Frontispiece. Photograph of habitus of *Entomoantyx cyanipennis* (Chaudoir), dorsal aspect. Mexico, Veracruz, NE Catemaco, Los Tuxtlas Biological Station (CNCI). Standardized Body Length = 4.4 mm.

# THE MIDDLE AMERICAN GENERA OF THE TRIBE OZAENINI WITH NOTES ABOUT THE SPECIES IN SOUTHWESTERN UNITED STATES AND SELECTED SPECIES FROM MEXICO

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*Quaestiones Entomologicae*
*26: 30—116*

## ABSTRACT

*Based on structural features of adults, the following new taxa are described:* Entomoantyx, *new genus (type species—* Ozaena cyanipennis *Chaudoir, 1852); and* Pachyteles *(*sensu stricto*)* enischnus, *new species (type locality— México, Jalisco, near Ixtapa). Combined in a single genus, but ranked as subgenera are:* Pachyteles *(*s. str.*) Perty, 1830 (type species—* P. striola *Perty, 1830);* Goniotropis *Gray, 1832 (type species—* G. braziliensis *Gray, 1832), with its junior synonym,* Scythropasus *Chaudoir, 1852 (type species—* S. elongata *Chaudoir, 1852); and* Tropopsis *Solier, 1849 (type species—* T. marginicollis *Solier, 1849). The following species-level synonymy is proposed, with the senior synonym and thus valid name listed first for each combination:* Pachyteles *(*Goniotropis*)* parca *LeConte, 1884 (type area— U.S.A., Arizona)* = P. beyeri *Notman, 1919 (type locality— México, Baja California Norte, San Felipe);* Pachyteles *(*s. str.*)* gyllenhali *(Dejean, 1825) (type area— Cuba)* = P. verticalis *(Chaudoir, 1848) (type area— Colombia)* = P. testaceus *Horn, 1868 (type locality— Fort Grant,Arizona U.S.A.); and* Ozaena lemoulti *Bänninger, 1931 (type locality— French Guiana, St. Jean du Maroni)* = O. halffteri *Ogueta, 1965b (type locality—México, Veracruz, Tlapacoyan). The genera are characterized in terms of adults, using defensive secretions and structural features, including chaetotaxy, antennae, mouthparts (labrum, mandibles, maxillae, and labium), antenna cleaner of the fore tibia, male genitalia, ovipositor, and internal genitalia of females. To facilitate future phylogenetic analysis, transformation series were postulated for each character, using the Metriini (genus* Metrius *Eschscholtz) as out-group. This provided a linear series for the genera, from most like to least like* Metrius*:* Entomoantyx*;* Pachyteles *(*s. lat.*);* Physea*;* Ozaena*; and* Platycerozaena. Ozaena *and* Platycerozaena *are postulated to be sister groups, but relationships to one another of the remaining genera have not been postulated. The following species are characterized, in terms of adult features and geographical distribution:* Entomoantyx cyanipennis *(Chaudoir);* Physea hirta *LeConte, 1853 and* P. latipes *Schaum, 1864;* Pachyteles *(*Goniotropis*)* parca *LeConte,* P. kuntzeni *Bänninger, and* P. elongatus *(Chaudoir);* Pachyteles *(*s. str.*)* gyllenhali *Dejean,* P. enischnus, *new species, and* P. mexicanus *(Chaudoir, 1848); and* Ozaena lemoulti *Bänninger. A key is provided to these species and to the Middle American genera. Based on general zoogeographic theory for Middle America, the following hypothesis is developed to explain the distribution patterns of the Middle American genera and the species* *whose ranges either enter the United States or are near the U.S.-Mexican border: Middle America was entered at various times during the Tertiary by the ancestor of* Entomoantyx *and members of each of the genera; i.e., the only genus to evolve as such in Middle America was* Entomoantyx. *Most of the extant species differentiated in Late Tertiary time as east-west vicariants, as a result of the influence of climatic change and mountain building on the ranges of the ancestral populations. Two species, P* gyllenhali *and* O. lemoulti, *arrived in the northern areas comparatively recently, each becoming widespread during Pleistocene time.*

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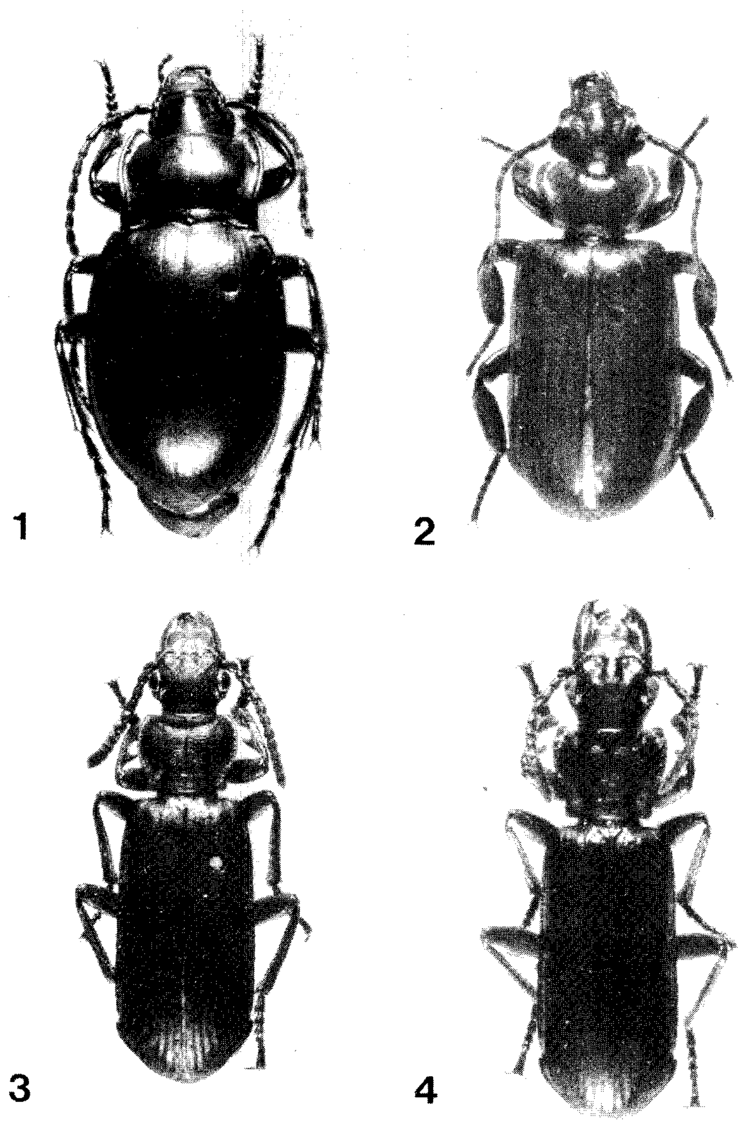
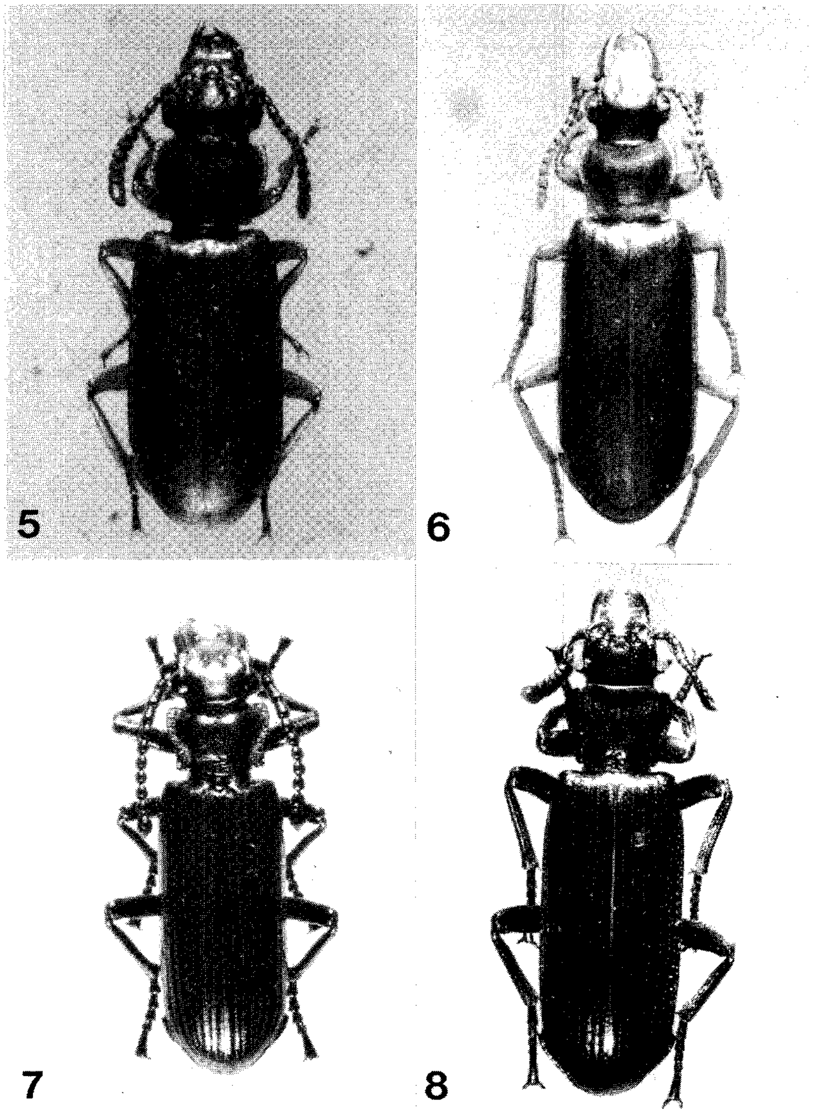
## INTRODUCTION

The roots of this study extend back in time to the early 1950's, when the first author found in the collections of the U. S. National Museum of Natural History a specimen of *Ozaena* collected in a Plant Quarantine Station at Nogales, Arizona. As far as was known then, this record represented a substantial range extension for the genus, and it seemed not unlikely that the specimen was an accidental import from the American tropics, to the south. Max Bänninger, at that time the foremost authority on Ozaenini, was consulted, and he reported the identity of the specimen as *Ozaena elevata* (*cf.* Bänninger, 1956: 400), a species otherwise known only from South America. The specimen was labelled by him as *Ozaena elevata* var.

In 1978, the second author collected a specimen of *Ozaena* at Peña Blanca, Pajarito Mountains, southern Arizona— a locality near Nogales, but far enough away to suggest that the species represented was indeed native to the area. Comparison of this specimen with the one taken at Nogales showed that the two were sufficiently similar to be regarded as conspecific. But, what species did they represent? Having entered into discussion about ozaenines in the United States, we



Figs. 1–4. Photographs of habitus, dorsal aspect, of: 1, *Metrius contractus* Eschscholtz; U.S.A. California, Siskiyou County, Pickewish Campground (UASM); Standardized Body Length = 10.9 mm. 2, *Physea latipes* Schaum; México, Venedio (CASC); SBL = 11.1 mm. 3, *Pachyteles (Goniotropis) parca* LeConte; U.S.A., Arizona, Santa Cruz County, Santa Rita Mts., Madera Canyon; SBL = 10.9 mm. 4, *P. (Goniotropis) kuntzeni* (Bänninger); U.S.A. Arizona, Santa Cruz County, Peña Blanca (UASM); SBL = 15.2 mm.



Figs. 5—8. Photographs of habitus, dorsal aspect, of: 5, *P.* (*sensu stricto*) *gyllenhali* (Dejean); U.S.A., Arizona, Graham County, Aravaipa Canyon, 17.7 km. N. Klondyke (UASM); SBL = 4.4 mm. 6, *P.* (*sensu stricto*) *enischnus*, new species; Mexico, Jalisco, nr. Ixtapa, gallery forest SBL = 7.0 mm. 7, *Ozaena lemoulti* Bänninger; U.S.A., Arizona, Pajarito Mts., Peña Blanca; SBL = 18.0 mm. (SMCC); 8, *Platycerozaena brevicornis* (Bates); French Guiana Monte de Kaw, Piste de Kaw, Km. 3 (UASM); SBL = 11.4 mm.

asked this question of one another some seven years ago. Encouraged by Terry L. Erwin, we decided to answer it, and at the same time to put into a more general context the ozaenines inhabiting the southwestern United States.

In the course of our preliminary investigation, we found striking differences among the genus-level taxa represented in the United States, and these discoveries led us into an investigation of the Middle American ozaenine genera. Gradually, the emphasis of the study changed from a species-level faunal study to a generic treatment, with data about these species appended.

This paper is intended to achieve two goals: first, to establish the basis for a phylogenetic analysis of the ozaenine genera of the world; and second, to summarize the information that can be gleaned from knowledge of ozaenine species at the northern limits of the Tribe in the New World. The only questions we attempt to answer are two: first, proximity of relationships of ozaenines and the genus *Metrius* Eschscholtz, made necessary by the potential out-group status of the latter; and two, the original question about the identity of the specimens of *Ozaena* that led to this study. Darlington's (1950) demonstration of close relationships between ozaenines and paussines is so well established as to be unchallengeable. The principal matter here is to establish at the generic or genus-group level the propinquity of ancestry of the two tribe-level groups.

## MATERIAL AND METHODS

### Material

We studied about 400 specimens of Metriini and Ozaenini, and representatives of several paussine genera. The material is in the collections noted below. Each collection is designated in the text by a coden; these are listed below, in alphabetical order, in association with the names and addresses of the institutions represented. Names of curators are indicated in parentheses.

AMNH- Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024, U.S.A. (L. H. Herman).
ASUT- Department of Zoology, Life Sciences Center, Arizona State University, Tempe, Arizona 85281, U.S.A. (F. Hasbrouck).
BMNH- Department of Entomology, British Museum (Natural History), Cromwell Road, London, SW7 5BD, United Kingdom. (N.E. Stork).
CASC- Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. (D.H. Kavanaugh)..
CISC- California Insect Survey, Division of Entomology, University of California, Berkeley, California, 94720, U.S.A. (J. Chemsak)..
CNCI- Canadian National Collection of Insects, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, K1A 0C6. (J. M. Campbell).
CUIC- Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York, 14850, U.S.A. (J.K. Liebherr).
EGRC- Edward G. Riley Collection, Department of Entomology, Texas A & M University, College Station, Texas 77843, U. S. A.
ETHZ- Entomologische Institut, Eidgenossische Technische Hochschule-Zentrum, Universitätstrasse 2, CH-8006, Zürich, Switzerland (W. Sauter).
FSCA- Florida State Collection of Arthropods, Division of Plant Industry, 1911 34th Street, S.W., P.O. Box 1269, Gainesville, Florida, 32602, U.S.A. (R.E. Woodruff).

MCZC- Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 02138, U.S.A. (S.R. Shaw; D.R. Maddison).
MCZC Fall- H.C. Fall Collection, MCZC, address as above..
MNHP- Entomologie, Museum National d'Histoire Naturelle, Paris 75005, France. (H. Perrin)..
OSUC- Ohio State University Collection of Insects and Spiders, 1735 Neil Avenue, Columbus, Ohio, 43210, U.S.A. (C.A. Triplehorn).
SMCC- Scott McCleve, 2210 13th Street, Douglas, Arizona, 85607, U.S.A.
TAIU- Department of Biology Collections, Texas A&I University, Kingsville, Texas, 78363, U.S.A. (James A. Gillaspy).
TAMU- Department of Entomology, Texas A&M University, College Station, Texas, 77843, U.S.A. (Horace R. Burke).
UASM- Strickland Entomological Museum, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3.
USNM- United States National Entomological Collection, Department of Entomology, United States National Museum of Natural History, Washington, D.C., 20560, U.S.A. (T.L. Erwin).
ZMHB- Museum für Naturkunde der Humboldt Universität zu Berlin, Bereich Zoologisches Museum, Invalidenstrasse 43, DDR-1040 Berlin (F. Hieke).

### Methods.

Methods were standard, involving visual comparison of structural features, using magnifying equipment from an 8X hand lens to stereobinocular microscopes to a Cambridge Scanning Electron Microscope. Data were recorded in print, as line drawings, and as photographs.

*Measurements.*— These were made with a Wild stereobinocular microscope Model M-5, at 25X magnification. They were taken to determine size and proportions.

Length is expressed as Standardized Body Length, determined as the sum of length of: head (from mandibular condyle to posterior margin of compound eye); pronotum (along mid-line); and elytra (along the suture, from apex of scutellum to apex of elytra). Width is maximum transverse width of elytra. Measurements presented in the species descriptions are of the smallest and largest males and females, as determined by visual inspection of the material at hand. The values obtained are thus rough approximations of total range in body size.

*Ranking.*— Used are subfamily, tribe, genus, subgenus and species. For the higher ranks, we accepted those proposed by Bänninger (1927), Kryzhanovskij (1976), and Erwin (1979a). For genus and subgenus, we sought major gaps in continuity of variation of structural features. The resulting taxonomic treatment is thus conservative.

*Relationships.*— Statements about this topic are based on inferred relative propinquity of descent, as determined by shared derived features. As out-group, we used the monobasic tribe Metriini. Because of our deliberately limited data base, we did not attempt a formal phylogenetic analysis of the taxa.

Species are regarded as evolving units reproductively isolated from other such units, the gaps being judged by discontinuity in structural features.

## HISTORICAL ASPECTS

### Tribal-level Synonymy

Tribe OZAENINI

"La cinquieme division" (in part) Latreille, 1817: 189.
Bipartis (in part) Latreille and Dejean, 1822: 79.—Latreille, 1829: 386.
Scaritides (in part) Dejean, 1825: 356.— Dejean and Boisduval, 1829: 230.
Brachinides (in part) Audouin and Brullé, 1834: 240.— Chenu, 1851: 87.
Ozenides Lacordaire, 1854: 154, 155.— Chaudoir, 1868: 43.
Ozaenidae Hope, 1838: 107.— LeConte, 1861: 5, 14.— Jeannel, 1941: 89.— 1946: 46 .— Regenfuss, 1975: 283.
Ozaeninae Bates, 1881: 24.— Winkler, 1924: 83.— Crowson, 1955: 6.— Basilewsky, 1962: 291.— Nagel, 1979a: 9, 10, 11.— 1979b: 15.— Crowson, 1981: 502, 504.
Ozaenini Schaum, 1860: 773.— LeConte, 1861: 14.— Horn, 1881: 124, 128.— LeConte and Horn, 1883: 23.— Sloane, 1920: 118.— Leng, 1920: 49.— Sloane, 1923: 242.— Csiki, 1927: 425.— Bänninger, 1927: 177.— Andrewes, 1929: 162.— van Emden, 1942: 24.— Blackwelder, 1944: 23.—Darlington, 1950: 49.— Ball, 1960: 94.— Bell, 1967: 105.— Lindroth, 1969: XXII.— Hlavac, 1971: 57.— Kryzhanovskij, 1976: 82, 87.— Eisner *et al.*, 1977: 1385.—Reichardt, 1977: 377.— Ball, 1979: 91, 95, 100.— Ward, 1979: 185, 186, 188, 190.— Moore, 1979: 198.— Goulet, 1979: 205.— Thompson, 1979: 212, 226, 231, 232.— Erwin, 1979b: 481, 557, 583, 591.- Erwin and Sims, 1984: 374.— Ball, 1985: 24.— Erwin, 1985: 451, 467.— Stork, 1985: 1113.
Ozaenina Iakobson, 1906: 316.— Bousquet, 1986: 378.
Mystropomini Horn, 1881: 116-117.— Sloane, 1923: 246.
Mystropominae Dupuis, 1911: 2.
Mystropomitae Jeannel, 1946: 47.
Paussidae (in part) Crowson, 1955: 6.— Deuve, 1988: 176.
Paussitae (in part) Erwin and Sims, 1984: 374.— Erwin, 1985: 467.
Paussinae (in part) Moore, in Moore *et al.*, 1987: 26.

### Classification and Relationships

*Tribal level.*— Latreille (1817: 189) included *Ozaena* in his fifth division of the Carabiques, which included also "Les Morions", "Les Aristes", "Les Harpales", "Les Feroniens"," Les Licinines", "Les Badistes", and "Les Panagees". Latreille and Dejean (1822), Dejean (1825), and Dejean and Boisduval (1829) included *Ozaena* in the Bipartis, along with the scaritines and genus *Morio*n Latreille. Dejean (1825: 355) stated implicitly, however, that *Ozaena* was an aberrant element, and later authors (Audouin and Brullé, 1834, and Chenu, 1851) included the ozaenines with the brachinines and various lebiomorphs. In part, this association was based on the crepitating behavior of adults ozaenines and brachinines, though the diagnostic feature given was habital— adults with rather thick bodies.

Hope (1838) first recognized ozaenines as a distinct assemblage, though he included with them *Nomius* Castelnau, *Melisodera* Westwood, and *Catapiesis* Brullé. Hope neglected to give reasons for erecting the Ozaenidae. Lacordaire (1854) followed suit, including in the group eight ozaenine genera and *Nomius*, characterized in part on a reduced mesosternum so that the mid-coxae are in contact with one another. He noted also the posterolateral elytral flanges, and that they did not occur in *Nomius*.

Schaum (1860) did not treat the Ozaenini in detail, though he (*l.c.*, p. 773) located the group (as defined by Lacordaire) in the carabine assemblage (*i.e.*, adults with mid-coxal cavities open) and in a sub-group including Omophronini, Elaphrini, Carabini, Loricerini, Promecognathini, and Mormolycini. He did not place them in the sub-group that followed that included the Scaritini, Siagonini, and Hiletini, nor with the brachinines and other truncatipennian groups. This was indeed a radical departure in classification at that time, and quite appropriate.

Chaudoir (1868) provided a synopsis of the Ozaenini, bringing together information about all of the taxa previously described, and describing new genera and species. For the group diagnosis, he gave special emphasis to the reduced mesosternum that Lacordaire had recorded, and noted as well, following Schaum (1860) that the mesothoracic suture extended to the mid-coxae. He stated also his belief that the ozaenines should be placed between the brachinines and helluonines, where they had been placed by previous authors. Perhaps Chaudoir's most important contribution in this work was to identify the distinctiveness of *Ozaena dentipes* Olivier (type species of *Ozaena*), separating it from the other species that had been described in the genus, and transferring the latter to other taxa—principally to *Pachyteles* Perty.

Bates (1881: 24) placed the ozaenines about as Schaum had done, between loricerines and scaritines, in their own subfamily. In the same year, Horn arrayed the ozaenines in two tribes: Mystropomini and Ozaenini. The basis for this division was an error: Horn, while correctly recording that the middle coxal cavities were open in *Mystropomus*, . mistakenly stated that they were closed in the remaining genera of ozaenines. He placed the Ozaenini (minus *Mystropomus*) in the subfamily Harpalinae, near the Panagaeini. *Mystropomus* was left in the Carabinae, or first major division of the Carabidae. Although Bates (*l.c.*) had pointed out the error (Horn sent him his MS before it was published), he did so in such a gentlemanly manner that the point seemed to have been lost. Thus, LeConte and Horn (1883) and Leng (1920) followed Horn's arrangement. Dupuis (1911) also recognized the mystropomines as a group separate from the Ozaenini, at least implicitly. Because he treated the Metriinae in the same publication, evidently he accepted Horn's opinion about a close relationship between the latter and the mystropomines.

Sloane (1923: 246) noted Horn's mistaken interpretation of the thoracic structure of the Ozaenini (*sensu* Horn), and re-combined the latter with *Mystropomus*. He placed the re-constituted Ozaenini in his "Carabidae Clausae", along with Metriini, Migadopini, Scaritini, Siagonini, Enceladini, Promecognathini, Elaphrini, Loricerini, and Omophronini. Csiki (1927) and Andrewes (1929) followed Sloane's sequencing.

Bänninger (1927) revised the Ozaenini, providing a much more comprehensive treatment than Chaudoir's. He gave a clear tribal diagnosis and detailed description, based on adult external features of the known genera. He confirmed that the affinities of the Ozaenini were with the carabines (broad sense), and particularly with the Cicindisini, Nototylini, and Metriini. Among diagnostic features for the Ozaenini that he emphasized were the elytral flanges.

Kolbe (1927) hypothesized that ozaenines and paussids were closely related.

Van Emden (1942) characterized the larvae of the Ozaenini, emphasizing the unusual modifications of the urogomphi and posterior abdominal segments.

Jeannel (1941) included in his new taxon Isochaeta (based on the apical position of both fore tibial spurs): trachypachines, gehringiines, metriines, ozaenines, and paussines. However, he did not pursue the matter of relationships of any of these groups to one another. Nonetheless, one can see from the sequence of taxa that probably he considered the last three to be related to one another.

Darlington (1950: 48) re-asserted the basis for hypothesizing close relationship between paussids and ozaenines, noting that Kolbe was the first so to insist. Nonetheless, he retained the ozaenines as a separate tribe, and in effect treated the paussids as an informal taxon to include the Protopaussini and Paussini. Darlington did not comment about classification of the ozaenine genera, but he developed a detailed classification for the paussine genera.

Basilewsky (1962: 291) transferred the Protopaussini from the subfamily Paussinae to the Ozaeninae, on the basis of the plesiotypic unreduced antennal pedicel. He did not take into account the apotypic features shared by protopaussines and paussines.

Transformation series in a variety of character systems support adequately the hypothesis of monophyly of paussines and ozaenines. Crowson (1955) accepted this, but rather than treating this complex as a group within the family Carabidae, he chose to recognize the paussine complex as a separate family, including therein the Ozaenini.

While there is little doubt that the ozaenine-paussine complex is monophyletic, there is some doubt that the Ozaenini are monophyletic relative to the paussines, *i.e.*, some extant ozaenine genus might be the sister group of the Protopaussini + Paussini. So, the more distal part of the reconstructed phylogeny of this complex is not resolved at the tribal level. What about the more basal part: is there an extant sister group for the ozaenine-paussine complex?

Luna de Carvalho (1959) pointed out the marked similarity between the genitalia of metriines and ozaenine-paussine males. Bell (1967) united in his new taxon Septisternia the tribes Metriini, Ozaenini and Paussini (implicitly Protopaussini + Paussini), implying thereby that *Metrius* was the sister group of the ozaenine-paussine complex. This hypothesis was accepted by Regenfuss (1975) and by various subsequent authors.

On the basis of superficial examination of larval features, Goulet (1979: 205) suggested that "metriines are simply ozaenines", and this opinion of striking similarity was borne out by Bousquet's (1986) detailed study of the larval characteristics of *Metrius*.

Similarity between adults of *Metrius* and those of the ozaenine-paussine complex in complex defensive secretions and their delivery systems provide more evidence of close relationships of these taxa (Eisner and Aneshansley, 1981).

Thus, metriines and the ozaenine-paussine complex can be treated as a monophyletic assemblage. Without going into detail here, we assert that the Metriini is the sister group of the hypothetical ancestor of the ozaenine-paussine complex.

Erwin and Sims (1984) and Erwin (1985) hypothesized a close relationship among the supertribes Metriitae (including Metriini, only), Paussitae (including Ozaenini + Paussini and four other tribes) and Brachinitae. These supertribes were included in the subfamily Paussinae. As indicated above, metriites belong with the paussite assemblage. Thus only two main lineages are represented in the Paussinae: Paussitae and Brachinitae. Are these two really sister groups? In addition to Erwin and Sims (*l.c.*), Eisner *et al.* (1977), Bousquet (1986) and Deuve (1988) have stated so. Others (Forsyth, 1972; Crowson, 1981, p. 503, Bell, 1983, p. 595, and Moore *et al.*, 1987, p. 26 and 48) indicate either implicitly or explicitly their belief that the similarity between brachinites and paussites, in complex defensive secretions and complex delivery systems— the best evidence available for close relationship— are the result of convergence. We favor the latter opinion.

Similarities between brachinites and Psydriformes (*sensu* Erwin, 1985) are in apotypic features of several systems that seem to be functionally independent (thoracic structure, organization of the antennal cleaner of the fore tibia, structure of the male genitalia and ovipositor). It seems to us that the best explanation for this array of similarities is inheritance from a common ancestry. Thus, we hypothesize that the brachinites are either members of the Psydriformes, or at least are the sister group of this group of carabids that, overall, is more highly derived than is the ozaenine-paussine complex.

Incredible as it seems, then, the elaborate defensive system of brachinites and paussites must have evolved independently if the similarities between brachinites and psydriforms are indicative of close relationship— as we hypothesize. Thus, there is a clear conflict of evidence. This conflict must be resolved, in terms of additional evidence yet to be found that will tip the balance one way or the other. Forbes (1926: 59) in his monumental publication about wing folding, pointed out the similarity between *Brachinus* and *Passus* adults in their distinctive folding pattern of the hind wings. He believed that this similarity did, in fact, indicate relationship (personal communication). It remains to be determined, however, if other brachinines and paussines have this same form of wing folding, and it remains to be determined, as well, if the pattern is plesiotypic or apotypic in the Carabidae. This lead is worth pursuing.

The question of ranking of the metriine + ozaenine + paussine complex remains to be answered. Erwin and Sims (*l.c.*) and Erwin (*l.c.*) recognize two supertribes, as noted above. Bousquet (1986: 378) proposes recognition of one tribe, the Paussini, to include two subtribes— Ozaenina and Paussina (Metriini + Protopaussini + Paussini of authors). We favor treating this complex as a subfamily, with three tribes, only: Metriini, Ozaenini, and Paussini. (We exclude thereby Nototylini, and Cicindisini that were included by previous authors). If we did not use the rank of subfamily in the Carabidae, we would follow Bousquet in his system of ranking.

The history of classification of the Ozaenini has been one of surprising discoveries and recurrent themes. The most surprising discovery is that of close relationship between metriines and ozaenines+paussines. It was presaged by Horn (1881: 117), when he pointed out the similarities in structural features between *Mystropomus* . and *Metrius*. However, this lead was not followed for many years. The recurrent theme is the relationship between ozaenines and scaritines on the one hand, and between paussines (present sense) and brachinines, on the other. The linear arrangement by Erwin (1985: 467) is very similar in part to that presented in the past, with ozaenines either in (Dejean, 1825) or near (Schaum, 1860) a complex including the scaritines, and either in (Audouin and Brullé, 1834) or near (Chaudoir, 1868) the brachinines. We conclude that our predecessors of the last century did rather well, though they had simpler equipment and lacked the knowledge of carabid diversity that we have now.

*Generic level.*— The only explicit attempt to classify the genera of Ozaenini was by Jeannel (1946: 46-48). Treating this assemblage as a family, he recognized three subfamilies: the monogeneric Australian Mystropomitae and Neotropical Physeitae, and the Neotropical-Afrotropical-Oriental Ozaenitae to include all of the remaining genera. For the Ozaenitae, he recognized three tribes: the Oriental Eustrini, including *Eustra* Schmidt-Goebel and *Dhanya* Andrewes; the monogeneric Neotropical Pachytelini for the genus *Pachyteles* Perty; and the Neotropical-Afrotropical-Oriental Ozaenini for the remaining genera.

For the Afrotropical-Madagascan fauna, Jeannel erected the subgenus *Afrozaena*, and included it, *Sphaerostylus* Chaudoir, and *Pseudozaena* Castelnau as subgenera of the genus *Pseudozaena*. Basilewsky (1962: 291-293) accepted implicitly Jeannel's classification, but added the Protopaussini to the Ozaenidae (treated by Basilewsky as a subfamily). However, he disagreed with Jeannel's treatment of *Pseudozaena*, ranking each of the three subgenera as a genus, and reranking *Itamus* Schmidt-Goebel as a genus separate from *Pseudozaena* (*sensu stricto*).

For the classification of genera, we agree that *Mystropomus* should be placed in a higher taxon of its own (as a subtribe), at the base of the tribe. The evidence that we have seen suggests that *Ozaena* and its close relative, *Platycerozaena* Bänninger, are not closely related to any of the other ozaenine genera, and we think that *Pachyteles* may be a plesiotypic sister group to at least some of the Old World genera. *Physea* and its close relative *Physeomorpha* Ogueta,are abundantly distinctive in features of adults, some of which indicate marked primitiveness. Overall though, we think that this group is not far removed from the pachyteline assemblage.

In the light of these observations, we cannot offer much support for Jeannel's classification of the ozaenine genera, though we have nothing to put in its place. See also Stork (1985: 1120). We think it best to avoid a formal classification of these genera at this time, though we realize that preparation of such a classification must be a high priority for future workers on this tribe.

## COMPARATIVE MORPHOLOGY

### Structural and Biochemical Features

In this section, we describe and compare in an evolutionary context, microsculpture, various setal patterns, structures, and defensive secretions useful in characterizing the genera of ozaenine carabids.The major purpose of this section is to explain the details of character complexes which either have not been used extensively in classifying ozaenines, or have been used only superficially. As a working hypothesis, we accept the tribe Metriini (genus *Metrius* Eschscholtz) as out-group for the tribes Ozaenini and Paussini (*sensu lato*, including Protopaussini and Paussini *sensu* Darlington, 1950, or Paussidae Jeannel, 1946), which we believe are sister groups.

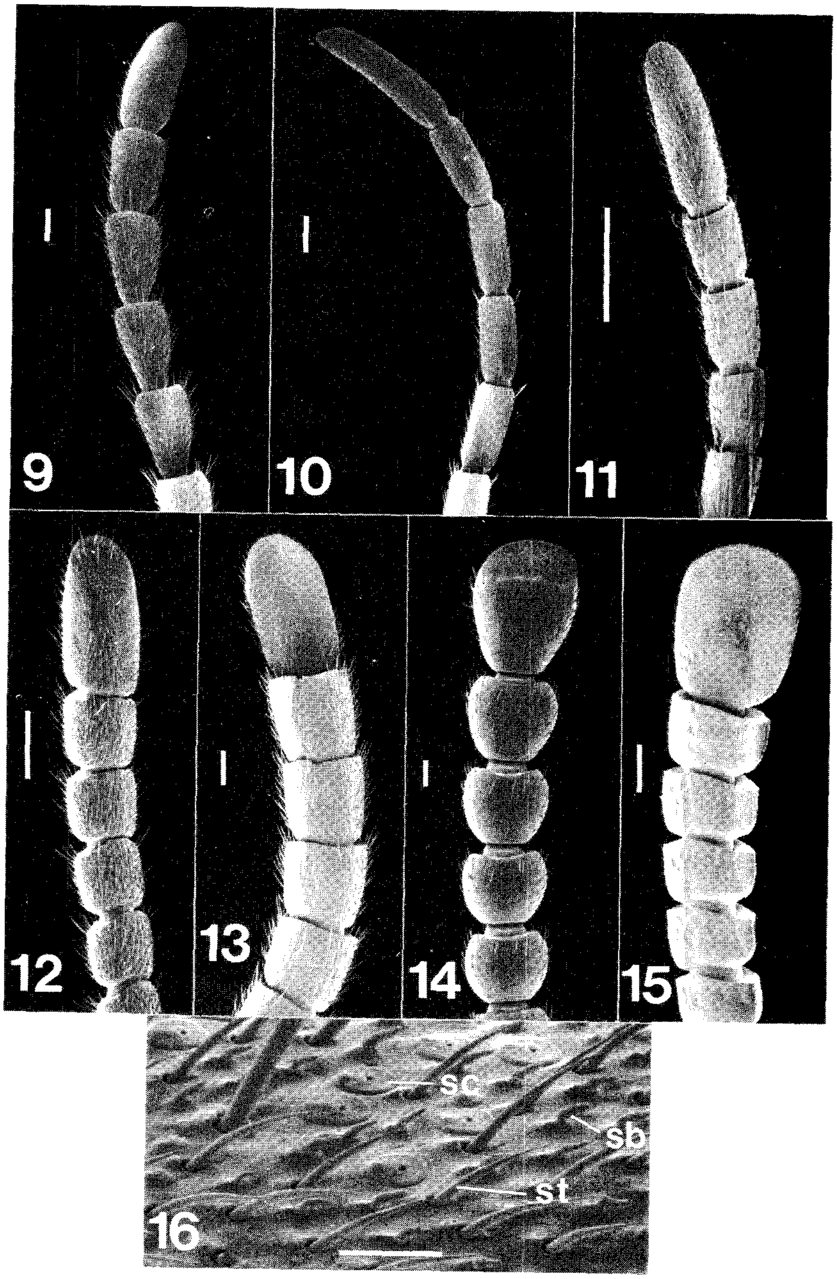
*Microsculpture.*— Adults of *Metrius* exhibit an isodiametric mesh pattern over almost the entire body surface. For the ozaenines, dorsal sculpture is isodiametric, with microlines either distinct or reduced and hard to see, or lost (Figs. 107A-C). For the ventral surface, mesh pattern varies from isodiametric to transverse, with most sclerites exhibiting a transverse pattern. No marked or taxonomically very useful trends were identified.

*Setae on dorsal surfaces of head and pronotum.— Metrius* adults have a generalized pattern of setal number: clypeus and vertex, one pair each; pronotum, two pairs of marginal setae. Ozaenines are more setose generally, or have fewer setae. Entomoantyx .i.Entomoantyx, new genus; adults have a pair of clypeal setae, a pair of supraorbitals, and several in a transverse row across the vertex. The lateral margins of the pronotum have three to five pairs of setae. Physea .i.Physea Brullé; and Pachyteles .i.Pachyteles Perty;adults have about 12 clypeal setae, one pair of supraorbitals, and several pairs of setae posterad the compound eyes. The lateral pronotal setae are several pairs, as in Entomoantyx.

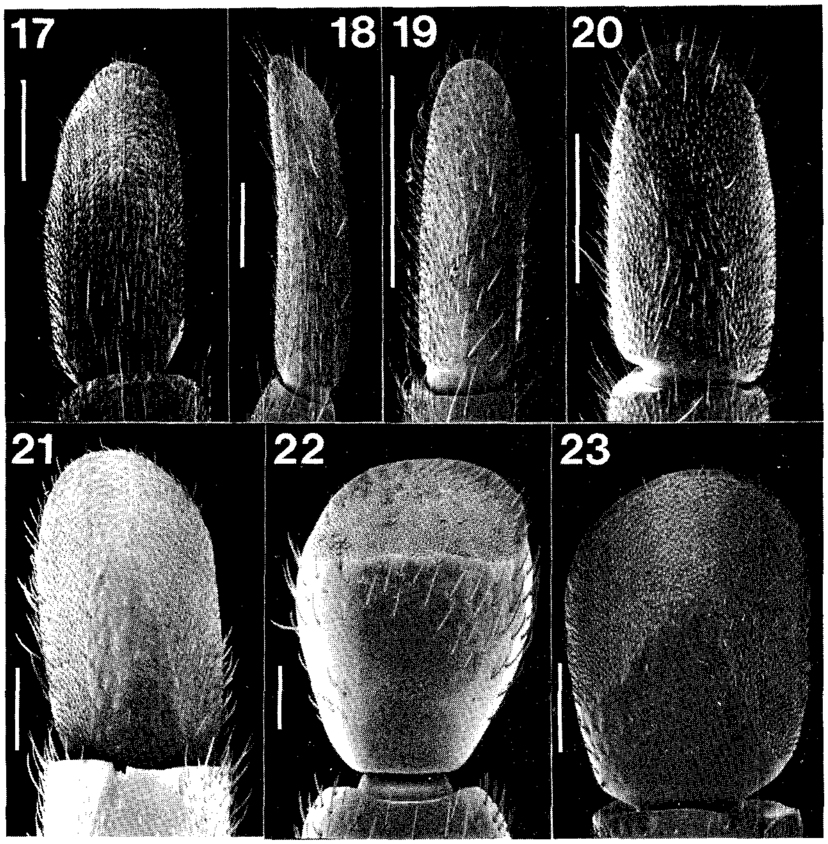
In contrast, adults of *Ozaena* and *Platycerozaena* lack clypeal, supraorbital and lateral pronotal setae.

The transformation series would seem to be:

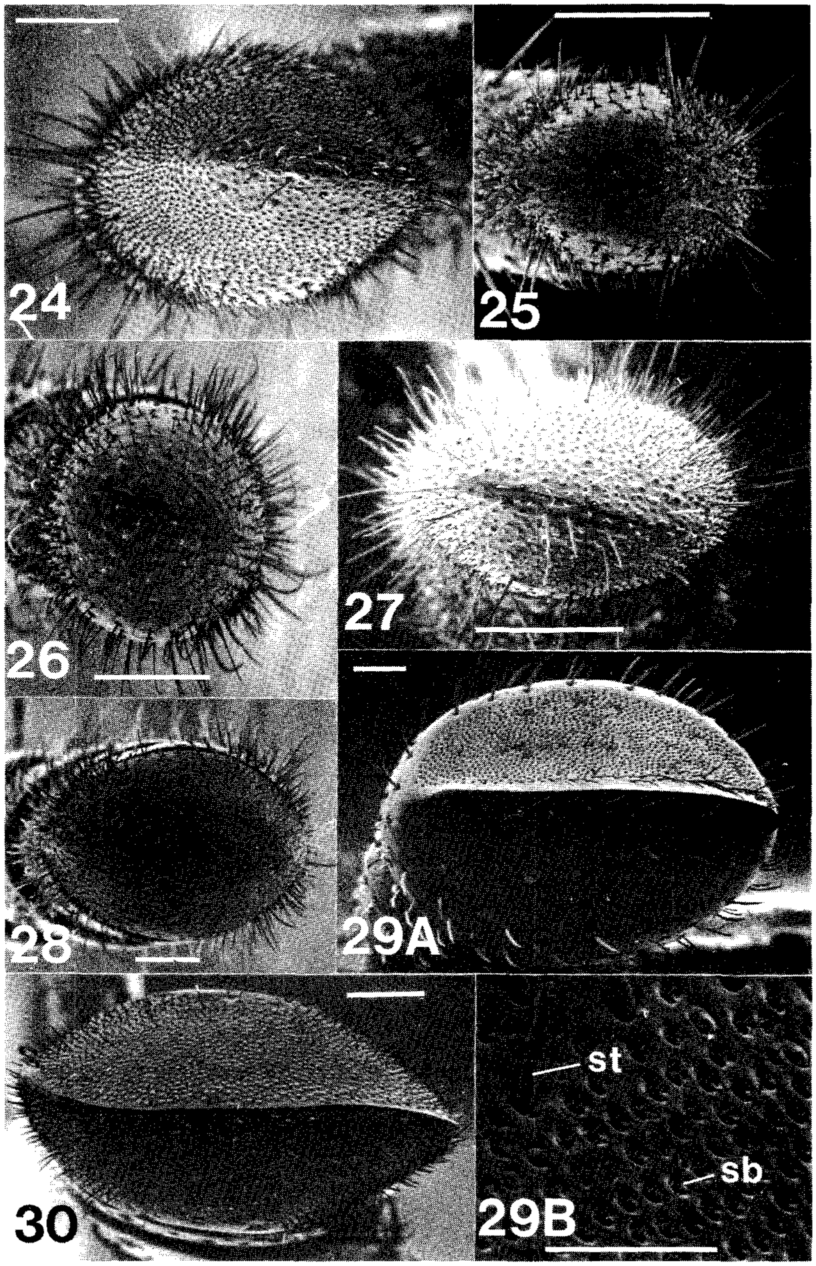
*Ozaena* ←——*Metrius* ——→*Entomoantyx*
*Platycerozaena* *Physea*
*Pachyteles*



Figs. 9—16. 9—15, Left antennomeres, 7—11, of: 9, *Metrius contractus* Esch.; 10, *Physea hirta* LeC.; 11, *Entomoantyx cyanipennis* (Chd.); 12, *Pachyteles* nr. *striola* Perty; 13, *Pachyteles kuntzeni* (Bänn.); 14, *Ozaena lemoulti* Bänn.; 15, *Platycerozaena panamensis* (Bates).16, Left antennomere 11, sense organs, of *Metrius contractus* Esch. Scale bars = 200 µm, Figs. 9-15; 20 µm, Fig. 16. Legend: sb- *sensillum basiconicum*; sc- *sensillum coeloconicum*; and st- *sensillum trichodeum*.



Figs. 17—23. Left antennomere 11, of: 17, *Metrius contractus* Esch.; 18, *Physea hirta* LeC.; 19, *Entomoantyx cyanipennis* (Chd.); 20, *Pachyteles* nr. *striola* Perty; 21, *Pachyteles kuntzeni* (Bänn.); 22, *Ozaena lemoulti* Bänn.; 23, *Platycerozaena panamensis* (Bates). Scale bars = 200 µm,



Figs. 24—30. Left antennomere 11, apical aspect, of: 24, *Metrius contractus* Esch.; 25, *Physea hirta* LeC.; 26, *Entomoantyx cyanipennis* (Chd.); 27, *Pachyteles* nr. *striola* Perty; 28, *Pachyteles kuntzeni* (Bänn.); 29, *Ozaena lemoulti* Bänn. .—A, lower mag.; B, higher mag., showing sense organs; 30, *Platycerozaena panamensis* (Bates). Scale bars = 100 µm, Figs. 24—29A, and 30; 50µm, Fig. 29B. Legend: sb- *sensillum basiconicum*; st- *sensillum trichodeum*.

*Antennae.*— Variation occurs in overall length, form of antennomeres, and distribution and frequency of types of sensilla. Overall length can be appreciated from examination of Figs. 1 to 8. These and Figs. 9 to 30 illustrate also differences in form and proportions of antennomeres. Note particularly the moniliform articles of Ozaena adults (Figs. 14 and 22), quadrate form of antennomeres 4-10 characteristic of *Pachyteles* (Figs. 12, 13, 20, and 21), and transverse antennomeres 4-10 characteristic of *Platycerozaena* (Fig. 15).

Antennomere 11 among Ozaenini differs from the more basal antennomeres in being longer (Figs. 10 and 11), and either as broad as (Figs. 12 and 13) or broader than (Figs. 14 and 22) the latter. Of special note are: slender curved antennomere 11 of *Physea* (Fig. 18), the basally constricted antennomere 11 of *Ozaena* (Fig. 22) and the very broad antennomere 11 of *Platycerozaena* (Figs. 15 and 23). Compared to Metrius (Fig. 17), antennomere 11 is narrow in *Physea* and *Entomoantyx*, slightly wider in *Pachyteles* (Fig. 20), and markedly wider in *Ozaena* and *Platycerozaena*.

Antennomere 11 exhibits differences in cross section also, which are best appreciated from an apical aspect (Figs. 24-30). For *Metrius* (Fig. 24), antennomere 11 is terete, without a sharply delimited apical ridge. For *Physea* and *Entomoantyx* (Figs. 25 and 26), antennomere 11 is nearly circular, and without a sharply differentiated apical ridge. For *Pachyteles* (Figs. 27 and 28) antennomere 11 is terete, but with a moderately sharply defined apical ridge. For *Ozaena* and *Platycerozaena* (Figs. 29A and 30), antennomere 11 is terete, with apical ridge sharply delimited as a carina: straight in *Ozaena* Fig. 29A), and sinuate in *Platycerozaena* (Fig. 30). The orientation of this carina is dorso-ventral.

Sensillar types of ozaenine antennomeres were identified through the publication of Zacharuck (1985: 25-26). Three types were recognized: trichodea (relatively long setiform hairs, st in Fig. 16); basiconica (relatively short and thick setiform hairs, sb in Fig. 16); and coeloconica (cones set in the floor of shallow depressions or pits in the cuticle, open to the outside through a small round hole, sc in Fig. 16 ). Only sensilla trichodea and basiconica are considered here.

Antennomeres 1 (scape) to 4 have few sensilla trichodea, and the intervening surfaces are relatively smooth. These antennomeres are not considered further. For antennomeres 5- 11, the surfaces bearing sensilla are more or less shagreened, the roughened appearance being the result of the raised cuticular rims around the bases of the sensilla.

Four types of distribution and frequency of sensilla are recognized.

**Type a**: sensilla trichodea numerous on antennomeres 5-11, each article with anterior and posterior faces with reduced setation at the middle, and in the triangle at the base of antennomere (Figs.9, 10, 12 and 13); sensilla basiconica numerous and rather long, ca. one-fifth length of sensilla trichodea, and confined to dorsal and ventral areas of antennomeres (*cf* Fig. 16). Taxa whose adults exhibit type a antennomeres are: *Metrius, Physea*, and *Pachyteles*.

**Type b:** for antennomeres 5-10, as in type a, above; for antennomere 11, toward apex, sensilla basiconica few and ordered in more or less parallel rows (Fig. 26); exhibited by *Entomoantyx* adults.

**Type c** (Fig. 29A-B): for antennomeres 5-10, sensilla trichodea and basiconica relatively few, basiconica very short, glabrous or nearly glabrous areas extensive; ventrally, or ventro-laterally, with small groups of sensilla basiconica; for antennomere 11, sensilla trichodea sparse dorso-ventrally, preapically, and a row each side of apical carina; about one-third of apex occupied by a dense concentration of sensilla basiconica. Type **c** is exhibited by *Ozaena* adults.

**Type d** (Fig. 23): for antennomeres 5-10, sensilla trichodea sparse and only about half length of those of types a-c; sensilla basiconica ventrally in dense groups, each side of a carina; antennomere 11 with relatively sparse, short sensilla trichodea apically, dorsally and ventrally, around triangular central area; sensilla basiconica very dense apically and along dorsal and ventral surfaces. Adults of *Platycerozaena* exhibit this sensillar type.

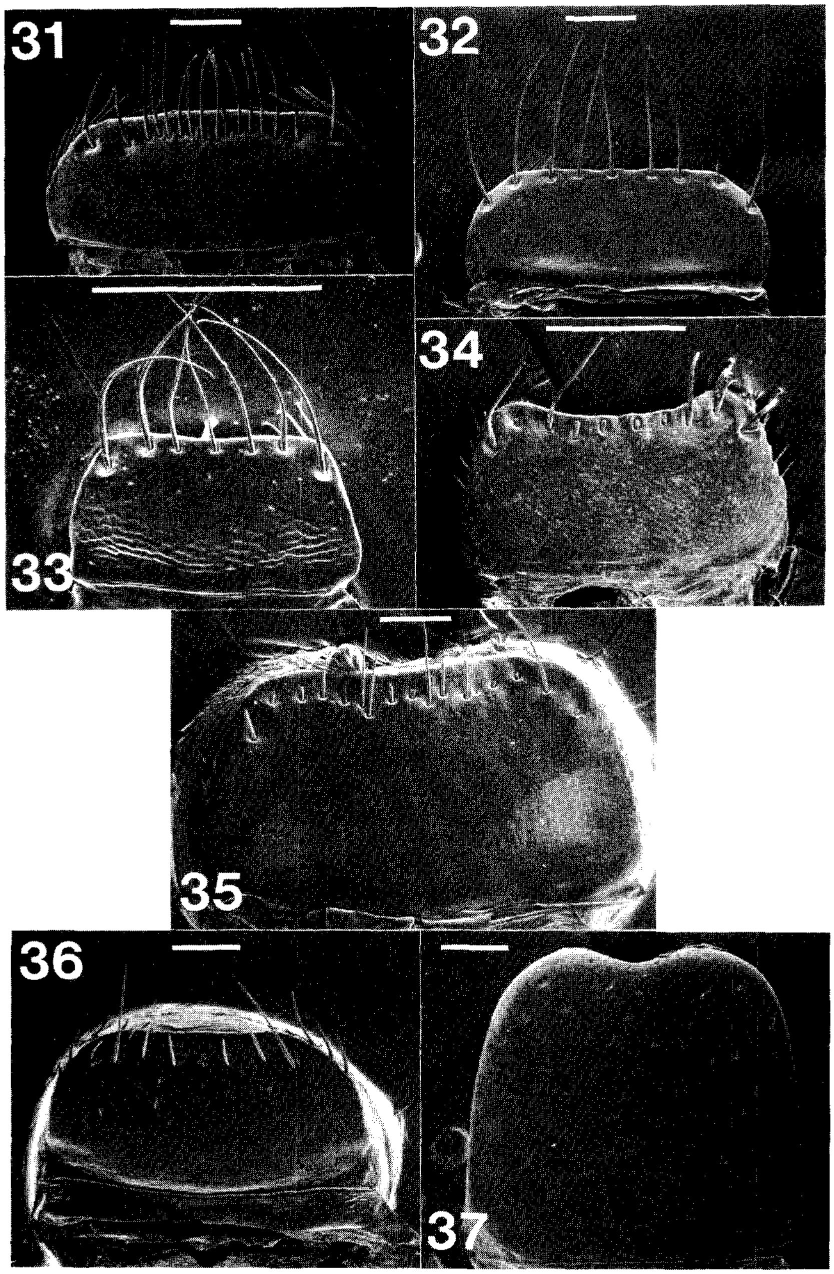
Based on extent of departure from the antennae of *Metrius*, these data suggest the following linear transformation series:

*Metrius* ——→*Physea*——→*Pachyteles*——→*Ozaena*
*Entomoantyx* *Platycerozaena*

*Labrum*.— This sclerite varies in form and setation. In form, it is transverse, i.e., wider than long, with the anterior margin truncate or nearly so (Figs. 31-33, 35 and 36), or broadly concave (Fig. 34), or elongate, with anterior margin notched (Fig. 37). Number of long preapical setae varies from 0 (*Platycerozaena*, Fig. 37) to 12 to 16 (*Metrius*, Fig. 31), with 7 to 12 intermediate (*Physea*, Fig. 32; *Entomoantyx*, Fig. 33; *Pachyteles*, Fig. 34; and *Ozaena*, Fig. 36). The highest number group is postulated as plesiotypic, since it is characteristic of the outgroup. Short setae (sensilla basiconica) are also evident on the dorsal surfaces of the labra of *Ozaena* and *Platycerozaena*. The data suggest the following branched transformation series:

*Physea*
*Entomoantyx*
↑
*Metrius*——→*Pachyteles*——→*Ozaena*——→*Platyceroz.*

*Mandibles*.— These are illustrated in Figs. 38 to 43, and characterized for each genus in Table 1. Mandibles of Carabidae have been described in several publications (*cf.* Shpeley and Ball, 1978; Forsythe, 1982; and Evans and Forsythe, 1985), and a detailed and more or less consistent nomenclature developed. The anterior incisor area, of varied width, terminates in the apical incisor tooth. The occlusal margin of the incisor is the terebral ridge or margin (**tm**, Figs. 38A-B). A terebral tooth (**tt**) is near the posterior part of the terebral margin. Below the tooth is the retinaculum (**r**, Fig. 38C), more or less prominent, with an anterior (**art**) and posterior (**prt**) retinacular tooth, joined by a retinacular ridge (Figs. 42A-B, 43E-F). The retinaculum is terminated by a groove, the premolar incision. Posterior to this incision is the molar area, divided or not by a molar incision: if divided, the anterior part of the molar area is the premolar (Figs. 38A-B, **pm**), the posterior part, the molar (Figs. 38A-B, **m**). Ventrally, various ridges occur in different taxa. In metriines and ozaenines, a ventral retinacular ridge (Fig. 39C, **vrr**) and a premolar ridge (Fig. 38C, **pr**) are recognized. A ventral groove (Fig. 38D, **vg**) of varied length bears a row of setae, the latter of varied length and density. The thicker lateral surface of each mandible contains a triangular depression, the scrobe. In *Metrius*, the scrobe bears a single long seta (Fig. 38A, **ss**); in ozaenines, it bears a single long seta (Fig. 40A) or a varied number of shorter setae (Figs. 39A and 41A). The dorsal surface is variously sparsely covered with setae shorter than those in the scrobe.



Figs. 31—37. Labrum, dorsal aspect, of: 31, *Metrius contractus* Esch.; 32, *Physea hirta* LeC.; 33, *Entomoantyx cyanipennis* (Chd.); 34, *Pachyteles* nr. *striola* Perty; 35, *Pachyteles kuntzeni* (Bänn.); 36, *Ozaena lemoulti* Bänn.; 37, *Platycerozaena panamensis* (Bates). Scale bars = 200 µm,

In all their features, the mandibles of *Metrius* adults are much like those of the still more primitive genus *Trachypachus*. Thus, we accept these features as plesiotypic. Mandibles of ozaenines are apotypic in the following features: terebral ridge short (not extended on to retinaculum); retinaculum reduced; and molar area not divided by an incision. The mandibles characteristic of all the genera examined, except *Platycerozaena*, exhibit additionally the following apotypic features: posterior retinacular tooth moderate to large, extended posteriorly; and ventral groove long. Considering the generally derived features of *Platycerozaena* and its close relationship to *Ozaena*, we believe that the seemingly plesiotypic conditions of the former genus (small posterior retinacular tooth and short ventral groove) are secondary losses, and are thus apotypic.

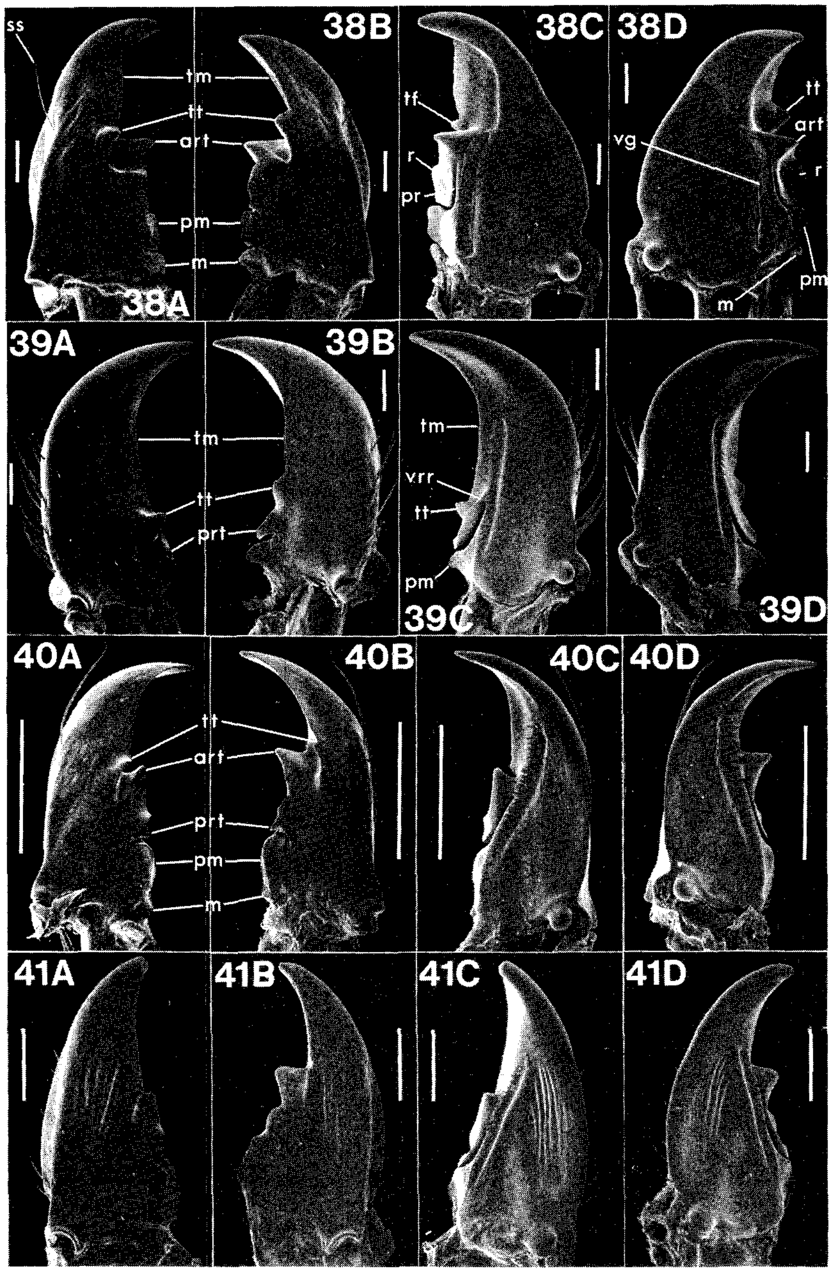
Within the Central American Ozaenini, we regard as most plesiotypic the mandibles of *Entomoantyx*: scrobe with single long seta, surface otherwise glabrous; and anterior retinacular tooth of the left mandible prominent. Most derived are the mandibles of *Physea*: falcate in form, and with the retinacular ridge reduced by loss of the anterior retinacular tooth. The mandibles of *Platycerozaena* also seem markedly apotypic, with broad, partially punctate dorsal surfaces, and somewhat reduced system of teeth and short ventral grooves. The mandibles of *Ozaena*, much like those of *Pachyteles*, are more derived in that the dorsal surfaces are punctate, as in *Platycerozaena*. We believe that the data presented are best summarized by the following branched transformation series:

$$\begin{tikzcd}
 & & \textit{Physea} & & \\
\textit{Metrius} \arrow[r] & \textit{Entomo.} \arrow[r] & \textit{Pachytel.} \arrow[u] \arrow[r] & \textit{Ozaena} \arrow[r] & \textit{Platycer.}
\end{tikzcd}$$

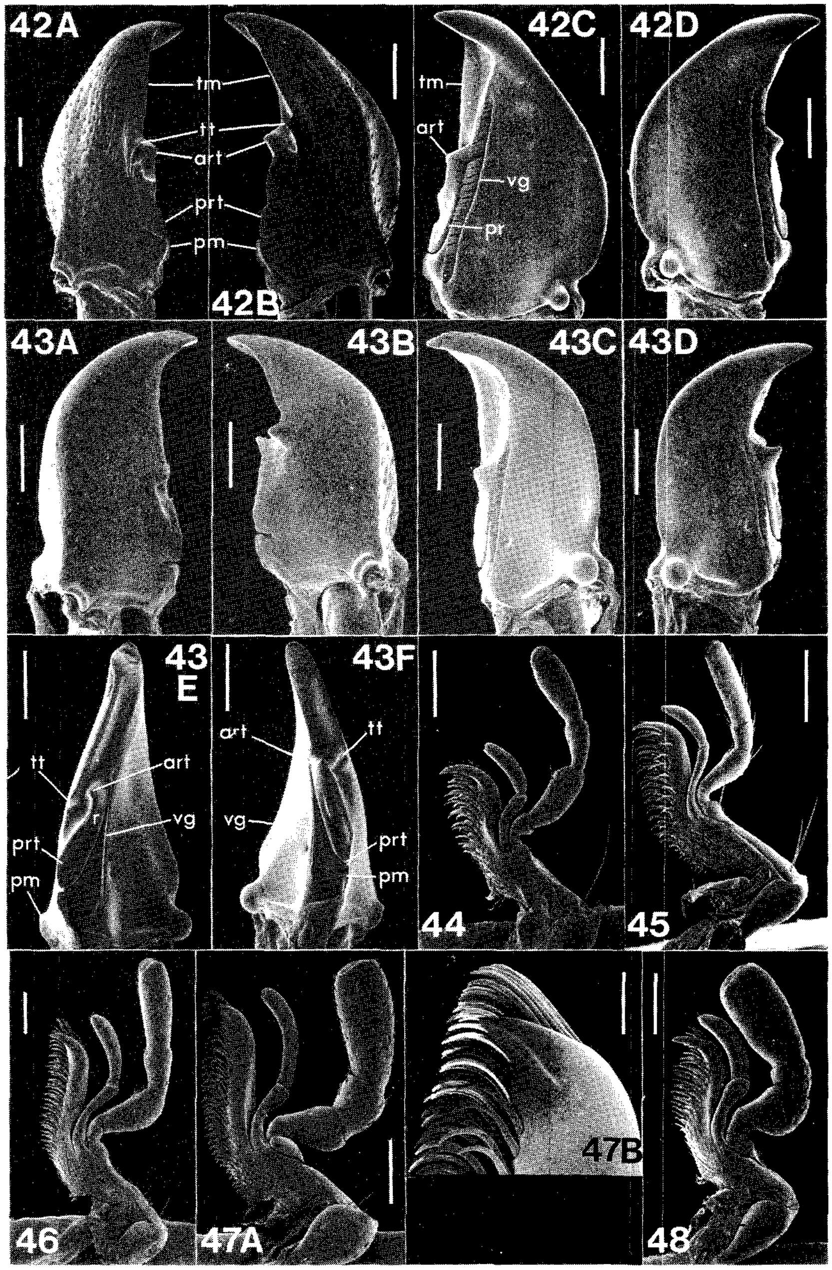
Nothing is known about feeding habits of adult *Metrius* and ozaenines, though the structural features of the mandibles and maxillae (see below) suggest that these beetles are "mixed feeders, ingesting food as fluid, semi-fluid, mush and fragments, or a mixture of all of them" (Evans and Forsythe, 1985: 122).

*Maxillae*.— Among ozaenines, these structures exhibit limited variation except in form of terminal palpomeres. For the Central American ozaenines, however, the more interesting variation is in details of the lacinia. Most taxa have a moderately long, sharp, slightly curved apical tooth and a moderately dense brush of marginal setae. Characteristic of *Physea* (Fig. 45) is a lacinia like that of *Metrius* (Fig. 44), with a long markedly curved apical tooth. The lacinia characteristic of *Ozaena* (Figs. 47 and 48) has a short, chisel-like, apical tooth, and a very dense brush of setae. Laciniae with fewer setae and longer teeth are more likely to be used as rakes to draw food particles into the mouth, whereas laciniae with more setae are more likely to be involved in a system of pre-oral digestion, with the dense setae serving to hold the digestive fluid used to liquefy partially the prey before ingesting it (Evans and Forsythe, 1985: 123). Certainly the most derived maxillae are those of *Ozaena*. The data seem to indicate the following linear transformation series:

$$\begin{tikzcd}
 & & \textit{Entomoantyx} & \\
\textit{Metrius} \arrow[r] & \textit{Physea} \arrow[r] & \textit{Pachyteles} \arrow[r] & \textit{Ozaena} \\
 & & \textit{Platycerozaena} &
\end{tikzcd}$$



Figs. 38—41. Mandibles, A, C, left mandible, dorsal and ventral aspects, respectively; B, D, right mandible, dorsal and ventral aspects, respectively: 38, *Metrius contractus* Esch; 39, *Physea hirta* LeC.; 40, *Entomoantyx cyanipennis* (Chd.); 41, *Pachyteles* nr. *striola* Perty. Scale bars = 200 μm, Legend: art- anterior retinacular tooth; m- molar; pm- premolar; pr- premolar ridge; prt- posterior retinacular tooth; r- retinaculum; tt- terebral tooth; vg- ventral groove; vrr- ventral retinacular ridge.



Figs. 42—48. 42—43, mandibles, A, C, E, left mandible, dorsal, ventral, and occlusal aspects, respectively; B, D, F, right mandible, dorsal, ventral, and occlusal aspects, respectively. 42, *Ozaena lemoulti* Bänn.; 43, *Platycerozaena panamensis* (Bates). 44, Left maxilla, ventral aspect, of *Metrius contractus* Esch. 45, Right maxilla, ventral aspect (reverse printing, for ease of comparison), of *Physea hirta* LeC. 46, Left maxilla, ventral aspect, of *Pachyteles kuntzeni* (Bänn.). 47, Left maxilla of *Ozaena lemoulti* Bänn.: A, complete structure; B, lacinia, apex. 48, Left maxilla of *Platycerozaena panamensis* (Bates). Scale bars = 400 μm, Figs. 42-47A, and 48; 100 μm, 47B. Legend: art- anterior retinacular tooth; m- molar; pm- premolar; pr- posterior retinacular ridge; prt- posterior retinacular tooth; r- retinaculum; tt- terebral tooth; vg- ventral groove.

**TABLE 1. Characteristics of Mandibles of *Metrius* Eschscholtz, and of Ozaenine Genera of North and Middle America**

| NAME OF GENUS | Scrobe | Dorsal Surface | Setation Dorsal Surface | Width Terebral Tooth | Terebral Margin | Retinacul. Thickness | Retinaculum Teeth Ant. | Retinaculum Teeth Post. | Molar Area | Ventral Groove |
|---|---|---|---|---|---|---|---|---|---|---|
| *Metrius* | 1 seta | – | moderate | moderate | slight curvature extended on to Retinacul. | marked | large | small | divided | short |
| *Entomoantyx* | 1 seta | – | moderate | small | slight curvature not extended on to Retinacul. | thin | large | moderate | not divided | long |
| *Physea* | many setae | – | moderate | moderate | marked curvature not extended on to Retinacul. | thin | absent | large | not divided | long |
| *Pachyteles* | many setae | – | moderate | small | slightly curved extended on to Retinacul. | thin | large | large | not divided | long |
| *Ozaena* | many setae | + | moderate | small | slightly curved extende on to Retinacul. | thin | moderate | large | not divided | long |
| *Platycerozaena* | many setae | + | wide | moderate | slightly curved not extended on to Retinacul. | thin | moderate | small | not divided | short |

We believe that this structural transformation series parallels a functional transformation series, involving a shift from ingestion of particulate to ingestion of more liquid food.

*Labium.*— Features of note involve the mentum, and terminal labial palpomeres (Figs. 49-55). On the menta of *Metrius*, *Entomoantyx*, and *P.* (*Goniotropis*) (Figs. 49, 51 and 53), one or two pairs of long tactile setae are located paramedially posterad the tooth. Such setae are absent from the menta of *Physea*, *Ozaena*, and *Platycerozaena* (Figs. 50, 54 and 55).

Lateral lobes of the mentum are moderately long in *Metrius*, *Physea*, *Entomoantyx*, and *Pachyteles*, and markedly long in *Ozaena* and *Platycerozaena*. In addition, in the last-named genus, the lateral lobes are markedly narrowed and pointed apically.

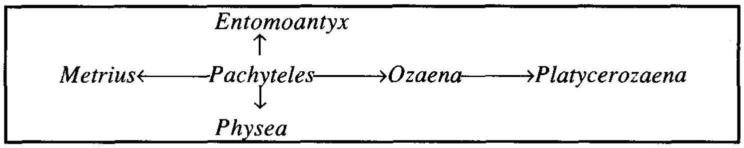
Epilobes (Fig. 49, **el**) are broader medially in *Metrius*, *Physea*, and *Pachyteles*. They are broader apically in *Entomoantyx*, and in *Ozaena* and *Platycerozaena* they are narrow.

The mental tooth is moderately long in *Metrius*, *Entomoantyx*, *Physea*, and *Pachyteles*; somewhat reduced in *Ozaena*, and markedly reduced in *Platycerozaena*. The apex of the tooth is notched in *Metrius contractus* Esch., and not notched in an undescribed species of *Metrius* (Y. Bousquet, personal communication) or in the New World ozaenine genera— though it is notched in the Australian genus *Mystropomus*. .

The glossal sclerites (Fig. 49, **gs**) are bisetose in members of *Metrius*, *Entomoantyx*, *Physea*, and *Pachyteles*. These setae are lacking from the glossal sclerites of *Ozaena* and *Platycerozaena*, evidently a reflection of the general reduction in setae characteristic of these genera.

Terminal palpomeres vary somewhat within the New World ozaenine genera. In most, they are like those of *Pachyteles* (Fig. 52), thus broader than those of *Metrius* (Fig. 49). The terminal palpomeres of *Physea*, however, are parallel-sided and more elongate (Fig. 50).

We believe that the following branched transformation series summarizes adequately the pattern of the various forms and details of the labium:



*Thoracic structures.*— *Metrius* adults exhibit an hypertrophied intercoxal process of the prosternum, which is so large that it covers the mesosternum. The mesosternal and metasternal intercoxal processes are firmly articulated to one another, as in most carabids. Ozaenines seem to be rather more loosely articulated than are adults of most carabid groups. The intercoxal process of the prosternum is of normal size. The intercoxal processes of the meso- and metasterna are rather loosely articulated in adults of *Entomoantyx*, *P.* (*Goniotropis*), *Ozaena*, and *Platycerozaena*. Among adults of *Physea* and *P.* (*Pachyteles*), the processes are reduced so that the middle coxae are in contact with one another medially.

The following linear transformation series summarizes this system:

*Entomoantyx*
*Metrius*——→*P.* (*Goniotropis*)——→*P.* (*Pachyteles*)
*Ozaena* *Physea*
*Platycerozaena*

Stork (1985: 1115 and Fig. 12) reports in adults of *Dhanya* prothoracic pits, one on each side, laterad the fore coxal cavities. He notes also the presence of such structures in adults of *Mystropomus*, but that they are positioned differently, and thus probably not homologues of the pits in *Dhanya*. He notes a possible involvement of these pits in a possible association with ants.

The metathorax of *Metrius* adults is small, the result of loss of the flight function and ultimately of the metathoracic wings and associated muscles. This group of losses and reductions is apotypic for *Metrius*.

*Metathoracic wings*.— The Middle American genera are characterized by wings with the wedge cell lacking, but otherwise with complete venation, and with the oblongum cell large, and quadrangular (*cf.* Ward, 1979: 183, Figs. 1-3 and 7). In contrast, members of the Oriental genus *Dhanya* exhibit markedly reduced venation, including a triangular, stalked oblongum cell (Stork, 1985: 1129, Fig. 43). In this latter feature, members of this genus resemble those of the Paussina (Darlington, 1950).

*Legs*.— Features of particular note include projections of the fore femora, antennal cleaner of the fore tibiae, and sexual dimorphism of the fore tarsomeres.

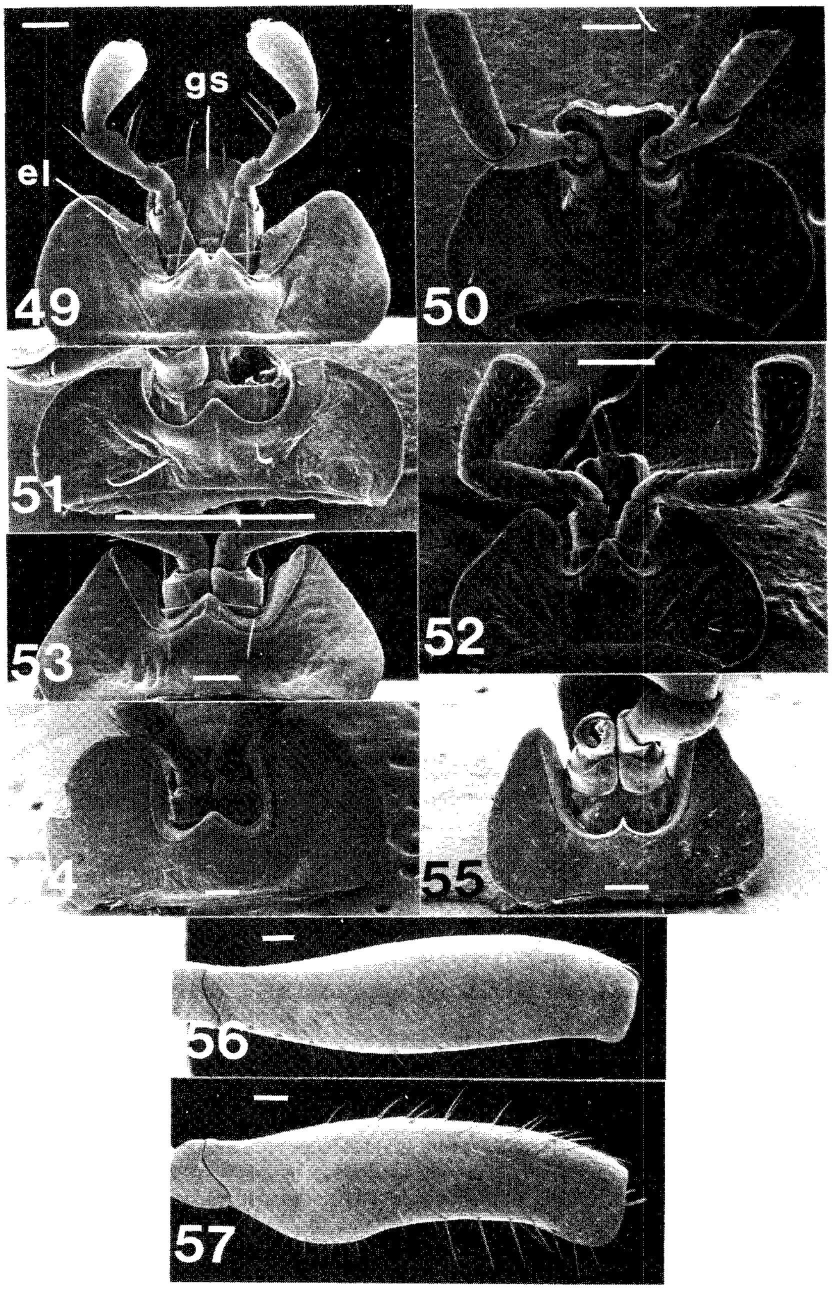
The fore femora without projections are those of adults of *Metrius* (Fig. 56), *Entomoantyx* (Fig. 58 ), and some South American species of *Pachyteles* (subgenus *Tropopsis*). Adults of *Physea* (Fig. 57) and of *Platycerozaena* (Fig. 62) exhibit a prominent broad swelling ventrally. Adults of *Pachyteles* (Figs. 59 and 60) have prominent narrow projections, whereas those of *Ozaena* (Figs. 61A-B) have shorter, setose projections.

The transformation series indicated by these data is the following:

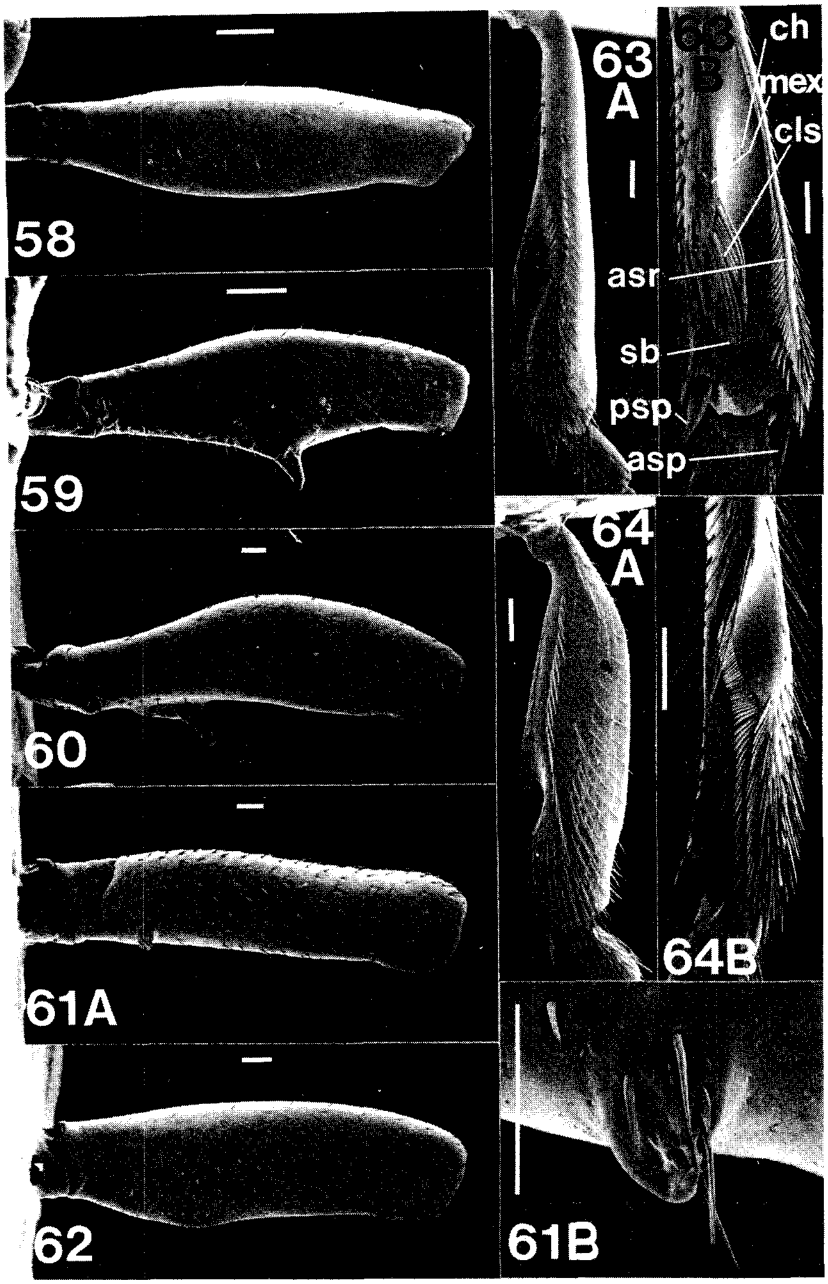
*Physea* ←—— *Metrius*——→ *Pachyteles*
*Platyceroz.* *Entomoantyx* *Ozaena*

*Antennal cleaner*.— This complex comb organ (Darlington, 1950: 60), includes some form of groove or notch on the front tibia, and associated setae and spines, projections, and/or spurs. Hlavac (1971) provides a detailed analysis for the Carabidae. Figures 63 to 69 illustrate antennal cleaners for *Metrius* and the ozaenines. Table 2 provides details for the taxa of interest.

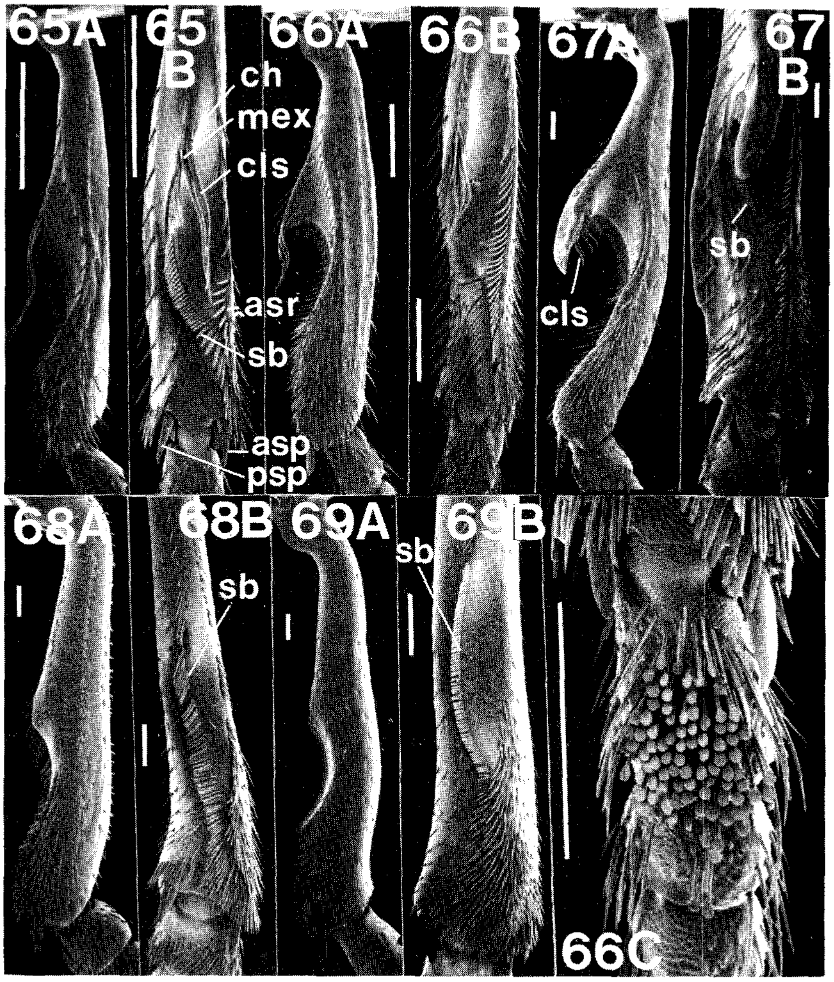
Structures are as follows: a more or less extensive groove in the mesal surface of the fore tibia, the cleaning channel (**ch**); a more or less expanded portion of the tibia adjacent to the channel (**mex**); a setal band (**sb**) extended across the channel and parallel to the posterior edge of the channel; several large sinuate clip setae (**cls**), origin posteriorly at the medial expansion; and anterior row of setae (**asr**) along the anterior edge of the channel; a zone of confluence distally, where the setal band and anterior setal row almost meet, and in some taxa seem to disappear in a dense patch of other setae (Fig. 69B).



Figs. 49—57. 49—55, Labium, ventral aspect, of: 49, *Metrius contractus* Esch; 50, *Physea hirta* LeC.; 51, *Entomoantyx cyanipennis* (Chd.); 52, *Pachyteles* nr. *striola* Perty; 53, *Pachyteles parca* LeC.; 54, *Ozaena lemoulti* Bänn.; 55, *Platycerozaena panamensis* (Bates). 56-57, left fore femur, anterior aspect, of: 56, *Metrius contractus* Esch; 57, *Physea hirta* LeC. Scale bars = 200 µm, Legend: el- epilobe of mentum; gs- glossal sclerite of mentum.



Figs. 58—64. 58—62, Left fore femur, 58, and 60-62, anterior aspect, 59, posterior aspect, of: 58, *Entomoantyx cyanipennis* (Chd.); 59, *Pachyteles* nr. *striola* Perty; 60, *Pachyteles kuntzeni* (Bänn.); 61, *Ozaena lemoulti* Bänn., A- entire sclerite, B- spine; 62, *Platycerozaena panamensis* (Bates). 63-64, Left fore tibia, A- anterior aspect, B- inner aspect, of: 63, *Metrius contractus* Esch; 64, *Physea hirta* LeC. Scale bars = 200 µm, Legend: asp- anterior tibial spur; asr- anterior setal row; ch- channel; cls- clip setae; mex- median expansion; psp- posterior tibial spur; sb- setal band.



Figs. 65—69. 65—66A-B, and 67—69, front tibiae, 65—66 and 68-69, left; 67, right (printed in reverse, for ease of comparison); A, anterior aspect, B, inner aspect, of: 65, *Entomoantyx cyanipennis* (Chd.); 66, *Pachyteles* nr. *striola* Perty; 67, *Pachyteles kuntzeni* (Bänn.); 68, *Ozaena lemoulti* Bänn.; 69, *Platycerozaena panamensis* (Bates). 66C, Left fore tarsomeres 1-3, ventral aspect of male *Pachyteles* nr. *striola* Perty. Scale bars = 200 µm, Legend: asp- anterior tibial spur; asr- anterior setal row; ch- channel; cls- clip setae; mex- median expansion; psp-posterior tibial spur; sb- setal band.

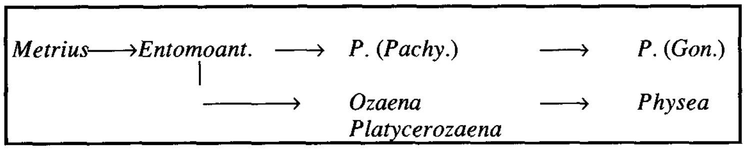
**TABLE 2. Characteristics of Antennal Cleaning Organ of *Metrius* Eschscholtz, and of Ozaenine Genera of North and Middle America**

| NAME OF GENUS | Grade | Channel | Median Expansion | No. Clip Setae | Anterior Setal Row | Setal Band |
|---|---|---|---|---|---|---|
| *Metrius* | B | large, ext. basad MEx | moderage | 5+ | setae large | short, sharply sinuate |
| *Entomoantyx* | C | large, ext. basad MEx | moderate | 5- | setae large | long, sinuation moderate |
| *Physea* | C | small, term. at MEx | slight | 0 | not evident | long, sinuation slight |
| *Pachyteles* (*s. str.*) | C | large, ext. basad MEx | marked | 5- | setae large | long, sinuation moderate |
| *Pachyteles* (*Goniotropis*) | C | large, ext. basad MEx | marked, w/ claw-like projection | 5+ | setae large | long, sinuation moderate |
| *Ozaena* | C | small, term. at MEx | slight | 0 | setae large | long, sinuation slight |
| *Platycerozaena* | C | small, term. at MEx | slight | 0 | setae small sparse | long, sinuation slight |

Hlavac (1971: 56) places *Metrius* and the Australian ozaenine genus *Mystropomus* . in grade B, characterized as follows: tibial spurs not part of cleaning mechanism; setal band long, with distinct vertical section and confluent zone, length of setal band/length of tibia 26-58 per cent, in most taxa less than 40 per cent; confluent zone short, 15 to 35 per cent length of band; median expansion evident, in most taxa not shifted far anterad; channel shallow, developed far basad of clip setae or not; fore tibia not compressed antero-posteriorly. *Metrius* and *Mystropomus* are classified as "advanced Grade B", presumably because of the extended channels that they exhibit. However, this condition would seem to be plesiotypic among ozaenines.

The remaining ozaenines are classified by Hlavac as members of Grade C: setal band long (length of setal band/length of tibia 33-69 per cent), divided into a large distal region or confluent zone, and a proximal cleaning arc; distal region from 33 to 69 per cent length of setal band; median expansion markedly developed anteriorly; channel deep, short, not extended above clip setae; anterior and posterior setal rows, if present, not in from of cleaning aggregations.

The various forms of cleaning organs seem to form the following branched transformation series:



Following development of the more complex cleaner (C from B), further development occurs with hypertrophy of the median expansion (Figs. 66A-B, and 67A-B). In contrast, the cleaning organ is reduced in the line *Ozaena* + *Platycerozaena*- *Physea* (Figs. 68A-B, 69A-B, and 64A-B), with decrease in size of channel, loss of clip setae and loss or reduction of the anterior setal row. This reduction probably coincides with modification of other parts of the fore tibiae (markedly broadened in *Physea*), or in modifications of the antennae (reduction in setae in *Ozaena* and *Platycerozaena*; thickening of the antennomeres in *Ozaena*, shortening of the antennae in *Platycerozaena*). In any event, it seems unlikely that the reduced organs can function as antennal cleaners. Darlington (1950: 65) claims that such reduction is a precursor to total loss of the antennal cleaner exhibited by paussine adults, many of which have markedly expanded tibiae, and markedly expanded antennomeres that lack standard tactile and chemosensory setae. We can appreciate that the antennal modifications of *Ozaena* and *Platycerozaena* render the cleaning organ superfluous, but the antennomeres of *Physea* seem to have a normal complement of sense organs. If other carabids with normal antennae need to groom them, how do *Physea* adults manage? Do they have some other mechanism, or is their grooming behavior so modified that they can use effectively the remnants of their cleaning organs?

*Genital segments of males*.— These are abdominal segments VIII and IX/X. The latter segment is either composite, or one of either IX or X (*cf* Bils, 1976). Although Bils' paper treats females, we assume that the tergum that bears the explosion chambers of the defensive system is the same in both sexes, and Bils labels this "T IX/X" (*l.c.*, Figs. 9 and 11, *EK*).

Tergum VIII is of about the same form in all taxa examined. We do not comment further about it. Sternum VIII and the "ring sclerite" (sclerites of segment IX/X) do exhibit some interesting variation.

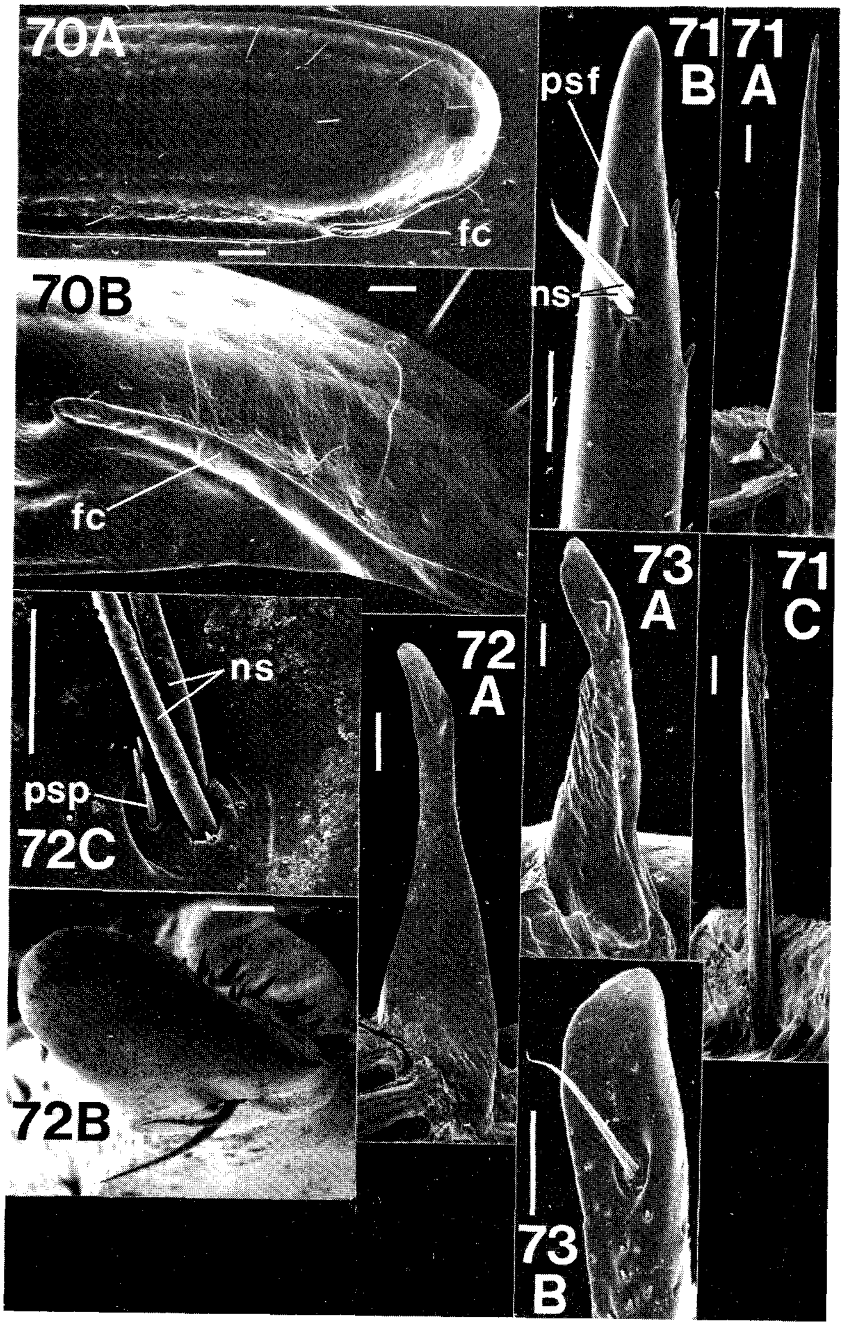
**TABLE 3. Characteristics of Male Genitalia of Metrius Eschscholtz, and of the Ozaenine Genera of North and Middle America**

| | Median Lobe | | Sc. Rod | Internal Sac | | | Parameres | |
|---|---|---|---|---|---|---|---|---|
| NAME OF GENUS | Shaft | Apex | Length | Basal Area (1) | Collar Area (2) | Apical Area (3) | Left | Right |
| *Metrius* | curvature preapically marked | prominent narrow, pointed posteriorly | *ca.* .25 L. median lobe | micro-trichia extensive microspines | semi-circle, right of | membranous lobe | few preapical | digitate; apical/preap. fringe of long setae |
| *Entomoantyx* | curvature moderate | broad, not prominent pointed ventrally | *ca.* .75 L. median lobe | sagittate microtrich. field | complete collar of micro-trichia | sclerot. terminal sclerite | asetose | digitate; longer than left; apical/preap. fringe of shorter setae. |
| *Physea* | curvature moderate | as for *Entomoant.* | *ca.* .50 L. median lobe | without micro-trichia | as for *Entomoant.* | membr. lobe on left; w/o terminal sclerite | few preapical setae | spatulate asetose; shorter than left. |
| *Pachyteles* (*sensu stricto*) | curvature moderate to marked | as for *Entomoant.* | subequal to length median lobe | micro-trichia few | as for *Entomoant.* | w/o term. sclerite; lightly scl. tube | asetose | spatulate to blade-like; setation various. |

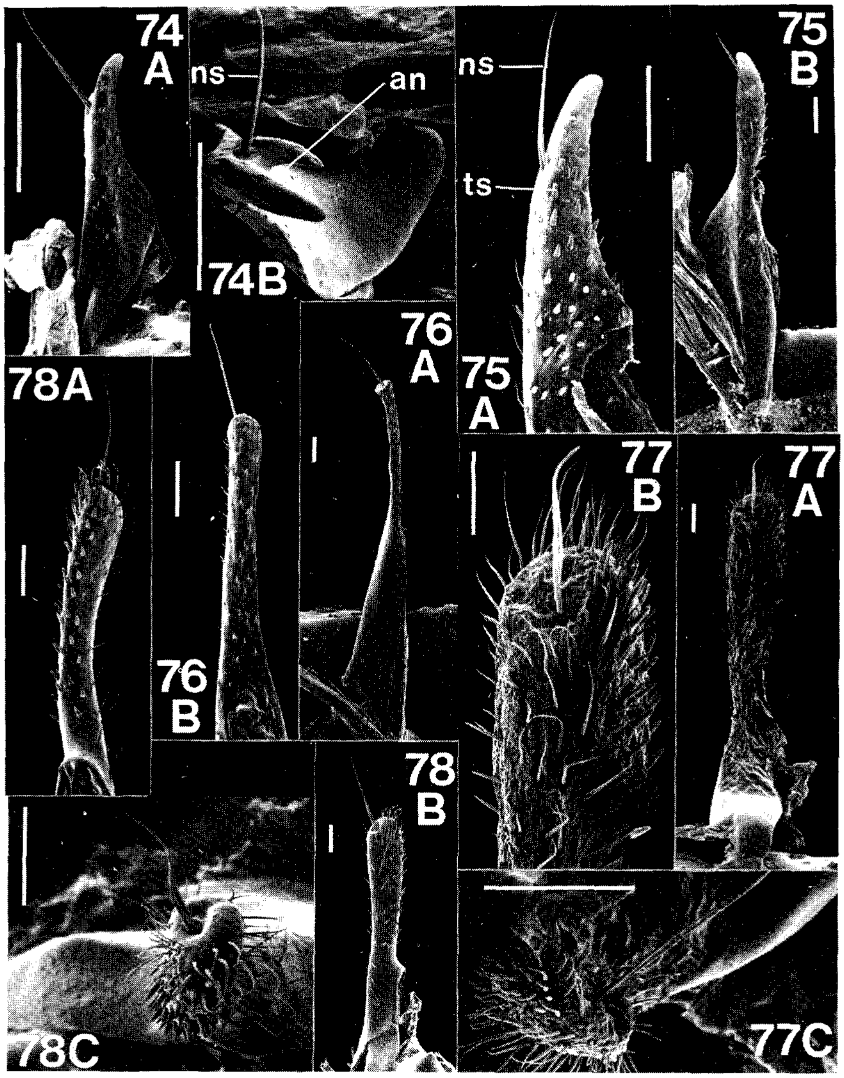
(continued on next page)

**TABLE 3** (continued)

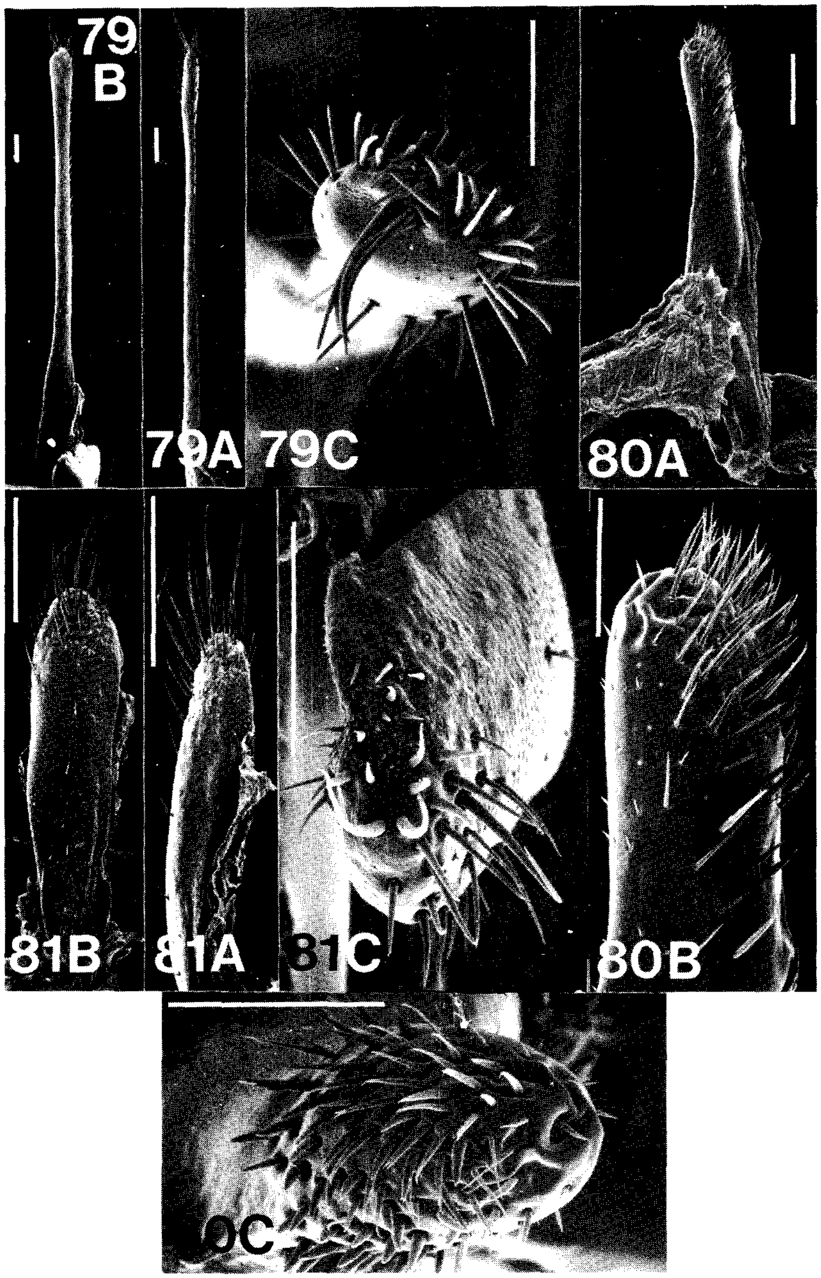
| | Median Lobe | | Sc. Rod | Internal Sac | | | Parameres | |
|---|---|---|---|---|---|---|---|---|
| NAME OF GENUS | Shaft | Apex | Length | Basal Area (1) | Collar Area (2) | Apical Area (3) | Left | Right |
| *Pachyteles* (*Goniotropis*) | curvature marked | prominent, broad, obl. truncate or broadly rounded | *ca.* .60 L. median lobe | microtrichia few | extensive collar of microtrichia | apical brush; terminal sclerite | few preapical setae | falcate setose on much of medial margin; longer than left |
| *Ozaena* | curvature very slight | not projected ventrally obsolete | *ca.* .90 L. median lobe | without microtrichia | extensive mainly on left | term scl. broad, w/ broad vent. dir. lobe | few preapical setae | falcate; setose on much of medial margin; longer than left. |
| *Platycerozaena* | curvature very slight | slightly projected ventrally | *ca.* .90 L. median lobe | without microtrichia | as in *Ozaena* | as in *Ozaena* | as in *Ozaena* | spatulate; setose on much of medial margin; longer than left. |



Figs. 70—73. 70, left elytron of *Entomoantyx cyanipennis* (Chd.): A, apical half, dorsal aspect; B, flange of Coanda, lateral aspect. 71-73, left stylomeres of females of: 71, *Physea hirta* LeC., A- ventral aspect, B- ventral aspect, apical portion, C- medial aspect; 72, *Metrius contractus* Esch., A, ventral aspect, B- caudo-ventral aspect, C- apical portion, ventral aspect; 73, *Entomoantyx cyanipennis* (Chd.), A- ventral aspect, B- apical portion, ventral aspect. Scale bars = 200µm, Figs. 70A, 71A,C, 72A; 40mm, 70B, 71B, 72B-C, 73A-B. Legend: fc- flange of Coanda; ns- nematiform setae; psf- preapical sensory furrow; psp- preapical sensory pegs.

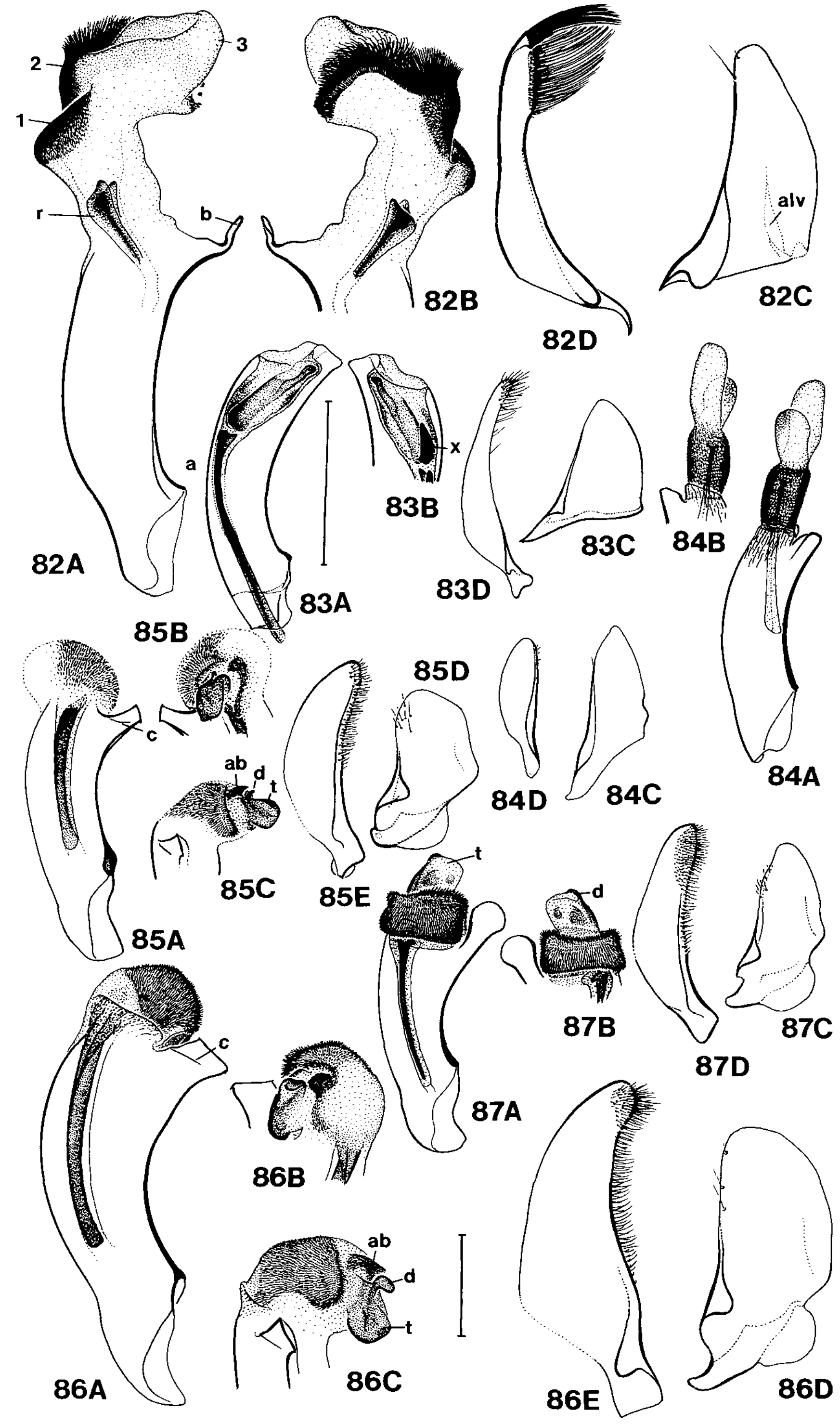


Figs. 74—78. Left stylomeres of females of: 74, *Pachyteles gyllenhali* (Dej.), A- medial aspect, B- caudal aspect; 75, *Pachyteles enischnus*, new species, A- medial aspect, B- ventral aspect; 76, *Pachyteles mexicanus* Chd., A- medial aspect, B- ventral aspect; 77, *Pachyteles kuntzeni* (Bänn.), A- ventral aspect, B- apical portion, ventral aspect, C- caudal aspect; 78, *Pachyteles parca* LeC., A- medial aspect, B-ventral aspect, C- caudal aspect. Scale bars = 100 μm, Legend: an- apical notch; ns- nematiform seta; ts, trichoid seta.



Figs. 79—81. Left stylomeres of females of: 79, *Pachyteles elongatus* (Chd.), A- medial aspect, B- ventral aspect, C- caudal aspect; 80, *Ozaena lemoulti* Bänn., A- ventral aspect, B-apical portion, ventral aspect, C- caudal aspect; 81, *Platycerozaena panamensis* (Bates), A- medial aspect, B-apical portion, medial aspect, C- caudal aspect. Scale bars = 200 mm, 79A-B, 80A-B, and 81A; 100 mm, 79C, 80C, and 81B-C.

Figs. 82—87. Male genitalia of: 82, *Metrius contractus* Esch., A- median lobe, left lateral aspect, internal sac everted, B- same, right lateral aspect, apical portion, C-D, left and right parameres, respectively, dorsal aspect; 83, *Entomoantyx cyanipennis* (Chd.), A- median lobe, left lateral aspect, internal sac inverted, B- same, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 84, *Physea hirta* LeC., A- median lobe, left lateral aspect, internal sac everted, B- same, apical portion, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 85, *Pachyteles parca* LeC., A- median lobe, left lateral aspect, internal sac everted, B- same, apical portion, right lateral aspect, C- same, apical portion, ventral aspect, D-E, left and right parameres respectively, dorsal aspect; 86, *Pachyteles kuntzeni* (Bänn.), A- median lobe, left lateral aspect, internal sac everted, B- same, apical portion, right lateral aspect, C- same, apical portion, ventral aspect; D-E, left and right parameres, respectively, dorsal aspect; 87, *Pachyteles elongatus* (Chd)., A- median lobe, left lateral aspect, internal sac everted, B- same, right lateral aspect; C-D, left and right parameres, respectively, dorsal aspect. Scale bars = 0.5 µm, Legend: 1-3, major regions of internal sac; a- median lobe, basal articulation point for parameres; ab, apical brush of internal sac; b- apical portion of median lobe; c- carinula of apical portion of median lobe; d- digital projection of terminal sclerite of internal sac; r- rod of apical portion of ejaculatory duct; t- terminal sclerite of internal sac.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85A
87B
87D
87C
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87A
86B
ab
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86A
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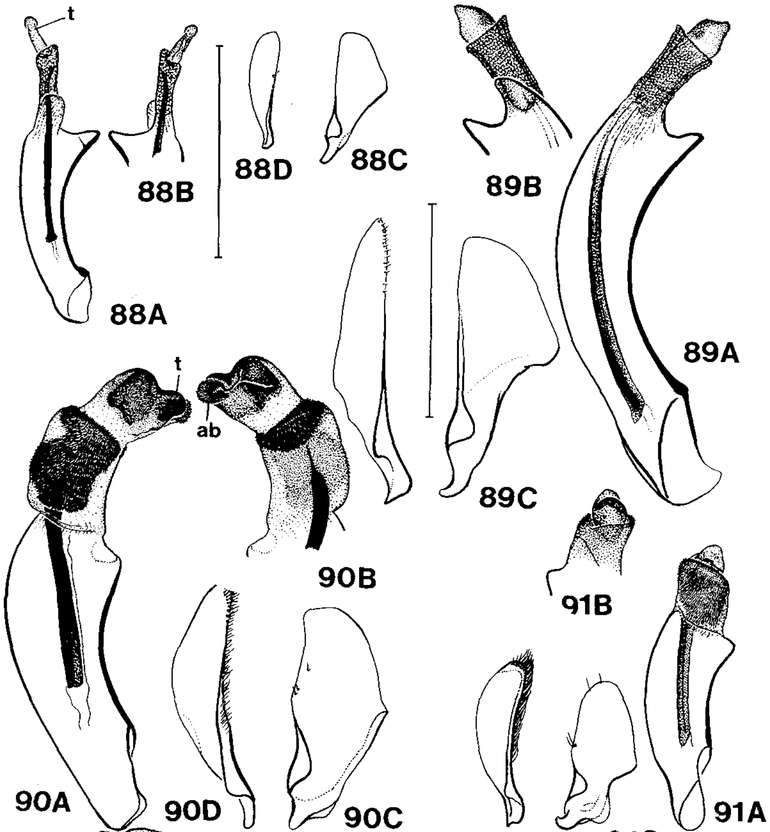
Figs. 88—96. 88—91, Male genitalia of: 88, *Pachyteles gyllenhali* (Dej.), A- median lobe, left lateral aspect, internal sac everted, B, same, apical portion, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 89, *Pachyteles mexicanus* Chd., A-median lobe, left lateral aspect, internal sac everted, B- same, apical portion, right lateral aspect; C-D, left and right parameres respectively, dorsal aspect; 90, *Ozaena lemoulti* Bänn., A- median lobe, left lateral aspect, internal sac everted; B, same, apical portion, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 91, *Platycerozaena panamensis* (Bates), A- median lobe, left lateral aspect, internal sac everted; B, same, apical portion; C and D, left and right parameres, respectively, dorsal aspect. 92-96, Ring sclerites of segments IX/X of: 92, *Metrius contractus* Esch., dorsal aspect; 93, *Entomoantyx cyanipennis* (Chd.), dorsal aspect; 94, *Physea hirta* LeC., ventral aspect; 95, *Pachyteles marginicollis* (Solier), dorsal aspect; 96, *Platycerozaena magna* (Bates). Scale bars = 0.5 µm, Legend: ab- apical brush of internal sac; ec- explosion chamber of pygidial gland system; hs- hemisternite of segment IX/X; t- terminal sclerite of internal sac.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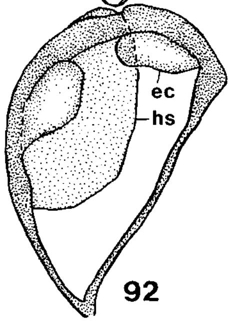
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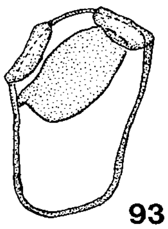
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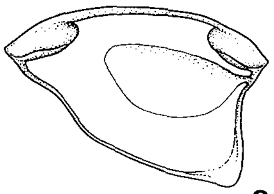
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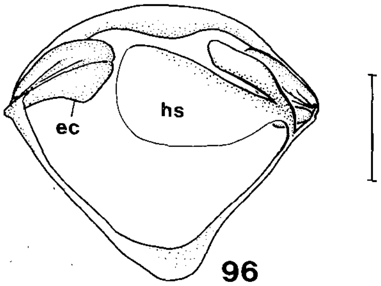
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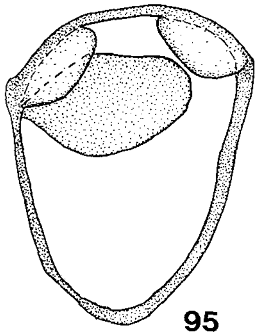
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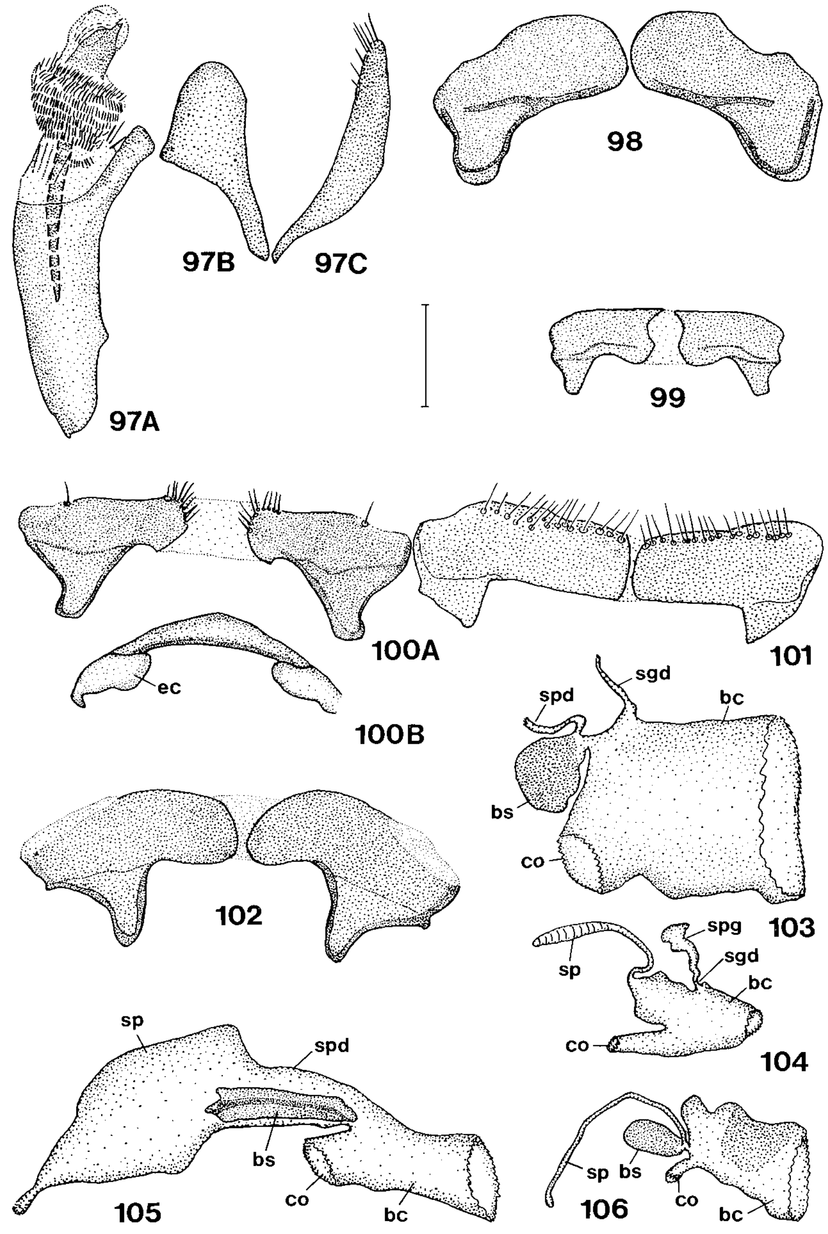


Figs. 97—106. 97, Male genitalia of *Pachyteles enischnus*, new species: A, median lobe, left lateral aspect, with internal sac everted; B-C, left and right parameres, respectively, ventral aspect. 98-100A and 101—102, Sternum VIII, ventral aspect, of: 98, *Metrius contractus* Esch.; 99, *Entomoantyx cyanipennis* (Chd.); 100A, *Physea latipes* Schaum; 101, *Pachyteles parca* LeC.; 102, *Pachyteles mexicanus* Chd. 100B, Tergum IX/X, dorsal aspect, of *Physea latipes* Schaum. 103-106, female reproductive tracts, lateral aspects, of: 103, *Metrius contractus* Esch; 104, *Entomoantyx cyanipennis* (Chd.); 105, *Physea latipes* Schaum; 106, *Pachyteles parca* LeC. Scale bars = 0.5 µm, Legend: bc- bursa copulatrix; bs- bursal sclerite; co- common oviduct; ec- explosion chamber; sgd- spermathecal gland duct; sp- spermatheca; spd- spermathecal duct.

In *Metrius* males, the posterior margin of sternum VIII is broadly notched. The two anterior projections join at their apices to form a ring. We interpret these projections as apodemes. Among males of the Ozaenini, sternum VIII consists of a pair of small lateral sclerites connected to one another by membrane, and without apodemes.

The ring sclerite (Figs. 92-96) surrounds the genitalia which, during copulation, protrude between tergum and sternum. The tergum is narrow, and laterally on each side bears the explosion chambers (Fig. 92, *ec*). The sternum comprises a pair of apodemes joined anteriorly to form the ring; to the right one is connected a hemisternite (Fig. 92, *hs*), which is more or less extensive. This hemisternite is larger in *Metrius* males, being smaller among the ozaenines.

The sternal apodemes of *Metrius* males, at their junction, form a narrow angle. This angle is greater among the ozaenines, the junction being broadly rounded in *Entomoantyx* males (Fig. 93). The ring is markedly asymmetrical in *Metrius* and *Physea* males (Fig. 94), slightly to the right in *Ozaena* and *Platycerozaena* (Fig. 96), and about symmetrical in *Entomoantyx* and *Pachyteles* males. These data suggest the following linear transformation series:

*Metrius*——→*Physea*——→*Ozaena*——→*Pachyteles*——→*Entomo.*
*Platycerozaena*

Although the ring sclerite of *Physea* is in form much like that of *Metrius*, in fact the former ring is a good deal shorter than the latter, and is thus more derived than is apparent at first.

*Male genitalia.*— This system comprises the sclerotized median lobe which has enfolded in it the actual organ of intromission, the internal sac or endophallus, and attached externally to the base is a pair of plate-like or digit-like parameres. Stork (1985: 1120 and Figs. 32-37) provides excellent data about the male genitalia of the species of *Dhanya*.

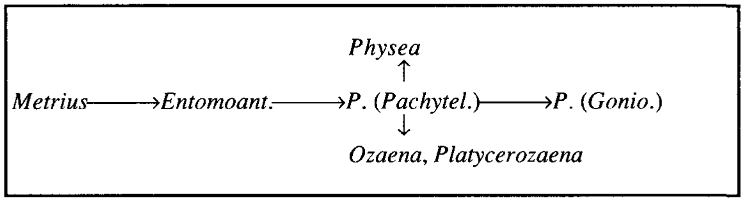
Among *Metrius* and ozaenine males, the median lobe is a compressed tube, with an open base, *i.e.*, without a distinct basal bulb (*cf.* Figs. 82A-91A and 97A).

In lateral aspect, the articulation point for the parameres (Fig. 82A, *a*) marks the ventral base of the shaft. The shaft is curved ventrad, more abruptly so apically in *Metrius* males, and narrowed in males of the ozaenine genera. The apical portion (Fig. 82A, *b)* located ventrad, is marked in *Metrius* males by a sharp constriction in the median lobe, and comprises a thin lobe with apex directed posterad, and bent sharply away from the ventral curve. Among ozaenine males, the apical portion varies from non-existent (Figs. 90A-B) to prominent and subtruncate (Figs. 86A-B), or round and spatulate (Figs. 87A-B). See Table 3 for details.

The internal sac is complicated in form and more so in its armature of microtrichial fields and microspines derived from microtrichia. An additional piece of armature associated with the internal sac is the rod (Fig. 82A, **r**) of the ejaculatory duct— a trough-like structure on the dorsal surface of the duct, and which is varied in length. It is designated posterior rod by Stork (1985: 1120), and is very long in males of *Dhanya* (*l.c.*, Figs. 32-37).

Details of armature are best appreciated with the internal sac everted and, if possible, fully inflated (Figs. 82A-B, 84A-B, *etc.*). (for ozaenines, it is difficult to extend fully the sac; for the few males of *Entomoantyx* that we had available, it proved to be impossible). Three areas or fields are recognized: a dorso-basal lobe of microtrichia (1); a median band or collar of microtrichia or microspines (2); and an apical lobe that bears the ostium or gonopore and various sclerites and microtrichial fields (3). Details for the genera are provided in Table 3. Stork (*l.c.*, Figs. 32-37) figures similar structures for the species of *Dhanya*.

The parameres are varied in form, setation, and relative size. Illustrations (Figs. 82-91 and 97) were made from the dorsal aspect. Details are in Table 3. Compared to the genitalia of *Metrius* males, those of the Ozaenini exhibit median lobes with less differentiated apices, longer sclerotized rods of the internal sac, internal sacs with the apical parts more elaborate, and right parameres of most taxa broader, and either asetose or with shorter setae. A possible transformation series is the following:



This series emphasizes the close association of *Entomoantyx* with *Metrius* in form and setation of the right paramere, and internal sac with a concentration of microtrichia on the dorso-basal area. Farthest from *Metrius* is subgenus *Goniotropis*, with its elaborate apical part of the internal sac. Males of subgenus *Pachyteles* seem to occupy a central point in the Ozaenini, with a structural plan of genitalia sufficiently complex to be ancestral to the other types. Although elaboration seems to be the main thrust of evolution of the genitalia, reduction seems to characterize *Physea*: shorter rod, reduced parameres, and a rather simple internal sac with the only projection being a large apical lobe. Also, the microtrichial field in the basal area seems to have been reduced in *Physea*, *Pachyteles*, *Ozaena*, and *Platycerozaena*.

*Genital segments of females*.— Abdominal terga VIII and IX/X (Fig. 100B) are essentially the same in *Metrius* and the ozaenines and are not noted further. Sternum VIII consists of a pair of hemisternites, each of which in *Metrius* females has an asetose broad median part and a broad, anteriorly directed apodeme. Among ozaenines, there is appreciable intergeneric variation. The median posterior parts are less extensive in most taxa than in *Metrius* (Fig. 98), and the apodemes are narrower. *Physea* females have the median parts shorter, with more membrane between (Fig. 100A), and *Physea* and *P.* (*Goniotropis*) females (Fig. 101) have setae variously distributed. Females of *Entomoantyx* have reduced hemisternites with the median margins markedly sinuate (Fig. 99). No transformation series is offered because the complexity of these structures cannot be summarized so simply.

*Ovipositor sclerites*.— These consist of a pair of slender valvifers articulated with tergum IX/X , and articulated to each valvifer a single-articled stylomere (Figs. 71-81), of varied length and setation, but each with a preapical sensory pit with one or more nematiform setae. The stylomeres are articulated in such a way that they are exserted straight posterad, without first being partially rotated from a flattened position in the body cavity. Presumably, this is a primitive feature of the paussine stock.

Stylomeres of *Metrius* females (Figs. 72A-B) are moderately long, broad at base, and broadly rounded at the apex; the surface, especially dorsally, has numerous basiconic sensilla; and the sensory furrow is preapical, with a pair of long nematiform setae and several basiconic sensilla (Fig. 72C) that are longer than usual for Carabidae. The stylomeres of *Entomoantyx* females (Figs. 73A-B) are similar to those of *Metrius*.

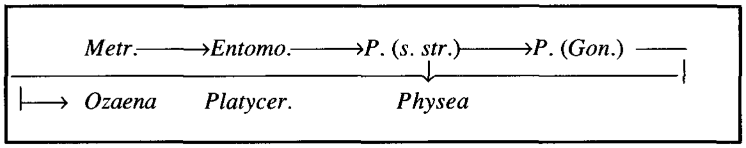
The stylomeres of *Physea* females (Figs. 71A-B) are much more elongate and slender, the surface with few sensilla, but including two preapical nematiform setae.

The stylomeres of *Pachyteles* females are various in form and proportions. Those of *P. enischnus* n. sp. (Figs. 75A-B) are most like the stylomeres of *Metrius*: mandible-like, falcate, with broad base and rounded apex, the nematiform setae preapical; however, the surface is covered with thick, short trichoid setae. The stylomeres of *P. gyllenhali* differ from those of *P. enischnus* n. sp. by the bifid apices (Fig. 74B). The stylomeres of *P. mexicanus* (Fig. 76A-B) are much more slender, digitiform, cylindrical (at least preapically), the surface with numerous slender trichoid setae in addition to those that are short and thick, and the sensory furrow and nematiform setae are apical rather than preapical.

The stylomeres of *P. parca* (Figs. 78A-C) and *P. kuntzeni* (Figs. 77A-C) are markedly similar to one another, and are much like those of *P. mexicanus*: cylindrical, with nematiform setae nearly apical; but they are shorter (palpiform) and with a much denser vestiture of setae. In contrast, the stylomeres of *Pachyteles elongatus* are long and very slender (Figs. 79A-C), like those of *Physea*, except that the nematiform setae are apical and the surface is moderately densely setose.

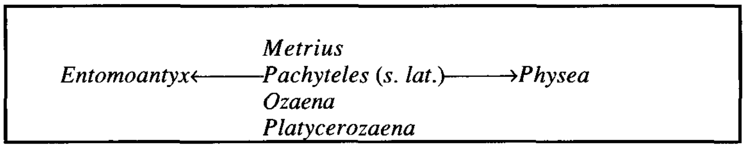
The stylomeres of *Ozaena* (Figs. 80A-C) are short, palpiform, cylindrical, with the nematiform setae apical, and with numerous trichoid setae apically and preapically. Those of *Platycerozaena* (Figs. 81A-C) are similar to the stylomeres of *Ozaena*, but the form is terete rather than cylindrical, and the apical and preapical setae are longer.

The following linear transformation series summarizes these data:



Along the main horizontal axis, there is an overall decrease in stylomere length, a shift of the sensory furrow toward the apex, and an increase in setation. *Physea* females are exceptional, with their long glabrous stylomeres, and *Pachyteles elongatus* varies in a similar way.

*Bursal sclerite and spermatheca.*— At the posterior end of the bursa copulatrix (**bc**) of female *Metrius* (Fig.103), a posterior chamber is extended dorsad the common oviduct (**co**), connected to the dorsal wall of the bursa is a spermatheca (not shown, but like **sp** in Fig. 104) with a short sinuous duct (**spd**), and an extensive spermathecal gland (not shown) connected by a short spermathecal gland duct (**sgd**). Table 4 provides details for the ozaenine genera studied. Based on absence or presence of the bursal sclerite and on form of the latter, the following branched transformation series is postulated:



nematiform setae and several basiconic sensilla (Fig. 72C) that are longer than usual for Carabidae. The stylomeres of *Entomoantyx* females (Figs. 73A-B) are similar to those of *Metrius*.

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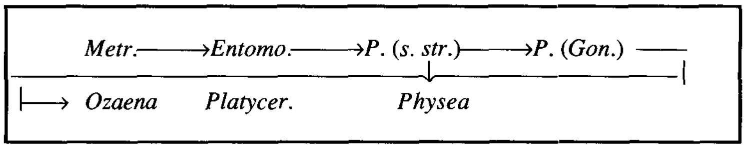
The stylomeres of *Ozaena* (Figs. 80A-C) are short, palpiform, cylindrical, with the nematiform setae apical, and with numerous trichoid setae apically and preapically. Those of *Platycerozaena* (Figs. 81A-C) are similar to the stylomeres of *Ozaena*, but the form is terete rather than cylindrical, and the apical and preapical setae are longer.

The following linear transformation series summarizes these data:



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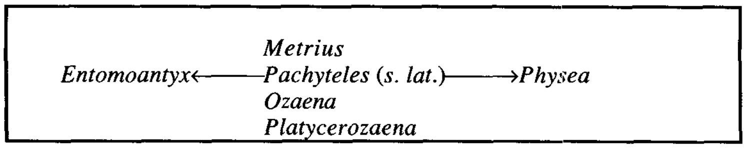


**TABLE 5.** **Defensive Secretions Recovered from Adult *Metrius* and Adults of Three Genera of Ozaenini. From Eisner, *et al.*, 1977; and Roach, *et. al.*, 1979.**

| NAME OF GENUS | 1-4 benzo-quinone | 2-Methyl-1,4-benzo-quinone | 2-3 Dimethyl-1,4-benzo-quinone | 2-Ethyl-1,4-benzo-quinone | n-penta-decane | Total Compounds |
|---|---|---|---|---|---|---|
| *Metrius*[1]. | X | | | | X | 2 |
| *Physea*[2]. | X | X | X | | | 3 |
| *Pachyteles (sensu lato)*[3]. | X | X | X | | X | 4 |
| *Platycerozaena*[4]. | X | X | X | X | X | 5 |

[1]., *Metrius contractus* Esch.; [2]., *Physea hirta* LeC.; [3]., *P.* (*Pachyteles*) nr. *striola* Perty, *P.* (*P.*) *longicornis* Bates, and *P.* (*Goniotropis*) sp?; [4]., *Platycerozaena panamensis* Bates.

*Defensive secretions and their delivery.*— Eisner *et al.* (1977), Roach *et al.* (1979), and Eisner and Aneshansley (1981) analyze in some detail the defensive secretions and their delivery for ozaenines. Forsyth (1972) describes the structure of the pygidial glands that produce the secretions, and Deuve (1988: 167, Fig. 10) contributes an analysis of the position of the openings of the pygidial glands.

The secretions are various benzoquinones and the hydrocarbon n-pentadecane. Table 5 shows the names of secretions that have been recovered from adults of *Metrius* and representatives of three ozaenine genera considered here. The limited data show a graded series with numbers of compounds increasing from two (in *Metrius*) to three and five in ozaenines. Lack of n-pentadecane from the armory of *Physea* would seem to be a loss.

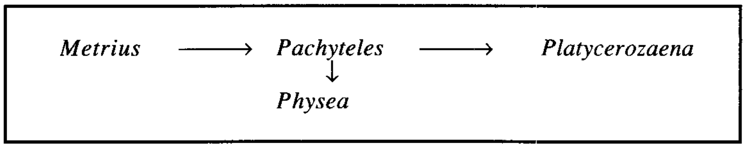
The mixtures are hot and are delivered with explosive force, in a cloud of corrosive vapor. Details of the process are explained by Eisner and Aneshansley (*loc. cit.*), though it was known for 150 years that these beetles were "bombardiers".

Ozaenines and paussines are able to direct the defensive jets forward by means of the flanges of Coanda on the elytra (Stork, 1985: 1115), as explained by Eisner and Aneshansley (*loc. cit.*).

Another part of the delivery system includes umbilical setae that are expanded (Figs. 107C-D), and to which droplets of the defensive secretions adhere when they are fired forward. Also, the beetles brush the secretions over the body, using the legs (Eisner and Aneshansley, *l.c.*). Characteristic of *Ozaena* and *Platycerozaena* adults are modified setae (basiconic Type 2; *cf.* Nagel, 1979b: 27). These are illustrated in Figs. 107A-B. They are on the lateral margins of the pronotum, as well as on the elytra. Their flattened, ridged surfaces would seem to be ideal for increasing the evaporative surface area for the defensive secretions, and thus enhancing the effectiveness of the latter. Unfortunately, Eisner and his co-workers did not mention these setae.

Forsyth, and Eisner and Aneshansley report that the pygidial glands of adult *Metrius* and the ozaenines are similar in structure, *i.e.*, two chambered. We have not studied them in detail, though we have seen the explosion chambers located laterally on Tergum IX/X (*cf.* Figs. 92-96 and 100B). This, combined with the numerous other similarities in structural features, is strong evidence for linking these taxa phylogenetically.

In summary, the defensive system shows remarkable complexity both in structure and function between *Metrius* and the Ozaenini + Paussini, linking these taxa in a single higher-level taxon. The ancestor of the group evidently evolved a system for development and release of simple hot benzoquinones. The delivery system was improved by evolution of the flanges of Coanda, and the chemical system became more complex with development of additional corrosive components. With data for only four of the six genera, the following branched transformation series is incomplete:



Sexual dimorphism: adhesive setae of fore tarsomeres.— Males of *Metrius* have fore tarsomeres 1 and 2 or 1, 2 and 3 (Y. Bousquet, personal communication)

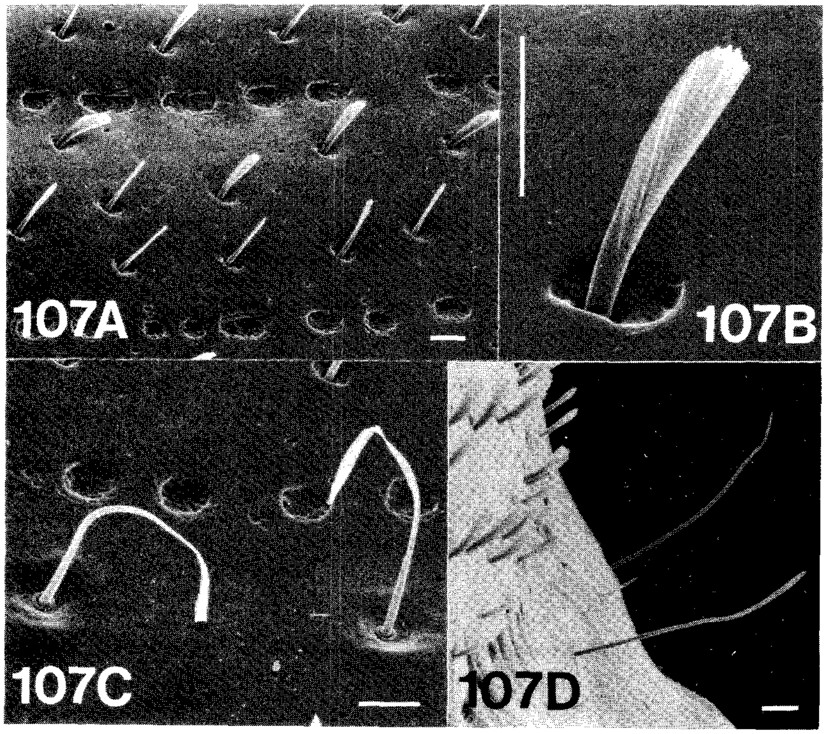


Fig. 107. Specialized setae on the elytron of *Ozaena lemoulti* Bänn.: A-B, sensilla basiconica, type 2; C, umbilical setae; D- sensilla basiconica, type 2. Scale bars = 50 μm,

markedly expanded, and on the ventral surface of each is a pad of adhesive articulo-setae (Stork, 1980: 287; *cf.* his Figs. 15B-E; referred to as "spongy pubescence" by previous authors). Among ozaenines, the vestiture-bearing tarsomeres are less expanded. Males of *Physea*, almost all of *Pachyteles* (*s. str.*) (Fig. 66C) and some of subgenus *Goniotropis* have adhesive setae on only fore tarsomeres 1 and 2. Males of some species of *Goniotropis*, and of *Entomoantyx* have vestiture on tarsomeres 1-3. Males of *Pachyteles gyllenhali*, *Ozaena* and *Platycerozaena* (and some species of *Dhanya*— see Stork, 1985: 1115) lack adhesive vestiture and none of the fore tarsomeres are expanded. The data are summarized in the following branched transformation series:

| | | | | |
|---|---|---|---|---|
| *P.* (*P*) *gyll.*<br>*Ozaena*<br>*Platyceroz.* | ⟵ | *Metrius*<br>*P.* (*Pachytel.*)<br>*P.* (*Goniotr.*)<br>*Physea* | ⟶ | *Entomoantyx*<br>*P.* (*Goniotr.*) |

Trends are in two directions: increase in number of tarsomeres with vestiture; and complete loss of adhesive vestiture.

## Summary

In the absence of evidence that the New World ozaenine genera are monophyletic relative to their Old World counterparts, only a limited evolutionary analysis seems practical. This analysis consists of statements about phylogenetic distance from the putative out-group, *Metrius*, and about striking features of evolutionary divergence in particular character systems.

In terms of overall divergence, as measured by a summation of the relative distance from *Metrius* in each of the postulated transformation series, the sequence of genera is as follows, from most like to least like: *Entomoantyx—Pachyteles—Physea—Ozaena-Platycerozaena*. Probably this sequence does not represent a system of sister-group relationships, though *Ozaena* and *Platycerozaena* must be sister groups. *Physea* is strikingly aberrant in details of mandibles, male and female genitalia and ovipositor, as well as body form. The few defensive secretions lend credence to the proposition that this genus, though aberrant, is from a basically primitive stock.

A reviewer of a previous draft of the manuscript on which this paper is based, conducted a numerical cladistic analysis of the data, using the program HENNIG 86, and reported that a single most parsimonious cladogram resulted, expressed linearly as a series of inclusions: *Metrius* + (*Entomoantyx* + (*Pachyteles* + (*Physea* + (*Ozaena* + *Platycerozaena*)))). The consistency index is 0.81 or 26/32, indicating that there are only six extra steps in the cladogram of the six genera.

The sequence of genera is exactly the same as in the linear arrangement presented above. Nonetheless, as explained above, we do not believe that evolutionary significance should be accorded to the branching pattern, *i.e.*, that *Physea* is really sister-group of *Ozaena* + *Platycerozaena*.

We note two striking developments in the New World Ozaenini. Both may involve close association with ants. One of these developments is an escape from the constraints of life under bark, and is represented by the genus *Physea*. Body form is markedly modified (*i.e.*, broadened, as in Fig. 2; *cf.* Figs. 3 and 4). Other divergent features of *Physea* are noted above. We do not know their functional significance in relation to life in an environment with fewer physical constraints, or if some of these modifications evolved in response to life with ants. An explanate body plus flattened appendages may have to do with provision of a dorsal shield under which the appendages can be concealed as a safeguard against attacks by ants. The elongate antennae, which we believe are secondarily elongated, are anomalous, especially considering the reduced antennal cleaner. One would think that short antennae would be more easily protected from the ravages of ants.

A second striking development involves the genera *Ozaena* and *Platycerozaena*. The more evolved chemical defensive system includes possibly setae that are specialized for enhanced effectiveness in dispersion of the defensive secretions, which in turn are more numerous than in other New World ozaenines (demonstrated for *Platycerozaena*; inferred for *Ozaena*). This more complex system suggests evolution to cope with more efficient enemies— as for *Physea*, possibly ants. Loss of the normal tactile setae from the dorsal surface of head, pronotum and elytra also suggests association with ants— by analogy with lack of setae in paussines. Other striking modifications of these two ozaenine genera involve: antennae, with general reduction in sensilla trichodea, modification in form, and antennomere 11 with its concentration of sensilla basiconica; various modifications of labrum, maxillae, and labium, suggesting changes in food or feeding mechanisms; and the peculiarly modified palpiform stylomeres of the

females, which suggest a sensory function rather than one of simple deposition of eggs.

We believe that the reduced antennal cleaner of the fore tibia has developed twice: once in the ancestral stock of *Physea* + *Physeomorpha*, and once in the ancestral stock of *Ozaena* + *Platycerozaena*. This feature, plus loss of tactile setae from the *Ozaena-Platycerozaena* lineage, presages similar losses from the paussine lineage, as pointed out by Darlington (1950) for *Physea*. He noted, as well, the myrmecophilous habits of *Physea* and the paussines. Another similarity to the paussine lineage is the peculiar sensilla basiconica of adults of *Ozaena* and *Platycerozaena*. Conceivably, either the *Physea* or *Ozaena* lineage could be the sister group of the paussines, though the similarities might reflect simply parallel developments, based on an underlying general similarity.

The general ecologically-based scenario that we think the data reflect is one of: evolution in the tropics of form, structure and habits for life under bark (*Entomoantyx* and *Pachyteles*); differentiation in the sub-cortical habitat (*Pachyteles*); secondary loss or modification of these features, associated with development of a myrmecophilic existence (*Physea* and *Physeomorpha*). We do not have information about habitat for the *Ozaena-Platycerozaena* lineage, but we judge from body form of adults that they are sub-cortical, and we believe that they are adapted for life with ants, too.

A different scenario, based on lack of association of *Physea* adults with sub-cortical habits, places its lineage at the base of the Ozaenini.

Finally, we believe that *Metrius* is a relict genus, surviving in the temperate zone, living in an ancestral-type habitat of leaf litter, beyond the periphery of the range of its more evolved ozaenine relatives. In many body features, adults are primitive, but not in body form, absence of wings, or in development of the large intercoxal process of the prosternum. Thus, this basically primitive group has evolved its own special features.

## TAXONOMIC TREATMENT

Provided in this section are: description of the Tribe Ozaenini based on features of adults of New World taxa; descriptions of the genera known from Middle America; and descriptions of selected species. These species are either known from the United States, or their northern limit of geographical range is near the U. S.-Mexican border, or their structural features indicate aspects that we found instructive in appreciating the divergence of the New World Ozaenini.

For the species, we report limited quantitative data: range of body size (Standardized Body Length and maximum width). The only generally useful ratio that we found and report here is width of elytra/ Standardized Body Length (W/SBL). Two groups are recognized in the material that we examined: species with low values (0.31-0.35), whose adults have long slender bodies; and species with higher values (0.37-0.46), whose adults have broader, stouter bodies.

### Tribe OZAENINI

*Description*.— Adults small to average for Carabidae (SBL *ca*. 3-18 mm.). Body form sub-cylindrical to terete and explanate.

Color. Body uniform black to testaceous, or various combinations of these somber colors, or aeneous-green; elytra somber-colored, or aeneous, like rest of body, or bright metallic blue-green.

Microsculpture. Most members with mesh pattern of dorsal sclerites (including elytra) isodiametric, mesh pattern of lateral and ventral sclerites predominantly transverse, though surface not grated (Allen and Ball, 1980: 487); some members with mesh pattern of body sclerites and elytra uniformly isodiametric; microlines distinctly developed, or partially effaced and thus difficult to see at magnification of 50X or less, or absent (Fig. 107A).

Luster. Dorsum (including elytra) dull (most members) or glossy, venter more glossy, or dull as dorsum.

Vestiture. Surfaces of body and elytra either with or without pile of short trichoid (hair-like) setae, pilosity dense or sparse; members of most taxa with ventral and lateral sclerites sparsely pilose. Articles of legs sparsely or densely pilose. Members of some taxa with setae on head and prothorax, and/or serially arranged setae on various intervals of elytra. Wider, flat, costate setae (Fig. 107A and B) on dorsal surfaces of pronotum and elytra of members of some taxa. Fore tarsomeres 1-3 of males (Fig. 66C) with or without adhesive vestiture. Mandibles, cardines, submentum and mentum with or without pilosity.

Fixed (or standard) setae (*i.e.*, those characteristic of most carabid taxa) and spines. Clypeus with one to three pairs of setae laterally, or asetose. Head with one pair of supraorbital setae (members of some taxa with supraorbital setae indistinguishable from other long trichoid setae of head), or asetose. Antennae: trichoid setae as follows— antennomere 1 with one to several; antennomeres 2 and 3 with ring of few near apex, antennomere 4 with one or several rings of few, preapically; antennomeres 5-11 with many to few, variously arranged, or antennomere 11 without; other setae— shorter, thicker basiconic sensilla on antennomeres 5-11, associated with rugose matt areas variously, from numerous and widely distributed on lateral surfaces to very few concentrated in small oval areas on ventro-lateral surfaces, or toward apex of antennomere 11 (Figs. 29A&B, 30). Labrum pre-apically with seven to 12 forward-directed setae, or asetose (*Platycerozaena* members). Mandibles each with or without single long seta in scrobe (Fig. 40A) (members of *Physea* with numerous long setae, one of which may be the normal seta of the scrobe). Maxillary setae: cardo asetose or with one to three; stipes, two; palpomere, several. Labial setae: submentum, two to five or six; mentum, two to five or six; glossal sclerite, two to four; palpomeres 2 and 3 plurisetose (Figs. 44-47); palpomere 1 glabrous or with few setae. Pronotum with more than two pairs of lateral marginal setae, or without marginal setae. Prosternum with apex glabrous or sparsely setae. Elytra with umbilical setae (each elytron with about 30), without parascutellar setae, with or without (members of few taxa) discal setae. Tibiae each with several rows of spines. Tarsomeres 1-5 ventro-laterally with one or two rows of setae on each margin, ventral surfaces of tarsomeres 1-4 with patches of longer setae. Standard setae of abdominal sterna not distinguishable from vestiture.

Head. Form approximately quadrate. Clypeus transverse, surface plane, anterior margin slightly concave. Frons and vertex uniformly slightly vaulted, or frons with pair of indistinctly delimited impressions near fronto-clypeal suture. Supra-antennal areas ridged laterally, flat or reflexed. Occipital area broad, not constricted, or with shallow groove dorsally. Temporal areas either small or swollen laterally, each as narrow lobe extended on posterior surface of eye. Antennal fossae close to anterior margin of eye, sub-antennal area either plane or depressed. Gula average. Eyes elliptical, with long axis either parallel or perpendicular to long axis of head.

Antennae. Varied in relative length, from shorter than combined length of head and pronotum, to about one third of body length; filiform to sub-clavate; antennomere 1 (scape) large; antennomere 2 (pedicel) shorter than scape, small; antennomeres 3 and 4 elongate or short and moniliform; antennomeres 5-10 sub-cylindrical, longer than wide (Fig. 10); or more or less compressed, extended ventro-laterally, broad surfaces anterior and posterior with antenna extended at right angles to longitudinal body axis, either longer than wide (Fig. 11), quadrate (Fig. 13), or wider than long (Fig. 15); or moniliform, short, thick and cylindrical (Fig. 14); antennomere 11 (Figs. 25-30) more or less enlarged, either longer or wider than antennomeres 5-10, shape various— pre-apically sub-cylindrical (Fig. 25) or more or less transverse (Figs. 29A-30), apex blunt or narrowly keeled, keel straight (Fig. 29A) or sinuate (Fig. 30).

Mouthparts. Labrum transverse, narrow (Fig. 32), or broader (Figs. 33, 35, and 36), or almost as long as wide (Fig. 37); anterior margin straight or broadly concave, or narrowly notched (Fig. 37). Mandibles: trigonal, with broad bases, symmetrical in general outline, scrobes broad, distinctly marked, retinaculum very large (Figs. 40A-D) or small (Figs. 39A-D); terebral margins prominent, posteriorly extended or not on dorsal surface of retinaculum (Fig. 42A); terebral tooth evident on both left and right mandibles (Figs. 39A,B- 43A,B); retinaculum prominent or not, posterior tooth more or less evident, directed posterad, anterior tooth prominent or not; molar area variously toothed; ventral groove more (Fig. 40C-D) or less (Fig. 39C-D) extensively densely setose. Maxillae: average for Carabidae; lacinia with apical tooth normal (long and slender, Fig. 46), or shorter and broader, chisel-like (Fig. 47B); galeomeres 1 and 2 of various proportions; palpomeres various, 4 relatively slender (Fig. 45) to broad (Figs. 47A and 48). Labium: submentum narrow, transverse; mentum transverse, lateral lobes of various lengths, more or less tapered apically; epilobes prominent; mental tooth large or small, apically not notched (in New World taxa); ligula uniformly sclerotized, paraglossae adnate to glossal sclerite, latter with blunt apex. Palpomeres 2 and 3 subequal, longer than 1; palpomere 3 slender or broad, apical margin broad, subtruncate.

Prothorax. Pronotum transverse or longer than wide, short compared to length of elytra; base and apex similar in width, but base distinctly narrower than apex; disc slightly convex, median longitudinal and anterior transverse impressions shallow, posterior transverse impression shallow to deep; lateral grooves distinct, postero-lateral impressions shallow to deep; sides plane or reflexed, lateral margins broad or narrow, evenly curved throughout length or more or less sinuate posteriorly; antero-lateral and postero-lateral angles various, from broadly obtuse to narrowly acute. Proepipleura broad, either sharply extended laterally and horizontal to pleuronotal margin, or extended dorsad in same plane as pleuron. Pleural sclerites average for Carabidae. Prosternum with intercoxal process broad or slender, with apex near posterior margins of coxae.

Pterothorax. Mesepisternum and mesosternum separated by suture. Mesepimeron extended to margin of mid-coxa, broad, posterior margin sinuate, medially overlapping metepisternum. Mesosternum narrow, intercoxal process in contact or not with process of metasternum. Metathorax of average proportions, or distinctly shortened. Metepisternum long and slender, with lateral margin much longer than width of basal margin; or short and broad, with lateral and basal margins subequal. Metepimeron distinct, wide in relation to apical width of metepisternum. Metasternum average for Carabidae.

Elytra. Elongate, parallel-sided, or expanded and inflated, with widest point near middle, and tapered both anteriorly and posteriorly. Disc flattened or somewhat inflated, tapered gradually apically. Basal ridge short, extended no farther than plane of base of interneur 4, and anterad discal plane. Humeri each denticulate or rounded. Apical margin oblique. Flange of Coanda (Fig. 70B) preapico-lateral. Intervals moderately convex to flat, interneurs shallow, punctate or not, obsolescent or absent. Epipleura average for Carabidae.

Metathoracic wings. Fully developed in adults of most taxa, variously reduced in few. Oblongum cell large, quadrangular; wedge cell absent.

Legs. Coxae, trochanters, middle and posterior femora and tibiae average for carabids, or tibiae markedly compressed (Figs. 64A-B). Anterior and posterior coxae separated from one another by intercoxal processes; middle coxae separated or not by intercoxal processes. Front femur more or less cylindrical or flattened, with or without antero-ventral projections (Figs. 58-61A,B) or swellings (Fig. 57). Front tibia isochaete (both spurs terminal), expanded apically or flattened and generally explanate. Antennal cleaner with channel large (Figs. 66A-B) or smaller; medial expansion prominent (Figs. 67A-B) or not (Figs. 68A-B); clip setae (Fig. 65) present or absent; anterior setal row with setae large (Figs. 67A-B) or small (Figs. 64A-B); setal band not sinuate (Fig. 68B) to markedly so (Figs. 67A-B). Tarsomeres thickened, with dorsal surfaces slightly depressed, 5 longer than any of 1-4, tarsal claws smooth, not denticulate.

Abdomen. Sterna II-VII and tergum VIII average for carabids, without distinctive features. Males with sternum VIII with pair of small hemisternites, without apodemes, joined medially by membrane. Ring sclerite (Segment IX-X, Figs. 92-96) of males with tergum narrow, laterally each side with sclerotized explosion chambers (*ec*) of pygidial gland system; sternal apodemes joined in form of symmetrical or markedly asymmetrical ring; right hemisternite various in form, bilobed or not. Females with sternum VIII (Figs. 98-102) with pair of more or less reduced hemisternites, joined medially by membrane; hemisternites setose or asetose, each with short apodeme projected anteriorly. Tergum IX/X narrow.

Male genitalia. Median lobe compressed, basal opening wide; apical portion various, from simple short point to more or less elaborate ventrally-directed projection (Fig. 87A) or cleft (Fig. 89B); apical orifice dorsal. Ejaculatory duct in median lobe surrounded by long, rod-like sclerite ( rod, **r**, Figs. 83A-91A, and 97A). Internal sac short, infolded but only partially inverted, with three areas: basal asetose membranous area; medial collar, with microtrichia; and apical portion variously lobed and with or without sclerites (Figs. 83-91, and 97). Parameres extensive, left broad basally but tapered apically, apex with or without few setae. Right paramere long, apex extended nearly to apex of median lobe, medial margin fringed with setae, more or less extensively (Figs. 83-91, and 97).

Ovipositor. Ventral surface ventrally directed in repose. Valvifer slender, moderately long. Stylomere single sclerite, slender, of various length, variously setose and spinose, apex pointed (Fig. 71A), more broadly rounded (Fig. 81A), subtruncate (Fig. 73A), or cleft (Fig. 74B ). Sensory furrow preapical (Figs. 71, 74A-B) or apical (Figs. 76A-B) with long nematoid setae and furrow peg setae, margins without ensiform setae.

*Way of life.*— Little is known about this topic (Ball, 1960: 94). Adults of various species of *Pachyteles* (*sensu lato*) have been collected from under bark of fallen tree trunks in lowland wet tropical forests and from under bark of fallen cottonwood poplars along waterways in semi-desert areas. Adults of *Pachyteles kuntzeni* have been collected at night, on dead oak trees and stumps. Adults of *Physea hirta* LeConte have been collected in association with leaf-cutter ants of the genus *Castelnau.* Most ozaenine adults, however, have been collected at ultraviolet light at night, showing that they are active nocturnally.

Adults and larvae of the non-myrmecophilous species probably are general predators under bark, an inference based on their general structural features. Forsythe (1982 and 1987) recognizes three types of feeding in carabids: fluid feeding; fragmentary feeding; and mixed feeding. Mixed feeders are of two types: either predominantly zoophagous or predominantly phytophagous. Each of these types has characteristic mandibles and maxillae. Details of mandibular and maxillary structure of adult ozaenines indicates that they are mixed feeders, predominantly zoophagous. This means that individuals take particulate animal matter, but secrete digestive juices extra-orally, on the prey. Thus, presumably, a certain amount of digestion is extra-oral.

*Geographical distribution.*— In the New World, the range of the Ozaenini extends from southern South America (Argentina in the east and Chile in the west) northward through Central America to southwestern United States (southern Texas in the east, and southern Arizona in the west).

*Included taxa.*—Six New World genera are included in the Ozaenini: *Entomoantyx*, new genus; *Physea* Brullé; *Physeomorpha* Ogueta; *Pachyteles* Perty; *Ozaena* Olivier; and *Platycerozaena* Bänninger. Of these, *Physeomorpha* is confined to South America, and *Entomoantyx* to Middle America. The remaining genera are in both South and Middle America, and *Physea*, *Pachyteles* and *Ozaena* reach their northern limits in southern-most southwestern United States.

## Key to Genera of Metriini and Ozaenini of Middle and North America, and Species of Southwestern United States and Northern Mexico

1 Fore tibia with both spurs terminal (Fig. 65B). Fore coxal cavities closed by medial extension of proepimera. Pterothorax with middle coxal cavities disjunct (mesepimeron extended to middle coxa)........................................................................ 2

1' Combination of character states otherwise. ...................................... ........................................................................other tribes of Carabidae.

2 (1) Elytron without flange of Coanda (*cf.* Fig. 70A). Mentum with tooth notched apically (Fig. 49) or not. Metathorax with metepisternum short, length of lateral margin subequal to width at basal margin. Mandible with single seta in scrobe....................

.........Tribe Metriini, *Metrius* Eschscholtz. (not treated further).

2' Elytron with flange of Coanda (Fig. 70A), body form various. Tooth of mentum not notched apically (Figs. 50-55). Mandibles with one or many setae in scrobe ..................................
..........................Tribe Ozaenini. .................................................................3

3 (2') Mandible with single long seta in scrobe (Fig. 40A). Antennae filiform, antennomeres 5-11 densely setose, 1-4 sparsely so. Elytra metallic blue-green, sharply contrasted with rufous head and prothorax..............*Entomoantyx cyanipennis* (Chaud.), p. 84

3' Mandible with several (five or more) setae in scrobe (Figs. 39A, 41A). Antennae various in form. Dorsal surface more or less uniform in color, black, piceous, or testaceous.............................4

4 (3') Tibiae markedly compressed and broad (Fig. 64A). Fore femur with prominent broad swelling near base (Fig. 57). Head with broad depression (antennal fossa) beneath anterior margin of eye ...................*Physea* Brullé.....................................................................5

4' Tibiae sub-cylindrical, not compressed and broad. Fore femur with broad swelling or spine (Figs. 58-62). Head without antennal fossa..............................................................................................6

5 (4) Elytra with uniform vestiture of short setae, in addition to long tactile setae.........................................*Physea hirta* LeConte, p. 87

5' Elytra without vestiture of short setae, only several rows of long, tactile setae............. .................*Physea latipes* Schaum, p. 87

6 (4') Anterior tibia with prominent clip setae associated with antennal cleaning channel (Fig. 65B), latter extended beyond median expansion. Head, pronotum and elytra with normal long setae, with or without more or less dense vestiture of short trichoid setae. Mandibles with dorsal surfaces impunctate.........
......... ..................................*Pachyteles* Perty.. .........................................7

6' Fore tibia without clip setae, channel of antennal cleaner terminated at plane of median expansion (Fig. 68A). Head, pronotum and elytra without normal long setae, glabrous, or with vestiture of short, thickened setae (Fig. 107A). Mandibles with dorsal surfaces more or less densely punctate (Figs. 42A, B-43A, B) ..................................................................................... 12

7 (6) Middle coxae in contact with one another, not separated by intercoxal extensions of meso- and metasterna..................................8

7' Middle coxae separated by extensions of meso- and metasterna.................................................................................................10

8 (7) Pronotum and dorsal surface of elytra with vestiture of short setae.. ............... ................ ....*Pachyteles gyllenhali* (Dejean), p. 94

8' Pronotum and elytra with sparse, longer setae, those of elytra in rows on intervals.........................................................................................9.

9 (8') Pronotum with anterior and posterior lateral angles acute............
..............................................*Pachyteles mexicanus* Chaudoir, p. 97

9' Pronotum with anterior angles rounded, posterior angles about rectangular....................*Pachyteles enischnus*, new species, p. 96

10 (7') Pronotum narrow, only slightly wider than, or about as wide as, head..................................*Pachyteles elongatus* (Chaudoir), p. 93

10' Pronotum broader, distinctly wider than head .................................. 11

11 (10') Smaller (SBL 9-12 mm.), pronotum narrower (Fig. 3). .................................................. *Pachyteles parca* LeConte, p. 90

11' Larger (SBL 15-18 mm.), pronotum broader (Fig. 4) ................................................ *Pachyteles kuntzeni* (Bänninger), p. 92

12 ( 6') Antennae long, about one third length of body; antennomere 11 with shagreened area confined to apical third (Fig. 22), apical ridge straight (Fig. 29A)........ *Ozaena lemoulti* Bänninger, p. 100

12' Antennae short, claviform, antennomeres 5-11 markedly broad and flat; antennomere 11 with shagreened area apical and extended along dorsal and ventral margins (Fig. 23); apical ridge sinuate (Fig. 30) .................................... *Platycerozaena* Bänninger, p. 101

## *Entomoantyx*, new genus

Frontispiece, and Figs. 11, 19, 26, 33, 40A-D, 51, 58, 65A-B, 70A-B, 73A-B, 83A-D, 93, 99, and 104.

TYPE SPECIES: *Ozaena cyanipennis* Chaudoir, 1852: 40. Here designated.
*Ozaena*; Chaudoir, 1852: 40.—1854: 307.
*Pachyteles*; Chaudoir, 1868: 66.— Bates, 1881: 27.— Csiki, 1927: 427.
*Tropopsis*; Bänninger, 1927: 207.— Blackwelder, 1944: 23.— Reichardt, 1977: 377.— Erwin, 1979B: 557.

*Notes about synonymy*.— The type species of *Entomoantyx* was removed from *Pachyteles* and included in *Tropopsis* Solier by Bänninger on the basis of plesiotypic features (middle coxae separated; fore femur without ventral spine; antennal cleaner of fore tibia less modified). But, in apotypic features of antennal form and development of the antennal cleaner, *T. marginipennis* Solier (type species of *Tropopsis*) is more like *Pachyteles* than like *E. cyanipennis*. Furthermore, *E. cyanipennis* is characterized by a unique derived feature (form of mental epilobes), reduced number of labral setae (seven or eight), and more plesiotypic features than *Pachyteles* or *Tropopsis* in retaining a scrobal seta, a hardly modified antennal cleaner, and probably structure of the male genitalia (presence of a dense dorso-basal patch of microtrichia, and styliform right paramere). We believe, thus, that *E. cyanipennis* is not closely related to either *Tropopsis* or *Pachyteles*. For these reasons, we remove *E. cyanipennis* from *Tropopsis*. Because *E. cyanipennis* does not have a named genus for assignment, we have proposed a new one. Because the differences between *Tropopsis* and *Pachyteles* are slight, we combine these taxa, with the former name being a junior synonym. See below for details.

*Derivation of generic name*.— From the Greek *entomon*, cut, and *antyx*, margin, a name that alludes to the scalloped lateral margins of the pronotum of adult *E. cyanipennis*.

*Recognition*.— Adults are recognized easily among Middle American ozaenines by the bright bluish-green elytra that contrast strikingly with the rufous head and pronotum. The lateral margins of the pronotum (Frontispiece) are scalloped. Body size is small. The antennae, though rather short, have antennomeres 5-11 longer than wide (Fig. 11). Males have fore tarsomeres 1-3 with adhesive setae ventrally, median lobe of genitalia with a broad truncate apex (Figs. 83A-B), and internal sac with a sagittate dense patch of microtrichia dorso-basally (**x**,Fig. 83B), and left paramere digitate and densely setose apically. Females are characterized by rather short, broad stylomeres (Figs. 73A-B), with subtruncate apex and sensory groove markedly preapical.

*Description.*— Habitus as in Frontispiece. Size small, SBL ca. 3.5-4.5 mm., width 1.5-2 mm.

Color. See "Recognition" section, above.

*Microsculpture and luster. Pterothoracic pleura and sterna with mesh pattern transverse;* otherwise, as described for tribe. Surface generally slightly shining.

Vestiture. Tarsomeres with dorsal surfaces sparsely setose; fore tarsomeres 1-3 of males ventrally with adhesive vestiture. Thoracic and abdominal sterna with sparse covering of rather long setae. Otherwise, as described for tribe.

Chaetotaxy. Clypeus with two pairs of setae. Vertex of head with one pair of supraorbital, one pair of paramedial, and one pair of paralateral setae, latter two groups in row across vertex. Antennae: antennomere 1 with several setae; antennomeres 2-4 with apical row of long setae; antennomeres 5-11 with dense covering of setae, except nearly glabrous areas on anterior and posterior faces. Mouthparts: labrum with seven to eight long setae near anterior margin; mandibles each with one long seta in scrobe (Figs. 40A-B); maxillary stipites each with two lateral setae; submentum, mentum, and glossal sclerite each with one pair of setae. Pronotum with three pairs of lateral setae: one pair anteriorly, one pair near middle, and one pair anterior to postero-lateral angles; one pair of paramedial setae near anterior margin. Each elytron with about five setae in intervals 3 and 5, umbilical setae *ca.* 15. Legs, number of setae (fore, middle and hind): coxae, *0-numerous-numerous; trochanters,* 1-1-1; *femora, numerous, numerous, numerous.*

Head. Frons without impressions. Eyes moderately prominent (Frontispiece); temporal area each side small, not swollen. Supraantennal area each side with sharp ridge.

Antennae (Figs. 11, 19 and 26). Filiform, antennomeres 5-10 slightly longer than wide, antennomere 11 distinctly so (Fig. 11). Antennomere 11 (Fig. 19) with apex about symmetrical, moderately broadly rounded; circular in cross section, apical margin without distinct keel (Fig. 26).

Mouthparts. Labrum (Fig. 33) transverse. Mandibles (Figs. 40A-D): see Table 1 for details. Maxillae: average for Ozaenini, as in Figs. 45 and 46. Labium (Fig. 51): mentum with prominent tooth, lateral lobes broadly rounded apically, epilobes each with sharp tooth near apex; palpomere 3 triangular, with apex subtruncate.

Prothorax. Pronotum (Frontispiece) transverse; lateral grooves moderately broad; disc convex; linear impressions (anterior transverse and median longitudinal) clearly impressed; lateral margins scalloped; postero-lateral impressions deep. Propleura and prosternum as described for tribe.

*Pterothorax. As described for tribe, and middle coxal cavities separate, with meso- and* meta- intercoxal processes in contact with one another. Metepisternum not overlapped by extension of mesepimeron.

Elytra. Intervals broad, indistinctly elevated, interneurs shallow, indistinct. Basal ridge extended to about base of interneur 5.

Legs. In most features, as described for Ozaenini. Fore femur terete in cross section, without ventral projections. Antennal cleaner of fore tibia (Figs. 65A and B): grade C (see under "Structural and Biochemical Features"); details in Table 2.

Abdomen. Segments II-VII with tergum and sternum unmodified. or description of segments VIII and IX/X, see under "Structural and biochemical features, genital segments".

Male genitalia (Figs. 83A-D) and ovipositor Figs. 73A-B). See these items under "Structural and biochemical features", and Table 3 for details of male genitalia.

Ovipositor (Figs. 72A-C). Stylomeres of moderate length, broad at base. For details, see this topic under "Structural and biochemical features".

Bursa copulatrix and spermatheca. See Fig. 104 and for details, Table 4.

*Way of life.*— Members of this genus live in lowland tropical forests. Adults have been collected under bark of fallen tree trunks, and at U-V light, at night. The distinctive color pattern of red and blue suggests aposomaty, and this may be indicative of a way of life that differs from other New World ozaenines— for example, more time spent by adults in situations where they are exposed to predators that hunt using visual stimuli.

*Geographical distribution*.— This genus is known only from the Gulf-Caribbean Versant of Middle America: from Nicaragua northward to the state of Veracruz, México.

*Relationships*.— This genus is either a very primitive member of the *Pachyteles* assemblage of Ozaenini, or possibly even the sister group of the other assemblages of ozaenine genera, excluding the Australian *Mystropomus* Chaudoir and Oriental *Anentmetus* Andrewes.

*Included species*.— *Entomoantyx* includes only the species *E. cyanipennis* (Chaudoir).

### *Entomoantyx cyanipennis* (Chaudoir)

*Ozaena cyanipennis* Chaudoir, 1852: 40. TYPE MATERIAL: three males, each labelled "Ex Musaeo Chaudoir [red print] in front of following box label: "*cyanipennis* Chaud. Mexique 57 Salle"; Chaudoir-Oberthür Coll., Box 132 bis (MNHP). LECTOTYPE (here selected), first specimen in series.— Species synonymy same as for genus, above.

*Ozaena cyanoptera* Thomson, 1856: 330. TYPE MATERIAL: HOLOTYPE female, labelled "Ex Musaeo Chaudoir" [red print], in front of following box label: "cyanipennis Chaud Bul Mus 1852 p. 40 cyanoptera Thomson Ann Soc Ent 1856 p. 330 Toxpam".

*Pachyteles cyanipennis* Chaudoir, 1868: 66.— Bates, 1881: 27.— Csiki, 1927: 428.

*Tropopsis cyanipennis*; Bänninger, 1927: 207.— Blackwelder, 1944: 23.— Reichardt, 1977: 377.

*Pachyteles cyanoptera;* Chaudoir, 1868: 66.

*Notes about synonymy*.— Chaudoir (1868: 66) recognized the taxonomic identity of the types of *Ozaena cyanipennis* and *O. cyanoptera*, and established the synonymy, accordingly.

*Recognition*.— Among New World ozaenines, adults of *E. cyanipennis* are unique in color pattern: rufous head and prothorax, and metallic blue elytra. Adults are small in size.

Habitus as in frontispiece. Standardized Body Length (male) 4.4 mm; females 3.8-4.1 mm. Width, male 1.92 mm., females 1.6-1.7 mm; W/SBL male 0.44, females 0.42-0.43. Other features as noted for genus *Entomoantyx*, above.

*Way of life and geographical distribution*.— As above, under *Entomoantyx*.

*Material examined*.— In addition to the types, we have seen 14 specimens from México, as follows.

**Chiapas**. 27 km. SW Simojovel, VII.17.1962; J.M. Campbell (CNCI). **Veracruz**. Cordova, VI.29.1966; J.S. Buckett, M.R.& R.C. Gordon (CISC). 33 km. NE Catemaco, Los Tuxtlas Biological Station, 160 m, VII.1983; S.& J. Peck (UASM). Coyame, at Lake Catemaco, VII.1-15.1963; D.R. Whitehead (UASM). Lake Catemaco, V.24-25.1969; H.F. Howden (UASM). Dos Amates, VI.16-17.1969; D. Bright & J.M. Campbell (CNCI). Sontecomapan, VI.10.1969; H.F. Howden (UASM).

## *Physea* Brullé, 1834

*Physea* 1834: 473. TYPE SPECIES: *Trachelizus rufa* Brullé [= *Ozaena testudinea* Klug, 1834: 80]; by monotypy.— Chaudoir, 1854: 289, 310.— 1868: 72.— Lacordaire, 1854: 160.— Bates, 1881: 27.— Csiki, 1927: 431.— Bänninger, 1927: 212.— Van Emden, 1942: 25.— Blackwelder, 1944: 23.— Jeannel, 1946: 47.— Darlington, 1950: 50, 51, 65.— Ball, 1960: 94.— Reichardt, 1977: 376.—Thompson, 1979: 214.— Erwin, 1979: 557.

*Trachelizus* Brullé, 1834: 258. TYPE SPECIES: *T. rufa* Brullé, 1834: 259; by monotypy.— Solier, 1836: 598.— Chevrolat, in d'Orbigny, 1848: 626.— Chaudoir, 1854: 310.

*Trachelyzus* Chenu, 1851: 89.

*Notes about synonymy*.— The generic name *Trachelizus* appeared first in the Dejean catalogue (1834: 243), credited to Chevrolat, for a genus of brentids. Brullé (in Audouin and Brullé, 1834: 258) used this name, credited to Solier, for a genus of ozaenine carabids, with *T. rufus* Solier as the only included species, and thus type of this genus. Subsequently, in an addendum to the same volume (1834: 473), *Physea* Brullé was proposed as a replacement name for *Trachelizus*, on the basis that the latter name was, in effect, a junior homonym of *Trachelizus* Dejean. Also implied in the text was that *Ozaena testudinea* Klug, 1834 was a senior synonym of *T. rufus* Brullé. In any event, the name of the type species of *Physea* must be *Trachelizus rufus,* though the correct name of the *species* is *P. testudinea* Klug.

*Derivation of generic name.*— From Greek, meaning ampoule or bulb-shaped lamp; a vial for holy oil; evidently in allusion to the body form of an adult, which resembles a rather broad bottle constricted toward the top. with a narrow opening, corked by the head. The word *Trachelizus* is from Greek, meaning to wring or twist, presumably in allusion to the seemingly marked constriction between head and pronotum.

*Recognition.*— Adults are rufous or rufo-brunneous in color, with partially darkened appendages. The elytra are inflated and broad in relation to length (Fig. 2). Antennomeres 5-10 (Fig. 10) are filiform, distinctly longer than wide. The legs are flattened, especially the tibiae (Figs. 64A and B), and the tarsomeres are relatively slender. These features render *Physea* the most easily recognized genus in the Ozaenini.

*Description.*— Habitus as in Fig. 2. Size moderate, SBL ca. 10-12 mm., maximum width 4.9-5.2 mm.

Color. Body uniform rufous or rufo-brunneous; appendages same color, or mandibles, antennomeres and tibiae darkened.

Microsculpture and luster. As for Ozaenini, with mesh pattern transverse on mesepimera, isodiametric on mesepisterna, and isodiametric to slightly transverse on metepisterna. Dorsal surface matte, ventral surface matte or pterothoracic and abdominal sterna slightly iridescent.

Vestiture. Dorsal surface setose or glabrous, mandibles with scrobes setose basally. Ventral surface generally setose, or at least abdominal sternum IV with paramedial patches of setae, and row of setae near posterior margin of each of sterna IV to VII. Male fore tarsomeres 1 and 2 with adhesive vestiture ventrally.

Chaetotaxy. Clypeus with about 12 setae. Vertex with one pair of supraorbital setae and transverse row of about four shorter setae. Antennae: antennomere 1 (scape) with several setae; 2 and 3 each with preapical ring of setae; antennomere 4 with scattered setae; antennomeres 5-11 generally setose except anterior and posterior glabrous areas. Mouthparts: labrum (Fig. 32) with row of about 10 setae near anterior margin; mandibles without fixed setae; maxillary stipes laterally with two setae; submentum, mentum, and glossal sclerite each with single pair of setae; mentum without paramedial setae; labial palpomere 2 trisetose. Pronotum with marginal setae numerous anteriorly and posteriorly, asetose medially. Each elytron with several rows of long setae on disc. Legs (number of setae, fore, middle, and hind): coxae, 0-numerous-numerous; trochanters, several-several-one or two; femora, numerous-numerous-numerous.

Head. Frontal impressions not indicated. Eyes in lobate setose clefts, large. Supraantennal area reflexed strikingly anteriorly, in form of broad plate each side (Fig. 2).

Antennae (Figs. 10, 18 and 25). Antennomeres 5-11 (Fig. 10) filiform, distinctly longer than wide. Antennomere 11 (Fig. 18) with apical margin markedly asymmetrical, apex narrowly rounded, without distinct ridge (Fig. 25).

Mouthparts. Labrum transverse (Fig. 32). Mandibles (Figs. 39A-D) falcate, most of occlusal margin smooth. or details, see Table 1. Maxillae average for Ozaenini, lacinia (*cf.* Fig. 46) terminated in long sharp tooth; palpomeres slender, elongate, apex of maxillary palpomere 4 subtruncate. Labium (Fig. 50): mentum with broadly rounded lateral lobes, each epilobe widened preapically; tooth prominent; labial palpomere 3 elongate, slender, apex truncate.

Prothorax. Pronotum (Fig. 2) markedly transverse, sides markedly reflexed, lateral margins smooth; lateral grooves broad; impressions shallow. Prosternum with intercoxal process narrow.

Pterothorax. As described for Ozaenini, and intercoxal processes of meso- and metasternum reduced, middle coxal cavities and middle coxae in contact medially. Metepisternum overlapped by lobe of mesepimeron.

Elytra. Markedly expanded, convex. Surface smooth, flat, no indication of intervals and interneurs. Basal ridge extended only to about base of interneur 6.

Legs. Middle coxae globose, more so than usual. Femora (Fig. 57) and tibiae (Figs. 64A and B) markedly compressed, especially tibiae. Femora with ventral surfaces grooved, fore femur (Fig. 57) with swelling ventrally, near base. Antennal cleaner of fore tibia (Figs. 64A and B) small. For details, see Table 2.

Abdomen. Sclerites of segments II-VII unmodified. or description of sclerites of segments VIII and IX-X, see under "Structural and biochemical features, genital segments". See also Figs. 94 and 100A and B.

Male genitalia (Figs. 84A-D). For details, see this topic under "Structural and biochemical features" and Table 3.

Ovipositor (Figs. 71A-C). Stylomeres long and slender, blade-like. or details. see this topic under "Structural and biochemical features".

Bursa copulatrix and spermatheca (Fig. 105). For details, see this topic under "Structural and biochemical features", and Table 4.

*Defensive secretions*.— Three compounds, only. See Table 5 for details.

*Way of life*.— Members of this genus seem to be associated with leaf-cutter ants of the genus *Atta*. See under species treatments, below, for additional details.

Geographical distribution.— This genus is confined to the New World, ranging on the mainland from Argentina to southwestern United States.

Relationships.— In body and leg form and structure of the antennal cleaner, adults of *Physea* are much like those of the monobasic genus (1965a: 113). They differ in form of antennomeres, however, those of *Physeomorpha* being very short and transverse. In spite of this difference, we believe that these genera are closely related, and may be congeneric.

Jeannel (1946: 47) placed *Physea* in a monobasic subfamily, because of its obvious distinctiveness within the Ozaenini. Enhancing the distinctiveness of body form and leg form are the distinctive mandibles, male genitalia, elongate stylomeres of the ovipositor, bursa copulatrix, and bursal sclerite, and myrmecophilous way of life. In other derived features (pterothoracic structure, absence of the scrobal seta from the mandibles, trisetose labial palpomeres and a complex set of defensive chemicals), adults of *Physea* are like other New World ozaenines.

The filiform antennae seem to be a remarkably plesiotypic feature, for they are more slender than the antennae of adult *Metrius*, the primitive sister-group of the Ozaenini. This feature should not be over-emphasized, for two reasons. First, the putative sister-genus of *Physea* exhibits more typical ozaenine antennae. Second, the antennal cleaner is suggestive of a taxon whose members once had antennal articles that were too extensive to be cleaned effectively by such a structure, and accordingly the latter was reduced. Subsequently, then, the antennomeres became slender, once more. Thus, their seeming primitiveness is secondary, and therefore, these structures are apotypic.

At this time, we are not in position to offer an hypothesis that provides a sister group for the lineage *Physea* + *Physeomorpha*.

*Included species*.— Six species are members of this genus, including two, *P. hirta* LeConte and *P. latipes* Schaum, that live in México (with the former also occurring in Texas), and that are treated below.

### *Physea hirta* LeConte
### Figs. 10, 18, 25, 32, 39A-D, 45, 50, 57, 64A-B, 71A-C, 84A-D, 94, and Map 1.

*Physea hirta* LeConte, 1853: 393. TYPE MATERIAL: HOLOTYPE male, labelled "Type 5488" [red paper]; "*Physea* hirta Lec" [handwritten]; (MCZ). TYPE LOCALITY (from original description): México, near U.S. border (Haldeman).— Chaudoir, 1854: 312.— 1868: 72.— Bates, 1881: 27.— Csiki, 1927: 431.— Bänninger, 1927: 212.— Blackwelder, 1944: 23.— Leng, 1920: 49.— Johnson, 1978: 67.

*Recognition.*— In habitus (Fig. 2), adults are similar only to those of *P. latipes* Schaum Fig. 2). The two species are distinguished by setation (see key) and pronotal form: elevated lateral portions much broader in *P. hirta*, and anterior margin sharply concave.

Habitus as in Fig. 2. Characteristics of *Physea*. Standardized Body Length, males 10.7-11.1 mm., females 10.5-11.7 mm; W/SBL males 0.44-0.45, females 0.44.

*Way of life.*— Adults were collected in Chiapas and Veracruz in and around the midden heaps of *Atta* nests, in daylight hours. Van Emden (1936), in a description of the larva of *P. setosa* Chaudoir, notes that both larvae and adults of this species live in *Atta* nests. Specimens have been collected at night, also. The late Jorge Hendrichs, of México City, advised the senior author that he had collected specimens of what was probably this species at night, in the vicinity of columns of *Atta* workers.

*Geographical distribution.*— This species is known from the Gulf and Pacific Versants of Middle America, from Guatemala to southeastern Texas.

*Material examined.*— From México and the United States, we have seen 20 specimens from the following localities.

UNITED STATES OF AMERICA. **Texas**. **Comal Co.** (USNM). **Kennedy Co.** 27°10'N, 97°40'W, VIII.28.1976; J.E. Gillaspy (TAIU).

MÉXICO. **Chiapas**. E. slope, Sierra de la Colmena, 16° 24'18"N, 91 24'16"W, Arroyo Santa Maria, 213 m., nr. *Atta* nest, VI.5-10.1972; G.E. & K.E. Ball, P.A. Meyer (UASM). Same, VI.1-10.1972 (UASM). 27 km. SE Teopisca, Rte. 24, VI.3-4.1969; H.. Howden (UASM). **Oaxaca**. Rte. 131, 82 km. S. Juchatengo, oak forest VII.16-17.1972; P.A. Meyer, G.E. Ball (UASM). Hwy. 125, 13 km. N. Hwy. 200, nr. Pinotepa Nacional, U-V light, 195 m., VII.19.1986; S. McCleve, P. Jump (UASM).**San Luis Potosi**. El Salto, VIII.8-9.1968; J.W. McReynolds (CASC). Same, U-V light, VII.7.1966; R.E. Woodruff (UASM). Tamazunchale, VII.13.1956; D.H. Janzen (CISC).**Veracruz**. Fortin de las Flores, 1010 m., VIII.1.1964; H.V. Daly (CISC). Same, U-V light, VII.7-12.1974; J.A. Chemsak, J. Powell (CISC). Rio Metlac Cn., NW. Fortin de las Flores, U-V light, VII.10.1974; J.A. Chemsak, E.& J. Linsley, & J. Powell (CISC). Canyon, SW. Rio Metlac, nr. Fortin, 975-1036 m., *ex* refuse deposit *Atta mexicana*, VIII.13-18, 1971, A. Newton (MCZC).

### *Physea latipes* Schaum
### Figs. 2, 100A-B, 105, and Map 1

*Physea latipes* Schaum, 1864: 117. TYPE MATERIAL: not seen. TYPE AREA: "Mexico" (from original description). Chaudoir, 1868: 74 .— Bates, 1881: 27 (as junior synonym of *P. hirta* LeC.).— Csiki, 1927: 431 (as junior synonym of *P. hirta* LeC).— Bänninger, 1927: 212.— Blackwelder, 1944: 23.

*Recognition.*— See key and treatment of this topic for *P. hirta.*

Habitus as in Fig. 2. Standardized Body Length, males 10.3-11.4 mm., females 11.0-11.4 mm; W/SBL, males 0.44-0.46, females 0.45-0.46.

Female sternum VIII and tergum IX-X as in Figs. 100A and B, respectively. Bursa copulatrix as in Fig. 105.

*Geographical distribution.*— We have seen material from the Pacific Versant of México, only. However, we expect that *Physea latipes* ranges into southern Arizona, as do many other carabids that occur in the vicinity of Mazatlan, Sinaloa. This prediction is supported by occurrence in southern Arizona of the host of other *Physea* species, *Atta mexicana* (Smith, 1951). .

*Material examined.*— We have seen 34 adults from the following localities.

MÉXICO. **Colima**. Manzanillo, VII.18.1953; C.& P. Vaurie (AMNH).**Guerrero.** Iguala, IX; Barrett (CASC). **Jalisco**. Ajijic, U-V light, VII.25.1964; W. L. Nutting (UASM). Estacion Biologia Chamela, VII.8-16.1985; J. Chemsak *et al.* (CISC). 61 km. SW Guadalajara, 1310 m., VII.24.1952; F.W. & F.G. Werner (UASM). Hwy. 200, 33.5 km. S. Puerto Vallarta, 724 m., U-V light, VII.21.1986; S. McCleve, P. Jump (UASM). **Sinaloa**. Mazatlan, IX.15.1918 (CASC). "Venedio" [=Venedillo], VII.10- VIII.27.1918 (CASC).

## *Pachyteles* Perty

*Pachyteles* Perty, 1830: 3. TYPE SPECIES: *Pachyteles striola* Perty, 1830: 4; fixed by Hope, 1838: 99; subsequent designation.— Chevrolat, in d'Orbigny, 1847: 392.— Lacordaire, 1854: 157.— Chaudoir, 1868: 51.— Bates, 1881: 26. — Horn, 1881: 129.— LeConte and Horn, 1883: 24.— Leng, 1920: 49.—Csiki, 1927: 427.— Bänninger, 1927: 208.— van Emden, 1942: 25.— Blackwelder, 1944: 23.— Ball, 1960: 94.— Erwin *et al.*, 1977: 4.3.— Reichardt, 1977: 376.— Eisner *et al.*, 1977: 385.— Ward, 1979: 185.— Thompson, 1979: 232.— Erwin, 1979a: 359. 1979b: 557.- Erwin and Sims, 1984: 374, 427.

*Goniotropis* Gray, 1832: 274. TYPE SPECIES: *Goniotropis braziliensis* Gray, 1832: 274; by monotypy.— Duponchel, in d'Orbigny, 1845: 274.—Lacordaire, 1854: 157.— Chaudoir, 1868: 51.— Bates, 1881: 25 .— Csiki, 1927: 427 (as junior synonym of *Pachyteles*).— Bänninger, 1927: 202.— Blackwelder, 1944: 23.— Ball, 1960: 94.— Erwin *et al.*, 1977: 4.3.— Reichardt, 1977: 377.— Moore, 1979: 194.— Erwin, 1979: 557.— Eisner and Aneshansley, 1981: 83.

*Tropopsis* Solier, 1849: 179. TYPE SPECIES: *Tropopsis marginicollis* Solier, 1849: 181 (here designated, the first of two species named by Solier).— Lacordaire, 1854: 159.— Chaudoir, 1868: 67 (as a section of *Pachyteles*).— Csiki, 1927: 427.— Bänninger, 1927: 207.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.— Reichardt, 1977: 377.

*Scythropasus* Chaudoir, 1852: 289. TYPE SPECIES: *Scythropasus elongatus* Chaudoir, 1852: 289 (by monotypy).— 1868: 48.— Bates, 1881: 24.— Csiki, 1927: 427.— Bänninger, 1927: 207.— Erwin, *et al.*, 1977: 4.3.

*Notes about synonymy.*— *Pachyteles*, *Goniotropis* and *Tropopsis* are treated as congeneric because the differences among them seem rather slight, compared to differences among other New World genera. Certainly, the group as a whole is markedly divergent, especially in features of the male genitalia and ovipositor. However, such differences do not seem to be correlated with other features. The name *Scythropasus* Chaudoir was synonymized with *Goniotropis* by Bänninger. The basis for selecting *Pachyteles* as the name for the genus is priority.

*Derivation of generic name.*— According to its author (Perty,1830: 4), the word *Pachyteles* is derived from incrassate antennomere 11, and means thick spear (Greek, *pachy* + *telum*).

*Recognition.*— Among Middle American ozaenines, adults of *Pachyteles* are recognized by a combination of: antennomeres 5-10 short, each about as wide as long; fore femur with ventral spines (Figs. 59 and 60); antennal cleaner of fore tibia with median expansion prominent; and base of mental tooth of labium with a pair of setae. Adults of the South American subgenus *Tropopsis* lack the femoral spine, and one undescribed species has long and slender antennal articles.

*Description.*— Habitus as in Figs. 3-6, body slender, elongate. Size varied, Standardized Body Length *ca.* 3.5-17.5 mm, maximum width 1.3-5.9 mm.

Color. Various somber shades: flavo-rufous to dark piceous, but not black; appendages of most specimens rather paler than body color.

Microsculpture and luster. As for Ozaenini, and pterothoracic pleura and sterna with mesh pattern isodiametric or transverse.

Vestiture. Dorsal surface various, from almost glabrous to densely setose, especially elytra. Fore tarsomeres 1 and 2 or 1-3 of males with adhesive vestiture ventrally, or fore tarsomeres glabrous.

Chaetotaxy. Clypeus with three pairs of setae. Vertex of head with several pairs of supraorbital setae and several behind eyes, also. Antennae, number of setae: antennomere 1, one to several; 2-3, apical ring; antennomere 4, *ca.* apical half setose; antennomeres 5-11 densely setose, except anterior and posterior glabrous triangular areas. Mouthparts: labrum (Figs. 34 and 35) with 10 or more (*ca.* 16) setae near anterior margin; maxillary stipes with two or three setae; submentum and mentum with one or more pairs of setae, each; glossal sclerite apically with one pair setae; labial palpomere 2 with numerous setae, but three preapical setae longer than rest; palpomere 3 also setose. Pronotum with marginal setae numerous (*ca.* 10). Each elytron with several rows of discal setae of about 10 in each of intervals 1, 3, 5, and 7; umbilical setae *ca.* 25. Legs (number of setae, fore, middle, hind): coxae, 0-numerous-numerous; trochanters, several-several-several, each with one long seta, others short; femora, numerous-numerous-numerous.

Head. Frontal impressions shallow, broad, but recognizable. Eyes (Figs. 3-6) subtruncate posteriorly, moderately prominent; temporal lobes small. Supraantennal area not reflexed, though ridges generally sharp.

Antennae (Figs. 12, 13, 20, 21, 27 and 28). Antennomeres 5-10 almost quadrate, 11 clearly longer than wide (Figs. 12 and 13),flattened antero-posteriorly, terete in cross section (*cf.*Figs. 27 and 28). Antennomere 11 (Figs. 20 and 21) with apex broadly rounded, terminated in straight keel (Figs. 27 and 28).

Mouthparts. Labrum transverse (Figs. 34 and 35). Mandibles (Figs. 41A-D) falcate, occlusal margins with prominent teeth. For details, see Table 1. Maxillae average for Ozaenini, as in Fig. 46. Labium (Figs. 52 and 53): mentum with lateral lobes more or less pointed apically, each epilobe widened preapically; tooth prominent; labial palpomere 3 narrowly securiform, apex subtruncate.

Prothorax. Pronotum (Figs. 3-6) transverse, distinctly wider than long, to distinctly longitudinal, slender and slightly longer than wide. Lateral grooves moderately wide. Lateral margins smooth to crenulate, sides posteriorly sinuate or not; antero- and posterolateral angles projected or not. Disc moderately convex, impressions distinct but shallow.

Pterothorax. As described for Ozaenini and anterior margin of metepisternum near coxa overlapped by posterior lobe of mesepimeron.

Elytra. Surface various: distinctly striate, indistinctly so, or smooth; intervals, if evident, moderately to slightly convex, but broad and not carinulate. Basal ridge extended to about plane of base of intervals 4 or 5.

Legs. In most features, as described for Ozaenini, no parts remarkably compressed. Fore femur (Figs. 59 and 60) with dentiform projection ventrally near base (subgenera *Pachyteles* and *Goniotropis*), or without such projection (subgenus *Tropopsis*). Antennal cleaner of fore tibia various. See Figs. 66A and B, and 67A and B. See Table 2 for details.

Abdomen. Sclerites of segments II-VII unmodified. or sclerites of segments VIII and IX/X, see Figs. 95, 101, and 102. or details, see under "Structural and biochemical features, genital segments".

Male genitalia (Figs. 85-89, and 97). For details, see Table 3.

Ovipositor (Figs. 74-79). Stylomeres various, from long and slender with narrow apex to short, rather broad, and with apex bifurcate.

Bursa copulatrix and spermatheca (Fig. 106). For details, see Table 4 .

*Defensive secretions.*— Four compounds. See Table 5 for details.

*Way of life.*— Adults of *Pachyteles* are probably insect predators, most of them living under bark of fallen tree trunks, and probably flying at night. At the northwestern periphery of the range, a few individuals have been collected in agricultural fields, but it is not clear from the labels whether they were collected at light, at night, or if they were found on the ground during the day. Adults of other species have been collected at night, in association with dead oaks.

*Geographical distribution.*— The range of this genus extends through the forested parts of the Neotropical Region from southern Chile to México, and into southwestern United States, in the Nearctic Region.

*Relationships.*— In external features, adults of *Pachyteles* resemble most closely those of the Afrotropical genus *Afrozaena* Jeannel. This apparent similarity, however, is not borne out by detailed study of structural features. *Pachyteles* is without close extant relatives in the New World, also..

*Included taxa.*— We recognize three subgenera, two of which [*Goniotropis* and *Pachyteles* (*sensu stricto*)] occur in southwestern United States, and are treated further below. Included in subgenus *Goniotropis* is *Pachyteles elongatus* (Chaudoir), the type species of *Scythropasus* Chaudoir. The subgenus *Tropopsis* is confined to South America, and is not considered further.

## Subgenus *Goniotropis* Gray

*Derivation of subgeneric name.*— In the original description of the type species, *G. braziliensis* Gray, the author notes (1832: 274) that the anterior femora and tibiae are strongly toothed and that each elytron terminates in an apical hook. The name is derived from Greek *gonio*, meaning angle, and *tropis*, meaning keel. We believe the word refers to the flanges of Coanda, which are keel-like, and are located posteriorly on the outer angles on each elytron.

*Recognition.*— Adults of *Goniotropis* have the middle coxal cavities closed medially, with the intercoxal process of meso- and metasterna in contact, and the antennal cleaner of the fore tibia (Figs. 67A and B) with a prominent projection extended from the medial expansion. A more detailed characterization is not required here.

*Way of life.*— Adults of a few species of *Goniotropis* have been collected under the bark of fallen tree trunks, and one was found in a bromeliad growing on the trunk of a standing pine tree, about 5 meters above the ground. Most specimens have been taken at U-V light, at night.

*Geographical distribution.*— The range of *Goniotropis* includes the northern half of South America, all of Middle America, and southern Arizona in southwestern United States.

*Relationships.*— We hypothesize *Goniotropis* to be sister group of subgenus *Pachyteles*, with their common ancestor being the sister group of subgenus *Tropopsis*. This hypothesis is based on transformation series for the intercoxal processes, armature of the fore tibia and structure of the antennal cleaner.

*Included species.*— Bänninger (1927: 203-204) included 14 species in this group. Two species occur in Arizona, in southwestern United States. We describe these because they are in the study area, and as well, the tropical Mexican *P. elongatus* (Chaudoir) because it is the type species of *Scythropasus*, a junior synonym of *Goniotropis*.

### *Pachyteles parca* LeConte
Figs. 3, 53, 78A-C, 85A-E, 101, 106, and Map 1

*Pachyteles parca* LeConte, 1884: 2. HOLOTYPE female, in LeConte-Horn Collection, labelled: "Ari."; "Type 5487" [red paper]; "*Pachyteles* parca LeC" [handwritten] (MCZC). TYPE AREA: Arizona, U.S.A.— Horn, 1894: 308.— Leng, 1920: 49.— Csiki, 1927: 430.

*Goniotropis parca*; Bänninger, 1927: 204.— Ball, 1960: 94.— Erwin, *et al.*, 1977: 4.3.

*Pachyteles beyeri* Notman, 1919: 225. HOLOTYPE male, labelled: "San Felipe Low Cal"; "*Pachyteles beyeri* TYPE" [handwritten, on blue paper] (Staten Island Museum, New York). NEW SYNONYMY.— Csiki, 1927: 204.

*Goniotropis beyeri* Bänninger, 1927: 204.— Ball, 1960: 94.— Erwin, *et alii.*, 1977: 4.3.

*Notes about synonymy.*— In form of median lobe and details of the internal sac, the male genitalia of the type of *P. beyeri* match those of males of *P. parca*, collected in Madera Canyon, Santa Rita Mountains, Arizona. In other features, specimens of the two nominal species are identical, also. We have no doubt that they are conspecific.

*Recognition.*— Adults of this species are slender, with transverse pronotum with sinuate lateral margins (Fig. 3), and of moderate size (Standardized Body Length less than 12 mm). In general form, they look like small specimens of *P. kuntzeni* (Bänninger):males differ from those of the latter species in form of the apical portion of the median lobe (Figs. 85A-B; *cf* Figs. 86A-B; also, *cf* Figs. 87A-B).

*Description.*— Habitus as in Fig. 3, with character states of *Goniotropis* and: SBL males, 9.9-11.4 mm., females 8.8-11.2 mm.; W/SBL males 0.31-0.32, females 0.33.

Male genitalia (Figs. 85A-D). Median lobe in lateral aspect with apical portion with carinula (**c**) on left side, apex nearly truncate; internal sac with small apical brush (**ab**) and digitus (**d**), terminal lobe small. Left paramere (Fig. 85D) with patch of setae preapically; right paramere (Fig. 85E) with about half medial margin setose.

Ovipositor. Stylomeres each as in *P. kuntzeni* (*cf.* Figs. 77A-C), cylindrical, straight, apex broad and circular, not tapered to point, sensory furrow nearly apical; surface with irregular rows of thick basiconic and slender trichoid sensilla, dense cluster of these near apex.

Bursa copulatrix. As in Fig. 106.

*Way of life.*— All known specimens have been collected at night, at light, principally at ultra-violet light, in the vicinity of oak-pine forests. Months of collection are from June to September.

*Relationships.*— Based on marked similarity in structural features and on evidently parapatric distribution pattern we hypothesize that this species and *P. kuntzeni* are sister taxa.

*Geographical distribution (Map 1).*— This species is known from northwestern México (Baja California and northern Sonora) western Durango, and southern Arizona, in southwestern United States. The Durango specimen, a male, was determined by Bänninger, in 1926, as "Goniotropis sp?"

*Material examined.*— In addition to the types, we have seen 29 specimens from the following localities.

UNITED STATES OF AMERICA. **Arizona.** *Cochise County.*— Chiricahua Mts., Portal, VII.15.1968; D.J. & J.N. Knull (OSUC). Guadalupe Canyon, at light, VII.1.1975; S. McCleve, M. Topham (SMCC). Same, at light, VII.31.1975; S. McCleve (SMCC). Huachuca Mts., VIII.18.1936; J.N. Knull (OSUC). Same, Miller Canyon, 1524 m., VIII.17.1974; E. R. Hoebeke (CUIC). Peloncillo Mts., 53 km. E. Douglas, at light, VII.17.1973; S. McCleve (SMCC). *Graham County.*— Galiuro Mts., Aravaipa Canyon, 17.7 km. N. Klondyke, U-V light, VII.24.1976; G.E. Ball, J.M. Campbell, P.M. Hammond (UASM). Same, on Turkey Creek, VI.22.1976; S. McCleve (SMCC). *Pima County.*— Santa Catalina Mts., Molino Basin, VII.31.1974; D.M. Bright (CNCI). Same, VIII.8.1969 (FSCA). *Santa Cruz County.*— Pajarito Mts., Peña Blanca Canyon, 1191 m., U-V light, VII.2.1980; S. McCleve (SMCC). Same, VII,13,1968 (FSCA). Same, VII.16.1964; R.H. Arnett, Jr. & E. R. Van Tassell (SCA). Same, VII.13.1970; K. Stephan (SCA). Same, VIII.7.1959; R.H. Arnett, Jr. (FSCA). Same, U-V light, VIII.11.1968; G.E. Ball family & R.B. Madge (UASM). Same, U-V light, VII.28.1978; S. McCleve (SMCC). 4.3km. above Peña Blanca, VIII.12.1983; E. Riley (EGRC). Santa Rita Mts., Madera Canyon, VIII.8.1977; .T. Hovore (SCA). Same, 1490 m., VIII.23.1959; J.G. Franclemont (CUIC). Same, VII.20.1959 (CUIC).Same, VIII.11-24.1963; G.E. and K.E. Ball (UASM).

MÉXICO. **Baja California Sur**. 3 km. E. La Burrera, 515 m., IX.2.1977 (CASC). San Jose del Cabo [Horn, 1894: 308. Sierra El Chinche [Horn, 1894: 308]. **Durango**. Canelas; J. Flohr [ZMHB]. **Sonora**. 55 km. SW Moctezuma, 1066 m., VI.10.1982; S. McCleve (SMCC). Rte. 16, 32.3 km. E. Rio Yaqui, U-V light, VII.26-27.1987; S. McCleve (UASM). Sierra Alamos, 2.7 km. S. 1.9 km. W. Alamos, U-V light; S. McCleve (UASM).

### *Pachyteles kuntzeni* (Bänninger) NEW COMBINATION
Figs. 4, 13, 21, 28, 35, 46, 60, 67A-B, 77A-C, 86A-E, and Map 1

*Goniotropis kuntzeni* Bänninger, 1927: 204. HOLOTYPE female, labelled: Canelas, Durango Mexico Flohr (Bänninger Coll., ETHZ) TYPE LOCALITY: México, Durango, Canelas.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.— Erwin and Halpern, 1978: 360.

*Notes about type material.*— We have not seen the holotype, but we have seen a male paratype in ZMHB from the type locality, and our material (from Sonora and southern Arizona) matches the features, including those of the male genitalia, of that specimen. Accordingly, we are confident that our identification is correct.

*Recognition.*— Adults of this species are large (SBL 16.0- 17.6 mm), the largest known of *Pachyteles*, with transverse pronotum with sinuate lateral margins (Fig. 4). They are much like large specimens of *P. parca*. Males of the two species are similar in details of the genitalia, but in males of *P. kuntzeni*, the apex of the median lobe (Fig. 86A) is obliquely truncate. or additional details, see the description, below. In shape of the stylomeres of the ovipositor, females of *P. kuntzeni* and *P. parca* are similar, but those of *P. kuntzeni* have more setae (Figs. 77A-C; *cf* Figs. 78A-C).

*Description.*— Habitus as in Fig. 4. With character states of subgenus *Goniotropis* and Standardized Body Length males 16.0-16.9 mm., females 15.7-17.2 mm; W/SBL males 0.33-0.35, females 0.32-0.33.

Male genitalia (Figs. 86A-E). Median lobe in left lateral aspect (Fig. 86A) with apical portion prominent, rather broad, carinulate on left side, apex obliquely truncate. Internal sac with large apical brush (**ab**), pendent terminal lobe (**t**) with large digitus (**d**). Left paramere (Fig. 86D) with few setae preapically along medial margin. Right paramere (Fig. 86E) with extensive brush of setae for most of length of medial margin.

Ovipositor (Figs. 77A-C). Stylomeres of moderate length, cylindrical, with broad circular apex, not tapered to point, and sensory groove preapical. Vestiture moderately dense, of longer sensilla trichodea and thicker sensilla basiconica.

Bursa copulatrix. About same as that of *P. parca* (above; *cf* Fig. 106).

*Way of life.*— Specimens have been collected in association with dead oak trees, at night.

Geographical distribution (Map 1).— This species is known only from northwestern México (Durango and Sonora) and southernmost United States (Arizona).

*Relationships.*— This species is postulated to be the sister taxon of *P. parca*.

*Material examined.*— In addition to the male paratype, we have seen 13 specimens, from the following localities.

UNITED STATES OF AMERICA. . **Arizona**. *Cochise County*.—Huachuca Mts., Ash Canyon, 1548m., VIII.2.1979; N. McFarland (SMCC). *Maricopa County*.— Tempe, XI.28.1966; T. Paca (ASUT). Santa Cruz County.— Atascosa Mts., Sycamore Canyon, on oak stump at night, VII.12.1977; S. McCleve (SMCC). Pajarito Mts., Walker Canyon, 1191 m., on dead oak, at night, VII.28.1978. S. McCleve (SMCC). Pajarito Mts., Peña Blanca, 1219 m., U-V light; G.E.&K.E. Ball, & R.B. Madge (UASM). *County not known*.— S. Graham Mts., 1524 m., VIII.20.1974; K. Stephan (FSCA).

MÉXICO. **Sonora**. 16.1 km. E. Cananea, VIII.16.1949; G.M. Bradt (AMNH).

### *Pachyteles elongatus* (Chaudoir)
### Figs. 79A-C, 87A-D

*Scythropasus elongatus* Chaudoir, 1854: 295. TYPE MATERIAL: HOLOTYPE male, in Chaudoir-Oberthür Collection Box 132, labelled "Mexique"; "Ex Musaeo Mniszech"; "Elongatus Chaud." [handwritten, not in Chaudoir's hand] (MNHP).—1868: 48.— Bates, 1881: 24.— Csiki, 1927: 427.

*Goniotropis elongatus*; Bänninger, 1927: 203.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.

*Notes about type material.*— The specimen indicated above as holotype is in a series with a female labelled "Temax, N. Yucatan Gaumer" (Bates Coll) and a male labelled "Yucatan (Bates Coll)", and is not labelled as type. However, Chaudoir (1868: 48) recorded that the single specimen on which the name was based was collected in México and was in the Mniszech collection. The specimen labelled as holotype fits these conditions.

*Recognition.*— The slender body and pronotum as long as or slightly longer than wide distinguishes adults of this species from other Mexican members of *Pachyteles* (*sensu lato*). Males have adhesive vestiture on fore tarsomeres 1-3, rather than on 1-2 only, as in most other species of *Pachyteles*, and the apical portion of the median lobe (Fig. 87A) is distinctive (*cf* Figs. 85A and 86A). The long slender stylomeres of the ovipositor (Figs. 79A-C) are distinctive for females.

*Description.*— With character states of subgenus *Goniotropis* and form slender, pronotum as long or longer than wide. Standardized Body Length males 10.6-11.0 mm., females 9.6-11.6 mm.; W/SBL males 0.30-0.32, females 0.32-0.33.

Male genitalia (Figs. 87A-D). Median lobe in lateral aspect (Fig. 87A) with apical portion broadly rounded, prominent. Internal sac (Figs. 87A-B) with collar area covered with slender microtrichia; without apical brush; terminal sclerite truncate, not lobed. Parameres (Figs. 87C-D): left paramere with narrowed apex, with few setae preapically on medial margin; right paramere elongate, medial margin extensively setose, most densely so preapically.

Ovipositor (Figs. 79A-C). Stylomeres long and slender, each with two or more nematiform setae (Fig. 79C), surfaces with few trichoid setae in median area, more densely setose preapically and apically.

Bursa copulatrix. Not studied.

*Way of life.*— Specimens known to us were collected at ultra-violet light, at night, in or in the vicinity of lowland tropical forest.

*Geographical distribution.*— This species is in the northern part of the Neotropical region, ranging in Central America from Nicaragua to Tamaulipas on the Gulf Versant, and to Nayarit on the Pacific Versant.

*Relationships.*— The distinctive body form, form of apex of median lobe, armature of the internal sac, and slender stylomeres of the ovipositor indicate that this species is not very close to *P. parca* and *P. kuntzeni*, the only other known species of *Goniotropis* in México.

*Material examined.*— In addition to the type and Yucatan specimens in the Chaudoir-Oberthür collection noted above, we have seen 10 specimens from localities in México.

**Chiapas**.. Palenque ruins, 122 m., U-V light, VI.8.1966; G.E. Ball & D.R. Whitehead (UASM). **Jalisco**. 24 km. S. Tomatlan, lowland 2nd growth forest and pasture, 110 m., at U-V light, VII.11.1984; S. McCleve & P. Jump (UASM). **Nayarit**.. 58 km. SW Las Piedras lowland forest 118 m, at U-V light, VII.7-8.1984; S. McCleve & P. Jump (UASM). **San Luis Potosi**.. Palitla, VIII.5.1966; O.S. lint (USNM). **Tamaulipas**.. *ca.* 40 km. N. Ciudad Monte Nacimiento, at light, VII.31.1970; C.W. O'Brien (UASM). **Veracruz**. Lake Catemaco, U-V light, VII.10-18.1963; D.R. Whitehead (UASM). Same, VI.9-25.1969; H. F. Howden (UASM). Same, Coyame, U-V light, VII.5.1967; R.E. Woodruff (UASM). Los Tuxtlas Biological Station, *ca.* 30 km. E. Catemaco, *ca.* 30 m., VI.29-30.1983; R.S. Anderson (UASM).

### Subgenus *Pachyteles* (*sensu stricto*)

*Recognition*.— See this topic above, for subgenus *Goniotropis*. Habitus is illustrated by Figs. 5 and 6. These forms are rather similar to one another, and though other members of the subgenus look like them generally, some have strikingly different pronota, and differ as well in punctation of the dorsal surface and striation pattern of the elytra.

*Way of life*.— See the general statement under the genus, and details in the following species treatments.

*Geographical distribution*.— The range of *Pachyteles* (*sensu stricto*) is coextensive with the range of the genus.

*Relationships*.— See this topic under *Goniotropis* and *Pachyteles* (*s. lat.*).

*Included species*.— According to Bänninger (1927: 210-212), 48 species are included in *Pachyteles* (*s. str.*), arranged in several groups. We treat only three here, including one that is new.

### *Pachyteles gyllenhali* (Dejean)

Figs. 5, 74A-B, and 88A-D

*Ozaena gyllenhali* Dejean, 1825: 436. TYPE MATERIAL: in Chaudoir-Oberthür Collection, Box 132, in front of the following box label— "Gyllenhali Dej. Antilles? C. Dejean." HOLOTYPE female, labelled: "Gyllenhali m. in Amer. inf." [green paper]; "Gyllenhali" [green paper]; "Ex Musaeo Chaudoir" [red print on white paper].— Chaudoir, 1854: 301.

*Pachyteles gyllenhali*; Chaudoir, 1868: 55.—Csiki, 1927: 428.— Bänninger, 1927: 211.— Blackwelder, 1944: 23.— Erwin, *et alii*., 1977: 4.3.— Erwin and Sims, 1984: 427.

*Ozaena verticalis* Chaudoir, 1848: 104. TYPE MATERIAL: two females— first labelled "Ex Musaeo Chaudoir" [red print on white paper]; second, "Goudet" [green paper], "Ex Musaeo Chaudoir" [red print on white paper]— in Chaudoir-Oberthür Collection, Box 132, in front of the following box label: "verticalis Chaud. Colombie Duport". LECTOTYPE (here selected) first female in series (MNHP).—1854: 301. NEW SYNONYMY.

*Pachyteles verticalis*; Chaudoir, 1868: 56.— Bates, 1881: 25.— Csiki, 1927: 428.— Bänninger, 1927: 210.— Blackwelder, 1944: 23.

*Pachyteles testaceus* Horn, 1868: 129. LECTOTYPE female, in LeConte-Horn Coll., labelled: "Ariz"; TYPE NO. 1029.1 [red paper]; "*Pachyteles* testaceus Horn" (MCZC). NEW SYNONYMY. TYPE LOCALITY: Fort Grant, Arizona.—Horn, 1881: 128.— LeConte and Horn, 1883: 24.— Horn, 1894: 308.— Leng, 1920: 49.— Blackwelder, 1944: 23.— Ball, 1960: 94.— Erwin, *et al*., 1977: 4.3.

*Notes about synonymy*.— The type specimens of the three nominal taxa noted above are very similar in size and external features. Horn (1868: 130) noted the marked similarity among them, but based on the limited material at his disposal he concluded that three species were represented. With the more extensive material available to us, especially of the nominal mainland taxa, we are unable to distinguish among them.

*Recognition*.— A combination of small body size (Standardized Body Length *ca*. 3.5- 6 mm.), densely setose dorsal surface, and pale (rufo-flavous) integument distinguishes adults of this species from other North-Middle American species of *Pachyteles*. Males lack adhesive setae of the fore tarsomeres, and the apical portion of the median lobe (Fig. 88A) is small, narrow and pointed. Females have the stylomere of the ovipositor with a bifurcate apex (Fig. 74B).

*Description*.— Habitus of adults as in Fig. 5, with features of subgenus *Pachyteles*.SBL males 4.0-5.4 mm., females 3.6-4.6 mm; W/SBL males 0.40, females 0.37-0.39.

Color. Integument pale, especially specimens from Arizona and northwestern México, but many from elsewhere with irregular fuscous cloud medially on elytra.

Microsculpture. Average for genus.

Vestiture. Dorsal surface of head, pronotum and elytra densely setose. Males without adhesive vestiture on fore tarsomeres.

Head. Average for Ozaenini.

Pronotum (Fig. 5). Subrotund, transverse; lateral margins sinuate posteriorly. Anterior angles acute; posterior angles rectangular.

Elytra. Moderately densely punctate, interneurs very shallow to obsolescent, intervals nearly flat.

Legs. Average for subgenus.

Male genitalia (Figs. 88A-D). Median lobe (Figs. 88A-B) with apical portion small, apex pointed. Internal sac with basal rod (**r**; *cf.* Fig. 82A) long, terminal lobe (**t**) penis-like, without preapical lobe, dorsal lobe, or microspines. Left paramere asetose (Fig. 88C); right paramere with single seta on medial margin.

Ovipositor (Figs. 74A-B). Stylomeres triangular in outline, each with base broad , cupped medially (Fig. 74A), somewhat flattened, apex bifurcate (Fig. 74B); sensory groove at base of furcation, preapical in position. Setation rather sparse, principally of sensilla basiconica.

*Way of life.*— Adults of this species have been collected on dead tree trunks, under bark, and in saguaro cactus. Many specimens have been collected at night, at light, and particularly ultra violet light. The wide range of this species, including islandic localities in both the Caribbean Sea and Pacific ocean, indicates that adults disperse readily.

*Geographical distribution.*— The range of this species is extensive, including the Greater Antillean island of Cuba, the Tres Marias Islands off the Pacific Coast of México, and on the mainland, from Brazil in South America (Blackwelder, 1944: 23), throughout Middle America to southern Arizona.

*Material examined.*— We have seen 193 specimens of this species, from the following localities in Cuba, the United States, and México.

UNITED STATES OF AMERICA. **Arizona.** *Cochise County.*— Guadalupe Canyon, U-V light, VII.31.1975; S. McCleve (SMCC). Same, VIII.2.1977 (SMCC). *Gila County.*— Globe, VII.1927; D.K. Duncan (MCZC). Wheatfield, near Globe, II.25.1932; . Parker, D.K. Duncan (MCZC). Same (CASC). *Graham County.*— Galiuro Mts., Aravaipa Canyon, east end, U-V light, VII.24-25.1974; S. McCleve (SMCC). Same (AMNH). Aravaipa Canyon, U-V light, VIII.12.1975; S. McCleve (SMCC). Same, Turkey Creek, 1.6 km. S. Aravaipa Creek, U-V light, VIII.11.1975; S. McCleve (SMCC). Same, ca. 16 km. NW Klondyke, 900 m., U-V light, VII.30-31.1975; G. E. Ball, H.E. Frania (UASM). Same, U-V light, VII.24.1976; G.E. Ball, J.M. Campbell, P.M. Hammond (UASM). Same, U-V light, VIII.24.1977; G.E. & K.E. Ball (UASM). Arivaipa, VIII.29.1933; Bryant (CASC). Safford, under bark of cottonwood, beside creek, I.10.1938; O. Bryant (CASC). *Maricopa County.*— Phoenix, XI.27.1919; E. Schiffel (MCZC). *Pima County.*— Ajo Mts., Alamo Canyon, in rotting saguaro cactus, VII.24; H.B. Leech (CASC). Same, VII.25; H.B. Leech, J.W. Green (CASC). Arivaca, XI.30.1969; K. Stephan (FSCA). Same, Arivaca Creek, VII.31.1952; H.B. Leech, J.W. Green (CASC). Baboquivari Mts., W. side, Baboquivari Canyon, VII.25-27.1952; H.B. Leech, J.W. Green (CASC). Redington, XII.7.1969; K. Stephan (FSCA). Tucson, VII.21.1917 (CUIC). Same, San Xavier Mission, VII.29.1924; E.P. Van Duzee (CASC). *Pinal County.*— Florence (Fall, MCZ). *Santa Cruz County.*— Cobabi Mts., Santa Cruz Village, X.12.1916 (USNM). Pajarito Mts., Peña Blanca Canyon, Lot 511, VII.26.1961; R.H. Arnett, E. Van Tassell (FSCA). Patagonia, VII.36; E.S. Ross (CASC). Same, VIII.9.1940; E.S. Ross (CASC). Same, VII.18.1948; C. & P. Vaurie (AMNH). Same, IX.28.1968 (SCA). *County not known.*— Galiuro Mts.; Hubbard and Schwarz (FSCA, USNM). Arizona, Charles Palm (AMNH).

CUBA. Cayamas, I.14; E.A. Schwarz (MCZC).

MÉXICO. **Baja California**. Pelican Island, VII.5.1921; J.C. Chamberlin (CASC). **Baja California Norte**. 14.5 km. SE Rancho Laguna, VII.1.1973; Fisher, Westcott (CASC). **Baja California Sur**. El Sargento, VII.29.1971; H.G. Real, R.E. Main (CASC). Miraflores, VIII.7.1971; H.G. Real, R.E. Main (CASC). 8 km. S. Miraflores, VII.10.1938; Michelbacher, Ross (CASC). 24 km. E. San Jorge, VII.24.1971; H.G. Real, R.E. Main (CASC). San Jose Island, V.28.1921; E.P. Van Duzee (CASC). Santa Rosa (Fall, MCZC). [Sierra] El Chinche, 609 m., under stones (CASC).**Chiapas**. Cerro Baul, ridge SE of, 21 km. W Rizo del Oro, 1615 m., cloud forest, IX.6-8.1970; C. Mullinex, D.E. Breedlove (CASC). 48 km. NW Ocosingo, VI.30.1977; E.M. Fisher (CASC). Sierra de la Colmena, e. slope, nr. La Caverna, Arroyo Santa Maria, 16°24'18"N, 91°24'16"W, 213 m., on ground, VI.1-10.1972; G.E.& K.E. Ball, P.A. Meyer (UASM). Sierra de la Colmena, San Cristobal trail, 701-853 m., VI.8.1972; P.A. Meyer, G.E.& K.E. Ball (UASM). 19 km. S. Solosuchiapa, Rte. 195, 640 m., IV.25.1966; G.E. Ball, D.R. Whitehead (UASM). **Colima**. 11.3 km. NE Colima, XII.3.1948; E.S. Ross (CASC). Mt. Colima, SE slope, XII.2.1948; H.B. Leech (CASC). **Jalisco**. nr. Ixtapa, ca. 30 m., gallery forest, dead tree; XII.22.1970; G.E.& K.E. Ball (UASM). 15 km. S. Mazamitla, 1676 m., VII.29-31.1952; F.W. & F.G. Werner (UASM). 20 km. S Tecalitlan, 1615 m., VIII.3.1967; Ball, T.L. Erwin, R.E. Leech (UASM). **Nayarit**. Jesus Maria, VII.6.1955; B. Malkin (CASC). San Blas, VI.15.1955; B. Malkin (CASC). Islas Tres Marias, Madre Maria Island, Arroyo Hondo, V.17.1925; H.H. Keifer (CASC). **Sinaloa**. 8 km. N. Mazatlan, U-V light; J.A. Chemsak (CISC). **Sonora**. 8 km. E. Alamos, VIII.11.1973; K. Stephan (FSCA). 21 km. SE. Alamos, X.30.1972; K. Stephan (FSCA). Bahia Kino, X.25.1980; P. Jump (SMCC). Sierra San Luis, Varela Ranch, Cañon Bonita, U-V light, and under bark of cottonwood logs; G.E. Ball & D.R. Maddison (UASM).**Tabasco**. 96 km. SE. Villahermosa, U-V light, VI.6-7.1972; P.A. Meyer, G.E.& K.E. Ball (UASM). **Veracruz**. Atoyac, VI.24.1982; M.A. Ivie (OSUC). Cordoba; D.A. Fenyes (CASC). Fortin de las Flores, VI.20-30.1963; D.R. Whitehead (UASM). park cañon, 3.2 km. W. Fortin de las Flores. Rte. 150, VIII.3-6.1965; Cornell Univ. Mexico Field Party, 1965 (CUIC). 56 km. SE. Jalapa, XII.26.1963; C.A.& M.J. Tauber (CUIC). Sierra de las Tuxtlas, Lake Catemaco, Coyame, under bark, VII.1-15.1963; D.R. Whitehead (UASM). Same, under bark, VII.10-18.1963; D.R. Whitehead (UASM). 0.5 km. W. Sontecomapan, 305 m., IX.20&26.1965; G.E. Ball, D.R. Whitehead (UASM). Same, IX.18-26.1965 (UASM). 4 km. W. Sontecomapan, IV.3&10.1966; G.E. Ball, D.R. Whitehead (UASM). Same, on log, VI.1-5 & 20.1966 (UASM). Same, U-V light (UASM).

## *Pachyteles enischnus*, new species
## Figs. 6, 75A-B, 97A-D, and Map 1

*Type material*.— HOLOTYPE male, labelled: "MEX. Jalisco nr. Ixtapa gallery forest dead tree ca. 100' [elevation above sea level] XII.22.70"; "Puerto Vallarta MEX trip 1970 G.E.&K.E. Ball collectors" (USNM). ALLOTYPE female, "15 km.S. Mazamitla Jal. MEX. 5500' pine-oak forest July 30, 1952 FE & FG Werner" (USNM). Two male PARATYPES (USNM) labelled same as holotype, and one male PARATYPE (UASM) labelled same as allotype. Eleven additional PARATYPES, labelled as follows. Male and female, "MEXICO Jalisco 33.8 km. S. Puerto Vallarta pine-oak forest 750 m., at U-V light 9,10.VII.1984 S. McCleve, P. Jump" (UASM). our males, three females, "MEXICO Nayarit 57.9 km. s.w. Las Piedras lowland forest 118 m., at U-V light 7-8.VII.1984 S. McCleve, P. Jump" (UASM). Male, "Sin. Mex. 200 ft. 5-3-49"; "GM Bradt Collector" (AMNH). Female, "5 mi. E. Alamos SONORA MEX VIII.11.1973 K. Stephan & D.S. Chandler" (OSUC).

*Derivation of specific epithet*.— This is based on the Greek adjective *enischnos*, meaning thin, in allusion to the slender adult body form (Fig. 6).

*Recognition*.— Body size, reduced setation of the dorsal surface, and pronotum with markedly sinuate lateral margins distinguish this species from other members of the genus that range into northern México and southwestern United States.

*Description*.— Habitus as in Fig. 6. Standardized Body Length of males 7.2-7.6 mm., females 7.0-7.7 mm.; W/SBL males 0.34-0.35, females 0.33-0.35.

Color. Body rufous to rufo-piceous, legs, antennae and palpi slightly paler than body.

Microsculpture and luster. Head dorsum with mesh pattern isodiametric, microlines fine, nearly effaced on center of vertex. Pronotum with mesh pattern transverse, partly effaced on disc. Elytra with mesh pattern isodiametric in lateral channels, transverse and partly effaced on disc. Dorsal surface generally shiny.

Vestiture. Dorsal surface of head and pronotum sparsely setose. Elytra with discal intervals serially, sparsely setose. Thoracic and abdominal sterna moderately densely setose.

Head (Fig. 6). Eyes average in size and convexity. Frontal impressions broad, irregular in outline, irregularly punctate. Vertex coarsely, sparsely punctate.

Pronotum (Fig. 6). Transverse, surface sparsely, irregularly punctate. Anterior and posterior margins nearly straight. Lateral margins markedly sinuate posteriorly. Postero-lateral angles about rectangular. Disc slightly convex. Lateral grooves broad anteriorly and posteriorly, narrow medially, margins not beaded. Postero-lateral impressions broad and irregular, continuous anteriorly with lateral grooves.

Elytra. In form, average for *Pachyteles*, humeri broadly rounded, slightly prominent. Interneurs shallow, rather broad, intervals only slightly convex. Intervals sparsely punctate.

Metathoracic wings. Macropterous, fully developed.

Legs. Average for subgenus *Pachyteles*.

Male genitalia (Figs. 97A-C). Median lobe (Fig. 97A) with apical portion distinct, extended ventrad, apex broadly rounded, nearly subtruncate. Internal sac with collar area with dense covering of slender seta-like microtrichia; apical portion with broad sclerite on left side, terminated in obtusely pointed lobe; basal part of sac with distinct longitudinally oriented ridges and several setae near apex of median lobe. Left paramere (Fig. 97B) shorter than right paramere (Fig. 97C), glabrous. Right paramere digitate, sparsely setose apically and on apical part of medial margin.

Ovipositor (Figs. 75A-B). Stylomeres falcate, each with apex broadly pointed, not bifurcate. Sensory groove ventral, remote from apex. Lateral and ventral surfaces with numerous thick sensilla basiconica (Fig. 75A).

*Way of life.*— Adults were collected from under bark of dead trees in gallery forest bordering deciduous tropical forest, near sea level, to pine-oak forest at *ca.* 1500 m. Most specimens, however, were taken at light, at night, indicating nocturnal flight activity during the rainy season in northwestern México.

*Geographical distribution.*— This species is known only from western México, from Jalisco to Sonora.

*Relationships.*— Adults of this species are like those of *P. filiformis* Chaudoir, in size and body form. The latter species occurs in the east, and farther southward in México. General similarity plus allopatric ranges suggest that these two species might be closely related to one another.

### *Pachyteles mexicanus* (Chaudoir)
Figs. 76A-B, 89A-D, and 102.

*Ozaena mexicana* Chaudoir, 1848: 106. TYPE MATERIAL: two males, two females, in Chaudoir-Oberthür Collection, Box 132, each labelled "Ex Musaeo Chaudoir [red print], in front of the following box label: "mexicana Chaud Mexique". LECTOTYPE (here selected): a male, first specimen in series (MNHP).— 1854: 306.

*Pachyteles mexicanus*; Chaudoir, 1868: 65.— Bates, 1881: 27.— Csiki, 1927: 429.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.

*Recognition.*— Adults are broad-bodied, with pronotum with anterior angles acute and projected laterally, and smooth or nearly smooth elytra.

*Description.*— With features of *Pachyteles* (*s. str.*) and body broad and sturdy. Standardized Body length of males 5.9-7.2 mm., females 6.6-7.6 mm; W/SBL males 0.39-0.43, females 0.42-0.46.

Metathoracic wings. Relatively small, with apical portion reduced.

Male genitalia (Figs. 89A-D). Median lobe in right lateral aspect (Fig. 89B) with apex broadly bifid. Internal sac (Figs. 89A-B) narrow, with slender collar with dense covering of seta-like microtrichia; apical part (only partly everted) with broadly pointed apex. Left paramere (Fig. 89C) with apex broadly pointed, asetose. Right paramere (Fig. 89D) slender, elongate, preapical part of medial margin sparsely setose, setae short.

Ovipositor (Figs. 76A-B). Stylomeres moderately elongate, apex blunt, obliquely truncate; nematiform setae terminal; surface with long slender trichoid sensilla and short broad basiconic sensilla.

*Way of life.*— Specimens have been collected under bark of fallen trees in lowland tropical rain forest, at about 720 m. elevation, and in cloud forest at

1400m., in a pile of leaf litter and oak branches. Specimens were collected at night, on the surface, also. The reduced wings of adults indicate that flight is not possible, and this indication is supported by absence of specimens from catches by light traps.

*Geographical distribution.*— The range of this species extends from Nicaragua northward to San Luis Potosi on the Gulf Versant of México.

*Relationships.*— The distinctive male genitalia and ovipositor, and smooth glabrous elytra place this species clearly apart from the others treated in this paper.

*Material examined.*— In addition to the types, we have seen 57 specimens of this species, from the following localities in México.

**Chiapas**. 11 km. S. Jitotol, Rte. 195, pine-sweetgum, *ca.* 1650 m., V.5.1977; Mexican Exp. 1977, J.S. Ashe, H.E. Frania, D. Shpeley (UASM). Sierra de la Colmena, San Cristobal trail, 701-853 m. [Lacandon forest], June 8, 1972; P.A. Meyer, G.E.& K.E. Ball (UASM). Yerba Buena Hospital, 2.4 km. N. Pueblo Nuevo, 1554-1829 m., June 21-22, 1972; P.A. Meyer, G.E. Ball (UASM). **Oaxaca**. 21 km. S. Valle Nacional, 1128 m., VIII.71; A. Newton (MCZC). 9.7 km. S. Valle Nacional, 650 m., V.18-20.1971; H.. Howden (UASM). Same, VII.20-31.1971; 299CS (UASM). 17.3 km. S. Valle Nacional, Rte. 175, montane trop. for., *ca.* 1000 m., IV.26.1977; Mexican Exp. 1977, J.S. Ashe, H.E. Frania, D. Shpeley (UASM). **Puebla**. 2.4 km. N. Tlaxcalantonga, VII.3-8.1971; 273 DH (UASM). **San Luis Potosi**. 29 km. S. Tamazunchale, XI.22.1946; E.S. Ross (CASC). **Veracruz**. 3.9 km. N. Coscomatepec, 1400 m., VIII.12.1987; Mexico Field Party, 1987: J. K. Liebherr, D.K. Millman (CUIC). 6.4 km. N. Huatusco, 1280 m., VII.2.1973; A. Newton (MCZC). 7.1 km. N. Huatusco, 1300 m., on clay bank, at night, VIII.15.1987; Mexican Field Party, 1987: J.K. Liebherr, D.K. Millman (CUIC). 7 km. S. Huatusco, cloud forest, *ca.* 2164 m., VII.24.1977; Mexican Exp., 1977, J.S. Ashe, H.E. Frania, D. Shpeley (UASM). Jalapa; M. Trujillo (AMNH). Jalapa, May (CASC).

## *Ozaena* Olivier

*Ozaena* Olivier, 1812: 617. TYPE SPECIES: *Ozaena dentipes* Olivier, 1812: 620; by monotypy.— Dejean, 1825: 356, 433.— Dejean and Boisduval, 1829: 186, 231.— Dejean, 1831: 471.— Brullé, in Audouin and Brullé, 1834: 258.— Castelnau-Laporte, 1834: 144.— Blanchard, in Cuvier, 1842: 127.— Chevrolat, in d'Orbigny, 1847: 376.— Lacordaire, 1854: 156.— Chaudoir, 1854: 289, 297.— 1868: 49.— Csiki, 1927: 427 .— Bänninger, 1927: 193.— 1931: 184.— Blackwelder, 1944: 22.— Bänninger, 1949: 132.— Ball, 1960: 95.— Ogueta, 1965: 75.— Reichardt, 1977: 377.— Erwin, *et al*, 1977: 4.3.

*Ictinus* Castelnau-Laporte, 1834: 53. TYPE SPECIES: *Ictinus tenebrioides* Castelnau-Laporte,1834: 53; by monotypy; = *O. dentipes* Olivier.— 1835: 144.— Hope, 1838: 99.— Duponchel, E., in d'Orbigny, 1846: 16.

*Ozena* Chenu, 1851: 87 (misspelling).

*Nomenclatural note.*— Hope (1838: 99) fixed "*Ic. Rogerii* Dejean" as type species of *Ictinus*, but this name was not among those originally associated with that generic name.

*Derivation of generic name.*— From Greek, meaning to smell, in allusion to the odorous defensive secretions of the adults. Here is a fine but simple example of the fact that even the museum taxonomists of the early 19th Century were cognizant of features of living organisms, and were prepared to use such features. The bizarre notion that museum taxonomists were interested in structural features only should be put to rest.

*Recognition.*— Mature adults have black integuments. The antennae are relatively long for ozaenines (Fig. 14). The labium (Fig. 54) has long lateral lobes of the mentum, broadly rounded apically. The elytra and lateral margins of the pronotum have short broad setae with ridged surfaces (Fig. 107A-B).

*Description.*— Habitus as in Fig. 7, size large, Standardized Body Length *ca.* 14-20 mm, maximum width 5.1-6.1 mm.

Color. Body and appendages black, or very dark piceous.

Microsculpture and luster. As in Tribe Ozaenini, and on mesopleura mesh pattern transverse, on metapleura isodiametric to transverse. Surface shining in most species, dull in some.

Vestiture. Scrobes of mandibles with normal setae. Dorsal surface of elytra and lateral margins of pronotum with short broad setae, surface ridged and flattened, and apex cleft (Fig. 107B). Males without adhesive vestiture on fore tarsomeres. Ventral surface generally setose, with normal trichoid setae, abdominal sterna densely setose.

Chaetotaxy. Clypeus and vertex of head asetose, temporal areas each side with several setae. Antennae (Figs. 7, 14, and 29A-B): with antennomeres sparsely setose, setae generally short; antennomere 11 with dense concentration of sensilla basiconica in apical third to half. Mouthparts: apical margin of labrum with about 12 setae; mandibular scrobes without setae; maxillary stipes with two setae laterally; labial submentum and mentum with several setae each; glossal sclerite apically without setae; labial palpomere 2 without long setae. Pronotum: without fixed trichoid setae. Disc of elytra: without fixed trichoid setae. But note sensilla basiconica, Figs. 107A-C. Legs (fore, middle hind): coxae, 0-numerous-numerous; trochanters, generally setose; femora, asetose.

Head. Frontal impressions elongate, shallow, irregular. Eyes (Fig. 7) prominent, posteriorly with moderately large temporal lobes. Supraantennal areas not reflexed, but extended laterally each side as obtuse point.

Antennae. Long, extended posteriorly clearly past elytral humeri (Fig. 7); antennomeres 1-4 cylindrical, 5-11 (Fig. 14) moniliform, with 11 (Figs. 29A-B) distinctly swollen and apically with distinct straight sharp keel.

Mouthparts. Labrum (Fig. 36) transverse. Mandibles (Figs. 42A-D) short, thick, occlusal margin toothed. For details, see Table 1. Maxillae average in most respects, but lacinia (Figs. 47A,B) with thick brush of curved setae and terminated in short chisel-like tooth. Palpomere 4 thick, apex obliquely truncate. Labium (Fig. 54) with lateral lobes of mentum large, broadly rounded apically; tooth short; epilobes narrow, not extended to apex; palpomere 3 thick, short in *O. lemoulti* adults, apex truncate.

Prothorax. Pronotum (Fig. 7) short, distinctly wider than long. Sides explanate, elevated or flat (*O. lemoulti*). Disc convex. Impressions distinct. Prosternum with intercoxal process broad, short.

Pterothorax. As for Tribe Ozaenini, and mid-coxal cavities closed medially by junction of intercoxal processes of meso-and metasternum. Metepisternum overlapped by posterior lobe of mesepimeron.

Elytra. Intervals broad, slightly elevated. Interneurs shallow, punctate, punctures large. Basal ridge very short, hardly evident. Humeri denticulate.

Metathoracic wings. Fully developed.

Legs. As described for Ozaenini, and fore femora (Fig. 61A) about cylindrical, thickened apically, each ventrally toward base with small setose denticulate process (Fig. 61B). Fore tibia with antennal cleaner (Figs. 68A-B) reduced. or details, see Table 2. Tarsi average for Ozaenini.

Abdomen. Sclerites of segments II-VII unmodified. or details of sclerites of segments VIII and IX/X, see under "Structural and biochemical features- genital segments".

Male genitalia (Figs. 90A-D). or details, see under Structural and biochemical features", and Table 3.

Ovipositor (Figs. 80A-C). Stylomeres short, moderately densely setose apically, sensory furrow apical, with single nematiform seta.

Bursa copulatrix and spermatheca. See Table 4 for details.

*Way of life.*— Evidently, most known specimens of this genus preserved in museums have been collected at light, in lowland (principally tropical) forest. Nothing else is known about habitat or activity.

*Geographical distribution.*— The range of *Ozaena* extends from Argentina in South America to southern Arizona in North America. Only one species, *O. lemoulti* Bänninger, is known to occur in Middle and southern North America.

*Relationships.*— The sister group of *Ozaena* seems to be *Platycerozaena*, based on similarities in setal reduction, type of setae, reduction of antennal cleaner, distribution of setation on the antennae, and form of the stylomeres, bursa copulatrix, and spermatheca. We have considered seriously the proposition that these two groups are congeneric. The relationships of the lineage represented by these two genera is not evident at this time.

*Included species.*— *Ozaena* includes ten species, eight of which have been described.

### *Ozaena lemoulti* Bänninger

Figs. 7, 14, 22, 29A-B, 36, 42A-D, 47A-B, 54, 61A-B, 68A-B, 80A-C, 90A-D, and 107A-D.

*Ozaena lemoulti* Bänninger, 1932: 185. TYPE MATERIAL: HOLOTYPE male, labelled "GUYANE FRANCSE St Jean du Maroni Collection LeMoult"; "*Ozaena lemoulti* Bänninger" [handwritten] (Bänninger Collection, Zurich). TYPE LOCALITY: as indicated on locality label of holotype.— Blackwelder, 1944: 23.— Bänninger, 1949: 133.— Ogueta, 1965b: 87.— Erwin *et al.* 1977: 4.3. Bänninger, 1956: 400.

*Ozaena elevata* Ball, 1960: 95 (not Bänninger, 1956).

*Ozaena halffteri* Ogueta, 1965b: 83. HOLOTYPE female, labelled "México, estado de Veracruz, Tlapacoyan, 5.IX.1953, leg. Ticul Alvarez y Gonzalo Halffter" (Ogueta Collection). NEW SYNONYMY.— Erwin, *et al.*, 1977: 4.3.

*Notes about synonymy.*— We have not seen the holotype of *O. halffteri*, but we have seen specimens from Arizona and from localities extending collectively through the whole of Middle America and northern South America. A detailed study shows that the supposed diagnostic features given by Ogueta in his key to species (*l.c.*, 76-77) exhibit too much variation to support the hypothesis that two species are represented in the material noted above. Thus, we regard the names *O. lemoulti* and *O. halffteri* as synonyms of one another.

The name *Ozaena elevata* was published for a specimen of *O. lemoulti*, collected at Nogales, Arizona (Ball, 1960: 95), based on Bänninger's determination as *Ozaena elevata* var? However, that determination was made before the material was available to indicate the limits of *O. lemoulti* and *O elevata*. We are satisfied that the present identification of the Nogales specimen is correct. Nonetheless, we are a bit doubtful if *O. lemoulti* and *O elevata* Bänninger are specifically distinct. The material available is not sufficient to permit this second synonymy. See Bänninger, 1956: 400.

*Recognition.*— The only species of *Ozaena* in Middle and North America, adults of this species might be confused only with those of *Pachyteles kuntzeni*, which are also large and uniformly dark in color. Form of the antennae (Figs. 14, 22, and 29A-B) distinguishes readily members of these taxa. The pronotum (Fig. 7) of adult *O. lemoulti* is shorter, broader, and with lateral margins evenly curved, not sinuate posteriorly. The elytra of adult *O. lemoulti* bear dorsally distinctive ribbed, apically branched setae (Fig. 107A-B), not exhibited by adults of *P. kuntzeni*.

*Description.*— Habitus as in Fig. 7. Standardized Body length males 16.8-18.4 mm., females 16.4-18.2 mm.; W/SBL males 0.31, females 0.31-0.33. Other features as described above, for genus.

*Geographical distribution.*— The range of this species extends from Ecuador and Cayenne in northern South America through Middle America to southern Arizona.

*Relationships.*— Based on details of body form, of distribution of antennal sensilla, and of mandibular structure, and allopatric geographical distribution, we postulate that *O. lemoulti* and *O. elevata*, if distinct, are sister species.

*Material examined.*— From México and the United States, we have seen 11 specimens from the following localities. We have seen also 22 additional specimens from localities in Brazil (Para), Cayenne, and Venezuela, in northern

South America; and from Belize, Costa Rica, Guatemala, and Panama, in Middle America.

UNITED STATES OF AMERICA. **Arizona.** *Santa Cruz County.*— Nogales, VI.19.1945, in house (USNM). Peña Blanca Canyon, Pajarito Mts., 1191 m., VII.27.1978; S. McCleve (SMCC).

MÉXICO . **Chiapas.** Palenque ruins, 100 m., U-V light, May 20, 1972; P. Meyer, G.E.&K.E. Ball (UASM). **Coahuila.** Saltillo; E. Palmer (MCZC). **Morelos.** Cuernavaca; V. Barrett (CASC). **San Luis Potosi.** El Salto, VIII.8.1966; O. S. Flint (USNM). Palitla, at light, VII.21.1970; Schafffner, Murray, Phelps, Hart (TAMU). Tamazunchale, V.20.1952; M. Cazier, W. Gertsch, R. Schrammel (AMNH). **Tamaulipas.** El Salto Falls, 42 km. W. Antiguo Morelos, 610 m., VII.11-14.1963; Duckworth & Davis (USNM). **Veracruz.** Fortin de las Flores, 1010 m., at light, VII.7-12.1974; J.A. Chemsak, E.& J. Linsley, and J. Powell (CISC).

## *Platycerozaena* Bänninger

Figs. 8, 15, 23, 30, 37, 43A-F, 48, 55, 62, 69A-B, 81A-C, 91A-D, and 96.

*Ozaena* (in part); Bates, 1874: 23.— 1881: 25.— Csiki, 1927: 427.

*Platycerozaena* Bänninger, 1927: 197. TYPE SPECIES: *Ozaena brevicornis* Bates, 1874: 24; by monotypy.— Blackwelder, 1944: 23.— Ogueta, 1965c: 361.— Reichardt, 1977: 377.— Erwin, 1979: 557.— Roach, *et al.*, 1979: 18.

*Ozaena* (*Platycerozaena*) Bänninger, 1949: 133.

*Nomenclatural note.*— Ogueta (1965c: 361) indicated *O magna* as type species of *Platycerozaena*. However, this name was not associated with this generic name when the latter was proposed.

*Derivation of generic name.*— From Greek, *platyceros*, meaning flat horn, to be interpreted as antenna, combined with *Ozaena*; literally, the *Ozaena* with flat antennae.

*Ranking.*— Bänninger (1949), without explanation, included *Platycerozaena* as a subgenus of *Ozaena*. We agree with Ogueta (1965c: 361) that the two groups, though no doubt closely related, are each monophyletic and abundantly distinct from each other. Accordingly, we choose to rank *Platycerozaena* as a distinct genus.

*Recognition.*— Adults of this genus are readily distinguished by black color, elongate labrum (Fig. 37), short antennae with markedly transverse antennomeres 5-10 (Fig. 15), mentum with very small tooth (Fig. 55), and small antenna cleaner (Figs. 69A-B).

*Description.*— Habitus as in Fig. 8, moderate in size, Standardized Body length *ca.* 6.0-8.0 mm., maximum width 1.8-2.5 mm, slender in form.

Color. Body and appendages of mature adults black.

Microsculpture and luster. As for Tribe Ozaenini, and pterothoracic pleura and sterna with transverse mesh pattern. Elytra with microlines fine, mesh pattern transverse. Surface shining to subiridescent.

Vestiture. Dorsum with sparse covering of short setae, these flattened, expanded, ribbed and branched on pronotum and elytra (*cf.* Fig. 107A-B). Ventral surface sparsely setose.

Chaetotaxy. Labrum (Fig. 37), clypeus, vertex and temporal areas of head, lateral margins of pronotum and elytra without long tactile ("fixed") setae. Antennae: antennomeres 1-10 with short trichoid setae; 5-10 each with patch of sensilla basiconica on ventral anterior and posterior surfaces; antennomere 11 with sensilla basiconica extensive laterally and preapically; central triangular area more or less glabrous (Figs. 23 and 30). Mouthparts: without fixed setae (as in *Ozaena*). Legs (*fore-middle-hind*): *coxae, numerous-numerous-numerous*; *trochanters*, numerous-numerous-sparse. Basal fore tarsomeres of males without adhesive setae.

Head. Frontal impressions broad, shallow. Eyes (Fig. 8) prominent, posteriorly with small temporal lobe each side. Supraantennal area each side not reflexed, ridged, extended laterally as obtuse point.

Antennae. Short, not extended posteriorly beyond basal margin of pronotum. Antennomeres 1-4 more or less cylindrical, rather short; antennomeres 5-11 (Fig. 15) slender, markedly compressed; antennomere 11 (Figs. 23 and 30) more elongate, broad, apical margin broadly rounded in lateral aspect, apex narrowly keeled, keel sinuate (Fig. 30).

Mouthparts. Labrum (Fig. 37) elongate. Mandibles (Figs. 43A-F) with occlusal margins toothed, short, broad (see Table 1 for details). Maxillae (Fig. 48) average for Ozaenini, palpomere 4 markedly broad, apical margin obliquely truncate. Labium (Fig. 55): mentum with long slender lateral lobes, each pointed apically; epilobes slender, terminated just short of apex; palpomere 3 broad, apex truncate.

Prothorax. Pronotum transverse, lateral margins narrow, beaded, sinuate posteriorly or evenly rounded; impressions distinct. Prosternum with intercoxal process short, rather slender.

Pterothorax. As for Ozaenini, and base of metepisternum narrowly overlapped by base of mesepimeron.

Elytra. Intervals broad, slightly elevated. Interneurs narrow, punctate. Basal ridge very short, hardly evident. Humeri denticulate.

Legs. In most features, as described for Ozaenini. Fore femora each clavate, with ventral margin protruded as broad projection (Fig. 62). Antennal cleaner of fore tibia (Figs. 69A-B) reduced (see Table 2 for details).

Abdomen. Sclerites of segments II-VII unmodified. or description of sclerites of segments VIII and IX/X, see under "Structural and biochemical features, genital segments". See also Fig. 96.

Male genitalia. See under "Structural and biochemical features" and Table 3. See also Figs. 91A-D.

Ovipositor (Figs. 81A-C). Stylomeres short, moderately densely setose toward apex, rather broad in ventral aspect, sensory furrow and nematiform setae not identified.

Bursa copulatrix and spermatheca. See Table 4 for details.

*Defensive secretions*.— Five compounds. See Table 5 for details.

*Way of life*.— Nothing has been reported about this topic for *Platycerozaena*. The reduced setation suggests some unusual mode of living, in which tactile sensation is not a premium. Paussines also exhibit reduction in sensilla, and they live with ants. Perhaps, then, members of *Platycerozaena* are myrmecophilous, too.

*Geographical distribution*.— This genus is known only from central Brazil northward to Nicaragua, in Lower Middle America.

*Relationships*.— This genus seems to be the sister group of *Ozaena* Olivier. For details, see under the latter genus.

*Included species*.— According to Ogueta (1965c: 362-363), *Platycerozaena* includes four species.

## ZOOGEOGRAPHY

Because the boundaries of this study are artificial both phylogenetically and geographically, it lacks the unity required to develop a coherent generalizing evolutionary hypothesis. Accordingly, we attempt only to relate to general patterns the taxonomic bits and pieces that we have treated.

### The Tribes

Metriines are confined to dry temperate forests of the west coast of United States, beyond the periphery of the range of the Ozaenini. The latter group is pantropical, and in the New World ranges from the margins of the Sonoran desert in southwestern United States to the Chilean rain forests in South America. The group is centered in the lowland tropics, with numbers of species declining with increasing altitude and latitude.

Two historical interpretations seem possible. First, the ancestral stock of the Metriini and Ozaenini occupied the whole of Pangaea before its breakup, toward the end of the Palaeozoic. With breakup, the northern vicar evolved into the

Metriini, and the southern one produced the Ozaenini (Erwin, 1979b: 577). Second, the ancestral stock of the Metriini + Ozaenini was Gondwanian, appearing after breakup of Pangaea. An initial split produced a less progressive line, the Metriini, which was replaced gradually in the tropics by the more progressive sister group, the Ozaenini. Metriines were replaced eventually, throughout the tropics, and survive today only in a small area of the north temperate zone, beyond the range of their ozaenine sister group. Either of these interpretations recognizes *Metrius* as a relict group.

A more specific hypothesis accounts for the occurrence of *Metrius* (and other relict taxa) in coastal areas in western United States. According to some geologists, various small Pacific terranes have drifted eastward, eventually encountering and becoming part of the west coast of North America. Perhaps these tectonic plates carried with them the remnants of old taxa that populated the coastal areas (Downes and Kavanaugh, 1988: 8). We give little credence to this possibility.

## The Genera

*Patterns.*— Four of the Middle American genera (*Physea*, *Pachyteles*, *Ozaena* and *Platycerozaena*) occur in both the South and North American continents. *Entomoantyx* is confined to the Middle American part of the North American continent. In terms of northward limits, *Physea*, *Pachyteles*, and *Ozaena* reach southwestern United States. The range of *Entomoantyx* extends north of the Isthmus of Tehuantepec in northeastern México, and *Platycerozaena* reaches only Nicaragua, at the southern edge of Nuclear Middle America. *Pachyteles* is the only ozaenine genus known from the West Indies, where it is represented in the Greater Antilles by two species. In South America, *Physea*, *Pachyteles*, and *Ozaena* reach Argentina, whereas *Platycerozaena* reaches only central Brazil.

In terms of diversity, all of the bi-continental genera are more speciose on the South American than the North American continent, though for *Physea* and *Platycerozaena* the difference is slight.

*Historical interpretation.*— Accepting a Gondwanian origin of the Ozaenini, we believe that occurrence of the tribe in Middle America and southwestern United States on the North American continent, must have been accomplished by dispersal— in part over sea and in part over land, in Tertiary time. There could have been an over land movement, if in fact there was an early Tertiary intercontinental connection, as has been postulated by some authors (for a discussion, see Donnelly, 1988, and Savage, 1982).

Based on phylogenetic position, diversity pattern and extent of northward penetration, we believe the genera arrived in the following sequence: first, the ancestral stock of *Entomoantyx*, a genus which we take to be a relict; second, *Pachyteles* and *Physea*; third, *Platycerozaena* (few Middle American species, limited penetration); and fourth, *Ozaena* (only one species, which occurs in northern South America, as well).

Number of incursions postulated varies. For the bi-continental genera, we indicate: one each, for *Physea* and *Ozaena*; for *Platycerozaena*, two (one endemic species in Middle America, and one shared between the northern and southern continents); for *Pachyteles*, several incursions, with several each for the nominotypical subgenus and for *Goniotropis*.

For time of arrival, we postulate Late Cretaceous to Early Tertiary for *Entomoantyx*; Middle Tertiary for *Physea*; Pliocene and Pleistocene for *Platycerozaena*; and Pleistocene for *Ozaena*. Because *Pachyteles* is represented by several of the same species on both continents, as well as by an array of endemic species in Middle America, we postulate a range of times from Early Tertiary to Pleistocene and possibly even Recent.

The Greater Antilles were invaded probably at two different times by *Pachyteles* : once early, possibly in mid-Tertiary (this invasion represented by an endemic flightless species, living in the Jamaican highlands, undescribed, and possibly now extinct); and once recently (Pleistocene or Recent), and represented by *P. gyllenhali*, on the island of Cuba. The Lesser Antilles were probably invaded comparatively recently by one or two species of *Pachyteles*.

Mid-Tertiary arrival of the ancestral stock of the species of *Pachyteles* on Jamaica could have been facilitated by a land bridge, now foundered, but represented by the Nicaraguan Rise (Donnelly, 1988), or possibly by a mobile Jamaica that was closer to the mainland than it is now (Rosen, 1985, and references therein). We are inclined to doubt the latter possibility.

In conclusion, then, we postulate that the Middle-North American fauna has developed partly by incursions of taxa from South America, and partly by *in situ* differentiation of invading stocks. This is a common biogeographic pattern, described by many biogeographers.

### Ozaenine Species of Southwestern United States and Vicinity

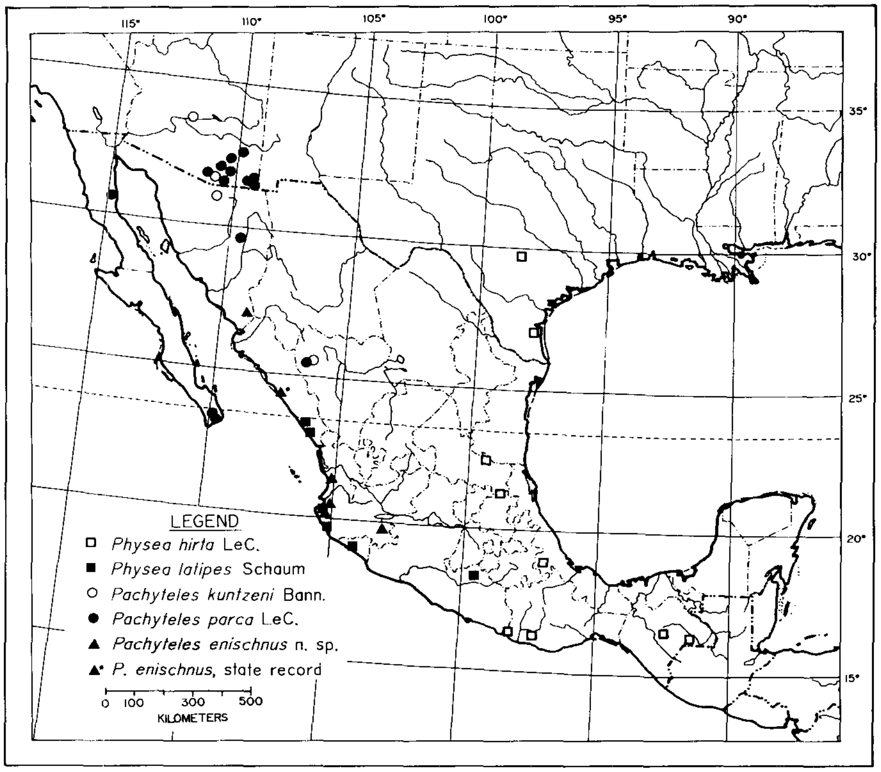
*The pattern.*— This is described partly in terms of extent of range and habitats. The latter are numbered below, according to the classification of Brown and Lowe (1980) and Brown, *et al.* (1980). Of the ozaenine species that are in or near southwestern United States, one (*Physea hirta*) reaches its northern limits in southern Texas, on the Gulf Versant. The remaining six are in the west, entering United States in Arizona, with the range of *Pachyteles gyllenhali* extended northward to approximately 33°30'N.

The northwestern species comprise two groups in terms of extent of range: those confined to the west (*Physea latipes*, *Pachyteles parca*, *P. kuntzeni*, and *P. enischnus*; Map 1), and those with ranges extended southward for various distances (*P. gyllenhali* and *Ozaena lemoulti*). *Physea hirta* belongs to this latter group, also.

In terms of habitat, the species confined to the west occupy dry habitats primarily, including tropical Sinaloan thorn scrub (134.3), Sinaloan deciduous forest (124.6), Madrean evergreen woodland (123.3), Sonoran desert scrub (154.11), Chihuahuan desert scrub (153.2), and interior chaparral (132.2). However, it is important to realize that desert areas are probably marginal for ozaenines, because no extensive diversification of the group has taken place in such areas, and no species are confined to desert habitats. The wide-ranging western species occupy some of these habitats, and as well Riparian cottonwood-willow series (224.53), and southward, evergreen tropical and cloud forest.

Another aspect of the pattern is distribution of putative sister species. *Physea hirta* and *P. latipes* are probably sister species, and their range overlap is only partial (Map 1). *Pachyteles parca* and *P. kuntzeni* seem to be sister species, whose ranges are in contact, probably narrowly, in southern Arizona and in northern México. *P. enischnus* has a probable sister species (*P. filiformis* Chaudoir) *filiformis* Chaudoir, *Pachyteles;*in eastern México. The sister species of *P. gyllenhali* as not been postulated, though we suspect it will be South American. That of *Ozaena lemoulti* is probably the more southern Brazilian *O. elevata* Bänninger, with the area of disjunction being the Amazon Basin.

The fact that most of the northern ozaenine species have vicariant or parapatric sister species suggests relatively recent differentiation of each of the stocks to which these species belong. From the standpoint of interpretation, it is



Map 1. Geographical positions of known localities in México and southwestern United States for five species of Ozaenini.

particularly interesting that each of the three species endemic on the Pacific Versant (*Physea latipes*, *Pachyteles parca*, and *P. enischnus*) have putative eastern counterparts.

In summary, the species at the northern end of the range of the Ozaenini occupy there principally dry forests and marginally, desert habitats. Most of the endemic Middle American-U.S. taxa are confined to such habitats. The two taxa whose ranges extend into South America plus *Physea hirta* occur in wet tropical forests, as well. The endemic Middle American-U.S. taxa exhibit east-west disjunction or near-disjunction, of closely related species.

*Geographical history.*— The general pattern described above is like the distribution patterns of many other taxa that occur in the same area (see Liebherr, 1986: 161-172, for details of the *Agonum extensicolle* group, and associated references to other authors and taxa. See also Ball and Nimmo, 1983, and Ball and Maddison, 1987).

The explanation seems rather simple. Each ancestral stock of the Recent endemic Middle American elements was divided and thus isolated, to the east and west of the north-south trending Sierra Madre Occidental, as a result of drying of the climate in the later part of the Tertiary Period. In isolation, the now vicariant elements differentiated from one another, becoming specifically distinct. Also, the western species probably became adapted to some extent to desert conditions, and succeeded in establishing in habitats marginal to their ancestral dry forests.

In Holocene time, and possibly earlier during the wetter glacials, the erstwhile vicariants *P. parca* and *P. kuntzeni* came into contact with one another, their ranges overlapping.During the wetter glacials of the Pleistocene, probably, the ranges of *Pachyteles gyllenhali* and *Ozaena lemoulti* expanded, (the former species reaching Cuba in the Caribbean Ocean, and the Tres Marias Islands in the Pacific), and these taxa reached the northern limits of the tribe Ozaenini in the New World, and came to overlap the ranges of the more northern endemics. Possibly the range of *Physea hirta* expanded similarly, with this predominantly eastern species spreading through the Isthmus of Tehuantepec to the lowlands on the Pacific Versant of México.

More generally, we believe that these northern ozaenine stocks provide some perception about how the dry adapted fauna of western México evolved. Certain species, ranging northward from the wet tropics, are able to enter drier habitats. In the course of changing circumstances, the expanded ranges of these species become disjunct. In the fullness of time, and under the influence of natural selection, the dry forest stocks become adapted to such conditions to the extent that they either become confined to them, or are able to enter still drier habitats. So far, ozaenines have not penetrated the extreme habitats encountered in the Sonoran and Chihuahuan deserts. Such penetration remains as a future evolutionary possibility.

*Corollaries.*— If this zoogeographic scenario is correct, the following should be found to be true.

1. Future work will not refute the hypothesized sister-group relationships.
2. *Pachyteles parca*, most collections of which have been made in Arizona, will be found further south along the Pacific coast, in Sinaloan deciduous forest.
3. The range of *Pachyteles kuntzeni* is in fact limited in northwestern México, to the eastern slopes of the Sierra Madre Occidental, as is suggested by present limited data. It will be found, farther south, in tropical forest, as well.

## CONCLUDING STATEMENT

Nearly 30 years ago, when Ross H. Arnett, Jr., published his treatment of the beetle genera of North America north of México, knowledge of the included Ozaenini was hardly more than what was known in the previous century, when most of the species of the group resident in southwestern United States were described. In this work, we add a few points about relationships and distribution of these species, but much more must be done, both ecologically and systematically, to bring this small but markedly divergent faunule (seven species, only, in three genera) to that stage of understanding at which ecologists can make use of the species as elements in ecosystems, *et cetera.*

At a more general level, we have added to understanding of the ozaenine genera of Middle America by detailed comparisons of a number of systems of structural features, and by entering into the structural characterizations the important data that have been generated by others concerning the defensive secretions of the pygidial glands. For the first time, we have used in detail the features of *Metrius* in out-group comparison to polarize in an evolutionary context the features of the ozaenine genera. Still to be done is to work out relationships of these genera on a worldwide basis, and to relate the reconstructed phylogenetic patterns to the movement of continents as described by plate tectonic theory.

In our investigations of structural features, we have uncovered a wealth of detail that could be analyzed profitably by functional morphologists: mouthparts and ovipositors are two such systems.

We hope we have provided an adequate basis for the next stage of systematic analysis of the New World Ozaenini, which must be treatment of the species, particularly of *Pachyteles* (*sensu lato*). We hope that those who use this publication find in the wealth of implied questions about ozaenines adequate recompense for the lack of answers that we have been able to provide.

## ACKNOWLEDGEMENTS

We thank the entomologists whose names appear in the list of codens and addresses of collections from which we received the material on which this study is based. The senior author adds a special note of appreciation to those who made possible his visits to study their collections, and who extended warm hospitality to him during those visits: M. E. Bacchus, P. M. Hammond, R. D. Pope, and N. E. Stork (BMNH); D. H. Kavanaugh (CASC); S. R. Shaw and D. R. Maddison (MCZC); and L. Sims and T. L. Erwin (USNM). Lee H. Herman (AMNH) made special efforts to arrange for the loan of the type of *Pachyteles beyeri* Notman.

Most of the line drawings of the male genitalia were prepared by D. R. Maddison, while he was a graduate student at the University of Alberta. D. Shpeley and G. D. Braybrook worked together in preparing the material and photographs of structural features, using the Department of Entomology's scanning electron microscope. J. S. Scott prepared the photographs of habitus and the plates of illustrations.

At our request, a draft of the manuscript was reviewed by Yves Bousquet (Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario) and by Donald R. Whitehead (Systematic Entomology Laboratory, United States Department of Agriculture, Washington, D. C.). Although we were not able to take advantage of all of their proposals for improvement, we adopted many of them and made corrections, as required.

We hope that our colleagues and associates who contributed so generously to this study find adequate recompense for their efforts in the resulting publication.

Financial support for field and museum work was received through grants to the senior author: A-1399, Natural Sciences and Engineering Research Council of Canada; and GB-3312, National Science Foundation, U.S.A. Publication costs were met with funds from NSERCC Grant A-1399. We are grateful for this important assistance.

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