PROCEEDINGS

OF THE

California Academy of Sciences

Vol. 42

SAN FRANCISCO
PUBLISHED BY THE ACADEMY
1979–1982

(US ISSN 0068-547X)

The California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

PRINTED IN THE UNITED STATES OF AMERICA
BY ALLEN PRESS, INC., LAWRENCE, KANSAS

CONTENTS OF VOLUME 42

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 1, pp. 1–55; 113 figs. March 2, 1979

SYSTEMATICS OF THE NEARCTIC *PTILODEXIA* BRAUER AND BERGENSTAMM (DIPTERA: TACHINIDAE)*

By
D. Dee Wilder

Department of Entomology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

ABSTRACT: A revised classification of the Nearctic prosenine genus *Ptilodexia* Brauer and Bergenstamm (Diptera: Tachinidae) is presented. A total of 8,000 specimens and type material for nearly all species were studied. All seventeen previously described valid species of *Ptilodexia* are diagnosed and illustrated. Five new species, *P. sabroskyi*, *P. pacifica*, *P. californica*, *P. westi*, and *P. maculata* are described and illustrated. A key to the Nearctic species is presented. The following new synonymies are made: *P. conjuncta* (Wulp) (= *Rhynchodexia simulans* Wulp); *P. contristans* (Wulp) (= *R. punctipennis* Wulp); *P. carolinensis* Brauer and Bergenstamm (= *P. neotibialis* West, *P. minor* West); *P. halone* (Walker) (= *P. hucketti* West); *P. harpasa* (Walker) (= *P. leucoptera* West, *Dinera robusta* Curran); *P. rufipennis* (Macquart) (= *Dexia cerata* Walker, *D. albifrons* Walker, *Rhynchodexia confusa* West, *R. translucipennis* West, *Rhynchodexia dubia* Curran); *P. major* (Bigot) (= *Dexiosoma fumipennis* Bigot, *Rhynchodexia fraterna* Wulp, *R. omissa* Wulp); *P. incerta* West (= *P. proxima* West; *Rhynchodexia elevata* West).

The biology of these parasitic flies is reviewed and possible host–parasite relationships are discussed. The taxonomic significance of numerous morphological characters in the genus and the subfamily is discussed. The phylogeny of *Ptilodexia* and its nearest relatives is discussed; six species groups are separated, and an evolutionary tree presented for these groups. The contemporary and historical zoogeography of the genus is discussed as it pertains to host and parasite distribution. A distribution map is presented for each species treated.

INTRODUCTION

Flies of the genus *Ptilodexia* are large calyptrate Diptera belonging to the Tachinidae, a family of exclusively parasitic flies. *Ptilodexia* adults are commonly collected on flowers during the summer months. The larvae parasitize the larvae of certain scarabaeid beetles. They are of economic interest because they are known parasites of such pests as *Phyllophaga* spp., *Popillia japonica* Newman, and *Macrodactylus subspinosus* (Fabricius). The genus is distributed throughout the New World.

Although specimens of *Ptilodexia* are common in collections, few are correctly identified. Sabrosky and Arnaud (1965) made no attempt to give synonymies or distributions in their catalog listing of 27 species names. The special problems leading to such confusion in *Ptilodexia* are (1) difficulty in associating the sexes, (2) a high degree of intraspecific variation, (3) an unusually low degree of interspecific variation, and

---

* Contribution from the Frost Entomological Museum, Pennsylvania State University. This research was supported by the Agricultural Experiment Station Project No. 2070, and constitues Contribution No. 5611 from that station. An earlier version of this paper was submitted to the Graduate School, Pennsylvania State University, as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

(4) the lack of consistent traditional morphological characters.

The purpose of this study is to revise the classification of *Ptilodexia* on the basis of all available material, to analyze the life history of its species, and to determine evolutionary and zoogeographical trends which may apply also to other members of the family Tachinidae.

MATERIALS

This study was based on over 8,000 specimens borrowed from various museums. In addition, type-specimens for most of the known species and numerous representatives of other genera in the Prosenini were studied.

Institutions loaning material used in this study were as follows: American Museum of Natural History (AMNH), Arizona State University (ASUT), British Museum (Natural History) (BMNH), California Academy of Sciences (CASC), University of California Berkeley (CISC), Canadian National Collection (CNCI), Cornell University (CUIC), University of Nebraska (DEUN), Field Museum of Natural History (FMNH), Florida State Collection (FSCA), Iowa State University (ISUI), Los Angeles County Museum of Natural History (LACM), Leningrad Museum of Natural History (LMNH), Museum of Comparative Zoology, Harvard University (MCZC), Michigan State University (MSUC), Ohio State University (OSUC), Oklahoma State University (OSEC), Oregon State University (OSUO), Paul H. Arnaud, Jr., Collection (PHAC), Yale University (PMNH), Purdue University (PURC), South Dakota State University (SDSU), University of Kansas (SEMC), Staten Island Institute of Science (SIIS), University of Oklahoma (SMSH), Texas A & M University (TAMU), University of Arizona (UAIC), University of Alberta (UASM), University of California Davis (UCDC), University of California Riverside (UCRC), University of Idaho (UICM), University of Montreal (UMIC), University of Michigan (UMMZ), Utah State University (USUC), National Museum of Natural History (USNM), Vienna Museum of Natural History (VMNH), Washington State University (WSUC).

METHODS

The male genitalia of *Ptilodexia* species are partially obscured on dry, pinned specimens. To examine them, the posterior half of the abdomen was removed, placed in a solution of 10 percent KOH, and heated until the structures were sufficiently softened to be dissected easily. They were later rinsed twice with water and twice with acetic acid, placed in glycerine, and examined. They were stored in a microvial pinned beneath the insect.

Illustrations of the genitalia were made using an ocular grid. The postabdomen was anchored to a small piece of soft wax on the bottom of the dish of glycerine to prevent it from drifting about.

Drawings of the heads were made by projecting photographic transparencies of them onto drawing paper. Manipulation of the projector provided images of uniform size. The image was then traced with a hard pencil; the details were filled in after thorough examination of the specimen with a dissecting microscope.

All measurements were made using an ocular grid, calibrated by a stage micrometer. Ratios were calculated from these measurements.

Because of the extreme intraspecific variability of *Ptilodexia*, a description which included all variation would be unwieldy and would be similar for each species. To make the description more useful and manageable in size, only one specimen, the holotype, is described.

A complete synonymy and list of citations are given for each species included in this study. New species are thoroughly described and diagnosed. For previously described species, only a diagnosis is presented. Known information on each species is summarized and notes regarding types and nomenclature are presented.

Intraspecific variation is discussed thoroughly for all new species. With previously described species, variation is discussed only where it is necessary for species identification. Complete data from each specimen, including sex, locality, collector, depository, and other information, have been recorded by Wilder (1976) and therefore are not presented here. Wilder (1976) also gives complete redescriptions for all previously described species of *Ptilodexia*.

The scope of this revision has been limited for practical reasons. Inclusion of the southern Mexican species would have doubled the number of species treated, and the material available for these species is wholly inadequate. All Nearctic species are treated herein.

ACKNOWLEDGMENTS

I extend my sincerest appreciation to Dr. C. W. Sabrosky, who initiated this study and without whose help this revision could not have been completed. Dr. Sabrosky also generously loaned types and was always available to answer questions about *Ptilodexia* and related tachinids.

I thank Dr. K. C. Kim for his valuable assistance during this project. His enthusiasm and drive served as a constant inspiration.

Persons and institutions loaning type material, for which I am grateful, are: Dr. R. W. Crosskey (BMNH), who was extremely generous in loaning 56 type-specimens for this project; Dr. R. Litchtenberg (VMNH); Dr. V. Richter (LMNH); Dr. L. L. Pechuman (CUIC) who kindly loaned me the types of 14 species for an extended period of time; also J. C. Scott (MCZC), Dr. P. Wygodzinsky (AMNH), and Dr. F. C. Thompson (USNM) who helped in uncovering some important syntypes.

I am indebted to Dr. P. H. Arnaud, Jr., and the Department of Entomology, California Academy of Sciences, for providing facilities and valuable assistance during my time on the West Coast. Thanks are also due to Dr. D. C. Rentz and D. H. Kavanaugh for their frequent assistance with many problems.

I finally thank my husband, George Zelznak, for his unending encouragement and optimism throughout this study.

BIOLOGY

The larvae of *Ptilodexia* flies parasitize and kill their scarabaeid larva hosts. The adult flies, however, feed on nectar and they spend considerable time probing at flowers, particularly composites. While feeding they become covered with pollen and probably act as pollinators. *Ptilodexia conjuncta* and *P. agilis* adults have been observed pollinating the flowers of dwarf mistletoe (*Arceuthobium cyanocarpum*). Adults of *Ptilodexia* have been collected with pollinia attached to the tarsi.

Adults are collected in many environments. Members of some species are collected at the seashore, while others have been taken at altitudes as high as 3,000 m in the Sierra Nevada and the Rocky Mountains. These flies have been taken at UV light, Malaise, and other flight traps. But the most productive method of collecting seems to be sweeping flowers, especially composites such as *Baccharis* and *Solidago*.

The occurrence of specimens of *Ptilodexia* is, as with most parasites, seasonal. At times, hundreds of individuals of one, two, or even three species may be collected simultaneously at one kind of flower. In other years the flies will be rare—perhaps representing the normal buildup and decline of a parasitic population. In some areas, such as Long Island, New York, and Riverside, California, specimens of certain species have been collected on the same dates every year for ten or more years. However, both these areas have been extensively surveyed regularly by specialists and may represent the actual situation, which is not seen in other areas simply because of poor sampling.

There is no information on the mating habits of *Ptilodexia* spp. Despite the numerous specimens collected, few have been pinned in copula. Males usually emerge before females, but the place and time of mating is unknown.

The female carries hundreds of tiny larvae in her abdomen during larviposition. It is not known if she simply broadcasts them or if she places them directly on the soil. Neither is it known if the female is able to locate areas of host density, nor if the larva has the sensory capacity to find a host. If the larvae are deposited in a jar, they will wander along the sides for two to three days before dying. First-instar larvae of *Prosena siberita* survive a week or more in the soil (Clausen 1927).

The larvae are presumably quite easy to rear if the host larvae can be kept alive under laboratory conditions. During the development of the parasite larva, a defensive response of the host causes a respiratory funnel to appear at the point of attachment to the host. This is a sclerotized funnel-shaped structure which encloses the caudal end of the larva and can be seen through the integument of the host. The larva feeds on the internal fluids and fat body of the host and finally leaves the host to pupate in the soil. By this time, the larva has ingested nearly all the contents of the host.

Based on Davis's (1919) data, *Ptilodexia* larvae overwinter within the host. The pupal stage is quite short, cold temperatures are not required to complete development.

The host scarabaeid larvae, or white grubs, belong to the subfamily Melolonthinae, which includes such common and economically important genera as *Phyllophaga*, *Popillia*, and *Macrodactylus*. The dynastinine scarabaeids of the genus *Aphonus* are also parasitized by these flies. Champlain and Knull (1944), and Peterson (1948) implicate *Ptilodexia canescens* as a parasite of the cerambycids *Saperda calcarata* and *Rhagium lineatum*.

Most species of *Phyllophaga* have a two- or three-year life cycle. *Popillia japonica* and some of the other hosts have one-year life cycles. The life cycle of *Ptilodexia* probably does not exceed one year. Early-instar white grubs are attacked in the fall and fed upon until the following spring or summer when the parasite pupates. Adult flies emerge shortly thereafter.

According to Davis (1919), when infested host larvae are brought indoors in the fall, the *Ptilodexia* larvae will continue their development within the host, pupate, and emerge as adults in the winter, without interruption. It is thus possible that in areas with long seasons, two or more broods could develop. My samples from Texas, southern California, and some southeastern states appear to support this. Two broods per year are possible only if there is an ample supply of grubs of the proper stage feeding in the soil. In these areas of bivoltinism, variant populations in the species concerned are apparently more common than in areas where only one brood is possible. One can extrapolate to the tropical regions where even more generations per year are possible, and the number of species and the variation among species is phenomenal.

It is not known if any species of *Ptilodexia* is host specific, but some species are known to have more than one host. For example, *P. carolinensis* can complete its life cycle either in *Phyllophaga rugosa* (fide Davis 1919, as *Ptilodexia abdominalis*) or in *Popillia japonica*. On the other hand, *Ptilodexia maculata* and *P. prexaspes* have restricted ranges and show little intraspecific variation—perhaps indicative of host specificity. *Ptilodexia harpasa* and one of its reported hosts, *Macrodactylus subspinosus*, are sympatric.

Many questions remain unanswered regarding the relationship of host preference and speciation in *Ptilodexia*. In some species, local aberrant populations are found that only vaguely resemble the typical population. The possibility exists that these aberrant populations have shifted to a host significantly different from the common one. It is conceivable that such a shift could be an early step in speciation.

Many factors involving the relationship of host and parasite presumably influence the appearance of the adult fly. These factors include number of fly larvae per host, instar of parasitized host, rate of host development, and rate of parasitoid development. Specimens of *P. carolinensis* developed in *Phyllophaga* grubs differ greatly from those developed in larvae of *Popillia*.

These factors contribute to the extreme intraspecific variability in *Ptilodexia*, perhaps ultimately leading to speciation in the group. Carefully controlled breeding experiments are needed to help understand the effects on the parasites of the host and host environment.

TAXONOMIC CHARACTERS

Most of the specific characters previously used by *Ptilodexia* taxonomists are subtle, difficult to see, and unstable, sometimes differing not only between individuals but also on each side of the same specimen. Of the characters traditionally used to separate species, many have been either stable within the genus (e.g., "arista plumose") or different within a species (e.g., color, wing venation). Most earlier workers lacked sufficient study material to recognize normal intraspecific variation. Certain characters these early workers used were good, but they are more useful used in combination with certain other characters.

Sexual dimorphism has caused problems in the taxonomy of *Ptilodexia*. Abdominal color and color pattern, and leg color frequently differ between sexes; hence the two sexes of some species have been described under different names.

I have freely used raw measurements in my descriptions, recognizing nonetheless that they are of limited use in this group. Proportional measurements are generally more useful, and I include them in my descriptions and diagnoses. The standards for these proportional measurements are head height and length of the first antennal segment—both measurements which are proportional to general size.

This study is limited to dried adult flies, so structural characters are the only ones which form the basis of my classification. What follows is a brief discussion of the taxonomic importance of the various physical characters and how their states are determined. The headings and general organization are similar to those used by Crosskey (1973a). It is hoped that other workers in the Tachinidae will adopt the same format, eventually bringing some order to the study of variation in the family.

Body Color and Vestiture

The general integumental color of *Ptilodexia* adults is a dull brown, although adults of certain more-advanced species may be black or testaceous, and teneral specimens are generally paler. The color of the scutellum compared to that of the rest of the notum sometimes is specifically useful (e.g., *P. planifrons–P. contristans*); however, in adults of some species (*P. rufipennis*), it also varies intraspecifically. The color of the abdomen varies from reddish or testaceous with a dark longitudinal stripe, to concolorous black to testaceous. Although abdominal color may be of occasional taxonomic value, it almost always varies between males and females of the same species. In the female it is frequently concolorous, with the longitudinal stripe indistinct or absent. General body color sometimes varies clinally, and in some species, smaller, darker populations exist in the northern parts of the range.

Vestiture characters can aid in distinguishing members of different species. These characters seem to vary independently of integumental color. Facial tomentum varies from extremely heavy—totally obscuring the underlying integumental color–to fine and sparse. Occasionally there is a pattern or spot of color in this vestiture which can be distinct for a species (e.g., *P. contristans, P. canescens*). Facial tomentum may be dull (*P. westi*) or strongly shining (*P. incerta*). The color of the facial tomentum varies intraspecifically.

The tomentum on the pleuron is of little taxonomic value, and that on the notum is only slightly more useful. The notal tomentum on adults of some species (e.g., *P. westi, P. arida*) is heavy, abundant, and almost flocculent, nearly obscuring the integumental color, whereas on those of others (*P. mathesoni*) it is so fine that the notum appears polished. In members of other species (*P. conjuncta*), the tomentum is flattened and shiny, giving the notum, or parts of it, a coppery hue. Usually notal tomentum is arranged in longitudinal stripes, but this striping varies among individuals and is of little diagnostic value. Notal tomentum also varies between the sexes, usually being heavier in the female. Tomentum on the mediotergite can be fine or heavy; in specimens of *P. agilis* and *P. mathesoni,* however, it is absent.

Abdominal tomentum varies more between species than between sexes. It is generally grayish and tessellate, although in some individuals it may be gold or brownish; and it may be shining or dull. Only in adults of one species (*P. mathesoni*) has the tessellate pattern been replaced by a more uniform distribution of tomentum, and even then, only in the males. In members of a few species (e.g., *P. pacifica, P. ponderosa*), the grayish tomentum is the only vestiture on the abdomen, but in most there are patterns of brown or gold tomentum which can aid in distinguishing species. In *P. rufipennis* adults the bases of the median marginal setae on the third and fourth abdominal tergites are surrounded with gold tomentum; adults of *P. agilis* have a marginal band of it on the third and fourth tergites; those of *P. arida* have brown tomentum overlying the longitudinal stripe.

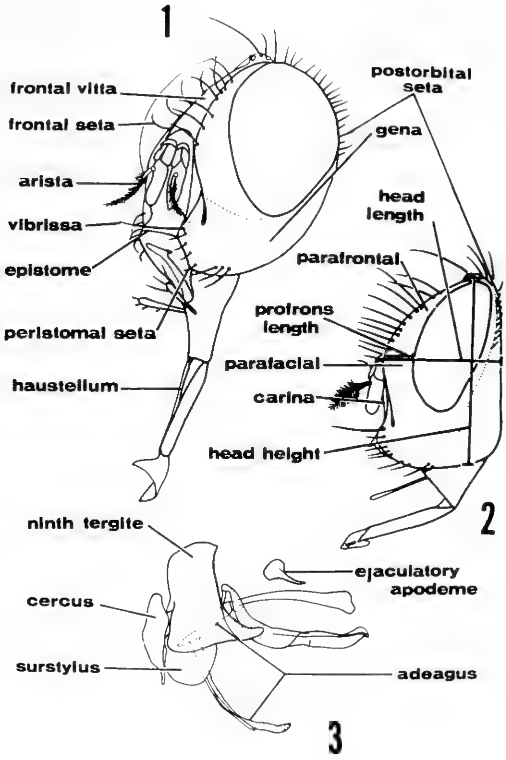
These characters of general color and vestiture show a greater degree of variation within *Ptilodexia* than within all other Nearctic Prosenini, with the possible exception of the most closely related genus, *Mochlosoma*.

When examining specimens for colors and patterns of tomentum, it is imperative that they be viewed from several different angles. Often a pattern can be distinguished only if it is seen obliquely.

Chaetotaxy and Hairing

Chaetotaxy is of minor taxonomic use in *Ptilodexia,* as it varies widely within species but little between them. Frequently, numbers and even the presence of setae vary from one side of the specimen to the other. This phenomenon is represented in the descriptions by separating the two states with a slash (1/0). Hairs differ from setae in being much smaller and finer.

The taxonomically useful setae on the head are the oral vibrissae (Fig. 1). There is usually one pair (two in specimens of *P. contristans*). The size and spatial relationships between the vibrissae and the peristomal setae can aid in identifying adults in some species. In *P. rufipennis* adults the peristomals immediately below



FIGURES 1–3. Structure of generalized *Ptilodexia*. Fig. 1. Head, anterolateral view. Fig. 2. Head, lateral view. Fig. 3. Genitalia, lateral view.

the vibrissae are short, becoming longer with distance from the vibrissae; in *P. conjuncta* adults, on the other hand, the peristomals are subequal and nearly as long as the vibrissae. Numbers of peristomal setae vary between and within species, but considerable overlap between species is common. The number and size of frontal setae vary, but these are even less reliable characters than are the number and size of the peristomal setae.

The ocellar, postocellar, internal vertical, and external vertical setae show some intraspecific differences in size and number. I have described these differences, but they are too variable to be used diagnostically. The postorbital setae vary in length between species, but not as much as between the sexes. The hairs which are sometimes inserted between them have minor significance. In adults of some species the postorbitals are long and closely spaced, while in those of others they are interspersed with fine setae half the length of the postorbitals, and in still others they are interspersed with tiny hairs.

Another group of taxonomically useful hairs on the head are those immediately ventral to the postorbitals. Members of species such as *P. planifrons* and *P. mathesoni* are characterized as having two to four irregular rows of dark hairs between the postorbital setae and the yellow or white occipital hair. Members of other species have only one row of these dark hairs (*P. californica*), and those of others have none or just a few scattered hairs (*P. maculata*). This character also shows much intraspecific variation and must be used cautiously.

Perhaps the best diagnostic character in *Ptilodexia* is the hairing of the parafacials (herein defined as the sides of the head bounded by the apex of the second antennal segment, the oral vibrissae, the frontal suture, and the anterior eye margin). The presence, size, distribution, and color of these hairs are extremely variable but species specific. There is slight variation in the characteristics of these hairs between males and females belonging to the same species; that is, the parafacial hairs of the female are slightly sparser, finer, and are not inserted as far ventrally on the parafacial as they are on the male. These hairs may be absent (*P. rufipennis*); long, dark, and abundant (*P. planifrons*); sparse and pale (*P. halone*); minute and occurring only on the upper anterior parafacial (*P. incerta*); strong and concentrated at the lower edge of the eye (*P. canescens*); strongly inclined anteriad (*P. contristans*); or inclined ventrad (*P. harpasa*). Many other combinations exist. It appears that this character can be of diagnostic value even in the Tropics, where there are many undescribed species. I have illustrated the character state for parafacial hairs in every Nearctic species herein described or diagnosed. The nature of the parafacial hairs is also of importance in *Mochlosoma*, where they are always present, but not in the other Nearctic Prosenini.

Parafacial-hair characteristics appear frequently in the key to species. When the hairs are small and pale, specimens must be examined carefully from several angles; often it is the bases of the hairs rather than the hairs themselves which are visible.

The parafrontal hairs are of much less taxonomic value. They are usually present, dark, and are either sparse or abundant.

Thoracic chaetotaxy is of little diagnostic importance in *Ptilodexia*. The numbers of such setae as sternopleurals, notopleurals, and postalars are generally constant within the genus. Others such as posthumerals, presuturals, acrostichals, dorsocentrals, and scutellars vary somewhat between species, but they also show considerable intraspecific variation. The number of humeral setae and discal scutellars are more constant, but must be used in combination with other characters to aid identification.

The length and density of hairs covering the *Ptilodexia* thorax vary between species. These, however, are difficult characters to divide into easily defined states. Propleural hairs do not occur in *Ptilodexia* adults, but are present in members of several closely related genera. They have diagnostic value at the generic level.

Another group of hairs on the thoraces of these flies is the infrasquamal setulae, small hairs inserted beneath the point of attachment of the squamae or calypters. In adults of some related genera in the Prosenini, these are always absent. In some *Ptilodexia* adults their absence may be a reliable specific character state (e.g., *P. canescens, P. maculata*), but in others, their absence carries less taxonomic importance. Sixty percent of the specimens of *P. rufipennis* examined had infrasquamal setulae, but they were present in only twenty percent of *P. incerta* specimens. This character is of equal value in both sexes. When using this character, one must realize that the 'absence' of infrasquamal setulae indicates absence on both sides of the body.

Hairs and setae on the legs have little diagnostic value; often the setal length reflects total body size more than any specific difference. The exception to this is the length of the antero- and posteroventral setae on the posterior leg of the male, which show species-level variation. These are difficult to measure, however, and have not been used in this revision. Other setae on the femora show some taxonomic potential, especially the presence or absence of anterior setae on the posterior femora.

Numbers of abdominal setae vary intraspecifically, but they usually vary around a certain number which can be defined for some species. The presence or absence of median marginal setae on the first syntergite can be a useful character.

The number of median discal and median marginal setae on the third and fourth tergites is useful in separating members of some closely related species (e.g., *P. californica* and *P. pacifica*), while in others it shows considerable intraspecific variation. The presence or absence of lateral discal setae on these tergites will separate members of distantly related species.

Length and density characters of abdominal hairs have about the same taxonomic value as those characters in thoracic hair. That is, they differ and seem to be constant among members of a species, but are difficult to separate into character states.

Although hairing on the genitalia varies only slightly between species, the presence of strong setae on the ninth tergite (epandrium) is an excellent diagnostic character in adults of *P. contristans* and *P. westi*.

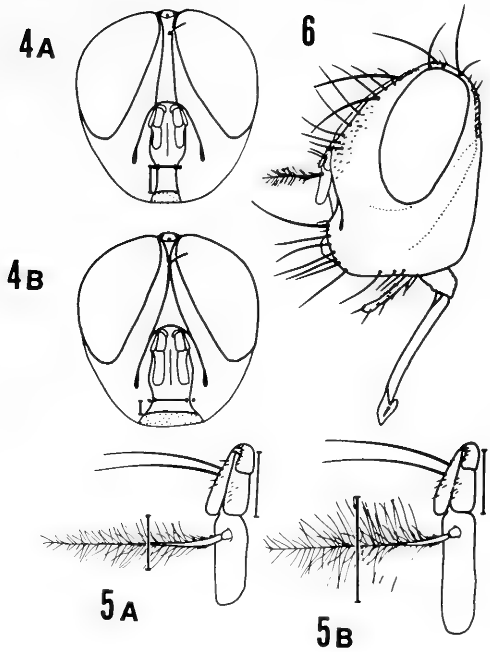
Head

Head characters in *Ptilodexia* are of more use taxonomically than characters of any other part of the fly. Included are those of chaetotaxy, which have been discussed in the previous section. Drawings of the head, with the terms used in this paper, are presented in Figures 1–2.

The head, in members of this genus, is wide and boxlike. The parafacials and genae are wide and covered with fine, dull-lustered tomentum. The genae are usually reddish, contrasting with the whitish parafacials and genal dilations. The velvety-appearing frontal vitta extends from the vertex to the frontal suture. The third antennal segment is rarely longer than twice the length of the second and bears an arista covered with long fine hairs. Between the antennae is a raised ridge or carina which does not protrude beyond the antennae. The epistome may or may not protrude. Mouthparts are similar to those of other calyptrate flies with the mentum length from 0.3 to 0.8 times the head height.

The width of the parafacial is of considerable diagnostic use in *Ptilodexia*. *Ptilodexia rufipennis* adults have narrow parafacials, while in *P. conjuncta* adults they are quite wide. This character is easier to evaluate in males than in females, and it varies more among *Ptilodexia* adults than among *Mochlosoma* adults.

The shape of the frontal vitta can be of use in this genus. Below the ocellar triangle and between the eyes, the frontal vitta is usually obliterated (Fig. 4b), the parafrontals becoming con-



FIGURES 4–6. Comparison of specimens of *Ptilodexia*. Fig. 4. Comparison of adults of two generalized species of *Ptilodexia* showing variation in width of epistome, position of oral vibrissae, and width of frontal vitta; A. head, anterior view, with frontal vitta not obliterated and distance of oral vibrissae from oral margin greater than distance between oral vibrissae; B. head, anterior view, with frontal vitta obliterated and distance of oral vibrissae from oral margin less than distance between oral vibrissae. Fig. 5. Comparison of antennae of adults of two generalized species of *Ptilodexia*; A. antenna, showing length of plumosity on arista shorter than length of second antennal segment; B. antenna showing length of plumosity on arista longer than length of second antennal segment. Fig. 6. *Ptilodexia ponderosa* (Curran), holotype, head of female, lateral view.

tiguous. In members of some species (e.g., *P. canescens*, *P. halone*), however, the parafrontals do not touch, and the frontal vitta is continuous from the antennal base to the ocellar triangle (Fig. 4a). This character varies to a similar degree in specimens of *Mochlosoma*.

The size and shape of the carina are useful at the supraspecific level. Among *Ptilodexia* species, the carina is sometimes distinctly shaped (e.g., *P. planifrons*). Carina characters vary more among *Mochlosoma* than *Ptilodexia* adults, in general being wider and better developed in individuals of the former genus. In members of several closely related genera such as *Dinera* and *Hesperodinera*, the carina is strongly developed, protruding from between the antennae, appearing almost bulbous, and visible from the lateral aspect. In *Rhamphinina* adults it is short, narrow, and strongly keeled. The carina shows no sexual dimorphism in size and shape, and except in a few cases it is species specific.

The oral vibrissae and adjoining areas hold characters of taxonomic value in *Ptilodexia*. These are the width of the depression between the bases of the oral vibrissae and the distance of the vibrissae from the epistome (sclerotized oral margin). Members of some species of *Ptilodexia* have this area wide and short; an example is *P. rufipennis*, in adults of which the vibrissae are far apart and close to the oral margin (Fig. 4b). The opposite state is shown in *P. prexaspes* adults, which are characterized by vibrissae that are far from the oral margin, but not far apart (Fig. 4a). In *Rhamphinina* specimens, the area is four times as high as wide. This character is diagnostic in a few species, but in others it varies intraspecifically. It shows no sexual dimorphism. In evaluating this character, physical measurement is necessary; estimate is inadequate. The invisible line connecting the vibrissae should pass through the center of their bases, and the sclerotized margin of the epistome should serve as the ventral boundary. Width is measured only at the vibrissae; height is measured mesially.

The epistome generally protrudes in *Ptilodexia* and *Mochlosoma* specimens, and although both genera show variation, in *Ptilodexia* adults it is sometimes species specific. In adults of species like *P. prexaspes*, *P. canescens*, and *P. halone*, the oral margin projects slightly if at all. As a result, the lower anterior portion of the head is vertical in profile (Fig. 71), and in some cases the anterior margin of the head protrudes further anteriad at the antennae than at the vibrissae. *Ptilodexia conjuncta* adults show the opposite state, the epistome projecting strongly, as does the lower anterior portion of the face (Fig. 26). In other prosenines the character shows less intraspecific variation than it does among species of *Ptilodexia*.

The length of the haustellum is an extremely valuable taxonomic character in *Ptilodexia* (and *Mochlosoma*), and it is also the chief difference distinguishing *Ptilodexia* from *Mochlosoma* specimens. In individuals of the former genus, the length of the haustellum varies from 0.3 to

0.9 times the head height, and the shape is broad and linear or slightly tapered; it is rigid in all individuals. *Mochlosoma* specimens have the haustellum much longer than the head height, and narrow and flexible. In other Prosenini this character serves to separate genera. In *Ptilodexia* I have compared the length of the haustellum with the head height and used the resulting ratio as a diagnostic character which varies consistently between species, little within species, and not at all between the sexes. When using this character in the key, actual measurements must be made; estimating the ratio is difficult because a slender haustellum appears longer than a broad one of the same length.

There is intraspecific variation in the length of the haustellum among members of a few species. Among *P. rufipennis* (as well as *P. arida, P. carolinensis,* and *P. pacifica*) specimens, the haustellum length varies locally. The length can be short in members of one population and noticeably longer in those of another. The character is still useful, though, since the variation remains within easily expressed values.

The length and shape of the palpi vary slightly between members of different species of *Ptilodexia*. The length is expressed, in this paper, as a fraction of the haustellum length. Some Prosenini, such as *Prosena* and *Senostoma* specimens, have short stubby palpi; and in *Ateloglossa* adults they are completely absent. This character varies among *Mochlosoma* specimens much as it does among those of *Ptilodexia*. In members of *P. arida* and *P. prexaspes,* the length of the palpi may nearly equal the length of the haustellum, while in those of *P. obscura,* it is rarely more than 0.3 times the haustellum length.

The antennae possess some useful taxonomic characters: length, shape, and arista plumosity. The length of the third segment is herein expressed in terms of its relationship to the relatively constant second segment. Measurement of the second segment is taken from a slightly anterodorsal aspect and is the longest dorsoventral length of the segment.

Among *Prosena* and *Senostoma* adults, length of the third segment is approximately twice the length of the second; in those of most other Prosenini, it is considerably shorter. Among *Mochlosoma* species the length varies, the most usual state being the third segment equal to 1.4 to 1.5 the second. The same is true in *Ptilodexia* species, where this character can be used to separate adults of some species. *Ptilodexia sabroskyi* adults have a short third segment, subequal to or shorter than the second, whereas those of *P. rufipennis* have the third segment up to twice the length of the second. Specimens of *P. obscura* sometimes have the third antennal article broadened apically instead of slightly pointed as it is in members of most species.

The length of the plumosity on the arista is an excellent diagnostic character in *Ptilodexia*. I have expressed it in relation to the length of the second antennal segment. The arista, including the plumosity, is measured at its greatest width (Fig. 5). In specimens of *P. rufipennis* and *P. harpasa,* two species with long third antennal segments, the length of the plumosity is greater than twice the length of the second antennal segment, while in those of *P. planifrons* and *P. prexaspes,* the length of the plumosity is less than or equal to the length of the second segment. This character is especially useful in separating adults of the closely related *P. californica* and *P. sabroskyi*.

Thorax

Most of the thoracic characters used in this revision have been discussed in the sections on vestiture and chaetotaxy, the remaining ones are those of the mediotergite, legs, and wings.

Adults of *Ptilodexia* have a typical calyptrate thorax with the mesothorax highly developed, and the prothorax and metathorax reduced. The scutellum is small; ventral to it is the bulging postscutellum, which distinguishes members of the family Tachinidae. The pleuron is typical of other calyptrate flies. The propleuron is bare, although the rest of the pleuron is beset with fine hairs and numerous groups of setae. The legs are long with extremely long tarsi. The wings are also long, the venation typical of calyptrate flies.

The mediotergite is the oval arched area ventral to the postscutellum. In members of some species the mediotergite is dorsally polished, although other parts of it may be tomentose. Care must be taken when observing this character, since on adults of some species the mediotergite has a thin layer of tomentum and still appears shiny.

Leg color is a taxonomically useful character. In species where the color is similar in members of both sexes, pale-colored legs are diagnostic. The color of the tarsi can also separate members of different species (e.g., *P. halone* and *P. prexaspes*). *Ptilodexia maculata* specimens are distinguished by distinct femoral patches which, although present on members of other species, are strikingly evident on those of *P. maculata*. Other species exhibit dimorphism in leg color, the males with dark legs, the females with pale legs (e.g., *P. agilis, P. arida*). Two other species, *P. rufipennis* and *P. pacifica*, have females with pale legs and males with legs of varied color.

Wing venation is useful in distinguishing members of some genera in this tribe (*Nimioglossa*). Within *Ptilodexia* (and *Mochlosoma*), however, it is of dubious value. Wing color is constant within species and can be used diagnostically. Adults of *P. contristans* have the wings distinctly darkened basally, while those of *P. mathesoni* have the entire wing darkened. The colors of the squamae, epaulet, and basicosta also show slight differences between members of certain species, but they can be varied among those of others.

Abdomen and Genitalia

In *Ptilodexia* adults as in most Nearctic Prosenini, the abdominal tergites meet ventrally, entirely obscuring the sternites. The first tergite is actually composed of two fused segments; the next three tergites—third, fourth, and fifth—are conspicuous. The sixth tergite is fairly broad, the edges not meeting ventrally (but embracing the fifth sternite); it and those remaining are withdrawn into the fifth tergite. The next two tergites are fused and become the seventh syntergite, which is fairly narrow in *Ptilodexia* members (not much wider than the epandrium), with its surface oriented posterodorsally, as is the epandrium (the ninth tergite). This pattern is similar in *Mochlosoma* members, but in other Prosenini it is different. In *Prosena* adults, for example, the ninth tergite appears to be fused with the seventh and eighth, and in members of *Hesperodinera*, the fused seventh and eighth tergites are exposed and greatly enlarged, the surface facing posterad, the epandrium forced beneath the abdomen.

Abdominal color is varied intraspecifically but is still useful as a key characteristic distinguishing members of some species. In the key presented herein, when the abdomen is described as reddish laterally, at least the second and third tergites (of the male—the character is not as consistently applicable to the female) have the integument reddish or rufotestaceous laterally. On specimens in which the abdomen is concolorous dark brown or gray, there may be a slight rufescent cast along the margins of the tergites. This state should not be confused with the previous one, in which the reddish color extends from the anterior to posterior margins of the tergites.

In specimens of *Ptilodexia*, the external male genitalia (Fig. 3) have taxonomic value. The characters which vary slightly between members of different species are the shape of the ninth tergite, the shape of the surstyli, and the shape of the cerci. These characters are useful in distinguishing members of a few species, but sometimes vary more intra- than interspecifically. Only in species with extraordinarily modified members (e.g., *P. westi, P. rufipennis*) can the external genitalia be called diagnostic, and even then, they must be dissected for characters to be examined properly. Often the genitalia of adults of *Mochlosoma* and *Ptilodexia* are identical. The above-mentioned characters vary greatly between specimens belonging to different genera and are of excellent supraspecific group characters.

Internal genitalia are generally not useful in separating members of species of *Ptilodexia*. The aedeagus is nearly identical in members of this genus and those of *Mochlosoma*. The ejaculatory apodeme, however, is useful in distinguishing specimens of some species or species groups. Its shape can be distinct, as in *P. contristans, P. planifrons*, and *P. rufipennis* members; between many of the species, though, it does not vary. Female genitalia show no striking diagnostic differences, with the notable exception of the surface sculpturing of the spermathecae which, with high-magnification studies, may reveal specific differences. The reproductive systems of both sexes of *Ptilodexia* have been described by Townsend (1938).

The larvae of *Ptilodexia* have never been described, even though there is a figure of a mature larva and the puparium in Davis (1919). The nature of the cephalopharyngeal skeletons of first instar larvae (from the abdomen of gravid females) has been used to separate species in some genera of tachinids (*Archytas*), but the character is of no use in *Ptilodexia*. Greene (1922) described the puparium of an unknown species of *Ptilodexia* (erroneously determined as *P. tibialis*).

Of the useful diagnostic characters, none works to separate members of all species from those of all others. Most of these characters are of high value in distinguishing members of the derived species, but when members of certain primitive species (*P. carolinensis, P. major*) are examined, they lose much of their value and more characters must be considered in making identifications.

PHYLOGENY

Present attempts to reconstruct the phylogeny of a genus or tribe in the Tachinidae are based on incomplete data and should be considered extremely tentative at best. Characters used at generic and tribal levels are so unstable that convergence, loss, and acquisition occur repeatedly. Most of the species, and probably many of the genera, are unknown or poorly defined on a worldwide basis. Host relationships are largely unknown.

For the phylogeny of *Ptilodexia*, Neotropical species and representatives of closely related genera were carefully examined to infer apomorphic and plesiomorphic states. Character matrices were then constructed and phylogenetic trees inferred. This method works well when trying to construct probable relationships in higher categories, but for relationships among species it is not adequate. This is becuase the characters distinguishing species are generally more unstable than those distinguishing families or tribes. Many specific characters can be lost or regained easily.

Relationships within the Prosenini can be inferred only after examining members of the tribe on a world basis. I have not had the opportunity to do this. I have seen a few representatives of the North American genera, none of the exclusively Neotropical genera, one of an Australian genus, and one of *Prosena*, a worldwide genus. Most of the species in these genera can not yet be identified with existing keys.

The characters used to infer relationships between genera are facial carina, space between vibrissae, propleural hairs, and haustellum length. The form of the facial carina provides a good generic character, much as it does in the tribe Rutiliini (Crosskey 1973a). In members of Prosenini, the carina was lost once, although slight expression is common in members of some species of *Ptilodexia* and *Mochlosoma*.

The area between the vibrissae is another stable generic character. In *Ptilodexia* and *Mochlosoma* adults, and in those of some of the other genera, this area is depressed and may be flat or slightly concave, while in members of the more primitive genera, it is slightly to strongly convex. In the primitive genera, the oral vibrissae are situated at or slightly above the oral margin, while in *Ptilodexia*, *Mochlosoma*, and *Rhamphinina* adults, they are inserted distinctly dorsal to the epistome. In *Arctophyto* and *Milada* adults, their placement is intermediate between that in members of the primitive and the derived genera.

Propleural hairs are lacking in members of *Sentstoma* and *Prosena*, two of the more primitive genera. They have been lost in *Hesperodinera* adults and are never seen in those of the advanced genera.

The haustellum is longer than the head height in specimens of *Prosena*, *Prosenoides*, *Nimioglossa*, and *Mochlosoma*, but is much shorter in those of the other genera. Also, there is great variation in haustellum length among *Ptilodexia* species (from 0.3 to 0.9 times head height).

The position of *Ptilodexia* within the Prosenini is advanced. Assuming an Oriental center of origin for the group, there is a wealth of forms (members of which have a broad, blunt, facial carina) in the Oriental and Palearctic regions. Some of these, such as *Prosena* and *Dinera*, are widespread. It was probably a form similar to *Dinera*, *Milada*, and *Arctophyto* which, along with its hosts, crossed the Bering Land Bridge during favorable conditions in the late Tertiary. Subsequent radiation before and during the Pleistocene must have been great, for *Ptilodexia* is the most diverse genus of prosenines in the western hemisphere.

Dinera and *Arctophyto-Milada* remain on both sides of the Pacific with relatively few species. Other small genera which proably originated from this complex are *Ateloglossa*, *Dolichocodia*, *Prosenoides*, and *Hesperodinera*, members of which have retained the inflated carina, and *Myoceropsis*, *Rhamphinina*, and *Nimioglossa*, whose members have lost it.

Ptilodexia and *Mochlosoma*, both large genera, probably had similar origins, *Mochlosoma* from a more restricted ancestral line. Although the strong carina has been lost, it is expressed to a moderate degree in members of some species in both genera. It is my opinion that the only character which separates *Ptilodexia* from *Mochlosoma* adults, the haustellum shape and length, is a phylogenetically sound one, that is, its origin in *Mochlosoma* is monophyletic. Although radiation of both genera has been great, divergence between *Mochlosoma* and *Ptilodexia* members is only slight.

Ateloglossa and *Hesperodinera* had their origins from a *Dinera*-like ancestor, members of the former having lost the palpi and the latter the propleural hairs, but both having retained the squarish head and inflated facial carina. *Prosenoides* adults, on the other hand, bear a closer resemblance to *Prosena* specimens, and the two may be closely related. Both *Nimioglossa* and *Rhamphinina* had their origins early in the *Ptilodexia-Mochlosoma* line, their members having diverged from the ancestral forms in having the area between the oral vibrissae depressed and the vibrissae placed considerably above the oral margin, as do representatives of *Ptilodexia* and *Mochlosoma*.

Within *Ptilodexia*, characters indicating relationship are difficult to determine. The ancestral and derived states of a few of these characters have been inferred.

Small size and dark color seem to be primitive states within *Ptilodexia*, while the derived states are large size and pale color. The primitive state of the length of the third antennal segment, the length of the plumosity on the arista, and length of the haustellum is an intermediate one, with the derived states being short and long. The presence of both parafacial hairs and infrasquamal setulae appear to be primitive within this genus. Primitively the oral margin is narrow and projecting, while the more advanced forms show it to be wide and not projecting. The primitive, typical shape of the ejaculatory apodeme can be seen in most species (Fig. 44). Members of some of the advanced species have this structure modified in various ways (Fig. 29, 35), although those of others do not.

The genus *Ptilodexia* in North America is comprised of six loosely knit groups. The first, and probably most primitive of these, is the *agilis* group, which consists of *P. agilis*, *P. obscura*, and *P. mathesoni*. The next group is the *carolinensis* group, with member species *P. carolinensis*, *P. halone*, *P. prexaspes*, and *P. canescens*. The *harpasa* group is composed of *P. rufipennis*, *P. arida*, *P. harpasa*, and *P. ponderosa*. In the *major* group are *P. major*, *P. incerta*, *P. maculata*, and *P. flavotessellata*. The *conjuncta* group contains *P. conjuncta*, *P. planifrons*, *P. contristans*, and *P. westi;* and the *californica* group, *P. californica*, *P. sabroskyi*, and *P. pacifica*.

The character states which segregate members of these groups are vague and difficult to define, but since the groups appear to have both a zoogeographical and morphological basis, they will be discussed. Their relationships to each other are somewhat less clear.

Members of the *agilis* group are small, dark flies with little red color on the abdomen and a short haustellum. The legs of the females of *P. agilis* and *P. mathesoni* are pale, while those of *P. obscura* are dark. The mediotergite is polished or shiny in members of all three species. This is probably the most primitive group of *Ptilodexia*; *P. agilis* members perhaps being similar to those of the prototype of the genus. *Ptilodexia agilis* is a widespread western form, occurring into central Texas; *P. mathesoni*, closely related, is a northern form found in New York, Michigan, and eastern Canada. *Ptilodexia obscura* has a distribution from the Appalachians to the Rocky Mountains and is nearly complimentary to that of *P. agilis*.

Species included in the *carolinensis* group have members with a nonprojecting epistome and a nearly vertical anterior head profile. All adults have relatively short plumosity on the arista and the abdomen reddish laterally. Two of these species, *P. halone* and *P. prexaspes*, have limited east coast distributions. *Ptilodexia canescens* occurs across the northern United States and Canada, while *P. carolinensis* is widely distributed from the east coast to the Rocky Mountains. *Ptilodexia carolinensis* is probably the oldest of the four, *P. canescens*, *P. halone*, and *P. prexaspes* being derived from it during the Pleistocene.

The *harpasa* group is the most ambiguous of all, containing most of the Antillean and many Mexican species. Members of these species all have long antennae and long plumosity on the arista; some lack parafacial hairs. *Ptilodexia rufipennis* occurs from the east coast to the Rocky Mountains and across Canada; *P. harposa* is more restricted, *P. arida* is restricted to the Southwest and Mexico, while *P. ponderosa* is

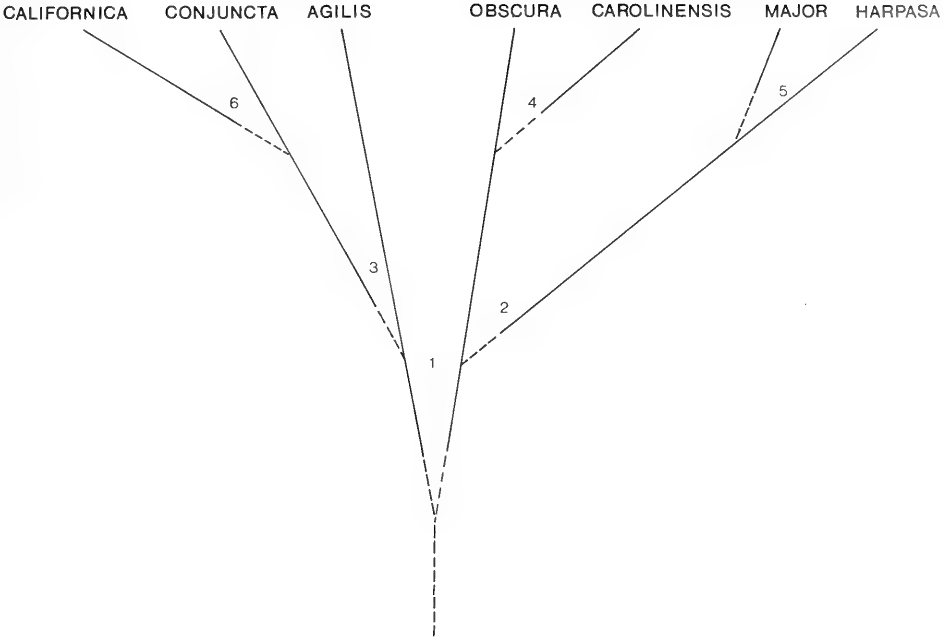


FIGURE 7. Inferred phylogeny of *Ptilodexia* species groups.

probably a West Indian species, with one record from Florida. Assuming that *P. harpasa* is the closest to the ancestor of the group, *P. rufipennis* became the most widespread and *P. arida* and *P. ponderosa* radiated in the southern latitudes.

Ptilodexia major, the most primitive member of the next group shows slight similarities to specimens of *P. harpasa*. It ranges widely throughout the Midwest, Southwest, and Mexico. *Ptilodexia incerta* has an eastern distribution almost exactly complementary to that of *P. major*, while *P. maculata* and *P. flavotessellata* are restricted in the Southwest and Midwest. These species all have members with short, pale, parafacial hairs.

The next group, *conjuncta*, is probably derived directly from the ancestral *agilis* group and consists of only western species. *Ptilodexia conjuncta*, its most primitive member, ranges throughout the Rocky Mountains from Canada into Mexico and west to California. *Ptilodexia planifrons* and *P. contristans* extend from the southwestern United States into Mexico; and *P. westi*, a close relative of *P. contristans*, is restricted to the extreme southern Midwest and the Southwest.

The last, or *californica* group, is related to the *conjuncta* group and probably had a similar origin. Its three species are confined to California and the West Coast, and members of these taxa show similarities only to members of the *conjuncta* group.

A graphic representation of the relationships of these species groups is given in Figure 7. Possible events at the numbered branching points are as follows:

1. Major east-west split. Eastern group members with parafacial hairs extending low on the face; western group members with parafacial hairs high on the face.
2. Widening of face; lighter general color. Some females with yellow legs; lengthening of plumosity on arista. Some advanced members radiating widely; radiation into Mexico and Antilles.
3. Lengthening of haustellum, increase in size, widening of face. Extensive radiation into Mexico.
4. Slight increase in size. Flattening of oral margin and anterior facial margin; shortening of haustellum and plumosity on arista.

5. Shortening of haustellum. Radiation and isolation in southwestern United States and Mexican Pleistocene refugia.
6. Pleistocene isolation in California. Decrease in abundance of parafacial hairs and length of haustellum.

ZOOGEOGRAPHY

Although the dispersal powers of Diptera are relatively great, the distribution patterns seen in *Ptilodexia* seem to be dependent upon those of their hosts, the Scarabaeidae. Distribution of some Scarabaeidae are well known, and their possible histories have been discussed in several papers (Howden 1963; 1966).

All statements made in this section are tentative. The patterns discussed are those of species of *Ptilodexia*, but interpretations of those patterns are those which have been offered for some of the species of Scarabaeidae. No host specificity has been found, and it is only speculation that similar patterns of *Ptilodexia* and their scarabaeid hosts are due to similar histories.

Howden (1966) stated that North American species of *Phyllophaga* show a decline in numbers from Georgia to Canada and from Texas or Arizona to Nebraska. This is true of *Ptilodexia*. He also stated that if certain areas of Texas were included with Arizona and New Mexico, there would be little overlap between the eastern and western faunas (approximate dividing line, 100th meridian). This holds true for the most part in *Ptilodexia*. However, a number of eastern species occur all the way into British Columbia in the northern parts of their ranges. As with *Phyllophaga*, many of the southern Arizona records represent the northern limits of Mexican species.

When plotting the centers of distribution of species of *Ptilodexia*, it was noted that six species groups could be defined geographically. These were the same six groups which had been structurally and zoogeographically defined above. Although these groups show that the phylogeny presented herein has a zoogeographical basis, they are not the best groupings for discussing zoogeography.

I have categorized the species of *Ptilodexia* into six zoogeographical groups, based on their complete distributions rather than centers of distribution. The relationships of these categories may give insight into the historical zoogeography of the group.

The first of these is an extreme northern pattern shown by *P. canescens* and *P. mathesoni*. The distribution is almost exclusively in areas which were previously glaciated. The range of *P. mathesoni* (Fig. 17) is restricted to Michigan, New York, and eastern Canada. Its ancestral and most closely related species, *P. agilis*, occupies a large area from the Rocky Mountains west, extending eastward into Texas (Fig. 12). *Ptilodexia canescens*, from the *carolinensis* group, inhabits the northern United States and Canada from Newfoundland to British Columbia. In the East it extends southward only to the previous front of the Wisconsin glaciation, while in the West it extends southward into eastern Idaho, western Wyoming, and northern Utah (Fig. 67). The distribution of a species in previously glaciated areas without representation south of the glacial front is fairly uncommon (Ross 1965). This deglaciated area may have offered considerable opportunity for expansion to certain Scarabaeidae and their *Ptilodexia* parasitoids.

The next group has a widespread distribution, throughout the eastern United States into the plains states and, in some cases, even further west. Of these species, only *P. harpasa* (Fig. 82) lacks representation in the lower Midwest. The other species, *P. carolinensis* (Fig. 62), *P. incerta* (Fig. 103), *P. obscura* (Fig. 22), and *P. rufipennis* (Fig. 88) occur widely throughout the Midwest and the East.

The remaining eastern distribution pattern is that of *P. halone* and *P. prexaspes*. Both of these species belong to the *carolinensis* group; they are closely related and complementary in distribution. *Ptilodexia prexaspes* occurs in Florida and along the Atlantic coast to Virginia (Fig. 77), while *P. halone* is found in Mississippi, Tennessee, and along the coast from Maryland to New York (Fig. 72). It is possible that these relatively uncommon species are host-specific parasites of some of the large, flightless scarabs found in the Southeast and discussed by Howden (1963).

Two species, *P. agilis* and *P. conjuncta*, have large western ranges, the former from British Columbia to Texas and west to the Pacific coast (Fig. 12), the latter from Mexico to British Columbia, west to the coast (excluding California), and eastward through Canada to Ontario (Fig. 27).

Ptilodexia californica (Fig. 47), *P. pacifica* (Fig. 52), and *P. sabroskyi* (Fig. 57) have ranges which are restricted to the west coast of the United States. It is possible that some unique local populations are parasitic on the large flightless genera of scarabs (such as *Pleocoma*) which survived in situ during the Pleistocene.

The remaining distribution group is the most common in *Ptilodexia,* occurring in at least seven species. This is a southwestern distribution, with species which may have had Mexican refugia. Four of these are Mexican species whose ranges extend northward into the mountainous regions of Arizona and New Mexico, rarely into Utah and Idaho. These four are *P. contristans* (Fig. 37), *P. planifrons* (Fig. 32), *P. maculata* (Fig. 108), and *P. arida* (Fig. 93), all recently differentiated. It is possible that the ranges of many other Nearctic Mexican species also extend into these areas, but specimens have not yet been taken by collectors.

Two of this southwestern group, *P. westi* and *P. flavotessellata,* apparently do not range into Mexico. The former occurs broadly along the international boundary from central Arizona to eastern Texas and into Oklahoma and southern Kansas (Fig. 42), while *P. flavotessellata* occurs in northern New Mexico, Colorado, and Nebraska (Fig. 113).

The last species in the southwestern group is *P. major.* Its distribution is a combination of the ranges of the previous two groups, extending from Mexico (where it is widespread) into the mountains of Arizona, New Mexico, and Colorado and through Texas into the Plains in Nebraska and Kansas (Fig. 98).

Unlike those of *Phyllophaga* (Howden 1966), eastern species of *Ptilodexia* frequently occur from Georgia to southern Ontario; others range broadly across the northern part of the United States and Canada. I see this deviation as a result of the vagility of these flies and the probable capability of developing in different hosts, factors which may account for other deviations from typical scarabaeid distributions.

Inferring the historical zoogeography of *Ptilodexia* is extremely speculative. The genus, as we know it, probably evolved on this continent, its ancestor reaching the area via the Bering Land Bridge during the Tertiary. By the onset of the Pleistocene, most of the species were probably already established. Pleistocene climatic fluctuations must have affected the distribution patterns we see in the genus today.

The eastern species in our fauna may have occupied southeastern Pleistocene refugia, most of them expanding westward in the north after the ice sheets retreated. *Ptilodexia agilis* seems to have been much more widespread at one time, one of the species derived from it being found only in the Northeast. While *P. agilis* may have had a wide refugium, *P. conjuncta* and *P. californica* perhaps survived the Pleistocene in Mexico and California, respectively, separated by the extensive desert barriers of the time. The three species endemic to California were probably separated from the other species at a relatively early time, closely resembling each other considerably more than any other species. Their refugia were in central and southern California, and subsequent recolonization proceeded no further north than the southern limits of the ice sheet. The southwestern groups could have survived the glacial periods in situ or in Mexican refugia. It appears that *P. major* was once a widespread species, extending well into Mexico before the Pleistocene and giving rise to many species there.

The Southwest, including Texas and Arizona, has the largest number of endemics. In the warmer parts of the country such as these, more generations per year are possible, and evolution can proceed at a faster pace than in the north. This may account, in part, for the large number of endemics; it also helps explain the numerous divergent populations seen in California and Texas as well as the tremendous diversity of the genus in Mexico.

Genus **PTILODEXIA** Brauer and Bergenstamm

Ptilodexia Brauer and Bergenstamm, 1889:119 (Type-species, *Ptilodexia carolinensis* Brauer and Bergenstamm, 1889, by original designation.)

Myoceropsis Townsend, 1915:23 (Type-species, *Rhynchiodexia flavotessellata* Walton by original designation.)

Rhamphinina, authors, not Bigot.

Rhynchiodexia, authors, not Bigot.

Rhynchodexia, emend. Wulp, 1891.

The genus *Ptilodexia* Brauer and Bergenstamm is confined to the New World. It is best represented in the Neotropical region, as is the entire tribe Prosenini.

Diagnosis.—Members of *Ptilodexia* can be distinguished from those of all closely related species of Nearctic Prosenini by the following combination of character states: propleuron bare; facial carina sometimes well developed (but never broad, blunt, and separating the antennae); haustellum shorter than the head height; apical cell open or closed at wing margin; and infrasquamal setulae usually present.

Description.—Color black to reddish, usually with thorax dark and abdomen pale with dark longitudinal stripe. *Head* with face broad in profile, anterior margin usually vertical; epistomal margin somewhat projecting; frontal vitta strongly narrowed between eyes, often obliterated; facial tomentum heavy to sparse, dull to shining, color varied, but usually grayish; parafacial hairs varied, absent or present; carina long, not much deeper than width of third antennal segment; postocular setae long; one or two pairs of oral vibrissae; epistome generally projecting to some degree; haustellum rigid, varied, from 0.3 to 0.8 times head height; palpi long. Antennae with length of third segment varied from one to two times length of second; arista with length of plumosity more than length of second antennal segment. *Thorax* with propleuron bare; mesonotum strongly or weakly tomentose, usually indistinctly striped; three or four pairs of presutural and postsutural acrostichals; a tuft of small hairs on postalar wall. *Wing* length 2.5 times width; apical cell open or closed at wing margin; infrasquamal setulae present or absent. *Legs* dark, tibiae lighter in most cases, posterior tarsi very long, 1.5 times length of tibia; claws and pulvilli long. *Abdomen* broad, conical, tomentum usually in large irregular patches; numerous median discal and marginal setae on abdominal tergites; four abdominal tergites visible, lateral margins meeting ventrally. *Genitalia* slightly withdrawn, terminal, axis vertical; cerci and surstyli variously modified. *Female* differs from male in following ways: frontal vitta wide with sides subparallel; eyes widely separated; profrons a little wider; frontal and peristomal setae not as abundant; vertex with few hairs or setae; postocular setae shorter and sparser; height of eyes distinctly less; frontal orbital setae present (Fig. 6). Thorax with fewer setae and hairs and more heavily tomentose; thorax and legs frequently lighter in color with fewer and shorter major setae and hairs; tarsal claws and pulvilli much shorter. Abdomen broader, shorter, and much more heavily tomentose; usually with fewer median discals and often lacking other setae; integumental color uniform brown or gray in many females, even when it is marked in males of the same species.

Brauer and Bergenstamm erected the genus *Ptilodexia* in 1889 for the North American species *P. carolinensis*. There has been much confusion since that time regarding the limits of the genus. This is because several characters normally constant within tachinid genera vary among *Ptilodexia* species. These characters include the presence or absence of parafacial hairs and infrasquamal setulae.

Prior to 1889, Macquart and Walker described species belonging to *Ptilodexia* in the genus *Dexia* Meigen, while Bigot (1885) created the genus *Rhamphinina* for those species he described. Bigot thought that *Rhamphinina*, a neotropical genus, and *Rhynchiodexia*, one of his Australian genera, could be distinguished from one another by the presence or absence of a facial carina. Wulp (1891) considered this to be an inconsistent character.

Wulp (1891) emended the name to *Rhynchodexia*, which he used for what we now call *Ptilodexia*. He felt that *Rhynchodexia* and *Rhamphinina* were congeneric and mistakenly placed one Mexican species, *contristans*, in *Hystrichodexia*.

West (1924; 1925), a North American worker, thought that the species with hairy parafacials belonged to *Ptilodexia* while those with bare parafacials were *Rhynchodexia*. Austen (1907) shared this opinion. Later, West (1950) agreed with Curran (1934) that the two were probably one and *Rhynchodexia* was the proper name for the complex. Reinhard (1943) stated that the name *Ptilodexia* was available for American species.

Examination of species of *Rhynchodexia*, now *Senostoma* (Crosskey 1973a), shows that this genus differs from *Ptilodexia* in having a pronounced facial carina as well as numerous other differences which will be discussed later. *Rhamphinina dubia*, the type-species of the genus, is not a *Ptilodexia*.

The name *Estheria tibialis* Robineau-Desvoidy is frequently used for species of *Ptilodexia* (Townsend 1921; Aldrich 1905; Austen 1907). The type of this species is lost, so we cannot know if *E. tibialis* belongs to *Ptilodexia*. However, since a characteristic of *Estheria* is the presence in its members of a petiolate apical cell, and since this rarely occurs in *Ptilodexia,* I agree with previous workers who have chosen to reject the name *E. tibialis.*

Key to the Nearctic Species of *Ptilodexia*

1a. Parafacial hairs present, although very small and pale in some individuals; legs of females varied in color 2

1b. Parafacial hairs absent; legs of females pale in color 27

2a. Infrasquamal setulae present 5

2b. Infrasquamal setulae absent 3

3a. Parafacial hairs dark, long, present on most of parafacial (Fig. 66); length of plumosity on arista subequal to length of second antennal segment; face with traces or spots of brownish tomentum (northeastern U.S., trans-Canada, northern mountain states) .... *canescens* (Walker)

3b. Parafacial hairs pale and/or short, present only on upper anterior portion of parafacial; length of plumosity on arista at least 1.5 times length of second antennal segment (Fig. 5b); facial tomentum concolorous silvery gray or yellowish 4

4a. Femora of members of both sexes brown or black (eastern U.S. to about 100th meridian) .... *incerta* (West) (in part)

4b. Femora of members of both sexes orange with definite black or brown patches on flexor surfaces, coxae also with dark patches (Arizona and New Mexico) .... *maculata* n.sp.

5a(2a). Flies pale colored; thorax, abdomen, and femora pale brown to orange, or width of depression between oral vibrissae less than distance between oral vibrissae and oral margin (Fig. 4a) 6

5b. Flies dark; thorax, abdomen, or legs brown or darker in color; width of depression between oral vibrissae equal to or greater than distance between oral vibrissae and oral margin (Fig. 4b) ... 10

6a. Integument of tarsi pale, concolorous with legs ventrally .... *halone* (Walker)

6b. Integument of tarsi brown or black 7

7a. Width of the depression between oral vibrissae greater than distance from vibrissae to oral margin 8

7b. Width of depression between oral vibrissae less than or equal to distance from vibrissae to oral margin (Fig. 4a) .... *prexaspes* (Walker)

8a. Parafacial hairs minute, confined to upper anterior parafacial; haustellum length 0.6 times head height (Fig. 6) (southern Florida) .... *ponderosa* (Curran)

8b. Parafacial hairs long, scattered on parafacial; haustellum length no more than 0.5 times head height (southwestern U.S. and Texas) 9

9a. Parafacial hairs dark, coarse and abundant (Fig. 61); femora or notum brown in many individuals; this color form uncommon (Texas) .... *carolinensis* Bauer and Bergenstamm (in part)

9b. Parafacial hairs pale or light brown, fine, sparse (Fig. 112); femora and notum pale orange-brown (southwestern U.S. into Colorado and Nebraska) .... *flavotessellata* (Walton)

10a(5b). Mediotergite polished immediately beneath postscutellum; parafacial hairs distant from eye; haustellum 0.5 times head height or less (Fig. 11); legs of females yellow; species with members small, dark 11

10b. Mediotergite with at least a fine dusting of tomentum; parafacial hairs and haustellum varied 12

11a. Abdomen and thorax black, strongly shining; abdomen with tomentum evenly distributed; parafacial hairs black, coarse (Fig. 16); squamae of males dark brown (northcentral and eastern U.S.) .... *mathesoni* (Curran)

11b. Abdomen with tomentum in large irregular patches; thorax with definite tomentose striping; parafacial hairs black, fine (Fig. 11); squamae of males white to pale brown (western U.S. and Texas) .... *agilis* Reinhard (in part)

12a(10b). Length of plumosity on arista less than or equal to 1.25 times length of second antennal segment (southwestern U.S. and Mexico) 13

12b. Length of plumosity on arista more than 1.25 times length of second antennal segment (widespread) 15

13a. Abdomen and scutellum concolorous dark gray or brown, slightly lighter on ventral margins of tergites in a few individuals; ninth tergite and parafacial hairs varied; haustellum length 0.7 to 0.8 times head height (Fig. 31) 14

13b. Abdomen and scutellum distinctly reddish laterally; ninth tergite with several strong setae (Fig. 33); parafacial hairs long, dark, occurring along parafacial ventrally to level of oral vibrissae; haustellum length 0.6 times head height (Fig. 36) .... *contristans* (Wulp)

14a. Parafacial hairs long, coarse, numerous, occurring on entire parafacial (Fig. 31) (Arizona, New Mexico into Mexico) .... *planifrons* (Wulp)

14b. Parafacial hairs fine, sparse, occurring only on anterior parafacial (Fig. 41) (Texas, Oklahoma, Kansas) .... *westi* n.sp. (in part)

15a(12b). Parafacial hairs short, pale or otherwise inconspicuous 16

15b. Parafacial hairs long, dark, although sparsely placed in some individuals 20

16a. Mediotergite polished; legs of females yellowish; haustellum length no more than 0.5 times head height (Fig. 11); scutellum concolorous with rest of notum .... *agilis* Reinhard (in part)

16b. Mediotergite tomentose to subshining; legs of females dark; haustellum length varied; scutellum lighter in color than rest of notum in most individuals 17

17a. Parafacial hairs pale and, in most individuals, small (Fig. 97) (west only to Arizona and Rocky Mountains) 18

17b. Parafacial hairs light brown to black, short or medium in length (Pacific coast states) 19

18a. Infrasquamal setulae absent or greatly reduced in number in most individuals; parafacial hairs only on upper anterior parafacial (Fig. 102); length of palpi equal to or slightly less than half length of haustellum, broadened at tip (central and eastern U.S.) .... *incerta* (West) (in part)

18b. Infrasquamal setulae present in most individuals; parafacial hairs extending ventrally on face to level of apex of antennae (Fig. 97); length of palpi greater than half length of haustellum, narrow (southwestern U.S. into Texas) .... *major* (Bigot)

19a(17b). Third antennal segment subequal to or shorter than second segment; smallest distance between eyes of male subequal to width of frontal vitta at antennal base; female with parafacial hairs confined to area near antennae; facial tomentum dull (southern California) .... *sabroskyi* n.sp.

19b. Third antennal segment longer than second segment; smallest distance between eyes of male less than width of frontal vitta at base of antennae; females with parafacial hairs scattered, often along center of parafacial; facial tomentum shining (throughout California) .... *californica* n.sp.

20a. Haustellum length greater than 0.6 times head height, thin, narrowed apically 21

20b. Haustellum length less than or equal to 0.6 times head height, broad and linear in most individuals 24

21a. Length of plumosity on arista more than twice length of second antennal segment; haustellum length 0.65 to 0.7 times head height, narrow (Fig. 81) (northern and eastern U.S.) .... *harpasa* (Walker)

21b. Length of plumosity on arista less than or equal to twice length of second antennal segment; haustellum length varied (western U.S.) 22

22a. Parafacial hairs long, dark, and abundant, uniformly covering parafacial (Fig. 26); haustellum length 0.6 to 0.8 times head height, narrowed apically in most individuals; abdomen reddish laterally .... *conjuncta* (Wulp)

22b. Parafacial hairs sparse (Fig. 41); haustellum length and abdomen varied 23

23a. Length of haustellum more than 0.7 times head height, strongly narrowed apically; parafacial hairs sparse, located only on anterior portion of parafacial (Fig. 41); male abdomen dark brown or gray with little if any reddish color; ninth tergite with several strong setae (Fig. 38) (Texas and Oklahoma) .... *westi* n.sp. (in part)

23b. Length of haustellum less than 0.65 times head height, broad; not narrowed apically in most individuals; parafacial hairs occurring along center of parafacial (Fig. 46); male abdomen distinctly reddish with longitudinal stripe; ninth tergite with hairs only (Pacific coast states) .... *californica* n.sp. (in part)

24a(20b). Abdomen blackish with little if any orange coloration laterally; parafacial hairs inserted close to anterior margin of eye in most individuals; palpi very short, less than half length of haustellum (Fig. 21); wings of many males basally darkened .... *obscura* West

24b. Abdomen, especially of male, with at least some red or orange coloration laterally; parafacial hairs not inserted close to anterior eye margin in most individuals; palpi longer than half length of haustellum (Fig. 51); wings of males not basally darkened 25

25a. Femora of members of both sexes orange or marked with orange; abdominal tomentum concolorous (California)...... .... *pacifica* n.sp.

25b. Femora of members of both sexes brown or black (some specimens from Texas may have orange femora); abdominal tomentum bicolored (widespread) 26

26a. Epistomal angle of head not prominent (Fig. 61); females with 6 to 8 dorsal and lateral marginal setae on abdominal segment III; males with 1 pair of dorsal marginal setae on abdominal segment II; haustellum length 0.4 to 0.5 times head height (central and eastern U.S.) .... *carolinensis* Brauer and Bergenstamm (in part)

26b. Epistomal angle of head prominent (Fig. 46); females with 10 to 12 dorsal and lateral marginal setae on abdominal segment III; most males with 2 pairs of dorsal marginal setae on abdominal segment II; haustellum length 0.5 to 0.65 times head height (western U.S.) .... *californica* n.sp. (in part)

27a(1b). Abdomen without any reddish or orange coloration laterally in most males; tip of abdomen and genitalia generally reddish yellow; facial tomentum strongly shining; length of plumosity on arista more than twice length of second antennal segment; face appearing narrow (Fig. 87); infrasquamal setulae absent in many individuals; femora of many males yellow (central and eastern U.S. into New Mexico and British Columbia) .... *rufipennis* (Macquart)

27b. Abdomen orange laterally in most males; tip of abdomen not noticeably lighter than rest of abdomen; facial tomentum rather dull; length of plumosity on arista at most equal to twice length of second antennal segment; face appearing broad (Fig. 92); infrasquamal setulae present; femora of males dark (Utah and southern Idaho south into Mexico) *arida* (Curran)

The Nearctic Species of *Ptilodexia*

agilis Group

Ptilodexia agilis Reinhard

(Figures 8–12)

Ptilodexia agilis REINHARD, 1943:22. SABROSKY AND ARNAUD (1965:988). [HOLOTYPE, male, deposited in CNCI, labeled, College Station, Texas, 8 Oct. 1933, H. J. Reinhard.]

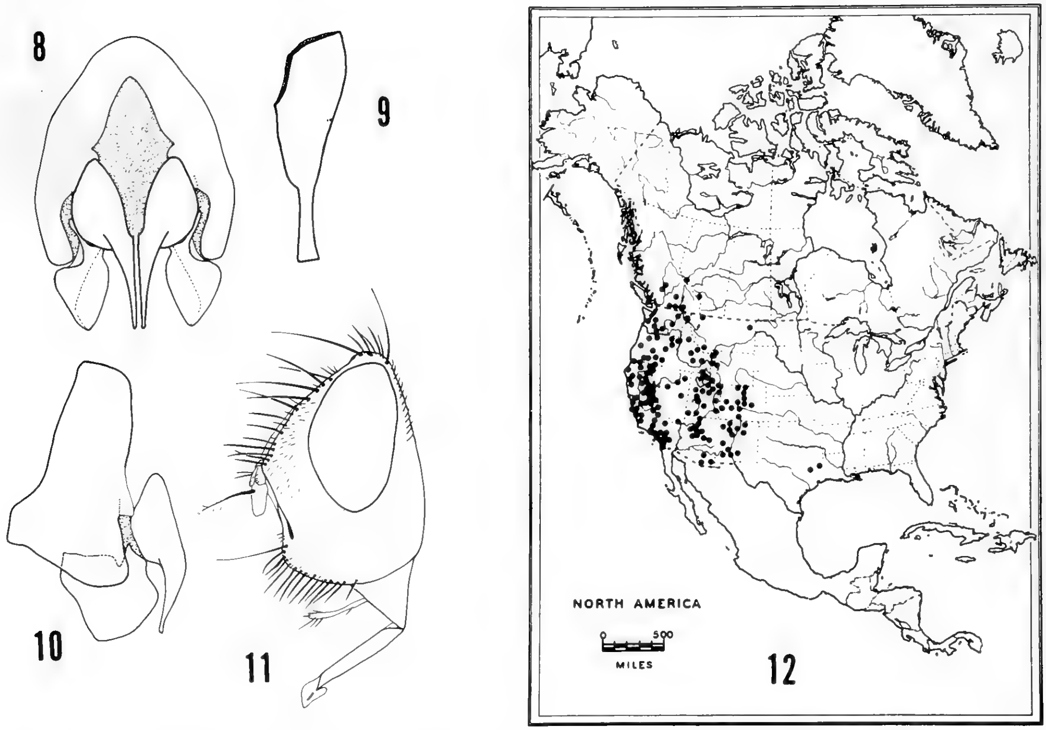
TAXONOMIC NOTES.—Although I have not seen the holotype of *P. agilis*, members of this species are quite distinctive, and the original description is adequate to assure the identity of the specimens examined. Even though *P. agilis* was described from a disjunct population, the type-specimens are typical of the species. Type material is reported to be in excellent condition.

DIAGNOSIS.—*Ptilodexia agilis* is a distinct species, members of which can be separated from their congeners by the following character states: size small; parafacial hairs fine, medium in length, inserted below apex of antennae or less than 0.25 mm from anterior margin of eye in only a few individuals; haustellum less than half head height; length of plumosity on the arista 1.5 to 2.0 times length of second antennal segment; mediotergite polished; abdomen and scutellum entirely blackish; female with legs pale colored.

MATERIAL EXAMINED.—Specimens examined include 812 males and 488 females, data as listed by Wilder (1976).

DISTRIBUTION.—*Ptilodexia agilis* ranges from Arizona and New Mexico north through California, the Great Basin, and the Rocky Mountains into Alberta and British Columbia. There are a few records from eastern Texas, where the topotypic population is found.

BIOLOGICAL NOTES.—The flight period lasts from April to October, and adults can be col-



FIGURES 8–12. *Ptilodexia agilis* Reinhard. Fig. 8. Genitalia of male, posterior view. Fig. 9. Ejaculatory apodeme. Fig. 10. Genitalia of male, lateral view. Fig. 11. Head of male, lateral view. Fig. 12. Distribution of *P. agilis*.

lected at any time during this period. July and August are the most frequent months of collection, but local variation is common. In California, for example, *P. agilis* adults are collected more frequently in September and October along the coast and in the south; but in the Sierra, northern California, and Oregon, June and July are the main periods of activity.

This species inhabits both mountains and lowlands. Adults have been collected at elevations up to 2,600 m in Arizona, 3,800 m in California, above the 3,000-m level in Colorado, and frequently above 3,000 m elsewhere. *Ptilodexia agilis* adults have frequently been taken at low elevations in such areas as the San Joaquin Valley, the Great Basin, and eastern Texas. Specimens have been collected by UV light trap, Malaise trap, wind vane trap, and by sweeping foliage.

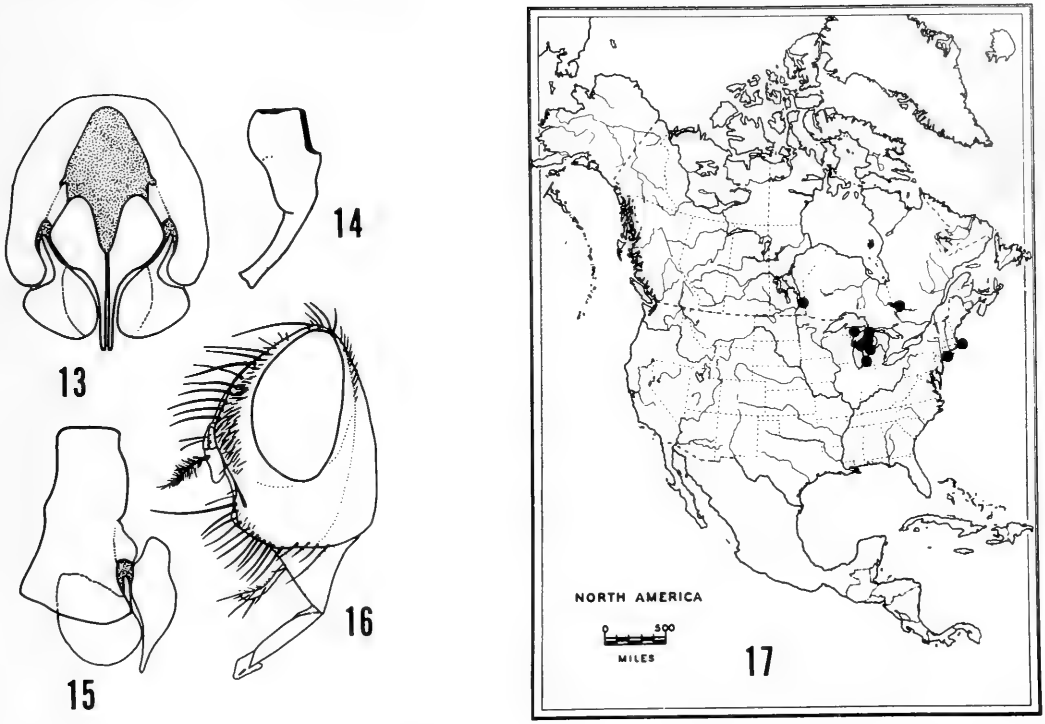
Flowers visited include the Compositae *Achillea Millefolium*, *Chrysothamnus viscidiflorus*, *Baccharis glutinosa*, *B. pilularis*, *Eriogonum nudum*, *Solidago trinervata*, and *Lepidospartum squamatum*. Unidentified Compositae visited were *Achillea* sp., *Baccharis* sp., *Solidago* sp., *Eriogonum* sp., and *Haplopappus* sp. Other flowers from which *P. agilis* adults have been collected are *Allium* (Liliaceae) and *Salix* (Salicaceae). At two localities in Colorado, specimens were collected on Dwarf Mistletoe (*Arceuthobium cyanocarpum*); and members of this species are believed to be pollinators of that plant. One specimen was collected in an emergence trap under a filbert tree in Oregon.

There are no data on the life history of this insect. Its members are probably not host specific, judging from the diverse assortment of habitats and wide geographical and temporal ranges of the species.

Ptilodexia mathesoni (Curran)

(Figures 13–17)

Rhynchiodexia mathesoni CURRAN, 1931:93. WEST (1950:110); SABROSKY AND ARNAUD (1965:989). [LECTOTYPE (here designated), male, deposited in CUIC, labeled, "Douglas Lake, Mich., 24–VII–22"/"Wing Slide, Cornell U., Lot. 919, Sub. 138, L. S. West"/"♂ Holotype *Rhynchiodexia mathesoni*



FIGURES 13–17. *Ptilodexia mathesoni* (Curran). Fig. 13. Genitalia of male, posterior view. Fig. 14. Ejaculatory apodeme. Fig. 15. Genitalia of male, lateral view. Fig. 16. Head of male, lateral view. Fig. 17. Distribution of *P. mathesoni*.

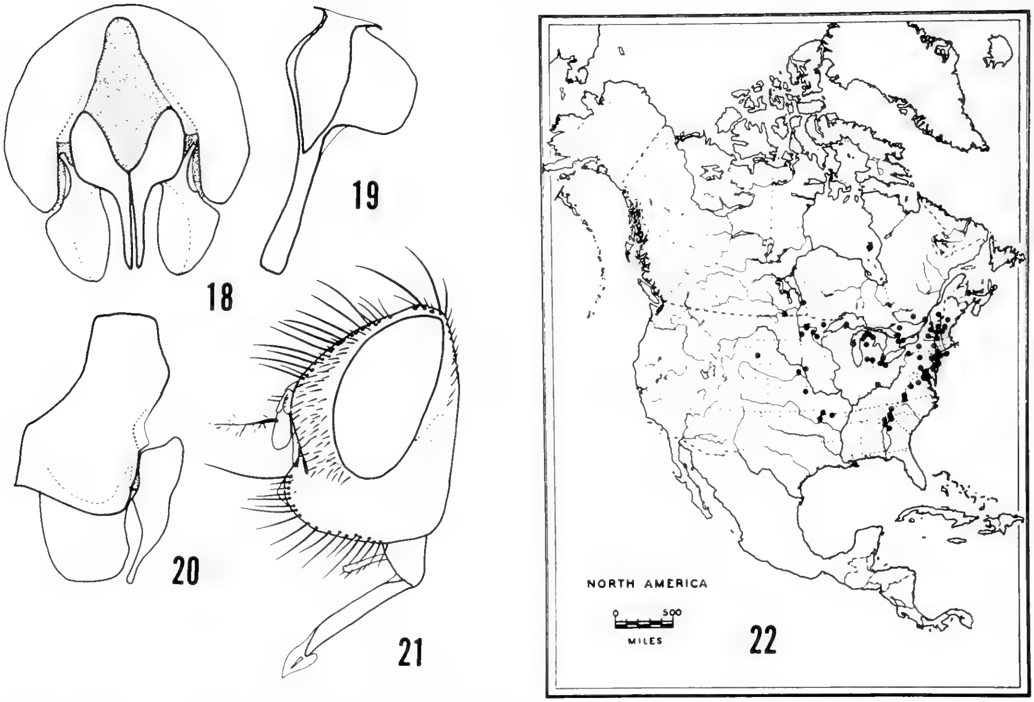
Curran"/"Holotype Cornell U. No. 1938"/"Cornell U. Lot. 922, Sub. 40"/"Lectotype *Rhynchiodexia mathesoni* Curran designated by D. Wilder, 1976."]

TAXONOMIC NOTES.—Even though the label on the type-specimen reads "Holotype *Rhynchiodexia mathesoni* Curran," this specimen is *not* a holotype. The author of the paper validating the species made no mention of type material or of type-locality. The type label with Curran as author was put on the specimen at a later date; it was West's "holotype," not Curran's. The name *P. mathesoni* was proposed by West and validated by Curran in his 1931 key. I have designated West's "holotype" as the lectotype. It is a large specimen in excellent condition.

There is one other specimen which I believe Curran had before him while writing his key. This specimen, also from Douglas Lake, Michigan, is deposited in AMNH and was collected on the same date as the specimen West labeled as holotype. I have designated this specimen as a paralectotype. It might be argued that this second specimen, because it is labeled with Curran as the author, was later sent to AMNH and not seen by Curran. However, the type labels of all five of the species validated in Curran's key give Curran as the author. I believe that all these labels were changed at a later date, and since Curran makes no mention of material, I feel that these two identically labeled specimens are actually syntypes.

DIAGNOSIS.—*Ptilodexia mathesoni* is a distinctive species, evidenced by the following combination of character states: body color black, shining; parafacial hairs long, black, inserted ventral to apex of antennae or less than 0.25 mm from anterior margin of eye in only a few individuals; haustellum less than half head height in length; width of arista and plumosity 1.5 to 2 times length of second antennal segment; mediotergite polished; wings dark in color; male abdomen with pollen evenly distributed; female with pale-colored legs.

MATERIAL EXAMINED.—Twenty-one males and eleven females were examined.



FIGURES 18–22. *Ptilodexia obscura* West. Fig. 18. Genitalia of male, posterior view. Fig. 19. Ejaculatory apodeme. Fig. 20. Genitalia of male, lateral view. Fig. 21. Head of male, lateral view. Fig. 22. Geographical distribution.

DISTRIBUTION.—The species, although records are few, seems to range through the northeastern United States and eastern Canada. There is one record from Victoria Beach, Manitoba.

BIOLOGICAL NOTES.—The flight period is from April to October with the main period of activity between mid-June and mid-August. All records for months other than July and August are from Suffolk County, New York.

There are no life-history data for *P. mathesoni*. One male was collected on *Solidago canadensis*.

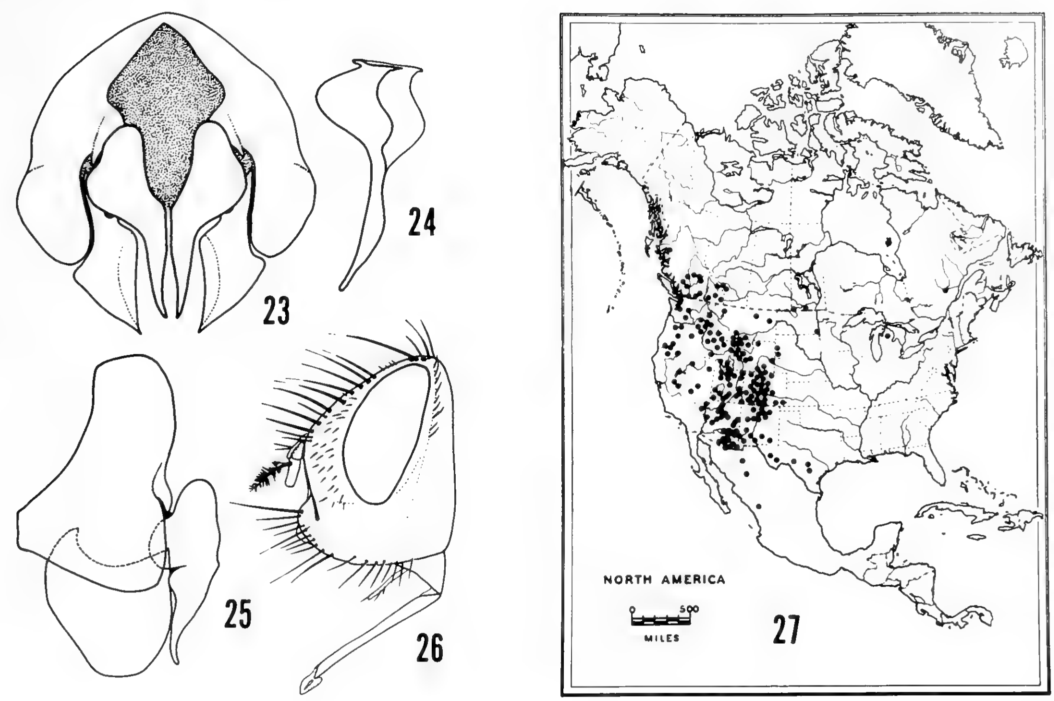
Ptilodexia obscura West

(Figures 18–22)

Ptilodexia obscura WEST, 1925:133. LEONARD (1928:822); CURRAN (1930:93); SABROSKY AND ARNAUD (1965:989). [HOLOTYPE, female, deposited in SIIS, labeled, "Wading River, L.I., June 29, 1917, W. T. Davis."]

TAXONOMIC NOTES.—West described *P. obscura* from three female specimens, one of which he designated holotype. The two paratypes are so labeled and are deposited in CUIC. They closely resemble the holotype. There is a male specimen from Victoria Beach, Manitoba, deposited in AMNH, which bears a handwritten label reading, "*R. obscura* West." It appears that West recognized the male of the species at a later time, even though this particular male specimen differs considerably from the female type-series. West still used the generic name *Ptilodexia* for *obscura* in 1950, but because his concept of the genus changed, it is possible that he might have written "*R. obscura*" instead of "*P. obscura*." It is doubtful that Curran labeled the specimen or ever looked at West's types, since in his 1931 key, he describes *P. obscura* specimens as being over 12.5 mm long.

DIAGNOSIS.—*Ptilodexia obscura* is a fairly distinctive species. Its members may be separated from their congeners by the following combination of character states: face narrow, with parafacial hairs abundant, long, fine, dark, and inserted below lower edge of eye and close to its anterior edge; third antennal segment dark in most specimens, broadened apically; length of plumosity on arista 1.5 times length of second



FIGURES 23–27. *Ptilodexia conjuncta* (Wulp). Fig. 23. Genitalia of male, posterior view. Fig. 24. Ejaculatory apodeme. Fig. 25. Genitalia of male, lateral view. Fig. 26. Head of male, lateral view. Fig. 27. Geographical distribution.

segment; haustellum broad, length 0.55 to 0.6 times head height; palpi short, half haustellum length or less; notum covered with short, appressed, grayish pollen, giving it a smooth, subshining appearance; legs of females brown; abdominal color, grossly appearing black, but actually rufescent laterally.

MATERIAL EXAMINED.—One hundred forty-two males and 53 females of *P. obscura* were examined.

DISTRIBUTION.—The range of *P. obscura* extends from New Brunswick south into the Georgia Appalachians west into Arkansas, eastern Kansas and Nebraska, western South Dakota and Saskatchewan, and Manitoba.

BIOLOGICAL NOTES.—The flight period lasts from April to September with June and July the most common months of collection, a later average seen only in Manitoba. Most specimens have been collected at low elevations, the exceptions coming from 800–1,700 m in the Appalachians in Tennessee, North Carolina, and Virginia.

Collecting methods yielding specimens of *P. obscura* include sweeping and Malaise trap. Specimens have been collected on the flowers of *Solidago canadensis* (Compositae), and *Aruncus* sp. and *Spiraea latifolia*, both Rosaceae.

conjuncta Group

Ptilodexia conjuncta (Wulp)

(Figures 23–27)

Rhynchodexia conjuncta WULP, 1891:228. ALDRICH (1905:499); GUIMARAES (1971:33). [LECTOTYPE (here designated), male, deposited in BMNH, labeled "Lectotype"/"♂"/"B.C.A. Dipt. II, *Rhynchodexia conjuncta* v.d.W."/"Central America. Pres. by F. D. Godman. O. Salvin. 1903–172"/"Ciudad, Mex., 8100 ft., Forrer"/"Lectotype *Rhynchodexia conjuncta* Wulp designated by D. Wilder, 1975."]

Rhynchodexia simulans WULP, 1891:229. ALDRICH (1905:499); GUIMARAES (1971:34). [LECTOTYPE (here designated), male, deposited in BMNH, labeled, "Lectotype"/"N. Sonora, Mexico. Morrison"/"♂"/"B. C. A. Dipt. II, *Rhynchodexia simulans*, v.d.W."/"Central America, pres. by F. D. Godman, O. Salvin. 1903–172"/"Lectotype *Rhynchodexia simulans* Wulp, designated by D. Wilder, 1975."] NEW SYNONYMY

Ptilodexia tibialis (partim): ALDRICH (1905:504).

TAXONOMIC NOTES.—Wulp described *P. conjuncta* from two male cotypes, one of which I have designated as lectotype. This specimen is in good condition except for a few broken setae.

Wulp described *P. simulans* and *P. conjuncta* in the same paper. The cotype (one of two) which I saw and designated lectotype is in good condition, although it has the dorsal setae and abdomen broken.

Wulp realized that *P. conjuncta* and *P. simulans* were very closely related. He separated members of each on the basis of size, curvature of the hind tibia, and some other minor characters. Size, of course, cannot be used effectively to separate these parasitic flies. A curved hind tibia is a character state which occurs frequently in members of many species of *Ptilodexia*, especially in those of *P. conjuncta*, where it constitutes part of normal intraspecific variation.

DIAGNOSIS.—*Ptilodexia conjuncta* is a variable species. Its members can be distinguished by the following: face wide; parafacial hairs long, fine, dark, abundant, inserted below level of lower edge of eye in some specimens and at least 0.12 mm from anterior edge of eye in all but a few specimens; haustellum long, ranging from 0.6 to 0.8 times head height, slender, narrowed apically in most specimens; carina fairly well developed; width of arista and plumosity 1.5 to 2 times length of second antennal segment; oral margin distinctly protruding; scutellum and sides of abdomen reddish.

MATERIAL EXAMINED.—Specimens examined included 1,238 males and 629 females.

DISTRIBUTION.—This species ranges from British Columbia and Alberta south through the Rocky Mountains into Mexico. There are scattered records from the plains states, the Great Basin, California, and Oregon. There are a few doubtful records from the eastern United States.

BIOLOGICAL NOTES.—The flight period ranges from February to October. Most of the activity occurs in July and August, earlier in the northern areas and later further south. In Arizona (and possibly Texas), *P. conjuncta* appears to have two broods, one in March and April, and another in August and September.

Ptilodexia conjuncta adults are generally found in mountainous areas at altitudes from 1,500 to 2,750 m and in some areas up to 3,660 m. They are also, although less commonly, collected at low elevations in coastal as well as inland areas. Label data indicate that they have been collected in meadow sweeps, in a meadow in spruce-fir zone (2,750 m), in pine-spruce-aspen zone, and above timberline. Productive collecting methods for *P. conjuncta* specimens are UV light and Malaise trap.

Specimens of *P. conjuncta* have been collected from many flowers. These include: *Senecio salignus, Heliopsis parvifolia, Cacalia decomposita, Encelia farinosa, Geraea canescens, Chrysothamnus greeni, Achillea Millefolium;* and unidentified species of *Encelia* sp., *Gutierrezia* sp., *Solidago* sp., *Baccharis* sp., *Helianthus* sp., *Senecio* sp., *Eriogonum* sp., *Achillea* sp., *Bigelovia* sp., *Aster* sp., and *Rudbeckia* sp. (all Compositae). Other flowers visited include, *Ceanothus fendleri* and unidentified *Ceanothus* sp. (Rhamnaceae); *Arctostaphylos* sp. (Ericaceae); *Melilotus* sp., and *Dalea* sp. (Fabaceae); *Lippia wrightii* (Verbenaceae); and *Arceuthobium* sp. (Loranthaceae). *Ptilodexia conjuncta* adults, along with those of *P. agilis,* have been observed pollinating Dwarf Mistletoe (*Arceuthobium cyanocarpum*).

Ptilodexia planifrons (Wulp)

(Figures 28–32)

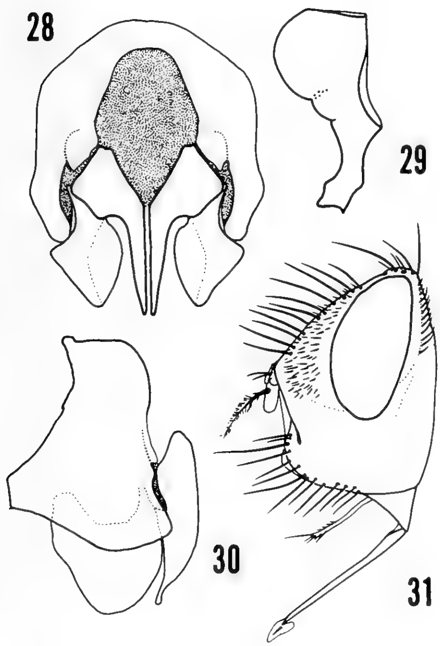
Rhynchodexia planifrons WULP, 1891:234. ALDRICH (1905:499); GUIMARAES (1971:33). [HOLOTYPE, male, deposited in BMNH, labeled, "Holotype"/"Ciudad, Mexico, 8100 ft., Forrer"/"♂"/"B. C. A. Dipt. II, *Rhynchodexia planifrons*, v.d.W"/"Central America pres. by F. D. Godman, O. Salvin. 1903–172."]

Dexia harpasa (partim): ALDRICH (1925:114). (Misidentification).

TAXONOMIC NOTES.—The holotype of this species, deposited in BMNH, is in poor condition, but is still recognizable. The facial band is obscured, the tibiae are quite light and distinctly curved (a frequently encountered anomaly in species of *Ptilodexia*), and the striping on the notum is more distinct.

Labels on the specimen say only "Ciudad, Mexico, 8100 ft.," but in the description, the origin of this specimen is stated as "Ciudad in Durango, 8100 ft." I follow Wulp's original publication in calling Durango the type-locality.

DIAGNOSIS.—*Ptilodexia planifrons* is a distinctive species and its members can be identified by the following character combination: face wide; presence of a contrasting tomentose diagonal band extending from antennal base to eye margin; parafacial hairs dark, coarse, abundant, inserted lower than level of oral vibrissae only in a few specimens; antenna with plumosity



FIGURES 28–32. *Ptilodexia planifrons* (Wulp). Fig. 28. Genitalia of male, posterior view. Fig. 29. Ejaculatory apodeme. Fig. 30. Genitalia of male, lateral view. Fig. 31. Head of male, lateral view. Fig. 32. Geographical distribution.

on arista less than or equal to length of second antennal segment; carina long, slightly keeled and prominent; two pairs of oral vibrissae in most specimens; frontal vitta very wide at antennal base; haustellum long, 0.7 to 0.85 times head height, narrowed apically; scutellum and abdomen entirely dark gray or black.

MATERIAL EXAMINED.—One hundred seventy-three males and 70 females of *P. planifrons* were examined.

DISTRIBUTION.—This species ranges from Flagstaff south through the mountains of central and southeastern Arizona, through the central mountainous region of New Mexico, the western tip of Texas, and south into Durango, Mexico. There is one record from Colorado; however, no exact locality is given.

BIOLOGICAL NOTES.—The flight period lasts from August through October, with the majority of records from mid-August to mid-September. The earliest seasonal record is one specimen collected on 27 June (error?) from El Paso, Texas, in 1921, and the latest is a series of 24 females collected on 22 October 1964, in Cochise County, Arizona.

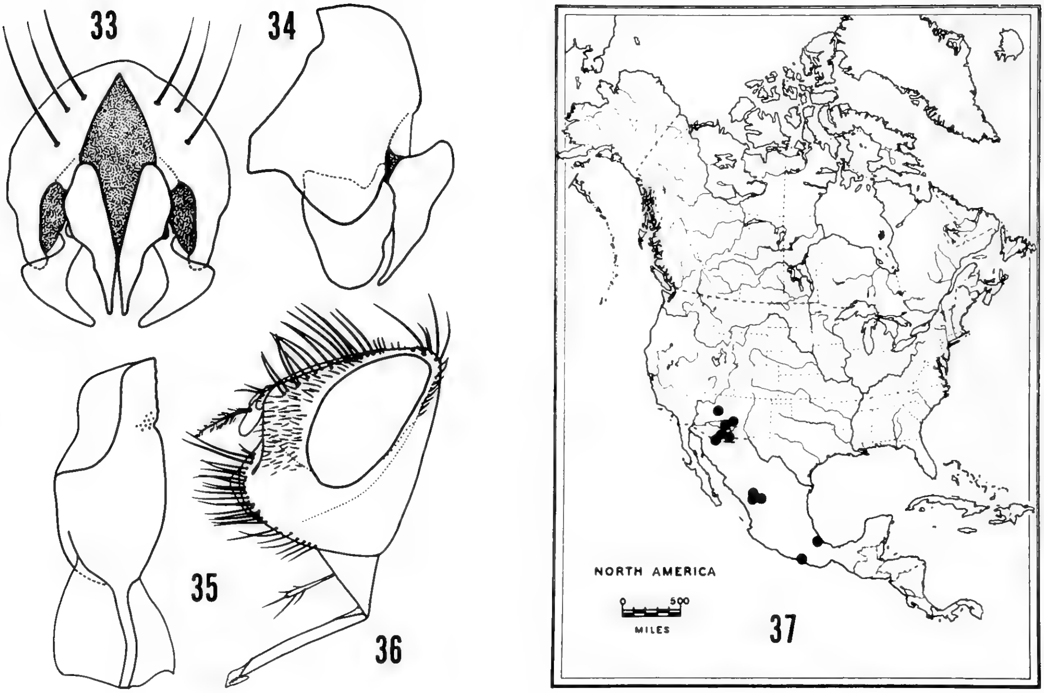
Ptilodexia planifrons adults generally occur in the mountains and have been collected at many elevations between 1,370 and 3,350 m. Flowers visited include *Gutierrezia sarothrae* (1,800–2,440 m, Apache County, Arizona), *Heliopsis parvifolia* (2,590 m, Chiricahua Mts., Cochise County, Arizona), *Solidago trinervata* (Sierra Madre, 2,230 m), and *Rudbeckia* sp. in Chihuahua, all Compositae. All except two of the flower-visiting flies were males (one female collected on *Heliopsis* sp. and another at *Rudbeckia* sp.). One specimen was collected at a light.

Ptilodexia contristans (Wulp)

(Figures 33–37)

Hystrichodexia contristans WULP, 1891:221. [HOLOTYPE, male, deposited in BMNH, labeled, "Holotype"/"Omilteme, Guerrero, 8000 ft., July, H. H. Smith"/"♂"/"B. C. A. Dipt. II., *Hystrichodexia contristans*, v.d.W."/"Central America, Pres. by F. Godman, O. Salvin. 1903–172."]

Rhynchodexia punctipennis WULP, 1891:233. ALDRICH (1905:499); GUIMARAES (1971:33). [LECTOTYPE (here designated), male, deposited in BMNH, labeled, "Cotype"/"Sierra de las Aguas Escondidas, Guerrero, 9500 ft., July. H. H. Smith"/"♂"/"B. C. A. Dipt. II. *Rhynchodexia punctipennis*, v.d.W."/"Central America. Pres. by F. D. Godman, O. Salvin. 1903–172"/"Lectotype *Rhynchodexia*



FIGURES 33–37. *Ptilodexia contristans* (Wulp). Fig. 33. Genitalia of male, posterior view. Fig. 34. Genitalia of male, lateral view. Fig. 35. Ejaculatory apodeme. Fig. 36. Head of male, lateral view. Fig. 37. Geographical distribution.

punctipennis Wulp designated by D. Wilder 1975.''] NEW SYNONYMY.

Ptilodexia constrictans (Wulp): GUIMARAES (1971:33) [*lapsus calamus*].

TAXONOMIC NOTES.—The holotype of this species is in fair condition except for a broken thorax and an abdomen which is oily, obscuring the tomentum patterns.

Wulp described *Rhynchodexia punctipennis* and *Hystrichodexia contristans* in the same paper. He felt that the two genera differed by two superficial characters, the general body shape and the hairs of the abdomen. The lectotype of *P. punctipennis,* although in poor condition is certainly a teneral specimen of *P. contristans.*

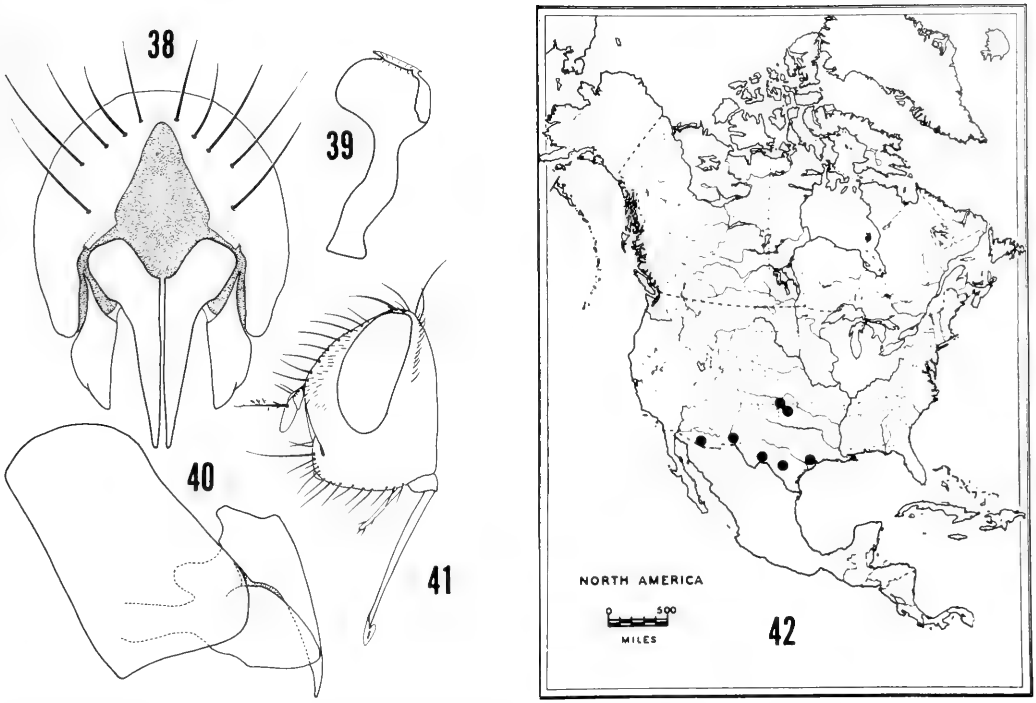
DIAGNOSIS.—Specimens of *P. contristans* can be separated from those of related species by the following combination of characters: face very wide; parafacial hairs long, dark, abundant, occurring to, and in most specimens, also below level of lower eye margin; third antennal segment broadened apically in some individuals; plumosity on arista short, its width subequal to length of second antennal segment; carina short but well developed; haustellum narrow, equal to 0.6 times head height; oral margin strongly protruding; scutellum and sides of abdomen reddish laterally, wing base distinctly darkened; ninth tergite with several strong setae.

MATERIAL EXAMINED.—Ninety-one males and 20 females were examined.

DISTRIBUTION.—This species ranges from the central and southeastern mountains of Arizona southward into the mountains in Durango, Veracruz, and Guerrero. There is one record from New Mexico.

BIOLOGICAL NOTES.—The flight period is from mid-August to early September, with a few scattered records in July. The holotype was collected in July.

All specimens were collected in mountainous areas. The lowest elevation indicated on labels is 2,130 m, in Veracruz, the highest, 2,900 m, in Guerrero. Specimens have been collected on the following Compositae: *Heliopsis parvifolia, Cacalia decomposita, Verbesina encelioides, He-*



FIGURES 38–42. *Ptilodexia westi,* n.sp. Fig. 38. Genitalia of male, posterior view. Fig. 39. Ejaculatory apodeme. Fig. 40. Genitalia of male, lateral view. Fig. 41. Head of male, lateral view. Fig. 42. Geographical distribution.

lenium hoopesii, and unidentified *Senecio* sp., *Cirsium* sp., and *Solidago* sp. There are no associated host data.

Ptilodexia westi, new species

(Figures 38–42)

TYPE-LOCALITY.—The holotype was collected at Imperial, Texas, 10 April 1954 by L. D. Beamer.

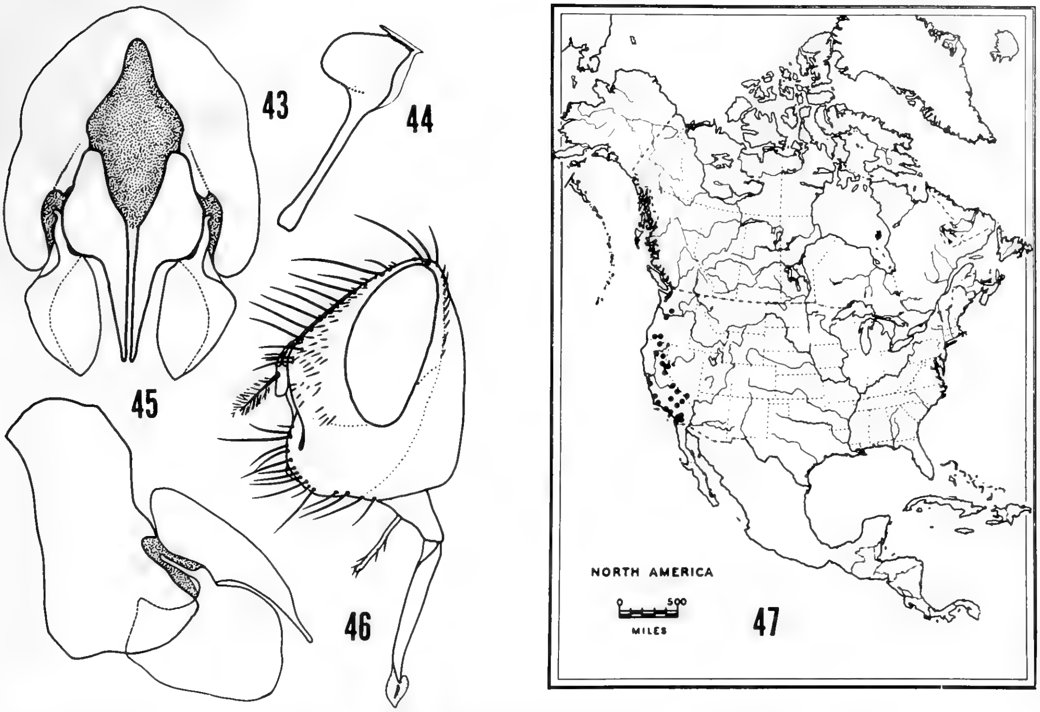
TYPE-SPECIMENS.—The male holotype is deposited in CNCI, the allotype, from Las Cruces, New Mexico, in USNM. Complete data from these specimens and the 21 paratypes are listed below.

DIAGNOSIS.—This is a distinctive species, its members easily separable from those of other species in the genus by the following combination of character states: face wide, tomentum grayish, very heavy; parafacial hairs from short to medium in length, occurring only on anterior half of parafacial, below apex of antennae in a few individuals; length of haustellum 0.7 to 0.8 times head height, narrowed apically, length of plumosity on arista varied, from 1 to 1.25 times length of second antennal segment; abdomen heavily tomentose, in males integument dark gray with no median stripe, in females brown or rufous; ninth tergite of males with several strong setae; genitalia unlike those of adults of any other species.

DESCRIPTION.—**Male:** Total body length 10.5 mm, grayish. *Head* height 2.6 mm; profrons 0.25 of head length. Facial tomentum very heavy, dull, grayish white, obscuring integumental color; parafrontal hairs long, sparse, dark; parafacial hairs medium in length, dark, rather sparse, located along anterior half of parafacial ventrally to slightly beyond apex of antennae. Width of frontal vitta at antennal base 0.4 mm, at narrowest part, 0.1 mm; carina strongly developed, slightly keeled, broad, not depressed below apex of antennae; facial cavities strongly darkened. Height of gena 0.25 times head height. One pair of strong ocellar setae, one pair of smaller postocellars and postverticals; one pair of strong and one pair of weak inner verticals; outer verticals subequal to postorbitals. Fifteen pairs of medium-length postorbital setae, some a little shorter than others; ventral to postorbitals is an irregular row of dark hairs merging into dense whitish occipital hair. Seven pairs of frontal setae; one pair of oral vibrissae 0.3 mm from oral margin, the shallow depression between them 0.4 mm wide; 9 additional oral setae, one above vibrissae quite strong, peristomals gradually increasing in length with distance from vibrissae. Epistome not protruding, its width twice length of first two antennal segments. Haustellum narrow, length 0.7 times head height, narrowed apically; palpi testaceous, narrow, length 0.5 times haustellum length. Antennae dark testaceous, third segment brownish apically, arista and plumosity dark brown. Third segment of antenna 1.5 times length of second antennal segment. *Thorax*: Mesonotum dark brown with heavy gray tomentum; striping obscure. Integument of scutellum and postalar calli concolorous with rest of notum. Six humeral setae, 2 posthumerals and 1 presutural, 3 pairs of discal scutellars. Pleura brown, sutures lighter, tomentum grayish; infrasquamal setulae present; squamae whitish, wings light brown; epaulet light brown, basicosta testaceous; mediotergite tomentose. *Legs* dark reddish brown, tibiae lighter apically. Anterior femur with 7 dorsal setae, 8 posterodorsals, 13 posteroventrals; tibia with slightly darkened dorsal line. Midlle femur with 5 short anterior setae in 2 rows. Posterior femur with 8 anterodorsals, 5 anteroventrals, 6 posteroventrals, and no anterior setae. Femora with color uniform, tibiae darkened on basal third, tarsi black. *Abdomen* dark brownish black with heavy gray tomentum which is slightly brownish around bases of median marginal setae on second tergite and along posterior margins of third tergite. First syntergite with 1 pair of lateral marginal setae. Second tergite with l pair of median discals, 1 pair of median marginals, and 1 pair of lateral marginal setae. Third tergite with 1 pair of median discal setae, and 8 dorsal and lateral marginal setae. *Genitalia*: Eighth tergite with sparse small brown hairs. Ninth tergite long, covered with long dense brown hairs and many long, strong setae; lateral swelling absent. Surstylus small, narrow, lateral angle smoothly rounded, internal depression absent, mesal surface slightly convex with strong hairs; basally with strong setae, in profile, elongate, heart-shaped, inclined strongly in posteroventral direction, partially obscuring cerci. Cerci with lateral lobes angular, only slightly differentiated from arms; arms wide, height more than twice that of lateral lobes; arms extending ventrally well past apex of surstyli; in profile, smoothly but strongly incurved with no bulge, tips pointed, facing in anteroventral direction. Ejaculatory apodeme with stem distinct from bulb and about 1.3 times its length; bulb open on part of one side and top. **Female:** Similar to male except for usual sexual differences and the following. General color reddish brown. Width of frontal vitta at narrowest point 0.3 mm, at antennal base 0.4 mm, narrowest point near antennal base, strongly widened to vertex. Height of gena 0.25 times head height. Nine pairs of stout postorbital setae with smaller setae irregularly interspersed; six pairs of frontal setae. Notum brown with tomentum heavy; six strong humeral setae; squamae whitish; pleura light reddish brown. Legs lighter in color than those of male, tibiae similarly marked. Anterior femur with 10 posteroventrals, 8 posterodorsals, and 10 dorsal setae. Middle femur with 5 strong anterior setae in 2 rows, 1 anteroventral, and 5 posteroventrals. Posterior femur with 6 anterodorsals, 4 posteroventrals, 5 anteroventrals, and no anterior setae. Abdomen brownish, lighter laterally, covered with heavy grayish tomentum. First syntergite with 1 pair of lateral marginal setae. Second tergite with 1 pair of lateral marginals and 1 pair of median marginal setae. Third tergite with 1 pair of median discals and 10 dorsal and lateral marginals.

VARIATION.—*Ptilodexia westi* adults are quite distinct, but even among the small number of specimens examined, a certain degree of variation is seen. Total body length ranges from 10 to 12 mm. Facial tomentum is yellow or gray in a few specimens; parafacial hairs do not extend to below the antennal apex in most individuals, and the hairs are varied in length, from short to long. The carina is shorter and not visible beyond the apices of the antennae in some specimens. There are two rows, instead of one, of dark hairs ventral to the postorbitals in a few adults. The haustellum length is varied, from 0.7 to 0.8 times the head height. The antennae are also varied, from rufotestaceous to light brown, with the third segment not darkened.

The wings of some specimens are light in color. The femora are darkened apically on all except the dorsal surfaces in some individuals; this is especially noticeable in females, where ground color of the femora can be pale in color.



FIGURES 43–47. *Ptilodexia californica,* n.sp. Fig. 43. Genitalia of male, posterior view. Fig. 44. Ejaculatory apodeme. Fig. 45. Genitalia of male, lateral view. Fig. 46. Head of male, lateral view. Fig. 47. Geographical distribution.

In a few specimens, the abdomen is without brownish tomentum, and the integument is reddish brown ventrally and laterally. The abdomen of many females is reddish with a vague narrow median stripe, and in most females, it has no median discal setae.

MATERIAL EXAMINED.—Fifteen males and 8 females were examined from the following localities. **Arizona:** *Pima Co.*: 1♂, Brown's Canyon, Baboquivari Mts., 18 Aug. 1955, G. Butler (UAIC). **Kansas:** *Clark Co.*: 1♀, Sitka, 12 June 1960, W. Van Velzen (MSUC). **New Mexico:** *Dona Ana Co.*: 1♀, Las Cruces, 21 Sep. (USNM). **Oklahoma:** *Woodward Co.*: 1♂, Range 1 mile NW Supply, 1 June 1961, D. Bryan, 7♂♂-3♀♀, 9 June, 2♂♂3♀♀, 15 June (OSEC). **Texas:** *Brazos Co.*: 1♂, College Station, 30 May 1936, student collector (TAMU). *Pecos Co.*: 1♂, Fort Stockton, 28 Sep. 1935 (TAMU); 1♂, Imperial, 10 Apr. 1954, L. Beamer (CNCI). *Uvalde Co.*: 1♂, Uvalde, 18 May 1914, Bishopp (USNM).

Although few specimens were available for study, this species appears to be the most unusual *Ptilodexia* in the Nearctic region. Its members are, in fact, so dissimilar from those of other species that it may ultimately be assigned to a new genus.

BIOLOGICAL NOTES.—The flight period stretches from April to September, with too small a sample available to generalize on peak activity. There is no information available regarding host, collecting techniques, or ecology of this species.

DERIVATION OF NAME.—This species is named in honor of Dr. L. S. West, who did much of the early work with this genus in the United State.

californica Group

Ptilodexia californica, new species

(Figures 43–47)

TYPE-LOCALITY.—Two miles (3.2 km) S of Luther Pass, Alpine County, California.

TYPE-SPECIMENS.—The male holotype and the allotype are deposited in the collection of the California Academy of Sciences. The holotype bears the CASC type number 12571. Complete data from these specimens and the 52 male and 37 female paratypes are listed below.

DIAGNOSIS.—*Ptilodexia californica* adults can usually be distinguished from those of other species in the genus using the following combination of character states: facial tomentum shining, dark brown or pale hairs scattered sparsely along center of parafacial; haustellum length 0.5 to 0.65 times head height; third antennal segment longer than second, and length of plumosity on arista equal to 1.4 times length of second antennal segment; frontal vitta obliterated at narrowest point; scutellum and abdomen of males reddish, legs of both sexes dark.

Description.—**Male:** Total body length 13.5 mm, dark brown with abdomen reddish laterally. *Head* height 3.3 mm; profrons 0.3 times head length. Facial tomentum whitish, shining, obscuring integumental color; parafrontal hairs long, dark; parafacial hairs dark, rather long, scattered along middle of parafacial. Width of frontal vitta at antennal base 0.5 mm, at narrowest point, obliterated; carina fairly well developed, short; facial cavities brown. Height of gena 0.25 times head height. One pair of strong ocellar setae; 2 pairs of postocellars, 1 pair of postverticals, inner and outer verticals all subequal. Thirteen pairs of postorbitals, frequently interspersed with smaller hairs; between postorbitals and the whitish occipital hair is an irregular row of dark setae. Twelve pairs of frontal setae; one pair of oral vibrissae 0.3 mm from oral margin, the depression between them 0.4 mm wide; 18 additional oral setae, at least one above vibrissae and peristomals subequal. Epistome strongly protruding, its width 1.6 times length of first two antennal segments. Haustellum long, of medium width, 0.6 times head height; palpi long, narrow, testaceous, length 0.5 times haustellum length. Antennae dark rufotestaceous, third segment, arista and plumosity dark brown. Third segment of antenna 1.4 times length of second segment; length of plumosity on arista 1.4 times length of second antennal segment. *Thorax*: Mesonotum dark brown with fine, dull-gray pollen, striping indistinct; integument of scutellum and postalar calli rufotestaceous. Six humeral setae, 1 posthumeral and 2 presuturals, 3 pairs of discal scutellars. Pleura dark brown with fine grayish tomentum; infrasquamal setulae present; squamae whitish, wings pale brown; epaulet dark brown, basicosta testaceous; mediotergite tomentose, subshining. *Legs* dark brown, tibiae rufotestaceous darkened slightly basally and apically; tarsi blackish. Anterior femur with 9 dorsal setae, 8 posterodorsals, and 21 posteroventrals; tibia with dark dorsal line. Middle femur with 3/4 anterior setae in 2 rows. Posterior femur with 11 anterodorsals, 8 anteroventrals, 5 posteroventrals, and 1 anterior seta. *Abdomen* rufous with narrow, dark-brown median stripe; tomentum shining white, shining brown around median marginals and posterior median discals of second and third tergites. First syntergite with 1 strong pair of lateral marginal setae. Second tergite with 3 pairs of median discals, 2 pairs of median marginals, 2 pairs of lateral marginals, and 2 pairs of lateral discal setae. Third tergite with 2 pairs of median discals, 12 dorsal and lateral marginals, and 6 pairs of miscellaneous discal setae. *Genitalia*: Eighth tergite with sparse long hairs. Ninth tergite with long brown hairs, lateral swelling absent. Surstylus large with lateral angle fairly sharp, depression deep; surface strongly pitted. Cerci with height of lateral lobes greater than that of arms; lateral lobes slightly attenuated dorsally, mesal margins concave; in profile, arms strongly bulging. Ejaculatory apodeme with bulb distinct from stem, which is twice height of bulb. Bulb open on one side and on top, where it is distinctly lipped. **Female:** Similar to male except for usual sexual differences and the following. Width of frontal vitta at narrowest point 0.4 mm, at antennal base 0.6 mm. Height of gena 0.3 times head height. Eleven pairs of short postorbital setae; 10 pairs of frontal setae. Legs colored similarly to those of male, tibiae not as pale. Anterior femur with 14 posteroventrals, 8 posterodorsals, and 6 dorsal setae. Middle femur with 5 anterior setae in 2 rows. Posterior femur with no anterior setae, 5 anterodorsals, 5 posteroventrals, and 6 anteroventrals. Abdomen dark reddish brown; median stripe broad and indistinct. First syntergite with 1 pair of lateral marginal setae. Second tergite with 1 pair of median marginals, 1 pair of median discals, and 1 pair of lateral marginal setae. Third tergite with 2 pairs of median discals, 2 pairs of lateral discals, and 12 dorsal and lateral marginal setae.

Variation.—*Ptilodexia californica* adults show relatively little variation in many of the diagnostic characters of this group. However, they do seem to exhibit a distinctly greater than usual degree of variation in minor characters as well as in the genitalia. It is possible that later, more-detailed studies may uncover cryptic or incipient species within *P. californica*. There are also a few specimens which appear to be intermediate between *P. californica* and *P. sabroskyi,* and between *P. californica* and *P. pacifica*.

Total body length ranges from 11 to 16 mm. In a few individuals, facial tomentum has a yellowish cast and the carina is keeled. Most specimens have no small hairs interspersed between the postorbital setae. The haustellum is varied, with the length ranging from 0.5 to 0.65 times head height. Notal tomentum may be partially or wholly dull brown and the mediotergite can be fairly shiny. The abdomen is varied from the state shown in the holotype to dark reddish brown with the median stripe broad and indistinct. The genitalia are extremely varied.

Material Examined.—Fifty-three males and 39 females were examined from the following localities. **California:** *Alpine Co.*: 1♂, 2 miles [3.2 km] S Luther Pass, 6 July 1959, at flower *Achillea Millefolium,* P. Arnaud (CASC); 1♂, Hope Valley, 9 July 1948, J. MacSwain (CISC). *Fresno Co.*: 1♀, Prather, 29 June 1956, R. Schuster (CISC); 2♀♀, Watts Valley, 22–23 June 1956, R. Schuster (CISC). *Inyo Co.*: 1♀, W Fork Coyote Creek, 2.1 miles [3.4 km] NE Coyote Lake, 37°14'N, 118°30'W, Sierra Nevada, 9,840 ft [ca. 3,000 m] sweeping, 16 Sep. 1969, S. Frommer (UCRC); 1♂, near Mono Pass, 12,000 ft, [ca. 3,658 m] 19 Aug. 1956, C. MacNeill (CISC); 1♂ Panamint Mts., 28 May 1937, B. Brookman (CASC). *Kern Co.*: 1♂, 4 miles [ca. 6.4 km] N Muroc, 30 Apr. 1950, T. Leigh (CISC); 2♂♂, Short Canyon, 7 miles [ca. 11 km] NW Inyokern, 13 Apr. 1954, J. MacSwain (CISC); 1♂, Walker Pass, 11 June 1962, G. Bohart (USUC). *Los Angeles Co.*: 3♂♂2♀♀, Oct., Coquillett (USNM); 5♀♀3♂♂, Crystal Lake, 29 June 1950, W. Bentnick, 13♂♂11♀♀, 9 July 1952, R. Wagner (CISC, LACM); 1♂, Little Rock, 10 May 1941, J. Wilcox (PHAC); 1♂1♀, 1 mile W Little Rock, 13 May 1956, J. MacSwain (CISC); 1♂, 2 miles [ca. 3.2 km] W Pearblossom, 12 May 1956, E. Linsley (CISC); 1♀, Rock Creek, 21 July 1936, A. Basinger (CASC). *Mariposa Co.*: 1♂, Yosemite Valley, 26 June 1921, E. Van Dyke (CASC). *Mono Co.*: 1♂1♀, Sardine Creek, 27 June 1957, D. Flaherty (UCRC, UAIC); 1♂, Sonora Pass, 9,000–10,000 ft [ca. 2,740–3,050 m], 16 July 1951, P. Ashlock, 1♀, 10 Aug. 1960, C. Toschi (USNM, CISC). *Nevada Co.*: 1♀, Prosser Dam, 15 July 1966, D. Miller (UCDC); 1♂, 7 miles [ca. 11 km] SE Truckee, 24 June 1954, G. Schaefers (CISC). *Plumas Co.*: 2♂♂1♀ (Allotype), Meadow Valley, 10 June 1924, E. Van Dyke (CASC). *Riverside Co.*: 1♂, Hemet, 26 Apr. 1961, Ewart (UCRC); 1♂, Hidden Valley, Joshua Tree National Monument, 18 May 1946, A. Melander (USNM); 1♂, Pinon Flat, 24 Apr. 1950, C. MacNeill (CISC); 1♂, Pinon Flat, San Jacinto Mts., 18 May 1939, E. Ross, 2♀♀, *Eriogonum,* 21 May 1940, H. Reynolds, 1♂, 27 May 1939, B. Brookman (CISC, UCRC); 1♂, Pinon Flat, Santa Rosa Mts., 27 May 1941, D. Knull (OSUC). *San Bernardino Co.*: 1♂, Helendale, 16 May 1955, W. Richards (CNCI). *San Diego Co.*: 1♀, 16.5 miles [ca. 26.6 km] N of Carlsbad, Timberlake (UCRC). *San Luis Obispo Co.*: 1♂, Oso Flaco Lake, 19 July 1964, M. Irwin (UCRC). *Santa Barbara Co.*: 1♀, Janama Beach, 9 July 1965, J. Powell (CISC); 1♀, Los Prietos, 23 June 1965, J. Powell (CISC). *Santa Cruz Co.*: 1♂, Bear Valley, Santa Cruz Mts., July 1913, F. Clark (CUIC). *Siskiyou Co.*: 2♂♂, Hebron Summit, 10 miles [ca. 16 km] S of Dorris, 5,300 ft [ca. 1,600 m] 27 July 1953, W. Gertsch (AMNH). *Tehama Co.*: 1♂3♀♀, Deer Creek, 6 July 1952, M. Cazier (AMNH). *Ventura Co.*: 1♀, Quatal Canyon, NW corner Ventura Co., *Stanleya pinnata*, 9 May 1959, J. Powell (CISC); 2♂♂, Hungry Valley, 5 miles [ca. 8 km] S of Gorman, 6 May 1959, C. O'Brien (CISC). **Nevada:** *Clark Co.*: 1♀, Kyle Canyon, Charleston Mts., 5,200 ft [ca. 1,580 m] 4 June 1941, Timberlake (UCRC). *Ormsby Co.*: 1♀, 6 July, Baker (USNM). **Oregon:** *Hood River Co.*: 1♂, Hood River, 17 June, Childs (CISC). *Jackson Co.*: 1♀, Colestin, 31 July 1918, E. Van Duzee (CASC). *Klamath Co.*: 1♂, Eagle Ridge, Klamath Lake, 20 May 1924, C. Fox (CISC). **Washington:** *Yakima Co.*: 1♀, Signal Peak Ranger Stn., 4,000 ft [ca. 1,200 m], 15 July 1933, J. Wilcox (PHAC).

Biological Notes.—The flight period lasts from April to October with most of the activity from April to July. Adults have been collected at low as well as high elevations (up to 3,660 m). Flowers from which they have been collected are *Eriogonum* sp. (Polygonaceae) and *Stanleya pinnata* (Cruciferae).

Ptilodexia pacifica, new species

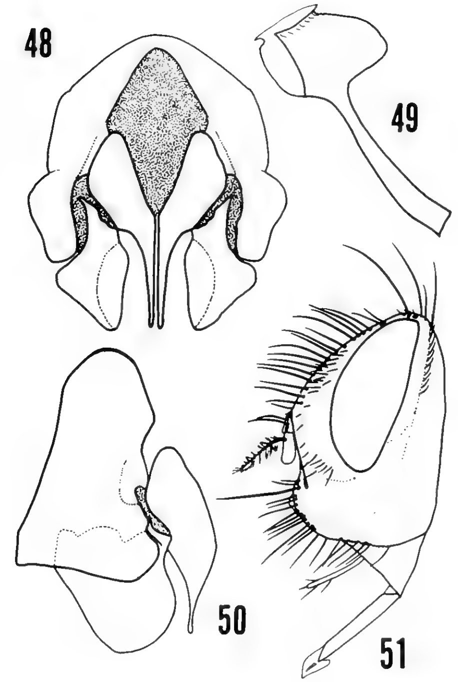
(Figures 48–52)

Type-Locality.—Point Pinos, Pacific Grove, Monterey County, California.

Type-Specimens.—The holotype, a male, and the allotype are deposited in the collection of the California Academy of Sciences. The holotype bears the CASC type number 12572. Complete data from these specimens and the 62 male and 16 female paratypes are listed below.

Diagnosis.—*Ptilodexia pacifica* is a complex species, but specimens can generally be separated from those of other species in the genus by the following combination of character states: parafacial hairs long, dark, inserted along center of parafacial as low as ventral eye margin; haustellum length varied, from 0.4 to 0.55 times head height; legs of most adults either pale in color or marked with rufotestaceous; notum of most specimens covered with flat, shiny, brownish tomentum, giving it a coppery appearance; abdominal tomentum concolorous—either whitish or brownish in most individuals—white marked with brown in only a few.

Description.—**Male:** Total body length 10.5 mm, dark brown, abdomen reddish. *Head* height 2.75 mm; profrons 0.25 times head length. Facial tomentum heavy, shining grayish, obscuring integumental color; parafrontal hairs long, dark, sparse; parafacial hairs long, dark, rather sparse, inserted along middle of parafacial to ventral margin of eye. Width of frontal vitta



FIGURES 48–52. *Ptilodexia pacifica*, n.sp. Fig. 48. Genitalia of male, posterior view. Fig. 49. Ejaculatory apodeme. Fig. 50. Genitalia of male, lateral view. Fig. 51. Head of male, lateral view. Fig. 52. Geographical distribution.

at base of antenna 0.4 mm, at narrowest part obliterated; carina low, broad, rounded; facial cavities dark brown. Height of gena 0.3 times head height. One pair of strong ocellar setae, 3 pairs of postocellars, 1 pair of postverticals, inner verticals, and outer verticals. Fifteen pairs of long postorbital setae, not interspersed with smaller hairs; between postorbitals and whitish occipital hairs are a few irregular dark setae. Thirteen pairs of frontal setae; 1 pair of strong oral vibrissae 0.2 mm from oral margin, the depression between them 0.4 mm wide. Thirteen additional oral setae; one above vibrissae and peristomals subequal to each other; oral margin protruding, its width equal to 2.2 times length of first two antennal segments. Haustellum of medium width, length 0.5 times head height; palpi long, rufotestaceous, the length 0.6 times haustellum length. Antennae rufotestaceous, third segment, arista and plumosity brown. Third segment of antenna 1.5 times length of second segment; length of plumosity on arista 1.75 times length of second antennal segment. *Thorax*: Mesonotum dark brown with tomentum appearing grayish from one angle and shiny brownish from others; striping indistinct. Integument of postalar calli, scutellum, and sides of notum rufotestaceous. Six humeral setae, 2 posthumerals and 2 presuturals, 2 pairs of discal scutellars. Pleura dark brown with grayish tomentum; infrasquamal setulae present; squamae white, wings light brown; epaulet brown, basicosta rufotestaceous; mediotergite thinly tomentose, shining. *Legs* dark rufotestaceous, anterior and middle femora brownish with pale apical markings; posterior femora with dark apicoventral patches; tibiae unmarked, tarsi dark brown. Anterior femur with 7 dorsal setae, 8 posterodorsals, and 15 posteroventrals; tibia without dark dorsal line. Middle femur with 5 anterior setae in 2 rows. Posterior femur with 15 anterodorsals, 8 anteroventrals, 4 posteroventrals, and no anterior setae. *Abdomen* rufotestaceous with a dark median stripe; tomentum whitish. First syntergite with 1 pair of lateral marginal setae. Second tergite with 2 pairs of median discals, 2 pairs of median marginals, 4 pairs of lateral marginals, and 2 pairs of lateral discal setae. Third tergite with 2 pairs of median discals, 10 dorsal and lateral marginals, and 2 pairs of lateral discal setae. *Genitalia*: Eighth tergite with sparse, long, fine hair. Ninth tergite with long brown hair and a distinct lateral swelling. Surstylus with lateral angle sharp, internal depression deep. Cerci with lateral lobes longer than arms; arms reaching to ventral margin of surstylus; in profile, cerci bulging, tips directly ventrally. Ejaculatory apodeme with bulb and stem distinct; stem twice as long as height of bulb, which is widely opened on one side and top; opposite side decumbent. **Female:** Similar to male except for usual sexual differences and the following: General color dark brown. Width of frontal vitta at narrowest point 0.4 mm, at antennal base 0.6 mm wide. Height of gena 0.35 times head height. Seven pairs of medium postorbital setae; 10 pairs of frontal setae. Notum dark brown with heavy brownish tomentum; six humeral setae. Legs rufotestaceous. Anterior femur with 11 posteroventrals, 4 posterodorsals, and 5 dorsal setae. Middle femur with 3 anterior setae in 2 rows, 1 anteroventral, and 4 posteroventrals, 4 anteroventrals, and no anterior setae. Abdomen dark brown, a little lighter laterally. Second tergite with 1 pair of median discals, 1 pair of median marginals, 3 pairs of lateral marginals, and 1 pair of lateral discal setae. Third tergite with 1 pair of median discals, 10 dorsal and lateral marginals, and 2 pairs of lateral discal setae. Tip of abdomen reddish.

VARIATION.—*Ptilodexia pacifica* is the most variable Nearctic speices of *Ptilodexia*. Several fairly distinct populations are present, each of which may eventually be recognized as a separate species. I fail to name these as species now because of the inadequate sample and numerous specimens which appear to be intermediates.

The form to which the type-specimens belong has males and females with pale-colored legs. These specimens have the parafacial hairs rather sparse; are small in body size (7–13 mm); and the abdominal tomentum is uniformly whitish in most individuals. This form occurs from southern California along the coast into Monterey County.

Members of the second form are larger; have parafacial hairs abundant; and only females have pale-colored legs, although the legs of some males are marked with orange or reddish. The facial tomentum is brownish in some specimens, and the abdominal tomentum is so in most. These specimens are more hairy and much darker in color than those of the previous form. Many have one to two rows of dark hairs ventral to the postorbitals, and have dark squamae and wings. This form ranges from Oregon south along the California coast to Monterey County, where both this and the previous form are found.

The third form is found in the Sierra Nevada from northern California south into Inyo County. These specimens resemble those of the first form in size and facial hair; however, most individuals are darker in color, and males and females have dark-colored legs. The abdominal tomentum is concolorous, whitish.

Specimens of the three forms have a number of character states in common which segregate them from specimens of other western species. It is for this reason and the lack of material that I have treated the complex as one species. It is hoped that further collecting, and ecological and life history studies will elucidate relationships and uncover a basis for the variability within this species.

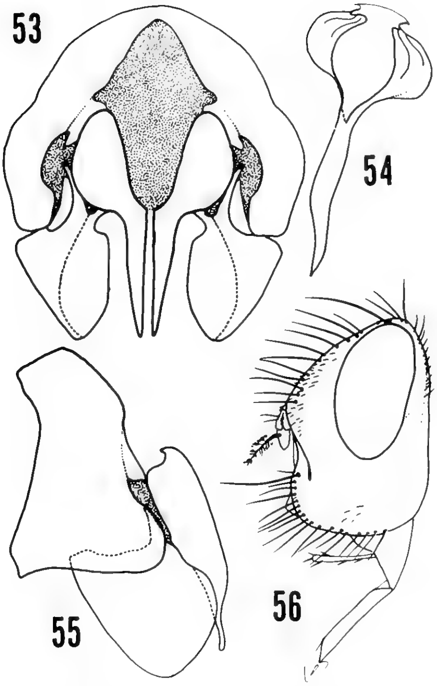
MATERIAL EXAMINED.—Two hundred twenty-six males and 115 females of *P. pacifica* were examined. Data from those specimens in the type-series are as follows: **California:** *Monterey Co.*: 35♂♂1♀, Point Pinos, Pacific Grove, 24 May, 1952, P. Arnaud, 4♂♂12♀♀, 13 June 1959, 25♂♂5♀♀, 19 Aug. 1957 (PHAC).

Data from the other specimens examined are recorded by Wilder (1976).

DISTRIBUTION.—The species ranges from southern California north along the coast to northern Oregon. It is also found in the Central Valley and through the Sierra Nevada in California.

BIOLOGICAL NOTES.—The flight period ranges from May to November with specimens occurring throughout that period with perhaps two activity peaks—one in late spring and early summer, and the other in the fall.

Specimens of *P. pacifica* have been collected on the following flowers belonging to the family Compositae: *Baccharis pilularis*, *Chrysothamnus viscidiflorus*, and *Achillea Millefolium*, and undetermined *Baccharis* sp. and *Solidago* sp. Specimens have also been collected from *Eriogonum elatum* (Polygonaceae). They have also been collected while resting on the leaves of *Rubus parviflorus* and *Umbellularia californica*. This species inhabits both low and high (up to



FIGURES 53–57. *Ptilodexia sabroskyi*, n.sp. Fig. 53. Genitalia of male, posterior view. Fig. 54. Ejaculatory apodeme. Fig. 55. Genitalia of male, lateral view. Fig. 56. Head of male, lateral view. Fig. 57. Geographical distribution.

3,660 m) elevations. Collecting methods used include UV and white light, sweeping, flight trap, and light trap. *Ptilodexia pacifica* adults have been collected in meadows, near streams, on sand dunes, and on rocks.

Ptilodexia sabroskyi, new species

(Figures 53–57)

TYPE-LOCALITY.—San Clemente, Orange County, California.

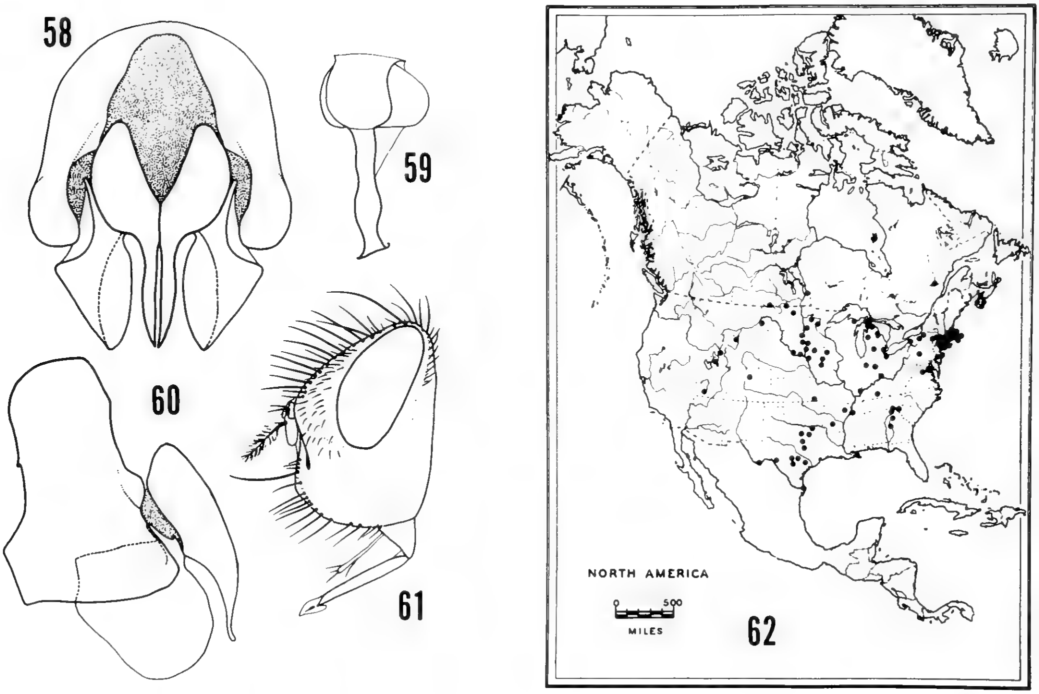
TYPE-SPECIMENS.—The holotype, a male, was collected by G. Eickwort on 25 July 1961, and is deposited in MSUC. The allotype, deposited in LACM, is from near Wrightwood, 1,719 m, San Bernardino County, California. Complete data from these specimens and the 37 male and 7 female paratypes are listed below.

DIAGNOSIS.—Specimens of *P. sabroskyi* are large, robust, and quite distinctive. They can be distinguished from those of other species of *Ptilodexia* by the following combination of character states: parafacial hairs brown, rather short, concentrated near upper anterior edge of parafacial and scattered randomly elsewhere, lower ones often yellowish; length of plumosity on arista less than twice length of second antennal segment, the third antennal segment short, subequal to the second in length; smallest distance between eyes greater than width of frontal vitta at antennal base; frontal vitta not obliterated at its narrowest point; length of haustellum varied from 0.5 to 0.6 times head height; legs of both sexes dark; notum light brown laterally in most individuals.

DESCRIPTION.—**Male:** Total body length 17 mm, dark brown with abdomen reddish laterally. *Head* height 4 mm; profrons 0.3 times head length. Facial tomentum dull whitish, heavy, obscuring integumental color; parafrontal hairs medium in length, dark, abundant; parafacial hairs brown, short, concentrated on upper anterior portion of face, short, pale hairs scattered elsewhere on parafacial. Width of frontal vitta at antennal base 0.6 mm, at narrowest point 0.1 mm; carina well developed, broad; facial cavities dark gray. Height of gena 0.3 times head height. One pair of strong ocellar setae, two pairs of smaller postocellars, one pair each of postverticals, inner verticals, and outer verticals. Eighteen pairs of long postorbital setae, not interspersed with smaller hairs; ventral to postorbitals are no dark hairs, only yellowish occipital hair. One pair of frontal setae, 1 pair of long oral vibrissae 0.4 mm from oral margin, the depression between them 0.6 mm wide; 16 additional oral setae, one above vibrissae rather strong, peristomals subequal to each other, about 0.5 times vibrissae length. Epistome strongly protruding, its width 1.7 times length of first two antennal segments. Haustellum broad, blackish, length 0.5 times head height; palpi long, narrow, rufotestaceous, length 0.6 times haustellum length. Antennae dark rufotestaceous; third segment, arista, and plumosity dark brown. Third segment of antenna very short, 0.8 times length of second segment; length of plumosity on arista 1.5 times length of second antennal segment. *Thorax*: Mesonotum dark brown, rufescent laterally; tomentum heavy, grayish, striping distinct; integument of humeri, postalar calli, and scutellum rufescent. Six humeral setae, 2 posthumerals and 2 presuturals, 6 pairs of discal scutellars. Pleura dark brown, sutures lighter, tomentum heavy, grayish; infrasquamal setulae present; squamae whitish, wings light brown, epaulet dark brown, basicosta testaceous; mediotergite subshining tomentose. *Legs* dark brown, tibiae rufous, darkened basally and slightly apically; tarsi blackish. Anterior femur with 12 dorsal setae, 11 posterodorsals, and 18 posteroventrals; tibia with dark dorsal line. Middle femur with 4 strong anterior setae in 2 rows. Posterior femur with 13 anterodorsals, 10 anteroventrals, 6 posteroventrals, and no anterior setae. *Abdomen* rufous with a narrow, dark brown, median stripe; tomentum white, heavy, patchy, brown around median marginal setae of second and third tergites. First syntergite with 1 pair of lateral marginal setae. Second tergite with 3 pairs of median discals, 2 pairs of median marginals, 3 pairs of lateral marginals and 2 pairs of lateral discals. Third tergite with 3 pairs of median discals, 12 dorsal and lateral marginals, and 4 pairs of lateral discals. *Genitalia*: Eighth tergite with numerous small, fine hairs. Ninth tergite with long dark hairs; lateral swelling pronounced. Surstylus large with lateral angle sharp, internal depression rather shallow, basally strongly convex; in profile, inclined slightly posterad. Cerci with height of lateral lobes subequal to height of arms; in profile, lateral lobe with a strong dorsal hook pointing anteriad, arms bulging slightly ventrally, tips rounded. Ejaculatory apodeme with bulb distinct from long, thin stem, which is 2.5 times height of bulb. Bulb large and somewhat flattened, open widely on one side and narrowly on top with a strong lip; opposite side strongly decumbent. **Female:** Similar to male except for usual sexual differences and the following. Width of frontal vitta at narrowest point 0.4 mm, at antennal base 0.6 mm. Height of gena 0.4 times head height. Nine pairs of short postorbital setae irregularly interspersed with short hairs; 8 pairs of frontal setae. Legs same color as in male, anterior femur with 10 posteroventrals, 8 posterodorsals, and 8 dorsal setae. Middle femur with 3 anterior setae in 2 rows, 5 posteroventrals, and 1 anteroventral. Posterior femur with no anterior setae, 7 anterodorsals, 4 posteroventrals, and 4 anteroventrals. Abdomen dark reddish brown with a vague median stripe; tomentum heavy, white. First syntergite with 1 pair of lateral marginal setae. Second tergite with 1 pair of median discals, 1 pair of median marginals, and 1 pair of lateral marginal setae. Third tergite with 1 pair of median discals and 12 dorsal and lateral marginals.

VARIATION.—*P. sabroskyi* exhibits relatively little variation. Total body length ranges from 12 to 18 mm. The scattered hairs on the parafacial are brown in some individuals, but are long in none. The third antennal segment is varied in length, at its longest being equal to the second segment. The number of discal scutellar setae is quite varied, as are the lengths of those setae. Abdominal color in males and females ranges from rufous to dark reddish brown, although few individuals exhibit the latter. There is no brownish tomentum on the abdomens of a few males and many females.

MATERIAL EXAMINED.—Material examined included 38 males and 8 females. Data from these specimens are as follows: **California:** *Unknown*: 1♂, Marina Beach, 17 June 1961, C. Philip (CASC); 1♂, Pine Lake, southern California, Johnson (USNM). *Inyo Co.*: 1♀, Wyman Canyon, White Mts., near stream, 21 July 1967, S. Frommer (UCRC). *Los Angeles Co.*: 1♂, Malibu Creek mouth, 17 July 1953 (LACM); 1♂, Claremont, Baker (LACM). *Orange Co.*: 1♂, Newport, 10 July 1916, D. Hall (USNM); 3♂♂, Newport Beach, 19 Aug. 1920, Timberlake (UCRC); 1♂, San Clemente, 25 July 1961, G. Eickwort (MSUC). *Riverside Co.*: 1♂, Coachella Valley, 7 Apr. 1928, R. Woglum (CISC); 1♂, Palm Springs, Andreas



FIGURES 58–62. *Ptilodexia carolinensis* Brauer and Bergenstamm. Fig. 58. Genitalia of male, posterior view. Fig. 59. Ejaculatory apodeme. Fig. 60. Genitalia of male, lateral view. Fig. 61. Head of male, lateral view. Fig. 62. Geographical distribution.

Canyon, 24 Apr. 1954, M. Wasbauer (CISC). *San Bernardino Co.*: 1♂, May, Coquillett (USNM); 1♂, Barton Flats, 20 July 1950, A. Melander (USNM); 5♂♂, Cajon, 11 May 1934, C. M. (UCRC); 3♂♂, Colton, 26–28 May 1917, E. VanDuzee (CASC); 1♂, Deep Creek Public Camp, 15 June 1957, A. Menke (LACM); 1♂, South Fork Camp, San Bernardino Mts., 2 Sep. 1946, Timberlake (UCRC); 1♂, upper Santa Ana River, 6 July 1948, A. Melander, 1♂, 9 July 1959, 1♂, 16 July 1947, 1♂, 18 July 1950, 1♂1♀, 22 July 1950, 1♂, 4 Aug. 1946, 1♂, 10 Aug. 1949, 1♂, 29 Aug. 1946, 1♂, 15 Sep. 1946 (USNM); 1♂, Verdemont, 22 May 1954, A. Melander (USNM); 1♀, near Wrightwood, 1,719 m (LACM). *San Diego Co.*: 1♂, A. Moldenke (USNM); 1♂, 1 mile S of Del Mar, *Eriogonum fasciculatum*, 10 July 1963, P. Hurd (CISC); 1♂1♀, Dulzura, 14 June 1917 (AMNH); 1♀, 2.8 miles [ca. 4.5 km] SW of Poway, Los Penasquitos Creek, 400 ft [ca. 120 m], 25 July 1965, R. Somerby (UCRC); 1♀, Tecate Peak, 10 July 1963, J. Powell (CISC). *Ventura Co.*: 1♀, Oxnard Beaches, 13 June 1955, R. Erdmann, 1♂, 16 July 1953, W. Gertsch, 1♀, 25 July 1956, R. Erdmann (LACM, AMNH).

DISTRIBUTION.—The range of *P. sabroskyi* is restricted to southern California and the White Mountains.

BIOLOGICAL NOTES.—The period of activity lasts from April to September. Adults have been collected near a stream and on *Eriogonum fasciculatum* (Polygonaceae).

DERIVATION OF NAME.—*Ptilodexia sabroskyi* is named in honor of Dr. C. W. Sabrosky for his enormous contribution to the study of the Tachinidae.

carolinensis Group

Ptilodexia carolinensis Brauer and Bergenstamm

(Figures 58–62)

Ptilodexia carolinensis BRAUER AND BERGENSTAMM, 1899:119. BRAUER (1899:508); ALDRICH (1905:499); SABROSKY AND ARNAUD (1965:988); COLE (1969:543). [LECTOTYPE (here designated), male, deposited in VMNH, labeled, "S. Carolina"/"*rufipennis* Mq, *carolinensis*, Coll. Winthem, (two indistinguishable words)"/"*Carolinensis* Type, det. Brauer. Bergenst."/"*carolinensis* Type Br Bgst"/"*Ptilodexia carolinensis* Br. Bgst."/"Lectotype *Ptilodexia carolinensis* designated by D. Wilder 1976."]

Estheria tibialis (partim): COQUILLETT (1910:598); TOWNSEND (1931:102). (misidentification)

Ptilodexia abdominalis (partim): DAVIS (1919:84). (misidentification)

Ptilodexia neotibialis WEST, 1924:184. LEONARD (1928:822);

CURRAN (1930:93); SABROSKY AND ARNAUD (1965:989); COLE (1969:543). [HOLOTYPE, male, deposited in MCZC, labeled, "Colebrook, Conn., Coll. W. M. Wheeler"/Black square/"MCZ Type 26963"/"Holotype *Ptilodexia neotibialis* West."] NEW SYNONYMY

Dexia harpasa (partim): ALDRICH (1925:114); JOHNSON (1925b:208). (misidentification)

Rhynchodexia confusa (partim): JOHNSON (1925b:208). (misidentification)

Ptilodexia minor WEST, 1925:132. LEONARD (1928:822); WEST (1950:pl. I, fig. 3, pl. IV, fig. 8); SABROSKY AND ARNAUD (1965:989). [HOLOTYPE, female, deposited in CUIC, labeled "Duck Lake, N.Y., 6–VIII–21"/"L. S. West Collector"/ "Wing Slide, Cornell U., Lot 919, Sub 86, L. S. West"/ "Holotype *Ptilodexia minor* West"/"Holotype Cornell U., No. 1875"/"Cornell U., Lot. 922, Sub. 43."] NEW SYNONYMY

TAXONOMIC NOTES.—*Ptilodexia carolinensis* has been confused routinely with other species by earlier workers. Neither Curran nor West had ever seen the type. West speaks of generic characters but never mentions *P. carolinensis*, the type-species of the genus, in any of his papers.

Aldrich (1925) saw the types, matched them with his specimens of *P. canescens* and *P. planifrons*, which he thought were *Estheria tibialis*. Following Austen (1907), he assigned this species to *Dexia harpasa* Walker. Townsend (1931) and Coquillett (1910) also felt that *P. carolinensis* was a synonym of *E. tibialis*. Sabrosky and Arnaud (1965) considered *P. carolinensis* separate from *P. harpasa*.

I have seen the type—there is only one male now, not the two which Aldrich (1925) reported—and it is in excellent condition. The specimen has been designated lectotype.

DIAGNOSIS.—*Ptilodexia carolinensis* is a diverse species (or perhaps species group), its members lacking distinct characters. Specimens can be more easily assigned here by characteristics which they lack rather than those which they possess.

Adults with rather broad, parallel-sided face, vibrissal angle protruding little or not at all; parafacial hairs long, fine, inserted along middle of parafacial; epistome protruding only slightly; third antennal segment 1.5 times length of second in most specimens; length of plumosity on arista varied from 1 to 1.5 times length of second antennal segment; haustellum length varied from 0.4 to 0.5 times head height; scutellum and sides of abdomen orange-brown in most adults; some specimens from Texas and South Dakota are totally orange-brown.

MATERIAL EXAMINED.—Two hundred fifty-six males and 133 females were examined.

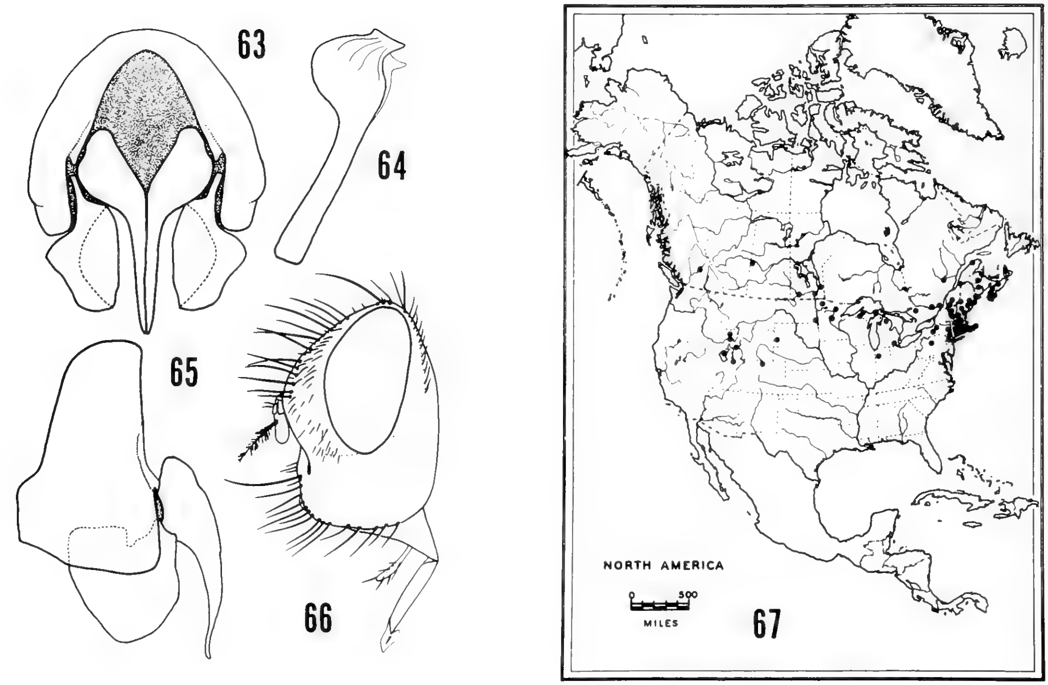
DISTRIBUTION.—This species ranges widely from Nova Scotia south to Georgia and west into Texas and the Rocky Mountains, with scattered records from Utah, Wyoming, and Saskatchewan.

BIOLOGICAL NOTES.—The flight period is from July to September with the majority of specimens collected from mid-August to mid-September. Specimens have been collected as early as 30 May on Long Island and as late as 23 October in Virginia.

In Texas, the insect seems to be double-brooded, some specimens being collected in April, May, and June, and others in September, October, and November. In material from other areas, such as New York, we find early-season and late-season specimens, but their numbers do not indicate a double brood. There may be a correlation between the brood and body color in the enigmatic Texas specimens. Unfortunately, the sample at hand, while giving weight to this possibility, is too small for any such conclusions to be drawn.

Specimens which have been brought into the lab complete their development and emerge much earlier than they would have in nature. Parasitized Japanese beetles, collected in October, yielded adult *Ptilodexia carolinensis* as early as 21 December. It is not known if these specimens were exposed to cold temperatures. It is feasible that in a warm climate two broods might occur. In the area where the above-mentioned specimens were collected (Connecticut), the adult would not have emerged, under normal conditions, until the following summer.

Nearly all of the specimens of this species were collected at low elevations. One was collected at 1,450 m in the southern Appalachians, and others in Colorado and Wyoming at 1,950 m and 2,060 m, respectively. A number of specimens have been collected by sweeping vegetation, and some have been taken on *Solidago* sp. Perhaps coincidentally, Japanese beetle feeds on the foliage of *Solidago juncea* (Fleming 1972). Available host data indicate that this insect parasitizes *Popillia japonica* in the Northeast and *Phyllophaga* sp. in Texas. Davis (1919:84) reports that adults (under the name of *P. abdominalis* were reared from the larvae of *Phyllophaga rugosa* collected in Manitoba.



FIGURES 63–67. *Ptilodexia canescens* (Walker). Fig. 63. Genitalia of male, posterior view. Fig. 64. Ejaculatory apodeme. Fig. 65. Genitalia of male, lateral view. Fig. 66. Head of male, lateral view. Fig. 67. Geographical distribution.

Ptilodexia canescens (Walker)

(Figures 63–67)

Dexia canescens WALKER, 1852:310. OSTEN SACKEN (1878:155); ALDRICH (1905:502); AUSTEN (1907:345); CHAMPLAIN AND KNULL (1944:214); PETERSON (1948:60); SABROSKY AND ARNAUD (1965:988). [HOLOTYPE, male, deposited in BMNH, labeled "*Dexia canescens*, Walk."/"Holotype"/"U.S."/"United States. Ex. Coll. Saunders 68.4"/Crosskey examination label, 1970]

Ptilodexia harpasa (partim): DAVIS (1919:82); ALDRICH (1925:114); JOHNSON (1925b:208). (misidentification)

Rhynchodexia confusa (partim): JOHNSON (1925b:208). (misidentification)

TAXONOMIC NOTES.—The holotype has many dorsal setae broken and one antenna missing. The wings are in excellent condition.

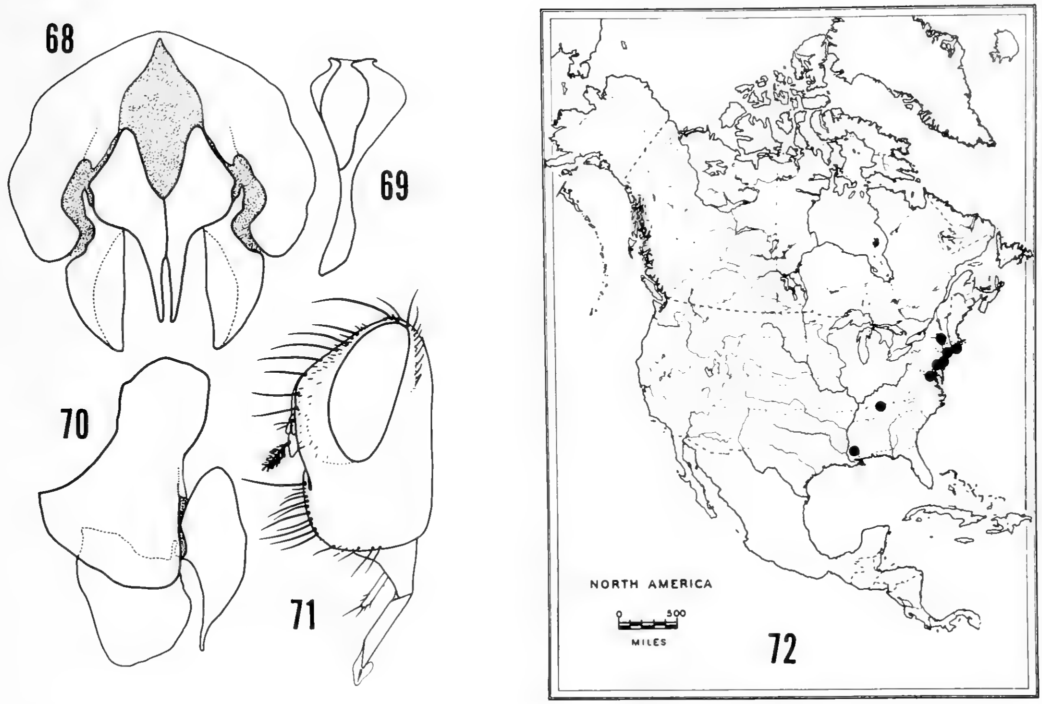
DIAGNOSIS.—Adults of *P. canescens* are unique in the following combination of characters: parafacial hairs long, coarse, denser near lower anterior edge of eye in most individuals. Oral margin in most adults not protruding; males with frontal stripe not obliterated at narrowest point; width of plumosity on arista less than or equal to length of second antennal segment; length of haustellum less than half head height; total absence of infrasquamal setulae; abdomen quite dark in most specimens, with a distinct median stripe in a few.

MATERIAL EXAMINED.—One hundred forty-eight males and 68 females were examined.

DISTRIBUTION.—This species ranges from Nova Scotia to Long Island and west to the Rocky Mountains. There are scattered records in British Columbia, Idaho, Wyoming, and Utah.

BIOLOGICAL NOTES.—The flight period is from June to August, with the majority of records in mid-July. Specimens have been collected as early as 24 April (Long Island, 1923) and as late as 8 September (Massachusetts, 1907) in nature.

The majority of specimens were collected at low elevations; however, there are records from mountainous areas, the highest being 2,040 m in Wyoming. Specimens from Massachusetts and Utah have been collected on the flowers of parsnip. Specimens from State College, Pennsylvania, were taken at a UV light. In Kindred, in eastern North Dakota, a male and a female were



FIGURES 68–72. *Ptilodexia halone* (Walker). Fig. 68. Genitalia of male, posterior view. Fig. 69. Ejaculatory apodeme. Fig. 70. Genitalia of male, lateral view. Fig. 71. Head of male, lateral view. Fig. 72. Geographical distribution.

collected on native prairie vegetation. Two males and six females have been reared and are associated with puparia. The only host data available indicate that this insect is a parasitoid of *Phyllophaga* sp.

Ptilodexia halone (Walker)

(Figures 68–72)

Dexia halone WALKER, 1849:837. OSTEN SACKEN (1878:155); ALDRICH (1905:502); SABROSKY AND ARNAUD (1965:988). [LECTOTYPE (here designated), male, desposited in BMNH, labeled, "*Dexia halone* Wlk."/"Lectotype"/"Georgia, U.S.A., Ex. Coll. Abbot"/"Georgia"/Crosskey examination label 1970/"Lectotype *Dexia halone* Walker designated by D. Wilder 1975."]

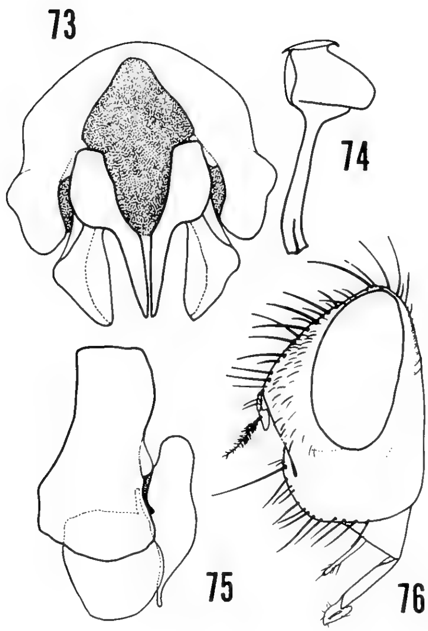
Ptilodexia hucketti WEST, 1952:131. LEONARD (1928:822); CURRAN (1930:93); WEST (1950:pl. I, fig. 1); SABROSKY AND ARNAUD (1965:988) [HOLOTYPE, male, deposited in CUIC, labeled, "Riverhead, L.I., N.Y., 30 July 1922, H. C. Huckett"/"Holotype *Ptilodexia hucketti* West, ♂"/"Holotype Cornell U. No. 1872"/"Cornell U., Lot. 922, Sub. 44"] NEW SYNONYMY

TAXONOMIC NOTES.—The lectotype and paralectotype are in poor condition but still easily recognizable. The lectotype has all dorsal setae broken or absent, most tarsi and the left posterior leg missing, and the abdomen broken and glued.

DIAGNOSIS.—Adults of *Ptilodexia halone* can be distinguished from those of all other species of *Ptilodexia* by the following combination of characters: totally orange or orange-brown in color; parafacial hairs short and pale, inserted rather randomly on parafacial; oral margin not or only slightly protruding; area between oral vibrissae and oral margin higher than wide (length and width may be equal); length of haustellum 0.3 to 0.4 times head height; third antennal segment only slightly longer than second; length of plumosity on arista 1.4 times length of second segment; inner vertical setae strongly convergent; tarsi concolorous with femora and tibiae; presence of median marginal setae on first abdominal segment.

MATERIAL EXAMINED.—Thirteen males and seven females were examined.

DISTRIBUTION.—Scant available records show that *P. halone* ranges from southern Mississippi presumably through the Appalachians into Tennessee and along the East Coast from Maryland



Figures 73–77. *Ptilodexia prexaspes* (Walker). Fig. 73. Genitalia of male, posterior view. Fig. 74. Ejaculatory apodeme. Fig. 75. Genitalia of male, lateral view. Fig. 76. Head of male, lateral view. Fig. 77. Geographical distribution.

to Albany, New York. There is one record from Georgia. Adults appear to be uncommon.

Biological Notes.—The flight period ranges from June to July in the southern part of its range and from mid-July to late August in the north. There are no ecological data associated with the material examined.

Ptilodexia prexaspes (Walker)

(Figures 73–77)

Dexia prexaspes Walker, 1849:837. Osten Sacken (1878:155); Brauer (1899:502); Austen (1907:345); Brimley (1938:368); Sabrosky and Arnaud (1965:989). [Lectotype (here designated), male, deposited in BMNH, labeled, "*Dexia prexaspes* Walk."/"Lectotype"/"Georgia, U.S.A., Ex. coll. Abbot"/"Georgia"/Crosskey examination label, 1970/ "Lectotype *Dexia prexaspes* Walker, designated by D. Wilder 1975."]

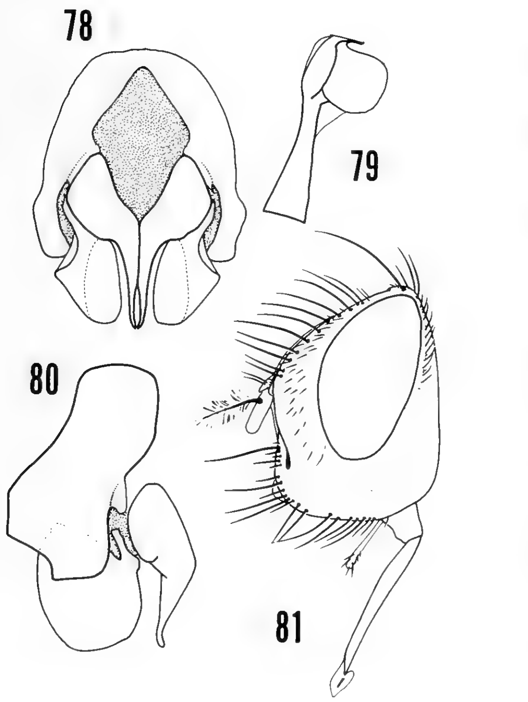
Taxonomic Notes.—The lectotype has the right front and rear tarsi missing, most frontals, dorsal abdominal, and thoracic setae missing, and the haustellum withdrawn.

Diagnosis.—Adults of *Ptilodexia prexaspes* are unique in the following combination of characters: Rather light-colored flies, females uniformly dark rufotestaceous except for darker tarsi; males may be partially brown dorsally, but with at least humeri and legs pale rufotestaceous; parafacial hairs dark, short in females, long and coarse in males, scattered on parafacial; third antennal segment 1.5 times length of second; length of plumosity on arista subequal to second antennal article; frontal vitta of males obliterated at some point between eyes; length of haustellum 0.3 to 0.4 times head height; oral margin protrudes slightly, if at all; area between oral vibrissae and oral margin distinctly higher than wide; legs of males and females light in color.

Material Examined.—Only six males and six females of *P. prexaspes* have been examined for this study.

Distribution.—This species appears to be localized and its members uncommon. The range extends from central Florida along the southern Atlantic coast to Cape Hatteras, North Carolina.

Biological Notes.—This insect appears to have two broods in Florida. The flight periods



FIGURES 78–82. *Ptilodexia harpasa* (Walker). Fig. 78. Genitalia of male, posterior view. Fig. 79. Ejaculatory apodeme. Fig. 80. Genitalia of male, lateral view. Fig. 81. Head of male, lateral view. Fig. 82. Geographical distribution.

are from late March and April to June in Florida, and late August and September to October in Florida and North Carolina.

Adults of *P. prexaspes* have been collected at a 15-watt UV light in March and June. In the fall they have been taken on *Solidago microcephala* and *Eupatorium*, both Compositae. One specimen was collected from a female asilid, *Efferia aestuans* (Linnaeus), which had presumably taken it as prey.

harpasa Group

Ptilodexia harpasa (Walker)

(Figures 78–82)

Dexia harpasa WALKER, 1849:840. OSTEN SACKEN (1878:155); ALDRICH (1905:502); AUSTEN (1907:344); DAVIS (1919:82); WEST (1924:186); ALDRICH (1925:114); JOHNSON (1925a:89); (1925b:208); (1927:203); LEONARD (1928:822); CURRAN (1930:93); TOWNSEND (1931:102); BRIMLEY (1938:368); PROCTER (1938:371); (1946:429); SABROSKY AND ARNAUD (1965:988). [HOLOTYPE, a female, deposited in BMNH, labeled, "*Dexia harpasa*, Walk."/"Holotype"/"40 3 30 1026"/"N. America. ex. Coll. Children 40.3.30.1026."/ Crosskey examination label 1970.]

Ptilodexia leucoptera WEST, 1925:132. LEONARD (1928:822); CURRAN (1930:93); WEST (1950:pl. I, fig. 2); SABROSKY AND ARNAUD (1965:989). [HOLOTYPE, female, deposited in CUIC, labeled, "Riverhead, L.I., N.Y., IX–17–13"/"Wing Slide, Cornell U., Lot. 919, Sub. 115, L. S. West"/"Holotype *Ptilodexia leucoptera* West ♀"/"Holotype Cornell U., No. 1874"/"Cornell U., Lot. 922, Sub. 42."] NEW SYNONYMY

Dinera robusta CURRAN, 1930:93. WEST (1950:111); SABROSKY AND ARNAUD (1965:989). [LECTOTYPE (here designated), male, deposited in CUIC, labeled, "Poughkeepsie, N.Y., July 1906, N.Y.S. Coll."/"♂ Allotype *Rhynchiodexia robusta* Curran"/"Allotype Cornell U., No. 1935"/"Cornell U., Lot. 922, Sub. 3"/"*Ptilodexia obscura* West, det. H. J. Reinhard"/"Lectotype *Dinera robusta* Curran designated by D. Wilder 1976."] NEW SYNONYMY

Ptilodexia tibialis (partim): TOWNSEND (1931:102).

TAXONOMIC NOTES.—*Ptilodexia harpasa* was first described and named from one female by Walker in 1849. The holotype is in poor condition, lacking posterior legs, right middle leg, and antennae (one antenna is glued to the double mount). All the setae from the dorsal surface of the thorax and abdomen are missing, and the coxal, sternopleural, and hypopleural areas of the left side are obliterated by the pin. The parafacial hairs have been rubbed off, but were obviously present at one time. Despite its condition, there is no question about the identity of the specimen.

Austen (1907) placed the name *P. harpasa* in synonymy with *P. tibialis*, apparently without seeing the type of the latter (which had been lost). Aldrich (in Davis 1919) disputed this and restored validity to *P. harpasa*. In 1925, upon visiting the Vienna Natural History Museum, he placed *P. carolinensis* in synonymy with *P. harpasa*, using for comparison specimens from USNM which were actually *P. canescens* and *P. planifrons*. At no time does Aldrich mention seeing the type of *P. harpasa*; he apparently based his conclusions solely on the word of Austen. In 1931, Townsend reiterated this synonymy and restored the name *P. tibialis* as the valid one, again without looking at the latter type. Since that time, the names *P. tibialis* and *P. harpasa* have both been used for many species of *Ptilodexia*.

Ptilodexia leucoptera was also described from a single female by West in 1925. The holotype, from Riverhead, Long Island, is in good condition and is deposited in CUIC.

Curran introduced the name *Dinera robusta* into the literature in his 1930 key. West (1950) claimed that he had never intended to describe *robusta* in the genus *Dinera*. This manuscript name was only tentative—until Curran validated it. The specific epithet, *robusta*, is totally misleading since this species is one of the smallest in the genus. West redescribed and illustrated *Rhynchiodexia robusta* in 1950, incorrectly designating his earlier types as holotype and allotype. Since Curran was the describer, the specimens he looked at (including West's holotype and allotype) became a syntype series, and the only valid designation could be lectotype and paralectotype. I have designated West's female "holotype" as paralectotype and his male "allotype" as lectotype. Other determined material in AMNH and CUIC which Curran probably used in developing his concept of the species have also been designated paralectotypes.

Diagnosis.—*Ptilodexia harpasa* adults are among the smallest, most slender flies in the genus. They have parafacial hairs medium to long, fine, distributed sparsely along center of parafacial, in a few individuals inserted below ventral eye margin; haustellum length 0.65 to 0.7 times head height, slender; third antennal segment long; length of plumosity on arista more than twice length of second antennal segment; abdomen and scutellum appear dark, but are actually partially rufescent.

Material Examined.—Four hundred seven males and 465 females were examined, a sex ratio different from the usual in the genus.

Distribution.—*Ptilodexia harpasa* ranges from the southern Appalachians into northern Quebec and west into Ohio, Michigan, northern Illinois, Minnesota, North Dakota, and Manitoba.

Biological Notes.—The flight period lasts from May to October, the most active months being August and September. *Ptilodexia harpasa* adults have been collected in Malaise traps, by net, on foliage, and as the prey of a crab spider. Flowers from which they have been collected are: *Solidago canadensis*, *Solidago rugosa*, *Eupatorium coelestinum* (Compositae); and *Melilotus alba* (Fabaceae).

Several specimens have been reared and are pinned with puparia. Two specimens from Ontario bear the label, "reared from R. C. larvae." This is perhaps an abbreviation for rose chafer, *Macrodactylus subspinosus*, a small scarab, whose range coincides with that of *P. harpasa*. Davis (1919) reports that adults have been reared from grubs (*Phyllophaga?*) from Connecticut.

Ptilodexia rufipennis (Macquart)

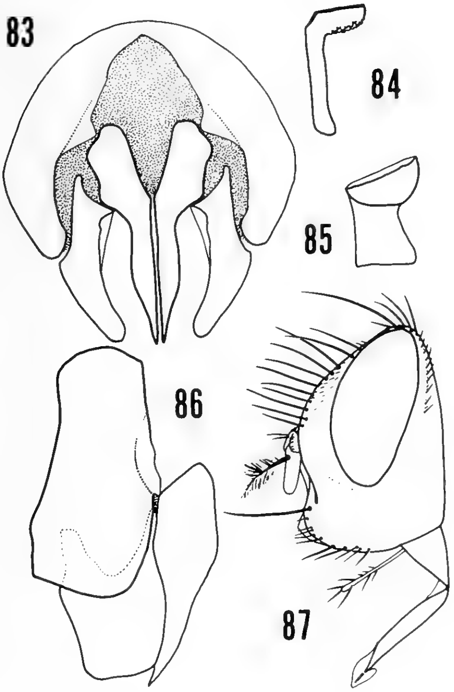
(Figures 83–88)

Dexia rufipennis Macquart, 1842:244. Osten Sacken (1878:155); Brauer (1899:508); Johnson (1925b:209); Aldrich (1905:504); Curran (1930:93); Brimley (1938:367); Sabrosky and Arnaud (1965:989). [Holotype, female, lost.]

Dexia cerata Walker, 1849:847. Osten Sacken (1878:155); Aldrich (1905:502); Austen (1907:344); Fattig (1944:3); Sabrosky and Arnaud (1965:989). [Holotype, female, deposited in BMNH, labeled, "*Dexia cerata* Walk."/"Holotype"/"N. Amer."/"N. America. Pres. by the Entomological Club, 44.12"/Crosskey examination label, 1970.] New Synonymy

Dexia albifrons Walker, 1852:317. Osten Sacken (1878:155); Aldrich (1905:501); Austen (1907:345); Sabrosky and Arnaud (1965:988). [Holotype, male, deposited in BMNH, labeled, "*Dexia albifrons* Walk."/"Holotype"/"U.S."/"United States Ex. Coll. Saunders. 68.4"/"*albifrons*"/Crosskey examination label, 1970.] New Synonymy

Rhynchodexia confusa West, 1924:185. Johnson (1925b:208); Leonard (1928:821); Curran (1930:93); Wray (1938:91); Reinhard (1943:22); West (1950:109); Sabrosky and Arnaud (1965:988). [Holotype, male, deposited in CUIC, labeled, "Selden, L.I., July 1, 1923, N.Y."/"Holotype



FIGURES 83–88. *Ptilodexia rufipennis* (Macquart). Fig. 83. Genitalia of male, posterior view. Fig. 84. Ejaculatory apodeme. Fig. 85. Ejaculatory apodeme. Fig. 86. Genitalia of male, lateral view. Fig. 87. Head of male, lateral view. Fig. 88. Geographical distribution.

Rhynchodexia confusa West, ♂"/"Holotype, Cornell U. No. 1245"/"Cornell U., Lot. 922, Sub. 35."] NEW SYNONYMY

Rhynchodexia translucipennis WEST, 1925:135. LEONARD (1928:821); CURRAN (1930:93); WEST (1950:pl. I, fig. 6); SABROSKY AND ARNAUD (1965:989). [HOLOTYPE, male, deposited in CUIC, labeled, "Ithaca, N.Y., 18 July '21"/"L. S. West Collector"/"Wing Slide, Cornell U., Lot 919, Sub. 116, L. S. West"/"Holotype, *Rhynchodexia translucipennis* West, ♂"/"Holotype Cornell U., No. 826"/"Cornell U., Lot 922, Sub. 37."] NEW SYNONYMY

Ptilodexia harpasa (partim): JOHNSON (1925b:209). (misidentification)

Ptilodexia neotibialis (partim): JOHNSON (1925:208). (misidentification)

Rhynchiodexia dubia CURRAN, 1930:93. WEST (1950:110); SABROSKY AND ARNAUD (1965:988). [LECTOTYPE (here designated), male, deposited in AMNH, labeled, "Sta. Study Insects, Tuxedo, N.Y., 28–VII–1928"/"Collector C. H. Curran"/"Lectotype *Rhynchiodexia dubia* Curran designated by D. Wilder 1976."] NEW SYNONYMY

TAXONOMIC NOTES.—The name *P. rufipennis* has been misused frequently in the literature. It also has a long list of synonyms. Part of the reason for this is clear—the species exhibits exceptionally high variability. Females and males differ from each other in taxonomic characters which were used previously in the group to define species. There is also strong clinal variation in males, which without being thoroughly sampled could lead workers to name certain populations as separate species. Specimens also are commonly collected. These factors, combined with the failure of earlier workers to examine type material, have contributed to the taxonomic problems in this species.

The name has been in general use since it was proposed in 1843. Brauer (1899) felt that this species was the same as *P. carolinensis*, and therefore placed the species in *Ptilodexia*. Subsequent workers used the name but failed to define the species. This was understandable since the type was lost and the original description was short.

Curran's 1930 key characterized members of the species as having infrasquamal setulae absent, parafacials haired, and the scutellum reddish. Macquart's description states that the female from Nova Scotia, which he named *Dexia* *rufipennis,* has, among other characteristics, the legs, basal antennal segments, and scutellum "testace." He also describes the epistome as "saillant" or protruding. The only species which ranges into Nova Scotia and whose members combine those characters with the others in Macquart's original description is the one presently being considered, specimens of which lack parafacial hairs.

The holotype of *Dexia cerata* Walker, described as being from "North America," fits Macquart's description perfectly. It is in poor condition, with antennae, facial setae, and left middle and hind legs broken. The haustellum is withdrawn.

Dexia albifrons Walker, another synonym of this species, is also from the "United States." The male holotype is a dark, small specimen of this varied species. It is in poor condition, entirely covered with dust or mold and missing most setae.

West used the genus *Rhynchodexia* for those species whose members lacked parafacial hairs. In describing *Rhynchodexia confusa,* he looked only at specimens from the northeastern United States and suspected that more than one species was involved. He also stated that this species had been represented in collections under the name *P. harpasa,* another Walker species described in the same paper as *P. cerata*. The description of *P. harpasa* is much less characteristic of members of this species than is that of *P. cerata,* and it is difficult to understand why that name was being used instead of *P. cerata*. The holotype and allotype of *P. confusa* are both large specimens with light-colored legs. They are in excellent condition.

West's other synonym of *P. rufipennis* is *Rhynchodexia translucipennis*. This species was described from two unusual-looking specimens of *P. rufipennis*. The holotype (and paratype) has translucent, milky-white wings and a light, reddish-brown thorax. It is possible that these specimens are teneral; however, they lack the characteristic collapsed face normally associated with teneral *Ptilodexia*. Tenerals do not generally have milky wings. Nevertheless, these specimens definitely belong in *P. rufipennis*. The type-specimens are in good condition.

The name *Rhynchiodexia dubia* was introduced into the literature by C. H. Curran in 1931. Between 1921 and 1925, West had been working with tachinids of New York and adjacent states and had placed type labels on certain specimens. His work was interrupted, and these specimens, with their manuscript names, were deposited in CUIC. Curran consulted this collection and used five of West's manuscript names in his paper "Diptera from Tuxedo," which was essentially a faunal list. Unfortunately, a key to adults of the species of *Rhynchiodexia* appears in this paper, making the names valid since they were accompanied by a statement of diagnostic characters.

Of the five species described in this paper, Curran mentions actual material for only one—*P. dubia*. He does not mention West's holotype (a female from Cimarron, Colorado), although he must have seen it to use the name. West's holotype belongs to *P. agilis* Reinhard; the specimens which Curran mentions belong to *P. rufipennis* and are from New York. I have designated the lectotype of *P. dubia* from the Curran material for the following reasons. Curran, in mentioning these specimens, made them syntypes; he does not indicate that he saw West's type, and there is a slight possibility that he did not. Also, West's type is in poor condition, whereas Curran's material is in good condition, and a lectotype designated from it would be supported by a long series of paralectotypes. I have given West's Colorado "holotype" the status of misassociated paralectotype.

The lectotype and paralectotypes are in excellent condition and are deposited in AMNH, FSCA, and CUIC. These specimens definitely belong to *P. rufipennis* (except West's "holotype").

In Curran's 1930 key, he separated *P. rufipennis,* as I have now defined it, into four species. The characters he used are: presence or absence of infrasquamals, color of male legs, color of scutellum, and presence or absence of parafacial hairs. All except the last are character states which vary among *P. rufipennis* adults.

Diagnosis.—Specimens of *P. rufipennis* are distinguished from those of all other species of *Ptilodexia* by the following combination of characters: face long and narrow, totally devoid of parafacial hairs ventral to second antennal segment; antennae long, width of plumosity on arista more than twice length of second antennal segment; abdomen grayish black or dark brown, reddish laterally in a few individuals; extreme tip of abdomen and genitalia yellowish; legs of females and often those of males pale in color;

ejaculatory apodeme with bulb in shape of a shallow cup.

VARIATION.—This species shows remarkable intraspecific variation. Northern specimens (those from Canada, Michigan, Wisconsin, North Dakota, and Montana) are dark in facial ground color; the antennae are dark in most adults; the legs of males are varied, ranging from light brown to almost black; and the length of the haustellum is almost half the head height. Specimens from Florida and Georgia into Texas are light in facial ground color; the antennae are rufotestaceous and the legs of males are pale, just as in females. These specimens have the haustellum short, about 0.3 times the head height.

In intermediate geographical areas, there is a mixture of the two forms. It is not uncommon to have a series split into half dark individuals and half light. There is no striking difference in the genitalia of members of these two forms, and in the areas of intergradation, intermediates occur. These intermediates are dark with short mouthparts or light with longer ones, and they are few in number. Many of the intermediate areas are represented by one or two specimens, and it is possible that a representative sample of these flies will show the presence of a smooth cline, northern areas having the largest percentage of dark specimens, southern areas the largest proportion of light ones, and the intermediate areas showing a north–south gradient of light and dark.

MATERIAL EXAMINED.—The sample of *Ptilodexia rufipennis* includes 694 males and 612 females.

DISTRIBUTION.—This species ranges from Newfoundland to southern Florida, across the continent to British Columbia, southeastern Washington, and central Montana. There are scattered records in central Colorado, New Mexico, and Texas.

BIOLOGICAL NOTES.—The flight period lasts from May to November. However, most specimens have been collected in the months of July, August, and September. In the Midwest and Canada, records for the months of July and August predominate, while in the Northeast and Mid-Atlantic states most are collected during August and September. In areas of heavy collecting (Suffolk County, New York), specimens seem to occur with similar frequency throughout the season. The small sample from Florida shows specimens collected in May and again in September, October, and November, perhaps indicating a bivoltine situation. In nearby Georgia the records show specimens taken from mid-May to mid-August with most occurring during June and July.

Ptilodexia rufipennis is predominately a lowland species. A few specimens have been collected in mountainous areas. In New Mexico, specimens were collected at 2,440 m in the White Mountains; specimens from Georgia were taken up to 1,460 m in the southern Appalachians; up to 1,890 m in North Carolina; and up to 1,830 m in Tennessee.

Ptilodexia rufipennis adults have been collected on a number of different flowers, including the following Compositae: *Solidago trinervata, Achillea Millefolium, Eupatorium perfoliatum, Chrysanthemum leucanthemum,* and unidentified *Solidago* sp., *Aster* sp., *Cirsium* sp., and *Anaphalis* sp. They have also been noted visiting *Melilotus alba* (Fabaceae), *Daucus carota* (Umbelliferae), *Ceanothus americanus,* and unidentified *Ceanothus* sp. (Rhamnaceae), and *Lonicera* sp. (Caprifoliaceae). Most of these flowers are yellow or white.

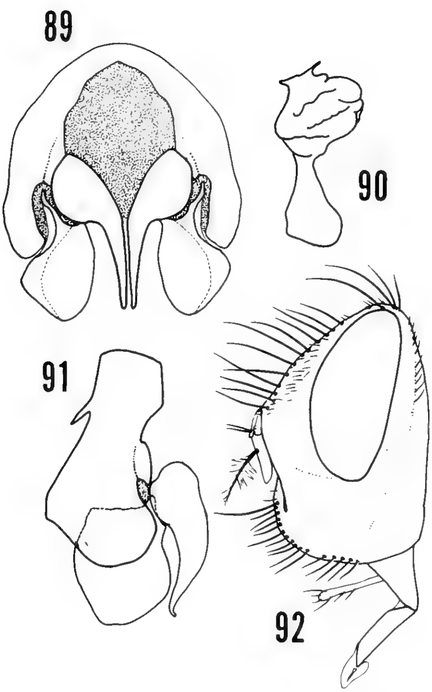
One specimen was collected from a female asilid (*Proctocanthus philadelphicus* Macquart), which had presumably captured it as prey. Other means of collecting have been by net (sweeping foliage), UV light trap, aerial light, and Malaise trap. *Ptilodexia rufipennis* adults have been collected in a cranberry bog, marshy meadow, creek bank, maple-elm floodplain along stream, and in a maple–mixed-oak–hickory forest.

Ptilodexia arida (Curran)

(Figures 89–93)

Rhynchiodexia arida CURRAN, 1931:93. WEST (1950:110); SABROSKY AND ARNAUD (1965:988); COLE (1969:543). [LECTOTYPE (here designated), a female, deposited in CUIC, labeled, "Pinnaleno Mts., Ft. Grant, Ariz."/"R. C. Shannon July 17, 1917"/"Altitude 7000 ft."/"Wing Slide, Cornell U., Lot. 919, Sub. 120, S. S. West"/"♀ Holotype *Rhynchiodexia arida* Curran"/"Holotype, Cornell U., No. 1937"/"Cornell U., Lot. 922, Sub. 39"/"Lectotype *Rhynchiodexia arida* Curran designated by D. Wilder 1976."]

TAXONOMIC NOTES.—Curran introduced the name into the literature in his 1930 key. West, however, was the one to segregate and name the species. West's "holotype," a female, has been designated as lectotype, even though it bears a holotype label with Curran as author. A speci-



Figures 89–93. *Ptilodexia arida* (Curran). Fig. 89. Genitalia of male, posterior view. Fig. 90. Ejaculatory apodeme. Fig. 91. Genitalia of male, lateral view. Fig. 92. Head of male, lateral view. Fig. 93. Geographical distribution.

men from Manitoba has been designated as paralectotype. This specimen has an undated Curran determination label, and I think that he compared the specimen with West's type, felt that they were the same, and consulted both when writing the 1930 key.

West's type is a female in poor condition, but the Manitoba male is in good condition. The Manitoba specimen is misassociated, actually belonging to *P. major*.

Diagnosis.—*Ptilodexia arida* adults are unique in the following combination of characters: broad, square face, no parafacial hairs ventral to second antennal segment; plumosity on arista long, up to twice length of second antennal segment; legs of females pale in color; abdomen of males and many females reddish laterally.

Material Examined.—Sixty-four males and 33 females were examined.

Distribution.—*Ptilodexia arida* ranges from Veracruz in Mexico into the mountains of Arizona and Utah. There is one record from Jefferson County, Idaho.

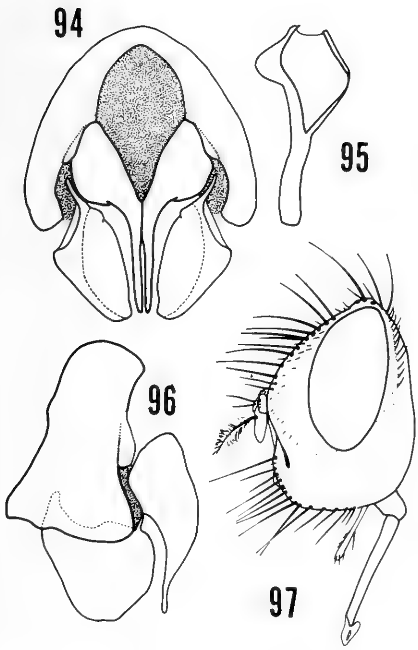
Biological Notes.—The flight period is from March to October, the majority of specimens being captured in July and August. There is only one March record and none for the months of April and May. One specimen from Morelos in Mexico was collected in November.

This species inhabits a mountainous region. Specimens have all been collected in the mountains, some at elevations up to 2,560 m. One exception is a male collected in Jefferson County, Idaho, an area of extensive lava fields. Other specimens have been collected by special devices, such as UV light and Malaise traps. One female was collected on *Ceanothus* (Rhamnaceae), and four males were swept from *Ipomoea* (Convolvulaceae). There are five reared specimens; however, they lack data. They are pinned with their hosts, small scarabaeid larvae.

Ptilodexia ponderosa (Curran)

(Figure 6)

Rhynchiodexia ponderosa Curran, 1930:93. West (1950:110); Sabrosky and Arnaud (1965:989). [Lectotype, female,



FIGURES 94–98. *Ptilodexia major* (Bigot). Fig. 94. Genitalia of male, posterior view. Fig. 95. Ejaculatory apodeme. Fig. 96. Genitalia of male, lateral view. Fig. 97. Head of male, lateral view. Fig. 98. Geographical distribution.

deposited in CUIC, labeled, "Chokoloskee, Fla."/"Wing Slide, Cornell U. Lot. 919, Sub. 129, L. S. West"/"♀ Holotype *Rhynchiodexia ponderosa* Curran"/"Holotype Cornell U. No. 1936"/"Cornell U. Lot. 922, Sub. 38"/"Lectotype *Rhynchiodexia ponderosa* Curran."]

TAXONOMIC NOTES.—This species was originally segregated and named by West, but the name was introduced into the literature by Curran and dates from his 1930 key. The unique specimen was not designated as a holotype. Since Curran did not mention the number of specimens which he had, even though there is only one, it must be designated lectotype. The specimen is in excellent condition.

DIAGNOSIS.—Since this species is represented by one specimen, it is difficult to diagnose. The *P. ponderosa* specimen can be distinguished from members of all other related species by the following combination of characters. Size large, color light reddish brown; face wide; parafacial hairs small, brown, inserted only on anterior half of parafacial; vibrissal angle of head quite pronounced; epistome protrudes noticeably; third antennal segment long; length of plumosity 1.6 times length of second antennal segment; haustellum length 0.6 times head height; legs uniformly testaceous.

DISTRIBUTION.—The lectotype was collected in extreme southern Florida and almost certainly represents a West Indian species. It more closely resembles specimens from these islands (most of which have small, pale, parafacial hairs, long plumosity on the arista, and a medium-long haustellum) than those from the United States. It differs from the specimens I have seen from the islands in being much larger and having uniformly pale legs.

major Group

Ptilodexia major (Bigot)

(Figures 94–98)

Rhamphinina major BIGOT 1888:265. WULP (1891:228); GIGLIO-TOS (1894:60); BRAUER (1899:509); ALDRICH (1905:504); SABROSKY AND ARNAUD (1965:989); COLE (1969:543); GUIMARAES (1971:33). [LECTOTYPE (here designated), male, deposited in BMNH, labeled, "Lectotype"/"*Rhamphinina major* Bigot"/"Mexico. Ex. coll. Bigot. Pres. by G. H. Verrall, Oct. 1904. 1904–274"/"Lectotype *Rhamphinina major* Bigot designated by D. Wilder 1975."]

Rhynchiodexia tincticornis BIGOT, 1888:266. WULP (1891:228); BRAUER (1899:509); ALDRICH (1905:504); GUIMARAES

(1971:34). [Lectotype (here designated), male, deposited in BMNH, labeled, "Lectotype"/"*Rhynchiodexia tincticornis* Bigot"/"Mexico. Ex. coll. Bigot. Pres. by G. H. Verrall, Oct. 1904. 1904–274"/Bigot's original inked label/ Austen's penciled note regarding Bigot's label/"Lectotype *Rhynchiodexia tincticornis* Bigot designated by D. Wilder 1975."]

Dexiosoma fumipennis Bigot, 1888:270. Wulp (1891:230); Brauer (1899:508); Aldrich (1905:504); Guimaraes (1971:34). [Holotype, female, deposited in BMNH, labeled, "Holotype"/"*Rhynchiodexia fumipennis*"/"Mexico. Ex. coll. Bigot. Pres. by G. H. Verrall, Oct. 1904. 1904–274"/2 folded labels.] New Synonymy

Rhynchodexia fraterna Wulp, 1891:229. Giglio-Tos (1894:61); Aldrich (1905:499); Thompson (1963:517); Guimaraes (1971:33). [Lectotype (here designated), male, deposited in BMNH, labeled, "Lectotype"/"Cuernavaca, Morelos. June H. H. S."/"♂"/"B. C. A. Dipt. II *Rhynchodexia fraterna*, v.d.W."/"Central America Pres. by F. D. Godman, O. Salvin. 1903–172"/"Lectotype *Rhynchodexia fraterna* Wulp, desig. by D. Wilder 1975."] New Synonymy

Rhynchodexia omissa Wulp, 1891:235. Aldrich (1905:499); Guimaraes (1971:33). [Lectotype (here designated), male, deposited in BMNH, labeled, "Lectotype"/"N. Yucatan, Gaumer"/"♂"/"B. C. A. Dipt. II *Rhynchodexia omissa* v.d.W."/"Central America Pres. by F. D. Godman, O. Salvin. 1903–172"/"Lectotype *Rhynchodexia omissa* Wulp designated by D. Wilder 1975."] New Synonymy

Ptilodexia harpasa (partim): Davis (1919:83). (misidentification)

Rhynchiodexia arida (partim): Curran (1930:93). (misidentification)

Taxonomic Notes.—The confusion and synonymy of this species in the literature is understandable. It is quite variable in color characteristics and size of its members. It also has a broad geographical range. Bigot proposed three names for *P. major* and Wulp two.

The syntype series for *P. major* consists of five males. Two of these are misassociated, one resembling specimens of *P. conjuncta* but with a shorter haustellum, the other resembling specimens of *P. scutellata* but with much hairier parafacials. The other three are conspecific. The specimen chosen as a lectotype has the upper parafacials a little hairier than the others, and its facial tomentum has a slightly yellowish cast. The series is in poor condition, the lectotype having only one leg and one antenna; most of the setae are broken.

Associated with the syntype series is a penciled label in Austen's handwriting. It mentions that Brauer (1899:509) felt the species belonged to *Ptilodexia*. He continued, however, saying that he (Austen) felt that the series was comprised of representatives of three distinct genera, only one specimen belonging to *Ptilodexia*. The specimen which Austen felt was a *Ptilodexia* is the misassociated type resembling specimens of *P. conjuncta*. His reasoning is not clear, but perhaps he failed to see the minute parafacial hairs on true *P. major* members and therefore felt it belonged in another genus. The type which resembles adults of *P. scutellata* could understandably be considered as representing a different genus by a worker who believed in restricted genera.

Bigot stated the type-locality as Mexico and Washington Territory. All five syntypes have labels reading "Mexico."

Both of the cotypes of *Rhynchiodexia tincticornis* are in poor condition. The specimen chosen as lectotype is oily, the tomentum therefore obscured. Wulp (1891) redescribed the species and restricted the type-locality to Paso del Macho, possibly taking the name of the locality from another Bigot label. Since this locality is within the range of the species, the restriction is accepted. Wulp stated that he had a female from Costa Rica. It is possible, but unlikely, that the species ranges that far south. Brauer (1899) placed *P. major* in *Ptilodexia* and listed *P. tincticornis* as a synonym.

Bigot described *R. fraterna* in 1891 from 21 males and 5 females. Of the four male specimens which I had the opportunity to see, one was misassociated, the other three belonged to *P. major*. Wulp himself stated after his description that three of his largest specimens "agree fully with a typical example of *Rhamphinina major*," and he then cited a few minor color differences. He also felt that some of the smaller specimens "bear a striking resemblance" to *P. fumipennis* adults. The lectotype, a male from Cuernavaca, is in good condition.

Rhynchiodexia omissa was described from three male and two female cotypes. The male which I saw and designated as lectotype belongs to *P. major*. The specimen was collected in northern Yucatan. It is in excellent condition and is similar in color to the lectotype of *P. tincticornis*. Guimaraes (1971) was the first to place *omissa* in *Ptilodexia*.

Another name must be considered while discussing *P. major*. This is *Rhamphinina dubia* Bigot, the type-species of that genus. Bigot described *R. dubia* from two females labeled only "Mexico." The two specimens now in the British Museum are, however, a male and a female. The male belongs to *P. major* and the female to *Macrometopa calogaster*, the latter placed by

Austen. Townsend (1931:100) spoke of a female holotype; however, this cannot be considered a lectotype designation of the type-series according to Crosskey (in litt.). I have designated the female of the original material as the lectotype, giving the male the status of misassociated paralectotype. Had the other specimen (♂, *P. major*) been chosen as the lectotype, the name *Rhamphinina* (1885) would have priority over *Ptilodexia* (1889) and our commonly used name would have to be changed. *Macrometopa* now becomes a synonym of *Rhamphinina*.

DIAGNOSIS.—*Ptilodexia major* exhibits much variation throughout its range, and after a more thorough sample is available, may be found to consist of more than one species. It is most difficult to diagnose, and specimens can be more easily identified by first eliminating other species.

Thorax dark, the notum distinctly striped; parafacial hairs small, pale, inserted only on anterior half of parafacial, ventrally on face to apex of antennae; they are light brown, medium length, and/or scattered on parafacial in few individuals; haustellum length varied, from 0.55 to 0.65 times head height, in some small specimens it is slightly longer; palpi longer than half haustellum length in most individuals; length of plumosity on arista more than twice length of second antennal segment; abdomen reddish with dark median stripe in most males, entirely dark or dark with fourth tergite reddish in a few.

VARIATION.—*Ptilodexia major* exhibits more variability than do most *Ptilodexia*. A summary of this variation is given by Wilder (1976).

There are some specimens, notably those from Texas, New Mexico, Colorado, and Nebraska, which seem to fall somewhere between specimens of *P. incerta* and *P. major*, two species which are, from available records, allopatric. It is possible that these represent an as yet unrecognized species and that true *P. major* is a more southern species. Most of the characters involved, however, are vague and in other species are part of normal intraspecific variation. This problem may be solved when a larger sample is available, thereby allowing the use of statistical techniques. I have placed these specimens in *P. major* because it is with members of this species that they share the most character states.

Most Nearctic *Ptilodexia* do not have ranges which extend into neotropical Mexico (*P. conjuncta* is an exception). Specimens of *P. major* from Chiapas, Campeche, and Yucatan, however, differ very little from those from Arizona, at least in characters which easily separate adults or other species in the genus. I feel justified in placing all these specimens in *P. major*, although when more Mexican material is available for study, it may show that more than one species is involved.

MATERIAL EXAMINED.—One hundred fifty-two males and 77 females of *P. major* were examined.

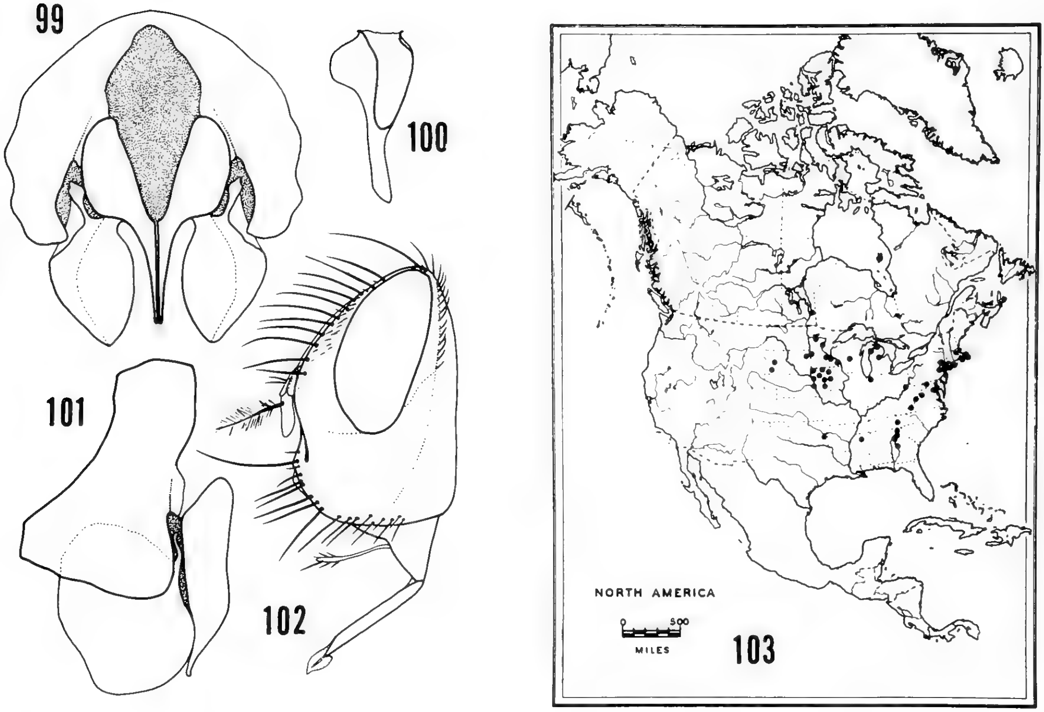
DISTRIBUTION.—This species ranges from Nebraska southward through Colorado, Kansas, Arizona, New Mexico, and Texas into southern Mexico.

BIOLOGICAL NOTES.—The flight period ranges from April to October, with the main activity in July and August in most parts of the range. Members of Texas populations exhibit two periods of activity, one in April and May, and another in September and October. Specimens reared indoors appear to emerge much earlier, in December, February, and March.

Specimens have been taken at both low and high elevations, the highest being 2,130 m in Coahuila, Mexico. Methods used to collect *P. major* adults are sweeping, UV light trap, Malaise trap, and rearing. Flowers from which *P. major* adults have been captured include: *Senecio* sp., *Baccharis glutinosa* (Compositae); *Lepidium thurberi* (Cruciferae); *Croton* sp. (Euphorbiaceae); *Medicago sativa*, *Dalea albiflora* (Fabaceae); *Marrubium vulgare* (Labiatae); *Gossypium* sp. (Malvaceae), and *Tamarix* sp. (Tamaricaceae). Unlike other *Ptilodexia*, composites are not the group of flowers most frequently visited.

Several specimens among the material examined have been reared and are associated with skins of host larvae. Unfortunately, these skins cannot be identified. Host data on some specimens list the host as "May beetle" and *Phyllophaga farcta*. David (1919) mentions *Phyllophaga* grubs collected on 29 April, at Austin, Texas:

> *Ptilodexia* larvae were first observed from May 18 to June 18. In these cases, adult flies issued between June 11 and July 10, the puparium stage varying from 20–32 days. Grubs collected in New Mexico May 10 and 24 showed parasitism from May 20 to July 7, while larvae from the same locality collected on September 7 and confined in indoor cages showed parasitic larvae from October 7 to February 23.



FIGURES 99–103. *Ptilodexia incerta* (West). Fig. 99. Genitalia of male, posterior view. Fig. 100. Ejaculatory apodeme. Fig. 101. Genitalia of male, lateral view. Fig. 102. Head of male, lateral view. Fig. 103. Geographical distribution.

Aldrich called these New Mexico and Texas specimens *Ptilodexia harpasa*, but they are typical of *P. major* adults. Davis also reports members of this species being reared from grubs of *Aphonus pryiformis* collected in Las Vegas and Caffrey, New Mexico.

Ptilodexia incerta West

(Figures 99–103)

Ptilodexia incerta WEST, 1925:131. LEONARD (1928:822); CURRAN (1930:93); SABROSKY AND ARNAUD (1965:989). [HOLOTYPE, male, deposited in CUIC, labeled, "Riverhead, L.I., N.Y. 6–30–21"/"Holotype *Ptilodexia incerta* West ♂"/"Holotype Cornell U. No. 1873"/"Cornell U. Lot. 922, Sub. 45"]

Ptilodexia proxima WEST, 1925:133. LEONARD (1928:822); CURRAN (1930:93); WEST (1950:pl. I, fig. 4); SABROSKY AND ARNAUD (1965:989). [HOLOTYPE, male, deposited in CUIC, labeled, "Riverhead, L.I., N.Y."/"Wm. T. Davis, Aug. 5, 1917"/"Wing Slide, Cornell U. Lot. 919, Sub. 121, L. S. West"/"Holotype *Ptilodexia proxima* West ♂"/"Holotype Cornell U. No. 1877"/"Cornell U. Lot 922, Sub. 47"] NEW SYNONYMY

Rhynchodexia elevata WEST, 1925:135. LEONARD (1928:821); SABROSKY AND ARNAUD (1965:988). [HOLOTYPE, male, deposited in CUIC, labeled, "Riverhead, L.I., N.Y., Aug. 20, 1922"/"Wing Slide Cornell U. Lot. 919, Sub. 123, L. S. West"/"Holotype *Rhynchodexia elevata* West ♂"/"Holotype Cornell U. No. 1871"/"Cornell U. Lot. 922, Sub. 36."] NEW SYNONYMY

Ptilodexia harpasa (partim): JOHNSON (1925b:208). (misidentification)

Rhynchiodexia levata West: CURRAN (1930:93). (lapsus calamus)

TAXONOMIC NOTES.—West described *P. incerta* and its two synonyms in the same paper. The type-localities of all three are Riverhead, Long Island. None of his holotypes, all males, show any significant differences. The type of *P. proxima* is large, that of *P. elevata* is small, while the type of *P. incerta* is intermediate in size.

West placed *P. elevata* in the genus *Rhynchodexia* because he thought that it lacked parafacial hairs. These hairs, however, are present and are similar in size, color, and number to those of the other two species. He also felt that the *P. elevata* adult differed in having the vibrissae inserted far above the oral margin, another characteristic which is the same in the other two species.

West stated no diagnostic difference between the *P. incerta* and *P. proxima* males, and the descriptions of the two are nearly identical.

The types of these three species names are in excellent condition, with the possible exception of the holotype of *P. incerta,* which is dusty. They are all deposited in CUIC. The three are unquestionably conspecific.

DIAGNOSIS.—Adults of *P. incerta* can be distinguished from those of other species of the genus overlapping in range by the following combination of character states: parafacial hairs tiny and pale (rarely brown), present only on extreme upper anterior portion of parafacial; length of third antennal segment about 1.5 times length of second; length of plumosity on arista twice length of second antennal segment. Haustellum length 0.5 to 0.6 times head height; palpi, broad in many individuals, equal to or less than half haustellum length. Thorax distinctly striped; in many specimens there are few or no infrasquamal setulae; in most abdomen reddish with a median longitudinal stripe.

MATERIAL EXAMINED.—Specimens examined include 105 males and 32 females.

DISTRIBUTION.—This species occurs throughout the eastern U.S., west to about the 100th meridian.

BIOLOGICAL NOTES.—The flight period lasts from May to September, with most specimens being collected during July. In certain areas, especially in the Southeast, specimens have been taken in every month from 10 May to 26 September.

Associated data show that *P. incerta* adults have been collected while at blooms of *Cirsium* sp. and *Solidago* sp., both Compositae. They have also been taken on high prairie in Hennepin County, Minnesota. A male was taken from a phymatid, which had presumably captured it as prey. Records show that *P. incerta* adults have only been collected at low elevations.

Ptilodexia maculata, new species

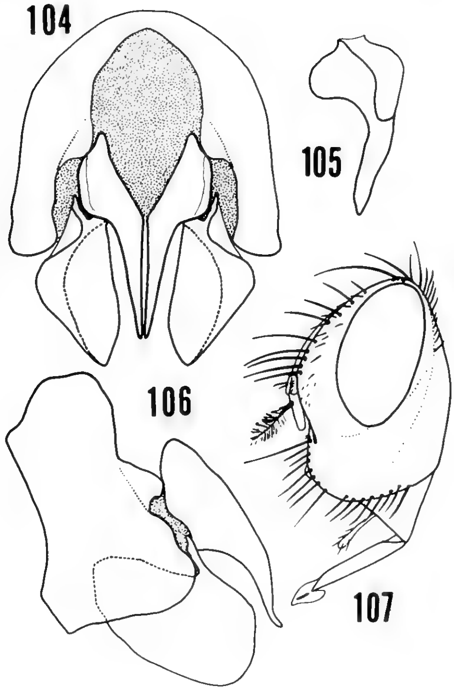
(Figures 104–108)

TYPE-LOCALITY.—The holotype was collected 14 miles [ca. 22.5 km] north of Silver City, Grant County, New Mexico.

TYPE-SPECIMENS.—The holotype, a male, is deposited in MSUC, the allotype, from Show-Low Arizona, in USNM. Complete data from these specimens and the 12 male and 10 female paratypes are listed below.

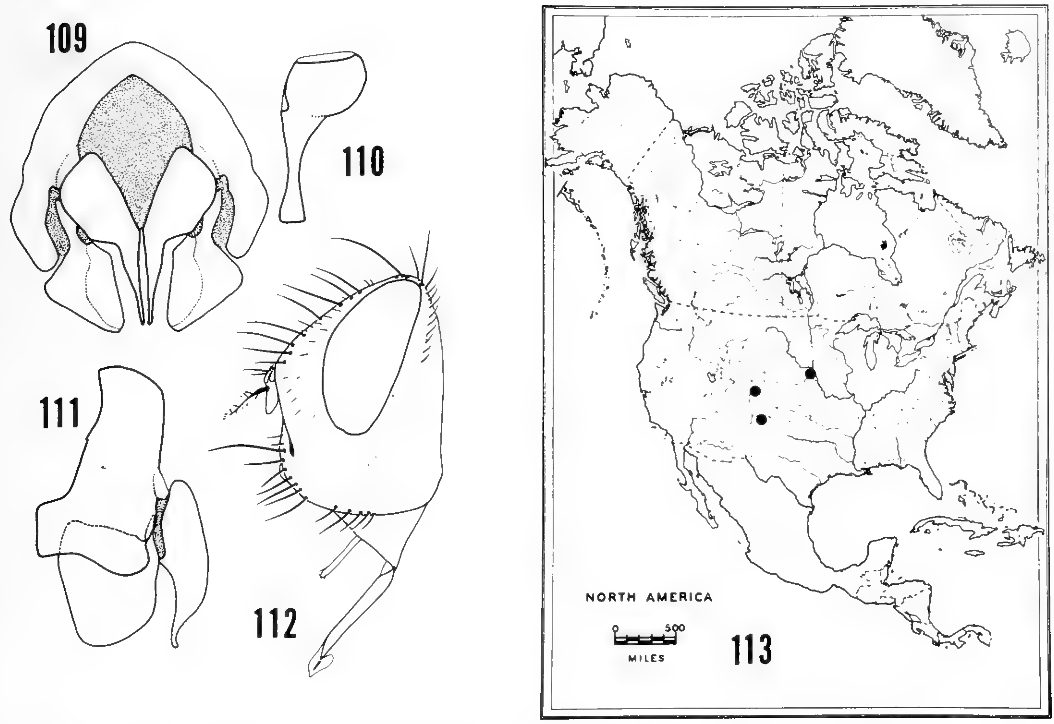
DIAGNOSIS.—*Ptilodexia maculata* is a distinctive species, its members differing from those of its congeners by the following combination of character states. Reddish brown; face wide, anteroventral angle not strongly protruding; parafacial hairs small, pale, occuring only along anterior edge of parafacial; oral margin only slightly protruding; infrasquamal setulae lacking; haustellum length 0.4 to 0.5 times head height. The legs of males and females are pale, the femora with striking dark brown apicoventral patches.

DESCRIPTION.—**Male:** Total body length 16 mm, brownish with median abdominal stripe. *Head* height 3.5 mm; profrons 0.3 times head length. Facial tomentum pale gold, shining, fine, not obscuring integumental color; parafrontal hairs long, dark, sparse; parafacial hairs small, pale, inserted only along anterior edge of parafacial and not ventral to antennal apex. Width of frontal vitta at base of antenna 0.55 mm, at narrowest part 0.25 mm; carina well developed, long, wide; facial cavities slightly darkened. Height of gena 0.35 times head height. One pair of ocellar setae, 2 pairs of postocellars subequal to ocellars, 1 pair of shorter postverticals, 1 pair of long inner verticals, and 1 pair of outer verticals subequal to postorbitals. Fifteen pairs of postorbital setae not interspersed with smaller hairs, those closest to ocellar triangle long, becoming smaller with distance from ocellar triangle, curved only slightly anterad; between postorbitals and the dense whitish occipital hair are a few scattered hairs. Twelve pairs of frontal setae; one pair of oral vibrissae 0.25 mm from oral margin, the depression between them 0.4 mm wide; 12 additional oral setae, 1 above vibrissae fairly strong, peristomals subequal to each other. Epistome only slightly protruding, its width 1.3 times length of first two antennal segments. Haustellum broad, brown, 0.4 times head height; palpi testaceous, 0.7 times haustellum length. Antennae unique; second segment light brown, testaceous apically; third segment testaceous on basal half, light brown apically; arista and plumosity pale brown. Third segment of antenna slightly narrowed apically, 1.3 times length of second segment; length of plumosity on arista 1.5 times length of second antennal segment. *Thorax*: Mesonotum rufotestaceous, brown posteriorly, subshining; tomentum beige, striping indistinct. Integument of humeri and postalar calli rufotestaceous. Six pairs of strong humeral setae, 1 posthumeral, 1 presutural, and 2 pairs of discal scutellars. Pleura rufotestaceous



FIGURES 104–108. *Ptilodexia maculata*, n.sp. Fig. 104. Genitalia of male, posterior view. Fig. 105. Ejaculatory apodeme. Fig. 106. Genitalia of male, lateral view. Fig. 107. Head of male, lateral view. Fig. 108. Geographical distribution.

marked with brown, tomentum beige, translucent; infrasquamal setulae absent; squamae and wings pale testaceous; epaulet light brown, basicosta testaceous, mediotergite tomentose, subshining. *Legs* rufotestaceous, tibiae darkened basally and apically, coxae and trochanters marked with dark brown; femora with dark brown, strongly contrasting ventral patches on apical half, bases of setae inserted on dark patches pale in color, pale setal bases on maculae of anterior femur coalesced into pale stripe; tarsi black. Anterior femur with 12 dorsal setae, 8 posterodorsals, and 13 posteroventrals, tibia with a distinct dark dorsal line. Middle femur with 2 anterior setae in 1 row. Posterior femur with a row of 7 anterodorsal setae, 9 anteroventrals, 6 posteroventrals, and 1 anterior seta; posterior tibia curved. *Abdomen* rufotestaceous with dark brown, narrow, median stripe; tomentum whitish, brown above median stripe. First syntergite with 3 pairs of lateral marginal setae. Second tergite with 3 pairs of median discals, 12 dorsal and lateral marginals, and 4 pairs of lateral discal setae. Ventral margins of tergite marked with brown. *Genitalia*: Eighth tergite with numerous fine, dark setae. Ninth tergite with many long, dark setae, lateral swelling small. Surstylus huge, lateral angle smoothly rounded, depression fairly deep, with only fine hairs; in profile, smoothly rounded with slight ventral swelling. Cerci elongate, lateral lobes laterally curved strongly anterad, mesal margins slightly concave; height of arms slightly greater than that of lobes, arms not reaching ventral margins of surstyli, in profile, slightly bulging, tips large, round. Ejaculatory apodeme with bulb and stem distinct, the latter slightly longer and curved. Bulb widely open on one side and top; opposite side strongly decumbent. **Female:** Similar to male except for usual sexual differences and the following. Width of frontal vitta at narrowest point 0.4 mm, at antennal base 0.7 mm. Height of gena 0.35 times head height. Ten pairs of short postorbital setae, with 1 or 2 small hairs interspersed; 7/8 frontal setae. Anterior femur with 9 posteroventrals, 7 posterodorsals, and 9 dorsal setae. Middle femur with 4 anterior setae in 2 rows, 4 posteroventrals, and no an-



FIGURES 109–113. *Ptilodexia flavotessellata* (Walton). Fig. 109. Genitalia of male, posterior view. Fig. 110. Ejaculatory apodeme. Fig. 111. Genitalia of male, lateral view. Fig. 112. Head of male, lateral view. Fig. 113. Geographical distribution.

teroventrals. Posterior femur with no anterior setae, 5 anterodorsals, 3 posteroventrals, and 3 anteroventrals. Abdomen rufous with vague dark-brown median stripe, pollen whitish, light brown around median marginal setae. First syntergite with 1 pair of strong lateral marginal setae. Second tergite with 1 pair of lateral marginals, median discals, and median marginals. Third tergite with 1 pair of median discals and 5 dorsal and lateral marginal setae.

VARIATION.—Intraspecific variation is slight. Total body length ranges from 10 to 16 mm. The parafacial hairs are brownish in some specimens, but they are small in all adults. The area between the oral vibrissae and the oral margin has the height equal to width in some specimens. The integument of the notum in some individuals is rufotestaceous striped with dark brown. All facial and body tomentum are shades of brown in some adults, in females, quite dark.

MATERIAL EXAMINED.—Thirteen males and eleven females were examined from the following localities. **Arizona:** *Cochise Co.*: 1♂, Garden Canyon, Huachuca Mts., 30 July 1949, W. Gertsch (AMNH); 1♂, Ramsey Canyon, 15 miles [ca. 24 km] S of Sierra Vista, 6,000 ft [ca. 1,830 m], 1 July 1964, Sternitzky (CNCI); 1♂, Rucker Canyon, Chiricahua Mts., 22 Aug. 1965, G. Wallace (UCRC). *Navajo Co.*: 1♀, Show-Low, 24 July 1956, Butler (UAIC). *Santa Cruz Co.*: 1♀, Madera Canyon, 4,880 ft [ca. 1,490 m], 15 June 1965, D. Harrington, 1♀, 25 July, 1♂, 6 Aug. 1961, at light, G. Nelson, 1♀, 11 Aug. 1965, D. Harrington, 2♀♀, 12 Aug., 1♂, 15 Aug., 1♂, 17 Aug. 1972, D. Knull, 1♂1♀, 26 Aug. 1965, D. Harrington, 1♂, 1 Sep., 1♂3♀♀, 7 Sep., 1♀, 15 Sep. (UCDC, OSUC). **New Mexico:** *Catron Co.*: 2♂♂, Mogollon Mts., 29 Aug. 1951 (CASC). *Grant Co.*: 1♂, 14 miles [ca. 22.5 km] N of Silver City, 8 July 1961, G. Eickwort (MSUC). *Hidalgo Co.*: 1♂, Guadalupe Canyon, 7 Aug. 1967, J. Smith (UCRC).

BIOLOGICAL NOTES.—The flight period lasts from July to September. Adults of this species have been collected at lights. They inhabit mountainous areas and have been taken at elevations from 1,490 m to 1,830 m.

DERIVATION OF NAME.—The name of this species refers to the striking femoral maculae on its members.

Ptilodexia flavotessellata (Walton)

(Figures 109–113)

Rhynchiodexia flavotessellata WALTON, 1914:176. TOWNSEND (1915:23); (1938:349); SABROSKY AND ARNAUD

(1965:988); Cole (1969:543). [Holotype, female, taken in copula and pinned with its mate, deposited in USNM, labeled, "Koehler, New Mexico, 8–14"/"Webster No. 7707"/"W. R. Walton collector."]

Taxonomic Notes.—Walton stated that he described this species from four specimens taken at Eagle Tail Mountain, Colfax County, New Mexico. He named a female, pinned in copula with its mate, the holotype. These specimens bear a label which reads only, "Koehler, New Mexico" as the locality; however, since Walton himself was the collector, his restriction is accepted. There are more specimens than the description records with identical labels, so the three males which he indirectly makes paratypes cannot be segregated. The type material is in excellent condition.

Townsend (1915) erected the genus *Myoceropsis* for *P. flavotessellata*. He believed that specimens of *Ptilodexia* had the haustellum longer than 0.75 times the head height and that *P. flavotessellata*, its members with the haustellum length 0.5 times the head height, differed sufficiently to be segregated generically.

Diagnosis.—Specimens of *P. flavotessellata* can be distinguished from those of other North American *Ptilodexia* by the following combination of character states: general color pale orange-brown, tarsi darker; parafacial hairs pale to brown, of medium length, sparse, scattered randomly on parafacial; third antennal segment not much longer than second; length of plumosity 1.25 to 1.5 times length of second antennal segment; haustellum light brown in color, narrow, about 0.5 times head height; area between oral vibrissae and oral margin wider than high; epistome protrudes only slightly.

Material Examined.—Five male and three female specimens were examined.

Distribution.—*Ptilodexia flavotessellata* ranges from northeastern New Mexico north into Colorado and Nebraska.

Biological Notes.—The collection dates on the specimens examined range from 22 June in Boulder, Colorado, to 9 September in Nebraska. There are no associated ecological data.

Literature Cited

Aldrich, J. M. 1905. A catalogue of North American Diptera. Smithson. Misc. Collect. 46(2):1–680.

———. 1924. Notes on some types of American muscoid Diptera in the collection of the Vienna Natural History Museum. Ann. Entomol. Soc. Am. 17:209–218.

———. 1925. Notes on some types of American muscoid Diptera in the collection of the Vienna Natural History Museum (cont.). Ann Entomol. Soc. Am. 18:107–130.

Austen, E. E. 1907. The synonymy and general position of certain species of Muscidae (*sens. lat.*) in the collection of the British Museum, described by the late Francis Walker. Ann. Mag. Nat. Hist., Ser. 7, 19:326–347.

Bigot, J. M. F. 1885. Diagnoses de trois genres nouveaux de Diptères du groupe des Déxiaires. Ann. Soc. Entomol. France (6)5:xi–xii.

———. 1889. Diptères nouveaux ou peu connus 34ª partie, XLII, Diagnoses de nouvelles espèces. Ann. Soc. Entomol. France (6)8:253–270.

Blanchard, E. E. 1966. Dipteros parasitos de escarabeoideos argentinos. Rev. Invest. Agric., Ser. 5, 3(11):175–229.

Brauer, F. 1899. Beiträge zur Kenntniss der Muscaria Schizometopa. Bemerkungen zu den original exemplaren der von Bigot, Macquart und Robineau-Desvoidy, beschreiben Muscaria Schizometopa aus der Sammlung des Herrn G. H. Verrall, III. Sitzunsber. K. Akad. Wiss. Wien, Math.–Naturwiss. Kl. 1(108):495–529.

——— and J. E. von Bergenstamm. 1889. Die Zweiflügler des Kaiserlichen museums zu Wien. IV. Vorarbeiten zu einer monographie der Muscaria Schizometopa. Pars I. Denkschr. K. Akad. Wiss. Wien 56(1):69–180.

Brimley, C. S. 1938. Insects of North Carolina. North Carolina Dep. Agric., Div. Entomol., Raleigh. 491 pp.

Champlain, A. B., and J. N. Knull. 1944. Notes on Pennsylvania Diptera. Entomol. News 34(7):211–215.

Clausen, C. P., J. L. King, and C. Teranishi. 1927. The parasites of *Popillia japonica* in Japan and Chosen (Korea) and their introduction into the United States. U.S. Dep. Agric. Agric. Res. Serv. Tech. Bull. 1429. 56 pp.

Cole, F. R. 1969. The flies of western North America. Univ. Calif. Press, Berkeley and Los Angeles. 693 pp.

Coquillett, D. W. 1910. The type species of the North American genera of Diptera. Proc. U.S. Natl. Mus. 37:499–647.

Crosskey, R. W. 1973a. A revisionary classification of the Rutiliini (Diptera: Tachinidae), with keys to the described species. Bull. Brit. Mus. (Nat. Hist.) Entomol. Suppl. 19: 1–167.

———. 1973b. A conspectus of the Tachinidae (Diptera) of Australia, including keys to the supraspecific taxa and taxonomic and host catalogues. Bull. Brit. Mus. (Nat. Hist.) Entomol. Suppl. 21:1–221.

Curran, C. H. 1930. Report on the Diptera collected at the Station for the Study of Insects, Harriman Interstate Park, N.Y. Bull. Am. Mus. Nat. Hist. 61:21–115.

———. 1934. The Diptera of Kartabo, Bartica district, British Guiana with descriptions of new species from other British Guiana localities. Bull. Am. Mus. Nat. Hist. 66:287–532.

Davis, J. J. 1919. Contributions to a knowledge of the natural enemies of *Phyllophaga*. Ill. Nat. Hist. Surv. Bull. 8(5):53–138.

Fattig, P. W. 1944. *Phyllophaga* of Georgia. Emory Univ. Mus. Bull. Georgia, no. 2, 32 pp.

Fleming, W. E. 1963. The Japanese Beetle in the United States. U.S. Dep. Agric. Agric. Res. Serv. Agric. Handb. 236. 30 pp.

Giglio-Tos, E. 1894. Ditteri del Messico. Pt. 3. 76 pp. Torino.

Greene, C. T. 1922. An illustrated synopsis of the puparia of 100 muscoid flies (Diptera). Proc. U.S. Natl. Mus. 60(10):1–39.

Guimaraes, J. H. 1971. Family Tachinidae. Pages 1–333 *in*

A catalogue of the Diptera of the Americas south of the United States. 104. Museum of Zoology, University of Sao Paulo, Brazil.

HOWDEN, H. F. 1963. Speculation on some beetles, barriers and climates during the Pleistocene and pre-Pleistocene periods in some nonglaciated portions of North America. Syst. Zool. 12:178–201.

———. 1966. Some possible effects of the Pleistocene on the distributions of North American Scarabaeidae. Can. Entomol. 98:1177–1190.

JOHNSON, C. W. 1925a. Diptera of the Harris collection. Proc. Bost. Soc. Nat. Hist. 38(2):57–99.

———. 1925b. Fauna of New England, List of the Diptera or two-winged flies. Occas. Pap. Bost. Soc. Nat. Hist. 7(15):1–326.

———. 1927. The insect fauna with reference to the flora and other biological features. *In* Procter, W., Biological survey of the Mount Desert Region. Part I. Wistar Institute Press, Philadelphia.

LEONARD, M. D. 1928. A list of the insects of New York. Cornell Univ. Agric. Exp. Stn. Mem. 101:1–1121.

MACQUART, J. 1843. Diptères exotiques nouveaux ou peu connus. Mém. Soc. Sci. Agric. Arts Lille 1842:162–460.

———. 1846. Diptères exotiques nouveaux ou peu connus. Supplement. Mém. Soc. Sci. Agric. Arts Lille (1845), 1844:133–364.

OSTEN SACKEN, C. R. 1878. Catalogue of the described Diptera of North America (ed. 2). Smithson. Misc. Collect. 16(2):1–276.

PETERSON, L. O. T. 1948. Some aspects of Poplar Borer (*Saperda calcarata* Say) (Cerambycidae) infestations under parkbelt conditions. Ann. Rep. Entomol. Soc. Ont. 78:56–61.

PROCTER, W. 1938. The insect fauna with references to methods of capture, food plants, the flora and other biological features. *In* Procter, W., Biological survey of the Mount Desert Region. Part VI. Wistar Institute Press, Philadelphia. 496 pp.

———. 1946. The insect fauna with references to methods of capture, food plants, the flora and other biological features. *In* Procter, W., Biological survey of the Mount Desert Region. Part VII. Wistar Institute Press, Philadelphia. 566 pp.

REINHARD, H. J. 1943. New North American Muscoidea. J. Kansas Entomol. Soc. 16:14–23.

ROBINEAU-DESVOIDY, J. B. 1830. Essai sur les Myodaires. Mém. Acad. Sci. Inst. Fr., Ser. 2, 2:1–813.

ROSS, H. H. 1965. Pleistocene events and insects. Pages 583–595 *in* Wright, H. E., Jr., and D. G. Frey, editors. The Quaternary of the U.S. Princeton University Press, Princeton, N.J.

SABROSKY, C. W., AND P. H. ARNAUD, JR. 1965. Family Tachinidae. Pages 961–1108 *in* Stone, A., C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson. Catalogue of the Diptera of America North of Mexico. U.S. Dep. Agric. Agric. Res. Serv. Agric. Handb. 276.

STEYSKAL, G. C. 1976. The terminology of the bristles on the upper back of the head in the higher Diptera. J. Kansas Entomol. Soc. 49(2):155–159.

THOMPSON, W. R. 1963. The tachinids of Trinidad. II. Echynomyiines, dexiines and allies. Can. J. Zool. 41:335–576.

TOWNSEND, C. H. T. 1915. Proposal of new muscoid genera for old species. Proc. Biol. Soc. Wash. 28:19–23.

———. 1921. Notes on American oestromuscoid types. Rev. Entomol. 1:65–104.

———. 1938. Manual of myiology in twelve parts. Pt. 7: Oestroid generic diagnoses and data (Gymnosomatini to Senostomatini), 434 pp. São Paulo.

WALKER, F. 1837. Descriptions, etc. of the insects collected by Cpt. P. P. King, R.N.F.R.S., in the survey of the Straits of Magellan, Diptera. Trans. Linn. Soc. London. 17:331–359.

———. 1849. List of specimens of dipterous insects in the collection of the British Museum. London. 4:689–1172.

———. 1852. Diptera. Pages 157–252, 253–414 *in* Saunders, W. W., ed. Insecta Saundersiana. Vol. 1. London.

WALTON, W. R. 1914. Report on some parasitic and predaceous Diptera from northeastern New Mexico. Proc. U.S. Natl. Mus. 48:171–186.

WEST, L. S. 1924. New northeastern Dexiini. Psyche 31:184–193.

———. 1925. New Phasiidae and Tachinidae from New York State. J. N.Y. Entomol. Soc. 33:121–135.

———. 1950. The status of *Rhynchiodexia robusta* Curran together with a consideration of certain cephalic and other characters useful in muscoid taxonomy. Pap. Mich. Acad. Sci. Arts Lett. 34:109–117.

WILDER, D. D. 1976. Systematics of the Nearctic *Ptilodexia* Brauer and Bergenstamm (Diptera: Tachinidae). Ph.D. dissertation. Pennsylvania State University. 390 pp.

WILLISTON, S. W. 1896. On the Diptera of St. Vincent (West Indies). Trans. Entomol. Soc. London; 253–446.

WRAY, D. L. 1938. Insects of North Carolina. North Carolina Dep. Agric. Third Supp., 181 pp. Raleigh, N.C.

WULP, F. M. VAN DER. 1891. Family Muscidae. Pages 225–248 *in* F. D. Godman, O. Salvin, editors. Biologia Centrali-Americana. Zoologia.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 2, pp. 57–67, 6 figs., 2 tables. March 2, 1979

THE SNAKE EELS (PISCES, OPHICHTHIDAE) OF THE HAWAIIAN ISLANDS, WITH THE DESCRIPTION OF TWO NEW SPECIES

By
John E. McCosker
Steinhart Aquarium, California Academy of Sciences, San Francisco, California 94118

ABSTRACT: The ophichthid eels of the Hawaiian Islands (including Johnston and the Leeward islands) are reviewed; included are species new to Hawaii and extralimital records of species previously considered to be endemic. A key to species identification is provided. Two new species captured in deepwater traps off Oahu are described: *Muraenichthys puhioilo*, subfamily Myrophinae, captured at 275 m, and *Ophichthus kunaloa*, subfamily Ophichthinae, captured at 350 m. Data concerning the following species are provided: *Schismorhynchus labialis*, *Muraenichthys cookei*, *M. macropterus*, *Apterichtus flavicaudus*, *Ichthyapus vulturis*, *Phaenomonas cooperae*, *Callechelys luteus*, *Myrichthys maculosus*, *M. bleekeri*, *Cirrhimuraena playfairii*, *Brachysomophis sauropsis*, *B. henshawi*, *Phyllophichthus xenodontus*, *Ophichthus polyophthalmus* and *O. erabo*. Differences in vertebral number of populations of *Myrichthys maculosus* are discussed and the eastern Pacific nominal species *M. xysturus* (Jordan & Gilbert), *M. tigrinus* Girard and *M. pantostigmius* Jordan & McGregor are placed in its synonymy. The endemism (5 of the 15 species) of the Hawaiian ophichthid fauna and the problems of populations and species differences are discussed.

INTRODUCTION

The snake eels, family Ophichthidae, of the Hawaiian Islands (including Johnston and the Leeward islands) were first treated by Jordan and Evermann (1905) and subsequently reviewed by Gosline (1951) and Gosline and Brock (1960). Recent collections by the George Vanderbilt Foundation, John E. Randall of the Bishop Museum, and Thomas A. Clarke of the University of Hawaii have added important additional specimens. The Hawaiian Archipelago contains a particularly interesting eel fauna in terms of its abundance and the range of distributional conditions which exist, including species that are endemic to the islands as well as those that are distributed eastward to Australia and the Red Sea. This, while recognizing the dispersal mechanism allowed by the leptocephalus larva, provides an intriguing study for marine zoogeographers. Those considerations, as well as the recent capture of other Hawaiian ophichthids and two apparently undescribed deepwater species, have prompted this review.

METHODS

All measurements are straight-line (point to point). Standard length, trunk length, and tail length were read on a 300-mm ruler with 0.5-mm gradations and were recorded to the nearest 0.5 mm. All other measurements were made with dial calipers and were recorded to the nearest 0.1 mm. Head length was measured from the snout tip to the posterodorsal margin of the gill opening; trunk length was taken from the end of the head to mid-anus; body depth does not include the fin. Vertebrae (which include the last centrum) were counted from radiographs.

Comparisons are based in part on specimens extralimital to the Hawaiian Islands when material was insufficient. Partial synonymies are provided where applicable to the Hawaiian Islands taxa and where new synonymies are proposed.

Specimens utilized in this study are deposited in the following institutions: Australian Museum, Sydney (AMS); Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History) (BMNH); Bernice P. Bishop Museum (BPBM); California Academy of Sciences (CAS), now including the George Vanderbilt Foundation (GVF) and the Stanford University collections (SU); Hawaii Institute of Marine Biology (HIMB); Los Angeles County Museum of Natural History (LACM); Scripps Institution of Oceanography (SIO); University of Hawaii (UH); and the National Museum of Natural History (USNM).

KEY TO THE OPHICHTHID EELS OF JOHNSTON AND THE HAWAIIAN ISLANDS

1a. Caudal fin rays conspicuous, confluent with dorsal and anal; tail tip flexible; gill openings mid-lateral, a constricted opening; pectoral fin absent in Hawaiian species. Subfamily MYROPHINAE 2

1b. Tail tip a hard or fleshy, finless point; gill openings mid-lateral to entirely ventral, unconstricted; pectoral fin present in some species. Subfamily OPHICHTHINAE 7

2a. A prominent median toothed groove on ventral side of snout, bordered by dermal folds, extending forward to anterior nostrils; anterior nostrils elongated tubes equal to eye in length .... *Schismorhynchus labialis*

2b. Ventral side of snout without a prominent groove bordered by dermal folds; anterior nostrils less than eye in length 3

3a. Teeth absent on vomer, absent or embedded on intermaxillary, those on maxillary and dentary minute or villiform; dorsal fin origin (DFO) behind anus .... *Schultzidia johnstonensis*

3b. Teeth present on intermaxillary, maxillary, dentary, and vomer; DFO either before or behind anus 4

4a. Posterior nostril entirely outside of mouth; teeth on maxillary, dentary, and vomer in broad bands; snout bluntly rounded .... *Muraenichthys schultzei*

4b. Posterior nostril inside mouth, covered externally by a flap; teeth uniserial or biserial, not in broad bands; snout either blunt or acute 5

5a. DFO anterior to anus, about midway to gill openings .... *Muraenichthys puhioilo* n.sp.

5b. DFO above or behind anus 6

6a. Snout blunt; DFO above or slightly before anus .... *Muraenichthys cookei*

6b. Snout acute; DFO slightly behind anus .... *Muraenichthys gymnotus*

7a. Body entire finless; coloration either uniform or darker dorsally, without large spots or saddles 8

7b. At least a minute, short, dorsal fin present; coloration variable, either uniform, banded, or spotted, or somewhat darker dorsally 9

8a. Posterior nostril opening outside mouth, with a flap; anterior nostril tubular; body extremely elongate; head 15–20 times in TL .... *Apterichtus flavicaudus*

8b. Posterior nostril opening inside mouth; anterior nostril flush with snout; body moderately elongate; head 11–12 times in TL .... *Ichthyapus vulturis*

9a. Only fin a short dorsal originating just behind occiput and ending in anterior trunk region; body extremely elongate, the depth 120–150 times in TL .... *Phaenomonas cooperae*

9b. Dorsal and anal fins present, the dorsal extending nearly to the tail tip; body moderately to extremely elongate, but the depth less than 120 times in TL 10

10a. Dorsal fin orgin (DFO) on nape; pectoral fins absent; gill openings inferior, converging forward; coloration pale to tan, overlain with small dark spots .... *Callechelys luteus*

10b. DFO behind nape, either on head or slightly behind gill openings; pectoral fins present; coloration either uniform, spotted, or banded 11

11a. DFO well in advance of gill openings; teeth molariform or granular; pectoral fins broad-based, short and rounded 12

11b. DFO before, above, or behind gill openings; teeth pointed; pectoral fin base restricted, opposite upper half of gill openings and longer than broad 13

12a. Coloration consists of several longitudinal series of dark spots along sides and dorsal surface *Myrichthys maculosus*

12b. Coloration consists of about 30 dark saddles reaching approximately to the lateral line *Myrichthys bleekeri*

13a. DFO well ahead of gill openings; edge of upper lip fringed with a conspicuous row of barbels *Cirrhimuraena playfairii*

13b. DFO above or behind gill openings; upper lip either naked or fringed 14

14a. Postorbital region with a conspicuous transverse depression; lips fringed; canine teeth in jaws and on vomer; coloration uniform 15

14b. Dorsolateral profile on head even; lips entire; jaw and vomerine teeth not excessively developed; coloration uniform, spotted, or banded 16

15a. Dorsal fine pale; snout contained about 15 times in head length *Brachysomophis sauropsis*

15b. Dorsal fin dark with a white border; snout contained about 10 times in head length *Brachysomophis henshawi*

16a. Conspicuous leaflike appendages on anterior nostrils; head and trunk equal to or greater than tail (coloration uniform; vomerine teeth absent) *Phyllophichthus xenodontus*

16b. No leaflike appendages on anterior nostrils; head and trunk equal to or less than tail 17

17a. Vomerine teeth absent or 1–3; head and body coloration light to tan, overlain with a series of black saddles *Leiuranus semicinctus*

17b. A series of teeth on the vomer; coloration uniform or spotted, not as above 18

18a. DFO above pectoral tips; pectoral fin elongate, attenuate; coloration uniform, darker dorsally *Ophichthus kunaloa* n.sp.

18b. DFO above gill openings; pectoral fin rounded; coloration not uniform, markedly spotted 19

19a. Head and body overlain with numerous ocellated spots; those on body in 3 regular alternating rows, the spots separated by pale interspaces; vertebrae of 1 specimen 148 *Ophichthus polyophthalmus*

19b. Head and body overlain with numerous dark spots; those on body in 2 irregular rows, the spots about equal in size to their interspaces; vertebrae of 6 specimens 152–155 *Ophichthus erabo*

Muraenichthys puhioilo, new species

(Figures 1–2)

Holotype: CAS 29115 (originally SIO 70-32), 355 mm total length, captured in a benthic shrimp trap set overnight at 275 m depth, N of Barber's Point, Oahu, Hawaiian Islands, by Thomas A. Clarke on 28 October 1969.

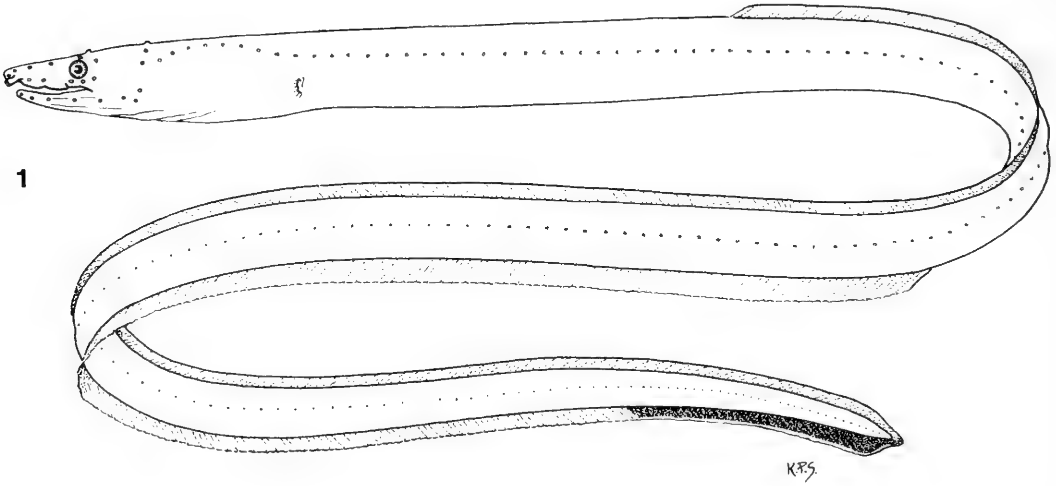
Counts and Measurements (in mm).—The description of this new species is based on the holotype and only known specimen. Total length 355 mm; head length 37.3; trunk length 120; tail length 198; body depth at gill openings 15; body width at gill openings 8; body depth at anus 12; body width at anus 7.5; origin of dorsal fin 86; snout length 8.2; upper jaw length 10.7; eye diameter 3.2; interorbital distance 4.4. Total vertebrae 160; preanal vertebrae 62.

General Description.—Body elongate, depth at gill openings 23.7 in total length, tapering and laterally compressed posteriorly. Head and trunk 2.26 and head 9.5 in total length. Snout moderately acute; lower jaw included, its tip reaching the posterior edge of anterior nostrils. Anterior nostrils tubular, slightly shorter than eye diameter. Posterior nostril entirely inside upper lip, before anterior margin of the eye, opening inward, appearing externally as a flap. Eye less than twice in fleshy interorbital distance. Interorbital region flat. Rictus of jaw slightly behind posterior margin of eye.

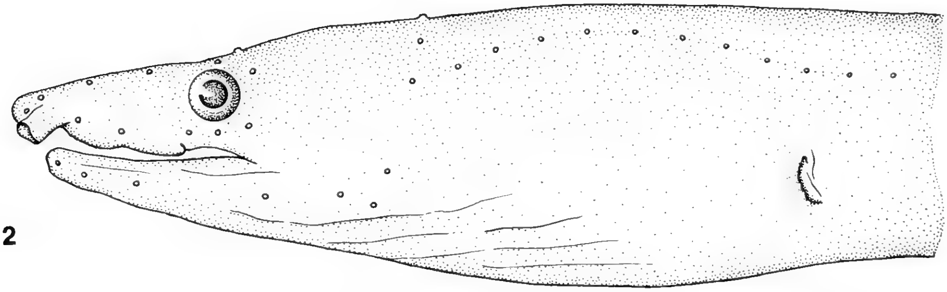
Median fins low, except near tail tip and anterior portion of anal fin. Dorsal fin arises closer to gill openings than to anus. Paired fins absent. Median fins confluent with caudal.

Head pores minute. Single temporal and interorbital pores present. Five pores along mandible, three overlying preopercle. Lateral-line pores difficult to discern posteriorly; 10 pores before gill opening; approximately 140 pores along left side, 65 before the anus. Last lateral-line pore occurs about a head length before tail tip.

Teeth slender, small and conical, uniserial throughout. The pattern of dentition is nearly



1



2

FIGURES 1 and 2. Fig. 1. Left lateral view of holotype of *Muraenichthys puhioilo* McCosker, new species, CAS 29115, 355 mm TL. Fig. 2. Head region of holotype of *Muraenichthys puhioilo* McCosker, new species.

identical to that of *Muraenichthys chilensis* (cf. McCosker 1970, fig. 4), except that the new species lacks the anteriormost intermaxillary tooth. None is extremely elongate although the anteriormost vomerine tooth is slightly larger than all jaw teeth. Four intermaxillary teeth, forming an inverted v, are followed by 14 uniserial vomerine teeth. The maxillary teeth are equal in size, 15 right and 17 left. Teeth of lower jaw separated at symphysis, about 17 on each side.

Body coloration in isopropyl alcohol uniform tan, although the belly and lateral-line are slightly darker. Median fins pale except for the posterior portion (slightly longer than head length) of anal fin which is dark. (The functional significance of this highly contrasting fin coloration is not known.) Eyes dark blue.

ETYMOLOGY.—From the Hawaiian *puhi oilo*, small eels about as large in diameter as a finger, here considered a noun in apposition. Eels, particularly *puhi oilo*, were highly esteemed as food by ancient Hawaiians. Mary Kawena Pukui (1902) wrote that "the eel was a fish of which chiefs were fond . . . so much prized by those of Koolau, Maui . . . that they said only beloved guests were served with eels . . . for eels were considered choicer than wives."

REMARKS.—This individual was captured at a depth far greater than that of any previously known *Muraenichthys*. The nearly 20 species of the genus are generally known from water shallower than 50 meters.

This specimen was reported by Clarke (1972:312), on the basis of my erroneous identification, as *Muraenichthys macropterus* Bleeker. I have subsequently examined a radiograph of Bleeker's type-specimen (BM 1867.II.28.303) and found it to possess 130 vertebrae, with 22 before the dorsal fin origin and 47 before the anal fin origin. Bleeker's type was from Ambon; a series from Palau (CAS 41186) had 127–132 vertebrae ($\bar{x}$ = 129.8, n = 5). My examination of more than 100 specimens of *M. macropterus* from throughout Oceania found them to differ from the new species in having fewer vertebrae, biserial vomerine dentition (becoming uniserial posteriorly), uniform fin coloration, and in occupying shallower water. The new species differs from all other species of *Muraenichthys*, subgenus *Scolecenchelys*, on the basis of its uniserial dentition, anterior dorsal fin location, coloration, and vertebral number.

In my review of *Muraenichthys* (McCosker 1970), I followed Schultz (1953) in considering *M. breviceps* Günther to be a probable synonym of *M. macropterus*. I have subsequently recognized *M. breviceps* as a distinct species and include *M. devisi* Fowler, *M. ogilbyi* Fowler, and *Aotea acus* Phillipps in its synonymy (McCosker and Allen, MS.). I also examined the other known synonyms of *M. macropterus*, *M. owstoni* Jordan and Snyder from Japan and *Echidna uniformis* Seale from Guam, and determined that they are *M. macropterus*. The holotype of *M. owstoni* (SU 6472) has 131 vertebrae.

Ophichthus kunaloa, new species

(Figures 3–4)

Holotype: CAS 29136 (originally SIO 70–33), 440 mm total length, captured in a benthic shrimp trap set overnight at 350-m depth, SE of Barber's Point, Oahu, Hawaiian Islands, by Thomas A. Clarke on 31 December 1969.

Paratypes: Collected with the holotype. BPBM 21086, 473 mm total length. USNM 218274, only the head and anterior trunk region of a partially eaten specimen.

COUNTS AND MEASUREMENTS (in mm).—The condition of the holotype is parenthetically followed by that of the intact paratype. Total length 440 mm (473 mm); head length 42.0 (45.7); trunk length 135 (144); tail length 263 (283); body depth at gill openings 16 (15); body width at gill openings 13.7 (12.5); origin of dorsal fin 58 (68); left pectoral fin length 20.0 (19.5); left pectoral fin base 4.6 (4.5); snout length 8.6 (7.7); upper jaw length 17.2 (20.0); gill opening height 5.6 (5.5); eye diameter 7.0 (8.0); interorbital distance 6.9 (6.9). Total vertebrae 185 (181); preanal vertebrae 66 (67).

GENERAL DESCRIPTION.—Body elongate, depth at gill openings 10.3–10.5 in total length, tapering posteriorly. Tail slender, laterally compressed posteriorly. Head and trunk 2.49 and head 10.3–10.5 in total length. Snout rounded; lower jaw included, its tip in advance of anterior nostril base. Anterior nostril tubular; posterior nostril at edge of lip, entirely outside of mouth, covered anteriorly by a small flap. Eye large; its center lies slightly behind midpoint of upper jaw. Head broad; interorbital area flat.

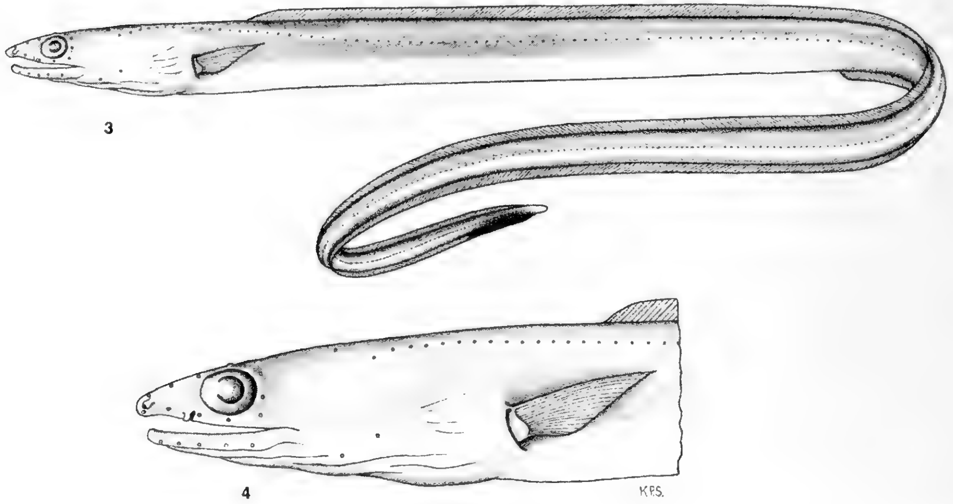
Median fins low, lying partially within a groove. Dorsal fin arises before end of pectoral. Median fins disappear within a flabby groove before the tail tip. Pectoral fins elongate, the dorsalmost rays tapering posteriorly. Caudal tip naked.

Head pores minute, difficult to locate on preserved specimens. Single temporal and interorbital pores. Five pores along mandible, two overlying preopercle. Lateral-line pores begin above second preopercular pore. Lateral-line pores difficult to discern, about 64 before anal opening.

Teeth small, conical; biserial in jaws, the outer row smaller and closer set. Vomerine teeth biserial anteriorly, followed by a uniserial row of about 10 teeth. Intermaxillary tooth patch surrounded anterolaterally by a ring of 6–8 teeth.

Body coloration in isopropyl alcohol tan, becoming lighter along chin, snout, throat, lower third of trunk region, below the lateral-line of the trunk region, along the dorsal midline, and at the tail tip. A black smudge exists along the lower edge of the tail, about ⅓ head length from the tail tip. Fins pale. Lateral-line pores lie within minute white dots. Eyes blue.

ETYMOLOGY.—Named *kunaloa* in reference to Kuna Loa, the Long Eel, of ancient Hawaiian legends. It is said that the sixth great deed of Maui the Wonder Boy was to behead Kuna Loa after the treacherous eel had assaulted the fair maiden Hina (see Colum 1937). The legend as-



FIGURES 3 and 4. Fig. 3. Left lateral view of holotype of *Ophichthus kunaloa* McCosker, new species, CAS 29136, 440 mm TL. Fig. 4. Head region of holotype of *Ophichthus kunaloa* McCosker, new species.

serts that from the cut tail evolved the common conger eel and from the blood which fell into the fresh and salt water came all of the other Hawaiian eels. This, clearly, was the first attempt at a phylogenetic interpretation of Hawaiian anguilliforms.

REMARKS.—The depth of capture of the new species is remarkable in that most benthic ophichthids live shallower than 100 meters. It is entirely likely that future deepwater collections in outlying areas might reveal this or a closely related species.

In his key to the Hawaiian ophichthids, Gosline (1951:309) mentioned a new species of ophichthine which possessed characters similar to the new species, that was "probably from moderately deep water," and had been killed by the Mauna Loa lava flow of 1950. This specimen was not mentioned in further publications, and neither Gosline (in litt.), John E. Randall of the Bishop Museum (BPBM), nor Leighton Taylor of the University of Hawaii (UH) have been able to locate it after the majority of the UH fish collection had been transferred to the BPBM.

The closest relatives to the new species appear to be those congeners which also possess large eyes, similar dentition, posterior nostrils along the lip (rather than opening into the mouth) and preceded by a flap, two rather than three preopercular pores, and a plain coloration. Those species of *Ophichthus*, mostly within the subgenus *Coecilophis* Kaup (cf. McCosker 1977), share a preference for moderate-depth sand or mud substrates. *Ophichthus kunaloa* is particularly similar to *O. urolophus* (Temminck and Schlegel), an oriental species, which differs in its proportionately shorter tail and much deeper body, and to the eastern Pacific *O. pacifici* Günther, a species with a comparatively longer head, deeper body, and white spots along the lateral-line.

The following comments comprise new records and systematic information concerning the Hawaiian ophichthid fauna.

SUBFAMILY MYROPHINAE

Schismorhynchus labialis (Seale)

Muraenichthys labialis Seale, 1917:79 (type-locality, Arno Atoll, Marshall Islands).
Leptenchelys labialis: Schultz 1953:80.
Schismorhynchus labialis: McCosker 1970:509.

REMARKS.—This wide-ranging species has been collected from the Society Islands (BPBM 12016), Marshall Islands, Johnston Island, and Easter Island, but has not been captured in Hawaii.

Muraenichthys cookei Fowler

Muraenichthys cookei Fowler, 1928:41 (type-locality, Oahu).

REMARKS.—I concur with Gosline (1951), that *M. cookei,* a Hawaiian endemic, is closely related to but distinct from *M. laticaudata.* A comprehensive discussion of specific differences exists in Gosline (1955:469–470).

SUBFAMILY OPHICHTHINAE

Apterichtus flavicaudus (Snyder)

Sphagebranchus flavicaudus Snyder, 1904:516 (type-locality, between Maui and Lanai).
Caecula (Sphagebranchus) flavicauda: Gosline 1951:311.
Verma flavicauda: Böhlke 1968:3.
Apterichtus flavicaudus: Böhlke and McCosker 1975:4.

REMARKS.—This species, previously considered a Hawaiian endemic, has now been collected at several South Pacific locations. I compared all of Snyder's specimens with specimens from Midway Island (SIO 68–487) and Rapa Island (BPBM 12306), and found them to differ only in vertebral number. Six Hawaiian and Midway specimens had 155–166 ($\bar{x}$ = 158.7) vertebrae, whereas six Rapa specimens had 163–166 ($\bar{x}$ = 164).

Ichthyapus vulturis (Weber and de Beaufort)

Sphagebranchus vulturis Weber and de Beaufort, 1916:319 (type-locality, Nasi besar Island, Sumatra).
Caecula (Sphagebranchus) platyrhyncha Gosline, 1951:312 (type-locality, Oahu, Hawaiian Islands).

REMARKS.—Randall and McCosker (1975) synonymized *Caecula platyrhyncha* with *Sphagebranchus vulturis* after comparing Hawaiian specimens with the holotype. Variation exists in the number of preopercular pores (either 3 or 4) of Hawaiian specimens, but the pore number of specimens from other localities was found to be constant.

Phaenomonas cooperae Palmer

Phaenomonas cooperae Palmer, 1970:219 (type-locality, Gilbert Islands).

REMARKS.—This unmistakable elongate species is known from Hawaii on the basis of a specimen (HIMB 68–52) dredged from a depth of 60 m, offshore from Keehi Lagoon, Oahu, in 1968. The specimen has 262 total vertebrae, 169 preanal, and falls within the range of meristic and morphometric variation of its Indo-West-Pacific conspecifics (McCosker 1975).

Callechelys luteus Snyder

Callechelys luteus Snyder, 1904:517 (type-locality, near the southern coast of Molokai).

REMARKS.—This elongate species, unique in dorsal fin condition and coloration, is known only from the Hawaiian Islands and Midway Island (SIO 68–497). Its closest relative appears to be the eastern Pacific endemic *C. galapagensis* McCosker and Rosenblatt. A radiograph of the holotype of *C. luteus* (USNM 50864) evidenced 216 vertebrae, with 123 before the anal fin origin.

Myrichthys maculosus (Cuvier)

Muraena maculosa Cuvier, 1817:232 (type-locality, European Seas?).
Pisoodonophis magnifica Abbott, 1861:476 (type-locality, Hawaiian Islands).
Ophichthus stypurus Smith and Swain, 1882:120 (type-locality, Johnston Island).

REMARKS.—This common species, perhaps better than any other Hawaiian ophichthid, depicts the isolation of the Hawaiian and Johnston population as evidenced by vertebral number. I am unable except by vertebral number to separate the Hawaiian, Midway, and Johnston specimens from those from the Red Sea, Indian Ocean, Oceania, and the eastern tropical Pacific (see Table 1). For this and related faunal studies I have examined many living and dead specimens of *Myrichthys* as well as the types of most of the nominal species. Until now, I have followed the conventional view that the eastern Pacific nominal species *M. xysturus* (Jordan and Gilbert) (which includes *M. tigrinus* Girard and *M. pantostigmius* Jordan and McGregor) differs from *M. maculosus,* although the only significant difference is that of vertebral number. In the absence of any apparent morphological differences, I am resigned to recognize these populations at a subspecific level, and therefore recognize this ophichthid as a trans-Pacific species. The differences in *M. maculosus* population vertebral numbers is thus parallel to the condition of several trans-Pacific species of muraenid eels (Rosenblatt et al. 1972; McCosker and Rosenblatt 1975). I suspect that as data are gathered concerning the duration of larval life, distance of larval transport, and the critical period of leptocephalus transformation, a more lucid view of *Myrichthys* taxonomy will be achieved.

I have examined the holotypes of *M. magni-*

TABLE 1. *Myrichthys maculosus* (CUVIER): VERTEBRAL DATA FOR EASTERN PACIFIC AND INDO-PACIFIC POPULATIONS. All counts made from radiographs of adults.

	mean	range	n
Eastern Pacific[1]	153.1	149–157	19
Revillagigedos and Clipperton Is.	163.1	161–168	10
Hawaii, Johnston, and Midway	178.5	174–182	16
Western Pacific[2]	192.8	190–199	8
Red Sea	194.5	194–195	2

[1] Specimens from the Gulf of California, Tres Marias Islands, Cocos Island, Panama, and the Galapagos Islands.

[2] Specimens from Wake, Palau, Philippines, RyuKyus, and the Line Islands.

ficus and *M. stypurus* and found them to be conspecific. The holotype of *M. stypurus* is aberrant in that its tail had been severed and subsequently healed.

Myrichthys bleekeri Gosline

Ophisurus fasciatus var. *semicinctus* Bleeker, 1864:64 [a homonym of *Ophisurus semicinctus* Lay and Bennett, 1839:66] (type-locality, Indonesia).
Myrichthys bleekeri Gosline, 1951:314 [a substitute name for *Ophisurus fasciatus* var. *semicinctus* Bleeker, 1864, preoccupied].

REMARKS.—This species is known from Johnston Island and the Indo-West-Pacific, but not from Hawaii.

Cirrhimuraena playfairii (Günther)

Ophichthys playfairii Günther, 1870:76 (type-locality, Zanzibar).
Microdonophis macgregori Jenkins, 1903:422 (type-locality, Lahaina, Maui).
Jenkinsiella macgregori: Jordan and Evermann, 1905:82.
Cirrhimuraena playfairii: Barnard, 1925:205.
Cirrhimuraena macgregori: Gosline, 1951:315.

REMARKS.—Smith (1962) synonymized the Hawaiian species *Microdonophis macgregori* with the wide-ranging Indo-Pacific species *Cirrhimuraena playfairii.* He based this action on his comparison of four specimens from Aldabra with published descriptions by Gosline (1951) of Hawaiian specimens and by Weed and Howarth (1961) of specimens from Ceylon. I have examined the type-specimens from Hawaii and compared them with material from Midway (SIO 68–497) and the Marquesas (BPBM 12304), and concur with Smith. The holotype of *M. macgregori* (USNM 50721) has 180 vertebrae; two Marquesan specimens have 186 and 187 vertebrae.

Brachysomophis sauropsis Schultz

Brachysomophis sauropsis Schultz, 1943:18 (type-locality, Samoa).

REMARKS.—Not known from Hawaii. I have been unable to examine Gosline's (1955:443) specimen of *B. sauropsis* from Johnston Island. However, based on his description, I would agree that *B. sauropsis* and *B. henshawi* are distinct species.

Brachysomophis henshawi Jordan and Snyder

Brachysomophis henshawi Jordan and Snyder, 1904:940 (type-locality, Honolulu).

REMARKS.—Apparently, this species is a Hawaiian endemic. A comprehensive revision of *Brachysomophis* is necessary, however, before assumptions concerning its species can be made.

Phyllophichthus xenodontus Gosline

Phyllophichthus xenodontus Gosline, 1951:316 (type-locality, Oahu).

REMARKS.—*Phyllophichthus* is currently recognized to contain a single wide-ranging species, known from the western Indian Ocean, throughout Oceania, and Hawaii (McCosker and Allen, MS). Four specimens from Johnston and Oahu islands had 168–175 vertebrae ($\bar{x}$ = 170.8).

Ophichthus polyophthalmus Bleeker

(Figure 5)

Ophichthys polyophthalmus Bleeker, 1864:43 (type-locality, Ambon).
Microdonophis polyophthalmus: Jordan and Snyder 1907:207.
Ophichthus polyophthalmus: Fowler 1927:5.

REMARKS.—The markedly spotted Hawaiian eels placed by recent authors in either *Microdonophis* or *Ophichthus* is a composite. *Ophichthus polyophthalmus* (Fig. 5), a medium-length adult ophichthid with ocellated spots on the head and body, was reported by Fowler (1927) on the basis of a Kahoolawe (BPBM 3700) dredge specimen. Fowler (1928) subsequently recorded eleven Honolulu market specimens (the largest, 1,039 mm) which possessed dark spots; he considered them to also be *O. polyophthalmus* and recognized the nominal species *Microdonophis fowleri* Jordan and Evermann

FIGURE 5. Adult specimen of *Ophichthus polyophthalmus*, taken from Bleeker (1864).

and *Ophichthus garretti* Günther to be synonyms which differed only in coloration. *Ophichthus garretti* is a valid and distinctly different species. My comparison of numerous specimens of the large form with solid dark spots (*Ophichthus erabo*, Fig. 6) with the medium-length eel with ocellated spots indicated that they are in fact separate species differing in coloration and vertebral number. Too few specimens of *O. polyophthalmus* were available for a proper morphological comparison, although *O. erabo* appears to possess a proportionately longer tail.

I herein report a second Hawaiian specimen of *O. polyophthalmus*, collected in 1968 by hook and line from Nanakuli, Oahu (BPBM 11981, 399 mm SL). The specimen has 148 vertebrae, 75 before the anal opening.

Ophichthus erabo (Jordan and Snyder)
(Figure 6)

Microdonophis erabo Jordan and Snyder, 1901:780 (type-locality, Misaki, Japan).
Microdonophis fowleri Jordan and Evermann, 1904:164 (type-locality, Honolulu).
Ophichthus erabo: McCosker 1977:81.

REMARKS.—The majority of Hawaiian records of *O. polyophthalmus* are based on specimens of *O. erabo*. I have compared the Japanese holotype (SU 6477) and cotypes (SU 6667 and 6744) of *O. erabo* with specimens from Hawaii (SU 8407; SU 8466; BPBM 12510; and USNM 50613, the holotype of *M. fowleri*) and Taiwan (CAS 15600), and found them not to differ. The vertebral range of six specimens was 152–155 ($\bar{x}$ = 154). The holotype of *O. erabo* has 155 vertebrae and the holotype of *M. fowleri* has 152.

DISCUSSION

The endemism of the Hawaiian shorefish fauna has been recognized by numerous authors and most recently summarized by Randall (1976). He calculated that 29 percent of the 442 reef and shorefish species were endemic at the specific or subspecific level. He elucidated the situation of the problematical species such as *Acanthurus triostegus*, wherein an identifiable difference in coloration exists between the Hawaiian and extralimital populations, but a consensus of opinion concerning the biological significance of that difference has not been reached. A similar problem exists with the Hawaiian ophichthids.

Of the 15 ophichthids present at Hawaii, five species are endemic. The new species described herein, *Ophichthus kunaloa* and *Muraenichthys puhioilo*, are known only from a single deep-water collection and are therefore of little value

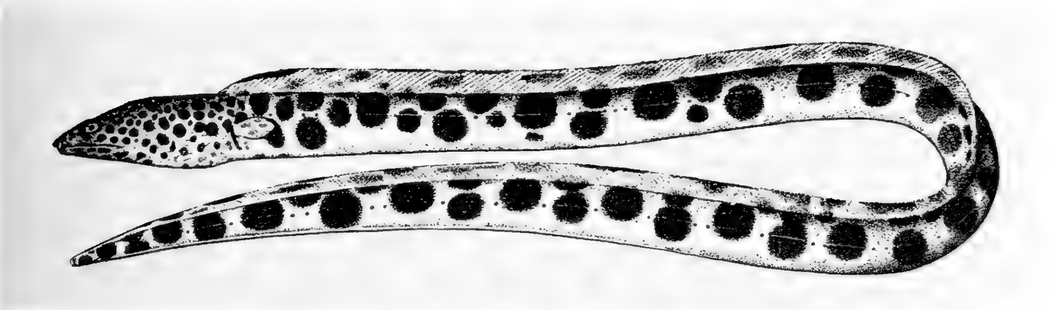


FIGURE 6. Adult specimen of *Ophichthus erabo*, taken from Jordan and Snyder (1901).

Table 2. Distribution of Hawaiian and Johnston Island Ophichthids.

	Hawaiian	Leewards	Johnston	Indo-West Pacific
Schultzidia johnstonensis	x	x	x	x
Schismorhynchus labialis			x	x
Muraenichthys schultzei			x	x
Muraenichthys cookei	x	x	x	
Muraenichthys gymnotus			x	x
Muraenichthys puhioilo	x			
Ichthyapus vulturis	x	x		x
Apterichtus flavicaudus	x	x		x
Callechelys luteus	x	x		
Myrichthys maculosus	x	x	x	x
Myrichthys bleekeri			x	x
Cirrhimuraena playfairii	x	x		x
Phyllophichthus xenodontus	x			x
Phaenomonas cooperae	x			x
Leiuranus semicinctus	x	x	x	x
Brachysomophis sauropsis			x	x
Brachysomophis henshawi	x			
Ophichthus erabo	x			x
Ophichthus polyophthalmus	x			x
Ophichthus kunaloa	x			

to a zoogeographic analysis. The endemics, *Muraenichthys cookei* and *Brachysomophis henshawi*, are perhaps no more different than are several of the other ophichthids discussed here from their Indo-West-Pacific "conspecifics." *Callechelys luteus* is the only Hawaiian ophichthid endemic distinctly different at the specific level from all known congeners. It is most closely related to *C. galapagensis*, another insular endemic (McCosker and Rosenblatt 1972). In my analysis of Hawaiian ophichthids, I have been able to recognize the Hawaiian populations of several species (viz., *Myrichthys maculosus, Phaenomonas cooperae, Phyllophichthus xenodontus, Ichthyapus vulturis*, and probably several others) to be distinct from other Indo-Pacific populations of their conspecifics on the basis of vertebral differences. Yet I am hesitant to assign them specific rank. It should be recognized, however, that the absolute differences in ophichthid vertebral numbers appear to be less when calculated on a percentage basis. For example, the difference of eight vertebrae between the Hawaiian specimen of *Phaenomonas cooperae* and the Gilbert Island holotype is only three percent, which is less than a difference of one vertebra for most perciform fishes. As Randall (1976:49–50) has discussed, these differences are real and apparently indicate limited gene flow with other insular populations. Whether the Hawaiian forms are in fact distinct biological species, incipient species, or whatever taxon a systematist deems them, awaits the discovery of biological data concerning leptocephalus transport, longevity, and gene flow.

Untaxing the taxonomy of the Hawaiian ophichthids, initiated by Maui the Wonder Boy and continued by Jordan, Evermann, and Gosline, remains a challenge.

Acknowledgments

This study depended primarily upon recent specimens collected by J. E. Randall (BPBM), the George Vanderbilt Foundation (CAS), and the 1968 STYX Expedition of the Scripps Institution of Oceanography. Other specimens and assistance were provided by the following individuals: J. Paxton and D. Hoese (AMS); J. Böhlke (ANSP); A. Wheeler (BMNH); W. Eschmeyer (CAS); R. Lavenberg (LACM); R. Rosenblatt and J. Copp (SIO); V. Springer and N. Gramblin (USNM); and L. Taylor of the Waikiki Aquarium, Hawaii. J. Gordon and C. Ruark assisted with the preparation of radiographs, M. Giles prepared the photographs, and K. Smith prepared Figures 1–4. I am very grateful to all of the above-mentioned individuals for their assistance, and in particular, to Thomas A. Clarke for providing the new species and to William A. Gosline for his pioneering studies of apodal fishes.

LITERATURE CITED

ABBOTT, C. C. 1861. Description of new species of apodal fishes in the museum of the Academy of Natural Sciences of Philadelphia. Proc. Acad. Nat. Sci. Phila. 12:475–479.

BARNARD, K. H. 1925. A monograph of the marine fishes of South Africa. Part I. Ann. S. Afr. Mus. 21:1–418.

BLEEKER, P. 1864. Atlas ichthyologique des Indes Orientales Neerlandaises. Vol. 4. Amsterdam. 132 pp.

BÖHLKE, J. E. 1968. A new species of the ophichthid eel genus *Verma* from the West Atlantic, with comments on related species. Not. Nat. (Phila.), no. 415. 12 pp.

———, AND J. E. MCCOSKER. 1975. The status of the ophichthid eel genera *Caecula* Vahl and *Sphagebranchus* Bloch, and the description of a new genus and species from fresh waters in Brazil. Proc. Acad. Nat. Sci. Phila. 127(1): 1–11.

CLARKE, T. A. 1972. Collections and submarine observations of deep benthic fishes and decapod crustacea in Hawaii. Pac. Sci. 26(3):310–317.

COLUM, P. 1937. Legends of Hawaii. Yale Univ. Press, New Haven. 220 pp.

CUVIER, G. 1817. Le règne animal. Vol. 2. Paris. 532 pp.

FOWLER, H. W. 1927. Fishes of the tropical central Pacific. Bernice P. Bishop Mus., Bull. 38. 32 pp.

———. 1928. The fishes of Oceania. Bernice P. Bishop Mus., Mem. 10. 540 pp.

GOSLINE, W. A. 1951. The osteology and classification of the ophichthid eels of the Hawaiian Islands. Pac. Sci. 5(4):298–320.

———. 1955. The inshore fish fauna of Johnston Island, a Central Pacific atoll. Pac. Sci. 9(4):442–480.

———, AND V. E. BROCK. 1960. Handbook of Hawaiian fishes. Univ. Hawaii Press, Honolulu. 372 pp.

GÜNTHER, A. C. 1870. Catalogue of the fishes in the British Museum. Vol. 8. London. 549 pp.

JENKINS, O. P. 1904. Report on collections of fishes made in the Hawaiian Islands, with descriptions of new species. U.S. Bur. Fish. Bull. 22:417–511.

JORDAN, D. S., AND B. W. EVERMANN. 1905. The aquatic resources of the Hawaiian Islands. Part I. The shore fishes. U.S. Fish. Comm. Bull. 23(1):1–574.

———, AND J. O. SNYDER. 1901. A review of the apodal fishes or eels of Japan, with descriptions of 19 new species. Proc. U.S. Natl. Mus. 23(1239):837–890.

———. 1904. Notes on collections of fishes from Oahu Island and Laysan Island, with descriptions of four new species. Proc. U.S. Natl. Mus. 27:939–948.

———. 1907. Notes on fishes of Hawaii, with descriptions of new species. U.S. Bur. Fish. Bull. 26:207–218.

LAY, G. T., AND E. T. BENNETT. 1839. The zoology of Captain Beechey's voyage. Fishes. London. Pp. 41–75.

MCCOSKER, J. E. 1970. A review of the eel genera *Leptenchelys* and *Muraenichthys*, with the description of a new genus, *Schismorhynchus*, and a new species, *Muraenichthys chilensis*. Pac. Sci. 24(4):506–516.

———. 1975. The eel genus *Phaenomonas* (Pisces, Ophichthidae). Pac. Sci. 29(4):361–363.

———. 1977. The osteology, classification, and relationships of the eel family Ophichthidae. Proc. Calif. Acad. Sci., Ser. 4, 41(1):1–123.

———, AND R. H. ROSENBLATT. 1972. Eastern Pacific snake-eels of the genus *Callechelys* (Apodes: Ophichthidae). Trans. San Diego Soc. Nat. Hist. 17(2):15–24.

———, AND ———. 1975. The moray eels (Pisces: Muraenidae) of the Galapagos Islands, with new records and synonymies of extralimital species. Proc. Calif. Acad. Sci., Ser. 4, 40(13):417–427.

PALMER, G. 1970. New records, and one new species, of teleost fishes from the Gilbert Islands. Bull. Brit. Mus. (Nat. Hist.) Zool. 19(6):211–234.

PUKUI, M. K. 1902. Ka hana kuhikuhi no ka lawai'a ana. Ka Nupepa Kuokoa, newspaper article, 23 May. (Not seen; reference from: TITCOMB, M. 1972. Native use of fish in Hawaii. Univ. Hawaii Press, Honolulu. 175 pp.)

RANDALL, J. E. 1976. The endemic shore fishes of the Hawaiian Islands, Lord Howe Island and Easter Island. Colloque Commerson 1973, ORSTOM Trav. et Doc. no. 47:49–73.

———, AND J. E. MCCOSKER. 1975. The eels of Easter Island with a description of a new moray. Los Angeles County Mus. Contrib. Sci., no. 264. 32 pp.

ROSENBLATT, R. H., J. E. MCCOSKER, AND I. RUBINOFF. 1972. Indo-West-Pacific fishes from the Gulf of Chiriqui, Panama. Los Angeles County Mus. Contrib. Sci., no. 234. 18 pp.

SCHULTZ, L. P. 1943. Fishes of the Phoenix and Samoan islands. U.S. Natl. Mus. Bull. 180. 316 pp.

———. 1953. Fishes of the Marshall and Marianas islands. Families from Asymmetrontidae through Siganidae. U.S. Natl. Mus. Bull. 202, 1. 685 pp. (With collaborators.)

SEALE, A. 1917. New species of apodal fishes. Bull. Mus. Comp. Zool. Cambridge 61:79–94.

SMITH, J. L. B. 1962. Sand-dwelling eels of the western Indian Ocean and the Red Sea. Rhodes Univ. Ichthyol. Bull. 24:447–466.

SMITH, R., AND J. SWAIN. 1882. Notes on a collection of fishes from Johnston's Island including descriptions of five new species. Proc. U.S. Natl. Mus. 5:119–143.

SNYDER, J. O. 1904. A catalogue of the shore fishes collected by the steamer "Albatross" about the Hawaiian Islands in 1902. U.S. Bur. Fish. Bull. 22:513–538.

WEBER, M., AND L. F. DE BEAUFORT. 1916. The fishes of the Indo-Australian Archipelago. Vol. 3. Leiden. 455 pp.

WEED, W. A. III, AND J. N. HOWARTH. 1961. Range extensions of the ophichthid eels *Phyllophichthus xenodontus* and *Cirrhimuraena macgregori*. Copeia 1961(3):357.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 3, pp. 69–85; 7 figs. December 22, 1979

REVIEW OF THE RHINOTRAGINI OF MEXICO (COLEOPTERA: CERAMBYCIDAE)

By
John A. Chemsak and E. G. Linsley
University of California, Berkeley, CA 94720

ABSTRACT: **The Rhinotragini known to occur in Mexico are reviewed. Keys are provided for the determination of the seven genera and also for species in the genera. Distribution maps are included for the more common species and most of the new taxa are illustrated. New species include: *Tomopterus exilis*, *Acyphoderes amoena*, *A. fulgida*, *A. prolixa*, and *A. parva*.**

New synonymies and one new combination are proposed.

INTRODUCTION

The Rhinotragini comprise a large group of Neotropical Cerambycidae which is particularly abundant and diverse in South America. The group is of special interest because of the remarkable degree of mimicry exhibited by most species. This is evident in modifications in form, coloration, and behavior, with the various taxa utilizing a wide range of models, particularly bees, wasps, and "protected" beetles of other families. Frequently, the mimicry is expressed in strong sexual dimorphism and dichromatism with males and females utilizing different models.

The number of species diminish as the group extends northward from South America, and only one is thus far known to occur in the United States. As presently defined, the Mexican fauna consists of 22 species in 7 genera. Some of the species appear to be restricted to Mexico, while others range into Central America to Costa Rica or Panama. One is also found in South America.

Tribe RHINOTRAGINI Lacordaire

Rhinotragides LACORDAIRE, 1869:497.
Rhinotraginae BATES, 1873:21.
Rhinotragini LINSLEY, 1963:164.

Body more or less elongate. Head prolonged below eyes to form a muzzle; antennae usually shorter than body in both sexes, outer segments more or less serrated; eyes finely faceted, with lower lobes very large, nearly contiguous in front in males; palpi short, last segment subcylindrical or ovate-cylindrical, apex truncate; mandibles short. Pronotum cylindrical or rounded, without a lateral spine or tubercle; prosternum with intercoxal process narrow, level, anterior coxae usually obliquely exserted, cavities feebly angulate externally; intermediate coxal cavities open externally; episterna of metathorax very large, triangular, and in front broad and narrowly separated from coxae. Elytra nearly always modified, attenuated, subulate, or squamiform.

KEY TO THE MEXICAN GENERA OF RHINOTRAGINI

1. Elytra short, not extended over abdomen 2
Elytra longer, extended at least partially over abdomen 4
2(1). Elytra narrowing posteriorly, apices dehiscent and narrowly rounded 3

Elytra not narrowing posteriorly, apices obliquely truncate .... *Tomopterus*

3(2). Pronotum with disk punctate, calluses, if present, small, rounded; posterior tibiae with very dense brush of long pubescence .... *Epimelitta*

Pronotum with three longitudinal, glabrous calluses on disk; posterior tibiae with apical brush small, the pubescence short .... *Bromiades*

4(1). Pronotum uniformly punctate or with rounded calluses on disk; femora moderately clavate 6

Pronotum usually with three distinct, longitudinal calluses on disk; anterior and intermediate femora often very strongly clavate 5

5(4). Antennae short, serrate apically; anterior and intermediate femora very strongly clavate .... *Acyphoderes*

Antennae slender, elongate, filiform apically; anterior and intermediate femora narrowly clavate .... *Stenopseutes*

6(4). Elytra with disk vitreous transparent; pronotum about as long as broad or slightly longer .... *Odontocera*

Elytra with disk shining, not transparent; pronotum narrow, distinctly longer than broad .... *Ommata*

Genus **Tomopterus** Audinet-Serville

Tomopterus Audinet-Serville, 1833:544; Newman 1840:21; White 1855:176; Thomson 1860:166, 168; 1864:163, 416; Lacordaire 1869:509; Bates 1870:329; 1880:44.

This genus may be recognized by the short, rather squat form, short, subserrate antennae, rounded pronotum, short, apically truncate elytra, and arcuate posterior femora.

Type-species: *Tomopterus staphylinus* Audinet-Serville, 1833 (monotypic).

The species of *Tomopterus* appear to mimic eumenine vespids. Two species occur in Mexico.

Tomopterus vespoides White

Tomopterus vespoides White, 1855:176, pl. 5, fig. 8; Bates 1880:44; 1885:291; Fisher 1930:17.

Male: Integument black, antennae reddish distally, apices of hind femora and tibiae pale, elytra usually narrowly reddish along lateral margins and with a reddish median stripe extending from humeri arcuately to middle of apex. Head with eyes contiguous on front; antennae with segments from fifth expanded, subserrate. Pronotum almost as broad as elytra; disk coarsely, contiguously punctate; apex and base with bands of yellow, appressed pubescence. Scutellum elongate, triangular, nonpubescent. Elytra moderately coarsely, densely punctate, sparsely pubescent. Abdomen with sternites margined with yellowish, appressed pubescence; parameres prominent. Length, 8–10 mm.

Female: Form more robust. Head with eyes separated on front by about width of antennal scape. Scutellum yellow-pubescent. Elytra black medially, remainder reddish. Abdomen bulbous, pointed apically. Length, 8–10 mm.

Type-locality: Guatemala.

Range: Tamaulipas, Mexico to Panama.

Flower Records (Costa Rica): *Bixa, Forsteronia, Byrsonima, Paullinia, Cordia*.

New Records: 1 female, 10 miles [16 km] N Cuidad Victoria, Tamaulipas, 20 Aug. 1941 (H. S. Dybas); 1 female, 9 miles [ca. 14 km] S Tuxpán, Veracruz, 11 June 1961 (Michener and Ordway); 1 female, Tehuantepec, Oaxaca, 8 July 1962.

Tomopterus exilis, new species

(Figure 1)

Female: Form small, rather slender; integument black, antennae brownish; elytra narrowly pale at base, each side with a broad, oblique, pale vitta extending from behind humerus to apex; anterior and intermediate legs brownish, posterior femora pale over basal one-half; pubescence silvery, appressed. Head with front rather short, moderately coarsely, densely punctate; eyes separated on front by little more than diameter of antennal scape; separated on vertex by about twice diameter of scape; antennae clavate, enlarging from fifth segment, outer segments broader than long, with small apical poriferous areas, third segment longer than first, fourth shorter than first, fifth longer than fourth, basal segments with a few, long, erect setae beneath. Pronotum as long as broad, cylindrical; disk coarsely, deeply reticulate-punctate; apex narrowly impressed, base rather broadly impressed; apex and base with narrow transverse silvery bands of appressed pubescence, each side with a narrower band behind middle extending from sides to coxal cavities; long, pale, erect hairs numerous; prosternum densely punctate, sparsely clothed with long, erect hairs;

mesosternum with a broad pubescent band over epimeron; metasternum sparsely punctate, with a long erect seta rising from each puncture, a narrow, oblique, pubescent band present posteriorly. Scutellum densely silver-pubescent. Elytra broader than long, densely, deeply, contiguously punctate; pubescence long, erect; pale vittae in form of a broad V; apices obliquely truncate. Legs slender; femora enlarged over apical one-half, hind pair arcuate, extending almost to apex of abdomen; tibiae slender. Abdomen only slightly enlarged posteriorly; punctures and pubescence fine, sternites more densely pubescent along posterior margins; last sternite rounded at apex. Length, 8 mm.

Holotype, female (National Museum of Natural History) from Cancún, Quintana Roo, Mexico, 25 Apr. 1974 (D. Pletsch).

The more slender form, cylindrical rather than transverse pronotum, and longer antennae will separate this species from *T. vespoides* White.

Genus **Epimelitta** Bates

Charis Newman, 1840:21; Thomson 1864:163; Lacordaire 1869:507 (name preoccupied). Type-species: *Charis euphrosyne* Newman, 1840, Thomson designation, 1864).
Epimelitta Bates, 1870:330; 1873:123.
Charisia Champion, 1892:161 (new name for *Charis* Newman, 1840, preoccupied).

The Mexican species in this genus may be recognized by the short elytra, lack of longitudinal calluses on the pronotum, and densely tufted posterior tibiae.

Type-species: *Epimelitta meliponica* Bates, 1870 (by present designation).

Most species of *Epimelitta* mimic meliponid bees. The group is dominantly South American with only two species presently known from Mexico.

Epimelitta nigerrima (Bates)

Charisia nigerrima Bates, 1892:160, pl.6, fig. 8.
Epimelitta nigerrima; Aurivillius 1912:284.

Female: Integument black, antennae reddish brown. Antennae short, serrate from fifth segment. Pronotum densely clothed with long erect pubescence; disk callused behind middle. Elytra strongly dehiscent, densely punctate. Legs short, femora and tibiae with dense tufts of dark pubescence. Length, 11 mm.

Type-locality: Atoyac, Veracruz, Mexico.

Only the holotype of this species is known.

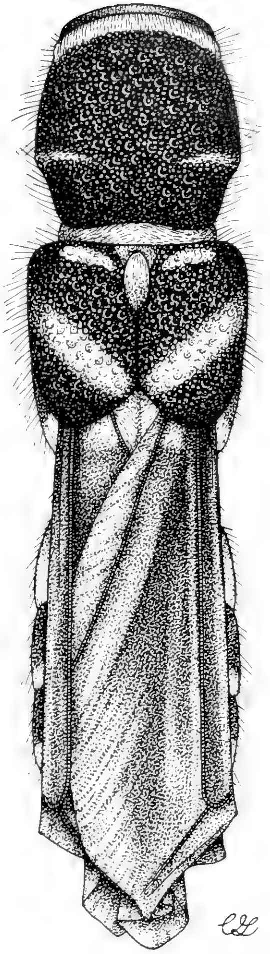


Figure 1. Dorsal view of pronotum and body of *Tomopterus exilis* Chemsak and Linsley, female.

Epimelitta aureopilis Fisher

Epimelitta (?) *aureopilis* Fisher, 1953:16.

Male: Form slender, elongate; head, prothorax, part of metasternum and often bases of hind femora black, antennae reddish brown, elytra testaceous except for narrow black lateral and sutural margins, legs and abdomen partially reddish, posterior tarsi yellow. Head small, front golden pubescent; antennae slender, moderately serrate. Pronotum densely, coarsely punctate; apex and base with a broad band of appressed golden pubescence, basal band reaching to about middle at center. Elytra dehiscent, sparsely pubescent. Legs with posterior pair very elongate, femora feebly clavate, tibiae with a dense tuft of long reddish-orange pubescence. Abdomen elongate, slender, last sternite barely impressed. Length, 16–21 mm.

FEMALE: Form and coloration similar. Abdomen with last sternite narrowly rounded at apex. Length, 18–23 mm.

TYPE-LOCALITY: Tolomé, Veracruz, Mexico.

This species differs greatly in facies from other known *Epimelitta*. Its long, slender form with very long posterior legs, make it especially distinctive. However, except for these characteristics, *aureopilis* is structurally similar to other species within the genus.

Fisher (1953) tentatively assigned *aureopilis* to *Epimelitta* because of the difficulty in delimiting genera of Rhinotragini. We have retained it in this genus since it is beyond the intent of this paper to attempt to clarify the generic classification of this primarily South American group.

NEW RECORDS: 3 females, 3 males, Cotaxtla Exp. Sta., Cotaxtla, Veracruz, 1 Aug. 1962 (D. H. Janzen); 1 male, Ixmal, Yucatán (G. F. Gaumer); 1 female, 30 miles [48 km] NE Tehuantepec, Oaxaca, 8 July 1955 (D. Giuliani).

Genus **Bromiades** Thomson

Bromiades THOMSON, 1864:165; LACORDAIRE 1869:506; BATES 1873:120; ZAYAS 1975:130.

The tricallused pronotum, strongly serrate antennae, and short, tapered elytra distinguish this genus.

TYPE-SPECIES: *Odontocera brachyptera* Chevrolat, 1838 (by original designation).

Bromiades brachyptera (Chevrolat)

Odontocera brachyptera CHEVROLAT, 1838:285; JACQUELIN DUVAL *in* SAGRA 1857:269, pl. 10, fig. 9.

Bromiades brachyptera; THOMSON 1864:165; BATES 1873:120; FISHER 1930:13; LINSLEY 1935:85, pl. 2, fig. 3; ZAYAS 1956:113; 1975:131, pl. 17, fig. a.

Bromiades meridionalis FISHER, 1930:14 (type-locality, Cabima, Panama). NEW SYNONYMY.

MALE: Integument black, shining, antennal segments four to usually eight, yellowish basally; elytra broadly testaceous medially; femora usually with basal one-half testaceous; anterior and intermediate tibiae basally and posterior pair except apically, testaceous. Pronotum densely clothed with golden, recumbent pubescence between calluses. Abdomen not modified apically. Length, 15–17 mm.

FEMALE: Form and coloration similar to male, abdomen broader. Antennae occasionally almost all black. Length, 16–18 mm.

TYPE-LOCALITY: Cuba.

RANGE: Central Mexico to Colombia and Cuba.

HOST PLANTS: *Andira inermis* (W. Wright) H.B.K. ex D.C. (Cuba).

FLOWER RECORDS. Costa Rica: *Cordia, Casearia, Forsteronia, Coccoloba,* asclepiad vine. Mexico: *Spondias*.

Color variation is apparent in the antennae and legs. Specimens from Panama have dominantly black antennae and orange posterior femora and tibial brushes. This type of color variation occurs in numerous species throughout the tribe.

We have seen no additional specimens from Mexico since those reported by Linsley (1935) from Bejucos.

Genus **Acyphoderes** Audinet-Serville

Acyphoderes AUDINET-SERVILLE, 1833:549; WHITE 1855:194; THOMSON 1860:179; 1864:165; LACORDAIRE 1869:505; BATES 1873:117; 1880:43.

This genus may be recognized by the dorsal callosities of the pronotum. The antennae are distally serrate and usually extend to about the middle of the elytra. The elytra are subulate or elongate, narrowed posteriorly and extend to the abdomen. The anterior and intermediate femora are usually strongly clavate. Males of most species have the last abdominal sternite modified in varying degrees.

TYPE-SPECIES: *Acyphoderes aurulenta* Kirby, 1818 (Thomson designation, 1864).

Acyphoderes, with ten species, is the largest group of Rhinotragini found in Mexico. Two other species, *velutinus* Bates, 1885, and *vespiventris* Bates, 1880, described originally from Guatemala, probably also occur in Mexico.

Key to the Mexican species of *Acyphoderes*

1. Pronotum black, with discal callosities shining, punctures sparse or absent 2
Pronotum reddish or infuscated, discal callosities opaque, densely punctate 5
2(1). Pronotum with transverse or longitudinal bands of dense, appressed pubescence 3
Pronotum rather sparsely pubescent,

without basal and apical transverse pubescent bands 4

3(2). Pronotum densely pubescent along apical and basal margins, dorsal calluses usually punctate, lateral pair rounded, punctures very dense, confluent. Length, 13–20 mm. Sinaloa to Oaxaca and Veracruz .... *cribricollis*

Pronotum densely pubescent except on calluses, calluses shining, elongate, not punctate, punctures obscured. Length, 14–18 mm. Sinaloa to Chiapas .... *amoena*

4(2). Elytra subulate, extending only to anterior margin of second abdominal segment; abdomen strongly inflated toward apex. Length, 17–21 mm. Nayarit to Oaxaca and Veracruz .... *sexualis*

Elytra more gradually tapering, extending over first three abdominal segments; abdomen narrowed toward apex. Length, 14–18 mm. Veracruz to Costa Rica .... *fulgida*

5(1). Elytra with apices rounded, as broad as or broader than diameter of antennal scape 6

Elytra with apices truncate to emarginate, narrower than diameter of antennal scape 7

6(5). Pronotum deeply impressed at base and apex, with bands of dense appressed pubescence in impressions; elytra black around scutellum. Length, 20–25 mm. Colima .... *prolixa*

Pronotum not deeply and broadly impressed at base and apex, without transverse bands of dense pubescence; elytra pale around scutellum. Length, 11–18 mm. Baja California .... *delicata*

7(5). Pronotum with apical and basal transverse bands of dense, appressed pubescence, dorsal calluses moderately elevated 8

Pronotum rather uniformly pubescent, without transverse bands, dorsal calluses prominently elevated. Length, 15–20 mm. Colima to Oaxaca and Veracruz .... *acutipennis*

8(7). Elytra 2.5 or more times longer than basal width, extending at least to third abdominal segment 9

Elytra short, 2.0 times as long as basal width, extending only to second abdominal segment. Length, 10–18 mm. Campeche to Honduras .... *yucateca*

9(8). Legs with hind femora pedunculate; abdomen abruptly inflated toward apex; elytra with two oblique, usually brownish, scabrous bands at base. Length, 11–16 mm. Sinaloa to Nayarit .... *parva*

Legs with hind femora gradually enlarged; abdomen gradually expanded toward apex; elytra punctate at base, with a triangular yellowish area around scutellum. Length, 13–22 mm. Sonora and Tamaulipas to Costa Rica .... *suavis*

Acyphoderes cribricollis Bates

Acyphoderes cribricollis Bates, 1892:160, pl. 6, fig. 6; Linsley 1935:84; Chemsak 1967:74 (lectotype).

Male: Form slender, elongate; integument black; antennae reddish brown, usually infuscated apically; elytra testaceous, shining, margins dark, legs pale, hind pair with femoral club and apices of tibiae brownish; abdomen with first two segments yellowish, usually infuscated apically, other segments usually reddish. Head with front densely pubescent, eyes separated by less than diameter of antennal scape. Pronotum longer than broad; apex and base broadly impressed; disk with median callus punctate, lateral pair more elevated anteriorly, glabrous, rounded; punctures dense, opaque; apical and basal margins with broad bands of dense, appressed, golden pubescence, bands joined laterally and usually extended longitudinally on disk on each side of middle; pro- and mesosternum pubescent; anterior one-half of metasternum and posterior end of episternum densely pubescent. Elytra extending to posterior margin of third abdominal segment; base and disk finely, sparsely punctate, margins densely punctate; apices rounded, about as broad as antennal scape. Legs with femora clavate, anterior and intermediate pairs moderately clavate. Abdomen slender, slightly enlarged toward apex; last sternite deeply, broadly excavated, margins prominent, elevated apically. Length, 14–20 mm.

Female: Form similar. Head with eyes widely separated on front. Abdomen with last sternite not modified. Length, 13–20 mm.

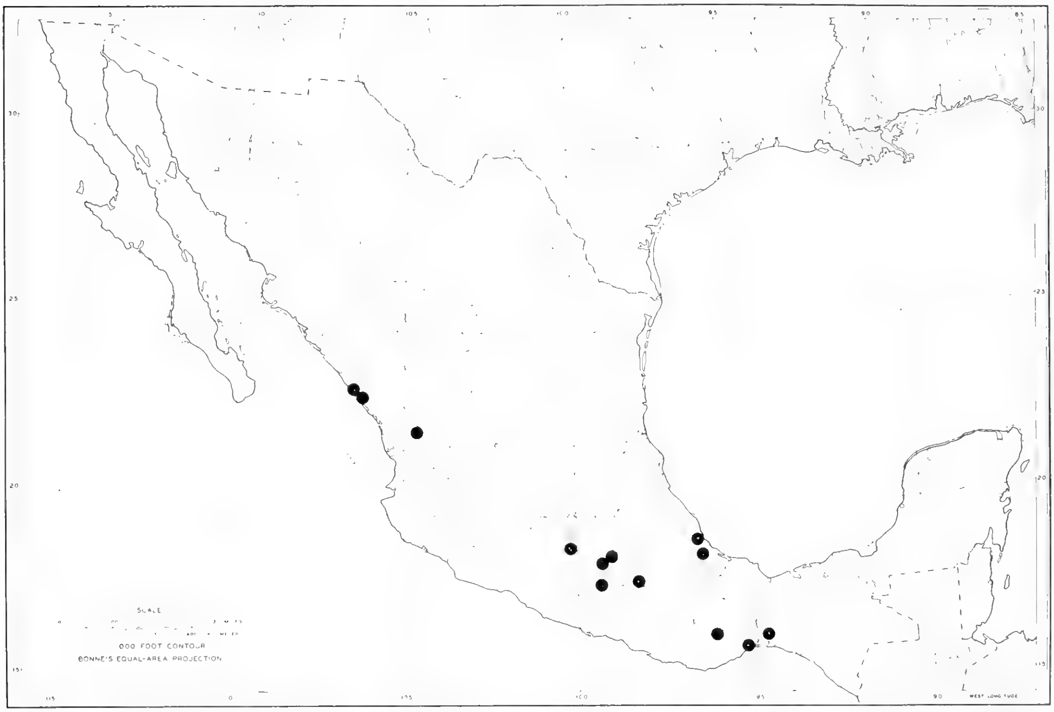


FIGURE 2. Known distribution of *Acyphoderes cribricollis* Bates.

TYPE-LOCALITY: Ventanas, Durango.

FLOWER RECORDS: *Croton, Xanthoxylum, Jatropha.*

The dense pubescence, rounded, glabrous calluses, and dense, opaque punctation of the pronotum distinguish this species.

NEW RECORDS: See Figure 2.

Acyphoderes amoena, new species
(Figure 3)

MALE: Form moderate sized; integument black; antennae reddish brown; elytra shining, yellow-brown, margins black, base often with two short dark vittae extending back from inside of humeri; legs orange-brown, posterior femora often dark over clavate portion; abdomen usually pale and dark. Head with eyes separated on front by less than diameter of antennal scape; front and vertex densely clothed with appressed golden pubescence. Pronotum longer than broad, sides impressed before and behind middle; disk uneven, dorsal calluses glabrous, elevated, sides with smaller calluses before middle, pubescence between calluses dense, appressed, golden, obscuring surface, long, erect hairs rather sparse; prosternum densely pubescent; mesosternum densely clothed with appressed golden pubescence; metasternum densely pubescent except for rectangular areas near base, episternum with dense pubescent patches posteriorly and anteriorly on upper margin. Elytra elongate, extending to fourth abdominal segment; lateral margins darkened, narrowly punctate, sutural margins elevated, narrowly dark; disk shining, very sparsely punctate except on base; apices rounded, broad. Legs with anterior and intermediate femora moderately clavate; posterior femora gradually clavate; posterior tibiae densely pubescent over apical one-half. Abdomen not apically enlarged; sternites with small patches of dense pubescence at sides of apical margins; last sternite broadly excavated, margins elevated toward apex, angles blunt. Length, 14–18 mm.

FEMALE: Form similar. Head with eyes widely separated on front. Abdomen with last sternite broadly rounded at apex. Length 16–18 mm.

Holotype, male (California Academy of Sciences) from 3 miles [ca. 5 km] E Villa Union, Sinaloa, Mexico, 24 July 1972,

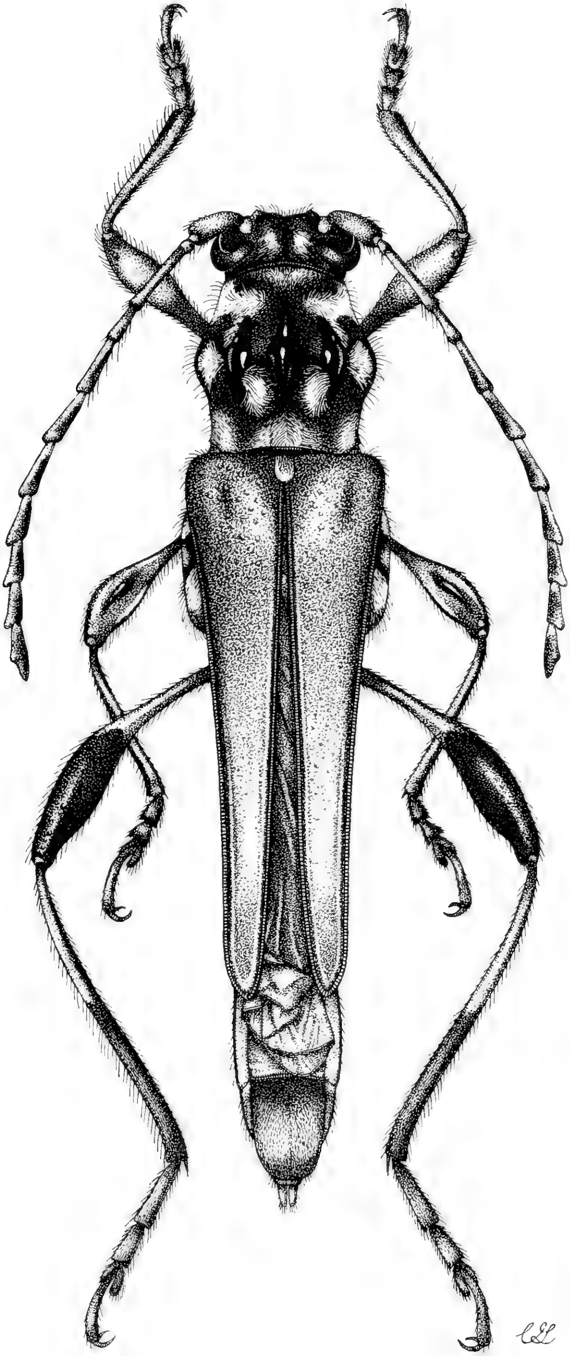


FIGURE 3. *Acyphoderes amoena* Chemsak and Linsley, male.

on *Jatropha curcas* flowers (J. A. and M. A. Chemsak, A. E. and M. M. Michelbacher). **Paratypes** as follow: 1 male, same data as type; 1 female, 16 miles [ca. 26 km] NE San Blas, Nayarit, 21 July 1963 (R. Westcott); 1 male, 14 miles [ca. 23 km] NW Tehuantepec, Oaxaca, 26 June 1961, on flowers of *Croton* (Univ. Kans. Mex. Exped.); 1 male, 23 miles [ca. 37 km] S Matías Romero, Oaxaca, 14 Aug. 1963 (Parker and Stange); 1 female, Playa La Ventosa, 3.5 miles [ca. 5.6 km]

NE Salina Cruz, Oaxaca, 28 July 1970 (Fisher, Sullivan); 1 female, 5 miles [ca. 8 km] NW Escuinapa, Sinaloa, 25 July 1971 (Fisher).

We are also assigning to this species five specimens from various localities in Mexico which differ in having the antennae black, with segments 8–11 all or partially yellow. In most of these, the two basal black vittae of the elytra are very distinct and the pubescence is more silvery than golden. Structurally they are identical with the typical forms.

Records are: 1 female, Tecolopa, Colima, 31 July 1954 (Cazier, Gertsch, Bradts); 1 female, 10 miles [ca. 16 km] W Colima, 1 Aug. 1954 (Cazier, Gertsch, Bradts); 1 male, Manzanillo, Colima, 12 July 1956 (R. and K. Dreisbach); 1 male, Acapulco, Guerrero, 30 July 1933 (M. A. Embury); 1 male, 31 miles [ca. 50 km] SE Comitán, Chiapas, 18 June 1965 (Burke, Meyer, Schaffner).

Acyphoderes sexualis Linsley

Acyphoderes sexualis LINSLEY, 1934:349; 1935:84, pl. 2, figs. 1, 1a.

MALE: Form rather elongate; integument black, antennae with basal segments infuscated beneath, reddish above, outer segments pale annulate basally; elytra with disk pale vitreous; abdomen with first segment reddish at middle; posterior legs with femora narrowly pale basally, tibiae yellowish at basal one-half. Head with eyes separated on front by about diameter of third antennal segment. Pronotum slightly broader than long, sides impressed behind middle, base narrower than apex; disk with three longitudinal, sparsely punctate, shining calluses; punctures between calluses fine, dense; pubescence fine, moderately dense, appressed, long erect hairs numerous; mesosternum with epimeron densely pubescent; metasternum with a broad, densely pubescent band anteriorly and a narrow band along posterior margin. Elytra subulate, extending to anterior portion of second abdominal segment; lateral margins broadly black and densely punctate, sutural margins narrowly black, impunctate; base scabrous, with two oblique black vittae behind scutellum; disk vitreous, almost impunctate. Legs with anterior and intermediate femora strongly clavate; posterior tibiae with a dense brush of hairs over apical one-half. Abdomen strongly inflated toward apex; sternites with first three segments margined at sides and apices with dense pubescence; last sternite with a large circular plate, sides prominently elevated; claspers large. Length, 20–21 mm.

FEMALE: Form similar. Head with eyes widely separated on front. Pronotum with dorsal calluses less prominent. Abdomen with last sternite excavated but lacking a plate. Length, 17 mm.

TYPE-LOCALITY: Bejucos, Temascaltepec, Mexico.

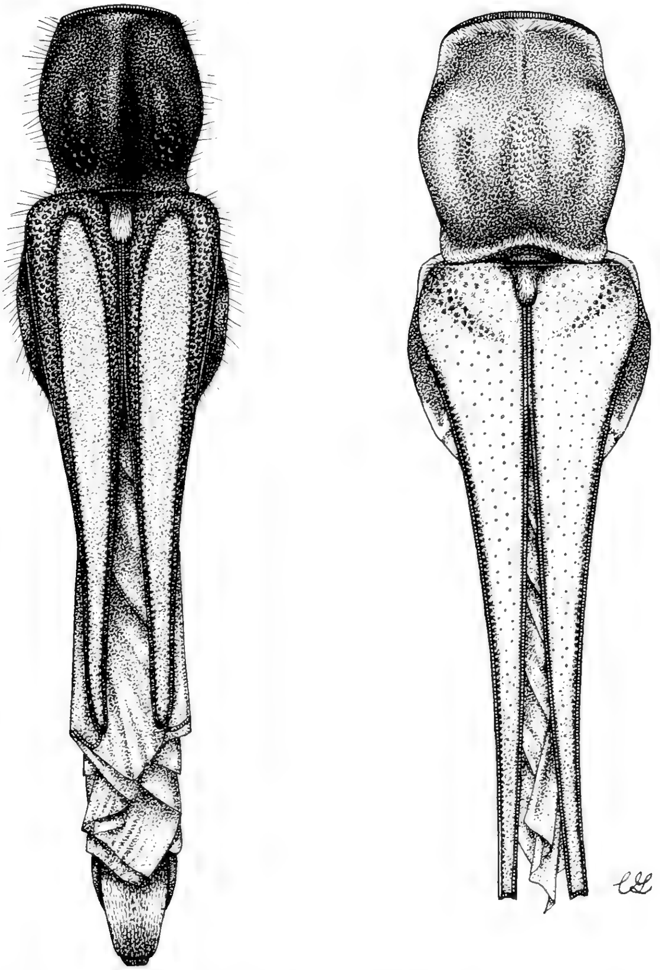
FLOWER RECORDS: *Acacia*, *Spondias*.

NEW RECORDS: 1 male, Arroyo Santiago, near Jesus María, Nayarit, 5 July 1955 (B. Malkin); 1 male, Mexcala, Guerrero, 29 June 1951 (H. Evans); 2 males, 20 miles [32 km] S Matías Romero, Oaxaca, 25 June 1961, on flowers of *Acacia* (Univ. Kans. Mex. Exped.); 1 female, 8 miles [ca. 13 km] NE Catemaco, Veracruz, 3 July 1971 (Clark, Murray, Hart, Schaffner).

Acyphoderes fulgida, new species

(Figure 4)

MALE: Form moderate sized, tapering; integument black, shining; antennae often brownish toward apex; elytra with disk testaceous, vitreous; hind femora usually testaceous over basal one-half except at extreme base. Head with eyes contiguous on front; inner margins of front elevated, nonpubescent. Pronotum longer than broad, sides impressed behind middle; disk with dorsal calluses elongate, barely punctate, shining; sides with oblique calluses on anterior one-half; punctures between calluses fine, dense; pubescence fine, pale, appressed, denser on sides, long, pale, erect hairs numerous; prosternum densely punctate at middle, densely clothed with long, pale, erect hairs; mesosternum with a dense, pale, pubescent patch on epimeron; metasternum densely pubescent over apical one-fourth, episternum with a small pubescent patch at end. Elytra elongate, extending to fourth abdominal segment; lateral margins broadly black at base, narrowly black toward apex, sutural margins more broadly black at base; punctures dense on dark margins, disk very sparsely punctate; apices rounded, broader than antennal scape. Legs with anterior and intermediate femora strongly clavate, clavae large; posterior femora gradually clavate; posterior tibiae with a moderately dense brush of dark hairs over apical one-half. Abdomen not enlarged apically; sternites one to three densely clothed with pale pubescence along lateral and apical margins and with a double row at middle; last sternite shallowly excavated with a large blunt tubercle on



FIGURES 4–5. Dorsal view of pronotum and body of (*left*) *Acyphoderes fulgida* Chemsak and Linsley, male, and (*right*) *Acyphoderes parva* Chemsak and Linsley, male.

each side at base, claspers densely pubescent. Length, 16–18 mm.

FEMALE: Form similar. Head with eyes separated on front by more than diameter of antennal scape. Pronotum very sparsely punctate between calluses. Abdomen with last sternite narrowly rounded at apex. Length, 14–18 mm.

Holotype, male; **allotype** (California Academy of Sciences) from La Pacífica, 4 km NW Cañas, Guanacaste Prov., Costa Rica, 25 May 1974, on *Casearia nitida* flowers (P. Opler). Six **paratypes** (3 males, 3 females) same locality, all collected by P. Opler, 25 May 1974, 2–4 June 1973, on asclepid vine, 3 June 1971, on *Trigonia floribunda*; 1 female, 2 miles [ca. 3.2 km] NW Cañas, 18–21 May 1974 (E. Giesbert); 2 females, Playa Hermosa, Guanacaste, 6–10 June 1974 (Giesbert).

Two additional specimens (1 male, 1 female) from Salto Eyiplantla, near Catemaco, Veracruz, Mexico, 17 Aug. 1976 (J. Hafernik and R. Garrison) are also assigned to this species.

In addition to the marked sexual dimorphism, this species varies slightly in coloration. Males occasionally have the posterior femora yellow and brownish. Some of the females have the femora and tibiae pale brownish except for the apical one-half of the hind tibiae.

The elongate elytra, punctation of the pronotum, and nonbulbous abdomen will separate *fulgida* from *sexualis*. The structure of the male copulatory apparatus is also strikingly different in the two species.

Acyphoderes prolixa, new species

MALE: Form very elongate; head reddish; antennae brownish; pronotum black; dorsal calluses reddish; elytra testaceous, margins brownish, base with a triangular black spot around scutellum; thoracic sterna black; legs pale, tibiae dark on dorsal edge, femora black internally on anterior portion of club; abdomen pale basally, reddish toward apex, sternites variably infuscated at bases. Head with eyes separated on front by about diameter of antennal scape; inner margins of front densely pubescent; antennae with segments from fourth opaque. Pronotum slightly longer than broad, sides rounded; apex and base broadly impressed; disk convex, dorsal calluses moderately elevated; calluses punctate, other punctures fine, dense; apex and base with densely pubescent bands; prosternum densely pubescent; mesosternum with epimeron densely clothed with pale appressed pubescence; metasternum densely pubescent anteriorly, episternum with a dense pubescent patch posteriorly. Elytra narrow, extending at least to middle of third abdominal segment; lateral margins brownish, densely punctate, sutural margins elevated, pale brownish; disk shining, testaceous, very sparsely punctate; apices rounded, about as wide as antennal scape. Legs with anterior and intermediate femora strongly clavate; posterior femora petiolate, clavae moderate. Abdomen elongate, not enlarged apically; sternites densely punctate, moderately densely pubescent; fourth sternite shallowly impressed at apex; last sternite broadly, deeply impressed, margins elevated basally, not forming angle at apex. Length, 21–25 mm.

FEMALE: Form more robust, less elongate. Head with eyes widely separated on front. Pronotum reddish, black on apical and basal margins; metepisternum partially reddish. Abdomen enlarged apically; last sternite not impressed. Length, 20–24 mm.

Holotype, male, **allotype** (American Museum of Natural History) and 6 paratypes (3 males, 3 females) from 10 miles [ca. 16 km] W Colima, Colima, Mexico, 1 Aug. 1954 (M. Cazier, W. Gertsch, Bradts).

This species may be recognized by the elongate form and black triangular patch around the scutellum. The coloration, more petiolate posterior femora, and broadly excavated, margined last abdominal sternite of the males will separate *prolixa* from *suavis*.

Acyphoderes delicata Horn

Acyphoderes delicatus HORN, 1894:400; HAMILTON 1896:168; LINSLEY 1942:54.

MALE: Form slender, gradually tapering; integument reddish; antennae orange-brown; elytra shining pale brownish, margins darker; underside partially infuscated; legs pale, femora with clavate portions brownish, hind tibiae broadly brown at apices. Head with eyes separated on front by more than diameter of antennal scape. Pronotum as long as broad, broadly rounded; disk opaque, median callus narrow, elongate, lateral pair broader, arcuate, densely punctate; pubescence fine, uniform, dense, short, erect; mesosternum with sides densely pubescent; metasternum densely pubescent over anterior one-half, episternum with a dense pubescent patch posteriorly. Elytra extending to fourth abdominal segment; base narrowly yellowish, sparsely punctate, margins densely punctate, disk sparsely punctate; apices rounded, much broader than antennal scape. Legs with anterior and intermediate femora clavate, clavae small; posterior tibiae densely pubescent at apical one-half. Abdomen slender, not enlarged apically; last sternite very shallowly impressed at apex, sides not margined. Length, 11–18 mm.

FEMALE: Not seen.

TYPE-LOCALITY: El Taste, Baja California Sur.

This species is distinctively characterized by the inflated, opaque pronotum and apically slender abdomen.

NEW RECORDS: 2 males, Santa Victoria Trail: La Burrera–La Laguna ridge, 1,200–1,350 m, Baja California Sur, 28 Aug. and 2 Sep. 1977 (R. L. Westcott).

Acyphoderes acutipennis Thomson

Acyphoderes acutipennis THOMSON, 1860:179; BATES, 1880:43; 1885:290.

MALE: Form elongate, strongly tapered; integument brownish; calluses of pronotum often yellowish; elytra yellowish brown. Head with eyes separated on front by about diameter of antennal scape; pubescence sparse. Pronotum longer than broad, sides impressed behind middle; disk with calluses prominently elevated, punctate, subopaque; pubescence moderately dense, pale, appressed, rather uniform; mesosternum with a dense patch of appressed pubescence at sides; metasternum with a small pubescent patch on posterior part of episternum. Elytra elongate, strongly tapered, extending to anterior margin of third abdominal segment; lateral margins broadly brownish, densely punctate, sutural margins narrowly brownish; base finely, densely asperate punctate; disk finely, sparsely punctate, each puncture bearing a short erect seta; apices truncate, narrower than diameter of antennal scape. Legs with anterior and intermediate femora strongly clavate. Abdomen gradually inflated toward apex; last sternite shallowly impressed at apex, sides barely margined. Length, 15–20 mm.

FEMALE: Form similar. Head with eyes more widely separated on front. Abdomen more bulbous, last sternite not impressed. Length, 16–20 mm.

TYPE-LOCALITY: Mexico.

The prominent, often pale calluses of the pronotum and rather elongate, apically narrow elytra make this species distinctive.

New records: 4 males, 2 females, Temascal, Oaxaca, 3 June 1964, 1 Nov. 1963 (D. Janzen); 1 male, Tezonapa, Veracruz, July 1906; 1 male, Colima, Colima (Conradt).

Acyphoderes yucateca (Bates), new combination

Odontocera yucateca BATES, 1892:159, pl. 6, fig. 7; CHEMSAK 1967:78 (lectotype).

MALE: Form moderately elongate, strongly tapered; integument light to dark reddish brown; elytra with disk testaceous. Head with eyes separated on front by about diameter of antennal scape. Pronotum longer than broad, sides lightly impressed behind middle, base slightly narrower than apex; disk with elongate calluses punctate, opaque; punctation dense, shallow, scabrous; base and apex with narrow bands of dense, appressed pubescence, long erect hairs rather sparse; meso- and metasternum with small, densely pubescent patches at sides of posterior margins. Elytra strongly tapered, extending to anterior margin of second abdominal segment; lateral margins dark from behind humeri to apices, densely punctate, sutural margins narrowly dark; impunctate; base moderately densely punctate, punctures sparse toward apex, each bearing a short seta; humeri and often a V-shaped basal vitta dark; apices truncate, narrower than diameter of antennal scape. Legs with anterior and intermediate femora strongly clavate. Abdomen moderately inflated toward apex; two basal segments yellowish; last sternite shallowly impressed, sides lightly margined; last tergite densely clothed with appressed pubescence. Length, 10–18 mm.

FEMALE: Form similar. Head with eyes more widely separated on front. Abdomen more inflated toward apex; last sternite unmodified. Length, 12–18 mm.

TYPE-LOCALITY: Temax, Yucatán, Mexico.

The pubescent bands and less elevated calluses of the pronotum will distinguish this species from *acutipennis*.

NEW RECORDS: 4 males, Yucatán (G. F. Gaumer); 3 males, 3 females, Piste, Yucatán, 6 and 26 Sep. 1967 (E. Welling); 1 male, Yaxche, Yucatán, 10 Sep. 1964 (J. and D. Pallister); 1 male, 1 female, X-Can, Quintana Roo, 25 June 1967, 26 Sep. 1967 (Welling); 1 male, Hwy. 180, Quintana Roo, 23 Mar. 1964 (E. L. Mockford); 1 male, 26 miles [ca. 42 km] S Yucatán line, Campeche, 30 June 1963 (Porter); 1 male, Campeche, Campeche, 30 June 1966 (McFadden); 1 male, El Zapotal, 2 miles [ca. 3.2 km] S Tuxtla Gutiérrez, Chiapas, 9 July 1957 (J. Chemsak); 1 female, Puerto Castilla, Honduras, Sep. 1945 (Crowell).

Acyphoderes parva, new species

(Figure 5)

MALE: Form rather small, short; integument pale brownish; head, pronotum, underside, and abdomen variously infuscated; elytra testaceous, dark margined, and with two dark, oblique basal bands. Head with eyes separated on front by a little more than diameter of antennal scape; inner margins of front densely pubescent. Pronotum longer than broad, sides slightly impressed behind middle; disk convex, dorsal calluses rather prominent, punctate; surface densely punctate, opaque; apical and basal margins with narrow pubescent bands; sternum with a narrow, densely pubescent band at sides; metasternum densely pubescent, with a pubescent patch at end of episternum. Elytra extending to anterior margin of third abdominal segment; base finely scabrous, densely punctate; lateral margins densely punctate, disk finely, sparsely punctate; apices truncate, narrower than antennal scape. Legs with anterior and intermediate femora strongly clavate, clavae large; hind femora petiolate, clavae short; hind tibiae arcuate. Abdomen enlarged toward apex; two basal segments with lateral patches of dense pubescence; last sternite broadly excavated, margins elevated at apex forming obtuse angles. Length 11–15 mm.

FEMALE: Form similar. Head with eyes more widely separated on front. Pronotum with dorsal calluses less prominent. Abdomen bulbous, last sternite not impressed. Length, 12–16 mm.

Holotype, male; **allotype** (California Academy of Sciences) from 5 miles [ca. 8 km] N Mazatlán, Sinaloa, Mexico, 1 Aug. 1972, on flowers of *Buddleia wrightii* (J. A. and M. A. Chemsak), 9–15 Aug. 1970, on *B. wrightii* (J. A. Chemsak). **Paratypes** as follow: 1 female, 5 miles [ca. 8 km] N Mazatlán, 9–15 Aug. 1970, on *Buddleia* (J. A. Chemsak); 10 males, Mazatlán, 28 Nov. 1962 (T. Gantenbein); 1 female, Acaponeta, Nayarit, 19 Nov. 1955 (E. C. Bay); 2 males, 15 miles [ca.24 km] NW Acaponeta, 19 Oct. 1964 (A. E. Michelbacher); 1 male, 15 miles [ca. 24 km] S Acaponeta, 20 Aug. 1964 (Burke and Apperson); 1 female, Teacapán, Sinaloa, 29 June 1956 (R. and K. Dreisbach); 2 females, Tuxpán, Nayarit, 20 Aug. 1964 (Burke and Apperson); 1 female, 60 miles [ca. 97 km] N Tepic, Nayarit, 15 Aug. 1957 (J. A. Chemsak).

This species averages smaller in size than most other Mexican *Acyphoderes*. It can be separated from *suavis* by the different coloration, more inflated abdomen, and petiolate posterior femora. Additionally, the excavation of the last abdominal sternite of males is deeper and the margins more highly elevated.

The coloration of *parva* varies from brownish to black and the basal oblique dark bands of the elytra are often vague.

Acyphoderes suavis Bates

Acyphoderes suavis BATES, 1885:290, pl. 20, fig. 20.

MALE: Form elongate; integument reddish; antennae with segments 6–8 usually infuscated; elytra pale brownish with a pale triangular basal area; underside variously infuscated; front and middle femora basally and dorsally dark, hind femora dark at middle; hind tibiae dark annulate on apical one-half. Head with eyes separated on front by slightly more than diameter of antennal scape. Pronotum longer than broad, sides lightly impressed behind middle; apex and base narrowly impressed; dorsal calluses moderately elevated, opaque; apex and base with a band of dense, appressed pubescence; mesosternum with epimeron densely pubescent; metasternum with a densely pubescent patch at posterior edge of episternum. Elytra extending to third abdominal segment; lateral margins lightly infuscated, densely punctate; disk finely, sparsely punctate; apices truncate, as broad as or narrower than antennal scape. Legs with anterior and intermediate femora strongly clavate, posterior pair gradually clavate. Abdomen gradually enlarged apically; last sternite impressed at apex, sides moderately produced apically. Length, 13–24 mm.

FEMALE: Form similar. Abdomen more bulbous, last sternite not impressed. Length, 15–22 mm.

TYPE-LOCALITY: Córdoba, Mexico.

FLOWER RECORDS: *Buddleia, Jatropha* (Mexico); *Casearia, Baltimora* (Costa Rica).

This species may be readily recognized by the color and pubescent bands of the pronotum.

In flight, adults greatly resemble and behave like those of *Polistes instabilis* Sauss.

NEW RECORDS: See Figure 6. Known from Mexico to Costa Rica.

Genus **Stenopseutes** Bates

Stenopseutes BATES, 1873:130; 1880:44.

This genus may be recognized by the slender antennae, longitudinally tricallose pronotum, reduced prosternal process, and slender, feebly clavate femora.

TYPE-SPECIES: *Stenopseutes aeger* Bates, 1873 (monotypic).

Two species are known, one from Mexico.

Stenopseutes sericinus Bates

Stenopseutes sericinus BATES, 1880:44.

FEMALE: Integument testaceous, antennae brownish. Pronotum densely clothed with appressed pubescence. Elytra vitreous with a triangular patch of appressed pubescence at base; margins narrowly dark. Legs yellowish, femora feebly clavate. Length, 14 mm.

TYPE-LOCALITY: Mexico.

No new material of this species has been seen. The above characterization was based upon a 35-mm color transparency of a specimen in the British Museum (Natural History).

Genus **Odontocera** Audinet-Serville

Odontocera AUDINET-SERVILLE, 1833:546; WHITE 1855:187; THOMSON 1860:176; 1864:417; LACORDAIRE 1869:503; BATES 1873:36; 1880:42; LINSLEY 1963:165.

The primary characteristic of this genus in Mexico is the vitreous disk of the elytra. *Odontocera* differs from *Ommata* by this character and also by the less elongate pronotum. *Acyphoderes* differs by the tricallused pronotum and usually more strongly clavate femora.

Type-species: *Odontocera vitrea* Audinet-Serville (Thomson designation, 1864).

Key to the Mexican species of *Odontocera*

1. Pronotum margined apically and basally by bands of dense, appressed pubescence 2
   Pronotum lacking dense pubescent bands, disk usually with a longitudinal median callus. Length, 11–16 mm. Mexico to Nicaragua .... *clara*

2(1). Elytra more than 3 times longer than basal width, erect hairs at base short; antennae extending beyond middle of elytra. Length, 11–20 mm. Southern Arizona to Chiapas and Veracruz .... *aurocincta*
   Elytra less than 3 times longer than basal width, erect hairs at base long; antennae not reaching to middle of elytra. Length, 12–13 mm. Tamaulipas to Veracruz .... *fuscicornis*

Odontocera fuscicornis Bates

Odontocera fuscicornis Bates, 1885:289.

Male: Form slender, rather short; integument black; antennae reddish; legs brownish, femora pale at bases; elytra yellowish, vitreous, narrowly margined by black, apices black, base with two dark humeral vittae; abdomen with first two segments partially pale. Head with front short, eyes contiguous; antennae short, segments from sixth expanded at apices, basal segments with a few long, erect hairs beneath. Pronotum moderately coarsely, subreticulately punctate; base deeply impressed, apical and basal pubescent bands silvery, long, erect hairs numerous. Elytra less than 3 times longer than basal width; punctures on vitreous areas sparse; pubescence at base long, erect. Legs with femora clavate; posterior tibiae moderately pubescent. Abdomen with last sternite impressed for most of its length, sides feebly elevated. Length, 12–13 mm.

Female: Form and coloration similar. Head with eyes well separated on front. Abdomen with last sternite not modified. Length, 13 mm.

Type-locality: Cordoba, Mexico.

The smaller size, shorter elytra and antennae will separate this species from *aurocincta*.

New Records: 2 males, 1 female, 22 miles [ca. 35 km] N El Limón, Tamaulipas, 9 June 1951 (P. D. Hurd).

Odontocera aurocincta Bates

Odontocera aurocincta Bates, 1873:42.

Male: Form elongate, slender, integument black; antennae pale with basal segments often infuscated; elytra pale, shining, base often black, lateral margins black to beyond middle; legs black or with only clavate portions of femora black; abdomen with segments one and two mostly pale. Head with front moderate, eyes subcontiguous; antennae slender, extending a little beyond middle of elytra, segments from sixth slightly produced apically. Pronotum longer than broad, sides rounded; disk coarsely, subconfluently punctate; apex and base with a band of dense, silvery or golden, appressed pubescence, bands extended along sides and united; long erect hairs numerous; mesosternum densely pubescent on epimeron; pubescent bands on anterior and posterior margins of metasternum and on episternum. Elytra more than 3 times longer than basal width; margins densely punctate, pale portion of disk rather sparsely, separately punctate; pubescence sparse, short, erect over basal half. Legs slender, femora clavate. Abdomen with last three sternites densely punctate, last sternite feebly impressed over most of its length, sides margined but not elevated. Length, 11–19 mm.

Female: Form similar; head and pronotum often reddish; antennae usually pale; legs pale, with femoral clavae black; abdomen usually mostly yellowish or reddish; pubescence golden. Head with eyes widely separated on front. Abdomen somewhat inflated toward apex; last sternite rounded at apex. Length, 12–20 mm.

Type-locality: Tehuantepec, Mexico.

This species is easily separated by the elongate form and pubescent bands of the pronotum.

Two distinct subspecies can be recognized.

Odontocera aurocincta aurocincta Bates

Odontocera aurocincta Bates, 1873:42; 1880:43.
Odontocera aurocincta aurocincta; Linsley 1961:163.
Odontocera aurocincta var. *nigroapicalis* Fisher, 1947:52; Linsley 1961:164 (type-locality, La Gloria, Cardel, Veracruz).

Males with pubescence golden; antennae usually all pale; elytra without basal black bands; legs with femoral clubs black. Females with head and pronotum black.

Type-locality: Tehuantepec.

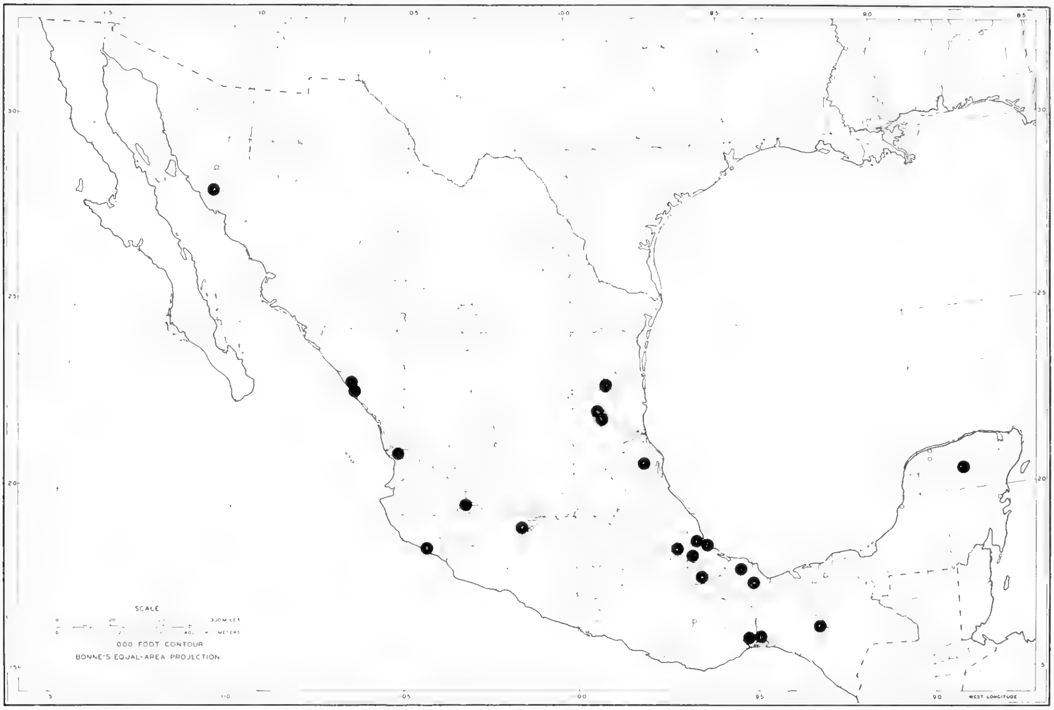


FIGURE 6. Known distribution of *Acyphoderes suavis* Bates in Mexico.

RANGE: State of Nayarit to Chiapas, north to Veracruz (Fig. 7).

FLIGHT PERIOD: June to August.

Adults have been taken on flowers of *Acacia*.

Odontocera aurocincta arizonensis Linsley

Odontocera aurocincta arizonensis LINSLEY, 1961:163; 1963:165.

Males with silvery pubescence; antennae with basal segments infuscated; legs usually all black; elytra black basally. Females with head and pronotum reddish.

TYPE-LOCALITY: Box Canyon, Santa Rita Mts., Arizona.

RANGE: southern Arizona to Sinaloa (Fig. 7).

FLIGHT PERIOD: July to September.

Adults frequent the flowers of *Acacia*, *Buddleia*, *Croton*, and *Jatropha*.

Although the models have not been specifically determined, it is clear that the two sexes of this subspecies mimic different insects. Females greatly resemble and fly like vespids, while males appear more like ichneumonids in the field.

Odontocera clara Bates

Odontocera clara BATES, 1873:38; 1874:222; 1880:43, pl. 5, fig. 4.

Odontocera carinicollis LINSLEY, 1934:348; 1935:84, pl. 2, fig. 6 (type-locality: Bejucos, Temascaltepec, Mexico). NEW SYNONYMY.

MALE: Form slender, elongate; integument black; pronotum often reddish; elytra pale vitreous except for narrow black margins; legs occasionally pale; antennae often with outer segments pale annulate. Head with front moderately long, eyes subcontiguous; antennae slender, extending beyond middle of elytra, segments from sixth slightly produced apically. Pronotum longer than broad, sides rounded; disk rather finely, irregularly punctate; middle usually with a longitudinal, slightly elevated callus which extends over most of the length; pubescence fine, erect, with appressed pubescence at sides; metasternum densely pubescent. Elytra more than 3½ times longer than basal width; base and black margins densely punctate, pale disk sparsely punctate; pubescence sparse. Legs slender; femora moderately clavate. Abdomen densely

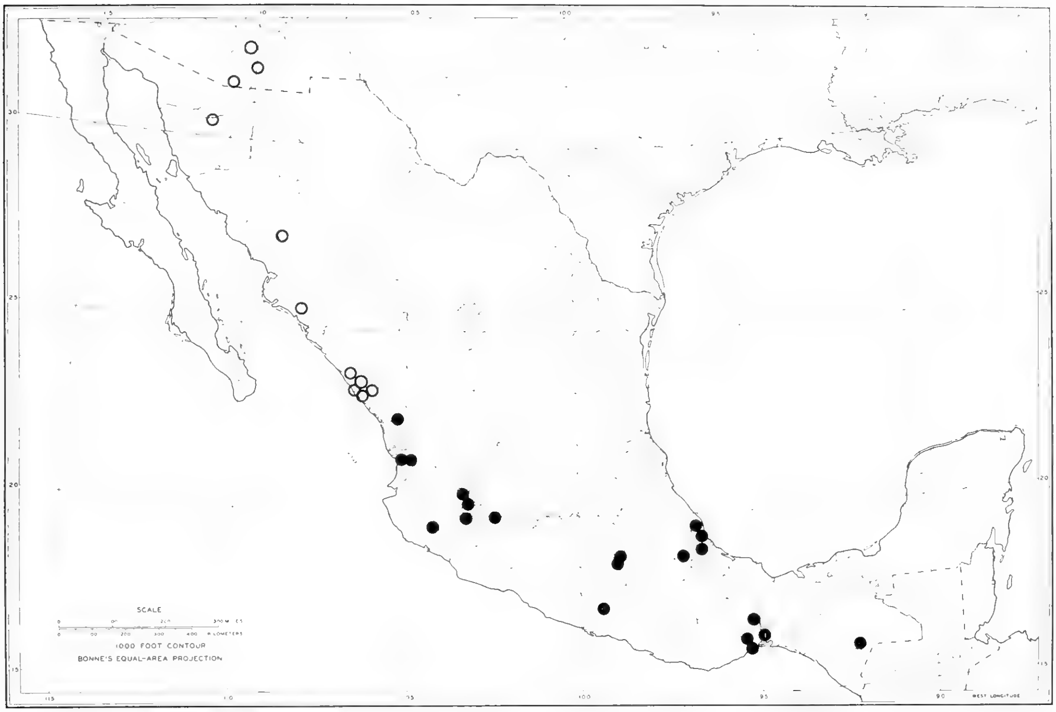


FIGURE 7. Known distribution of *Acyphoderes aurocincta aurocincta* Bates (closed circles), and *A. aurocincta arizonensis* Linsley (open circles).

pubescent; last sternite shallowly impressed at apex, sides barely elevated. Length, 11–14 mm.

FEMALE: Form similar. Pronotum a little broader. Abdomen with last sternite narrowly rounded at apex. Length, 14–16 mm.

TYPE-LOCALITY: Chontales, Nicaragua.

This species varies in having the pronotum reddish or black. The elongate, median callus of the pronotum characterizes it.

NEW RECORDS: 1 male, 1 female, 6 miles [ca. 10 km] N La Ventosa, Oaxaca, 19 July 1963 (W. A. Foster); 1 female, Suchiapa, Chiapas, 17 July 1957 (J. A. Chemsak); 1 female, 5.5 miles [ca. 8.9 km] NW Acala, Chiapas, 23 June 1965 (Burke, Meyer, Schaffner); 1 female, 30 miles [ca. 48 km] NE Tehuantepec, Oaxaca, 8 July 1955 (D. Giuliani); 1 female, 4.4 miles [ca. 7.1 km] E Cuernavaca, Morelos, 6–8 July 1974 (Clark, Murray, Ashe, Schaffner).

Genus **Ommata** White

Ommata WHITE, 1855:194; THOMSON 1864:166; LACORDAIRE 1869:502; BATES 1870:319; 1873:26; 1880:42; ZAJCIW 1966:875; 1970:37.

This is probably the most difficult genus of Rhinotragini to define. It has been divided into a number of subgenera, but a study of the entire group will be necessary to correctly determine the systematic position of the Mexican *Ommata*. In Mexico, the genus may be recognized by the usually long antennae, non-callused, elongate pronotum and usually non-vitreous elytra.

TYPE-SPECIES: *Ommata elegans* White, 1855 (monotypic).

Three species are presently known from Mexico.

Key to the Mexican species of *Ommata*

1. Pronotum elongate, cylindrical, not broadly impressed at base and apex; elytra subglabrous, with fine erect hairs arising from each puncture 2

   Pronotum about as long as broad, broadly impressed at base and apex; elytra densely clothed with appressed, golden pubescence. Length, 11 mm. Veracruz to Panama .... *sallaei*

2. Integument, especially pronotum and underside, metallic bluish to greenish; pos-

terior tibiae densely clothed with suberect, black setae. Length, 11–13 mm. Veracruz to Oaxaca .... *cyanea*

Integument non-metallic, abdomen often reddish; posterior tibiae sparsely pubescent. Length, 7–10 mm. Morelos to Guatemala .... *championella*

Ommata championella Bates

Ommata (Eclipta) championella BATES, 1880:42; ZAJCIW 1970:38.
Ommata (Ommata) rubriventris LINSLEY, 1934:347; 1935:84; ZAJCIW 1966:91 (type-locality: Tejupilco, Temascaltepec, Mexico). NEW SYNONYMY.

MALE: Integument black; antennae with outer segments basally yellow annulate; elytra with disk longitudinally pale brownish; femora yellowish basally; abdomen often reddish. Head with antennae enlarged from seventh segment. Pronotum narrow, shallowly reticulate-punctate. Elytra moderately coarsely, densely punctate, punctures becoming denser toward apex. Abdomen elongate; last sternite impressed at apex. Length, 7–9 mm.

FEMALE: Form more robust. Prothorax often reddish. Abdomen broader, reddish; last sternite narrowly rounded at apex. Length, 8–10 mm.

TYPE-LOCALITY: Calderas, Guatemala.

RANGE: Morelos, Mexico to Guatemala.

The small, slender form, punctation of the pronotum, and paler longitudinal stripes of the elytra will separate this species from other known Mexican *Ommata*.

NEW RECORDS: 1 female, 7 miles [ca. 11 km] SW Yautepec, Morelos, 2 July 1961, 3,500 ft [ca. 1,067 m] (Univ. Kansas Mex. Exped.); 1 male, 1 female, 3 miles [ca. 5 km] SE La Trinitaria, Chiapas, 18, 19 June 1965 (Burke, Meyer, Schaffner); 1 female, Las Margaritas, Chiapas, 18 June 1965 (Burke, Meyer, Schaffner); 1 female, 7 miles [ca. 11 km] SW Teopisca, Chiapas, 23 May 1969 (J. M. Campbell).

Ommata cyanea Bates

Ommata cyanea BATES, 1885:288.
Ommata (Eclipta) cyanea; ZAJCIW, 1970:38.

MALE: Integument greenish or bluish metallic; antennae bluish, yellow annulate from fourth segment; legs bluish; elytra brownish down middle. Head with antennae as long as elytra, segments from sixth apically expanded. Pronotum cylindrical; coarsely punctate at middle; sparsely pubescent; strongly narrowed toward apex; apices truncate. Legs with posterior femora elongate, feebly clavate. Abdomen with last sternite deeply impressed. Length, 11 mm.

FEMALE: Form similar. Antennae black; basal segments densely pubescent. Abdomen broader; last sternite narrowly rounded at apex. Length, 12–13 mm.

TYPE-LOCALITY: Cordova, Mexico.

The metallic coloration makes this species distinctive.

NEW RECORDS: 1 female, 5 miles [ca. 8 km] S Lake Catemaco, Veracruz, 6 July 1961 (D. H. Janzen); 1 female, 1 male, Temescal, Oaxaca, 6 July 1965 (G. Nelson and family).

Ommata sallaei Bates

Ommata sallaei BATES, 1885:289, pl. 20, fig. 15.

FEMALE: Integument yellowish; mandibles, eyes, antennae basally and at apices of outer segments, apical and basal margins and rounded median spot on pronotum, elytra except for triangular basal area, apices and dorsal edges of femora and bands on clubs of hind femora, and parts of underside black. Antennae slender, segments feebly produced at apices. Eyes widely separated on front. Pronotum coarsely punctate, sparsely pubescent. Elytra opaque, densely punctate and pubescent, apices truncate. Length, 11 mm.

TYPE-LOCALITY: Cordova, Veracruz.

This species is distinctive among Mexican *Ommata* in its color and opaque elytra. It is also known from Cerro Campana in Panama.

ACKNOWLEDGMENTS

These studies were carried out in conjunction with a National Science Foundation-sponsored study on North American Cerambycidae through Grant DEB 76-23849 A01. The authorities of the following institutions and individuals are gratefully acknowledged for the loan of specimens: American Museum of Natural History, New York; California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa; Cornell University, Ithaca; Essig Museum of Entomology, Berkeley; Field Museum of Natural History, Chicago; Los Angeles County Museum of Natural History; Museum of Comparative Zoology, Cambridge; Texas A & M University, College Station; United States National Museum of Natural History, Washington, D.C.; University of Arizona, Tucson; University of California, Davis; University of Kansas, Lawrence; E. Giesbert, D. Marqua, G. Nelson, and R. Westcott.

Celeste Green prepared the illustrations and Kathleen Sorenson the maps.

LITERATURE CITED

AUDINET-SERVILLE, J. G. 1833. Nouvelle classification de la famille des longicornes. Ann. Soc. Entomol. France. 2:528–573.

AURIVILLIUS, C. 1912. Coleopterorum catalogus 39:1–574. Berlin.

BATES, H. W. 1870. Contributions to an insect fauna of the Amazon Valley (Coleoptera, Cerambycidae). Trans. Entomol. Soc. London. 1870:243–335, 391–444.

———. 1873. Notes on the longicorn Coleoptera of Tropical America. Ann. Mag. Nat. Hist. (4) 11:21–45, 117–133.

———. 1874. Supplement to the longicorn Coleoptera of Chontales, Nicaragua. Trans. Entomol. Soc. London. 1874 (2):219–235.

———. 1879–1885. Longicornia. Biologia-Centrali-Americana, Insecta, Coleoptera. 5:iii–xii, 1–436, pls. 1–25.

———. 1892. Additions to the Longicornia of Mexico and Central America with remarks on some of the previously recorded species. Trans. Entomol. Soc. London. 1892 (2):143–183, 3 pls.

CHAMPION, G. C. 1892. [Footnote proposal of *Charisia* to replace *Charis* Newman]. Trans. Entomol. Soc. London. 1892:161.

CHEMSAK, JOHN A. 1967. Lectotype designations of Cerambycidae in the British Museum (Natural History). J. Kansas Entomol. Soc. 40:73–81.

CHEVROLAT, L. A. A. 1838. Insectes coléoptères inédits, découverts par M. Lanier dans l'intérieur de l'ile de Cuba. Rev. Zool. 1838:279–286.

FISHER, W. S. 1930. Notes on the rhinotragine beetles of the family Cerambycidae, with descriptions of new species. Proc. U.S. Natl. Mus. 77:1–20.

———. 1947. New cerambycid beetles belonging to the tribe Rhinotragini. Proc. U.S. Natl. Mus. 97:47–57.

———. 1953. New cerambycid beetles belonging to the tribe Rhinotragini. Pan-Pac. Entomol. 29:14–17.

HAMILTON, J, *in* LENG AND HAMILTON, 1896. Synopsis of the Cerambycidae of North America. Part 3, The Lamiinae. Trans. Am. Entomol. Soc. 23:101–178.

HORN, G. H. 1894. The Coleoptera of Baja California. Proc. Calif. Acad. Sci. (2) 4:302–449.

JACQUELIN DU VAL, P. N. C. *in* SAGRA, 1857. Insectes. Ordre des coléoptères. Histoire. . .de l'ile de Cuba. 7:137–328.

KIRBY, W. 1818. A century of insects, including several new genera described from his cabinet. Trans. Linn. Soc. London 12:375–453.

LACORDAIRE, J. T. 1869. Histoire naturelle des insectes. Genera des coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insects. 8:1–552.

LINSLEY, E. G. 1934. A new genus and several new species of Neotropical rhinotragine beetles. Rev. Entomol. 4: 345–351.

———. 1935. Studies in the Longicornia of Mexico. Trans. Am. Entomol. Soc. 61:67–102, 1 pl.

———. 1942. Contributions toward a knowledge of the insect fauna of Lower California. No. 2. Coleoptera: Cerambycidae. Proc. Calif. Acad. Sci. (4) 24:21–96, pls. 4–5.

———. 1961. A new rhinotragine cerambycid from Arizona and Sonora. Entomol. News 72:163–164.

———. 1963. The Cerambycidae of North America. Part IV. Taxonomy and classification of the subfamily Cerambycinae, tribes Elaphidionini through Rhinotragini. Univ. Calif. Publ. Entomol. 21:165, 52 figs.

NEWMAN, E. 1840. Entomological notes. The Entomologist 1:1–16; 2:17–32.

THOMSON, J. 1860. Essai d'une classification de la famille des cérambycides et matériaux pour servir a une monographie de cette famille. Pp. 1–404, illus. Paris.

———. 1864. Systema cerambycidarum ou exposé de tous les genres compris dans la famille des cérambycides et familles limitrophes. Mém. Soc. Roy. Sci. Liège. 19:1–540.

WHITE, A. 1855. Catalogue of coleopterous insects in the collection of the British Museum. Pt. VIII, Longicornia II, pp. 175–412, pls. 5–10. London.

ZAJCIW, D. 1966. Estudos do genero "Ommata" White, 1855. II: Subgenero "Ommata". Rev. Brasil. Biol. 26:87–92, 1 fig.

———. 1970. Estudos do genero *Ommata* White, 1855. V: Notas sobre o subgenero *Eclipta* Bat., 1873. Atas Soc. Biol. Rio de Janeiro 13:37–40.

ZAYAS, F. DE. 1956. El genero *Essostrutha* Thoms., adición de una especie nueva. Mem. Soc. Cubana Hist. Nat. 23:105–114, 1 pl.

———. 1975. Revisión de la familia Cerambycidae. Acad. Cien. Cuba, Inst. Zool. 443 pp., 35 figs.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 4, pp. 87–133, 70 figs. December 22, 1979

STUDIES ON THE NEBRIINI (COLEOPTERA: CARABIDAE), III.[1] NEW NEARCTIC *NEBRIA* SPECIES AND SUBSPECIES, NOMENCLATURAL NOTES, AND LECTOTYPE DESIGNATIONS[2]

By
David H. Kavanaugh
Department of Entomology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

ABSTRACT: The purpose of this paper, third of a series on the nebriine carabid beetles, is to upgrade the status of nomenclature for Nearctic members of genus *Nebria* in preparation for subsequent papers on classification, phylogeny, zoogeography, and natural history of members of the Nearctic fauna. Names are provided for five undescribed species [*Nebria carri* (type-locality—Dollarhide Summit, Idaho), *N. darlingtoni* (type-locality—South Fork American River, California), *N. gouleti* (type-locality—Rattlesnake Creek, Washington), *N. lituyae* (type-locality—Mount Blunt, Lituya Bay, Alaska), and *N. navajo* (type-locality—19 miles SW of Kayenta, Arizona)]. Twenty-three subspecies are also described as new [*Nebria acuta quileute*, *N. arkansana edwardsi*, *N. arkansana oowah*, *N. arkansana uinta*, *N. fragilis teewinot*, *N. gebleri cascadensis*, *N. gebleri fragariae*, *N. gebleri siskiyouensis*, *N. gyllenhali lassenensis*, *N. gyllenhali lindrothi*, *N. kincaidi balli*, *N. lacustris bellorum*, *N. meanyi lamarckensis*, *N. meanyi sylvatica*, *N. nivalis gaspesiana*, *N. obliqua chuskae*, *N. sahlbergii modoc*, *N. sahlbergii triad*, *N. schwarzi beverlianna*, *N. spatulata sierrae*, *N. trifaria utahensis*, *N. vandykei wyeast*, and *N. zioni oasis*]. Diagnosis and comment on geographical distribution are provided for each new taxon. Lectotypes are designated for *Carabus gyllenhali* Schönherr, *C. nivalis* Paykull, *Helobia castanipes* Kirby, *Nebria bifaria* Mannerheim, *N. eschscholtzii* Ménétriés, *N. gregaria* Fischer von Waldheim, *N. hudsonica* LeConte, *N. ingens* Horn, *N. livida* LeConte, *N. mannerheimii* Fischer von Waldheim, *N. metallica* Fischer von Waldheim, *N. mollis* Motschulsky, *N. moesta* LeConte, *N. obliqua* LeConte, *N. sahlbergii* Fischer von Waldheim, *N. suturalis* LeConte, *N. trifaria* LeConte, *N. vandykei* Bänninger, *N. violacea* Motschulsky, and *N. viridis* Horn. *Nebria longula* LeConte and *N. obtusa* LeConte are recognized as junior synonyms of *N. suturalis* LeConte and *N. obliqua* LeConte, respectively. *Nebria rathvoni* LeConte is reduced in status to a subspecies of *N. gebleri* Dejean. Emendations or restrictions of type-localities are provided for *Nebria catenata* Casey, *N. eschscholtzii* Ménétriés, *N. expansa* Casey, *N. hudsonica* LeConte, *N. incerta* Casey, *N. ingens* Horn, *N. longula* LeConte, *N. obliqua* LeConte, *N. oregona* Casey, *N. ovipennis* LeConte, and *N. tenuipes* Casey. Additional notes on type-specimens and nomenclature are provided for other species group names.

INTRODUCTION

My interest in beetles of the genus *Nebria* Latreille began in 1967. While collecting carabid beetles in the Rocky Mountains of Colorado, I concentrated on my own preferred haunts—namely, riparian, nival, and peri-nival habitats. This specialization provided frequent encou-

---

[1] Papers which serve as contributions I and II in this series are, respectively, Kavanaugh (1971) and Kavanaugh and Martinko (1972).

[2] Data presented here have been extracted from the author's unpublished Doctoral Dissertation, submitted to the University of Alberta, Edmonton, September 1978 (Kavanaugh 1978).

ters with members of various *Nebria* species because, in these habitats, few insect groups approach *Nebria* in their conspicuous abundance. With the aid of Lindroth's (1961) treatment of the genus for Canada and Alaska, I was able to identify most of my material. It soon became evident that *Nebria* species formed a biologically important and interesting element of the montane fauna. Species diversity and population densities in suitable microhabitats were impressively high, and I began to recognize patterns of altitudinal zonation among the resident species. Observations made on collecting trips to montane areas in Utah and California suggested that similar patterns of *Nebria* species diversity and habitat distribution existed in these and other areas in western North America.

The opportunity to begin serious study of Nearctic *Nebria* appeared in July 1970, when I enrolled at the University of Alberta, Edmonton. Although Nearctic *Nebria* species were at that time already among the taxonomically better-known carabid groups, I hoped to build on my previous interest and experience through additional studies which seemed both feasible and potentially rewarding scientifically. My plan was to obtain data with which to further define the structural and distributional limits of Nearctic species and explore the evolutionary relationships among them. Initial goals were the formulation of an improved infrageneric classification of the New World species and generation of hypotheses concerning the historical development of diversity and distributional patterns observed in the fauna.

Nebria, in the broadest sense, comprises a group of over 500 nominal taxa which, in aggregate, demonstrate Holarctic distribution. The Palaearctic component of the genus is more diverse, both in species and major lineages, than the Nearctic. Consequently, all hypotheses on relationships among Nearctic species and on historical development of the Nearctic fauna would be highly speculative in the absence of a working knowledge of the Palaearctic fauna. Fortunately, as work toward the initial project goals progressed, new sources of taxonomic data became available as by-products of field work and efforts to obtain comparative material on loan. These additional resources have permitted expansion of the project to include coverage of the Palaearctic *Nebria* fauna, comparisons with members of other nebriine genera and related carabid tribes, and the use of additional character systems in study of the Nearctic *Nebria* fauna. These other systems include external structure of immature stage individuals, life history features (especially life cycle timing), habitat preferences, and adult internal structure.

Various facets of the expanded project have progressed at different rates, and some of these are yet incomplete or barely begun. This paper represents a first report on the Nearctic *Nebria* fauna, specifically on nomenclature relating to same. My purpose is twofold. First, I provide names for five species and 23 subspecies not previously described. These names are needed immediately for use in several other manuscripts and by several other workers. To this end, data and discussion presented for each name are limited to little more than the minimum required by the *International Code of Zoological Nomenclature* for availability. My second purpose is to provide additional notes on nomenclature for previously described Nearctic species, including emendations and/or restrictions of type-localities, notes on type-specimens, and designations of lectotypes.

In a subsequent paper (manuscript in preparation) I will present additional information on Nearctic *Nebria* taxa, including those presented here as new. Each taxon will be more fully described and illustrated. A classification and key for identification of adults will be provided, as will results of comparative studies on structure, distribution, and natural history. A review of the known fossil record of Nearctic *Nebria* will also be included.

MATERIALS

This study is based on examination of over 66,000 Nearctic and 5,800 Palaearctic adult *Nebria* specimens. Approximately 35,000 specimens were borrowed from various institutional and private collections in North America, Europe, and Asia. Following is a list of abbreviations used in the text which refer to various collections from which specimens were received. Most, but not all, correspond to abbreviations proposed by Arnett and Samuelson (1969). Where appropriate, names of curators or assistants who sent specimens are also included.

AHab—A. Habu, National Institute of Agricultural Sciences, Tokyo, Japan.

ALar—A. Larochelle, Collège Bourget, Rigaud, Québec J0P 1P0.
AMor—A. Morgan and A. V. Morgan, University of Waterloo, Waterloo, Ontario N2L 3G1.
AMNH—American Museum of Natural History, New York, New York 10024; L. H. Herman, Jr.
ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania 19103; W. W. Moss.
BFCa—B. F. Carr, 24 Dalrymple Green NW, Calgary, Alberta T3A 1Y2.
BMNH—British Museum (Natural History), London, England; P. M. Hammond, H. K. Kenward, M. E. Bacchus.
BRot—B. Rotger, CR., Immaculate Heart of Mary Church, P.O. Box 451, Pagosa Springs, Colorado 81147.
CArm—C. Armin, 191 West Palm Avenue, Reedley, California 93654.
CAS—California Academy of Sciences, San Francisco, California 94118; H. B. Leech.
CDA—California State Department of Food and Agriculture, Sacramento, California 95814; F. G. Andrews.
CNC—Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6; R. de Ruette, A. Smetana.
CSU—Colorado State University, Fort Collins, Colorado 80521; T. O. Thatcher.
CUB—University of Colorado, Boulder, Colorado 80302; H. Rodeck.
CUIC—Cornell University, Ithaca, New York 14850; L. L. Pechuman.
DBUM—Université de Montreal, Montreal, Québec H3C 3J7; M. Coulloudon.
DENH—University of New Hampshire, Durham, New Hampshire 03824; W. J. Morse.
DEUN—University of Nebraska, Lincoln, Nebraska 68503; B. C. Ratcliffe.
DHKa—D. H. Kavanaugh, California Academy of Sciences, San Francisco, California 94118.
DJLa—D. J. Larson, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7.
DMan—D. Mann, University of Washington, Seattle, Washington 98195.
DRWh—D. R. Whitehead, Systematic Entomology Laboratory, U.S.D.A., % United States National Museum, Washington D.C. 20560.
DZEC—Montana State University, Bozeman, Montana 59715; N. L. Anderson.
EAMa—E. A. Martinko, University of Kansas, Lawrence, Kansas 66045.
EDNC—North Carolina Department of Agriculture, Raleigh, North Carolina 27602; J. F. Greene.
EMUS—Utah State University, Logan, Utah 84332; W. J. Hanson.
ETHZ—Eidgenössische Technische Hochschule Entomologisches Institut, Zürich, Switzerland; W. Sauter.
FMNH—Field Museum of Natural History, Chicago, Illinois 60605; H. Dybas.
GASh—G. A. Shook, 1209 West Hays, Boise, Idaho 83702.
GRNo—G. R. Noonan, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.
HGou—H. Goulet, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6.
HoKn—R. L. Hoffman and L. Knight, Radford College, Radford, Virginia 24141.
HNHM—Hungarian Natural History Museum, Budapest, Hungary; S. Horvatovitch.
ICCM—Carnegie Museum, Pittsburg, Pennsylvania 15213; G. E. Wallace.
INHS—Illinois Natural History Survey, Urbana, Illinois 61803; M. W. Sanderson.
ILar—I. La Rivers, University of Nevada, Reno, Nevada 89507.
ISUI—Iowa State University, Ames, Iowa 50010; R. Miller.
IUIC—Indiana University, Bloomington, Indiana 47401; F. N. Young.
JBel—J. Belicek, 9345-98A Street, Edmonton, Alberta T6E 3N2.
JKus—J. Kuster, University of Alberta, Edmonton, Alberta T6G 2E3.
JNeg—J. Nègre, 9 Boulevard de Lesseps, Versailles, France.
JSch—J. Schuh, 4039 Shasta Way, Klamath Falls, Oregon 97601.
JSpe—J. Spence, University of Alberta, Edmonton, Alberta T6G 2E3.
JVMa—J. V. Matthews, Jr., Geological Survey of Canada, Ottawa, Ontario K1A 0E8.
KMFe—K. M. Fender, 911 Ashwood Avenue, McMinnville, Oregon 97128.
KSUC—Kansas State University, Manhattan, Kansas 66502; H. D. Blocker.
KUSM—University of Kansas, Snow Museum, Lawrence, Kansas 66045; G. Byers.
LACM—Los Angeles County Museum of Natural History, Los Angeles, California 90007; C. L. Hogue.
LEMC—Macdonald College, Lyman Entomological Museum, Ste. Anne de Bellevue, Québec J7V 3N8.
LRus—L. Russell, 828 NW 27th Street, Corvallis, Oregon 97330.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; J. F. Lawrence.
MGF—Museum G. Frey, Entomologisches Institut, Tutzing bei München, West Germany; M. Würmli.
MHNG—Museum d'Histoire Naturelle, Geneva, Switzerland; C. Besuchet.
MNHP—Muséum National d'Histoire Naturelle, Paris, France; A. Bons, H. Perrin.
MLLu—M. L. Luff, University of Newcastle, Newcastle-upon-Tyne, England.
MSU—Michigan State University, East Lansing, Michigan 48823; R. L. Fischer.
NMB—Naturhistorisches Museum Basel, Basel, Switzerland; W. Wittmer.
NMDo—N. M. Downie, 505 Lingle Terrace, Lafayette, Indiana 47901.
NMPC—National Museum in Prague, Prague, Czechoslovakia; Z. Mlynar.
NRSS—Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Nyholm.
NSDA—Nevada State Department of Agriculture, Reno, Nevada 89504; R. C. Bechtel.
ODA—Oregon State Department of Agriculture, Salem, Oregon 97310; R. L. Westcott.
OSEC—Oklahoma State University, Stillwater, Oklahoma 74074; W. A. Drew.

OSUC—Ohio State University, Columbus, Ohio 43210; C. A. Triplehorn.
OSUO—Oregon State University, Corvallis, Oregon 97331; P. Oman.
PADA—Pennsylvania State Department of Agriculture, Harrisburg, Pennsylvania 17120; T. J. Henry.
PMCh—P. M. Choate, Jr., University of Florida, Gainesville, Florida 32601.
PMNH—Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; C. L. Remington, K. W. Brown.
PSMi—P. S. Miliotis, Depot Street, Dunstable, Massachusetts 01827.
PSUC—Pennsylvania State University, University Park, Pennsylvania 16802; K. C. Kim.
PUCA—Pacific Union College, Angwin, California 94508; L. E. Eighme.
PURC—Purdue University, Lafayette, Indiana 47907; A. Provonsha.
RCGr—R. C. Graves, 627 Crestview, Bowling Green, Ohio 43402.
RCra—R. Crawford, University of Washington, Seattle, Washington 98195.
RDav—R. Davidson, University of Vermont, Burlington, Vermont 05401.
RFre—R. Freitag, Lakehead University, Thunder Bay, Ontario P7B 5E1.
ROM—Royal Ontario Museum, Toronto, Ontario M5S 2C6; G. B. Wiggins.
RPPa—R. P. Papp, Bernice P. Bishop Museum, Honolulu, Hawaii 96818.
RTBe—R. T. Bell, University of Vermont, Burlington, Vermont 05401.
SFVS—California State University, Northridge, California 91324; P. F. Bellinger.
SDSU—South Dakota State University, Brookings, South Dakota 57006; E. U. Balsbaugh, Jr.
SJSU—San Jose State University, San Jose, California 95114; J. G. Edwards.
TCBa—T. C. Barr, Jr., University of Kentucky, Lexington, Kentucky 40506.
TNak—T. Nakane, National Science Museum, Tokyo, Japan.
TMZM—Tromsø Museum, Tromsø, Norway; J. H. Andersen.
UAFA—University of Arkansas, Fayetteville, Arkansas 72701; R. T. Allen.
UASM—University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball.
UBC—University of British Columbia, Spencer Museum, Vancouver, British Columbia V6T 1W5; G. G. E. Scudder.
UCB—University of California, Essig Museum of Entomology, Berkeley, California 94720; J. A. Chemsak.
UCD—University of California, Davis, California 95616; R. O. Schuster.
UCR—University of California, Riverside, California 92502; S. Frommer.
UIMI—University of Idaho, Moscow, Idaho 83843; W. F. Barr.
UMHF—Universitetets Zoologiska Museum Entomologiska Avdelningen, Helsingfors, Finland; H. Silfverberg.
UMMZ—University of Michigan, Ann Arbor, Michigan 48104; R. D. Alexander.
UMRM—University of Missouri, Columbia, Missouri 65201; W. R. Enns.
UMTF—University of Turku, Turku (Abo), Finland; H. Hippa.
USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; T. L. Erwin.
UWBM—University of Washington, Burke Museum, Seattle, Washington 98105; M. H. Hatch, S. Rohwer.
UWEM—University of Wisconsin, Madison, Wisconsin 53706; L. J. Bayer.
UWLW—University of Wyoming, Laramie, Wyoming 83070; R. J. Lavigne.
VMKi—V. M. Kirk, Northern Grain Insects Research Laboratories, Brookings, South Dakota 57006.
WSU—Washington State University, Pullman, Washington 99163; W. J. Turner.
ZILR—Zoological Institute, Academy of Science, Leningrad, U.S.S.R.; O. L. Kryzhanovskij, V. G. Shilenkov.
ZMKD—Universitetets Zoologiske Museum, København, Denmark; O. Martin.
ZMLS—Zoological Institute, University of Lund, Lund, Sweden; C. H. Lindroth.
ZMUM—Zoological Museum, Moscow University, Moscow, U.S.S.R.; S. Keleinikova.
ZSBS—Zoologische Sammlung des Bayerischen Staates, München 19, West Germany; G. Scherer.

I have been able to study the type-specimens of all 85 previously described Nearctic nominal taxa through the cooperation of many of the curators listed above. The following three minor nomenclatural problems must remain unsolved, but none, I think, will require further attention. *Nebria melsheimeri* Sturm (1826:173) and *Nebria eschscholtzii* Sturm (1826:173) (not of Ménétriés) must be considered *nomina nuda* because these names appear only in Sturm's catalog to his collection, unaccompanied by either description or statement of locality; and no type-specimens exist. The problem with and current status of the name *Nebria elias* Motschulsky is discussed with a treatment of *Nebria gyllenhali* (Schönherr) below.

Where necessary, lectotypes have been chosen and so labelled, and their formal designations appear here. I have also labelled holotypes for previously described species names where prior labels were unclear or lacking. Holotypes designated for taxa described here as new (with the exception of the holotype of *N. trifaria utahensis* n. ssp.) have been deposited in the type collection of the California Academy of Sciences.

METHODS

A detailed discussion of preparative and procedural methods used in this project will be included in a subsequent paper (Kavanaugh, manuscript in preparation). I present here comment on only those methods which relate specifically to data and results presented in this paper.

DISSECTING TECHNIQUES.—Characters used in diagnoses of many taxa named here include form of the hindwings and genitalia of adults. Successful examination of these structures required some dissection. Specimens were prepared for dissection by soaking them for 5 or 10 minutes in boiling water. Addition of a very small amount of liquid detergent hastened the relaxation process. Specimens collected in ethyl acetate fumes were relaxed easily, but material collected in potassium cyanide fumes or in ethyl alcohol required a brief (two to five minute) treatment in warm potassium hydroxide (10% solution).

A general impression of the size (but not shape) of the hindwings was obtained by simply lifting the left elytron to expose the wing. For a study of venation and wing shape, the left hindwing was torn free at the wing base using fine forceps, then spread and mounted in alcohol on a slide. Permanent mounts (in Euparal medium) were made for representatives of all taxa studied; however, most hindwings were later dried, glued to cards, and pinned with their respective specimens.

The apex and shaft of the median lobe and parameres in male specimens or the coxostyli in female specimens were quickly examined in relaxed specimens by simple eversion of these structures using fine forceps. For study of the base of the median lobe in males or the spermatheca, bursa copulatrix, and other internal structures in females, the genitalia were extracted as a unit by tearing the membranous connections between eighth tergum and sternum and the "ring sclerite" (in males) or the valvifers, paraprocts, and proctiger (in females). Genitalia were next treated for 5 to 10 minutes in hot (10%) potassium hydroxide solution to remove nonsclerotized tissue, rinsed in water, further dissected as needed, then transferred to and examined in glycerine. After genitalic specimens were studied and drawn, they were placed in polyethylene microvials in a drop of glycerine and pinned with their respective specimens.

SEX DETERMINATION.—Determination of the sex of individuals was made simply by reference to form of the front tarsi. Adult males have the basal three or four tarsomeres dilated, laterally expanded, and have pads of adhesive setae on ventral surfaces of the basal two or three tarsomeres. Females have all tarsomeres slender and without ventral pads of adhesive setae.

MEASUREMENTS.—The only mensural character used in this study is "standardized body length." This expression refers to the sum of three measurements (Fig. 1A): length of head, measured along midline from apical margin of clypeus to a point opposite posterior margin of eye; length of pronotum, measured along midline from apical to basal margin; and length of elytron, measured along midline from apex of scutellum to a point opposite elytral apex. While this measure of relative size avoids error due to variation in extension or retraction of body parts among specimens, it consistently underestimates the apparent total body length of specimens (such as could be measured from the most anterior to the most posterior point) by from 12 to 18 percent.

Range in standardized body length in my sample for each taxon was established by visual selection of smallest and largest specimens for each sex. All measurements were made with the aid of a Leitz stereoscopic dissecting microscope at a magnification of 16 diameters, using a calibrated ocular grid with a scale interval of 0.1 mm.

ILLUSTRATIONS AND MAPS.—Line drawings illustrating structural characters were made with the aid of an ocular grid mounted in a Leitz stereoscopic dissecting microscope. Unless otherwise noted, scale lines which accompany illustrations equal 1.0 mm. All drawings of homologous structures are consistent in scale and aspect to facilitate comparisons. In some drawings, uniform sparse stippling is used to indicate membranous areas. Where only part of a structure is illustrated (such as the basal region of an elytron), a wavy line serves as the artificial margin of the drawing.

Maps are presented to illustrate known distributions of taxa. Symbols used denote approximate locations of samples (see taxon descriptions for respective lists of sample localities). (Written permission has been obtained for use of Goode Base Map No. 202 [or parts thereof] [copyright by the University of Chicago, Department of Geography].)

FORMAT FOR PRESENTATION OF NEW TAXA.—Included for each new name are: a synonymy (i.e., list of names which have been misapplied in the literature to members of this taxon, including all known literature records); designations and listings of type-specimens and their places of deposition; designation of type-locality; the diagnostic combination (i.e., those character states which, in combination, distinguish members of the taxon from members of other taxa); derivation of the taxon name; a brief synopsis of geographical distribution; and a list of localities (including months of collection and place of deposition) for paratypes.

Several comments are required on the format and data content of the locality lists. For convenience, all data (including countries, states or provinces, counties, and localities) are arranged alphabetically. All records are from specimens I have personally studied. Records solely from the literature are not included here. The geographical subdivisions "County" or "Comté" are used where possible as an aid in organizing the data. Provinces and states for which these subdivisions are not used include: Alberta, British Columbia, Manitoba, Saskatchewan, Yukon Territory, and Alaska. All national parks are treated as counties; and all localities within park boundaries are listed under the park rather than under their appropriate counties. Because altitude data are often important in defining the habitat ranges of *Nebria* taxa, these data are recorded here where known. No attempt has been made, however, to present altitude data not actually recorded on the specimen labels. Where necessary, altitude values have been converted to their metric equivalents.

Only the months in which specimens were actually collected at a given locality have been noted here. This level of precision adequately describes the temporal distributions of most samples. The addition of year and day data would have expanded the size of this paper greatly but contributed little. I have also omitted the names of collectors in order to conserve space. Collections in which specimens are deposited are noted for each locality, but holdings for each collection are not itemized.

Specimens with illegible or essentially meaningless locality labels are grouped with specimens bearing no locality labels under the heading "SPECIMENS WITHOUT LOCALITY DATA." Specimens listed under the heading "DOUBTFUL RECORDS" are of two types: (1) those labelled as from localities outside the known and probable ranges of the taxon; and (2) those labelled as from localities within the known geographical range of a taxon but from areas where I am certain no suitable habitat for the beetles exists. For some specimens in category (2), however, where appropriate habitat can be found within reasonable proximity of the stated locality, I have chosen to add the word "area" after the entry. Although imprecise, this convention accommodates the common practice among some collectors of simply recording the nearest city or town on specimen labels rather than more precise locality data.

CRITERIA FOR RANKING TAXA.—All available evidence supports the universality of sexual reproduction among nebriine species. Because apparently all *Nebria* species are bisexual, I accept as appropriate Mayr's (1969:26) proposed definition of the biological species (as amended by Whitehead 1972:139), namely, that species are populations or groups of populations through which gene flow actually or potentially exists, but which are reproductively [intrinsically] isolated from all other such populations [or groups of populations]. As noted by Whitehead (1972:139) and Larson (1975:251), the species so defined is a category with a nonarbitrary, objective basis; but this applies only to the extent that interspecific hybridization is excluded or nonintrogressive. Success in application of this species definition to the recognition of contemporary species and, therefore, the "objective" bases of taxa recognized depend on the degree to which reproductive isolation can be demonstrated or inferred where it exists and excluded where it does not. Direct, unequivocal evidence for this intrinsic isolation or lack of same can seldom, if ever, be provided, even from breeding tests. Only criteria by which indirect evidence can be evaluated are generally useful.

The following working criteria were used in recognizing species. Two sympatric or parapatric forms were considered separate species if all individuals (of one or both sexes) of one differ from all members (of the same or both sexes) of the other in one or more structural characters (other than color or size). In practice, members of sympatric or parapatric *Nebria* species generally differ in several characters and therefore easily fulfill this criterion. Two allopatric forms were considered separate species if differences between members of each are roughly equivalent to differences between members of two closely related sympatric species AND if members of geographically intermediate populations of either fail to exhibit intermediate character states for the differentiating characters. Use of the above criteria required the following assumption: that continuity or discontinuity in characters of external structure, internal genitalic structure, geographical and habitat distribution, and life history provided by the study of population samples (comprised of individuals and groups of same) is evidence of reproductive continuity or isolation, respectively, among natural populations. Clearly, recognition of allopatric species is more arbitrary than distinguishing sympatric or parapatric species; but hypotheses about relationship must be drawn from available evidence, and some estimate of these relationships is preferable to none.

I accept the subspecies definition of Edwards (1956b:230) in slightly altered form; namely, that subspecies are populations or groups of populations whose members are recognizably different from members of other conspecific populations and would interbreed with the latter IF they occurred sympatrically and synchronously (under natural conditions) BUT are distinctly isolated from them during their mating periods.

THE SUBSPECIES CATEGORY.—I frequently used the subspecies category in ranking allopatric *Nebria* populations and population groups because patterns of geographical variation are often such that discontinuities in structural and other characters correlate well with discontinuities in habitat or physiography (see also Ball 1966; and Ball and Nègre 1972). Other workers (Erwin 1970; Madge 1967; Noonan 1973; and Whitehead 1976) have avoided use of the subspecies category in their studies of lowland, mainland groups. Recognition of the usefulness of a subspecies concept appears to depend on one's particular perspective; more specifically, on the distribution of habitats or areas occupied by the organisms one studies. Where gaps between areas of suitable habitat are broad and clear, such as with predominantly montane groups like *Nebria*, correlated discontinuity in variation is more confidently recognized and suggestive of active, effective barriers to gene flow.

Because names for subspecies are accorded the same rights and strictures as species names and compete with the latter for priority under the present *International Code of Zoological Nomenclature*, the description of new subspecies (and resultant introduction of new names into the literature) must be justified. I suggest that recognition of subspecies as defined above is justified because they represent incipient species. They are at present independent evolutionary units whose members are already differentiated from members of other conspecific populations. Because these units are generally of zoogeographic and historical significance, the formal subspecies trinomen is as welcome a "shorthand notation" (Larson 1975:252) as the species binomen or any other formal name.

In addition to the question of usefulness is that of practicality, recognizing inherent difficulties in the formulation and application of a subspecies concept. Use of the subspecies category has been warmly debated for decades (see for example, Brown and Wilson 1954; Edwards 1954, 1956a, 1956b; Inger 1961; and Wilson and Brown 1953). Without question, great variation in subspecies concepts has existed among taxonomists, so that taxa recognized by various workers are seldom equivalent or even comparable units. The inability of taxonomists to formulate and apply a common subspecies concept to their studies is unfortunate but understandable in light of evolutionary theory, which predicts a spectrum of intermediate stages in the process of speciation. Assignment of formal subspecific rank to populations at one particular stage in the process is complicated by the potential for almost infinite variety in evolutionary rate and direction of change.

I agree with Edwards (1954, 1956a, 1956b) that the subspecies as defined above is a relatively objective ("comparatively but not absolutely nonarbitrary" [Simpson 1961:116]) category. Extensive barriers to gene flow between subspecies can, as suggested earlier, be recognized in some instances through detailed studies of habitat and geographical distributions and life histories. These may in fact be easier to demonstrate than intrinsic isolating mechanisms (i.e., reproductive isolation) between separate species. Arbitrariness arises in decisions on "how different" members of allopatric or allochronous populations must be for recognition as either distinct species or conspecific subspecies.

Working criteria I used for recognizing subspecies were as follows. Two populations or groups of populations were considered separate subspecies if (1) their respective geographical ranges are allopatric and separated by recognizable environmental barriers, (2) differences between members of each are constant but less distinctive than differences between members of two closely related sympatric species in one or more characters of structure, color, or size, AND (3) the geographical pattern of variation in distinguishing characters is nonclinal or distinctly step-clinal. In general, all members of a subspecies can be recognized on structural characters alone. However, in some instances, where two subspecies were recognized as distinct by a step-clinal pattern of variation, all members of one subspecies may be distinguished only from all members of the most proximate populations of the other. A good example of this type of variation pattern is seen for *Nebria lacustris* Casey (see below; details to be presented elsewhere [Kavanaugh, manuscript in preparation]). The following assumption was required for use of the above criteria: that the amount of phenotypic divergence between members of two allopatric populations is a measure not only of the completeness and duration of their extrinsic isolation but also of the probability that reproductive (intrinsic) isolation has evolved between them. Where this assumption is invalid, the resultant error in ranking (i.e., recognizing as subspecies taxa which, in fact, conform to the biological species definition) is, in my opinion, less objectionable than its opposite. If two *de facto* species are ranked as subspecies, close relationship between the taxa is merely overemphasized, and species-group names are still provided and protected by priority. Only changes in status are required if actual relationships are correctly determined later.

NEW NEARCTIC *NEBRIA* SPECIES AND SUBSPECIES

The order of presentation of new taxa in this section follows a new classification of Nearctic *Nebria* to be presented elsewhere (Kavanaugh, manuscript in preparation).

Nebria gouleti, new species

(Figures 2, 13, 51)

HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Asotin Co., Hwy. 129, 10 mi. sw. Antone, Rattlesnake Cr., 3000′, 25 August 1973 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gouleti Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12504." ALLOTYPE (same data as holotype) also in CAS. In total, 514 PARATYPES (227 males and 288 females) are deposited in the following collections: AMNH, ANSP, BFCa, CAS, CUIC, DHKa, DJLa, LRus, MCZ, MSU, OSUO, PURC, RTBe, SJSC, UASM, UIMI, UMMZ, USNM, UWBM, and WSU.

TYPE-LOCALITY.—Rattlesnake Creek (10 miles [ca. 16 km] SW of Antone), Asotin County, Washington.

DIAGNOSTIC COMBINATION.—Head uniformly dark, without pale spot(s) on vertex, antennal scape moderately long, symmetrically ellipsoid (Fig. 2); pronotum distinctly cordate, midlateral seta present (Fig. 13), without longitudinal tubercle medial to midlateral seta; elytra dull, microsculpture deeply impressed, meshes isodiametric or very slightly transverse, fifth elytral interval without setae; metepisternum impunctate; hind coxa bi- or trisetose basally, tarsomeres of hind tarsus glabrous dorsally; second visible abdominal sternum with patch of setae medially (between hind coxae), third to fifth visible sterna each with two to six pairs of posterior paramedial setae (Fig. 37).

DERIVATION OF TAXON NAME.—I take great pleasure in naming this species in honor of my good friend and frequent field companion, Henri Goulet, from whom I have learned to observe and appreciate carabid beetles while they are still alive!

GEOGRAPHICAL DISTRIBUTION.—Figure 51; restricted to portions of the Columbia Plateau region in Washington, Oregon, and Idaho; the lower Columbia River valley; and the mountains of northern and central Idaho. I have studied specimens from the following localities.

United States of America

IDAHO: Adams County, New Meadows ([1,170 m]) [June] (1; UIMI); Bonner County, Sandpoint [Sep.] (1; CAS); Clearwater County, Canyon Ranger Station [Sep.] (1; UIMI); Custer County, Lower Stanley (10 miles [ca. 16 km] E on Salmon River [1,800 m]) [Aug.] (1; DHKa), Salmon River (at Bayhorse Creek [1,620 m]) [Aug.] (45; DHKa); Idaho County, Fenn Ranger Station (Selway Fork Clearwater River) [Aug.] (3; UIMI), Lochsa River (at Canyon Creek [520 m]) [July] (2; DHKa), Lowell (39 miles [ca. 63 km] NE on Lochsa River [850 m]) [July] (1; DHKa), Meadow Creek (1.5 miles [ca. 2.4 km] S of Selway Falls) [Sep.] (1; CAS), Orogrande Creek [Aug.] (3; UWBM), Selway Falls [July] (1; UWBM); Kootenai County, Coeur d'Alene [June–July] (5; CAS, MCZ, USNM), Hayden Lake [Aug.] (9; AMNH, MCZ, UIMI, USNM); Latah County, Kendrick [Sep.] (2; UIMI), Moscow (1; USNM); Lemhi County, Salmon (and 21 miles [ca. 34 km] N) [July–Aug.] (2; UASM, UIMI); Nez Perce County, Lenore [May] (2; UIMI), Lewiston (and 2 and 3 miles [ca. 3.2 and 4.8 km]

E on Clearwater River [300 m–380 m]) [May–Aug., Oct.] (52; DHKa, UIMI), Waha [Aug.] (5; CAS, MCZ, PURC, USNM), Waha Lake [July] (4; CAS, MCZ); Shoshone County, Avery [Sep.] (2; UWBM), Clarkia [June] (1; UIMI), St. Joe River (17 miles [ca. 27 km] E of St. Maries) [July] (10; CAS); Valley County, Dagger Falls [July] (2; BFCa), Zena Creek [June] (1; UIMI); County unknown, Bungalow [Aug.] (15; UWBM). OREGON: Baker County, East Fork Eagle Creek [July] (2; UWBM), Halfway [July] (1; BFCa); Hood River County, Hood River [Sep.] (2; MCZ); Multnomah County, Portland [July] (3; CUIC); Umatilla County, Cottonwood Creek [June] (3; USNM, UWBM), Kamela [June] (1; CAS), Milton (Walla Walla River) [May–June] (4; UWBM), S of Kooskooskie (Washington) [June] (2; UWBM); Union County, Elgin (and 0.1 mile [0.16 km] S at Grande Ronde River [1,130 m]) [May, Aug.] (2; DHKa), Hilgard Junction State Park [Aug.] (3; RTBe), La Grande (1 mile [ca. 1.6 km] NE on Grande Ronde River [1,070 m]) [May] (5; DHKa); Wallowa County, Minam (0.2 miles [ca. 0.3 km] SE at junction of Minam and Wallowa rivers [790 m]) [May] (5; DHKa). WASHINGTON: Asotin County, Antone (10 miles [ca. 16 km] SW at Rattlesnake Creek [910 m]) [Aug.] (21; DHKa), Asotin (Asotin Creek [370 m]) [May–June] (18; ANSP, CAS, DHKa), Buford Creek (3.6 miles [ca. 5.8 km] S of Grande Ronde River [760 m]) [May] (8; DHKa), Grande Ronde River (at Highway 129 [550 m]) [May, Sep.] (2; DHKa, SJSC); Chelan County, Leavenworth [July] (20; ANSP, CAS, MCZ, PURC, USNM, UWBM), Peshastin Creek [July] (1; UASM), Tumwater Canyon ([610 m]) [May] (2; LRus); Columbia County, Dayton (Touchet River [580 m]) [May, July] (5; DKHa, WSU); Franklin County, Palouse Falls State Park [May] (2; LRus); Klickitat County, Trout Lake [July] (1; UWBM), White Salmon [Aug.] (2; UWBM); Skamania County, Underwood (15 miles [ca. 24 km] W on Columbia River [90 m]) [May] (4; DHKa); Spokane County, Spokane Falls (1; CAS); Walla Walla County, Burbank [May] (1; ANSP), Coppei [May] (1; UAFA), Coppei Creek [May] (1; UIMI), Kooskooskie [June, Aug.] (33; UIMI, UWBM), Touchet River (near Waitsburg) [July] (98; DJLa), Walla Walla (and 2 miles [ca. 3.2 km] S [320 m], Mill Creek) [May–Sep.] (139; CAS, CUIC, DHKa, MCZ, OSUO, PURC, UIMI, UMMZ, UWBM, WSU); Whitman County, Almota [May] (2; MCZ, MSU), Wawawai (2.8 miles [ca. 4.5 km] NW at Snake River [300 m]) [May] (11; DHKa), Wilma [Apr.–May] (6; ANSP, UWBM).

Doubtful Records

CANADA—ALBERTA: Longview (Highwood River) [July] (7; CAS). UNITED STATES OF AMERICA—CALIFORNIA: (2; USNM).

Nebria lacustris bellorum, new subspecies

(Figures 14, 52)

Nebria lacustris; BELL 1955:265 (in part).

HOLOTYPE, a male, in CAS, labelled: "U.S., Tenn., Great Smoky Mts. N. P., Chimneys Picnic Area, W. Prong Little Pigeon R., 3000', 24May73 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria lacustris bellorum Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12506." ALLOTYPE (same data as holotype) also in CAS. In total, 276 PARATYPES (139 males and 137 females) are deposited in the following collections: CAS, CUIC, DHKa, HoKn, MCZ, RTBe, TCBa, UAFA, UASM, USNM.

TYPE-LOCALITY.—West Prong Little Pigeon River (at Chimneys Picnic Area), Great Smoky Mountains National Park, Tennessee.

DIAGNOSTIC COMBINATION.—Head uniformly dark, without pale spot(s) on vertex; pronotum (Fig. 14) distinctly cordate, midlateral seta present, without longitudinal tubercle medial to midlateral seta; elytra very shiny or faintly iridescent, microsculpture consists of thin, transverse lines without (or with only scattered) meshes, striae very deeply impressed, intervals markedly convex, fifth interval without setae; metepisternum impunctate; tarsomeres of hind tarsus glabrous dorsally; second visible abdominal sternum glabrous medially, third to fifth visible sterna each with single pair of posterior paramedial setae; specimen from locality in southeastern United States, south of French Broad River (North Carolina or Tennessee) (Fig. 52).

DERIVATION OF TAXON NAME.—I take pleasure in naming this subspecies in honor of Ross and Joyce Bell (Burlington, Vermont), who have long been interested in the *Nebria* of eastern North America, and who have generously provided encouragement and information for this study.

GEOGRAPHICAL DISTRIBUTION.—Figure 52; restricted to that portion of the southern Appalachian region including Great Smoky Mountains National Park and adjacent mountain ranges. I have studied specimens from the following localities.

United States of America

NORTH CAROLINA: Great Smoky Mountains National Park [June] (1; MCZ), Indian Gap [Sep.] (1; USNM), Kephard Prong Oconaluftee River [Aug.] (14; DHKa, TCBa), Newfound Gap ([1,520 m–1,580 m]) [Aug.] (1; MCZ), Oconaluftee River (11 miles [ca. 18 km] SE of Newfound Gap on Highway 441 [550 m], at Smokemont [840 m] and 2.3 miles [ca. 3.7 km] NW of Smokemont [610 m]) [May, Sep.] (61; DHKa, USNM), Smokemont Loop Trail ([760 m–910 m]) [July] (18; UAFA); Haywood County, Beach Gap (7 miles [ca. 11 km] S of Sunburst at Middle Prong West Fork Pigeon River [1,520 m]) [June, Aug.] (4; HoKn), Bubbling Spring Branch ([1,520 m]) [July] (10; DHKa, TCBa), Graveyard Fields (Blue Ridge Parkway at Yellowstone Prong Pigeon River [1,540 m]) [May] (1; DHKa), Mount Sterling ([910 m]) [Oct.] (7; CAS, CUIC), Retreat [May] (6; USNM); Swain County, Bryson City (Deep Creek [610 m]) [Aug.] (2; MCZ). TENNESSEE: Great Smoky Mountains National Park, Alum Cave Creek ([1,220 m–1,250 m]) [May] (4; DHKa), Chimneys Camp ([910 m]) [May, Sep.] (18; CAS, CUIC, USNM), Newfound Gap ([1,520 m–1,580 m]) [Aug.] (2; MCZ, UASM), Tennessee Branch Bradley Creek ([980 m]) [May] (15; USNM), Walker Prong Little Pi geon River [Aug.] (1; DHKa), West Prong Little Pigeon River ([1,040 m–1,220 m]), Chimneys Picnic Area [910 m], (3 miles [ca. 4.8 km] S of Gatlinburg [520 m], 3.7 miles [ca. 6.0 km] N of Newfound Gap [1,220 m]) [May, July, Sep.] (109; DHKa, MCZ, UAFA, USNM); Sevier County, Gatlinburg [June] (1; DHKa).

Doubtful Records

UNITED STATES OF AMERICA—COLORADO: Jefferson County, Golden (Clear Creek) [June] (1; USNM). LOUISIANA: St. Tammany Parish, Highway 90 (10 miles [ca. 16 km] W of Mississippi border) [June] (1; CAS).

Nebria nivalis gaspesiana, new subspecies

(Figures 15, 53)

Nebria suturalis; LENG (not LeConte). —LENG 1920:47 (in part). —LINDROTH 1955a:39.

Nebria nivalis bifaria MANNERHEIM. —LINDROTH 1955a:39 (in part).

Nebria nivalis; *auctorum*. —LAROCHELLE 1972:62 (in part); 1976:48; 1977:12 (in part). —LINDROTH 1961:81 (in part); 1971:1459.

Nebria bifaria; LINDROTH 1961:81 (in part).

HOLOTYPE, a male, in CAS, labelled: "Can., Que., Peninsule de Gaspe, Mt. Albert, Ruisseau du Diable, 3200′–3500′, 11–12 June 73 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria nivalis gaspesiana Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12510." ALLOTYPE (same data as holotype) also in CAS. In total, 287 PARATYPES (119 males and 168 females) are deposited in the following collections: ALar, CAS, CNC, DBUM, DHKa, MCZ, RTBe, UASM, USNM.

TYPE-LOCALITY.—Ruisseau du Diable (980 m–1,070 m), Mont Albert, Parc de La Gaspésie, Comté de Gaspé-Ouest, Québec.

DIAGNOSTIC COMBINATION.—Head uniformly dark, without pale spot(s) on vertex; pronotum (Fig. 15) distinctly cordate, midlateral seta present, with small longitudinal tubercle medial to midlateral seta; fifth elytral interval with one to four setae; metepisternum impunctate; tarsomeres of hind tarsus glabrous dorsally; specimen from locality in Maine (Mount Katahdin), Gaspé Peninsula, Island of Newfoundland, or Labrador (west only to east shore of Ungava Bay) (Fig. 53).

DERIVATION OF TAXON NAME.—This subspecies is named for the Gaspé Peninsula, on which the type-locality is found.

GEOGRAPHICAL DISTRIBUTION.—Figure 53; disjunct; restricted to the western part of the Island of Newfoundland, Mount Katahdin (Maine), the high mountains of the Gaspé Peninsula, and coastal Labrador (northwest to the eastern shore of Ungava Bay). I have studied specimens from the following localities.

Canada

NEWFOUNDLAND: Island of Newfoundland, Little Codroy River [July] (4; MCZ, USNM), St. John Bay (Doctors Brook) [July] (5; CNC, ZMLS), South Branch (Grand Codroy River) [July] (4; MCZ), Spruce Brook (1; MCZ). QUÉBEC: Comté de Bonaventure [July] (1; ALar); Comté de Gaspé-Ouest, Parc de La Gaspésie (Mont Albert at Ruisseau du Diable [980 m–1,070 m]) [June–July] (261; ALar, CNC, DBUM, DHKa, RTBe); Territoire du Nouveau-Québec, Rivière Abloviak [July] (1; DBUM).

United States of America

MAINE: Piscataquis County, Baxter State Park (Mount Katahdin [910 m–1,580 m]) [June–Aug.] (10; CAS, MCZ, USNM).

Nebria gyllenhali lassenensis, new subspecies

(Figures 3, 54)

HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Lassen Volcanic N. P., Cascade Range, s. slope Mt. Lassen, Emerald Lk., 2450m, 22Aug.74 D.H.Kavanaugh Coll."/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gyllenhali lassenensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12511." ALLOTYPE (same data as holotype) also in CAS. In total, 34 PARATYPES (18 males and 16 females) are deposited in the following collections: CAS, DHKa, FMNH, USNM.

TYPE-LOCALITY.—Emerald Lake, Mount Lassen (south slope), Lassen Volcanic National Park, California.

DIAGNOSTIC COMBINATION.—Head, pronotum, and elytra without metallic reflection; head uniformly dark, without pale spot(s) on vertex, moderate in size and convexity, with genae and occiput not broadened, eyes full-sized; antennal scape (Fig. 3) short, straight, symmetrically ovoid or anteriorly more convex; penultimate labial palpomere trisetose; pronotum small, slightly narrow, moderately cordate (lateral margin moderately arcuate at middle), slightly dull to moderately shiny, microsculpture moderately to faintly impressed, meshes isodiametric, alveolae flat, midlateral seta present, without longitudinal tubercle medial to midlateral seta; elytral intervals flat, third interval continuous or faintly catenate (setiferous pores slightly to moderately foveate), fifth interval without setae; hindwing full-sized; metepisternum impunctate; tarsomeres of hind tarsus glabrous dorsally; second visible abdominal sternum glabrous medially, third to fifth visible sterna each with single pair of posterior paramedial setae; specimen from locality in northern Sierra Nevada (California) or Cascade Range south of Columbia River (Fig. 54).

DERIVATION OF TAXON NAME.—This subspecies is named for Mount Lassen, on the south slope of which the type-locality is found.

GEOGRAPHICAL DISTRIBUTION.—Figure 54; restricted to the southern Cascade Range (south of the lower Columbia River valley) and the northern Sierra Nevada (south to Sonora Pass). I have studied specimens from the following localities.

United States of America

CALIFORNIA: Lassen Volcanic National Park, Emerald Lake ([2,450 m]) [Aug., Oct.] (6; CAS, DHKa, FMNH), Little Hot Springs Area (East Sulphur Creek [2,440 m–2,530 m]) [Aug.] (6; CAS, DHKa), Mount Lassen (3 miles [ca. 4.8 km] SE) [July] (1; USNM), Ridge Lake [Aug.] (16; CAS); Tuolumne County, Sonora Pass [Aug.] (3; CAS). OREGON: Deschutes County, Todd Lake (and 1 mile [ca. 1.6 km] S) [Aug.] (4; JSch).

Nebria gyllenhali lindrothi, new subspecies

(Figures 4, 54)

Nebria sahlbergi; WICKHAM 1902:232.
Nebria gyllenhali; *auctorum*. —ARMIN 1963:90.

HOLOTYPE, a male, in CAS, labelled: "U.S., Wyo., Albany Co., Medicine Bow Mts., Snowy Range, Brooklyn Lk, 10500', 11July72 DHKavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gyllenhali lindrothi Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12512." ALLOTYPE (same data as holotype) also in CAS. In total, 1579 PARATYPES (795 males and 784 females) are deposited in the following collections: AMNH, ANSP, CArm, CAS, CDA, CNC, CUB, CUIC, DHKa, DRWh, EAMa, FMNH, ICCM, KSUC, MCZ, MSU, PADA, PMCh, PMNH, PURC, RCGr, RDav, RTBe, SDSU, UAFA, UASM, USNM, UWBM, UWL, ZMLS.

TYPE-LOCALITY.—Brooklyn Lake (3,200 m), Albany County, Wyoming.

NOTES ON NOMENCLATURE AND TYPES.—This subspecies is the form noted by Lindroth (1969b:1109) as an undescribed species related to *N. gyllenhali*.

DIAGNOSTIC COMBINATION.—Head, pronotum, and elytra without metallic reflection; head uniformly dark, without pale spot(s) on vertex, moderate in size and convexity, with genae and occiput not broadened, eyes full-sized; antennal scape (Fig. 4) long, straight, slightly arcuate, moderately or markedly narrowed basally; penultimate labial palpomere trisetose; pronotum small, slightly narrow, moderately cordate (lateral margin moderately arcuate at middle), slightly dull to moderately shiny, microsculpture moderately to faintly impressed, meshes isodiametric, alveolae flat, midlateral seta present, without longitudinal tubercle medial to midlateral seta; elytral intervals flat, third interval continuous or faintly catenate (setiferous pores slightly to moderately foveate), fifth interval without setae; hindwing reduced in size and venation pattern; metepisternum impunctate; tarsomeres of hind tarsus glabrous dorsally; second visible abdominal sternum glabrous medially, third to fifth visible sterna each with single pair of posterior paramedial setae; specimen from locality in southern Rocky Mountains—in Medicine Bow Mountains or Sierra Madre (Wyoming), or Uinta Mountains (Utah), or further south (Fig. 54).

DERIVATION OF TAXON NAME.—I am honored to name this subspecies after Carl H. Lindroth, a friend whose knowledge of and studies on Holarctic Carabidae, and *Nebria* in particular, have been a guiding light in this study, and who first called my attention to the distinctiveness of members of this taxon. I deeply regret that Carl did not live to see the completion of this study, to which he contributed so much.

GEOGRAPHICAL DISTRIBUTION.—Figure 54; restricted to the southern Rocky Mountains, from northern New Mexico north to the Medicine Bow Mountains and Sierra Madre of southern Wyoming, west to the Uinta Mountains of eastern Utah. I have studied specimens from the following localities.

United States of America

COLORADO: (2; KUSM, PURC); Boulder County, ([3,810 m]) [July] (1; CUB), Arapaho Pass ([2,740 m–3,350 m]) [Aug.] (1; RTBe), Arapaho Peak ([3,510 m]) [Aug.] (3; CArm), Beaver Creek ([2,530 m]) [July] (1; CArm), Fourth of July Mines ([3,430 m]) [Aug.] (2; CArm), Jenny Lake ([3,200 m]) [July] (2; CArm), Middle St. Vrain Creek ([3,600 m]) [July] (1; CArm), Niwot Ridge ([3,050 m]) [July] (5; CArm, CUB), Rainbow Lakes ([3,350 m]) [Aug.] (3; CNC), Rollins Pass ([3,410 m–3,540 m]) [Aug.] (2; CUB, DHKa), South Fork Middle Boulder Creek ([2,900 m–3,960 m]) [Aug.] (1; CArm); Clear Creek County, Leavenworth Valley (Argentine Road [3,660 m–3,960 m]) (2; USNM), Loveland Pass ([3,660 m–3,840 m]) [July] (42; CAS, RTBe, UWBM), Mount Evans ([3,600 m–4,330 m], Summit Lake [3,900 m–3,960 m]) [July–Aug.] (76; CAS, CNC, DHKa, FMNH, MCZ, PURC, RCGr, UASM); Conejos County, Cumbres Pass ([3,050 m]) [June] (1; CAS); Custer County, Ophir Creek (7.3 miles [ca. 11.7 km] SW of Fairview [3,140 m]) [June] (9; DHKa), St. Charles River (1.9 miles [ca. 3.1 km] SW of San Isabel [2,710 m–2,830 m]) [June] (14; DHKa), Wet Mountains ([3,470 m]) [July] (2; USNM); Dolores County, Lizard Head Pass ([3,050 m]) [Sep.] (1; CAS), Rico area ([2,590 m–3,050 m]) [July] (10; ANSP, MCZ, USNM); El Paso County, Pikes Peak ([3,960 m]) [July] (8; AMNH, CAS), South Cheyenne Creek (at Gold Camp Road [2,530 m–2,650 m]) [June] (1; DHKa); Garfield County, Trappers Lake ([2,530 m–2,650 m]) [June] (49; DHKa); Gilpin

County, Central City ([2,620 m]) [July] (1; CAS), Corona ([3,350 m]) [Sep.] (7; CAS, CUIC), South Boulder Creek (at Rollinsville and 2.5 miles [ca. 4.0 km] W [2,440 m]) [July–Aug.] (5; CArm, DHKa, UAFA); Grand County, Ptarmigan Peak (20; MCZ, ZMLS); Gunnison County, Gothic ([2,930 m]) [July] (2; USNM), Mexican Cut Lakes (1 mile [ca. 1.6 km] NW of Elko Park [3,440 m]) [Aug.] (1; PMNH); Huerfano County, Apishapa Pass [June] (3; CUB), Bear Lake [June] (13; DHKa, EAMa), Blue Lake [June] (10; DHKa, EAMa), Cucharas Pass ([3,050 m] and 1.5 miles [ca. 2.4 km] N) [June] (109; DHKa, EAMa), Cucharas River (near Blue Lake [3,190 m]) [June] (5; DHKa); Jackson County, Cameron Pass ([3,140 m]) [Aug.] (1; UASM), Rabbit Ears Pass ([2,740 m]) [June–Aug.] (8; CAS, USNM); La Plata County, Hermosa Creek Trail (NW of Hermosa [2,960 m]) [Aug.] (9; UASM); Larimer County, Browns Lake Trail [Aug.] (9; RTBe), Crown Point [July] (21; RTBe), Zimmerman Lake [Aug.] (3; RTBe); Los Animas County, Apishapa Pass (2.1 miles [ca. 3.4 km] SE [3,230 m]) [June] (9; DHKa), Bear Creek (5 miles [ca. 8 km] S of Cucharas Pass [2,800 m]) [June] (83; DHKa); Mesa County [Aug.] (5; PMCh, RDav), Grand Mesa ([3,050 m]) [July–Aug.] (6; CAS, CUB, USNM), Skyway ([3,050 m]) [June] (2; DHKa, FMNH); Mineral County, Pagosa Springs (20 miles [ca. 32 km] N) [June] (1; DRWh), Wolf Creek Pass ([3,250 m–3,660 m] and 2 miles [ca. 3.2 km] W, Thunder Mountain [3,570 m]) [June–Aug.] (96; CAS, CDA, CNC, DHKa, EAMa, UASM, USNM); Ouray County, American Flats ([3,660 m]) [July] (4; AMNH), Ouray area [June–July] (4; AMNH, CAS); Park County, Middle Fork North Platte River (near Hoosier Pass [3,540 m]) [July] (1; DHKa), Mount Lincoln ([3,350 m]) [Aug.] (1; UASM); Rio Grande County, Rio Grande River (1 mile [ca. 1.6 km] S of South Fork [2,400 m]) [Aug.] (29; DHKa, EAMa), Summitville ([3,050 m–3,350 m]) [Aug.] (7; CNC, MCZ); Rocky Mountain National Park ([3,200 m–3,510 m]) [June–Aug.] (11; CAS, CNC, UASM), Fall River Pass ([3,600 m]) [July] (5; CUB), Longs Peak ([3,840 m], Chasm Lake [3,810 m]) [July–Aug.] (14; CArm), Milner Pass ([3,280 m]) [July] (1; AMNH), Ouzel Falls ([3,050 m]) [Aug.] (1; CArm), Sandbeach Lake ([3,050 m]) [June] (7; CArm), Trail Ridge Road ([3,660 m–3,960 m]) [Aug.] (2; CUB, USNM); Routt County, Buffalo Pass (Summit Lake [3,140 m]) (4; CAS), Walton Creek (above Dumont Lake [2,900 m–2,960 m]) [Aug.] (5; DHKa); San Juan County, Silverton ([3,660 m]) [July] (1; USNM); Summit County, Quandary Peak (south slope [3,410 m–3,960 m]) [Aug.] (35; DHKa); Teller County ([3,410 m]) [June] (1; PADA), Phantom Canyon ([2,960 m]) [June] (1; CAS); County unknown, "Hot Springs" (1; ICCM), "King's Lake" ([3,350 m]) [Aug.] (2; CArm), La Plata Mountains ([3,200 m–3,660 m]) [July–Aug.] (4; DHKa, USNM), "Laramie Co." (2; ICCM), Medicine Bow Range ([2,440 m–3,660 m]) [July] (3; MCZ), Mount Baldy (summit [3,750 m]) [July] (1; CArm), San Juan Mountains ([3,660 m]) [July] (1; USNM), "foothills of Rocky Mts." (1; PMNH). New Mexico: (9; ANSP, ICCM, KUSM, MCZ, USNM); Mora County, Pecos Baldy (2; AMNH); Rio Arriba County, Gregorio Lake ([2,790 m]) [June] (5; DHKa), Rio Puerco (at Rio Puerco Campground [2,350 m–2,440 m]) [June] (3; DHKa); San Miguel County, Beaver Creek (SW of Rincon Montoso [2,620 m]) [Aug.] (15; UASM), Cowles area ([2,440 m], Spirit Lake Trail) [June] (4; AMNH, UASM), Las Vegas area ([2,130 m]) [July] (1; KUSM), Willow Creek (near Torrero [2,740 m]) [June] (8; UASM); Santa Fe County, Lake Katherine ([3,600 m]) [June] (30; DHKa), Lake Peak (5; AMNH), Nambe Divide ([3,350 m]) [July] (2; ANSP), Santa Fe Ski Basin (5 miles [ca. 8 km] NW) (1; AMNH); Taos County, Red River (2.2 miles [ca. 3.5 km] [2,610 m], 4.1 miles [ca. 6.6 km] [2,580 m], and 5 miles [ca. 8 km] W of Red River, 8 miles [ca. 13 km] S of Red River [2,870 m]) [June] (40; AMNH, DHKa), Tres Ritos [July] (4; CAS), Wheeler Peak ([3,050 m–3,640 m], NW slope, Middle Fork Lake [3,340 m], Middle Fork Red River [3,260 m–3,690 m]) [June] (172; AMNH, DHKa). Utah: Duchesne County, Garfield Basin (stream below Tungsten Lake [3,450 m]) [Sep.] (3; USNM); Grand County, Mill Creek (at Oowah Lake [2,680 m]) [Aug.] (12; DHKa); San Juan County ([2,800 m]) [Aug.] (1; FMNH), Dark Canyon ([2,960 m], NE slope [3,240 m]) [Aug.] (30; UASM), Geyser Pass ([3,050 m], N slope [3,120 m], E slope [3,220 m], at Blue Lake [2,960 m]) [July–Aug.] (79; AMNH, UASM), Mill Creek Valley ([2,900 m]) [Aug.] (2; UASM). Wyoming: Albany County, Brooklyn Lake ([3,200 m]) [July] (41; DHKa), Centennial area ([3,050 m]) [Aug.] (22; MSU, SDSU), Douglas Creek (1 mile [ca. 1.6 km] SSE of Keystone [2,680 m]) [July] (32; DHKa), Little Brooklyn Lake ([3,120 m]) [July] (113; DHKa), Medicine Bow Peak ([3,350 m–3,660 m]) [July–Aug.] (3; FMNH, KSUC, UWL), Mirror Lake ([3,290 m]) [July] (37; USNM), Nash Fork Little Laramie River (7.5 miles [ca. 12.1 km] NW of Centennial [2,990 m]) [July] (1; DHKa), Snowy Range Pass ([3,200 m]) [June, Aug.] (33; RTBe, UASM); Carbon County, Elk Mountain (35.0 miles [ca. 56.3 km] NE of Saratoga [3,400 m]) [July] (32; USNM), Hidden Treasure Gulch (11.5 miles [ca. 18.5 km] WSW of Encampment [2,870 m]) [July] (2; DHKa), Lake Marie ([3,230 m] and 8 miles [ca. 13 km] SW [2,740 m]) [July] (7; DHKa), North French Creek (4 miles [ca. 6.4 km] W of Mirror Lake [3,050 m]) [July] (3; DHKa), Silver Lake ([3,170 m]) [July] (32; USNM).

Doubtful Records

United States of America—Massachusetts: (1; UMRM).

Nebria acuta quileute, new subspecies

(Figures 16, 38, 46, 55)

Nebria acuta Lindroth 1961:71 (in part).

Holotype, a male, in CAS, labelled: "U.S., Wash., Olympic N. P., Olympic Mts., Boulder Cr. at Olympic Hot Springs, 2000′, 20July71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria acuta quileute Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12494." Allotype (same data as holotype) also in CAS. In total, 135 Paratypes (81 males and 54 females) are deposited in the following collections: CAS, CNC, DHKa, LACM, MCZ, UASM, UIMI, USNM, UWBM.

Type-Locality.—Boulder Creek (at Olympic Hot Springs), Olympic National Park, Washington.

Diagnostic Combination.—Pronotum (Fig. 16) moderately cordate, basal sinuation of lateral margin moderately short and deep, basal angle rectangular or slightly acute, midlateral seta absent; elytra slightly shiny, microsculpture moderately impressed, meshes isodiametric (broken) or slightly transverse, elytral silhouette subrectangular, not narrowed basally, humeral angle not rounded or obtuse, humeral carina markedly developed and projected anterolaterally; hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; male with apex of median lobe as in Figure 38; female without anterodorsal sclerite in bursa copulatrix (Fig. 46); specimen from locality on Olympic Peninsula, Washington (Fig. 55).

Derivation of Taxon Name.—This subspecies is named for the people native to the area including the type-locality, the Quileute tribe.

Geographical Distribution.—Figure 55; restricted to the Olympic Peninsula, Washington. I have studied specimens from the following localities.

United States of America

Washington: Olympic National Park [Aug.] (5; LACM, MCZ), Dosewallips River (at Mascott Campground) [July] (10; UWBM), Eagle Point ([1,830 m]) [July] (1; CNC), Olympic Hot Springs (Boulder Creek [610 m–780 m]) [May–Aug.] (120; CAS, CNC, DHKa, UIMI, USNM, UWBM), Sol Duc Hot Springs [June] (1; CAS).

Nebria sahlbergii modoc, new subspecies

(Figures 17, 56)

Holotype, a male, in CAS, labelled: "U.S., Calif., Modoc Co., Warner Mts., 4 mi. e. New Pine Creek, Pine Cr., 5700′, 22May71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria sahlbergii modoc Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12513." Allotype (same data as holotype) also in CAS. In total, 15 Paratypes (10 males and 5 females) are deposited in the following collections: CAS, DHKa, UASM, USNM.

Type-Locality.—Pine Creek (4 miles [ca. 6.4 km] E of New Pine Creek), Modoc County, California.

Diagnostic Combination.—Pronotum (Fig. 17) size moderate, basal sinuation of lateral margin long and deep, basal angles rectangular, not denticulate, lateral explanation broad throughout its length, midlateral seta absent; proepisternum faintly punctulate anteriorly; elytra slightly short and narrowed basally, elytral silhouette subrectangular, humeral angle not markedly rounded or obtuse, humeral carina moderately developed, slightly projected anterolaterally; specimen from locality in Warner Mountains (northeastern California or southcentral Oregon) (Fig. 56).

Derivation of Taxon Name.—This subspecies is named for the county in which the type-locality is found, as well as for the people native to the region, the Modoc tribe.

Geographical Distribution.—Figure 56; restricted to the Warner Mountains of northeastern California and southcentral Oregon. I have studied specimens from the following localities.

United States of America

California: Modoc County, Cedar Pass [June] (6; USNM), New Pine Creek (4 miles [ca. 6.4 km] E at Pine Creek [1,740 m]) [May] (11; DHKa).

Nebria sahlbergii triad, new subspecies

(Figures 18, 56)

Holotype, a male, in CAS, labelled: "U.S.A., Calif., Trinity Co., Trinity Alps, S. F. Salmon R. at Big Flat Cmpgd., 1490m, 18July75 D.H. & B.A. Kavanaugh Stop #75-36"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria sahlbergii triad Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12514." Allotype (same data as holotype) also in CAS. In total, 212 Paratypes (98 males and 114 females) are deposited in the following collections: CAS, DHKa, FMNH, MCZ, PUCA, UASM, USNM.

Type-Locality.—South Fork Salmon River (at Big Flat Campground), Trinity County, California.

Diagnostic Combination.—Pronotum (Fig. 18) large, broad, basal sinuation of lateral margin moderate in length and depth, basal angles rectangular, not denticulate, lateral explanation broad throughout its length, midlateral seta absent; proepisternum smooth anteriorly; elytra moderate in length and basal width, elytral silhouette subrectangular, humeral angle not markedly rounded or obtuse, humeral carina moderately developed, slightly projected anterolaterally; specimen from locality in Klamath Mountains system of the Coast Ranges (northwestern California or southwestern Oregon) (Fig. 56).

Derivation of Taxon Name.—This subspecies is named for the Trinity Alps, in which the type-locality is found. I use a synonym of 'trinity' for this purpose.

Geographical Distribution.—Figure 56; restricted to the Klamath Mountains system of northwestern California, probably also in southwestern Oregon. I have studied specimens from the following localities.

United States of America

California: Siskiyou County, Gulick Creek (at road to Josephine Lake [1,550 m]) [Aug.] (1; CAS); Trinity County, Boulder Creek (at Goldfield Campground [1,070 m]) [July] (56; CAS, DHKa), Coffee Creek (at Coffee Creek Ranch [1,070 m]) [July] (32; CAS, DHKa), Morris Meadows ([1,340 m]) [Aug.] (1; PUCA), South Fork Salmon River (at Big Flat Campground [1,490 m]) [June–Aug.] (124; CAS, DHKa, FMNH, MCZ, UASM, USNM).

Nebria lituyae, new species

(Figures 29, 57)

HOLOTYPE, a male, in CAS, labelled: "4 June 1977 3356′ under stones, summit Mt. Blunt, 2 mi. s. Lituya Bay, SE Alaska D. Mann coll. 102"/ "Holotype Nebria lituyae Kavanaugh det. D. H. Kavanaugh 1979" [red label]/ "California Academy of Sciences Type No. 13460." ALLOTYPE (same data as holotype) also in CAS. In total, 21 PARATYPES (11 males and 10 females) are deposited in the following collections: CAS, DHKa, DMan, UASM, USNM.

TYPE-LOCALITY.—Mt. Blunt, 2 miles [ca. 3.2 km] s of Lituya Bay, Alaska.

DIAGNOSTIC COMBINATION.—Head width moderate or slightly broadened, eyes moderately convex, each epilobe of mentum with apical tooth short or moderately long; pronotum with lateral explanation broad throughout its length, basal angles rectangular, basal sinuation of lateral margin moderate in length and depth, midlateral seta absent; prosternal intercoxal process (Fig. 29) lanceolate, completely margined (even at apex); elytra slightly elongate, narrow, with or without faint metallic violet reflection, elytral silhouette subovoid, slightly to moderately narrowed basally, humeral angle not markedly rounded or obtuse, humeral carina slightly developed and projected anterolaterally; hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; specimen from locality in southeastern Alaska (mainland) (Fig. 57).

DERIVATION OF TAXON NAME.—This species is named for Lituya Bay, near which the type-locality is found.

GEOGRAPHICAL DISTRIBUTION.—Figure 57; known only from southeastern Alaska, near Lituya Bay. I have studied specimens from the following locality.

United States of America

ALASKA: Mount Blunt (2 miles [ca. 3.2 km] s of Lituya Bay [720 m–760 m]) [June] (23; CAS, DHKa, DMan, UASM, USNM).

Nebria arkansana edwardsi, new subspecies

(Figures 30, 33, 39, 47, 58)

Nebria sahlbergi; *auctorum*.—EDWARDS 1975:48. —MANK 1934:74.

Nebria arkansana; LINDROTH 1961:70 (in part).

HOLOTYPE, a male, in CAS, labelled: "U.S., Mont., Glacier N. P., Livingston Range, Logan Pass Area, ne. slope Mt. Clements, 7100′, 17July72 DHKavanaugh & JGEdwards"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana edwardsi Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12495." ALLOTYPE (same data as holotype) also in CAS. In total, 1872 PARATYPES (1060 males and 812 females) are deposited in the following collections: AMNH, ANSP, BFCa, CAS, CNC, CUIC, DBUM, DHKa, DJLa, FMNH, INHS, JSch, JVMa, KUSM, LRus, MCZ, MSU, OSUO, PMNH, PURC, ROM, RTBe, SJSC, UAFA, UASM, UBC, UIMI, USNM, UWBM.

TYPE-LOCALITY.—Logan Pass, Glacier National Park, Montana.

NOTES ON NOMENCLATURE AND TYPES.—Lindroth (1961:70) designated the valley of the Upper San Juan River, Archuleta County, Colorado, as type-locality for *N. arkansana* Casey. As a result, the nominal subspecies of *N. arkansana* is one restricted to the southern Rocky Mountains (southcentral Wyoming and further south). The name presented here is for the widely distributed subspecies left unnamed by Lindroth's choice of type-locality.

DIAGNOSTIC COMBINATION.—Head moderate in size and relative width; pronotum with lateral explanation broad throughout its length, basal angles rectangular or slightly acute, basal sinuation of lateral margin moderately deep, midlateral seta absent; elytra slightly to moderately dull, microsculpture with meshes isodiametric or slightly transverse, elytral silhouette rectangular or subrectangular, broad basally, basal margination (Fig. 30) straight or slightly concave, merged smoothly with lateral margination, humeral angle not markedly rounded or obtuse, humeral carina absent or very slightly developed; hindwing with full reflexed apex distal to stigma (Fig. 33); hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; male with median lobe (Fig. 39) broad, with apex short and narrow; female with posterodorsal sclerite of bursa copulatrix as in Figure 47; specimen from locality in Rocky Mountain region, but only north or west of Utah and southern Wyoming (Fig. 58).

DERIVATION OF TAXON NAME.—I take great pleasure in naming this subspecies in honor of J. Gordon Edwards, whose keen interest in life at high altitude has fostered my own.

GEOGRAPHICAL DISTRIBUTION.—Figure 58; widespread, distributed in Rocky Mountain region from southern Yukon Territory south to northeastern Nevada, Idaho, and northern Wyoming. I have studied specimens from the following localities.

Canada

Alberta: Banff National Park, Banff [Aug.–Sep.] (3; CUIC, UASM), Boom Lake ([1,830 m]) [July] (1; CNC), Bow Lake [Aug.] (1; UASM), Bow River ([1,830 m]) [Aug.] (6; CNC), Johnson Creek Trail (at Johnson Creek Campground) [July] (1; ROM), Lake Agnes [Aug.] (1; PMNH), Lake Louise [June–Sep.] (16; AMNH, CAS, CNC, MCZ, UBC), Ptarmigan Mountain ([2,590 m]) [Aug.] (13; CNC), Spray Lake [July] (1; JVMa), Sunset Pass ([1,950 m]) [Aug.] (4; CNC); Jasper National Park [Aug.] (2; AMNH), Amethyst Lake (and Amethyst Lake Trail [1,710 m]) [July] (10; DHKa, UASM), Angel Glacier [Sep.] (1; RTBe), Hardisty Creek (1 mile [ca. 1.6 km] S on Highway 93) [July] (1; RFre), Jasper [Aug.] (3; USNM), Miette Hot Springs [Aug.] (1; RTBe), Miette River (at Meadow Creed [1,100 m]) [July–Aug.] (22; DHKa, UASM), Mount Edith Cavell ([1,360 m] and below Angel Glacier) [July] (3; DHKa, UAFA), Portal Creek Trail ([1,950 m]) [July] (3; USNM); Waterton Lakes National Park [July–Aug.] (5; UASM, UWBM), Cameron Lake (creek below lake) [July] (7; USNM), Red Rock Canyon [July] (2; CAS), Waterton Park (Cameron Creek) [July] (36; CNC, MCZ, UASM); Other localities, Bellevue (2 miles [ca. 3.2 km] W at Gold Creek [1,370 m]) [July] (1; DHKa), Blackstone Gap [Aug.] (2; CNC), Blairmore (1; USNM), Blakiston Brook [July] (10; UASM), Carbondale River (near Lost Creek) [Sep.] (1; DJLa), Cline River (at Highway 11) [Aug.] (2; DHKa), Gap [Aug.] (1; CAS), Gorge Creek [July] (2; UASM), Happy Valley (Pincher Creek) [Aug.] (11; CAS, UASM), Highwood Pass ([2,380 m]) [July] (15; CNC), Highwood River [Aug.] (1; CAS), Marmot Creek (10 miles [ca. 16 km] SW of Kananaskis Forest Experiment Station [1,520 m]) [Aug.] (10; CNC), Mill Creek Ranger Station [Aug.] (2; CAS), Pincher Creek ([1,620 m]) [July] (3; DJLa), Ram River area [July] (2; BFCa), Sheep River (4.5 miles [ca. 7.2 km] above Gorge Creek) [Aug.] (7; DHKa), West Branch Castle River ([1,340 m]) [Aug.] (6; DJLa). British Columbia: Glacier National Park, Asulkan Glacier area [Aug.] (1; CNC), Glacier [July–Aug.] (6; CAS, CNC, PURC), Rogers Pass ([1,370 m]) [Aug.] (2; ANSP, CAS); Kootenay National Park [Aug.] (3; CNC), Kimpton Creek ([1,220 m]) [July] (2; CNC), Kindersley Pass ([2,130 m]) [July] (4; CNC), Kootenay River (at Highway 1B) [Aug.] (1; UASM), Marble Canyon [July] (1; CNC), Sinclair Creek ([1,830 m] and at Highway 13) [June–Aug.] (25; CAS, CNC, UASM, UBC), Vermillion Creek [July] (4; CAS, MSU, UBC); Yoho National Park [July] (3; CAS), Amiskwi River (and at Amiskwi Falls [1,830 m]) [Aug.] (34; CNC), Field (and 3 miles [ca. 4.8 km] E on Kicking Horse River) [June, Aug.] (4; CAS, USNM), Lake Oesa ([2,130 m]) [July] (18; CNC), Lake O'Hara [July] (10; CAS, CNC, UBC), Otterhead River ([1,680 m]) [Aug.–Sep.] (29; CNC, DHKa), Yoho River ([1,400 m], 4 to 12 miles [ca. 6.4 to ca. 19 km] E of Field, at Takakkaw Falls [1,520 m]) [July–Aug.] (25; CNC, DHKa, UASM); Other localities, Bosewell [Aug.] (1; UASM), Cabin Creek (NE of Fernie, near Michel) [July] (13; CNC, UASM), Creston (8 miles [ca. 13 km] W) [June] (3; CNC), Crowsnest Pass (2 miles [ca. 3.2 km] W [1,280 m] and 5 miles [ca. 8 km] W on Elk River [1,220 m]) [July] (51; DHKa), Edgewood [July–Aug.] (3; CAS), Elk Creek (E of Fernie) [July] (4; UASM), Elk River (10.7 miles [ca. 17.2 km] W of Fernie) [July] (3; ROM), Erickson (Arrow Creek) [Aug.] (12; CAS, UBC), Fernie (Coal Creek [1,680 m], Fairy Creek, Lizard Creek) [July–Aug.] (63; BFCa, CAS, CNC, DBUM, FMNH, MSU, UBC), Flathead [June] (1; CUIC), Fort Steele [June, Sep.] (2; CAS, UBC), Fortysixmile Camp (at Hope Trail) [July] (4; CAS, CNC, UBC), Hope Mountains [July–Sep.] (6; CNC, INHS, MCZ), Hosmer (Elk River) [July] (1; CAS), Lorna [June] (2; CAS, UBC), Manning Provincial Park (Nicomen Ridge) [July] (10; CAS, CNC, MSU, UBC), Michel (5; UASM), Mount Copeland ([1,980 m]) [Aug.] (21; CNC), Radium Hot Springs [Aug.] (6; CAS, CNC, UBC), Slocan [Aug.] (2; BFCa), South Fork Creek [Aug.] (1; UWBM), Summit Creek (near Creston) [Aug.] (5; UASM), Tetsa River (Alaska Highway mile 378 and mile 390) [Aug.] (3; DHKa, MSU), Vernon [July] (1; CAS), Whipsaw Creek (at Hope Trail [1,460 m]) [July] (1; UBC), Wyndel [Sep.] (1; CNC). Yukon Territory: Rancheria (Swift River) [Aug.] (6; CNC, UASM).

United States of America

Idaho: Blaine County, Alturas Lake (at Alturas Inlet Campground [2,130 m]) [Aug.] (11; DHKa), Cherry Creek (0.1 miles [ca. 0.2 km] NW of Highway 93 [2,230 m]) [Aug.] (6; DHKa), Dollarhide Summit (2 miles [ca. 3.2 km] E at North Fork Warm Springs Creek [2,350 m–2,410 m]) [Aug.] (9; DHKa), Galena [July] (1; BFCa), Galena Summit (2.4 miles [ca. 3.9 km] NE [2,320 m]) [Aug.] (12; DHKa), Hyndman Creek [July] (22; UWBM), Ketchum (2 miles [ca. 3.2 km] NNW at Big Wood Creek [1,830 m]) [Aug.] (28; DHKa), North Fork Warm Springs Creek (10 miles [ca. 16 km] W of Ketchum [1,890 m]) [Aug.] (92; DHKa), Sun Valley [Sep.] (2; JSch); Camas County, Carrie Creek (32 miles [ca. 51 km] [2,440 m] and 36 miles [ca. 58 km] [2,100 m] ESE of Ketchum) [Aug.] (106; DHKa), South Fork Boise River (14 miles [ca. 23 km] E of Featherville at Skeleton Creek [1,550 m], 34 miles [ca. 55 km] E of Featherville at Bear Creek [1,830 m]) [Aug.] (157; DHKa); Cassia County, Rock Creek (15 miles [ca. 24 km] S of Hansen, at Rock Creek Ranger Station) [June–July] (6; UIMI); Custer County, Bayhorse Creek (7 miles [ca. 11 km] NW of Highway 93 [2,440 m]) [Aug.] (3; DHKa), Fourth of July Creek (3 miles [ca. 4.8 km] E of Highway 93 [2,230 m]) [Aug.] (58; DHKa), Stanley [July] (1; UWBM), Trail Creek Summit (2 miles [ca. 3.2 km] NE at Summit Creek [2,320 m]) [Aug.] (9; DHKa); Fremont County, Island Park [July] (3; BFCa); Shoshone County, Avery (7 miles [ca. 11 km] E) [July] (1; UIMI); Valley County, Dagger Falls [July] (2; BFCa), Middle Fork Salmon River (near Boundary Creek) [Aug.] (7; RTBe); County unknown, Twin Creek Forest Camp ([1,520 m]) [July] (57; UWBM). Montana: Carbon County, Quad Creek (17 miles [ca. 27 km] SW of Red Lodge [3,050 m]) [July] (66; DHKa); Fergus County, East Fork Rock Creek ([1,710 m]) [July] (42; DHKa); Flathead County, Marias Pass (10 miles [ca. 16 km] W of summit [1,370 m]) [July] (11; LRus), South Fork Flathead River (at Hungry Horse Reservoir [1,220 m]) [July] (3; LRus); Gallatin County, Fairy Lakes [Aug.] (1; CUIC); Glacier National Park [July–Aug.] (6; CUIC), Baring Creek (at St. Mary Lake) [Aug.] (3; UWBM), Grinnel Falls ([1,860 m]) [Aug.] (1; SJSC), Grinnel Glacier ([1,860 m–1,890 m]) [Aug.] (21; DHKa, SJSC, USNM), Grinnel Lake (at inlet [1,540 m]) [Aug.] (1; DHKa), Lake McDonald (and at Sprague Creek Campground) [July–Aug.] (4; CAS, RTBe), Lake Sherburne (at Canyon Creek) [July] (1; CAS), Logan Pass ([2,030 m–2,130 m] and 5 miles [ca. 8 km] W [1,770 m]) [July–Sep.] (16; DHKa, JSch, RTBe, UASM), Morning Eagle Falls ([1,680 m]) [July] (1; SJSC), Mount Clements (NE slope [2,160 m]) [July] (5; DHKa), Piegan Pass ([2,410 m]) [Aug.] (1; SJSC), St. Mary [Aug.] (8; SJSC, UASM); Madison County, Beaver Creek ([1,920 m]) [Aug.] (1; KUSM), Ennis [July] (2; UIMI); Mineral County, Haugan [Aug.] (14; KUSM), Lookout Pass ([1,280 m]) [July] (1; LRus), Saltese [July, Sep.] (3; MSU, SJSC); Sweetgrass County, Big Timber Creek (at Half Moon Campground [2,230 m–2,290 m]) [July] (1; DHKa). NEVADA: Elko County, Lamoille Creek (at Lower Lamoille Campground [1,920 m]) [Aug.] (35; DHKa), Thomas Creek (at Thomas Creek Campground [2,320 m–2,380 m]) [Aug.] (130; DHKa). OREGON: Baker County, Cornucopia [June–July] (35; BFCa, UWBM); Union County, Elgin (and 9 miles [ca. 14 km] NW at Little Phillips Creek [1,300 m]) [May, Aug.] (6; DHKa), Langdon Lake area (SE of summit) [Aug.] (2; UWBM), Tollgate-Elgin Road [June] (3; UWBM); Wallowa County [Aug.] (1; JSch), Aneroid Lake ([2,320 m]) [July] (2; FMNH), East Fork Eagle Creek [July] (9; UWBM), Indian Crossing (Imnaha River) [Aug.] (2; MSU, OSUO), Lostine River ([1,310 m], at French Campground, at Two Pan Campground [1,710 m–1,980 m]) [Aug.] (112; DHKa, USNM, UWBM), Lost Lake [Aug.] (1; UWBM), Wallowa Lake [July–Aug.] (10; DHKa, UWBM), Wallowa River (above inlet to Wallowa Lake) [May] (1; DHKa). WASHINGTON: Walla Walla County, Walla Walla [Aug.] (1; UWBM). WYOMING: Big Horn County, Granite Pass (8 miles [ca. 13 km] SW on Granite Creek [2,380 m]) [July] (5; DHKa), Shell Creek (11 miles [ca. 18 km] SW of Granite Pass [2,130 m]) [July] (14; DHKa), West Tensleep Creek ([3,140 m–3,200 m]) [July] (17; DHKa); Johnson County, Clear Creek (12 miles [ca. 19 km] W of Buffalo [2,190 m]) [July] (1; DHKa), South Fork Clear Creek (16 miles [ca. 26 km] W of Buffalo [2,350 m], at South Fork Campground [2,350 m]) [July–Aug.] (6; DHKa, FMNH); Park County, Fox Creek (at Highway 212) [Aug.] (1; CAS); Sheridan County, Little Tongue River (13 miles [ca. 21 km] WSW of Dayton [2,380 m]) [July] (22; DHKa); Washakie County, Tensleep (6 miles [ca. 10 km] [1,550 m] and 11 miles [ca. 18 km] [1,890 m] NE on Tensleep Creek) [July] (4; DHKa); Yellowstone National Park [Aug.] (25; USNM); County unknown, Bighorn Reserve (1; MCZ).

Nebria arkansana oowah, new subspecies

(Figures 40, 48, 58)

HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Grand Co., LaSal Mts., Mill Cr. at Oowah Lk., 8800′, 2August71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana oowah Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12496." ALLOTYPE (same data as holotype) also in CAS. In total, 75 PARATYPES (54 males and 21 females) are deposited in the following collections: CAS, DHKa, MCZ, UASM, USNM.

TYPE-LOCALITY.—Mill Creek (at Oowah Lake), Grand County, Utah.

DIAGNOSTIC COMBINATION.—Head moderate in size and relative width; pronotum with lateral explanation broad throughout its length, basal angles rectangular or slightly acute, basal sinuation of lateral margin moderately deep, midlateral seta absent; elytra with humeral angle not markedly rounded or obtuse, humeral carina moderately developed, elytral silhouette subrectangular, broad basally, hindwing full-sized; hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; male with median lobe broad, apex as in Figure 40; female with posterodorsal sclerite of bursa copulatrix as in Figure 48; specimen from locality in La Sal Mountains (eastern Utah) (Fig. 58).

DERIVATION OF TAXON NAME.—This subspecies is named for the small, sheltered lake at the type-locality.

GEOGRAPHICAL DISTRIBUTION.—Figure 58; restricted to the La Sal Mountains of eastern Utah. I have studied specimens from the following localities.

United States of America

UTAH: Grand County, Mill Creek (at Oowah Lake [2,680 m]) [Aug.] (74; CAS, DHKa, MCZ, USNM); San Juan County, Mill Creek Valley ([2,900 m]) [Aug.] (3; UASM).

Nebria arkansana uinta, new subspecies

(Figures 35, 41, 58)

HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Summit Co., Uinta Mts., Hwy. 150, Lost Lk., 9800′, 14Aug71 DHKavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana uinta Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12497." ALLOTYPE (same data as holotype) also in CAS. In total, 93 PARATYPES (44 males and 49 females) are deposited in the following collections: CAS, DHKa, MCZ, UASM, USNM.

TYPE-LOCALITY.—Lost Lake, Summit County, Utah.

DIAGNOSTIC COMBINATION.—Head moderate in size and relative width; pronotum with lateral explanation broad throughout its length, basal angles rectangular or slightly acute, basal sinuation of lateral margin moderately deep, midlateral seta absent; elytra with humeral angle not markedly rounded or obtuse, humeral carina moderately developed; elytral silhouette subrectangular or subovoid, slightly narrowed basally; hindwing reduced in length and width (Fig. 35); hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; male with median lobe as in Figure 41; specimen from locality in Uinta Mountains or in Wasatch Mountains at or north of Weber River, Utah (Fig. 58).

DERIVATION OF TAXON NAME.—This subspecies is named for the Uinta Mountains, in which the type-locality is found.

GEOGRAPHICAL DISTRIBUTION.—Figure 58; restricted to the Uinta Mountains and the Wasatch Mountains at or north of Weber River (northern Utah). I have studied specimens from the following localities.

United States of America

UTAH: Cache County, Logan River (13.7 miles [ca. 22 km] E of Logan at Cottonwood Creek [1,740 m]) [Aug.] (65; CAS, DHKa, MCZ, UASM); Duchesne County, Painter Basin ([3,470 m]) [Sep.] (1; USNM); Summit County, Lost Lake ([2,990 m]) [Aug.] (7; DHKa), Upper Provo River (20.8 miles [ca. 33 km] E of Kamas [2,600 m], at Highway 150) [Aug.] (6; DHKa, USNM); Uintah County, Big Brush Creek (7 miles [ca. 11 km] WNW of Highway 44 [2,620 m]) [Aug.] (14; DHKa); Weber County, Ogden (6 miles [ca. 10 km] E on Ogden River [1,490 m]) [Aug.] (2; DHKa).

Nebria fragilis teewinot, new subspecies

(Figures 35, 42, 59)

HOLOTYPE, a male, in CAS, labelled: "U.S., Wyo., Teton N. P., Teton Mts., Mt. Teewinot, stream on se. slope, 7100′–9000′, 3Aug.73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria fragilis teewinot Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12500." ALLOTYPE (same data as holotype) also in CAS. In total, 377 PARATYPES (219 males and 158 females) are deposited in the following collections: CAS, DHKa, KUSM, MCZ, SJSC, UASM, USNM.

TYPE-LOCALITY.—Mount Teewinot (southeast slope), Grand Teton National Park, Wyoming.

DIAGNOSTIC COMBINATION.—Head moderate in size and relative width; pronotum with lateral explanation broad throughout its length, basal angles rectangular or slightly acute, basal sinuation of lateral margin moderately deep, midlateral seta absent; elytra slightly shiny, microsculpture faintly impressed, with meshes irregularly isodiametric or slightly transverse, with or without faint metallic green or violet reflection, elytral silhouette subrectangular or subovoid, slightly narrowed basally, humeral angle not markedly rounded or obtuse, humeral carina moderately developed; hindwing reduced in length and width (Fig. 35); hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; male with median lobe as in Figure 42; specimen from locality in westcentral Wyoming (Fig. 59).

DERIVATION OF TAXON NAME.—This subspecies is named for the type-locality.

GEOGRAPHICAL DISTRIBUTION.—Figure 59; restricted to mountain ranges of the Rocky Mountain system in westcentral Wyoming. I have studied specimens from the following localities.

United States of America

WYOMING: Grand Teton National Park, Mica Lake ([2,970 m]) [July] (1; DHKa), Mount Teewinot (SE slope [2,160 m–2,740 m]) [Aug.] (79; DHKa), South Fork Cascade Canyon ([3,080 m]) [July] (1; SJSC), South Fork Garnet Canyon ([2,820 m]) [July] (1; SJSC), Timberline Lake area [July] (1; DHKa); Lincoln County, White Creek (20 miles [ca. 32 km] SE of Alpine Junction [1,950 m–2,190 m]) [Aug.] (40; DHKa), Wolf Creek (16.1 miles [ca. 26 km] SW of Hoback Junction [1,770 m–1,780 m]) [July–Aug.] (137; CAS, DHKa, MCZ, UASM, USNM); Sublette County, Green River Lakes (west shores [2,440 m–2,590 m]) [July] (53; DHKa), Hoback River (14 miles [ca. 23 km] SW of Highway 187/189 [2,440 m]) [July] (11; DHKa); Teton County, Alaska Basin (near Sunset Lake [2,940 m]) [July] (1; SJSC), Granite Creek (at Granite Falls [2,160 m]) [July] (37; DHKa), Togwotee Pass ([2,960 m] and 3.7 miles [ca. 6.0 km] WNW at Blackrock Creek [2,770 m]) [Aug.] (20; DHKa, KUSM).

Nebria zioni oasis, new subspecies

(Figures 5, 60)

HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Washington Co., Pine Valley Mts., Leeds Cr. at Oak Grove Cmpgd., 6300′–6500′, 20June71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria zioni oasis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12518." ALLOTYPE (same data as holotype) also in CAS. In total, 46 PARATYPES (18 males and 28 females) are deposited in the following collections: CAS, DHKa, UASM, USNM.

TYPE-LOCALITY.—Leeds Creek at Oak Grove Campground, Washington County, Utah.

DIAGNOSTIC COMBINATION.—Body and appendages dark (piceus or black); antennal scape (Fig. 5) medium length, straight, almost cylindrical (slightly narrowed basally); each epilobe of mentum with tooth moderately long; pronotum with lateral explanation moderately broad throughout its length, basal angles rectangular or slightly acute and projected posteriorly, lateral margin without subapical sinuation but with basal sinuation moderately long and deep, midlateral seta absent; elytra not vaulted, slightly flattened, elytral silhouette ovoid, markedly narrowed basally, humeral angle markedly rounded and obtuse, humeral carina markedly developed, fifth and seventh elytral intervals without setiferous pores; hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; specimen from locality in Pine Valley Mountains (Utah) (Fig. 60).

DERIVATION OF TAXON NAME.—This species is named for the oasislike nature of the type-locality—a spot of green, as it were, in an otherwise dry land.

GEOGRAPHICAL DISTRIBUTION.—Figure 60; restricted to the Pine Valley Mountains of southwestern Utah. I have studied specimens from the following locality.

United States of America

UTAH: Washington County, Leeds Creek (at Oak Grove Campground [1,920 m–1,980 m]) [June] (46; CAS, DHKa, UASM, USNM).

Nebria obliqua chuskae, new subspecies

(Figures 19, 34, 61)

HOLOTYPE, a male, in CAS, labelled: "USA Arizona Apache Co., sw. Red Rock Chuska Mts. Wagon Wheel Camp Gr. aspen-fir forest 2260m. Loc. 11 July 11–12, 1976"/ "SOUTHWESTERN USA EXP.—1976 G.E.Ball, J.M. Campbell, P.M.Hammond"/ "Holotype Nebria obliqua chuskae Kavanaugh det. D. H. Kavanaugh 1979" [red label]/ "California Academy of Sciences Type No. 13461." ALLOTYPE (same data as holotype) also in CAS. In total, 16 PARATYPES (10 males and 6 females) are deposited in the following collections: CAS, MCZ, UASM, USNM.

TYPE-LOCALITY.—Lukachukai Creek (at Wagon Wheel Campground), Apache County, Arizona.

DIAGNOSTIC COMBINATION.—Mandible markedly explanate laterally, broad; tooth of mentum bifid, with notch V-shaped; pronotum (Fig. 19) relatively long and narrow, moderately cordate, moderately narrowed basally, widest anterior to middle, slightly shiny (microsculpture faintly or moderately impressed, meshes isodiametric), basal margin not or only slightly sinuate laterally, lateral bead narrow, obliterated basally in most specimens, basal foveae broad, smooth or faintly rugulose or punctulate, basal angles obtuse, basal sinuation of lateral margin absent, lateral explanation moderately wide and more broadened posteriorly only, midlateral seta absent; elytral silhouette subovoid, slightly narrowed basally, lateral margins slightly rounded; hindwing (Fig. 34) reduced in length; hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; specimen from locality in Chuska Mountains, Arizona (Fig. 61).

DERIVATION OF TAXON NAME.—This subspecies is named for the Chuska Mountains, in which the type-locality is found.

GEOGRAPHICAL DISTRIBUTION.—Figure 61; restricted to the Chuska Mountains, Arizona. I have studied specimens from the following locality.

United States of America

ARIZONA: Apache County, Lukachukai Creek (at Wagon Wheel Campground [2,260 m–2,320 m]) [July–Aug.] (18; CAS, MCZ, UASM, USNM).

Nebria darlingtoni, new species

(Figures 20, 62)

HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., El Dorado Co., Sierra Nevada, S. F. American River., 3 mi. w. of Riverton, 910m, 16July75 D. H. & B.A. Kavanaugh Stop #75-29"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria darlingtoni Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12499." ALLOTYPE (same data as holotype) also in CAS. In total, 170 PARATYPES (105 males and 65 females) are deposited in the following collections: AMNH, CAS, DHKa, ICCM, KSUC, KUSM, MCZ, UASM, USNM.

TYPE-LOCALITY.—South Fork American River (3 miles [ca. 4.8 km] w of Riverton), El Dorado County, California.

DIAGNOSTIC COMBINATION.—Body black, legs dark brown or piceus; microsculpture on pronotum and elytra very deeply impressed, meshes isodiametric, alveolae convex; pronotum (Fig. 20) with lateral explanation narrow at middle, broadened posteriorly, basal angles rectangular or slightly acute, basal sinuation of lateral margin moderately short and deep, midlateral seta absent; elytra with humeral carina slightly developed, slightly projected anteriorly, elytral silhouette ovoid, markedly narrowed basally, humeral angles moderately rounded and obtuse; hind coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; specimen from Sierra Nevada, California (Fig. 62).

DERIVATION OF TAXON NAME.—I take great pleasure in naming this species in honor of Philip J. Darlington, Jr., biogeographer, student of carabid evolution, and friend, whose work and personal encouragement have provided inspiration in this study.

GEOGRAPHICAL DISTRIBUTION.—Figure 62; apparently restricted to the canyon of the South Fork of the American River, Sierra Nevada, California. I have studied specimens from the following localities.

United States of America

CALIFORNIA: El Dorado County [Aug.] (9; CAS, ICCM, KSUC, MCZ, USNM), Kyburz (2 miles [ca. 3.2 km] E on South Fork American River [1,340 m]) [July] (5; CAS, DHKa), Pacific House [Sep.] (5; CAS), Riverton (South Fork American River [980 m], 3 miles [ca. 4.8 km] w at Bridal Falls Picnic Area [910 m]) [July–Aug.] (151; AMNH, CAS, DHKa, KUSM, MCZ, UASM), White Hall [June] (2; UASM).

Nebria navajo, new species

(Figures 43, 63)

HOLOTYPE, a male, in CAS, labelled: "Kayenta Ariz. 19 mi. sw VI-18-33"/ "Navajo Co. Alt. 6500 ft."/ "Ansel F Hall Exp. 1933"/ "Holotype Nebria navajo Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12509." One male PARATYPE (same data as holotype) also in CAS.

TYPE-LOCALITY.—Kayenta (19 miles [ca. 31 km] sw, Navajo County, Arizona.

Diagnostic Combination.—Body pale tan-orange, legs pale yellow; microsculpture on pronotum and elytra moderately impressed, meshes isodiametric, alveolae flat; pronotum with lateral explanation narrow at middle, broadened posteriorly, basal angles rectangular or slightly acute, basal sinuation of lateral margin moderately short and deep, midlateral seta absent; elytra with humeral carina slightly developed, slightly projected anteriorly, elytral silhouette ovoid, markedly narrowed basally, humeral angles moderately rounded and obtuse; hindwing short, narrow; hind coxa bi- or plurisetose basally; apex of fourth tarsomere of hind tarsus with ventrolateral lobe long; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; male with apex of median lobe as in Figure 43; specimen from Arizona (Fig. 63).

Derivation of Taxon Name.—This species is named for the people native to the region including the type-locality.

Geographical Distribution.—Figure 63; known only from the type-locality in northeastern Arizona. I have studied specimens from the following locality.

United States of America

Arizona: Navajo County, Kayenta (19 miles [ca. 31 km] SW [1,980 m]) [June] (2; CAS).

Nebria gebleri cascadensis, new subspecies

(Figures 21, 64)

Nebria gebleri; *auctorum*. —Hatch 1939:118 (in part). —Lindroth 1961:83 (in part). —Van Dyke 1925:119 (in part); 1926:10 (in part).

Holotype, a male, in CAS, labelled: "U.S., Wash., Mt. Rainier N. P., Paradise R. above Narada Falls, 4580′–4800′, 8Aug72 DHKavanaugh &HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri cascadensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12502." Allotype (same data as holotype) also in CAS. In total, 1696 Paratypes (944 males and 752 females) are deposited in the following collections: AMNH, ANSP, BFCa, CAS, CNC, CUIC, DHKa, DJLa, FMNH, INHS, JSch, KSUC, KUSM, LRus, MCZ, MSU, NMDo, ODA, OSUC, OSUO, PURC, ROM, RTBe, SDSU, SJSC, UAFA, UASM, UBC, UCR, UIMI, UMMZ, USNM, UWBM, UWEM, WSU.

Type-Locality.—Paradise River (above Narada Falls), Mount Rainier National Park, Washington.

Diagnostic Combination.—Head moderate in size, dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 21) markedly cordate, with or without faint violet metallic reflection, sinuation of lateral margin very deep, midlateral seta present, basolateral seta present; elytra moderately convex, with distinct violet or brassy metallic reflection, elytral silhouette subovoid, slightly narrowed basally, basal margination moderately concave, humeral angle roundly obtuse, humeral carina moderately to markedly developed, fifth elytral interval without setae (in few individuals with one to three setae), not (or in few individuals moderately) catenate, striae moderately impressed; specimen from locality in Cascade Range of central Oregon to southern British Columbia (Fig. 64).

Derivation of Taxon Name.—This subspecies is named for the Cascade Mountain Range, in which members of this taxon are widely distributed.

Geographical Distribution.—Figure 64; restricted to the Cascade Range (from central Oregon to southern British Columbia), the adjacent mountain ranges west of the Okanagan lowland in southwestern British Columbia, and to Vancouver Island (not yet recorded from the Olympic Peninsula, Washington, although I predict that it will be found to occur there). I have studied specimens from the following localities.

Canada

British Columbia: Copper Mountain [Aug.] (4; UBC), Cultus Lake Provincial Park (Entrance Bay Campground) [June] (4; ROM), Garibaldi (Cheakamus River) [Sep.] (2; JSpe), Garibaldi Provincial Park (Diamond Head Trail [1,070 m]) [July] (3; CNC), Hope [June–July] (8; BFCa, IHNS), Hunter Creek (at Restmore Lodge) [July] (3; CAS), Manning Provincial Park (Blackwell Peak [910 m], Lightning Lake, Nicomen Ridge, Skagit River) [May–Sep.] (35; CAS, CNC, DHKa, KUSM, MCZ, MSU, RTBe, UBC, UMMZ), Midday Valley (near Merritt) [Aug.] (1; INHS), Nicolum River (at Hope Trail) [July] (2; UBC), North Bend [July] (19; USNM), Skagit River (at Hope Trail [760 m]) [July] (3; UBC), Snass Creek (at Warburton Trail [760 m]) [July] (5; UBC), Spious Creek [May] (1; CAS), Vancouver area (2; ANSP), Whipsaw Creek (at Hope Trail [1,220 m]) [May, July] (4; UASM, UBC); Vancouver Island, Port Alberni (Robertson Creek Spawning Channel) [June] (1; ROM).

United States of America

Oregon: Clackamas County, Austin Hot Springs [July] (1; OSUO), Brightwood (Salmon River) [July] (8; DHKa), Mount Hood (S slope below Timberline Lodge [1,190 m]) [Aug.] (2; DHKa), Rhododendron ([490 m] and 1 mile [ca. 1.6 km] SE at Zig Zag River [600 m]) [July–Aug.] (55; CAS, DHKa, SJSC, UWBM); Deschutes County, Elk Lake [July] (1; UWBM), Upper Deschutes River [May] (1; UWBM); Hood River County, Hood River [May, July] (8; CAS, USNM), Mount Hood (Cloud Cap, Hood River Meadows Ski Area [1,710 m], Sand Creek, Tillie Jane Creek, Umbrella Falls) [June–Sep.] (70; CAS, DHKa, MCZ, NMDo, ODA, UCR, UIMI, UWBM); Marion County, Detroit ([460 m] and 5 miles [ca. 8.0 km] N) [July–Aug.] (3; LRus, UWBM); Multnomah County, Horsetail Falls ([120 m]) [May–July] (87; DHKa, JSch, ODA, OSUO). Washington: (32; ANSP, CAS, INHS, MCZ, OSUC, USNM); Chelan County, Fish Lake [July] (1; UWBM), Leavenworth [July] (8; ANSP, KUSM, MCZ, SDSU, USNM), Tumwater Canyon ([610 m]) [May] (1; LRus); Cowlitz County, Ariel [May] (1; UWBM], Cougar [Sep.] (2; OSUO), Hoffstadt Creek (at Toutle River) [July] (2; MSU, OSUO), North Fork Toutle River (14 miles [ca. 23 km] E of Toutle [300 m]) [Aug.] (33; CAS, DHKa), Toutle River [July] (11; UWBM); King County, Baring [July] (2; FMNH), Green River Gorge (Green River) [May, Aug.] (5; UWBM), Greenwater River (at Greenwater Campground) [June] (1; UWBM), North Bend [July] (17; CAS, CUIC, MCZ), Renton (Cedar River) [May] (1; UWBM), Skykomish [July, Sep.] (2; UASM, UWBM), Snoqualmie [June] (4; UIMI), Stevens Pass (and 4 miles [ca. 6.4 km] W) [June, Aug.] (5; LRus, UASM), Wellington [July] (10; CAS, MCZ, USNM, UWEM), White River (5 miles [ca. 8 km] W of Greenwater [1,490 m], Slippery Creek) [July–Aug.] (42; DHKa, UWBM); Kittitas County, Blewett Pass (Niger Creek) [July] (2; USNM), Easton (22; CAS, INHS, MCZ, USNM), Snoqualmie Pass [July] (4; CAS), Teanaway Ridge ([910 m]) [July] (10; LRus); Klickitat County, Klickitat Valley [July] (1; MCZ); Lewis County, Lake Creek (3 miles [ca. 4.8 km] NE of Packwood [370 m]) [July] (5; DHKa), White Pass (and 1.5 miles [ca. 2.4 km] W at Millridge Creek [1,280 m]) [June–July] (42; DHKa, SJSC, USNM); Mount Rainier National Park ([760 m–1,830 m]) [June–Sep.] (30; ANSP, CAS, CUIC, KSUC, MCZ, OSUO, SJSC, UIMI, UWBM), Bear Flat ([1,520 m–1,830 m]) [July] (1; CAS), Carbon River [June] (4; UWBM), Cayuse Pass [1,400 m] [June] (4; USNM), Fish Creek (at West End Road) [June] (1; ROM), Fryingpan Creek ([1,160 m–1,190 m]) [July–Aug.] (38; CNC, DHKa, SJSC), Horse Creek (near Longmire) [July] (15; CAS), Ipsut Creek Campground [Aug.] (1; OSUO), Kautz Creek (at Nisqually River) [Sep.] (2; UWBM), Longmire ([760 m]) [June–Aug.] (25; CAS, SJSC, USNM), Narada Falls ([1,370 m–1,460 m]) [July–Aug.] (118; DHKa, USNM, UWBM), Nisqually River (0.1 miles [ca. 0.2 km] above Paradise River [980 m], toe of Nisqually Glacier [1,220 m–1,520 m]) [July–Aug.] (7; AMNH, CAS, CUIC, DHKa, MCZ), North Fork Puyallup River (below toe of Puyallup Glacier [1,100 m–1,650 m]) [July–Aug.] (22; CNC, DHKa, USNM), Ohanapecosh [June, Aug.] (18; DJLa, LRus, SJSC, UIMI, USNM), Paradise area (below Sluskin Falls, Paradise Park [1,220 m–1,830 m], Paradise River [1,400 m–1,680 m], Paradise Valley) [June–Sep.] (88; CAS, CUIC, DHKa, FMNH, MCZ, USNM, UWBM), St. Andrews Creek (at West End Road [1,160 m]) [Aug.] (5; DHKa), Silver Creek [Aug.] (10; UWBM), Sluskin Falls [July] (8; UWBM), Stevens Creek ([1,190 m–1,220 m]) [June–July] (4; DHKa, USNM), Sunbeam Falls ([1,220 m]) [May] (1; CNC), Sunrise area [July] (2; LRus), Tahoma Creek ([910 m]) [July] (1; USNM), West End Road [July] (1; CAS), White River ([1,190 m] and at White River Campground [1,520 m]) [July–Aug.] (12; FMNH, SJSC, USNM, UWBM), Van Trump Creek (above Christine Falls [1,220 m–1,280 m]) [July–Aug.] (62; DHKa, UWBM); Pierce County, Goat Creek (at Nisqually River [610 m]) [July] (130; DHKa), Fairfax [Oct.] (1; FMNH), Poch Creek (at Carbon River) [Aug.] (5; UCB, UWBM), Tenas Creek (5 miles [ca. 8.0 km] E of Ashford [610 m]) [July] (1; DHKa), White River (at Silver Springs Campground [790 m]) [June, Aug.] (15; DHKa, USNM); Skamania County, Carson [Aug.] (6; UIMI), Council Lake (SE on Forest Road 123 [1,260 m]) [Aug.] (4; UASM), Mount St. Helens (Maratta Creek) [July] (3; DHKa), North Fork Cipsus River [June] (14; UWBM), North Fork Toutle River (at Spirit Lake Lodge [940 m]) [Aug.] (31; CAS, DHKa), Spirit Lake [July, Sep.] (3; DHKa, UWBM), Stabler [June] (1; OSUO), Wind River (8 miles [ca. 13 km] N of Carson [340 m]) [May, July] (14; DHKa); Snohomish County, Darrington (Clear Creek Falls) [May] (5; UWBM), Glacier Peak [July–Aug.] (2; CAS, UWBM); Whatcom County, Glacier (North Fork Nooksack River) [July] (13; CAS, LRus), Lookout Creek (4 miles [ca. 6.4 km] E of Glacier [380 m]) [Aug.] (18; CAS, DHKa), Mount Baker (Austin Pass [1,520 m], Bagley Creek [670 m], Razor Hone Creek [1,680 m]) [July–Sep.] (125; CAS, DHKa, JSpe, LRus, UCR, UWBM), North Fork Nooksack River (4 miles [ca. 6.4 km] E of Glacier [380 m], Silver Fir Campground [610 m]) [Aug.] (3; CAS, DHKa), Shuksan ([760 m]) [Aug.] (3; LRus), Shuksan Creek [Aug.] (12; UWBM), Skagit River (at Newhalem) [July] (2; UWBM); Yakima County, American River (at Hell's Crossing [1,040 m]) [July–Aug.] (17; DHKa, ICCM, KUSM, MCZ, UIMI, UMMZ, UWBM), Bumping River (0.8 miles [ca. 1.3 km] SW of Highway 410 [1,010 m]) [July–Sep.] (92; CAS, DHKa, ICCM, MCZ, MSU, PURC, UAFA, USNM, WSU), Dog Lake ([1,310 m]) [July] (25; DHKa), Mount Adams (Bird Creek [910 m–2,440 m], Chaparral Creek [880 m], Klickitat River) [June–July, Sep.] (82; AMNH, ANSP, CAS, CUIC, FMNH, ICCM, MCZ, UASM, UIMI, USNM, UWBM, WSU), Naches River [July] (2; USNM), Tampico [July] (1; USNM), Tieton Dam [Aug.] (2; AMNH, WSU), Wildcat Creek (at Tieton River [880 m]) [July] (3; DHKa, OSUO), Yakima area (11; JSch, MCZ, USNM, WSU), Yakima Indian Reservation ([910 m]) [July] (1; CAS).

Doubtful Records

United States of America—Colorado: Leavenworth Valley (1; ANSP). Washington: Pullman (1; ICCM).

Specimens Without Locality Data: (4; CDA, MCZ, MSU, UWBM).

Nebria gebleri fragariae, new subspecies

(Figures 22, 44, 49, 64)

Holotype, a male, in CAS, labelled: "U.S., Ore., Grant Co., Blue Mts., Strawberry Cr., 5800' 28 May 1971, DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri fragariae Kavanaugh det. D. H. Kavanaugh 1979" [red label]/ "California Academy of Sciences Type No. 12501." Allotype (same data as holotype) also in CAS. In total, 27 Paratypes (21 males and 6 females) are deposited in the following collections: CAS, DHKa, UASM, USNM.

Type-Locality.—Strawberry Creek (1,770 m), Grant County, Oregon.

Diagnostic Combination.—Size moderate, standardized body length male less than 10.5 mm, female less than 11.0 mm; head moderate in size, dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 22) moderately cordate, with or without faint green metallic reflection, midlateral seta present, basolateral seta present; elytra with distinct green metallic reflection, elytral silhouette subrectangular, broad basally; male with apex of median lobe as in Figure 44; female with anterodorsal sclerite in bursa copulatrix (Fig. 49); specimen from locality in Strawberry Range, Blue Mountains, eastern Oregon (Fig. 64).

Derivation of Taxon Name.—This subspecies is named for the Strawberry Range of the Blue Mountains, in which the type-locality is found. The subspecific epithet is a form of the scientific name for the strawberry genus, *Fragaria* Linnaeus.

Geographical Distribution.—Figure 64; restricted to the Strawberry Range of the Blue Mountains of eastern Oregon. I have studied specimens from the following locality.

United States of America

Oregon: Grant County, Strawberry Creek ([1,770 m]) [May] (29; CAS, DHKa, UASM, USNM).

Nebria gebleri siskiyouensis, new subspecies

(Figures 23, 64)

Holotype, a male, in CAS, labelled: "U.S.A., Calif., Trinity Co., Trinity Alps, S. F. Salmon R. at Big Flat Cmpgd., 1490m, 18July75 D. H. & B. A. Kavanaugh Stop #75-36"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri siskiyouensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12503." Allotype (same data as holotype) also in CAS. In total, 33 Paratypes (19 males and 14 females) are deposited in the following collections: CAS, DHKa, FMNH, UASM, USNM.

Type-Locality.—South Fork Salmon River (at Big Flat Campground), Trinity County, California.

Diagnostic Combination.—Head dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 23) with apical angles moderately narrow, midlateral seta present, basolateral seta present; elytra without metallic reflection, elytral silhouette subovoid, relatively short and broad; hindwing full-sized; specimen from locality in Klamath Mountains system of Coast Ranges in northwestern California or southwestern Oregon (Fig. 64).

Derivation of Taxon Name.—This subspecies is named for the Siskiyou Mountains, in which members of this taxon were first collected.

Geographical Distribution.—Figure 64; restricted to the Klamath Mountains system of the Coast Ranges in northwestern California and southwestern Oregon. I have studied specimens from the following localities.

United States of America

California: Trinity County, Boulder Creek (at Goldfield Campground [1,070 m]) [July] (2; CAS, DHKa), South Fork Salmon River (at Big Flat Campground [1,490 m]) [June–July] (30; CAS, DHKa, FMNH, UASM, USNM), Taylor Lake Road (branch of Taylor Creek [1,750 m]) [Aug.] (1; CAS). Oregon: Jackson County, Little Applegate River ([700 m]) [Aug.] (2; CAS, FMNH).

Nebria carri, new species

(Figures 10, 24, 65)

Holotype, a male, in CAS, labelled: "U.S., Ida., Blaine Co., Sawtooth Mts., Smoky Range, 2 mi. e. Dollarhide Summit, N. F. Warm Springs Creek, 7700′–7900′, 21 Aug.73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria carri Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12498." Allotype (same data as holotype) also in CAS. In total, 152 Paratypes (63 males and 89 females) are deposited in the following collections: BFCa, CAS, DHKa, FMNH, GASh, MCZ, UASM, USNM.

Type-Locality.—Dollarhide Summit, Blaine County, Idaho.

Diagnostic Combination.—Head dark, with a pair of pale paramedial spots on vertex; penultimate labial palpomere bisetose; mentum (Fig. 10) with M_3 setae absent; pronotum (Fig. 24) with midlateral seta present, basolateral seta absent; specimen from locality east of Columbia Basin (Fig. 65).

Derivation of Taxon Name.—I take pleasure in naming this species in honor of John and Betty Carr (Calgary, Alberta), who first collected specimens of same, and who have provided help and encouragement to me and to other students during our respective studies.

Geographical Distribution.—Figure 65; known at present only from ranges of the Sawtooth Mountains system and from the Seven Devils Mountains of southcentral and western Idaho, respectively. I have studied specimens from the following localities.

United States of America

Idaho: Adams County, Towsley Springs (9 miles [ca. 14 km] nne of Cuprum [2,070 m]) [July–Aug.] (4; BFCa, DHKa); Blaine County, Dollarhide Summit (1.0 to 2.0 miles [ca. 1.6 to 3.2 km] e on North Fork Warm Springs Creek [2,350 m–2,500 m]) [Aug.] (138; CAS, DHKa, MCZ, UASM, USNM), Twin Lakes Trail (w of Petit Lake) [July] (2; BFCa); Camas County, Carrie Creek (32 miles [ca. 51 km] wsw of Ketchum [2,400 m]) [Aug.] (9; DHKa); Elmore County, Trinity Lakes [Aug.] (1; GASh).

Nebria kincaidi balli, new subspecies

(Figures 11, 31, 65)

Nebria kincaidi; *auctorum*. —Blackwelder and Blackwelder 1948:2 (in part). —Erwin and Ball 1972:85 (in part). —Hatch 1939:121 (in part). —Lindroth 1961:88 (in part). —Van Dyke 1919:8 (in part).

Nebria columbiana; *auctorum* (not Casey). —HATCH 1939:121 (in part). —VAN DYKE 1919:8 (in part).

HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Mt. Rainier N. P., Paradise R. above Narada Falls, 4580′–4800′, 8Aug72 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria kincaidi balli Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12505." ALLOTYPE (same data as holotype) also in CAS. In total, 366 PARATYPES (189 males and 177 females) are deposited in the following collections: AMNH, CAS, CNC, CUIC, DHKa, FMMH, KUSM, LACM, LRus, MCZ, MSU, ODA, OSUO, SJSC, UASM, USNM, UWBM, WSU.

TYPE-LOCALITY.—Paradise River (above Narada Falls), Mount Rainier National Park, Washington.

DIAGNOSTIC COMBINATION.—Head dark, with a pair of pale paramedial spots on vertex; penultimate labial palpomere trisetose; mentum (Fig. 11) with M_3 setae present; pronotum with midlateral seta present, basolateral seta absent; elytra with basal margination (Fig. 31) moderately long, smooth or faintly wavy, slightly to moderately concave; specimen from Cascade Range of central Washington to northern Oregon (Fig. 65).

DERIVATION OF TAXON NAME.—I take great pleasure in naming this subspecies in honor of George E. Ball, my mentor and friend.

GEOGRAPHICAL DISTRIBUTION.—Figure 65; restricted to the Cascade Range of central Washington and northern Oregon. Present known range extends from Mount Rainier (Washington) south to Mount Hood (Oregon). I have studied specimens from the following localities.

United States of America

OREGON: Hood River County, Mount Hood ([910–1,830 m], Cloud Cap Road at Tillie Jane Road, Hood River Meadows Ski Area [1,620 m–1,710 m], Tillie Jane Creek [1,830 m], Umbrella Falls) [June–Sep.] (67; AMNH, CAS, CUIC, DHKa, MCZ, MSU, ODA, USNM, UWBM, WSU). WASHINGTON: Mount Ranier National Park [July–Sep.] (4; CUIC, SJSC, WSU), Cayuse Pass ([1,400 m]) [June] (1; USNM), Fryingpan Creek ([1,160 m–1,190 m]) [July–Aug.] (2; CNC, DHKa), Indian Henry's ([1,370 m–1,520 m]) [July] (1; UASM), Louise Lake [July] (5; UASM), Mowich Lake [July] (4; OSUO, UWBM), Mystic Lake [July] (1; WSU), Nisqually River ([1,220 m]) [May] (4; CNC), Paradise area (above Narada Falls [1,520 m], Paradise Park [1,520 m–1,830 m], Paradise River [1,460 m–1,830 m]) [June–Aug.] (265; CAS, CNC, CUIC, DHKa, FMNH, KUSM, LRus, MCZ, OSUO, UASM, USNM, UWBM), Ricksecker Point [Sep.] (1; UWBM), Sluskin Falls [July] (1; UWBM), Snow Lake ([1,520 m]) [Aug.] (1; CNC), Spray Park ([1,980 m]) [Aug.] (1; LRus), Sunrise area [July] (2; CAS, LRus), Van Trump Creek (above Christine Falls [1,220 m–1,280 m]) [July] (7; DHKa), Van Trump Park ([1,830 m]) [Aug.] (1; CNC), West End Drive [July] (1; CAS); Pierce County, Coplay Lake [May] (1; UWBM); Skamania County, Spirit Lake ([910 m–1,770 m]) [Aug.] (1; OSUO).

Doubtful Records

UNITED STATES OF AMERICA—OREGON: Deschutes County, Bend [July] (8; LACM).

Nebria spatulata sierrae, new subspecies

(Figures 6, 66)

Nebria spatulata; ERWIN AND BALL 1972:83 (in part).

HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Mono Co., Sierra Nevada Mts., ne. face White Mt., along stream in cirque above Big Horn Lake, 3290m–3480m, 21 July 74 D.H.Kavanaugh Collector"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria spatulata sierrae Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12516." ALLOTYPE (same data as holotype) also in CAS. In total, 58 PARATYPES (28 males and 30 females) are deposited in the following collections: CAS, DHKa, MCZ, RPPa, UASM, UCB, USNM.

TYPE-LOCALITY.—White Mountain (east slope, above Big Horn Lake), Mono County, California.

DIAGNOSTIC COMBINATION.—Size moderate: standardized body length male less than 12.0 mm, female less than 12.4 mm; head with a pair of pale paramedial spots (or pair fused to form a single median spot), genae and occiput not swollen, eyes moderate in size and convexity; antennal scape (Fig. 6) moderate in length, slightly arcuate, markedly narrowed basally; pronotum with midlateral seta present, basolateral seta present; elytra rufous or piceus, very dull, with microsculpture deeply impressed, meshes isodiametric, without metallic reflection, elytral silhouette markedly ovoid, narrowed basally; hindwing vestigial; specimen from locality on Eastern Divide or more northern portion of Sierra Nevada (Fig. 66).

DERIVATION OF TAXON NAME.—This subspecies is named for the Sierra Nevada, California, to which its geographical range is restricted.

GEOGRAPHICAL DISTRIBUTION.—Figure 66; restricted to the Eastern Divide of the Sierra Nevada in California; presently known from as far north as Sonora Pass (Tuolumne County) and as far south as Big Pine Creek (Inyo County). I have studied specimens from the following localities.

United States of America

CALIFORNIA: Inyo County, Big Pine Creek (at Finger Lake [3,290 m]) [Aug.] (4; CAS); Mono County, H. M. Hall Natural Area ([3,350 m]) [July–Sep.] (9; RPPa), Saddlebag Lake [Sep.] (3; CAS), White Mountain (NE slope in cirque above Big Horn Lake [3,290 m–3,480 m]) [July] (13; DHKa); Tuolumne County, Sonora Pass ([2,740 m–3,350 m]) [July] (3; UCB, USNM); Yosemite National Park, Maclure Creek Basin ([3,290 m–

3,350 m]) [Sep.] (1; DHKa), Mount Lyell ([3,350 m]) [July–Aug.] (23; CAS, MCZ, UASM), Tioga Pass ([3,050 m]) [Aug.] (2; CAS).

Doubtful Records

United States of America—California: San Bernardino County [July] (2; CAS).

Nebria meanyi lamarckensis, new subspecies

(Figures 25, 32, 67)

Holotype, a male, in CAS, labelled: "U.S., Calif., Inyo Co., Sierra Nevada, Lamarck Cr. above Upper Lamarck Lk., 10700′–11000′ 6July71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria meanyi lamarckensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12507." Allotype (same data as holotype) also in CAS. In total, 21 Paratypes (6 males and 15 females) are deposited in the following collections: CAS, DHKa, UASM.

Type-Locality.— Lamarck Creek (above Upper Lamarck Lake), Inyo County, California.

Diagnostic Combination.—Size moderate, standardized body length male less than 12.0 mm, female 9.5 to 12.3 mm; head dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 25) markedly cordate, basal angles acute, projected posteriorly, midlateral seta present, basolateral seta present; elytra with faint or moderate violet, blue, or green metallic reflection, elytral silhouette subrectangular, broad basally, basal margination (Fig. 32) straight or slightly concave; specimen from locality in southern Sierra Nevada (California) (Fig. 67).

Derivation of Taxon Name.—The name for this subspecies refers to the type-locality, Lamarck Creek, which in turn refers to Jean Baptiste Pierre Antoine Lamarck, the noted French naturalist and pioneer evolutionist.

Geographical Distribution.—Figure 67; restricted to the east slope of the southern Sierra Nevada. I have studied specimens from the following localities.

United States of America

California: Inyo County, Big Pine Creek (below Finger Lake [3,140 m]) [Aug.] (2; CAS), Lamarck Creek (above Upper Lamarck Lake [3,260 m–3,350 m]) [July] (21; CAS, DHKa, UASM).

Nebria meanyi sylvatica, new subspecies

(Figures 26, 67)

Nebria meanyi; Hatch 1939:118 (in part).

Holotype, a male, in CAS, labelled: "U.S.A., Wash., Olympic N. P., Olympic Mts., Boulder Cr. at Olympic Hot Springs, 610m, 15Aug.74 D. H. Kavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria meanyi sylvatica Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12508." Allotype (same data as holotype) also in CAS. In total, 177 Paratypes (83 males and 94 females) are deposited in the following collections: CAS, CNC, CUIC, DHKa, ICCM, JSch, UASM, USNM, UWBM.

Type-Locality.—Boulder Creek (at Olympic Hot Springs), Olympic National Park, Washington.

Diagnostic Combination.—Head moderate in size and width, dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 26) markedly cordate, basal sinuation of lateral margin very short and deep, midlateral seta present, basolateral seta present; elytra moderately convex, elytral silhouette subrectangular to subovoid, moderately broad basally, basal margination slightly short, humeral angles faintly or moderately obtuse, humeral carina present, slightly to markedly developed, elytral intervals markedly convex, fifth interval with three to six setae, markedly catenate, striae deeply impressed; specimen from locality on Vancouver Island (British Columbia) or Olympic Peninsula (Washington) (Fig. 67).

Derivation of Taxon Name.—This subspecies name is derived from the Latin word, *sylvaticus,* meaning "of the forest"—a reference to the deep forest habitat occupied by taxon members.

Geographical Distribution.—Figure 67; restricted to Vancouver Island, British Columbia, and the Olympic Peninsula, Washington. I have studied specimens from the following localities.

Canada

British Columbia: Vancouver Island, Alberni (38 miles [ca. 61 km] w) [May] (1; CNC).

United States of America

Washington: Olympic National Park [Aug.] (11; ICCM, MCZ, UASM, USNM), Elwha River (at Elwha Campground) [Aug.] (1; CUIC), Dosewallips River (at Muscott Campground) [July] (3; UWBM), Olympic Hot Springs (Boulder Creek [670 m–760 m]) [May–Aug.] (160; CAS, CNC, DHKa, JSch, UWBM), Sol Duc Hot Springs [July] (3; JSch, UWBM).

Nebria vandykei wyeast, new subspecies

(Figures 7, 68)

Nebria vandykei; auctorum. —Erwin and Ball 1972:87 (in part). —Hatch 1939:118 (in part). —Lindroth 1961:86 (in part).

Nebria trifaria vandykei Bänninger. —Hatch 1953:56 (in part).

Holotype, a male, in CAS, labelled: "U.S.A., Ore., Clackamas Co., Cascade Range, s. slope Mt. Hood, headwaters Salmon R. near Timberline Lodge, 1830m–1950m, 3 Aug.74

D. H. Kavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria vandykei wyeast Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12517." ALLOTYPE (same data as holotype) also in CAS. In total, 186 PARATYPES (104 males and 82 females) are deposited in the following collections: CAS, DHKa, MCZ, OSUO, UASM, USNM, UWBM.

TYPE-LOCALITY.—Salmon River headwaters, Mount Hood, Clackamas County, Oregon.

DIAGNOSTIC COMBINATION.—Size very large, standardized body length male greater than 12.0 mm, female greater than 12.5 mm; head dark, with a pair of pale paramedial spots on vertex; antennal scape (Fig. 7) narrowed basally, straight or slightly arcuate; pronotum with midlateral seta present, basolateral seta present; elytra without metallic reflection, elytral silhouette markedly ovoid; specimen from locality in Cascade Range south of Columbia River (Fig. 68).

DERIVATION OF TAXON NAME.—For this subspecies, I have selected that name given to Mount Hood by local native peoples—*Wy'east*, which means "The Mountain."

GEOGRAPHICAL DISTRIBUTION.—Figure 68; restricted to the Cascade Range south of the Columbia River; present known range from Mount Hood south to the Three Sisters area (Oregon). I have studied specimens from the following localities.

United States of America

OREGON: Deschutes County, Middle Sister Peak (E slope at North Fork Squaw Creek [1,950 m–2,190 m]) [Aug.] (19; CAS, DHKa); Hood River County, Mount Hood ([1,740 m], Hood River Meadows Ski Area [1,920 m–1,950 m], headwaters of Salmon River near Timberline Lodge [1,830 m–1,950 m], Sand Creek) [June–Aug.] (130; CAS, DHKa, UWBM); Marion County, Mount Jefferson (N slope [1,860 m–1,920 m], S end of Jefferson Park [1,830 m], Russell Creek [1,680 m–1,740 m], West Branch Whitewater River [1,830 m–1,890 m]) [Aug.] (39; CAS, DHKa, OSUO).

Nebria schwarzi beverlianna, new subspecies

(Figures 1, 27, 36, 69)

HOLOTYPE, a male, in CAS, labelled: "U.S., Wyo., Sublette Co., Gros Ventre Mts., Hwy. 187/189, 8 mi. nw. Bondurant, Hoback R., 6900', 1–2 August 73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria schwarzi beverlianna Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12515." ALLOTYPE (same data as holotype) also in CAS. In total, 254 PARATYPES (133 males and 121 females) are deposited in the following collections: CAS, DHKa, FMNH, MCZ, ROM, UASM, USNM.

TYPE-LOCALITY.—Hoback River (8 miles [ca. 13 km] NW of Bondurant), Sublette County, Wyoming.

DIAGNOSTIC COMBINATION.—Figure 1; size very large, standardized body length male greater than 12.0 mm, female greater than 12.5 mm; head moderate in size and width, dark, with a pair of pale paramedial spots on vertex; pronotum (Fig. 27) slightly flattened, only slightly cordate, broad basally, midlateral seta present, basolateral seta present; elytra with marked violet, blue, or green metallic reflection, elytral silhouette subrectangular, broad basally; hind coxa (Fig. 36) with four to six basal and one (in very few individuals two or three) apical seta(-ae); specimen from locality in western Wyoming (Fig. 69).

DERIVATION OF TAXON NAME.—I take great pleasure in naming this subspecies in honor of my wife, Beverly Ann Kavanaugh, in grateful acknowledgment of her constant support through the course of this study.

GEOGRAPHICAL DISTRIBUTION.—Figure 69; at present known only from Hoback River at the south slope of the Gros Ventre Mountains. I have seen specimens from the following locality.

United States of America

WYOMING: Sublette County, Bondurant (8 miles [ca. 13 km] NW at Hoback River [2,100 m]) [July–Aug.] (255; CAS, DHKa, FMNH, MCZ, UASM, USNM).

Specimens Without Locality Data: (1; ROM).

Nebria trifaria utahensis, new subspecies

(Figures 8, 28, 45, 50, 70)

HOLOTYPE, a male, in CNC, labelled: "Lonesome Beaver, 7500', Henry Mts., Utah VII 20–22, 68 H. F. Howden"/ "Holotype Nebria trifaria utahensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]. ALLOTYPE (same data as holotype) also in CNC. In total, 13 PARATYPES (9 males and 4 females) are deposited in the following collections: CAS, CNC, UASM.

TYPE-LOCALITY.—Lonesome Beaver, Henry Mountains, Garfield County, Utah.

DIAGNOSTIC COMBINATION.—Head moderate in size and width, dark, with a pair of pale paramedial spots on vertex; antennal scape (Fig. 8) slightly arcuate or straight, slightly to markedly narrowed basally; pronotum (Fig. 28) with basal sinuation of lateral margin moderately deep, midlateral seta present, basolateral seta present; elytra without metallic reflection, microsculpture deeply impressed, meshes isodiametric, elytral silhouette subovoid; hindwing reduced in width and length, truncate distal to stigma; male with apex of median lobe as in Figure 45; female with posterodorsal sclerite in bursa copulatrix as in Figure 50; specimen from Henry Mountains (Utah) (Fig. 70).

DERIVATION OF TAXON NAME.—This subspecies is named for the State of Utah, in which its geographical range is restricted.

GEOGRAPHICAL DISTRIBUTION.—Figure 70; restricted to the Henry Mountains of southcentral Utah. I have studied specimens from the following localities.

United States of America

UTAH: Garfield County, Hanksville (24 miles [ca. 39 km] s [2,290 m]) [July] (3; CNC), Lonesome Beaver ([2,290 m]) [July] (12; CAS, CNC, UASM).

NOMENCLATURAL NOTES AND LECTOTYPE DESIGNATIONS

Carabus gyllenhali SCHÖNHERR, 1806:196. [=*Nebria gyllenhali* (Schönherr).] LECTOTYPE (here designated), a male, in NRSS, labelled: "♂"/ [triangular blue label]/ "Lectotype Carabus gyllenhali Schönherr designated by D. H. Kavanaugh 1976" [red label]. Five paralectotypes (same data as lectotype) also in NRSS.

The name *Carabus rufescens* Strøm (1768:331) did not appear in the literature between the date of its original description and 1880, when Schøyen (1880:183) revived its use (Carl Lindroth, personal communication). Jeannel (1937:4), however, accepted *N. rufescens* as the senior synonym of *N. gyllenhali*; and, following him, a number of authors have subsequently applied the name "*rufescens*" to this species (Blair 1950:220; Friden 1971:30; Greenslade 1968:41; Horvatovitch 1973:252; Luff 1972:174; Luff and Davies 1972:47; Nakane 1963:18, 1971:180; and Ueno 1953:59, 1955:47). The combination *N. rufescens gyllenhali* has sporadically appeared (Jeanne 1966:12; and Jeannel 1937:4, 1941:19) as has the unfortunate combination *N. gyllenhali rufescens*, where "*rufescens*" referred variously to a subspecies, race, variety, or aberration of *N. gyllenhali* (Andrewes 1939:161; Bänninger 1925:345, 1960:261; Csiki 1927:359; Munster 1933:267; and Reitter 1908:93).

The name given to this particular species is of considerable importance. The accumulated literature on this species is very extensive, and its members are among the most broadly distributed and commonly collected of all carabid beetles. Both names have been so often used in the literature that a decision for or against either will cause some confusion, but it is still more important to reach some decision which will provide for consistency in all future usage. Lindroth (1939:59, 1954:121, 1961:78) and Bänninger (1949:144) have refused to recognize *N. rufescens* as the valid name for this species. For the reasons they have cited, because no type-specimen has been found or perhaps ever existed, and because Strøm's original description "cannot be interpreted (not even as a *Nebria*)" (Carl Lindroth, personal communication), I concur that the name *N. gyllenhali* (Schönherr) should be conserved as the valid name for the species. Any future use of the epithet *rufescens* should be discouraged; and the name *Carabus rufescens* Strøm should be listed as a *nomen dubium*.

Carabus nivalis PAYKULL, 1790:52. [=*Nebria nivalis* (Paykull).] LECTOTYPE (here designated), a male, in NRSS, labelled: "Mus. Payk."/ "Riksmuseum Stockholm" [green label]/ "Lectotype *Carabus nivalis* Paykull designated by D. H. Kavanaugh 1976" [red label].

The specimen chosen as lectotype of *Carabus nivalis* is one of three specimens so identified in NRSS from the Paykull Collection. The other two specimens are actually *Nebria gyllenhali gyllenhali* (Schönherr) adults. Because all three specimens bear identical labels and have traditionally been considered syntypes, the two *N. gyllenhali* specimens could perhaps be considered paralectotypes. Paykull (1798:119) subsequently described a "variety B" of *C. nivalis*, which is clearly synonymous with *N. gyllenhali gyllenhali* and was based on specimens from a different locality and collector. The original description of *C. nivalis* does not fit the two hetero-specific specimens, but the description of "variety B" does so. I conclude that these specimens are probably not part of Paykull's original type-series of *C. nivalis*; but they may be the specimens he described later as "variety B."

Helobia castanipes KIRBY, 1837:20. [=*Nebria gyllenhali castanipes* (Kirby).] LECTOTYPE (here designated), a female, in BMNH, labelled: "Type" [red-trimmed disk]/ "70"/ "N. Amer." [pale blue disk with "5699" on underside]/ "apparently Type of castanipes Kby. Lindroth 1952"/ "Lectotype Helobia castanipes Kirby designated by D. H. Kavanaugh 1976" [red label].

The lectotype bears no label in Kirby's hand. However, according to P. M. Hammond (personal communication), the number "5699" on the underside of one label refers to an entry in manuscript catalogs of the Coleoptera in BMNH. An original label in Kirby's hand is pasted in the catalog at this entry and reads "73. 1. ♀?/ castanipes." The fate of the second of two specimens mentioned by Kirby in his original description is unknown.

Nebria arkansana Casey, 1913:52.

Lindroth (1961:70) was certainly correct in denying the validity of Casey's records for Arkansas and Indiana for this species; and his choice for the new type-locality ("Valley of the Upper San Juan River," Archuleta County, "Colorado") is quite reasonable. The specimens in Casey's series are labelled "Ind" and "S. Ark"; and it is at least possible that the latter refers to the South Arkansas River (a quite suitable locality for the species, in Chaffee County, Colorado) rather than to the State of Arkansas as supposed by Casey. It is also possible that "Ind" refers to the "Indian Territory," although general use of that name for the region was abandoned long before 1913.

Nebria bifaria Mannerheim, 1853:120. [=*Nebria nivalis nivalis* (Paykull).] Lectotype (here designated), a male, in ZILR, labelled: "38"/ "Nebria carbonaria Esch. Insel. Paul"/ "Lectotype ?" [red label]/ "Lectotype Nebria bifaria Mannerheim designated by D. H. Kavanaugh 1976" [red label].

Nebria catenata Casey, 1913:49. [=*Nebria trifaria catenata* Casey.] Type-Locality.—Colorado; restricted by Erwin and Ball (1972:97) to San Juan Mountains, and here further restricted to Wolf Creek Pass, Mineral County, Colorado.

Nebria diversa LeConte, 1863a:2 [as a replacement name for *N. livida* LeConte]. Lectotype (same as for *N. livida* LeConte; see below for data).

Nebria elias Motschulsky, 1865:274. The type-specimen of *N. elias* has been completely destroyed and only its pin and labels remain (in ZMUM). Motschulsky's original description is too vague to permit assurance that *N. elias* and *N. gyllenhali castanipes* are synonymous. The occurrence of the latter in Alaska (the type area of *N. elias*) is restricted and local, which casts further uncertainty as to appropriate application of the name. I therefore refrain from designation of a neotype and list *N. elias* as a *nomen dubium*, but, for convenience, place it as a synonym of *N. gyllenhali castanipes*, following Lindroth (1961:78).

Nebria eschscholtzii Ménétriés, 1844:55. Lectotype (here designated), a female, in ZILR, labelled: [gold-coated square]/ "California" [pink label]/ "Eschscholtzii Menet. Californ."/ "Syntypus" [red label]/ "Lectotype Nebria eschscholtzii Menetries designated by D. H. Kavanaugh 1976" [red label]. One paralectotype also in ZILR. Type-Locality.—California; here restricted to South Fork of American River, 3 miles [ca. 4.8 km] w of Riverton, El Dorado County, California.

Nebria expansa Casey, 1913:56. [=*Nebria lacustris* Casey, 1913:56.] Type-Locality.—Indiana; here restricted to Turkey Run State Park, Parke County, Indiana.

The name *N. lacustris* Casey has priority over *N. expansa* by precedence of position as well as by action of first reviser (Bell 1955:265; see also Lindroth 1961:77). In his original description, Casey recorded *N. expansa* from "Texas and Indiana," based on his study of two females. Bell (1955:267) and Lindroth (1961:77, 1975:112) accepted the record from Texas. In my judgment, this record must be erroneous. Acting on my suggestion, Lindroth (1975:147) amended his lectotype designation (1975:112) and selected the Casey specimen labelled "L.," interpreted by Casey as from Indiana, instead of the "Texas" specimen. Individuals recognizable as the "*expansa*" form of *N. lacustris* have often been collected at the restricted type-locality chosen.

Nebria fusiformis Van Dyke, 1926:11. [=*Nebria spatulata spatulata* Van Dyke.]

Because this name appeared unaccompanied by any description or indication, it should be considered a *nomen nudum*. It is clear to me, however, from the text in which the name appeared, that Van Dyke was referring to his *N. spatulata*, the original description of which appeared the previous year.

Nebria gebleri DEJEAN, 1831:573. HOLOTYPE, a female, in MHNP, labelled: "Sitka"/ "Gebleri Eschs"/ "Ex Musaeo Mniszech"/ "Holotype Nebria gebleri Dejean det. D. H. Kavanaugh 1976" [red label].

It is clear from his original description that the specimen of *N. gebleri* seen by Dejean was at that time complete. In his review of the Dejean types, Lindroth (1955b:12) noted that the head and prothorax of the type-specimen had been lost. In my study of the type (in 1976), I found it to be complete again! Unfortunately, the parts replaced are not only from a different specimen but also from one representing a different species [namely, *Nebria picicornis* (Fabricius)]. There is no doubt, however, that the pterothorax and abdomen (through which the pin passes) are the recognizable remains of the valid type-specimen.

Nebria gregaria FISCHER VON WALDHEIM, 1821:72. LECTOTYPE (here designated), a male, in ZMUM, labelled: "47. gregaria Fisch."/ "Lectotype Nebria gregaria Fischer v. Wald. designated by D. H. Kavanaugh 1976" [red label].

Fischer (1821:73) indicated that his description of *N. gregaria* was based on material in his own and Eschscholtz's collections. I have been unable to locate any Eschscholtz specimens of *N. gregaria* from among those in UMHF. Apparently, the single Fischer specimen (ZMUM) chosen as lectotype is the only survivor from the type-series.

Nebria hudsonica LECONTE, 1863b:3. LECTOTYPE (here designated), a male, in MCZ, labelled: "Saskatchewan"/ "Type 643" [red label]/ "N. hudsonica *LeC.*"/ "Lectotype Nebria hudsonica LeConte designated by D. H. Kavanaugh 1976" [red label]. TYPE-LOCALITY.—Saskatchewan, Hudson's Bay Territory; here restricted to North Saskatchewan River at Rocky Mountain House, Alberta.

In 1863, the area now occupied by the Province of Saskatchewan was part of Hudson's Bay Territory (or the Northwest Territories), and at least up to that date, the name "Saskatchewan" was apparently applied only to the Saskatchewan River system. Therefore, LeConte's use of the name as a type-locality probably refers to the river system rather than the province. Only those parts of the system in Alberta are within the continuous range of *N. hudsonica*, although I have seen two specimens from localities in the Province of Saskatchewan. My selection of the restricted type-locality reflects these facts and considerations.

Nebria incerta CASEY, 1913:53. [=*Nebria obliqua* LeConte.] TYPE-LOCALITY.—Colorado; here restricted to North Fork of South Platte Canyon at Santa Maria, Park County, Colorado. This restricted type-locality is the same as for *N. obliqua*.

Nebria ingens HORN, 1870:98. LECTOTYPE (here designated), a female, in MCZ, labelled: "Cala."/ "Type No. 1026" [red label]/ "Nebria ingens Horn"/ "Lectotype Nebria ingens Horn designated by D. H. Kavanaugh 1976" [red label]. One female paralectotype, also in MCZ, labelled: "Cala."/ "Type 8127 [red label]/ "N. ingens Horn." TYPE-LOCALITY.—Sierra Nevada Mountains east of Visalia, California; here restricted to Franklin Lakes, Tulare County, California.

In his original description, Horn mentioned two specimens, a male and a female. The MCZ specimen seen by Lindroth (1961:87), his "allotype," is a female. The other specimen, from the Horn Collection (formerly at ANSP, now at MCZ), is also a female; so Horn did not actually see a male of this species. The lectotype chosen is the specimen from the Horn Collection.

Nebria livida LECONTE, 1859:84 [preoccupied by *Carabus lividus* Linnaeus, 1758:414; =*Nebria diversa* LeConte]. LECTOTYPE (here designated), a male, in MCZ, labelled: [blue disk]/ "Type 642" [red label]/ "N. diversa *LeC.* ‖ livida LeC."/ "Lectotype Nebria livida LeConte designated by D. H. Kavanaugh 1976" [red label]. One male paralectotype (same data as lectotype) also in MCZ.

Nebria longula LECONTE, 1878:478. [=*Nebria suturalis* LeConte—NEW SYNONYMY.] TYPE-LOCALITY.—Colorado; here restricted to Longs Peak, Rocky Mountain National Park, Colorado.

To date, all Colorado records for *N. suturalis* have been from the Front Range of the Rocky Mountains. The restricted type-locality is a protected wilderness area in that range.

Nebria mannerheimii FISCHER VON WALDHEIM, 1828:253. LECTOTYPE (here designated), a male, in ZMUM, labelled: "Sitcha"/ "48. mannerheimii Fisch."/ "Lectotype Nebria mannerheimii Fischer v. Wald. designated by D. H. Kavanaugh 1976" [red label]. One male paralectotype in UMHF.

Both specimens that I recognize as comprising the type-series of *N. mannerheimii* were probably those collected by Eschscholtz (Fischer von Waldheim 1828:253). The specimen chosen as lectotype is from the Fischer Collection (ZMUM). The paralectotype is from the Mannerheim Collection (UMHF) and bears an "Eschsch." label.

Nebria metallica FISCHER VON WALDHEIM, 1821:71. LECTOTYPE (here designated), a male, in ZMUM, labelled: "Unalaschka. F."/ "73 metallica Fisch."/ "Lectotype Nebria metallica Fischer v. Wald. designated by D. H. Kavanaugh 1976" [red label]. One male and one female paralectotype are in UMHF.

Fischer's description of *N. metallica* was based on material in his own and Eschscholtz's collections (Fischer von Waldheim 1821:72). Specimens from the latter, identified as such, are now in UMHF as part of the Mannerheim Collection. I have chosen the Fischer Collection specimen as lectotype, the two Eschscholtz specimens as paralectotypes. A fourth specimen, in the Fischer Collection (ZMUM), bears a "Kadjak" [=Kodiak] label and is thus excluded from the type-series.

Nebria moesta LECONTE, 1850:209. [=*Nebria gyllenhali castanipes* (Kirby).] LECTOTYPE (here designated), a male, in MCZ, labelled: [light green disk]/ "Type 645" [red label]/ "N. moesta LeC."/ "N. castanipes Kby."/ "Lectotype Nebria moesta LeConte designated by D. H. Kavanaugh 1976" [red label]. One male and two female paralectotypes (same data as lectotype) also in MCZ.

Nebria mollis MOTSCHULSKY, 1865:274. [=*Nebria nivalis nivalis* (Paykull).] LECTOTYPE (here designated), sex undetermined (specimen incomplete, badly damaged), in ZMUM, labelled: "A. borealis" [green label]/ "Nebria mollis Motsch. Am. arc. cont." [green label]/ [red rectangle]/ "Lectotype Nebria mollis Motschulsky designated by D. H. Kavanaugh 1976" [red label].

In his original description, Motschulsky presented the species epithet as "*molbis*." I have found no published statement by Motschulsky that "*molbis*" was a misspelling. However, the type-specimen is labelled "*mollis*"; from as early as 1868, every subsequent citation of the name has used the latter spelling. This suggests early recognition, possibly initiated (privately) by Motschulsky himself, of an original error. The first clear indication of an intended emendation is that of Csiki (1927:389).

Nebria mühlenbergii STURM, 1826:173 [here emended to *Nebria muehlenbergii* Sturm].

Because Sturm never selected type-specimens, none exists for this name. Furthermore, no description ever accompanied the use of this name. However, Sturm (1843:16) subsequently cited *N. muehlenbergii* as a synonym of *N. pallipes*, thereby providing the only clue to his application of the name to a taxon. The name should be treated as a *nomen nudum*.

Nebria obliqua LECONTE, 1866c:363. LECTOTYPE (here designated), a male, in MCZ, labelled: "Col."/ "Type 646" [red label]/ "Nebria obliqua Lec. Lewis Col."/ "obliqua 2"/ "Lectotype Nebria obliqua LeConte designated by D. H. Kavanaugh 1976" [red label]. One female paralectotype (same data as lectotype) also in MCZ. TYPE-LOCALITY.—Colorado; here restricted to North Fork of South Platte Canyon at Santa Maria, Park County, Colorado.

The type-locality of *N. obliqua*, as originally stated, was Colorado. LeConte (1878:478) subsequently listed "North Fork of South Platte Cañon (7,000 to 8,000 ft.)" as a locality for the species, and Lindroth (1961:73) accepted this as the type-locality. I here formally restrict the type-locality to that area.

Nebria obtusa LECONTE, 1878:478. [=*Nebria obliqua* LeConte—NEW SYNONYMY.]

My interpretation of LeConte's original description of *N. obtusa* is that the name is based on a single specimen (see LeConte 1878:479, lines 7–8). I therefore consider the type-specimen (in MCZ) to be a holotype. The synonymy noted here was actually suggested by LeConte

(1878:479) and is supported by abundant data (Kavanaugh, manuscript in preparation).

Nebria oregona CASEY, 1913:52. [=*Nebria mannerheimii* Fischer von Waldheim.] TYPE-LOCALITY.—Clackamas County, Oregon; here restricted to Zigzag River at Rhododendron, Clackamas County, Oregon.

Nebria ovipennis LECONTE, 1878:477. TYPE-LOCALITY.—Sierra Nevada, California; here restricted to Mount Conness (east slope, above Greenstone Lake), Mono County, California.

The holotype of *N. ovipennis* (in MCZ) is representative of populations north of Mount Lyell, Yosemite National Park, but not south of that point in the Sierra Nevada. The restricted type-locality chosen is therefore both more precise and appropriate for the form represented by the type-specimen.

Nebria pallipes SAY, 1823:78.

Lindroth (1969a:1149, and in Lindroth and Freitag 1969:326) discussed the problem of establishing the actual publication date of Say's paper in which the original description of *N. pallipes* appeared. His comments, however, support the date cited above, rather than 1825, the year Lindroth (1961:76) cited.

Nebria rathvoni LECONTE, 1853:400. [=*Nebria gebleri rathvoni* LeConte—NEW STATUS.] HOLOTYPE, a male, in MCZ, labelled: "6456 ft. Lake Tahoe, Cal. May 24, 1879"/ [light green square]/ "79." [red-tipped label]/ "N. rathvoni LeC."/ "Type 7403" [red label]/ "Holotype Nebria rathvoni LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE-LOCALITY.—Sacramento, California; here emended to Truckee River at Truckee, Nevada County, California.

There is no reason to doubt that the specimen recognized here as the holotype of *N. rathvoni* is actually the specimen seen by LeConte, although locality and date data on one label indicate otherwise. It is the only specimen of this taxon in the LeConte Collection (MCZ). Furthermore, the troublesome specimen label itself appears to be relatively new, and I suspect that it has been more recently added to the original type-specimen and thereby represents a mislabelling.

LeConte's type-locality, Sacramento, is well outside the habitat range of the taxon; so the type was surely not collected there (although Sacramento was probably the closest important town to the true collection site. Truckee, the emended type-locality, is about at the midpoint of both the habitat and geographical ranges of the taxon.

Nebria sahlbergii FISCHER VON WALDHEIM, 1828:254. LECTOTYPE (here designated), a male, in UMHF, labelled: "♂"/ "Eschsch."/ "Sitka"/ "Lectotype Nebria sahlbergii Fischer v. Wald. designated by D. H. Kavanaugh 1976" [red label]/ "Lectotype Nebria violacea Motsch. designated by D. H. Kavanaugh 1976" [red label].

Fischer's description of *N. sahlbergii* was based on a study of Eschscholtz material (Fischer von Waldheim 1828:254). I have located only two specimens probably representing the original type-series—one in the Fischer Collection (ZMUM), the other in the Mannerheim Collection (UMHF). I have chosen the UMHF specimen as lectotype because, first, the original description better fits this specimen, and, second, the Fischer (ZMUM) specimen is actually a representative of *N. gyllenhali castanipes* rather than *N. sahlbergii* as the latter name was applied by Lindroth (1961:68). The Fischer specimen must be considered a paralectotype of *N. sahlbergii* in spite of its identity. In fact, the strange misuse of the name "*sahlbergii*" by numerous North American authors in referring to *N. gyllenhali castanipes* (Kirby) (e.g., Casey 1913:51; Hatch 1939:120; Horn 1870:102; LeConte 1853:400, 1878:479) can only now be explained—that is, if these authors assumed that the Fischer specimen was the type of *N. sahlbergii*. I choose not to follow their interpretation in order to preserve the name *Helobia castanipes* Kirby (see above), which would become an objective junior synonym of *N. sahlbergii* if the Fischer specimen were designated as lectotype.

Nebria suturalis LECONTE, 1850:209. LECTOTYPE (here designated), a male, in MCZ, labelled: [light green disk]/ "Type 650" [red label]/ "suturalis 3"/ "Lectotype Nebria suturalis LeConte designated by D. H. Kavanaugh 1976" [red label]. Two female paralectotypes (same data as lectotype) also in MCZ.

Nebria tenuipes Casey, 1913:51. [=*Nebria eschscholtzii* Ménétriés.] Type-Locality.—Alameda County, California; here restricted to Niles Canyon, Alameda County, California.

Nebria texana Casey, 1913:54. [=*Nebria obliqua* LeConte.] Type-Locality.—"Texas."

The holotype of *N. texana* (in USNM) bears the label "Tex," interpreted by Casey as referring to the State of Texas (a highly improbable record). It is more probable that the specimen was collected in Colorado, perhaps at Texas Creek, a small tributary of the Arkansas River, Fremont County, Colorado. However, I prefer not to amend or restrict the type-locality at present, pending further field search in the mountainous regions of western Texas.

Nebria trifaria LeConte, 1878:478. Lectotype (here designated), a female, in MCZ, labelled: "9500 ft. Amer. Fork Canon Utah, Aug. 2–3, 1877"/ "Type 651" [red label]/ "N. trifaria *LeC.*"/ "Lectotype Nebria trifaria LeConte designated by D. H. Kavanaugh 1976" [red label].

Nebria vandykei Bänninger, 1928:5. Lectotype (here designated), a male, in ETHZ, labelled: "Paradise Val. Mt. Rainier Wash. VII-18-1920"/ "Col. by E. C. Van Dyke"/ "1. Fühl.gld. as. 1 + 2 B."/ "FG. Basig. bil. *OP*!"/ "Nebria trifaria LeC."/ "Type Nebria Van Dykei 10.1927" [red-trimmed label]/ "Lectotype Nebria vandykei Bänninger designated by D. H. Kavanaugh 1976" [red label]. Two paralectotypes also in ETHZ.

In his original description, Bänninger mentioned four specimens in the type-series, but only three of these are accounted for at present (W. Sauter, personal communication).

Nebria violacea Motschulsky, 1850:73. [=*Nebria sahlbergii sahlbergii* Fischer von Waldheim.] Lectotype (here designated), same specimen as lectotype of *Nebria sahlbergii* Fischer von Waldheim (see above).

Mannerheim apparently obtained and examined the Eschscholtz specimen of *N. sahlbergii* now in UMHF, studied the specimen identified as *N. sahlbergii* in Fischer's Collection (ZMUM), and then noted (Mannerheim 1843:189) that two "varieties" existed. He called the form represented by the Eschscholtz specimen in his possession "var. B." Motschulsky (1850:73), referring to Mannerheim's brief description of variety "B," named this form *N. violacea*. Consequently, the specimen now in UMHF appears to be the specimen upon which both *N. violacea* and *N. sahlbergii* are based. I have therefore designated and so labelled the specimen as lectotype for both names.

Nebria viridis Horn, 1870:101. [=*Nebria frigida* R. F. Sahlberg.] Lectotype (here designated), a male, in MCZ, labelled: "R. [superscript "M"] A."/ "Type No. 1027-" [red label]/ "N. viridis Horn"/ "Lectotype Nebria viridis Horn designated by D. H. Kavanaugh 1976" [red label]. One male paralectotype (same data as lectotype) also in MCZ.

In Horn's original description, only two specimens are mentioned. There are now three specimens in MCZ (one from the Horn Collection, two from the LeConte Collection). I have designated the Horn specimen as lectotype and the first LeConte specimen as the paralectotype. The second LeConte specimen (labelled "viridis 2") has no type status. All three specimens bear identical first labels; but LeConte may have received his second specimen directly from Ulke (see Horn 1870:14), his first specimen from Horn.

Acknowledgments

I gratefully acknowledge the assistance of those curators and other individuals listed above (under Materials and Methods) who loaned material in their care to me for study. In addition, the following individuals made type-material available to me on loan or provided critical information on type-specimens: T. L. Erwin (USNM), P. M. Hammond (BMNH), H. Hippa (UMTF), S. Keleinikova (ZMUM), O. L. Kryzhanovskij and V. G. Schilenkov (ZILR), J. F. Lawrence and J. Scott (MCZ), H. B. Leech (CAS), O. Martin (ZMKD), T. Nyholm (NRSS), H. Perrin (MHNP), S. Rohwer (UWBM), W. Sauter (ETHZ), G. Scherer (ZSBS), and H. Silfverberg (UMHF). T. L. Erwin (USNM), M. H. Hatch (UWBM), J. F. Lawrence (MCZ), H. B. Leech (CAS), P. Oman (OSUO), L. L. Pechuman (CUIC), A. Provonsha (PURC), and A. Smetana (CNC) were helpful hosts during my visits to study material in their respective institutions. I thank also the many colleagues and friends who assisted me in the field by providing companionship, physical labor, and other resources in support of the project, and my colleagues at both the University of Alberta and the California Academy of Sciences for their encouragement and assistance. Special thanks are due to P. H. Arnaud, Jr., G. E. Ball, T. L. Erwin, H. Goulet, G. R. Noonan, and D. R. Whitehead for their continued interest in the project and their willingness to share with me their own observations and experiences.

This study was supported by the National Research Council of Canada with funds from Grant A-1399 to G. E. Ball. Additional financial support was obtained from the Boreal Institute for Northern Studies (University of Alberta), through a Grant In Aid of Research (1973–74) for fieldwork in Alaska, and from the California Academy of Sciences.

Literature Cited

Andrewes, H. E. 1939. The generic names of the British Carabidae, with a check list of the British species. The Generic Names of British Insects, 6:153–192.

Armin, C. 1963. A study of the family Carabidae (Coleoptera) in Boulder County, Colorado. Unpublished Ph.D Dissertation. Department of Biology, University of Colorado, Boulder, Colorado. 476 pp.

Arnett, R. H., and G. A. Samuelson. 1969. Directory of Coleoptera collections of North America (Canada through Panama). Purdue University Press, Lafayette, Indiana. vii + 123 pp.

Ball, G. E. 1966. The taxonomy of the subgenus *Scaphinotus* Dejean with particular reference to the subspecies of *Scaphinotus petersi* Roeschke. Transactions of the American Entomological Society, 92:687–722.

———, and J. Nègre. 1972. The taxonomy of the Nearctic species of the genus *Calathus* Bonelli (Coleoptera: Carabidae: Agonini). Transactions of the American Entomological Society, 98:412–533.

Bänninger, M. 1925. Neunter Beitrag zur Kenntnis der Carabinae: die Nebriini. Entomologische Mitteilungen, 14:180–195, 256–281, 329–343.

———. 1928. Über die Nebriini. 13. Beitrag zur Kenntnis der Carabinae. Koleopterologische Rundschau, 14:1–7. Entomologicae, 11:143–242.

———. 1949. Ueber Carabinae (Col.). Ergänzungen und Berichtigungen III, mit Bemerkungen zu R. Jeannels neuer Einteilung der Carabiden. Mitteilungen der Münchner Entomologischen Gesellschaft, 35–39:127–157.

———. 1960. Die schweizerischen Arten der Gattung *Nebria* Latr. (Col. Carab.). Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 32:337–356.

Bell, R. T. 1955. Species of the *pallipes*-group of *Nebria* in the eastern United States. Proceedings of the Entomological Society of Washington, 57:265–267.

Blackwelder, R. E., and R. M. Blackwelder. 1948. Fifth supplement to the Leng Catalogue of Coleoptera of America, north of Mexico. John D. Sherman, Mount Vernon, New York. 87 pp.

Blair, K. G. 1950. *Nebria nivalis* Paykull (Col., Carabidae) in Scotland. Entomologist's Monthly Magazine, Ser. 4, 86:220–222.

Brown, W. L., Jr., and E. O. Wilson. 1954. The case against the trinomen. Systematic Zoology, 3:174–176.

Casey, T. L. 1913. Studies in the Cicindelidae and Carabidae of America. Memoirs on the Coleoptera, 4:1–192.

Csiki, E. 1927. Pars 92. Carabidae: Carabinae II. Pp. 315–622 *in* W. Junk and S. Schenkling, editors, Coleopterorum Catalogus 1. W. Junk, Berlin. 345 pp. + 648 pp. [1926–33].

Dejean, P. F. M. A. 1831. Species general des Coléoptères de la Collection de le Comte Dejean. 5. Mequignon-Marvis, Paris. viii + 883 pp.

Edwards, J. G. 1954. A new approach to infraspecific categories. Systematic Zoology, 3:1–20.

———. 1956a. Clarification of certain aspects of infraspecific systematics. Systematic Zoology, 5:92–94.

———. 1956b. What should we mean by subspecies? Turtox News, 34:200–202, 230–231.

———. 1975. The Carabidae of Glacier National Park, Montana. The Coleopterists Bulletin, 29:47–58.

Erwin, T. L. 1970. A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). Quaestiones Entomologicae, 6:4–215.

———, and G. E. Ball. 1972. Classification of the ovipennis and trifaria groups of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini). Proceedings of the Biological Society of Washington, 85:77–108.

Fischer von Waldheim, G. 1820–22. Entomographia imperii russici. I. Moscow. viii + 210 pp.

———. 1825–28. Entomographia imperii russici. III. Moscow. vii + 315 pp.

Friden, A. 1971. Beetle fauna on the borders of some Scandinavian glaciers. Norsk Entomologisk Tidsskrift, 18:29–32.

Greenslade, P. J. M. 1968. Habitat and altitude distribution of Carabidae (Coleoptera) in Argyll, Scotland. Transactions of the Royal Entomological Society of London, 120:39–54.

Hatch, M. H. 1939. A key to the species of *Nebria* of northwestern North America. The Pan-Pacific Entomologist, 15:117–121.

———. 1953. The beetles of the Pacific Northwest. Part I: Introduction and Adephaga. University of Washington Press, Seattle, Publication No. 16. vii + 340 pp.

Horn, G. H. 1870. Descriptive catalogue of the species of *Nebria* and *Pelophila* of the United States. Transactions of the American Entomological Society, 3:97–105.

Horvatovich, S. 1973. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. 306. *Nebria nivalis changaica* ssp. n. aus der Mongolei (Coleoptera: Carabidae). Folia Entomologica Hungarica, Series nova, 26:251–255.

Inger, R. F. 1961. Problems in the application of the subspecies concept in vertebrate taxonomy. Pp. 262–285 *in* W. F. Blair, editor, Vertebrate speciation. Conference on vertebrate speciation, University of Texas, 1958. University of Texas Press, Austin. xvi + 642 pp.

Jeanne, C. 1966. Carabiques de la Peninsule Ibérique. (3' note). Actes de la Société Linnéenne de Bordeaux, 103:3–18.

Jeannel, R. 1937. Notes sur les Carbiques (Première note). Revue Française d'Entomologie, 4:1–23.

———. 1941. Faune de France, 39. Coléoptères Carabiques. Première partie. P. Lechevalier et Fils, Paris, 571 pp.

Kavanaugh, D. H. 1971. A new species of *Nebria* Latreille from Utah. Journal of the Kansas Entomological Society, 44:40–46.

———. 1978. The Nearctic species of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini): classification, phylogeny, zoogeography, and natural history. Unpublished Ph.D. Dissertation. Department of Entomology, University of Alberta. xlviii + 1041 pp.

———, and E. A. Martinko. 1972. Notes on distribution and a peculiar behavior pattern in *Nebria purpurata* LeConte (Coleoptera: Carabidae). The Coleopterists Bulletin, 26:147–149.

Kirby, W. 1837. Part 4. The insects. [xxxix + 325 pp.] *In* J. Richardson, Fauna Boreali-Americana; or the zoology of the northern parts of British America. Josiah Fletcher, Norwich and London.

Larochelle, A. 1972. Notes sur les périodes d'accouplement de quelques Carabidae du Québec. Le Naturaliste Canadien, 99:61–63.

———. 1976. Dates of egg-production in some carabid beetles (Coleoptera: Carabidae) from Québec. Cordulia, 2:47–49.

———. 1977. A list of teneral carabid beetles (Coleoptera: Carabidae) from Québec and their dates of capture. Cordulia, 3:109–113.

Larson, D. J. 1975. The predaceous water beetles (Coleoptera: Dytiscidae) of Alberta: systematics, natural history and distribution. Quaestiones Entomologicae, 11:245–498.

LeConte, J. L. 1850. General remarks upon the Coleoptera of Lake Superior. Pp. 201–242 *in* J. L. R. Agassiz, Lake Superior, Natural History 4. Gould, Kendall, and Lincoln, Boston. x + 248 pp. + 8 plates.

———. 1853. Notes on the classification of the Carabidae of the United States. Transactions of the American Philosophical Society (new series), 10:363–403.

———. 1859. Catalogue of the Coleoptera of Fort Tejon, California. Proceedings of the Academy of Natural Sciences of Philadelphia, 11:69–90.

———. 1863a–66a. List of the Coleoptera of North America. Smithsonian Miscellaneous Collections, No. 140, 6:1–49 (1863), 50–70 (1866).

———. 1863b–66b. New species of North American Coleoptera, Part 1, Smithsonian Miscellaneous Collections, No. 167, 6:1–86 (1863), 87–168 (1866).

———. 1866c. Additions to the coleopterous fauna of the United States. I. Proceedings of the Academy of Natural Sciences of Philadelphia, 1866:361–394.

———. 1878. The Coleoptera of the alpine regions of the Rocky Mountains. Bulletin of the United States Geological and Geographical Survey of the Territories, 4:447–480.

Leng, C. W. 1920. Catalogue of the Coleoptera of America, North America. John D. Sherman, Mount Vernon, New York. x + 470 pp.

Lindroth, C. H. 1939. Zur Systematik fennoskandischer Carabiden. 2. *Nebria nivalis* Payk. und *gyllenhali* Schönh. Entomologisk Tidskrift, 60:54–62.

———. 1954. Random notes on North American Carabidae. Bulletin of the Museum of Comparative Zoology, 111:117–161.

———. 1955a. The carabid beetles of Newfoundland including the French islands St. Pierre and Miquelon. Opuscula Entomologica, Supplement 12. 160 pp. + 9 plates.

———. 1955b. Dejean's types of North American Carabidae. Opuscula Entomologica, 20:10–34.

———. 1961. The ground-beetles of Canada and Alaska, Part 2. Opuscula Entomologica, Supplement 20. Pp. 1–200.

———. 1969a. The theory of glacial refugia in Scandinavia. Comments on present opinions. Notulae Entomologicae, 49:178–192.

———. 1969b. The ground-beetles of Canada and Alaska, Part 6. Opuscula Entomologica, Supplement 35. Pp. 945–1192.

———. 1971. On the occurrence of a continental element in the ground-beetle fauna of eastern Canada (Coleoptera: Carabidae). The Canadian Entomologist, 103:1455–1462.

———. 1975. Designation of holotypes and lectotypes among ground beetles (Coleoptera, Carabidae) described by Thomas L. Casey. The Coleopterists Bulletin, 29:109–147.

———, and R. Freitag. 1969. North American ground-beetles (Coleoptera, Carabidae, excluding Cicindelinae) described by Thomas Say: designation of lectotypes and neotypes. Psyche, 76:326–361.

Linnaeus, C. 1758. Systema naturae. Tenth edition. Part 1. Stockholm. 824 pp.

Luff, M. L. 1972. The larvae of the British Carabidae (Coleoptera) II. Nebriini. The Entomologist, 105:161–179.

———, and L. Davies. 1972. Ecological observations on some Carabidae (Col.) from St. Kilda, with notes on other beetles new to the island. The Entomologist's Monthly Magazine, 108:46–51.

Madge, R. B. 1967. A revision of the genus *Lebia* Latreille in America north of Mexico (Coleoptera, Carabidae). Quaestiones Entomologicae, 3:139–244.

Mank, E. W. 1934. The Coleoptera of Glacier Park, Montana. The Canadian Entomologist, 66:73–81.

Mannerheim, C. G. 1843. Beitrag zur Kaefer-Fauna der Aleutischen Inseln, der Insel Sitkha und Neu-Californiens. Bulletin de la Société Impériale des Naturalistes de Moscou, 16:175–314.

———. 1853. Dritter Nachtrag zur Kaefer-Fauna der nordamerikanischen Laender des russischen Reiches. Bulletin de la Société Impériale des Naturalistes de Moscou, 26:96–273.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York. xi + 428 pp.

Ménétriés, M. 1844. Sur un envoi d'Insectes de la côte N. O. d'Amérique. Bulletin de la Classe Physico-Mathématique de l'Académie Impériale des Sciences de Saint-Petersbourg, 2:50–63.

Motschulsky, V. 1850. Die Kaefer Russlands. I. Insecta Carabica. Gautier, Moscow. vii + 91 pp.

———. 1865. Enumération des nouvelles espèces de Coléoptères. IV. Bulletin de la Société Impériale des Naturalistes de Moscou, 38:227–380.

Munster, T. 1933. Tillaeg og Bemaekninger til Norges Koleopterfauna. III. Norsk Entomologisk Tidsskrift, 3:267–278.

Nakane, T. 1963. Carabidae. Pp. 5–52 and plates 3–26 *in* Iconographia insectorum Japonicorum colore naturali edita. II. (Coleoptera). Hokurykan, Tokyo.

———. 1971. Notes on the Coleoptera from the alpine zone of the Daisetsu Mountains. Pp. 179–183 *in* Faunal Survey of the Mt. Daisetsu area, JIBP Main area—XII. Annual Report of JIBP–CTS for Fiscal Year 1970.

Noonan, G. R. 1973. The anisodactylines (Insecta: Coleoptera: Carabidae: Harpalini): classification, evolution, and zoogeography. Quaestiones Entomologicae, 9:266–480.

Paykull, G. 1790. Monographia Caraborum Sueciae. J. Edman, Uppsala. 138 pp.

———. 1798. Fauna Suecica. Insecta. I. Uppsala. x + 234 pp.

Reitter, E. 1908. Fauna Germanica. Die Käfer des deutschen Reiches. I. Stuttgart. viii + 248 pp.

Say, T. 1823. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille inhabiting United States. Transactions of the American Philosophical Society, new series, 2:1–109.

Schönherr, C. J. 1806. Synonymia insectorum, oder: Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum geordnet. I. H. A. Nordstrom, Stockholm. xii + 293 pp.

Schøyen, W. M. 1880. Coleopterologiske notitser. Entomologisk Tidskrift (Stockholm), 1:177–185.

Simpson, G. G. 1961. Principles of animal taxonomy. Columbia University Press, New York. xii + 247 pp.

Strøm, H. 1768. Beskrivelse over Norske insecter. II. Det Kongelige Norske Videnskabers Selskab Skrifter, 4:313–371.

Sturm, J. 1826. Catalog meiner Insecten-Sammlung, erster Theil, Käfer. Nürnberg. 207 pp. + 4 plates.

———. 1843. Catalog der Käfersammlung von Jacob Sturm. Nürnberg. xiii + 386 pp. + 6 plates.

Ueno, S.-I. 1953. Carabidae. Shin Konchu (Tokyo), 6:52–60.

———. 1955. Two new species of the genus *Nebria*. The Entomological Review of Japan, 6:45–50.

Van Dyke, E. C. 1919. The distribution of insects in western North America. Annals of the Entomological Society of America, 12:1–12.

———. 1925. Studies of western North American Carabinae with descriptions of new species. The Pan-Pacific Entomologist, 1:111–125.

———. 1926. Certain peculiarities of the coleopterous insect fauna of the Pacific Northwest. Annals of the Entomological Society of America, 19:1–12.

Whitehead, D. R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). Quaestiones Entomologicae, 8:131–348.

———. 1976. Classification and evolution of *Rhinochenus* Lucas (Coleoptera: Curculionidae: Cryptorhynchinae), and Quaternary Middle American zoogeography. Quaestiones Entomologicae, 12:118–201.

Wickham, H. F. 1902. A catalogue of the Coleoptera of Colorado. Bulletin from the Laboratories of Natural History of the State University of Iowa, 5:217–310.

Wilson, E. O., and W. L. Brown, Jr. 1953. The subspecies concept and its taxonomic application. Systematic Zoology, 2:97–111.

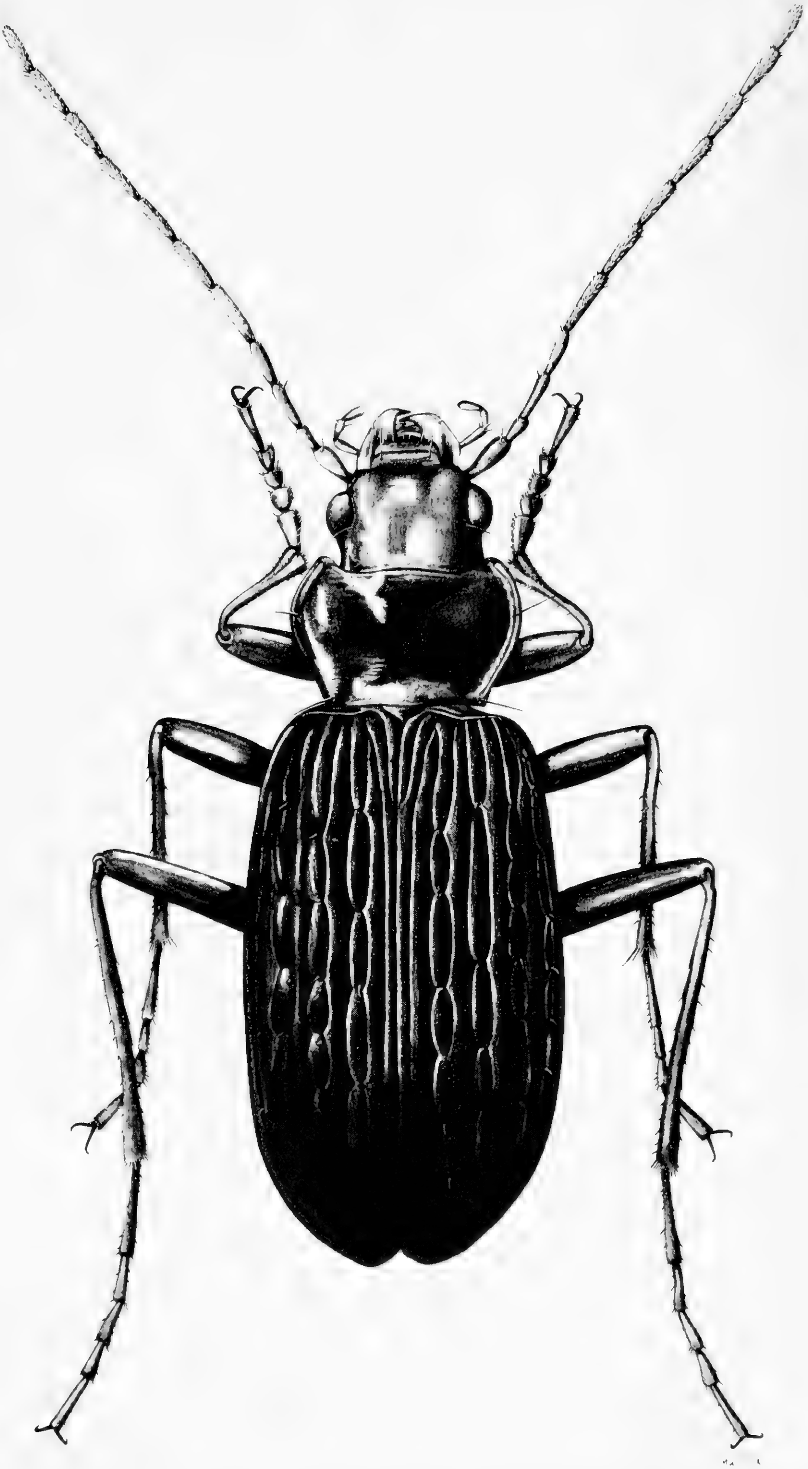
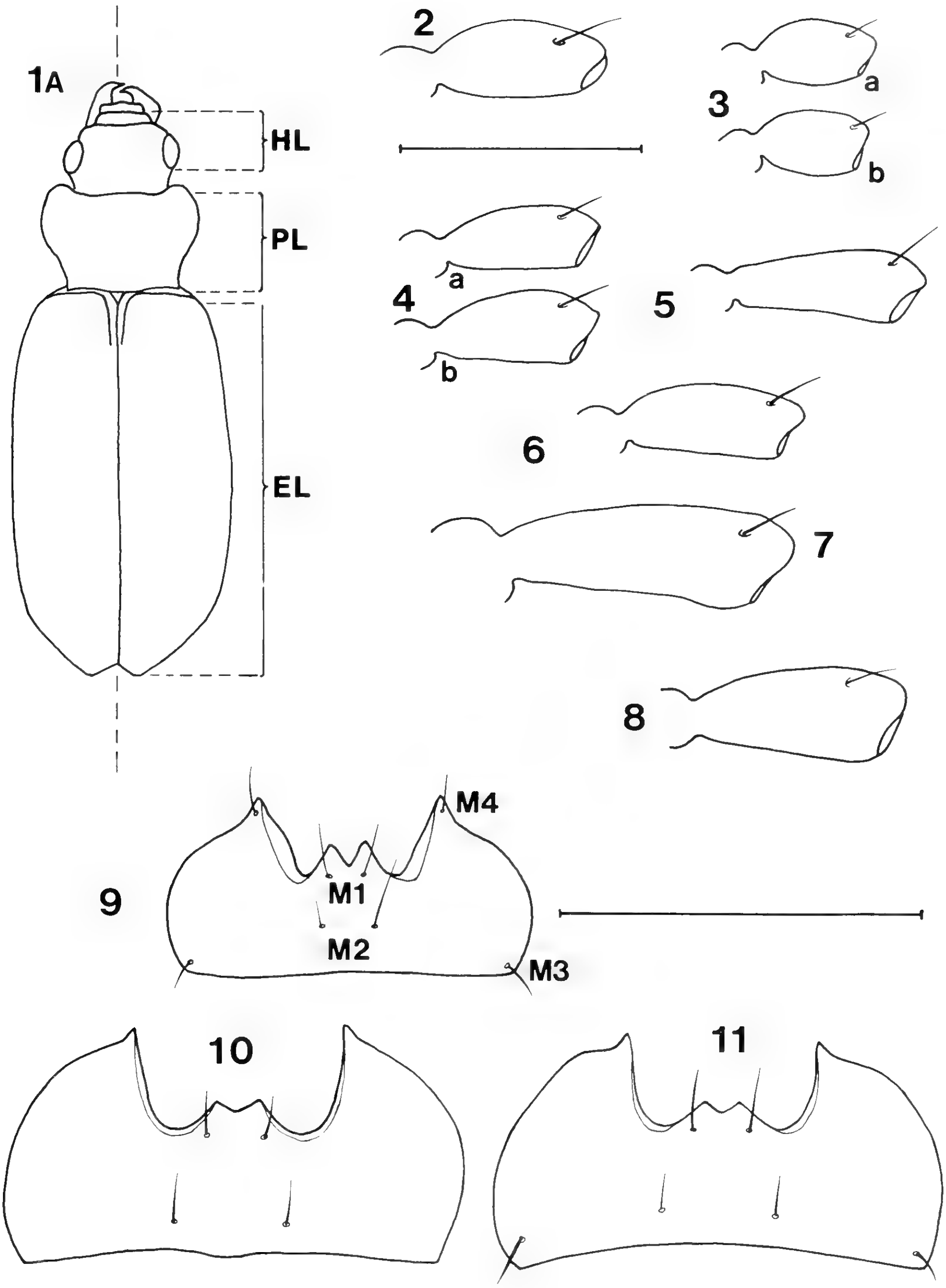
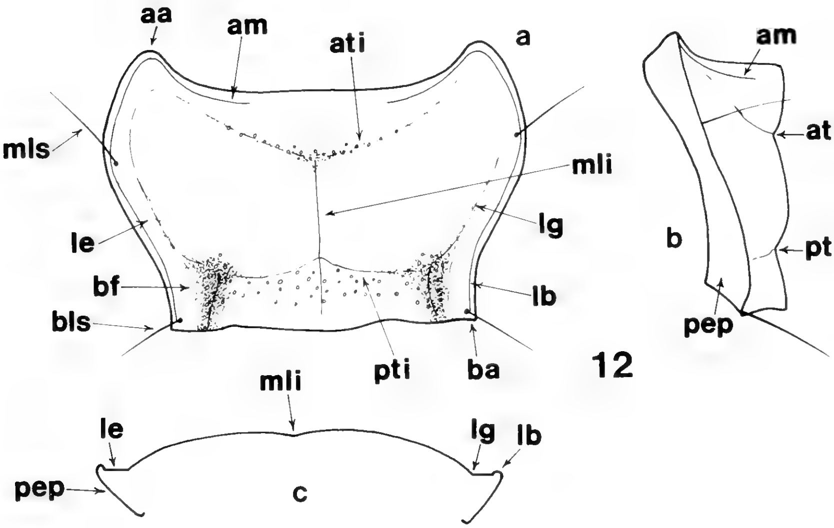


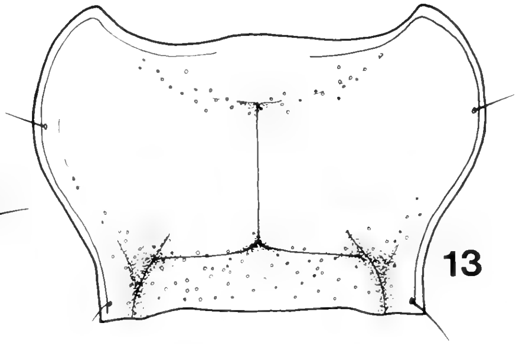
FIGURE 1. *Nebria schwarzi beverlianna*, new subspecies: adult male, dorsal aspect (approximately 6 times actual size). (Illustration by C. L. Mullinex.)



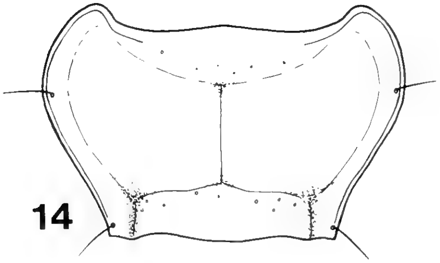
FIGURES 1–11. Fig. 1. Components of "standardized body length" measurement: HL = head length; PL = pronotal length; EL = elytral length. Figs. 2–8. Right antennal scape, dorsal aspect. 2. *Nebria gouleti* n.sp. (Underwood, Washington). 3. *Nebria gyllenhali lassenensis* n.ssp. (a. Mount Lassen, California; b. Todd Lake, Oregon). 4. *Nebria gyllenhali lindrothi* n.ssp. (a. Brooklyn Lake, Wyoming; b. Rio Puerco, New Mexico). 5. *Nebria zioni oasis* n.ssp. (Pine Valley Mountains, Utah). 6. *Nebria spatulata sierrae* n.ssp. (Big Horn Lake, California). 7. *Nebria vandykei wyeast* n.ssp. (Mount Hood, Oregon). 8. *Nebria trifaria utahensis* n.ssp. (Henry Mountains, Utah). Figs. 9–11. Mentum, ventral aspect. 9. General form and chaetotaxy; M_1 through M_4 are designations for specific pairs of setae. 10. *Nebria carri* n.sp. (Dollarhide Summit, Idaho). 11. *Nebria kincaidi balli* n.ssp. (Mount Hood, Oregon). All scale lines equal 1.0 mm.



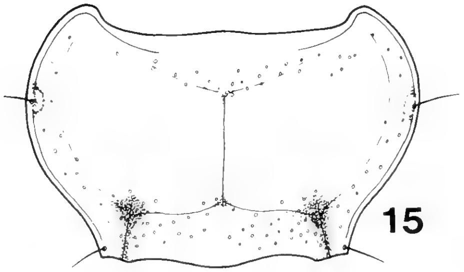
12



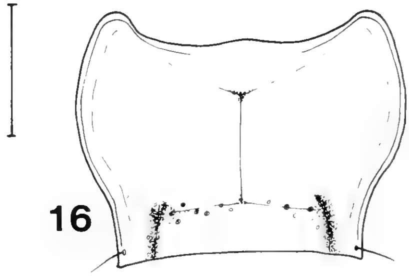
13



14

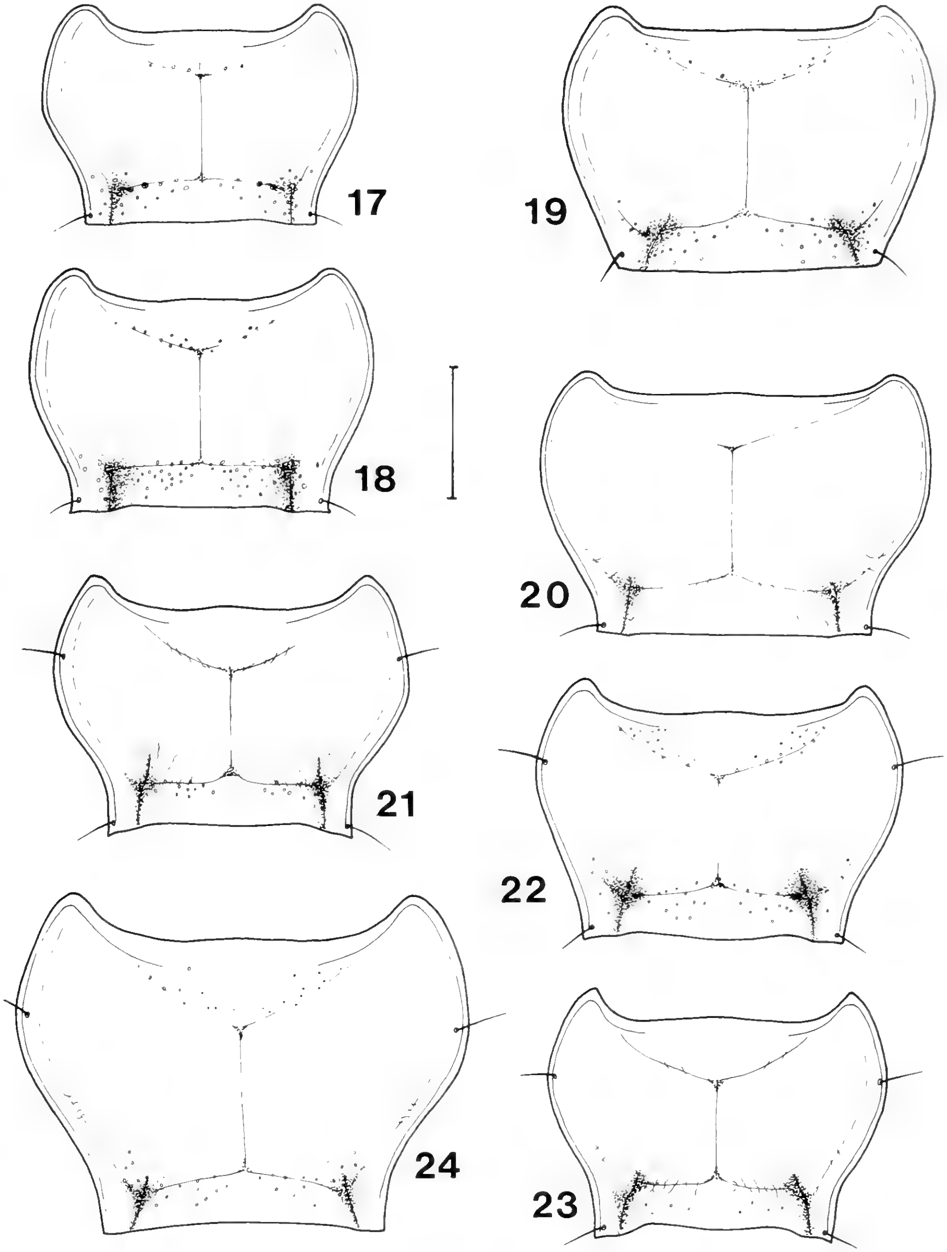


15

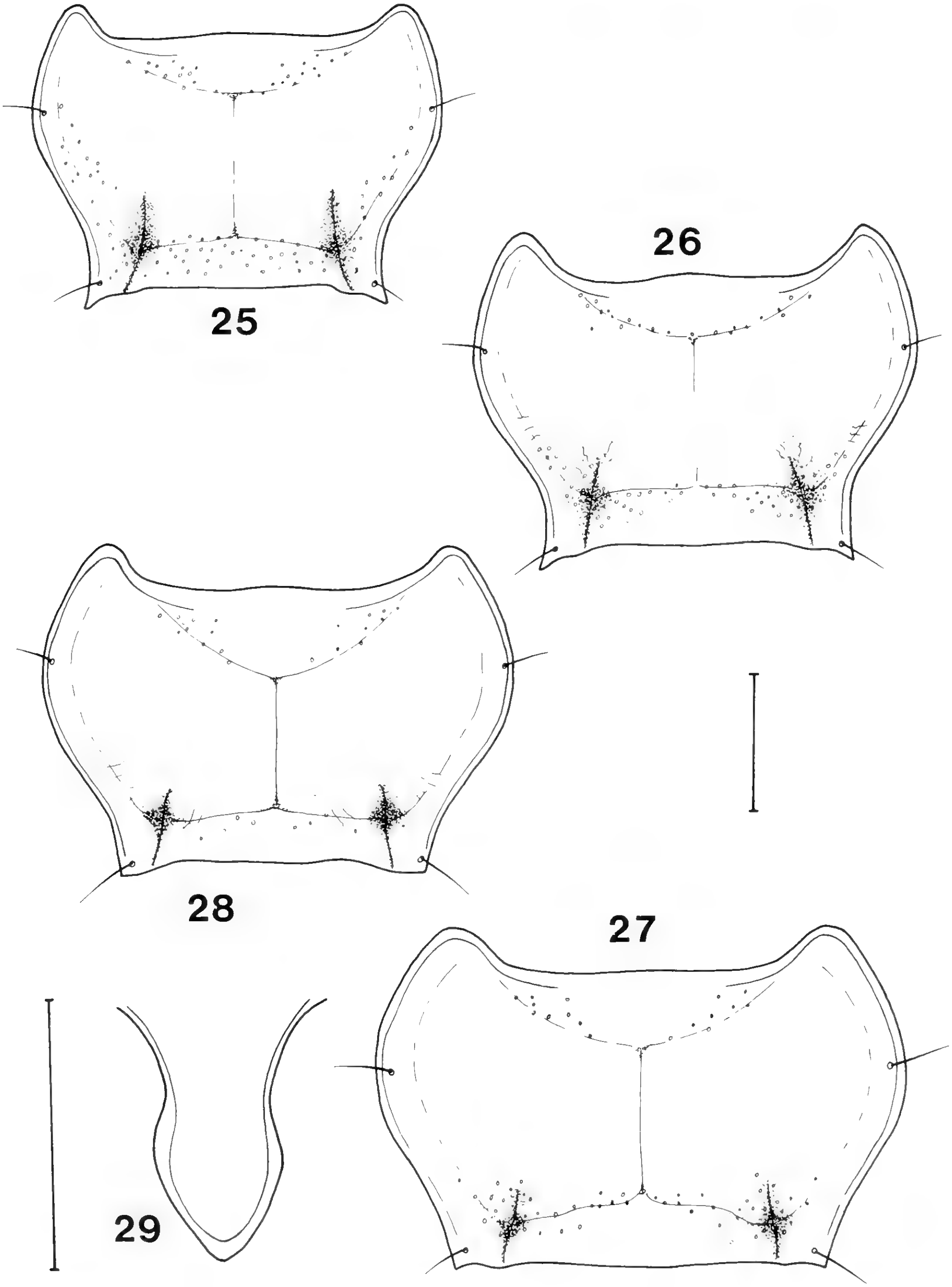


16

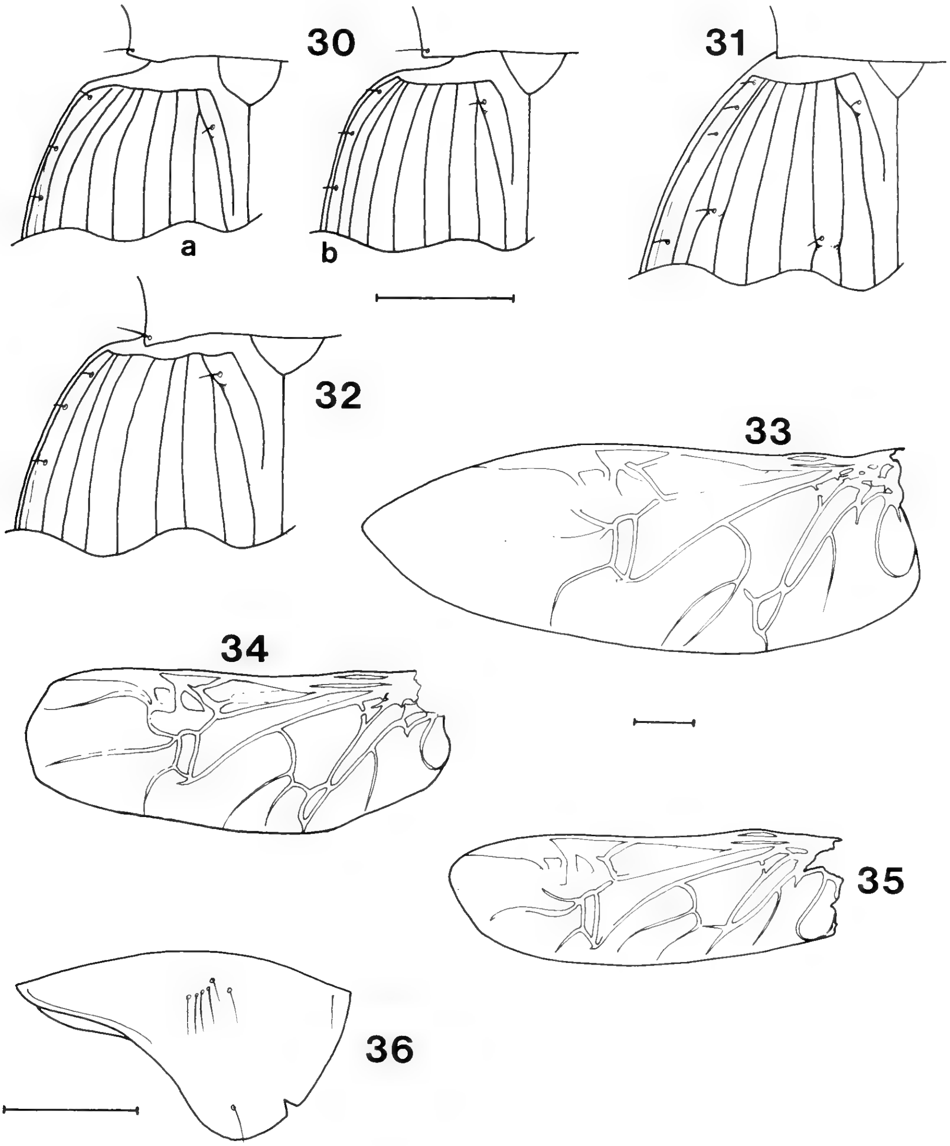
FIGURES 12–16. Fig. 12. Pronotum, general form and associated terms (a. dorsal aspect; b. left lateral aspect; c. cross-sectional aspect); abbreviation code: *aa* = apical angle; *am* = apical margination; *ati* = anterior transverse impression; *ba* = basal angle; *bf* = basal fovea; *bls* = basolateral seta; *lb* = lateral bead (= lateral margination); *le* = lateral explanation; *lg* = lateral groove; *mli* = median longitudinal impression; *mls* = midlateral seta; *pep* = proepipleuron; *pti* = posterior transverse impression. Figs. 13–16. Pronotum, dorsal aspect. 13. *Nebria gouleti* n.sp. (Salmon River, Idaho). 14. *Nebria lacustris bellorum* n.ssp. (Great Balsam Mountains, North Carolina). 15. *Nebria nivalis gaspesiana* n.ssp. (Mont Albert, Québec). 16. *Nebria acuta quileute* n.ssp. (Olympic Hot Springs, Washington). Scale line equals 1.0 mm.



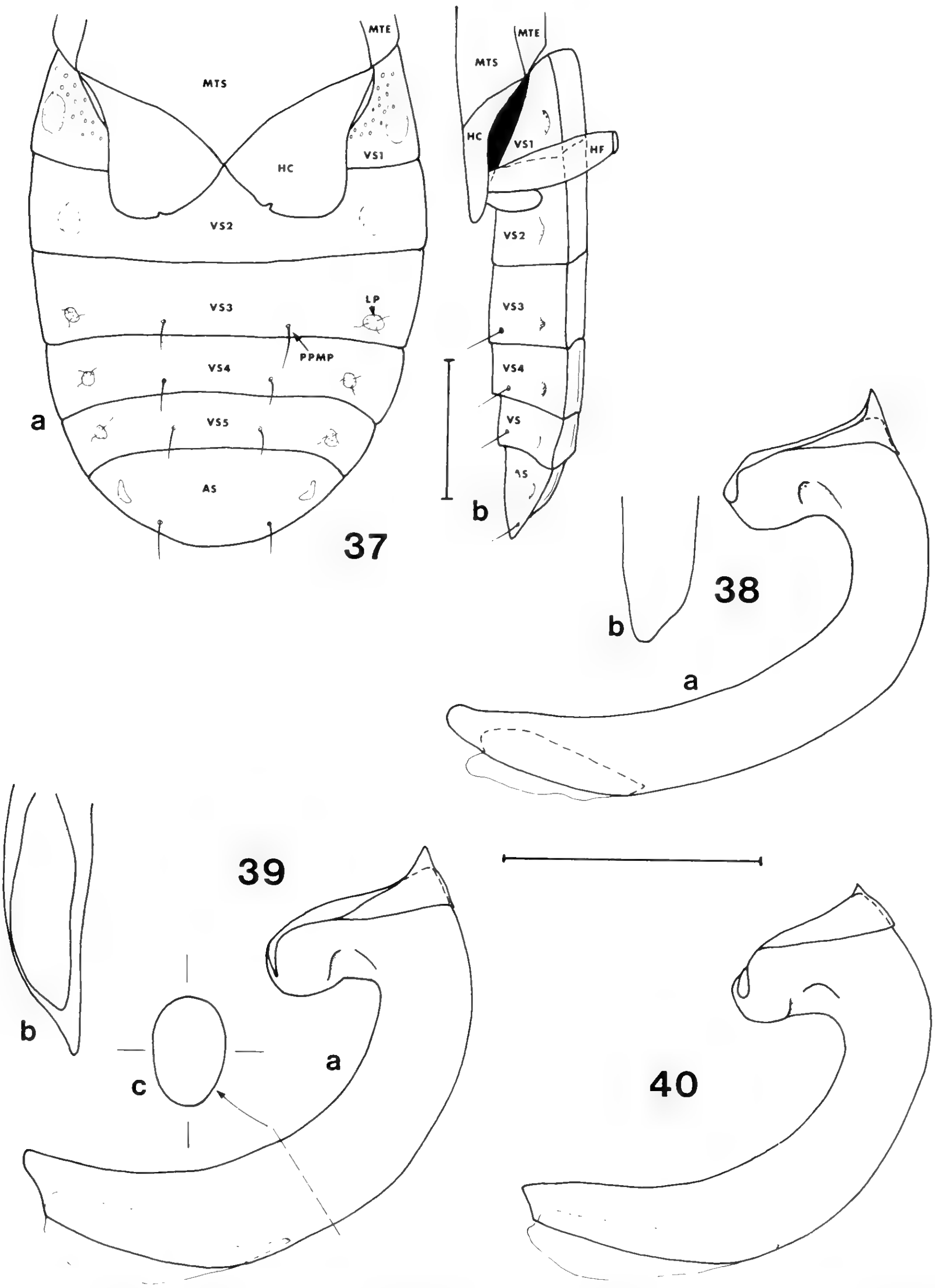
FIGURES 17–24. Pronotum, dorsal aspect. 17. *Nebria sahlbergii modoc* n.ssp. (Warner Mountains, California). 18. *Nebria sahlbergii triad* n.ssp. (Trinity Alps, California). 19. *Nebria obliqua chuskae* n.ssp. (Chuska Mountains, Arizona). 20. *Nebria darlingtoni* n.sp. (Kyburz, California). 21. *Nebria gebleri cascadensis* n.ssp. (Glacier, Washington). 22. *Nebria gebleri fragariae* n.ssp. (Strawberry Mountains, Oregon). 23. *Nebria gebleri siskiyouensis* n.ssp. (Trinity Alps, California). 24. *Nebria carri* n.sp. (Dollarhide Summit, Idaho). Scale line equals 1.0 mm.



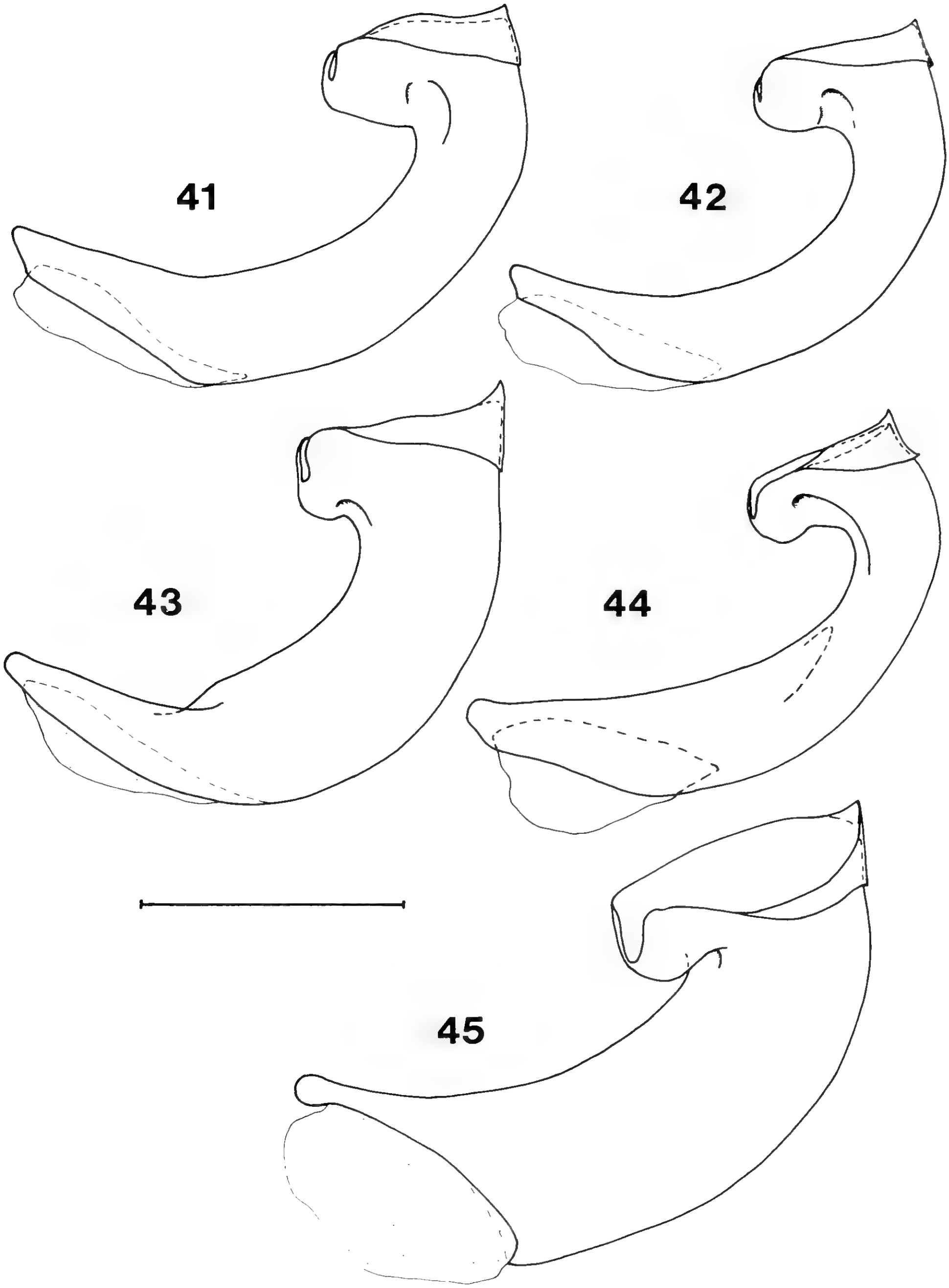
FIGURES 25–29. Figs. 25–28. Pronotum, dorsal aspect. 25. *Nebria meanyi lamarckensis* n.ssp. (Upper Lamarck Lake, California). 26. *Nebria meanyi sylvatica* n.ssp. (Olympic Hot Springs, Washington). 27. *Nebria schwarzi beverlianna* n.ssp. (Hoback River, Wyoming). 28. *Nebria trifaria utahensis* n.ssp. (Henry Mountains, Utah). Fig. 29. Prosternal intercoxal process, *Nebria lituyae* n.sp. (Mount Blunt, Lituya Bay, Alaska). All scale lines equal 1.0 mm.



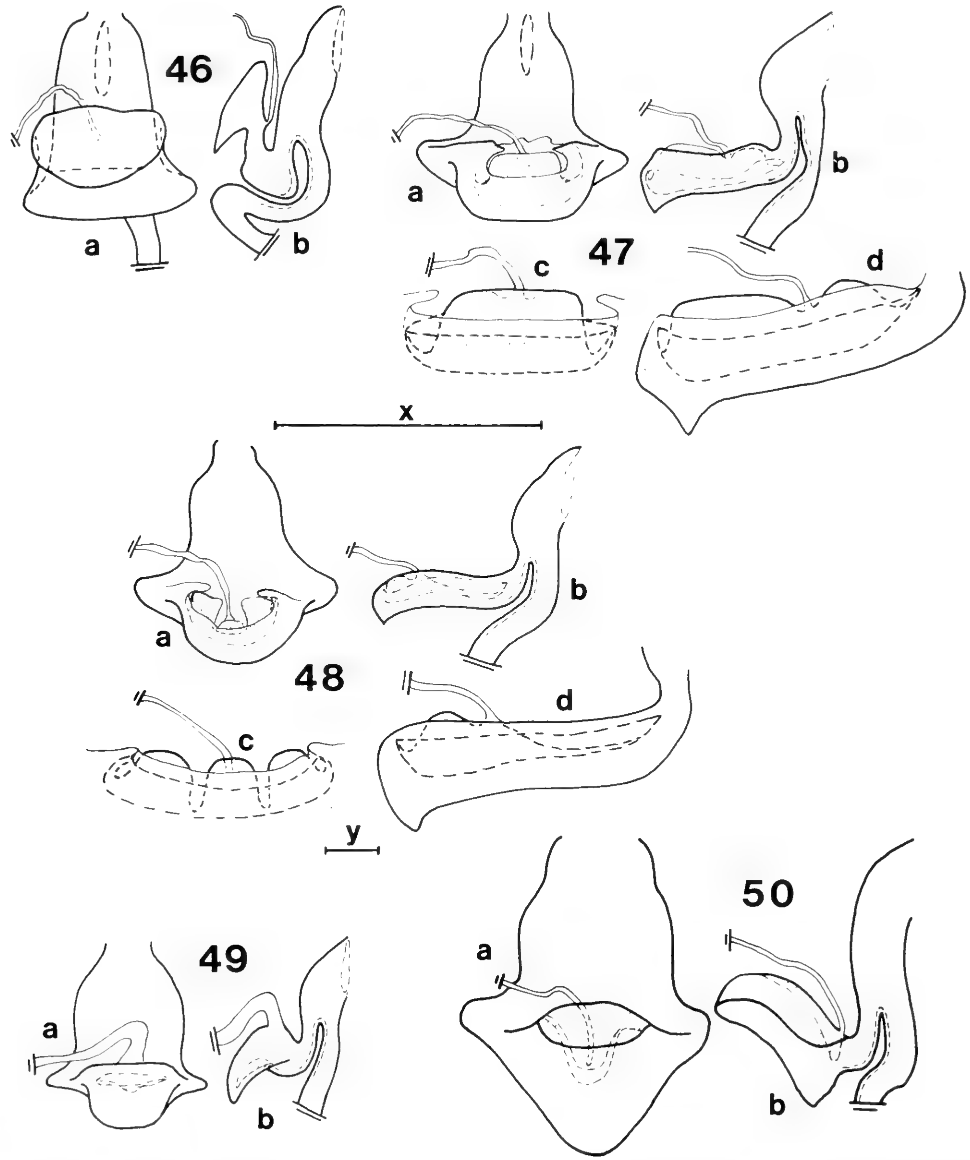
FIGURES 30–36. Figs. 30–32. Basal region of left elytron, dorsal aspect. 30. *Nebria arkansana edwardsi* n.ssp. (a. Rancheria, Yukon Territory; b. Gorge Creek, Alberta). 31. *Nebria kincaidi balli* n.ssp. (Mount Rainier, Washington). 32. *Nebria meanyi lamarckensis* n.ssp. (Upper Lamarck Lake, California). Figs. 33–35. Left hindwing. 33. Full-sized wing, *Nebria arkansana edwardsi* n.ssp. (Logan Pass, Montana). 34. Wing reduced in length, *Nebria obliqua chuskae* n.ssp. (Chuska Mountains, Arizona). 35. Wing reduced in length and width, *Nebria arkansana uinta* n.ssp. (Logan River, Utah). Fig. 36. Right hind coxa, ventral aspect, *Nebria schwarzi beverlianna* n.ssp. (Hoback River, Wyoming). All scale lines equal 1.0 mm.



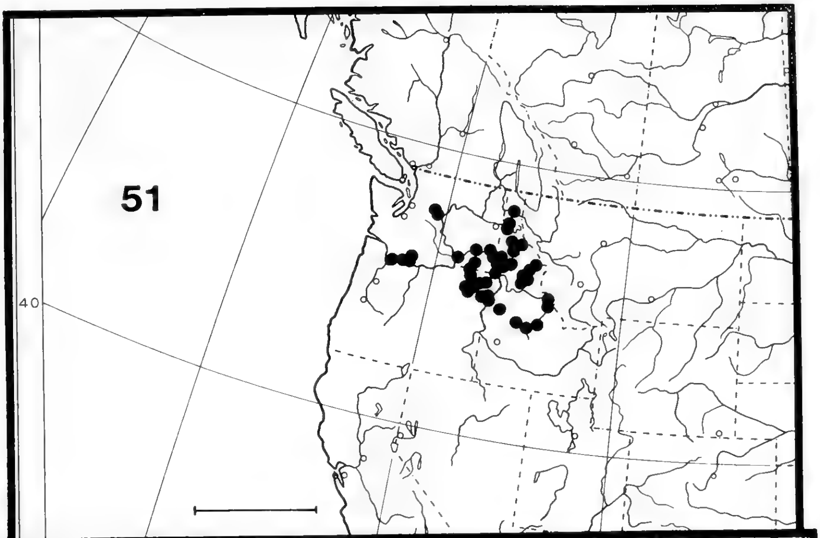
FIGURES 37–40. Fig. 37. Abdominal venter, form and associated terms (a. ventral aspect; b. left lateral aspect); abbreviation code: *AS* = anal sternum; *HC* = hind coxa; *HF* = hind femur; *LP* = lateral pit; *MTE* = metepisternum; *MTS* = metasternum; *PPMP* = posterior paramedial puncture and associated seta; *VS1* to *VS5* = first to fifth visible abdominal sterna. Figs. 38–40. Median lobe of male genitalia. 38. *Nebria acuta quileute* n.ssp. (Olympic Hot Springs, Washington) (a. left lateral aspect; b. ventral aspect, apical region only). 39. *Nebria arkansana edwardsi* n.ssp. (Yoho National Park, British Columbia) (a. left lateral aspect; b. dorsal aspect, apical region only; c. cross section at middle of shaft). 40. *Nebria arkansana oowah* n.ssp. (La Sal Mountains, Utah) (left lateral aspect). All scale lines equal 1.0 mm.

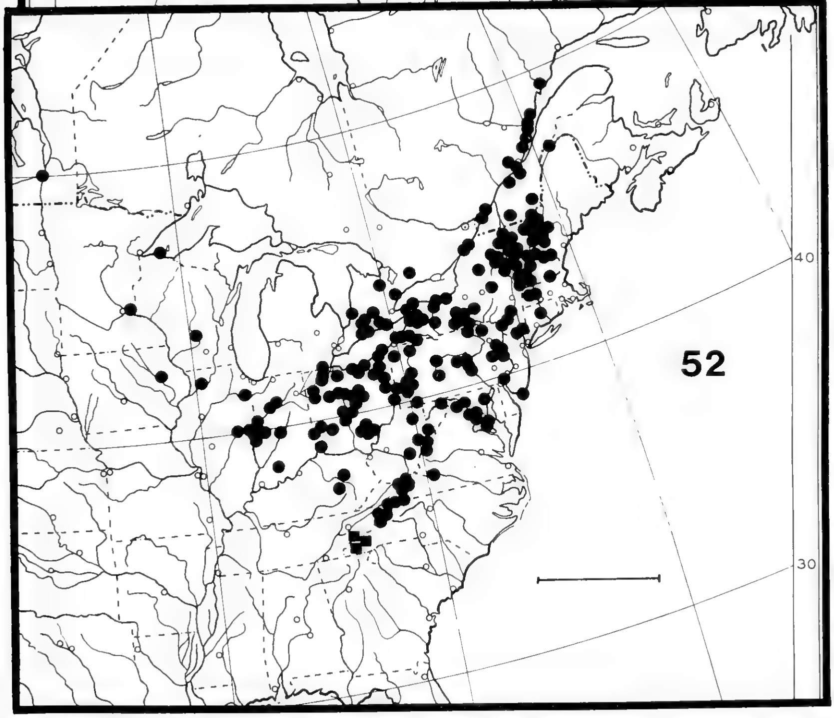


FIGURES 41–45. Median lobe of male genitalia, left lateral aspect. 41. *Nebria arkansana uinta* n.ssp. (Logan River, Utah). 42. *Nebria fragilis teewinot* n.ssp. (Mount Teewinot, Wyoming). 43. *Nebria navajo* n.sp. (19 miles [ca. 31 km] sw of Kayenta, Arizona). 44. *Nebria gebleri fragariae* n.ssp. (Strawberry Mountains, Oregon). 45. *Nebria trifaria utahensis* n.ssp. (Henry Mountains, Utah). Scale line equals 1.0 mm.

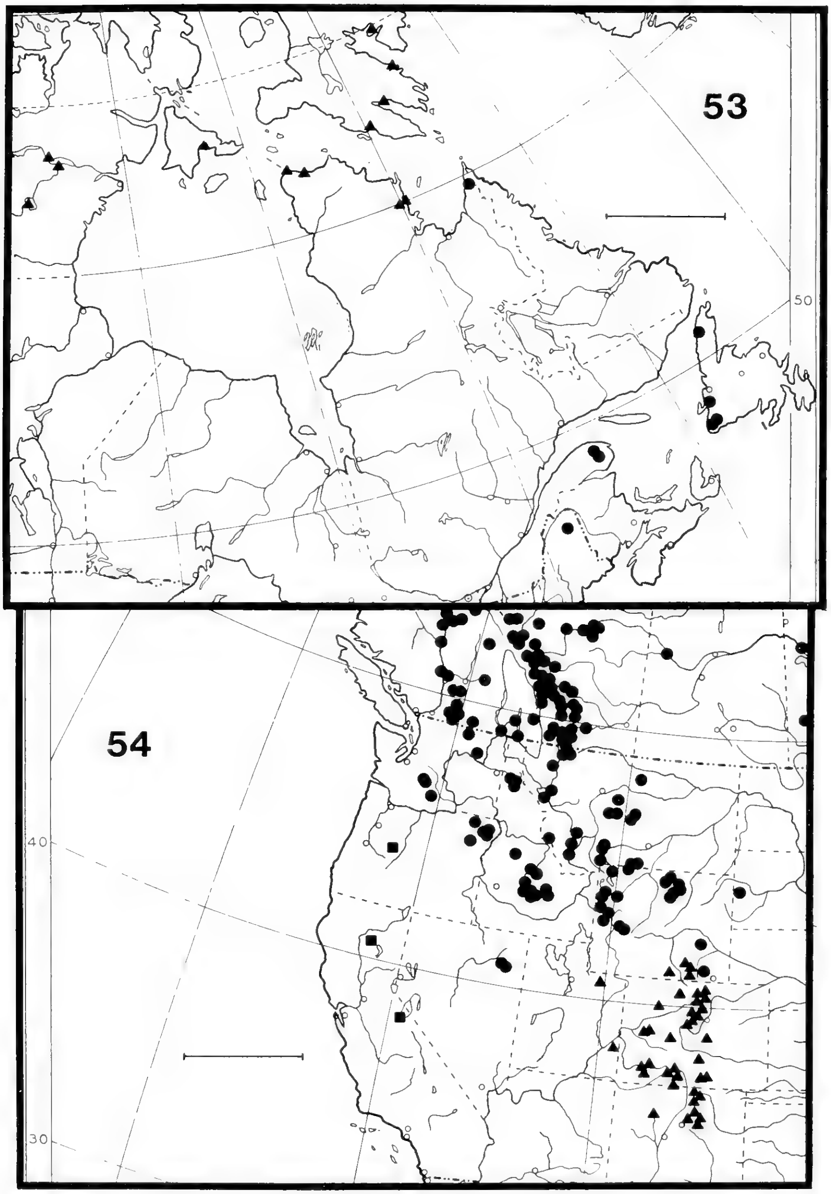


FIGURES 46–50. Bursa copulatrix (a. dorsal aspect; b. left lateral aspect; c. bursal sclerite enlarged, dorsal aspect; d. bursal sclerite enlarged, left lateral aspect); in a. or b., stippled area denotes shape and location of distinct sclerite or moderately to markedly sclerotized, but less clearly defined, area; in c. or d., stippled area denotes weakly sclerotized membrane, sclerite is not stippled. 46. *Nebria acuta quileute* n.ssp. (Olympic Hot Springs, Washington). 47. *Nebria arkansana edwardsi* n.ssp. (Amiskwi Falls, British Columbia). 48. *Nebria arkansana oowah* n.ssp. (La Sal Mountains, Utah). 49. *Nebria gebleri fragariae* n.ssp. (Strawberry Mountains, Oregon). 50. *Nebria trifaria utahensis* n.ssp. (Henry Mountains, Utah). Scale line "x" equals 1.0 mm and applies to all figures "a" and "b." Scale line "y" equals 0.10 mm and applies to all figures "c" and "d."

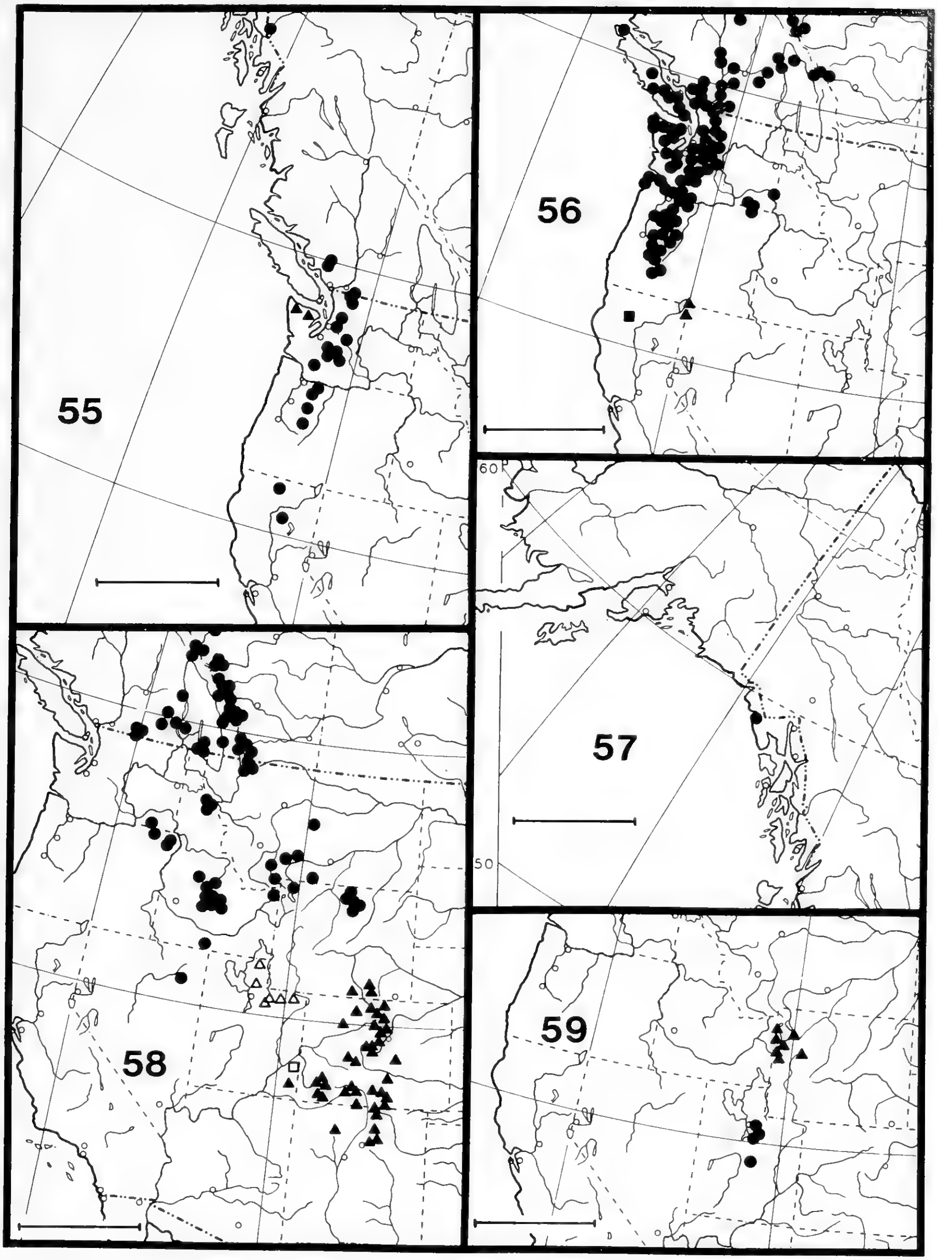




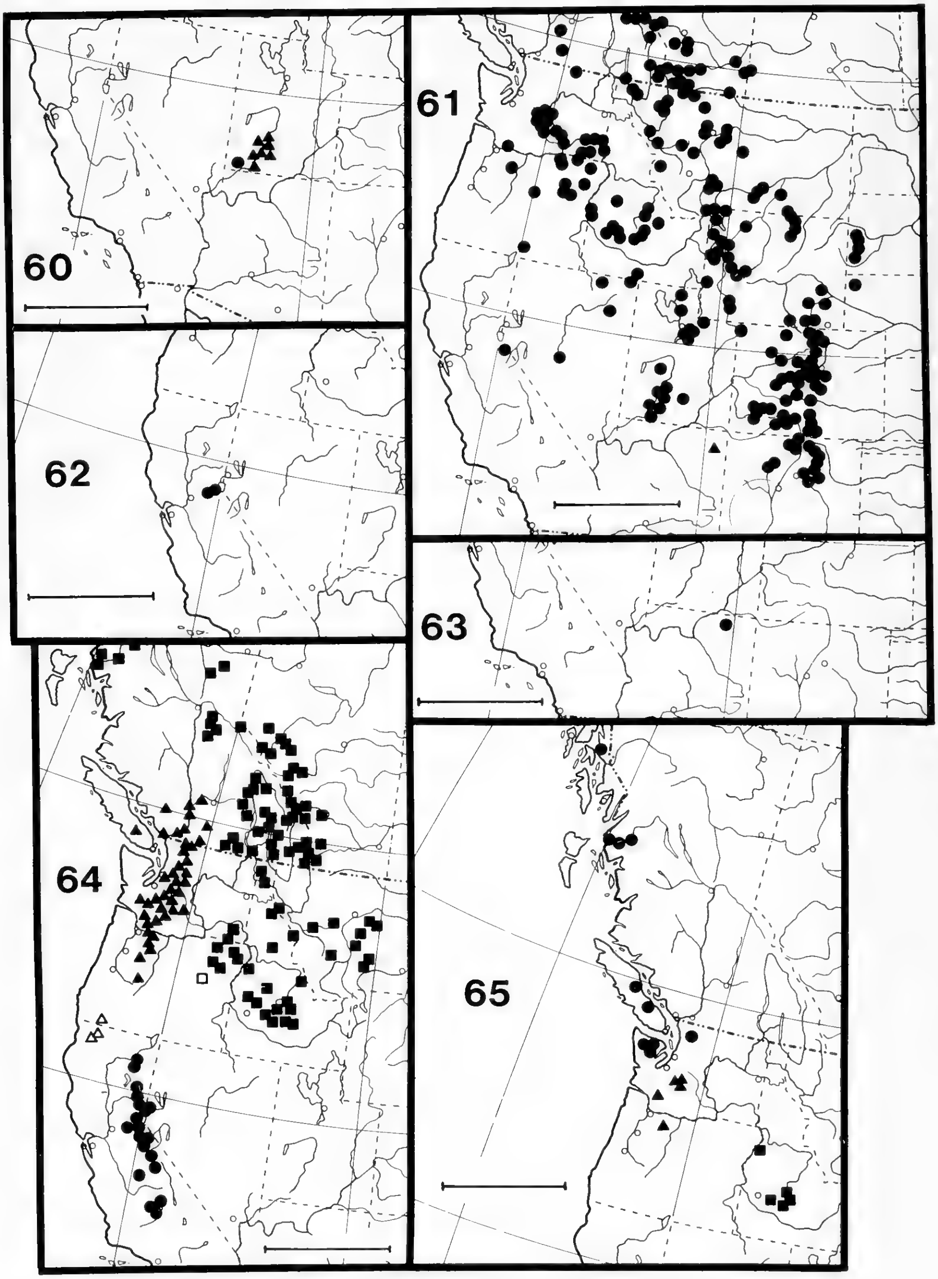
FIGURES 51–52. Geographical distribution maps. 51. *Nebria gouleti n.sp.* 52. *Nebria lacustris* Casey [*N. lacustris lacustris* = solid circles; *N. lacustris bellorum* n.ssp. = solid squares]. All scale lines equal 500 km.



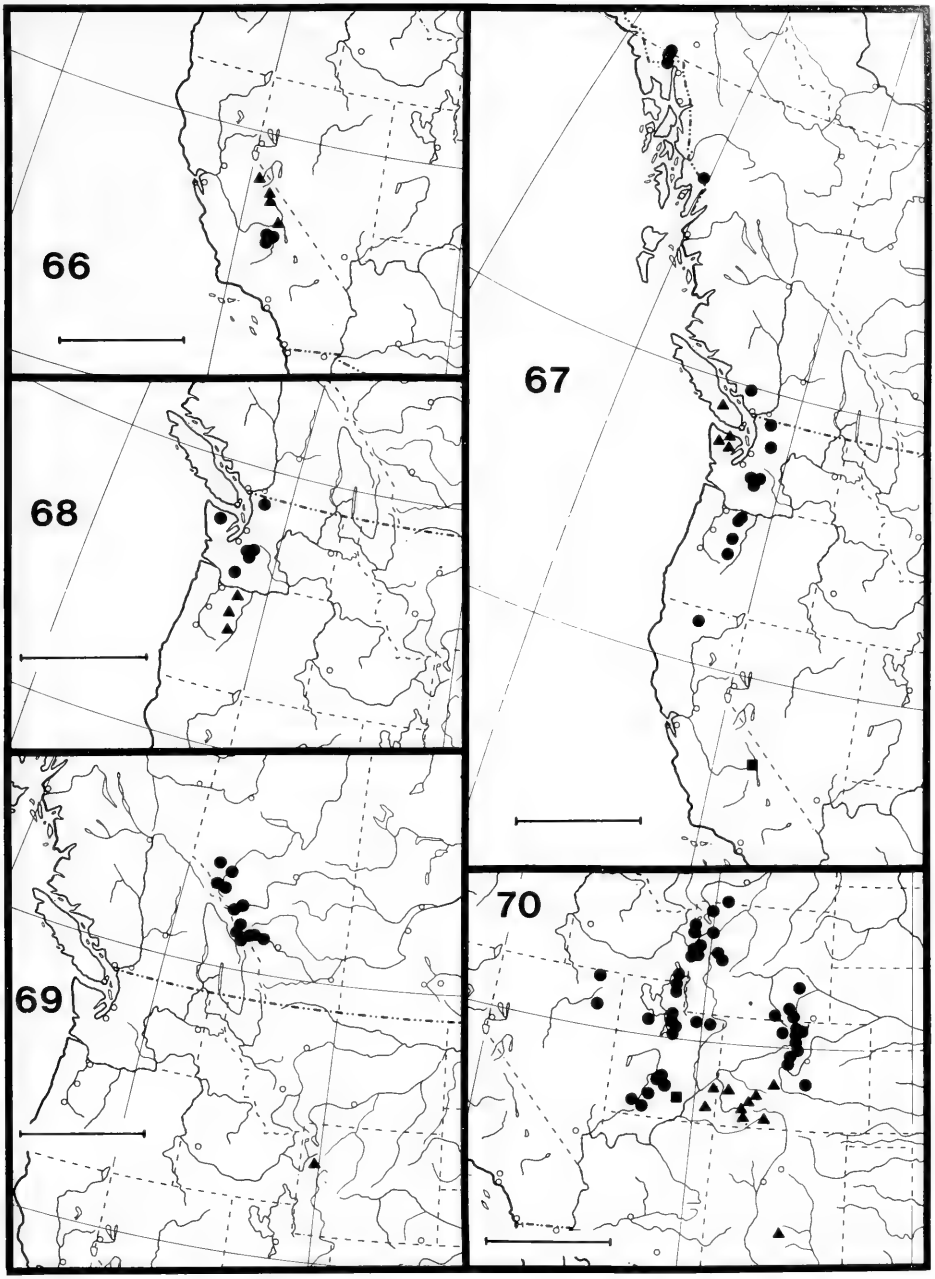
FIGURES 53–54. Geographical distribution maps. 53. *Nebria nivalis* (Paykull) [*N. nivalis nivalis* = solid triangles; *N. nivalis gaspesiana* n.ssp. = solid circles]. 54. *Nebria gyllenhali* (Schönherr) [*N. gyllenhali castanipes* (Kirby) = solid circles; *N. gyllenhali lassenensis* n.ssp. = solid squares; *N. gyllenhali lindrothi* n.ssp. = solid triangles]. All scale lines equal 500 km.



FIGURES 55–59. Geographical distribution maps. 55. *Nebria acuta* Lindroth [*N. acuta acuta* = solid circles; *N. acuta quileute* n.ssp. = solid triangles]. 56. *Nebria sahlbergii* Fischer von Waldheim [*Nebria sahlbergii sahlbergii* = solid circles; *N. sahlbergii modoc* n.ssp. = solid triangles; *N. sahlbergii triad* n.ssp. = solid square]. 57. *Nebria lituyae* n.sp. 58. *Nebria arkansana* Casey [*N. arkansana arkansana* = solid triangles; *N. arkansana edwardsi* n.ssp. = solid circles; *N. arkansana oowah* n.ssp. = open square; *N. arkansana uinta* = open triangles]. 59. *Nebria fragilis* Casey [*N. fragilis fragilis* = solid circles; *N. fragilis teewinot* n.ssp. = solid triangles]. All scale lines equal 500 km.



FIGURES 60–65. Geographical distribution maps. 60. *Nebria zioni* Van Dyke [*N. zioni zioni* = solid triangles; *N. zioni oasis* n.ssp. = solid circle]. 61. *Nebria obliqua* LeConte [*N. obliqua obliqua* = solid circles; *N. obliqua chuskae* n.ssp. = solid triangle]. 62. *Nebria darlintoni* n.sp. 63. *Nebria navajo* n.sp. 64. *Nebria gebleri* Dejean [*N. gebleri gebleri* = solid squares; *N. gebleri cascadensis* n.ssp. = solid triangles; *N. gebleri fragariae* n.ssp. = open square; *N. gebleri rathvoni* LeConte = solid circles; *N. gebleri siskiyouensis* = open triangles]. 65. *Nebria carri* n.sp. [solid squares] and *Nebria kincaidi* Schwarz [*N. kincaidi kincaidi* = solid circles; *N. kincaidi balli* n.ssp. = solid triangles]. All scale lines equal 500 km.



FIGURES 66–70. Geographical distribution maps. 66. *Nebria spatulata* Van Dyke [*N. spatulata spatulata* = solid circles; *N. spatulata sierrae* n.ssp. = solid triangles]. 67. *Nebria meanyi* Van Dyke [*N. meanyi meanyi* = solid circles; *N. meanyi lamarckensis* n.ssp. = solid square; *N. meanyi sylvatica* n.ssp. = solid triangles]. 68. *Nebria vandykei* Bänninger [*N. vandykei vandykei* = solid circles; *N. vandykei wyeast* n.ssp. = solid triangles]. 69. *Nebria schwarzi* Van Dyke [*N. schwarzi schwarzi* = solid circles; *N. schwarzi beverlianna* n.ssp. = solid triangle]. 70. *Nebria trifaria* LeConte [*N. trifaria trifaria* = solid circles; *N. trifaria catenata* Casey = solid triangles; *N. trifaria utahensis* n.ssp. = solid square]. All scale lines equal 500 km.

PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 5, pp. 135–179 December 22, 1979

EASTERN PACIFIC MACROURINE GRENADIERS WITH SEVEN BRANCHIOSTEGAL RAYS (PISCES: MACROURIDAE)

By

Tomio Iwamoto

Department of Ichthyology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

ABSTRACT: Seventeen species representing eight genera of macrourine grenadiers with seven branchiostegal rays are treated as part of the eastern Pacific fauna. Among the eight genera, *Nezumia* is the most diverse, with 10 species represented. *Nezumia ventralis* new species, is described from two Galápagos specimens; the high pelvic fin ray count of 15 contrasts this species with all other eastern Pacific *Nezumia*. Two apparently disjunct populations of *N. loricata* are given subspecific recognition: subspecies *loricata* from the Galápagos and subspecies *atomos* (new) from central Chile. *Echinomacrurus, Hymenocephalus, Paracetonurus, Ventrifossa, Malacocephalus, Mataeocephalus,* and *Mesobius* are each represented by only one species—the first four genera listed are first recorded from the eastern Pacific. *Echinomacrurus occidentalis* (a second species in the genus) is newly described from a single specimen taken off Peru in 4,334 m. *Macrurus fragilis* Garman, 1899, is tentatively aligned with members of *Paracetonurus*. *Ventrifossa* is recognized as consisting of three subgenera: *Ventrifossa, Lucigadus,* and *Sokodara* (new). Only subgenus *Lucigadus* is represented in the eastern Pacific.

INTRODUCTION

The large grenadier subfamily Macrourinae is divisible into two distinct groups based on branchiostegal ray counts. Those macrourines with six branchiostegal rays, typified by *Macrourus* Bloch and *Coryphaenoides* Gunnerus, form one group; those with seven branchiostegal rays and one monotypic genus (*Pseudonezumia* Okamura) with seven or eight form a second group. This second group may be further divided by species differences in the development and location of the periproct region (the specialized area surrounding the anal and urogenital openings) and the development of ventral light organs. *Hymenocephalus* is the most distinctive member of this second group and forms a phylogenetic line well removed from the others. Another line of related genera, characterized by the members having a broad periproct situated close to the origin of the anal fin, includes such diverse genera as *Echinomacrurus* Roule, *Paracetonurus* Marshall, *Cetonurus* Günther, *Trachonurus* Günther, and *Sphagemacrurus* Fowler. These genera contrast with *Nezumia* Jordan, *Malacocephalus* Günther, *Ventrifossa* Gilbert and Hubbs, *Kumba* Marshall, and *Pseudonezumia* Okamura, members of which have a smaller periproct removed by some distance from the origin of the anal fin and preceded by an anteriorly extended light organ of various size. *Mataeocephalus* Berg falls somewhere between these two divisions in that members of one species (*M. adjustus*) have a periproct that is well removed from the anal fin origin, and they also have a distinct dermal window of the light organ extended forward of the periproct, while members of the other species apparently have a periproct situated close before the anal fin, and their light organ lacks a distinct dermal window.

The 16 species here considered constitute about 40 percent of the total (approximately 40 spp.) macrourid fauna of the eastern Pacific. The genus *Coelorinchus* from this region (6 spp.) was reviewed in a previous paper (Iwamoto 1979). A review of the large complex of macrourines with six branchiostegal rays and the trachyrincines (2 spp.) from the eastern Pacific is currently underway. A summary of past studies of the Macrouridae from eastern Pacific waters is given in Iwamoto and Stein (1974). In addition, the recent works of Hubbs and Iwamoto (1977), Chirichigno and Iwamoto (1976), Shcherbachev et al. (1979), Ojeda and Camus (1977), and Parin et al. (1973, 1976) should be consulted.

Methods

Methods for making counts and measurements generally follow procedures described by Hubbs and Lagler (1958) and modified for macrourids by Iwamoto (1970, 1978). Six or seven branchiostegal rays are found in all but one species of macrourid. The exception is *Pseudonezumia* Okamura, 1971a, which has seven or eight (personal communications, Osamu Okamura, September 1978). Four of the rays are attached laterally on the epihyal and ceratohyal; the remaining two or three (or probably four in *Pseudonezumia*; condition not known) are attached anteriorly and medially on the ceratohyal—thus only the latter group of rays need be counted to determine the total number. However, these anteriormost rays (i.e., those closest to the isthmus) are generally small and slender, making them difficult to see without probing or dissection.

Synonymies are limited to primary synonyms and other combinations. Materials for this study are based primarily on collections made by the Anton Bruun in 1966 and the Te Vega in 1968; most of these are deposited in the ichthyological collection of the California Academy of Sciences (CAS). Other sources have been extensively used, and abbreviations for the depositories are as follows: AMNH, American Museum of Natural History, New York; BMNH, British Museum of Natural History, London; CAS-SU, Natural History Museum, Stanford University, now housed at CAS; FAKU, Faculty of Agriculture, Kyoto University, Maizuru; FSFRL, Far Seas Fisheries Research Laboratory, Shimizu; IMARPE, Instituto del Mar, Callao; LACM, Natural History Museum of Los Angeles County, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; SIO, Scripps Institution of Oceanography, La Jolla; UMML, School of Marine and Atmospheric Science, University of Miami, Miami; USNM, National Museum of Natural History, Washington, D.C.

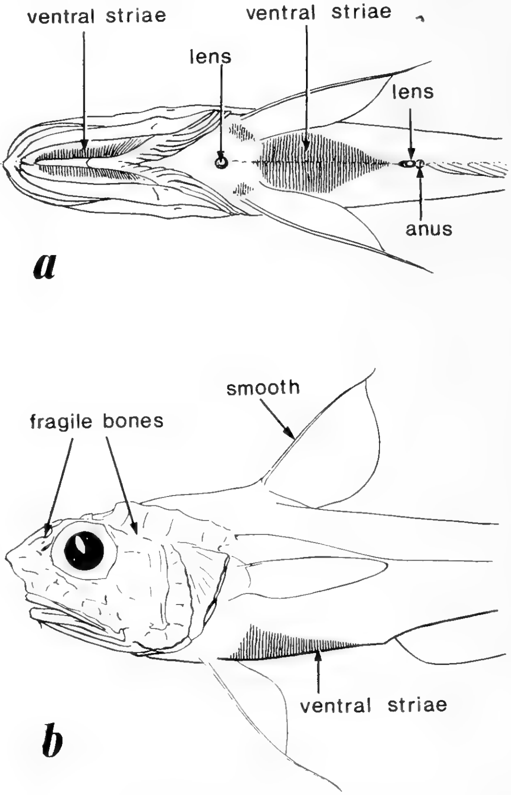


Figure 1. Diagrammatic ventral (*a*) and lateral (*b*) views of a hypothetical representative of the genus *Hymenocephalus*, showing diagnostic features of the genus.

Key to the Adults of Eastern Pacific Macrourine Species with Seven Branchiostegal Rays

1a. Ventral striae (fine black transverse lines, most readily visible under magnification) present over gular membranes, isthmus, and parts of chest and abdomen (Fig. 1). Anus situated immediately before anal fin and preceded by a small,

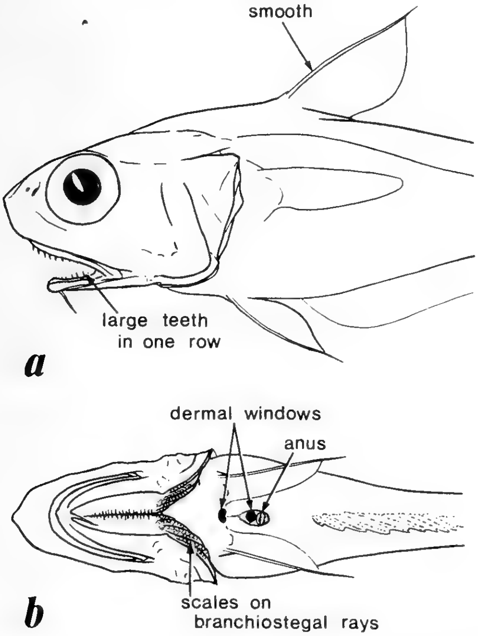


FIGURE 2. *Malacocephalus laevis*. (*a*) Lateral view showing smooth leading edge of second spinous dorsal ray and enlarged teeth of lower jaw. (*b*) Ventral view showing scales on branchiostegal rays and location of anus and light organ structures.

raised lenslike structure; this structure connected by a thin (often obscure) black median line to similar structure on chest. Head bones extremely fragile, some almost membranous. Gill-rakers numerous, more than 20 (total count) on first arch. Second spinous dorsal ray smooth ...... *Hymenocephalus* sp. (p. 140)

1b. No ventral striae. Anus removed by a short to moderate distance from anal fin; lenslike structure, if present, far removed from anal fin origin and usually located in a shallow fossa. Head bones relatively strong. Gill-rakers fewer than 20 (total) on first arch. Second spinous dorsal ray smooth or serrated 2

2a. Spinous second ray of first dorsal fin with smooth leading edge (Fig. 2a) 3

2b. Spinous second ray of first dorsal fin with serrated leading edge 5

3a. Chin barbel absent .... *Mesobius berryi* Hubbs and Iwamoto (p. 141)

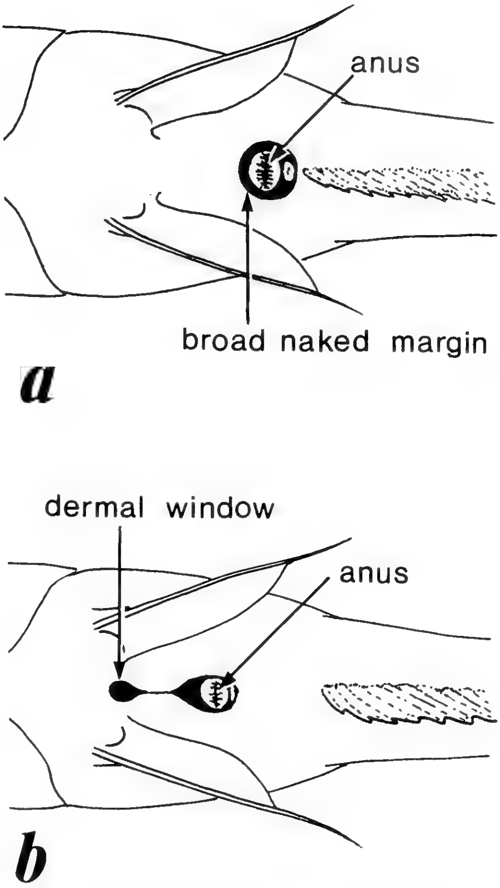


FIGURE 3. Diagrammatic ventral views of abdomen of grenadiers showing periproct location (*a*) abutting or close to (separated by a few scale rows in some individuals) origin of anal fin, and (*b*) periproct far removed from origin of anal fin.

3b. Chin barbel present, well developed 4

4a. Teeth large, in a single row on lower jaw (Fig. 2a); scales on branchiostegal membrane (Fig. 2b) .... *Malacocephalus laevis* (Lowe) (p. 149)

4b. Teeth small, in a narrow band on lower jaw; no scales on branchiostegal membranes .... *Nezumia liolepis* (Gilbert) (p. 157)

5a. Periproct close to or abutting (Fig. 3a) origin of anal fin; anus usually closer to origin of anal fin than to insertion of pelvic fins 6

5b. Periproct far removed from origin of anal fin (Fig. 3b); anus usually closer to in-

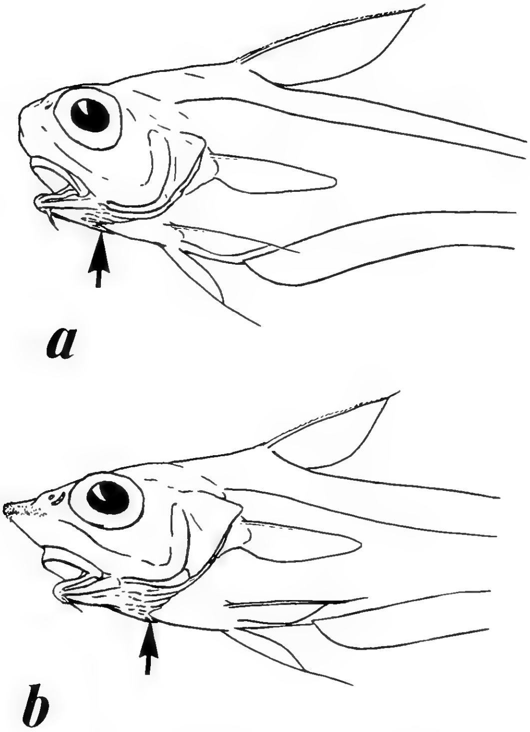


FIGURE 4. Ventrolateral views of (*a*) *Ventrifossa nigromaculata* and (*b*) *Nezumia latirostrata* comparing relative lengths of first dorsal fin, anterior extent of gill openings (arrows), and relative positions of pelvic and anal fins.

sertion of pelvic fins than to origin of anal fin 8

6a. Head massive, globose; snout broadly rounded. Scales on body distinctly nonimbricate (not overlapping), the exposed field of each scale separated by a fleshy border from the exposed fields of adjacent scale ....
Echinomacrurus occidentalis n. sp. (p. 143)

6b. Head relatively slender, angular; snout pointed. Body scales distinctly imbricate; exposed fields of adjacent scales not distinctly separated from each other by a fleshy border 7

7a. Head bones stout; head ridges strongly armed with coarse scutelike scales. Mouth small, notably inferior, and distinctly U-shaped. Scales densely covered with spinules ....
.... *Mataeocephalus tenuicauda* (Garman) (p. 145)

7b. Head bones fragile; head ridges naked or with unmodified scales. Mouth moderate in size, not notably inferior, and more normally shaped. Scales with few or no spinules on exposed field ....
.... *Paracetonurus fragilis* (Garman) (p. 147)

8a. Height of first dorsal fin much greater than length of head. Opercular opening extends far forward to vertical through hind edge of maxillae (Fig. 4a) ....
.. *Ventrifossa* (*Lucigadus*) *nigromaculata* (McCulloch) (p. 153)

8b. Height of first dorsal fin about equal to or less than length of head. Anteriormost extent of opercular opening much posteriad of vertical through hind edge of maxillae (Fig. 4b) 9

9a. Second ray of first dorsal fin with 0 to 4 weak denticles on leading edge (Fig. 5a). Scales thin, highly deciduous with few or no spinules on exposed fields of body scales ....
.... *Nezumia liolepis* (Gilbert) (p. 157)

9b. Second ray of first dorsal fin with numerous prominent denticulations on leading edge (Fig. 5b). Scales relatively adherent, with spinules densely covering exposed fields 10

10a. Species bathypelagic. Gill filaments short; length about half diameter of eye lens. Outer pelvic ray prolonged, 70–160% HL. Body scales small, bearing 1–15 slender, erect spinules that render body surface velvety; 11–14 scale rows below origin of second dorsal fin. Color black to brownish black ....
.... *Nezumia parini* Hubbs and Iwamoto (p. 176)

10b. Species benthopelagic. Gill filaments moderate to long; length about equal to or greater than diameter of eye lens. Outer pelvic ray usually less than 70% HL. Body scales small to moderate; spinules on scales few to numerous, moderately to greatly inclined, conical, lanceolate, or shield shaped, usually rough in texture; fewer than 11 scale rows below origin of second dorsal fin. Color

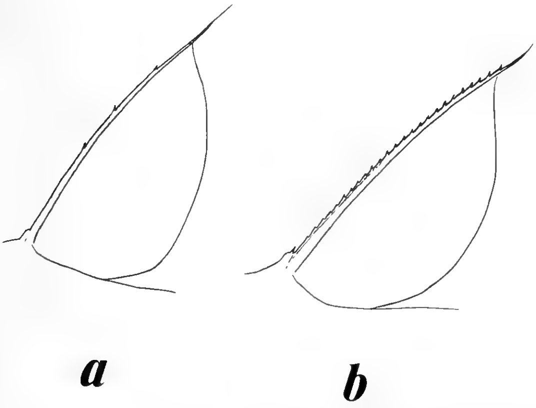


FIGURE 5. Comparison of denticulations on leading edge of second spinous dorsal rays of (*a*) *Nezumia liolepis* and (*b*) *Nezumia loricata*.

various shades of blue, violet, brown, or black 11

11a. Mandibular rami usually completely naked; pores of lateralis system large and prominent on mandibular rami and along ventral border of suborbital region (Fig. 6a). Mouth relatively large, length upper jaw usually 30–36% HL. Outer gill-slit relatively wide, 17–22% HL 12

11b. Most of mandibular rami scaled, although anterior end naked in some; pores of cephalic lateralis system small, relatively inconspicuous (Fig. 6b). Mouth relatively small, length upper jaws 23–32% HL. Length outer gill-slit 12–16% HL 13

12a. Patches of small scales on base of lowermost branchiostegal rays (Fig. 6a). Spinules on body scales relatively broad, lanceolate, arranged in a somewhat quincunx pattern, rows not discretely parallel or slightly convergent and ridgelike. Chin barbel long, 20–25% HL. Rays of pelvic fin 10–11. Orbit diameter 25–29% HL .... *Nezumia stelgidolepis* (Gilbert) (p. 161)

12b. Few isolated scales or no scales on branchiostegal rays. Spinules on body scales narrow, usually conical, arranged in discrete parallel or slightly convergent rows. Length of chin barbel 10–16% HL. Rays of pelvic fin 11–12. Orbit diameter 30–34% HL .... *Nezumia pulchella* (Pequeño) (p. 159)

13a. Gill-rakers on inner side of first (outermost) arch 9 or fewer (total count), 5–6 (rarely 7) on lower limb .... *Nezumia convergens* (Garman) (p. 171)

13b. Gill-rakers on inner side of first arch 9 or more (total), 8 or 9 on lower limb 14

14a. Pelvic fin rays 9. First dorsal with prominent black blotch distally, pale basally. Interorbital region narrow, width 17–19% HL .... *Nezumia orbitalis* (Garman) (p. 167)

14b. Pelvic fin rays 9–12. First dorsal fin usually uniformly blackish. Interorbital width moderate, 17–26% (usually more than 20%) HL 15

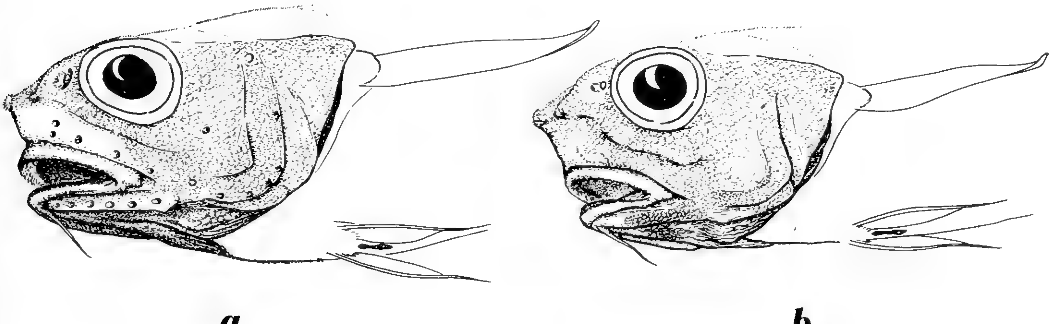


FIGURE 6. Ventrolateral views of (*a*) *Nezumia stelgidolepis* and (*b*) *Nezumia pudens* comparing pore development (slightly exaggerated) and squamation of head in the two species.

15a. Snout relatively blunt, high. Suborbital region smoothly and almost completely scaled; scales along ridges not especially stout and coarse (Fig. 6b). Barbel long, 19–25% HL .... *Nezumia pudens* Gilbert and Thompson (p. 163)

15b. Snout pointed, low. Suborbital region often with ventral surfaces partially naked; scales along ridges stout, coarse. Barbel shorter, less than 17% HL 16

16a. Pelvic fin rays 9–10. First dorsal fin rays II,8–11 (usually 9–10) Length barbel 5–10% HL .... *Nezumia latirostrata* (Garman) (p. 168)

16b. Pelvic fin rays 10–12. First dorsal fin rays II,9–12 (usually 10–12). Length barbel 10–17% HL .... *Nezumia loricata* (Garman) (p. 174)

Hymenocephalus Giglioli

Hymenocephalus Giglioli, 1882:199 (type-species *Hymenocephalus italicus* Giglioli, 1884, by monotypy).

Mystaconurus Günther, 1887:124 (as subgenus of *Macrurus*) (type-species *Hymenocephalus italicus* Giglioli, 1884, by subsequent designation of Jordan and Evermann 1898:2580).

Hymenogadus Gilbert and Hubbs, 1920:521 (as subgenus) (type-species *Hymenocephalus gracilis* Gilbert and Hubbs, 1920, by original designation). —Okamura 1970a:58 (recognized as genus).

Diagnosis.—Macrourine grenadiers with anus immediately before anal fin. Striae, consisting of fine parallel black lines over silvery pigment, on most ventral areas of body. Two lenslike dermal windows of light organ on midventral line; one immediately before anus and one on chest before pelvic fin bases; dermal window connected by black ridge along midventral wall of abdominal cavity. Head large, cavernous; bones thin, head covering membranous. Mouth large, subterminal. Gill openings and outer gill-slit relatively wide. Gill-rakers numerous, more than 15 on lower limb of outer arch except in slender, cylindrical-bodied species (subgenera *Hymenogadus* and *Spicomacrurus*). Second dorsal spine smooth or weakly denticulate (in *Hymenogadus*). Small species, usually less than 200 mm TL. (Adapted after Iwamoto 1970:374–375.)

Remarks.—Okamura (1970a) elevated the subgenus *Hymenogadus* to full generic status, including in it *H. gracilis* Gilbert and Hubbs, 1920, *H. tenuis* Gilbert and Hubbs, 1917, and *H. kuronumai* Kamohara, 1938. The three species are obviously closely related and form a distinct group readily distinguished from most other *Hymenocephalus* (sensu lato), but it is not the differences between the species groups in *Hymenocephalus* but the similarities among them that are most striking. Used in its widest sense, the genus *Hymenocephalus* encompasses a group of species that is notably distinct and distantly removed from other groups of macrourine grenadiers. By recognizing both *Hymenocephalus* and *Hymenogadus,* differences are emphasized and the obvious close relationship of the two groups is masked. This is regrettable and entails a needless proliferation of names. Recognition of *Hymenogadus* (with *gracilis* and *tenuis*) and *Spicomacrurus* (with *kuronumai*) as subgenera within *Hymenocephalus* is to me a more practicable and meaningful treatment of the species groups involved.

Hymenocephalus sp.

Diagnosis.—Refer to generic diagnosis.

Counts and Measurements.—1D. II,8; gill-rakers on outer arch about 20. The following in millimeters: estimated HL 25; estimated TL 170; horizontal orbit diameter 10.3; length upper jaw 15.0; width suborbital 3.8; orbit to angle of preopercle 12.3; length barbel 3.7.

Remarks.—The single specimen of this genus from eastern Pacific waters was in such poor condition when examined in June 1975, that an adequate description could not be prepared. The head was damaged and had become separated from the trunk, and the paired fins were gone; but there was no question as to its genus because of the presence of striae on the gular membrane and along the abdomen; the presence of two lenslike light organs on the chest and before the anus; the number, shape, and coloration of the gill-rakers; and the shape of the preopercle ridge—these combined features uniquely characterize the genus *Hymenocephalus*.

This specimen represents the first record of the genus from eastern Pacific waters. The genus is common throughout the warm-water regions of the Atlantic, Indian, and most of the central and western Pacific oceans. That only a single specimen has been collected—and that a fair-sized adult taken in a midwater haul—suggests that the species is not a regular inhabitant of eastern Pacific waters. The specimen may represent a stray or an expatriate, possibly from populations far to the westward.

Material Examined.—USNM 149049 (1 specimen, est. 170 mm TL); Peru, off Aguja Pt., 5°57′30″S, 81°50′W; vertical haul, 732–0 m over bottom depth of 4,023 m; Albatross sta. 4655, 12 Nov. 1904.

Mesobius Hubbs and Iwamoto

Mesobius Hubbs and Iwamoto, 1977:235 (type-species *Mesobius berryi* Hubbs and Iwamoto, 1977, by original designation).

Diagnosis.—Bathypelagic. Periproct region broad, somewhat raised, close to anal fin origin (removed from origin by 2–4 scale rows in some individuals); anus centrically located within periproct. Large light organ abutting rectum, but no anterior extensions between pelvic fin bases or on chest. Abdomen short, distance isthmus to anal fin origin 1.0–1.5 of orbit diameter in adults. Chin barbel absent. Dentition in both jaws consist of narrow bands of small teeth. Scales of head elongate, each bearing 1–3 rows of spinules that form low, sharp ridges with 2–9 spinules per row. Head and body laterally compressed. Swim bladder greatly reduced, bearing 2 retia and 2 gas glands. Postlarvae and prejuveniles pass through a polka-dotted ("phalacromacrurus") stage; adults mostly black. (Adapted from original description.)

Remarks.—Since publication of the genus description, Dr. Carl L. Hubbs and I have received information concerning additional specimens of the genus. Dr. Nikolai V. Parin has written (to Hubbs, 25 Nov. 1977) that representatives of the genus have been collected by Russian vessels in the Atlantic and Indian oceans between latitudes 31° and 37°S. These specimens are presumably those recently reported by Shcherbachev et al. (1979) who recorded *M. berryi* from the Indian Ocean, and *M. antipodum* from the Indian Ocean and the Atlantic Ocean off the southwestern tip of Africa. Unlike the type-specimens of both species, the Russian specimens were captured in bottom trawls. The largest *M. antipodum* recorded by Shcherbachev et al. was more than 661 mm in total length and 136 mm in head length, and their six specimens ranged 104–136 mm HL and 465+ to 661+ mm TL. Their five specimens of *M. berryi* ranged 64.5–75.5 mm HL and 330+ to 412+ mm TL. The *M. antipodum* specimens are considerably larger than any of the *M. antipodum* and *M. berryi* Dr. Hubbs and I had examined (the largest *M. berryi* we had was 392 mm in total length and 70 mm in head length; the holotype of *M. antipodum* was 390 mm long, with an incomplete tail, and 75 mm in head length). Dr. Christine Karrer has also informed us (personal communication, Oct. 1977) of having examined specimens of *Mesobius* in the Institut für Seefischerei (ISH), Hamburg, that were captured in the Atlantic by the Walther Herwig. Four of these (ISH 1816/68; 88–107 mm HL) were borrowed through the kindness of Dr. M. Stehman and were identified as *M. antipodum*. Takao Arai (1979) recently reported the collection of 12 specimens of *M. antipodum* off New Zealand, the largest of which was 128 mm in head length. It thus appears that *M. antipodum* attains a much larger size than *M. berryi*, and that speculation (Hubbs and Iwamoto 1977:246) as to the probable distribution of *M. antipodum* extending widely across the Southern Hemisphere is supported.

Mesobius berryi Hubbs and Iwamoto

(Figure 7*a*)

Mesobius berryi Hubbs and Iwamoto, 1977:236–244, figs. 1–8, 10A (original description; holotype and 18 paratypes from eastern North Pacific).

Diagnosis.—A species of *Mesobius* with 12–17 pyloric caeca; mesial gill-rakers on first arch 10–13 ($\bar{x}$ = 11.8), on second arch 10–12 ($\bar{x}$ = 11.0). Length posterior nostril less than 4 into least suborbital width. Differentiated squamation of posttemporal region not extending posteriad of vertical through origin of pectoral fin. Outer margin of gill cover not notably incised at subopercle.

Remarks.—General features of the fish can be seen in Figure 7a. This species has been adequately described in the original description, and in the recent reports by Arai (1979) and Shcherbachev et al. (1979). *Mesobius berryi* and *Nezumia parini* are the only eastern Pacific species of macrourid normally living bathypelagically as adults (adults of other species make excursions into bathypelagic depths, but their normal habitat is near bottom, i.e., benthopelagic; see Marshall and Merrett (1977) and Merrett (1978) for recent discussions on this subject). The unique squamation of the head of *Mesobius berryi* is unlike that of any other species encountered in the eastern Pacific and makes adults of the species easily recognizable. The specific differences originally reported between *M. berryi* from the North Pacific and *M. antipodum* from the South Pacific have generally

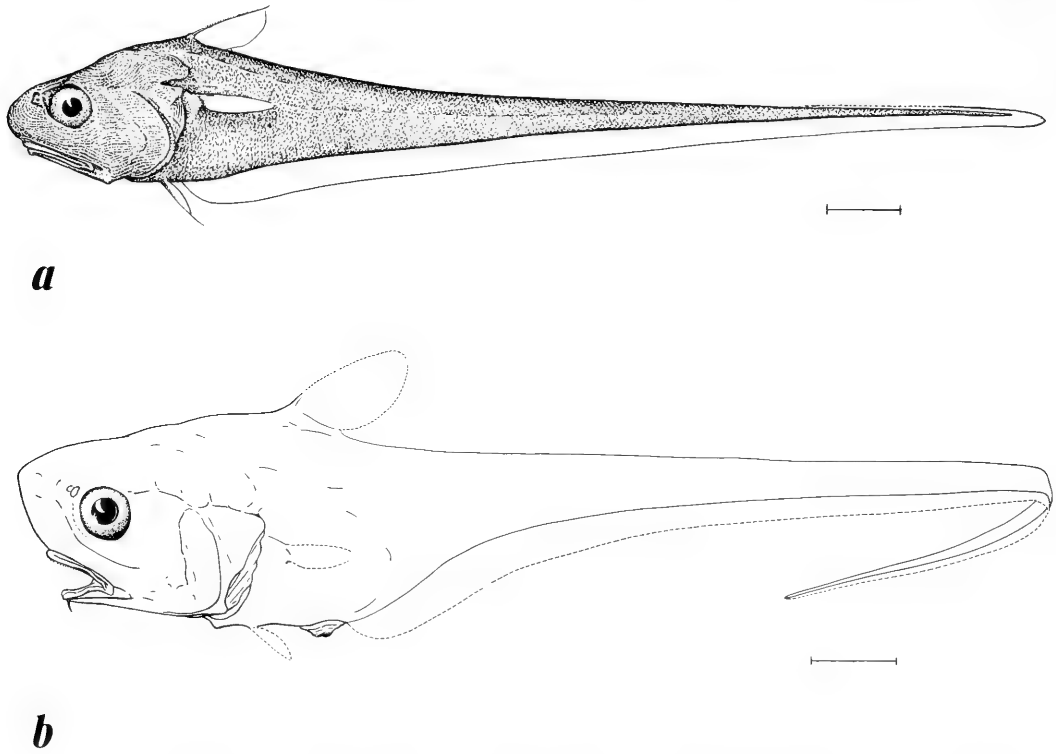


FIGURE 7. (*a*) *Mesobius berryi* Hubbs and Iwamoto. (Adapted from fig. 1 in Hubbs and Iwamoto 1977.) (*b*) *Echinomacrurus occidentalis* Iwamoto, new species. Reconstruction of holotype, USNM 135612, collected by the ALBATROSS off Peru in 4,334 m.

been confirmed by Arai (1979) upon his examination of 12 specimens of *M. antipodum* captured off the New Zealand shelf and by Shcherbachev et al. (1979) from examination of specimens from the Indian Ocean and the southwestern Atlantic. Meristic features show the best differences (see Table 1), with the pyloric caeca count showing no overlap (12–17 in eight specimens of *M. berryi*, 30–43 in more than six specimens of *M. antipodum*) (data from Hubbs and Iwamoto (1977), Shcherbachev et al. (1979), and Arai (1979)); the last author gave only the range of counts in his 12 specimens of *M. antipodum*).

Echinomacrurus Roule

Echinomacrurus ROULE, 1916:22 (type-species *Echinomacrurus mollis* Roule, 1916, by monotypy).

DIAGNOSIS.—Macrourine grenadiers with anus located within a broad naked area that lies immediately adjacent to anal fin origin; head massive, swollen by the expansive cephalic lateral-line canals; second spinous ray of first dorsal fin serrated along leading edge; scales nonimbricate, with slender, erect spinules; scales along dorsal fins not especially enlarged (as in *Cetonurus*); no scales on gular and branchiostegal membranes; swim bladder reduced or absent. (See Marshall (1973:599) for additional characters.)

REMARKS.—The genus *Echinomacrurus* has hitherto been known only from the eastern North Atlantic and the western Indian Ocean (Marshall 1973). The eastern Pacific specimen here reported is the first Pacific and, at 4,334 m, the shallowest record of the genus. Other specimens of *Echinomacrurus* have been taken at depths from 5,000 to 5,413 m, and except for one Indian Ocean specimen, all were taken in nets fished at the bottom—Marshall (1973) thus considers *E. mollis* bathypelagic to benthopelagic in habit.

The genus is closely related to *Cetonurus* Vaillant, 1888; the two agree in most diagnostic characters given above but not in squamation

Table 1. Comparison of Selected Counts in *Mesobius berryi* and *M. antipodum*. Data from Hubbs and Iwamoto (1977), Arai (1979), and Shcherbachev et al. (1979).

Total gill-rakers on first arch

	range	$\bar{x}$	S.D.	*n*
M. berryi	10–13	11.7	0.82	19
M. antipodum	12–15	13.9	0.85	31

Total gill-rakers on second arch

	range	$\bar{x}$	S.D.	*n*
M. berryi	10–12	11.2	0.62	20
M. antipodum	12–16	13.9	0.89	31

Pectoral fin rays

	range	$\bar{x}$	S.D.	*n*
M. berryi	12–14	12.9	0.63	33
M. antipodum	13–16	14.5	0.68	31

Pelvic fin rays

	range	$\bar{x}$	S.D.	*n*
M. berryi	7–9	7.7	0.57	35
M. antipodum	6–7	6.9	0.35	30

and swim-bladder characters. *Cetonurus* has imbricate scales over most of the body and notably enlarged scales along the base of the second dorsal fin; it also has scales over the lower branchiostegal rays and on the gular membrane, and a well-developed swim bladder.

Echinomacrurus occidentalis new species

(Figure 7*b*)

Diagnosis.—An *Echinomacrurus* with 12 pelvic fin rays. Orbits about 20 percent HL. Eleven gill-rakers on mesial side of second arch. Interspace between first and second dorsal fins 31 percent HL.

Counts.—1D. ca. II,9; 1P. i18/i18; 2P. ca. 12/12. Gill-rakers on first arch 1 + 9; on second arch 2 + 9. Pyloric caeca 6.

Measurements (all in mm; measurements preceded by ca. are estimates).—Total length ca. 400; head length ca. 80; snout length ca. 27; preoral length ca. 23; horizontal orbit diameter 16; least postorbital length 39; orbit to angle of preopercle 36; suborbital width 10; length upper jaw 22.5; length barbel 7; length outer gill-slit 9; preanal length ca. 110; length snout to anus ca. 102; outer pelvic to anal 29; isthmus to anal ca. 54; greatest body depth ca. 62; depth over anal origin ca. 53; 1D.–2D. interspace 31.

Description.—Head deep, massive, presumably swollen in appearance when fresh; snout high, broad; nostrils high, located at about level of dorsal margin of orbits; interorbital space broad, convex. Mouth rather small, subinferior, but upper jaw extends near to vertical through hind edge of orbit; ascending limb of premaxilla high (height about 0.9 of ramus length), inclined forward. Interopercle mostly covered by, and closely adhered to, preopercle. A distinct notch in outline of gill cover formed by posteroventral border of subopercle.

Scales small, nonimbricate, almost in mosaic pattern on parts of head, more widely spaced on body. Thin, erect spinules cover most scales, giving shagreenlike feel to skin. Scales everywhere cover exposed surfaces of head and body except on fins, lips, parts of subopercle, wide margin surrounding anus, small areas behind pectoral and dorsal fins, and gill membranes. Shoulder girdle beneath gill cover naked; border between naked and scaled areas of shoulder sharply demarcated. Periproct large, raised, immediately adjacent to anal fin and occupying almost half distance between insertion of pelvic fins and origin of anal fin; anus slightly protruding. Premaxillary teeth small, conical, recurved, in a narrow, tapered band of about four rows deep anteriorly, tapering to a single row posteriorly; band extends about three-fourths length of premaxillary ramus; outer series of teeth slightly enlarged. Mandibular dentition about the same as that of premaxillary, but without enlarged outer teeth.

Gill-rakers short, spiny, tubercular. Outer gill-slit relatively long; about 8 rudimentary rakers on outer side of first arch, 1 + 9 on inner side, these armed with slender conical spines. Pyloric caeca 6, large, thick. Specimen a male with 2 well-developed testes.

Linings of gill, buccal, and peritoneal cavities black. Stomach black.

Remarks.—It is with some reluctance that I describe this single eastern Pacific specimen of *Echinomacrurus* as a new species, because of its extremely poor condition. It is unlikely, however, that any additional material of this rare species will be soon forthcoming, and there is little doubt that the specimen represents an undescribed taxon. The pelvic fin ray count of 12, which I have confirmed on the right fin by staining, is distinctly higher in the eastern Pacific specimen than the 9–10 reported for *E. mollis* by Nybelin (1957) and Marshall (1973:599). The larger orbit (20 percent HL cf. 10–15 percent), which goes into the distance orbit to angle of preopercle about 2.2 times (compared with 2.5 or more in *E. mollis*), the slightly more rays of the first dorsal fin (II,9 in *E. occidentalis*, II,10 or II,11 in *E. mollis*), and the somewhat higher gill-raker count on the second arch (11 compared with 9–10 for *E. mollis*) are other noteworthy differences. Additionally, comparison of the holotype of *E. occidentalis* with a specimen of *E. mollis* from the Swedish Deep-Sea Expedition of 1947–48 (reported on by Nybelin (1957) and borrowed through the courtesy of Dr. Hubendick of the Natural History Museum, Göteborg) has revealed that the scales on the abdomen of the new species are smaller, with about seven scale rows separating the periproct from the pelvic fin bases as compared with three at the most separating the two regions in *E. mollis*. The pelvic girdle of *E. occidentalis* is much shorter than that of *E. mollis*—its length from anterior point to base of pelvic fin goes about 2.5 into distance orbit to angle of preopercle, as compared with about 2.0 for the same measurement in *E. mollis*. The new species is otherwise closely similar to its congener, for which Nybelin (1957) gives an excellent description and a photograph of two freshly caught specimens.

DISTRIBUTION.—Known from only the holotype taken off the northern coast of Peru in 4,334 m.

MATERIAL EXAMINED.—**Holotype:** USNM 135612 (1, ca. 80 mm HL, ca. 400 mm TL); off Peru, 8°30′S, 85°36′W, 4,334 m, ALBATROSS sta. 4658, 14 Nov. 1904.

Mataeocephalus Berg

Coelocephalus GILBERT AND CRAMER, 1897:422 (*non* Agassiz, 1843) (type-species *Coelocephalus acipenserinus* Gilbert and Cramer, 1897, by monotypy).

Mataeocephalus BERG, 1898:43 (replacement name for *Coelocephalus* Gilbert and Cramer, 1897, preoccupied).

DIAGNOSIS.—Macrourine grenadiers with anus located within a moderately broad to broad naked area (periproct) whose posterior edge is immediately adjacent to or close to anal fin origin; anus usually closer to origin of anal fin than to insertion of pelvic fins. Spinous ray of first dorsal fin with a serrated leading edge or serrations obsolete (in *M. adjustus*). Snout produced, dorsoventrally depressed, with a stout, two-pronged scute. Mouth small (less than 30 percent HL), inferior; suborbital ridge stout, sharply angular in cross section. Premaxillary and mandibular teeth in broad bands which are usually confined to anterior portion of jaws and which usually fall well short of posterior corners of mouth opening. Gill openings restricted; gill membranes broadly connected to isthmus. Outer gill-rakers on first arch rudimentary or absent.

COMPARISONS.—*Mataeocephalus* appears superficially close to *Coelorinchus* Giorna but is immediately distinguished from that genus by the branchiostegal ray count of 7 (6 in *Coelorinchus*), the strongly serrated spinous ray in first dorsal fin (except in *M. adjustus* with serrations obsolete; cf. smooth or, rarely, with few distal teeth in *Coelorinchus*), and the two-pronged terminal snout scute (one- or three-pronged in *Coelorinchus*). The genus *Mataeocephalus* is closest to *Nezumia* but differs in: (1) anus closer to anal fin origin than to pelvic fin insertion (anus generally closer to pelvic fin insertion in *Nezumia*); (2) premaxillary and mandibular teeth in short, broad bands except in *M. adjustus* (cf. narrow tapering bands that extend posteriorly to rictus except in *N. burragei* (Gilbert, 1905)); (3) generally longer snout, and smaller, more inferior mouth; and (4) outer rakers of first arch rudimentary or absent (cf. tubercular rakers present in *Nezumia* species). Members of the genus are unlikely to be confused with any other macrourine grenadier with the combination of seven branchiostegal rays and periproct adjacent or close to anal fin origin because of their small, inferior mouth, much produced snout, and sharp, angular suborbital ridge.

REMARKS.—*Mataeocephalus* includes a small group of about five closely related species confined to the tropical waters of the Pacific and Indian oceans. The genus is not known from the Atlantic Ocean.

Mataeocephalus adjustus (Smith and Radcliffe, 1912) from the Philippines appears to be the most primitive member judged by the following characters: relatively large mouth that is not strongly U-shaped; dentition in both jaws extending posteriad in a tapered band; head and snout not dorsoventrally depressed to the extent found in the other members; ventral surfaces of snout and suborbital regions completely scaled; terminal snout scute rather small; and periproct area relatively small. Most of these supposedly

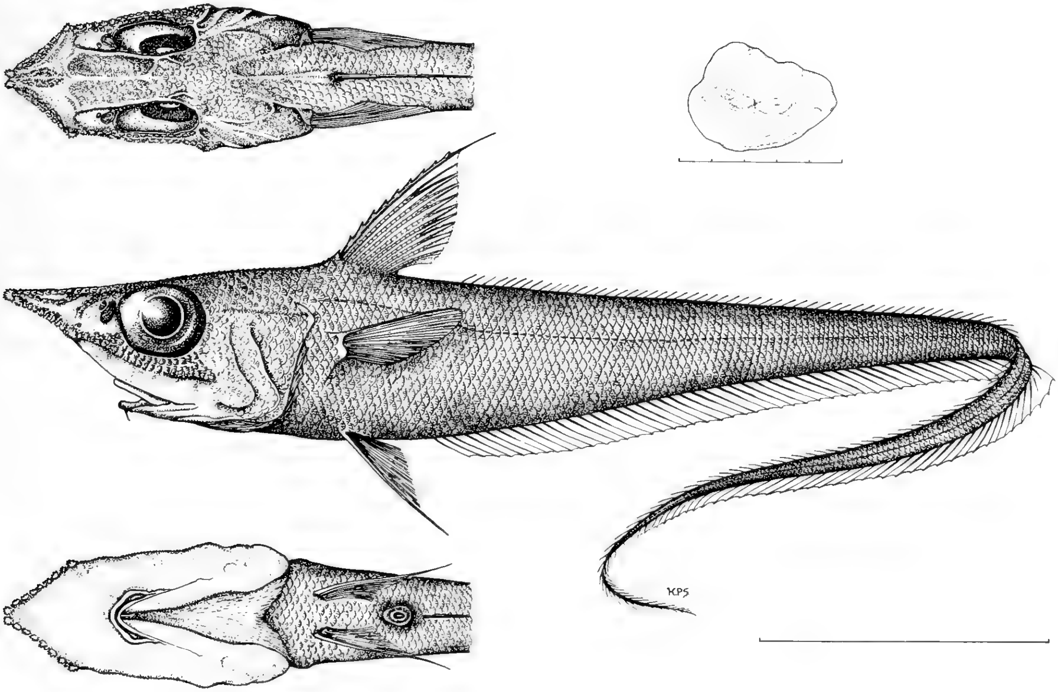


FIGURE 8. *Mataeocephalus tenuicauda* (Garman). Composite drawing from specimens catalogued AMNH 8451, 8467, and 8468, collected by the ARCTURUS, 96 km south of Cocos Island. Scale bar under otolith represents 5 mm; that under tail, 25 mm.

primitive features of *M. adjustus* cloud the otherwise strong differences between the genera *Mataeocephalus* and *Nezumia*, but viewing the group as a whole, and on the basis of the diagnosis given above, recognition of each as distinct genera seems justified.

Mataeocephalus tenuicauda (Garman)
(Figure 8)

Macrurus tenuicauda GARMAN, 1899:216–217, pl. 49, fig. 1 (original description; type-locality Gulf of Panama, 838 m, ALBATROSS sta. 3384).

Mataeocephalus tenuicauda: GILBERT AND HUBBS, 1916:146 (name only).

DIAGNOSIS.—A species of *Mataeocephalus* with 8 (9 in three fins of 18 specimens) pelvic fin rays; 22–26 pectoral fin rays. Chin barbel about 4–6 percent HL. Upper jaw 19–28 percent HL. No small naked fossa (anterior dermal window of light organ) anterior to periproct.

DESCRIPTION.—General features of fish seen in Figure 8. Head shallow, depressed; greatest width of head about equal to or more than greatest depth of head. Dorsal and ventral surfaces of head sharply demarcated by a strong ridge running from snout tip posteriad to preopercle, but not connected to preopercular ridge. Mouth small, inferior, protrusible, U-shaped. Periproct region large, situated almost midway between origin of anal fin and insertion of pelvic fins, but slightly closer to former. No separate dermal window of light organ apparent in specimens examined. Swim bladder large, with two long, slender, uncoiled retia and two small, flattened gas glands. Males with large drumming muscles on each side of anterior end of swim bladder. Pyloric caeca simple, short, thick; 16 to 21 in five specimens. Intestine with two major loops, the first extending posterodorsally from pylorus, the second extending anteroventrally along dextral wall of abdomen, passing anteriad and sinistrally around front of stomach and caecal mass. Opercular openings restricted dorsally and ventrally; gill membranes broadly connected and attached to isthmus with no free posterior fold. A fleshy ridge on shoulder girdle along posterodorsal margin of gill cavity. Outer gill-rakers of first arch rudimentary, platelike, 3 or 4 in number.

Dorsal fin with thornlike spinous first ray

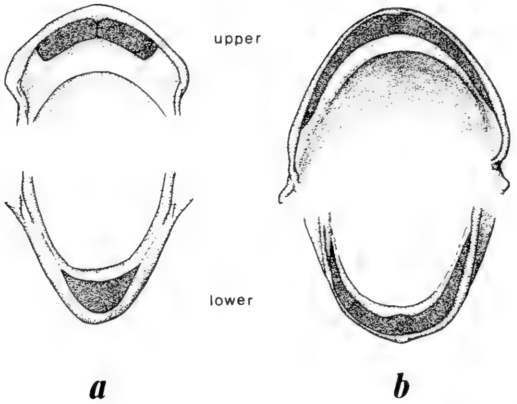


FIGURE 9. View of upper and lower jaws showing shape of tooth bands in (*a*) *Mataeocephalus tenuicauda* (Garman), specimen 48 mm HL and (*b*) *Nezumia latirostrata* (Garman), specimen 40.5 mm HL.

closely appressed to spinous second ray, the latter with widely spaced teeth along leading edge. Outer ray of pelvic fins prolonged, extending well beyond anal fin origin.

Scales on body with slender, conical spinules arranged in sharp, ridgelike rows. Scales on head variously developed; those on ridges more coarsely developed with spinule rows arranged in a stellate pattern in some and a broad posteriorly radiating pattern in others; those on top of head generally with low, longitudinal spinule rows that diverge slightly posteriorly. Ventral surfaces of head naked except for a small patch of scales at anteroventral corner of preopercle and along leading edge of snout where large, coarse, spinous, nonimbricate scales overlap slightly onto ventral surfaces. Tip of snout armed with two closely appressed, conical scutes. Suborbital region covered dorsally with two distinct rows of large, coarse, nonimbricate, strongly adherent scales. Supraorbital and supranarial ridges coarsely scaled. A prominent lunate naked groove dorsally along each side of anterior snout margin.

Premaxillary teeth in broad, short, cardiform bands truncated at posterior ends (Fig. 9a). Mandibular teeth in a broad, short band with tapered ends; tooth band falling well short of lateral corners of mouth.

Coloration in alcohol. All specimens examined have lost most of their body scales. Overall color brown to swarthy, often with a violet tinge on trunk and tail. Abdominal region blackish. Naked ventral surfaces of head pale to dusky. Fins dusky to blackish. Oral, branchial, and peritoneal cavities blackish.

COUNTS (from 18 specimens unless otherwise indicated).—1D. II,8–10; 1P. 22–26 ($\bar{x}$ = 23.76); 2P. 8–9 (9 rays in 3 of 36 fins). Gill-rakers on first and second arch 0–1 + 6–7 (6–8 total; $\bar{x}$ = 7.18); on second arch 0–1 + 5–7 (6–8 total; $\bar{x}$ = 7.29). Scales below first dorsal 7–11 (6 specimens); below midbase of first dorsal 6½ to 9 (6 specimens); below second dorsal 8½ to 11 (9 specimens); over distance equal to predorsal length of head 37–48 (4 specimens).

MEASUREMENTS (from 18 specimens unless otherwise indicated).—Total length 131+ to 303 mm; head length 30.0–65.3 mm. The following in percent of head length: postrostral length of head 60–66 ($\bar{x}$ = 61.8; S.D. = 1.56); snout length 36–42 ($\bar{x}$ = 39.9; S.D. = 1.46); preoral length 35–43 ($\bar{x}$ = 38.6; S.D. = 2.31); internasal width 19–22 ($\bar{x}$ = 20.5; S.D. = 0.80); orbit diameter 26–30 ($\bar{x}$ = 27.2; S.D. = 1.48); interorbital width 19–22 ($\bar{x}$ = 20.3; S.D. = 0.93); postorbital length 29–36 ($\bar{x}$ = 32.7; S.D. = 1.51); orbit to angle of preopercle 28–33 ($\bar{x}$ = 30.0; S.D. = 1.25); suborbital width 13–16 ($\bar{x}$ = 14.6; S.D. = 0.96); upper jaw length 19–28 ($\bar{x}$ = 22.4; S.D. = 2.07); barbel length 3.7–5.7 ($\bar{x}$ = 4.7; S.D. = 0.61); length outer gill slit 8.5–12.7 ($\bar{x}$ = 10.4; S.D. = 1.08; n = 13); preanal length 122–138 ($\bar{x}$ = 129.5); outer 2P. to A. 21–29 ($\bar{x}$ = 25.9; S.D. = 2.16; n = 15); greatest body depth 42–56 ($\bar{x}$ = 52.2; S.D. = 3.47; n = 14); 1D.–2D. interspace 19–29 ($\bar{x}$ = 25.1); height 1D. 52–63 ($\bar{x}$ = 58.5; n = 8); length 1P. 37–41 ($\bar{x}$ = 38.7; n = 12); length 2P. 37–49 ($\bar{x}$ = 43.2).

COMPARISONS AND RELATIONSHIPS.—*Mataeocephalus tenuicauda* closely resembles the Hawaiian endemic *M. acipenserinus* (Gilbert and Cramer, 1897) but differs in having a longer upper jaw (22–28 percent HL vs. about 19–21.5), a somewhat longer chin barbel (3.7–5.7 percent HL vs. 2.6–4.0), and in lacking a small naked fossa anterior to the periproct. *M. nigrescens* (Smith and Radcliffe, 1912) from the Philippines also closely resembles both *M. tenuicauda* and *M. acipenserinus*, and the three are considered as close allies by Gilbert and Hubbs (1920:564). My cursory examination of five paratypes of *M. nigrescens* (USNM 149310; 149311 [2 specimens]; 149312; 149313) revealed minimal differences between *nigrescens* and *tenuicauda*. Morphometric features of the two are indistinguishable. Scale-row counts, however, show notable separation; *nigrescens* specimens had about 7½ rows between the origin of the second dorsal fin and 5½ below the midbase of the first dorsal fin, whereas *tenuicauda* specimens had 8½ to 11 and 6½ to 9, respectively.

Mataeocephalus adjustus (Smith and Radcliffe, 1912) is readily distinguished from *tenuicauda, nigrescens,* and *acipenserinus* by the following characters: fewer pelvic rays (7 cf. 8 or 9), fewer pectoral rays (19 or fewer cf. 21–26), bands of teeth in both jaws extending posteriad about to end of rictus. Because of the many features distinguishing *M. adjustus* on the one hand and *M. tenuicauda, M. nigrescens,* and *M. acipenserinus* on the other, a wide phylogenetic divergence between the two groups is suggested. The lack of specimens of *M. microstomus* (Regan, 1908) from the Indian Ocean and the paucity of information in the original description preclude an adequate comparison of this species with its congeners.

Distribution.—Mainland Pacific coasts of Panama and Ecuador between latitudes 6°36′N and 3°15′S; in the Galápagos; and south of Cocos Island.

Size.—To at least 65 mm HL and 303 mm TL.

Material Examined (55 specimens, 7 localities).—**Panama:** USNM 148879 (2, 57–59 mm HL, 202–253 mm TL), 6°36′N, 81°45′W, 581 fms (1,063 m), Albatross sta. 4621, 21 Oct. 1904. **Ecuador:** CAS 38325 (1, 34 HL, 155 TL), 3°15′S, 80°55′W, 945–960 m, Anton Bruun cr. 18B, sta. 770 (field no. LWK66–120), 10 Sep. 1966. Cocos Island (60 miles [96 km] S of): AMNH 8451 (7, 35–64 HL), AMNH 8467 (6 specimens), AMNH 8468 (23 specimens), AMNH 8469 (5 specimens), AMNH 8470 (7 specimens), all from Arcturus sta. 74, May 1925. **Galápagos:** CAS-SU 25239 (1, 55 HL, 230 TL), 0°29′S, 89°54′30″W, 392 fms [717 m], Albatross sta. 2818, 15 Apr. 1888.—USNM 135340 (1, 43 HL, 185+ TL), 0°36′30″S, 89°19′00″W, 634 fms [1,159 m], Albatross sta. 2808, 4 Apr. 1888.—CAS 42075. (2, 30–31 HL, 158–131+ TL), 1°06′S, 89°22′W, 700–800 m, Te Vega cr. 19, sta. 102, 12 Apr. 1968.

Paracetonurus Marshall

Paracetonurus Marshall, 1973:615 (type-species *Macrurus parvipes* Smith and Radcliffe, 1912, by original designation).

Diagnosis.—A macrourine grenadier with anus and urogenital openings within a broad, black periproct immediately preceding anal fin origin. Spinous ray of first dorsal fin with a serrated leading edge. Snout relatively high, broad; suborbital region relatively deep, without a strong spinous ridge. Scales flanking base of second dorsal fin not enlarged. (Adapted from Marshall 1973.)

Remarks.—Marshall (1973:615) erected this genus to include *Macrurus flagellicauda* Koefoed, 1927, *M. parvipes* Smith and Radcliffe, 1912, and *Lionurus cetonuropsis* Gilbert and Hubbs, 1916—three species that are closely related to *Cetonurus* Günther, 1887, but which are distinguished by their somewhat less-inflated head and their lack of enlarged scales along the base of the second dorsal fin. The monotypic genus *Kumba* Marshall, 1973, is also closely related to *Paracetonurus* but differs primarily in lacking serrations on the second spinous ray of the first dorsal fin.

I have included *Macrurus fragilis* Garman, 1899, in *Paracetonurus* for reasons given in the description of that species. By doing so, the definition of the genus is expanded and its contrast with the genera *Cetonurus* and *Kumba* is lessened. I recognize, however, that a detailed study comparing features of *P. fragilis* and the three other species of the genus may necessitate a further rearrangement of the taxon, but the material available does not allow such a study at this time.

Paracetonurus fragilis (Garman)

(Figure 10)

Macrurus fragilis Garman, 1899:203–204, pl. 46, fig. 1 (original description; Albatross specimens from off Panama and Colombia, 3,058–3,334 m).

Lionurus (Lionurus) fragilis: Gilbert and Hubbs 1916:146 (listed).

Sphagemacrurus fragilis: Marshall 1973:623 (listed).

Diagnosis.—A species of *Paracetonurus* with 8–9 pelvic rays. Nasal rostrum extremely fragile; head covering thin, almost membranous.

Counts.—1D. II,6–9; 1P. 19–21; 2P. 8–9. Gill-rakers on inner side of first arch 1–2 + 8–10 (10–11 total); on inner side of second arch 1–2 + 8–9 (9–11 total).

Measurements (from three specimens; most measurements are estimates).—Head length about 26–35 mm; total length 175+ to 200 mm. The following in percent of head length: snout length about 28–40; orbit diameter about 22–23; interorbital width 24–27; orbit to angle of preopercle 33–44; suborbital width 14–18; length upper jaw 31–39; length barbel 19–24; length outer gill-slit 17–20; greatest body depth 66–69.

Description.—Head moderately wide, trunk short, tail very long and straplike. Head bones thin, fragile, particularly nasal rostrum, which most often is bent to side giving appearance of

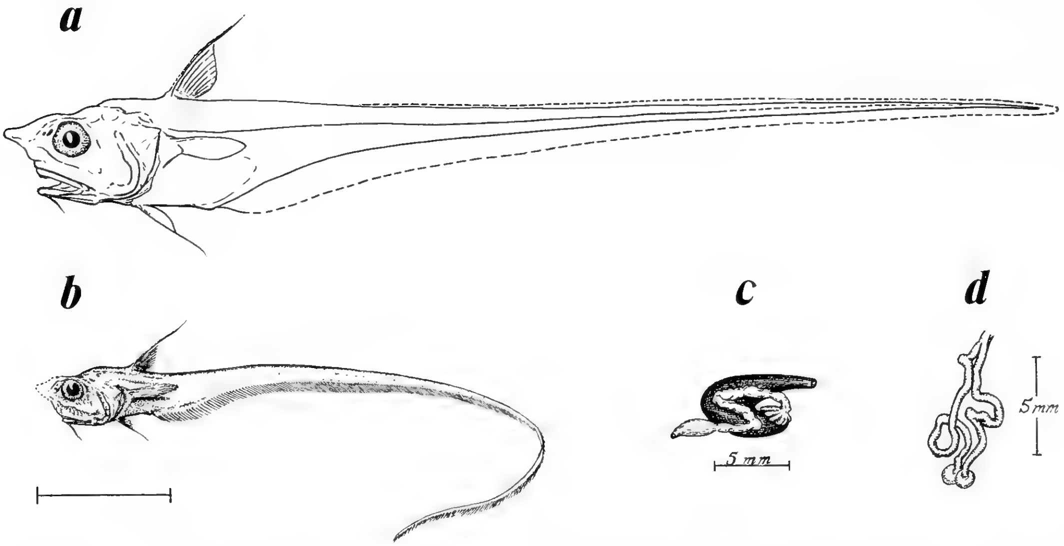


FIGURE 10. *Paracetonurus fragilis* (Garman). (*a*) Diagrammatic reconstruction from paratype MCZ 28585 and UMML uncat. (*b*) SIO 55-265, snout reconstructed. (*c*) Stomach and intestines of UMML uncat. (*d*) Retia and gas glands of UMML uncat. Scale rule for *a* and *b* equals 25 mm.

blunt snout. Snout relatively high and wide. Interorbital region broad, width usually greater than diameter of orbit. Suborbital region deep, without a strongly angular ridge. Mouth moderately large, upper jaws extend to vertical through hind margin of orbits or slightly beyond. Barbel moderately long, slender, length equal to or slightly greater than length outer gill-slit. Gill openings extend forward to below posterior third of orbit. Gill membranes little restricted (probably with a moderate free fold posteriorly over isthmus). Gill-rakers tubercular, gill lamellae short. Pyloric caeca short, thick, 10–15 in UMML specimen. Intestine short, only two loops from pyloric caeca to anus. Esophagus and caecal portion of stomach black; pyloric portion of stomach grayish brown. Rectum black, remainder of intestine and pyloric caeca pallid. Retia long, well developed, 2; gas glands 2.

First dorsal fin short, base low; second spinous ray weakly serrated and produced beyond segmented rays. Second dorsal fin rudimentary, originating posterior to vertical through origin of anal fin. Pectoral and pelvic fins small; the latter far forward, origin below preopercle angle, with outer ray slightly produced and extended past origin of anal fin.

Snout and probably most of anterior and ventral parts of head naked and covered with thin black integument. (I could find no scale pockets on the head of specimens I examined, but Garman's (1899:pl. 46, fig. 1) figure suggests that there are some over the gill covers.) Garman (1899:204) describes the scales as "small, thin, deciduous, with concentric striae; five scales in a row from the lateral line to the base of the first dorsal or thirty-one in a series from this dorsal to the anal." Garman's figure of a scale shows a single point on the posterior edge, but an otherwise spinuleless exposed field.

Teeth short, slender, sharp, in roughly two rows in premaxillae, in narrow band in mandibles; no enlarged series.

Coloration in alcohol. Head and abdominal region black, remainder of body brownish. Oral, branchial, and peritoneal cavities black. Gill arches and rakers blackish but lamellae pallid.

DISTRIBUTION.—The species is known only from the tropical eastern Pacific where it is found in waters of considerable depths. Specimens were obtained in three trawls fished on bottom in 3,058–3,334 m, and a single specimen was taken in an open midwater trawl fished to a depth of 1,335 m.

COMPARISONS AND REMARKS.—As the name implies, members of this species are extremely fragile. The few specimens available for examination were in such poor condition that an adequate description and illustration could not be prepared. The thin, flexible rostrum is often damaged and folded to the side (as is the rostrum on the specimen illustrated by Garman 1899:pl. 46, fig. 1), but when intact, the rostrum is moderately long and pointed. The fragile head, and particularly the rostrum, is highly reminiscent of the condition obtaining in specimens of *Hymenocephalus,* but members of that genus and *P. fragilis* differ in many other fundamental features. The small adult size of *P. fragilis* is indicated by the ripe condition of a 200-mm-TL female paratype (MCZ 28585), whose ovaries contained eggs as large as 1.3 mm in diameter.

This species is quite unusual and may represent a genus distinct from *Paracetonurus,* but it is placed in that taxon out of convenience, because an adequate study comparing it with other related forms could not be made. It differs from other members of *Paracetonurus* in having a less inflated head; thin, membranous, and mostly naked head covering (cf. moderately thick, completely scaled head covering); more pelvic fin rays (8–9 cf. 6–7); and a larger mouth (upper jaw extends posteriad to below hind third of orbits, cf. below middle third of orbits). The species is also fairly close to members of the genus *Sphagemacrurus* Fowler (in which Marshall (1973) has placed the species), but it differs in lacking a strong spinous suborbital ridge, a high first dorsal fin base, and a short blunt snout—all characteristic of *Sphagemacrurus.* The origin of the vent is also more anteriorly placed in species of *Sphagemacrurus* (below anterior third of first dorsal fin compared with below hind edge of first dorsal fin in *P. fragilis*).

Material Examined (7 specimens, 4 localities).—**Panama:** MCZ 28586 (holotype, about 230 mm TL); 6°17′N, 82°05′W, 3,058 m, beam trawl, Albatross sta. 3360, 24 Feb. 1890. —UMML uncat. (1, about 26 HL, 175+ TL); 6°53′N, 79°27′W, 3,193 m, R/V Pillsbury sta. 526, 5 May 1967. **Colombia:** MCZ 28585 (3 paratypes, about 29–35 HL, 190+ to 200 TL) and USNM 57857 (1, est. 26 HL, est. 175 TL); 2°35′N, 83°53′W, 3,334 m, beam trawl, Albatross sta. 3374, 3 Mar. 1890. **Eastern Pacific:** SIO 55–265 (1, 117 TL); 00°02′S, 100°23′W, 0–1,335 m, 3-m midwater trawl, R/V Horizon sta. ET(b)-H-65.

Malacocephalus Günther

Malacocephalus Günther, 1862:396 (as subgenus of *Macrurus*) (type-species *Macrourus laevis* Lowe, 1843, by monotypy).

Diagnosis.—A macrourine grenadier with anus remote from anal fin and closer to pelvic fins; periproct large. Two large dermal windows of light organ, the anterior one in a bean-shaped depression situated between bases of pelvic fins, the posterior one in a shallow circular depression close before the anus. Teeth large, widely spaced, in single row in lower jaw; usually larger posteriorly. Teeth in upper jaw in two rows or in narrow band; outer series distinctly spaced and enlarged. Pyloric caeca numerous (50–100 or more), multiply branched. Lowermost three or four branchiostegal rays scaled. Mouth large, upper jaw usually more than 45 percent of head length. No strongly developed scutelike scales on head ridges.

Remarks.—*Malacocephalus* comprises a close-knit group of about six species, one of which is undescribed (see Iwamoto 1970:410). Relationships of the genus lie closest to *Ventrifossa* Gilbert and Hubbs, 1920, a taxon represented in the eastern Pacific by a single member (of the subgenus *Lucigadus*), although the genus is common in most other warm-water areas. Members of the genus *Malacocephalus* are confined to upper-slope waters of tropical and warm-temperate regions. Three of the six species (*laevis* (Lowe, 1843), *nipponensis* Gilbert and Hubbs, 1916, and *hawaiiensis* Gilbert, 1905) are closely related and may eventually prove to represent one widely distributed species. Okamura (1970a:69) has, in fact, synonymized *M. nipponensis* with *M. laevis.*

Malacocephalus laevis (Lowe)

(Figure 11)

Macrourus laevis Lowe, 1843:92 (original description; off Madeira).

Malacocephalus laevis: Günther 1862:397–398. —Hubbs, Follett, and Dempster 1979:14 (list; first record from eastern Pacific).

Macrurus (*Malacocephalus*) *laevis*: Günther 1887:148, pl. 38, fig. b. See Marshall 1973:653 for extensive synonymy.

Malacocephalus sp.: Hubbs and Iwamoto 1977:243 (1 spec. from California).

Diagnosis.—A species of *Malacocephalus* with spinous second ray of first dorsal fin smooth; teeth in upper jaw in two distinct rows; pectoral fin rays 19–20; upper jaw less than 50 percent of head length.

Description of Eastern Pacific Specimen.—General features of fish seen in Figure 11. Head compressed and deep. Ridges not sharp or coarsely scaled; head contours smoothly rounded. Snout narrow, pointed (in somewhat

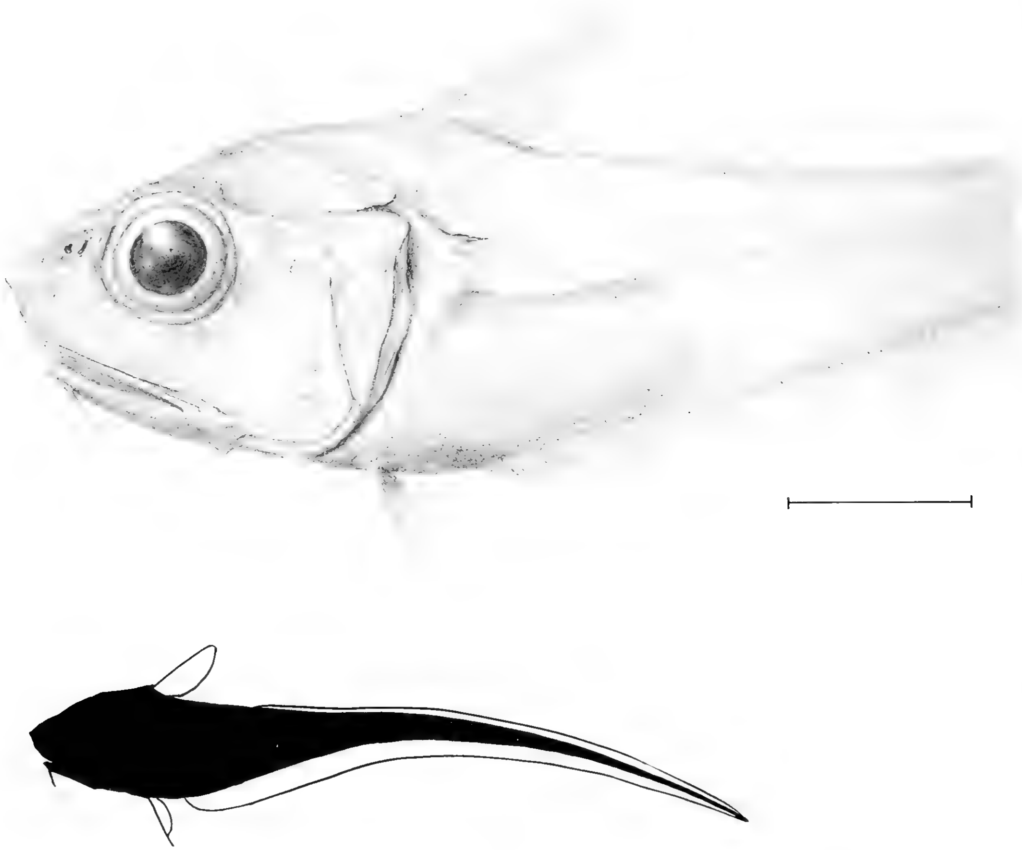


FIGURE 11. *Malacocephalus laevis* (Lowe). SIO 79-344, 58 mm HL, from off Santa Barbara County, California, in 229 m.

shriveled eastern Pacific specimen; probably rounded in life). Gill openings wide, extending anteroventrally to below hind margin of orbit. Gill membranes loosely connected to isthmus with a posterior free fold. Interopercle broadly exposed and scaled ventrally. Periproct region large, long-ovate, anus and urogenital opening at broader posterior end of region; anterior dermal window of light organ in deep, lunate to bean-shaped fossa between bases of pelvic fins and separated from periproct by a broad isthmus of scales. Several partially digested euphausids in stomach. Pyloric caeca fragile, thin, branched, difficult to count, but more than 50 terminal digits.

Scales uniformly small and finely spinulated. Snout and suborbital region completely scaled, without prominent naked areas. Coarse, scute-like scales completely absent; ridges of head all smoothly rounded. Lower jaw uniformly scaled. Lowermost branchiostegal rays scaled; gular membrane apparently without scales (but scales here normally highly deciduous and may have been present in life).

Color gray-brown overall; violet over abdominal region, shoulder girdle, and opercle; and blackish over chest, on branchiostegal membrane, and on gular region (violet regions probably not as prominent in undenuded and fresh specimens). Peritoneum brownish black. Oral valves and lower lips peppered with melanophores, remainder of oral cavity pale. First dorsal fin, pectoral fin, pelvic fin, and anterior portion of anal fin brownish black; second dorsal fin and most of anal fin pale or dusky.

COUNTS.—1D. II,11; 1P. 20/19; 2P. 9/8. Gill-rakers on first arch 3 + 9; on second arch 3 + 7. Scales below first dorsal approximately 16.

Measurements.—Total length 335 mm; head length 58 mm. The following in percent of head length: postrostral length of head 78; snout length 26; preoral length 17; internasal width 17.5; orbit diameter 36; interorbital width 27; postorbital length of head 41; distance orbit to angle of preopercle 43; suborbital width 12; upper jaw length 48; barbel length 17; length first gill-slit 26; preanal length 123; outer pelvic ray to anal origin 28; anus to anal origin 17; greatest body depth 85; interspace between 1D. and 2D. 48.

Comparisons and Relationships.—I have tentatively identified this single eastern Pacific specimen of *Malacocephalus* as *M. laevis*. All morphometric and meristic characters examined fell within the range of variation enumerated in a previous paper (Iwamoto 1970) for specimens I examined from the Atlantic Ocean. However, the snout length and interorbital width in the Pacific specimen were at the lower limits of the range for these characters in Atlantic specimens, and the orbit diameter was at the upper limit. Close comparison of the eastern Pacific specimen with others from the Atlantic Ocean showed only one difference—scales were absent on the gular membrane whereas most Atlantic specimens had a small patch of scales there. The deciduous nature of the scales in this area, however, may account for their absence in the somewhat denuded eastern Pacific specimen. Comparison of SIO 79-344 with specimens of *M. hawaiiensis* (USNM 51618, holotype; CAS-SU 8522, 3 paratypes) showed slightly lower values in relative snout length (26 percent head length cf. 28–29), preoral length (17 cf. 19–21), internasal width (17.5 cf. 21–25), interorbital width (27 cf. 31–35), length snout to anus (111 cf. 117–120), and 1D.–2D. interspace (48 cf. 57–75). Similar comparison of proportional measurements with specimens of *M. nipponensis* (FAKU 13316, 13318, 13321, and 13878) showed lower values in the eastern Pacific specimen in snout length (26 percent HL cf. 28–31), preoral length (17 cf. 20–21), interorbital width (27 cf. 30–35), and barbel length (17 cf. 21–24), but a greater value for the orbit diameter (36 cf. 29–34). The gill-raker count of 12 was also slightly higher than the 10–11 of the *M. nipponensis* specimens. Whether or not these slight differences are meaningful in delimiting species is as yet conjectural. Adequate series of each population should be compared before definitive statements are made regarding the number of valid species in the genus. Until then it seems wisest to retain the established names.

Remarks.—*Malacocephalus laevis* is listed by Hubbs, Follett, and Dempster (1979:14) in their "List of the fishes of California" on the basis of the present specimen. Mr. Eiichi Fujii has informed me (in litt., 6 Mar. 1979) of having collected specimens of the species from seamounts off the coast of Baja California while aboard the Kaiyo Maru in January and February of 1979.

Material Examined.—SIO 79-344 (1, 57.8 mm HL, 335 mm TL), California, Santa Barbara County, between Gaviota and Point Conception, 229 m, otter trawl, 10 Dec. 1968.

Ventrifossa Gilbert and Hubbs

Ventrifossa Gilbert and Hubbs, 1920:553 (type-species *Coryphaenoides garmani* Jordan and Gilbert, 1904, by original designation).

Diagnosis.—A genus of macrourine grenadier with anus removed from anal fin origin and closer to pelvic fin insertion; anus situated posteriorly in an oval-shaped area of naked black skin (the periproct) that extends forward to a small fossa (anterior dermal window) between pelvic fin bases. An often-inconspicuous lenslike posterior dermal window in front of anus. Second spinous ray of first dorsal fin slightly produced and finely toothed along leading edge (except in *V. atherodon*). Jaw teeth small, in narrow to moderately broad bands in upper jaw, outer series slightly enlarged in most species; lower-jaw teeth small, none enlarged, in one to several irregular series laterally. Branchiostegal membranes naked (in subgenus *Ventrifossa*) or usually with patches of scales (in subgenus *Lucigadus*) along exposed lowermost branchiostegal rays. No sharp, coarsely scaled, angular ridges on head; suborbital region with flat to gently rounded contours—scales here not modified to form stout shelves or ridges (as in *Nezumia*). Snout angular to rounded in profile, either without a spiny terminal scute or with a small unilateral one; supranarial ridge without modified scutelike scales; lateral angles of snout without spinous tubercular scale at tip. Body and head scales generally small, densely covered with fine, slender, conical or shield-shaped spinules.

Remarks.—*Ventrifossa* as here diagnosed comprises three major groups which I treat as subgenera: *Ventrifossa*, *Lucigadus*, and *Soko-*

dara (new). In describing *Ventrifossa,* Gilbert and Hubbs (1920:543) recognized four subgenera, three of which were monotypic: *Atherodus* (with *Optonurus atherodon* Gilbert and Cramer, 1897), *Lucigadella* (with *Macrourus nigromarginatus* Smith and Radcliffe, 1912), and *Lugigadus* (with *Macrourus lucifer* Smith and Radcliffe, 1912). *Atherodus* was distinguished from the other subgenera on the basis of dentition (teeth of lower jaw in two series, arrowhead-shaped canines on upper jaw), scale spinules (few and short), orbit size (3 in head), and dorsal spine (without denticulations). My studies of the genus have shown that all but the last character are nondiagnostic for the subgenus in that the character states are shared with other members of the genus, or that they are part of a graduated character spectrum within the genus. The absence of denticulations on the dorsal spine appears to be the sole character distinguishing *V. atherodon* from other members of the genus. The sister-group relationship of *V. atherodon* and *V. ctenomelas* (Gilbert and Cramer, 1897) is strongly suggested in other shared specializations and in the common occurrence of the two species in the Hawaiian Islands, where *V. atherodon* is apparently endemic (*V. ctenomelas* is also found in the western Pacific).

Characters that Gilbert and Hubbs (1920) used to separate *V. lucifer* into a distinct subgenus, *Lucigadus,* include the ventral light organ ("a conspicuous pearly body in a sheath"), mouth angle ("highly oblique"), and spinules on scales ("in quincunx order"). My reexamination of the type-specimens of *V. lucifer* has shown that the "sheath" in which the "pearly body" lies is an artifact of preservation, the "sheath" having formed by the ripping midventrally of the thin abdominal wall below the light organ. The pearly color of the organ is from the reflective layer surrounding the organ. The light organ in *V. lucifer* is not notably different from that of other closely related members of the genus, including *V. nigromarginata.* The arrangement of spinules on the scales appears to show no meaningful relationships in this genus nor in the closely related *Nezumia*—the character is useful, however, at the species level. The notably oblique mouth of *V. lucifer* represents one extreme in a graded series that includes—from mouth little oblique to mouth notably oblique—*Macrourus nigromarginatus, Macrurus fasciatus* Weber, 1913, *Macruroplus ori* Smith, 1968, *Macrourus nigromaculatus* McCulloch, 1907, and *Macrourus lucifer.* I consider these five species as representatives of the subgenus *Lucigadus* Gilbert and Hubbs.

The subgenera of *Ventrifossa* as I recognize them can be characterized in the following manner:

Subgenus *Ventrifossa* Gilbert and Hubbs, 1920:553 (type-species *Coryphaenoides garmani* Jordan and Gilbert, 1904).

1. Mandibular teeth in one to three irregular series laterally.
2. Premaxillary teeth in a narrow band with outer series slightly to prominently enlarged; tooth band extends posteriad beyond maxillary process.
3. Mouth slightly oblique, moderate to large, upper jaw length 42–53 percent head length.
4. Tip of snout with a blackish spot, or entire leading edge black.
5. Branchiostegal and gular membranes completely naked.
6. Gill-rakers 13–20 total on inner series of outer (first) arch.
7. Pores of cephalic lateral line system small and inconspicuous.
8. Pyloric caeca numerous, 40–70 in distal count, usually branched near base.
9. Snout without spinous tubercular scute at tip.
10. Abdominal vertebrae 11–12.
11. Ventral aspects of body not appearing to have shifted notably forward.
12. Infraorbital shelf not exceedingly narrow anteriorly.

Included species: *V. atherodon* (Gilbert and Cramer, 1897), *V. ctenomelas* (Gilbert and Cramer, 1897), *V. divergens* Gilbert and Hubbs, 1920, *V. garmani* (Jordan and Gilbert, 1904), *V. macropogon* Marshall, 1973, *V. mucocephalus* Marshall, 1973, *V. petersonii* Alcock, 1891, and one or two undescribed speces (specimens in the CAS collection).

Subgenus *Lucigadus* Gilbert and Hubbs (type-species *Macrourus lucifer* Smith and Radcliffe, 1912).

1. Mandibular teeth in several irregular series laterally or in a narrow to moderately wide band.

2. Premaxillary teeth in a narrow to moderately wide band with outer series slightly enlarged; teeth not present posteriad of hind margin of maxillary process.
3. Mouth slightly to greatly oblique, moderate in size, 33–45 percent HL.
4. Tip and leading edge of snout without distinct pigmentation.
5. Lowermost of branchiostegal rays scaled.
6. Gill-rakers 7–16 total on inner series of outer (first) arch.
7. Pores of cephalic lateral line system prominent in most species.
8. Pyloric caeca 30–55, generally unbranched.
9. Snout tip without stout, spinous, scutelike scale.
10. Abdominal vertebrae 10–11.
11. Ventral aspects of body appearing to have migrated far forward resulting in anal origin below first dorsal; pelvic origin below operculum; gill membranes united below orbits; snout high, rounded; base of first dorsal high.
12. Infraorbital shelf not especially narrow anteriorly.

Included species: *V. fasciata* (Weber and de Beaufort, 1929), *V. lucifer* (Smith and Radcliffe, 1912), *V. nigromarginata* (Smith and Radcliffe, 1912), *V. nigromaculata* (McCulloch, 1907), and *V. ori* (Smith, 1968).

Subgenus *Sokodara* Iwamoto, new subgenus (type-species *Coryphaenoides misakius* Jordan and Gilbert, 1904).

1. Mandibular teeth in a narrow band of two to three irregular series laterally.
2. Premaxillary teeth in a narrow band; outer series scarcely enlarged.
3. Mouth slightly oblique, large, 35–42 percent head length.
4. Tip of snout blackish.
5. Branchiostegal and gular membranes completely naked.
6. Gill-rakers 14–16 total on inner series of outer (first) arch.
7. Pores of cephalic lateral line system small and inconspicuous.
8. Pyloric caeca 54–65 in distal count, branched near base.
9. Snout with a small, unilateral, spinous scute at tip.
10. Abdominal vertebrae 14.
11. Ventral aspects of body not appearing to have shifted notably forward.
12. Infraorbital shelf greatly narrowed anteriorly.

Included species: *V. misakia* and one or two undescribed species (specimens in CAS and USNM collections).

Distribution.—The genus *Ventrifossa* is represented in the eastern Pacific by one wide-ranging, Southern Hemisphere species, *V.* (*Lucigadus*) *nigromaculata*. That representatives of the more diverse subgenus *Ventrifossa* are entirely absent from this region forms a striking parallel with a similar situation in the eastern Atlantic, where the genus is entirely unknown (except off Cape Point, South Africa)—this despite the presence in the western Atlantic of two species of subgenus *Ventrifossa* (*V. macropogon* and *V. mucocephalus*) and one of subgenus *Lucigadus* (species cf. *V. ori*). *Ventrifossa* is known in most other warm-water regions of the Pacific and Indian oceans.

Ventrifossa nigromaculata (McCulloch)

(Figures 12*a*, 18*d*)

Macrourus nigromaculatus McCulloch, 1907:346–348, pl. 63, figs. 1, 1a (original description; holotype and 4 paratypes; 56 km E of Sydney, Australia, in 1,463 m).

Lionurus nigromaculatus: McCulloch 1919:32 (listed), pl. 11, fig. 114a.

?*Macruroplus nigromaculatus*: Smith 1949: 135 (brief description; southern Africa).

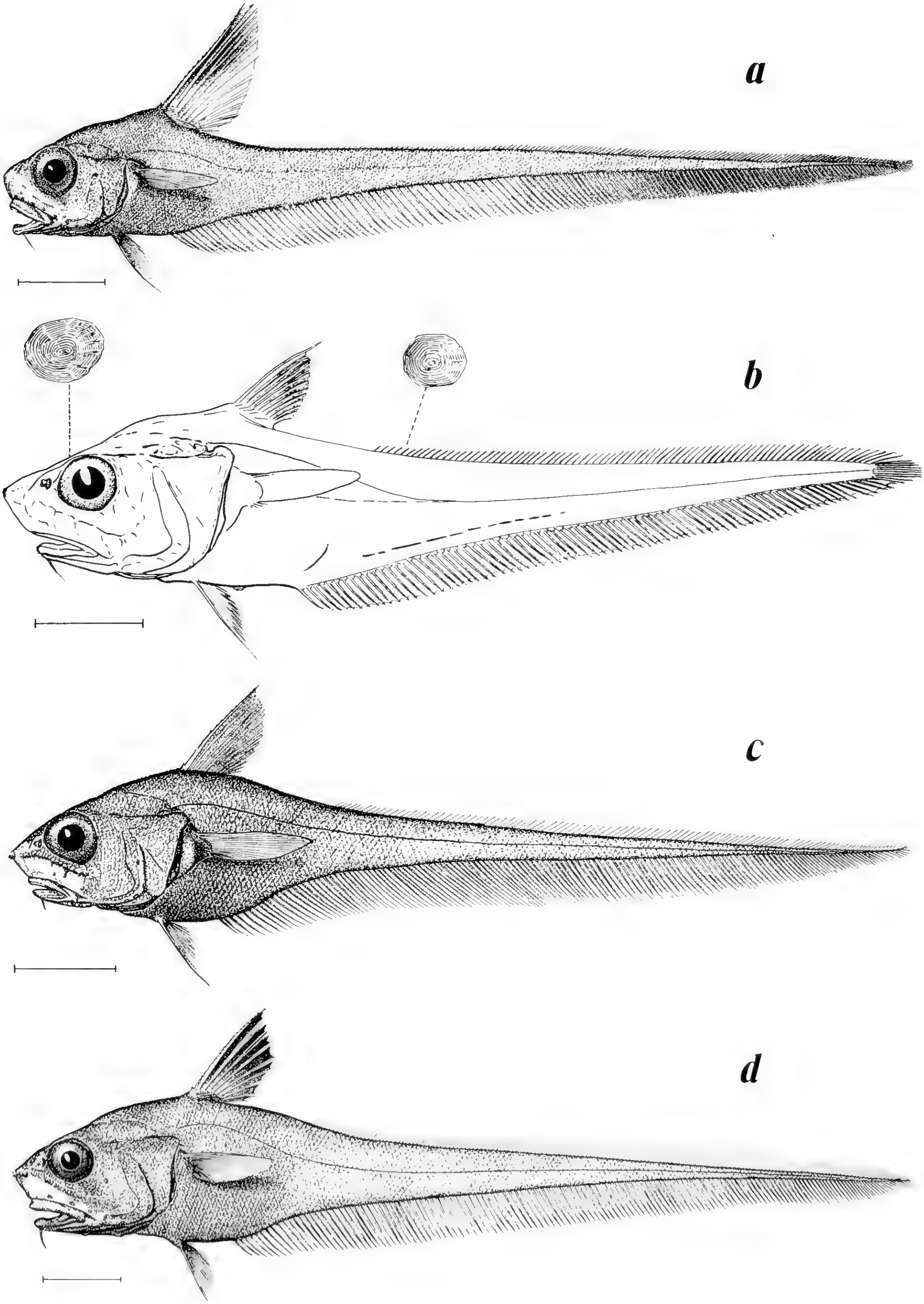
Nezumia nigromaculata: Makushok 1967:207 (name).

Macruroplus potronus Pequeño, 1971:290–291, fig. 15 (original description; holotype only, off Chile, 34°58′S, 72°36′W, in 200 m).

Diagnosis.—A species of *Ventrifossa*, subgenus *Lucigadus*, with 13–15 pelvic fin rays. Total gill-rakers on first arch 12–16; on second arch 12–14. Upper jaw length 39–45 percent HL. Scales below first dorsal fin about 16–20; below second dorsal fin 10–12. First dorsal fin with a prominent black blotch.

Description.—General features of the fish are best seen in Figure 12a. Gill membranes unite across isthmus at a point below middle of orbits and slightly ahead of posterior end of maxillae. Head ridges virtually nonexistent; all surfaces smoothly rounded; suborbital region almost flat. Pores on head well developed but not especially prominent.

Pyloric caeca well developed, numerous, rather large; unbranched except at very base.


a
b
c
d

Configuration of intestinal tract a rather simple 'S' pattern. Gas glands a flattened kidney shape; mesial surfaces of the two glands closely abutting; retia attached mesially at about middle of each gland. Retia slender, short, uncoiled.

Spinules on body scales very small, slender, conical, greatly reclined, and arranged in more or less parallel horizontal rows in middle part of vertically elongate exposed field. Spinule rows number 11–12 on larger scales of CAS specimens. Scales present on lowermost three or four branchiostegal rays and also densely cover exposed ventral surfaces of interopercle.

Anterior dermal window of light organ large, situated between pelvic fin bases, and connected to periproct by isthmus of naked black skin. Posterior dermal window relatively prominent in most specimens examined, discernible as a discrete translucent area lying immediately anteriad of anus and occupying most of anterior portion of periproct.

Fins well developed. First dorsal fin large; height about equal to or greater than length of head. Anal fin high along almost entire length. Pelvic fins broad but not especially long; outer ray slightly produced, extending slightly beyond anal fin origin.

Coloration in alcohol. Ground color tawny to grayish. Trunk region with violet tinge becoming bluish over abdomen and blackish around periproct and pelvic fins. First dorsal fin with a prominent black blotch on distal one-half to two-thirds; blotch not extending to margin of fin. Anal rays lightly punctate anteriorly and blackish along distal margins. Median fins blackish posteriorly towards tail tip. Pelvic fins blackish or covered with bold punctations. Gill covers and gill membranes blackish or densely punctate. Oral cavity generally pale with few scattered small areas blackish or densely punctate. Outer wall of gill cavity black along first gill-slit and around outer margins, but pale otherwise. Gill-rakers and gill-arches blackish, but gill filaments pale. Lips dusky to somewhat blackish.

COUNTS (from 13 specimens).—1D. II,10–11; 1P. 19–23; 2P. 13–15 (one specimen with 12 on left fin, 13 on right fin). Total gill-rakers on first arch 12–16; on second arch 12–14. Scales below first dorsal about 16–20; below second dorsal 10–12; over distance equal to predorsal length 42–45. Pyloric caeca 30, 32, and about 57 in three specimens.

MEASUREMENTS.—Twelve specimens examined ranged 17–50 mm HL; 94+ to 339 mm TL. The following are in percent of head length: postrostral length 73–81 ($\bar{x} = 77.2$; S.D. = 2.57); snout length 25–30 ($\bar{x} = 28.1$; S.D. = 1.55); ventral length of snout 18–22 ($\bar{x} = 19.1$; S.D. = 1.38); orbit diameter 40–47 ($\bar{x} = 42.9$; S.D. = 2.71); interorbital width 20–26 ($\bar{x} = 22.1$; S.D. = 2.07); suborbital width 12–18 ($\bar{x} = 15.7$; S.D. = 2.14); length upper jaw 39–45 ($\bar{x} = 41.2$; S.D. = 1.80); length barbel 18–26 (usually 20–26); length outer gill-slit 23–30 ($\bar{x} = 26.0$; S.D. = 1.68); preanal length 140–158; outer pelvic ray to anal origin 41–54; anus to anal origin 20–30; greatest body depth 92–112 (usually over 100); depth over anal origin 75–105; 1D.–2D. interspace 32–58; height 1D. 101–134; length 1P. 63–73; length 2P. 44–58.

REMARKS.—*Macruroplus potronus* Pequeño, 1971, was described from a single specimen taken off Chile in 200 m. The specimen was examined and photographed by Dr. William N. Eschmeyer in 1974. Examination of his photographs and the original description leaves no doubt as to the conspecificity of that specimen with those I have examined from the eastern Pacific and called *Ventrifossa nigromaculata*. Should these eastern Pacific specimens prove distinct from western Pacific specimens now referred to this species, the name *potronus* remains available.

Ventrifossa nigromaculata is a distinctive species widely distributed in temperate waters of the South Pacific. Although considerable variation was found in several characters in the specimens examined, the material available did not suggest a difference in populations from opposite sides of the Pacific. Atlantic Ocean spec-

←

FIGURE 12. (*a*) *Ventrifossa nigromaculata* (McCulloch). Specimen CAS 41668, 35 mm HL, from off Chile in 750 m. (*b*) *Nezumia liolepis* (Gilbert), CAS-SU 21402, 55 mm HL, from off Santa Cruz Island, California in 1,397–1,629 m. Enlarged views of scales from interorbital region and region just below anterior end of second dorsal fin. (*c*) *Nezumia pulchella* (Pequeño), CAS 28763, 46 mm HL, from off Peru in 272 m. (*d*) *Nezumia stelgidolepis* (Gilbert), CAS 33109, 56 mm HL, off Pescadero Point, California, in 439 m.

imens previously referred to this species are apparently distinct and may represent an undescribed species.

Distribution.—Australia, New Zealand, and Chile, in 230–1,463 m.

Size.—To about 50 mm in head length and about 340 mm total length.

Material Examined (13 specimens, 8 localities).—**Chile:** USNM uncat. (2, 20–35 mm HL, 140–246 mm TL), NW of Valparaíso, ca. 400 m; M/V Ruiz I; 11 Feb. 1966. —CAS 41669 (1, 33 HL, 240 TL), 32°08.5′S, 71°43′W, 960 m, Anton Bruun cr. 18A, sta. 703 (field no. LWK66–47), 12 Aug. 1966. —CAS 41668 (1, 35 HL, 262 TL), 34°06.5′S, 72°18.5′W, 750 m, Anton Bruun cr. 18A, sta. 687 (field no. LWK66–25), 5 Aug. 1966.

New Zealand: BMNH 87.12.7.118 (1, 17 HL, 94+ TL), Challenger sta. 166, 275 fms (503 m). —LACM 11336-3 (1, 38 HL, 280 TL), 41°35′S, 175°00′E, 256–490 m, Eltanin sta. 1848, 19–20 Dec. 1961. —LACM 10968–12 (5, 25–37 HL, 192–283 TL), 44°00′S, 178°06′W, 230–421 m, Eltanin sta. 1398, 29 Nov. 1964. —FAKU 42147 (1, 41 HL, 300 TL), Kaiyo Maru sta. 29, July 1968. —FSFRL B3052 (1, 50 HL, 339 TL), 44°20.5′S, 179°17.5′W, 750 m, Kaiyo Maru sta. 33, 15 July 1968.

Nezumia Jordan

Nezumia Jordan, 1904, *in* Jordan and Starks: 620 (type-species *Nezumia condylura* Jordan and Gilbert, 1904, by original designation).

?*Macruroplus* Bleeker, 1874:369 (type-species *Macrourus serratus* Lowe, 1843, by monotypy) (nomen nudum; see Poll 1953:238).

Lionurus:auct. (*non* Günther, 1887).

Diagnosis.—A macrourine grenadier with anus removed from anal fin origin (closer to pelvic fin insertion in most species) and situated in an oval-shaped area of naked black skin (the periproct). A small fossa (anterior dermal window of ventral light organ), round to teardrop shaped, forming anterior point of periproct in most species, detached from periproct in some species. Teeth small, in narrow to broad bands in both jaws; outer series of teeth in upper jaw of most species uniformly spaced and slightly enlarged. Teeth on premaxillary bone do not arise posteriad of maxillary process. Mouth moderate to small, upper jaw length less than 40 percent of head length in most species. Snout pointed or bluntly rounded, with stout, spiny, tuberclelike scales at tip and lateral angles, prominent in almost all species. Barbel present. Suborbital shelf covered with two (in most species) or more rows of stout, deeply embedded (except in *N. liolepis*), nonimbricate, spinous scales; these scales form a prominent edge or crest that runs longitudinally from lateral angle of snout to preopercle bone and divides suborbital region into upper and lower halves. Body scales covered with needlelike to shield-shaped spinules (spinules almost obsolescent in *N. liolepis*). Snout and suborbital areas with some naked areas along ventral margins in most species, almost entirely naked ventrally in these areas in several species. Total gill-raker number on mesial side of outer (first) arch less than 12 in all but a few species. Color various shades of black, brown, blue, or violet; some species with last two colors have silvery reflections on body. Pyloric caeca unbranched and fewer than 30 in distal count in most species, as many as 60 in the few species with branched caeca. Retia two (occasional individuals may have four), slender, uncoiled; gas glands globular, sometimes somewhat flattened.

Remarks.—The genus *Nezumia* is a diverse group of slightly more than 40 species of which ten are known and confined to the eastern Pacific. Most of these ten species have restricted distributions, but *N. stelgidolepis* is known from southern Peru to southern British Columbia, and *N. convergens* is common in waters from northern Peru to Costa Rica and is here recorded from the Islas Tres María and the Gulf of California. The distribution of six species (*latirostrata, liolepis, orbitalis, parini, pudens, pulchella*) each spans fewer than 30 degrees of latitude. *N. loricata* is known only from isolated captures in the Galápagos and off central Chile.

Although most other genera are poorly represented in the eastern Pacific, the region has proved rich in *Nezumia* species. The ten species here recorded rank the fauna among the largest found in broadly comparable geographical areas. Based on my examination of specimens and from the literature, a breakdown of the number of *Nezumia* species by area is as follows:

Eastern Pacific—10 spp.
Atlantic—14 spp.
  Eastern—10 spp.
  Western—9 spp.
Japan (8) + Philippines (4)—10 spp.
Hawaii—7 spp.
Western Indian Ocean— ?4 spp.
Central Indian Ocean— ?4 spp.

The few species recorded from the Philippines is surprising, as the area is otherwise exceedingly rich in grenadier species, especially of the genus *Coelorinchus*. Despite the extensive collecting by the ALBATROSS in the early part of the century, the area remains poorly known in terms of its deepwater fauna, and doubtless, other species of *Nezumia* will subsequently be found there. The South China Sea and the Indo-Australian Archipelago likewise remain relative unknowns, and more deepwater collecting is badly needed in these biologically rich areas. Indian Ocean grenadiers have not been comprehensively reviewed by recent workers; the generic allocations of many species are still questionable.

Members of the genus are of small to moderate size; only a few attain lengths of more than 340 mm in total length (only *N. stelgidolepis* in the eastern Pacific, but other species in the Atlantic and western Pacific). The larger species tend to have a larger, more terminal mouth and stronger, longer teeth—these features being suggestive of a predatory habit on larger, more active prey. The smaller species with their smaller, more inferior mouth, and longer, more pointed snout most likely feed on small prey captured on or in the bottom substratum. *Nezumia parini* is an enigma, however, in that it is strictly bathypelagic (the only member of the genus to be so), yet it retains a physiognomy much like that of its bottom-dwelling congeners (see Hubbs and Iwamoto (1977) for additional discussion of this peculiar species).

The genus is primarily one of upper- and middle-slope fishes, with few species ranging deeper than 2,000 m. Of the eastern Pacific species (Table 2), *N. convergens* not only has the second broadest horizontal range, but also the greatest vertical range, and it is probably the deepest-living species. In contrast, *N. stelgidolepis*, which has the broadest horizontal range of the eastern Pacific species, has only a moderate depth range and has been captured at the shallowest depth.

The sole bathypelagic member of the genus, *N. parini*, has been captured in midwater nets fished primarily in depths of 1,000 m or greater. In the type-series, 14 of 23 captures of the fish were made in nets fished to an estimated depth of 1,000 m or greater; in seven, the nets were fished to depths estimated at between 675 and 940 m; and only in two were the nets fished shallower (estimated depths of 420 and 455 m) (Hubbs and Iwamoto 1977).

Genera most closely related to *Nezumia* are *Ventrifossa* Gilbert and Hubbs, 1920, and *Malacocephalus* Günther, 1887; the three constitute a close-knit unit which I (Iwamoto 1972) have called the tribe Malacocephalini. The unifying characters of this tribe are the presence in the members of seven branchiostegal rays, a well-developed periproct region that is remote from the anal fin origin, and the presence of one or two dermal windows of the light organ anterior to the anus.

TABLE 2. COMPARISON OF CAPTURE DEPTHS OF NINE SPECIES OF *NEZUMIA* FROM THE EASTERN PACIFIC OCEAN.

Species	Capture depths (m) min.	max.	difference
stelgidolepis	227	909	632
pulchella	272	735	463
orbitalis	523	800	277
ventralis	549	717	168
pudens	580	1,238	758
loricata	600	1,480	880
convergens	600	1,865	1,265
latirostrata	605	1,400	795
liolepis	682	1,629	947

Nezumia liolepis (Gilbert)

(Figures 12*b*, 18*c*)

Macrurus (Lionurus) liolepis GILBERT, 1890:117 (original description, off southern California, ALBATROSS sta. 2980, in 1,103 m).
Lionurus liolepis: GOODE AND BEAN 1896:409 (occurrence).
Macrurus liolepis: GARMAN 1899:199–200 (description; records from ALBATROSS sta. 3418, 3424, 3436).
Macrurus barbiger GARMAN, 1899:197, pl. 45, figs. 2–2b (original description; off Islas Tres Marías, Mexico, ALBATROSS sta. 3424, in 676 fm [1,236 m]).
Lionurus (Lionurus) barbiger: GILBERT AND HUBBS 1916:146 (listed).
Lionurus (Lionurus) liolepis: GILBERT AND HUBBS 1916:146 (listed).
Nezumia liolepis: FITCH AND LAVENBERG 1968:142 (listed).
Ventrifossa barbiger: MARSHALL 1973:654 (listed).

DIAGNOSIS.—A *Nezumia* with 10–11 (rarely 12) pelvic fin rays. Few serrations on second spinous ray of first dorsal fin. Thin, deciduous scales on body with few or no spinules on exposed field. Small ventral light organ. Upper jaw 31–40 percent HL.

DESCRIPTION.—General features of fish seen in Figure 12b. Head moderately compressed and deep. Suborbital ridge rounded; shallow, obtuse angle formed by dorsal and ventral surfaces. Interorbital region shallowly concave; width about equal to or less than orbit diameter. Snout narrow, bluntly pointed, protruding slightly beyond rather large, almost lateral mouth. Jaws only slightly restricted by lip-folds at posterior angle. Opercular openings wide, extending above a horizontal through dorsal edge of orbit; gill membranes loosely attached to isthmus. Nape high, strongly arched in large adults. First dorsal fin base low. Periproct region about equidistant from pelvic fin insertion and anal fin origin; ventral light organ poorly developed, inconspicuous without dissection. Gill-rakers small, tubercular. Gill filaments long; length of longest more than half diameter of orbit, about equal to or longer than least width of suborbital region. Pyloric caeca slender; rather short, less than diameter of orbits; biramously branched, each main stem branching one or two times.

Fin rays all relatively slender and delicate. Second spinous ray of dorsal fin slightly prolonged; leading edge smooth except for a few small denticles near distal end. Outer ray of pelvic fin slender; filamentous tip extends slightly beyond origin of anal fin.

Overall coloration grayish brown tinged with violet; surface over abdomen much darker, over operculum blackish, but anteriorly over rest of head and especially snout paler. Lips dark brown to blackish; fins dusky to blackish. Gill membranes black. Outer-wall lining of gill chamber blackish; inner-wall lining grayish to pale. Lining of oral cavity blackish.

Scales highly deciduous; few specimens with any scales remaining. A sizable patch remaining dorsally on head and snout of CAS-SU 2545, 50 mm HL. Larger of these scales with 5–7 rows, each with 2–3 long conical spinules (Fig. 12b). Scales over dorsal surface of snout either with one to several low ridges that are sometimes armed with one or a few short spinules, or scales completely lack ridges and spinules. Dorsal surface of snout lacks scales along leading edge and along snout ridges. Ventrally, snout entirely naked back onto suborbital region to vertical through end of maxillary, but a narrow, thin wedge of small, thin, cycloid scales extends forward to about level of anterior border of orbits. Rami of lower jaw with small, fine, spinuleless scales located mainly about median axis of each ramus.

COUNTS (from 38 specimens).—1D. II,8–11 (total 10–13; $\bar{x}$ = 11.87; S.D. = 0.75); 1P. 20–25 ($\bar{x}$ = 22.72; n = 61; S.D. = 1.23); 2P. 10–11 (rarely 12). Gill-rakers on first arch 1–3 + 7–10 (total 9–12, usually 10–11); on second arch 1–3 + 7–10 (9–12 total). Scales below first dorsal 8–10; below second dorsal 7–10; over distance equal to predorsal length of head 39–44 (3 specimens). Pyloric caeca 25–37 (6 specimens).

MEASUREMENTS (from 38 specimens).—Total length 114–290 mm; head length 26–63 mm. The following in percent of head length [range ($\bar{x}$; n; S.D.)]: postrostral length of head 73–81 (77.68; 34; 1.77); snout length 24–28 (25.95; 36; 1.12); preoral length 13–23 (19.12; 34; 2.00); internasal width 17–23 (19.00; 26; 1.50); orbit diameter 25–31 (27.18; 38; 1.50); interorbital width 21–27 (23.28; 37; 1.25); postorbital length of head 43–56 (50.17; 35; 3.42); distance orbit to angle of preopercle 36–44 (39.39; 37; 1.88); suborbital width 11–15 (12.92; 37; 0.96); upper jaw length (28) 31–40 (34.12; 38; 2.31); barbel length 10–20 (14.68; 37; 2.59); length first gill-slit 14–23 (17.38; 37; 1.65); preanal length 119–142 (131.52; 27; 5.81); outer pelvic ray to anal origin 32–57 (42.26; 26; 6.24); anus to anal origin 13–27 (19.76; 24; 4.66); greatest body depth 60–82 (70.89; 29; 4.86); 1D.–2D. interspace 28–48 (34.63; 36; 6.15); 1D. height 58–73 (62.267; 21; 4.27); 1P. length 43–53 (49.15; 24; 3.30); 2P. length 42–55 (48.03; 25; 6.13).

COMPARISONS AND RELATIONSHIPS.—*Nezumia liolepis* belongs with that group of *Nezumia* species characterized by (1) a moderate-sized mouth, (2) a relatively deep, compressed head, (3) a rather blunt, high, and usually weakly armed snout, and (4) relatively wide gill openings. This group includes such geographically separated species as *N. stelgidolepis* (Gilbert), *N. atlantica* (Parr, 1946), *N. africana* (Iwamoto, 1970), *N. bubonis* Iwamoto, 1974, *N. dara* (Gilbert and Hubbs, 1916), *N. burragei* (Gilbert, 1905), *N. hebetata* (Gilbert, 1905), *N. holocentrus* (Gilbert and Cramer, 1897), *N. kamoharai* Okamura, 1970, and *N. macronema* (Smith and Radcliffe, 1912). *N. liolepis* is readily distinguished from these species in having the combination of (1) few serrations on the dorsal spine, (2) reduced spinulation on the scales of the head and body, (3) extensive naked areas on the dorsal and ventral surfaces of the snout and suborbital region, (4) a distinctive shape of the operculum, and (5) a relatively posteriad position of the anus.

REMARKS.—Garman (1899:197) described *Macrurus barbiger* from a 10-inch (25-cm) specimen taken off the state of Guerrero, Mexico.

He contrasted the species with *N. liolepis*, reporting that *barbiger* has "the head more round, the cheeks more convex, the snout narrower, and the barbel longer, besides which differences there are others in the fins and the colors." I compared the holotype of *M. barbiger* (MCZ) 28597) with specimens Garman identified as "*Macrurus liolepis*" and found that these differences do not hold up. There is little doubt that the *M. barbiger* holotype and the "*M. liolepis*" specimens are conspecific.

Distribution.—The species is known from off Monterey Bay, California (36°49′20°N), to south of Guerrero, Mexico (17°24′N), including the Gulf of California south of Guaymas (Garman 1899:200, Albatross sta. 3436). Capture depths have ranged from 768–823 m (CAS 26638) to 1.655 m (Albatross sta. 3436).

Material Examined (40 specimens from 9 localities).—**California** (north to south): CAS-SU 5351 (4, 28–52 mm HL), off Monterey Bay, 36°49′20″N, 122°12′30″W, 834 m, Albatross sta. 3126, 13 Mar. 1889. —CAS-SU 21402 (5, 53–63), off Santa Cruz Islands, 1,397–1,629 m, Albatross sta. 4428, 14 Apr. 1904. —USNM 44271, syntypes (2, 45–50), E of Santa Cruz Islands, 33°49′45″N, 119°24′30″W, 1,103 m, Albatross sta. 2980, 12 Feb. 1889. —CAS 26638 (4, 41–56), off San Mateo Point, 33°15′30″N, 117°38′W, 768–823 m, N. B. Scofield sta. 53B59, 23 June 1953. —CAS-SU 2545 (6, 27-50), off San Diego, 32°49′N, 117°27′30″W, 656 m, Albatross sta. 2936, 4 Feb. 1889. —USNM 77495 (3, 33–33), off Point Loma, San Diego, 940–989 m, Albatross sta. 4333, 9 Mar. 1904.

Mexico: MCZ 28597 (holotype of *Macrurus barbiger* Garman, 1899, 54 mm HL), off Islas Tres Marías, 21°15′N, 106°23′W, 1,236 m, Albatross sta. 3424, 18 Apr. 1891. —CAS 40230 (10, 38–47), off Jalisco, 19°43.5′N, 105°35.5′W, 700–900 m, Te Vega cr. 19, sta. 17, 10 July 1968. —CAS 40231 (5, 51–58), off Guerrero, 17°24′N, 101°31′W, 940–1,000 m, Te Vega cr. 19, sta. 19, 12 July, 1968.

Nezumia pulchella (Pequeño, 1971)

(Figures 12*c*, 18*b*)

Macruroplus pulchellus Pequeño, 1971:293–294, fig. 17 (original description; off Chile; type-locality 25°26′S, 70°37′W, 374–424 m).

Diagnosis.—A species of *Nezumia* with 11–12 pelvic fin rays. Gill-rakers on first arch 9–11 total; on second arch 8–10. Spinules on body scales conical, in distinct, slightly convergent rows. Ventral surfaces of snout, suborbital region, mandibular rami, and gular and branchiostegal membranes usually naked, but occasionally with few scattered scales. Barbel 9–16 percent of HL; upper jaw 30–34 percent HL.

Description.—General features of fish seen in Figure 12c. Head moderately compressed, trunk deep in large adults, less so in smaller individuals. Suborbital ridge prominent in study material, accentuated by shrunken lower portion of region; suborbital ridge of fresh specimens probably not as pronounced. Other head ridges rather smoothly rounded without reinforcing spiny scutelike scales. Snout narrow and short, relatively blunt; armed with small spiny scutes at tip and at lateral angles. Mouth moderately large, lateral, unrestricted by lip folds at angle. Posterodorsal corner of opercle slightly produced. Interopercle broadly exposed posteriorly and ventrally. Gill openings wide, membranes broadly connected over isthmus with a moderately broad free fold. Anterior dermal window of light organ small, in shallow fossa between bases of pelvic fins and slightly removed from periproct. Gill filaments long; length of longest about equal to diameter of pupil, greater than width of suborbital region. Pyloric caeca well developed, but fairly short (about 0.6 into orbit diameter), branched only at bases; 23–31 in nine specimens.

Scales of body with distinct, slightly convergent rows of small conical spinules on exposed fields. Scales generally lacking on gular membrane, mandibles, lower part of snout and suborbital region, and branchiostegal membrane, but one specimen (CAS 38323) with two small scales on right gill membrane near base of fifth branchiostegal ray. Small areas dorsally behind leading edge of snout naked. Stout, spiny scales at tip and lateral angles of snout and in two rows along dorsal surface of suborbital region, but scales otherwise not modified. Sensory pores along ventral margins of suborbital region and preopercle, and along inner margins of mandibles large and prominent.

Teeth in both jaws in rather narrow band; teeth small except for outer premaxillary series, which is composed of enlarged, spaced, sharp, conical teeth.

Coloration in alcohol medium brown overall with bluish tinge over abdomen and blackish ventrally on trunk. Gill membranes black; fins blackish. Lining of buccal cavity pale except for grayish oral valves. Peritoneal cavity pale but peppered with small melanophores.

Counts (from 16 specimens).—1D. II,10–11 (9 in one specimen); 1P. 19–28 ($\bar{x} = 24.52$; $n = 31$; S.D. = 2.06); 2P. 11–12. Mesial gill-rakers on first arch 1–3 + 7–9 (9–11 total); on second arch 1–2 + 7–9 (8–10 total). Scales below first dorsal 6½–8½; below second dorsal 5½–7½;

below midbase of first dorsal 4½–6; over distance equal to predorsal length 35–44 (usually 37–40).

Measurements (from 15 specimens, 22-mm-HL specimen from SIO 65–675 excluded).—Total length 137+ to 286+ mm; head length 29–61 mm. The following in percent of head length [range ($\bar{x}$; n; S.D.)]: postrostral length of head 79–82 (80.47; 15; 1.06); snout length 21–26 (23.59; 15; 1.38); preoral length 16–19 (17.61; 15; 0.62); internasal width 15–21 (18.47; 15; 1.42); orbit diameter 30–34 (32.29; 15; 1.47); interorbital width 20–25 (22.79; 15; 1.31); postorbital length 40–46 (43.34; 15; 1.88); orbit to angle of preopercle 34–38 (36.05; 15; 1.30); suborbital width 11–13 (11.85; 15; 0.66); upper jaw length 30–34 (32.15; 15; 1.29); length barbel 9–16 (11.73; 15; 3.38); length first gill-slit 17–23 (19.95; 15; 1.54); preanal length 117–150 (131.93; 15; 7.51); greatest body depth 68–88 (79.80; 15; 5.43); 1D.–2D. interspace 31–56 (41.83; 15; 7.40); height first dorsal fin 65–76 (69.30; 10; 4.00); length pectoral fin 51–70 (61.53; 15; 5.17); length pelvic fin 39–53 (45.87; 15; 3.48).

Comparisons and Relationships.—*Nezumia pulchella* is closely related to *N. stelgidolepis* but differs primarily in having 11–12 pelvic fin rays rather than the 9–10 of *N. stelgidolepis*. Scale spinules also show notable differences between the two species. In *N. pulchella* the spinules are all conical and in distinct rows that converge slightly towards the midline, whereas in *stelgidolepis* the spinules are conical to lanceolate and arranged in a more quincunx pattern. Retia and gas glands of *pulchella* are also much larger and stouter, the barbel is shorter, and the branchiostegal rays are naked except for occasional scattered scales (as opposed to short rows of deciduous scales along the bases of the lowermost branchiostegal rays in *stelgidolepis*).

Nezumia pulchella is readily distinguishable from *N. pudens* in having extensive naked areas on the ventral surface of the head and on the mandibles (as compared with surfaces mostly scaled in *pudens*), fewer scale rows below the first and second dorsal fins (6½ to 8½ vs. 10½ to 12 below the first dorsal; 5½ to 7½ vs. 8½ to 10½ below the second dorsal, fewer pyloric caeca (23–31 vs. 37–44), and a shorter barbel (9–16 vs. 20–25).

Size.—To at least 286 mm in total length (in a specimen, IMARPE uncat., 61 mm in head length). A specimen in the type-series measured 67 mm HL and 272 mm TL (Pequeño 1971:294, table).

Distribution.—Northern Peru (7°49′S) to central Chile (about 33°S) in 250–960 m.

Material Examined (16 specimens from 8 localities).—**Peru:** CAS 38323 (3, 54–57 mm HL, 207+ to 270 mm TL), 7°49′S, 80°38′W, 605–735 m, Anton Bruun cr. 18B, sta. 754 (field no. LWK66–93), 5 Sep. 1966. —CAS 28761 (1, 43 HL, 187 TL) and IMARPE uncat. (1, 61 HL, 286+ TL), 13°49.4′S, 76°46.9′W, 570 m, 24 Jan. 1972. —CAS 28763 (1, 46 HL, 226 TL), 13°53.3′S, 76°42.0′W, 272 m, 25 Jan. 1972. —CAS 28764 (1, 35 HL, 164 TL), 16°31.0′S, 73°12.2′W, 510 m, 1 Feb. 1972. —IMARPE uncat. (1, 34 HL, 161 TL), 18°07′S, 71°02.5′W, 28 Jan. 1972. **Chile:** CAS 38320 (6, 26–39 HL, 135–185 TL), 23°41′S, 70°34′W, 250–400 m, Anton Bruun cr. 18A, sta. 717 (field no. LWK66–63), 17 Aug. 1966. —CAS 38318 (1, 38 HL, 158 TL), 32°08.5′S, 71°43′W, 960 m, Anton Bruun cr. 18A, sta. 703 (field no. LWK66–47), 12 Aug. 1966. —SIO 65–675 (1, 22 HL, 104 TL), about 29 km off Valparaíso Harbor (ca. 33°N), 22–23 Dec. 1965.

Nezumia stelgidolepis (Gilbert)

(Figures 12*d*, 13, 18*i*)

Macrurus stelgidolepis Gilbert, 1890:116 (original description; off Pt. Conception, California, Albatross sta. 2960, in 488 m).

Macrurus gracillicauda Garman, 1899:206–207, pl. H, fig. 1 (original description; Gulf of Panama, Albatross sta. 3384 and 3385, in 837 and 523 m).

Lionurus (Nezumia) stelgidolepis: Gilbert and Hubbs 1916:145 (listed).

Lionurus stelgidolepis: Barnhart 1936:24 (brief description).

Nezumia stelgidolepis: Roedel 1951:509, fig. 183 (16 records off California).

Nezumia gracillicauda: Marshall and Iwamoto *in* Marshall 1973:626 (listed).

Diagnosis.—A species of *Nezumia* with 9–10 pelvic fin rays. Gill-rakers on first arch 8–12 total; on second arch 8–11 total. Spinules on body scales conical to narrowly lanceolate. Ventral surfaces of snout, most of suborbital region, and anterior half or more of mandibular rami naked. Lowermost branchiostegal rays scaled. Barbel 15–26 percent HL; upper jaw 31–37 percent.

Description.—General features of fish seen in Figures 12d and 13. Head moderately compressed and deep; ridges of head not strongly developed, usually somewhat rounded; suborbital region relatively flat. Snout narrow, bluntly pointed (more pointed in young), protruding slightly beyond rather large mouth, which is only slightly restricted at posterior angle by lip folds. Posterodorsal corner of opercle somewhat

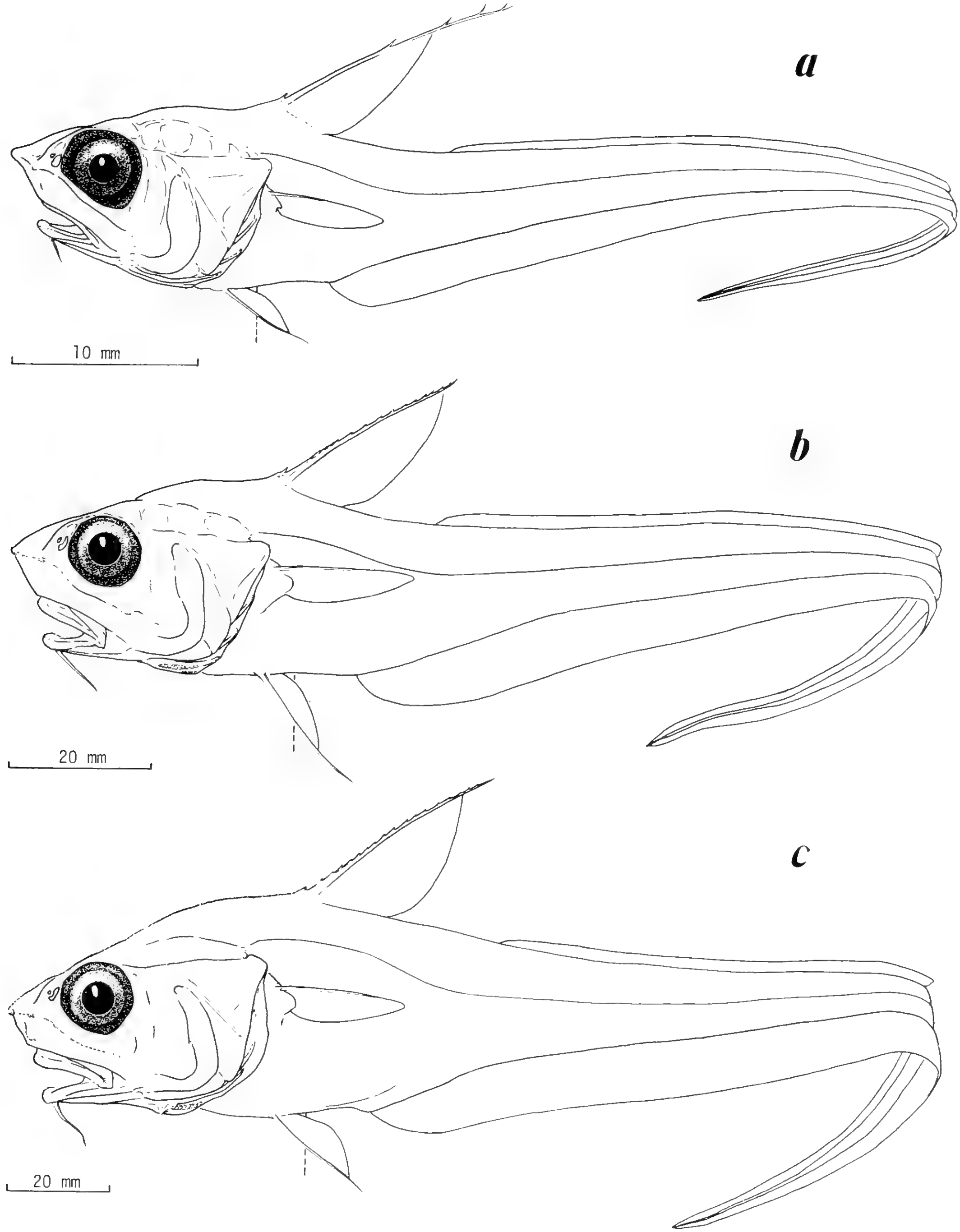


FIGURE 13. *Nezumia stelgidolepis* (Gilbert). (*a*) CAS 44197, 14.7 mm HL, 73 mm TL (fins and head region somewhat reconstructed after 13.5-mm-HL specimen from same station). (*b*) USNM 120272, 28.7 mm HL, 280 mm TL, partially reconstructed. (*c*) CAS 40022, 53 mm HL, 255 mm TL.

flaplike, posterior margin of gill cover steeply oblique along opercle, gently rounded along subopercle, connecting to broadly exposed (and scaled) interopercle. Shape of gill cover similar to that in *N. liolepis*. Gill openings wide; gill membranes rather narrowly connected over isthmus, with free posterior fold. Nape region slightly arched. Anus within lenticular area of black naked skin, situated slightly behind bases of pelvic fins, but closer to these than to anal fin. Anterior dermal window of light organ small, in shallow fossa between pelvic fin bases. Gill filaments well developed; length longest filament equal to or longer than least suborbital width and about equal to pupil diameter. Pyloric caeca numerous, branched; counts highly variable, in eight specimens 24, 34, 36, 38, 38, 40, 43, and 58. Periproct region relatively large, close behind pelvic fin bases; anterior window of light organ small, circular, lying between inner edges of pelvic fin bases.

Scales densely covered with long, narrowly lanceolate to conical spinules arranged in short, slightly convergent rows. Ventral surfaces of snout and most of suborbital region, and anterior half to two-thirds of lower jaw naked. Sensory pores rather prominent over these naked areas. Short rows of small deciduous scales along bases of one or more branchiostegal ray.

Coloration of fresh specimen (CAS 40022) swarthy overall with blackish predominant over ventral aspects of abdomen, chest, head, and gill covers. Bluish tinge over blackish abdominal walls. Fins dusky to blackish; first dorsal slightly paler basally. Lining of buccal cavity pale, but oral valves gray. Pharyngeal region dark gray; gill-rakers gray but gill filaments pale. In juveniles (CAS 41196 and 41197), oral cavity densely peppered with small melanophores.

Dentition in broad bands in both jaws, narrowly tapered posterolaterally. Outer series of upper jaw teeth slightly enlarged and evenly spaced.

Four juvenile specimens presumably of this species were captured in midwaters. The largest of these (LACM 30611–16) measured 19 mm in HL, 106 mm in TL, and was taken in an Isaacs-Kidd midwater trawl off the northwestern coast of Baja California between the surface and about 600 m, over a bottom depth of 1,600 to 1,100 fms (2,962–2,012 m). This specimen was dark colored, superficially resembling *N. parini*, but the coarse scale spinules, the large pores on the head and mandibles, the distinct lateral line, the number of pelvic fin rays, and the large gill filaments distinguish the species as *N. stelgidolepis*. The three other specimens (CAS 41196 and 41197) captured in midwaters were too small to positively identify without more comparative material, but the general appearance (see Fig. 13c) and counts (of dorsal and pelvic fin rays, and gill-rakers) also suggest *N. stelgidolepis* as the correct identification. Proportional measurements of these juveniles were generally divergent from those of the adults, indicating substantial allometric growth in such features as preoral length of snout, orbit diameter, interobital width, postorbital length of head, distance orbit to angle of preopercle, upper jaw length, and barbel length.

The smallest examined specimen (USNM 57861) captured in a bottom trawl measured 39 mm in head length and 176 mm in total length.

COUNTS (from 33 specimens).—1D. II,9–10 (8 in one specimen, 11 in two specimens); 1P. 20–26 ($\bar{x}$ = 21.00; *n* = 59; S.D. = 3.30); 2P. 9–10 (8 in one specimen, 11 in two others). Gill-rakers on first arch 10–11 total (8 in one, 9 in one, 12 in three specimens); on second arch 9–11 total. Scales below first dorsal 8–9 (rarely 10); below second dorsal 7–8 (9 in one); below midbase of first dorsal 6–7; over distance equal to predorsal length of head 34–47, usually between 36 and 42.

MEASUREMENTS (from 38 specimens, juveniles excluded).—Total length 176–405+ mm; head length 39–96 mm. The following in percent of head length [range ($\bar{x}$; *n*; S.D.)]: postrostral length of head 73–82 (78.60; 35; 1.80); snout length 22–28 (24.51; 36; 1.34); preoral length 12–18 (14.86; 36; 1.28); internasal width 14–19 (16.46; 30; 1.19); orbit diameter 26–32 (28.06; 38; 1.68); interorbital width 20–26 (23.46; 38; 1.55); postorbital length 43–52 (46.56; 33; 2.17); orbit to angle of preopercle 35–45 (39.81; 37; 2.01); suborbital width 11–16 (12.84; 37; 1.01); upper jaw length 31–37 (34.93; 38; 1.49); length barbel 15–26 (20.98; 36; 2.72); length first gill-slit 12–18 (16.37; 36; 1.54); preanal length 119–157 (135.95; 37; 9.51); greatest body depth 70–90 (77.68; 33; 5.77); 1D.–2D. interspace 26–58 (45.92; 38; 11.19); height first dorsal fin 48–68 (60.73; 29; 4.26); length pectoral fin 44–56 (49.69; 35; 3.23); length pelvic fin 35–49 (43.48; 34; 3.61).

COMPARISONS AND RELATIONSHIPS.—In the eastern Pacific, *Nezumia stelgidolepis* is most closely related to *N. liolepis* and *N. pulchella*, but is readily distinguished from these two by differences in scale spinulation, squamation pattern, pelvic ray count, and other features noted in the key. *Nezumia stelgidolepis* is representative of that group of *Nezumia* spp. characterized by relatively blunt snout, large mouth, broadly unrestricted gill openings, deep body, and large size. Some of the species in this group (e.g., *Nezumia atlantica* (Parr, 1946), *N. africana* (Iwamoto, 1970)) have been treated in other works (Parr 1946; Iwamoto 1970; Marshall 1973) as members of the genus *Ventrifossa*.

Size.—*Nezumia stelgidolepis* is the largest eastern Pacific member of the genus, attaining a total length of at least 445 mm (see Roedel 1951:509). *Nezumia atlantica*, a close relative from the western Atlantic, attains a comparable size, probably exceeded in the genus only by the peculiar species *N. bubonis* Iwamoto, 1974, from the Hawaiian Islands and the western Atlantic.

Distribution.—British Columbia (off Vancouver Island) to southern Peru (18°10.0′S), in 277–909 m (Makushok (1967:table 18) gives the depth distribution as "(61–91)379–909").

Material Examined (excluding material previously listed in Iwamoto and Stein 1974:49–50).—**California:** CAS 23396 (1, 63 mm HL, 310 mm TL), off Ft. Bragg in 475–494 m. —CAS 33110 (1, 43 HL, 243 TL), off Bodega Bay, 494–585 m, 23 Feb. 1965. —CAS 31509 (1, 73 HL, 365+ TL), off Point San Simeon, 530 m, N. B. Scofield sta. 54BB71, 25 Oct. 1954. —CAS 40022 (1, 53 HL, 255 TL), off Santa Barbara County, 34°18.4′N, 120°14.4′W, 439–443 m, Commando, 10 Aug. 1977. —USNM 87579 (1, 68 HL), Albatross. —USNM 127072 (1, 39 HL, 280+ TL), off southern California, Albatross.

Mexico: LACM 30611–16 (1, 19 HL, 106 TL), Guadalupe I., 28°57′15″N, 118°05′19°W, est. fishing depth 0–600 m, bottom depth 2,926–2,012 m, IKMT, Velero sta. 12494, 21 Nov. 1968. —AMNH 12902 (4, 55–70 HL, 250–305+ TL), San Cristobal Bay, 27°07′08″gN, 114°33′10″W, 519 m, Albatross sta. 5675, 15 Mar. 1911.

Galápagos: USNM 135605 (1, 77 HL, 346 TL), Albatross.

Ecuador: CAS 44196 (1, 14 HL, 67+ TL), 4°14′S, 81°26′W, 0–1,830 m, IKMT, Anton Bruun cr. 18B, sta. 756B (field no. LWK66–113), 8 Sep. 1966.

Peru: LACM 33883 (1, 66 HL, 303 TL), 6°42′S, 80°59′05″W, 780 m, sta. SNP1–25, 22 Jan. 1974. —LACM 33886 (1, 41 HL, 168 TL), 7°44′05″S, 80°30′05″W, 750–760 m, sta. SNP1-28, 23 Jan. 1974. —CAS 38324 (7, 48–66 HL, 180+ to 280 TL), 7°49′S, 80°38′W, 605–735 m, Anton Bruun cr. 18B, sta. 754 (field no. LWK66–93), 5 Sep. 1966. —CAS 41197 (2, 13.5–14.7 HL, 66–73 TL), 11°53′S, 78°05′W, 0–1,125 m, IKMT, Anton Bruun cr. 16, sta. 656–0, 14 June 1966. —IMARPE uncat. (1, 74 HL, 290+ TL), 18°10′S, 71°29′W, 610 m, 23 Aug. 1972.

Nezumia pudens Gilbert and Thompson

(Figures 6*b*, 14*c*, 18*h*)

Nezumia pudens Gilbert and Thompson, 1916:472–473, pl. 5, fig. 2 (types from Albatross sta. 2791 off Lota, Chile, 38°08′S, 75°53′W, 1,240 m).

Lionurus (*Nezumia*) *pudens:* Gilbert and Hubbs 1916:146 (name only).

Macruroplus pudens: Fowler 1944:48, fig. (list).

Diagnosis.—A species of *Nezumia* with 10–11 pelvic fin rays. Gill-rakers on first and second arches 9–10 total. Spinules on body scales slender, sharp, conical, in dense cluster on exposed fields. Head surface fully scaled except for small area along ventromedian line of snout and over gill membranes. Barbel 20–25 percent of HL; upper jaw 30–39 percent HL.

Description.—General features of fish seen in Figure 14a. Head rather compressed, surfaces smoothly rounded. Suborbital ridge low, rounded. Snout short, blunt narrow; blunt scutes at terminal and lateral angles not especially spiny or set off from adjacent scales. Mouth subterminal, rather short; posterior corners somewhat restricted by lip folds; lips thick, papillaceous, especially in large adults. Barbel rather thick throughout, not tapering to filamentous tip. Interopercle broadly exposed posteriorly and ventrally. Posterodorsal corner of opercle angular, without broad tablike extension. Gill membranes rather broadly connected over isthmus, with a narrow free fold. Anus located in middle third of distance between pelvic fin base and anal fin origin. Anterior dermal window small, round, lying between or slightly in advance of line connecting insertion of pelvic fins. Gill filaments well developed but relatively short; length of longest less than diameter of eye lens, about 0.6 into least suborbital width. Pyloric caeca slender, numerous, 37, 39, and 44 in three specimens, branched two or three times at base; length of longest about equal to interorbital width.

Exposed fields on body scales densely covered with relatively erect, slender, stiletto-shaped spinules arranged in quincunx pattern or in close, strongly convergent rows. Almost all of head uniformly covered with small, relatively adherent scales (Fig. 6b). Small area along ventral midline and ventral margin of snout naked. Scales along dorsal half of suborbital region heavier, larger, more adherent, and in two distinct rows. Mandibles and exposed surfaces of

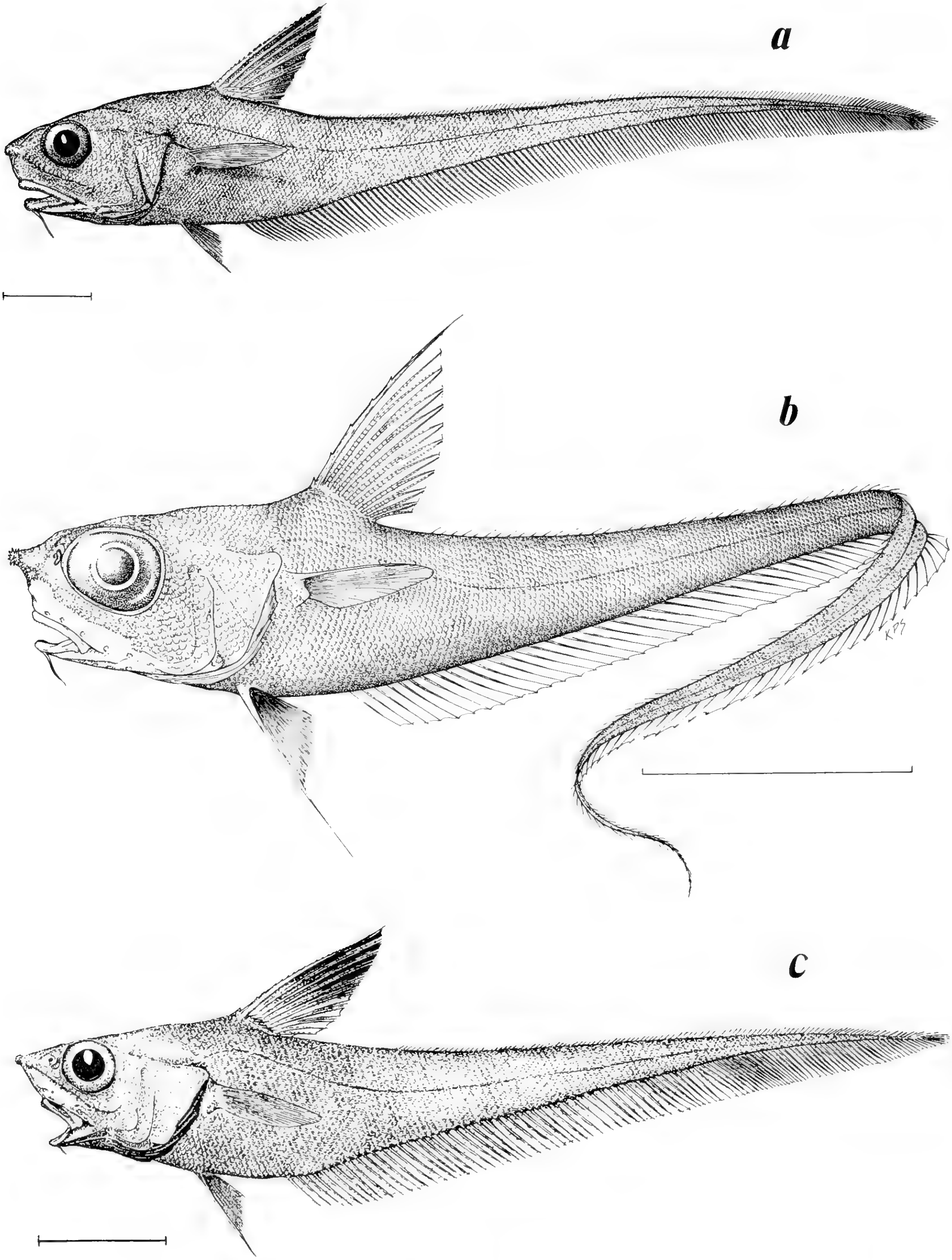


FIGURE 14. (*a*) *Nezumia pudens* (Gilbert and Thompson). CAS 38310, 50 mm HL, from off Chile in 750 m. (*b*) *Nezumia ventralis* Hubbs and Iwamoto, new species. Holotype, CAS-SU 68361, 26.4 mm HL, taken off the Galápagos in 549 m. (*c*) *Nezumia orbitalis* (Garman), LACM 33885-2, 48 mm HL, off Peru in 800 m.

interopercle covered with small scales, but gill membranes naked.

Fins moderate in size. First spinous ray of dorsal fin slender, sharp, spikelike; second spinous ray slightly prolonged, armed along leading edge with slender, sharp spikes spaced sufficiently apart so that spikes do not overlap. Outer ray of pelvic fins with filamentous tip extending well beyond origin of anal fin. First dorsal fin placed rather far posteriad; origin about on same vertical as anus and about one eye-lens diameter behind vertical through origin of pectoral fins.

Jaw teeth in rather broad, coarse bands that narrow posteriorly. Outer series of upper jaw slightly enlarged, particularly along anterior border.

Coloration in alcohol medium brown with abdominal and cheek area blackish tinged with violet. Gill membranes black; naked margins of snout, nostrils, lower jaw, opercular bones, and rim of orbit blackish or darkly swarthy. Fins all blackish; distal and anterior portions of membranes of first dorsal fin more intensely blackish. Lining of mouth and gullet blackish; that of gill cavity blackish along external margins but pale towards inner portions; that of abdominal cavity black to swarthy.

Counts (from 7 specimens).—1D. II,9–11; 1P. 19–24; 2P. 10–11. Medial gill-rakers on first arch 1–2 + 7–9, usually 2 + 8 (9–10 total); on second arch 1–2 + 8–9 (9–10 total). Scale rows (from 4 specimens) below first dorsal 10½ to 12; below second dorsal 8½ to 10½; below midbase of first dorsal 7½ to 8½; over distance equal to predorsal length 43–46.

Measurements (from 6 specimens; 22-mm-HL specimen excluded).—Total length 165–400 mm; head length 32–68 mm. The following in percent of head length: postrostral length of head 74–76; snout length 28–30; preoral length 18–22; internasal width 19–23; orbit diameter 31–35; interorbital width 22–23; postorbital length of head 40–48; distance orbit to angle of preopercle 37–43; suborbital width 15–16; upper jaw length 30–39; length barbel 20–25; length first gill-slit 14–18; preanal length 143–158; greatest body depth 73–81; 1D.–2D. interspace 34–43; height first dorsal fin 80–93; length pectoral fin 56–64; length pelvic fin 44–58.

Comparisons and Relationships.—*Nezumia pudens* is readily distinguished from its most closely related eastern Pacific congeners *N. stelgidolepis*, *N. pulchella*, and *N. liolepis* by: (1) ventral surface of snout, suborbital region, and mandibular rami scaled (vs. mostly naked in these other species); (2) mucous pores in these areas not prominent (vs. prominent); (3) posterodorsal angle of opercle not produced into a short tab or flap (vs. a distinct flap or tab); (4) gill filaments relatively short, length less than diameter of eye lens (greater than eye lens in others); (5) first dorsal fin originating more posteriad than others; and (6) buccal cavity completely blackish (mostly pale in *stelgidolepis* and *pulchella*, but blackish in *liolepis*). Its relationship to other Pacific species of *Nezumia* is uncertain and probably distant.

Nezumia pudens bears some resemblance in general physiognomy of the head and body to *N. sclerorhynchus* (Valenciennes, 1838), and *N. suilla* Marshall and Iwamoto, 1973, from the Atlantic, but the higher pelvic fin ray count and the more complete squamation on the ventral aspects of the head in *N. pudens* are distinguishing.

Size.—To at least 68 mm HL and 400 mm TL.

Distribution.—Known only off central Chile between latitudes 32°S and 38°S, in 580–1,238 m.

Material Examined (7 specimens, all from Chile).—USNM uncat. (formerly CAS 38317) (1, 39 mm HL, 240 mm TL), 32°08.5′S, 71°43′W, 960 m, Anton Bruun cr. 18A, sta. 703 (field no. LWK66–47), 12 Aug. 1966. —CAS 38315 (2, 22–39 HL, 106+ to 234 TL), 32°17′S, 71°39.5′W, 580 m, Anton Bruun cr. 18A, sta. 702 (field no. LWK66–44), 11 Aug. 1966. —CAS 38310 (2, 50–68 HL, 267–400 TL), 34°06.5′S, 72°18.5′W, 750 m, Anton Bruun cr. 18A, sta. 687 (field no. LWK66–25), 5 Aug. 1966. —USNM 76860 (holotype, 32 HL, 170 TL) and CAS-SU 22727 (paratype, 34 HL, 165 TL), 38°08′S, 75°53′W, 1,238 m, Albatross sta. 2791, 14 Feb. 1888.

Nezumia ventralis Hubbs and Iwamoto, new species

(Figure 14*b*)

Diagnosis.—A *Nezumia* with 15 pelvic fin rays and 24–27 pectoral fin rays. Mandibular rami, ventral surfaces of snout, and most of ventral surfaces of suborbital region naked; mucous pores over these surfaces large. Scales small, about 9½ below origin of second dorsal fin; spinules on body scales slender, conical, greatly reclined, in parallel to subparallel rows.

Description of Holotype.—General features of fish seen in Figure 14b. Head and trunk moderately compressed and deep. Suborbital region divided into an upper portion covered with two longitudinal rows of stout scales and a lower portion with almost no scales; the surfaces of the two halves meet along the suborbital ridge at an obtuse angle. Opercular opening moderately restricted, extends ventrally to below a point anteriad of preopercular ridge. Gill membranes restricted, without a free fold over isthmus. Trunk short, distance isthmus to anal fin origin less than postrostral length of head. Periproct moderate in size, anus much closer to insertion of pelvic fins than to origin of anal fin. Ventral light organ well developed; a large, oval dermal window forms anterior extension of periproct; dermal window extends forward almost to a line connecting pelvic fin insertions. Gill filaments long, well developed; longest filament about 3.5–4.0 mm, about as long as diameter of eye lens. About 23 slender pyloric caeca.

Teeth in moderately broad bands in both jaws; bands narrower posteriorly on jaws. Outer series of teeth in upper jaw slightly enlarged.

Scales of body covered with slender, conical, reclined spinules arranged in parallel to subparallel ridgelike rows that give a somewhat striated appearance to body surfaces. Four to five rows of spinules on larger body scales. Spinules on head scales more erect than those on body scales, and spinules often arranged in divergent rows. Scales behind bases of paired fins, behind first dorsal fin, and beneath outer margin of gill covers without spinules. Scales dorsally on suborbital region stout, adherent, and covered with coarse spinules. Scales at tip and lateral angles of snout large, tuberclelike, and coarsely spined. Exposed posterior tip of interopercle scaled. Mandibular rami, ventral surfaces of snout, and most of ventral surface of suborbital region naked; mucous pores large and prominent in these areas. There appear to be some scale pockets along lowermost branchiostegal rays of holotype, but condition of specimen left doubts as to their actual presence (the "pockets" may simply be torn skin).

Fins generally well developed. First dorsal fin high, length almost as long as head length (longest ray broken at tip in holotype and paratype). Leading edge of spinous second ray armed with sharp, widely spaced denticles. Outer ray of pelvic fin slightly prolonged, extends beyond origin of anal fin. Pelvic and anal fins originate relatively far forward; pelvic fin origin below subopercle, anal fin origin below hind third of first dorsal fin base.

Holotype too badly faded for accurate description of coloration. See color description of paratype.

Description of Paratype.—The single paratype is in poor condition and falling apart. The snout region is destroyed, and the posterior half of the tail has broken off and almost completely disintegrated. The fins and scales are intact, however, and most of the diagnostic features of the species could be examined. The specimen is notably larger than the holotype (postrostral length of head 31.0 mm compared with 20.8 mm) and the two exhibit some ontogenetic differences. Thus, the spinules on scales are more numerous than in the holotype, and the larger spinules on body scales tend to be lanceolate rather than conical. Spinule rows on body scales are also more numerous, six to eight on the larger scales of paratype compared with four to five in comparable scales of holotype.

The paratype had 29 pyloric caeca compared with the approximate count of 23 obtained in the holotype (I did not enlarge the original slit in the abdominal wall of the holotype for fear of damaging the specimen further). Two spinulated scales were present at the base of the left fourth branchiostegal ray, but none were on the opposite member.

Ground color of paratype dark brown with violet tinge over abdomen. Fin membranes, gill membranes, and naked surfaces of snout, suborbital region, and mandibular rami chocolate-brown. Gill cavity brown on inner wall and along periphery of outer wall but pallid everywhere else. Gill filaments and gill arches pale, the tubercular rakers dusky.

Counts (paratype counts, if different, in brackets).—1D. II,10; 1P. 24 (left), 27 (right) [25, 25]; 2P. 15. Mesial gill-rakers on first arch 2 + 9 [2 + 10], on second arch 2 + 8 [2 + 9]. Scales below first dorsal about 12 [about 13]; below second dorsal 9½; below midbase of first dorsal about 8 [about 9½]; lateral line scales over distance equal to predorsal length 41 [not taken in paratype]. Pyloric caeca about 23 [29].

Measurements of Holotype.—Total length 142 mm, head length 26.4 mm. The following in percent of head length: postrostral length of head 79.0; snout length 23.8; preoral length 20.4; internasal width 19.7; orbit diameter 36.7; interorbital width 22.0; postorbital length of head 38.2; distance orbit to angle of preopercle 34.0;

suborbital width 12.1; upper jaw length 27.2; barbel length 14.0; length first (outer) gill-slit 15.9; preanal length 129; isthmus to anus 47.4; outer pelvic ray to anal origin 34.0; greatest body depth 68; depth over anal origin 57; 1D.–2D. interspace 34; length pectoral fin about 53; length outer pelvic ray about 53.

COMPARISONS AND RELATIONSHIPS.—*Nezumia ventralis* appears most closely related to two Atlantic species, *N. sclerorhynchus* (Valenciennes, 1838) and *N. suilla* Marshall and Iwamoto, 1973. The combination of general head and body shape, the presence of broad naked areas on the ventral surfaces of the snout and suborbital region, the naked mandibular rami, the large pores on the head, the general coloration, and the placement and size of the fins suggest this relationship. The new species is readily distinguished from the two by its high pelvic fin ray count of 15, compared with 7 in *suilla* and usually 9 (rarely 7, 8, or 10) in *sclerorhynchus*. *N. propinqua* (Gilbert and Cramer, 1897) is the only other species of the genus having a pelvic fin ray count as high as that of *N. ventralis*, but *N. ventralis* lacks the distinct black blotch on the tip of the first dorsal fin that is so prominent in *propinqua*, and it has more pectoral fin rays (23 or fewer in *propinqua*), a shallower body, a more anteriorly placed pelvic fin, and fewer scale rows below the second dorsal fin.

DISTRIBUTION.—The species is known from only two specimens taken by the ALBATROSS in the Galápagos Islands.

ETYMOLOGY.—From the Latin *ventralis*, adj., of or belonging to the belly—in reference to the ventral light organ.

REMARKS.—The paratype was first examined (circa 1920) by Dr. Carl L. Hubbs, who recognized the distinctness of the specimen and gave it the manuscript name of "*Lionurus ventralis*." Because of other commitments, Dr. Hubbs was unable to formally describe the species at the time and consequently returned the specimen to the National Museum along with other macrourids collected by the ALBATROSS in the eastern Pacific in 1888 and 1904.

MATERIAL EXAMINED.—**Holotype:** CAS-SU 68361, 26.4 mm HL, 142 mm TL, Galápagos Islands, off Hood (Española) I., 1°30′30″S, 89°39′W, 549 m, ALBATROSS sta. 4642, 7 Nov. 1904.

Paratype: USNM 135345, 1 badly deteriorated specimen, Galápagos Islands, 00°29′S, 89°54′30″W, 717 m, ALBATROSS sta. 2818, 15 Apr. 1888.

Nezumia orbitalis (Garman)

(Figure 14c)

Macrurus orbitalis GARMAN, 1899:207–208, pl. 47, figs. 1–1b (original description; Gulf of Panama, ALBATROSS sta. 3385, in 523 m).

Lionurus (*Nezumia*) *orbitalis*: GILBERT AND HUBBS 1916:146 (listed).

Nezumia orbitalis: MAKUSHOK 1967:table 18.

DIAGNOSIS.—A species of *Nezumia* with 9 pelvic fin rays. Gill-rakers on first arch 1–2 + 8–10 (10–11 total); on second arch 1–3 + 7–9 (9–11 total). Spinules on body scales slender, conical to narrowly lanceolate; no enlarged middle row of spinules on scales. Barbel length 6–12 percent HL; upper jaw length 27–32 percent HL. First dorsal fin with distinct black tip.

DESCRIPTION.—General features of fish seen in Figure 14c. A petite species probably not exceeding 200 mm in total length. Head about 21–25 percent of total length in specimens with complete tails. Snout pointed; head ridges relatively well developed with spinous tubercles at terminal and lateral points of snout. Dorsal profile arched high over nape to give distinctive humpbacked appearance. Gill membranes broadly attached across isthmus, with only a narrow posterior free fold. Anterior dermal window of light organ small, circular, situated in a shallow fossa between bases of pelvic fins; anus close behind.

Spinous second ray of first dorsal fin armed along leading edge with small, closely spaced teeth. Outer pelvic ray slightly prolonged, extends past origin of anal fin. Pelvic fin origin forward of pectoral fin origin, which in turn is slightly forward of first dorsal fin origin.

Body scales with slender, conical to narrowly lanceolate spinules densely covering exposed fields, disposed in as many as 15 rows in large specimens, with spinule rows converging towards middle of field; no enlarged middle row of spinules. Most ventral surfaces of snout and suborbital region naked. Lower jaw surfaces naked except for a line of loose scales along midline of each ramus.

Coloration. Garman (1899:208) has given a good color description from the types: "Blackish over the body cavity; reddish brown over the muscular portions of the caudal section; lighter to translucent on the head and snout; entire surface tinted with grayish, from the spinules of the scales. Fins light; first dorsal and pectorals tipped with black. Orbit surrounded by a narrow border of black." The peritoneal lining of the lectotype is silvery with bold punctations.

Dentition of jaws consists of small teeth in moderately wide bands with outer series of upper jaw slightly enlarged.

Counts (from 15 specimens).—1D. II,9–10 (11 in one specimen); 1P. 20–22 ($\bar{x}$ = 20.8); 2P. 9. Gill-rakers on first arch 1–2 + 8–10 (9–11 total; $\bar{x}$ = 10.3); on second arch 1–3 + 7–9 (9–11 total; $\bar{x}$ = 10.2). Scales below first dorsal 7–9; below second dorsal 6½ to 7; below midbase of first dorsal 4½ to 5½; lateral-line scales over distance equal to predorsal length of head 36–45. Pyloric caeca 17, 17, and 23 in three specimens.

Measurements (from 15 specimens).—Total length 115–186 mm; head length 27–41 mm. The following in percent of head length [range ($\bar{x}$; n; S.D.)]: postrostral length of head 73–78 (76.0; 14; 1.47); snout length 25–30 (27.8; 15; 1.27); preoral length 20–25 (22.9; 15; 1.81); internasal width 18–22 (19.9; 15; 0.97); orbit diameter 29–34 (31.9; 15; 1.28); interorbital width 17–19 (17.7; 15; 0.72); postorbital length 39–45 (41.5; 13; 2.11); orbit to angle of preopercle 33–40 (34.5; 15; 1.96); suborbital width 11–14 (12.4; 15; 0.83); upper jaw length 27–32 (28.5; 15; 1.55); length barbel 6–12 (9.0; 13; 1.59); length outer gill-slit 14–18 (15.9; 15; 1.33); preanal length 119–146 (123.8; 15; 12.42); outer pelvic ray to anal origin 28–41 (33.9; 15; 5.19); anus to anal origin 14–29 (21.5; 15; 4.81); greatest body depth 63–82 (72.2; 15; 6.45); 1D.–2D. interspace 34–57 (44.1; 15; 7.35); height first dorsal fin 75–90 (80.4; 10; 6.15); length pectoral fin 48–78 (55.6; 12; 7.35); length pelvic fin 41–58 (49.2; 11; 4.49).

Relationships and Comparisons.—*Nezumia orbitalis* is closely related to *N. latirostrata* and the two have narrow, coincident, geographic ranges, although *N. orbitalis* is usually found at shallower levels than *N. latirostrata* (the two species were represented together in only one haul, SNP1-28, off Peru in 800 m, the deepest record for *N. orbitalis*). Meristic and morphological features of the two species are close, and the general appearance is similar. Color differences are the most noticeable. The first dorsal fin of *N. orbitalis* is distinctly pallid basally and black tipped distally, whereas in *N. latirostrata* the fin is uniformly blackish. The head of *N. orbitalis* is paler than that of *N. latirostrata*, and the prominent black orbital ring of the former is essentially lacking in the latter. The area ventrally on the naris appears smudged with black in *N. latirostrata* but is scarcely pigmented in *N. orbitalis*. Silvery reflections persist on the preopercle of *N. orbitalis* specimens but not in *N. latirostrata* specimens, and the belly denuded of scales has a more bluish cast in *N. orbitalis*. *Nezumia latirostrata* is generally a much darker fish.

The low pelvic fin ray count, the number of gill-rakers, and the short barbel together serve to distinguish *N. orbitalis* from other eastern Pacific members of the genus.

The species appears close to the widespread Atlantic species *N. aequalis* (Günther), the two sharing many meristic, morphometric, and coloration features. Even the humpbacked appearance of *N. orbitalis* is shared with one population of *N. aequalis*—that population being coincidentally also one from the eastern side of an ocean (the Gulf of Guinea) (see Marshall and Iwamoto *in* Marshall 1973:641). *N. orbitalis* is readily distinguished from *N. aequalis*, however, by its somewhat shorter snout length (20–25 percent HL cf. 25–32 in *aequalis*), its relatively longer head length compared with the total length (head length 21–25 percent of total length, cf. 15–18), and its smaller adult size (probably less than 200 mm TL, as judged from the 175-mm length of the ripe female lectotype, cf. more than 270 mm TL in *aequalis* [Marshall and Iwamoto *in* Marshall 1973:643]).

Distribution.—Gulf of Panama to Peru, in 523–800 m.

Size.—To at least 41 mm HL and 186 TL.

Material Examined (15 specimens, 4 localities).—**Panama:** MCZ 28578 (lectotype, 41 mm HL, 175+ mm TL), MCZ 50956 (5 paralectotypes, formerly MCZ 28578, 28–35 HL, 115+ to 153 TL), and USNM 57856 (2 paralectotypes, 28–34 HL, 129+ to 130+ TL), all from Gulf of Panama, 7°32′36″N, 79°16′W, 286 fms (523 m), Albatross sta. 3385, 8 Mar. 1891.

Peru: LACM 33885 (2, 40–40 HL, 174+ to 186 TL), 7°46′S, 80°31′W, 800 m, sta. SNP1-27, 23 Jan. 1974. —LACM 33886 (4, 27–39 HL, 118–178 TL), 7°44′05″S, 80°30′05″W, 750–760 m, sta. SNP1-28, 23 Jan. 1974. —IMARPE (1, 40 HL, 175+ TL), 13°57.2′S, 76°42.0′W, 580–600 m, 7 Aug. 1972.

Nezumia latirostrata (Garman)

(Figures 4*b*, 15*a*, 18*e*)

Macrurus latirostratus Garman, 1899:211–212, pl. 48, fig. 2 (original description; types from Albatross sta. 3354, 3384 and 3394 in Gulf of Panama, 322–511 fms [589–935 m]).

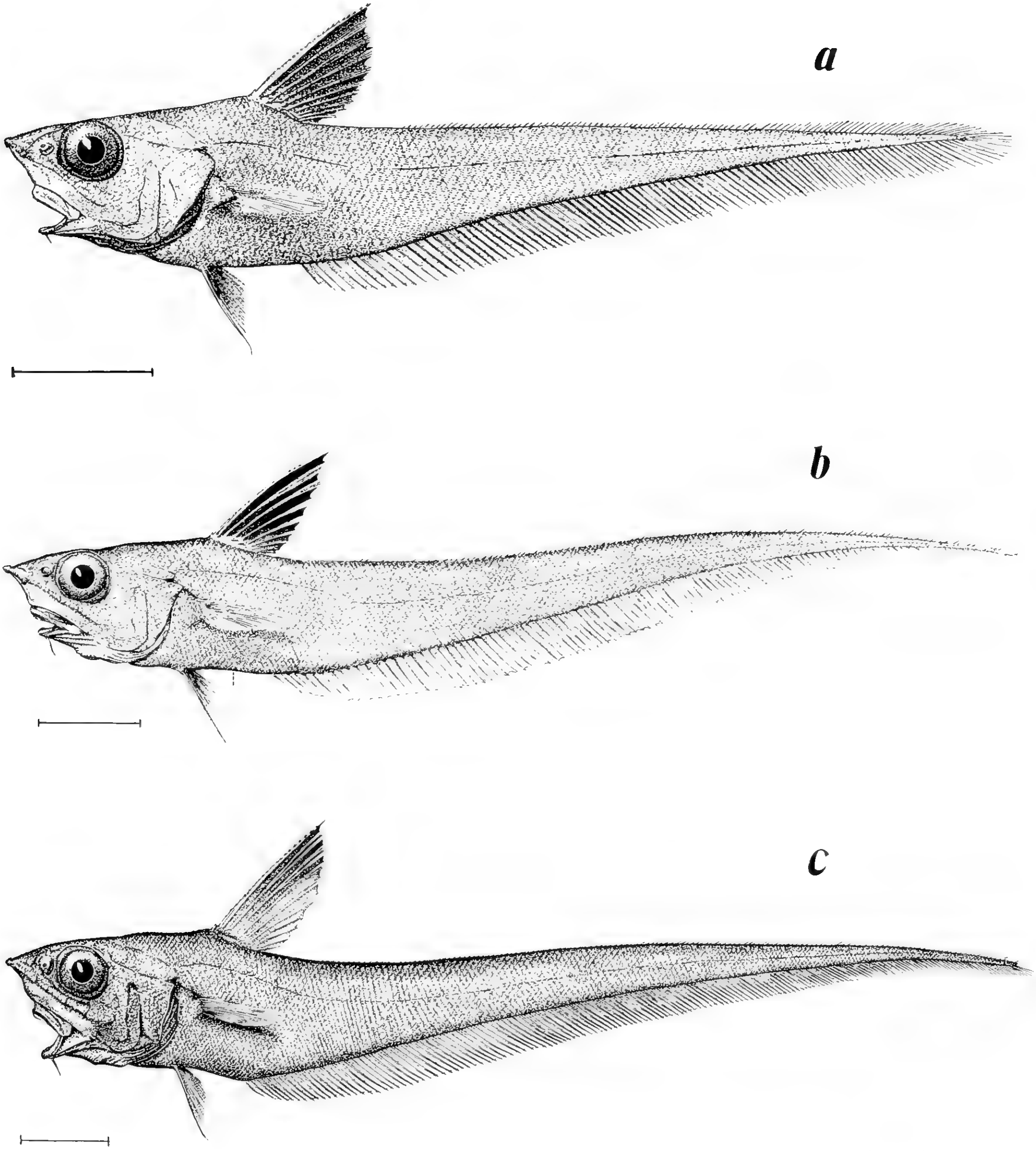


FIGURE 15. (*a*) *Nezumia latirostrata* (Garman), CAS 38330, 40 mm HL, from off Ecuador in 700–1,000 m. (*b*) *Nezumia convergens* (Garman), CAS 36816, 44 mm HL, from off Ecuador in 850–1,400 m. (*c*) *Nezumia loricata atomos* new subspecies. Holotype, CAS 38312, 51 mm HL, 297+ TL, from off Chile in 1,170–1,480 m.

Lionurus (*Nezumia*) *latirostratus*: GILBERT AND HUBBS 1916:146 (name only).
Nezumia latirostrata: MAKUSHOK 1967:table 18.

DIAGNOSIS.—A species of *Nezumia* with 9–10 pelvic fin rays. Gill-rakers on first and second arch 9–11 total (7–9 on lower limb). Barbel length 5–10 percent of HL; upper jaw length 27–32. Spinules on body scales lanceolate, arranged in indistinct rows without enlarged middle row. Scales below first dorsal 7½ to 9; below second dorsal 6 to 7½. First dorsal fin uniformly blackish.

DESCRIPTION.—General features of fish seen in Figure 15a. Head and trunk moderately compressed, tail greatly so. Head ridges prominent, suborbital ridge strongly angular. Mouth subterminal; rictus extends to below anterior edge of eye lens; maxilla extends to below middle of eye. Terminal and lateral angles of snout armed with small but stout, spiny tubercular scales. Interorbital region slightly concave, width about 60 percent of orbit diameter. Gill membranes broadly attached over isthmus (Fig. 4b), with a narrow posterior free fold; gill opening extends anteroventrally slightly anteriad of a vertical through posterior edge of preopercle. Body moderately deep in adults, generally more slender in the young; greatest body depth more than postrostral length of head in all specimens larger than about 30 mm HL. Light organ externally represented by a small, black, oblate, naked fossa between bases of pelvic fins and anterior to anus. Anus situated notably closer to insertion of pelvic fins than to origin of anal fin. Gill filaments short; length of longest slightly shorter than diameter of eye lens.

First dorsal fin of moderate height, length of longest ray less than head length; second spinous ray slightly produced into a thin filament; leading edge of ray armed with small, closely spaced teeth; in some specimens, tip of each tooth overlaps base of adjacent tooth. Paired fins of moderate size; outer ray of pelvic fin produced, extends posteriad well beyond origin of anal fin.

Body scales moderately deciduous, as judged from generally denuded state of specimens examined. Spinules on body scales distinctly lanceolate, densely covering exposed fields, arranged in indistinct longitudinal rows that converge towards middle of field. Scales absent on ventral surface of snout, but surface copiously dotted with dark sensory papillae. Suborbital region below ridge with a wedge-shaped cluster of small scales. Mandibles with small loose scales along midline of each ramus but naked at anterior end.

Teeth small, in bands of moderate width in both jaws. Outer series of teeth in upper jaw scarcely enlarged.

Coloration in alcohol swarthy. Bluish tinge over trunk and violet tinge over head and tail pronounced in denuded specimens. All fins dark brown to brownish black. Lining of oral cavity dusky, that of gill cavities black except for pale areas ventrally and along medial wall. Peritoneal cavity pale but peppered with large melanophores.

COUNTS (from 57 specimens).—1D. II,9–10 (II,8 in two specimens, II,11 in two others); 1P. 18–23 ($\bar{x}$ = 20.65; n = 105; S.D. = 1.0); 2P. 9–10. Gill-rakers on first and second arch 1–3 + 7–9 (total 9–11). Scales below first dorsal 7½ to 9 (rarely 7); below second dorsal 6 to 7½; lateral-line scales over distance equal to predorsal length of head 32–38 ($\bar{x}$ = 35.88; n = 34; S.D. = 1.5). Pyloric caeca 17–25 ($\bar{x}$ = 21.23; n = 30; S.D. = 2.4).

MEASUREMENTS (from 56 specimens).—Total length 128–231 mm; head length 26–48 mm. The following in percent of head length [range ($\bar{x}$; n; S.D.)]: postrostral length of head 71–77 (73.53; 56; 1.78); snout length 27–34 (29.97; 56; 4.36); preoral length 23–31 (26.16; 56; 1.78); internasal width 20–26 (23.39; 55; 1.23); orbit diameter 30–36 (33.78; 55; 1.46); interorbital width 17–25 (20.84; 56; 1.57); postorbital length of head 36–43 (38.94; 54; 1.52); orbit to angle of preopercle 33–39 (35.25; 55; 1.36); suborbital width 13–17 (15.18; 56; 1.11); upper jaw length 27–32 (29.55; 56; 1.30); length barbel 5–10 (8.19; 49; 1.57); length first gill-slit 11–16 (13.59; 54; 1.13); preanal length 123–157 (140.93; 56; 7.57); outer pelvic ray to anal fin origin 27–48 (37.14; 55; 4.59); anus to anal fin origin 16–33 (22.27; 52; 3.78); greatest body depth 66–96 (77.22; 56; 11.01); 1D.–2D. interspace 34–55 (one specimen with 72) (45.41; 56; 6.30); height first dorsal fin 75–98 (83.78; 18; 6.10); length pectoral fin 52–68 (59.32; 50; 4.96); length pelvic fin 41–67 (55.57; 49; 6.92).

COMPARISONS AND RELATIONSHIPS.—*Nezumia latirostrata* and *N. convergens* are closely related and specimens of the two are difficult to differentiate. Chief differences between the two species lie in (1) gill-raker counts, (2) barbel length, (3) scales below first dorsal, (4) scales over distance equal to predorsal length, and (5) body length. *Nezumia latirostrata* generally has 7–9 gill-rakers on the lower limb of the first and second arches, whereas *N. convergens* has 5–7. Barbel lengths contrast at 5–10 percent HL for *N. latirostrata* and 8–20 percent (12–18 in most) for *N. convergens*. Scale rows below the origin of the first dorsal fin are less numerous in *latirostrata* (7½ to 9) than in *convergens* (8½ to 10, a few individuals with 11). The number of anterior lateral-line scales over a distance equal to the predorsal length is generally lower in *latirostrata* (32–38 in most specimens compared with 36–42 in *convergens*), but there is considerable overlap with *convergens* in this feature. The body is somewhat shorter in *latirostrata*; the ratio HL:TL is between 1:4.5 and 1:5.5 (fewer than 12 percent of the specimens with an intact tail had a ratio of more than 1:5.2), whereas in *convergens* it is 1:5.3 to 1:5.8.

Nezumia latirostrata also closely resembles *N. loricata*. The principal differences between the two rest in the pelvic fin ray counts (9–10 in *latirostrata*, 10–12 in *loricata*); barbel length (5–10 percent HL vs. 10–17); number of scale rows below midbase of first dorsal fin (usually 4½ to 5½ vs. 6½ to 7½) and below the origin of the second dorsal fin (6 to 7½ vs. 8–9); and the ratio of head length to body length (1:4.8 to 1:5.5 vs. 1:5.1 to 1:6.1).

Nezumia latirostrata is readily distinguished from other eastern Pacific species of *Nezumia* by characters given in the key. *Nezumia latirostrata* is distinguishable from the Hawaiian species of the genus by a combination of characters that includes snout shape (blunter and shorter in *holocentrus* (Gilbert and Cramer, 1897); *burragei* (Gilbert, 1905); *hebetata* (Gilbert, 1905); and *ectenes* (Gilbert and Cramer, 1897)) and pelvic fin ray count (more in *propinqua* (Gilbert and Cramer, 1897) and *obliquata* (Gilbert, 1905)). Of the Japanese species reported by Okamura (1970a), all but four (*proxima* (Smith and Radcliffe, 1912, in Radcliffe), *tomiyamai* (Okamura, 1963), *burragei* (Gilbert, 1905), and *dara* (Gilbert and Hubbs, 1916)) can be differentiated from *latirostrata* by the number of pelvic fin rays, but *N. tomiyamai*, *N. burragei*, and *N. dara* have more scale rows below the origin of the second dorsal fin than does *N. latirostrata*, and *N. proxima* has a longer barbel (less than two times into orbit diameter compared with three or more times in *latirostrata*).

Most Atlantic members of the genus (see Marshall and Iwamoto *in* Marshall 1973:624–649) are distinguishable from *N. latirostrata* by a combination of pelvic fin ray count, barbel length, and shape of scale spinules. The western Atlantic species *N. cyrano* Marshall and Iwamoto, 1973, is "probably most closely related to *N. latirostratus*" (ibid.:629), but the two differ in snout length (longer in *cyrano*, 32–36 percent HL, as opposed to 27–34, most specimens below 33, in *latirostrata*), upper jaw length (24–28 in *cyrano* vs. 27–32 in *latirostrata*), and length of first gill-slit (6–10 vs. 11–16).

DISTRIBUTION.—Panama (SE of Punta Mala) to northern Peru (SE of Lobos de Afuera) in 605–1,400 m.

SIZE.—To at least 48 mm HL and more than 234 mm TL.

MATERIAL EXAMINED (182 specimens from 11 localities).—**Panama:** USNM 57855 (2 syntypes, 39–41 mm HL, 198+ to 205 mm TL), 7°21′N, 79°35′W, 935 m, ALBATROSS sta. 3394, 10 Mar. 1891. —GCRL 14259 (2, 47–48 HL, 215–198+ TL), 7°18′N, 79°38′W, 732–805 m, CANOPUS sta. 1285, 24 Mar. 1974. —GCRL 14260 (1, 41 HL, 167+ TL), 7°13′N, 79°18′W, 805–841 m, CANOPUS sta. 1291, 12 Mar. 1974. —CAS-SU 25246 (2, 44–46 HL, 195+ to 245 TL), "between Galapagos and Panama ALBATROSS 1888" (no other data).

Ecuador: CAS-SU 24091 (8, 28–41 HL) and CAS-SU 25223 (9, 38–42 HL), 00°37′S, 81°00′W, 733 m, ALBATROSS sta. 2792, 2 Mar. 1888. —CAS 38328 (1, 42 HL, 175+ TL), 2°20′S, 81°16′W, 850–1,400 m, TE VEGA cr. 19, sta. 84, 4 Aug. 1968. —CAS 38330 (49, 25–45 HL, 133–215 TL), 2°25′S, 81°10′W, 700–1,000 m, TE VEGA cr. 19, sta. 148, 1 Sep. 1968. —CAS 40826 (60, 38–45 HL, 190–234 TL), 3°15′S, 80°55′W, 945–960 m, ANTON BRUUN cr. 18B, sta. 770 (LWK66–120), 10 Sep. 1966.

Peru: USNM 118019 (1, 42 HL, 215+ TL), 5°47′S, 81°24′W, 1,030 m, ALBATROSS sta. 4653, 12 Nov. 1904. —LACM 33885 (2, 37–38 HL, 175–192 TL), 7°46′S, 80°31′W, 800 m, sta. SNP1-27, 23 Jan. 1974. —CAS 38321 (35, 16–46 HL, 81–205 TL) and CAS 38322 (10, 27–46 HL, 100+ to 203 TL), 7°49′S, 80°38′W, 605–735 m, ANTON BRUUN cr. 18B, sta. 754 (LWK66–93), 5 Sep. 1966.

In addition, the following ALBATROSS specimens were examined but no measurements or counts were taken from them: MCZ 28570 (6 syntypes), sta. 3354; MCZ 28571 (10 syntypes), sta. 3384; and MCZ 28572 (3 syntypes), sta. 3394.

Nezumia convergens (Garman)

(Figures 15*b*, 18*f*)

Macrurus convergens GARMAN, 1899:210–211, pl. 48, fig. 1 (Gulf of Panama, 695–1,020 fms [1,271–1,865 m], ALBATROSS sta. 3353, 3357, and 3393).

Macrurus cuspidatus GARMAN, 1899:209–210 (Gulf of California, 27°34′N, 110°53′40″W, 905 fms [1,655 m], ALBATROSS sta. 3436).

Macrurus trichiurus GARMAN, 1899:215 (Gulf of Panama, 555 fms [1,014 m], ALBATROSS sta. 3358).

Lionurus (Nezumia) convergens: GILBERT AND HUBBS 1916:146 (listed).

Lionurus (Nezumia) cuspidatus: GILBERT AND HUBBS 1916:146 (listed).

Lionurus (Nezumia) trichiurus: GILBERT AND HUBBS 1916:146 (listed).

Nezumia convergens: MAKUSHOK 1967:table 18.

Nezumia cuspidata: MAKUSHOK 1967:table 18.

Nezumia trichiura: MAKUSHOK 1967:table 18.

Sphagemacrurus trichiurus: MARSHALL 1973:623 (listed).

DIAGNOSIS.—A species of *Nezumia* with pelvic fin rays 10–11. Gill-rakers on first arch 7–9 (5–7 on lower limb); on second arch 8–9. Spinules on body scales slender, conical to narrowly lanceolate, in discrete longitudinal rows, middle row often enlarged. Barbel length 8–20 percent HL (usually 2.5–3.0 in orbit); upper jaw length 26–32. First dorsal fin uniformly blackish.

Description.—General features of fish seen in Figure 15b. Head slightly compressed, ridges of head generally well developed; suborbital ridge prominent. Mouth subterminal, upper jaw extends posteriad to below middle of eye. Snout moderately pointed; terminal and lateral angles with stout tubercles armed with radiating rows of small spinules. Interorbital region flat to slightly concave, narrow, somewhat more than half orbit diameter. Gill membranes broadly attached over isthmus, with only a narrow posterior free fold; gill openings extend anteroventrally to beneath posteroventral angle of preopercular ridge (Fig. 4b). Body slender; greatest body depth (at origin of first dorsal fin) less than postrostral length of head; 7–8 in total length in large adults. Light organ not well developed externally; no scaleless fossa between pelvic fins. Anus within middle third of distance between pelvic fin insertion and anal fin origin. Gill filaments rather short, length of longest shorter than diameter of eye lens.

Second spinous ray of first dorsal fin longer than postrostral length of head; leading edge armed with rather closely spaced, nonoverlapping slender, sharp teeth. Pectoral and pelvic fins originate about on same vertical, which is anterior to origin of first dorsal fin. Outer pelvic ray in adults extends slightly past anal fin origin. Second dorsal fin rudimentary throughout.

Body scales somewhat deciduous. Slender, sharp, conical spinules uniformly cover exposed fields, aligned in slightly convergent longitudinal rows; spinules in middle row usually larger than those of lateral rows; 10–12 rows of spinules on scales of large adults. Almost all of ventral snout surface and part of anteroventral portion of suborbital region without scales. Mandibular rami covered posteriorly with narrow band of small, loose scales; mandibles generally naked anteriorly, but liberally pocketed there with small pores.

Dentition composed of small teeth in broad bands in both jaws; outer series of teeth in upper jaw not notably enlarged.

Coloration in alcohol generally brownish black with hint of violet (especially on tail); bluish tinge over abdomen. Fins uniformly black or brownish black. Oral cavity dusky; peritoneal cavity flesh colored, often lightly peppered with large melanophores.

Counts (from 80 specimens). —1D. II,9–10 (rarely 8 or 11); 1P. 18–22 ($\bar{x}$ = 20.18; *n* = 142; S.D. = 1.02); 2P. 10–11 (rarely 9). Gill-rakers on first and second arch 1–2 + 5–7 (total 7–9; $\bar{x}$ = 8.04; *n* = 80; S.D. = 0.56). Scales below first dorsal 8½–10 (rarely 11); below second dorsal 5½–9 (usually 6½–9); lateral line scales over distance equal to predorsal length of head 33–44 (usually 36–42). Pyloric caeca 21–32 (usually 25–30) ($\bar{x}$ = 26.97; *n* = 35; S.D. 2.55).

Measurements (from 80 specimens, 25 localities, 17.5–51.6 mm HL, 97–300 mm TL), expressed as percentage of head length [range ($\bar{x}$; *n*; S.D.)]: postrostral length of head 69–76 (72.60; 79; 1.43); snout length 27–34 (30.46; 80; 1.37); preoral length 22–31 (26.99; 78; 1.59); internasal width 17–23 (20.50; 70; 1.31); orbit diameter 31–37 (33.74; 80; 1.31); interorbital width 16–23 (19.73; 79; 1.29); postorbital length 34–40 (37.78; 78; 1.59); orbit to angle of preopercle 32–40 (35.17; 77; 1.72); suborbital width 12–17 (14.41; 77; 0.96); upper jaw length 26–32 (28.83; 78; 7.37); length barbel 8–20 (14.08; 74; 2.64); length first gill-slit 11–19 (13.22; 76; 1.36); preanal length 133–181 (150.13; 73; 8.47); distance outer pelvic ray to anal origin 27–55 (40.11; 75; 5.24); vent to anal origin 14–28 (20.54; 66; 3.11); greatest body depth 60–78 (71.21; 64; 5.23); 1D.–2D. interspace 28–68 (45.74; 75; 9.00); height first dorsal fin 68–93 (79.68; 53; 5.13); length pectoral fin 46–60 (52.30; 64; 3.52); length pelvic fin 36–61 (46.03; 59; 4.85).

Relationships and Comparisons.—In the eastern Pacific, *Nezumia convergens* appears closest to *N. latirostrata* (Garman), *N. loricata* (Garman), and *N. orbitalis* (Garman), but it is readily distinguished from these three by its fewer gill-rakers on the first arch (9 or fewer total, 5–6 [rarely 7] on lower limb, as compared with 9 or more total, 7–11 on lower limb). Spinules on body scales are generally more slender and conical than those of *N. latirostrata* and *N. loricata*, and they are arranged in discrete parallel rows with the middle row often enlarged (this compares with spinules in a somewhat quincunx arrangement or in rows that converge strongly toward the midline in the other two species). In addition, the body is somewhat more slender than that of the other three species (greatest depth less than 75 percent of head length in most adults of *N. convergens* compared with more than 75 percent in most adults of other species), the anus is usually more posteriorly placed, often closer to the anal fin origin than to the insertion of the pelvic fins (always closer to the pelvic fin insertion in the others), and the anterior dermal window of the light organ is poorly defined externally (well defined in others). The barbel is slightly longer than that of *N. latirostrata,* and the first dorsal fin is uniformly blackish, not black blotched as in *N. orbitalis*.

Nezumia convergens seems closely related to the western Atlantic species *N. suilla* Marshall and Iwamoto, 1973, with which it shares a close similarity in general physiognomy, coloration, scale spinulation, and extent of naked areas on the ventral surfaces of the head. The lower pelvic fin ray count (7) and broader scale spinules in that species, nonetheless readily distinguish it from *N. convergens*.

REMARKS ON SYNONYMY.—In my studies of the grenadiers described by Garman (1899), I have encountered three instances where he described different specimens of a single species-group taxon as different species. In the present instance, the nominal species concerned are *Macrurus cuspidatus, M. convergens,* and *M. trichiurus*. As first revisor, I have chosen to establish the name *M. convergens* over the other two, primarily because the type-series for the species is large and representative, while *M. cuspidatus* and *M. trichiurus* were each described from single specimens, the last from a juvenile.

The holotype of *M. cuspidatus* agrees well with the many well-preserved type-specimens of *M. convergens* except for its much deeper body. The entire trunk area of the holotype, in fact, appears to be abnormally swollen, as if it had been over-injected with preservative. If this is true, the deeper body is of no consequence. The Gulf of California capture of *M. cuspidatus* represents the northernmost record of the species and the only record from the Gulf.

The holotype of *M. trichiurus* is a young specimen (17.5 mm HL, 111 mm TL) slightly damaged ventrally. It agrees in all salient features with small specimens of *N. convergens* I have examined. Although Garman (1899:215) gave a pelvic fin ray count of 8 for the species, I counted 10 on both fins of the holotype. The gill-raker count on that specimen was 1 + 6 on the mesial side of both the first and the second arches.

DISTRIBUTION.—*Nezumia convergens* is one of the most numerous and widely distributed grenadier in the eastern Pacific Ocean. The species has the greatest latitudinal range of any *Nezumia* in the eastern Pacific except *N. stelgidolepis,* although present collections show a broad gap between the Islas Tres Marías and Costa Rica. This gap is of little significance, however, in that deep trawling along the Central American coast between the Gulf of Panama and the Gulf of California has been extremely limited. One Gulf of California record; others from off northern Mexico, Costa Rica, Panama, Cocos Ridge, Galápagos, Ecuador, Peru, and Chile (to 34°53.5′S). Capture depths from 600 m to 1,865 m.

SIZE.—To at least 50 mm HL and 300 mm TL.

MATERIAL EXAMINED.—**Mexico:** MCZ 28575 (1, 52 mm HL; holotype of *Macrurus cuspidatus* Garman, 1899), Gulf of California off Guaymas, Sonora, 27°34′N, 110°53′40″W, 1,655 m, ALBATROSS sta. 3436, 22 Apr. 1891. —LACM 31124–4 (3, 43–45 HL, 250–270 TL), N of Islas Tres Marías, 21°52′30″N, 106°47′36″W, 800–550 m, VELERO IV sta. 13770, 21 Jan. 1970.

Costa Rica: LACM 33588 (4, 28–50 HL, 161–295 TL), 9°45′18″N, 85°52′24″W, 1,865–1,372 m, VELERO IV sta. 18932, 12–13 May 1973.

Panama: MCZ 28574 (1 damaged syntype), 7°15′N, 79°36′W, 1,865 m, ALBATROSS sta. 3393, 10 Mar. 1891. —GCRL 14258 (1, 26 HL, 132+ TL), 7°13′N, 79°18′W, 805–841 m, CANOPUS sta. 1291, 12 Mar. 1974. —MCZ 28573 (3 syntypes, 31–42 HL, 170+ to 220+ TL), 7°06′15″N, 80°34′W, 1,271 m, ALBATROSS sta. 3353, 23 Feb. 1891. —MCZ 28556 (1, 17.5 HL, 111 TL; holotype of *Macrurus trichiurus* (Garman, 1899), 6°30′N, 81°44′W, 1,006 m, ALBATROSS sta. 3358, 24 Feb. 1891.

Cocos Island: AMNH 3471 (3, 29–43 HL), 96 km S of Cocos, ARCTURUS sta. 74, May 1925.

Galápagos: CAS 36814 (1, 47 HL, 248 TL), 27 km SSE of Isla San Cristobal, 1°06′S, 89°22′W, 700–800 m, TE VEGA cr. 19, sta. 102, 12 Aug. 1968.

Ecuador: CAS 36817 (1, 47 HL, 265 TL), off Gulf of Guayaquil, 2°10′S, 81°13′W, 800–1,000 m, TE VEGA cr. 19, sta. 144, 31 Aug. 1968. —CAS 36816 (8, 19–44 HL, 101–252 TL), 2°20′S, 81°16′W, 850–1,400 m, TE VEGA cr. 19, sta. 84, 4 Aug. 1968. —CAS 36815 (2, 22–30 HL, 108–175 TL), 2°25′S, 81°10′W, 700–1,000 m, TE VEGA cr. 19, sta. 148, 1 Sep. 1968. —CAS 36812 (35, 23–48 HL, 134–230+ TL), 3°15′S, 80°55′W, ANTON BRUUN cr. 18B, sta. 770 (field no. LWK66–120).

Peru: CAS 36813 (3, 40–43 HL, 205–230 TL), 4°10′S, 81°27′W, 1,815–1,860 m, ANTON BRUUN cr. 18B, sta. 766 (field no. LWK66–115), 9 Sep. 1966. —CAS 28760 (1, 21 HL, 97 TL), 17°08′05″S, 73°28′04″W, 860 m, 27 Jan. 1972. —IMARPE (1, 37 HL, 206+ TL), 18°17.3′S, 71°11′W, 600 m, 28 Jan. 1972. —CAS 28762 (1, 33 HL, 177 TL), 18°19′S, 71°12′W, 810 m, 28 Jan. 1972. —IMARPE (1, 32 HL) (bottle label illegible), 800 m, 1972.

Chile: SIO 72–184 (3, 35–39 HL, 182–205+ TL), 18°40.4′S, 70°36.0′W, 768–967 m, THOMAS WASHINGTON, field no.

TABLE 3. RANGE, MEAN ($\bar{x}$), AND STANDARD DEVIATION (S.D.) OF SELECTED MEASUREMENTS (VALUES IN PERCENTAGE OF HEAD LENGTH) AND COUNTS OF TWO SUBSPECIES OF *NEZUMIA LORICATA* (GARMAN).

Character	Subspecies	*n*	Range	$\bar{x}$	S.D.
1D. rays (total)	*loricata*	11	12–14	12.73	0.8
	atomos	9	11–13	11.78	0.8
1P. rays	*loricata*	23	20–24	21.48	1.1
	atomos	18	21–25	22.22	1.0
2P. rays	*loricata*	24	10–11	10.92	0.3
	atomos	18	11–12	11.28	0.5
GR I (total)	*loricata*	12	9–12	10.58	0.9
	atomos	9	11–14	12.44	0.9
GR II (total)	*loricata*	12	10–12	10.83	0.7
	atomos	9	11–13	12.56	0.7
Postrostral len.	*loricata*	10	70–75	72.60	1.4
of head	*atomos*	9	67–72	69.56	1.3
Snout length	*loricata*	12	29–32	30.75	1.1
	atomos	9	32–37	33.89	1.4
Internasal	*loricata*	11	20–24	22.00	1.2
length	*atomos*	9	22–25	23.56	1.0
Interorbital	*loricata*	12	19–24	21.00	1.4
width	*atomos*	9	22–26	23.78	1.6
Orbit to	*loricata*	12	32–36	33.92	1.0
preopercle	*atomos*	9	34–38	35.89	1.2

MV72–II–27, 7 May 1972. —CAS 36807 (6, 27–50 HL, 150+ to 287 TL), 24°29.5′S, 70°40′W, 950 m, ANTON BRUUN cr. 18A, sta. 714 (field no. LWK66–60), 16 Aug. 1966. —CAS 36810 (7, 34–41 HL, 184+ to 220 TL), 32°08.5′S, 71°43′W, 960 m, ANTON BRUUN cr. 18A, sta. 703 (field no. LWK66–47), 12 Aug. 1966. —CAS 36809 (3, 36–42 HL, 218–220 TL), 32°17′S, 71°39.5′W, 580 m, ANTON BRUUN cr. 18A, sta. 702 (field no. LWK66–44), 11 Aug. 1966. —CAS 36805 (28, 29–50 HL, 162–300+ TL), 33°39′S, 72°09.5′W, 1,170–1,480 m, ANTON BRUUN cr. 18A, sta. 699 (field no. LWK66–41), 10 Aug. 1966. —CAS 36811 (2, 35–39 HL, 208–224 TL), 34°06.5′S, 72°18.5′W, 750 m, ANTON BRUUN cr. 18A, sta. 687 (field no. LWK66–25), 5 Aug. 1966. —CAS 36808 (8, 28–39 HL, 148+ to 203 TL), 34°53.5′S, 72°44′W, 780–925 m, ANTON BRUUN cr. 18A, sta. 698 (field no. LWK66–40), 9–10 Aug. 1966.

Nezumia loricata (Garman)

(Figures 15*c*, 16, 18*g*; Table 3)

Macrurus loricatus GARMAN, 1899:208–209, pl. 47, figs. 2–2b (original description; specimens from ALBATROSS sta. 3409 and 3410, off Galápagos Islands, 327–331 fms).

Lionurus (Nezumia) loricatus: GILBERT AND HUBBS 1916:146 (listed).

Nezumia loricata: MAKUSHOK 1967:table 18.

DIAGNOSIS.—A species of *Nezumia* with 10–12 (usually 11) pelvic fin rays. Gill-rakers on first arch 11–14 (8–11 on lower limb); on second arch 10–13 (8–11 on lower limb). Spinules on body scales moderately to broadly lanceolate; no enlarged middle row of spinules on scales. Barbel length 10–17 percent HL; upper jaw length 29–33. First dorsal fin uniformly blackish.

DESCRIPTION.—General features of fish seen in Figure 15c. Body rather deep, especially in adults; greatest depth at origin of first dorsal fin significantly greater than postrostral length of head. Head length varies from 17 to 20 percent of total length. Rictus extends to below middle of orbit; maxillary extends to vertical slightly behind middle of orbit. Tubercular scutelike scales at tip and lateral angles of snout spiny and stout; the terminal scute bifid. Interorbital space flat to slightly concave, relatively narrow, 1.3–1.7 into orbit. Gill membranes broadly attached across isthmus with little, if any, free fold. Gill openings extend anteroventrally to a point slightly behind vertical through posterior margin of orbits. Dermal window of light organ small, roundish, situated between pelvic fin bases. Anus much closer to origin of pelvic fin than to origin of anal fin. Gill filaments short, length of longest less than half diameter of orbit.

Second spinous ray of dorsal fin stout, armed on leading edge with sharp, pointed, reclined teeth; tip of ray slightly produced. Paired fins moderate in size; outer ray of pelvic fin extends beyond first three or four anal rays, other pelvic rays barely (or do not) reach anal fin origin.

Body scales relatively adherent (compared with those of *N. convergens* and *N. latirostrata*). Spinules on body scales dagger-shaped to narrowly triangular, densely cover exposed fields, arranged in longitudinal series that converge towards middle of field. Scales absent on ventral surface of snout and posteriorly along part of suborbital region; naked areas dotted with sensory papillae, arranged in discrete rows and clusters in most specimens. Mandibular rami covered with small, thin, rather deciduous scales.

Teeth small, in bands of moderate width in both jaws. Outer series of teeth in upper jaw slightly enlarged.

Color in alcohol swarthy to medium brown. Ventral aspects of trunk and head much darker. All fins blackish. Oral cavity dusky. Peritoneal lining blackish and densely punctate in Chilean specimens (subspecies *atomos*), but more flesh colored with scattered large punctations in TE VEGA Galápagos specimens (subspecies *loricata*).

GEOGRAPHIC VARIATION.—I here recognize two subspecies of *Nezumia loricata* based on differences in certain counts, measurements, and structural features enumerated and discussed below.

Key to the Subspecies of *Nezumia loricata*

1a. Terminal snout scute composed of two distinctly separated halves. Gill-rakers on first arch 9–12 total. Postrostral length of head 70–75% of head length ($\bar{x}$ = 72.6); snout length 26–32% ($\bar{x}$ = 30.8). Head length 17.6–20.0% of total length ($\bar{x}$ = 19.0). Galápagos Islands .... *N. loricata loricata*

1b. Each half of terminal snout scute closely adpressed, without a deep, median gap between them. Gill-rakers on first arch 11–14 total. Postrostral length of head 67–71% HL ($\bar{x}$ = 69.6); snout length 32–37 ($\bar{x}$ = 33.9). Head length 16.6–18.2% of total length ($\bar{x}$ = 17.5). Off Chile .... *N. loricata atomos*, new subspecies

The few specimens of restricted size representing the populations off Chile and the Galápagos Islands limit comparisons, but there appear to be sufficient differences in the study material to warrant formal recognition of the two populations. Frequency distributions of counts and measurements showing notable differences between the subspecies are enumerated in Table 3. Chief among the other differences is the shape of the terminal snout scute (Fig. 16)—in Galápagos specimens, the scute is composed of two coarsely spined halves medially split almost to the base, whereas in Chilean specimens, the scute is rather finely spined with the two halves closely adjoined medially, with little gap between. The tubercular scales along the leading edge of the snout and at the lateral angles are also more coarsely spined in the Galápagos specimens, and the Chilean specimens have a broader double row of thickened scales along the suborbital region.

The two populations of *N. loricata* are widely disjunct, and apparently, no material from intervening areas has been collected despite numerous trawl hauls at appropriate depths along the coasts of Ecuador, Peru, and Chile.

The subspecific name *atomos* is derived from the Greek word meaning indivisible or uncut, in reference to the relatively undivided terminal snout scute of this subspecies.

FIGURE 16. *Nezumia loricata* (Garman). Dorsal views of terminal snout scute in two subspecies: (*a*) *N. loricata loricata;* (*b*) *N. loricata atomos.*

COUNTS (of both subspecies combined).—1D. II,9–12; 1P. 20–25; 2P. 10–12. Gill-rakers on first arch 1–3 + 8–11; on second arch 2 + 8–11. Scales below first dorsal 9 to 12½; below second dorsal 7½ to 9; below midbase of first dorsal 6½ to 7½; over distance equal to predorsal length of head 35–41. Pyloric caeca 20–32 ($\bar{x}$ = 25.9, *n* = 9).

MEASUREMENTS (of both subspecies combined, other than those given in Table 3).—Total length 175+ to 297+ mm, head length 34–52. The following in percent of head length: preoral length 25–30; orbit diameter 31–36; postorbital length of head 36–40; suborbital width 14–17; upper jaw length 29–33; length pelvic fin 44–68; length barbel 10–17; length outer gill slit 14–17; preanal length 140–157; base outer pelvic ray to anal origin 31–44; anus to anal origin 16–28; greatest body depth 67–87; height first dorsal fin 80–101; length pectoral fin 48–63.

COMPARISONS AND RELATIONSHIPS.—*Nezumia loricata* appears most closely related to *N. latirostrata*, but the two are readily distinguished by differences given in the key and in the description of *N. latirostrata*. *Nezumia loricata* may be distinguished from another close relative, *N. convergens*, by differences in gill-raker numbers, spinules on body scales, relative body depth, and placement of anus (see comparisons in description of *N. convergens*). Other eastern Pacific species of the genus are differentiated from *N. loricata* by characters given in the key.

DISTRIBUTION.—Galápagos (subspecies *loricata*) and central Chile (subspecies *atomos*).

SIZE.—To at least 52 mm HL and 300 mm TL.

MATERIAL EXAMINED.—**Galápagos** (subspecies *loricata*): MCZ 28577 (4 syntypes, 45–55 mm HL, 215+ to 250 mm TL), and USNM 57859 (1 syntype, 47 HL, 240+ TL), 00°19′N, 90°34′W, 331 fms (605 m), ALBATROSS sta. 3410, 3 Apr. 1891. —MCZ 28576 (1 syntype, 48 HL, 260 TL), 00°18′40″N, 90°34′W, 327 fms (598 m), ALBATROSS sta. 3409, 3 Apr. 1881.

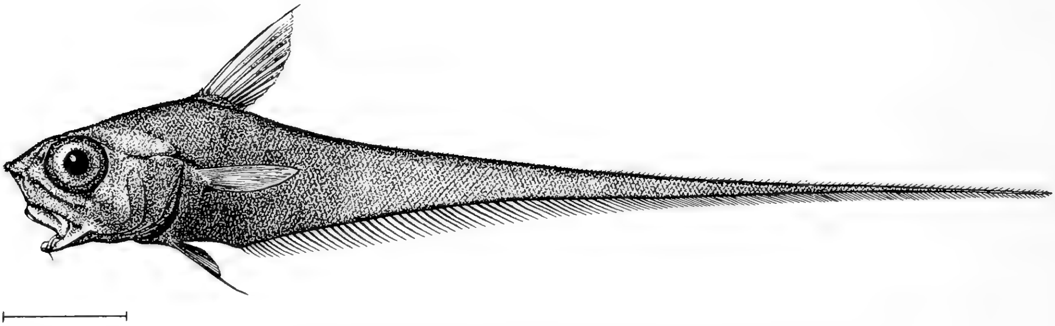


FIGURE 17. *Nezumia parini* Hubbs and Iwamoto, 1977. Paratype, CAS 29414, 35 mm HL, 216 mm TL, from off Peru.

—USNM 135603 (remains of about 6 specimens, mostly disintegrated), 00°29′S, 89°54′30″W, 392 fms (717 m), ALBATROSS sta. 2818, 15 Apr. 1888. —CAS 38329 (7, 34–50 HL, 175+ to 250 TL), 1°06′S, 89°22′W, 700–800 m, TE VEGA cr. 19, sta. 102, 12 Aug. 1968. —CAS-SU 25246 (2, 44–46 HL, poor condition), captured "between Galapagos and Panama, ALBATROSS 1888."

Chile (subspecies *atomos*): HOLOTYPE, CAS 38312 (51 mm HL, 297+ mm TL) and 8 PARATYPES, CAS 43427 (47–51 HL, 270–290 TL), 33°39′S, 72°09′W, 1,170–1,480 m, ANTON BRUUN cr. 18A (field no. LWK66–41), 10 Aug. 1966.

Nezumia parini Hubbs and Iwamoto

(Figures 17, 18*a*)

Nezumia parini HUBBS AND IWAMOTO, 1977:246–250, fig. 8, 11, table 4.

DIAGNOSIS.—A bathypelagic species of *Nezumia* with 11–12 pelvic fin rays. First and second gill arches each with 10–13 rakers. Small, circular body scales each with 1–15 long, erect, needlelike spinules. Scale rows below second dorsal about 11–14. Barbel length 7–13 percent HL; upper jaw length 31–36 percent HL; outer pelvic fin ray length 71–160 percent HL. Overall color dark brown to black.

REMARKS.—General features of the fish can be seen in Figure 17. This distinctive species, described in detail in the original description, is the only *Nezumia* with bathypelagic adults, although in other species (e.g., *N. stelgidolepis*) the early-life stages are probably bathypelagic. The relationships of *N. parini* are obscure, but probably lie closest to the *convergens-latirostrata-loricata-orbitalis* complex of species. The dense, fine, erect spinules on the small scales give a distinctive furry texture and feel to body surfaces.

SIZE.—*Nezumia parini* is a small species attaining a head length of 35 mm and a total length of 216 mm.

DISTRIBUTION.—Midwaters of the equatorial eastern Pacific and off the western shores of the Americas between Panama (7°30′N) and northern Chile (20°00′S).

MATERIAL EXAMINED.—See original description. In addition, one specimen recently discovered in the CAS-SU collections filed under unidentified Gadidae: CAS-SU 57651 (formerly New York Zoological Society cat. no. 28704), (1, 35.6 mm HL, 202 mm TL), off Colombia, 4°45′N, 78°02′W, meter net fished over bottom depth of 500 fms (914 m), ZACA sta. 233, 3 Apr. 1938.

ACKNOWLEDGMENTS

I thank the many persons who helped in different aspects of this study. The following helped in the loan of specimens and/or provided information and assistance during museum visits: T. Arai (Nippon Luther Shingaku Daigaku, Tokyo); N. Chirichigno-F. (IMARPE); D. M. Cohen (National Marine Fisheries Service, Washington, D.C.); C. E. Dawson (GCRL); D. Hubendick (Natural History Museum, Göteborg); C. L. Hubbs (deceased), R. H. Rosenblatt and assistants (SIO); C. Karrer (formerly ISH); R. J. Lavenberg and assistants (LACM); R. Lee (University of Alaska); K. Leim and K. Hartel (MCZ); T. McLellan (formerly MCZ and Massachusetts Institute of Technology); C. R. Robins (UMML); C. L. Smith and G. Nelson (AMNH); V. G. Springer and assistants (USNM); M. Stehman (ISH)

W. N. Eschmeyer examined and photographed the holotype of *Macruroplus potronus*, critically reviewed the manuscript, and provided useful advice during the study. L. J. Dempster assisted in literature searches, reviewed the

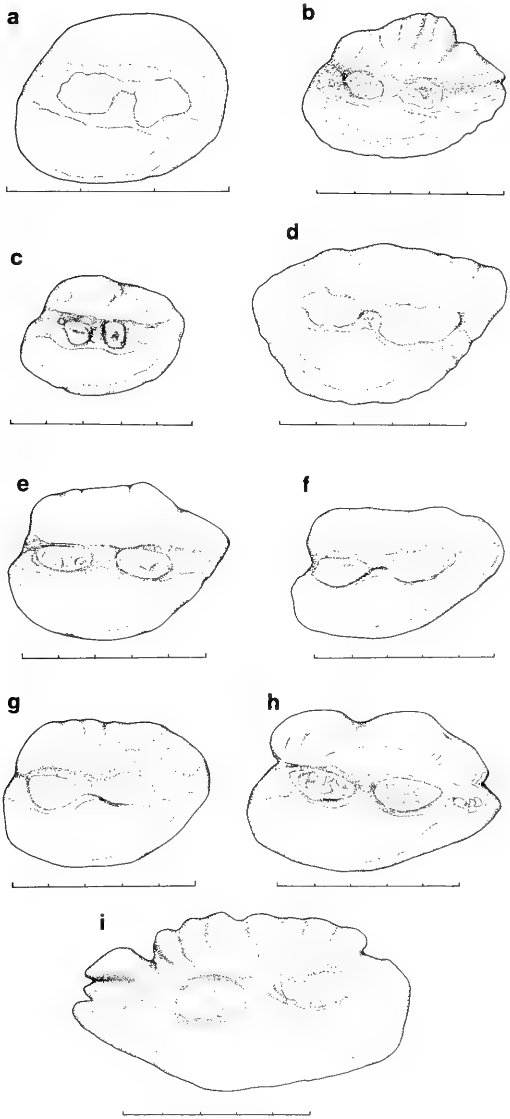


FIGURE 18. Otoliths (left saggita) from (*a*) *Nezumia parini*, (*b*) *N. pulchella*, (*c*) *N. liolepis*, (*d*) *Ventrifossa nigromaculata*, (*e*) *Nezumia latirostrata*, (*f*) *N. convergens*, (*g*) *N. loricata atomos*, (*h*) *N. pudens*, and (*i*) *N. stelgidolepis*. Increments on scale bars equal 1 mm.

manuscript, and advised on grammatical, nomenclatural, and editorial matters. O. Okamura reviewed the manuscript, offered advice and information, and provided many profitable hours of discussions on the Macrouridae. K. P. Smith rendered the fine illustrations of *Mataeocephalus tenuicauda* (Fig. 8) and *Nezumia ventralis* (Fig. 14b). Curatorial and technical assistance was provided by J. E. Gordon, T. Keating, B. Powell, W. C. Ruark, and P. Sonoda. My sincerest thanks to all.

This study was supported in part by a grant from the National Science Foundation (BMS 075-03153), Tomio Iwamoto, principal investigator.

LITERATURE CITED

AGASSIZ, JOHN LOUIS R. 1843. Bericht über die fossilen Fische des Old Red Sandstone, in Auftrage der britischen Versammlung, im Jahre 1842, erstattet. Biblioth. Univ. Genève, 1843, 43:353–369.

ALCOCK, ALFRED W. 1891. On the deep-sea fishes collected by the "Investigator" in 1890–91. Ann. Mag. Nat. Hist., ser. 6, 8:16–34; 119–138, pls. vii–viii.

ARAI, TAKAO. 1979. Additional information on a rare macrourid fish, *Mesobius antipodum*, from New Zealand. Japn. J. Ichthyol. 25(4):286–390, figs. 1–3.

BARNHART, PERCY SPENCER. 1936. Marine fishes of southern California. Univ. Calif. Press, Berkeley. 209 pp.

BERG, CARLOS. 1898. Substitución de nombres genéricos. Comm. Mus. Nac. Buenos Aires 1:41–43.

BLEEKER, PIETER. 1874. Typi nonnulli generici piscium neglecti. Versl. Akad. Amsterdam, ser. 2, 8:367–371.

CHIRICHIGNO F., NORMA, AND TOMIO IWAMOTO. 1977. *Coryphaenoides delsolari*, a new species of macrourid fish from the Pacific coast of South America. Proc. Biol. Soc. Wash. 89(45):519–528.

FITCH, JOHN E., AND ROBERT J. LAVENBERG. 1968. Deep-water teleostean fishes of California. Univ. Calif. Press, Berkeley. 155 pp.

FOWLER, HENRY W. 1944. Fishes of Chile. Systematic catalog. Apartado Rev. Chil. Hist. Nat. Santiago.

GARMAN, SAMUEL. 1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross" during 1891. Lieut.-Commander Z. L. Tanner, U.S.N., commanding. Part 26, The Fishes. Mem. Mus. Comp. Zool. Harv. Coll. 24:1–431, pls. 1–84, A–N.

GIGLIOLI, ENRICO H. 1882. New deep-sea fish from the Mediterranean. Nature (London), 27(1882):198–199.

———, AND A. ISSEL. 1884. Pelagos, saggi sulla vita et sui prodotti del mare. Genova. 433 pp.

GILBERT, CHARLES H. 1890. A preliminary report on the fishes collected by the steamer "Albatross" on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proc. U.S. Natl. Mus. 13(797):49–126.

———. 1905. The deep-sea fishes of the Hawaiian Islands. Part 2, section 2, pp. 576–713, figs. 230–276, pls. 66–101, *in* Jordan, David Starr, and Barton Warren Evermann, The aquatic resources of the Hawaiian Islands. Bull. U.S. Fish Comm. (1903)22.

———, AND FRANK CRAMER. 1897. Report on the fishes dredged in deep water near the Hawaiian Islands, with descriptions and figures of twenty-three new species. Proc. U.S. Natl. Mus. 19(1114):403–435, pls. 36–48.

———, AND CARL L. HUBBS. 1916. Report on the Japanese macrouroid fishes collected by the United States fisheries steamer "Albatross" in 1906, with a synopsis of the genera. Proc. U.S. Natl. Mus. 51(2149):135–214, pls. 8–11.

———, AND ———. 1917. Description of *Hymenocephalus* *tenuis*, a new macrouroid fish from the Hawaiian Islands. Proc. U.S. Natl. Mus. 54(2231):173–175.

———, and ———. 1920. The macrourid fishes of the Philippine Islands and the East Indies. U.S. Natl. Mus. Bull. 100, 1(pt. 7):369–588.

———, and William F. Thompson, 1916. Family Macrouridae, pp. 471–476, pls. 5–6, *in* Thompson, William F., Fishes collected by the United States Bureau of fisheries steamer "Albatross" during 1888, between Montevideo, Uruguay, and Tome, Chile, on the voyage through the Straits of Magellan. Proc. U.S. Natl. Mus. 50(2133):401–476, pls. 2–6.

Goode, G. Brown, and Tarleton H. Bean. 1896. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world . . . . Smithson. Contrib. Knowl. 1895[1896], 30(981), 1(text):1–553; 2(atlas):1–26, pls. 1–123. [Also issued as U.S. Natl. Mus. Spec. Bull. 2, and Mem. Mus. Comp. Zool. Harv. Coll. 22.].

Günther, Albert. 1862. Catalogue of the fishes of the British Museum 4:1–534.

———. 1887. Report on the deep-sea fishes collected by H.M.S. Challenger during the years 1873–76. Rep. Sci. Res. Challenger 22(Zool.):pt. 1(text): 1–335, pt. 2(plates): pls. 1–73.

Hubbs, Carl L., W. I. Follett, and Lillian J. Dempster. 1979. List of the fishes of California. Occas. Pap. Calif. Acad. Sci. 133:1–51.

———, and Tomio Iwamoto. 1977. A new genus (*Mesobius*), and three new bathypelagic species of Macrouridae (Pisces, Gadiformes) from the Pacific Ocean. Proc. Calif. Acad. Sci., ser. 4, 41(7):233–251, figs. 1–11.

———, and Karl F. Lagler. 1958. Fishes of the Great Lakes region. Rev. ed. Cranbrook Inst. Sci. Bull. 26:1–213.

Iwamoto, Tomio. 1970. The R/V Pillsbury Deep-Sea Biological Expedition to the Gulf of Guinea, 1964–65. 19. Macrourid fishes of the Gulf of Guinea. Stud. Trop. Oceanogr. Miami 4(pt. 2):316–431, figs. 1–27.

———. 1972. Macrourid fishes of the tribe Malacocephalini (Macrouridae: Gadiformes). Ph.D. Thesis, Univ. Miami.

———. 1974. *Nezumia* (*Kuronezumia*) *bubonis*, a new subgenus and species of grenadier (Macrouridae: Pisces) from Hawaii and the western North Atlantic. Proc. Calif. Acad. Sci., ser. 4, 39(22):507–516, figs. 1–3.

———. 1978. Eastern Pacific macrourids of the genus *Coelorinchus* Giorna (Pisces:Gadiformes), with description of a new species from Chile. Proc. Calif. Acad. Sci., ser. 4, 41(12):307–337, figs. 1–20.

———, and David L. Stein. 1974. A systematic review of the rattail fishes (Macrouridae: Gadiformes) from Oregon and adjacent waters. Occas. Pap. Calif. Acad. Sci. no. 111:1–79.

Jordan, David Starr, and Barton Warren Evermann. 1898. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47(3):2183–3134.

———, and Charles Henry Gilbert. 1904. Macrouridae. Pp. 602–621 *in* Jordan, David Starr, and Edwin C. Starks, List of fishes dredged by the steamer Albatross off the coast of Japan in the summer of 1900, with descriptions of new species and a review of the Japanese Macrouridae. Bull. U.S. Fish Comm. (1902) 22:577–630, pls. 1–8.

———, and Edwin C. Starks. 1904. See Jordan and Gilbert, 1904.

Kamohara, Toshiji. 1938. On the offshore bottom-fishes of Prov. Tosa, Shikoku, Japan. Tokyo. 86 pp.

Koefoed, Einar. 1927. Fishes from the sea-bottom. Report on Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition. 1910, 4(Pt. 1):1–147, pls. 1–6.

Lowe, Richard T. 1843. Notices of fishes newly observed or discovered in Madeira during the years 1840, 1841 and 1842. Proc. Zool. Soc. Lond. 11:91.

Makushok, M. 1967. Whiptails (family Macrouridae or Coryphaenoididae auct.). Chapter IV, pp. 200–227 *in* V. G. Kort (chief ed.), Biology of the Pacific Ocean. Book III. Fishes of the open waters. Moscow. (Transl. from Russian.) U.S. Naval Oceanogr. Off., Transl. 528, Wash., D.C.

Marshall, Norman B. 1973. Family Macrouridae. Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res., no. 1(pt. 6):496–665.

———, and Tomio Iwamoto. 1973. Genus *Nezumia*. Pp. 624–649, figs. 39–47 *in* Marshall, Norman B. Family Macrouridae. Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res., no. 1(pt. 6):496–665.

———, and Nigel Merrett. 1977. The existence of a benthopelagic fauna in the deep-sea. Pp. 483–497 *in* Martin, Angel, (ed.), A voyage of discovery: George Deacon 70th Anniversary Volume. Pergamon Press, Oxford.

McCulloch, Allan R. 1907. The results of deep sea investigation in the Tasman Sea. II. The expedition of the "Woy Woy." 1. Fishes and crustaceans from eight hundred fathoms. Rec. Aust. Mus. Syd. 6:345–355, pls. 63–65.

———. 1919. Check-list of the fish and fish-like animals of New South Wales, Parts 1 and 2. Australian Museum Sydney. 58 pp. 24 pls.

Merrett, Nigel R. 1978. On the identity and pelagic occurrence of larval and juvenile stages of rattail fishes (Family Macrouridae) from 60°N, 20°W and 53°N, 20°W. Deep-Sea Res. 25:147–160.

Nybelin, Orvar. 1957. Deep-sea bottomfishes. Rep. Swed. Deep-Sea Exped. 1947–48, 2(Zool.)(20):247–345, pls. 1–7.

Ojeda R., Federico P., and Juan Camus Y. 1977. Morfometria y nicho trofico de *Coelorhynchus patagoniae* Gilbert y Thompson (Pisces: Macrouridae). Bol. Mus. Nac. Hist. Nat. Chile 35:99–104.

Okamura, Osamu. 1963. Two new and one rare macrourid fishes of the genera *Coelorhynchus* and *Lionurus*, found in the Japanese waters. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 4:21–35.

———. 1970a. Fauna Japonica. Macrourina (Pisces). Academic Press of Japan, Tokyo. 216 pp., 64 pls.

———. 1970b. Studies on the macrouroid fishes of Japan. Morphology, ecology and phylogeny. Rep. Usa Mar. Biol. Sta. 171(1–2):1–179.

Parin, N. V., V. E. Becker, O. D. Borodulina, and V. M. Tchuvassov. 1973. Deep-sea pelagic fishes of the southeastern Pacific Ocean [in Russian, English summary]. Tr. Inst. Okeanol., Akad. Nauk SSSR 94:71–159.

———, G. N. Pokhilskaya, Y. I. Sazonov, and B. I. Fedoryako. 1977. Rare and poorly know midwater fishes from the central and eastern Pacific Ocean [in Russian, English summary]. Tr. Inst. Okeanol., Akad. Nauk SSSR 104:206–236.

Parr, Albert E. 1946. The Macrouridae of the western North Atlantic and Central American seas. Bull. Bing. Oceanogr. Coll. 10(1):1–99.

Pequeño-R., Germán. 1971. Sinopsis de Macrouriformes de Chile (Pisces, Teleostomi). Bol. Mus. Nac. Hist. Nat. Santiago 32:269–298.

Poll, Max. 1953. Poissons III. Téléostéens malacopterygiens. Rés. Sci. Expéd. Océonogr. Belge eaux côtières Africaines de l'Atlant. Sud (1948–1949) 4(2):1–258.

Radcliffe, Lewis. 1912. See Smith and Radcliffe, 1912.

Regan, C. Tate. 1908. The Percy Sladen Trust Expedition to the Indian Ocean in 1905 under the leadership of Mr. J. Stanley Gardiner. No. XIV.—Report on the marine fishes collected by Mr. J. Stanley Gardiner in the Indian Ocean. Pp. 217–255, pls. 23–32.

Roedel, Phil M. 1951. Noteworthy southern California records of four species of marine fishes. Calif. Fish Game 37(4):509–510.

Roule, Louis. 1916. Notice préliminaire sur quelques espèces nouvelles ou rares des Poissons provenant des croisières de S.A.S. le Prince de Monaco. Bull. Inst. Océanogr. Monaco 320:1–32.

Shcherbachev, Yu. N., Yu. I. Sazonov, and A. S. Piotrovskij. 1979. Occurrence of *Trachonurus villosus* (Günther) and *Mesobius* (Hubbs et Iwamoto) (Macrouridae, Osteichthyes) in the Indian Ocean. [In Russian.] Akad. Nauk SSSR [Problems in Ichthyology] 19:20–28, figs. 1–2, tables 1–2.

Smith, Hugh M., and Lewis Radcliffe. 1912. *In* Radcliffe, Lewis. Descriptions of a new family, two new genera, and twenty-nine new species of anacanthine fishes from the Philippine Islands and contiguous waters. Proc. U.S. Natl. Mus. 43(1924):105–140, pls. 22–31.

Smith, J. L. B. 1949. The sea fishes of southern Africa. Central News Agency, Cape Town, 550 pp. (Also 1953, 1961, and 1965 editions.)

———. 1968. New and interesting fishes from deepish water off Durban, Natal and southern Mozambique. Oceanogr. Res. Inst. Invest. Rep. 19:1–30, pls. 1–6.

Vaillant, Léon L. 1888. Expédition scientifiques du Travailleur et du Talisman pendant les années 1880, 1881, 1882, 1883. Poissons. Paris. Pp. 1–406, pls. 1–28.

Valenciennes, Achille. 1838. Ichthyologie des îles Canaries. Pp. 1–109, pls. 1–27, *in* Philip Barker Webb and Sabin Berthelot, Histoire Naturelle des îles Canaries, Zool., tome 2, pt. 2. Bethune, Paris.

Weber, Max. 1913. Die Fische der Siboga-Expedition. Siboga Exped. 57:1–719, pls. 1–12.

———, and L. F. de Beaufort. 1929. The fishes of the Indo-Australian Archipelago, vol. 5. E. J. Brill, Leiden. 458 pp.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 6, pp. 181–227, 17 figs. July 2, 1980

REVISION OF THE EASTERN PACIFIC SYNGNATHIDAE (PISCES:SYNGNATHIFORMES), INCLUDING BOTH RECENT AND FOSSIL FORMS

By
Ronald A. Fritzsche

Department of Biology, The University of Mississippi,
University, Mississippi 38677

Abstract: The marine and estuarine eastern Pacific Syngnathidae comprises 17 extant and 3 extinct species. Diagnostic characters for species and genera, including meristic and morphometric characters, and osteological features, are given. All species both living and fossil are diagnosed and described.

The recognized species and their ranges are: *Hippocampus ingens* Girard [=*H. hildebrandi*] (San Francisco Bay, California, south to Pucusana, Peru, including the Gulf of California); *Doryrhamphus melanopleura* (Bleeker) (Indo-Pacific; in the eastern Pacific from Bahía Magdalena, Baja California, south to Isla la Plata, Ecuador, including the Gulf of California, Galápagos Islands, and Clipperton Island); *Doryrhamphus paulus* n.sp. (Islas Revillagigedo, Mexico); *Leptonotus blainvilleanus* (Eydoux and Gervais) [=*S. acicularis*] (Hornitos, Chile, to Golfo Nuevo, Argentina); *Bryx arctus* (Jenkins and Evermann) (Tomales Bay, California, south to Mazatlán, Mexico, including the Gulf of California); *Bryx heraldi* n.sp. (Islas Juan Fernández and Isla San Félix, Chile); *Bryx coccineus* (Herald) (Bahía Banderas, Mexico, south to Punta Aguja, Peru, and the Galápagos Islands); *Bryx veleronis* Herald (Galápagos Islands; Islas Revillagigedo; Isla Murciélago and Isla del Caño, Costa Rica; and Islas San José and Canal de Afuera, Panama); *Bryx clarionensis* n.sp. (Isla Clarión, Mexico); *Syngnathus auliscus* (Swain) (Santa Barbara Channel, California, south to Paita, Peru, including the Gulf of California); *Syngnathus carinatus* (Gilbert) (confined to upper Gulf of California); *Syngnathus exilis* (Osburn and Nichols) (Half Moon Bay, California, to Bahía Magdalena, Baja California, and Isla Guadalupe, Mexico); *Syngnathus californiensis* Storer (Bodega Bay, California, south to Bahía Santa María, Baja California); *Syngnathus macrobrachium* n.sp. (Tumbes, Peru, south to Puerto Montt, Chile); *Syngnathus euchrous* n.sp. (Redondo Beach, California, to Punta Eugenia, Baja California); *Syngnathus leptorhynchus* Girard [=*S. griseolineatus, S. barbarae*] (southeastern Alaska south to Bahía Santa María, Baja California); *Syngnathus insulae* n.sp. (Isla Guadalupe, Mexico).

Studies of growth and variation show that *S. leptorhynchus* is highly variable with each population distinct. Marked seasonal variation, when combined with growth data, indicates that individuals probably live for one year or less.

The fossil pipefishes of Southern California are all only known from the Miocene. *Hipposyngnathus imporcitor* n.sp. from the upper Modelo Formation is most closely related to two species from the Oligocene of Europe. *Syngnathus emeritus* n.sp. is known only from the Puente Formation. *Syngnathus avus* Jordan and Gilbert is known from the lower Modelo Formation.

A comparison between inferred relationships of the various species and their geographical distribution suggests that the evolution of the eastern Pacific *Syngnathus* is a result of at least two separate invasions. *Doryrhamphus melanopleura* invaded the eastern Pacific by crossing the East Pacific Barrier and gave rise to *Doryrhamphus paulus*. *Leptonotus blainvilleanus* is related to other species of *Leptonotus* in New Zealand and southern Australia and was probably derived from an ancestor in these areas via waif dispersal.

The reduction and loss of elements of the branchial skeleton is useful in characterizing urophorine genera and may be of general use when relationships within the family Syngnathidae are studied in more detail.

INTRODUCTION

Pipefishes of the family Syngnathidae inhabit most temperate and tropical seas. In the eastern Pacific, pipefishes occur from southeastern Alaska to Tierra del Fuego. They are primarily marine or euryhaline, but some species are confined to fresh water.

Even though the family Syngnathidae contains the seahorses, of general interest to aquarists, the family has, in general, been poorly studied. There are a number of undescribed species and the intrafamilial relationships are poorly understood, due, in part, to the great variability in meristic and morphometric characters.

A revision of the Syngnathidae was published by Duncker (1915), but the American species were not included. Ginsburg (1937) and Herald (1940–1965) have been the major contributors to the taxonomy of the American syngnathids. To date, a definitive treatment of the eastern Pacific syngnathids has not appeared.

Detailed osteological work on adult syngnathids is limited to that of Jungersen (1910), Rauther (1925), and Banister (1967). Jungersen's study included the genera *Hippocampus, Syngnathus,* and *Nerophis,* two of which occur in the eastern Pacific. Rauther also studied the osteology of *Syngnathus,* as did Banister. The osteology of the other four genera of eastern Pacific syngnathids has not been treated. It is generally recognized that for the study of higher taxa, osteological characters are a good indicator of phylogeny because of their conservative nature.

The goal of this study has been to characterize the eastern Pacific genera and species of Syngnathidae, both fossil and recent, and to examine intraspecific variation. In addition, a preliminary examination of the osteology of a few of the syngnathid genera was made to help in understanding the relationships between at least a few of the genera, and as a test of the relationships proposed by Herald (1959) based on the method of brood-pouch closure.

MATERIALS AND METHODS

Specimens that have contributed to the data are listed in the Material Examined section for each species. In those lists, the number of specimens is given, followed by the size range (SL in mm) enclosed in parentheses. If the size range was not determined or the specimens are damaged, the range of standard length is not given. Abbreviations for listed collections are: AMS, the Australian Museum, Sydney; BC, University of British Columbia: BMNH, British Museum (Natural History); BOC, Bingham Oceanographic Collection, Yale University; CAS, California Academy of Sciences; EMBCh, Estacíon de Biología Marina, Chile; GCRL, Gulf Coast Research Laboratory Museum; HSU, Humboldt State University; IMARPE, Instituto del Mar, Peru; LACM, Natural History Museum of Los Angeles County; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Muséum National d'Histoire Naturelle, Paris; MNMH P, Museo Nacional de Historia Natural, Santiago, Chile; SCCWRP, Southern California Coastal Water Research Project; SIO, Scripps Institution of Oceanography Marine Vertebrates Collection; SU, Stanford University (now housed at CAS); UCLA, Department of Zoology, University of California, Los Angeles; UMMZ, University of Michigan Museum of Zoology, USNM, National Museum of Natural History, Smithsonian Institution; UW, University of Washington.

Measurements were made with dial calipers to the nearest 0.1 mm for lengths less than 17 cm; an ocular micrometer was used for measurements less than 2 mm. Measurements greater than 17 cm were made to the nearest mm with a centimeter rule.

The principle characters used in identifying syngnathids are illustrated in Figures 1 and 2 (based on a generalized syngnathid). The terminology used for the various ridges on the body is that of Herald (1943).

The condition of the lateral trunk ridge (Fig. 2) is important in characterizing syngnathid genera. It is subcontinuous with the superior tail ridge in *Bryx* and *Syngnathus,* but continuous in *Leptonotus*. In *Hippocampus* and *Doryrhamphus* the lateral trunk ridge is continuous with the inferior tail ridge. Clausen (1956) has shown that these ridge patterns are not wholly consistent within species, however, they are of value when used with other characters.

Scutella (Fig. 1), small oval plates interpolated between the larger dermal plates, may be present or absent. Their size is important in species determinations and is therefore included in the species descriptions. Size is given as a comparison of an individual scutellum with an adjacent plate.

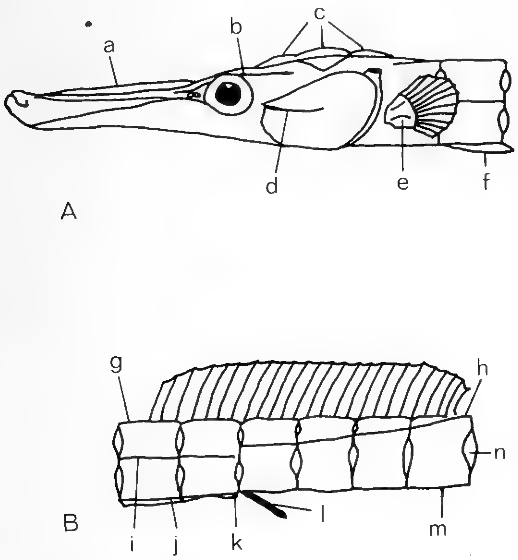


FIGURE 1. Characters used in syngnathid identification (modified after Herald 1943). (*A*) Characters in the region of the head: *a*. snout ridge; *b*. supraorbital ridge; *c*. supraoccipital, nuchal, and prenuchal ridges; *d*. opercular ridge; *e*. pectoral cover plate ridges; *f*. ventral trunk ridge. (*B*) Characters in the region of the dorsal fin: *g*. superior trunk ridge; *h*. superior tail ridge; *i*. lateral trunk ridge; *j*. inferior trunk ridge; *k*. anus; *l*. anal fin; *m*. inferior tail ridge; *n*. scutellum.

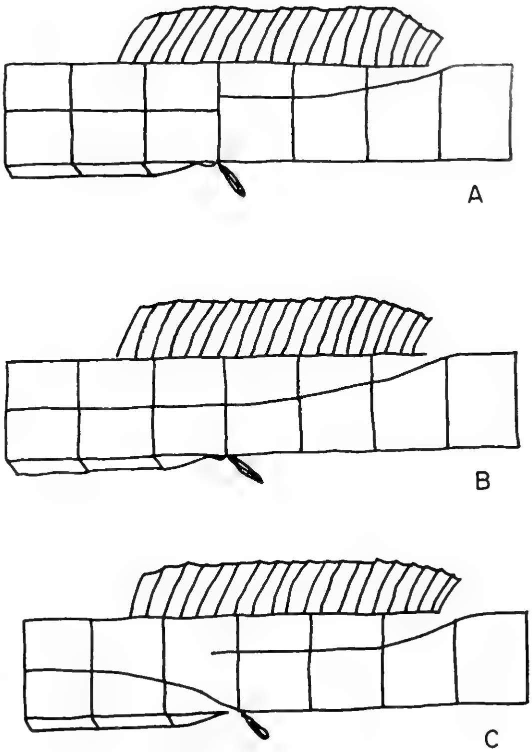


FIGURE 2. Configuration of ridges above the anus (modified after Herald 1943). (*A*) Lateral trunk ridge subcontinuous with superior tail ridge. (*B*) Lateral trunk ridge continuous with superior tail ridge. (*C*) Lateral trunk ridge continuous with inferior tail ridge.

A ring is defined as one unit in the series of dermal plates which form definite bands around the body.

Pouch protecting plates are not illustrated. They are merely ventral extensions of the inferior trunk or tail ridge which support the brood pouch and protect the eggs.

The pectoral cover plate is defined as the plate covering the base of the pectoral fin.

The methods of making counts and measurements are those of Hubbs and Lagler (1958), with the following exceptions:

Number of trunk and tail rings: The ring bearing the pectoral fins is counted as the first trunk ring; the ring bearing the anus is the last trunk ring. The ring bearing the anal fin is the first tail ring. If the anus and the anal fin are borne on the same ring, then that ring is the first tail ring and the preceeding ring is the last trunk ring.

Number of dorsal and anal fin rays: last two rays are counted as two.

Number of rings covered by dorsal fin: fractions of a ring estimated to the nearest tenth of a ring.

Number of lateral-line papillae: range of the number of lateral-line papillae per dermal plate.

For *Hippocampus* the standard length is the distance from the tip of the coronet, with the head held perpendicular to the trunk, to the tip of the tail, with the tail held straight (Ginsburg 1937).

In species diagnoses the modal range of a particular meristic character is given in parentheses after the range of that character.

Osteology was studied from trypsin-digested and alizarin-stained specimens (Taylor 1967) listed below. Osteological nomenclature follows Jungersen (1910) and Banister (1967). Bones were drawn with the aid of a camera lucida.

Diagnoses are based on adults unless otherwise noted.

Statistical procedures follow the text of Dixon and Massey (1957) except that the regression analyses are based on the Bartlett regression analysis as given by Hoese (1971). Unless otherwise specified, differences are considered significant at $P \leq .05$.

Cleared and Stained Material Examined.—*Heraldia nocturna,* SIO 75-54, 1, Sydney, Australia; *Maroubra perserrata,* SIO 75-53, 1, Sydney, Australia; *Choeroichthys brachysoma* SIO 73-196, 1, Timor Sea; *Doryrhamphus melanopleura,* SIO 65-343, 1, Gulf of California; *Dunckerocampus dactylophorus,* CAS uncat., 1, unknown; *Dentirostrum janssi,* CAS 14148, 3 paratypes, Thailand; *Syngnathoides biaculeatus,* SIO 61-693, 1, 10°N, 103°50′E; *Leptonotus blainvilleanus,* USNM 176569, 1, Isla Chiloé, Chile; *Leptonotus blainvilleanus,* USNM 176564, 1, Bahía Lin, Chile; *Parasyngnathus elucens,* CAS 13696, 1, Virgin Islands; *Ichthyocampus belcheri,* CAS uncat., 2, Philippine Is.; *Micrognathus brevirostris,* SIO 73-196, 4, Timor Sea; *Penetopteryx taeniocephalus,* SIO 66-587, 1, Great Tulear Reef; *Syngnathus carinatus,* S. Guevarra pers coll., 1, Gulf of California; *S. acus,* SIO 73-310, 1, Yugoslavia; *S. auliscus,* SIO 68-168, 1, Sonora, Mexico; *S. californiensis,* SIO H47-180, 1, Santa Cruz Island; *S. leptorhynchus,* E. B. Brothers pers. coll., 1, Mission Bay; *S. pelagicus,* SIO 65-358, 1, western Atlantic; *Bryx veleronis,* SIO 71-52, 1, Panama; *B. clarionensis,* SIO 74-116, 1, paratype, Clarion Is.; *B. dunckeri,* SIO 70-376, 1, Panama; *B. arctus,* SIO H52-218, 1, Baja California; *B. coccineus,* USNM 220972, 1, Galapagos Is.; *Cosmocampus brachycephalus,* CAS 24025, 2, Panama; *Corythoichthys flavofasciatus,* R. Nolan pers. coll., 1, Eniwetak; *Corythoichythys* sp., SIO 73-206, 1, Timor Sea, *Pseudophallus starksi,* USNM 208371, 2, Panama; *P. elcapitanensis,* USNM 208369, 1, Panama; *Hippocampus kuda,* SIO-60-250, 1, Hawaii; *H. ingens,* NMFS uncat., 1, eastern Pacific; *Phyllopteryx foliatus,* SIO 73-361, 1, Australia.

SYSTEMATICS

Family **Syngnathidae** Bonaparte, 1838

Type-Genus: *Syngnathus* Linnaeus, 1758.

Diagnosis.—Syngnathiforms with body encased in armor formed of dermal plates arranged in rings; pelvic and spinous dorsal fins absent; dorsal and pectoral fins moderately developed to absent; caudal and anal fins weakly developed to absent (tail often prehensile when caudal fin absent); opercular slit reduced to a small opening at dorsoposterior margin of opercle, four complete gill arches bearing lobate gills; pseudobranchiae present; supracleithra and postcleithra absent; ribs absent; teeth lacking on jaws, but premaxillae and dentaries may bear odontoid processes (Dawson and Fritzsche 1975); pharyngobranchial tooth plates present or absent; upper part of cleithrum forms part of the external armor; posttemporals suturally united to neurocranium; 1–3 branchiostegals; no basisphenoid; no metapterygoid; eggs incubated by males in a special area under the trunk or tail, which may or may not be developed into a pouch; no pyloric sphincter; no distinct stomach; right kidney only present, aglomerular; predorsals reduced to 2–3 nuchal plates.

The family is usually divided into two groups: Gastrophori—those which develop the brood pouch under the abdomen; Urophori—those with the brood pouch under the tail.

Key to Genera of Eastern Pacific Syngnathidae

1a. Caudal fin absent; tail prehensile; head at right angle to main body axis .... *Hippocampus* Rafinesque

1b. Caudal fin present; tail never prehensile; head in line with main body axis 2

2a. Brood pouch under abdomen 3

2b. Brood pouch under tail 4

3a Trunk rings more numerous than tail rings .... *Doryrhamphus* Kaup

3b. Trunk rings fewer than tail rings .... *Oostethus* Hubbs

4a. Lateral trunk ridge continuous with superior tail ridge; brood pouch without protecting plates; mature females with deep, compressed trunk .... *Leptonotus* Kaup

4b. Lateral trunk ridge subcontinuous with superior tail ridge; brood pouch with protecting plates; mature females with subcylindrical trunk 5

5a. Dorsal rays 23 or fewer; snout short, contained 2.3–4.0 times in head; anal fin present or absent; small, never longer than 124 mm SL .... *Bryx* Herald

5b. Dorsal rays 26 or more; snout longer, contained 1.6–2.8 times in head; anal fin present; larger, most species reach 200 mm or more SL .... *Syngnathus* Linnaeus

Records of Doubtful Validity

Regan (1908) included *Oostethus brachyurus* (Bleeker) and *Syngnathus spicifer* Rüppell in his list of the fishes occurring at Tehuantepec, Mexico. Herald (1940) repeated these records but doubted their validity. Herald (1943) indicated that there was considerable doubt that these two species were collected at Tehuantepec, because he had been able to confirm that Regan's specimens had come from an animal dealer. Duncker (1915) had also realized that the specimens had come from an animal dealer, but the records have persisted. The animal dealer had received specimens from both Mexico and the Philippines. *O. brachyurus* and *S. spicifer* occur in the Philippines, and it seems most probable that the specimens were collected there.

There is, however, a valid record of *Oostethus* from the eastern Pacific. McCosker and Dawson (1975) reported a single individual of the euryhaline Atlantic *Oostethus lineatus* collected on the Pacific side of Panama in 1971 and concluded that the specimen represents a transit of the Panama Canal.

Dermatostethus punctipinnis Gill (1863) was described from four specimens collected at San Diego. Presently there are three type-specimens at the USNM (lectotype, here designated as USNM 8128; paralectotypes here designated as USNM 214484). Much confusion has been generated by these specimens. The types are quite large (302–344 mm SL), have a very flexible "neck," and dark spotting on the dorsal fin. Herald (1940, 1941) referred *D. punctipinnis* to the synonymy of *Syngnathus californiensis* because the latter is a large species with counts like that of the type material of *D. punctipinnis*. Miller and Lea (1972:212) suggested that *D. punctipinnis* might be a valid species, but did not include it in their key to California species. I have examined the types of *D. punctipinnis* and have compared them to specimens of *S. acus* from Europe and have been unable to find significant differences. I therefore relegate *D. punctipinnis* to the synonymy of *S. acus*.

Syngnathus acus has been recorded from the Indo-Pacific (Weber and De Beaufort 1922), and my examination of a specimen from that region (Pakoi, China) suggests the existence of a distinct *acus*-like species. But the putative California material is typical of *acus* and could not represent trans-Pacific migration.

Duméril (1870) described *Syngnathus bairdianus* from a locality given as "Côte du Mexique, voisine de la Californie." The locality as listed in the catalog of the MNHN is "Mexique près la Californie, Lucas 1867." I examined the two types (lectotype, here designated as MNHN 6112; paralectotype, here designated as MNHN 2756) and found them to be indistinguishable from *S. pelagicus* Linnaeus. I therefore relegate *S. bairdianus* to the synonymy of *S. pelagicus*. *S. pelagicus* inhabits the Sargasso Sea and apparently can be transported over long distances. It has been recorded from Tierra del Fuego (Fowler 1944) and from New Zealand (Weber and De Beaufort 1922). *Histrio histro*, another inhabitant of the Sargasso Sea, is widely distributed and has been recorded from the Galápagos Islands (Schultz 1957). It is therefore remotely possible that *S. pelagicus* could have been collected near the coast of Mexico.

None of the above species will be treated further because of their doubtful standing as members of the eastern Pacific fauna.

Hippocampus Rafinesque

Hippocampus RAFINESQUE, 1810:18 (type-species by monotypy, *H. heptagonus* Rafinesque [=*Syngnathus hippocampus* Linnaeus]); DUNCKER 1912:237 (diagnosis); 1915:115 (diagnosis); GINSBURG 1937:525 (diagnosis; discussion).

Farlapiscus WHITLEY, 1931:313 (type-species by original designation, *Hippocampus breviceps* Peters).

Hippohystrix WHITLEY, 1940:44 (type-species by original designation, *Hippocampus spinosissimus* Weber).

DIAGNOSIS.—Urophori characterized by a prehensile tail; absence of caudal fin, scutella, brood pouch protecting plates, and basibranchials; head at right angle to trunk; brood pouch sealed along midline except for small anterior opening; occiput raised to form coronet; dorsal fin base raised.

DISTRIBUTION.—Marine; world-wide in tropical and subtropical seas.

Hippocampus ingens Girard

(Figures 3 & 7*C*)

Hippocampus ingens GIRARD, 1859:342 (original description; San Diego, California) (lectotype here designated as USNM 982); JORDAN AND GILBERT 1880:23 (San Diego); 1881:453 (San Diego); JORDAN AND JOUY 1881:1 (California); JORDAN AND GILBERT 1882:69 (San Diego); 1883:386 (description; range); EVERMANN AND JENKINS 1891:127, 135 (Guaymas, Mexico); GILBERT 1891:450 (ALBATROSS sta. 2795); EIGENMANN AND EIGENMANN 1892:144 (San Diego); VAILLANT 1894: 70 (Gulf of California); JORDAN 1895:417 (description; Mazatlán, Mexico); JORDAN AND EVERMANN 1896:776 (synonymy; description); GILBERT AND STARKS 1904:57 (Panama Bay); GILL 1905:807 (range); STARKS AND MORRIS 1907:186 (range); OSBURN AND NICHOLS 1916:155 (Concepción Bay); NICHOLS AND MURPHY 1922:506 (Peru); MEEK AND HILDEBRAND 1923:256 (description; synonymy); BREDER 1928:23 (Cape San Lucas, Concepción Bay); ULREY AND GREELEY 1928:41 (synonymy; range); ULREY 1929:6 (Lower California, Gulf of California); 1932:77 (Baja California); GINSBURG 1937:534 (range; synonymy; description); ATZ 1937:62 (size); FOWLER 1944:496 (range); KOEPCKE 1962:200 (references; range); CLEMENS AND NOWELL 1963:262 (off Mexico; in stomachs of fish); HUBBS AND HINTON 1963:12 (California record; range); CHIRICHIGNO-F. 1963:8, 34 (Peru; range); CASTRO-AGUIRRE ET AL. 1970:132 (common in Gulf of California); MILLER AND

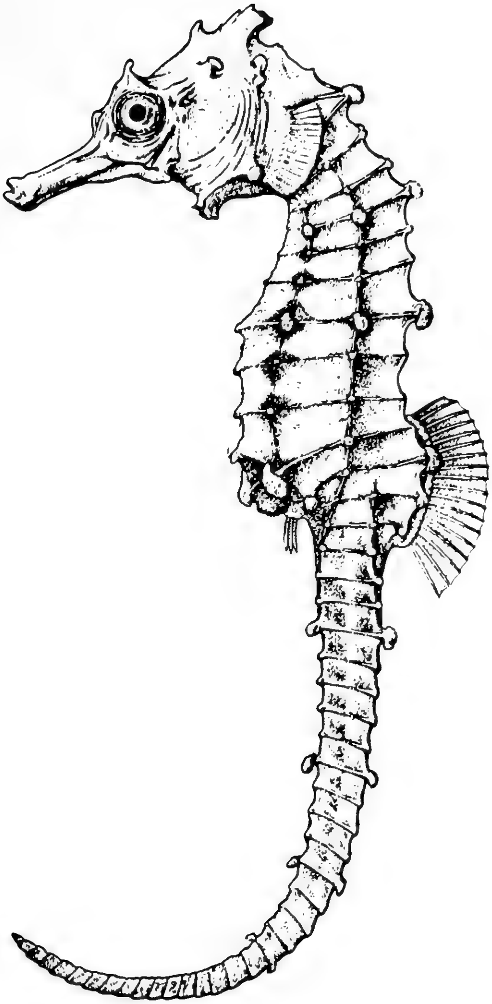


FIGURE 3. *Hippocampus ingens*, MCZ 35292, collected in 1860 at San Francisco, California, by Alexander Agassiz (not examined).

LEA 1972:89 (description; range); CHIRICHIGNO-F. 1974: 86, 337 (Peru; in key; range).

Hippocampus gracilis GILL, 1863:282 (original description; Cape San Lucas, Baja California).

Hippocampus ecuadorensis FOWLER, 1921:446 (original description; Bahía, Ecuador).

Hippocampus hildebrandi GINSBURG, 1933:562 (original description; Chame Point, Panama); holotype USNM 82063); 1937:579 (description; range).

DIAGNOSIS.—A *Hippocampus* with 17–22 (19) dorsal rays; 15–17 pectoral rays; 4–5 anal rays; 11–12 (11) trunk rings; 37–41 (39) tail rings; dorsal fin on 1.2–2 + 1.5–4 rings; total rings covered by dorsal fin 3–4; brood pouch on 5–8 rings; head 4.2–5.8 in SL; dorsal fin base 1.8–2.9 in head; snout 1.8–2.5 in head; maximum size examined 247 mm SL; smallest mature male 54 mm, said to attain 12″ (297 mm) (Miller and Lea 1972), which is approximately the size of my largest specimen if the head is included in the measurement.

DESCRIPTION.—Body ridges typically well developed with a blunt recurved tubercle at center of each plate. First, fourth, seventh, and tenth trunk rings usually with larger and better developed tubercles. Sixth, tenth, fourteenth, and eighteenth tail rings may have strongly developed tubercles, but are usually more obsolescent than trunk tubercles. Coronet with five radially arranged tubercles. Males with the more weakly developed tubercles. Tubercles in both sexes generally become obsolete with growth. Strong nuchal ridge, without spines. Opercle with faint radiating striae. No prominent snout ridge. Internasal spine blunt. Prominent broad-based supraopercular spine directed laterally. Lateral trunk ridge and superior tail ridges overlap for one ring. Trunk rings octangular under dorsal fin, heptangular anteriorly. Trunk moderately compressed. First tail ring heptangular, remainder quadrangular. Superior trunk and tail ridges overlap for two to three rings. Dermal flaps, when present, on enlarged tubercles and head ridges, consisting of a stout base with numerous filamentous outgrowths.

Coloration in life. Red, yellow, or green. One specimen captured at La Paz, Baja California, had undersides and tips of tubercles yellowish, most of body mottled with dark brown to black, and covered with many small dark spots as well as smaller white ones. The white spots tend to coalesce into longitudinal streaks; yellowish coloration more pronounced on underside of tail. White bands around body every six or seven rings. Dorsal fin with distinct dark submarginal band. Pectoral fins hyaline.

Coloration in alcohol. Enlarged tubercles usually whitish, often with white ring around body at that point. Ground color dark brown with small white papillae often forming streaks and reticulations, and radiating lines around orbit. Ventral surface of tail without white markings. Dorsal fin with a dark band near margin. Median abdominal ridge often dark brown in males. However, color variable; some specimens may be uniform light tan.

HABITAT.—Collections of *H. ingens* are uncommon. Some have been made in shallow water, but most specimens have been captured at depth with dredges or trawls, or at the surface in the open ocean. Dredge and trawl collections have usually been made at depths of 10 m or more. Juveniles (ca. 40 mm) and larger individuals (115 mm) are not uncommonly taken at the surface. Alverson (1963) studied the food items in stomachs of eastern Pacific yellowfin tuna, *Thunnus albacares,* and found *H. ingens* in 18 stomachs out of the 2846 he examined. Judging from the small displacement volumes of these fish, they were all juveniles. One 34-mm individual (SIO 71-186) was taken from the gut of a bluefin tuna, *Thunnus thynnus.* The habitat is not yet precisely known. *H. ingens* appears to spend much of its life in the open sea.

Comparisons.—Ginsburg (1933) described *H. hildebrandi* from Chame Point, Panama, as differing from *H. ingens* in having lower, broader tubercles. My examination of 38 specimens from the eastern Pacific has shown that all specimens are referrable to *H. ingens.* I have examined the types of *H. ingens* and *H. hildebrandi* and conclude that the types of *H. hildebrandi* are juveniles of *H. ingens.*

Since *H. ingens* is the only species of seahorse in the eastern Pacific, it is easily identifiable. The closest relative of *H. ingens* is possibly *H. reidi* Ginsburg from the western Atlantic, from which it differs in number of dorsal rays (17–22 vs 15–19) and in number of tail rings (36–41 vs 34–37). The relationship of *H. ingens* to seahorses of the Indo-Pacific is impossible to determine because knowledge of the genus *Hippocampus* is very incomplete.

Range.—San Francisco Bay, California, south to Pucusana, Peru, including the Gulf of California. Infrequently taken north of central Baja California. During periods of unusually warm water, *H. ingens* may enter California waters.

Material Examined.—**California:** San Diego, USNM 982, 1(167), lectotype; USNM 214485, 2(125–146), paralectotypes; Point Loma, SIO 63-1085, 1(195).

Baja California: Laguna Guerrero Negro, SIO 61-10, 3(155–185). Bahía Sebastián Vizcaíno, SIO 63-1046, 1(29). Bahía Magdalena, SIO 62-713, 1(108); SIO 64-73, 1(27); SIO 60-305, 1(55). Punta Hughes, SIO 64-45, 1(109).

Gulf of California: La Paz, SIO 74-81, 1(200). Punta Mangles, SIO 65-335, 1(122). Isla Santa Inéz, SIO 65-306, 1(99). San Felipe, SIO 67-1, 1(168).

Mazatlán South: Boca Teacapán, SIO 60-90, 1(118). Nayarit, SIO 60-89, 1(92). Bahía de Banderas, SIO 62-29, 1(148). Acapulco, UCLA W52-119, 1(70). Golfo de Tehuantepec, SIO 73-258, 5(116–136); SIO 68-16, 1(47); SIO 63-1031, 1(115); SIO 72-123, 1(80). Guatemala, SIO 63-623, 1(70); UCLA W56-273, 1(120). Costa Rica, UCLA W54-139, 1(114). Panama, SIO 71-260, 1(115); SIO 71-186, 1(36); USNM 82063, 1(66), holotype of *H. hildebrandi*; USNM 82037, 1(44), paratype of *H. hildebrandi*; USNM 82039, 1(47), paratype of *H. hildebrandi.*

Galápagos Islands: BC 56-440, 2(238–247); SIO 54-174, 1(128). Isla Santa Cruz, SIO H51-388, 1(89).

Doryrhamphus Kaup

Doryrhamphus Kaup, 1853:233 (nomen nudum); 1856:54 (type-species by monotypy, *D. excisus* Kaup; Red Sea); Duméril 1870:585 (description); Jordan and Evermann 1896:773 (in part; description); Duncker 1912:231 (description; synonymy); 1915:244 (description; synonymy); Jordan, Evermann, and Clark 1930:243 (synonymy); Herald 1953:244 (description; synonymy).

Pristidoryrhamphus Fowler, 1944:158 (type-species by original designation, *P. jacksoni* Fowler =*Doryrhamphus negrosensis* Herre).

Diagnosis.—Gastrophori with lateral trunk ridge continuous with inferior tail ridge; inferior trunk and tail ridges discontinuous; superior trunk and tail ridges discontinuous; trunk rings more numerous than tail rings; snout ridge strongly serrate, markedly so in mature males; each dermal plate armed with strong retrorse spine; no pouch-protecting plates; caudal fin large and brightly colored; branchial skeleton with all elements present; scutella present; two nuchal plates; three infraorbitals; strongly developed opercular ridge; 14–19 trunk rings; 10–17 tail rings; 21–29 dorsal rays; 4 anal rays; 10 caudal rays.

Range.—Four or five species ranging throughout the tropical Indo-Pacific among coral and rocky reefs.

Discussion.—Kaup first published the name *Doryrhamphus* in 1853, but his reference to *D. excisus* Hemprich and Ehrenberg cannot be taken to be an indication as defined by the *International Code of Zoological Nomenclature* Art. 16a(v). The species *D. excisus* was an unpublished manuscript name in 1853. The requirements of the Code were not fulfilled until Kaup (1856) published descriptions of *Doryrhamphus* and *D. excisus.*

Key to Eastern Pacific Species of *Doryrhamphus*

1a. Trunk rings 16–18 (usually 17) tail rings 14–17 (usually 15); head 4.0–4.4 in SL .. .. *melanopleura* (Bleeker)
Tropical Indo-Pacific

1b. Trunk rings 16–17 (usually 16); tail rings

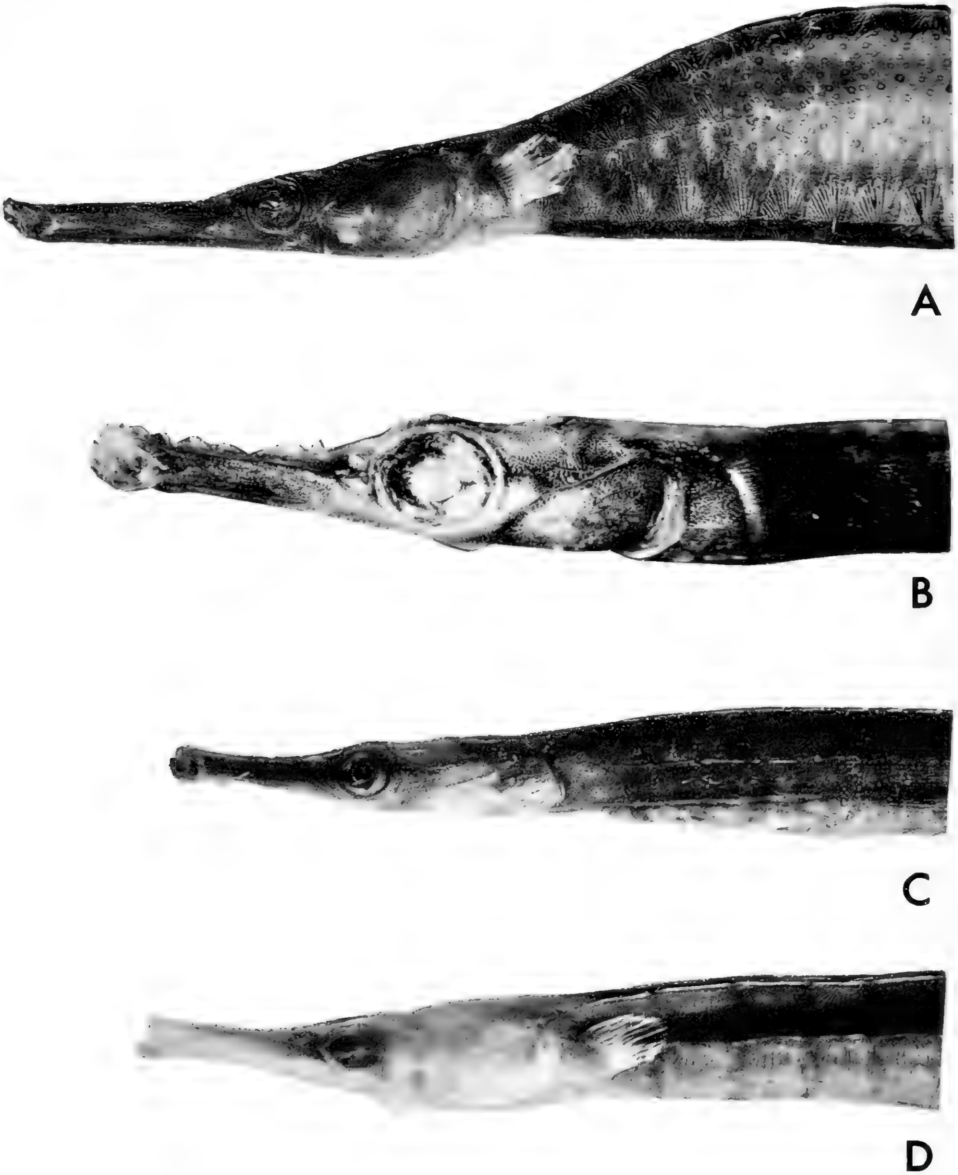


FIGURE 4. Anterior part of body of four species of eastern Pacific Syngnathidae. (*A*) *Leptonotus blainvilleanus*, a 168-mm-SL female, SIO 72-168. (*B*) *Doryrhamphus paulus*, holotype, SIO 72-67. (*C*) *Doryrhamphus melanopleura*, a 52-mm-SL male, SIO 65-343. (*D*) *Syngnathus auliscus*, a 110-mm-SL female, SIO 65-181.

13–15 (usually 14); head 3.4–4.0 in SL .... *paulus* n.sp.
Islas Revillagigedo, Mexico

Doryrhamphus melanopleura (Bleeker)

(Figure 4*C*)

Syngnathus melanopleura BLEEKER, 1858:464 (original description; "Kokos-eilanden").

Doryrhamphus californiensis GILL, 1863:284 (original description; Cabo San Lucas; holotype SU 19255); JORDAN AND EVERMANN 1896:773 (description; range); DUNCKER 1915:62 (as "species dubia"); ULREY 1929: 6 (Cape San Lucas); JORDAN, EVERMANN, AND CLARK 1930:243 (range); ULREY 1932:77 (Cabo San Lucas); NICHOLS AND MURPHY 1944:239 (Panama); FOWLER 1944:496 (range).

Doryichthys californiensis: GÜNTHER 1870:186 (new combination; description; range).

Microphis extensus SNYDER 1911:525 (original description; Naha, Okinawa; holotype USNM 98266).

Doryrhamphus melanopleura: HERALD 1940:59 (in key; synonymy; range); 1953:246 (description; subspecies; range).

DIAGNOSIS.—A *Doryrhamphus* with 22–27 (24–25) dorsal rays; 19–23 pectoral rays; 16–18 (17) trunk rings; 14–17 (15) tail rings; dorsal covering 3–5 + 2–4 rings; total rings covered by dorsal fin 6–7.5; brood pouch covering 17–19 rings; head 4.0–4.4 in SL; dorsal fin base 1.6–1.9 in head; snout 2.0–2.5 in head; maximum known size 69 mm SL; smallest mature male 31 mm SL.

DESCRIPTION.—A sharply ridged and strongly spined fish. Head with prominent prenuchal, nuchal, and occipital crests. Snout ridge strongly serrated, markedly so in mature males. Pectoral cover plate with well-developed superior and inferior ridges. Strong spination on maxillae and along dorsal edge of infraorbitals. Ventral edge of quadrate occasionally with strong serrations. Each ring bears a single posteriorly directed spine on each ridge, becoming obsolete along ventral ridges. Scutella large. No dermal flaps.

Brood pouch abdominal, without protecting plates. Eggs about 0.5 mm in greatest diameter, arranged in three layers, four across. Males with eggs and young collected from March through August.

Fins all large and well developed. Caudal a little longer than snout. Dorsal base about equal to snout and orbit combined. Anal conspicuous, its length about half orbital diameter. Pectoral fins broad based.

Coloration in life. Essentially the same as coloration in alcohol except that caudal has a white border, two yellowish spots near base, and an oval orange area in middle part of fin.

Coloration in alcohol. Uniform dusky with darker streak from tip of snout to pectoral base. Fins colorless except for caudal, which is distinctively marked with two light basal spots and one larger median spot. Individual fin rays often lined with melanophores on each side. Young less than 20 mm SL have a banded color pattern with eight brown bands on a lighter background.

HABITAT.—In crevices in rocks, under overhangs, and among coral heads.

RANGE.—In eastern Pacific from Bahía Magdalena, Baja California, south to Isla la Plata, Ecuador (UMML), and at the Galápagos Islands and Clipperton Island. In the Gulf of California north to Isla Ángel de la Guarda (UCLA W60-6, not examined) in the west to Punta Guillermo, Sonora (UCLA W51-11 not examined), in the east. Widely distributed throughout Indo-Pacific.

COMPARISONS.—*D. melanopleura* is an interesting and complex species. It has been divided into several subspecies (Herald 1953) that are probably not valid. A detailed study of the populations is needed before much can be said about possible relationships. It is related to *D. paulus* from which it can be distinguished by the characters given in the description of that species.

MATERIAL EXAMINED.—**Mexico:** Bahía Magdalena, SIO 64-54, 3(55–62). Cabo San Lucas, SIO 61-227, 10(18–56). Los Frailes, SIO 61-249, 14(32–64). Bahía de los Muertos, SIO 74-90, 3(32–46). Isla San José, SIO 65-265, 5(48–55). Isla Santa Cruz, SIO 65-343, 6(19–61). Isla Carmen, SIO 65-302, 15(45–62). Isla San Ignacio de Farallón, SIO 59-228, 3(40–42). Lobos Rock, SIO 61-280, 20(16–53). Bahía de Banderas, SIO 62-29, 2(29–45).

Costa Rica: Isla del Caño, LACM 32548, 36(33–55).

Panama: Taboguilla Island, SIO 67-34, 21(16–48).

Galápagos Islands: Plaza Island, SIO 64-1015, 3(53–63); BC 54-392, 1(64).

Comparative material from Indo-West Pacific: Hawaii, CAS 20402, 1(54). Eniwetak, R. S. Nolan personal collection, 3(39–45). Guam, CAS 15835, 2(44–44). Australia, AMS IA-2713, 1(38); AMS I10740, 2(31–39). Japan, CAS 14512, 2(68–69).

Doryrhamphus paulus n.sp.

(Figure 4*B*)

Doryrhamphus melanopleura pleurotaenia: (in part) HERALD 1953:248 (size; meristic data).

Doryrhamphus melanopleura: Ricker 1959:2 (Socorro Island).

DIAGNOSIS.—A dwarf species of *Doryrhamphus* with 23–26 dorsal rays; 20–21 pectoral rays; 16–17 (16) trunk rings; 13–15 (14) tail rings; 29–31 (30) total rings; dorsal on 3–4.2 + 2.5–4 rings; total rings covered by dorsal fin 6.5–7.5; brood pouch on 14–17 rings; head 3.4–4.0 in SL; dorsal fin base 1.7–2.2 in head; snout 2.1–2.7 in head; smallest mature male 24.5 mm SL; maximum known size 38.9 mm SL.

DESCRIPTION.—Strongly ridged and spined. Occipital, nuchal, and prenuchal ridges low but sharply defined. Snout ridge serrate in males, with 4–5 spines on anterior tip and three or so larger isolated spines further posterior; females and juveniles with or without obvious snout-ridge serrations. Pectoral cover plate with superior and inferior ridges. Each body plate with a sharp retrorse spine. No dermal flaps.

Only one brooding male known, collected in March.

Fins well developed. Caudal shorter than snout. Dorsal fin base equal to combined snout and orbit. Pectoral fins broad based but short, only extending posteriorly to junction of first and second trunk rings.

Coloration. Essentially same as that given for eastern Pacific populations of *D. melanopleura*.

Habitat and Range.—Three to 17 m, among rock reefs in Islas Revillagigedo, Baja California.

Comparisons.—*D. paulus* is most closely related to, and was probably derived from, *D. melanopleura,* which is widespread in the Indo-Pacific but is not represented at the Islas Revillagigedo. Although *D. melanopleura* ranges throughout the Indo-Pacific and is quite variable, the number of trunk rings is fairly stable at 18. Some populations have modal counts of 17 or 19 rings; however, 16 trunk rings have never been found in *D. melanopleura*.

Doryrhamphus paulus can be distinguished from *D. melanopleura* by the characters given in the key.

D. excisus from the Red Sea also has 16 trunk rings, but differs from *D. paulus* in having 10–11 tail rings rather than 13–15, and 18–20 dorsal rays rather than 23–26.

Etymology.—From the Latin *paulus,* little.

Material Examined.—**Holotype:** SIO 72-67, a 32.7-mm-SL mature male collected at a depth of 6–12 m with Chemfish, ca. 100 m SE of "Humpback Cove," Isla Socorro, Islas Revillagigedo, Mexico, 19 Feb. 1972, by D. Diener and party. **Paratypes. Mexico.** Islas Revillagigedo: SU 67255, 24.5 mm SL, mature male, 8 m, rotenone, "Grayson's Cove," Isla Socorro, 11 Mar. 1940, by Vernon Brock. SU 36442, 1(31), same data as SU 67255. CAS 13699, 9(20–34) and LACM 31781-2, 3(22–32), "Grayson's Cove," ca. 200 m N of "Old Man of the Rocks," Isla Socorro, R/V Searcher sta. 52, 8–12 m, rotenone, 14 Feb. 1971. LACM 317821-12, 5(26–32), s of Cape Henslow, Isla Socorro, R/V Searcher sta. 53, 13–17 m, rotenone, 15 Feb. 1971. GCRL 15753, 1(27), Braithwaite Bay, Isla Socorro, 3 m, rotenone, 13 Feb. 1956, by George Lindsay. SIO 72-67, 6(16–26), collected with holotype. SIO 74-155, 2(29–39), Sulfur Bay, Isla Clarión, 10–17 m, rotenone, 11 Dec. 1974, by Robert Kiwala.

Leptonotus Kaup

Leptonotus Kaup, 1853:232 (type-species by monotypy, *Syngnathus blainvilleanus* Eydoux and Gervais, 1837); 1856:46; Duncker 1912:235; 1915:88.

Acmonotus Phillipi, 1896:382 (type-species by original designation, *Acmonotus chilensis* Philippi [=*S. blainvilleanus* Eydoux and Gervais]).

Novacampus Whitley, 1955:110 [type-species by original designation, *Syngnathus norae* (Waite)].

Diagnosis.—Urophori without pouch-protecting plates; trunk compressed and much expanded in females; lateral ridge system of the ascending pattern (Fig. 2*B*); all elements of branchial skeleton present, none reduced; dorsal fin usually located on two or more trunk rings; 10 caudal rays; opercular ridge weak or absent; most body ridges smooth and reduced; two branchiostegals.

Distribution.—Approximately five species known only from south temperate seas; South America, South Australia, Tasmania, and New Zealand.

Leptonotus blainvilleanus (Eydoux and Gervais)

(Figure 4*A*)

Syngnathus blainvilleanus Eydoux and Gervais, 1837:79 (original description; "Mare Indicum"; holotype MNHN 6050); Guichenot 1848:348 (description).

Syngnathus acicularis Jenyns, 1842:147 (original description; Valaparaíso, Chile; holotype BMNH 1917.7.14.28).

Leptonotus Blainvillei: Kaup 1853:232 (range); 1856:16 (description; range).

Syngnathus blainvillianus; Günther 1870:162 (description; range); Steindachner 1898:331 (Chile); Thompson 1816:423 (Patagonia).

Hemithylacus Petersi Duméril, 1870:600 (original description; Puerto Montt, Chile).

Acmonotus chilensis Philippi, 1896:382 (original description; Pelluhue, Chile).

Leptonotus blainvillianus: Abbott 1899:338 (references; range); Duncker 1915:88 (synonymy; description; range); Norman 1937:40 (Patagonia); Herald 1940:59 (synonymy; range); 1942:132 (diagnosed in key); Fowler 1944:496 (range); Mann 1954:189 (description; range); De Buen 1963:89 (synonymy; description); Koepcke 1962:200 (range); Chirichigno-F. 1974:339 (in keys; range).

Syngnathus blainvillei: Delfin 1901:43.

Siphostoma blainvilliana: Evermann and Radcliffe 1917:53.

Leptonotus blaenvillianus: Siccardi 1954:211–242 (brood pouch; variation).

Leptonotus blainvilleanus: Duméril 1870(2):581 (description; habitat); Vaillant 1888:16 (Orange Bay, Patagonia; coloration); Herald 1965:364 (common name).

Diagnosis.—A *Leptonotus* with 34–41 (35–37) dorsal rays; 12–14 pectoral rays; 2–3 anal rays; 18–20 (19) trunk rings; 48–52 (50) tail rings; 67–70 total rings; dorsal on 0.5–2 + 7–8.2 rings; total rings covered by dorsal fin 7.3–10; brood pouch on 10–14 rings; head 7.0–9.0 in SL; dorsal fin base 1.0–1.6 in head; snout 1.8–2.2 in head; maximum known size 217 mm SL (Duncker 1915); smallest mature male 108 mm SL. See Table 1 for meristic variation.

Description.—Ridges on head and body mostly obsolete. Nuchal and prenuchal ridges low and smooth. Opercles strongly convex; opercular ridge reduced to basal one-fourth of

TABLE 1. MERISTIC VARIATION IN *Leptonotus blainvilleanus*.

	Trunk rings			Tail rings					Dorsal rays							
Locality	18	19	20	48	49	50	51	52	34	35	36	37	38	39	40	41
Chile:																
Antofagasta	1	12	1	1	3	6	4	—	2	6	1	4	1	—	—	—
Valparaíso	—	—	2	—	—	1†	1	—	—	—	—	1†	—	—	—	—
Concepción	—	1	—	—	—	—	1	—	—	—	—	1	—	—	—	—
Coquimbo	—	2	—	—	—	1	1	—	1	—	—	—	—	—	—	—
Puerto Montt	1	4	2	1	2	4	—	—	—	—	1	3	3	—	—	—
Isla Chiloé	—	9	3	4	4	4	—	—	—	2	3	4	2	—	—	—
Totals	2	28	8	6	9	16	7	—	3	8	5	13	6	—	—	—
		$\bar{x}$ = 19.1				$\bar{x}$ = 49.6						$\bar{x}$ = 36.3				
Argentina*:																
Golfo Nuevo																
(females)	27	4	—	—	4	16	10	1	—	1	1	8	14	5	1	1
(males)	3	34	3	5	12	20	—	2	—	—	7	7	13	8	1	1
Totals	30	38	3	5	16	36	10	3	—	1	8	15	27	13	2	2
		$\bar{x}$ = 18.6				$\bar{x}$ = 49.8						$\bar{x}$ = 37.8				
"Mare Indicum"**	—	1**	—	—	—	—	—	—	1**	—	—	—	—	—	—	—

† Holotype of *S. acicularis*.
* Data from Siccardi 1954.
** Holotype of *L. blainvilleanus*.

opercle, striations faint. Snout ridge smooth, low, and reaches posteriorly to interorbit. Supraorbital ridges smooth, one-half orbit diameter in length. Pectoral cover plate without ridges. Trunk of mature females compressed and expanded dorsoventrally, with sharp dorsal and ventral borders. Scutella small, indistinct. Plates with reduced ridgelets. Entire body very fleshy over plates. Lateral line papillae 2–4 per plate. No dermal flaps.

Brood pouch without lateral protecting plates. Males brooding eggs have been collected in January and March.

Dorsal fin high, its height equal to width of two trunk rings.

Coloration in alcohol. Juveniles with alternating pattern of dark and light bands along length of body. Darker bands about four rings in width, light bands only one-half a ring in width. Caudal dark brown with a light border. Snout and interorbit darker than remainder of head. Fins colorless.

Adult females sometimes entirely light tan with dark brown venter and dorsum on trunk, and with posterior half of tail dark brown. Usually the head is a dark olive-brown and the trunk is dark brown with small, dark-bordered ocelli. Dorsal fin may have a few melanophores along the ray margins. Adult males yellowish brown with dark brown area surrounding the nares; ocelli may develop on the first few tail rings.

HABITAT.—Kelp beds along the open coast; occasionally into brackish water (Fischer 1963).

REMARKS.—Meristic data from the Golfo Nuevo, Argentina, population of *L. blainvilleanus* (Table 1) (from Siccardi 1954) show a difference in mean number of trunk rings between males and females from Golfo Nuevo ($P \ll .005$).

The lower number of trunk rings in the Golfo Nuevo females contributes to the significant difference between the Chilean and Argentinean populations ($P \ll .005$). However, the dorsal ray count also differs significantly between these two regions.

Siccardi (1954) studied a large number of specimens of *L. blainvilleanus* from both coasts of southern South America and was able to provide some data on morphometric variation. She found that the depth of the trunk in males remains fairly constant during growth, from 112–140 mm, so that the standard length/trunk depth ratio was 22.4 in 112-mm fish and 26.7 in 140-mm fish. Also, the maximum depth of the trunk in females was attained by a standard length of 140–150 mm. This was correlated with reaching sexual maturity. The trunk in males became relatively shorter and the tail longer with growth, whereas relative lengths of the trunk and tail in females remained constant with growth.

COMPARISONS.—Because the genus *Leptonotus* has not received systematic treatment, it can only be said that *L. blainvilleanus* seems to be most closely related to the southern Australian species *L. semistriatus*. *L. blainvilleanus* can be distinguished from *L. semistriatus* by the snout length (1.8–2.2 in head rather than 1.6–1.7) and by the dorsal fin placement (on 0.5–2 + 7–8.2 rings rather than 3–4 + 7).

Leptonotus blainvilleanus has long been considered to be a member of the New Zealand fauna (Waite 1909). However, a comparison of the holotype of *L. blainvilleanus* with specimens of *Leptonotus* from New Zealand reveals that *L. blainvilleanus* and examined New Zealand species of *Leptonotus* are distinct. The New Zealand specimens of *Leptonotus* are referable to *L. elevatus* (Hutton) and *L. norae* (Waite).

Mr. A. Wheeler (BMNH) examined the holotype of *Syngnathus acicularis* Jenyns at my request. His counts and description of lateral ridge pattern confirm the fact that the holotype of *S. acicularis* is conspecific with *L. blainvilleanus*.

RANGE.—Hornitos, Chile, to Golfo Nuevo, Argentina.

MATERIAL EXAMINED.—"Mare Indicum," MNHN 6050, holotype.

Chile: Hornitos, SIO 72-168, 1(168). Antofagasta, EBMCh 1520-28, 9(86-207); GCRL 12466, 4(117–215). Coquimbo, MNMHP 5302, 1(169); MNMHP 5305, 1(246); Valparaíso, EBMCh 222, 1(190). Concepción, MNMHP 5574, 1(126). Bahía Lin, USNM 176564, 4(75–121). Puerto Montt, USNM 205179, 3(104–129). Isla de Chiloé, USNM 176569, 4(108–142); MNMHP 5304, 3(84–173); MNMHP 5303, 5(141–162). No collection data, CAS (Indiana label), 1(184).

Argentina: Patagonia, CAS 36440, 1(130).

Bryx Herald

Bryx HERALD, 1940:52 (type-species by original designation *Bryx veleronis* Herald); 1959:468 (subgenus of *Syngnathus*).

Microsyngnathus HERALD, 1959:468 (subgenus of *Syngnathus*, type-species by original designation *Syngnathus dunckeri* Metzelaar).

DIAGNOSIS.—Urophori characterized by a very short snout; small size (generally less than 100 mm); first epibranchial reduced or not; second hypobranchials and epibranchials reduced; frontals not reaching anteriorly past middle of lateral ethmoids; ossified epaxialis tendons present or absent; one infraorbital; two nuchal plates; pouch protecting plates present; dermal flaps present or absent; 14–17 trunk rings; 27–40 tail rings; 19–31 dorsal rays; 10–14 pectoral rays; anal fin present or absent; 10 caudal rays; 10–19 rings covered by brood pouch; 0–2 + 3–7 rings covered by dorsal fin.

DISTRIBUTION.—Ten tropical species, and one species at Islas Juan Fernández and Isla San Félix.

DISCUSSION.—*Bryx* is closely related to *Cosmocampus*, and the two were probably derived from a common ancestor.

Bryx was erected by Herald in 1940 for the sole reception of *B. veleronis*. Later, Herald (1959) transferred *B. veleronis* to *Syngnathus* and retained *Bryx* as a subgenus. In the same paper *Microsyngnathus* was erected as a subgenus, with *Syngnathus dunckeri* as type-species, and *S. arctus* and *S. coccineus* included therein. *S. hildebrandi* Herald, 1965, *S. randalli* Herald, 1965, and *S. banneri* Herald and Randall, 1972, were described as being related to, or tentatively referred to, the subgenus *Microsyngnathus* species in Herald (1965) and Herald and Randall, 1972. The species of *Bryx* and *Microsyngnathus* (and *Micrognathus balli* Fowler, 1925, and *Syngnathus darrosanus* Dawson and Randall, 1975) are separated from other syngnathids and united by shared characters given in the diagnosis above. This combination of characters defines a related lineage of syngnathids worthy of generic recognition. The type-species of *Microsyngnathus* further agrees with *Bryx veleronis* in lacking an anal fin: *Microsyngnathus* Herald, 1959, thus becomes a junior synonym of *Bryx* Herald, 1940. The subgenus *Simocampus* is proposed for those species of *Bryx* possessing an anal fin.

Key to Eastern Pacific Species of *Bryx*

1a. Anal fin present (subgenus *Simocampus*) 2
1b. Anal fin absent (subgenus *Bryx*) 4
2a. Head shorter than length of dorsal fin base .... *heraldi* n.sp.
Islas Juan Fernández and Isla San Félix
2b. Head longer than length of dorsal fin base 3
3a. Dorsal fin usually entirely on tail rings,

TABLE 2. FREQUENCY DISTRIBUTIONS OF TRUNK AND TAIL RINGS, AND DORSAL FIN RAYS IN EASTERN PACIFIC SPECIES OF *Bryx*.

	Trunk rings			Tail rings									Dorsal fin rays										
	14	15	16	33	34	35	36	37	38	39	40	41	18	19	20	21	22	23	24	25	26	27	28
heraldi	—	18*	—	—	—	—	2	10	6*	—	—	—	—	—	—	—	10*	8	—	—	—	—	—
arctus	1	31*	20	—	—	—	3	5	10	18*	19	1	4	19	10*	10	9	2	—	—	—	—	—
coccineus	1	11*	1	—	—	—	1	3	2	5*	2	—	—	8*	4	—	—	—	—	—	—	—	—
veleronis	1	16*	—	2	—	1	9*	5	—	—	—	—	—	—	—	—	1	1*	1	3	4	4	2
clarionensis	—	9*	—	—	—	3	6*	—	—	—	—	—	—	—	—	—	—	—	—	1	2	4*	2

* Primary type.

except in some southern California specimens with the dorsal on a fraction of a trunk ring; 18–23 dorsal rays; double row of dark spots on trunk .... *arctus* (Jenkins and Evermann)

Tomales Bay, California, and San Felipe, Gulf of California, to Mazatlán, Mexico

3b. Dorsal fin always on at least a fraction of last trunk ring; 18–20 dorsal rays; no double row of dark spots on trunk .... *coccineus* (Herald)

Banderas Bay, Mexico, to Punta Aguja, Peru, and Galápagos Islands

4a. Snout longer than postorbital length .... *clarionensis* n.sp.

Clarión Island, Revillagigedo Islands, Mexico

4b. Snout shorter than postorbital length .... *veleronis* Herald

Galápagos and Revillagigedo Islands, and coasts of Panama and Costa Rica

Simocampus n.subgen.

TYPE-SPECIES.—*Siphostoma arctum* Jenkins and Evermann.

DIAGNOSIS.—A *Bryx* with anal fin.

INCLUDED SPECIES.—*B. arctus* (Jenkins and Evermann); *B. coccineus* (Herald); *B. balli* (Fowler); *B. banneri* (Herald and Randall); *B. hildebrandi* (Herald); and *B. darrosanus* (Dawson and Randall).

ETYMOLOGY.—From the Greek *simos*, pug-nosed, and *campos*, sea-creature.

Bryx (Simocampus) heraldi n.sp.

(Figure 5C)

DIAGNOSIS.—A *Bryx* with 22–23 (22) dorsal rays; 11 pectoral rays; 3 anal rays; 15 trunk rings; 36–38 (37) tail rings; 52–54 total rings; dorsal on 0–1 + 5.2–6 rings; 17–18 rings covered by brood pouch; head 10.3–12.3 in SL; dorsal fin base 0.8–1.0 in head; snout 2.4–2.8 in head; maximum known size 99.8 mm SL; smallest mature male 70 mm SL. See Tables 2 and 3 for additional counts and measurements.

DESCRIPTION.—All ridges of head and body moderately developed and smooth. Prenuchal and nuchal ridges elevated and easily discernible. Opercular ridge extends posteriorly about half length of opercle. Snout ridge moderately developed, extending posteriorly to interorbit. Ridges of pectoral cover plate obsolete. Trunk and tail ridges low but easily visible. Superior

TABLE 3. NUMBER OF SPECIMENS (N) AND STANDARD LENGTH RANGE, TOGETHER WITH RANGE AND MEAN ($\bar{x}$) OF SELECTED CHARACTERS EXPRESSED IN THOUSANDTHS OF STANDARD LENGTH IN *Bryx*.

		Head length		Snout length		Snout depth		Body depth		Dorsal base length		Pectoral fin length		
Species	SL	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	N
heraldi	70–100	81–97	89	29–37	33	12–16	14	29–38	34	91–113	100	16–21	18	7
coccineus	50–116	90–115	100	35–42	38	12–22	16	30–47	36	72–82	77	12–22	18	7
arctus	62–88	84–99	92	23–41	33	12–17	15	35–48	41	80–87	83	11–23	17	11
veleronis	37–49	96–113	104	41–44	43	16–19	17	35–44	38	108–130	123	17–24	20	7
clarionensis	38–50	119–131	125	39–44	42	15–20	17	36–45	40	121–136	126	23–28	25	8

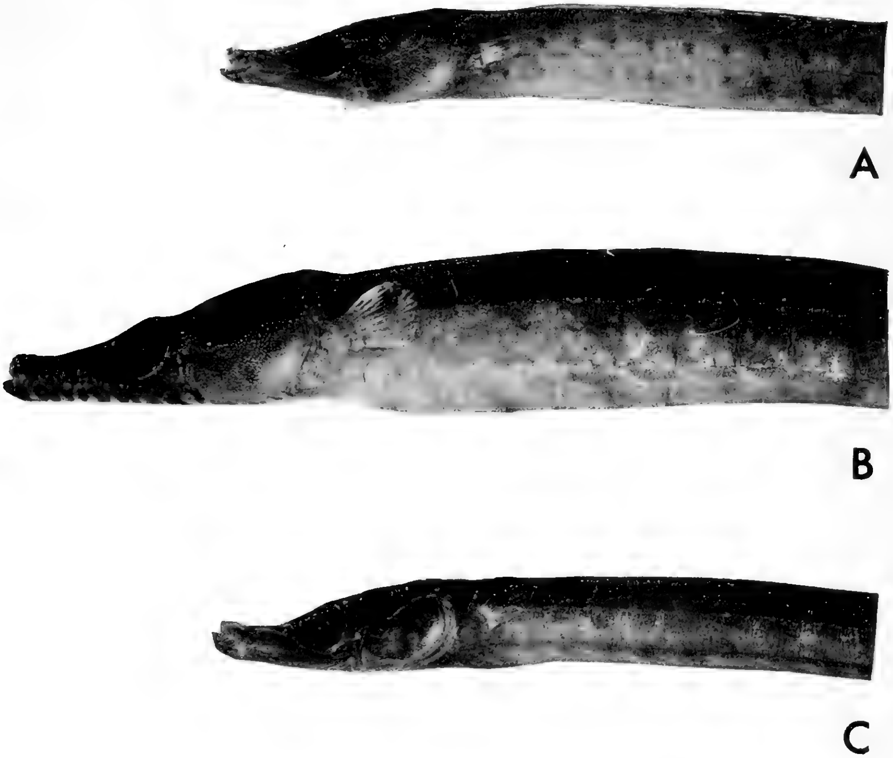


FIGURE 5. Anterior part of body of three species of eastern Pacific Syngnathidae. (*A*) *Bryx arctus*, an 88-mm-SL female, SIO H46-65. (*B*) *Bryx coccineus*, a 116-mm-SL female, USNM 220970. (*C*) *Bryx heraldi*, holotype, SIO 65-626.

tail ridge and lateral trunk ridge overlap on one plate. Scutella indistinct and about one-fourth as deep as adjoining plates. Lateral line consisting of 2–4 papillae per plate. No dermal flaps.

Protecting plates of brood pouch weakly developed; pouch folds lightly scalloped. Eggs 0.5 mm in greatest diameter, arranged in two layers four across. Males with eggs and young have been taken in early to mid-December.

Caudal fin short, as long as last two tail rings.

Coloration in alcohol. Background a light tan with few to many dark blotches on body, which, in some individuals, may make the fish appear darker brown. The dark blotches may be lighter centrally, and they may appear as dark bands 2–4 rings wide, or as thin bands between light tan areas. Brown freckling may also occur dorsally. All fins are colorless. The head coloration is essentially like that of the rest of the body. Pigmented part of cornea a darkish tan ring with radially arranged light blotches.

HABITAT.—Rocky reefs and sandy bottoms at depths of 6–23 m.

COMPARISONS.—*B. heraldi* is most closely related to *B. coccineus* and *B. arctus* of the eastern Pacific. It differs from *coccineus* is having a shorter head (10–13 rather than 8.6–11.1 in SL), 22–23 rather than 19–20 dorsal rays, and a longer dorsal fin base (0.8–1.0 rather than 1.1–1.4 in head length); and from *arctus* in lacking the double row of dark spots on the trunk and dermal flaps, and in having fewer tail rings (36–38 rather than 36–41).

RANGE.—Islas Juan Fernández and Isla San Félix.

ETYMOLOGY.—Named in honor of the late Earl S. Herald in recognition of his life-long interest in pipefish.

MATERIAL EXAMINED.—**Holotype:** SIO 65-626, a 99.8-mm-SL mature male collected from a rock ledge at Isla San Félix, Chile, from a depth of 9–12 m, with emulsified rotenone and SCUBA on 6 Dec. 1965 by Wayne Baldwin and party.

Paratypes: SIO 65-626, 2(79–82) taken with the holotype. SIO 65-624, 1(85); Isla San Félix, 9 m. SIO 65-634, 1(77); Cumberland Bay, Isla Juan Fernández, 6–11 m. GCRL 15755, 1(70); Isla Juan Fernández, 20–23 m. SIO 65–655, 1(72); Carvajal Bay, Isla Juan Fernández, 9–12 m. All taken 5–15 Dec. 1965 with emulsified rotenone and SCUBA by Wayne Baldwin and party.

Bryx (Simocampus) arctus (Jenkins and Evermann)

(Figures 5*A*, 6, 16*B*)

Siphostoma arctum JENKINS AND EVERMANN, 1888:137 (original description; Guaymas, Sonora, Mexico; holotype USNM 39369); JORDAN AND EVERMANN 1896:771 (description).

Syngnathus arctus: ULREY AND GREELEY 1928:42 (synonymy; range); ULREY 1929:6 (Lower California; Gulf of California); JORDAN, EVERMANN, AND CLARK 1930:242 (range); STARKS AND MORRIS 1907:185 (range); HUBBS 1916:160 (eelgrass; San Diego, California); ULREY 1932:77 ("costa occidental y Golfo de California"); HERALD 1940:60 (synonymy); 1959:468 (placed in subgenus *Microsyngnathus*); FEDER, TURNER, AND LIMBAUGH 1974:128 (in coralline algae under kelp beds); MILLER AND LEA 1972:89 (description; range).

Syngnathus arcta: BERRY AND PERKINS 1965:668 (larvae in California Current).

DIAGNOSIS.—A *Simocampus* with 18–23 (19) dorsal rays; 3 anal rays; 9–11 pectoral rays; 14–16 (15) trunk rings; 36–41 (39–40) tail rings; dorsal on 0–0.8 + 5–5.3 rings; 17–23 rings covered by brood pouch; head 10.1–13.2 in SL; dorsal fin base 1.0–1.2 in head; snout 2.4–4.0 in head; maximum known size 121 mm SL; smallest sexually mature male 59 mm SL. See Tables 2 and 3 for additional counts and measurements.

DESCRIPTION.—Ridges of trunk and tail distinct and smooth. Prenuchal and nuchal ridges smooth, not separated by an indentation. Opercular ridge distinct and about half length of opercle. Snout ridge elevated and smooth from interorbital to tip of vomer. Supraorbital ridge extends posteriorly to center of opercle. Pectoral cover-plate ridges joined to form an anteriorly directed semicircle. Dermal flaps often present at junction of plates along ridges.

Protecting plates of brood pouch moderately developed; edges of pouch folds slightly scalloped. Eggs 0.5 mm in greatest diameter, arranged in two layers four across. Males with eggs and young taken from May to July.

Coloration in alcohol. Variable light tan to dark brown. May be uniformly colored or variously mottled with light and dark. Usually a double row of dark spots on sides of trunk. When patterned, background color is usually light, with dark bands on about every fourth ring. Northern fish usually darker and not mottled (Starks and Morris 1907).

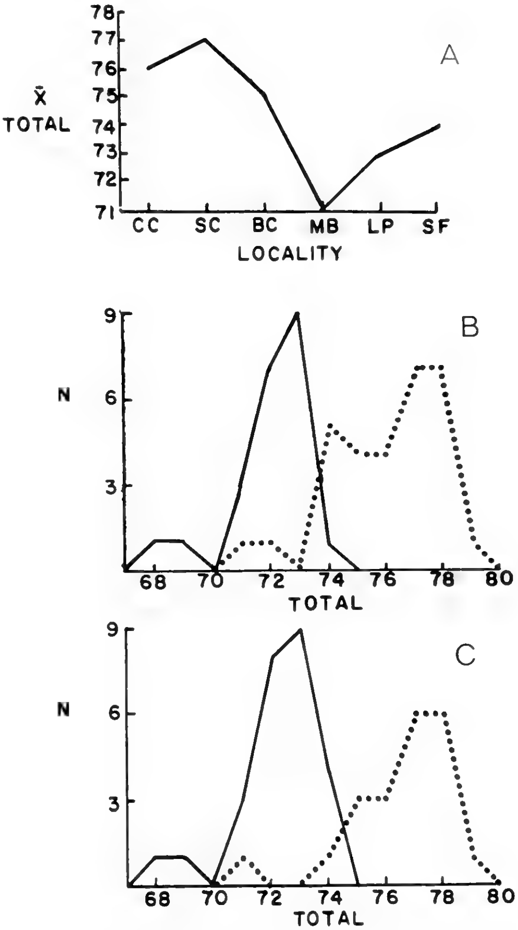


FIGURE 6. Clinal variation of *Bryx* (*Simocampus*) *arctus*. (*A*) Mean number of dorsal rays plus total rings plotted against locality. CC = central California; SC = southern California; BC = Baja California south of Bahía Sebastián Vizcaíno; MB = Bahía Magdalena; LP = La Paz to Bahía de Los Ángeles; SF = San Felipe. (*B*) Number of dorsal rays plus total rings; northern Gulf of California specimens included with southern specimens. (*C*) Number of dorsal rays plus total rings; northern Gulf of California specimens included with southern specimens. Dotted line indicates specimens from the north; solid line indicates specimens from the south.

HABITAT.—Shallow water, 0–10 m, in bays in eelgrass, and on reefs in clumps of algae, often coralline.

VARIATION.—Meristic features: There are significant differences ($P \ll .001$) in mean numbers of trunk rings, tail rings, and dorsal rays between populations from the Gulf of California and central California. The differences are produced by the clinal decrease in number of rings and dorsal rays from north to south (Fig. 6). It seems reasonable to attribute this cline to the direct effect of the environmental temperature.

Comparisons.—*B. arctus* is most closely related to *B. coccineus* and *B. heraldi* in the eastern Pacific and *B. hildebrandi* in the western Atlantic. *B. arctus* can be distinguished from *B. coccineus* and *B. heraldi* by the characters given in the key and in the descriptions of these species. *B. arctus* can be distinguished from *B. hildebrandi* by the lower number of trunk rings (14–16 rather than 17), the higher number of tail rings (36–41 rather than 33–34), and the smaller head (10.1–13.7 rather than 9.5–10.7 in SL) in the former.

Range.—Tomales Bay, California, south to Mazatlán, Mexico, and throughout the Gulf of California.

Material Examined.—**California:** Tomales Bay, SU 36445, 1(74); Elkhorn Slough, CAS 45064, 1(84); SIO H45-53, 1(52). Santa Monica, UCLA W49-112, 1(60). San Pedro, SIO 74-120, 1(85); Santa Catalina Island, SIO 53-185, 2(58–79). Newport Bay, SIO H45-70, 7(70–84). San Clemente, SIO 55-73A, 2(90–94). La Jolla, SIO 58-504, 1(73); SIO H45-32, 1(85).

Outer Coast of Baja California: Bahía de Todos Santos, SIO 62-475, 1(111). Bahía San Quintín, SIO 63-1055, 3(119–121). Bahía Playa María, SIO 52-168, 1(96). Punta San Rosarito, SIO 52-162, 3(76–88). Laguna San Ignacio, SIO H50-71, 2(59–60). Bahía Santa María, SIO 62-734, 1(102). Bahía Magdalena, SIO 62-726, 7(54–91); SIO 58-61, 1(97).

Gulf of California: Isla San José, SIO 65-265, 1(62). Bahía San Carlos, CAS 48976, 4(71–84). Isla Santa Cruz, SIO 74-124, 1(59); Isla Ildefonso, SIO 65-330, 1(68). Bahía de los Ángeles, SIO 61-185, 2(90–98). San Felipe, SIO 72-79, 4(66–81). Isla Tiburón, UCLA W56-26, 2(60–67).

Sonora: Bahía, Bocochibampo, SIO 70-84, 1(79). Guaymas, USNM 39639, 1(88), holotype.

Bryx (Simocampus) coccineus (Herald)

(Figure 5*B*)

Syngnathus coccineus Herald, 1940:57 (original description; Charles Island, Galápagos Islands; holotype, USNM 101688); Fowler 1944:496 (Galápagos Islands).

Syngnathus independencia Hildebrand, 1946:153 (original description; Bahía Independencia, Peru; holotype, USNM 127853); Koepcke 1962:200 (range); Chirichigno-F. 1974:89, 351 (diagnosed in key; range).

Diagnosis.—A *Simocampus* with 19–20 (19) dorsal rays; 2–3 anal rays; 10–11 pectoral rays; 14–16 (15) trunk rings; 36–40 (39) tail rings; 51–54 total rings; dorsal on 0–1 + 4.5–5 rings; 14–16 rings covered by brood pouch; head 8.6–11.1 in SL; dorsal fin base 1.1–1.4 in head; snout 2.3–3.0 in head; maximum known size 124 mm SL; smallest sexually mature male 78 mm SL. See Tables 2 and 3 for additional counts and measurements.

Description.—All ridges of trunk and tail moderately developed. Prenuchal, nuchal, supraorbital, and snout ridges well developed. Opercular ridge one-half length of opercle on smaller specimens, becoming one-third length of opercle with growth. Two horizontal ridges on pectoral cover plate, becoming obsolete with growth. Superior tail ridge and lateral trunk ridge overlap for 0–1 plate. Lateral line with 3–6 papillae per plate. Dermal flaps may be present.

Protecting plates of brood pouch weakly developed and no deeper than one-half depth of adjacent tail; edges of pouch folds smooth to weakly scalloped. Eggs 0.6 mm in greatest diameter, arranged in one layer two or three across. Males with young have been taken at the Galápagos Islands in January. Brooding males have been collected in July in Panama.

Caudal fin as long as last four tail rings.

Coloration in alcohol. Coloration in *B. coccineus* is very variable. Background color varies from a light tan to dark brown. Specimens may be a uniform light tan to dark brown, or more usually, light with darker markings. Light tan specimens may have darker spots at the bases of the dorsal rays and pectoral rays. The specimens with tan background and darker blotches do not have any unifying color pattern. One specimen has the venter dark brown and dorsum light tan, with dark bands extending over the dorsum on every three or four rings. Many specimens, however, have a whitish blotch on the pectoral cover plate and immediately posterior to the orbit. Hyoid region may be dark with a series of whitish spots.

Habitat.—Beds of red algae and coral heads at depths from 0–18 m.

Comparisons.—*B. coccineus* is most closely related to its eastern Pacific congeners *B. heraldi* and *B. arctus*. *B. coccineus* differs from the former by the characters discussed in the description of *B. heraldi*, and from the latter in lacking the double row of dark spots on the trunk and in having a longer head (8.6–11.1 rather than 10.1–13.2 in SL). Examined type material of *S. independencia* agrees in all respects with the holotype of *B. coccineus*. It is likely that the exceptional occurrence of *B. coccineus* in Independencia Bay, Peru, in 1941 was the result of transport of individuals southward during the extreme El Niño of that year (Lobell 1942).

Range.—Bahía Banderas, Mexico, to Punta Aguja, Peru (occasionally to Bahía Independencia), and the Galṕagos Islands.

Material Examined.—**Mexico:** Bahía de Banderas, SIO 62-42, 1(116).

Costa Rica: Puerto Culebra, USNM 101690, 1(57). Puerto Jimenez, USNM 92120, 1(50). Both paratypes of *S. coccineus*.

Panama: Isla Canal de Afuera, SIO 71-52, 1(65).

Peru: 6°55′S, 80°42′W, USNM 220970, 1(116). Bahía Independencia, USNM 127853, 1(124), holotype of *S. independencia*; USNM 127854, 2(88–108), paratypes of *S. independencia*.

Galápagos Islands: Isla Santa María, USNM 101688, 1(87), holotype of *S. coccineus*. Isla Fernandina, USNM 220971, 6(62–98); USNM 220972, 1(77).

Subgenus **Bryx** Herald

Type-species.—*Bryx veleronis* Herald.

Diagnosis.—A *Bryx* without an anal fin.

Included Species.—*B. veleronis* Herald; *B. clarionensis* n.sp.; *B. dunckeri* (Metzelaar); *B. randalli* (Herald).

Bryx (Bryx) veleronis Herald

(Figures 7*B* & 8)

Bryx veleronis Herald, 1940:55 (original description; Albemarle Island, Galápagos Islands; holotype LACM 20012).

Diagnosis.—A *Bryx* with 22–28 dorsal rays; 11–13 pectoral rays; 14–15 trunk rings; 33–37 tail rings; 48–52 total rings; dorsal on 0–0.5 + 5.5–7.0 rings; 11.5–15 rings covered by brood pouch; head 8.3–10.3 in SL; dorsal fin base 0.8–1.0 in head; snout 1.2–1.5 in postorbital; maximum known size 60 mm SL; smallest sexually mature male 45 mm SL. See Figure 8, and Tables 2 and 3 for additional counts and measurements.

Description.—Ridges of trunk and tail moderately developed, serrate and with an indentation at plate junctions. Prenuchal and nuchal plates with sharply defined serrate ridge. Snout ridge well developed, wholly on mesethmoid. Opercular ridge three-fourths length of opercle. Supraorbital ridge weak. Two parallel horizontal ridges on pectoral cover plate. Superior tail and median trunk ridges overlap for one ring. Scutella indistinct and half as deep as adjoining plates. Lateral line consisting of 1–2 papillae per plate. Dermal flaps may be present, especially on upper surface of head.

Figure 7. Anterior part of body of three species of eastern Pacific Syngnathidae. (*A*) *Bryx clarionensis*, holotype, SIO 74-116. (*B*) *Bryx veleronis*, a 34-mm-SL female, SIO 67-40. (*C*) *Hippocampus ingens*, in life.

Protecting plates of brood pouch weakly developed and no deeper than half depth of adjacent plate; edges of pouch folds smooth. Eggs 0.5–0.75 mm in greatest diameter, arranged in one layer two across. Males with young taken in July.

Coloration in alcohol. Body a light to dark tan, with various amounts of mottling, but no definite pattern. Opercular membrane and hyoid region may be brownish, with white spots and bars almost serially arranged. Pectoral and dorsal fins clear, caudal colored the same as rest of body. Body may have sprinkling of punctate melanophores ventrally. One or two brownish streaks may extend posteriorly from orbit.

HABITAT.—In red-algae beds and coral heads at depths of 3–18 m.

COMPARISONS.—Most closely related to *B. clarionenesis*. For further comparisons see discussion under that species.

RANGE.—Taken only at islands, including the Galápagos Islands; Islas Revillagigedo; Isla Murciélago and Isla del Caño, Costa Rica; and Islas San José and Canal de Afuera, Panama.

MATERIAL EXAMINED.—**Islas Revillagigedo:** Isla Clarión, LACM 20013 (formerly AHF VELERO sta. 305-34), 13(45–49), paratypes. Isla Socorro, UCLA W55-124, 1(41).

Costa Rica: Isla del Caño, LACM 31579-15, 6(37–48).

Panama: Archipiélago de las Perlas, SIO 67-38, 1(37); SIO 67-40, 1(34). Isla Canal de Afuera, SIO 71-52, 1(46).

Galápagos Islands: Isla Santa María, USNM 101689, 1(48), paratype.

Bryx (Bryx) clarionensis n.sp.

(Figures 7A & 8)

DIAGNOSIS.—A *Bryx* with 25–28 dorsal rays; 11–13 pectoral rays; 15 trunk rings; 35–36 tail rings; 50–51 total rings; dorsal on 0–1 + 6–7 rings; head 7.6–8.4 in SL; dorsal fin base 0.9–1.1 in head; snout 0.8–0.9 in postorbital; maximum known size 47 mm SL; males unknown. See Figure 8, and Tables 2 and 3 for additional counts and measurements.

DESCRIPTION.—All ridges of head and body distinct and moderately serrate. Prenuchal and nuchal ridges slightly elevated. Opercular ridge extends posteriorly for entire length of opercle. Snout ridge extends from interorbital region to anterior end of mesethmoid. Pectoral cover plate with two obsolete horizontal ridges. Trunk and tail ridges not markedly indented between rings. Superior tail and lateral trunk ridges do not overlap. Scutella small, indistinct. Lateral line not visible. Many cirruslike dermal flaps on dorsal surface of head in a few specimens.

Coloration in alcohol. Background color orangish tan, with a series of light and dark bands in a few specimens, each about two rings in width around tail. Brown frecklelike spots may appear on dorsal surface of head and along sides of snout. Abdominal region slightly darker than rest of body. Dorsal and pectoral fins colorless, caudal rays orangish brown.

HABITAT.—Known only from the types taken at the surface near Isla Clarión, Mexico.

COMPARISONS.—*B. clarionenesis* differs from the closely related species *B. veleronis* in having a longer snout (0.8–0.9 rather than 1.4–1.5 in postorbital) and the snout ridge not quite so elevated and serrate. Figure 8 provides a comparison of the snout length versus standard length for each species. Both species have been collected at Isla Clarión.

RANGE.—Isla Clarión, Islas Revillagigedo, Mexico.

ETYMOLOGY.—Named for the type-locality.

MATERIAL EXAMINED.—**Holotype:** SIO 74-116, formerly UCLA W55-136, a 47-mm-SL mature female dip-netted under a night light over 15 fathoms (27 m) at the SE anchorage, Isla Clarión, 20 Apr. 1955, by John Fitch, Wayne Baldwin, and B. Craig.

Paratypes: SIO 74-116, 7(38–50), and GCRL 15754, 1(41), same data as holotype.

Syngnathus Linnaeus

Syngnathus LINNAEUS, 1758:336 (type-species by Int. Comm. Zool. Nom. Opinions 45 and 77: *Syngnathus acus* Linnaeus); DUNCKER 1912:236 (description); 1915:78 (description; subgenera); JORDAN, EVERMANN, AND CLARK 1930:240 (North American species; synonymy); HERALD 1943:141 (in part; description; subgenera).

Siphostoma RAFINESQUE, 1810:18 (type-species by monotypy, *Syngnathus pelagicus* Linnaeus); JORDAN AND EVERMANN 1896:761 (description; synonymy).

Siphonostoma KAUP, 1853:233 (emmendation of *Siphostoma*); 1856:48 (description).

Dermatostethus GILL, 1863:283 (type-species by monotypy, *Dermatostethus punctipinnis* Gill [=*Syngnathus acus* Linnaeus]); JORDAN, EVERMANN, AND CLARK 1930:240 (range).

Syrictes JORDAN AND EVERMANN, 1927:504 (type-species by original designation, *Syngnathus fuscus* Storer).

DIAGNOSIS.—Syngnathids with subcaudal brood pouch protected by plates; nuchal and prenuchal plates and scutella present; superior ridges of trunk and tail discontinuous; lateral ridge of trunk and superior ridge of tail continuous or subcontinuous; inferior trunk and tail ridges continuous; opercular ridge present or re-

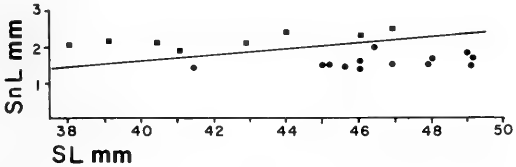


FIGURE 8. Comparison of snout length plotted against standard length for *Bryx veleronis* (closed circles) and *Bryx clarionensis* (closed squares).

duced to only basal part; pectoral, dorsal, anal, and caudal fins developed; dorsal fin base not raised; first hypobranchial reduced to absent; remainder of branchial skeleton present, without tooth plates; jugular plates well developed, separated by a median plate; body ridges generally smooth to finely serrate, both neither strongly toothed nor serrate; 2–3 infraorbitals; 25–47 dorsal rays; 2–4 anal rays; 11–14 pectoral rays; 10 caudal rays; 14–23 trunk rings; 33–50 tail rings. This genus contains some of the largest species in the family; *S. californiensis* reaches a length of 533 mm SL. Marine and fresh water, cosmopolitan, but most abundant in temperate seas.

DISCUSSION.—Herald (1943, 1959), following the preliminary analysis of Duncker (1915), divided the genus into four subgenera differentiated on the basis of brood-pouch closure. On osteological grounds, I conclude that two of these subgenera (*Bryx* and *Microsyngnathus*) together constitute a distinct genus (*Bryx*). *Syngnathus* is the most speciose pipefish genus, with perhaps 40 species.

Key to Eastern Pacific Species of *Syngnathus*

1a. Trunk rings 14–16 ($\bar{x}$ = 15) ---------- *auliscus* (Swain)

Santa Barbara Channel, California, to northern Peru; in eelgrass of bays and sloughs

1b. Trunk rings 17 or more (6 of 914 specimens of *S. leptorhynchus* have 16) ------ 2

2a. Snout long, compressed, usually contained less than 1.8 in head length -------- 3

2b. Snout shorter, round, usually contained more than 1.8 times in head length -------- 5

3a. Total rings fewer than 63; all ridges of trunk and tail distinctly keeled ---------- *carinatus* (Gilbert)

Northern Gulf of California

3b. Total rings more than 63; all ridges of trunk and tail rounded ---------- 4

4a. Total rings 63 or more, usually 64–66; 35–41 dorsal rays, usually 37–40 (see Fig. 11), dark bar extending diagonally from orbit across opercle ---------- *exilis* (Osburn and Nichols)

Halfmoon Bay, California, to Bahía Magdalena, Baja California; on sand bottoms

4b. Total rings 67–72, usually 68–70; 39–48 dorsal rays, usually 42–46 (see Fig. 11), no dark bar across opercle ---------- *californiensis* Storer

Bodega Bay, California, to Bahía Santa María, Baja California; associated with kelp beds, often epipelagic

5a. Pectoral fins long, extending posteriorly across two full trunk rings ---------- *macrobrachium* n.sp.

Tumbes, Peru, to Puerto Montt, Chile

5b. Pectoral fins short, never extending posteriorly across two full rings ---------- 6

6a. Total rings more than 60 ---------- 7

6b. Total rings 60 or fewer ---------- 8

7a. Trunk length 1.5 or more in tail length; total rings 60–68; dorsal rays 33–45 ---------- *euchrous* n.sp.

Redondo Beach, California, to Bahía de Ballenas, Baja California; near bottom off rocky shores

7b. Trunk length 1.5 or less in tail length; total rings 53–64; dorsal rays 28–43 ---------- *leptorhynchus* Girard (in part)

8a. Interorbital 3 in postorbital; head usually more than 8.6 in SL -- *leptorhynchus* Girard

Southeastern Alaska to Bahía Santa María, Baja California; in eelgrass of bays

8b. Interorbital more than 3 in postorbital; head usually less than 8.6 in SL ---------- *insulae* n.sp.

Isla Guadalupe, Mexico, in algae and eelgrass, 20–34 m

Syngnathus auliscus (Swain)

(Figures 4*D* & 9)

Siphostoma auliscus SWAIN, 1882:547 (original description; Santa Barbara and San Diego, California; types lost); JORDAN AND GILBERT 1883:905 (description; range); SWAIN AND MEEK 1884:238 (diagnosed in key); JORDAN AND EVERMANN 1896:767 (description; range); EIGENMANN AND EIGENMANN 1892:144 (San Diego).

Syngnathus auliscus; STARKS AND MORRIS 1907:184 (range); HUBBS 1916:160 (description); ULREY AND GREELEY

TABLE 4. FREQUENCY DISTRIBUTIONS OF TRUNK AND TAIL RINGS, AND DORSAL FIN RAYS IN EASTERN PACIFIC SPECIES OF *Syngnathus*.

	Trunk rings									Tail rings																		
	14	15	16	17	18	19	20	21	22	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
auliscus	17	56	16	—	—	—	—	—	—	1	16	19	23	20	10	—	—	—	—	—	—	—	—	—	—	—	—	—
carinatus	—	—	7	57*	1	—	—	—	—	—	—	—	—	—	1	6	22	33	3	—	—	—	—	—	—	—	—	—
exilis	—	—	—	2	94	21	10*	1	—	—	—	—	—	—	—	—	—	—	3	10	22	33*	38	15	3	—	—	—
californiensis	—	—	—	—	—	1	20	48	6	—	—	—	—	—	—	—	—	—	—	—	—	6	10	36	25	5	2	1
macrobrachium	—	—	1	19	12	—	—	—	—	—	—	—	—	—	—	5	11	13*	3	—	—	—	—	—	—	—	—	—
euchrous	—	—	—	—	39	133*	25	—	—	—	—	—	—	—	—	—	5	27	44	37	26	33	12*	6	2	—	—	—
leptorhynchus	—	—	9	146	443	267	55	1	—	—	—	11	41	109	112	104	75	123	168	157	29	1	—	—	—	—	—	—
insulae	—	—	—	11	18	2*	—	—	—	—	—	—	—	—	—	5	10*	13	—	—	—	—	—	—	—	—	—	—

	Dorsal fin rays																						
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
auliscus	3	13	18	23	18	6	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
carinatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	10	10	15	11*	15	1	—	—
exilis	—	—	—	—	—	—	—	—	—	—	16	30	26	20	15	10*	2	1	—	—	—	—	—
californiensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	6	13	9	9	13	17	5	2
macrobrachium	—	—	—	—	—	—	—	—	—	—	1	1	1	7*	5	8	3	1	2	—	—	—	—
euchrous	—	—	—	—	—	—	—	1	9	10	24	24	29	30	18	11	14*	9	6	5	—	—	—
leptorhynchus	—	—	4	18	39	50	87	76	73	58	86	98	113	99	56	30	14	2	—	—	—	—	—
insulae	—	—	—	—	—	6	7*	12	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* Primary type.

TABLE 5. NUMBER OF SPECIMENS (N) AND STANDARD LENGTH RANGE, TOGETHER WITH RANGE AND MEAN ($\bar{x}$) OF SELECTED CHARACTERS EXPRESSED IN THOUSANDTHS OF STANDARD LENGTH IN *Syngnathus*.

		Head length		Snout length		Snout depth		Body depth		Dorsal-base length		Pectoral-fin length		
Species	SL	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	N
auliscus	46–134	98–136	113	44–56	48	10–19	15	18–46	31	98–124	112	13–21	18	9
carinatus	116–230	113–141	128	65–89	76	8–10	9	16–26	22	114–138	127	15–26	21	17
exilis	75–238	102–148	121	50–88	68	7–13	10	20–44	29	95–120	107	13–21	16	37
californiensis	78–382	111–143	120	55–93	69	6–12	9	15–41	24	100–128	115	9–18	14	33
macrobrachium	92–190	112–144	137	60–82	72	10–14	12	26–35	30	121–140	130	21–34	29	15
euchrous euchrous	111–249	100–132	114	47–78	55	8–14	11	22–40	29	111–128	118	10–23	17	20
e. ollotropis	116–244	93–108	103	44–57	49	10–12	11	22–30	26	96–127	112	10–15	13	10
leptorhynchus	57–245	104–148	122	48–87	65	8–15	12	20–55	27	97–141	118	10–20	16	92
insulae	88–180	107–117	111	46–57	52	10–14	11	19–30	24	105–114	109	13–19	16	7

1928:42 (synonymy; range); ULREY 1929:6 (Lower California); JORDAN, EVERMANN, AND CLARK 1930:240 (range); ULREY 1932:77 (Golfo de California); BARNHART 1936:34 (description; range); HERALD 1940:60, 63 (key; synonymy; range); CASTRO-AGUIRRE ET AL. 1970:131 (not common in Gulf of California); MILLER AND LEA 1972:89 (description; range); CHIRICHIGNO-F. 1974:351 (range).

Singnathus auliscus; VAILLANT 1894:70 (Gulf of California).

Siphostoma sinaloae JORDAN AND STARKS 1896:268 (original description; Mazatlán; holotype SU 2945).

Syngnathus tweedlei MEEK AND HILDEBRAND, 1923:259 (original description; Chame Point, Panama; holotype USNM 82088).

DIAGNOSIS.—A *Syngnathus* with 26–33 (27–30) dorsal rays; 10–14 pectoral rays; 2–3 anal rays; 14–16 (15) trunk rings; 34–39 (36–37) tail rings; 0.2–1.5 + 5–7.2 rings covered by dorsal fin; total rings covered by dorsal fin 6–7.9; 15–21 pouch rings; head 7.1–10.1 in SL; dorsal fin base 0.8–1.6 in head; snout 2.0–2.8 in head; maximum known size 178 mm SL; smallest sexually mature male 71 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges of body smooth, rounded, low but distinct. Prenuchal and nuchal ridges low but distinct. Opercles strongly convex, with median ridge reaching half the length. Snout ridge running full length of snout to interorbital. Head not raised at orbit, so that snout ridge almost horizontal. Supraorbital ridge originating just anterior to nostrils and ending above anterior edge of opercle. Pectoral cover plate with one obsolete ridge. Lateral trunk and superior tail ridges overlap for one ring. Slightly acute ventral trunk ridge. Three lateral line papillae per plate. Dermal flaps rarely present.

Plates protecting brood pouch well developed, often as deep as overlying tail rings. Eggs 0.6–0.7 mm in greatest diameter, arranged in two layers four across. Brooding males collected in April through August.

Fins of moderate size, caudal as long as last three tail rings. Pectoral base about 1.5 in its length.

Juveniles less than 25 mm SL (Fig. 9) are much spinier than adults. Large broad-based spine on each frontal; opercle has a broad-based lateral projection, and each ring has a well-developed spine on each ridge. Dorsal fin high. Mouth large and upturned. Body whitish with light brown pigmented spots forming a band dorsal to gut anteriorly and continuing posteriorly along ventral surface of tail. Occasionally with sprinkling of pigment spots on body, concentrated on ventral surface of gut and along dorsal base.

Coloration in life. Variations of brown or green, never red.

Coloration in alcohol. Usually light tan to brown, lighter ventrally. Median caudal rays brown; outer two rays light tan; all other fins colorless. Usually a dusky blotch below nostrils. Sometimes a brownish streak at lower-posterior corner of orbit. Often there is on the body much darker mottling, which may alternate with light areas, especially posteriorly, giving a dark-light banded appearance. Lighter bands usually narrower and separated by five to six rings.

HABITAT.—Eelgrass of bays and sloughs. Occasionally in floating *Sargassum*.

COMPARISONS.—Although *S. auliscus* is a chiefly tropical species, it occurs rather frequently in the southern part of San Diego Bay, where the temperature is raised by a thermal

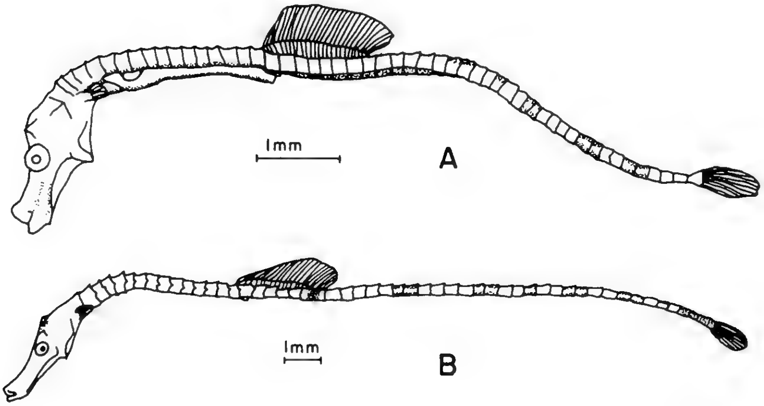


FIGURE 9. Juvenile *Syngnathus auliscus* from San Diego Bay, California. (*A*) 9.2 mm SL. (*B*) 16.3 mm SL.

effluent; this is the only place in California where this species has been found in larger numbers than other pipefishes. It may be confused in this region with the similar *S. leptorhynchus. S. auliscus* differs from *S. leptorhynchus* in having 14–16 trunk rings rather than 17 or more; in having a deeper and more robust trunk; and in reaching a much smaller size as adults.

RANGE.—Santa Barbara Channel, California, to Paita, Peru, and throughout the Gulf of California.

MATERIAL EXAMINED.—**California:** Newport Bay, LACM W55-257, 1(162). Peñasquitos Lagoon, SIO 73-411, 1(178). San Diego, SIO H46-94, 2(127–134); G. McGowen personal collection, 89(7.4–31.8).

Mexico: Bahía de Tortugas, SIO H48-53, 1(92). Bahía Almejas, SIO 65-181, 2(98–111). Cholla Bay, CAS 45071, 2(91–99). Puerto Peñasco, GCRL V73:10729, 2(65–82). Guaymas, R. Behrstock, personal collection, 38(29–112). Sinaloa, GCRL V71:6572, 1(123); GCRL V68:2639, 1(81); GCRL V71:6565, 2(46–52). Mazatlán, SU 2945, 1(87), holotype of *S. sinaloae*.

Nicaragua: Corinto, CAS 6346, 1(74).

Costa Rica: Puntarenas, GCRL V69:3526, 3(44–83).

Panama: Chame Point, USNM 82088, 1(71), holotype of *S. tweedlei*.

Peru: Tumbes, IMARPE uncat., 2(?–100). Paita, IMARPE uncat., 1(87).

Syngnathus carinatus (Gilbert)

(Figure 10*B*)

Siphostoma carinatum GILBERT, 1892:547 (original description; 31°31′45″N, 114°19′W; lectotype here designated as SU 240); JORDAN AND EVERMANN 1896:763 (description).

Syngnathus carinatum; BREDER 1928:24 (Isla Tiburón, Bahía Adair, San Felipe).

Syngnathus carinatus; ULREY 1929:6 (Gulf of California); JORDAN, EVERMANN, AND CLARK 1930:240 (range); ULREY 1932:77 (Golfo de California); FOWLER 1944:496 (range).

Syngnathus acus; (not of Linnaeus) HERALD 1940:60 (diagnosed in key; range).

Syngnathus griseolineatus leptorhynchus; (not of Girard) CASTRO-AGUIRRE ET AL. 1970:132 (Gulf of California).

DIAGNOSIS.—A *Syngnathus* with 40–46 (41–45) dorsal rays; 13–15 pectoral rays; 3–4 anal rays; 16–18 (17) trunk rings; 39–43 (41–42) tail rings; 56–60 total rings; dorsal on 0.1–1.8 + 7.5–11.1 rings; total rings covered by dorsal 9–12.1; 21.5–22 rings covered by brood pouch; head 7.1–8.6 in SL; dorsal fin base 0.9–1.2 in head; snout 1.6–1.8 in head; maximum known size 230 mm SL; smallest sexually mature male 182 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges on body usually well developed and serrate. Supraoccipital, nuchal, and prenuchal ridges low and finely serrate. Opercular and supraorbital ridges low. Snout ridge slightly elevated and serrate, extending posteriorly to region above anterior edge of orbit. Pectoral cover plate with only superior ridge. Superior trunk ridge extending forward dorsally to gill opening and ending just below nuchal plate. Lateral trunk and superior tail ridges usually not overlapping, but may overlap for half width of last trunk ring. Scutella easily discernible, about half as deep as median trunk plate. Lateral line consisting of 6–7 papillae per plate. No dermal flaps.

Protecting plates of brood pouch well developed, more than half as high as adjacent tail; margin of folds of brood pouch smooth. Eggs 0.9–1.0 mm in greatest diameter, arranged in two layers six across. Males with eggs have been collected in November.

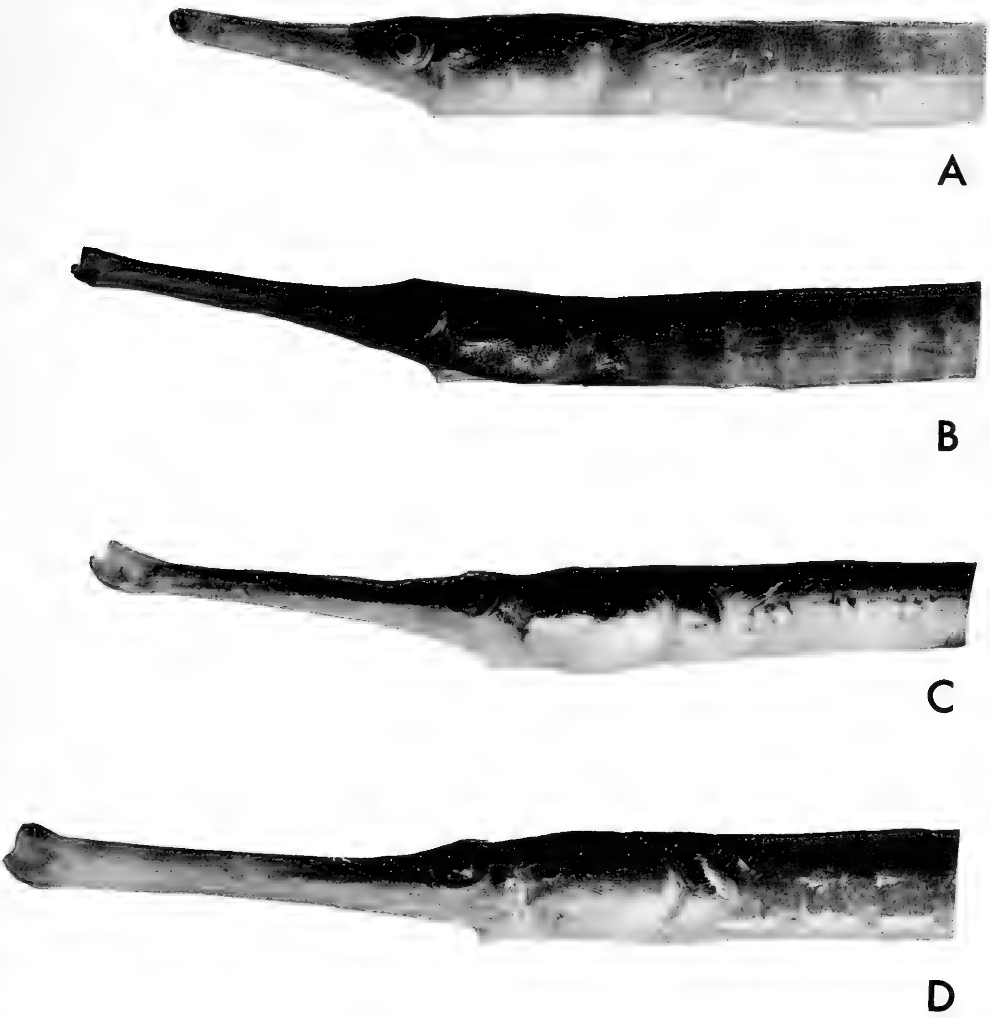


FIGURE 10. Anterior part of body of four species of eastern Pacific Syngnathidae. (*A*) *Syngnathus macrobrachium*, holotype, USNM 176501. (*B*) *Syngnathus carinatus*, a 200-mm-SL female, SIO 72-60. (*C*) *Syngnathus exilis*, a 238-mm-SL female, SIO 75-661. (*D*) *Syngnathus californiensis*, a 285-mm-SL female, SIO 62-552.

Fins all well developed. Pectoral fin extends posteriorly to edge of first trunk ring or middle of second trunk ring.

Coloration in alcohol. Older specimens a uniform light tan to dark brown, with caudal dusky and dark spots at bases of dorsal rays. Fresh specimens with immaculate white undersides becoming silvery on opercle and pectoral cover plate. Dorsum light green-brown with white areas around scutella, which may be connected by white streaks to adjacent scutella. Thus, a chainlike pattern often evident dorsolaterally. Caudal fin green-brown centrally with light edges. Snout with the same green-brown color dorsally. Other fins colorless.

MERISTIC VARIATION.—The number of trunk rings in *S. carinatus* is relatively stable, usually 17, except that three of the four specimens from Bahía Kino had 16. The same trend is shown by the number of tail rings. The normal range is from 41–42, but two of the four specimens from Bahía Kino had 40 tail rings.

COMPARISONS.— As indicated in the account of *S. macrobrachium*, *S. carinatus* is closely related to *macrobrachium*, *schlegeli*, and *folletti*. It seems to be most closely related to the

Japanese *S. schlegeli*. It differs from *schlegeli* in coloration (light coloration with chainlike pattern rather than dark brown), longer snout, and in that the superior trunk ridge is continued anteriorly above the gill opening. The relationship of *S. carinatus* to a Japanese fish parallels the distribution indicated by Dawson (1944) for some algae.

RANGE.—Northern part of Gulf of California, from head of Gulf and from Bahía San Luis Gonzaga in the west to Bahía Kino in the east.

MATERIAL EXAMINED.—Gulf of California: Mouth of Río Colorado, SIO 63-484, 2(132–139). Between El Golfo and San Felipe, S. Guevara personal collection, 20(161–216). Off Bahía Adair, BOC 1184, 11(86–148). 31°32′30″N, 114°20′W, USNM 48250, 3(185–287); USNM 127139, 2(187–189); USNM 125028, 2(178–183), paralectotypes. 31°31′45″N, 114°19′W, SU 240, 1(198), lectotype; SU 67670, 3(186–201), paralectotypes. San Felipe, SIO 72-60, 2(203–209); SIO 58-164, 1(127); SIO H47-53, 47(132–165); SIO 74-118, 3(182–230); BOC 1017, 5(81–156). Punta Diggs, UCLA W62-61, 5(131–152). Isla Willard, LACM 22298, 1(210). Isla Tiburón, BOC 1010, 1(123). Bahía Kino, SIO 60-113, 4(115–133).

Syngnathus exilis (Osburn and Nichols)

(Figures 10*C* & 11)

Siphostoma exile OSBURN AND NICHOLS, 1916:153 (original description; west San Benito Island, Baja California; holotype USNM 87543, formerly AMNH 5203).

Syrictes exilis; JORDAN, EVERMANN, AND CLARK 1930:243 (range).

Syngnathus californiensis californiensis; HERALD 1940:60 (in part); 1941:62 (in part).

Syngnathus exilis; ULREY 1929:6 (listed); MILLER AND LEA 1972:212 (range).

DIAGNOSIS.—A *Syngnathus* with 36–41 (rarely 35, 42 or 43) (37–40) dorsal rays; 11–14 pectoral rays; 3 anal rays; 17–21 (18) trunk rings; 43–49 (rarely 50) (45–47) tail rings; 63–68 (64–66) total rings; dorsal on 0–1.9 + 7–9.5 rings; brood pouch covering 19–26 rings; head 6.8–9.8 in SL; dorsal fin base 0.9–1.4 in head; snout 1.6–2.0 in head; eggs 1.0–1.2 mm in greatest diameter, arranged in two layers four across. Maximum known size 253 mm SL; smallest sexually mature male 125 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—Ridges of trunk and tail smooth and rounded. Nuchal and prenuchal ridges obsolete to absent, smooth. Opercular ridge distinct, reduced to basal third of opercle. Snout ridge low, smooth to slightly serrate, reaching from vomer to anterior part of interorbital; slightly elevated posteriorly. Superior ridge of pectoral cover plate absent, inferior ridge obsolete. Lateral trunk and superior tail ridges overlap on first tail ring. Trunk and tail ridges smooth to slightly rugose. Scutella small, about one-third as deep as adjoining plates. Snout moderately compressed. Abdomen typically and rather distinctly with posterior swelling, especially in juveniles and females. Lateral line consisting of 4–5 papillae per plate. Often with a pair of stitches on first trunk ring and nuchal plates. No dermal flaps.

Pouch protecting plates well developed, about as high as adjacent tail. Eggs 1.0–1.2 mm in greatest diameter, arranged in two layers four across. Brooding males found throughout year.

Pectoral fins reach posteriorly to just past junction of first and second trunk rings. Caudal fin as long as last three tail rings.

Coloration in life. From C. L. Hubbs's field notes for SIO H47-43.

> The specimens become sooty toward the caudal. Of the half grown, one is blackish green the other tan, much variegated with lighter and darker. All are much speckled with light on top of head. The female varies from greenish brown anteriorly to reddish brown posteriorly. The male is brown, becoming orange toward the brood pouch. The lower part of the opercle of all is silvery with a more or less distinct dark stripe behind the lower part of the eye. Dark markings on lower part of opercle are incipient. All but the adult male have a diffuse dark streak on belly. The adults show the half crescents on the body just above the ventrolateral keel. The adult male is rather conspicuously banded with light. The others indefinitely so.

Coloration in alcohol. The most striking feature of alcoholic specimens is the dusky stripe on the snout extending from the nostrils anteriorly on the greater part of the snout, and the bar that courses diagonally from the posteroventral margin of the orbit to the opercle. These markings may be wanting in older specimens. The general body color is typical for most species of *Syngnathus*; i.e., a ground color tan to dark brown, with various mottlings of darker brown.

HABITAT.—On the bottom off sandy beaches, often associated with pieces of detached algae. Occasionally, juveniles are taken in the plankton, sometimes associated with flotsam. Two specimens (SIO H51-203 and CAS 32983) were taken from the guts of albacore (*Thunnus alalunga*).

COMPARISONS.—*S. exilis* is a long-snouted pipefish of the outer coast, resembling *S. californiensis* in general appearance. It can be distinguished from that species by its smaller size at maturity, generally fewer trunk rings ($\bar{x}$ = 18.3 vs $\bar{x}$ = 20.8), coloration (especially the presence of the dark oblique bar at the posterior corner of the orbit), the abdomen usually with a posterior swelling, and the sand-bottom vs kelp-bed habitat. Figure 11 provides information for easy separation of *S. exilis* from *S. californiensis*.

RANGE.—Half Moon Bay, California, to Bahía Magdalena, Baja California, including the channel islands of California and Isla Guadalupe, Mexico.

MATERIAL EXAMINED.—**California:** Half Moon Bay, SIO 54-106, 1(217). Guide Seamount, CAS 32983, 1(97). Del Monte Beach, SIO 74-195, 2(92–196). Monterey, CAS 27950, 1(89). San Luis Obispo, SIO 55-35, 1(164); SIO H50-195, 2(217–227). Los Angeles, SCCWRP sta. T_1-75, 4(176–199); SCCWRP sta. T-0, 4(132–203). Long Beach, UCLA W50-128, 2(228–235). Newport Beach, SIO H45-70, 17(120–239). Dana Point, SCCWRP sta. Fv. 3, 5(105–190). Torrey Pines Lagoon, UCLA W63-49, 2(170–175). La Jolla, SIO H47-43, 4(96–163); SIO H47-106, 48(107–242); SIO H51-153, 13(136–227); SIO H46-63, large series; SIO H47-158, 34(96–225); SIO H47-134, 1(170); SIO H48-163, large series. Santa Cruz Island, SIO H51-259, 1(115). Santa Catalina Island, LACM 30510-9, 1(85); LACM 30865-3, 1(42). Mission Bay, SIO 61-412, 1(113); San Diego Bay, SIO H50-112, 1(219).

Baja California: Islas Coronados, SIO H46-125, 1(145). Punta Banda and Isla de Todos Santos, SIO 61-284, 1(120); SIO 68-302, 1(160); SIO H51-24, 2(102–118). Punta Santo Tomas, SIO 65-440, 1(103). Cabo Colnett, SIO H51-303, 1(181); CAS 3295, 8(114–161). Bahía San Quintín, SIO H50-25, 1(239); SIO 60-453, 1(135). Bahía San Carlos, SIO H52-210, 4(114–247). Bahía Blanca, SIO 60-327, 3(158–250). Bahía Playa María, SIO H52-169, 2(120–224). Isla Guadalupe, SIO 65-72, 1(130). Bahía Santa Rosalía, SIO 62-282, 1(164). Bahía Sebastián Vizcaíno, SIO H52-135, 9(131–228). Islas San Benitos, USNM 87534, 1(166), holotype. Isla Cedros, SIO 68-345, 1(175); UCLA W60-126, 1(123); SU 67915, 1(117); SIO 65-591, 1(220); SIO 62-756, 1(145); SIO H53-110, 1(193). Punta Eugenia, SIO 61-398, 1(70). Cabo Tortolo, SIO H48-55, 1(180). Bahía Tortugas, SIO H48-51, 1(98); SIO 63-806, 1(141); SIO 59-25, 1(155); SIO H48-33, 3(192–238); SU 2488, 1(123); AMNH 5588, 5(99–118), paratypes. Bahía San Roque, SIO 63-16, 1(84); SIO 64-185, 1(152). Bahía Asunción, SIO 68-303, 1(161); SIO 62-535, 2(100–110); SIO 68-301, 2(96–151); SIO H51-96, 1(174); SIO H48-92, 1(115); SIO 66-147, 1(190); SIO 64-68, 3(161–226). Bahía San Hippolito, SIO 64-750, 14(70–253). Bahía de Ballenas, SIO 64-405, 1(173); SIO 64-765, 1(180); SU 767, 1(147). Bahía Santa María, SIO H50-149, 1(136). Bahía Magdalena, SIO H50-96, 1(67).

Syngnathus californiensis Storer

(Figures 10*D*, 11, 16*C*)

Syngnathus californiensis STORER, 1848:73 (original description; California; holotype lost); STARKS AND MORRIS 1907:183 (meristic features); STARKS 1911:177 (not included in Puget Sound fauna); HUBBS 1916:158 (description); 1921:4 (range; counts); ULREY AND GREELEY 1928:42 (synonymy; range); ULREY 1929:6 (included in list); JORDAN, EVERMANN, AND CLARK 1930:240 (range); BARNHART 1936:34 (description); HERALD 1940:64 (in part; diagnosed in key); 1941:62 (description; range; synonymy); MILLER AND LEA 1972:89 (description; range).

Siphostoma californiense; JORDAN AND GILBERT 1881:453 (synonymy); JORDAN AND JOUY 1881:1 (Santa Barbara, Monterey, and San Francisco); JORDAN AND GILBERT 1882:69 (in part; *S. griseolineatus* included); SWAIN 1882:308 (description; synonymy); JORDAN AND GILBERT 1883:384 (description; synonymy; range); SWAIN AND MEEK 1884:238 (diagnosed in key); JORDAN AND EVERMANN 1896:764 (description; synonymy; range).

Siphostoma californiensis; EVERMANN AND LATIMER 1910:136 (San Pablo Bay, California, probably *S. leptorhynchus*).

DIAGNOSIS.—A *Syngnathus* with 40–48 (42–46) dorsal rays; 12–14 pectoral rays; 3 anal rays; 19–22 (21) trunk rings; 46–52 (48–49) tail rings; 66–71 total rings; dorsal on 0.2–1.9 + 7.5–9.5 rings; total rings covered by dorsal 8.5–10.5; 19.5–25 rings covered by brood pouch; head 6.2–8.9 in SL; dorsal fin base 0.9–1.2 in head; snout 1.5–2.0 in head; maximum known size 533 mm SL; smallest mature male 191 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges on body distinct, smooth, and rounded. Supraoccipital, nuchal, and prenuchal ridges absent. Opercular ridge reduced to absent. Snout ridge low, not elevated, and smooth, extending posteriorly to interorbit. Supraorbital ridge absent. Pectoral cover-plate ridges absent. Superior trunk ridge indistinct anterior to pectoral fin. Lateral trunk ridge and superior tail ridge overlap on first tail ring. Scutella small, about one-third depth of adjoining plates. Lateral line consisting of 7–8 papillae per plate. No dermal flaps.

Protecting plates of brood pouch well developed, about as high as half adjacent tail; margin of brood pouch folds smooth. Eggs 1.1–1.3 in greatest diameter, arranged in 2 layers 3–4 across. Males with young or eggs have been collected in July–October.

The fins are normally developed. Pectoral fin reaching posteriorly just past junction of first and second trunk rings. Caudal fin as long as last three tail rings.

Coloration in life. From C. L. Hubbs's field notes for SIO H45-69.

> Belly generally yellow-green, sometimes pale blue or even pale brownish. Especially conspicuous are the small dark speckles, occasionally weak or absent, along the carinae of the trunk between the plates. These provide an almost invariable distinction. The streak along the mid-line of the belly is lacking or very weakly developed. In almost all

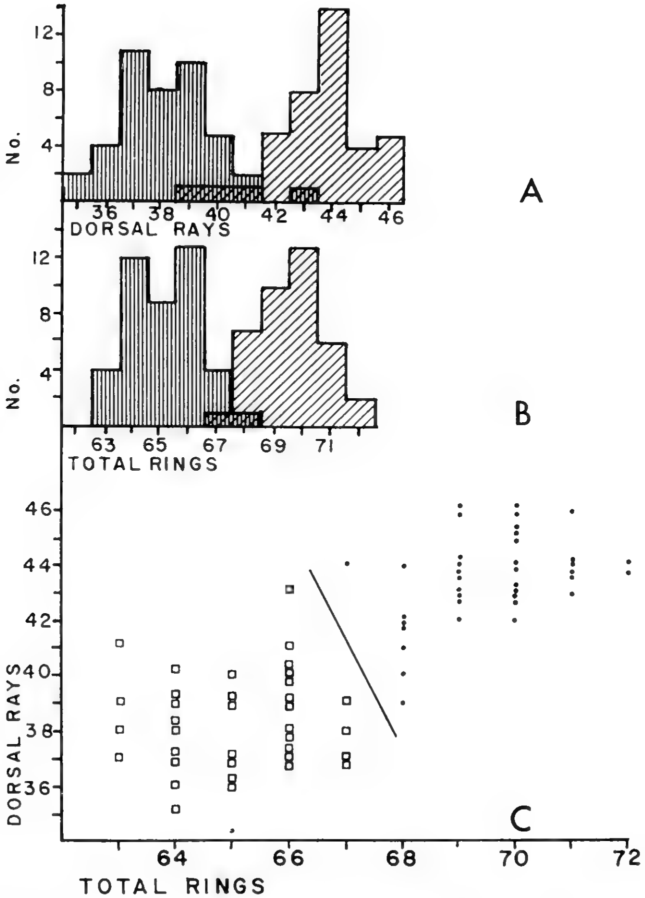


FIGURE 11. Comparison of meristic characters between *Syngnathus exilis* and *Syngnathus californiensis*. (*A*) Frequency of dorsal ray counts. *S. exilis* vertical lines, *S. californiensis* diagonal lines. (*B*) Frequency of total ring number. *S. exilis* vertical lines, *S. californiensis* diagonal lines. (*C*) Number of dorsal rays plotted against total number of rings. *S. exilis* open squares, *S. californiensis* dots.

specimens the light streakings in the upper and lateral aspects of the head and body form more or less definite and extensive wavy lengthwise lines, typically forming a ring on the first nuchal plate. When light markings are developed along the ventral carina of trunk (in about one-third of specimens) there tend to be more definite elliptical or oval marks more or less separated from the light color of the belly, and when they are developed similar marks are usually evident along the median and dorsal carinae.

Coloration in alcohol. The young, which are associated with drifting kelp, often are light gray to tan with a dark streak alongside the snout.

Adults vary from tan to brown, often with indistinct darker blotches and wavy lines about the head and opercle; especially pronounced along the sides of the trunk. The dark snout stripe most often remains as a dark area around and below the nostrils. The caudal has the same color as the body. The remaining fins are colorless except for melanophores along the rays.

HABITAT.—Offshore kelp (*Macrocystis*) beds, and frequently associated with drifting kelp.

COMPARISONS.—*S. californiensis* is a very distinctive fish as an adult. The combination of large size and high number of rings and dorsal rays serves to distinguish *S. californiensis* from all other California pipefishes. *S. euchrous* most closely approaches *S. californiensis* in size and number of rings, but its short round snout easily distinguishes it from the longer compressed snout of *S. californiensis*. *S. californiensis* juveniles are easily confused with adults of *S. exilis* (see comparison in account of *S. exilis*).

RANGE.—Bodega Bay, California, south to Bahía Santa María, Baja California, and including the offshore islands (essentially the same distribution as that of the giant kelps *Macrocystis pyrifera* and *M. angustifolia*).

MATERIAL EXAMINED.—**California:** Bodega Bay, CAS 32933, 1(162). San Francisco, CAS 60233, 2(154–171); USNM 27199, 1(401). Moss Landing, SIO 62-510, 1(284); SIO 53-194, 3(131–192). Monterey Bay, SU 19261, 1(128); SU 36465, 6(94–325); SU 5327, 3(157–184); CAS 13409, 1(177); SU 58461, 3(57–84). Guide Sea Mount, CAS 32983, 1(98). 36°N, 123°W, LACM 30458-1, 1(212). W. R. Hearst State Park, SIO 73-301, 13(174–254). Morro Bay, UCLA W50-196, 2(162–185). Diablo Cove, LACM 31300-24, 2(160–203). Avila Bay, SIO H50-195. Santa Barbara, SIO 61-426, 30(119–362); SIO H44-12, 1(173); SIO H51-128, 3(119–327). Santa Rosa Island, UCLA W50-99, 2(161–171). Santa Cruz Island, UCLA W50-87, 1(247); UCLA W50-97, 1(183). San Pedro, SIO H44-38. Long Beach, CAS 31512, 1(241). Del Mar, SIO 58-107, 2(400–410). Catalina Basin, S. Imsand personal collection, 16(78–100). La Jolla, SIO H52-181, 1(115); SIO H50-7, 1(437); SIO H47-153, 1(172). Bird Rock, SIO 75-427, 1(533). Mission Beach, SIO 67-29, 1(530). Mission Bay, SIO H45-8, 5(121–184); CAS 11428, 1(122); SIO H44-28, 1(125); SIO H46-75, 2(168–180). Point Loma, SIO H51-347, 7(151–387).

Mexico: Bahía de Todos Santos, SIO H53-229, 2(223–269); SIO 61-284, 13(111–323); SIO 64-806, 5(125–349). Punta Banda, SIO 59-302, 1(194). Cabo Colnett, SIO H50-62, 1(222). Isla San Martín, SIO H52-219, 1(89); SIO H52-218, 3(104–162). Bahía San Quintín, SIO H51-108, 1(141). Punta Baja, SIO H51-401, 1(198). Isla San Geronimo, SIO H52-159, 2(190–252). Bahía San Carlos, SIO H52-210, 16(175–282). Punta Eugenia, SIO H52-118, 1(125). Isla Cedros, CAS 32952, 1(224). Bahía Thurloe, CAS 15424, 1. Bahía Santa María, LACM W51-264, 1(234).

Syngnathus macrobrachium n.sp.

(Figure 10*A*)

Syngnathus acicularis (not of Jenyns); DELFIN 1901:42 (range); HILDEBRAND 1946:155 (in part; description; synonymy; range); MANN 1954:190 (description; range); KOEPCKE 1962:200 (range); DEBUEN 1963:91 (synonymy; description); MORROW 1957:228 (Peru); CLEMENS AND NOWELL 1963:262 (night light off Peru); CHIRICHIGNO-F. 1974:189, 351 (diagnosed in key; range).

Siphostoma aciculare (not of Jenyns); EVERMANN AND RADCLIFFE 1917:53 (synonymy; description); NICHOLS AND MURPHY 1922:506 (Chincha Island).

Syngnathus acus (in part, not of Linnaeus); HERALD 1940:60 (diagnosed in key); FOWLER 1944:496 (range).

DIAGNOSIS.—A *Syngnathus* with 36–44 (39–42) dorsal rays; 12–15 pectoral rays; 2–4 anal rays; 16–18 (17–18) trunk rings; 40–43 (41–42) tail rings; 57–62 total rings; dorsal on 0.5–2.3 + 7–9 rings; total rings covered by dorsal fin 9–10.3; 17–21 pouch rings; head 6.6–8.2 in SL; dorsal fin base 0.9–1.2 in head; snout 1.8–2.0 in head; maximum known size 255 mm SL; smallest mature male 84 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges of body rounded and smooth. Nuchal and prenuchal ridges low, smooth. Opercular ridge extending posteriorly about one-fourth length of opercle. Supraorbital and snout ridges low, smooth. Ridges of pectoral cover plate obsolete. Trunk and tail ridges smooth, without indentations between rings. Superior trunk ridge does not extend anteriorly past gill opening. Scutella moderately developed, about equal in depth to adjacent plate. Lateral line consisting of 4–5 papillae per plate. No dermal flaps.

Protecting plates of brood pouch about as high as adjacent tail; margin of brood pouch folds smooth. Egg size unknown. Males with embryos and with recently emptied pouches have been taken from October through April.

The fins are well developed. The pectoral is particularly large, extending posteriorly over two full rings.

Coloration in alcohol. Generally a light brown to dusky with caudal fin darker. A dark streak on mid-ventral snout, another just anterior to orbit. Dorsal and pectoral fins colorless, with chromatophores present along sides of individual rays.

MERISTIC VARIATION.—There is little variation in the number of trunk rings. There is some indication that the Chilean population is characterized by having 18 trunk rings and the Peruvian by 17.

There is a greater variation in the number of tail rings. The range for Peruvian fish is usually 40–42, whereas the counts of the Chilean fish are fairly stable at 42.

The increase in number of rings with higher latitudes is not found in the count of dorsal rays. The Peruvian fish have 40–42 dorsal rays, whereas those from Chile have 39–40, if the fish from Hornitos and Valparaíso, Chile, are exluded.

COMPARISONS.—*S. macrobrachium* is very close to *S. carinatus* and *S. folletti* of the western Atlantic. It differs from *S. carinatus* in having a longer snout (1.6–1.8 rather than 1.8–2.0 in head), coloration dark rather than lighter gray, and a longer pectoral fin (extending posteriorly over two full rings rather than one to one and one-half). It differs from *S. folletti* in having longer pectoral fins, 36–44 dorsal rays rather than 37–38, and in having a longer head (6.6–8.2 in SL rather than 8.2–9.9).

RANGE.—Tumbes, Peru, south to Puerto Montt, Chile.

ETYMOLOGY.—From the Greek *makros*—long, and *brachion*—arm, in reference to the long pectoral fin.

MATERIAL EXAMINED.—**Holotype:** USNM 176501, 1(225), a mature male collected at Huasco, Chile (28°28′S, 71°14′W), on 9–10 Oct. 1844, by M. J. Lobell.

Paratypes: UCLA W59-49, 1(153), night light off Punta Berejo, Peru (10°34′S, 77°56′W), 16 Sep. 1959, by J. Seapin. SIO 72-168, 2(177–190), off Hornitos, Chile, 5 m, otter trawl, 27 Apr. 1972, by local fishermen aboard the LUZ III. USNM 213485, 4(193–255), collected with holotype. UCLA W58-116, 3(92–103), bait net off Ilo, Peru (17°38′S, 71°18′W), 15 Dec. 1957, by J. Seapin. IMARPE uncat., 2(122–186), Zona de Lima, Peru, July 1973, by K. Freyman. IMARPE uncat., 10(123–161), Cantolao la Punta, Peru, 27 Apr. 1964, by B. M. Vildoso. EBMCh 10108–10109, 2(96–111), Iquique, Chile, Dec. 1957.

ADDITIONAL MATERIAL: **Peru:** Cabo Blanco, UCLA W59-46, 3(52–60). Callao, UCLA W59-48, 7(74–89). Lima, CAS 45073, 4(116–176). Bahía Chilca, USNM 127856, 3(89–175); USNM 127855, 1(107).

Chile: Valparaíso, CAS 12017, 1(126).

Syngnathus euchrous n.sp.

Syngnathus californiensis californiensis (in part, not of Storer); HERALD 1940:64; 1941:62.

DIAGNOSIS.—A *Syngnathus* with 33–45 dorsal rays; 11–14 pectoral rays; 3 anal rays; 18–20 trunk rings; 41–49 tail rings; 60–68 total rings; dorsal on 0.2–1.5 + 6–9 rings; brood pouch covering 20–23 rings; head 8.3–11.2 in SL; dorsal fin base 0.8–1.3 in head; snout 1.8–2.5 in head.

DESCRIPTION.—All ridges of body smooth to slightly rugose. Nuchal and prenuchal ridges low to obsolete. Opercle strongly convex, with weak ridge restricted to anterior fourth of opercle. Snout ridge development different in the two subspecies. Supraorbital ridge reduced. Interorbital flat to slightly concave. Pectoral cover plate with superior ridge obsolete to absent. Lateral trunk ridge ending on last trunk or first tail ring. Lateral line papillae 5–8 per plate. No dermal flaps.

Protecting plates of brood pouch varying from about one-third as high to about as high as adjacent tail. Eggs 1.2 mm in greatest diameter, arranged in 2–4 layers 4–6 across. Males with eggs and young collected from February through August.

COMPARISONS.—*S. euchrous* is most closely related to *S. leptorhynchus* from which it can be distinguished by the characters given in the key.

ETYMOLOGY.—From the Greek *eu*—well, and *chroa*—the color of the skin, in reference to the well-marked coloration.

Key to the Subspecies of *Syngnathus euchrous*

1a. Dorsal rays usually 39–42; tail rings usually 45–46; 21–23 rings covered by brood pouch .... *euchrous*
Redondo Beach, California to Punta Eugenia, Baja California

1b. Dorsal rays usually 36–38; tail rings usually 42–44; 20–21 rings covered by brood pouch. .... *ollotropis* n.subsp.
Bahía Tortugas to Bahía de Ballenas, Baja California

Syngnathus euchrous euchrous

(Figure 12*A*)

DIAGNOSIS.—An *S. euchrous* with 38–45 (39–42) dorsal rays; 11–14 pectoral rays; 3 anal rays; 18–20 (19) trunk rings; 42–49 (45–46) tail rings; 61–68 total rings; snout ridge concave in outline, smooth; maximum known size 296 mm SL; smallest sexually mature male 128 mm SL. See Tables 4, 5, and 6 for additional counts and measurements.

Coloration in life. From C. L. Hubbs's field notes for SIO H47-43:

> Four are rich brown, grading from greenish brown to reddish brown with very conspicuous pearly cross-blotching. There are a variable number of blue-white specks. The crown and nape regions are more or less completely covered with fine to coarse speckles. Along the ventrolateral keel there are single to compound specks on the plates . . . . The opercles are flecked with silver-blue and a more or less distinct wedge of the same color extends downward and backward from eye. The dorsal fin is entirely or almost entirely immaculate.

Coloration in alcohol. As is true with most species of *Syngnathus,* excessive variability precludes using color patterns as diagnostic features. A dusky patch or streak below the nares. A series of small whitish spots over the entire dorsal surface of head and body, often extending onto sides. Protecting plates of brood pouch chocolate-brown. Caudal brownish with white on tips of outermost rays. Dorsal and pectoral fins translucent, with some pigmentation along rays.

HABITAT.—Near bottom off rocky shores.

RANGE.—Redondo Beach, California, south to Punta Eugenia, Baja California.

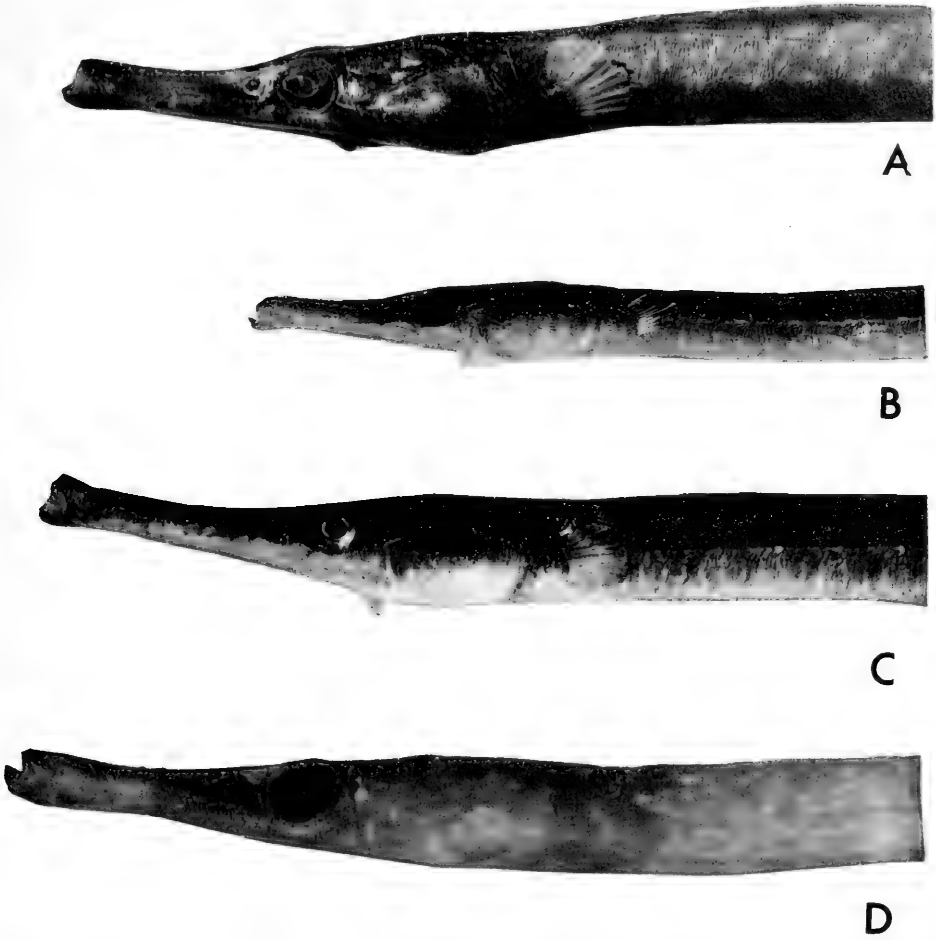


FIGURE 12. Anterior part of body of four species of eastern Pacific Syngnathidae. (*A*) *Syngnathus euchrous,* holotype, SIO H47-68. (*B*) *Syngnathus euchrous ollotropis,* holotype, SIO H48-53. (*C*) *Syngnathus leptorhynchus,* a 166-mm-SL male, SIO 63-1053. (*D*) *Syngnathus insulae,* holotype, SIO 63-169.

MATERIAL EXAMINED.—**Holotype:** SIO H47-68, a 232-mm-SL mature male collected at Bahía Todos Santos, Baja California (31°52′N, 116°38′W), with a 25-ft (7.6-m) beach seine at a depth of 0.3–1.5 m on 22 May 1947, by Carl L. and Laura C. Hubbs.

Paratypes: SIO H47-68, 86(83–228), same data as holotype. SIO H48-319, 16(95–204), E side of southern Isla Coronado, Baja California, dredge, 11 m, 22 Dec. 1948, by Clark Hubbs and party aboard M/V ORCA. GCRL 15757, 22(96–175), Scripps Pier, La Jolla, California, dip net under night light, 17 Aug. 1947, by J. L. McHugh. CAS 27405, 11(39–186), Estero de Punta Banda, Baja California, 8 Sep. 1949, by Chaffy, Scott, and Mead.

ADDITIONAL MATERIAL.—**California:** Redondo Pier, SIO H48-204, 1(225). Scripps Pier, SIO H46-63, 20(54–179). La Jolla Shores, SIO H50-214, 2(175–249); SIO H50-227, 5(119–139).

Baja California: Islas Coronados, SIO H49-217, 17(142–224); SIO H49-19, 15(152–223); SIO H46-125, 4(86–118); SIO H46-119, 11(132–222); SIO H48-217, 14(107–238). Bahía de Todos Santos, SIO H45-223a, 4(111–213); SIO H51-48, 5(99–130). Bahía Blanca, SIO 60-327, 5(162–203). Isla Cedros, SIO 53-110, 6(123–186); SIO 68-280, 1(113).

INTERGRADES with *S. e. ollotropis*: Punta Malarrimo, UCLA W51-223, 6(61–223); UCLA W51-221, 12(76–149).

Syngnathus euchrous ollotropis n.subsp.

(Figure 12*B*)

DIAGNOSIS.—An *S. euchrous* with 33–40 (36–38) dorsal rays; 11–13 pectoral rays; 3 anal rays; 18–20 (19) trunk rings; 41–45 (43) tail rings; 60–65 total rings; snout ridge well developed from vomer to anterior third of orbit, rugose, typically without distinct rise anterior to orbit; maximum known size 224 mm SL; smallest sexually mature male 102 mm SL. See Tables 5 and 6 for additional counts and measurements.

DESCRIPTION.—Young. 14–16 mm SL at birth. All fins developed and with rays. Rings without prominent spines but distinct triangular ridges. Uniform orange-tan with middle rays of caudal fin more darkly pigmented than outer. Dorsal and pectoral fins colorless. Anal fin darkly pigmented.

Coloration in life. From C. L. Hubbs's field notes for SIO H48-53:

> The lower part of opercles dark and mottled . . . . Streaked color phase frequent and light bars usually faint and seldom well developed . . . the lower parts are almost always marked with dark and usually variegated rather than being clear. In general the color pattern is more longitudinal and less transverse. In some specimens the lower keel carries a series of light blotches one per segment or may be largely clear. The general color varies from light tan to very deep purple-brown, almost black. The prominent marking of the lower surface is perhaps the most outstanding color feature.

Coloration in alcohol. Typically brownish above and light below, becoming entirely brownish on posterior third of body. Dorsal fin hyaline. Anal and pectoral rays bordered by melanophores. Often a dark midventral stripe on trunk. A chocolate-brown band on trunk between lateral trunk ridge and superior tail ridge. Caudal with light and dark reticulations. A reticulated area around orbit and on snout. Most often an orange-brown body with longitudinal lighter streaks.

HABITAT.—Eelgrass beds and drifting algae.

COMPARISONS.—*S. e. euchrous* is easily distinguishable from *S. e. ollotropis* by the characters given in the key. There is, however, a zone of intergradation along the coast near Punta Malarrimo. The specimens examined from there are intermediate in meristic characters between the two subspecies (Table 6). Although these intergrades are closer to *S. e. euchrous* in the ranges of these meristic characters, they have the distinctive straight snout ridge characteristic of *S. e. ollotropis*.

The semi-isolation of *S. e. ollotropis* in Turtle Bay has produced a distinctive morphology which would have to be considered specifically distinct had not the intergrades been collected.

The existence of definite intergrades between *S. e. euchrous* and *S. e. ollotropis* is concrete indication that subspecific recognition is warranted.

RANGE.—Bahía Tortugas south to Bahía de Ballenas, and Isla Cedros, Baja California.

MATERIAL EXAMINED.—**Holotype:** SIO H48-53, a 224-mm-SL mature male collected ¾ mile [1.2 km] E of Cabo Tortolo, Bahía Tortugas, Baja California (27°38′53″N, 114°51′46″W), from eelgrass at a depth of 1 m, with an 8-ft [2.4-m] minnow seine, 8 Feb. 1948, by Clark and Earl L. Hubbs.

Paratypes: All collected in Baja California. SIO H48-53, 35(43–220), same data as holotype. SIO H48-55, 47(66–216), same locality as holotype, 1.5 m, 25-ft [7.6-m] bag seine, 9 Feb. 1948, by Clark and Earl Hubbs. GCRL 15758, 15(61–158), same locality, 1 m, 25-ft [7.6 m] bag seine, 7 Feb. 1948, by Clark and Earl Hubbs. SIO H47-112, 1(207), Bahía Tortugas, from drifting brown algae, 23 May 1947, by Robert S. Arthur. SIO 54-131, 1(139), SE part of Bahía Tortugas, shell dredge, R/V ORCA, 18 July 1954, by J. W. Sefton, Jr. SU 19260, 1(144), off Isla Cedros, 27 Mar. 1952, by James E. Böhlke and party, Sefton-Stanford ORCA Expedition.

ADDITIONAL MATERIAL.—Bahía Tortugas, CAS 5438-5440, 3(104–112). Bahía de Ballenas, SIO 64-847, 1(135).

Syngnathus leptorhynchus Girard

(Figures 12*C*, 13, 14)

Syngnathus brevirostris GIRARD, 1854:156 (original description; San Diego, California; cotypes USNM 969; nec *S. brevirostris* Rüppell, 1840).

Syngnathus leptorhynchus GIRARD, 1854 (Oct. 6):156 (original description; San Diego, California; holotype USNM 970, lost); JORDAN AND EVERMANN 1896:764 (description; range; synonymy); JORDAN AND GILBERT 1880:23 (synonymy); STARKS AND MORRIS 1907:184 (habits; range); HUBBS 1916:158 (description); 1921:1 (synonymy; description); ULREY AND GREELEY 1928:42 (synonymy; range); ULREY 1929:6 (listed); JORDAN, EVERMANN, AND CLARK 1930:240 (synonymy; range); BARNHART 1936:34 (description); MILLER AND LEA 1972:87 (description; range).

Syngnathus californiensis leptorhynchus; HERALD 1940:64 (new combination; diagnosed in key); 1941:66 (description; range; synonymy).

Siphostoma leptorhynchus; JORDAN AND GILBERT 1881:453 (synonymy); JORDAN AND JOUY 1881:1 (*S. dimidiatus* as synonym); JORDAN AND GILBERT 1882:69 (range); SWAIN AND MEEK 1884:238 (key); JORDAN AND GILBERT 1883:384 (description; range; synonymy).

Siphostoma leptorhynchum; SWAIN 1882:311 (synonymy; description).

Syngnathus griseolineatus AYRES, 1854 (Oct. 27):14 (original description; probably near San Francisco, California; holotype ANSP 835); STARKS 1911:177 (breeding habits); HUBBS 1916:159 (measurements; compared with *S. barbarae*); 1921:1 (counts and measurements); JORDAN, EVERMANN, AND CLARK 1930:240 (range).

Syngnathus californiensis griseolineatus; HERALD 1940:64 (diagnosed in key); 1941:65 (description; range; synonymy).

Siphostoma griseolineatum; SWAIN 1882:308, 310, 315 (key; synonymy; description); SWAIN AND MEEK 1884:238 (key); KERMODE 1909:83 (British Columbia); EVERMANN AND LATIMER 1910:136 (Tomales Bay, California); KERMODE 1929:24 (Victoria, British Columbia); 1930:22 (Longborough Inlet, British Columbia); JORDAN AND EVERMANN 1896:764 (description; range; synonymy).

Syngnathus abbotti GIRARD, 1859:346 (original description; San Francisco, California; holotype USNM 971).

Syngnathus arundinaceus GIRARD, 1859:346 (original description; coast of California; holotype USNM 972); JORDAN, EVERMANN, AND CLARK, 1930:240 (range).

Syngnathus dimidiatus GILL, 1863:284 (replacement name for *Syngnathus brevirostris* Girard, preoccupied).

Siphostoma bairdianum (not of Duméril) SWAIN, 1882:311 (description; Santa Barbara, California).

Siphostoma barbarae SWAIN *in* SWAIN AND MEEK, 1884:238 (based on specimen described by Swain (1882) as *S. bairdianum*; holotype USNM 31253); JORDAN AND EVERMANN 1896:765 (description; synonymy; range).

Syngnathus barbarae: STARKS AND MORRIS 1907:185 (Santa Barbara); HUBBS 1916:159 (description); ULREY AND GREELEY 1928:42 (synonymy; range); JORDAN, EVERMANN, AND CLARK 1930:240 (range).

Syngnathus californiensis (in part, not of Storer): FOWLER 1921:443 (description); STARKS 1911:177 (Puget Sound).

DIAGNOSIS.—A *Syngnathus* with 28–43 dorsal rays; 11–13 pectoral rays; 2–3 anal rays; 16–21 trunk rings; 36–46 tail rings; 53–63 total rings; dorsal on 0–1.5 + 6–9 rings; brood pouch covering 18–26 rings; head 5.6–9.3 in SL; dorsal fin base 0.9–1.3 in head; snout 1.6–2.4 in head; maximum known size 299 mm SL; smallest mature male 80 mm SL. See Tables 4, 5, 7, and 8 for additional counts and measurements.

DESCRIPTION.—All ridges of head and body moderately developed, rounded, and rather smooth to slightly rugose. Nuchal and prenuchal ridges low. Supraoccipital ridge obsolete and not continuous with nuchal ridge. Opercular ridge extends posteriorly about one-third length of opercle. Snout ridge smooth, low, with small hump over nares. Superior ridge of pectoral cover plate smooth, curved; inferior ridge obsolescent to absent. Supraorbital ridges smooth. Northern populations tend to have more obsolescent ridges. Trunk and tail ridges slightly rugose. Superior tail and lateral trunk ridges usually not overlapping; when overlapping, only for length of last trunk ring. Scutella of medium size, subequal to half depth of adjoining plates. Lateral line consisting of 6–9 papillae per plate. No dermal flaps.

Protecting plates of brood pouch moderately developed and as much as two-thirds as deep as attached tail ring; edges of brood pouch folds entire. Eggs 1.3–1.5 mm in greatest diameter, arranged in 1–2 layers 4 across. Males with eggs and young collected year round.

Fins moderately developed. Caudal as long as last three tail rings. Pectoral fin extends posteriorly over about 1⅓ rings.

TABLE 6. MERISTIC VARIATION IN *Syngnathus euchrous*.

Subspecies and locality	Trunk rings			Tail rings									Dorsal rays												
	18	19	20	41	42	43	44	45	46	47	48	49	33	34	35	36	37	38	39	40	41	42	43	44	45
S. e. euchrous																									
La Jolla	9	16	2	—	1	—	1	2	13	7	1	2	—	—	—	—	—	—	1	2	3	5	3	6	2
Coronados Is.	—	14	11	—	—	—	—	7	9	3	3	—	—	—	—	—	—	3	10	8	—	2	1	—	2
Todos Santos	8	7*	4	—	—	1	2	6	8	1*	1	—	—	—	—	—	—	2	5	4	2	3*	2	—	—
Blanca Bay	3	2	—	—	—	—	—	2	2	1	—	—	—	—	—	—	—	1	—	—	2	—	2	—	—
Cedros Island	4	4	—	—	—	—	4	3	—	—	1	—	—	—	—	—	—	—	—	2	—	4	1	—	1
Intergrades																									
Puerto Malarrimo	5	6	—	—	1	3	3	3	1	—	—	—	—	—	—	—	2	2	2	—	4	—	—	—	—
S. e. ollotropis																									
Turtle Bay	10	84**	8	5	25	40	27**	3	—	—	—	—	1	9	10	24	22**	21	12	2	—	—	—	—	—

* Holotype of *S. e. euchrous*.

** Holotype of *S. e. ollotropis*.

Table 7. Meristic Variation in *Syngnathus leptorhynchus*.

	Trunk rings						Tail rings										
Locality	16	17	18	19	20	21	36	37	38	39	40	41	42	43	44	45	46
Vancouver Is.	—	—	11	17	—	—	—	—	—	—	3	8	8	4	2	—	—
Puget Sound	—	5	21	4	—	—	—	—	—	—	2	10	12	7	—	—	—
Coos Bay	—	1	51	9	1	—	—	—	—	—	—	4	12	14	27	3	—
Humboldt Bay	—	3	64	19	1	—	—	—	—	—	—	4	28	28	21	6	—
Tomales Bay	—	2	31	4	—	—	—	—	—	—	7	11	16	3	—	—	—
San Francisco Bay	—	2	10	190*	52	1	—	—	—	—	—	3	32*	109	107	20	1
Morro Bay	—	1	35	3	1	—	1	1	10	15	10	3	—	—	—	—	—
Pt. Mugu Lagoon	—	—	14	—	—	—	—	—	1	4	6	3	—	—	—	—	—
Santa Barbara	—	—	1†	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Newport Bay	—	2	17	11	—	—	—	—	1	2	7	5	11	3	—	—	—
Mission Bay	3	91	144	9	—	—	4	19	61	74	64	21	3	—	—	—	—
San Diego Bay	1	14**	9**	1	—	—	—	2	12	9**	2	—	—	—	—	—	—
Estero de Punta Banda	2	12	5	—	—	—	—	4	8	4	—	1	1	—	—	—	—
Bahía San Quintín	—	10	29	—	—	—	6	14	15	3	1	—	—	—	—	—	—
Scammon Lagoon	3	3	1	—	—	—	—	1	1	1	2	2	—	—	—	—	—
Total	9	146	443	267	55	1	11	41	109	112	104	75	123	168	157	29	1
			$\bar{x} = 18.2 \pm 0.8$									$\bar{x} = 41.2 \pm 2.3$					

	Dorsal rays															
Locality	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Vancouver Is.	—	—	—	—	—	—	2	1	6	4	7	3	1	1	1	—
Puget Sound	—	—	—	—	—	—	2	3	8	7	4	2	2	—	—	—
Coos Bay	—	—	—	—	—	—	—	—	5	4	16	14	10	8	2	—
Humboldt Bay	—	—	—	—	—	—	—	—	7	9	12	17	14	12	8	2
Tomales Bay	—	—	—	—	—	—	—	1	4	9	11	3	4	1	2	—
San Francisco Bay	—	—	—	—	—	—	1	9	31	55	61*	60	25	8	1	—
Morro Bay	—	—	—	—	3	5	10	10	6	5	—	—	—	—	—	—
Pt. Mugu Lagoon	—	—	—	—	2	2	2	5	2	1	—	—	—	—	—	—
Santa Barbara	—	—	—	—	—	—	—	—	1†	—	—	—	—	—	—	—
Newport Bay	—	—	—	—	3	5	6	6	7	3	1	—	—	—	—	—
Mission Bay	2	15	26	38	53	51	37	18	6	1	—	—	—	—	—	—
San Diego Bay	—	—	5	3	8	6	2	1**	—	—	—	—	—	—	—	—
Estero de Punta Banda	2	2	7	5	3	—	—	—	—	—	—	—	—	—	—	—
Bahía San Quintín	—	—	—	4	14	7	8	3	2	—	1	—	—	—	—	—
Scammon Lagoon	—	1	1	—	1	—	3	1	—	—	—	—	—	—	—	—
Total	4	18	39	50	87	76	73	58	85	98	113	99	56	30	14	2
								$\bar{x} = 35.8 \pm 3.3$								

* Holotype of *S. barbarae*.

† Holotype of *S. abbotti*.

** Syntypes of *S. brevirostris*.

Coloration in life. Mostly browns, purples, and greens, with varying amounts of mottling, spots, etc.

Coloration in alcohol. Coloration highly variable, mainly shades of brown. Great inter- and intra-population variability. Highly mottled, blotched, and striped. Dorsal fin always with some brownish spots at base and fin rays bordered with melanophores.

Habitat.—Ordinarily inhabiting eelgrass in bays and occasionally near shore outside.

Variation and Growth.—Variation: *Syngnathus leptorhynchus* shows extreme variation in meristic characters (see Table 7) approaching the North Atlantic species *S. typhle* in this regard. Duncker (1908) statistically analyzed several meristic characters of *S. typhle* populations from the Baltic Sea, Plymouth, and Naples and showed a definite clinal pattern in the variation of numbers of trunk rings and pectoral rays. Other meristic features showed populational differences, but in a mosaic pattern of different sequences.

Meristic variation in *S. leptorhynchus* is mosaic, and no single character allows or justifies recognition of more than one species or subspecies. Herald (1940, 1941) and others have used the same meristic characters herein analyzed in support of recognizing northern and southern species or subspecies. A mosaic pattern of variation is not limited to *Syngnathus* species, e.g., Rosenblatt (1963) reported a similar pattern for populations of the Central American tripterygiid *Enneanectes sexmaculatus*.

Each bay along the west coast of North America appears, on the basis of available evidence, to support a distinctive population of *S. leptorhynchus*. Meristic features of each population are not stable, but do fluctuate with changes in environmental temperature.

To underscore this point, C. L. Hubbs analyzed three collections from the northwest corner of Mission Bay on 22–24 April 1923. All three collections were made with exactly the same method (seine) and at the same location in the bay. For analysis, all specimens 97 mm SL or less are considered to be winter reared, and in view of the demonstrated growth (see below) it may be presumed that all specimens longer than 97 mm SL were at least mostly reared in warmer water. The summary of meristic data (Table 8) compiled for these collections indicates that the winter-reared young have higher means in all meristic characters studied than do the larger (adult) fish. The means for these two size groups are all significantly different ($P \ll .005$).

Although Mission Bay has been highly modified in recent years, the data are indicative of changes in meristic characters as a result of environmental temperature. Similar seasonal meristic variation has been documented by Brothers (1975) for the goby *Quietula y-cauda*—using samples taken throughout the year, he determined that the mean vertebral number of the postlarvae is inversely correlated with seasonal changes in environmental temperature.

Each local population of *Syngnathus leptorhynchus* is therefore distinctive and also highly modified by local environmental conditions. *S.*

TABLE 8. SEASONAL VARIATION IN MERISTIC CHARACTERS OF *Syngnathus leptorhynchus*.

	Trunk rings							Tail rings										
	17	18	19	N	$\bar{x}$	SD	t	36	37	38	39	40	41	42	N	$\bar{x}$	SD	t
Young	25	84	8	117	17.8	0.51	10.75			10	34	52	18	3	117	39.7	0.91	10.15
Adults	54	53	1	111	17.5	0.57		3	15	42	36	11	3		110	38.4	1.02	

	Total rings												Dorsal rays												
	53	54	55	56	57	58	59	60	N	$\bar{x}$	SD	t	29	30	31	32	33	34	35	36	37	N	$\bar{x}$	SD	t
Young			2	13	41	39	18	4	117	57.6	1.04	10.75	2	4	8	24	29	27	16	6	1	117	33.2	1.55	7.80
Adults	3	10	31	36	16	11	3		110	55.9	1.29		8	20	25	25	21	10	2			111	31.6	1.47	

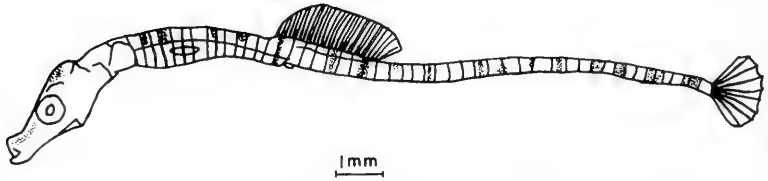


FIGURE 13. *Syngnathus leptorhynchus* at time of emergence from brood pouch. 16.3 mm SL.

leptorhynchus may be a useful indicator species for the effects of pollution.

Growth: On 16 June 1974, a male *S. leptorhynchus* (165 mm SL) gave birth to 85 young in the laboratory of the National Marine Fisheries Service, La Jolla. The young were immediately separated from their father and kept alive until a failure in the seawater system on 6 Sep. The young were fed *Artemia* nauplii and fresh-caught plankton. An overabundance of food was always present. Samples of the young were removed frequently during the period from 16 June to 6 Sep. and preserved in 10% formalin for later analysis.

Figure 14 represents the measured growth of the young for the period. The data have been analyzed and fitted to a Laird-Gompertz equation (Laird, Barton, and Tyler 1968) calculated after the methods of Zweifel and Lasker (1976). The Laird-Gompertz equation is preferred when analyzing growth for periods less than one year.

On 16 Aug. development of the brood pouch had already begun in a 76-mm-SL individual. Four males (80–93 mm SL), each with a fully developed brood pouch, were found on 24 Aug. By the termination of the experiment on 6 Sep., the largest specimen was a fully-mature, 114-mm male.

That the ranges of meristic variation for the adults do not completely subtend the ranges for the young together with rapid growth to sexual maturity strongly indicate that individuals of *S. leptorhynchus* (at least from Mission Bay) probably live for only one year. This is in agreement with the data presented by Brown (1972) for *S. louisianae, S. scovelli, S. floridae,* and *Micrognathus crinigerus* for Cedar Key, Florida. Based on length-frequency analyses, Brown estimated a life span of perhaps one year.

COMPARISONS.—A highly variable species that is similar to the Japanese *S. schlegeli.* In fact, it is rather difficult to separate members of northern populations of *leptorhynchus* from those of *schlegeli.* However, *S. schlegeli* has a longer snout and longer fins, and the ridges of the body are better developed. *S. insulae,* also closely related to *S. leptorhynchus,* may be distinguished by the characters given in the account of that species.

RANGE.—Southeastern Alaska south to Bahía Santa María, southern Baja California.

MATERIAL EXAMINED.—**Alaska:** UW 14486, 1(179); UW 1610, 1(212).

British Columbia: Vancouver, BC 53-253a, 28(60–206); SIO 62-206, 2(137–192).

Washington: Puget Sound, CAS 10935, 3(125–140); UW 4927, 3(136–151); UW 5296, 2(146–245); UW 4258, 3(86–130); UW 4918, 4(139–167); SIO 74-73, 19(73–215).

Oregon: Tillamook, UMMZ 93951, 33(49–235). Coos Bay, UMMZ 93956, 63(35–235).

California: Klamath Lagoon, CAS 45070, 1(216). Humboldt Bay, HSU OT62-7, 44(136–207); HSU OT61-18, 14(121–218); HSU OT64-5, 12(110–210). Mendocino County, SU 20515, 5(165–214). Tomales Bay, SIO 75-459, 37(54–234); UCLA W55-198, 35(61–207); CAS 19860, 2(211–293); CAS 26207, 2(104–252). Drakes Bay, CAS 7518, 1(130). San Pablo Bay, CAS 45072, 33(59–272). San Francisco Bay, SU 4190, 24(115–159); USNM 971, 1(228), holotype of *S. arundinaceus*; UMMZ 64416, 1(215); UMMZ 6044, 1(151); CAS ALBATROSS Biological Survey of San Francisco Bay*, D5826, 1(131); H5159, 2(139–165); D5816, 1(129); H5311, 1(119); H5013, 4(111–184); D5847, 1(92); H5003, 1(87–121); H5318, 2(110–128); H5185, 1(61); D5848, 2(101–118); H5312, 2(66–94); H5004, 2(77–110); H5308, 1(67); H5230, 1(62); H5248, 1(64); H5259, 1(61); H5310, 1(80); H5316, 2(69–98); H5309, 2(106–120); H5250, 7(51–123); H5009, 9(33–109); H5257, 1(86); H5261, 2(41–43); H5345, 13(25–133); H5313, 6(69–93); H5251, 6(73–125); H5010, 2(33–66); H5005, 3(44–69); H5275, 3(38–70); H5315, 5(63–113); H5252, 5(62–95); H5317, 4(76–103); H5311, 8(75–90); H5274, 8(67–77); H5007, 11(28–108); H5314, 13(67–105); H5272, 17(64–146); H5276, 25(49–130); H5006, 76(27–116). Elkhorn Slough, SIO 62-510, 3(77–103). Del Monte, SIO 48-372, 2(92–196). Morro Bay, SIO H50-191, 1(243); UCLA W50-196, 50(98–236); SU 48888, 10(162–217). Point Mugu, CAS 45076, from E. S. Herald personal collection, 4(151–181). Santa Barbara, USNM 31253, type of *S. barbarae.* San Pedro, SIO H48-180, 1(257). Newport Bay, UCLA W50-171, 50(99–278); UCLA W50-172, 3(101–132); SIO H46-33, 5(215–280). San Juan Capistrano, SIO H52-109, 1(101). Mission Bay, SIO H45-8, 50(72–198); SIO H46-10,

---

* Station data may be found in Anonymous 1921.

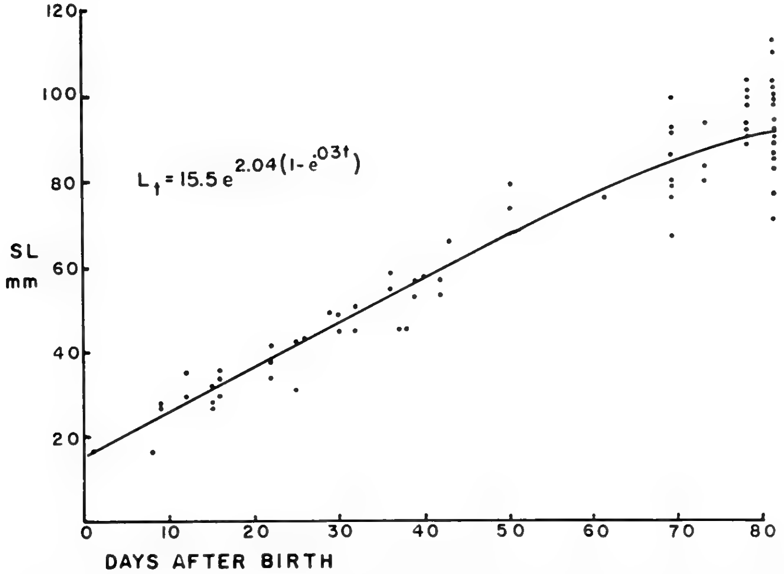


FIGURE 14. Growth of *Syngnathus leptorhynchus*. Standard length plotted against time in days. The Laird-Gompertz Equation fitted to these data is included.

3(116–125). San Diego Bay, USNM 969, 3, types of *S. brevirostris*; SIO 64-337, 25(100–158).

Baja California: Estero de Punta Banda, SIO H45-15, 19(104–158). Bahía San Quintín, SIO 60-453, 128(69–245); SIO 60-450, 6: SU 15251, 10(123–299). Laguna Scammon, SIO H52-140, 1(95). Bahía Santa María, SIO H50-149; SIO 60-294, 1(94).

Syngnathus insulae n.sp.

(Figure 12*D*)

DIAGNOSIS.—A *Syngnathus* with 31–34 (32–33) dorsal rays; 10–12 pectoral rays; 2–4 anal rays; 17–19 (18) trunk rings; 40–42 (41–42) tail rings; 58–60 total rings; dorsal on 0.2–1.2 + 6.5–8 rings; 19 rings covered by brood pouch; head 8.6–9.3 in SL; dorsal fin base 1.0 in head; snout 1.7–2.3 in head; maximum known size 204 mm SL; smallest sexually mature male 125 mm SL. See Tables 4 and 5 for additional measurements.

DESCRIPTION.—All ridges of head and body poorly developed, smooth. Prenuchal and nuchal crests obsolete. Opercular ridge reduced to short basal portion. Ridges of pectoral cover plate low. Trunk and tail ridges low, rounded but distinguishable. Superior tail ridge not reaching beyond first tail ring, only overlapping lateral trunk ridge for one-half ring. Scutella quite distinct and about half as deep as adjoining plate. Lateral line consisting of 5–6 papillae per plate. No dermal flaps.

Protecting plates of brood pouch well developed, each about as deep as adjacent tail ring; edges of brood pouch folds entire. Eggs 1.2–1.3 mm in greatest diameter, arranged in one layer two across. Males with eggs and young have been collected in April.

Fins normally developed. Caudal fin as long as last three tail rings. Pectoral fin reaches posteriorly to end of first trunk ring.

Young. About 12 mm SL at birth. About five dark bands posterior to vent. Body sprinkled with small round melanophores, especially in the area of the bands. Snout short, mouth distinctly upturned.

Coloration in life. From C. L. Hubbs's field notes for SIO H46-143:

> The greener specimen has a dark streak running downward and backward from eye. In this specimen the streak extending upward and backward from eye is less distinct. The streak running forward from eye to chin is conspicuous posteriorly but interrupted anteriorly. The redder specimen has a dark spot just behind and below eye, but no definite streaks radiating from eye.

Coloration in alcohol. A light tan to tan fish without any distinguishing pattern. The caudal fin may be lighter at its border. Darker specimens may have a sprinkling of small melanophores bordering rays.

HABITAT.—Occasionally in floating *Sargas-*

sum, but much more often taken at depths of 20–34 m in beds of *Sargassum* and algae.

COMPARISONS.—Appears most closely related to *S. leptorhynchus*. The two are very close in meristic characters. *S. leptorhynchus* has the longer snout and postorbital. *S. insulae* differs from *leptorhynchus* in the broader interorbital, smaller orbit, and less robust body.

RANGE.—Endemic to Isla Guadalupe, an oceanic island well off the coast of Baja California.

ETYMOLOGY.—From the Latin *insulae*, genitive of *insula* (island).

MATERIAL EXAMINED.—**Holotype:** SIO 63-169, a 160-mm-SL mature male collected at Caleta Malpómene, a cove at the south end of Isla Guadalupe, Mexico, from a depth of 22–50 m using a try-net on 22 Apr. 1963, by C. L. Hubbs and party aboard the R/V HORIZON.

Paratypes: All taken from Isla Guadalupe. SIO 63-169, 32(77–204), same data as holotype. SIO H46-143, 2(98–98.4), Caleta Melpómene, under nightlight, 6 Dec. 1946, by C. L. Hubbs aboard R/V E. W. SCRIPPS. SIO H46-144, 1(118), Caleta Melpómene, 3–6 m, dredge, 7 Dec. 1946, by C. L. Hubbs aboard R/V E. W. SCRIPPS. GCRL 15756, 2(93–117), Caleta Melpómene, under nightlight, 27 Jan. 1950, by C. L. Hubbs and party aboard R/V ORCA. SIO H50-31, 1(99), Caleta Melpómene, 3–7 m, dredge, 29 Jan. 1950, by C. L. Hubbs and party aboard R/V ORCA. SIO 54-214, 2(51–87), ⅛ mile [200 m] "off Barracks" (Northeast Anchorage), under nightlight, 13 Nov. 1964, by C. L. Hubbs and party. SIO 63-188, 1(116), just inside s side Punta Amarillo on rocky bottom, 15 m, Chemfish and SCUBA, 26 Apr. 1963, by J. R. Stewart and party.

FOSSIL SYNGNATHIDAE OF SOUTHERN CALIFORNIA

The following discussion of the fossil pipefishes of southern California is based on a large collection in the Section of Vertebrate Paleontology at the Natural History Museum of Los Angeles County (LACM), including the collections formerly housed at the California Institute of Technology (CIT).

The fossil syngnathids from southern California are all of Miocene to possibly Pliocene age. Most specimens have been collected in diatomites and diatomaceous siltstones of the upper Modelo and Puente formations, although a number have been collected from argillaceous diatomites of the lower Modelo Formation. Localities are given by number, and more precise data can be obtained by referring to the Locality Catalogue in the Vertebrate Paleontology Section (LACM).

These formations have provided the bulk of material used in the descriptions of California fossil fish (Jordan and Gilbert 1919; David 1943). Since most of the fishes contained in these deposits are pelagic to bathypelagic, previous authors have inferred that during the Miocene this area was a large basin with depths ranging from 200–500 m (David 1943) to 1000 m (Crane 1966).

Materials and Methods

The anal and pectoral fins of fossil pipefishes are usually not visible. Since the anal fin marks the first tail ring, it is impossible to make precise counts of trunk and tail rings. However, the number of plates in a ring around the trunk is usually seven and there are four around the tail. When these plates could be seen, accurate counts were made. When such counts were not determinable, the trunk rings were counted as ending at the first ring under the dorsal fin or the posterior end of the median ventral ridge (in *Hipposyngnathus*).

The count of dorsal fin rays in fossil pipefishes is difficult because of frequent splitting of the two ray-halves. However, with proper precaution, a fairly accurate count is often possible.

Accurate counts of the rings and dorsal rays are of particular importance in syngnathid taxonomy, as these counts provide the primary basis for classification of living forms.

Correct generic allotment of fossil syngnathid species is based primarily on the author's knowledge of the general appearance of syngnathid genera. The characters often used for placement of syngnathids into a genus (i.e., lateral ridge pattern, placement and position of brood pouch) are very rarely preserved in fossilized pipefishes.

This section on fossil pipefishes is intended only to describe those forms known to occur in deposits along the eastern Pacific and is not meant to be a critical review or stratigraphic analysis of them.

Subfamily **Hipposyngnathinae** nom. nov.

Eogastrophinae JERZMANSKA 1968:436 ("genre typique: *Hipposyngnathus* Danil'chenko 1960").

Since the subfamily name was incorrectly proposed as Eogastrophinae (the sole-included genus is *Hipposyngnathus*), and since subfamilial ranking is obviously called for, I propose the name Hipposyngnathinae, with *Hipposyngnathus* as the type-genus.

Jerzmanka diagnosed the subfamily adequate-

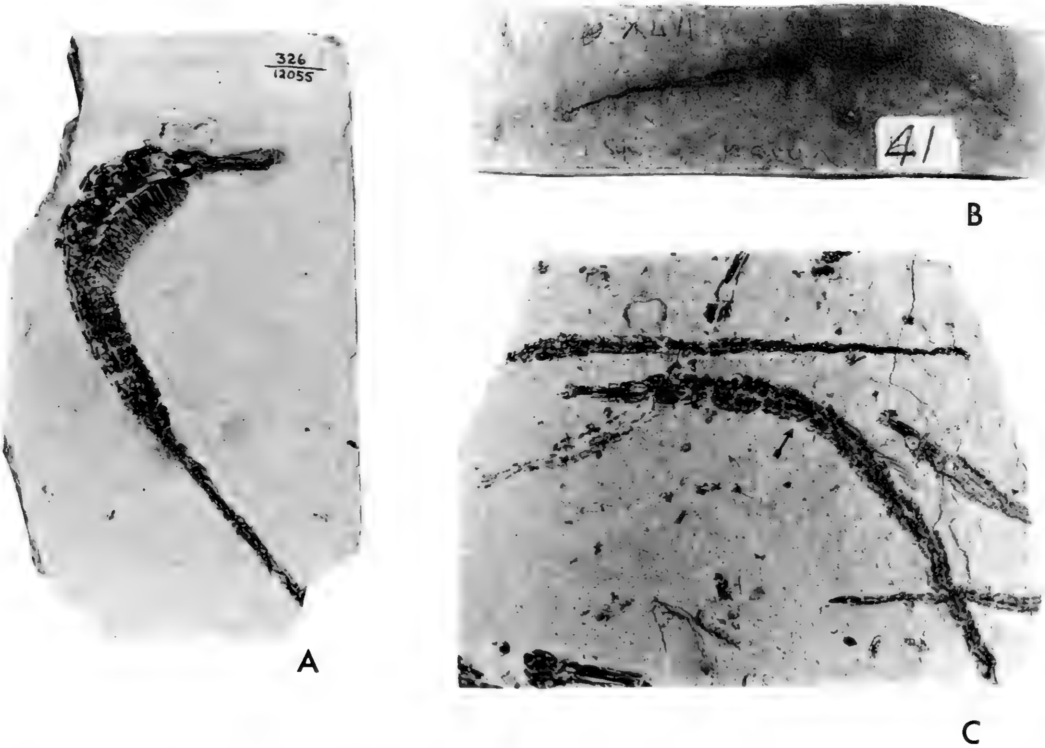


FIGURE 15. Holotypes of three species of California fossil syngnathids. (*A*) *Hipposyngnathus imporcitor,* LACM 12055. (*B*) *Syngnathus avus,* CAS Geology Dept. No. 58372. (*C*) *Syngnathus emeritus,* LACM 27445.

ly except that she incorrectly stated that scutella are absent.

Hipposyngnathus Danil'chenko

Hipposyngnathus DANIL'CHENKO, 1960:87 (type-species by original designation *H. convexus* Danil'chenko); JERZMANSKA 1968:436.

DIAGNOSIS.—Lateral protecting plates of brood pouch absent, however, a very pronounced median ventral trunk ridge probably indicates position of brood area. Dorsal, pectoral, and caudal fins present. Dorsal mainly on the tail. Ridges of body generally moderately developed and rugose, but without spines or serrations. Three described species from the Oligocene and Miocene.

DISTRIBUTION.—Oligocene of the Caucasus and Carpathian Mountains of southeastern Europe. Miocene of southern California.

Hipposyngnathus imporcitor n.sp.

(Figure 15*A*)

Syngnathus avus (in part, not of Jordan and Gilbert, 1919): DAVID 1943:70 (description).

Holotype: LACM 12055, an almost-complete specimen from the upper Modelo Formation of the northeast slope of Santa Monica Mountains, Los Angeles County, California (Locality LACM (CIT) 326).

REFERRED MATERIAL (all from California).—Upper Modelo Formation, NE slope Santa Monica Mountains, Los Angeles County, 24 identifiable specimens, 33 fragments, LACM loc. no. (CIT)326: LACM cat. nos. 10060–10061, 10063, 10114, 10134, 10143, 10145, 12054, 25341–25351; and LACM loc. no. 1267: LACM cat. nos. 13362–13373, 13451–13465, 13469–13473, 13475, 13477–13478, 25789–25791. Near Lompoc, LACM loc. no. 6589, 10 fragmentary specimens: LACM cat. nos. 12160–12169. Near Emery Park, Alhambra, Los Angeles County, LACM loc. nos. 1031, 1033, 14 specimens: LACM cat. nos. 1056–1058, 1349, 12459–12464, 25668. Dixie Canyon, Santa Barbara County, LACM loc. no. (CIT)329, 6 specimens: LACM cat. nos. 25357–25359, 25363–25365.

DIAGNOSIS.—A *Hipposyngnathus* from the upper Modelo Formation of southern California with about 22 dorsal rays; 20–22 trunk rings; 42–44 tail rings; snout 1.5–1.9 in head; orbit 7.8–12.0 in head; pouch rings equal to trunk rings; pectoral fin present but rays not countable; pouch ridge as long as adjacent trunk. Maximum size known 242 mm SL.

DESCRIPTION.—Body ridges moderately developed and rugose. Plates rhomboid-ovate with 10–13 ridgelets on either side of median ridge, large; each trunk plate about as wide as orbit. Opercular ridge smooth, about half as long as opercle. Snout without distinct ridge. Scutella small. Two infraorbitals. Vertebrae as in *Syngnathus*. Dorsal high, about 1.5 times higher than adjacent tail. Caudal normally developed.

DISCUSSION.—*H. imporcitor* is the most common syngnathid in the upper Modelo Formation. The extinct *Hipposyngnathus* was previously known from two European Oligocene species. *Hipposyngnathus imporcitor* can be easily distinguished from its congeners *H. neriticus* and *H. convexus* by the characters given in the diagnosis.

The genus *Hipposyngnathus* is unusual in having a very exaggerated ventral trunk ridge. Jerzmanska (1968) suggested that the males alone had this ridge and that it was the site of egg deposition. She also speculated that pouch flaps were present on either side of the ridge. However, the extant genus *Maroubra* also has an enlarged ventral trunk ridge, although not so well developed as in *Hipposyngnathus*, and its eggs are not protected by flaps. It seems improbable that *Hipposyngnathus* had brood-pouch flaps.

The Gastrophori are typically spiny with the exception of *Nerophis* and *Entelurus*. *Hipposyngnathus* is most like *Nerophis* in general body form.

PALEOECOLOGY.—Crane (1966) has discussed the paleoecology of *Chauliodus eximius*, a chauliodontid from the diatomite of the upper Modelo. Most of his specimens were from the same localities as those where *Hipposyngnathus* was collected. The upper Modelo is approximately 15 million years old (Crane 1966).

David (1943) discussed the paleoecology and climate of the upper Sisquoc Formation and the deposits at Lompoc. She concluded that the Lompoc deposits were younger and that the fishes found there were neritic and pelagic, and those of the upper Modelo more bathypelagic. Her conclusion that the fish fauna of the upper Modelo indicated a basin depth of 200–500 m is probably in error. Recent evidence (Crane 1966) supports the view that the basin was probably at least 1000 m in depth.

With the above evidence in mind, it seems most probable that *H. imporcitor* was a pelagic species, which may have accompanied floating algae, much as do the Recent species *Syngnathus pelagicus* and *S. californiensis*. This conclusion is supported by the evidence presented by Danil'chenko (1960) for the fishes of the Maikop basin. He showed that this basin was anoxic below a depth of 300 m, therefore *H. convexus* may be assumed to be a pelagic species.

ETYMOLOGY.—From the Latin *Imporcitor*—"a diety that presides over the drawing of furrows," in reference to the greatly expanded trunk ridge. To be treated as a noun in apposition and as of masculine gender.

Syngnathus Linnaeus

Syngnathus emeritus n.sp.

(Figure 15*C*)

Holotype: LACM 27445, an almost complete specimen from the Puente Formation near San Dimas, Los Angeles County, California (Locality LACM 7153).

REFERRED MATERIAL.—Puente Formation near San Dimas, Los Angeles County, California, LACM loc. nos. 5153, 7046, 14 specimens and fragments: LACM 26146–26148, 27431–27434, 27437–27440, 27446–27448.

DIAGNOSIS.—A *Syngnathus* with 43–47 dorsal rays; 10 caudal rays; pectoral rays not detectable; 14–15 trunk rings; 51 tail rings; snout 1.5–1.8 in head; orbit 5.8–8.7 in head; brood pouch not seen; largest specimen examined 181 mm SL.

DESCRIPTION.—Ridges of body smooth and generally not accentuated. Osteology basically the same as in extant species of *Syngnathus*. Plates small, width of trunk plate less than orbit diameter. Dorsal about as high as depth of adjacent body.

COMPARISONS.—*S. emeritus* is unusual in having 15 trunk rings combined with 51 tail rings. These characters and the number of dorsal rays distinguish it from *S. avus*.

The relationships of *S. emeritus* perhaps lie with the extant species *S. leptorhynchus* and *S. auliscus*. It is possible that *S. emeritus* was on the ancestral line leading to one or both of these species.

ETYMOLOGY.—From the Latin *emeritus*—honorably retired.

PALEOECOLOGY.—*S. emeritus* is found in the diatomaceous shale of the Puente Formation. Its habits probably were much like those of *S. avus*, i.e., living in relatively shallow water among marine vegetation.

Syngnathus avus (Jordan and Gilbert)

(Figure 15*B*)

Syngnathus avus JORDAN AND GILBERT, 1919:34 (Miocene chalk near Titus Avenue, Bairdstown, California, U.C. loc. no. 3525; type-specimen by original designation, SU XLIV, B of original description): JORDAN 1921:259 (reconstruction); DAVID 1943:70 (in part; description; synonymy).

Syngnathus californiensis avus: HERALD 1941:69 (description; discussion).

Holotype: CAS Geology Dept. no. 58372 (SU no. XLIV, B of original description), all fossil fish types and other Jordan paleoichthyological material is now in the Geology Department, California Academy of Sciences.

Paratypes: CAS Geology Dept. no. 58373 (SU no. V, also marked 115, A of original description); CAS Geology Dept. no. 58374 (SU no. 115A, C of original description).

REFERRED MATERIAL.—Lower Modelo Formation, Santa Monica Mountains, Los Angeles County, California, LACM loc. no. 1681, 15 specimens: LACM cat. nos. 11598–11605, 26438–26444.

DIAGNOSIS.—A *Syngnathus* with 36 dorsal rays; 10 caudal rays; 18 trunk rings; 43 tail rings; dorsal on 0.5 + 7.5 rings; pouch covering 22 rings; head 6.4–7.0 in SL; snout 1.7–1.8 in head; dorsal fin base 1.3 in head; maximum known size 225 mm SL.

DESCRIPTION.—Generally as given by Jordan and Gilbert (1919). Osteology of neurocranium same as that described for extant species of *Syngnathus* (Jungersen 1910). Opercles without median ridge.

DISCUSSION.—The type material is now in such poor condition that the characters as given by Jordan and Gilbert (1919) cannot accurately be determined. However, specimen No. 58373 (paratype) does have a brood pouch with protecting plates developed; they are not missing as stated by Herald (1941).

Syngnathus avus is a rather common member of the fossil fauna of the argillaceous diatomites of the lower Modelo Formation. The original field notes indicate that one slab measuring 4 by 4 ft [1.2 × 1.2 m] contained 42 specimens.

It must be pointed out that Figure 2 on Plate XXIX of Jordan and Gilbert (1919) is not of the type of *S. avus*. In fact, Jordan and Gilbert mistakenly included a figure of a fossil pipefish from Austria rather than the correct figure of *S. avus*. This mistake was pointed out by Duncker (1923) and was subsequently corrected by Jordan (1926, 1927).

DISTRIBUTION AND RELATIONSHIPS

The eastern Pacific syngnathids are generally distributed, with some exceptions, in commonly recognized zoogeographic provinces. Most of the pipefishes are found in bays and sloughs where the water temperature may be higher than along the adjacent open coast. As a result their distribution often extends past the higher-latitude, colder-water boundary established for the open-coast fauna. This kind of distribution is shown by other bay-dwelling fishes such as the blennies and gobies (distributions in Miller and Lea 1972). For example, *Hypsoblennius gentilis* ranges from the Gulf of California to Monterey, *Ilypnus gilberti* ranges from the Gulf of California to Tomales Bay, *Clevelandia ios* ranges from the Gulf of California to British Columbia, and *Quietula y-cauda* ranges from the Gulf of California to Morro Bay. *Syngnathus leptorhynchus* ranges from the outer coast of Baja California to southern Alaska. Thus, these bay-dwelling fishes cross the Point Conception faunal boundary (Briggs 1974).

There are more species of *Syngnathus* in the Northern Hemisphere than in the Southern Hemisphere. The close similarity of Japanese *Syngnathus schlegeli* to generalized members of two distinct eastern Pacific lineages supports the hypothesis that the eastern Pacific *Syngnathus* are derivable from two separate invasions from the northwest. An alternative hypothesis is invasion of Japan from the eastern Pacific followed by a reinvasion of the eastern Pacific. However, the first hypothesis appears to be the most parsimonious. One lineage consists of *S. carinatus*, *S. macrobrachium*, and *S. folletti*. The other consists of *S. leptorhynchus*, *S. euchrous*, and *S. insulae*. The related *S. californiensis* and *S. exilis* occupy a somewhat isolated position in the genus and may be the products of another radiation.

The problem of defining these lineages and relating them to *S. schlegeli* is one of not being able to determine plesiomorphic and apomorphic character states at the species level within the genus *Syngnathus*. Thus, overall similarities, including meristic characters and strength of ridge development, become the most important criteria used.

The *carinatus-macrobrachium-folletti* lineage is characterized by a relatively long snout; large, well-developed fins; large orbit; and rather well-developed ridges. The presence of *carinatus* in the upper Gulf of California and *macrobrachium* and *folletti* in South America parallels the distribution given by Chen (1975) for the *exsul-spinorbis* and *capensis* complexes of the subgenus *Sebastomus*. Chen speculated that these lineages probably shared a common ancestor that was able to both invade the Gulf and cross the tropics using the same climatic event. He was, however, unable to rule out multiple crossings. The lack of any close relative of *S. carinatus* along the outer coast of Baja California or California is puzzling and quite different from the *Sebastomus* example given above. It is possible that the *carinatus-macrobrachium-folletti* lineage may have had a southern origin, although more evidence is needed in support of this hypothesis.

The *leptorhynchus-euchrous-insulae* lineage is characterized by the medium-length snout, which is round in cross section, and an almost straight snout ridge which does not rise much anterior to the orbit. The restriction of this group essentially to Baja California northward is interpreted to mean that, assuming a more northern origin, this lineage is much more recent than the preceding one.

It is apparent that *S. leptorhynchus* has given rise to the Guadalupe Island endemic *S. insulae*, probably as a result of waif dispersal via the California Current.

Syngnathus leptorhynchus and *S. euchrous* probably share a common ancestor. The isolation of a population of *S. euchrous* in Turtle Bay has produced the subspecies *S. e. ollotropis*. Turtle Bay is unusually warm and the *Macrocystis pyrifera* found there has a different growth form than that along the coast (Neushul 1971). A zone of intergradation between *S. e. euchrous* and *S. e. ollotropis* exists at Puerto Malarrimo.

Syngnathus exilis and *S. californiensis* are characterized by an elongate, compressed snout, and rounded ridges. It is possible that they are related to the *carinatus-macrobrachium-folletti* lineage, but their relationships cannot be determined at this time.

The relationships of the fossil *S. avus* and *S. emeritus* are difficult to determine. It seems highly probable that *S. avus* is related to the generalized *S. leptorhynchus* based mainly on meristic characters. The low trunk ring and high tail ring counts of *S. emeritus* are unlike those seen in living eastern Pacific *Syngnathus* spp.

Syngnathus auliscus is the only truly tropical member of the genus *Syngnathus* in the eastern Pacific. The characteristic spination of young *S. auliscus* can also be seen in young *S. fuscus* from the northwestern Atlantic. This spination has also been reported (D'Ancona 1933) for the Mediterannean *S. agassizi* and *S. phlegon*. Spination in young *Syngnathus* may be indicative of a distinct lineage within the genus. A systematic study of the juveniles of *Syngnathus* spp. is definitely called for.

Syngnathus auliscus is not uncommonly taken in southern California. It is apparent that this species is little affected by the tropical-temperate transition between about Sebastián Vizcaíno Bay and Magdalena Bay. This distribution pattern is shown by other fishes such as *Paralabrax maculatofasciatus* (distribution in Miller and Lea 1972). However, in San Diego Bay the warm-water effluent produced by the San Diego Gas and Electric power plant provides an ideal environment for tropical species. As a result there is a large population of *S. auliscus* in San Diego Bay, and the typical California bay species *S. leptorhynchus* is now less abundant.

The genus *Bryx* is a circumtropical genus with only *B. arctus* and *B. heraldi* having temperate populations. There are eight species in the New World; one, *B. balli*, is in Hawaii, *B. banneri* is in the Indo-West Pacific, and *B. darrosanus* is in the Indian Ocean. The two subgenera, *Bryx* and *Simocampus*, were present before the closure of the Panamanian seaway in the late Pliocene to early Pleistocene (Woodring 1966), since the eastern Pacific and western Atlantic now have members of both subgenera.

The subgenus *Bryx* is composed of four species, two in the Atlantic and two in the Pacific Ocean. This subgenus is presumably derived from the subgenus *Simocampus* and is distinguished from it by the absence of the anal fin. The two species in each ocean are more closely related to each other than either is to the species in the other ocean. In fact the radiations in the two oceans have paralleled each other. The primary difference between the two species is the relative length of the snout.

Without a knowledge of the plesiomorphic condition with regard to meristic characters, it is impossible to speculate on the relationships within the subgenus *Simocampus*. However, the Juan Fernández endemic *B. heraldi* was probably derived from *B. coccineus* or their immediate common ancestor. This is unusual since the ichthyofauna on the Chilean islands of Juan Fernández and San Félix has a strong Indo-Pacific component (McCosker 1970, 1971). The eastern Pacific *B. arctus* and *B. coccineus* are more closely related to each other than either is to members of the genus in other oceans.

Doryrhamphus melanopleura is an Indo-Pacific species that has apparently invaded the eastern Pacific by crossing the East Pacific Barrier, since there are no members of this genus in the Atlantic, even though suitable habitat would seem to be available. The eastern Pacific populations of *D. melanopleura* differ in coloration from their Indo-West Pacific conspecifics. The Islas Revillagigedo endemic *D. paulus* has the same color pattern as the eastern Pacific *D. melanopleura* and was probably derived from mainland populations of *D. melanopleura*.

The genus *Leptonotus* is a southern cold-temperate group with species in South Australia (Munro 1958), New Zealand, and southern South America. This genus is represented in South America by *L. blainvilleanus*. The mechanism by which cold-temperate organisms have achieved a distribution spanning the South Pacific Ocean is currently under debate. Rosen (1974) has argued that the distribution of at least the freshwater galaxiids covers most of the components of the original Gondwanaland mass. Thus, the distribution of southern cold-temperate organisms reflects the break-up of Gondwanaland. However, the possibility of chance dispersal probably utilizing the eastward-flowing South Pacific current seems to be more likely for most marine fishes. This has been documented by McCosker (1970, 1971) for *Parapercis* and *Muraenichthys*. McCosker pointed out that most of the groups showing this particular distribution pattern are derived from Indo-West Pacific groups dispersing southward to southern Australia and New Zealand, and the subsequent movement eastward of cold-adapted forms across the cold-temperate South Pacific Ocean to Chile. Eschmeyer and Poss (1976) have shown that with some cooling during the Pleistocene, a number of near-surface sea mounts, reefs, and islands would have been available to eastward-moving temperate biota in the southern Pacific Ocean. Although they were dealing with the scorpionfish genus *Maxillicosta*, the effects of Pleistocene or earlier cooling would also facilitate dispersal of *Leptonotus*. The ability of marine fishes to cross oceanic barriers has been well documented (Rosenblatt et al. 1972). Pipefishes (e.g., *S. pelagicus*) are known to be borne great distances by the currents. It is therefore likely that the marine *L. blainvilleanus* was derived from an ancestor from the South Australia–New Zealand region by chance dispersal of waifs to South America.

The relationships of *Hippocampus* must await a revisionary study of the genus *Hippocampus*. Our knowledge of the genus *Hippocampus* is so poor that it is now impossible to determine the exact relationship of *H. ingens* to other members of the genus. Since the genus is circumtropical, it is at least pre-Tethyan in origin.

Hipposyngnathus has become extinct since the Tertiary. Because of our almost complete ignorance of the relationships between genera of living syngnathids, it is impossible to relate *Hipposyngnathus* to living genera. The reason or reasons for the extinction of this genus remain unknown.

BRANCHIAL SKELETON

Previous investigators (Duncker 1910, 1912; and Herald 1959) have used the position and development of the male brood pouch as the diagnostic character when defining genera and subfamilies. The method of brood pouch closure was used by Herald (1959) in constructing a phylogeny of the Syngnathidae.

The few osteological studies which have included the Syngnathidae have generally been based on only one or a few of the genera (Jungersen 1910; Banister 1967). These studies were therefore not adequately comparative and provided little information on intrafamilial relationships.

In order better to characterize the genera and subfamilies within the Syngnathidae, I have begun a study of the osteology of the syngnathid genera. This study is also designed to be a test of the hypotheses of relationships presented by previous authors who studied the brood pouch. Although the present investigation is still preliminary, data can be presented at this time.

Because the syngnathids are such highly specialized fishes, many aspects of their osteology (e.g., caudal skeleton) are so reduced that they can provide little phylogenetic information. However, the branchial skeleton does seem to provide useful information. All the genera ex-

TABLE 9. SYNGNATHID BRANCHIAL FORMULAE.

Genus	B1	B2	B3	H1	H2	E1	E2	E3	I2	I3	Remarks
GASTROPHORI:											
Heraldia (1)*	+	+	+	+	+	+	+	+	+	+	
Maroubra (1)	+	+	–	+	+	+	+	+	+	+	
Choeroichthys (1)	+	+	–	+	+	+	+	+	+	+	
Dentirostrum (1)	+	+	–	+	+	+	+	+	+	+	
Doryrhamphus (1)	+	+	–	+	+	+	+	+	+	+	
Dunckerocampus (1)	+	+	–	+	+	+	+	+	+	+	
Syngnathioides (1)	+	+	–	+	–	–	–	–	+	+	1
Nerophis (1)**	+	+	–	+	–	–	–	–	+	–	
UROPHORI:											
Leptonotus (1)	+	+	–	+	+	+	+	+	+	+	
Parasyngnathus (1)	+	+	–	+	+	+	+	+	+	+	2
Ichthyocampus (1)	+	+	–	+	+	+	+	+	+	+	
Micrognathus (1)	+	+	–	+	+	+	+	+	+	+	3
Syngnathus (7)†	+	+	–	–/r	+	+	+	+	+	+	
"*Corythoichthys*" (Atl.) (1)	+	+	–	+	r	+	+	+	+	+	
Bryx (*Bryx*) (3)	+	+	–	+	r	+/r	r	+	+	+	
Bryx (*Simocampus*) (2)	+	+	–	+	r	+/r	r	+	+	+	
Pseudophallus (2)	+	+	–	–	+	+	+	–	+	+	
Hippocampus (2)	–	–	–	+	+	+	+	+	+	+	
Phyllopteryx (1)	–	–	–	+	–	–	–	?	+	+	4
Corythoichthys (Pac.) (2)	+	–	–	–	+	–	–	–	–	–	
Penetopteryx (1)	+	+	–	+	+	+	+	+	+	+	

+ = present.
– = absent.
r = reduced.
* Number in parenthesis represents number of species examined.
** Data from Jungersen (1910).
† Only *Syngnathus acus* has reduced H1.
1 I2&3 with tooth plates.
2 with additional I element.
3 I2&3 with tooth plates.
4 I2&3 with tooth plates.

amined so far (Table 9) have a full complement of ceratobranchials (i.e., five pairs). The remaining elements in the branchial skeleton are variously lost or reduced within the family and possibly along distinct lineages within the family. The Urophori in particular show reduction and loss of every element except the ceratobranchials. The structure of the branchial skeleton is constant within a genus. Although the information provided by the branchial skeleton is based on characters undergoing reduction and not on uniquely derived characters, it is reasonable to use these characters when defining relationships. It seems quite probable that an element which is lost from such a highly evolved structure would not be regained.

The presence of well-developed first hypobranchials and reduced second hypobranchials and epibranchials clearly distinguish the genus *Bryx* from *Syngnathus* (Fig. 16). *Bryx* was included by Herald (1959) as a subgenus of *Syngnathus*.

The loss of all elements except the first basibranchial and second hypobranchials in the Pacific species usually referred to the genus *Corythoichthys* is clear evidence that the Atlantic and Pacific species should be placed in separate genera (Fig. 17). In fact, Dawson (1977) provisionally referred Atlantic species of *Corythoichthys* to the catchall genus *Syngnathus* and more recently placed them in a new genus, *Cosmocampus* (Dawson 1979). Herald's hypothesis that *Corythoichthys* is ancestral to, or on the lineage leading to, *Syngnathus* is clearly erroneous. However, Atlantic species of *Cosmocampus* could very well be on the lineage leading to *Bryx*.

Herald's hypothesis that *Leptonotus* and *Mi-*

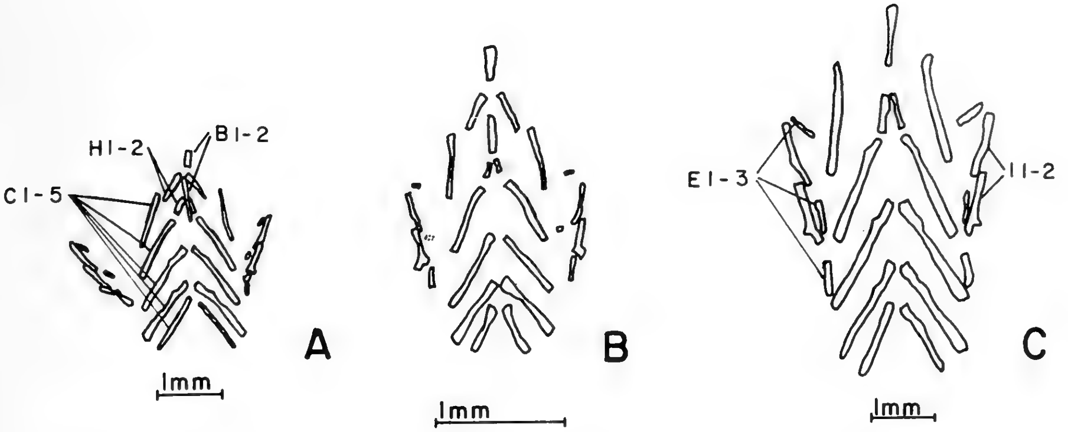


FIGURE 16. Dorsal view of the branchial skeleton of several syngnathids with the epibranchials and infrapharyngobranchials shown from their ventral aspect. (*A*) *Parasyngnathus elucens*, CAS 13696. (*B*) *Bryx arctus*, SIO H52-218. (*C*) *Syngnathus californiensis*, SIO H47-180. Abbreviations: B—basibranchial; H—hypobranchial; C—ceratobranchial; E—epibranchial; I—infrapharynogobranchial.

crognathus are derivable from *Parasyngnathus* can neither be supported nor refuted on the basis of their branchial skeletons. *Parasyngnathus* has a primitive branchial skeleton (Fig. 16). The retention of the upper pharyngeal tooth plates in *Micrognathus* is the only major difference between it and *Parasyngnathus*.

One interesting point is the extreme reduction of the branchial skeleton in the gastrophorine genus *Syngnathoides* and in the urophorine genera *Phyllopteryx* and *Hippocampus* (Fig. 17). These three genera are presently placed in separate subfamilies because of differences in the position and development of the brood pouch. However, in addition to the reduction of branchial elements, all three genera have the head at an angle to the main body axis and a prehensile tail without a caudal fin. This evidence may indicate that the three genera are much more closely related than has previously been recognized.

The amount of variation in the branchial skeleton is much greater in the Urophori than in the Gastrophori. The Gastrophorine genus *Heraldia* is the only syngnathid genus with three basibranchials, and it might well be the most primitive of the syngnathid genera.

The genus *Nerophis* is usually considered to be the most primitive genus in the family. However, the species referred to this genus have the most specialized branchial skeleton, in terms of reduction, in the Gastrophori (Table 9).

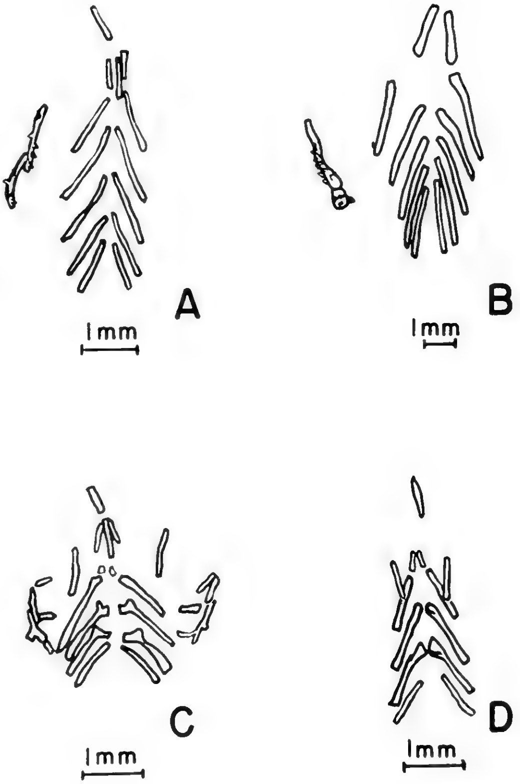


FIGURE 17. Branchial skeletons of four syngnathids. (*A*) *Syngnathoides biaculeatus*, SIO 60-693. (*B*) *Phyllopteryx foliatus*, SIO 73-361. (*C*) *Cosmocampus brachycephalus*, CAS 24025. (*D*) *Corythoichthys intestinalis*, SIO 73-206.

The evidence as is cited above indicates that the structure and development of the branchial skeleton in the Syngnathidae is of great utility in determining relationships. The fact that relationships as determined by the branchial skeleton transcend recognized subfamilial boundaries is a strong indication that the within-family relationships of this group are far from being understood.

Acknowledgments

I thank the following individuals for loan of material and/or providing information on specimens: John Paxton, AMS; Alex Peden, BC; Alwyne Wheeler, BMNH; Keith Thompson, BOC; William N. Eschmeyer, Tomio Iwamoto, and Pearl Sonoda, CAS; Fernando Balbontín, EMBCh; C. E. Dawson, GCRL; Robert Behrstock, HSU; Norma Chirichigno-F., IMARPE; Robert J. Lavenberg, Camm Swift, and Shelton Applegate, LACM; Myvanwy Dick, MCZ; M. L. Bauchot, MNHN; James Allen, SCCWRP; Leslie Knapp, SOSC; W. R. Taylor and Susan Karnella, USNM; Robert R. Miller, UMMZ; J. Moreland, NMNZ.

I thank the following individuals for material aid in the completion of this work: Donald Dockins (deceased), Joseph Copp, and Jan Pulsifer provided curatorial aid; James Zweifel provided the Laird-Gompertz analysis; John Butler raised the pipefish used in the study of growth; Myvanwy Dick supplied the figure of *Hippocampus ingens* collected at San Francisco; fellow graduate students who discussed various aspects of this problem with me and provided insights from their own research. Dr. Robert Lavenberg provided assistance in preparing the manuscript for publication.

I am particularly indebted to Dr. Richard H. Rosenblatt who made this study possible through his aid and advice, and to Dr. Carl L. Hubbs (deceased), who generously provided data collected on pipefishes for over 30 years and for his advice, support, and encouragement.

And finally, I wish to thank my wife, Edith, for her support and encouragement throughout the course of this research. Without her I am sure this work would never have been completed.

This study is based on a dissertation submitted to the University of California, San Diego, in 1976, in partial fulfillment of the requirements for the Ph.D. degree.

Literature Cited

Anonymous. 1921. Dredging and hydrographic records of the U.S. Fisheries Steamer "Albatross" 1911–1920. Appendix 3, Rep. U.S. Comm. Fish. 1920, Doc. 897, 190 p.

Abbott, J. F. 1899. The marine fishes of Peru. Proc. Acad. Nat. Sci. Phila. 1899:324–364.

Alverson, F. G. 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. Inter-Amer. Trop. Tuna Comm. Bull. 7:293–396.

Atz, J. W. 1937. Neptune's knight: the seahorse. Bull. N.Y. Zool. Soc. 40(2):57–65.

Ayres, W. O. 1854. Description of *Syngnathus griseo-lineatus*. Pacific 3(51):202.

Banister, K. E. 1967. The anatomy and classification of the order Gasterosteiformes (Pisces). Ph.D. Dissertation. University of Newcastle upon Tyne, England. 211 p.

Barnhart, P. S. 1936. Marine fishes of southern California. Univ. Calif. Press, Berkeley. 209 p.

Berry, F. H., and H. C. Perkins. 1965. Survey of pelagic fishes of the California Current area. U.S. Fish Wildl. Serv. Fish. Bull. 65(3):625–682.

Bleeker, P. 1858. Vijfde bijdrage tot de kennis der ichthyologische fauna van de Kokos-eilanden. Nat. Tijdsch. Neder. Indie. 15:457–468.

Bonaparte, C. L. J. L. 1838. Synopsis vertebratorum systematis. Nuov. Ann. Sci. Nat. 2:105–133.

Breder, C. M., Jr. 1928. Scientific results of the second oceanographic expedition of the "Pawnee" 1926. Nematognathi, Apodes, Isospondyli, Synentognathi, and Thoracostraci from Panama to Lower California with a generic analysis of the Exocoetidae. Bull. Bing. Oceanogr. Exped. 2(2):1–25.

Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill, New York. 475 p.

Brown, J. 1972. A comparative life history study of four species of pipefishes (family Syngnathidae) in Florida. Ph.D. Dissertation. University of Florida, Gainesville. 163 p.

Brothers, E. B. 1975. The comparative ecology and behavior of three sympatric California gobies. Ph.D. Dissertation. University of California, San Diego. 370 p.

Castro-Aguirre, J. L., J. Arvizu-Martínez, and J. Páez-Barrera. 1970. Contribución al conocimiento de los peces del Golfo de California. Rev. Soc. Méx. Hist. Nat. 31:107–181.

Chen, L. 1975. The rockfishes, genus *Sebastes* (Scorpaenidae), of the Gulf of California, including three new species, with a discussion of their origin. Proc. Calif. Acad. Sci., Ser. 4, 40(6):109–141.

Chirichigno-F., N. 1963. Estudios de la fauna ictíologia de los esteros y parte baja de los rios de departmento de Tumbes (Perú). Servicio de Pesquería Perú, Serie de Divulgación Cientifica, No. 22. 87 p.

———. 1974. Clave para identificar los peces marinos del Perú. Inf. Inst. Mar Perú-Callao, No. 44:1–387.

Clemens, H. B. and J. C. Nowell. 1963. Fishes collected in the eastern Pacific during tuna cruises, 1952 through 1959. Calif. Fish Game 49(4):240–264.

Crane, J. M., Jr. 1966. Late Tertiary radiation of viperfishes (Chauliodontidae) based on a comparison of recent and Miocene species. Los Angeles Cty. Mus. Contrib. Sci., no. 115:1–29.

D'Ancona, U. 1933. Family Syngnathidae. *In* Fauna e Flora del Golfo di Napoli, 38. Monografia: Uova, larve, e stadi giovanili di teleostei (Monografia eleborata con l'uso del materiale raccolto e seriato da Salvatore Lo Bianco). Stn. Zool. Napoli, pt. 2:284–299. [Translation of the Israel Program for Scientific Translation 1969]

Danil'chenko, P. G. 1960. Kostistye ryby maikopskich otlozenii kavkaza. Tr. Paleontol. Inst. Akad. Nauk SSSR 78:3–207.

David, L. R. 1943. Miocene fishes of southern California. Geol. Soc. Am. Spec. Pap. no. 43:1–143.

Dawson, C. E. 1977. Review of the pipefish genus *Corythoichthys* with description of three new species. Copeia 1977(2):295–338.

———. 1979. Notes on western Atlantic pipefishes with description on *Syngnathus caribbaeus* n.sp. and *Cosmocampus* n.gen. Proc. Biol. Soc. Wash. 92(4):671–676.

———, and R. A. Fritzsche. 1975. Odontoid processes in pipefish jaws. Nature 257:390.

———, and J. E. Randall. 1975. Notes on Indo-Pacific pipefishes (Pisces: Syngnathidae) with description of two new species. Proc. Biol. Soc. Wash. 88(25):263–280.

Dawson, E. Y. 1944. The marine algae of the Gulf of California. Allan Hancock Pac. Exped. 3(10):189–464.

DeBuen, F. 1963. Peces Chilenos Beloniformes, Syngnathiformes y Gobiidae. Bol. Soc. Biol. Concepción 35–36(1960–61):82–101.

Delfin, F. T. 1901. Catálogo de los peces de Chile. Rev. Chilena Hist. Nat. 3(1899) and 4(1900). 133 p.

Dixon, W. J., and F. J. Massey, Jr. 1957. Introduction to statistical analysis. 2nd ed. McGraw-Hill, New York. 488 p.

Duméril, A. H. A. 1870. Histoire naturelle des poissons ou ichthyologie générale. Vol. 2. Paris. 624 p.

Duncker, G. 1908. Syngnathiden-Studien. I. Variation und Modifikation bei *Siphonostoma typhle* L. Mitt. Naturh. Mus. (Jahrb. Wiss. Anst.) Hamburg 25:1–115.

———. 1912. Die Gattungen der Syngnathidae. Ibid. 29(2):219–240.

———. 1915. Revision der Syngnathidae. Erster teil. Ibid. 32:9–120.

———. 1923. Warnung. Zool. Anz. 56:238–239.

Eigenmann, C. H., and R. S. Eigenmann. 1892. A catalogue of the fishes of the Pacific coast of America, north of Cerros Island. Ann. N.Y. Acad. Sci. 6:349–358.

Eschmeyer, W. N., and S. G. Poss. 1976. Review of the scorpionfish genus *Maxillicosta* (Pisces:Scorpaenidae), with a description of three new species from the Australian-New Zealand region. Bull. Mar. Sci. 26(4):433–449.

Evermann, B. W., and O. P. Jenkins. 1891. Report upon a collection of fishes made at Guaymas, Sonora, Mexico, with descriptions of new species. Proc. U.S. Natl. Mus. 1891:121–165.

———, and H. B. Latimer. 1910. On a collection of fishes from the Olympic Peninsula, together with notes on other west coast species. Proc. Biol. Soc. Wash. 23:131–139.

———, and L. Radcliffe. 1917. The fishes of the west coast of Peru and the Titicaca Basin. Bull. U.S. Natl. Mus. 95:1–166.

Eydoux, F., and P. Gervais. 1837. Voyage de "La Favorite." Poissons. *Echeneis sexdecim-lamellata* et *Syngnathus blainvilleanus*. Mag. Zool. 7:1–4.

Feder, H. M., C. H. Turner, and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game Fish. Bull. no. 160:1–144.

Fischer, W. 1963. Die Fische des brackwassergebiets Lenga bei Concepcion (Chile). Int. Rev. Gesamten Hydrobiol. 48:419–511.

Fowler, H. W. 1921. Notes on hemibranchiate and lophobranchiate fishes. Proc. Acad. Nat. Sci. Phila. 73:437–448.

———. 1944a. Fishes obtained in the New Hebrides by Dr. Edward L. Jackson. Proc. Acad. Nat. Sci. Phila. 96:155–199.

———. 1944b. Results of the Fifth George Vanderbilt Expedition (1941). The fishes. Monogr. Acad. Nat. Sci. Phila. no. 6:57–583.

Gilbert, C. H. 1891. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. No. XIX.—A supplementary list of fishes collected at the Galapagos Islands and Panama, with descriptions of one new genus and three new species. Proc. U.S. Natl. Mus. 1890, 13:449–455.

———. 1892. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. No. XXII.—Descriptions of thirty-four new species of fishes collected in 1888 and 1889, principally among the Santa Barbara Islands and in the Gulf of California. Proc. U.S. Natl. Mus. 14:539–566.

———, and C. C. Starks. 1904. The fishes of Panama Bay. Mem. Calif. Acad. Sci. 4:1–304.

Gill, T. N. 1863. Synopsis of the species of lophobranchiate fishes of western North America. Proc. Acad. Nat. Sci. Phila. 1862:282–284.

———. 1905. The life-history of the sea-horses (Hippocampids). Proc. U.S. Natl. Mus. 28:805–814.

Ginsburg, I. 1933. Descriptions of five new species of seahorses. J. Wash. Acad. Sci. 23(12):560–563.

———. 1937. Review of the seahorses (*Hippocampus*) found on the coasts of the American continents and of Europe. Proc. U.S. Natl. Mus. 83:497–594.

Girard, C. F. 1854. Observations upon a collection of fishes made on the Pacific Coast of the United States by Lieut. W. P. Trowbridge, U.S.A., for the museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Phila. (for 1854), 7(4):142–156.

———. 1859. Fishes. *In* General Report upon the Zoology of the several Pacific railroad routes, 1857. U.S. Senate Miscell. Doc. no. 78, 1859, 33 Congr., 2 Sess. 400 p.

Guichenot, A. 1848. Fauna Chilena. Peces. *In* Gay, C., Historia fisica y politica de Chile . . . , Paris, ("en casa del Autor") Zoología 2:137–372.

Günther, A. 1870. Catalog of the fishes in the British Museum. Vol. 8. Taylor and Francis, London. 549 p.

Herald, E. S. 1940. A key to the pipefishes of the Pacific American coasts with descriptions of new genera and species. Allan Hancock Pac. Exped. 9(3):51–64.

———. 1941. A systematic analysis of variation in the western American pipefish, *Syngnathus californiensis*. Stanford Ichthyol. Bull. 2(3):49–73.

———. 1943. Studies on the classification and relationships of the American pipefishes. Ph.D. Dissertation. Stanford University. 339 p.

———. 1953. Family Syngnathidae:Pipefishes. Pp. 231–278 *in* Leonard P. Schultz et al. Fishes of the Marshall and Marianas Islands. Bull. U.S. Natl. Mus. 202, 1.

———. 1959. From pipefish to seahorse—a study of phylogenetic relationships. Proc. Calif. Acad. Sci. ser. 4, 29(13):465–473.

———. 1965. Studies on the Atlantic American pipefishes with descriptions of new species. Proc. Calif. Acad. Sci. ser. 4, 32(12):363–375.

Hildebrand, S. F. 1946. A descriptive catalog of the shore fishes of Peru. Bull. U.S. Natl. Mus. 189:1–530.

Hoese, D. E. 1971. A revision of the eastern Pacific species of the gobiid fish genus *Gobiosoma*, with a discussion of relationships of the genus. Ph.D. Dissertation. University of California, San Diego. 213 p.

Hubbs, C. L. 1916. Notes on the marine fishes of California. Univ. Calif. Publ. Zool. 16:153–169.

———. 1912. Notes on the pipe-fishes of California. Occas. Pap. Mus. Zool. Univ. Mich. no. 100:1–4.

———, and K. F. Lagler. 1958. Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci. 26:1–213.

———, and S. D. Hinton. 1963. The giant sea horse returns. Pac. Discov. 16(5):12–15.

Jenkins, O. P., and B. W. Evermann. 1888. Descriptions of eighteen new species of fishes from the Gulf of California. Proc. U.S. Natl. Mus. 1:137–158.

Jenyns, L. 1842. Fish. *In* Darwin, C., ed., The zoology of H.M.S. "Beagle," during the years 1832–1836. Part 4. 172 p.

Jerzmanska, A. 1968. Ichtyofaune des couches à ménilite (flysch des Karpathes). Acta Palaeontol. Pol. 13(3):379–488.

Jordan, D. S. 1895. The fishes of Sinaloa. Proc. Calif. Acad. Sci. ser. 2, 5:377–514.

———. 1921. The Miocene shore-fishes of California. Sci. Mon. 13(5):459–563.

———. 1926. Ein unglückliches Versehen. Zool. Anz. 6:221–224.

———. 1927. A confusing error. Copeia 1927(161):190–191.

———, and B. W. Evermann. 1896. The fishes of North and Middle America. Part 1. Bull. U.S. Natl. Mus. 47:1–954.

———, and ———. 1927. New genera and species of North American fishes. Proc. Calif. Acad. Sci. ser. 4, 16(5):501–507.

———, ———, and H. W. Clark. 1930. Checklist of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela. Rep. U.S. Comm. Fish. (1928) pt. 2:1–670.

———, and C. H. Gilbert. 1880. Notes on a collection of fishes from San Diego, California. Proc. U.S. Natl. Mus. 3:23–34.

———, and ———. 1881. List of the fishes of the Pacific Coast of the United States, with a table showing the distribution of the species. Proc. U.S. Natl. Mus. 3:452–458.

———, and ———. 1882. Notes on the fishes of the Pacific Coast of the United States. Proc. U.S. Natl. Mus. 4:29–70.

———, and ———. 1883. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus. 16:1–1018.

———, and J. Z. Gilbert. 1919. Fossil fishes of southern California. II. Fossil fishes of the Miocene (Monterey) formations of southern California. Stanford Univ. Publ. (Univ. Ser.):13–60.

———, and P. L. Jouy. 1882. Checklist of duplicates of fishes from the Pacific Coast of North America, distributed by the Smithsonian Institution in behalf of the United States National Museum. Proc. U.S. Natl. Mus. 4:1–18.

———, and E. S. Starks. 1896. Description of a new species of pipefish (*Siphostoma sinaloae*) from Mazatlan. Proc. Calif. Acad. Sci. ser. 2, 6:268.

Jungersen, H. F. E. 1910. Structure of Aulostomidae, Syngnathidae, and Solenostomidae. K. Danske Vidensk. Skrift. Naturv., ser. 7, 8(5):268–384.

Kaup, J. J. 1853. Übersicht der Lophobranchier. Arch. Naturges. 19(1):226–234.

———. 1856. Catalogue of the lophobranchiate fishes in the collection of the British Museum. London. 76 p.

Kermode, F. 1929. Report of the Provincial Museum of Natural History for the year 1928. [British Columbia] F1–F27.

———. 1930. Report of the Provincial Museum of Natural History for the year 1929. [British Columbia] F1–F26.

Koepcke, H. W. 1962. Lista de los peces marinas conocidos del Perú con datos de su distribución geográfica. Pt. 3. Biota 4(33):193–204.

Laird, A. K., A. D. Baron, and S. A. Tyler. 1968. Growth and time: An interpretation of allometry. Growth 32:347–354.

Linnaeus, C. 1758. Systema naturae. Regnum animale. 10th ed. Guiliemi Engelman, Lipsae. 824 p.

Lobell, M. J. 1942. Some observations on the Peruvian coastal current. Trans. Am. Geophys. Union, pt. II:332–336.

Mann, F. G. 1954. La vida de los peces en aguas chilenas. Ministerio de Agricultura, Univ. of Chile, Santiago. 342 p.

McCosker, J. E. 1970. A review of the eel genera *Leptenchelys* and *Muraenichthys*, with the description of a new genus, *Schismorhynchus*, and a new species, *Muraenichthys chilensis*. Pac. Sci. 24(4):506–516.

———. 1971. A new species of *Parapercis* (Pisces:Mugiloididae) from the Juan Fernandez Islands. Copeia 1971(4):682–686.

———, and C. E. Dawson. 1975. Biotic passage through the Panama Canal, with particular reference to fishes. Mar. Biol. 30:343–351.

Meek, S., and S. F. Hildebrand. 1923. The marine fishes of Panama, pt. 1. Field Mus. Nat. Hist. Publ. 215, zool. ser. 15:1–330.

Miller, D. J. and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game Fish Bull. no. 157. 235 p.

Morrow, J. E. 1957. Shore and pelagic fishes from Peru, with new records and the description of a new species of *Sphoeroides*. Bull. Bing. Oceanog. Coll. 26(2):5–55.

Munro, I. S. R. 1958. Syngnathiformes. Pp. 81–96 *in* Handbook of Australian fishes. Fish. Newsl. 17(2–5).

Neushul, M. 1971. The species of *Macrocystis* with particular reference to those of North and South America. Pp. 211–222 *in* North, W. J., ed. The biology of giant kelp beds (*Macrocystis*) in California. Beihefte zur Nova Hedwigia 32.

Nichols, J. Y., and R. C. Murphy. 1922. On a collection of marine fishes from Peru. Bull. Am. Mus. Natl. Hist. 46:501–516.

———, and ———. 1944. A collection of fishes from the Panama Bight, Pacific Ocean. Bull. Am. Mus. Nat. Hist. 83(4):217–260.

Norman, J. R. 1937. Coast fishes. Part II. The Patagonian region (including the Straits of Magellan and the Falkland Islands). Discovery Rep. 16:1–150.

Osburn, R. C., and J. T. Nichols. 1916. Shore fishes collected by the "Albatross" expedition in Lower California with descriptions of new species. Bull. Am. Mus. Nat. Hist. 35(16):139–181.

Philippi, R. A. 1896. Peces nuevos de Chile. Anal. Univ. Chile 93:375–390.

Rafinesque, C. S. 1810. Caratteri de alcuni nuovi generi e nuove specie di animali e plante della Sicilia, con varie osservazioni sopra i medisimi. Palermo. 105 p.

Rauther, M. 1925. Die syngnathiden des Golfes von Neapel. Publ. Stn. Zool. Napoli 36:1–365.

REGAN, C. T. 1908. Pisces. Biologia Centrali-Americana, 1906–1908. 203 p.

RICKER, K. E. 1959. Fishes collected from the Revillagigedo Islands during the 1954–1958 cruises of the "Marijena." Univ. Brit. Col. Inst. Fish. Mus. Contrib. no. 4:1–10.

ROSEN, D. E. 1974. Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides*. Bull. Am. Mus. Nat. Hist. 153(2):267–325.

ROSENBLATT, R. H. 1963. Some aspects of speciation in marine shore fishes. Pp. 171–180 *in* Speciation in the sea. Systematics Assoc. Publ. no. 5.

———, J. E. MCCOSKER, AND I. RUBINOFF. 1972. Indo-west Pacific fishes from the Gulf of Chiriqui, Panama. Los Angeles Cty. Mus. Contrib. Sci. no. 234:1–18.

SCHULTZ, L. P. 1957. The frogfishes of the family Antennariidae. Proc. U.S. Natl. Mus. 107:47–105.

SICCARDI, E. M. 1954. Consideraciones sobre el modo de reproducción de "*Leptonotus blaenvillianus*" Eydoux and Gervais, 1837 (Pisces: Syngnath.). Comun. Inst. Nac. Invest. Cien. Nat. Cien. Zool. 2(14):211–242.

SNYDER, J. O. 1911. Descriptions of new genera and species from Japan and the Riu Kiu Islands. Proc. U.S. Natl. Mus. 40:525–549.

STARKS, E. C. 1911. Results of an ichthyological survey about the San Juan Islands, Washington. Ann. Carnegie Mus. 7:162–213.

———, AND E. L. MORRIS. 1907. The marine fishes of southern California. Univ. Calif. Publ. Zool. 3:159–252.

STEINDACHNER, F. 1898. Die Fische der Sammlung Plate. Fauna Chilensis. Zool. Jahrb. (Suppl.) 4:281–337.

STORER, D. H. 1848. Description of a new species of *Syngnathus,* brought from the western coast of California by Capt. Phelps. Proc. Boston Soc. Nat. Hist. 1845, 2(10):73.

SWAIN, J. 1882. A review of the Syngnathinae of the United States, with a description of one new species. Proc. U.S. Natl. Mus. 5:307–315.

———, AND S. E. MEEK. 1884. Notes on the pipefishes of Key West, Florida, with description of *Siphostoma McKayi,* a new species. Proc. U.S. Natl. Mus. 7:237–239.

TAYLOR, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122:1–17.

THOMPSON, W. F. 1916. Fishes collected by the United States Bureau of Fisheries Steamer "Albatross" during 1888, between, Montevideo, Uruguay, and Tome, Chile, on the voyage through the Straits of Magellan. Proc. U.S. Natl. Mus. 50:401–476.

ULREY, A. B. 1929. A check-list of fishes of southern California and Lower California. J. Pan-Pac. Res. Inst. 4(4):2–11.

———. 1932. Lista de los peces de las costas de la Baja California. Ann. Inst. Biol. 3(1):75–80.

———, AND P. O. GREELEY. 1928. A list of the marine fishes (Teleostei) of southern California with their distribution. Bull. South. Calif. Acad. Sci. 27(1):1–53.

VAILLANT, L. L. 1883. Remarques sur les affinités naturelles des familles composant le sous-ordre des poissons malacoptérygiens abdominaux. Ann. Sci. Nat. (Zool.), sér. 6, 15(7):1–13.

———. 1888. Mission scientifique du Cap Horn, 1882–1883. VI. Zool., Poissons. Paris. 35 p.

———. 1894. Sur une collection de poissons recueillie en Basse-Californie et dans le Golfe par M. Léon Diguet. Bull. Soc. Philom. Paris, sér. 3, 6:69–75.

WAITE, E. R. 1909. Subantarctic islands of New Zealand. Art. XXV. Vertebrata of the subantarctic islands of New Zealand. Pisces:585–598.

WEBER, M. AND L. F. DE BEAUFORT. 1922. The fishes of the Indo-Australian Archipelago. IV. Leiden. 410 p.

WHITLEY, G. P. 1931. New names for Australian fishes. Aust. Zool. 6(4):310–334.

———. 1940. Illustrations of some Australian fishes. Aust. Zool. 9(4):397–428.

———. 1955. Sidelights on New Zealand ichthyology. Aust. Zool. 12(2):110–119.

WOODRING, W. P. 1966. The Panama land bridge as a sea barrier. Am. Phil. Soc. 110(6):425–453.

ZWEIFEL, J. R. AND R. LASKER. 1976. Prehatch and posthatch growth of fishes—A general model. Fish. Bull., U.S. 74(3):609–621.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 7, pp. 229–285; 30 figs., 7 tables July 2, 1980

A REVISION OF THE FISH GENUS *OGCOCEPHALUS* WITH DESCRIPTIONS OF NEW SPECIES FROM THE WESTERN ATLANTIC OCEAN (OGCOCEPHALIDAE; LOPHIIFORMES)

By
Margaret G. Bradbury[1]
Department of Biological Sciences, San Francisco State University,
San Francisco, California 94132

ABSTRACT. The New World genus *Ogcocephalus* comprises twelve species. Two species are island endemics in the eastern Pacific, *Ogcocephalus darwini* Hubbs in the Galápagos archipelago and *Ogcocephalus porrectus* Garman off Cocos Island, but the remaining ten are western Atlantic species. Five of the Atlantic species are described as new: *Ogcocephalus pantostictus* and *Ogcocephalus declivirostris* from the northern and western Gulf of Mexico, *Ogcocephalus rostellum* from the Atlantic coast of the southeastern United States, *Ogcocephalus corniger* also from the Atlantic coast of the southeastern United States but ranging into the eastern Gulf of Mexico, and *Ogcocephalus pumilus* from the Caribbean and coasts of the Guianas. *Ogcocephalus parvus* Longley and Hildebrand has a wider range than formerly known, from the coast of the southeastern United States and eastern Gulf of Mexico through the Caribbean to the Atlantic coast of South America. *Ogcocephalus vespertilio* (Linnaeus) has a more restricted range than formerly thought, the coast of Brazil from the mouth of the Amazon to the mouth of the Rio de la Plata. *Ogcocephalus notatus* (Cuvier and Valenciennes) also has a southerly distribution in the western Atlantic, the coast of northern South America from Colombia to northern Brazil. The variable species *Ogcocephalus nasutus* (Cuvier and Valenciennes) appears to be allopatric with *O. vespertilio* (Linnaeus), which it most resembles; *O. nasutus* ranges from the mouth of the Amazon through the Caribbean to the Bahamas and southeastern Florida. *Ogcocephalus cubifrons* (Richardson) ranges from the Bahamas and the coast of the southeastern United States into the eastern Gulf of Mexico to at least Pensacola, Florida, and Campeche Banks. The name *Ogcocephalus radiatus* (Mitchill) is placed in the synonymy of *Ogcocephalus cubifrons*. Illustrated keys, photographs, diagnoses, and distribution maps are provided.

INTRODUCTION

Ogcocephalids from the western Atlantic Ocean have become available in large numbers during the last two or more decades, much of the new material a handsome dividend from the work of exploratory vessels of the U.S. National Marine Fisheries Service sampling new fishing grounds. Prior to this exploratory period, specimens of ogcocephalids were uncommon in collections except for those captured inshore by swimmers or divers, particularly off Florida and off islands in the Caribbean. Few in number and little studied, these specimens were difficult to assign names to because variation in characters then used in diagnoses was not understood. Variation in the length of the prominent rostrum was a frequent source of error. The information developed in this study is that some species may be diagnosed by their long rostrums at all sizes,

---

[1] Research Associate, Department of Ichthyology, California Academy of Sciences.

but the rostrum in other species varies allometrically so that juveniles have long rostrums, but adults have short ones.

Analysis of morphometric data, including data about the rostrum, reveals that the genus *Ogcocephalus* is represented in the western Atlantic by ten species, five of which are described here as new. More recently, new material from the eastern Pacific has also become available. Study of this material confirms that two derivative species are present in the eastern Pacific (Garman 1899; Hubbs 1958).

Studies on the remaining genera of Ogcocephalidae of the Atlantic Ocean are underway currently. Discussions of the zoogeography of the group and intrafamilial relationships of all the Atlantic species will be published with the results of those studies.

ACKNOWLEDGMENTS

This study has been pursued intermittently since the late 1950's. During this time I became indebted to many colleagues to whom it is a pleasure to extend my grateful thanks at last. I deeply appreciate the encouragement given me by the late Loren P. Woods, who first suggested this problem and made available the specimens, skeletal material, and photographs of ogcocephalids in the Field Museum of Natural History; he also read an early version of the manuscript and devoted a great deal of time to assisting me. My dear friend, the late Marion Grey, gave valuable bibliographic assistance as well as the enthusiastic encouragement that so often characterized her relations with her colleagues. Pearl M. Sonoda sent specimens on each of a number of occasions and cheerfully gave much other assistance. Hymen Marx discussed ideas with zest and humor during one memorable Chicago summer. George S. Myers and the late Rolf L. Bolin, who were my professors at Stanford University, gave valuable help; Prof. Bolin gave skillful criticism of an early version of this report. With characteristic generosity, Giles W. Mead kindly made possible a study trip to museums in the eastern United States and gave support and encouragement in various ways. The late Carl L. Hubbs gave advice about taking counts and measurements and graciously examined for me a Linnaean type-specimen at Uppsala. He along with W. I. Follett and Lillian Dempster helped with the coining of names.

Photographs and radiographs were generously provided by the following: Harvey R. Bullis, Jr., Bruce B. Collette, William N. Eschmeyer, David W. Greenfield, Åke Holm, Robert J. Lavenberg, Garnett W. Link, Jr., Robert N. Lea, Giles W. Mead, and Loren P. Woods. For their valuable time, I am grateful to the following people who loaned specimens or made arrangements for me to work at their institutions: William W. Anderson, Richard T. Barber, Frederick H. Berry, James E. Böhlke, the late Anton Brunn, Harvey R. Bullis, Jr., Daniel M. Cohen, Bruce B. Collette, C. E. Dawson, Myvanwy M. Dick, Robert H. Gibbs, Carter R. Gilbert, David W. Greenfield, Jena Guibé, Carl L. Hubbs, Robert K. Johnson, Robert J. Lavenberg, Giles W. Mead, George C. Miller, Martin A. Moe, Jr., C. Richard Robins, Richard H. Rosenblatt, Jay M. Savage, Leonard P. Schultz, Robert L. Shipp, Victor G. Springer, Camm C. Swift, Ethelwynn Trewavas, Vladimir Walters, and Loren P. Woods. I thank Lillian J. Dempster and W. I. Follett for clarifications on nomenclatural questions.

This investigation was supported by Public Health Service Fellowship No. 8543 from the Division of General Medical Sciences, Public Health Service, and by National Science Foundation grant GB-4777 from the Division of Biological and Medical Sciences. Support from these agencies was essential for the completion of this work, and I am deeply appreciative.

SPECIAL TERMINOLOGY

The depressed anterior portion of the fish is called the disk and consists of the cranium, opercular apparatus, and the trunk back to the pectoral axillae. The lateral margins of the disk are formed by the opercular bones, which are very elongate relative to the cranium. The cranium is of ordinary proportions relative to the standard length, so the large total size of the disk is due primarily to the elongate opercular series, which sweeps backward from the cranium and envelops the trunk on either side to form the disk.

The (usually) conspicuous protuberance from the front of the head dorsal to the nasal openings is called the rostrum. Appearing as a median horn in most species, it varies in relative length from short to very long. It may bear cirri at its distal end, but its function remains unknown at this time. No skull bones are involved in the

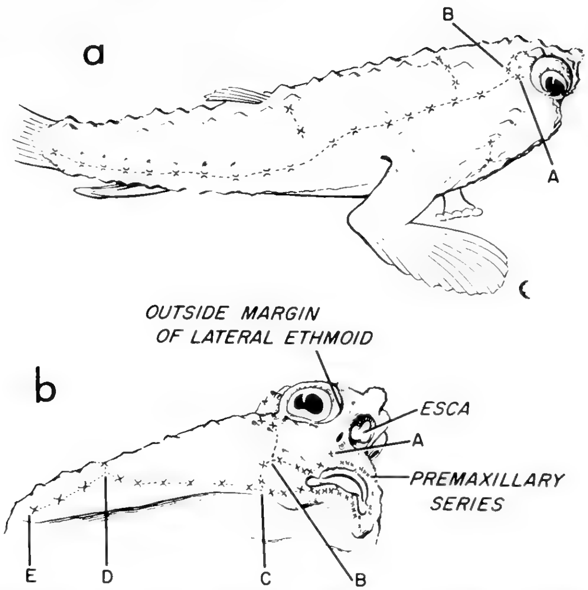


FIGURE 1. Lateralis system of *Ogcocephalus cubifrons*, 275 mm SL. Each lateral-line scale indicated by pair of opposing U-shaped symbols representing flaps of skin associated with such scales. Canals indicated by dashed line. *(a)* Lateral view showing lateral line beginning at A; portion of supraorbital series also shown, beginning at B. *(b)* Oblique view of head showing cheek series, A to C, premaxillary series, and subopercular series, C to E.

structure of the rostrum; it is formed solely of modified scales.

Just beneath the rostrum is a cavity lined with scaleless skin into which the angling lure or illicium may be drawn. This cavity is here called the illicial cavity. The somewhat bulbous structure seen within the illicial cavity is the bait of the angling apparatus, or esca (Fig. 1*b*), a movable glandular appendage attached to the distal end of the illicium. The illicium is a bony rod, quite short, but when extended, can be seen to be covered with scaleless skin like the skin which lines the illicial cavity; the skin of the illicium is thrown into accordionlike folds when the illicium is retracted.

In members of the Ogcocephalidae the scales are highly modified structures of three main types (Bradbury 1967: fig. 5). The simplest type is a pyramid- or cone-shaped scale called a tubercle, typically with a spine at its apex, although there may be several. The kind of scale that characterizes *Ogcocephalus*, called a buckler, is larger and more complex; bucklers are cone-shaped, too, but covered with small spinules rather granular in appearance and arranged in rows that radiate out from the apex of the buckler. These granular spinules fill the spaces between bucklers. The morphological relationship between tubercles and bucklers is not clear; the spinules of bucklers often resemble tubercles, suggesting that the buckler may be a compound structure consisting of one enlarged tubercle overlain with small tubercles arranged in the radiating pattern, but the matter cannot be clarified until developmental studies of the scales are undertaken.

Finally, besides tubercles and bucklers, specially shaped lateral-line scales occur. With appropriate preparations it can be shown that lateral-line scales are bowl- or dish-shaped (Bradbury 1967: fig. 5), but under ordinary viewing conditions their shapes are difficult to discern. However, they are often made conspicuous because of associated flaps or fringes of epidermis; when epidermal decorations are absent, lateral-line scales may often be distinguished because of the large single neuromast lying in the center of the cup of each scale.

METHODS

COUNTS.—Vertebral counts were made from radiographs and include the hypural plate.

Scales of the lateral-line system can generally be seen in most species of Ogcocephalidae, al-

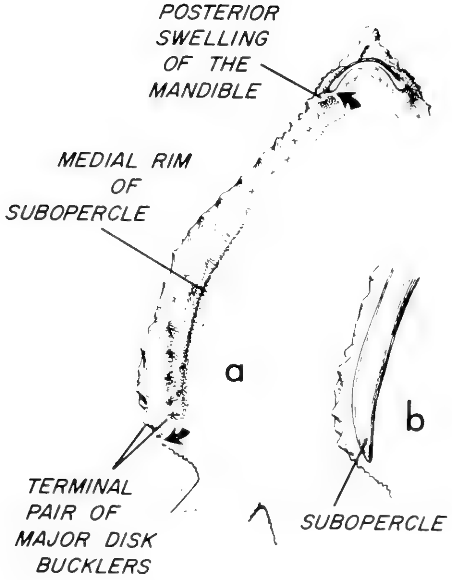


FIGURE 2. Ventral view of *Ogcocephalus cubifrons*, 275 mm SL, showing disk margin. *(a)* Length of disk margin is distance between two points indicated by the two arrows. *(b)* Position of subopercle relative to disk margin.

though the canals are difficult to discern as a rule. Thus it may be difficult to follow and count lateral-line scales when they are small and spaced far apart on the surface of the disk where they tend to become lost in the rough integument, but elsewhere on the body it is generally possible to see the scales and follow the lines of the canals by using adequate magnification. In this paper I have used four series of counts of scales of the lateral-line system as taxonomic characters.

1. Lateral line (Fig. 1*a*). The lateral line begins just posterior to the eye at A. Care must be taken not to include scales of the supraorbital series which begins at B. The line of scales continues back across the dorsal surface of the disk and suddenly descends ventrally just posterior to the gill pore, continuing along the lateral sides of the tail and on to the base of the caudal fin.

2. Subopercular series (Fig. 1*b*). This portion of the cephalic lateral-line system branches from the preoperculomandibular canal at C and continues posteriorly along the ventral side of the subopercle to E. A secondary branch leaves the subopercular series at D and runs up onto the dorsal side of the disk for a short distance. Care must be taken to avoid including the first scale of this branch series in the subopercular lateral-line scale count. The subopercular lateral-line scale count was always taken as the count between C and D because the posterior section (between D and E) does not vary from a count of 3. Thus, the subopercular lateral-line scale count in the figure is 6.

3. Cheek series (Fig. 1*b*). I have called the section of lateral line that extends in a sigmoid curve from A to C the cheek series, although its topographic position suggests that it consists of lateral-line scales from the infraorbital canal plus the opercular section of the preoperculomandibular canal. The cheek series excludes scales of the branch extending from B towards the eye.

4. Premaxillary series (Fig. 1*b*). The premaxillary series is a short section of infraorbital canal just above the upper lip.

MEASUREMENTS.—The highly specialized body form of these fishes requires some modification of standard measuring procedures as pointed out by Hubbs (1958). I have followed his procedures in large part, but made adjustments that permit comparative measurements of members of other genera.

Measurements were made either with sharp-pointed steel calipers and a steel rule, or with dial calipers, and were recorded to the nearest 0.1 mm; measurements of approximately 15 mm or less were taken viewed through a low-power dissecting microscope. All measurements involving the upper or lower jaws were taken from the anteriormost median point of the lips without pressing the calipers into the lip tissue. All measurements involving bucklers were taken to the base of the buckler and not to its apex, unless otherwise stated.

Standard length is the distance from the upper lip to the base of the caudal rays. The latter point is difficult to establish in large specimens in which the integument is thick and stiff; the calipers were pressed firmly back against the swelling formed by the bases of the rays. Predorsal distance is the distance from the center of the upper lip to the base of the first dorsal ray; preanal distance is the distance from the center of the lower lip to the base of the first anal ray. The distance from the jaw to the anus is the distance between the center of the lower lip and the center of the anal opening.

The point of articulation of the mandible with the suspensorium is visible externally as a pronounced swelling at the posterior end of the

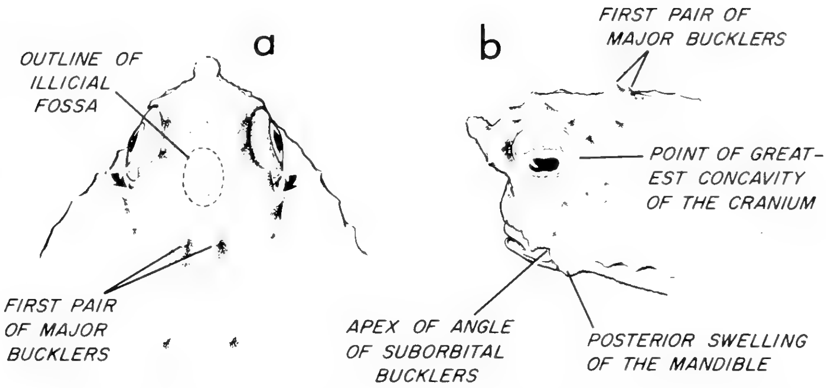


FIGURE 3. Views of head of *Ogcocephalus cubifrons,* 275 mm SL, showing specific locations of points used in taking measurements of head. Head depth is taken with one needle of calipers set between bucklers of first major pair *(a)* and *(b),* with other needle on apex of swelling of mandible *(b).* Width of cranium is taken between points of greatest concavity just posterior to orbits *(b)*; also shown by arrows in *(a).* Suborbital width is least distance between orbit and apex of angle formed by suborbital bucklers *(b).*

mandible; the measurement of the disk margin was taken with one point of the calipers pressed against the front of this swelling and the other point pressed against the posterior end of the subopercle (arrows, Fig. 2*a*). Care must be taken in determining the posterior end of the subopercle in specimens with a thick stiff integument, but the tip of the subopercle can be felt with the caliper point just posterior to the terminal pair of large bucklers at the angle of the disk. This measurement of the disk margin was substituted for head length, which proved to be an awkward measurement in some species. Trunk width is the "width behind P_1 [pectoral] fins" (Hubbs 1958) which "is taken where the body margin reaches a maximum curvature near the solid part of the urosome, behind the disk."

Length of rostrum was taken as the distance from the dorsal rim of the posterior nostril to the distal tip of the terminal spine of the rostrum. The nostril landmark was chosen, in spite of being off-center, because it is in precisely the same relative position in all species. Although the rostrum appears to be highly variable in length in *Ogcocephalus,* results of this study show that some of the variation results from allometric growth patterns. When this allometry is borne in mind, the length of the rostrum proves a useful distinguishing feature in these fishes.

Width of cranium (Fig. 3*a*) corresponds to "skull prominence width" of Hubbs (1958). It is the distance taken between the "points of greatest concavity" which lie just posterior to the orbits (Fig. 3*a*, arrows, and 3*b*). Head depth is the oblique distance from a median point on the roof of the cranium between the first pair of major bucklers (Fig. 3*a*) to the apex of the cone-shaped swelling formed by the mandible where it articulates with the suspensorium (Fig. 3*b*). The first pair of major bucklers invariably occurs just posterior to a noticeably soft spot on the dorsal surface of the cranium, which is actually the fossa into which the illicium retracts (Fig. 3*a*). Although off-centered, this measurement of head depth taken as described is a useful, repeatable measurement. The eye measurement is the greatest diameter of the bony orbit; since there are no circumorbital bones, the lateral process of the sphenotic bone forms all there is of a posterior bony margin of the orbit. The rear needle of the calipers was always pressed against this bone. Suborbital width is the least distance between the margin of the cornea (well marked by its rim of tubercles) and the apex of the sharp angle formed by the suborbital bucklers just above the angle of the lips (Fig. 3*b*). Lateral ethmoid width is the least distance between the outside margins of the lateral ethmoid bones, which are the bones that form the sides of the illicial cavity (Fig. 1*b*). Mouth width is the greatest overall width, i.e., the distance between the posterior tips of the maxillaries. Taking this measurement and the following one require some care because the maxillary tips are usually concealed beneath the suborbital integument.

The length of the jaw is taken from the median point of the upper lip to the posterior tip of the maxillary. The snout length measurement is the least distance from the anterior bony margin of the orbit to a point on the median line just above the upper lip and exactly at the base of a strip of scaleless skin lying between the two armored halves of the snout. Length of dorsal and length of anal are the lengths of these fins from the base of the first ray to the tip of the longest ray with the fin depressed.

The patterns of dentition in species of *Ogcocephalus* show little variation from the pattern described for *O. darwini* by Hubbs (1958). Bradbury (1967) described the dentition in the genus and compared it with patterns in other genera with the use of alizarin-stained and cleared specimens. Since there are no readily discernible distinctions in the dentitions of species of *Ogcocephalus* that are taxonomically useful, features of dentition are omitted from this report.

As is often the case with endeavors of this kind, sampling was not random, and specimens were studied as they came available regardless of their size or the locality from which they came. Usually habitat differences were not known. Meristic differences proved to be less useful for discriminating among populations than body proportions and color patterns, and the latter were used repeatedly in diagnosing specimens. It was convenient to express body proportions as ratios, and these ratios are used in the species diagnoses. However, for systematic comparisons, proportions are also given in terms of percent of standard length in tabular format. Counts of pectoral fin rays and the various lateral-line scale series were made on both right and left sides, and counts from both sides are included in the tables; most of the tables present these data in right-and-left pairs.

Abbreviations for fish collections are as follows: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History): CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; FSBC, Florida State Board of Conservation Marine Laboratory; GCRL, Gulf Coast Research Laboratory Museum; LACM, Los Angeles County Museum; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Muséum National d'Histoire Naturelle, Paris; SIO, Scripps Institution of Oceanography; SU, Stanford University (this collection is now housed in the California Academy of Sciences and therefore listed as CAS-SU); UF, Florida State Museum, University of Florida; UMML, Marine Laboratory, University of Miami; USNM, U.S. National Museum of Natural History, Smithsonian Institution; ZMUC, Universitetets Zoologiske Museum, Copenhagen.

Ogcocephalus Fischer

Ogcocephalus FISCHER, 1813:78 [type-species *Lophius vespertilio* Linnaeus, by subsequent designation of Jordan and Evermann 1896:511]; BRADBURY 1967.

Malthe CUVIER, 1816:311 (part) [type-species *Malthe vespertilio* Cuvier and Valenciennes (non Linnaeus), 1837, by subsequent designation of Gill 1878:232].

Malthea (or *Malthaea*) CUVIER AND VALENCIENNES, 1837:440 [emended spelling of *Malthe* and therefore taking the same type-species].

Oncocephalus JORDAN, 1895:506 [unjustified emendation of *Ogcocephalus* Fischer].

Onchocephalus GILL, *in* GOODE AND BEAN, 1896:498 [unjustified emendation of *Ogcocephalus* Fischer].

Of the two unjustified emendations of *Ogcocephalus* which have appeared in the literature, at least one had the objective of correcting an alleged improper transliteration from the Greek. Jordan and Evermann (1898:2736) state with regard to the original spelling of *Ogcocephalus,* "properly written *Oncocephalus,* but Fischer chose the above monstrous spelling." The second emended spelling may have been introduced for the same reason, but in fact no reason was put forward. In any event, the original spelling of the name is a correct original spelling, and the name stands as *Ogcocephalus* Fischer (see also Briggs 1961).

DIAGNOSIS.—A genus of Ogcocephalidae with gill rakers in the form of oval pads which are studded with teeth resembling the fine teeth elsewhere in the buccal cavity (Bradbury 1967; fig. 7). Gills 2½, none on the first arch; complete holobranchs on the second and third arches, a hemibranch on the fourth arch. Scales on ventral surface of tail consisting of numerous, tiny, closely spaced tubercles; if any bucklers occur, they are scattered or may occur in a single short median row, but in any case, never are arranged in two longitudinal rows that cover the entire ventral surface as in *Zalieutes* or *Malthopsis.* Esca distinctly trilobed, with a median dorsal, somewhat leaf-shaped, lobe and two ventral lobes arranged symmetrically below the median lobe (Bradbury 1967: fig. 3).

TABLE 1. FREQUENCY DISTRIBUTION OF STANDARD LENGTHS IN SPECIES OF *Ogcocephalus*.

		Standard lengths in millimeters																								
	N	11 20	21 30	31 40	41 50	51 60	61 70	71 80	81 90	91 100	101 110	111 120	121 130	131 140	141 150	151 160	161 170	171 180	181 190	191 200	201 210	211 220	221 230	231 240	241 250	251 260	261 270
notatus	53	1	4	4	3	3	8	11	7	6	4	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
darwini	30	—	—	1	—	—	1	1	—	—	6	4	6	4	5	1	1	—	—	—	—	—	—	—	—	—	—
porrectus	35	—	1	—	1	1	2	4	8	4	2	6	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—
vespertilio	46	—	—	—	—	1	—	4	2	3	5	3	1	5	7	4	6	3	1	—	—	—	1	—	—	—	—
nasutus	108	—	2	4	3	1	3	6	5	6	4	7	8	11	9	4	6	7	9	2	3	3	3	2	—	—	—
cubifrons	57	—	1	—	4	1	2	2	3	—	—	4	2	3	6	3	5	7	3	3	1	5	2	—	—	—	—
pantostictus	48	—	—	1	2	—	1	2	3	10	7	3	1	3	—	2	4	1	2	1	2	—	2	—	—	—	1
rostellum	70	—	—	1	3	3	4	1	3	7	8	9	9	12	8	2	—	—	—	—	—	—	—	—	—	—	—
corniger	38	—	2	—	2	1	1	1	3	6	7	5	9	1	—	—	—	—	—	—	—	—	—	—	—	—	—
parvus	56	—	1	—	6	19	17	10	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
declivirostris	56	—	—	1	6	3	13	8	5	8	6	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—
pumilus	49	—	3	4	27	13	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

DESCRIPTION.—*Body form.* Body depressed anteriorly, forming a disk which is subtriangular in outline. Cranium well elevated above general slope of disk, proportions between width of cranium and head depth showing little variation within genus (width of cranium into head depth 1.4–2.1). Also, there is little variation in length of snout and width of suborbital relative to width of cranium (suborbital width into width of cranium 1.0–1.9; snout length into width of cranium 1.4–2.4). Rostrum variable in length, from a relatively small knob to a long median horn. Gill pores opening dorsally, lying in the axillae a short distance in advance of rear margin of disk. No membranes connecting pectoral peduncles with trunk as occur in *Halieutichthys*. Ventral surface of disk flat.

Tail stout and muscular, relatively wide at its junction with disk, tapering to a narrow caudal base. Ventral surface of tail flattened so that a cross section through anterior half of tail would be nearly a half circle. Predorsal distance 1.4–1.7 in standard length; preanal distance 1.2–1.4 in standard length. Anus slightly in front of a line drawn between posterior tips of pectoral elbows when pressed against trunk; distance from jaw to anus 1.6–1.9 in standard length.

Head Features. Eyes directed laterally and a little anteriorly and downward. Cornea much smaller than orbit, skin extending from cornea around eyeball studded with small tubercles. Depending upon its condition at time of preservation, iris shows a more or less pronounced pupillary operculum (except in *O. notatus*) on its ventral margin, giving pupil an approximate kidney shape. Sometimes a less noticeable dorsal operculum (again excepting *O. notatus*) extends downward towards its ventral mate so that pupil is dumbbell-shaped; presumably these opercula regulate pupil size, but I know of no experiments that demonstrate this function.

Anterior nostril round, the aperture encircled by a rim of skin which often forms a short tube; posterior nostril slitlike, larger than anterior nostril. Jaws very protractile, mouth moderate to small, usually semicircular, its width 2.6–5.2 in length of disk margin except in *O. notatus*, which has a relatively wide mouth and in which the ratio is 1.8–2.5. In normal position, posterior ends of maxillaries concealed beneath the suborbital bucklers. Upper jaw terminal or subterminal relative to snout; lower jaw included; gape oblique.

TABLE 2. FREQUENCY DISTRIBUTIONS FOR DORSAL AND ANAL FIN RAY COUNTS AND VERTEBRAL COUNTS IN SPECIES OF *Ogcocephalus*.

	Dorsal fin						Anal fin		Vertebrae			
	1	2	3	4	5	6	3	4	18	19	20	21
notatus	—	1	—	35	17	2	5	50	6	11	—	—
darwini	—	—	1	16	1	—	2	16	—	14	3	—
porrectus	—	—	11	22	—	—	—	33	2	14	—	—
vespertilio	—	—	3	26	8	—	—	37	3	15	—	—
nasutus	—	1	1	57	11	—	4	66	3	30	—	—
cubifrons	—	—	3	23	10	—	1	35	—	5	14	1
pantostictus	—	—	3	23	11	—	—	37	—	2	12	3
rostellum	—	—	5	20	1	—	1	25	—	5	17	2
corniger	—	—	7	30	1	—	1	37	3	16	—	—
parvus	—	1	1	64	3	—	2	67	3	9	1	—
declivirostris	—	—	1	39	13	—	4	49	1	14	28	—
pumilus	1	—	9	37	3	—	28	21	—	14	—	—

Fins. Dorsal fin small, placed far posteriorly on tail to rear of level of anus; dorsal rays usually 4–5, unbranched. Anal fin "like a narrow lappet" (Hubbs 1958) or a prop for the tail, usually fleshy, particularly along anterior edge and tips of first two rays. Apparently this fin lies twisted on its side while fish rests on the substrate. Typically the anal fin has 4 unbranched rays, but *O. pumilus* frequently has only 3 (Table 2). Pectorals sturdy, variable in shape from relatively long and narrow to broad and fan shaped; pectoral rays with skin especially fleshy on distal ventral surfaces in 9 of the 12 species, this fleshy tissue not developed on ventral surface of pectorals in very small specimens as a rule. Pectoral rays 10–15, unbranched (Table 3). Pelvics also sturdy, narrow at their base for more than half their length, then abruptly flared distally with tips of rays very fleshy in most species, so much so in adults of some species that fin resembles a small paddle. Pelvic fin count always I,5; rays unbranched. Caudal fin with rounded margin and 9 rays, at least 6 of which are branched; formula either i,7,i or i,6,ii.

Teeth. Teeth conical, retrorse, villiform, in bands on jaws, in broad plates on tongue, and in smaller patches on prevomer and palatines. Gill rakers in the form of oval plates, variable in size but always bearing teeth similar to those on jaws and in buccal cavity. Patches of slightly larger teeth on second and third pharyngeobranchials, these patches always well developed

TABLE 3. FREQUENCY DISTRIBUTION OF PAIRS OF PECTORAL FIN RAY COUNTS IN SPECIES OF *Ogcocephalus*.

	Paired pectoral ray counts											
	$\frac{10}{10}$	$\frac{10}{11}$	$\frac{11}{11}$	$\frac{11}{12}$	$\frac{12}{12}$	$\frac{12}{13}$	$\frac{13}{13}$	$\frac{13}{14}$	$\frac{14}{14}$	$\frac{14}{15}$	$\frac{15}{15}$	other	$\bar{x}$
notatus	—	—	—	—	—	2	22	3	18	1	—	$\frac{12}{14}$	13.4
darwini	—	—	—	—	—	—	—	—	8	6	14	—	14.6
porrectus	—	—	—	—	—	—	—	5	23	2	2	—	14.0
vespertilio	—	—	—	—	—	1	4	5	28	4	4	—	14.0
nasutus (South Amer.)	—	—	1	—	3	4	20	6	5	—	—	—	13.1
nasutus (Cent. Amer.)	—	—	1	1	17	2	4	—	—	—	—	—	12.1
nasutus (W. Indies)	—	—	—	1	24	4	9	—	1	—	—	—	12.3
cubifrons	—	—	—	1	24	12	44	9	2	—	—	$\frac{11}{13},\frac{11}{13},\frac{12}{14}$	12.7
pantostictus	—	—	1	3	17	4	21	—	1	—	—	—	12.5
rostellum	—	—	—	1	2	2	32	3	3	—	—	—	13.0
corniger	2	5	25	2	3	—	—	—	—	—	—	—	11.0
parvus (northern)	23	6	12	—	—	—	—	—	—	—	—	—	10.4
parvus (southern)	—	—	11	3	1	—	—	—	—	—	—	—	11.2
declivirostris	2	4	41	2	2	—	—	—	—	—	—	$\frac{9}{11}$	11.0
pumilus	—	1	30	8	9	—	—	—	—	—	—	—	11.3

TABLE 4. FREQUENCY DISTRIBUTION OF LATERAL-LINE SCALE COUNTS IN SPECIES OF *Ogcocephalus*. Counts were attempted on both right and left sides of specimens, but counts which were not repeated within two subsequent attempts were discarded.

		Lateral-line scale counts																									
	N	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	$\bar{x}$
notatus	54	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	6	9	13	6	5	3	5	3	—	—	32.4
darwini	26	—	—	—	—	1	—	—	—	1	2	3	5	8	2	2	2	—	—	—	—	—	—	—	—	—	26.3
porrectus	53	—	—	—	—	—	—	1	1	5	8	12	8	12	5	1	—	—	—	—	—	—	—	—	—	—	25.5
vespertilio	62	—	—	—	—	—	—	—	—	—	—	—	—	1	3	6	9	6	14	9	8	2	1	3	—	—	31.8
nasutus	114	—	—	—	—	—	—	—	—	—	2	5	2	9	5	8	17	19	19	11	8	3	2	2	2	—	30.8
pantostictus	83	—	—	—	—	—	—	—	—	—	—	—	—	2	4	8	5	12	10	14	7	6	8	5	1	1	32.5
cubifrons	71	—	—	—	—	—	—	—	—	2	2	5	8	19	6	6	14	2	3	2	1	—	1	—	—	—	28.1
rostellum	73	—	—	—	—	—	—	1	1	2	10	16	18	9	4	5	2	4	1	—	—	—	—	—	—	—	25.9
corniger	44	—	—	—	4	5	15	8	8	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20.5
parvus	118	7	24	37	35	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17.2
declivirostris	59	—	—	—	—	—	—	—	3	6	16	16	7	9	2	—	—	—	—	—	—	—	—	—	—	—	24.9
pumilus	34	—	—	—	—	2	10	9	10	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21.1

even in species in which gill rakers are smallest (Bradbury 1967).

Integument. Most species with dermal cirri, but these variable among individuals of the same species; also, cirri are probably fragile and most likely do not preserve uniformly well, so their variability is difficult to assess. In any event, when they appear in preserved materials, they may occur singly or in clusters or thick fringes, most often in association with lateral-line system, particularly on face, disk margin, and lateral sides of tail. Scales consisting of close-set tubercles and bucklers, their bases sometimes slightly overlapping, forming a heavy armor. Large bucklers in dense groups over cranium and face and around disk margins, where they may be ankylosed to underlying bone. Heavy bucklers also on dorsal surface of trunk and tail where they form a median band which varies in width, extending in some species down sides of tail to lateral line. All species with large bucklers scattered elsewhere over dorsal surface of disk and pectoral peduncles with tubercles and small bucklers interspersed among them. Tubercles always invest skin covering surface of eyeballs between cornea and edges of bony orbits. Ventral surface of disk invariably covered with fine tubercles so that skin looks and feels like shagreen. Ventral surface of tail similarly covered, but there may be a short median line or a scattering of small bucklers. Dorsal and pectoral fins may or may not have minute tubercles running out along rays, but the fleshy anal and pelvic fins always have fine tubercles covering at least basal ⅓ or ¼ of fin, except in *O. notatus* in which fins are nearly naked. Caudal fin with thick bands of small bucklers and tubercles running out along rays, but in alternating fashion so that rays 1, 3, 5, etc., have their thickest covering on one side of the fin while alternate rays have their thickest covering on opposite side, permitting fin to be tightly folded in spite of its dense armor.

Color in preservative. Most species with markings on "wings" of disk and in axillae in the form of clusters of spots. Less commonly, tracts of spots or reticula occur along lateral walls of tail, and in *Ogcocephalus porrectus* and *O. darwini* the disk and tail markings have coalesced into a pair of prominent stripes. Color of dorsal and pectoral fins variable from species to species, but color of anal and pelvic fins generally the same as color of ventral surface of

TABLE 5. FREQUENCY DISTRIBUTION OF PAIRS OF CHEEK LATERAL-LINE SCALE COUNTS IN SPECIES OF *Ogcocephalus*.

		Paired cheek lateral-line scale counts									
	N	$\frac{7}{7}$	$\frac{7}{8}$	$\frac{8}{8}$	$\frac{8}{9}$	$\frac{9}{9}$	$\frac{9}{10}$	$\frac{10}{10}$	$\frac{10}{11}$	other	$\bar{x}$
notatus	43	—	—	—	—	—	3	37	3	—	10.0
darwini	24	1	4	15	2	1	—	—	—	$\frac{6}{8}$	7.9
porrectus	19	—	—	18	—	—	—	—	—	$\frac{6}{8}$	8.0
vespertilio	34	—	—	—	2	31	1	—	—	—	9.0
nasutus (South Amer.)	38	—	—	—	4	31	2	1	—	—	9.1
nasutus (Cent. Amer.)	20	—	—	4	5	9	—	1	—	$\frac{8}{10}$	8.7
nasutus (W. Indies)	37	—	—	8	6	22	1	—	—	—	8.7
cubifrons	50	—	3	31	9	6	1	—	—	—	8.2
pantostictus	39	—	1	2	10	9	13	3	—	$\frac{8}{10}$	9.0
rostellum	25	—	—	19	5	1	—	—	—	—	8.1
corniger	26	—	1	22	2	—	—	—	—	—	8.0
parvus (northern)	35	1	6	24	2	—	—	—	—	$\frac{6}{8}$, $\frac{7}{9}$	7.9
parvus (southern)	15	—	1	11	3	—	—	—	—	—	8.1
declivirostris	42	—	—	36	5	—	—	—	—	$\frac{7}{9}$	8.1
pumilus	32	—	—	23	7	2	—	—	—	—	8.2

body. Ventral surface of body usually much paler than ground color of dorsal surface. Dorsal and pectoral fins may have spotted or reticulate pattern, but anal and pelvics seldom have any discrete spotting or banding. Caudal fin markings nearly constant throughout genus, consisting of a dark basal third about the same intensity as ground color of dorsal surface of body, a pale middle third, and a dark distal third. Spots sometimes superimposed on this basic pattern in a few species.

Color in life. Observations of life colors in these fishes suggest that, as a group, they are remarkably colorful if one considers how drab they become in preservative. In most cases the underparts are some shade of red: reddish orange, or crimson, or even purplish red, with fins, lips, and buccal membranes likely to be colored a shade of red as well. One relatively deep-water form, *O. pumilus*, is pinkish colored when freshly caught. Life colors are known from too few species, however, to be able to generalize yet about life colors in these fishes.

DISTRIBUTION.—*Ogcocephalus* is confined to the West Indian–Panamanian fauna, with ten species in the western Atlantic Ocean and two

TABLE 6. FREQUENCY DISTRIBUTION OF PAIRS OF SUBOPERCULAR LATERAL-LINE SCALE COUNTS IN SPECIES OF *Ogcocephalus*.

		Paired subopercular lateral-line scale counts													
	N	$\frac{4}{5}$	$\frac{5}{5}$	$\frac{5}{6}$	$\frac{6}{6}$	$\frac{6}{7}$	$\frac{7}{7}$	$\frac{7}{8}$	$\frac{8}{8}$	$\frac{8}{9}$	$\frac{9}{9}$	$\frac{9}{10}$	$\frac{10}{10}$	$\frac{10}{11}$	other	$\bar{x}$
notatus	44	—	—	—	—	—	3	4	3	8	19	3	—	—	$\frac{7}{9}$, $\frac{7}{9}$, $\frac{7}{9}$, $\frac{8}{10}$	8.5
darwini	21	1	1	—	7	3	4	2	1	1	—	—	—	—	$\frac{6}{8}$	6.5
porrectus	31	—	—	2	19	8	1	1	—	—	—	—	—	—	—	6.1
vespertilio	40	—	—	—	—	—	—	4	6	8	13	5	—	—	$\frac{6}{10}$, $\frac{7}{9}$, $\frac{7}{10}$, $\frac{8}{10}$	8.6
nasutus (South Amer.)	38	—	—	—	2	3	1	7	2	9	6	4	—	—	$\frac{6}{8}$, $\frac{6}{9}$, $\frac{7}{9}$, $\frac{7}{9}$	8.0
nasutus (Cent. Amer.)	22	—	—	1	1	2	4	2	3	3	1	2	—	—	$\frac{6}{8}$, $\frac{7}{9}$, $\frac{7}{9}$	7.6
nasutus (W. Indies)	37	—	—	1	4	6	10	7	2	2	1	1	1	—	$\frac{6}{8}$, $\frac{6}{8}$	7.2
cubifrons	57	—	—	—	—	4	17	14	11	6	—	—	—	—	$\frac{6}{8}$, $\frac{6}{9}$, $\frac{7}{9}$, $\frac{8}{10}$	7.5
pantostictus	48	—	—	—	—	—	—	—	3	8	22	7	3	1	$\frac{7}{9}$, $\frac{7}{9}$, $\frac{9}{11}$, $\frac{10}{13}$	9.1
rostellum	42	—	—	3	9	9	12	4	—	1	—	—	—	—	$\frac{5}{7}$, $\frac{5}{7}$, $\frac{6}{8}$, $\frac{7}{9}$	6.6
corniger	33	—	—	6	12	10	3	1	—	—	—	—	—	—	$\frac{4}{7}$	6.2
parvus (northern)	35	3	10	15	4	1	—	1	—	—	—	—	—	—	$\frac{5}{7}$	5.4
parvus (southern)	15	2	8	2	3	—	—	—	—	—	—	—	—	—	—	5.1
declivirostris	38	—	—	2	8	7	13	4	2	—	—	—	—	—	$\frac{5}{7}$, $\frac{6}{8}$	6.7
pumilus	30	1	4	8	13	4	—	—	—	—	—	—	—	—	—	5.8

TABLE 7. MORPHOMETRIC PROPORTIONS FOR SPECIES OF *Ogcocephalus*. Body measurements are given as thousandths of standard length.

	Jaw to anus			Snout to dorsal			Length of disk margin			Width of urosome		
	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$
notatus	29	.549–.796	.585	22	.633–.680	.657	50	.365–.438	.403	36	.191–.318	.268
darwini	28	.547–.836	.703	28	.589–.668	.639	29	.328–.456	.385	28	.155–.244	.210
porrectus	31	.457–.716	.585	31	.615–.699	.647	35	.419–.539	.450	35	.189–.277	.243
vespertilio	37	.542–.617	.586	37	.635–.733	.670	46	.414–.490	.456	37	.180–.282	.231
nasutus (South Amer.)	11	.520–.618	.564	14	.611–.682	.643	40	.419–.506	.464	40	.185–.271	.236
nasutus (Cent. Amer.)	14	.535–.625	.571				25	.415–.482	.446	7	.207–.241	.221
nasutus (W. Indies)	8	.550–.588	.566	9	.626–.684	.656	40	.415–.508	.465	26	.160–.262	.228
pantostictus	5	.529–.574	.558	5	.646–.671	.657	48	.420–.483	.441	25	.196–.281	.247
cubifrons	16	.543–.621	.577	16	.613–.684	.653	54	.396–.482	.438	31	.169–.294	.237
rostellum	20	.528–.608	.551	20	.624–.686	.651	71	.405–.493	.448	19	.211–.282	.249
corniger	32	.545–.641	.591	33	.641–.732	.680	37	.388–.481	.441	33	.192–.258	.228
parvus (northern)	18	.480–.652	.603	17	.646–.704	.674	40	.452–.524	.486	29	.183–.284	.241
parvus (southern)	7	.610–.636	.621	8	.644–.691	.666	15	.453–.501	.479	13	.199–.280	.245
declivirostris	17	.540–.601	.564	16	.605–.679	.635	56	.390–.447	.419	29	.193–.342	.264
pumilus	29	.523–.588	.547	29	.611–.844	.635	49	.398–.463	.429	29	.204–.264	.235

	Head depth			Width of cranium			Length of rostrum			Width of mouth		
	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$
notatus	49	.198–.260	.223	53	.121–.185	.146	50	.050–.195	.079	53	.172–.213	.196
darwini	29	.196–.291	.223	29	.103–.155	.123	29	.088–.181	.128	29	.106–.137	.121
porrectus	35	.207–.250	.224	35	.120–.207	.137	32	.131–.164	.149	35	.127–.153	.139
vespertilio	35	.224–.255	.239	46	.104–.157	.140	46	.169–.293	.213	37	.134–.165	.152
nasutus (South Amer.)	41	.213–.282	.234	41	.127–.172	.142	39	.079–.230	.135	41	.134–.177	.149
nasutus (Cent. Amer.)	24	.212–.262	.240	25	.110–.150	.135	25	.068–.258	.136	24	.122–.162	.144
nasutus (W. Indies)	34	.208–.262	.229	40	.118–.176	.133	37	.083–.229	.132	34	.120–.164	.137
pantostictus	36	.200–.250	.223	48	.119–.155	.136	47	.067–.170	.104	40	.130–.168	.142
cubifrons	47	.206–.258	.225	52	.119–.177	.141	51	.075–.224	.111	41	.097–.141	.117
rostellum	53	.185–.234	.204	71	.105–.165	.130	69	.053–.123	.073	52	.100–.147	.118
corniger	37	.223–.290	.251	38	.121–.171	.136	36	.189–.267	.228	37	.130–.183	.152
parvus (northern)	41	.238–.301	.276	41	.136–.180	.157	40	.074–.152	.119	41	.109–.149	.123
parvus (southern)	15	.241–.270	.253	15	.133–.158	.146	15	.094–.136	.118	15	.095–.120	.106
declivirostris	56	.198–.244	.218	56	.107–.157	.133	56	.029–.131	.077	56	.117–.151	.133
pumilus	49	.205–.244	.222	49	.123–.155	.137	49	.135–.219	.184	49	.125–.158	.144

	Length of jaw			Width of eye			Width of interorbital			Depth of caudal peduncle		
	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$
notatus	52	.110–.137	.124	53	.072–.112	.086	53	.046–.090	.061	52	.069–.094	.082
darwini	28	.081–.110	.090	29	.081–.103	.090	29	.050–.080	.064	28	.066–.090	.079
porrectus	35	.087–.117	.098	35	.078–.105	.088	35	.055–.090	.064	34	.065–.083	.076
vespertilio	46	.095–.113	.106	46	.076–.106	.095	46	.060–.093	.071	46	.069–.094	.080
nasutus (South Amer.)	41	.091–.121	.101	40	.079–.118	.091	41	.054–.074	.064	40	.070–.090	.081
nasutus (Cent. Amer.)	25	.096–.112	.104	25	.070–.110	.094	25	.056–.077	.064	8	.081–.089	.085
nasutus (W. Indies)	40	.087–.115	.098	40	.076–.130	.088	40	.053–.097	.067	35	.079–.122	.089
pantostictus	48	.085–.110	.096	43	.068–.106	.087	48	.054–.080	.066	47	.077–.096	.086
cubifrons	53	.069–.100	.081	36	.074–.116	.091	53	.062–.092	.075	43	.078–.105	.091
rostellum	71	.070–.107	.080	69	.073–.109	.085	71	.044–.083	.059	59	.055–.088	.074
corniger	38	.093–.125	.104	38	.082–.124	.101	38	.044–.082	.064	38	.061–.087	.076
parvus (northern)	41	.082–.102	.091	41	.098–.134	.116	41	.042–.076	.056	40	.075–.102	.083
parvus (southern)	15	.071–.084	.078	15	.091–.116	.103	15	.055–.073	.062	15	.078–.095	.087
declivirostris	56	.080–.108	.092	56	.081–.107	.095	56	.039–.070	.050	55	.077–.100	.086
pumilus	49	.070–.111	.093	49	.094–.128	.106	49	.037–.054	.044	49	.070–.088	.079

TABLE 7. Cont.

	Width of suborbital			Width between lateral ethmoids			Length of snout			Length of dorsal fin			Length of anal fin		
	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$
notatus	35	.067–.112	.087	36	.086–.110	.096	36	.068–.097	.080	48	.105–.219	.146	48	.114–.180	.150
darwini	29	.065–.096	.084	29	.057–.088	.071	29	.059–.083	.066	26	.087–.121	.105	25	.144–.191	.162
porrectus	34	.085–.103	.093	34	.073–.092	.080	34	.049–.079	.070	33	.087–.121	.102	34	.150–.190	.171
vespertilio	46	.089–.114	.103	37	.064–.084	.077	37	.065–.082	.074	34	.099–.152	.123	35	.147–.183	.167
nasutus (South Amer.)	31	.084–.123	.097	32	.069–.100	.083	31	.063–.084	.073	31	.081–.147	.108	31	.114–.178	.146
nasutus (Cent. Amer.)	8	.099–.116	.104	21	.073–.096	.085	7	.076–.100	.083	7	.095–.119	.109	7	.140–.172	.156
nasutus (W. Indies)	40	.087–.117	.103	34	.074–.103	.083	34	.065–.083	.074	25	.089–.153	.111	30	.123–.193	.160
pantostictus	31	.084–.112	.097	25	.076–.095	.084	24	.065–.084	.074	41	.088–.160	.120	36	.133–.191	.164
cubifrons	35	.085–.110	.096	29	.072–.096	.079	28	.061–.097	.073	41	.097–.159	.126	29	.152–.204	.170
rostellum	38	.070–.097	.085	44	.065–.099	.076	20	.057–.077	.065	19	.088–.141	.103	17	.122–.169	.147
corniger	33	.088–.112	.101	33	.069–.110	.081	33	.064–.084	.073	37	.072–.125	.091	38	.124–.177	.150
parvus (northern)	29	.110–.136	.120	29	.082–.117	.097	29	.078–.098	.089	36	.109–.175	.145	39	.132–.177	.158
parvus (southern)	13	.091–.110	.101	13	.079–.089	.084	13	.071–.083	.079	14	.120–.176	.143	15	.143–.202	.165
declivirostris	34	.069–.105	.084	34	.068–.100	.083	34	.058–.084	.070	53	.114–.186	.150	54	.141–.187	.166
pumilus	29	.078–.099	.087	29	.069–.094	.078	29	.060–.075	.067	43	.096–.192	.132	44	.108–.178	.150

in the eastern Pacific. In the Atlantic the genus occurs along the coast of the United States from Cape Hatteras south to the Gulf of Mexico, West Indies, the coasts of Central America and South America to Uruguay. In the Pacific the genus is known from the vicinity of Cocos Island, the Galápagos Islands, and Peru (but not from south of the Gulf of Panama as stated by Lundy (1956) or from off Cabo Corrientes as stated by Hubbs (1958); of course, it is possible, even likely, that *Ogcocephalus* will be found eventually at these localities, but I know of no such records to date. I suspect the error is owed simply to a misreading of coordinates on the map of the eastern Pacific Ocean concerning the locality of the type-series of *Ogcocephalus porrectus* (Garman, 1899).

Relative to other genera in the family, *Ogcocephalus* has the shallowest bathymetric range. Although data on depth distribution are still scanty for some species, some generalizations may be attempted. Four species appear to occur most commonly at depths shallower than 50 m; these species are *O. cubifrons*, *O. pantostictus*, *O. vespertilio*, and *O. darwini*, with *cubifrons* often recorded from depths of 10 m or less. Two species that have their depth distribution centered at 50–60 m are *O. nasutus* and *O. notatus*, and three that have their depth distributions centered at 60–100 m are *O. parvus*, *O. pumilus*, and *O. declivirostris*. *Ogcocephalus porrectus* has been taken only between 100 and 170 m, but the species has been taken from few localities. Finally, there are two species, *O. rostellum* and *O. corniger*, that have relatively wide bathymetric ranges from 30 to 250 m. Thus, for the genus as a whole, most specimens have been taken at depths shallower than 100 m, but some have been taken as deep as 200 m, and a few individuals have been taken from depths over 350 m.

Key to Species of *Ogcocephalus*

Few species were found to be unique in the characters studied, and constructing a key proved difficult. This key will permit identification of most specimens of juvenile and adult specimens of *Ogcocephalus*, but some couplets utilize characters that do not discriminate completely between members of the couplet. In these cases, species intermediate between members of a couplet are carried from there through both sides of the key.

1a. Distribution: western Atlantic Ocean .. 2
1b. Distribution: eastern Pacific Ocean 13

2a. Pectoral rays 10/10 to 11/11 or 11/12 (3% of specimens belonging to species included here have pectoral rays 12/12) 3
2b. Pectoral rays 12/12 to 15/15 (2% of specimens belonging to species included here have pectoral rays 11/12 or 11/11) 6

3a. Rostrum very long, length 0.9–1.6 in head depth, 1.6–3.1 in length of disk margin 4
3b. Rostrum moderate to short, length 1.7–4.0 in head depth, 3.2–8.5 in length of disk margin 5

4a. Anal rays 3–4. Body pale tan or gray without markings except dark spots occasionally present dorsally on either side of disk. No fleshy pads on ventral surface of pectoral rays; fin membrane relatively thin and translucent (Fig. 4*a*). A small species reaching 70 mm SL. Known from northern Bahamas through Puerto Rico and Lesser Antilles to Surinam. One record from Honduras .... *Ogcocephalus pumilus* new species (Fig. 26), p. 272
4b. Anal rays 4. Dorsal body surface brownish, evenly covered with small whitish spots (which are the tips of bucklers). Distal ends of pectoral rays with thickened fleshy pads on their ventral surfaces; fin membrane thick and opaque (Fig. 4*b*). A moderate-sized species reaching 140 mm SL. Known from eastern Cuba, eastern Gulf of Mexico, and eastern coast of United States as far north as Cape Lookout, North Carolina .... *Ogcocephalus corniger* new species (Fig. 26), p. 274

5a. Rostrum short, usually tilted upward; never sloping downward. Body surface rough, contours craggy with prominent bucklers. Head raised relatively high above disk, head depth 3.1–4.2 in standard length. Mouth small, its width 2.0–2.8 in head depth. Distal ends of pectoral rays with thickened fleshy pads on ventral surfaces; fin membrane thick and opaque (Fig. 4*b*). A small species reaching 85 mm SL. Western Atlantic from South Carolina to Recife, Brazil, except absent from western Gulf of Mexico .... *Ogcocephalus parvus* (Fig. 28), p. 276
5b. Rostrum horizontal or sloping downward relative to long axis of body. Bucklers giving body a roughened surface, but not craggy contours. Head relatively low to the disk, head depth 4.3–5.1 in standard length. Mouth width 1.4–1.9 in head depth. Distal ends of pectoral rays without fleshy pads; fin membrane thin and translucent (Fig. 4*a*). A moderate-sized species reaching 140 mm SL. Known only from northern and western Gulf of Mexico .... *Ogcocephalus declivirostris* new species (Fig. 24), p. 269

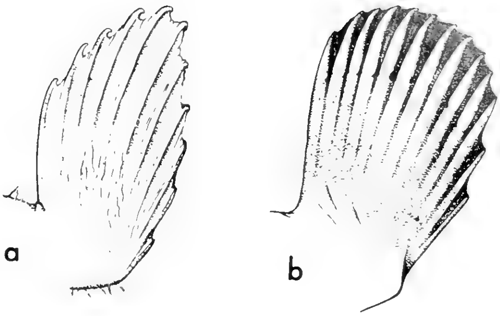


FIGURE 4. *(a)* Ventral view of pectoral fin of type found in *O. notatus, O. pumilus,* and *O. declivirostris.* Skin relatively thin, membranes translucent, and articulations of fin rays visible through skin. *(b)* Ventral view of pectoral fin of type found in all other species. Skin thick, spongy along the rays, especially distally where small pads form. Membranes thick and elastic. (These features often undeveloped in small individuals.)

6a. Mouth wide, its width 1.8–2.5 in length of disk margin, 1.0–1.4 in head depth. Lateral-line scales in premaxillary series 4/4, in cheek series usually 10/10 (Fig. 1*b*). Pupil oval; no opercula. Atlantic coast of South America from Caribbean coast of Venezuela to mouth of Rio Plata in Uruguay .... *Ogcocephalus notatus* (Fig. 5), p. 243
6b. Mouth width 2.6 or more in length of

disk margin, 1.4 or more in head depth. Lateral-line scales in premaxillary series 3/3, in cheek series 8/8 to 9/9 or 9/10, rarely 10/10 (Fig. 1*b*). Pupil kidney- or dumbbell-shaped because of presence of opercula (flaps of iris tissue) encroaching over pupil 7

7a. Rostrum very long, length 1.4–3.1 in length of disk margin, 0.8–1.7 in head depth 8

7b. Rostrum moderate to short, length 3.2 or more in length of disk margin, 1.8 or more in head depth 10

8a. Anal rays 3–4. Subopercular lateral-line scales 5/5 to 6/6, occasionally 6/7. Interorbital relatively narrow, 2.5–3.7 in width of cranium. Distal pectoral rays without fleshy pads ventrally; fin membrane thin and translucent (Fig. 4*a*). A small species reaching 70 mm SL. Known from northern Bahamas through Puerto Rico and Lesser Antilles to Surinam. One record from Honduras .... *Ogcocephalus pumilus* new species (Fig. 26), p. 272

8b. Anal rays 4, rarely 3. Subopercular lateral-line scales 7/7 to 9/9 or 9/10, seldom fewer. Interorbital wide, its width 1.4–2.6 in width of cranium. Distal ends of pectoral rays generally with fleshy pads ventrally; fin membrane thick and opaque (Fig. 4*b*) 9

9a. Pectoral count most often 14/14. Color pattern usually consisting of network of light-colored lines on patches of dark background, these reticulated patches present dorsally on either side of disk, sides of tail, bases of pectoral fins, and on face. Known from mouth of Amazon River to São Paulo, Brazil .... *Ogcocephalus vespertilio* (Fig. 5), p. 247

9b. Pectoral count most often 12/12 to 13/13. May be devoid of color markings, but more often with clusters of dark rounded spots, these spots sometimes with light borders, present dorsally on either side of disk in some, extending on to face, pectoral fins, or even entire dorsal surface of body in others 10

10a. Round dark spots occurring over entire dorsal surface of disk and prominent on dorsal surface of pectoral fins 11

10b. Round dark spots either absent or, if present, restricted to center of disk on either side; some specimens of *O. nasutus* from the West Indies are darkly mottled and may have networks of pale lines on face, tail, and around gill pores. Pectorals without spotted pattern, or if spots occur, they are dim and restricted to the bases of pectorals 12

11a. Mouth relatively narrow, its width 1.7 or more in head depth; interorbital wide relative to the short jaw, interorbital 0.8–1.3 in length of jaw. Subopercular lateral-line scales usually 7/7 to 8/8. Northern Bahamas and coasts of southeastern United States from Cape Lookout, North Carolina, to Pensacola, Florida, and south to Campeche Banks, Mexico .... *Ogcocephalus cubifrons* (Fig. 18), p. 258

11b. Mouth wide, width 1.7 or less in head depth; width of interorbital 1.2–1.8 in length of jaw. Subopercular lateral-line scales usually 8/9, 9/9, or more. Northern and western Gulf of Mexico from Pensacola, Florida, to Tamaulipas, Mexico .... *Ogcocephalus pantostictus* new species (Fig. 23), p. 264

12a. Rostrum a well-developed median horn. Head often marked by stripes radiating from eye in specimens from West Indies. Jaw relatively long, length 1.2–1.6 in width of cranium. A variable species with a broad range as understood here; known from the Bahamas, southeastern Florida, the Caribbean, and northern coast of South America to mouth of Amazon River .... *Ogcocephalus nasutus* (Figs. 12, 13), p. 251

12b. Rostrum extremely short, not produced into a median horn except in very small specimens. No stripes radiating from eye, although spots may occur on iris. Jaw short, length 1.4–1.9 in width of cranium. Eastern coast of United States from Cape Hatteras to the Florida Keys .... *Ogcocephalus rostellum* new species (Fig. 24), p. 267

13a. Skin shagreenlike, bucklers not spiny and protuberant .. *Ogcocephalus darwini* (Fig. 29), p. 279

13b. Spiny bucklers protuberant; skin not smooth and shagreenlike .... *Ogcocephalus porrectus* (Fig. 29), p. 282

Ogcocephalus notatus (Cuvier and Valenciennes)

(Figure 5)

[?] *Lophius histrio* (non Linnaeus): ROSENTHAL 1822:pl. 19, fig. 2 [skeleton and legend; see comment after synonymy].
Malthe notata CUVIER, 1829:252 [nomen nudum].
Malthe angusta CUVIER, 1829:252 [nomen dubium; after plate in Rosenthal 1822].
Malthe truncata CUVIER, 1829:252 [nomen nudum].
Malthaea notata CUVIER AND VALENCIENNES, 1837:453 [Surinam; holotype MNHN 4764]; DEKAY 1842:167 [partial description, compiled]; LÜTKEN 1866:208 [Maruim, Brazil; description; *truncata* placed in synonymy of *notata*].
Malthaea angusta CUVIER AND VALENCIENNES, 1837:454 [Surinam; holotype MNHN 4767].
Malthaea truncata CUVIER AND VALENCIENNES, 1837:454 [holotype MNHN 4772].
Malthea notata: STORER 1846:132 (separate) [partial description, compiled]; CASTELNAU 1855:26, pl. 12, fig. 3 [Bahía, Brazil]; GILL 1862:47 [listed, after Storer 1846].
Malthe notata: GILL 1873:14 [range: southern Atlantic coast, compiled].
Malthe vespertilio [?] (non Linnaeus): GILL 1883:556 [cites Rosenthal 1822, in list of osteological works].
Oncocephalus truncatus: MIRANDA RIBEIRO 1915: on page 575 of unnumbered text, 2 figs. [Santos, Brazil; description; photographs]; 1918:154 [synonymy].
Ogcocephalus radiatus: PUYO 1936:233 [off Cayenne River, French Guiana; description; figures; synonymy; behavior]; MENEZES 1964:157 [Brazil; description; figures; comparisons with *Ogcocephalus vespertilio* (Linnaeus); photographs].
Ogcocephalus nasutus var. *cayennensis* PUYO, 1936:241 [Cayenne, French Guiana; figures; holotype unknown].
Oncocephalus radiatus: FOWLER 1941:184 [compiled; after *Oncocephalus truncatus* of Miranda Ribeiro 1915].
Oncocephalus notatus: DELSMAN 1941:76 [mouth of Amazon River; said to resemble photograph of *O. truncata* (Cuvier & Valenciennes) in Miranda Ribeiro 1915].
Onchocephalus radiatus: PUYO 1949:257 [French Guiana; description; figures; synonymy; behavior].
Onchocephalus nasutus var. *cayennensis:* PUYO 1949:260 [Cayenne, French Guiana; description; figures; synonymy].
Ogcocephalus truncatus: LOWE (MCCONNELL) 1962:679 [British Guiana; partial description; ecology].
Ogcocephalus nasutus: CERVIGNON M. 1966:867 [Venezuela; description; figures; key]; DAHL 1971:316 [Colombia; figures; key].
Ogcocephalus notatus: BRADBURY 1967:417 [type-series enumerated].

The figure of a skeleton labeled *Lophius histrio* in Rosenthal (1822:pl. 19, fig. 2) is assigned to the Ogcocephalidae; the strongly depressed body and the elongate pectoral radials and opercular bones are unmistakably those of an ogcocephalid. The details of the skull, however, are not clear enough to identify the figure to genus. The high cranium with what appears to be a secondary roof over the illicial groove is characteristic of *Ogcocephalus,* and the relatively large mouth suggests that the skeleton may be that of *O. notatus,* but other possibilities cannot be excluded. I place *Lophius histrio* (non Linnaeus) of Rosenthal, 1822, in the synonymy of *Ogcocephalus notatus* so as to retain it with the synonym *Malthe angusta* Cuvier, 1829, which was based on Rosenthal's figure. Since the name *M. angusta* Cuvier, 1829, was given in a footnote with no other designation, and since the figure cannot be identified with certainty, the name becomes a nomen dubium. Two other names given in the same footnote, *M. notata* and *M. truncata,* are without designations and are therefore nomina nuda.

All three names were published with designations at a later date (Cuvier and Valenciennes 1837). Their holotypes are all representatives of the same species, in spite of the variation the specimens exhibit in length of the rostrum and number of spots on the disk. Since *M. notata* has page priority over the other two available names, it is the valid name.

DIAGNOSIS AND COMPARISONS.—Distinguished from all other species of *Ogcocephalus* by its wide mouth (Fig. 6) and an additional lateral-line scale in the premaxillary series (4 in *notatus,* 3 in all other species). Four species of *Ogcocephalus* have geographic ranges overlapping that of *notatus*; these are *parvus, pumilus, vespertilio,* and *nasutus.* Of the four, only *nasutus* seems to occupy the same grounds and is occasionally taken in the same net hauls with *notatus,* but *vespertilio,* which seems to be an inshore species, may also eventually be shown to co-occur with *notatus. O. notatus* is distinguishable from *nasutus* and *vespertilio* by the shorter length of its disk margin (Fig. 7). The other two species, *parvus* and *pumilus,* with geographic ranges overlapping that of *notatus,* probably do not co-occur with *notatus* because they have relatively deep bathymetric distributions. *O. notatus* is distinguishable from *parvus* and *pumilus* by its higher number of pectoral rays (nearly always 13 or more in *notatus,* 12 or fewer in *parvus* and *pumilus,* Table 3).

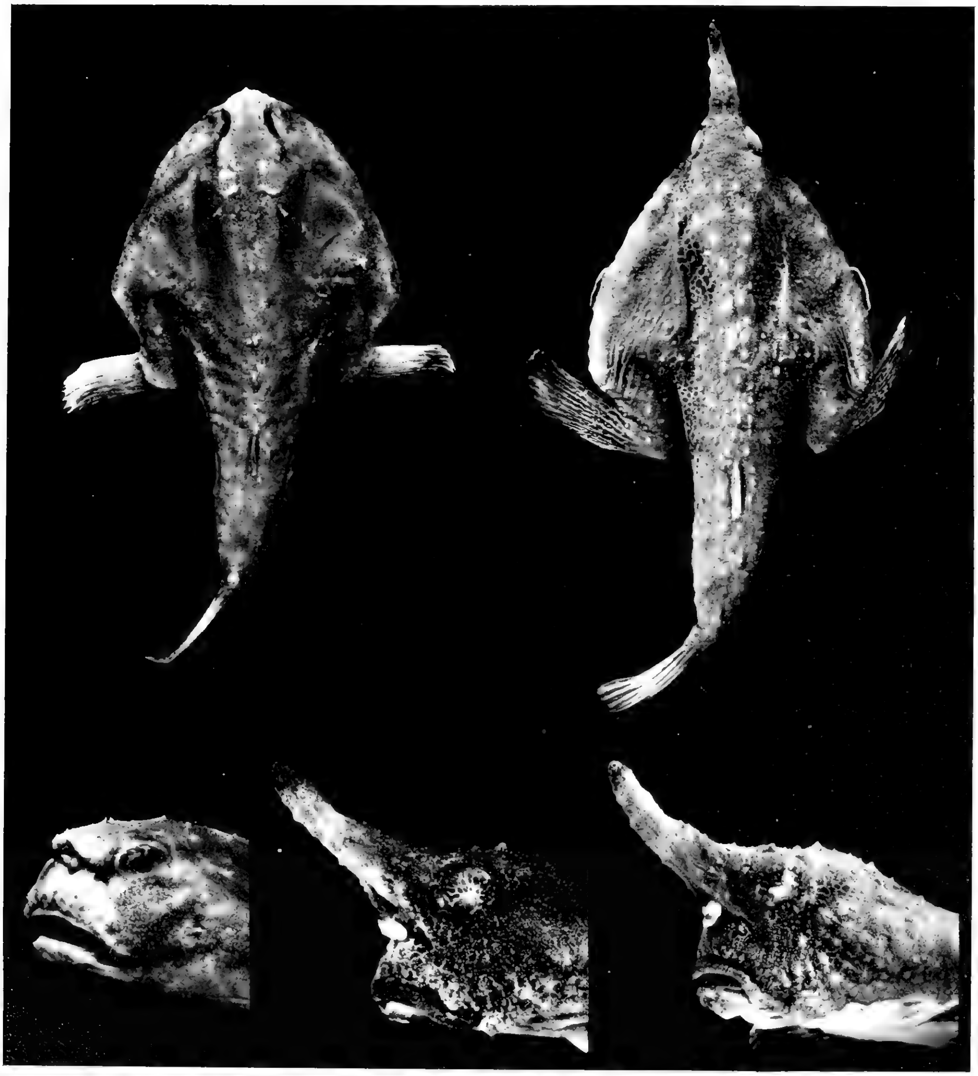


FIGURE 5. *Ogcocephalus notatus* (Cuvier and Valenciennes), MCZ 45075, 104.5 mm SL, from off northern Brazil, *left top*; view of face, *left bottom*, showing shelflike rostrum (small specimens usually have short median horn). *Ogcocephalus vespertilio* (Linnaeus), CAS-SU 59624, 175.0 mm SL, from off northern Brazil, *right top*; view of face, *right bottom*, showing reticulated pigment pattern. *O. vespertilio, bottom center*, also CAS-SU 59624, 150.0 mm SL, showing reticulated pattern commonly found on face and iris in this species.

O. notatus is further distinguished from all other species in the genus in having an oval-shaped pupil, whereas all the others have the iris modified by the presence of opercula so that the pupil is irregular in shape, approximately kidney- or dumbbell-shaped. It is inferred that these opercula regulate the amount of light passing through the pupil; if so, it appears that *O. notatus* lacks this mechanism. However, I have never observed this species alive. It is possible that appropriate tests of the iris in this species when subjected to bright illumination would show that opercula are present even though they fail to show in preserved materials.

DESCRIPTION.—Counts and measurements from 72 specimens, 20.0 to 133.8 mm SL (Table 1).

Counts. Counts given in Tables 2–6. *Ogcocephalus notatus* has relatively high meristic counts; the high count for lateral-line scales in

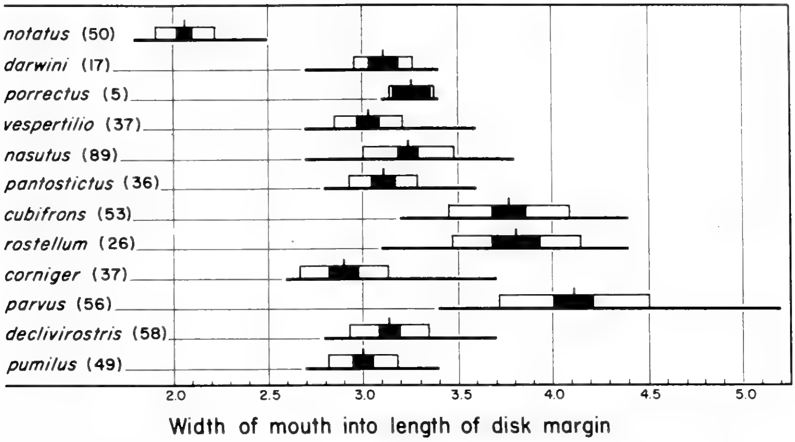


FIGURE 6. Variation in ratio of width of mouth into length of disk margin in *Ogcocephalus* (horizontal axis). Black bar = 2 standard errors of mean, white bar = 2 standard deviations, center vertical line = mean, and heavy horizontal line = range. This figure was drafted before all material of *darwini* and *porrectus* became available, but material studied subsequently does not change the point: *O. notatus* has a wider mouth than any other species in genus.

cheek series (usually 10) is diagnostic for the species (Table 5). The mean count of lateral-line scales in subopercular series in *O. notatus* (8.5) is exceeded only by *pantostictus* (9.1) and *vespertilio* (8.6) (Table 6). The mean count for pectoral rays in *notatus* (13.4) is less distinctive, resembling the *nasutus* population from off South America (13.1) and *rostellum* (13.0), but exceeded by *darwini, porrectus,* and *vespertilio* (all with mean pectoral counts of 14.0 or more) (Table 3).

Proportions. Proportions expressed as ratios given as the mean followed by the range in parentheses.

Disk margin shorter on average than in other species of *Ogcocephalus* except *darwini,* its length 2.5(2.3–2.8) in standard length. Tail wider on average than in other species, its width 1.6(1.2–2.3) in length of disk margin. Caudal peduncle of average depth, 2.7(2.4–3.2) in head depth. Rostrum produced into a short horn in small specimens, becoming extremely truncated and shelflike in larger specimens; length of rostrum 5.6(2.1–7.9) in length of disk margin. Aperture of illicial cavity oval to subdiamond shaped, wider than high in specimens of medium to large size, higher than wide in specimens about 50 mm SL or less. Cranium less sharply demarcated from disk than in other members of *Ogcocephalus,* its elevation above disk surface (when viewed from front) presenting a convex and gradual contour, not concave or abrupt. Head depth 1.8(1.6–2.1) in length of disk margin. Cranium broad, its width 2.8(2.2–3.3) in length of disk margin. Eye 1.7(1.4–2.0) in width of cranium, prefrontal width 1.5(1.3–1.7) in width of cranium. Interorbital space concave, moderately wide, its width 2.4(2.1–2.9) in width of cranium, 3.7(2.8–4.6) in head depth. Mouth wider than in other species of *Ogcocephalus,* 1.1(1.0–1.4) in head depth, 2.1(1.8–2.5) in length of disk margin; length of jaw 1.8(1.6–2.2) in head depth. Upper lip thin, lower lip a little fleshy laterally. Dorsal fin relatively long, its length 2.8(2.0–3.8) in length of disk margin; anal fin 2.7(2.3–3.5) in length of disk margin.

Integument. Dermal cirri conspicuous along lateral line of face, disk margin, and tail. Large bucklers present on disk margin and median dorsal area of body. Pectoral fins with tiny tubercles running out along rays dorsally but bare ventrally. Dorsal, anal, and pelvic fins devoid of tubercles except for a few tiny scattered ones at bases of pelvics and anal. Caudal fin as in generic description. Skin covering the eyeballs bearing tiny tubercles; edge of cornea not beaded by a row of small bucklers as occurs in other species. Pectoral membranes moderately thick, opaque, but no fleshy pads on ventral surfaces of ray tips.

Color in preservative. Dorsal surface uniformly gray with apices of bucklers paler than ground color. Distinct round spots with pale narrow margins in a cluster on either side of disk, 1 to

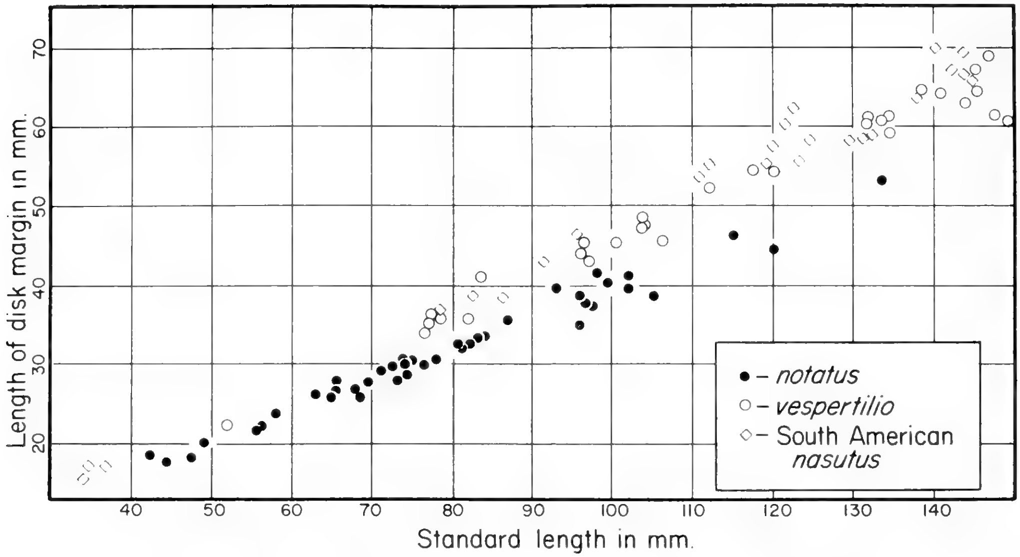


FIGURE 7. Comparisons between *Ogcocephalus nasutus* (only specimens from coast of South America), *O. vespertilio*, and *O. notatus* of relationship between length of disk margin and standard length. *O. notatus* over 75 mm SL shown to have relatively short disk margin.

7 on each side, occasionally none, particularly in very small specimens. One specimen 41.5 mm SL with dark rings scattered on dorsal surface of body and along sides of tail into the axillae. Ventral surface uniformly creamy pale, chin dusky in a few specimens. Lips the same pale ground color as the ventral body surface. Iris golden or dark gray, never with spots or radiating lines. Pectorals dusky, shading to darker gray distally, almost to black in some very small specimens, but tips of rays pale. Pelvic and anal fins the same creamy pale ground color as ventral body surface; anal sometimes with a dusky spot distally, especially in small specimens. Dorsal dusky, often with indistinct dark splotches; an oblique black stripe slashed across dorsal fin rays and membrane in specimens about 25.0 mm SL or less. Caudal fin as in generic description.

Color in life. Unknown.

DISTRIBUTION (Fig. 8).—Specimens studied ranged from Trinidad on the northeastern coast of South America to the mouth of the Amazon River, but the species is known from farther south and also from farther west into the Caribbean. Miranda Ribeiro (1915) reports one specimen, about 125 mm SL (his *Oncocephalus truncatus*), from Santos, Brazil; Cervigon (1966) reports specimens from the Caribbean coast of Venezuela at Laguna de Unare, and Menezes (1964) reports on a collection (his *Ogcocephalus radiatus*) from Aracajú. Bathymetric range: 18–64 m. Puyo (1949) reports specimens from estuaries, particularly of the Cayenne River, French Guiana, at depths of less than 2.5 m. He also reports one example from a swampy upstream section of a creek 8 km inland from Cayenne at a depth of approximately 1.8 m.

MATERIAL EXAMINED.—Numbers in parentheses are numbers of specimens. Data for OREGON stations (=O) in Bullis and Thompson (1965).

Trinidad: ANSP 53381 (1), Oropuche; CAS 23928 (2), O-2208.

Venezuela: CAS 23929 (2), O-2223; CAS-SU 62120 (1), O-2215; FMNH 65975 (13), O-2212; FMNH 65976 (2), O-2213; FMNH 65977 (1), O-2224.

Guyana: ANSP 103629 (5), O-2226; BMNH 1950.5.15.56 (2), Georgetown; BMNH 55.8.28.70 (1), Demerara; FMNH 65978 (24), O-2225; FMNH 65979 (77), O-2226; FMNH 65980 (1), O-2234; USNM 197108 (4), "Cape St. Mary."

Surinam: CAS-SU 62126 (3), O-2279, FMNH 65974 (3), O-2208; MCZ 45077 (4), COQUETTE sta. 193, 6°24′N, 55°03′W, 24 m; MNHN A.4764 (holotype); MNHN A.4767 (holotype of *Malthaea angusta* Cuvier and Valenciennes); MNHN A.4768 (1); MNHN 5259 (1); USNM 188772 (1), COQUETTE sta. 142, 6°23.5′N, 54°56′W, 26 m; USNM 188791 (1), COQUETTE sta. 167, 6°18.5′N, 55°28′W, 18 m; USNM 188781 (8), COQUETTE sta. 2, 6°23′N, 55°05.5′W, 27 m.

French Guiana: USNM 188773 (2), O-2038.

Brazil: *Amapá:* CAS-SU 51215 (5), O-2058; FMNH 65971 (1), O-2056; FMNH 65972 (4), O-2057; MCZ 45078 (4), O-2059. *Pará:* FMNH 65973 (13), O-2075; USNM 188797 (1), O-2076.

Specimens without locality data: CAS-SU 59629 (1), Brazil; MNHN A.4772 (holotype of *Malthaea truncata* Cuvier and Valenciennes); MNHN 5242 (said to be from New York, but this undoubtedly an error).

Ogcocephalus vespertilio (Linnaeus)

(Figure 5)

Lophius vespertilio LINNAEUS, 1758:236 ["American Ocean"; holotype in Zoologiska Institutionen Uppsala]; HOLM 1957:12 [holotype listed].

Malthaea longirostris CUVIER AND VALENCIENNES, 1837:450, pl. 365 [Bahia, Brazil; holotype MNHN 6369]; LÜTKEN 1866:208 [Maruim, Brazil; description].

Malthea guacucuja: CASTELNAU 1855:26 [Bahia, Brazil; cited as being the same as *Malthaea longirostris* Cuvier and Valenciennes].

Malthe vespertilio: GÜNTHER 1861:200 (part) [partial description; places the following names of Cuvier and Valenciennes, 1837, in the synonymy of *vespertilio*: *longirostris, nasuta, notata, angusta,* and questionably *truncata*]; JORDAN 1885:927 (part) [*longirostris* referred to synonymy of *vespertilio*]; LÖNNBERG 1896:39 [holotype listed].

Oncocephalus longirostris: MIRANDA RIBEIRO 1915: on page 574 of unnumbered text [Recife, Brazil; description]; 1918:153 [synonymy]; FOWLER 1941:184 [fishes of the coast of Brazil, compiled].

Ogcocephalus vespertilio: DE SOTO 1922:52 [Amazon R., 1300–1450 km upstream]; [?] CARVALHO 1943:71 [São Paulo, Brazil; partial description]; MENEZES 1964:155 [Brazil; synonymy; description; photographs]; BRADBURY 1967:417 [listed]; DE SCARABINO 1974:306 [mouth of Rio de la Plata; description; photographs].

DIAGNOSIS AND COMPARISONS.—*Ogcocephalus vespertilio* is distinguished from the majority of species of *Ogcocephalus* by its extremely long rostrum. Only two other species in the genus have rostrums that reach the relatively great lengths seen in *vespertilio*; these two long-nosed species are *corniger* and *pumilus* (Fig. 9 and Table 7), but they are easily separated from *vespertilio* on the basis of fewer pectoral rays (10–12 pectoral rays in *corniger* and *pumilus* compared to 13–15 in *vespertilio*). *O. vespertilio* also differs from *corniger* in color pattern, having dark spots separated by pale lines that usually form a reticulum occurring in patches on the face and sides of the tail and in the pectoral axillae, while *corniger* is evenly covered by closely set pale spots on a darker background. *O. pumilus* is a far smaller species than *vespertilio,* reaching only about 70 mm SL; from deeper waters than *vespertilio* (generally from waters 40 m or more in depth rather than the inshore, shallower depths attributed to *vespertilio*), *pumilus* is a pale gray species generally lacking markings of any kind; at the most, it has only light gray spots.

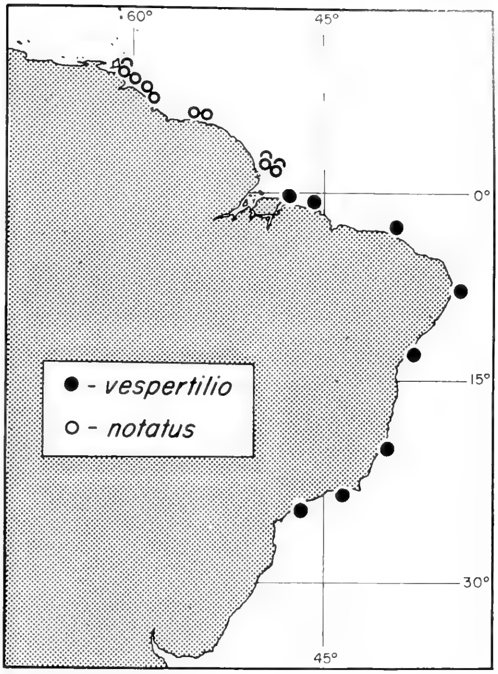


FIGURE 8. Distribution of study material of *Ogcocephalus notatus* and *O. vespertilio. O. notatus* also known from Caribbean and from Brazil, and *O. vespertilio* from mouth of Rio de la Plata (see text).

Ogcocephalus nasutus, cubifrons, and *pantostictus* all closely resemble *vespertilio* in their large size and body shape, but the relative length of the rostrum in *nasutus,* while highly variable, is seldom as great as in *vespertilio* (Fig. 10); *cubifrons* and *pantostictus* show allometric growth of the rostrum, with the smallest specimens having long rostrums and juvenile and adult specimens having progressively shorter ones. *O. vespertilio* is distinguished from *nasutus* by its relatively wide interorbital distance compared to the distance between the lateral ethmoids (Fig. 11) and by the modal number of pectoral rays (14 in *vespertilio,* 12–13 in *nasutus,* Table 3).

None of the long-nosed forms of *Ogcocephalus* are sympatric with *vespertilio,* including *cubifrons* and *pantostictus,* which are long-nosed only when small. These latter as well as *corniger* are at the northern edge of the range

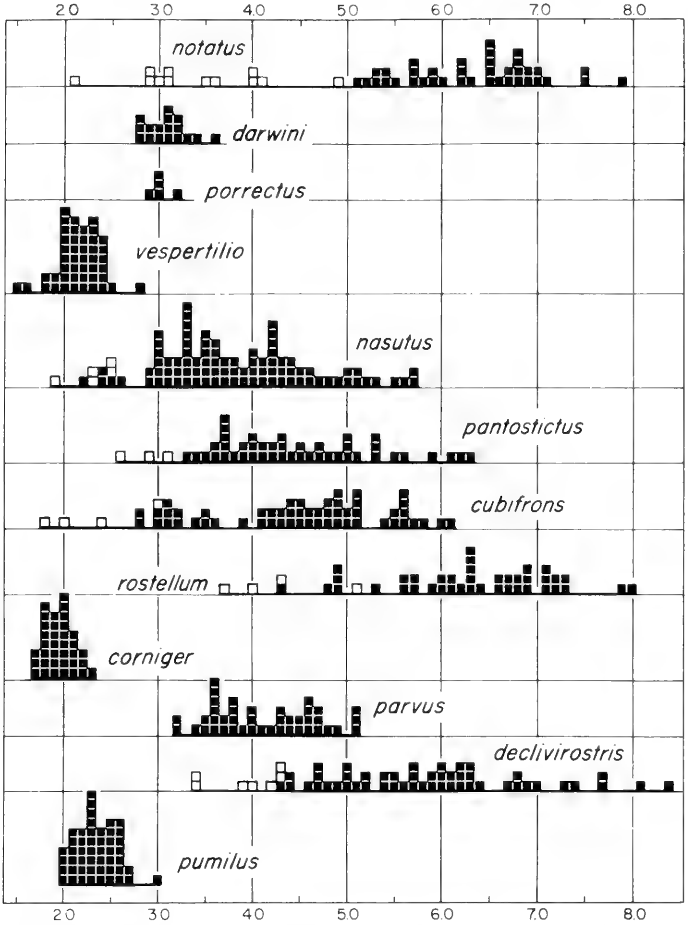


FIGURE 9. Histogram showing ratio of length of rostrum into length of disk margin (horizontal scale). One square = one specimen. White squares = specimens less than 50 mm SL (not shown for long-nosed species *vespertilio, corniger,* and *pumilus,* nor small species *parvus*). This figure was drafted before all material of *darwini* and *porrectus* became available, but new material does not change general picture. (With inclusion of new material, data for 30 *darwini* are: range 2.8 to 3.6, $\bar{x}$ = 3.1; for 35 *porrectus*: range 2.8 to 3.4, $\bar{x}$ = 3.0.)

for the genus (east coast of the United States and the Gulf of Mexico), while *vespertilio* occupies the southernmost range for the genus (coasts of Brazil and Uruguay). *O. pumilus* and *nasutus* have intermediate ranges (together ranging from Cuba and the Bahamas to Surinam). Only *nasutus* has a range which, as presently known, reaches almost to the northern edge of the range of *vespertilio,* that is, the vicinity of the mouth of the Amazon River.

The one species of *Ogcocephalus* which is sympatric with *vespertilio* is the short-nosed form, *notatus,* also distinguished from *vespertilio* by its wide mouth (Fig. 6) and higher number of lateral-line organs in the cheek series (4 in *notatus* but 3 in *vespertilio*).

DESCRIPTION.—Counts and measurements from 46 specimens, 52.0–222.5 mm SL (Table 1).

Counts. Counts given in Tables 2–6. Menezes (1964) recorded the pectoral count for *O. vespertilio* as 13–14, but I find a wider range of 12–15 with a strong mode of 14, which places the species second only to *O. darwini* in high number of pectoral rays. *O. vespertilio* also has relatively high counts for all lateral-line scale se-

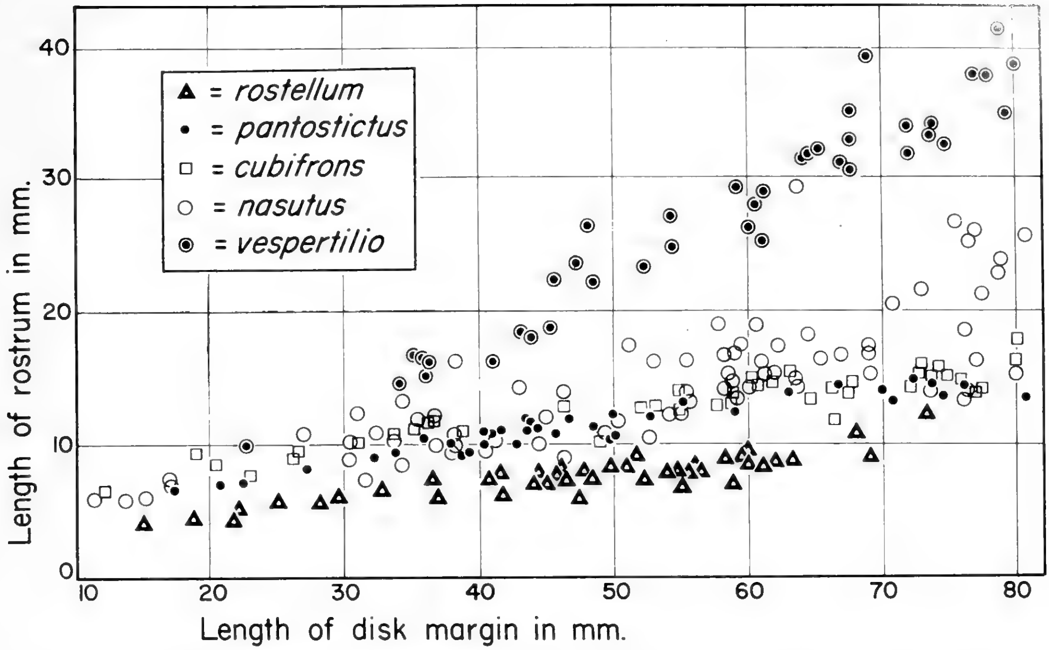


FIGURE 10. Comparisons among five closely similar species of *Ogcocephalus* to show relationship of length of rostrum to length of disk margin (see also Fig. 9). *O. vespertilio* shows long rostrum at all stages of growth, *cubifrons* and *pantostictus* show shortening of rostrum with growth, *rostellum* shows short rostrum at all stages of growth. Length of rostrum in *nasutus* extremely variable.

ries: subopercular lateral-line scale count modally 9 as in *notatus* and *pantostictus*; modal count for the cheek series 9. Scales in lateral line relatively numerous as in three other large species: *nasutus, pantostictus,* and *cubifrons*.

Proportions. Proportions expressed as ratios given as the mean followed by the range in parentheses. Length of disk margin intermediate within the range of variation for the genus, 2.2(2.0–2.4) in SL. Width of tail also intermediate, 2.0(1.5–2.5) in length of disk margin; caudal peduncle moderately deep, 3.0(2.5–3.5) in head depth. Rostrum with a thick base, proportionately longer than in any other species save *corniger,* its length 2.1(1.5–2.8) in length of disk margin. Aperture of illicial cavity elongate, triangular, always higher than wide. Cranium rising steeply above the disk, becoming massive in large adults; head depth 1.9(1.7–2.0) in length of disk margin. Width of cranium 3.3(2.9–4.0) in length of disk margin. The following in width of cranium: eye 1.5(1.3–1.8), lateral ethmoid width 1.9(1.6–2.3). Interorbital moderate to wide, flat posteriorly but distinctly convex anteriorly, grading into the roundness of the rostrum; interorbital width 2.0(1.5–2.4) in width of cranium, 3.4(2.6–4.0) in head depth. Mouth moderate, its width 1.6(1.5–1.7) in head depth, 3.0(2.7–3.6) in length of disk margin; jaw 2.2(2.0–2.4) in head depth. Upper lip fleshy, of an even width for its entire length; lower lip also fleshy, thickened medially. Dorsal fin of moderate size, 3.8(3.0–4.6) in length of disk margin; anal fin 2.7(2.4–3.1) in length of disk margin.

Integument. Dermal cirri present on tip of the rostrum, disk margins, and lateral sides of tail, usually sparse except on rostrum. Large bucklers prominent, arranged as in generic description. All fins with tiny tubercles, those on pectorals restricted to the base, those on ventrals and anal running out from base for about half length of fin. Tubercles on dorsal fin sparse except for anterior edge of fin where they thickly encrust the first ray and run out nearly to end of ray. Caudal as in generic description. Skin covering eyeballs studded with tiny tubercles,

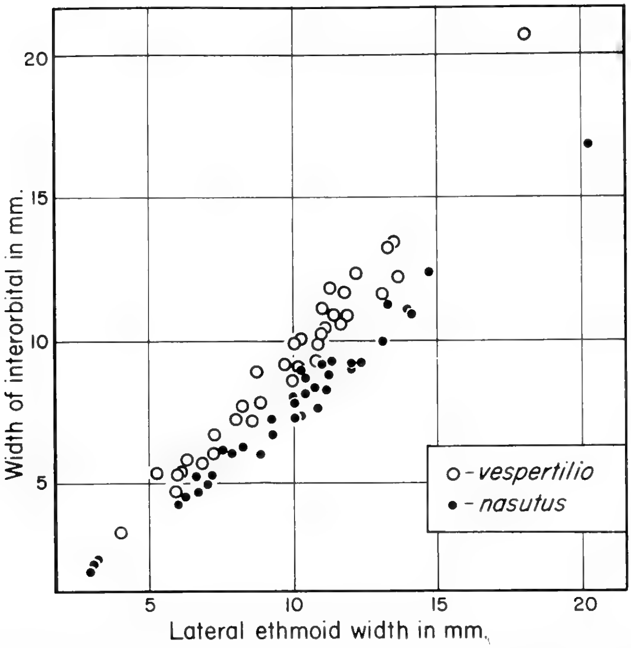


FIGURE 11. Comparison between *Ogcocephalus vespertilio* and *O. nasutus* (only specimens from South America) to show relatively wide interorbital distance compared to lateral ethmoid width in *vespertilio*.

the rim around cornea with small bucklers, but these not so prominent as in other species. Pectoral membranes thick, opaque, ventral surface of ray tips with well-developed fleshy pads.

Color in preservative. Ground color medium brown. Markings consist of dark spots separated by pale lines that form a reticulum. These markings occur on face, often within illicial cavity, and on esca, and generally extend in a band across each eye. On the eye, including the iris, light lines radiate from pupil. The markings extend posteriorly from each eye and are often continuous on each side with a patch of markings on each shoulder. Similar markings extend from axillae along lateral sides of tail. Sometimes patch in axilla also continuous with shoulder patch on each side. Ventral surface of body uniformly light yellowish brown, or sometimes chin and tail slightly darker. Lips pale; rostrum with a diffuse dark subterminal ring. Iris marked with an extension of the same pattern that covers face. Pectorals with reticulate markings basally, grading into a dark border; rays tips pale. Dorsal also with reticulate pattern. Ventrals and anal the same ground color as ventral surface of body; tips of ventrals dusky, tip of anal dusky to black. Caudal as in generic description, but with reticulate markings superimposed on basal two thirds.

Color in life. Unknown.

DISTRIBUTION (Fig. 8).—Coasts of Brazil and Uruguay from Amazon River south to La Plata River. Little bathymetric data available; appears to be an inshore species. One specimen identified as *Ogcocephalus vespertilio* recorded from 1300–1450 km upstream in Amazon River (de Soto 1922).

MATERIAL EXAMINED.—The holotype, Linnésamling no. 163, Museum Alströmer-Linné no. 40, Uppsala University, examined for me by C. L. Hubbs; exact locality unknown. All other material from **Brazil**; numbers in parentheses are numbers of specimens. *Pará:* USNM 12575 (1), Amazon. *Maranhão:* CAS-SU 59627 (1) and CAS-SU 59628 (4), Rio Bacanga, Madre Deus; CAS-SU 59630–59632 (3), Madre Deus. *Ceará:* CAS-SU 59616–59620 (5) and CAS-SU 59622–59626 (10), Mucuripe, Fortaleza; CAS-SU 59621 (2), Fortaleza. *Pernambuco:* USNM 104286 (1), Recife. *Bahia*, all from Salvador: CAS-SU 59633 (1), market; MCZ 1037 (1); MCZ 25741 (1); MNHN 6369 (holotype of *Malthaea longirostris* Cuvier and Valenciennes); ZMUC 18 (1). *Espírito Santo:* CAS-SU 59612 (1) and CAS-SU 59614 (1), Enseada, Vitória; CAS-SU 59615 (1), Vitória. *Rio de Janeiro:* MCZ 11755 (1) and MCZ 11756 (2), Rio de Janeiro. *São Paulo:* CAS-SU 59610 (1) and CAS-SU 59613 (1), Ponta da Praia, Santos; CAS-SU 59611 (1), Ponta do Rabo Azedo, 113 km NE São Paulo.

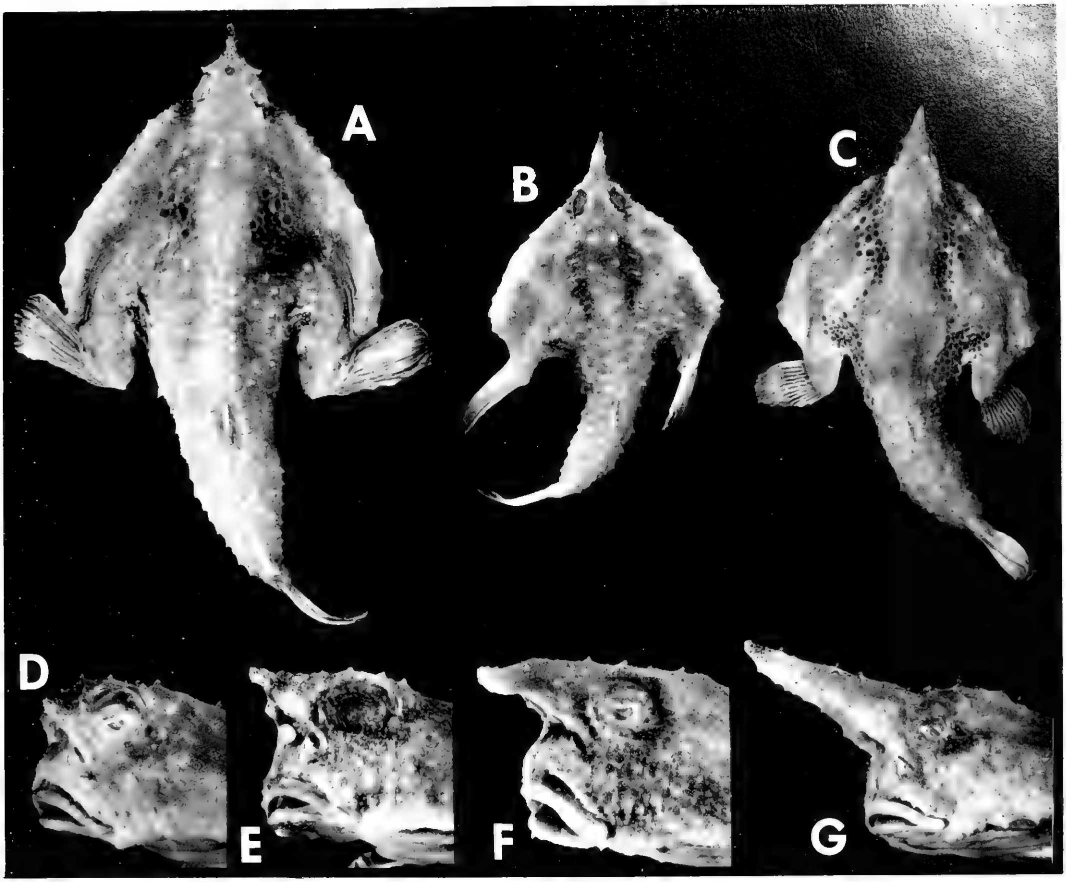


Figure 12. Variation in *Ogcocephalus nasutus* (Cuvier and Valenciennes). *(A)* Specimen from off Surinam, FMNH 87034, 135.0 mm SL, and *(B)* specimen (juvenile) from Caribbean off Venezuela, MCZ 41510, 84.0 mm SL, both showing common pattern of clusters of spots on shoulders. *(C)* Specimen from northern Brazil, FMNH 66386, 130.0 mm SL, showing uncommon condition of clusters of spots extending from eyes backwards to axillae, reminiscent of *O. vespertilio*. *(D)* From Honduras, CAS 28520, 148.5 mm SL. *(E)* and *(F)* From Surinam, CAS-SU 51208, 130.5 mm SL, and FMNH 64900, 203.0 mm SL. *(G)* From Nicaragua, CAS 28494, 205.0 mm SL. Extremely short rostrum *(D)*, bent rostrum *(F)*, and extremely long rostrum *(G)* are unusual, but all occur in both Central American and South American material.

Ogcocephalus nasutus (Cuvier and Valenciennes)

(Figures 12 and 13)

[?] *Rana piscatrix* Seba, 1734:pl. 74, fig. 2 [Curaçao; see comment after synonymy].

Lophius vespertilio (non Linnaeus): Bloch 1787:8, pl. 110 [description]; Parrá 1787:pl. 4 [not seen; a hand-drawn copy by Señorita Poey was consulted; Cuba]; Cuvier 1816:311 [based on Bloch 1787].

[?] *Lophius rostratus* Shaw, 1804:383 [description; nomen dubium; see comment following synonymy].

[?] *Malthe nasuta* Cuvier, 1829:252 [nomen dubium, based on Seba 1734; see comment following synonymy].

Malthea vespertilio (non Linnaeus): Cuvier and Valenciennes 1837:440 ["Porto-Rico, Martinique, Terre-Neuve"; description].

Malthaea nasuta Cuvier and Valenciennes, 1837:452 [Martinique, "Saint-Domingue, New-York"].

Ogcocephalus vespertilio (non Linnaeus): Jordan and Evermann 1898:2737 ["Havanna, Cuba"; description]; Meek and Hildebrand 1928:1017 [Porto Bello, Panamá; description]; Beebe and Tee-Van 1928:272 [Port-au-Prince Bay, Haiti; key; field characters; color in life]; Herre 1942:305 [Bridgetown, Barbados]; Martin S. 1956:142 [Los Roques off coast of Venezuela; description]; [?] Lowe (McConnell) 1962:680 [British Guiana (Guyana); partial description; ecology]; [?] Cervigon M. 1966:870 [Venezuela; description; key]; [?] Dahl 1971:317 [Colombia; key].

Ogcocephalus nasutus: Beebe and Tee-Van 1928:273 [Port-au-Prince Bay, Haiti; key; field characters; color in life]; Bradbury 1967:417 [listed]; Randall 1967:825 [West Indies; food habits]; 1968:295 [photograph; description];

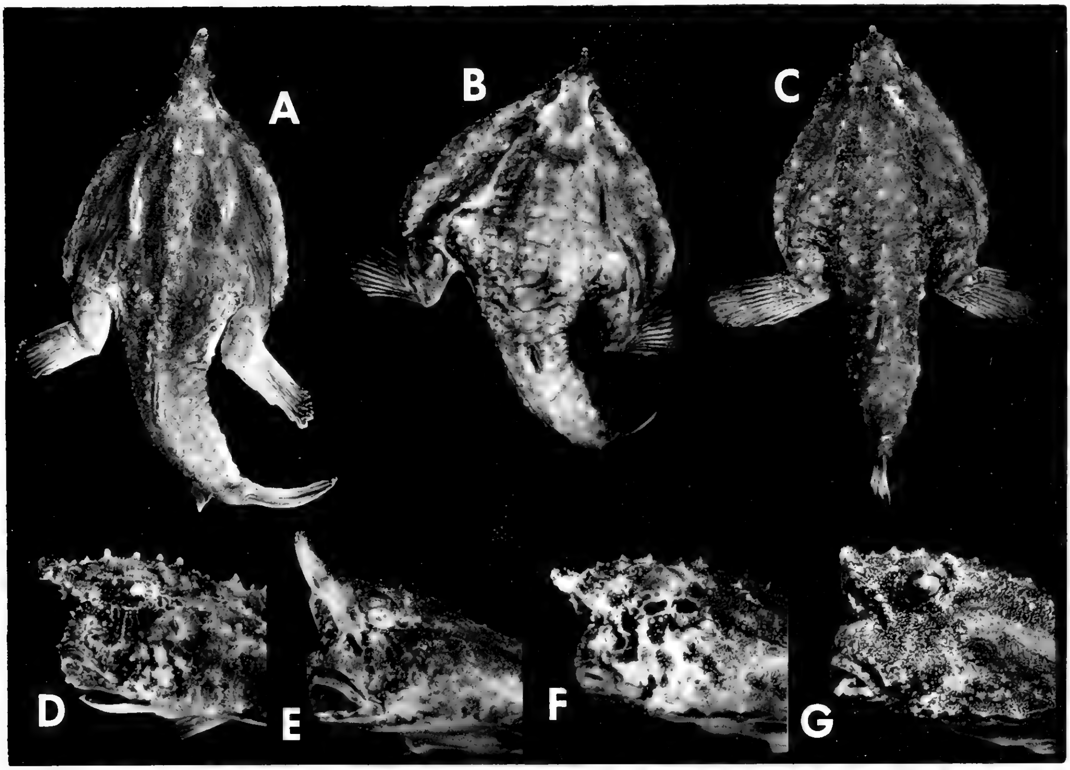


FIGURE 13. Variation in *Ogcocephalus nasutus* (continued from Fig. 12). *(A)* From Belize, CAS 42579, 182.0 mm SL, and *(B)* from the Bahamas, ANSP 90674, 187.0 mm SL, both lacking color pattern except for few dim ocellated spots on disk of Belize specimen. In spite of absence of color pattern on body, striped and spotted patterns on face common in specimens from West Indies and Central America: *(D)* from Panama, MCZ 11768, 112.0 mm SL; *(E)* from Belize, same specimen as *(A)*; *(F)* from the Bahamas, UF 24185, 108.0 mm SL. *(D)* Also shows exaggeratedly spiny bucklers occasionally seen among specimens from West Indies and Central America; *(F)*, a less pronounced example of spiny squamation. *(C)* From the Bahamas, ANSP 90670, 170.0 mm SL, showing clusters of spots frequently seen in West Indies material; however, this specimen also has square-browed conformation of head characteristic of *O. cubifrons* and is intermediate between *cubifrons* and *nasutus* in other characters. *(G)* From the Bahamas, ANSP 90671, 162.0 mm SL, also intermediate between *cubifrons* and *nasutus*, with extremely dark coloration sometimes seen in West Indies material, but photographed while wet and intensely highlighted; compare conformation of rostrum with Figure 23*G*.

BÖHLKE AND CHAPLIN 1968:728 [description; bathymetric range; habits; key; figure].

Oncocephalus vespertilio (non Linnaeus): FOWLER 1947:14, fig. 9 [Nassau or Hog I., Bahama Is.; description].

Ogcocephalus radiatus: BREDER 1949:95, pl. 10, figs. 1–4 [Bimini, Bahama Is.; behavior; photographs]; DAHL 1971:317 [Colombia; key; figs.].

The name *Lophius rostratus* Shaw, 1804, is based upon a textbook compilation drawn from Linnaeus together with the pre-Linnaean authors Seba (1734), Browne (1756), and Marcgrave (1648). The description in Marcgrave of a fish from Brazil gives proportions of the rostrum indicating it was the same species Linnaeus later described and named *vespertilio*. Linnaeus used the term "*rostratus*" (beaked) in describing *vespertilio*, suggesting that Shaw's name derives from Linnaeus's description. In any case, *rostratus* Shaw in part refers to the long-nosed Brazilian form described by Marcgrave and Linnaeus. However, the other two authors to whom Shaw referred, Seba and Browne, described and figured specimens said to be from Curaçao and Jamaica, respectively; the localities and the figures suggest *nasutus* but do not limit the possibilities to *nasutus*. The illustration in Shaw also appears to depict *nasutus* because it shows a rostrum of only moderate proportions, but apart from that the illustration is highly stylized and difficult to interpret. Finally, the range given by Shaw, "South-American seas," is too general to apply to any particular species. As I am unable to determine Shaw's *Lophius rostratus* either from his sources or from his description, I hereby reject the name *Lophius rostratus* Shaw as a nomen dubium.

The name *Malthe nasuta* Cuvier, 1829, was published in a footnote with no other designation than a figure in Seba (1734) labeled *Rana piscatrix*. This stylized drawing may represent the Antillean-Caribbean form of the species of *Ogcocephalus* under consideration here, but it is a very generalized figure and could be a representation of any of several other species. Because it is impossible to establish the identity of the figure upon which the name *Malthe nasuta* Cuvier, 1829, was based, the original description of *Ogcocephalus nasutus* is here considered to be that of Cuvier and Valenciennes, 1837.

COMPARISONS AND DIAGNOSIS.—At the beginning of this study, only specimens from the West Indies and the Venezuela-Guiana coast of South America were available for examination. These specimens showed some differences in color pattern and sometimes in squamation. Specimens from the West Indies included many with relatively dark overall color and reticulated markings around the gill pores, in the axillae, and on the lateral sides of the tail; these sometimes had jagged clusters of spinules at the tips of bucklers that made the body very rough (Fig. 13*D* shows this condition). Specimens from the northern coast of South America were a lighter, more uniform brown in color with less jagged bucklers; these generally were from depths of 30 m or more, but no comparisons with the West Indies specimens could be made on this point, as the latter usually lacked bathymetric data.

Eventually, specimens from the Caribbean coast of Central America became available. They generally came from offshore in depths over 30 m, but some were from shallower water. These Central American specimens resembled the South American specimens in color and squamation, their integument relatively pale and smooth, but the dark, rough-skinned variants occur here too, known from older museum specimens that also lack bathymetric data. In any case, the three groups of specimens were treated separately, so tables of data in this report show three sets of data for *O. nasutus*, which are designated as West Indies *nasutus*, Central American *nasutus*, and South American *nasutus*.

Besides varying in color pattern, *O. nasutus* is more variable than other species in the genus in lateral-line scale counts and in rostrum proportions, features relied upon in this study to characterize species. Apparently, *nasutus* also has a greater bathymetric range than any of its congeners, occurring inshore as well as offshore to depths of approximately 200 m in parts of its range. Perhaps bathymetric variations will eventually help explain morphological variation in this form.

One of the largest species of *Ogcocephalus* (Table 1), *nasutus* most resembles *cubifrons* to the north of its range and *vespertilio* to the south. At this time it appears that *nasutus* is allopatric with the Brazilian species *vespertilio*, but this assertion needs verification. In the north *nasutus* occurs with *cubifrons* off southeastern Florida and in the western Bahamas; whether or not it is entirely distinct from *cubifrons* in the western Bahamas is in doubt because a few specimens which are intermediate between *nasutus* and *cubifrons* have been taken there. *O. nasutus* differs from *cubifrons* in having a longer jaw (Fig. 14) and a narrower interorbital distance (Fig. 15), a rostrum longer on the average but more variable (Fig. 10), and higher modal number of lateral-line scales in the cheek series (9 instead of 8 as in *cubifrons*, Table 5). Color pattern also assists in separating *nasutus* from *cubifrons*: clusters of dark spots occur on the face, disk, and tail in both species, but *nasutus* lacks the bright pattern of spots on the pectoral fins seen in *cubifrons*. From *vespertilio, nasutus* differs in usually having a shorter rostrum (Fig. 10), a narrower interorbital distance (Fig. 11), and a lower modal count of pectoral rays (12–13 in *nasutus*, 14 in *vespertilio*, Table 3).

Ogcocephalus nasutus also resembles *pantostictus* and *rostellum* in general appearance. Compared to *pantostictus*, which shows allometric growth of the rostrum, the rostrum in *nasutus* is variable but generally longer than in *pantostictus* (Fig. 10). *O. nasutus* also differs from *pantostictus* in having a lower modal number of lateral-line scales in the subopercular series (8 compared to 9, Table 6), and *nasutus* has a pattern of spot clusters or may lack spots entirely, while *pantostictus* has a pattern resembling polkadots covering the entire dorsal sur-

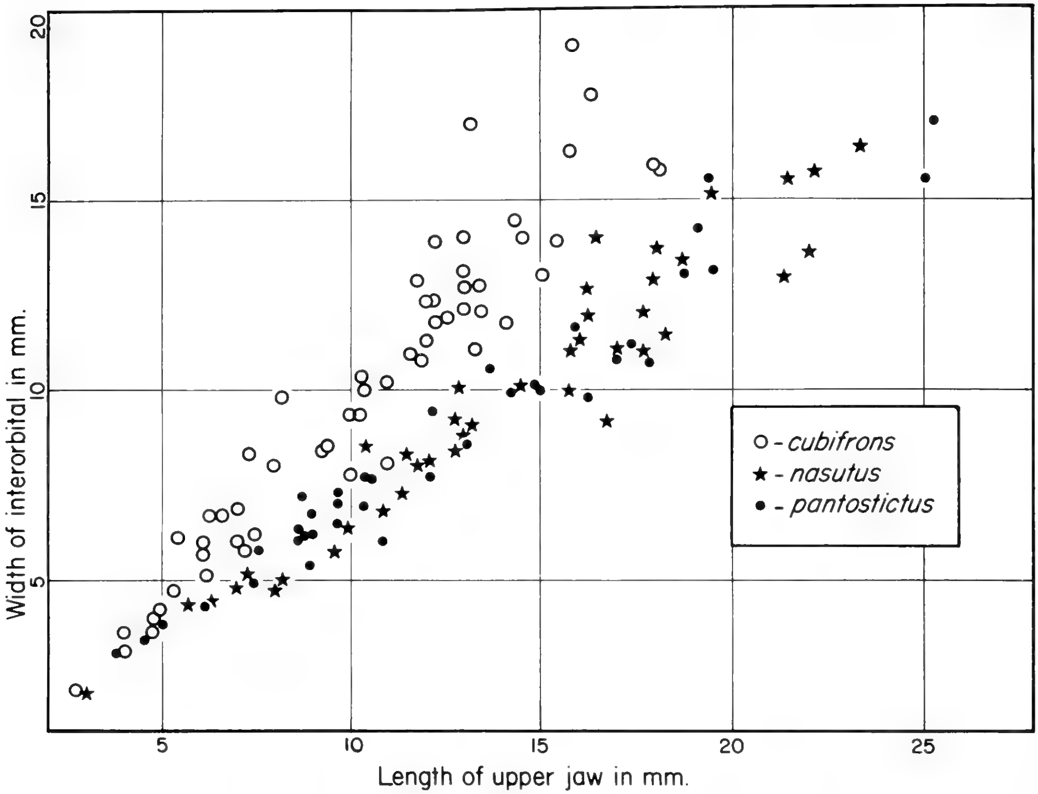


FIGURE 14. Comparisons between *Ogcocephalus nasutus* (only specimens from West Indies), *O. cubifrons*, and *O. pantostictus* to show that jaw is short in *O. cubifrons* relative to width of interorbital.

face of the body. *O. nasutus* differs from *rostellum* in having a longer rostrum (Fig. 10), a higher modal number of lateral-line scales in the cheek series (9 compared to 8 as found in *rostellum*, Table 5), and a relatively longer jaw (Fig. 16)

Ogcocephalus parvus and *O. pumilus* occur within the range of *nasutus*, but both are smaller species, reaching only 85 mm in standard length. Both differ further from *nasutus* in some meristic counts: pectoral rays usually 12–13 in *nasutus*, 10–12 in *parvus* and *pumilus*; lateral-line scales in the cheek series 9 in *nasutus*, 8 in the other two (Tables 3 and 5).

The range of *O. nasutus* slightly overlaps that of *corniger* in the vicinity of southeastern Florida and the western Bahamas; however, *corniger* is distinguished by its color pattern of close-set pale spots on a darker background evenly covering the entire dorsal surface, while *nasutus* has spot clusters on a lighter background or no spots at all. *O. nasutus* and *O. corniger* also differ in some meristic counts: pectoral rays usually 12–13 in *nasutus*, 10–12 in *corniger*; lateral-line scales in the cheek series 9 in *nasutus*, 8 in *corniger* (Tables 3 and 5).

The southern portion of the range of *nasutus* overlaps the range of *notatus*, but the two are distinguished by the relative length of the disk margin (longer in *nasutus*, Fig. 7) and width of the mouth (narrower in *nasutus*, Fig. 6) as well as the lateral-line scale count of 3 in the premaxillary series in *nasutus* (4 in *notatus*) and 9 in the cheek series (10 in *notatus*).

DESCRIPTION.—Counts and measurements based on 106 specimens as follows: 40 specimens, 26.2–232.0 mm SL from the West Indies; 25 specimens 42.7–223.0 mm SL from the coast of Central America and Yucatán; 41 specimens, 29.0–233.5 mm SL from the coast of South America.

Counts. Counts given in Tables 2–6. A

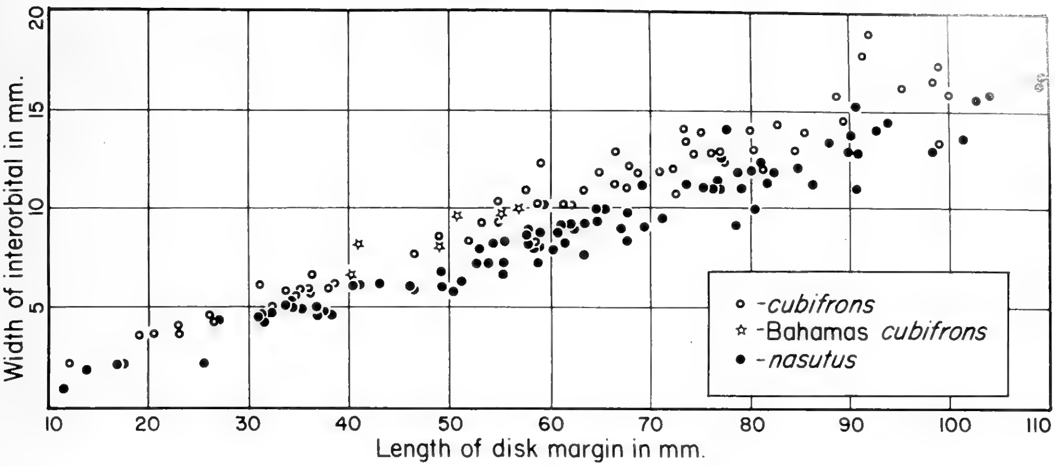


FIGURE 15. Comparison between *Ogcocephalus cubifrons* and *O. nasutus* to show that interorbital is widest in *O. cubifrons* relative to length of disk margin.

marked difference in pectoral count exists between Antilles–West Indian and Central American specimens on the one hand and South American specimens on the other, most frequently 12 in Antilles–West Indian and Central American specimens, usually 13 in South American specimens. A small cline is formed between these two groups of *nasutus* and *vespertilio*, which most frequently has 14 pectoral rays, but clinal variation is not found in other counts. *O. nasutus* shows a wider range of variation with a higher degree of asymmetry in counts of lateral-line scales in the subopercular series than other species in the genus, but resembles most other species in having a relatively narrow range of variation in the count for the cheek series of lateral-line scales (modally 9, a feature in which *nasutus* resembles *vespertilio*). *O. nasutus* has a relatively high count for lateral-line scales, perhaps associated with the large size of the species, since other large species (*vespertilio*, *pantostictus*, and *cubifrons*) also have high lateral-line scale counts.

Proportions. Proportions expressed as ratios given as the mean followed by the range in parentheses.

Length of disk margin intermediate for the range of variation in the genus, 2.2(2.0–2.4) in SL. Tail moderately wide to narrow, its width 2.0(1.7–2.7) in length of disk margin; depth of caudal peduncle quite variable but averaging relatively deep, 2.8(2.2–3.5) in head depth. Rostrum extremely variable in length and contour. It may be as short as the rostrum of examples of *cubifrons* of comparable size (especially true among Bahaman and western Caribbean specimens) or as long as that of *vespertilio*. It may be thick-based and conical or slender and finger-shaped. Usually it is straight, either horizontal or tilted upward, but a few specimens have it crooked with its tip bent sharply upward or drooping downward (Fig. 12, 13). Length of rostrum 3.7(1.9–5.7) in length of disk margin. Aperture of illicial cavity subtriangular, higher than wide. Cranium rising steeply above disk, head depth 2.0(1.7–2.2) in length of disk margin. Width of cranium 3.4(2.5–4.0) in length of disk margin. The following in width of cranium: eye 1.5(1.3–1.9), lateral ethmoid width 1.7(1.4–2.0). Interorbital variable, from slightly concave to flat or even a little convex anteriorly where the interorbital contours grade into the roundness of the rostrum. Width of interorbital 2.1(1.7–2.7) in width of cranium, 3.6(2.8–4.4) in head depth. Mouth moderate, its width 1.6(1.4–1.8) in head depth, 3.2(2.7–3.8) in length of disk margin; jaw 2.3(2.1–2.5) in head depth. Upper lip fleshy, of an even width for its entire length; lower lip fleshy, swollen medially. Dorsal fin 4.4(2.9–5.6) in disk margin; anal fin 3.0(2.4–3.9) in disk margin.

Integument. Dermal cirri sometimes present. Large bucklers prominent, arranged as in generic description. All fins with tiny tubercles.

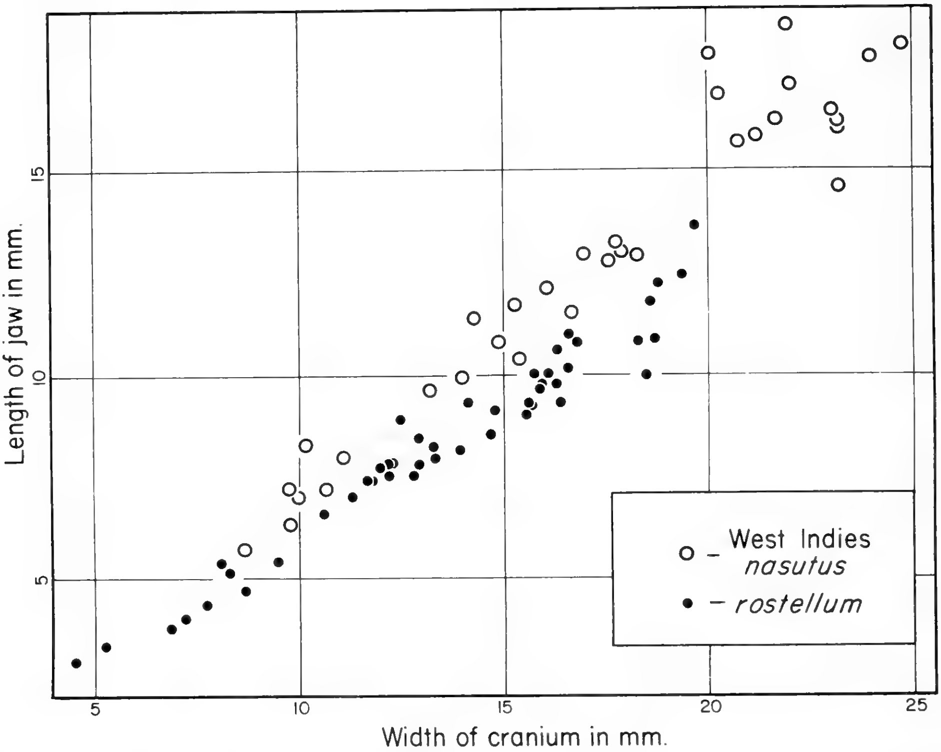


FIGURE 16. Comparison between *Ogcocephalus nasutus* (only specimens from West Indies) and *O. rostellum* to show that jaw is long in *O. nasutus* relative to width of cranium.

On pectorals, ventrals, and anal, tubercles are variable in distribution, sometimes restricted to bases of fins, sometimes running out along rays for half their length. Dorsal fin with tubercles on anterior edge of first ray, sometimes running out along ray nearly to its tip. Caudal as in generic description. Skin covering eyeballs bearing tiny tubercles with rim around the cornea beaded by a row of small bucklers. Pectoral membranes thick, opaque, ventral surface of rays with fleshy pads.

Color in preservative. Specimens from West Indies often very darkly pigmented, but specimens from off coast of South America and Central America usually have dorsal surface of body tan or medium brown, with ventral surface of body usually paler than dorsal surface. As pointed out elsewhere, it is likely that this color variation is correlated with depth and not geographical locality; a corroborative observation is that several specimens from Central America from presumed shallow water (exact depths not given) were relatively darkly pigmented.

Roundish dark spots often present clustered in a patch on either shoulder. Markings on face, lateral walls of tail, and in axillae tend to be reticula of pale lines between dark irregular patches. Specimens from West Indies sometimes have dark stripes with narrow light borders on face and iris which form a radiating pattern around pupil. Ventral surface pale to dark gray in West Indian specimens, the chin often particularly dark; ventral surface uniformly pale in South American and Central American specimens. Lips in West Indian specimens usually darkly pigmented in dark specimens, but otherwise lips pale. Rostrum generally with a diffuse black subterminal ring. Iris black or marked with an extension of color markings of face. Pectorals of West Indian specimens generally dark to nearly black, always with a black margin even when fin pale basally; pectorals of South American and Central American specimens usually pale dusky to medium gray or tan, shading to a darker margin. Dorsal variable, pale to dark, ordinarily without markings. Ventrals and anal the same ground color as ventral surface of body; in dark specimens the ventrals and anal

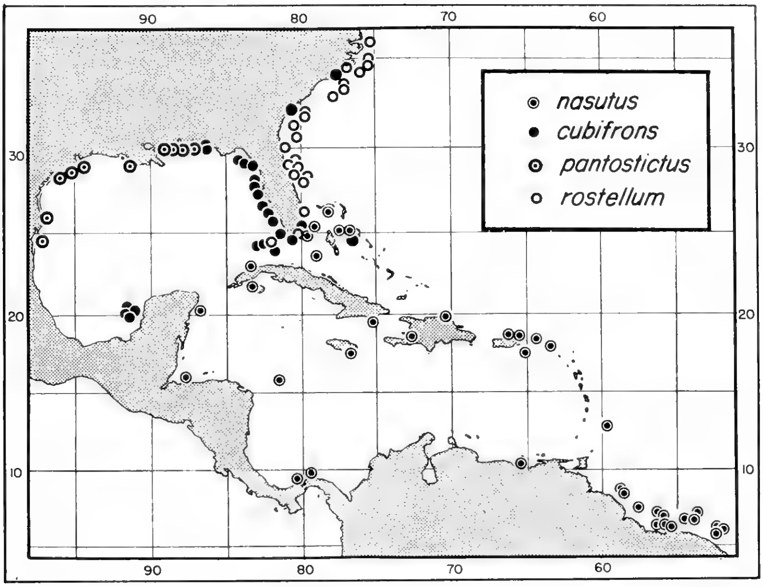


FIGURE 17. Localities for study material of *Ogcocephalus nasutus, O. cubifrons, O. pantostictus,* and *O. rostellum.* Scale of map too small to show that *O. cubifrons* and *O. pantostictus* are parapatric in northern Gulf of Mexico; see text for localities.

may have dark tips, and small specimens nearly always have anal black-tipped. Caudal fin as in generic description.

Color in life. Kodachrome transparencies made of a freshly captured specimen from off coast of South America show dorsal surface of body uniformly grayish olive-green, a mudlike color, with conspicuous clusters of black spots on either shoulder. Pectorals and caudal the same greenish shade basally, shading to black margins. Lips, ventral surface of body, and anal fins rosy tan.

Breder (1949) writes of a specimen captured from off Bimini and kept in an aquarium, "For the most part the fish remained an intense black, so much so that it was only with difficulty that any of the ordinarily visible fish structures could be seen. Thus the pupil, iris, and skin about the eye were so much the same that none of the details could ordinarily be seen at all. The inside of the mouth and the membranes shown when 'yawning' were at all times a rich mahogany and very contrasting to the entirely black fish. At night on a few occasions the iris became mahogany colored, and vague lighter bands appeared across the back."

Perhaps color variation is governed to some extent by variations in the amount of ambient light, with dark specimens coming from shallow, well-lighted waters and lighter colored specimens coming from deeper water. Dr. John E. Randall (personal communication) says of a specimen 164 mm SL which was taken in water about 21 m deep in Reef Bay, St. John, Virgin Islands, "The fish was brown on top with no spots. There were some short white lines near the gill opening and around the ventral half of the eye and snout below the rostral prominence. The mouth was bright red. The ventral part of the fish was red."

Dr. Bruce B. Collette (personal communication) noted that a specimen he took from water 1–1.5 m deep off the Isle of Pines had lips that were brilliant vermillion.

DISTRIBUTION (Fig. 17).—Material used for counts and measurements in this study came from the West Indies and the coasts of Central and northern South America to the mouth of the Amazon River. However, during the final preparation of this report, the following specimens were seen which extend the range to southeastern Florida: UMML 16813, 1 specimen, bridge at Bear Cut, Dade Co., and UMML 33252, 1 specimen, Bear Cut at Virginia Key, Dade Co. Bathymetric range: shore to 275 m.

REMARKS.—Early in this study I examined the type material in the Muséum National d'Histoire Naturelle, Paris, which consisted of the following three specimens: A.4665, Martinique, Keraudren; A.4765, Saint Domingue, Ricord (Pichon); and A.4766, New York, Milbert. The Martinique specimen, a dried example mounted on a wooden stand and about 200 mm SL, was difficult to perform counts and measurements on, but had a relatively short rostrum, wide mouth, and narrow interorbital. The Saint Domingue specimen, 192.5 mm SL, had an extremely short rostrum, wide mouth, and wide interorbital. The New York specimen, 34.0 mm SL, had a relatively long, slender rostrum, but the specimen is too small for other proportions to be useful. This specimen is also problematical because the locality is outside the known range of *nasutus* as understood here. Although a stray occurrence off New York is certainly possible, it is also possible that the original locality information is wrong. None of the specimens had discernible markings.

Recognizing now that *nasutus* is variable and difficult to characterize, and that setting its limits is yet to be accomplished, I cannot assert that the three types are conspecific. To compound the difficulty, I recently checked the status of these specimens and was informed by Dr. M.-L. Bauchot (personal communication) that specimen A.4665 (the Martinique specimen) unfortunately has disappeared from the collection.

Material Examined.—Numbers in parentheses are numbers of specimens. For data from Oregon stations (=O), refer to Bullis and Thompson (1965).

West Indies: Bahamas: AMNH 18025 (1); ANSP 72336 (1), Nassau and Hog I.; ANSP 90669 (1) and ANSP 90673 (1), N shore of Hog I.; ANSP 90672 (1) and 90674 (1), S shore of Hog I.; MCZ 11767 (2), Nassau; UF 24185 (1), Silver Bay sta. 2464, 23°34′N, 79°05′W, 274 m. **Cuba:** ANSP 89011 (1), Havana; CAS-SU 3096 (1), Havana; CAS 27215 (1) and CAS 42578 (1), Havana; MCZ 11758–11760 (5); MCZ 11763 (3); MCZ 35096 (1), Guantánamo Bay; USNM 13051 (1). **Jamaica:** CAS-SU 4744 (3). **Haiti:** USNM 132575 (1), Port-au-Prince; USNM 178027 (1). **Dominican Republic:** AMNH 8297 (2) and AMNH 17462 (1); ZMUC 10 (1) and ZMUC P9229 (1), Puerto Plata. **Puerto Rico:** FMNH 64842 (1), O-2626; CAS 23918 (1), O-2668. **Virgin Islands:** FMNH 53947 (1), St. Croix; UMML 6821 (1), W end Reef Bay, St. John; USNM 116432 (1), Shoy Lagoon, St. Croix; ZMUC 5 (1), St. Croix. **Lesser Antilles:** ANSP 10622–10623 (2), St. Martin; MCZ 27332 (1), "St. Bart." [=Saint Barthélemy?]; CAS-SU 39893 (1), Bridgetown, Barbados; FMNH 64847 (1), O-2631.

Central America: British Honduras: AMNH 8209 (1), Porta Cortez; CAS 28495 (2), O-6405, 17°18′N, 88°01′W, 183 m; CAS 42579 (2), Undaunted cr. 6703, sta. 72, 17°12′N, 88°11.2′W, 18–20 m; USNM 37123 (1), off Cozumel; BMNH 1927.9.16.18–22 (4), Watercey I. **Honduras:** CAS 28520 (1), Hurricane, 15°48′N, 83°54′W, 24 m; CAS 28521–22 (4), Shady Lady, 15°49.5′N, 83°44′W, 31 m; CAS 28523 (2), Shady Lady, 15°54′N, 83°40′W, 37 m; FMNH 64329 (2), O-1934; FMNH 64330 (4), O-1937. **Nicaragua:** CAS 28494 (2), O-6426, 12°56′N, 82°21′W, 190 m. **Panama:** MCZ 11768 (1), Isthmus of Darien; USNM 81728 (1), Porto Bello.

South America: Venezuela: CAS 28527 (1), Calamar sta. 502, 11°15′N, 65°15′W, 82–104 m; FMNH 64900 (4), O-2348; MCZ 41510 (4), Atlantis sta. 5599, 10°19′N, 65°32.5′W, 64 m. **Guyana:** CAS 28525 (1), Calamar sta. 425, 95–101 m; FMNH 64894 (1), O-2251; FMNH 65950 (2), O-2249; FMNH 65960 (4), O-2231; FMNH 65961 (2), O-2233; FMNH 65962 (2), O-2254; FMNH 66386 (1), O-1996; UF 24184 (1), O-2241. **Surinam:** CAS 23915 (1), O-2279; CAS 23917 (1), Coquette sta. 178, 6°19′N, 55°50.5′W, 27 m; CAS-SU 51208 (1), Coquette sta. 30, 6°49.5′N, 54°54′W, 48 m; CAS-SU 51211 (1), Coquette sta. 213, 6°46′N, 54°29.5′W, 44 m; FMNH 64896 (1), O-2275; FMNH 64898 (8), O-2329; FMNH 65959 (1), O-2016; FMNH 65963 (1), O-2266; MCZ 45076 (1), Coquette sta. 182, 6°15′N, 55°54′W, 24 m; UMML 4012 (1), O-2268. **French Guiana:** CAS 23916 (1), O-2043; FMNH 64889 (1), O-2035; FMNH 64890 (1), O-2036; FMNH 64897 (1), O-2303; FMNH 65964 (1), O-2301. **Brazil:** MCZ 45075 (4), O-2074.

Undetermined material. Seven specimens from the Bahama Islands are intermediate in color pattern between *nasutus* and *cubifrons*, and also cannot be diagnosed with certainty on the basis of morphometric characters; these are ANSP 72335 (1), Hog I., ANSP 90670–90671 (2), south shore of Hog I., and FMNH 64139 (4), Grand Bahama I.

Ogcocephalus cubifrons (Richardson)

(Figures 18 and 22)

[?] *Lophius radiatus* Mitchill, 1818:326 ["Strait of Bahama"; nomen dubium; see comment after synonymy].

Lophius (*Malthe*) *cubifrons* Richardson, 1836:103, pl. 96 [Labrador (see comment after synonymy); holotype BMNH 1855.9.19.848].

Malthaea cubifrons: Cuvier and Valenciennes 1837:452 [based on Richardson 1836; *cubifrons* placed in synonymy of *nasutus*].

Malthea nasuta (non Cuvier and Valenciennes): Storer 1846:131 [synonymy; partial description; range, compiled].

Malthe cubifrons: Günther 1861:203 [partial description of holotype]; Gill 1873:14 [Labrador; name only]; Goode and Bean 1879:121 [west Florida; fin formulae]; 1882:235 [Gulf of Mexico; name only]; Jordan and Gilbert 1882:850 [coasts of Florida; partial description].

Malthea radiata: Gill 1862:47 [name only; based on *Malthea nasuta* of Storer 1846].

Malthe vespertilio (non Linnaeus): Gill 1873:14 [Labrador, compiled]; Jordan and Swain 1885:234 [Cedar Keys, Florida; partial description; *cubifrons* and *nasutus* referred to synonymy of *vespertilio*]; Henshall 1895:220 [Tampa, Florida]; Jordan 1899:172 [name listed].

Malthe vespertilio nasuta (non Cuvier and Valenciennes): Jordan and Gilbert 1882:850 [range: South Atlantic coast of United States; partial description].

Malthe vespertilio radiata: Jordan 1885a:927 (part) [variety *cubifrons* referred to the synonymy of *radiatus*]; 1885b:144 [Key West, Florida; partial description]; 1885c:45 [Egmont Key, Florida].

Malthe radiata: Henshall 1891:383 [southern Florida]; 1895:220 [Tampa, Florida; partial description].

Onchocephalus radiatus: Goode and Bean 1896:498 [Pensacola, Florida; description; notes on holotype of *cubifrons* Richardson, 1836].

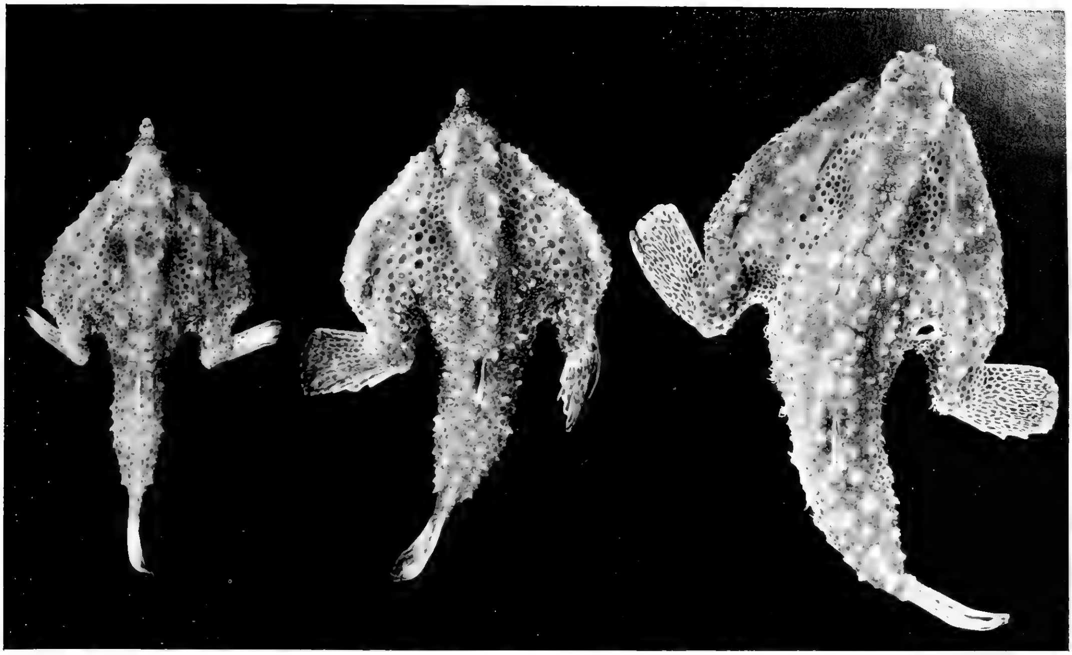


FIGURE 18. *Ogcocephalus cubifrons* (Richardson) from west coast of Florida showing interorbital width increases with size and rostrum length decreases. *Left to right:* 78.0 mm SL, FSBC 342, 64–81 km NE Dry Tortugas; 98.0 mm SL, UF 2730, off Pensacola; 194.0 mm SL, FSBC 1369, off Don-ce-Sar, Pinellas County.

Ogcocephalus vespertilio (non Linnaeus): Jordan and Evermann 1896:511 (part) [list, compiled]; Evermann and Kendall 1900:99 (part) [locality records, compiled]; Gunter, Williams, Davis, and Smith 1948:314 [Fort Myers, Florida; mortality].

Ogcocephalus radiatus: Jordan and Evermann 1898:2738 [Cedar Key, Florida; description; range; *radiatus* (=*cubifrons*) removed from synonymy of *vespertilio*]; Evermann and Kendall 1900:99 (part) [Key West, Florida; other localities compiled]; Fowler 1906:108 [Florida Keys; color in life; behavior; figure]; 1915:251 [Palm Beach, Florida]; Breder 1929:303 [Florida]; Jordan, Evermann, and Clark 1930:507 [compiled]; Storey and Gudger 1936:648 [mortality]; Gunter, Williams, Davis, and Smith 1948:312 [Englewood, Florida; mortality]; Briggs 1958:301 [range, compiled]; Böhlke and Chaplin 1968:727 [Bahama Is.; description; key; figure]; Walls 1975:117 [partial description; color photograph].

Oncocephalus radiatus: Fowler 1926:254 [Captiva Pass, Florida]; 1945:335 (part) [Sanibel I., Florida].

Ogcocephalus cubifrons: Longley and Hildebrand 1941:311–312, pl. 33, fig. 2 [Tortugas, Florida; key; description]; Hildebrand 1955:219 ([Campeche Banks, Yucatán; partial description]; Springer and McErlean 1962:41 [south Florida; listed]; Moe and Martin 1965:147 [off Pinellas Co., Florida; ecological survey; listed]; Moe et al. 1966:120 [Florida; list of museum specimens]; Bradbury 1967:417 [listed]; Stark 1968:33 [Alligator Reef, Florida; composition of reef fauna].

Ogcocephalus nasutus (non Cuvier and Valenciennes): Reid 1954:73 [Cedar Key, Florida; description; ecology]; Herald 1972:110 [color photograph].

Ogcocephalus sp.: Springer and Woodburn 1960:91 [Tampa Bay, Florida; ecology].

Although the name *radiatus* Mitchill, 1818, has often been used for this form, I agree with Longley (Longley and Hildebrand 1941) that the usage is mistaken. Longley wrote concerning Mitchill's description that the ". . . facts of distribution make it improbable that Mitchill's *Lophius radiatus* is the same [as *cubifrons* Richardson]." Unfortunately, the holotype for *radiatus* Mitchill cannot be found. The fairly extensive search that I made yielded no results, and there is no record in the literature or elsewhere that any later author ever saw the specimen(s) that Mitchill (1818) described. Therefore, we have only the original description of *radiatus* on which to rely, but it is impossible to tell from it what Mitchill had in hand. All but one of the characters in the original description are generic or familial characters: the nature of the modified scales and their surface sculpturing, the way that scales with their crystalline tubercles form the rostrum, the location of the rostral cavity, the "minute" jaw teeth, the "distinct" tongue, and the size and placement of the various fins. The one character given which is helpful in discrim-

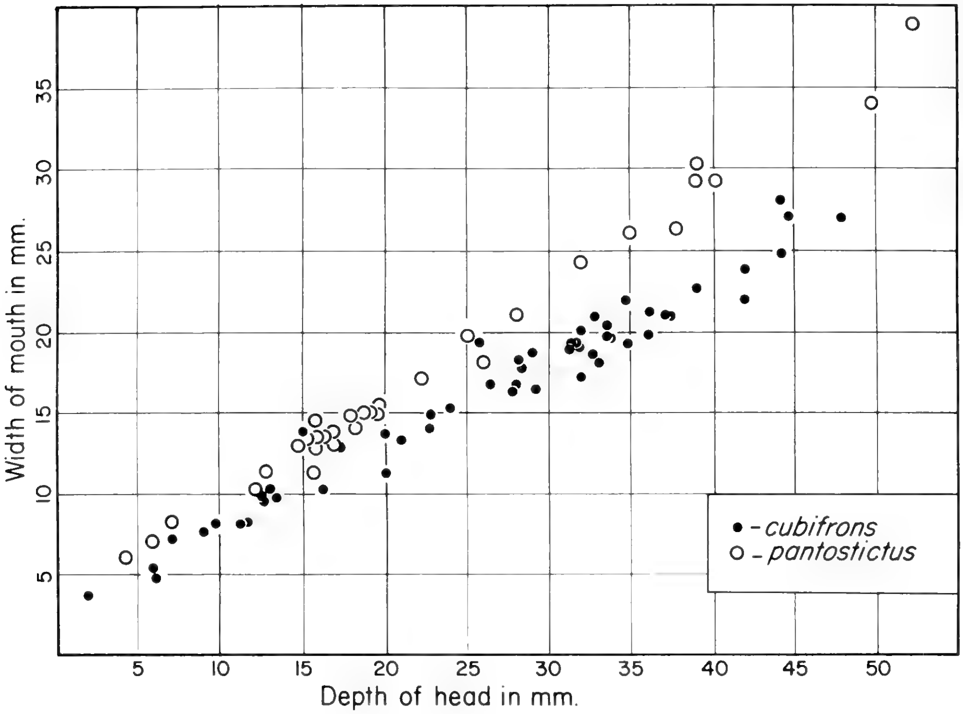


FIGURE 19. Comparison between *Ogcocephalus cubifrons* and *O. pantostictus* to show mouth is widest in *O. pantostictus* relative to depth of head.

inating species is the pectoral fin ray count, given as nine or ten. But these numbers are too low to correspond to *cubifrons*, for which the range in the pectoral fin count is 11 to 14. However, Mitchill (1818) described a total of three species of ogçocephalids in his paper and several times gave fin counts that are impossibly low, indicating that fin ray counts cannot be used with confidence in this case. The locality given in the original description of *radiatus* is "the depths of the Strait of Bahama." Strait of Bahama is an old name for the Straits of Florida, an area from which could be taken at least three species that fit the description; these are *rostellum*, *nasutus*, and *parvus*, the latter having the low number of pectoral fin rays that best fits the description if we could be sure that it were accurate. Of course, *cubifrons* also is taken in the general area, but it is an inshore form and less likely to be taken in "the depths of the Strait" by a "drag net," if we interpret that to mean relatively deep water as Longley evidently did (Longley and Hildebrand 1941). Since the original description of *Lophius radiatus* Mitchill, 1818, is inadequate for specific assignment, and since the single diagnostic character in the description (the pectoral fin ray count) fails to characterize the species at hand, I hereby reject the earlier name in favor of *Lophius* (*Malthe*) *cubifrons* Richardson, 1836.

The name *cubifrons* Richardson is represented by a holotype, BMNH 1855.9.19.848, in reasonable condition except for fading, and the original description with illustration is unequivocally of this form, but there is a question regarding locality. Jordan and Evermann (1898) first drew attention to the problem: "*Malthe cubifrons*, Richardson, [is] . . . said to be from Labrador (Coll. J. J. Audubon), but this is certainly an error; Audubon collected also in Carolina and Florida." Labrador is indeed far beyond the range of this species, but "Carolina" and Florida are both likely type-localities. However, I am unable to assign the holotype to any specific locality, or even general locality, within the range of the species.

DIAGNOSIS AND COMPARISONS.—A large species of *Ogcocephalus* reaching 230 mm SL

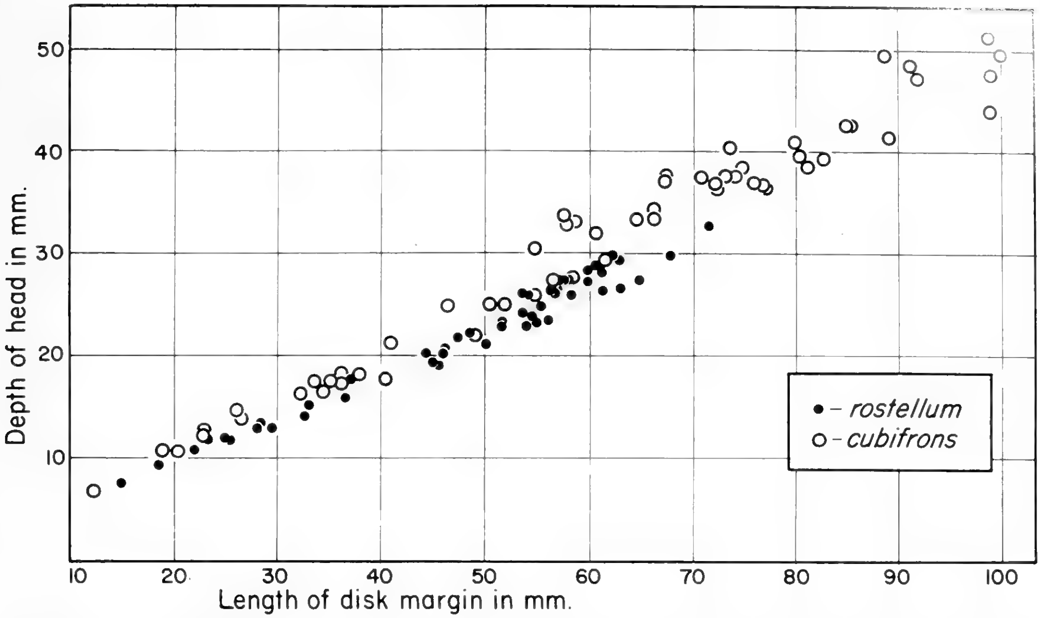


FIGURE 20. Comparison between *Ogcocephalus rostellum* and *O. cubifrons* to show that depth of head is greatest in *O. cubifrons* relative to length of disk margin.

(Table 1) and distinguished by the combined features of a bright pattern of dark spots on the pale pectoral fins, a small mouth (Fig. 6), a wide interorbital distance, and a thick, massive head on which, in large individuals, is perched a small, knoblike rostrum, because the rostrum is characterized by ontogenetic allometry: very long in juveniles, very short in large adults (Fig. 22).

In general appearance, *O. cubifrons* most closely resembles *nasutus, rostellum,* and *pantostictus,* especially the latter, which is also large and heavy. *O. cubifrons* is distinguished from *pantostictus* by its smaller mouth (Fig. 19) and lower count of lateral-line scales in the subopercular series (usually 7–8 in *cubifrons,* modally 9 in *pantostictus,* Table 6). *O. cubifrons* is distinguished from both *pantostictus* and *nasutus* by the lower number of lateral-line scales in the cheek series (modally 8 in *cubifrons,* 9 in *pantostictus* and *nasutus,* Table 5), and is further distinguished from *nasutus* by having a shorter jaw and wider interorbital (Figs. 14 and 15) and in having allometric growth of the rostrum (Fig. 22).

Although the ranges of *cubifrons* and *rostellum* overlap off the southeastern United States, the two evidently seldom co-occur, *cubifrons* being taken in shallower water than *rostellum. O. rostellum* has a more flattened disk as expressed by the head height (Fig. 20), a less massive head as expressed by the rostrum measurement (Fig. 9), and a smaller caudal peduncle (Fig. 21); it is a smaller species than *cubifrons,* reaching only 160 mm SL.

Ogcocephalus parvus and *corniger* occur off both coasts of Florida and off the Carolinas and Yucatán, as does *cubifrons,* but *parvus* and *corniger* are taken in deeper water than *cubifrons.* Both *parvus* and *corniger* have fewer pectoral fin rays than *cubifrons* (usually 12–13 in *cubifrons,* 10–11 in *parvus* and *corniger,* Table 3) and differing color patterns; *parvus,* a small species reaching only 85 mm SL, has blotches of varying tones as the color pattern on the dorsal surface of the body, but it lacks the prominent clusters of dark circles seen on the body and pectoral fins in *cubifrons. O. corniger* differs from *cubifrons* in having close-set pale spots on a dark background evenly covering the entire dorsal surface of the body.

Ogcocephalus declivirostris is restricted to the northwestern Gulf of Mexico and is evidently allopatric with *cubifrons. O. decliviros-*

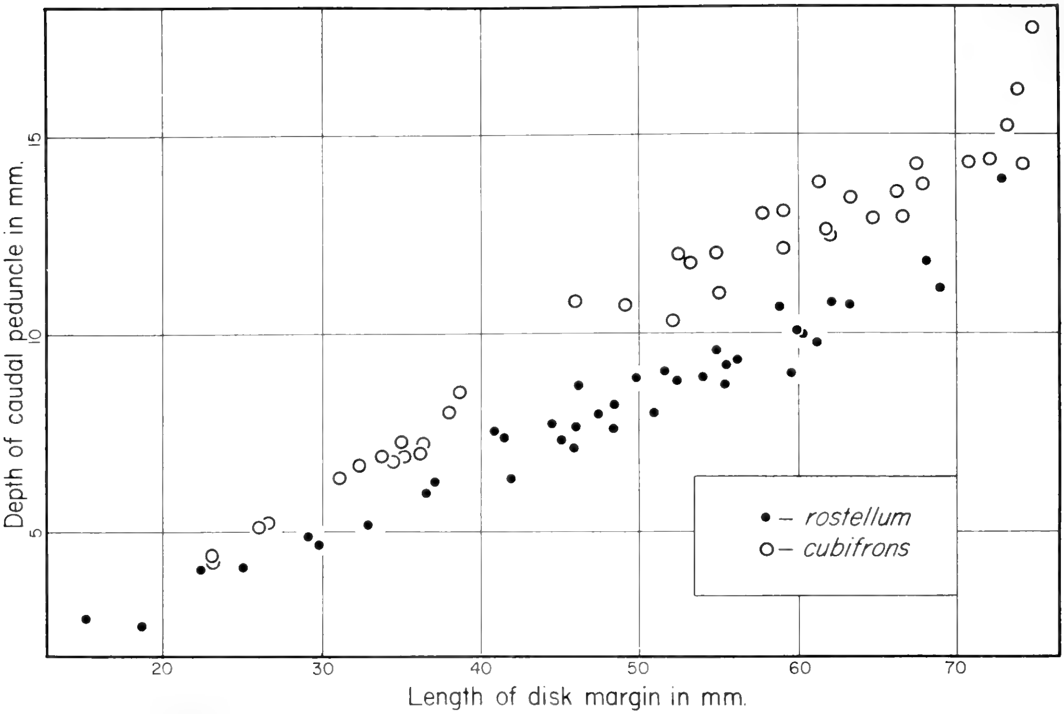


FIGURE 21. Comparison between *Ogcocephalus rostellum* and *O. cubifrons* to show that depth of caudal peduncle is greatest in *O. cubifrons* relative to length of disk margin.

tris is distinguished, in any case, in having fewer pectoral fin rays (modally 11 in *declivirostris*, usually 12–13 in *cubifrons*, Table 3); *declivirostris* lacks the fleshy ventral pads on the distal tips of the pectoral fin rays as well as the spotted pattern of the pectoral fins so prominent in *cubifrons* (although occasionally *declivirostris* has a few very pale spots on the pectorals). Finally, *declivirostris* differs from *cubifrons* in having its rostrum jutting horizontally or downwards instead of upwards as in *cubifrons*.

DESCRIPTION.—Counts and measurements from 95 specimens 29.9 to 224.0 mm SL (Table 1).

Counts. Counts given in Tables 2–6. Two counts for *cubifrons* lie in the middle of the range for the genus; pectoral fin ray count is generally 12–13 in *cubifrons*, which is the middle of the generic range of 10–15, and the subopercular lateral-line scale count in *cubifrons* is usually 7–8, which is the middle of the generic range (excluding extremes) of 5–10. The lateral-line scale count, although showing wide variation, is also near the middle of the range for the genus (Table 4). However, *cubifrons* agrees with *pantostictus*, *rostellum*, and *declivirostris* in having a high modal vertebral count of 20, whereas the more usual count for the genus is 19.

Proportions. Proportions expressed as ratios given as the mean followed by the range in parentheses.

Length of disk margin intermediate within range of variation for the genus, 2.3(2.0–2.5) in SL. Width of tail also intermediate, varying from thin in smallest specimens to thick and broad in large specimens, 1.8(1.5–2.4) in length of disk margin; caudal peduncle thick and deep, its depth 2.5(2.2–2.9) in head depth. Rostrum long, conical, and upturned in small specimens, becoming relatively small and knoblike in large ones (Fig. 22); length of rostrum 4.3(1.8–6.1) in length of disk margin. Aperture of illicial cavity subtriangular in small specimens, much higher than wide, becoming merely oval or round in large ones. Cranium rising steeply above the disk, its contours becoming massive and boxlike in adults; head depth 2.0(1.7–2.2) in length of

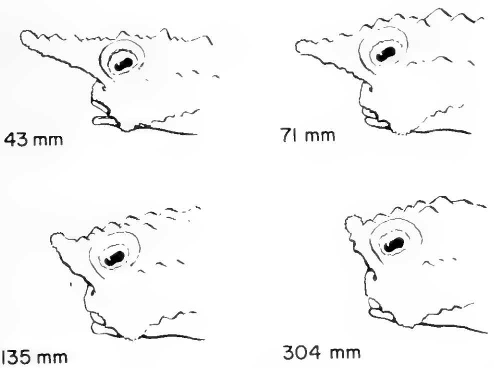


FIGURE 22. Heads of four examples of *Ogcocephalus cubifrons* showing allometric growth of rostrum.

disk margin. Width of cranium 3.1(2.6–3.6) in length of disk margin. The following in width of cranium: eye 1.6(1.4–1.9), lateral ethmoid width 1.8(1.5–2.0). Interorbital very wide, slightly concave, 1.9(1.5–2.2) in width of cranium, 3.0(2.3–3.4) in head depth. Mouth small, its width 1.9(1.6–2.2) in head depth, 3.8(3.2–4.4) in length of disk margin; jaw 2.8(2.5–3.2) in head depth. Upper lip fleshy, of an even width for its entire length; lower lip fleshy, usually thickened medially although no median lobe is developed. Dorsal fin 3.4(2.7–4.8) in length of disk margin; anal fin 2.6(2.2–3.1) in length of disk margin.

Integument. Dermal cirri generally well developed on lateral sides of tail, less so on disk margin; cirri also frequently scattered thickly on dorsal surface of body, particularly in half-grown specimens. Large bucklers prominent, arranged as in generic description. Tubercles relatively sparse on fins, occurring at bases of dorsal and pectoral fins with only a few scattered along fin rays. Anal and ventrals with tubercles at bases and running out on fin rays for a third to a half their length. Caudal as in generic description. Skin covering eyeballs bearing tiny tubercles with rim of cornea beaded by a row of small bucklers. Pectoral membranes thick, opaque, the ventral surface of ray tips with well-developed fleshy pads.

Color in preservative. Ground color of dorsal surface of body light tan to dark brown or gray with black spots sprinkled on face, on skin covering eyeballs, on shoulders and lateral sides of tail, in the axillae, on pectoral fins, and usually on lateral margins of disk. Spotted pattern on shoulders does not form a reticulum as it does in *O. vespertilio*. Shoulder spots often with pale centers in small specimens. Ground color of pectoral fins and sides of tail usually pale with dark spots so close together that the background appears as a reticulum; even in specimens so dark as to obscure most of the spotted pattern of body, the pattern on pectoral fins remains prominent. Pectoral fins with a broad dark brown or black border in medium-sized and small specimens. Lips pale; rostrum with a diffuse black subterminal ring; iris black, or golden with black spots, in which case color pattern of face extends over eyes to margin of pupil. Ventral surface of body uniformly pale or creamy. Ventral and anal fins the same ground color as ventral surface of body, ventrals often with a pale patch distally in dark specimens, anal fin sometimes dark or at least tipped with brown or black in small specimens. Ventral pads of pectoral fin rays white or pale. Dorsal fin spotted or sometimes with merely vague blotches. Caudal fin as in generic description but generally with spotted pattern of tail carried back and superimposed on caudal's basic pattern.

Color in life. I have not seen this species alive. The following is a description by Longley (Longley and Hildebrand 1941), "The young are dark gray on the under side; older fish coppery red, with much individual variation in color on the dorsal side, usually lighter or darker brown, variegated with reddish orange or yellow-orange patches, disappearing in preserved specimens; the chief patches behind the eyes, the two sometimes meeting across the nape to form a great U-shaped mark open to the rear; usually an additional one above and behind the branchial aperture; and one about base of soft dorsal fin. Even at a standard length of 50 mm. there is some, and in fish of medium and large size much spotting with light-bordered dark spots in a long, narrow tract from eye to gill opening. Here the spots usually are less crowded than elsewhere, and more nearly circular. On the sides of the head, margin of the disk, and sides of the trunk, the pattern is less open, being principally a network of light lines on the dark ground. Small fish have pectorals and caudal yellow proximally and dark brown distally, with a netted pattern appearing first at the base of these fins and extending gradually to their tips, the yellow advancing before it at the expense of the darker brown, which gives way to the lighter color on which the marbling spreads."

A photograph in Walls (1975:263) shows a specimen (his *O. radiatus*) with margins of pectorals bright yellow; the size of the fish is not given, but the small relative size of the rostrum indicates that the specimen is probably a large adult. A smaller specimen is shown in color in Herald (1972). In this specimen the yellow color lies just proximal to the dark brown fin margins about as Longley described (Longley and Hildebrand 1941). Both photographs show the "netted" pattern on the base of the pectorals.

Distribution (Fig. 17).—Northern Bahamas, coast of the southeastern United States from the vicinity of Cape Lookout, North Carolina, around the Florida peninsula to Pensacola, Florida, and south to Campeche Banks, Yucatán. Bathymetric range: shore to 68 m.

Material Examined.—BMNH 1855.9.19.848, the holotype, said to be from Labrador, but this undoubtedly an error (see p. 260). For following material, numbers in parentheses are numbers of specimens. For data of Oregon stations (= O), refer to Springer and Bullis (1956).

United States: North Carolina: UF 24912 (1), near Cape Lookout Bight, Carteret Co. **South Carolina:** UF 24903 (1), 31°58′N, 79°43′W, about 77.3 km SE Edisto Beach, Beaufort Co. **Georgia:** UF 25931 (1), off Brunswick. **Florida:** *Dade County:* FMNH 46128 (1), inshore reef between Miami and Angelfish Creek; FMNH 46854 (1), Triumph Reef off Elliot Key; USNM 89710–89711 (2), Biscayne Bay near Cocoanut Grove, Miami. *Monroe County:* ANSP 90667 (1), E end Grassy Key, Florida Bay; CAS 18585 (1), near Key West; FMNH 7020 (1), Key West; FMNH 21645–21647 (3), near Marathon; FMNH 64123 (1), O-1004; FSBC 342 (4), FSBC 381 (1), FSBC 410 (1) all from 24°41′–24°52′N, 82°00′–82°35′W; FSBC 626 (1) and FSBC 762 (1), both from 24°43′10″–24°52′00″N, 82°00′–82°35′W; UF 4071 (1), Marquesas Keys; UF 7022 (1), Big Pine Key; UMML 1201 (10), 24°45′–24°50′N, 82°10′–82°30′W; UMML 4786 (1), 5.3 km SW of Greyhound Key; USNM 57243 (1), Matecumbe Key; USNM 84035 (1), 24°36′N, 81°48′W; USNM 117003 (7), Tortugas; USNM 117006 (3), channel W of White Shoal, Tortugas; USNM 117170 (2), Tortugas; USNM 126488 (2), Key West. *Collier County:* FSBC 1157 (1), Everglades. *Lee County:* CAS-SU 5841 (1), Captiva Pass; CAS-SU 36404 (6), Sanibel I.; FMNH 510, 512, and 513 (3), Captiva Pass; FMNH 38584–38586 (3) and FMNH 38587 (1), Boca Grande; USNM 76025 (1), Boca Grande Pass; USNM 86159 (1), Boca Grande. *Hillsborough County:* USNM 143160 (2), Port Tampa. *Pinellas County:* FSBC 61 (1), Blind Pass, St. Petersburg Beach; FSBC 878 (1), John's Pass, Madeira Beach; FSBC 1369 (1), due W of Don-ce-Sar; USNM 158543 (1), Bay at Clearwater. *Levy County:* the following all from Cedar Key: ANSP 90668 (2); CAS-SU 99 (5); UF 229 (1); UF 753 (1); UF 916 (1); UF 919 (1); UF 1522 (1); UF 1612 (1); UF 3169 (1); UF 3374 (1); UF 7832 (1); UF (1), R-I-650-4; UF (1), R-I-651-3; UF (2), R-I-2351-1; UF (1), R-II-551-6; UF (1), R-II-2051-4; UF (1), R-III-451-1; UF (1), R-III-451-4; UF (2), R-IV-551-1; UF (1), R-IV-551-7; UF (2), R-VI-650-3; UF (4), R-VI-750-2; UF (4), R-VI-1750-4; UF (1), R-VII-150-5; UF (4), R-VII-150-6; UF (6), R-VIII-2650-1; UF (4), R-VIII-2650-1; UF (2), R-VIII-2650-2; UF (1), R-IX-1250-1; UF (1), R-IX-1250-1; UF (2), R-X-850-7; UF (1), R-X-2250-5-5; UF (1), R-XI-750-6; UF (1), R-XI-750-7; UF (1), R-XII-1050-1; UF (2); R-XII-1050-2; USNM 88499 (1); USNM 164928 (1). *Franklin County:* CAS 23914 (1), Apalachicola Bay. *Okaloosa County:* UF 5586 (1), UF 5587 (1), UF 5596 (1), all from Choctawatchee Bay at Destin; UF 2730 (1), Pensacola.

Florida Straits: UF 28649 (1), Silver Bay sta. 144, 27°44′N, 82°46′W, 7.3 m.

Bahamas: ANSP 103627 (1), George M. Bowers sta. 659, W side Eleuthra I.; ANSP (3), Chaplin Program sta. 513B, Hatchet Bay, Eleuthra I.; ANSP (2), Chaplin Program sta. 526, Hatchet Bay, 4.8 km offshore, Eleuthra I.; UMML 4719 (1), Exuma Sound adjacent to Eleuthra I., 7.3 m.

Mexico: Campeche Banks: FMNH 46745 (5), O-436; FMNH 64107 (8), O-713–716; FMNH 64134 (3), O-710; UF 28647 (1), Silver Bay sta. 362, 20°00′N, 91°43′W, 44 m; UF 28648 (1), O-417. **Yucatán:** USNM 148497 (1).

Undetermined material. Seven specimens from the Bahama Islands are intermediate in color pattern between *cubifrons* and *nasutus*, and also cannot be diagnosed with certainty on the basis of morphometric characters. These specimens are: ANSP 72335 (1), Hog I.; ANSP 90670–90671 (2), S shore of Hog I.; and FMNH 64139 (4), Grand Bahama I.

Ogcocephalus pantostictus new species

(Figure 23)

Ogcocephalus vespertilio (non Linnaeus): Woods 1942:192 [off Corpus Christi, Texas].

Ogcocephalus cubifrons (non Richardson): Hildebrand 1954:321 [off Texas].

Ogcocephalus radiatus: Anonymous 1976:131 and 427 [Mexican coast of Gulf of Mexico; color photograph; key]; Hoese and Moore 1977:144, fig. 101 [NW Gulf of Mexico; key; partial description; range].

Diagnosis and Comparisons.—A very large *Ogcocephalus* (Table 1) with the entire dorsal surface of the body covered with a polkadotlike pattern of dark spots (sometimes dim in museum specimens). Resembling *cubifrons* in many features, it has allometric growth of the rostrum: a relatively long rostrum in small specimens, but short and sometimes merely knoblike in large specimens. *O. pantostictus* is distinguished from *cubifrons* by its wider mouth (Fig. 19; also expressed by the jaw measurement, Fig. 14) and in having higher modal counts of lateral-line scales in the cheek series (9 in *pantostictus*, 8 in *cubifrons*, Table 5) and in the subopercular series (9 in *pantostictus*, 8 in *cubifrons*, Table 6).

With its range restricted to the northern and western Gulf of Mexico, *pantostictus* is largely sympatric with *declivirostris*, but the two are distinguished by the pectoral fin ray count (usually 12–13 in *pantostictus* and 11 in *declivirostris*, Table 3) and the lateral-line scale count in the subopercular series (modally 9 in *pantostictus*, 7 in *declivirostris*, Table 6), *O. pantostictus*

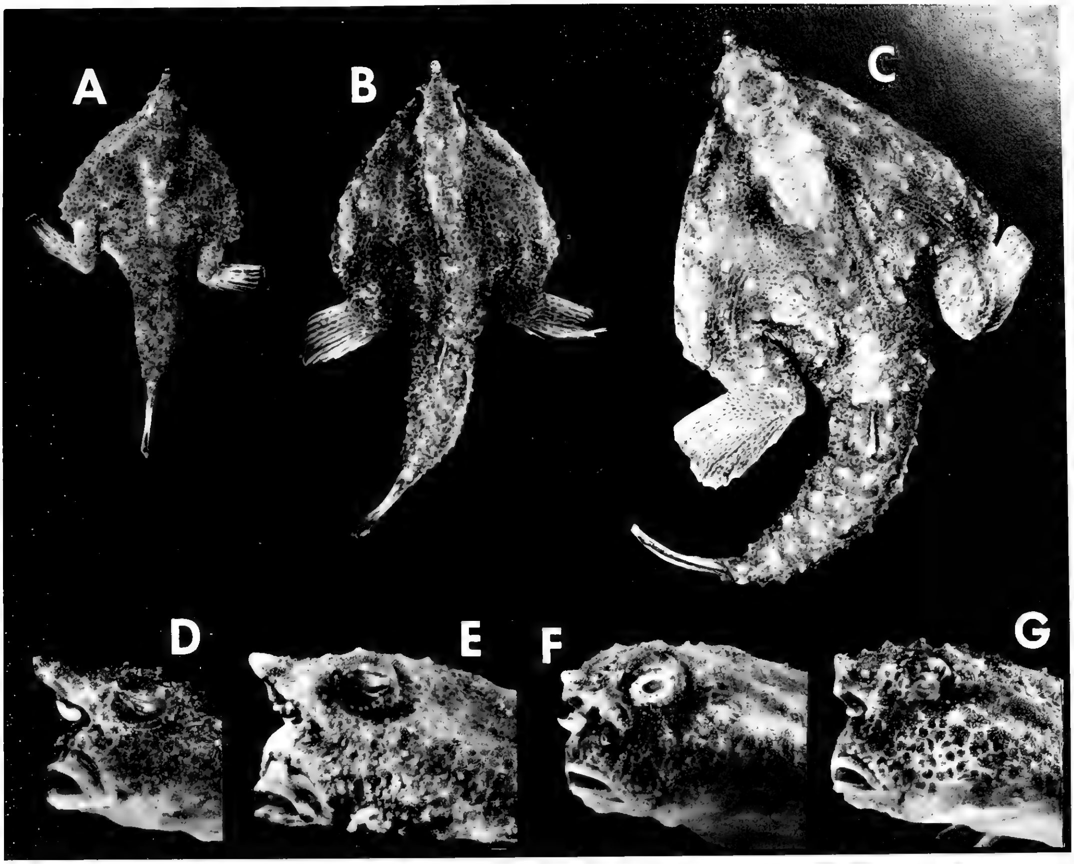


FIGURE 23. *Ogcocephalus pantostictus* new species, all from Gulf of Mexico. *(A)* and *(D)* Paratype 77.0 mm SL, CAS-SU 40559, Galveston, Texas. *(B)* Paratype 96.0 mm SL, FMNH 64111, off Mobile Bay, Alabama. *(C)* and *(E)* Holotype 226.0 mm SL, FMNH 50765, off Pensacola, Florida. *(F)* Paratype 187.0 mm SL, CAS-SU 40559, showing variation of rostrum resembling *O. cubifrons*. Compare with *(G)*, *O. cubifrons* (same specimen as in Fig. 18*C*).

also has the ventral surfaces of the pectoral fin rays thickened with fleshy pads which are not present in *declivirostris*.

The species *corniger* and *parvus* have ranges slightly overlapping that of *pantostictus* in the northern Gulf of Mexico, but both are separable from *pantostictus* by their lower pectoral fin ray counts (usually 12–13 in *pantostictus* and 10–11 in *corniger* and *parvus*, Table 3). *O. parvus* is a far smaller species than *pantostictus*, reaching only about 85 mm SL. *O. corniger* has a much longer rostrum than does *pantostictus* (Fig. 9) and has a distinctive color pattern of pale spots on a darker background distributed evenly over the dorsal surface of the body in contrast to the darkish circles on a lighter background found in *pantostictus*.

DESCRIPTION.—Counts and measurements from 65 specimens, 38.6 to 261.0 mm SL (Table 1).

Counts. Counts given in Tables 2–6; in the following description, counts for the holotype given in brackets. Pectoral fin ray counts in *pantostictus* in middle of range for genus, 12–13 in a range of 10–15 [12,12]. Subopercular lateral-line scale count, modally 9 [10,10] in *pantostictus*, high relative to range of 5–10 (excluding extremes) for genus; only two other species have as high a count: *vespertilio* usually has 9 scales in subopercular series, *notatus* usually 10. The count for cheek lateral-line scales nears high end of range, too, with count in *pantostictus* usually 8 or 9 [9,10]; in this character *pantostictus* agrees with *nasutus*, and only *vespertilio* and *notatus* have higher counts in cheek series. Lateral-line scale count [35,36] varies widely, but mean is highest for genus. *O. pantostictus* resembles *cubifrons, rostellum,* and *declivirostris* in vertebral count of 19–21, modally 20, in contrast to remaining eight species which nearly always have 19, occasionally 18, vertebrae. [D.4; A.4.]

Proportions. Proportions expressed as ratios given as the mean followed by the range in parentheses and the proportion for the holotype in brackets.

Length of disk margin intermediate within range of variation for the genus, 2.3(2.1–2.4)[2.4] in SL. Tail moderately thick and broad in large specimens, relatively narrow in small ones, its width 1.8(1.5–2.0)[1.7] in length of disk margin; caudal peduncle thick and deep, its depth 2.6(2.3–2.9)[2.5] in depth of head. Ontogenetic allometry in growth of rostrum resembles that in *cubifrons*; however, I have not seen specimens of *pantostictus* less than 38.6 mm in standard length and therefore do not know whether or not the remarkably long rostrum seen in very small *cubifrons* (30 mm SL) is also characteristic of small *pantostictus*. Rostrum cone-shaped in small examples, becoming relatively small and finger-shaped in large ones. Length of rostrum 4.3(2.6–6.3)[5.0] in length of disk margin. Aperture of illicial cavity subtriangular in small specimens, higher than wide, becoming oval in adults. Cranium rising steeply above disk, becoming heavy and massive in large specimens; head depth 2.0(1.8–2.1)[2.1] in length of disk margin. Width of cranium 3.2(2.9–3.7)[3.4] in length of disk margin. The following in width of cranium: eye 1.6(1.4–1.8)[1.8], lateral ethmoid width 1.6(1.4–1.8)[1.6]. Interorbital slightly concave, wide, 2.0(1.8–2.5)[1.9] in width of cranium, 3.3(2.9–4.1)[2.9] in head depth. Mouth moderate, its width 1.6(1.4–1.8)[1.6] in head depth, 3.1(2.8–3.6)[3.3] in disk margin; jaw 2.3(2.1–2.7)[2.5] in head depth. Upper lip fairly fleshy, of an even width along its entire length; lower lip fleshy, usually thickened medially although no median lobe is developed. Dorsal fin 3.7(2.9–4.8)[4.8] in length of disk margin; anal fin 2.7(2.3–3.2)[3.2] in length of disk margin.

Integument. Dermal cirri often present on disk margin and lateral sides of tail. Large bucklers prominent, arranged as in generic description. Tubercles relatively sparse on fins, occurring at very base in dorsal and anal fins and on about proximal third of anal and ventrals. Caudal as in generic description. Skin covering eyeballs bearing tubercles with rim around cornea usually beaded by a row of small bucklers. Pectoral membranes thick, opaque; ventral surfaces of ray tips with well-developed fleshy pads.

Color in preservative. Dorsally the ground color of body gray or tan sprinkled fairly evenly with round dark spots over entire tail and disk, including face and skin covering eyeballs. Markings on shoulders, sides of tail, and in axillae generally darkest and showing greatest contrast with background color. Ventral surface uniformly pale, usually paler than ground color of dorsal body surface. Lips pale; rostrum with a diffuse dark subterminal ring; iris golden with black spots, or entirely black.

Pectorals with same spotted pattern as dorsal surface of body. In small or medium-sized specimens, spotted pattern on pectorals grades into a dark border. In many individuals spots close together so that background appears as a light-colored reticulum. Ventrals and anal same color as ventral surface of body; anal sometimes dusky near tip in specimens under about 100 mm SL. Dorsal fin usually spotted, especially when spotted pattern of dorsal body surface relatively intense.

Color in life. Unknown.

DISTRIBUTION (Fig. 17).—Coasts of northern and western Gulf of Mexico from approximately longitude 87°W to latitude 25°N. Bathymetric range: from limited data available, about 9–31 m.

NAME.—The name *pantostictus* means all spotted, in reference to the distinctive over-all spotted color pattern.

MATERIAL EXAMINED.—HOLOTYPE: FMNH 50765, Santa Rosa Sound, Pensacola, Florida; a male 226.0 mm SL.

PARATYPES. Numbers in parentheses are numbers of specimens. **United States: Florida:** ANSP 71329 (1), Pensacola; MCZ 45080 (1), OREGON sta. 1648, 30°11′N, 86°55′W, 31 m. **Alabama:** FMNH 64111 (1), OREGON sta. 882, 30°10′N, 87°50′W, 10 m. **Mississippi:** CAS 23934 (1), off Horn I.; FMNH 21636 (1), Horn I.; FMNH 46734 (1), outside Petit Bois I.; GCRL 562 (1), outside Petit Bois I.; GCRL 563 (1), sw of Ship I.; GCRL 564 (1), off Horn I.; GCRL 565 (1), off w end of Horn I.; UF uncat. (1), SILVER BAY sta. 167, 30°12′N, 88°40′W, 7.3 m. **Louisiana:** FMNH 50997 (2); GCRL 566 (1), s of Grand Isle, 17 m; USNM 188755 (1), PELICAN sta. 66-7, 28°59′N, 91°48′W. **Texas:** CAS 23932 (1); USNM 94443 (1); USNM 118610 (9). *Vicinity of Galveston:* CAS-SU 40559 (10); USNM 118603 (1); USNM 118604 (1); USNM 118606 (1); USNM 120071 (1); USNM 176982 (1); USNM 188803 (2), PELICAN sta. 56-5, 29°10.5′N, 94°50.5′W; USNM 188805 (1), PELICAN sta. 62-2, 29°19′N, 94°31.5′W. *Vicinity of Freeport:* MCZ 45079 (1), USNM 117804 (14), USNM 118605 (1), USNM 118611 (1). *Southern Texas:* USNM 120070 (1),

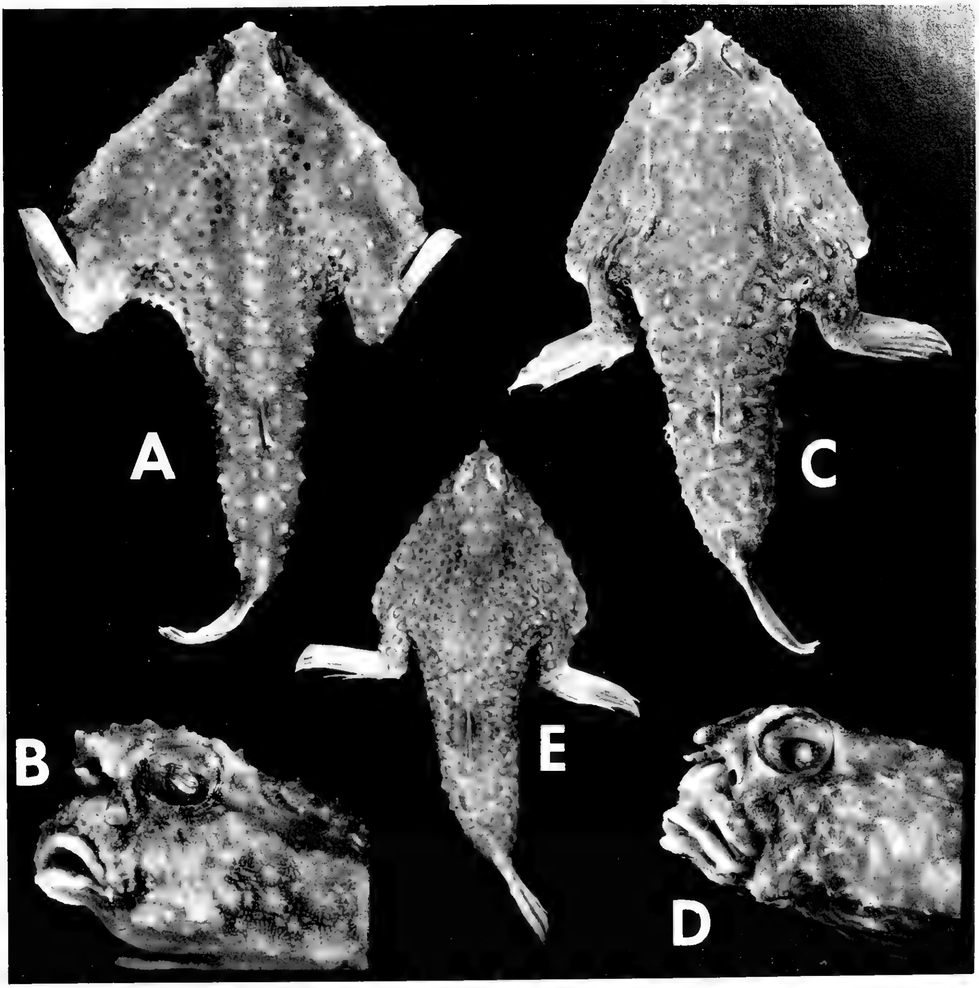


FIGURE 24. *(A)* and *(B) Ogcocephalus rostellum* new species, holotype, 133.0 mm SL, USNM 188809, off Atlantic coast of Florida, 29°10′N, 80°19′W. *(C)* and *(D) Ogcocephalus declivirostris* new species, holotype, 129.5 mm SL, FMNH 64136, Texas coast of Gulf of Mexico, 28°02′N, 96°03′W. *(E)* Paratype of *O. declivirostris*, 107.5 mm SL, FMNH 61577, Texas coast of Gulf of Mexico, 28°02′N, 96°04′W, showing pattern of dim spots sometimes seen on dorsal surface of body.

Aransas Pass; FMNH 37728–37729 (2), Port Aransas; FMNH 40298 (1), within 80 km of Corpus Christi; ANSP 90675 (1), Brownsville Ship Channel, Pt. Isabel; USNM 188800 (1), Pt. Isabel.

Mexico: USNM 188775 (1) and USNM 188783 (1), both from off Huts Bayon, approximately 24°30′N, 6–18 m.

Material without exact localities: USNM 188756 (1), PELICAN sta. 37; USNM 188758 (1), PELICAN sta. 104-2; USNM 188769 (1), MC 9; USNM 188798 (1), 8.1 km offshore.

Ogcocephalus rostellum new species

(Figure 24*A–B*)

Malthaea nasuta (non Cuvier and Valenciennes): DEKAY 1842:166, pl. 28, fig. 89 [synonymy; description; range, compiled].

DIAGNOSIS AND COMPARISONS.—A moderate-sized *Ogcocephalus* with a very abbreviated rostrum resembling the shelflike condition seen in *notatus*. (In the smallest specimens of both *rostellum* and *notatus*, 40 mm SL or less, a short median horn is developed on the rostrum.) *O. rostellum* is distinguished from *notatus* by its narrower mouth (Fig. 6) and lower number of scales in the cheek lateral-line series (modal number 8 in *rostellum*, 10 in *notatus*, Table 5) and in the premaxillary series (3 in *rostellum*, 4 in *notatus*).

In general appearance and color pattern, *rostellum* most closely resembles *cubifrons*; the ranges of the two species overlap along the Atlantic coast of the southeastern United States, but *rostellum* is ordinarily taken from deeper water than *cubifrons*. The two are distinguished by some differences in body proportions: *rostellum* has a relatively more flattened disk as expressed by the head height measurement (Fig. 20) and a less massive head as expressed by the rostrum measurement (Fig. 10); also it has a narrower caudal peduncle than *cubifrons* (Fig. 21). *O. rostellum* is a smaller species than *cubifrons*, reaching 160.0 mm in standard length compared to 230.0 mm in *cubifrons*. Finally, the color pattern of the pectoral fin helps discriminate between *rostellum* and *cubifrons*; often there are no dark spots on the pectoral fins in *rostellum* compared to the bright pattern of dark spots on a light background covering the pectoral fins in *cubifrons*, but when spots do occur on the pectorals in *rostellum*, they are generally dim and also less numerous than in *cubifrons* and restricted to the basal portions of the fins.

Ogcocephalus rostellum has its range adjacent to that of *nasutus* but is a smaller species than *nasutus* (Table 1) and lacks the long rostrum seen in *nasutus* (Fig. 10); *rostellum* differs further from *nasutus* in having a shorter jaw (Fig. 16).

The range of *rostellum* overlaps the ranges of *parvus* and *corniger*; all occur at moderate depths on the continental shelf off the southeastern United States. *O. rostellum* may be separated from *parvus* and *corniger* by the pectoral fin ray count (usually 13 in *rostellum*, usually 10–11 in *parvus* and *corniger*, Table 3). *O. rostellum* is further distinguished from *corniger* in lacking a long rostrum (Fig. 9), and is further distinguished from *parvus* in its flatter disk with less elevated cranium (head depth 4.3–5.4 into SL in *rostellum*, 3.1–4.2 in *parvus*).

DESCRIPTION.—Counts and measurements from 69 specimens, 33.3 to 154.2 mm SL (Table 1).

Counts. Counts given in Tables 2–6; in the following description, counts for holotype given in brackets. Pectoral fin ray count usually 13 [13, 13], range 11–15, about intermediate within range of variation for genus. Count of lateral-line scales in subopercular series moderately low for genus, usually 6 or 7 [5,6], range 5–9. Count of cheek series of lateral-line scales 8 [8,8], the most common count for the genus; range 7–9. Lateral-line scale count, 21–32 [26, 25]. Mean for each of the counts of series of lateral-line scales in *rostellum* lower than in the closely similar *cubifrons*. *O. rostellum* agrees with *cubifrons*, *pantostictus*, and *declivirostris* in having a modal count of 20 vertebrae, compared to other species in genus in which modal count is 19. [D. 4; A. 4.]

Proportions. Proportions expressed as ratios given as the mean followed by the range in parentheses and the proportion for the holotype in brackets.

Length of disk margin intermediate relative to range of variation for genus, 2.2(2.0–2.4)[2.4] in SL. Tail moderate in width, 1.8(1.6–2.1)[1.6] in length of disk margin; caudal peduncle slender, 2.7(2.4–2.9)[2.7] in head depth. Rostrum produced into a short cone in small specimens, becoming more shelflike in large specimens with the median horn extremely abbreviated, rostrum 6.1(3.7–8.0)[7.1] in length of disk margin. Aperture of illicial cavity almost diamond-shaped. Cranium well demarcated from disk, but head less deep than in other species in the genus, head depth 2.2(2.0–2.4)[2.2] in length of disk margin. Cranium relatively narrow, its width 3.5(2.7–3.9)[3.6] in length of disk margin (one specimen had this ratio 4.4). The following in width of cranium: eye 1.5(1.3–1.7)[1.5], lateral ethmoid width 1.6(1.5–1.8)[1.8]. Interorbital space slightly concave, its width moderate, 2.2(1.9–2.7)[2.4] in width of cranium, 3.4(2.8–4.1)[3.9] in head depth. Mouth small, its width 1.7(1.5–2.0)[1.8] in head depth, 3.8(3.1–4.4)[4.0] in length of disk margin; jaw 2.6(2.3–2.8)[2.7] in head depth. Upper lip fleshy, of an even width for its entire length; lower lip fleshy, very thickened medially. Dorsal fin 4.3(3.2–4.9)[4.5] in length of disk margin; anal fin 3.0(2.5–3.5)[3.4] in length of disk margin.

Integument. Dermal cirri sometimes present but never conspicuous. Large bucklers prominent, arranged as in generic description. In more than half the specimens studied, the ventral surface of tail with low bucklers making surface markedly coarse relative to smooth shagreenlike texture of ventral surface of disk. All fins with at least a few tubercles; dorsal with only a few tubercles at base, but pectoral, ventral, and anal fins with tubercles at their bases and running out along rays for a third to three-fourths their length. Caudal as in generic description. Skin covering eyeballs bearing tiny tubercles with rim around cornea beaded by a row of small bucklers. Pectoral membranes thick, opaque, ventral surfaces of ends of rays with fleshy pads.

Color in preservative. Ground color of dorsal surface of body light tan to dark brown with round dark spots (occasionally rings) in an elongate cluster on either shoulder and in a band down either side of tail, each continuous with a cluster in axillae. Sometimes the same spotted pattern occurs on face. Ventral surface uniformly pale; lips pale. The small rostrum sometimes with a dusky tip, but no dark subterminal ring except in a few small specimens; iris golden or black. Basal portions of pectoral fins pale, occasionally with a few faint spots, darkening distally so that frequently a distinct black border is formed. Ventrals and anal the same pale ground color as ventral surface of body, anal with a dusky spot distally in a few small specimens. Dorsal dusky with faint splotches or simply pale. About one-half the specimens at hand have no dark markings on caudal, but remainder show pattern common for genus.

Color in life. The following description from three color transparencies of a freshly killed specimen captured in winter off North Carolina; one transparency shows a dorsal, one a lateral, and one a ventral view.

Ground color of dorsal surface of body medium brown with whitish patches where skin evidently abraded from protruding tops of bucklers. Darker mottlings of pigment in axillae. Fine black lines radiating from apices of large bucklers. An elongate cluster of round dark spots on either shoulder; among these spots are sprinkled a few smaller, intensely orange spots, about four on each side (cast shadows on the photographs may be obscuring other orange spots). Pectoral and caudal fins with mottled brownish basal portions fading to translucent white with pale tan striations on middle portions and terminating in broad, bright orangy-red borders blending to pure dark red and finally to narrow black distal margins.

Face the same brownish ground color as dorsal surface of body. Lips bright orangy red; iris a rosy-brass color with tan spots in a circle around pupil. Ventral operculum well extended in example and the same rosy-brass color as rest of iris.

Ventral surface of body with a transparent wash of pinkish orange over a pale gray surface.

Distribution (Fig. 17).—Atlantic coast of the United States from Cape Hatteras, North Carolina, to the Florida Keys. (One specimen from Jamaica, USNM 160732, 150.0 mm SL, has the general shape of the head and the small mouth that characterize *rostellum,* but it differs from *rostellum* in other body proportions and has no diagnostic color markings; I am unable to assign this specimen.) Bathymetric range: 28–228 m.

Name.—The name *rostellum* is the diminutive of the word rostrum, referring to the particularly small rostrum in this species.

Material Examined.—Numbers in parentheses are numbers of specimens. For data from Combat stations (=C) and Silver Bay stations (=SB), refer to Bullis and Thompson (1965); for data from Pelican stations (=P), refer to Anderson (1956). Holotype. USNM 188809, C-336, Atlantic coast of Florida; a male 129.5 mm SL.

Paratypes. **North Carolina:** FMNH 64338 (1), C-384; USNM 72288 (1), Cape Lookout; USNM 111848 (1), Beaufort; USNM 132093 (1), Albatross sta. 2417, 33°18′30″N, 77°07′W, 174 m; USNM 148317 (2), Albatross sta. 2600, 34°39′40″N, 75°35′30″W, 159 m; USNM 148320 (3), Albatross sta. 2602, 34°38′30″N, 75°33′30″W, 227 m; USNM 151919 (1), Albatross III sta. 35, 34°45.5–48′N, 75°28′–33′W, 77–88 m; USNM 151962 (1), Albatross III, 31-B, sta. 14, 33°26′N, 77°03.5–06′W, 59 m; USNM 151971 (1), Albatross III, 31-D, sta. 3, 34°11′N, 76°06′W, 82–119 m. **South Carolina:** CAS 23925 (3), SB-1782; FMNH 64100 (1), Bowers sta. 50, 31°50′N, 79°45′W, 46 m; USNM 84510 (4), Albatross sta. 2312, 32°54′N, 77°53′30″W, 161 m. **Georgia:** ANSP 103634 (1), P-178-10; CAS-SU 62117 (2), SB-1768; FMNH 66385 (15), Bowers sta. 32, 30°14′N, 80°16′W, 73 m; UF 24189 (1), Brunswick; USNM 149959 (2); USNM 188810 (1), P-198-5. **Florida:** FMNH 66388 (2), SB-3442; MCZ 32940 (1), inlet near New Smyrna; MCZ 45088 (3), SB-3022; MCZ 45089 (1), SB-2775; MCZ 45090 (1), P-168-2; MCZ 45091 (1), Cape Canaveral Pier; MCZ 45092 (1), SB-2771; MCZ 45093 (1), P-169-3; USNM 18031 (1), St. Augustine; USNM 38026 (1), 3.2 km s of Mosquito Inlet, Hillsborough River; USNM 131628 (2), Albatross sta. 2641, 25°11′30″N, 80°10′W, 110 m; USNM 188790 (1), P-208-8; USNM 188794 (1), P-171-2; USNM 188806 (L), P-169-8; USNM 188807 (1), C-334; USNM 188813 (2), C-336 (same haul as holotype). **Florida Straits:** CAS-SU 62123 (1), SB-2039; UF 24190 (1), C-455. **Florida Keys:** USNM 117004 (2), Tortugas; USNM 117005 (1), Tortugas.

Other: USNM 83785–83786 (3), Albatross sta. 2311 and 2318, 32°55′N, 77°54′W (South Carolina) and 24°25′45″N, 81°46′00″W (Florida Keys), 145 and 82 m.

Ogcocephalus declivirostris new species

(Figure 24*C–E*)

Ogcocephalus sp.: Hildebrand 1954:322 [off Texas; partial description; stomach contents]; Walls 1975:120 [n Gulf of Mexico; called *Ogcocephalus* sp. B; partial description; figs.]; Hoese and Moore 1977:144, fig. 100 [nw Gulf of Mexico; key; partial description; range].

DIAGNOSIS AND COMPARISONS.—An *Ogcocephalus* with rostrum generally sloping downward with respect to the long axis of the body instead of being horizontal or tilted upward. *O. declivirostris* differs from all its congeners except *pumilus* and *notatus* in lacking the development of fleshy pads on the ventral surfaces of the pectoral and pelvic rays. It may be separated from the long-nosed species, *pumilus, corniger,* and *vespertilio,* by the length of the rostrum (length of rostrum into length of disk margin 3.4–8.4 in *declivirostris,* 1.5–3.0 in the long-nosed species, Fig. 9) and from *notatus* by the width of the mouth (width of mouth into length of disk margin 2.8–3.7 in *declivirostris,* 1.8–2.5 in *notatus*). It is distinguished from all species except *pumilus, parvus,* and *corniger* by its low pectoral ray count (usually 11 in *declivirostris,* 12 or more in other species except *pumilus, parvus,* and *corniger,* Table 3). *O. declivirostris* is sympatric with *O. pantostictus,* both being species of the northern and western coasts of the Gulf of Mexico; besides the lower pectoral fin ray count in *declivirostris,* just mentioned, *declivirostris* has a lower count for the subopercular lateral-line series than *pantostictus* (modally 7 in *declivirostris,* 9 in *pantostictus*). The range of *parvus* overlaps with that of *declivirostris* in the northern Gulf of Mexico; *declivirostris* is distinguished from *parvus* by its flatter head (head depth into SL 4.3–5.1 in *declivirostris,* 3.1–4.2 in *parvus*) and larger mouth (width of mouth into head depth 1.4–1.9 in *declivirostris,* 2.0–2.8 in *parvus*).

DESCRIPTION.—Counts and measurements from 99 specimens, 39.6 to 137.0 mm SL (Table 1).

Counts. Counts given in Tables 2–6; in following description, counts for holotype given in brackets. In *declivirostris* all counts except vertebral count at low end of range of variation within genus. Pectoral fin ray count usually 11 [11,11]; range 9–12. Subopercular lateral-line scale count usually 8 [8,9]; range 7–9. Mean for lateral-line scale count 25 [25,27]; range 22–28. Vertebral count most frequently 20; range 18–20. [D. 5; A. 3.]

Proportions. Proportions expressed as ratios given by the mean followed by the range in parentheses and the proportion for the holotype in brackets.

Length of disk margin intermediate relative to range of variation for genus, 2.4(2.3–2.6)[2.4] in standard length. Tail stout and broad, its width 1.6(1.3–2.0)[1.3] in length of disk margin, tapering slightly but rounding off more abruptly at caudal fin than in other species. Caudal peduncle thick, its depth 2.5(2.3–2.8)[2.5] in head depth. Rostrum a rod-shaped protuberance with a narrow base, generally pointing downward but sometimes horizontal relative to long axis of body; never tilted upward. Length of rostrum 5.7(3.4–8.4)[7.0] in length of disk margin; the series at hand shows that during ontogeny the rostrum becomes relatively shorter. Aperture of illicial cavity approximately oval to subtriangular, wider than high in medium- and large-sized specimens, higher than wide in specimens less than about 65 mm SL. Cranium when viewed from front rising in a gradual curve above disk, head depth 1.9(1.8–2.1)[1.9] in length of disk margin. Width of cranium 3.2(2.7–3.7)[3.3] in length of disk margin. The following in width of cranium: eye 1.4(1.1–1.6)[1.6], lateral ethmoid width 1.6(1.3–1.9)[1.6]. Interorbital space concave, narrow, its width 2.7(2.1–3.4)[3.2] in width of cranium, 4.5(3.3–5.7)[5.7] in head depth. Mouth average size, its width 1.6(1.4–1.9)[1.5] in head depth, 3.1(2.8–3.7)[2.8] in length of disk margin; length of jaw 2.4(2.1–2.7)[2.1] in head depth. Upper lip moderately fleshy, of an even width for its entire length; lower lip thickened medially, the thickening becoming a pronounced lobe in largest specimens. Dorsal fin relatively large, its length 2.8(2.4–3.4)[2.8] in length of disk margin; anal fin also large, its length 2.5(2.1–2.9)[2.6] in length of disk margin.

Integument. Dermal cirri well developed on lateral sides of tail and disk, more so than in other species of *Ogcocephalus.* Cirri present on tip of rostrum in small specimens. Large bucklers arranged as described in generic description. Dorsal fin devoid of tubercles, anal fin with only a few at base. Pectoral fins with tubercles at base on both dorsal and ventral surfaces, a few tubercles extending out along anterior and posterior rays. Pelvics with tubercles present on basal quarter of ventral surface but none on dorsal surface. Caudal as in generic description. Skin covering eyeballs bearing tiny tubercles with rim around cornea beaded by a row of small bucklers in small specimens, disappearing in large specimens. Pectoral membranes relatively thin and translucent; no fleshy pads on ventral tips of rays.

Color in preservative. Ground color of dorsal

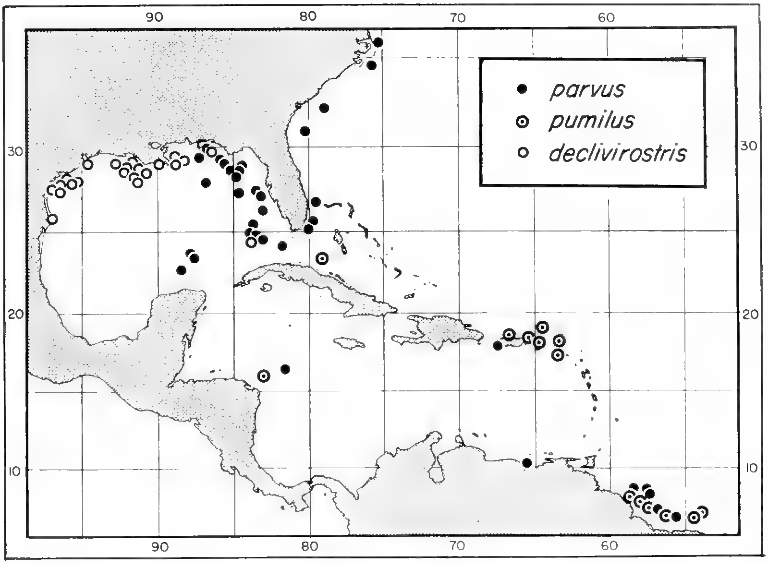


Figure 25. Localities for study material of *Ogcocephalus parvus, O. pumilus,* and *O. declivirostris. O. parvus* also known from Recife, Brazil (Günther 1880).

surface of body gray or tan, apices of bucklers paler than ground color. Dim rounded spots sometimes clustered on shoulders, face, in axillae, and along sides of tail, occurring mostly in small specimens. A few small specimens have these spots covering entire disk dorsally. Ventral surface of body uniformly pale; lips pale, occasionally with dusky splotches. Rostrum with a diffuse black tip in small specimens, this mark disappearing in larger specimens. Iris black or golden, sometimes golden with a ring of dim spots circling pupil. Pectoral fins dusky, sometimes darkened towards tips, but no pronounced dark borders except in some small individuals. Pelvics and anal the same pale ground color as ventral surface of body, anal sometimes with a dusky tip in small specimens. Dorsal dusky with inconspicuous splotches. Caudal as described in generic description except for a few specimens that have the caudal uniformly dusky.

Color in life. Unknown.

Distribution (Fig. 25).—Northern and western coasts of Gulf of Mexico from longitude 86°W to latitude 26°N. One record from Florida Straits. Bathymetric range: 3.5–180 m except for Florida Straits record (388 m).

Name.—The name *Ogcocephalus declivirostris* means an *Ogcocephalus* with rostrum sloping downward.

Material Examined.—Holotype: FMNH 64136, off Texas, 28°02′N, 96°03′W, 40 m; a male 129.3 mm SL.

Paratypes. Numbers in parentheses are numbers of specimens. For data from Oregon stations (=O), refer to Springer and Bullis (1956) and Bullis and Thompson (1965). **Gulf coast of Florida:** ANSP 103628 (1), O-331; FMNH 61579 (1), O-858; FMNH 64120 (2), O-944. **Florida Straits:** UMML 3897 (1), O-1550. **Louisiana:** CAS 23930 (1), O-2700; CAS 23931 (1), O-2704; CAS-SU 62119 (3), Pelican sta. 84-3, 28°14′N, 91°41′W, 55 m; FMNH 46735 (1), 0-72; FMNH 46736 (3), O-75; FMNH 46737 (3), O-283–284; GCRL 557 (2) and GCRL 559 (1), s of Grand Isle, 37 m; GCRL 558 (2) and GCRL 560 (1), s of Grand Isle, 27 m; MCZ 45072 (3), Pelican sta. 74-3, 29°04′N, 88°44.5′W, 110 m; MCZ 45073 (1), Pelican sta. 72-6, 29°11.5′N, 88°52′W, 73 m; MCZ 45074 (1), Pelican sta. 69-6, 28°48′N, 89°51′W, 55 m; USNM 131166 (21), Morgan City, 3.7–9.1 m; USNM 188761 (1), sw of Eugene I. Beacon, Atchafalaya Bay; USNM 188764 (1), Pelican sta. 85-4, 28°11′N, 91°24.5′W, 86 m; USNM 188765 (1), Pelican sta. 85-3, 28°09′N, 91°27′W, 91 m; USNM 188767 (1), Pelican sta. 81-8, 28°50′N, 91°29.5′W, 18 m; USNM 188771 (1) and USNM 188774 (1), ssw of Eugene I. Beacon, Atchafalaya Bay; USNM 188777 (1), Pelican sta. 86-3, 28°28′N, 91°13.5′W, 40 m; USNM 188784 (2), Pelican sta. 34, 28°33′N, 90°55′W, 26 m; USNM 188792 (2), Pelican sta. 84-1, 28°22.5′N, 91°44.5′W, 59 m; USNM 188796 (1), Pelican sta. 94-1, 28°27′N, 92°14′W, 53 m; USNM 188799 (1), Pelican sta. 93-8, 28°33′N, 92°15.5′W, 44 m; USNM 188801 (2), Pelican sta. 93-3, 28°55′N, 92°15.5′W, 26 m. **Texas:** CAS-SU 62140 (30), Galveston; FMNH 61576 (1), 27°04′N, 96°23′W, 55 m; FMNH 61577 (2), 28°02′N, 96°04′W, 40 m; FMNH 61578 (1), 28°02′N, 96°04′W, 37 m; FMNH 61580 (1), 27°22′N, 96°34′W, 49 m; FMNH 61582 (1), 27°30′N, 96°28′W, 73 m; FMNH 61583 (1), 27°39′N, 96°28′W, 68 m; FMNH 64135 (1), 27°49′N, 96°31′W, 40 m; FMNH 64137 (1), 27°34′N, 96°43′W, 42 m; FMNH 64138 (2), off Mustang I., 46–48 m; USNM

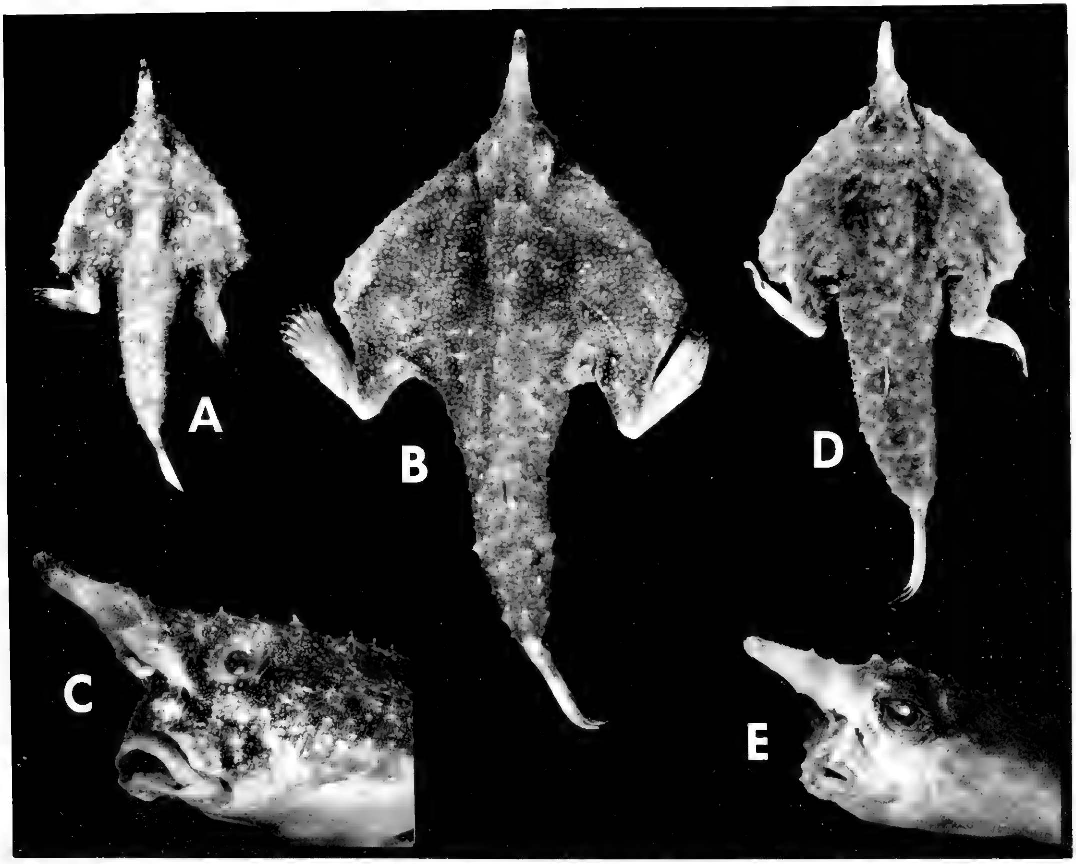


FIGURE 26. *(A)* Paratype of *Ogcocephalus corniger* new species, 61.0 mm SL, UF 24183, from w of Andros I., Bahamas, 24°25′N, 79°13′W, showing color pattern of juvenile. *(B)* and *(C) Ogcocephalus corniger* new species, holotype, 124.5 mm SL, USNM 188808, Gulf of Mexico, 29°00′–10′N, 85°01′W. *(D)* and *(E) Ogcocephalus pumilus* new species, holotype, 57.5 mm SL, USNM 188812, Surinam, 7°05′N, 54°08′W.

118606 (23), Galveston; USNM 171763 (2), near Brownsville; USNM 188776 (1), SILVER BAY sta. 200, 27°59′N, 95°15′W, 79–84 m. **Material without exact locality:** USNM 188766 (1), Madame Canaia.

Ogcocephalus pumilus new species

(Figure 26*D–E*)

DIAGNOSIS AND COMPARISONS.—A long-nosed *Ogcocephalus* distinctive for its small size and lack of pigment markings. *Ogcocephalus pumilus* is the smallest member of the genus; maximum standard lengths for specimens seen in this study are all under 70 mm (Table 1). *O. pumilus* differs from all its congeners except *declivirostris* and *notatus* in lacking the fleshy ventral pads on the tips of the rays of the pectoral and pelvic fins.

Ogcocephalus pumilus is sympatric with *parvus* and *nasutus*, but as it does not occur on the coasts of the southeastern United States and Gulf of Mexico, its range is less extensive than that of *parvus*. It is distinguished from *parvus* by its long rostrum (length of rostrum into length of disk margin 2.0–3.0 in *pumilus*, 3.2–5.0 in *parvus*) and shorter disk margin (length of disk margin into SL 2.2–2.7 in *pumilus*, 1.9–2.2 in *parvus*) as well as its pale color contrasted with the mottlings and spotted patterns seen in *parvus*. *O. pumilus* is also distinguished from most examples of *nasutus* by its lack of color pattern as well as its diminutive size (*nasutus* being among the largest species in the genus). Also, many specimens of *pumilus* may be separated from *nasutus* by the pectoral fin ray count (modally 11 in *pumilus*, 12 or 13 in *nasutus*, Table 3).

Off the northern coast of South America, the range of *pumilus* overlaps that of *notatus*. The two species are separable on the basis of the pectoral fin ray count (11–12 in *pumilus*, 13–14, rarely 12, in *notatus*) and subopercular lateral-line scale count (range 5–7, modally 6, in *pumilus*, 7–10, modally 9, in *notatus*). *O. pumilus* also has a markedly smaller mouth than *notatus* (width of mouth into length of disk margin 2.6–3.4 in *pumilus*, 1.8–2.5 in *notatus*).

DESCRIPTION.—Counts and measurements from 63 specimens, 25.8 to 66.7 mm SL (Table 1).

Counts. Counts given in Tables 2–6. In following description, counts for holotype given in brackets. All counts in *pumilus* low compared to counts for genus as a whole. Pectoral fin ray count most often 11 [11,11]; range 10–12. Subopercular lateral-line scale count most often 6 [6,7]; range 4–7. Cheek lateral-line scale count most often 8 [8,8]; range 8–9. Mean for lateral-line scale count 21 [21,21]; range 19–24. Anal fin ray count 3 more than half the time [3], remarkable because count normally 4 throughout family. [D. 4.] Vertebral counts on 14 specimens all 19.

Proportions. Proportions expressed as ratios given as mean followed by range in parentheses and proportion for holotype in brackets.

Length of disk margin 2.3(2.2–2.5)[2.3] in SL. Tail moderately wide, its width 1.8(1.6–2.1)[1.8] in length of disk margin. Caudal peduncle 2.8(2.5–3.2)[2.6] in head depth. The grotesque rostrum thin and long, its length 2.4(2.0–3.0)[2.4] in length of disk margin, its long axis about horizontal with body axis rather than tilted upward. Aperture of illicial cavity subtriangular, higher than wide. Head depth 1.9(1.7–2.1)[2.1] in length of disk margin. Width of cranium 3.1(2.7–3.5)[3.3] in length of disk margin. The following in width of cranium: eye 1.3(1.1–1.5)[1.3]; lateral ethmoid width 1.7(1.5–1.9)[1.6]. Interorbital space slightly concave, narrow, its width 3.1(2.4–3.7)[2.8] in width of cranium, 5.1(3.8–6.2)[4.4] in head depth. Mouth moderate-sized, its width 1.5(1.4–1.7)[1.7] in head depth, 3.0(2.7–3.4)[3.2] in length of disk margin; length of jaw 2.4(2.1–2.6)[2.4] in head depth. Upper lip moderately fleshy, of an even width for its entire length; lower lip fleshy, no median lobe. Dorsal and anal fins about average in proportion to body size, length of dorsal fin 3.3(2.3–4.3)[3.9] in length of disk margin; length of anal fin 2.9(2.4–3.7)[3.0] in length of disk margin.

Integument. Dermal cirri usually present on lateral sides of tail and disk margin. No cirri on tip of rostrum. Large bucklers arranged as described for genus. Dorsal fin devoid of tubercles, anal fin with only a few near base. Pectorals and pelvics with tubercles at base and running out on the fins for ¼ to ½ their length. Caudal as in generic description. Skin covering eyeballs bearing tiny tubercles with rim around cornea often beaded by a row of small bucklers. Pectoral membranes thin, translucent; pectoral rays without fleshy pads on their ventral tips.

Color in preservative. Dorsal surface of body white to pale gray or grayish brown; in the latter case, apices of bucklers paler than ground color. Pigment markings usually absent; if present, they are dusky and ill-defined spots, occurring on shoulders, lateral sides of tail, and (very infrequently) face. Ventral surface of body uniformly pale; lips also pale. Rostrum with a dusky subterminal ring. Iris black or silvery. Pectorals colorless in white examples, dusky in gray ones; in the latter, the gray color may shade to a darker tone towards tips of pectorals. Pelvics and anal the same pale whitish color as ventral surface of body; anal sometimes with a dusky tip. Dorsal colorless in white specimens, dusky in others, sometimes with a faintly darker stripe or two. Caudal colorless to dusky in white examples; gray or brownish individuals with caudal as in generic description.

Color in life. From a color transparency taken shortly after capture: body pale bluish gray, ventral surface of body paler than dorsal surface, the whole suffused with a wash of translucent pinkish orange. Rostrum a deeper orange. Distal thirds of pectorals and caudal deep orange.

DISTRIBUTION (Fig. 25).—Known from the Bahamas just north of Cuba, from Puerto Rico, the Leeward Islands, the western Caribbean, and the northern coast of South America to Surinam. Bathymetric range: 35–348 m.

NAME.—The name *pumilus*, which is derived from a word meaning dwarf, is given in reference to the diminutive size and grotesque appearance of this species.

MATERIAL EXAMINED.—Numbers in parentheses are numbers of specimens. For data from OREGON (=O) and SILVER

BAY (=SB) stations, refer to Bullis and Thompson (1965). HOLOTYPE: USNM 188812, Surinam, O-2018, 57.5 mm SL.

PARATYPES. **Northern Bahamas:** USNM 188759 (2), SB-2455. **Puerto Rico:** FMNH 64843 (2) and FMNH 64844 (10), O-2626; FMNH 64845 (2), O-2627; MCZ 45085 (3), O-2668; MCZ 45087 (8), O-2626. **Virgin Islands:** CAS 23920 (1), O-2618; FMNH 64841 (4), O-2616; USNM 108353 (1), 18°25′30″N, 63°32′36″W. **Leeward Islands:** FMNH 64846 (5), O-2631; FMNH 64848 (2), O-2633; FMNH 64891 (33), O-2231; UMML 7488 (14), O-2632; USNM 190467 (1), O-2632. **Honduras:** CAS 23921 (1), O-1865. **Guyana:** ANSP 103632 (3), O-2231; ANSP 103633 (1), O-2262; CAS 23919 (1), O-2249; CAS-SU 62122 (3), O-2345; CAS-SU 62125 (1), O-2259; FMNH 64893 (3), O-2249; FMNH 65965 (1), O-2001; FMNH 65966 (1), O-2234; FMNH 65967 (3), O-2248; FMNH 65968 (1), O-2250; FMNH 65969 (3), O-2261; FMNH 65970 (4), O-2344; MCZ 45086 (3), O-2261; USNM 185984 (3), 8°33′N, 58°46′W. **Surinam:** FMNH 64899 (2), O-2330.

Ogcocephalus corniger new species

(Figure 26*A–C*)

Ogcocephalus vespertilio (non Linnaeus): LONGLEY AND HILDEBRAND 1941:311, 314 [Tortugas, Florida; key; description].

Ogcocephalus sp.: LONGLEY AND HILDEBRAND 1941:311, 315 [Tortugas, Florida; key; partial description by Hildebrand]; WALLS 1975:118 [northern Gulf of Mexico; partial description; figs.; called *Ogcocephalus* sp. A; color photograph].

Oncocephalus vespertilio (non Linnaeus): FOWLER 1952:14 [off southern Florida; partial description].

Probable references:

Lophius nostratus MITCHILL 1818:325 [''Straits of Bahamas''; a misspelling of *Lophius rostratus* Shaw].

Malthe vespertilio (non Linnaeus): UHLER AND LUGGER 1876:77 [southern Chesapeake Bay; partial description].

Oncocephalus vespertilio (non Linnaeus): GARMAN 1896:87 [off Key West, Florida; partial description].

Ogcocephalus vespertilio (non Linnaeus): H. M. SMITH 1907:401, figs. 185–186 [off Beaufort, North Carolina; partial description; figures the same as Jordan and Evermann 1898:pl. 392, figs. 958 and 958b (legend: *Ogcocephalus vespertilio*)].

DIAGNOSIS AND COMPARISONS.—A long-nosed *Ogcocephalus* distinctive for its dorsal color pattern, which consists of small pale round spots close together and evenly distributed over the darker background color of the dorsal surface of the body (specimens under about 65 mm SL lack this pattern; see sections on color below).

The long rostrum in *corniger* separates it from all other species of *Ogcocephalus* except *vespertilio, pumilus,* long-nosed morphs of *nasutus,* and small examples of *cubifrons* less than 50 mm SL (Fig. 9). The range of *corniger* (coasts of southeastern United States and eastern Gulf of Mexico) is widely separated from that of *vespertilio* (coast of Brazil) and, at this time, appears to be separated from that of *pumilus* (northern Bahamas, Caribbean, and coast of South America to Surinam). Besides separate ranges, other aspects separate these long-nosed species. *O. corniger* differs from *vespertilio* in its lower number of pectoral rays (10–12 in *corniger,* 13–15 in *vespertilio*) and lower number of subopercular lateral-line scales (usually 5–7 in *corniger,* usually 8–9 in *vespertilio,* Table 6); it differs from *pumilus* in its larger body size (*pumilus* is less than 70 mm in SL) and in having fleshy pads on the ventral tips of the pectoral rays which *pumilus* lacks.

The range of *corniger* overlaps the ranges of *nasutus* and *cubifrons,* but long-nosed forms of *nasutus* and *cubifrons* may be distinguished from *corniger* by the pectoral fin ray count (modally 11 in *corniger,* usually 12 or 13 in *nasutus* and *cubifrons,* Table 3). *O. corniger* differs further from *nasutus* in the number of cheek lateral-line scales (usually 8 in *corniger,* modally 9 in *nasutus,* Table 5) and from *cubifrons* by its longer jaw (length of jaw into width of cranium 1.2–1.5 in *corniger,* 1.6–2.0 in *cubifrons*).

Two short-nosed species of *Ogcocephalus, parvus* and *rostellum,* occur within the range of *corniger* but are separable from *corniger* not only by the proportions of the rostrum but also by color pattern—neither ever has the pattern of small round pale spots on a darker background seen in *corniger.* Other characters that separate *corniger* from *parvus* include the smoother shagreenlike quality of the integument in *corniger* compared to the rough, lumpy surface of the integument in *parvus,* and the larger mouth in *corniger* (width of mouth into head depth 1.5–2.0 in *corniger,* 2.0–2.8 in *parvus*). An additional character separating *corniger* from *rostellum* is the pectoral fin ray count (modally 11 in *corniger,* modally 13 in *rostellum,* Table 3).

DESCRIPTION.—Counts and measurements from 57 specimens 26.2 to 134.0 mm SL (Table 1).

Counts. Counts given in Tables 2–6. In the following description, counts for holotype given in brackets. Counts in *corniger* low compared to those of genus as a whole. Pectoral fin ray count usually 11 [11,11]; range 10–12. Subopercular lateral-line scale count usually 6 or 7 [6,6]; range 4–8. Cheek lateral-line scale count 8 [8,8] (the commonest count for genus); range 7–9. Mean for lateral-line scale count nearly 21 [20,20]; range 18–24. Majority of sample of *corniger* had 19 vertebrae, the most usual vertebral count for the genus. [D. 3; A. 4.]

Proportions. Proportions expressed as ratios given as mean followed by range in parentheses and proportion for holotype in brackets.

Length of disk margin intermediate relative to range of variation in genus, 2.3(2.1–2.5)[2.4] in SL. Tail narrow to moderately wide, the width 2.0(1.7–2.4)[1.7] in length of disk margin, tapering to a relatively thin caudal peduncle; depth of caudal peduncle 3.3(2.8–4.1)[3.3] in head depth. Rostrum with a wide base but becoming slender distally, upturned and very long, the length 2.0(1.7–2.3)[2.1] in length of disk margin. Aperture of illicial cavity triangular, always higher than wide. Cranium, when viewed from front, rising steeply above disk; head relatively deep, its depth 1.8(1.6–1.9)[1.7] in disk margin. Width of cranium 3.3(2.9–3.5)[3.2] in length of disk margin. Eye comparably large, 1.3(1.1–1.7)[1.5] in width of cranium. Lateral ethmoid width 1.7(1.5–2.0)[1.7] in width of cranium. Interorbital space flat to moderately convex, its width 2.1(1.7–2.5)[1.9] in width of cranium, 3.9(3.1–4.6)[3.6] in head depth (except one specimen, which has these proportions 2.9 and 5.7, respectively). Mouth average size, its width 1.6(1.5–2.0)[1.5] in head depth, 2.9(2.6–3.7)[2.6] in length of disk margin; length of jaw 2.4(2.2–2.6)[2.5] in head depth. Upper lip fleshy, of an even width for its entire length; lower lip also fleshy, thickly swollen medially. Dorsal fin small compared to other species in genus, its length 4.8(3.7–5.8)[5.8] in length of disk margin; anal fin also small, its length 3.0(2.5–3.5)[3.0] in length of disk margin.

Integument. Dermal cirri absent, or at least inconspicuous, except near tip of rostrum, where fairly long cirri occur in subterminal ring. Large bucklers arranged as in generic description. Dorsal fin devoid of tubercles; anal fin with tiny tubercles covering proximal third or half of fin. Pectorals and pelvics with tiny tubercles at base on both dorsal and ventral surfaces, running out along fin rays for a third to half their length. Caudal as in generic description. Skin covering eyeballs bearing fine tubercles with rim around cornea beaded by a row of slightly larger ones. Pectoral membranes thick, opaque, ventral surfaces of the ray tips with well-developed fleshy pads (pads not developed in small specimens).

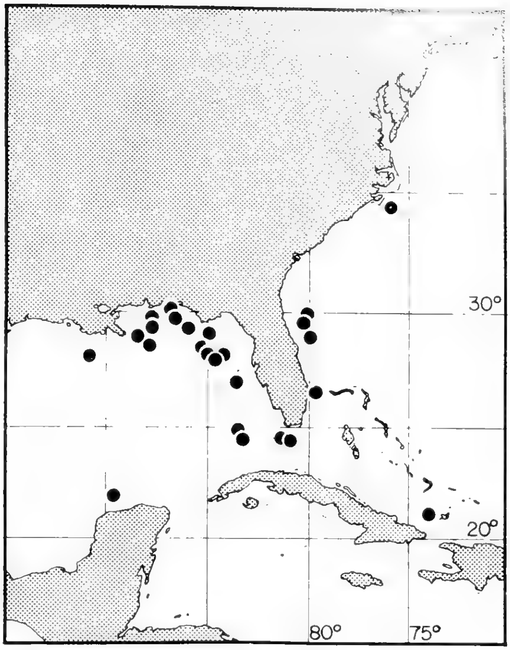


FIGURE 27. Localities for study material of *Ogcocephalus corniger*.

Color in preservative. Dorsal surface of body uniformly covered with small pale spots on a darker ground color, the ground color generally brown or gray, becoming darker on shoulders in many examples; sometimes spots so close together that ground color may appear as a reticulum. The pale spots are unpigmented apices of bucklers. Specimens under about 65 mm SL generally lack this color pattern and are uniformly pale or dusky, but occasionally, dark rings occur clustered on shoulders. Ventral surface of body uniformly pale; lips pale. Rostrum with a diffuse dark subterminal ring, incomplete below. Iris black or golden, or golden with spots, but never with radiating lines. Pectorals pale to dusky proximally with broad dark brown or black margins; ray tips white, ventral pads of rays white. Pelvic and anal fins the same ground color as ventral surface of body; pelvics sometimes with darkened or blotched tips in dark specimens; anal most often with distal third very dark to black. Dorsal dusky, often with a pale diagonal stripe or two. Caudal as in generic description, the border always dark to black.

Color in life. The following description from three color transparencies made of a freshly killed specimen captured in winter off North Carolina. One transparency shows a dorsal view of the fish and one a ventral view; the remaining one shows a lateral view of the head.

Ground color of dorsal surface of body chocolate brown with fine, close-set pearl-gray spots completely covering the surface, including face and skin covering eyeballs. Even iris of eye has the spotted pattern, with a brassy highlight around pupil. Lips bright red-orange, with a translucent wash of red-orange pigment over lower face and lower edge of disk, where it becomes continuous with the same red-orange wash over ventral surface of body, including pelvic and anal fins. This red-orange coloration on ventral surface is more intense on chin, on a ring encircling anus, and on tail including anal fin, which also has a black tip. Pectoral fins with translucent red-orange color basally, the rays becoming deep red-orange distally and the fins each with a broad blackish margin. Caudal dark basally, becoming pale red-orange in middle portion with rays a darker shade than membranes, and black again distally in a broad margin.

Longley (Longley and Hildebrand 1941) stated for examples from off Tortugas (his *Ogcocephalus vespertilio*) that the pectorals and caudal were, "buff-yellow over basal half, passing through maroon-purple to prune purple at the tips, the contrast between the darker outer third and the yellow basal two-thirds being sharper on the under side of the pectorals; belly, maxillary membranes and buccal cavity coppery red." Walls (1975) presents a photograph of an example from the Gulf of Mexico (his *Ogcocephalus* sp. A) which shows the pectorals red-orange basally, succeeded by bright yellow, which gives way to more red-orange, which in turn gives way to black borders.

DISTRIBUTION (Fig. 27).—Known from the Atlantic coast of the United States from Cape Lookout, North Carolina, to Florida, Campeche Banks, and the northeastern Gulf of Mexico to Louisiana; one record from off Great Inagua I., Bahamas. Bathymetric range: 29–230 m.

NAME.—This form is named *corniger*, meaning horn-bearer, in reference to the long, upturned rostrum.

MATERIAL EXAMINED.—Numbers in parentheses are numbers of specimens. For data from early OREGON stations (=O), refer to Springer and Bullis (1956); for data from later OREGON stations and for COMBAT (=C) and SILVER BAY (=SB) stations, refer to Bullis and Thompson (1965). HOLOTYPE: USNM 188808, Gulf coast of Florida, O-729–730; a male 124.5 mm SL.

PARATYPES. **North Carolina:** CAS 23927 (1), SB-2930; USNM 152030 (1). **Atlantic coast of Florida:** ANSP 103626 (1), C-101; CAS-SU 62124 (1), C-497; CAS-SU 62128 (1), SB-1931; USNM 161375 (1), Palm Beach. **Bahamas:** FMNH 66387 (1), SB-3496; UF 24183 (1), SB-2470. **Florida Straits:** CAS 23926 (1), SB-437; UF 24182 (1), SB-2362. **Florida Keys:** FMNH 64124 (6), O-1020; USNM 37853 (1), ALBATROSS sta. 2316, 24°25′30″N, 81°47′45″W, 91 m; USNM 74089 (1), s of Key West; USNM 117001 (1) and 117002 (3), Tortugas. **Gulf coast of Florida:** FMNH 64103 (1), O-603; FMNH 64104 (1), O-727–728; FMNH 64109 (1), O-732; FMNH 64113 (1), O-897; FMNH 64116 (2), O-917; FMNH 64119 (1), O-936; FMNH 64122 (2), O-945; 64126 (4), O-1021; FMNH 64129 (3), O-1022; MCZ 45070 (1), O-326; USNM 134087 (1), 28°47′30″N, 84°37′00″W. **Alabama:** FMNH 46744 (1), O-265; MCZ 45071 (1), O-2838; USNM 159159 (1), 29°47′N, 87°17′W. **Louisiana:** USNM 188793 (1), SB-175. **Yucatán:** USNM 188804 (1), SB-404.

Ogcocephalus parvus Longley and Hildebrand

(Figure 28)

Malthe vespertilio (non Linnaeus): GÜNTHER 1880:7 [Pernambuco (=Recife), Brazil].

Ogcocephalus parvus LONGLEY AND HILDEBRAND, 1940:283, fig. 28 [s of Tortugas, Florida; holotype USNM 109313]; 1941:311 and 314 [Tortugas, Florida; key]; ERDMAN 1956:338 [Joyuda, Puerto Rico; partial description]; BRIGGS 1958:301 [Florida, compiled]; MOE ET AL. 1966:120 [Florida; list of museum specimens]; BRADBURY 1967:417 [listed]; STARKS 1968:33 [Alligator Reef, Florida; composition of reef fauna]; WALLS 1975:116 [N Gulf of Mexico; partial description].

Oncocephalus parvus: FOWLER 1945:336 [Key West, Florida; listed]; 1952:15 [Sombrero Key Light, Florida; description of color].

Probable reference:

Ogcocephalus vespertilio: DAHLBERG 1975:45, fig. 93 [coast of Georgia; partial description; range, compiled].

DIAGNOSIS AND COMPARISONS.—An *Ogcocephalus* with exceptionally angular, craggy body contours and large, prominent bucklers. *O. parvus* differs from all its congeners except *cubifrons* in having a very small mouth relative to head depth (width of mouth into head depth 2.0–2.8 in *parvus*, 1.0–2.0 in all others except *cubifrons*). *O. parvus* may be separated from *cubifrons* by its narrower interorbital space (interorbital width into head depth 3.6–6.6 in *parvus*, 2.3–3.4 in *cubifrons*). It may be distinguished from all but *corniger*, *declivirostris*, and *pumilus* by its low pectoral fin ray count (usually 10–11 in *parvus*, 12 or more in all others except *corniger*, *declivirostris*, and *pumilus*). *O. parvus* is distinguished from *corniger* and *pumilus* by its short rostrum (length of rostrum into length of disk margin 3.2–5.1 in *parvus*, 1.7–3.0 in *corniger* and *pumilus*) and from *declivirostris*

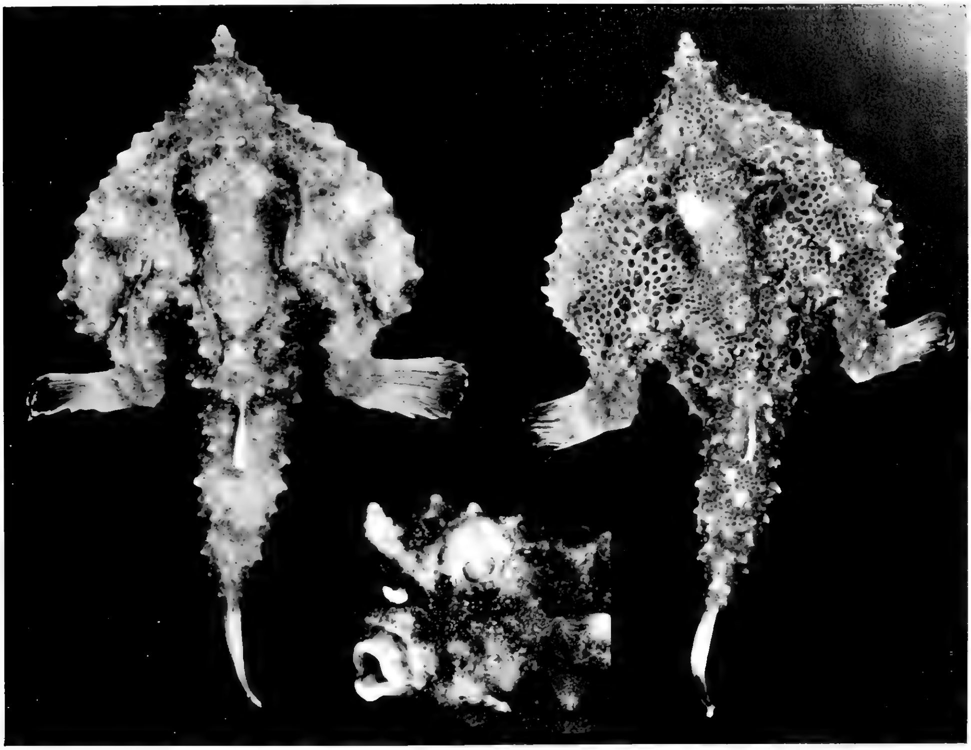


FIGURE 28. *Ogcocephalus parvus* Longley and Hildebrand. *Left* and *center:* FMNH 46742, Gulf of Mexico, 75.0 mm SL. *Right:* FMNH 65957, Guyana, 64.0 mm SL.

by the fleshy ventral pads developed on the distal ends of the pectoral fin rays (absent in *declivirostris*).

DESCRIPTION.—Counts and measurements from 69 specimens, 27.3 to 84.7 mm SL (Table 1). Because specimens in the northern part of the range (coasts of southeastern United States and eastern Gulf of Mexico) differed in pigment pattern from those in the southern part (Caribbean Sea and Atlantic coast of South America), the two groups were analyzed separately with the expectation that samples would accumulate that were large enough to differentiate the groups well. However, too few specimens from the southern part of the range were obtained, so only the color patterns and counts are treated separately in the following description. Data for body proportions were combined for the two groups.

Counts. Counts given in Tables 2–6. Counts for *parvus* the lowest found in genus. Pectoral fin ray count usually 10 in northern *parvus* and 11 in southern *parvus*; range 10–12 for species. Subopercular lateral-line count usually 5 or 6; range 4–8. Cheek lateral-line scale count usually 8; range 7–9. Mean count for lateral-line scales 17; range 15–19. Vertebral count modally 19; range 18–20 (all vertebral counts are from holotype and paratypes).

Proportions. Proportions expressed as ratios given as mean followed by range in parentheses. Relative length of disk margin longest for the genus, its length 2.1(1.9–2.2) in SL. Tail moderately wide, its width 2.0(1.7–2.5) in length of disk margin. Caudal peduncle 3.1(2.5–4.0) in head depth. Rostrum variously finger- to cone-shaped, but always short, its length 4.2(3.2–5.1) in length of disk margin. Aperture of illicial cavity oval or subcircular. Cranium rising steeply above disk, head depth 1.8(1.6–2.0) in length of disk margin. Width of cranium 3.2(2.6–3.6) in length of disk margin. The following in width of cranium: eye 1.4(1.1–1.6); lateral ethmoid width 1.7(1.4–1.9). Interorbital space narrow, concave, its width 2.7(2.1–4.1) in width of cranium, 4.8(3.6–6.6) in head depth. Mouth small and narrow, its width 2.3(2.0–2.8) in head depth, 4.1(3.4–5.2) in length of disk margin; jaw short, its length 3.1(2.8–3.5) in head depth. Upper lip fleshy, of an even width for its entire length; lower lip with a fleshy median lobe. Dorsal fin average size, its length 3.4(2.4–4.3) in length of disk margin; anal fin short, its length 3.1(2.4–3.6) in length of disk margin.

Integument. Dermal cirri usually sparse or absent, but a few examples have cirri well developed over dorsal surface of body. Most specimens from southern population have subterminal rostral cirri. Large bucklers arranged as in generic description. Dorsal fin devoid of tubercles; anal fin with only a few tiny ones at base. Pectorals and pelvics with tiny tubercles covering basal third or fourth of their length. Caudal as in generic description. Skin covering eyeballs bearing tiny tubercles with rim around cornea beaded by a row of small bucklers. Pectoral membranes thick, opaque; ventral surfaces of ray tips with well-developed fleshy pads.

Color in preservative. Northern examples: ground color of dorsal surface of body pale tan to medium brown. Markings variable but irregular or rounded dark brown spots, with or without whitish margins, clustered on shoulders, face, in axillae, and sometimes along lateral sides of tail. Occasionally some of these markings are rings instead of spots. Dark splotches, sometimes indistinct, may occur elsewhere on dorsal surface. A few specimens with minute dark spots scattered over dorsal surface in addition to other markings. Ventral surface of body uniformly creamy pale, sometimes becoming dusky on anterior part of head, particularly on chin, in which case two distinct white patches may occur, one on either side of mandible. Pectorals pale to nearly white with a broad black margin extending through all but the three shortest rays; ray tips white, ventral pads white. Pelvics and anal same pale ground color as ventral surface of body; anal often with a dusky or dark spot distally. Dorsal colorless or a little dusky basally. Caudal colorless in about half the specimens at hand, otherwise as in generic description. Iris black or golden, or golden with dark spots.

Southern examples: ground color of dorsal surface of body usually a much darker brown than in northern specimens (this difference does not show well in Fig. 28 because photographed specimens were chosen to show pigment markings contrasted as well as possible with ground color; fish on right in Fig. 28 is relatively pale). Minute but very distinct black dots on lateral portions of disk and on top of cranium, continuing posteriorly along dorsal surface of tail. Large, sharply defined brown or black spots and rings on shoulders and face and also in axillae, extending from these on to sides of tail. A few specimens with an absolutely pigmentless white patch a little larger than top of cranium in area and located in middorsal region just posterior to cranium. Ventral surface of body, fins, and eyes as in northern examples.

Color in life. From an aquarium specimen newly captured in Gulf of Mexico off Mobile, Alabama, kindly shown me by Dr. Robert L. Shipp and his students at the University of South Alabama: ground color of face and dorsal surface of body dark brown, the large irregularly shaped spots on shoulders and axillae lavender separated by cream-colored reticula in approximately the pattern seen on the right in Figure 28; smaller pepperlike spots on tail and disk seen in figure are black in living specimen. Down face on either side from eye to angle of jaw a cascade of orange spots having dark brown rims and separated by white-colored reticula. Lips orange. Iris gold flecked with orange. Pectorals a translucent orange with broad black margins. Caudal dark brown basally, white in middle third, orange on distal third.

Several Kodachrome transparencies made from specimens immediately after capture have been available. From specimens from off the southeastern United States, the following notes are offered: ground color of dorsal surface of body bright tan suffused with red-orange in large patches; dark spots arranged as described for preserved specimens. Dorsal fin red-orange. Pectorals with a red-orange stripe just proximal to black margin; ray tips white.

From a specimen newly captured from off coast of Guyana: dorsal surface of body very dark, the markings difficult to discern except those on shoulders (the usual cluster of irregular spots). Skin surrounding gill pores tan. Tips of many bucklers faintly red-orange. Pectorals with red-orange stripe just proximal to black margins; ray tips white. Ventral surface of body, including pectoral peduncles and bases of pectoral fins, entirely bright red-orange. Anal fin red-orange with white stripe through second quarter. Lips red-orange, corresponding to an observation by Erdman (1956) of a specimen from Puerto Rico with "bright red lips." A rectangularly shaped white patch on either side of mandible and an oblong white patch in median line about halfway between chin and bases of pelvics.

Distribution (Fig. 25).—Known from the Atlantic coast of the United States from Cape Hatteras south to the eastern Gulf of Mexico, the Caribbean Sea, and the coast of South America to Recife, Brazil. Bathymetric range: 29–126 m.

Material Examined.—Numbers in parentheses are numbers of specimens. For data from early Oregon stations (= O), refer to Springer and Bullis (1956); for data from later Oregon stations as well as Combat (=C) and Silver Bay (=SB) stations, refer to Bullis and Thompson (1965).

Northern examples

North Carolina: CAS 23922 (1), SB-2927; CAS 23924 (1), SB-3339; FMNH 64336 (1), C-384; UF 24186 (1), C-385. **South Carolina:** MCZ 45082 (1), C-166. **Georgia:** FMNH 66383 (9), Bowers sta. 32, 30°14′N, 80°16′W, 73 m; MCZ 45083 (1), Pelican sta. 178-15, 31°20′N, 80°17′W, 38 m; UMML 114 (1), between Jacksonville, Florida, and Brunswick, Georgia. **Atlantic coast of Florida:** ANSP 103631 (1), SB-2721. **Florida Straits:** CAS-SU 62118 (2), C-457; UF 24187 (2), SB-2363; UF 24188 (1), SB-2382. **Florida Keys:** FMNH 64125 (6), O-1020; USNM 109313 (holotype) and USNM 109314 (12 paratypes), Tortugas, 134–201 m. **Gulf coast of Florida:** FMNH 46742 (1), 29°04′N, 84°23.5′W, 37 m; FMNH 46743 (2), O-35; FMNH 64105 (1), O-729–730; FMNH 64108 (2), O-732; FMNH 64112 (1), and FMNH 64114 (2), O-897; FMNH 64115 (1), O-916; FMNH 64117 (3), O-917; FMNH 64118 (2), O-936; FMNH 64127 (3) and FMNH 64128 (3), O-1021; FMNH 64130 (1), O-1022; GCRL (1), O-35; MCZ 45084 (1), O-1024; USNM 188795 (1), Pelican sta. 153-3, 29°24′N, 85°54′W, 37 m. **Alabama:** USNM 188778 (1), Pelican sta. 137-2, 29°36′N, 87°29′W, 66 m. **Yucatán:** CAS 23923 (1), SB-438; FMNH 46741 (1), O-222.

Southern examples

Puerto Rico: USNM 164504 (1), Joyuda. **Honduras:** ANSP 103630 (1), O-1874. **Guyana:** CAS-SU 62121 (1), O-2000; FMNH 64892 (2), O-2247; FMNH 64895 (3), O-2261; 65954 (1), O-2245; FMNH 65955 (1), O-2232; FMNH 65956 (1), O-2257; FMNH 65957 (4), O-2000; FMNH 65958 (1), 1999; MCZ 48081 (1), O-2262; USNM 188768 (2), O-2000. **Brazil:** BMNH 79.5.14.527 (1), Challenger sta. 122, off Pernambuco (=Recife).

Ogcocephalus darwini Hubbs

(Figure 29 [*left*])

Ogcocephalus darwini Hubbs, 1958:161 [Isla Isabella, Galápagos Islands; holotype SIO H51-214; photographs]; Bradbury 1967:417 [listed]; McAllister 1968:161 [Tagus Cove, Albemarle (=Isabella) I., Galápagos Islands; branchiostegals described].

Diagnosis and Comparisons.—An *Ogcocephalus* distinguished by the unique character of its smooth integument, likened to shagreen by Hubbs in the original description (1958); the bucklers are obscured by a covering of fine spinules in contrast to the prominent, coarse bucklers of other species. *O. darwini* is also distinguished from all its congeners except the single other eastern Pacific species, *O. porrectus,* by a pair of solid dark stripes on the dorsal surface of the disk which continue on to the lateral sides of the tail; all Atlantic species of *Ogcocephalus* either are spotted on the dorsal surface of the body or else lack markings altogether. Differences between *darwini* and *porrectus* include a shorter disk margin in *darwini* (Fig. 9) and a higher modal pectoral fin ray count (15 in *darwini,* 14 in *porrectus*; Table 3).

Description.—A detailed description and comparison with the two other eastern Pacific ogcocephalines is given in the original description of *Ogcocephalus darwini* (Hubbs 1958), but in order to keep the presentations of species in this revision strictly parallel for ease of reference, a description is given again below, including some new observations. Counts and measurements from 30 specimens 35.1 to 166.1 mm SL (Table 1).

Counts. Counts given in Tables 2–6. *O. darwini* has the highest mean for pectoral fin ray count of any in genus; range 14–15 (but Hubbs (1958) gives 14–16; however, his sample included three specimens I have not seen). *O. darwini* most often has 6–7 subopercular lateral-line scales but shows considerable variation in count; range 4–9. Cheek lateral-line count usually 8, as for most species in genus; range 6–9. Range for lateral-line scale count 19–30, which is about center of distribution for genus. Modal vertebral count 19; range 19–20.

Proportions. Proportions expressed as ratios given as mean followed by range in parentheses.

Disk margin shorter on the average than in any other species of *Ogcocephalus,* its length 2.6(2.3–2.9) in SL. Tail thin, its width 2.0(1.7–2.4) in length of disk margin, tapering evenly to caudal fin; caudal peduncle of moderate depth, 2.7(2.4–3.1) in head depth. Rostrum thick and blunt, moderately long, its length 3.1(2.8–3.6) in disk margin. Aperture of illicial cavity subtriangular, higher than wide or the two dimensions about equal. Cranium, when viewed from front,

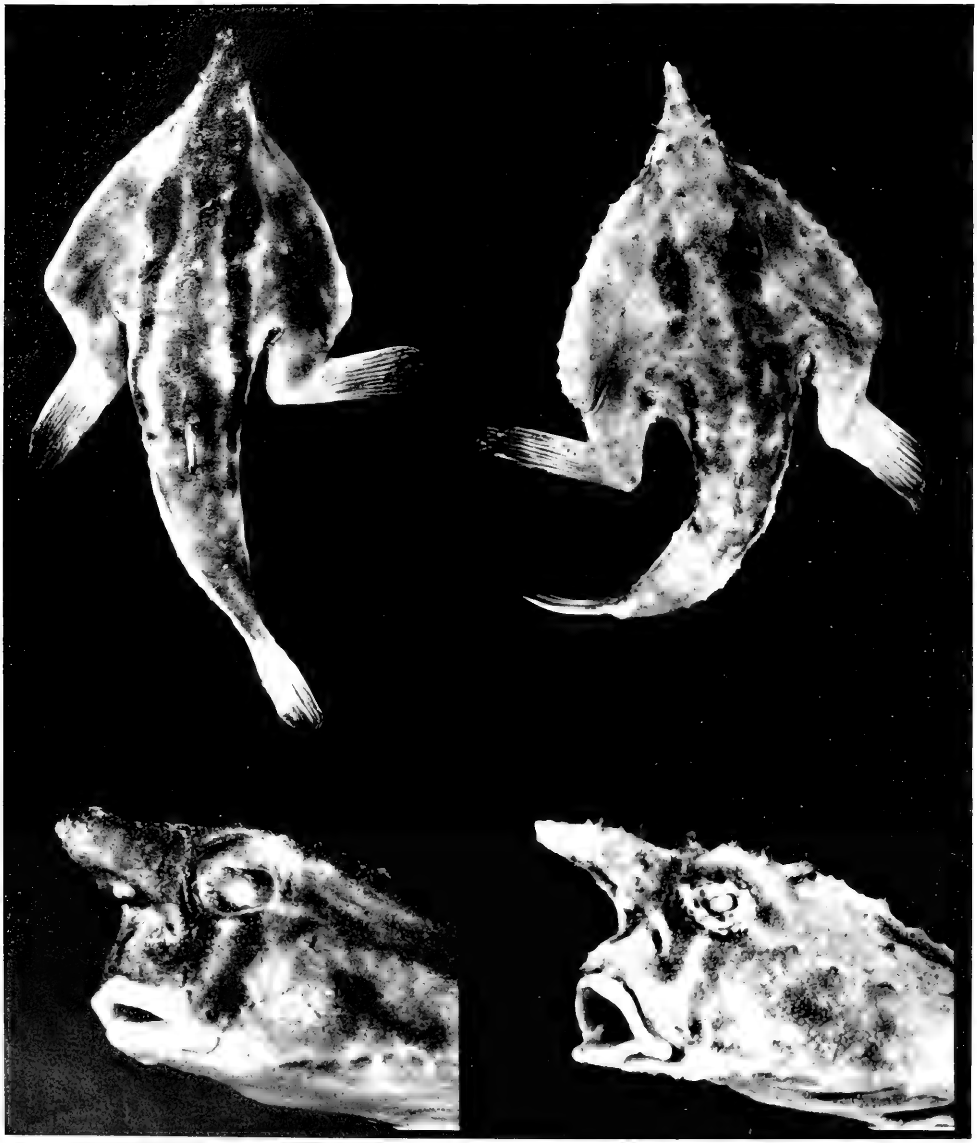


FIGURE 29. *Ogcocephalus darwini* Hubbs, *left*, top and bottom, paratype 128.5 mm SL, CAS-SU 17112. *Ogcocephalus porrectus* (Garman), *right*, top and bottom, paratype 108.0 mm SL, MCZ 28733.

rising steeply above disk, head depth 1.8(1.6–2.1) in length of disk margin. Width of cranium 3.2(2.9–3.5) in length of disk margin. The following in width of cranium: eye 1.3(1.3–1.5), lateral ethmoid width 1.6(1.4–1.8). Interorbital space wide, concave, the width 1.8(1.6–2.1) in width of cranium, 3.2(2.9–3.6) in head depth. Mouth average in width, the width 1.7(1.4–2.0) in head depth, 3.1(2.7–3.4) in length of disk margin; length of jaw 2.4(2.0–2.6) in head depth. Upper lip moderately fleshy, of an even width for its entire length; lower lip fleshy, no median lobe. Dorsal fin average size, its length 3.8(3.0–4.3) in length of disk margin; anal fin comparatively long, 2.4(2.1–2.6) in length of disk margin.

Integument. Dermal cirri present or absent. Large bucklers present but inconspicuous because of their covering of skin embedded with

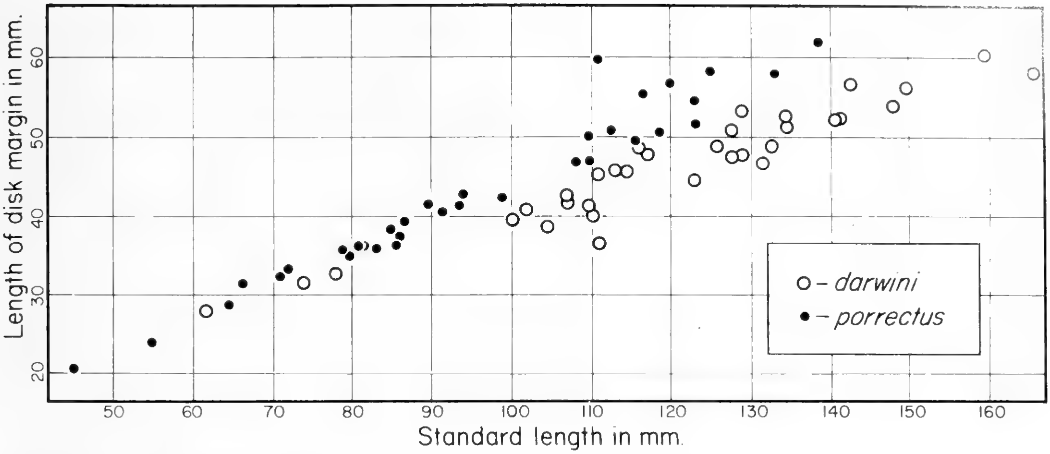


FIGURE 30. Comparison between *Ogcocephalus darwini* and *O. porrectus* to show that length of disk margin is greatest in *O. porrectus* relative to standard length.

fine spinules (except small specimens 35 mm SL or less have perfectly visible bucklers not yet covered by the fine-grained, shagreenlike integument); bucklers arranged as in generic description. All fins with fine tubercles at their bases and extending out variable distances along fin rays. Caudal as in generic description. Skin covering eyeballs bearing tiny, densely set tubercles, with rim around cornea beaded by a row of somewhat larger ones. Pectoral membranes thick, opaque; ventral surfaces of ray tips with well-developed fleshy pads.

Color in preservative. Ground color of dorsal surface tan to brown, the conspicuous markings a pair of dark stripes, one on each side, originating behind eyes and extending posteriorly over disk and on to lateral walls of tail where they are sometimes interrupted to form a series of blotches. Top of head dark, from whence a median dusky stripe extends posteriorly, becoming wider and more intense around dorsal fin. Face also dark, marked by a narrow light stripe on either side extending obliquely from eye to lip just anterior to corner of mouth, a pattern very similar to that observed in *Ogcocephalus porrectus.* Ventral surface uniformly pale except for chin, which is sometimes dusky; the pale shade extends up sides of tail to the lateral line or even a little above. Rostrum the same dark shade as face and head. Iris black or gold, or black with golden spots. Dorsal surfaces of pectorals pale basally, grading to black distally, the ventral pads near tips of rays pale or white. Pelvics and anal the same ground color as ventral surface of body, anal sometimes dusky or black on distal third. Dorsal fin dusky to dark, sometimes blotched. Caudal fin pale basally with distal third dark except in one specimen, which displays color pattern described for genus.

Color in life. Hubbs (1958) states for one specimen which retained some color, "upper parts, purplish gray; rather blue-gray on tubercles and in an irregular blotch near each side of the disk; the two dark streaks, reddish brown; underparts, bright rose-red, becoming white or whitish on the lower (but not the upper) surface of the pelvics, on the outer tip of the anal, and, weakly, on the lower border of the caudal, also on the esca (but not the red stem) of the illicium; pectoral rays pink-gray, encroached by the widening, blackish interradial streaks; the fin becoming almost solidly blackish inside the narrow red outer border."

I observed two live specimens in August 1968 which had been freshly taken from coral rubble in 25 m of water off Isla Isabela by pipe dredge. In these the dorsal surfaces of disk and tail medium brown, the two longitudinal stripes dark cocoa brown. Ventral surfaces of body creamy white, as were esca and tops of eyeballs, all contrasting sharply with brown head and brown rostrum. Lips cherry-red; striking white blotches along sides of disk posterior to mouth. Pelvics creamy white tipped with brown on dorsal surfaces. Pectorals brown on dorsal surfaces, grading to rich dark shade distally, creamy white on ventral surfaces.

Distribution.—Galápagos Islands. Bathymetric range: 3.5–73.5 m.

Material Examined.—Numbers in parentheses are numbers of specimens. All material from the Galápagos Islands. **Isla Isabela:** SIO H51-214 (holotype) and SIO 54-175 (1), Caleta Tagus; SIO H50-18 (1), Punto Moreno, shallow water near shore; SIO 55-16 (1), Punto Moreno, under 9 m; SIO H50-132 (1), Bahía Elizabeth, 5.5 m; SIO 54-199 (1) and SIO 58-116 (1), Bahía Elizabeth; SIO 57-20 (1), Bahía de Banks, approx. 00°01′S, 91°29′W; CAS-SU 14977 (1), Bahía de Banks, under 77 m; SIO H51-51 (1), just outside Caleta Webb; SIO 57-111 (1), Caleta Webb; CAS 39904 (13), Te Vega cr. 17, sta. 91, 00°15′22″S, 91°22′26″W, Canal Bolívar; SIO 56-60 (1), 4.6–5.6 m; SIO 58-39 (1), w side I. Isabela or e side I. Fernandina. **Isla Fernandina:** SIO H53-196 (1), Punta Mangle. **Isla Santa Cruz:** USC (1), Allan Hancock Pacific Exped. 1935, sta. 345-35, 00°24′50″S, 90°21′40″W, 55 m.

Other material: SIO 57-166 (1), exact locality unknown; CAS-SU 17112 (1), exact locality unknown; CAS-SU 46654 (1), from stomach of shark (*Gyropleurodus quoyi*) taken in Caleta Tagus.

Ogcocephalus porrectus (Garman)

(Figure 29 [*right*])

Oncocephalus porrectus Garman, 1899:86 [5°32′45″N, 86°54′30″W; lectotype MCZ 28733].

Ogcocephalus porrectus: Hubbs 1958:161 [redescription of type-series; photographs; selection of lectotype]; Bradbury 1967:417 [listed].

Diagnosis and Comparisons.—One of only two species of *Ogcocephalus* known from the eastern Pacific Ocean (the other is *O. darwini*). *O. porrectus* and *O. darwini* are morphologically distinguishable by the nature of the squamation, shagreenlike and relatively smooth in *darwini* but rough with prominent spiny bucklers in *porrectus*. Other differences include the relatively longer disk margin in *porrectus* (Fig. 9) and lower modal number of pectoral rays (14 in *porrectus*, 15 in *darwini*, Table 3).

Although a smaller species than *nasutus* (Table 1), *porrectus* most resembles *nasutus* in body proportions and quality of the squamation. However, the color pattern in *porrectus*, consisting of a longitudinal stripe on each side of the body, is unknown in *nasutus* or any other Atlantic species. The relationship in color pattern between Atlantic and Pacific species in this: the clusters of spots or reticulations where found in tracts in Atlantic species are represented in *porrectus* (and in *darwini*) by solid stripes.

Description.—Counts and measurements from 35 specimens 25.6 to 138.5 mm SL (Table 1).

Counts. Pectoral fin ray count relatively high with modal number 14 in range of 10 to 15 for genus (Table 3). Lateral-line scale counts below average, however, with lateral-line count always under 30 (Table 4) and subopercular lateral-line count modally 6 (Table 6). Cheek lateral-line scale count usually 8 as in most species in the genus (Table 5) and vertebral count usually 19 (Table 2).

Proportions. Proportions expressed as ratios given as mean followed by range in parentheses. Disk outline subtriangular, length of disk margin 2.2(2.1–2.4) in SL. Tail thin to moderately wide, its width 2.0(1.6–2.4) in length of disk margin, tapering evenly to caudal fin; caudal peduncle of average thickness, its depth 3.0(2.6–3.4) in head depth. Rostrum moderately long with a thick base, its length 3.0(2.8–3.4) in length of disk margin; seen from side, rostrum arches slightly with its distal end pointing downwards except that terminal buckler is turned abruptly upwards (Fig. 29). Aperture of illicial cavity subtriangular in outline, higher than wide. Cranium, when viewed from front, rising steeply above disk; head depth 2.0(1.9–2.2) in length of disk margin. Width of cranium 3.2(2.3–3.9) in length of disk margin. The following in width of cranium: eye 1.6(1.3–2.0), lateral ethmoid width 1.7(1.5–1.9). Interorbital space flat, not convex as in *vespertilio*, of average width, the width 2.1(1.8–2.5) in width of cranium, 3.6(3.0–4.0) in head depth. Mouth moderate, its width 1.6(1.4–1.8) in head depth, 3.2(2.8–3.6) in length of disk margin; length of jaw 2.3(2.1–2.5) in head depth. Upper lip moderately fleshy, of an even width for its entire length; lower lip fleshy, thickened medially. Dorsal fin small, its length 4.4(3.4–4.8) in length of disk margin; anal fin relatively long, its length 2.6(2.4–3.0) in length of disk margin.

Integument. Dermal cirri inconspicuous, usually present on disk margin, chin, lateral sides of tail near lateral line, and on sides of large bucklers on dorsal surface of body. Large bucklers prominent, with coarse spines bristling from apex of each; bucklers arranged as in generic description. All fins except dorsal with fine tubercles running out for ⅓ to ⅔ length of fin rays; dorsal fin with none or only a few prickles on anterior edge of first ray. Caudal as in generic description. Skin covering eyeballs bearing fine tubercles with rim around cornea beaded by a row of small but prominent bucklers. Pectoral membranes thick, opaque; ventral surfaces of ray tips with well-developed fleshy pads.

Color in preservative. Freshest material has dorsal surface of body uniformly brown except for darker brown longitudinal stripes, one on each side as in *darwini,* beginning anteriorly on dorsal surface of disk behind eyes as an elongate "shoulder" blotch which then narrows posteriorly and trails back along sides of tail where sometimes interrupted in one or two places. Garman's four specimens faded (Garman 1899), but holotype (Hubbs 1958) shows the longitudinal markings, and original description refers to markings.

Markings on faces of fresh specimens also resemble markings in *darwini*; suborbital space (between eye and mouth) dark except for a markedly pale stripe descending from eye to corner of mouth. Lips the same creamy-white shade as ventral surface of body; pelvics and ventral surfaces of pectorals also creamy white. Dorsal surface of pectorals dusky, grading distally to black tips. Anal often tipped with black, especially in small specimens. Dorsal dusky, occasionally blotched with dark pigment. Iris golden with very dark spots in a ring around the eccentrically shaped pupil (Garman described the iris as having "radiating bars of brown"). Caudal as in generic description.

Color in life. Two 35-mm color slides provided by Dr. Robert Lea show that, as in other species of *Ogcocephalus, O. porrectus* has considerable bright-reddish coloring. One slide shows entire ventral surface of body to be orange-red except for ventral surfaces of pelvic and anal fins, which are whitish. The other slide, a dorsal view of body, shows skin around gill openings to be reddish and fin rays nearest sides of pectoral and caudal fins to have their tips scarlet.

DISTRIBUTION.—Vicinity of Cocos Island from depths of 88–146 m. Hubbs (1958) erred in stating that the material described by Garman (1899) from ALBATROSS station 3368 was from "south of the Gulf of Panamá, in the vicinity of Cabo Corrientes, Colombia." The coordinates for this station (5°32′45″N and 86°54′30″W, correctly quoted by Prof. Hubbs) designate a locality near Cocos Island, not the coast of Colombia. But this small error may foreshadow things to come. A specimen from Peru, USNM 200363 (data given below) agrees fairly well with *O. porrectus* in squamation, color pattern, and morphometric characters. Whether a population of batfishes that properly may be assigned to *O. porrectus* occurs along the coast of western South America is a question that awaits future work.

MATERIAL EXAMINED.—Numbers in parentheses are numbers of specimens. **Cocos Island:** MCZ 28733 (lectotype) and MCZ 41594 (3 paralectotypes) both from ALBATROSS sta. 3368, 5°32′45″N, 86°54′30″W, 121 m. The following from R/V SEARCHER cruise 72-4: LACM 32263 (23), 5°33′32″N, 87°04′44″W, 110 m; LACM 32264 (6), 5°33′30″N, 87°05′50″W, 137–146 m; LACM 32268 (1), 5°31′10″N, 87°01′58″W, 88–91 m; LACM 32269 (1), 5°28′30″N, 87°04′00″W, 119–121 m. **Peru:** USNM 200363 (1), Caleta Cruz (Tumbes), 37–55 m.

LITERATURE CITED

ANDERSON, W. W. 1956. January to April distribution of the common shrimp on the south Atlantic continental shelf. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 171:1–14.

ANONYMOUS. 1976. Catalogo de peces marinos Mexicanos. Secretaría de Pesca Instituto Nacional de Pesca. 462 p.

BEEBE, W., AND J. TEE VAN. 1928. The fishes of Port-au-Prince, Haiti, with a summary of the known species of marine fish of the island of Haiti and Santo Domingo. Zoologica 10(1):1–279, figs.

BLOCH, M. E. 1787. Ichthyologie, ou Histoire naturelle, générale et particulière des poissons. Pt. 4 (de la Garde ed.). Berlin. 134 p.

BÖHLKE, J. E., AND C. C. G. CHAPLIN. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publ. Co., Wynnewood. 771 p.

BRADBURY, M. G. 1967. The genera of batfishes (Ogcocephalidae). Copeia 1967(2):399–422.

BREDER, C. M. 1929. Field book of marine fishes of the Atlantic coast from Labrador to Texas. G. P. Putman Sons. 332 p., figs.

———. 1949. On the relationship of social behavior to pigmentation in tropical shore fishes. Bull. Am. Mus. Nat. Hist. 94:87–106, 8 pls.

BRIGGS, J. C. 1958. A list of Florida fishes and their distribution. Bull. Florida St. Mus. Biol. Sci. 2(8):223–318.

———. 1961. Emendated generic names in Berg's classification of fishes. Copeia 1961(2):161–166.

BROWNE, P. 1756. The civil and natural history of Jamaica, vol. 8. 509 p., 49 pls.

BULLIS, H. R., JR., AND J. R. THOMPSON. 1965. Collections by the exploratory fishing vessels *Oregon, Silver Bay, Combat,* and *Pelican* made during 1956–1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510:1–130.

CARVALHO, J. P. 1943. Nota preliminar sobre a fauna ictiologica do litoral sul do Estado de São Paulo. Bol. Indústria Animal 150:27–80.

CASTELNAU, F. DE. 1855. Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para. Poissons. Paris. 112 p., 50 pls.

CERVIGON M., F. 1966. Los peches marinos de Venezuela. Tomo II (Monografía No. 12). Estación de Investigaciones Marinas de Margarita Fundación La Salle de Ciencias Naturales. Caracas. Pp. 449–951.

CUVIER, G. 1816. Le règne animal distribué d'après son organisation, . . . Poissons, vol. 2. Paris. 532 p.

———. 1829. Le règne animal distribué d'après son organisation, . . . Ed. 2. Poissons, vol. 2. 406 p.

———, AND A. VALENCIENNES. 1837. Histoire naturelle des poissons, vol. 12. Pp. i–xxiv, 1–507. Paris.

DAHL, G. 1971. Los peces del norte de Colombia. Inst. Desarrollo de los Recursos Nat. Renov., Bogotá. 392 p.

DAHLBERG, M. D. 1975. Guide to coastal fishes of Georgia and nearby states. Univ. Georgia Press. 186 p.

DEKAY, J. E. 1842. Zoology of New York. Pt. 4, Fishes. Albany, N.Y. 415 p. (plates in a separate volume).

DELSMAN, H. C. 1941. Pisces. Mem. Mus. Roy. Hist. Nat. Belgique, sec. 2, fasc. 21, Résultats scientifiques des Croisières du Navire-École Belge 3(3):65–77.

ERDMAN, D. S. 1956. Recent fish records from Puerto Rico. Bull. Mar. Sci. Gulf Caribb. 6(4):315–340.

EVERMANN, B. W., AND W. C. KENDALL. 1900. Check-list of the fishes of Florida. Rep. U.S. Comm. Fish Fish. 25:35–103.

FISCHER, G. 1813. Zoognosia, tabulis synopticis illustrata. Ed. 3. Vol. 1. Moscow. 465 p.

FOWLER, H. W. 1906. Some cold-blooded vertebrates of the Florida Keys. Proc. Acad. Nat. Sci. Phila. 58:77–113.

———. 1915. Cold-blooded vertebrates from Florida, the West Indies, Costa Rica, and eastern Brazil. Proc. Acad. Nat. Sci. Phila. 67:244–269.

———. 1926. Fishes from Florida, Brazil, Bolivia, Argentina, and Chile. Proc. Acad. Nat. Sci. Phila. 78:249–285.

———. 1941. A list of fishes known from the coast of Brazil. Arquiv. Zool. São Paulo 3(6):115–184.

———. 1945. A study of the fishes of the southern Piedmont and coastal plain. Acad. Nat. Sci. Phila. Monogr. 7:1–408.

———. 1947. Notes on Bahama fishes obtained by Mr. Charles G. Chaplin in 1947, with descriptions of two new species. Not. Nat. 199. 14 p.

———. 1952. Fishes from deep water off southern Florida. Not. Nat. 246. 16 p.

GARMAN, S. 1896. Report on the fishes collected by the Bahama expedition of the State University of Iowa, under Professor C. C. Nutting, in 1893. Bull. Lab. Nat. Sci. St. Univ. Iowa 4:77–93.

———. 1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, by the U.S. Fish Commission steamer "Albatross" during 1891. XXVI. The Fishes. Mem. Mus. Comp. Zool. Harvard 24:1–431, 97 pls.

GILL, T. 1862. Catalogue of the fishes of the eastern coast of North America, from Greenland to Georgia. Proc. Acad. Nat. Sci. Phila. 1861(1862)(Suppl.):1–63.

———. 1873. Catalogue of the fishes of the east coast of North America. Smithson. Misc. Collect. 283. 50 p.

———. 1878. Note on the Maltheidae. Proc. U.S. Natl. Mus. 1:231–232.

———. 1883. Supplementary note on the Pediculati. Proc. U.S. Natl. Mus. 5:551–556.

GOODE, G. B., AND T. H. BEAN. 1879. Catalogue of a collection of fishes sent from Pensacola, Florida, and vicinity, by Mr. Silas Stearns, with descriptions of six new species. Proc. U.S. Natl. Mus. 2:121–156.

———, AND ———. 1882. A list of the species of fishes recorded as occurring in the Gulf of Mexico. Proc. U.S. Natl. Mus. 5:234–240.

———, AND ———. 1896. Oceanic Ichthyology. Special Bull. U.S. Natl. Mus. 2:1–555, atlas with 123 pls.

GUNTER, G., R. H. WILLIAMS, C. C. DAVIS, AND F. G. W. SMITH. 1948. Catastrophic mass mortality of marine animals and coincident phytoplankton bloom on the west coast of Florida, November 1946 to August 1947. Ecol. Monogr. 18(3):309–324.

GÜNTHER, A. 1861. Catalogue of the acanthopterygian fishes in the collection of the British Museum. British Museum (Natural History), London. 586 p.

———. 1880. Report on the shore fishes. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. Zoology 1(pt. 6):18–82.

HENSHALL, J. A. 1891. Report upon a collection of fishes made in southern Florida during 1889. Bull. U.S. Fish Comm. 1889, 9:371–389.

———. 1895. Notes on fishes collected in Florida in 1892. Bull. U.S. Fish Comm. 1894, 14:209–221.

HERALD, E. S. 1972. Fishes of North America. Doubleday, New York. 256 p.

HERRE, A. W. C. T. 1942. Notes on a collection of fishes from Antigua and Barbados, British West Indies. Stanford Univ. Publ. Univ. Ser. Biol. Ser. 7(2):287–305.

HILDEBRAND, H. H. 1954. A study of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci. Univ. Texas 3(2):233–366.

———. 1955. A study of the fauna of the pink shrimp (*Penaeus duorarum*) grounds in the Gulf of Campeche. Publ. Inst. Mar. Sci. Univ. Texas 4(1):169–232.

HOESE, H. D., AND R. H. MOORE. 1977. Fishes of the Gulf of Mexico, Texas, Louisiana, and adjacent waters. Texas A&M Univ. Press. 327 p.

HOLM, Å. 1957. Specimina Linnaeana i Uppsala bevarade Zoologiska samlingar från Linnéstid. [In Swedish with summary.] Uppsala Univ. Årsskr. 1957(6):1–68.

HUBBS, C. L. 1958. *Ogcocephalus darwini*, a new batfish endemic at the Galápagos Islands. Copeia 1958(3):161–170.

JORDAN, D. S. 1885a. A catalogue of the fishes known to inhabit the waters of North America, north of the Tropic of Cancer, with notes on the species discovered in 1883 and 1884. Rep. U.S. Comm. Fish Fish. 1884:789–973.

———. 1885b. List of fishes collected at Key West, Florida, with notes and descriptions. Proc. U.S. Natl. Mus. 7:103–150.

———. 1885c. List of the fishes from Egmont Key, Florida, in the Museum of Yale College, with descriptions of two new species. Proc. Acad. Nat. Sci. Phila. 1884:42–46.

———. 1895. The fishes of Sinaloa. Stanford Univ. Publ., Contrib. Biol. Hopkins Lab. Biol. 1:377–514. (Published simultaneously in Proc. Calif. Acad. Sci., ser. 2, 5:377–514.)

———. 1899. A manual of the vertebrate animals of the northern United States including the district north and east of the Ozark mountains, south of the Laurentian hills, north of the southern boundary of Virginia, and east of the Missouri river, inclusive of marine species. Ed. 8. Chicago. 397 p.

———, AND B. W. EVERMANN. 1896. A check-list of the fishes and fish-like vertebrates of North and Middle America. Rep. Comm. Fish Fish. 1895, Append. 5:207–584.

———, AND ———. 1898. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47(pt. 3):2183–3136 and (pt. 4):i–ci, 3137–3313, pls. I–CCCXCII.

———, ———, AND H. W. CLARK. 1930. Checklist of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rep. U.S. Comm. Fish. 1928 (pt. 2):1–670.

———, AND C. H. GILBERT. 1882. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus. 16:1–1018.

———, AND J. SWAIN. 1885. Notes on fishes collected by David S. Jordan at Cedar Keys, Florida. Proc. U.S. Natl. Mus. 7:230–234.

Linnaeus, C. 1758. Systema naturae. Vol. 1. Ed. 10. Holmiae. 824 p.

Longley, W. H., and S. H. Hildebrand. 1940. New genera and species of fishes from Tortugas, Florida. Pap. Tortugas Lab. 32(Carnegie Inst. Washington Publ. 517):223–285.

———, and ———. 1941. Systematic catalog of the fishes of Tortugas, Florida, with observations on color, habits, and local distribution. Pap. Tortugas Lab. 34 (Carnegie Inst. Washington Publ. 535):1–331.

Lönnberg, A. J. E. 1896. Linnean type-specimens of birds, reptiles, batrachians, and fishes in the Zoological Museum of the R. University in Upsala. K. Sven. Vetenskapakad. Handl. 22(4)(1):1–45.

Lowe (McConnell), R. H. 1962. The fishes of the British Guiana continental shelf, Atlantic coast of South America, with notes on their natural history. J. Linn. Soc. London Zool. 44(301):669–700.

Lundy, W. E. 1956. Galápagos produces the "Thing." Nat. Hist. 65:468–469.

Lütken, C. 1866. Ichthyologiske notiser. II. Om arterne af slaegten *Malthaea* og saerligt om *M. notata* (*truncata*). Vidensk. Medd. Naturhist. Foren. Kjøbenhavn 1865:205–223.

Marcgrave, G. 1648. Historiae rerum naturalium Brasiliae. Batavia and Amsterdam. 293 p. plus an index of 7 unnumbered pages.

Martin S., F. 1956. Ictiología del archipiélago de Los Roques. Pp. 87–144 *in* El archipiélago de Los Roques y La Orchila por la Sociedad de Ciencias Naturales La Salle. Caracas.

McAllister, D. E. 1968. Evolution of branchiostegals and associated opercular, gular, and hyoid bones and the classification of telestome fishes, living and fossil. Bull. Natl. Mus. Canada 221 (biol. ser. 77):1–239.

Meek, S. E., and S. F. Hildebrand. 1928. The marine fishes of Panama. Field Mus. Nat. Hist. Publ. 249, zool. ser. 15:709–1045.

Menezes, N. 1964. Sobre ogcocephalideos das costas do Brazil (Pisces, Ogcocephalidae). Papeis Avulsos do Departamento de Zoologia 16(16):153–171.

Mirando Ribeiro, A. de. 1915. Fauna Brasiliense—Peixes. Physoclisti. Pt. 5. Arch. Mus. Nac. Rio de Janeiro 17:1–679.

———. 1918. Summario. Fauna Brasiliense—Peixes. Physoclisti. Pt. 5. Arch. Mus. Nac. Rio de Janeiro 21:1–227.

Mitchill, S. L. 1818. Dr. Mitchill's memoir on the fishes of New-York. Am. Monthly Mag. Critical Rev. 2(5):321–328.

Moe, M. A., Jr., P. C. Heemstra, J. E. Tyler, and H. Wahlquist. 1966. An annotated listing of the fish reference collection at the Florida Board of Conservation Marine Laboratory. Florida Bd. Conserv. Mar. Lab. Spec. Sci. Rep. 10, 121 p. [mimeo.].

———, and G. T. Martin. 1965. Fishes taken in monthly trawl samples offshore of Pinellas County, Florida, with new additions to the fish fauna of the Tampa Bay area. Tulane Stud. Zool. 12(4):129–151.

Parrá, A. 1787. Peces y crustaceos de la Isla de Cuba. Havanna. [Not seen; pages 11–13 in a volume of pages hand-copied from Parrá by Señorita Poey in the Library of the California Academy of Sciences were used.]

Puyo, J. 1936. Contribution à l'étude ichthyologique de la Guyane française—Peches et Pecheries. Bull. Soc. Hist. Nat. Toulouse 70. 258 p.

———. 1949. Faune de l'Empire français. 12. Poissons de la Guyane française. Office de la Recherche Scientifique outre-Mer. Paris. 280 p.

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. Miami 5:665–847.

———. 1968. Caribbean Reef Fishes. T.F.H. Publ., New Jersey. 318 p.

Reid, G. K. 1954. An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4(1):1–94.

Richardson, J. 1836. Fauna Boreali-Americana; or the zoology of the northern parts of British America. Pt. 3. The Fish. London. 327 p., pls. 74–97.

Rosenthal, F. 1822. Ichthyotomische Tafeln. Section 2, Pt. 4. Berlin.

Scarabino, S. M. de. 1974. Sobre la presencia de "pez murcielago" *Ogcocephalus vespertilio* (Linné) (Pisces, Ogcocephalidae) en la boca de la Plata. Rev. Inst. Invest. Pesqueras 2(3):306–313.

Seba, A. 1734. Locupletissimi rerum naturalium thesauri accurata descriptio et iconibus artificiosissimis expressio, per universam physicis historiam . . . . Vol. 1. Amstelaedami.

Shaw, G. 1804. General zoology 5(2):251–463.

Smith, H. M. 1907. The fishes of North Carolina. North Carolina Geol. Econ. Surv. 2:1–453.

Soto, A. de. 1922. A batfish from the Amazon. Copeia (108):51.

Springer, S., and H. R. Bullis, Jr. 1956. Collections by the *Oregon* in the Gulf of Mexico. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 196:1–134.

Springer, V. G., and A. J. McErlean. 1962. Seasonality of fishes on a south Florida shore. Bull. Mar. Sci. Gulf Caribb. 12(1):39–60.

———, and K. D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. Florida State Bd. Cons. Mar. Lab., Prof. Pap. Ser. 1. 104 p.

Stark, W. A., II. 1968. A list of fishes of Alligator Reef, Florida, with comments on the nature of the Florida reef fish fauna. Undersea Biol. 1(1):4–40.

Storer, D. H. 1846. A synopsis of the fishes of North America. Mem. Am. Acad. Arts Sci. Boston 2(7):44–298.

Storey, M., and E. W. Gudger. 1936. Mortality of fishes due to cold at Sanibel Island, Florida, 1886–1936. Ecology 17(4):640–648.

Uhler, P. R., and O. Lugger. 1876. List of fishes of Maryland. Rep. Comm. Fish Maryland 1876:67–176.

Walls, J. G. 1975. Fishes of the northern Gulf of Mexico. T.F.H. Publ., New Jersey. 432 p.

Woods, L. P. 1942. Rare fishes from the coast of Texas. Copeia 1942(3):191.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 8, pp. 287–293, 5 figs. July 2, 1980

XENAPLOACTIS, A NEW GENUS FOR *PROSOPODASYS ASPERRIMUS* GÜNTHER (PISCES: APLOACTINIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES

By
Stuart G. Poss
Division of Biological Sciences and Museum of Zoology,
University of Michigan, Ann Arbor, Michigan 48109

and
William N. Eschmeyer
California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

ABSTRACT. A new genus, *Xenaploactis*, is created for *Prosopodasys asperrimus* Günther, 1860, which is redescribed. *X. anopta* from Luzon Island in the Philippines and *X. cautes* from the Andaman Sea and the Gulf of Thailand are described as new. These species exhibit differences in the configuration of ridges between the eyes, body depth, head pores, and other features. Species of *Xenaploactis* differ from those of other genera of the Aploactinidae by the presence of several features in combination: 3 anterior dorsal fin spines forming a separate fin, rather sharp head spines, a markedly upturned mouth, and a body densely covered with modified pointed scales.

INTRODUCTION

Günther (1860) described *Prosopodasys asperrimus*, assigning it to a genus otherwise composed of tetrarogid scorpaenoids. Because of this and because the species remains known from only the holotype, *Prosopodasys asperrimus* has not been generally recognized as an aploactinid scorpaenoid.

Günther described the head and body as "covered with small prickles," and this caused Poss and Eschmeyer (1978) to suspect that this species was an aploactinid. Other features mentioned in Günther's brief description—absence of palatine teeth, presence of one spine and three soft rays in the pelvic fins, and presence of flexible anal spines—tended to support this view. More recent examination of the holotype confirms this suspicion.

Species assigned to *Prosopodasys*, a name originally proposed by Cantor (1849:1026) as a replacement name for *Apistus* Cuvier and Valenciennes, have been placed into a number of genera. *Prosopodasys asperrimus* does not belong in any of these nor does it belong in any existing genus of aploactinid.

Two undescribed and closely related species have been discovered among specimens in the collections of the National Museum of Natural History (USNM) and the California Academy of Sciences (CAS). Together with *Prosopodasys asperrimus*, they form a natural cluster quite distinct from other aploactinids. Provided below are descriptions of these species and a new genus to contain them.

METHODS

The methods used in this study follow those of Eschmeyer (1969) as modified by Poss and Eschmeyer (1978). Spines and rays are difficult to distinguish and median fin-ray counts were checked against radiographs. The last fin ray in the dorsal and anal fins is double, borne on a single pterygiophore, and counted as one ray.

Xenaploactis new genus

TYPE-SPECIES.—*Prosopodasys asperrimus* Günther, 1860.

DIAGNOSIS.—Aploactinid fishes with spinous dorsal fin in 2 parts; the first 3 dorsal fin spines inserting on cranium and forming a separate fin, widely separate from the 4th spine of the second part of the spinous dorsal fin; rather pungent head spines, including 2 prominent preorbital spines and strong spine on lateral face of third infraorbital bone; head and body densely covered with modified scales; mouth strongly upturned. Maxillary with prominent angular point at end of anteroventral margin, with ridge on lateral face. Dorsal III, X, 8–9 (last double) or III, XI, 8–9 (last double). Anal I, 9–10 (last double). Pelvic I, 3. Pectoral 13–14. Vertebrae 27–28. Branchiostegal rays 6. Four dorsal spines and associated pterygiophores anterior to third neural spine. Upper posterior margin of opercular bone very close to base of dorsal fin. Teeth on jaws and vomer, none on palatines.

DESCRIPTION.—(See also species descriptions below.) Dorsal fin in 2 parts, originating on cranium above posterior border of eye; first 3 spines close together, widely separate from 4th spine, which originates just anterior to end of head; 2nd spine longest, all spines rather weak, flexible, without cirri. Dorsal fin membrane of second part of fin notably incised, dorsal spines free from fin membrane at about midlength; degree of fin incision decreases posteriorly. Pectoral fin rays all unbranched, longest 5–7 from above, reaching just past anus.

Head covered with modified scales, scales absent in interorbit and behind eye. Mouth strongly upturned. Movable lachrymal bone (infraorbital 1) bladelike, with 3 spines; 1st small, directed anteriorly, followed by 2 prominent sharp spines, 2nd spine about equal in length to 3rd, directed downward; 3rd spine directed down and slightly back. Third infraorbital with prominent spine on ventral margin of bone projecting ventrally and laterally; lateral face of bone with prominent ridge and 2 blunt spines. Infraorbital (suborbital) stay appearing as a strong ridged bar. One postorbital bone (infraorbital 4 or 5). Interorbit with prominent ridges. Nasal bones tubed, without spines. Preopercle with 5 rather strong spines, uppermost largest, diminishing in size ventrally. Upper arm of preopercle forming strong ridge. Opercle with 2 weak ridges, lower ending in small blunt spine on opercular margin. Opercular flap extending nearly to base of dorsal fin between spines 4 and 5. Interopercle forming spinous projection on posterior opercular margin. Posterior dorsal border of cleithrum ending in small, poorly defined blunt spine. Angular bone prominent, strongly jutting ventrally with mouth closed. Maxillae reaching anterior border of eye, with ridged dorsal border, ridge near ventral border. Maxillary cirrus minute.

Pelvic fin origin slightly in advance of lowermost pectoral fin rays. Pelvic fin membrane not adnate to body. Caudal fin rounded, with 18 total fin-ray elements (9 upper and 9 lower), all unbranched. Caudal skeleton with parahypural, 1st and 2nd hypurals fused; 3rd and 4th hypurals fused; 5th hypural small, autogenous; 1st preural neural spine long; 2 epurals. Seven upper and 7 lower fin-ray elements are attached to the hypurals, 2 (procurrent) rays are free above and below.

ETYMOLOGY.—The generic name *Xenaploactis* is derived from the Greek *xenos* (stranger) + *Aploactis* (a related genus). *Xenaploactis* is feminine.

Key to the Species of *Xenaploactis*

1a. Interorbit with ridges nearly parallel (Fig. 4). Body depth less than ⅓ of standard length. Dorsal fin III, IX, 8–9 (based on limited material; some variation to be expected) ---- *X. cautes* (Figs. 4 *lower* and 5)

1b. Interorbit with ridges divergent anteriorly, convergent over middle of orbit, divergent posteriorly (Figs. 2 and 4 *upper*). Body depth equal to or greater than ⅓ of standard length. Dorsal fin III, X, 8–9 (based on limited material; some variation to be expected) ---------------------------------- 2

2a. Second infraorbital bone with 1 or 2

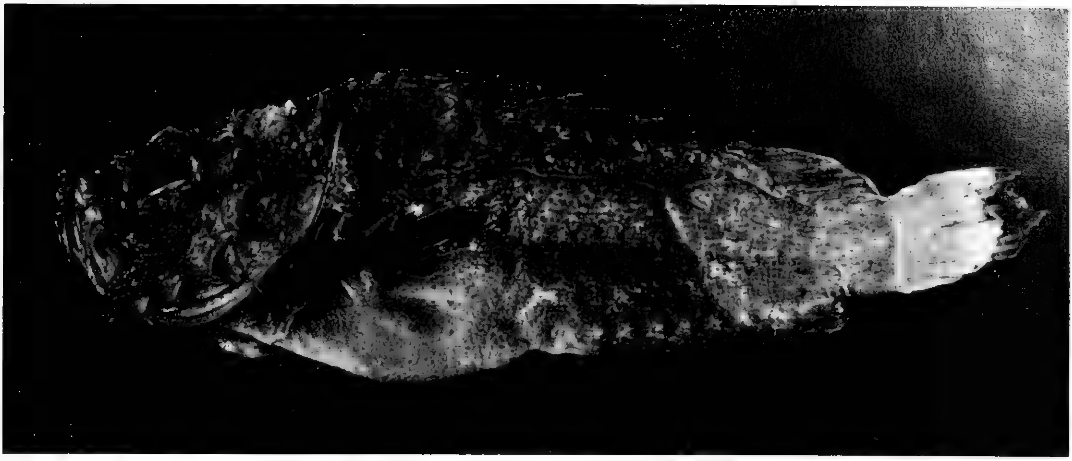


FIGURE 1. Lateral view of holotype of *Prosopodasys asperrimus* (=*Xenaploactis asperrima*) (BMNH 1979.5.5:1, 39.9 mm SL). Specimen formerly dried, somewhat distorted.

spines. Pore of infraorbital lateral line canal at second infraorbital bone as simple obscure pore. Body depth greater than ⅓ of standard length. No fingerlike cirri above uppermost preopercular lateral line pores. Dorsal fin III, X, 9. Anal I, 10 (based on limited material; some variation to be expected) .... *X. asperrima* (Figs. 1 and 2)

2b. Second infraorbital bone without spines. Pore of infraorbital lateral line canal at second infraorbital bone as prominent elongate slit. Body depth equal to ⅓ of standard length. Fingerlike cirri present above uppermost preopercular lateral line pores. Dorsal III, X, 8. Anal I, 9 (based on limited material; some variation to be expected) .... *X. anopta* (Figs. 3 and 4 *upper*)

Xenaploactis asperrima (Günther)

(Figures 1 and 2)

Prosopodasys asperrimus GÜNTHER, 1860:140–141 (original description; type-locality East Indies).

MATERIAL.—**Holotype:** BMNH 1979.5.5:1 (39.9 mm SL). East Indies, Sir E. Belcher, no other data.

COUNTS.—Dorsal fin III, X, 9 (last double). Anal fin I, 10 (last double). Pectoral fin 13 (left), 14 (right). Pelvic fin I, 3. Lateral line scales 10 (left), 11 (right). Vertebrae 27.

DESCRIPTION.—(See also generic diagnosis above.) Body notably elevated behind head, body depth more than ⅓ of standard length. Body densely covered with modified scales which form spinous points, best developed on upper back behind head. Lateral line with 10–11 tubed scales, each with 2 small laterally projecting spinules, best developed anteriorly, last scale extending over base of caudal fin. Gill rakers short, difficult to count, total 8–10; 3 on upper arch, 5–7 on lower arch. No modified scales on snout. Lachrymal bone (infraorbital 1) with 2 large spines, first notably curved. A small spine in front at base of first spine, a small spine at base of second spine. Second infraorbital bone with a small double or single spine, with obscure small circular lateral line pore. Third infraorbital bone with a large spine directed out and down; a strong ridge attached to preopercle. Mouth very strongly upturned, nearly vertical. Interorbit with prominent ridges, divergent anteriorly, convergent over middle of interorbit, divergent posteriorly (Fig. 2). Postocular spine appearing as a sculptured ridge, weakly connected to supraorbital ridge. Parietal spine lumplike. Pterotic spine as a strong, slightly curved ridge. Posttemporal spine well ossified, sculptured, appearing as a ridged lump, followed by small bladelike supracleithral spine. Dorsal posterior border of cleithrum appearing as a marked ridge, ending in a blunt, poorly defined spine. Preopercular lateral line pores simple, no fingerlike cirri above uppermost pores. Ventral surface of dentary without distinct cirri.

Color in life unknown. Color of head and body

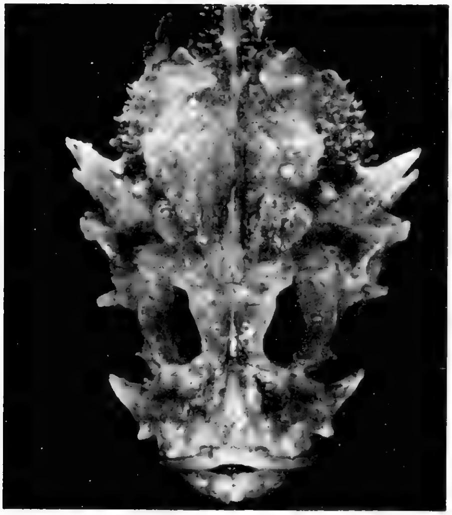


FIGURE 2. Dorsal view of head of holotype of *Prosopodasys asperrimus* (=*Xenaploactis asperrima*).

in preservative light brown, fins slightly darker and possibly speckled in life.

Measurements in millimeters as follows (percent standard length in parentheses): standard length 39.9; head 13.2 (34); snout 3.5 (9); orbit 3.0 (7); interorbital width 2.2 (5); jaw 6.0 (15); postorbit 7.0 (17); body depth 14.6 (37); predorsal 6.2 (15); anal fin 14.0 (35); caudal fin 9.5 (24); pectoral fin 9.2 (23); pelvic fin 4.5 (11); 1st dorsal spine 3.2 (8); 2nd dorsal spine 4.1 (10); 3rd dorsal spine 3.1 (8); 4th dorsal spine 1.8 (4); 5th dorsal spine 2.7 (7); penultimate dorsal spine 3.1 (8); last dorsal spine 3.5 (9); anal spine 2.1 (5); least depth of caudal peduncle 4.2 (10); snout to base of 2nd dorsal spine 7.2 (18); snout to base of 3rd dorsal spine 7.8 (19); snout to base of 4th dorsal spine 11.5 (29); snout to base of 5th dorsal spine 14.6 (37); width of 1st dorsal spine at midlength 0.2 (1); incision of dorsal fin membrane at 4th dorsal spine (from tip to membrane) 1.8 (4).

DISTRIBUTION.—Known only from the holotype from the "East Indies."

Xenaploactis anopta, new species

(Figures 3 and 4 *upper*)

No literature applies to this species.

MATERIAL.—**Holotype:** CAS 32633 (37.0 mm SL). Philippines, Luzon I., Zambales, 4 km w of Calguaguin Cove, 64–81 m, 0835–0910 hrs, J. E. Norton, 9 June 1966.

COUNTS.—Dorsal fin III, X, 8 (last double). Anal fin I, 9 (last double). Pectoral fin 13 (left), 14 (right). Pelvic fin I, 3. Lateral line scales 10 (left), 11 (right). Vertebrae 27.

DESCRIPTION.—(See also generic description above.) Body somewhat elevated behind head, body depth ⅓ of standard length. Body densely covered with modified scales which form spinous points, best developed anteriorly; lateral line with 10–11 tubes, each with 2 small, laterally projecting spinules which are best developed anteriorly; last scale extending over base of caudal fin. Gill rakers short, difficult to count, total 10, 3 on upper arch, 7 on lower arch. Few modified scales on snout, none on interorbit. Movable lachrymal bone (infraorbital one)

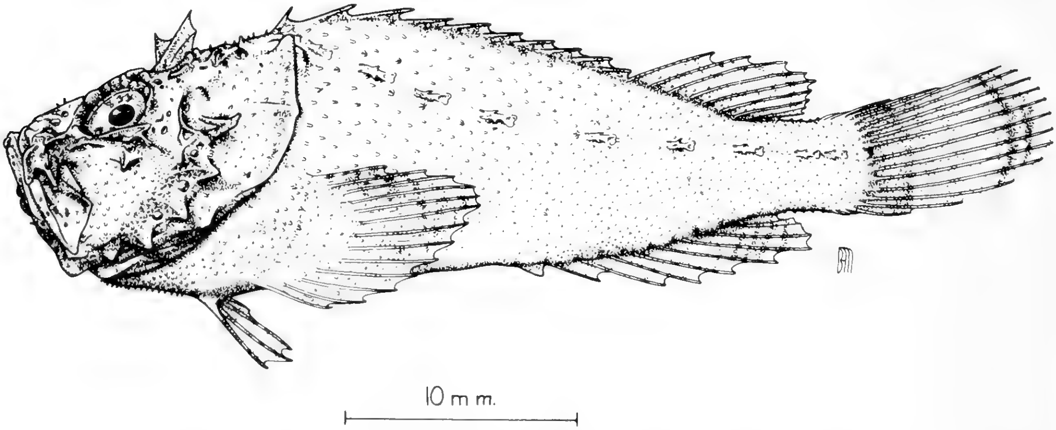


FIGURE 3. Lateral view of holotype of *Xenaploactis anopta* (CAS 32633, 37.0 mm SL).

bladelike with 3 spines: 1st small, directed toward premaxilla; followed by 2 large, sharp spines, 2nd about equal in length to 3rd, directed downward; 3rd spine directed down and slightly back. Spine on second infraorbital bone absent; a large elongate lateral line pore present. Mouth strongly upturned. Interorbit with prominent ridges, divergent anteriorly, convergent over middle of interorbit, strongly divergent posteriorly (Fig. 4 *upper*). Postocular spine and pterotic spine ridgelike. Posttemporal spine a large well-ossified lump ending in blunt spine, followed by blunt supracleithral spine. Dorsal posterior border of cleithrum ending in a small, poorly defined blunt spine. Preopercular lateral line pores opening as small tubes, fingerlike cirri above uppermost pores. In ventral view, surface of dentary with 5 small fingerlike cirri along outer margin; 5 pairs of similar cirri anteriorly, between dentaries.

Color in life unknown. Color of head and body in preservative (Fig. 3) brown, with scattered black specks. Fins darker, possibly speckled in life; caudal with vertical bands.

Measurements in millimeters as follows (percent standard length in parentheses): standard length 37.0; head 13.0 (35); snout 3.7 (10); orbit 3.3 (9); interorbital width 2.5 (6); jaw 5.3 (14); postorbital 7.3 (20); body depth 12.3 (33); predorsal 6.4 (17); anal fin 14.1 (38); caudal fin 9.2 (25); pectoral fin 8.5 (23); pelvic fin 5.2 (14); 1st dorsal spine 1.9 (5); 2nd dorsal spine 3.5 (9); 3rd dorsal spine 2.4 (6); 4th dorsal spine 1.5 (4); 5th dorsal spine 2.2 (6); penultimate dorsal spine 2.2 (6); last dorsal spine 2.3 (6); anal spine 1.9 (5); least depth of caudal peduncle 4.1 (11); snout to 2nd dorsal spine 6.8 (18); snout to 3rd dorsal spine 8.4 (23); snout to 4th dorsal spine 12.9 (35); snout to 5th dorsal spine 13.7 (37); width of 1st dorsal spine at midlength 0.3 (1); incision of dorsal fin membrane at 4th dorsal spine (from tip to membrane) 1.5 (4).

ETYMOLOGY.—The species-group name is derived from the Greek *anoptos* (unseen).

DISTRIBUTION.—Known only from the type-locality in the Philippines at 64–81 m.

Xenaploactis cautes, new species

(Figures 4 *lower* and 5)

No literature applies to this species.

MATERIAL.—**Holotype:** CAS 16105 (28.0 mm SL). Gulf of Thailand, 12°19′15″N, 100°43′40″E, 28.6 km from Goh Chuang, 33 m, muddy sand bottom, MV STRANGER, 16-ft (4.9-m) otter trawl, George Vanderbilt Foundation sta. 60-449, GVF reg. no. 2724, Scripps locality 60-185 C.N. 633f.5-9a, 0117–0202 hrs, 13 Dec. 1960. **Paratype:** USNM 221143 (24.3). Andaman Sea, 14°07′N, 97°05′E, 69–73 m, International Indian Ocean Expedition, ANTON BRUUN cruise 1, sta. 38, Gulf of Mexico shrimp trawl, 30 Mar. 1963.

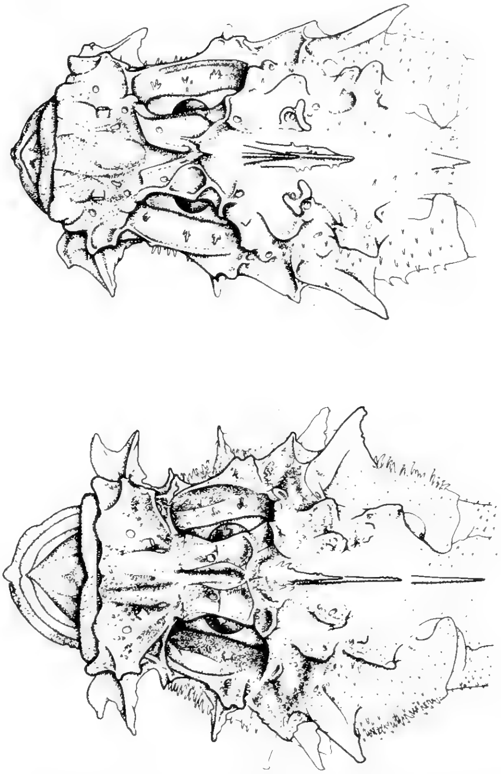


FIGURE 4. Dorsal view of head of holotypes of *Xenaploactis anopta* (*upper*) and *X. cautes* (*lower*).

COUNTS.—Dorsal fin III, XI, 8–9 (last double). Anal fin I, 10 (last double). Pectoral fin 14. Pelvic fin I, 3. Lateral line scales 9–10. Vertebrae 27–28.

DESCRIPTION.—(See also generic description above.) Body not notably elevated behind head, body depth less than ⅓ of standard length. Body covered with modified pointed scales. Lateral line with 9–10 tubed scales, each with 2 small laterally projecting spinules which are best developed anteriorly, last scale extending over base of caudal fin. Gill rakers short, difficult to count, total 10–12, 3–4 on upper arch, 6–8 on lower arch.

Many modified scales on snout. Lachrymal bone (infraorbital 1) with 3 spines; 1st, of moderate size, points mostly forward, continuous

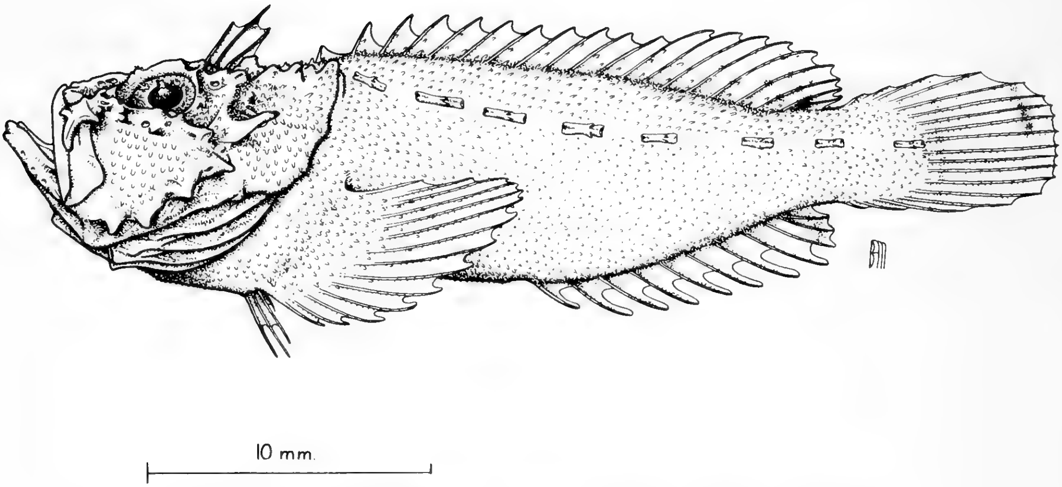


FIGURE 5. Lateral view of holotype of *Xenaploactis cautes* (CAS 16105, 28.0 mm SL).

with ridge at base of larger 2nd spine; 2nd spine about equal in length to 3rd, directed downward, slightly curved; 3rd spine points mostly back. Second infraorbital bone with 2 spinous points, 1 above other, with obscure circular lateral line pore. Interorbit with nearly parallel ridges, stronger posteriorly (Fig. 4 *lower*). Postocular spines as slightly curved ridges, meeting at midline of interorbit, connected to interorbital ridges. Pterotic spine ridgelike. Posttemporal spine ridgelike, followed by blunt supracleithral spine. Cleithrum ending in small blunt spine. In ventral view, surface of dentary with 5 tiny fingerlike cirri along outer margin, 5 pairs of similar cirri anteriorly between dentaries.

Color in life unknown. Color in preservative pale, probably strongly faded. Head and body without scattered specks. Fins not darker than body.

Measurements in millimeters as follows (holotype first, percent standard length in parentheses): standard length 28.0, 24.3; head 9.9, 9.4 (35, 39); snout 2.4, 2.4 (9, 10); orbit 2.4, 2.4 (9, 10); interorbital width 1.8, 2.1 (6, 9); jaw 3.6, 4.2 (13, 17); postorbit 4.7, 4.9 (17, 20); body depth 7.8, 7.4 (28, 30); predorsal 5.0, 4.2 (18, 17); anal fin 11.1, 10.8 (40, 44); caudal fin 6.7, 6.2 (24, 26); pectoral fin 6.2, 5.5 (22, 23); pelvic fin 3.0, 3.4 (11, 14); 1st dorsal spine 1.7, 1.7 (6, 7); 2nd dorsal spine 2.9, 2.6 (10, 11); 3rd dorsal spine 1.7, 1.6 (6, 6); 4th dorsal spine 1.3, 1.3 (4, 5); 5th dorsal spine 1.7, 1.5 (6, 6); penultimate dorsal spine 2.2, 1.6 (8, 6); last dorsal spine 2.3, 1.4 (8, 6); anal spine 1.8, 2.0 (6, 8); width between interorbital ridges 0.7, 0.8 (3, 3); least depth of caudal peduncle 3.3, 2.7 (12, 11); snout to 2nd dorsal spine 5.6, 5.2 (20, 21); snout to 3rd dorsal spine 6.0, 5.4 (21, 22); snout to 4th dorsal spine 8.9, 8.4 (32, 34); snout to 5th dorsal spine 10.3, 8.5 (37, 35); width of 1st dorsal spine at midlength 0.2, 0.2 (1, 1); incision of fin membrane at 4th dorsal spine (from tip to membrane) 1.3, 1.3 (4, 5).

ETYMOLOGY.—The species-group name is derived from the Latin *cautes* (a rough, pointed rock) and is to be treated as a noun in apposition.

DISTRIBUTION.—Known only from the type material from the Andaman Sea and Gulf of Thailand. This species appears to inhabit muddy sand bottom at depths of 33–79 m.

ACKNOWLEDGMENTS

We thank a number of friends and colleagues who assisted us in the course of this study: Alwyne Wheeler and Mary Connolly (BMNH) for giving us the opportunity to examine the holotype of *Prosopodasys asperrimus*; Leslie Knapp, of the Smithsonian Oceanographic Sorting Center, for sending us the second specimen of *Xenaploactis cautes*; James Gordon, Betty Powell, William Ruark, and Pearl Sonoda (all of CAS) for their continous help. Tomio Iwamoto and Lillian Dempster (CAS) reviewed the manuscript and offered critical suggestions. We also wish to thank Ellie Koon and Joanne Zupan, of the University of Michigan, for their assistance. The drawings were made by Beth Meinhard (CAS).

LITERATURE CITED

CANTOR, T. 1849. Catalogue of Malayan fishes. J. R. Asiatic Soc. Bengal 18(2): 983–1443, 14 pls.

ESCHMEYER, W. N. 1969. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae). Occas. Pap. Calif. Acad. Sci. 79. 130 p.

GÜNTHER, A. 1860. Catalogue of the acanthopterygian fishes in the British Museum. Vol. 2, Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae. London. xxi + 548 p.

POSS, S. G., AND W. N. ESCHMEYER. 1978. Two new Australian velvetfishes, genus *Paraploactis* (Scorpaeniformes: Aploactinidae), with a revision of the genus and comments on the genera and species of the Aploactinidae. Proc. Calif. Acad. Sci. 41(18):401–426, 14 figs., 6 tables.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 9, pp. 295–302, 6 figs. March 5, 1981

SUNDASALANGIDAE, A NEW FAMILY OF MINUTE FRESHWATER SALMONIFORM FISHES FROM SOUTHEAST ASIA

By

Tyson R. Roberts

California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118

ABSTRACT: **Sundasalangidae, a new family of minute freshwater salmoniform fishes related to the Salangidae or East Asian icefishes, is based upon a new genus and two new species recently discovered in Southeast Asia, *Sundasalanx praecox* and *S. microps*, both described in the present paper. With males and females sexually ripe at standard lengths of only 14.9 mm, *S. praecox* is the smallest known adult salmoniform and is among the smallest of all adult vertebrates. The new family differs from all other teleosts including Salangidae in the following features of its skeletal anatomy, which is largely cartilaginous: the two halves of the pectoral girdle are united to each other by a median scapulocoracoid cartilage; in branchial arches 1–3 the basibranchials and hypobranchials of either side are represented by a single cartilaginous element; and each half of the pelvic girdle is provided with a pair of rod-shaped parapelvic cartilages. Despite these and many other differences, Sundasalangidae and Salangidae are clearly closely related. They agree with each other but differ from all other known teleosts in having the jaw suspension with bilaterally paired palatohyomandibuloquadrate cartilages.**

INTRODUCTION

Among the freshwater fishes recently collected by the author in Southeast Asia are two samples, one from far up the mainstream of the Kapuas River in Kalimantan (Indonesian Borneo) and the other from a creek draining into the Tale Sap in peninsular Thailand, of minute transparent teleosts with a skeleton that is almost entirely cartilaginous (Figs. 1–2). Superficially resembling drawings of early or mid-metamorphic leptocephalus larvae of *Elops* (cf. Gehringer 1959:figs. 10–11), closer study of the fishes in these samples reveals that they are sexually mature, represent two very distinct species, and are actually salmoniforms most closely related to the East Asian icefishes of the family Salangidae. Yet they differ so markedly from Salangidae, and in certain respects from all other known teleosts, that a new family is proposed for them.

METHODS AND MATERIALS; ACKNOWLEDGMENTS

Observations on the largely cartilaginous skeletal anatomy of Salangidae and Sundasalangidae have been made on specimens prepared by means of the newly developed alcian blue–alizarin technique for counterstaining cartilage and bone in whole, cleared specimens of small vertebrates (Dingerkus and Uhler 1977). I am grateful to Robert Drewes of the California Academy of Sciences for preparing specimens of both species of Sundasalangidae and of all of the genera and nearly half of the species of Salangidae, and also to William N. Eschmeyer, Curator of Fishes of the California Academy of Sciences, for making the specimens of Salangidae available. A complete list of these skeletal preparations will be presented in an extensively illustrated account of the skeletal anatomy of Salangidae and Sundasalangidae now

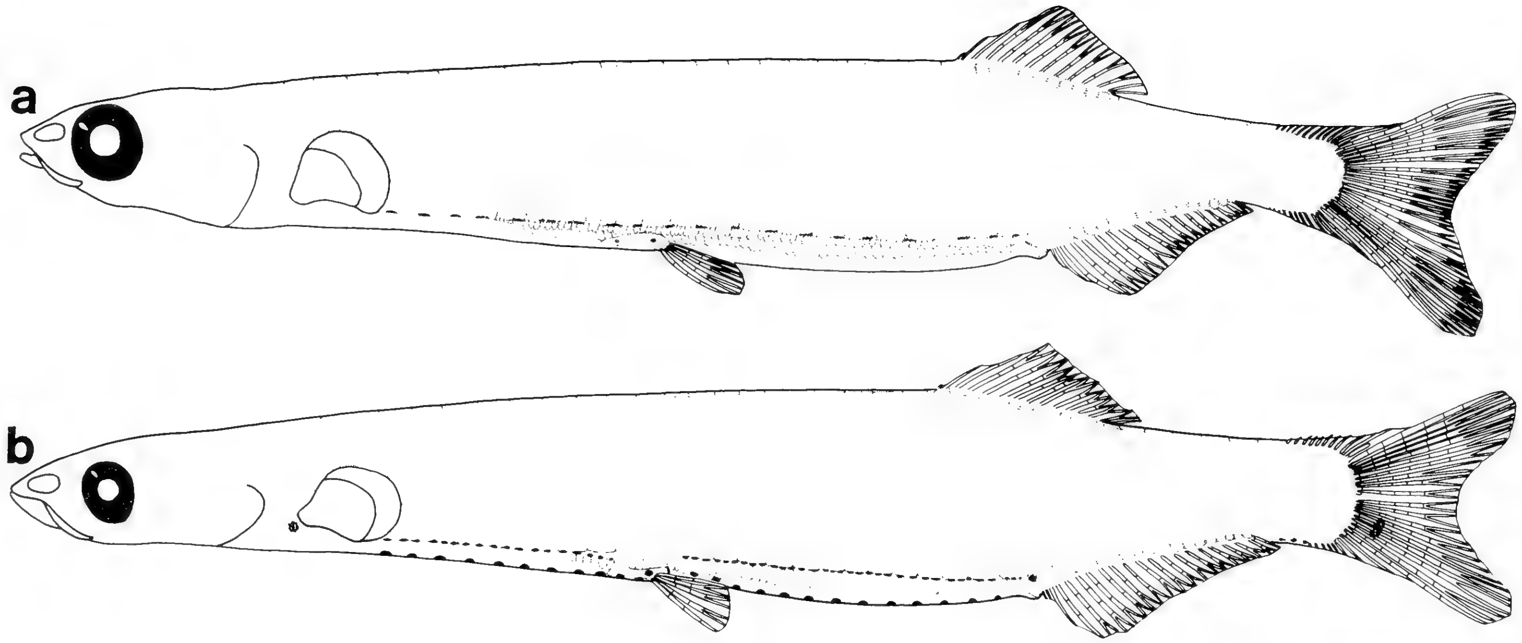


FIGURE 1. (*a*) *Sundasalanx praecox,* based mainly on 17.0-mm paratype, MCZ 54390; (*b*) *Sundasalanx microps,* based mainly on 17.0-mm paratype, CAS 44220.

being prepared (Roberts, ms). I also thank Karsten E. Hartel and William Fink for loaning the specimens of *Sundasalanx praecox* which had been deposited by me in the Museum of Comparative Zoology at Harvard. My fieldwork in Thailand and Indonesia which led to the discovery of *Sundasalanx* was supported or aided by the following institutions: Museum of Comparative Zoology; Kasetsart University College of Fisheries; National Research Council, Thailand; Indonesian National Research Council (LIPI); and Smithsonian Tropical Research Institute (STRI). I particularly thank Supap Monkolprasit of Kasetsart and Ira Rubinoff of STRI for facilitating my travel and fieldwork. The preparation of this paper was supported by grant DEB77-24574 in the Systematic Biology Program of the National Science Foundation.

SUNDASALANGIDAE, new family

TYPE-GENUS: *Sundasalanx*, new genus.

Sundasalangids differ from all other teleosts, so far as known, in having a pectoral girdle with a median cartilaginous scapulocoracoid and a single pair (one on each side) of fan-shaped, "externalized" radial cartilages (Fig. 3) which form the peduncular portion of the pedunculated pectoral fins; a pair of rod-shaped parapelvic cartilages (Fig. 2) which apparently serve to anchor each half of the pelvic girdle to the free ventral end of a myotomal muscle; and branchial arches with hypobranchial elements 1–3 absent as separate elements, evidently fused to basibranchials 1–3 (Fig. 4). In Salangidae the scapulocoracoids are paired, separate elements, and the two halves of the pectoral girdle are separate from each other; each pectoral fin is supported by three or more radial cartilages; parapelvic cartilages are absent; and the first three branchial arches have separate basibranchial and hypobranchial elements.

Members of the Sundasalangidae agree with most Salangidae but apparently differ from all other teleosts in having a jaw suspension consisting of a single cartilaginous element or palatohyomandibuloquadrate (Fig. 5); they agree with Salangidae but apparently differ from adults of all other known teleosts (Nelson 1960:61) in having well-developed separate fourth hypobranchials (Fig. 4). Sundasalangids agree with the Salangidae but differ from adults of most other teleosts in having pedunculate pectoral fins; a scaleless body; no symplectics; no circumorbital bones; myotomal muscles failing to meet at ventral midline of body; and maxillary bones with distal two-thirds curved inwards underneath the head so that the portion of the maxillary toothrow they bear projects medially rather than ventrally when the mouth is closed. In addition to the unique characters associated with their pectoral and pelvic girdles and gill arches, which have been described above, Sundasalangidae differ from Salangidae in their much smaller size (the smallest salangids are over 35 mm in standard length [SL] when sexually mature); olfactory organs each with a single nasal opening instead of two openings; interopercle absent; pectoral fin without segmented bony rays; adipose fin absent; sexually mature males without enlarged or otherwise modifed anal fin, or a row of large pored scales on the base of the anal fin (present in all salangids); pelvic fins five-rayed (seven-rayed in all salangids); myotomes <-shaped (ʒ-shaped in salangids); and vertebrae only 37–43 (48–77 in Salangidae). Sundasalangidae comprises two species, *Sundasalanx praecox* and *S. microps*, described below.

Sundasalanx, new genus

TYPE-SPECIES: *Sundasalanx praecox*, new species.

Minute, transparent, freshwater fishes with a largely cartilaginous skeleton; a single large nasal opening on each side of snout; body bilaterally compressed, scaleless; branchiostegal rays four (usually three in Salangidae); pectoral fins pedunculate, without bony rays; pelvic fins midabdominal, with five rays; myotomal musculature of opposite sides widely separated ventrally; each half of pelvic girdle anchored to free ventral end of a myotomal muscle by a pair of parapelvic cartilages; a median membranous keel extending on abdomen from pelvic fins to vent; gut a simple straight tube with no differentiated stomach; vent immediately anterior to anal fin origin; no secondary sexual dimorphism or dichromatism; vertebrae (including hypural centrum as one) 37–43.

Dentition (Figs. 4–5): Premaxillary and maxillary with a single row of minute conical teeth; lower jaw with two rows of minute conical teeth, inner row curved inwards away from outer row; fifth ceratobranchials with 0–10 conical teeth. Roof of mouth and upper pharyngeal elements edentulous.

Median fins: Dorsal and anal fins originating

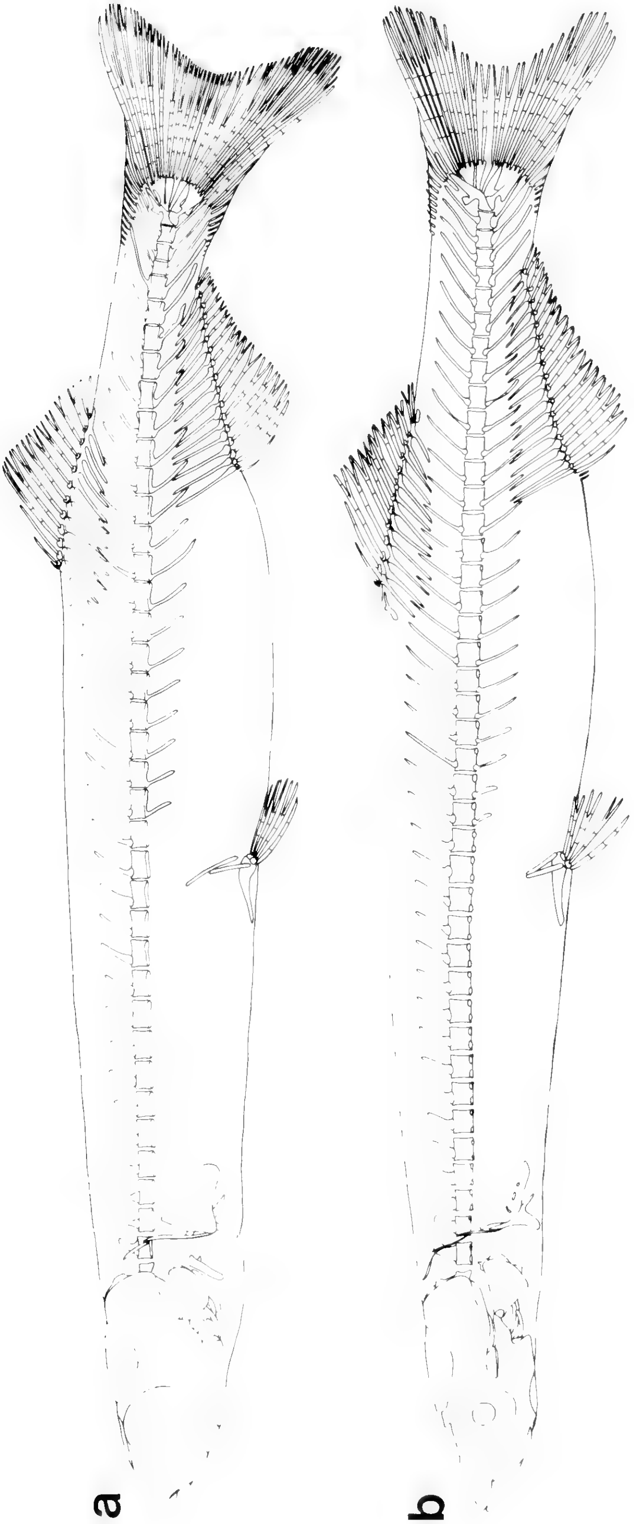


FIGURE 2. (*a*) *Sundasalanx praecox*, MCZ 54390, 17.0 mm; (*b*) *Sundasalanx microps*, CAS 44220, 17.0 mm.

on posterior third of body; origin of anal fin on a vertical through or slightly posterior to middle of dorsal fin base. Dorsal fin with three simple and 8–11 branched rays (last ray, counted as one, split to base); anal fin with 3–4 simple rays and 12–17 branched rays (last ray split to base). Adipose fin absent. Caudal fin moderately forked, with 10 + 9 principal rays and 9–12 + 7–11 procurrent rays.

ETYMOLOGY.—Sunda (=Sundaland, the continental landmass of Southeast Asia connected to the Asian mainland by the isthmus of Kra) plus *Salanx* (Greek, masc.), type-genus of the family Salangidae.

Sundasalanx praecox, new species

(Figures 1a, 2a, 4a, 5a, 6a)

MATERIAL.—**Holotype:** MCZ 47129, 17.2-mm male with well-developed testes, from Khlong Falamee, a swift, muddy creek 1–2 m deep and 3–5 m wide with hard-packed mud bottom flowing into inner lake of Tale Sap, at about 2 km W of Pak Payoon on the isthmus of Kra, southern Thailand; nylon flyscreen pushnet; 20 June 1970.

Paratypes: MCZ 54390, 119: 14.9–18.3 mm, same collection data as holotype; nine utilized for alcian blue–alizarin preparations.

DIAGNOSIS.—*S. praecox* is distinguished from *S. microps,* its only congener, by its much larger eyes: horizontal diameter of eye measured in 10 specimens including smallest and largest specimen of each species, 4.3–5.0% of SL in *S. praecox* vs. 2.7–3.2% in *S. microps*. In *S. praecox* eyeballs separated from each other by a distance about equal to transverse diameter of their pigmented portion, while in *S. microps* distance separating them equal to at least twice transverse diameter. In *S. praecox* head deeper, more compressed, and nasal septum much narrower (Figs. 1, 6). Maxillary teeth about 15–19 vs. about 30 (Fig. 5). Palatohyomandibuloquadrate cartilage entire vs. palatine separate from hyomandibuloquadrate (Fig. 5). Fifth ceratobranchial with about 8–10 large conical teeth vs. 0–3 small conical teeth (Fig. 4). First gill arch with 1 + 9 well-developed gill rakers vs. 0 + 1–2 rudimentary gill rakers; all ceratobranchials with well-developed gill rakers vs. gill rakers greatly reduced in size, and ceratobranchials moderately elongate vs. slender and very elongate (Fig. 4). Posterior parapelvic cartilage originating dorsal to anterior parapelvic cartilage and extending further into myotomal muscle mass instead of lying parallel with anterior parapelvic cartilage (Fig. 2). No midventral row of large, round pigment spots on abdomen and postpelvic abdominal keel corresponding in number to myotomal muscles (present in *S. microps*) (Fig. 1). Anal fin with 12–15 branched rays vs. 14–17. Caudal peduncle more slender (Figs. 1, 2). Vertebral centra more elongate (Fig. 2.) Total vertebrae (excluding basioccipital half centrum but counting upturned hypural centrum as one) 37(n = 2) or 38(7) vs. 41(2), 42(4) or 43(1).

Sex: The 120 *S. praecox* from Khlong Falamee were all caught in a segment of the creek less than 100 m long and presumably represent a random sample from a single breeding population. The sample includes 32 males 14.9–18.3 mm SL with well-developed testes, 19 females 14.9–17.3 mm with well-developed eggs, and 68 specimens 15.2–17.9 mm of undetermined sex in which the gonads are inactive or relatively undeveloped. The testes extend nearly the entire length of the abdomen dorsolaterally to the gut. Obscured anteriorly by the liver, the testes are otherwise readily visible through the transparent ventral body wall and translucent ventral portion of the myotomal muscles (Fig. 1a); they are uniformly divided throughout their length into obliquely aligned divisions or partitions, of which there are about five or six per myotome. Similarly partitioned testes, present in some minute or small freshwater African Clupeidae (personal observation with Peter Whitehead) have not been observed in Salangidae. The largest specimen in the entire sample is a male of 18.3 mm with very well developed testes; the smallest male, 14.9 mm, has testes almost as well developed. In females the ovaries also extend virtually the entire length of the abdomen and lie dorsolateral to the gut. Eggs in varying stages of development are present. In the ripest ovaries observed, the largest eggs, 0.20–0.25 mm in diameter, are aligned in a single row of about 25 eggs in each ovary. The smallest female, 14.9 mm, has ovaries with well-developed eggs.

Food: Gut contents, either whole macroscopic animals or fragments of them, readily observed through the transparent body and gut walls, are present in 34 (28%) of the 120 specimens. In the other 86 (72%), the guts appear to be entirely empty. Items ingested consist exclusively of animals, almost all apparently either aquatic insect larvae or segmented vermiform organisms (also aquatic insects?). None of the

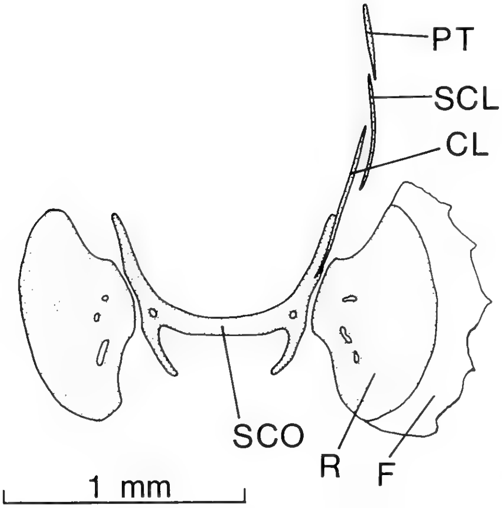


FIGURE 3. *Sundasalanx microps,* CAS 44220, 17.0 mm, pectoral girdle and fin (ventral view). PT, SCL, CL = posttemporal, supracleithrum, cleithrum; R, F = pectoral radial, frayed margin of fin; SCO = scapulocoracoid (secondary pectoral girdle and frayed margin of fin of right side omitted).

guts contain plant material, sediment, or significant amounts of nonidentifiable debris.

ETYMOLOGY.—Latin *praecox,* too early ripe, premature.

Sundasalanx microps, new species

(Figures 1b, 2b, 3, 4b, 5b, 6b)

MATERIAL.—**Holotype:** Museum of Zoology, Bogor, Indonesia, 3000, 17.0 mm, near shore of mainstream Kapuas River at Kampong Nibung, about 100 km NE of Sintang and 7 km NE of Selimbau, Kalimantan, Indonesia, lat. 0°39′N, long. 112°10.5′E; current moderate, water muddy, 26°C, pH 5.5–6, bottom soft mud, depth to 1 m; nylon flyscreen seine; 5–6 July 1976.

Paratypes: Museum of Zoology, Bogor, Indonesia, 3001, and CAS 44220, 34:14.6–19.9 mm, same collection data as holotype, seven utilized for alcian blue–alizarin preparations.

DIAGNOSIS.—*S. microps* is distinguished from *S. praecox,* its only known congener, in the diagnosis of that species given above.

Sex and food: The gonads in the sample of 35 *S. microps* are not well developed, and I have been unable to distinguish males and females. The guts of nearly all appear to be empty; a few contain unidentified fragments, but no whole insect larvae or other animals, plant material, or sediment.

ETYMOLOGY.—Greek *mikros,* small, little, and *ops,* eye.

Sundasalanx species undetermined

Vaillant (1893:110–112, pl. 2, fig. 4) described some delicate little fishes collected in the Ka-

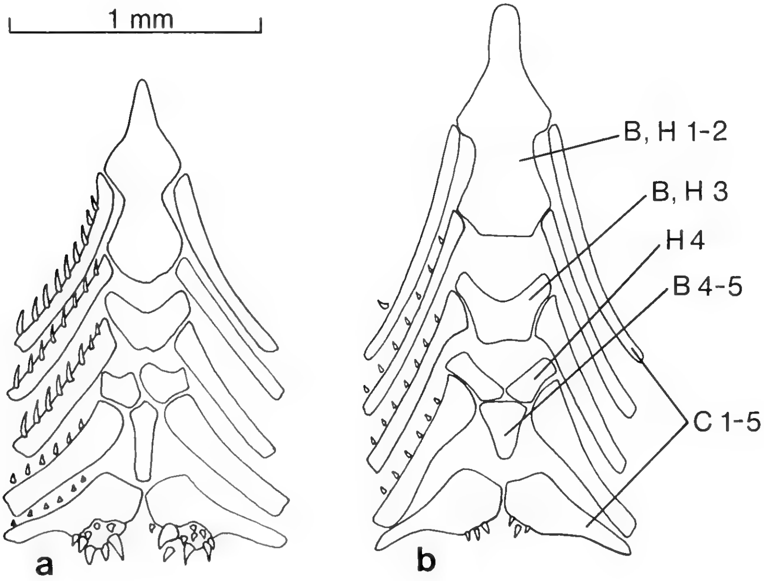


FIGURE 4. Ventral parts of gill arches, dorsal view (gill rakers of right side omitted): (*a*) *Sundasalanx praecox,* MCZ 54390, 17.2 mm; (*b*) *Sundasalanx microps,* CAS 44220, 17.2 mm. B, H, C = basibranchial, hypobranchial, ceratobranchial (see text for explanation).

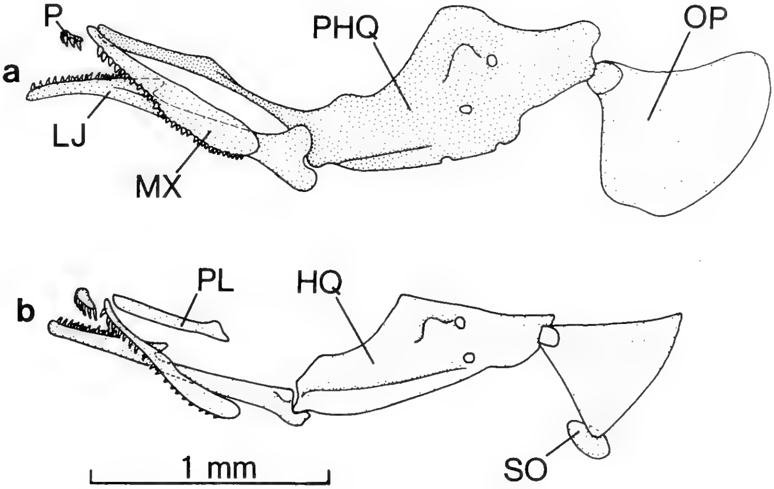


FIGURE 5. Jaws, jaw suspension, and gill cover, lateral view: (*a*) *Sundasalanx praecox*, MCZ 54390, 17.1 mm; (*b*) *Sundasalanx microps*, MCZ 44220, 17.0 mm. P, MX, LJ = premaxillary, maxillary, lower jaw; PHQ = palatohyomandibuloquadrate; PL, HQ = palatine, hyomandibuloquadrate; OP, SO = opercle, subopercle.

puas River by Chaper in 1890–91 which he hesitantly identified as young needlefish (?*Belone caudimaculata*). Subsequent to completing the manuscript of this paper, I visited the Muséum National d'Histoire Naturelle in Paris, where Chaper's Kapuas collection is deposited, and examined this material. The specimens (MNHN 91-596, 27:18.8–23.4 mm), although not in the best state of preservation, are clearly *Sundasalanx* but do not agree well with my diagnoses of either *S. microps* or *S. praecox*. They agree with *S. microps* rather than *S. praecox* in their relatively large size, vertebral counts of about 42–45, modally 43 (determined by counting the myotomes), and number of branched anal fin rays, about 15–18. On the other hand, the eyes seem to be much larger than in *S. microps* and possibly even larger than in *S. praecox*, and the number of maxillary teeth fewer than in *S. microps* and *S. praecox*. In nearly all of the specimens, the eyes are ruptured or their shape so distorted that horizontal diameter cannot be measured accurately. In a 22.5-mm specimen in which the eye is intact and nearly normal in shape, its horizontal diameter is 5.0% of SL (2.7–3.2% in *S. microps*, 4.3–5.0% in *S. praecox*). The eyeballs are so large that they nearly meet in the middle of the head, whereas in both *S. microps* and *S. praecox* they are considerably further apart. The number of teeth on the maxillary bone is only 10–14 (n = 3) vs. about 30 in *S. microps* and about 15–19 in *S. praecox*. A row of melanophores is visible on the side of the body external to the free ventral ends of the myotomal muscles, but not on the ventral midline of the abdomen and postpelvic abdominal keel (the latter present in *S. microps* but not in *S. praecox*). I was unable to detect testes or eggs in any of the specimens, although many of

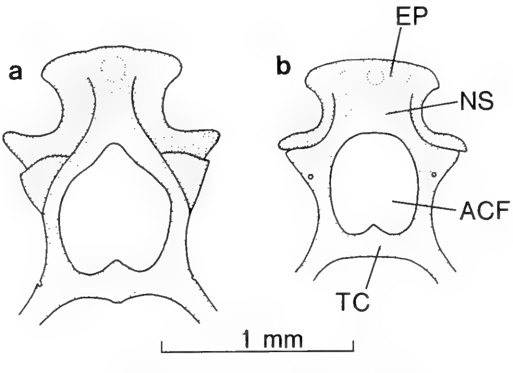


FIGURE 6. Anterior end of cranium, dorsal view: (*a*) *Sundasalanx praecox*, MCZ 54390, 17.2 mm; (*b*) *Sundasalanx microps*, CAS 44220, 17.0 mm. EP, NS = ethmoid plate, nasal septum; ACF, TC = anterior cranial fontanel, tectum cranii.

them have ruptured abdomens. The precise locality where they were collected is unknown, but judging from Vaillant's remarks (1893:60) they must have been taken in or near the mainstream of the Kapuas River somewhere between its confluence with the Sebruang River and Semitau, or in the same general area as *S. microps,* the type-locality of which is less than 40 km upriver from Semitau. So far as I have been able to find out, no additional material of *Sundasalanx* has been reported upon or collected by anyone else.

DISCUSSION

Alizarin is a specific stain for bone but does not always stain bone in an early stage of development or poorly calcified bone. Alcian blue usually stains cartilage, but apparently also sometimes stains uncalcified bone or bone in an early stage of development. In some instances structures which are clearly bone or cartilage fail to be noticeably stained by either alizarin or alcian blue. Thus, it is not possible to state in every instance which skeletal elements in Sundasalangidae and Salangidae are cartilage and which are bone based merely on their staining reaction to alcian blue and alizarin. In Sundasalangidae the only skeletal elements deeply stained with alizarin are vertebral centra, distal ends of neural and haemal spines, caudal fin rays, hypural fan, teeth, and bony toothplates on fifth ceratobranchials. Maxillary bone, toothbearing portion of the lower jaw, secondary pectoral fin girdle (posttemporal, supracleithrum and cleithrum) and pelvic fin rays are weakly stained with alizarin. Gill rakers, branchiostegal rays, and subopercle are either weakly stained with alcian blue or are not stained at all, in which case they may be difficult to observe even with transmitted light. In alcian blue–alizarin preparations of adult Salangidae, the distribution of elements stained by alcian blue and alizarin is basically similar to that in Sundasalangidae, but alizarin is taken up more extensively.

Sundasalanx praecox is among the smallest of adult vertebrates and is the smallest known salmoniform fish. *Sundasalanx microps* is the smallest of more than 250 fish species present in the Kapuas River (personal observations), thus providing an excellent example of survival of a peripheral-division fish family in the midst of a rich primary-division freshwater ichthyofauna by evolution of minute body size and a wholly freshwater life history (for further discussion see Roberts 1978:20–21). Salangidae are anadromous and freshwater fishes inhabiting coastal waters and rivers of East Asia from North Vietnam northwards to Korea, Vladivostok, and Sakhalin. They are unknown from Thailand and Borneo. The basic references to systematics and geographical distribution of Salangidae are Fang (1934) and Wakiya and Takahasi (1937).

LITERATURE CITED

DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52(4):229–232, 3 figs.

FANG, P. W. 1934. Study on the fishes referring to Salangidae of China. Sinensis 4(9):231–268, 7 figs., 6 tables.

GEHRINGER, J. W. 1959. Early development and metamorphosis of the ten-pounder, *Elops saurus* Linnaeus. U.S. Fish Wildl. Serv. Fish. Bull. 59 (155):619–647, 32 figs., 14 tables.

NELSON, G. J. 1970. Gill arches of some teleostean fishes of the families Salangidae and Argentinidae. Jpn. J. Ichthyol. 17(2):61–66, 2 figs.

ROBERTS, T. R. 1978. An ichthyological survey of the Fly River in Papua New Guinea with descriptions of new species. Smithson. Contrib. Zool. 281, 72 pp., 32 figs.

VAILLANT, L. 1893. Contribution à l'étude de la faune ichthyologique de Bornéo. Nouv. Arch. Mus. Hist. Nat., ser. 3, 5:23–114, 2 pls.

WAKIYA, Y., AND N. TAKAHASI. 1937. Study on fishes of the family Salangidae. J. Coll. Agric. Tokyo Univ. 14(4):265–295, 3 figs., pls. 16–21, 2 tables.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 10, pp. 303–314, 4 figs. March 5, 1981

NEW AND RECONSIDERED SPECIES OF *MICONIA* (MELASTOMATACEAE) FROM COSTA RICA AND PANAMA

By
Frank Almeda
Department of Botany, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

ABSTRACT: Diagnoses, descriptions, and discussions are presented for five new Central American species of *Miconia (M. chiriquiensis* and *M. coloradensis* from Panama, and *M. confertiflora, M. grandidentata,* and *M. longibracteata* from Costa Rica). Diagnostic illustrations are provided for four of the novelties, and the new name *Miconia concinna* is proposed for a Panamanian endemic heretofore known as *Topobea micrantha.*

INTRODUCTION

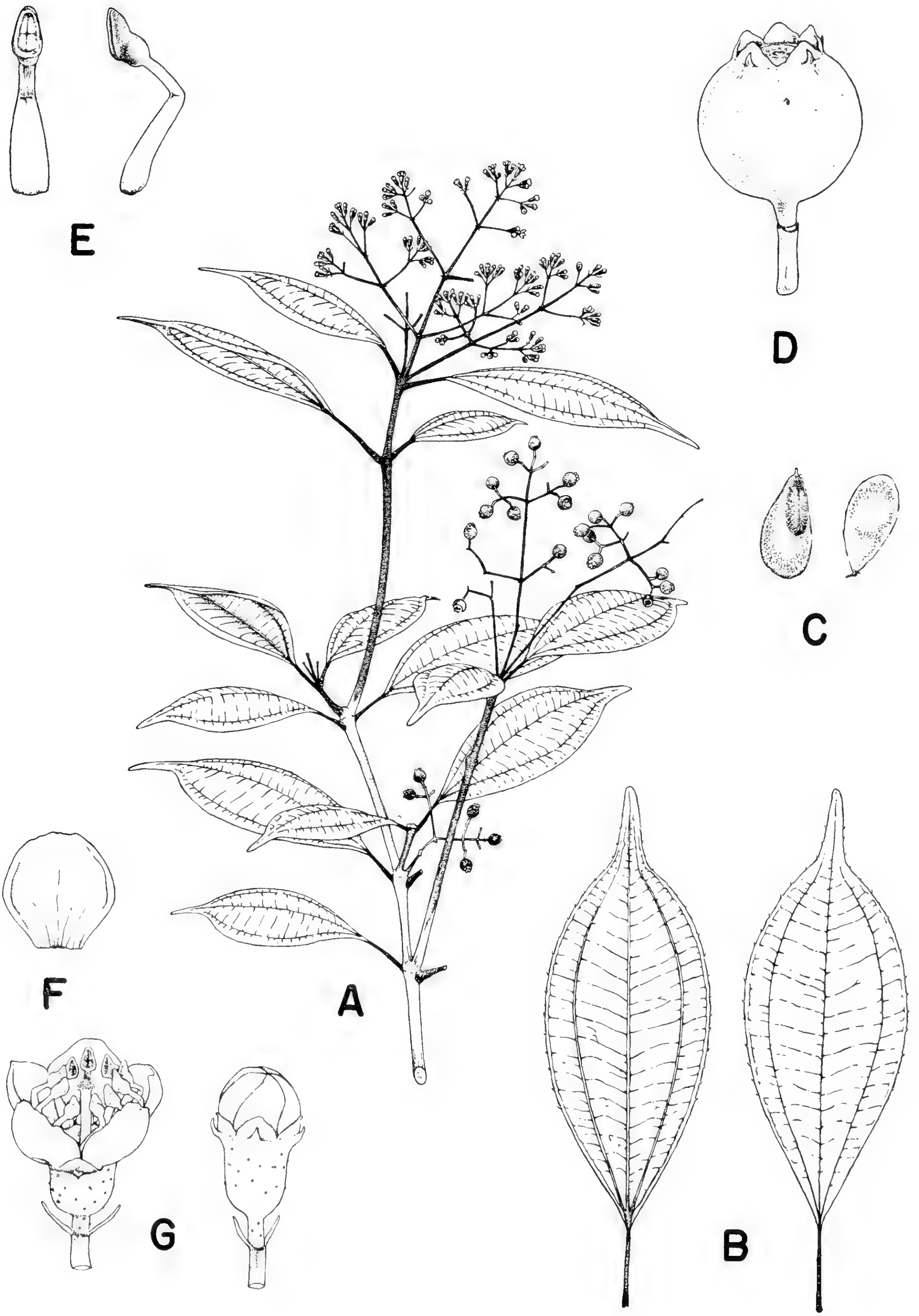
In the four decades since Standley (1938) attempted to summarize knowledge of the Costa Rican Melastomataceae, increased botanical exploration in Costa Rica and adjacent Panama has resulted in the collection of much new material of the montane species of *Miconia.* Field and herbarium study of this genus for a comprehensive treatment of Melastomataceae for *Flora Costaricensis* reveals the need for nomenclatural changes, emended species descriptions, and recognition of several undescribed taxa. This paper places some of this new information on record now to make the names available to other researchers prior to completion of the floristic treatment.

Miconia chiriquiensis Almeda, sp. nov.

(Figure 1)

Sect. *Cremanium. Frutex vel arbor parva 2–4(–10) m. Ramuli teretes vel obscure rotundato-quadrangulati sicut folia primum paulo furfuracei mox glabrati. Petioli (5–)7–18(–25) mm; lamina 3.7–7.5(–10) × 1.5–4.6 cm chartacea elliptica apice caudato-acuminato basi acuta margine obscure serrulato. Panicula 4–6.5 cm longa glabra laxe multiflora; flores 5-meri, pedicellis 0.5–1 mm longis, bracteolis 0.5–1.5 × 0.5 mm caducis. Hypanthium (ad torum) 1 × 1 mm, lobis interioribus 0.5–1 mm altis late deltoideis apice obtuso, dentibus exterioribus acutis ca. 0.5 mm eminentibus. Petala 1.5 × 1.5 mm suborbicularia glabra. Stamina isomorphica glabra; filamenta 1.5 mm longa; antherarum thecae 0.75 × 0.5 mm paulo cuneatae poro 0.5 mm diam. ventraliter inclinato, connectivo non prolongato. Stylus 0.7–1 × 0.5 mm glaber; stigma subcapitatum; ovarium omnino inferum apice glabro.*

Shrub or tree 2–4(–10) m tall. Internodes and distal branches ± terete, essentially glabrous at maturity, but vegetative buds and young leaves commonly beset with a brownish furfuraceous indument. Leaves chartaceous, distantly ciliate-serrulate, 3.7–7.5(–10) cm long and 1.5–4.6 cm wide, elliptic, bluntly caudate-acuminate apically and acute basally, glabrous at maturity,


E
D
C
A
F
G
B

3-nerved or 3-plinerved (excluding inconspicuous submarginal pair) punctate and with a conspicuous network of secondaries below; petioles (5–7)7–18(–25) mm long and 1 mm broad. Inflorescence a laxly branched suberect to ± pendant panicle 4–6.5 cm long; rachis ± quadrate, glabrous throughout; bracteoles sessile, early-deciduous, 0.5–1.5 mm long and 0.5 mm wide, linear-oblong, entire. Pedicels 0.5–1 mm long. Hypanthia (at anthesis) campanulate, 1 mm long to the torus, glabrous. Calyx lobes (on fruiting hypanthia) persistent, glabrous, semicircular or depressed-triangular with entire to irregularly, ± hyaline margins, 0.5–1 mm long and about 1 mm wide; calyx teeth persistent, subulate, ± appressed to and shorter than mature calyx lobes. Petals 5, erect to antrorsely spreading, glabrous, ± concave, white or greenish white, suborbicular, entire, 1.5 mm long and wide. Stamens 10, isomorphic, incurved toward central axis of flower at anthesis; filaments glabrous, subulate, white to translucent, mostly 1.5 mm long and 0.5 mm wide basally; anthers about 0.75 mm long and 0.5 mm wide distally, white, ± infundibuliform to obliquely cuneate in profile view, shallowly emarginate dorsally, the pore oblong and ventrally inclined; connective simple, inconspicuous and lacking prolongations or appendages. Ovary inferior. Style straight, glabrous, 0.7–1 mm long; stigma subcapitate. Berry globose, 2–3 mm long to the torus and 2–3.5 mm in diameter. Seeds ± pyriform, beige, papillate, mostly 0.7–1 mm long.

Types.—**Panama.** Chiriquí: about 8 km w of Cerro Punta, vicinity of Las Nubes, elevation 6100–6400 ft [1859–1951 m], 11 Feb. 1978, *Almeda & Nakai 3535* (holotype: CAS!; isotypes: C!, DUKE!, F!, MO!, PMA!, US!).

Additional Specimens Examined.—**Panama.** Chiriquí: vicinity of Las Nubes, 2.7 miles [4.3 km] NW of Río Chiriquí Viejo, w of Cerro Punta, *Croat 22392* (CAS, DUKE, MO), *Croat 22425* (MO, US); Bajo Chorro, Boquete, *Davidson 181* (US), *Davidson 390* (MO).

Distribution.—A little-collected cloud-forest species apparently restricted to Chiriquí province in western Panama at elevations of 1850–2200 m. Available specimens, all of which were collected in February, are in flower and fruit.

Miconia chiriquiensis is apparently rare and occurs in a region which continues to yield new and narrowly endemic taxa. Diagnostic features include the ciliate-serrulate, elliptic leaves that are caudate-acuminate apically, short (0.5–1 mm), linear-oblong, early-deciduous bracteoles, concave, suborbicular petals, geniculate filaments, and minute (0.75 × 0.5 mm), 4-celled anthers.

In his account of *Miconia* for the Melastomataceae of Panama, Gleason (1958) referred this entity to *M. rubens* (Sw.) Naud. Study of his description and examination of selected cited specimens indicate that Gleason also confused *M. chiriquiensis* with the taxon treated here as *M. concinna*. The latter differs markedly from *M. chiriquiensis* by virtue of its epiphytic habit, trichotomously branched, corymbiform panicle, and distinctive androecial morphology. In foliar size and shape the new species bears a strong resemblance to *M. rubens*, which is known only from Jamaica and Venezuela. *Miconia rubens* does differ conspicuously, however, by the somewhat swollen nodes, ferrugineous pubescence on distal nodes and juvenile foliage, marginally fimbriate bracteoles, dioecious floral condition, peltate stigma, and cuneate, apically truncate anthers. Although *M. chiriquiensis* resembles *M. rubens* most closely in the totality of its vegetative characters, it is difficult to present meaningful speculation regarding the origin and exact relationships of these taxa. Aside from the possibility of evolutionary convergence, the most logical alternative hypothesis is that *M. rubens* is a close relative and possibly dioecious derivative of *M. chiriquiensis*.

Miconia coloradensis Almeda, sp. nov.

(Figure 2)

Sect. *Amblyarrhena. Herba 1 m alta (fide collectore). Ramuli glabri primum obscure subquadrangulati demum teretes. Petioli 3–7.5 × 1.5–3 cm; lamina 13.5–20.5 × 9.8–17 cm*

←

Figure 1. *Miconia chiriquiensis* Almeda. *A*, habit, ×½; *B*, representative leaves, lower surface (left) and upper surface (right), ×1; *C*, seeds, ×12; *D*, mature berry, ×8; *E*, stamens, ventral view (left) and lateral view (right) × ca. 10; *F*, petal, × ca. 8; *G*, fully expanded flower showing natural posture of petals and stamens (left), floral bud and pedicellar bracteoles (right), ×9. (*A–G* from *Almeda & Nakai 3535*.)

chartacea vel subcoriacea denticulata cordata apice acuminato vel cuspidato, 9–11-nervata, supra glabra et paulo reticulato-bullata, subtus in superficie pilis stellatis obsita. Panicula 7–19 cm longa multiflora; flores (4–)5-meri, 1.5–5 mm pedicellati, bracteolis 3–6 mm longis obovatis vel spathulatis valde caducis. Hypanthium (ad torum) 2.5 × 2 mm, lobis interioribus 1 mm altis rotundatis vel truncatis, dentibus exterioribus crassis ca. 0.5 mm eminentibus. Petala 3–5.5 × 2–4 mm obovata. Stamina isomorphica glabra; filamenta 2.5 mm longa; antherarum thecae 2.5 × 1 mm anguste obovatae poro 0.5–0.75 mm diam. paulo ventraliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 5 × 0.5 mm glaber; stigma subcapitatum.

Herb to 1 m tall (according to collectors). Cauline internodes glabrous, subquadrangular to ± terete. Leaves ± bullate above, chartaceous to subcoriaceous, denticulate, 13.5–20.5 cm long and 9.8–17 cm wide, cordate, acuminate to cuspidate apically, 9–11-nerved with a prominulous network of secondary and tertiary nerves below, glabrous and green above, red to purple and moderately beset with sessile stellate trichomes on and between primary and secondary nerves below; petioles 3–7.5 cm long and 1.5–3 cm broad, each petiole bearing an abaxial, humplike protuberance proximal to nodal junction. Inflorescence a laxly branched terminal panicle 7–19 cm long; rachis ± rounded to subquadrangular, moderately stellate pubescent; bracteoles sessile, early deciduous, 3–6 mm long and 1.5–3 mm wide, obovate to spatulate, erose to denticulate, ± enveloping young buds and pedicels, glabrous above, sparsely to moderately stellate below. Pedicels 1.5–5 mm long, beset with sessile stellate trichomes. Hypanthia (at anthesis) narrowly campanulate, mostly 2.5 mm long to the torus, moderately to sparsely stellate pubescent. Calyx lobes (on fruiting hypanthia) persistent, glabrous, erect, broadly semicircular but ± truncate apically, entire to somewhat erose, 1 mm long and about 2 mm wide; calyx teeth persistent, bluntly subulate or knoblike, appressed to and shorter than the calyx lobes on mature berries. Petals mostly 5, but 4 in some flowers, reportedly pink, obovate, entire, rounded to irregularly emarginate at apex, 3–5.5 mm long and 2–4 mm wide. Stamens 10, but 9 in 4-merous flowers, isomorphic; filaments straight, subulate, thickened and somewhat fleshy, at least basally, 2.5 mm long; anthers 2.5 mm long and mostly 1 mm wide distally, yellow, obovoid, border of apical pore ± emarginate ventrally but truncate dorsally; connective inconspicuous and without prolongations or appendages. Ovary inferior. Style straight, 5 mm long, glandular-ciliate basally, otherwise glabrous; stigma subcapitate. Berry ± globose, 4.5–5.5 mm long to the torus and 5–5.5 mm in diameter. Seeds galeiform, nitid, smooth to obscurely papillate, 0.5 mm long.

TYPES.—**Panama.** Bocas del Toro/Chiriquí border: Cerro Colorado along intersection of Bocas Road with main ridge road, 15.4 km from Chami along ridge road, elevation 1400–1700 m, 24 Oct. 1977, *Folsom 6143* (holotype: CAS!; isotype: MO).

ADDITIONAL SPECIMENS EXAMINED.—**Panama.** Chiriquí: Cerro Colorado, Bocas Road, *Folsom & Collins 1748* (CAS, MO).

DISTRIBUTION.—Known only from Cerro Colorado in western Panama at an elevation of 1400–1700 m. Flowering and fruiting specimens have been collected in February and October.

This distinctive species is characterized by a lax, elongate inflorescence, truncate calyx lobes, nitid, galeiform seeds and cordate, denticulate leaves clothed abaxially with sessile, stellate trichomes. In the few collections available for study, the inflorescence is consistently terminal but superficially appears to diverge from a lateral position because of the overtopping effect created by lengthening of proximal axillary shoots. The characteristic number of floral parts has been difficult to determine on the basis of material at hand. The inflorescence on the holotype has both 4-merous flowers with nine stamens and 5-merous flowers with ten stamens, but the significance of this variation cannot be properly assessed without a more extensive series of specimens.

The relationships of this species are unclear. Assuming sect. *Amblyarrhena* represents a natural grouping, it is tempting to suggest that *M. coloradensis* diverged from the Andean stock that gave rise to *M. andreana* Cogn. of Colombia and *M. gibba* Markgraf of Ecuador. The former differs from *M. coloradensis* in having longer leaves (2–3.5 dm), a furfuraceous pubescence, linear-oblong to subulate bracteoles, and a compact inflorescence with ultimate units consisting of congested glomerules. Aside from striking differences in inflorescence size and structure,

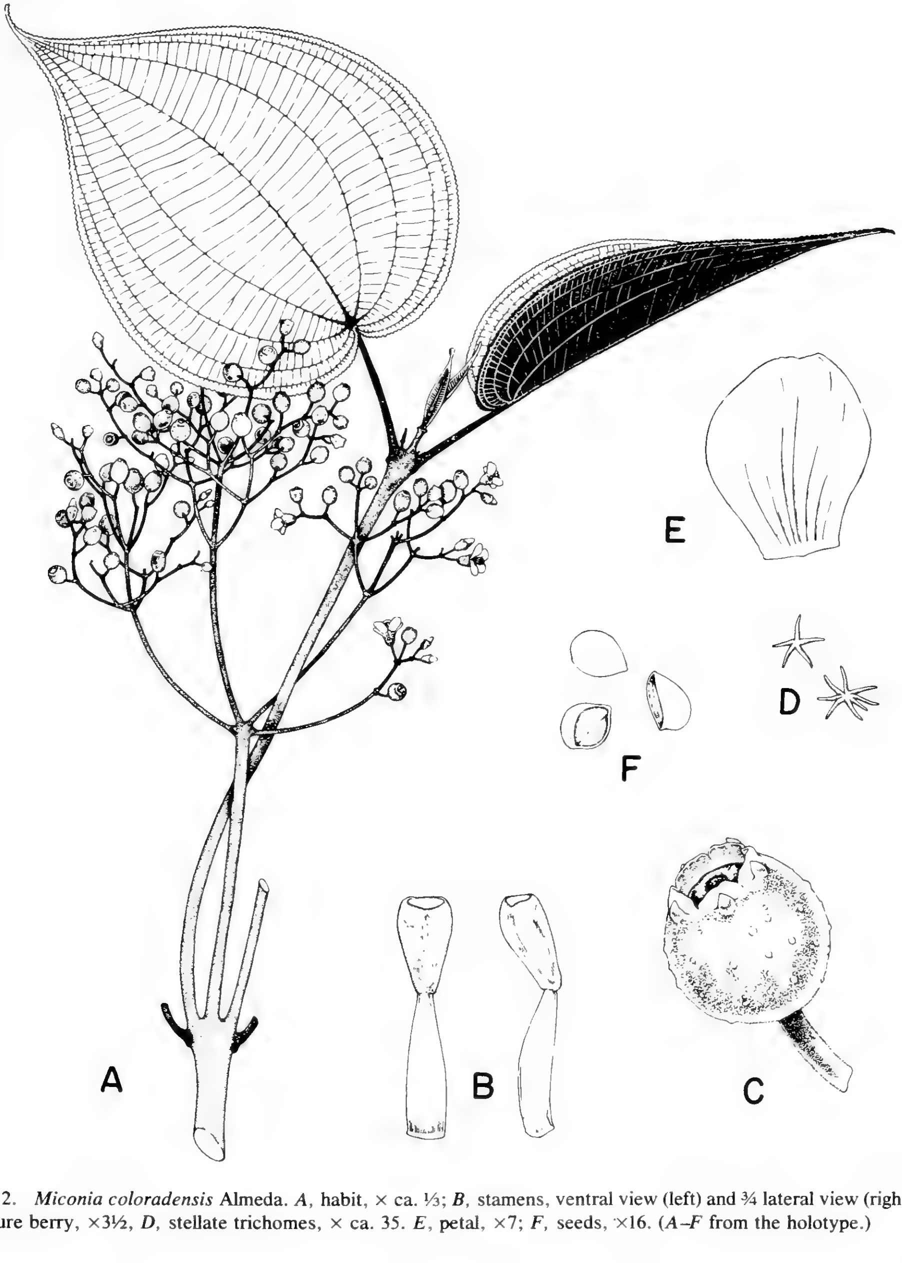


FIGURE 2. *Miconia coloradensis* Almeda. *A*, habit, × ca. ⅓; *B*, stamens, ventral view (left) and ¾ lateral view (right), × ca. 6; *C*, mature berry, ×3½, *D*, stellate trichomes, × ca. 35. *E*, petal, ×7; *F*, seeds, ×16. (*A–F* from the holotype.)

the new species approaches *M. gibba* in overall foliar length and shape. Petioles of the latter are shorter (1.5–2 cm), and the leaves are 7-nerved, caducously furfuraceous below, and bigibbous dorsally at the base.

Miconia concinna Almeda, nom. nov.

Topobea micrantha Pittier, J. Wash. Acad. Sci. 14:451. 1924. Nec *Miconia micrantha* Cogn. (Bull. Torrey Bot. Club 23:16. 1896) nec *M. micrantha* Pilger (Verh. Bot. Ver. Brand. 47:173. 1905; *M. wittii* Ule, nom. nov., Notizbl. Bot. Gart. Berl. 6:367. 1915) nec *M. micrantha* Pittier (Bol. Soc. Venez. Cienc. Nat. 11:27. 1947; *M. tabayensis* Wurdack, nom. nov., Phytologia 21:359. 1971).

Study of the holotype and recently collected material of this entity reveals some inaccuracies in Pittier's incomplete Latin diagnosis. It seems appropriate, therefore, to present the following emended species description.

Epiphytic shrub with lax arching branches to 2 m long. Cauline internodes terete, the distal branches glabrous and ± vernicose on drying. Leaves of a pair isomorphic to anisomorphic, chartaceous, ciliate-serrulate (the trichomes mostly 1–2 mm long), 1.7–4.7 cm long and 1.4–3 cm wide, elliptic to elliptic-ovate acuminate apically and acute basally, sparsely pubescent to glabrate at maturity but usually lepidote to brown-punctate below, sparsely brown furfuraceous to glabrous above, the pubescence usually tardily deciduous and imparting a brown-punctate appearance, 3-nerved with a network of secondaries mostly 1–2 mm apart; petioles 5–20 mm long, 1 mm broad. Inflorescence a pendant, congested, trichotomously branched corymbiform panicle 1–1.5 cm long (shorter than foliage leaves borne at the node initiating the inflorescence) borne on a stout peduncle 2–5 mm long; bracteoles sessile, foliaceous, persisting on the infructescence, oblanceolate to narrowly spatulate, 3–6(–10) mm long, 1–2 mm wide, glabrous to sparsely furfuraceous. Pedicels terete, glabrous, mostly 0.5 mm long. Hypanthia (at anthesis) glabrous, campanulate, 1–1.5 mm long to the torus and 1–1.5 mm broad. Calyx lobes (on fruiting hypanthia) ± ascending, persistent, semicircular but varying to rounded-deltoid, entire to minutely lacerate, 1 mm long and 1.5 mm wide at base between sinuses; calyx teeth persistent, triangular, 0.5 mm long. Petals 5, ± erect to antrorsely spreading, glabrous, ± concave, white but sometimes yellowish on drying, suborbicular, entire, 2–2.5 mm long and wide. Stamens 10, isomorphic; filaments glabrous, subulate, distally geniculate, 2–2.5 mm long; anthers 0.5 mm long, ± cuneate, broadly flared and terminated by a ± ovoid ventrally inclined pore; connective thickened and prolonged (0.5 × 0.5 mm) below thecae, truncate to shallowly bilobed in ventral view, dilated dorsally into a blunt projecting appendage in profile view. Ovary ca. 4/5 inferior. Style straight, glabrous, 3 mm long; stigma ± clavate to subcapitate. Berry reportedly black at maturity, 2–2.5 mm long to the torus, 2.5–3 mm in diameter. Seeds ± pyriform, smooth and nitid, mostly 0.75 mm long.

SPECIMENS EXAMINED.—**Panama.** Chiriquí: humid forests on precipitous slopes of Cerro de la Horqueta, *Pittier 3276* (US, holotype of *T. micrantha*); S slopes of Cerro Horqueta N of Boquete, *Wilbur, Teeri & Foster 13490* (CAS, DUKE); Cerro Pando, on continental divide and Panama/Costa Rica border, ca. 16 km NW of El Hato del Volcán, *Mori & Bolten 7291* (CAS), *Mori & Bolten 7301* (CAS).

DISTRIBUTION.—Apparently a localized cloud-forest epiphyte endemic to Chiriquí province in western Panama at elevations of 2000–2500 m. Flowering and fruiting specimens have been collected in January, March, and July.

Miconia concinna is recognized by its lax, arching branches, adaxial furfuraceous indument on juvenile foliage, large, persistent, foliaceous floral bracts, and pendant, few-flowered corymbiform inflorescences that are markedly shorter than subtending foliage leaves.

Pittier's (1924) initial placement of this species in *Topobea* is difficult to understand, since his discussion makes note of several features which made this decision questionable. In choosing this course, Pittier was apparently impressed by the presence of conspicuous foliaceous floral bracteoles and by the position of the inflorescence, which he erroneously described as axillary. In describing this species as a tree, it also seems likely that Pittier mistook its habit for that of its host. Label Information for all recently gathered material indicates that this species is an epiphyte, and until noted otherwise, it seems advisable to accept this habital description as characteristic of the species.

On the basis of limited material, Standley (1938) misinterpreted *M. concinna* to be conspecific with the Costa Rican endemic described here as *M. longibracteata*. This confusion was compounded when he referred specimens of these two taxa to *M. myrtillifolia* Naud., a species of Andean Colombia and Venezuela which differs in having quadrate branchlets, a longer (2–4 cm), erect panicle, and very different oblong anthers with diminutive apical pores and unprolonged connectives. More recently, Gleason (1958) included *M. concinna* in his misconstrued concept of *M. rubens* (Sw.) Naud. The latter, a dioecious species, is known only from Jamaica and Venezuela and differs most notably by its elongate multiflowered inflorescence, inconspicuous bracteoles, ± swollen nodes, and different anther morphology.

In foliar shape and floral details, *M. concinna* and *M. longibracteata* are more similar to each other than to any other species of the genus, and there is little doubt that they were derived from common ancestral stock. Available collections suggest that these two species are allopatric, with the range of *M. concinna* lying south of that of *M. longibracteata*. The prevailingly glabrous leaves, early-deciduous floral bracteoles, and laxly branched, elongate panicle of *M. longibracteata* serve to separate these species most readily.

Miconia confertiflora Almeda, sp. nov.
(Figure 3)

Sect. *Chaenopleura. Frutex epiphyticus ca. 2 m altus. Ramuli sulcato-quadrangulati sicut folia inflorescentia plerumque glabri. Petioli 3–16(–20) mm; lamina 1.7–7 × 1–3.4 cm elliptica, elliptico-ovata vel obovata apice acuta vel acuminata basi acuta, 3(–5)-nervata, chartacea et serrulata. Panicula corymbiformis, pedunculo plus minusve 1.5 cm longo; flores 5-meri breviter (1 mm) pedicellati, bracteolis 1.5–2.5(–4) mm longis valde caducis. Hypanthium (ad torum) 1.5 × 1 mm, lobis interioribus 0.5–1 mm altis late deltoideis vel rotundatis, dentibus exterioribus acuminatis 0.5–1.5 mm longis. Petala 1–1.5 × 0.5–1 mm ovata apice acuto vel paulo uncinato. Stamina isomorphica glabra; filamenta 1–1.5 mm longa; antherarum thecae 0.75–1 × 0.25–0.50 mm anguste oblongae, connectivum nec prolongatum nec appendiculatum. Stylus 2 × 0.5 mm glaber; stigma truncatum non expansum.*

Epiphytic shrub to 2 m tall, distal branches quadrangular with carinate to narrowly alate angles, entirely glabrous but bearing a pair of ± pustulate setiform appendages at opposing nodal faces. Leaves chartaceous, glabrous, 1.7–7 cm long and 1–3.4 cm wide, basally entire but distally serrulate, elliptic but sometimes varying to elliptic-ovate or obovate, acute to acuminate apically and acute basally, 3(–5)-nerved with a conspicuous network of secondary nerves, dark green above, pale green and occasionally punctate below; petioles 3–16(–20) mm long and about 1 mm broad. Inflorescence a multiflowered corymbiform panicle with flowers borne in congested terminal glomerules; rachis glabrous, quadrangular, mostly less than 1.5 cm long; bracteoles sessile, glabrous, early-deciduous, 1.5–2.5(–4) mm long and 0.5–1 mm wide, linear-subulate. Pedicels 1 mm long. Hypanthia (at anthesis) campanulate, glabrous, 1.5 mm long to the torus. Calyx lobes (on fruiting hypanthia) persistent, erect, broadly deltoid to ± rounded, entire with conspicuous hyaline margins, 0.5–1 mm long and 1 mm wide; calyx teeth persistent, subulate to setiform, equaling or commonly exceeding calyx lobes on mature berries. Petals 5, glabrous, erect and ± concave at anthesis, white but tinged with red externally, narrowly to broadly ovate, entire, acute to bluntly uncinate apically, 1–1.5 mm long and 0.5–1 mm wide. Stamens 10, isomorphic, erect to slightly incurved at anthesis; filaments white, ± translucent, subulate, 1–1.5 mm long; anthers 0.75–1 mm long and 0.25–0.50 mm wide basally, glabrous, white, narrowly oblong but ± obovoid in profile view, distally rounded with a subterminal, oblong ventrally inclined cleftlike pore, the margins of which often form a ± elevated hyaline border; connective thickened, not conspicuously dilated or prolonged dorsally but commonly ± prolonged ventrally below thecae. Ovary wholly inferior. Style straight, 2 mm long; stigma truncate. Berry purple at maturity, ± globose, 3–3.5 mm long to the torus and 3.5 mm in diameter. Seeds narrowly ovoid with an enlarged, ± flattened lateral raphe, densely papillate on the convex surface, mostly 2 mm long and 1 mm broad.

TYPES.—**Costa Rica.** San José: about 18 km N of San Isidro de Coronado off C.R. #216 on lower W slopes of Volcán Irazú, elevation 1700–1800 m, 5 July 1977, *Almeda et al. 2908* (holotype: CAS!; isotypes: CR!, F!, MO!, US!).

ADDITIONAL SPECIMENS EXAMINED.—**Costa Rica.** Heredia: slopes NE of Cerro Chompipe about 16 km NNE of San Rafael, *Wilbur, Almeda & Daniel 22249* (CAS, DUKE); Cerro Zurquí, NE of San Isidro, *Standley & Valerio 50542* (US), *Standley & Valerio 50644* (US); saddle area between Cerro Chompipe and SE flank of Volcán Barba off secondary road N of C.R. Hwy #113 connecting with Calle Gallito, *Baker, Utley & Utley 232* (CAS, DUKE). San José: 5 km NE of Cascajal, *Almeda & Nakai 3611* (CAS); 3–6 km beyond Las Nubes in vicinity of Cascajal, *Almeda 2636* (CAS); about 7 km by road NE of Cascajal and 14 km NE of San Isidro de Coronado, *Wilbur 19816* (DUKE); 3–5 km NE of Cascajal in vicinity of Río Cascajal, *Wilbur 24420* (DUKE); about 3 km NE of Cascajal and 9 km NE of San Isidro de Coronado, *Wilbur 19787* (DUKE).

DISTRIBUTION.—A local cloud-forest epiphyte apparently endemic to the Cordillera Central of Costa Rica at elevations of 1600–2400 m. Flowering and/or fruiting specimens have been collected in February, March, July, October, and December.

Field observations and label information of known collections indicate that this species is an obligate epiphyte. Extirpation of moist forests within the limited range of this taxon poses a real threat to its survival. Fortunately, some individuals persist as inhabitants of remnant pas-

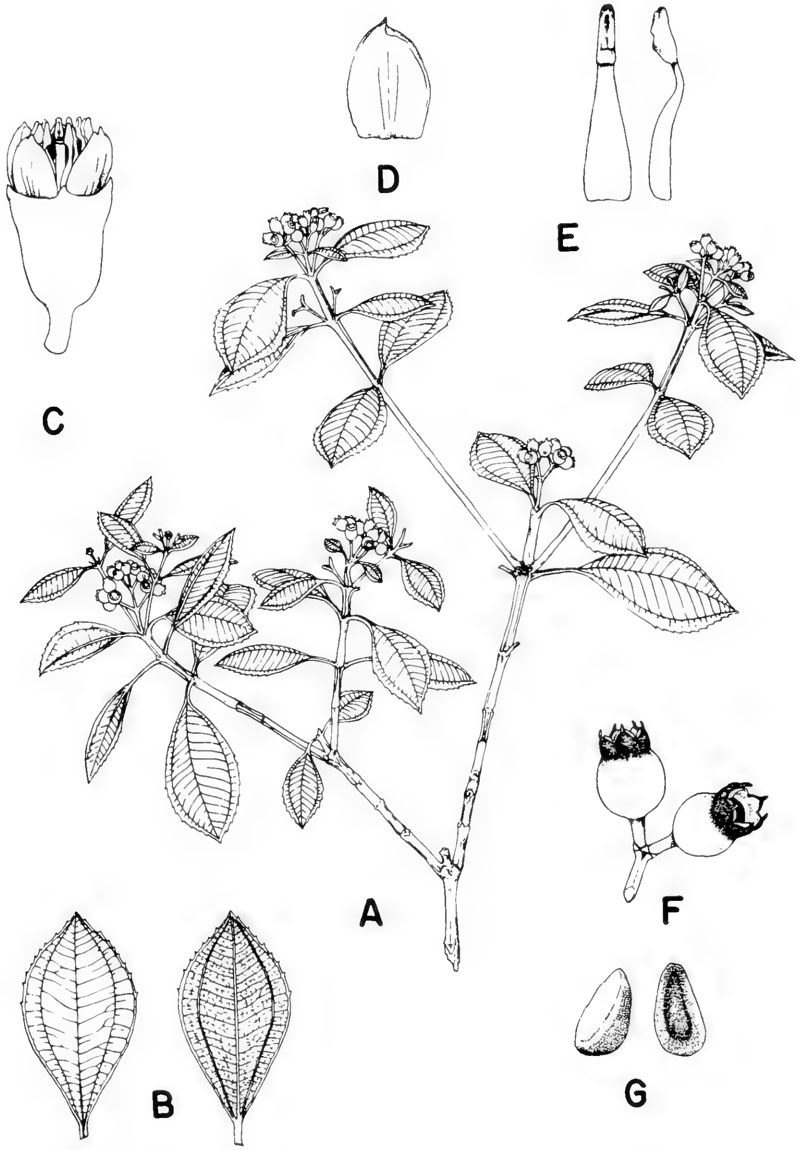


FIGURE 3. *Miconia confertiflora* Almeda. *A*, habit, ×¼; *B*, representative leaves, upper surface (left) and lower surface (right), ×¾; *C*, fully expanded flower showing petals and stamens, ×9; *D*, petal, × 16; *E*, stamens, ventral view (left) and lateral view (right), ×13; *F*, mature berries with persistent calyx lobes and calyx teeth, ×3; *G*, seeds, ×6. (*A–G* from *Almeda et al. 2908.*)

ture trees long after surrounding vegetation has been cut away.

This new species is readily separated from congeners by its quadrangular branchlets, distally serrulate leaves, congested corymbiform inflorescence, glabrous hypanthia, prominent calyx teeth, and narrowly ovoid seeds that are densely papillate on the convex side. The small, inconspicuous anthers are also noteworthy in having subterminal, oblong pores, the margins of which are elevated into a low, continuous, hyaline border. This feature becomes distorted with pressing and drying and is best observed in pickled or hydrated material.

Miconia confertiflora superficially resembles *M. chionophylla* Naud. of sect. *Chaenopleura,* which ranges from Andean Colombia to Bolivia. The latter differs in its procumbent or scandent habit, puberulent branchlets and petioles, smaller leaves (1–1.5 × 0.7–1.3 cm), 4-merous flowers, and capitate stigma. The congested inflorescence of *M. confertiflora* is also reminiscent of that found in *M. parvifolia* Cogn. (of sect. *Cremanium*), another high-elevation Colombian species easily separated by its dwarf shrubby habit (2–3 dm tall), smaller, revolute leaves (8–15 mm long), ovate, apically truncate petals, and copious stellate pubescence on distal branchlets.

Miconia grandidentata Almeda, sp. nov.

Sect. *Chaenopleura. Frutex epiphyticus ca. 1 m altus. Ramuli sulcato-quadrangulati sicut folia novella primum modice vel dense pilis stellatis induti mox glabrati. Petioli 4–15(–19) mm; lamina 3–6 × 1.8–3.5 cm elliptica vel elliptico-ovata apice acuto vel acuminato basi acuta, 3(–5)-nervata, chartacea obscure distanterque serrulata. Panicula 3–5.3 cm longa multiflora; flores 5-meri breviter (1–2 mm) pedicellati, bracteolis conspicuis (1–)3–6 mm longis persistentibus. Hypanthium (ad torum) 2–2.5 × 2 mm, lobis interioribus 0.5 mm altis late deltoideis vel rotundatis, dentibus exterioribus subulatis 2 mm longis. Petala 1.5–2 × 1 mm plus minusve ovata apice uncinato. Stamina isomorphica glabra; filamenta 2 mm longa; antherarum thecae 0.75–1 × 0.5 mm oblongae, rectae vel paulo curvatae poro ventraliter inclinato, connectivo ad basim dorsaliter dente hebeti truncato glabro ornato. Stylus 2 × 0.5 mm glaber; stigma truncatum non expansum.*

Epiphytic shrub to 1 m tall, distal branchlets moderately to densely stellate, quadrangular with carinate to narrowly alate angles. Older branches somewhat corky on drying, cracking and excorticating in age. Leaves chartaceous, entire but obscurely serrulate distally, 3–6 cm long and 1.8–3.5 cm wide, elliptic to elliptic-ovate, acute to acuminate apically and acute basally, glabrous at maturity but clothed with brown stellate trichomes when young, 3(–5)-nerved with a conspicuous network of secondary nerves below; petioles 4–15(–19) mm long and 1–2 mm broad. Inflorescence an erect, terminal thyrse mostly 3–5.3 cm from base to apex; the rachis prominently quadrangular; bracteoles sessile, essentially glabrous, persistent, gradually reduced in size upward, (1–)3–6 mm long and 0.5–2 mm wide, narrowly lanceolate to subulate and ± concave adaxially. Pedicels 1–1.5 (–2) mm long caducously stellate pubescent, each pedicel commonly subtended by three bracteoles. Hypanthia (at anthesis) ± globose, 2–2.5 mm long to the torus, beset with sessile stellate trichomes (these early-deciduous and generally not present on fruiting hypanthia) or persistent only as remnant arms of stellate trichomes, which superficially resemble punctiform glands. Calyx lobes (on fruiting hypanthia) persistent, sparsely stellate pubescent, erect to somewhat incurved, broadly deltoid to ± rounded, entire to bluntly undulate with hyaline margins, 0.5 mm long and 1 mm wide; calyx teeth persistent, subulate, 2 mm long and 1.5 mm wide at base, markedly exceeding calyx lobes on mature berries. Petals 5, glabrous, erect and ± concave at anthesis, white, ± ovate in outline, entire, but bluntly uncinate apically, 1.5–2 mm long and mostly 1 mm wide. Stamens 10, isomorphic, erect but ± incurved and exceeding the style; filaments white to translucent, subulate, 2 mm long; anthers 0.75–1 mm long and mostly 0.5 mm wide basally, glabrous, white, oblong to rhomboid in profile view, but broadened distally to an oval or oblong, ventrally inclined apical pore; connective thickened and prolonged dorsally at the base into a deflexed ± truncate appendage. Ovary wholly inferior. Style straight, 2 mm long; stigma truncate. Berry pink when young but deep purple at maturity, globose, mostly 4 mm long to the torus and 4 mm in diameter. Seeds cuneate and conspicuously angled, reddish brown, vernicose, 1.5–1.75 mm long.

TYPE.—**Costa Rica.** San José: About 5 km NE of Cascajal, elevation 5400 ft [1646 m], 17 Feb. 1978, *Almeda & Nakai 3627* (holotype: CAS!).

ADDITIONAL SPECIMENS EXAMINED.—**Costa Rica.** Heredia: pastured slopes above Río Pará Blanco on lower slopes of Cerro Zurquí about 7 km NE of San Josecito, *Wilbur & Luteyn 18634* (DUKE). San José: slopes and thickets at Alto La Palma about 15 km in a straight line NE of San José, *Wilbur 20340* (CAS, DUKE).

DISTRIBUTION.—A rare cloud-forest epiphyte known only from the south-facing slopes of the Cordillera Central of Costa Rica at elevations of 1600–1800 m. Flowering material has been collected in February, July, and December.

Initial study of this species led me to interpret it as an atypical large-leafed variant of *M. confertiflora*, a species that grows in the same general area. Subsequent field observations of additional flowering and fruiting material indicate that this is a distinctive taxon worthy of specific rank. *Miconia confertiflora* and *M. grandidentata* share an epiphytic habit, quadrangular branchlets, and elliptic to elliptic-ovate, distally serrulate leaves having a conspicuous network of secondary nerves below. *Miconia grandidentata* differs consistently in several diagnostic characters. It lacks the nodal, setiform appendages so characteristic of distal branchlets in *M. confertiflora*. It also differs in having stellate pubescence on branchlets and young hypanthia, an elongate thyrsoid panicle, persistent floral bracteoles, longer calyx teeth, and angulate, vernicose seeds that lack a well-defined prolonged lateral raphe. The stamens of *M. grandidentata* also provide several distinguishing features. Hydrated anthers, which are oblong to rhomboid in profile view, are broadened distally to an oval or oblong, ventrally inclined terminal pore, and the connective is thickened and prolonged dorsally into a deflexed caudiform appendage.

Miconia longibracteata Almeda, sp. nov.

(Figure 4)

Sect. *Chaenopleura. Frutex 1–3 m altus. Ramuli glabri obscure quadrangulati demum teretes. Petioli 7–16(–27) × 1 mm; lamina (1.3–) 2.5–4.2 × 1.1–2.8 cm chartacea elliptica, elliptico-obovata aliquando suborbicularia apice acuta vel acuminata basi acuta vel obtusa, trinervata supra primum sparse ferrugineo-furfuracea mox glabrata, subtus primum sparse vel modice lepidota mox glabrata. Panicula 3.5–8 cm longa multiflora; flores 5-meri, pedicelli (1–) 2.4 mm longi, bracteolis 4–11(–18) mm longis oblongis vel anguste spatulatis usque ad anthesim persistentibus. Hypanthium (ad torum) 1–1.5 × 1–1.5 mm, lobis interioribus 1–1.5 mm altis rotundatis vel deltoideis, dentibus exterioribus acutis 0.5 mm longis. Petala 2–2.5 × 2 mm suborbicularia glabra. Stamina isomorphica glabra; filamenta 2.5 mm longa; antherarum thecae 0.5 × 0.25 mm apice late biporosae, connective sub loculis 0.5 mm prolongato dorsaliter ad basim (0.5 mm) hebeti-tuberculato. Stylus 2–2.5 × 0.5 mm glaber; stigma plus minusve clavatum.*

Shrub 1–3 m tall. Cauline internodes glabrous, glossy black and obscurely quadrangular when young, becoming brown and terete with age. Leaves firmly chartaceous, ciliate-serrulate (the trichomes mostly 0.5–1 mm long), (1.3–)2.5–4.2 cm long and 1.1–2.8 cm wide, elliptic, elliptic-obovate or sometimes varying to suborbicular, acuminate to acute apically and acute to obtuse basally, glabrous at maturity but caducously lepidote below and glabrous to sparsely brown furfuraceous above when young, 3-nerved, the secondaries conspicuous below and mostly 2 mm apart; petioles 7–16(–27) mm long and 1 mm broad. Inflorescence an erect, laxly branched, elongate panicle 3.5–8 cm long, exceeding foliage leaves borne at the node initiating the inflorescence; rachis glabrous, quadrate to ± rounded; bracteoles sessile, foliaceous, deciduous following anthesis and mostly absent on the infructescence, linear-oblong to narrowly spatulate, ± concave to navicular, 4–11(–18) mm long, 0.5–3 mm wide, glabrous above and below. Pedicels terete, glabrous, (1–)2–4 mm long. Hypanthia (at anthesis) glabrous, campanulate, 1–1.5 mm long to the torus and 1–1.5 mm broad distally. Calyx lobes (on fruiting hypanthia) erect to ascending, persistent, semicircular but varying to ± deltoid, entire, 1–1.5 mm long and 1–1.5 mm wide basally between sinuses; calyx teeth persistent, triangular, 0.5 mm long. Petals 5, antrorsely spreading, glabrous, ± concave, white to yellowish white, suborbicular, entire, 2–2.5 mm long, 2 mm wide. Stamens 10, isomorphic; filaments glabrous, subulate, white, distally incurved, 2.5 mm long; anthers about 0.5 mm long or less, 0.25 mm wide distally, white, ± cuneate, flared distally and terminated by a broad, ± ovoid, ventrally inclined pore; connective markedly thickened and prolonged (0.5 × 0.5 mm) below thecae, dilated dorsally into a blunt knobby protuberance. Ovary totally inferior. Style straight, glabrous, 2–2.5 mm long; stigma ± clavate. Berry deep purple to purple-black at maturity, 3.5–5 mm long to the torus, 3–4(–5) mm in diameter. Seeds ± pyriform, obscurely muriculate, mostly 1 mm long.

TYPES.—**Costa Rica.** Alajuela: wooded slopes of Volcán Poás about 12 km W of Varablanca, elevation ca. 2400 m, 21 Jan. 1968, *Wilbur & Stone 9845* (holotype: DUKE!; isotypes: CAS!, US!).

ADDITIONAL SPECIMENS EXAMINED.—**Costa Rica.** Alajuela: Volcán Poás, forest between crater and cold lake, *Davidse & Pohl 1169* (US); Volcán Poás, cloud forest along road 2.5–3.5 miles [4.0–5.6 km] W of Poasito, *Webster, Miller & Miller 12242* (DUKE, US); SE slope of Volcán Poás, *Hatheway 1388*

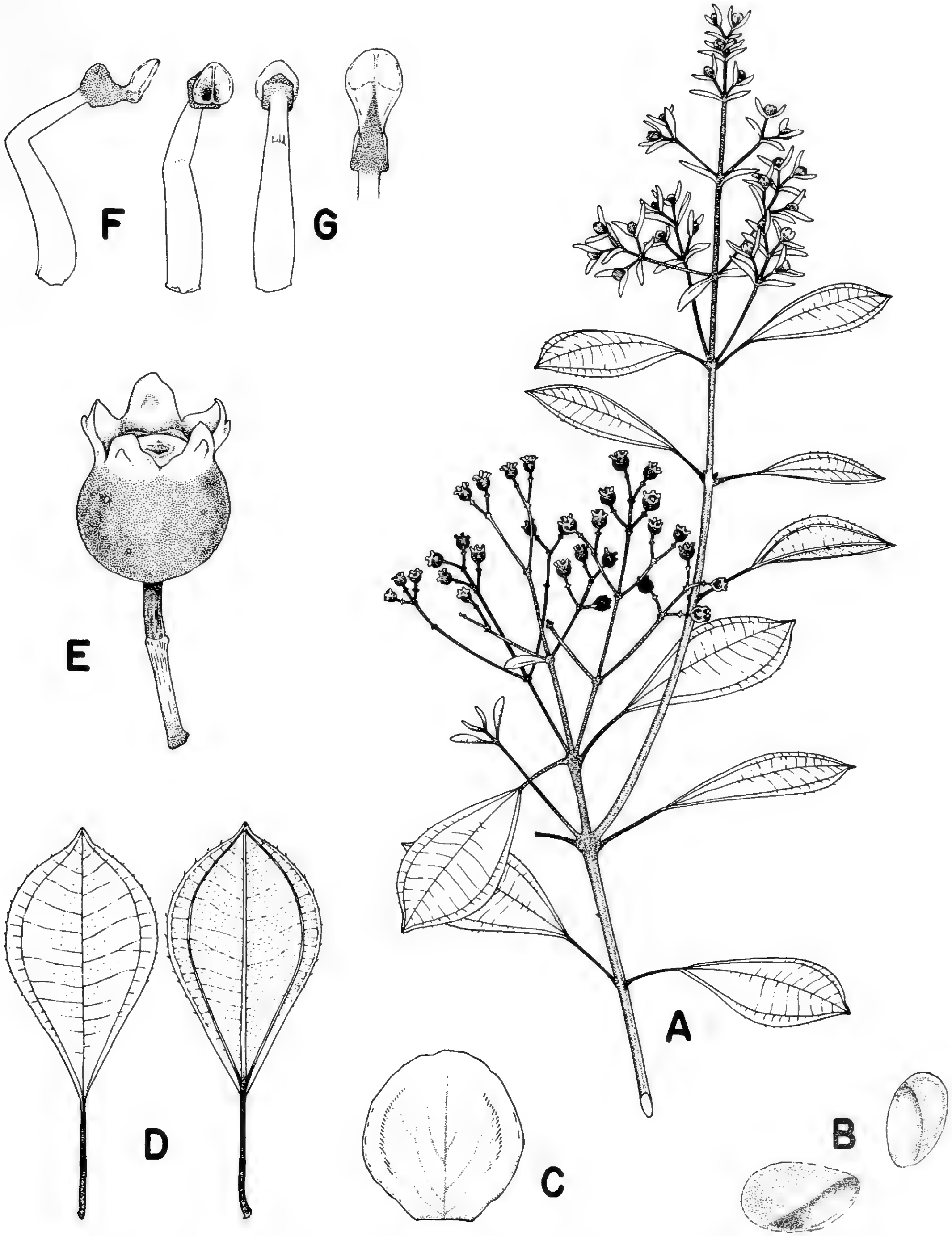


FIGURE 4. *Miconia longibracteata* Almeda. *A*, habit, × ca. ⅔; *B*, seeds, ×14; *C*, petal, ×9; *D*, representative leaves, upper surface (left) and lower surface (right), ×1; *E*, mature berry, × ca. 4; *F*, stamens, lateral view (left) and ¾ ventral view (right), ×10: *G*, stamens, dorsal view (left) and ventral view of anther and prolonged connective (right), ×10. (*A & D* from *Schnell 727*; *B, C, E–G* from *Wilbur & Stone 9845*.)

(DS, US). Cartago: El Empalme, *Schnell 727* (US—2 sheets); Talamanca Range, Panamerican Highway, *Carlson 3611* (US); El Cañon (Carretera Panamericana), *O. Jimenez 42* (US); La Chonta, *Schnell 725* (US); Panamerican Highway about 24 km W of Villa Mills, *Wilbur & Stone 8800* (DUKE); S of El Empalme, *A. Jimenez 1979* (US). Cartago/San José border: 6 km NW of Dos Amigos, *Wilbur & Luteyn 18321* (DUKE); 5 km NW of Ojo de Agua or 19 km SE of El Empalme, *Wilbur 28674* (DUKE); 5 km SE of Trinidad along Carretera Interamericana, *Wilbur 27780* (DUKE).

DISTRIBUTION.—Endemic to Costa Rica where it is presently known from the slopes of Volcán Poás and the Cordillera de Talamanca at elevations of 2000–3000 m. Available collections indicate that flowering and fruiting occurs sporadically throughout the year.

Among Costa Rican taxa of *Miconia*, this species is recognized by the combination of large foliaceous floral bracteoles, prevailingly glabrous foliage, suborbicular petals, and peculiar androecial morphology (see Fig. 4*F*). Staminal posture and morphology are best observed in pickled or boiled material hydrated with the aid of a wetting agent. Materials so treated show short, compressed, anther thecae terminating in a broad apical pore; the connective which is conspicuously thickened and prolonged below the thecae is narrowly triangular in ventral view, knobby and somewhat angulate in profile view, and ± horseshoe shaped in dorsal view. In many respects the elaborate connective is reminiscent of a pedestal providing anchorage and support for the anther. This distinctive anther morphology appears to represent an extreme in the evolutionary line that has led to great reduction in anther size. The very broad apical pores and pronounced geniculation of the filaments consistently bring anthers to an incurved position within the flower and may contribute to prevalent self-pollination.

In size and shape of floral bracteoles and anthers, *M. longibracteata* is most similar to *M. concinna* (also treated herein). The characters distinguishing these species are enumerated in the discussion under *M. concinna*. *Miconia longibracteata* also resembles *M. superposita* Wurdack in vegetative aspect. The latter, a Colombian species, differs in having squamulose pubescence on juvenile branchlets, shorter bracteoles (3.7 × 0.8 mm), and 4-celled anthers with the dorsal loculus of each theca overlapping but distal to the ventral one.

ACKNOWLEDGMENTS

I thank Terry Bell for preparing the line drawings, Dr. J. J. Wurdack for review of the manuscript, the Museo Nacional de Costa Rica and the Organization for Tropical Studies for logistical support, and curators of the following herbaria for special loans or use of their facilities: CR, DUKE, F, MO, US. This study was supported by U.S. National Science Foundation Grants DEB 76-83040 and DEB 78-25620.

LITERATURE CITED

GLEASON, H. A. 1958. Melastomataceae. Flora of Panama. Ann. Missouri Bot. Gard. 45:203–304.

PITTIER, H. 1924. New or little known Melastomataceae from Venezuela and Panama. II. J. Wash. Acad. Sci. 14:447–451.

STANDLEY, P. C. 1938. Flora of Costa Rica. Field Mus. Nat. Hist., Bot. Ser. 18(3):783–1133.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 11, pp. 315–322, 5 figs. June 24, 1981

STUDIES ON CAVE HARVESTMEN OF THE CENTRAL SIERRA NEVADA WITH DESCRIPTIONS OF NEW SPECIES OF *BANKSULA*

By

Thomas S. Briggs

Research Associate, Department of Entomology, California Academy of Sciences, San Francisco, California 94118

and

Darrell Ubick

Biology Department, San Jose State University, San Jose, California 95114

ABSTRACT: New ecological and biogeographic information on Sierra Nevada cave harvestmen in *Banksula* was obtained while environmental impact and mitigation work was being done for the Army Corps of Engineers New Melones Dam project. Isolation appears to be the principal factor leading to speciation in *Banksula*, but the distribution of species in the vicinity of the New Melones Reservoir is not readily explained. Four new species of *Banksula* are described: *B. rudolphi*, *B. martinorum*, *B. grubbsi*, and *B. elliotti*.

INTRODUCTION

Troglobitic organisms are scarce in California caves, possibly due to the relatively small size and geologic youth of these habitats. Laniatorid harvestmen of the genus *Banksula* are distinctive because they are relatively abundant obligate cavernicoles of the Calaveras Formation of the Sierra Nevada. Intensive collecting by biospeleological investigators contracted by the Army Corps of Engineers, the Fish and Wildlife Service, and the Office of Endangered Species has yielded numerous new records and four new species of *Banksula*. Project teams worked primarily in the vicinity of the New Melones Reservoir site on the Stanislaus River, Calaveras and Tuolumne counties, where several caves are threatened by completion of the New Melones Dam. Biological surveys were begun in May 1975 when a mine tunnel in limestone was selected for transplanting biota, including *Banksula grahami* and *B. melones*, from McLean's Cave, the largest of the threatened caves. As additional workers transplanted animal and plant life from McLean's Cave and studied other nearby caves, some distributional, behavioral, and ecological information were obtained which allow us to present some biogeographic discussion of *Banksula*.

Briggs (1974) reviewed and expanded the genus *Banksula* and described four species with functional eyes. He showed that the single previously known species, *Banksula californica* (Banks), lacked corneas and retinae. His contention that all *Banksula* are confined to caves is supported by all subsequent investigations. Only *Banksula melones*, which has relatively well-developed eyes, has been collected near or at the cave twilight zone. *Sitalcina sierra* Briggs and Hom is the only laniatorid harvestman found in epigean habitats adjacent to cave localities.

METHODS AND DEPOSITION

The structures measured and morphological terminology used in this paper are generally those described by Briggs (1968) for laniatorid harvestmen, with one modification that appears in this paper and in Briggs (1974): we substitute "second endites" for that portion of the second coxae previously referred to as the maxillary processes. Another structure, the labial process, first described by Briggs (1971), is located between the second endites.

Unless otherwise noted, all specimens recorded in this paper were preserved in ethyl alcohol and are deposited in the collection of the California Academy of Sciences.

Key to the Species of *Banksula*

1a. Operculum small, held almost entirely between mesal margins of fourth coxae; males with apex of aedeagus not enclosed in sheath, velum on dorsal plate smooth (*californica* group) 2
1b. Operculum large, with posterior margin well behind mesal extreme of posterior margin of fourth coxae; males with apex of aedeagus enclosed in sheath, velum on dorsal plate in transverse folds (*melones* group) 7

2a. Retinae entire; eye tubercle obliquely truncate in lateral view .... *B. galilei* Briggs
2b. Retinae absent or incomplete; if retinae present, eye tubercle a rounded cone .. 3

3a. Small spines or tubercles between principal dorsal spines on palpal femur; corneas absent .... *B. californica* (Banks)
3b. No small spines or tubercles between principal dorsal spines on palpal femur; corneas present or absent 4

4a. Proximal ventral spinose tubercle on palpal tibia equal to ventral spinose tubercle on patella; retinae absent; corneas present or absent 5
4b. Proximal ventral spinose tubercle on palpal tibia always smaller than ventral spinose tubercle on patella; retinae incomplete or absent; corneas present 6

5a. Submarginal row of tubercles on eighth tergite and last sternite .... *B. rudolphi* new species
5b. No submarginal rows of tubercles on tergites or sternites .... *B. martinorum* new species

6a. Eye tubercle a rounded cone; small spur ectal to proximal ventral spine on palpal femur; incomplete retinae usually present .... *B. tuolumne* Briggs
6b. Eye tubercle obliquely truncate in lateral view; no spur ectal to proximal ventral spine on palpal femur; retinae absent .... *B. grubbsi* new species

7a. First legs longer than 4 mm; retinal diameter greater than 0.03 mm; aedeagus and enclosing sheath fold anterior to recurved prongs of dorsal plate .... *B. melones* Briggs
7b. First legs shorter than 4 mm; retinal diameter less than 0.03 mm or missing; aedeagus and enclosing sheath held within bifurcate dorsal plate 8

8a. Eye tubercle and elevated area behind without tubercles; retinae present .... *B. grahami* Briggs
8b. Eye tubercle and elevated area behind tuberculate; retinae reduced or missing .... *B. elliotti* new species

Banksula rudolphi new species

(Figure 2)

HOLOTYPE.—Male. Body length 1.67 mm; scute length 1.40 mm; scute width 1.14 mm; eye tubercle length 0.23 mm; eye tubercle width 0.28 mm; operculum length 0.18 mm; operculum width 0.21 mm.

Palp: trochanter 0.19 mm, femur 0.79 mm, patella 0.44 mm, tibia 0.65 mm, tarsus 0.44 mm.

Leg II: trochanter 0.19 mm, femur 1.42 mm, patella 0.44 mm, tibia 1.26 mm, metatarsus 1.02 mm, tarsus 1.58 mm.

Scute with segmentation delineated by tubercles, eye tubercle and area behind tuberculate. Eye tubercle a rounded cone without retinae (some individuals also without corneas). Tergites with row of tubercles at margin, eighth tergite also with medial row of tubercles. Posterior

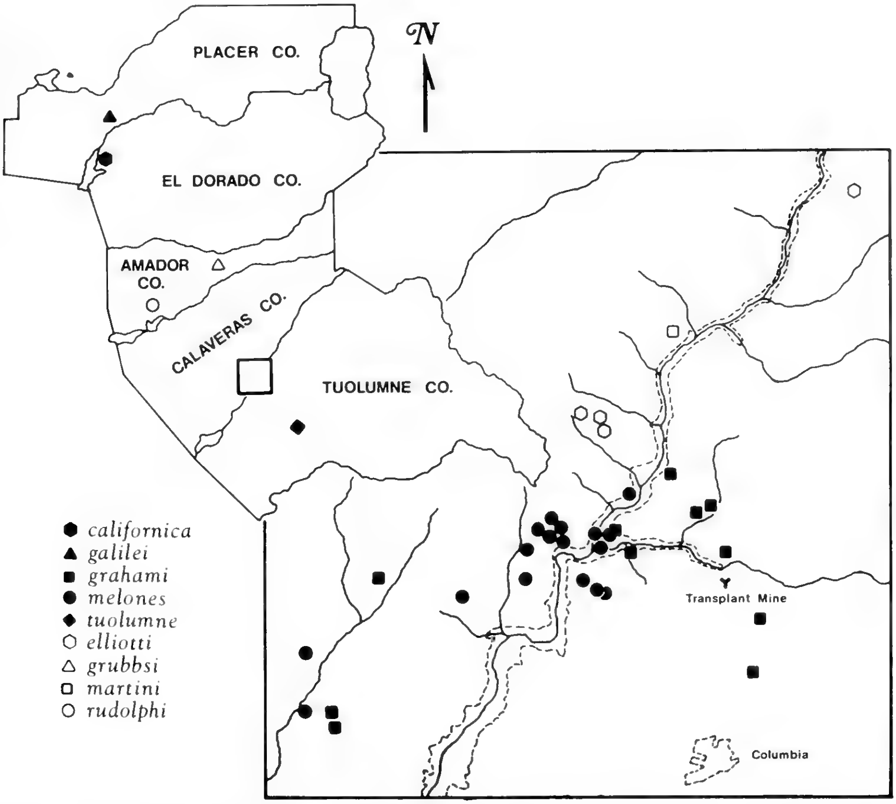


FIGURE 1. Map showing counties in the central Sierra Nevada where *Banksula* have been collected. The inset shows the region along the Stanislaus River where environmental impact and mitigation work on *Banksula* has been concentrated.

sternite with two rows of tubercles. Anal plate with medial tubercles. Second endites with concave ectal margin. Labial processes rounded. Operculum with narrow, rounded anterior; posterior margin adjacent to mesal extreme of posterior margin of fourth coxae.

Palpal femur with six prominent proximal dorsal spines (some individuals with only five spines) and one small distal dorsal spine; no setae or tubercles between dorsal spines; ectal spur at base of first ventral spine small and rounded; venter with numerous small tubercles. Proximal ventral tubercle on palpal tibia reduced, spine from tubercle absent. Ventral spine on palpal patella arising from a reduced tubercle.

Tarsal formula 4-6-5-6.

Body concolorous yellow-orange.

Penis typical of *californica* group (see Briggs 1974:11–12).

ALLOTYPE.—Female. Slightly smaller than holotype. Proximal ventral spinose tubercle on palpal tibia present, equal in size to robust ventral spinose tubercle on palpal patella. Operculum with truncate apex (rounded in some individuals); posterior margin behind mesal extreme of posterior margin of fourth coxae.

TYPE-SPECIMENS.—Holotype, allotype, 21 paratypes (9 ♂, 9 ♀, 3 juv.): Chrome Cave, near Jackson, Amador County, California, 5 Apr. 1979, D. C. Rudolph, S. Winterath, and B. Martin. Paratypes, 2 ♂, 2 ♀, 3 juv.: same locality, 21 Sep. 1980, T. S. Briggs and D. Ubick. Paratype, 1 ♂: same locality, 24 Jan. 1981, T. S. Briggs and D. Ubick.

ETYMOLOGY.—This species is named for biospeleologist D. Craig Rudolph.

ECOLOGICAL NOTES.—Chrome Cave is a small cave situated in about 0.02 km² of limestone. The outcrop is surrounded by serpentine which also forms much of the cave's walls. The humidity is relatively high and a mean temperature of 18 C was recorded on 24 January 1981. *Bank-*

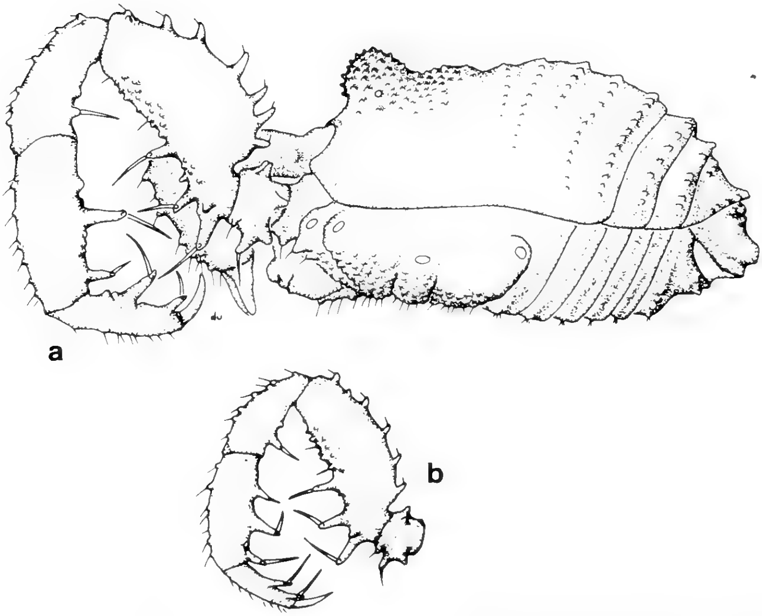


FIGURE 2. *Banksula rudolphi* Briggs and Ubick, new species. *a*. Lateral view of body and left palpus of male holotype; *b*. Lateral view of left palpus of female allotype.

sula rudolphi is found throughout the upper regions of the cave, predominantly on the undersides of rocks. Associated with *Banksula* is a rich assortment of predators, of which spiders (Araneae) are most abundant. We recorded the following species: *Archoleptoneta schusteri* Gertsch, *Liocranoides* sp., *Trogloneta paradoxa* Gertsch, and *Usofila* (*Telema*) sp. Of the other cavernicoles encountered, the most interesting were specimens of *Prokoenenia* sp. (Palpigradida).

Banksula martinorum new species

(Figure 3)

HOLOTYPE.—Male. Body length 1.75 mm; scute length 1.49 mm; scute width 1.23 mm; eye tubercle length 0.26 mm; eye tubercle width 0.33 mm; operculum length 0.18 mm; operculum width 0.19 mm.

Palp: trochanter 0.19 mm, femur 0.88 mm, patella 0.53 mm, tibia 0.65 mm, tarsus 0.42 mm.

Leg II: trochanter 0.21 mm, femur 1.81 mm, patella 0.39 mm, tibia 1.67 mm, metatarsus 1.23 mm, tarsus 2.37 mm.

Scute with segmentation delineated by small tubercles; eye tubercle and area behind slightly tuberculate. Eye tubercle subconical, without retinae or corneas. Tergites with submarginal row of tubercles. Second endites large, ectal margin slightly concave. Labial processes with acute anterior margin. Operculum with rounded anterior, posterior margin slightly behind mesal extreme of posterior margin of fourth coxae. First coxae with two prominent spinose tubercles. Anal plate smooth.

Palpal femur with five prominent proximal dorsal spines and two slightly smaller distal dorsal spines; no setae or tubercles between dorsal spines; ectal spur at base adjacent to second ventral spine. Proximal ventral spinose tubercle on palpal tibia equal to ventral spinose tubercle on patella.

Tarsal formula 4-6-5-6.

Body concolorous pale yellow.

Penis typical of *californica* group.

ALLOTYPE.—Female. Similar to male.

TYPE-SPECIMENS.—Holotype, allotype, 3 paratypes (1 ♀, 2 juv.): Heater Cave, 8 km N Columbia, Calaveras County, California, 15 Mar. 1979, D. C. Rudolph, B. Martin, and S. Winterath.

ETYMOLOGY.—This species is named for arachnologist Barbara Martin and for Army Corps of Engineers environmental planner Robert Martin.

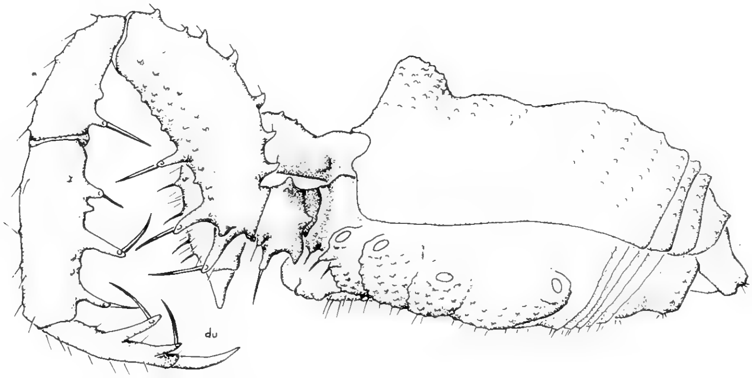


FIGURE 3. *Banksula martinorum* Briggs and Ubick, new species. Lateral view of body and left palpus of male holotype.

Banksula grubbsi new species
(Figure 4)

HOLOTYPE.—Male. Body length 1.49 mm; scute length 1.26 mm; scute width 1.23 mm; eye tubercle length 0.25 mm; eye tubercle width 0.35 mm; operculum length 0.18 mm; operculum width 0.21 mm.

Palp: trochanter 0.19 mm, femur 0.70 mm, patella 0.39 mm, tibia 0.53 mm, tarsus 0.65 mm.

Leg II: trochanter 0.18 mm, femur 1.49 mm, patella 0.44 mm, tibia 1.23 mm, metatarsus 0.96 mm, tarsus 1.49 mm.

Scute with segmentation delineated by small tubercles, area behind eye tubercle tuberculate. Eye tubercle obliquely truncate, declining posteriorly; entire surface tuberculate. Eyes with small corneas and no retinae. Tergites with submarginal row of tubercles. Second endites setose, with acute ectal invagination behind midpoint. Labial processes large, rounded. Small operculum with rounded anterior, margin adjacent to fourth coxae, posterior margin slightly behind mesal extreme of posterior margin of fourth coxae.

Chelicerae setose, only slightly tuberculate.

Palpal femur with four prominent proximal dorsal spines and three reduced distal dorsal spines; no setae or tubercles between proximal dorsal spines; ectal spur at base replaced by a broad, low tubercle; ventral margin straight. Palpal tibia without significant proximal ventral spine.

Tarsal formula 4-6-5-6.

Body concolorous light yellow.

Penis typical of *californica* group, aedeagal velum held in smooth dorsal plate.

TYPE-SPECIMEN.—Holotype: Black Chasm Cave, near Volcano, Amador County, California, 19 Feb. 1978, A. G. Grubbs.

FEMALE.—Unknown.

ETYMOLOGY.—This species is named for biospeleologist Andrew G. Grubbs.

Banksula elliotti new species
(Figure 5)

HOLOTYPE.—Male. Body length 1.61 mm; scute length 1.23 mm; scute width 1.28 mm; eye tubercle length 0.26 mm; eye tubercle width 0.35 mm; operculum length 0.30 mm; operculum width 0.32 mm.

Palp: trochanter 0.23 mm, femur 0.63 mm, patella 0.39 mm, tibia 0.53 mm, tarsus 0.39 mm.

Leg II: trochanter 0.16 mm, femur 1.14 mm, patella 0.35 mm, tibia 0.96 mm, metatarsus 0.72 mm, tarsus 1.14 mm.

Scute with segmentation delineated by tubercles, eye tubercle and area behind tuberculate. Eye tubercle rounded, slightly conical, with small corneas and without retinae. Tergites with row of tubercles at margin. Second endites setose, mesally broad and rounded; labial processes spatulate. Operculum large, extending posterior to hind coxae. Hind sternite and anal plate with row of tubercles. All coxae tuberculate.

Chelicerae with strongly tuberculate anterior margin.

Palpal femur with six prominent proximal dorsal spines and four reduced distal dorsal spines; no setae or tubercles between proximal dorsal spines; ectal spur well developed at base of

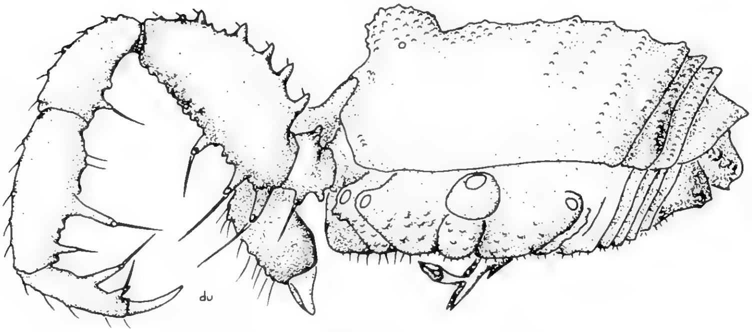


FIGURE 4. *Banksula grubbsi* Briggs and Ubick, new species. Lateral view of body and left palpus of male holotype.

proximal ventral spine, ventral surface tuberculate.

Tarsal formula 4-6-5-6.

Body concolorous yellow-orange.

Penis with folds at base of dorsal plate; apex of aedeagus enclosed in rounded sheath and held within distal bifurcation of dorsal plate.

ALLOTYPE.—Female. Similar to male.

TYPE-SPECIMENS.—Holotype, allotype, 4 paratypes (2 ♂, 1 ♀, 1 juv.): Pinnacle Point Cave, near Camp Nine Power House, 9.6 km N Columbia, Tuolumne County, California, 8 Feb. 1979, D. C. Rudolph, B. Martin, and S. Winterath. Paratypes, 2 ♂, 2 juv.: same locality, 20 Jan. 1978, W. Elliott, A. Grubbs, and S. Winterath. Paratypes, 2 ♂, 1 ♀: same locality, 1 May 1977, A. Grubbs, N. Boice, M. McEachern and J. Davis. Paratypes, 1 ♀: Digger Pine Cave, 6.5 km N Columbia, Calaveras County, 22 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell. Paratypes, 3 ♂, 5 ♀: Rabbit Hole Cave, 6.5 km N Columbia, Calaveras County, 22 Mar. 1979, D. Rudolph, B. Martin, and S. Winterath. Paratypes, 1 ♂, 1 ♀: Grapevine Gulch Cave, 6.5 km N Columbia, Calaveras County, 22 Nov. 1979, D. Rudolph, B. Martin, and S. Winterath. Paratypes, 1 ♂, 4 ♀: same locality, 27 Apr. 1977, B. Hawson, A. Grubbs, J. Munthe, and M. McEachern.

ETYMOLOGY.—This species is named for biospeleologist William R. Elliott.

VARIATIONS.—Specimens taken in Pinnacle Point Cave are without retinae, although half of the specimens taken in the remaining caves have retinal pigment in their eyes. The specimen from Digger Pine Cave has a relatively more conical eye tubercle. Some specimens have only three distal dorsal spines on the palpal femur.

Banksula grahami Briggs

Banksula grahami BRIGGS 1974:7.

RECORDS.—*Calaveras County:* Moaning Cave, near Vallecitos, 22 Aug. 1963, 22 Dec. 1968, 6 Dec. 1977, R. Graham, T. Briggs, W. Elliott, A. Grubbs, and S. Winterath; Linda's Cave, 6 km W Columbia, 16 May 1977, A. Grubbs, N. Boice, and D. Broussard; Carlow's Cave, 6 km W Columbia, 16 May 1977, A. Grubbs, N. Boice, and D. Broussard. *Tuolumne County:* Experimental Mine Cave, 3 km N Columbia, 25 Jun. 1975, R. Lem; Mine tunnel along road to Experimental Mine, 2.5 km N Columbia, 25 Jun. 1975, T. Briggs (identification only); Snell's Cave, 3 km N Columbia, 26 Feb. 1978, 14 Feb. 1978, 2 Apr. 1979, S. Winterath, D. Rudolph, and J. Reddell; Crystal Palace Cave, 5 km N Columbia, 4 Nov. 1967, 21 Dec. 1977, 4 Feb. 1979, 25 Mar. 1979, T. Briggs, V. Lee, D. Rudolph, S. Winterath, A. Grubbs, W. Elliott, B. Martin, and J. Reddell; Porcupine Cave, 5 km N Columbia, 4 Feb. 1979, 28 Feb. 1979, D. Rudolph, S. Winterath, and B. Martin; mine on ridge, 4.5 km N Columbia, 22 Feb. 1979, D. Rudolph, S. Winterath, and B. Martin; Banksula Cave, 6 km N Columbia, 21 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, and W. Elliott; McLean's Cave, 4.5 km N Columbia, 13 May 1967, 14 Dec. 1977, 18 Dec. 1977, 6 Mar. 1979, 27 Mar. 1979, 2 Apr. 1979, K. Hom, T. Briggs, W. Elliott, A. Grubbs, S. Winterath, D. Rudolph, and B. Martin; Transplant Mine, 3 km N Columbia, 17 Apr. 1979, D. Rudolph, S. Winterath, and E. vanIngen.

NOTES.—The migration of *Banksula grahami* into two of the mine tunnels recorded above is the only known example of probable interstitial movement by a species of *Banksula*.

Banksula melones Briggs

Banksula melones BRIGGS 1974:8.

RECORDS.—*Calaveras County:* Cave of Skulls, 5 km NW Columbia, 16 Apr. 1977, 29 Mar. 1979, T. Briggs, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Quail (Gerritt's) Cave, 5 km NW Columbia, 3 Jul. 1975, 17 Apr. 1977, 30 Mar. 1979, W. Rauscher, D. Cowan, B. Martin, and S. Winterath; Barren Cave, 5 km NW Columbia, 30 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Beta Cave, 5 km NW Columbia, 7 May 1977, 29 Mar. 1979, A. Grubbs, D. Broussard, S. Winterath, D. Rudolph, W. Elliott, J. Reddell, and B. Martin; Poison Oak Cave, 5 km NW Columbia, 29 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Coral Cave, 5 km N Columbia, 24 Feb. 1978, 22 Mar. 1979, A. Grubbs, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Bryden's Cave, 5 km NW Columbia, 29 May 1977, A. Grubbs and B. Hopkins; Cone Cave, 5 km NW Columbia, 30 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Reddell; Eagle View Cave No. 2, 5 km NW Columbia, 29 Mar. 1979, D. Rudolph, B. Martin, S. Winterath, W. Elliott, and J. Red-

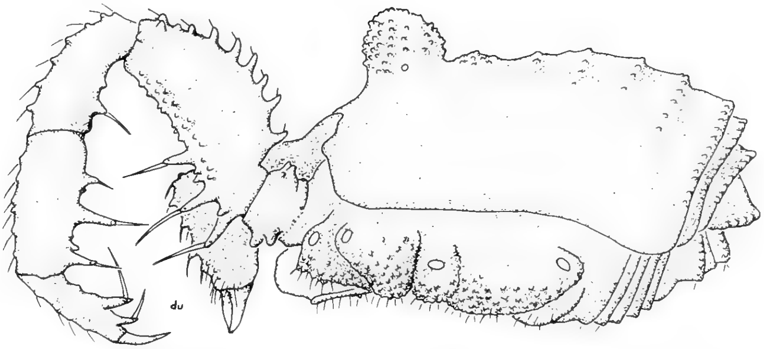


FIGURE 5. *Banksula elliotti* Briggs and Ubick, new species. Lateral view of body and left palpus of male holotype.

dell; Lost Piton Cave, 6.5 km W Columbia, 6 May 1977, 26 Mar. 1979, A. Grubbs, N. Boice, D. Broussard, S. Winterath, W. Elliott, and J. Reddell; Bone Cave, 6 km W Columbia, 20 Apr. 1980, T. Briggs and D. Ubick. *Tuolumne County:* Quarry (McNamee's) Cave, 3 km NW Columbia, 24 May 1969, G. Leung, W. Rauscher, and T. Briggs; Gate Pit Cave, 3 km NW Columbia, 1 Apr. 1979, D. Rudolph; Mine Cave, 3 km NW Columbia, 1 Apr. 1979, D. Rudolph, B. Martin, and S. Winterath; Scorpion Cave, 4.5 km N Columbia, 8 Feb. 1979, 25 Mar. 1979, D. Rudolph, S. Winterath, D. Cowan, and T. Briggs; Vulture Cave, 4.5 km N Columbia, 10 Feb. 1979, 17 Feb. 1979, 22 Feb. 1979, 19 Mar. 1979, S. Winterath, D. Rudolph, B. Martin, and W. Elliott; McLean's Cave, 4.5 km N Columbia, 13 May 1967, 17 June 1967, 24 June 1967, 14 Dec. 1977, 18 Dec. 1977, 6 Mar. 1979, 27 Mar. 1979, K. Hom, T. Briggs, V. Lee, W. Elliott, A. Grubbs, S. Winterath, D. Rudolph, and B. Martin; Transplant Mine, 3 km N Columbia, 17 Apr. 1979, D. Rudolph, S. Winterath, and E. vanIngen.

NOTES.—Some of the specimens collected in Vulture Cave and Bone Cave were found under rocks in the twilight zone. All other collections were made in permanently dark regions of caves.

ECOLOGICAL REVIEW

Several ecological studies on *Banksula* (Briggs 1975; Elliott 1978; Rudolph 1979) have been conducted in McLean's Cave at the confluence of the Middle Fork and the South Fork of the Stanislaus River (approximate elevation, 300 m). This cave is one of the largest in the Calaveras limestone of the central Sierra Nevada and contains the only sympatric populations of *Banksula* species. *Banksula melones* and *B. grahami* are mixed in habitats near the base of a broad talus cone formed by debris gradually moving through two small entrances to the lowest levels of the cave. Because there is no flowing water in the cave, the talus cone and deep-penetrating roots are important food sources for the inhabitants. The cave temperature ranges from 14 C to 16 C and the humidity from 82% to 97% (Elliott 1978). Specimens of *Banksula melones* and *B. grahami* were found under rocks or wandering on the floor or walls. They were rarely captured in baited pitfall traps (Briggs 1975; Elliott 1978). Although biased by more intensive winter collecting, records from McLean's and other caves suggest greatest activity in winter and spring.

At least 30 species of arthropods, most of which were listed by Elliott (1978), coexist with *Banksula melones* and *B. grahami* in McLean's Cave. Elliott (1978) identified some species, but many have not yet been identified. His feeding experiments showed that captive *Banksula*, kept in McLean's Cave, will eat live Collembola but not equally abundant Psocoptera. Rudolph (1979) maintained eight immature *Banksula* in McLean's Cave using Collembola as food; three molted within 43 days. One adult and two immature individuals maintained at the same time without food survived.

Rudolph (1979) searched the mine tunnel into which Briggs and Elliott transplanted *Banksula melones*, *B. grahami*, and miscellaneous arthropods from McLean's Cave. The transplanted population, which included a few hundred *Banksula*, appeared to be reproducing. The future of this transplant may depend on how well conditions in the mine duplicate conditions in McLean's Cave. If they both flourish, the transplanted *Banksula* species may demonstrate that their sympatry in a small cave is stable.

BIOGEOGRAPHY

The distribution of *Banksula* species is similar to the invertebrate troglobite distributions reported from caves in the Appalachian Mountains of the eastern United States in that these cave species tend to be bounded within "karst islands," within which subterranean dispersal and genetic communication readily occurs (Barr 1967; Culver et al. 1973). Such karst-island speciation exists for *Banksula* in the Sierra Nevada if the limestone outcrops are widely separated. Thus, the species *B. galilei* Briggs, *B. californica* (Banks), *B. rudolphi* new species, *B. grubbsi* new species, and *B. tuolumne* Briggs occupy karst that is separated by many kilometers of nonporous rock (Fig. 1). The isolation of these cave species is, therefore, more complete than that of the species in the Appalachian caves. The area of the karst in which *B. galilei*, *B. californica*, and *B. rudolphi* are found is 0.02–0.1 km^2 and is considerably smaller than the smallest karst island (10 km^2) studied in the eastern United States (Culver et al. 1973). Furthermore, quarrying shows that these small outcrops have small volume and little internal water flow.

All known *Banksula* species are allopatric except for *B. melones* and *B. grahami* in McLean's Cave. This suggests that sympatric species compete, and the sympatry in McLean's Cave is a result of a recent invasion. About half of the 70 or so Calaveras Formation caves carefully checked yielded a species of *Banksula*. Thirty-one of these are located in the karst of the Stanislaus River. Eighteen apparently habitable caves in this region did not contain *Banksula* (Rudolph 1979). The absence of harvestment in caves located in karst outside of the Stanislaus River region may be due to an uneven distribution of their epigean ancestors.

The distribution of the four species of *Banksula* (*B. melones*, *B. grahami*, *B. martinorum*, and *B. elliotti*) that occupy the karst of the Stanislaus region is not readily explained. Volcanic rock divides Coyote Creek (west of the Stanislaus River) from the Stanislaus River. It forms an irregular barrier between *B. elliotti* and *B. melones*, and separates *B. melones* from *B. grahami* southeast of the Stanislaus River. Several continuous bands of amphibolite divide the remaining limestone regions into parallel lenses in which allopatric populations of *B. melones* and *B. grahami* occupy most of the available caverns. These populations seem to split into eastern and western clusters that do not correlate well with geology or water systems. The karst that contains the easternmost population of *B. elliotti* is isolated by one kilometer of metavolcanic rock from the karst that contains the rest of *B. elliotti* and *B. martinorum*. Coyote Creek, the much larger Stanislaus River, and the south fork of the Stanislaus that branches to the east have no apparent effect on the distribution of species of *Banksula*. The four Stanislaus species show increasing cavernicolous specialization in relative eye loss, from *B. melones* with the largest eyes, to *B. elliotti* with missing retinae, and *B. martinorum* with complete eye loss. One might infer that adaptive radiation began with a *B. melones*-like ancestor and progressed to *B. elliotti*. If correct, one must explain how the increasingly troglobitic species *B. grahami* and *B. elliotti* were able to cross geologic and drainage barriers. Further studies on the harvestmen of the Stanislaus River region are needed to explain this unexpected distribution of species. It is regrettable that this portion of the river will soon be inundated by the New Melones Reservoir and some of the harvestmen caves will be lost.

LITERATURE CITED

BARR, T. C., JR. 1967. Observations on the ecology of caves. Am. Nat. 101(922):475–491.

BRIGGS, T. S. 1968. Phalangids of the laniatorid genus *Sitalcina* (Phalangodidae:Opiliones). Proc. Calif. Acad. Sci. 36(1):3–7.

———. 1971. Relict harvestmen from the Pacific Northwest. Pan-Pac. Entomol. 47(3):168–169.

———. 1974. Phalangodidae from caves in the Sierra Nevada (California) with a redescription of the type genus. Occas. Pap. Calif. Acad. Sci. 108:1–15.

———. 1975. Biological transplant project, New Melones Lake, California—final report. Serial #DACW05-75-P-1845, U.S. Army Corps of Eng., Sacramento Dist., Calif.

CULVER, D., J. R. HOLSINGER, AND R. BAROODY. 1973. Toward a predictive cave biogeography: the Greenbrier Valley as a case study. Evolution 27(4):689–695.

ELLIOTT, W. R. 1978. Final report on the New Melones cave harvestman transplant. Contract #DACW05-78-C-0007, U.S. Army Corps of Eng., Sacramento Dist., Calif.

RUDOLPH, D. C. 1979. Final report on the status of the Melones cave harvestman in the Stanislaus River drainage. Contract #14-16-0009-79-009, U.S. Fish Wildl. Serv., Wash. D.C.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 12, pp. 323–339, 34 figs. June 24, 1981

TROPICAL EASTERN PACIFIC LIMPETS OF THE FAMILY ACMAEIDAE (MOLLUSCA, ARCHAEOGASTROPODA): GENERIC CRITERIA AND DESCRIPTIONS OF SIX NEW SPECIES FROM THE MAINLAND AND THE GALÁPAGOS ISLANDS

By

David R. Lindberg*

Center for Coastal Marine Studies, University of California,
Santa Cruz, California 95064

and

James H. McLean

Section of Malacology, Natural History Museum of Los Angeles County,
Los Angeles, California 90007

Abstract: We define genera on conservative shell structure characters and on qualitative radular characters. *Lottia*, previously considered monotypic, is expanded to include Panamic species with a secondary gill (branchial cordon) formerly assigned to *Scurria*. *Scurria* has a similar gill, but the shell structure differs. The new species *Notoacmea ubiquita* from Mexico and *N. pumila* from Ecuador are small-shelled allopatric species with radular teeth modified for feeding on coralline algae. Two new species of *Notoacmea* (*N. rothi* and *N. immaculata*), endemic to the Galápagos Islands, constitute a species pair differing chiefly in radular features: the radular teeth of *N. immaculata* are adapted for feeding on calcareous algae; those of *N. rothi* for noncalcareous algae. A pair of endemic new species of *Lottia* from the Galápagos Islands (*L. mimica* and *L. smithi*) also differ mainly in radular characters. *Lottia mimica* is a noncalcareous-alga feeder and *L. smithi* is a calcareous-alga feeder. These four endemic species are the principal acmaeid limpets of the Galápagos. Two mainland species, *Notoacmea filosa* and *Lottia mesoleuca*, are known only sporadically from the Galápagos Islands.

Introduction

The last comprehensive, illustrated review of the Acmaeidae of the tropical eastern Pacific was given by McLean (1971). At the time of preparation of that account, two of the species described herein—*Notoacmea ubiquita* and *Lottia mimica*—were recognized as new but were not described. The generic placement of these two species was puzzling because they had previously unknown combinations of radular, shell, and gill characters.

Further study of generic relationships has now provided a basis for the convincing allocation of these species. Although a full review of generic

---

* Research Associate, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118.

criteria in the family is beyond the scope of this paper, we include some discussion pertaining to the Panamic species. A major distinction has become apparent between *Lottia* Sowerby, 1834, and *Scurria* Gray, 1847, two genera having a secondary gill (accessory gill lappets on the mantle margin). These two genera are redefined here, the name *Lottia* thus being made available for use for some tropical species previously considered to belong to *Scurria*.

A closer examination of the acmaeids of the Galápagos Islands has resulted in the recognition of four new endemic species, representing two species pairs wherein the principal differences are in radular tooth morphology. The shell characters of each pair are insufficiently distinct to permit reliable identification by shell alone. Radular characters in the Acmaeidae have been found by all workers to be species-specific. In no species has ontogenetic or situs variation in radulae been found. Similar shell morphologies have been reported, however, in both congeneric and noncongeneric species of Acmaeidae (McLean 1966; Lindberg 1979). We therefore consider each radular morphotype to represent a separate species. Because the shell characters of each pair are insufficiently distinct to permit reliable identification, both species are discussed in a combined discussion section following their formal descriptions.

Abbreviations are as follows: AHF, Allan Hancock Foundation, University of Southern California, Los Angeles (collection on loan to LACM); AMNH, Department of Invertebrates, American Museum of Natural History, New York; ANSP, Department of Malacology, Academy of Natural Sciences, Philadelphia; CAS, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco; LACM, Section of Malacology, Natural History Museum of Los Angeles County, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; SU, Stanford University, Stanford (collection on loan to CAS); USNM, Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C.

Generic Criteria for the Panamic Acmaeidae

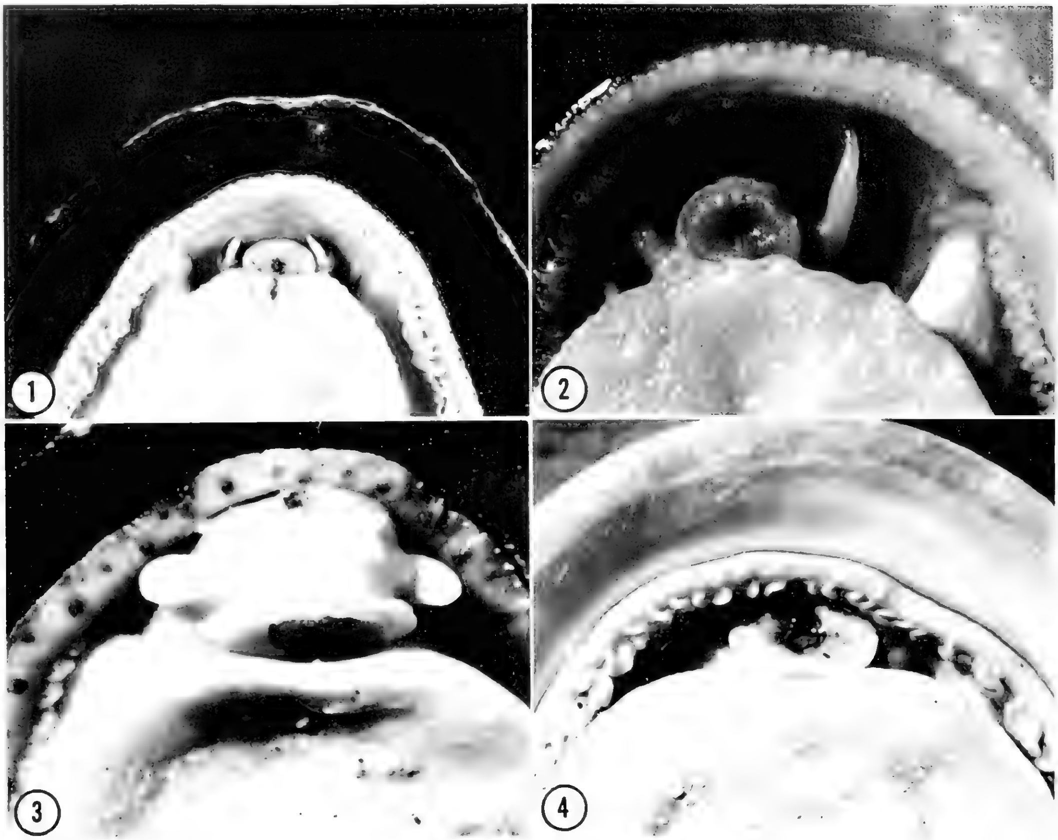
Generic assignments in McLean's (1971) review were based on shell sculpture, presence or absence of the secondary gill, and whether marginal radular teeth are represented by two pairs of fully developed teeth, a single pair of rudimentary teeth (uncini), or are absent altogether. We now realize that a system based on these three characters alone is not adequate.

Christiaens (1975) proposed a generic classification of the Acmaeidae in which tooth shape and configuration were especially emphasized. He felt some genera had three pairs of lateral teeth and some two, the latter group having a bicuspid second lateral tooth. We maintain that all acmaeids have three pairs of lateral teeth. We fail to see how the third lateral tooth can be interpreted as part of the second, because in all acmaeid radulae we have examined, we find that the ventral plates of the radular ribbon have three lateral plate components, one corresponding to each lateral tooth. We believe that the reduction of the outermost tooth that occurs in some species is a result of dietary specialization. Relation of diet to tooth shape was discussed by McLean (1966), and we are now aware of similar tooth shape and configuration in species of diverse genera. We do not consider lateral tooth shape to be useful as a generic character.

We continue to maintain full generic separation of species groups in which the marginal teeth have three possible expressions: (1) two pairs of fully functional marginals (*Patelloida* Quoy and Gaimard, 1834); (2) a single pair of marginal remnants or uncini (*Collisella* Dall, 1871; *Lottia* Sowerby, 1834; *Scurria* Gray, 1847); and (3) no marginals or uncini (*Acmaea* Eschscholtz, 1833; *Notoacmea* Iredale, 1915; *Problacmaea* Golikov and Kussakin, 1972; *Rhodopetala* Dall, 1921; and *Tectura* Gray, 1847). We therefore disagree with Christiaens's ranking of *Notoacmea* as a subgenus of *Collisella*.

Recent work by Lindberg (1976, 1978) has employed shell structure characters first used for patellacean limpets by MacClintock (1967). We believe that the relationships suggested by shell structure are conservative and are basic to a modern classification of the family.

We are now inclined to define genera using shell structure, branchial characters, radula basal plate structure, and the three possibilities for marginal teeth listed above, recognizing that shell sculpture characters are convergent in all genera and that lateral tooth shape is likewise



FIGURES 1–4. Ventral views of preserved specimens of *Lottia* and *Scurria* species showing secondary gill in relation to head. FIGURE 1. *Lottia gigantea*, Isla de Guadalupe, Mexico (LACM 55618). FIGURE 2. *Lottia mesoleuca*, Bahía Tenacatita, Jalisco, Mexico (LACM 66-55). FIGURE 3. *Lottia mimica* new species, paratype, Academy Bay, Isla Santa Cruz, Galápagos Islands, Ecuador (LACM 1926). FIGURE 4. *Scurria scurra*, Punta El Lacho, Santiago Province, Chile (LACM 75-32).

convergent and widely variable interspecifically (although not intraspecifically).[1]

Acmaea and *Notoacmea* differ in lateral plate morphology. In *Acmaea* the lateral plates are similar in size and shape and are arranged in a posteriorly diverging V-configuration. In *Notoacmea* the lateral plates are unequal in size and shape—the first and second lateral plates tend to lie in the same line and the third lateral plates are always lateral and slightly posterior to the second lateral plates.

Acmaea and *Tectura* also differ in lateral plate morphology. In both genera dentition consists of three pairs of equal-sized and equal-shaped lateral teeth; however, in *Tectura* the lateral plates that support these teeth are complex and similar in shape and position to those found in the genus *Collisella*.

All species of *Acmaea* are known to feed on coralline algae and have blunt, equal-sized teeth. Some of the tropical eastern Pacific and Caribbean species of *Notoacmea* are now known to have teeth similarly blunt and of equal size. These species may also be coralline alga feeders. Three of the four new species of *Notoacmea* described in this paper (*N. ubiquita*, *N. pumila*, and *N. immaculata*) have blunt equal-sized lateral teeth. The other new species of *Notoacmea*, *N. rothi*, has the outermost lateral tooth

---

[1] In his discussion of *Notoacmea fascicularis* (Menke, 1851) McLean (1971:327) alluded to two different radular types within that species, suggesting that a "complex involving more than one species" was a possibility. Lindberg will report separately on the two species of the *N. fascicularis* complex.

greatly reduced and the first two pairs more elongate, which is the pattern characteristic of most temperate and tropical species of *Notoacmea*.

Similar modification of the lateral teeth for feeding on coralline algae is known in some tropical species of *Collisella*. Eastern Pacific species of this uncinate genus with lateral teeth so modified are: *C. atrata* (Carpenter, 1857), *C. discors* (Philippi, 1849), *C. mitella* (Menke, 1847), and *C. pediculus* (Philippi, 1846).

Two generic names have been used for acmaeid limpets in which there is a secondary gill (branchial cordon) in addition to the normal acmaeid ctenidium: *Lottia* Sowerby, 1834 (type-species *L. gigantea* Sowerby, 1834), and *Scurria* Gray, 1847 (type-species *Patella scurra* Lesson, 1830). *Lottia* has usually been considered monotypic, with the single Californian species *L. gigantea*. It has been diagnosed (Dall 1871) as having a secondary gill incomplete or interrupted in front of the head, whereas in *Scurria* the gill is complete or continuous. The radular dentition in both genera consists of three pairs of lateral teeth and one pair of uncini.

We have examined the secondary gill in living and preserved specimens of *L. gigantea* and find that many specimens have a greatly reduced but distinct gill in front of the head (Fig. 1). The secondary gill of a tropical eastern Pacific species usually assigned to *Scurria*, *S. mesoleuca* (Menke, 1851), is normally much less prominent in front of the head than along the sides (Fig. 2). The secondary gill of *Lottia mimica*, new species (Fig. 3), is also much reduced in front of the head. The secondary gill of *Scurria scurra* (Fig. 4) is complete over the head, but it is also somewhat reduced in prominence in this region. We therefore do not regard the reduction of the secondary gill near the head as a useful generic character.

MacClintock (1967) found that *Scurria* in the Peruvian faunal province differ in shell structure from other eastern Pacific species with the secondary gill. The Peruvian *Scurria* species are in MacClintock's shell structure "group 3," whereas *Lottia gigantea* and the two species placed by McLean (1971) in *Scurria* (*S. mesoleuca* and *S. stipulata* (Reeve, 1855)) are in shell structure "group 1" (along with most other species of *Collisella* and *Notoacmea*). Because we believe that shell structure is more conservative than branchial characters, and we place even less emphasis on shell sculpture and coloration, we infer that the Panamic acmaeids previously assigned to *Scurria* are more closely related to *L. gigantea* than to *Scurria*. The two Panamic species plus *L. mimica* and *L. smithi* described in this paper are therefore assigned to *Lottia*. *Lottia* is redefined to include uncinate species in shell structure "group 1," with a secondary gill that is usually reduced but not necessarily absent over the head.

NEW SPECIES OF ACMAEIDAE FROM THE TROPICAL EASTERN PACIFIC

Notoacmea ubiquita new species

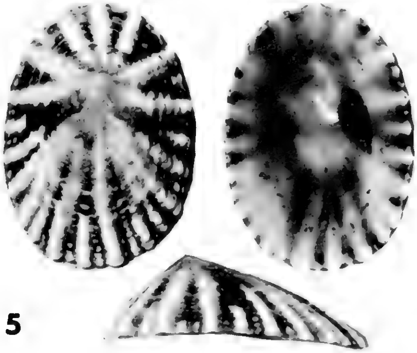
(Figures 5–7, 23, 29)

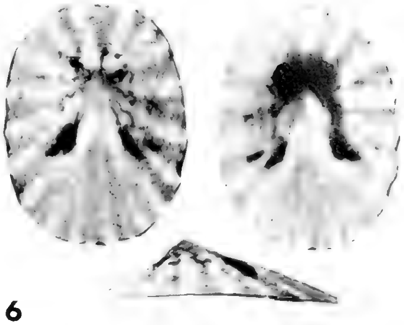
There are two situs forms of this species, a laterally compressed form and an oval form. A description for each follows.

Shell (oval form) (Figs. 5, 6): Relatively small (maximum length 12 mm), profile of medium height; apex anterior to center; all slopes convex; large shells frequently with a flattened area posterior to apex; sides of shell somewhat parallel. Sculpture of rounded radial ribs, with weaker secondary ribs beginning below apex; ribs extending slightly beyond the shell edge, crenulating the aperture; concentric sculpture of well-defined but nearly microscopic, sharply raised ridges. Exterior translucent white with red-brown markings on early shell, the markings becoming darker, reticulate, and limited to rib-interspaces with growth; ribs white, overlain with dark brown radial markings that may be concentrated into lateral rays. Interior margin white with dark markings that correspond to exterior interspaces; intermediate area white; central area with yellow stain, exterior markings visible through shell.

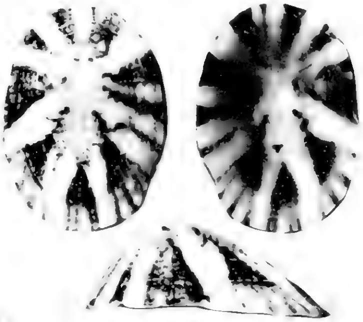
Shell (compressed form) (Fig. 7): Lateral profile high, ends raised relative to sides; all slopes convex; some specimens compressed in early stage, changing abruptly to oval form. Sculpture and coloration as in oval form.

Radula (Figs. 23, 29): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges straight to slightly concave, cusps rounded, blunt; second pair of lateral teeth posterior and lateral to first pair, medial and lateral edges convex, cusps rounded, blunt; third lateral teeth lateral to sec-

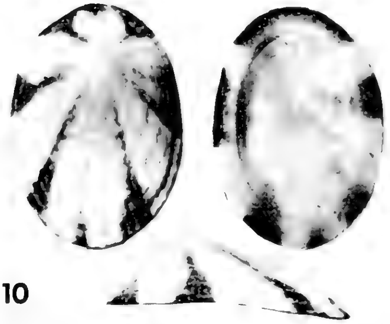

5


6


7


8


9


10

FIGURES 5–10. FIGURE 5. *Notoacmea ubiquita* new species. Holotype, LACM 1917. Santiago Peninsula, Colima, Mexico. Length 11.7 mm. FIGURE 6. *Notoacmea ubiquita.* LACM 54773. Guaymas, Sonora, Mexico. Length 6.9 mm. FIGURE 7. *Notoacmea ubiquita.* LACM 54773. Guaymas, Sonora, Mexico. Length 5.4 mm. FIGURE 8. *Notoacmea pumila* new species. Holotype, LACM 1919. Punta Ancon, Ecuador. Length 4.7 mm. FIGURE 9. *Notoacmea pumila.* Paratype, LACM 1920. Punta Ancon, Ecuador. Length 3.6 mm. FIGURE 10. *Notoacmea pumila.* LACM 72-17. Bahía Jobo, Costa Rica. Length 5.6 mm.

ond pair, medial edges concave, lateral edges straight, extending to edges of ventral plates, cusps blunt. Marginal teeth lacking. First lateral plates overlap anterior ribbon segment, posterolateral edges concave; second lateral plates irregular, posterior edges convex; third lateral plates lobate with lateral lobes extending to edges of ventral plates; second and third lateral plates separated by a partial suture. Ventral plates closely set with both anterior and posterior processes.

Animal: Pigmentation lacking, snout with oral lappets.

HOLOTYPE DIMENSIONS.—Length 11.7, width 8.1, height 3.6 mm.

TYPE-LOCALITY.—Mexico: Colima; Manzanillo, Santiago Peninsula, Playa Las Hadas (19°05′57″N, 103°19′36″W) (LACM 63-10), intertidal zone to 5 m. *Leg.* J. H. McLean and C. Tenney, 21–24 Mar. 1963, 3 specimens.

TYPE-MATERIAL.—Holotype (oval form), LACM 1917; 2 paratypes, LACM 1918 (both oval and compressed forms). The holotype is the largest specimen examined.

DISTRIBUTION.—Baja California Sur, Mexico, from Punta Pequeña (26°14′N) (LACM 71-6) to Bahía Magdalena and Cabo San Lucas, north in the Gulf of California to Puertecitos (30°25′N) (LACM 65-34) and Guaymas, south to Bahía Tangola Tangola, Oaxaca (15°45′N) (AHF 215).

MATERIAL EXAMINED.—58 lots, approximately 350 specimens, 3 radula preparations.

ETYMOLOGY.—The name is based on the Latin adverb *ubique* (everywhere). The species is indeed ubiquitous—shells, at least, have been recovered from sediment residues taken by divers from nearly all LACM station localities throughout the range.

DISCUSSION.—Although *Notoacmea ubiquita* has been known for many years, it was not described earlier because of uncertainties about its generic position. Its shell shape and sculpture suggested *Collisella*, and its lack of uncini and subtidal habitat suggested *Acmaea*. We are now satisfied to place it in *Notoacmea* because of the basal plate configuration. Although most species of *Notoacmea* are finely ribbed, the rather more prominent ribbing of *N. ubiquita* is not as strong as occurs in many species of *Collisella*.

Notoacmea ubiquita is the only Panamic acmaeid with an oval form and a laterally compressed form. *Notoacmea ubiquita* has broader, stronger ribs than any other tropical species of *Notoacmea*. On the basis of shell characters, it is more similar to some of the Panamic *Collisella*, which differ in having an uncinate radula. The fine brown concentric markings of the early stages do not occur in any other species. *Collisella turveri* (Hertlein and Strong, 1951) differs in having broader, more projecting ribs. *Collisella acutapex* (Berry, 1960) has a higher shell profile with sharper, more prominent ribbing, and its pattern of brown lines is more coalescing. *Collisella mitella* (Menke, 1847) also has white ribs, but its ribs are more numerous and the interspaces are dark colored. *Patelloida semirubida* (Dall, 1914) has sharper radial and concentric sculpture, with red rather than brown markings; its radula is also markedly different, having two pairs of marginal teeth per ribbon segment.

Large lots show a complete series of possible shell shapes between the elevated narrow forms with raised ends and the low oval forms. Some shells have an early compressed phase, with later growth stages like the oval form; some relatively large shells are angulate at the sides, giving the shell a flat-topped appearance. Color variation is relatively minor; one color variant characteristic of specimens from Jalisco is ordinary in early stages, changing to solid maroon at later stages. Largest shells seen are from Jalisco and Colima; specimens from localities in the Gulf of California attain about two-thirds the size of southern specimens.

Notoacmea ubiquita has features in common with two more northern species, *Collisella triangularis* (Carpenter, 1864) and *Tectura rosacea* (Carpenter, 1864), both of which differ in lacking the radial ribbing. All three species have laterally compressed forms, are primarily subtidal, and have equal-sized lateral teeth adapted for feeding on calcareous algae. In *C. triangularis* the compressed form predominates, whereas in *T. rosacea* the oval form is more abundant, but in both species the compressed forms occur on branching coralline algae and the oval forms occur on crustose coralline algae, and all intermediate conditions are known. Although we have not directly observed the compressed form of *N. ubiquita* on branching coralline algae, it probably so occurs, judging from its ability to change from compressed to oval during growth, which implies a change of situs.

Notoacmea pumila new species

(Figures 8–10, 24, 30)

Shell (Figs. 8–10): Small (maximum length 7 mm); profile medium-high; apex anterior to center; anterior slope straight to convex, lateral slopes convex; usually encrusted with coralline algae. Sculpture of fine, sharp radial ribs originating below apex, secondary ribs arising in the interspaces, not reaching thickness of primary ribs. Aperture oval, not crenulate. Color pattern independent of ribbing: most frequently white near apex, gray at margin, with 6 to 10 white rays in a stellate pattern, some rays not reaching margin; some specimens with fine brown lines bordering white rays and fine brown lines that produce a concentric network. Interior translucent white, showing the exterior pattern.

Radula (Figs. 24, 30): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges concave, cusps rounded. Second pair of lateral teeth posterior to first pair, medial edges convex, lateral edges straight, cusps rounded. Third pair of lateral teeth positioned posterior and lateral to second pair, medial edges convex, lateral edges straight to slightly concave. Third laterals broader than second laterals, with lateral extensions to edges of ventral plates; cusps rounded. Marginal teeth lacking. First lateral plates irregular, anterior portions overlapping anterior ribbon segments; second lateral plates elongate, ovoid; third lateral plates triangular, with convex posterior edge. Ventral plates with strong anterior and posterior processes. Lateral portions with strong sutures parallel to edges.

Animal: Pigmentation lacking, oral fringe simple.

HOLOTYPE DIMENSIONS.—Length 4.7, width 3.3, height 2.0 mm.

TYPE-LOCALITY.—Ecuador: Santa Elena Peninsula; Punta Ancon, north and south sides (2°20′S, 80°54′W), intertidal zone. *Leg.* J. H. McLean and D. Shasky, 6–7 Mar. 1970 (LACM 70-11, 70-12), 72 LACM specimens, 12 Shasky specimens.

TYPE-MATERIAL.—Holotype, LACM 1919, paratypes, LACM 1920; paratypes have also been deposited in the collections of CAS and USNM, and in Shasky collection (Redlands, California).

DISTRIBUTION.—El Velero, Nicaragua (12°01′N) (LACM 74-86), south to Ecuador (type-locality). There are numerous dead specimens from Bahía Salinas, Costa Rica (11°02′N, 85°45′W) (LACM 72-17, 72-19); two specimens only from Panama at San Carlos (8°29′N, 79°57′W) (LACM 75-55), and a number of localities in Ecuador collected by D. Shasky.

MATERIAL EXAMINED.—19 lots, approximately 200 specimens, 3 radula preparations.

ETYMOLOGY.—The name is a Latin adjective, *pumilus,* meaning small or dwarfish—fitting for this, the smallest tropical eastern Pacific member of the family.

DISCUSSION.—*Notoacmea pumila* could be confused only with two other relatively small forms, *N. ubiquita* new species and *Patelloida semirubida*. It differs from the first in having much sharper ribbing and not being compressed. Although both *N. pumila* and *P. semirubida* have fine sharp radial ribs, *N. pumila* lacks the sharp concentric sculpture and pink markings of *P. semirubida*.

The radula of *N. pumila* is similar to that of two new species described herein, *N. ubiquita* and *N. immaculata*. It differs from both by having a complete rather than partial suture between the second and third lateral plates and having strong ventral plate sutures parallel to the lateral edges. The ventral plates of *N. pumila* have anterior and posterior processes which *N. immaculata* lacks, and the third lateral plates are triangular rather than biformed as in *N. immaculata* and *N. ubiquita*. The radula of *N. pumila* differs from that of *P. semirubida* by lacking marginal teeth.

Large lots show similar color patterns both in the material from Costa Rica and from stations in Ecuador. A small percentage of specimens change with growth from dark rayed to solid dark (see Fig. 9); fewer specimens are rayed only with brown linear markings and fine brown reticulate markings. Shell proportions vary only slightly.

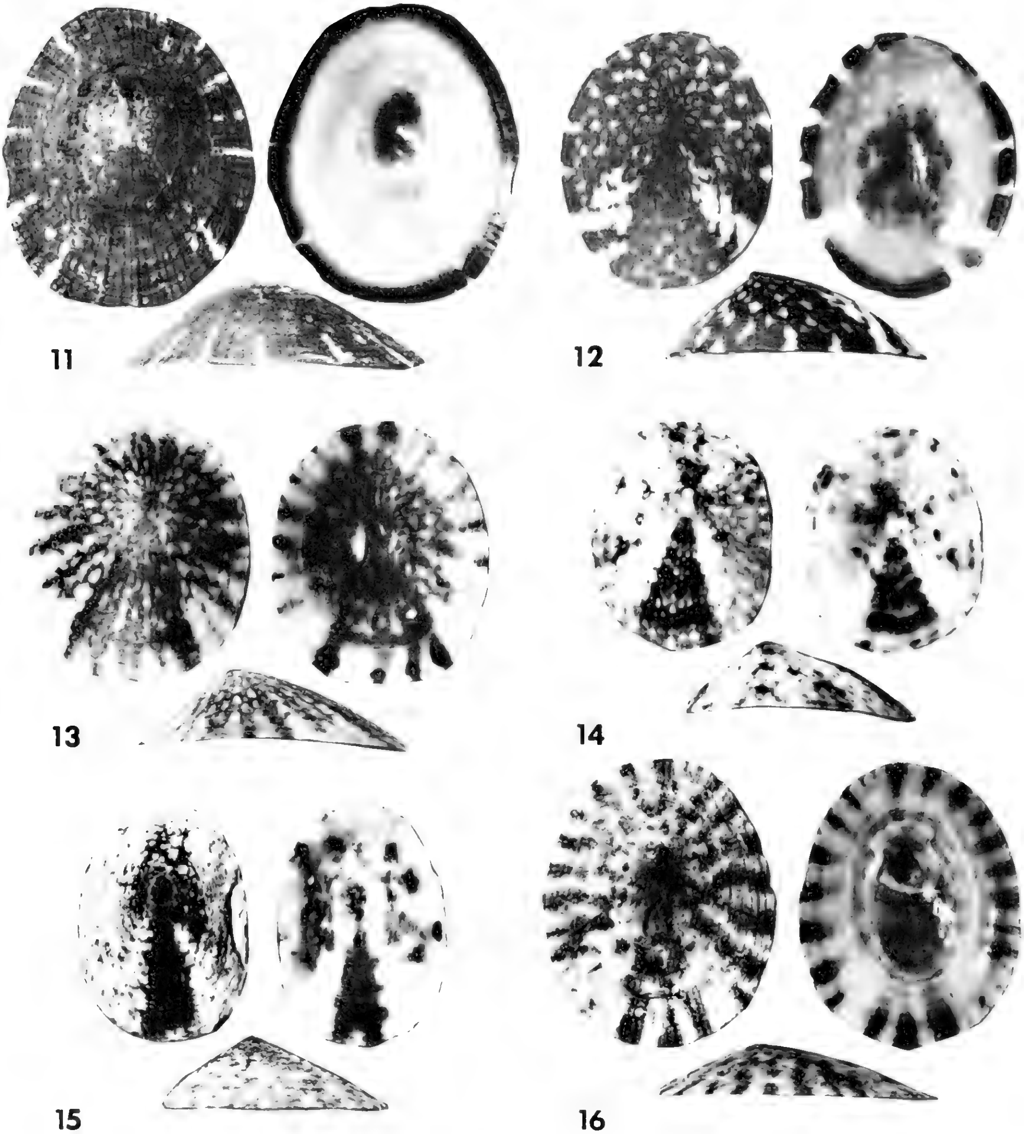
Notoacmea pumila undoubtedly feeds on coralline algae—the lateral teeth are blunt and of equal size. Living specimens have been collected in the low intertidal zone and the species probably also occurs in the immediate subtidal zone on coralline-encrusted rocks.

Notoacmea rothi new species

(Figures 11–13, 25, 31)

Shell (Figs. 11–13): Size medium (maximum length 20 mm), height medium; apex anterior to center; all slopes convex, aperture ovoid. Sculpture of unequal riblets and concentric growth lines; one to three secondary riblets between each two primary riblets. Exterior dark gray with scattered white markings; apical pattern tessellate; white markings often aligned in lateral rays that define a broad, dark posterior ray. Interior margin broad, dark, streaked with white corresponding to exterior pattern; intermediate area blue-white; central area blue-white with brown stain.

Radula (Figs. 25, 31): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges slightly con-



FIGURES 11–16. *Notoacmea* from the Galápagos Islands. FIGURE 11. *Notoacmea rothi* new species. Holotype, LACM 1921. Wreck Bay, Isla San Cristóbal. Length 16.8 mm. FIGURE 12. *Notoacmea rothi*. LACM 54774. East side, Isla Fernandina. Length 11.5 mm. FIGURE 13. *Notoacmea rothi*. LACM 54777. Bahía Cartago, Isla Isabela. Length 8.8 mm. FIGURE 14. *Notoacmea immaculata* new species. Holotype, LACM 1923. Isla Baltra. Length 5.6 mm. FIGURE 15. *Notoacmea immaculata*. AHF 173-34. Isla Baltra. Length 7.8 mm. FIGURE 16. *Notoacmea filosa* (Carpenter, 1865). LACM 54775. Isla San Cristóbal. Length 15.5 mm.

cave, rounding to pointed cusps. Second pair of lateral teeth lateral to first pair, both edges convex, broad, with pronounced pointed cusps; third lateral teeth lateral to second pair, reduced, medial edges convex, lateral edges straight, cusps angular. Marginal teeth lacking. First lateral plates subrectangular; second lateral plates rounded, separated from third lateral plates by partial suture; third lateral plates biformed, posterior section rounded, lateral section pointed, extending to lateral edges of ventral plates. Ventral plates closely set, subrectangular, with weak anterolateral extensions.

Animal: Body pigmentation lacking; snout with oral lappets.

HOLOTYPE DIMENSIONS.—Length 16.8, width 14.0, height 4.8 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla San Cristóbal, Wreck Bay (0°54′S, 89°36′W). *Leg.* J. DeRoy, 12 May 1968, 4 specimens.

TYPE-MATERIAL.—Holotype, LACM 1921 (shell and radular slide), 1 paratype, LACM 1922; paratypes also deposited in the collections of CAS and USNM.

DISTRIBUTION.—Galápagos Islands; Isla Fernandina (ANSP 152554), Isla Isabela (SU 239), Isla Rabida (LACM 71-69), Isla Bartolomé (AMNH 163290), Isla Santa Cruz (ANSP 154889), Isla Baltra (AMNH 163263), Isla Santa María (CAS 23025), Isla Santa Fé (AHF 48-33), Isla Española (USNM 102359), Isla San Cristóbal (MCZ 205068).

MATERIAL EXAMINED.—40 lots, 435 specimens, 9 radula preparations.

ETYMOLOGY.—We are pleased to name the species in honor of Barry Roth of the California Academy of Sciences in recognition of his work in molluscan systematics.

Notoacmea immaculata new species
(Figures 14, 15, 26, 32)

Shell (Figs. 14–15): Small (maximum length 12 mm), thin, diaphanous, height medium. Apex anterior to center, anteriorly directed; all slopes convex. Aperture ovoid; sides straight, sides elevated. Sculpture of faint gray, broad riblets and concentric growth lines. Exterior light gray, mottled with yellow-brown, brown, and white; darker markings concentrated into broad posterior ray bordered with white. Interior margin broad, dull, marked with exterior pattern; intermediate area translucent, glossy white; exterior pattern readily visible through shell; central area glossy, translucent, marked with sparse yellow streaks, central stain lacking.

Radula (Figs. 26, 32): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges straight to slightly concave, tapering to rounded cusps; second pair of lateral teeth posterior and slightly lateral to first pair, both edges convex, tapering to rounded cusps. First and second lateral teeth approximately equal in width. Third pair of lateral teeth posterior and lateral to second pair, medial edges convex, lateral edges elongate, straight to slightly concave, extending to edges of ventral plates, cusps rounded. Marginal teeth lacking. First lateral plates ovoid; second lateral plates rounded posteriorly, separated from third lateral plates by partial suture; third lateral plates lobate. Ventral plates closely set, subrectangular with strong anterior sutures.

Animal: Body pigmentation lacking; snout with oral lappets.

HOLOTYPE DIMENSIONS.—Length 5.6, width 4.3, height 1.4 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla Baltra (0°26′S, 90°17′W), Caleta del Norte, 0–3 m. *Leg.* ANTON BRUUN, cr. 18B, sta. 791, 21 Sep. 1966, 1 specimen.

TYPE-MATERIAL.—Holotype, LACM 1923 (shell and radula slide), 1 paratype, CAS 15920 (shell and radula slide). Paratype from Isla Santa Cruz, Academy Bay.

DISTRIBUTION.—Galápagos Islands; Isla Fernandina (LACM 62-196), Isla Isabela (LACM 71-70), Isla Bartolomé (AMNH 163290), Isla Santa Cruz (ANSP 154889), Isla Baltra (LACM 66-206), Isla San Cristóbal (ANSP 153328).

MATERIAL EXAMINED.—14 lots, 63 specimens, 5 radula preparations.

ETYMOLOGY.—The name is a Latin adjective, *immaculatus* (unstained), referring to the lack of a central stain in the area within the myostracum.

DISCUSSION.—The radular difference that is the chief basis of the separation of the two species is unmistakable and qualitative: in *N. rothi* the third lateral teeth are reduced (Fig. 25) and in *N. immaculata* the third lateral teeth are large (Fig. 26). The lateral plate morphologies are correspondingly different. In *N. rothi* the second and third lateral plates are approximately equal in size, and the lateral edges of the third lateral plates form small pointed projections. In *N. immaculata* the third lateral plates are larger than the second lateral plates and the lateral projections are rounded.

The shells of *N. rothi* and *N. immaculata* have similar overall proportions and sculpture. The color pattern consists of radiating and scattered whitish tessellations, with the greatest concentration of white tessellations in two latero-posterior rays, the posterior area between the two rays having the least amount of tessellate flecking so that it may appear to be a single, uniformly dark posterior ray. Those specimens confirmed on radular examination to have the tooth pattern of *N. rothi* have the dark gray-green ground color predominating, whereas those identified as *N. immaculata* have a light gray or white ground color. The largest specimens examined have proven to be *N. rothi*; the largest specimen verified as *N. immaculata* is 12 mm in length. The large specimens of *N. rothi* have a dark interior stain, which is generally lacking in *N. immaculata*. One small, stunted specimen verified as *N. immaculata* (LACM 71-48) shows a slight trace of brown interior stain. It is possible that the brown stain is indicative of the attainment of size rather than a species-specific character. Too few specimens verified as *N. immaculata* are available to enable us to be certain that any shell characters may be used as proof of identity.

Of the mainland acmaeid species, the *Notoacmea rothi–immaculata* complex resembles *Notoacmea filosa* (Carpenter, 1865) (Fig. 6), which has similar shell characters. They differ from *N. filosa* in the following ways: *N. rothi–immaculata* has a profile of medium height; *N. filosa* has a low profile. In *N. rothi–immaculata* the interspaces are broader than the riblets; in *N. filosa* the riblets are more numerous and the interspaces approximately equal in width to the riblets. *Notoacmea filosa* has a color pattern of radiating dark and lighter rays, often interrupted, but not tessellated in circular or oval patterns. The tessellate markings are characteristic of *N. rothi–immaculata*. The dark posterior ray of *N. rothi–immaculata* is not a feature of *N. filosa*.

Although the configuration of the lateral teeth of *N. filosa* has little in common with that of *N. immaculata*, there is a similarity between *N. filosa* and *N. rothi*. However, the shape of the second lateral teeth differs: in *N. filosa* the second lateral teeth are triangular; in *N. rothi* the second lateral teeth are broad with convex edges.

No detailed observations on the habitat of either species are available to us. We know from collection data on museum specimens that *N. rothi* occurs intertidally. Specimens are relatively free of encrustations except for some coralline algae and spirorbid worm tubes. The edges of the apertures are smooth and oval, not molded to fit a habitual site of attachment, suggesting that the normal habitat is likely to be on the undersides of stones in tidepools. Station data for the holotype of *N. immaculata* indicate a depth of 0 to 3 m. The absence of specimens in the intertidal collections of J. DeRoy suggests that *N. immaculata* is essentially a subtidal species.

The elongated teeth of *N. rothi* are similar to those of such temperate species as *Collisella pelta* (Rathke, 1833), *Notoacmea persona* (Rathke, 1833), and *Lottia gigantea*. All have pointed cusps on the first and second laterals and reduced third laterals. These temperate species are known to feed upon sessile diatoms and noncalcareous algae in the middle and high intertidal zones, so we infer that *N. rothi* does also.

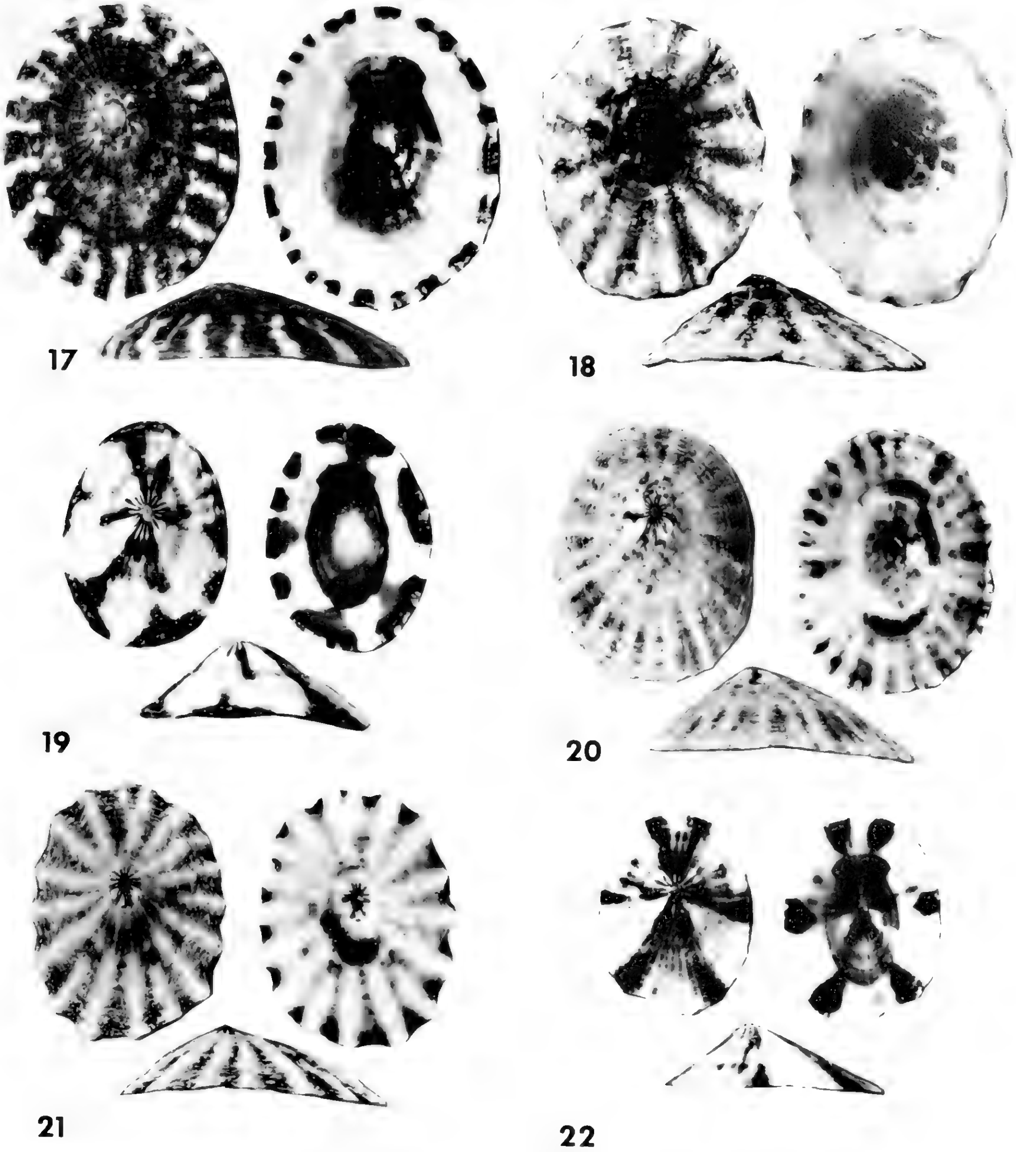
The short blunt teeth of *N. immaculata* are similar to those of species known to feed on coralline algae. The presumed subtidal occurrence of *N. immaculata* is in accordance with the abundant subtidal occurrence of coralline algae.

Lottia mimica new species

(Figures 17–19, 27, 33)

Shell (Figs. 17–19): Size medium (maximum length 25 mm), height medium; apex anterior to center; all slopes convex. Aperture ovoid, lateral edges somewhat parallel. Sculpture of raised angular ribs with one or two secondary ribs between each pair of primary ribs; ribs extending slightly, crenulating the margin. Exterior gray-brown with white radial markings that may or may not correspond to ribs. Apex white, with fine, dark radial lines typically concentrated in rays. Interior margin dark, with white markings corresponding to exterior color pattern; intermediate area blue-white; central area stained with dark brown; apical region white; exterior markings visible through shell.

Radula (Figs. 27, 33): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges straight, cusps pointed. Second pair of lateral teeth positioned posterior to and slightly lateral to first pair, medial edges convex, lateral edges slightly convex, cusps pointed. Third lateral teeth lateral to second pair, medial edges strongly convex, lateral edges concave, cusps pointed. All lateral teeth approximately equal in width. Marginal



FIGURES 17–22. New species of *Lottia* from the Galápagos Islands. All from Academy Bay, Isla Santa Cruz. FIGURE 17. *Lottia mimica* new species. Holotype, LACM 1925. Length 16.2 mm. FIGURE 18. *Lottia mimica*. Paratype, LACM 1926. Length 14.8 mm. FIGURE 19. *Lottia mimica*. Paratype, LACM 1926. Length 9.6 mm. FIGURE 20. *Lottia smithi* new species. Holotype, LACM 1927. Length 12.4 mm. FIGURE 21. *Lottia smithi*. Paratype, LACM 1928. Length 12.9 mm. FIGURE 22. *Lottia smithi*. Paratype, LACM 1928. Length 7.5 mm.

teeth small, narrow, extending over ventral plates in vicinity of third pair of lateral teeth. First lateral plates square, slightly overlapping anterior ribbon segments; second lateral plates rounded, separated from third lateral plates by partial suture; third lateral plates irregular, with prominent lateral extensions extending to edges of ventral plates. Ventral plates closely set, with broad, rounded anterior process, lateral edges concave, posterior process weak.

Animal: Base of every second or third mantle tentacle with dark red-brown pigmentation;

snout with oral lappets; secondary gill complete but reduced in front of head, composed of lappets (approximately 14 per mm); every other lappet reduced, less than one-half the size of the larger ones.

HOLOTYPE DIMENSIONS.—Length 16.2, width 12.4, height 4.2 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla Santa Cruz (0°38′S, 90°23′W), Academy Bay, Coamaño Island, intertidal zone. *Leg.* J. DeRoy, Oct. 1967.

TYPE-MATERIAL.—Holotype, LACM 1925 (shell and radula slide), 17 paratypes, LACM 1926, paratypes also deposited in the collections of CAS and USNM. Paratypes collected at several stations in Academy Bay by J. DeRoy between 1967 and 1969.

DISTRIBUTION.—Galápagos Islands; Isla Fernandina (AMNH 163363), Isla Isabela (AHF 74-33), Isla Bartolomé (AMNH 163290), Isla Santa Fé (AMNH 163362), Isla Española (AHF 359-35), and Isla San Cristóbal (CAS 23103).

MATERIAL EXAMINED.—33 lots, 198 specimens, 23 radula preparations.

ETYMOLOGY.—The name *mimica* is a Latin adjective, imitative, indicative of the difficulty of distinguishing the two members of the *Lottia* pair by their external appearance.

Lottia smithi new species

(Figures 20–22, 28, 34)

Shell (Figs. 20–22): Size medium (maximum length 25 mm), height medium; apex positioned in anterior third of shell; all slopes convex. Aperture ovoid. Sculpture of rounded primary ribs, secondary ribs of equal strength but beginning below apex. Primary and secondary ribs white, interspaces brown; apex white, with fine dark radial lines gathered into rays; interior margin dull yellow with irregular brown markings that correspond to exterior interspaces; intermediate area and central areas white; interior of myostracum bordered by yellow-brown halo. Exterior markings visible through shell.

Radula (Figs. 28, 34): First pair of lateral teeth closely set at anterior edge of ribbon segment, both edges convex, rounding to blunt cusps; second pair of lateral teeth posterior and slightly lateral to first pair, both edges convex, rounding to blunt cusps. Third pair of lateral teeth positioned lateral and posterior to second pair, both edges convex, rounding to blunt cusps. Marginal teeth small, narrow, overlapping ventral plates just anterior of third pair of lateral teeth. First lateral plates ovoid, slightly overlapping anterior ribbon segment; second lateral plates distinctly smaller than other lateral plates, medial edges rounded, separated from third lateral plates by a partial suture. Posterior edge of third lateral plates concave, with lateral extensions terminating in strongly hooked edges. Ventral plates closely set with strong posterior process; anterior process also present. Lateral edges in vicinity of marginal teeth concave; anterior sutures parallel with anterior edges of ventral plates.

Animal: Mantle tentacle pigmentation sometimes present; snout with oral lappets; secondary gill complete, but reduced in front of head, composed of lappets (approximately 11 per mm).

HOLOTYPE DIMENSIONS.—Length 12.4 mm, width 9.7 mm, height 4.5 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla Santa Cruz (0°38′S, 90°23′W), Academy Bay, Punta Nuñez, intertidal zone. *Leg.* J. DeRoy, 13 Oct. 1969.

TYPE-MATERIAL.—Holotype, LACM 1927 (shell and radula slide), 9 paratypes, LACM 1928; paratypes also deposited in the collections of CAS and USNM. All type-material from Isla Santa Cruz, Academy Bay.

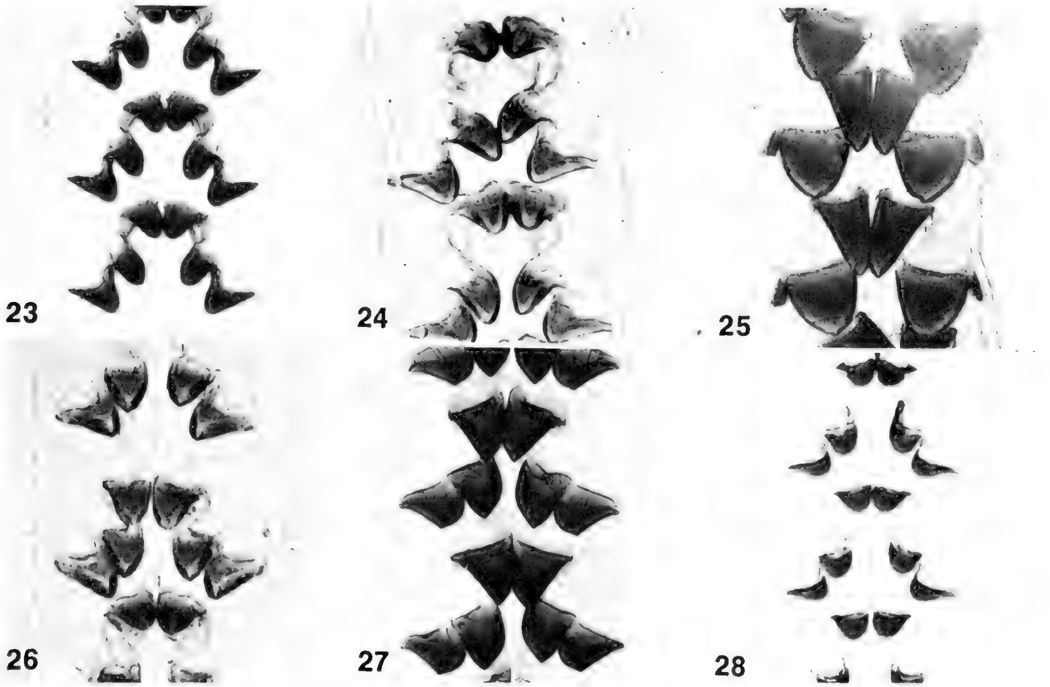
DISTRIBUTION.—Galápagos Islands; Isla Fernandina (LACM 72-196), Isla Isabela (CAS 27221), Isla Bartolomé (AMNH 163290), Isla Santa Cruz (LACM 28839), Isla Santa María (ANSP 153370), Isla San Cristóbal (ANSP 153328).

MATERIAL EXAMINED.—15 lots, 70 specimens, 14 radula preparations.

ETYMOLOGY.—We are pleased to name this species in honor of the late Allyn G. Smith of the California Academy of Sciences in recognition of his work with eastern Pacific mollusks, including those of the Galápagos Islands.

DISCUSSION.—The radular difference that separates *L. mimica* and *L. smithi* is readily apparent. In *L. mimica* the lateral teeth are pointed distally; in *L. smithi* they are rounded. The third lateral teeth of *L. mimica* are of the same width as the second; in *L. smithi* the third lateral teeth are much broader than the second. *Lottia mimica* lacks the strong posterior process on the ventral plates that is present in *L. smithi.*

In addition to radular difference, there is

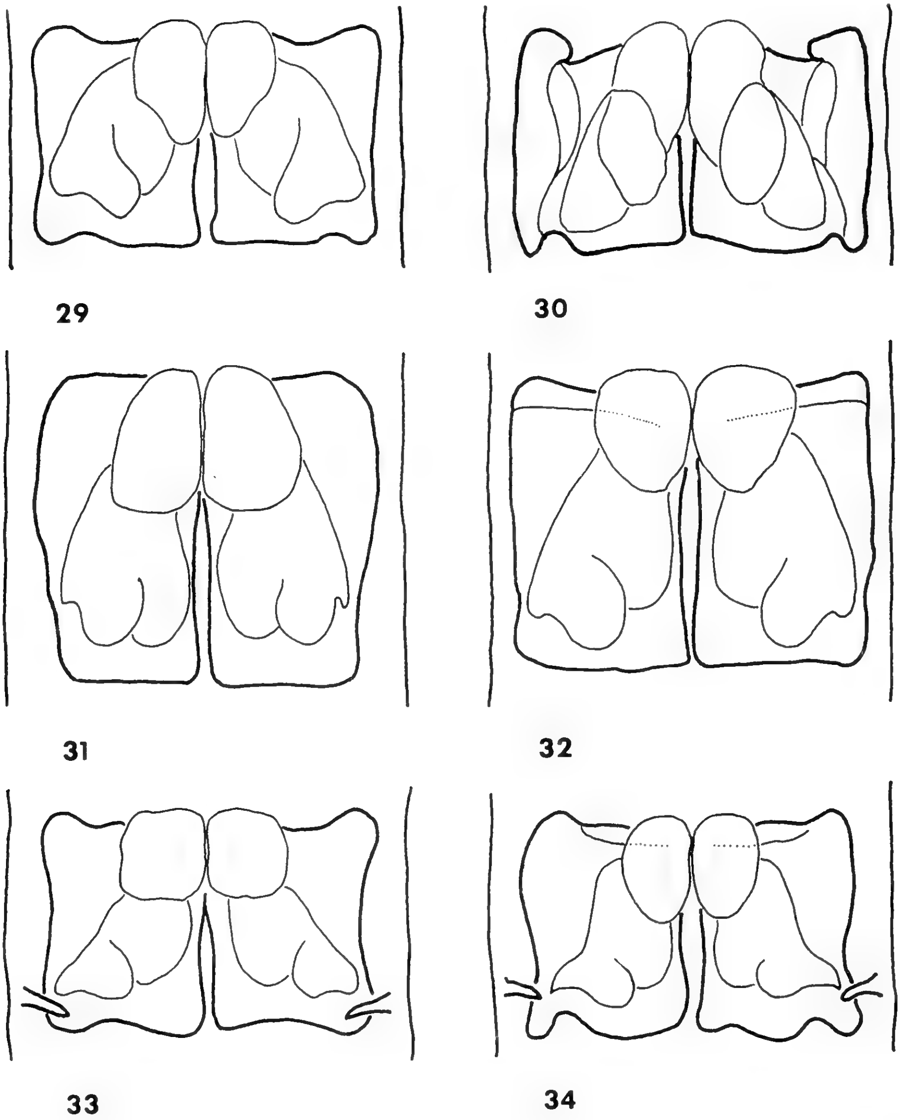


FIGURES 23–28. Radular dentition. FIGURE 23. *Notoacmea ubiquita* new species. FIGURE 24. *Notoacmea pumila* new species. FIGURE 25. *Notoacmea rothi* new species. FIGURE 26. *Notoacmea immaculata* new species. FIGURE 27. *Lottia mimica* new species. FIGURE 28. *Lottia smithi* new species. Anterior towards top of page.

another significant anatomical difference: in *L. mimica* the mantle tentacles are darkly pigmented (Fig. 3) in much the same way as in *L. gigantea* (Fig. 1). This pigmentation is weakly developed or entirely lacking in *L. smithi*. This distinction could prove useful in future field studies because it provides a reliable, nonfatal method of species determination.

Shells of *L. mimica* and *L. smithi* are essentially indistinguishable and are characterized by moderately strong radial ribs, variable in the number reaching the margin. Some specimens of both species have relatively few primary and secondary ribs, and these ribs project, crenulating the margin (Figs. 18, 21). In others the secondary ribs are more numerous and the primary ribs less prominent. In these specimens the ribs project only slightly and the shell margin is relatively even (Figs. 17, 19, 20, 22). The normal pattern on the apical region of juvenile shells is identical in both species (Figs. 19–22). The apical tip is dark colored with a pattern of thin, dark lines, concentrated in six bundles in the 1, 3, 5, 7, 9, and 11 o'clock positions. In most specimens this pattern changes abruptly to one in which rib surfaces are lighter colored and the interspaces darker, often showing concentric variations in intensity. In a few specimens of both species (Figs. 19, 22), the juvenile pattern changes to a solid 6-rayed pattern in the adult. The holotype of *L. mimica* is unusual; in the early stage it is uniformly dark, changing abruptly to a rayed pattern in which the lighter rays do not necessarily correspond to the ribs. Four specimens of the type lot of *L. mimica*, including the holotype, are predominantly dark colored; none in the type lot of *L. smithi* may be so described. The range of variability of *L. mimica* is therefore somewhat broader than that of *L. smithi*.

The peculiar markings in the juvenile shell of *L. mimica–smithi* as well as its particular adult pattern are unlike those of any other acmaeid species. The extreme specimens with few ribs are similar to *Collisella pediculus*, although that species has fewer, more prominent ribs. *Colli-*



FIGURES 29–34. Radular basal plates. FIGURE 29. *Notoacmea ubiquita* new species. FIGURE 30. *Notoacmea pumila* new species. FIGURE 31. *Notoacmea rothi* new species. FIGURE 32. *Notoacmea immaculata* new species. FIGURE 33. *Lottia mimica* new species. FIGURE 34. *Lottia smithi* new species. Anterior towards top of page.

sella mitella has a greater number of ribs and has a more uniform color pattern, with lighter ribs and darker interspaces.

There is no particular similarity to the large, dark brown shells of *Lottia gigantea* or the blue-green shells of *L. mesoleuca* and *L. stipulata*, but that is not surprising in view of the lack of consistent shell characters within all acmaeid genera.

We have no information about the habitat of either *L. mimica* or *L. smithi*. The original collecting information supplied by J. DeRoy indicates that they were collected on rocks exposed to heavy surf. All of the shells in both type lots were heavily encrusted with coralline algae, as are those of the Panamic species of *Collisella* that live under exposed surf conditions, such as *C. pediculus*. Limpets in this habitat have an habitual site of attachment with the shell edge molded to fit the home site. The margins of *L. mimica* and *L. smithi* are sufficiently irregular to suggest that they conform to specific sites.

The short, blunt, equal-sized radular teeth of *L. smithi* are well adapted for feeding on coralline algae. The shape of the lateral teeth, particularly the expansion of the third laterals, is similar to that found in other coralline-feeding *Collisella* of the tropical eastern Pacific. The lateral teeth of *L. mimica,* however, are not those of a coralline feeder, nor are they like those of most of the diatom-feeding species of *Notoacmea* or *Collisella,* in which the third lateral teeth are reduced. The medium length teeth with pointed cusps, all equally large, are like those of many of the Peruvian *Scurria* and the Californian *Notoacmea insessa* (Hinds, 1842). The last species is known to feed on the stipes of brown algae. The teeth of *L. mimica* are most likely adapted for feeding on some of the fleshy, encrusting, but noncalcareous algae.

Limpets of the *L. mimica–smithi* type are present in late Pleistocene deposits on Isla San Salvador (Hertlein and Strong 1939). The range of variation in the fossil specimens is similar to that seen in Recent specimens of both *L. mimica* and *L. smithi.* However, specific identifications are not possible from the shells alone.

ACMAEIDAE OF THE GALÁPAGOS ISLANDS

The Galápagos Islands, or Archipiélago de Colón, are located approximately 800 km west of Cabo San Lorenzo, Ecuador. The fifteen islands and numerous islets extend from 1°40′N to 1°36′S and from 89°17′W to 90°01′W. The islands have been the subject of numerous scientific explorations (see Slevin 1959) and are renowned for their unique fauna and flora. The marine molluscan fauna comprises tropical eastern Pacific elements, endemics, and a few forms from the Indo-Pacific faunal region (Emerson 1978).

Some nine different taxa of acmaeid limpets have been reported from the Galápagos Islands since 1855 (Reeve 1855; Carpenter 1864; Wimmer 1880; Stearns 1893; Pilsbry and Vanatta 1902; Dall 1909; Schwengel 1938; Hertlein and Strong 1955; Keen 1958; McLean 1971). None of the species reported have been recognized as endemics, having been considered instead as vagrants from the Californian, Panamic, and Peruvian molluscan faunal provinces. Many of the records have been based on beachworn shells or small shells dredged dead and in poor condition. Such specimens are difficult to refer to known species and could hardly be recognized as distinct new species. After examining a number of museum collections, we are able to confirm the presence of only two previously reported species at the Galápagos Islands, *Notoacmea filosa* and *Lottia mesoleuca.*

Specimens of *L. mesoleuca* from the Galápagos were originally misidentified as the Australian species *Patelloida striata* Quoy and Gaimard, 1834, and were so treated by Reeve (1855:pl. 33, fig. 99) (as "*Patella striata*"), Carpenter (1864) (as "*Acmaea striata* Reeve"), and Stearns (1893) (as "*Acmaea striata* Reeve"). Occurrences of *L. mesoleuca* at the Galápagos are rare. It is represented in the collections examined by three specimens: two from Isla Genovesa (AHF 782-38) and a single beach specimen from the "Galapagos" (ANSP 39189). Isla Genovesa is the most northeastern of the islands, and it is conceivable that the species may be established there and not elsewhere in the archipelago.

Notoacmea filosa is also rare in collections. It is represented by only two museum lots, one from Isla Santa Cruz (AMNH 177320) and one from Isla San Cristóbal (LACM 54775) (Fig. 16) collected in 1929. Further information about the occurrence of these two species at the Galápagos Islands is desirable. Considering that recent collecting efforts have not produced these species, we only provisionally list them in the Galápagos Islands fauna.

We consider all other records of Acmaeidae from the Galápagos Islands to be misidentifications of the four new species described herein. Because separation of members of the species pairs is based on radular characters, it is not possible to list species-specific synonymies for each member.

In both species pairs, additional characters segregate with the radular morphotypes. In the *Notoacmea* siblings, there are differences in shell size and coloration associated with the radular types. In the *Lottia* pair, there are no significant differences in shell size, sculpture, or coloration; however, there are differences in mantle pigmentation and secondary gill morphology. We interpret these separate character states as evidence against a simple radular polymorphism and instead recognize the pairs as separate species. There is also evidence that the habitat differs in the *Notoacmea* pair but not in the *Lottia* pair.

Whether speciation of the two pairs of sibling species was sympatric or allopatric is unknown. However, we hope that future workers will pursue this problem in the field and the laboratory. Electrophoretic analysis could prove productive.

Acknowledgments

We are indebted to Jacqueline DeRoy of Isla Santa Cruz, Galápagos Islands, who furnished preserved specimens of the new species from those islands. Donald R. Shasky of Redlands, California, loaned pertinent specimens from his collection. Courtesies were extended to Lindberg on his museum visits by George M. Davis (ANSP), William K. Emerson (AMNH), Welton L. Lee (CAS), Joseph Rosewater and Kathy Lamb (USNM), Barry Roth (CAS), and Ruth Turner (MCZ). Barry Roth also made available the late Leo G. Hertlein's unpublished notes on the Galápagos molluscan fauna. Bertram C. Draper, Los Angeles, made the prints of shell specimens, and Sally Walker, University of California, Santa Cruz, prepared the line drawing. We thank Eugene V. Coan, Myra Keen, and Barry Roth for reading the manuscript and offering helpful suggestions.

Resumen

La definición de género está basada en las características conservativas de la estructura de la concha y también en las características cualitativas de la rádula. La *Lottia*, que anteriormente se había considerado monotípica, se extende a incluir las especies panámicas con la agalla secundaria (un cordón branquial), que anteriormente se había atribuido a la *Scurria*. La *Scurria* tiene la agalla semejante, pero la estructura de la concha se diferencia. Las nuevas especies *Notoacmea ubiquita* de México y *N. pumila* de Ecuador tienen las conchas pequeñas y son especies alopátricas con los dientes radulares que están modificados para alimentarse de la alga coralina. Dos nuevas especies de *Notoacmea* (*N. rothi* y *N. immaculata*), que son endémicas a las Islas Galápagos, constituyen un par de especies que se diferencian principalmente por los rasgos de la rádula: los dientes radulares de *N. immaculata* están adoptados para alimentarse de la alga calcárea; los dientes radulares de *N. rothi*, para alimentarse de la alga no calcárea. Un par de nuevas especies de *Lottia* endémicas a las Islas Galápagos (*L. mimica* y *L. smithi*) también se diferencian principalmente por las características radulares. La *Lottia mimica* se alimenta de la alga y es no calcárea; y la *L. smithi* se alimenta de alga y es calcárea. Estas cuatro especies endémicas son las principales lapas acmaeidas de las Islas Galápagos. Dos especies de la tierra firme, *Notoacmea filosa* y *Lottia mesoleuca*, se han observado no más esporadicamente en las Islas Galápagos.

Literature Cited

Carpenter, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Rep. Brit. Assoc. Adv. Sci. 1864:517–686.

Christiaens, J. 1975. Révision provisoire des mollusques marins récents de la famille des Acmaeidae. Inf. Soc. Belge Malacol. 4(4):3–20.

Dall, W. H. 1871. On the limpets; with special reference to the species of the west coast of America, and to a more natural classification of the group. Am. J. Conchol. 6(3):227–282.

———. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. Proc. U.S. Natl. Mus. 37:147–294.

Emerson, W. K. 1978. Mollusks with Indo-Pacific faunal affinities in the eastern Pacific Ocean. Nautilus 92:91–96.

Hertlein, L. G., and A. M. Strong. 1939. Marine Pleistocene mollusks from the Galápagos Islands. Proc. Calif. Acad. Sci., ser. 4, 23:367–380.

———, and ———. 1955. Marine mollusks collected at the Galápagos Islands during the voyages of the *Velero III*, 1931–1932. Pp. 111–115 *in* Essays in the Natural Sciences in Honor of Capt. Allan Hancock, Univ. So. Calif., Los Angeles, Calif.

Keen, A. M. 1958. Sea shells of tropical west America. 1st ed. Stanford Univ., Stanford, Calif. 624 pp.

Lindberg, D. R. 1976. Cenozoic phylogeny and zoogeography of the Acmaeidae in the eastern Pacific. Ann. Rep. West. Soc. Malacol. 9:15–16.

———. 1978. On the taxonomic affinities of *Collisella edmitchelli*, a late Pleistocene limpet from San Nicolas Island, California. Bull. So. Calif. Acad. Sci. 77:65–70.

———. 1979. Variation in the limpet *Collisella ochracea* and the northeastern Pacific distribution of *Notoacmea testudinalis* (Acmaeidae). Nautilus 93:50–56.

MacClintock, C. 1967. Shell structure of patelloid and bellerophontoid gastropods (Mollusca). Peabody Mus. Nat. Hist. Yale Univ. Bull. 22:1–140.

McLean, J. H. 1966. West American prosobranch Gastropoda: Superfamilies Patellacea, Pleurtomariacea, and Fissurellacea. Ph.D. dissertation, Stanford Univ., Stanford, Calif. 255 pp.

———. 1971. Family Acmaeidae, *in* Keen, A. M., Sea shells of tropical west America. 2nd ed. Stanford Univ. Press, Stanford, Calif. 1064 pp.

———. 1973. Family Acmaeidae, *in* Marincovich, L., Intertidal marine mollusks of Iquique, Chile. Nat. Hist. Mus. Los Angeles Co. Sci. Bull. 16:1–49.

Pilsbry, H. A., and E. G. Vanatta. 1902. Papers from the Hopkins Stanford Galápagos Expedition, 1898–99, no. 13, marine Mollusca. Proc. Washington Acad. Sci. 4:549–560.

Reeve, L. 1855. Conchologia iconica: or, illustrations of the shells of molluscous animals. Vol. 8. Monograph of the genus *Patella*. London. Pages not numbered, 41 pls.

Schwengel, J. S. 1938. Zoological results of the George Vanderbilt South Pacific Expedition, 1937. Part I. Galápagos Mollusca. Proc. Acad. Nat. Sci. Philadelphia 90:1–3

Slevin, J. R. 1959. The Galápagos Islands: A history of their exploration. Occas. Pap. Calif. Acad. Sci. 25:1–150.

Stearns, R. E. C. 1893. Report on the mollusk fauna of the Galápagos Islands with descriptions of new species. Proc. U.S. Natl. Mus. 16:353–450.

Wimmer, A. 1880. Zur Conchylien-Fauna der Galapagos-Inseln. Sitzungsber. K. Akad. Wiss. Wien Math.-Natwiss. Kl. 80(Abt. I)(10)(1879):465–514.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 13, pp. 341–348, 5 figs. June 24, 1981

A REVIEW OF THE BATHYAL FISH GENUS *ANTIMORA* (MORIDAE: GADIFORMES)

By
Gregg J. Small*

Systematics Laboratory, National Marine Fisheries Service, NOAA,
National Museum of Natural History, Washington, DC 20560

ABSTRACT: There are two valid species of the genus *Antimora*: *A. microlepis* Bean in the North Pacific, and *A. rostrata* (Günther) from the southeastern Pacific, Southern Ocean, and Atlantic Ocean. Junior synonyms of *A. rostrata* include: *A. australis* Barnard, *A. meadi* Pequeño, *A. rhina* Garman, and *Haloporphyrus viola* Goode and Bean. *Antimora microlepis* has 90 to 103 gill filaments on the first arch; *A. rostrata* has 76 to 90. Differences in the regression equations of gill filament length on standard length, and of head length on standard length between fish from several geographic areas are shown. Other characters examined include numbers of vertebrae, fin rays, gill rakers, and scale rows; and morphometric ratios, using lengths of eye, snout, predorsal, first dorsal fin ray, maxillary, and gill rakers, and width of interorbital.

INTRODUCTION

Fishes of the benthopelagic morid genus *Antimora* are widely distributed in the world oceans, ranging in depth between 402 and 2905 m (Grey 1956), and are very abundant in some regions (Wenner and Musick 1977). They appear to be most common on the continental slopes of subarctic, subantarctic, and temperate regions, but are generally rare in the subtropics and tropics, although they are apparently common in the vicinity of the Hawaiian and Galápagos islands.

The genus *Antimora* is distinguished from other members of the family Moridae by the combination of a pronounced pointed snout, a pelvic fin with six rays, a well-developed mental barbel, a long-based second dorsal fin with more than 50 rays, and a deep indentation in the outline of the anal fin (Svetovidov 1948). There is little information on food habits because specimens brought to the surface routinely evert their stomachs. Sedberry and Musick (1978) found only 10 specimens with intact stomachs in numerous deep-water trawlings. Individuals with ripe eggs are unknown, and specimens smaller than 100 mm are rare. Males longer than 325 mm are uncommon, although females are often longer than 600 mm. Within its depth range, there is a segregation by sex and also by size of individuals (Iwamoto 1975; Wenner and Musick 1977). Available information on the taxonomy and distribution of the genus was summarized by Iwamoto (1975).

Although this study shows that only *Antimora rostrata*, occurring in all areas except the North Pacific, and *A. microlepis*, occurring only in the North Pacific, are valid species of the genus *Antimora*, the following species and their associated localities have been previously proposed: *Haloporphyrus rostrata* Günther, 1878,

---

* Present address: Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, Washington 98112.

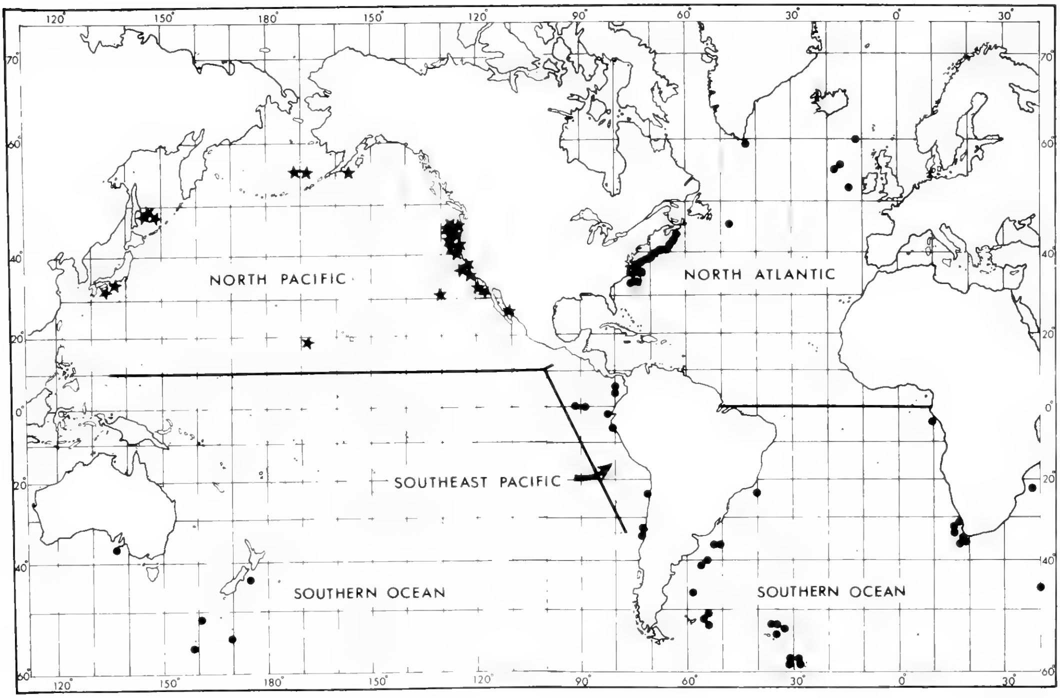


FIGURE 1. World localities from which specimens of *Antimora* spp. were studied. Stars = *A. microlepis*, dots = *A. rostrata*. Heavy black lines divide regions.

from subantarctic seas; *Haloporphyrus viola* Goode and Bean, 1878, from the temperate western North Atlantic; *Antimora microlepis* Bean, 1890, from the temperate eastern North Pacific; *Antimora rhina* Garman, 1899, from the Gulf of Panama; *Antimora australis* Barnard, 1925, from off the Cape of Good Hope; and *Antimora meadi* Pequeño, 1970, from off the coast of Chile.

No comparison has ever been made of populations represented by these six names. The closest approach was that of Schroeder (1940) who examined limited material of the first four nominal species (he apparently overlooked *A. australis*) and suggested that they be referred to the same species. The object of the present paper is to resolve the number of valid species of *Antimora* using measurements, counts, and the known species distributions.

Biological and distributional information are useful in clarifying the taxonomy of *Antimora*. It has been shown that in the western North Atlantic *Antimora* becomes larger with increasing depth but does not reproduce within the area of its greatest known abundance (Wenner and Musick 1977). Migrations may be a regular part of the life history of the western North Atlantic population. The mobility of *Antimora* has been confirmed by Cohen (1977) who has shown that these fish are able swimmers. Perhaps there is a single interbreeding North Atlantic population. If *Antimora* from other regions have the same swimming ability, then there may be single populations in the southeastern Pacific, the southern oceans, and the northern Pacific. Although data for this study were originally segregated on the basis of six geographical regions (see Materials), characters of *Antimora* in the western and eastern North Pacific were found to be similar as were those from the western and eastern North Atlantic. A preliminary analysis indicated that the four geographical groupings mentioned above provide a more appropriate basis for comparison (Fig. 1).

METHODS

Measurements and counts were made according to Hubbs and Lagler (1970) and include:

standard length, head length, snout length, predorsal length, eye diameter, upper jaw length, interorbital distance, first dorsal fin ray length, number of scales along the lateral line, and number of scale rows between lateral line and dorsal origin. Numbers of vertebrae (including the hypural plate), anal rays, and dorsal rays were read from radiographs.

Numbers of gill filaments and gill rakers on the first gill arch, lengths of the longest gill raker and gill filament (measured from base to tip, Fig. 2), length of longest gill raker at the gill angle, and dorsal fin ray length (from the anterior base to the tip of the first ray) were compared. Broken and otherwise damaged rays were not measured.

Coloration, often used in early descriptions, was not recorded due to color changes which occur in preserved specimens. However, an attempt was made to recheck other characters presented in original descriptions.

MATERIALS

A total of 449 specimens were examined (refer to figures for length summary).

WESTERN NORTH PACIFIC (between 33°N to 48°N and 135°E to 145°E; 6 specimens): U.S. National Museum (USNM): 161494 (1); 160607 (1); 160606 (1); 149228 (1); 117886 (2).

EASTERN NORTH PACIFIC (between 18°N and 56°N; 96 specimens): California Academy of Sciences (CAS): 3883 (2); 37559 (1); 34354 (2); 34353 (2); 32308 (2); 27525 (1); 26226 (1); uncat. (3); CAS-SU 5276 (5); 77 (1). Museum of Comparative Zoology (MCZ): 28250 (1). Scripps Institution of Oceanography (SIO): 70-249 (22); 70-247 (2); 68-443 (1); 59-265 (1). University of Washington (UW): 19309 (2); 19235 (1); 19228 (7); 19139 (4); 18492 (8); 18201 (2) 18190 (2); 17180 (7); 19149 (1); 18493 (5). USNM: 45361 (2 syntypes of *Antimora microlepis*); 54573 (1); 54364 (1); 53876 (3); 48562 (1); 47238 (1); 47237 (1).

WESTERN NORTH ATLANTIC (between 27°N and 59°N; 117 specimens): Institut für Seefischerei, Hamburg (ISH): 79/73 (2). MCZ: 53949 (1); 38282 (3); 38073 (3); 37633 (1); 37619 (2); 37595 (1); 37520 (1); 37585 (2). University of Maine, Darling Center (UMDC): 313-1 (1); 306-2 (1). USNM: 21837–8 (2 syntypes of *Haloporphyrus viola*); uncat. (35); 31725 (1). x-ray counts only: 143250 (1); 45872 (1); 45845 (1); 45808 (1); 36163 (1); 38142 (1); 38068 (1); 38064 (3); 38019 (1); 35595 (1); 35566 (1); 33446 (4); 33443 (7); 33340 (3); 33337 (5); 33014 (1); 31768 (1); 28612 (1); 28611 (1); 28610 (1); 28609 (1); 28608 (1); 24746 (1). Virginia Institute of Marine Sciences (VIMS): 3458 (2); 3243 (1); 1471 (7); 1460 (3); 872 (4); 870 (1); uncat. (3).

EASTERN NORTH ATLANTIC (between 50°N and 60°N; 6 specimens): ISH: 112/74 (1); 111/74 (1); 146/74 (2); 745/74 (2).

SOUTHEASTERN PACIFIC (between 0°S to 56°S and 70°W to 91°W; 123 specimens): USNM: uncat. (120). MCZ: 28610 (1) and 28611 (2) (3 syntypes of *Antimora rhina*).

SOUTHERN OCEANS (specimens from southern Atlantic, Indian, and Pacific oceans, excluding southeastern Pacific specimens; 101 specimens): ISH: 2191/68 (2); 1250/66 (1); 1241/66 (2); 1142/66 (11); 1129/66 (1); 361/71 (2); 344/71 (1); 286/71 (1); 152/67 (8); 151/67 (3); 150/67 (1); 33/76 (5); WH32/76 (5). Los Angeles County Museum (LACM): 10033 (12); 10032 (8); 10985-5 (3); uncat. (9). University of Florida (UF-TABL): 503 (1). UMDC: uncat. station numbers 01343 (1); 01342 (1); 00198 (1); 00165 (1); 00157 (1); 00152 (1). USNM: 188827 (1 syntype of *Antimora australis*); 188829 (3); 188823 (5); 188822 (2); uncat. (3). British Museum Natural History (BMNH): 1887.12.-17.36 (holotype of *Haloporphyrus rostratus*, x-ray only).

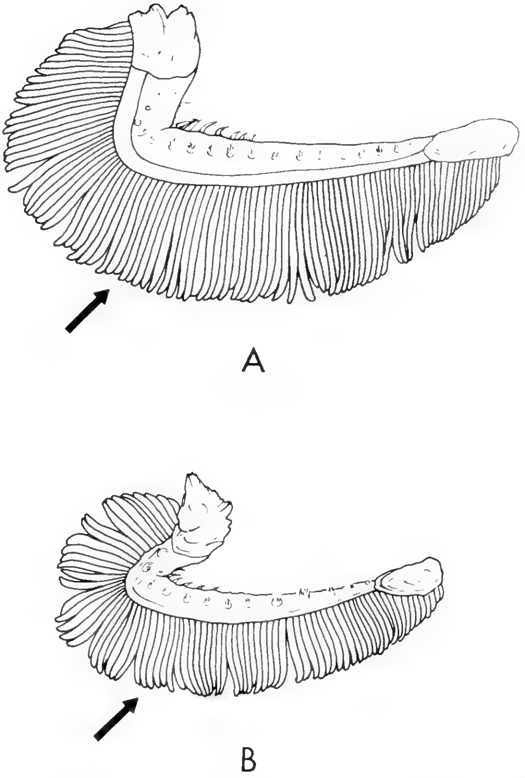


FIGURE 2. Medial view of first gill arch of left side to illustrate location of gill filament measurement. (*A*) *Antimora microlepis*, UW 17180, off Columbia River, 46°N, 124°W, 310 mm SL; (*B*) *Antimora rostrata*, LACM 10985-5, southwest of New Zealand, 56°19′S, 158°29′E, 330 mm SL. Drawn by Keiko Hiratsuka Moore.

RESULTS

Antimora may be divided into two distinct species instead of the six described, based on the number of gill filaments and secondarily on the ratio of gill filament length to standard length. Other measurements can be used but with less distinct separation of species.

COUNTS.—North Pacific specimens possess 90–103 gill filaments on the first gill arch, compared with 76–90 in specimens from the other

TABLE 1. COMPARISON OF THE FREQUENCY OF GILL FILAMENT NUMBER BY STANDARD LENGTH GROUP FOR *Antimora microlepis* FROM NORTH PACIFIC (1), AND *Antimora rostrata* FROM THE NORTH ATLANTIC (2), SOUTHEAST PACIFIC (3), AND SOUTHERN OCEANS (4).

	Number of gill filaments																													
SL (mm)	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106
100–150			3	3	2	44 4		4		23 4		22 4	23 4					1		1				1		1					
151–200			4	3		4	3	33 4	24 44	2	34				4					11			1		1	1					
201–250			3			34	4	23	34 4		2	2		3		1				11	1	11	1					1			
251–300			4	2	2	3		22 4	3	23	3		22	24		1	11	1	11	1	11 11	11	11 11	11 11	11 1	11 1					11
301–350	3			3		3	34		2	33 4	24	22	3	2	11 2				11	11 11	11 1	1		1		1		1			
351–400										23				2	3			1			11	1									
401 +						4	4													1			1		1						

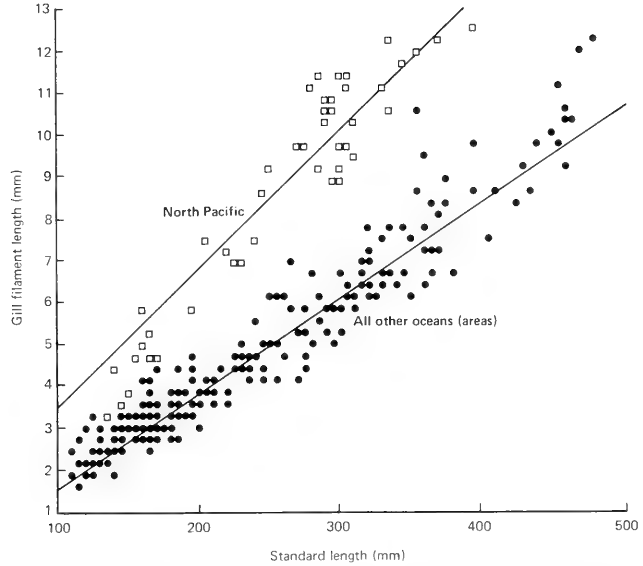


FIGURE 3. Regression of gill filament length on standard length in *Antimora* from four divisions of the world oceans: North Pacific, squares; southeast Pacific, Southern Ocean, and North Atlantic, dots. North Pacific: $y = 0.03x - 0.10$, $n = 51$. All other oceans (areas): $y = 0.02x - 0.70$, $n = 230$.

regions (Table 1). Number of gill filaments appears to be constant over the size range of specimens in all populations.

Only slight differences between samples were found from the four geographical areas in total vertebral number, number of gill rakers on the first arch, and anal and dorsal fin rays (Table 2).

Although the size and number of scales have been used in several of the species descriptions previously mentioned, they are not useful characters for the differentiation of these species. Specimens of *Antimora* are very fragile and on capture the scales and scale pockets do not remain intact for use as a reliable character.

MEASUREMENTS.—Specimens collected from the eastern and western North Pacific north of latitude 10°N have a gill filament length relatively greater than that in fish caught elsewhere. Above the size range of approximately 150 mm standard length, the length of the filaments distinctly separate North Pacific fishes from all other groups. Least square regression lines were fit

TABLE 2. SUMMARY OF SELECTED COUNTS AND LENGTH PROPORTIONS IN *Antimora* FROM THE FOUR GEOGRAPHICAL REGIONS SHOWN IN FIGURE 1 (lengths presented as ratio of standard length to size of part).

	N Pacific			SE Pacific			N Atlantic			S Ocean		
Character	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD
Snout length	11.9	71	0.86	11.8	105	1.33	12.7	78	1.16	12.6	93	1.53
Predorsal length	3.9	69	1.47	3.7	108	0.20	3.7	76	0.17	3.9	94	0.20
Maxillary length	7.1	70	0.36	6.9	110	0.50	7.2	76	0.38	7.4	94	0.49
First dorsal fin ray length	5.9	47	1.43	7.1	94	1.58	5.1	63	1.45	6.1	54	1.40
Eye diameter	15.0	66	1.20	15.3	96	1.34	16.0	69	1.42	16.2	49	1.36
Interorbital width	17.6	38	1.45	18.6	71	1.61	15.5	32	1.56	18.3	32	1.64
Longest gill raker length	73.4	23	14.07	–	0	–	76.9	1	–	103.0	11	16.00
Total number of vertebrae	59.1	47	0.86	58.8	76	0.96	59.8	64	1.26	59.6	31	1.02
Total number of gill rakers	16.5	38	1.93	16.2	74	1.29	16.6	46	2.11	16.0	79	1.54
Total number of anal fin rays	40.6	41	1.40	39.3	56	1.39	41.9	67	1.56	40.0	28	1.70
Total number of dorsal fin rays	52.4	40	1.15	51.7	59	1.37	53.8	60	1.45	53.2	32	1.45

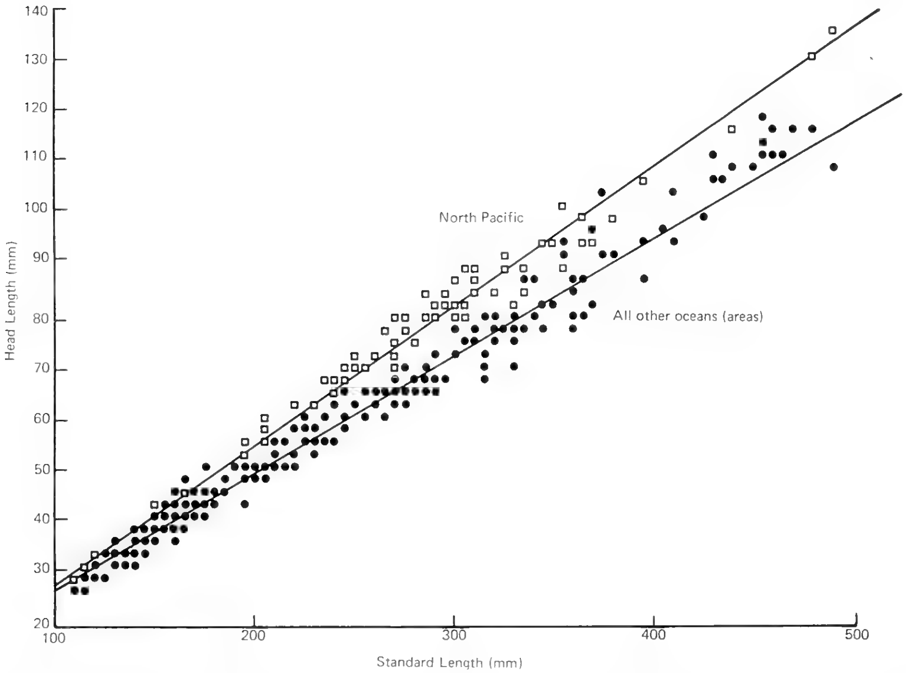


FIGURE 4. Regression of head length on standard length in *Antimora* from four divisions of the world oceans: North Pacific, squares; North Atlantic, southeast Pacific, and Southern Ocean, dots. North Pacific: $y = 0.26x + 2.22$, $n = 98$. All other oceans (areas): $y = 0.23x + 2.9432$, $n = 277$.

to the data, and the regression of gill filament length on standard length was determined following the methods of Zar (1974) (Fig. 3).

Head length against standard length (Fig. 4) also separates North Pacific specimens from all other *Antimora*. This difference is most marked in fish larger than 200 mm standard length.

Bean (1890), Garman (1899), Barnard (1925), and Pequeño (1970) noted head length to total length or standard length proportions in original descriptions with no apparent differences among the described species.

Comparisons of the length of snout, predorsal distance, maxillary, first dorsal fin ray, eye diameter, longest gill raker, and width of interorbital are summarized in Table 2. None of the measurements serve unequivocally to separate the North Pacific specimens from other *Antimora*. Fish from all other areas do show some differences: southeast Pacific, North Atlantic, and Southern Ocean populations may have slightly different lengths of first dorsal fin ray; North and southeast Pacific fish appear to have larger eyes than do other *Antimora*; and North Atlantic specimens have larger interorbital widths. Gill raker length may also show some differences, however, data for this character are incomplete.

Within the range of *A. rostrata*, there are local differences in some morphometric characters, but these differences are not consistent throughout the range of size or geography. For example, the first dorsal fin ray to standard length ratio is higher in North Atlantic specimens than those from other areas. This longer fin ray is most pronounced in specimens in the 200–400 mm range. North Atlantic fish also have a shorter snout and wider interorbital distance over certain segments of their size range as compared to specimens from other regions. Although only one specimen from low latitudes in the mid-Atlantic was examined in this study, there may be contact between North Atlantic and South Atlantic populations of *Antimora*, as specimens have been taken in the Bahamas and the Gulf of Guinea (personal communication, Daniel M.

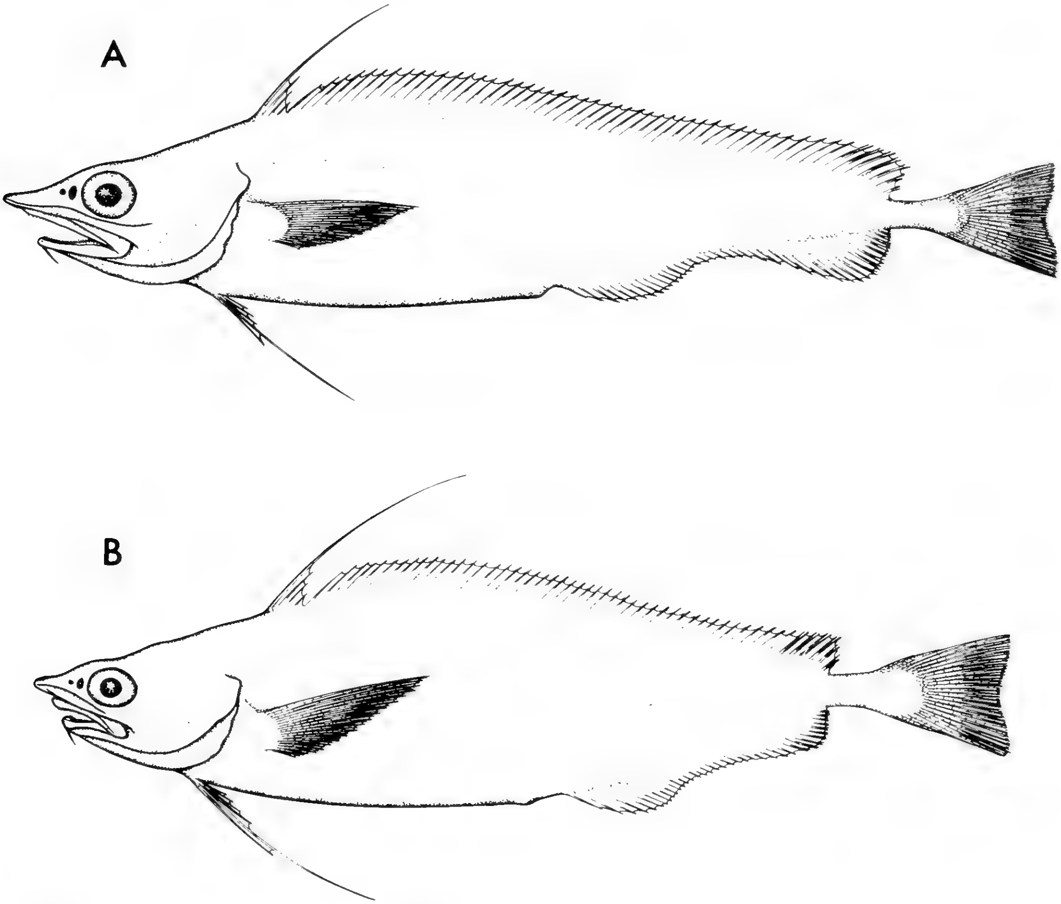


FIGURE 5. (*A*) *Antimora rostrata,* USNM 218479, SL 346 mm, male, western North Atlantic, 36°39′N, 74°28′W, 1530–1610 m; (*B*) *Antimora microlepis* CAS 32308, SL 371 mm, male, off California. Drawn by Keiko Hiratsuka Moore.

Cohen, Systematics Laboratory, National Marine Fisheries Service, NOAA, Washington, D.C.).

Conclusions

The species can be characterized as follows:

Antimora microlepis Bean, 1890

(Figure 5*B*)

Antimora microlepis Bean, 1890:38 (type-locality: 51°23′N, 130°34′W, Albatross sta. 2860, off Cape St. James, Queen Charlotte Islands, 876 fms [1602 m], 13 Aug. 1888).

Characters.—Gill filaments on first gill arch 90–103; gill filaments relatively long, regression equation of gill filament length on standard length $y = 0.03x - 0.10$; head length relatively long, regression equation of head length on standard length $y = 0.26x + 2.22$.

Range.—Eastern and western North Pacific Ocean, north of latitude 10°N.

Antimora rostrata (Günther, 1878)

(Figure 5*A*)

Haloporphyrus rostratus Günther, 1878:18 (type-locality: "midway between the Cape of Good Hope and Kerguelen Island; east of the mouth of the Rio de la Plata," Challenger sta. 146, 1375 fms [2515 m], and sta. 320, 600 fms [1097 m]).

Haloporphyrus viola Goode and Bean, 1878:257–260 (type-locality: "outer edge of Le Have Bank, at a depth of four or five hundred fathoms" [approximately 43°N, 64°W]).

Antimora rhina Garman, 1899:185–186 (type-locality: Gulf of Panama, Albatross sta. 3353, 7°06′15″N, 80°34′W, 695 fms [1271 m], sta. 3393, 7°15′N, 79°36′W, 1020 fms [1865 m]).

Antimora australis BARNARD, 1925:499 (type-locality: "off Cape Point, 475–900 fathoms" [869–1646 m]).

Antimora meadi PEQUEÑO, 1970:14–16 (type-locality: ANTON BRUUN cruise 13, between 34°06′S, 72°26′W, and 34°12′S, 72°25′W, in 1400–1475 m, 3 Feb. 1966).

CHARACTERS.—Gill filaments on first gill arch 76–90; gill filaments relatively short, regression equation of gill filament length on standard length $y = 0.02x - 0.70$; head length relatively short, regression equation of head length on standard length $y = 0.23x + 2.9432$.

RANGE.—All oceans except the North Pacific north of 10°N.

ACKNOWLEDGMENTS

I am thankful for the advice and support given me by Daniel M. Cohen of the Systematics Laboratory, National Marine Fisheries Service (NMFS), for initially suggesting this study, and his valuable guidance throughout the course of this work. Tomio Iwamoto (CAS) recommended that I examine gill filament length, arranged for the loan of specimens from the California Academy of Sciences, and reviewed the manuscript. Bruce B. Collette (Systematists Laboratory, NMFS) and Hugh H. DeWitt (University of Maine, Orono) also reviewed the manuscript and made valuable comments.

Special thanks are due Charles A. Wenner and John A. Musick for allowing me to read their then-unpublished manuscript on the life history of North Atlantic *Antimora* and examine specimens in their collection at the Virginia Institute of Marine Science. The Allan Hancock Foundation and Los Angeles County Museum provided Antarctic material, William Fink (MCZ) provided important materials from the North Atlantic as did Alfred Post (ISH). Richard Rosenblatt (SIO), Arthur Welander (UW), Carter Gilbert (UF), Jean Dunn (NMFS, Seattle Laboratory), and the National Museum of Natural History were all instrumental in providing additional materials. Keiko H. Moore prepared the illustrations and figures.

LITERATURE CITED

BARNARD, K. H. 1925. Descriptions of new species of marine fishes from South Africa. Ann. Mag. Nat. Hist. ser. 9, 15:498–504.

BEAN, T. H. 1890. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. No. XI—New fishes collected off the coast of Alaska and adjacent region southward. Proc. U.S. Natl. Mus. 13:37–45.

COHEN, D. M. 1977. Swimming performance of the gadoid fish *Antimora rostrata* at 2400 meters. Deep-Sea Res. 24:275–277.

GARMAN, S. 1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross" during 1891, Lieut-Commander Z. L. Tanner, U.S.N. Commanding. Part 26, The Fishes. Mem. Mus. Comp. Zool. Harvard 24:1–431.

GOODE, G. B., AND T. H. BEAN. 1878. Descriptions of two gadoid fishes, *Phycis chesteri* and *Haloporphyrus viola* from the deep-sea fauna of the northwestern Atlantic. Proc. U.S. Natl. Mus. 1:256–260.

GREY, M. 1956. The distribution of fishes found below a depth of 2000 meters. Fieldiana Zool. 36:74–336.

GÜNTHER, A. 1878. Preliminary notices of deep sea fishes collected during the voyage of H.M.S. Challenger. Ann. Mag. Nat. Hist. ser. 5, 2:17–28.

HUBBS, C. L., AND K. F. LAGLER. 1970. Fishes of the Great Lakes region. 4th ed. Ann Arbor: Univ. Michigan Press. 213 pp.

IWAMOTO, T. 1975. The abyssal fish *Antimora rostrata* (Günther). Comp. Biochem. Physiol. 52B:7–11.

PEQUEÑO-R., G. 1970. *Antimora meadi* n.sp. en Chile. Not. Men. Mus. Nac. Hist. Nat. (Santiago) 15:14–16.

SCHROEDER, W. C. 1940. Some deep sea fishes from the North Atlantic. Copeia 1940:231–238.

SEDBERRY, G. R., AND J. A. MUSICK. 1978. Feeding strategies of some demersal fishes of the continental slope and rise off the Mid-Atlantic coast of the USA. Mar. Biol. (N.Y.) 44:357–375.

SVETOVIDOV, A. N. 1948. Treskoobraznye. Faune SSSR, Ryby 9(4), 221 pp. Akad. Nauk SSSR. (Transl. from Russian: 1962, Gadiformes, Fauna USSR, Fishes. 304 pp. U.S. Dep. Comm., Natl. Tech. Inf. Serv., Springfield, Virginia; OTS 63-11071.)

WENNER, C. A., AND J. A. MUSICK. 1977. Biology of the morid fish, *Antimora rostrata*, in the western North Atlantic. J. Fish. Res. Bd. Canada 34:2362–2368.

ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey: Prentice Hall Inc. 620 pp.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 14, pp. 349–377; 18 figs., 2 tables **October 26, 1981**

THE *KAIANUS*-GROUP OF THE GENUS *CALLIONYMUS* (PISCES: CALLIONYMIDAE), WITH DESCRIPTIONS OF SIX NEW SPECIES

By
Ronald Fricke
Saalestrasse 3 a, D-3300 Braunschweig,
Federal Republic of Germany

ABSTRACT: The *kaianus*-group of the genus *Callionymus*, subgenus *Callionymus*, is revised. The recognized species and their ranges are: *Callionymus kaianus* Günther, 1880 (Kai Islands, eastern Indonesia); *Callionymus moretonensis* Johnson, 1971 (northern half of Australia, New Ireland, New Caledonia); *Callionymus whiteheadi* n.sp. (southwestern Indonesia); *Callionymus guentheri* n.sp. (Philippine Islands); *Callionymus formosanus* n.sp. (Formosa Strait, Taiwan); *Callionymus sokonumeri* Kamohara, 1936 (southern Japan); *Callionymus altipinnis* n.sp. (South China Sea: China coast); *Callionymus ochiaii* n.sp. (southern Japan); *Callionymus regani* Nakabo, 1979 (Saya de Malha Bank, western-central Indian Ocean); *Callionymus kotthausi* nom. nov. (for *Callionymus indicus* (Kotthaus, 1977), a secondary homonym; India); *Callionymus africanus* (Kotthaus, 1977) (east Africa); *Callionymus bentuviai* n.sp. (southern Red Sea); *Callionymus carebares* Alcock, 1890 (northern Indian Ocean).

INTRODUCTION

The dragonets of the family Callionymidae are a group of benthic marine fishes (except for two euryhaline species which enter and even live in freshwater rivers). About 130 species are known. The two largest genera, *Callionymus* and *Synchiropus,* are nearly circumtropical in warm and temperate seas, but some species also live in cold waters; e.g., *Callionymus lyra* and *C. maculatus* of the northern Atlantic follow the warm Gulf Stream to Iceland and northern Norway. Callionymids usually live on sand or mud bottoms, sometimes also on coral sand bottom in coral reefs, or among seaweed, from very shallow waters and even tide pools down to about 800 m.

Callionymus is the largest genus of the family, comprising about 75 species. Fricke (1980) distinguished three subgenera (*Callionymus, Calliurichthys,* and *Spinicapitichthys*) which differ principally in the shape of the preopercular spine. The subgenus *Callionymus* is the largest, comprising about 55 species which can be arranged into various species groups. The *kaianus*-group is one of the larger species groups and contains deepwater mud-bottom species of the Indian and western Pacific oceans.

Seven of the species included in the *kaianus*-group have been described. *Callionymus kaianus* Günther, 1880, was originally described from Kai Islands, west of New Guinea, and later recorded from India, Indonesia, Saya de Malha Bank (western-central Indian Ocean), Zanzibar, Arabian Sea, Japan, Pescadore Islands (near Taiwan), Gulf of Tonkin, and the coast of China. Johnson (1971) described a new subspecies, *Callionymus kaianus moretonensis,* from northeastern Australia. *Callionymus carebares* Alcock, 1890, was described from the Bay of Bengal; *C. sokonumeri* Kamohara, 1936, from Japan; and *C. regani* Nakabo, 1979, from the Saya de Malha Bank. Under the generic name *Diplogrammus*, Kotthaus (1977) described two further species, *D. africanus* and *D. indicus*.

I found several closely allied new species, which are described and compared in the present paper, from examination of specimens (most previously identified as *Callionymus kaianus*) in the Australian Museum, Sydney (AMS); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Faculty of Agriculture of Kyoto University, Kyoto (FAKU); Fish Collection, Hebrew University of Jerusalem (HUJF); Institut Royal des Sciences Naturelles, Brussels (IRSN); Marine Science Laboratory, Chinese University of Hong Kong (MSL); Staatliches Naturhistorisches Museum, Braunschweig (NMB); Zoologisches Institut und Zoologisches Museum der Universität Hamburg (ZIM); and Museum für Naturkunde, Zoologisches Museum, East Berlin (ZMB).

METHODS

Methods used are the same as those in my previous papers (especially Fricke 1980; Fricke 1981a).

The preopercular spine formula, explained by Fricke (1981a), is calculated by the following formula:

$$a\frac{b}{c}d,$$

where a is the number of antrorse spines at the base, b is the number of points or serrae at the dorsal edge, c is the number of points or serrae at the ventral edge, and d is 1 and reflects the main tip of the spine. The formula treats simplified *left* spines. Right spines have to be treated as left (e.g., the number of antrorse spines at the base, a, is always on the left side of the formula).

The pectoral fin base is divided in two by a membrane connecting it with the fifth pelvic fin ray. The formula a/b is used where a is the pectoral fin base length above the connecting membrane, b is the corresponding length below.

THE *CALLIONYMUS KAIANUS*-GROUP

The *Callionymus kaianus*-group, including the new species described in this paper, comprises thirteen deepwater mud-bottom species in the subgenus *Callionymus* (see Fricke 1980:59) distributed in the Indian and west Pacific oceans (Figs. 1 & 2): *Callionymus kaianus, C. moretonensis, C. whiteheadi, C. guentheri, C. sokonumeri, C. formosanus, C. altipinnis, C. ochiaii, C. regani, C. kotthausi, C. africanus, C. bentuviai*, and *C. carebares*. The group is characterized by the presence in its members of large eyes; dorsal and anal fin formulae D IV + viii,1, A (vii,1–)viii,1; one or two unbranched median caudal fin rays which are often filamentous; a characteristic shape of the preopercular spine (see Fig. 3); and (usually) a characteristic black blotch on the third membrane of the first dorsal fin.

Species of the *kaianus*-group are similar to the deepwater mud-bottom species groups of the genus *Synchiropus* (e.g., *phaeton*-group, *altivelis*-group), agreeing with them in some aspects of body shape and even color markings (black spot on third membrane of first dorsal fin, etc.). The *Synchiropus* species groups are easily distinguished from the *kaianus*-group by the shape of the preopercular spine and by generic differences between *Callionymus* and *Synchiropus* discussed in detail in my revision of the genus *Synchiropus* (Fricke 1981b).

Characters and distribution of the species of the *kaianus*-group are compared in Tables 1–2. Further distinguishing features (not compared in the tables) include other proportions, the preopercular spine shape, and body color pattern.

Key to the Species of the *Callionymus kaianus*-Group

1a. Head in SL 2.7–3.1; branchial opening very broad, same size as or larger than pupil; upper edge of preopercular spine with 2 large curved points, but without a small antrorse point ...... *C. carebares*
1b. Head in SL 3.4–4.6; branchial opening small, about ⅓–½ of pupil; upper edge of preopercular spine with 1 small antrorse and 1 or 2 large curved points 2

2a. D_2 and anal fins very high, males with convex distal margins 3
2b. D_2 and anal fins relatively low, with straight distal margins 6

3a. First spine of D_1 filamentous 4
3b. First spine of D_1 not filamentous 5

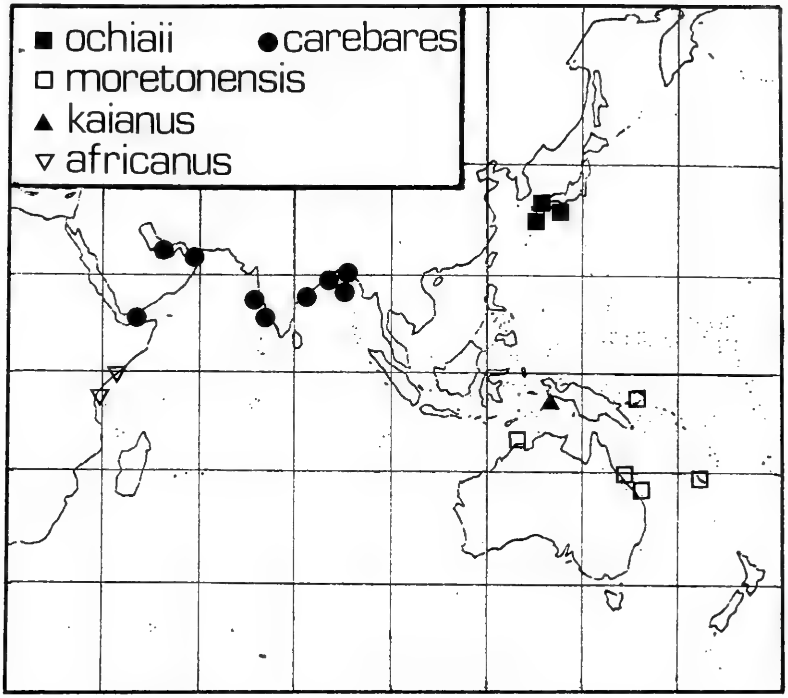


FIGURE 1. Geographical distribution of species of the *kaianus*-group of the genus *Callionymus*.

4a. D_2 relatively low, 1st ray about 1.0, 5th ray about 0.9 in head length; preopercular spine with 2 curved points (and 1 small antrorse point) at its upper side; black blotch on 3rd membrane of D_1 large, nearly covering entire membrane; anal fin with a distal black streak on each membrane; distal ⅔ of anal fin dark brown, tips of rays white .... *C. formosanus*

4b. D_2 high, 1st ray about 1.1, 5th ray about 0.8 in head; preopercular spine with 1 large curved point (and 1 small antrorse point) at its upper side; black blotch on 3rd membrane of D_1 small, distal in position; anal fin without a distal black streak on each membrane; distal margin of anal fin black, tips of fin rays also black .... *C. altipinnis*

5a. Main tip of preopercular spine long and slender; distal half of anal fin black, tips of rays white; distal margin of caudal fin regular; black blotch on 3rd membrane of D_1 relatively large, central in position (not reaching distal margin) .... *C. guentheri*

5b. Main tip of preopercular spine short; anal fin with a distal black streak on each membrane, distal ⅔ of membranes and tips of fin rays brown; distal margin of caudal fin irregular; black blotch on 3rd membrane of D_1 very small, extremely distal in position .... *C. sokonumeri*

6a. Caudal fin convex, without filaments .. 7

6b. Caudal fin convex or slightly pointed, with 1 or 2 filaments 10

7a. Anal fin with a small distal yellow margin or colorless; sides of body with a row of large indistinct brownish blotches .... *C. regani*

7b. Anal fin with a broad dark brown or black margin; sides of body with a row of small distinct black blotches 8

8a. Main tip of preopercular spine long and slender; lower part of caudal fin colorless .... *C. kotthausi*

8b. Main tip of preopercular spine short; lower part of caudal fin with a broad black streak 9

9a. Pectoral fin base with a large dark brown

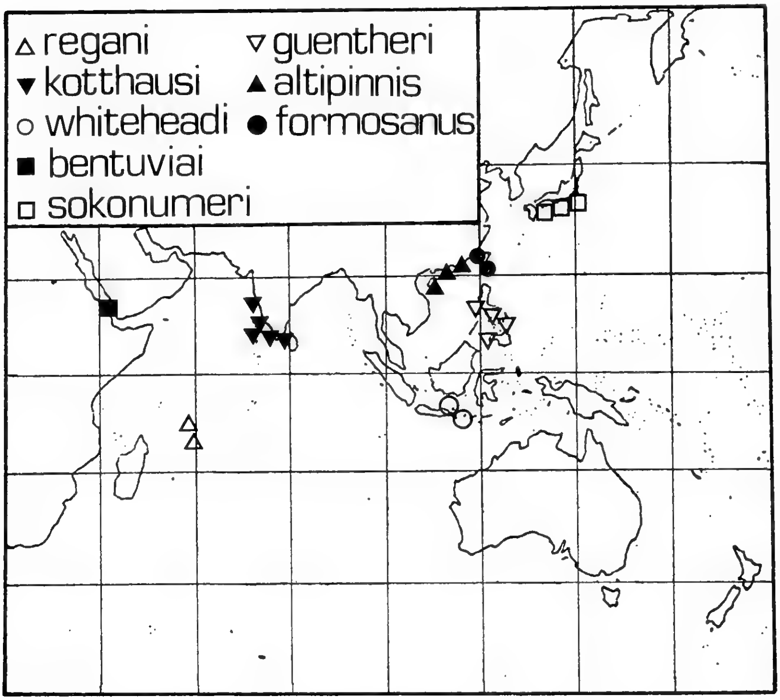


FIGURE 2. Geographical distribution of species of the *kaianus*-group of the genus *Callionymus*.

area; back marbled with olive-green; operculum with large white spots; lower part of caudal fin black distally; D_2 with a basal row of dark blotches .... *C. whiteheadi*

9b. Pectoral fin base with 2 black streaks; back yellowish brown, with white blotches surrounded by semicircular dark brown bands; operculum with small black spots; lower part of caudal fin with a broad, curved black band, but colorless distally; D_2 without a basal row of black spots .... *C. africanus* (female)

10a. First spine of D_1 with a long filament 11

10b. First spine of D_1 without a filament .. 13

11a. Main tip of preopercular spine short, largest point on its dorsal side with a basal hook; D_2 colorless, with transverse white lines; sides of body with a row of distinct black blotches .... *C. kaianus*

11b. Main tip of preopercular spine long and slender, largest point on its dorsal side without a basal hook; D_2 with rows of blotches; sides of body with a row of indistinct brownish blotches 12

12a. Anal fin with a dark margin; D_2 with 2 rows of white blotches and a darkish distal margin; main tip of preopercular spine about 2.5–3.0 times as long as largest point at its dorsal side; body with light blotches edged with semicircular dark lines .... *C. moretonensis*

12b. Anal fin pale, without a dark margin; D_2 with a basal and 2–3 more distal rows of dark spots; main tip of preopercular spine about 1.0–1.5 times as long as largest point at its dorsal side; body with minute blackish spots forming rings and blotches .... *C. ochiaii*

13a. Second membrane of D_1 deeply incised; caudal fin with 2 long filaments which are nearly twice as long as rest of fin; D_1 with 2 or more black blotches, largest reaching from 1st to 4th spine; D_2 with vertical dark streaks .... *C. bentuviai*

13b. Second membrane of D_1 not incised; caudal fin with 1 or 2 relatively short filaments which are not longer than rest of fin; D_1 with a black blotch on 3rd membrane (rarely also with an additional black blotch distally on the same membrane), occasionally reaching to 2nd spine; D_2 with rows of dark and/or light blotches (but without vertical dark streaks) 14

14a. Lateral line in area behind eye with a long branch running downwards; D_1 with a large black blotch basally on 3rd membrane, 1 or 2 branches of which reach 2nd membrane; pectoral fin base with 2 dark streaks; anal fin with a distal black margin (usually including tips of fin rays); caudal fin without 2 median transverse black lines; D_2 with 1 basal, 1 median, and 1 distal row of light spots and 2 median rows of black spots .... *C. africanus* (male)

14b. Lateral line without a branch in the postorbital area; D_1 with a relatively small distal black blotch on 3rd membrane; pectoral fin base with a dark area; distal half of anal fin black, tips of fin rays white; caudal fin with 2 median transverse black lines; D_2 with a basal and a median row of black blotches .... *C. guentheri* (female)

Callionymus carebares Alcock, 1890

(Figures 4–5)

Callionymus carebares ALCOCK, 1890:209 ("off Madras coast, 98–102 fms"); 1898:73; 1899:pl. 20, fig. 4; REGAN 1906:329 (Sea of Oman, 98–180 fms [179–329 m]); SMITH 1963:555, pl. 84K (after Alcock).

MATERIAL EXAMINED.—**Syntypes:** BMNH 1890.11.28.18–24, 2 ♂, 5 ♀, "Investigator," off Ganjam Coast, India.

Other specimens: BMNH 1903.5.14.34, 1 spec., 39.0 mm SL, J. W. Townsend, Karachi. BMNH 1903.9.24.2–4, 3 spec., J. W. Townsend, Iranian Mekran coast, Gulf of Oman (25°19′N, 58°21′E), 98 fms (179 m). BMNH 1904.5.25.218–220, 3 spec., J. W. Townsend, Sea of Oman, 180 fms (329 m). BMNH 1939.5.24.1384, 1 spec., John Murray Exped., 23 Nov. 1933, Gulf of Oman, 193 m. BMNH 1939.5.24.1385–1409, 24 spec., John Murray Exped., Arabian Sea, 135–183 m. BMNH 1939.5.24.1410–1421, 15 spec., John Murray Exped., Gulf of Aden, 220 m. IRSN 1797, 2 ♀, M. Frank, 4 Apr. 1894, Gulf of Bengal. FMNH 5740, 1 ♀, J. W. Townsend, 1906, Sea of Oman (Dr. D. J. Stewart, FMNH, kindly examined the specimen).

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a very large branchial opening (same size as, or larger than, pupil), an unusually large head (head length in SL 2.7–3.1), and two large curved points, but without a small antrorse spine at dorsal edge of preopercular spine.

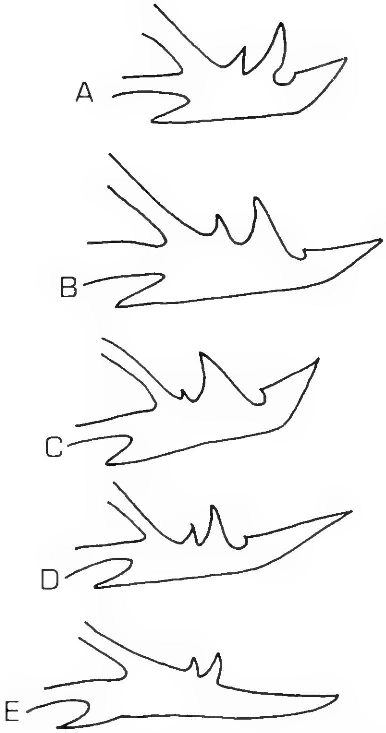


FIGURE 3. Preopercular spines of species of the *kaianus*-group. The main characteristics are the straight ventral side of the spine, the strong straight antrorse point, the upcurved main tip, and the antrorse spine in combination with two (rarely one) large curved points on the dorsal side. (*A*) Left preopercular spine of *Callionymus kaianus*. (*B*) Left preopercular spine of *C. guentheri*. (*C*) Left preopercular spine of *C. africanus*. (*D*) Left preopercular spine of *C. moretonensis*. (*E*) Left preopercular spine of the most primitive species of the *kaianus*-group, *C. carebares* (without an antrorse point on the dorsal side).

DESCRIPTION.—Counts and measurements (see also Table 1): D_1 IV; D_2 viii,1; A viii,1; P_1 ii–iii,14–16,iii; P_2 I,5; C ii,2–3,0–ii,2–4,iii.

Body elongate and depressed. Head very large, depressed, 2.7–3.1 in SL. Eye large, 2.7–3.5 in head. Pupil large, about 2.5 in eye. Branchial opening very large, same size as pupil or larger. Occipital region with a bony plate and two low bony protuberances. Preopercular spine nearly as long as eye diameter, with a long, slightly upcurved main tip, two curved points at its dorsal side and a large antrorse spine at its

TABLE 1. CHARACTER AND DISTRIBUTIONAL COMPARISONS OF SPECIES OF THE *Callionymus kaianus*-GROUP (see also Table 2). SL = standard length; HL = head length.

	C. regani	*C. kotthausi*	*C. bentuviai*	*C. africanus*	*C. whiteheadi*	*C. carebares*
Distribution area	Saya de Malha Bank	S India	S Red Sea	E African coast	W Indonesia	N Indian Ocean
Fin rays: D	IV + viii,1	IV + viii,1	IV + viii,1	IV + viii,1	IV + viii,1	IV + viii,1
A	viii,1	viii,1	viii,1	viii,1	viii,1	viii,1
P	19–21	19–21	18–20	19–22	19–20	21
Preopercular spine formula	$1\frac{3}{-}1$	$1\frac{2\text{–}3}{-}1$	$1\frac{3}{-}1$	$1\frac{3}{-}1$	$1\frac{2\text{–}3}{-}1$	$1\frac{2}{-}1$
Head length in SL	ca. 4.1	3.8–3.9	3.6–4.0	3.9–4.1	3.9–4.2	2.7–3.1
Predorsal (1) length in SL	ca. 3.7	3.3–3.4	3.4–3.7	3.5–3.6	3.5–3.6	2.2–2.6
Predorsal (2) length in SL	ca. 2.3	2.2–2.3	2.1–2.3	2.1–2.3	2.2–2.3	1.8–1.9
Preanal length in SL	ca. 2.1	2.0–2.1	1.8–2.1	1.9–2.1	1.9–2.0	1.6–1.8
Eye diameter in HL	ca. 2.7	2.3–2.5	2.1–2.9	2.0–2.2	2.2–2.3	2.7–3.5
Pelvic fin length in HL	ca. 1.0	1.1–1.2	0.8–0.9	1.0–1.1	1.1–1.2	1.3–1.5
First D_1 spine in HL	ca. 1.15	1.3–1.4	0.9–1.1	1.3–1.5	1.2–1.3	1.7–1.8
Longest C ray in SL	ca. 3.0 (♂♂ and ♀♀)	2.0 (♂♂)–3.3 (♀♀)	1.2–1.7	2.4–3.3	3.4–3.7	2.5–3.4
First D_1 spine filament	lacking	lacking or very short	lacking	lacking	lacking	very short, only in ♀♀
Caudal fin filaments	lacking	lacking or (rarely in ♂♂) 2 (very short)	2 (very long)	2 (short)	lacking	2 (very short)
Second D_1 membrane	present as usual	present as usual	deeply inserted	present as usual	present as usual	present as usual
Distal dark streak on A	absent	present	present (very broad)	present (narrow)	present	present
Dark blotch on D_1	only on 3rd membrane	♂: 2 blotches on 2nd & 3rd membranes; ♀: 1 blotch from 1st to 3rd membrane	2 dark blotches on 3rd membrane; lower one reaching to 1st spine	1 dark blotch on 3rd membrane; occasionally reaching to 2nd spine	on 3rd membrane, basal in position, w/basal branch to 2nd membrane	♀♀: on 2nd & 3rd membrane. ♂♂: black spot lacking
Head color pattern	cheeks dark brn. w/ light spots	brn. w/some irregular darkish spots	brn. w/black spots on operculum	w/few irregular darkish spots	many dark spots on cheeks	monochromatic gray
Caudal fin color pattern	nearly colorless	w/3–4 vertical rows of lt. brownish spots	upper part w/small, lower part w/broad dark curved line	upper part w/small dark spots, lower part w/broad dark band	upper part w/large dark blotches; lower part distally dark	distal margin dark
Fifth ray D_2 in HL	ca. 1.35	ca. 1.65	ca. 1.2	ca. 1.5	1.5–1.7	1.8–2.0
Fifth ray A in HL	ca. 2.05	ca. 2.25	ca. 1.9	ca. 2.3	2.5–2.6	2.2–2.3
D_2 color pattern	w/white spots & lines	w/3 rows dark blotches	w/9 vertical dark streaks	w/rows of dark & white spots	basal row of dark spots	distal margin darkish

TABLE 2. CHARACTER AND DISTRIBUTIONAL COMPARISONS OF SPECIES OF THE *Callionymus kaianus*-GROUP (see also Table 1). SL = standard length; HL = head length.

	C. kaianus	*C. moretonensis*	*C. guentheri*	*C. altipinnis*	*C. sokonumeri*	*C. ochiaii*	*C. formosanus*
Distribution area	Kai Is.	N Austr., sw Pac.	Philippines	S. China Sea	s Japan	s Japan	Taiwan
Fin rays: D	IV + viii,1	IV + viii,1	IV + viii,1	IV + viii,1	IV + viii,1	IV + viii,1	IV + viii,1
A	viii,1	viii,1	viii,1	viii,1	viii,1	viii,1	viii,1
P	21–22	19–21	21	17–18	18–20	18–21	20–21
Preopercular spine formula	$1\frac{3}{-}1$	$1\frac{3}{-}1$	$1\frac{3}{-}1$	$1\frac{2}{-}1$	$1\frac{3}{-}1$	$1\frac{3}{-}1$	$1\frac{3}{-}1$
Head length in SL	ca. 4.6	3.4–4.7	ca. 4.0	ca. 4.2	3.6–4.4	3.5–4.4	ca. 4.5
Predorsal (1) length in SL	ca. 3.8	3.0–3.8	ca. 3.45	ca. 3.6	ca. 3.9	ca. 3.7	ca. 3.75
Predorsal (2) length in SL	ca. 2.4	2.1–2.4	ca. 2.2	ca. 2.25	ca. 2.3	ca. 2.25	ca. 2.4
Preanal length in SL	ca. 2.2	1.8–2.2	ca. 2.0	ca. 2.0	ca. 2.15	ca. 2.05	ca. 2.25
Eye diameter in HL	ca. 2.35	2.0–2.4	ca. 2.3	ca. 2.55	2.1–2.9	2.3–3.0	ca. 2.3
Pelvic fin length in HL	ca. 1.0	ca. 0.95	ca. 1.0	ca. 0.95	0.9–1.1	ca. 1.0	ca. 0.9
First D_1 spine in HL	ca. 0.85	0.8–1.5	ca. 1.2	ca. 0.65	ca. 1.0	ca. 1.4	ca. 0.7
Longest C ray in SL	ca. 2.4	2.5–3.7	ca. 2.0	ca. 2.6	ca. 2.45	ca. 3.0	ca. 2.15
First D_1 spine filament	present	present (short)	lacking	present	lacking	present (very short)	present
Caudal fin filaments	2	2 (short)	1–2 in ♂♂	1(–2)	2 (long)	2 (short)	1(–2?)
Second D_1 membrane	present as usual	present as usual	present as usual	present as usual	present as usual	present as usual	present as usual
Distal dark streak on A	absent	present	present	present	present	absent	present
Dark blotch on D_1	on 3rd membrane, basally reaching to 2nd membrane	on 3rd membrane, a basal branch reaching to 2nd spine	distally on 3rd membrane	distally on 3rd membrane	distally on 3rd membrane	on 3rd membrane; occasionally w/ a branch to 2nd membrane	only on 3rd membrane
Head color pattern	lt. brn. w/irregular dark blotches & spots	monochromatic brn.	w/few dark spots	monochromatic	w/few dark blotches	like body pattern	brn. w/few light spots
Caudal fin color pattern	upper part w/ irregular dark spots, lower part w/a dark band	upper & lower parts w/dark streaks	upper part w/few small dark spots, lower part w/a dark band	dusky	w/irregular whitish spots	upper part: w/ irregular dark spots; lower part w/a dark band	upper part w/few dark spots; lower part w/a dark lower & distal area
Fifth ray D_2 in HL	ca. 1.2	1.2–1.7	ca. 1.4	ca. 0.8	0.7–1.3	1.2–2.2	ca. 0.9
Fifth ray A in HL	ca. 1.75	1.4–2.4	ca. 1.85	ca. 1.2	ca. 1.2	ca. 2.0	ca. 1.3
D_2 color pattern	white streaks	2 rows white spots	dark spots or vertical dark streaks	colorless	gray, w/vertical dark streaks	w/irregular dark markings	w/vertical light streaks; anterior distal part black

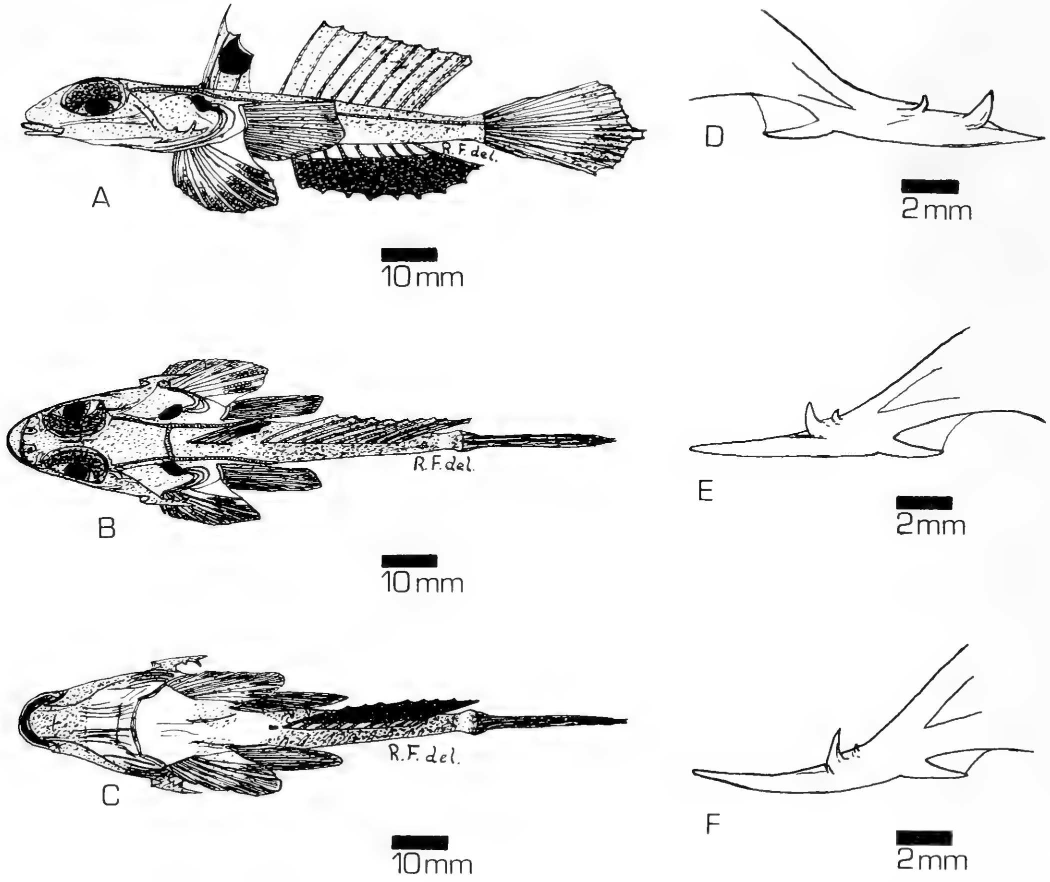


FIGURE 4. *Callionymus carebares*, IRSN 1797, Gulf of Bengal. Specimen 1, female, 85.8 mm SL: (*A*) lateral view; (*B*) dorsal view; (*C*) ventral view; (*D*) left preopercular spine; (*E*) right preopercular spine. Specimen 2, female, 86.2 mm SL: (*F*) right preopercular spine.

base (formula: $1\overset{2}{\text{———}}1$; see Fig. 4*D–F*). Lateral line reaching from hind margin of eye to base of caudal fin; the line of the opposite side is interconnected by a transverse branch across the occipital region. Caudal peduncle length 5.8–6.6 in SL, minimal caudal peduncle depth 21.0–22.6 in SL.

First spine of first dorsal fin nearly as long as first ray of second dorsal fin, filamentous only in females. Distal margin of second dorsal fin straight. Anal fin beginning on vertical through second ray of second dorsal fin. Distal margin of caudal fin slightly convex, the two median rays elongate but usually not filamentous. Outer edge of pelvic fin convex; longest pelvic fin ray reaching to base of first anal fin ray. Pectoral fin reaching nearly to fifth ray of second dorsal fin when laid back.

Color in alcohol. Head and body dark gray, belly white. Eye darkish. First dorsal fin in male monochromatic dark, in female nearly colorless, with a large distal dark blotch reaching from second to fourth spine. Second dorsal fin colorless, distal margin darkish. Distal one-third of caudal fin dark. Distal two-thirds of anal fin black, anal fin base colorless. Pelvic fin colorless, pectoral fin with few dark spots.

DISTRIBUTION.—Northern parts of Indian Ocean: Gulf of Aden, Gulf of Oman, coast of India, Arabian Sea (see Fig. 1); 135–330 m on muddy bottoms.

DISCUSSION.—*Callionymus carebares* seems to be the most primitive member of the *kaianus*-group based on the shapes of its preopercular spine (no antrorse spine at its dorsal side) and caudal fin (often no median unbranched ray

FIGURE 5. First dorsal fin in *Callionymus carebares*. (*A*) BMNH 1890.11.28.18, male, 95.0 mm SL, syntype, Ganjam coast, India. (*B*) BMNH 1890.11.28.19, female, 86.2 mm SL, syntype, Ganjam coast, India.

present). It is also unique, however, in its very large head and its extremely large branchial opening (which is porelike and very small in other callionymid fishes). Therefore, it seems to belong to another evolutionary branch in the *kaianus*-group, and I assign it to a subgroup of its own. Juvenile specimens, which have a smaller head and a smaller branchial opening, are more similar to the other species of the *kaianus*-group.

Callionymus kaianus Günther, 1880

(Figure 6)

Callionymus kaianus GÜNTHER, 1880:44, pl. 19, fig. B (Kai Is., 129 fms [236 m]); DE BEAUFORT 1951:66–67, fig. 12 (after Günther); SMITH 1963:553, pl. 84*J* (in part; after Günther); SUWARDJI 1965:308–310 (Kai Is., 180–290 m).

MATERIAL EXAMINED.—**Holotype:** BMNH 1879.5.14.565, 1 ♂, 128.6 mm SL, *Challenger* Exped., Kai Is.

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening, a short head (about 4.6 in SL), preopercular spine with a small antrorse and two large curved points on dorsal side, straight distal margin of second dorsal fin, two short caudal fin filaments, long filamentous first spine of first dorsal fin, short main tip of preopercular spine, and pale anal fin.

DESCRIPTION.—Counts and measurements (see also Table 2): D_1 IV; D_2 viii,1; A viii,1; P_1 ii,17–18,ii; P_2 I,5; C ii,2,ii,3,iii.

Body elongate and depressed. Head depressed, about 4.6 in SL. Eye large, 2.35 in head. Pupil relatively small, 3.3 in eye. Branchial opening of normal size, about two times in pupil. Occipital region with two low bony protuberances. Preopercular spine 1.45 in eye diameter, with a relatively short, slightly upcurved main tip, a small antrorse and two large curved points (the larger with a small additional basal point) on its dorsal side and a large antrorse spine at its base (formula: $1\frac{3}{-}1$; see Fig. 6*B*). Lateral line reaching from area behind eye to end of third branched caudal fin ray (seen

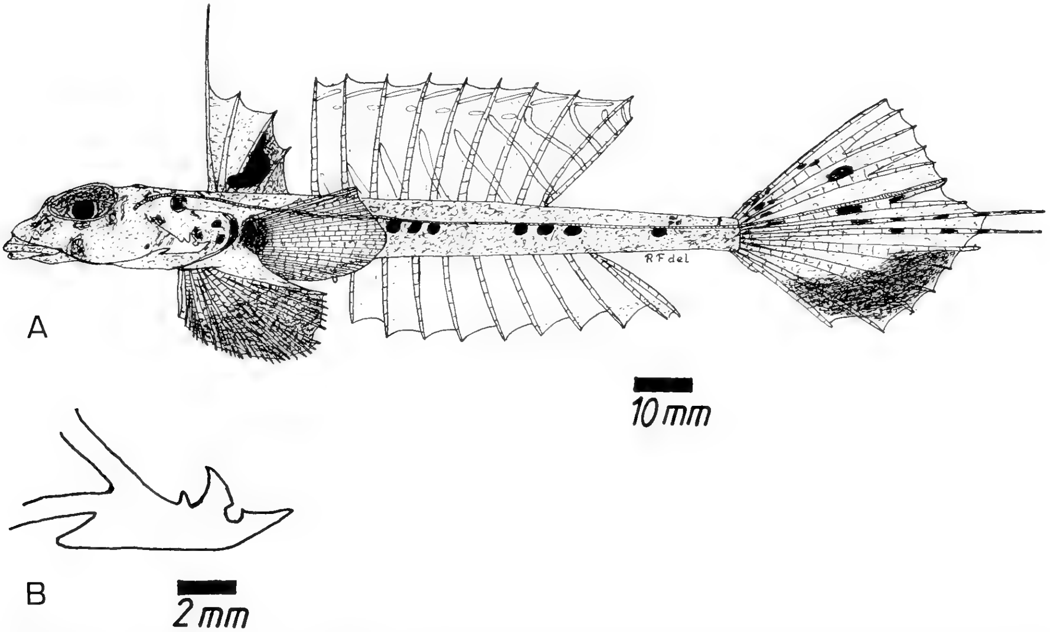


FIGURE 6. *Callionymus kaianus*, BMNH 1879.5.14.565, holotype, male, 128.6 mm SL, Kai Islands: (*A*) lateral view; (*B*) left preopercular spine.

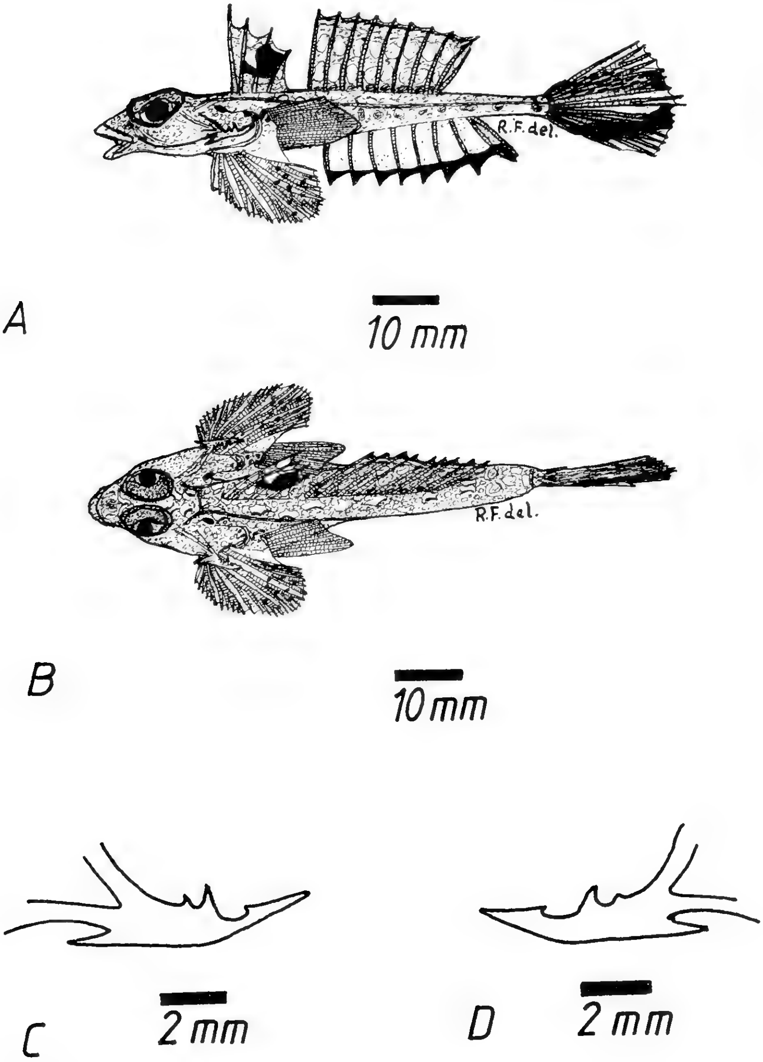


FIGURE 7. *Callionymus moretonensis*, NMB 37074, 69.4 mm SL, New Caledonia: (*A*) lateral view; (*B*) dorsal view; (*C*) left preopercular spine; (*D*) right preopercular spine.

from above); the line of one side is interconnected to its opposite member by a transverse branch across the occipital region and one across the dorsal side of caudal peduncle. Caudal peduncle length 5.2 in SL, minimal caudal peduncle depth 23.8 in SL.

First spine of first dorsal fin long and filamentous. Distal margin of second dorsal fin straight. Anal fin beginning on the vertical through midbase of second membrane of second dorsal fin. Distal margin of caudal fin pointed, the two unbranched median rays filamentous (filaments relatively short). Distal margin of pelvic fin convex; longest pelvic fin ray only reaching the anal papilla. Pectoral fin reaching to second anal fin ray when laid back.

Color in alcohol. Head and body light brown, back with some lighter blotches. Belly white, thorax brownish. Eye light gray. Pectoral fin base with a large dark blotch. A row of dark blotches in groups along body side. Operculum with some dark spots, head with indistinct brownish blotches and lines. First dorsal fin light, with a black blotch on third membrane, a basal branch of which reaches nearly to second spine. Second dorsal fin colorless, with white lines in characteristic arrangement (see Fig. 6*A*). Anal fin colorless, with few yellow pigment on the membranes between the five posterior rays. Upper and median parts of caudal fin with dark spots and blotches; lower part with a broad curved dark band. Distal part of pelvic fin dark; pectoral fin colorless.

DISTRIBUTION.—Kai Islands (west of New Guinea), at three different localities (Fig. 1); 180–290 m, muddy bottom.

DISCUSSION.—*C. kaianus* differs from *C. moretonensis* of northern Australia, the species geographically nearest, by its shorter main tip of preopercular spine, and by various color markings (e.g., pale anal fin without a black distal margin); it differs from *C. whiteheadi* by the presence of filaments in the first dorsal and caudal fins, the barbed largest point on dorsal side of preopercular spine, and various color markings.

Specimens referred to *C. kaianus* from the Gulf of Thailand seem to belong to another species.

Callionymus moretonensis Johnson, 1971

(Figure 7)

Callionymus calauropomus: (nec Richardson, 1844) PETERS, 1876:841 (New Ireland); JORDAN AND SEALE 1905:415 (after Peters); FOWLER 1928:422 (after Peters); MUNRO 1958:253 (after Peters).

Callionymus kaianus moretonensis JOHNSON, 1971:108–113, figs. 1–2 (s Queensland); 1973:217–230 (biology).

MATERIAL EXAMINED.—**Holotype:** AMS I15608–001, 1 spec., 158.3 mm SL, C. R. Johnson, 1 Aug. 1969, E of Cape Moreton, Queensland, 68–72 fms (124–132 m). **Paratypes:** CAS 24764, 1 spec., 131.2 mm SL; CAS 24765, 1 spec., 134.0 mm SL; CAS 24766, 1 spec., 141.7 mm SL; CAS 24767, 1 spec., 164.9 mm SL; all with same data as holotype.

Other specimens: BMNH 1892.1.14.26–27, 2 spec., 52.4–58.2 mm SL, Mr. Walker, Holothuria Banks (NW Australia). ZMB 9399, 1 ♂, 1 juv., 35.0–81.9 mm SL, R/V GAZELLE, "shortly before the year 1876," New Ireland. NMB 37074, 1 spec., 69.4 mm SL, P. Fourmanoir, 1979, Havannah, s New Caledonia, 150 m.

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (3.4–4.7 in SL); preopercular spine with a small antrorse and two large curved points on its dorsal side and a long, slender main tip; second dorsal fin with a nearly straight distal margin; caudal fin with two short median filaments; first dorsal fin with a relatively long, filamentous first spine; anal fin with a dark distal margin; and second dorsal fin with rows of white blotches and a dark distal margin.

DESCRIPTION.—Counts and measurements (see also Table 2): D_1 IV; D_2 viii,1; A vii,1–viii,1; P_1 ii,18–20; P_2 I,5; C i–ii,3–4, (0–)i–ii,2–3,ii–iii.

Body elongate and depressed. Head depressed, about 3.4–4.7 in SL. Eye large, 2.0–2.4 in head. Pupil relatively small, 2.9–3.0 in eye. Branchial opening of normal size, about 2–3 times in pupil. Occipital region with two low bony protuberances. Preopercular spine about 1.1–1.2 in eye diameter, with a long slightly upcurved main tip, a small antrorse and two large curved points at its dorsal side, and a large antrorse spine at its base (formula: $1\frac{3}{-}1$; see Fig. 7*C, D*). Lateral line reaching from area behind eye to end of third branched caudal fin ray (counted from above); the line of the opposite side is interconnected by a transverse branch across the occipital region and one across the dorsal side of the caudal peduncle. Caudal peduncle length 5.8–6.5 in SL, minimal caudal peduncle depth 23.0–30.0 in SL.

First spine of first dorsal fin relatively long and filamentous (in adults). Distal margin of second dorsal fin straight. Anal fin beginning on a vertical through second ray of second dorsal fin. Distal margin of caudal fin convex in small specimens (somewhat pointed in adults), with two short median filaments. Distal margin of pelvic fin convex; longest pelvic fin ray reaching nearly to midbase of first membrane of anal fin. Pectoral fin reaching to fourth ray of second dorsal fin.

Color in alcohol. Head and body light brown, ventral side of body and belly whitish. Thorax white. Back with white spots bordered by semicircular black lines. Eye grayish. A row of irregular brownish spots along sides of body. Head with small white spots. Some dark spots at upper part of pectoral fin base. First dorsal fin light brown, with a large black blotch on third membrane, a basal branch of which reaches to second spine, and some smaller white blotches surrounding it. Second dorsal fin with two or three rows of white spots and a darkish distal margin. Anal fin colorless, with a black distal border. Pelvic fin with small dark spots on distal parts of fourth and fifth rays. Pectoral fin colorless or with three vertical rows of darkish spots. Caudal fin whitish, with some dark spots forming a broad curved band in the upper part, a broad curved black band in the lower part.

DISTRIBUTION.—Northern half of Australia (Holothuria Banks to southern Queensland), New Caledonia, and New Ireland (see Fig. 1); 101–150 m, mud bottom.

DISCUSSION.—The differences between *C. kaianus* and *C. moretonensis* are discussed in the description of the former species. *Callionymus moretonensis* differs from *C. whiteheadi* by the presence of filaments in first dorsal and caudal fins, by the shape of the main tip of the preopercular spine, and by color markings.

The record of *Synchiropus calauropomus* (Richardson, 1844) from New Ireland (Peters 1876) is based on two specimens of *Callionymus moretonensis*. *Synchiropus calauropomus* does not occur in that area.

Johnson (1971) originally described *C. moretonensis* as a subspecies of *C. kaianus*, but the differences are sufficient to regard *C. moretonensis* as a distinct species.

Callionymus whiteheadi new species

(Figure 8)

?*Callionymus kaianus*: (non Günther, 1880) WEBER 1913: (Madura Sea, 7°2.6′S, 115°23.6′E, 100 m).

MATERIAL EXAMINED.—**Holotype:** BMNH 1980.6.20.1, 112.3 mm SL, P. J. P. Whitehead, 14 July 1979, off Bali (8°50′S, 114°14′E), 110–220 m. **Paratype:** BMNH 1980.11.25.2, 1 spec., 105.5 mm SL, P. J. P. Whitehead, summer 1979, SE coast of Java (near type-locality).

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (3.9–4.2 in SL); preopercular spine with a small antrorse and one or two large curved points, and a short main tip; second dorsal fin with a nearly straight distal margin; caudal fin with a convex distal margin, but without filaments; first dorsal fin without a filament and with a basal black blotch on third membrane; light brown cheeks with few dark spots; anal fin with a black distal margin; second dorsal fin with a basal row of dark spots; and sides of body with a row of distinct black blotches.

DESCRIPTION.—Counts and measurements (see also Table 1): D_1 IV; D_2 viii,1; A viii,1; P_1 i–ii,15–17,ii; P_2 I,5; C ii,3,i–ii,2–3,iii.

Body elongate and depressed. Head depressed, 3.9–4.2 in SL. Eye large, 2.2–2.3 in head. Pupil relatively small, about 3.2 in eye. Branchial opening of normal size, about 3 times in pupil. Occipital region with two low bony protuberances. Preopercular spine 1.7–1.9 in eye diameter, with a short, slightly upcurved main tip, a small antrorse and one or two large curved points at its dorsal side, and a large antrorse spine at its base (formula: $1\overset{2\text{–}3}{\text{———}}1$; see Fig. 8*B*). Lateral line reaching from area behind eye to third branched caudal fin ray (counted from above); the line of the opposite side is interconnected by a transverse branch across the occipital region and another across the dorsal side of caudal peduncle. Caudal peduncle length 5.5–6.1 in SL, minimal caudal peduncle depth 25.5–26.3 in SL.

First spine of first dorsal fin somewhat longer than first ray of second dorsal fin, but not filamentous. Distal margin of second dorsal fin nearly straight. Anal fin beginning on the vertical through second ray of second dorsal fin. Distal margin of caudal fin convex; no median filaments. Distal margin of pelvic fin convex; longest pelvic ray only reaching to anal papilla when laid back. Pectoral fin reaching to midbase of second membrane of second dorsal fin when laid back.

Color in alcohol. Head and body dark olive-green; lower surface of body white. Back marbled with brown. Thorax and belly white. A dark area at upper part of pectoral fin base. Some large whitish spots bordered by black on operculum. Head with dark brown spots and lines. Eye dorsally black, ventrally dark blue. A row of irregular black blotches along sides of body. First dorsal fin olive-green; first spine marbled alternating black and white; a large black blotch basally on third membrane, a basal branch of which reaches to second spine. Second dorsal fin with two rows of indistinct darkish blotches and a basal row of distinct blackish blotches. Anal fin white, with a broad distal black margin. Caudal fin rays in upper part of caudal fin with black blotches; lower part of caudal fin blackish distally. Distal two-thirds of pelvic fin darkish; upper half of pectoral fin with four vertical rows of black spots.

DISTRIBUTION.—Bali and southeastern Java, possibly also Madura Sea (see Fig. 2); 110–220 m, mud bottom.

DISCUSSION.—The differences between *C. whiteheadi*, *C. kaianus*, and *C. moretonensis* have been discussed in the descriptions of the last two species. *C. whiteheadi* differs from *C. regani* by the shape of the preopercular spine and by various color markings (e.g., black border of anal fin; shape and position of black blotch in first dorsal fin; color patterns of second

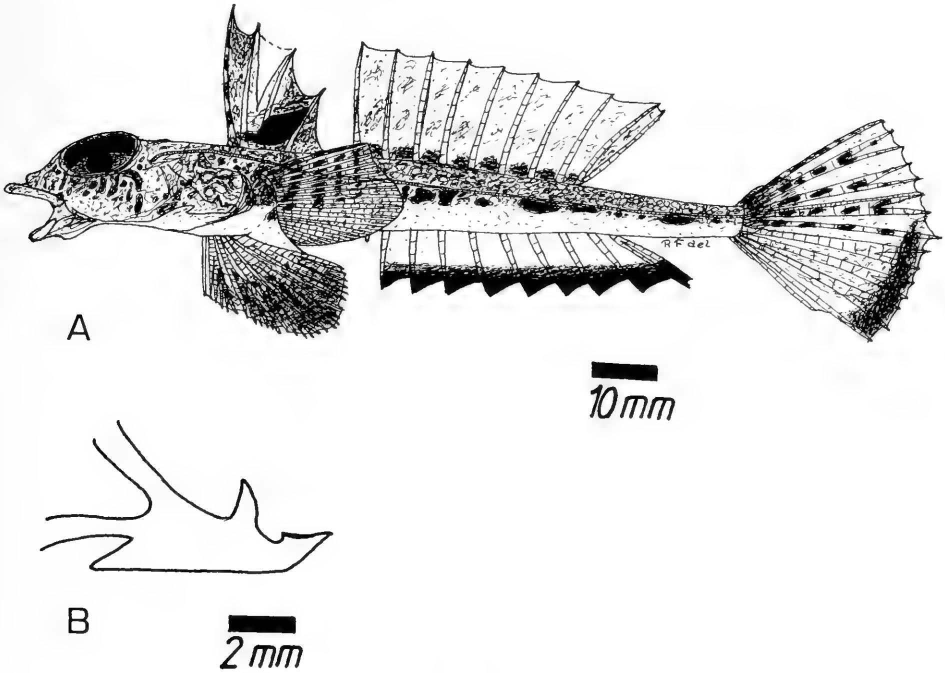


FIGURE 8. *Callionymus whiteheadi*, holotype, BMNH 1980.6.20.1, 112.3 mm SL, off Bali: (*A*) lateral view; (*B*) left preopercular spine.

dorsal and caudal fins; body color pattern, etc.). It differs from *C. guentheri* in lacking caudal fin filaments, in the different shape of the preopercular spine, and in various color markings.

ETYMOLOGY.—This new species is named after Dr. Peter J. P. Whitehead, British Museum (Natural History), who collected the type-specimens and allowed me to examine them.

Callionymus regani Nakabo, 1979

(Figure 9)

Callionymus kaianus: (non Günther, 1880) REGAN 1908:248 (Saya de Malha Bank, 123 fms [225 m]); SMITH 1963 (part):553 (after Regan).

Callionymus regani NAKABO, 1979:231–234, fig. 1, table 1 (Saya de Malha Bank).

MATERIAL EXAMINED.—BMNH 1908.3.23.263, 1 ♂, 101.3 mm SL, Gardiner-Expedition, Saya de Malha Bank (western-central Indian Ocean), "over 123 fms" (225 m).

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (about 4.1 in SL); preopercular spine with a small antrorse and two large curved points at dorsal side, and a short main tip; second dorsal fin with a nearly straight distal margin; caudal fin with a convex distal margin but without filaments; first dorsal fin without a filament and with a distal black blotch on third membrane surrounded by white lines; dark brown cheeks with characteristic light blotches; colorless anal fin without a distal black margin; second dorsal fin with rows of white spots and lines; and sides of body with few large indistinct brownish blotches.

DESCRIPTION.—Counts and proportions (see Table 1): D_1 IV; D_2 viii,1; A viii,1; P_1 i–iii,17–19,0–i; P_2 I,5; C 0–ii,3,i–ii,2–3,ii–iii.

Body elongate and depressed. Head depressed, 4.1 in SL. Eye large, about 2.7 in head. Pupil relatively small, 3.4 in eye diameter. Branchial opening of normal size, about 3 in pupil. Occipital region with two low bony protuberances. Preopercular spine 1.4 in eye diameter, with a short, slightly upcurved main tip, a small antrorse and two larger curved points at its dorsal side, and a large antrorse spine at its base (formula: $1\underset{-}{\overset{3}{\text{———}}}1$; see Fig. 9*B*). Lateral line reaching from area behind eye to end of third branched caudal fin ray (seen from above); the line of the opposite side is interconnected by a transverse branch across the occipital region and another across the caudal peduncle. Caudal

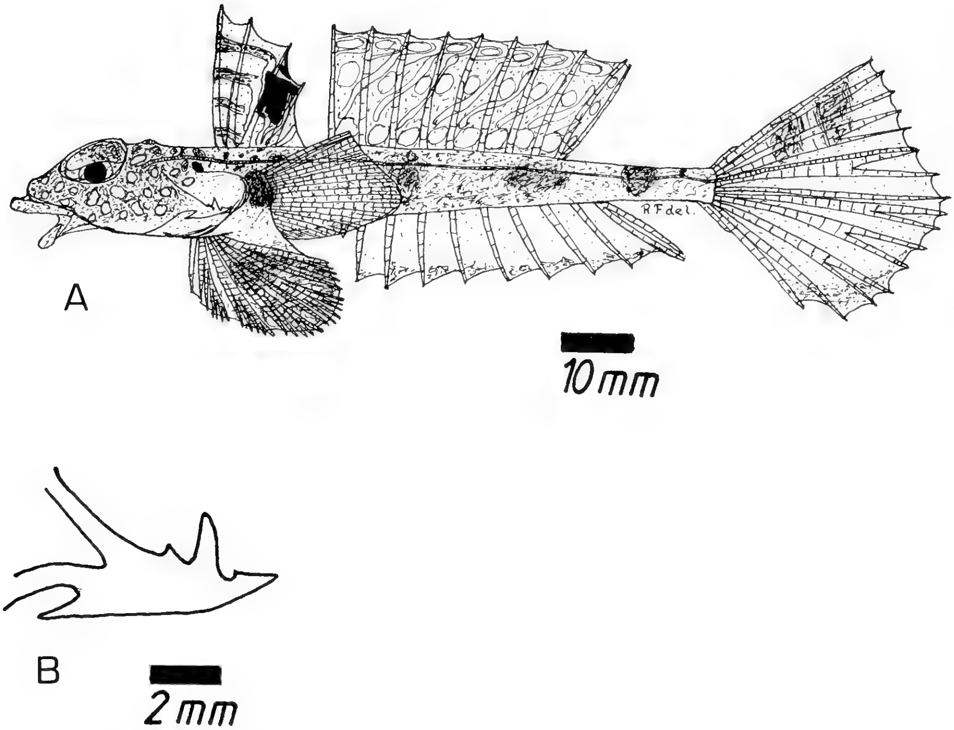


FIGURE 9. *Callionymus regani*, BMNH 1908.2.23.263, male, 101.3 mm SL, Saya de Malha Bank: (*A*) lateral view; (*B*) left preopercular spine.

peduncle length 6.25 in SL; minimal depth of caudal peduncle 22.5 in SL.

First spine of first dorsal fin somewhat longer than first ray of second dorsal fin, but not filamentous. Distal margin of second dorsal fin nearly straight. Anal fin beginning on vertical through second ray of second dorsal fin. Distal margin of caudal fin nearly convex; no median filaments. Distal margin of pelvic fin convex; longest pelvic fin ray reaching to base of first anal fin ray when laid back. Pectoral fin reaching to midbase of third membrane of second dorsal fin when laid back.

Color in alcohol. Head and body brown. Belly white, thorax light brown. Three to four large indistinct darkish areas along sides of body. Head brown; males with many light blotches, females with few light blotches. Occipital region with dark spots. Eye posteriorly gray, anteriorly yellowish. A large dark brown blotch at pectoral fin base. First dorsal fin pale; about four horizontal dark lines on first and second membranes. A black blotch distally on third membrane, occasionally reaching to posterior part of second membrane; distal edge of third membrane also black. Remaining parts of third and fourth membranes covered with curved white lines. Second dorsal fin mostly colorless, with rows of white blotches and/or lines. Anal fin pale; distal margin yellowish. Caudal fin pale, occasionally with two darkish blotches at upper edge; lower part sometimes dusky. Distal parts of fourth and fifth rays of pelvic fin darkish; pectoral fin colorless.

DISTRIBUTION.—Saya de Malha Bank, western-central Indian Ocean (see Fig. 2); 126–225 m.

DISCUSSION.—The differences from *Callionymus whiteheadi* were discussed in the description of that species. *Callionymus regani* differs from *C. africanus* by the absence of caudal fin filaments and by a completely different color pattern; it differs from *C. kotthausi* in its shorter main tip of preopercular spine, shorter first spine of first dorsal fin, shorter caudal fin (especially

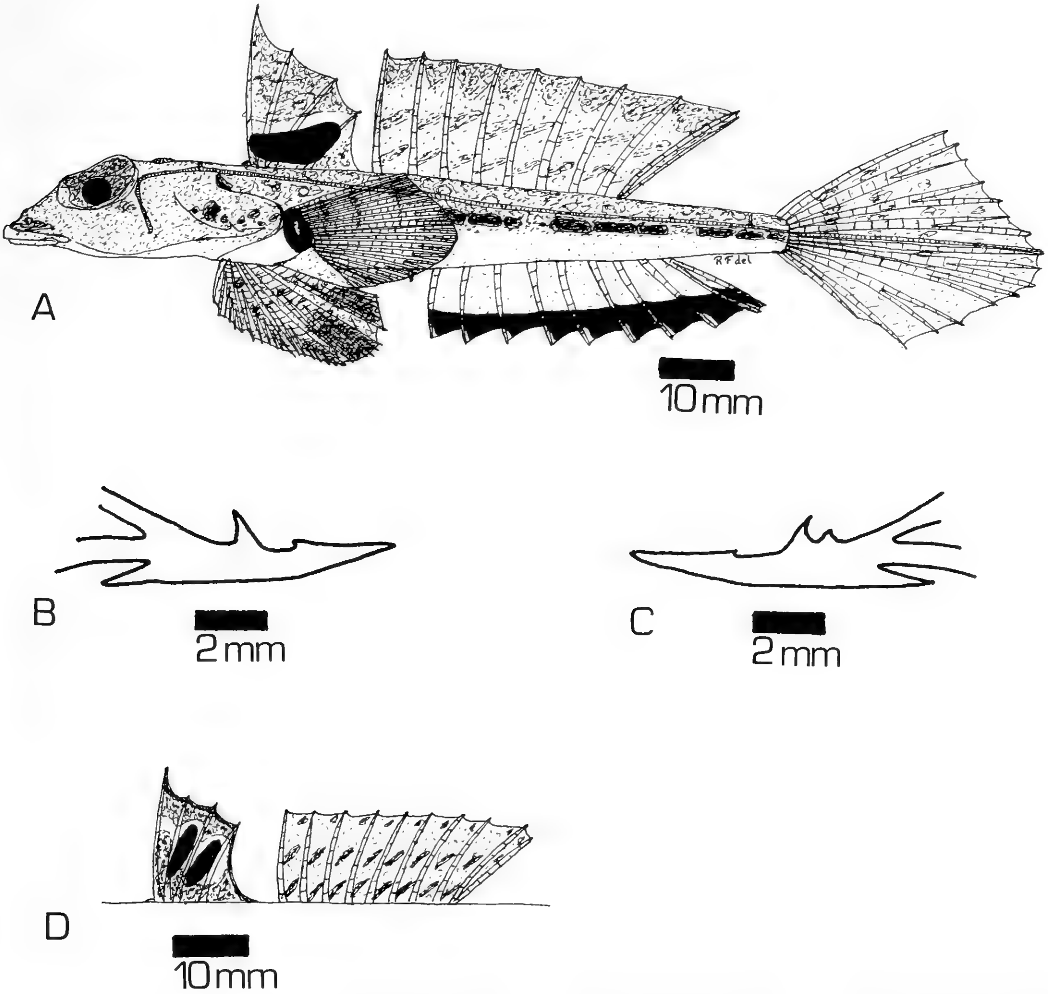


FIGURE 10. *Callionymus kotthausi*, ZIM 5535, holotype, 114.8 mm SL, off Cochin (India): (*A*) lateral view; (*B*) left preopercular spine; (*C*) right preopercular spine. ZIM 5536, paratype, specimen 1, male, 81.2 mm SL, Cochin: (*D*) first and second dorsal fins.

in males), and various color markings (e.g., color patterns of first and second dorsal fins, and anal fin, head, and sides of body).

Callionymus kotthausi new name

(Figure 10)

Callionymus kaianus: (non Günther, 1880) ALCOCK 1899:74 (Malabar Coast, India, 102 fms [187 m]).

Diplogrammus indicus KOTTHAUS, 1977:40–41, figs. 423*b*, 424*b*, 425 (wsw of Cochin, India).

MATERIAL EXAMINED.—**Holotype:** ZIM 5535, ♀, 114.8 mm SL, A. Kotthaus, R/V METEOR, 10 Feb. 1965, about 40 km wsw of Cochin, India (09°40′N, 75°38.8′E to 09°45.3′N, 75°38.5′E), 211–138 m. **Paratypes:** ZIM 5536, 2 ♂, 9 ♀, 71.3–87.0 mm SL; same data as holotype.

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (3.8–4.1 in SL); preopercular spine with a small antrorse and one or two large curved points, and a long main tip; second dorsal fin with a nearly straight distal margin; caudal fin without filaments; anal fin with a broad dark margin; sides of body with a row of small distinct black blotches; and colorless lower part of caudal fin.

DESCRIPTION.—Counts and measurements

(see also Table 1): D_1 IV; D_2 viii,1; A viii,1; P_1 i–ii,17,ii; P_2 I,5; C ii,3,i,3,iii.

Body elongate, depressed. Head depressed, 3.8–4.1 in SL. Eye large, about 2.4 in head. Pupil about 2.8 in eye. Branchial opening of normal size, about 2–3 times in pupil. Occipital region with a low bony protuberance. Preopercular spine about 1.4 in eye diameter, with a long upcurved main tip, a small antrorse and one or two large curved points on its dorsal side, and a large antrorse spine at its base (formula $1\frac{2-3}{\quad}1$; see Fig. 10*B*,*C*). Lateral line reaching from area behind eye to end of median unbranched caudal fin ray, with a long branch at its ventral side in postorbital region; the line of the opposite side is interconnected by a transverse branch across the occipital region and another across the caudal peduncle. Caudal peduncle length about 6.5 in SL; minimal caudal peduncle depth about 24.0 in SL.

First spine of first dorsal fin long (longer than first ray of second dorsal fin), but not filamentous. Distal margin of second dorsal fin nearly straight. Anal fin beginning on the vertical through third ray of second dorsal fin. Distal margin of caudal fin convex or slightly pointed, without filaments. Distal margin of pelvic fin convex; longest pelvic fin ray reaching only to anal papilla when laid back. Pectoral fin reaching to middle of third membrane of second dorsal fin when laid back.

Color in alcohol. Head and dorsal side of body yellowish brown; back with some dark-edged whitish blotches. Sides of body with a row of dark spots. Thorax, belly, and lower parts of body yellowish white. Eye dark gray. Operculum with dark spots. First dorsal fin brownish; males with one or two black blotches surrounded by white on second and third membranes; females with an elongate ocellated basal black blotch on first to third membranes. Second dorsal fin transparent, distally darkish, with two rows of elongate dark spots. Distal margin of anal fin black, tips of rays white. Caudal fin mostly colorless, with 3–4 vertical rows of light brown spots in its upper part. Distal half of fourth and fifth pelvic fin rays dark; pelvic fin basally with irregular darkish spots.

DISTRIBUTION.—Southwest coast of India (see Fig. 2); 138–211 m.

DISCUSSION.—Kotthaus (1977) assigned *Diplogrammus indicus* to the genus *Diplogrammus* using Smith's (1963:549) key: "A skinny keel along lower flank from tip of pelvic to caudal base," in combination with "an antrorse spine at base of preopercular spine." The latter feature is also valid for species of the genus *Callionymus*, but the specimens of "*Diplogrammus indicus*" have neither a skinny keel along lower flank of body, as in species of *Diplogrammus*, nor any other diagnostic feature of *Diplogrammus* (e.g., a free flap of skin at the operculum, a lateral line with many branches). Kotthaus's species belongs in the genus *Callionymus*, and it posseses all features of the *kaianus*-group of the subgenus *Callionymus*. The binomen *Callionymus indicus* (Kotthaus, 1977), however, becomes a secondary homonym of *Callionymus indicus* Linnaeus, 1758 (a Platycephalidae now well known as *Platycephalus indicus*) and must be replaced.

ETYMOLOGY.—The species is named after Dr. A. Kotthaus, who first described the species. In accordance with Dr. Kotthaus, who is presently unable to create a new name for the species because of his health, I propose the new name *Callionymus kotthausi* to replace *Callionymus indicus* (Kotthaus, 1977).

Callionymus africanus (Kotthaus, 1977)

(Figure 11)

Callionymus kaianus: (non Günther 1880) NORMAN 1939:73 (Zanzibar area); SMITH 1963 (part):553 (after Norman).
Diplogrammus africanus KOTTHAUS, 1977(part):38–40, figs. 421, 422, 423*a*, 424*a* (NE of Mombasa).

MATERIAL EXAMINED.—**Holotype:** ZIM 5533, ♀, 102.3 mm SL, A. Kotthaus, R/V METEOR, 14 Jan. 1965, about 180 naut. miles NE of Mombasa (01°18′S, 41°56′E to 01°19.8′S, 41°53′E). **Paratypes:** ZIM 5534, 11 ♂, 19 ♀, same data as holotype.

Other specimens: BMNH 1939.5.24.1422, 1 ♂, 75.5 mm SL, John Murray Exped., 12 Jan. 1934, near Zanzibar (5°38′54″S, 39°15′42″E to 5°40′18″S, 39°17′36″E); green mud bottom; bottom temperature 15.52°C; bottom salinity 35.21‰.

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (about 4.0 in SL); preopercular spine with a small antrorse and two larger curved points at dorsal side, and a relatively short main tip; nearly straight distal margin of second dorsal fin; two short median caudal fin filaments; first dorsal fin without a filament and with a normal (not incised) second membrane; anal fin with a narrow black distal margin; no vertically elongated dark blotches in median part of caudal fin; back with

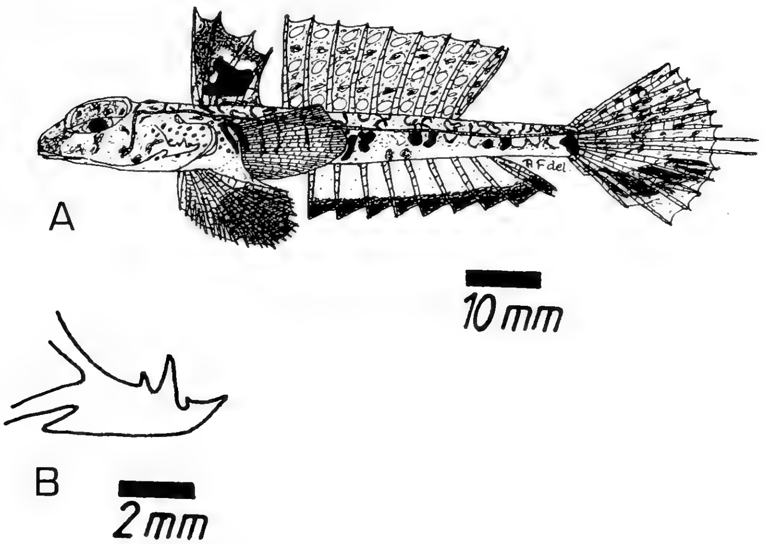


FIGURE 11. *Callionymus africanus,* BMNH 1939.5.24.1422, male, 75.5 mm SL, Zanzibar: (*A*) lateral view; (*B*) left preopercular spine.

dark-bordered light spots; and pectoral fin base with two transverse dark streaks.

Description.—Counts and proportions (see also Table 1): D_1 IV; D_2 viii,1; A viii,1; P_1 i–ii,16–20,i–ii; P_2 I,5; C ii,3,ii,2,iii.

Body elongate and depressed. Head depressed, 3.9–4.1 in SL. Eye large, 2.0–2.2 in head. Pupil relatively small, about 3.7 in eye diameter. Branchial opening of normal size, about 3 in pupil. Occipital region with two low bony protuberances. Preopercular spine 1.8 in eye diameter, with a short, slightly upcurved main tip, a small antrorse and two large curved points on its dorsal side, and a large antrorse spine at its base (formula: $1\overset{3}{\text{———}}1$; see Fig. 11*B*). Lateral line reaching from area behind eye to end of third branched caudal fin ray (counted from above); the line of the opposite side is interconnected by a transverse branch across occipital region and another across dorsal side of caudal peduncle. Lateral line with a long branch at its ventral side behind eye. Caudal peduncle length 6.0–6.1 in SL, minimal caudal peduncle depth 19.9–21.3 in SL.

First spine of first dorsal fin somewhat longer than first ray of second dorsal fin, but not filamentous. Distal margin of second dorsal fin nearly straight. Anal fin beginning on the vertical through second ray of second dorsal fin. Distal margin of caudal fin convex; males with two relatively short median filaments, females without filaments. Distal margin of pelvic fin convex; longest pelvic fin ray reaching to base of first anal fin ray when laid back. Pectoral fin reaching to fourth ray of second dorsal fin when laid back.

Color in alcohol. Head and body brown; ventral side of body lighter, belly and thorax white A row of paired dark brown blotches on side of body. Back with light spots bordered with dark brown. Pectoral fin base with two transverse dark lines. Eye dark blue, dorsally with dark brown blotches. First dorsal fin brown; a large white-edged black blotch basally on third membrane, a basal and a distal branch of which reaches to second spine; occasionally, also with a small distal black blotch on third membrane. Second dorsal fin with three rows of white and two rows of darkish spots; these rows alternately arranged. Anal fin pale, with a narrow black distal margin. Lower part of caudal fin with a broad curved dark bar, upper part scattered with dusky spots. Distal parts of fourth and fifth pelvic fin rays dark; upper part of pectoral fin with three vertical rows of dark spots.

Sexual Dimorphism.—As described by Kotthaus (1977:40).

Distribution.—Known from Zanzibar and southern Somalia (see Fig. 1), possibly distributed along entire east African coast; 212 m, mud bottom.

Discussion.—The differences from *Callionymus regani* are discussed in the description of that species. The two paratypes described by Kotthaus (1977:39) from the southern Red Sea are small specimens of *Callionymus bentuviai*.

Callionymus bentuviai new species

(Figure 12)

Diplogrammus africanus Kotthaus, 1977 (part):39 (s Red Sea).

Material Examined.—**Holotype:** HUJF 9935, 87.8 mm SL, A. Ben-Tuvia, 1957, Eritrea (Ethiopia; s Red Sea). **Paratypes:** HUJF 8068, 2 spec., 79.7–85.2 mm SL, same data as holotype; ZIM 5532, 2 spec., 34.2–46.9 mm SL, A. Kotthaus, R/V Meteor, 6 Dec. 1964, s Red Sea, 70–75 m.

Diagnosis.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (3.6–4.0 in SL); preopercular spine with a small antrorse and two larger curved points at its dorsal side, and a relatively long main tip; second dorsal fin with a nearly straight distal margin; two very long median caudal fin filaments; first dorsal fin without a filament and with a deeply incised second membrane; and second dorsal fin with vertical dark streaks.

Description.—Counts and proportions (see also Table 1): D_1 IV; D_2 viii,1; A viii,1; P_1 i–ii,15–17,i–ii; P_2 I,5; C ii,2–4,i–ii,2–3,ii–iii.

Body elongate and depressed. Head depressed, 3.6–4.0 in SL. Eye large, 2.15–2.85 in head. Pupil relatively small, about 2.7 in eye. Branchial opening of normal size, about 1.5 in pupil. Occipital region with two low bony protuberances. Preopercular spine 1.2–1.6 in eye diameter, with a long slightly upcurved main tip, a small antrorse and two larger curved points on its dorsal side, and a large antrorse spine at its base (formula: $1\overset{3}{\text{———}}1$; see Fig. 12*C,D*). Lateral line reaching from area behind eye to end of third branched caudal fin ray (counted from above); the line of the opposite side is interconnected by a transverse branch across occipital region and another across caudal peduncle. Caudal peduncle length 4.9–5.8 in SL, minimal caudal peduncle depth 23.1–24.9 in SL.

First spine of first dorsal fin longer than first ray of second dorsal fin, but not filamentous. Second membrane of first dorsal fin deeply incised (not in young specimens). Distal margin of second dorsal fin nearly straight. Anal fin beginning on the vertical through midbase of second membrane of second dorsal fin. Distal margin of caudal fin convex, with two very long median filaments. Distal margin of pelvic fin mostly convex; longest ray reaching to middle of second membrane of anal fin when laid back. Pectoral fin reaching to fourth ray of second dorsal fin when laid back.

Color in alcohol. Head and body dark brown; ventral side of body dark brown, belly whitish. Back nearly monochromatic, with very few small dark spots. A row of small pale blotches along side of body, occasionally also a row of two groups of three dark spots each. Many black spots on operculum and at pectoral fin base. First dorsal fin light brown, with two darkish transverse lines distally between first and third spines. A large, elongate, curved black blotch basally from first to fourth spine, mainly on third membrane. Another black blotch distally on third membrane. Second dorsal fin pale, with nine vertical dark streaks. Anal fin dark brown, with a black distal margin. Caudal fin pale; dorsal part with a narrow curved dark line, ventral part with a broad curved dark bar. Pelvic fin pale; upper one-third with three vertical rows of dark spots.

Distribution.—Known only from the southern Red Sea (see Fig. 2); 70–75 m.

Discussion.—*Callionymus bentuviai* differs from all other species of the *kaianus*-group in its deeply incised second membrane of the first dorsal fin, the absence of a dorsal fin filament in combination with two very long median caudal fin filaments, and an unusual color pattern (e.g., in the dorsal fins).

Etymology.—This species is named for Professor Adam Ben-Tuvia (Hebrew University of Jerusalem), who collected the holotype and sent it to me for examination.

Callionymus ochiaii new species

(Figure 13)

Callionymus kaianus: (non Günther, 1880) Ochiai, Araga, and Nakajima 1955:111–113, figs. 8–10, table 6 (various s Japan localities); Matsubara 1955:713 (after Ochiai, Araga, and Nakajima); Kamohara 1964:90 (Kochi Pref. to Kagoshima; deep-sea bottom, very rare); Masuda, Araga, and Yoshino 1975:261, pl. 84*D* (Kumano Bay south).

Material Examined.—**Holotype:** FAKU 23261, ♂, 95.0 mm SL, 1–3 Sep. 1954, Shibushi, Kagoshima Pref., Japan. **Paratypes:** FAKU 23257–23260 and FAKU 23275, 2 ♂, 3 ♀, 77.8–116.8 mm SL, same data as holotype.

Diagnosis.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head

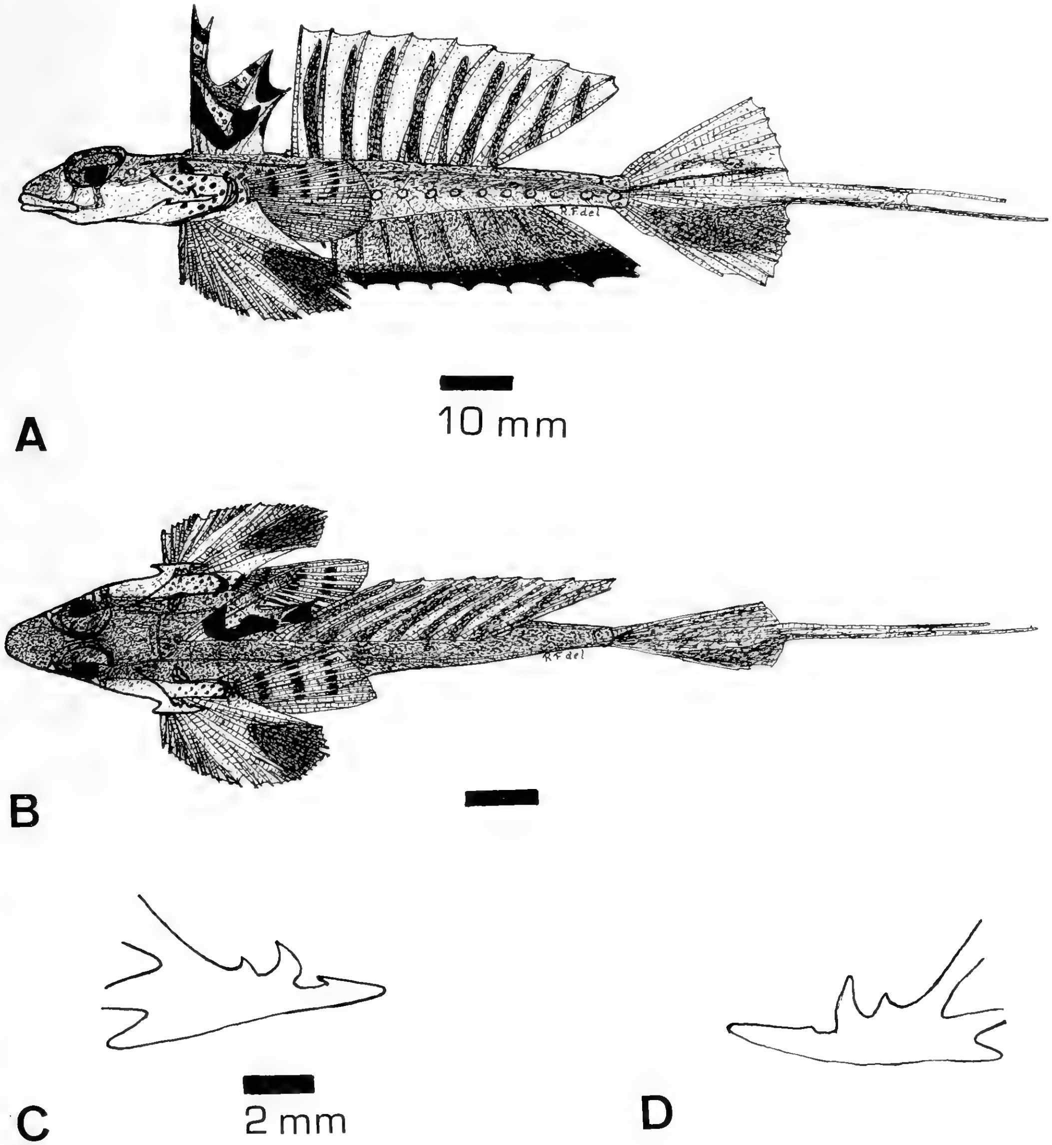


FIGURE 12. *Callionymus bentuviai*, HUJF 9935, holotype, 87.8 mm SL, Eritrea: (*A*) lateral view; (*B*) dorsal view; (*C*) left preopercular spine; (*D*) right preopercular spine.

(3.5–4.4 in SL); preopercular spine with a small antrorse and two larger curved points at its dorsal side, and a relatively long main tip; nearly straight distal margin of second dorsal fin; one or two short median caudal fin filaments; first dorsal fin with a long filament (males) or a filament of median size (females); anal fin without a distal dark margin; and long, slender main tip of preopercular spine, which is longer than the longest point on its dorsal edge.

DESCRIPTION.—Counts and proportions (see also Table 2): D_1 IV; D_2 viii,1; A viii,1; P_1 ii,16–18,i; P_2 I,5; C ii,3(–4),i,(2–)3,iii.

Body elongate and depressed. Head depressed, 3.5–4.4 in SL. Eye large, 2.3–3.0 in head. Pupil relatively small, about 3.65 in eye diameter. Branchial opening of normal size, about 2.5 in pupil. Occipital region with two low bony ridges. Preopercular spine 1.3–1.8 in eye diameter, with a long, slightly upcurved main

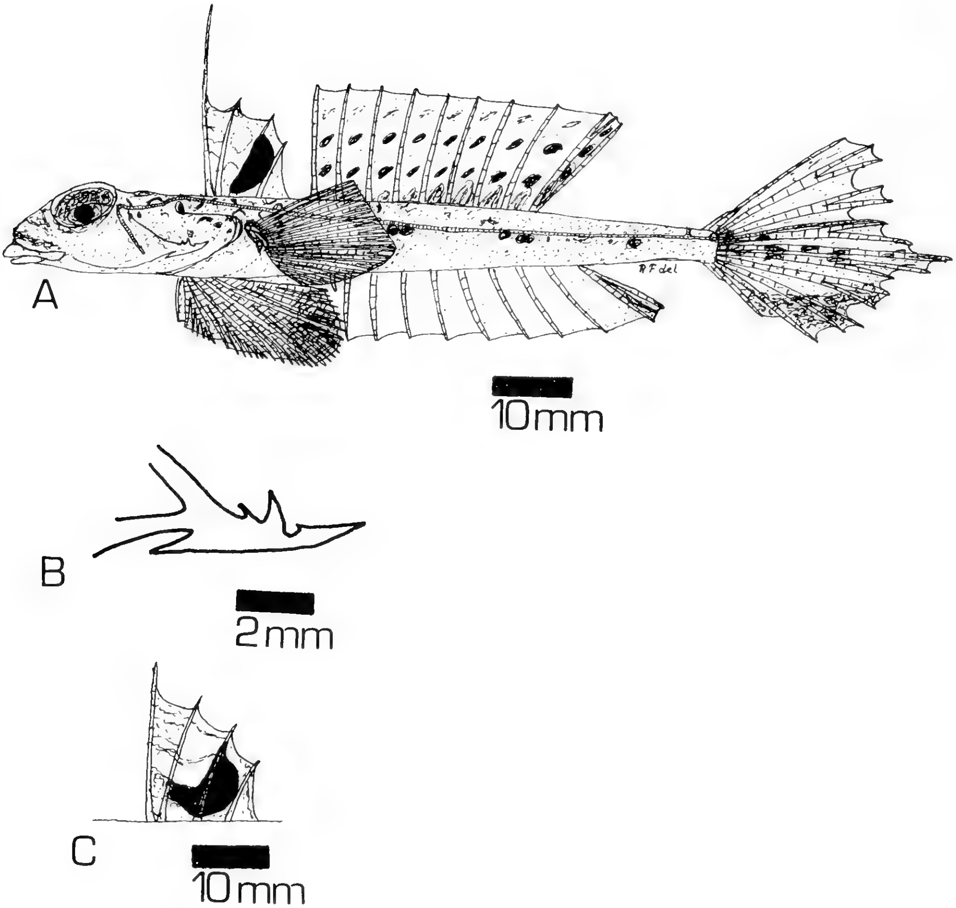


FIGURE 13. *Callionymus ochiaii,* holotype, FAKU 23261, male, 95.0 mm SL, Shibushi (Japan): (*A*) lateral view; (*B*) left preopercular spine. Paratype, FAKU 23258, female, 116.8 mm SL, Shibushi (Japan): (*C*) first dorsal fin.

tip, a small antrorse and two larger curved points at its dorsal side, and a large antrorse spine at its base (formula: $1\overset{3}{\text{———}}1$; see Fig. 13*B*). Lateral line reaching from area behind eye (from where a branch runs down to base of preopercular spine) to end of third branched caudal fin ray (counted from above); the line of the opposite side is interconnected by a transverse branch across occipital region and another across dorsal part of caudal peduncle. Caudal peduncle length 5.3–6.1 in SL; minimal caudal peduncle depth 24.3–27.8 in SL.

First spine of first dorsal fin filamentous (filament in females relatively short). Second membrane of first dorsal fin not incised. Distal margin of second dorsal fin nearly straight. Anal fin beginning on a vertical through midbase of second membrane of second dorsal fin. Distal margin of caudal fin irregular, with two short median filaments. Distal margin of pelvic fin convex; longest pelvic fin ray reaching to midbase of first anal fin membrane. Pectoral fin reaching to fourth ray of second dorsal fin when laid back.

Color in alcohol. Body brownish yellow above, whitish below. Back with minute blackish spots, forming rings and blotches. A row of dark brown blotches along sides of body. Pectoral fin base with a dark area. Head with some irregular dark spots and blotches. First dorsal fin gray, with a black blotch basally or centrally on third membrane, a basal branch of which occasionally reaches to second spine. Second dorsal fin gray, with large irregular dark blotches and submarginal dark bands. Caudal fin pale except for the darker lower part where the fin is scattered with several pale pearl-white round spots. Anal fin dusky, sometimes indefinitely but broadly edged with brown (but not with black). Pectoral fin uniformly pale; pelvic fin pale, outer posterior margin more or less dark.

DISTRIBUTION.—Southern Japan (see Fig. 1); about 100 m, sand and mud bottoms.

DISCUSSION.—From the most similar species, *C. moretonensis, C. ochiaii* differs in having a somewhat shorter main tip of preopercular spine, an irregular distal margin of caudal fin, and several different color markings (especially the absence of a distal black band in the anal fin; the color patterns of the caudal and second dorsal fins and of the pectoral fin base; the body color pattern, etc.). *Callionymus ochiaii* differs from *C. kaianus* in the shape of the largest point on the dorsal side of the preopercular spine, in the length of the filament in the first dorsal fin, and in various color markings.

The first dorsal fin filament of the male specimen figured in Ochiai, Araga, and Nakajima (1955:fig. 8) is very short. Because the specimen (91.0 mm SL) is nearly as long as the holotype (95.0 mm SL), the filament might have been broken in that specimen.

ETYMOLOGY.—This new species is named for Dr. Akira Ochiai, who first described the species under the name *Callionymus kaianus*.

Callionymus formosanus new species

(Figure 14)

?*Callionymus kaianus:* (non Günther, 1880) CHU 1957:22 (Pescadores Islands).

MATERIAL EXAMINED.—**Holotype:** CAS 46972, ♂, 104.0 mm SL, F. B. Steiner, Apr. 1971, Formosa Str. (25°N, 120°E), approximately 90 m.

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (about 4.5 in SL); preopercular spine with a small antrorse and two larger curved points at dorsal side; relatively high second dorsal and anal fins with convex distal margins; filamentous first spine of first dorsal fin; large black blotch nearly on entire third membrane of first dorsal fin; anal fin with a distal black streak on each membrane; distal two-thirds of anal fin brown; and white anal fin ray tips.

DESCRIPTION.—Counts and proportions of the holotype (see also Table 2): D_1 IV; D_2 viii,1; A viii,1; P_1 ii,16–17,ii; P_2 I,5; C ii,3,ii,2,iii.

Body elongate and depressed. Head depressed, about 4.5 in SL. Eye large, about 2.3 in head. Pupil relatively small, about 3.4 in eye diameter. Branchial opening of normal size, about 2.5 in pupil. Occipital region with two low bony ridges. Preopercular spine about 1.7 in eye diameter, with a slightly upcurved main tip of medium size, a small antrorse and two larger curved points at its dorsal side, and a large antrorse spine at its base (formula: $1\frac{3}{-}1$; see Fig. 14*B*). Lateral line reaching from area behind eye (from where a long branch runs downwards) to middle of upper median unbranched caudal fin ray; the line of the opposite side is interconnected by a transverse branch across occipital region and another across dorsal side of caudal peduncle. Caudal peduncle length 4.9 in SL, minimal caudal peduncle depth 13.0 in SL.

First spine of first dorsal fin filamentous. Second dorsal fin relatively high, distal margin convex. Anal fin beginning on a vertical through midbase of first membrane of second dorsal fin. Distal margin of caudal fin convex, with one relatively long filament. Distal margin of pelvic fin convex; longest pelvic fin ray reaching to midbase of first membrane of anal fin. Pectoral fin reaching to third ray of second dorsal fin when laid back.

Color in alcohol. Body dark brown, belly whitish. Side of body with a row of irregular blackish blotches. Head dark brown, with some lighter spots. A vertical dark streak under the eye. A dark blotch at pectoral fin base. Back and sides of body with whitish dark-edged blotches. First dorsal fin pale, with a large dark blotch on third membrane and three white blotches on first and second membranes. Second membrane with a distal black margin. Second dorsal fin pale, with a vertical white streak on each fin ray. Distal margin of first three rays of second dorsal fin black. Anal fin pale, distal two-thirds brownish, with a distal black streak on each membrane; tips of fin rays white. Caudal fin pale, with a vertical row of dark spots; lower margin and lower distal margin dark. Pelvic fin with irregular darkish spots and a dark distal margin of third, fourth, and fifth rays. Upper part of pectoral fin with three vertical rows of dark spots.

DISTRIBUTION.—Known only from Formosa Strait (see Fig. 2): about 90 m.

DISCUSSION.—This interesting new species belongs to the subgroup of species with a high second dorsal fin in the *kaianus*-group. It seems

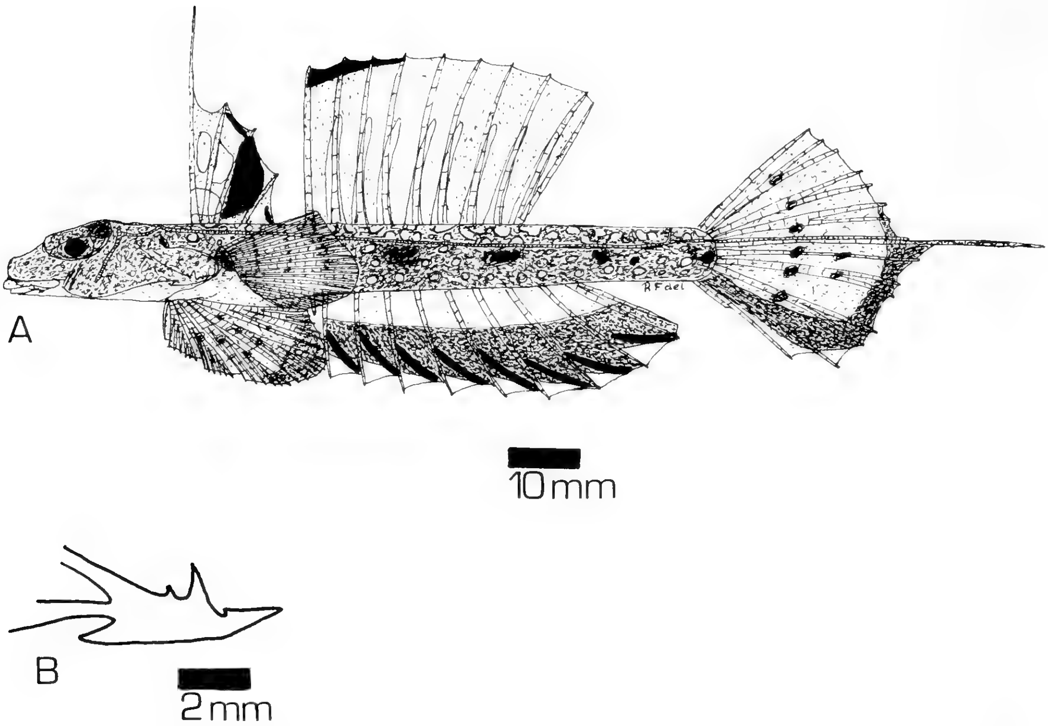


FIGURE 14. *Callionymus formosanus*, holotype, CAS 46972, male, 104.0 mm SL, Formosa Strait: (*A*) lateral view; (*B*) left preopercular spine.

to be a primitive member of that subgroup because the second dorsal fin is still relatively low.

The specimen recorded as *Callionymus kaianus* by Chu (1957) from Pescadores Islands (southern part of Formosa Strait) is probably this species.

ETYMOLOGY.—This new species is named after its type-locality (Formosa Strait).

Callionymus guentheri new species

(Figures 15–17)

Callionymus curvicornis: (non Valenciennes, 1837) GÜNTHER 1880: 53 (Philippines, 82 fms [150 m]); HERRE 1953:777 (after Günther).

MATERIAL EXAMINED.—**Holotype:** BMNH 1879.5.14.567, ♀, 87.3 mm SL, CHALLENGER Exped., 26 Oct. 1874, W of Zamboanga, Philippine Is. (7°03′N, 121°48′E; entrance from Sulu Sea into Basilan Str., about 7 miles W of Mindanao I., and to the NW of Caldera Pt.), 82 fms (150 m). **Paratypes** (all from the Philippines collected by J. E. Norton, 1966): CAS 46966, 4 spec., 3 Nov., Sandoval Pt., Catanauan, Quezon, 70–78 fms (128–143 m); CAS 32897, 11 spec. (7 ♂, 4 ♀), 51.2–128.0 mm SL, 27 June, Lemery Town, Balayan Bay, Batangas, Luzon, 90–85 fms (165–155 m); CAS 33879, 1 ♀, 112.8 mm SL, 15 Dec., N of San Andres I., Marinduque, 151–158 fms (276–289 m); CAS 34286, 3 ♂, 100.0–108.3 mm SL, 14 Dec., NW of San Andres I., Marinduque, 137–139 fms (250–254 m); CAS 34197, 1 ♂, 8 ♀, 90.2–129.3 mm SL, 24 Nov., Siburio Pt., Ragay Gulf, Camarines Sur Prov., 319–324 fms (583–593 m); CAS 32905, 4 ♂, 3 ♀, 69.3–117.2 mm SL, 15 Nov., Buri Pt., Ragay Gulf, Camarines Sur Prov., 304–309 fms (556–566 m); CAS 34426, 1 ♀, 84.1 mm SL, 4 July, S of Bauan Town, Batangas Bay, Batangas Prov., 90–88 fms (165–161 m); CAS 34278, 4 ♀, 89.9–124.5 mm SL, 11 Dec., N of Melchor I., Marinduque, 120–126 fms (219–231 m); CAS 33864, 3 ♀, 90.0–127.3 mm SL, 23 Nov., Caurusan Pt., Ragay Gulf, Camarines Sur Prov., 302–308 fms (552–564 m); CAS 32916, 5 ♀, 91.0–118.2 mm SL, 11 Nov., Pusgo Pt., Ragay Gulf, Quezon, Luzon I., 60–67 fms (110–123 m); CAS 33703, 1 ♀, 122.0 mm SL, 25 June, S of Barrio Nomong Casto, Balayan Bay, 105–100 fms (183–192 m); CAS 34401, 1 ♀, 117.7 mm SL, 24 June, SE of Calaca Town, Balayan Bay, 65–55 fms (119–100 m); CAS 32997, 1 ♀, 107.5 mm SL, 15 June, Batangas, Balayan Bay, S of Barrio Sinisian, 95–99 fms (174–181 m); CAS 34190, 1 ♂ (113.2 mm SL), 1 ♀ (99.7 mm SL), 6 Nov., SE of Alibijaban I., Ragay Gulf, 81–88 fms (148–161 m); CAS 34272, 1 ♂, 108.0 mm SL, 14 Nov., Nagas Pt., Ragay Gulf, 297–299 fms (543–547 m); CAS 34154, 7 ♀, 91.1–129.2 mm SL, 3 Sep., N of San Andres Pt., Marinduque, 108–112 fms (197–205 m); CAS 32668, 2 ♀, 94.5–102.0 mm SL, 26 July, SE of Talaga, Batangas Bay, 138–131 fms (253–240 m); CAS 32801, 1 ♂, 91.9 mm SL, 25 Aug., NE of Salomague I., Marinduque, 142–150 fms (260–275 m); CAS 34205, 1 ♀, 127.0 mm SL, 10 Dec., NW of Baltazar I., Marinduque, 142–150 fms (260–275 m); CAS 34468, 1 ♀, 102.8 mm SL, 27 July, Lemery

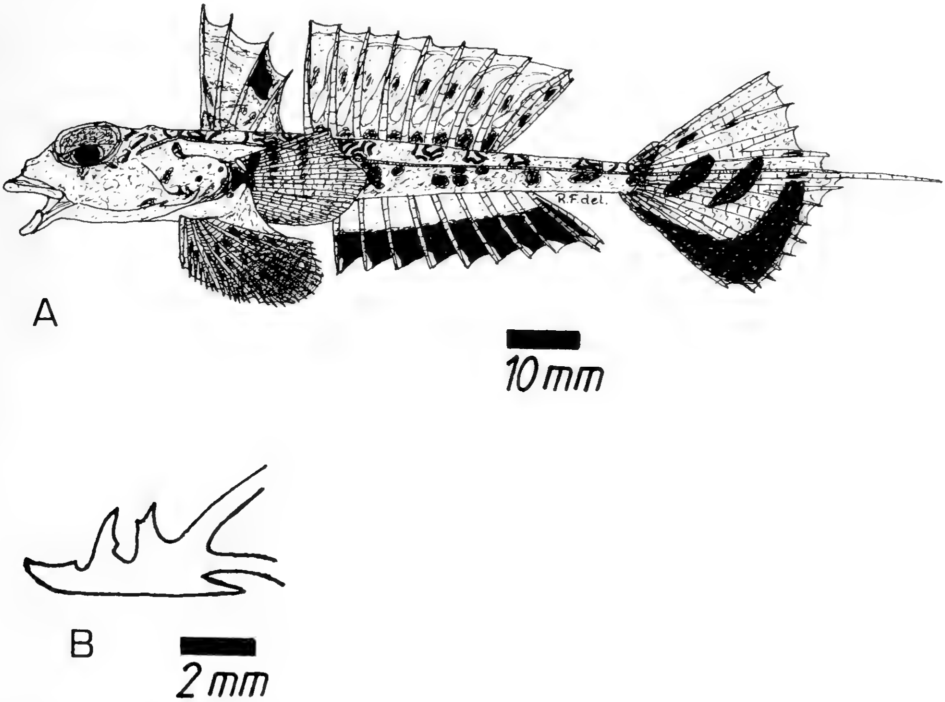


FIGURE 15. *Callionymus guentheri*, holotype, BMNH 1879.5.14.567, female, 87.3 mm SL, off Zamboanga, Philippines: (*A*) lateral view; (*B*) left preopercular spine.

Town, Balayan Bay, 85–90 fms (155–164 m); CAS 34074, 1 ♀, 123.2 mm SL, N of Sayao Bay, Marinduque, 61–70 fms (111–128 m); CAS 33067, 1 ♀, 125.2 mm SL, 18 July, S of Barrio Salong, Luzon I., 120–114 fms (220–208 m).

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (3.9–4.2 in SL); preopercular spine with a small antrorse and two larger curved points on dorsal side; very high second dorsal fin with a convex distal margin (males) or a relatively low second dorsal fin with a nearly straight distal margin (females); first dorsal fin without a filament (or with a very short one in smaller specimens); long and slender main tip of preopercular spine; anal fin with a black distal half and white fin ray tips; regular distal margin of caudal fin, with filaments only in small specimens (caudal fin elongate in adults); and relatively large central black blotch on third membrane of first dorsal fin.

DESCRIPTION.—Counts and proportions of the holotype (female) (see also Table 2): D_1 IV; D_2 viii,1; A viii,1; P_1 i–ii,17–19,i–ii; P_2 I,5; C ii,2–3,i–ii,2–4,iii.

Body elongate and depressed. Head depressed, 3.9–4.2 in SL. Eye large, 2.3–2.6 in head. Pupil of normal size, 2.7–3.5 in eye diameter. Branchial opening of normal size, about 2.0 in pupil. Occipital region with two low bony ridges. Preopercular spine 1.5–1.7 in eye diameter, with a slightly upcurved main tip which is relatively long or of medium size, a small antrorse and two larger curved points on its dorsal side, and a large antrorse spine at its base (formula: $1\frac{3}{\quad}1$; see Fig. 15*B*, Fig. 16*B*). The two large spines on the dorsal side of the preopercular spine of the holotype possess small basal hooks (see Fig. 15*B*). Lateral line usually reaching from area behind eye to end of third branched caudal fin ray (counted from above); because of the different caudal fin formula of the holotype (C ii,2,i,4,iii instead of C ii,3,ii,2,iii), the lateral line reaches to middle of median unbranched caudal fin ray in that specimen. The lateral line of the opposite side is interconnected by a transverse branch across occipital region and another across dorsal side of caudal peduncle. Caudal peduncle length 5.1–6.0 in SL, minimal caudal peduncle depth 23.0–26.0 in SL.

First spine of first dorsal fin somewhat longer than first ray of second dorsal fin but not fila-

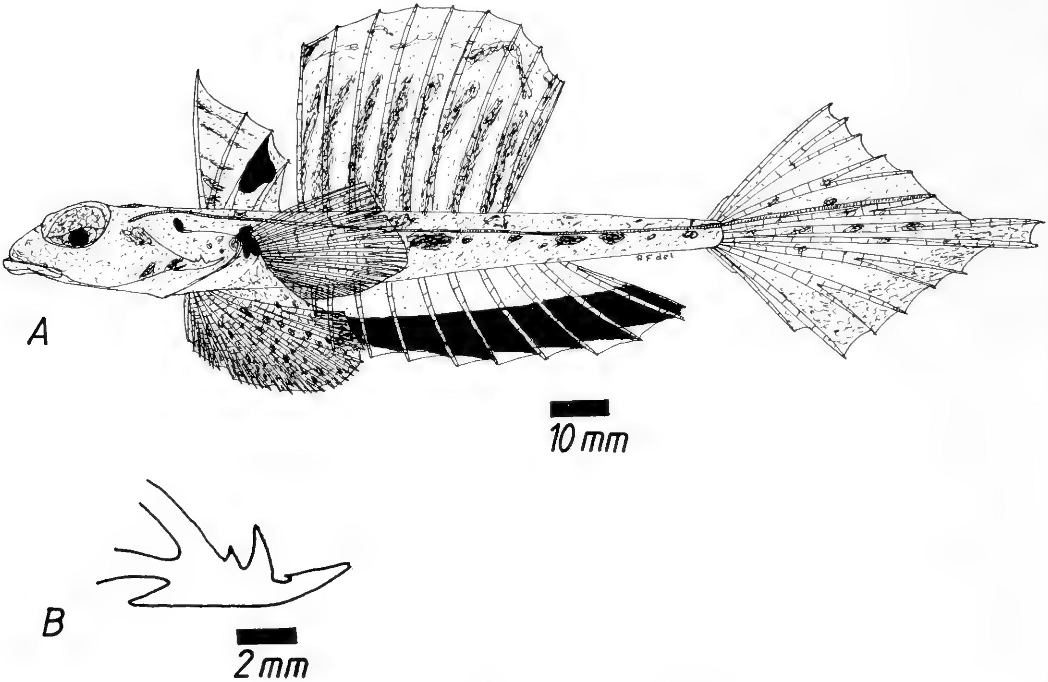


FIGURE 16. *Callionymus guentheri*, paratype, CAS 32897 (specimen 1), male, 128.0 mm SL, Balayan Bay, Philippines: (*A*) lateral view; (*B*) left preopercular spine.

mentous (only occasionally in small specimens a very short filament). Second dorsal fin in males relatively high, with a convex distal margin, in females lower, with a nearly straight distal margin. Anal fin beginning on the vertical through base of second ray of second dorsal fin. Distal margin of caudal fin in small specimens convex, with one or two long filaments; in larger specimens all median caudal fin rays elongate (the two median rays longest), but not filamentous; even the longest rays are connected by membranes. Distal margin of pelvic fin convex; longest pelvic fin ray reaching to midbase of first or second membrane of anal fin. Pectoral fin reaching to fourth or fifth ray of second dorsal fin when laid back.

Color in alcohol. Head and body brown. One or two rows of large, irregular dark blotches along side of body. A large dark area on pectoral fin base. Back with dark brown semicircular lines in groups which are bordered by white on one side. Eye dark gray. Belly and thorax white; lower side of body brown. Head with few irregular darkish spots. First dorsal fin light brown, with five brownish cross-lines in the anterior part; a dark blotch on third membrane distally or centrally. Second dorsal fin pale, females with a basal and a median row of dark spots and some curved white lines (see Fig. 15*A*); males with vertical darkish streaks (see Fig. 16*A*). Distal half of anal fin black; tips of fin rays white. Caudal fin in females with a broad dark band in the lower and lower distal parts and two median short transverse dark bands; in the upper part some irregular dark spots. Males have the same caudal fin color pattern, but less intense. Pectoral fin dorsally with two rows of dark spots. Distal three-fourths of pelvic fin darkish, with irregular dark brown spots and blotches.

DISTRIBUTION.—Known from various localities in the Philippine Islands (southern coast of Luzon to northern coast of Mindanao; see Fig. 2); 100–593 m, on mud bottoms.

DISCUSSION.—The differences between *C. guentheri*, *C. whiteheadi*, and *C. kaianus* have been discussed in the descriptions of the last two species. *Callionymus guentheri* differs from *C. regani* in the caudal fin shape, the high second

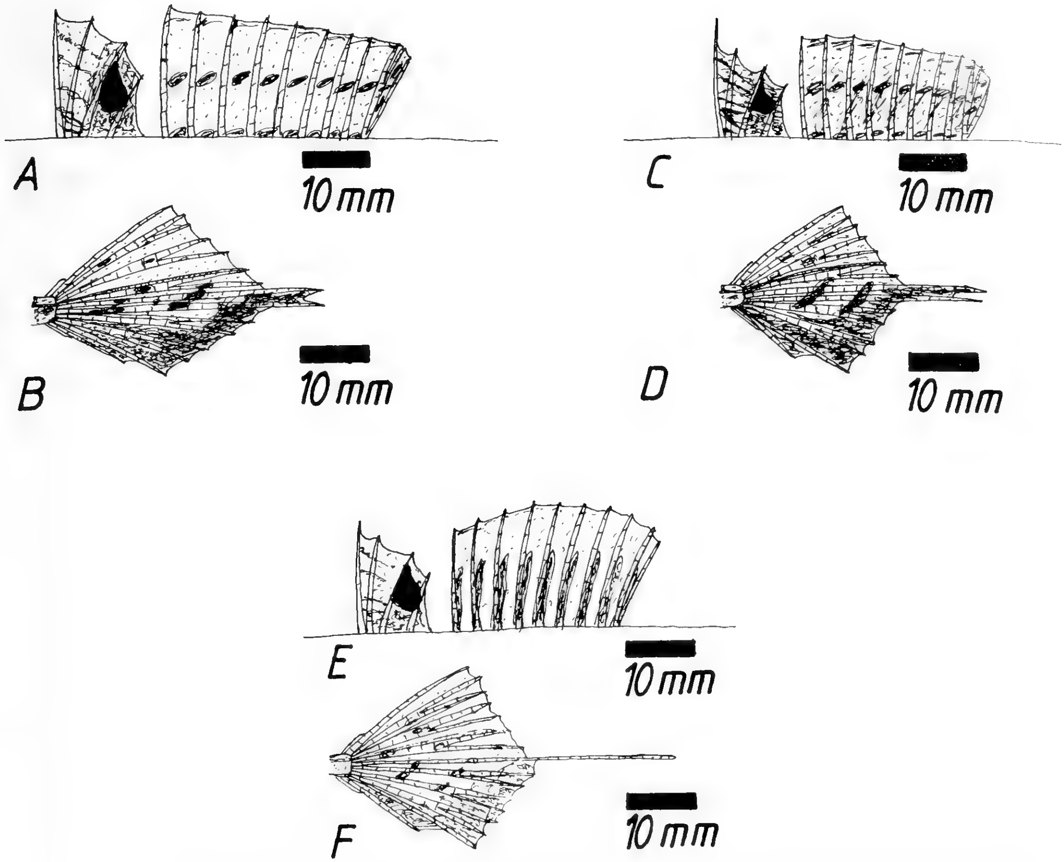


FIGURE 17. *Callionymus guentheri*, paratypes, CAS 32897, Balayan Bay, Philippines. Female (specimen 2), 108.8 mm SL: (*A*) first and second dorsal fins; (*B*) caudal fin. Male (specimen 4), 77.6 mm SL: (*C*) first and second dorsal fins; (*D*) caudal fin. Male (specimen 10), 85.3 mm SL: (*E*) first and second dorsal fins; (*F*) caudal fin.

dorsal fin (in males), and various color markings; from *C. ochiaii* in the caudal fin shape, the lack of a dorsal fin filament (in males), the high second dorsal fin (in males), and several color markings.

In the extensive collections of J. E. Norton (paratypes of *C. guentheri*), a great depth range can be found (100–593 m); 593 m is the greatest depth recorded for any species of the *kaianus*-group. Because few specimens are known of most species of that group, it is possible that in the future, specimens of other species will be recorded from comparable depths.

ETYMOLOGY.—This new species is named after Dr. Albert Günther, who, in 1880, reported the first specimen under the name *Callionymus curvicornis*.

Callionymus altipinnis new species

(Figure 18)

Callionymus kaianus: (non Günther, 1880) CHU ET AL. 1962:723–724, fig. 585 (South China Sea); BESEDNOV 1968:63 (Gulf of Tonkin).

Callionymus huguenini: (non Bleeker, 1858) SHEN 1964:202–203, fig. 2 (Hong Kong).

MATERIAL EXAMINED.—**Holotype:** MSL 0001, ♂, 123.8 mm SL, S.-C. Shen, Hong Kong Fish Market. **Paratypes:** CAS 46967, 10 spec., 104.1–144.5 mm SL, R. L. Bolin, 23 July 1958, South China Sea, E of Hainan (20°32′N, 112°45′30″E); CAS 46968, 1 spec., 135.9 mm SL, R. L. Bolin, 21 July 1958, off Tungku Pt., Hainan (19°31′N, 111°24′30″E); CAS 46969, 1 spec., 124.8 mm SL, R. L. Bolin, 23 July 1958, South China Sea, E of Hainan (20°32′N, 112°51′E).

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (about 4.2 in SL); preopercular spine with a rel-

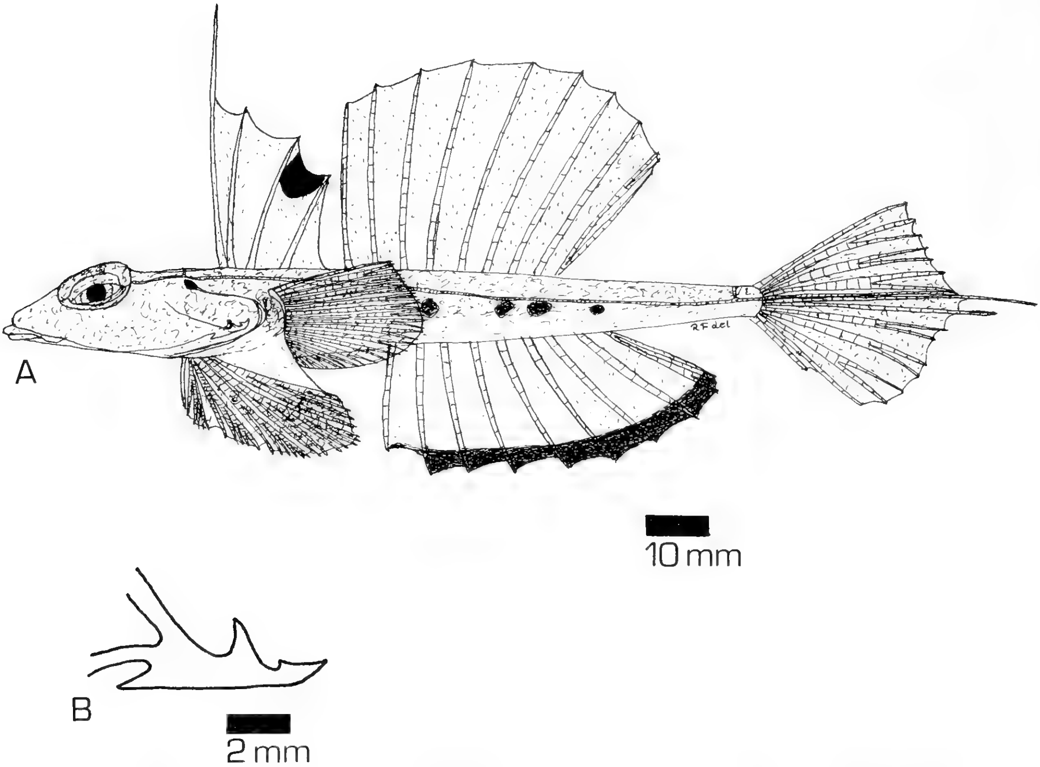


FIGURE 18. *Callionymus altipinnis*, holotype, MSL 0001, male, 123.8 mm SL, Hong Kong: (*A*) lateral view; (*B*) left preopercular spine.

atively short main tip; small antrorse and one (rarely two) larger curved points at dorsal side; very high second dorsal and anal fins with convex distal margins; filamentous first spine of first dorsal fin; small distal black blotch on third membrane of first dorsal fin; anal fin with a black distal margin (including tips of fin rays), but without a distal black streak on each membrane surrounded by dark brown; and one or two caudal fin filaments of medium size.

DESCRIPTION.—Counts and proportions of the holotype (see also Table 2): D_1 IV; D_2 viii,1; A viii,1; P_1 i,14–15,ii; P_2 I,5; C i,3,ii,3,ii.

Body elongate and depressed. Head depressed, about 4.2 in SL. Eye large, about 2.5 in head. Pupil of normal size, about 3.8 in eye. Branchial opening about 3 in pupil. Occipital region with two low bony ridges. Preopercular spine about 1.7 in eye diameter, with a relatively short, slightly upcurved main tip, a small antrorse and one (rarely two) larger points on its dorsal side, and a large antrorse spine at its base (formula: $1\frac{2(-3)}{}1$; see Fig. 18*B*). Lateral line reaching from area behind eye to middle of upper median unbranched caudal fin ray; the line of the opposite side is interconnected by a transverse branch across occipital region and another across dorsal side of caudal peduncle. Caudal peduncle length about 5.0 in SL; minimal caudal peduncle depth about 25.0 in SL.

First spine of first dorsal fin filamentous. Second dorsal fin very high, distal margin convex. Anal fin begins on vertical through middle of second membrane of second dorsal fin. Distal margin of pelvic fin convex; longest pelvic fin ray reaching nearly to base of first anal fin ray. Pectoral fin reaching to middle of third membrane of second dorsal fin when laid back. Distal margin of caudal fin somewhat pointed, with one or two filaments.

Color in alcohol. Head, body, and fins pale except for a distal black blotch on third membrane of first dorsal fin, a row of dark blotches along side of body, eyes grayish, a black distal margin of anal fin, and a darkish area on pectoral fin base.

DISTRIBUTION.—Known only from the South China Sea off China, from Hong Kong (type-locality) to the Gulf of Tonkin; island of Hainan (see Fig. 2). The exact collecting depth of specimens of *C. altipinnis* is not known, but the species should occur at about the same depth as other species of the *kaianus*-group.

DISCUSSION.—*Callionymus altipinnis* differs from *C. sokonumeri* in the filamentous first spine of the first dorsal fin, the shorter caudal fin filaments, and various color markings.

The record of *C. huguenini* Bleeker (by Shen 1964) from Hong Kong is based on a misidentified specimen of *C. altipinnis* (the specimen is now the holotype of *C. altipinnis*).

ETYMOLOGY.—From the Latin *altus,* high, and *pinna,* fin, in reference to the unusually high second dorsal, anal, and first dorsal fins.

Callionymus sokonumeri Kamohara, 1936

Callionymus sokonumeri KAMOHARA, 1936:448, fig. 2 (Mimase Market); 1952:90, fig. 87 (Prov. Tosa); 1955:63, fig.; MATSUBARA 1955:713 (after Kamohara); OCHIAI, ARAGA, AND NAKAJIMA 1955:109–110, figs. 6–7, table 5 (Mimase and Owase); KAMOHARA 1964:90 (Kochi Pref.).

DIAGNOSIS.—A *Callionymus* of the *kaianus*-group with a small branchial opening; short head (3.6–4.4 in SL); preopercular spine with a small antrorse and two larger curved points at dorsal side, and a short main tip; high second dorsal fin with a convex distal margin; no filament in first dorsal fin; anal fin with a distal black streak on each membrane; distal two-thirds of membranes of anal fin brown, including tips of fin rays; an irregular distal margin of caudal fin; and a very small black blotch on third membrane of first dorsal fin, extremely distal in position.

DESCRIPTION.—Counts and proportions (see also Table 2): D_1 IV; D_2 viii,1; A viii,1; P_1 18–20; P_2 I,5; C 10.

Body elongate and depressed. Head depressed, 3.6–4.4 in SL. Eye large, 2.1–2.9 in head. Pupil about 3.1 in eye diameter. Branchial opening about 3 in pupil. Preopercular spine with a short main tip, a small antrorse and two larger curved points at its dorsal side, and a large antrorse spine at its base (formula: $1\overset{3}{\overline{\qquad\quad}}1$). Lateral line reaching from area behind eye to end of one of the median caudal fin rays (?); the line of the opposite side interconnected by a transverse branch across occipital region and another across dorsal side of caudal peduncle. Caudal peduncle length about 4.8 in SL, minimal caudal peduncle depth 23.0 in SL.

First spine of first dorsal fin lower than first ray of second dorsal fin, not filamentous. Second dorsal fin very high, with a convex distal margin. Anal fin begins on vertical through second ray of second dorsal fin. Distal shape of caudal fin irregular; two median caudal fin rays elongate, occasionally filamentous. Distal margin of pelvic fin convex; longest pelvic fin ray reaching to midbase of first membrane of anal fin when laid back. Pectoral fin reaching to fourth ray of second dorsal fin when laid back.

Color in alcohol. Body olive-yellow above, whitish below. Back with both blackish spots and blotches, the former forming darkish rings. A row of several dark brown blotches along side of body. Pectoral fin base with a brown area. First dorsal fin gray, with three oblique dark bars; a black blotch distally on third membrane. Second dorsal fin gray, with several vertical dark streaks on membranes. Distal part of anal fin blackish, occasionally with a transverse streak distally on each membrane except the first. Caudal fin gray, mottled with blackish spots and small whitish blotches. Pectoral fin pale, the dorsal part mottled with dark spots. Pelvic fin gray, distal parts of fourth and fifth rays dark.

DISTRIBUTION.—Known only from central Honshu, Japan (Pacific coast; see Fig. 2); collection depths not known.

DISCUSSION.—I unfortunately had no material of this species. The present description is compiled from Kamohara (1936) and Ochiai, Araga, and Nakajima (1955).

The differences between *C. sokonumeri* and *C. altipinnis* are discussed in the description of the latter species. *Callionymus sokonumeri* differs from *C. ochiaii* in its higher second dorsal and anal fins, the shape of the caudal fin, a shorter main tip of the preopercular spine, and various color markings.

Callionymus sp.

Callionymus kaianus: (non Günther, 1880) WONGRATANA 1968:58 (Gulf of Thailand).

DISCUSSION.—I did not examine material of the *kaianus*-group from the Gulf of Thailand. Wongratana's (1968) paper records *Callionymus kaianus,* but gives no descriptions or figures.

Callionymus kaianus should not occur in the Gulf of Thailand. I have been unable to determine if the specimens from that area belong to any of the known species of the *kaianus*-group, or if they represent yet another species.

Acknowledgments

For discussion of problems, loan of specimens, information, or permission to examine specimens in their collections, I thank the following persons: H.-J. Paepke (ZMB, East Berlin); P. J. P. Whitehead, A. Wheeler, and O. Crimmen (BMNH, London); A. Ben-Tuvia and D. Golani (HUJF, Jerusalem); K.-C. Au (MSL, Hong Kong); H. K. Larson (AMS, Sydney); J. P. Gosse (IRSN, Brussels); W. N. Eschmeyer, L. J. Dempster, T. Iwamoto, T. R. Roberts, P. M. Sonoda, M. Hearne, and G. Raabe (CAS, San Francisco), T. Iwai and T. Nakabo (FAKU, Kyoto), A. Kotthaus (Eppstein, W. Germany), H. Wilkens and R. Dohse (ZIM, Hamburg). W. N. Eschmeyer and T. Iwamoto (CAS, San Francisco) also reviewed the manuscript.

I am greatly obliged to P. Fourmanoir (ORSTOM, Nouméa) for the gift of a specimen of *Callionymus moretonensis* and a further callionymid fish specimen. I am also grateful to D. J. Stewart (FMNH, Chicago) who examined a specimen of *Callionymus carebares* from his collection for me. I thank O. von Frisch (NMB, Braunschweig) for accepting specimens loaned to me. A financial contribution for expenses during my visit to the California Academy of Sciences was provided by that organization.

Literature Cited

Alcock, A. W. 1890. On the bathybial fishes collected in the Bay of Bengal during the season 1889–1890. Ann. Mag. Nat. Hist. (6)6:197–222.

———. 1898. Illustrations of the zoology of H.M. Indian surveying steamer "Investigator." Pt. 4, Fishes. Calcutta: Indian Museum.

———. 1899. A descriptive catalogue of the Indian deep-sea fishes in the Indian Museum, collected by the Royal Indian Marine Survey ship Investigator. Calcutta: Indian Museum. 211 pp.

Beaufort, L. F. de. 1951. The fishes of the Indo-Australian Archipelago, 9. Percomorphi (concluded), Blennioidea. Leiden: E. J. Brill. 484 pp.

Besednov, L. N. 1968. Ichthyofauna of the Gulf of Tonkin (in Russian). Uchenye Zapiski Dal'nevostocnyi Universitet, Vladyvostok 15(2):47–85.

Bleeker, P. 1858. Vijfde bijdrage tot de kennis der ichthyologische fauna van Japan. Act. Soc. Sci. Indo-Neerl. 5:1–12.

Chu, K. Y. 1957. A list of fishes from Pescadore Islands. Rep. Inst. Fish. Biol. Minist. Econ. Aff. Natl. Taiwan Univ. 1(2):14–22.

Chu, Y. T., and others. 1962. Fishes of the South China Sea. [In Chinese] Peking. Pp. i–xxxvii, 1–1184, figs. 1–860.

Fowler, H. W. 1928. The fishes of Oceania. Mem. B. P. Bishop Mus. 10:1–540, figs. 1–82, pls. 1–49.

Fricke, R. 1980. Neue Fundorte und noch nicht beschriebene Geschlechtsunterschiede einiger Arten der Gattung *Callionymus* (Pisces, Perciformes, Callionymidae), mit Bemerkungen zur Systematik innerhalb dieser Gattung und Beschreibung einer neuen Untergattung und einer neuen Art. Ann. Mus. Civ. Stor. Nat. 'Giacomo Doria' 83:57–105, figs. 1–14, pls. 1–9.

———. 1981a. On a new species of the family Callionymidae (Pisces, Perciformes, Callionymoidei), *Callionymus stigmatopareius* spec. nov. from Mozambique. J. Nat. Hist. 15(1):161–167, figs. 1–2, tables 1–2.

———. 1981b. Revision of the genus *Synchiropus* (Teleostei: Callionymidae). Braunschweig: J. Cramer. 196 pp.

Günther, A. (C. L. G.). 1880. Report on the shore-fishes procured during the voyage of H.M.S. Challenger in the years 1873–1876. Rep. Sci. Results H.M.S. Challenger, Zool. 1(6):1–82, pls. 1–32.

Herre, A. W. C. T. 1953. A check-list of the fishes of the Philippines. U.S. Dept. Int. Fish Wildl. Serv., Res. Rep. 20:1–977.

Johnson, C. R. 1971. Revision of the callionymid fishes referable to the genus *Callionymus* from Australian waters. Mem. Queensl. Mus. 16(1):103–140.

———. 1973. Biology of the dragonet *Callionymus kaianus moretonensis* Johnson (Pisces, Callionymidae). Zool. J. Linn. Soc. 52:217–230.

Jordan, D. S., and A. Seale. 1905. The fishes of Samoa. Description of the species found in the archipelago, with a provisional check-list of the fishes of Oceania. Bull. U.S. Bur. Fish. 25:175–455, figs. 1–111, pls. 33–53.

Kamohara, T. 1936. Two new deep-sea fishes from Japan. Annot. Zool. Japon., Tokyo 15(4):446–448, figs. 1–2.

———. 1952. Revised descriptions of the offshore bottom fishes of province Tosa, Shikoku, Japan. Rep. Kochi Univ. Nat. Sci. (3):1–122, figs. 1–100.

———. 1955. Coloured illustrations of the fishes of Japan. Osaka.

———. 1964. Revised catalogue of fishes of Kochi Prefecture, Japan. Rep. Usa Mar. Biol. Stn. 11(1):1–99.

Kotthaus, A. 1977. Fische des Indischen Ozeans. A. Systematischer Teil XIX: Percomorphi (9). "Meteor" Forschungsergebn., Reihe D(25):24–44, figs. 406–428.

Linnaeus, C. 1758. Systema naturae . . . . 1. Regnum animale. 824 pp.

Masuda, H., C. Araga, and T. Yoshino. 1975. Coastal fishes of southern Japan. Tokyo: Tokai Univ. Press. 379 pp., 143 pls.

Matsubara, K. 1955. Fish morphology, and hierarchy. Pt. 1. Tokyo: Ishizaki-Shoten. 789 pp. [2nd. ed., Tokyo 1971.]

Munro, I. S. R. 1958. The fishes of the New Guinea region. Territ. Papua and New Guinea, Fish. Bull. 1:97–369. [Reprinted from Papua and New Guinea Agric. J. 10(4):97–369.]

Nakabo, T. 1979. A new and two rare species of the genus *Callionymus* (Callionymidae) from the western Indian Ocean. Japan. J. Ichthyol. 26(3):231–237, figs. 1–4, table 1.

Norman, J. R. 1939. Fishes. Sci. Rep. John Murray Exped. 7(1):1–116, figs. 1–41.

Ochiai, A., C. Araga, and M. Nakajima. 1955. A revision of the dragonets referable to the genus *Callionymus* found in the waters of Japan. Publ. Seto Mar. Biol. Lab. 5(1):95–132.

Peters, W. C. H. 1876. Uebersicht der während der von 1874–1876 unter dem Commando des Hrn. Capitän z.S. Freiherrn von Schleinitz ausgeführten Reise der S.M.S. "Gazelle" gesammelten und von der Kaiserlichen Admiralität der Königlichen Akademie der Wissenschaften übersandten Fische. Monatsber. Dtsch. Akad. Wiss. Berl. 1876:831–854.

Regan, C. T. 1906. On fishes from the Persian Gulf, the Sea of Oman, and Karachi, collected by Mr. F. W. Townsend. J. Bombay Nat. Hist. Soc. 16:318–333, pls. A–C.

———. 1908. The Percy Sladen Trust Expedition to the Indian Ocean in 1905 under the leadership of Mr. J. Stanley Gardiner. Report on the marine fishes collected by Mr. J. Stanley Gardiner in the Indian Ocean. Trans. Linn. Soc. London, Zool. (2)12(3):217–255, pls. 23–32.

Richardson, J. 1844–1848. The zoology of the voyage of H.M.S. Erebus & Terror, under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839 to 1843. Fishes. London. 139 pp., 60 pls.

Shen, S.-C. 1964. A list of the fishes from Hong Kong. Pt. 1. Quart. J. Taiwan Mus. (Taipei) 17:193–208

Smith, J. L. B. 1963. Fishes of the families Draconettidae and Callionymidae from the Red Sea and western Indian Ocean. Rhodes Univ., Dep. Ichthyol., Ichthyol. Bull. (28):547–564, figs. 1–8, pls. 83–86.

Suwardji. 1965. Notes on the genus *Callionymus* (Pisces, Callionymidae), mostly from Indonesian waters, with the description of three new species and a new subspecies. Vidensk. Medd. Dansk Naturhist. Foren. 128:303–323, pls. 46–48.

Valenciennes, A. *in* Cuvier, G., and A. Valenciennes. 1837. Histoire naturelle des poissons 12. Paris. i–xxiv + 507 pp.

Weber, M. 1913. Die Fische der Siboga-Expedition. Siboga Exped. 57:1–719. Leiden.

Wongratana, T. 1968. Check list of fishes caught during the trawl surveys in the Gulf of Thailand and off the east coast of the Malay peninsula. Contrib. Mar. Fish. Lab. Bangkok 13:1–96.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 15, pp. 379–407, 18 figs., 4 tables. October 26, 1981

DISTRIBUTION, REPRODUCTIVE ANATOMY, AND VARIATION OF *MONADENIA TROGLODYTES* HANNA AND SMITH (GASTROPODA: PULMONATA) WITH THE PROPOSAL OF A NEW SUBGENUS

By
Barry Roth

*Department of Invertebrate Zoology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118*

Abstract: *Shastelix,* new subgenus of *Monadenia* (type-species, *M. troglodytes troglodytes*) is proposed, based principally on genital characters. The new subgenus is mostly confined to the Klamath Mountains of California and is parapatric with *Monadenia,* sensu stricto. *Monadenia troglodytes* is common in a limited area of Shasta County, associated with limestone terrane. Three subspecies are recognized based on morphometry and geography—*M. t. troglodytes* along the McCloud River arm of Shasta Lake; *M. t. wintu,* new subspecies, between the Pit River and Squaw Creek, with one disjunct, outlying population south of Shasta Lake; and *M. t. chaceana* (formerly ranked as a distinct species) near the confluence of the Shasta and Klamath rivers in Siskiyou County. Sympatric *Monadenia churchi* and *M. troglodytes* differ little in reproductive anatomy; elaborations of the female genitalia are probably not important in species recognition or reproductive isolation. A phylogenetic hypothesis and evolutionary scenario for the three subgenera of *Monadenia* are presented.

INTRODUCTION

The western North American helicacean snail genus *Monadenia* Pilsbry, 1895, includes conspicuous species that have long attracted the attention of malacologists. Its type-species, *Helix fidelis* Gray, 1834, was the first land mollusk described from the Pacific coast. It includes the most northern helicacean species—and some of the most northern large land snails—on the North American continent. *Monadenia* is one of the few temperate genera of snails with an elaborate color pattern (Comfort 1951), and *M. fidelis* is the only snail in the far west with a dramatic polymorphism of shell color and banding (Roth in press).

Pilsbry (1939) and Berry (1940a) divided *Monadenia* into two groups of species, based on reproductive anatomy and shell characters—*Monadenia,* sensu stricto, and *Corynadenia* Berry, 1940. The range of the genus extends from southern Alaska to central California, principally west of the Cascade Range but penetrating inland along major river valleys. One branch reaches south along the east side of the Sacramento Valley; the other follows the southern Klamath Mountains and Coast Ranges to the San Francisco Bay region (Figure 1). The subgenus *Corynadenia* exists as an apparently disjunct group of species on the west side of the Sierra Nevada. Roth (1975) showed that *Monadenia churchi* Hanna and Smith, 1933, which occupies a fairly wide range around the north end of the Sacramento Valley, and which Pilsbry (1939) and Berry (1940a) had grouped with the

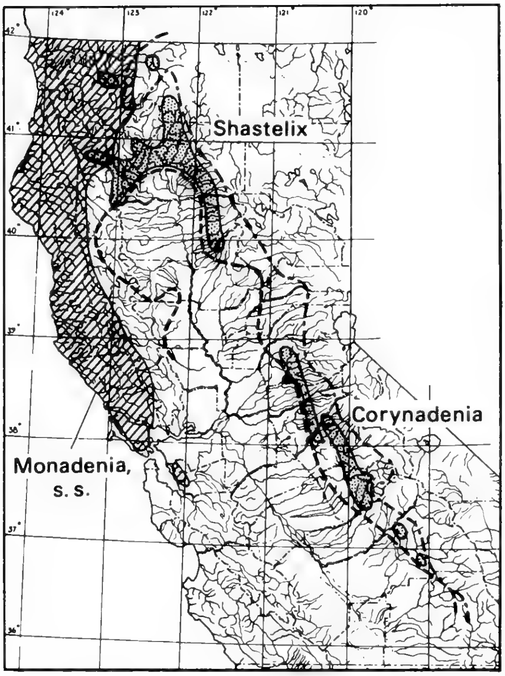


FIGURE 1. Distribution of the subgenera of *Monadenia* in California. Diagonal hachure, generalized range of *Monadenia,* sensu stricto; stippling, in Klamath Mountains region, *Shastelix,* in Sierra Nevada, *Corynadenia.* Dashed line represents 36 C mean maximum July isotherm; dot-dashed line, −4 C mean minimum January isotherm (thermal data after Elford 1970).

Sierran subgenus, combines anatomic and shell characters of *Monadenia,* s.s., and *Corynadenia.* A number of other species from northern California described by Berry (1940b) have not yet been dissected or assigned unequivocally to subgenus. Parapatry and possible sympatry of species have been demonstrated (Roth and Eng 1980; and herein), and it is clear that the zoogeography of *Monadenia* is more complex than earlier authors imagined.

Monadenia is ecologically diverse, comprising species of rock crevices and rockslides, others that inhabit deep leafmold, semi-arboreal forms, and snails that crawl out exposed on low plant cover. The relations between habit and habitat, on the one hand, and morphology and variation, on the other, are important for understanding the evolutionary history of the group. This paper is one of a projected series of studies aimed at elucidating those relationships.

Monadenia troglodytes Hanna and Smith, 1933, was described from fossil shells of presumed Pleistocene age collected in Samwel Cave, Shasta County, California (sec. 5, T. 35 N, R. 3 W, Mount Diablo Base and Meridian, USGS Bollibokka Mountain Quadrangle). Other shells of the species, likewise interpreted as Pleistocene, were reported from Potter Creek Cave (sec. 23, T. 34 N, R. 4 W, MDB&M, USGS Lamoine Quadrangle), Shasta County (Hanna and Smith 1933). Empty shells were later found by Stanford University speleologists a short distance outside Samwel Cave (Smith 1957), and in 1963 the species was discovered alive in the same general area (Walton 1970). Smith (1970) and Roth (1972a, 1972b) cited *M. troglodytes* as rare and of limited distribution.

In May 1973 the late Allyn G. Smith of the California Academy of Sciences found the species at a new locality, in limestone rockslides near Ellery Creek (SE¼ sec. 6, T. 35 N, R. 3 W, MDB&M, Bollibokka Mountain Quadrangle), west of the McCloud River arm of Shasta Lake (Fig. 2). He collected many empty shells in various states of preservation and one living specimen. Since then, additional collections, including a substantial amount of material secured independently by S. E. Hirschfeld, D. C. Rudolph, and R. L. Seib, indicate that the species is fairly common in a limited area in Shasta County and is strongly associated with limestone terrane.

Dissections of the reproductive system show that *M. troglodytes,* along with *M. churchi,* belongs to a new subgenus, which is named herein. Selected shell characters were measured to analyze shell variability. A new subspecies is described, distinguished from typical *M. troglodytes* by details of color, shell microsculpture, and morphometry. *Monadenia chaceana* Berry (1940b) is similar in general shell character but differs consistently in certain shell measurements and is regarded as a third subspecies. One other species of *Monadenia* occurs within the range of *M. troglodytes,* permitting a consideration of species criteria within the genus. An hypothesis of phylogenetic relationships within *Monadenia* is presented.

The use of a trinomial to designate the nominate subspecies—a convention sparingly observed in American land malacology, but one necessary to distinguish the subspecies from the species sensu lato—is here introduced for *Monadenia troglodytes troglodytes.*

FIGURE 2. Gilman Road crossing of Ellery Creek (Locality 26); typical *Monadenia troglodytes* habitat in brush-covered talus at foot of prominent limestone outcrop.

The following institutional abbreviations are employed:

AMNH—American Museum of Natural History
ANSP—Academy of Natural Sciences, Philadelphia
CAS—California Academy of Sciences, Department of Invertebrate Zoology
CASGTC—California Academy of Sciences, Geology Type Collection, Department of Geology
FMNH—Field Museum of Natural History
LACM—Los Angeles County Museum of Natural History
SSB—Private collection of S. Stillman Berry, Redlands, California
SUPTC—Stanford University Paleontological Type Collection, now in Department of Geology, California Academy of Sciences
UCMP—Museum of Paleontology, University of California, Berkeley
USNM—United States National Museum of Natural History

Monadenia Pilsbry

Monadenia PILSBRY, 1895:198.—PILSBRY 1939:31–35.

TYPE-SPECIES: *Helix fidelis* Gray, 1834, by original designation.

Shastelix, new subgenus

TYPE-SPECIES: *Monadenia troglodytes troglodytes* Hanna and Smith, 1933.

DIAGNOSIS.—*Monadenia* with large, globose atrium; mucus gland much longer than dart sac, its lower part adnate to atrium; penial retractor inserted near middle of epiphallus; flagellum (epiphallic caecum) substantially longer than penis plus epiphallus and borne in a series of helical coils. Penis sessile on atrium, not invaginated into it. Spermatophore helically coiled (?). Shell of moderate size for the genus, smooth or granulose, protoconch sculpture of minute, somewhat confluent granules, tending to align in diagonal series.

The genitalia of *Monadenia troglodytes* (Figs. 4–6) differ most obviously from those of species

TABLE 1. CHARACTER COMPLEXES IN THE SUBGENERA OF *Monadenia*.

Characters	*Monadenia*, s.s.	*Shastelix*	*Corynadenia*
Atrium large and globose (+), or small and narrow (−)	+	+	−
Mucus gland many times longer than (+), or about equal to (−), dart sac	+	+	−
Lower part of mucus gland adnate to (+), or free from (−), atrium	−	+	−
Dart sac 5 mm or less in length (+), or longer than 5 mm (−)	−	+	−
Flagellum ≥1.5 times length of (+), or about as long as (−), penis plus epiphallus	−	+	+
Flagellum (and spermatophore) helically coiled (+), or straight (−)	−	+	+
Basal chamber of penis invaginated into (+), or sessile on (−), atrium	+	−	+
Penial retractor inserted near middle (+), or on distal third (−), of epiphallus	−,+	+	+

of the nominate subgenus (*M. fidelis, M. infumata* (Gould, 1855), *M. setosa* Talmadge, 1952) in the long, helically coiled flagellum. The flagellum in *Monadenia*, sensu stricto, is thick and straight or simply curved and about as long as the penis plus epiphallus (Pilsbry 1939:figs. 15A, B, *M. fidelis*; Roth and Eng 1980:fig. 3, *M. setosa*; the genitalia of *M. infumata* are similar). The flagellum is the organ which secretes the spermatophore; the spermatophore of *M. fidelis* (Webb 1952:fig. 8A) is straight. In the Sierran *Monadenia* (*Corynadenia*) *hirsuta* Pilsbry, 1927, a species with helically coiled flagellum, the spermatophore is coiled like a corkscrew. It seems probable, therefore, that species of *Shastelix* also secrete coiled spermatophores.

Both *Shastelix* and *Monadenia*, s.s., have a large, globose atrium. (I follow Pilsbry [1939], Berry [1940a] and other authors in using the term "atrium" for the large, saccular elaboration of the lower genitalia upon which the penis, dart sac, and vagina insert and which when everted forms the copulatory pad or disk. This organ is mainly developed above the insertion of the penis and is homologous to the lower part of the vagina in other helicoid genera. In these other genera the term "atrium" is conventionally restricted to the common passage to the external genital pore below the insertion of the penis.) In *Shastelix* the lower ductlike portion of the mucus gland is adnate to the atrium, whereas in *Monadenia*, s.s., it runs along the surface of the atrium but is not fused to it. The dart sac in *Shastelix* is smaller than that in the nominate subgenus. In *Monadenia*, s.s., the basal part of the penis is invaginated into the wall of the atrium, which clasps it like a collar; in *Shastelix* the basal part of the penis is sessile on the atrium.

In the subgenus *Corynadenia* Berry, 1940a (type-species, *Helix hillebrandi* Newcomb, 1864; see Pilsbry 1939:fig. 15C), the atrium is smaller, narrow and elongate, and the mucus gland is shorter or very slightly longer than the dart sac. The flagellum is longer than the penis plus epiphallus and, at least in some species, helically coiled. The basal part of the penis is invaginated into the wall of the atrium, as in *Monadenia*, s.s.

Character complexes differentiating the three subgenera are summarized in Table 1.

Monadenia churchi also belongs to *Shastelix* and resembles *M. troglodytes* in genitalia (Fig. 8) and protoconch sculpture. It is probable that some undissected species from the Klamath Mountains (particularly *M. cristulata* Berry, 1940, and *M. marmarotis* Berry, 1940) will also prove to belong to *Shastelix*. The known range of the subgenus (Fig. 1) extends from Butte County on the south and east, around the north

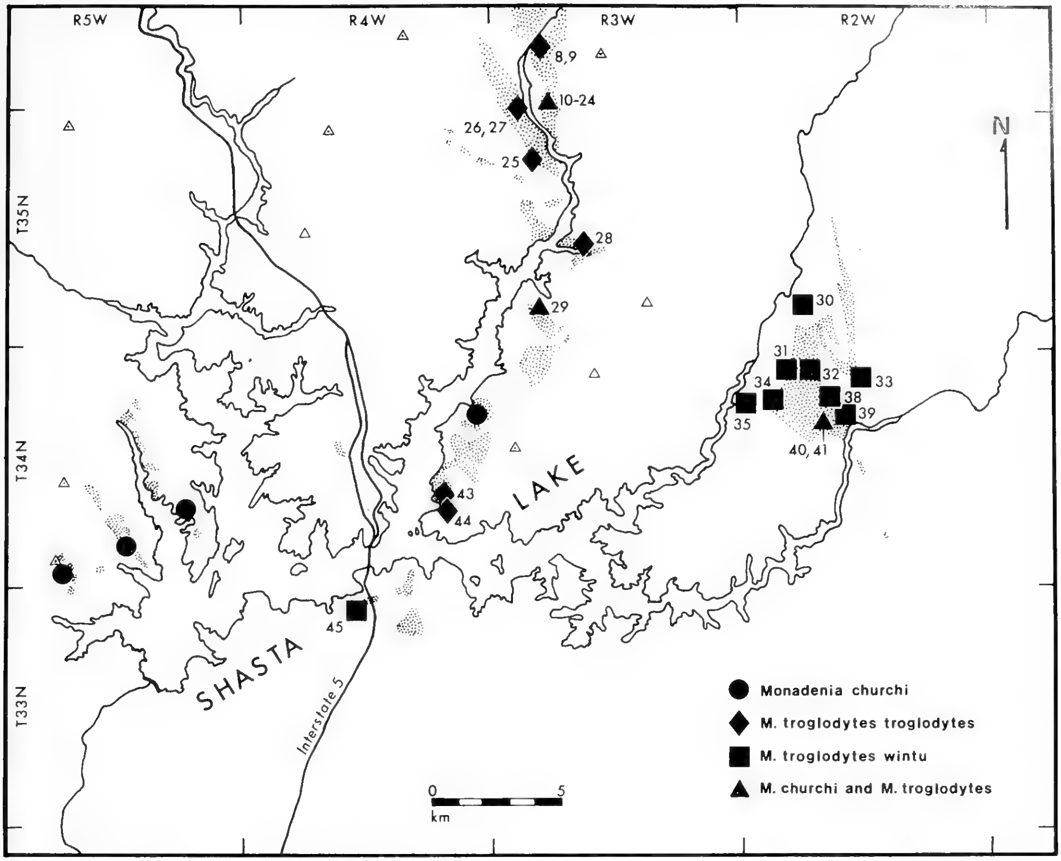


FIGURE 3. Distribution of *Monadenia* species in vicinity of Shasta Lake, Shasta County, Calif. Stippling indicates surface outcrops of limestone. Open triangles denote peaks of more than 1000 m elevation. Geology after: Diller (1906); Kinkel et al. (1956); Coogan (1960); Albers and Robertson (1961); Demirmen and Harbaugh (1965); Irwin and Galanis (1976).

end of the Sacramento Valley, to near Burnt Ranch, Trinity County, on the west, and the Shasta River–Klamath River confluence on the north. *Monadenia churchi* and *M. troglodytes* are sympatric in the vicinity of Shasta Lake. In the drainage of the Trinity River, *Shastelix* is parapatric with *Monadenia,* s.s. There *M. fidelis* and *M. setosa* tend to occur in riparian woodland close to streambeds, while *M. churchi* occurs on drier, more exposed slopes and in rockslides. Only the subgenus *Corynadenia* is known to occur in the Sierra Nevada.

The subgenus name is derived from the place-name *Shasta*—lake, mountain, river, and county—plus the Greek *helix,* a spiral, hence a snail. Its gender is feminine.

DISTRIBUTION, ANATOMY, AND GEOGRAPHIC VARIATION OF *Monadenia troglodytes*

The material now available, summarized in the Appendix, makes it clear that *Monadenia troglodytes* is not only extant (Walton 1970) but occupies a considerable range in the vicinity of Shasta Lake (Fig. 3). At several of the localities, living individuals were found to be common.

The ranges of *M. t. troglodytes* and a second subspecies described herein lie within the "Eastern Klamath Belt," the easternmost of several concentric lithic belts that constitute the Klamath Mountains physiographic province of northwest California and southwest Oregon (Irwin 1972). The Klamath Mountains are a rugged mountain region including clusters of high peaks 1800–2700 m in altitude. Peaks and ridgecrests of 1200–1350 m occur in the area mapped in Figure 3. The canyons of the Sacramento, McCloud, and Pit rivers and Squaw Creek dominate the area's topography. Shasta Lake is an artificial impoundment of these rivers; their courses prior to damming may be seen on pre-1940 topographic maps. The spillway of Shasta Dam is at an elevation of 325 m, so that local relief of 1000 m and more is present in the area under study. Southward from Shasta Lake, the Sacramento River descends through foothills to the broad, alluviated floor of the Sacramento Valley. The Sacramento River–Trinity River watershed—closely coinciding with the Shasta County–Trinity County boundary and dividing the north coast drainage from the interior, Great Valley, drainage—is located a few kilometers off the west margin of the map. North, east, and southeast of the map area lie portions of the Cascade Range physiographic province (Wahrhaftig and Birman 1965); due north is the Pleistocene stratovolcano Mount Shasta, 4300 m in altitude.

The Klamath Mountains are noted for the diversity of their flora and the number of local endemic plant species (Whittaker 1961; Axelrod 1976). In the region under study, the vegetation is largely northern yellow pine forest with some Sierran montane forest (Küchler 1977), particularly between the Pit and McCloud rivers. Lower elevations and exposed slopes are covered by a growth of scrub oak and chaparral. The land at higher elevations was originally densely timbered with coniferous forest, but in many areas logging, fires, and the effects of smelter smoke have removed the original timber, so that second-growth forest and brush are widespread. Manzanita (*Arctostaphylos*) is the dominant brush plant.

The normal annual precipitation is between 120 and 180 cm, more than 90 percent of it falling in the months October through April (Elford 1970; Major 1977). Mean monthly temperatures at Shasta Dam range from around 5 C in January to about 25 C in July (Major 1977). Daytime temperatures in excess of 40 C are not uncommon from June through September. Local microclimatic variation is considerable.

Geology of the region is complex, including intrusive and extrusive, sedimentary, and metamorphic rock suites, of ages from Paleozoic to Quaternary. Of particular interest are bodies of limestone that crop out discontinuously in three principal areas. These are finely crystalline, resistant limestones that often form prominent outcrops (Kinkel et al. 1956:fig. 20). Local topographic names such as "Gray Rocks" (Lamoine and Bollibokka Mountain quadrangles), "Limerock Gulch," "Marble Creek," and "Upper and Lower Limestone Valley Creeks" (Lamoine Quadrangle) acknowledge their presence.

All samples of *Monadenia troglodytes* for which adequate data are available were taken on or adjacent to these limestone areas (Fig. 3). The localities fall into two groups: those associated with the Triassic Hosselkus limestone in the vicinity of Brock Mountain, between the Pit River and Squaw Creek arms of Shasta Lake; and those on or near the Permian McCloud limestone, along the McCloud River arm of the Lake. The type-locality, Samwel Cave, belongs to the latter group; so does Locality 45, south of the Pit River arm, the southernmost definite site for *M. troglodytes*. (A bleached, broken shell from somewhat farther south—Loc. 46, in the Anderson Quadrangle—is similar but cannot be assigned unequivocally to species.) Locality 35 is from a limestone quarry, evidently in one of the limestone lenses in the predominantly clastic Pit Formation (Albers and Robertson 1961).

Limestones in the Shasta Lake region are discontinuous because of faulting and erosion. The McCloud and Brock Mountain locality groups are separated by approximately 10 km of nonlimestone terrane—chiefly volcanics, pyroclastics, and mudstones. Squaw Creek, its canyon, and a watershed of 830 m minimum elevation also stand between the two groups. Morphologic distinctions between the Brock Mountain and McCloud River herds, discussed below, indicate that a certain amount of genetic isolation exists as well. Localities yielding *M. troglodytes* range in elevation from about 330 to 760 m, so it does not seem likely that the altitude of the watershed alone constitutes an isolating factor. Exposure and seasonal lack of moisture on ridgetops may restrict the snails' mobility, but since some collections of *M. troglodytes* were made in zones of high insolation, with snails active in shaded spots even during July, limestone substrate seems a more likely limiting factor.

Cooper (1869) remarked on the strong association of *Monadenia* with carbonate terrane in the Sierra Nevada; and Pilsbry (1939) surmised that discontinuity of limestone substrata was involved in the formation of local races. Many other records exist of land mollusks whose distribution is more or less tied to areas of high calcium availability (e.g., Boycott 1934; Tweedie 1961; Heller 1975).

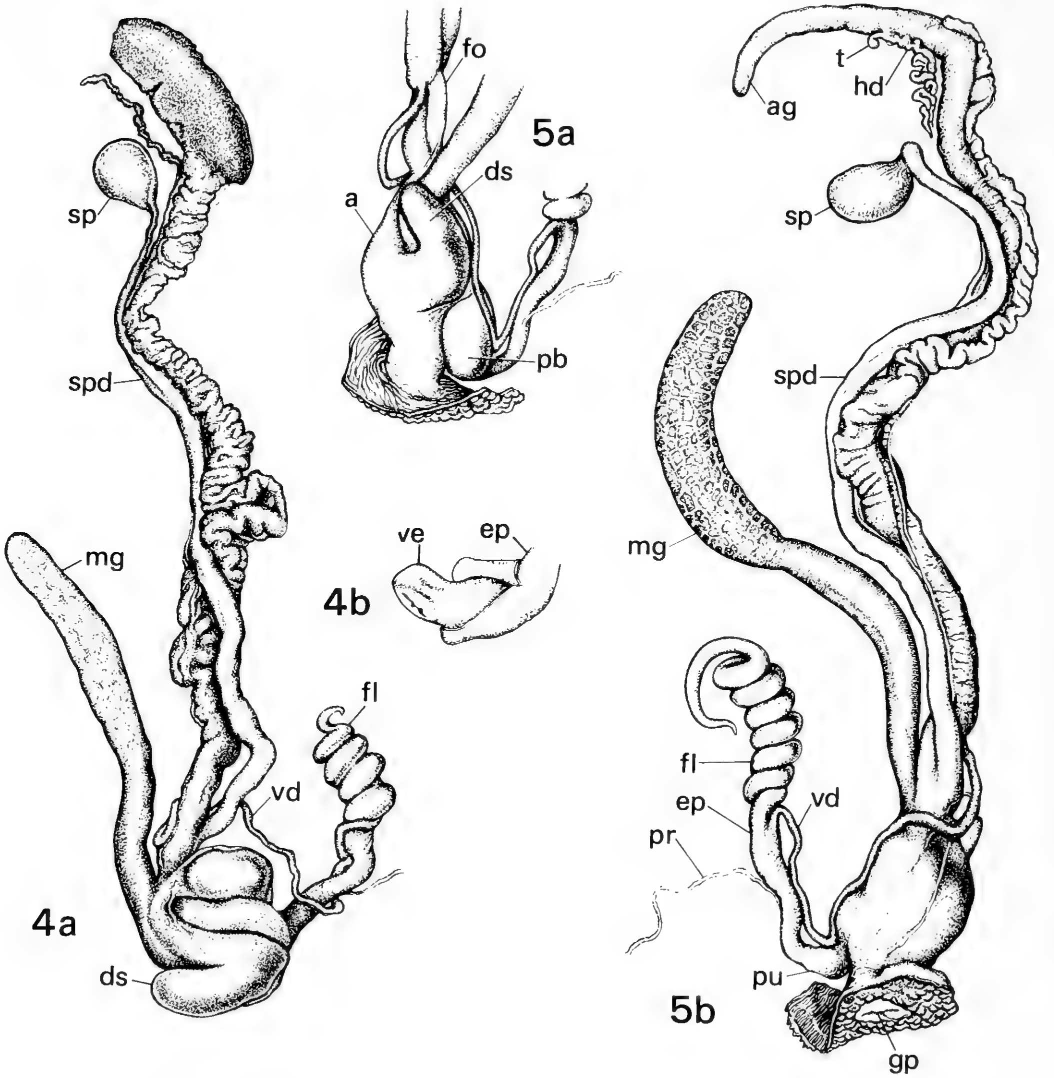
To the west, limestone outcrops of the Devonian Kennett Formation in the Mammoth Buttes–Backbone Ridge area west of the Sacramento River arm of Shasta Lake have yielded *Monadenia churchi* but not *M. troglodytes*. *Monadenia churchi* also occurs in the McCloud River and Brock Mountain areas. At a minimum of three stations it is sympatric or parapatric with *M. troglodytes* and was received in the same samples. *M. churchi* is not restricted to limestone substrata; it has been found elsewhere in lava rockslides (type lot; Hanna and Smith 1933) and coniferous forest debris (Roth and Eng 1980). At each locality on limestone where both *M. troglodytes* and *M. churchi* were taken together, *M. troglodytes* is the more common species. The implications of the sympatry of *M. churchi* and *M. troglodytes* for classification of *Monadenia* are discussed below.

No specimens from Shasta County referable to the Sierran *Monadenia* (*Corynadenia*) *mormonum* (Pfeiffer, 1857) have been found in the course of this study, and it appears that all such records in the literature are based on misidentifications of either *M. troglodytes* or *M. churchi*. (For example: "The most northern locality for *mormonum* now known is at Shasta, Cal., lat. 41° (nearly), alt. 1160 feet, where in the volcanic region Dr. Yates found a very few stunted specimens with but five and a half whorls and the bristle-granulations of the young very strongly developed" [Cooper 1879:285]. "In Shasta County, far north of the localities mentioned, a race of *mormonum* has been found in the Upper Sonoran Zone at and near the junction of the Pitt [*sic*] with the Sacramento river (Brewer, Gabb). They agree with the typical form in the absence or extreme faintness of spiral striae and in coloration; the shell is smaller and the spire generally higher. They are within the area of *M. churchi*" [Pilsbry 1939:56].) A lot collected in the nineteenth century, UCMP 2491, *ex* D. O. Mills collection no. 290, labeled "Shasta County, Calif." and formerly identified as *M. mormonum*, is probably the same as the Shasta County shells referred to by Pilsbry (1939:56). It is *M. troglodytes*, similar to those from the Brock Mountain area. The original description of *M. troglodytes* was based on samples with very low spire index (H/D = 0.411–0.500); the figured holotype is nearly planispiral. In the samples now at hand, intermediate examples connect these very flat shells with the higher-spired, *mormonum*-like specimens.

ANATOMY.—Specimens were prepared for anatomical study by drowning followed by transfer in stages to 70% ethanol. Specimens of *M. troglodytes* from the following localities were dissected: 10, 26, 28, 34, 39, 43. Except as noted, the data given apply to all individuals examined.

Body grayish tan, shaded darker on dorsum; light buff mid-dorsal stripe; sole light buff. Mantle over lung translucent buff, with gray dendritic pencilling occupying 0–35% (usually about 20%) of surface. (All degrees of mantle pigmentation present in sample from Loc. 10; other samples less variable.) Mantle collar colored like body. External genital pore a vertical 1–2 mm slit often showing white rim.

Right ocular retractor running between male and female systems, passing over crook at penis-epiphallus junction. Genitalia as in Figures 4–6. Penis stout, basal chamber separated by crook from upper chamber, adnate to atrium but not invaginated therein; upper chamber thin-walled, finely ridged internally, containing cylindrical to ovate-conic, slightly rugulose verge 3–3.5 mm long. Tip of verge with slitlike lateral meatus on anterior edge, dorsal facet concavely beveled (Fig. 4*b*). (End of verge of specimens from Loc. 43 blunt, as broad or broader than stalk, with flaplike expansion of tip opposite meatus.) Wall of upper penial chamber bearing a single large pilaster that fits against beveled facet of verge and extends into basal chamber. Epiphallus from ½ to ¾ as thick as penis at their junction. Penial retractor (originating on floor of lung) long, narrow, slightly expanded just before insertion on medial part of epiphallus. Flagellum (epiphallic caecum) longer than penis plus epiphallus, as thick as epiphallus, borne in 4 to 7 helical coils; distal end tapering to fine point. Vas deferens with 2–3 convolutions where it passes under atrium. Spermatheca (bursa cop-



FIGURES 4–5. Genitalia of *Monadenia troglodytes*. Figs. 4*a–b*. *M. t. troglodytes*; (*a.*) dorsal aspect, Loc. 28, atrium rotated 90° downward with respect to oviduct; (*b.*) detail of verge, Loc. 10. Figs. 5*a–b*. *M. t. wintu*, n. subsp., holotype CAS 018431, Loc. 34; (*a.*) dorsal aspect; (*b.*) ventral aspect. Abbreviations: *a*—atrium; *ag*—albumen gland; *ds*—dart sac; *ep*—epiphallus; *fl*—flagellum; *fo*—free oviduct; *gp*—external genital pore; *hd*—hermaphroditic duct; *mg*—mucus gland; *pb*—basal chamber of penis; *pr*—penial retractor muscle; *pu*—upper chamber of penis; *sp*—spermatheca; *spd*—duct of spermatheca; *t*—talon (fertilization pouch); *vd*—vas deferens; *ve*—verge.

ulatrix) globose; spermathecal duct long, straight, unbranched, capacious for lower three-fourths, narrower below spermatheca. Dart sac small to moderate-sized, sessile at convergence of two atrial crura which, when everted, form a copulatory pad or disk (Fig. 7); sac containing a 2-mm, tubular, calcareous dart. Mucus gland large, bent near middle, lower portion adnate to atrium and running along lower edge of superior atrial crus to insertion at base of dart sac.

Measurements of selected organs are given in Table 2. All show considerable variation. There appears to be no systematic difference between samples except that those from the Brock Mountain area tend to have more coils to the epiphallus.

TABLE 2. LENGTHS (in mm) OF SELECTED ORGANS OF *Monadenia troglodytes* AND *M. churchi* (range, with sample mean in parentheses).

	M. t. troglodytes		*M. t. wintu*		*M. churchi*	
Loc. (n)	10 (6)	43 (5)	34 (3)	45 (1)	Mammoth Butte (3)	29 (1)
Free portion of mucus gland	16.0–21.2 (18.82)	10.9–21.0 (17.12)	16.1–30.0 (21.0)	15.7	15.7–18.1 (16.77)	17.3
Dart sac	2.6–4.5 (3.18)	2.1–2.4 (2.33)	2.5–3.2 (2.87)	2.1	1.8–2.7 (2.23)	1.9
No. of coils of flagellum	3.5–5 (4.13)	3.5–5 (4)	5–7 (6)	5	3.5–4 (3.67)	6
Free (upper) chamber of penis	3.3–4.8 (3.55)	3.4–4.7 (3.84)	3.7–4.6 (4.23)	4.0	3.5–3.6 (3.6)	3.5
Epiphallus	5.6–8.7 (7.93)	5.7–8.6 (6.72)	8.4–8.9 (8.63)	8.1	5.2–6.5 (5.63)	6.6
Base of epiphallus to insertion of penial retractor	2.6–4.9 (4.07)	2.9–4.1 (3.5)	3.5–4.7 (4.03)	4.1	2.2–3.2 (2.7)	2.6

In their exserted state the atrial crura form a copulatory pad (Fig. 7). The female genital pore is located on the bottom of the pocket between the two crura. The male opening, through which the verge is exserted, is located near the middle of the forward edge of the anterior crus. The pore of the dart sac is at the convergence of the crura; further eversion of the dart apparatus was not observed.

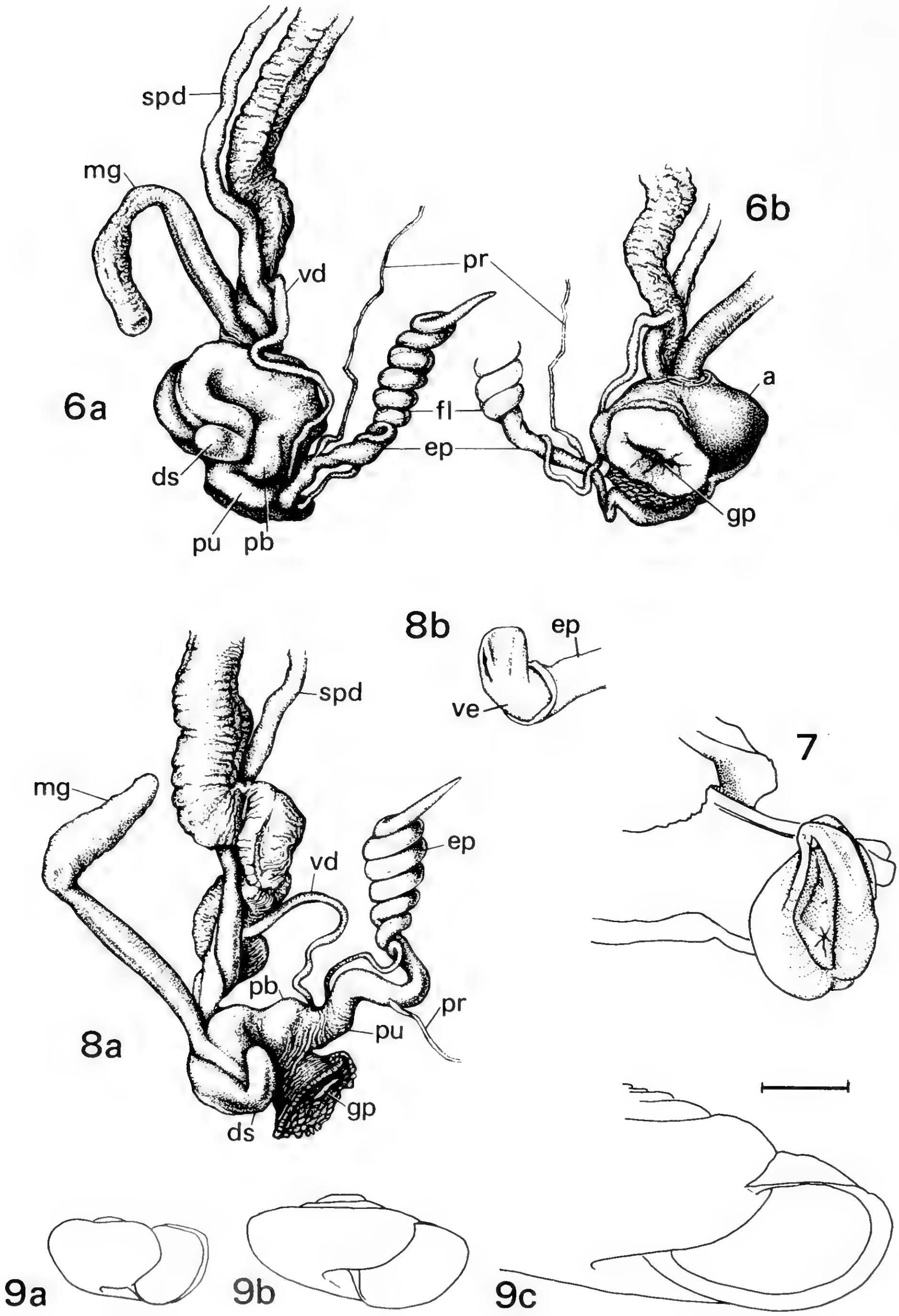
The lower genitalia are enveloped in thin tissue that binds the male system to the atrium and in some specimens forms a collar around the penis just below its junction with the epiphallus.

The jaw is crescentic, golden brown, with four to six major ribs that denticulate both margins. From one to five smaller intercalary ribs are present on some specimens.

The radula of a specimen from Locality 28 has 41 teeth in a half row. The central tooth is somewhat wider than in *M. fidelis* (see Pilsbry 1939:fig. 15E), the mesocone as long as the basal plate. On the fourteenth tooth an endocone appears, and on the fifteenth an ectocone. The marginal teeth are somewhat spatulate, the cleft between mesocone and endocone deep, and both mesocone and endocone are sometimes bifid or trifid. The outer marginals are very short.

SHELL CHARACTERS AND VARIATION.—Hanna and Smith (1933) described the protoconch of *Monadenia troglodytes* as consisting of 1½ whorls marked by wavy radiating riblets. In a group of 19 *M. t. troglodytes* hatched in captivity from eggs laid by an individual from Locality 10 (slope below Samwel Cave), the protoconch consists of 1.5–1.8 whorls (counting by the method of Diver 1932) and measures 2.8–3.5 mm in diameter. The extreme nuclear tip is smooth. Thereafter, sculpture of the protoconch consists of minute granules, round and somewhat confluent, irregularly disposed at first but after about one half whorl tending to form wavy, radial riblets. Those just outboard of the suture retain this character nearly to the end of the embryonic shell. Elsewhere on the top surface the granules become discrete and spirally elongated and tend to align in oblique, protractive and retractive series. Below the periphery the granules are discrete, spirally elongated, sometimes arranged in diagonal series but more often scattered. All other *M. troglodytes* in which the protoconchs are not abraded show essentially the same sculpture. Slight erosion sometimes emphasizes the effect of wavy radiating riblets, as described by Hanna and Smith for the type lot. The embryonic sculpture is very similar to that of *M. fidelis* (see Pilsbry 1939).

The onset of neanic growth is marked by an abrupt enlargement of whorl diameter. The intensity of surface granulation on early neanic whorls is less than that on the protoconch; the granules are sometimes obscure or localized in a few patches. Irregular, axial growth ridges are the dominant sculptural feature. Between these



FIGURES 6–9. Figs. 6*a*–*b*. Genitalia of *Monadenia troglodytes wintu*, n. subsp., Loc. 45; (*a*.) dorsal aspect; (*b*.) ventral aspect, atrium partially everted. Fig. 7. Copulatory pad of *M. t. wintu*. Figs. 8*a*–*b*. Genitalia of *Monadenia churchi*, Loc. 29. (*a*.) dorsal aspect; (*b*.) detail of verge. Figs. 9*a*–*c*. Ontogenetic shape change in *Monadenia troglodytes troglodytes*, Loc. 10. Scale line = 5 mm for Fig. 9*a*, 10 mm for Figs. 9*b*, 9*c*. Abbreviations as in Figs. 4–5.

ridges there is an extremely fine, wrinklelike, parallel lineolation, particularly evident on the base. Closely set, wavy, spiral striation appears on the base, usually by the end of the first postnuclear whorl. These striae are irregular in both strength and spacing.

Variably expressed, these elements—granulation, growth rugae, wrinkle-lineolation, and spiral striae—constitute the microsculpture of adult shells. When not pitted or breached by erosion, the periostracum is smooth and glossy; in adult shells it is often scratched and abraded on base and spire. Fine, wavy, spiral striation on the base is apparently standard but frequently removed by abrasion. On some shells, stronger, incised striae occur on the shoulder of the last whorl and may be prominent behind the lip.

After about the three-whorl stage, granulation is rare below the shoulder. It persists on the spire for a varying number of whorls, usually becoming sparser with ontogeny, the granules becoming lower, more elongate, and less clearly defined until, in some cases, they finally merge into the general undulation of the periostracal surface. In most instances, however, granulation stops at or near a growth rest, and when growth is resumed the granules are few, irregular, or absent.

The last granulose whorl varies from locality to locality (Fig. 10), and there is a half-whorl to two-whorl range in all samples large enough for consideration. The means of the last granulose whorl increase in populations from north to south along the McCloud River. (Far to the north, *M. t. chaceana* has a mean of 1.83 granulose whorls, seemingly continuing the cline.) Variation in the Brock Mountain herd is less obviously clinal: the westernmost samples, Localities 34 and 35, have few granulose whorls ($\bar{x}$ = 2.38 and 2.10, respectively); the few measurable shells from the more eastern localities 33, 38, 40, and 41 are in the 2.5–3.5 whorl range; and Locality 39, situated geographically amid the other eastern localities, has a predominance of shells pustulose at 4.5 whorls and beyond ($\bar{x}$ = 4.17). Locality 45, south of Shasta Lake, also has populations whose granulation persists onto the later whorls ($\bar{x}$ = 3.73). The difference in number of granulose whorls between the McCloud River and Brock Mountain locality groups is highly significant ($P < 0.001$).

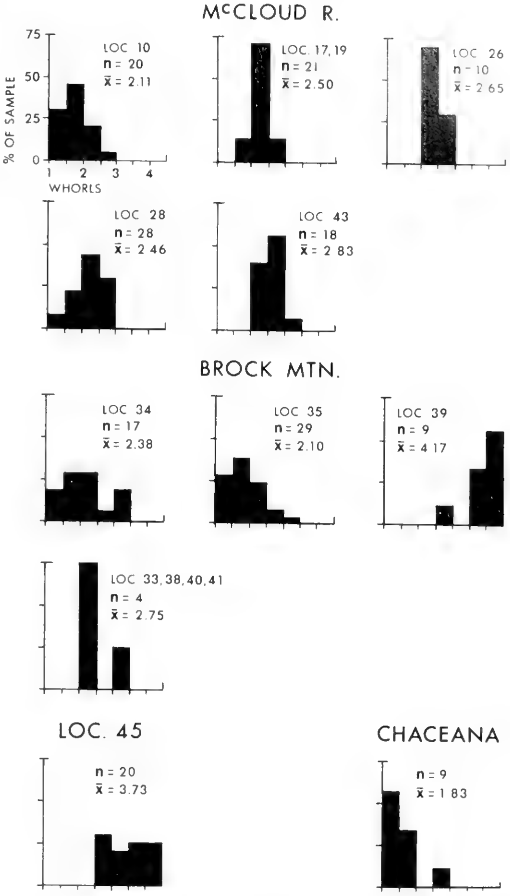


FIGURE 10. Histograms of last granulose whorl (to the nearest half whorl) in *Monadenia troglodytes* samples from along the McCloud River (*M. t. troglodytes*), Brock Mountain region and Loc. 45 south of Shasta Lake (*M. t. wintu*, n. subsp.), and Siskiyou County (*M. t. chaceana*).

In hatchlings, the protoconch is golden tan; some show a faint reddish-brown spiral band at the periphery of the last half whorl. From the first, the teleoconch shell material is lighter tan than the protoconch. Beginning with the first neanic whorl, narrow whitish zones border the reddish-brown band above and below, the lower zone seeming to appear earlier than the upper. Gradually the narrow band becomes darker and more prominent, partly by contrast with the increasing whitish opacity of the rest of the shell. The advancing suture partly or wholly obscures the band.

Color of adult *Monadenia troglodytes* is variable, although fairly uniform within a sample.

The basic shell material is white, covered in fresh, uneroded specimens with a transparent, yellowish periostracum. All fresh specimens have a dark reddish-brown band (chestnut of Rayner [1970]; Munsell midpoint 9.5R/2.3/3.8) just above the periphery, ranging from 0.5 to about 1.5 mm wide on the body whorl. Bands wider than 1 mm occur mainly in the eastern, Brock Mountain, samples and at Locality 45 south of Shasta Lake. Unpigmented zones, either white or showing only the yellowish color of the periostracum, border the dark supraperipheral band above and below. These zones are usually narrower than the dark band, but in some instances they are equally wide or wider. The lower zone is commonly wider than the upper; on shells with a light-colored base, its anterior edge may be indistinct.

Color of the base is generally uniform, sometimes slightly darker toward the periphery. The color ranges from nearly white (even with periostracum intact) to a medium reddish brown (rust of Rayner [1970]; Munsell midpoint 9.0R/4.3/8.0), with little variation within a sample. The lightest bases occur in samples from Localities 35, 38, 40, and 41 (all, Brock Mountain area); and the darkest at Localities 39 (Brock Mountain) and 45 (McCloud limestone south of Shasta Lake). Samples from elsewhere on the McCloud limestone are intermediate in shade.

The shoulder and spire are medium reddish brown, as dark as or darker than the base. They are never as dark as the supraperipheral band. The darkest spires occur in the Brock Mountain area and the lightest along the McCloud River. In both groups there is a tendency for the center of the shoulder to be lighter, producing a shadowy secondary banding that is most evident on the lighter shells of the McCloud River herd. The secondary banding is never as distinct as that in *Monadenia fidelis* (see Talmadge 1960; his "multibanded phase"). One other color effect is observable: some individuals have radial streaks of darker pigment on the shoulder. These streaks usually precede a growth rest and evidently represent concentrated pigment deposition at times when shell growth is slowing down. They are often followed by a whitish radial streak (as growth starts up again rapidly?). When combined with secondary banding, as in some McCloud River shells, the streaks produce a mottled effect.

It seems likely that the same shell pigment, in various dilutions, produces the supraperipheral band, base, and shoulder coloration.

The expanded lip of adult specimens is white.

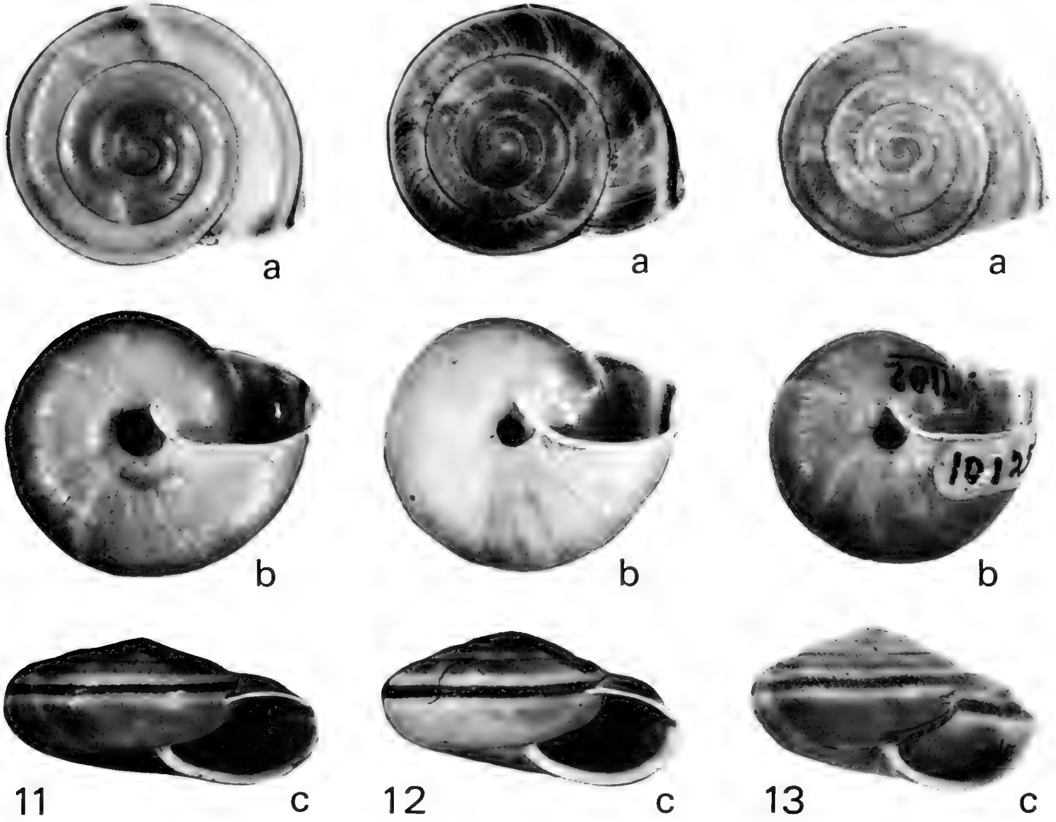
Color variation in *M. troglodytes* segregates geographically: populations in the Brock Mountain area have the darkest spires, both the darkest and the lightest bases, and the broadest bands near the periphery. Populations along the McCloud River have the lightest-colored shells and the greatest incidence of secondary banding and mottling.

In the course of ontogeny, the shell of *Monadenia troglodytes* undergoes several significant changes in shape. The protoconch—that portion of the shell which forms within the egg—is almost hemispherical, with nearly flat spire and deeply convex base. Gould (1969) suggested that mechanical limitations of space within the egg largely determine protoconch shape in the zonitid snail *Poecilozonites*, and in fact, the protoconch of *M. troglodytes* is shaped very much like that of *Poecilozonites bermudensis bermudensis* (Gould 1969:pl. 6, figs. 6, 7).

Post-embryonic juvenile shells are wide, flat- to low-spired, angulate at the shoulder, and tumid at the base. Again as in *Poecilozonites*, postembryonic growth begins with a marked increase in relative width. As growth proceeds, the whorl changes in cross section (Fig. 9) from crescentic and taller than broad, in the embryonic shell, to auriculate and broader than tall in the adult. Also with growth, the periphery, which is above the middle in juvenile shells, migrates downward until it is medial in adults and changes gradually from angulate to rounded.

Spire height increases allometrically with respect to shell diameter, producing a domed spire. Since from about the third whorl on, the height-diameter ratio of the shell remains practically constant, the allometry is due chiefly to the downward migration of the periphery.

In *Monadenia*, as in most other helicacean snails, growth is determinate. The shell enlarges up to a point, generally coincident with sexual maturity, when the lip is thickened and turned outward. Thereafter, no additional spiral growth takes place. In *M. troglodytes*, the greatest absolute height of aperture and often the greatest total shell height are achieved one-half to one-quarter whorl before the cessation of growth. For the last quarter turn, translation along the



FIGURES 11–13. Shells of *Monadenia troglodytes*, ×1.5. Figs. 11*a–c*. *M. t. troglodytes*, Loc. 26. Figs. 12*a–c*. *M. t. wintu*, n. subsp., holotype CAS 018431, Loc. 34. Figs. 13*a–c*. *M. t. chaceana*, paratype CASGTC 10125.

vertical axis is halted or reversed, and at the same time, the whorl is compressed apico-basally. The final 3–4 mm increment of growth strikes downward at about a 30° angle to the suture, bringing the peristome nearly into tangency with the face of the body whorl. Similar terminal growth occurs in many genera of helicacean snails, particularly those from xeric environments. It is presumably an adaptation to enhance the snails' mucous seal to the substratum, in order to retard water loss or exclude predators. The final half-whorl "leap" of growth is most strongly expressed in populations along the McCloud River north of Shasta Lake and contributes to their generally low height-diameter ratios compared to Brock Mountain populations.

As already noted above, *Monadenia troglodytes* undergoes a much greater range of variation in shape than was evident from the type lot alone. Data on basic shape measurements and indices—height (H), diameter (D), H/D ratio, number of whorls, umbilical width (U), and U/D ratio—are summarized in Table 3. Data from adult shells (those with reflected lip) only are included. Samples were collected without special procedures to insure randomness, but there is no reason to suspect bias with regard to any of the dimensions or ratios used here.

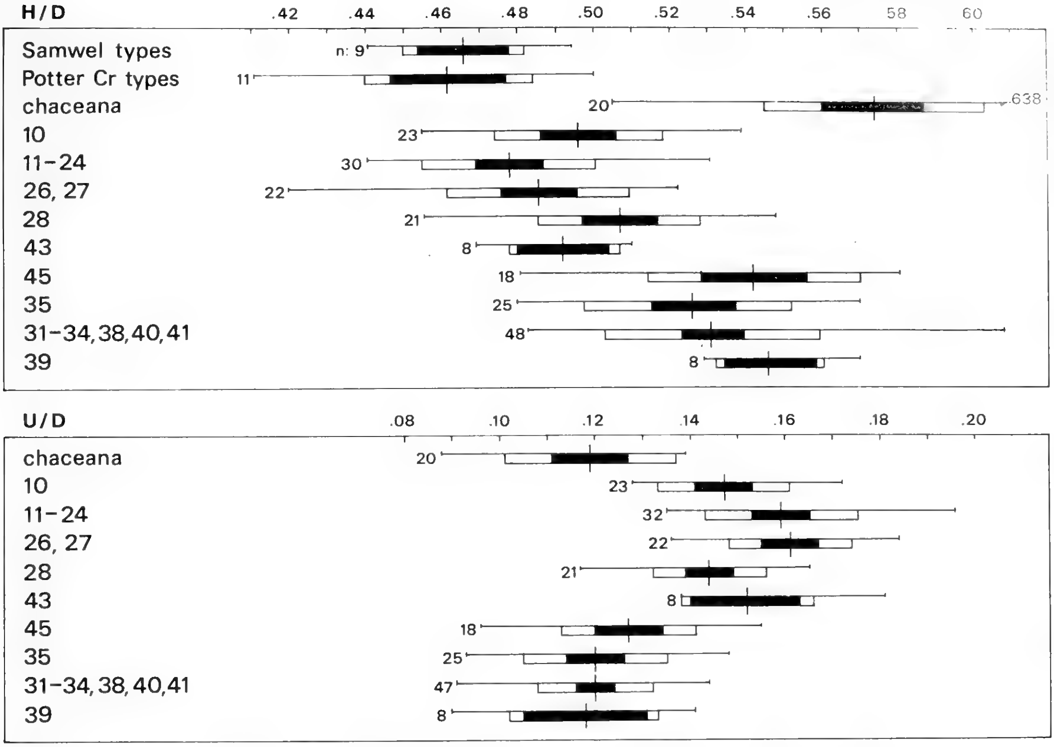
All shells were measured with a hand-held caliper with vernier scale. Height (H) was measured parallel to, and maximum diameter (D) perpendicular to, the axis of coiling of the shell. The expanded lip of adult shells was excluded from these dimensions. Umbilical width (U) is an inside caliper measurement taken parallel to

TABLE 3. SHELL DIMENSIONS (in mm) AND RATIOS IN *Monadenia troglodytes*. Statistics are range with sample mean ± one standard deviation in parentheses. Only adult shells included.

Locality	n	Height (H)	Diameter (D)	Umbilical width (U)	Number of whorls	H/D	U/D	H + D
				M. t. troglodytes				
Slope below Samwel Cave (10)	23	10.0–12.3 (11.01 ± 0.58)	20.9–24.5 (22.23 ± 0.84)	2.8–4.0 (3.27 ± 0.37)	5.0–5.5 (5.3 ± 0.15)	0.455–0.539 (0.496 ± 0.022)	0.128–0.172 (0.147 ± 0.014)	31.5–36.5 (33.24 ± 1.25)
Vicinity of Samwel Cave (11–24)	*	10.2–13.1 (11.75 ± 0.79)	21.9–27.2 (24.65 ± 1.14)	3.0–4.8 (3.91 ± 0.39)	5.0–6.0 (5.42 ± 0.21)	0.441–0.531 (0.478 ± 0.023)	0.135–0.196 (0.159 ± 0.016)	32.1–40.0 (36.36 ± 1.76)
Ellery Creek (26, 27)	22	11.5–14.0 (12.69 ± 0.77)	23.7–28.1 (26.13 ± 1.14)	3.5–5.1 (4.20 ± 0.40)	5.3–5.9 (5.57 ± 0.14)	0.420–0.522 (0.486 ± 0.023)	0.136–0.184 (0.161 ± 0.013)	35.2–41.9 (38.85 ± 1.74)
Dekkas Rock (28)	21	10.1–12.6 (11.62 ± 0.70)	20.6–25.0 (22.95 ± 1.38)	2.5–4.1 (3.32 ± 0.37)	5.2–5.8 (5.41 ± 0.19)	0.456–0.548 (0.507 ± 0.021)	0.117–0.164 (0.144 ± 0.012)	31.6–37.6 (34.57 ± 1.97)
Potter Creek (43)	8	11.3–12.6 (11.81 ± 0.47)	22.8–24.9 (24.04 ± 0.80)	3.2–4.5 (3.66 ± 0.40)	5.2–5.7 (5.46 ± 0.15)	0.469–0.510 (0.492 ± 0.014)	0.140–0.181 (0.125 ± 0.014)	34.3–37.3 (35.85 ± 1.17)
				M. t. wintu				
Calveris cement quarry (45)	18	12.0–15.5 (13.42 ± 1.00)	22.6–27.2 (24.78 ± 1.36)	2.4–3.7 (3.14 ± 0.34)	5.5–6.1 (5.72 ± 0.15)	0.481–0.581 (0.542 ± 0.028)	0.096–0.155 (0.127 ± 0.014)	34.6–42.2 (38.20 ± 2.17)
Above Squaw Creek (35)	25	11.2–14.9 (12.84 ± 0.88)	21.9–27.6 (24.53 ± 1.47)	2.2–3.6 (2.93 ± 0.42)	5.2–5.8 (5.47 ± 0.21)	0.480–0.570 (0.526 ± 0.026)	0.094–0.148 (0.120 ± 0.015)	33.9–42.5 (37.37 ± 2.22)
NE of Brock Mtn (31–34, 38, 40, 41)	**	12.0–16.4 (14.07 ± 1.00)	22.6–29.3 (26.47 ± 1.48)	2.3–4.0 (3.16 ± 0.41)	5.2–5.9 (5.61 ± 0.16)	0.483–0.608 (0.531 ± 0.028)	0.091–0.144 (0.120 ± 0.012)	36.4–44.7 (40.57 ± 2.23)
Above Brock Creek (39)	8	13.0–14.2 (13.60 ± 0.41)	23.6–25.6 (24.91 ± 0.76)	2.3–3.6 (2.94 ± 0.36)	5.4–5.9 (5.69 ± 0.16)	0.529–0.570 (0.546 ± 0.014)	0.090–0.141 (0.118 ± 0.015)	36.8–39.7 (38.51 ± 1.07)
				M. t. chaceana				
Hornbrook and Yreka Quadrangles (1, 4–7)	20	10.5–14.6 (13.34 ± 1.10)	18.0–26.0 (23.27 ± 1.99)	1.7–4.0 (2.77 ± 0.51)	5.2–5.8 (5.54 ± 0.19)	0.506–0.638 (0.574 ± 0.029)	0.088–0.139 (0.119 ± 0.018)	28.5–40.2 (36.61 ± 2.97)

* For H, H/D, H + D, n = 30; for D, U, U/D, n = 32; for number of whorls, n = 29.

** For H, n = 49; for D, H/D, H + D, n = 48; for U, U/D, n = 47; for number of whorls, n = 46.



FIGURES 14*a* (upper), 14*b* (lower). Relative height of spire (H/D) and relative width of umbilicus (U/D) in *Monadenia troglodytes*. Line designates sample range; vertical strike, mean; open bar, mean ± one standard deviation; solid bar, 95% confidence interval of population mean.

the maximum diameter and occasionally required breaking away a portion of the inner lip. Number of whorls was determined, with the use of a binocular microscope, by the method of Diver (1932) except that the final fraction of a whorl was estimated without pencil lines being drawn on the shell. The measurement is rounded to the nearest 0.1 whorl. Pilsbry (1939:xi, fig. B) evidently counted whorls by approximately the same method, although he usually expressed results to the nearest one-quarter or one-third of a whorl and sometimes quoted uncritically the figures of other authors.

The simple measurements of size (H, D, H + D) show that as a group the McCloud River herd averages smaller than the Brock Mountain herd, although there is extensive overlap of ranges in all categories. The smallest averages belong to the samples from Localities 10 (below Samwel Cave) and 28 (Dekkas Rock). Shells of large diameter (and large H + D) occur near Ellery Creek (Locs. 26, 27).

Relative height of spire (H/D) segregates geographically (Fig. 14*a*), with McCloud River shells significantly lower-spired than those from Brock Mountain. As in most other parameters, shells from Locality 45 segregate with the Brock Mountain herd. The U/D ratio, the relative width of the umbilicus, segregates along the same lines (Fig. 14*b*)—not surprisingly, since the two ratios, H/D and U/D, may be aspects of the same variable. A tapering tube of a given size and rate of expansion may be coiled steeply (high rate of translation along coiling axis and small distance of generating curve from axis: Raup 1966) or flatly (low rate of translation, large distance from axis). The first mode generates a high-spired shell with small umbilicus, the second a low-spired shell with wide umbilicus. A correlation coefficient of −0.951 for sample mean H/D and mean U/D further attests to the association between the two parameters in *M. troglodytes* in the Shasta Lake region. The high spire and small umbilicus of *M. t. chaceana*

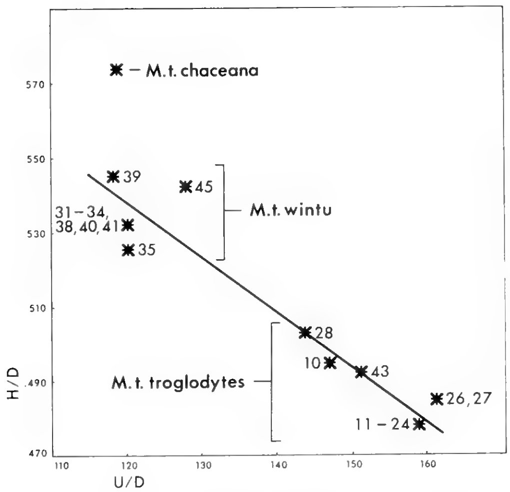


FIGURE 15. Relation between mean relative height of spire (H/D) and mean relative width of umbilicus (U/D) in *Monadenia troglodytes*.

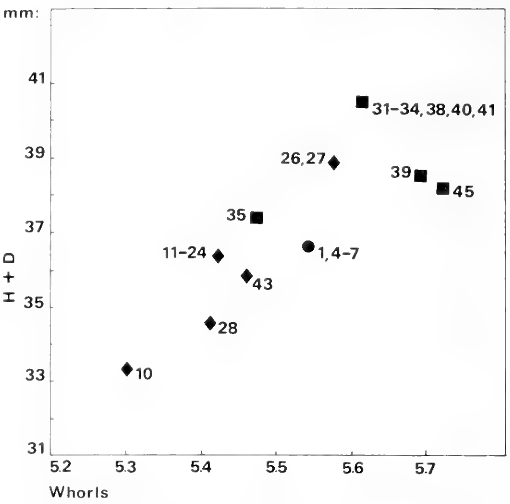


FIGURE 16. Relation between mean size (H + D) and mean number of whorls in *Monadenia troglodytes*. Diamonds, *M. t. troglodytes*; squares, *M. t. wintu*, n. subsp.; circle, *M. t. chaceana*.

are in harmony with this association, although the umbilicus is broader and/or the spire higher than regression of the Shasta Lake statistics predicts (Fig. 15).

Figure 16 plots the relationship between mean size (H + D) and whorl number. Although the scatter of individual (specimen) points overlaps extensively, again there is geographic segregation of means. Locality 45 sorts with the Brock Mountain herd, nearest to the pustulose shells from Locality 39. Mean size and mean whorl number correlate strongly in the McCloud River herd (r = 0.954); the more heterogeneous Brock Mountain herd displays no such tight correlation.

Based on the dimensions given by Hanna and Smith (1933), the type lot of *M. troglodytes* from Samwel Cave and their material from Potter Creek Cave are flatter (lower H/D) than any of the samples here studied. Both the mean diameter and mean H/D ratio of the type lot differ significantly from those of the nearest living sample, from Locality 10. It would be premature, however, to conclude that the difference represents evolutionary change. Hanna and Smith accepted a Pleistocene age for the cave specimens, first because they believed the species extinct and, second, because the shells had been associated with bone deposits. (The Samwel Cave and Potter Creek Cave vertebrate faunas have been assigned a Rancholabrean [late Pleistocene] age; Hibbard et al. 1965.) But the burrowing or crevice-seeking habit of land snails makes them unreliable stratigraphically. State of preservation is not very informative: in the several cave samples now at hand, there are shells in every gradation from slightly dusty to heavily encrusted with calcium carbonate, and there may be a more or less continual influx of shells drifting or washing into the caves. Independent evidence of age, such as radiometric dating, and collections with good stratigraphic control are needed before one can place the cave samples in a time framework.

SYSTEMATICS

TAXONOMIC CRITERIA IN *Monadenia*.—Individuals of *Monadenia troglodytes* in the Shasta Lake region group strongly into two geographic units based on shell color and texture, microsculpture, and morphometry. *Monadenia chaceana* constitutes a third such unit. Although its internal anatomy is not yet known, its shell characters are highly similar to *M. troglodytes*, and it is thus given coordinate rank with the latter two groups.

The subspecies category has been employed somewhat unevenly in terrestrial malacology. Early workers responded to the manifold variability of some tropical snail groups, for instance, by naming dozens of subspecies, and the morass of names led in turn to a reaction against taxonomic recognition of infraspecific units (Gould 1969). I agree with Kavanaugh (1979:93) that "recognition of the usefulness of a subspecies concept . . . [depends] on one's particular perspective; more specifically, on the distribution of habitats or areas occupied by the organisms one studies. Where gaps between areas of suitable habitat are broad and clear, . . . correlated discontinuity in variation is more confidently recognized and suggestive of active, effective barriers to gene flow." The three groups of *Monadenia troglodytes* meet the criteria for subspecies. Shell character differences are mainly quantitative and correlated with geography. Except for the different verge configuration at Locality 43 (the significance of which remains unresolved), the identity of the genitalia between the two Shasta Lake region herds suggests that interbreeding would be possible if the two were brought together sympatrically in nature. Limestone substratum is apparently the required habitat, its absence a probable barrier to gene flow, at least under present environmental conditions. Rivers are at least short-term barriers, but over the long term may be important agents of dispersal. The population at Locality 45 may well have been established by riverborne waifs rafted down the Pit River—perhaps from the population of Locality 39, with which it groups morphologically (Figs. 10, 14–16). Clinal variation in granulation along the McCloud River arm suggests incomplete genetic isolation between those localities. Populations on the McCloud limestone, exclusive of Locality 45, constitute one unit; since it includes the type-locality, this unit is the nominate subspecies, *Monadenia* (*Shastelix*) *troglodytes troglodytes*. Populations between the Pit River and Squaw Creek arms of Shasta Lake, and the southern population at Locality 45, are named as a new subspecies below.

The sympatric or parapatric occurrence of *Monadenia churchi* and *M. troglodytes* at several localities in the Shasta Lake region should, theoretically, permit an estimate of the degree of morphologic difference that can be expected between species of the genus, and by analogy aid in ranking allopatric taxa. Reproductive structures are particularly suitable for such an analysis, because a major difference in genitalia (taking into account the possible effects of seasonal variation and genital polymorphism) implies functional incompatibility. Solem (1975) used data on reproductive anatomy of sympatric species to define taxonomic criteria in the snail genus *Oreohelix* Pilsbry, 1904. Like many other helicacean snails, monadenias have elaborate terminal genitalia, replete with accessory organs which are employed in a courtship of some complexity (Webb 1952, 1966). Specialized reproductive organs and complex precopulatory behavior are sometimes regarded as isolating mechanisms in other animal groups; theoretically, they prevent unproductive mating between sympatric species. Solem (1978:67) predicted that, among pulmonates, elaboration of stimulatory and glandular or dart structures would occur where the need for species recognition signs was the greatest, for example, under conditions of sympatry in areas of historically fluctuating climate and vegetational cover or in island situations involving explosive speciation. The differences in the genitalia of *M. churchi* (Fig. 8) and *M. troglodytes* (Figs. 4–6), however, are relatively limited and far less marked than those between members of different subgenera.

The values for organ lengths in *M. churchi* (Table 2) fall mostly within the range of variation of *M. troglodytes*. The dart sac averages smaller in *M. churchi*, but the size range overlaps that of *M. troglodytes*. Length of the mucus gland is highly variable in both species and may vary according to recency of copulation. *M. churchi* from Mammoth Butte, west of Shasta Lake, and others from the Trinity River drainage have a thin, cylindric verge with the end squared and compressed, the meatus transverse. The verge of a specimen from near Campbell Creek on the east side of the McCloud River arm (Loc. 29) is also squared at the tip but thicker, with lateral meatus and concave facet as in *M. troglodytes* (Fig. 8*b*). All specimens examined have a single large pilaster in the penial chamber. It appears, therefore, that reproductive anatomy in *Shastelix* is too variable and too weakly differentiated to offer reliable characters for diagnosis.

The two species are much more readily distinguished on shell characters: *M. churchi* has strong, pustulose microsculpture over the entire shell, even when adult; a dull periostracal surface; and uniform brown color on base and spire. Quantitative differences, not always present but usually helpful in distinguishing the two species, include higher spire, stronger growth rugae, and more tightly coiled last whorl.

I have detected no systematic conchological differences between *M. troglodytes* found with *M. churchi* and those occurring alone. In each case the *M. troglodytes* shells retain the standard characters of their herd. On the other hand, *M. churchi* from within the range of *M. troglodytes* tend to be larger, shinier, more inflated, and less densely pustulose than specimens from elsewhere. Whether this apparent convergence with *M. troglodytes* goes beyond independent geographic variation will be examined in a later paper.

The finding that in reproductive anatomy *M. churchi* and *M. troglodytes* differ from each other chiefly in verge shape also implies that the elaborations of the female side of the genital system—dart sac, copulatory pad, etc.—may not be involved in species recognition during courtship or maintenance of reproductive isolation. According to the sexual selection model of Charnov (1979), hermaphroditic animals may copulate not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another's eggs). "There must often exist a conflict of interest between mating partners—as a recipient each should be inclined to accept sperm (not necessarily for fertilization of its own eggs) in order to give its sperm away" (Charnov 1979:2482). In order to pair with and fertilize a partner, a *Monadenia* may have to display its own *apparent* receptivity to the partner's sperm. Like any character that individuals use to choose sperm donors, the organs involved in such a display would be subject to exaggeration through time. Selective pressure toward species-specific differentiation of the organs would depend on (1) frequency of the opportunity for interspecific mating, based both on degree of sympatry and the effectiveness of other organ or behavior systems in maintaining isolation; and (2) relative fitness of resulting hybrids.

Monadenia (Shastelix) troglodytes troglodytes Hanna and Smith

(Figures 4*a–b*, 9*a–c*, 11*a–c*)

Monadenia troglodytes Hanna and Smith, 1933:84–85, pl. 5, figs. 6–8.—Pilsbry 1939:54, fig. 22(6–8).—Smith 1957:26; 1970:40.—Walton 1970:111.—Roth 1972a:7; 1972b:7; 1979:13.

Original Description.—"Shell light buff, medium size, widely umbilicate; spire greatly depressed; whorls 5½ with moderately deep suture; the last whorl slightly depressed near the aperture; outer margin expanded very little, the basal margin somewhat more so; one pale brown spiral band appears just above the periphery, which is bounded above and below by white bands that are slightly wider; surface without markings except growth lines; nucleus consisting of 1½ whorls marked by radiating wavy riblets. Diameter 24.2; altitude 10.8 mm" (Hanna and Smith 1933). This description was repeated by Pilsbry (1939).

Type Material.—**Holotype:** UCMP 32394 (shell): California: Shasta County: Samwel Cave (UCMP loc. 1008).

Paratype: CASGTC 5842 (shell); same locality as holotype.

Referred Material.—California: Shasta County: Bollibokka Mountain Quadrangle: Loc. 8 [2 specimens], 9 [5], 10 [32], 11 [6 in addition to holotype and paratype], 12 [2], 13 [2], 14 [2], 15 [2], 16 [1], 17 [4], 18 [2], 19 [31], 20 [2], 21 [6], 22 [1], 23 [2], 24 [9], 25 [2], 26 [30], 27 [5], 28 [38], 29 [3]. Lamoine Quadrangle: Loc. 42 [1], 43 [22], 44 [12], 47 [1], 48 [1]. Figure 3 maps these localities.

Discussion.—As described above in the section on geographic variation and graphically shown in Figures 14–16, *M. t. troglodytes* has the lowest-spired and most broadly umbilicate shells of any subspecies. The shells average smaller than those of the Brock Mountain herd (*M. t. wintu*, next described), but large shells occur near Ellery Creek. The lightest-colored shells and the greatest incidence of secondary banding and mottling occur in *M. t. troglodytes*. The nominate subspecies tends to have fewer coils to the epiphallus than *M. t. wintu*.

Monadenia (Shastelix) troglodytes wintu, new subspecies

(Figures 5*a–b*, 6*a–b*, 7, 12*a–c*)

Diagnosis.—*M. troglodytes* with moderately high spire (sample mean H/D = 0.526–0.546), shell solid, lustrous, shoulder reddish brown, strong white zones above and below brown supraperipheral band, base either nearly white, or reddish brown, as dark as shoulder. Granulation often persisting past third whorl.

Description.—Shell of moderate size for the genus, solid, moderately to distinctly thick, lustrous; spire convexly conic, moderately elevated; whorls 5.2–6.1 in adult, tightly coiled; body whorl slightly expanded over last ½ turn. Protoconch of 1.5–1.9 whorls, nuclear tip smooth, followed by fine granulation tending to form wavy, radial riblets below suture; granules elsewhere spirally elongated, in diagonal series or irregularly scattered. Early neanic whorls less densely granulated, granulation becoming sparser with growth, usually persisting past the 2.5-whorl stage and often past the 3-whorl stage in at least some members of each sample. Body whorl sculptured with fine growth rugae and microscopic, wavy, parallel, spiral lineolation, most evident behind lip. Juvenile shells with base tumid, spire low, shoulder angulate; periphery becoming first obtusely angular and finally rounded with maturity. Base of adult shells rounded, umbilicus open, steep-walled, diameter 0.090–0.155 times major diameter of shell. Last 3–4 mm of body whorl striking downward at about 30° angle to suture. Aperture broadly auriculate, apico-basally compressed, oblique. Peristome slightly thickened, everted; inner lip covering 10–25% of umbilicus. Color of spire and shoulder medium reddish brown (rust of Rayner [1970]; Munsell midpoint 9.0R/4.3/8.0); dark reddish brown (chestnut of Rayner [1970], Munsell midpoint 9.5R/2.3/3.8) band just above periphery, 1–1.5 mm wide in adult, bordered above and below with white or light tan zones, upper zone either narrower or about as wide as brown band, lower zone usually as wide or somewhat wider; base whitish with light tan suffusion or (at some localities) reddish brown as dark as shoulder. Periostracum smooth, colorless or very light yellowish tan. Dimensions: holotype, height 12.8 mm, diameter 25.1 mm, diameter of umbilicus 3.0 mm, 5.6 whorls; largest paratype (Loc. 35), height 14.9 mm, diameter 27.6 mm, diameter of umbilicus 2.9 mm, 5.6 whorls. Dimensions of other referred material summarized in Table 3.

Body of animal dove gray to sooty black with a reddish or purplish cast, darker on dorsum; light mid-dorsal stripe; sole light buff with gray margin. Mantle over lung translucent buff with gray pencilling covering less than 10% of surface. Genitalia (Figs. 5, 6) as in typical subspecies.

Jaw as in *M. t. troglodytes*. Radula substantially as in *M. t. troglodytes*, with 42 teeth in a half row (Locs. 34, 45), an endocone developed on tooth 21 (Loc. 34) or 14 (Loc. 45), an ectocone on tooth 22 (Loc. 34) or 17 (Loc. 45). Bifid and trifid endocones occur sporadically.

TYPE MATERIAL.—**Holotype:** CAS 018431 (shell, radula, and soft parts); CALIFORNIA: Shasta County: NW¼ NE¼ sec 8, T. 34 N, R. 2 W, USGS Bollibokka Mountain Quadrangle (15-minute Series [Topographic]; ed. 1957), cave between two limestone buttes at south end of Gray Rocks, above Pit River arm of Shasta Lake. S. E. Hirschfeld coll., Oct. 1975. [Loc. 34.]

Paratypes: CAS 018432, 018433 (shells and soft parts), same locality as holotype. CAS 018434, 16 shells, same locality as holotype. CAS 018435, 5 shells, Loc. 35. USNM, ANSP, AMNH, FMNH, LACM, one shell each, Loc. 35.

REFERRED MATERIAL.—CALIFORNIA: Shasta County: Bollibokka Mountain Quadrangle: Loc. 30 [2 specimens], 31 [19], 32 [8], 33 [1], 36 [3], 37 [5], 38 [7], 39 [13], 40 [14], 41 [20]. Project City Quadrangle: Loc. 45 [40]. Figure 3 maps these localities.

ETYMOLOGY.—The subspecies is named for the people native to the region where it is found, the Wintu tribe.

DISCUSSION.—The major features of variation within the subspecies and its morphological relationship to other subspecies are discussed above and graphically shown in Figures 14–16. In coloration and spire height, *M. t. wintu* and *M. t. chaceana* are more similar than either is to *M. t. troglodytes*, whereas in microsculpture and relation of whorl number to overall size, *M. t. chaceana* and *M. t. troglodytes* group more closely.

Monadenia (Shastelix) troglodytes chaceana Berry

(Figures 13*a–c*)

Monadenia chaceana BERRY, 1940b:9–11, figs 9, 10.—PILSBRY 1948:1092.—SMITH 1960:97.—ROTH 1972a:5; 1972b:6.

ORIGINAL DESCRIPTION.—"Shell of but moderate size, weight, and thickness; spire low-conic to moderately elevated; whorls 5½ to 6, subangulate and carinate above the middle during juvenility, subcarinate at adolescence, but becoming obtusely angular and finally quite well rounded at maturity; base tumid, the umbilicus open, steep-walled, permeable to apex, and contained on the average about 8.4 times (7.45 to 9.88 in those measured) in the major shell-diameter. Aperture somewhat descending above, oblique, rounded to round-ovate, slightly or not at all flattened below; peristome nearly simple above, elsewhere usually little thickened and but moderately everted, terminating below in a very moderate columellar flare which covers only the edge of the umbilicus.

"Embryonic shell swollen, of 1¾ to 2 whorls; the surface initially smooth, but almost at once breaking into a few, irregular axial waves succeeded by a close, fine, crowded granulation, which abruptly ceases with the first post-embryonic whorl, the often heavy but extremely variable growth-striae thenceforth becoming the dominant feature; a few indistinct, elongate, and commonly confluent papillae arranged in rather distant forward-descending series appear on the early turns, but gradually give way on the later whorls to a weak and not very regular spiral striation which may become quite indistinct on the base; general surface between the striae and growth-lines very finely *microscopically* wrinkled in a cloth-like pattern.

"Periostracum smooth and lustrous; deep brown, encircled by a conspicuous dark-brown band about 2 mm. wide just above the periphery, bordered by a much narrower yellowish band and yet narrower band of the same pale tone just above, while on the shoulder some shells show varying traces of yet another band of intermediate brownish tone, best seen in juvenals" (Berry 1940b).

TYPE MATERIAL.—**Holotype:** SSB 8678 (shell); CALIFORNIA: Siskiyou County: among rocks about halfway up a spur of Badger Mountain on west side of Shasta River Canyon not far above its mouth (Berry 1940b).

Paratypes: CASGTC 10125 (formerly A. G. Smith no. 7102; shell); SUPTC 6555 (shell); according to Berry (1940b), additional paratypes are in the Berry Collection, with others originally to be deposited in the USNM and the Emery P. Chace Collection.

DISTRIBUTION.—*Monadenia t. chaceana* is known only from the general vicinity of the type-locality, in the Hornbrook Quadrangle, Siskiyou County (Locs. 1–5), and from one site (Loc. 6) in the Yreka Quadrangle, Siskiyou County (see also Fig. 1). Locality 7, "near Yreka" is too generalized to assign to a quadrangle with confidence. Limestone areas west of Gazelle and southeast of Scott Valley need additional prospecting for *Monadenia*.

DISCUSSION.—In coloration, *M. t. chaceana* most closely resembles the darker samples of *M. t. wintu*. The base is as dark as the spire, although neither is as dark as the supraperipheral band. At Localities 5 and 7, along with the usual dark-spired individuals, a form is present with light shoulder and one narrow, medium-brown, secondary band about two-thirds the distance from the suture to the periphery.

The substance of the shell is thinner and more translucent than in the Shasta Lake region groups.

Monadenia troglodytes chaceana has the highest mean H/D ratio of any subspecies (Table 3, Fig. 14*a*), differing highly significantly from any sample of *M. t. troglodytes* or *M. t. wintu*. At equivalent diameters, adult *M. t. chaceana* average 0.49 whorl more than *M. t. wintu* from the Brock Mountain area.

Berry (1940b) compared his *M. chaceana* to *Monadenia mormonum cala* (Pilsbry, 1900) and *M. churchi*. He also intimated a possible relationship to *Monadenia fidelis minor* (Binney, 1885) and surmised that the type-locality of that subspecies might be the Mount Shasta region. The latter supposition was evidently based on a statement by Binney (1885; Binney and Bland 1869) that small *Monadenia fidelis* occur at Mount Shasta.

Binney (1885:121, fig. 91) proposed "*Aglaia fidelis* var. *minor*" without a diagnosis and his original figure is unlocalized, but elsewhere (1885:141, footnote; 493) he recorded it from The Dalles, Oregon, collected by Henry Hemphill. Henderson (1936) and Pilsbry (1939) accepted The Dalles as the type-locality. The California Academy of Sciences collection contains two probable syntypes of *A. f.* var. *minor*, CASGTC 6001–6002, formerly H. Hemphill Collection no. 8598 and labeled "Helix fidelis Gray,/ var. minor W. G. Binn/depressed near mormonum/Near The Dalles, Oregon/Types/HH" in Hemphill's handwriting. They are small *M. fidelis*, agreeing well with Pilsbry's (1939) diagnosis of *M. fidelis minor* and moderately well with Binney's original engraving. That figure shows a pale shoulder with a light-centered spiral band and an indication of strong radial growth striae on the early whorls—all characteristic of the Dalles form.

The Binney and Bland Collection of terrestrial mollusks, now at the American Museum of Natural History (Gratacap 1901), contains one specimen of *M. fidelis* labeled "H. fidelis/Mt. Shasta/ Cooper." An oval, gold-edged, adhesive label on the specimen states "Mt. Shasta/WHB JGC"; the shell was evidently collected by William H. Brewer and given to James G. Cooper, who passed it on to Binney. This specimen, AMNH 57788, is 25.8 mm in diameter, 16.1 mm high, with 6.0 whorls. The shoulder is unpigmented except for faint, discontinuous traces of a light-centered spiral band. It is not the specimen illustrated by Binney (1885).

To my knowledge, *M. fidelis* does not live at Mt. Shasta proper, the nearest localities being Beaver Creek near the Klamath River, Siskiyou County (subspecies *M. f. leonina* Berry, 1937), and near the shores of Klamath Lake, Oregon (unnamed subspecies cited by Pilsbry [1939:42, fig. 18e] as *M. f. minor*). The Binney specimen is similar to the latter but more narrowly umbilicate. Brewer probably collected this shell on his 1863 trip through the Klamath Mountains, rather than on his 1862 climb of Mount Shasta (Brewer 1930). Cooper (1869) mentioned receiving from Brewer *M. fidelis* collected at Crescent City, the western terminus of Brewer's Klamath route. I conclude (1) that the name *minor* applies to a race of small *Monadenia fidelis* (Gray) from around The Dalles, Oregon, and (2) that Berry was mistaken about the similarity of his *M. chaceana* to Binney's "Mount Shasta" material.

PHYLOGENETIC HYPOTHESES CONCERNING *Monadenia*

Early statements about evolution within *Monadenia* tended to accord the widespread and conspicuous *M. fidelis* a central—and in some unspecified way archetypal—position, while the smaller, more remote and cryptic *M. hillebrandi*, *M. mormonum*, and similar forms were viewed as derivative (and possibly degenerate) offshoots (for example, see Cooper 1887; Stearns 1900). A questionable exception is that of Cooper (1873), who evidently attempted to adduce general principles for the direction of character-state transformation in west coast snail genera. One can readily speculate as to what extent an ethnocentric outlook colored such views. A second generation of malacologists studying *Monadenia* (chief among them Pilsbry, S. S. Berry, G D. Hanna, and Junius Henderson) concerned themselves more with description and less with interpretation of evolutionary relationships. But in their work too, a typological bias, with *M. fidelis* the "type" in more than a nomenclatural sense, may be detected. In a recently proposed alternative hypothesis (Roth 1979), the ancestral *Monadenia* was seen as a ground-dwelling, low-spired, and somewhat variable form, from which the exposed-crawling, partly diurnal, and semi-arboreal *M. fidelis* evolved: "Once emancipated from life in holes in the ground, the *fidelis* group achieved large size, relatively high spire, and an extensive range which now reaches farther north than any other American helicacean" (Roth 1979:13). Roth and Eng (1980) offered a conjectural, "narrative" (sensu Ball 1976) hypothesis for the origin of *Monadenia setosa* Talmadge. Such narrative explanations are not analytical and have little predictive power. To date, none of these competing models has specified the criteria for judging relationships, and none has been couched in testable propositions.

TABLE 4. CHARACTER COMPLEXES IN *Monadenia* (apomorphous states listed first).

1. Atrium small and narrow (large and globose).
2. Mucus gland about equal to (many times longer than) dart sac.
3. Lower part of mucus gland adnate to (free from) atrium.
4. Dart sac 5 mm or less in length (longer than 5 mm).
5. Flagellum about as long as (≥1.5 times length of) penis plus epiphallus.
6. Flagellum and spermatophore straight (helically coiled).
7. Basal chamber of penis sessile on (invaginated into) atrium.
8. Penial retractor inserted near middle (on distal third) of epiphallus.
9. Habit at least partly arboreal (ground-dwelling).
10. Granulose microsculpture present on teleoconch (limited to protoconch).
11. Shoulder band pigmentation monomorphic (polymorphic).

Phylogenetic systematics, the methodology of Willi Hennig (1966), seeks to analyze the probable direction of evolutionary character transformation in a particular group of organisms and, from this analysis, to reconstruct the evolutionary history of the group. An important virtue of this method is that it generates testable hypotheses about phylogenetic relations. (See Kavanaugh [1972] for an exposition of Hennig's approach to systematics and Gaffney [1979] for a useful bibliography of papers dealing with cladistic methodology.) In land malacology, Van Goethem (1977), Breure (1979), and Bishop (1979) have applied these principles to the land snail groups Urocyclinae, Bulimulidae, and American Camaenidae, respectively, and the same approach is implicit in the writings of a number of other malacologists.

Of 55 morphological and natural history characters studied, 11 (Table 4) were incorporated in a cladistic analysis. Characters excluded were those in which polarity of the transformations could not be interpreted, those that occur only

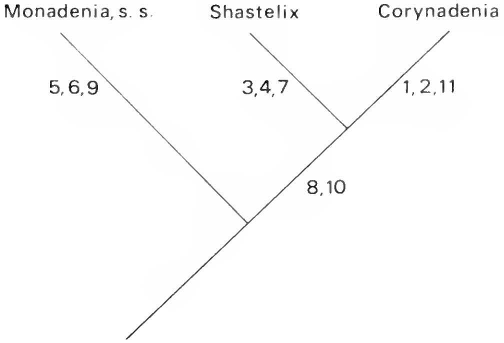


FIGURE 17. Suggested cladogram for the subgenera of *Monadenia*. Numbers refer to apomorphous states of character complexes listed in Table 4.

in states judged to be symplesiotypic for the genus, and those that are unique (as apomorphies) to one species and hence provide no information for grouping.

Figure 17 illustrates the relationship of character states in the three subgenera of *Monadenia*. It is well to emphasize that the hypothesis presented here is preliminary and undoubtedly will be modified as study of the genus progresses. This cladogram is based mainly on reproductive anatomy. In general, shell characters are much more labile, phenotypic responses to environment are common, and the number of conchologically polytypic species in *Monadenia* hampers the use of shell features in this kind of analysis. As Bishop (1979:275) noted, snail shells offer relatively few characters for analysis and are difficult to characterize objectively, "though both shape and texture may be most informative to the eye of an experienced worker in a manner which is hard to express in words." Moreover, shell characters are subject to numerous parallelisms and convergences, usually associated with habit and habitat (for example, the often-remarked similarity between the rock crevice-dwelling species, *Monadenia circumcarinata* (Stearns, 1879) and *Oreohelix elrodi* (Pilsbry, 1900)). A closer study is needed to discriminate analogous from homologous shell character states and extend the cladistic analysis to the species level.

Three character complexes, especially, illustrate the problems left unsolved by this analysis. The arboreal habit in *Monadenia*, s.s., is regarded as an apomorphy, but many of the associated apomorphic characteristics (potential for large size, high spire) are differentially expressed in the various subspecies of the polytypic *Monadenia fidelis*. Are these characters secondarily lost in such subspecies as the low-spired *M. f. scottiana* Berry and the small-shelled, unnamed race near Klamath Lake, or do these races preserve the plesiomorphous condition? Perhaps the arboreal habit and its associated character states are better viewed as expressions of a physiologically based eurytopy which permits life in the trees but also allows *M. fidelis* to inhabit low herbage near the coast (*M. f. pronotis* Berry) or rockpiles (Klamath Lake race). A specialized arboreal habit, such as the dependence of *M. setosa* on standing broadleaf deadwood for juvenile habitat (Roth and Eng 1980), is probably a second level of apomorphy, derived from a more generalized arboreal potentiality.

A transparent periostracum, through which shell banding is visible, is probably plesiomorphous for the genus. Banding, which is widespread in Helminthoglyptidae and other helicacean families, presumably evolved in the face of visual predation pressure (Roth, in preparation). An opaque periostracum that masks the banding (still present in the shell underneath) seems to be associated with cryptic habits and independently derived in *Monadenia*, s.s., and *Corynadenia*.

Carination of the margin of the adult shell is a paedomorphy (compare Gould 1969, *Poecilozonites*), independently derived in *Monadenia*, s.s., *Corynadenia*, and probably *Shastelix*. "Hypercarination" (carina set off by pinched grooves) is a further derived state among several deep rock-crevice-dwelling forms of the Sierra Nevada.

While a cladogram, such as that in Figure 17, is nothing more than a branching diagram depicting the nested pattern of synapomorphies among the taxa under study, a phylogeny is an explicit statement concerning the exact nature of the evolutionary relationship among the taxa (Eldredge 1979). A phylogenetic tree is "a diagram (not necessarily branching!) depicting the actual pattern of ancestry and descent among a series of taxa" (Eldredge 1979:168) and embodies assumptions and information not required in (and theoretically excluded from) the construction of a cladogram. With the further addition of explanatory narrative, one can often devise a scenario to suggest how the phylogenetic relationship, and the pattern of synapomorphies in the underlying cladogram, came to be.

Strictly speaking, the construction of phylogenetic trees is limited to species; species, not genera or other higher taxa, give rise to other species. Therefore, when we speak of a dichotomy arising between subgenera (as herein), we are really maintaining that the dichotomy arose between two species which would be classed in the separate subgenera.

The suggested cladogram for the subgenera of *Monadenia* specifies three detected autapomorphies in the subgenus *Monadenia*, s.s., two synapomorphies shared by *Shastelix* and *Corynadenia*, and three autapomorphies each in *Corynadenia* and *Shastelix*. The effect of this distribution of apomorphies is to falsify all possible phylogenetic trees for the group except that which is isomorphous with the cladogram (see Platnick 1977:440–441, fig. 2). Consequently, the proposed phylogenetic history of *Monadenia* consists of (1) a dichotomy between *Monadenia*, s.s., and the common ancestor of *Corynadenia* and *Shastelix*, followed in time by (2) the dichotomy between *Corynadenia* and *Shastelix*.

THE SCENARIO.—In the John Day Formation (late Oligocene to early Miocene) of central Oregon, three fossil forms referred to *Monadenia* are present: *M. antecedens* (Stearns, 1900), large-shelled and so similar in general appearance to *M. fidelis* that it was formerly ranked as a subspecies of the latter; *M. dubiosa* (Stearns, 1902), said to be another *fidelis*-like form (Pilsbry 1939); and *M. marginicola* (Conrad, 1871), which Hanna (1920) believed to be related to "the *mormonum* group" (i.e., *Corynadenia*). No anatomical details are available, of course, and the shell microsculpture, if preserved, is not specified in the literature, but the distinction between large *fidelis*-type shells and smaller shells with the character of present-day ground-dwelling forms is consistent with the hypothesized early split between *Monadenia*, s.s., and the *Shastelix*-*Corynadenia* stock.

At the time of deposition of the John Day Formation (36.4–22 million years before present; Hammond 1979), the Cascade Arc had rotated from its earlier northwest-southeast orientation almost to its present north-south position, east of the presumably coastal Klamath Mountains–Coast Range block (Hammond 1979:figs. 8, 9). The John Day accumulated as clayey and tuffaceous sediments in an inland basin contemporaneously with formation of the volcanic and pyroclastic rocks of the middle Western Cascades Group. During this episode, Cascade volcanism was centered in randomly spaced stratovolcanoes and calderas; the string of high volcanic edifices that characterizes the modern Cascade Range had not yet developed. Contemporaneous floras from the Coast Range block to the west are similar in floristic composition and leaf physiognomy to the Bridge Creek Flora from the lower member of the John Day (Brown 1959; Wolfe and Hopkins 1967), indicating that the Cascade Range was not a significant climatic or vegetational barrier at this time.

The Bridge Creek Flora, associated with a radiometric date of 31.5 million years (Evernden and James 1964), represents a mixed mesophytic forest dominated by broad-leaved deciduous trees, in a temperate climate with ample summer rainfall (Chaney 1948; Brown 1959; Wolfe and Hopkins 1967). Its greatest similarities are with modern hardwood forests of eastern North America and eastern Asia (Chaney 1948; Whittaker 1961). Temperature parameters suitable for forests of this composiion are now lacking in the Pacific coast states except in isolated, small, interior valleys (Wolfe 1979).

The source of the John Day land mollusks is evidently the vertebrate-rich middle member, of early Arikareean (late Oligocene) age (Wood et al. 1941) and about 25 million years old (Berggren and Van Couvering 1974). Contemporaneous floras are also mixed mesophytic, possibly somewhat warmer than the Bridge Creek Flora. The diverse vertebrate remains likewise indicate a temperate and wet climate, quite unlike the semiarid interior of Oregon of the present. It seems plausible that such an environment could have supported greater intrageneric snail diversity than now seen in any forests of the west, much as the hardwood forests of the eastern United States now support a substantial diversity of snails in genera of the Polygyridae. Part of the early diversification of *Monadenia* forms probably involved habitat partitioning between ground-dwelling and arboreal species.

The subsequent vegetational and climatic history of western North America (greatly simplified) includes warming from late Oligocene to middle Miocene, followed by gradual, fluctuating cooling through the Pleistocene, and a shift from summer-wet to summer-dry climate. By the Pliocene the woody flora was depauperate, with extinctions most marked in broad-leaved lineages with paratropical and subtropical affinities (Wolfe 1979). Latitudinal and altitudinal zonation became pronounced in the later Tertiary, accompanied by a differentiation of forest types into several adaptive zones (Axelrod 1976:fig. 7). As the rising Cascade Range cast a more profound rain shadow on the interior, humid forests became confined to the windward, west slope of the Cascades and lands to the west—the modern range of *Monadenia,* s.s.

At this time (late Miocene–Pliocene), a substantial allopatry between the two existing stocks of *Monadenia* may have arisen, with the *Shastelix-Corynadenia* stock inhabiting the drier, interior regions, and *Monadenia,* s.s., perhaps exploiting a tendency toward eurytopy in humid environments. Equability of climate may also have been a factor. Parapatry like that which now occurs in the Klamath Mountains, where *M.* (*Monadenia*) *fidelis* and *M.* (*M.*) *setosa* inhabit riparian woodland while *M.* (*Shastelix*) *churchi* occupies drier, more exposed slopes and rockslides, may have been common where the environments interfingered. (In this connection, according to Whittaker [1961] and Axelrod [1976], the modern Klamath Mountains preserve a climate and vegetation more like that of the later Cenozoic than any other region in the west.) Some time in this interval *Monadenia* became extinct in central Oregon.

On a graph of mean annual temperature versus mean annual range of temperature (compare Wolfe 1979), only the thermal range of *Shastelix* overlaps that of present-day mixed mesophytic forest (Fig. 18). Because the John Day fossil occurrence represents only one datum, we do not know what the total Oligocene thermal range of *Monadenia* might have been; but certainly the large, *fidelis*-type snails of the typical subgenus have shifted away (toward the right—equable—side of the graph) from the thermal zone of mixed mesophytic forest. *Shastelix* has shifted less, if at all. The narrow overlap of thermal ranges of *Monadenia,* s.s., and *Shastelix* parallels their narrow geographic zone of parapatry and suggests progressive range/habitat differentiation along a climatic gradient. In contrast, the thermal range of *Corynadenia* overlaps those of both other subgenera extensively. It occupies a considerable range of mean annual temperatures, but a limited zone of mean annual temperature *ranges.* If *Corynadenia* differentiated from *Shastelix* along a climatic gradient, it was presumably not chiefly a gradient of mean temperature and equability.

The autapomorphies of *Corynadenia* can be interpreted as adaptations to the rockslide/rock-crevice habitat and prolonged summer drought. The range of *Corynadenia* receives the least precipitation of any zone inhabited by *Monadenia* (Elford 1970). Reduction or partial loss of the genital apparatus is associated with adaptation to xeric environments in other groups of Helminthoglyptidae (Gregg 1960; Bequaert and Miller 1973). Retention of granulose microsculpture on the teleoconch is evidently a paedomorphy, and is most strongly developed in species (*M. hillebrandi, M. circumcarinata*) with paedomorphic carination of the adult shell. Small size and low-spired, lenticular shape are other crevice-related characteristics that occur in some species and races of *Corynadenia.*

Additional evidence for the relationship of temperature and distribution in *Monadenia* is seen in the close correspondence between maximum summer and minimum winter isotherms and the range limits of *Shastelix* and *Corynadenia* (Fig. 1). The 36 C mean maximum July isotherm practically coincides with the "downhill" limit of the genus in the Klamath Mountains and Sierra Nevada, and the −4 C mean minimum January isotherm, more loosely, with the "uphill" limit. (At this scale, the isotherms are highly generalized and each stands for a range of related microhabitat temperatures.) The southern limit of *Corynadenia* occurs just north of where these two isotherms pinch together. Similarly, between the southern limit of *Shastelix* and the northern limit of *Corynadenia,* the July isotherm bulges eastward, almost but not quite intersecting the January isotherm. At this point, the 33 C mean maximum July isotherm, which most closely coincides with the very southern limit of *Shastelix,* is actually east ("uphill") of the −4 C January isotherm. If it persisted long enough, a thermal configuration like this could have produced vicariance within

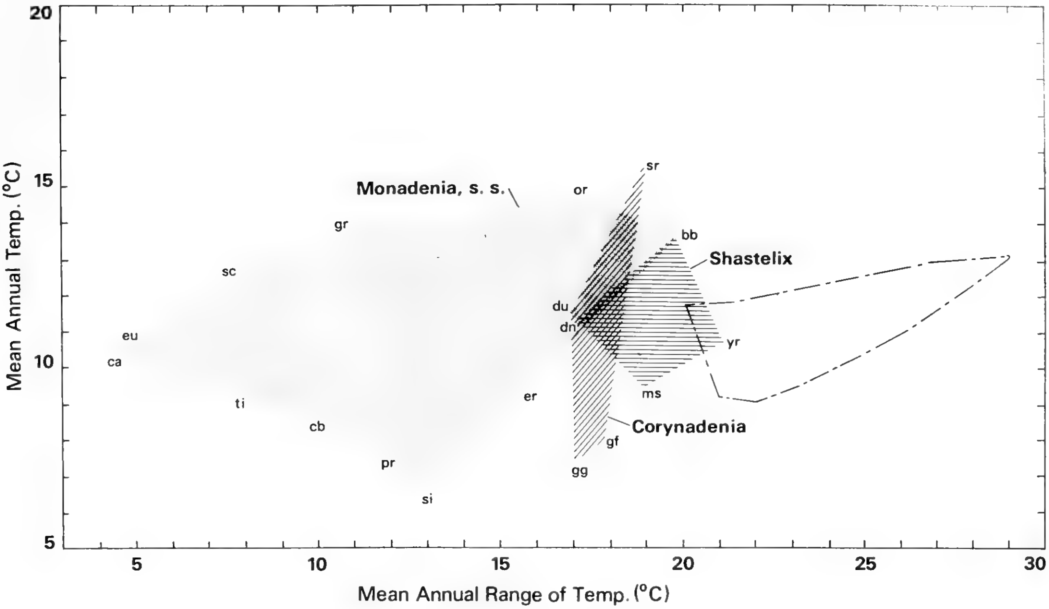


FIGURE 18. Graph of thermal ranges of the three subgenera of *Monadenia* in relation to temperature parameters. Stippling, *Monadenia*, sensu stricto; diagonal hachure, *Corynadenia*; horizontal hachure, *Shastelix*. Dot-dashed line encloses thermal range of present-day mixed mesophytic forest of eastern Asia (after Wolfe 1979). Abbreviations for stations defining the subgeneric polygons (in California unless otherwise indicated): *bb*, Big Bar; *ca*, Cape Blanco, Oreg.; *cb*, Clallam Bay 1 NNE, Wash.; *dn*, Dunsmuir; *du*, Dudley; *er*, Elwha Ranger Station, Wash.; *eu*, Eureka; *gf*, Giant Forest; *gg*, Grant Grove; *gr*, Graton 1 W; *ms*, Mount Shasta; *or*, Orleans; *pr*, Prince Rupert, Brit. Col.; *sc*, Scotia; *si*, Sitka, Alaska; *sr*, Sonora Ranger Station; *ti*, Tatoosh Island, Wash.; *yr*, Yreka. Thermal data from Elford (1970), Wolfe (1979).

the *Shastelix-Corynadenia* stock. The present configuration of the isotherms must be short-lived in geologic terms, particularly in the face of the great climatic fluctuations of the Pleistocene; while it may now enforce the geographic separation of *Shastelix* and *Corynadenia*, their initial cleavage undoubtedly took place earlier. Alone, or in combination with climatic factors, Miocene or later topographic developments could have fostered the vicariance. (Pliocene through Holocene volcanic rocks of the High Cascades Group overlap the edges of the northern Sierra Nevada and eastern Klamath Mountains, separating the metamorphic and plutonic rocks of these two provinces for a distance of about 80 km [Hammond 1979]. They were extruded initially as basaltic flows and later as andesitic, cone-building eruptions, filling a structural trough and lowland between the Klamath and Sierran blocks. For a calcicolous ancestral *Monadenia*, these volcanic rocks could have been a barrier leading to allopatric differentiation or interrupting a cline along which some differentiation had already proceeded.) Given the complexity of relations between land snails and their environment, it is unlikely that a single event can be pinpointed as the cause, but no details of phylogeny, distribution, or thermal relations contraindicate vicariance in the general geographic setting of the present.

ACKNOWLEDGMENTS

I gratefully acknowledge the friendship and guidance of Allyn G. Smith (1895–1976), who nourished my interest in terrestrial malacology and helped to frame an early draft of this study. In addition I thank S. E. Hirschfeld, R. L. Seib, and D. C. Rudolph, all of whom, knowing of my interest in Shasta County snails, contributed material for study. Special thanks are owed to P. U. Rodda, D. H. Kavanaugh, H. W. Schorn, P. H. Pressley, and D. W. Taylor for helpful discussion; to A. J. Cain, G. M. Davis, and W. L. Lee for stimulus in several areas; to A. J.

Ferreira for radular preparation; to W. K. Emerson and H. Feinberg for lending historically significant material; and to L. L. Eng, E. V. Coan, and L. H. Roth for aiding the investigation in various ways. Susan Middleton contributed photographic assistance. Steven Sechovec rendered most of the anatomical drawings.

Literature Cited

Albers, J. P., and J. F. Robertson. 1961. Geology and ore deposits of East Shasta copper-zinc district, Shasta County, California. U.S. Geol. Surv. Prof. Pap. 338. 107 p.

Axelrod, D. I. 1976. History of the coniferous forests, California and Nevada. Univ. Calif. Publ. Bot. 70:1–62.

Ball, I. R. 1976. Nature and formulation of biogeographical hypotheses. Syst. Zool. 24:407–430.

Bequaert, J. C., and W. B. Miller. 1973. The mollusks of the arid southwest, with an Arizona check list. Univ. Arizona Press, Tucson.

Berggren, W. A., and J. A. Van Couvering. 1974. The late Neogene. Elsevier Sci. Publ. Co., Amsterdam.

Berry, S. S. 1940a. A proposed dichotomy of the snail-genus *Monadenia*. Bull. South. Calif. Acad. Sci. 38:203–205.

———. 1940b. Nine new snails of the genus *Monadenia* from California. J. Entomol. Zool., Pomona Coll. 32:1–17.

Binney, W. G. 1885. A manual of American land shells. U.S. Natl. Mus. Bull. 28. 528 p.

———, and T. Bland. 1869. Land and fresh water shells of North America. Part I. Pulmonata Geophila. Smithson. Misc. Collect. 194. 316 p.

Bishop, M. J. 1979. A new species of *Caracolus* (Pulmonata: Camaenidae) from the Oligocene of Nebraska and the biotic history of the American camaenid land snails. Zool. J. Linn. Soc. London 67:269–284.

Boycott, A. E. 1934. The habitats of land Mollusca in Britain. J. Ecol. 22:1–38.

Breure, A. S. H. 1979. Systematics, phylogeny and zoogeography of Bulimulinae (Mollusca). Zool. Verh. Rijksmus. Nat. Hist. Leiden 168. 215 p.

Brewer, W. H. 1930. Up and down California in 1860–1864. The journal of William H. Brewer, Professor of Agriculture in the Sheffield Scientific School from 1864 to 1903. Edited by F. P. Farquhar. Yale Univ. Press, New Haven.

Brown, R. W. 1959. A bat and some plants from the upper Oligocene of Oregon. J. Paleontol. 33:125–129.

Chaney, R. W. 1948. The ancient forests of Oregon. Condon Lecture Publ., Oregon State Syst. High Educ. 56 p.

Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. Proc. Natl. Acad. Sci. U.S.A. 76:2480–2484.

Comfort, A. 1951. Observations on shell pigments of land pulmonates. Proc. Malacol. Soc. London 29:35–43.

Coogan, A. H. 1960. Stratigraphy and paleontology of the Permian Nosoni and Dekkas Formations (Bollibokka Group). Univ. Calif. Publ. Geol. Sci. 36:243–316.

Cooper, J. G. 1869. On the distribution and localities of west coast helicoid land shells, &c. Am. J. Conchol. 4:211–240.

———. 1873. On the law of variation in the banded California land shells. Proc. Calif. Acad. Sci. 5:121–125.

———. 1879. Notes on some land-shells of the Pacific slope. Proc. Am. Philos. Soc. 18:282–288.

———. 1887. West coast Pulmonata; fossil and living. Bull. Calif. Acad. Sci. 2:355–376.

Demirmen, F., and J. W. Harbaugh. 1965. Petrography and origin of Permian McCloud limestone of northern California. J. Sediment. Petrol. 35:136–154.

Diller, J. S. 1906. Description of the Redding Quadrangle. U.S. Geol. Surv. Geol. Atlas of United States, folio 138. 14 p.

Diver, C. 1932. A method of determining the number of whorls of a shell and its application to *Cepaea hortensis* Müll. and *C. nemoralis* L. Proc. Malacol. Soc. London 19:234–239.

Eldredge, N. 1979. Cladism and common sense. Pp. 165–198 *in* J. Cracraft and N. Eldredge, eds., Phylogenetic analysis and paleontology. Columbia Univ. Press, New York.

Elford, C. R. 1970. Climate of California. Climatography of the United States, no. 60-4, U.S. Dept. Commerce. 57 p.

Evernden, J. F., and G. T. James. 1964. Potassium-argon dates of the Tertiary floras of North America. Am. J. Sci. 262:945–974.

Gaffney, E. S. 1979. An introduction to the logic of phylogenetic reconstruction. Pp. 79–111 *in* J. Cracraft and N. Eldredge, eds., Phylogenetic analysis and paleontology. Columbia Univ. Press, New York.

Gould, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P.* (*Poecilozonites*) in Bermuda. Bull. Mus. Comp. Zool. 138:407–532.

Gratacap, L. P. 1901. Catalogue of the Binney and Bland Collection of terrestrial air-breathing mollusks of the United States and Territories. . . . Bull. Am. Mus. Nat. Hist. 14:335–403.

Gregg, W. O. 1960. Derivation of the Helminthoglyptinae with particular reference to the desert forms. Am. Malacol. Union Inc. Annu. Rep. 25(for 1959):45–46.

Hammond, P. E. 1979. A tectonic model for evolution of the Cascade Range. Soc. Econ. Paleontol. Mineral. Pacific Coast Paleogeog. Sympos. 3:219–237.

Hanna, G D. 1920. Fossil mollusks from the John Day basin in Oregon contained in the Condon Museum of the University of Oregon. Univ. Oregon Publ. 1(6):1–8.

———, and A. G. Smith. 1933. Two new species of *Monadenia* from northern California. Nautilus 4:79–86.

Heller, J. 1975. The taxonomy, distribution and faunal succession of *Buliminus* (Pulmonata: Enidae) in Israel. Zool. J. Linn. Soc. 57:1–57.

Henderson, J. 1936. The non-marine Mollusca of Oregon and Washington—Supplement. Univ. Colo. Stud. 23:251–280.

Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana.

Hibbard, C. W., C. E. Ray, D. E. Savage, D. W. Taylor, and J. E. Guilding. 1965. Quaternary mammals of North America. Pp. 509–525 *in* H. E. Wright, Jr., and D. G. Frey, eds., The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey.

Irwin, W. P. 1972. Terranes of the western Paleozoic and Triassic belt in the southern Klamath Mountains, California. U.S. Geol. Surv. Prof. Pap. 800-C:103–111.

———, and S. P. Galanis, Jr. 1976. Map showing limestone and selected fossil localities in the Klamath Mountains Province, California and Oregon. U.S. Geol. Surv. Misc. Field Studies Map MF-749.

Kavanaugh, D. H. 1972. Hennig's principles and methods of phylogenetic systematics. Biologist 54:115–127.

———. 1979. Studies on the Nebriini (Coleoptera:Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. Proc. Calif. Acad. Sci. 42:87–133.

Kinkel, A. R., Jr., W. E. Hall, and J. P. Albers. 1956. Geology and base-metal deposits of West Shasta copper-zinc district, Shasta County, California. U.S. Geol. Surv. Prof. Pap. 285. 156 p.

Küchler, A. W. 1977. The map of the natural vegetation of California. Pp. 909–939, map, *in* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California. John Wiley and Sons, New York.

Major, J. 1977. California climate in relation to vegetation. Pp. 11–74 *in* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California. John Wiley and Sons, New York.

Pilsbry, H. A. 1895. Guide to the study of helices [continuation]. Manual of Conchology, ser. 2, 9:161–336.

———. 1900. Note on the varieties of *Epiphragmophora mormonum*. Nautilus 13:128.

———. 1939. Land Mollusca of North America (north of Mexico). Acad. Nat. Sci. Phila., Monogr. 3, 1(1):1–573.

———. 1948. Land Mollusca of North America (north of Mexico). Acad. Nat. Sci. Phila., Monogr. 3, 2(2):521–1113.

Platnick, N. 1977. Cladograms, phylogenetic trees, and hypothesis testing. Syst. Zool. 26:438–442.

Raup, D. M. 1966. Geometric analysis of shell coiling: general problems. J. Paleontol. 40:1178–1190.

Rayner, R. W. 1970. A mycological colour chart. Commonwealth Mycological Institute, Kew, Surrey.

Roth, B. 1972a. Rare and endangered land mollusks in California. The Resources Agency of California, Dept. Fish and Game, Inland Fisheries Admin. Rep., no. 72-10. 21 p.

———. 1972b. Rare and endangered land mollusks in California. Sterkiana 48:4–16.

———. 1975. On the affinities of *Monadenia churchi* Hanna and Smith (Gastropoda: Stylommatophora). Bull. South. Calif. Acad. Sci. 74:93–94.

———. 1979. Thoughts on *Monadenia* and other snails of northern California (abstract). West. Soc. Malacol. Annu. Rep. 11:13.

———, and L. L. Eng. 1980. Distribution, ecology, and reproductive anatomy of a rare land snail, *Monadenia setosa* Talmadge. Calif. Fish Game 66:4–16.

Smith, A. G. 1957. Snails from California caves. Proc. Calif. Acad. Sci., ser. 4, 29:21–46.

———. 1960. Note on *Trilobopsis tehamana* (Pilsbry), a rare northern California land snail. Veliger 2:97.

———. 1970. American Malacological Union Symposium, Rare and Endangered Mollusks. 6. Western land snails. Malacologia 10:39–46.

Solem, A. 1975. Notes on Salmon River Valley oreohelicid land snails, with description of *Oreohelix waltoni*. Veliger 18:16–30.

———. 1978. Classification of the land Mollusca. Pp. 49–97 *in* V. Fretter and J. Peake, eds., Pulmonates, vol. 2A, Systematics, evolution and ecology. Academic Press, London.

Stearns, R. E. C. 1900. Fossil land shells of the John Day region with notes on related living species. Proc. Wash. Acad. Sci. 2:651–660.

Talmadge, R. R. 1960. Color phases in *Monadenia fidelis* (Gray). Veliger 2:83–85.

Tweedie, M. W. F. 1961. On certain Mollusca of the Malayan limestone hills. Bull. Raffles Mus. 26:49–65.

Van Goethem, J. L. 1977. La systématique des Urocyclinae (Mollusca, Pulmonata, Urocyclidae). Malacologia 16:133–138.

Wahrhaftig, C., and J. H. Birman. 1965. The Quaternary of the Pacific mountain system in California. Pp. 299–340 *in* H. E. Wright, Jr., and D. G. Frey, eds., The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey.

Walton, M. L. 1970. Longevity in *Ashmunella*, *Monadenia*, and *Sonorella*. Nautilus 83:109–112.

Webb, G. R. 1952. Pulmonata, Xanthonycidae: Comparative sexological studies of the North American land-snail, *Monadenia fidelis* (Gray)—a seeming ally of Mexican helicoids. Gastropodia 1:[1–3].

———. 1966. Courtship between *Monadenia fidelis* and *M. infumata*. Nautilus 79:103–105.

Whittaker, R. H. 1961. Vegetation history of the Pacific Coast states and the "central" significance of the Klamath region. Madroño 16:5–22.

Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australasia. U.S. Geol. Surv. Prof. Pap. 1106. 37 p.

———, and D. M. Hopkins. 1967. Climatic changes recorded by Tertiary land floras in northwestern North America. Pp. 67–76 *in* K. Hatai, ed., Tertiary correlations and climatic changes in the Pacific. 11th Pac. Sci. Congress, Tokyo, 1966, Sympos. 25.

Wood, H. E., II, R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Bull. Geol. Soc. Am. 52:1–48.

Appendix: Localities

Localities for material studied are listed below, grouped according to geographic area. The numbers assigned are for purposes of this study; samples are on deposit in the mollusk collection of the California Academy of Sciences. Map quadrangle names refer to the most recent edition of the U.S. Geological Survey 7.5- and 15-minute Series (Topographic). The number in brackets following the collection data is the total number of specimens examined from that locality; it does not always agree with sample size numbers cited in the text because not every character could be measured for every specimen and because many of the computations utilized adult shells or anatomies only. Distances are cited as received in the collectors' notes and have not been converted to the metric system.

California: *Siskiyou County:* Hornbrook Quadrangle

1 Along creek 1.5 mi sw of Hornbrook. G D. Hanna, Apr. 1928 [5].

2 SW¼ sec. 18, T. 46 N, R. 6 W, 1000 ft up Klamath River from mouth of Shasta River. D. E. Marsh, 1931 [2].

3 Among rocks about half-way up a spur of Badger Mountain on west side of Shasta River canyon not far above its mouth. E. P. Chace, 29 Sep. 1937 [3]. (Type-locality, *M. t. chaceana.*)

4 Shasta River near junction with Klamath River. E. P. Chace [3].

5 Sec. 25(?), T. 46 N, R. 7 W, banks of Shasta River, 2–3 mi from mouth, in shaded rockslides. A. G. Smith, 11 Sep. 1934 [5].

California: *Siskiyou County:* Yreka Quadrangle

6 Chastain's Quarry, west of Gazelle. E. P. and E. M. Chace, 28 Sep. 1937 [3].

7 [?] "Near Yreka." E. J. Elliott, autumn 1933 [5].

California: *Shasta County:* Bollibokka Mountain Quadrangle

8 Near McCloud River bridge, 30 mi NE of Redding. D. C. Rudolph, B. Martin, S. Winterath, 9 Apr. 1979 [2].

9 Sec. 32, T. 36 N, R. 3 W, west slope of Bollibokka Mountain, 0.75 mi E of bridge across McCloud River. J. W. Durham, E. C. Allison, 18 Apr. 1964 [5].

10 Sec. 5, T. 35 N, R. 3 W, slope below Samwel Cave, above McCloud River arm of Shasta Lake. R. L. Seib, 11 Mar. 1978 [32].

11 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, ch. 1, sec. 2–5 (=UCMP loc. 1008). E. L. Furlong [8]. (Type-locality, *M. t. troglodytes.*)

12 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, in gravel slope filling grotto at south end, ch. 2, sec. 4 (=UCMP loc. 1009). E. L. Furlong [2].

13 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, with bone matter, 50 ft in from twilight zone. R. E. Graham, 5–6 Jan. 1957 [2].

14 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, twilight zone floor. R. de Saussure, 10 May 1957 [2].

15 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. de Saussure, 5 June 1957 [2].

16 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, entrance to main cave. R. de Saussure, 5 June 1957 [1].

17 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, surface, second exit. R. de Saussure, A. Dacey, 5 June 1957 [4].

18 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. N. Slusser, 4–7 June 1957 [2].

19 Sec. 5, T. 35 N, R. 3 W, within 25 ft of entrance to Samwel Cave. R. E. Graham, 8 June 1958 [31].

20 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, bone chamber pit containing bone and rubble matrix, 7 to 12 inches depth. R. E. Graham, 10–14 June 1958 [2].

21 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. E. Graham, 27 Dec. 1958 [6].

22 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. E. Graham, 18 June 1959 [1].

23 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. E. Graham, 19 Dec. 1959 [2].

24 Sec. 5, T. 35 N, R. 3 W, Samwel Cave and vicinity. D. C. Rudolph, B. Martin, S. Winterath, 9 Apr. 1979 [9].

25 SE¼ sec. 7, T. 35 N, R. 3 W, limestone outcrop, summit of Hirz Mountain, 2 mi sw of Samwel Cave. R. E. Graham, June 1960 [2].

26 SE¼ sec. 6, T. 35 N, R. 3 W, Ellery Creek on Gilman Road, 15 mi NE of junction with Interstate Hwy. 5, limestone rock slides. A. G. Smith, 17 May 1973; B. Roth, Mar. 1980 [30].

27 SE¼ sec. 6, T. 35 N, R. 3 W, Ellery Creek, w side of McCloud River arm of Shasta Lake. R. L. Seib, 24 Mar. 1978 [5].

28 SW¼ sec. 21, T. 35 N, R. 3 W, Dekkas Rock at junction of Dekkas Creek with E side of McCloud River arm of Shasta Lake. R. L. Seib, 24 Mar. 1978 [38].

29 NW¼ NE¼ sec. 32, T. 35 N, R. 3 W, limestone outcrop 0.3 mi ssw of junction of Campbell Creek with E side of McCloud River arm of Shasta Lake. R. L. Seib, 24 Mar. 1978 [3].

30 Sec. 28, 29(?), T. 25 N, R. 2 W, Low Pass Creek. J. Gorman, 29 Jan. 1953 [2].

31 SE¼ NW¼ sec. 4, T. 34 N, R. 2 W, caves at headwaters of Brock Creek drainage. S. E. Hirschfeld, July 1975 [19].

32 SE¼ NW¼ sec. 4, T. 34 N, R. 2 W, shelter below and to left of Goblin Shelter, headwaters of Brock Creek drainage. S. E. Hirschfeld, July 1975 [8].

33 NE¼ SW¼ sec. 3, T. 34 N, R. 2 W, small cave in Hosselkus limestone in gray rocks on E side of eastern NE–SW-trending ridge. S. E. Hirschfeld, 3 Apr. 1970 [1].

34 NW¼ NE¼ sec. 8, T. 34 N, R. 2 W, cave between two limestone buttes at south end of Gray Rocks, above Pit River arm of Shasta Lake. S. E. Hirschfeld, Oct. 1975 [49]. (Type-locality, *M. t. wintu.*)

35 SW¼ NW¼ sec. 7, T. 34 N, R. 2 W, limestone quarry 1 mi N, ⅝ mi E of Brock Mountain Lookout, above Squaw Creek arm of Shasta Lake. R. L. Seib, 25 Mar. 1978 [39].

36 Squaw Creek. A. M. Strong, 1898 [3].

37 Squaw Creek. J. Gorman, 14–15 Mar. 1953 [5].

38 N ctr., SE¼ sec. 9, T. 34 N, R. 2 W, caves in Brock Creek limestone, above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [7].

39 NW¼ SE¼ sec. 9, T. 34 N, R. 2 W, lower limestone across from Brock Spring, above Brock Creek, above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [13].

40 NE¼ SW¼ sec. 9, T. 34 N, R. 2 W, "Monadenia Cave" and vicinity, above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [14].

41 NE¼ SW¼ sec. 9, T. 34 N, R. 2 W, "Elk Antler Cave," above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [20].

CALIFORNIA: *Shasta County:* Lamoine Quadrangle

42 SW¼ sec. 13, T. 34 N, R. 4 W, Shasta Lake Caverns. D. C. Rudolph, B. Martin, S. Winterath, 10 Apr. 1979 [1].

43 SE¼ SE¼ sec. 23, T. 34 N, R. 4 W, Potter Creek, along McCloud River arm of Shasta Lake. R. L. Seib, 11 Mar. 1978 [22].

44 Sec. 23, T. 34 N, R. 4 W, Potter Creek Cave, "past kitchen" (=UCMP loc. 1055) [12].

CALIFORNIA: *Shasta County:* Project City Quadrangle

45 SE¼ sec. 4, T. 33 N, R. 4 W, Calveris Cement Co. quarry above Interstate Hwy. 5 just south of Shasta Lake bridge, 2.5 mi NNE of Mountain Gate. R. L. Seib, 11 Mar. 1978 [40].

CALIFORNIA: *Shasta County:* Anderson Quadrangle

46 Clear Creek, on road between Redding and Beegum. G D. Hanna, Sep. 1952 [1].

CALIFORNIA: *Shasta County:* quadrangle uncertain

47 Crystal Shasta Cave. K. Howard, 1958(?) [1].

48 Chute Cave. R. de Saussure, Nov. 1957 [1].

49 "Shasta County, Calif.," *ex* D. O. Mills collection, UCMP [3].

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 16, pp. 409–433, 2 figs., 9 tables October 26, 1981

FOOD HABITS OF SMALLER MARINE MAMMALS FROM NORTHERN CALIFORNIA

By

Robert E. Jones

Museum of Vertebrate Zoology, University of California,
Berkeley, California 94720

Abstract: General food habits are discussed for 11 species of small marine mammals beach-cast in northern California. The collection method allowed tabulation only of the kinds, numbers, and percentages of fish, molluscan, and crustacean prey.

Dominant food species for all male *Zalophus californianus* were the following: *Merluccius productus* (62.8 percent of occurrence), *Engraulis mordax* (23.8 percent), Scorpaenidae (6.3 percent), *Porichthys notatus* (3.2 percent). *Octopus* and *Loligo* also occurred in 7 (23.0 percent) of 30 California sea lions examined.

Nine of 19 individuals of *Eumetopias jubatus* contained food remnants of fish; 10 new dietary items are reported. Seven of the nine also fed on invertebrates, including four kinds of cephalopods. Scorpaenidae 31.2 percent of occurrence), *Merluccius productus* (21.7 percent), Pleuronectidae (17.3 percent), and *Chilara taylori* (11.8 percent) were the principal fishes identified.

Eight of 12 *Phoca vitulina* stomachs contained food (6 with fish, 2 with invertebrates). Embiotocids (41.9 percent of occurrence), *Lycodopsis pacifica* (27.9 percent), Pleuronectidae (9.3 percent), and *Hexagrammos decagrammus* (9.3 percent) were the dominant fishes. The only cephalopod identified from *Phoca* was *Octopus*.

The stomachs of all seven individuals of *Lagenorhynchus obliquidens* examined contained food. Osmerid fishes, *Porichthys*, and juvenile rockfishes were the most frequent items identified. The presence of five genera of cephalopods suggests that *Lagenorhynchus* can take a wide variety of prey from several habitats.

Juvenile Scorpaenidae, *Engraulis*, *Merluccius*, and *Microgadus* made up 97 percent of the diet of 20 individuals of *Phocoena phocoena*. The abundant cephalopod *Loligo* was a primary invertebrate food item and was ingested whole.

INTRODUCTION

The objective of this study is to summarize the literature on the diets of smaller marine mammals in the eastern Pacific and to report on the contents of 102 stomachs from five pinniped and six small cetacean species. The purpose has been to make a thorough scrutiny of published dietary knowledge and analyze stomachs of beach-cast specimens. Particular attention has been directed to reviewing all records on feeding controversy. It has been argued for many decades that marine mammals compete with commercial fishing industries (Anonymous 1901; Townsend 1918).

Marine biologists in California have questioned the impact of marine mammals on the state's fisheries for at least 100 years (Redding et al. 1875; Rutter et al. 1904; California Division of Fish and Game 1927; Hedgpeth 1944; Anderson 1960; Frey 1971; National Oceanic and Atmospheric Administration 1974). The report of the California Commissioners of Fisheries for the years 1874–1875 (Redding et al. 1875) stated clearly that sea lions and seals were protected by special enactment, with penalties imposed on any person who should kill or disturb the beasts. On the basis of the observed "hundred-fold" increase in the populations of seals and sea lions at the entrance to San Francisco Bay over the previous ten-year period, the Commissioners recommended the killing of nine-tenths of the existing population. It is unclear as to what action, if any, resulted from this recommendation. Scammon (1874) stated, "A few years ago great numbers of sea lions were taken along the coast of Upper and Lower California, and thousands of barrels of their oil were obtained." The statement describes the period before the enactment of regulations protecting California pinnipeds. On the west coast of North America, most of the commercial seal and sea-lion killing stopped about 1860 (Bonnot 1928).

The problem of a declining fishery was aired before another commission at San Francisco in 1899, and on 27 April 1899, permission was granted to kill sea lions along the coast, including lighthouse reservations (Bonnot 1928). The data from stomach inspections, gathered by Professor L. L. Dyche in 1899, were published by C. H. Merriam (1901a, 1901b). These publications were an attempt toward a critical examination of stomachs from slaughtered sea lions. A view held by many was that stomach analysis was utterly useless, for the observed fact was that sea lions pursued salmon through the Golden Gate as far as Sacramento (Anonymous 1901). Thousands were killed before the Treasury Department prohibited wholesale slaughter on government lands on 31 May 1899 (Merriam 1901a). The destruction of sea lions was justified by the belief that the declining shad (*Alosa sapidissima*), salmon (*Oncorhynchus* spp.), and striped bass (*Morone saxatilis*) fisheries would thereby increase, but little evidence was gathered to verify or deny such claims. The U.S. Fish Commission, the Secretary of the U.S. Department of Agriculture, and the New York Zoological Society opposed the decisions of the California Fish Commission (Anonymous ["Steelhead" pseudonym] 1901).

The controversy over control of sea lion populations pitted biologists C. Hart Merriam, Barton W. Evermann, and William T. Hornaday against David Starr Jordan, Charles H. Gilbert, Harvey W. Harkness, and N. Baird Scofield (Starks 1918; Townsend 1918, 1919). The 1904 report of a Federal commission appointed to review the situation contains the first published list of stomach contents of a series of California sea lions (*Zalophus*) and northern sea lions (*Eumetopias*) (Rutter et al. 1904).

In 1914–1916, the Newcombe Commission gathered basic biological field data in British Columbia (Newcombe and Newcombe 1914; Newcombe et al. 1918). Twelve of the 14 northern sea lions examined contained intact herring; however, food items consumed by these sea lions throughout the year were not documented.

Early in the 20th century, suggestions were made to harvest young sea lions, following the example of the Newfoundland harp-seal industry. Harp seals (*Phoca*) had been cropped annually for 100 years with an annual take of pups exceeding 200,000. Recommendations for control of pinnipeds in California gained the support of many prominent biologists (Townsend 1919).

Following an investigation at the lighthouse reservation on Año Nuevo Island (Evermann 1921), it was stated that surplus bulls on this rookery could be killed (Evermann and Hanna 1925). This is the earliest example of a recommendation to harvest marine mammals along the California coast based on biological information. Because sea lions and seals are polygamous, it was felt that 10 percent of the excess males could be killed, but for economic reasons the cropping was not carried out (Rowley 1929). Target clubs obtained military surplus guns and ammunition and "practiced" on the Santa Cruz and San Mateo coast pinniped populations. Apparently this activity frightened the pinnipeds enough to cause their departure (Herb Steindorf, local rancher, pers. comm., 1969). Fishermen still ask permission to kill sea lions, and numerous reports of damage to the fishery continue to this day.

Between the late 1920's and 1972, when the Marine Mammal Protection Act was passed, certain marine mammals were fully protected, but commercial and sport fishermen (actively fishing from boats) could kill sea lions and harbor seals interfering with their operations (California Fish and Game Code, Sections 3002, 4500). Thus fishermen could protect their nets, tackle, and fish from damage by marine mammals. The California Fish and Game Commission reserved the right to reduce the population and to require permits for educational display or scientific taking of sea lions or seals. The sea otter (*Enhydra lutris*), Guadalupe fur seal (*Arctocephalus townsendi*), and elephant seal (*Mirounga angustirostris*) were fully protected. State laws applied only to the seals, sea lions, and sea otter; no regulations concerning cetaceans were in effect until the enactment of the Marine Mammal Protection Act of 1972. This protection placed an immediate moratorium upon the taking and importation of all marine-mammal products into the United States (National Oceanic and Atmospheric Administration 1974). The oft-repeated complaint about the lack of life history data on most of our common species of marine mammals is still valid (Starks 1918; Anderson 1960; Peterson and Bartholomew 1967; Briggs and Davis 1972). Even the age at puberty and physical maturity of the California sea lion (*Zalophus californianus*) is unknown (Harrison 1972). There are few published accounts of marine mammal life histories, and these studies seldom contain precise information on food habits (Bartholomew 1967; Orr and Poulter 1965, 1967; Peterson and Bartholomew 1967; Peterson and LeBoeuf 1969; Odell 1971; Seed 1972). General publications on marine mammals seldom contain significant or specific information on food habits (Sergeant and Fisher 1957; Slijper 1962; King 1964; Evans and Bastian 1969; Daugherty 1972; Orr 1972; Ridgway 1972).

Notes on food habits of pinnipeds have been reported in the literature since the early work of L. L. Dyche in 1903 (Bonnot 1928, 1932a, 1932b, 1951; Scheffer and Neff 1948; Scheffer 1950a; Mathisen 1959; Mathisen et al. 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966; Morejohn and Baltz 1970; Briggs and Davis 1972).

The literature on distribution, food habits, and life histories of small cetaceans is less extensive, and wholly inadequate. While the federal status report to the Secretary of Commerce (National Oceanic and Atmospheric Administration 1974) is the most complete summary of studies to date, natural history data are lacking even for the most common species. Cetaceans have not had a reputation for eating commercially important fishes nor for harassing fishermen. Until 1972 there were no federal laws protecting or regulating the capture of small whales or porpoises. Recently large numbers of porpoises have been killed during tuna-fishing operations (Perrin 1970). Papers dealing with food habits of cetaceans are widely scattered (Scheffer 1950b, 1953; Brown and Norris 1956; Tomilin 1957; Wilke and Kenyon 1952, 1957; Wilke and Nicholson 1958; Norris and Prescott 1961; Fitch and Brownell 1968; Loeb 1972; Perrin et al. 1973).

More study is needed on feeding rates and feeding phenomena (Sergeant 1968, 1969). Fasting periods and basic metabolic rates obviously affect calculations of the impact of marine mammals on the food resources of the sea. The role of marine mammals in overall ocean ecology needs further study. Current knowledge of food chains and trophic relationships of marine mammals has only recently been given attention by marine ecologists (Steele 1970).

Materials and Methods

During this study, I examined 102 specimens found dead on California beaches (Table 1). The 11 species of marine mammals studied (Figures 1 and 2) include two phocids, *Mirounga angustirostris* and *Phoca vitulina*, and three otariids, *Eumetopias jubatus*, *Zalophus californianus*, and *Callorhinus ursinus*. The six cetacean species represent three families: Phocoenidae, *Phocoena phocoena* and *Phocoenoides dalli*; Delphinidae, *Delphinus delphis*, *Grampus griseus*, and *Lagenorhynchus obliquidens*; and Physeteridae, *Kogia simus*.

Where feasible, specimens up to about 100 pounds (45 kg) were removed to the laboratory and data were recorded on standardized sheets (Norris 1961; Scheffer 1967). Where terrain or tidal conditions did not allow removal, carcasses were measured in place. All possible standard measurements were taken.

The skull, baculum (when present), and stomach were collected from specimens too large to move. All material was labeled and taken to the laboratory for careful examination. Osteological material from each specimen was tagged and cleaned by standard museum techniques. Thirteen stomachs were donated by personnel of the California Academy of Sciences.

After initial external cleaning, 25 stomachs were filled with cool tap water and measured to obtain an average stomach volume (Table 2). Each water-filled stomach was drained of its

TABLE 1. NUMBER OF MARINE MAMMAL STOMACHS EXAMINED IN NORTH-CENTRAL CALIFORNIA, 1968–1973; (n = 102). A total of 68 stomachs contained food items; of these, 61 had fish remains, 33 invertebrates.

CETACEANS	*Phocoena*	*Phocoenoides*	*Lagenorhynchus*	*Delphinus*	*Grampus*	*Kogia*	Total
Examined	20	5	7	1	1	1	35
With contents	16	2	7	1	1	1	28
Empty	4	3	0	0	0	0	7
With fish	14	2	5	1	0	1	23
With invertebrates	8	0	3	1	1	1	14
PINNIPEDS	*Zalophus*	*Eumetopias*	*Phoca*	*Callorhinus*	*Mirounga*		Total
Examined	30	19	12	4	2		67
With contents	20	9	8	1	2		40
Empty	10	10	4	3	0		27
With fish	20	9	6	1	2		38
With invertebrates	7	7	2	2	0		19
With rock or plant material	1	3	0	0	0		4

contents into a graduated cylinder for accurate volumetric reading.

Stomach contents were segregated, using a parasite-recovery technique of flotation and decanting, and then washed repeatedly with clean water. This method of sedimentation-decantation allows speedy recovery of all items. Small otoliths (lapilli) were occasionally detected, but all otoliths reported here were sagittae. Other workers (Fitch and Brownell 1968; Morejohn and Baltz 1970; Smith and Gaskin 1974) have screened gastro-intestinal materials through cheesecloth gauze or graded wire screens.

Disarticulated bones were separated from internal parasites with forceps. Fish bones and otoliths were dried overnight. Soft tissues were preserved in alcohol.

The heavy fish otoliths (sagittae) were easily seen by moving the clear glass container over backgrounds of several different colors. Even the tiny otoliths (asterisci or lapilli) could be detected when they were gently moved by the covering water. I removed the otoliths with a camel hair brush or fine forceps. They were carefully cleaned of mucus (film), dried, and stored in gelatin pill containers. John E. Fitch, California Department of Fish and Game, provided identifications.

Most cephalopod beaks, which were stored in alcohol, were identified using the pictorial guide developed by the California Department of Fish and Game (Iverson and Pinkas 1971). Several types were identified by Clifford Fiscus, National Marine Mammal Laboratories, U.S. Department of Commerce. I later checked these samples using the keys developed by Clarke (1962) and by comparing them with squid beaks furnished by Jerome L. Spratt of the California Department of Fish and Game. Four hundred thirty-five cephalopod beaks and 2828 fish otoliths were identified. Thirty-one otoliths and 217 cephalopod beaks were not identifiable. I was able to identify most cephalopod beaks only to genus.

Few stomachs contained intact fish. Fish skeletal material was air-dried, and its volume was measured in a graduated cylinder (Table 9). Fish remains were identified with the aid of Clothier 1950; Roedel 1953; Clemens and Wilby 1961; Fitch and Lavenberg 1971; and Miller and Lea 1972. Common names used follow those of the American Fisheries Society (Robins et al. 1980) except for Atka-mackerel and jackmackerel, which follow Hubbs, Follett, and Dempster (1979). All recovered materials (specimens and contents) are deposited in the Museum of Vertebrate Zoology, Berkeley, or the California Academy of Sciences, San Francisco.

A total of 35 cetacean and 67 pinniped carcasses was beach-cast along north-central California. Voucher material has been collected and deposited at these institutions: CAS, California Academy of Sciences, San Francisco; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; HSC, Humboldt State University, Vertebrate Zoology Museum, Arcata; PORE, Point Reyes National Seashore, Point Reyes.

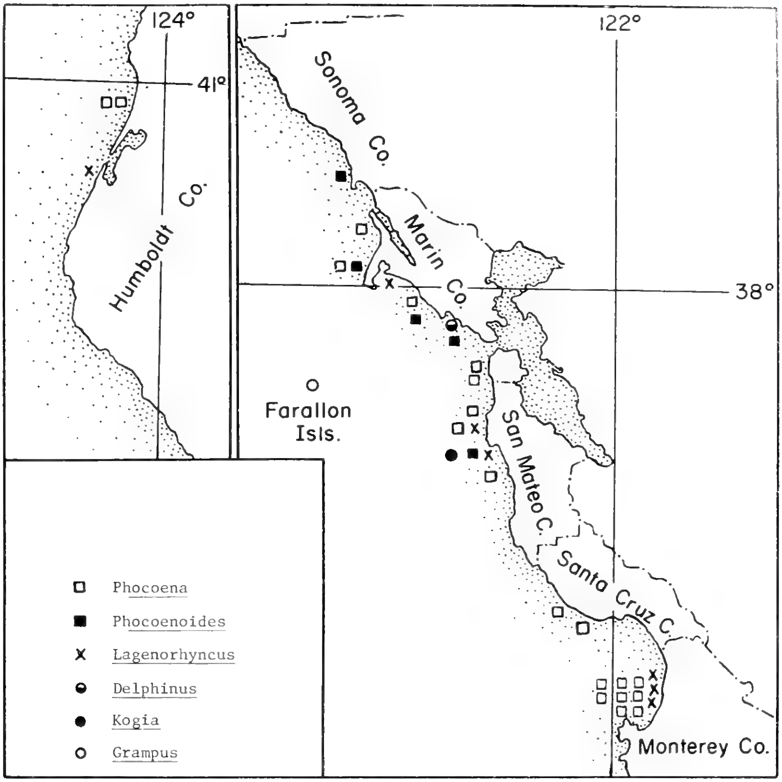


FIGURE 1. Localities of cetacean beach-cast specimens in north-coastal California, 1968–1973.

CETACEAN

Humboldt Co.—*Phocoena*: HSC 68-7, F, 2 Sep. 1968, 122 cm, 12 otoliths; HSC 73-4, M, 21 Aug. 1973, 150 cm est., 14 otoliths.—*Lagenorhynchus*: HSC 68-9, M, 26 Dec. 1968, 179 cm, 36 otoliths, 1 cephalopod beak.

Sonoma Co.—*Phocoenoides*: MVZ 153258 (REJ 670), F, 28 June 1973, 102 cm, empty.

Marin Co.—*Phocoena*: CAS 16602 (2385), M, 1 June 1973, 138 cm, 1083 otoliths; CAS 16603 (2385), 1 June 1973, 146 cm, empty; CAS 21380 (REJ 448), F, 3 July 1970, 158 cm, 15 otoliths.—*Phocoenoides*: MVZ 153259 (REJ 678), F, 7 Aug. 1973, 186 cm, empty; CAS 16604 (2385), M, 1 June 1973, 198 cm, empty; CAS 16297 (2335), M, 21 Sep. 1972, 188 cm, 6 otoliths.—*Lagenorhynchus*: MVZ 140845 (REJ 218), F, 9 Feb. 1970, 181 cm, no ID.—*Delphinus*: CAS 16242 (2340), F, 6 Nov. 1972, 168 cm, 11 otoliths, 4 cephalopod beaks.

San Francisco Co.—*Phocoena*: CAS 16629 (2384), M, 26 May 1973, 140 cm, 2 otoliths; CAS 16572 (2398), F, 20 Aug. 1973, 137 cm, 17 otoliths.—*Grampus*: MVZ 153257 (REJ 659), F, 20 May 1973, 275 cm, barnacle and hydroid.

San Mateo Co.—*Phocoena*: CAS 15992 (2237), F, 19 July 1971, 143 cm, 33 otoliths; CAS 16609 (2390), F, 13 July 1973, 159 cm, 26 otoliths and 1 hake; CAS 16633 (2392), F, 13 July 1973, 126 cm, 4 otoliths, 35 pair cephalopod beaks and 13 whole *Loligo*.—*Phocoenoides*: CAS (REJ 674), F, 1 Aug. 1973, (79 in.), 223 cm,* 61 otoliths.—*Lagenorhynchus*: CAS 16593 (2336), M, 28 Sep. 1972, 190 cm, 47 otoliths; CAS 16342 (2380), F, 20 Apr. 1973, 193 cm,* 4 otoliths.—*Kogia*: CAS 16635 (2382), M, 25 May 1973, 204 cm, 2 otoliths and 231 cephalopod beaks.

Santa Cruz Co.—*Phocoena*: CAS 21381 (KB 19-73), M, 13 Apr. 1973, 134 cm, 17 otoliths; (KB 17-73), F, 1973, 104 cm, empty.

Monterey Co.—*Phocoena*: CAS 21387 (REJ 687), F, 22 Sep. 1973, 107 cm, empty; CAS 21383 (REJ 673), M, 24 July 1973, 126 cm, 48 otoliths, 1 pair cephalopod beaks; CAS 21385 (REJ 661), F, 17 June 1973, 104 cm, 16 otoliths, 3 cephalopod beaks; CAS 21386 (REJ 654), F, 24 Apr. 1973, 137 cm, 15 otoliths; CAS 21389 (REJ 653), M, 25 Apr. 1973, 145 cm, 13 cephalopod beaks; CAS 21388 (REJ 450), ? sex, 24 July 1971, no tl, 127 otoliths, 52 cephalopod beaks; CAS 21384 (REJ 449), ? sex, 24 July 1971, 108 cm, empty; CAS 21382 (REJ 241), F, 6 June 1970, 172 cm, 16 cephalopod beaks.—*Lagenorhynchus*: CAS 21370 (REJ 652), F, 21 Apr. 1973, 187 cm, 4 otoliths; CAS 21378 (REJ 625), M, 14 May 1973, 177 cm, 147 cephalopod beaks; MVZ (REJ 237), F, 29 May 1970, 180 cm, 7 cephalopod beaks.

---

* Indicates original data taken in inches.

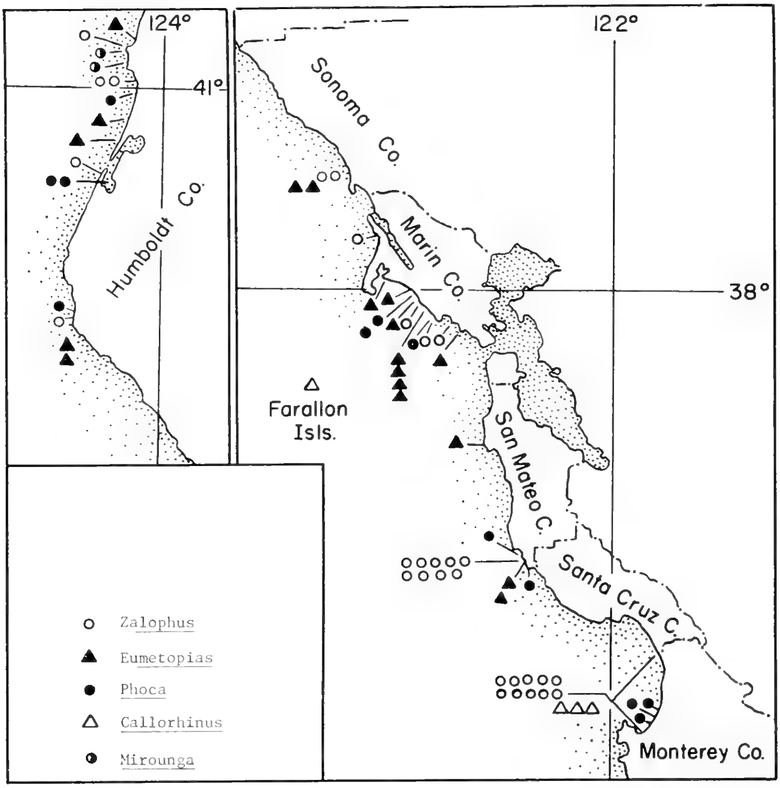


FIGURE 2. Localities of pinniped beach-cast specimens in north-coastal California, 1968–1973.

PINNIPEDS

Humboldt Co.—*Zalophus*: CAS 21401 (REJ 248), M, 16 June 1970, 256 cm, 17 otoliths; HSC 3206 (69-34), M, 1 June 1969, 233 cm,* 52 otoliths; HSC 3205 (REJ 69-33) M, 27 May 1969, 228 cm,* 122 otoliths; HSC 3204 (REJ 69-32), M, 23 May 1969, 249 cm,* 93 otoliths; HSC 3125 (REJ 69-31), M, 14 May 1969, 239 cm,* 152 otoliths.—*Eumetopias*: CAS 21391 (REJ 683), F, 16 Sep. 1973, 111 cm, empty; CAS 21390 (REJ 672), M, 20 July 1973, 309 cm, empty; HSC, (REJ 655), F, 1 May 1973, 200 cm, stones only; HSC, (REJ 247), M, 14 June 1970, 257 cm, 76 otoliths, 2 cephalopod beaks; MVZ 140847 (REJ 249), F, 16 June 1970, 259 cm, 66 otoliths, 13 cephalopod beaks; HSC, (REJ 69-8), F, 16 Feb. 1969, 251 cm,* 2 otoliths, 1 cephalopod beak.—*Phoca*: CAS 21421 (REJ 684), F, 17 Sep. 1973, 147 cm, empty; HSC 1188 (REJ 69-24), F, 25 Apr. 1969, 149 cm, 13 otoliths; HSC, (REJ 68-38), M, 28 July 1968, 162 cm, 3 otoliths; HSC, (REJ 68-14), F, 6 Apr. 1968, 102 cm, 17 otoliths.—*Mirounga*: HSC 2165 (REJ 69-6), F, 19 Feb. 1969, 152 cm, 1 *Apristurus brunneus* egg; HSC 1356 (?), F, 5 May 1970, no tl, 26 otoliths.

Sonoma Co.—*Zalophus*: CAS 21402 (REJ 680), M, 17 Aug. 1973, 238 cm, empty; CAS 21403 (REJ 660), M, 5 June 1973, 215 cm, 98 otoliths, 1 cephalopod beak.—*Eumetopias*: CAS 21392 (REJ 688), M, 23 Sep. 1973, 152 cm, 4 otoliths; CAS 21393 (REJ 679), F, 17 Aug. 1973, 229 cm, empty.

San Francisco Co..—*Callorhinus*: MVZ 140846 (REJ 212), F, 5 Feb. 1970, 131 cm, 7 isopods.

Marin Co.—*Zalophus*: CAS 21404 (REJ 700), M, 29 Sep. 1973, 210 cm, empty; PORE 138 (REJ 657), M, 9 May 1973, 230 cm, 1 otolith; CAS 21405 (REJ 641), M, 1 Mar. 1973, 220 cm, empty; CAS 16184 (2316), M, 19 July 1973, 158 cm, 1 otolith, 1 cephalopod.—*Eumetopias*: CAS 21399 (REJ 682), M, 6 Sep. 1973, 325 cm, empty; CAS 21395 (REJ 677), F, 7 Aug. 1973, 235 cm, broken otoliths and rocks; PORE 136 (REJ 676), M, 6 Aug. 1973, 280 cm, empty; CAS 21395 (REJ 668), F, 22 June 1973, 234 cm, empty; ?(REJ 637), 21 Oct. 1972, no tl, 22 otoliths, 4 cephalopod beaks; CAS 21397 (REJ 635), F, 16 Sep. 1972, 232 cm, empty; CAS 21396 (REJ 629), M, 22 July 1972, 228 cm, 59 otoliths, 5 cephalopod beaks; PORE 137 (REJ 453), F, 14 Aug. 1971, 226 cm, empty.—*Phoca*: PORE 214 (REJ 681), F, 29 Aug. 1973, 140 cm, empty; CAS 21423 (REJ 669), M, 22 June 1973, 97 cm, 3 *Crago* sp.; CAS 21422 (REJ 642), M, 1 Mar. 1973, 158 cm, empty.

San Mateo Co.—*Zalophus*: CAS 21412 (REJ 698), M, 28 Sep. 1973, 160 cm, empty; CAS 21411 (REJ 697), M, 28 Sep. 1973, no tl, empty; CAS 21410 (REJ 695), M, 28 Sep. 1973, 218 cm, empty; CAS 21409 (REJ 693), M, 28 Sep. 1973, 213 cm,* empty; ?(REJ 692), M, 28 Sep. 1973, 152 cm (est.), 2 otoliths, 2 cephalopod beaks; CAS 21408 (REJ 691), F, 28 Sep. 1973, no tl, empty; CAS 21407 (REJ 690), M, 28 Sep.

TABLE 2. AVERAGE STOMACH VOLUME OF THREE SPECIES OF MARINE MAMMALS AS MEASURED BY WATER DISPLACEMENT

			Total length of animal (cm)		Volume of stomachs (l)	
Species	*n*	Sex	Range	Average	Range	Average
Zalophus						
Adults	6	M	198–256	223	9.42–19.84	12.63
Subadults	4	M	126–160	145	1.72–9.12	5.75
Eumetopias						
	3	M	280–325	305	22.20–46.72	33.67
	4	F	200–235	230	9.80–23.74	17.78
Phocoena						
	3	M	126–145	136	1.10–1.43	1.28
	5	F	95–159	120	7.00–2.25	2.44

1973, 196 cm, empty; CAS 16302 (2383), M, 27 May 1973, 122 cm, empty; MVZ 139211 (LGB 317), M, 24 Mar. 1970, no tl, 18 otoliths.—*Eumetopias*: ?(REJ 699), F?, 28 Sep. 1973, 192 cm, 24 otoliths, 1 cephalopod beak; CAS 21400 (REJ 694), M, 28 Sep. 1973, no tl, empty; CAS 21398 (REJ 675), F, 2 Aug. 1973, 220 cm, 1 otolith.—*Phoca*: ?(REJ 696), F, 28 Sep. 1973, 133 cm, 9 otoliths, 13 cephalopod beaks; CAS 21424 (REJ 689), F, 28 Sep. 1973, 139 cm, 15 *Eptatretus stoutii* eggs.

Monterey Co.—*Zalophus*: CAS 21415 (REJ 686), M, 22 Sep. 1973, no tl, 7 otoliths; ?(REJ 685), M, 22 Sep. 1973, 142 cm, 18 otoliths; CAS 21420 (REJ 667), M, 19 June 1973, 195 cm, 7 otoliths; CAS 21417 (REJ 666), M, 19 June 1973, 256 cm, 3 otoliths; CAS 21416 (REJ 665), M, 19 June 1973, 198 cm, 48 otoliths, 40 cephalopod beaks; CAS 21419 (REJ 664), M, 19 June 1973, 151 cm, 221 otoliths; CAS 21418 (REJ 662), M, 19 June 1973, 126 cm, 1 otolith, 3 cephalopod beaks; CAS 21414 (REJ 647), M, 1 Apr. 1973, 115 cm, 1 otolith, 3 cephalopod beaks; UC tag 6588 (REJ 244), M, 6 June 1970, 125 cm, 2 otoliths, 3 cephalapod beaks; CAS 21413 (REJ 68-40), M, 12 June 1968, 233 cm,* 39 otoliths.—*Phoca*: CAS 21427 (REJ 671), M, 13 June 1973, 98 cm, 1 otolith; CAS 21426 (REJ 663), F?, 19 June 1973, 87 cm, empty; CAS 21425 (REJ 646), F, 1 Apr. 1973, 142 cm, 10 cc fish bones, 3 cephalopod beaks.—*Callorhinus*: MVZ 153256 (REJ 645), F, 1 Apr. 1973, 121 cm, empty; ?(REJ 243), F, 6 June 1970, 101 cm, 12 otoliths, 14 cephalopod beaks; MVZ 138677 (REJ 69-36), F, 12 July 1969, 137 cm, empty.

RESULTS ·

Sixty-eight percent of the 102 stomachs examined in this study contained material (Table 1), approximately the same percentage as recorded for stomachs from collected living marine mammals. For example, 331 of 437 stomachs (76 percent) of the fur seals taken off California in 1966 contained food (Marine Mammal Biological Laboratory 1969), and 18 of 44 (41 percent) California sea lions taken recently in Oregon contained food (Mate 1973). Normally about 60 percent of the northern sea lions collected during daylight hours have food in their stomachs (Spalding 1964), but Mathisen et al. (1962) found food in 82 percent (114 stomachs). Forty percent of 1300 fur seal stomachs examined in Alaska contained food (Scheffer 1950a).

Fish otoliths or other dietary remains were recovered from 61 stomachs, and 33 stomachs had remnants of identifiable invertebrates (Tables 3, 4, 5, and 9). The items in the stomachs included fish bones and otoliths, parasites, seaweeds, fish egg cases, cephalopod tissue and beaks, eye lenses of fish and cephalopods, rocks, wood, and parts of other invertebrates.

Fitch and Brownell (1968) have presented a valid case for the use of otoliths in determination of dietary habits. Other investigators also have found undigested parts such as otoliths and cephalopod beaks in the forestomachs of cetaceans (Rae 1965; Harrison et al. 1970; Iverson and Pinkas 1971; Loeb 1972; Smith and Gaskin 1974).

Phoca vitulina, Harbor seal

Harbor seals in the Aleutians contained fewer prey species than in other areas studied. Wilke (1957) examined seven harbor seals collected in March at Amchitka Island and found that octopus was the most frequent item, but that gadid and hexagrammid fishes made up the greatest volume of food present. A later study by Kenyon (1965) found only octopus (*Octopus* sp.) and Atka-mackerel (*Pleurogrammus monopterygius*) in 11 seals at Amchitka Island. He theorized that harbor seals feed during the daylight hours as suggested by the freshness and large volumes of food in the stomachs. Kenyon failed to consider Wilke's earlier study which indicat-

TABLE 3. TOTAL NUMBER OF FISH OTOLITHS FOUND IN 22 SPECIMENS OF CETACEANS, NORTH-CENTRAL CALIFORNIA, 1968–1973.

Prey species	*Phocoena* (14)		*Phoecoenoides* (2)		*Lagenorhynchus* (5)		*Delphinus* (1)	
	No. otoliths	Percent total	No. otoliths	Percent total	No. otoliths	Percent total	No. otoliths	Percent total
Rockfishes (Scorpaenidae)	1017	(71.8)	0	–	8	(9.2)	0	–
Northern anchovy	253	(17.8)	0	–	5	(5.7)	0	–
Pacific hake	74	(5.8)	61	(91.1)	3	(3.5)	0	–
Smelts (Osmeridae)	9	(0.15)	0	–	34	(39.0)	1	(9.1)
Pacific tomcod	34	(2.3)	6	(8.9)	0	–	0	–
Plainfin midshipman	2	(0.14)	0	–	34	(39.0)	0	–
Flatfishes (Pleuronectidae)	13	(0.92)	0	–	1	(1.2)	0	–
Medusafish	0	–	0	–	0	–	10	(90.9)
Surfperches (Embiotocidae)	9	(0.63)	0	–	0	–	0	–
Spotted cusk-eel	2	(0.14)	0	–	0	–	0	–
Jackmackerel	0	–	0	–	2	(2.3)	0	–
Total	1413	(99.68)	67	(100)	87	(99.9)	11	(100.0)

ed that the abundant rock greenling (*Hexagrammos lagocephalus*) made up 96 percent of food volume from harbor seals. Total sample size during March for both Wilke (1957) and Kenyon (1965) was 10 specimens, which is hardly adequate for the construction of generalities. Yet Kenyon's (1965) study is the basis for Morejohn and Baltz's (1970) model for selective feeding. They looked at a single elephant seal and compared its feeding behavior to that of harbor seals at Amchitka. The sample sizes in these studies are barely adequate for comparison, and are inadequate for feeding models.

The diet of harbor seals varies greatly with season and location of populations. Pelagic, bottom-dwelling, and anadromous fishes have all been reported in its diet. Captain Scammon (1874) noted that the "Leopard Seal" pursued and devoured small fish.

During a two-year study in Alaska (Imler and Sarber 1947), 166 (41.5 percent) of 400 harbor seal stomachs contained identifiable food items. In the Copper River flats of Alaska, 67 seals fed almost entirely on eulachon (*Thaleichthys pacificus*). Ninety-nine other specimens from southeastern Alaska had fed on walleye pollock (*Theragra chalcogramma*) and Pacific tomcod (*Microgadus proximus*) (22.6 percent), Pacific herring (*Clupea harengus pallasii*) (16.4 percent), and flounders (11.1 percent). Lesser numbers (29.5 percent) of salmonids, sculpins, rockfish, blennies, and skates were reported. Imler and Sarber (1947) also found shrimp and octopus (20.6 percent) in harbor seals from Alaska.

Spalding (1964) collected harbor seals throughout the year in British Columbia; 57 of the 126 stomachs were empty. He found that minimal food was consumed during the June to September pupping season. In summer, the stomachs contained cephalopods (35.4 percent), rockfish (22.6 percent), and salmon (16.1 percent). Stomachs collected from September to December contained invertebrates (34.8 percent), herring (10.8 percent), and salmon (30.4 percent). Fish of commercial value composed 54 percent of the harbor seals' diet on a yearly basis.

In Puget Sound also the harbor seal is a generalized feeder (Scheffer 1928). Scheffer and Sperry (1931) point out that fishes made up 93.6 percent, molluscs 5.8 percent, and crustaceans 0.6 percent of the total volume of harbor seal stomach contents. Only two percent of the harbor seal stomachs contained salmon (Scheffer and Slipp 1944). Studies in Washington (Scheffer 1928; Scheffer and Sperry 1931; Scheffer and Slipp 1944; Seed 1972) revealed that the major prey species were flatfishes: English sole (*Parophrys vetulus*), flathead sole (*Hippoglossoides elassodon*), Pacific herring, Pacific tomcod, Pacific hake (*Merluccius productus*), sculpins (*Leptocottus armatus*, *Myoxocephalus* sp.), walleye pollock, surfperches (*Cymatogaster aggregata*, *Rhacochilus* sp.), Pacific cod (*Gadus*

TABLE 4. TOTAL NUMBER OF FISH OTOLITHS FOUND IN 38 SPECIMENS OF PINNIPEDS, NORTH-CENTRAL CALIFORNIA, 1968–1973.

	Phoca (6)		*Zalophus* (20)		*Eumetopias* (9)		*Callorhinus* (1)		*Mirounga* (2)	
Prey species	No. otoliths	Percent total	No. otoliths	Percent total	No. otoliths	Percent total	No. otoliths	Percent total	No. otoliths	Percent total
Pacific hake	1	(2.3)	574	(62.8)	55	(21.7)	0	–	26	(96.3)
Northern anchovy	0	–	218	(23.8)	1	(0.4)	12	(100)	–	–
Rockfishes (Scorpaenidae)	1	(2.3)	57	(6.2)	79	(31.2)	0	–	0	–
Flatfishes (Pleuronectidae)	4	(9.3)	1	(0.1)	44	(17.3)	0	–	0	–
Spotted cusk-eel	0	–	6	(0.6)	30	(11.8)	0	–	0	–
Plainfin midshipman	0	–	30	(3.2)	1	(0.4)	0	–	0	–
Sablefish	0	–	0	–	22	(8.7)	0	–	0	–
Surfperches (Embiotocidae)	18	(41.9)	3	(0.3)	0	–	0	–	0	–
Pacific herring	0	–	16	(1.7)	1	(0.4)	0	–	0	–
Lingcod	0	–	1	(0.1)	13	(5.1)	0	–	0	–
Blackbelly eelpout	12	(27.9)	0	–	1	(0.4)	0	–	0	–
Jackmackerel	0	–	3	(0.3)	3	(1.2)	0	–	0	–
Smelts (Osmeridae)	0	–	2	(0.2)	2	(0.2)	0	–	0	–
Kelp greenling	4	(9.3)	0	–	0	–	0	–	0	–
Pacific tomcod	2	(4.7)	1	(0.1)	0	–	0	–	0	–
Brown cat shark	0	–	0	–	1	(0.4)	0	–	1	(3.7)
Pacific hagfish	1	(2.3)	0	–	0	–	0	–	0	–
Chinook salmon	0	–	1	(0.1)	0	–	0	–	0	–
Queenfish	0	–	1	(0.1)	0	–	0	–	0	–
Blacktail snailfish	0	–	0	–	1	(0.4)	0	–	0	–
Total	43	(100)	914	(99.6)	254	(99.6)	12	(100)	27	(100)

macrocephalus), and lingcod (*Ophiodon elongatus*). These authors list 13 kinds of crustacea and 4 kinds of mollusca from the stomachs of harbor seals. Harbor seals eat flounder, sole, herring, eel, goby, cod, whiting, squid, whelks, crab, and mussels (King 1964). Fishes, squid, octopus, and shellfish constitute the diet of harbor seals in California (Daugherty 1972). Bonnot (1951) indicated that the fishes, molluscs, and crustaceans consumed by harbor seals in California are usually slow-moving or sedentary forms. The above authors do not specify scientific names nor document sources for their dietary information.

I examined stomachs of 12 harbor seals of which eight with food had eaten eight kinds of fish (*Merluccius productus, Microgadus proximus, Lycodopsis pacifica, Sebastes* spp., *Hexagrammos decagrammus, Embiotoca jacksoni, Phanerodon furcatus, Glyptocephalus zachirus*), one kind of octopus (*Octopus* sp.), and one kind of shrimp (*Crago* sp.). Embiotocid perch constituted 41.9 percent of my sample, compared with 11 percent in Washington (Scheffer and Sperry 1931). One harbor seal (REJ 689) had

TABLE 5. MINIMUM NUMBER OF INDIVIDUAL FISH AND CEPHALOPODS FOUND IN ELEVEN SPECIES OF MARINE MAMMALS, NORTH-CENTRAL CALIFORNIA, 1968–1973.

	Cephalopods		Fishes	
	Minimum no. individuals represented	No. beaks	Minimum no. individuals represented	No. otoliths
Zalophus	32	51	476	922 (8*)
Eumetopias	11	27	132	258 (5*)
Phoca	12	16	23	43 (1*)
Callorhinus	7	14	6	12
Mirounga	0	0	13	26
Phocoena	92	168	712	1429 (16*)
Phocoenoides	0	0	34	67
Lagenorhynchus	86	155	45	88 (1*)
Delphinus	3	4	6	11
Kogia	112	217	1	2
Grampus	0	0	0	0
Totals	355	652	1448	2858 (31)

* Unidentifiable.

TABLE 6. NUMBER OF INDIVIDUAL FISH, GROUPED BY NICHE, FOUND IN THE STOMACHS OF MARINE MAMMALS FROM NORTH-CENTRAL CALIFORNIA, 1968–1973.

	Sample size	Schooling (open water)	Bottom-dwelling (rocky)	Inshore (schooling)
Zalophus	30	296	52	121
Eumetopias	19	28	97	3
Phoca	12	2	24	0
Mirounga	2	13	0	0
Callorhinus	4	0	0	6
Phocoena	20	52	13	646
Lagenorhynchus	7	3	22	20
Phocoenoides	5	33	0	0
Delphinus	1	5	0	1
Grampus	1	0	0	0
Kogia	1	0	1	0

ingested Pacific hagfish (*Eptatretus stoutii*) egg cases (15 eggs). I observed that Pacific hagfish or Pacific lamprey (*Lampetra tridentata*) was a prey item of seals near river mouths in northern California. Scheffer and Sperry (1931) note that two percent of stomachs in which items occurred contained Pacific lamprey.

At birth, harbor seals average 81.6 cm in length (Bigg 1969). I examined two pups (98 and 97 cm) which contained solid food: an otolith (*Sebastes* spp.) in one stomach and a number of shrimp (*Crago* sp.) in the other. This suggests that harbor seals catch their own food at an early age.

In summary, knowledge to date indicates that harbor seals feed on shallow-water fishes and bottom-dwelling invertebrates (Tables 1, 6 and 9).

Mirounga angustirostris, Elephant seal

Pike and MacAskie (1969) reported hagfish eggs (*Eptatretus*) and probably digested hagfish remains in an elephant seal from Canada. Huey (1930) pointed out that several of the fish species found in elephant seal stomachs inhabit water from 50 to 120 fathoms (ca. 91 to 219 m) deep. Small sharks (*Squalus*, *Cephaloscyllium*), skates (*Raja*), rays (Myliobatidae), and ratfish (*Hydrolagus*) have been reported as food items in elephant seals (Kenyon and Scheffer 1955; King 1964; Daugherty 1972; Seed 1972). Huey (1925) found that three of four Guadalupe Island elephant seals contained squid (*Loligo*).

Contrary to the report of Morejohn and Baltz (1970), teleost fishes had been reported from elephant seals. Huey (1930) reported a single bass, and Daughterty (1972) stated that elephant seals eat rockfish. Freiburg and Dumas (1954) found a dead adult elephant seal in Oregon which may have died from bones of Pacific hake (*Merluccius productus*) blocking the internal nasal region.

More information is needed on fish ecology and fish population abundance before the nature of feeding behavior of elephant seals can be clarified. The elephant seal may be a selective feeder (Morejohn and Baltz 1970), but seasonal, sex, and age factors need to be resolved. Commercial catches are the reference for fish abundance by Morejohn and Baltz. However, commercial fish catches are a poor indication of fish abundance when most reported fish are of commercial value (Bell 1971). Anyone accompanying commercial vessels realizes that many unreported fish are caught besides those marketed. All fishes Morejohn and Baltz found were bottom or rock-dwelling species (*Chilara*, *Porichthys*, *Sebastes*, and *Lyopsetta* or *Glyptocephalus*).

Elephant seals may feed during particular periods of the day. If they are nocturnal feeders, they may catch hake high in the water column, but diurnal feeding would suggest that hake are taken in deep water (Nelson and Larkins 1970). Studies are needed to determine when and where elephant seals feed. Large fish otoliths may indicate offshore feeding by the elephant seal.

To date, few elephant seals have been examined for stomach contents. One of my seals, an immature female (HSC–1970) found dead in Humboldt County on 5 May 1970, contained 26 otoliths from Pacific hake, representing at least 12 adult fish. Hake migrate north along the coast in spring and summer and might be expected to be present in marine mammal diets at that time of year. Pacific hake form massive schools just above the bottom and show a pronounced daily vertical migration (Nelson and Larkins 1970). Most adult hake are located beyond the continental shelf at depths of 230–410 m. Although Pacific hake are present in commercially abundant numbers, they are not being exploited currently by American fisheries. Pacific hake ranked second in abundance in California larval surveys (Ahlstrom 1965).

My other specimen, also an immature female, was found in Trinidad, Humboldt County, 19 Feb. 1969 (HSC–69-6). It contained a single egg case of the brown cat shark (*Apristurus brunneus*), which was identified using the description and photos in Cox (1963). This species of shark is found in deep water from British Columbia to Baja California.

Eumetopias jubatus, Northern sea lion

The northern sea lion has been studied more intensively than most other North Pacific pinnipeds. This sea lion occurs along the eastern Pacific coasts from Alaska to California, where its relationships to commercial fisheries have been studied extensively. In general, these studies reveal that fish and cephalopods are the preferred foods.

In 1899 L. L. Dyche inspected 25 sea lion stomachs from near Monterey Bay, California. All specimens referred to by Dyche contained squid or octopus.

The original manuscript Dyche sent to C. H. Merriam in 1901 did not specify which sea lion was involved. This partially handwritten document mentioned only the common identification "California Sea Lion" (Unpublished manuscript, Dyche 1901. C. H. Merriam file at Museum of Vertebrate Zoology, University of California, Berkeley). When Merriam (1901a, 1901b) first published Dyche's data, he did not indicate whether the northern sea lion (*Eumetopias*) or the California sea lion (*Zalophus*) was involved. Later, Dyche (1903) used the name "*Zalophus californianus* Lesson" beneath the general title of "Food for California Sea Lions," suggesting that California sea lions were examined. Thus it was long believed that all sea lions examined by Dyche were *Zalophus*. Briggs and Davis (1972) have pointed out that at least some of Dyche's specimens were *Eumetopias jubatus*. Since only 7 of these 25 sea lions deposited at the University of Kansas are extant today, it is not possible to make positive identifications for all of Dyche's specimens (R. S. Hoffmann, Curator Univ. of Kansas, pers. comm. [1973]). Although the 7 extant specimens are northern sea lions, it is possible that all 25 of the originally collected specimens may not have been this species.

Northern sea lions have been reported to feed at night (Rowley 1929; Bonnot 1951; Mathisen 1959; Mathisen et al. 1962; Spalding 1964; Seed 1972; Mate 1973). Fiscus and Baines (1966) sighted feeding groups of up to several thousand animals 8–22 km out in Unimak Pass, Alaska. It would be of interest to know if the individuals observed feeding returned to the hauling-out area each afternoon with engorged stomachs. Daytime feeding behavior has been noted by many fishermen, specifically long-line and drag-boat operators (Kenyon 1952a).

An interesting examination at the cannery dock at the mouth of the Klamath River was reported by Bonnot (1951). Two half-grown northern sea lions were killed, and only lampreys were found in their stomachs. J. C. Snyder also examined sea lions at river mouths and identified the remains of lampreys in their stomachs (Kenyon 1952b). More recently, Jameson and Kenyon (1978) reported that 82 percent of observed feeding behavior at the Rogue River, Oregon, was on lampreys.

Rutter et al. (1904) presented data on 18 northern sea lions (6 males and 12 females) from north-central California. The eight female sea lions containing food were taken from Año Nuevo Island in July or August. Five male sea lions from Pt. Arena ate at least 147 fish but only 5 squid. The majority of their food was fish (257 fish present in the 13 animals). The only cephalopod material was from five sea lions from both areas. This low incidence of cephalopods does not agree with the findings of Dyche (1903), but the identity of Dyche's specimens is in doubt. In contrast, in southern California Rutter et al. (1904) found only 39 fish but thousands of cephalopods in a sample of 24 *Zalophus*. They concluded that the northern sea lion feeds chiefly on fish, and the California sea lion on cephalopods, and that both feed opportunistically.

Bonnot (1928) examined two northern sea lion stomachs from San Miguel Island, California, on 20 June 1928. The adult male was empty but the female contained three greenish eggs of a skate or shark. Bonnot stated that this was an old, blind sea lion and perhaps she was dying. In northern California, at the Saint George Reef rookery (Del Norte County), Bonnot found thousands of shells of a tiny pelecypod embedded in sea lion feces. Other investigators have not reported analysis of scats, perhaps because of the difficulty of locating adequate samples (Bonnot 1928).

The literature contains a composite list of 32 fishes from stomachs of northern sea lions (Table 7). Because of the nonspecific categories of some fish names, I have not attempted to produce an accurate species list. Only the papers

TABLE 7. SUMMARY OF FOOD CONTENTS OF *Eumetopias* (modified from Pike (1958) with recent additions).

Locality	Season and year	Source	No. of stomachs (size and/or sex)	No. of stomachs, kinds of food
St. Paul I., Alaska	July 1949–1951	(6)	22 (2 females)	19—empty, 1—ceph. beak, 1–10 lbs., sandlance trace-starry flounder, sculpin, 1–20 lbs. halibut, cod, flounder, pollack, 4—large stones
Sitka to Kodiak I., Alaska	May, July, Aug. 1945–1946	(4)	23 (adults)	8–empty, 15—salmon, cod, halibut, pollack, 4—octopus
Kodiak to Krenitzin I., Alaska	May–July 1959	(8)	382 (372 males, 10 females)	326—empty, 28—fish (7 spp.), 21—invertebrates, 20—squid and octopus, 10—no ID fish, 154—stones and gravel
Chernaburg I., Alaska	May, July 1958	(7)	114 (46 males, 51 females, 17 yearlings)	20—empty, 31—fish (7 spp.), 61—invertebrates, 73—rock and sand, 24—no ID fish, 5—milk
Beresford I., B.C.	Aug. 1913	(2)	3 (adults)	2—empty, 1—salmon, "cod" and "bass"
Scott I., B.C.	June, July 1956	(5)	56 (adults)	50—empty, 4—fish and squid, 1—herring, 1—octopus
Scott I., B.C.	June 1957	(5)	8 (4 females, 4 males)	6—empty, 1—salmon, 1—no ID fish
Barkley Sound, B.C.	Dec. 1915	(2)	14 (11 males, 3 females)	12—herring, 1—clamshell, 1—crab, octopus
Barkley Sound, B.C.	Feb., Apr. 1958	(5)	14 (13 females, 1 male)	6—empty, 3—herring, 2—rockfish, 2—fish/octopus, 1—octopus, skate, hake
Isnor Rock, B.C.	July, Aug. 1957	(5)	3 (young males)	1—rockfish, 1—squid and rockfish, 1—squid
British Columbia	Feb.–Dec. 1959	(9)	393 (equal numbers, males/females)	213—empty, 75—fish (17 spp.), 49—no ID, milk or kelp
Offshore California–N. Pacific	Mar., Sep. 1958–1963	(10)	34 (7 males, 15 females)	11—lost at sea, 22—fish (15 spp.), 2—no ID fish, 1—clamshell and fish, 9—rocks and pebbles
Pt. Arena and Año Nuevo I., Calif.	July–Aug. 1901	(1)	18 (6 males, 12 females)	5—empty, 13—fish, 6—squid and octopus

TABLE 7. CONTINUED.

Locality	Season and year	Source	No. of stomachs (size and/or sex)	No. of stomachs, kinds of food
Año Nuevo I., Calif.	"several years ago" prior to 1918	(3)	15 (14 females, 1 young male)	7—empty, 8—rock, sardines, salmon, 3—fish and squid
North-Central California	1968–1973	(11)	19 (7 males, 12 females)	10—empty, 9—fish, 7—squid and octopus, 2—rocks

(1) Rutter et al. 1904.
(2) Newcombe et al. 1918.
(3) Starks 1918.
(4) Imler and Sarber 1947.
(5) Pike 1958.
(6) Wilke and Kenyon 1952.
(7) Mathisen et al. 1962.
(8) Thorsteinson and Lensink 1962.
(9) Spalding 1964.
(10) Fiscus and Baines 1966.
(11) Current study 1973.

of Wilke and Kenyon (1952), Spalding (1964), and Fiscus and Baines (1966) present scientific names and volumetric determinations which enable me to present a well-documented dietary list. Pike (1958) also presented a table with stomach contents. All of these data are updated and presented as Table 7.

My study adds 10 genera of fishes to those previously reported from northern sea lions, as follows: *Microstomus, Parophrys, Careproctus, Lyopsetta, Eopsetta, Glyptocephalus, Porichthys, Engraulis, Spirinchus*, and *Chilara*. These 10 genera constituted 31.1 percent of the otoliths found in *Eumetopias*.

All northern sea lion stomachs which contained cephalopod beaks also had remains of from 2 to 13 species of fish (Table 5). Four species of cephalopods were identified: *Loligo opalescens, Octopus* sp., *Chiroteuthis* sp., and *Onychoteuthis* sp. Most beaks were so thoroughly digested that specific identifications were impossible. One male sea lion (REJ 629) had eaten at least 3 octopus plus 13 species of fish. More surprising than the variety of prey eaten was the fact that the sea lion had been eating during the breeding season when most *Eumetopias* males fast (Spalding 1964).

In my study demersal fish were found in six of the nine stomachs containing fish. When the 127 identified fishes from northern sea lions are grouped according to schooling (open-water), bottom-dwelling (rocky), and inshore-schooling species (Table 6), it is apparent that the northern sea lion feeds mainly on bottom-dwelling fishes. The rather high incidence of rocks in the stomachs also suggests a bottom-feeding habit (Tables 1 and 9).

Zalophus californianus, California sea lion

California sea lions make annual north–south migrations along the Pacific Coast of North America. Adult and subadult males move northward during September and October after the breeding season (Bonnot 1928; Fry 1939; Orr and Poulter 1965, 1967; Bartholomew 1967; Peterson and Bartholomew 1967; Peterson and LeBoeuf 1969; Odell 1971) and return south in March to the more southern breeding rookeries.

Virtually nothing is known about the feeding behavior of migrating California sea lions. Peterson and LeBoeuf (1969) indicated that influxes of sea lions into northern areas are correlated with periods of abundance of food, but they did not document their statement.

No published studies have been reported on California sea lions between Monterey Bay and the Oregon border. B. R. Mate (Oregon State Univ., pers. comm. [1971]) collected 44 male California sea lions in Oregon, but he has not yet identified the fish otoliths. From the data presented by Mate (1973), one can calculate that 40.9 percent of the combined sample of deliberately collected sea lions contained food. My method of obtaining stomach data showed that 66.6 percent of the beached California sea lions contained food.

Fiscus and Baines (1966) examined six California sea lions taken during a recent study on fur seals. The stomach volume was recorded; thus the estimate for feeding rates and food intake to body weight can be determined more clearly. *Loligo opalescens* (common squid), unidentified squid, northern anchovy, and Pacific hake were found in these pelagic California sea lions.

Several observations have been made of feeding sea lions. Fink (1959) reported a single observation, on 25 Feb. 1959, in Monterey Bay of California sea lions attacking a school of Pacific sardines. Although feeding on sardines is surely not uncommon, his vivid description of harbor porpoises controlling the fish school and the sea lions feeding on the periphery of the school is the only published account of such behavior. Ryder (1957) reported feeding aggregations of pinnipeds and birds. At the Farallon Islands, California, an adult male California sea lion was seen repeatedly eating several jackmackerel during the daylight hours on 17 and 19 September 1973 (T. James Lewis and Barbara Lewis, Point Reyes Bird Observatory, pers. comm.). At Cerros (Cedros) Island, Baja California, a female California sea lion was observed feeding beneath the surface by Bonnot (1932b), who watched this cow eat at least six large flying fish (Exocoetidae).

Scheffer and Neff (1948) noted that the analysis of only 58 California sea lion stomachs had been reported in the literature. Of these, Dyche's 25 specimens from the Monterey area are either misidentified or of questionable identity. Scheffer and Neff examined four sea lion stomachs from southern California. Two females were empty, but the other female contained evidence of at least 21 small squid. The single male found dead near La Jolla on 26 Nov. 1943 had 36 nearly whole Pacific herring plus fragments representing 30 other herring. All California sea lions analyzed by Scheffer and Neff were from south of Point Conception.

Rutter et al. (1904) examined stomachs of 24 California sea lions, 13 with food, in July and August 1901 at southern California localities. The eight females each had 100 to 300 small squid parts. Squid pens were food remnants in the stomachs of three of the five males. The remaining stomach contents consisted of hake, rockfish, ratfish, unidentified small fish, and milk. Bonnot (1928) reported on these same specimens and stated that 5 had eaten fish and 11 had eaten squid. Starks (1918) pointed out that stomachs of two of the breeding bulls that Rutter et al. examined did not contain any food.

According to a recent survey by scientists at the Scripps Institution of Oceanography and presented to the California Senate Fact Finding Committee on Natural Resources (Anderson 1960), 24 of 30 stomachs from *Zalophus* contained food. The only identified items were fish otoliths, but many unidentified cephalopod beaks also were present. Carl L. Hubbs (Scripps Institution of Oceanography) and John E. Fitch (California Dept. of Fish and Game, Long Beach, pers. comm. [1973]) revealed that this study was done by the late Art Kelly in southern California and northern Mexico. The 424 fish otoliths which Kelly recovered were identified by Fitch as representing 24 kinds of fishes. Pacific hake were found in 17 of the 24 stomachs and constituted 48.1 percent of the total otoliths. The other fishes were cusk-eels, midshipmen, and species of rockfish. Sixty-six (15.6 percent) of the otoliths were of Pacific mackerel, anchovy, perch, and white croaker. These sea lions also fed extensively on squid and octopus, as represented by beaks in their stomachs.

Briggs and Davis (1972) spent 500 hours aboard sport and commercial salmon boats in Monterey Bay from 14 April to 22 September 1969. They observed seven instances of predation on salmon by California sea lions. Of the hooked fish, 4.1 percent were lost to sea lions. I found 10 dead California sea lions along Monterey Bay during the commercial salmon season (April to September). I also located an additional 20 California sea lion carcasses farther north (Figure 1). I found a single female California sea lion north of Monterey Bay. Only one salmon otolith was present among the 922 otoliths (461 fish represented) from my sample of California sea lions.

Male California sea lions feed on a variety of schooling fishes (Pacific hake, anchovy, rockfish, flatfish, cusk-eel, midshipmen, herring, lingcod, jackmackerel, salmon, and osmerids). Pacific hake and anchovy make up 86.6 percent by frequency of occurrence of otoliths from sea lion stomachs. Schooling fishes, both inshore and open-water types (417 otoliths) were found in California sea lions (Table 6).

Callorhinus ursinus, Northern fur seal

Wilke and Kenyon (1957) identified five species of fish from 204 seals (114 with food) collected from the Bering Sea and St. Paul Island. Seals collected at sea contained large numbers of capelin (*Mallotus villosus*) and walleye pollock (*Theragra chalcogramma*). Only one salmon (*Oncorhynchus* sp.) was found in the stomachs. Three seals killed on land at St. Paul Island collectively held one salmon (*Oncorhynchus* sp.), one walleye pollock, and two sandfish (*Trichodon*). Indian hunters took 41 seals (13 empty) 30 miles (about 48 km) off Washington in 1930. Although the stomach contents were digested, squid eyes and beaks were reported from 21, and identifiable herring vertebrae were present in 15 stomachs (Schultz and Rafn 1936). Clemens and Wilby (1933) looked at 25 stomachs from the west coast of Vancouver Island and reported that 8 contained squids, 9 had salmon, and the rest had small schooling fish. No data on the volume of the stomachs or the number of empty stomachs were reported.

Hanna (1951) recorded fur seals in the Gulf of the Farallons during February and April. Seals were described as competitors with W. I. Follett as he dip-netted for myctophid fish (*Tarletonbeania, Symbolophorus*), sablefish (*Anoplopoma fimbria*), and red Irish lord (*Hemilepidotus hemilepidotus*). Hanna also theorized that fur seals, porpoises, and sea birds were all feeding on pteropods (Mollusca).

More recently 437 stomachs from pelagic fur seals taken off California were examined (Marine Mammal Biological Laboratory 1969). Anchovy, saury, hake, and squid constituted 98 percent of the total food volume.

Scheffer (1950a) reviewed the dietary literature on fur seals. He presented data on only two northern fur seal stomachs from California, one of which contained an unidentified bird and the other had fed on Pacific saury (*Cololabis saira*).

Fur seals found on California beaches usually have little food in their stomachs. Likewise a fur seal from Southeast Farallon Island contained no food in its stomach (REJ 212), but had seven isopods (*Riggia*?) which are external parasites on fish. One beach-cast fur seal had 7 beaks of the common squid and 12 northern anchovy otoliths in its stomach (REJ 243).

Phocoena phocoena, Harbor porpoise

Although the diet of harbor porpoises in California waters is poorly known, herring, small cods, soles, and squid are food items of harbor porpoises generally (Ridgway 1972). Scammon (1874) wrote, "They feed upon fish, and are occasionally taken in seines that are hauled along the shores of San Francisco Bay by the Italian fishermen."

Harbor porpoises seldom are sighted more than 20 miles (about 32 km) offshore and usually are seen near harbor entrances (Fiscus and Niggol 1965). Local fish abundance and seasonal fish movements affect the diet of these porpoises (Rae 1965).

In Scottish waters, Rae (1965) examined 45 porpoises from November to March and 7 additional ones in the summer months. A few invertebrates were found which Rae thought might have been taken incidentally with other food items. Fish or fish remains were recognized in 41 of the 43 stomachs with recognizable food. One of the two remaining stomachs contained milk and the other the remains of a very small cephalopod. Ten species of fish were present, with herring (*Clupea harengus*) and whiting (*Gadus merlangus*) the most common. Most fish were less than 25 cm in length, with the largest individuals 35 cm. These harbor porpoises had been trapped in nets set for cod or salmon.

British naturalists have recorded food habits of harbor porpoises in the North Sea for more than 100 years, and small fish, mainly clupeoids (65 percent) and gadoids (30 percent), constitute the major foods taken (Rae 1965). Rae concluded that harbor porpoises take pelagic forms of fish. Tomilin (1957) found benthic fish predominating in the diet of harbor porpoises from the Black Sea and Sea of Azov. In a study in the Bay of Fundy, small schooling fishes (*Clupea harengus, Gadus morhua, Scomber scombrus*) were principal food items for harbor porpoises (Smith and Gaskin 1974). These schooling fishes accounted for 78 percent of the total diet.

Tomilin (1957) listed dietary items of harbor porpoises in the Black Sea, where 4000 stomachs were inspected. These porpoises fed upon eight benthic species and six pelagic species of fish. The pelagic fish were consumed when they occurred in large dense schools. One of two harbor porpoises found at Pt. Barrow, Alaska, contained bones of whitefish (*Leucichthys*) (Hall and Bee 1954). Pike and MacAskie (1969) reported a Canadian harbor porpoise caught in a gill net. This animal had one herring in its stomach.

Scheffer (1953) inspected a female porpoise from Grays Harbor County, Washington, which had fed on 37 capelin. Its death apparently was caused by an American shad blocking its throat passages. Five years earlier Scheffer had found on the same beach another porpoise which also had choked to death on a fish. A female porpoise from Port Townsend, Washington, May 1950, had eaten five Pacific herring (Wilke and Kenyon 1952).

Orr (1937) reported that a porpoise apparently choked to death on a gray smoothhound shark (*Mustelus californicus*). This single report of sharks as a food item may be abnormal. Fink (1959) observed for 30 minutes several hundred harbor porpoises feeding on a school of Pacific sardines northwest of Pt. Pinos, Monterey Bay. He vividly described the attack and herding of the sardines, and counted from 5 to 12 fish eaten by an individual porpoise in its attack through the sardines.

In my study, juvenile rockfish constituted 71.8 percent of the diet of harbor porpoises (Table 3). Five porpoises collected in June and July contained 1017 rockfish otoliths. Northern anchovy was the second most frequent fish and was found in seven porpoises from April to August. Over two-thirds of all fish found in stomachs of harbor porpoises live in open water or are inshore schooling species (Table 6). Juvenile Pacific hake, Pacific tomcod, rockfish, and northern anchovy accounted for 97 percent of all stomach otoliths found during my investigation (Table 3).

Invertebrate remains were found in 8 of the 20 porpoises examined (Table 9). A total of 141 *Loligo opalescens* beaks was identified from 168 cephalopod fragments. These beaks represent at least 92 individual cephalopods compared to at least 712 fish represented by 1429 otoliths (Table 5). One harbor porpoise (CAS 2392) had 13 intact *Loligo* and an additional 35 pairs of beaks in its stomach. The intact bodies of the 13 squids indicated harbor porpoises do not chew this food item.

Phocoenoides dalli, Dall's porpoise

This porpoise is much more common than early records indicate. Brownell (1964) reported its occurrence in southern California waters in the winter. Lustig (1948) saw 10 or 12 porpoises feeding on baitfish, anchovy or sauries, on 13 July 1939, in the Anacapa Passage.

Deep-water benthic fish and bathypelagic cephalopods were reported as major food items from a large sample of Dall's porpoise stomachs from Japan (Wilke and Nicholson 1958). Eleven percent of the food volume was squid: *Watasenia, Ommastrephes*, and unidentified genera. Myctophidae (lanternfishes) composed 70 and 73 percent of the stomach contents in 1949 and 1952, respectively.

Cowan (1944) took five (3 males and 2 females) Dall's porpoise off the coast of British Columbia in the summer of 1939. Four of the five stomachs were full of herring. Pike and MacAskie (1969) examined three males and two females from British Columbia, and they too found mostly herring or squid in three stomachs.

Scheffer (1953) recorded the stomach contents of six Dall's porpoises from Monterey and northward. These contained Pacific hake, squids (*Loligo opalescens* and unidentified species), jackmackerel, and unidentified fish. Two Dall's porpoises from Alaska had fed only on capelin. Brown and Norris (1956) mentioned anchovy as a food item of the Dall's porpoise. An adult porpoise taken in southern California waters had eaten at least 14 Pacific hake, 2 jackmackerel, and 13 cephalopods (Norris and Prescott 1961). These authors also noted the porpoise circling amid schools of sauries, probably feeding. Fiscus and Niggol (1965) observed Dall's porpoises off the north coast and collected five specimens off Cape Mendocino, California. Three females and one of the males had only squid beaks in their stomachs; the stomach of the other male was empty.

The Dall's porpoise is present in Monterey Bay all year. Stomach samples, examined each month, indicated that Pacific hake, rockfish, and squid are important food items. Loeb (1972) examined 25 stomachs of Dall's porpoise from Monterey Bay and found Pacific hake in 23, squid in 16. Most of the cephalopods present were *Loligo,* with lesser numbers of *Abraliopsis, Gonatus, Onychoteuthis,* and *Octopus.* Pacific hake, juvenile rockfish, and squid made up 93 percent of the total diet of the Dall's porpoise from Monterey Bay (Table 5 in Loeb 1972).

On 28 June 1973, an immature female Dall's porpoise was found on the beach north of the University of California Marine Station at Bodega Bay. Presumably this animal (REJ 670, 102 cm total length) was dependent on its mother for nourishment, although no milk was noted in its stomach.

I examined four adult Dall's porpoises (2 males, 2 females), and only two had identifiable food remains. One (REJ 674) had 61 Pacific hake otoliths representing 31 fish in its stomach, and the other (CAS 2335) contained 6 juvenile Pacific tomcod. The two other porpoises had empty stomachs (CAS 2384, REJ 678).

Loeb (1972) did not mention Pacific tomcod as a dietary item from Dall's porpoises but did note a wide variety of fishes (15 species) eaten by Dall's porpoises from Monterey Bay. Pacific hake have been reported as important food for Dall's porpoise (Scheffer 1953; Norris and Prescott 1961; Fiscus and Niggol 1965; Loeb 1972). The hakelike fish (*Laemonema,* family Moridae) occurs in the diet of Dall's porpoise from Japanese waters (Wilke and Nicholson 1958).

No cephalopods were found in any of the five Dall's porpoise stomachs from my northern California sample.

Delphinus delphis, Pacific common dolphin

Common dolphins seldom are sighted north of the California-Oregon border and are rare beyond the 100-fathom (183-m) line (National Oceanic and Atmospheric Administration 1974). Four *Delphinus* stomachs collected off California contained fish and cephalopods (Fiscus and Niggol 1965). One female had unidentified fish otoliths and another stomach contained (by volume) 60 percent squid, 25 percent saury, and 15 percent northern anchovy. One male dolphin taken at sea contained 90 percent *Loligo* and 10 percent saury. Another stomach contained 60 percent lanternfish (Myctophidae) and 40 percent squid (*Gonatus* sp., 20 percent; *Onychoteuthis* sp., 10 percent; unidentified squid, 10 percent) (Fiscus and Niggol 1965).

Observations in California waters indicate that common dolphins are present in inshore waters throughout the year (Norris and Prescott 1961). The major foods seem to be sardines, anchovies, sauries, small bonito, and squid (Norris and Prescott 1961).

Schmidt (1923) removed 15,191 otoliths from the stomach of one *Delphinus.* These otoliths represented five species of small fish (7596 individuals). Frost (1924) looked at 4338 of these same otoliths and identified six species in three families. Myctophid fish accounted for 4324 of these 4338 otoliths. The fishes represented probably did not constitute a "full" meal for this dolphin (Fitch and Brownell 1968).

Many common dolphins stranded in southern California had empty stomachs (Robert Brownell, Jr., Smithsonian Institution, pers. comm. [1970]). Fitch and Brownell (1968) examined two which had 133 and 119 otoliths. Anchovy remains (141 sagittae) were the most abundant. One dolphin had eaten 63 fishes representing six families. Anchovy, myctophids, and saury were represented in the other common dolphin examined. These authors speculated that both *Lagenorhynchus* and *Delphinus* feed on mesopelagic fish at depths exceeding 120 m (Fitch and Brownell 1968).

The Pacific common dolphin (CAS 2340) I examined had 11 otoliths assigned to two species; medusafish (*Icichthys lockingtoni*) and an osmerid. This specimen also had four *Loligo* beaks. Medusafish are most abundant around jellyfish and in the upper 150 ft (ca. 46 m) of the ocean (John Fitch, California Dept. of Fish and Game, pers. comm. [1973]). Apparently this dolphin had fed near the surface.

Lagenorhynchus obliquidens, Pacific white-sided dolphin

This dolphin has received careful attention from west coast biologists during the last 25 years (Scheffer 1950b, 1953; Brown and Norris 1956; Houck 1961; Norris and Prescott 1961). These authors reported sardine, Pacific herring, salmon, northern anchovy, "scad" (=jackmackerel), Pacific saury, squid, and jellyfish remnants as food items (Table 8).

Large feeding aggregations of California sea lions, elephant seals, common dolphins, and Pacific white-sided dolphins have been observed by various authors (Norris and Prescott 1961; Fiscus and Niggol 1965). Mixed schools of common and white-sided dolphins have been noted

TABLE 8. STOMACH CONTENTS OF *Lagenorhynchus obliquidens* FROM THE WEST COAST OF NORTH AMERICA (CALIFORNIA).

Locality	Sex	Date	Source	Type of contents
w Trinidad	F	11 Sep 1958	(3)	Pacific sauries, "scad"
Humboldt Co.	M	26 Dec. 1968	(6)	Pacific sanddab, Pacific hake, eulachon, squid
Marin Co.	F	9 Feb. 1970	(6)	no ID (fish)
San Mateo Co.	M	29 Sep. 1972	(6)	shortbelly rockfish, northern anchovy, plainfin midshipman
San Mateo Co.	F	6 May 1973	(6)	Pacific hake, jackmackerel
w Santa Cruz	M	4 Mar. 1959	(4)	trace squid
w Santa Cruz	F	5 Mar. 1959	(4)	northern anchovy, Pacific hake, squid
Monterey Co.	F	21 Apr. 1973	(6)	night smelt
Monterey Co.	F	29 May 1970	(6)	squid, octopus
w Pt. Piedras	F	27 Feb. 1959	(4)	northern anchovy, squid
NW Morro Bay	M	22 Feb. 1959	(4)	northern anchovy, Pacific hake, squid
w Morro Bay	F	14 Feb. 1959	(4)	trace squid
s Anacapa I.	M	27 Feb. 1952	(1)	jellyfish, squid
Santa Monica	?	22 Aug. 1963	(5)	Pacific hake, northern anchovy, white seaperch, cephalopods
s San Pedro	F	6 June 1953	(2)	anchovies, squid
Long beach	F	21 Aug. 1967	(5)	northern anchovy, Pacific hake, cephalopods, queenfish

(1) Scheffer 1953.
(2) Brown and Norris 1956.
(3) Houck 1961.
(4) Fiscus and Niggol 1965.
(5) Fitch and Brownell 1968.
(6) Current study 1973.

off southern California where the white-sided dolphins are common, but north of San Francisco only small groups of *Lagenorhynchus* have been seen (Fiscus and Niggol 1965).

In southern California waters, white-sided dolphins have a distinct seasonal movement during the summer and fall which correlates with a shift from anchovies and squids as a principal food to the offshore schools of Pacific saury. This conclusion is from field observations only and from one stomach analysis (Brown and Norris 1956). No seasonal migration of white-sided dolphins has been observed in northern California. A migration of white-sided dolphins to northern California may correlate with oceanic current shifts and/or fish migratory patterns.

Pacific sanddab, eulachon, night smelt, shortbelly rockfish, and plainfin midshipman can now be added to the known species of food fishes reported from white-sided dolphins. I recovered 89 otoliths, only 3 of which represent open-water fishes. The great number of otoliths from inshore schooling fishes (Table 6) tends to indicate that this dolphin eats abundant, small fishes (osmerids, midshipman, and juvenile rockfish).

The fact that white-sided dolphins feed on five kinds of cephalopods gives the impression that these invertebrates are a major food resource (Tables 5 and 9). My data indicate that the white-sided dolphin apparently is not dependent on cephalopods in northern California; only three of seven stomachs had molluscan remains. One dolphin (REJ 625) contained 147 of the 155 cephalopod beaks found.

Grampus griseus, Risso's dolphin

Until recent stranding records were published (Orr 1966; Paul 1968; Stroud 1968; Hatler 1971) this dolphin was known only from the type of *Grampus stearnsii* (Dall) collected at Monterey Bay in 1873. All four previous specimens reported were males, and only two contained identifiable food remains. Orr (1966) reported a Risso's dolphin from San Mateo County that contained two pairs of beaks from the squid *Dosidicus gigas*. Stroud (1968) listed seven categories of cephalopod beaks from a male Risso's dolphin recovered in Washington: *Onychoteuthis* (1), *Octopodoteuthis* (1), *Chiroteuthis* (16), *Gonatus* (4), Gonatidae—form A (7), Gonatidae—form B (13), and unidentified beaks (2). No fishes have been found in any Risso's dolphin.

I examined a single specimen at Southeast Farallon Island on 20 May 1973. All standard measurements (275 cm total length) were taken, and the reproductive tract, blood sample, and complete skeleton were saved. No parasites were discovered, but a goose-neck barnacle (*Pollicipes polymerus*) and a single hydroid (*Aglaophenia latirostris*) were in the stomach. Orr (1951) theorized that such material is swallowed incidentally as the animal thrashes close to shore. The barnacle and hydroid reported here were probably accidentally ingested. Both kinds of invertebrates are plentiful on the intertidal shores of the Farallon Islands. Hatler (1971) reported that plant material seems to be an "herbal remedy" in *Grampus*. Risso's dolphin is probably an invertebrate feeder like *Globicephala*, which eats only squid as reported by Sergeant and Fisher (1957). *Grampus* lack teeth in the upper jaw and may feed solely on soft invertebrates.

Kogia simus, Dwarf sperm whale

Brownell obtained three dwarf sperm whales from Japanese waters. Although a good comparative collection of Japanese fishes was lacking, Fitch and Brownell (1968) presented a table indicating that 18 different species of fish in 7 families were in the stomachs. Because two families (Macrouridae and Moridae) are inhabitants of deep water, these authors speculated that *Kogia* feeds 800 ft (244 m) or more beneath the surface. Other authors have stated that most specimens of *Kogia* had eaten cephalopods or pelagic crustaceans (National Oceanic and Atmospheric Administration 1974).

Scheffer and Slipp (1948) examined a male pygmy sperm whale specimen from Washington. It had 500 cc of nematodes and food fragments in its stomach; 11 eye lenses (including 5 from squid), 15 squid beaks, 21 otoliths of an unidentified fish, 1 crab limb, maxillary bones of 2 specimens of *Trichodon* (?), and fragments of shrimp *Pasiphaea, Pandalus, Pandalopsis*.

Kogia has a discontinuous distribution and is rather poorly known from the west coast. Few have been seen alive. Beach-cast specimens have provided material for anatomical, taxonomic, and distributional studies, but essentially nothing is known of its life history (Handley 1966).

Because of difficulty of identification prior to Handley's work (1966), most earlier literature could apply to either the pygmy sperm whale (*K. breviceps*) or the dwarf sperm whale. Only in recent studies can identification be trusted.

One *K. simus* recovered at Thorton Beach, San Mateo County, by the California Academy of Sciences (CAS 2382, male, 204 cm total length) contained 217 beaks representing 112 individuals of these families: Octopoteuthidae, Onychoteuthidae, Enoploteuthidae, Histioteuthidae, Gonatidae, Chiroteuthidae. In addition, a single pair of otoliths in its stomach was from a plainfin midshipman (*Porichthys*). This is the most northern record of *Kogia simus* along the west coast.

DISCUSSION

Statements about marine-mammal diets frequently have been vague and misleading and give a false impression of the role these animals play in the marine ecosystem. Much more information is needed to understand predator-prey relationships in California waters (Steele 1970). California waters are rich in commercially important fishes, and these fishes are well studied. However, it is also pertinent to consider the stocks of noncommercial fishes and the dynamics of such populations. The distribution of both predator and prey, including the availability of the latter throughout the year, is of prime importance.

Adult marine mammals are usually migratory. The causes of these movements are largely unknown, but to some extent marine mammals respond to the seasonal abundance of food. The breeding cycle and its influence on food gathering have not been studied. The smaller whales are not associated with breeding rookeries as are pinnipeds. Cetaceans constantly search for prey and apparently lack the feeding-nursing cycle characteristically found in seals and sea lions.

The behavior and feeding techniques of all marine mammals are poorly documented. Escape strategies of prey species are not well known. The sheer abundance of smaller prey items allows the escape of some individuals from predators. Some fishes and invertebrates reduce predation upon themselves by camouflage or disguise. Armor and spines must also help some prey to reduce losses. Representatives of the following common families of fishes were completely absent from the marine mammal stom-

Table 9. Stomach Contents of Marine Mammals Found in this Study (volume of dry fish bones, cephalopod identification, and miscellaneous items).

Field number	Fish bones (cc)	Cephalopod beaks		Identification
		Upper	Lower	
Zalophus				
68–40	950	–	–	—
317 LGB	400	–	–	—
647	35	2	3	*Octopus* sp.
660	4000	–	1	*Octopus* sp.
662	trace	3	–	*L. opalescens*
664	250	–	–	—
665	30	23	17	*L. opalescens*
666	5	–	–	—
667	trace	–	–	—
685	120 1—*Polinices* shell, *Ulva*, eelgrass	–	–	—
686	820	–	–	—
692	45	–	1	*Octopus* sp.
244	–	1	3	*L. opalescens*
Eumetopias				
69-8	600	–	1	*Chiroteuthis*
247	–	1	1	*L. opalescens*
249	–	6	7	*L. opalescens*
629	–	2	2	*Octopus* sp.
637	2850	2	2	*L. opalescens*
655	1—rock	–	1	*Onychoteuthis*
675	trace	–	–	—
677	5—rocks, trace	–	–	—
688	240	–	–	—
699	3200	–	1	*Octopus* sp.
Phoca				
69-24	trace	–	–	—
646	40	2	1	*Octopus* sp.
671	10	–	–	—
696	400	10	3	*Octopus* sp.
Callorhinus				
212	7—external fish isopods (*Riggia* ?)	–	–	—
243	–	7	7	*L. opalescens*
Delphinus				
CAS 2340	3	1	1	*L. opalescens*
Lagenorhynchus				
HSC 68-9	–	1	–	*Abraliopsis*
237	–	1	1	*Octopoteuthis*
		1	3	*L. opalescens*
		–	1	unknown Gonatidae
625	–	1	1	*Onychoteuthis*
		79	66	*L. opalescens*
		–	1	*Gonatus* sp.
652	trace	–	–	—
Phocoena				
241	–	9	7	*L. opalescens*
450	15	35	17	*L. opalescens*
653	–	8	5	*L. opalescens*
661	–	–	1	*L. opalescens*
673	75	1	1	*L. opalescens*

TABLE 9. CONTINUED.

Field number	Fish bones cc	Cephalopod beaks		Identification
		Upper	Lower	
HSC 73-4	180	–	–	—
CAS 2384	–	2	3	*L. opalescens*
CAS 2385 (476)	trace	–	–	—
CAS 2392	–	35	36	*L. opalescens* plus 13 whole *Loligo*
CAS 2398	–	2	–	*Morotheuthis* sp.

achs examined in this study: Cottidae, Agonidae, Serranidae, Blenniidae, Clinidae, and Scombridae. These marine fishes are probably detected and perhaps discriminated as nonprey items. Possibly these fishes possess mechanisms to escape.

Sick or injured marine mammals will starve rapidly. Animals not showing obvious causes of death presumably were sick or injured and seldom had anything in their stomachs. Specimens showing evidence of violent sudden death had intact squid or fish. Others had only digestion-resistant items such as beaks or otoliths. One harbor porpoise (CAS 2390) had swallowed a 46-cm Pacific hake, the anterior end of which was partially digested. No food item in this study showed evidence of having been chewed or cut by the consumer. Field observations indicate that food is torn apart by much head shaking, and the teeth only aid in the capture and holding of prey. The lack of specialized forelimbs with which to manipulate food is evident in the swallowing of whole food.

Sexual dimorphism in the size of pinnipeds (Scheffer 1958) should be reflected in feeding rates and the species or size of prey selected, but no published data are available to substantiate this. However, such resource partitioning is shown between species (Table 6).

It appears that prey selection in marine mammals is specialized, and this conclusion is supported by the available data. Comparison of the food of *Phoca* with that of *Eumetopias* and *Zalophus* (Tables 1, 4, and 7) shows less dependence on pelagic fishes by *Phoca*. Perch, eelpout, and greenling (80 percent of the fish eaten by *Phoca*) are typically shallow-bottom species which live near rocky habitats. *Zalophus* characteristically feeds on Pacific hake, northern anchovy, and rockfish (93 percent of the fish). These open-water fishes are very abundant (Ahlstrom 1965; Bell (1971). *Eumetopias*, while also using Pacific hake and rockfish, relied more heavily on bottom-dwelling flatfish and cusk-eel (29.1 percent of the fish). *Octopus* was the only cephalopod found in the stomachs of harbor seals, although several other cephalopods are taken by California and northern sea lions (Table 9). Stomachs of *Eumetopias* frequently had stones in them (Table 9). Apparently there is some selection for these nonfood items by these sea lions. The depth of the sea at which these pinnipeds feed is unknown. All prey items normally eaten by *Eumetopias* inhabit water less than about 200 m deep. Thus *Zalophus* feeds on schooling fishes while *Eumetopias* feeds on bottom fishes (Table 6).

The mean feeding rate of small cetaceans as described by Sergeant (1969) is 10.8 percent of their body weight per day. No comparative information is available on feeding rates of juvenile individuals, nor have sexual or seasonal differences in feeding rates been published. Captive Arctic seals (*Cystophora*, *Pagophilus*) require food in amounts of 3–5 percent of their body weight per day in order to maintain good health (Blix et al. 1973). Daily food consumption of fur seals (10 percent of body weight), northern sea lion (4 percent of body weight), and harbor seal (11 percent of body weight) are recorded on field-collected specimens by Spalding (1964). These data do not include information on body size, reproductive state, or activity factors which influence the food consumption of these pinnipeds.

The smaller odontocetes fed on more cephalopods (17 percent of the diet) than did the pinnipeds (5 percent) (Tables 5 and 9). The diet of the sea lions in this study was 95 percent fish, compared with 83 percent in the cetaceans.

Phocoena fed heavily on rockfish, anchovy, and juvenile Pacific hake. Most of these fishes are semi-pelagic, small, and probably occur near the surface. The recoveries of harbor porpoises were limited to the period April to September and therefore do not reflect a year-round dietary sample. These porpoises prey extensively on *Loligo,* which is present throughout the year.

Lagenorhynchus associates with many other species of marine animals and perhaps feeds on a wide variety of prey. Data from this study (Table 8) indicate that white-sided dolphins are generalized feeders. Osmerids and midshipmen, representing two distinct habitats (inshore schooling and bottom-dwelling), were major food items. Although midshipmen live from the intertidal regions to a depth of 170 fathoms (about 311 m), they also leave the bottom in search of food (Fitch and Lavenberg 1971). We do not know where or when this fish is eaten, but it is an important component in the diets of all marine mammals studied.

ACKNOWLEDGMENTS

So many individuals have contributed to this study that it is impractical to list them all. The telephone calls from federal, state, and county officials and other interested persons reporting carcasses are deeply appreciated. Personnel at the Point Reyes Bird Observatory deserve special thanks. The facilities of these institutions were used: California Academy of Sciences; Museum of Vertebrate Zoology, University of California, Berkeley; Humboldt State University.

Personnel of each institution extended aid, especially my dissertation committee at Humboldt State University, chaired by Dr. W. J. Houck. The patience showed by the manuscript reviewers is appreciated; thank you, Drs. S. Harris, J. Waters, and W. Z. Lidicker, Jr. The assistance of Mr. John E. Fitch, Research Director, State Fisheries Laboratory, California Department of Fish and Game, was essential for the identification of fish otoliths. Mr. Clifford H. Fiscus, National Marine Fisheries Service, Seattle, Washington, aided with the identification of the cephalopod beaks.

My able field assistants located as many old carcasses as I did. Thanks, Pica, Chepen, Dusty, and Ginger. And lastly, the support of Lise made all the tasks easier.

LITERATURE CITED

AHLSTROM, E. H. 1965. Kinds and abundance of fishes in the California Current region based on egg and larval survey. Calif. COFI Prog. Rep. 10:31–37.

ANDERSON, H. 1960. Sea lions—creatures of controversy. Calif. Senate Fact Finding Committee on Natural Resources. Fort Bragg, California. 14 p.

ANONYMOUS. 1901. Sea lions as fish destroyers. For. Stream 56(22):428.

ANONYMOUS ("Steelhead," pseudonym). 1901. Food of sea lions. For. Stream 56(26):507–508.

BARTHOLOMEW, G. A. 1967. Seal and sea lion populations of the California Islands. Pp. 229–244 *in* R. N. Philbrick (ed.), Proc. Symp. on the Biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara.

BELL, R. R. 1971. California marine fish landings for 1970. Calif. Dep. Fish Game Fish Bull. 154. 50 p.

BIGG, M. A. 1969. The harbor seal in British Columbia. Fish. Res. Bd. Canada Bull. 172. 33 p.

BLIX, A. S., J. A. IVERSON, AND A. PASCHE. 1973. On the feeding and health of young hooded seals (*Cystophora cristata*) and harp seals (*Pagophilus groenlandicus*) in captivity. Norw. J. Zool. 21:55–58.

BONNOT, P. 1928. Report on the seals and sea lions of California. Calif. Dep. Fish Game Fish Bull. 14. 61 p.

———. 1932a. Food habits of the Pacific harbor seal. Calif. Fish Game 18:98.

———. 1932b. A note on the fishing of the California sea lion. Calif. Fish Game 18:98–99.

———. 1951. The sea lions, seals, and sea otter of the California coast. Calif. Fish Game 37:371–389.

BRIGGS, K. T., AND C. W. DAVIS. 1972. A study of predation by sea lions on salmon in Monterey Bay. Calif. Fish Game 58:37–43.

BROWN, D. H., AND K. S. NORRIS. 1956. Observations of captive and wild cetaceans. J. Mammal. 37:311–326.

BROWNELL, R. L., JR. 1964. Observations of odontocetes in central California waters. Norsk Hvalfangst-Tidende 53(3):60–66.

CALIFORNIA DIVISION OF FISH AND GAME. 1927. What do sea lions eat? Calif. Fish Game 13:119–120.

CLARKE, M. R. 1962. The identification of cephalopod 'beaks' and the relationship between beak size and total body weight. Bull. Brit. Mus. (Nat. Hist.) Zool. 8(10):419–480.

CLEMENS, W. A., AND G. V. WILBY. 1933. Food of the fur seal off the coast of British Columbia. J. Mammal. 14:43–46.

———, AND ———. 1961. Fishes of the Pacific coast of Canada. Second ed. Fish. Res. Bd. Canada Bull. 68. 443 p.

CLOTHIER, C. R. 1950. A key to some southern California fishes based on vertebral characters. Calif. Fish Game Fish Bull. 79. 83 p.

COWAN, I. M. 1944. The Dall porpoise, *Phocoenoides dalli* (True), of the northern Pacific Ocean. J. Mammal. 25:295–306.

COX, K. W. 1963. Egg-cases of some elasmobranchs and a cyclostome from Californian waters. Calif. Fish Game 49:271–289.

DAUGHERTY, A. E. 1972. Marine mammals of California. Second ed. Dept. Fish and Game, Sacramento, California. 87 p.

DYCHE, L. L. 1901. Notes on the food habits of California sea lions. [Manuscript *in* C. H. Merriam files Mus. Vert. Zool. Univ. Calif., Berkeley. 6 p.]

———. 1903. Notes on the food habits of California sea lions. *Zalophus californianus* Lesson. Trans. Kansas Acad. Sci. 18:179–182.

Evans, W. E., and J. Bastian. 1969. Marine mammal communication: social and ecological factors. Pp. 425–475 *in* H. T. Andersen. The biology of marine mammals. Academic Press, New York.

Evermann, B. W. 1921. The Año Nuevo Steller sea lion rookery. J. Mammal. 2:16–19.

———, and G D. Hanna. 1925. The Steller sea lion rookery on Año Nuevo Island, California in 1924. J. Mammal. 6:96–99.

Fink, B. D. 1959. Observation of porpoise predation on a school of Pacific sardines. Calif. Fish Game 45:216–217.

Fiscus, C. H., and G. A. Baines. 1966. Food and feeding behavior of Steller and California sea lions. J. Mammal. 47:195–200.

———, and K. Niggol. 1965. Observations of cetaceans off California, Oregon, and Washington. U.S. Fish Wild. Serv. Spec. Sci. Rep. Fish. 498. 27 p.

Fitch, J. E., and R. L. Brownell, Jr. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Bd. Canada 25:2561–2574.

———, and R. J. Lavenberg. 1971. Marine food and game fishes of California. California Natural History Guides 28. Univ. Calif. Press, Berkeley and Los Angeles. 179 p.

Freiburg, R. E., and P. C. Dumas. 1954. The elephant seal (*Mirounga angustirostris*) in Oregon. J. Mammal. 35:129.

Frey, H. W. (ed.). 1971. California's living marine resources and their utilization. Calif. Dept. Fish and Game. Sacramento, California. 148 p.

Frost, G. A. 1924. Fish otoliths from the stomach of a porpoise. Nature 113:310.

Fry, D. H., Jr. 1939. A winter influx of sea lions from Lower California. Calif. Fish Game 25:245–250.

Hall, E. R., and J. W. Bee. 1954. Occurrence of the harbor porpoise at Point Barrow, Alaska. J. Mammal. 35:122–123.

Handley, C. O., Jr. 1966. A synopsis of the genus *Kogia* (Pygmy Sperm Whales). Pp. 62–69 *in* K. S. Norris (ed.). Whales, porpoises, and dolphins. Univ. Calif. Press, Berkeley and Los Angeles.

Hanna, G D. 1951. Alaska fur seals, *Callorhinus ursinus*, observed off San Francisco Bay, California. J. Mammal. 32:364–365.

Harrison, R. J. (ed.). 1972. Functional anatomy of marine mammals. Vol. 1. Academic Press, London and New York. 451 p.

———, F. R. Johnson, and B. A. Young. 1970. The oesophagus and stomach of dolphins (*Tursiops, Delphinus, Stenella*). J. Zool. 160:377–390.

Hatler, D. F. 1971. A Canadian specimen of Risso's dolphin. Canadian Field-Nat. 85:188–189.

Hedgpeth, J. W. 1944. Sea lions. Nat. Mag. 37(8):443–445.

Houck, W. J. 1961. Notes on the Pacific striped porpoise. J. Mammal. 42:107.

Hubbs, C. L., W. I. Follett, and L. J. Dempster. 1979. List of the fishes of California. Occas. Pap. Calif. Acad. Sci. 133. 51 p.

Huey, L. M. 1925. Late information on the Guadalupe Island elephant seal herd. J. Mammal. 6:126–127.

———. 1930. Capture of an elephant seal off San Diego, California, with notes on stomach contents. J. Mammal. 11:229–231.

Imler, R. H., and H. R. Sarber. 1947. Harbor seals and sea lions in Alaska. U.S. Fish Wild. Serv. Spec. Sci. Rep. 28. 23 p.

Iverson, I. L. K., and L. Pinkas. 1971. A pictorial guide to beaks of certain eastern Pacific cephalopods. Calif. Fish Game Fish Bull. 152:83–105.

Jameson, R. J., and K. W. Kenyon. 1978. Prey of sea lions in the Rogue River, Oregon. J. Mammal. 58:672.

Kenyon, K. W. 1952a. Diving depths of the Steller sea lion and Alaskan fur seal J. Mammal. 33:245–246.

———. 1952b. The Steller sea lion. Pac. Discovery 5(4):4–13.

———. 1965. Food of harbor seals at Amchitka Island, Alaska. J. Mammal. 46:103–104.

———, and V. B. Scheffer. 1955. The seals, sea lions, and sea otter of the Pacific coast. U.S. Fish Wild. Serv. Circ. 32. 34 p.

King, J. E. 1964. Seals of the world. Brit. Mus. (Nat. Hist.) London. 154 p.

Loeb, V. J. 1972. A study on the distribution and feeding habits of the Dall porpoise in Monterey Bay, California. Unpublished Master's Thesis, San Jose State College. 62 p.

Lustig, B. L. 1948. Sight records of Dall porpoises off the Channel Islands, California. J. Mammal. 29:183.

Marine Mammal Biological Laboratory. 1969. Fur seal investigations, 1966. U.S. Fish Wild. Serv. Spec. Sci. Rep. Fish. 584. 123 p.

Mate, B. R. 1973. Population kinetics and related ecology of the northern sea lion, *Eumetopias jubatus*, and the California sea lion, *Zalophus californianus*, along the Oregon coast. Ph.D. Thesis. Univ. of Oregon. 94 p.

Mathisen, O. A. 1959. Studies on Steller sea lion (*Eumetopias jubata*) in Alaska. Trans. N. Am. Wildl. Res. Conf. 24:346–356.

———, R. T. Baade, and R. J. Lopp. 1962. Breeding habits, growth, and stomach contents of the Steller sea lion in Alaska. J. Mammal. 43:469–477.

Merriam, C. H. 1901a. Food of sea lions. Science 8:777–779.

———. 1901b. Food of sea lions. For. Stream 56(21):428.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Fish Game Fish Bull. 157:1–235.

Morejohn, G. V., and D. M. Baltz. 1970. Contents of the stomach of an elephant seal. J. Mammal. 51:173–174.

National Oceanic and Atmospheric Administration. 1974. Report of the Secretary of Commerce. Administration of the Marine Mammal Protection Act of 1972. Federal Register 39:23896–23932.

Nelson, O. M., and H. A. Larkins. 1970. Distribution and biology of Pacific hake: a synopsis. Pp. 23–24 *in* Pacific hake. U.S. Fish Wildl. Serv. Circ. 332.

Newcombe, C. F., W. H. Greenwood, and C. M. Fraser. 1918. The sea-lion question in British Columbia. Contrib. Canadian Biol. Sessional Paper 38a. 39 p.

———, and W. A. Newcombe. 1914. Sea-lions on the coast of British Columbia. Rep. Comm. Fish. B.C. for 1913:131–145.

Norris, K. S. (ed.). 1961. Committee on marine mammals. Standardized methods for measuring the recording data on the smaller cetaceans. J. Mammal. 42:471–476.

———, AND J. H. PRESCOTT. 1961. Observations on Pacific cetaceans of Californian and Mexican waters. Univ. Calif. Publ. Zool. 63:291–401.

ODELL, D. K. 1971. Censuses of pinnipeds breeding on the California Channel Islands. J. Mammal. 52:187–190.

ORR, R. T. 1937. A porpoise chokes on a shark. J. Mammal. 18:370.

———. 1951. Cetacean records from the Pacific coast of North America. Wasmann J. Biol. 9(2):147–148.

———. 1966. Risso's dolphin on the Pacific coast of North America. J. Mammal. 47:341–343.

———. 1972. Marine mammals of California. Calif. Nat. Hist. Guides 29. Univ. Calif. Press, Berkeley and Los Angeles. 64 p.

———, AND T. C. POULTER. 1965. The pinniped population of Año Nuevo Island, California. Proc. Calif. Acad. Sci., ser. 4, 32:377–404.

———, AND ———. 1967. Some observations on reproduction, growth, and social behavior in the Steller sea lion. Proc. Calif. Acad. Sci., ser. 4, 35:193–226.

PAUL, J. R. 1968. Risso's dolphin, *Grampus griseus*, in the Gulf of Mexico. J. Mammal. 49:746–748.

PERRIN, W. F. 1970. The problem of porpoise mortality in the U. S. tropical tuna fishery. Pp. 45–48 *in* Proceedings 6th Annual Conference on Biological Sonar and Diving Mammals, Stanford Res. Inst., Menlo Park, Calif.

———, R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS. 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 71:1077–1092.

PETERSON, R. S., AND G. A. BARTHOLOMEW. 1967. The natural history and behavior of the California sea lion. Am. Soc. Mammal. Spec. Publ. no. 1. 79 p.

———, AND B. J. LEBOEUF. 1969. Population study of seals and sea lions. Trans. N. Am. Wildl. Res. Conf. 34:74–79.

PIKE, G. C. 1958. Food of the Northern sea lion. Pp. 18–20 *in* Prog. Rep. 112, Fish. Res. Bd. Canada Biol. Sta. Nanaimo, B.C.

———, AND I. B. MACASKIE. 1969. Marine mammals of British Columbia. Fish. Res. Bd. Canada Bull. 171. 54 p.

RAE, B. B. 1965. The food of the common porpoise (*Phocoena phocoena*). J. Zool. (Proc. Zool. Soc. London) 146:114–122.

REDDING, B. R., S. R. THROCKMORTON, AND J. D. FARWELL. 1875. P. 13 *in* Report of the Commissioners of Fisheries of the State of California, 1874–1875. Sacramento.

RIDGWAY, S. H. (ed.). 1972. Mammals of the sea: biology and medicine. Charles C Thomas, Springfield, Illinois, 812 p.

ROBINS, C. R., R. M. BAILEY, C. E. BOND, J. R. BROOKES, E. A. LACHNER, R. N. LEA, AND W. B. SCOTT. 1980. A list of common and scientific names of fishes from the United States and Canada (Fourth edition). Am. Fish. Soc. Spec. Publ. 12. 174 p.

ROEDEL, P. M. 1953. Common ocean fishes of the California coast. Calif. Fish Game Fish Bull. 91. 184 p.

ROWLEY, J. 1929. Life history of the sea lions of the California coast. J. Mammal. 10:1–36.

RUTTER, C., R. E. SNODGRASS, AND E. C. STARKS. 1904. Report on the sea lion investigation. Pp. 116–119 *in* Hugh M. Smith. Report on inquiry respecting food-fishes and fishing-grounds. Rep. U.S. Comm. Fish Fish. Part 18.

RYDER, R. A. 1957. Avian-pinniped feeding associations. Condor 59:68–69.

SCAMMON, C. M. 1874. The marine mammals of the northwestern coast of North America, described and illustrated; together with an account of the American whale-fishery. John H. Carmany and Co., San Francisco. 319 p. [Reprinted by Dover Co., New York. 1968.]

SCHEFFER, T. H. 1928. Precarious status of seal and sea-lion on our northwest coast. J. Mammal. 9:10–16.

———, AND C. C. SPERRY. 1931. Food habits of the Pacific harbor seal, *Phoca richardii*. J. Mammal. 12:214–226.

SCHEFFER, V. B. 1950a. The food of the Alaska fur seal. U.S. Fish Wild. Serv. Wild. Leaflet 329. 16 p.

———. 1950b. The striped dolphin, *Lagenorhynchus obliquidens* (Gill 1865), on the coast of North America. Am. Midl. Nat. 44:750–758.

———. 1953. Measurements and stomach contents of eleven delphinids from Northeast Pacific. Murrelet 34(2):27–30.

———. 1958. Seals, sea lions, and walruses, a review of the pinnipedia. Stanford Univ. Press, Stanford, California. 179 p.

——— (ed.). 1967. Committee on marine mammals. Standard measurements of seals J. Mammal. 48:459–462.

———, AND J. A. NEFF. 1948. Food of California sea-lions. J. Mammal. 29:67–68.

———, AND J. W. SLIPP. 1944. The harbor seal in Washington State. Am. Midl. Nat. 32:373–416.

———, AND ———. 1948. The whales and dolphins of Washington State, with a key to the cetaceans of the west coast of North America. Am. Midl. Nat. 39:257–337.

SCHMIDT, J. 1923. Consumption of fish by a porpoise. Nature 112:902.

SCHULTZ, L. P., AND A. M. RAFN. 1936. Stomach contents of fur seals taken off the coast of Washington. J. Mammal. 17:13–15.

SEED, A. (ed.). 1972. Seals, sea lions, and walruses in eastern North Pacific and Arctic waters. Pacific Search, Seattle. 40 p.

SERGEANT, D. E. 1968. Feeding ecology of marine mammals. Pp. 89–96 *in* Proc. 2nd Symposium on Disease and Husbandry of Aquatic Mammals. Marineland Florida Res. Lab.

———. 1969. Feeding rates of cetacea. Fiskeridir Skr. Ser. Havunders. 15(3):246–258.

———, AND H. D. FISHER. 1957. The smaller cetacea of eastern Canadian waters. J. Fish. Res. Bd. Canada 14:83–115.

SLIJPER, E. J. 1962. Whales, translated by A. J. Pomerans. Basic Books, New York. 475 p.

SMITH, G. J. D., AND D. E. GASKIN. 1974. The diet of harbor porpoises [*Phoecoena phocoena* (L)] in coastal waters of eastern Canada, with special reference to the Bay of Fundy. Canadian J. Zool. 52:777–782.

SPALDING, D. J. 1964. Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia coast. Fish. Res. Bd. Canada Bull. 146. 52 p.

STARKS, E. C. 1918. The sea lions of California. Am. Mus. J. 18(3):226–237.

STEELE, J. H. (ed.). 1970. Marine food chains. Univ. Calif. Press, Berkeley and Los Angeles. 552 p.

STROUD, R. K. 1968. Risso dolphin in Washington State. J. Mammal. 49:347–348.

THORSTEINSON, F. V., AND C. J. LENSINK. 1962. Biological observations of Steller sea lions taken during an experimental harvest. J. Wildl. Manage. 26:353–359.

Tomilin, A. C. 1957. Mammals of U.S.S.R. and adjacent countries. Vol. 9. Cetaceans. Translated from Russian (Israel program for scientific translation, Jerusalem. 1967). 717 p.

Townsend, C. H. 1918. Sea lions and the fishery industries. N.Y. Zool. Soc. Bull. 21:1679–1682.

———. 1919. The utilization of the sea lion. N.Y. Zool. Soc. Bull. 22:32–33.

Wilke, F. 1957. Food of sea otters and harbor seals at Amchitka Island. J. Wildl. Manage. 21:241–242.

———, and K. W. Kenyon. 1952. Notes on the food of fur seal, sea-lion, and harbor porpoise. J. Wildl. Manage 16:396–397.

———, and ———. 1957. The food of fur seals in the eastern Bering Sea. J. Wildl. Manage. 21:237–238.

———, and A. J. Nicholson. 1958. Food of porpoises in waters off Japan. J. Mammal. 39:441–443.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 17, pp. 435–442, 21 figs. October 26, 1981

STUDIES ON THE NEBRIINI (COLEOPTERA: CARABIDAE), IV. FOUR NEW *NEBRIA* TAXA FROM WESTERN NORTH AMERICA

By
David H. Kavanaugh
Department of Entomology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

ABSTRACT: This paper, fourth of a series on the nebriine carabid beetles, provides names for four undescribed taxa from western North America, including: *Nebria danmanni* (type-locality: Deception Basin, Olympic National Park, Washington), *N. sonorae* (Chipmunk Flat, Tuolumne County, California), *N. turmaduodecima* (Caribou Basin, Siskiyou County, California), and *N. meanyi giulianii* (Milner Creek, Mono County, California). Diagnostic combination of characters and comment on geographical distribution are provided for each new taxon and distinguishing features are illustrated.

INTRODUCTION

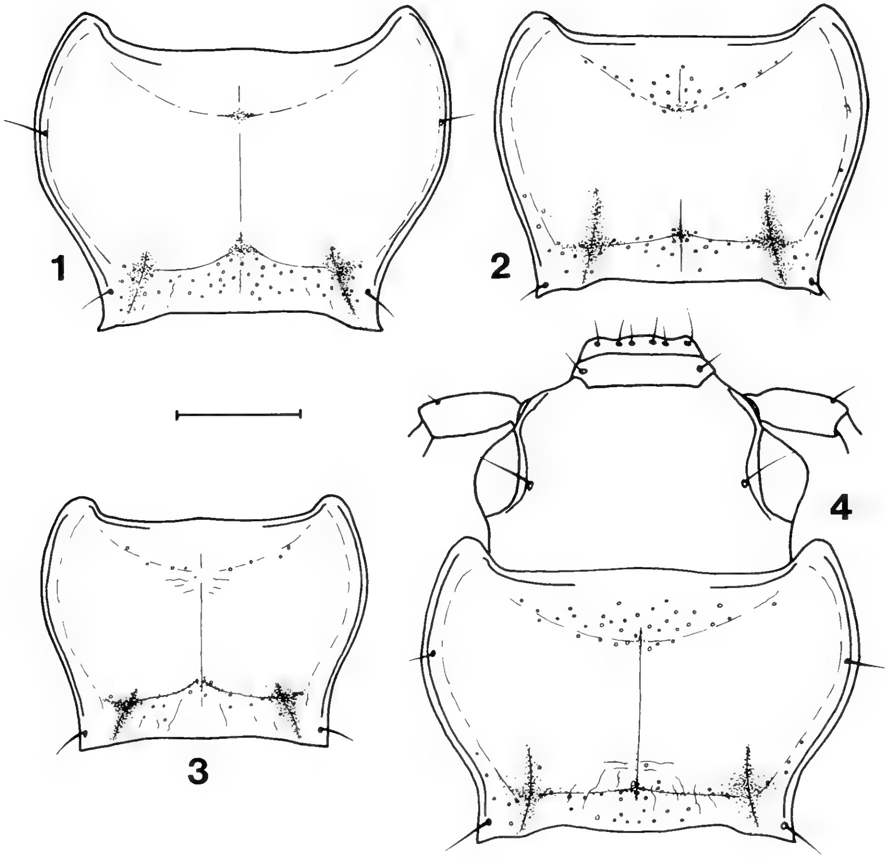
As part of an ongoing project on the Nebriini of the world, Kavanaugh (1979) provided names for 5 new species and 23 new subspecies of genus *Nebria* Latreille from North America and updated nomenclature for Nearctic members of the genus. Since the appearance of that paper, three new species and one new subspecies of *Nebria* have been discovered.

The purpose of this report, an addendum to Kavanaugh (1979), is to provide names for these new taxa. Names are needed immediately for use in several other manuscripts and by other workers. To this end, data and discussion presented for each name are limited to little more than the minimum required by the International Code of Zoological Nomenclature for availability. Additional information on all Nearctic *Nebria* taxa, including those presented here as new, will be presented in a subsequent paper now in preparation.

MATERIALS

This study is based on examination of 187 adult *Nebria* specimens. Following is a list of abbreviations used in the text which refer to the collections from which specimens were received and/or in which paratype specimens have been deposited. Names of curators who sent specimens are also included.

CAS—California Academy of Sciences, San Francisco, California 94118; D. H. Kavanaugh.
CDA—California State Department of Food and Agriculture, Sacramento, California 95814; F. G. Andrews.
DMan—D. Mann, University of Washington, Seattle, Washington 98195.
UASM—University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball.
UCD—University of California, Davis, California 95616; R. O. Schuster.
USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; T. L. Erwin.



FIGURES 1–4. Figs. 1–3. Pronotum, dorsal aspect; scale line = 1.0 mm. 1. *Nebria turmaduodecima* n.sp. (Upper Caribou Lake, California). 2. *Nebria danmanni* n.sp. (Deception Basin, Washington). 3. *Nebria sonorae* n.sp. (Chipmunk Flat, California). Fig. 4. Head and pronotum, dorsal aspect, *Nebria meanyi giulianii* n.ssp. (Milner Creek, California).

Methods

Methods which relate specifically to data and results presented in this paper (including dissection techniques and criteria for ranking taxa) are described in Kavanaugh (1979). A broader and more detailed discussion of preparative and procedural methods used will be included in a subsequent paper (Kavanaugh, manuscript in preparation).

New *Nebria* Taxa

The order of presentation of new taxa follows a new classification of Nearctic *Nebria* to be presented at a later date (Kavanaugh, manuscript in preparation).

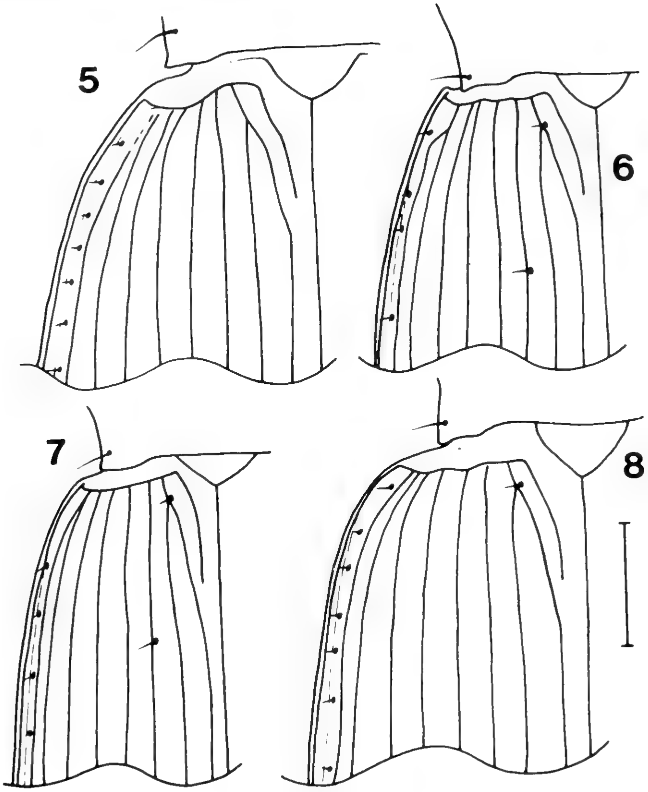
Nebria turmaduodecima, new species

(Figures 1, 5, 9, 13, 17, 21)

HOLOTYPE, a male, in CAS, labelled: "U.S.A., California, Siskiyou Co., Trinity Alps, Caribou Basin (south rim), at snowfield edges, 2290m, 12 Aug. 1980, Stop #80-27 D. H. Kavanaugh collector"/"D. H. Kavanaugh Collection" [orange label]/"Holotype Nebria turmaduodecima Kavanaugh det. D. H. Kavanaugh 1981" [red label]/"California Academy of Sciences Type No. 13729." PARATYPES: 140 (65 males, 75 females), deposited in CAS, CDA, UASM, UCD, USNM.

TYPE-LOCALITY.—Caribou Basin, 2290 m, Trinity Alps, Siskiyou County, California.

DIAGNOSTIC COMBINATION.—Size medium, standardized body length of male less than 12.0 mm, of female less than 12.4 mm; head dark, with pair of pale spots present on vertex (partially fused medially in some individuals); elytra slightly shiny (microsculpture moderately impressed, meshes isodiametric or very slightly transverse), without metallic reflection (very slightly developed in a few individuals only); pronotum (Fig. 1) with midlateral and basolateral setae present; elytral silhouette markedly ovoid, narrowed basally (Fig. 5); hindwing (Fig. 9) vestigial; median lobe of male genitalia as in



FIGURES 5–8. Basal region of left elytron, dorsal aspect; scale line = 1.0 mm. 5. *Nebria turmaduodecima* n.sp. (Upper Caribou Lake, California). 6. *Nebria danmanni* n.sp. (Deception Basin, Washington). 7. *Nebria sonorae* n.sp. (Chipmunk Flat, California). 8. *Nebria meanyi giulianii* n.ssp. (Milner Creek, California).

Figure 13; bursa copulatrix of female as in Figure 17; specimen from Trinity Alps, northwestern California.

DERIVATION OF TAXON NAME.—The species epithet is a combination of the Latin words for "troop" (=*turma*) and "twelve" (=*duodecima*). It is a pleasure for me to name this species in honor of the boys of Troop 12, Boy Scouts of America, Petaluma, California, who assisted me in collecting the first known specimens of this species.

GEOGRAPHICAL DISTRIBUTION.—Figure 21. Known only from Caribou Basin in the Trinity Alps of northwestern California; range probably restricted to the Trinity Alps. I have studied specimens from the following localities.

United States of America

CALIFORNIA: Siskiyou County, Caribou Basin (south rim [2290 m]) [Aug.] (45; CAS), Upper Caribou Lake (east shore [2100–2130 m]) [Aug.] (96; CAS, CDA, UASM, UCD, USNM).

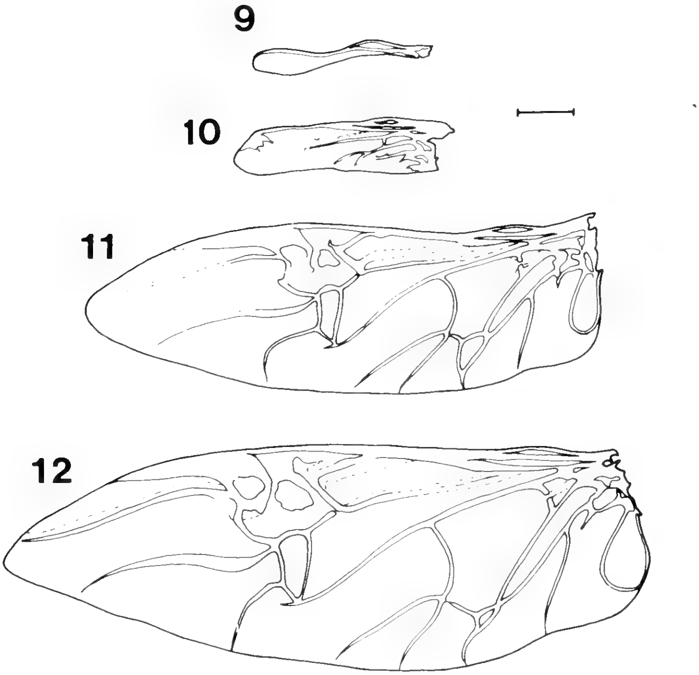
Nebria danmanni, new species

(Figures 2, 6, 10, 14, 18, 21)

HOLOTYPE, a male, in CAS, labelled: "U.S.A., Washington, Olympic National Park, Deception Basin, 6000 ft., 4 Sept. 1976 D. Mann collector"/"Holotype Nebria danmanni Kavanaugh det. D. H. Kavanaugh 1981" [red label]/"California Academy of Sciences Type No. 13730." PARATYPES: 28 (13 males, 15 females), deposited in CAS, DMan, UASM, USNM.

TYPE-LOCALITY.—Deception Basin, 1830 m, Olympic National Park, Washington.

DIAGNOSTIC COMBINATION.—Dorsal surface very shiny, elytral microsculpture formed of markedly transverse meshes; pronotum (Fig. 2) with apical angle markedly projected anteriorly, basal angle rectangular, denticulate, and moderately projected posteriorly, basal sinuation of lateral margin very long and shallow, midlateral seta absent; elytral silhouette subrectangular, markedly elongate, slightly narrowed basally, humeral angle (Fig. 6) markedly distinct, humeral carina markedly developed and projected



FIGURES 9–12. Left hindwing; scale line = 1.0 mm. 9. *Nebria turmaduodecima* n.sp. (Upper Caribou Lake, California). 10. *Nebria danmanni* n.sp. (Deception Basin, Washington). 11. *Nebria sonorae* n.sp. (Chipmunk Flat, California). 12. *Nebria meanyi giulianii* n.ssp. (Milner Creek, California).

anteriorly; hindwing (Fig. 10) markedly shortened and narrowed; middle tibia moderately concave to slightly sulcate dorsally at middle, brush of dorsal setae moderately dense subapically; hindcoxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; median lobe of male genitalia as in Figure 14; bursa copulatrix of female as in Figure 18.

DERIVATION OF TAXON NAME.—I take great pleasure in naming this species in honor of my friend and field companion, Daniel H. Mann, who collected the first known specimens, including the holotype, of this species.

GEOGRAPHICAL DISTRIBUTION.—Figure 21. Known only from Deception Basin in southeastern Olympic National Park, Washington; range probably restricted to the Olympic Mountains at high elevations. I have studied specimens from the following localities.

United States of America

WASHINGTON: Olympic National Park, Deception Basin ([1830 m]) [Sep.] (11; CAS, DMan), Mount Mystery (east slope [1800–1860 m]) [July] (18; CAS, USNM)

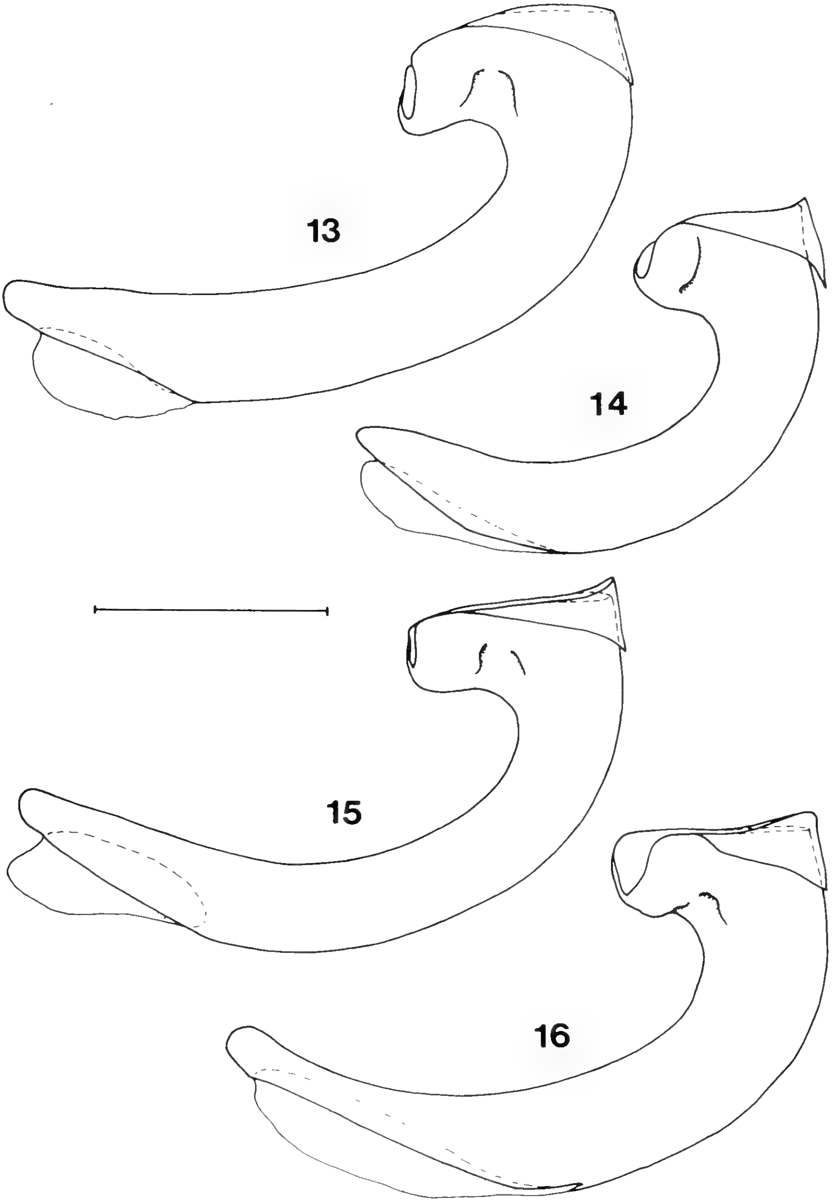
Nebria sonorae, new species

(Figures 3, 7, 11, 15, 19, 21)

HOLOTYPE, a male, in CAS (on indefinite loan deposit from UCD) labelled: "Chipmunk Flat Tuolumne Co., Calif. VIII-9-60"/"R. R. Montanucci Collector"/"Holotype Nebria sonorae Kavanaugh det. D. H. Kavanaugh 1981" [red label]/"California Academy of Sciences Type No. 13731." PARATYPES: two females, deposited in CAS, UCD.

TYPE-LOCALITY.—Chipmunk Flat, Tuolumne County, California.

DIAGNOSTIC COMBINATION.—Dorsal surface moderately shiny, elytral microsculpture moderately impressed, formed of isodiametric (or nearly so) meshes; pronotum (Fig. 3) with apical angle moderately projected, basal angle rectangular or slightly acute, not projected posteriorly, basal sinuation of lateral margin moderate in length and depth, midlateral seta absent; elytral silhouette subrectangular, moderately elongate, moderately narrowed basally, humeral angle (Fig. 7) moderately distinct, humeral carina well developed and projected anteriorly; hindwing (Fig. 11) full-sized and width; middle tibia moderately sulcate dorsally at middle, brush of dorsal setae moderately dense subapically; hind

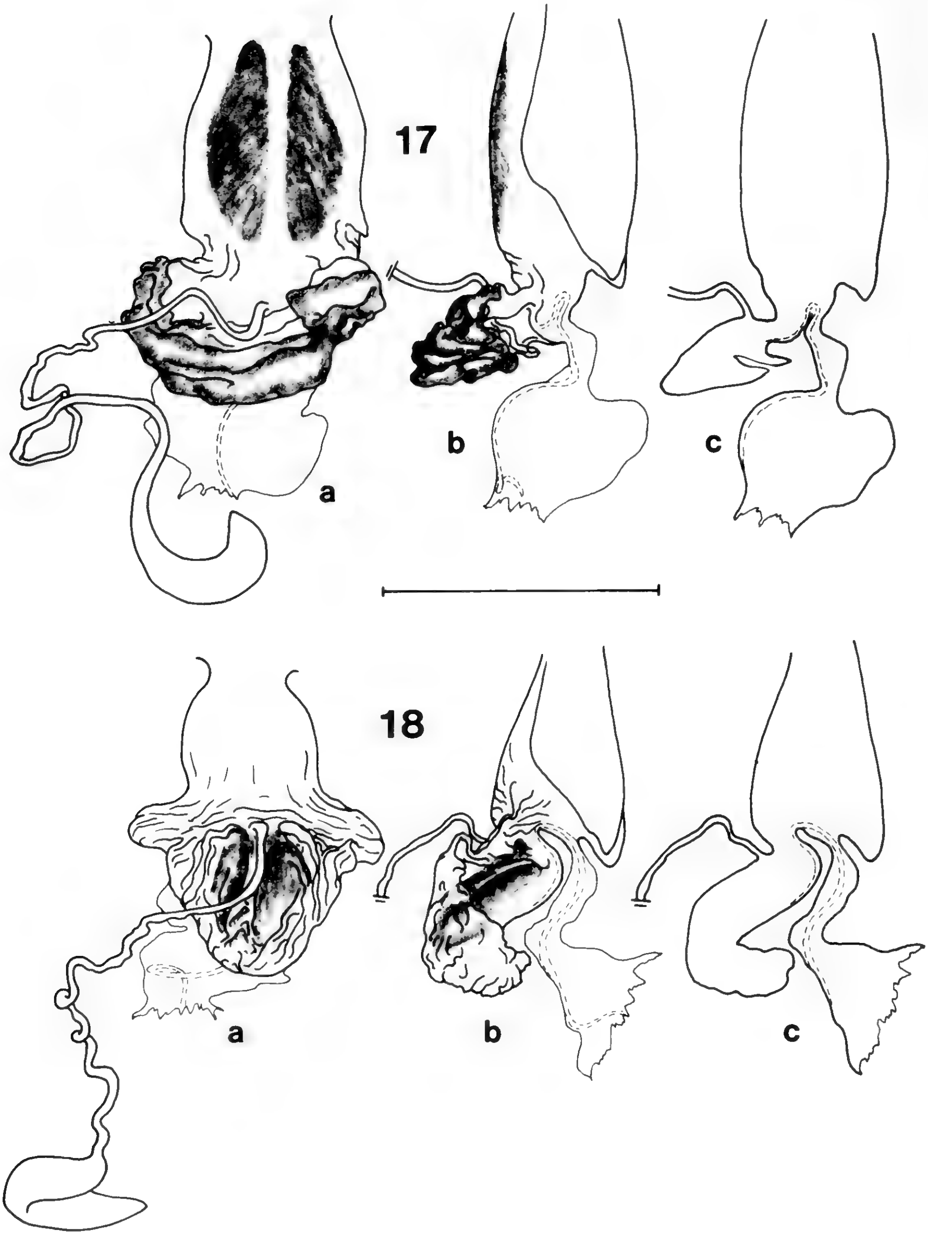


FIGURES 13–16. Median lobe of male genitalia, left lateral aspect; scale line = 1.0 mm. 13. *Nebria turmaduodecima* n.sp. (Upper Caribou Lake, California). 14. *Nebria danmanni* n.sp. (Deception Basin, Washington). 15. *Nebria sonorae* n.sp. (Chipmunk Flat, California). 16. *Nebria meanyi giulianii* n.ssp. (Montgomery Creek, California).

coxa bi- or plurisetose basally; third to fifth visible abdominal sterna each with two or more pairs of posterior paramedial setae; median lobe of male genitalia as in Figure 15; bursa copulatrix of female as in Figure 19.

DERIVATION OF TAXON NAME.—This species is named for Sonora Pass, which is the low point on the main divide of the Sierra Nevada between Tuolumne and Mono counties and is the dominant landmark in the vicinity of the type-locality.

GEOGRAPHICAL DISTRIBUTION.—Figure 21.

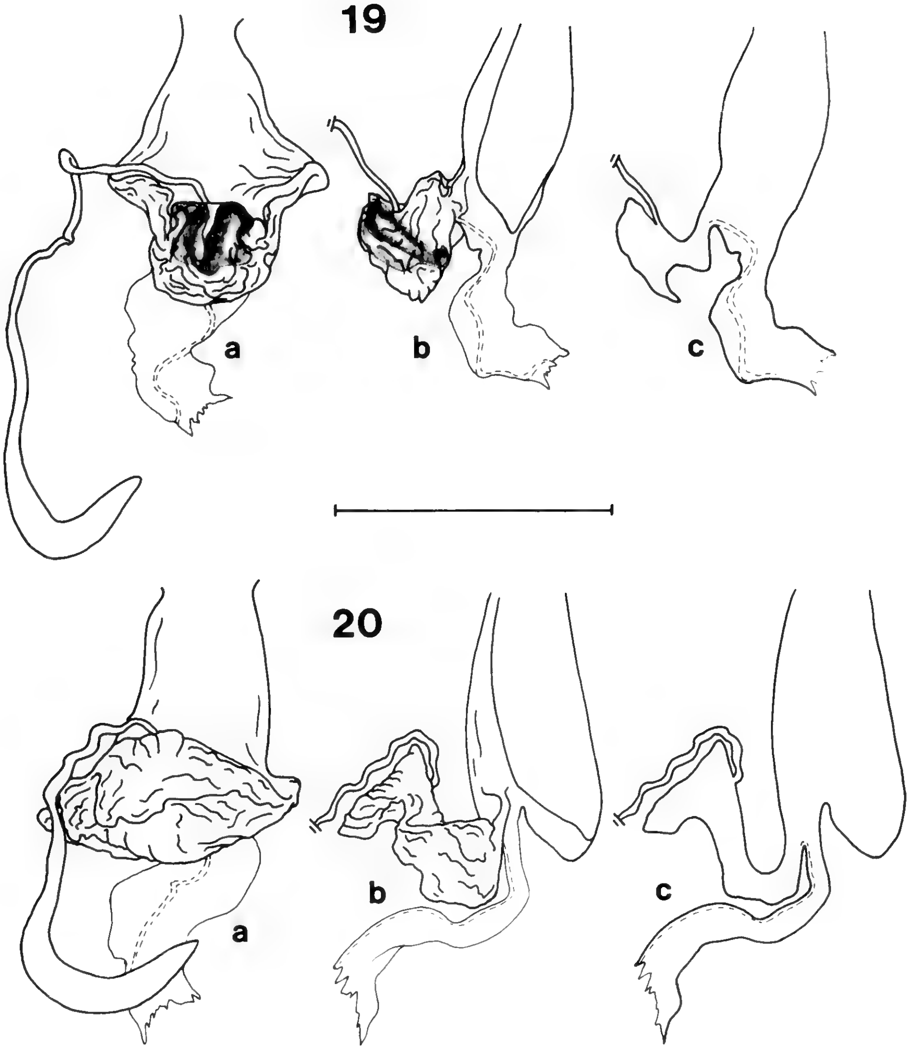


FIGURES 17–18. Bursa copulatrix (*a*, dorsal aspect; *b*, left lateral aspect; *c*, mid-sagittal outline, left lateral aspect); scale line = 1.0 mm. 17. *Nebria turmaduodecima* n.sp. (Upper Caribou Lake, California). 18. *Nebria danmanni* n.sp. (Deception Basin, Washington).

Known only from Chipmunk Flat, Tuolumne County, California, and the stream (southeast of and above the Flat) which drains the northwest flank of Leavitt Peak massif; range probably restricted to that portion of the Sierra Nevada between Sonora Pass and Buckeye Pass. I have studied specimens from the following localities.

United States of America

CALIFORNIA: Tuolumne County, Chipmunk Flat (and stream SE [2440–2680 m]) [June, Aug.] (3; CAS, UCD).



FIGURES 19–20. Bursa copulatrix (*a*, dorsal aspect; *b*, left lateral aspect; *c*, mid-sagittal outline, left lateral aspect); scale line = 1.0 mm. 19. *Nebria sonorae* n.sp. (Chipmunk Flat, California). 20. *Nebria meanyi giulianii* n.ssp. (Milner Creek, California).

Nebria meanyi giulianii, new subspecies

(Figures 4, 8, 12, 16, 20, 21)

HOLOTYPE, a male, in CAS, labelled: "U.S.A., California, Mono County, White Mts., Montgomery Creek, 2380m, 21 June 1980 D. Giuliani collector"/"Holotype Nebria meanyi giulianii Kavanaugh det. D. H. Kavanaugh 1981" [red label]/ "California Academy of Sciences Type No. 13732." PARATYPES: 13 (3 males, 10 females), deposited in CAS.

TYPE-LOCALITY.—Montgomery Creek, 2380 m, Mono County, California.

DIAGNOSTIC COMBINATION.—Size medium, standardized body length of male less than 12.0 mm, of female less than 12.3 mm; head dark, with pair of pale spots present on vertex; elytra with slight to moderate metallic blue, green, or violet reflection; head (Fig. 4) relatively broad, antennal scape short, cylindrical; pronotum (Fig. 4) relatively short, wide, moderately cordate, slightly broad basally, hind angle rectangular, moderately projected posteriorly, midlateral seta present; elytral silhouette subrectangular, broad basally, basal margination (Fig. 8) moderately concave; hindwing (Fig. 12) full-sized; median lobe of male genitalia as in Figure 16; bursa copulatrix of female as in Figure 20; specimen from White Mountains of eastern California (Fig. 21).

Derivation of Taxon Name.—I take great pleasure in naming this subspecies in honor of Derham Giuliani, a naturalist and friend whose long-term interest has been the exploration and biotic inventory of remote and poorly sampled parts of California and Nevada. On one of his recent forays, he discovered populations of this new subspecies.

Geographical Distribution.—Figure 21. Known only from two localities on the western slope of the White Mountains of eastern California; range probably restricted to that mountain chain. I have studied specimens from the following localities.

United States of America

California: Mono County, Milner Creek ([2440 m]) [July] (9; CAS), Montgomery Creek ([2380 m]) [June] (5; CAS).

ACKNOWLEDGMENTS

In addition to those individuals whose contributions I acknowledged in naming three of the taxa described above, I thank Terry L. Erwin and my son, Thomas W. Kavanaugh, for their help and companionship during field work in the Olympic Mountains (Washington) and Sonora Pass area (California), respectively.

LITERATURE CITED

Kavanaugh, D. H. 1979. Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. Proc. Calif. Acad. Sci. 42:87–133.

Figure 21. Map of geographical distributions: *Nebria turmaduodecima* n.sp. = solid circle; *Nebria danmanni* n.sp. = solid triangle; *Nebria sonorae* n.sp. = solid star; *Nebria meanyi giulianii* n.ssp. = solid square.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 18, pp. 443–454, 4 figs. May 14, 1982

DENDROGASTER (CRUSTACEA: ASCOTHORACIDA) FROM CALIFORNIA: SEA-STAR PARASITES COLLECTED BY THE *ALBATROSS*

By
Mark J. Grygier
Scripps Institution of Oceanography, A-008, University of California, San Diego, La Jolla, California 92093

ABSTRACT: Californian specimens of the ascothoracid crustacean genus *Dendrogaster*, discovered by W. K. Fisher in sea-stars collected by the ALBATROSS, are reviewed. *Dendrogaster arbusculus* Fisher, represented by a female and nauplii from *Hippasteria californica* Fisher, is redescribed, with special attention to the female internal anatomy. Also, two new species are described: *D. fisheri* n.sp., represented by two females, from *Pedicellaster magister megalabis* Fisher; and *D. punctata*, represented by females, a male, metanauplii, and ascothoracid larvae, from *Poraniopsis inflata* (Fisher). These are the only ascothoracids so far described from the west coast of the Americas south of Alaska.

INTRODUCTION

Ascothoracida Lacaze-Duthiers, 1880, is often classified (under the name Ascothoracica Gruvel, 1905) as a primitive order of Cirripedia (e.g., Lacaze-Duthiers 1880, 1883; Knipowitsch 1892; Gruvel 1905; Newman et al. 1969), but arguments for its elevation to an independent subclass have also been made (Wagin 1937, 1947, 1976; Grygier 1980b, 1981a). The taxon now comprises about 40 species in 10 genera, all parasites of echinoderms or coelenterates (reviewed by Wagin 1976).

Dendrogaster Knipowitsch, 1890, parasitic in the coelomic cavity of sea-stars (Asteroidea), is the largest genus in the subclass. It includes over 20 species about the world, the taxonomy and biology of which have been studied principally by the Russian worker Wagin (especially 1950, 1954, 1957; summarized 1976). Other workers on this genus have included Knipowitsch (1890, 1891, 1892), Le Roi (1905, 1907), Okada (1925, 1938, 1941), Yosii (1931), Korschelt (1933), Hickman (1959), Achituv (1971), Karande and Oguro (1979, 1981a, 1981b), and Grygier (1981a, 1981b).

Females of *Dendrogaster* have a large, branched mantle (modified carapace) containing gut diverticula, gonads, and a spacious brood chamber. The main body is reduced, only the first antennae and mouth parts being strongly developed. Eggs hatch as nauplii, metanauplii, or bivalved ascothoracid larvae (Wagin 1948, 1954). Larvae remain within the brood chamber until the ascothoracid stage. Males, which also live in the brood chamber, have an ascothoracid larvalike main body with five pairs of natatory appendages and a muscular abdomen terminating in a furca. Their carapace lining is expanded posteriorly into a pair of winglike protrusions containing testes and a branch of the gut (Wagin 1946, 1954).

Dendrogaster arbusculus Fisher, 1911, parasitic in *Hippasteria californica* Fisher, 1905, is the only named ascothoracid from the west coast of the Americas outside Alaska, although I have seen a specimen of *Ascothorax* Djakonov, 1914, from Monterey Bay, and there are two undescribed species of *Dendrogaster* in the Puget Sound region (P. Illg, Univ. of Washington, personal communication). *Dendrogaster arbusculus* is incompletely known; the original description (Fisher 1911) consisted only of the locality of collection, the host sea-star, and a drawing of the holotype in situ. Yosii (1931) presented a schematic diagram of the mantle branching pattern based on Fisher's drawing. This species was included in the genus *Myriocladus* Okada, 1925 (Okada 1925; Yosii 1931; Krüger 1940), which was later synonymized with *Dendrogaster* (Wagin 1950; Hickman 1959).

Fisher (1911, 1928) found two other California sea-stars infested by *Dendrogaster*, *Poraniopsis inflata* (Fisher), 1906, and *Pedicellaster magister megalabis* Fisher, 1928, but he only specified their collection localities. His tentative identification of these parasites as *D. arbusculus* was never confirmed and, as shown below, was mistaken.

METHODS AND MATERIALS

All of Fisher's finds were from sea-stars collected by the U.S. Bureau of Fisheries vessel ALBATROSS off California in 1904; station data are listed below.

Specimen 1, holotype of *Dendrogaster arbusculus*; 5.4 km SSE of Gull Islet, off SE coast of Santa Cruz Island, 1220 m, ALBATROSS sta. 4429, 14:IV:04; host species *Hippasteria californica* (Fisher 1911:237, 404, pl. 111).

Specimen 2, holotype of *Dendrogaster punctata*; 9.9 km NW of Pt. Pinos Lighthouse, Monterey Bay, 118–554 m, ALBATROSS sta. 4471, 14:V:04; host species *Poraniopsis inflata* (Fisher 1911:264).

Specimen 3, paratype fragments of *Dendrogaster punctata*; same station as holotype.

Specimen 4, holotype of *Dendrogaster fisheri*; 25.2 km SSW of Pt. Loma Lighthouse, San Diego, 940–960 m, ALBATROSS sta. 4334, 14:IV:04; host species *Pedicellaster magister megalabis* (Fisher 1928:66).

Specimen 5, paratype of *Dendrogaster fisheri*; 7.4 km SW of Pt. San Pedro, Santa Cruz Island, 817–932 m, ALBATROSS sta. 4427, 9:III:04; host species *Pedicellaster magister megalabis* (Fisher 1928:66).

Dendrogaster-infested sea-stars or isolated specimens of the parasites were obtained from the California Academy of Sciences (CAS) and the National Museum of Natural History (USNM). In cases where a sea-star still contained its parasites, the host was dissected and the specimen of *Dendrogaster* removed. One previously isolated but dried-out mantle fragment was reconditioned in a 10% trisodium phosphate solution overnight.

At least one female of each species was dissected to remove appendages and, in the case of the holotype of *D. arbusculus*, the internal organs. Incisions were made sparingly in each female in a search for males and larvae. A male and several larvae from the species parasitic in *Poraniopsis inflata*, as well as several larvae from *D. arbusculus*, were examined whole in lactic acid; some larvae of each species were dissected. Permanent mounts were made in Turtox CMC-10 with acid fuchsin or in glycerine jelly. Drawings were done with the aid of a camera lucida.

SYSTEMATIC SECTION

Ascothoracida Lacaze-Duthiers, 1880
Dendrogastridae Gruvel, 1905
Dendrogaster Knipowitsch, 1890

Dendrogaster arbusculus Fisher, 1911

(Figures 1 & 2)

Myriocladus arbusculus: OKADA 1925:371.

MATERIAL.—One female, holotype, deposited as CAS 013159.

DIAGNOSIS.—Female large. Middle piece four times as long as main branches; small "extra branch" opposite middle piece. Six complexly ramifying major branches, including four posterior secondary branches and both anterior primary branches. Terminal protuberances conical, scattered. Third article of first antenna with fusion seam, proximodorsal muscle, and dorsal seta. Nauplii about 1 mm long, with setose appendages. Males and ascothoracid larvae unknown.

DESCRIPTION OF FEMALE.—General appearance. Fisher's illustration of the holotype of *D. arbusculus* (1911:pl. 111, fig. 1) accurately portrays the parasite and its position within its host. The mantle is a whitish branched sac extending

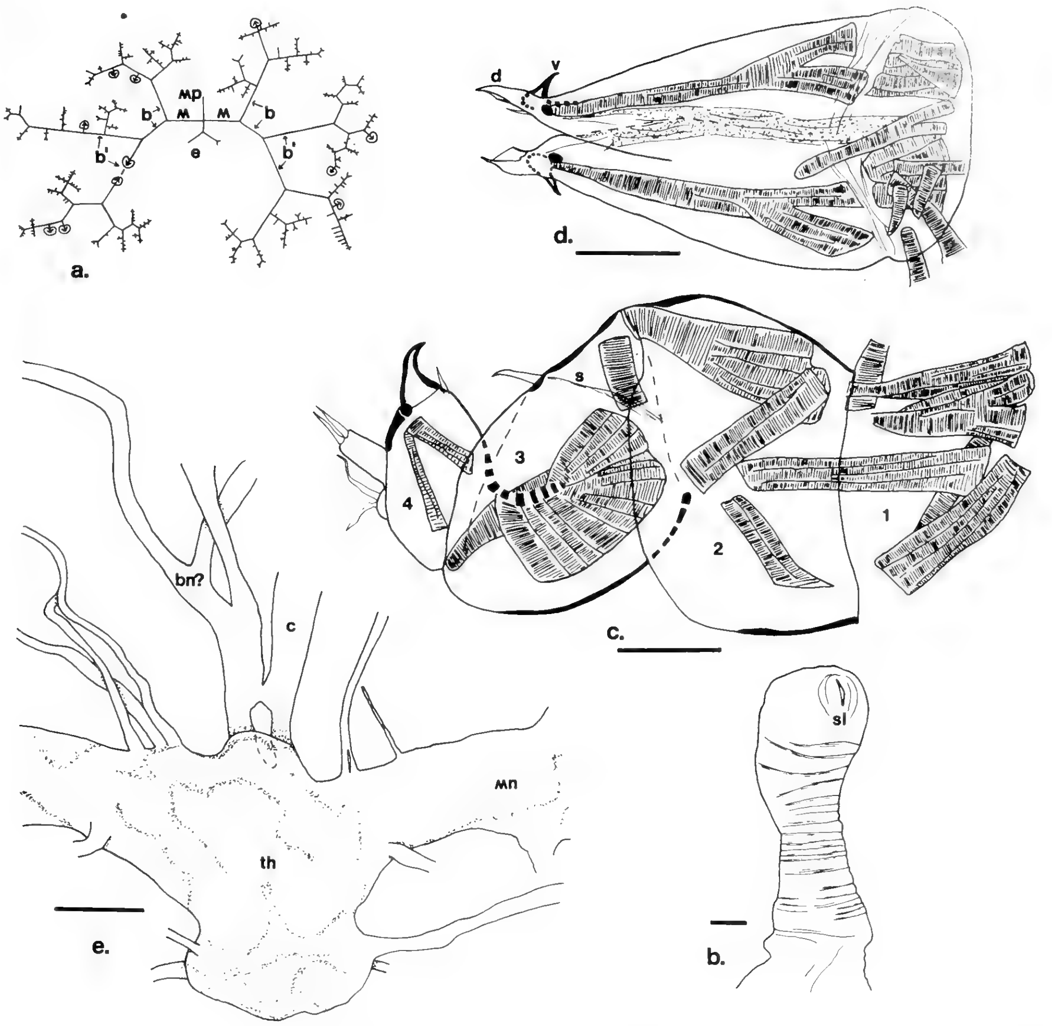


FIGURE 1. *Dendrogaster arbusculus* Fisher; holotype, female. (*a*) Schematic diagram of mantle branching pattern, terminal protuberances omitted, encircled arrows representing broken ends, opposed arrows (lower left) indicating reconstruction (orientation of distal part arbitrary). (*b*) Middle piece, dorsal view. (*c*) First antenna with musculature, articles numbered. (*d*) Second maxillae with musculature, anterior view. (*e*) Thoracic part of nervous system, dorsal view. Explanation: b, primary branches; b', secondary branches; bn?, buccal nerve?; c, circumesophageal connectives; d, distal prong; e, "extra" branch; m, main branches; mp, middle piece; s, fusion seam; sl, distal slit; th, thoracic nerve mass; v, ventral prong. Scale bars 0.1 mm, except 1.0 mm in *b*.

about 50 mm in the preserved state. The branches are constricted at nodes and expanded elsewhere, especially distally. The very thin outer cuticle of the mantle covers a loose network of longitudinal and circular muscle fibers. The focal point of the branching pattern (Fig. 1*a*) is a clavate medial protuberance (middle piece) about 10 mm long with a vertical distal slit (Fig. 1*b*). The musculature of the middle piece is better developed than that of the rest of the mantle; prominent circular muscles overlie longitudinal muscular sheets.

Branching pattern (Fig. 1*a*). The descriptive terminology of the branching pattern is modified from that of Wagin (1950, 1976). A pair of laterally directed main branches arise at the base

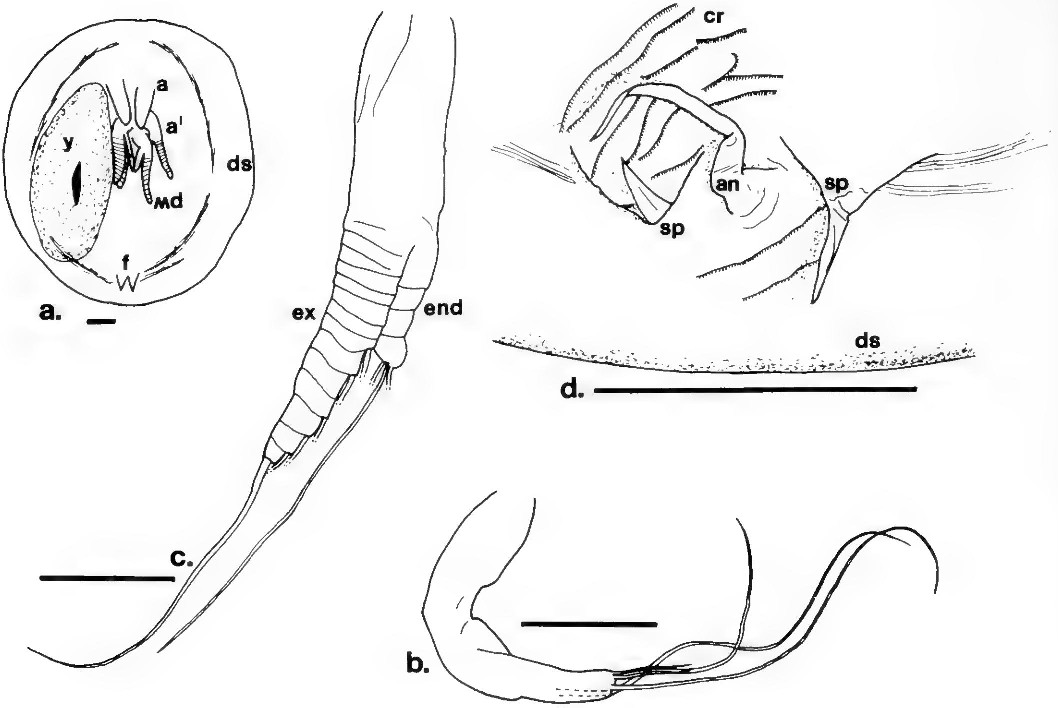


FIGURE 2. *Dendrogaster arbusculus* Fisher; nauplii. (*a*) Nauplius, ventral view, diagrammatic. (*b*) First antenna. (*c*) Second antenna. (*d*) Posterior end including furcal rudiments. Explanation: a, first antenna; a', second antenna; an, anal spine or seta; cr, ctenate ridges; ds, dorsal shield; end, endopod; ex, exopod; f, furca; md, mandible; sp, furcal spines; y, yolk. Scale bars 0.1 mm.

of the middle piece, each about 2.5 mm long. Opposite the middle piece is a short, bifurcate "extra branch." The main branches split into anterior and posterior primary branches, the latter quickly dividing into a pair of large secondary branches on each side. Further ramifications of these six major branches occur by an irregular series of bifurcations and lateral branchings, leading finally to conical terminal protuberances sometimes arranged in loose trefoils.

Internal structure of mantle. The main body, located within the slit at the distal end of the middle piece, is fused to the mantle dorsally and laterally. The subchelate first antennae and piercing-and-sucking oral cone are directed anteriorly. The thorax and abdomen are almost completely reduced, forming a sac around the gut and nervous mass. A pair of large, diaphanous gut diverticula pass posteriorly along the inside of the middle piece, extend into the main branches, and follow the branching of the mantle exactly. The ovaries, attached all along the gut diverticula, are tissue strands or tubules, the lateral follicles of which each contain a developing oocyte (cf. Okada 1941, for description of similar arrangement in another species). The mantle cavity is a brood chamber for eggs and nauplii.

First antennae (Fig. 1*c*). The first antennae are four-segmented and subchelate, 0.7 mm long. The shape of the first article could not be determined; its musculature consists of two dorsal flexors and two ventral extensors of the second article and a long flexor inserted on the proximoventral corner of the third article. The second article is rectangular. A flexor and an extensor muscle run from its proximodorsal corner to the proximal corners of the third article; another flexor runs from its proximoventral side to the proximoventral corner of the third article. The third article is subrectangular, with its distal edge facing somewhat dorsally. A seam indicating the fusion of two articles cuts across the proximodorsal corner; there is a seta near the distal end of the seam and a muscle within the corner set off by it. The fourth article is oval, fitting lengthwise into the distal end of the third. There are two anterior processes, the first a small mound with two setae, the other cylindrical with two setae on the right first antenna, three on the left. There is a seta at the base of the heavy distal claw. Two claw-retracting muscles run from a thickening anterior to the claw (cf. Grygier 1981b); one attaches to the side of the article, the other to its basal apodeme. This apodeme extends far into the third article; a very powerful fan of flexor muscles reaches from it to the ventral and proximal sides of that article. A less powerful extensor muscle runs alongside the flexors from the ventral base of the fourth article to the proximal end of the third.

Oral cone. The oral cone is directed anteriorly. The labrum forming the sheath of the cone is drawn out laterally and ventrally, almost enclosing the mouth parts. The basal part is swollen with the insertions of the buccal pump muscles. The only mouth parts are the harpoon-shaped second maxillae (Fig. 1*d*), which protrude from the cone. They are fused for half their length. The distal prong at the tip of each consists of a thick point and a membranous flange. The ventral hook is bent laterally downwards and is more heavily chitinized than the distal prong. A muscle runs from its base to the base of the mouth part, where it ends at a transverse wrinkle indicating an articulation. There are many short muscles more proximally.

Internal anatomy. The buccal pump is a mass of circular, longitudinal, and radial muscles occupying the bulk of the oral cone. It encloses the chitin-lined esophagus which leads into the midgut, from which the digestive diverticula emerge. In other species of *Dendrogaster*, the gut is blind (Knipowitsch 1892; Le Roi 1907; Okada 1925; Wagin 1954); it was not possible to confirm that this is the case here.

The nervous system (Fig. 1*e*) is highly concentrated in the thorax. A pair of round, medially connected cerebral ganglia lie anterior to the esophagus; though they are said to give off large antennular nerves (Wagin 1954), these were not found. Lateral connectives from the cerebral ganglia pass around the esophagus, giving off a pair of bifurcate buccal (?) nerves. The connectives are linked by a commissure before they enter the anteroventral part of the thoracic nerve mass. From this mass, which is not divided into ganglia, a pair of very large nerves arise laterally to innervate the mantle. Several small nerves arise on each side near their bases, two or three anteriorly and one posterodorsally. Two pairs of fairly large nerves arise laterally from the posterior end of the thoracic mass, one dorsal and one ventral. It is impossible to say what structures all these nerves innervate; no such proliferation of nerves has been described in *Dendrogaster* previously (cf. Wagin 1954).

A pair of large, wrinkled saclike organs were removed with the second maxillae. These may be the maxillary glands, though no ducts could be followed nor openings on the maxillae located.

A cavity within the main body contained a white, friable substance which resembled yolk except for its color. A similar organ has been described in a new Antarctic species of *Dendrogaster*, where it was considered a vitellogenous organ (Grygier 1981b; also see Grygier 1980a). It more likely represents the proximal part of the oviduct.

GAMETES AND LARVAE.—Eggs. Hundreds of eggs were found within the mantle cavity. They are yellow and subspherical, averaging 0.51 mm × 0.45 mm.

Sperm. Patches of sperm cells are attached to membranes within the mantle. Their heads are about 4.2 μm long, 1.7–2.0 μm wide, tapered slightly anteriorly, with a small terminal acrosome. The midpiece is granular and tapers posteriorly for about 6.4 μm. The tail is at least 20.4 μm long and probably much longer. These sperm are similar to those of other species of *Dendrogaster* studied by light microscopy (Le Roi 1907; Okada 1941) and by electron microscopy (Grygier 1981a). If these sperm are not autochthonous but are actually ingested starfish sperm, they should have round heads (Dan 1968), not the observed oblong heads.

MALES.—It is puzzling that no males were found in this female. Nauplii occupied the brood chamber; therefore, fertilization must have taken place. Parthenogenesis has been suggested in *D. murmanensis* Wagin, 1950 (Kluge, unpublished data cited by Wagin 1947), and *D. repertus* Le Roi, nom. nud. (Le Roi, unpublished data cited by Krüger 1920), but since sperm were present, it is unlikely to have been the case here. One possible case of hermaphroditism is reported. Okada (1941) found that the anterior region of the ovary in *D. okadai* (Yosii, 1931) produced spermlike cells rather than ova. He did not explain why he did not consider these true sperm. No obvious testes were found in the present specimen, but internal investigations were minimized to preserve the integrity of the holotype. It is also possible that a dwarf male was lost when the mantle was damaged upon removal from the host.

NAUPLII (Fig. 2).—About 24 nauplii, each about 1.0 mm long and 0.9 mm wide, were found (Fig. 2*a*). The dorsal shield is bowl-shaped, oval in dorsal view, with a broad rim. The main body of the nauplius completely fills the bowl's concavity. It has three pairs of naupliar appendages, a simple labrum, and a rudimentary furca, but no nauplius eye. The first antennae are uniramous and unsegmented, and have three long and two short distal setae (Fig. 2*b*). The second antennae and mandibles are alike (Fig. 2*c*), with an obscurely divided protopod, an exopod formed of about 13 annuli, the last 6 or so each bearing a long seta, and an endopod half as long as the exopod with about four indistinct articles and three setae. The labrum is small, its posterior margin acute. The furca (Fig. 2*d*) consists of a pair of conical mounds, each with a spine at the apex. A long, flexible anal spine arises between and dorsal to them. Between the labrum and furca, more pronounced along the midline and posteriorly, are a number of ctenate cuticular ridges.

AFFINITIES.—The elucidation of interspecific relationships among the species of *Dendrogaster* has so far proved intractable. Okada's (1925) segregation of several species (including *D. arbusculus*) into a new genus, *Myriocladus*, is no longer accepted. Provisional attempts to correlate morphology of the parasites with the phylogeny of their host sea-stars have been unsatisfactory (Yosii 1931; Grygier 1981b).

Wagin (1976) proposed another approach based on his investigations (Wagin 1947, 1948, 1954) of embryonic and larval development in ascothoracids, including species of *Dendrogaster*. He distinguished three kinds of larval development in this genus. *Dendrogaster astropectinis* (Yosii, 1931) and *D. beringensis* Wagin, 1957, hatch from the eggshell as nauplii. Other species hatch as metanauplii, and yet others as ascothoracid larvae. Wagin considered the first variation the most primitive and suggested that the deep bathyal habitat (2000–4000 m) of the two species exhibiting it was the critical factor in its retention. *Dendrogaster arbusculus* hatches as a nauplius that is more perfectly formed than that of *D. astropectinis*, and the present specimen was captured at shallow bathyal depths (1200 m). These facts may not indicate affinities between *D. arbusculus* and either *D. astropectinis* or *D. beringensis*, however, because the presence of a free naupliar stage is a plesiomorphic feature.

Neither of the other two species remotely resembles *D. arbusculus* in its branching patterns. Like *D. arbusculus*, females of *D. astropectinis* have a fusion seam and a proximodorsal muscle in the third article of the first antenna. This conformation, which is also plesiomorphic, is not limited to these two species, however, being found also in *D. iwanowi* Wagin, 1950, *D. tasmaniensis* Hickman, 1959, and both new species described below. The occurrence of a single seta on this article is limited to *D. arbusculus* and one of the new species below. *Dendrogaster ludwigi* Le Roi, 1905, and *D. dogieli* Wagin, 1950, the only other species in the genus with an "extra branch" like *D. arbusculus*, otherwise have unique branching patterns not resembling that of the present species.

Dendrogaster fisheri, new species

(Figure 3)

Dendrogaster cf. *arbusculus:* FISHER 1928:66.

MATERIAL.—Two females. Holotype from ALBATROSS sta. 4334 deposited as USNM 184574; paratype from ALBATROSS sta. 4427 as USNM 184575. Holotype occupied four arms of host, middle piece directed outward in interradius (Fig. 3*a*); paratype occupied only two arms of host.

DIAGNOSIS.—Females small to medium-sized, with four equally developed primary branches. Short middle piece more than twice as long as main branches; short, lobate secondary branches arising alternately from primary branches. Third article of first antenna with fusion seam, proximodorsal muscle, and two or three dorsal setae, one removed from rest. Males, nauplii, and ascothoracid larvae unknown.

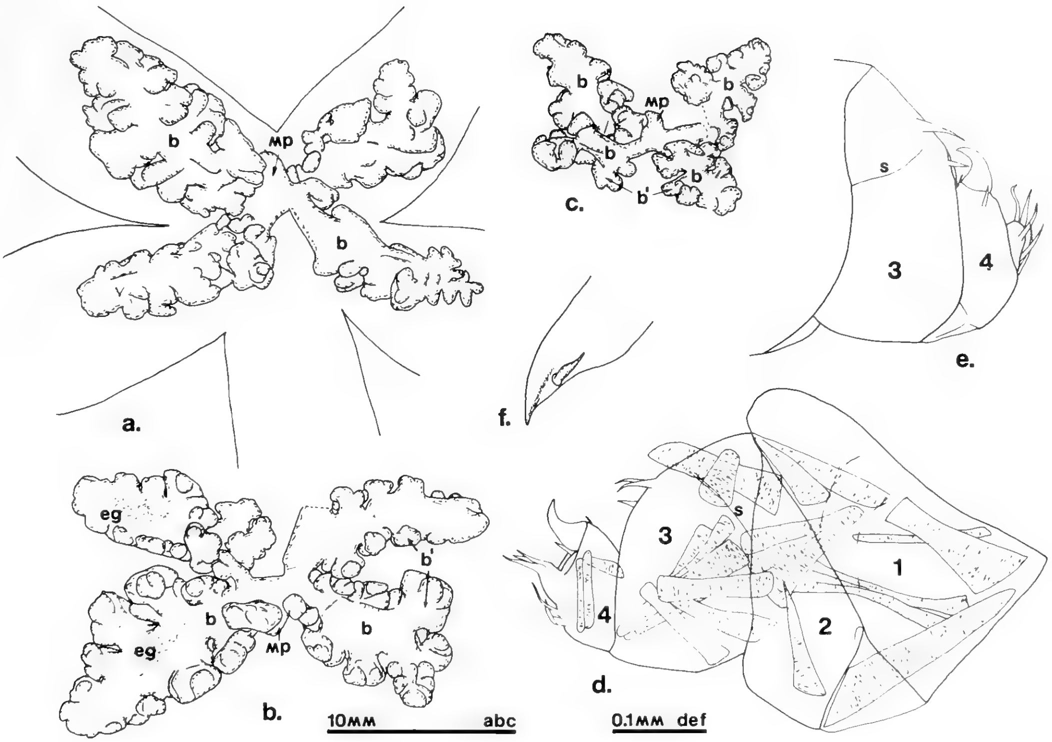


FIGURE 3. *Dendrogaster fisheri,* new species; female. (*a*) Holotype in situ in host sea-star *Pedicellaster magister megalabis* Fisher, dorsal view. (*b*) Holotype, ventral view. (*c*) Paratype, ventral view. (*d*) First antenna of paratype with musculature, articles numbered. (*e*) First antenna of holotype, distal articles (numbered). (*f*) Tip of second maxilla, lateral view. Explanation: b, primary branches; b′, secondary branches; eg, eggs; mp, middle piece; s, fusion seam.

DESCRIPTION.—General appearance. *Dendrogaster fisheri* is of small to medium size, the greatest extent of the branches being 26 mm in the holotype (Fig. 3*a, b*) and 14 mm in the paratype (Fig. 3*c*). The mantle surface is smooth with clearly visible longitudinal muscles. Its color in the preserved state is pale brown to pale yellow. The oral cone and left first antenna of the holotype protruded through the distal slit of the middle piece before dissection, but no part of the paratype's main body was visible externally.

Branching pattern. The middle piece of the holotype is 2 mm long, bluntly conical with a distal slit. The main branches are very short (less than 1 mm), each dividing into a pair of primary branches 9–12 mm long in the holotype, 6–9 mm long in the paratype. The anterior and posterior primary branches are equally developed. Many short secondary branches arise alternately from the anterior and posterior sides of the primary branches, the proximal ones slightly larger than the distal ones, each bearing several blunt terminal protuberances.

First antennae (Fig. 3*d, e*). The four-segmented, subchelate first antennae are massive, 0.5 mm long in the paratype (Fig. 3*d*), larger in the holotype (Fig. 3*e*). The basal article is triangular, attached to the head by its longest side, and with its sharpest apex uppermost; it contains the flexor and extensor muscles of the second article and a flexor muscle of the third article. The second article is rectangular, smaller and shorter than the first, and contains flexor and extensor muscles of the third article. The third article is an irregular quadrilateral higher than long, with a fusion seam across its proximodorsal corner and two or three dorsal setae distal to the seam (one isolated far distally); it contains flexor and extensor muscles of the fourth article and an isolated muscle in the corner delimited by the fusion seam. The fourth, distalmost article is short, almost square, with a distal claw and two claw retractor muscles. It is armed with a small seta lateral to the claw, a process on the distal face with three setae, and a small seta at the base of the claw.

Oral cone. The only obvious mouth parts, the second maxillae, are enclosed in a sheathlike oral cone formed from the labrum. The tips of the second maxillae are bifurcate (Fig. 3*f*); the ventral hook can be bent laterally and posteriorly with respect to the distal prong. The tips are directed away from each other when the mouth parts protrude from the oral cone.

GAMETES AND LARVAE.—In both specimens a large number of eggs about 0.5 mm in diameter distend the primary branches and bend the secondary branches ventrally (Fig. 3*b*). No dwarf males or larvae were found in a cursory search of both specimens.

AFFINITIES.—Fisher (1928) tentatively assigned these specimens to *D. arbusculus*. There is no real similarity, however, since *D. fisheri* has only four major branches with no complicated higher-order branching, a relatively shorter middle piece than *D. arbusculus,* and no "extra branch" opposite the middle piece. At the time of Fisher's publication, only four other species of *Dendrogaster* had been named and the extent of intraspecific variation of branching patterns, still incompletely known (but see Karande and Oguro 1981b), could not be estimated. Since the two available specimens of *D. fisheri* are alike in most respects, including their common host, I am proposing a new species for them. In recognition of his having informed zoologists of the existence of these specimens, I take pleasure in naming the species after W. K. Fisher.

Dendrogaster fisheri superficially resembles young specimens of *D. arctica* Korschelt, 1933, which also have four equal primary branches with lobular side branches (Wagin 1950), but in *D. arctica* the secondary branches are simple, lacking terminal protuberances. The first antenna has no fusion seam or associated muscle, only two setae on the third article, and a single seta proximal to the process on the fourth article (Wagin 1950). *Dendrogaster arctica* inhabits the Bering Sea (Fisher 1930; Wagin 1950) and Hudson Bay (undocumented record on distribution map by Wagin 1970), and parasitizes the sea-star *Leptasterias groenlandica* (Lütken), 1857.

Dendrogaster ludwigi also has four primary branches. The secondary branches, though short, are so densely covered with terminal protuberances that the primary branches are completely obscured, whereas in *D. fisheri* the primary branches are easily discernible. *Dendrogaster ludwigi* lives in shallow water from Japan to Australia (Le Roi 1905, 1907; Yosii 1931; Kenny 1959); its range is unlikely to extend to the east Pacific, especially in waters as deep as *D. fisheri*'s habitat (800–1000 m).

In no other known species of *Dendrogaster* is the mantle constructed around four relatively simple primary branches.

Dendrogaster punctata, new species

(Figure 4)

Dendrogaster cf. *arbusculus:* FISHER 1911:264.

MATERIAL.—One female, holotype, deposited as USNM 184573; several mantle fragments from same host, paratype lot, deposited as CAS 018895.

DIAGNOSIS.—Females medium-sized with complexly branched mantle. Short, cylindrical middle piece little longer than main branches. Primary and secondary branches dichotomous, better developed posteriorly; more distal branches either unbranched and elongate or variously branched, ending in trefoil-shaped clusters of terminal protuberances. Mantle extensively pitted. Third article of first antenna with weak fusion seam, proximodorsal muscle, and dorsal seta. Males with elongate, cylindrical posterior protrusions; testes ribbonlike. Third article of first antenna in males and ascothoracid larvae without proximodorsal muscle, but with two long, bifid setae. Anterior face of fourth article with straplike aesthetasc, seta, and process with three setae. Late metanauplii lacking antennae.

DESCRIPTION OF FEMALE.—General appearance (Fig. 4*a*). The mantle extends 26 mm when the branches are spread out, but in situ the branches are curled and intertwined (fixation artifact?). The mantle is beige and fairly tough in the preserved state. Its surface is uneven, pitted by irregular small depressions (Fig. 4*b*). [The

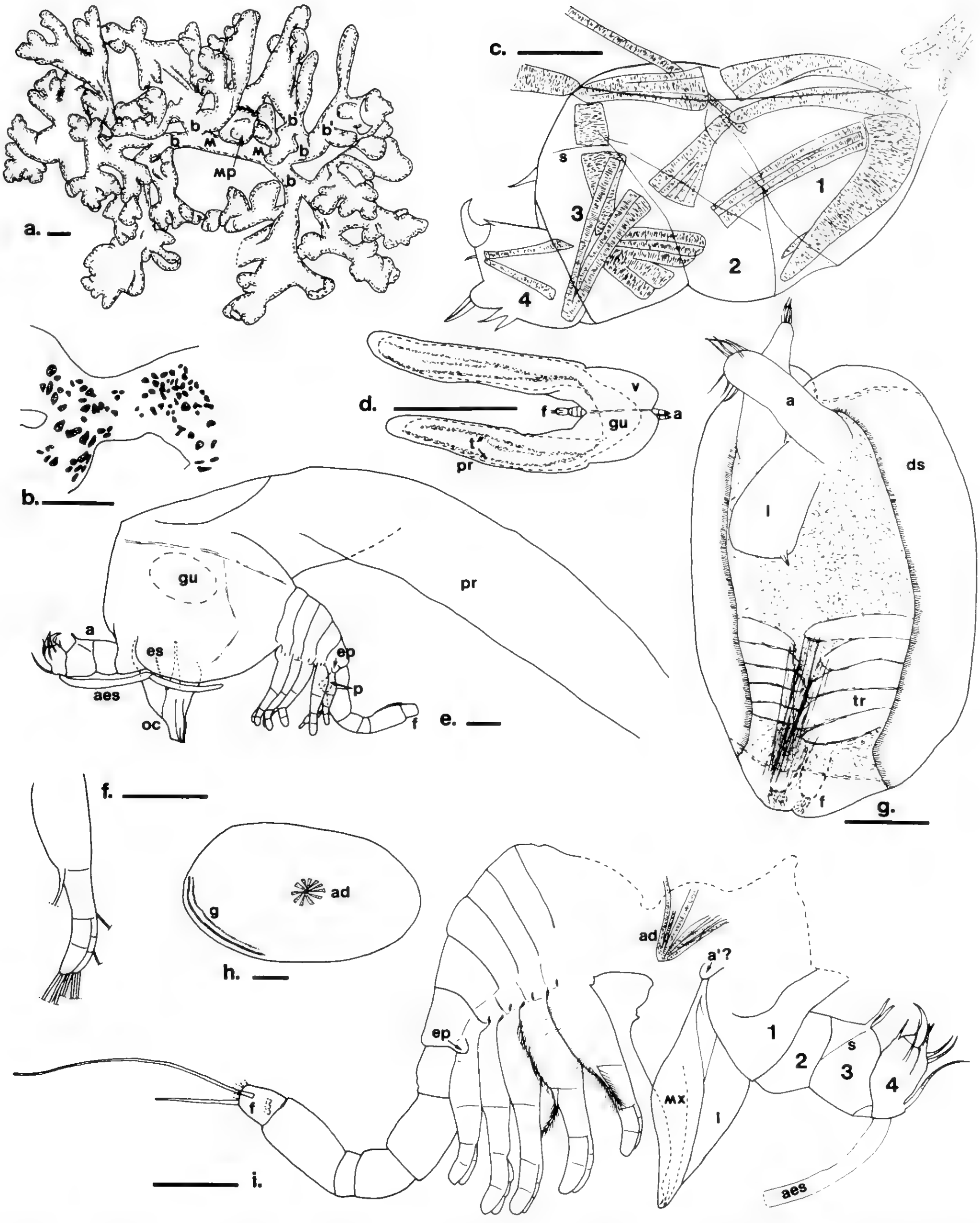


FIGURE 4. *Dendrogaster punctatus*, new species. (*a*) Holotype, female, overall view. (*b*) Detail of same showing depressions in mantle (stippled). (*c*) First antenna of same with musculature, articles numbered. (*d*) Male, dorsal view. (*e*) Male, lateral view, left valve removed, natatory setae omitted on thoracopods and furca. (*f*) Male, second thoracopod with natatory setae. (*g*) Late metanauplius, ventral view. (*h*) Carapace valve of ascothoracid larva, interior view, anterior end right. (*i*) Main body of ascothoracid larva, most thoracopod setation omitted, first antennal articles numbered. Explanation: a, first antenna; a'?, second antenna?; ad, adductor muscle; aes, aesthetasc; b, primary branches; b', secondary branches; ds, dorsal shield; ep, epaulet; es, esophagus; f, furcal rami; g, guard spinules; gu, midgut (diverticula indicated by dashed lines in *d*); l, labrum; m, main branch; mp, middle piece; mx, second maxilla; oc, oral cone; p, penis; pr, posterior protrusion; s, fusion seam; t, testes; tr, thoracopod rudiments; v, carapace valve. Scale bars 1.0 mm in *a*, *b*, *d*; otherwise 0.1 mm.

specific name is derived from this sculpturing (Latin *punctatus*: prick or point).]

Branching pattern. The middle piece is rather thick and 3.5 mm long, slightly longer than the main branches. The latter bifurcate into short primary branches, each of which bifurcates again into secondary branches, the posterior ones ramifying a little more complexly than the anterior ones. Some secondary branches bifurcate or trifurcate; others are palmate. Some tertiary branches are simple elongate lobes; usually, though, higher-order branches end in terminal protuberances arranged in trefoils.

First antennae (Fig. 4*c*). The first antennae are four-segmented and subchelate. The dorsal part of the triangular first article overlaps part of the tall, rectangular second article. The third article is a rounded quadrilateral with a faint fold indicating a fusion seam, a muscle in the corner so delimited, and one large dorsal seta. The fourth article is rhombic with a strong distal claw. Its anterior face is armed, progressively more distally, with two setae, a process with two or three terminal setae, and a smaller seta arising from the side of the article. There is a small seta near the base of the claw. The musculature is similar to that described in *D. arbusculus* and *D. fisheri*.

Oral cone. The sheath of the oral cone is formed from the expanded labrum. The mouth parts were not examined.

Description of Female Fragments.—It is not possible to determine how the several mantle fragments found together with the holotype fit together to form one or more complete specimens, especially since no middle pieces were among them. Two small fragments may be from a single specimen similar to the holotype. Two others may be from a larger specimen with fewer terminal protuberances in trefoils than the holotype and a greater proportion of unbranched, elongate higher-order branches. All fragments had pitted surfaces like the holotype.

Description of Male.—General appearance (Fig. 4*d*, *e*). The single dwarf male found in one of the female mantle fragments is bivalved with a cylindrical protrusion arising posteriorly from each valve. The valves are about 0.63 mm long and are held open for a total width of 0.70 mm. One posterior protrusion is 1.6 mm long, the other 1.4 mm. A midgut diverticulum partially enveloped by longitudinal strips of testicular tissue reaches nearly to the end of each protrusion (Fig. 4*d*). The main body, suspended beneath the valves, has four-segmented, subchelate first antennae, an oral cone, five thoracomeres with natatory limbs, and a five-segmented abdomen terminating in a pair of furcal rami (Fig. 4*e*).

First antennae (Fig. 4*e*). The first antennae are massive pincers protruding from the carapace. The first, triangular article is the largest; the second and third are rectangular, the latter with a proximodorsal fusion seam and a pair of large terminally bifid setae. The fourth article is smaller than the others and bears a distal claw opposing the two setae on the third article. A straplike sensory aesthetasc almost twice as long as the first antenna arises from the ventroproximal corner. Distal to this on the anterior face is a large seta and, farther distally, a fixed process bearing three setae. Two long setae flank the claw, and a third arises at its base. All these setae narrow abruptly to a sharp point. Little can be made of the musculature, but there is no muscle in the part of the third article delimited by the fusion seam.

Oral cone (Fig. 4*e*). The oral cone is narrow. The labral margins do not meet posteriorly. The distal and posterior prongs of the second maxillae, the only mouth parts, are strongly chitinized.

Thorax. The oral cone and first pair of thoracopods are widely separated (Fig. 4*e*). A pair of ventrolateral flanges extend from the thoracopods to the first antennae, partly overlapping the oral cone. The last thoracomere has a small posterolateral epaulet (Fig. 4*e*). The thoracopods consist of a coxa, a basis, a triarticulate endopod (biarticulate in the fifth pair), and a biarticulate exopod (Fig. 4*f*). The coxae of the first two pairs each bear a large lateral seta; the first four pairs have a medial seta on the basis and their endopods have one seta on the second article and three terminal setae. All the exopods terminate in three setae.

Abdomen. There is a short, distinctly bilobed penis rudiment on the venter of the first abdominal segment (Fig. 4*e*). The furcal rami are almost square with four long medial setae, three arising basally, the fourth distally near the dorsal margin. Of the four terminal setae, the most ventral is less than half the length of the others.

Description of Larvae.—Metanauplii (Fig. 4*g*). All the mantle fragments contained numerous late metanauplii about 0.55 mm long and 0.35 mm wide. The dorsal shield is folded ventrally at the sides and has a pronounced anterior indentation, presaging the bivalved carapace of the ascothoracid larva. The first antennal rudiments are cylindrical with several short terminal setae. Eyes and second antennae are lacking. A pair of stylets (second maxillae?) protrude from beneath the large labrum. No other mouth parts are visible. There are five pairs of stubby thoracopod rudiments bearing setae, as well as a pair of unerupted furcal rami with numerous short distal setae.

Ascothoracid larvae (Fig. 4*h*, *i*). These larvae are very similar to the male except that they lack posterior protrusions. The carapace valves (Fig. 4*h*) are about 0.60 mm long and 0.35 mm high. The posteroventral margin of the inner cuticle is lined with two rows of guard spinules. On the main body (Fig. 4*i*), small lobes posterior to the first antennae may be vestiges of second antennae (Okada 1938; Hickman 1959). The oral cone and thoracopods are not as far removed from each other as they are in the male, but a space remains corresponding to the lost first pair of thoracopods. The coxae of the first two pairs of developed thoracopods are armed externally with a fringe of fine hairs and a seta. Other details of setation are unclear, but are probably similar to those in the male. The main bodies of the ascothoracid larvae and males are alike in all other respects.

AFFINITIES.—Fisher (1911) suggested that these specimens belonged to *D. arbusculus*. The complexity of the branching pattern is comparable, but numerous differences argue against this identification. The mantle of the holotype of *D. arbusculus* is much more delicate than that of *D. punctata* and lacks depressions. The middle piece is relatively much shorter in *D. punctata*, which also lacks an "extra branch" opposite the middle piece. The terminal protuberances are well expressed and rounded in *D. punctata*, but are less pronounced in the other species. The third article of the first antenna is identically armed in both species, but the two proximal setae on the fourth article are on a mound in *D. arbusculus*, not in *D. punctata*. The metanauplii and ascothoracid larvae of *D. punctata* are only about half the size of the nauplii of *D. arbusculus*.

Four other species of *Dendrogaster* have terminal protuberances arranged in trefoils. *Dendrogaster rimskykorsakowi* Wagin, 1950, is not complexly branched and the clusters of terminal protuberances are widely spaced (Wagin 1950). *Dendrogaster okadai* has oppositely pinnate higher-order branches (Yosii 1931), and *D. ludwigi* does not branch beyond the tertiary order. The new Antarctic species agrees with *D. punctata* in having several dichotomies followed by trichotomies in the higher branching orders, but it is much more robust than *D. punctata* and has very distinctive first antennae (Grygier 1980a, 1981b).

The metanauplii of *D. punctata* are peculiar in lacking rudiments of the second antennae and the first pair of thoracopods (possibly also lacking mandibles and first maxillae, but these mouth parts may be hidden under the labrum). Wagin (1954, 1976) reported the presence, albeit in reduced form, of all these appendages through the metanaupliar stages in several other species of *Dendrogaster*, although the first thoracopods were always lost in the molt to the ascothoracid larva. He may have been conservative in describing only three ontogenetic sequences among the species of this genus.

Among ascothoracid larvae and males, the long bifid setae on the third article of the first antennae are unique to *D. punctata*. In sum, this species seems to have no known close relatives elsewhere in the genus.

ACKNOWLEDGMENTS

I extend thanks to Mr. Dustin D. Chivers (CAS) and Dr. David Pawson (USNM) for locating the specimens of *Dendrogaster* discussed in this paper, Dr. Paul Illg (University of Washington) for enlightening personal discussions of his own work on this genus, and Dr. William A. Newman (Scripps Institution of Oceanography) for allotting me space in his laboratory and criticizing earlier drafts of this paper. This work, a Contribution of Scripps Institution of Oceanography, new series, was done during the tenure of an NSF Graduate Fellowship and was partly supported by NSF Grant DEB78-15052.

LITERATURE CITED

ACHITUV, Y. 1971. *Dendrogaster asterinae* n. sp., an ascothoracid (Cirripedia) parasite of the starfish *Asterina burtoni* of the Gulf of Elat. Crustaceana 21:1–5.

DAN, K. 1968. Echinoderma (Part 3, Asteroidea). Pp. 303–

308 *in* Kumé, M. and Dan, K., eds., Invertebrate Embryology. NOLIT Publishing House, Belgrade.

Fisher, W. K. 1911. Asteroidea of the North Pacific and adjacent waters. Part 1: Phanerozonia and Spinulosa. U.S. Natl. Mus. Bull. 76(1):1–419.

———. 1928. Asteroidea of the North Pacific and adjacent waters. Part 2: Forcipulata (part). U.S. Natl. Mus. Bull. 76(2):1–245.

———. 1930. Asteroidea of the North Pacific and adjacent waters. Part 3: Forcipulata (concluded). U.S. Natl. Mus. Bull. 76(3):1–356.

Gruvel, A. 1905. Monographie des Cirrhipèdes ou Thecostracés. Masson et Cie, Editeurs, Paris (reprinted 1965, A. Asher & Co., Amsterdam). 472 p.

Grygier, M. J. 1980a. A representative of the genus *Dendrogaster* (Cirripedia: Ascothoracica) parasitic in an Antarctic starfish. Eos Trans. Am. Geophys. Union 61(16):174 [Abstr.].

———. 1980b. Comparative spermatology of Ascothoracica (Crustacea: Maxillopoda) and its phylogenetic implications. Am. Zool. 20(4):815 [Abstr. 450].

———. 1981a. Sperm of the ascothoracican parasite *Dendrogaster*, the most primitive known in Crustacea. Int. J. Invertebr. Reprod. 3:65–73.

———. 1981b. A representative of the genus *Dendrogaster* (Cirripedia: Ascothoracica) parasitic in an Antarctic starfish. Antarct. Res. Ser. 32(1):1–15.

Hickman, J. L. 1959. *Dendrogaster tasmaniensis* sp. nov. (Ascothoracida) from the sea-star *Allostichaster polyplax* (Müller and Troschel). Parasitology 49:316–329.

Karande, A. A., and C. Oguro. 1979. Some observations on the larvae of ascothoracid parasites in asteroids. Zool. Mag. 88(4):435 [Abstr.].

———, and ———. 1981a. Larvae of *Myriocladus astropectinis* (Yosii 1931) reared under laboratory conditions. Proc. Indian Acad. Sci. Anim. Sci. 90(1):23–31.

———, and ———. 1981b. Comments on taxonomic characters of *Myriocladus astropectinis* Yosii, 1931 (Ascothoracica). Crustaceana 41(1):108–110.

Kenny, R. 1959. A new Australian record of an ascothoracid parasite. Austral. J. Sci. 21:221.

Knipowitsch, N. M. 1890. [*Dendrogaster astericola* n. gen. et sp., a new form of parasitic Cirripedia of the group Ascothoracida.] [In Russian.] Vestnik Estestvoispyt. 8 [Not seen.].

———. 1891. *Dendrogaster astericola* nov. g. et sp., eine neue Form aus der Gruppe Ascothoracida. Biol. Centralbl. 10:707–711.

———. 1892. Beiträge zur Kenntniss der Gruppe Ascothoracida. [In Russian with German summary.] Tr. Petrogr. O-va. Estestvoispyt. 23(2):1–155.

Korschelt, E. 1933. Über zwei parasitäre Cirripedien, *Chelonibia* und *Dendrogaster*, nebst Angaben über die Beziehungen der Balanomorphen zu ihrer Unterlage. Zool. Jahrb. Abt. Syst. Oekel. Geogr. Tiere 64(1):1–39.

Krüger, P. 1920. Studien an Cirripedien. Indukt. Abstammungs-. Vererbungsl. 24(2):105–158.

———. 1940. Ascothoracida. Bronns Klassen und Ordnungen des Teirreichs, Band 5, Abt. 1, Buch 3, Teil 4:1–46.

Lacaze-Duthiers, H. de. 1880. Histoire de la *Laura gerardiae* type nouveau de crustacé parasite. Arch. Zool. Exp. Gén. 8:537–581.

———. 1883. Histoire de la *Laura gerardiae* type nouveau de crustacé parasite. Mém. Acad. Sci. Inst. France 42(2):1–160.

Le Roi, O. 1905. Zwei neue parasitische Cirripedien aus der Gruppe der Ascothoracida. Zool Anz. 29:399–401.

———. 1907. *Dendrogaster arborescens* und *Dendrogaster ludwigi*, zwei entoparasitische Ascothoraciden. Z. Wiss. Zool. 86(1):100–133.

Newman, W. A., Zullo, V. A., and Withers, T. H. 1969. Cirripedia. Pp. R206–R295 *in* Moore, R. C., ed., Treatise on Invertebrate Paleontology, Part R (Arthropoda 4), Book 1.

Okada, Y. K. 1925. Contribution à l'étude des cirripèdes ascothoraciques. 1. Note sur le *Dendrogaster arborescens* Le Roi; établissement d'un nouveau genre. Bull. Mus. Nat. Hist. Nat. 31:364–371.

———. 1938. Les cirripèdes ascothoraciques. Trav. St. Zool. Wimereux 13:489–514.

———. 1941. Sur la construction particulière de l'organe génital femelle de *Myriocladus* et la différentiation des cellules sexuelles. Fac. Sci. Imp. Univ. Tokyo Sect. IV Zool. 5(3):249–263.

Wagin, V. L. [spelled Vagin]. 1937. Die Stellung der Ascothoracida ord. nov. (Cirripedia Ascothoracica Gruvel 1905) im System der Entomostraca. C. R. (Dokl.) Acad. Sci. URSS 15(5):273–278.

——— [spelled Vaghin]. 1946. On males of Dendrogasteridae (Ascothoracida, Entomostraca). C. R. (Dokl.) Acad. Sci. URSS 52(3):273–276.

———. 1947. *Ascothorax ophioctenis* and the position of Ascothoracida Wagin in the system of the Entomostraca. Acta Zool. (Stockh.) 27 [dated 1946]:155–267.

———. 1948. [On types of larval development in Dendrogasteridae (Ascothoracida, Entomostraca).] [In Russian.] Dokl. Akad. Nauk SSSR 59(2):387–390.

———. 1950. [On new parasitic crustaceans of the family Dendrogasteridae (order Ascothoracida).] [In Russian.] Tr. Leningr. O-va. Estestvoispyt. 70(4):3–89.

———. 1954. [On structure, larval development, and metamorphosis in Dendrogasteridae (parasitic crustaceans of the order Ascothoracida).] [In Russian.] Uchen. Zap. Leningr. Gos. Univ. 35(172):42–89.

———. 1957. Dendrogasteridae (Entomostraca, Ascothoracida) aus den Asteroidea der Beringsee. [In Russian with German summary.] Tr. Leningr. O-va. Estestvoispyt. 73(4):58–63.

———. 1970. [Dispersal routes and phylogeny of Ascothoracida.] [In Russian.] Pp. 153–163 *in* [Questions on Evolutionary Morphology and Biocenology]. Kazan University Press, Kazan.

———. 1976. [Ascothoracida.] [In Russian.] Kazan University Press, Kazan. 141 p.

Yosii, N. 1931. Note on *Myriocladus*. J. Fac. Sci. Imp. Univ. Tokyo Sect. IV Zool. 2:337–349.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 19, pp. 455–496, 74 figs., 22 tables May 14, 1982

SMALL TERRESTRIAL GROUND-BEETLES OF CENTRAL AMERICA (CARABIDAE: BEMBIDIINA AND ANILLINA)

By
Terry L. Erwin
Department of Entomology, Smithsonian Institution,
Washington, D.C. 20560

ABSTRACT: This paper provides a synopsis of the tribe Bembidiini with an overview of the three included subtribes, Bembidiina, Tachyina, and Anillina for Central America. Anillina is thought to be a polyphyletic grade derived from genus *Paratachys* of the Tachyina, but no formal classificatory action on this hypothesis is taken. Based on structural characters, *Horologion*, previously classified as Psydrini or Trechini, probably also belongs to this grade. Thirteen new species of *Bembidion* are described from the following type-localities: *purulha*, 22.0 km south of Purulha, Baja Verapaz, Guatemala; *lavernae*, Cerro Buenavista, San José Province, Costa Rica; *quetzal*, 20.0 km west of San Pedro Sacatepéquez at Río Nahuala, Quezaltenango, Guatemala; *diabola*, Volcán Irazú, Cartago Province, Costa Rica; *edwardsi*, Cerro Buenavista, San José Province, Costa Rica; *aeger*, Cerro de la Muerte, Cartago Province, Costa Rica; *chiriqui*, 8.0 km west of Boquete, Chiriquí Province, Panama; *nahuala*, 27.0 km northwest of San Marcos, San Marcos, Guatemala; *franiae*, 4.8 km east of San Mateo Ixtatán, Huehuetenango, Guatemala; *cortes*, La Lima, Cortés, Honduras; *armuelles*, Puerto Armuelles, Chiriquí Province, Panama; *barrensis*, Barro Colorado Island; *ixtatan*, 4.8 km east of San Mateo Ixtatán, Huehuetenango, Guatemala. Four new species of *Geocharidius* are described from the following type-localities: *romeoi*, 13.0 km south of Purulha, Baja Verapaz, Guatemala; *gimlii*, 7.7 km south of San Juan Ixcoy, Huehuetenango, Guatemala; *phineus*, 1.6 km south of Pantin, Baja Verapaz, Guatemala; *tagliantii*, Totonicapán, Totonicapán, Guatemala. The 22 *Bembidion* species presently known from Central America are arrayed in nine species groups. Corresponding groups for the five known *Geocharidius* species are not used because of the small size of the fauna and their questionable relationships with poorly known northern taxa. Distribution and relationships are discussed in general, but detailed analysis is deferred until species-group taxonomy is undertaken on a broader geographic scale. Notes are provided on natural history and distribution for each species; dot maps illustrate the known range of each taxon.

INTRODUCTION

Nearly 100 years have passed since the last comprehensive paper on Central American *Bembidion* was produced by H. W. Bates. Darlington (1934) described a single species. Other than these two contributions, the genus has received no taxonomic attention for Central America. Presently, 22 species are known from the area, an increase of 17 since the time of Bates's papers. The anilline genus *Geocharidius* was discussed more recently by Taglianti (1973), but his coverage did not add new species for Central America. Presently, five species are known from the area, an increase of four since Bates's contributions to *Biologia Centrali-Americana* (Bates 1882, 1884). It therefore can be assumed that after nearly 100 years the *Bembidion* fauna of Central America (defined here as the mainland and coastal islands from Guatemala to Panama) is still not completely known; the anilline fauna is essentially untouched, probably a result of their living in deep soil humus, thus hard to collect except by special means. The tachyine fauna, here discussed at the generic level only, is huge (Erwin 1974b) and is presently under revision (e.g., Erwin 1973, 1974a, 1975, 1977).

In order to provide data for a series of studies now underway by D. H. Kavanaugh and me on the genus *Bembidion* (Erwin and Kavanaugh 1980, 1981), I am publishing here an extract from my "Ground Beetles of Central America" in advance of the volume in which it belongs. The present study is a faunal documentation which will provide data for future analyses. Comments pertaining to biogeography are given below, but since the Central American bembidiine fauna represents the "tail-ends" of more northernly or southernly distributed groups, phylogenetic and detailed biogeographic analyses will be discussed elsewhere (e.g., Erwin and Kavanaugh 1981).

MATERIALS

This paper is based on examinations of 1002 specimens of *Bembidion* and 44 specimens of *Geocharidius* from Central America, as well as numerous specimens of other Bembidiini from other parts of the world. Following is a list of depositories for these materials; acronyms based on Erwin (1970) are given preceding each entry: CAS—California Academy of Sciences, San Francisco, California 94118, D. H. Kavanaugh; MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts, M. Thayer, A. Newton; MNHP—Museu National d'Histoire Naturelle, Paris, H. Perrin, J. Menier; UASM—Strickland Museum, University of Alberta, Edmonton, Canada, G. E. Ball; BMNH—British Museum (Natural History), London, P. Hammond, M. Bacchus; HPST—Canal Zone, Henry P. Stockwell; AMNH—American Museum of Natural History, New York, L. Herman; FMNH—Field Museum of Natural History, Chicago, H. Dybas; FDAG—Florida Department of Agriculture Insect Collection, Gainesville, Florida, R. Woodruff; UMAA—University of Michigan, Ann Arbor, R. D. Ward; UAIC—University of Arkansas, Fayetteville, R. T. Allen; GRNO—Milwaukee Public Museum, Wisconsin, G. R. Noonan; JNEG—78 Versailles, 9, B^{b} De Lesseps, France, J. Nègre.

METHODS

General procedural methods are as I used before (Erwin 1970, 1973, 1974a, 1975; Erwin and Kavanaugh 1981). Measures for various body parts are coded as follows and are presented in the species descriptions as single specimen measures, if that is all I saw, or ranges based on the smallest and largest of all specimens studied—all specimens were measured with an electronic measuring device (Erwin 1978) and measures are presented in millimeters. *ABL* = apparent body length, that length used by most previous authors as total length as measured by holding up a ruler alongside the specimen (see Erwin and Kavanaugh 1981). *SBL* = standardized body length, that length introduced by Ball (1972) and modified by Kavanaugh (1979), and equal here to the sum of LH, LP, and LE. *TW* = total width across the widest portion of the elytra, actually measured as the left elytron (WE) and doubled to obtain value. *LH* = length of head from front edge of clypeus to base of head at point of cervical constriction and taken along midline. *LP* = length of pronotum from base to apex along midline. *LE* = length of elytron, longest one, along suture from apex of scutellum to apex of sutural projection. *WE* = width of elytron at widest portion. All label, specimen measurement, and field data about specimens are computerized (L. J. M. Erwin 1976), and these records formed the base for study and analysis. Data concerning material examined are presented in tables and maps; tables summarize data deduced from specimen labels, however, localities are presented as latitude and longitude except in the case of types where place names are also used. Elevations are given in meters even though specimen labels may have them in English units; occasionally, specimen labels give imprecise altitudinal data or none at all, thus, in these cases tables include the abbreviation 'ca.' to indicate approximate altitude derived from topographic maps. Chaetotaxy reference follows that of Erwin (1974a) and the term 'interneur,' used for the structure between elytral intervals, is described in Erwin (1974a). Microsculpture micrographs were made only for species where sufficient study material allowed coating of body parts.

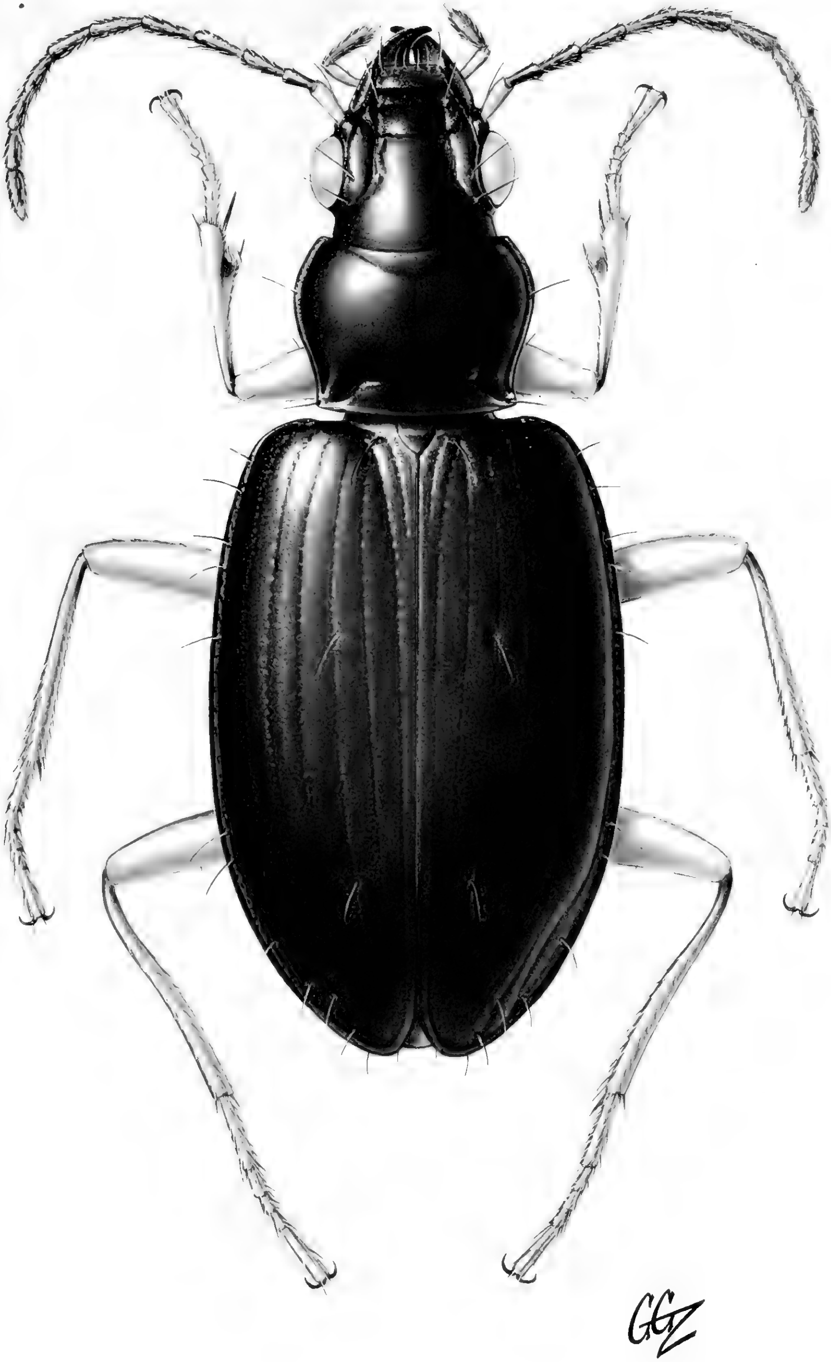


FIGURE 1. Habitus of *Bembidion vernale* Bates, dorsal aspect, female from Cerro Punta, Chiriquí, Panama.

TRIBE BEMBIDIINI

The bembidiines are a diverse lot of mostly small beetles distributed worldwide and whose primary apotypic feature is the subulate apical palpomere. The tribe is represented by three subtribes in Central America: Bembidiina, Tachyina, and Anillina.

Bembidiinas are much larger, as a rule, than members of the other subtribes, often are colorful, almost always have large eyes, and do not possess an elytral recurrent groove (however, the apex of interneur 5 is often depressed). *Bembidion* includes hundreds, if not thousands, of species worldwide, but most of these are distributed in the Holarctic and South Temperate regions. In Central America, there are only 22 species known, but undoubtedly some more-alticolous species will be discovered with additional collecting in remote upland areas. These beetles live in such diverse habitats as sea beaches and mountain tops above timber line. They are particularly common and diverse along gravelly streams and rivers and in upland forest above 2000 meters. The major taxonomic problem remaining in this genus is to segregate and define its components on a worldwide basis. Netolitzky (1942, 1943) and Lindroth (1963) provided an excellent foundation with which to start; D. H. Kavanaugh and I have taken up the task. The former authors have shown beyond doubt that male genitalic characteristics are of great value in several Holarctic groups for determining relationships. Erwin and Kavanaugh (1981) showed the same to be true for the female reproductive system. Reclassification of this complex and diverse genus will require a world overview, reevaluation of character systems, and close scrutiny of geographic ranges. Much more collecting will need to be done, especially in the western United States, South American Andes, and Palearctic Asia. The larval stages of many groups of Bembidiina are known (see Lindroth 1963); these will aid systematic studies because taxonomically useful characters are present (Erwin 1975).

Tachyinas are small to medium-sized bembidiines with much greater diversity and richness than bembidiinas. Tachyinas almost always have eyes, many are colorful (some metallic), and most possess a recurrent groove near the elytral apex. Most Central American genera are composed of numerous species. This subtribe constitutes one of the two largest groups of the Central American fauna (the other being Agonina, *Platynus*, and its relatives). Tachyina beetles live in diverse habitats, from intertidal zones to rain forest canopy; they are extremely diverse along riparian systems, and some have adapted to living with ants. They are a lowland faunal component and have not become true alticoles as have *Bembidion* and other carabid groups such as the trechines, indicating that they are a later taxon pulse element of the fauna than are the Bembidiina (Erwin 1979, 1981; Erwin and Adis 1982). Erwin (1973, 1974a, 1974b, 1975) has begun a world revisionary study of this group of beetles. As with bembidiinas, reclassification of this complex and diverse tribe will require a world overview, reevaluation of character systems, and close scrutiny of geographic ranges. Much more collecting will need to be done, especially in the tropics. The larval stages of Tachyina are mostly unknown (see Erwin 1975).

Anillinas are minute, apterous, blind beetles which inhabit deep humus in upland forests and are also found in caves and fissures. Difficulty in finding these beetles prevents accumulation of enough material to adequately revise most genera. Undoubtedly, more species will be discovered in upland forests by use of special collecting techniques (e.g., Berlese funnel). Anillinas, as currently classified, are easily recognized by their small size, pale coloration, and lack of eyes. Some cave-dwelling Ardistomina (Scaritini) have also lost eyes, but remain easily recognized by body shape (pedunculate). Some trechines in Middle America have also adapted to caves and become blind, but they can be immediately recognized by their long apical palpomeres and sulcate head. There are a few wingless, pale, nearly blind *Mioptachys* (Tachyina) in the same habitat with *Geocharidius* (the only genus of Central American Anillina); the former always have some eye facets, however, and possess a deeply engraved and sulcate recurrent groove on the lateroapical portion of the elytron. Jeannel (1937, 1963a, 1963b) attempted a phylogenetic and biogeographic synthesis of this group, however, he was partially thwarted by lack of material, his assumption that the group is monophyletic, and the 'reduction' of most character suites leaving poorly defined taxa. Recent discovery of an apparently eyed Anillina from lowland Brazil suggests a relationship of the subtribe to the tachyina group "*Polyderidius.*" Possibly, Anillina represents a grade of numerous parallel lineages derived from *Paratachys* and allies, each of which adapted independently to deep-humus environments. This possibility would explain several puzzles. For example, all anillinas have the anterior tibia notched obliquely—an apotypic trend found among all the higher tachyinas, which reaches its ultimate development in *Micratopus* and *Lymnastis.* Also explained would be the occurrence of these small, blind, wingless beetles on remote islands and all continents (except Antarctica). At present, the only explanation is that they are an ancient group predating the initial rift of Pangaea. This explanation is not concordant with many other aspects of carabid evolution and radiation. It seems to me that a polyphyletic origin hypothesis now best fits observations, and *Paratachys* and allies are the source of the anillina grade, as they are also the probable source of "Lymnastine" radiation.

Horologion, a monotypic genus (known from only one specimen) from West Virginia represented by *H. speokoites,* has long troubled classifiers (Valentine 1932; van Emden 1936; Ball 1963). Considering the evidence presented above and the fact that many character states are shared among *Horologion* and Anillinas, and especially, that these share the derived tibial configuration mentioned above, I here suggest that *Horologion* belongs in the anillina grade and that its origin lies in the Tachyina.

For recent treatments of Bembidiini or its components see Basilewsky (1968, 1972—Madagascan and St. Helena Bembidiini), Darlington (1962—New Guinea Bembidiini), Erwin (1973, 1974a, 1974b, 1975, 1976, 1977—Tachyina), Erwin and Kavanaugh (1980, 1981—North American *Bembidion*), Kryzhanovskiy (1970—U.S.S.R. Tachyina), Lindroth (1963, 1966, 1975, 1976, 1980—North American, Australian, and Asian Bembidiini), de Miré (1976—African Tachyina), Pawlowski (1974—Polish Bembidiini).

Genus **Bembidion** Latreille

Bembidium Latreille, 1802:82. [Type-species *Cicindela quadrimaculata* Linné, 1761:211, subsequent designation by Andrewes (1935:17).]

For detailed generic synonymies see Andrewes (1935:92), Ball (1963), Lindroth (1963:206), Müller (1918), and Netolitzky (1942, 1943).

Diagnostic Combination.—Small to medium-sized, more or less depressed beetles with broad elytra, narrow forebody, and long slender appendages. Color various, often with metallic luster, elytra sometimes spotted. Terminal palpomere subulate; eyes moderate to large, antennomeres 3–11 entirely pubescent, mentum with well-developed tooth; mandibles unisetose. Pronotum with two midlateral and usually two basilateral setae; elytron with two or more discal setae in third interval or adjacent interneur. Elytron without recurrent groove, although apex of fifth interneur usually sulcate. Microsculpture various. Female stylus small, spatulate, unisetose. Male parameres 2- or 3-setose. Flight wings present, absent, or dimorphic; reduction in size and length of various degrees. ABL = 2.43–6.11 mm in Central American species.

Natural History.—Species of this genus live on sea beaches, along streams and rivers, and in forests; they can be found during their quiescent periods under leaf litter, logs, or stones. Several species in Central America are true alticoles; most of these are wingless. The larvae of many European and some North American species are known and described, but none in Central America have been discovered in either larval or pupal stages. Adults of *Bembidion* species are carnivorous; in addition to small arthropods, they also eat arthropod eggs (Frank 1971). Their usual life cycle requires one year; larvae are present in the fauna in summer for the most part, however, some species overwinter in this stage in the north (Lindroth 1963). *Bembidion* species are dominant members of most northern riparian, alpine, and lake shore communities. In the tropics, this dominance does not exist at lower elevations, however, I have seen it in upland riparian habitats in Panama and in the Subparamo habitat in Costa Rica.

Notes.—*Bembidion* of the southern United States, Mexico, and South America are in need of a detailed taxonomic study. Therefore, I have restricted coverage here to only Central America within the limits set forth in the Introduction. The North American *Bembidion* fauna consists of more than 200 species (Lindroth 1967), that of Central America 22! This drastic reduction in species numbers occurs in Mexico, most dramatically at the southern edge of the Transverse

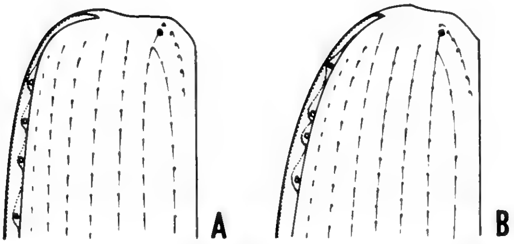


FIGURE 2. Elytron, left, dorsal aspect of (*a*) *Bembidion rogersi* Bates, alate form, 7.5 km south of Ojo de Agua, Cartago, Costa Rica, male; (*b*) same, brachypterous form, same locale, male.

Volcanic Belt and Isthmus of Tehuantepec. From this line southward, *Bembidion* is never as diverse as it is in North America, although species are found as far south as Tierra del Fuego (Darlington 1965).

The *Bembidion* fauna of North America is very complex and difficult to work with because of many closely related species in most species groups. That of Central America, however, is quite the contrary because there are only a few species in each of the nine represented groups, the tail-ends of otherwise diverse northern and southern groups. Male genitalic character states are excellent for delimiting species and species groups, female genitalic characteristics for species groups; both these suites usually correlate well with external structure (Erwin and Kavanaugh 1981) which then can be utilized for diagnostic features. Externally, the beetles differ in states of the frontal furrows, metasternal process, dorsal elytral chaetotaxy and structure of the interneurs, microsculpture, and pronotal shape, even though the beetles themselves are similar in habitus. In Central America, two habitus types occur: the winged type (Fig. 2*a*) with large square humeri and narrow forebody and head, and the brachypterous type (Fig. 2*b*) with rounded and narrow humeri, arcuate-sided elytra, and more robust forebody and head. These two types occur among different individuals of the same population of wing-dimorphic species such as *B. rogersi* and *B. nahuala*.

Adults can easily be sexed in two ways. Males have two basal tarsomeres of the anterior leg dilated and with modified setae beneath, forming a loosely biserrate "spongy" pad, and two setae along the caudal edge of sternum VI; females have no "spongy" pad or dilated tarsomeres and have four setae on sternum VI.

ARRANGEMENT OF TAXA: *BEMBIDION*.—I here follow Lindroth's arrangement of species groups and add the *rogersi, vernale, nahuala, franiae,* and *cognatum* groups, none of which were covered by him. Arrangement of taxa within groups is based on complexity of male genital structure, from simple to complex. Athough this may not be phylogenetically accurate, it suits the purpose of this paper in its attempt to simply document the fauna for further study. Such further study must necessarily be based on revisionary work with a much broader geographic base than Central America.

CHECKLIST OF *BEMBIDION* SPECIES OF CENTRAL AMERICA.

The *semistriatum* group
  1. *B. purulha,* new species
The *rogersi* group
  2. *B. rogersi* Bates, 1878:602
The *vernale* group
  3. *B. mexicanum* Dejean, 1831:126
  4. *B. vernale* Bates, 1882:149
  5. *B. satellites* Bates, 1884:291
  6. *B. lavernae,* new species
  7. *B. quetzal,* new species
  8. *B. diabola,* new species
  9. *B. vulcanium* Darlington, 1934:157
  10. *B. edwardsi,* new species
  11. *B. aeger,* new species
  12. *B. chiriqui,* new species
The *nahuala* group
  13. *B. nahuala,* new species
The *franiae* group
  14. *B. franiae,* new species
The *incrematum* group
  15. *B. aratum* LeConte, 1852:189
The *dorsale* group
  16. *B. cortes,* new species
  17. *B. sparsum* Bates, 1882:151
  18. *B. armuelles,* new species
The *affine* group
  19. *B. barrensis,* new species
The *championi* group
  20. *B. cyclodes* Bates, 1884:290
  21. *B. championi* Bates, 1882:148
The *cognatum* group
  22. *B. ixtatan,* new species

Key to Species of *Bembidion* of Central America

1. Pronotum with hind angles completely rounded, base markedly lobed as in Figure 21 2

TABLE 1. NUMBERS AND PERCENTAGES OF WINGED VERSUS NON-WINGED INDIVIDUALS IN THREE POPULATIONS OF (A) *Bembidion rogersi* BATES AND (B) *Bembidion nahuala*, NEW SPECIES.

	– Wing female	+ Wing female	% Female – wing	– Wing male	+ Wing male	% Male – wing	% Total – wing
Locality							
(A)							
Cerro de la Muerte	54	7	88%	99	20	83%	85%
Volcán Irazú	4	4	50%	7	1	87%	69%
Volcán de Chiriquí	6	4	60%	3	2	60%	60%
(B)							
Río Nahuala	5	1	83%	0	0	—	83%
San Marcos	26	9	74%	16	2	89%	79%
Cerro Zunil	1	0	100%	0	0	—	100%
Finca San Rafael	1	0	100%	0	0	—	100%

– Pronotum with hind angles acute or square, base not lobed 3

2(1). Elytron with interneur 7 absent, interneur 6 extended to at least middle .... 19. *B. cyclodes* Bates
– Elytron with interneurs 6 and 7 present, short, not extended beyond basal sixth .... 20. *B. championi* Bates

3(1). Frontal furrows doubled on clypeus and behind posterior supraorbital seta, furrows moderately or markedly convergent; humerus somewhat paler than disc of elytron; small beetles, less than 3.0 mm 4
– Frontal furrows not doubled, not convergent; humerus various; larger beetles, usually more than 3.0 mm 5

4(3). Frontal furrows deeply impressed and convergent, doubled throughout their length .... 22. *B. ixtatan*, new species
– Frontal furrows shallow and single between eyes, nearly parallel except on clypeus where they converge and are doubled .... 19. *B. barrensis*, new species

5(3). Metasternal process between mesocoxae entirely unmargined 6
– Metasternal process clearly margined, margin removed from apex and abruptly or gradually raised 8

6(5). Dorsal surface without microsculpture, surfaces shiny .... 13. *B. nahuala*, new species
– Dorsal surface with well-developed microsculpture, surfaces dull 7

7(6). Elytron bifoveate, foveae around setae deep and wide, each extended across about three intervals; elytral microsculpture of wide meshes, on head and pronotum variously effaced or nearly isodiametric .... 2. *B. rogersi* Bates
– Elytron bipunctate, punctures around dorsal setae deep and small, not extended beyond middle of adjacent interval; elytral microsculpture of finely impressed lines or wide meshes, surface subiridescent, on head clearly and evenly isodiametric, slightly granular, more evenly transverse and less impressed on pronotum .... 14. *B. franiae*, new species

8(5). Elytron with setae Ed3 and Ed5 in interval 3 and not touching adjacent interneurs 9
– Elytron with these setae in or touching interneur 3 12

9(8). Elytron without microsculpture, markedly shiny .... 15. *B. aratum* LeConte
– Elytron with perfectly isodiametric and well-engraved microsculpture, surfaces dull 10

10(9). Pronotum (Fig. 19) narrow, about as wide as head across eyes; length 3.47 to 4.23 mm .... 17. *B. sparsum* Bates
– Pronotum broad, much wider than head across eyes; length 3.75 to 4.41 mm 11

11(10). Pronotum (Fig. 20) markedly convex

TABLE 2. VARIATION IN TOTAL LENGTH (SBL in mm) WITHIN AND AMONG *Bembidion* SPECIES OF CENTRAL AMERICA.

	Sex	(*n*)	Minimum	Maximum	Mean	±SE	SD	CV
01. *B. purulha*	m	1	4.19	4.19	—	—	—	—
	f	1	4.53	4.53	—	—	—	—
02. *B. rogersi*	m	135	3.78	4.26	4.25	0.02	0.22	5.24
	f	88	3.60	4.63	4.20	0.02	0.24	5.69
03. *B. mexicanum*	m	33	5.04	6.11	5.50	0.05	0.29	5.36
	f	29	4.95	5.95	5.41	0.05	0.26	4.88
04. *B. vernale*	m	182	4.39	5.64	5.06	0.02	0.24	4.72
	f	113	4.43	5.66	5.14	0.02	0.24	4.68
05. *B. satellites*	m	30	4.20	5.12	4.61	0.04	0.24	5.25
	f	25	4.22	5.17	4.79	0.05	0.23	4.87
06. *B. lavernae*	m	X	—	—	—	—	—	—
	f	1	4.18	4.18	—	—	—	—
07. *B. quetzal*	m	9	4.74	5.59	5.21	0.09	0.27	5.26
	f	18	4.77	5.53	5.23	0.06	0.24	4.61
08. *B. diabola*	m	31	3.56	4.38	3.71	0.04	0.22	5.47
	f	22	3.64	4.49	4.10	0.05	0.24	5.93
09. *B. vulcanium*	m	18	3.73	4.49	4.12	0.05	0.20	4.75
	f	15	3.11	4.36	4.02	0.08	0.32	7.85
10. *B. edwardsi*	m	X	—	—	—	—	—	—
	f	3	3.77	4.00	3.87	0.07	0.12	3.09
11. *B. aeger*	m	18	3.05	3.74	3.49	0.04	0.18	4.19
	f	16	3.26	3.75	3.44	0.03	0.12	3.38
12. *B. chiriqui*	m	34	3.42	4.15	3.84	0.03	0.19	4.89
	f	10	3.68	4.25	3.98	0.05	0.17	4.22
13. *B. nahuala*	m	19	2.87	3.77	3.24	0.06	0.27	8.28
	f	41	3.04	4.00	3.50	0.03	0.21	5.93
14. *B. franiae*	m	1	4.12	—	—	—	—	—
	f	1	3.98	—	—	—	—	—
15. *B. aratum*	m	2	4.03	5.03	4.53	0.50	0.71	15.61
	f	3	4.24	4.48	4.35	0.07	0.12	2.77
16. *B. cortes*	m	10	3.75	4.41	4.17	0.04	0.13	3.22
	f	22	3.75	4.40	4.13	0.04	0.19	4.67
17. *B. sparsum*	m	9	3.47	4.10	3.74	0.08	0.23	6.16
	f	8	3.52	4.23	3.82	0.08	0.24	6.20
18. *B. armuelles*	m	X	—	—	—	—	—	—
	f	1	4.32	4.32	—	—	—	—
19. *B. barrensis*	m	1	2.94	2.94	—	—	—	—
	f	X	—	—	—	—	—	—
20. *B. cyclodes*	m	X	—	—	—	—	—	—
	f	1	3.05	3.05	—	—	—	—
21. *B. championi*	m	X	—	—	—	—	—	—
	f	X	—	—	—	—	—	—
22. *B. ixtatan*	m	3	2.43	2.90	2.70	0.01	0.24	9.03
	f	4	2.54	2.85	2.69	0.07	0.14	5.06

"X" = sex not available for measurement.

TABLE 3. VARIATION IN TOTAL WIDTH (TW in mm) WITHIN AND AMONG *Bembidion* SPECIES OF CENTRAL AMERICA.

	Sex	(*n*)	Minimum	Maximum	Mean	±SE	SD	CV
01. *B. purulha*	m	1	1.79	1.79	—	—	—	—
	f	1	1.82	1.82	—	—	—	—
02. *B. rogersi*	m	135	1.58	2.13	1.82	0.01	0.22	5.24
	f	88	1.57	1.98	1.80	0.01	0.11	5.93
03. *B. mexicanum*	m	33	2.07	2.80	2.44	0.02	0.14	5.62
	f	29	2.09	2.80	2.42	0.02	0.13	5.52
04. *B. vernale*	m	182	1.89	2.61	2.18	0.01	0.12	5.45
	f	113	1.80	2.51	2.22	0.01	0.12	5.47
05. *B. satellites*	m	30	1.64	2.12	1.96	0.02	0.11	5.50
	f	26	1.77	2.30	2.04	0.02	0.11	5.18
06. *B. lavernae*	m	X	—	—	—	—	—	—
	f	1	1.78	1.78	—	—	—	—
07. *B. quetzal*	m	9	2.04	2.38	2.24	0.04	0.11	4.72
	f	18	2.08	2.45	2.24	0.03	0.13	5.72
08. *B. diabola*	m	31	1.52	1.89	1.74	0.02	0.10	5.59
	f	22	1.52	1.93	1.76	0.02	0.11	6.26
09. *B. vulcanium*	m	18	1.63	2.00	1.89	0.02	0.08	4.48
	f	15	1.58	2.04	1.89	0.03	0.13	6.67
10. *B. edwardsi*	m	X	—	—	—	—	—	—
	f	3	1.59	1.66	1.62	0.02	0.04	2.34
11. *B. aeger*	m	18	1.28	1.65	1.51	0.02	0.09	5.82
	f	16	1.34	1.81	1.50	0.03	0.11	7.45
12. *B. chiriqui*	m	34	1.54	1.83	1.70	0.01	0.08	4.58
	f	10	1.65	1.94	1.77	0.03	0.09	5.25
13. *B. nahuala*	m	19	1.20	1.78	1.45	0.03	0.16	11.18
	f	41	1.28	1.94	1.58	0.02	0.12	7.40
14. *B. franiae*	m	1	1.85	1.85	—	—	—	—
	f	1	1.83	1.83	—	—	—	—
15. *B. aratum*	m	2	1.68	1.98	1.83	0.15	0.21	11.59
	f	3	1.62	1.85	1.77	0.08	0.13	7.21
16. *B. cortes*	m	10	3.98	4.14	4.17	0.02	0.07	3.79
	f	22	1.65	1.99	1.84	0.02	0.08	4.29
17. *B. sparsum*	m	9	1.50	1.74	1.62	0.03	0.09	5.42
	f	8	1.53	1.89	1.71	0.05	0.13	7.84
18. *B. armuelles*	m	X	—	—	—	—	—	—
	f	1	1.80	1.80	—	—	—	—
19. *B. barrensis*	m	1	1.21	1.21	—	—	—	—
	f	X	—	—	—	—	—	—
20. *B. cyclodes*	m	X	—	—	—	—	—	—
	f	1	1.39	1.39	—	—	—	—
21. *B. championi*	m	X	—	—	—	—	—	—
	f	X	—	—	—	—	—	—
22. *B. ixtatan*	m	3	1.20	1.26	1.24	0.02	0.03	2.60
	f	4	1.07	1.21	1.14	0.03	0.06	5.21

"X" = sex not available for measurement.

TABLE 4. VARIATION IN TOTAL DEPTH (TD in mm) WITHIN AND AMONG *Bembidion* SPECIES OF CENTRAL AMERICA.

	Sex	(*n*)	Minimum	Maximum	Mean	±SE	SD	CV
01. *B. purulha*	m	1	1.04	1.04	—	—	—	—
	f	1	1.12	1.12	—	—	—	—
02. *B. rogersi*	m	135	0.81	1.19	0.95	0.01	0.08	8.49
	f	88	0.74	1.16	0.96	0.01	0.09	9.02
03. *B. mexicanum*	m	33	1.18	1.54	1.33	0.02	0.10	7.17
	f	29	1.15	1.47	1.31	0.01	0.08	6.14
04. *B. vernale*	m	182	0.86	1.40	1.10	0.01	0.01	8.63
	f	113	0.89	1.37	1.10	0.01	0.10	9.32
05. *B. satellites*	m	30	0.87	1.21	1.04	0.01	0.07	7.04
	f	26	0.88	1.21	1.03	0.02	0.09	8.26
06. *B. lavernae*	m	X	—	—	—	—	—	—
	f	1	0.83	0.83	—	—	—	—
07. *B. quetzal*	m	9	1.01	1.38	1.19	0.04	0.12	10.37
	f	18	0.94	1.39	1.16	0.03	0.11	9.50
08. *B. diabola*	m	31	0.76	1.15	0.96	0.02	0.10	9.88
	f	22	0.82	1.20	0.96	0.02	0.10	10.17
09. *B. vulcanium*	m	18	0.86	1.14	1.00	0.02	0.08	7.51
	f	15	0.78	1.09	0.96	0.02	0.09	8.90
10. *B. edwardsi*	m	X	—	—	—	—	—	—
	f	3	0.84	0.87	0.85	0.01	0.02	1.79
11. *B. aeger*	m	18	0.52	0.84	0.73	0.02	0.09	12.11
	f	16	0.65	0.88	0.76	0.02	0.07	9.18
12. *B. chiriqui*	m	34	0.80	1.05	0.90	0.01	0.06	7.00
	f	10	0.78	1.03	0.90	0.03	0.09	10.15
13. *B. nahuala*	m	19	0.60	0.95	0.72	0.02	0.10	13.97
	f	41	0.64	0.95	0.81	0.01	0.07	8.52
14. *B. franiae*	m	1	0.93	0.93	—	—	—	—
	f	1	0.85	0.85	—	—	—	—
15. *B. aratum*	m	2	0.92	0.94	0.93	0.01	0.01	1.52
	f	3	0.82	0.89	0.86	0.02	0.04	4.39
16. *B. cortes*	m	10	0.92	1.12	1.00	0.02	0.07	6.81
	f	22	0.84	1.13	1.00	0.02	0.07	7.36
17. *B. sparsum*	m	9	0.76	0.98	0.89	0.02	0.07	8.06
	f	8	0.89	1.02	0.95	0.02	0.05	4.88
18. *B. armuelles*	m	X	—	—	—	—	—	—
	f	1	1.08	1.08	—	—	—	—
19. *B. barrensis*	m	1	0.71	0.71	—	—	—	—
	f	X	—	—	—	—	—	—
20. *B. cyclodes*	m	X	—	—	—	—	—	—
	f	1	0.80	0.80	—	—	—	—
21. *B. championi*	m	X	—	—	—	—	—	—
	f	X	—	—	—	—	—	—
22. *B. ixtatan*	m	3	0.58	0.62	0.60	0.01	0.02	3.49
	f	4	0.48	0.60	0.55	0.03	0.05	9.52

"X" = sex not available for measurement.

with arcuate side margins, markedly convergent behind and abruptly sinuate just before hind angles .... 18. *B. armuelles,* new species

– Pronotum (Fig. 18) moderately convex, side margins not markedly arcuate nor much convergent behind, shallowly sinuate before hind angle .... 16. *B. cortes,* new species

12(8). Elytra with pale spots contrasting against dark background 13

– Elytra concolorous 14

13(12). Pronotum (Fig. 5) broad, wider than head across eyes; elytral pale spot extended to apex in most specimens; interneur punctures coarsely impressed and large; pronotum with fine and feeble carina at hind angle .... 3. *B. mexicanum* Dejean

– Pronotum (Fig. 9) narrow, about as wide as head across eyes; elytral pale spot isolated; interneur punctulae finely impressed, medium-sized; pronotum with well-developed carina delimiting deep basal fovea .... 7. *B. quetzal,* new species

14(12). Elytral interneurs coarsely punctate basally, absent behind middle, dorsal surface without microsculpture, shiny .... 1. *B. purulha,* new species

– Elytral interneurs finely punctate or not, extended to near apex; dorsal surface with or without microsculpture, if without, hind wings absent 15

15(14). Pronotum (Fig. 6) with short, sharp, well-developed carina at hind angle; dorsal surface with metallic-blue cast; flight wings fully developed .... 4. *B. vernale* Bates

– Pronotum with rudimentary or no carina at hind angle; dorsal surface non-metallic brown or black; flight wings reduced or virtually absent 16

16(15). Elytron with interneurs 7 and 8 virtually absent (a few minute punctulae present in some individuals); small beetles with narrow ovoid elytra and narrow pronotum .... 11. *B. aeger,* new species

– Elytron with all interneurs present, though finer laterally, all easily traceable beyond disc; larger beetles, with broadly ovoid elytra and broad pronotum 17

17(16). Form short, broad, and subconvex; pronotum abruptly sinuate, sides straight for only a short distance, hind angles acute or square 18

– Form long, narrow, and depressed; pronotum with lateral margins nearly straight in basal fifth, hind angles acute 21

18(17). Metasternum with intercoxal process narrowly margined, bead well developed and of even width .... 8. *B. diabola,* new species

– Metasternum with intercoxal process broadly margined, bead widely removed from apex medially, narrowed laterally 19

19(18). Eyes flattish, not produced much beyond outline of head capsule (range: Cerro Buenavista, Costa Rica) .... 10. *B. edwardsi* new species

– Eyes prominent, produced well beyond outline of head capsule 20

20(19). Range: central cordillera of Costa Rica; male aedeagus as in Figure 30 .... 9. *B. vulcanium* Darlington

– Range: Volcán de Chiriquí, Panama; male aedeagus as in Figure 33 .... 12. *B. chiriqui,* new species

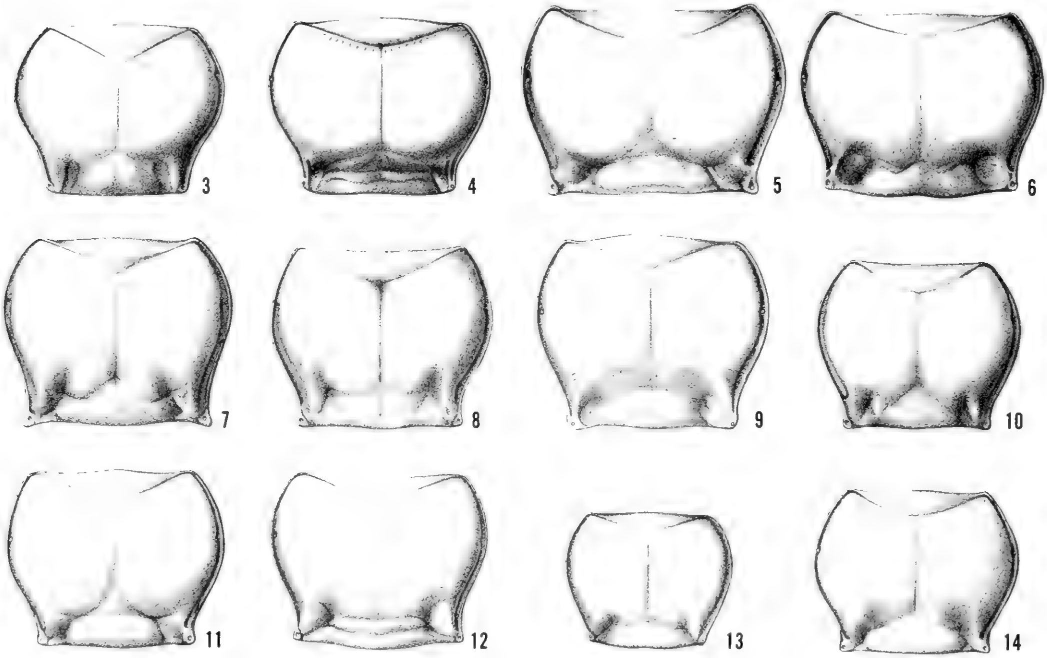
21(17). Elytron with interneurs markedly striatopunctulate, intervals subconvex .... 5. *B. satellites* Bates

– Elytron with interneurs shallowly striatopunctulate, intervals flat .... 6. *B. lavernae,* new species

The *semistriatum* group

(Subgenus *Hydriomicrus* Casey, 1918:87. Type-species *Bembidium semistriatum* Haldeman, 1843:303, by subsequent designation of Lindroth 1963:305.)

Diagnostic Combination.—Metasternal process completely bordered; elytral interneurs effaced in apical half, markedly punctulate in basal half; microsculpture absent; male genital sclerites as in or similar to Figure 23.



FIGURES 3 to 14. Pronotum, dorsal aspect. 3. *Bembidion purulha* n.sp., 66.4 km south of Cobán, Alta Verapaz, Guatemala, male. 4. *B. rogersi* Bates, 7.5 km south of Ojo de Agua, Cartago, Costa Rica, male. 5. *B. mexicanum* Dejean, 22.0 km west of San Pedro Sacatepéquez at Río Nahuala, male. 6. *B. vernale* Bates, San Isidro de Coronado, San José, Costa Rica, male. 7. *B. satellites* Bates, Chomogo area, 10°18′N, 084°47′W, Alajuela, Costa Rica, male. 8. *B. lavernae* n.sp., Cerro Buenavista, San José, Costa Rica, female. 9. *B. quetzal* n.sp., 20.0 km west of San Pedro Sacatepéquez at Río Nahuala, male. 10. *B. diabola* n.sp., Volcán Irazú, Cartago, Costa Rica, male. 11. *B. vulcanium* Darlington, 7.5 km south of Ojo de Agua, Cartago, Costa Rica, male. 12. *B. edwardsi* n.sp., Cerro Buenavista, San José, Costa Rica, male. 13. *B. aeger* n.sp., Cerro Buenavista, San José, Costa Rica, male. 14. *B. chiriqui* n.sp., 8.0 km west of Boquete, Chiriquí, Panama, male.

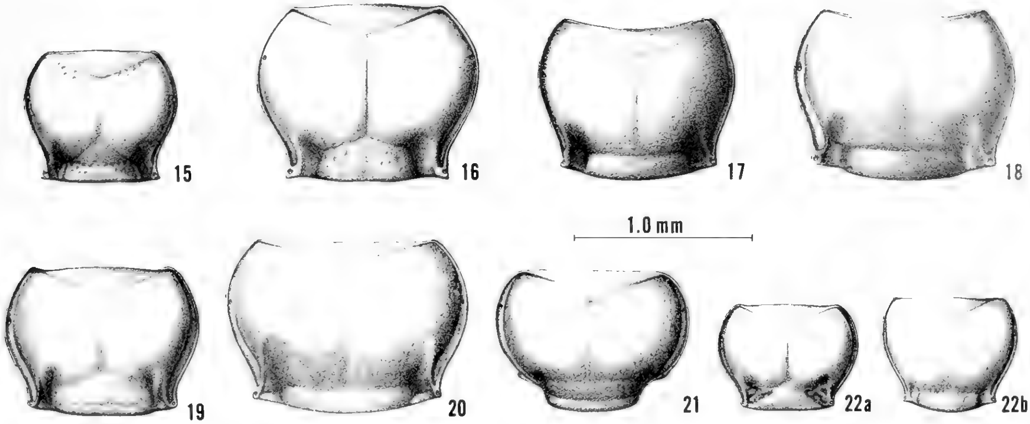
These beetles are hygrophilous, occurring along streams in fine gravel and sand, or in *Sphagnum* bogs. Previously, this group of five species was known from only North America; the Central American one described below extends the group's range considerably. All species are fully winged and occur in the lowland or adjacent low hills. The male median lobe of the species covered herein lacks the pigmented ostium flag characteristic of Central American *Bembidion* (*Peryphus*) species, yet the endophallus strongly suggests relationship with this group.

1. **Bembidion purulha**, new species

(Figures 3, 23, 64)

DIAGNOSTIC COMBINATION.—Interneurs with large, coarse, sparse punctulae; pronotum markedly constricted with small basal punctiform fovea; dorsal surface without microsculpture; male median lobe without pigmented ostium flags. *Color and luster:* piceous; appendages testaceous; venter and dorsum of forebody rufopiceous; surface very shiny. *Form:* medium-sized for genus with narrow forebody and broad elytra; pronotum (Fig. 3) slightly wider than head or elytron; eyes large and prominent. *Structure:* frontal furrows deeply sulcate and arcuate between eyes, shallower where prolonged on clypeus. Hind angles of pronotum finely and abruptly carinate, carinae very short; basal fovea deep, extended to lateral margin. Interneurs effaced apically; except first which is striate in apical third, otherwise coarsely punctulate, punctures deep and large, separated by their own diameter or more. Dorsal microsculpture absent. Male median lobe as in Figure 23. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 64. Known only from the Sierra de las Minas in east-central Guatemala. I have seen specimens from localities listed in Table 5.



FIGURES 15 to 22. Pronotum, dorsal aspect. 15. *Bembidion nahuala* n.sp., 27.0 km northwest of San Marcos, San Marcos, Guatemala, male. 16. *B. franiae* n.sp., 4.8 km east of San Mateo Ixtatán, Huehuetenango, Guatemala, male. 17. *B. aratum* LeConte, La Lima, Cortés, Honduras, male. 18. *B. cortes* n.sp., La Lima, Cortés, Honduras, male. 19. *B. sparsum* Bates, Tikal, Del Petén, Guatemala, male. 20. *B. armuelles*, n.sp., Puerte Armuelles, Chiriquí, Panama, female. 21. *B. championi* Bates, 8.6 miles [13.8 km] east of San Cristóbal, Chiapas, Mexico, female. 22*a*. *B. ixtatan* n.sp., 27.0 miles [43.5 km] west of Sololá, Sololá, Guatemala, male. 22*b*. *B. barrensis* n.sp., Barro Colorado Island, Panama, male.

NATURAL HISTORY NOTES.—These beetles were collected in May and August at elevations of 1372 m and 1420 m in Lower Montane Wet and Subtropical Wet forests, respectively; neither is teneral. The holotype was collected from oak leaf litter near a stream; the paratype was collected by splashing fine silty gravel at the edge of a small brook in pine-oak forest. Both specimens are fully winged.

TYPE-MATERIAL.—**Holotype** ♀, GUATEMALA, Baja Verapaz, 22.0 km S of Purulha, 15°07′N, 090°12′W, Aug. (*Ball, Frania, & Whitehead*) (USNM), ADP 026375. **Paratype:** 1♂, GUATEMALA, Alta Verapaz, 66.4 km S Cobán, 15°12′N, 090°18′W, May (*Erwin & Erwin*) (USNM), ADP 013626. See also Table 5.

DERIVATION OF TAXON NAME.—Spanish, *Purulha*, after the town near which the holotype was collected.

The *rogersi* group

DIAGNOSTIC COMBINATION.—Metasternal process without border; elytral interval 3 bifoveate, fovea broad and depressed; male median lobe with broad lobe on ventral face.

These beetles are independent of running or standing water and occur in Subparamo grasslands of volcanic highlands. Two Colombian species belong to this group: *B. subapterum* Darlington and *B. sanctaemarthae* Darlington. The three species are either wing-dimorphic or brachypterous and form a group closely related to the *vernale* group. The *vernale* group is northern and islandic in distribution while the *rogersi* group is southern; *B. rogersi* is the northernmost representative of the group.

2. **Bembidion rogersi** Bates

(Figures 2, 4, 24, 40, 64)

Bembidium rogersi BATES, 1878:602. [Lectotype ♂, COSTA RICA, Volcán de Irazú, 09°58′N, 083°53′W (BMNH), here designated.]

DIAGNOSTIC COMBINATION.—Interneur 3 catenate, constrictions at large unisetose foveae; color black. *Color and luster:* black; appendages and venter piceous; surface of elytron dull, forebody shiny. *Form:* medium-sized for genus with narrow forebody and elytra; elytra either with square humeri or sloped; pronotum (Fig. 4)

TABLE 5. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 01. *Bembidion purulha* n.sp.; map Figure 64.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°07′N 90°12′W	1420	USNM	Aug	1
15°12′N 90°18′W	1372	USNM	May	1
		Total specimens examined:		2

TABLE 6. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 02. *Bembidion rogersi* n.sp.; map Figure 64.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
10°11′N 84°13′W	2600	USNM	Mar	1
09°59′N 83°53′W	3000–3030	USNM	?	1
09°58′N 83°53′W	3364	UASM	Aug	6
09°58′N 83°53′W	3440	MCZ	Jan	2
09°58′N 83°53′W	3350	USNM	May	9
09°55′N 84°02′W	1400–1500	USNM	Feb	2
09°54′N 83°41′W	0640	USNM	May	1
09°54′N 83°41′W	0640	MCZ	Jun, Jul	3
09°35′N 83°48′W	2682	USNM	Jun	182
09°33′N 83°44′W	2700	UAIC	Jul	1
09°32′N 83°46′W	?	MCZ	Dec	2
09°32′N 83°46′W	?	UAIC	Mar	1
08°51′N 82°33′W	2240	USNM	Jun	4
08°51′N 82°34′W	2134	UAIC	May	1
08°51′N 82°34′W	2134–2438	UAIC	May	5
08°51′N 82°36′W	1848–2464	USNM	May	5
08°47′N 83°30′W	2220	USNM	Jun	1
			Total specimens examined:	227

wider than head, about equal in width to elytron; eyes moderately large and prominent. *Structure:* frontal furrows moderately well impressed, diffuse, rugose, parallel, prolonged on clypeus; anterior supraorbital pore well impressed. Hind angles of pronotum markedly carinate; basal fovea deep, rather small, extended to base; side slightly sinuate. Elytron (Figs. 2*a*, *b*) either long, humerus squared, sides slightly arcuate, or short, humerus rounded/sloped, sides markedly arcuate; interneurs entire, much shallower apicolaterally and striate; interneurs 2 and 3 catenate at Ed3a and Ed5b. Dorsal microsculpture (Fig. 40) of rather large, coarse, transverse meshes, effaced from center of pronotum. Male median lobe as in Figure 24. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 64; known from the Cordillera Central of Costa Rica from Volcán Irazú, Volcán Poás, and in the area of Turrialba, south along the Cordillera de Talamanca to Volcán de Chiriquí in Panama.

NATURAL HISTORY NOTES.—These beetles are commonly collected above 1600 m in life zones from Lower Montane Wet Forest up and into Subparamo. They occur as high as 3350 m; are found independent of running water; and have been collected in January, February, March, May through August, and December. Very teneral beetles were found in late May on Volcán de Chiriquí, indicating that larvae and pupae may be found just prior to that time, that is, in the early rainy season. Great numbers of specimens were collected at night on fine-textured wet soil among bunch grass at the edge of dwarf Montane Rain Forest on Cerro de la Muerte, Costa Rica (2682 m), and among flood debris and under stones during the day near Cerro Punta, Chiriquí, Panama. Individuals of this species may be long-winged and presumably fly, or brachypterous, having only a small veinless pad in place of the flight wing. Table 1 illustrates the distribution of these character states at several localities.

MATERIAL EXAMINED.—Lectotype (see above) and 227 specimens (Table 6).

The *vernale* group

(Subgenus *Peryphus* Stephens, 1828:2. [Type-species *Carabus litorale* auct. = *Bembidium tetracolum* Say, 1823:89, by subsequent designation of Westwood 1840:7.]

DIAGNOSTIC COMBINATION.—Metasternal process completely bordered; elytron with discal setae contiguous with or in interneur 3; parameres trisetose or bisetose; endophallus as in Figures 25 to 33; elytral microsculpture of transverse lines or meshes, effaced from head and pronotum; interneurs shallow or effaced laterally and apically.

A study of the life histories of these beetles would add much to test the theory of taxon pulses (Erwin 1979, 1981a). It is readily apparent that the group is plesiotypically hygrophilous. With development of aptery and movement to montane habitats, there is a corresponding shift away from water into forest-floor litter or open dry spots in the forest or above treeline, thus the species become mesophilous alticoles. In Central America, this shift was accomplished by three separate lineages of the *vernale* group. The plesiotypic parent stock was probably a middle altitude riparian species which radiated and is now represented by four widespread species at middle altitudes one of which is wing-dimorphic and six brachypterous alticoles.

As suggested by Lindroth (1963:312), a world-wide revision of this group would be desirable. Only then will we know the subgroup relationships, and these can be recognized only by the structure of the endophallus in combination with other characters. The median lobe of all species in this group has one or two ostium flags extending from near the apical orifice to the median area on the left surface. In addition, three Central American forms have a nonsclerotized patch ventrally on the median lobe. These apotypic features should assist in discovering relationships in revisions with wider geographic coverage (e.g., Erwin and Kavanaugh 1981).

Widespread species exhibit considerable variation in pronotal shape and elytral coloration. *Bembidion mexicanum* and *B. vernale* exemplify this in part in regard to pronotal variation, and the former is paler in the north, darker in the south.

3. **Bembidion mexicanum** Dejean

(Figures 5, 25, 41, 65)

Bembidium mexicanum DEJEAN, 1831:126. [Lectotype ♂, MEXICO (MNHP) selected and so labelled by G. E. Ball.]
Bembidium sallaei BATES, 1882:148. [Lectotype ♂, MEXICO (MNHP) selected and so labelled by G. E. Ball.]

DIAGNOSTIC COMBINATION.—Pronotum (Fig. 5) broad, wider than head across eyes; elytral pale spot extended to apex in most specimens; interneur punctures coarsely impressed and large; pronotum with fine and feeble carina at hind angle. *Color and luster:* dorsum piceous; appendages and at least part of elytron testaceous; venter piceous anteriorly, abdomen rufous posteriorly; surfaces shiny, elytron slightly iridescent. *Form:* large beetles with broad head and pronotum, and broad elytra; pronotum (Fig. 5) wider than head, about equal to width of elytron; eyes large and prominent. *Structure:* frontal furrows well impressed, bowed medially around frontal callus, prolonged on clypeus, generally parallel. Hind angle of pronotum finely carinate, carina curved posteriolaterally; basal fovea well impressed, narrowed anteriorly. Interneurs effaced apicolaterally, 7 virtually absent, 1 to 3 striatopunctulate, 4 to 6 punctulate. Dorsal microsculpture of extremely fine and dense transverse lines on elytron (Fig. 41), effaced from head and pronotum. Male median lobe as in Figure 25. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 65. At present, this species is known from Colorado south to middle Costa Rica.

NATURAL HISTORY NOTES.—These beetles are commonly found at middle elevations in Lower Montane Wet, Premontane Moist, Tropical Dry, and Subtropical Dry forests in the pine zone between 1300 m and 2400 m. Specimens were collected in March, May, June, and August; a teneral specimen from Guatemala collected in May indicates that larvae and pupae may be found just prior to that time, that is, in the early rainy season. They are found at the edge of small to medium-sized streams in gravel and under stones where there is some silt and at least some sparse vegetation. All known specimens are fully winged; P. J. Spangler collected two individuals at UV light traps near Guatemala City indicating that the beetles fly.

MATERIAL EXAMINED.—Lectotypes (see above) and 62 specimens (Table 7).

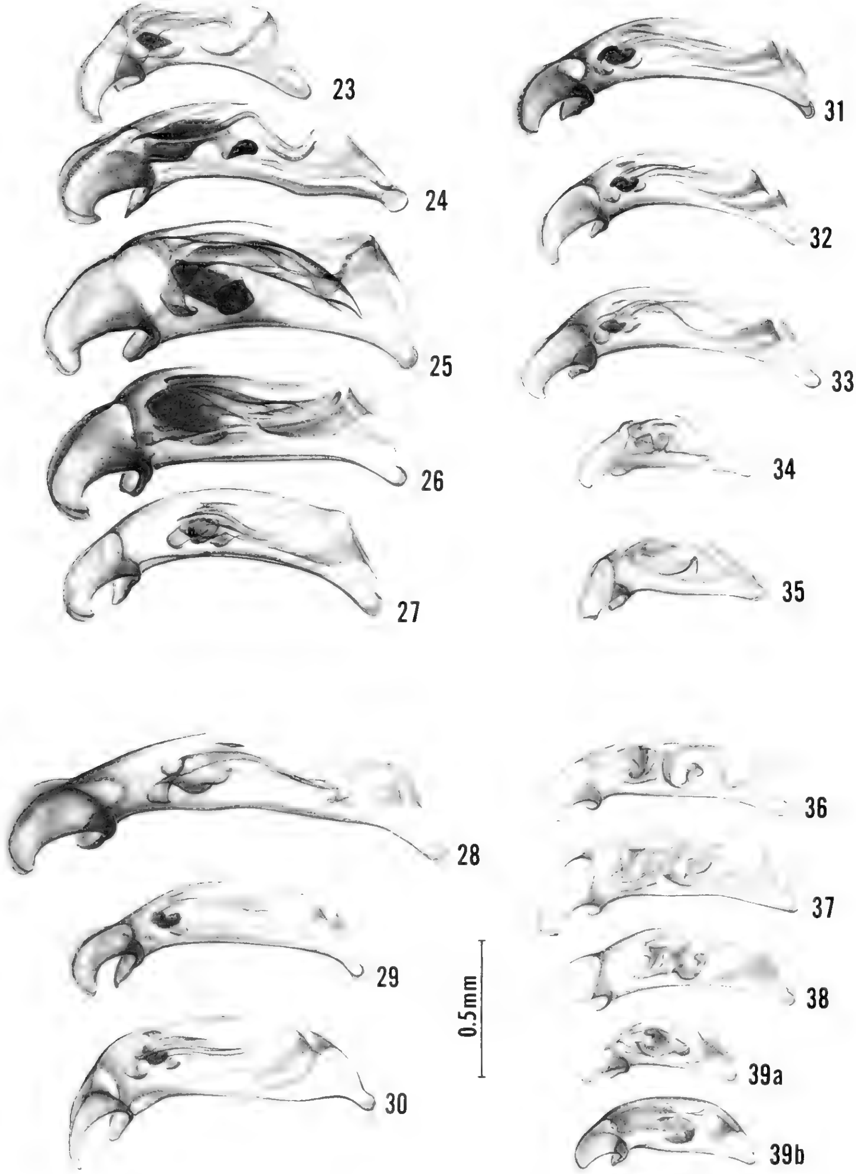
TAXONOMIC NOTES.—Bates's *B. sallaei* is a color variety of the widespread and variable *B. mexicanum,* and was recognized as such by Bates (1882:148).

4. **Bembidion vernale** Bates

(Figures 1, 6, 26, 42, 66)

Bembidium vernale BATES, 1882:149. [Lectotype ♂, PANAMA, Peña Blanca, 08°27′N, 081°41′W (BMNH), here designated.]

DIAGNOSTIC COMBINATION.—Elytra blue, nonspotted; length more than 4.2 mm. *Color and luster:* dorsum submetallic blue; penultimate palpomeres and antennomeres 2 to 11 infuscated, otherwise appendages testaceous; venter piceous; surface shiny. *Form:* large-sized beetles for genus with narrow forebody and slightly broad elytra. Pronotum (Fig. 6) slightly wider than head, about equal to width of elytron; eyes large and prominent. *Structure:* frontal furrows well impressed, rugose, slightly convergent anteriorly, extended on clypeus. Hind angle of



FIGURES 23 to 39. Median lobe of male genitalia, left lateral aspect. 23. *Bembidion purulha* n.sp., 66.4 km south of Cobán, Alta Verapaz, Guatemala. 24. *B. rogersi* Bates, 7.5 km south of Ojo de Agua, Cartago, Costa Rica. 25. *B. mexicanum* Dejean, 22.0 km west of San Pedro Sacatepéquez at Río Nahuala. 26. *B. vernale* Bates, San Isidro de Coronado, San José, Costa Rica. 27. *B. satellites* Bates, Chomogo area, 10°18′N, 084°47′W, Alajuela, Costa Rica. 28. *B. quetzal* n.sp., 25.0 km south of Totonicapán, Huehuetenango, Guatemala. 29. *B. diabola* n.sp., Volcán Irazú, Cartago, Costa Rica. 30. *B. vulcanium* Darlington, 7.5 km south of Ojo de Agua, Cartago, Costa Rica. 31. *B. edwardsi* n.sp., Cerro Buenavista, San José, Costa Rica. 32. *B. aeger* n.sp., Cerro Buenavista, San José, Costa Rica. 33. *B. chiriqui* n.sp., 8.0 km west Boquete, Chiriquí, Panama. 34. *B. nahuala* n.sp., 27.0 km northwest of San Marcos, San Marcos, Guatemala. 35. *B. franiae* n.sp., 4.8 km east of San Mateo Ixtatán, Huehuetenango, Guatemala. 36. *B. aratum* LeConte, La Lima, Cortés, Honduras. 37. *B. cortes* n.sp., La Lima, Cortés, Honduras. 38. *B. sparsum* Bates, Tikal, Del Petén, Guatemala. 39*a*. *B. ixtatan* n.sp., 27.0 miles [43.5 km] west of Sololá, Sololá, Guatemala. 39*b*. *B. barrensis* n.sp., Barro Colorado Island, Panama.

pronotum markedly carinate; basal fovea large and deep. Interneurs entire, shallow laterally and apically, punctulate throughout length. Dorsal microsculpture of extremely fine and dense transverse lines or meshes (more on female than male) on elytron (Fig. 42), effaced from head and pronotum. Male medium lobe as in Figure 26. *Size:* see Tables 2, 3, and 4.

Geographical Distribution.—Figure 66; the range of this species extends in the north from at least Guatemala, south to western Panama; no specimens from Mexico were examined.

Natural History Notes.—These beetles are found in large numbers at middle altitudes along rivers with stony and gravelly banks where there is little or no vegetation. Altitudinal range extends from 1700 m to 2600 m in Premontane Wet, Lower Montane Moist, Lower Montane Wet, and Montane Wet forests. Specimens were collected in April, May, and June; teneral ones collected in May indicate that larvae and pupae may be found just prior to that time, that is, in the early rainy season. Individuals occur at the edge of the water, hiding under stones during the day. All individuals studied were fully winged and numerous collection records indicate capture at UV lights; these beetles are probably good fliers.

Material Examined.—Lectotype (see above) and 295 specimens (Table 8).

Taxonomic Notes.—Bates, in his original description, gave as type-locality of this species, "Mexico (Sallé)," however, he specifically mentioned later (Bates 1884:291) that additional material from Peña Blanca, Panama, was identifiable as *B. vernale*. The type-specimen from the Sallé collection is apparently lost, therefore, I selected one of the Peña Blanca specimens as lectotype, thereby restricting the type-locality.

Table 7. Locality Data Deduced from Specimen Labels. 03. *Bembidion mexicanum* Dejean; map Figure 65.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°20′N 91°26′W	ca. 1900	USNM	Jun	5
15°12′N 90°18′W	1372	USNM	May	20
15°07′N 91°32′W	ca. 2000	USNM	Jun	2
15°02′N 90°27′W	1400	USNM	Jun	1
14°58′N 91°46′W	2200	USNM	May	24
14°49′N 91°02′W	2370	USNM	Aug	1
14°37′N 90°30′W	1479	MCZ, UAIC	?	3
14°37′N 90°30′W	1479	USNM	?	1
14°37′N 90°30′W	1525	USNM	?	1
14°33′N 90°35′W	ca. 1300	USNM	Aug	2
09°55′N 84°02′W	1000–1200	USNM	Feb–Mar	1
09°55′N 84°02′W	1000–1200	USNM	Jun	1
		Total specimens examined:		62

5. **Bembidion satellites** Bates

(Figures 7, 27, 43, 67)

Bembidium satellites Bates, 1884:291. [Lectotype ♀, Panama, Peña Blanca, 08°27′N, 081°41′W (BMNH), here designated.]

Diagnostic Combination.—Form long, narrow, and depressed; pronotum with lateral margins nearly straight in basal fifth, hind angles acute. Elytron with interneurs markedly striatopunctulate, intervals subconvex. Dorsal surface without metallic-blue cast. *Color and luster:* dorsum flavous; antennomeres 3 to 11 infuscated, otherwise appendages testaceous; venter piceous; surface shiny, elytra slightly iridescent. *Form:* medium-sized beetles with narrow forebody and very narrow, depressed elytra; pronotum (Fig. 7) convex, slightly wider than head and elytron; eyes large and prominent. *Structure:* frontal furrows well impressed, arcuate medially, extended on clypeus. Hind angle of pronotum markedly carinate; basal fovea large and deep. Interneurs effaced apicolaterally, or nearly so; interneur 7 with small number of widely spaced minute punctulae, 1 to 6 striatopunctulate. Dorsal microsculpture of extremely fine and dense transverse lines or meshes on elytron (Fig. 43), effaced from head and pronotum. Male median lobe as in Figure 27. *Size:* see Tables 2, 3, and 4.

Geographical Distribution.—Figure 67; the range of this species extends from Monte-

Table 8. Locality Data Deduced from Specimen Labels. 04. *Bembidion vernale* Bates; map Figure 66.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°15′N 91°27′W	2560	USNM	Aug	1
10°15′N 83°28′W	0010	USNM	Jun	1
09°59′N 84°00′W	1524	UASM	Jun	13
08°51′N 82°36′W	2240	USNM	Jun	4
08°51′N 82°36′W	1848–2464	USNM	May	112
08°51′N 82°36′W	1720	UASM	May	14
08°51′N 82°36′W	1720	HPST	Apr, May	9
08°51′N 82°36′W	1700	USNM	Jun	35
08°51′N 82°34′W	2134–2438	UAIC	May	5
08°51′N 82°34′W	2134–2438	UAIC	May	13
08°51′N 82°34′W	2134–2438	USNM	May	12
08°47′N 82°26′W	1848	UAIC	Jun	5
08°47′N 82°26′W	1848	USNM	Jun	69
08°47′N 82°26′W	1100	USNM	Jun	1
08°46′N 82°38′W	1360	HPST	May	1
		Total specimens examined:		295

Table 9. Locality Data Deduced from Specimen Labels. 05. *Bembidion satellites* Bates; map Figure 67.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
10°18′N 84°48′W	1300–1600	USNM	Mar	4
10°18′N 84°47′W	1620	USNM	Jun	7
08°51′N 82°35′W	1848–2464	USNM	May	32
08°51′N 82°35′W	1848–2464	USNM	May	5
08°51′N 82°34′W	2134–2438	UAIC	May	6
08°51′N 82°34′W	2134–2438	USNM	May	2
		Total specimens examined:		56

verde, Costa Rica, south along the Cordillera de Talamanca to Volcán de Chiriquí, Panama.

Natural History Notes.—These beetles are found at middle altitudes along slow, small streams with silty and gravelly banks where there is little or no vegetation. Altitudinal range extends from 1600 m to 2500 m in Premontane Rain and Lower Montane Wet forests. Specimens were collected in March, May, and June; teneral ones collected in May and mid-June at Chiriquí indicate that larvae and pupae may be found just prior to that time, that is, in the early rainy season. Individuals occur at the edge of the water, hiding among small stones during the day. Individuals studied were either fully winged or with some state of reduction of the wing membrane. Within populations the length of the wing membrane varied from a small veined pad to a longer veined membrane one-third the length of the elytron, to a fully developed wing with reflexed apex. Such variation was noted from both Monteverde, Costa Rica, and Chiriquí, Panama.

Material Examined.—Lectotype (see above) and 56 specimens (Table 9).

6. **Bembidion lavernae,** new species

(Figures 8, 67)

Diagnostic Combination.—Elytral intervals flat; elytra elongate and spatulate; pronotum with lateral margins nearly straight in basal fifth, hind angles acute. *Color and luster:* rufopiceous; head, prothorax, venter flavous, in part infuscated; appendages flavotestaceous, in part infuscated; surfaces shiny. *Form:* medium-sized for genus with head and prothorax robust; elytra long and spatulate, with markedly sloped humeri and markedly arcuate sides; pronotum (Fig. 8) markedly narrowed basally, slightly wider than head, much wider than elytron; eyes medium-sized, slightly prominent. *Structure:* frontal furrows well impressed, rugose, parallel, ended abruptly at frontoclypeal line; clypeus convex. Hind angle of pronotum noncarinate, square; fovea broad and deep; side margins straight in basal fifth. Interneurs 1 and 2 entire, striate, 3 to 6 abbreviated before apex, 7 and 8 effaced. Dorsal microsculpture of moderately transverse meshes. Male unknown. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 67; known only from the type-locality.

NATURAL HISTORY NOTES.—These beetles live microsympatrically with *B. edwardsi* on Cerro Buenavista at high elevation (3416 m) in the Subparamo plant association (Janzen 1973), Montane Rain Forest of Holdridge (1971). The type is brachypterous, as are no doubt the rest of the members of the species since humeral reduction is more marked than in any other species studied except *B. aeger.*

TYPE-MATERIAL.—**Holotype** ♀, COSTA RICA, San José Province, Cerro Buenavista, 09°33′N, 083°45′W, Mar. (*Edwards*) (USNM), ADP 055189.

DERIVATION OF TAXON NAME.—I take great pleasure in naming this species in honor of La Verne J. Magarian who trudged up many mountains in search of carabid beetles, and who designed the computerized system employed in this and my other carabid studies.

7. **Bembidion quetzal,** new species

(Figures 9, 28, 44, 67)

DIAGNOSTIC COMBINATION.—Pronotum narrow, about as wide as head across eyes; elytral pale spot preapical and isolated; interneur punctulae finely impressed, medium-sized; hind angle of pronotum with well-developed straight carina delimiting deep basal fovea; antennomeres 2 to 11 darkly infuscated. *Color and luster:* dorsum piceous; antennomeres 2 to 11, palpomeres, tibiae, and tarsomeres infuscated, otherwise testaceous; venter rufopiceous; surfaces shiny. *Form:* moderately large beetles with narrow head and pronotum and rather long, almost parallel-sided elytra; pronotum (Fig. 9) slightly wider than head, about equal to width of elytron; eyes large and prominent. *Structure:* frontal furrows well impressed, rugose, almost parallel, and extended on clypeus. Hind angle of pronotum markedly carinate; basal fovea large and deep. Interneurs effaced apicolaterally or nearly so; interneur 7 with small number of widely spaced, minute punctulae, 1 to 6 striatopunctulate, at least basally. Dorsal microsculpture of extremely fine and dense transverse lines or meshes on elytron (Fig. 44), effaced from head and pronotum. Male median lobe as in Figure 28. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 67; known only from west-central Guatemala.

NATURAL HISTORY NOTES.—These beetles are found commonly at middle altitudes along small rivers with stony and gravelly banks where there is little or no vegetation. Altitudinal range extends from 2200 m to 2900 m in Lower Montane Wet and Montane Moist forests. Specimens were collected in May and August, none were teneral. Individuals occur at the edge of water, hiding under stones during the day. All individuals studied were fully winged.

TYPE-MATERIAL.—**Holotype** ♂, GUATEMALA, Quezaltenango, 20.0 km w San Pedro Sacatepéquez at Río Nahuala and Hwy 1, 14°48′N, 091°46′W, May (*Erwin & Erwin*) (USNM), ADP 012345. **Paratypes:** 8♂, 18♀, same data as holotype or as listed in Table 10 and deposited as USNM-12, UASM-2, CAS-2, MCZ-2, AMNH-2, BMNH-2, MNHP-2, JNEG-2.

DERIVATION OF TAXON NAME.—Mayan, *Quetzal,* after the beautiful Guatemalan bird, *Pharomachrus mocinno,* with which these beetles share the forest.

8. **Bembidion diabola**, new species

(Figures 10, 29, 45, 68)

DIAGNOSTIC COMBINATION.—Form short, broad, and subconvex; eyes small and flattish; pronotum abruptly sinuate, sides straight for only a short distance, hind angle acute or square, carina feebly developed; metasternum with intercoxal process narrowly margined, bead well developed and of even width. *Color and luster:* dorsum rufopiceous; scape testaceous, otherwise appendages partially infuscated; venter rufopiceous; surfaces shiny. *Form:* small, rather robust beetles with large head, small eyes, markedly cordate pronotum, ovate elytra; pronotum (Fig. 10) much wider than head or elytron; eyes flattish. *Structure:* frontal furrows well impressed, slightly rugose, almost parallel, angularly prolonged on clypeus. Hind angle of pronotum with feebly developed carinae or no carinae; basal fovea large and deep; side margins abruptly and markedly sinuate. Interneurs entire, though much shallower apicolaterally, striatopunctulate, punctulae small and sparse. Dorsal microsculpture of large transverse meshes on elytra (Fig. 45), effaced from head and pronotum. Male median lobe as in Figure 29. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 68;

TABLE 10. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 07. *Bembidion quetzal* n.sp.; map Figure 68.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°07′N 91°32′W	ca. 2000	USNM	Jun	2
15°04′N 91°52′W	2800–2900	USNM	May	1
14°58′N 91°46′W	2200	USNM	May	23
14°49′N 91°02′W	2370	USNM	Aug	1
		Total specimens examined:		27

TABLE 11. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 08. *Bembidion diabola* n.sp.; map Figure 68.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
09°58′N 83°53′W	3440	MCZ	Jan	3
09°58′N 83°53′W	3350	USNM	May	37
09°58′N 83°53′W	2850	UMAA	Feb	1
09°58′N 83°53′W	2850	UASM	Sep	3
09°58′N 83°53′W	2844	AMNH	Nov	1
? [Costa Rica]	?	UAIC	?	2
? [Costa Rica]	?	UMAA	Jul	6
		Total specimens examined:		53

these beetles occur only in the Cordillera de la Talamanca, Costa Rica.

NATURAL HISTORY NOTES.—These beetles live microsympatrically with *B. vulcanium* on Volcán Irazú at high elevations in the Subparamo plant association (Janzen 1973), Montane Wet Forest of Holdridge (1971), between 2800 m and 3500 m. They were collected in January, May, September, and November; teneral specimens were found in all those months except November, indicating a nonseasonal life cycle. These beetles are found independent of water among bunch grasses on finely textured soil. All individuals studied have small nonveined pads in place of flight wings.

TYPE-MATERIAL.—**Holotype** ♂, COSTA RICA, Volcán Irazú, 09°58′N, 083°53′W, May (*Cartwright*), ADP 003062. **Paratypes:** 30♂, 22♀, same data as holotype or as listed in Table 11 and deposited as USNM-27, UASM-6, CAS-4, MCZ-3, AMNH-3, BMNH-2, MNHP-2, JNEG-2, UAIC-2, UMAA-1.

DERIVATION OF TAXON NAME.—Latin, *diabolus,* meaning the devil, whose lair lay in the caldera of Volcán Irazú near which these beetles live.

9. **Bembidion vulcanium** Darlington

(Figures 11, 30, 46, 68)

Bembidion vulcanium DARLINGTON, 1934:157. [Holotype ♂, COSTA RICA, Volcán Irazú, 09°58′N, 083°53′W, Jan. (*Nevermann*) (MCZ), ADP 003145.]

DIAGNOSTIC COMBINATION.—Eyes prominent, produced well beyond outline of head capsule; pronotum robust, very broad; elytral microsculpture shallowly engraved, surface very shiny. *Color and luster:* dorsum rufopiceous or piceous; scape and femora testaceous, otherwise appendages infuscated; venter rufopiceous or piceous; surfaces shiny. *Form:* moderately small beetles with broad head and markedly broad pronotum, elytra ovoid; pronotum (Fig. 11) much wider than head or elytron, markedly convex and cordiform; eyes large and prominent. *Structure:* frontal furrows moderately well impressed, broad, parallel, extended on clypeus. Hind angle of pronotum feebly carinate, carinae not extended to base; basal fovea deep, extended to side margin; side margins abruptly and markedly sinuate. Interneurs entire, though much shallower laterally and apically, almost effaced in some individuals, striatopunctulate medially, punctulate laterally, punctulae rather large and coarse on disc, widely separated. Dorsal microsculpture of shallowly engraved transverse meshes on elytra (Fig. 46), effaced from head and pronotum. Male median lobe as in Figure 30. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 68; known only from the three high volcanos of Costa Rica: Poás, Irazú, and Cerro de la Muerte.

NATURAL HISTORY NOTES.—These beetles live microsympatrically with *B. diabola* on Volcán Irazú and at high elevations in the Subparamo plant association (Janzen 1973), Montane Rain and Montane Wet forests of Holdridge (1971), between 2600 m and 3400 m on other Costa Rican volcanos. They were collected in January, February, March, June, July, and August; teneral specimens were not found. These beetles are found independent of water among bunch grasses on finely textured soil under stones and pieces of wood. All individuals studied have small nonveined pads in place of flight wings.

MATERIAL EXAMINED.—Holotype (see above) and 32 specimens (Table 12).

TABLE 12. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 09. *Bembidion vulcanium* Darlington; map Figure 68.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
10°11'N 84°13'W	2400	UASM	Aug	7
09°58'N 83°53'W	2200	USNM	Jan–Feb	1
09°58'N 83°53'W	2800–3000	USNM	Jan	7
09°58'N 83°53'W	2800–3000	MCZ	Jan	4
09°35'N 83°48'W	2682	USNM	Jun	1
09°33'N 83°44'W	2700	USNM	Jul	3
09°33'N 83°42'W	2900–3000	GRNO	Aug	1
09°32'N 83°46'W	?	UAIC	Mar	3
09°32'N 83°46'W	3203	USNM	Mar	1
09°32'N 83°46'W	3355	USNM	Jun	5
		Total specimens examined:		33

10. **Bembidion edwardsi**, new species

(Figures 12, 31, 68)

DIAGNOSTIC COMBINATION.—Eyes small and nearly flat; metasternal process broadly margined; elytra very short and narrow in proportion to head and pronotum. *Color and luster:* dorsum of elytron rufopiceous, forebody piceous; antennomeres 1, 2, and base of 3, legs, and base of palpomeres testaceous; venter piceous; surface shiny. *Form:* medium-sized for genus with large robust forebody, small elytra; pronotum (Fig. 12) broader than head, much broader than elytron; eyes small, flattish. *Structure:* frontal furrows well impressed, rugose, markedly delimited laterally by convex carina; anterior supraorbital seta in deep fovea. Hind angle of pronotum without carina, slightly obtuse; basal fovea and base markedly rugose; side margins markedly sinuate at basal third. Elytron short, with slightly sloped humerus, and arcuate side margin. Interneurs 1 and 2 entire, 3 to 8 abbreviated before apex, shallower laterally, all striatopunctulate. Dorsal microsculpture of elytron transverse, not regularly formed of meshes, effaced from head and pronotum. Male median lobe as in Figure 31. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 68; known only from the type-locality.

NATURAL HISTORY NOTES.—These beetles live microsympatrically with *B. lavernae* on Cerro Buenavista at 3416 m elevation in the Subparamo plant association (Janzen 1973). They were collected in March. These beetles are found independent of water among bunch grasses on finely textured soil under stones. All individuals studied have small nonveined pads in place of flight wings.

TYPE-MATERIAL.—**Holotype** ♂, COSTA RICA, San José Province, Cerro Buenavista, 09°33'N, 083°45'W, Mar. (*Edwards*) (USNM), ADP 055177. **Paratypes:** 2♀, same data as holotype and deposited as CAS-1, USNM-1.

DERIVATION OF TAXON NAME.—I take great pleasure in naming this species in honor of J. Gordon Edwards, who first showed me a ground beetle and who collected the type-series.

11. **Bembidion aeger**, new species

(Figures 13, 32, 47, 69)

DIAGNOSTIC COMBINATION.—Pronotum with rudimentary or no carina at hind angle; dorsal surface nonmetallic brown or black; flight wings reduced or virtually absent; elytron with interneurs 7 and 8 virtually absent (a few minute punctulae present in some individuals); small beetles with narrow ovoid elytra and narrow pronotum. *Color and luster:* dorsum piceous; scape and legs testaceous or slightly infuscated, other appendages darkly infuscated; venter piceous. *Form:* small, rather cylindrical beetles with broad forebody in proportion to elytra; pronotum (Fig. 13) slightly wider than head or elytron; eyes small and slightly prominent. *Structure:* frontal furrows shallow, slightly convergent, extended on clypeus. Hind angle of pronotum noncarinate; basal fovea small, shallow; side margins shallowly sinuate. Interneurs effaced apicolaterally and laterally, striatopunc-

TABLE 13. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 11. *Bembidion aeger* n.sp.; map Figure 69.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
09°35′N 83°45′W	3335	GRNO	Jan	10
09°33′N 83°45′W	3416	USNM	Mar	24
09°32′N 83°46′W	3141	USNM	Mar	1
09°32′N 83°46′W	3203	USNM	Mar	6
09°32′N 83°46′W	3355	USNM	Jun	2
09°32′N 83°46′W	?	UAIC	Mar	1
		Total specimens examined:		44

tulate, punctulae small and sparse. Dorsal microsculpture of shallowly engraved transverse meshes, nearly effaced from elytra (Fig. 47), effaced from head and pronotum. Male median lobe as in Figure 32. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 69; known only from the upper slopes of Cerro de la Muerte and adjacent ridges.

NATURAL HISTORY NOTES.—These beetles live microsympatrically with *B. vulcanium*, *B. lavernae*, and *B. edwardsi*, on Cerro de la Muerte and its adjacent ridges at high elevations in the Subparamo plant association (Janzen 1973), Montane Rain Forest of Holdridge (1971), between 3200 m and 3400 m. They were collected in January, March, and June; teneral specimens were not found. All individuals studied have small nonveined pads in place of flight wings.

TYPE-MATERIAL.—**Holotype** ♂, COSTA RICA, Cartago, Cerro de la Muerte, 09°32′N, 083°46′W, June (*Erwin & Erwin*) (UASM), ADP 017224. **Paratypes:** 25♂, 18♀, same data as holotype or as listed in Table 13 and deposited as USNM-22, UASM-2, CAS-2, MCZ-2, AMNH-2, BMNH-2, MNHP-2, JNEG-2, UAIC-1, GRNO-6.

DERIVATION OF TAXON NAME.—Latin, *aeger*, meaning sick or troubled, in reference to the small slight form of these beetles.

12. **Bembidion chiriqui**, new species

(Figures 14, 33, 48, 69)

DIAGNOSTIC COMBINATION.—Eyes prominent, produced well beyond outline of head capsule; form short and subconvex; elytron with all interneurs present, though finer laterally, all easily traceable beyond disc, broadly ovoid; pronotum broad, with abruptly sinuate side margins, sides straight for only a short distance, hind angle acute; metasternum with intercoxal process broadly margined, bead widely removed from apex. *Color and luster:* dorsum piceous, nearly black; scape and legs testaceous, otherwise appendages infuscated; venter piceous; surfaces shiny. *Form:* moderately small beetles with moderately broad head and pronotum; elytra with arcuate sides; pronotum (Fig. 14) slightly wider than head and about equal to width of elytron, markedly convex and cordiform, base prolonged apically with sides straight before acute hind angle; eyes large and prominent. *Structure:* frontal furrows moderately well impressed, slightly convergent on clypeus. Hind angle of pronotum moderately carinate, carina not extended to base; basal fovea deep, extended to side margin. Interneurs entire, impressed laterally, striatopunctulate, punctulae small, shallowly impressed, widely spaced. Dorsal microsculpture of elytron (Fig. 48) of moderately impressed, dense, transverse lines, on head of shallowly engraved slightly transverse meshes, effaced from pronotum. Male median lobe as in Figure 33. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 69; known only from the type-locality.

NATURAL HISTORY NOTES.—These beetles were found commonly at 2220 m altitude in Lower Montane Wet Forest where there was sparse ground vegetation. Specimens were collected in June; teneral specimens were not found. These beetles are found independent of water in oak forest on finely textured soil under leaf litter. All individuals studied have small nonveined pads in place of flight wings.

TYPE-MATERIAL.—**Holotype** ♂, PANAMA, Chiriquí, 8.0 km w Boquete, near Quebrada Emporio, 08°47′N, 082°30′W, June (*Erwin & Erwin*) (USNM), ADP 017618. **Paratypes:** 33♂, 10♀, same data as holotype and deposited as USNM-29, UASM-2, CAS-2, MCZ-2, AMNH-2, BMNH-2, MNHP-2, JNEG-2.

DERIVATION OF TAXON NAME.—Spanish, *Chiriquí*, after the Volcán de Chiriquí on which these beetles live.

The *nahuala* group

DIAGNOSTIC COMBINATION.—Metasternal process without border; elytral interval 3 nonfoveate; male median lobe without ostium flags; dorsal microsculpture absent.

These beetles are independent of running or standing water and occur in Subparamo grasslands of volcanic highlands. The single species included in this group and the one in the *franiae* group are externally quite dissimilar, although both are similar to diverse members of the subgenus *Peryphus* or *vernale* group discussed above. However, males of both *nahuala* and *franiae* have very similar genitalia. Further study of these forms and other related ones from outside the geographic area of this coverage will need to be undertaken to resolve their relationships.

13. **Bembidion nahuala**, new species

(Figures 15, 34, 49, 70)

DIAGNOSTIC COMBINATION.—Metasternal process unmargined; dorsal microsculpture effaced; pronotum small. *Color and luster:* dorsum piceous; tibiae, tarsomeres, and antennomeres 1 to 3 testaceous, otherwise appendages infuscated; venter piceous; surfaces shiny. *Form:* small beetles with narrow, small head and pronotum, and broad elytra; pronotum (Fig. 15) about equal to head in width, both slightly narrower than elytron; elytron either long with squared humerus and slightly arcuate sides, or short with rounded humerus and markedly arcuate sides; eyes large and prominent. *Structure:* frontal furrows well impressed, rugose, parallel, prolonged on clypeus. Hind angle of pronotum acute, markedly carinate; basal fovea large, deep, extended to basal margin; lateral margin evenly sinuate. Interneurs nearly effaced laterally, represented by minute punctulae, effaced apically, discally finely striatopunctulate. Dorsal microsculpture absent (Fig. 49). Male median lobe as in Figure 34. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 70; known only from the Guatemalan highlands.

NATURAL HISTORY NOTES.—These beetles are independent of running or standing water and occur in Subparamo grasslands of volcanic highlands in Lower Montane Wet Forest between 2100 m and 3100 m. Specimens were collected in May, June, and August; teneral specimens were not found. At the type-locality these beetles were found among bunch grass where there was little remaining forest due to activities of man. Specimens were collected from beneath stones along the roadway. The species is dimorphic with respect to wing length; brachypterous individuals have only a small veinless pad in place of the flight wing and constitute a large percentage of the populations sampled (Table 1).

TABLE 14. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 13. *Bembidion nahuala* n.sp.; map Figure 70.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°12′N 90°18′W	3052	USNM	May	3
15°04′N 91°52′W	2800–2900	USNM	May	50
14°58′N 91°46′W	2200	USNM	May	6
14°46′N 91°28′W	2170	USNM	Aug	1
14°20′N 90°31′W	2105	USNM	Jun	1
		Total specimens examined:		61

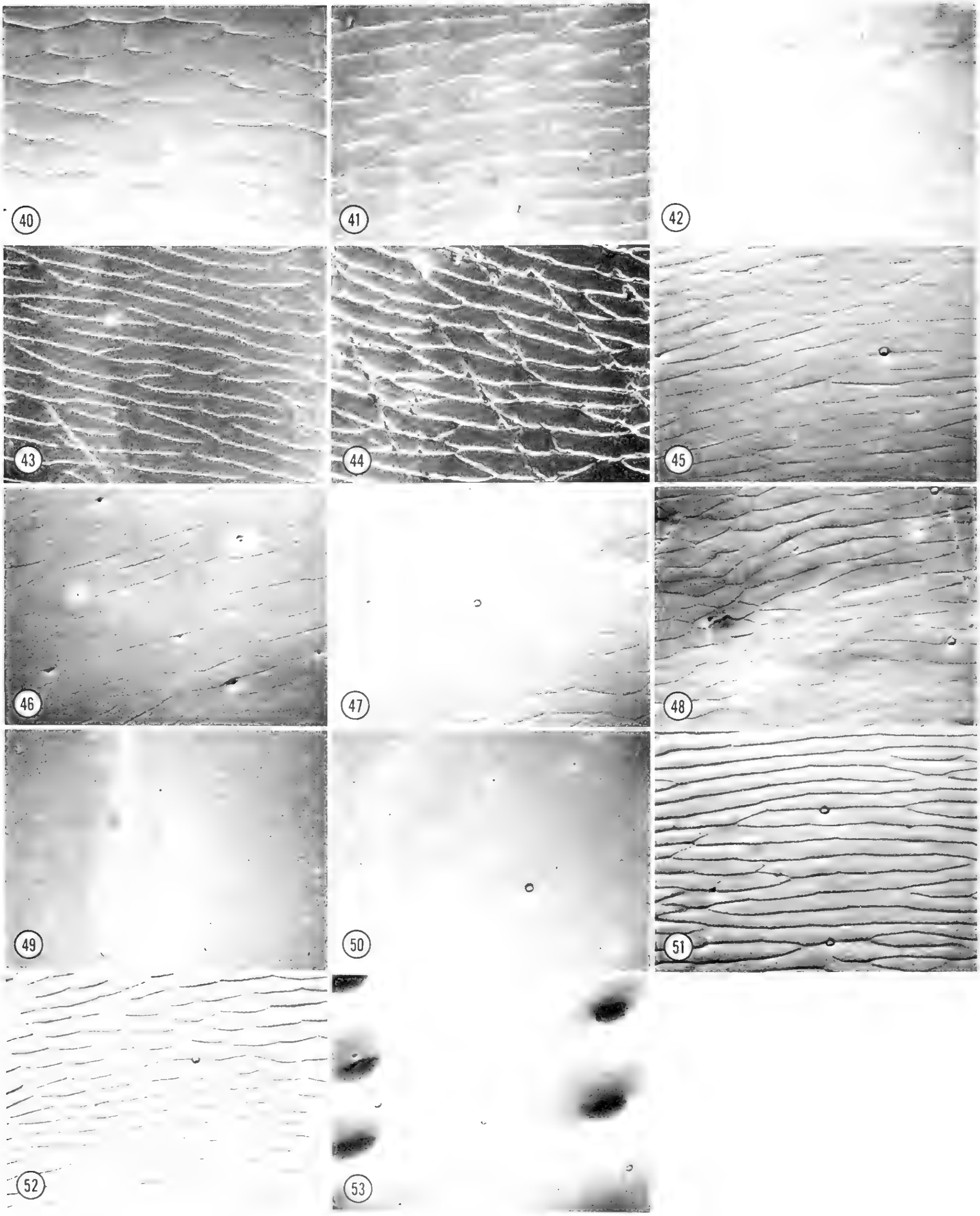
TYPE-MATERIAL.—**Holotype** ♂, GUATEMALA, San Marcos, 27.0 km NW San Marcos, 15°04′N, 091°52′W, May (*Erwin & Erwin*) (USNM), ADP 013024. **Paratypes:** 18♂, 42♀, same data as holotype or as listed in Table 14 and deposited as USNM-40, UASM-2, CAS-4, MCZ-4, AMNH-2, BMNH-2, MNHP-2, JNEG-2, FMNH-2.

DERIVATION OF TAXON NAME.—Uto-aztecan, *Nahuala,* after the Río Nahuala where the type-series was collected; the word derives from the general name for the indigenous peoples of the region, the Nahuatl, of which the Aztecs were part.

The *franiae* group

DIAGNOSTIC COMBINATION.—Metasternal process without border; elytral interval 3 nonfoveate; male median lobe with ostium flags; dorsal microsculpture present.

These beetles are independent of running or standing water and occur in litter in Lower Montane Moist Forest. The single species included in this group and the one in the *nahuala* group are externally quite dissimilar, although both are similar to diverse members of the subgenus *Peryphus* or *vernale* group discussed above. However, males of both *nahuala* and *franiae* have very similar genitalia. Further study of these forms and other related ones from outside the geographic area of this coverage will need to be undertaken to resolve their relationships.



FIGURES 40 to 53. Microsculpture of elytron, left, dorsal aspect posterior to Ed3, 3rd interval, ca. 1000×, males. 40. *B. rogersi* Bates, 7.5 km south of Ojo de Agua, Cartago, Costa Rica. 41. *B. mexicanum* Dejean, 22.0 km west of San Pedro Sacatepéquez at Río Nahuala. 42. *B. vernale* Bates, San Isidro de Coronado, San José, Costa Rica. 43. *B. satellites* Bates, Chomogo area, 10°18′N, 084°47′W, Alajuela, Costa Rica. 44. *B. quetzal* n.sp., 25.0 km south of Totonicapán, Huehuetenango, Guatemala. 45. *B. diabola* n.sp., Volcán Irazú, Cartago, Costa Rica. 46. *B. vulcanium* Darlington, 7.5 km south of Ojo de Agua, Cartago, Costa Rica. 47. *B. aeger* n.sp., Cerro Buenavista, San José, Costa Rica. 48. *B. chiriqui* n.sp., 8.0 km west of Boquete, Chiriquí, Panama. 49. *B. nahuala* n.sp., 27.0 km northwest of San Marcos, San Marcos, Guatemala. 50. *B. aratum* LeConte, La Lima, Cortés, Honduras. 51. *B. cortes* n.sp., La Lima, Cortés, Honduras. 52. *B. sparsum* Bates, Tikal, Del Petén, Guatemala. 53. *B. ixtatan* n.sp., 27.0 miles [43.5 km] west of Sololá, Sololá, Guatemala.

14. **Bembidion franiae**, new species

(Figures 16, 35, 70)

Diagnostic Combination.—Metasternal process between mesocoxae entirely unmargined; elytron bipunctate, punctures around dorsal setae deep and small, not extended beyond middle of adjacent interval; dorsal surface with well-developed microsculpture, that of elytra of finely impressed lines or wide meshes, surface subiridescent, on head clearly and evenly isodiametric, slightly granular, more evenly transverse and less impressed on pronotum. *Color and luster:* dorsum piceous; outer antennomeres and penultimate palpomeres infuscated, otherwise appendages testaceous; venter piceous; surfaces shiny, elytra subiridescent. *Form:* moderately small beetles for genus, with large head and pronotum in proportion to elytra; pronotum (Fig. 16) wider than head and elytron; eyes large and prominent. *Structure:* frontal furrows shallow and broad, prolonged on clypeus; anterior supraorbital pore deeply foveate. Hind angle of pronotum markedly carinate; basal fovea large and deep; lateral margins sinuate, straight for some distance behind sinuation. Interneurs of large punctulae laterally, effaced at extreme apex; disc markedly striatopunctulate, punctulae wide-spaced, not coarsely impressed. Dorsal microsculpture of elytra finely engraved, markedly transverse meshes, of head isodiametric, slightly granular meshes, and on pronotum well-engraved transverse meshes. *Size:* see Tables 2, 3, and 4.

Geographical Distribution.—Figure 70; known only from the type-locality.

Natural History Notes.—These beetles are independent of running or standing water and occur in oak forests in volcanic highlands in Lower Montane Wet Forest at 2500 m and 2600 m. Specimens were collected in August; the paratype is teneral. At the type-locality these beetles were found in oak leaf litter. The species is probably flightless, judging from the markedly developed state of brachyptery in the two known individuals which have only a small veinless pad in place of the flight wing.

Type-Material.—**Holotype** ♂, Guatemala, Huehuetenango, 4.8 km e San Mateo Ixtatán, 15°50′N, 091°27′W, Aug. (*Ball, Frania, & Whitehead*) (USNM), ADP 026917. **Paratype:** 1♀, same data as type (UASM).

Derivation of Taxon Name.—I take pleasure in naming this species in honor of one of the collectors of the types, Henry Frania.

The *incrematum* group

(Subgenus *Eupetedromus* Netolitzky, 1911:190. Type-species *Carabus dentellus* Thunberg, 1787:50, by subsequent designation of Lindroth 1963:348.)

Diagnostic Combination.—Metasternal process not bordered; elytra iridescent from densely transverse microsculpture or microsculpture absent; male genitalia similar to those in members of subgenus *Nothaphus* (Fig. 36; see also Lindroth 1963:367).

These beetles are hygrophilous, occurring along streams or standing water in fine gravel and sand, or on silt. Previously, this group was regarded as Holarctic; the addition to the group of *B. aratum* of the southwestern United States, Mexico, and Central America extends the group's range considerably. All species are fully winged and occur in the lowland or adjacent low hills. The male median lobe of the species covered herein has the pigmented ostium flag characteristic of North and Central American *Bembidion* (*Notaphus*) species, and the endophallus strongly suggests relationship with this group.

15. **Bembidion aratum** LeConte

(Figures 17, 36, 50, 71)

Bembidium aratus LeConte, 1852:189. [Lectotype ♀, Arizona, Gila River Valley (MCZ), designated by Erwin 1982.]

Bembidium scintillans Bates, 1882:150. [Lectotype ♀, Mexico, Capulapam, 17°18′N, 096°27′W (BMNH), designated by Erwin 1982.]

Bembidion vinnulum Casey, 1918:116. [Lectotype ♀, Arizona (*Southern*) (USNM), designated by Erwin 1982.]

Bembidion definitum Casey, 1918:166. [Holotype ♂, Arizona, Tucson, 32°13′N, 110°57′W (USNM).]

Diagnostic Combination.—Elytron with setae Ed3 and Ed5 in interval 3 and not touching adjacent interneurs; elytron without microsculpture, markedly shiny. *Color and luster:* dorsum piceous; elytra maculate, tibial base, femur apex, distal antennomeres, penultimate palpomeres infuscated, otherwise appendages testaceous; venter piceous; surfaces markedly shiny, elytra with faint metallic cast. *Form:* medium-sized beetles for genus with narrow head and pronotum and long-tapered elytra; pronotum (Fig. 17) slightly wider than head, markedly convex, about equal to width of elytron; eyes large and prominent. *Structure:* frontal furrows shallow, broad, parallel, extended to clypeus. Hind angle of pronotum markedly carinate; basal fovea small, deep, extended to basal margin; lateral margins shallowly sinuate. Interneurs en-

TABLE 15. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 15. *Bembidion aratum* LeConte; map Figure 71.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°30′N 86°35′W	0140–0160	UAIC	Jun	1
15°26′N 87°55′W	0020	FDAG	Jun	2
15°26′N 87°55′W	0020	UASM	Jun	1
15°25′N 91°43′W	1440	USNM	Aug	2
		Total specimens examined:		6

TABLE 16. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 16. *Bembidion cortes* n.sp.; map Figure 71.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°26′N 87°55′W	0020	FDAG	Jun	18
15°26′N 87°55′W	0020	UASM	Jun	14
		Total specimens examined:		32

tire, deeply impressed, striatopunctulate anteriorly, striate posteriorly. Dorsal microsculpture of head of shallowly impressed, moderate-sized, slightly transverse meshes, effaced from pronotum and elytron (Fig. 50). Male median lobe as in Figure 36. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 71; southwestern United States to Honduras along the central and eastern parts of the continent.

NATURAL HISTORY NOTES.—These beetles are found from sea level to middle elevations in Tropical Dry, Tropical Very Dry, and Subtropical Dry forests up to 1500 m. Specimens were collected in June and August; no teneral specimens were found. These beetles occur at the edge of moderately large streams in gravel and under stones where there is some silt and at least some sparse vegetation. All known specimens are fully winged; they were attracted to UV light traps in Mexico, Honduras, and Guatemala, indicating that the beetles fly.

MATERIAL EXAMINED.—Types (see above) and 6 specimens (Table 15).

The *dorsale* group

(Subgenus *Notaphus* Stephens, 1828:2. Type-species *Carabus varius* Olivier, 1795:110, by subsequent designation of Westwood 1840:7.)

DIAGNOSTIC COMBINATION.—Metasternal process completely bordered; elytra and forebody with isodiametric microsculpture; elytra with light-colored mosaic pattern on dark background; male genitalia uniform and similar to those in members of subgenus *Eupetedromus* (Fig. 36, see also Lindroth 1963:367).

These beetles are hygrophilous, occurring along streams or standing water in fine gravel and sand or among stones, or on sea beaches. Previously, this group was regarded as predominantly Holarctic, however, several species occur in the Tropics and in South Temperate regions, mainly on beaches. All species are fully winged and occur in the lowland or adjacent low hills. The male median lobes of the species covered herein have the pigmented ostium flag characteristic of North American *Bembidion* (*Notaphus*) species.

16. **Bembidion cortes,** new species

(Figures 18, 37, 51, 71)

DIAGNOSTIC COMBINATION.—Elytron with setae Ed3 and Ed5 in interval 3, not touching adjacent interneurs, and with perfectly isodiametric and well-engraved microsculpture; pronotum broad, moderately convex, much wider than head across eyes, side margins not markedly arcuate nor much convergent behind, shallowly sinuate before hind angle. *Color and luster:* dorsum of elytron with mosaic color pattern, head and pronotum dark green; distal antennomeres infuscated, otherwise appendages flavous or testaceous; venter rufopiceous or piceous, in some specimens apex of abdomen paler; surface of elytra shiny, forebody metallic. *Form:* medium-sized beetles for this genus with head, pronotum, and elytra broad; pronotum (Fig. 18) somewhat wider than head and elytron; eyes large and prominent. *Structure:* frontal furrows very shallow and broad, extended on clypeus. Hind angle of pronotum markedly carinate; basal fovea broad and deep; lateral margins shallowly sinuate. Interneurs entire, deeply impressed throughout their length, striatopunctulate anteriorly, striate posteriorly. Dorsal microsculpture of elytron nearly isodiametric, with some transverse meshes (Fig. 51), that of head and pronotum perfectly isodiametric, slightly granulate, deeply engraved. Male median lobe as in Figure 37. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 71; southern Mexico north at least to Vera Cruz, south to Honduras.

NATURAL HISTORY NOTES.—These beetles are found at low elevations in Tropical Dry Forests at 20 m. Specimens were collected in June and December; no teneral specimens were found. All known specimens are fully winged; they were attracted to UV light traps in Mexico and Honduras, indicating that the beetles fly.

TYPE-MATERIAL.—**Holotype** ♂, HONDURAS, Cortés, La Lima, 15°26′N, 087°55′W, June (*Blanton, Broce, & Woodruff*) (FDAG), ADP 047025. **Paratypes:** 9♂, 22♀, same data as holotype or as listed in Table 16 and deposited as USNM-12, UASM-2, CAS-2, MCZ-2, BMNH-2, MNHP-2, JNEG-2, FDAG-7.

DERIVATION OF TAXON NAME.—Spanish, *Cortés,* after the sea-faring explorer from Spain who touched the Middle American coast and Caribbean islands in so many places; in reference to the probable habitat and distribution of these beetles.

17. **Bembidion sparsum** Bates

(Figures 19, 38, 52, 71)

Bembidium sparsum BATES, 1882:151. [Lectotype ♂, MEXICO, Oaxaca (BMNH), designated by Erwin 1982.]

DIAGNOSTIC COMBINATION.—Elytron with setae Ed3 and Ed5 in interval 3 and not touching adjacent interneurs, and with perfectly isodiametric and well-engraved microsculpture; pronotum narrow, about as wide as head across eyes, markedly constricted behind. *Color and luster:* dorsum of elytron with mosaic color pattern, head and pronotum dark green; distal antennomeres infuscated, otherwise appendages flavous or testaceous; venter rufopiceous or piceous, in some specimens apex of abdomen paler; surface of elytra shiny, forebody metallic. *Form:* medium-sized beetles for this genus with head, pronotum, and elytra broad; pronotum (Fig. 19) narrow, equal in width to head and elytron; eyes large and prominent. *Structure:* frontal furrows very shallow and broad, extended on clypeus. Hind angle of pronotum markedly carinate; basal fovea broad and deep; lateral margins deeply sinuate. Interneurs entire, deeply impressed throughout their length, striatopunctulate anteriorly, striate posteriorly. Dorsal microsculpture of elytron nearly isodiametric, with some transverse meshes (Fig. 52), that of head and pronotum perfectly isodiametric, slightly granulate, deeply engraved. Male median lobe as in Figure 38. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 71; most of Middle America from Sonora, Mexico, south to at least Nicaragua and along the east coast at Vera Cruz, Mexico, as well as on the islands of Jamaica and Hispaniola (Haiti), and in Colombia. Curiously, there are no records from Costa Rica or Panama.

NATURAL HISTORY NOTES.—These beetles are found at low elevations in Tropical Dry, Tropical Very Dry, and Tropical Moist forests between 20 m and 500 m. Specimens were collected in June, July, August, and September on the mainland, February on Jamaica, and September on Hispaniola; some teneral specimens were found on Jamaica and Hispaniola, and some of the September mainland specimens were also teneral. These beetles frequent low-lying areas on dry sand which are adjacent to intermittently wet streams; the general vegetation is thorn scrub. All known specimens are fully winged; they were attracted to UV light traps in many localities, indicating that the beetles fly. This together with their occurrence in the Greater Antilles and their preference for intermittently wet areas indicate they are highly vagile dispersants.

MATERIAL EXAMINED.—Lectotype (see above) and 17 specimens (Table 17).

18. **Bembidion armuelles,** new species

(Figures 20, 71)

DIAGNOSTIC COMBINATION.—Elytron with setae Ed3 and Ed5 in interval 3 and not touching adjacent interneurs, and with perfectly isodiametric and well-engraved microsculpture; pronotum very broad and convex with abruptly sinuate lateral margins basally, much wider than head across eyes, markedly constricted behind. *Color and luster:* dorsum of elytron with mosaic color pattern, head and pronotum dark green; distal antennomeres infuscated, otherwise appendages flavous or testaceous; venter rufopiceous or piceous, in some specimens apex of abdomen paler; surfaces of elyta shiny, forebody metallic. *Form:* medium-sized beetles for this genus with head, pronotum, and elytra

TABLE 17. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 17. *Bembidion sparsum* Bates; map Figure 71.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
17°25′N 88°29′W	0000–0300	USNM	Jun	1
17°20′N 89°39′W	0250	USNM	Jun	3
17°20′N 88°33′W	0000–0300	USNM	Jun	1
17°15′N 88°45′W	0000–0300	USNM	Jun	1
15°44′N 87°27′W	0000–0020	UMAA	Mar	2
15°26′N 87°55′W	0020	UASM	Jun	4
13°52′N 90°05′W	0030–0040	USNM	Jul	2
13°36′N 89°50′W	0000–0010	UASM	May	1
12°36′N 86°02′W	0457	USNM	Jul	1
12°23′N 86°03′W	0122	USNM	Jun	1
		Total specimens examined:		17

broad; pronotum (Fig. 20) very broad and convex, wider than head and elytron; eyes large and prominent. *Structure:* frontal furrows very shallow and broad, extended on clypeus. Hind angle of pronotum markedly carinate; basal fovea broad and deep; lateral margins deeply sinuate. Interneurs entire, deeply impressed throughout their length, striatopunctulate anteriorly, striate posteriorly; intervals convex. Dorsal microsculpture of elytron nearly isodiametric, with some transverse meshes, that of head and pronotum perfectly isodiametric, slightly granulate, deeply engraved. Male unknown. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 71; known only from the type-locality.

NATURAL HISTORY NOTES.—The town of Armuelles is a port on the Pacific Ocean with extensive sea beach; behind the town lies Tropical Moist Forest. I do not know the habitat in which the unique specimen was collected; however, it is fully winged, it was collected in June, and it is not teneral.

TYPE-MATERIAL.—**Holotype** ♀, PANAMA, Chiriquí, Puerto Armuelles, 08°17′N, 082°52′W, June (*Bierig*) (MCZ), ADP 003142.

DERIVATION OF TAXON NAME.—Spanish, *Armuelles,* the name of the town near which the holotype was collected.

The *affine* group

(Subgenus *Furcacampa* Netolitzky, 1931:158. Type-species *Bembidium affine* Say, 1823:86, by original designation.)

DIAGNOSTIC COMBINATION.—Metasternal process completely bordered, margin removed from apex; elytra and forebody with isodiametric microsculpture; elytra with light-colored mosaic pattern on dark background; male genitalia similar to those in members of *versicolor* group (fig. 191 in Lindroth 1963:379).

These beetles are hygrophilous, occurring along streams or standing water on fine clay or sand, at the margins of marshy pools, or on lake beaches. Previously, this group was regarded as Nearctic, however, the new species described below from Panama extends the range considerably. Both species of the group are fully winged and occur in the lowland or adjacent low hills.

19. **Bembidion barrensis**, new species

(Figures 22*b*, 39*b*, 74)

DIAGNOSTIC COMBINATION.—Frontal furrows shallow, single, and nearly parallel between eyes, convergent and doubled on clypeus. *Color and luster:* dorsum of elytron with mosaic color pattern, head and pronotum dark piceous; appendages testaceous (on holotype, outer antennomeres missing, palpomeres missing); venter piceous; surfaces of elytra shiny, forebody slightly metallic. *Form:* small-sized for genus with narrow forebody and elytra; elytra with square humeri; pronotum (Fig. 22*b*) narrower than head, about equal in width to elytron; eyes large and prominent. *Structure:* frontal furrows well impressed, slightly rugose, almost parallel between eyes, angularly prolonged and doubled on clypeus. Hind angle of pronotum acute, with feebly developed, short, sharp carinae; basal fovea large and deep; side margins abruptly and markedly sinuate. Interneurs entire, though much shallower or effaced apicolaterally, striatopunctulate, punctulae medium-sized, coarse, and close-spaced. Dorsal microsculpture of large transverse meshes on apex of elytron, head and pronotum, effaced from disc of elytron. Male median lobe as in Figure 39*b*. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 74; known only from the type-locality.

NATURAL HISTORY NOTES.—The single specimen was found in Tropical Moist Forests at 28 m. It was collected in October and is not teneral. It is fully winged. The habitat consists of marshy lake shore (on the back side of the island opposite the Canal) with rich growth of *Calathea* and other emergent broadleaf plants growing in shallow, but rich, organic soil on top of red laterite. The marsh is heavily shaded in this area. The beetle was in a thin layer of leaves less than a meter from the water.

TYPE-MATERIAL.—**Holotype** ♂, PANAMA, Canal Zone, Barro Colorado Island, 09°10'N, 079°51'W, Oct. (*Erwin & Erwin*) (USNM), ADP 041711.

DERIVATION OF TAXON NAME.—Spanish, *barro*, meaning clay or mud and part of the name of the place where the holotype was collected.

The *championi* group

(Subgenus *Cyclolopha* Casey, 1918:144. Type-species *Bembidium sphaeroderum* Bates, 1882:147, here designated.)

DIAGNOSTIC COMBINATION.—Metasternal process completely bordered, margin not removed from apex; pronotum markedly lobed basally, hind angle absent or markedly obtuse; frontal furrows deep, markedly convergent, prolonged on clypeus.

Little is known regarding the life history and habits of these beetles. Few specimens are available for study. I collected one individual of the group in Mexico from beneath a rosette of prostrate grasses on a volcanic hillside in the Transverse Volcanic Belt. There was no water close by. A partially complete manuscript by G. G. Perrault (in litt.) indicates there are eight species in the group, distributed from Colorado, USA, to Guatemala.

20. **Bembidion cyclodes** Bates

(Figure 72)

Bembidium cyclodes BATES, 1884:290. [Lectotype ♀, MEXICO, Oaxaca (BMNH), selected and labelled by Perrault, herewith designated.]

Bembidium aztecanum CASEY, 1918:145. [Lectotype ♂, MEXICO, Cuernavaca (USNM), selected and labelled by Perrault, here designated.]

DIAGNOSTIC COMBINATION.—Pronotum with hind angle rounded with small angle along margin at posterior seta, base markedly lobed; elytron with interneur 7 absent, interneur 6 extended to at least middle. *Color and luster:* dorsum of elytra and propleura rufous; distal antennomeres infuscated, otherwise appendages testaceous; head, pronotum, and venter piceous; surfaces markedly shiny. *Form:* small beetles with broad forebody and elytra; pronotum slightly wider than head or elytron; eyes markedly large and prominent. *Structure:* frontal furrows sulcate, narrow, convergent, extended to clypeal setigerous pore. Hind angle of pronotum markedly obtuse, nearly absent; dorsum markedly convex; lateral margins markedly arcuate posteriorly; base prominently lobed. Interneurs 1 to 6 each a row of punctulae in basal half of elytron, 7 absent, 1 striatopunctulate, in apical half 2 to 6 absent; punctulae separated by their own diameter. Dorsal microsculpture absent. *Size:* see Tables 2, 3, and 4.

TABLE 18. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 20. *Bembidion cyclodes* Bates; map Figure 72.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
[Types from Mexico]	?	BMNH, USNM	?	2
15°23'N 91°02'W	1829	AMNH	Aug	1
		Total specimens examined:		3

GEOGRAPHICAL DISTRIBUTION.—Figure 72; known specifically from only one locality in Guatemala; older records give only "Guat." Perrault recorded this species from localities in Mexico, north as far as Cuernavaca.

NATURAL HISTORY NOTES.—These beetles are found at middle elevations in Lower Montane Moist Forests between 1450 m and 1900 m. Specimens were collected in August and October; no teneral specimens were found. All known specimens are fully winged.

MATERIAL EXAMINED.—Types (see above) and 1 specimen (Table 18).

21. **Bembidion championi** Bates

(Figures 21, 72)

Bembidium championi BATES, 1882:148. [Lectotype ♂, GUATEMALA, Quiché Mountains (MNHP), selected and labelled by Perrault, here designated.]

TABLE 19. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 21. *Bembidion championi* Bates; map Figure 72.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
[Type from Guatemala]	?	BMNH	?	1
[Mexico. Chiapas, 8.6 mi. E San Cristobal]		UASM		2
		Total specimens examined:		3

TABLE 20. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 22. *Bembidion ixtatan* n.sp.; map Figure 72.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°50′N 91°27′W	2460	USNM	Aug	6
14°47′N 91°15′W	ca. 2400	USNM	Aug	1
		Total specimens examined:		7

DIAGNOSTIC COMBINATION.—Pronotum with hind angle rounded, without small angle along margin at posterior seta, base markedly lobed; elytron with interneurs 6 and 7 present, short, not extended beyond basal sixth. *Color and luster:* dorsum of elytra and propleura rufous; distal antennomeres infuscated, otherwise appendages testaceous; head, pronotum, and venter piceous; surface markedly shiny. *Form:* small beetles with broad forebody and elytra; pronotum slightly wider than head or elytron; eyes markedly large and prominent. *Structure:* frontal furrows sulcate, narrow, convergent, extended to clypeal setigerous pore. Hind angle of pronotum markedly obtuse, nearly absent; dorsum markedly convex; lateral margins markedly arcuate posteriorly; base prominently lobed. Interneurs 1 to 7 each a row of punctulae in basal half of elytron, 1 striatopunctulate, in apical half 2 to 7 absent; punctulae separated by more than their own diameter. Dorsal microsculpture absent. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 72; known specifically from only the type-locality in Guatemala; other records give only "Guat." Perrault recorded this species from localities in Mexico, north as far as Jalisco.

NATURAL HISTORY NOTES.—These beetles are found at middle elevations in Lower Montane Moist Forests between 2100 m and 2700 m. Specimens were collected in June, August, and September; no teneral specimens were found. All known specimens have the wings reduced to small pads, each of which retains the bases of two major veins.

MATERIAL EXAMINED.—Lectotype (see above) and 2 specimens (Table 19).

The *cognatum* group

DIAGNOSTIC COMBINATION.—Metasternal process completely bordered, margin not removed from apex; pronotum not lobed basally, hind angles nearly square; frontal furrows deep, markedly convergent, prolonged on clypeus; microsculpture effaced from pronotum and elytra.

These beetles are hygrophilous, occurring along streams in fine gravel and sand, or in mosses. Previously, this group of two species was known from only North America and Mexico; the Central American one described below extends the group's range considerably. Both species are fully winged and occur at middle elevations. The male median lobe of the species covered herein has two pigmented ostium flags.

This group has not been assigned to subgenus. Its members are intermediate between *transparens* group (head structure) and *versicolor* group (body structure and color pattern). The unique male genitalia does not indicate relationship to either of these mentioned groups. Placement must await revisions of the several species groups with convergent frontal furrows (see Erwin and Kavanaugh 1981).

22. **Bembidion ixtatan**, new species

(Figures 22*a*, 39*a*, 53, 72)

DIAGNOSTIC COMBINATION.—Pronotum with hind angle squared; base not lobed; elytron with all interneurs coarsely punctulate well beyond middle; frontal furrows markedly convergent; microsculpture effaced from elytra and pronotum. *Color and luster:* elytra piceous, obscurely maculate, maculae not well defined; forebody and venter piceous; appendages infuscated; surfaces markedly shiny. *Form:* small beetles for the genus with head large, pronotum narrow, elytra convex and narrow; pronotum (Fig. 22*a*) slightly wider than head and elytron; eyes moderately large and prominent. *Structure:* frontal furrows well impressed, markedly convergent toward clypeus, doubled on clypeus. Hind angle of pronotum nearly square, finely carinate, carinae markedly short; basal fovea small and deep; lateral margins shallowly, abruptly sinuate. Interneurs effaced apicolaterally, markedly and coarsely punctulate on disc. Dorsal microsculpture effaced (Fig. 53). Male median lobe as in Figure 39*a*. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 72; known only from the Guatemalan highlands.

NATURAL HISTORY NOTES.—These beetles are found at upper to middle elevations in Lower Montane Moist Forests at 2500 m. Specimens were collected in August; no teneral specimens were found. These beetles live near mountain streams where they can be found during the day by washing mosses. All known specimens are fully winged.

TYPE-MATERIAL.—**Holotype** ♂, GUATEMALA, Huehuetenango, 4.8 km E San Mateo Ixtatán, 15°50′N, 091°27′W (*Ball, Frania, & Whitehead*) (USNM) ADP 026911. **Paratypes:** 2♂, 4♀, same data as for holotype or as listed in Table 20 and deposited as USNM-2, UASM-2, CAS-2.

DERIVATION OF TAXON NAME.—Probably Uto-Aztecan, *Ixtatan,* from the name of the town near which the type-series was collected.

Genus **Geocharidius** Jeannel

Geocharidius JEANNEL, 1963a:107. [Type-species *Anillus integripennis* Bates, 1882:145, by original designation.]

For details on related groups see Jeannel (1937, 1960, 1963a), and Taglianti (1973).

DIAGNOSTIC COMBINATION.—Small-sized, more or less depressed or markedly convex beetles with narrow or broad elytra, narrow forebody, and with medium-length, slender appendages. Color pale rufotestaceous. Terminal palpomere subulate; eyes absent; antennomeres 2 to 11 entirely pubescent and with numerous long setae, mentum with well-developed but small tooth; mandibles unisetose. Pronotum with two midlateral and usually two basilateral setae; elytron without discal setae, with scattered pubescence. Elytron without recurrent groove. Microsculpture various. Female stylus small, spatulate, unisetose. Male parameres as in Taglianti (1973). Flight wings absent, metathorax markedly reduced in size, elytra fused along midline. ABL = 1.0–1.5 mm in Central American species.

NATURAL HISTORY.—Species of this genus live in deep humus and decaying leaf litter or under deeply embedded stones in forests; they can be found by the use of sifting and Berlese funnel techniques. All species in Central America are true alticoles; all are wingless. The larvae are unknown.

NOTES.—The *Geocharidius* fauna of Middle America is very complex and difficult to work with because of the lack of a firm taxonomic base with which to start and the lack of representatives of the majority of the fauna. New collecting methods are turning up these small hypogean or deep-litter forms in great numbers. Of the five species treated below, four were discovered as recently as 1974. Use of these new collecting methods and new tools for revisionary studies (e.g., scanning electron micrographs) should allow detailed studies and a subsequent reconstruction of the phylogeny soon. Externally, the beetles differ in states of the frontal furrows, body form, pronotum shape, dorsal elytral chaetotaxy and structure of the interneurs, and microsculpture even though the beetles themselves are similar in habitus. In Central America, two habitus types occur: the depressed body form type such a *G. integripennis* and the globose type (Figs. 54, 55).

Adults can easily be sexed in two ways. Males have three basal tarsomeres of the anterior leg dilated and with modified setae beneath, forming a loosely biserrate row, and two setae along the caudal edge of sternum VI; females have no specially modified setae or dilated tarsomeres and have four setae on sternum VI.

ARRANGEMENT OF TAXA: *GEOCHARIDIUS.*—The Anillina are in need of a worldwide review and revision. No system heretofore proposed is adequate to reflect true relationships. Therefore, the arrangement of taxa below is strictly arbitrary.

CHECKLIST OF *GEOCHARIDIUS* SPECIES OF CENTRAL AMERICA.

1. *G. integripennis* (Bates 1882:145)
2. *G. romeoi,* new species
3. *G. gimlii,* new species
4. *G. phineus,* new species
5. *G. tagliantii,* new species

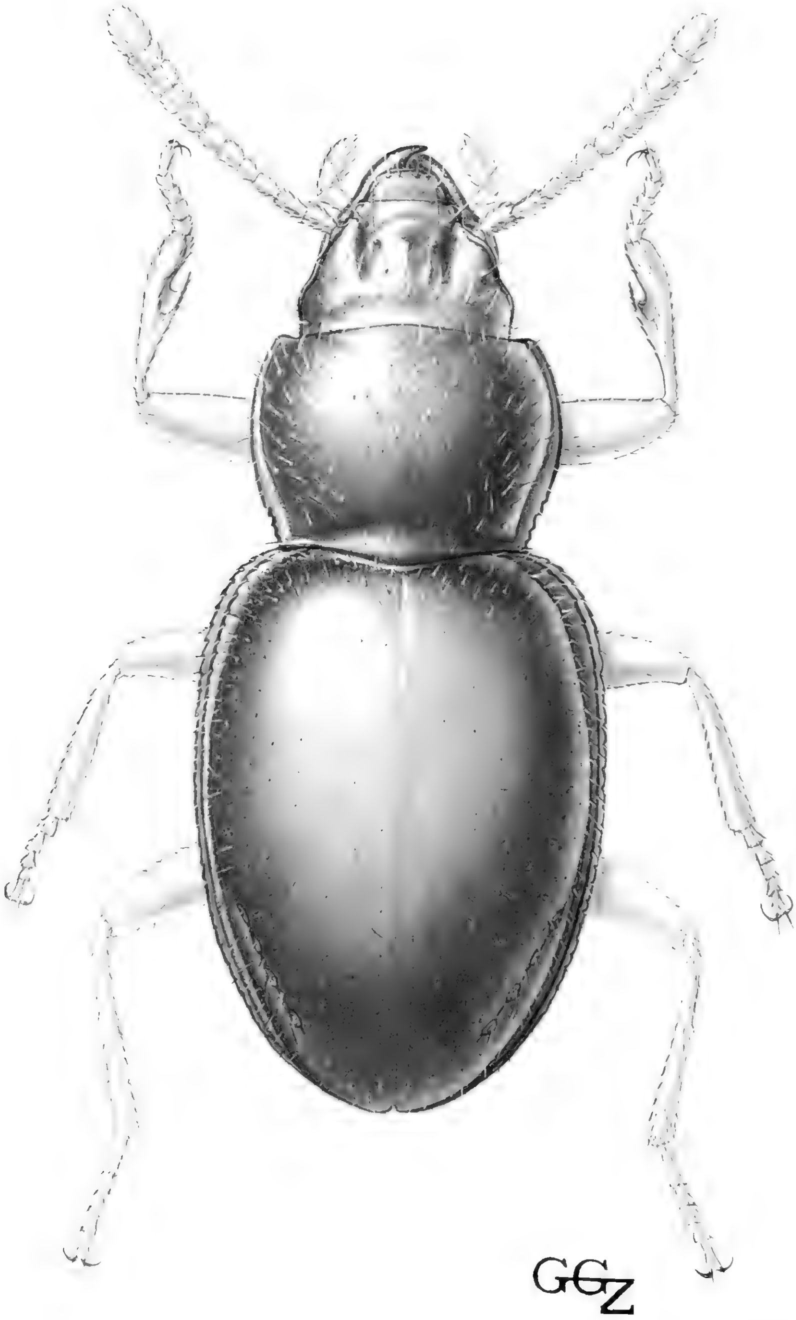


FIGURE 54. Habitus of *Geocharidius phineus* n.sp., dorsal aspect, male from 1.6 km south of Pantin, Baja Verapaz, Guatemala.

Key to Species of *Geocharidius* of Central America

1. Pronotum with lateral edge in front of hind angle multidentate ---------- 5. *G. taglianti*, new species
– Pronotum with lateral edge unidentate or smooth ---------- 2

2(1). Pronotum and elytra highly convex (lateral aspect), especially elytra which appear to be 'inflated' to a higher plane than pronotum ---------- 3
– Pronotum and elytra much less convex, dorsum of elytra on same plane with pronotum (lateral aspect) ---------- 4

3(2). Pronotum with markedly obtuse hind angle, side margin in front of them not sinuate; small beetles, SBL = 1.3 mm ---------- 2. *G. romeoi*, new species
– Pronotum with slightly obtuse hind angle, side margin in front of them sinuate; larger beetles, SBL = 1.5 mm ---------- 4. *G. phineus*, new species

4(2). Pronotum with small denticle on side margin in front of hind angle; body long, narrow, and depressed ---------- 1. *G. integripennis* Bates
– Pronotum without denticle, side margin entire; body broader and less depressed ---------- 3. *G. gimlii*, new species

1. **Geocharidius integripennis** (Bates)

(Figure 73)

Anillus integripennis BATES, 1882:145. [Lectotype ♂, GUATEMALA, Totonicapán, Totonicapán, 14°54′N, 091°22′W (*Champion*) (BMNH), here designated.]

DIAGNOSTIC COMBINATION.—Pronotum with lateral edge unidentate; pronotum and elytra slightly convex, dorsum of elytra on same plane with pronotum in lateral aspect; body long, narrow, and depressed. *Color and luster:* body dark testaceous; appendages pale testaceous. *Form:* medium-sized beetles for this genus with narrow and depressed forebody and elytra; pronotum wider than head and elytron; eyes absent. *Structure:* frontal furrows moderately well impressed anteriorly, smooth. Hind angle of pronotum sharp, with secondary denticle anterior to it; side margin sinuate. Elytron with side margin narrowly flanged in basal third, flange microserrulate, humerus evenly rounded; surface with scattered setae, striae absent. Dorsal microsculpture of head and scutellum isodiametric, sculpticells large and well impressed; effaced elsewhere. Male lectotype not dissected. *Size:* see Tables 2, 3, and 4.

GEOGRAPHICAL DISTRIBUTION.—Figure 73; known only from the type-locality.

NATURAL HISTORY NOTES.—The type-locality is located in Lower Montane Wet Forest in the Guatemalan highlands at about 2800 m.

MATERIAL EXAMINED.—Lectotype (see above) and 3 paralectotypes (BMNH).

TAXONOMIC NOTES.—Bates (1882) described this species from specimens collected by Champion. Four of these were deposited at BMNH and labelled with "Biologia Centrali-Americana" labels; another specimen with the printed Champion collector label but without a "BC-A" label was found in MNHP by Taglianti (1973). Taglianti also found a specimen with a handwritten label indicating it was from Totonicapán, Guatemala. Both specimens found in MNHP had handwritten labels (believed by Taglianti to be in Jeannel's handwriting) determining the specimens as "integripennis Bates." Bates (1882:145) did not indicate how many specimens he studied, but he provided a description and a handpainted illustration of a specimen of his new species.

Bates's description and illustration agree with the specimens labelled "BC-A" in BMNH: ". . . flavo-testaceus, subnitidus; frontalibus elongatis, sat profundis, interspatio subangusto convex." Bates's illustration indicates that the specimen(s) he described was uniformly flavotestaceous as well.

Unfortunately, Taglianti obtained two specimens from MNHP that were probably studied by Jeannel and selected them as lectotype and paralectotype, and he used a page of text describing how the specimens did not match Jeannel's 1963 redescription of the species. Taglianti apparently did not study the "BC-A" material at BMNH.

The MNHP specimens are not Bates's *integripennis* (and probably are not what Jeannel studied earlier). Since the specimens do not match Bates's description (e.g., Taglianti states that they have a darkly colored head and shal-

TABLE 21. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 01. *Geocharidius romeoi* n.sp.; map Figure 73.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°14′N 90°12′W	1600	USNM	Aug	21
15°10′N 90°12′W	1500	USNM	Aug	8
		Total specimens examined:		29

lowly impressed frontal furrows with "flattened forehead"), I consider Taglianti's selection of lectotype null and void. The two MNHP specimens are further considered under *G. tagliantii*, below.

It is likely that Jeannel studied "4 femelles" either from the BMNH collection (although he writes the type is in MNHP) or his material has been lost. It is clear that from his description and drawings he was describing the same species as Bates (note frontal furrows in drawings and his statement that the pronotum "les cotés faiblement argués, sans sinuosité postérieure, non crénelés . . . ." It is no wonder that Taglianti could not match Jeannel's description with the specimens at MNHP.

Reconstruction of the probable chain of events is that part of Champion's material (representing two species) went to BMNH, part to MNHP. Only the BMNH material was used by Bates in the original description. Jeannel probably only studied MNHP material, but the material represented the same species Bates studied, i.e., *integripennis*. Perhaps Jeannel overlooked the fact that he had two species represented. Taglianti saw only the second species and misapplied the name.

2. **Geocharidius romeoi**, new species

(Figure 73)

DIAGNOSTIC COMBINATION.—Elytra and pronotum highly convex; pronotum with obtuse hind angle, and nonsinuate side margin. *Color and luster:* body and head bright rufotestaceous; appendages pale testaceous. *Form:* small beetles for this genus with broad forebody and inflated elytra; pronotum highly convex, narrower than elytra; eyes absent. *Structure:* frontal furrows obsolete, front with moderate-sized tubercule at middle. Hind angle of pronotum doubled, each denticle sharp; side margin evenly arcuate, not sinuate. Elytron highly convex, short, side margin arcuate, narrowly flanged in basal third, flange microserrulate, humerus evenly rounded. Elytron surface with numerous scattered setae, striae absent. Dorsal microsculpture of head and scutellum isodiametric, sculpticells large and well impressed; effaced elsewhere. Male holotype not dissected. SBL = 1.002–1.282 mm; TW = 0.403–0.590 mm.

GEOGRAPHICAL DISTRIBUTION.—Figure 73; known only from the type-locality.

NATURAL HISTORY NOTES.—These beetles are found commonly at lower to middle altitudes in leaf litter with Berlese techniques. Altitudinal range extends from 1500 m to 1600 m in Tropical Wet Forests. Specimens were collected in August; several were teneral.

TYPE-MATERIAL.—**Holotype** ♂, GUATEMALA, Baja Verapaz, 13.0 km s Purulha, 15°10′N, 090°12′W, Aug. (*Ball, Frania, & Whitehead*) (USNM), ADP 026533. **Paratypes:** 17♂, 11♀, same data as holotype or as listed in Table 21 and deposited as USNM-14, UASM-4, CAS-4, MCZ-2, BMNH-2, MNHP-2.

DERIVATION OF TAXON NAME.—*Romeoi,* after Shakespeare's Romeo, who in Act I told Benvolio, "He that is stricken blind cannot forget the precious treasure of his eyesight lost," in reference to the demise of the Central American forests and its probable impact on these blind beetles, which are restricted to deep forest humus and litter.

3. **Geocharidius gimlii**, new species

(Figure 73)

DIAGNOSTIC COMBINATION.—Pronotum and elytra in lateral aspect on same plane; posterior angle of the pronotum without denticle. *Color and luster:* body and head flavotestaceous; appendages pale testaceous. *Form:* medium-sized beetles for this genus with narrow forebody and elytra; pronotum wider than head, narrower than elytron; eyes absent. *Structure:* frontal furrows shallowly impressed anteriorly, smooth. Hind angle of pronotum slightly obtuse, not denticulate; side margins straight and markedly convergent behind middle. Elytron moderately long and narrow, subdepressed, disc somewhat convex; side margin moderately flanged in basal third, flange strongly microserrulate, humerus evenly rounded. Elytral surface with scattered setae, striae absent. Dorsal microsculpture of large isodiametric meshes on head, base of

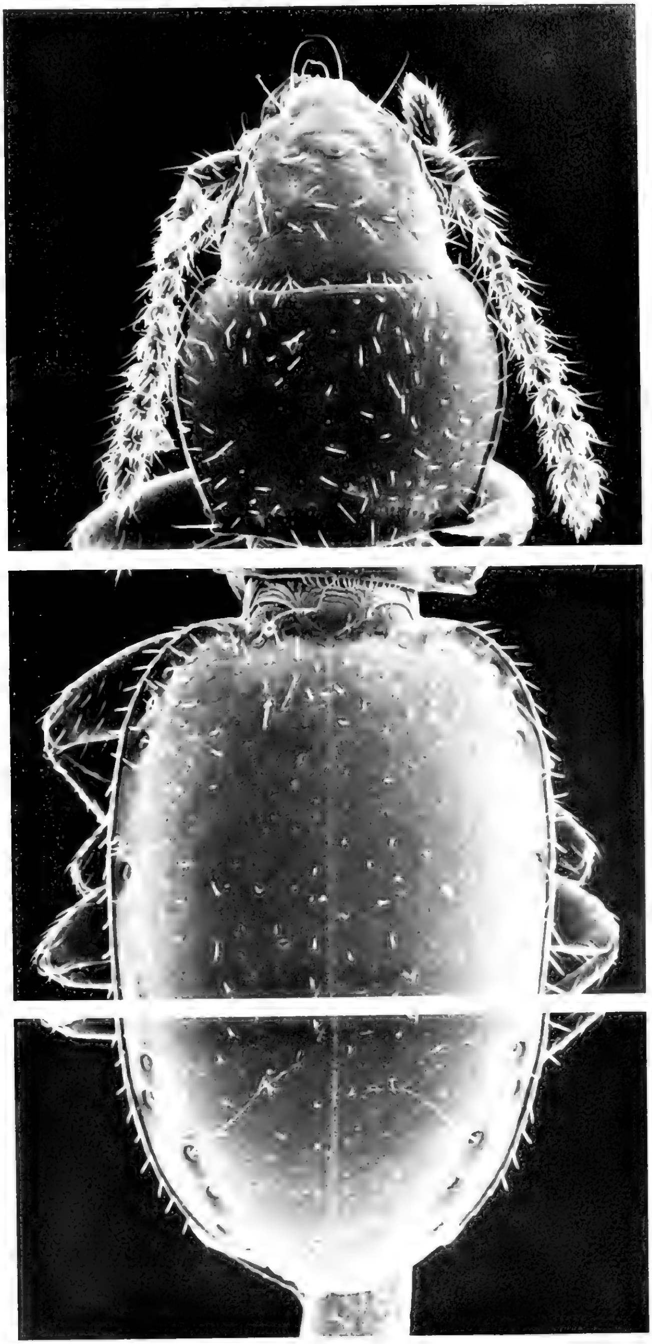
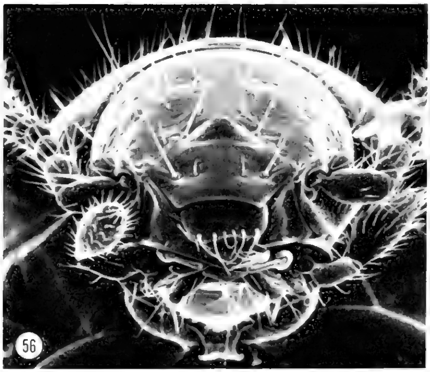
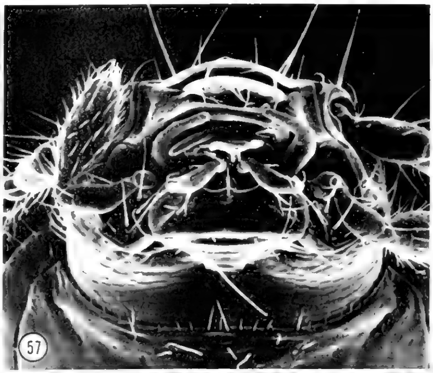
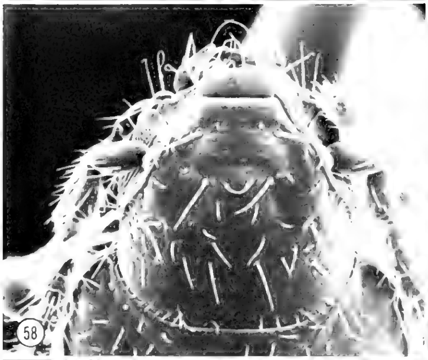
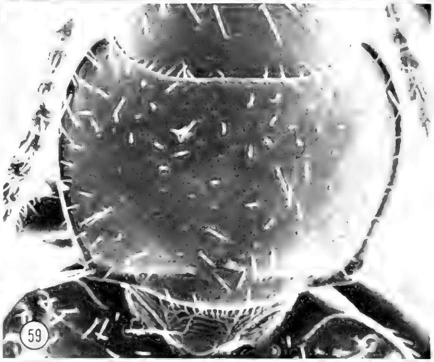


FIGURE 55. Habitus of *Geocharidius phineus* n.sp., dorsal aspect, male from 1.6 km south of Pantin, Baja Verapaz, Guatemala, SEM composite ca. 120×.

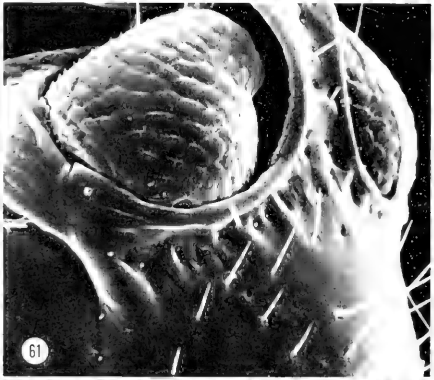

56

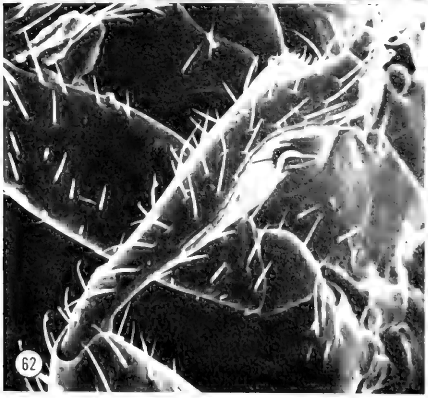

57

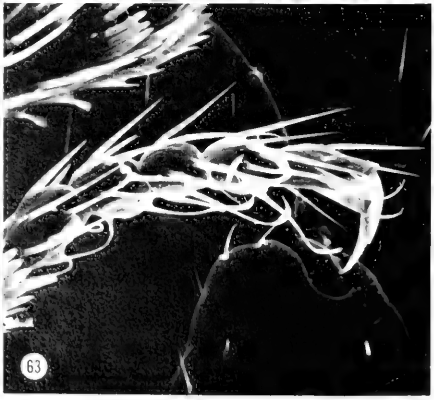

58


59


60


61


62


63

pronotum, and elytra. Male holotype not dissected. SBL = 1.319 mm; TW = 0.590 mm.

GEOGRAPHICAL DISTRIBUTION.—Figure 73; known only from the type-locality.

NATURAL HISTORY NOTES.—The unique type was found in leaf litter with Berlese techniques at an altitude of 2780 m in Lower Montane Wet Forest. It was collected in August and was not teneral.

TYPE-MATERIAL.—**Holotype** ♂, GUATEMALA, Huehuetenango, 7.7 km s San Juan Ixcoy, 15°35′N, 091°27′W, Aug. (*Ball, Frania, & Whitehead*) (USNM), ADP 026556.

DERIVATION OF TAXON NAME.—*Gimlii,* after the dwarf Gimli, son of Gloin (one of the 12 companions of Thorin Oakenshield), who accompanied the Hobbit, Frodo, on his trip south, in Book I of *The Lord of the Rings* by Tolkien, in reference to the small size of these beetles.

4. **Geocharidius phineus**, new species

(Figures 54–63, 74)

DIAGNOSTIC COMBINATION.—Pronotum and elytra highly convex, elytra inflated to higher plane than pronotum; lateral margin of pronotum with denticle before hind angle; front of head with tubercule. *Color and luster:* body rufotestaceous; appendages pale testaceous. *Form:* large beetles for this genus with highly convex pronotum and elytra; pronotum very broad, much wider than head and elytron; eyes absent. *Structure:* frontal furrows well impressed, front tuberculate at middle. Hind angle of pronotum sharp, margin in front of angle denticulate and sinuate. Elytron moderately long, narrow, highly convex; side margin broadly flanged in basal third, flange markedly microserrulate, humerus evenly rounded. Elytral surface with scattered setae, striae absent. Dorsal microsculpture of large isodiametric meshes, restricted to head, effaced elsewhere. Male holotype not dissected. SBL = 1.194–1.517 mm; TW = 0.561–0.675 mm.

TABLE 22. LOCALITY DATA DEDUCED FROM SPECIMEN LABELS. 02. *Geocharidius phineus* n.sp.; map Figure 73.

Lat./Long.	Elev. (m)	Orig. deposit.	Month coll.	No. spec.
15°16′N 90°14′W	1680	USNM	Aug	8
15°14′N 90°12′W	1600	USNM	Aug	2
15°10′N 90°12′W	1500	USNM	Aug	1
		Total specimens examined:		11

GEOGRAPHICAL DISTRIBUTION.—Figure 74; known only from the Sierra de Las Minas of central Guatemala.

NATURAL HISTORY NOTES.—These beetles were collected from leaf litter with Berlese techniques at altitudes between 1500 m and 1700 m in Subtropical Wet Forest. They were collected in August; one was teneral.

TYPE-MATERIAL.—**Holotype** ♂, GUATEMALA, Baja Verapaz, 1.6 km s Pantin, 15°16′N, 090°14′W, Aug. (*Ball, Frania, & Whitehead*) (USNM), ADP 026665. **Paratypes:** 4♂, 6♀, same data as holotype or as listed in Table 22 and deposited as USNM-6, UASM-2, CAS-2.

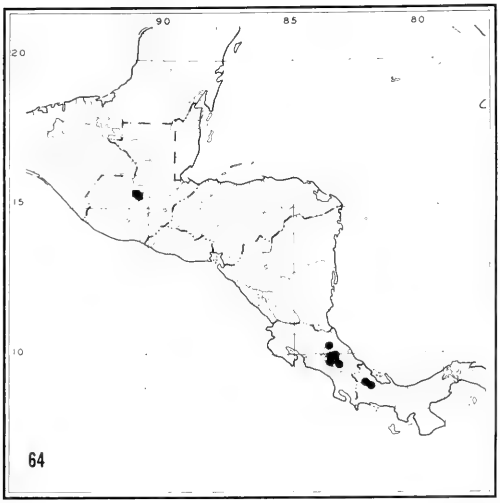
←

FIGURES 56 to 63. *Geocharidius phineus* n.sp., male from 1.6 km south of Pantin, Baja Verapaz, Guatemala. 56. Head, anterior aspect, 240×. 57. Mouthparts, oblique ventral aspect, 240×. 58. Head, dorsal aspect, 210×. 59. Pronotum, oblique dorsal aspect, 210×. 60. Prosternum, oblique anterior aspect, 230×. 61. Anterior coxae, left lateral aspect, 560×. 62. Tibia, left, anterior aspect, 380×. 63. Tarsomeres, left anterior, oblique ventral aspect, 690×.

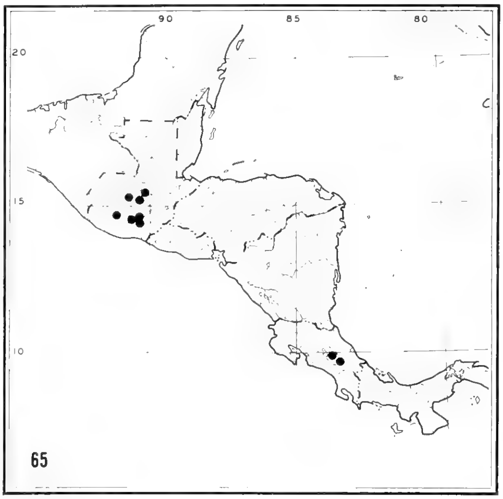
→

FIGURES 64 to 69. Geographical distribution maps. 64. *Bembidion purulha* n.sp., squares; *B. rogersi* Bates, circles. 65. *B. mexicanum* Dejean. 66. *B. vernale* Bates. 67. *B. satellites* Bates, squares; *B. lavernae* n.sp., circles; *B. quetzal* n.sp., triangles. 68. *B. diabola* n.sp., squares; *B. vulcanium* Darlington, circles; *B. edwardsi* n.sp., triangles. 69. *B. aeger* n.sp., squares; *B. chiriqui* n.sp., circles.

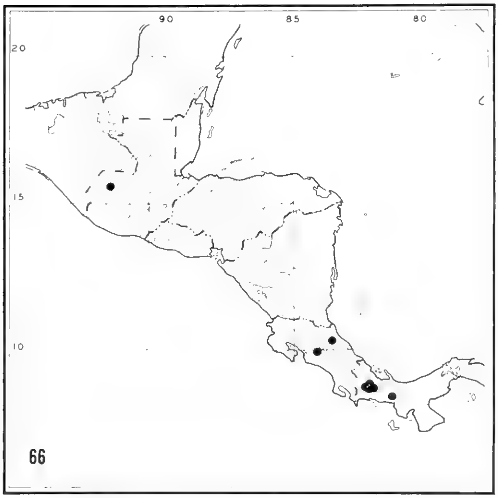
FIGURES 70 to 74. Geographical distribution maps. 70. *B. nahuala* n.sp., squares; *B. franiae* n.sp., circles. 71. *B. aratum* LeConte, squares; *B. cortes* n.sp., circles; *B. sparsum* Bates, triangles; *B. armuelles* n.sp., arrow; 72. *B. cyclodes* Bates, squares; *B. championi* Bates, circles; *B. ixtatan* n.sp., triangles. 73. *Geocharidius integripennis* Bates, squares; *G. romeoi* n.sp., circles; *G. gimlii* n.sp., triangles. 74. *G. phineus* n.sp., squares; *G. tagliantii* n.sp., circles; *B. barrensis* n.sp., triangle.



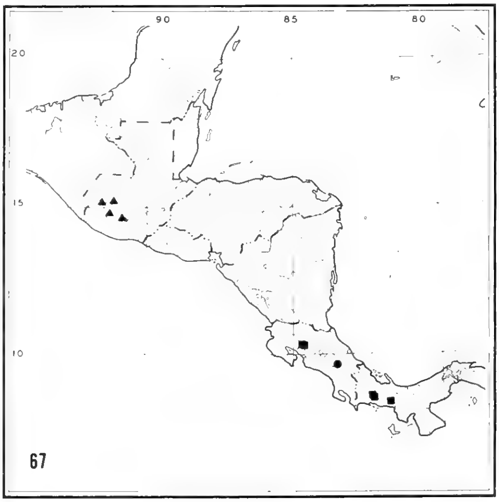
64



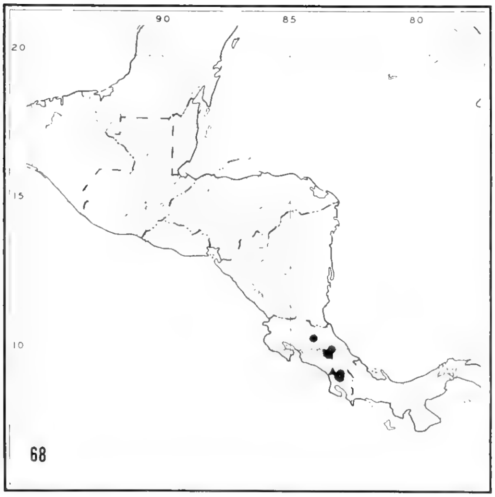
65



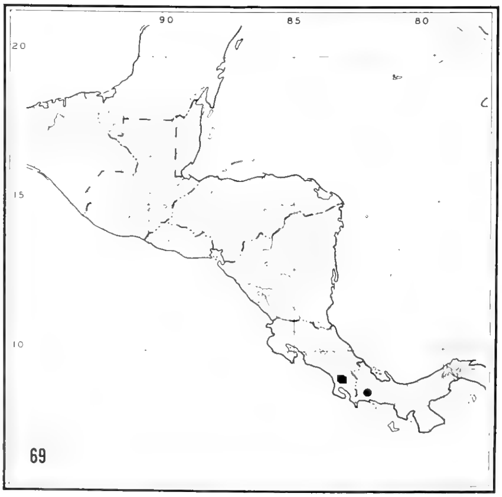
66



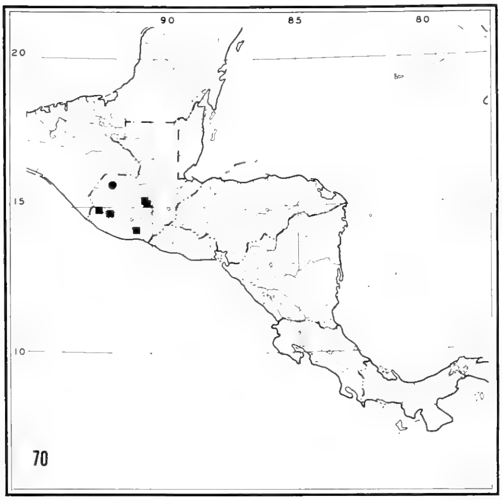
67



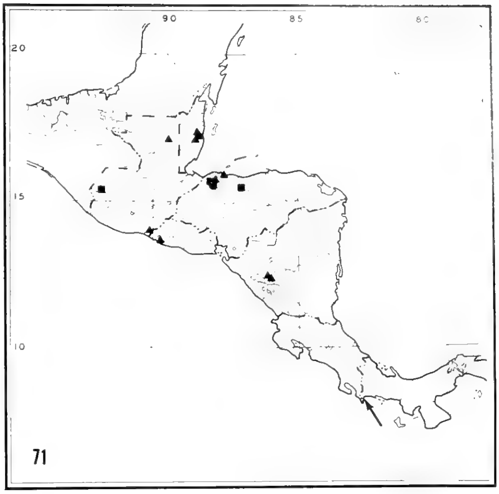
68



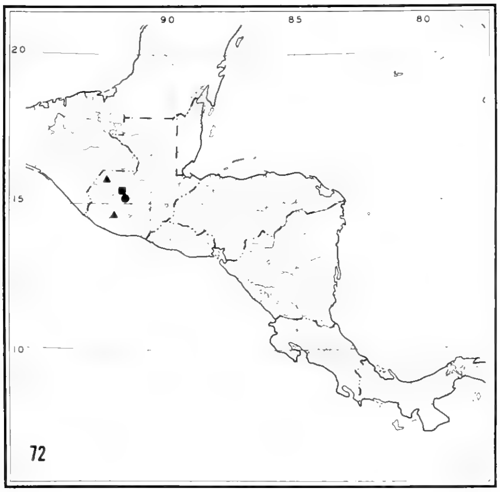
69


90
85
80
20
15
10

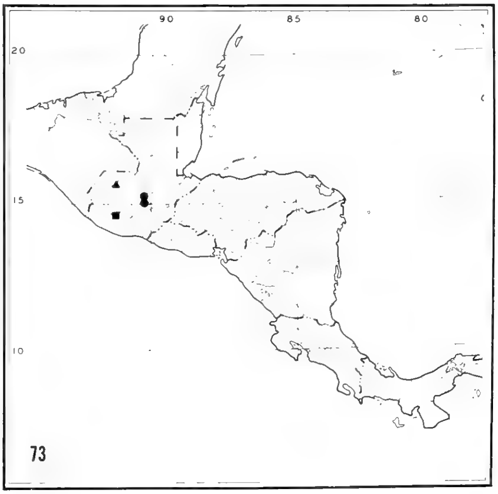
70


90
85
80
20
15
10

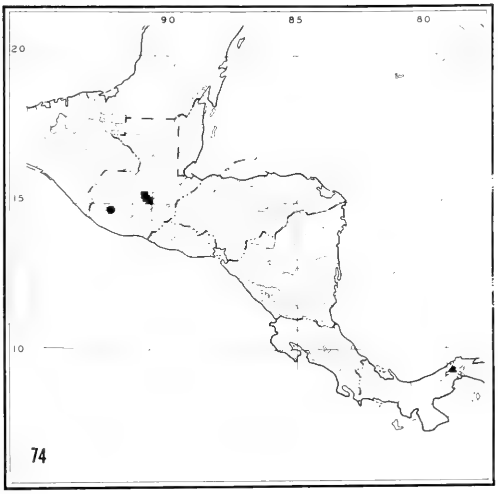
71


90
85
80
20
15
10

72


90
85
80
20
15
10

73


90
85
80
20
15
10

74

Derivation of Name.—*Phineus,* mythical prophet struck blind by Zeus, in reference to the lost eyesight of members of this species.

5. **Geocharidius tagliantii**, new species

(Figure 74)

Diagnostic Combination.—Pronotum in basal third with multidentate lateral margins. *Color and luster:* head and body dark rufous; appendages pale testaceous. *Form:* large beetles for this genus with broad forebody and elytra; pronotum wider than head and elytron; eyes absent. *Structure:* frontal furrows not well impressed, rough due to coarse microsculpture. Hind angle of pronotum denticulate, side margin in front of it multidenticulate and sides straight. Elytron medium-sized, narrow; side margin narrowly flanged in basal third, flange microserrulate, humerus squared, side margins nearly parallel. Elytral surface with scattered setae, striae absent. Dorsal microsculpture restricted to head and scutellum, of coarse isodiametric meshes. Male aedeagus figured by Taglianti (1973). SBL = 1.44–1.47 mm.

Geographical Distribution.—Figure 74; known only from the type-locality.

Natural History Notes.—The type-locality is located in Lower Montane Wet Forest in the Guatemalan highlands at about 2800 m.

Material Examined.—None; this description is based on that of Taglianti (1973).

Type-Material.—**Holotype** ♂, Guatemala, Totonicapán, Totonicapán, 14°54′N, 091°22′W (*Champion*) (MNHP).

Derivation of Taxon Name.—Named in honor of Agusto Vigna Taglianti of Italy who revised the Anillina of Mexico and Guatemala, and who mistakenly regarded this new species as Bates's *G. integripennis.*

Acknowledgments

I thank La Verne Jean Magarian for her foresight and creativity in developing a computerized data base and its underlying philosophy with which I have begun production of a Central American faunal study on ground beetles, this being the first contribution even though it is not part of the series. She also participated in collecting most of the specimens upon which this study is based. In addition, I warmly thank all those curators and assistants from whose museums specimens were borrowed and which are listed under methods.

I heartily thank George Venable and Gloria Gordon Zimmer for their excellent illustrative efforts and Linda L. Sims, Gloria N. House, Jeannine Weaver, and Noreen Connell for their efforts in compiling these pages.

Literature Cited

Andrewes, H. E. 1935. The fauna of British India, including Ceylon and Burma. Coleoptera. Carabidae Vol. II. Harpalinae I. Taylor and Francis Publishers, London. 323 p.

Ball, G. E. 1963. Carabidae. Pp. 55–182 *in* Arnett, R. H. The beetles of the United States. The Catholic University of America Press, Washington D.C.

———. 1972. Classification of the *Harpalus* subgenus *Glanodes* Casey (Carabidae: Coleoptera). Coleopterists Bulletin 26(4):179–204.

Basilewsky, P. 1968. Contributions a l'étude des Coléoptères Carabiques de la région Malgache. V. Les Bembidiinae de Madagascar et des Îles voisines. Annales de la Société Entomologique de France 4(3):515–548.

———. 1972. La faune terrestre de l'île de Sainte-Hélène. II. Insectes. 1. Fam. Carabidae. Annales du Musée Royal de l'Afrique Centrale, sér. 8, (192):11–84.

Bates, H. W. 1878. On new genera and species of geodephagous Coleoptera from Central America. Proceedings of the Zoological Society of London 1878:587–609.

———. 1882. Biologia Centrali-Americana, Insecta, Coleoptera, Carabidae 1(1):40–152.

———. 1884. Biologia Centrali-Americana, Insecta, Carabidae, Cicindelidae suppl. 1(1):257–299.

Casey, T. L. 1918. A review of the North American Bembidiinae. Memoirs on the Coleoptera 8:1–223.

Darlington, P. J., Jr. 1934. Four new Bembidiini (Coleoptera: Carabidae) from Costa Rica and Colombia. Occasional Papers of the Boston Society of Natural History 8:157–162.

———. 1962. The carabid beetles of New Guinea. Part I. Cicindelinae, Carabinae, Harpalinae through Pterostichini. Bulletin of the Museum of Comparative Zoology 126(3):321–564.

———. 1965. Biogeography of the southern end of the world: distribution and history of far-southern life and land, with an assessment of continental drift. Harvard University Press, Cambridge. 236 p.

Dejean, P. F. M. A. 1831. Spécies générale des coléoptères de la collection de M. le comte Dejean, 5:1–883.

DuVal, P. N. C. 1851. Diagnosis of *Anillus.* Bulletin de la Société Entomologique de France 1851:lxxii–lxxiii.

Erwin, L. J. M. 1976. Application of a computerized general purpose information management system (SELGEM) to a natural history research data bank (Coleoptera: Carabidae). Coleopterists Bulletin 30(1):1–32.

Erwin, T. L. 1970. A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). Quaestiones Entomologicae 6:4–215.

———. 1973. Studies of the Tachyina (Coleoptera: Carabidae: Bembidiini), part I: A revision of the Neotropical genus *Xystosomus* Schaum. Smithsonian Contributions to Zoology 140:1–39.

———. 1974a. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), part II: A revision of the New

World–Australian genus *Pericompsus* LeConte. Smithsonian Contributions to Zoology 162:1–96.

———. 1974b. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini) supplement A: Lectotype designations for New World species, two new genera, and notes on generic concepts. Proceedings of the Entomological Society of Washington 76(2):123–155.

———. 1975. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiina), part III: Systematics, phylogeny, and zoogeography of the genus *Tachyta* Kirby. Smithsonian Contributions to Zoology 208:1–68.

———. 1976. A case of homonymy in the Tachyina (Coleoptera: Carabidae: Bembidiini). Coleopterists Bulletin 30(1):94.

———. 1977. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini) supplement B: Lectotype designation of *Masoreus ridiculus* Schaufuss and transfer of the species to *Polyderis*. Coleopterists Bulletin 31(1):90.

———. 1978. Techniques. Coleopterists Bulletin 32(4):372.

———. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analysis of lowland forest sites in temperate and tropical regions. Pp. 539–587 *in* Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid beetles: Their evolution, natural history, and classification. Proceedings of the First International Symposium of Carabidology. Dr. W. Junk Publishers, The Hague.

———. 1981. Taxon pulses, vicariance, and dispersal: An evolutionary synthesis illustrated by carabid beetles. Pp. 159–196 *in* Nelson, G., and D. E. Rosen. Vicariance biogeography: A critique. Columbia University Press, New York.

———. 1982. Studies of the tribe Bembidiini (Coleoptera: Carabidae): Lectotype designations and species group assignments for *Bembidion* species described by Thomas L. Casey et al. The Pan-Pacific Entomologist.

———, and J. Adis. 1982. Amazonian inundation forests: Their role as short-term refugia and generators of species diversity and taxon pulses. Columbia University Press, New York.

———, and D. H. Kavanaugh. 1980. On the identity of *Bembidion puritanum* Hayward (Coleoptera: Carabidae: Bembidiini). Coleopterists Bulletin 34(2):241–242.

———, and ———. 1981. Systematics and zoogeography of *Bembidion* Latreille: I. The *carlhi* and *erasum* groups of western North America (Coleoptera: Carabidae: Bembidiini). Entomologia Scandinavica, suppl. 15:33–72.

Frank, J. H. 1971. Carabidae (Coleoptera) as predators of the red-backed cutworm (Lepidoptera: Noctuidae) in Central Alberta. The Canadian Entomologist 103:1039–1044.

Haldeman, S. S. 1843. Descriptions of North American species of Coleoptera, presumed to be undescribed. Proceedings of the Academy of Natural Sciences of Philadelphia 1:298–304.

Holdridge, L. R. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, New York. 747 p.

Janzen, D. H. 1973. Rate of regeneration after a tropical high elevation fire. Biotropica 5(2):117–122.

Jeannel, R. 1937. Les Bembidiides endogés (Col. Carabidae). Monographie d'une lignée gondwanienne. Revue Française d'Entomologie 3(4):241–399.

———. 1960. Sur les anillini de l'Inde et Ceylan. Revue Française d'Entomologie 27(1):16–23.

———. 1963a. Monographie des "Anillini" Bembidiides Endogés (Coleoptera Trechidae). Mémoires du Muséum National d'Histoire Naturelle, sér. A, Zool. 28(2):36–100.

———. 1963b. Supplément a la monographie des Anillini (1). Sur quelques espèces nouvelles de l'Amérique du Nord. Revue Française d'Entomologie 30(3):145–152.

Kavanaugh, D. H. 1979. Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. Proceedings of the California Academy of Sciences, 42:87–133.

Kryzhanovskiy, O. L. 1970. Taxonomy and distribution of species of the subtribe Tachyina (Coleoptera, Carabidae) in the USSR. Entomologicheskoe Obozrente 49(1):94–103.

Latreille, P. A. 1802. Histoire naturelle, générale et particulière des crustaces et des insectes, vol. 3. Paris. 467 p.

LeConte, J. L. 1852. Descriptions of new species of Coleoptera, from California. Annals of the Lyceum of Natural History of New York 5:185–216.

Lindroth, C. H. 1963. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 3. Opuscula Entomologica Supplementum 24:201–408.

———. 1966. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 4. Opuscula Entomologica Supplementum 24:409–648.

———. 1967. On the number of *Bembidion* species (Coleoptera, Carabidae) occurring in North America. Coleopterists Bulletin 21:28–31.

———. 1975. Designation of holotypes and lectotypes (Coleoptera, Carabidae) described by Thomas L. Casey. Coleopterists Bulletin 29(2):109–147.

———. 1976. Genus *Bembidion* Latreille (Coleoptera: Carabidae) in New Zealand: A revision. New Zealand Journal of Zoology 3:161–198.

———. 1980. A revisionary study of the taxon *Cillenus* Samouelle, 1819 and related forms (Coleoptera: Carabidae, Bembidiini). Entomologica Scandinavica 11:179–205.

Linné, C. 1761. Fauna Suecica, &c. Ed. 2. Stockholm. 578 p.

Miré, B. de. 1966. Revision des Tachylopha Motschulsky d'Afrique (Carabidae Tachyini). Revue de Zoologie et de Botanique Africaines 73(1–2):59–100.

Müller, J. 1918. Bestimmungstabelle der *Bembidion*-Arten Europas und des Mittelmeergebietes. Koleopterologische Rundschau 7:26–117.

Netolitzky, F. 1911. *Bembidion*-studien. Entomologische Zeitschrift 30:179–194.

———. 1931. Kritisches zum Katalog der Harpalinae von Csiki. (Coleopterorum Catalogus von Junk-Schenkling. Paris 97 et 98.) (Col., Carab.) Deutsche Entomologische Zeitschrift 2/3:153–167.

———. 1942. Bestimmungstabelle der *Bembidion*-Arten des paläarktischen Gebietes. Koleopterologische Rundschau 28:29–124.

———. 1943. Bestimmungstabelle der *Bembidion*-Arten des paläarktischen Gebietes. Koleopterologische Rundschau 29:1–70.

Olivier, A. G. 1795. Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie, et leur figure enluminée. Coleopteres 3(35):1–116.

Pawlowski, J. 1974. Biegaczowate—Carabidae podrodziny Bembidiinae, Trechinae. Klucze do oznaczania owadów Polski, No. 82, 19(3b):1–94.

Say, T. 1823. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. Transactions of the American Philosophical Society ser. 2, 2:1–109.

Stephens, J. F. 1828. Illustrations of British entomology; or a synopsis of indigenous insects: containing their generic and species distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Coleoptera 2:1–112.

Taglianti, A. V. 1973. The Anillini of Mexico and Guatemala (Coleoptera, Carabidae). Accademia Nazionale dei Lincei 171:307–324.

Thunberg, C. P. 1787. Museum naturalium academiae Upsaliensis. Cujus partem quartam, pp. 43–58. Upsaliae.

Valentine, J. M. 1932. *Horologion*, a new genus of cave beetles (fam. Carabidae). Journal of the New York Entomological Society 26:179–182.

van Emden, F. I. 1936. Bemberkingen zur Klassifikation der Carabidae: Carabini und Harpalinae piliferae Entomologische Blätter 32(2):12–52.

Westwood, J. O. 1840. Synopsis of the genera of British insects. Supplement. Pp. 1–158 *in* Westwood, J. O. 1838–1840. An introduction to the modern classification of insects: Founded on the natural habits and corresponding organization of the different families. Longman, Orme, Brown, Green, and Longman, publishers, London. 2 vol. 462 and 587 p.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 20, pp. 497–524, 20 figs., 1 table

May 14, 1982

THE BORNEAN GASTROMYZONTINE FISH GENERA *GASTROMYZON* AND *GLANIOPSIS* (CYPRINIFORMES, HOMALOPTERIDAE), WITH DESCRIPTIONS OF NEW SPECIES

By
Tyson R. Roberts
California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

ABSTRACT: **The endemic Bornean gastromyzontine genera *Gastromyzon* and *Glaniopsis* are revised. *Neogastromyzon* is shown to be generically distinct from *Gastromyzon*. *Gastromyzon monticola,* formerly placed in the synonymy of *Gastromyzon borneensis,* is a valid species. Five new species of *Gastromyzon* (*G. contractus, G. ctenocephalus, G. lepidogaster, G. megalepis,* and *G. ridens*) and three new species of *Glaniopsis* (*G. denudata, G. gossei,* and *G. multiradiata*) are described, bringing the total known species in these genera to nine and four, all of which are illustrated photographically.**

INTRODUCTION

Gastromyzontinae are bottom-dwelling fishes of swift-flowing highland and lowland streams in China, Vietnam, and Borneo. Most of the approximately 15 genera and 52 species are highly specialized, with ventrally flattened head and body; inferior mouth frequently with numerous barbels or papillae; head, body, and fins heavily tuberculate; and paired fins modified. Several genera have greatly enlarged pectoral and pelvic fins with more numerous rays than in any other Cypriniformes, and the pelvic fins may be united posteriorly, a condition otherwise unknown in the Ostariophysi. A synopsis of all Gastromyzontinae is given by Silas (1953); Chinese forms are reviewed and new species described by Chen (1980).

I collected samples of Gastromyzontinae during an ichthyological survey of the Kapuas River basin, western Borneo, in 1976. Work on their identification led to the present revision of *Gastromyzon* and *Glaniopsis*. Borneo is inhabited by five or six gastromyzontine genera: *Gastromyzon* Günther, 1874; *Glaniopsis* Boulenger, 1899; *Neogastromyzon* Popta, 1905; *Parhomaloptera* Vaillant, 1902; *Progastromyzon* Hora and Jayaram, 1951a, and *Protomyzon* Hora, 1932. I have studied only the first three of these genera. *Neogastromyzon* was placed in the synonymy of *Gastromyzon* by Inger and Chin (1961) but is shown here to be a valid genus. *Progastromyzon* was placed in the synonymy of *Protomyzon* by Inger and Chin (1962). All of these genera, with the possible exception of *Protomyzon,* seem to be endemic to Borneo. Two new species of *Protomyzon* are described from China by Chen (1980); otherwise *Protomyzon* is also known only from Borneo.

Gastromyzon was revised by Inger and Chin (1962). They described two new species referable to *Gastromyzon,* but misidentified *G. borneensis,* the generic type-species, and omitted *G. monticola,* previously placed in the synonymy of *G. borneensis* but here shown to be a distinct species. Five new species of *Gastromyzon* are described in this paper, bringing the total number of described species to nine, four of which occur in the Kapuas basin. *Glaniopsis,* hitherto considered monotypic (Weber and de Beaufort 1916; Inger and Chin 1962), is known only from northern Borneo; three new species of *Glaniopsis* are described, and additional material is reported but not named which may represent additional species.

Apart from systematics little has been published about Gastromyzontinae. Osteology and classification of some genera, including *Gastromyzon* and *Glaniopsis,* are treated by Ramaswami (1948, 1952); classification of *Glaniopsis* is discussed also by Hora and Jayaram (1951b). Wickler (1971) described locomotion, feeding, and territorial behavior in *Gastromyzon*; the species he studied is probably *G. fasciatus* (and not *G. borneensis*). Reproductive behavior has not been studied.

MATERIAL AND METHODS

This paper is based on material deposited in the following institutions: British Museum (Natural History) (BMNH); California Academy of Sciences (CAS), including material formerly deposited in the Natural History Museum, Stanford University (SU); Field Museum of Natural History, Chicago (FMNH); Institut Royal des Sciences Naturelles de Belgique (IRSNB); Museum of Comparative Zoology, Harvard (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Zoology, Bogor, Indonesia (MZB); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); and Zoological Museum, University of Amsterdam (ZMA).

Specimen lengths are standard length and proportional measurements are expressed as times in standard length, unless indicated otherwise. Eye diameter is the greatest horizontal or nearly horizontal measurement of the exposed portion of the eyeball. Interorbital width is the measurement between the exposed portion of the eyeballs. Mental barbels are referred to as "flap-like" rather than "barbel-like" if the length of their base is greater than their height (in some species of *Glaniopsis*). "Lateral scale series" refers to the scale row bearing tubes or pores for the lateral line sensory canal. Observation of scales in *Glaniopsis* was facilitated by staining some specimens superficially with alizarin. "Principal caudal-fin rays" includes all branched principal caudal rays plus one upper and one lower simple principal ray.

The following anatomical features or characters found in Gastromyzontinae have not been named previously, are relatively unfamiliar, or otherwise require comment:

Adhesive pads—pads of thickened, depigmented skin on ventral surface of anteriormost pectoral- and pelvic-fin rays: in many rheophilic, bottom-dwelling cyprinoids, probably including all Gastromyzontinae. The pads apparently increase the frictional properties of the paired fins in contact with substrate; in *Gastromyzon contractus* they are covered with horny, hook-shaped, posteriorly directed projections arising from single epidermal cells (Roberts, in press).

Ctenoid tubercles—tubercles forming minute, comblike projections on dorsolateral portions of head: first reported by Inger and Chin (1962) as "numerous short, curved rows of sensory papillae" on male *Neogastromyzon pauciradiatus*; I also found them on male *Gastromyzon ctenocephalus.* In both species I observed that areas with finely ctenoid tubercles grade into areas with more and more coarsely ctenoid tubercles and finally into quite ordinary-looking small conical tubercles.

Gill opening angular—gill opening lying posterior to opercle and extending anteriorly a short distance ventral to subopercle, so that free margin of gill cover is angular: in some *Gastromyzon.*

Gill opening vertical—gill opening lying entirely posterior to opercle, so that free margin of gill cover is vertical or nearly so: in some *Gastromyzon.*

Horny jaw sheaths—more or less thick sheaths of horny skin, sometimes forming a sharp "cutting edge," on upper and lower jaws: in many cyprinoids, probably including all Gastromyzontinae.

Lateral oral fold—a flap of skin with discrete margins, extending from rostral cap to pectoral-fin origin lateral to corner of mouth: in *Gastromyzon* only (Fig. 1*b*).

Postoral pouch—an anteriorly open, transverse pocket or pouch on ventral surface of head immediately posterior to mouth, formed by a fleshy transverse fold or "postoral flap": in *Gastromyzon borneensis, G. monticola,* and *Neogastromyzon nieuwenhuisi* (Fig. 1). *Gastromyzon fasciatus* sometimes has a weakly developed postoral flap without formation of a postoral pouch.

Rostral cap—a fold or cap of skin, usually horny, with a more or less pronounced ventral groove, overlying upper lip: in nearly all cyprinoids, probably in all Gastromyzontinae (Fig. 1). Sometimes misidentified as upper lip.

Secondary rostrum—a discrete projection at snout tip, supported internally by anteriorly directed, flangelike projections of the lacrimal bones, and heavily tuberculate in large adults: in *Gastromyzon borneensis* but no other Gastromyzontinae (Fig. 1*a, b*); superficially similar projections, possibly involving the lacrimal bones, occur in some Garrinae and Labeoinae.

Serrae—posteriorly or dorsoposteriorly directed bony projections, arising from individual lepidotrichia, usually strongly developed on pelvic fin, sometimes also present but weakly developed on pectoral fin: in all *Gastromyzon* except *G. megalepis*; morphologically similar and perhaps functionally analogous projections occur mainly on the anal fin but sometimes also on the pelvic and other fins in many Neotropical Characidae, but they have not been reported previously in any cyprinoids.

Sublacrimal groove—a more or less deep fold or groove between lacrimal bone and rostral cap: in *Gastromyzon* only (Fig. 1*a, b*).

Subopercular groove—groove extending from lower corner of gill opening to pectoral-fin origin, sometimes discontinuous or interrupted near its middle: in several *Gastromyzon,* possibly in other Gastromyzontinae with restricted gill opening.

Suprapelvic flap—a fleshy flap of skin immediately dorsal to anteriormost portion of pelvic fin: in many Gastromyzontinae; in *Gastromyzon* and *Neogastromyzon* the suprapelvic flap is continuous anteriorly with a flat lateral extension of the body wall which forms the ventrolateral margin of the abdomen.

Tubercles—multicellular horny tubercles of epidermal origin (frequently referred to as "nuptial tubercles," "breeding tubercles," or "pearl organs" in the literature) occur on the head, body, and fins of many cyprinoids including all Gastromyzontinae. They vary in size from the relatively large ones on the secondary rostrum and side of the body in male *Gastromyzon borneensis* (Fig. 5) to minute ones, barely visible with a dissecting microscope, such as those found in dense patches on the dorsal surface of the pectoral-fin rays in males of several species of *Gastromyzon,* including *G. contractus* (Fig. 2), or the very fine pricklelike tubercles widely scattered on the head and body of *Glaniopsis.*

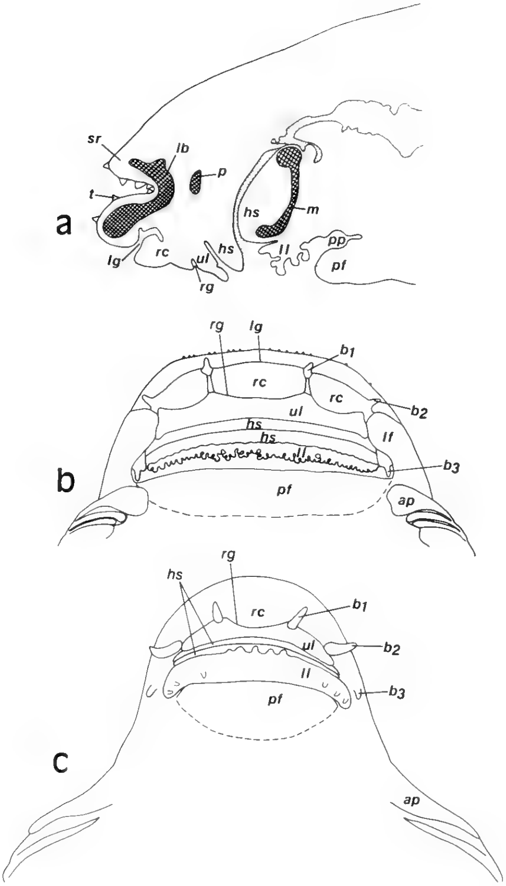


FIGURE 1. (*a*) *Gastromyzon borneensis,* sagittal section of head; (*b*) *Gastromyzon borneensis,* ventral surface of head; (*c*) *Neogastromyzon nieuwenhuisi,* ventral surface of head. (ap = adhesive pad; b_1, b_2, b_3 = rostral, maxillary, mandibular barbels; hs = horny sheaths of upper and lower jaws; lb, lg = lacrimal bone, sublacrimal groove; lf = lateral oral fold; ll, ul = lower and upper lips; m = mandible; pf, pp = postoral fold, postoral pouch; rc, rg = rostral cap, rostral groove; sr = secondary rostrum; t = tubercle; stippling = alimentary canal.)

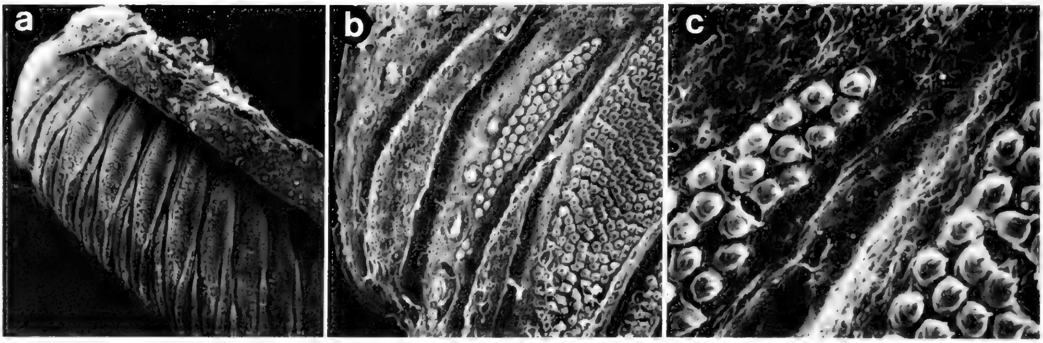


FIGURE 2. Dense patches of small, conical tubercles on dorsal surface of anteriormost pectoral-fin rays, *Gastromyzon contractus*, 32.2-mm male paratype (CAS 44186). Horizontal field width = 4.2 mm (*a*), 1.1 mm (*b*), and 330 μm (*c*).

No direct observations have been made concerning their function in Gastromyzontinae, so a term which does not imply a known function is preferred. Tubercles exhibit striking sexual dimorphism in Gastromyzontinae, as in many other groups of Cypriniformes, but they are also present in immature specimens of both sexes and presumably function in various modes of behavior.

KEY TO BORNEAN GENERA OF GASTROMYZONTINAE

1a. Pelvic fins united posteriorly, each with 14–24 branched rays; suprapelvic flap present, continuous anteriorly with lateral extension of body wall which forms ventrolateral abdominal margin 2

1b. Pelvic fins separate, each with 7–11 branched rays; suprapelvic flap present or absent 3

2a. Sublacrimal groove present; rostral and maxillary barbels project from anterior margin of rostral cap (Fig. 1*b*); head width at most 4; adhesive pad of anteriormost pectoral-fin ray with anterior margin free from abdomen; dorsal surface of pelvic fin usually serrate .... *Gastromyzon*

2b. Sublacrimal groove absent; rostral and maxillary barbels project from posterior margin of rostral cap; head width at least 5; adhesive pad of anteriormost pectoral-fin ray with anterior margin continuous with skin of abdomen; dorsal surface of pelvic fin not serrate ..... *Neogastromyzon*

3a. Mouth subterminal; nasal barbels present; two mandibular barbels near each corner of mouth (Fig. 15); suprapelvic flap absent .... *Glaniopsis*

3b. Mouth inferior; nasal barbels absent; a single mandibular barbel near each corner of mouth; suprapelvic flap absent? or present 4

4a. Gill opening extends ventrally onto ventral surface of body anterior to pectoral fin; branched pectoral-fin rays 16–18; suprapelvic flap absent? ..... *Parhomaloptera*

4b. Gill opening extends ventrally to base of pectoral fin, not onto ventral surface of body; branched pectoral-fin rays 18–24; suprapelvic flap present but not continued anteriorly to pelvic fin .... *Protomyzon*

Gastromyzon Günther

Gastromyzon GÜNTHER, 1874:454 (type-species *Gastromyzon borneensis* Günther, 1874, by monotypy).

Lepidoglanis VAILLANT, 1889:81 (type-species *Lepidoglanis monticola* Vaillant, 1889, by monotypy).

DIAGNOSIS.—*Gastromyzon* differs from all other Gastromyzontinae including *Neogastromyzon* in having a sublacrimal groove between lacrimal bone and rostral cap; rostral and maxillary barbels projecting from anterior (rather than from posterior) margin of rostral cap; a lateral oral fold; and lepidotrichia of pelvic-fin rays (and to a lesser extent, of pectoral-fin rays) bearing serrae (present in all but one species of *Gastromyzon*; absent in *Neogastromyzon* and not reported or observed in any other Gastromyzontinae).

Pectoral, pelvic, and anal fins close-set or even overlapping. Pectoral fin with 1 simple and 22–30 branched rays, its origin underneath head on or near a level with anterior margin of eye. Adhesive pads present on about 10–12 anteriormost pectoral-fin and 8–10 anteriormost pelvic-fin rays. Adhesive pad of first (unbranched) pectoral-fin ray with anterior margin free from abdomen (continuous with skin of abdomen in *Neogastromyzon*). Pelvic fins united posteriorly, each with 1 simple and 17–24 branched rays. Suprapelvic flap large, continuous anteriorly with lateral extension of body wall forming ventrolateral abdominal margin (as in *Neogastromyzon* but no other Gastromyzontinae). Dorsal fin with 2 simple and 7–9½ branched rays. Anal fin with 2 simple and 4–5½ branched rays. Principal caudal-fin rays usually 9+8.

Head and abdomen flattened ventrally. Mouth inferior, transverse, very broad. Nasal barbels absent; rostral and maxillary barbels small; mandibular barbels rudimentary or absent. Upper and lower jaws with broad, straight-edged horny jaw sheaths. Lower lip densely papillose except in *G. ctenocephalus* (sparsely papillose in *Neogastromyzon*). Gill opening restricted, lying well above base of pectoral fin (as in *Neogastromyzon* but no other Bornean Gastromyzontinae). Postoral pouch, if present, with postoral flap originating at base of first pectoral-fin ray (postoral pouch originates far anterior to pectoral-fin origin in *Neogastromyzon nieuwenhuisi,* the only other gastromyzontine with a postoral pouch). Specimens over 30 mm of both sexes usually tuberculate, males generally more so than females. Tuberculation heaviest on snout, dorsal surface of pectoral fin (absent or weakly developed on dorsal, anal, and caudal fins), and sometimes side of body.

GEOGRAPHICAL DISTRIBUTION.—Geographical distribution of *Gastromyzon,* based on material examined in this study, is illustrated in Figure 3. The most widely distributed species, *G. fasciatus* and *G. lepidogaster,* occur in northern, western, and eastern Borneo. *Gastromyzon borneensis,* previously reported from eastern and western Borneo (Weber and de Beaufort 1916; Inger and Chin 1961) apparently is restricted to northern Borneo (Sarawak and North Borneo). Absence of *Gastromyzon* in southern Borneo may be an artifact due to lack of collecting; much of this region, particularly the headwaters, is ichthyologically unexplored.

Key to *Gastromyzon*

1a. Secondary rostrum present ..... *G. borneensis*
1b. No secondary rostrum 2

2a. Sublacrimal groove extending onto side of head ..... *G. ridens*
2b. Sublacrimal groove confined to ventral surface of head 3

3a. Subopercular groove absent 4
3b. Subopercular groove present 6

4a. Postoral pouch present ..... *G. monticola*
4b. Postoral pouch absent 5

5a. Scales in lateral series 54–62; scale rows above lateral series 16–20; specimens over 40 mm with abdomen partly or entirely covered with fine scales ..... *G. lepidogaster*
5b. Scales in lateral series 44–48; scale rows above lateral series 11–12; abdomen scaleless except some specimens with a few relatively large scales between posteriormost pelvic-fin rays ..... *G. megalepsis*

6a. Snout relatively truncate in larger specimens; dorsal surface of head and body with relatively large, round, pale spots (vermiculate spots on head in small specimens); pectoral fin with thin pale band at margin; male without dense patches of small tubercles on dorsal surface of pectoral fin ..... *G. punctulatus*
6b. Snout rounded; dorsal surface of head and body without spots or with very small round spots; pectoral fin without thin pale band at margin; male with dense patches of small tubercles on dorsal surface of pectoral fin 7

7a. Adpressed dorsal fin extending posteriorly to or beyond level of anal-fin origin; pelvic fin reaching to or beyond anal-fin origin; snout sloping downward in front of eyes relatively strongly ..... *G. contractus*
7b. Adpressed dorsal fin falling short of level of anal-fin origin; pelvic fin falling short of or just reaching anal-fin origin; snout sloping downward in front of eyes relatively gently 8

8a. Predorsal scales 40–55; branched dorsal-fin rays 8½; branched anal-fin rays 5–5½; male without ctenoid tubercles on head ..... *G. fasciatus*

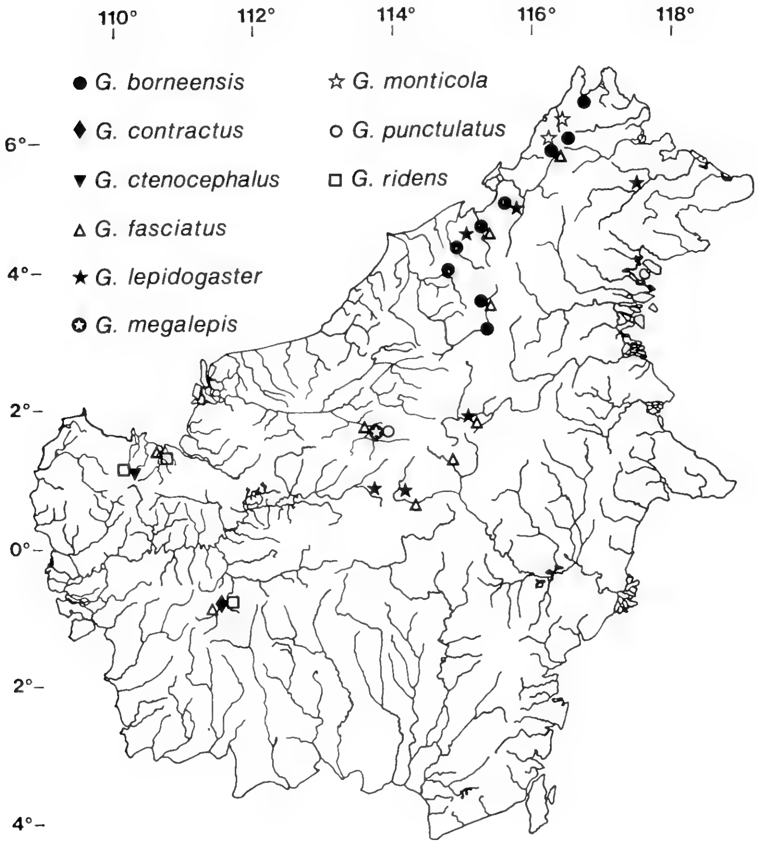


FIGURE 3. Distribution of *Gastromyzon* (based on material examined).

8b. Predorsal scales about 32–36; branched dorsal-fin rays 7½; branched anal-fin rays 4½; male with ctenoid tubercles on head .... *G. ctenocephalus*

Gastromyzon borneensis Günther

(Figures 1*a*, *b*, 4–5)

Gastromyzon borneensis GÜNTHER, 1874:6 (type-locality "sources of Mingalong River" = Mengalong River, Beaufort District, North Borneo).

TYPE-MATERIAL.—The type-series of five syntypes (BMNH 1874.11.24:1–5) comprises two species. Four specimens have a prominent secondary rostrum and the abdomen entirely scaleless; they are conspecific. The largest of these (BMNH 1874.11.24:1, 79.1 mm) is hereby designated lectotype of *G. borneensis*; the other three (BMNH 1874.11.24:2–4, 78.3, 72.6, and 65.5 mm) are paralectotypes. The fifth syntype (BMNH 1874.11.24:5, 78.0 mm) lacks a secondary rostrum, has the abdomen entirely covered with fine scales, and is not conspecific with the others; it is now the holotype of *G. lepidogaster* new species.

ADDITIONAL MATERIAL EXAMINED.—NORTH BORNEO: MCZ 34793, 34820, 34823, 27:27.9–70.4 mm, Mount Kinabalu; SU 31473, ZMA 114.365, 6:32.1–52.9 mm, Bongan River, Mandu Bay; FMNH 68129, 4:16.5–38.4 mm, Parutan River, Tambunan; FMNH 68128, 5:20.6–46.5 mm, Sungei Kaingeran, Tambunan. SARAWAK: IRSNB 19723, 64:36.6–89.0 mm, Arur Dalan, a torrential tributary of Padapur River, near Bario, Baram basin; IRSNB 19724, 30:19.7–68.3 mm, Sungai Ramudu, an affluent of Sungai Kalapang, upstream from Paramudu village, Baram basin; BMNH 1978.3.20:232–235, 4:35.4–52.9 mm, Medalam River, Gunong Mulu; BMNH 1895.7.2:82, 1:65.1 mm, Akar River; BMNH 1933.8.9:1–3, 3:57.8–66.9 mm, Lejok River, Tinjar River; FMNH 45852, 1:70.4 mm, Truson River, Lawas; FMNH 45853, 2:64.9–70.5 mm, Pa Brayong, Truson River; FMNH 68583, 3:44.1–51.0 mm, Akah River, Meligong.

DIAGNOSIS.—Attaining 89 mm, and thus possibly the largest species in the genus, *Gastromyzon borneensis* differs from all of its congeners in having a secondary rostrum and, in sexually mature males, developing heavy tuber-

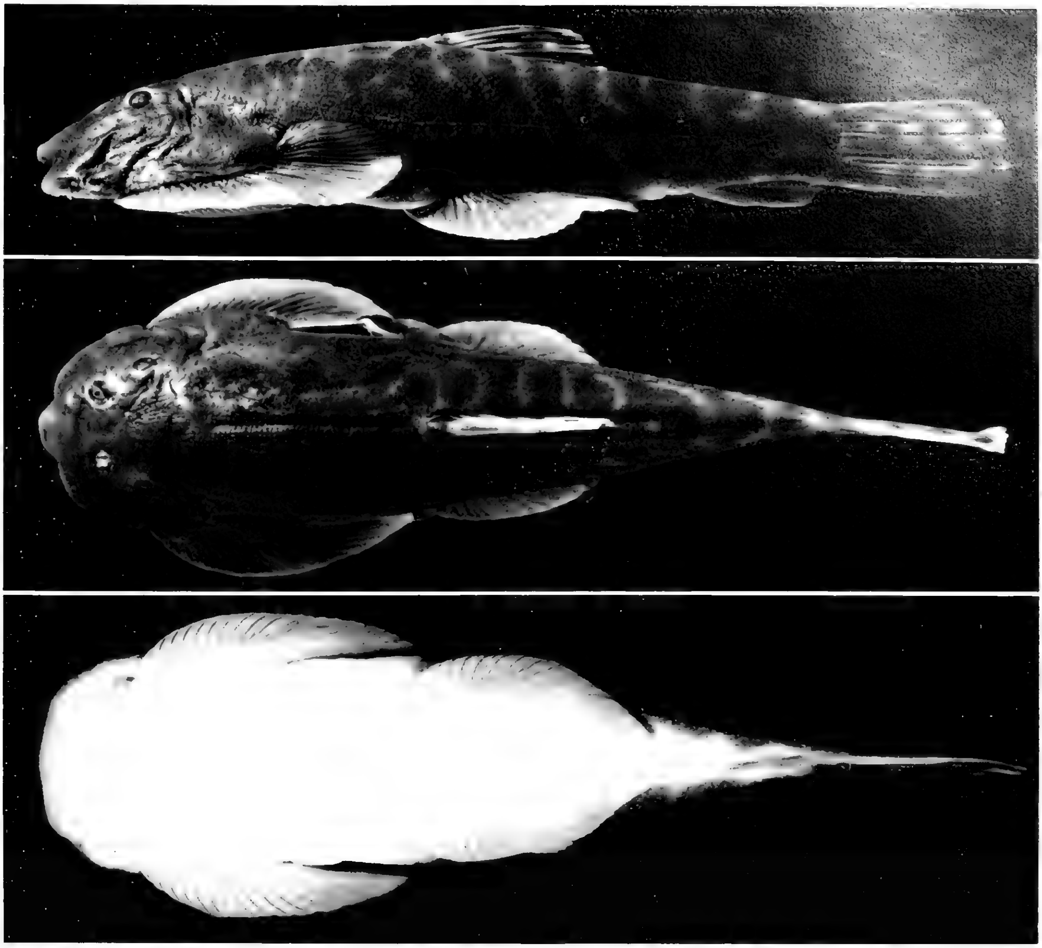


FIGURE 4. *Gastromyzon borneensis*, 88.2-mm female (IRSNB 19723).

culation on posteroventral portion of body. The secondary rostrum, present in all specimens examined over 30 mm of both sexes, is tuberculate in both sexes, but becomes slightly larger and more tuberculate in males than in females. Postoral pouch present (absent in all other *Gastromyzon* except *G. monticola*).

Snout terminating in secondary rostrum, otherwise gently sloping downward in front of eyes and relatively truncate. Gill opening vertical, its length about equal to eye diameter; no subopercular groove. Scales in lateral series 51–62; predorsal scales at least 40; scale rows above lateral series about 20; circumpeduncular scales 28–32. Pectoral fin falls far short of pelvic fin, pelvic fin short of anal fin, and depressed dorsal fin far short of level of anal-fin origin.

Dorsal and lateral surfaces of body with dull brownish or brownish-gray background broken by pale, interconnected narrow bands forming irregularly hexagonal or pentagonal figures; dorsal surface of head with hexagonal or pentagonal figures similar to those on body but much smaller and more closely spaced together. Most coloration on fins narrowly confined along fin rays; dorsal fin with faintly banded pattern; caudal fin with three to six dusky vertical bands. Paired fins without longitudinal bands or pale margins, pale or colorless posteriorly.

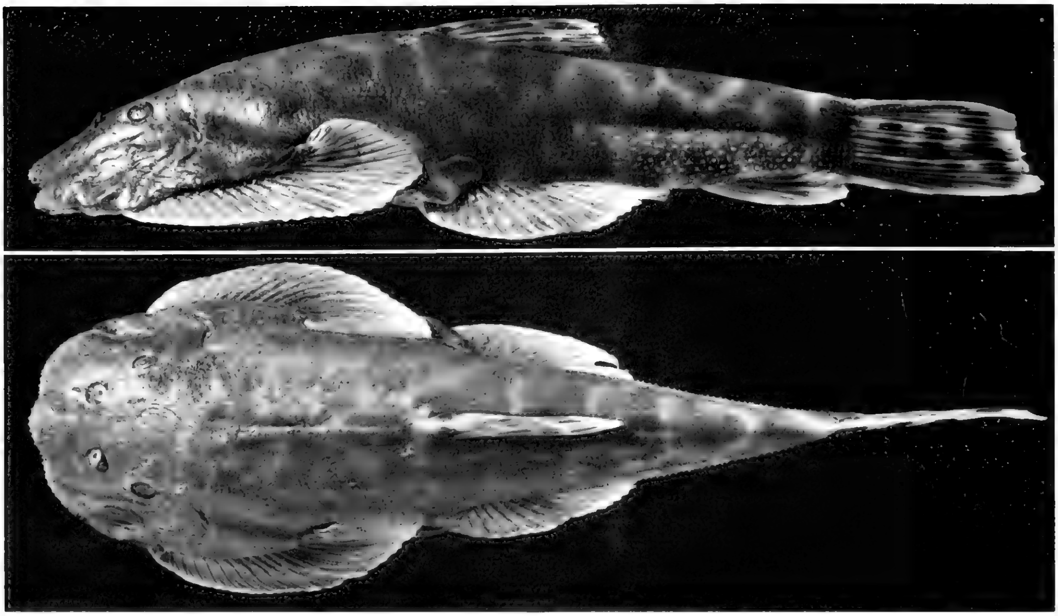


FIGURE 5. *Gastromyzon borneensis*, 71.5-mm male (IRSNB 19723).

Gastromyzon contractus new species

(Figures 2, 6)

TYPE-MATERIAL.—The types and only known specimens of this new species were collected in the mainstream and one small tributary of the Sungai Pinoh, a large high-gradient stream in the southern Kapuas basin, by Soetikno Woerjoatmodjo and me in July 1976.

Holotype.—MZB 3447, 34.4-mm gravid ♀, Sungai Tebelian, small forest stream 3–4 m wide and 50 cm deep, where it flows into Sungai Pinoh, 19 km upstream from Nangapinoh.

Paratypes.—CAS 49319, 1:30.2 mm, same data as holotype; MZB 3448, CAS 44186, USNM 230247, RMNH uncat., BMNH uncat., and MNHN uncat., 17:29.1–36.9 mm, mainstream of Sungai Pinoh 20–60 km upstream from Nangapinoh; MZB 3449 and CAS 49320, 2:25.9–29.8 mm, rocky channel in mainstream of Sungai Pinoh 37 km S of Nangapinoh.

DIAGNOSIS.—Perhaps the smallest species of *Gastromyzon* (largest known specimen 36.9 mm), *G. contractus* differs from all of its congeners in having depressed dorsal fin as well as pelvic fin reaching to or beyond level of anal-fin origin (depressed dorsal fin not reaching level of anal-fin origin, and pelvic fin reaching at most to anal fin in all other *Gastromyzon*).

Snout sloping downward in front of eyes more strongly than in most other *Gastromyzon*, but not so strongly as in *G. monticola* and *G. ridens*, and broadly rounded. Postoral pouch absent. Gill opening slightly angular, extending anteriorly ventral to subopercle only a short distance, its length about equal to eye diameter; subopercular groove present, continuous but shallow or interrupted near its middle. Scales in lateral series 52–63; predorsal scales 36–44; scale rows above lateral series 16–20; circumpeduncular scales about 25–30. Pectoral fin overlaps pelvic fin. Male with dense patches of small conical tubercles on dorsal surface of anteriormost pectoral-fin rays (Fig. 2).

Dorsal and lateral surfaces of body with thick, pale, interconnected lines forming irregular hexagonal or pentagonal figures; dorsal surface of head with numerous small, round, dark spots. Dorsal fin with two or three spotted longitudinal bands; caudal fin with two or three dark vertical bands; coloration in dorsal and caudal fins concentrated along fin rays. Paired fins with faint markings, pelvic fins sometimes almost entirely colorless or colorless except basal portion dusky. Some specimens with dorsal and lateral surfaces of body and head blotchy or blanched, suggesting physiological or behavioral color change.

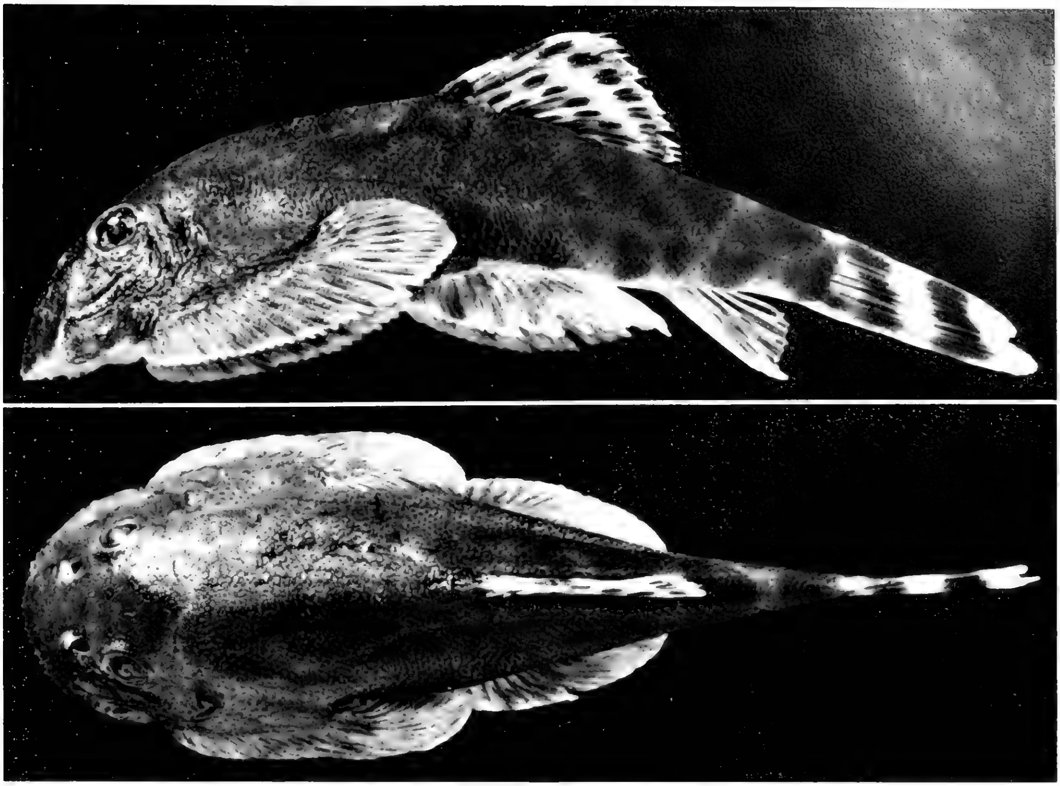


FIGURE 6. *Gastromyzon contractus*, 34.4-mm gravid female holotype (MZB 3447).

ETYMOLOGY.—From the Latin *contractus*, drawn together, in reference to the overlapping or nearness of the fins.

Gastromyzon ctenocephalus new species

(Figure 7)

TYPE-MATERIAL.—This species is known only from the type-series, collected at Senah, Sarawak, by A. Everett.

Holotype.—BMNH 1893.3.6:269, 42.3-mm ♂, Senah, Sarawak.

Paratypes.—BMNH 1893.3.6:261–268, 8:28.9–37.8 mm, same data as holotype.

DIAGNOSIS.—*Gastromyzon ctenocephalus* differs from all other *Gastromyzon* in having only 8–12 papillae on lower lip, widely spaced on or near its free anterior margin (vs. extremely numerous papillae densely distributed over entire lower lip); gill opening strongly angular, continued farther anteriorly ventral to subopercle than in any other *Gastromyzon*; subopercular groove continuous and relatively deep (vs. subopercular groove continuous but relatively shallow, interrupted in its middle, or absent); and sexually mature male with ctenoid tubercles on head and pectoral-fin base (ctenoid tubercles otherwise known only in male *Neogastromyzon pauciradiatus*).

Snout more or less strongly sloping downward in front of eyes, broadly rounded. No postoral pouch. Length of gill opening about 1.5–2 times eye diameter. Scales in lateral series about 50–60; predorsal scales about 32–36; scale rows above lateral series 15–20; circumpeduncular scales 28–30. Pectoral fin reaching or slightly overlapping pelvic fin; pelvic fin reaching anal fin; depressed dorsal fin falling short of level of anal-fin origin.

The holotype, a 42.3-mm male, has dense patches of small conical tubercles on dorsal surface of anteriormost branched pectoral-fin rays, as well as ctenoid tubercles on dorsolateral portion of head and on pectoral-fin base. A 32.6-mm male? has dense patches of small tubercles

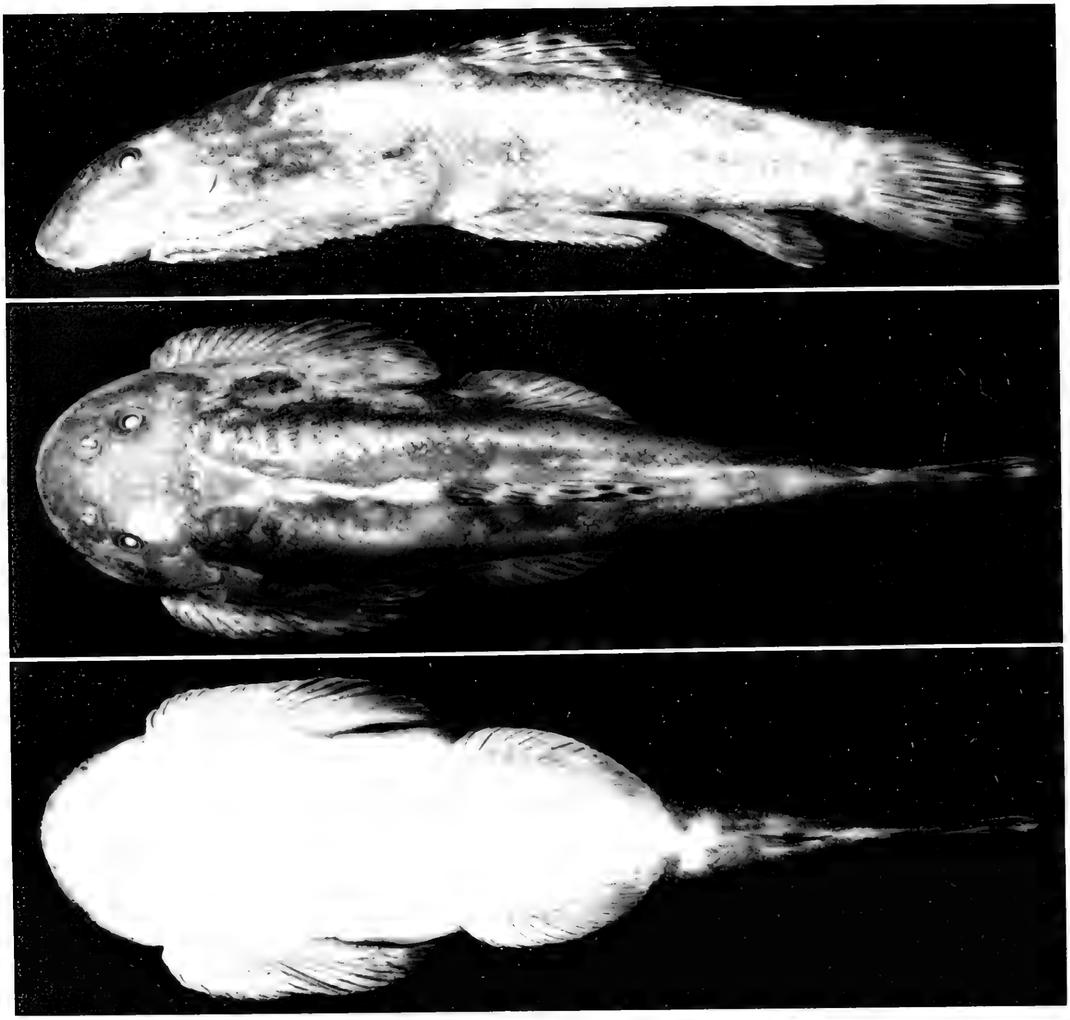


FIGURE 7. *Gastromyzon ctenocephalus*, 42.3-mm ripe male holotype (BMNH 1893.3.6.269).

on pectoral fin but no ctenoid tubercles. All other specimens, the three largest of which, 36.3–37.8 mm, are gravid females, lack ctenoid tubercles as well as dense patches of small tubercles on pectoral fin, but have numerous small conical tubercles widely scattered on dorsal surface of head and anteriormost portion of body (one tubercle per scale) as well as in uniserial rows of small conical tubercles on dorsal surface of pectoral-fin rays.

Dorsal surface of head with numerous small, round, pale spots; dorsal and lateral surface of body uniformly pale brownish (faded?) or, in one paratype, with small, round, pale spots on dorsal surface of body and pectoral-fin base, similar to those on head but slightly larger and more widely spaced apart. In holotype, dorsal and anal fins with two longitudinal spotted bands, spots centered on rays; caudal fin with two or three faintly spotted vertical bands, and melanophores narrowly distributed along length of all rays; paired fins with faint longitudinal bands. In all paratypes, dorsal-fin rays and interradial membranes heavily pigmented except for depigmented areas forming an alternating series of transparent round spots; anal fin with in-

FIGURE 8. *Gastromyzon fasciatus*, 59.0-mm mature male (MZB 3450).

terradial membranes each bearing a single vertical, oblong, darkly pigmented spot and rays without coloration; caudal fin with simple principal rays and interradial membranes between principal rays unpigmented, but unbranched principal rays and interradial membranes between branches of individual rays darkly pigmented; paired fins longitudinally banded in some paratypes, without noticeable banding in others; one paratype with pectoral fin spotted. Coloration of dorsal, anal, and caudal fins of paratypes very different from that in other species of *Gastromyzon* and in holotype. This difference, perhaps due to individual variation or sexual dichromatism, should be investigated when additional material becomes available.

ETYMOLOGY.—From the Greek *cteno-*, comb, and *cephalus*, head, in reference to the ctenoid tubercles on the head of mature males.

Gastromyzon fasciatus Inger and Chin

(Figure 8)

Gastromyzon fasciatus INGER AND CHIN, 1961:173 (type-locality "Sungai Dapu, a tributary of the Baleh River near the mouth of the Sungai Putai, Third Division, Sarawak").

MATERIAL EXAMINED.—SARAWAK: FMNH 68115, 68120, and BMNH 1960.12.30:1, 6:48.1–65.9 mm, paratypes, Baleh River, Rajang basin; FMNH 45852, 1:70.4 mm, Truson River, Lawas; FMNH 45853, 2:64.9–70.5 mm, Pa Brayong, Truson River; FMNH 68583, 3:44.1–51.0 mm, Akah River, Meligong; SU 32378, 1:45.1 mm, Sadong River; IRSNB 19725, 6:38.6–69.2 mm, Arur Dalan, torrential tributary of Padapur River, Baram basin. NORTH BORNEO: FMNH 68128, 5:20.6–46.5 mm, Sungai Kaingeran, Tambunan; FMNH uncat., 4:17.2–32.8 mm, Parutan River, Tambunan. KAPUAS BASIN: MZB 3450 and CAS 49321, 7:24.5–59.0 mm, Sungai Pinoh, RMNH 7636, 4:22.5–54.1 mm, Bongan. MAHAKAM BASIN: RMNH 7638, 2:53.2–56.8 mm, Bŏ; RMNH 7794, 2:39.2–54.3 mm, Bluu or Bloeoe.

DIAGNOSIS.—There does not seem to be any single character by which all specimens of *G. fasciatus* can be distinguished from all other species of *Gastromyzon*, but it is nevertheless a highly distinctive species. Predorsal scales 40–55 (usually less than 40 in all other *Gastromyzon*). Pelvic-fin and anal-fin rays usually more numerous than in other *Gastromyzon* (Table 1): branched pelvic-fin rays 20–24, modally 22 (vs. 17–22, modally 20 or less); branched anal-fin rays 5–5½, modally 5½ (vs. 4–5½, modally 5 or less). Specimens of *G. fasciatus* with well-developed coloration differ from all other *Gastromyzon* in having dorsal surface of head and body very darkly pigmented, black or bluish black, with narrow vertical white bars or white spots

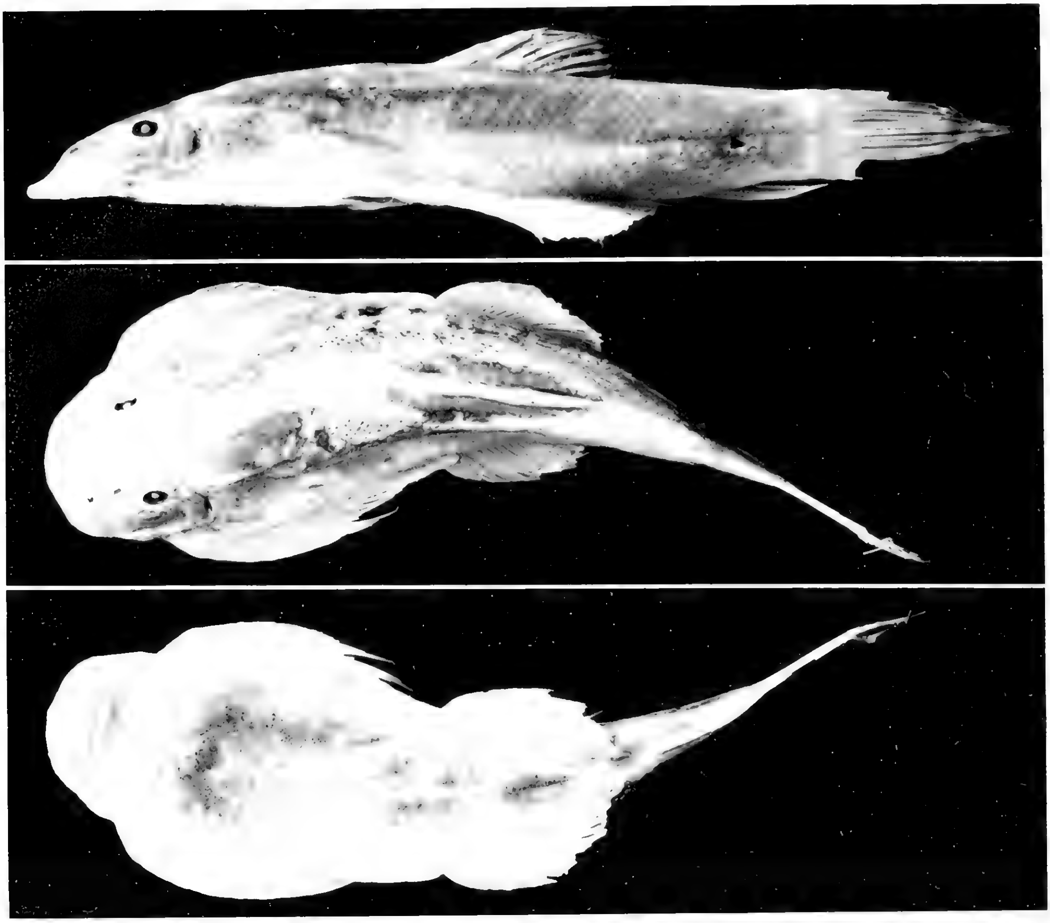


FIGURE 9. *Gastromyzon lepidogaster*, 78.0-mm holotype (BMNH 1874.11.24:5).

on body and disconnected white vermiculations on head. This coloration is well developed in freshly preserved specimens from Sarawak, North Borneo, and the Kapuas basin but is less well developed or indistinct in older material from the Mahakam basin.

Snout gently sloping downward in front of eyes, broadly rounded. No postoral pouch. Gill opening angular, extending anteriorly a short distance ventral to subopercle, its length about 1.5 times eye diameter. Subopercular groove always present, continuous or interrupted in the middle of its length. Scales in lateral series 55–68; scales above lateral series 20–23; circumpeduncular scales 30–43. Pectoral fin fails to reach pelvic fin; pelvic fin falls short of anal fin; depressed dorsal fin falls far short of level of anal-fin origin. Male with dense patches of small tubercles on dorsal surface of anteriormost branched pectoral-fin rays.

Freshly preserved specimens, including paratypes from the Rajang basin and the Kapuas material, have very distinctive coloration different from all other *Gastromyzon*: dorsal and lateral surfaces of head and body darkly pigmented, black or bluish-black, with several pale or white vertical bands (sometimes breaking up into a few large spots) on body; dorsal fin with three or four longitudinal spotted bands, caudal fin with two or three almost solid, thick, vertical or irregularly broken black bands; paired fins irregularly spotted or mottled (not longitudinally

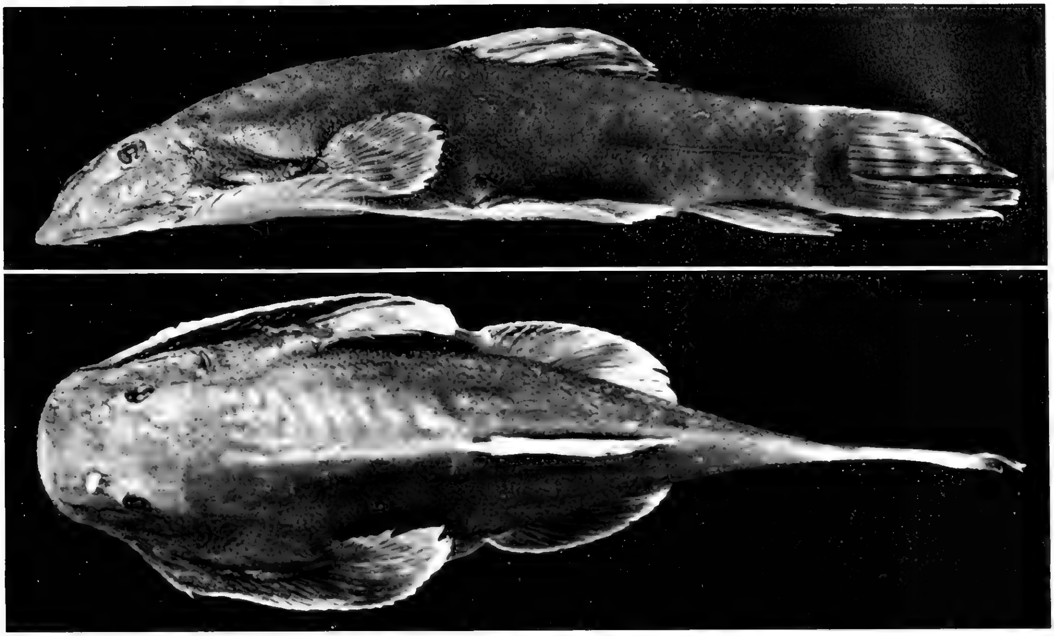


FIGURE 10. *Gastromyzon lepidogaster*, 62.9-mm ripe female paratype (FMNH 68113).

banded). Specimens from the Mahakam and some other collections, however, have less distinctive coloration, perhaps partly but not entirely due to fading after long preservation.

Gastromyzon lepidogaster new species

(Figures 9–10)

Gastromyzon borneensis GÜNTHER, 1874:6 (in part); POPTA 1906; WEBER AND DE BEAUFORT 1916 (Fig. 1, text; in part); INGER AND CHIN 1961; 1962 (in part).

TYPE-MATERIAL.—**Holotype:** BMNH 1874.11.24:5, 78.0 mm, sources of Mengalong River, Beaufort District, North Borneo.

Paratypes.—NORTH BORNEO: FMNH 68111–68114, 7:38.0–64.4 mm, Kinabatangan basin; FMNH 51683, 1:46.4 mm, East Coast Residency. BRUNEI: IRSNB uncat., 1:37.2 mm, upper course of Sungai Temburong. KAJAN BASIN: RMNH 7639, 3:79.0–83.3 mm, upper course of Boeloengan River above Ben Barum. MAHAKAM BASIN: RMNH 7635, 5:39.3–70.1 mm, upper Mahakam; RMNH 7637, 19:22.3–46.2 mm, Howong; RMNH 7794, 7:36.1–83.4 mm, Bluu or Bloeoe; RMNH 7638, 1:71.8 mm, Bŏ. KAPUAS BASIN: RMNH uncat., 1:72.3 mm, Bongan.

DIAGNOSIS.—*Gastromyzon lepidogaster* differs from all other *Gastromyzon* in having the abdomen more or less extensively covered with fine scales in all specimens examined over 40.2 mm and in many below this size (abdomen entirely scaleless in all other *Gastromyzon* except in some specimens of *G. megalepis* which have a few relatively large scales between bases of posteriormost pelvic-fin rays).

Snout gently sloping downward in front of eyes, gently rounded. No postoral pouch. Gill opening vertical, its length about equal to eye diameter. No subopercular groove. Scales in lateral series 54–62; predorsal scales 39–42; scale rows above lateral series 16–20; circumpeduncular scales 30–32. Pectoral fin reaches or falls short of pelvic fin; pelvic fin reaches anal fin; depressed dorsal fin falls short of level of anal-fin origin.

All *Gastromyzon lepidogaster* from North Borneo and Sarawak have the abdomen completely covered with fine scales up to the level of the anterior margin of the pectoral girdle, except the smallest specimen (27.7 mm), which has the abdomen entirely scaleless. Specimens of this species from the Mahakam, Kajan, and Kapuas basins above 40.2 mm, and many below this size, have the abdomen completely covered with fine scales between the bases of the pelvic fins, and sometimes have scattered scales farther anteriorly, but never have the abdomen

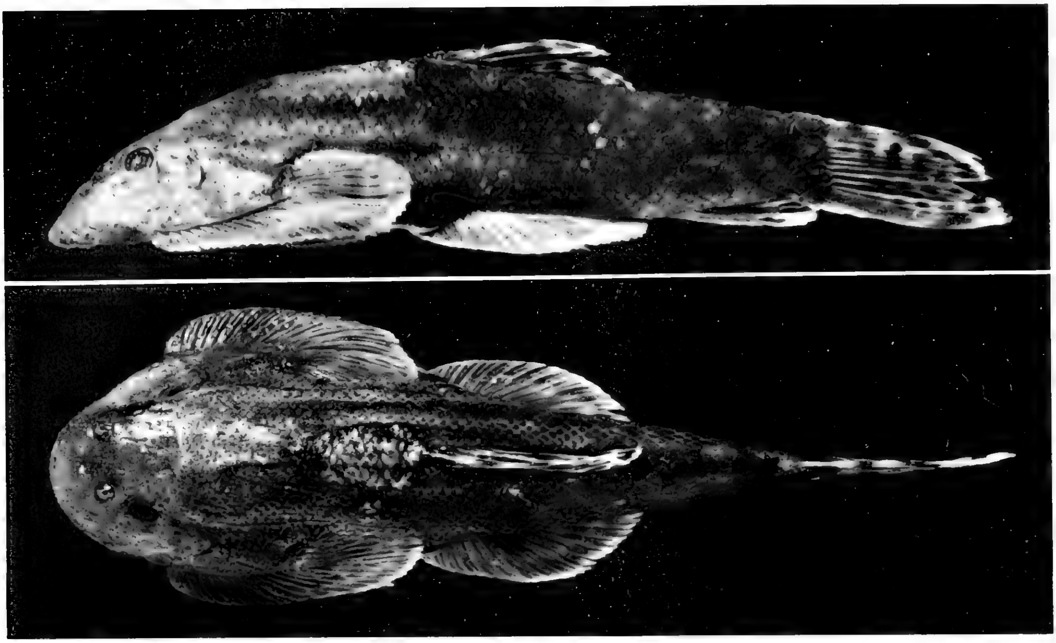


FIGURE 11. *Gastromyzon megalepis*, 54.6-mm mature male holotype (FMNH 68126).

completely covered with scales. They are similar in other respects to *G. lepidogaster* from North Borneo and Sarawak.

Dorsal and lateral surfaces of head and body uniformly brownish, or body with thin pale vertical bands (similar but slightly more numerous than those in *G. fasciatus*); bands on posterior portion of body in a few specimens interconnected to form irregularly pentagonal or hexagonal figures. Distal half of dorsal fin with two longitudinal spotted bands; caudal fin with broad dusky vertical band basally (on portion of fin covered by scales) and three or four lunate spotted bands on rest of fin. Anal and paired fins with faint markings, pectoral with spotted longitudinal bands, pelvic and anal with dusky coloration largely confined along rays.

ETYMOLOGY.—From the Greek *lepido-*, scale, and *gaster*, stomach, in reference to the extensive abdominal squamation.

Gastromyzon megalepis new species

(Figure 11)

Gastromyzon borneensis INGER AND CHIN, 1961:171 (in part).

TYPE-MATERIAL.—**Holotype:** FMNH 68126, 54.6-mm ♂, tributary of Baleh River between Sungai Entunau and Sungai Putai, Rajang basin, Third District, Sarawak, R. F. Inger, 5 Aug. 1956.

Paratypes.—FMNH uncat., 5:45.1–60.5 mm, same data as holotype; FMNH 68127, 3:28.6–33.1 mm, Baleh River, Rajang basin, Third District, Sarawak.

DIAGNOSIS.—*Gastromyzon megalepis* has relatively larger scales than any other *Gastromyzon*; it is also the only *Gastromyzon* with pelvic fin lacking serrae. Scales in lateral series 44–48 (vs. 50 or more in all other *Gastromyzon*); predorsal scales 24–28 (vs. 30 or more); scale rows above lateral series 11–12 (vs. 15 or more); and circumpeduncular scales 20–21 (vs. 25 or more). Pelvic-fin rays 4–15 each with a sharp, dorsoposteriorly projecting continuous lamina or flange, without bony projections from individual lepidotrichia.

Snout gently sloping downwards in front of eyes, broadly rounded. No postoral pouch. Gill opening vertical, its length about 1.5 times eye diameter. Subopercular groove absent. Pectoral fin extends to pelvic-fin origin; pelvic fin extends almost to anal fin; depressed dorsal fin falls far short of level of anal-fin origin. Male with dense patches of minute tubercles on dorsal surface of anteriormost branched pectoral-fin rays.

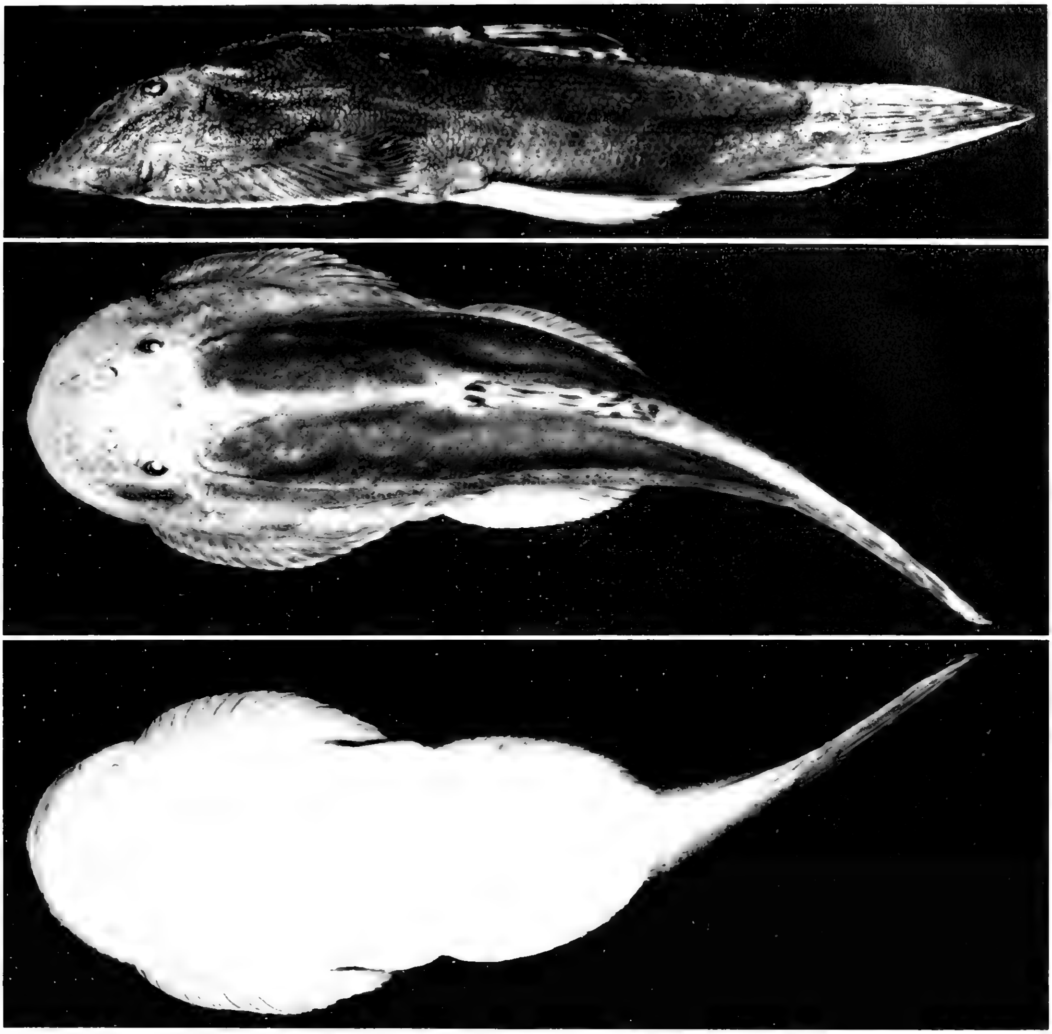


FIGURE 12. *Gastromyzon monticola*, 70.9-mm ripe female (BMNH 1894.6.30:196).

Dorsal and lateral surfaces of head and body uniformly brownish, sometimes mottled on caudal portion of body. Dorsal fin with four longitudinal spotted bands and caudal fin with about six lunate spotted bands, the spots nearly confined to fin rays; anal fin with melanophores uniformly distributed along rays; paired fins with faint longitudinal bands, pale margins.

ETYMOLOGY.—From the Greek *mega*-, large, and *lepis*, scale, in reference to the relatively large scales of this species.

Gastromyzon monticola (Vaillant)
(Figure 12)

Lepidoglanis monticola VAILLANT, 1889:81 (type-locality "Kina-Balou" = Mt. Kinabalu, North Borneo).

Gastromyzon monticola VAILLANT, 1891; 1893:94, pl. 1 (description and figures of syntypes).

Gastromyzon borneensis WEBER AND DE BEAUFORT, 1916 (in part).

This species has not been recognized by ichthyologists since it was placed in the synonymy of *Gastromyzon borneensis* by Weber and de

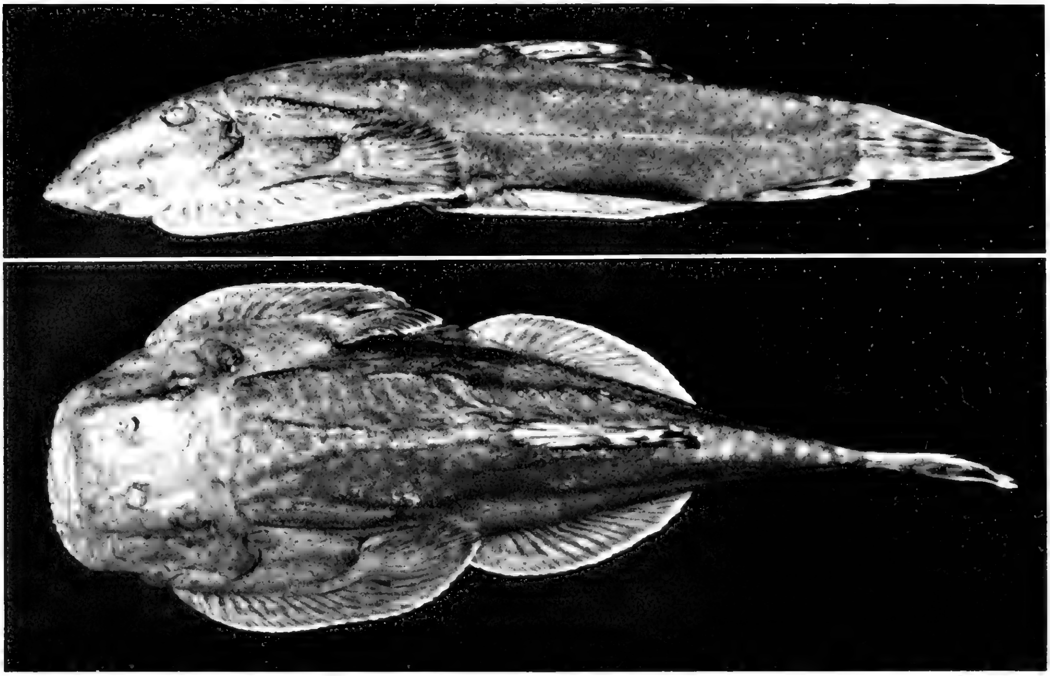


FIGURE 13. *Gastromyzon punctulatus*, 53.0-mm gravid female paratype (FMNH 68117).

Beaufort; it was entirely overlooked by Inger and Chin (1961).

MATERIAL EXAMINED.—All from NORTH BORNEO: MNHN 1889.83–85, 3:63.5–67.1 mm, syntypes, Mt. Kinabalu (Vaillant 1889, indicated 10 syntypes but only these 3 could be located during my visit to the MNHN in November 1979); BMNH 1894.6.30:196–197, 2:66.9–70.9 mm, Mt. Kinabalu (these two specimens were compared directly with the syntypes during my visit to the MNHN); FMNH 44725, 4:33.2–56.3 mm, Tempassuk River, Kota Belud District, West Coast Residency.

In addition to the specimens just listed, I tentatively identify MCZ 54091, 2:43.1–47.2 mm, Sarawak, as this species; these specimens were seen briefly during a visit to the MCZ and have not been considered in the account below.

DIAGNOSIS.—*Gastromyzon monticola* differs from all other *Gastromyzon* except *G. borneensis* in having a postoral pouch; it lacks a secondary rostrum and differs in many respects from *G. borneensis*. It differs from all other *Gastromyzon* except *G. ridens* and *G. contractus* in having the snout very strongly sloping downward in front of the eyes.

Snout broadly rounded or slightly pointed. Gill opening vertical, its length about equal to eye diameter. Subopercular groove absent. Scales in lateral series about 55–58; predorsal scales about 40; scale rows above lateral series 20; circumpeduncular scales 30–32. Pectoral fin overlaps pelvic fin; pelvic fin reaches anal fin; and depressed dorsal fin falls far short of level of anal-fin origin.

Dorsal and lateral surfaces of body uniformly brownish; dorsal surface of head with interconnected thick pale lines forming irregularly hexagonal or pentagonal figures, very numerous and close-set. Dorsal, anal, and caudal fins with numerous small round spots centered on rays, forming about four longitudinal bands on dorsal fin, two (faint) bands on anal fin, and up to eight lunate spotted bands on caudal fin. A particularly prominent dark spot at dorsal-fin origin (a spot at dorsal-fin origin occurs in other *Gastromyzon* but is usually not so noticeable). Paired fins longitudinally banded, with a moderately wide pale distal marginal band, and a dark submarginal band of about equal width; pectoral fin spotted internal to these bands.

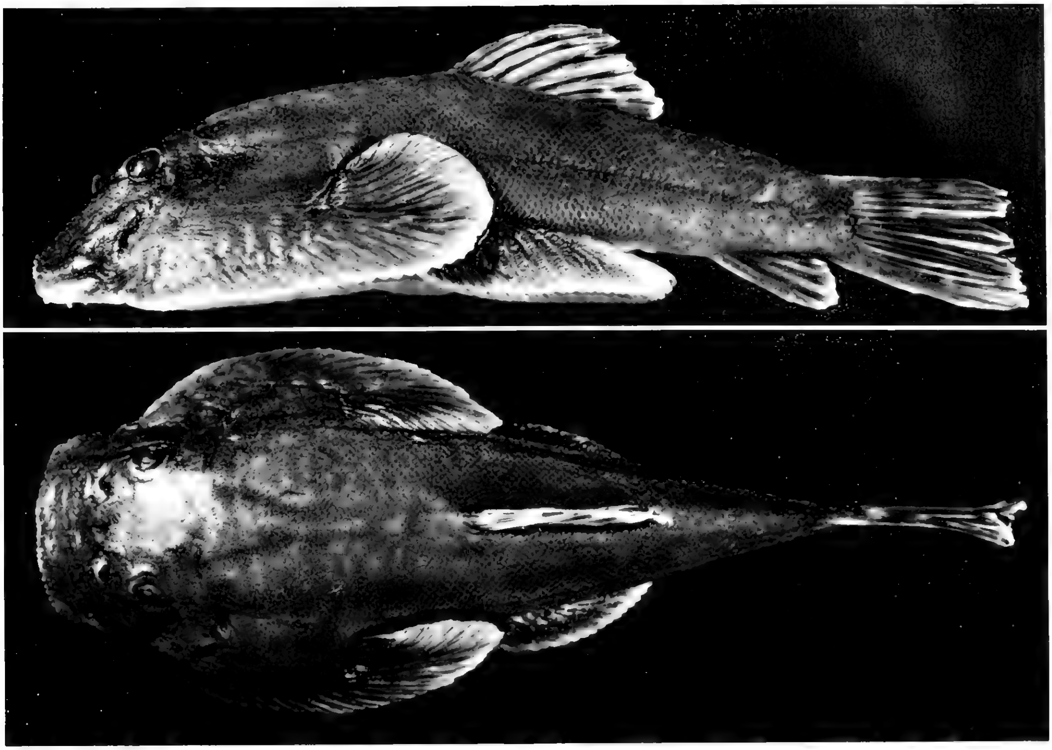


FIGURE 14. *Gastromyzon ridens*, 50.0-mm ripe male holotype (MZB 3455).

Gastromyzon punctulatus Inger and Chin
(Figure 13)

Gastromyzon punctulatus INGER AND CHIN, 1961:173 (type-locality "Sungai Dapu, a tributary of the Baleh River near the mouth of the Sungai Putai, Third Division, Sarawak").

This species is known only from the type-specimens collected in tributaries of the Baleh River, Rajang basin, Sarawak.

MATERIAL EXAMINED.—FMNH 68117, 3:32.9–53.6 mm, paratypes, same data as holotype.

DIAGNOSIS (partly after Inger and Chin 1961).—Larger specimens of *Gastromyzon punctulatus* differ from all other *Gastromyzon* except *G. ridens* in having a relatively truncate snout (vs. relatively more rounded in all other *Gastromyzon* and in smaller *G. punctulatus*) and a transverse row of papillae posterior to lower lip (not observed in any other *Gastromyzon*).

Snout gently sloping downward in front of eyes. No postoral pouch. Gill opening slightly angular, its length about 1.5 times eye diameter. Subopercular groove broadly interrupted or absent in larger specimens, continuous in small specimens. Scales in lateral series about 58–59; predorsal scales about 40–42; scale rows above lateral series 21–22; circumpeduncular scales about 33. Pectoral fin reaches pelvic fin; pelvic fin falls short of anal fin; depressed dorsal fin falls short of level of anal-fin origin. Tubercles on dorsal surface of head, body, and fins minute or absent except for two or three rows of widely spaced small conical tubercles on anterior rim of snout. Dorsal surface of pectoral fin without dense patches of small tubercles.

Two largest specimens examined by me (53.0-mm gravid ♀ and 53.7-mm ripe ♂) with faint, pale round spots, relatively large, all about the same size, and lying close together, over entire dorsal surface of head and body including caudal peduncle; sides of body otherwise uniformly brownish; paired fins longitudinally banded, with pale (unpigmented) distal margins; dorsal-

TABLE 1. FREQUENCIES OF BRANCHED FIN RAY COUNTS IN *Gastromyzon*.

	Dorsal							Anal				Pectoral									Pelvic							
	6½	7	7½	8	8½	9	9½	4	4½	5	5½	22	23	24	25	26	27	28	29	30	17	18	19	20	21	22	23	24
G. borneensis	1	5	68	2	3				67	7	2	1	8	20	41	17	3				5	44	34	6				
G. contractus					17	2	1		2	12	5			4	8	6	2					1	4	11	4			
G. ctenocephalus			9						9				1	3	5							3	5	1				
G. fasciatus					28					3	25	1			4	13	8	1						6	12	7	1	1
G. lepidogaster			1	15	12	14	1	1	5	36	2	1	1	12	21	11						2	20	22	3	1		
G. magalepis			1	1	6	1				8	1		1	6	2							1	2	5	1			
G. monticola			6	3				2	6	1			2	6	5	1					2	4	6	1	1			
G. punctulatus			1	1	1				3					1		2							1	2				
G. ridens			3	17	1			3	16	2					1	3	12	5	1	1	5	14	2	1				

fin and anal-fin rays dusky, interradial membranes depigmented except for a few oblong dark spots; caudal fin with four or five dark narrow vertical bands. A small specimen, 32.9 mm, is similarly colored, but spots are more distinct, and those on head more variable in shape, vermiculate rather than round.

Gastromyzon ridens new species

(Figure 14)

TYPE-MATERIAL.—**Holotype:** MZB 3455, 50.0-mm ripe ♂, mainstream of Sungai Pinoh 20–60 km upstream from Nangapinoh, Kapuas basin, T. R. Roberts, S. Woerjoatmodjo, 21 July 1976.

Paratypes.—CAS 49322, FMNH 94228, USNM 230249, BMNH uncat., MNHN uncat., RMNH uncat., 7:24.3– 35.7 mm, same data as holotype; BMNH 1893.3.6.270–275, 6:35.4–48.6 mm, Senah, Sarawak; SU 32378, 9:21.2–36.5 mm, Sadong River, Sarawak.

DIAGNOSIS.—*Gastromyzon ridens* differs from all other *Gastromyzon* in having sublacrimal groove very deep and enlarged, extending posteriorly onto cheek (vs. sublacrimal groove restricted to ventral surface of head in all other *Gastromyzon*); length of gill opening less than or barely equal to eye diameter (vs. equal to or greater than eye diameter); and snout relatively truncate, often with a slight ventral concavity at its tip (snout more rounded in all other *Gastromyzon* except *G. punctulatus*, which lacks ventral concavity at snout tip). Pectoral-fin rays 25–30, modally 27 (vs. 22–28, modally 26 or less in all other *Gastromyzon*; Table 1).

Snout strongly sloping downwards in front of eyes (more gently sloping in all other *Gastromyzon* except *G. contractus* and *G. monticola*). No postoral pouch. Gill opening vertical. No subopercular groove. Scales in lateral series 56–78; predorsal scales 32–52; scale rows above lateral series 15–26; circumpeduncular scales about 30–40. Pectoral fin considerably overlaps pelvic fin, perhaps more so than in any other *Gastromyzon* except *G. contractus*; pelvic fin falls short of anal fin; depressed dorsal fin falls far short of level of anal-fin origin. Male holotype, 50.0 mm, has serrae on pelvic fin relatively larger and more heavily developed than in any other specimen of *Gastromyzon* examined, and tubercles minute or absent on head, body, and fins except for numerous moderately large conical tubercles in a narrow band near snout tip. Serration and tuberculation of paratypes similar to that of holotype but less well developed, and some (♀♀?) lack tuberculation on snout tip.

Dorsal and lateral surfaces of head and body entirely or almost entirely covered with small, pale round spots; some specimens with posterior portion of body, body posterior of head, or entire head and body more or less uniformly pale or blanched, suggesting behavioral or physiological color change (as in *G. contractus*). Fins dusky or faintly marked, median fins with melanophores mainly confined along fin rays.

ETYMOLOGY.—From the Latin *ridens,* laughing or smiling, in reference to the peculiar countenance of this species caused by the extension of the sublacrimal groove onto the side of its head.

Glaniopsis Boulenger

Glaniopsis BOULENGER, 1899:228 (type-species *Glaniopsis hanitschi* Boulenger, 1899, by monotypy).

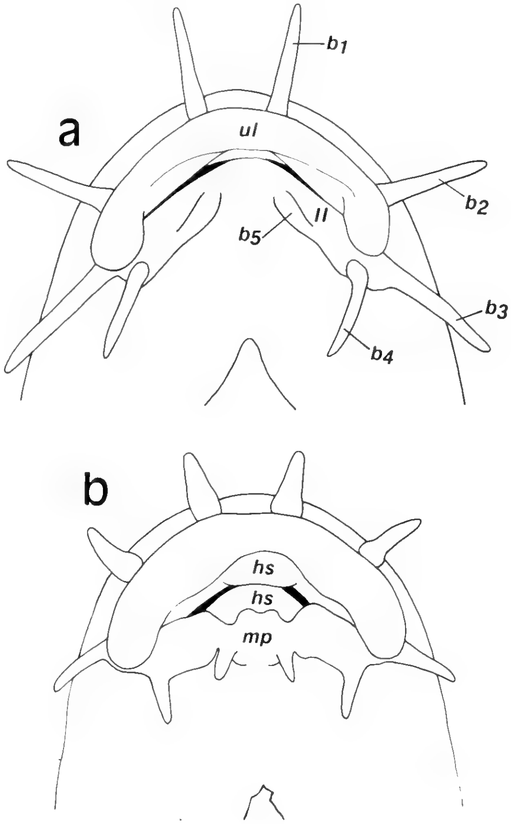


FIGURE 15. Ventral surface of head. (*a*) *Glaniopsis hanitschi*; (*b*) *Glaniopsis multiradiata* (b_1, b_2, b_5 = rostral, maxillary, mental barbels; b_3, b_4 = mandibular barbels; hs = horny sheaths of upper and lower jaws; ll, ul = lower lip, upper lip; mp = mental pad).

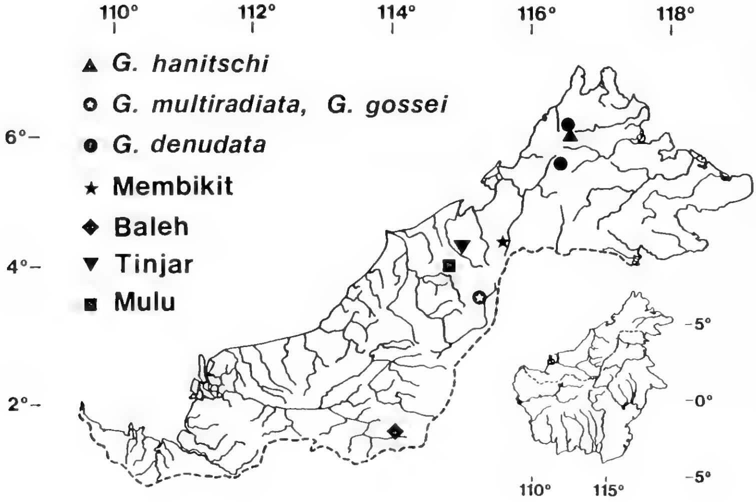


FIGURE 16. Distribution of *Glaniopsis*.

DIAGNOSIS.—*Glaniopsis* differs from all other Gastromyzontinae in having a subterminal (rather than inferior) mouth, and from all other Bornean Gastromyzontinae in having two (instead of only one) mandibular barbels at each corner of mouth (Fig. 15).

Dorsal fin with two simple and six or seven branched rays; anal fin with two simple and five branched rays; posteriormost dorsal-fin and anal-fin rays not split to base. Pectoral and pelvic fins widely separated; pectoral fin with one simple and 11–17 branched rays, with an outer "adhesive" and inner "vibratory" portions (Hora and Jayaram 1951), its origin posterior to head. Pelvic fins separate, each with 1 simple and 7–10 branched rays. Suprapelvic flap absent. Adhesive pads present on first three to five pectoral-fin rays and first three pelvic-fin rays. Sexually mature males with small or minute tubercles widely distributed on head, body, and fins; males with most highly developed tuberculation have median-fin rays and dorsal surface of paired-fin rays with uniserial rows of conical tubercles; tubercles on body minute, pricklelike, usually one per scale (many scales without tubercles). Females nontuberculate except for a few small conical tubercles in uniserial rows on dorsal surface of anteriormost four or five pectoral-fin rays.

Key to *Glaniopsis*

1a. Dorsal fin with 7 branched rays 2
1b. Dorsal fin with 6 branched rays 3

2a. Pectoral fin with 15–17 and pelvic fin with 8–10 branched rays .... *G. multiradiata*
2b. Pectoral fin with 12–14 and pelvic fin with 6–9 branched rays .... Baleh, Tinjar, and Mulu *Glaniopsis* (see accounts below for additional information)

3a. Maximum of nine lateral scale rows (midlateral scale row plus three scale rows above and five scale rows below it); principal caudal-fin rays usually less than 9+9 (most often 8+8) .... *G. denudata*
3b. At least 20 lateral scale rows; principal caudal-fin rays almost always 9+9 4

4a. Caudal peduncle depth 7.6–9.4; adpressed nasal barbel extends posteriorly at least to posterior margin of eye; eye diameter 30–42, 3.5–4.6 in interorbital width; horny sheath of upper jaw varying from gently convex to strongly projecting (beaklike) .... *G. hanitschi*, Membikit *Glaniopsis* (see accounts below for additional information)
4b. Caudal peduncle depth 9.2–12.2; adpressed nasal barbel extends posteriorly no farther than middle of eye; eye diameter 24–30, 2.2–3.1 in interorbital width; horny sheath of upper jaw varying from slightly concave to strongly notched medially .... *G. gossei*

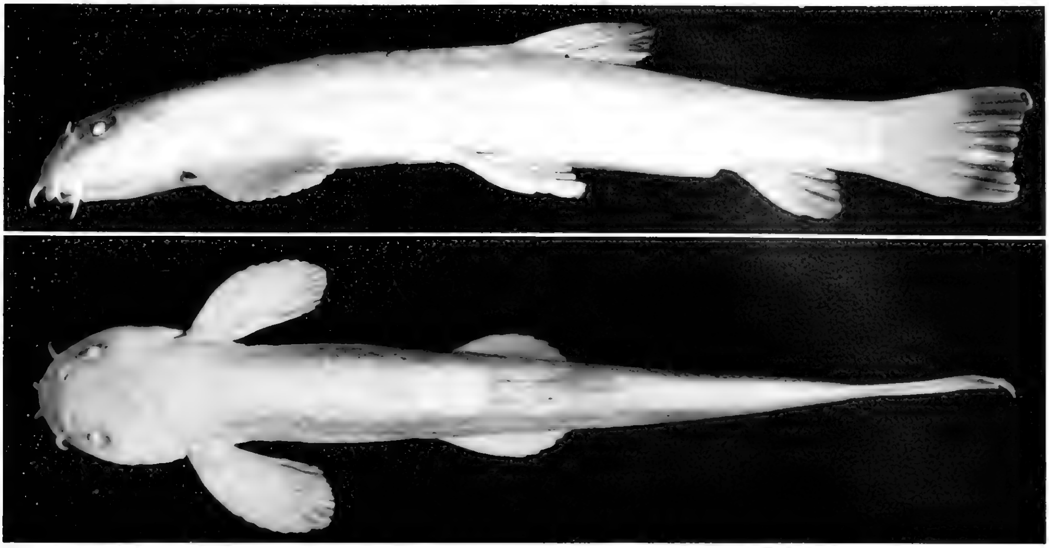


FIGURE 17. *Glaniopsis denudata*, 34.5-mm mature male holotype (BMNH 1957.2.27:1).

Glaniopsis denudata new species
(Figure 17)

TYPE-MATERIAL.—**Holotype:** BMNH 1957.2.27:1, 34.5 mm. Sungai Kidikarok, North Borneo; altitude 4500 ft [ca 1370 m]; 26 Aug. 1956; Cambridge North Borneo Expedition.

Paratypes.—BMNH 1957.2.27:2–15, 14:19.4–34.9 mm. Same collection data as holotype; IRSNB 618, 1:41.8 mm. Sungai Silau Silau, a headwater tributary of Sungai Liwagu, Labuk basin, near Tenompak, Mount Kinabalu, altitude 5000 ft [ca. 1500 m]; 7 Oct. 1971; Léopold III, J. P. Gosse.

DIAGNOSIS.—*Glaniopsis denudata,* perhaps the smallest species of *Glaniopsis,* differs from all other *Glaniopsis* in having extremely reduced squamation and usually fewer than 9+9 principal caudal-fin rays. Largest specimen a gravid female, 41.8 mm. Squamation consists of lateral scale series plus maximum of about three scale rows above and five below it, or total of about nine scale rows (vs. 20 or more in all other *Glaniopsis*). Principal caudal-fin rays variable, most often 8+8, perhaps always less than 9+9. Sexually mature males with minute, pricklelike tubercles scattered on abdomen in front as well as behind pelvic fins. Dorsal-fin origin distinctly posterior to a vertical through base of last pelvic-fin ray. Pelvic-fin origin much nearer pectoral-fin origin than to anal-fin origin.

Eye 17–25, 1.9–2.6 in interorbital space. Interorbital space 9.7–12.7. Branched dorsal-fin rays 6(13). Principal caudal-fin rays variable, most often 8+8: ?9+?9(1), 9+8(1), 9+8 or 9+9(1), 8+9(1), 8+8(6), 7+8(1). Pectoral-fin rays il3(6), il4(6), or il5(1). Pelvic-fin rays i7(13).

Length of nasal, outer mandibular, and sometimes maxillary barbels about equal to or slightly more than eye diameter, otherwise length of barbels less than eye diameter. Adpressed nasal barbel failing to reach exposed portion of eye or at most reaching only slightly beyond front margin of eye. Mental barbel flaplike.

Lateral scale series incomplete, with 102–111 scales, some scales absent or missing posteriorly, which, if present, would yield counts of about 115–120 (observations on three specimens lightly stained with alizarin). Dorsum and abdomen entirely scaleless. Tubed scale series complete or continuous on anterior one-fourth to one-half of body, always arrested before level of dorsal-fin origin and entirely absent posteriorly. In specimens less than 24 mm, tubed scale series absent or absent except for short anterior segment of up to about six tube-bearing scales. Myotomal muscle masses more sharply defined externally than in any other *Glaniopsis,* divisions between them clearly visible for entire length of body (vs. scarcely noticeable at all, or clearly visible only on posterior third of body).

All specimens in type-series with nearly identical coloration. Head without markings, dusky dorsally and laterally to just below level of eyes, without melanophores ventrally. Oral barbels and lips without melanophores. Upper fourth to half of body dusky, with fine melanophores uniformly distributed everywhere except in vicinity

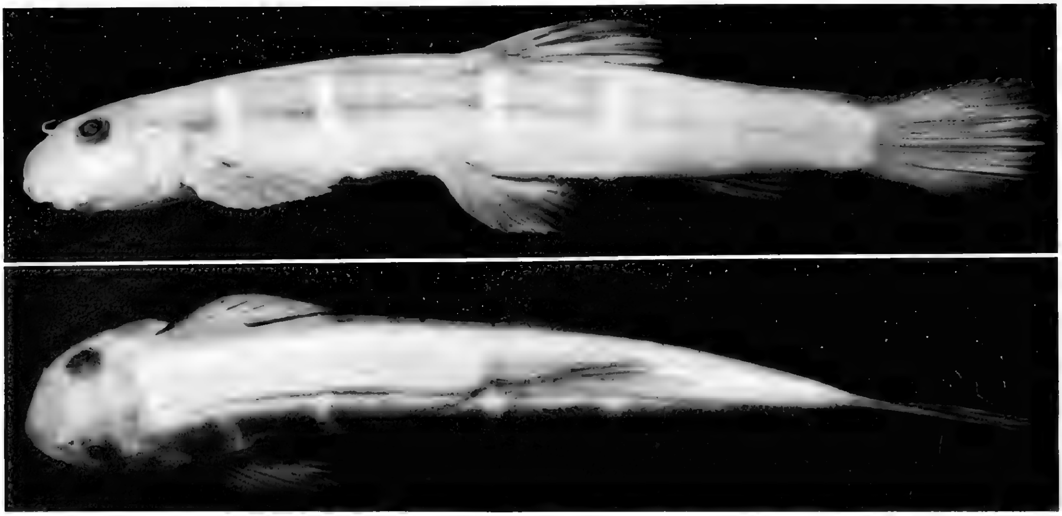


FIGURE 18. *Glaniopsis gossei*, 40.5-mm mature male holotype (IRSNB 621).

of dorsal-fin base: a dark area due to densely clustered fine melanophores circumscribing dorsal-fin base; a pallid area with few or no melanophores extending on dorsum in front of dorsal fin for a distance about equal to dorsal-fin base (some juvenile specimens of *G. hanitschi* display a tendency toward this coloration, but with much less marked contrast between dark and pallid areas; similar coloration not observed in juveniles or adults of other *Glaniopsis*). Lower half of body pale, without melanophores except near midline of body, dusky area dorsal to pectoral-fin base, very faint dusky area lateral to pelvic-fin base, and dark area lateral to anal-fin base due to concentrations of melanophores. Fins unpigmented or dusky, without distinct markings except for concentration of melanophores on caudal-fin base immediately posterior to hypural fan.

ETYMOLOGY.—The feminine adjective *denudata*, Latin, "nude," refers to the very limited squamation and sharply defined myotomal muscles characteristic of the species.

Glaniopsis gossei new species

(Figure 18)

TYPE-MATERIAL.—**Holotype:** IRSNB 621, 40.5 mm. Arur Dalan, a torrential headwater of Sungai Padapur, Baram basin, near Bario, Sarawak; altitude 3500 ft [ca. 1100 m]; 11 Oct. 1971; Léopold III, J. P. Gosse.

Paratypes.—IRSNB 622, 19:28.6–46.5 mm. Same collection data as holotype.

DIAGNOSIS.—*Glaniopsis gossei* differs from all other *Glaniopsis* in having a series of depigmented vertical bars on sides of body (these may be lost or obscured in specimens which are pallid, as if bleached or faded) and horny sheath of upper jaw strongly notched or concave medially, rather than strongly convex medially (beaklike) or evenly curved. It also differs from *G. hanitschi* in having larger eyes, narrower interorbital space, and shallower caudal peduncle; from *G. multiradiata* in having fewer dorsal, pectoral, and pelvic-fin rays, larger eyes, and longer barbels; and from *G. denudata* in having more extensive squamation.

Eye diameter 24–30, 2.2–3.1 in interorbital space. Interorbital space 9.2–11.0. Depth caudal peduncle 9.2–12.2. Branched dorsal-fin rays invariably 6 (20). Principal caudal-fin rays 9+9 (19; one specimen with broken fin not counted). Pectoral-fin rays i11 (2), i12 (14), or i13 (3). Pelvic-fin rays i7 (20). Dorsal-fin origin on a vertical through origin of last pelvic-fin ray or slightly posterior to it. Pelvic-fin origin closer to anal-fin origin than to pectoral-fin origin.

Length of nasal and outer mandibular barbels about 1.5 times eye diameter. Length of other barbels except mental barbel about equal to eye diameter. Adpressed nasal barbel extends posteriorly at least to middle of eye but not beyond exposed portion of eye. Mental barbel barbel-

FIGURE 19. *Glaniopsis hanitschi.* (*a*) 59.4-mm mature male (IRSNB 17540); (*b, c*) 59.4-mm mature female (IRSNB 17541).

like, about one-half as long as inner mandibular barbel.

Sides of body completely covered with scales which tend to be embedded (without free posterior margins) and slightly dispersed (not overlapping), especially on posterior half of body, making them difficult to count. Over 100 scales in lateral series. Dorsum in front of dorsal fin scaleless, behind dorsal fin covered with scales. Entire abdomen scaleless(?) except for a few scales near vent and anal-fin origin. Tubed scale series complete on anterior half of body, variably interrupted on posterior half.

ETYMOLOGY.—Named for Jean-Pierre Gosse, who collected much of the material reported upon in this paper, including the type-series of this species.

Glaniopsis hanitschi Boulenger

(Figures 15*a*, 19)

Glaniopsis hanitschi BOULENGER, 1899:228 (type-locality Kadamaian River, Mount Kinabalu, altitude 2100 ft [ca. 640 m]).

MATERIAL EXAMINED.—IRSNB 17540, 52:31.7–70.8 mm, Sungai Silau Silau, a headwater tributary of Sungai Liwagu, Labuk basin, near Tenompak, Mount Kinabalu, altitude 5000 ft [ca. 1500 m]; IRSNB 17541, 28:17.6–69.3 mm, headwater tributary of Sungai Liodan, below Bundu Tahun, Mount Kinabalu, altitude 4000 ft [ca. 1200 m]; FMNH 68950, 1:53.7 mm, Sungai Kelangaan, near Mesilan base camp, Mount Kinabalu, altitude 5000 ft [ca. 1500 m]; FMNH 47985, 1:58.7 mm, Jesselton District.

DIAGNOSIS.—*G. hanitschi* is the largest and most robust *Glaniopsis*, attaining 97 mm, with the deepest caudal peduncle, broadest interorbital width, smallest eyes, and longest barbels.

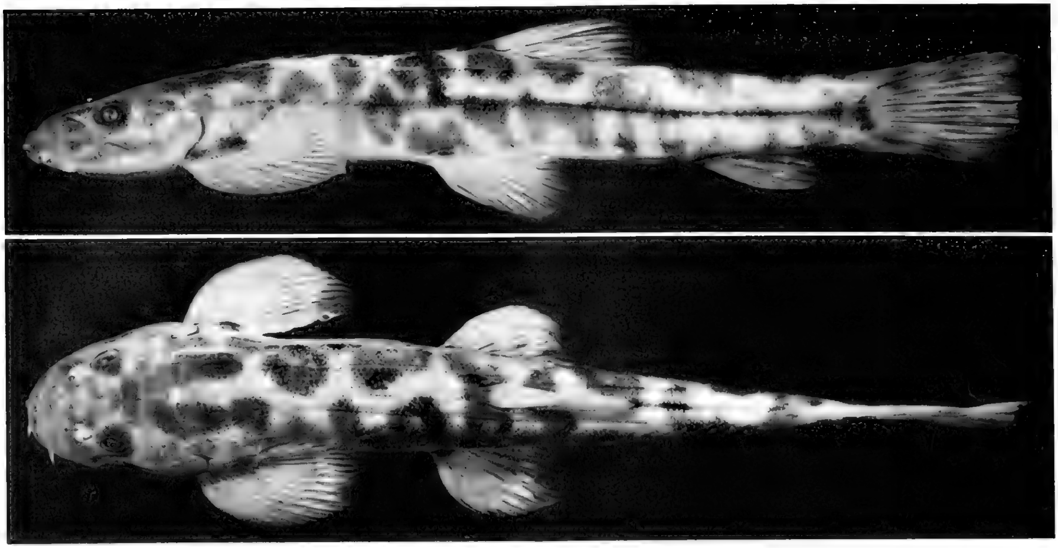


FIGURE 20. *Glaniopsis multiradiata,* 44.5-mm female holotype (IRSNB 619).

Caudal peduncle depth 7.6–8.9 (vs. 9.2–12.7 in all other species); interorbital width 7.9–9.6 (vs. 9.2–12.7; eye diameter 30–42, 3.7–4.6 in interorbital width (vs. 17–37, 1.9–3.1 in interorbital width); and adpressed nasal barbel invariably extending posteriorly beyond exposed portion of eye. Mental barbel flaplike.

Branched rays in dorsal fin 6 (30) (7 in two specimens with posteriormost ray abnormal), in pectoral fin 12 (20) or 13 (12), and in pelvic fin 6 (1), 7 (30), or 8 (1). Principal caudal-fin rays 9+9 (22) or 10+9 (1) (8+9 in one specimen with anomalous vertebral column).

Sides of body entirely covered with close-set, regularly overlapping scales with exposed posterior margins except for a small scaleless area immediately above base of pectoral fin. Nearly 30 complete scale rows near middle of body and 20 or more on caudal peduncle. Midlateral scale row complete, with about 125–146 scales (19). Dorsal surface of body anterior to dorsal fin varying from scaleless to covered with scales for five-sixths of distance to occiput, but never completely scaled. Dorsal surface of body posterior to dorsal fin completely covered with scales, or with only small scaleless areas immediately posterior to dorsal fin and on keel-like ridge over upper procurrent caudal-fin rays. Abdomen scaleless or nearly scaleless except for a few dispersed, embedded scales near anal-fin base and just anterior to vent. Lateral line canal tube-bearing scale series usually complete on anterior half of body, variably interrupted or incomplete on posterior half of body.

Head without markings. Body with 7–18 vertical or slightly oblique dark bars, mainly on dorsal half of sides, partially breaking up into upper and lower portions in some specimens, and regularly or irregularly arranged, sometimes dropping out or "fusing"; some bars may extend below midlateral line, and an occasional bar may lie entirely below it, especially in the caudal region, but bars do not continue onto or across dorsum either in front or behind dorsal fin. Anteriormost bar usually immediately behind head, posteriormost just in front of caudal-fin insertion; usually a bar near dorsal-fin origin. In some specimens two or more bars "fuse" to form a single broad mark. Bars absent or faint in specimens less than 32 mm. A few larger specimens with a narrow darkly pigmented area paralleling occiput and traversing dorsum immediately posterior to head. Two large specimens with separate markings which resemble bars on side of body and traverse dorsum anterior to dorsal fin. All specimens with a dense cluster of melanophores, sometimes faint, on lateral surface of pelvic-fin base and sometimes extending onto basal portion of first 1–2 pelvic-fin rays. Dorsum and sides of body with lozenge-shaped clusters of melanophores centered on each scale. Dorsal and lateral surfaces of head, nasal barbel, upper lip, dorsal and caudal fins, and dorsal surface of paired fins dusky. Ventral and ventrolateral portions of body, ventral surface of head excluding upper lip, lower lip, all barbels except nasal barbel, and ventral surface of paired fins colorless or depigmented (without melanophores).

Glaniopsis multiradiata new species

(Figures 15*b*, 20)

Type-Material.—**Holotype:** IRSNB 619, 44.5 mm. Arur Dalan, a torrential headwater of Sungai Padapur, Baram basin, near Bario, Sarawak; altitude 3500 ft [ca. 1100 m]; 11 Oct. 1971; Léopold III, J. P. Gosse.

Paratypes.—IRSNB 620, 30:24.3–59.1 mm. Same collection data as holotype.

Diagnosis.—*Glaniopsis multiradiata* has more rays in the paired fins and shorter barbels than any other *Glaniopsis*: pectoral-fin rays i15–17, usually i16 (vs. i11–14 in other species of *Glaniopsis*); pelvic-fin rays usually i9, exceptionally i8 or i10 (vs. usually i7, exceptionally i6 or i8); and length of all barbels equal to or less than eye diameter, adpressed nasal barbel usually failing to reach exposed portion of eye.

Eye diameter 20–37, 2.0–3.1 in interorbital space. Interorbital space 9.3–12.6. Depth caudal peduncle 9.7–12.3. Branched dorsal-fin rays invariably 7 (31). Branched anal-fin rays invariably 5 (31). Principal caudal-fin rays 9+9 (14), 9+8 (1). Pectoral-fin rays i15 (4), i16 (8), or i17 (7). Pelvic-fin rays i8 (2), i9 (28), or i10 (1). Dorsal-fin origin on a vertical through origin of last pelvic-fin ray or slightly posterior to it. Pelvic-fin origin closer to anal-fin origin than to pectoral-fin origin.

Length of all barbels usually less than eye diameter. Outer mandibular barbel longest, its length usually less than, but sometimes equal to, eye diameter. Adpressed nasal barbel usually failing to extend posteriorly to exposed portion of eye, at most extending slightly beyond free anterior margin of eye. Mental barbel barbel-like, half as long as inner mandibular barbel.

Sides of body completely covered with close-set, regularly overlapping scales with exposed posterior margins, except for a small naked area just above pectoral-fin base; about 30 complete scale rows near middle of body and 20 on caudal peduncle. Lateral scale row complete, with about 106–130 scales (17). Dorsum in front of dorsal fin usually covered with scales almost to occiput, always scaled for at least half its length in front of dorsal fin. Dorsum posterior to dorsal fin completely scaled except for a small scaleless area immediately posterior to dorsal fin in some specimens. Abdomen posterior to pelvic fins covered with embedded scales. Abdomen anterior to pelvic fins scaleless except for a few embedded scales median to pelvic-fin bases. Ventral surface of body posterior to anal fin completely scaled. Tubed scale series either complete, complete except for a few scales without tubes near end of series, or with short tubeless segments on posterior half of body in a few specimens.

Glaniopsis multiradiata has a variably mottled coloration distinct from that of other *Glaniopsis*. Mottles largest and best defined on dorsum, especially anterior to dorsal fin; fainter and smaller but similar mottles extend onto the head, including gill covers, cheeks, and snout in a few specimens; almost all specimens have mottles on dorsum, although varying in distinctness, except for two smallest specimens, 24.3 and 29.2 mm, which are pallid, as if bleached. Majority of specimens partially decolored, either on one or both sides, as if bleached. Path of lateral line marked by a thin dark longitudinal band which is absent or much less distinct in other *Glaniopsis* and which persists in specimens otherwise largely decolored. In specimens with mottlings on sides of body, these tend to be less prominent than those on dorsum. Abdomen colorless. Fins darkly pigmented compared to other *Glaniopsis*. Caudal fin in many specimens with three wavy vertical bands. Dorsal and anal fins with slight concentrations of melanophores suggesting incipient barred pattern. Dorsal, anal, and dorsal surfaces of paired fins often with fine melanophores concentrated along fin rays, giving them a dusky appearance. Dorsal surface of pectoral-fin base dusky or darkly pigmented, more so than in other *Glaniopsis*. A cluster of melanophores on lateral surface of pelvic-fin base.

Compared to *Glaniopsis hanitschi*, *G. multiradiata* has body slightly more elongate or slender, especially posteriorly; snout more depressed; ventral surface of head flatter; lips (especially lower) slightly less arcuate; lower lip interrupted medially by feebly developed mental pad from posterolateral corners of which mental barbels arise; bases of outer and inner mandibular barbels more widely separated; dorsal fin slightly smaller; caudal fin (correlated with shallower caudal peduncle) much smaller; caudal fin slightly forked, its upper lobe slightly larger (rather than truncate); and paired fins larger. Pectoral fin about 10–15% longer, its surface area when expanded about one-third greater; first pectoral-fin ray noticeably curved or bowed posteriorly instead of nearly straight or only slightly curved; fringes on distal ends of branched rays less well developed; adhesive pads on ventral surface of outermost rays thicker; and base of pectoral fin fully one-third longer.

ETYMOLOGY.—The feminine adjective *multiradiata* comes from *multus,* Latin, "much," plus *radiata,* Latin, "rayed," in reference to the more numerous pectoral-fin and pelvic-fin rays characteristic of the species.

Membikit **Glaniopsis**

Glaniopsis hanitschi (in part) INGER AND CHIN, 1962:107–108 (specimens from Sungai Membikit).

MATERIAL EXAMINED.—FMNH 68135, 3:46.5–52.4 mm. Sungai Membikit [tributary of Sungai Pegalan, Padas basin, near southern end of Crocker range], Keningau District, Sabah, 5°22′N, 116°06′E.

These three specimens resemble *G. hanitschi* more closely than they do any other *Glaniopsis* but differ from typical *G. hanitschi* from Mount Kinabalu in having head narrower and more depressed, fins smaller, and abdomen more extensively covered with scales anterior to pelvic fins. Two of the three specimens also have fewer pectoral-fin rays and a more incomplete tubed scale series.

Eye 34–43, 3.5–4.1 in interorbital space. Interorbital space 10.3–10.8 (vs. 7.9–9.6 in *G. hanitschi*). Depth caudal peduncle 9.0–9.4 (7.6–8.9 in *G. hanitschi*). Branched dorsal-fin rays 6 (3). Branched anal-fin rays 5 (3). Principal caudal-fin rays 9+9 (2), 9+7 (1, with caudal fin probably injured or abnormally developed). Pectoral-fin rays i11 (2) or i12 (1) (i12 or more in *G. hanitschi*). Pelvic-fin rays i7 (3).

Adpressed nasal barbel reaching to or slightly beyond free posterior margin of eye. Upper and lower horny jaw sheaths markedly convex near symphysis.

Dorsum and sides of body nearly completely covered with scales, lateral series complete with about 130–142 scales, about 35 complete scale rows near middle of body and 28 on caudal peduncle. Entire abdomen posterior to pelvic fins covered with embedded scales; half of abdomen anterior to pelvic fins with embedded scales. Tubed scale series complete or nearly complete on anterior half of body, absent or considerably interrupted on posterior half.

Coloration darker (duskier) than in *G. hanitschi,* without well-defined vertical bars on a relatively pale background; a continuous dark midlateral longitudinal band (absent in *G. hanitschi*). Fine melanophores extending from sides of body further toward and onto abdomen than in *G. hanitschi.* Nearly all scales with lozenge-shaped cluster of fine melanophores. Largest specimen, 52.4 mm female, uniformly dusky, without vertical bars or marks on dorsum or sides of body. Smallest specimen, 46.5 mm female, with about 20 vertical marks in side of body (less well defined, and lower lying than vertical bars in *G. hanitschi*); dorsum with 10 dark transverse marks anterior and 4 posterior to dorsal fin (absent in *G. hanitschi*). Specimen intermediate in size, a well-tuberculated 47.5 mm male, with markings on sides fewer and less well defined, but similar to those in smallest specimen, and marks on dorsum barely visible or absent.

Baleh and Tinjar **Glaniopsis**

MATERIAL EXAMINED.—FMNH 68137, 68151–68153, 69868, 24:20.4–38.0 mm, mainstream and tributaries of Baleh River, Rajang basin, Sarawak; BMNH 1933.8.9.9–10, 15:19.9–39.3 mm, Lejok River, altitude 50–1500 ft [ca. 15–460 m], Tinjar River District, Sarawak.

These specimens superficially resemble *G. hanitschi* but differ from it in their much smaller size, shorter barbels, having seven instead of only six branched dorsal-fin rays, fewer scales, and other minor differences.

Eye 24–32, 2.4–3.0 in interorbital width. Interorbital width 9.7–11.2. Depth caudal peduncle 8.9–10.0. Branched dorsal-fin rays invariably 7. Principal caudal rays usually 9+9. Pectoral-fin rays i12–i14; pelvic-fin rays i7 or i8. Adpressed nasal barbel extends posteriorly to middle of eye or almost to posterior border of exposed portion of eye. Upper and lower horny jaw sheaths moderately convex near symphysis.

Dorsum and sides of body completely covered with scales, or scales absent from dorsum only a short distance posterior to occiput; lateral scale series with 102–115 scales, about 18–25 scale rows near middle of body, 22–24 on caudal peduncle. Abdomen between pelvic fins covered with scales, otherwise largely scaleless.

Dorsal and lateral surfaces of body mottled or with vertical or variably broken vertical bands of equal or variable width. Largest specimen, 39.3 mm, a gravid female.

Mulu **Glaniopsis**

MATERIAL EXAMINED.—BMNH uncat., 2:18.4–33.2 mm. Extreme headwater of Sungai Tapin [Baram basin], Gunong Mulu, Sarawak.

These two small specimens possibly represent an undescribed species. They differ from all other *Glaniopsis* examined in having a more slender body. Unlike *Glaniopsis* from Membikit, Baleh, and Tinjar, which seem closest to *G. hanitschi,* Mulu *Glaniopsis* perhaps is closest to *G. multiradiata*. It agrees with *G. multiradiata* in general appearance, color pattern, and in having relatively high paired-fin ray counts but differs in having longer barbels, smaller eyes, larger scales, less extensive squamation, and paired fins with slightly fewer rays, as well as a more slender body. Eye 30–31 (20–25 in 5 *G. multiradiata* 24.3–36.9 mm), 3.4–3.7 in interorbital space. Interorbital space 8.4–9.0. Body depth 9.5–9.7 (6.4–8.1 in *G. multiradiata*). Depth caudal peduncle 10.2–11.4. Branched dorsal-fin rays 7 (2). Branched anal-fin rays 5 (2). Principal caudal-fin rays 9+9 (2). Pectoral-fin rays i13 (1), i14 (1) (i15–17 in *G. multiradiata*). Pelvic-fin rays i8 (2) (usually i9 in *G. multiradiata*). Pelvic-fin origin closer to pectoral than to anal-fin origin (equidistant between pectoral and anal-fin origins or closer to anal-fin origin in *G. hanitschi* and *G. multiradiata*).

Length of nasal, rostral, maxillary and outer mandibular barbels equal to or greater than eye diameter. Adpressed nasal barbel reaches at least to middle of eye. Larger specimen, 33.2 mm, with mental barbels barbel-like. Smaller specimen, 18.4 mm, with unusually broad, thin lower lip and large flaps in position normally occupied by mental barbels. Lower lip interrupted by a median mental pad as in *G. multiradiata*.

Larger specimen with dorsum, abdomen, and ventral surface of body posterior to anal fin scaleless; lateral scale series nearly complete with about 100 scales, allowing for 4–5 scales missing or having failed to develop slightly anterior to hypural fan (125–146 in *G. hanitschi,* 106–130 in *G. multiradiata*); at most 6–7 scale rows below and 5 above lateral scale series, or a maximum total of about 13 scale rows on side of body (vs. 25 or more in *G. hanitschi* and *G. multiradiata*); tubed scale series complete on anterior half of body, largely discontinuous or incomplete on posterior half. Smaller specimen entirely or almost entirely scaleless.

Larger specimen with dorsal and lateral surfaces of head and body dusky, on body mainly due to large lozenge- or scale-shaped clusters of melanophores overlying nearly every scale; dorsum anterior to dorsal fin with large mottles similar to those in *G. multiradiata*; cluster of melanophores lateral to pelvic-fin base; cluster of melanophores toward base of each caudal-fin lobe, fins otherwise without distinct markings. Smaller specimen with fine melanophores uniformly distributed over dorsal and lateral surfaces of head and body, and concentrations of melanophores along dorsal-fin base and lateral line canal, otherwise without distinct markings.

ACKNOWLEDGMENTS

It is a pleasure to thank the following individuals who helped in various ways during the course of this study: Oliver Crimmen, Alwyne Wheeler, Keith Banister, and Gordon Howes, BMNH; Marie-Louise Bauchot and Martine Desoutter, MNHN; Marinus Boeseman and Peter van Helsdingen, RMNH; Han Nijssen, ZMA; Jean-Pierre Gosse and L. Walschaerts, IRSNB; Karsten F. Hartel and William L. Fink, MCZ; Robert K. Johnson, Donald J. Stewart, and Robert F. Inger, FMNH; and Lillian J. Dempster, W. I. Follett, and Michael E. Hearne, CAS. Photography is by Alphonse Coleman, MCZ; and Orrin Moon, The Darkroom, San Rafael; and scanning electron micrography by Mary-Jacque Mann, SEM lab, National Museum of Natural History. I am especially indebted to Jean-Pierre Gosse for the opportunity to report on the extensive and beautifully preserved material of *Gastromyzon* and *Glaniopsis* collected by Léopold III and himself, and to Soetikno Woerjoatmodjo and Rajai for helping collect *Gastromyzon* in the Sungai Pinoh.

The ichthyological survey of the Kapuas basin was sponsored by the Museum of Zoology, Bogor, Indonesian National Research Council, and

Smithsonian Tropical Research Institute. Most of the research, supported by grant DEB77-24759 in the Systematic Biology Program, National Science Foundation, was done at the California Academy of Sciences and Tiburon Center for Environmental Studies.

Literature Cited

Boulenger, G. A. 1899. Descriptions of two new homalopteroid fishes from Borneo. Ann. Mag. Nat. Hist. (7)4:228–229.

Chen, Y. 1980. Systematic studies on the fishes of the family Homalopteridae of China. II. Classification of the fishes of the subfamily Gastromyzoninae. [In Chinese, with English summary.] Acta Hydrobiol. Sin. 7:95–120.

Günther, A. 1874. Descriptions of new species of fishes in the British Museum. Ann. Mag. Nat. Hist. (4)14:1–8.

Hora, S. L. 1932. Classification, bionomics, and evolution of homalopterid fishes. Mem. Indian Mus. (Calcutta) 12:263–330, pls. 10–12.

———, and K. C. Jayaram. 1951a. On two new gastromyzonid fishes from Borneo. Rec. Indian Mus. (Calcutta) 49:191–196.

———, and ———. 1951b. A note on the systematic position of the genus *Glaniopsis* Boulenger (Fishes: Cyprinoidea). Rec. Indian Mus. (Calcutta) 48:85–88.

Inger, R. F., and P. K. Chin. 1961. The Bornean cyprinoid fishes of the genus *Gastromyzon* Günther. Copeia 1961(2):166–176.

———, and ———. 1962. The fresh-water fishes of North Borneo. Fieldiana Zool. 45:1–268.

Popta, C. M. L. 1905. Suite des descriptions préliminaires des nouvelles espèces de poissons recueillies au Bornéo Central par M. le Dr. A. W. Nieuwenhuis en 1898 et en 1900. Notes Leyden Mus. 25:171–186.

———. 1906. Résultats ichthyologiques des voyages scientifiques de Monsieur le Professeur Dr. A. W. Nieuwenhuis dans le centre de Bornéo (1898 et 1900). Notes Leyden Mus. 27:1–304, pls. 1–10.

Ramaswami, L. S. 1948. The homalopterid skull. Proc. Zool. Soc. London 118:515–538.

———. 1952. Skeleton of cyprinoid fishes in relation to phyletic studies. IV. The skull and other skeletal structures of gastromyzonid fishes. Proc. Natl. Inst. Sci. India 18(6):519–538.

Roberts, T. R. In press. Unculi (horny projections arising from single cells), an adaptive feature of the epidermis of ostariophysan fishes. Zool. Scripta.

Silas, E. G. 1953. Classification, zoogeography and evolution of the fishes of the cyprinoid families Homalopteridae and Gastromyzonidae. Rec. Indian Mus. (Calcutta) 50:173–263, pl. 5.

Vaillant, L. 1889. Sur les poissons d'eaux douces de Bornéo. C. Rend. Congr. Internat. Zool. Paris, 1889:81–82.

———. 1891. [Note on *Lepidoglanis*]. C. Rend. Soc. Philomath. Paris, 1890–1891, 2:6.

———. 1893. Contribution a l'étude de la faune ichthyologique de Bornéo. Nouv. Arch. Mus. Paris 5(3):23–114, pls. 1–2.

———. 1902. Résultats zoologiques de l'expedition scientifique néerlandaise au Bornéo Central. Poissons. Notes Leyden Mus. 24:1–166, pls. 1–2.

Weber, M., and L. F. de Beaufort. 1916. The fishes of the Indo-Australian Archipelago. III. Ostariophysi: II Cyprinoidea, Apodes, Synbranchi. E. J. Brill, Leiden. xv + 455.

Wickler, W. 1971. Verhaltenstudien am einem hochspezialisierten Grundfisch, *Gastromyzon borneensis* (Cyprinoidea, Gastromyzonidae). Z. Tierpsychol. 29:467–480.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94952

PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 21, pp. 525–535, 33 figs. May 14, 1982

LATE MIOCENE BALANID CIRRIPEDIA FROM THE BASAL WILSON RANCH BEDS ("MERCED" FORMATION), SONOMA COUNTY, NORTHERN CALIFORNIA

By

Victor A. Zullo

Department of Earth Sciences,
University of North Carolina at Wilmington,
Wilmington, North Carolina 28403

and

Raj B. Guruswami-Naidu

Department of Geology, California Academy of Sciences,
San Francisco, California 94118

ABSTRACT: The basal conglomerate of the Wilson Ranch beds (Merced Formation of authors) contains abundant barnacle remains including three identifiable species of the family Balanidae. *Balanus* sp. aff. *B. nubilus* Darwin, 1854, is similar to extant *B. nubilus* and the California late Miocene–early Pliocene species *B. proxinubilus* Zullo, 1979, but differs in the internal morphology of the scutum. *Balanus irradians* new species is a member of the *Balanus balanus* (Linnaeus, 1758) complex distinguished by its lack of radii. *Notomegabalanus*(?) *insperatus* new species is a megabalanine with Southern Hemisphere cool-temperate affinities distinguished by its prominently ribbed parietes. A late Miocene age is assigned to the basal conglomerate on the basis of its stratigraphic relationship to a radiometrically dated tuff within the Wilson Ranch beds and on biostratigraphic evaluation of the molluscan fauna. The fauna of the basal conglomerate suggests deposition in an immediately subtidal environment subjected to wave and current action, and a cool temperate marine hydroclimate.

INTRODUCTION

A fossiliferous marine conglomerate of late Miocene age in southwestern Sonoma County, northern California (Fig. 1) contains an abundance of balanid barnacle remains. The specimens consist of shells, disarticulated compartmental plates, and a few dissociated scuta representing four species. One of these species cannot be identified beyond the generic level. A second is similar to, but not conspecific with, the extant Pacific coast species *Balanus nubilus* Darwin, 1854. The third, based on shell characters alone, is sufficiently unique to permit its description as a new species with affinities to the modern *Balanus balanus* (Linnaeus, 1758) complex. The fourth is a new species of megabalanine that appears to represent one of the newly delimited extant austral genera.

STRATIGRAPHY

Outcrops of marine sandstone in southwestern Sonoma County were for many years considered correlatives of the type Merced Formation of the San Francisco peninsula and

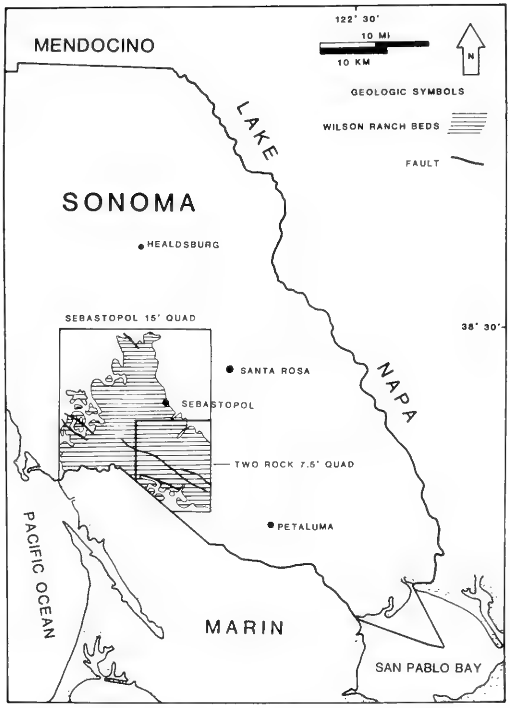


FIGURE 1. General locality map for CASG locality 54135, lower Wilson Ranch beds, southwestern Sonoma County, California.

referred to that unit (e.g., Dickerson 1922; Weaver 1949; Travis 1952). Higgins (1960) documented lithologic and faunistic differences between the type Merced Formation and the Sonoma deposits, and provided compelling arguments that the two units were deposited in separate basins. Higgins, however, did not propose a separate formational name for the Sonoma County deposits.

A tuff interbedded with the sandstone was described by Osmont (1905) as the Sonoma Tuff. In ensuing years, following the work of Dickerson (1922), the name Sonoma has been used to refer to the Neogene volcanic assemblage of eastern Sonoma and Napa counties. The original Sonoma Tuff can be regarded as one of a series of tuffaceous intertongues of the eastern volcanic assemblage into the western marine sequence. Osmont (1905) also described a molluscan fossil locality in the marine sandstone containing the Sonoma Tuff, to which he applied the name Wilson Ranch beds. As this is the earliest formal stratigraphic name that has been used for this Neogene marine unit, we will refer to these deposits as the Wilson Ranch beds.

K-Ar dates from the pumiceous, vitric tuff interbed described by Osmont have given an age range of 5.7 ± 0.6 to 6.1 ± 0.1 m.y. (Sarna-Wojcicki 1976). Bartow and others (1973) reported molluscan assemblages in the Wilson Ranch beds that ranged in age from the early Pliocene below, to late Pliocene above the dated tuff. The early and late Pliocene molluscan assemblages were correlated with Hemphillian (late Miocene to early Pliocene) and Blancan (late Pliocene to early Pleistocene) land mammal assemblages, respectively, from the Petaluma Formation immediately to the east. These relative ages are in terms of conventional Pacific coast usage. If, however, 5.0 m.y. is acceptable as the age of the Miocene-Pliocene boundary as proposed by Berggren (1972, 1978) and Van Eysinga (1975), then that part of the Wilson Ranch beds below the dated tuff is of Miocene age. This conclusion is supported by biostratigraphic evaluation of the molluscan fauna by Barry Roth (California Academy of Sciences, pers. commun., 1981). Roth would correlate the lower Wilson Ranch beds with the Pancho Rico Formation of Monterey County, California, which he and others now regard as late Miocene in age (Addicott 1976; Roth and Guruswami-Naidu 1978).

The barnacles described herein are from California Academy of Sciences Department of Geology (CASG) locality 54135. This locality is in a coquina near the top of the basal conglomerate of the Wilson Ranch beds in the Two Rock quadrangle, U.S. Geological Survey 7.5′ series, 1954 edition, revised 1971, and is in that part of the section referred by Osmont (1905) to the San Pablo Formation of the eastern San Francisco Bay region. A precise locality description is on file with the Department of Geology. At the exposure containing CASG locality 54135, the Wilson Ranch beds unconformably overlie the Franciscan assemblage (Fig. 2). The basal 0.5 m consists of a fining-upwards conglomerate composed of coarse sand, rounded pebbles, and angular pebble- to cobble-sized fragments of Franciscan-assemblage rocks in a fine-grained sandstone matrix. The upper part of the conglomerate is the coquina (CASG locality 54135) which is composed of predominantly horizontally bedded invertebrate shells. A vertebrate fossil lag, consisting of scattered intact elements and abundant, well-rounded bone fragments, overlies the coquina. The vertebrate lag grades upward into 3.4 m of massive, moderately indurated, fine-grained sandstone containing scattered invertebrates and rare vertebrate remains. This sandstone is overlain by tuffaceous sandstone to the top of the exposure. The basal conglomerate at this locality is estimated to be 50 m stratigraphically below the dated tuff in the Wilson Ranch beds (Peter Rodda, California Academy of Sciences, pers. commun., 1981).

PALEOECOLOGY

The petrology and fauna of the basal conglomerate suggest that the barnacles inhabited a rocky intertidal or immediately subtidal environment exposed to moderate or heavy surf. The coquina itself, and its relationship to the underlying fining-upwards conglomerate, suggest a time of stillstand after rapid transgression in a shallow depositional basin affected by wave base and/or current action. According to Barry Roth (pers. commun., 1981) the molluscan fauna suggests a marine hydroclimate similar to that of modern Puget Sound (i.e., cool temperate). These environmental conditions are supported by the composition, morphology, and preservation of the barnacle fauna.

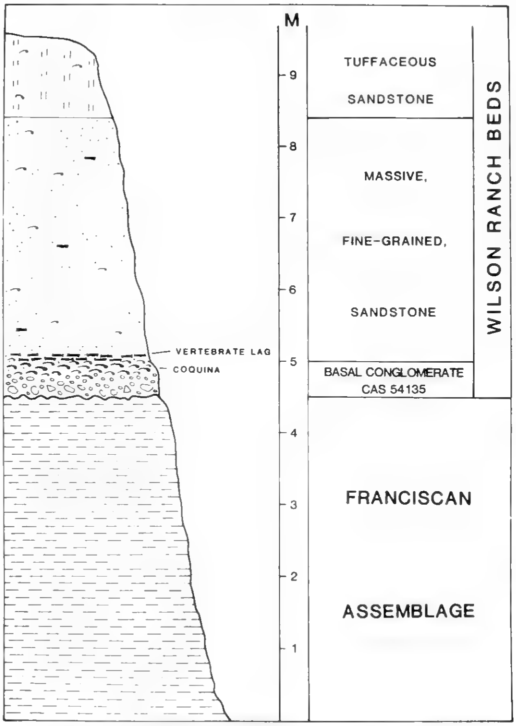


FIGURE 2. Stratigraphic setting for CASG locality 54135, lower Wilson Ranch beds, southwestern Sonoma County, California.

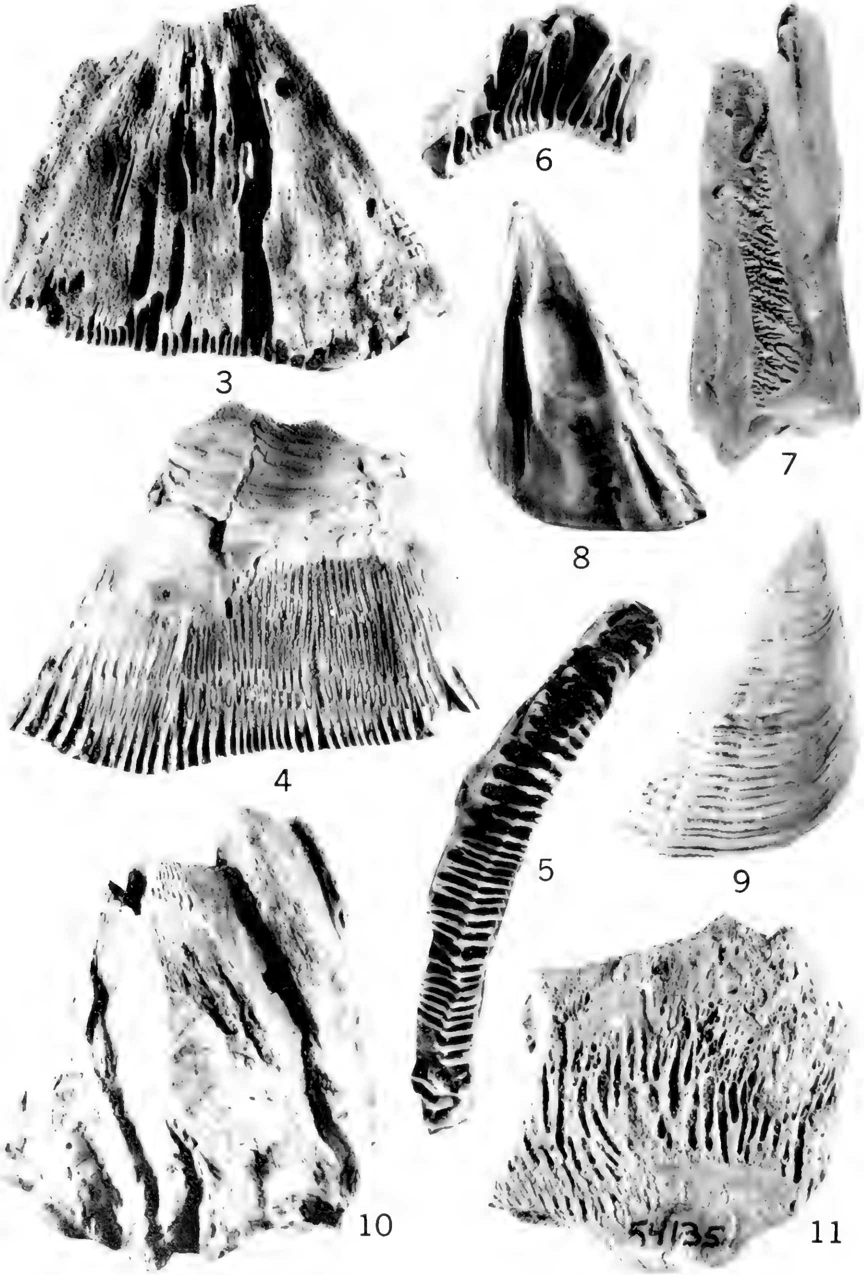
SYSTEMATIC ACCOUNT

Subclass CIRRIPEDIA Burmeister, 1834
Order THORACICA Darwin, 1854
Superfamily BALANOIDEA (Darwin), Newman and Ross, 1976
Family BALANIDAE Darwin, 1854
Subfamily BALANINAE Darwin, 1854

Balanus sp. aff. **B. nubilus** Darwin, 1854
(Figures 3–11)

Four complete shells, one partial shell, several disarticulated compartmental plates, one entire scutum, four fragmentary scuta, and a few fragments of basis from CASG locality 54135 are here referred to a species that is similar to, but probably not conspecific with, *Balanus nubilus*. The shells are conic, the radii are moderately well developed with oblique, jagged summits, and the orifice is toothed. The ribbing of the shell interior is not prominent, and the basis in larger individuals is cup-shaped and profusely porous near the margins. The parietal septa are crowded and thin, and the narrow, elongate parietal tubes rarely possess transverse septa.

The scuta that appear to be associated with these shells are higher than wide, slightly bowed outwards near the apex, and with a slightly reflexed tergal margin. The exterior is ornamented by prominent, closely spaced growth ridges that are faintly crenate, and the basitergal angle is rounded. The articular ridge is short, less than one-half the length of the tergal margin, and slightly reflexed over the narrow, shallow, articular furrow. The adductor ridge is erect, highest along the margin of the large, oval, and deeply impressed adductor muscle pit, but extending both apically and basally beyond the boundaries of the adductor pit. The depressor muscle pit is large, triangular, shallow, and bordered on its occludent margin by a low ridge. The depressor muscle pit has one or more narrow, low longitudinal ridges within. The depressor muscle pit located at the basioccludent angle is triangularly



FIGURES 3–11. *Balanus* sp. aff. *B. nubilus* Darwin, 1854. Figs. 3–5. Exterior, interior, and basal views of lateral plate, hypotype CASG 60881; greatest height 47.5 mm. Figs. 6–7. Basal and alar sutural edge views of carinorostral and carinal plates, hypotype CASG 60882; greatest height 61 mm, greatest wall thickness 17 mm (note transverse septa in parietal tubes). Figs. 8–9. Interior and exterior views of scutum, hypotype CASG 60883; height 23 mm. Fig. 10. Side view of shell, hypotype CASG 60884; greatest height 49 mm. Fig. 11. Fragment of basis, hypotype CASG 60885; greatest diameter of fragment 35.5 mm.

elongate, deeply impressed, and partially overhung by the occludent margin of the plate.

The shell of this species is similar to that of *Balanus nubilus* and the related fossil species *B. proxinubilus* Zullo, 1979, from the upper Miocene Pancho Rico Formation of central California and the upper Pliocene San Diego Formation of southern California. The only qualitative difference is that the radii of the Wilson Ranch species appear to be consistently broader than those of either *B. nubilus* or *B. proxinubilus*. The Wilson Ranch scuta differ in having the adductor ridge separate from the articular ridge, and in the much shorter articular ridge. In this regard the internal morphology is somewhat similar to that of the scutum of *B. rostratus* Hoek, 1883, but the presence of vertical ridges or crests in the depressor muscle pit serves to distinguish the Wilson Ranch scuta and to suggest relationship with *B. nubilus*.

Balanus irradians new species

(Figures 12–15, 18–21)

DIAGNOSIS.—Shell of six compartmental plates without radii; alae restricted to sheath area; sutures between compartmental plates obscured or represented by linear grooves; parietes with large, square to rectangular, transversely septate parietal tubes; number of interior ribs greater than number of parietal septa; basis calcareous, solid; distinguished from other members of the *Balanus balanus* complex by the lack of radii.

DESCRIPTION.—Shell thick, low to high conic or dome-shaped, with narrow carinolaterals and a small, untoothed, diamond-shaped orifice; sutures between the six compartmental plates obscured or represented by narrow grooves; radii absent; sutural edges between adjacent compartmental plates broad, bearing coarse, complexly arborescent denticulations; alae narrow, with horizontal summits, and restricted to region of sheath; exterior of parietes usually corroded; uncorroded parietes with external ornamentation of irregular, transverse growth rugae crossed by fine longitudinal striae; some specimens bear one to three external ribs on larger compartmental plates; length of sheath at least one-half height of compartmental plate; lower edge of sheath free-standing, acute, with cavity between it and interior of shell wall; interior of shell wall below sheath strongly ribbed, with the largest internal ribs corresponding to the parietal septa, and from one to three smaller ribs between parietal septa; parietal tubes large, nearly square to rectangular, crossed by transverse septa and sometimes secondarily filled in upper third; parietal septa denticulate basally; inner surface of external lamina bears denticulae between parietal septa; basis calcareous, solid.

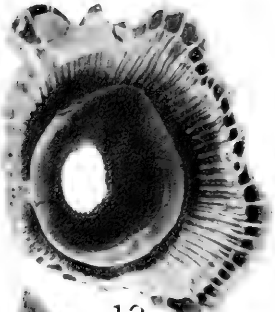
MATERIAL EXAMINED.—Twelve whole shells and 26 disarticulated compartmental plates from CASG locality 54135.

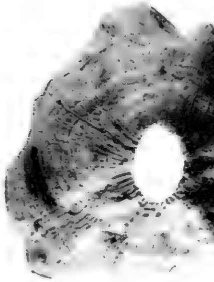
TYPE MATERIAL.—**Holotype**, CASG no. 60891; **paratypes**, CASG nos. 60892 through 60909, and paratype lot CASG no. 60910 in the California Academy of Sciences paleontological type collection.

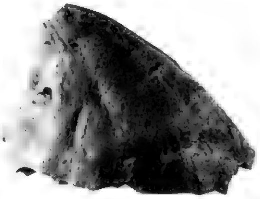
ETYMOLOGY.—The specific name is derived from the Latin prefix *ir-*, without, and *radius*.

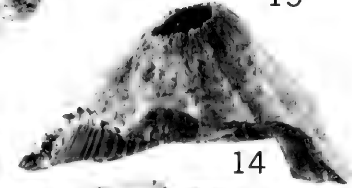
DISCUSSION.—*Balanus irradians* and the extant boreo-arctic species *B. balanus* and *B. rostratus*, constitute a small group in the genus *Balanus* that is characterized by solid, calcareous bases, large, square, parietal tubes, and secondary ribs between the primary septal ribs of the interior lamella of the parietal wall. The lack of radii and the overall morphology associated with a shell lacking radii are the major features distinguishing *B. irradians* from *B. balanus* and *B. rostratus*. In other respects, *B. irradians* shares characteristics with the extant species. The prominent external ribs present on some specimens are reminiscent of the ribbed wall of *B. balanus*, rather than the smooth shell of *B. rostratus*. On the other hand, both *B. irradians* and *B. rostratus* have transverse parietal septa that are lacking in *B. balanus*.

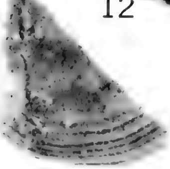
The corroded nature of the shells and the type of sediment in which they occur suggest that *B. irradians* lived in moderate- to high-energy environments. The thick shell wall, the suppression of radii, and the consequent development of a broad, coarsely denticulate sutural area for rigid articulation of the compartmental plates are comparable to shell development in species of *Tetraclita* Schumacher, 1817, that often inhabit areas of moderate to heavy wave shock and abrasion in the intertidal zone. A consequence of the lack of radii is that the orifice cannot be enlarged by lateral growth along the sutural edges of the plates as the shell increases in basal diameter and height. As Ross (1969) showed for *Tetraclita*, monometric growth forms enlarge their orifices by abrasion of the older, upper parts of the shell wall. The secondary filling and

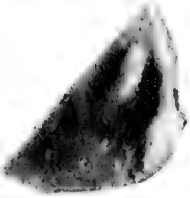

12

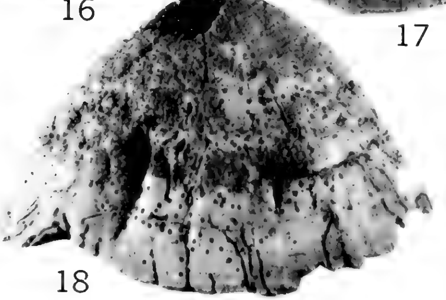

13

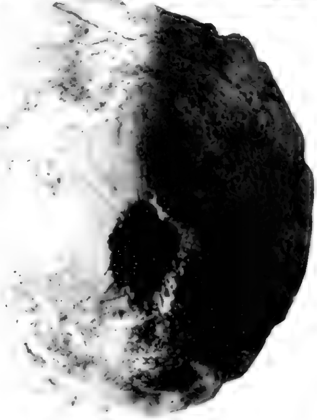

15


14

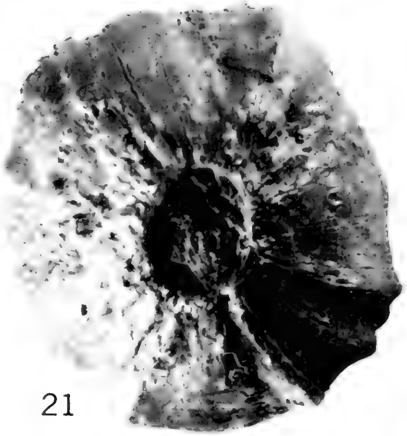

16


17


18


19


20


21

FIGURES 12–21. *Balanus irradians* new species. Figs. 12–14. Basal, top, and side views of paratype CASG 60892; greatest diameter of base 29 mm, greatest height of shell 15 mm (note fragment of basis in upper part of Fig. 12). Fig. 15. Side view of shell, paratype CASG 60893; greatest height 13 mm. Figs. 16–17. Exterior and interior views of scutum tentatively identified with *B. irradians*, hypotype CASG 60920; height 10 mm. Figs. 18–20. Side, top, and basal view of shell, holotype CASG 60891; greatest height 24 mm, carinorostral diameter 38 mm. Fig. 21. Top view of eroded shell with prominent ribs, paratype CASG 60894; greatest diameter 38.3 mm.

the transverse septa of the parietal tubes prevent exposure of the internal tissues of the barnacle when the upper and outer shell wall are removed.

The affinities of *B. irradians* with *B. balanus* and *B. rostratus* are in keeping with the conclusion that the fauna of the basal Wilson Ranch beds lived in hydroclimatic conditions similar to those of modern Puget Sound. *Balanus rostratus* is a subtidal North Pacific boreo-arctic species ranging south to northern Japan in the west and to Puget Sound in the east. *Balanus balanus* is a lower intertidal and subtidal species of the Arctic, boreal Atlantic, and boreal Pacific, with a distribution similar to that of *B. rostratus* in the North Pacific. The fossil record of *B. rostratus* is limited to the late Pleistocene on the Pacific coast of North America where it is recorded as far south as central California (Zullo 1969b), but extends back to the Pliocene in Japan (Yamaguchi 1977). *Balanus balanus* is found in Pleistocene deposits of both the North Atlantic and North Pacific basins, but has not been recorded from deposits south of southern Oregon (Zullo 1969b). Miocene and Pliocene European records of *B. balanus* are spurious (Menesini 1968, in part), but the species does occur in glacio-marine sediments of the Miocene part of the Yakataga Formation in southeastern Alaska, and is reported from the Miocene of Japan by Yamaguchi (1971).

The morphology of *B. irradians,* particularly those features peculiar to this species, suggests that *B. irradians* is a derivative of either *B. balanus* or *B. rostratus*. The modifications seen in the new species reflect adaptations to life under conditions of pronounced wave shock and abrasion, perhaps in the intertidal zone in relatively open coastal conditions.

Balanus sp. cf. **B. irradians**

(Figures 16–17)

A single, nearly intact scutum from CASG locality 54135 is tentatively referred to *B. irradians*. It is thin, about as broad as high, and slightly concave externally between base and apex. The exterior bears closely spaced, semi-erect growth ridges that are finely crenate. The tergal margin is slightly reflexed and the basitergal angle is rounded. The articular ridge is convex, reflexed over the articular furrow, and protrudes beyond the tergal margin. The articular furrow is narrow, shallow, and short. The articular ridge is long, fully two-thirds the length of the tergal margin. A short, low, blunt adductor ridge is present along the margin of the large oval adductor muscle pit in the upper half of the scutum and is separated from the articular ridge. The depressor muscle pit is a large triangular area between the adductor muscle pit and the basitergal angle. This pit is not bordered by a ridge on its occludent side. The pit for the depressor muscles in the basioccludent angle is large, triangular, and deep.

This scutum bears some resemblance to those of *B. balanus* and *B. rostratus,* but differs from both in its greater breadth, thinness, its short, blunt adductor ridge that is well removed from the articular ridge, and in the greater size and depth of the depressor muscle pit that is not bordered by a ridge on its occludent side. This scutum differs from others found at CASG locality 54135 and identified as *Balanus* sp. aff. *B. nubilus* by its greater width, its convex rather than straight articular ridge that is much more reflexed and much longer, its shorter, blunter adductor ridge, and the lack of striations or ridges in the depressor muscle pit.

Balanus sp.

(Figures 31–33)

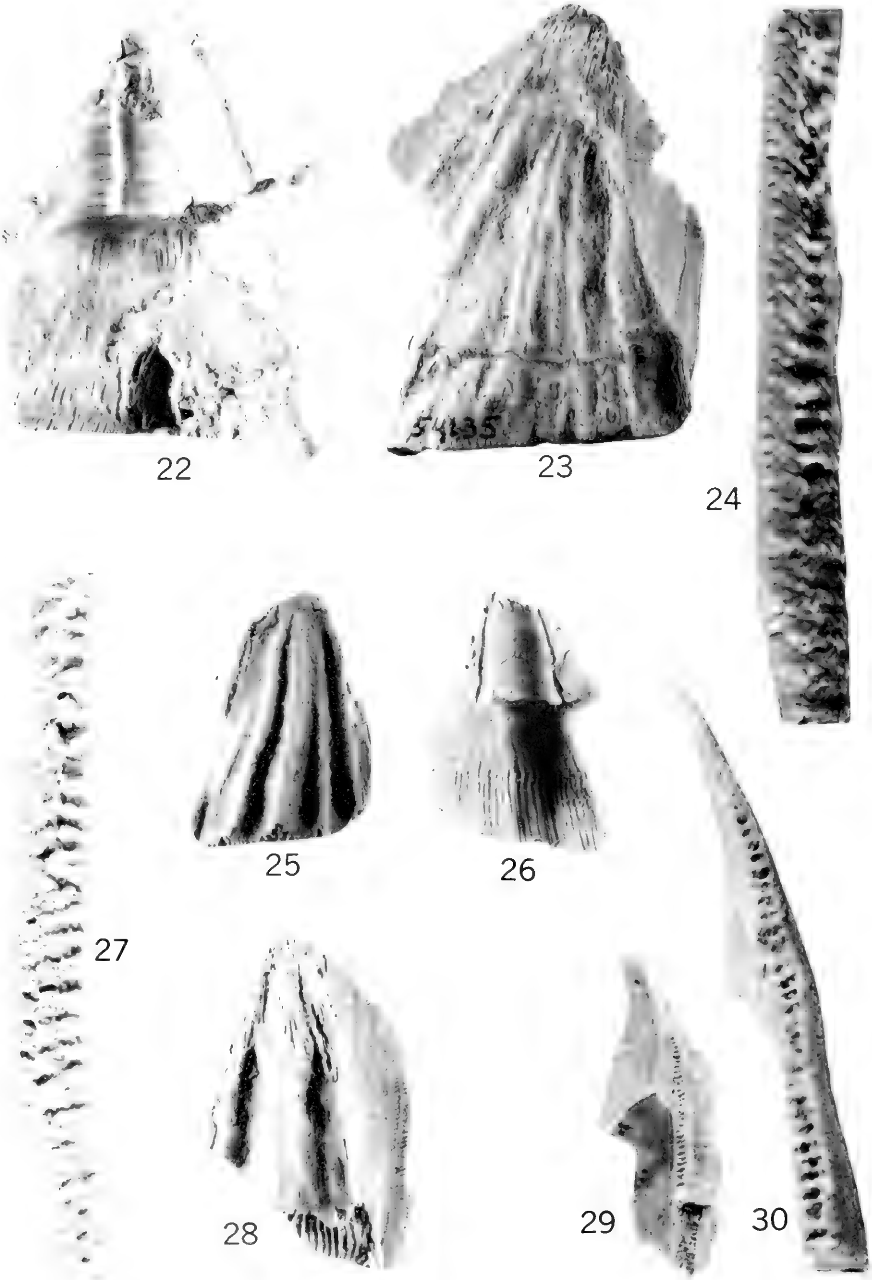
Several whole, high conic and cylindric shells cannot be identified beyond the generic level. Their orifices are toothed, the radii are moderately sunken with oblique summits, and the parietes are smooth to irregularly plicate, to inconspicuously ribbed. These shells may represent either *B.* sp. aff. *B. nubilus* or *Notomegabalanus*(?) *insperatus,* but their preservation is not conducive to the identification of specific characters.

Subfamily MEGABALANINAE Newman, 1980

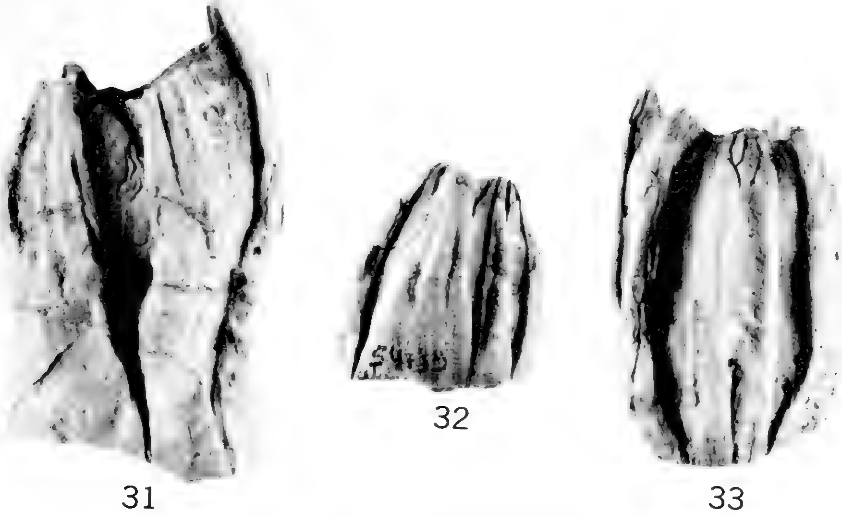
Notomegabalanus(?) **insperatus** new species

(Figures 22–30)

DIAGNOSIS.—Shell of six compartmental plates with broad, tubiferous radii; summits of radii oblique; septa of radial sutural edge bearing denticulae on lower sides only; exterior of parietes of larger compartmental plates with three to five prominent ribs, and ornamented by fine, closely spaced radial striae; parietal tubes numerous, rectangular, without transverse septa,



FIGURES 22–30. *Notomegabalanus*(?) *insperatus* new species. Figs. 22–24. Interior, exterior, and right radial sutural edge views of rostrum, holotype CASG 60914; greatest height of plate 36.4 mm. Figs. 25–26. Exterior and interior views of lateral plate, paratype CASG 60915; greatest height of plate 20.5 mm. Figs. 27–28. Radial sutural edge and exterior views of lateral plate, paratype CASG 60916; greatest height of plate 28.5 mm. Figs. 29–30. Side view and enlargement of radial sutural edge of lateral plate, paratype CASG 60917; greatest height of plate 18 mm.



Figures 31–33. *Balanus* sp., side views of three shells, hypotypes CASG 60911 through 60913, respectively; greatest height of shells: (Fig. 31) 42 mm, (Fig. 32) 20.5 mm, (Fig. 33) 29 mm.

but secondarily filled in upper half; basis unknown, but presumed calcareous; opercular plates unknown; distinguished from other species of *Notomegabalanus* Newman, 1980, and *Austromegabalanus* Newman, 1980, by the prominent external ribbing of the shell wall.

Description.—Reconstructed shell high conic with broad, tubiferous radii and moderately toothed orifice; summits of radii oblique; radial sutural edges septate, with septa bearing denticulae on lower sides only; alae moderately broad with oblique summits, confined to area of sheath; length of sheath less than one-half height of compartmental plates; lower margin of sheath free-standing, with shallow cavity between basal margin of sheath and interior of shell wall; exterior of parietes with from three to five prominent ribs on the larger compartmental plates, and ornamented by fine, closely spaced radial striae crossed by weak, widely spaced growth lines; interior of shell wall ribbed between base and sheath, internal ribs low, moderately developed, each corresponding to a parietal septum; parietal tubes numerous, without transverse septa, but secondarily filled in upper half; parietal septa thin, basally denticulate; outer lamina with one to four thin, half or quarter septa; basis unknown but presumed calcareous from basal denticulation of parietal septa; opercular plates unknown.

Material Examined.—Twenty-four disarticulated compartmental plates and one possibly complete shell from CASG locality 54135.

Type Material.—**Holotype,** CASG no. 60914; **paratypes,** CASG nos. 60915 through 60918, and paratype lot CASG no. 60919 in the California Academy of Sciences paleontological type collection.

Etymology.—The specific name is Latin for unhoped for or unexpected.

Discussion.—Recently, Newman (1980) subdivided the genus *Megabalanus* Hoek, 1913, into three genera. *Megabalanus* s.s. includes most of the *Megabalanus tintinnabulum* (Linnaeus, 1758) complex together with related species of modern tropical and warm temperate seas. The two new genera, *Austromegabalanus* and *Notomegabalanus,* include fossil and extant species restricted to austral cool temperate and subpolar waters. The only obvious shell character separating *Megabalanus* s.s. from the two austral genera is that the septa of the radial sutural edge of *Megabalanus* are denticulate on both their lower and upper sides, whereas the septa of the austral genera are denticulate only on their lower sides. The two austral genera are separated on characters of their terga; that of *Austromegabalanus* has a beak and a closed spur furrow, whereas that of *Notomegabalanus* is not beaked and has an open spur furrow. There are features of the mouth parts as well that can be used to distinguish true *Megabala-*

nus from the austral genera, but when dealing with the generic assignment of fossil species, only shell and opercular plate characteristics are available.

The revision of *Megabalanus* proffered by Newman is sound, both from a systematic and biogeographic point of view. However, the Neogene fossil megabalanid record from California presents a problem. The species described here and "*Megabalanus*" *wilsoni* (Zullo, 1969a) from the Pliocene San Diego Formation have radial sutural dentitions characteristic of Newman's austral genera. Furthermore, the tergum of "*M. wilsoni* is typical of *Notomegabalanus*, although the spur furrow is closed in adult specimens, and its resemblance to that of *N. algicola* (Pilsbry, 1916) from South Africa was noted previously (Zullo 1969a).

The *Notomegabalanus* species closest geographically to the California coast is *N. concinnus* (Darwin, 1854) from the Peruvian province. This species was not included by Newman, but it has the sutural dentition, tergum, labrum, and protuberant lower margin of the first maxilla that characterize *Notomegabalanus*. Are these California Neogene species true *Notomegabalanus* derived from some austral, perhaps South American ancestor? Does the *Austromegabalanus-Notomegabalanus* complex represent an ancestral, previously worldwide stock from which tropical and warm temperate *Megabalanus* s.s. evolved? Or do the California species represent a separate group exhibiting convergence of characters with the austral genera? At present it is possible only to consider the California species on the basis of their morphologies and to assign them to *Notomegabalanus* on the characters delimiting that taxon. The association of *N.*(?) *insperatus* with a cool temperate fauna does, however, suggest affinities with the austral megabalanid genera.

Notomegabalanus(?) *insperatus* differs from all other megabalanid species in bearing distinct, prominent, external ribs. *Megabalanus validus* (Darwin, 1854) and *M. zebra* (Darwin, 1854) have ribbed shells, but their ribs are low, rounded, and usually confluent, rather than erect and separate. In addition, both of these species have the sutural dentition typical of *Megabalanus* s.s. This new species is questionably assigned to *Notomegabalanus* rather than to *Austromegabalanus* solely on the basis of the presence of another *Notomegabalanus, N. wilsoni,* in the California Neogene.

ACKNOWLEDGMENTS

We thank Peter Rodda, California Academy of Sciences, for information concerning the geologic setting and stratigraphy of the Wilson Ranch beds and for his review of the manuscript; and Barry Roth, California Academy of Sciences, for his assessment of the age and depositional environment of the Wilson Ranch molluscan fauna and for his review of the manuscript.

LITERATURE CITED

ADDICOTT, W. O. 1976. Neogene molluscan stages of Oregon and Washington. Soc. Econ. Paleont. and Mineral., Pacific Sec., Neogene Sympos., pp. 95–115.

BARTOW, J. A., A. SARNA-WOJCICKI, W. O. ADDICOTT, AND K. R. LAJOIE. 1973. Correlation of marine and continental deposits in northern California tephrochronology. Am. Assoc. Pet. Geol. Bull. 57(4):769.

BERGGREN, W. A. 1972. A Cenozoic time-scale—some implications for regional geology and paleobiogeography. Lethaia 5:195–215.

———. 1978. Marine micropaleontology an introduction. Pp. 1–17 *in* Haq, B. U., and A. Boersma, editors, Introduction to marine micropaleontology. Elsevier, New York.

DARWIN, C. 1854. A monograph on the sub-class Cirripedia, The Balanidae, The Verrucidae. Ray Society, London. 684 p.

DICKERSON, R. E. 1922. Tertiary and Quaternary history of the Petaluma, Point Reyes and Santa Rosa quadrangles. Proc. Calif. Acad. Sci., ser. 4, 11(19):527–601.

HIGGINS, C. G. 1960. Ohlson Ranch Formation, Pliocene, northwestern Sonoma County, California. Univ. Calif. Publ. Geol. Sci. 36(3):199–232.

HOEK, P. P. C. 1883. Report on the Cirripedia collected by H.M.S. *Challenger* during the years 1873–1876. Rep. Sci. Results Voy. H.M.S. *Challenger,* Zool. 8(25):1–169.

———. 1913. The Cirripedia of the *Siboga*-Expedition. B. Cirripedia Sessilia. Pp. 129–275 *in Siboga*-Expeditie 31b. E. J. Brill, Leyden.

LINNAEUS, C. 1758. Systema Naturae. 10th Ed. Holmiae. 428 p.

MENESINI, E. 1968. *Balanus curvirostratus* nuova specie del Pliocene della Toscana. Atti Soc. Toscana Sci. Nat. Mem. P-V, ser. A, 75(2):617–632.

NEWMAN, W. A. 1980. On the biogeography of balanomorph barnacles of the southern ocean including new balanid taxa; a subfamily, two genera and three species. Proc. Internatl. Sympos. Mar. Biogeogr. and Evol. Southern Hemisphere, New Zealand DSIR Inform. Ser. 137, 1:279–306.

OSMONT, V. C. 1905. A geological section of the Coast Ranges north of the Bay of San Francisco. Univ. Calif. Publ. Bull. Dep. Geol. 4(3):39–87.

PILSBRY, H. A. 1916. The sessile barnacles (Cirripedia) in the collections of the U.S. National Museum; including a monograph of the American species. U.S. Natl. Mus. Bull. 93:1–366.

ROSS, A. 1969. Studies on the Tetraclitidae (Cirripedia: Thoracica): revision of *Tetraclita*. Trans. San Diego Soc. Nat. Hist. 15(15):237–251.

ROTH, B., AND R. GURUSWAMI-NAIDU. 1978. A new Miocene species of *Nuttallia* (Mollusca: Bivalvia) from the Salinas Valley, California. J. Paleont. 52(1):61–66.

SARNA-WOJCICKI, A. M. 1976. Correlation of late Cenozoic tuffs in the central Coast Ranges of California by means of trace- and minor-element chemistry. U.S. Geol. Surv. Prof. Pap. 972:1–30.

SCHUMACHER, C. F. 1817. Essai d'un nouveau systeme des havitations des vers testaces. Copenhagen. 287 p.

TRAVIS, R. B. 1952. Geology of the Sebastopol quadrangle, California. Calif. Div. Mines Bull. 162:1–33.

VAN EYSINGA, F. W. B. 1975. Geological time table, 3rd Ed. Elsevier, Amsterdam.

WEAVER, C. E. 1949. Geology of the Coast Ranges immediately north of the San Francisco Bay region, California. Geol. Soc. Am. Mem. 35:1–242.

YAMAGUCHI, T. 1971. Fossil barnacles from the Pleistocene Miyata Formation. Sci. Rep. Yokosuka City Mus. 18:122–130.

———. 1977. Taxonomic studies on some fossil and recent Japanese Balanoidea. Trans. Proc. Palaeontol. Soc. Jpn, new ser. 107–108:135–201.

ZULLO, V. A. 1969a. Thoracic Cirripedia of the San Diego Formation, San Diego County, California. Nat. Hist. Mus. Los Angeles Cty. Contrib. Sci. 159:1–25.

———. 1969b. A late Pleistocene marine invertebrate fauna from Bandon, Oregon. Proc. Calif. Acad. Sci., ser. 4, 36(1):347–361.

———. 1979. Thoracican Cirripedia of the Pancho Rico Formation, Salinas Valley, Monterey County, California. Nat. Hist. Mus. Los Angeles Cty. Contrib. Sci. 303:1–13.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

INDEX TO VOLUME 42

(Compiled by Lillian J. Dempster)

New names in **boldface** type.