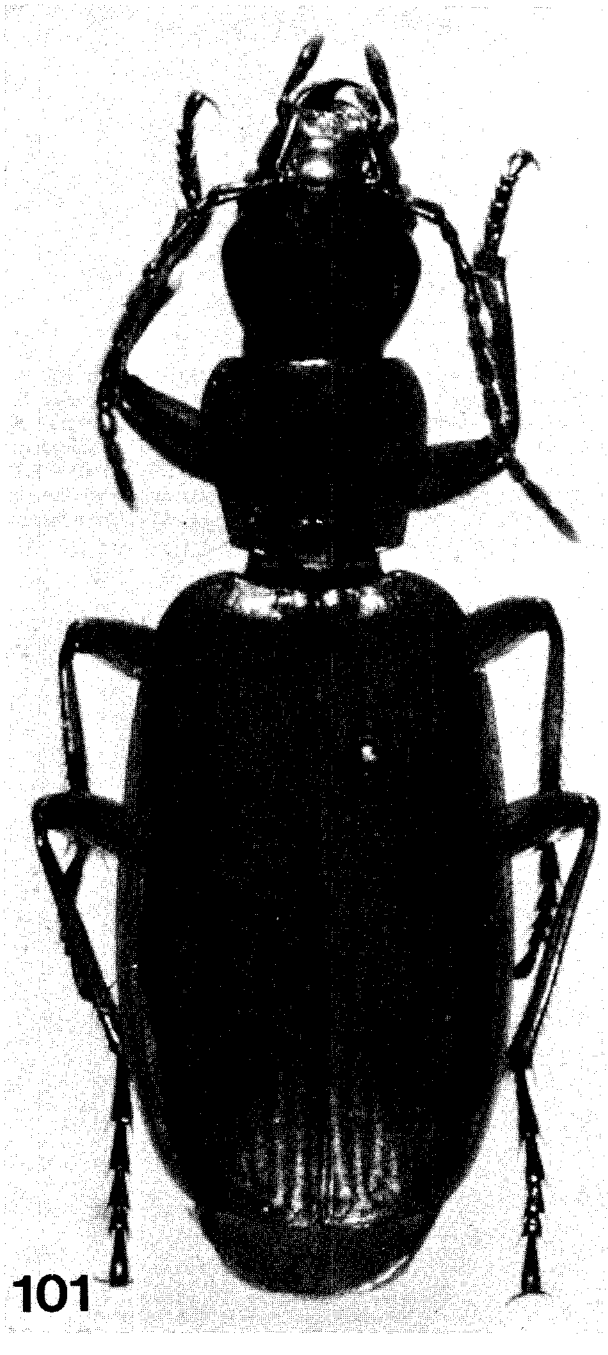

96 E


96F

Figs. 93–96. SEM photographs of structures of Calleidina, genus *Trigonothops*.—Fig. 93: *T. (Diabaticus) pauper* Blackburn, mandibles–A and C, left, dorsal and ventral aspects, respectively; B and D, right, dorsal and ventral apical aspects respectively. Figs 94 and 95: *T. (Phloeocarabus) nigricollis* MacLeay, head and pronotum, respectively, dorsal aspect. Fig. 96: *T. (sensu stricto) longiplaga* Chaudoir, left stylomere 2–A, B–lateral aspect; C, D–medial aspect; E–ventral aspect; F–apical branched seta. Scale bars: 93A–96A, and 96C = 100 μm, 96B, D, E, F = 5 μm. Legend, features of mandibles: m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tt, terebral tooth; vg, ventral groove. Legend, stylomere 2: e, branched seta.


97A
d
97 B
e
97C
97D
97E
98 E
98A
98B
e
d
98C
98D
99A
99 B
99C
a
d
b
99 D
a
b
99 E
100A
a
d
100B
100C
a
e
b
100D
b
e
a
d
100E

Figs. 97–100. SEM photographs of structures of Calleidina, genus *Trigonothops*.—Ovipositors, left stylomeres. Figs. 97 and 98, *T. (Phloeocarabus) nigricollis* Blackburn and *T. (Abaditicus) meyeri*, new species, respectively, stylomere 2: A, B, C, D, and E, lateral, lateral (apical portion); medial, medial (apical portion), and ventral aspect respectively. Fig. 99, *T. (Diabaticus) australis* Erichson: A, valvifer, and stylomeres 1 and 2, lateral aspect; B–E, stylomere 2—B, lateral aspect; C, lateral aspect, apical portion; D, medial aspect; E, ventral aspect. Fig. 100, *T. (Diabaticus) pauper* (Blackburn): A, B, C, D, and E, lateral (apical portion), medial aspect, medial (apical portion), and apico-ventral aspect, respectively. Scale bars: 97A–C, 98A-C, 99B, D, and 100 A–E=50 μm; 97B, D, E, 98B, D, E, and 99C and E=5 μm. Legend: a, lateral ensiform seta; b, medial ensiform seta; d, ventral setae; e, branched apical seta.

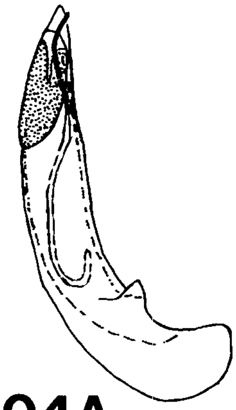

101


102C
102B
102A

Figs. 101–102. Photographs of Calleidina, *Trigonothops (Speotarus) lucifuga* (Moore).—Fig. 101: habitus, dorsal aspect (SBL=6.98 mm.). Fig. 102: ovipositor, left stylomere 2—A, lateral aspect; B, lateral aspect, apical portion; C, apico-ventral aspect. Scale bars=50 um.

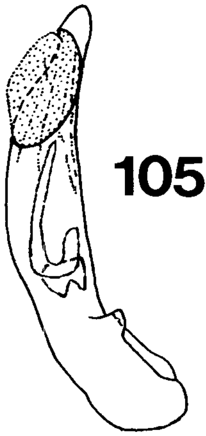
103A

103B



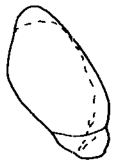
104A

104B



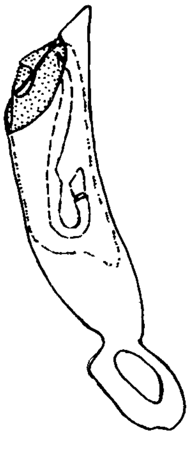
105A

105B

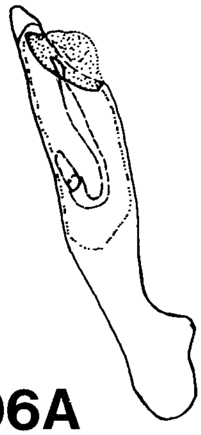


105C

105D



106A

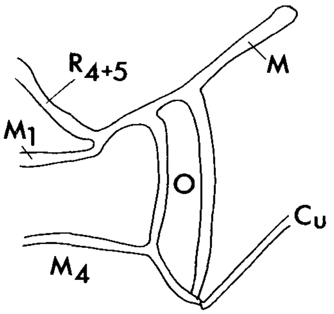


106B

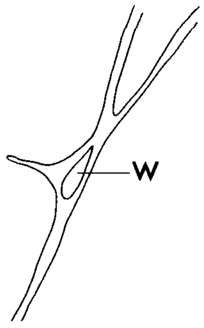
106C

106D

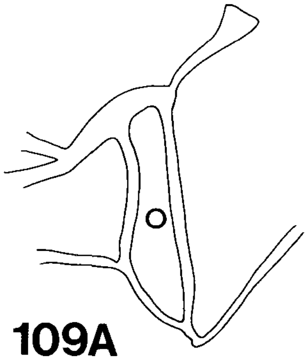
Figs. 103–106. Line drawings of Calleidina, genus *Trigonothops*.—Male genitalia—A and B, median lobe, left lateral and ventral (106B, dorsal) aspects, respectively; C and D, left and right parameres, respectively, ventral aspect, of: 103, *T. (sensu stricto) longiplaga* Chaudoir; 104, *T. (Phloeocarabus) nigricollis* Blackburn; 105, *T. (Abaditicus) meyeri*, new species; 106, *T. (Speotarus) lucifuga* (Moore).



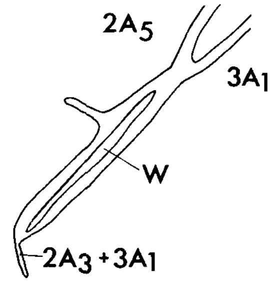
107A



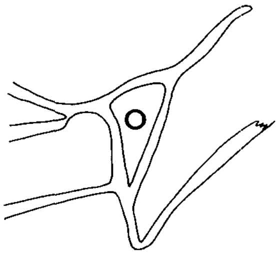
108B



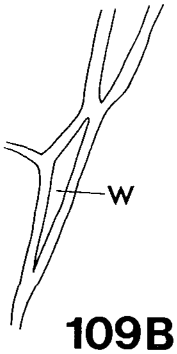
109A



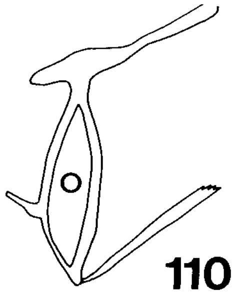
107B



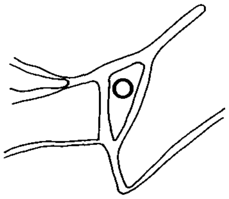
108A



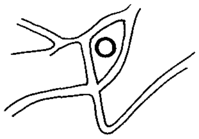
109B



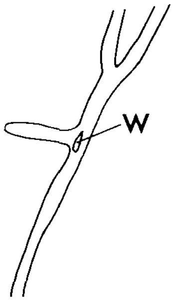
110A



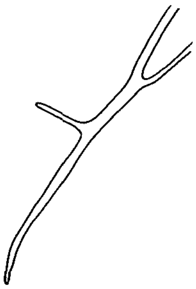
111A



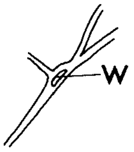
112A



110B



111B



112B

1mm

Figs. 107–112. Line drawings of Calleidina.--Wing cells and associated veins--A, oblongum cell, B, wedge cell, respectively, of: 107, *Trigonothops (sensu stricto) longiplaga* Chaudoir; 108, *Anomotarus (sensu stricto) crudelis* Newman; 109, *T. (Phloeocarabus) nigricollis* Blackburn; 110, *T. (Speotarus) lucifuga* (Moore); 111, *Anomotarus (sensu stricto) stigmula* Chaudoir; 112, *A. (Dromiotes) maculipennis* Mateu. Legend: cells-O, oblongum; W, wedge. Veins--A, anals; Cu, Cubitals; M, Media; R. Radius.

sub-truncate or moderately to deeply notched; median lobe of male genitalia with apical orifice hemiopic, on left and ventral side; ovipositor with stylomere 1 glabrous, stylomere 2 approximately cylindrical, tapered, ensiform setae short or absent; apical or preapical portion more or less setose; nematoid setae present or absent.

The *Trigonothops* assemblage

Figs. 89-92

It is easy to see why *Phloeocarabus* ± and *Diabaticus* were included in the cymindines: tarsi, though moderately broad, are not markedly so, and tarsomere 4 is only notched, without well developed lobes and pads of specialized setae. The tarsi of *Trigonothops* adults are clearly different from those of cymindines, but in other features this group and the former two seem quite close to one another.

It is also easy to see why Moore (1964: 73) placed *Speotarus* (Fig. 101) near *Anomotarus*: in external features, adults of the two groups look much alike. However, the stout tarsi of described *Speotarus* adults suggest a calleidine affinity, and this is borne out by structure of the male genitalia and stylomeres of the ovipositor.

Adults of the four calleidine groups of the *Trigonothops* assemblage exhibit so much similarity to one another that they are here included in a single genus. Furthermore, these groups are confined to the same zoogeographic area, the Australian Region, and this provides additional evidence for inferring close relationship. Additional details are provided below.

Trigonothops MacLeay

Trigonothops MacLeay, 1864: 110. GENERITYPE: *Calleida pacifica* Erichson: 1842: 124 (original designation).– Chaudoir, 1877: 221.– Sloane, 1898: 493. 1920: 170.– Csiki, 1932: 1488.– Darlington, 1968: 184.

Phloeocarabus MacLeay, 1871: 85. GENERITYPE: *Phloeocarabus mastersi* MacLeay, 1871: 85 (monotypy).– Sloane, 1898: 494- 499.– Blackburn, 1901: 112.– Csiki, 1932: 1488.- Darlington, 1968: 183- 184 NEW SYNONYMY.

Notoxena Chaudoir, 1877: 226. GENERITYPE: *Trigonothops nigricollis* MacLeay, 1864: 111 (monotypy).– Sloane, 1898: 499.– Darlington, 1968: 183- 184.

Diabaticus Bates, 1878: 324. GENERITYPE: *Plochionus australis* Erichson, 1842: 124 (monotypy)– Csiki, 1932: 1489. NEW SYNONYMY.

Speotarus Moore, 1964: 71. GENERITYPE: *Speotarus lucifugus* Moore, 1964: 73 (original designation).- Matthews, 1980: 10. NEW SYNONYMY.

Abaditicus, new subgenus. GENERITYPE: *Diabaticus collaris* Blackburn, 1901: 111 (here designated).

Notes about classification.— Inclusion of these taxa in a single genus makes the latter difficult to define in terms of external features. However, we feel confident that this assemblage is monophyletic, and we feel that it is more important to emphasize relationships inferred from complex internal structures than to emphasize differences, which, though easily perceived, seem of less importance. Attention is thus drawn to an underlying unity, and we hope that this will stimulate future workers on Australian carabids to undertake study of the group as a whole.

To draw attention to divergence within *Trigonothops*, we recognize four previously named assemblages as subgenera: *Trigonothops (sensu stricto)*, *Phloeocarabus*, *Diabaticus*, and *Speotarus*. However, the nominal genus *Diabaticus* seems to be paraphyletic, including two species that are less closely related to its type, *D. australis* Erichson, than to other group of *Trigonothops*. Therefore, we erect a fifth subgenus, *Abaditicus*, no previously published names being available.

The generitype of *Notoxena* Chaudoir is included in *Phloeocarabus* ±. Chaudoir (1877: 226), when he described *Notoxena,* did not cite MacLeay (1871). Hence, he must have been unaware that a genus had already been proposed that would include *T. nigricollis.*

Descriptive notes.— To the characterization of *Trigonothops* by Darlington (1968: 183), we add the following. Adults with eyes large, prominently bulged, temples small (Fig. 94), or only slightly convex, with temples well developed (Fig. 101). Tarsomere 4 notched or bilobed; tarsal claws pectinate or smooth. Male genitalia with median lobe hemiopic, internal sac with large flagellum- like sclerite (Figs. 103-106). Ovipositor with stylomere 1 asetose, stylomere 2 cylindrical, ensiform setae two or absent, ventral surface setose; apical portion extended and attenuate (Figs. 97A, C) or not (Figs. 98A, C).

Way of life.— Adults of *Trigonothops (sensu stricto), Phloeocarabus,* ± and *Abaditicus* are arboreal. We do not know where adults of *Diabaticus* live, but we assume that they spend at least part of their lives on trees. Adults of *Speotarus* are known only from caves.

Evolutionary trends.— If, as we believe, calleidines are basically arboreal, then the arboreal groups of *Trigonothops* are likely to be closer to the ancestral stock of the genus, with the cave-inhabiting *Speotarus* being the more remote. If this is correct, the smooth tarsal claws and rather flattened eyes of adults of *Speotarus* are probably apotypic, denticles having been lost from the ancestral stock of this subgenus, and the compound eyes reduced.

Key to Subgenera of *Trigonothops*

1 (0) Tarsal claws smooth; eyes slightly convex, temples large (Fig. 101); pronotum with narrow lateral grooves, only slightly transverse (Fig.101) .... *Speotarus* Moore, p. 191

1′ Tarsal claws pectinate; eyes markedly convex and bulged, temples small (Figs. 89-92, and 94); pronotum with wider lateral grooves, more transverse (Figs. 89-92, and 95) 2

2 (1′) Tarsomere 4 cleft apically, with pair of large lobes, ventrally with modified setae .... *Trigonothops (sensu stricto)*, p. 188

2′ Tarsomere 4 notched apically, lobes short, without modified vestiture ventrally . 3

3 (2′) Head with pair of distinct longitudinally directed lateral ridges, especially prominent between supraorbital setigerous punctures, and extended to posterior pair (Fig. 94); eyes very large, entire lateral area of head occupied; pronotum very broad, basal margin distinctly lobed (Fig. 95) .... *Phloeocarabus* MacLeay, p. 188

3′ Head without longitudinally directed ridges, or these shorter, not extended to posterior pair of supraorbital setigerous punctures; temples short, eyes average in size (Figs. 89-92), though prominent; pronotum narrower, more elongate, basal margin convex, but not distinctly lobed 4

4 (3′) Head sharply constricted posteriorly, in form of neck (Figs. 91, 92); elytron with microsculpture meshes isodiametric, not transverse .... *Abaditicus,* new subgenus, p. 189

4′ Head not sharply constricted in form of neck (Figs. 89, 90); elytron with microsculpture meshes transverse .... *Diabaticus* Bates, p. 188

Subgenus *Trigonothops (sensu stricto)*, NEW STATUS
Figs. 96A-F, 103A-B and 107A-B

Descriptive notes.— To Darlington's (1968: 184-185) characterization of this taxon, we add the following, based on study of 12 specimens (CAS) of two species, from various localities in Queensland and New South Wales. Hind wing with average oblongum cell, and wedge cell long, narrow (Figs. 107A, B) or both cells reduced (Figs. 108A, B). The basal portion of the flagellar sclerite of the internal sac is almost as long as the main part (Figs. 103A, B), that is, this structure is relatively short. Stylomere 2 of the ovipositor is as follows: form as in Figs. 96A, C, base broad, tapered markedly about half length, then paralled-sided; apex blunt; microsculpture with meshes distinct at base, isodiametric, each scale with acuminate tip; in apical 0.50, meshes elongate microlines shallow; apical 0.33 with few spines (Figs. 96D, E), one large ensiform seta dorso-laterally (Fig. 96D), and apical 0.20 with branched (Figs. 96B and F) and unbranched long setae extended from microscales.

Subgenus *Phloeocarabus* MacLeay NEW STATUS
Figs. 94, 95, 97A-E, 104A-B, and 109A-B

±

Descriptive notes.— To Darlington's (1968: 183) characterization of this taxon, we add the following, based on examination of his series of *T. nigricollis*, from various localities in New Guinea and Australia. Wing with cells large (Figs. 109A, B). The internal sac of the male genitalia contains a large reverse "J" shaped sclerite (Figs. 104A, B). Stylomere 2 of the ovipositor as in Figs. 97A-E, elongate, tapered gradually to narrow apex; microsculpture rather irregular, microlines fine, meshes isodiametric basally, elongate apically, (Figs. 97B, C); few setae mainly on lateral and dorsal surfaces, about half way between base and apex, without ensiform setae; short seta-like projections extended from microscales in apical 0.20 (Figs. 97B, D, and E).

Subgenus *Diabaticus* Bates, NEW STATUS
Figs. 89, 90, 93A-D, 99A-E and 100D-E

Having had the opportunity to see specimens of the three described species that were previously included, and of a fourth related but undescribed species, and having reached the conclusion that two subgenera are represented rather than one, it seems appropriate to offer a more extended analysis of this complex.

Structures that seem best to show relationships in *Trigonothops* are male genitalia and ovipositor. Unfortunately, we have both males and females of only one species of the *Diabaticus* complex, *T. meyeri,* new species. *T. australis* (Erichson) and *T. pauper* (Blackburn) are represented by females, only; and *T. collaris,* by a single male. However, because of the general pattern that we perceive, we feel certain that the missing pieces of evidence will fit in, when they are eventually found.

Stylomere 2 of ovipositors of *T. australis* (Fig. 99) and *T. pauper* (Fig. 100) is markedly different in form and sculpture from stylomere 2 of a *T. meyeri* female (Fig. 98). The latter stylomere is more like that of *Trigonothops (sensu stricto)* and *Phloeocarabus females. We think it likely that T. australis* and *T. pauper* females exhibit the plesiotypic form, and that the other forms are apotypic.

With *T. meyeri,* we group *T. collaris* Blackburn because of striking similarities in the genitalia and in form of head.

Descriptive notes.— Form as in Figs 89 and 90.

Color: body piceous, appendages rufous, elytra concolorous. Microsculpture and luster: dorsum of head (including labrum and clypeus) with meshes isodiametric, surface dull; pronotum with meshes transverse, surface shining, but not iridescent; lateral and ventral thoracic sclerites (including mesepisterna) with meshes transverse; abdominal sterna with meshes transverse, surface iridescent; scutellum with meshes isodiametric. Dorsal surface glabrous (except standard fixed setae), or sparsely setose. Pronotum subcordate, sides sinuate posteriorly, margins broadly curved upward; posterior angles approximately right. Ovipositor: stylomere 2 as in Figs. 99 and 100, blade-like, apical 0.33 straight (Fig. 99C), or slightly twisted (Fig. 100E); microsculpture predominantly of isodiametric meshes (Figs. 99D-E), elongate on apico-medial surface of *D. pauper* (Fig. 100D), lines deep, each scale with acuminate tip; apico-dorsal 0.33 with 15-20 trichoid setae, two ensiform setae pre-apically, one lateral, one medial, short (Fig. 99E), or longer (Fig. 100E); apex with (Figs. 100D, E) or without (Figs. 99C, E) fine setae extended from microscales.

Geographical distribution.— This subgenus is known from Tasmania and southeastern Australia, only.

Key to Species of Subgenus *Diabaticus*

1 (0) Dorsum of body and dorsal surfaces of tarsomeres generally punctate and setose; metepisternum short, with anterior and lateral margins subequal .... *T. (Diabaticus) pauper*, Blackburn, p. 189

1′ Dorsum of body and dorsal surfaces of tarsomeres glabrous, generally impunctate; metepisternum long, lateral margin longer than width at anterior margin .... *T. (Diabaticus) australis* (Erickson), p. 189

Trigonothops (Diabaticus) australis (Erichson), NEW COMBINATION
Figs. 89 and 99A-E

Plochionus australis Erichson, 1842; 124.
Diabaticus australis; Bates, 1878: 324.– Blackburn, 1901: 17.– Csiki, 1932: 1489.

Descriptive notes.— Standardized Body Length of two females: 8.60 and 8.96 mm. Values for Vwm/Hw 0.59 and 0.62. Lateral margins of pronotum only slightly elevated; broad lateral grooves markedly narrowed near anterior setigerous punctures, these in bottom of lateral grooves, clearly removed from margin. Elytron with basal ridge complete, extended from humerus to suture, near scutellum.

Bates (1878: 325) noted the superficial similarity in body form between adults of this species and those of *Cymindis (Pinacodera) punctigera* (LeConte).

Specimens examined.— Two females (BMNH), both determined by T.G. Sloane: one labelled Hobart, 91-88 [ovipositor dissected]; the other, V D Ld 77- 19; 146 [abdomen lacking].

Trigonothops (Diabaticus) pauper (Blackburn), NEW COMBINATION
Figs. 90 and 100A-E

Diabaticus pauper Blackburn, 1901: 111. HOLOTYPE female, labelled: Tazm [red print] T; Type [circular label, ringed with red]; Blackburn Coll 1910- 236; Diabaticus pauper, Blackb. [handwritten] (BMNH).– Csiki; 1932: 1489.

Descriptive notes.— Form as in Fig. 90. Standardized Body Length (five females): 5.60-(6.17)- 6.76 mm. Range of values for ratio width of neck to width of head: 0.53-0.65. Dorsal surface of frons and pronotum laterally rugulose, and elytral striae deeper than in adults of *T. australis*. Pronotum more narrowed posteriorly, and lateral margins more elevated; lateral margins of elytra crenulate; humeri narrowed (associated with wing loss and reduction of metathorax), and marginal ridge terminated near base of interneur 4. Ovipositor with stylomere 2 as in Figs. 100A-E.

Geographical distribution.— This species is known from Tasmania, only.

Material examined.— In addition to the holotype, we have seen four females (BMNH): two labelled Franklin, Tasmania, 91- 88; and two labelled Hobart, 91- 88.

Abaditicus, new subgenus
Figs. 91, 92, 98A-E, and 105A-D

This taxon is established to include *Diabaticus collaris* (Blackburn) and *Trigonothops meyeri*, new species.

Derivation of subgeneric name.— This is an anagram of *Diabaticus,* the name of the group to which *T. collaris* was originally assigned.

Recognition.— The markedly constricted posterior part of the head (Figs. 91 and 92) is sufficient to distinguish adults from those of other subgenera of *Trigonothops.* Additionally, the basal ridge of the elytron is extended only to the base of interneur 3; females have stylomere 2 of the ovipositor short and stout and without ensiform setae (Fig. 98); and males have a moderately long sclerite (Fig. 105B) in the internal sac.

Descriptive notes.— Form as in Figs. 91 and 92.

Color: body and appendages rufous; elytra concolorous (rufous) or bicolored (Fig. 92). Microsculpture and luster: dorsum of head (including labrum and clypeus) with meshes isodiametric, surface dull; pronotum with meshes transverse, surface shining but not iridescent; most lateral and ventral thoracic sclerites with meshes transverse, mesepisternum with meshes isodiametric; abdominal sterna with meshes transverse, surface iridescent. Dorsal surface glabrous (except standard fixed setae). Pronotum subcordate, sides sinuate posteriorly, lateral margins broadly curves upward; posterior angles approximately right. Elytron with basal ridge terminated near base of interneur 3, not extended to sutural margin. Internal sac of male genitalia with large, reverse "J" -shaped sclerite (Fig. 105B).

Stylomere 2 of ovipositor as in Figs. 98A-E, short, broad, constricted slightly medially, broadened apically, apical margin very broad (Fig. 98B). Microsculpture meshes isodiametric or slightly elongate, microlines generally distinct, scales without acuminate tips. Apical 0.25 with setae on lateral and dorsal surface, but not on medial surface, without ensiform setae; apex with long setae extended from microscales.

Geographical distribution.— This subgenus is known from southeastern Australia (Victoria), only.

Relationships.— We believe *Abaditicus* is the primitive sister group of the subgenus *Phloeocarabus,* ± based on inferred transformation series in armature of the internal sac, and details of stylomere 2.

Key to Species of Subgenus *Abaditicus*

1 (0) Elytra concolorous, rufo-piceous .... *T. (Abaditicus) collaris* (Blackburn), p. 190

1′ Elytron sharply bicolored, most of surface piceous, with apex and extensive area of disc rufous (Fig. 92) .... *T. (Abaditicus) meyeri,* new species, p. 190

Trigonothops (Abaditicus) collaris (Blackburn), NEW COMBINATION
Fig. 91

Diabaticus collaris Blackburn, 1901: 111. HOLOTYPE male labelled: 6954 H. Wick [red print] T; Type [circular, ringed with red]; Blackburn coll 1910- 236; Diabaticus collaris Blackb. [handwritten] (BMNH).– Csiki, 1932: 1489.

Descriptive notes.— Form as in Fig. 91. Standardized Body Length 6.88 mm. Value for ratio width of neck to maximum width of head 0.49. Pronotum with lateral grooves broader than in adults of *T. australis,* and hardly narrowed anteriorly; anterior pair of setigerous punctures nearly marginal. Median lobe as in Fig. 105, internal sac with reverse "J"-shaped sclerite.

Material examined.— Holotype, only.

Trigonothops (Abaditicus) meyeri, new species
Figs. 92, 98A-E, and 105A-E

Type material.— HOLOTYPE male, labelled: Woodhouse Ck., Nunniong Plt. Vic. 16.5.66. P. Meyer; under bark of E. delegatensis (CSIRO). Three paratypes, from the same locality:

collected on May 16- female (CAS); collected on May 26- male (BMNH); female (MCZ).

Derivation of specific epithet.— From the surname of the collector, Peter A. Meyer, Heidelberg, Victoria, Australia, to whom the senior author is grateful for the gift of these and other specimens.

Recognition.— This is the only known species of *Abaditicus* whose adults have spotted elytra.

Description.— Character states of subgenus, and the following. Form as in Fig. 92. Standardized Body Length, males 6.9- 7.12 mm., females 6.88- 7.08 mm. Body form *Calleida*- like. Neck evident (W vertex min./Hw males 0.52-0.53, female 0.52. Hw/Pl- males, 0.87- 0.89, females, 0.86- 0.92; Pl/El- males, 0.300- 0.32, females 0.29- 0.30.

Color. Appendages and body except elytra rufous; elytron with following rufous– epipleura, lateral groove, apical 0.16, and irregular discal area from interval 2 to 6, extended to humerus on interval 5; following black– interval 1, in basal 0.84, triangular area near scutellum, transverse band in apical 0.33, and intervals 7- 9 throughout most of length.

Microsculpture. As described for subgenus. Surface slightly shining, pronotum more so than head or elytra.

Fixed setae. Average for Calleidina: both pairs of pronotal setae on lateral margins.

Head. Frons and anterior part of vertex depressed. Frontal impressions extended diagonally to anterior pair of supraorbital setigerous punctures. Eyes average for subgenus; occipital area markedly constricted. Mouthparts average, including mental tooth, axiniform ultimate labial palpomeres, and bisetose penultimate palpomeres.

Pronotum. Moderately transverse, anterior margin shallowly concave, posterior margin convex, but not clearly lobed; lateral margins distinctly to slightly sinuate; anterior angles broadly rounded, posterior angles about right; lateral margins elevated, more broadly so posteriorly; disc broad, only slightly convex medially; median longitudinal impression sharply delimited, extended from near anterior to near posterior margin; posterior-lateral impressions indistinct, shallow, broadly continuous with broad lateral grooves.

Elytra. Humeri broadly rounded, apical margin subtruncate; basal ridge terminated near base of interneur 3, not extended to parascutellar setigerous puncture; interneurs shallow, intervals hardly convex.

Male genitalia. As in Figs. 105A-D, average for Calleidina.

Ovipositor. Stylomere 2 as in Figs. 98A-E.

Notes about habitat.— According to the labels, specimens in the type series were collected under bark of a eucalyptus tree. Probably, then, this species is arboreal. Interestingly the color pattern of these specimens is like that of many arboreal Australian lebiines (for example, *Trigonothops longiplaga Chaudoir).* Darlington (1971: 250-251) suggested that mimicry might be involved as an explanation for similarity in color pattern exhibited by some tree trunk-inhabiting lebiines, though he did not refer specifically to the pattern characteristic of *T. meyeri.* This suggestion seems reasonable to us, and we extend it in terms of Müllerian mimicry, to the many groups of Australian lebiines that are colored like adults of *T. meyeri.* Erwin (1978 and 1979) discussed tests of defense mechanisms that showed them to be powerful for adults of *Agra* and other lebiines. This is supporting evidence that this group of insects has the necessary equipment to form the basis for development of complexes of protected mimics.

Geographical distribution.— This species is known only from the type locality, which is in the general range of the previously described species of *Abaditicus.*

Phylogenetic relationships.— Adults of this species share with those of *T. collaris* a head with constricted occipital area, and elytra with basal ridges incomplete. These synapotypic features satisfy us that these two species are more closely related to one another than to the other known species of *Trigonothops.*

Subgenus *Speotarus* Moore, new status
Figs. 101, 102A-C, 106A-D, and 110A-B

Descriptive notes.— The following details are added to the original description of *Speotarus* (Moore, 1964: 91). These notes are based on two specimens of *T. lucifugus* Moore, 1964: male, Cocklebiddy Cave, Eucla Basin, S. Australia, bat piles 12.1.66, J. Lowrey; female, bat cave, Naracoorte, 9 Mar, 1963, E. Hamilton-Smith.

Habitus as in Fig. 101. Standardized Body Length, male 6.86 mm., female, 7.06 mm.

Microsculpture. Dorsum of clypeus and anterior part of frons smooth, microlines not evident, vertex with meshes isodiametric, microlines shallow; thoracic and abdominal sclerites, and elytra with meshes transverse. Surface generally shining, especially head.

Head. Eyes though extensive in area, only slightly convex, not protuberant (Fig. 101).

Pronotum. Narrow, slightly transverse, lateral grooves narrower than in *Trigonothops (sensu stricto)* adults.

Legs. Anterior and middle femora with more setae than usual, posterior face of middle femur with more than 12 setae.

Wings. Completely developed, not reduced. Oblongum cell fusiform (Fig. 110A), wedge cell very small (Fig. 110B).

Median lobe of male genitalia hemiopic, apical orifice to left and ventrad (Figs. 106A, B). Internal sac with reverse "J"-shaped sclerite, and small sclerite. Parameres as in Figs. 106C, D.

Ovipositor (Figs. 102A-C). Stylomere 1 asetose. Stylomere 2 elongate, apical portion tapered, preapically with pair of ensiform setae (one lateral, one medial), and several trichoid setae on ventral surface. Microsculpture with sculpticells elongate, each with small spine directed apically; microsculpture otherwise simple.

Notes about way of life.— Also included in subgenus *Speotarus* is a second species, *T. princeps* (Moore, 1964). Both species are known only from caves. Although pale color of integument and rather reduced eyes are cavernicolous adaptations, the normally proportioned metathorax and rather long wings of *Speotarus* adults suggest that they are not troglobitic. Moore (*in litt.*) advised us: "the species are undoubtedly troglophiles (guanophiles) and are plentiful in certain caves, notably on the Nullarbor Plain, where there are no trees and no surface litter." Further, he stated that the beetles have not been found in the course of extensive surveys of the litter-fauna, in southern Australia. This counters our first thought that habitus of the beetles suggests adaptation to life in deep litter.

Moore (personal communication) advises us that additional specimens of *Speotarus* have been found in additional caves. These beetles exhibit some differences from the previously described species, and may represent undescribed taxa.

Evolutionary considerations.— In the letter cited above, Moore advanced an hypothesis to explain the cave-inhabiting way of life of a stock that might have been arboreal. He suggested that the extant species of *Speotarus* were derived from tree-dwelling calleidines that took up life in tree-roosting bat colonies, and became adapted to living in association with guano. It would be but a rather short evolutionary step from that stage to life in caves inhabited by bats. As he noted, support for this hypothesis would come from discovery of *Speotarus* specimens in association with arboreal bats. We think that Dr. Moore's idea has merit, and hope that he succeeds in his quest for confirmatory evidence.

The *Anomotarus* assemblage

For reasons stated below, we combine the named genera of this complex in a single genus, *Anomotarus* Chaudoir. Further, we have considered seriously the possibility of a close relationship between *Anomotarus (sensu lato)* and *Trigonothops (sensu lato)*. However, we were unable to identify synapotypic features to support this alliance.

Anomotarus Chaudoir

Figs. 108A, B, and 113-117

Anomotarus Chaudoir, 1875: 48. GENERITYPE: *Anomotarus olivaceus* Chaudoir, 1875: 48 (monotypy).– Sloane, 1898: 494.– 1917: 435.– 1920: 170.– Csiki, 1932: 1492- 1493.– Jedlička, 1963: 300, 450.– Moore, 1964: 73.– Habu, 1967: 118- 121.– Darlington, 1968: 186- 191.– Mateu, 1970b: 148.– 1972: 44.– Moore, 1967a: 183- 184.

Uvea Fauvel, 1881: CXVIII. GENERITYPE: *Cymindis stigmula* Chaudoir, 1852: 57 (monotypy).

Nototarus Chaudoir, 1875: 19. GENERITYPE: *Nototarus australis* Chaudoir, 1875: 19 (monotypy).– Sloane, 1898: 494.– Csiki, 1932: 1492.– Moore, 1963: 442.– 1967b: 442-445.– Darlington, 1968: 185- 186. NEW SYNONYMY.

Lithostrotus Blackburn, 1894: 200. GENERITYPE: *L. coerulescens* Blackburn, 1894: 200 (monotypy).– Sloane, 1898: 494.– Csiki, 1932: 1492. NEW SYNONYMY.

Lestianthus Sloane, 1894: 451. GENERITYPE: *Lestianthus sculpturatus* Sloane, 1894: 452 (monotypy) (=*Lithostrotus coerulescens* Blackburn).

Dromiotes Jeannel, 1949: 914. GENERITYPE: *Lebia stigmula* Fairmaire, 1901: 126 (=*A. jeanneli* Mateu, 1972: 47, not *A. stigmula* Chaudoir, 1852: 57) (original designation).– Mateu, 1972: 44.

Cephalotarus Mateu, 1970b: 150. GENERITYPE: *Cephalotarus maculipennis* Mateu, 1970b: 151 (monotypy).– 1972: 46.

Notes about names and classification.— By inclusion in *Anomotarus* of *Dromiotes,* the type species of the latter (*Lebia stigmula* Fairmaire, 1901) becomes a secondary junior homonym of *A. (sensu stricto) stigmula* (Chaudoir, 1852). For the name *L. stigmula* Fairmaire, therefore, Mateu (1972: 94) proposed the new name *Anomotarus (Dromiotes) jeanneli.* Character states diagnostic for these taxa seem too slight and too few to warrant ranking as genera. Thus, we think it best to include all of the species in a single genus. However, we also think it desirable to indicate the pattern of divergence in the genus by recognition of three subgenera: *Dromiotes* Jeannel; *Anomotarus (sensu stricto)*; and *Nototarus* Chaudoir (including *Lithostrotus* Blackburn).

Justification of synonymy of *Nototarus* and *Lithostrotus* is required. Distinctive features of adults of *Lithostrotus* are: dorsal integument metallic blue, surface densely, coarsely punctate (Fig. 113), and setose, with microsculpture generally effaced; eyes small, temples large; Pronotum (Fig. 113) with very sharp posterior angles and sharply defined basal lobe. Our material of *Nototarus* includes adults of eight species (mostly unnamed). None exhibit metallic color, but two have a pattern of punctation similar to that of *Lithostrotus,* with the pronotum similar in form, and eyes similarly reduced. Adults of two species are less coarsely punctate, and are glabrous; the others are impunctate, and have rather larger eyes. In brief, the differences are bridged between the *Lithostrotus* adults and those of the more typical *Nototarus* species. Thus, a transformation series seems to be indicated, with one end represented by *Lithostrotus.* It will no doubt be desirable to recognize species groups, in conjunction with revision of the species of this subgenus.

Key to Subgenera of *Anomotarus (sensu lato)*

1 (0) Mentum toothed. Metepisternum elongate, lateral margin longer than width at anterior margin. Elytron with microsculpture meshes more or less transverse. Eyes large. Internal sac with or without sclerite. Stylomere 2 of ovipositor with sculpticells flat (Figs. 114 and 115) 2

1′ Mentum edentate. Metepisternum short, lateral and anterior margins subequal. Wings reduced. Elytron without microlines, or meshes transverse. Eyes reduced, though head large. Internal sac with large sclerite. Stylomere 2 of ovipositor with surface rugose, sculpticells raised as keels; pair of long slender, curved setae near apex (Fig. 116D) or not (Fig. 117D) .... Subgenus *Nototarus* Chaudoir.

2 (1′) Wing with oblongum cell broad (Fig. 112A), wedge cell small (Fig. 112B). Internal sac of male with well developed sclerites, flagellum-like or not. Stylomere 2 without long, curved setae (Figs. 115A-E). Species Afrotropical .. .. Subgenus *Dromiotes* Jeannel.

2′ Wing with oblongum cell narrow, wedge cell absent (Figs. 111A, B); or small (Fig. 108B). Internal sac without sclerites. Stylomere 2 of ovipositor with long, slender, curved setae (Figs. 114B and D). Species Oriental or Australian .... *Anomotarus (sensu stricto).*

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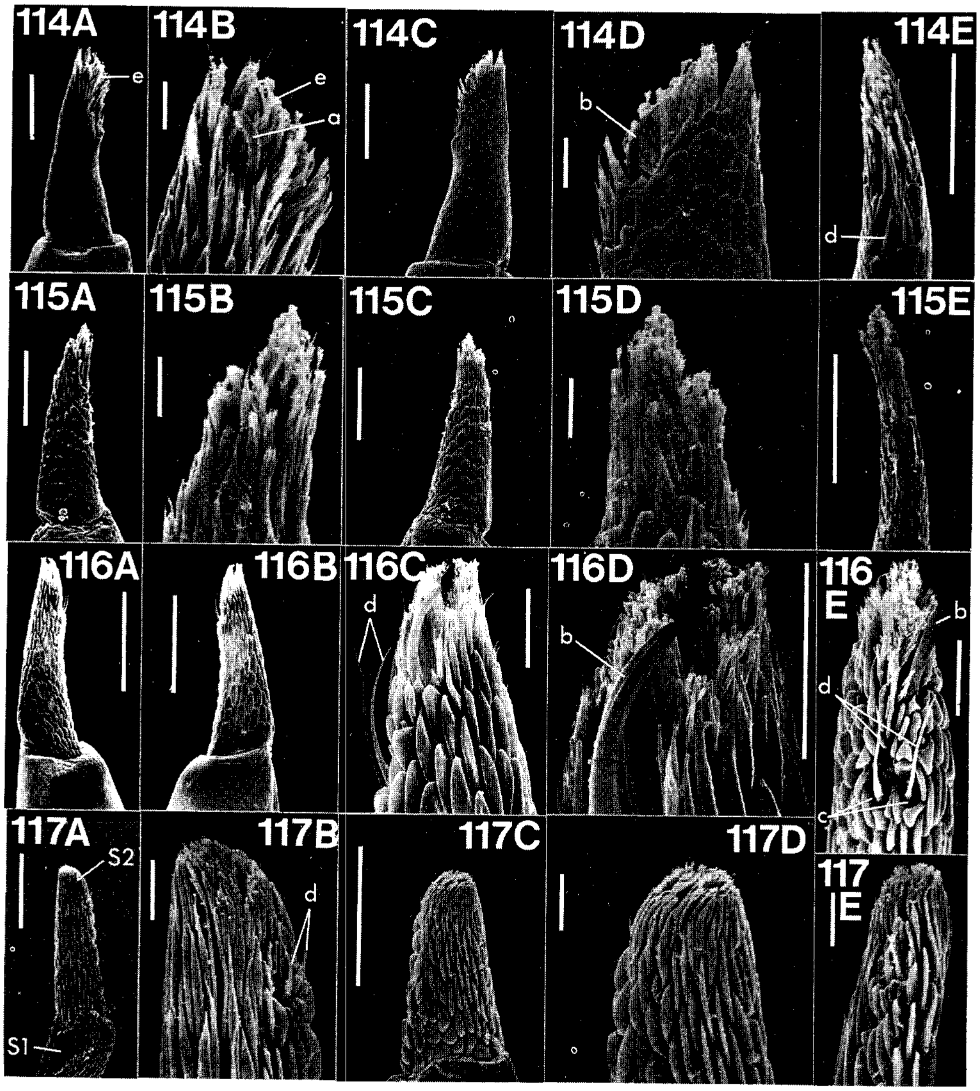
Fig. 113. Photograph of Calleidina.— *Anomotarus (Nototarus) coerulescens* (Blackburn), habitus, dorsal aspect (SBL=4.89 mm.).



Figs. 114–117. SEM photographs of Calleidina, genus *Anomotarus*.—Ovipositors, left stylomeres 1 and 2, or 2, only, A, B, C, D, and E—lateral, lateral (apical portion), medial, medial (apical portion), and apico-ventral aspects, respectively, of: 114, *A. (sensu stricto) stigmula* Chaudoir; 115 *A. (Dromiotes) maculipennis* Mateu; 116, *A. (Nototarus) coerulescens* (Blackburn); 117, *A. (N.) tumidiceps* (Blackburn). Scale bars: 114A, C, E, 115A, C, E, 116A, B, and 117A, C=50 μm; 114B, D, 115B, D, 116C, D, E, and 117B, D, E=10 μm. Legend: a, lateral ensiform seta; b, medial ensiform seta; c, sensory furrow; d, nematoid setae; e, branched apical seta; Sl, stylomere 1; S2, stylomere 2.

Darlington (1968: 185-187) provided useful descriptions of *Anomotarus* and *Nototarus,* to which we add that species with brachypterous members and with mental tooth probably belong to *Anomotarus (sensu stricto).* Hence, both of these subgenera have brachypterous members. Moore (1964: 73) suggested that it may be necessary to erect a new genus to include several species that seem to have adult characteristics similar to those of *A. tumidiceps* Blackburn.

The seeming scarcity of specimens of *A. coerulescens* makes it desirable to have a detailed account available, for the benefit of workers on Australian carabids.

Anomotarus (Nototarus) coerulescens Blackburn, NEW COMBINATION
Figs. 113, and 116A-E

Lithostrotus coerulescens Blackburn, 1894: 200. HOLOTYPE female, labelled: 5274 Vict [red print] T; Type [circular, ringed with red]; Blackburn coll 1910- 236; Lithostrotus coerulescens Blackb [handwritten] (BMNH).

Lestianthus sculpturatus Sloane, 1894: 451 (type not seen).– 1898: 494.

Lithostrotus planior Blackburn, 362. HOLOTYPE female, labelled: B7 MCS 7755 [red print] T; Type HT [circular, ringed with red]; Australia Blackburn coll BM 1910- 236; Lithostrotus latior Blackb [handwritten]; This must be the type of *planior*. The name latior was evidently written in error. No such name as *latior* has been published. A.M. Lea 6/9/12 [handwritten] (BMNH). TYPE LOCALITY: Australia New South Wales, Blue Mountains, 3000 feet.- - Lea, 1912: xxviii. NEW SYNONYMY.

Notes about synonymy.— We have seen the above-listed holotypes. They are so similar to one another that it seems they must be conspecific, and we regard them as such.

Recognition.— The following combination of character states sets adults of this species apart from others included in *Anomotarus*: dorsum metallic blue-green; microlines on dorsal surface not visible at magnification of 50X, except labrum with meshes isodiametric; dorsal surface punctate, each puncture with long seta; elytral intervals each uniseriately punctate, each puncture extended about width of interval, except punctures of interval 1 smaller; frontal impressions of head, median longitudinal impression of pronotum, and scutellar interneur very deep; eyes small, temples tumid, large; pronotum markedly cordate, base sharply lobed, posterior angles acute; metasternum short, metepisternum quadrate; hind wings short stubs; elytra with humeri sharply ridged, projected forward; stylomere 2 of ovipositor with microsculpture very coarse (Figs. 116A-E), extended apically as ridges and spines. Standardized Body Length 3.80- 4.04 mm. (three specimens).

Notes about relationships.— Adults of this southeastern Australian species most closely resemble those of a probably undescribed species, known from a single female collected in southern West Australia (Margaret River; MCZ). The single male of *A. angusticollis* (Sloane) (Wiluna; MCZ) shares with the above species the coarse, generally punctate dorsum. However, it is much larger, and the basal lobe of the pronotum is less distinctly developed.

Subtribe DROMIINA

The exact composition of this subtribe has not been settled. Jeannel (1949: 990) chose to include in the subfamily Dromiitae (family Lebiidae) the dromiines *(sensu stricto)* and the demetriines, ranking these groups as tribes. He excluded *Apristus* Chaudoir, placing this genus in the family Lionychidae. Habu (1967) chose to rank demetriines and dromiines as subtribes of Lebiini, and to include the lionychid genera in the Dromiina. We elect to follow Habu, though we exclude *Celaenephes* Schmidt- Goebel.

Jeannel (1949: 915) also erected the tribe Singilini (subfamily Lebiinae) to include a number of genera whose adults are characterized by small size, and pale, hairy integument.

Mateu (1963) revised this complex, pointing out that three groups were included, which he ranked as tribes: Lichnasthenini, Singilini *(sensu stricto)*, and Somotrichini. Ball (1975: 152) transferred the somotrichine to the subtribe Pericalina *(sensu lato)*. It seems to us that lichnasthenines and singilines, as understood by Mateu, can best be accommodated in the Dromiina, and we place them here. For the present, the names Singilini and Lichnasthenini are treated as junior synonyms of Dromiina.

On the basis of shared similarities in details of ovipositor sclerites and form of median lobe, we add to the singiline assemblage of the Dromiina the following taxa that were included by Csiki (1932: 1497- 1498) in the subtribe Cymindina: *Metaxymorphus* Chaudoir, 1850; *Periphobus* Péringuey, 1896; and *Callidomorphus* Péringuey, 1896. Members of these taxa are so similar to one another that it is inappropriate to rank them as genera. Nonetheless, adults of each group are distinguished from one another on the basis of body form (see key, below). Consequently, we rank each as a subgenus of *Metaxymorphus*, the senior name.

Notes are also included about *Coptoptera*, for reasons given below.

Metaxymorphus Chaudoir, *SENSU NOVO.*

Figs. 118A-B and 126A-B

Metaxymorphus (sensu stricto) Chaudoir, 1850: 370. GENERITYPE: *Dromius frenatus* Dejean, 1831: 351 (original designation). Péringuey, 1896: 205.– Csiki, 1932: 1497.– Basilewsky, 1958a: 295.– 1961c: 216- 217.

Periphobus Péringuey, 1896: 204, 211. GENERITYPE: *P. ferox* Péringuey, 1896: 211 (monotypy).– Csiki, 1932: 1498.– Basilewsky, 1956: 236- 242.– 1958a: 296. NEW SYNONYMY.

Callidomorphus Péringuey, 1896: 204, 210. GENERITYPE: *Metaxymorphus vittiger* Chaudoir, 1877: 234 (monotypy).– Csiki, 1932: 1498.

We are not in position to give diagnostic features of adults of this genus, for we do not know the other genera of dromiines well enough. We note, however, that the basis for assigning *Metaxymorphus* to the Dromiina is: head without suborbital setigerous punctures; elytron with penultimate umbilical setigerous puncture not laterad of antepenultimate and ultimate punctures; scutellar interneur separate from interneur 1, base of latter present; tibiae average, spinose; tarsomeres slender, glabrous dorsally, male front tarsomeres expanded slightly, with biseriate adhesive vestiture ventrally; tarsal claws pectinate; median lobe of males with basal bulb very small (Figs. 124A - 226A), right paramere very small (Fig. 125D); ovipositor with stylomeres 1 and 2 subequal, both glabrous, stylomere 2 with preapical "orifice" (membranous area, Figs. 121-123), preapical sensory furrow absent.

Description.— Smaller than average, Standardized Body Length ca. 3.2-4.5 mm. Form about average for Carabidae. Color somber: uniformly rufous to testaceous, or elytra striped alternately rufo-testaceous and testaceous; appendages paler than dorsum.

Microsculpture. Dorsum with meshes generally isodiametric to transverse on pronotum and elytra, microlines clearly visible at 50X. Venter and lateral sclerites of thorax with meshes transverse.

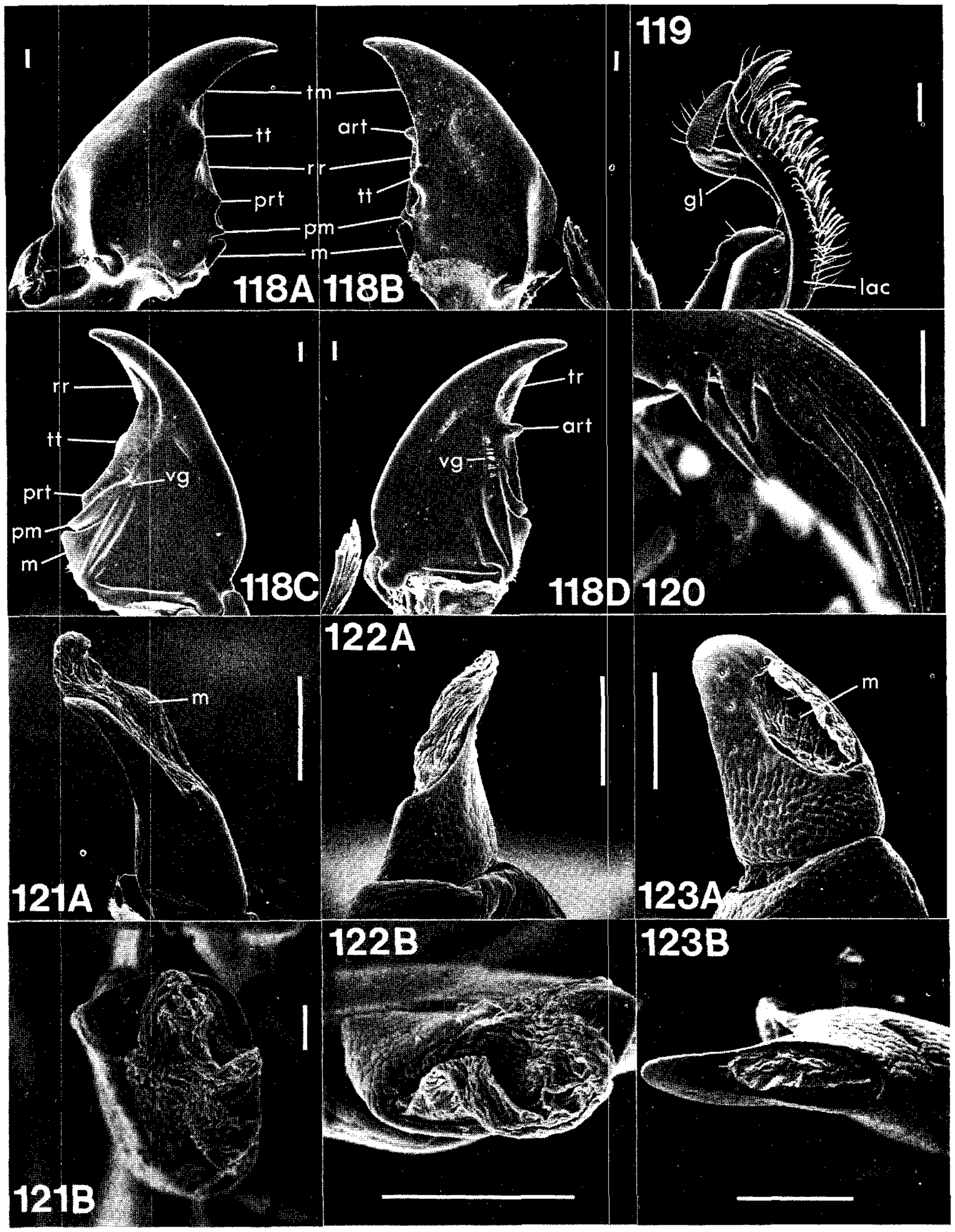
Luster. Dorsal surface dull; ventral surface faintly iridescent.

Fixed setae. Average for lebiines. Head with two pairs of supraorbital setigerous punctures; submentum and mentum each with single pair. Pronotum with two pairs of lateral setigerous punctures, posterior pair near posterior angles. Elytron with two discal setigerous punctures in interval 3; umbilical series continuous, of 13 or 14 setigerous punctures. Legs with average setation: tibiae with full complement of spines; tarsomere 5 with row of setae on each ventro-lateral margin. Abdominal sternum VII of both males and females with four setigerous punctures.

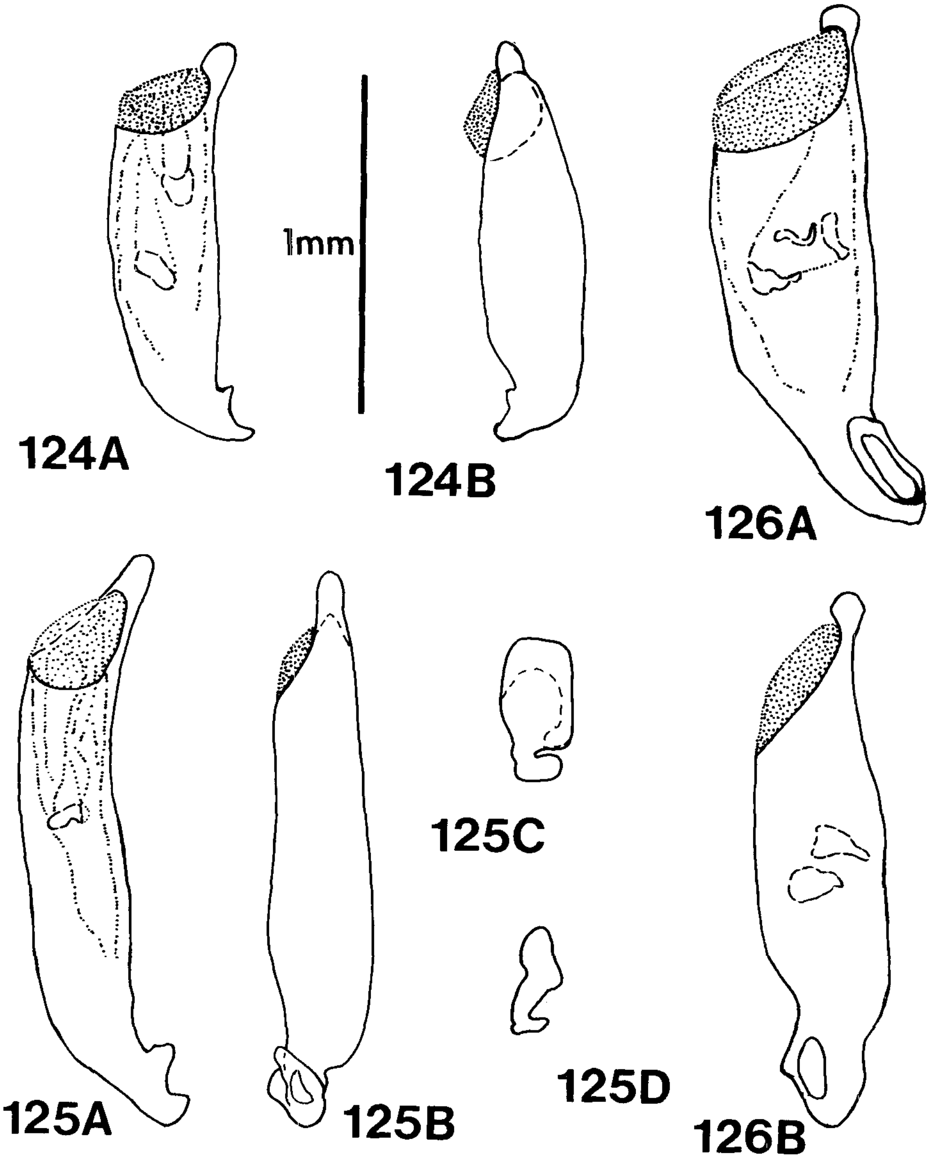
Vestiture and surface. Dorsal and ventral surfaces essentially glabrous, impunctate. Antennomere 1 with single seta; antennomeres 2 and 3 each with ring of setae preapically; remaining antennomeres average for lebiines.

Head. Average in form for lebiines, as broad or broader than average. Frontal impressions indistinct or well developed. Clypeus transverse, about rectangular, or with anterior margin distinctly incised, concave. Eyes average. Antenna filiform, antennomere 3 distinctly longer than 4; antennomeres each longer than wide.

Mouthparts. Labrum transverse, about rectangular. Mandibles (Figs. 118A-D) trigonal, but overall asymmetric, left with anterior portion of terebra much narrower than anterior portion of right terebra (Figs. 118A and B). Left mandible



Figs. 118–123. SEM photographs of structures of Dromiina, genus *Metaxymorphus*.—Fig. 118: *M. (Periphobus) confusus* (Basilewsky), mandibles—A and C, left, dorsal and ventral aspects, respectively; B and D, right, dorsal and ventral aspects, respectively. Fig. 119: *M. (P.) confusus*, right maxilla, ventral aspect. Fig. 120: *M. (P.) confusus*, tarsal claw, terminal aspect. Figs. 121–123: Left stylomere 2. Fig. 121: *Metaxymorphus (sensu stricto)* species–A and B, lateral and ventral aspect, respectively. Fig. 122: *M. (P.) confusus*–A and B, medial and apico-ventral aspects, respectively. Fig. 123: *M. (Callidomorphus) vittiger* (Péringuey)–A and B, lateral and ventral aspects, respectively. Scale bars: 118A–D, and 119 = 100 μm; 120–123B = 50 μm. Legend, mandibles: art, anterior retinacular tooth; m, molar; pm, premolar; prt, posterior retinacular tooth; tm, terebral margin; tt, terebral tooth; vg, ventral groove. Legend stylomere 2: m, preapical membrane.



Figs. 124–126. Line drawings of structures of Dromiina, genus *Metaxymorphus*.—Male genitalia, A and B, median lobe, left lateral and ventral aspects, respectively; C and D, left and right parameres, respectively, ventral aspect. Fig. 124: *M. (sensu stricto)* species. Figs. 125: *M. (Periphobus) confusus* (Basilewsky). Fig. 126: *M. (Callidomorphus) vittiger* (Péringuey).

(Figs. 118A and C) with blunt, broad terebral tooth, terebral margin distinct for most of length of terebra; cutting edge retinacular ridge, anterior retinacular tooth small; posterior retinacular tooth prominent, with well developed ridge internally; molar tooth prominent, clearly isolated from premolar tooth; ventral groove (Fig. 118C) short, asetose. Right mandible (Figs. 118B and D) with cutting edge terebral margin anteriorly, retinacular ridge posteriorly; terebral tooth blunt, not as broad as that of left mandible; retinacular ridge prominent, anterior tooth conical, prominent, posterior tooth well developed, with well developed ventral ridge; ventral groove short, setae few. Maxilla average in form; lacinia with single row of setae on ventral surface (Fig. 119); galeomere 2 shorter than 1 coarsely sculptured; palpomeres slender, palpomere 4 appreciably longer than 3, fusiform, narrowed apically. Labium average, mentum with well developed tooth, and epilobes widened apically; glossal sclerite broad, apically with pair of long setae, and several shorter setae; paraglossae adnate to glossal sclerite, about as long as latter, each with row of rather large setae apically; palpomeres average in form, sparsely setose, palpomere 2 longer than 3, with two long setae; palpomere 3 fusiform, narrowly truncate at apex.

Thorax. Pronotum markedly to slightly transverse, constricted posteriorly; all margins sharply beaded; anterior margin slightly concave; posterior margin curved, but not lobate; sides rounded, incurved evenly posteriorly, not sinuate; disc slightly convex, lateral grooves narrow; median longitudinal impression well developed. Prosternum with apex of intercoxal process immarginate. Metathorax reduced, metepisternum either quadrate or wider than long (i.e., length of anterior margin greater than that of lateral margin).

Legs. Average for lebiines. Tibiae with well developed spines. Front tarsomeres 1- 3 of males slightly expanded, each with two rows of adhesive vestiture ventrally. Tarsomere 4 with apical margin truncate. Claws pectinate, pectinations small (Fig. 120) few (one-three per claw).

Elytra. Average for lebiine adults, though humeri more sloped than average; apical margin subtruncate to truncate. Interneurs shallow, impunctate; intervals flat to slightly convex; basal ridge sinuate, extended from humerus to edge of scutellum.

Wings. Short stubs.

Abdominal sterna II- VII average for lebiines.

Male genitalia. Median lobe (Figs. 124A, B - 126A, B) cylindrical, anopic; basal bulb markedly reduced; apical orifice on left side. Internal sac with various sclerites. Right paramere reduced (Fig. 125D).

Ovipositor and associated sclerites. Stylomeres 1 and 2 without ensiform or nematoid setae (Figs. 121-123), subequal. Stylomere 2 with part of ventral surface membranous, membrane seemingly exsertile; without preapical sensory furrow and associated sense organs of ventral surface.

Key to Subgenera of *Metaxymorphus (sensu lato)*

1 (0) Clypeus sloped ventrally rather abruptly, depressed medially, or not. Head broad, body robust .... *Periphobus (sensu lato)* Péringuey.

1′ Clypeus sloped gradually anteriorly, surface plane, not depressed medially. Head narrower, body slender, agonoid .... 2.

2 (1′) Elytra bicolored, laterally testaceous, medially with more or less extensive, irregular, rufo-testaceous to piceous dark mark .... Subgenus *Metaxymorphus* Chaudoir. p. 197

2′ Elytra bicolored, pattern regular, margin and intervals 1, 3, 5, and 7 testaceous, intervals 2, 4, 6, and 8 rufo- piceous to piceous .... Subgenus *Callidomorphus* Péringuey.

Notes about classification.— We explained above our reasons for including the species of *Metaxymorphus, Callidomorpha,* and *Periphobus* in a single genus.

Csiki (1932: 1497- 1498) listed the names of 19 valid species of *Metaxymorphus (sensu stricto),* to which Basilewsky (1961c: 216- 217) added *M. flaviceps* Motschulsky, and *M. discopennis* Motschulsky, having transferred them from *Charopterus.* Most of the species were described by Péringuey. According to Basilewsky (1958a: 295), it is impossible to interpret with certainty most of Péringuey's descriptions. It will be necessary, therefore, to revise this group, on the basis of a careful study of type material.

Basilewsky (1956: 236- 242) revised *Periphobus* Péringuey. Noting that the striking sexual dimorphism recorded by Péringuey was the result of combining material of two species under a single name, Basilewsky included the female co-type of *P. ferox* Péringuey (type locality-

Oudtshoorn) in the new species *P. confusus* Basilewsky. He provided illustrations of habitus (Fig. 1, *P. ferox*; Fig. 4, *P. confusus*) and of the male genitalia (Fig. 2a, *P. confusus*; Fig. 2b, *P. ferox*) for both species. (As noted on reprints, captions for Figs. 3 and 4 were reversed). The habitus illustration was reproduced as Fig. 39 in "South African Animal Life" (Basilewsky, 1958a: 296).

According to the description and key (Basilewsky, 1956: 238), heads of *P. ferox* specimens are more markedly modified than are heads of *P. confusus*. Furthermore, the heads are sexually dimorphic, especially those of *P. ferox*. However, this dimorphism is not as extreme as Péringuey believed.

Notes about habitat.— We did not locate information for *Metaxymorphus*. We surmise, however, on the basis of brachyptery, color, and form of adults, that they inhabit dry, open area, and live on the ground.

Geographical distribution.— This genus is known only from localities in the Union of South Africa.

Specimens examined.— We have seen 40 specimens of *Metaxymorphus (sensu lato)*, from the following localities in South Africa.

M. (Metaxymorphus) atriceps Péringuey. Male, Cape Colony, Uitenhaage, Rv. J. O. Neil 1917- 55 (BMNH). Male, Cape Colony, Port Elizabeth G. A. K. Marshall 1917- 55 (BMNH).

M. (M.) cursor Péringuey. Male, female, Capetown, G. A. K. Marshall 1917- 55 (BMNH).

M. (Metaxymorphus) species?– 12 males, 15 females, all from Cape Province. IV. 1958 E. S. Ross, R. E. Leech (CAS). Male, two females, 19 mi. SE Garies 220 m V.2. 58; E. S. Ross, R. E. Leech (CAS). Four males, two females, 3 mi. SW Ladysmith 475 m. IV.24.58; E. S. Ross, R. E. Leech(CAS). Four males, female, Strandfontein XI.13.49 B. Malkin (CAS). Three males, nine females, Urendenburg XI.19.49 B. Malkin (CAS).

M. (Callidomorphus) vittiger Chaudoir. Male, Capland, Algoa Bay Dr. Brauns (BMNH). Female, Cape Colony Uiteahage Rev. J. O. Neil 1917- 55 (BMNH).

M. (Periphobus) confusus Basilewsky. Four males, Cape Province 5 mi. W. Herold 600 m. IV.24.58; E. S. Ross, R. E. Leech (CAS). Three females, Cape Province 3 mi. SW Ladysmith 475 m. IV.24.58; E. S. Ross, R. E. Leech (CAS).

Coptoptera Chaudoir

Coptoptera Chaudoir, 1837: 5. GENERITYPE: *Coptoptera brunnea* Chaudoir, 1837: 5 (monotypy).-- Péringuey, 1896: 230 (in part).-- Basilewsky, 1956: 401.

Klepsiphrus Péringuey, 1896: 223, 237. GENERITYPE: *Klepsiphrus pugnax* Péringuey, 1896: 237 (monotypy).

Syndetus Péringuey, 1896: 204, 222. GENERITYPE: *Syndetus simplex* Péringuey, 1896: 222 (monotypy).-Basilewsky, 1958b: 340-341.

Notes.— The genus *Syndetus* was included in the Cymindina by Péringuey (1896: 223), though he pointed out that specimens of *S. simplex* had dromiine featues, as well. Basilewsky, who examined the type of *S. simplex*, subsequent to his revision of *Coptoptera* (1956), concluded that this species was not only a dromiine, but also that it was a species of *Coptoptera*. We have not seen specimens of this species, but we accept Basilewsky's judgement.

Tribe ZUPHIINI

The genus *Agastus* Schmidt-Goebel was included by Jedlička (1963: 451) in the Cymindina, but this genus clearly belongs in the Zuphiini-- where Csiki (1932: 1567) placed it. The senior author saw in the British Museum (Natural History) a specimen of *A. ustulatus* Gestro from Java, and another with an indecipherable locality label, that was compared with the type.

CONCLUDING REMARKS

This paper began with the seemingly limited objective of seeking for the sister group of a New World taxon of lebiines. It developed into a taxonomic treatment, based on barely adequate material of groups ranging in rank from intra-specific to subtribal. Because so much of the work centered around dismembering of a taxon treated previously as if it were a taxonomically valid entity, and because of a shortage of time as well as of material for study, the paper was frustrating to write. Taxonomists, like most other scientists, prefer to build, rather than to take apart. Building for taxonomists consists primarily of description of new taxa, and locating such in the system of previously described taxa. Nonetheless, re-organization of groups like the cymindines of authors is required if future workers are to have a more secure basis for proceeding with classification of the Lebiini.

We reiterate our belief that future progress will be along lines that Habu pioneered. We wish to present briefly our views about how research on lebiines should proceed to produce maximally useful results in minimum time. It seems to us that development of a general system of classification for the Lebiini could be obtained in two stages. The first is undertaking of regional studies, zoogeographical region by region. Publications could consist of broad-spectrum reviews, based on dissections of representative members of each of the described genera, in order to test further those characters that seem to be important, and to assign these taxa to proper subtribes. At the same time, keys to genera ought to be written, and species names catalogued.

Stage 2 would have a taxonomic focus, with all of the genera of the world of each subtribe being assembled on the basis of inferred phylogenetic relationships. Persons doing this work would have the data base assembled by regional studies to guide them. Additionally, inter-regional comparisons would likely unearth additional character systems for use in classification. At this stage, the search for sister groups both within and between tribes would be of substantial importance and might lead to re-defining the limits of the Lebiini, either by exclusion of some subtribes, or by inclusion of other lebiomorph tribes.

Because much taxonomic research is on a regional basis, we believe that the initial regional approach advocated here to re-classification of lebiine genera will lead quickly to publications that are of immediate interest and use. Such publications are likely to provide the impetus for accumulation of additional data that will be of use in the world-wide treatment of genera of individual subtribes.

A second general issue about which comments seem appropriate is ranking of taxa. So long as one works within a geographically limited fauna, one can adopt the generic concepts that have been applied by previous workers in that area. However, a study of a group on a world-wide basis requires adoption of a uniform treatment. In this study, we were required to deal with the discrepancy between a broad concept of genera advocated by Lindroth (1969b: XVII) as applied to Holarctic carabids, and the more restricted one advocated explicitly by Basilewsky (1968b: 185) in his studies of African taxa, and applied by Mateu in his studies of tropical lebiines, generally. We believe that more broadly defined genera are more useful to biologists other than taxonomists, and that units more difficult to recognize and more restricted geographically can be named, but ranked at a lower level. Thus, we have defined genera broadly, in spite of the discomfort that will be caused to some of our colleagues.

Procedure in ranking is not a matter of right and wrong, but one of taste and preference--unless one adheres strictly to the tenets of cladistics. We hope that our re-ranking of well-known taxa will be judged on the merits advocated, and will be found satisfactory for general use. We hope that our judgements will not be rejected out of hand.

Reference above to biologists other than taxonomists recalls the interrelationships between these two groups, specifically with reference to the Lebiini. So far, study of lebiines has been principally the playground of taxonomists. In the course of their studies, such workers have discovered clues suggestive of modes of life and behavior that ought to excite interest of ecologists and ethologists, as well as of economic entomologists. When such workers take up the challenges inherent in determining life histories, host-parasite relationships, other ecological relationships, and behavior patterns, the data produced will be of great value to taxonomists, and will no doubt help in resolving vexing taxonomic problems.

Finally, we return to the initial purpose of this paper: a search for a sister group, specifically that of *Pinacodera* Schaum. We think that we have found it, though we are not sure. At least we have shed some light on the problem, and will develop hypotheses on the basis of our work. Hennig (1966: 139) noted that an important task of phylogenetic systematics is search for sister groups of monophyletic taxa. By accepting his formulation of tasks of systematics, we have been able to examine a range of interesting problems. As others have stated, Hennig's methods seem fruitful. They should be used widely to seek understanding of important practical taxonomic problems, rather than to serve as the basis for the futile and arid debate that rages in current issues of "Systematic Zoology" and elsewhere, the tone of which is reminiscent of the writings of Medieval scholastics addressing theological problems that seem now of little consequence.

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NOTE ADDED IN PROOF

After this paper was nearly ready for publication, R. B. Madge (*in litt.*) advised us that Habu (1982:113) had erected the Celaenephina as a new subtribe for *Celaenephes* Schmidt-Goebel, though he expressed doubt (*loc. cit.*: 110) that this genus belonged in the Lebiini. He also diagrammed (*loc. cit.*: 114, Fig. 29) his views about evolution of the stylomeres of truncatipennian carabids, with those of *Celaenephes* either in an ancestral position, or outside this taxonomic complex. Thus, our views, expressed above, are basically in agreement with those of Habu.

REFERENCES

Allen, R.T. and G.E. Ball. 1980. Synopsis of Mexican taxa of the *Loxandrus* series (Coleoptera: Carabidae: Pterostichini). Transactions of the American Entomological Society 105: 481–576.

Alluaud, C. 1917. Les carabiques de la faune alpine des hautes montagnes de l'Afrique orientale. Annales de la Société entomologique de France 86: 73–116.

Andrewes, H.E. 1923. Papers on Oriental Carabidae XII. Annals and Magazine of Natural History (9) 12: 679–690.

__________________. 1929. Coleoptera Carabidae. Volume 1.–*In* Stephenson, J. (Editor). The fauna of British India, including Ceylon and Burma. Taylor and Francis, London. xviii + 431 pp., 5 plates.

__________________. 1930. Catalogue of Indian Insects. Part 18–Carabidae. Calcutta. 389 pp.

__________________. 1935. Keys to some Indian genera of Carabidae. V. The genera *Cymindoidea, Platytarus,* and *Taridius*. Stylops 4: 201–205.

Antoine, M. (1938) 1939. Notes d entomologie marocaine. XXIX. Bulletin de la Société des Sciences naturelles et physiques du Maroc 18: 170–191.

_______________. 1962. Coléoptères carabiques du Maroc. Cinquième partie. Mémoires de la Société des Sciences naturelles et physiques du Maroc, Zoologie, Nouvelle Serie No. 9: 539–692.

Ball, G.E. 1960. Carabidae, Fascicle 4, pp. 55–210. *In* Arnett, R.H. 1960. The beetles of the United States (a manual for identification). The Catholic University of America Press, Washington, D. C. xi + 1112 pp.

_______________. 1975. Pericaline Lebiini: notes on classification, a synopsis of the New World genera, and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). Quaestiones Entomologicae 11 (2): 143–242.

_______________. 1978. The species of the Neotropical genus *Trichopselaphus* Chaudoir (Coleoptera: Carabidae: Harpalini): classification, phylogeny and zoogeography. *Ibid.* 14 (4): 447–489.

_______________. 1982. Evaluation of the Baron Maximilien de Chaudoir's contribution to classification of cymindine Lebiini and Masoreimorphi. The Coleopterists Bulletin 36

(3): 512–529.

__________ and D. Shpeley. In press. The species of eucheiloid Pericalina: classification and evolutionary considerations. The Canadian Entomologist.

Basilewsky, P. 1953a. Carabidae (Coleoptera Adephaga). Exploration du Parc national de l'Upemba. Mission G. F. de Witte, *et alii.* (1946–1949). Fascicule 10. Institute des Parcs nationaux du Congo Belge. Bruxelles. pp. 1–252.

__________. 1953b. Contributions a l'etude des Coléoptèra carabiques de la region malgache. Mémoires de l'Institut scientifique de Madagascar Serie III: 53–65.

__________. 1954a. Le genre *Leptosarcus* Péringuey (Coléoptèra Carabidae Lebiinae). Bulletin de la Société entomologique de Belgique 90: 83–88.

__________. 1954b. Revision des genres *Hystrichopus* Boheman et *Plagiopyga* Boheman (Coleoptera: Carabidae Lebiinae). Annales du Musée Royal du Congo Belge, Tervuren (Série 8°) Science Zoologie 31: 7-99.

__________. 1954c. Le genre *Pseudomasoreus* Desbrochers. Revue Zoologique et Botanique d'Afrique 49 (1–2): 89–96.

__________. 1956. Contributions à la connaissance des Lebiinae d'Afrique (Coleoptera Carabidae) II. Bulletin et Annales de la Société Royale d'Entomologie de Belgique 92: 236–248.

__________. 1957. Contributions à la connaissance des Lebiinae d'Afrique III. (Dromiinae: *Klepterus* Péringuey et *Klepteromimus* Péringuey). *Ibid.* 93: 239–256.

__________. 1958a. Coleoptera Carabidae, 5: 212–317. *In* Hänstrom B., P. Brinck, and G. Rudebeck. 1955–1973. South African Animal Life, Results of the Lund University Expedition in 1950–1951. Volumes 1–15. Almqvist and Wiskells Boktryckeri AB.

__________. 1958b. Contributions à la connaissance des Lebiinae d'Afrique. IV. (Coleoptera Carabidae). Bulletin et Annales de la Société Royale d'Entomologie de Belgique 94: 323–341.

__________. 1960. Coléoptères Carabidae du Mont Kabobo recueillis par N. Leleup. Revue Zoologique et Botanique d'Afrique 62: 66–90.

__________. 1961a. Contribution a la connaissance des Lebiinae d'Afrique (Coleoptera: Carabidae) VII. *Ibid.* 64: 153–171.

__________. 1961b. Coléoptères Carabidae africains nouveaux XII. *Ibid.* 63: 113–127.

__________. 1961c. Sur les types de Carabidae africains décrit pars V. Motschulsky. Bulletin et Annales de la Société Royale d'Entomologie de Belgique 97: 205–224.

__________. 1962. LX. Coleoptera Carabidae. Mission zoologique de l'I.R.S.A.C. en Afrique orientale (P. Basilewsky et N. Leleup, 1957). Annales du Musée Royale d'Afrique Centrale (Ser. 8°) Science Zoologie No. 107: 46-337.

__________. 1968a. Missione 1965 del Prof. Giuseppe Scortecci nello Yemen (Arabie meridionale). Atti della Societa Italina di Scienze Naturale di Milano. 107 (III-IV): 349-361.

__________. 1968b. III. Les calosomes des îles Galapagos (Coleoptera Carabidae). *In* Mission zoologique belge aux îles Galapagos et en Ecuador (N. et J. Leleup, 1964–1965). Vol. I, pp. 179–207. L'Imprimerie des Sciences, s. a., Bruxelles.

__________. 1976. 19. Coleoptera Carabidae. Mission entomologique du Musée

Royal d l'Afrique Centrale aux Monts. Uluguru, Tanzanie (L. Berger, N. Leleup, et J. Debecker, V–VIII. 1971). Revue de Zoologique Africaine 90 (3): 671–721.

__________________. 1982. Contributions a l'etude des Coléoptères carabiques de la region malgache XIV. Description d'un genre nouveau de Madagascar. Bulletin de la Société entomologique de France 87: 20-24.

Bates, H.W. 1871. Notes on Carabidae, and descriptions of new species (No. 7). Entomologists' Monthly Magazine 8: 77–81.

_______________. 1872. Notes on Carabidae, and descriptions of new species (No. 12). *Ibid.* 8: 199–202.

_______________. 1878. New genera and species of Carabidae from Tasmania. Cistula Entomologica II: 317–326.

_______________. 1883. Insecta, Coleoptera, Carabidae, Cicindelidae, supplement, Vol. 1, part 1, pp. 153–256, plates vi–vii. *In* Godman, F.D. and O. Salvin. 1879–1911. Biologia–Centrali Americana. Coleoptera. 7 volumes in 17 parts. London.

_______________ 1884. *Ibid.* pp. 257-299, plate xiii. *Ibid.*

_______________. 1886. On the geoadephagous Coleoptera collected by Mr. George Lewis in Ceylon. Annals and Magazine of Natural History (series 5) 17: 68–81, 143–156, and 199–212.

_______________. 1892. List of the Carabidae. Viaggio di Leonardo Fea in Birmania e regioni vicine. Annali del Museo Civico di Storia Naturale di Genova Series 2a 12 (32): 267–428.

Bedel, L. 1906. Catalogue raisonné des coléoptères du nord de l'Afrique (Maroc, Algérie, Tunisie, et Tripolitaine) avec notes sur la faune des Isles Canarie et de Madère. pp. 201–264. Paris.

Blackburn, T. 1894. Further notes on Australian Coleoptera, with descriptions of new genera and species. Parts XV–XVI. Transactions of the Royal Society of South Australia 18: 139–168; 200–240.

_____________________. 1901. Further notes on Australian Coleoptera, with descriptions of new genera and species. Parts XXVIII-XXIX. Transactions and Proceedings of the Royal Society of South Australia 25: 99–131.

_____________________. 1908. Further notes on Australian Coleoptera, with descriptions of new genera and species. No. XXXVIII. Transactions of the Royal Society of South Australia 32: 362–386.

Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part I. Bulletin of the United States National Museum No. 185, pp. 1–188.

Blanchard, C.E. 1853. Description des insectes. Voyage au Pole Sud ..... Zoologie vol. 4. Paris. 422 pp.

Blatchley, W.S. 1910. An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of the Rhynchophora) known to occur in Indiana, with bibliography and descriptions of new species. The Nature Publishing Company, Indianapolis, Indiana. 1386 pp.

Boheman, C.H. 1848. Insecta Caffraria annis 1838–1845a J.A. Wahlberg collecta. Coleoptera, Vol. 1, part 1. Fritze und Nordstedt, Holmiae. 298 pp.

Burgeon, L. 1937. Catalogues raisonnés de la faune entomologique du Conge Belge. Coléoptères carabiques (Troisième Partie). Annales de Musée du Congo Belge.

Zoologie Série III Section II, Tome II, Fascicule 5: 315-406.

Casey, T.L. 1920. Random studies among the American Caraboidea. *In* Casey, T.L. Memoirs on the Coleoptera, Volume IX, pp. 133–299. New Era Publishing Company, Lancaster, Pennsylvania. 516 pp.

Castelnau (Comte de), F.L.N. de C. Laporte 1832. Mémoire sur cinquante espèces nouvelles ou peu connues d'insectes. Annales de la Société entomologique de France 1: 386–415, 448.

Chaudoir, M. de. 1837. Description de quelques genres nouveaux et de quelques espèces nouvelles ou inèdites de carabiques. Bulletin de la Société des Naturalistes de Moscou 10 (3): 3–20.

____________________. 1850. Mémoire sur la famille des carabiques (2e partie, cont.). *Ibid.* 23: 349–460.

____________________. 1852. Memoire sur la famille des carabiques, Part 3. *Ibid.* 25: 3-104.

____________________. 1871. Remarques sur le catalogue de MM. de Harold et Gemminger, Tome 1. *Ibid.* 44 (II): 279–287.

____________________. 1873. Essai monographique sur le genre *Cymindis* proprement dit. Berliner Entomologischer Zeitschrift 17: 53–120.

____________________. 1875. Genres aberrants du groups des cymindides. Bulletin de la Société Impériale des Naturalistes de Moscou 49 (II): 1–61.

____________________. 1877. Genres nouveaux et espèces inédites de la famille des carabiques. *Ibid.* 51: 188–268.

____________________. 1878. Révision des genres *Onychopterygia, Dicranoncus,* et *Colpodes*. Annales de la Société entomologique de France (5) 8: 275-382.

Csiki, E. 1932. Coleoptera, Carabidae, Pars. 124, Harpalinae VII, pp. 1279–1598. *In* Junk W. und S. Schenkling. 1909–Coleopterorum Catalogus. W. Junk, Berlin und 's–Gravenhage.

Darlington, P.J., Jr. 1952. The carabid beetle of New Guinea. Part 2. The Agonini. Bulletin of the Museum of Comparative Zoology 107 (3): 89–252, 4 plates.

____________________. 1968. *Ibid.* Part III. Harpalinae (continued): Perigonini to Pseudomorphini. *Ibid.* 137(1): 1–253.

____________________. 1971. *Ibid.* Part IV General considerations; analyses and history of fauna; taxonomic supplement. *Ibid.* 142 (2): 130-337.

Dejean, P.F.M.A. 1825. Spécies général des coléoptères de la collection de M. le comte Dejean. Vol. 1. Méquignon–Marvis, Paris. xxx + 463 pp.

____________________. 1826. *Ibid.* Vol. 2. *Ibid.* viii + 501 pp.

____________________. 1831. *Ibid* Vol. 5. *Ibid.* viii + 883 pp.

Desbrochers des Loges, J. 1904. Faunule des Coléoptères de la France et de la Corse. Carabides de la Tribu des Lebiinae et des Tribus voisines. Le Frelon, 1904, No. 9, pp. 133–144; Nos. 10 and 11, pp. 145–176; and No. 12, pp. 177–196.

Dilger, W.C. 1952. The Brij hypothesis as an explanation for the tropical faunal similarities between the Western Ghats and the eastern Himalayas, Assam, Burma and Malaya. Evolution 6 (1): 125–127.

Emden, F.I. van. 1937. Neue und bekannte Carabidae aus Java (Coleoptera). Arbeiten über morphologische und taxonomische Entomologie 4 (2): 111–125.

Emetz, V.M. 1972. A revision of the ground beetles of the genus *Cymindis* Latr. (Coleoptera, Carabidae) of the fauna of the USSR. 1. The subgenera *Mastus* Motsch. and *Pseudomastus* Emetz, subgen. n. Entomological Reviews 51: 194–202 (translated from Russian).

———————. 1973. Materials for the revision of the genus *Cymindis Latr. (Coleoptera, Carabidae) of the fauna of the USSR. 2. Subgenera Iscariotes* Reiche and *Neopsammoxenus* Emetz, subgen. n. *Ibid.* 52 (1): 102–107. (translated from Russian)

Erichson, W.F. 1842. Beitrag zur Fauna von Vandiemensland, mit besonderer Rucksicht auf die geographische Verbreitung der Insekten. Archiv für Naturgeschichte, Vol. 8, Part 2: 83–287.

Erwin, T.L. 1974. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part II: a revision of the New World–Australian genus *Pericompsus* LeConte. Smithsonian Contributions to Zoology No. 162. Washington, D.C. iv + 96 pp.

———————. 1978. Systematic, natural history, and zoogeographic notes on the genus *Agra* Fabricius, with a description of a new species from Panama (Coleoptera: Carabidae: Lebiini). The Coleopterists Bulletin 32 (4): 261–268.

———————. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions (Coleoptera: Carabidae), pp. 539–592. *In* Erwin, T.L., G.E. Ball, D.R. Whitehead, and A.L. Halpern (Editors). Carabid beetles: their evolution, natural history, and classification (Proceedings of the First International Symposium of Carabidology, Smithsonian Institution, Washington, D. C., August 21, 23, and 25, 1976). W. Junk b.v., publishers, The Hague. X + 644pp.

———————. 1982. *Agra*, arboreal beetles of Neotropical forests: *erythropus* group systematics. Systematic Entomology 7 (1): 39-71.

——————— and L.J.M. Erwin. 1976. Relationships of predaceous beetles to tropical forest wood decay. The natural history of Neotropical *Eurycoleus macularis* Chevrolat (Carabidae: Lebiini) and its implications in the evolution of ectoparasitoidism. Biotropica 8 (4): 215–224.

———————, D.R. Whitehead, and G.E. Ball. 1977. Family 4. Carabidae, The Ground Beetles, pp. 4.1–4.68. *In* Blackwelder, R.E. and R.H. Arnett. Checklist of the beetles of Canada, Unites States, Mexico, Central America, and the West Indies. World Digest Publications, Oxycopis Pond, Wallace Road, Kinderhook, New York 12106.

Fairmaire, L. 1850. *Platytarus,* nouveau genre de Coléoptères, établi pour *Cymindis Famini.* Bulletin de la Société entomologique de France (2) 8: 17

———————. 1901. Materiaux pour la faune coleopterique de la region Malgache (11e note). Revue d'Entomologie 20: 101–248.

——————— and J.J.A. Laboulbène. 1854. Faune entomologique francaise ou description des insectes qui se trouvent en France, coléoptères, Vol. 1. Deyrolle, Paris. 180 pp.

Fauvel. A. 1881. Communications. Annales de la Société entomologique de France. (6) 1: CXVIII.

Fourcroy, A.F. de. 1785. Entomologia Parisensis, sive catalogus insectorum, quae in agro parisiense reperiuntur. 2 vols. Paris. 544 pp.

Gemminger, M. and E. von Harold. 1868. Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. I Cicindelidae–Carabidae. Paris, E. Deyrolle fils, 19 Rue de la Monnaie. XXXVI + 424 pp., index.

Habu, A. 1967. Fauna Japonica. Carabidae, Truncatipennes Group (Insecta: Coleoptera). Tokyo Electrical Engineering College Press, Hakushin-Sha Printing Co., Tokyo, Japan. xiv + 338 pp. Plates I–XXVII, some in color.

__________. 1978. Fauna Japonica Carabidae: Platynini. Yugaku-Sha Ltd., Tokyo, Japan. viii + 447 pp. Plates I–XXXVI, some in color.

__________. 1982. Revised and supplementary notes on, and descriptions of the Truncatipennes group of Japan (Coleoptera, Carabidae). The Entomological Review of Japan 36 (2): 85–142.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, Chicago, London. Preface, Contents and 263 pp.

Horn, G.H. 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. Transactions of the American Entomological Society 9: 91–196, plates 1–10.

__________ 1882. Synopsis of the tribe Lebiini. *Ibid.* 10: 126–164.

Iakobson, G.G. 1907. Die Käfer Russlands und Westeuropas. Ein Handbuch zum Bestimmen der Käfer. Lieferung V.A.F. Devrient, St. Petersburg. pp. 321–400, plates 37–46 (in Russian).

Jeannel, R. 1941. Sur le genre *Pseudomasoreus* Desbrochers. Bulletin de la Société entomologique de France 1941. pp. 62–67.

__________. 1942a. Coléoptères carabiques, 2me partie. Faune de France 40: 573–1173. Paris

__________. 1942b. La genese des faunes terrestres. Presses Universitaires de France, Paris. viii + 513 pp., 8 plates.

__________. 1949. Coléoptères carabiques de la Region malgache (troisieme partie). Faune de l'Empire francais XI, pp. 767–1146, figs. 365–548.

__________. 1955. L'édéage. Initation aux recherches sur la systematique des Coléoptères. Publications du Muséum National d'Histoire Naturelle, Editions du Museum, 36, Rue Geoffroy-Saint-Hilaire (Ve) Paris. 155 pp.

Jedlička, A. 1963. Monographie der Truncatipennen aus Ostasien Lebiinae–Odacanthinae–Brachyninae. Entomologische Abhandlungen und Berichte aus dem Staatl. Museum für Tierkunde in Dresden, 28 (7): 269–579, 244 text-figs., 54 plates, 6 colored.

__________. 1968. Neue Carabiden aus der Palaearktischen Region (Coleoptera, Carabidae). Reichenbachia 8 (34): 285–296.

Kolbe, H. J. 1898. Coleopteren (Kafer und Netzflugler). Deutsch-Ost-Afrika IV. Lief. VI, VII, VIII. Coleoptera 364 pp., 3 plates. Neuroptera, 42 pp., 1 plate (from Zoological Record, 1897, vol. 34: 34).

Lacordaire, T. 1854. Histoire naturelle des Insectes, genera des Coléoptères ou exposè méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Vol. 1. Cicindeletes–Palpicornes. Libraire encyclopedique de Roret, Paris. x + 486pp.

Larson, D.J. 1969. A revision of the genera *Philophuga* Motschoulsky and *Tecnophilus* Chaudoir, with notes on the North American Callidina (Coleoptera: Carabidae). Quaestiones Entomologicae 5 (1): 15–84.

Latreille, P.A. 1806. Genera crustaceorum et insectorum secundem ordinem naturalem in familias disposita, iconibus exemplisque plurimus explicata. Vol. 1. Paris. XVIII + 303 pp.

Lea, H.M. 1912. The late Rev. Canon Thomas Blackburn, B.A., and his entomological work. Transactions of the Royal Society of South Australia 36: v–xl.

LeConte, J.L. 1851. Descriptions of new species of Coleoptera from California. Annals of the Lycaeum of Natural History of New York 5: 125–184.

__________. 1853. Notes on the classification of the Carabidae of the United States. Transactions of the American Philosophical Society (2) 10: 363–403.

__________. 1861. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections III (No. 136): 1–286. Part 1.

__________ and G.H. Horn. 1883. Classification of the Coleoptera of North America. Prepared for the Smithsonian Insititution. *Ibid.* 26 (4) (No. 507): xxxvii + 567 pp.

Leng, C.W. 1920. Catalogue of the Coleoptera of America north of Mexico. John D. Sherman, Jr., Mount Vernon, New York. 470 pp.

__________ and A.J. Mutchler, 1927. Supplement 1919–1924 (inclusive) to Catalogue of the Coleoptera of America north of Mexico. John D. Sherman, Mount Vernon, New York. 78 pp.

Liebherr, J. MS. Larval description of *Calybe (Ega) sallei* (Chevrolat) with a preliminary assessment of anchonoderine affinities (Carabidae: Anchonoderini).

Liebke, M. 1938. Denkschrift über die Carabiden–tribus Colliurini. Festschrift zum 60. Geburstage von Professor Dr. Embrik Strand. Vol. 4, pp. 37–41. Riga.

__________. 1951. Beiträge zur Fauna Perus. nach der Ausbeute der Hamburger Sudperu–Expedition 1936 ander Sammlungen wie auch auf Gründ von Literaturangeben von Prof. Erich Titschack. Band II. Wissenschaftliche Bearbeitungen. Verlag Gustav Fischer, Jena. 344 pp.

Lindroth, C.H. 1969a. The ground beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. Part 6. Opuscula Entomologica, Supplementum 34: 945–1192.

__________. 1969b. *Ibid.* Part 1. *Ibid.* Supplementum 35: I–XLVIII.

MacLeay, W.J. 1863–1866 (1864). Descriptions of new genera and species of Coleoptera from Port Denison. Transactions of the Entomological Society of New South Wales 1: 106–130, pl. IX.

__________. 1871. Notes on a collection of insects from Gayndah. *Ibid.* 2: 79–158.

Mahar, J.M. 1978. The life history of *Pinacodera limbata* Dejean and *Pinacodera platicollis* Say (Coleoptera: Carabidae) in oak forests in Michigan. Unpublished M.S. Thesis, Michigan State University, East Lansing, Michigan. 47 pp.

Mandl, K. 1973. Bausteine zur Kenntnis der Familie Carabidae (Col.). Entomologischen Arbeiten aus den Museum Georg Frey 24: 88–100.

Mannerheim, C.G. 1837. Mémoire sur quelques genres et espèces de carabiques. Bulletin de la Société Impériale des Naturalistes de Moscou 10 (2): 3–49.

Mateu Sanpere, J. 1952. El género *Trymosternus* Chaudoir. Eos 28: 109–141.

__________. 1958. Más datos sobre los *Trymosternus* Chaud. (Col., Carabidae) de la Peninsula Ibérica. Miscelánea Zoologica 1 (5): 1-6.

__________. 1963. Notas sobre tres séries filéticas de Lebiidae (Lichnasthenini Thomson, Singilini Jeannel, Somotrichini nov.) (Coleoptera–carabides) y rectificaciones sinonimicas. Annali del Museo Civico di Storia Naturali di Genova

74: 122–139.

________________. 1970a. Notes sur Lebiens malgaches (Coleoptera Carabidae) (premiere note). Revue Zoologique et Botanique d'Afrique 81 (1–2): 173–179.

________________. 1970b. Description d'un genre nouveau de Coléoptères Carabidae Lebiinae, representant d'une tribu inédite en Afrique. *Ibid.* 82 (1–2): 148–156.

________________. 1972. Remarques sur trois genres de Troncatipennes afro-asiatiques (Coléoptères Carabiques). Nouvelle Revue d'Entomologie 2: 43–52.

________________. 1974. Révision des espèces africaines et malgaches du genre *Euplynes* Schmidt-Goebel (Col. Carabidae Agonini). Revue Zoologique Africains 88 (3): 487–506.

________________. 1980. Notes sur les lébiens malgaches (5e note). Sur trois nouveaux *Pseudomasoreus* Desbrochers. Revue francais d'Entomologie (N. S.) 2 (1): 15–23.

Matthews, E.G. 1980. A guide to the genera of beetles of South Australia. Part 1. Archostemata and Adephaga. Special Educational Bulletin Series South Australian Museum Adelaide, Australia. 48 pp., figs. 3–108.

Moore, B.P. 1963. New or little-known Australian Carabidae in the Frey Museum (Col.). Entomologischen Arbeiten aus den Museum Georg Frey 14: 435–444.

________________. 1964. New cavernicolous Carabidae (Coleoptera) from mainland Australia. Journal of the Entomological Society of Queensland 3: 69–74.

________________. 1967a. New Australian cave Carabidae (Coleoptera). Proceedings of the Linnaean Society of New South Wales 91: 179–184.

________________. 1967b. New or little-known Australian Carabidae in the Frey Museum (Col.). Entomologischen Arbeiten aus den Museum Georg Frey 18: 308–322.

Motschulsky, V. von. 1864. Enumération des nouvelles espèces de Coléoptères rapportés de ses voyages. Bulletin de la Société Impériale des Naturalistes de Moscou 337 (2): 171–240, 297–355.

Noonan, G.R. 1973. The anisodctylines (Insecta: Coleoptera: Carabidae: Harpalini): classification, evolution, and zoogeography. Quaestiones Entomologicae 9 (4): 266–480.

Péringuey, L. 1892. Fourth contribution to the South African Coleopterous Fauna. Descriptions of new species in the South African Museum. Transactions of the South African Philosophical Society 6 (2): 95–134.

________________. 1896. A descriptive catalogue of the Coleoptera of South Africa, part II. *Ibid* 7: i–xiv and 99–623, plates 3–10.

Porta, A. 1923. Fauna Coleopterorum Italica. Volume 1. Adephaga. Piacenza, San Remo. 285 pp., 278 figs.

Reichardt, H. 1974. The systematic position of *Asklepia* Liebke, 1938, with the description of a new species (Coleoptera, Carabidae). The Coleopterists Bulletin 28 (4): 177–179.

________________. 1977. A synopsis of the genera of Neotropical Carabidae (Insecta: Coleoptera). Quaestiones Entomologicae 13 (4): 347–485.

Say, T. 1823. Descriptions of insects of the families Carabici and Hydrocanthari of Latreille inhabiting United States. Transactions of the American Philosophical Society (new series) 2: 1-109.

Schaum, H. 1856–1860. Naturgeschichte der Insecten Deutschlands. Erste Abtheilung Coleoptera Erster Band. Nicolaische Verlagsbuchhandlung (G. Parthey), Berlin. 791

pp.

Schmidt–Goebel, H.M. 1846. Faunula Coleopterorum Birmaniae, adjectis nonnuliis Bengaliae indigenis. Lieferung 1. Prague. 94 pp., plates 1–3.

Seidlitz, G. von. 1887–1891. Fauna Baltica. Die Käfer (Coleoptera) der deutschen Ustseeprovinzen Russlands. Königsberg. CXCII + 818 pp.

_______________. 1888–1891. Fauna Transsylvanica. Die Käfer Siebenburgens. Königsberg. LVI + 915 pp., 1 plate.

Sloane, T.G. 1894. Studies in Australian entomology. No. VII. New genera and species of Carabidae. Proceedings of the Linnaean Society of New South Wales (2) 9: 393–455.

_______________. 1898. On Carabidae from West Australia, sent by Mr. A.M. Lea. *Ibid.* 23 (3): 444–520.

_______________. 1917. Carabidae from tropical Australia. *Ibid.* 42: 406–443.

_______________. 1920. The Carabidae of Tasmania. *Ibid.* 45: 113-180.

_______________. 1923. The classification of the Family Carabidae. Transactions of the Royal entomological Society of London, 1923, pp. 234–250.

Straneo, S.L. 1943. Su alcuni Carabidi del Museo Civico di Genova faccolti in Africa occidentale da L. Fea. Annali del Museo di Storia Naturali di Genova 62: 55–61.

Tanner, V.M. 1927. A preliminary study of the genitalia of female Coleoptera. Transactions of the American Entomological Society 53: 5–50, 15 plates.

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