Zoogeography and Systematics of the Lanternfishes of the Genus *Nannobrachium* (Myctophidae: Lampanyctini)

BERNARD J. ZAHURANEC

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Zoogeography and Systematics of the Lanternfishes of the Genus *Nannobrachium* (Myctophidae: Lampanyctini)

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ABSTRACT

Zahuranec, Bernard J. Zoogeography and Systematics of the Lanternfishes of the Genus *Nannobrachium* (Myctophidae: Lampanyctini). *Smithsonian Contributions to Zoology,* number 607, 69 pages, 25 figures, 34 tables, 2000. Of those lanternfishes in the genus *Lampanyctus* (sensu lato) with short or no pectoral fins, 17 species are recognized, removed to the separate genus *Nannobrachium,* and placed into five species groups. These groups are designated Nigrum (four species), Regale (five species), Cuprarium (two species), Achirus (five species), and Isaacsi (one species).

The genus *Nannobrachium* includes those species of the tribe Lampanyctini that are characterized by the following features: either a lack of pectoral fins or short fins with a narrow base in adults; vertically elongate, squarish otoliths with smooth margins; reduced musculature resulting in a soft, flaccid body; body profile appearing "pinched" with concave dorsal and ventral profiles behind the head; and swimbladder atrophied in adults.

The four species in the Nigrum group are *N. nigrum,* from the tropical and subtropical Pacific and eastern Indian oceans; *N. atrum,* from the temperate North and South Atlantic, South Indian, and Southwest Pacific oceans; *N. gibbsi,* herein described from the tropical Pacific; and *N. indicum,* herein described from the tropical Indian Ocean. All have extremely reduced pectoral fins with downward pointing fin rays in the adult.

All five species in the Regale group are confined to the Pacific Ocean: *N. regale* in the Subarctic and North Temperate; *N. ritteri* in the eastern North Pacific Subarctic and Temperate; *N. fernae* in the eastern North Pacific Temperate; *N. idostigma* in the eastern tropical Pacific; and *N. bristori* herein described from the North Subtropical Pacific. In the Regale group, the pectoral fin is not as reduced compared with other *Nannobrachium* groups, and the VLO photophore is low on the side of the body.

The two species in the Cuprarium group are *N. cuprarium,* bipolar in the subtropical Atlantic, and *N. lineatum,* from the tropical-subtropical Atlantic, Indian, and Pacific oceans. Both species have black pigmentation on the posterior of the supracaudal and infracaudal luminous glands.

Four of the five species in the Achirus group are herein described: *N. hawaiiensis, N. crypticum,* and *N. phyllisae* from the North Central, Equatorial, and Southeast Pacific, respectively; and *N. wisneri,* circumglobal from the southern temperate and subtropical regions. The previously described *N. achirus* is circumglobal in the Subantarctic. In all five species, the pectoral fin becomes greatly reduced or is completely lost and covered over by skin in adults.

The Isaacsi group contains only *N. isaacsi* from the eastern tropical Atlantic. It has the VO_2 photophore raised in position, above and slightly forward of the VO_1.

Most of the species and species groups show remarkably little overlap in their distributions. Analysis of the distribution patterns revealed distinct patterns concordant, or largely so, with patterns recognized for other oceanic organisms.

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Contents

Zoogeography and Systematics of the Lanternfishes of the Genus *Nannobrachium* (Myctophidae: Lampanyctini)

Bernard J. Zahuranec

Introduction

Among the open-ocean midwater fishes, the lanternfishes (family Myctophidae) are notably common and numerous both in terms of species and individuals (Hulley, 1995). Of the many genera in the family Myctophidae, the genus *Diaphus* contains the greatest number of species, whereas the genus *Lampanyctus* (sensu lato) is probably the most widespread and second in number of species (Backus et al., 1977).

Lampanyctus was erected by Bonaparte (1840), with *Gasteropelecus crocodilus* Risso (1810) the type-species by monotypy. As Moser and Ahlstrom (1974) pointed out, it has been a catch-all taxon ever since, even in Fraser-Brunner's (1949) and Paxton's (1972) reviews of the family. Since Fraser-Brunner's review, however, a number of species have been removed from *Lampanyctus* or described in separate genera. Several of these (*Stenobrachius, Triphoturus,* and *Lepidophanes*) were recognized as subgenera by Fraser-Brunner (1949) and were elevated to generic status by Bolin (1959). Hubbs and Wisner (1964) erected the genus *Parvilux* for two new species from the northeastern Pacific, and Paxton (1972) erected the genus *Bolinichthys* for several species in Fraser-Brunner's subgenus *Lepidophanes*.

Within the narrowly defined *Lampanyctus,* Paxton (1972), essentially following Bolin (1959), recognized three groups: those with moderate to long pectoral fins and with cheek photophores, to which the name *Lampanyctus* applies; those with long pectoral fins but lacking cheek photophores, for which no generic or subgeneric name has been proposed; and those with short or no pectoral fins and no cheek photophores, to which the name *Nannobrachium* applies. Although it was beyond the scope of his study to examine all species of *Lampanyctus,* Paxton (1972) did compare material of several species from each group; however, he thought that recognition of these three groups as subgenera necessitated a more thorough investigation of the species involved.

The species of the genus *Lampanyctus* have frequently caused taxonomic problems, with the species of the short-pectoral-finned group especially difficult to distinguish and identify. Robert H. Gibbs, Jr., in his capacity as the co-advisor for my doctoral dissertation, informed me (pers. comm., 1973) that numerous taxonomists have expressed reservations about the validity of many of the short-pectoral-finned species. There are several reasons for this confusion. In the first place, the fish are particularly fragile and are easily damaged in collecting nets, so most specimens are in poor condition. Second, the group contains many morphologically similar species from many parts of the world's oceans. Third, although there is limited variability in most characters, there is enough variability in some cases for similar species to overlap, even in those characters wherein they differ most significantly. The problems have been compounded because specimens of many of the species were rare until the buildup of modern oceanographic collections.

The short-pectoral-finned group is defined and recognized herein as a monophyletic assemblage, the genus *Nannobrachium*. By amassing a large amount of comparative material from all over the world, those characters found useful for separating the species and for assessing their variability have been evaluated. A total of 17 species in five species groups are recognized and are defined herein, whereas 10 species were recognized previously, and their distributions are described and compared. Definitive corroboration of the monophyletic status of the five species groups of *Nannobrachium,* however, awaits further study with additional material.

Bernard J. Zahuranec, Office of Naval Research, International Field Office, 800 North Quincy St., Arlington, Virginia, 22217.

Review Chairman: Richard P. Vari, Department of Vertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560-0159.

Reviewers: John Paxton, Australian National Museum, Sydney; Robert Karl Johnson, Grice Marine Laboratory, University of Charleston, Charleston, South Carolina, 29412. P. Alexander Hulley, South African Museum, Cape Town 8000, South Africa.

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At the Smithsonian Institution, many people helped in many ways: Charles Roberts with statistics, David Dance and Kenneth McCormick with computer expertise, Lee Ann Hayek with the principal components analysis, Kurt Bruwelheide and Diane Bohmhauer Tyler with a variety of miscellaneous tasks, as well as Edgar N. Gramlin and Susan Jewett. I am especially indebted to Richard Vari and Joseph Russo for their assistance and encouragement.

Special thanks to Deborah Bowman Cox, Donna Dennison, Denise Peterson, and Bobi Randall for help with typing the manuscripts and tables. Due to changeover between incompatible word processing systems, the manuscript had to be put back into working condition again. This was smoothly done, thanks to Jacqueline Myles' dedicated assistance. The fish drawings were done by Brian Stone, South Carolina Department of Natural Resources, Charleston. Thanks are due to Lawrence Behunek and Jennifer Rielly, Office of Naval Research, for final preparation of the illustrations. Finally, for an enormous amount of patient help, thanks to my wife Jean and to Robert K. Johnson, University of Charleston, who went far beyond what a friend might be expected to do in encouragement and in helping me prepare the manuscript for publication.

Materials and Methods

More than 9000 specimens were examined in the course of this study. A complete listing of material examined is available upon request from the Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, or from the Grice Marine Laboratory (Attention: Dr. Robert K. Johnson), University of Charleston, Charleston, SC 29412. Institutional acronyms cited in the present paper are as listed in Leviton et al. (1985), except as follows: IOM is used for the Institute of Oceanology, Academy of Sciences, Moscow, instead of IOAN; HIMB is used for the Hawaiian Institute of Marine Biology, University of Hawaii; MLML is used for the Moss Landing Marine Laboratory, Moss Landing, California; NMFS is used for the Fishery Oceanography Center, National Marine Fisheries Service, La Jolla, California; NZ is used for the New Zealand Fisheries Research Division, Wellington, New Zealand; ORSTOM is used for the Office de la Recherche Scientifique et Technique Outre-Mer, New Caledonia; UCSB is used for the University of California, Santa Barbara, California; and OS is used for the Department of Oceanography, Oregon State University.

Traditionally, various investigators, including Günther (1887), Gilbert (1891, 1906, 1915), Tåning (1928), and Fraser-Brunner (1949), classified the species in the family Myctophidae by using differences in the position and numbers of photophores. Although photophore differences are still of primary importance, increased emphasis is herein placed on other taxonomic characters, including morphometry.

Except as noted, meristic methodology follows Hubbs and Lagler (1958), and photophore nomenclature follows Wisner (1976) and Nafpaktitis et al. (1977) (Figure 1). All dorsal- and anal-fin rays were enumerated, including any of the anteriormost tiny rays that may be buried in the skin at the origin of the fin. This differs from the technique of Wisner (1976) and Bolin (fide Wisner, pers. comm., 1975), where the first, weak half-ray, when present, was ignored. It proved extremely difficult to decide when a first ray was so small and weak that it should be ignored rather than counted as one of the ordinary shorter rays that precede the longest robust rays. Thus, all rays that could be seen and had separate bases at the body surface were counted. The last rays are commonly split almost to the base and were counted as one.

In comparing the positional differences of photophores, they have usually been related to other photophores, instead of relating them to other anatomical structures. This is at variance with methodologies of more recent investigators (Nafpaktitis and Nafpaktitis, 1969; Wisner, 1976) but was found to be a more useful technique. Descriptions of the photophore patterns given for each species are for the typical or commonest pattern. Atypical photophore arrangements are discussed in the sections on geographic variation.

In *Lampanyctus* the last AOa photophore is clearly raised above the level of the rest of the AO series and is considered to be the first of two Pol photophores, not part of the AO series; however, any reference to the position of the Pol in these fishes refers to the second or upper Pol, consistent with common usage. The infracaudal and supracaudal luminous structures are called glands following Wisner (1976) and Nafpaktitis et al. (1977). The structures making up the glands resemble scales and are referred to as such, following those authors. All devel-

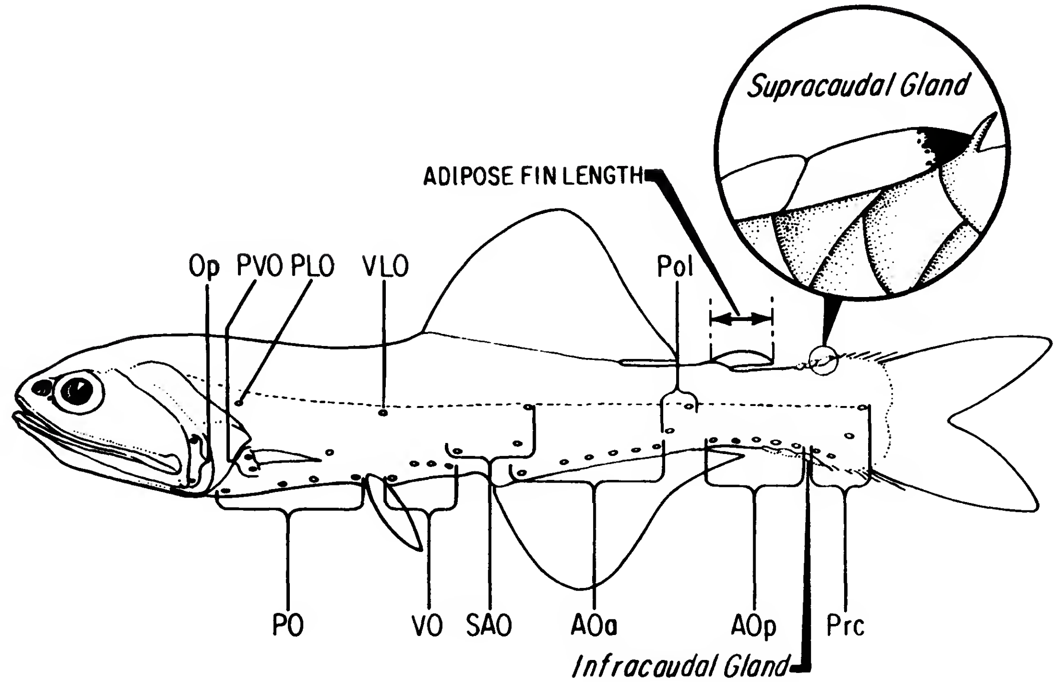

FIGURE 1.—Idealized *Nannobrachium cuprarium* (adapted from sketch of lectotype by Nafpaktitis, 1973, fig. 39) showing nomenclature of photophores, enlargement of black pigment cap on supracaudal gland, and technique used to measure adipose-fin length.

oped gill rakers on the first arch were counted, with the central raker at the angle included in the lower-limb count.

The number of tooth patches on the lower limb of the second gill arch was found to be an extremely useful diagnostic character. The second gill arch typically has three or four tooth patches, plus one gill raker on the upper limb, one gill raker at the angle, and one gill raker plus 8 to 12 tooth patches on the lower limb. In a few specimens, the posteriormost tooth patch on the lower limb may be developed into a second gill raker; however, this usually does not change the total number of elements from the typical number for the species. Consequently, counts of the tooth patches on the lower limb of the second arch that are given for each species are typical counts, even though a few specimens of virtually all species have one fewer tooth patch but two gill rakers on that lower limb. In order to determine whether the anteriormost tooth patch should be counted or not, the gill arch was lifted and rocked back and forth. If the tooth patch moved with the gill arch, it was counted, but if the tooth patch was forward of the hinge joint and, therefore, did not move with the gill arch, it was not counted. Occasionally, a tooth patch clearly was on the hinge but did not move when the gill arch was rotated. In that case, it was counted as ½ of a tooth patch. This occurred infrequently and made little difference for identifying specimens.

Except as noted, all measurements were taken following the techniques of Hubbs and Lagler (1958), using needle-point dividers and a binocular dissecting microscope. Using a steel rule, the measurements were estimated to the nearest 0.2 millimeters. Specimen length was measured as standard length (SL). Post-adipose length was measured from the notch at the posterior base of the adipose fin to the caudal base, following Wisner (1976). This avoided the difficulty of having to select some arbitrary spot on the "ramp" preceding the fin proper as the origin of the adipose fin. On the other hand, in order to measure the length of the adipose fin, the point where the fin itself arises from the "ramp" was taken as the origin of the adipose fin (Figure 1). Thus, the adipose-fin length measurements are probably prone to greater error than most of the other measurements taken on these fish.

Measurements were taken of 20 point-to-point dimensions, including standard length (in mm), for more than 20 specimens of each species. The means, standard deviations, and ranges of these, as thousandths of standard length, were calculated using the Statistical Package for the Social Sciences (SPSS) (Nie et al., 1977) and are given for each species in the measurements tables in the text. These statistics do not take into account any effects of allometry. Information concerning allometry was obtained from individual scatter plots of each measurement versus standard length for that species, and from a REGRESS program that employed a t-test for allometry. Both programs were developed by Richard Goodyear, formerly at the Smithsonian Institution. In the measurements tables, the abbreviations for indicating the significance level of tests of allometry are as follows: Sig ($p < 0.05$), Slt ($0.05 < p < 0.10$), 0=nonsignificant with + or – indicating positive or negative allometry. In indicating the results of regression analyses, Y denotes the dependent variable (head depth, predorsal depth, etc.), X denotes the independent variable (SL).

Measurement data also were used to obtain an independent, quantitative assessment of assignment of species to the five *Nannobrachium* species groups that had been based on criteria other than these morphometrics. The 19 measurements treated as fractions of standard length for at least 20 specimens of each species were subjected to a stepwise discriminant analysis (Rao, 1965), using standard techniques (Nie et al., 1977). Stepwise discriminant analysis determines the important variables for deciding assignment of cases (i.e., specimens) to groups (species groups). The similarity of specimens within a group is demonstrated by the production of a plot of the first two discriminant scores on a graph. Although the techniques are similar to a principal components analysis, it is more appropriate to apply these techniques herein because the categories (i.e., species) are assumed to be known and the cases have already been assigned to categories (i.e., specimens measured have been identified to species).

The practical use of the measurement data to aid in the identification of species proved extremely difficult. All species are quite similar morphologically, and most species within the same species group appear virtually identical in shape. Although there are subtle differences between even the most similar appearing species, individual specimens often are damaged and/or preserved in a distorted condition, which masks these differences.

In an attempt to solve this problem and to extract any information present on morphological differences, a number of statistical procedures were used. I visually scanned the data in the tables of measurements for each species and found a series of 76 ratios of various pairs of the measurements that showed promise for significant mensural differences between species as based on t-tests. Next, I used SPSS (Nie et al., 1977) to perform a discriminant function analysis for all possible combinations of pairs of species within each previously determined species group. An index value of discrimination was produced from those five ratios that were found to give the best separation for each pair of species. These index values were plotted for each pair of species, and an average value of group means was obtained, termed herein the Discrimination Value (D.V.). Information obtained from these discriminant function analyses for species pairs is in Appendix tables A12–A14. These can be used to assist in identifying a particularly difficult unknown specimen where using the appropriate identification keys and meristics tables has brought the number of choices to two similar species. Use instructions are with the tables in the Appendix. Text and figure abbreviations are as follows:

A	anal-fin rays
D	dorsal-fin rays
GR	gill rakers (upper limb + lower limb)
LL	lateral line scale pockets or pores (lateral line scales missing in virtually all specimens examined)
P_1	pectoral fin
P_2	pelvic fin
SC/IC	supracaudal / infracaudal "gland scale" counts; preceding isolated "luminous scales" are denoted in lower-case Roman numerals (e.g., i=1, ii=2)
Sig	allometry t-test significance level of $p < 0.05$
SL	standard length
Slt	allometry t-test significance level of $p > 0.05$, < 0.10
V	vertebrae (precaudal + caudal)

The Genus *Nannobrachium*

Nannobrachium Günther, 1887:199 [type-species *Nannobrachium nigrum* Günther, 1887, by monotypy].

Paralampanyctus Kotthaus, 1972a:13 [type-species *Lampanyctus niger* (Günther, 1887), by original designation].

The species of the tribe Lampanyctini were defined by Paxton (1972) to have the following features: (1) short (never reaching far beyond pelvic-fin base), rudimentary, or no pectoral fins with narrow base always equal to or shorter than distance between lower orbital margin and toothed margin of upper jaw in the adult; (2) solid, squarish otolith, longest vertically, without prominent notch or rostrum, often somewhat rounded into a kidney-bean shape; (3) weak musculature resulting in a soft, flaccid body; (4) body profile appearing "pinched" because both predorsal and preanal profiles tend to be concave, with body depth a short distance anterior to dorsal fin less than at dorsal-fin origin and less than at nape; and (5) swimbladder in adults either greatly reduced or completely lost, but never well developed and filled with gas.

Post (1972) found an "extra" chromosome in members of the "*Lampanyctus ater* group," which he thought would help separate that group from the rest of *Lampanyctus*. The situation appears, however, to be variable because Chen and Ebeling (1974) found that, although *L. ritteri* also had an atypical karyotype (apparently not an "extra" chromosome), *L. regalis* had the typical complement of the rest of *Lampanyctus*. Both species are herein considered to belong to the genus *Nannobrachium*. Some of the above-listed characters, especially the otolith shape, were utilized by Kotthaus (1972a) to erect the genus *Paralampanyctus*, which is a junior synonym of *Nannobrachium*.

The variability of otolith shape was examined to assess the value of this character for defining the genus. Large series of otoliths were available from fresh material in the Ocean Acre collections (Gibbs et al., 1971) of the three North Atlantic species of *Nannobrachium*: *N. atrum*, *N. cuprarium*, and *N. lineatum*. There is considerable variability in fine detail of otolith shapes (Figure 2) in these three species, but all are generally of similar form. This same squarish, vertically elongate shape is clearly evident in comparative material from four species of *Nannobrachium* from the Pacific, especially when contrasted with other species of *Lampanyctus* from the North Atlantic, except *L. macdonaldi*, which has otoliths similar to *Nanno-*

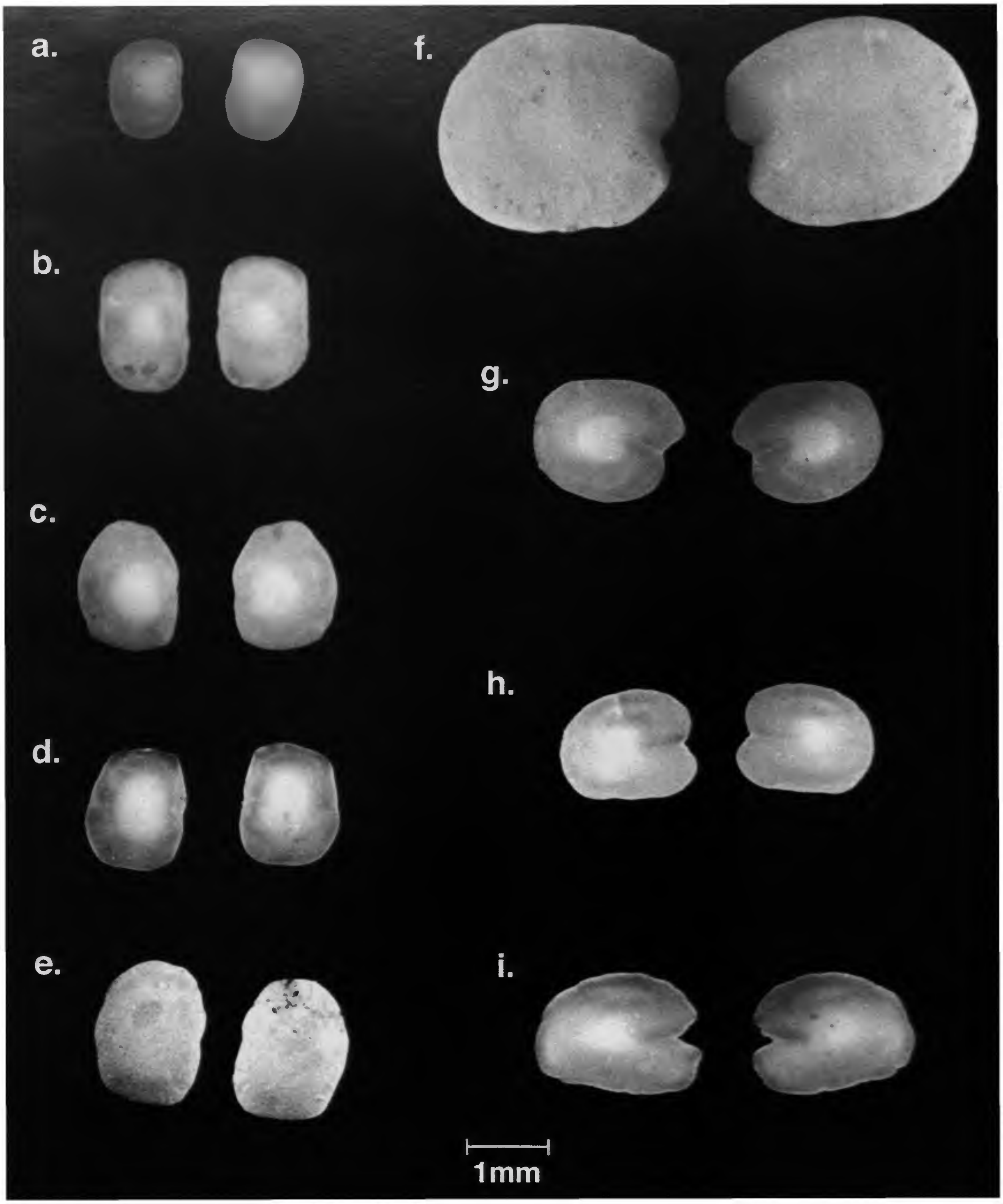

FIGURE 2.—Lateral view of otoliths (sagittae): *a, Nannobrachium atrum,* Ocean Acre, USNM; *b, N. cuprarium,* Ocean Acre, USNM; *c, N. gibbsi, Eltanin* Cruise 31, sta 13A, USNM; *d, N. nigrum, Eltanin* Cruise 31, sta 11A, USNM; *e, N. lineatum,* Ocean Acre, USNM; *f, Lampanyctus crocodilus,* MCZ RHB 1248; *g, L. festivus,* MCZ RHB 1128; *h, L. photonotus,* MCZ RHB 1149; *i, L. nobilis,* MCZ RHB 1415.

TABLE 1.—Diagnostic characters of species groups of *Nannobrachium*.

Character	Nigrum	Regale	Cuparium	Achirus	Isaacsi
P_1 lengths in adults	less than ½ distance to P_2 origin	reaching P_2 origin or beyond	between ½ to full distance to P_2	absent or short, pointing vertically downward	approximately reaching P_2 origin
P_1 rays in adults	extremely fine, flexible	well developed, strong	moderately well developed, intermediate in flexibility	absent or short, thick, stiff	as in Cuprarium but slightly longer and thicker
VLO position relative to lateral line (LL)	closer to LL than to PLO, less than 2 photophore diameters below LL	farther from LL than to PLO, more than 2 photophore diameters below LL	closer to LL than to PLO, usually touching LL	closer to LL than to PLO, less than 2 photophore diameters below LL	closer to LL than to PLO, usually touching LL
SAO_1	above VO_{2-3} interspace, on SAO_2 level	above VO_{2-3} interspace to above VO_{3-4} interspace	above VO_{3-4} interspace, slightly lower than SAO_2	as in Nigrum	above VO_{3-4} interspace, on SAO_2 level
Prc_3	directly under Prc_4	under but slightly forward of vertical from Prc_4	forward, on vertical midway between Prc_2 and Prc_4	directly under or slightly behind vertical from Prc_4	forward, on vertical midway between Prc_2 and Prc_4
Pol_2	under or slightly before vertical from adipose origin	well forward to below end of adipose-fin base	well forward of vertical from adipose origin	usually well forward of vertical from adipose origin	well forward of vertical from adipose origin
PVO_2	usually closer to PVO_1, ¼ PVO_1–PLO distance	as in Nigrum	as in Nigrum	usually farther from PVO_1; ¼–½ PVO_1–PLO distance	as in Nigrum
VO_2	approximately midway between VO_1–VO_3	as in Nigrum	as in Nigrum	as in Nigrum	directly above VO_1
Black pigment hood on supracaudal and infracaudal glands	absent	absent	present	absent	absent

brachium. The otoliths of the two species of *Parvilux* also are superficially similar, but Fitch (1969) pointed out that the otoliths of *Parvilux* are slightly concave rather than straight as in *Nannobrachium*.

Nannobrachium can be distinguished from all other genera in the Myctophidae, except *Triphoturus* and *Parvilux*, by the combination of characters listed above. *Nannobrachium* shares with those two genera and with the Macdonaldi species group of *Lampanyctus* the features of short pectoral fins and weak musculature resulting in a soft, flaccid body. In common with *Triphoturus* and *Parvilux*, *Nannobrachium* has a "pinched" body profile and narrow pectoral-fin base, whereas it shares a squarish, vertically elongate otolith and an atrophied swimbladder in adults with *Parvilux* and the Macdonaldi group.

Complete descriptions of larvae of *Nannobrachium* species have been published only for *N. bristori*, *N. hawaiiensis*, *N. idostigma*, *N. regale*, *N. ritteri* (Moser and Ahlstrom, 1996), and possibly *N. achirus* (see Moser and Ahlstrom, 1974). Larvae of *Nannobrachium* species share some common characteristics that may prove characteristic of the genus as a whole when the larvae of other species are known. Larvae are robust and have large heads with a more or less pointed snout. The pectoral fins are relatively large in most species of *Nannobrachium*, and they are very large and fan-shaped in some others (e.g., *N. hawaiiensis*). The large jaws have strong teeth and a tooth patch at the tip of the upper jaw. The tooth patch is borne on paired elements that are produced into a beak-like structure in some species (e.g., *N. achirus*).

Because there has been so much confusion regarding the identification of these species, it was not always possible to determine whether species in the literature were correctly identified without an examination of the material in question. Where literature references could be determined with some likelihood or certainty based on description, locality data, or other information, the citation was listed but was noted as questionable (i.e., with "?") or "in part" as explained below. In the species synonymies, known partial misidentifications by a given author are indicated by "in part," and, where necessary, by question marks as follows: [?in part]—identification probably at least partly correct but unconfirmed; [in part?]—identification known to be at least partly correct (some specimens), but the series of specimens reported also likely contained (unconfirmed) one or more additional species; [?in part?]—a combination of both uncertainties. The following references could not be confirmed, and the identifications must be considered uncertain.

Lampanyctus achirus.—Bekker, 1967b:179.

Lampanyctus ater.—Fraser-Brunner, 1931:224.—Belyanina, 1981:78–79.

Lampanyctus idostigma.—Stiassny, 1996:426.

Lampanyctus lineatus.—Parin, 1976:199.

Lampanyctus niger.—Gilbert, 1913:100.—Fowler, 1928:68; 1936:382, 391–392.—Borodin, 1931:76–77.—Kulikova, 1960:29–33.—Bekker 1967b:179. Bradbury et al., 1971:434.—Parin, 1971:82; 1975:321; 1976:199.—Borodulina, 1972:696, 698, 700, 701.—Parin et al., 1973:114–115.—Clarke and Wagner, 1976:642.—Willis et al., 1988:87.

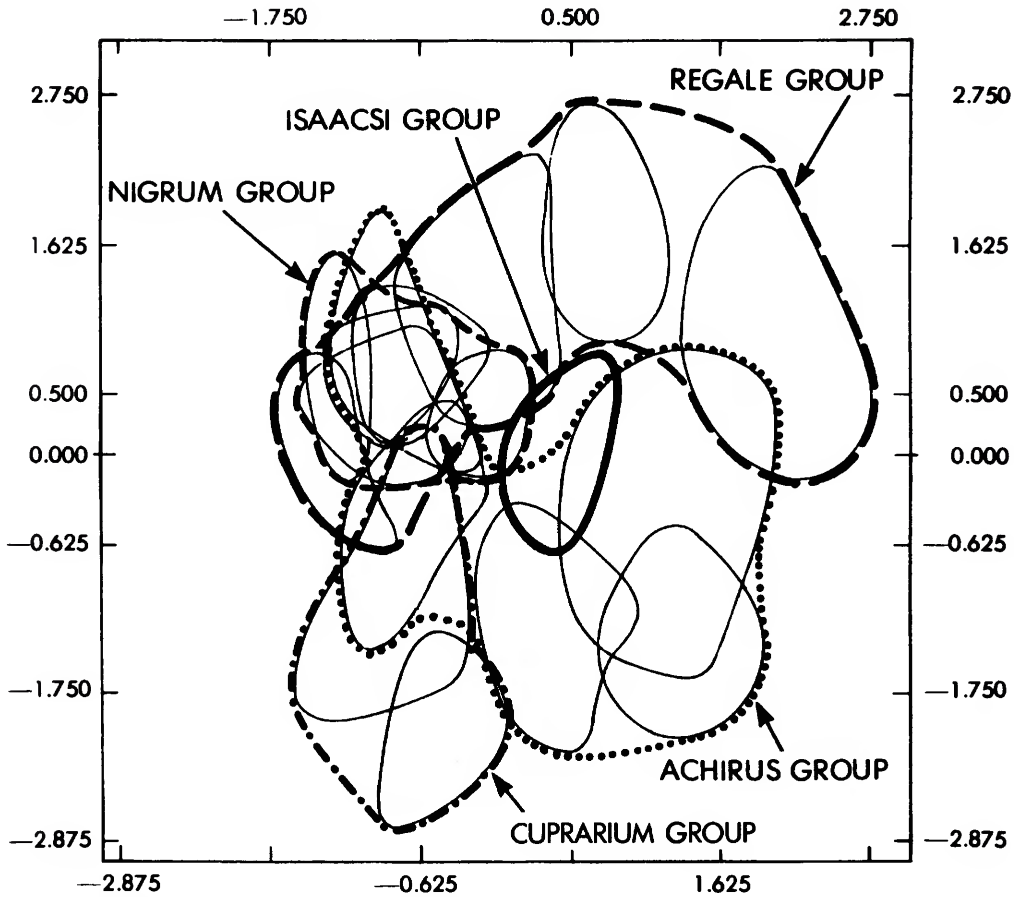

FIGURE 3.—Artist's rendering of plot of first two discriminant scores of selected proportional measurements for all species of *Nannobrachium* (see "Methods" for explanation). The species clusters are denoted by the solid thin lines. Envelopes for all species groups are denoted by separately labeled bold solid and dashed curves.

Lampanyctus niger species group/complex.—Clarke, 1982: 299, 303.

Lampanyctus nigrum.—Stiassny 1996:426.

Lampanyctus regale.—Stiassny, 1996:426.

Lampanyctus regalis.—King and Iversen, 1962:320.

Lampanyctus ritteri.—King and Iversen, 1962:320.—Parin et al., 1973:115.—Beebe and Vander Pyle, 1944:86–87.

Macrostoma nigrum.—Fowler, 1936:1231.

Myctophum (*Lampanyctus*) *nigrum*.—Pappenheim, 1914: 199.—Barnard, 1925:239.

Myctophum nigrum.—Herre, 1953:144.

The Species Groups of *Nannobrachium*

Five species groups are recognized in *Nannobrachium* as a result of this study. These are not proposed as formal taxa but are phenetic groups named after the oldest described species in each group: the Nigrum, Regale, Cuprarium, Achirus, and Isaacsi species groups.

All species in each group share at least one distinguishing character unique to that group among the species of *Nannobrachium*. In addition, all species in each group share a suite of one or more characters that are not unique to that group (also being found in other species of *Nannobrachium*). Thus, although some characters making up this suite are shared with species in other groups, the entire suite of characters is unique to that group. The characters for each group are discussed in the sections preceding the species accounts and are given in Table 1.

Recognition of five species groups is based on differences and similarities in photophore positions, condition of pectoral fins, and (one case) pigmentation. The groups have been corroborated by a step-wise discriminant analysis (Rao, 1965) of morphometric data. In this analysis, the most important variable for discriminating among species was length of the solid infracaudal gland; the second most important was caudal-peduncle depth. That is, these two variables contributed (or explained) the greatest amount of variation between species as expressed by the first discriminant scores. Because of the morphological similarity between species of *Nannobrachium* a plot of the discriminant scores resulted in a high degree of overlap; therefore, Figure 3 is an artist's rendering using thin solid lines to enclose the cluster of symbols for each species but with the symbols deleted. Thicker curves enclosing all species envelopes within each species group clearly show the grouping of the species clusters. Thus, the species groups, originally recognized largely on the basis of photophore arrangement differences, are independently supported by these clustering techniques using only morphometry. It is clear from the amount of overlap, however, that morphometry alone cannot be used to separate species or species groups.

Identification of *Nannobrachium* Species

To facilitate the identification of material, keys have been constructed. The first includes all species and species groups in a "natural" system, using those characters by which the species groups may be distinguished.

Because these species are so similar to each other, they are frequently difficult to identify properly. Knowing the geographical region from which the specimens were obtained can usually simplify the process, especially if the number of possible species in the key has been reduced accordingly. Consequently, an additional set of four keys was constructed for the major ocean areas to include the species of *Nannobrachium* that occur there.

In addition, where uncertainty exists in the identification of a specimen, perhaps because of its damaged condition, but where it has been identified to one of two possibilities, then the Discrimination Value (D.V.) in the Appendix may help resolve the dichotomy. Alternatively, Tables A2–A8, giving meristics obtained in this study, may help with identifications. Finally, it must be borne in mind that there are probably a number of undescribed species of *Nannobrachium* in the world's oceans. Specimens of undescribed species may be expected, particularly from the southern hemisphere, and especially from the Indo-Pacific region. In this regard, however, it is worth repeating Fraser-Brunner's (1949:1082) admonition (for *Lampanyctus* sensu lato but which holds especially for *Nannobrachium*) that "under no circumstances should a doubtful specimen of this genus be described as a new species unless adequate comparative material is available."

Key to Species Groups and Species of *Nannobrachium*

1. VO_2 photophore raised in forward position above VO_1 (Isaacsi group) (Atlantic) .... ***N. isaacsi***

   VO_2 photophore not raised or only slightly raised but in normal position, approximately midway between VO_1 and VO_3 2
2. Black pigment cap covering posterior tips of supracaudal and infracaudal luminous glands [Figure 1]; SAO_1 over VO_{3-4} interspace; Prc_3 on vertical midway between Prc_2 and Prc_4 (Cuprarium group) 3

   No black pigment cap covering posterior tips of supracaudal and infracaudal luminous glands; SAO_1 above or forward of vertical from VO_3 (except in *N. idostigma*), usually above VO_{2-3} interspace (except in *N. ritteri* and *N. fernae*); Prc_3 closer to vertical from Prc_4 than vertical from Prc_2, usually directly under Prc_4 4
3. Length of caudal peduncle shorter than, or equal to, upper-jaw length; Prc_3 on line connecting Prc_2 and Prc_4; Prc continuous with AOp; AO 5–6+5–6, total 10–11; anal-fin rays 18–19 (17–20); lateral line organs 32–33; vertebrae 14–16+18–19, total 32–34 (Atlantic) .... ***N. cuprarium***

   Length of caudal peduncle longer than upper-jaw length; Prc_3 below line connecting Prc_2 and Prc_4; Prc not usually continuous with AOp; AO 7–9+6–9, total 14–17; anal-fin rays 20–21 (19–23); lateral line organs 37–44; vertebrae 14–19+21–26, total 37–44 (Atlantic and Indo-Pacific) .... ***N. lineatum***
4. Pectoral fins always absent in large adults (greater than approximately 100 mm); pectoral fins present or absent in smaller specimens (between approximately 40 mm and 100 mm; if present, pectorals point directly downward and rays thicker and stiffer, although relatively shorter, in progressively larger specimens); PVO_1–PVO_2 distance averages more than ¼, usually about ⅓ to ½, the PVO_1–PLO distance; Prc_3 usually about equidistant between Prc_2 and Prc_4, directly on or slightly behind vertical from Prc_4; Pol_2 usually before vertical from origin of adipose fin (Achirus group) 5

Pectoral fins always present, rays fine and flexible, never thick and stiff (in specimens greater than approximately 40 mm, rays finer, more flexible, and relatively shorter; in smaller specimens pectoral fins tending to point backward, whereas in progressively larger specimens pectoral fins tending to point more directly downward); PVO_1–PVO_2 distance averages about ¼ the PVO_1–PLO distance; Prc_3 usually closer to Prc_2 than to Prc_4, usually slightly before vertical from Prc_4; Pol_2 usually behind vertical from origin of adipose fin 9

5. Pectoral fins always absent (vestigial rays may be present in some very small juveniles); small species, maximum size about 80 mm 6

Pectoral fins always present in specimens less than about 50 mm; in specimens between 50–100 mm, pectoral fins in various stages of becoming vestigial and covered with skin; in specimens longer than about 100 mm pectoral fins always absent; one intermediate-length species always retaining at least vestigial pectoral fins to maximum size of about 100 mm, with no vestige of pectoral fins above around 100 mm; two large species, maximum size greater than 150 mm 7

6. Infracaudal luminous gland short, 4–5 scales; AO 5–6+6–7, total 11–13; vertebrae 14–16+19–20, total 34–35 (N. Pacific) .... ***N. hawaiiensis***, new species

Infracaudal luminous gland long, 6–9 scales; AO 5–8+7–9, total 13–16; vertebrae 15–16+20–22, total 36–38 (cold temperate, south circumpolar) .... ***N. wisneri***, new species

7. Gill rakers 4+10 (8–11), total 14 (12–15); 8 tooth patches on lower limb of second gill arch; AO 5–6 (7)+5–6 (7), total 11–12 (10–13) (equatorial Pacific) .... ***N. crypticum***, new species

Gill rakers 5–6 (4–7)+12–14 (11–15), total 17–19 (15–21); 9–11 tooth patches on lower limb of second gill arch; AO 7 (6–8)+7–8 (6–9), total 14–15 (13–16)........ 8

8. Gill rakers 5–6 (7)+13 (11–15), total 18–19 (16–21); 10 (9–12) tooth patches on lower limb of second gill arch; AO 7 (6–8)+8 (7–9), total 15 (14–16); 6–9 scales in infracaudal luminous gland; lateral line organs 36–37 (34–38); vertebrae 15–17+20–22, total 36–38 (subantarctic, circumpolar) .... ***N. achirus***

Gill rakers 5 (4–6)+12 (11–13), total 17 (15–18); 9 (8–10) tooth patches on lower limb of second gill arch; AO 7 (6–8)+7 (6), total 14 (13); 5–7 scales in infracaudal luminous gland; lateral line organs 34–35; vertebrae 15+20–21, total 35–36 (southeast Pacific) .... ***N. phyllisae***, new species

9. Pectoral fin well developed, stiffer rays reaching to or beyond pelvic-fin insertion; VLO usually more than 3 photophore diameters below lateral line; VLO to lateral line distance always greater than PLO to lateral line distance (Regale group) 10

Pectoral fin very weakly developed, extremely fine, flexible rays reaching barely half way to pelvic-fin insertion; VLO touching or close to lateral line, less than 2 photophore diameters below; VLO to lateral line distance always less than PLO to lateral line distance (Nigrum group) 14

10. Infracaudal luminous gland short, 2–4 scales; lateral line organs 31–33; vertebrae 14–15+18–19, total 32–34; SAO series far posteriad, SAO_1 above VO_{3-4} interspace, SAO_2 on or slightly behind vertical from AOa_1, SAO_3 on or slightly behind vertical from AOa_2 (eastern Pacific) .... ***N. idostigma***

Infracaudal luminous gland long, almost always more than 4 scales (usually 5–9; if only 3 or 4 scales, then VLO much closer to lateral line than to pelvic-fin insertion); lateral line organs 35–40; vertebrae 14–16+20–23, total 36–39; SAO series not especially far posteriad, SAO_1 on or before vertical from VO_3, SAO_2 well before vertical from AOa_1, SAO_3 above either AOa_1 or AOa_{1-2} interspace 11

11. Gill rakers 4–5+11–12 (10–13), total 15–16 (14–18); 9 (8) tooth patches on lower limb of second gill arch 12

Gill rakers 4 (3–5)+10 (9–11), total 14 (13–15); 8 (7–9) tooth patches on lower limb of second gill arch 13

12. Infracaudal luminous gland very long, nearly filling infracaudal space, 7–10 scales; 13 (12–14) dorsal-fin rays; 37–38 lateral-line organs (N. Pacific) . . . . . . ***N. fernae***
    Infracaudal luminous gland short, covering less than one-half infracaudal space, 3–5 scales; 14–15 dorsal-fin rays; 35–36 lateral line organs (N. Pacific) . . . . ***N. bristori***, new species
13. VLO well above line passing through SAO_{1-2}; adipose fin large, length 1.5–2 times into caudal peduncle depth; supracaudal luminous scales 3–5; frequently 1 or 2 separate isolated luminous scales before solid infracaudal luminous gland (N. Pacific) . . . . ***N. regale***
    VLO approximately on line passing through SAO_{1-2}; adipose fin small, its length more than 3 times into caudal peduncle depth; supracaudal luminous scales 2–3; no isolated separate luminous scales before solid infracaudal luminous gland (N. Pacific) . . . . ***N. ritteri***
14. Gill rakers 5 (4)+12 (11–13), total 17 (15–18) 15
    Gill rakers 4 (3–5) + 10–11 (8–12), total 14–15 (13–17) 17
15. AO 6–7 (5–9)+7–8 (6–9), total 12–15 (12); lateral line organs 36–39; vertebrae 16 (15)+21–22 (20–23), total 37–38 (36–39); anal-fin rays 19 (17–21) (Atlantic, Indian, S. Pacific) . . . . ***N. atrum***
    AO 5 (4–6)+5–6 (7), total 10–11 (9–13); lateral line organs 29–34; vertebrae 15 (14–16)+18–20 (17–21), total 33–35 (32–37); anal-fin rays 16–17 (14–18) 16
16. Infracaudal luminous gland scales 4 (i+3–5); vertebrae 15 (14–16)+19–20 (18–21), total 34–35 (33–37); lateral line organs 32–34 (Pacific) . . . . ***N. nigrum***
    Infracaudal luminous gland scales 3 (i+2–5); vertebrae 14–15+18–19 (17), total 33 (32–34); lateral line organs 30–31 (29–32) (Indian) [specimens with high gill raker counts will key out here] . . . . ***N. indicum***, new species
17. Gill rakers 4 (5)+11 (10–12), total 15 (14–17); lateral line organs 30–31 (29–32) (Indian) [specimens with low gill raker counts will key out here] . . . . ***N. indicum***, new species
    Gill rakers 4 (3)+10 (8–11), total 14 (12–15); lateral line organs 33–34 (32–35) 18
18. AO 6–8+6–8, total 13–14; dorsal-fin rays 14–15 (16); anal-fin rays 18–19 (17–20); vertebrae 15–17+20–22, total 36–38; PVO_1 near PVO_2, the interspace ⅓ to ¼ of PVO_2–PLO distance; PVO_2 before or below center of pectoral-fin base; VLO approximately 1–2 photophore diameters below lateral line (tropical Pacific) . . . . ***N. gibbsi***, new species
    AO 5–7+5–7, total 10–13; dorsal-fin rays 13 (12–15); anal-fin rays 17 (15–19, usually 16–18); vertebrae 14–16+18–21, total 33–36; PVO_1–PVO_2 distance ½ to ⅓ of PVO_2–PLO distance; PVO_2 at or above upper edge of pectoral-fin base; VLO approximately 1 photophore diameter below lateral line (equatorial Pacific) [specimens with well-developed pectoral fins may key out here] . . . . ***N. crypticum***, new species

Key to the Species of *Nannobrachium* in the Atlantic Ocean

1. Pectoral fins present 2
   Pectoral fins absent 6
2. VO_2 photophore raised and forward to a position above VO_1 . . . . ***N. isaacsi***
   VO_2 photophore not, or only slightly, raised and in normal position, approximately midway between VO_1 and VO_3 3
3. Black pigment cap covering posterior tips of supracaudal and infracaudal luminous glands [Figure 1]; SAO_1 over VO_{3-4} interspace; Prc_3 on vertical midway between Prc_2 and Prc_4 4
   No black pigment cap covering posterior tips of supracaudal and infracaudal luminous glands; SAO_1 over VO_{2-3} interspace; Prc_3 directly under Prc_4 5

4. Length of caudal peduncle shorter than, or equal to, upper-jaw length; Prc_3 on line connecting Prc_2 and Prc_4; Prc continuous with AOp; AO 5–6+5–6, total 10–11; anal-fin rays 18–19 (17–20); lateral line organs 32–33; vertebrae 14–16+18–19, total 32–34 .... ***N. cuprarium***

   Length of caudal peduncle longer than upper-jaw length; Prc_3 below line connecting Prc_2 and Prc_4; Prc not usually continuous with AOp; AO 7–9+6–9, total 14–17; anal-fin rays 20–21 (19–23); lateral line organs 37–44; vertebrae 14–19+21–26, total 37–44 .... ***N. lineatum***

5. Gill rakers 5 (4)+12 (11–13), total 17 (16–18); 9 (7–10) tooth patches on lower limb of second gill arch; anal-fin rays 19 (17–21); 3–6 scales in infracaudal luminous gland, filling approximately ½ of infracaudal space; adipose fin further forward, origin usually above Pol_2 and before end of anal-fin base .... ***N. atrum***

   Gill rakers 5–6 (7)+13 (11–15), total 18–19 (16–21); 10 (9–12) tooth patches on lower limb of second gill arch; anal-fin rays 17–18 (15–19); 6–9 scales in infracaudal luminous gland, filling more than ¾ of infracaudal space; adipose fin further back, origin usually behind vertical line from Pol_2 and above end of anal-fin base [small specimens, usually less than 40 mm, with pectoral fins still prominent, will key out here] .... ***N. achirus***

6. Gill rakers 5–6 (7)+13 (11–15), total 18–19 (16–21); 10 (9–12) tooth patches on lower limb of second gill arch; infracaudal luminous gland frequently with separate isolated luminous scale preceding solid gland [large species, specimens usually longer than 60 mm, with pectoral fins vestigial under the skin, will key out here] .... ***N. achirus***

   Gill rakers 4 (5)+11–12, total 15–16 (17); 9 (8–10) tooth patches on lower limb of second gill arch; infracaudal luminous gland rarely having separate isolated luminous scale preceding solid gland [small species, less than 80 mm] .... ***N. wisneri*, new species**

Key to the Species of *Nannobrachium* in the Indian Ocean

1. Pectoral fins present 2

   Pectoral fins absent 6

2. Black pigment cap covering posterior tips of supracaudal and infracaudal luminous glands [Figure 1]; SAO_1 over VO_{3-4} interspace; Prc_3 on vertical midway between Prc_2 and Prc_4; anal-fin rays 20–21 (19–23); dorsal-fin rays 16–18; vertebrae 16–17 (14–19)+22–23 (21–26), total 39–40 (37–44) .... ***N. lineatum***

   No black pigment cap on supracaudal and infracaudal luminous glands; SAO_1 over VO_{2-3} interspace; Prc_3 approximately below Prc_4; anal-fin rays 16–19 (14–21); dorsal-fin rays 13–14 (12–15); vertebrae 15–16 (14–17)+18–22 (17–23), total 33–38 (32–39) 3

3. AO 4–6+5–7, total 9–12; lateral line organs 30–33 (29–34); vertebrae 15 (14–16)+18–20 (17–21), total 33–35 (32–37) 4

   AO 5–9+6–9, total 12–16; lateral line organs 35–39 (34); vertebrae 16 (15–17)+21–22 (20), total 37–38 (36–39) 5

4. Gill rakers 4 (5)+11 (10–12), total 15 (14–17); 8 (9) tooth patches on lower limb of second gill arch; 3 (2–5) infracaudal luminous gland scales; lateral line organs 30–31 (29–32) .... ***N. indicum*, new species**

   Gill rakers 5 (4)+12 (11–13), total 17 (15–18); 9 (10) tooth patches on lower limb of second gill arch; 4 (3–5) infracaudal luminous gland scales; lateral line organs 33 (32–34) .... ***N. nigrum***

5. Gill rakers 5 (4)+12 (11–13), total 17 (16–18); 9 (7½–10) tooth patches on lower limb of second gill arch; anal-fin rays 19 (17–21); 3–6 scales in infracaudal luminous gland, filling approximately ½ of infracaudal space .... ***N. atrum***

Gill rakers 5–6 (7)+13 (11–15), total 18–19 (16–21); 10 (9–12) tooth patches on lower limb of second gill arch; anal-fin rays 17–18 (15–19); 6–9 scales in infracaudal luminous gland, filling more than ¾ of infracaudal space [small specimens, usually less than 40 mm, with pectoral fins still prominent will key out here] .... *N. achirus*

6. Gill rakers 5–6 (7)+13 (11–15), total 18–19 (16–21); 10 (9–12) tooth patches on lower limb of second gill arch; infracaudal luminous gland frequently with separate isolated luminous scale preceding solid gland [large species, specimens usually longer than 60 mm, with pectoral fins vestigial under the skin, will key out here] . ... *N. achirus*

   Gill rakers 4 (5)+11–12, total 15–16 (17); 9 (8–10) tooth patches on lower limb of second gill arch; infracaudal luminous gland rarely with separate isolated luminous scale preceding solid gland [small species, less than 80 mm] .... ***N. wisneri***, new species

Key to the Species of *Nannobrachium* in the North Pacific Ocean

1. Pectoral fins absent .... ***N. hawaiiensis***, new species

   Pectoral fins present 2

2. VLO high, always 1 photophore diameter or less below lateral line 3

   VLO low, always more than 1 photophore diameter below lateral line 6

3. AO photophores 7–9+7–9, total 15–17; dorsal-fin rays 17 (16–18); anal-fin rays 20–21 (19–23); black pigment caps covering posterior tips of infracaudal and supracaudal luminous glands [Figure 1]; lateral line organs 37–44 ...... ***N. lineatum***

   AO photophores 4–8+5–8, total 10–14; dorsal-fin rays 13–15 (12–16); anal-fin rays 16–19 (14–20); no black pigment caps on infracaudal and supracaudal luminous glands; lateral line organs 32–36 4

4. Gill rakers 5 (4)+12 (11–13), total 17 (15–18); 9 (10) tooth patches on lower limb of second gill arch .... ***N. nigrum***

   Gill rakers 4 (3)+10 (8–11), total 14 (12–15); 8 tooth patches on lower limb of second gill arch 5

5. AO 6–8+6–8, total 13–14; dorsal-fin rays 14–15 (16); anal-fin rays 18–19 (17–20); vertebrae 15–17+20–22, total 36–38; PVO_1–PVO_2 interspace ⅓ to ¼ of PVO_2–PLO interspace; PVO_2 before or below center of pectoral-fin base .... ***N. gibbsi***, new species

   AO 5–7+5–7, total 10–13; dorsal-fin rays 13 (12–15); anal-fin rays 17 (16–18); vertebrate 14–16+18–21, total 33–36; PVO_1–PVO_2 interspace ½ to ⅓ of PVO_2–PLO interspace; PVO_2 at or above upper edge of pectoral-fin base .... ***N. crypticum***, new species

6. Gill rakers 4 (3–5)+10 (9–11), total 14 (12–15); 8 tooth patches on lower limb of second gill arch 7

   Gill rakers 4–5+11–12 (10–13), total 15–16 (14–18); 9 (8) tooth patches on lower limb of second gill arch 10

7. VLO no more than 2 photophore diameters below lateral line; VLO above line from PLO to SAO_1 [specimens with VLO farther from lateral line will key out here] .... ***N. gibbsi***, new species

   VLO more than 2 photophore diameters below lateral line; VLO on or below line from PLO to SAO_1 8

8. Infracaudal luminous gland short, filling less than ½ infracaudal space with 3 (2–4) scales; lateral line organs 31–33; vertebrae 14–15+18–19, total 32–34 [specimens with unusually low gill raker counts will key out here] .... ***N. idostigma***

   Infracaudal luminous gland longer, filling more than ½ infracaudal space with 5–7 (4) scales; lateral line organs 35–40; vertebrae 15–16+21–23, total 36–38 9

9. VLO well above line through SAO_1 and SAO_2; adipose fin large, length 1.5–2 times into caudal peduncle depth; supracaudal luminous scales 3–5; frequently 1, sometimes 2, separate isolated luminous scales before solid part of gland ..... ***N. regale***
   VLO approximately on line through SAO_1 and SAO_2; adipose fin small, length more than 3 times into caudal peduncle depth; supracaudal luminous scales 2–3; no isolated separate luminous scales before solid part of gland .... ***N. ritteri***
10. Infracaudal luminous gland very long, 7–10 scales, filling most of infracaudal space; total AO 14–15 (13–16) .... ***N. fernae***
   Infracaudal luminous gland short to moderately long, 2–5 scales, filling less than ½ infracaudal space; total AO 11–13 (10–14) 11
11. SAO series relatively far posteriad; SAO_1 above VO_{3-4} interspace, SAO_2 above or behind vertical from AOa_1, SAO_3 on or slightly behind vertical from AOa_2; dorsal-fin rays 13–14; AO 5–6+6 (5–8), total 11–12 (10–14); lateral line organs 31–33; vertebrae 14–15+18–19, total 32–34 [specimens with typical gill raker counts will key out here] .... ***N. idostigma***
   SAO series relatively far anteriad; SAO_1 above or before vertical from VO_3, SAO_2 well before vertical from AOa_1, SAO_3 above or slightly behind vertical from AOa_1; dorsal-fin rays 14–15; AO 6 (5–7)+7 (6–8), total 13 (14); lateral line organs 35–36; vertebrae 15–16+20–23, total 36–38 .... ***N. bristori,*** new species

Key to the Species of *Nannobrachium* in the South Pacific Ocean

1. Pectoral fins absent 2
   Pectoral fins present 4
2. Gill rakers 4 (5)+11–12, total 15–16 (17); small species, always less than about 80 mm with only trace of pectoral fins at smallest sizes (after postlarval transformation) .... ***N. wisneri,*** new species
   Gill rakers 5–6 (4–7)+12–13 (11–15), total 17–19 (15–21); large species, to more than 150 mm; pectoral fins present in smaller specimens (less than 50 mm) and may be found in larger ones, especially if skin of pectoral region is abraded 3
3. Gill rakers 5–6 (7)+13–14 (11–15), total 18–19 (16–21); 10 (9–12) tooth patches on lower limb of second gill arch; AO 7 (6–8)+8 (7–9), total 15 (14–16); 6–9 scales in infracaudal luminous gland; lateral line organs 36–37 (34–38); vertebrae 15–17+20–22, total 36–38 [moderately large to large specimens without pectoral fins apparent will key out here] .... ***N. achirus***
   Gill rakers 5 (4–6)+12 (11–13), total 17 (15–18); 9 (8–10) tooth patches on lower limb of second gill arch; AO 7 (6–8)+7 (6), total 14 (13); 5–7 scales in infracaudal luminous gland; lateral line organs 34–35; vertebrae 15+20–21, total 35–36 [moderately large to large specimens without pectoral fins apparent will key out here] .... ***N. phyllisae,*** new species
4. VLO more than 3 photophore diameters below lateral line, well below line connecting PLO with SAO_1; 3 (2–4) infracaudal luminous gland scales .... ***N. idostigma***
   VLO at or near lateral line, always less than 3 photophore diameters below it and well above line connecting PLO with SAO_1; 4–7 (3–9) infracaudal luminous gland scales 5
5. SAO_1 over VO_{3-4} interspace; Prc_3 on vertical midway between Prc_2 and Prc_4; dorsal-fin rays 17 (16–18); anal-fin rays 20–21 (19–22); vertebrae 17 (14–19)+22–23 (26), total 39–40 (38–44); black pigment cap on posterior tips of supracaudal and infracaudal luminous glands (fragile and frequently missing) .... ***N. lineatum***
   SAO_1 over VO_{2-3} interspace or, less commonly, over VO_3; Prc_3 on vertical line much closer to Prc_4 than Prc_2, usually under Prc_4; dorsal-fin rays 13–16 (12–17); anal-fin rays 16–19 (14–21); vertebrae 15–16 (14–17)+18–22 (23), total 33–38 (39); no black pigment cap on posterior tips of infracaudal or supracaudal luminous glands 6

6. Gill rakers 3–4+8–11, total 12–15; 8 tooth patches on lower limb of second gill arch 7
   Gill rakers 4–6+11–15, total 15–21; 9–10 (8–12) tooth patches on lower limb of second gill arch 8
7. AO 6–8+6–8, total 13–14; dorsal-fin rays 14–15 (16); anal-fin rays 18–19 (17–20); vertebrae 15–17+20–22, total 36–38; PVO_1–PVO_2 interspace ⅓ to ¼ of PVO_2–PLO interspace; PVO_2 before or below middle of pectoral-fin base .... ***N. gibbsi,*** new species
   AO 5–7+5–7, total 10–13; dorsal-fin rays 13 (14–15); anal-fin rays 17 (16–18); vertebrae 14–16+18–21, total 33–36; PVO_1–PVO_2 interspace ½ to ⅓ of PVO_2–PLO interspace; PVO_2 at or above upper edge of pectoral-fin base .... ***N. crypticum,*** new species
8. Gill rakers 5–6 (7)+13 (11–15), total 18–19 (16–21); AO 7 (6–8)+8 (7–9), total 15 (14–16); 10 (9–12) tooth patches on lower limb of second gill arch [small specimens, usually less than about 40 mm, still bearing prominent pectoral fins, will key out here] .... ***N. achirus***
   Gill rakers 5 (4–6)+12 (11–13), total 17 (15–18); AO 5–7 (4–8)+6–8 (5–9), total 11–14 (10–15); 8–9 (10) tooth patches on lower limb of second gill arch 9
9. Anal-fin rays 16–17 (14–18); 4 (3–5) infracaudal luminous gland scales; AO 5 (4–6)+6 (5–7), total 11 (10–13); lateral line organs 32–34 .... ***N. nigrum***
   Anal-fin rays 18–19 (17–21); 5–6 (3–7) infracaudal luminous gland scales; AO 6–7 (5–9)+7–8 (6–9), total 13–15 (12); lateral line organs 34–39 10
10. PVO_1–PVO_2 interspace about ¼ to ½ that of PVO_1–PLO interspace; Prc_3 usually about equidistant between Prc_2 and Prc_4, often slightly behind a vertical line from Prc_4; Pol_2 usually forward of adipose-fin origin; SAO_2 often closer to AOa_1 than to VO_4; lateral line organs 34–35 [small specimens, less than about 40 mm, still bearing prominent pectoral fins, will key out here] .... ***N. phyllisae,*** new species
    PVO_1–PVO_2 interspace about ¼ that of PVO_1–PLO interspace; Prc_3 usually noticeably closer to Prc_2 than to Prc_4, usually slightly before vertical from Prc_4; Pol_2 usually below adipose-fin base; SAO_2 usually closer to VO_4 than to AOa_1; lateral line organs 36–39 .... ***N. atrum***

The Nigrum Group

This group is distinguished by the extremely reduced pectoral fin. The pectoral fins of adults are more weakly developed and have thinner rays than in any other group. The fin length is less than one-half the distance to the pelvic-fin insertion, and the rays are extremely fine and flexible. In contrast, the species in other groups either lack pectoral fins or, if present, the fins are either longer than one-half the distance to the pelvic-fin insertion or they are shorter but have thick and stiff rays. In addition, in large adults of the Nigrum group, there is a pronounced tendency for the pectoral fins to point downward.

Other characters shared by all species in the Nigrum group are as follows: (1) VLO close to, or touching, the lateral line; always less than 2 photophore diameters below the lateral line and closer to the lateral line than the PLO is to the lateral line; (2) SAO_1 above the VO_{2-3} interspace; (3) Prc_3 directly under Prc_4, usually closer to Prc_2 than to Prc_4; (4) Pol_2 under the adipose fin or on a vertical from its origin. These and other characters are compared in Table 1 for all the species groups of *Nannobrachium.*

The Nigrum group contains four species: *N. nigrum* Günther, 1887; *N. atrum* (Tåning, 1928); *N. gibbsi,* new species; and *N. indicum,* new species. Modal characters of all species in the Nigrum group are listed in Table A1. Characters for *N. crypticum,* a new species in the Achirus group, and *N. bristori,* a new species in the Regale group, are included in Table A1 because both species have features that are similar to those of the species in the Nigrum group.

Nannobrachium nigrum Günther, 1887

FIGURE 4, TABLE 2

Nannobrachium nigrum Günther, 1887:199–200, pl. LII, fig. B [original description].—Gilbert, 1905:591 [description, Hawaiian Islands].—Herre, 1953:144 [original description listed].—Paxton, 1979:13 [holotype listed].

Myctophum (Lampanyctus) nigrum.—Brauer, 1906:242–243, 385 [in part] [distribution: Atlantic, Indian, and Pacific oceans].

Lampanyctus niger.—Parr, 1928:87 [key, similarities to *L. ater*].—Nafpaktitis, 1973:39–40 [figure, comparison with *L. ater*].—Parin, 1975:321, 325, 326 [?in part?] [tropical Pacific].—Clarke and Wagner, 1976:642 [?in part?] [vertical distribution].—Wisner, 1976:175–176 [description, distribution, figure].—Parin et al., 1977:122, 123, 165, 166 [in part] [western Pacific].—Nafpaktitis et al., 1977:204–206 [discussion, figure of holotype].—Clarke, 1978:

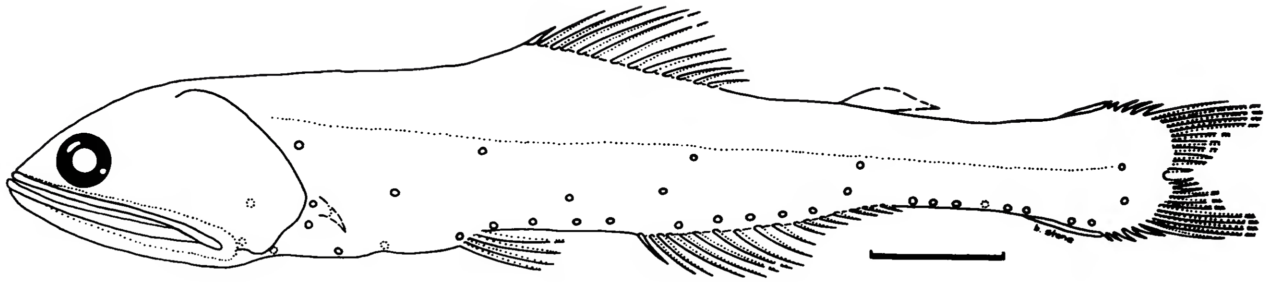

FIGURE 4.—*Nannobrachium nigrum* Gunther, 1887. Drawing of 81.5 mm specimen, USNM 298046, Pacific Ocean, 20°20′–20°30′N, 158°20′–158°30′W. (Scale bar=1 cm.)

499–502 [feeding patterns]; 1983a:327, 328, 332 [abundance estimates]; 1983b:205–206 [in part?] [sex ratio, size]; 1987:65 [central Pacific biogeography].—Chen, 1983:199 [?in part] [South China Sea] [fide J. Paxton].—Huang and Yang, 1983:234 [?in part] [Dongsha Islands, South China Sea] [fide J. Paxton].—Fujii, 1984:69, pl. 66-M [?in part] [description, distribution].—Cheng and Zheng, 1987, unpaginated [?in part] [China records] [fide J. Paxton].—Kailola, 1987:103 [?in part] [Solomon Sea].—Yang et al., 1996, unpaginated [?in part] [Nansha Islands, northeast South China Sea] [fide J. Paxton].

Lampanyctus (*Lampanyctus*) *niger*.—Fraser-Brunner, 1949:1085 [in part] [illustrated key].—Bekker, 1983:87–89, 198–200 [in part] [key, description, distribution].

Paralampanyctus niger.—Kotthaus, 1972a:14 [designated genotype].

Lampanyctus niger (Form B).—Clarke, 1973:416–418 [ecology north of Hawaii].

COMPARATIVE DIAGNOSIS.—*Nannobrachium nigrum* (Figure 4) can be distinguished from the other species of the Nigrum group and from *N. crypticum* in the Achirus group primarily by its gill-raker count (total 15–18) and number of tooth patches on the lower limb of the second gill arch (9–10) (both higher than in *N. gibbsi, N. indicum,* and *N. crypticum*). It can be distinguished from *N. atrum* by the lower number of AO photophores (10–13), anal-fin rays (14–18), lateral line organs (32–34), and vertebrae (33–37) and by having the SAO series farther back than in *N. atrum* (Table 3). It can be distinguished from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 31 specimens from the Pacific Ocean and are given in Tables A1–A8.

Proportions: Given in Table 2.

Fins: Origin of anal fin behind vertical from middle of base of dorsal fin. Pectoral fins not reaching beyond vertical from PO_3, with extremely weak and flexible rays. Adipose-fin base above end of anal-fin base, with adipose origin usually only slightly before end of anal-fin base.

Luminous Organs: PLO 1–3 photophore diameters below lateral line. PO_4 slightly higher than level of PVO_2 or on same level and above or slightly behind vertical from PO_3. VLO less than one photophore diameter below, frequently nearly touching, lateral line. SAO_2 closer to AOa_1 than to VO_4 or equidistant from VO_4 and AOa_1. SAO_3 approximately above AOa_1. AOa_1 slightly depressed and AOa_{1-2} interspace enlarged.

TABLE 2.—Measurements of *Nannobrachium nigrum* as thousandths of standard length with notes on allometry (for explanation see "Materials and Methods").

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	64.1	18.3	31 (24–84)		
Head depth	160	13	129–183	Y = 0.0 + 0.16x	0
Predorsal depth	137	14	110–157	Y = −0.7 + 0.15x	Slt +
Caudal peduncle depth	81	7	61–101	Y = −0.1 + 0.08x	0
Caudal peduncle length	231	13	203–257	Y = 0.2 + 0.23x	0
Postadipose length	223	15	192–259	Y = −1.2 + 0.24x	Sig +
Predorsal length	456	29	388–563	Y = 0.8 + 0.44x	0
Prepelvic length	407	15	385–442	Y = 1.5 + 0.38x	Sig −
Preanal length	569	28	538–695	Y = 1.4 + 0.55x	Slt −
Pelvic to anal length	150	10	127–167	Y = −0.5 + 0.16x	Slt +
Head length	273	15	245–303	Y = 0.3 + 0.27x	0
Upper-jaw length	206	9	194–229	Y = 0.6 + 0.20x	Sig −
Snout length	46	6	36–66	Y = 0.5 + 0.04x	Sig −
Eye diameter	53	7	43–75	Y = 0.0 + 0.05x	0
Supracaudal-gland length	63	7	47–76	Y = 0.1 + 0.06x	0
Infracaudal gland, solid length	86	13	50–116	Y = 0.3 + 0.08x	0
Infracaudal gland, extreme length	87	13	50–116	Y = 0.2 + 0.08x	0
Anal-fin base length	215	12	183–233	Y = −0.4 + 0.22x	Slt +
Dorsal-fin base length	180	10	155–197	Y = −0.3 + 0.19x	Slt +
Adipose-fin length	63	10	43–85	Y = −0.7 + 0.08x	Slt +

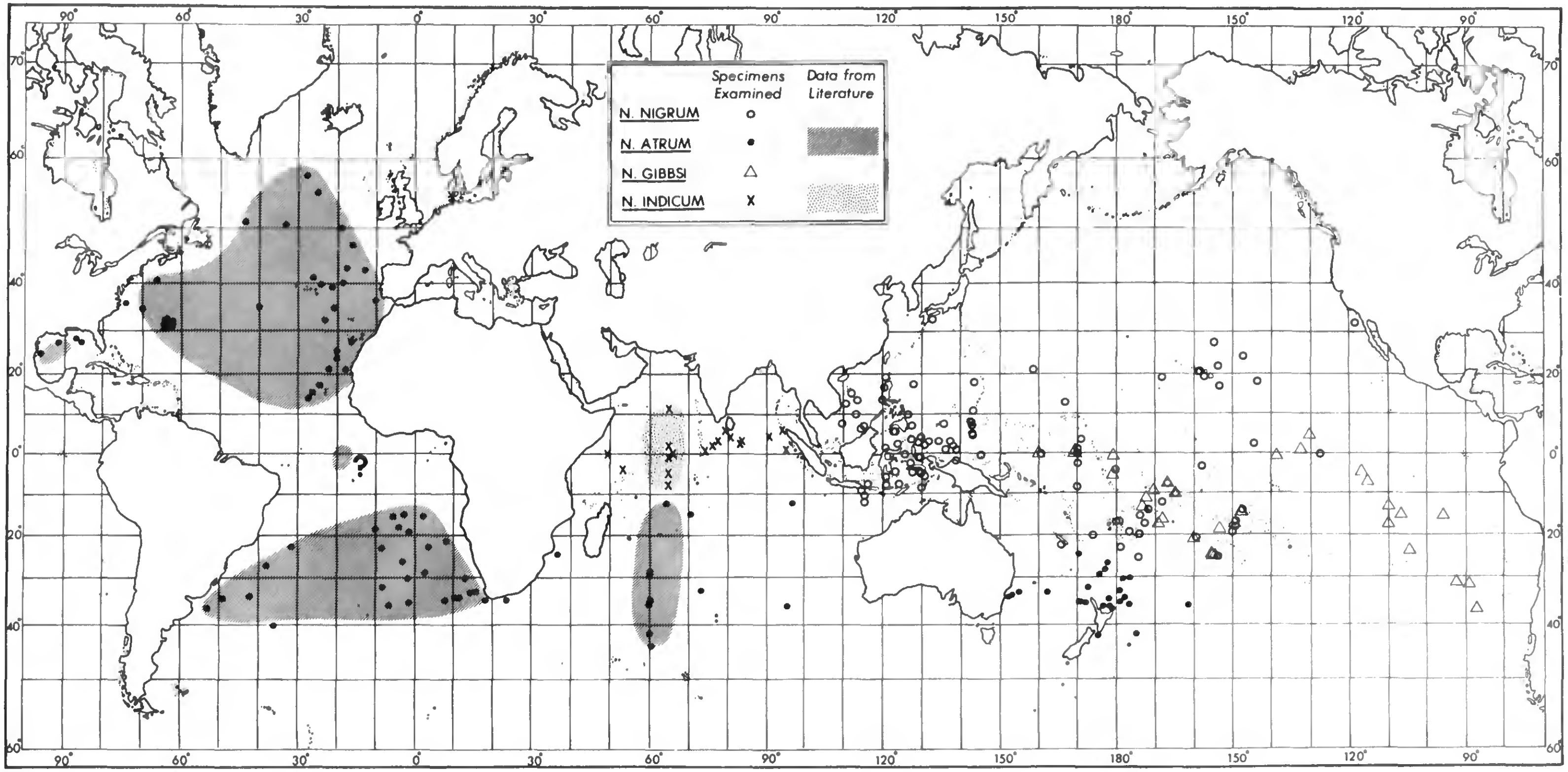

FIGURE 5.—Distributions and localities for material examined for species of the Nigrum Group.

TABLE 3.—Photophore position characters helpful to separate specimens of *N. atrum* from *N. nigrum*.

N. atrum	*N. nigrum*
VLO above pelvic-fin base or above origin of pelvic fin	VLO at end of pelvic-fin base or behind vertical from pelvic-fin base
PO_4 tends to be above PO_3 or slightly anterior to vertical from PO_3	PO_4 above or slightly posterior to vertical from PO_3
SAO_3 tends to be well before vertical from AOa_1	SAO_3 slightly before vertical from AOa_1 or on vertical (sometimes slightly behind)
SAO_2 tends to be closer to VO_4 than to AOa_1	SAO_2 tends to be equidistant or closer to AOa_1
Pol under adipose-fin base—usually under center of adipose-fin base	Pol under origin to center of adipose-fin base
Line through VLO and SAO_1 tends to pass through VO_3 or slightly behind it—usually well before VO_4	VLO-SAO_1 line passes through VO_4 or slightly behind it—as far as midway between VO_4 and AOa_1

AOp_1 at or behind end of anal-fin base. Prc well separated from AOp; Prc_{1-2} on horizontal line or Prc_2 slightly below level of Prc_1; Prc_{3-4} on vertical or nearly vertical line, well behind Prc_2. Supracaudal and infracaudal scales well developed, infrequently with a single, or even two (found once), separated luminous scales preceding the solid infracaudal gland. No secondary photophores found.

Size: The largest specimen examined was 111 mm. Previously the maximum size for this species was reported by Clarke (1973) as being less than 90 mm for a specimen given as *L. niger* (Form B) from north of Hawaii.

Material: 1,798 (13–111 mm) specimens were examined, including the holotype, 103 mm, BMNH 1887.12.7:219, collected south of the Philippines in 1875 by H.M.S. *Challenger.*

DISCUSSION.—It is now clear that, in many cases, both of the two new species in the Nigrum group were confused with *N. nigrum,* as were various other species of *Nannobrachium*. Table 3 can assist in distinguishing specimens of *N. nigrum* from *N. atrum,* which have frequently been confused in the literature.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium nigrum* is restricted to the tropical Pacific Ocean, primarily the western and central portions, and to the extreme eastern tropical Indian Ocean (Figure 5). No consistent differences in frequencies of meristic characters were found between specimens from the central and western Pacific and those from the eastern Indian Ocean; however, a few differences in photophore positions were noted. Specimens from north of Hawaii tended to have the VLO photophore behind a vertical from the end of the pelvic-fin base more often than did specimens from the western Pacific. In addition, those from around Hawaii more frequently had the SAO_2 equidistant between the VO_4 and AOa_1, whereas western Pacific specimens commonly had the SAO_2 closer to the AOa_1 than to the VO_4.

One 65 mm specimen from off New Caledonia (ORSTOM, collection number FAB 22) had such a high gill-raker count (6 + 14, left side, 5 + 14, right side + 10 tooth patches) that for some time it was seriously thought to represent another new species; however, photophore characters that could be checked were most similar to *N. nigrum,* although the SAO arrangement in this specimen somewhat resembled that of *N. atrum*. In addition, four specimens from various locations in the southwest Pacific proved to have a mixture of typical and high gill-raker counts (6+14, 1 count; 6+13, 2 counts; 5+13, 3 counts; 5+12, 2 counts). These extremely high counts were not entered in either Tables A1 or A3. Unfortunately, these specimens were in a poorer condition than the original 65 mm specimen. The interim conclusion, therefore, is to consider these specimens examples of intraspecific variability.

Fujii (1984:69) discussed the distribution of this species and gave a description based on two large specimens taken by midwater trawl near the Ogasawara Islands (~27°N, 143°E). Although his general discussion undoubtedly dealt with this species, the two above-mentioned specimens are almost certainly a different species because of their large size ("SL 19, 21 cm," which is twice as large as the largest specimens I examined), high dorsal-fin ray, anal-fin ray, and AO counts, Pol "well in advance of origin of adipose fin" (rather than below adipose-fin base, see Table 3), and lower VLO position relative to the lateral line (frequently nearly touching the lateral line in *N. nigrum*). The identification of the two specimens is problematical; the large size and the Pol and VLO positions suggest *N. lineatum* as a possibility, but the dorsal-fin ray, anal-fin ray, and AO counts are too low for the ranges I recorded for Indo-Pacific specimens of *N. lineatum* (Table A10).

***Nannobrachium atrum* (Tåning, 1928), new combination**

FIGURE 6, TABLES 4, 5

Lampanyctus ater Tåning, 1928:68 [original description, North Atlantic]; 1932, pl. 128 [description, figure].—Parr, 1928:88, 104–106 [key, western Atlantic, figured, description].—Nybelin, 1948:40 [eastern Atlantic].—Bolin, 1959:33 [discussion, distribution].—Bullis and Thompson, 1965:28 [northern Gulf of Mexico].—Bekker, 1967a:116 [equatorial Atlantic and Sargasso Sea].—Nafpaktitis and Nafpaktitis, 1969:44–45, fig. 53 [description, South Indian, lectotype figured, listed as holotype].—Quero, 1969:4 [northeastern Atlantic].—Badcock, 1970:1026 [discussion, depth distribution, Canary Islands].—Gibbs and Roper, 1971:129 [diurnal vertical migration].—Gibbs et al., 1971:43, 105–106 [key, vertical distribution near Bermuda, figure].—Hulley, 1972:225 [description]; 1981:188–190 [description, Atlantic

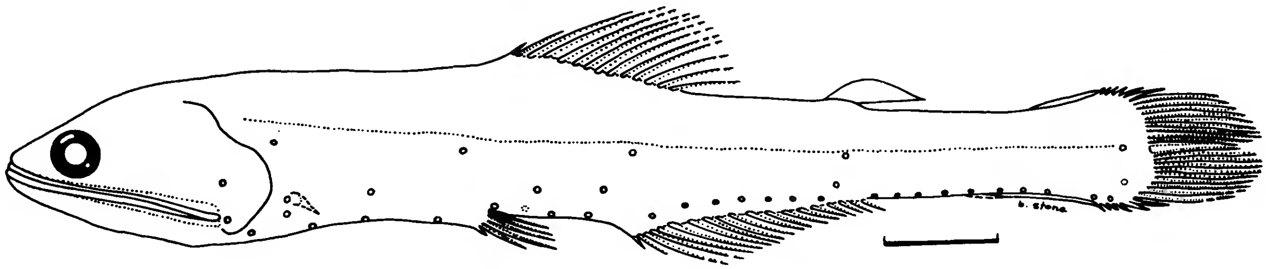

FIGURE 6.—*Nannobrachium atrum* (Tåning, 1928). Drawing of 102 mm specimen, USNM 298182, Atlantic Ocean, 32°16′N, 64°21′W. (Scale bar=1 cm.)

distribution]; 1984a:62, 79–82, figs. 12, 13 [in part] [description]; 1984b:461 [description, northeast Atlantic distribution]; 1986b:243 [zoogeography]; 1986c:307, fig. 86.75 [description, South Africa, figure]; 1990:163, 164 [figured, Southern Ocean].—Krefft and Bekker, 1973:187 [biology, synonymy].—Nafpaktitis, 1973:38–40 [redescription, designation of lectotype, figure].—Nielsen, 1974:38 [listing of lectotype].—Parin et al., 1974:106 [southwest Atlantic].—Bekker et al., 1975:314 [distribution, Caribbean Sea].—Badcock and Merrett, 1976:42 [30°N, 23°W].—Brooks, 1976:569, 575, 581 [swimbladder size].—Parin and Golovan, 1976:263 [off West Africa].—Wisner, 1976:175 [figure, discussion].—Nafpaktitis et al., 1977: 203–206, fig. 139 [description, distribution, figure].—Backus et al., 1977:267, 275, 277 [zoogeography].—Parin et al., 1978:175 [?in part?] [eastern tropical Atlantic].—Paxton, 1979:14 [lectotype].—Gushchin and Kukuev, 1981:37 [in part?] [53°N, 30°W].—Brandt, 1983:235, 240 [?in part?] [in warm core eddy east of Australia].—Moser et al., 1984:239 [relationships, larval description].—Hulley and Krefft, 1985:35, 40–46 [North Atlantic zoogeography].—Rubies, 1985:578, 584 [Valdivia Bank off Namibia, gill raker numbers].—Gartner et al., 1987:86, 88, 91, 95 [eastern Gulf of Mexico].—Kailola, 1987:103 [?in part] [Solomon Sea].—Karnella, 1987:52, 102–105, 149–159, 164 [ecology and biology near Bermuda].—Scott and Scott, 1988:221 [description, Nova Scotian shelf].—Paxton and Hanley, 1989:264 [Australian distribution].

Lampanyctus niger.—Norman, 1930:331 [in part] [Discovery Expeditions].—[Not Günther, 1887.]

Macrostoma atrum.—Fowler, 1939:1231 [repeats original description].

Lampanyctus (*Lampanyctus*) *ater*.—Fraser-Brunner, 1949:1086 [illustrated key].—Bekker, 1983:87, 88, 199, 200 [key, description, distribution].

?*Lampanyctus niger*.—Smith, 1949:123 [description, South Africa, figure] [determination fide Hulley, 1986c:307].—[Not Günther, 1887.]

Paralampanyctus ater.—Kotthaus, 1972b:29 [western tropical Indian].—Kotthaus, 1972a:14 [in part?] [eastern North Atlantic].

Lampanyctus niger-ater complex.—McGinnis, 1982:41–43, 66 [distribution south of 30°S, relationships, zoogeography].

COMPARATIVE DIAGNOSIS.—*Nannobrachium atrum* (Figure 6) can be distinguished from the other species of the Nigrum group and from *N. crypticum* in the Achirus group primarily by its gill raker count (total 16–18) and number of lower limb tooth patches on the second gill arch (7.5–10) (both higher than in *N. gibbsi, N. indicum,* and *N. crypticum*) and by the number of its AO photophores (12–15), lateral line organs (36–39), and vertebrae (36–39) (all higher than in *N. nigrum, N. indicum,* and *N. crypticum*) (Table A1). In addition, the SAO series is farther forward in *N. atrum* than it is in *N. nigrum*. It can be distinguished from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 56 specimens from the North and South Atlantic, Indian, and South Pacific oceans and are given in Tables A1–A8.

Proportions: Given in Table 4.

TABLE 4.—Measurements of *Nannobrachium atrum* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	80.1	24.2	35 (33.6–124.0)		
Head depth	143	9	123–163	Y = 0.5 + 0.14x	Slt –
Predorsal depth	135	11	112–163	Y = –1.0 + 0.15x	Sig +
Caudal peduncle depth	76	5	61–84	Y = –0.3 + 0.08x	Slt +
Caudal peduncle length	216	13	182–266	Y = 0.2 + 0.21x	0
Postadipose length	219	9	203–240	Y = –0.1 + 0.22x	0
Predorsal length	451	21	393–519	Y = 2.1 + 0.42x	Sig –
Prepelvic length	403	17	351–452	Y = 2.0 + 0.38x	Sig –
Preanal length	552	25	447–592	Y = 2.3 + 0.52x	Slt –
Pelvic to anal length	147	11	128–185	Y = –0.5 + 0.16x	Slt +
Head length	253	13	234–281	Y = 1.3 + 0.24x	Sig –
Upper-jaw length	194	8	179–214	Y = 1.2 + 0.18x	Sig –
Snout length	40	5	31–54	Y = 0.5 + 0.03x	Sig –
Eye diameter	48	6	36–60	Y = –0.0 + 0.05x	0
Supracaudal-gland length	66	9	53–88	Y = 1.0 + 0.05x	Sig –
Infracaudal gland, solid length	98	12	69–123	Y = 0.5 + 0.09x	Slt –
Infracaudal gland, extreme length	106	17	69–143	Y = 1.0 + 0.09x	Slt –
Anal-fin base length	227	16	159–256	Y = –0.9 + 0.24x	Slt +
Dorsal-fin base length	163	9	141–177	Y = 0.0 + 0.16x	0
Adipose-fin length	60	12	28–82	Y = 0.9 + 0.05x	Slt –

TABLE 5.—*Nannobrachium atrum*, comparison of selected meristics of specimens from the North and South Atlantic, Indian, and South Pacific oceans.

Area	AO photophores																								
	Anterior			Posterior			Total				Dorsal-fin rays					Anal-fin rays					Infracaudal-gland scales				
	6	7	8	6	7	8	13	14	15	16	13	14	15	16	17	17	18	19	20	21	i	4	5	6	7
N. Atlantic																									
West	16	20		6	22	4	18	10	2		2	13	3			1	6	11	1		3		1	8	7
East	14	20		2	23	9	10	20	2		2	7	9		1	4	5	8	1		6	1	5	6	4
S. Atlantic	10	29	3		21	21	2	25	14	1		7	13	1			4	14	3		9	5	7	9	
Indian	2	24	2	4	22	2	2?	24	2			2	6	5			7	5	1	1	9	8	5	1	
S. Pacific	11	33	2	2	11	5		16	2		2	14	12			1	5	15	5	1	1	3	13	1	

Fins: Origin of anal fin behind vertical from middle of base of dorsal fin. Pectoral fin barely reaching vertical from PO_3, its rays weak, flexible. Base of adipose fin above end of anal-fin base, its origin well before end of anal-fin base.

Luminous Organs: PLO 1–3 times its diameter below lateral line. PO_4 slightly higher than level of PVO_2 and above PO_3 or slightly anterior to vertical from PO_3. VLO less than one photophore diameter below, frequently nearly touching, lateral line. SAO_2 always behind vertical from VO_4 but usually closer to VO_4 than to AOa_1. SAO_3 before vertical from AOa_1. AOa_1 slightly depressed and AOa_{1-2} interspace enlarged. AOp_1 at or behind end of anal-fin base. Prc well separated from AOp; Prc_{1-2} on horizontal line; Prc_{3-4} on or nearly on vertical line, well behind Prc_2. Supracaudal and infracaudal luminous scales well developed, often with single separated scale preceding infracaudal gland. No secondary photophores found.

Size: The largest specimen examined was 133 mm from off New Zealand, whereas the largest specimen examined from the Atlantic was 119 mm, taken by the *Walther Herwig* in the North Atlantic. Nafpaktitis et al. (1977) suggested that this species may attain a maximum size of 140 mm. Hulley (pers. comm., 1980) reports a size of 129 mm and suggests sexual maturity at about 90–100 mm. The largest specimen that he examined from South Atlantic *Walther Herwig* material was 120.2 mm (Hulley, 1981).

Material: 741 (20–133 mm) specimens were examined, including the lectotype, 89 mm, ZMUC P2330209, *Dana* sta 1152 I, 30°17'N, 20°44'W, 22 October 1921.

DISCUSSION.—Although the distinctness of *N. atrum* from *N. nigrum* has been questioned in the past (Bolin, 1959; Nafpaktitis and Nafpaktitis, 1969; Nafpaktitis, 1973; Wisner, 1976), there is no doubt that they are distinct. Individual specimens, however, are not always easily separable, especially if damaged or distorted in preservation, as is frequently the case. The number of lateral line pores is an excellent diagnostic character, as are the number of vertebrae and, to a lesser extent, anal-fin rays. Table 3 can help identify specimens, especially those that are well preserved and not distorted.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium atrum*, the most widely distributed species of *Nannobrachium*, is found in the South Pacific and Indian oceans and in the Atlantic Ocean, where it is bipolar and absent from the central area (Figure 5). Nafpaktitis et al. (1977) reported *N. atrum* to have a daytime maximum abundance in the North Atlantic at 700–800 m and to be as shallow as 100 m at night. Karnella (1987) reported greater depth ranges for Ocean Acre material, with a late spring maximum at 1051–1100 m.

Despite the broad distribution, no differences were found in absolute numbers or frequencies of gill rakers on the first arch, lower limb tooth patches of the second arch, or body shape that would show up as proportional differences. Only slight differences were found in the frequencies of AOp and total AO photophore counts, dorsal- and anal-fin ray counts, and numbers of infracaudal luminous gland scales (Table 5). Southwest Pacific specimens tended to have the VLO rather far posteriad, which was the only photophore positional difference. No differences were noted in specimens from the eastern and western North Atlantic and the Gulf of Mexico.

Two specimens, one from the Indian Ocean and one from the Pacific, with exceptionally high numbers of anal-fin rays (21), deserve special comment. The Indian Ocean specimen (LACM 31332-4, 69 mm) was collected by the *Anton Bruun* and, thus, was part of the material described by Nafpaktitis and Nafpaktitis (1969:44). In addition to the high number of anal-fin rays, it is atypical both in the lower-limb tooth patch count on the second gill arch (10 on both sides versus the common number of 9 or rarely 10 on one side in typical *N. atrum*) and in its count of 8 AOa plus 6 AOp (both sides). A further mystery is the origin of this specimen. The bottle label lists only one specimen (86 mm) instead of the two it actually contains. Nafpaktitis and Nafpaktitis (1969:44) listed the material of *N. atrum* that they examined from the Indian Ocean and included the 86 mm specimen as the only one from that collection (label number 7133). They recorded neither the 69 mm specimen nor the atypical AO count of 8+6 in their table 9, so it appears that they did not see it.

The Pacific Ocean specimen with 21 anal-fin rays (ZMUC, *Dana* 3631 III, 96.5 mm) is from 35°40'S, 176°40'E, which is north of New Zealand. Besides the anal-ray count, it has two abnormalities: a gill raker count of 5+11 on the right side (the left side is the typical *N. atrum* count of 5+12) and the SAO_2 slightly far back in position so that it is closer to the AOa_1 than to the VO_4 (as is typical in *N. nigrum*). Determination of the status of these specimens requires study of more material.

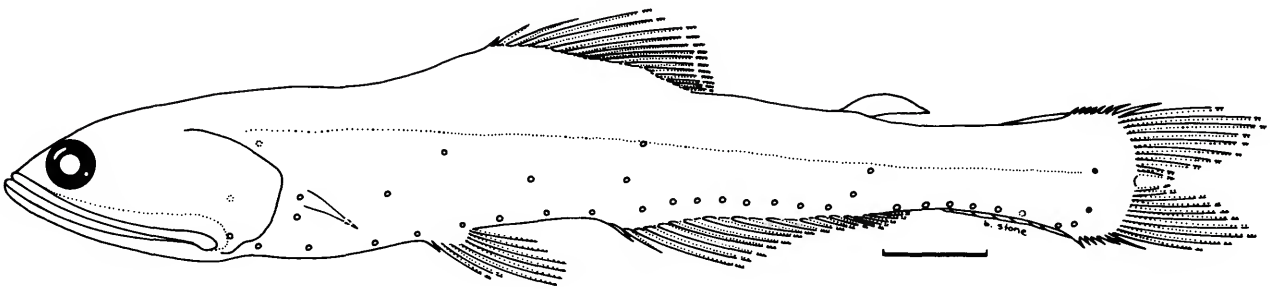

FIGURE 7.—*Nannobrachium gibbsi*, new species. Drawing of holotype, 107.5 mm, ZMUC, Dana sta 3570 I, Pacific Ocean, 14°01'S, 147°51'W. (Scale bar=1 cm.)

One other atypical and damaged specimen is in the collections of the South African Museum (SAM 23712), and it came from the South Atlantic. It appears to be a typical specimen of *N. atrum*, except that the intact left VLO is far below the lateral line (about 4 photophore diameters). The pectoral-fin base is narrow, but the fins are badly broken, so it is impossible to estimate their original length, but the rays appear to be stiff enough that they resemble some specimens of the Regale group. In all other characters, considering the damaged condition, it is a fairly typical specimen of *N. atrum*, except for a gill raker count on the right side of 5+13 (but with a more typical 5+12 on the left side). Again, determination of status awaits further study.

Nannobrachium gibbsi, new species

FIGURE 7, TABLE 6

Lampanyctus achirus.—Craddock and Mead, 1970:28 [in part] [southeast Pacific].—[Not Andriashev, 1962.]

Lampanyctus (*Lampanyctus*) *niger*.—Bekker, 1983:87–89, 198–200 [?in part] [key, description, distribution].—[Not Günther, 1887.]

TYPE SPECIMENS.—*Holotype:* Female 107.5 mm; ZMUC *Dana* sta 3570 I, 14°01'S, 147°51'W, 10 July 1928.

Paratypes: SIO 72-303, 1 (122 mm); SIO 72-306, 2 (23–54 mm); SIO 72-312, 2 (62–62 mm); SIO 72-313, 3 (31–111 mm); SIO 72-316, 2 (29–29 mm); SIO 72-320, 1 (117 mm); SIO 75-631, 1 (32 mm); UBC 13, 1 (93 mm); USNM uncat. (16°S, 168°04'W, 7 Dec 1967), 1 (89 mm); USNM 298168, 1 (93 mm); USNM 303311, 5 (38–59.5 mm); ZMUC 35-761, 1 (104 mm); ZMUC 35-858, 2 (98–99 mm); ZMUC 35-862, 1 (47 mm); ZMUC 35-879, 1 (74 mm); ZMUC 35-881, 1 (81 mm).

COMPARATIVE DIAGNOSIS.—*Nannobrachium gibbsi* (Figure 7) can be distinguished from the other species of the Nigrum group primarily by its gill raker count (total 13–15) and number of tooth patches on the lower limb of the second gill arch (7–8) (both lower than in *N. atrum* and *N. nigrum*); by the number of AO photophores (13–14), anal-fin rays (17–20), and vertebrae (36–38) (all higher than in *N. nigrum* and *N. indicum*); and by the number of lateral line organs (33–35) (lower than in *N. atrum* but higher than in *N. indicum*) (Table A1). It can be distinguished from all other species of *Nannobrachium* by the combination of characters in Table 1 and can be further distinguished from *N. crypticum* in the Achirus group by its higher number of AO photophores, anal-fin rays, and vertebrae (Table A1).

DESCRIPTION.—Counts are based on up to 62 specimens from the Pacific Ocean and are given in Tables A1–A8. Counts for the holotype are D 15, A 19, P_1 13?, 14?, GR 4+10, tooth patches 8, AO 8+6, SC/IC 4/6, LL 35?, V 16+21.

Proportions: Given in Table 6. Holotype measurements (in mm) as follows: SL 107.5, HD 16.0, PDD 16.8, CPD 8.9, CPL 21.4, PADL 23.0, PDL 50.4, PPL 42.5, PANL 59.2, PAL 17.1, HL 28.6, UJL broken, SOL 4.8, ED 5.6, SGL 6.5, IGS 12.4, IGEL 12.4, AFB, 26.0, DFB 19.6, AF 10.2.

Fins: Origin of anal fin behind vertical from middle of base of dorsal fin. Pectoral fins with weak and flexible rays, not reaching beyond vertical from PO_3, except in small specimens where they may reach beyond PO_4. Adipose-fin base above end of anal-fin base, with adipose origin well in advance of end of anal-fin base.

Luminous Organs: PLO 1–2 photophore diameters below lateral line (approximately 2 diameters below in holotype). PO_4 slightly below or approximately on level of PVO_2 and above or slightly behind a vertical from PO_3 (PO_4 on level of PVO_2 and behind vertical from PO_3 in holotype). PVO_2 before upper edge or center of pectoral-fin base (PVO_2 before upper edge in holotype); PVO_{1-2} interspace ¼–⅓ of PVO_2–PLO distance (approximately ¼ in holotype). VLO 1–2 photophore diameters below lateral line (two diameters below in holotype). SAO_2 above but variable in relation to vertical from AOa_1 (SAO_2 before vertical from AOa_1 in holotype). AOa_1 not notably depressed; AOa_{1-2} interspace slightly enlarged. AOp_1 behind end of anal-fin base. Prc well separated from AOp; Prc_{1-2} on horizontal line; Prc_{3-4} on or nearly on vertical line, well behind Prc_2 although Prc_3 occasionally forward as much as a full photophore diameter before vertical from anterior margin of Prc_4 (Prc_3 on vertical through anterior margin of Prc_4 in holotype). Supracaudal and infracaudal luminous glands well developed, infrequently with

TABLE 6.—Measurements of *Nannobrachium gibbsi* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	77.8	31.1	25 (31.2–122.0)		
Head depth	143	11	126–177	Y = 0.4 + 0.14x	Slt -
Predorsal depth	132	18	102–167	Y = –0.3 + 0.15x	Slt +
Caudal peduncle depth	79	6	71–97	Y = –0.4 + 0.09x	Slt +
Caudal peduncle length	221	11	202–240	Y = 0.4 + 0.22x	Slt -
Postadipose length	217	12	191–244	Y = –0.5 + 0.23x	Slt +
Predorsal length	459	25	377–497	Y = 2.0 + 0.43x	Slt -
Prepelvic length	417	15	392–467	Y = 0.9 + 0.40x	Slt -
Preanal length	566	34	460–629	Y = 2.8 + 0.53x	Slt -
Pelvic to anal length	151	9	133–170	Y = 0.4 + 0.15x	Slt -
Head length	262	20	232–309	Y = 1.1 + 0.25x	Slt -
Upper-jaw length	204	14	179–242	Y = 1.1 + 0.19x	Slt -
Snout length	45	6	31–56	Y = 0.7 + 0.03x	Sig -
Eye diameter	45	5	32–53	Y = –0.4 + 0.05x	Slt +
Supracaudal-gland length	51	7	38–66	Y = 0.2 + 0.05x	0
Infracaudal gland, solid length	86	11	59–108	Y = 0.2 + 0.08x	0
Infracaudal gland, extreme length	87	12	59–111	Y = –0.0 + 0.09x	0
Anal-fin base length	218	14	192–258	Y = –0.8 + 0.23x	Slt +
Dorsal-fin base length	161	12	140–199	Y = –0.9 + 0.18x	Slt +
Adipose-fin length	58	15	30–82	Y = –0.5 + 0.07x	Slt +

single separated luminous scale preceding solid infracaudal gland. No secondary photophores found.

Size: The largest known specimen is 122 mm.

Material: 190 (17–120 mm) specimens not designated as type material were examined.

DISCUSSION.—This species has been confused with both *N. nigrum* and *N. atrum,* which have nearly identical photophore patterns. They differ primarily in number of gill rakers on the first arch and number of tooth patches on the lower limb of the second gill arch. Although the differences are rather slight, they are consistent; however, fresh or freshly preserved specimens of *N. gibbsi* apparently look different from similar specimens of *N. nigrum*. When both species were collected together in the same midwater trawl sample aboard the R.V. *Eltanin* during a transect of the central Pacific, R.H. Gibbs, Jr., was able to recognize them as distinct, although he did not know which, if either, represented the true *N. nigrum* (pers. comm., 1977).

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium gibbsi* occurs mainly in the tropical Pacific (Figure 5). Examination of material from the extreme eastern and western ends of its range revealed no consistent variation.

ETYMOLOGY.—It is a pleasure to name this species after the late Dr. Robert H. Gibbs, Jr., of the Smithsonian Institution, in honor of his many contributions to our understanding of open-ocean midwater ichthyology. It is particularly appropriate in this case because he was first, as far as I am aware, to recognize the distinctness of specimens of this species.

Nannobrachium indicum, new species

FIGURE 8, TABLE 7

Lampanyctus sp.—Norman, 1939:29 [in part] [Gulf of Aden, Arabian Sea].

Lampanyctus sp. I.—Nafpaktitis and Nafpaktitis, 1969:42–43 [description and distribution].

Lampanyctus sp. II.—Nafpaktitis and Nafpaktitis, 1969:43–44, fig. 52 [description, figure].

Paralampanyctus sp.—Kotthaus, 1972b:29 [?in part] [southern tropical Indian Ocean].

Lampanyctus (*Lampanyctus*) *niger*.—Bekker, 1983:87–89, 198–200 [in part] [key, description, distribution].—[Not Fraser-Brunner, 1949.]

Lampanyctus sp. A.—Hulley, 1984a:63, 83–84, fig. 14 [description]; 1986c: 309–310, figs. 86, 88 [description, figure, off South Africa].

TYPE SPECIMENS.—*Holotype:* Female, 67 mm, ZMUC *Dana* sta 3912 II, 6°52′N, 79°30′E, 24 February 1929.

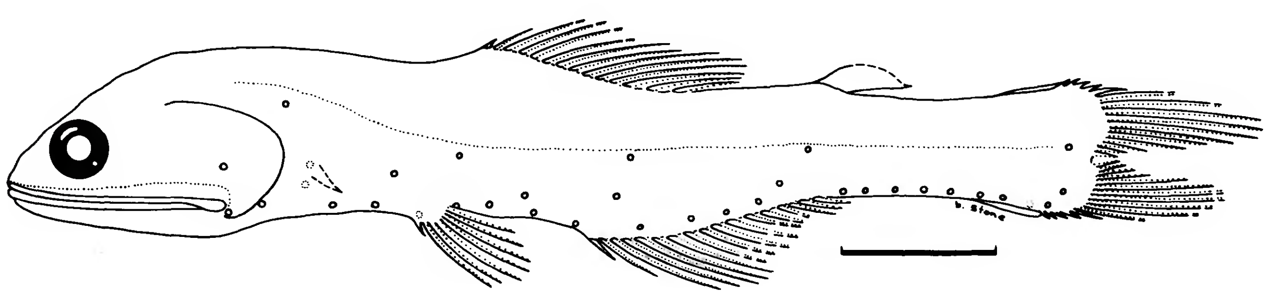

FIGURE 8.—*Nannobrachium indicum,* new species. Drawing of holotype, 67 mm, ZMUC, Dana sta 3912 II, Indian Ocean, 6°52′N, 79°30′E. (Scale bar = 1 cm.)

TABLE 7.—Measurements of *Nannobrachium indicum* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	60.2	12.8	29 (26–79)		
Head depth	160	12	121–192	Y = 0.7 + 0.15x	Slt –
Predorsal depth	148	16	121–177	Y = –0.9 + 0.16x	Slt +
Caudal peduncle depth	85	8	67–99	Y = –0.8 + 0.10x	Slt +
Caudal peduncle length	215	14	174–239	Y = 1.1 + 0.20x	Slt –
Postadipose length	221	15	181–246	Y = 0.5 + 0.21x	0
Predorsal length	463	18	407–493	Y = 1.1 + 0.45x	Slt –
Prepelvic length	409	17	356–442	Y = 0.9 + 0.39x	Slt –
Preanal length	560	18	497–600	Y = 0.8 + 0.55x	Slt –
Pelvic to anal length	139	11	119–162	Y = –0.2 + 0.14x	0
Head length	274	15	229–303	Y = 1.6 + 0.25x	Slt –
Upper-jaw length	204	13	175–235	Y = 1.5 + 0.18x	Sig –
Snout length	49	5	44–65	Y = 0.7 + 0.04x	Sig –
Eye diameter	56	7	43–70	Y = 0.5 + 0.05x	Slt –
Supracaudal-gland length	56	9	41–79	Y = 0.7 + 0.04x	Slt –
Infracaudal gland, solid length	72	8	56–96	Y = 0.5 + 0.06x	Slt –
Infracaudal gland, extreme length	74	12	56–114	Y = 1.0 + 0.06x	Slt –
Anal-fin base length	230	13	188–247	Y = –0.5 + 0.24x	0
Dorsal-fin base length	173	14	143–212	Y = –0.8 + 0.19x	Slt +
Adipose-fin length	74	11	51–89	Y = –0.8 + 0.09x	Slt +

Paratypes: LACM 31-3411, 1 (50 mm); LACM 31-3451, 1 (56 mm); LACM 31-3461, 5 (26–65 mm); LACM 31-3551, 2 (63–67 mm); LACM 31-3582, 1 (37 mm); LACM 31-3612/7217, 3 (59–61 mm); LACM 31-3661, 2 (54–55 mm); LACM 31-3892, 1 (58 mm); USNM 268397, 3 (60–69 mm); ZMUC 35-776, 1 (104 mm); ZMUC 39-12, 18 (44–78 mm).

COMPARATIVE DIAGNOSIS.—*Nannobrachium indicum* (Figure 8) can be distinguished from the other species of the Nigrum group and from *N. crypticum* in the Achirus group primarily by its gill raker count (total 14–17) (typically higher than in *N. crypticum* and *N. gibbsi* but lower than in *N. atrum* and *N. nigrum*) (Table A1) and by the number of luminous caudal-gland scales (1–3 / o–i+2–5), AO photophores (9–12), lateral line organs (29–32), and vertebrae (32–34) (typically lower than in all other species of *Nannobrachium,* except the same number of infracaudal luminous gland scales and vertebrae as in *N. idostigma*). In addition, it can be distinguished from all other *Nannobrachium* species by the combinations of characters in Table 1.

DESCRIPTION.—Counts are based on up to 29 specimens from the Indian Ocean and are given in Tables A1–A8. Counts for the holotype are D 14, A 17, P_1 ?, GR 4+11, tooth patches 8, AO 4+7, SC/IC 3/3, LL 32, V15+18.

Proportions: Given in Table 7. Holotype measurements (in mm) as follows: SL 67, HD 11.4, PDD 10.0, CPD 6.6, CPL 14.6, PADL 13.6, PDL 31.4, PPL 27.4, PANL 40.3, PAL 10.9, HL 19.7 (damaged), UJL 14.3, SOL 4.1, ED 4.2 (damaged), SGL 3.9, IGS 5.4, IGEL 5.4, AFB 5.6, DFB 11.9, AF 6.7.

Fins: Origin of anal fin under middle of base of dorsal fin. Pectoral fin barely reaching vertical from VO_3, its rays very weak and flexible. Base of adipose fin above end of anal-fin base, with adipose origin well in advance of end of anal-fin base.

Luminous Organs: PLO 1–2 photophore diameters below lateral line (about 2 diameters below in holotype). PO_4 slightly higher than level of PVO_2 and above or behind vertical from PO_3 (PO_4 slightly behind vertical from PO_3 in holotype). VLO touching, or nearly touching, lateral line (VLO nearly touching lateral line in holotype). SAO_2 position midway between VO_4 and AOa_1 variable, but frequently closer to AOa_1 (SAO_2 closer to AOa_1 in holotype). SAO_3 variably over AOa_1 (SAO_3 before vertical from AOa_1 in holotype). AOa_1 slightly depressed, and AO_{1-2} interspace enlarged. AOp_1 behind end of anal-fin base. Prc well separated from AOp; Prc_{1-2} on an approximately horizontal line; Prc_{3-4} on a vertical or nearly vertical line, well behind Prc_2. Supracaudal and infracaudal luminous scales well developed; infrequently with a single separated scale preceding the infracaudal gland. No secondary photophores found.

Size: *Nannobrachium indicum* is a small-bodied species of *Nannobrachium*, probably reaching a maximum size just over 100 mm.

Material: 57 (26–80 mm) specimens, excluding type material, were examined.

DISCUSSION.—Nafpaktitis and Nafpaktitis (1969) recognized this as two possible undescribed species, which they listed as *Lampanyctus* sp. I and *Lampanyctus* sp. II, but they did not describe them because of taxonomic uncertainty among the short-pectoral-finned species of *Lampanyctus*. Examination of their specimens, as well as additional material, shows that both *L.* sp. I and *L.* sp. II are *N. indicum,* representing examples of intraspecific variability.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium indicum* is the only species of *Nannobrachium* evidently restricted to the Indian Ocean, where it is limited to the Equatorial Region (Figure 5). No geographic variation was noted in material examined from the extreme eastern and western ends of the range. The two specimens from off the east coast of South Africa, which Hulley (1984a, fig. 14) reported as *Lampanyctus* sp. A, appear to be fairly typical specimens of this species, although they were captured far to the south of any other specimens I examined. They may represent expatriates carried south by the Agulhas current system.

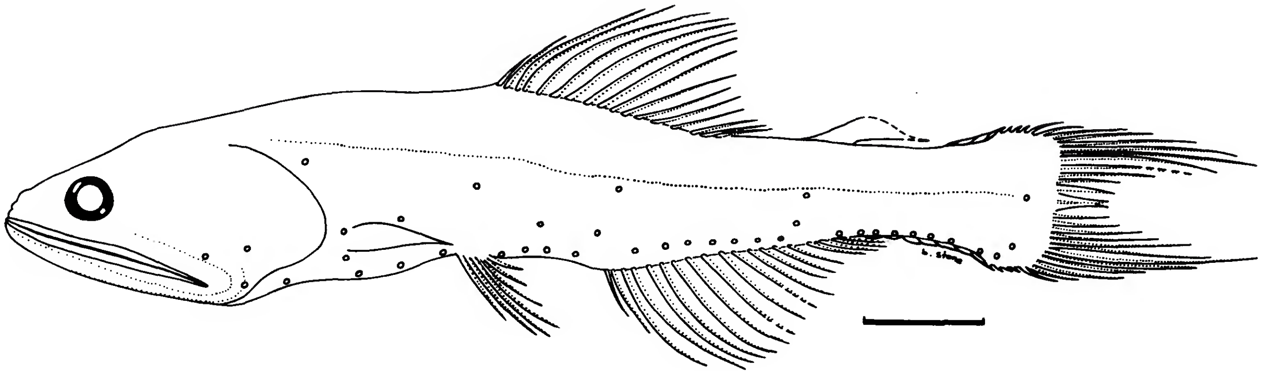

FIGURE 9.—*Nannobrachium regale* (Gilbert, 1891). Drawing of 81 mm specimen, USNM 108161. Specimen is a paratype of *L. micropunctatus* Chapman, Pacific Ocean, 56°06'N, 152°09'W. (Scale bar=1 cm.)

ETYMOLOGY.—The name is an adjective referring to the Indian Ocean.

The Regale Group

Two unique characters distinguish the species of this group: low position of the VLO on the side of the body and relatively robust pectoral-fin development. At a distance of three photophore diameters or more below the lateral line, the VLO is remote from the lateral line, always further than the PLO is from the lateral line. The pectoral fins are relatively strong and well developed, usually reaching beyond the pelvic-fin insertion, with moderately thick but rather flexible rays. Pectoral fins are better developed in this group than in any other *Nannobrachium* group. They are poorly developed, however, compared to the pectoral-fin development in most species of *Lampanyctus,* and accurate counts of pectoral-fin rays can only be made with difficulty. The species in the other *Nannobrachium* groups either lack pectorals or have pectorals with short, thick, and stiff rays, or they have pectorals with short, thin, and flexible rays.

Another character shared by species in the Regale group, but not unique to them, is the position of Prc_3 below Prc_4 but on a vertical from the anterior edge of Prc_4.

These and other characters are compared in Table 1 for all the species groups of *Nannobrachium*.

The Regale group contains five species: *N. regale* (Gilbert, 1891), *N. ritteri* (Gilbert, 1915), *N. idostigma* (Parr, 1931), *N. fernae* (Wisner, 1971), and *N. bristori,* new species. Modal characters of all species in the Regale group are listed in Table A9.

Nannobrachium regale (Gilbert, 1891)

FIGURE 9, TABLE 8

Myctophum regale Gilbert, 1891:544 [original description].—Böhlke, 1953:21 [paratype originally at Stanford University, now in California Academy of Sciences].—Paxton, 1979:13 [holotype and paratypes].

Nannobrachium regale Goode and Bean, 1896:512 [original description cited].—Jordan and Evermann, 1896a:300 [original description cited]; 1896b:563 [key, description].—Jordan et al., 1930:168 [original description cited].

Myctophum (Lampanyctus) regale Brauer, 1904:396 [?in part] [California]; 1906:385 [?in part] [California].

Lampanyctus regalis.—Parr, 1928:89 [synonymy in key]; 1929:24–25 [discussion, holotype figured].—Barnhart, 1936:21 [description, San Diego to Monterey, California].—Bolin, 1939:144–147 [description, comparison, figures].—Follett, 1952:412 [off central California].—Rass, 1955:328 [not seen, fide Pearcy et al., 1979; Kurile-Kamchatka area, Bering Sea]; 1968: 233, 237, 241 [distributional analysis].—Aron, 1959:414 [North Pacific, west of Aleutians].—Kulikova, 1960:34–39 [distribution, description].—Parin, 1961:262 [distribution].—Bekker, 1964:474 [distribution]; 1967b:179 [distribution].—Berry and Perkins, 1966:662 [eastern Pacific].—Paxton 1967a:432 [vertical distribution off southern California].—Fitch and Lavenberg, 1968:44 [California waters].—Ahlstrom, 1969:42 [California Current larvae].—Fitch, 1969:7 [otoliths].—Bailey et al., 1970:19 [common name—Pinpoint lampfish].—Ebeling et al., 1970b:12–15 [ecology off southern California].—Makushok, 1970:541 [Kurile-Kamchatka Trench].—Butler and Pearcy, 1972:1145–1149 [swimbladder].—Fedorov, 1973a:3; 1973b:42 [neither seen, fide Pearcy et al., 1979] [Bering Sea].—Briggs, 1974:316 [north boreal distribution].—Brown, 1974:28 [ecology off southern California].—Chen and Ebeling, 1974:841, 845, fig. 12 [karyotype].—Moser and Ahlstrom, 1974:406–407 [larvae figured].—Wisner, 1976:173 [description, distribution, figure].—Richardson and Pearcy, 1977:129 [larvae off Yaquina Bay, Oregon].—Frost and McCrone, 1978:755 [North Pacific, stations P and Q].—Childress and Somero, 1979:276 [enzymatic activities].—Lancraft and Robison, 1979:714 [net feeding].—Pearcy et al., 1979:129, 131 [Bering Sea, literature records].— Childress et al., 1980:28–33 [growth and energy relations].—Robins et al., 1980:21 [common name—Pinpoint lampfish].—Novikov et al., 1981:33 [Emperor Seamount Ridge].—Parin and Fedorov, 1981:74–78 [zoogeography].—Neighbors and Nafpaktitis, 1982:208–210, 212–213 [lipid composition].—Willis and Pearcy, 1982:92–93 [vertical distribution off Oregon].—Amaoka et al., 1983 [not seen, fide, H.G. Moser] [description, occurrence in northwestern Pacific].—Sawada, 1983:90–91, 236–237 [Japanese], 185, 318 [English], pls. 43, 126 [description, distribution, distinguished from *L. ritteri*].—Moser et al., 1984:238–239, fig. 124c [larva figured, relationships].—Fujii, 1984:69, pl. 66-L [description, distribution].—Stein, 1985:190 [large net capture].—Willis et al., 1988:122 [distribution].—Matarese et al., 1989, unpaginated [not seen, fide H.G. Moser] [larvae, occurrence in northeastern Pacific].—Moser et al., 1993:162–163 [distribution and abundance in California Current region].—Paxton et al., 1995:1315 [listed; not seen, fide J. Paxton].

Lampanyctus micropunctatus Chapman, 1939:527–530 [original description, northeast Pacific].—Fraser-Brunner, 1949:1085 [synonymized with *L. regalis*].—Böhlke 1953:19–20 [paratype originally at Stanford University, now at California Academy of Sciences].—Paxton, 1979:13 [holotype and paratypes].

TABLE 8.—Measurements of *Nannobrachium regale* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	129.3	37.3	25 (50–183)		
Head depth	170	11	152–194	Y = –0.2 + 0.17x	0
Predorsal depth	183	14	158–217	Y = –1.7 + 0.20x	Slt +
Caudal peduncle depth	100	8	81–114	Y = –0.9 + 0.11x	Slt +
Caudal peduncle length	207	12	183–228	Y = –1.6 + 0.22x	Slt +
Postadipose length	211	12	191–243	Y = –2.0 + 0.23x	Slt +
Predorsal length	463	17	433–500	Y = 3.2 + 0.44x	Sig –
Prepelvic length	432	20	396–483	Y = 2.5 + 0.41x	Slt –
Preanal length	584	18	557–628	Y = 3.2 + 0.56x	Sig –
Pelvic to anal length	147	14	119–178	Y = 0.7 + 0.14x	0
Head length	296	11	268–317	Y = 1.7 + 0.28x	Slt –
Upper-jaw length	212	10	194–238	Y = 2.1 + 0.19x	Sig –
Snout length	54	5	45–64	Y = 0.9 + 0.05x	Sig –
Eye diameter	51	4	44–58	Y = 0.4 + 0.05x	Slt –
Supracaudal-gland length	65	9	48–77	Y = –0.4 + 0.07x	0
Infracaudal gland, solid length	107	17	81–138	Y = –1.2 + 0.12x	0
Infracaudal gland, extreme length	117	19	81–151	Y = –0.2 + 0.12x	0
Anal-fin base length	218	14	197–244	Y = –2.5 + 0.24x	Slt +
Dorsal-fin base length	181	10	161–199	Y = –0.5 + 0.19x	0
Adipose-fin length	42	30	6–104	Y = 7.7 + –0.02x	Sig –

Lampanyctus (Lampanyctus) regalis.—Fraser-Brunner, 1949:1058 [illustrated key].—Bekker, 1983:84, 85, 194, 196 [key, description, distribution].

Nannobrachium regalis.—Moser and Ahlstrom, 1996:422–423 [early life history and larvae illustrated].

COMPARATIVE DIAGNOSIS.—*Nannobrachium regale* (Figure 9) can be distinguished from all other species in the Regale group, except *N. ritteri*, by its lower number of gill rakers (total 13–15), higher number of dorsal-fin rays (15–16), and forward position of the SAO photophores (Table A9). It can be separated from *N. ritteri* by the higher position of its VLO (above a line connecting PLO and SAO_1 in *N. regale*) and its larger adipose fin (adipose-fin length less than twice into the caudal peduncle depth in *N. regale*). It can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 25 specimens from the North Pacific Ocean and are given in Tables A2–A9.

Proportions: Given in Table 8.

Fins: Origin of anal fin behind vertical from middle of base of dorsal fin. Pectoral fins reaching beyond end of pelvic-fin base; well developed with rather robust, stout rays. Base of adipose fin above or slightly before end of anal-fin base.

Luminous Organs: PLO 1–3 photophore diameters below lateral line. PO_4 usually higher than level of PVO_2 and on or behind vertical from PO_3. VLO well below lateral line but typically well above midway between lateral line and pelvic-fin base and, therefore, closer to lateral line than to pelvic-fin base; VLO above line connecting PLO and SAO_1 and above line extended through SAO_{1-2}. SAO_1 above VO_{2-3} interspace; SAO_2 behind vertical from VO_4 but typically much closer to VO_4 than to AOa_1. Both SAO_1 and SAO_2 rather low on body, much closer to level of VO series than to SAO_3, which is immediately below lateral line and forward of vertical from AOa_1. Line connecting the VLO and SAO_1 typically passing through VO_4 or anal-fin origin, certainly much below SAO_2. AOa_1 usually slightly depressed and AOa_{1-2} interspace frequently somewhat enlarged. AOp_1 at or near end of anal-fin base. Upper Pol under adipose-fin base, typically on or behind vertical from middle. Prc usually continuous with AOp; Prc_3 approximately on vertical midway between Prc_2 and Prc_4 but much closer to Prc_2. Supracaudal and infracaudal scales well developed; usually with one or, less commonly, with two separated scales preceding infracaudal gland and very rarely one separated scale preceding supracaudal gland. Minute, secondary photophores on posterior border of some scale pockets, especially on upper half of body.

Size: This is a large species of *Nannobrachium*. The largest specimen examined was 183 mm from Sagami Bay, Japan (see discussion under "Distribution and Geographic Variation"). A number of specimens examined from the eastern Pacific were larger than 150 mm, with a maximum of 170 mm. Wisner (1976) recorded the size to about 165 mm but also discussed a larger form from off Oregon and possibly northern California reaching at least 170 mm (see discussion below).

Material: 198 (18–183 mm) specimens were examined, including the holotype, a female, 154 mm, USNM 44289, *Albatross* sta 2923, off San Diego, California.

DISCUSSION.—This is the only valid species of *Nannobrachium* that has been described more than once. Specimens from the North Pacific were described by Chapman (1939) as *L. micropunctatus*. The holotype (USNM 108142) and a series of paratypes of *L. micropunctatus* were carefully examined, and all proved to be typical specimens of *N. regale*.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium regale* is restricted to the North Pacific (Figure 10), from the Bering Sea to the region east of Hokkaido, Japan, in the western Pacific (fide M. Fedorov, 1977, pers. comm., 1979; Wisner, 1976). In the eastern Pacific, Wisner (1976) gave the range from the Gulf of Alaska southward to off Magdalena

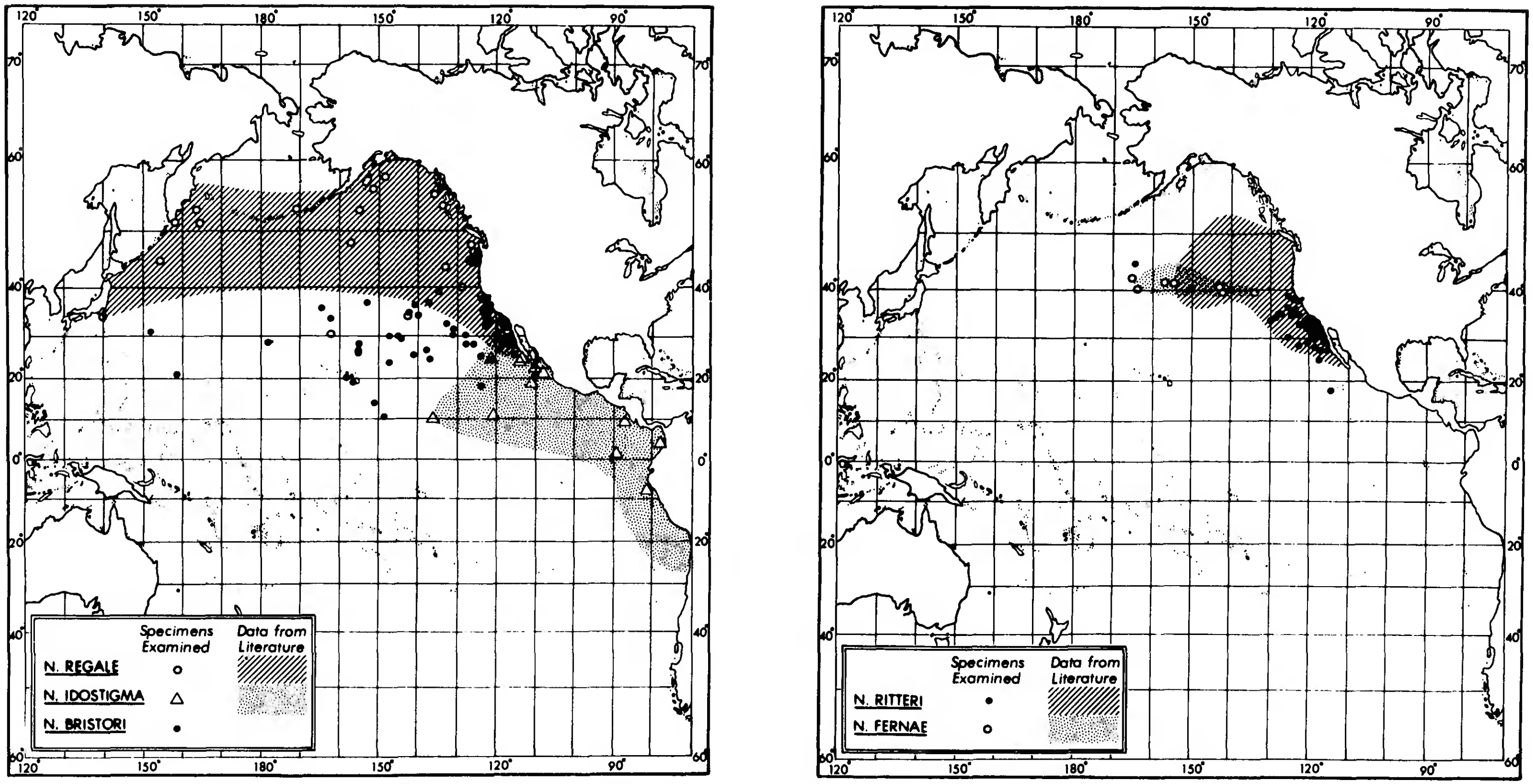

FIGURE 10.—Distributions and localities for material examined for species of the Regale Group.

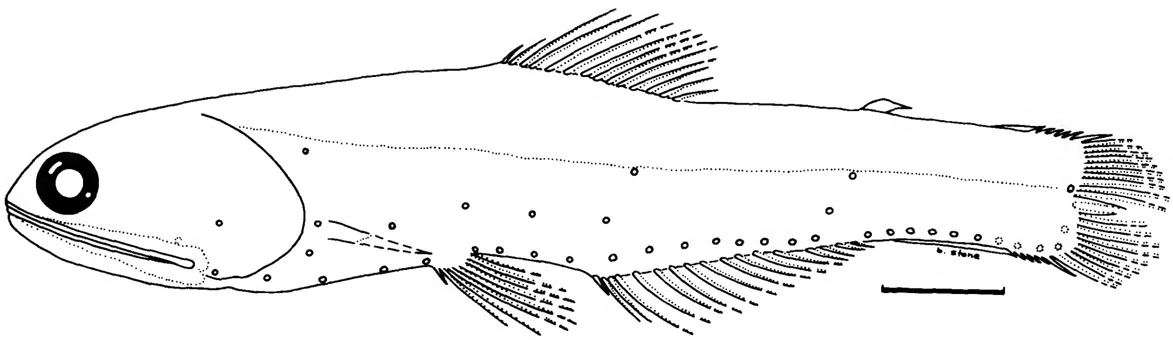

FIGURE 11.—*Nannobrachium ritteri* (Gilbert, 1915). Drawing of 87 mm specimen, USNM 303312, Pacific Ocean, 30°39'N, 118°45.5'W. (Scale bar=1 cm.)

Bay, Baja California, with a depth of capture as shallow as 50 m at night. The very large (183 mm) specimen from Sagami Bay (University of Tokyo, Nomi 26–ORI–200) was carefully examined for evidence of geographic variation, as was material from the western Pacific in the collections of the Zoological Institute, St. Petersburg, Russia. No consistent differences could be found between eastern and western North Pacific specimens. The specimen from Sagami Bay had a total of 15 AO photophores (both sides) and 19 anal-fin rays, both at the upper limit of counts for this species, but both counts also have been recorded from eastern Pacific specimens.

Wisner (1976:173) discussed a possible second form under this species having slightly higher numbers of dorsal-, anal-, and pectoral-fin rays, higher AO photophore and gill raker counts, and minor photophore positional differences. This suggestion was not corroborated by the present study.

Nannobrachium ritteri (Gilbert, 1915)

FIGURE 11, TABLE 9

Lampanyctus ritteri Gilbert, 1915:318 [original description, off San Clemente Island].—Parr, 1928:89 [key]; 1929:23–24 [discussion of holotype].—Jordan et al., 1930:167 [original description cited].—Barnhart, 1936:21 [description, San Diego to Monterey, California, figure].—Bolin, 1939:41–143 [description, comparison, figure].—Follett, 1952:412 [off central California].—Böhlke, 1953:20 [2 paratypes originally at Stanford University, now at California Academy of Sciences].—Aron, 1959:414–415 [North Pacific capture depths].—Parin, 1961:268–279 [distribution, gill structure]; 1971:82 [probable misidentification from Peru Current].— Aron, 1962:279, 301, 307 [?in part] [distribution in northeast Pacific].—Bekker, 1964:474 [boreal and central Pacific]; 1967b:179 [distribution].—Pearcy, 1964:87 [?in part] [off Oregon].—Berry and Perkins, 1966:661–662 [eastern Pacific].—Paxton, 1967a: 429 [vertical distribution off southern California]; 1967b:214–216 [feeding habits, parasites]; 1979:13 [holotype and paratypes].—Rass, 1968:233, 237, 241 [distributional analysis].—Ahlstrom, 1969:42 [California Current larvae].—Fitch, 1969:7 [otoliths].—Ebeling et al., 1970a:5, 7, 14 [off Santa Barbara, California]; 1970b:11–18, 29, 35 [ecology off southern California].—Barham, 1971:109 [swimbladder].—Day, 1971:17 [?in part] [off Canada and Washington].—Butler and Pearcy, 1972:1145–1149 [swimbladder].—Miller and Lea, 1972:70–71 [description, California Current system, figure].—Beklemishev, 1973:294–298 [characteristics of distribution].—Brown, 1974:17, 28 [ecology off southern California].—Chen and Ebeling, 1974:841, 845, fig. 8 [karyotype].—Moser and Ahlstrom, 1974:406–407 [larva figured].—Friedl et al., 1976:611 [deep scattering layer relationships].—Wisner, 1976:170–172 [description, distribution, figure].—McNulty and Nafpaktitis, 1977:510–514 [pineal morphology].—Pearcy et al., 1977: 238–239 [depth distribution off Oregon].—Frost and McCrone, 1978:755, 759 [North Pacific, stations P and Q].—Childress and Somero, 1979:276–277, 281 [enzymic activities].—Lancraft and Robison, 1979:714 [net feeding].—Childress et al., 1980:28–35 [growth and energy relations].—Parin and Bekker, 1981:66 [zoogeographic relations].—Parin and Fedorov, 1981:74–75 [Gulf of Alaska].—Robison and Bailey, 1981:136–138 [sinking rate of feces].—Neighbors and Nafpaktitis, 1982:208–214 [lipid composition].—Eschmeyer and Herald, 1983:94 [family representative].—Sawada, 1983:91, 237 [Japanese], 185, 318 [English] [distinguished from *L. regalis*].—Moser et al., 1984:238–239, fig. 124A [larva figured, relationships].—Willis, 1984:167 [assemblage membership in northeastern Pacific].—Moser et al., 1987:97 [assemblage relationships] [not seen, fide J. Paxton].—Willis et al., 1988:90 [distribution].—Matarese et al., 1989, unpaginated [not seen, fide, H.G. Moser] [larvae, from northeastern Pacific].—Moser and Smith, 1993:654 [assemblage relationships in California Current].—Moser et al., 1993:44 [distribution and abundance in California Current].—Paxton et al., 1995:1315 [listed; not seen, fide J. Paxton].

Lampanyctus (*Lampanyctus*) *ritteri* Fraser-Brunner, 1949:1085 [illustrated key].—Bekker, 1983:85, 86, 193, 198 [in part?] [key, description, distribution].

Nannobrachium ritteri.—Moser and Ahlstrom, 1996:424–425 [early life history and larvae illustrated].

COMPARATIVE DIAGNOSIS.—*Nannobrachium ritteri* (Figure 11) can be distinguished from all other species in the Regale group, except *N. regale*, by its lower number of gill rakers and intermediate number of infracaudal luminous gland scales (Table A9). It can be separated from *N. regale* by the lower position of its VLO (below a line connecting PLO and SAO_1 in *N. ritteri*) and its smaller adipose fin (adipose-fin length more than twice into the caudal peduncle depth in *N. ritteri*). It can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 25 specimens from the North Pacific Ocean and are given in Tables A2–A9.

Proportions: Given in Table 9.

Fins: Origin of anal fin under middle of base of dorsal fin. Pectoral fins reaching beyond end of pelvic-fin base; well de-

TABLE 9.—Measurements of *Nannobrachium ritteri* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	82.3	12.6	25 (64.5–107.5)		
Head depth	161	5	152–170	Y = 0.5 + 0.16x	Slt –
Predorsal depth	177	13	156–199	Y = –0.5 + 0.18x	0
Caudal peduncle depth	109	5	97–118	Y = –0.2 + 0.11x	0
Caudal peduncle length	232	10	211–252	Y = 1.5 + 0.21x	Slt –
Postadipose length	222	14	199–246	Y = 2.3 + 0.19x	Slt –
Predorsal length	453	15	408–478	Y = 2.6 + 0.42x	Slt –
Prepelvic length	406	13	372–431	Y = 0.8 + 0.40x	0
Preanal length	542	30	414–567	Y = 9.9 + 0.42x	Sig –
Pelvic to anal length	132	7	116–143	Y = 0.6 + 0.13x	Slt –
Head length	273	8	257–287	Y = 1.6 + 0.25x	Slt –
Upper-jaw length	195	6	180–205	Y = 1.6 + 0.18x	Sig –
Snout length	47	4	40–58	Y = 1.0 + 0.03x	Sig –
Eye diameter	60	4	47–66	Y = 0.9 + 0.05x	Sig –
Supracaudal-gland length	54	7	41–67	Y = –0.7 + 0.06x	Slt +
Infracaudal gland, solid length	139	10	115–160	Y = 1.5 + 0.12x	Slt –
Infracaudal gland, extreme length	140	10	115–160	Y = 1.8 + 0.12x	Slt –
Anal-fin base length	221	11	195–237	Y = 0.1 + 0.22x	0
Dorsal-fin base length	158	6	144–168	Y = –1.3 + 0.18x	Sig +
Adipose-fin length	48	7	36–61	Y = 0.5 + 0.04x	0

veloped with rather robust, stout rays. Base of adipose fin above end of anal-fin base.

Luminous Organs: PLO 1–3 photophore diameters below lateral line. PO_4 usually slightly higher than level of PVO_2 and on vertical from PO_3. VLO slightly below midway between lateral line and pelvic-fin base. SAO_1 above or slightly before vertical from VO_3; SAO_2 usually above AOa_1; and SAO_3 above AOa_{1-2} interspace. Both SAO_1 and SAO_2 approximately midway between lateral line and level of the VO and AOa series. Line connecting VLO and SAO_1 passing through or near lower margin of SAO_2 and always much above AOa_1. AOa_1 often slightly depressed; AOa_{1-2} interspace often slightly enlarged. AOp_1 at end of anal-fin base. Upper Pol before or on vertical from origin of adipose fin. Prc usually continuous with AOp; Prc_3 approximately on vertical midway between Prc_2 and Prc_4 but low and much closer to Prc_2. Supracaudal and infracaudal scales well developed, lacking any separated scales preceding infracaudal gland. No secondary photophores found.

Size: Wisner (1976) listed the maximum size to about 120 mm, which is consistent with the maximum-sized specimen of 117 mm examined in this study (the holotype).

Material: 929 (18–117 mm) specimens were examined, including the holotype, 117 mm, USNM 75807, Monterey Bay, California, collected by the *Albatross,* sta 4513, 23 May 1904.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium ritteri* is restricted to the northeast Pacific Ocean (Figure 10). Bekker, however (1983:198, fig. 91), gave a distribution pattern for *N. ritteri* that I cannot explain. In addition to the range off California, which corresponds well with my findings, Bekker showed *N. ritteri* to range off Central and South America, a distribution reminiscent of the southern part of an eastern tropical Pacific pattern, such as that of *N. idostigma.* I have seen no specimens of *N. ritteri* from that southern region, however, nor did Wisner (1976). The only supportive references I found were in Russian publications. Parin (1971) listed *L. ritteri* with a question mark as having been collected in the waters of the Peru Current during the fourth cruise of the R/V *Akademik Kurchatov.* In that paper, he did not indicate the number of specimens of any of the species, nor the localities at which the purported *L. ritteri* were taken, presumably because of their rarity. Beklemishev (1973:294–298), in a discussion of what he termed "far-neritic" (or "distant neritic") species, used the "lampanictine ritteri group" as an example from the eastern Pacific, "which, possibly, belong to a single polymorphic species *L. ritteri* (Figure 2)." The "ritteri group" distribution map (Beklemishev, 1973, fig. 2) appears to be an approximate composite of the distribution of *N. ritteri, N. idostigma,* and perhaps the eastern portion of *N. regale.* Beklemishev attributed the distribution map to information from Andriashev, 1962; Bekker, 1967a; and Bekker, pers. comm., 1977. Then, in dealing with some specific examples of mesopelagic zoogeography in the Pacific, using myctophid distributions, Parin and Bekker (1981:64–70) discussed distributions of "far-neritic groups" in which they estimated that around 20 species show such distribution patterns. After discussing eastern tropical Pacific and western tropical Pacific distributions, they discussed two examples of a transition type of far-neritic distribution: one in the "neutral region between the subtropical and subpolar waters near South America (*Hygophum bruuni,* 1 species out of the *Symbolophorus boops* group)" and one "near California (*Lampanyctus ritteri* and possibly *L. ingens*)." In this discussion, there is no suggestion that *L. ritteri* might occur in the far-neritic waters off South America, so it is especially puzzling to see such a distribution pattern in Bekker's (1983) monograph. Bekker not only illustrated the range off Central America and northern South America (1983, fig. 91), he discussed that distribution (1983:198), specifically giving a north-south extent from about 50°N to 30°S, extending westward from the continent to 150°W at the north, to 100°W at the

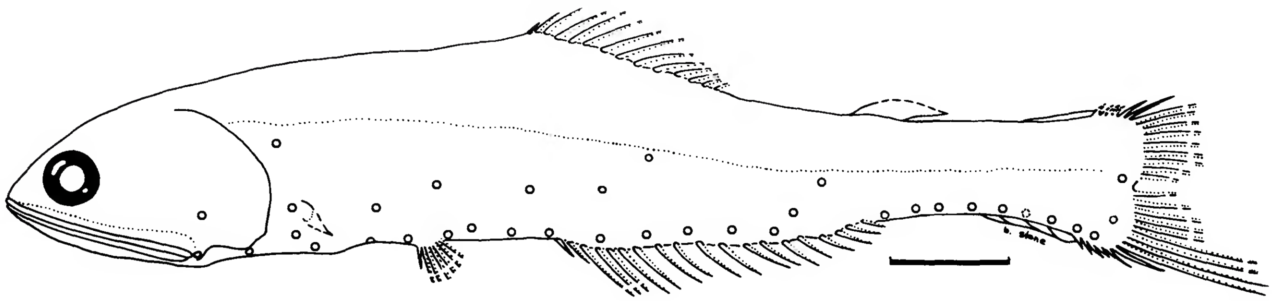

FIGURE 12.—*Nannobrachium idostigma* (Parr, 1931). Drawing of 92.5 mm specimen, SIO H52-404, Pacific Ocean, 30°00'N, 100°00'W. (Scale bar=1 cm.)

equator and to 80°W in the extreme south. In the absence of specimens, however, or at least the unequivocal identification of specific material of *N. ritteri* from off Central or South America, I must consider the southern distribution shown by Bekker to be in error.

Wisner (1976) reported the shallowest depth of capture of about 20 m during the night.

Nannobrachium idostigma (Parr, 1931)

FIGURE 12, TABLE 10

Lampanyctus idostigma Parr, 1931:32–34 [original description, eastern tropical Pacific].—Bolin, 1939:138–139 [description, comparison, figure].—Beebe and Van der Pyle, 1944:81 [eastern Pacific].—Bussing, 1965:203–204 [off Peru].—Berry and Perkins, 1966:662 [off Baja California].—Lavenberg and Fitch, 1966:96, 103 [Gulf of California].—Bekker, 1967b:179 [distribution].—Fitch and Brownell, 1968:2567 [otoliths in cetacean stomachs].—Ahlstrom, 1969:42 [California Current larvae]; 1972:1190 [possible larvae from eastern tropical Pacific].—Parin, 1971:82, 86–88, 90 [Peru Current]; 1975:321 [depth of capture at equator].—Robison, 1972:454–455 [Gulf of California].—Brewer, 1973:21–22 [Gulf of California].—Parin et al., 1973: 114–115 [eastern tropical Pacific].—Friedl et al., 1976:611 [deep scattering layer relationship].—Wisner, 1976:173–174 [description, distribution, figure].—Paxton, 1979:14 [holotype and paratypes].—Parin and Bekker, 1981: 66 [zoogeographic relations].—Neighbors and Nafpaktitis, 1982:208–210, 212–214 [lipid composition].—Robison and Craddock, 1983:285–296 [?in part] [Fraser's dolphin food item].—Loeb, 1986:179 [North Pacific depth distribution].—Paxton et al., 1995:1315 [listed] [not seen, fide J. Paxton].

Lampanyctus (Lampanyctus) idostigma.—Fraser-Brunner, 1949:1085 [illustrated key].—Bekker, 1983:84, 85, 194, 196 [key, description, distribution].

Nannobrachium idostigma.—Moser and Ahlstrom, 1996:416–417 [early life history, larvae illustrated].

COMPARATIVE DIAGNOSIS.—*Nannobrachium idostigma* (Figure 12) can be distinguished from all other species in the Regale group by its lower number of AO photophores, anal-fin rays, infracaudal luminous gland scales, lateral line organs, and vertebrae (Table A9). It can be separated from *N. bristori* by its low number of AO photophores, tooth patches on the lower limb of the second gill arch, and lateral line organs, and it can be distinguished from all the other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 25 specimens from the eastern Pacific Ocean and are given in Tables A2–A9.

TABLE 10.—Measurements of *Nannobrachium idostigma* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	65.1	13.8	25 (45.9–96.2)		
Head depth	157	11	135–174	Y = 2.9 + 0.11x	Sig –
Predorsal depth	156	12	131–177	Y = –0.6 + 0.17x	Slt +
Caudal peduncle depth	88	5	80–101	Y = 0.1 + 0.09x	0
Caudal peduncle length	220	13	200–251	Y = –2.0 + 0.25x	Sig +
Postadipose length	213	12	187–238	Y = –1.3 + 0.24x	Slt +
Predorsal length	474	18	428–497	Y = 4.5 + 0.40x	Sig –
Prepelvic length	404	17	362–438	Y = 4.6 + 0.33x	Sig –
Preanal length	547	28	476–590	Y = 6.2 + 0.45x	Sig –
Pelvic to anal length	130	10	112–156	Y = –1.0 + 0.15x	Slt +
Head length	283	19	234–309	Y = 5.3 + 0.20x	Sig –
Upper-jaw length	200	14	168–222	Y = 3.7 + 0.14x	Sig –
Snout length	50	5	42–63	Y = 1.0 + 0.03x	Sig –
Eye diameter	61	7	47–75	Y = 1.5 + 0.04x	Sig –
Supracaudal-gland length	52	10	31–78	Y = –0.9 + 0.07x	Slt +
Infracaudal gland, solid length	77	10	61–101	Y = –0.9 + 0.09x	Slt +
Infracaudal gland, extreme length	77	10	61–101	Y = –0.9 + 0.09x	Slt +
Anal-fin base length	233	20	182–274	Y = 1.2 + 0.21x	Slt –
Dorsal-fin base length	163	12	142–193	Y = –0.9 + 0.18x	Slt +
Adipose-fin length	59	9	42–74	Y = 0.1 + 0.06x	0

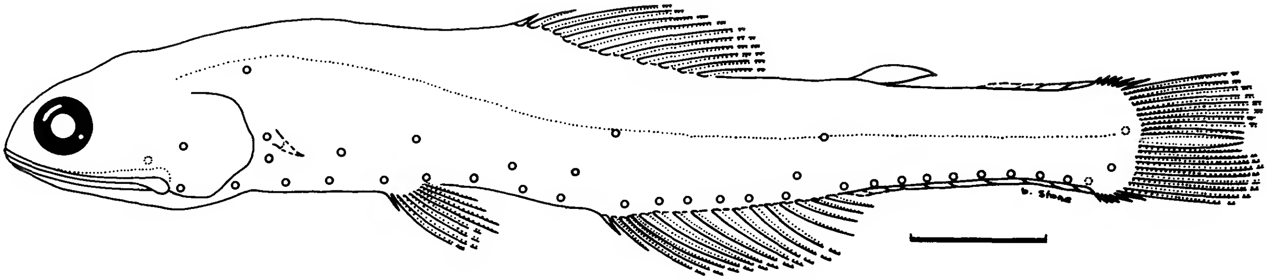

FIGURE 13.—*Nannobrachium fernae* (Wisner, 1971). Drawing of 78 mm paratype, SIO 51-373, Pacific Ocean, 50°00'N, 150°00'W. (Scale bar=1 cm.)

Proportions: Given in Table 10.

Fins: Origin of anal fin before vertical from middle of base of dorsal fin. Pectoral fins reaching beyond end of pelvic-fin base; well developed with rather robust rays. Base of adipose fin above end of anal-fin base.

Luminous Organs: PLO ½–2 photophore diameters below lateral line. PO_4 usually slightly higher than level of PVO_2 and behind vertical from PO_3. VLO well below lateral line, typically midway between it and pelvic-fin base. SAO_1 above VO_{3-4} interspace; SAO_2 variably above AOa_1, often slightly before or behind vertical from leading edge of AOa_1. Both SAO_1 and SAO_2 about midway between ventral profile and lateral line. SAO_3 approximately over AOa_2. AOa_1 usually slightly depressed; AOa_{1-2} interspace slightly enlarged. AOp_1 above end of anal-fin base. Pol_2 typically well before vertical from origin of adipose fin. Prc usually continuous with AOp. Prc_3 usually slightly forward of vertical from Prc_4 but low and slightly closer to Prc_2. Supracaudal and infracaudal gland scales well developed; no separated scales preceding solid gland. No secondary photophores found.

Size: Wisner (1976) recorded the species to about 90 mm in length, which corresponds closely to the length of 96 mm in the largest specimen examined in this study.

Material: 585 (15–96 mm) specimens were examined.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium idostigma* is restricted to the eastern tropical Pacific (Figure 10). Wisner (1976) reported that this species was taken only in tows that sampled at 300 m or deeper. No evidence could be cited for consistent geographic variation in this species.

Nannobrachium fernae (Wisner, 1971), new combination

FIGURE 13, TABLE 11

Lampanyctus fernae Wisner, 1971:50 [original description, North Pacific]; 1976: 172–173 [description, distribution, figure].—Paxton, 1979:14 [holotype and paratypes].—Willis et al., 1988:87 [distribution].

Lampanyctus (*Lampanyctus*) *fernae*.—Bekker, 1983:85, 86, 193, 198 [key, description, distribution].

COMPARATIVE DIAGNOSIS.—*Nannobrachium fernae* (Figure 13) can be distinguished from all other species in the Regale group primarily by the higher number of scales in its infracaudal luminous gland (Table A9), which is higher than in any other species of *Nannobrachium*. In addition, it can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 30 specimens from the North Pacific Ocean and are given in Tables A2–A9.

Proportions: Given in Table 11.

Fins: Anal-fin origin behind vertical from middle of base of dorsal fin. Pectoral fin reaching to or beyond pelvic-fin insertion, its rays relatively well developed and robust. Origin of adipose fin usually above end of anal-fin base.

Luminous Organs: PLO ½–2 photophore diameters below lateral line. PO_4 usually slightly higher than, but occasionally at, level of PVO_2 and behind vertical from PO_3. VLO well below lateral line, typically slightly closer to lateral line than to pelvic-fin base. SAO_1 variably above VO_3; SAO_2 closer to VO_4 than to AOa_1; level of SAO_{1-2} rather low on body, closer to ventral profile than to lateral line. SAO_3 on or before vertical from AOa_1; AOa_1 slightly depressed; AOa_{1-2} interspace slightly enlarged. AOp_1 above end of anal-fin base. Pol_2 well before vertical from origin of adipose fin. Prc frequently not continuous with AOp. Prc_3 on vertical line approximately midway between Prc_2 and Prc_4 but much closer to Prc_2. Supracaudal and infracaudal luminous gland scales well developed; no separated scales preceding solid glands.

Size: Wisner (1976) records the species as reaching a size of about 90 mm in length, which corresponds to the maximum length of 91 mm examined in this study.

Material: 62 (38–91 mm) specimens were examined.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium fernae* appears to have the most restricted distribution of any species of *Nannobrachium* (Figure 10). It is known only from an area of the North Pacific between 40°N–45°N and 135°W–165°W, with a depth of capture as shallow as 200 m at night (Wisner, 1976). Additional material I have examined comes from the same general region, so apparently this species

TABLE 11.—Measurements of *Nannobrachium fernae* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	55.8	13.9	30 (38–84)		
Head depth	146	11	130–173	Y = 1.4 + 0.12x	Sig –
Predorsal depth	137	9	114–156	Y = –0.4 + 0.14x	Slt +
Caudal peduncle depth	84	5	73–93	Y = –0.3 + 0.09x	Slt +
Caudal peduncle length	246	17	214–289	Y = –0.4 + 0.26x	0
Postadipose length	222	17	187–265	Y = –1.2 + 0.25x	Slt +
Predorsal length	461	18	427–520	Y = 2.1 + 0.42x	Sig –
Prepelvic length	389	9	368–415	Y = 0.6 + 0.38x	Slt –
Preanal length	542	30	436–587	Y = –0.9 + 0.56x	Slt +
Pelvic to anal length	150	12	129–173	Y = –0.3 + 0.16x	0
Head length	252	13	225–282	Y = 1.6 + 0.22x	Sig –
Upper-jaw length	180	11	161–206	Y = 1.9 + 0.14x	Sig –
Snout length	42	5	33–50	Y = 0.2 + 0.04x	Slt –
Eye diameter	61	6	52–79	Y = 0.7 + 0.05x	Sig –
Supracaudal-gland length	76	10	51–92	Y = –0.9 + 0.09x	Slt +
Infracaudal gland, solid length	200	14	173–231	Y = –1.0 + 0.22x	Slt +
Infracaudal gland, extreme length	200	14	173–231	Y = –1.0 + 0.22x	Slt +
Anal-fin base length	204	14	153–224	Y = –1.0 + 0.22x	Slt +
Dorsal-fin base length	146	9	125–159	Y = –0.2 + 0.15x	0
Adipose-fin length	50	12	29–75	Y = –0.0 + 0.05x	0

is truly so restricted. No geographic variation was found in material examined.

Nannobrachium bristori, new species

FIGURE 14, TABLE 12

Lampanyctus niger.—Berry and Perkins, 1966:662 [?in part] [fide H.G. Moser; Pacific off California and northern Mexico].—Moser and Ahlstrom, 1974: 406–407 [larva figured].—[Not Günther, 1887.]

Lampanyctus niger (Form C).—Clarke, 1973:416, 418 [ecology north of Hawaii].—[Not Günther, 1887.]

Lampanyctus (*Lampanyctus*) *niger*.—Bekker, 1983:87–89, 198–200 [?in part?] [key, description, distribution].—[Not Fraser-Brunner, 1949.]

Lampanyctus sp.—Moser et al., 1984:238, fig. 124D [larva figured].

Nannobrachium "*niger*."—Moser and Ahlstrom, 1996:418–419 [early life history and larvae illustrated].

TYPE SPECIMENS.—*Holotype:* Male, 110 mm, SIO 71-301, 27°26.6'N, 155°24.6'W, 30 September 1971.

Paratypes: HIMB 70-913, 2 (34–67 mm); HIMB 70-914, 18 (21–40 mm); HIMB 70-916, 4 (33–40 mm); HIMB 70-927, 2 (58–86 mm); OS 12816, 1 (74 mm); OS 12815, 4 (33–116 mm); SIO 51-84, 1 (57 mm); SIO 66-20, 2 (72–76 mm); SIO 67-56, 1 (73 mm); SIO 71-301, 3 (40–120 mm); SIO 71-310, 1 (111 mm); SIO 73-145, 1 (142 mm); SIO 73-160, 1 (105 mm); SIO 76-6, 1 (46 mm); SIO 73-329 (28°03'N, 154°39'W, 22 June 1973), 1 (68 mm); USNM 298174, 8 (30–91 mm); USNM 298191, 1 (101.5 mm); USNM 298192, 2 (32.5–47 mm); USNM 359634 (25°02'N, 137°55'W, 19 Nov 1967), 1 (106 mm).

COMPARATIVE DIAGNOSIS.—*Nannobrachium bristori* (Figure 14) can be most easily distinguished from the other species in the Regale group by its number of AO photophores (fewer than in *N. ritteri*, more than in *N. idostigma*), number of gill rakers and lower limb tooth patches on the second gill arch (more of both than in *N. regale* and *N. ritteri*, more tooth patches than in *N. idostigma*), and number of infracaudal luminous gland scales and lateral line organs (fewer of both than in *N. regale* and *N. ritteri*, fewer lateral line organs than in *N. fernae* and more than in *N. idostigma*) (Table A9). *Nannobrachium bristori* can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 23 specimens from the North Pacific Ocean and are given in Tables A2–A9. Counts for the holotype are D 14, A 18, P_1 16?, GR 4+11, tooth patches 9, AO 5+7 (L), 6+7 (R), SC/IC 3/4?, LL 37?, V 16+21.

Proportions: Given in Table 12. Holotype measurements (in mm) as follows: SL 110, HD 17.5, PDD 17.7, CPD 9.6, CPL 26.4, PADL 24.3, PDL 47.0, PPL 41.0, PANL 58.5, PAL 16.3, HL 31.3, UJL 22.9, SOL 4.9, ED 6.4, SGL 4.9, IGS 7.6, IGEL 7.6, AFB 26.4, DFB 21.7, AF 7.6.

Fins: Origin of anal fin behind middle of base of dorsal fin. Pectoral fins reaching just beyond PO_3 with weak and flexible rays. Adipose fin above end of anal-fin base.

Luminous Organs: PLO 1–2 photophore diameters below lateral line (1 diameter in holotype). PO_4 approximately on level of PVO_2 and above, or more frequently slightly behind, vertical from PO_3 (PO_4 behind vertical from PO_3 in holotype). VLO 2–3 photophore diameters below lateral line (VLO 2½ diameters below in holotype); its distance to lateral line equal to or greater than distance of PLO to lateral line. SAO_2 midway between VO_4 and AOa_1, exact position variable, but frequently closer to AOa_1 (SAO_2 closer to VO_4 in holotype). AOp_1 at or behind end of anal-fin base (AOp_1 slightly behind end of base in holotype). Prc separate from AOp; Prc_{1-2} on horizontal line; Prc_{3-4} on vertical or nearly vertical line, more than 1 photophore diameter behind vertical from Prc_2 (Prc_4 slightly behind vertical from Prc_3, 2 photophore diameters behind vertical from Prc_2 in holotype). Supracaudal and infracaudal luminous glands well developed, infrequently having single separated

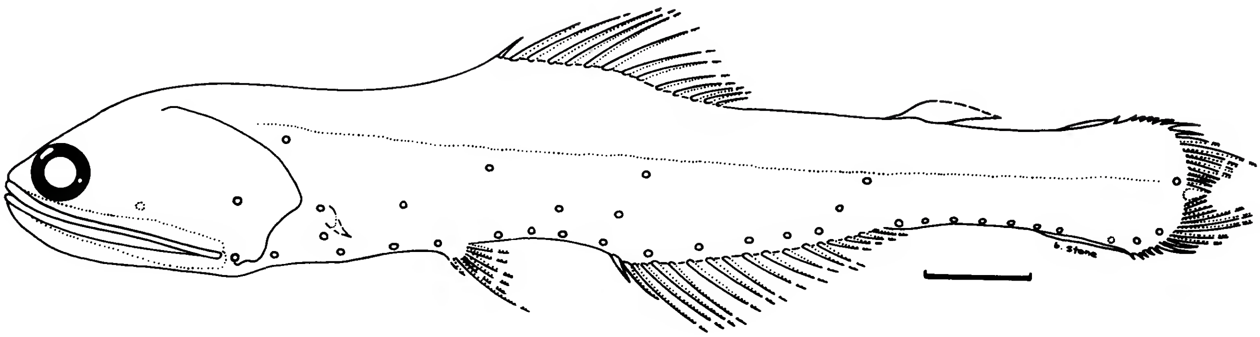

FIGURE 14.—*Nannobrachium bristori*, new species. Drawing of holotype, 110 mm, SIO 71-301, Pacific Ocean, 27°26.6'N, 155°24.6'W. (Scale bar=1 cm.)

luminous scale preceding solid infracaudal gland. No secondary photophores found.

Size: *Nannobrachium bristori* is a large-bodied species, reaching a maximum size in excess of 140 mm. The largest specimen encountered was 142 mm.

Material: 98 (16–126 mm) specimens were examined, excluding type material.

DISCUSSION.—This species has been confused with *N. nigrum* in the past, but it is clearly a distinct species of the Regale group. Of the species in the Regale group, *N. bristori* has the highest VLO. In this, it is reminiscent of the species in the Nigrum group, although the VLO in that group is always considerably higher. In addition, although the pectoral fin of *N. bristori* is rather short, with somewhat weak and flexible rays, it is stronger and longer than in any of the Nigrum group species and does not seem to show a tendency to point downward in large specimens. Both the VLO position and condition of the pectoral fin in *N. bristori*, however, suggest possible affinities to species of the Nigrum group. In addition, on the graph plotted for the discriminant function analysis (Figure 3), the data points for *N. bristori* lie far to the left, in the midst of data points for the Nigrum group species, indicating morphological similarities with those species. For these reasons, the characteristics of *N. bristori* have been included in Table A-1 for comparison with the species of the Nigrum group, as well as in Table A9, the Regale group.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium bristori* appears to be restricted to the tropical and subtropical waters of the North Pacific (Figure 10). It does not seem to be a particularly abundant species. Most collections contain only one or a few specimens.

No significant geographic variation could be found in *N. bristori*; however, the gill-raker count appears to exhibit higher variance than other species of *Nannobrachium*, but the cause of this variation is unclear.

ETYMOLOGY.—Named for my good friend, the late William B. Bristor, Jr., of Washington, D.C.

TABLE 12.—Measurements of *Nannobrachium bristori* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	71.7	33.8	23 (31.5–142.0)		
Head depth	160	12	127–184	Y = 1.0 + 0.14x	Sig –
Predorsal depth	131	16	104–152	Y = –1.0 + 0.15x	Slt +
Caudal peduncle depth	80	5	70–87	Y = –0.2 + 0.08x	Slt +
Caudal peduncle length	232	12	215–250	Y = 0.1 + 0.23x	0
Postadipose length	214	11	177–231	Y = –0.5 + 0.22x	Slt +
Predorsal length	447	22	406–508	Y = 2.4 + 0.41x	Sig –
Prepelvic length	400	21	364–451	Y = 1.0 + 0.38x	Sig –
Preanal length	551	29	452–610	Y = 1.0 + 0.54x	Slt –
Pelvic to anal length	148	15	123–175	Y = –0.6 + 0.16x	Slt +
Head length	281	19	242–318	Y = 1.6 + 0.25x	Sig –
Upper-jaw length	212	15	181–238	Y = 1.6 + 0.19x	Sig –
Snout length	47	7	36–62	Y = 0.6 + 0.04x	Sig –
Eye diameter	46	6	32–54	Y = –0.4 + 0.05x	Slt +
Supracaudal-gland length	50	9	38–68	Y = 0.4 + 0.04x	Slt –
Infracaudal gland, solid length	76	9	55–94	Y = 0.1 + 0.07x	0
Infracaudal gland, extreme length	77	11	55–101	Y = 0.3 + 0.07x	0
Anal-fin base length	217	16	189–250	Y = –0.7 + 0.23x	Slt +
Dorsal-fin base length	183	11	162–203	Y = 0.4 + 0.18x	Slt –
Adipose-fin length	61	14	41–84	Y = 1.0 + 0.04x	Sig –

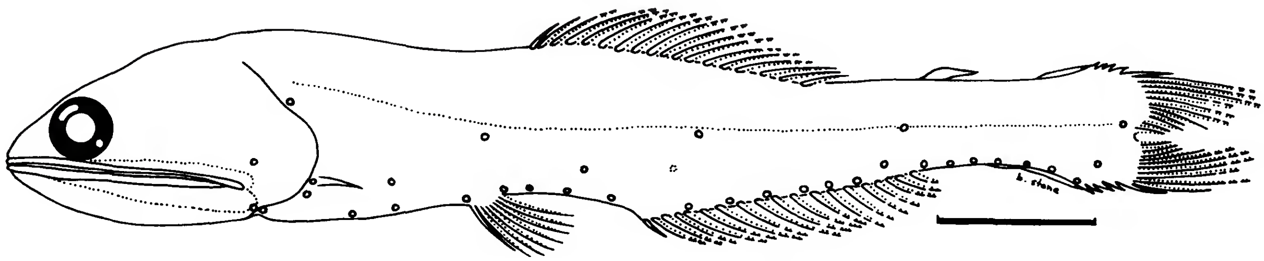

FIGURE 15.—*Nannobrachium cuprarium* (Tåning, 1928). Drawing of 67.5 mm specimen, USNM 253150, Atlantic Ocean, 32°09'N, 64°11'W. (Scale bar=1 cm.)

The Cuprarium Group

All species in this group share the unique character of dense black pigmentation on the posterior tips of both the supracaudal and infracaudal luminous glands. The pigmentation looks like a black "hood" or "cap" and somewhat resembles the caudal gland pigmentation of some species in the genera *Taaningichthys* and *Lampadena.* The pigmentation in the species of the Cuprarium group, however, is more weakly developed, and the structure appears to be more fragile than in those genera. Consequently, it may be missing in damaged specimens.

Pectoral-fin length in the species of this group is intermediate. The pectoral fins are longer than one-half the distance from the pectoral-fin base to the pelvic-fin insertion, but they never reach the pelvic-fin insertion. The pectoral rays resemble those of the Regale group species, but coincident with the slightly shorter fin length, the rays are proportionally thinner and more flexible.

Other shared characters not unique to this group include (1) VLO usually touching lateral line, (2) posterior position of SAO_1 above the VO_{3-4} interspace, usually at a slightly lower level than SAO_2, (3) Prc_3 on a vertical midway between Prc_2 and Prc_4, and (4) Pol_2 usually well forward of vertical from adipose fin origin.

These and other characters are compared in Table 1 for all species groups of *Nannobrachium.*

The Cuprarium group contains two species: *Nannobrachium cuprarium* (Tåning, 1928) and *N. lineatum* (Tåning, 1928).

Modal characters of all species in the Cuprarium group are listed in Table A10 along with those for *N. isaacsi,* the only species in the Isaacsi group.

Nannobrachium cuprarium (Tåning, 1928), new combination

FIGURE 15, TABLE 13

Lampanyctus cuprarius Tåning, 1928:68 [original description, North Atlantic].—Parr, 1928:88, 106–108 [key, western Atlantic, description, figure].—Bolin, 1959:33–34 [discussion, distribution].—Backus et al., 1965:144 [western Atlantic].—Bullis and Thompson, 1965:28 [northern Gulf of Mexico].—Bekker, 1967a:116–117 [distribution].—Backus et al., 1969:95 [western Sargasso Sea].—Nafpaktitis and Nafpaktitis, 1969:42 [discussion, figure of lectotype].—Badcock, 1970:1039 [off Canary Islands].—Gibbs and Roper, 1971:129 [diurnal vertical migration].—Gibbs et al., 1971:43, 103–104 [key, vertical distribution near Bermuda, figure].—Krefft and Bekker,

TABLE 13.—Measurements of *Nannobrachium cuprarium* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	64.6	9.5	25 (42.1–75.5)		
Head depth	160	9	136–170	Y = 0.1 + 0.16x	0
Predorsal depth	135	12	112–153	Y = −2.7 + 0.18x	Sig +
Caudal peduncle depth	85	5	70–95	Y = 0.2 + 0.08x	0
Caudal peduncle length	183	12	154–204	Y = 1.1 + 0.17x	Slt −
Postadipose length	169	9	149–184	Y = 1.1 + 0.15x	Slt −
Predorsal length	478	24	402–504	Y = 0.8 + 0.47x	0
Prepelvic length	419	24	342–475	Y = 4.4 + 0.35x	Sig −
Preanal length	563	26	477–593	Y = 4.3 + 0.50x	Slt −
Pelvic to anal length	138	9	121–151	Y = 1.0 + 0.12x	Slt −
Head length	275	16	237–297	Y = 0.5 + 0.27x	0
Upper-jaw length	213	11	177–232	Y = 1.2 + 0.19x	Slt −
Snout length	45	5	35–59	Y = 0.4 + 0.04x	Slt −
Eye diameter	55	5	44–68	Y = −0.5 + 0.06x	Slt +
Supracaudal-gland length	55	8	35–70	Y = 1.8 + 0.03x	Sig −
Infracaudal gland, solid length	87	10	70–114	Y = 2.1 + 0.05x	Sig −
Infracaudal gland, extreme length	88	10	70–114	Y = 2.1 + 0.06x	Sig −
Anal-fin base length	240	13	205–263	Y = 0.7 + 0.23x	0
Dorsal-fin base length	212	14	168–236	Y = 0.2 + 0.21x	0
Adipose-fin length	52	7	39–64	Y = 0.6 + 0.04x	Slt −

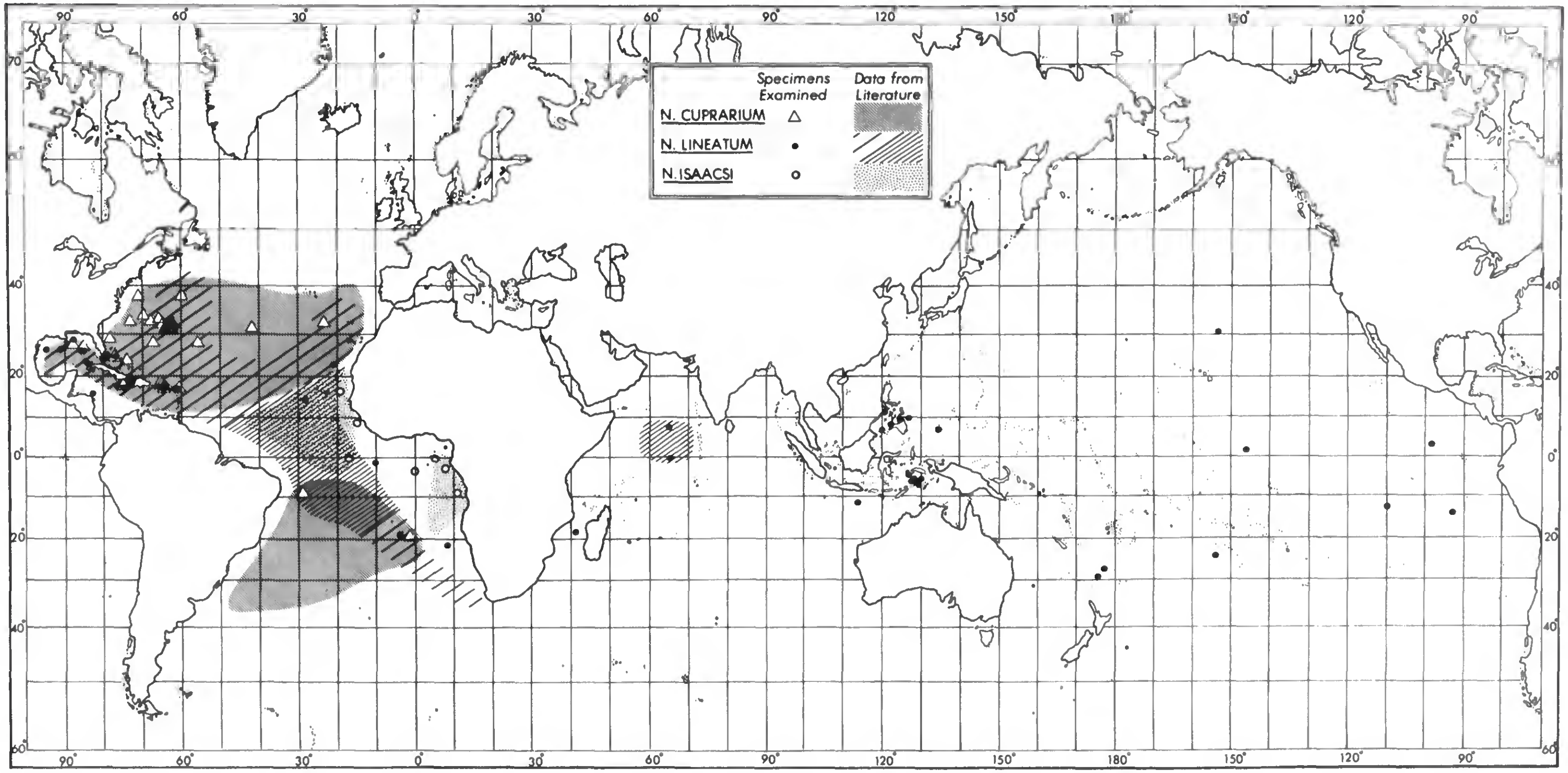

FIGURE 16.—Distributions and localities for material examined for *N. cuprarium*, *N. lineatum*, and *N. isaacsi*. The closer spacing of lines represents data from relatively more abundant catches.

1973:87 [biology, synonymy].—Nafpaktitis, 1973:41 [redescription, figure and designation of lectotype].—Briggs, 1974:328 [tropical Atlantic endemic].—Merrett and Roe, 1974:117, 119–125 [depth and feeding habits].—Nielson, 1974:38 [listing of lectotype].—Parin et al., 1974:106–107 [in part?] [southwest Atlantic].—Roe, 1974:107, 110 [vertical migration].—Bekker et al., 1975:314 [distribution, Caribbean Sea].—Badcock and Merrett, 1976:42–43, 45 [depth].—Brooks 1976:569, 575, 581 [swimbladder size].—Nafpaktitis et al., 1977:197–199 [description, distribution, figure].—Backus et al., 1977:267, 275, 277 [zoogeography].—Paxton, 1979:14 [lectotype].—Hulley, 1981:193–195 [description, Atlantic distribution]; 1984b: 462 [description, northeast Atlantic distribution].—Moser et al., 1984:239 [relationships, larval description].—Hulley and Krefft, 1985:36–37, 42–46 [North Atlantic zoogeography].—Karnella, 1987:52, 107–110, 149–159, 163–165 [ecology and biology near Bermuda].—Gartner et al., 1987:86, 88–89, 91, 95 [eastern Gulf of Mexico].

Lampanyctus (Lampanyctus) cuprarius.—Fraser-Bruner, 1949:1086 [illustrated key].—Bekker, 1983:87, 89, 193, 200, 201 [key, description, distribution].

COMPARATIVE DIAGNOSIS.—*Nannobrachium cuprarium* (Figure 15) can be distinguished from *N. lineatum* by its fewer AO photophores, lateral line organs, and vertebrae (Table A10). In addition, its caudal peduncle is shorter than the upper-jaw length (longer than the upper jaw in *N. lineatum*), and Prc_3 lies on a line connecting Prc_2 and Prc_4 (but is below that line in *N. lineatum*). *Nannobrachium cuprarium* can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 25 specimens from the Atlantic Ocean and are given in Tables A2–A8 and Table A10.

Proportions: Given in Table 13.

Fins: Origin of anal fin before vertical from middle of base of dorsal fin. Pectoral fin not reaching vertical from PO_4, its rays rather weak, flexible. Adipose fin above or slightly before end of anal-fin base.

Luminous Organs: PLO ½–2 photophore diameters below lateral line. PO_4 slightly higher than level of PVO_2, above and usually behind vertical from PO_3. VLO not more than its diameter below, frequently nearly touching, lateral line. SAO_2 approximately above AOa_1. AOa_1 somewhat depressed; AOa_{1-2} interspace enlarged. AOp_1 at or near end of anal-fin base. Pol_2 well before vertical from origin of adipose fin. Prc continuous with AOp; Prc_{2-3-4} on straight line at angle of about 110° to line connecting Prc_{1-2}. Supracaudal and infracaudal luminous scales well developed, very rarely single separated scale before infracaudal gland; prominent covering of black pigment on posterior tips of infracaudal and supracaudal glands resembling hood or cap. Solitary minute secondary photophores in horizontal rows, one such photophore on each posterior margin of at least some enlarged lateral line scales and on at least some scales below lateral line on anterior part of body; rows of minute photophores between rays of caudal fin.

Size: This appears to be a small-bodied species of *Nannobrachium*, seldom longer than 80 mm. The largest specimen examined here was 79 mm. Bekker (1967a) reported individuals as large as 92.7 mm, whereas Parin et al. (1974) reported one of 128 mm from the southwest Atlantic, and Kotthaus (1972a) reported one sample with a specimen of 110 mm. Gibbs et al. (1971) found the maximum size of the *N. cuprarium* collected in the Bermuda Ocean Acre study to be 79 mm, whereas Nafpaktitis et al. (1977) reported gravid females 70–75 mm. Hulley (pers. comm., 1980) examined 28 specimens from collections made by the *Walther Herwig* in the South Atlantic. Although his largest specimen was a 78 mm female, he judged it was not fully mature because the eggs lacked oil droplets, and he suggested that maximum size for the species might be about 90 mm. Given these recurrent findings (that virtually all specimens of *N. cuprarium* are approximately 80 mm or less), it may be that those larger specimens listed by Parin et al. (1974) and Kotthaus (1972a) are misidentifications.

Material: 534 (14–78 mm) specimens were examined, including the lectotype, a 63 mm female, ZMUC P2330213, *Dana* sta 1231 I, 24°30′N, 80°00′W, 6 February 1922 (Nafpaktitis, 1973).

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium cuprarium* is restricted to the Atlantic Ocean (Figure 16), where it is a bipolar, subtropical species. It is reported to occur during the day at 600–1200 m near Bermuda and at 700–900 m near the Canary Islands and during the night at shallower depths at both locations (Nafpaktitis et al., 1977). Karnella (1987) reported similar depth distributions in Ocean Acre material near Bermuda but with a maximum depth to 1500 meters in late summer. No consistent variations could be detected in specimens examined from the eastern and western North Atlantic, Gulf of Mexico, or South Atlantic.

Nannobrachium lineatum (Tåning, 1928), new combination

FIGURE 17, TABLE 14

Lampanyctus lineatus Tåning, 1928:68 [original description, North Atlantic].—Parr, 1928:88, 108–110 [key, western Atlantic, description, figure].—Bolin, 1959:34 [discussion, distribution].—Backus et al., 1965:144 [western Atlantic].—Bekker 1967a:117 [equatorial Atlantic].—Backus et al., 1969:95 [western Sargasso Sea].—Nafpaktitis and Nafpaktitis, 1969:41–42 [tropical Indian, description, figure].—Badcock, 1970:1039 [off Canary Islands].—Gibbs et al., 1971:43, 107 [key, vertical distribution near Bermuda, figure].—Krefft and Bekker, 1973:188–189 [biology, synonymy].—Nafpaktitis, 1973: 40 [redescription, figure and designation of lectotype].—Nielson, 1974:38 [listing of lectotype].—Bekker et al., 1975:314 [distribution, Caribbean Sea and Gulf of Mexico].—Badcock and Merrett, 1976:42 [30°N, 23°W].—Brooks, 1976:570, 575, 581 [swimbladder size].—Parin and Golovan, 1976:262 [off West Africa].—Backus et al., 1977:267, 275, 277 [zoogeography].—Nafpaktitis et al., 1977:199–201 [description, distribution, figure].—Parin et al., 1977:122, 123 [tropical Pacific] [in part?].—Parin et al., 1978:175 [eastern tropical Atlantic].—Paxton, 1979:14 [lectotype].—Hulley, 1981:206–208 [description, Atlantic distribution]; 1984b:464 [description, northeast Atlantic distribution]; 1986b:236, 242, 245 [zoogeography, Benguela region]; 1986c:308, fig. 86.80 [description, South Africa, figure].—Gloerfelt-Tarp and Kailola, 1984:77 [illustration from Nafpaktitis and Nafpaktitis].—Moser et al., 1984:239 [relationships, larval description].—Hulley and Krefft, 1985:35, 43–46 [North Atlantic zoogeography].—Rubies, 1985:578, 584 [Valdivia Bank off Namibia; gill raker count].—Clarke, 1987:66–67 [biogeography in central Pacific, listed as c.f. *lineatus*].—Gartner et al., 1987:86, 88, 91, 95 [eastern Gulf of Mexico].—Karnella, 1987:52, 112 [ecology and biology near Bermuda].

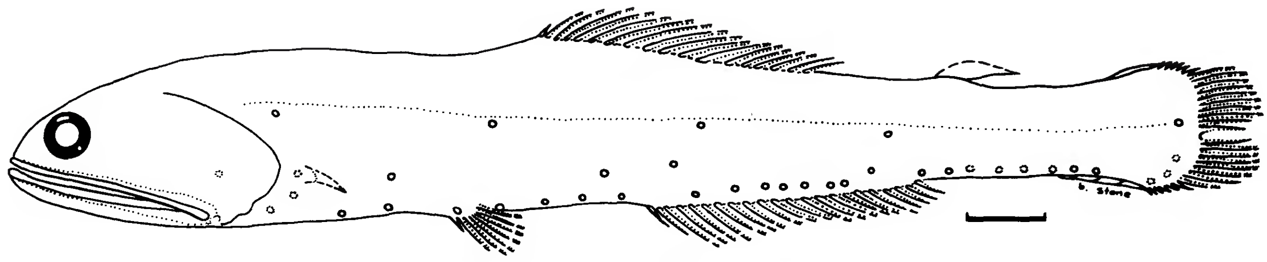

FIGURE 17.—*Nannobrachium lineatum* (Tåning, 1928). Drawing of 157 mm specimen, USNM 298184, Atlantic Ocean, 32°09′N, 64°11′W. (Scale bar=1 cm.)

Lampanyctus (*Lampanyctus*) *lineatus*.—Fraser-Brunner, 1949:1086 [illustrated key].—Bekker, 1983:87, 89, 201, 202 [key, description, distribution].
Lampanyctus niger.—Parin et al., 1977:122, 123 [?in part] [western Pacific].—[Not Günther, 1887.]

COMPARATIVE DIAGNOSIS.—*Nannobrachium lineatum* (Figure 17) can be distinguished from *N. cuprarium* by its higher number of AO photophores, lateral line organs, and vertebrae (Table A10). In addition, its caudal peduncle is longer than the upper-jaw length (shorter than the upper jaw in *N. cuprarium*), and the Prc_3 lies below a line connecting Prc_2 and Prc_4 (on that line in *N. cuprarium*). *Nannobrachium lineatum* can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 29 specimens from the Atlantic and up to 22 specimens from the Indo-Pacific and are given in Tables A2–A8, A10.

Proportions: Given in Table 14, for Atlantic material only.

Fins: Origin of anal fin under middle of base of dorsal fin. Pectoral fin not reaching vertical from PO_4, its rays rather weak, flexible. Adipose fin above end of anal-fin base.

Luminous Organs: PLO ½–2 photophore diameters below lateral line. PO_4 slightly higher than level of PVO_2 and approximately above PO_3 or slightly behind vertical from PO_3. VLO not more than one photophore diameter below, frequently touching, lateral line. SAO_2 slightly before vertical from AOa_1. AOa_1 slightly depressed; AOa_{1-2} interspace sometimes enlarged. AOp_1 above end of anal-fin base. Pol_2 well before vertical from origin of adipose fin. Prc_{1-3} forming gentle curve; Prc_4 at lateral line with Prc_3 midway between Prc_2 and Prc_4 but below line connecting them. Supracaudal and infracaudal luminous scales well developed; frequently one, rarely two, separate scales before infracaudal gland; rather inconspicuous covering of black pigment on posterior tips of infracaudal and supracaudal glands, resembling hood or cap; black pigment least developed in some Indo-Pacific specimens. Rows of minute photophores between rays of caudal fin.

Size: *Nannobrachium lineatum* appears to be the largest bodied species of *Nannobrachium*, reaching a maximum size well in excess of 200 mm in the Atlantic but apparently not so large in the Indo-Pacific. The largest specimen examined in this study was 237 mm. Nafpaktitis et al. (1977) reported a size of over 235 mm, with three gravid females 171–237 mm. Hulley (pers. comm., 1980) reported a maximum size of 221 mm for 157 specimens from the North and South Atlantic. Gibbs et

TABLE 14.—Measurements of *Nannobrachium lineatum* as thousandths of standard length with notes on allometry (for Atlantic material only).

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	100.1	35.8	29 (48.0–161.2)		
Head depth	140	10	111–152	Y = 1.0 + 0.13x	Slt −
Predorsal depth	118	13	96–141	Y = −0.4 + 0.12x	0
Caudal peduncle depth	74	5	66–83	Y = 0.4 + 0.07x	Slt −
Caudal peduncle length	218	10	200–247	Y = −0.3 + 0.22x	0
Postadipose length	189	8	174–211	Y = −0.2 + 0.19x	0
Predorsal length	460	20	405–509	Y = 1.4 + 0.44x	Slt −
Prepelvic length	403	18	347–440	Y = 2.3 + 0.37x	Sig −
Preanal length	548	17	523–610	Y = 1.0 + 0.54x	Slt −
Pelvic to anal length	138	14	110–183	Y = −1.7 + 0.16x	Sig +
Head length	260	18	212–297	Y = 1.9 + 0.24x	Slt −
Upper-jaw length	196	11	175–216	Y = 1.9 + 0.17x	Sig −
Snout length	42	7	33–56	Y = 1.2 + 0.03x	Sig −
Eye diameter	43	4	38–50	Y = 0.2 + 0.04x	Slt −
Supracaudal-gland length	50	7	35–62	Y = −0.1 + 0.05x	0
Infracaudal gland, solid length	78	12	55–105	Y = 0.4 + 0.07x	0
Infracaudal gland, extreme length	85	15	64–117	Y = 1.0 + 0.07x	Slt −
Anal-fin base length	243	12	215–262	Y = −0.5 + 0.25x	Slt +
Dorsal-fin base length	189	10	172–211	Y = −0.7 + 0.20x	Slt +
Adipose-fin length	56	13	32–86	Y = 1.6 + 0.04x	Sig −

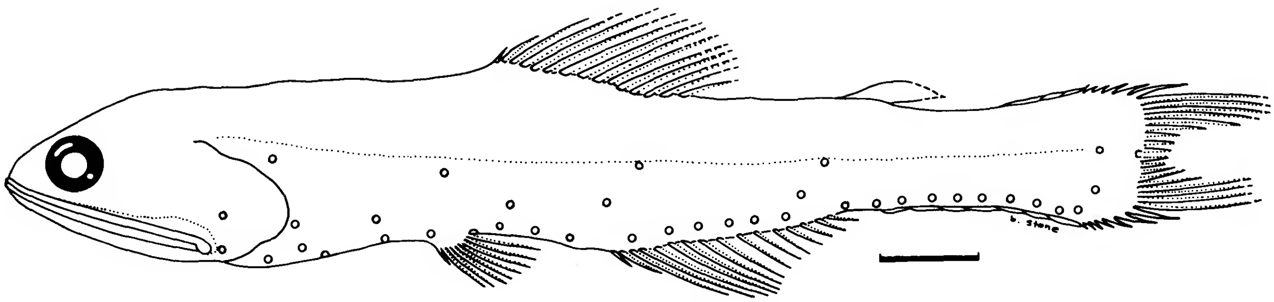

FIGURE 18.—*Nannobrachium achirus* (Andriashev, 1962). Drawing of 109 mm specimen, LACM 11488, Pacific Ocean, 63°01'S, 102°01.3'W. (Scale bar=1 cm.)

al. (1971) found the maximum size in the Bermuda Ocean Acre material to be 161 mm. From those few specimens available, it appears that Indo-Pacific forms referable to this species do not reach such a large size. The largest specimens reported by Nafpaktitis and Nafpaktitis (1969) among their material from the Indian Ocean was 97 mm. The largest specimen from the Indo-Pacific examined in this study was 122 mm.

Material: 203 (26–237 mm) specimens were examined, including the lectotype, a male, 121.5 mm, ZMUC P2330212, *Dana* sta 1186 I, 17°54'N, 65°54'W, 30 November 1921 (Nafpaktitis, 1973).

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium lineatum* is an uncommon species (Nafpaktitis et al., 1977), never particularly abundant. Most collections examined contained only one or a few specimens. It appears to have a tropical to subtropical distribution (Figure 16). In analyzing the *Walther Herwig* collections, Hulley (1981) found that *N. lineatum* was much more abundant in the collections between 9°N and 10°S, indicating a tropical distribution. It occurs at reported daytime depths of 700–1150 m (Nafpaktitis et al., 1977). Nighttime depths appear bimodal, as shallow as 65–350 m and as deep as 900–1000 m, indicating both migrants and non-migrants. Karnella (1987) reported similar ranges for Ocean Acre material from near Bermuda.

No consistent variation was apparent between North and South Atlantic specimens of *N. lineatum*, but there are considerable differences between Atlantic and Indo-Pacific material. These are manifested largely in a greater range of lateral line organ and vertebral counts, and to a lesser extent, gill raker counts (Table A10), suggesting that more than one species may be present. An attempt was made to analyze the differences between the Atlantic and Indo-Pacific specimens but was inhibited by the lack of adequate material. Until material of adequate quantity and quality becomes available, it seems best at this time to treat all forms as *N. lineatum*. (See also discussion of Fujii's two specimens of "*Lampanyctus nigrum*" from near the Ogasawara Islands in the western Pacific under *N. nigrum*).

The Achirus Group

The unique character distinguishing all species in this group is the nature of the extremely reduced pectoral-fin development. In all species, at a size that varies with each species, the pectoral-fin development slows or stops, usually resulting in no pectoral fins being visible in adults. The time at which this shift in growth rate occurs ranges from postlarval transformation (in *N. hawaiiensis*) to full adult, i.e., the change had not been completed in the largest specimens examined (90–100 mm) in *N. crypticum*, with the vestigial pectoral rays still visible.

From the examination of specimens in those species in which the change occurs at a larger size, it is clear that the nature of this change is unique to the species of this group. When the pectoral fin stops growing, the rays do not get longer but they do steadily thicken and become stiffer ontogenetically. The pectoral fin tends to point directly ventrally as the rays become broader, like flattened bones, and eventually anastomose along the edge of the scapula. Skin develops and thickens over the now-vestigial pectoral fin so that no trace of a pectoral fin is externally visible in large adults (except in *N. crypticum*). It also appears that in these species, fusion of bony rays continues with growth so that in the largest adults, no trace of the pectoral fin may be present, even upon dissection of the pectoral region (except in *N. crypticum*, of course).

Other shared characters useful in distinguishing, but not unique to, the species of the Achirus group include (1) SAO_1 over VO_{2-3} interspace, (2) Prc_3 directly below or slightly behind vertical from Prc_4, (3) Pol_2 usually before vertical from origin of adipose fin, and (4) PVO_1–PVO_2 distance greater than in other species groups, usually about ⅓ to ½ the PVO_1–PLO distance.

These and other characters are compared in Table 1 for all the species groups of *Nannobrachium*.

The Achirus group contains five species: *N. achirus* (Andriashev, 1962); *N. phyllisae*, new species; *N. hawaiiensis*, new species; *N. wisneri*, new species; and *N. crypticum*, new species.

Modal characters of all species in the Achirus group are listed in Table A11.

TABLE 15.—Measurements of *Nannobrachium achirus* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	109.8	25.7	78 (50–154)		
Head depth	155	8	138–179	Y = 0.2 + 0.15x	0
Predorsal depth	144	14	106–171	Y = −2.8 + 0.17x	Sig +
Caudal peduncle depth	89	10	67–111	Y = −2.1 + 0.11x	Sig +
Caudal peduncle length	238	11	210–265	Y = −0.5 + 0.24x	Slt +
Postadipose length	214	12	180–240	Y = −0.7 + 0.22x	Slt +
Predorsal length	461	20	372–509	Y = 1.3 + 0.45x	Slt −
Prepelvic length	404	17	368–487	Y = 1.9 + 0.39x	Sig −
Preanal length	548	17	488–588	Y = 2.0 + 0.53x	Sig −
Pelvic to anal length	138	10	107–175	Y = 0.4 + 0.13x	Slt −
Head length	256	11	232–291	Y = 1.3 + 0.24x	Sig −
Upper-jaw length	192	10	169–220	Y = 2.4 + 0.17x	Sig −
Snout length	40	6	27–59	Y = 1.0 + 0.03x	Sig −
Eye diameter	49	4	37–58	Y = 0.6 + 0.04x	Sig −
Supracaudal-gland length	65	9	45–88	Y = 0.5 + 0.06x	Slt −
Infracaudal gland, solid length	167	18	107–203	Y = 0.1 + 0.17x	0
Infracaudal gland, extreme length	173	16	137–211	Y = −0.7 + 0.18x	0
Anal-fin base length	225	15	180–318	Y = −1.6 + 0.24x	Slt +
Dorsal-fin base length	178	14	152–241	Y = −0.9 + 0.19x	Slt +
Adipose-fin length	47	8	28–64	Y = −0.6 + 0.05x	Slt +

Nannobrachium achirus (Andriashev, 1962), new combination

FIGURE 18, TABLE 15

Lampanyctus ater.—Norman, 1930:331 [subantarctic South Atlantic].—[Not Tåning, 1928.]

Lampanyctus achirus Andriashev, 1962:256–259 [original description, subantarctic South Pacific].—Bekker, 1964:474 [in part?] [zoogeography]; 1967a:116 [in part?] [southwest Atlantic].—Bussing, 1965:203–204 [in part?] [geographical variability].—Nafpaktitis and Nafpaktitis, 1969:45–46 [in part] [description, South Indian].—Parin and Andriashev, 1972:885 [zoogeographic relationships].—Krefft, 1974:252 [?in part] [distribution characterized].—Parin et al., 1974:106 [in part?] [southwest Atlantic].—Wisner, 1976:176–180 [in part] [description, distribution, figure].—Paxton, 1979:14 [holotype and paratypes].—Hulley, 1981:182–184 [description, South Atlantic]; 1984a:61, 78–79, fig. 11 [description, off South Africa]; 1986b:240, 242 [zoogeography]; 1986c:306, fig. 86.73 [description, South Africa, figure]; 1989:53 [South Indian, 38°09′39″S, 78°02′63″E]; 1990:162, 163 [figured, Southern Ocean].—McGinnis, 1982:42–44, 66–70 [in part?] [distribution south of 30°S, relationships, zoogeography].—[?] Moser et al., 1984: 238–239, fig. 124E [relationships, larva figured from Moser and Ahlstrom, 1974].—Paxton and Hanley, 1989:263 [?in part] [Australian distribution].—Paxton et al., 1995:1315 [listed] [not seen, fide J. Paxton].

Lampanyctus sp. [possibly *achirus*].—Moser and Ahlstrom, 1974:406–407 [larva figured].

Lampanyctus (Lampanyctus) achirus.—Bekker, 1983:86, 87, 198, 199 [in part] [key, description, distribution].

COMPARATIVE DIAGNOSIS.—*Nannobrachium achirus* (Figure 18) can be distinguished from all other species in the Achirus group by its higher number of gill rakers and tooth patches on the lower limb of the second gill arch, and from all other species, except *N. wisneri*, by its higher number of AO photophores, infracaudal luminous gland scales, lateral line organs, and vertebrae (Table A11). It also can be separated from *N. wisneri* and *N. hawaiiensis* by the visible presence of pectoral fins in small specimens (up to about 60 mm). *Nannobrachium achirus* can be distinguished from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 78 specimens and are given in Tables A2–A8, A11.

Proportions: Given in Table 15.

Fins: Origin of anal fin behind vertical from middle of base of dorsal fin. Pectoral fins relatively long and well developed in juvenile stages (easily visible in specimens up to about 60 mm), reaching more than one-half distance to pelvic-fin insertion, progressively becoming relatively shorter, with thicker rays, and covered by skin (in various stages of becoming vestigial between about 50–80 mm). Adults (longer than about 80 mm) with vestigial rays buried in skin and not externally visible unless skin abraded or otherwise torn. In largest adults, vestigial pectoral-fin elements cannot be found (perhaps lost through resorption). Adipose fin over end of anal-fin base.

Luminous Organs: PLO about 2 photophore diameters below lateral line. PO_4 approximately on level of PVO_2 and above PO_3. PVO_{1-2} interspace wide, that distance 2–3 times into PVO_2–PLO distance. SAO_1 above VO_{2-3} interspace, frequently closer to VO_3. SAO_2 midway above interspace between VO_4 and AOa_1. SAO_3 above AOa_1 but somewhat variable in position. AOa_1 slightly depressed; AOa_{1-2} interspace not visibly enlarged. AOp_1 above or behind end of anal-fin base. Prc separate from AOp; Prc_{1-2} on horizontal line; Prc_3 below Prc_4 but slightly in advance of vertical from center of Prc_4. Supracaudal and infracaudal luminous glands well developed, commonly having single separate luminous scale preceding solid infracaudal gland. Secondary photophores in single row on either side of back; single photophore on posterior edge of each scale in first full scale row below middle row of scales; best developed and most prominent in region of adipose fin and less well developed further forward but appear to extend forward to nape.

Size: *Nannobrachium achirus* is a large-bodied species, reaching a maximum size in excess of 160 mm. The largest specimen recorded by Hulley (pers. comm., 1980) from the

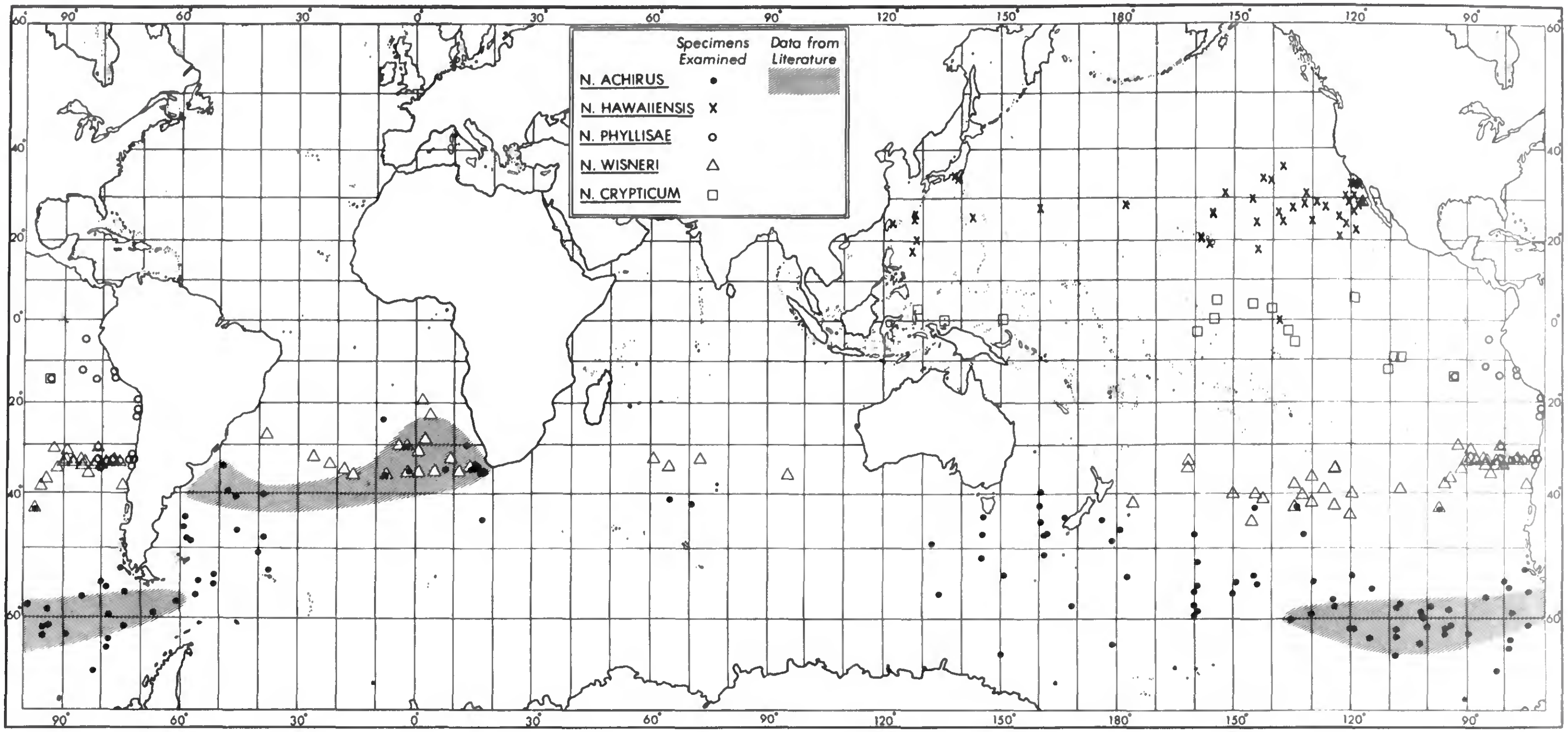

FIGURE 19.—Distributions and localities for material examined for species of the Achirus Group.

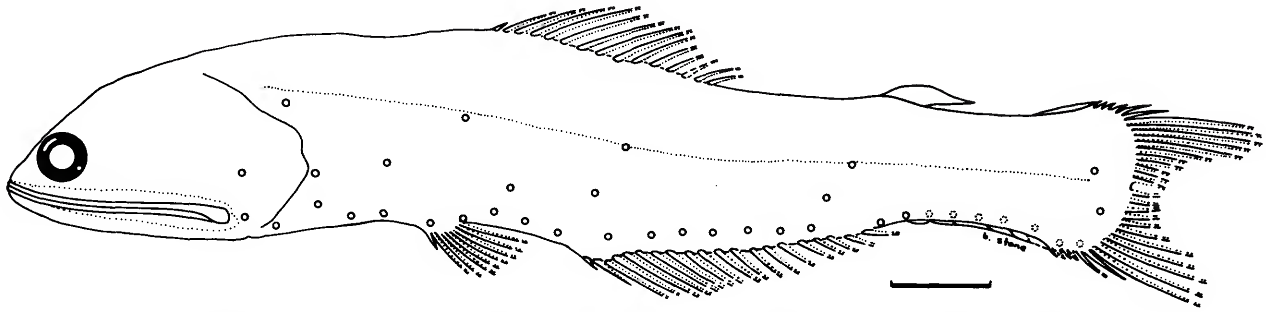

FIGURE 20.—*Nannobrachium phyllisae*, new species. Drawing of holotype, 108 mm, MCZ 96457, Pacific Ocean, 33°24'S, 73°33'W to 33°32'S, 73°35'W. (Scale bar=1 cm.)

South Atlantic was 162 mm. The largest specimen examined in this study was 154 mm.

Material: 451 (30–154 mm) specimens were examined, including the holotype, 124 mm, ZIN 36111, R/V *Ob*, sta 409, 64°36'S, 108°52'W, 24 April 1958, 1000 m.

DISCUSSION.—Within this species, the only one of the Achirus group previously described, there is the possibility of two sibling species, one having slightly more gill rakers than the other, as has been noted by Hulley (1981; and pers. comm., 1980). Based on material from the Patagonian Shelf off South America, as well as two specimens from the central South Atlantic, there appear to be two forms with different gill raker counts (one, typically 5+12/13, the other 6+13/14). These are obviously very close, but several additional differentiating characters were noted. In general, the more-numerous-gill-raker form tended to be black or gray in color versus brown or tan, had a larger vomerine tooth patch, and had the SAO_3 farther back. These characters, however, were not always correlated. Specimens were frequently found with a mixture of these characters, to the extent of having characters of each form on opposite sides of the same fish. Further analysis failed to establish consistent differences. Consequently, it is necessary to recognize only one species and to ascribe observed differences to a kind of mosaic pattern of variability.

The paratype listed by Andriashev (1962) as having been taken along with the holotype was not in the collections of the Zoological Institute, Russian Academy of Sciences, St. Petersburg, nor was any mention made of the disposition of the specimen in the original description. Checking the records further, Andriashev (pers. comm., 1976) found that the specimen had been sent (apparently on permanent loan) to Rolf Bolin at the Hopkins Marine Station (Stanford University) at the time the species was described. The specimen is now permanently in the California Academy of Sciences Fish Collection, Pacific Grove, California, CAS 15646.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium achirus* is a circumglobal, deep-water, subantarctic species (Figure 19). Because it has such a broad distribution, special efforts were made to compare material from the Atlantic, Pacific, and Indian sections of the Southern Ocean, but no patterns of differences were found in the specimens examined.

Nannobrachium phyllisae, new species

FIGURE 20, TABLE 16

Lampanyctus achirus.—Bussing, 1965:203–204 [in part] [midwaters of Peru-Chile Trench].—Craddock and Mead, 1970:28 [in part] [southeast Pacific].—Parin, 1971:82, 87, 89, 90 [in part?] [Peru Current].—Parin et al., 1973:114, 115 [?in part] [eastern tropical Pacific].—Wisner, 1976:177–180 [in part] [discussion, fig. 166A].—[Not Andriashev, 1962.]

TYPE SPECIMENS.—*Holotype:* Male, 108 mm, WHOI, *Anton Bruun* Cruise XIII, sta 52, 33°24'S, 73°33'W to 33°32'S, 73°35'W, 01 February 1966.

Paratypes: SIO 52-372, 2 (83–92 mm); SIO 63-1013, 2 (74–88 mm); SIO 63-1014, 1 (65 mm); SIO 65-667, 4 (112–147 mm); SIO 68-320, 1 (85 mm); SIO 69-321, 1 (28 mm); SIO 69-330, 7 (26–84 mm); USNM 303164, 3 (31–35 mm); USNM 303310, 5 (97–149 mm); WHOI 1344, 1 (39 mm); WHOI 1359, 1 (126 mm).

COMPARATIVE DIAGNOSIS.—*Nannobrachium phyllisae* (Figure 20) can be distinguished from *N. achirus* by its lower number of AO photophores, gill rakers, tooth patches, infracaudal luminous gland scales, lateral line organs, and vertebrae (Table A11); however, in all characters, there is overlap in ranges of counts. Similar differences are found between *N. phyllisae* and *N. wisneri*, namely, *N. phyllisae* has a lower number of infracaudal luminous glands and fewer vertebrae but has one more gill raker on the upper limb of the first gill arch. *Nannobrachium phyllisae*, however, can be separated from both *N. wisneri* and *N. hawaiiensis* by the presence of pectoral fins in small specimens (up to about 50 mm). It can be further separated from *N. hawaiiensis*, as well as from *N. crypticum*, by its higher AO photophore, gill raker, lateral line organ, and vertebral counts. It can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 21 specimens from the eastern Pacific Ocean and are given in Tables A2–A8, A11. Counts for the holotype are D 16, A 20, P_1 none, GR

TABLE 16.—Measurements of *Nannobrachium phyllisae* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	90.2	39.4	21 (30–149)		
Head depth	166	13	136–189	Y = 1.0 + 0.15x	Slt –
Predorsal depth	163	22	143–201	Y = –2.3 + 0.20x	Sig +
Caudal peduncle depth	97	10	76–119	Y = –0.8 + 0.11x	Sig +
Caudal peduncle length	209	17	174–257	Y = –0.5 + 0.22x	Slt +
Postadipose length	187	20	161–254	Y = –2.6 + 0.22x	Sig +
Predorsal length	465	21	421–514	Y = 1.9 + 0.44x	Sig –
Prepelvic length	418	23	384–459	Y = 2.8 + 0.38x	Sig –
Preanal length	542	28	471–582	Y = 1.6 + 0.52x	Slt –
Pelvic to anal length	120	9	97–135	Y = –0.1 + 0.12x	0
Head length	283	13	255–310	Y = 1.6 + 0.26x	Sig –
Upper-jaw length	210	15	183–240	Y = 2.2 + 0.18x	Sig –
Snout length	46	7	36–63	Y = 0.7 + 0.04x	Sig –
Eye diameter	46	3	41–53	Y = 0.1 + 0.04x	Slt –
Supracaudal-gland length	57	8	49–77	Y = 0.8 + 0.05x	Sig –
Infracaudal gland, solid length	130	16	100–159	Y = 0.2 + 0.13x	0
Infracaudal gland, extreme length	135	19	100–162	Y = 0.4 + 0.13x	0
Anal-fin base length	239	17	206–271	Y = –2.0 + 0.27x	Sig +
Dorsal-fin base length	201	14	176–228	Y = –1.7 + 0.22x	Sig +
Adipose-fin length	56	11	39–75	Y = 0.9 + 0.04x	Slt –

4+12, tooth patches 9, AO 7+7, SC/IC 3/i+5, LL 34, V 15+21.

Proportions: Given in Table 16. Holotype measurements as follows: SL 108, AD 18.6, PDD 19.5, CPD 11.4, CPL 21.6, PADL 20.5, PDL 53.5, PPL 41.4, PANL 56.2, PAL 12.9, HL 31.4, UJL 22.7, SOL 5.0, ED 5.2, SGL 5.3, IGS 12.1, IGEL 13.9, AFB 28.7, DFB 21.7, AF 8.7.

Fins: Origin of anal fin under middle of dorsal-fin base. Pectoral fins relatively long and well developed in juvenile stages (easily visible in specimens up to about 50 mm), progressively becoming relatively shorter, with thicker rays, (covered by skin in various stages of becoming vestigial, between about 40–70 mm); vestigial rays buried in skin and not externally visible. Largest adults with vestigial pectoral-fin elements undetectable (perhaps lost through resorption). Adipose fin over end of anal-fin base.

Luminous Organs: PLO 1–2 photophore diameters below lateral line (slightly more than 1 in holotype). PO_4 on level of PVO_2 (above level in holotype) and above PO_3. PVO_{1-2} interspace wide, that distance 2–3 times into PVO_2–PLO distance (about 2½ times in holotype). SAO_1 above VO_{2-3} interspace (slightly closer to VO_2 in holotype) SAO_2 above VO_4–AOa_1 interspace but usually closer to AO_1 (notably closer to AOa_1 in holotype). SAO_3 behind vertical from AOa_1. AOa_1 not noticeably depressed; AOa_{1-2} interspace only very slightly enlarged, if at all. AOp_1 above end of anal-fin base (slightly behind end in holotype). Prc slightly separate from AOp; Prc_{1-2} on horizontal line; Prc_3 below Prc_4 but variable, although frequently behind vertical from Prc_4 (Prc_3 on vertical from posterior margin of Prc_4 in holotype). Supracaudal and infracaudal luminous glands well developed, commonly having single separated luminous scale preceding solid infracaudal gland. Secondary photophores not found.

Size: *Nannobrachium phyllisae* is a large species, reaching a maximum size of at least 151 mm based on examined material. Wisner (1976), in discussing the *Lampanyctus achirus* species complex, listed a maximum size of about 155 mm for specimens from the southeast Pacific, which probably included this species.

Material: 30 (28–151 mm) specimens, excluding type material.

DISCUSSION.—In the past, *N. phyllisae* has been confused with *N. achirus* and frequently included in discussions of that species (Bussing, 1965; Craddock and Mead, 1970; and Wisner, 1976). There is no doubt that *N. phyllisae* is most closely related to *N. achirus,* which it resembles in size at which loss of pectoral fins occurs, in general body size and shape, and in having similar meristics. Because of the similarity of these two species, *N. phyllisae* may be expected to have similar larvae and to show other characteristics that have been noted for *N. achirus,* including secondary photophores on the back.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium phyllisae* is restricted to the Peru-Chile Current area of the southeastern Pacific Ocean (Figure 19). As might be expected for a species with such a restricted geographic range, no consistent geographic variability was found in specimens examined from different parts of the range.

ETYMOLOGY.—I have the pleasure of naming this species in honor of my former wife Phyllis E. Fabian, as a token of recognition for her many years of support, which culminated in this study.

Nannobrachium hawaiiensis, new species

FIGURE 21, TABLE 17

Lampanyctus sp. (no pectorals).—Berry and Perkins, 1966:662 [Pacific off California and northern Mexico].

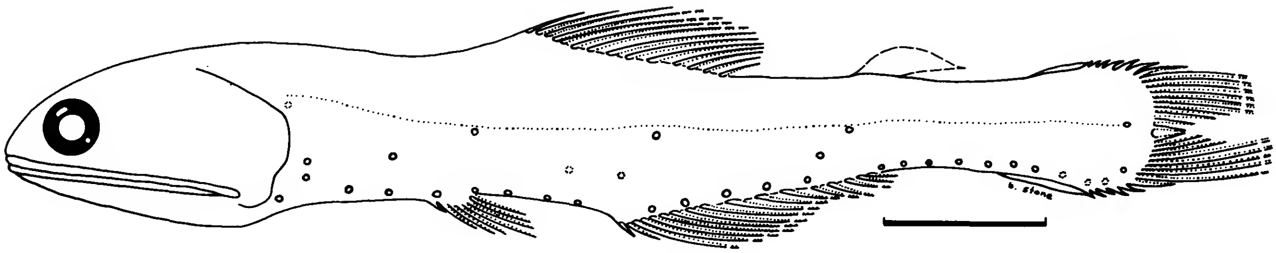

FIGURE 21.—*Nannobrachium hawaiiensis*, new species. Drawing of holotype, 63 mm, SIO 71-300, Pacific Ocean, 27°24.5′–27°24.9′N, 155°25.5′–155°13.7′W. (Scale bar=1 cm.)

Lampanyctus niger (Form A).—Clarke, 1973:416–418 [ecology north of Hawaii].—[Not Günther, 1887.]
Lampanyctus achirus Species Complex "northern Pacific" form.—Wisner, 1976:177–180, fig. 166B [in part?] [size, characterization].—[Not Andriashev, 1962.]
Lampanyctus niger.—Parin et al., 1977:122, 123 [in part?] [western Pacific].—[Not Günther, 1887.]
Lampanyctus "lacks pectorals" (sp. nov. A).—Loeb, 1979a:178, 186 [in part?] [larvae, central North Pacific]; 1979b:780–782, 783 [in part?] [larval depth distribution]; 1980:192–195, 199 [in part?] [central Pacific larval distribution].
Lampanyctus (sp. 1).—Fujii, 1984:69, pl. 66-N [description, distribution].
Lampanyctus sp.—Moser et al., 1984:238, fig. 124F.
Lampanyctus (sp. A).—Clarke, 1987:63, 65 [biogeography in central Pacific].
Nannobrachium "no pectorals".—Moser and Ahlstrom, 1996:420–421 [early life history and larvae illustrated].

TYPE SPECIMENS.—*Holotype:* Male, 63 mm, SIO 71-300, *Aries* Expedition, sta 9, 27°24.5′N, 155°25.5′W to 27°24.9′N, 155°13.7′W, 30 September 1971.

Paratypes: HIMB 70-1221, 76 (28–70 mm); HIMB 71-22, 18 (34–70 mm); HIMB 71-617, 32 (35–60 mm); HIMB 71-618, 62 (22–70 mm); HIMB 71-622, 22 (21–62 mm); HIMB 71-631, 30 (36–69 mm); LACM 30-988, 1 (72 mm); LACM 92-6216, 1 (57 mm); OS 012814, 5 (28–68 mm); SIO 71-300, 3 (14–69 mm).

COMPARATIVE DIAGNOSIS.—*Nannobrachium hawaiiensis* (Figure 21) can be distinguished from all species in the Achirus group, except *N. crypticum*, by its lower number of AO photophores, infracaudal luminous gland scales, lateral line organs, and vertebrae (Table A11). It can be separated from *N. achirus* and *N. phyllisae* by its lower number of gill rakers and tooth patches on the lower limb of the second gill arch. It can be distinguished from all species, especially from *N. crypticum*, by the complete absence of pectoral fins through the juvenile and adult states. It also can be separated from *N. crypticum* by its higher number of gill rakers and tooth patches on the lower limb of the second gill arch. *Nannobrachium hawaiiensis* can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1, but especially by the absence of pectoral fins.

DESCRIPTION.—Counts are based on up to 26 specimens and are given in Tables A2–A8, A11. Counts for the holotype are D 14, A 16, P_1 none, GR 4+11, tooth patches 9, AO 5+7, SC/IC 3/4, LL 33, V 15+20.

TABLE 17.—Measurements of *Nannobrachium hawaiiensis* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	50.7	14.8	26 (24.6–70.0)		
Head depth	160	10	134–177	Y = 0.7 + 0.15x	Slt –
Predorsal depth	119	13	89–137	Y = –0.6 + 0.13x	Slt +
Caudal peduncle depth	74	6	61–89	Y = –0.3 + 0.08x	Slt +
Caudal peduncle length	221	20	190–270	Y = 0.0 + 0.22x	0
Postadipose length	199	14	171–230	Y = 0.0 + 0.20x	0
Predorsal length	477	20	427–507	Y = 1.7 + 0.44x	Sig –
Prepelvic length	414	18	363–446	Y = 0.9 + 0.40x	Slt –
Preanal length	556	30	480–610	Y = 2.7 + 0.50x	Sig –
Pelvic to anal length	146	13	118–167	Y = 0.4 + 0.14x	Slt –
Head length	271	15	235–304	Y = 0.8 + 0.26x	Slt –
Upper-jaw length	212	14	178–246	Y = 1.2 + 0.19x	Sig –
Snout length	46	7	35–61	Y = 0.6 + 0.03x	Sig –
Eye diameter	51	8	36–69	Y = –0.9 + 0.07x	Sig +
Supracaudal-gland length	59	5	49–68	Y = 0.3 + 0.05x	Slt –
Infracaudal gland, solid length	90	12	73–121	Y = 0.8 + 0.07x	Slt –
Infracaudal gland, extreme length	91	13	73–121	Y = 0.7 + 0.08x	Slt –
Anal-fin base length	221	18	155–245	Y = –0.5 + 0.23x	Slt +
Dorsal-fin base length	175	14	154–211	Y = –0.2 + 0.18x	0
Adipose-fin length	69	12	44–89	Y = 0.2 + 0.07x	0

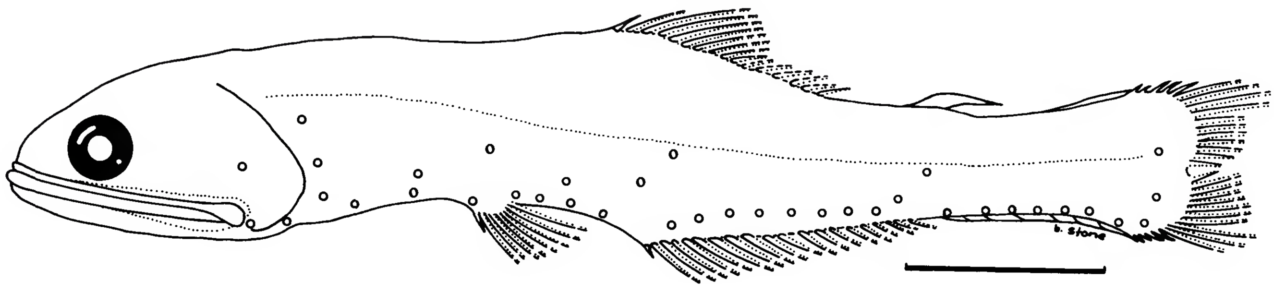

FIGURE 22.—*Nannobrachium wisneri*, new species. Drawing of holotype, 63 mm, MCZ 55478, Atlantic Ocean, 35°50′S, 2°16′W. (Scale bar=1 cm.)

Proportions: Given in Table 17. Holotype measurements (in mm) as follows: SL 63, HD 10.2, PDD 10.1, CPD 4.8, CPL 14.0, PADL 10.4, PDL 30.6, PPl 24.5, PANL 33.3, PAL 8.6, HL 18.0, UJL 13.6, SOL 2.7, ED 4.7, SGL 3.3, IGS 4.9, IGEL 4.9, AFB 13.7, DFB 11.2, AF 5.6.

Fins: Origin of anal fin below middle of base of dorsal fin. Pectoral fins completely lacking in juvenile, subadult, and adult stages, apparently lost at about time of postlarval transformation. Larvae with enormous, fan-shaped pectorals (Moser and Ahlstrom, 1996:421, figure Myctophidae 17). Pectoral-fin rays present buried in the skin in small juveniles (approximately 25–35 mm). Adipose-fin base over end of anal-fin base.

Luminous Organs: PLO about 2 photophore diameters below lateral line. PO_4 approximately on, or slightly below, level of PVO_2 (about on level of PVO_2 in holotype) and above PO_3. PVO_{1-2} interspace wide, that distance 2–3 times into PVO_2–PLO distance (slightly more than 2 times in holotype). SAO_1 approximately over VO_3 (behind vertical from VO_3 in holotype). SAO_2 above interspace between VO_4 and AOa_1 but much closer to AOa_1, sometimes over AOa_1 (SAO_2 before vertical from AOa_1 in holotype). SAO_3 behind vertical from AOa_1. AOa_1 not noticeably depressed nor AOa_{1-2} interspace noticeably enlarged. AOp_1 above end of anal-fin base. Prc slightly separate from AOp (notably separate in holotype); Prc_{1-2} approximately on horizontal line; Prc_3 below Prc_4 but slightly before vertical from center of Prc_4. Supracaudal and infracaudal luminous glands well developed, rarely having single separate luminous scale preceding solid infracaudal gland. Secondary photophores possibly present.

Size: Nannobrachium hawaiiensis is a small-bodied species of *Nannobrachium*, probably not greatly exceeding 80 mm in length. The longest specimen encountered in this study was 81 mm. Wisner (1976) gave about 70 mm as the maximum size for the "northeastern Pacific form" of the "*Lampanyctus achirus* Species Complex" and reported that specimens 58–65 mm had well-developed, although immature, ova.

Material: 942 (10–81 mm) specimens, excluding type material.

DISCUSSION.—For a number of years, *N. hawaiiensis* has been recognized as a distinct species in the North Pacific. Berry and Perkins (1966) identified the specimens that they listed as "*Lampanyctus* sp. (no pectorals)," pointing out that these specimens are specifically distinct from *N. achirus*. Wisner (1976, fig. 166B), however, discussed the very complex situation in the eastern Pacific, with an indication of clinal variation in certain meristics in specimens from the North Pacific to the southeast off South America. Indeed, the number of gill rakers and AO photophores in four of the species involved (Wisner did not identify specimens of *N. crypticum* with the *achirus* complex) generally increase monotonically from north to south, with *N. hawaiiensis*, the northernmost species, having the lowest numbers and *N. achirus*, the southernmost, having the highest numbers. Once the four species involved are distinguished, however, it is clear that there is no cline in characteristics of a single species but rather four species, each with different meristics.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium hawaiiensis* is the only species of the Achirus group found exclusively in the northern hemisphere. It is restricted to the North Pacific Central water mass (Figure 19). Material was compared from the eastern and western parts of the range, but no consistent geographic variation was evident.

ETYMOLOGY.—The name refers to the Hawaiian Islands near the center of the range, where this species is abundant in the surrounding midwaters.

Nannobrachium wisneri, new species

FIGURE 22, TABLE 18

Lampanyctus ater.—Norman, 1930:331 [in part] [South Atlantic].—[Not Tåning, 1928.]

Lampanyctus intricarius.—Norman, 1930:330 [in part, fide McGinnis, 1982] [South Atlantic].—[Not Tåning, 1928.]

Lampanyctus niger.—Norman, 1930:331 [in part] [South Atlantic].—[Not Günther, 1887.]

Lampanyctus sp.—Norman, 1930:331 [South Atlantic].

Lampanyctus achirus.—Bussing, 1965:203–204 [in part] [midwaters of Peru-Chile Trench].—Nafpaktitis and Nafpaktitis, 1969:45–46 [in part] [description, South Indian, fig. 55].—Craddock and Mead, 1970:28 [in part] [southeast Pacific].—Parin, 1971:82, 87, 89, 90 [?in part?] [Peru Current].—

TABLE 18.—Measurements of *Nannobrachium wisneri* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	56.4	9.7	25 (37.8–79.6)		
Head depth	150	8	131–161	Y = 1.2 + 0.13x	Sig –
Predorsal depth	127	12	108–150	Y = –0.4 + 0.13x	0
Caudal peduncle depth	84	5	76–93	Y = 0.0 + 0.08x	0
Caudal peduncle length	213	14	181–241	Y = 0.7 + 0.20x	Slt –
Postadipose length	187	12	160–211	Y = 0.4 + 0.18x	0
Predorsal length	504	25	415–532	Y = 5.6 + 0.40x	Sig –
Prepelvic length	408	19	346–439	Y = 1.4 + 0.38x	Slt –
Preanal length	542	43	418–594	Y = 5.5 + 0.44x	Slt –
Pelvic to anal length	145	10	131–170	Y = 0.5 + 0.14x	Slt –
Head length	269	14	238–294	Y = –0.3 + 0.28x	0
Upper-jaw length	204	6	193–214	Y = 0.8 + 0.19x	Slt –
Snout length	43	5	34–56	Y = 1.0 + 0.02x	Sig –
Eye diameter	55	7	40–65	Y = 0.9 + 0.04x	Slt –
Supracaudal-gland length	67	10	50–89	Y = –0.6 + 0.08x	Slt +
Infracaudal gland, solid length	167	13	139–198	Y = 1.6 + 0.14x	Slt –
Infracaudal gland, extreme length	170	14	139–206	Y = 1.9 + 0.13x	Sig –
Anal-fin base length	222	16	170–253	Y = 2.5 + 0.18x	Sig –
Dorsal-fin base length	171	11	144–194	Y = 1.4 + 0.15x	Slt –
Adipose-fin length	46	8	34–66	Y = 0.5 + 0.04x	Slt –

Parin et al., 1974:106 [?in part] [southwest Atlantic].—Rubies, 1985: 578–584 [?in part?] [Valdivia Bank off Namibia, gill raker numbers].—[Not Andriashev, 1962.]

Lampanyctus cf. *achirus*.—Hulley, 1972:225 [in part?] [description, South Atlantic].—[Not Andriashev, 1962.]

Lampanyctus ?achirus.—Hulley, 1981:184–185 [description, southwest Atlantic].—[Not Andriashev, 1962.]

Lampanyctus sp. A.—McGinnis, 1982:43–45, 66 [in part?] [distribution south of 30°S, relationships, zoogeography].

Lampanyctus (Lampanyctus) achirus.—Bekker, 1983:86–87, 198–199 [in part] [key, description, distribution].—[Not Andriashev, 1962.]

Lampanyctus sp. B.—Hulley, 1986b:243 [zoogeography]; 1986c:310, fig. 86.89 [description, South Africa, figure].

TYPE SPECIMENS.—*Holotype:* Female (?), 57 mm, MCZ 55478 (RHB 2229), R.V. *Atlantis II*, sta 60, 35°50'S, 2°16'W, 23 April 1971, depth 600–650 m.

Paratypes: LACM 11-259, 7 (30–37 mm); LACM 11-273, 6 (30–85 mm); MCZ 55478 (RHB 2229), 2 (34–35 mm); SIO 58-256, 1 (64 mm); SIO 61-46, 31 (34–71 mm); SIO 63-542, 2 (37–57 mm); SIO 63-544, 2 (34–60 mm); SIO 69-321, 22 (25–69 mm); USNM 209390, 139 (20–65 mm); USNM 209395, 31 (25–65 mm); USNM 209400, 21 (38–68 mm); WHOI 13-41, 4 (43–54 mm).

COMPARATIVE DIAGNOSIS.—*Nannobrachium wisneri* (Figure 22) can be distinguished from *N. crypticum*, *N. achirus*, and *N. phyllisae* by its gill raker count (lower than in *N. achirus* and *N. phyllisae*, higher than in *N. crypticum*) and by the virtually complete lack of pectoral fins in specimens larger than small juvenile stages (about 35 mm). It can be most easily distinguished from *N. hawaiiensis* by the higher number of infracaudal luminous gland scales, lateral line organs, and vertebrae (Table A11). *Nannobrachium wisneri* can be separated from all other species of *Nannobrachium* by the combination of characters in Table 1, but especially by the virtual absence of pectoral fins.

DESCRIPTION.—Counts are based on up to 26 specimens and are given in Tables A2–A8, A11. Counts for the holotype are D 15, A 19, P_1 none, GR 4+11, tooth patches 9, AO 8+6 (L), 7+7 (R), SC/IC 4(?)/7(?), LL 36, V 15+20.

Proportions: Given in Table 18. Holotype measurements (in mm) as follows: SL 57, HD 9.1, PDD 8.1, CPD 5.1, CPL 11.1, PADL 11.0, PDL 29.2, PPL 22.9, PANL 30.3, PAL 7.9, HL 15.8, UJL 12.1, SOL 3.0, ED 4.0, SGL 3.8 (damaged), IGS 9.9, IGEL 9.9, AFB 14.6, DFB 11.9, AF 4.

Fins: Origin of anal fin under or before vertical through center of base of dorsal fin (before vertical in holotype). Pectoral fins completely lacking in subadult and adult stages; vestigial in small juveniles (less than about 30 mm). Fin rays present but buried in the skin in larger juveniles (approximately 30–35 mm). Adipose-fin base over end of anal-fin base.

Luminous Organs: PLO typically more than 2 photophore diameters below lateral line (nearly 3 diameters in holotype). PO_4 approximately on, or slightly below, level of PVO_2 and above PO_3. PVO_{1-2} interspace wide, that distance 1½–3 times into PVO_2–PLO interspace (about 1½ times in holotype). SAO_1 above VO_3 but somewhat forward of vertical from center of VO_3. SAO_2 midway above interspace between VO_4 and AOa_1 but variable in position (closer to vertical from AOa_1 in holotype). SAO_3 above AOa_1. AOa_1 not noticeably or only slightly depressed; AOa_{1-2} interspace not noticeably enlarged. AOp_1 above end of anal-fin base (behind base on left side of holotype). Prc slightly separate from AOp; Prc_{1-2} approximately on horizontal line, but Prc_2 often slightly lower; Prc_3 below Prc_4 but slightly in advance of vertical from center of Prc_4. Supracaudal and infracaudal luminous glands well developed, rarely having single separated luminous scale preceding solid infracaudal gland. Possible traces of secondary photophores on back in similar position to those of *N. achirus*.

Size: *Nannobrachium wisneri* probably does not exceed 90 mm in length. The largest specimen examined for this study was 88 mm.

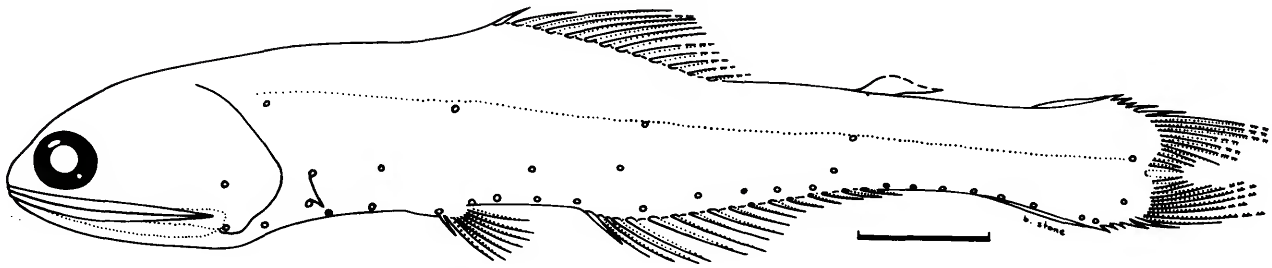

FIGURE 23.—*Nannobrachium crypticum*, new species. Drawing of holotype, 87 mm, HIMB TC 47-61, Pacific Ocean, 3°30′N, 145°00′W. (Scale bar=1 cm.)

Material: 1020 (20–83 mm) specimens, excluding type material.

DISCUSSION.—*Nannobrachium wisneri* has long been confused with both *N. achirus* and *N. phyllisae*. For example, Nafpaktitis and Nafpaktitis (1969), in discussing Indian Ocean myctophids, had only two specimens that they referred to "*N. achirus*." The larger specimen (144 mm) was correctly identified, but the smaller specimen (63 mm, label number 7324) was actually *N. wisneri*. In fact, it is this specimen of *N. wisneri* that was illustrated in their fig. 55 as *L. achirus*. A different problem is an 80 mm specimen collected by the *Walther Herwig* (sta 348/71) in the South Atlantic and listed by Hulley (1981) as *Lampanyctus*? *achirus*. It appears to be a specimen of *N. wisneri* with an atypically low number of gill rakers (4+10 versus 4+11 or 12 in typical specimens of *N. wisneri*) and vertebrae (given as 34 by Hulley, whereas the modal number of *N. wisneri* is 37); however, it has 9 tooth patches on the lower limb of the second gill arch, the modal number for *N. wisneri*. Furthermore, in examining the specimen very carefully, no trace of pectoral-fin rays could be found, even where the skin was abraded. Thus, it seems best to consider this specimen an example of *N. wisneri* with an abnormally low number of gill rakers and vertebrae, despite the collection locality of *Walther Herwig* sta 348, which is off the mouth of the Rio de la Plata, far to the south of other specimens of *N. wisneri* examined from the western South Atlantic. I agree with Hulley that it may yet prove to represent a distinct species.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium wisneri* is nearly circumglobal in Subtropical Convergence waters (Figure 19). The gap in its range south, and especially east, of Australia appears to be real, not an artifact of sampling effort. Particular attention was paid to comparing specimens from the Atlantic, Pacific, and Indian oceans, but no consistent meristic differences were found, except the one Atlantic specimen discussed above.

ETYMOLOGY.—It is an honor and a pleasure to name this species for Robert L. Wisner of the Scripps Institution of Oceanography in recognition of his contributions to the systematics of myctophids and other oceanic fishes.

Nannobrachium crypticum, new species

FIGURE 23, TABLE 19

Lampanyctus "niger".—Hartmann and Clarke, 1975:637 [in part] [ecology at 39°30′N, 145°].—[Not Günther, 1887.]

Lampanyctus sp. D.—Clarke, 1987:59, 61, 62 [in part] [biogeography in central Pacific].

TYPE SPECIMENS.—*Holotype:* Female, 87 mm, HIMB TC 47-61, 3°30′N, 145°00′W, 8 February 1970, Thomas A. Clarke, collector.

Paratypes: HIMB 47-52, 40 (28–93 mm); HIMB 47-6, 28 (30–89 mm); HIMB 47-61, 13 (20–87 mm); HIMB 47-67, 31 (23–98 mm); SIO 52-320, 1 (41 mm); SIO 60-236, 3 (31–87 mm); SIO 73-164, 2 (87–90 mm); USNM 303313, 7 (27–61 mm).

COMPARATIVE DIAGNOSIS.—*Nannobrachium crypticum* (Figure 23) can be distinguished from all other species of the Achirus group by the number of AO photophores, gill rakers, and lower limb tooth patches on the second gill arch (all fewer than in any other species of the Achirus group) (Table A11), and by the presence of externally visible pectoral fins in all life stages (except perhaps in the largest adults—greater than 90 mm). *Nannobrachium crypticum* is superficially similar to many species in the Nigrum group, but in addition to the differences in Table 1, it can be distinguished from them by the number of gill rakers and lower limb tooth patches on the second gill arch (both lower than in *N. nigrum* and *N. atrum;* one fewer gill raker, on average, than in *N. indicum*), by the number of its AO photophores and vertebrae (both lower than in *N. atrum* and *N. gibbsi*), and by the number of infracaudal luminous gland scales and lateral line organs (on average, both higher than in *N. indicum;* fewer lateral line organs than in *N. atrum*) (Table A1). *Nannobrachium crypticum* also can be distinguished from all other species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 99 specimens from the Pacific Ocean and are given in Tables A2–A8, A11. Counts for the holotype are D 13, A 17, P_1 12?, GR 4+10, tooth patches 8, AO 5+6 (L), 5+7 (R), SC/IC 3/i+5, LL 32, V 15+19.

TABLE 19.—Measurements of *Nannobrachium crypticum* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	76.4	15.4	29 (42–95)		
Head depth	142	8	129–157	Y = 1.1 + 0.13x	Sig –
Predorsal depth	144	13	105–167	Y = –0.8 + 0.15x	Slt +
Caudal peduncle depth	78	4	70–87	Y = –0.5 + 0.08x	Slt +
Caudal peduncle length	219	12	194–244	Y = 1.5 + 0.20x	Slt –
Postadipose length	219	11	194–239	Y = –1.1 + 0.23x	Slt +
Predorsal length	451	16	429–489	Y = 2.2 + 0.42x	Slt –
Prepelvic length	407	19	381–462	Y = 3.7 + 0.36x	Sig –
Preanal length	555	17	522–589	Y = 2.1 + 0.53x	Slt –
Pelvic to anal length	146	13	123–187	Y = 0.7 + 0.14x	Slt –
Head length	258	12	238–288	Y = 1.4 + 0.24x	Slt –
Upper-jaw length	200	9	184–229	Y = 1.8 + 0.18x	Sig –
Snout length	46	4	37–53	Y = 1.1 + 0.03x	Sig –
Eye diameter	56	6	45–70	Y = 0.8 + 0.05x	Slt –
Supracaudal-gland length	52	10	38–74	Y = 1.7 + 0.03x	Sig –
Infracaudal gland, solid length	76	15	45–113	Y = 0.5 + 0.07x	0
Infracaudal gland, extreme length	77	15	47–112	Y = 0.2 + 0.08x	0
Anal-fin base length	234	15	189–255	Y = –2.6 + 0.27x	Sig +
Dorsal-fin base length	165	11	137–189	Y = 0.1 + 0.16x	0
Adipose-fin length	57	13	27–85	Y = 0.1 + 0.06x	0

Proportions: Given in Table 19. Holotype measurements (in mm) as follows: SL 87, HD 14.4, PDD 12.5, CPD 6.9, CPL 19.2, PADL 18.7, PDL 39.8, PPL 34.3, PANL 47.7, PAL 13.8, HL 25.3, UJL 18.1, SOL 4.4, ED 5.0, SGL 5.3, IGS 8.5, IGEL 10.2, AFB 21.1, DFB 14.6, AF 6.4.

Fins: Origin of anal fin behind vertical through middle of base of dorsal fin. Pectoral fins not reaching beyond PO_3, pointing directly downward in larger specimens; rays progressively thicker, stiffer, and relatively shorter in larger specimens but remnants always visible externally, apparently not covered with skin even in 90–100 mm specimens. (Remnant rays in holotype are 2–3 mm long.)

Luminous Organs: PLO 1–2 photophore diameters below lateral line (1 in holotype). PO_4 approximately on level of PVO_2 (on level in holotype) but somewhat variable and above but slightly behind vertical from PO_3. PVO_2 before or above middle of pectoral-fin base (above middle in holotype); PVO_{1-2} interspace ½–⅓ of PVO_2–PLO distance (approximately ⅓ in holotype). VLO within 1 photophore diameter below lateral line. SAO_2 midway between VO_4 and AOa_1, often closer to AOa_1 (closer to AOa_1 in holotype). SAO_3 above, and slightly forward of vertical from AOa_1. AOa_1 slightly depressed; AOa_{1-2} interspace slightly enlarged. AOp_1 at end of anal-fin base. Prc separated from AOp; Prc_{1-2} on horizontal line; Prc_{3-4} on or nearly on vertical, 1 to 2 photophore diameters behind Prc_2 (Prc_{3-4} vertical in holotype, approximately 1 photophore diameter behind Prc_2); Prc_3 approximately equidistant between Prc_2 and Prc_4. Pol_2 approximately on vertical from adipose-fin origin. Supracaudal and infracaudal luminous glands well developed, infrequently having single separated luminous scale preceding solid infracaudal gland. Secondary photophores seen on back of 1 specimen, 1 photophore near posterior margin of each scale in 2 rows, 1 on either side of dorsal midline in region behind center of dorsal-fin base but additional extent of secondary photophores uncertain.

Size: *Nannobrachium crypticum* probably reaches a maximum size in excess of 100 mm. The largest specimen encountered in this study was 98 mm.

Material: 252 (19–93 mm) specimens, excluding type material.

DISCUSSION.—Just as *N. nigrum* and *N. atrum* have been confused in the past, specimens of *N. crypticum* have been misidentified in collections under both of those names. It was recognized, however, as related to, but distinct from, other species of *Nannobrachium* by Hartmann and Clarke (1975) and by Clarke (1987).

Despite the close similarity and initial confusion between *N. crypticum* and *N. gibbsi,* there is no doubt that *N. crypticum* belongs to the Achirus, not the Nigrum, species group. Although the Pol_2 is relatively far posterior in relation to the adipose-fin origin in this species, it is a typical Achirus group species in all other characters: Prc arrangement, wide PVO_{1-2} interspace, and, most importantly, the devolution of the pectoral fins as they become progressively more vestigial in larger specimens. The pattern is clearly the same in this species as in *N. achirus,* differing only in the larger size at which the vestigial pectoral rays would become covered with skin in *N. crypticum.* Because the large specimens available are in poor condition, with the skin torn, it is not clear whether *N. crypticum* ever has the vestigial pectoral fins completely covered over with skin as in the remaining Achirus group species. It may be that in very large specimens (probably in excess of 100 mm) without torn skin, the vestigial pectoral fins would not be visible externally.

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium crypticum* is apparently restricted to the equatorial Pacific (Figure 19), where it occurs across the breadth of the ocean from east to west. Variability, which may be geographical, was noted in some meristic characters. In a sample of five specimens taken on expedition Piquero V (lot 137, SIO 69-341) in

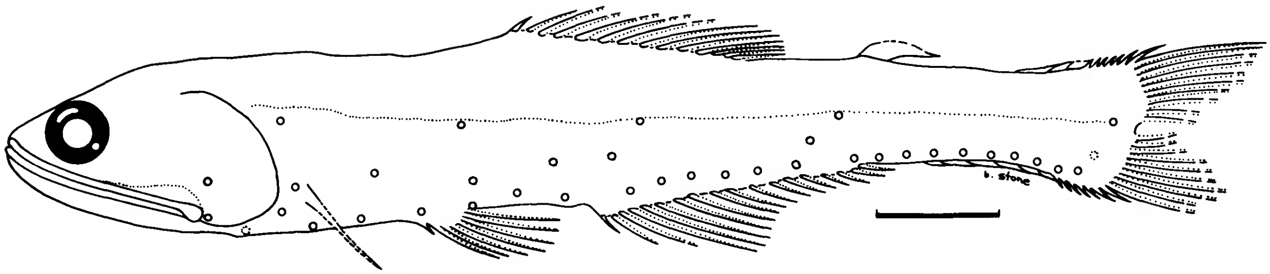

FIGURE 24.—*Nannobrachium isaacsi* (Wisner, 1974). Drawing of 98.5 mm specimen, LACM 34917-1, Atlantic Ocean, 20°01'N, 18°15'W. (Scale bar=1 cm.)

the southeast portion of the range at 13.5°S, 110.5°W, four specimens had dorsal- and anal-fin ray counts, as well as AO photophore counts, that were at the high end of the range for the species. On the other hand, another sample of six specimens from Piquero V (lot 527, SIO 69-338) taken at 9°S, 108°W, shows little indication of a higher than average number of dorsal- or anal-fin rays or AO photophores. More material is required to clarify whether this variability is significant.

ETYMOLOGY.—The name is derived directly from the Latin adjective *crypticum,* meaning "obscure" or "hidden," alluding to the unrecognized existence and relationships of this species.

The Isaacsi Group

The unique character distinguishing the species in this group is the position of the VO_2 directly above the VO_1 instead of midway between VO_1 and VO_3 as in all the other groups.

The pectoral-fin development in this group is essentially identical to that of the species in the Cuprarium group except that the pectoral fin is usually slightly longer. Normally, the pectoral fin reaches to or nearly to the pelvic-fin insertion, and the pectoral rays are slightly thicker and stiffer than those of the Cuprarium group.

One other character shared with the species of the Cuprarium group is the position of the Prc_3; it is found approximately on a vertical midway between Prc_2 and Prc_4.

These and other characters are compared in Table 1 for all the species groups of *Nannobrachium.*

The Isaacsi group contains a single species: *N. isaacsi* (Wisner, 1974).

Modal characters for *N. isaacsi* are listed in Table A10 along with the species in the Cuprarium group.

Nannobrachium isaacsi (Wisner, 1974), new combination

FIGURE 24, TABLE 20

Lampanyctus micropterus Brauer, 1906 [in part] [2 of 3 syntypes, fide Hulley, 1981].

Lampanyctus isaacsi Wisner, 1974:14–17 [original description, eastern equatorial Atlantic].—Nafpaktitis et al., 1977:201–203 [description, distribution, figure].—Backus et al., 1977:267, 275, 277 [zoogeography].—Paxton, 1979: 14 [holotype and paratypes].—Hulley, 1981:204–206 [description, Atlantic distribution].—Kinzer and Schulz, 1985:314, 316 [depth distribution, central equatorial Atlantic].—Rubies, 1985:578, 584 [Benguela Current, off Namibia, gill raker number low—questionable identification].

Lampanyctus (Lampanyctus) isaacsi.—Bekker, 1983:87–89, 193, 200 [key, description, distribution].

TABLE 20.—Measurements of *Nannobrachium isaacsi* as thousandths of standard length with notes on allometry.

Character	Mean	Standard deviation	Range	Regression equation	Allometry
Standard length	91.1	20.8	25 (35.0–119.6)		
Head depth	144	6	130–157	Y = 0.5 + 0.14x	Slt –
Predorsal depth	132	14	103–151	Y = –2.0 + 0.16x	Slt +
Caudal peduncle depth	81	5	71–90	Y = –0.6 + 0.09x	Slt +
Caudal peduncle length	230	10	207–253	Y = –1.0 + 0.24x	Slt +
Postadipose length	211	11	187–228	Y = –0.5 + 0.22x	0
Predorsal length	448	16	401–486	Y = 2.5 + 0.42x	Sig –
Prepelvic length	396	15	355–423	Y = 2.3 + 0.37x	Sig –
Preanal length	533	19	480–571	Y = 2.9 + 0.50x	Sig –
Pelvic to anal length	131	7	119–146	Y = –0.5 + 0.14x	Slt +
Head length	251	13	216–286	Y = 2.1 + 0.23x	Sig –
Upper-jaw length	188	11	154–214	Y = 1.8 + 0.17x	Sig –
Snout length	48	4	40–60	Y = 0.6 + 0.04x	Slt –
Eye diameter	54	5	44–65	Y = 0.2 + 0.05x	0
Supracaudal-gland length	61	12	47–85	Y = –0.4 + 0.07x	0
Infracaudal gland, solid length	122	20	83–155	Y = –1.0 + 0.13x	0
Infracaudal gland, extreme length	127	19	84–164	Y = –0.9 + 0.14x	0
Anal-fin base length	238	12	216–266	Y = –1.0 + 0.25x	Slt +
Dorsal-fin base length	184	11	161–206	Y = –2.0 + 0.21x	Sig +
Adipose-fin length	52	15	33–82	Y = 2.4 + 0.02x	Slt –

COMPARATIVE DIAGNOSIS.—*Nannobrachium isaacsi* (Figure 24) can be distinguished from all other species of *Nannobrachium* by the position of the VO_2 photophore forward above the VO_I. It can be further separated from the species of the Cuprarium group by the combination of characters in Table A10 and from all species of *Nannobrachium* by the combination of characters in Table 1.

DESCRIPTION.—Counts are based on up to 25 specimens from the eastern Atlantic and are given in Tables A2–A8, A10.

Proportions: Given in Table 20.

Fins: Origin of anal fin before vertical from middle of dorsal-fin base. Pectoral fin barely reaching vertical from PO_5, its rays rather weak, flexible. Base of adipose fin above end of anal-fin base.

Luminous Organs: PLO ½–1½ photophore diameters below lateral line. PO_4 slightly higher than level of PVO_2 and behind vertical from PO_3. VLO usually touching lateral line. SAO_2 before vertical from AOa_I. AOa_I slightly depressed; AOa series slightly concave downward. AOp_I above end of anal-fin base. Pol_2 well before vertical from origin of adipose-fin base. Prc nearly continuous with AOp; Prc_{2-3-4} usually forming straight line at angle of about 120° with line connecting Prc_{I-2}. Supracaudal and infracaudal scales rather weakly developed, sometimes with single separated scale preceding infracaudal gland. No secondary photophores found.

Size: *Nannobrachium isaacsi* apparently reaches a maximum size in excess of 130 mm. The largest specimen examined herein was 125 mm. Nafpaktitis et al. (1977) reported a maximum size of 130 mm, whereas Hulley (pers. comm., 1980) gave the maximum size as 132 mm among the 179 specimens he examined.

Material: 99 (16–125 mm) specimens were examined.

DISCUSSION.—Hulley (1981) examined Brauer's (1906) type material of *Lampanyctus micropterus*. It consists of three syntypes collected by the *Valdivia,* two from the Gulf of Guinea that "are identical with *L. isaacsi* in all respects" (Hulley, 1981:205). The third specimen from the Indian Ocean east of the Seychelles proved to be the same as *Triphoturus microchir* (Gilbert, 1913). Subsequently, Hulley (1986a) made both names junior synonyms of *Triphoturus nigrescens* (Brauer, 1904).

DISTRIBUTION AND GEOGRAPHIC VARIATION.—*Nannobrachium isaacsi* is found principally in the eastern tropical Atlantic (Figure 16), although Nafpaktitis et al. (1977) reported a few specimens from the western tropical Atlantic off eastern Brazil, which they regard as waifs. Based on the findings of Nafpaktitis et al. (1977), Hulley (1981; and pers. comm., 1980), and the material examined herein, *N. isaacsi* may have a disjunct distribution, with the two centers separated by a gap in the Gulf of Guinea. It is reported to occur between 550 and 750 m during the day and between 40 and 325 m at night (Nafpaktitis et al., 1977). No geographic variation was evident. As material in better condition becomes available, however, specimens from the two apparent centers of distribution should be carefully compared for possible differences.

Zoogeography of the Species of the Genus *Nannobrachium*

In the first comprehensive overview of marine biogeography, Ekman (1959) presented a rather coarse picture of open-ocean pelagic regions. Since then, a wide variety of investigations (see below) have added greatly to our knowledge of open-ocean biogeography, especially in the Atlantic and Pacific oceans. There are fewer collections from the Indian Ocean, and it is not so well known.

Although close correlation might be expected between surface features of the open-ocean and epipelagic biogeography, it seems less likely that the distribution of deeper-living mesopelagic animals would be closely correlated with near-surface oceanographic features. Numerous studies have demonstrated, however, that faunal breaks between regions often correlate with major physical oceanographic phenomena. These frequently have near-surface manifestations, such as at the edge of the Gulf Stream and at the boundary between the Subarctic and North Atlantic Temperate regions (Backus et al., 1977). On the other hand, boundaries between the subdivisions of the regions (faunal provinces) correspond to less prominent physical oceanographic features, frequently with little or no surface manifestation (Backus et al., 1977).

Drawing on many studies, I have compiled a map (Figure 25) showing the major open-ocean mesopelagic regions following the terminology and Atlantic boundaries of Backus et al. (1977). Boundaries for the Indian Ocean were modified from Gibbs and Hurwitz (1967), Nafpaktitis (1978), Nafpaktitis and Nafpaktitis (1969), Rochford (1966a), Sverdrup, Johnson, and Fleming (1942), and Wyrtki (1971). Those for the Pacific follow Brinton (1962), McGowan (1971, 1976), Parin (1961), Parin et al. (1973), and Wisner (1976). Boundaries for the Southern Ocean regions follow Backus (pers. comm., 1979) and McGinnis (1974, 1982) with modifications fromWyrtki (1971).

The mesopelagic southern temperate regions were examined in detail. The existence of a South Atlantic Temperate Region is rather poorly documented, and a possible South Indian Temperate is even more poorly documented. Parin et al. (1974) recognized the subtropical affinities of some species in the South Atlantic Temperate Region and included them in what was called the Peripheral Central or Subtropical pattern. There is, however, considerable confusion, as Krefft (1976) and Gibbs and McKinney (1988) pointed out, because some species in the Subantarctic Water Mass are confined to its northernmost edges, i.e., the southern part of the Subtropical Convergence (STC), whereas other species occur in the STC and extend to the north and south of it, and still other species have their southern limit in the STC but are primarily found to the north in subtropical waters. Krefft (1976) discussed those species mentioned by Parin et al. (1974) and gave examples of several other species as better fitting a "Convergence Pattern" (Krefft, 1976, fig. 3). This "Convergence Fauna" had first been recognized by Gibbs (1968) as a distinct zoogeographic region. It is approximately equivalent to what is herein recognized as the

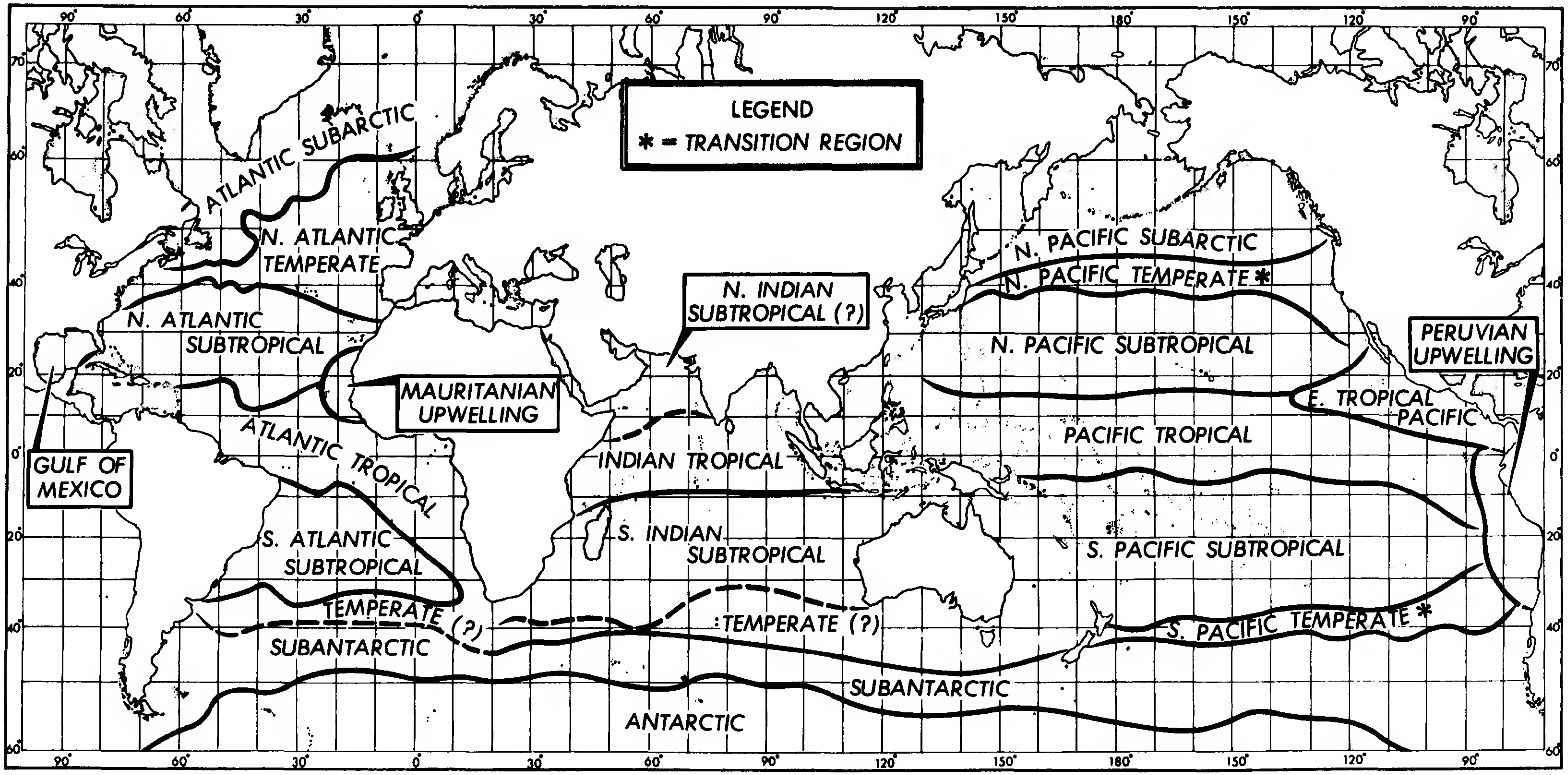

FIGURE 25.—Mesopelagic zoogeographic regions (see text for explanation).

South Atlantic Temperate Region (Figure 25), and what McGinnis (1977, 1982) recognized as the Subtropical Convergence. Hulley (1981), however, considered the Atlantic South Temperate pattern to be broader in scope, consisting of a Convergence Subpattern and a Subantarctic Subpattern. Gibbs and McKinney (1988) considered that any species that mainly occurred between 35°S–45°S to have convergence distributions even if specimens also had been captured to the north or south of those limits.

Boundaries for the South Atlantic and South Indian Temperate regions were set following the suggestions of Richard Backus (pers. comm., 1979). The boundary between the Temperate and South Subtropical regions follows the 13°C isotherm at 200 m (Backus et al., 1977). This is close to, but not exactly the same as, the northern edge of the Subtropical Convergence as delimited by McGinnis (1974, 1982) based on salinities of 34.6–34.8 per mil at 200 m. It also corresponds reasonably well with the Subantarctic Convergence of Ivanov and Neiman (1965) based on dynamical considerations. The southern edge of the STC forms the boundary between the South Temperate regions and the Subantarctic Region. Thus, in the Atlantic and Indian oceans, the entire Subtropical Convergence and adjacent waters to the north are included in the South Temperate regions. In the Pacific, the edges of mesopelagic fish distribution do not seem to correspond closely to the southern edge of the STC of McGinnis (1974, 1982). Consequently, the boundaries for the South Pacific Temperate Region are taken from the "South Pacific Transition Faunal Province core" of McGowan (1976:426). His provinces are based on the presence of faunal assemblages, and the core is where 100% of the assemblage occurs.

The discussion of the species distributions and their relationships to recognized mesopelagic zoogeographic regions will start with the North Atlantic. In order to deal with the geographic aspects in an orderly fashion, the discussions will proceed through the South Atlantic and South Indian oceans, including subantarctic affinities, then the remainder of the Indian Ocean, and, finally, the Pacific from south to north.

In the Atlantic, where the mesopelagic zoogeography is best known, my findings generally agree with those of Nafpaktitis et al. (1977) and Backus et al. (1977). The species of *Nannobrachium* with the most restricted distribution is *N. isaacsi* (Figure 16), characterized by Nafpaktitis et al. (1977) and Backus et al. (1977) as a tropical species. *Nannobrachium isaacsi* is widespread in the eastern tropical Atlantic and less common in the central tropical Atlantic. Certainly, the Mauritanian Upwelling Region is a center of abundance, but whether it truly occurs in two disjunct regions in the eastern Atlantic is not clear from the distribution shown by Nafpaktitis et al. (1977, fig. 138) nor from the samples available to me. Such an apparent distribution may result from uneven sampling efforts.

Of the three remaining species of *Nannobrachium* widely distributed in the Atlantic (*N. atrum, N. lineatum,* and *N. cuprarium*), only *N. cuprarium* (Figure 16) is unequivocally a bipolar subtropical species largely confined to the central gyres. In the North Atlantic, Hulley and Krefft (1985) found *N. cuprarium* to be the only myctophid characteristic of the South Sargasso Sea Province, part of the North Atlantic Subtropical. In the South Atlantic, because of its abundance in the central part of the South Atlantic Central Gyre, Hulley (1981:195) termed it a "gyral-eye" species.

Both *N. lineatum* and *N. atrum* have broader distributions that extend into the Indian and Pacific oceans, although as discussed under the species accounts, it is likely that the Indo-Pacific specimens of *N. lineatum* belong to more than one species, perhaps all different from the Atlantic form. Nafpaktitis et al. (1977) characterized *N. lineatum* in the Atlantic as not fitting any distribution pattern particularly well; however, in the *Walther Herwig* collections, *N. lineatum* (Figure 16) is most abundant in the Tropical Region and less abundant in the North Atlantic Subtropical (Hulley, 1981; and pers. comm., 1980), suggesting that it is primarily a tropical species. It seems to be virtually absent from the South Atlantic Subtropical, where the *Walter Herwig* took large numbers of the closely related *N. cuprarium.* Small numbers of both species were taken together by the *Walter Herwig* in the eastern North Atlantic Subtropical Region.

The distribution of *N. atrum* (Figure 5) in the Atlantic was characterized by Nafpaktitis et al. (1977:206) as "bipolar questionably subtropical" or as "bipolar temperate–semisubtropical." The uncertainty is due to a lack of specimens from some parts of the subtropics (including the southern Sargasso Sea) and an abundance in the temperate northeastern Atlantic. In the South Atlantic, McGinnis (1974, 1982, as *L. niger-ater* complex) found the southern limit of its distribution to coincide with the Subtropical Convergence. Both this study (Figure 5) and the *Walther Herwig* material (Hulley, 1981, and pers. comm., 1980) confirm that *N. atrum* is bipolar in distribution in subtropical and temperate waters and is not found in the tropics except as waifs. Thus, its range in the North Atlantic, as well as its presence in both the South Atlantic Subtropical and less well known South Atlantic Temperate regions, suggests a bipolar temperate–semisubtropical distribution.

The Subtropical Convergence also coincides with the southernmost limit for the Atlantic distribution of *N. wisneri*, an example of a South temperate–semisubtropical species (Figure 19). *Nannobrachium wisneri* is one of two Southern Hemisphere circumglobal (or nearly circumglobal) species. It shows a tendency to extend northward in the eastern Atlantic as does *N. achirus,* the second circumglobal species, undoubtedly because of the cold, northward-flowing Benguela Current (Hulley, 1981; and pers. comm., 1980). In the South Subtropical regions, *N. wisneri* occurs only in the southern parts, hence the designation "semisubtropical." In his investigations, Hulley (1986b:243) basically agreed with the distribution but characterized the pattern of *N. wisneri* (his *Lampanyctus* sp. B) as temperate, specifically, an example of a South Temperate Convergence Subpattern. As McGinnis (1982:69, *Lampanyctus* sp.

A) noted, the southern limits of the distribution of *N. wisneri* tend to correspond to the northern limits of *N. achirus*.

Nannobrachium achirus is a subantarctic species whose distribution (Figure 19) lies largely between the Subtropical Convergence in the north and the Antarctic Polar Front to the south (McGinnis, 1974, 1982). (The Antarctic Polar Front is the Antarctic Convergence of Deacon (1937) and MacKintosh (1946), based on salinity and temperature gradients, and of Ivanov and Neiman (1965), based on dynamical considerations.) The few specimens from north of the Subtropical Convergence in the southwestern Atlantic and southeastern Pacific were probably carried northward by the Falkland Current (Krefft, 1976:445) and by the Peru Current (McGinnis, 1982:44), respectively. McGinnis (1982) points out, however, that of the 10 species of myctophids whose distribution he designated Pattern III (from the Subtropical Convergence on the north to the Antarctic Polar Front on the south, i.e., a subantarctic distribution) only *N. achirus* regularly extends south of the Antarctic Polar Front. Hulley (1981:184) also noted this, characterizing *N. achirus* as having a broadly antarctic distribution based on *Walther Herwig* material but then suggested that its "spawning area indicates a subantarctic pattern." Subsequently, Hulley (1986b: 242) characterized the distribution as Widespread Temperate, with a South Temperate Subantarctic Subpattern.

Both samples of *N. achirus* available from the South Indian Ocean (Figure 19) were captured near the south edge of the Subtropical Convergence as delimited by McGinnis (1974, 1982). His one South Indian Ocean sample (McGinnis, 1982, fig. 31) also was taken in the STC. This is consistent with the characterization of *N. achirus* as a subantarctic species.

As in the Atlantic, in the Indian Ocean, *N. wisneri* occurs north of the Subtropical Convergence and, therefore, north of most of the collections of *N. achirus* (Figure 19). The few collections available were consistent with a temperate–semisubtropical distribution for this species. Because both this species and *N. achirus* occur to the east and west of the South Indian Ocean, both are presumed to have an unbroken circumglobal distribution; however, *N. wisneri* may be rare or absent in the region south of Australia and between Australia and New Zealand. A number of collections were available from those regions that contained specimens of either *N. achirus* (Figure 19) or *N. atrum* (Figure 5) but not of *N. wisneri*.

Nannobrachium atrum is common and widespread in the Subtropical and Temperate regions of the Indian Ocean, as it is in the Atlantic. This agrees with Nafpaktitis and Nafpaktitis (1969) but not with Kotthaus (1972b), who reported *N. atrum* from near the equator and at about 4°S. Of the material examined, the southernmost record was near the southern edge of the Subtropical Convergence, consistent with a temperate-semisubtropical species.

The three remaining Indian Ocean species are tropical or subtropical in their distribution. *Nannobrachium indicum*, the only species of *Nannobrachium* endemic to the Indian Ocean, is restricted to the Indian Tropical Region (Figure 5). The southern boundary of the Indian Tropical Region (Figure 25) is north of the Equatorial Frontal Water, which Rochford (1966a:6) delimited on the basis of salinity and oxygen differences. He located this Frontal water at about 9°S, "just south of the northern boundary of the south Equatorial current." This is about at the boundary of the Indian Equatorial and Central Water Masses (Sverdrup et al., 1942). It is probably a significant zoogeographic boundary. Not only does the boundary correlate with the break in distribution patterns for *N. indicum* and *N. atrum*, but it also has been shown by Gibbs and Hurwitz (1967) to correspond to a boundary between two morphologically distinct species of *Chauliodus* in the western Indian Ocean. Nafpaktitis and Nafpaktitis (1969) found that a number of other species of myctophids were found either to the north or to the south of approximately 10°S in the western Indian Ocean, and Nafpaktitis (1978) found the same for a number of species of *Diaphus*.

The four samples of *N. lineatum* from the Indian Ocean are consistent with the distribution pattern for this species in the Atlantic: more abundant in the Tropical Region, with sparse numbers in the South Indian Subtropical Region (Figure 16). The tendency to extend toward the south along the east coast of Africa is probably due to the southward-flowing Agulhas Current. According to Rochford (1966b), Banda Intermediate water of lower salinity moves toward the west at depths of 900–1100 m from about 10°S–15°S toward Madagascar. In addition, Rochford (1964) found evidence that high salinity water masses from the Gulf of Aden and from the Persian Gulf move toward the south along the East African coast. Part of this water turns east at the equator and part follows the African coast past Madagascar at intermediate depths varying from 300–700 m, depending on the origins of the water and the salinity maxima. Thus, both of these general water movements could help account for the occurrence of a tropical species to the south along the East African coast.

The few samples of *N. nigrum* from the Indian Ocean indicate that this species is present only in the extreme northeast portion of the the South Indian Subtropical. Given its wide occurrence in the tropical Pacific and the various East Indian seas and with more extensive collecting, *N. nigrum* may be expected to turn up in the extreme eastern portion of the Indian Tropical as well.

Over the past few years, Pacific zoogeography has been studied in greater detail, although that detail is still not equal to that of the Atlantic, and there has been no attempt to divide zoogeographic regions into provinces as Backus et al. (1977) have done for the Atlantic. In this regard, McGowan (1986:195) compared the characteristics of the three major pelagic faunal regions of the North Pacific (Subarctic, Central, and Eastern Tropical Pacific) and found no compelling evidence for sub- units, such as provinces, although he did discuss the presence of "several cyclonic sub-systems" within the Subarctic system; however, because they contain no endemics or unique species assemblages, he considered them to be "too 'unpredictable' to have served as habitats or centers for diversification." In the Pacific, McGowan (1974, 1976) and Reid et al. (1978) recognized five major faunal assemblages (Central, Transition, Equatorial, Eastern Tropical Pacific, and Subpolar—i.e., Subarctic and Subantarctic) and their core regions (where 100% of the faunal group species are found). All the faunal regions correspond to water masses and provide a useful framework to compare distribution patterns. The species of *Nannobrachium* can contribute to our understanding of Pacific zoogeography because there are many Pacific species, most of which are endemic.

The southernmost species, *N. achirus* (Figure 19), is clearly in the Subantarctic Region, although as discussed earlier, it also is known from south of the Antarctic Polar Front (McGinnis, 1982). In the southeastern Pacific, *N. achirus* is found only in the southern part of the Subantarctic Region, although McGinnis records specimens from as far north as 33°S. This is the region where the West Wind Drift squeezes through the Drake Passage. The Subantarctic Region is broad here, extending north along the west coast of South America until it blends in with the Peruvian Upwelling Region of the Peru-Chile Current (Figure 25).

The distribution of *N. wisneri* (Figure 19) is in, and to the north of, the South Pacific Temperate Region, so it is clearly a temperate–semisubtropical species. Many specimens occurred south of the Subtropical Convergence as delimited by McGinnis (1974, 1982), but their distribution corresponds almost precisely with the core of the Southern Transition Faunal Province of McGowan (1976, fig. 1). The distribution of *N. wisneri* also agrees with that of the "Convergence Fauna" (Gibbs, 1968:3) in the Pacific. Thus, although there is strong evidence for a recognizable Temperate Region in the South Pacific, its fauna does not seem to follow the same physical parameters as the fauna of the Atlantic and Indian Temperate regions.

In the Pacific, *N. atrum* (Figure 5) is found only in the southwestern portion, where it is common and appears to have a temperate–semisubtropical distribution. *Nannobrachium atrum* and *N. wisneri* are almost mutually exclusive in the South Pacific, in contrast with the South Atlantic where they co-occur widely. They apparently also co-occur in the Indian Ocean. In the South Pacific, the boundary between the two species appears to be around 170°W, with only one collection of *N. wisneri* to the west and one collection of *N. atrum* to the east of 170°W.

Nannobrachium idostigma is found throughout the Eastern Tropical Pacific Region and in the northern part of the Peruvian Upwelling Region (Figure 10). For this reason, it is perhaps best described as an Eastern Tropical Pacific species having affinities to the Peruvian Upwelling Region. Its restricted eastern Pacific distribution resembles that of *N. isaacsi* in the Atlantic. Beklemishev (1973), Parin and Bekker (1981), and Bekker (1983) considered that both this species and *N. ritteri*, which is also eastern Pacific but further north off the west coast of North America, display what they termed a "far-neritic" or "extended neritic" pattern. (See the discussion under the species account for *N. ritteri* for greater details.)

None of the species of *Nannobrachium* has a distribution limited to the South Pacific Subtropical Region. *Nannobrachium nigrum* (Figure 5), however, has a broad-ranging distribution that encompasses much of both the North and South Pacific Subtropical regions and the intervening Tropical Region. *Nannobrachium nigrum* is absent from the Eastern Tropical Pacific Region but appears to be very widespread and common throughout the seas of the western Pacific, extending into the eastern Indian Ocean.

The only other species of *Nannobrachium* that has a comparably wide distribution in the Pacific is *N. lineatum* (Figure 16). Specimens of various forms of this species were taken infrequently from widely distant localities in the Pacific Tropical and the North and South Pacific Subtropical regions, consistent with the pattern in the Atlantic and Indian oceans. One locality immediately south of the Eastern Tropical Pacific Region suggests that *N. lineatum* may ultimately be found in that region as well.

Nannobrachium gibbsi is widespread in the southern half of the Tropical and northern half of the South Pacific Subtropical regions (Figure 5), suggesting a south tropical–semisubtropical distribution. A few specimens taken in the extreme eastern part of the South Pacific Temperate Region near the subtropical–temperate border may represent waifs.

Nannobrachium crypticum is a tropical species largely confined to the Pacific Tropical Region (Figure 19). The few records from immediately south of the tropical–subtropical border probably represent imprecision in the location of that border or perhaps the boundary fluctuates or is not sharp.

Two species are largely restricted to the North Pacific Subtropical Region, *N. bristori* (Figure 10) and *N. hawaiiensis* (Figure 19), although both are commonly found in the southern part of the California Current, an area of mixing along the west coast of North America. Both species also have been taken beyond the borders of the Subtropical Region in adjacent regions, but these sporadic records can be considered waifs, and both species are designated as having North Pacific Subtropical distributions. The small number of locality records for *N. bristori* in the western Pacific is probably a function of the fewer samples available from that region, as well as the relative rarity of this species in collections; however, it also may be due to differences between eastern gyre and western gyre faunas in the North Pacific Subtropical Region (Sverdrup et al., 1942; Barnett, 1975, 1983, 1984).

All three remaining species of *Nannobrachium* in the North Pacific belong to the Regale group (Figure 10). *Nannobrachium regale* is broadly distributed across the North Pacific in all parts of the North Pacific Temperate and Subarctic regions. According to Fedorov (pers. comm., 1979) the breeding range for *N. regale* in the western Pacific corresponds almost exactly to the Subarctic Region; however, there also is a region to the south where expatriates can be found that corresponds closely to the North Pacific Temperate Region.

Nannobrachium ritteri appears to be a species of the North Pacific Temperate Region, but it is restricted to the eastern part, especially the California Current system along the west coast of North America. It is absent from the Subarctic Region and extends west from the U.S. coastline to about 45°N, 155°W (Wisner, 1976). The locality record at about 45°N, 165°W represents a range extension based on a single large specimen that probably was a waif.

The extremely limited distribution pattern of *N. fernae* appears to be real and not the result of sampling effort. *Nannobrachium fernae* is restricted to the east-central portion of the North Pacific Temperate Region, which corresponds almost precisely with the core region of the "North Transition Faunal Province" (McGowan, 1976:426). Although several invertebrates show a similar distribution (Brinton, 1962; McGowan, 1971), *N. fernae* appears to be the only fish found so far that shows such a distribution.

McGowan (1971:17) discussed the "Transition Faunal Province" in detail, giving numerous examples of North Pacific Temperate (=Transition Zone fauna) species from the zooplankton. He also pointed out the possibility of a wind driven westward countercurrent with a transport as large as 4–6 × 10^5 cubic meters per second at about 38°N based on data from Dodimead et al. (1963) and Fofonoff (1960) to account for the maintenance of planktonic organisms in a region generally shown on a broad scale as having only eastward-flowing surface currents (Sverdrup et al., 1942; Fleming, 1955).

When the distribution patterns for all species within each species group are compared, it is clear that there is remarkably little overlap between species, especially within the Nigrum (Figure 5) and Achirus (Figure 19) species groups. The only major exceptions are within the Regale group (Figure 10, *N. ritteri*) and the Cuprarium group (Figure 16, *N. lineatum*). Furthermore, there is little overlap when the species-group distributions as a whole are compared. Again, this is especially clear in comparing the distribution patterns of the Nigrum group as a whole with that of the Achirus group, although it also holds in large part when they are compared with the distribution of the Regale group.

It is shown that the species of *Nannobrachium* have discrete and distinctive distribution patterns that, for the most part, correlate with physical features of the open ocean. Furthermore, their distribution patterns correspond to and elucidate various zoogeographic regions that have been previously recognized on the basis of the distribution patterns of other organisms.

Summary and Conclusions

In the lanternfish fish family Myctophidae, the genus *Lampanyctus* (sensu lato) is one of the most speciose. Within that genus, those species with reduced pectoral fins have long been taxonomically confusing. More than 9000 specimens were studied worldwide in an attempt to resolve the taxonomic problems. The short-pectoral-finned group was found to contain 17 species that could be divided into five species groups based on shared and unique characters.

As herein recognized, the genus *Nannobrachium* includes those species in the tribe Lampanyctini with the following combination of characters: no pectoral fins or short fins with a narrow base; a vertically elongate squarish otolith with smooth margins; reduced musculature resulting in a soft, flaccid body; a "pinched" body profile with concave dorsal and ventral profiles behind the head; and swimbladder atrophied in adults.

Within the genus *Nannobrachium*, the Nigrum species group contains four species, including the type-species for the genus, *Nannobrachium nigrum* Günther, 1887. The other three species in the Nigrum group are *N. atrum* (Tåning, 1928) (long confused with *N. nigrum*) and two new species, *N. gibbsi* and *N. indicum*. All species in the Nigrum group share the unique character of very thin and flexible rays in extremely short pectoral fins in the adult, usually reaching less than one-half the distance to the pelvic-fin insertion.

The species of the Nigrum group are widely distributed. *Nannobrachium atrum* is the most widespread, being found in the North and South Atlantic, South Indian, and western part of the South Pacific oceans. *Nannobrachium nigrum* is found in the tropical Pacific, excluding the Eastern Tropical Pacific Region, through the East Indian archipelago as far west as the extreme eastern tropical Indian Ocean. *Nannobrachium gibbsi* is found in the tropical and subtropical South Pacific to slightly north of the equator. *Nannobrachium indicum* is the only species of *Nannobrachium* endemic to the Indian Ocean, where it is restricted to the tropics.

All species of the Regale group have well-developed (for *Nannobrachium*) pectoral fins that reach to, or nearly to, the pelvic-fin insertion and have the VLO photophore low on the side of the body. Of the five species in the group, only one, *N. bristori*, is a new species. The entire group is restricted to the Pacific Ocean and, except for *N. idostigma* (Parr, 1931), which is restricted to the Eastern Tropical Pacific and Peruvian Upwelling regions, all species are found only in the North Pacific. *Nannobrachium regale* Gilbert, 1891, is found across the entire North Pacific, primarily in the Subarctic Region. *Nannobrachium bristori* also is found across the North Pacific, but it also occurs to the south, in the subtropics. The two remaining species have restricted distributions: *Nannobrachium ritteri* (Gilbert, 1915) is found in the eastern Pacific throughout the eastern portions of the North Pacific Temperate Region and in the California Current, whereas *Nannobrachium fernae* (Wisner, 1971) (with the most restricted distribution of all species of *Nannobrachium*) is found in the eastern portion of the main part of the North Pacific Temperate Region.

Both species of the Cuprarium group share the unique character of pigmentation on the posterior portions of the supracaudal and infracaudal luminous glands. The smaller species, *N. cuprarium* (Tåning, 1928), is restricted to the subtropical regions of the North and South Atlantic oceans. The larger species, *N. lineatum* (Tåning, 1928), is the largest species of *Nannobrachium*, reaching a size, in the Atlantic, well in excess of 200 mm. Although it is widespread throughout the Atlantic, it seems to be especially abundant in the tropics. In the Indian and Pacific oceans, *N. lineatum* also is widespread but seems to be represented by two or more forms.

The Achirus species group contains five species, of which four are newly described herein; only *N. achirus* (Andriashev, 1962) had been described previously. All species in this group share an ontogeny resulting in lack of pectoral-fin development. In all species at a particular size, which varies with the species, the pectoral fins slow or stop their growth and eventually become overgrown with skin, so that usually no pectoral fins are visible in the adult. During the slowing of pectoral-fin growth, the rays point downward, become thicker, broad, and bone-like, and eventually fuse to the posterior edge of the scapula. *Nannobrachium achirus* is the most southerly of the species of *Nannobrachium*, being found circumglobally in the subantarctic. *Nannobrachium wisneri* is found to the north and occurs nearly circumglobally in the temperate regions, except in the vicinity of Australia and New Zealand. The remaining three species are found only in the Pacific. *Nannobrachium phyllisae* is restricted to the Peruvian Upwelling Region along the west coast of South America. *Nannobrachium hawaiiensis* is found across the North Pacific Subtropical Region and always has the most extreme loss of pectoral fins, perhaps occurring at or near the time of postlarval transformation. The remaining species, *N. crypticum,* also is found across the Pacific but is restricted to the Equatorial Region. The latter has the greatest retention of its pectoral fins, with the presence of some exterior vestige in the largest specimens available.

The Isaacsi species group is represented by a single species, *N. isaacsi* (Wisner, 1974). It is characterized by the position of the VO_2 photophore, above and slightly before the VO_1, which is unique for *Nannobrachium*. *Nannobrachium isaacsi* is restricted to the eastern tropical Atlantic Ocean and is especially common in the Mauritanian Upwelling Region.

In general, the distribution patterns of the species of *Nannobrachium* are distinctive and correspond to previously recognized zoogeographic regions, having boundaries that correlate with oceanographic features. In addition, the distribution patterns for the species and species groups of *Nannobrachium* show remarkably little overlap in distributions.

Appendix Tables

TABLE A1.—Nigrum group, *N. crypticum* and *N. bristori:* modal characters with extremes in parentheses.

Character	*N. nigrum*	*N. atrum*	*N. gibbsi*	*N. indicum*	*N. crypticum*	*N. bristori*
Gill rakers	5+12, total 17; (4–5)+(11–13) total (15–18)	5+12, total 17; (4–5)+(11–13) total (16–18)	4+10, total 14; (3–4)+(9–11) total (13–15)	4+11, total 15; (4–5)+(10–12) total (14–17)	4+10, total 14; (4)+(8–11) total (12–15)	4–5+11, total 15–16; (4–5) (10–12) total (14–17)
Tooth patches, 2nd gill arch (lower limb)	9 (9–10)	9 (7–10)	8 (7–8)	8 (8–9)	8 (7½–8)	9 (7½–9½)
AO photophores	5+6, total 11; (4–6)+(5–7), total (10–13)	6–7+7–8, total 13–15; (5–9)+(6–9), total (12–15)	6–7+7, total 13–14; (6–8)+(6–8), total (13–14)	4–5+5–7, total 10–11; (4–6)+(5–7) total (9–12)	5–6+5–6, total 11–12; (5–7)+(5–7), total (10–13)	6+7, total 13; (5–7)+(6–8), total (13–14)
Dorsal-fin rays	13 (12–15)	14–15 (13–16)	13–14 (13–15)	13–14 (13–15)	13–14 (12–15)	14–15 (14–15)
Anal-fin rays	16 (14–18)	19 (17–21)	18–19 (17–20)	17 (16–18)	17 (16–18)	18 (16–19)
Supracaudal/infracaudal gland scales	3/4 (2–4)/(o–i)+(3–5)	3–4/i+5 (2–5)/(o–ii)+(3–6)	2–3/4–5 (2–4)/(o–i)+(3–6)	2/3 (1–3)/(o–i)+(2–5)	3/4–5 (2–4)/(o–i)+(4–6)	3/3–4 (2–4)/(o–i)+(3–5)
Lateral line organs	33 (32–34)	37–38 (36–39)	33–34 (33–35)	30–31 (29–32)	33 (32–34)	35 (35–36)
Vertebrae	15+19–20, total 34–35; (14–16)+(18–21), total (33–37)	16+21–22, total 37–38; (15–16)+(20–23), total (36–39)	16+21, total 37; (15–17)+(20–22), total (36–38)	15+18–19, total 33;(14–15)+(17–19), total (32–34)	15+19–20, total 34–35; (14–16)+(18–21), total (33–36)	16+21, total 37; (15–17)+(20–23), total (36–38)
SAO_2 position relative to VO_4 and AOa_1	closer to AOa_1	closer to VO_4	midway, slightly closer to AOa_1	closer to AOa_1	midway, often closer to AOa_1	midway, often closer to AOa_1
Average PO_4 position	above and slightly behind PO_3	above and slightly anterior to PO_3	above and slightly behind PO_3	above PO_{3-5}, interspace often midway	above and slightly behind PO_3	above and slightly behind PO_3
VLO relative to lateral line (LL)	touching or 1 photophore diameter below, closer to LL than PLO–LL distance	as in *N. nigrum*	approximately 1–2 photophore diameters below; closer to LL than PLO–LL distance	as in *N. nigrum*	as in *N. nigrum*	2–3 photophore diameters below; further to LL than PLO–LL distance

Table A2.—AO photophores, all species of *Nannobrachium*.

Group	AOa						AOp					Total AO									
Species	4	5	6	7	8	9	5	6	7	8	9	9	10	11	12	13	14	15	16	17	18
Regale																					
N. regale		2	20	26	2				14	31	1				2	3	23	18			
N. ritteri			10	36	3					29	21							36	14		
N. idostigma		29	21				2	34	11	2			1	21	21	5	1				
N. fernae		5	45	10						38	21					2	31	23	3		
N. bristori		6	31	7				2	33	6						35	5				
Cuprarium																					
N. cuprarium		12	38				40	10					2	48							
N. lineatum				46	47	9		2	45	38	12						13	52	31	4	
Atlantic				31	22	5		2	33	19	3						13	34	11		
Indo-Pacific				15	25	4			12	19	9							18	20	4	
Isaacsi																					
N. isaacsi		2	43	1					2	30						4	28				
Nigrum																					
N. nigrum	2	50	5				2	41	3				5	35	4						
N. atrum		3	22	38	6	1		9	31	25	3				3	14	31	19			1†
N. gibbsi			32	16	1			6	39	4						32	15				
N. indicum	11	43	4				22	26	10			3	22	24	9						
Achirus																					
N. achirus			29	106	14				18	104	22						28	97	19		
N. phyllisae			4	22	7			8	18							6	19				
N. wisneri		1	10	33	6				28	15	6					3	24	20	2		
N. hawaiiensis		28	24					23	24					9	30	8					
N. crypticum		33	19	4			17	31	8				6	26	18	4					

†Aberrant specimen with 7+8, total 15 AO photophores on other side.

TABLE A3.—Gill rakers, all species of *Nannobrachium*.

Group	Upper					Lower								Total									
Species	3	4	5	6	7	8	9	10	11	12	13	14	15	12	13	14	15	16	17	18	19	20	21
Regale																							
N. regale	1	47	2				1	46	3						2	43	5						
N. ritteri		48	1				2	43	4						2	42	5						
N. idostigma		49						8	39	3						7	39	3					
N. fernae		51	8						5	46	8						5	43	6	5			
N. bristori		25	21					2	36	8						2	21	16	7				
Cuprarium																							
N. cuprarium			50						1	43	6							1	43	6			
N. lineatum		1	94	7					3	42	55	2						4	38	54	6		
Atlantic			55	3						7	49	2							7	46	5		
Indo-Pacific		1	39	4					3	35	6							4	31	8	1		
Isaacsi																							
N. isaacsi			45	5						2	23	23	2						2	21	24	1	2
Nigrum																							
N. nigrum		5	57						9	51	2						4	6	50	2			
N. atrum		4	66						3	61	6							7	57	6			
N. gibbsi	1	48					1	47	1						2	45	1						
N. indicum		52	6					5	46	7						5	44	5	4				
Achirus																							
N. achirus			83	72	1				3	22	104	24	3					3	20	56	56	18	3
N. phyllisae		2	38	2					12	29	1						2	10	27	3			
N. wisneri		46	4						18	32							18	28	4				
N. hawaiiensis		52							42	9							42	9					
N. crypticum		55				1	3	49	3					1	3	48	3						

TABLE A4.—Tooth patches, lower limb of second gill arch, all species of *Nannobrachium*.

Group											
Species	7	7½	8	8½	9	9½	10	10½	11	11½	12
Regale											
N. regale			22	1	1						
N. ritteri	3	2	19								
N. idostigma			18	3	3						
N. fernae			4		15	1					
N. bristori		1	1		21	1					
Cuprarium											
N. cuprarium			2	1	13	5	3				
N. lineatum			1	2	29	5	30	1			
Atlantic						5	30	1			
Indo-Pacific			1	2	29						
Isaacsi											
N. isaacsi					3		21				
Nigrum											
N. nigrum					19	3	2				
N. atrum		1	3	6	93	8	1				
N. gibbsi		1	23								
N. indicum			17	2	1						
Achirus											
N. achirus					11	5	42	3	4		1
N. phyllisae			3		15	2	2				
N. wisneri			3	5	42	1	2				
N. hawaiiensis				1	22		1				
N. crypticum		1	13								

TABLE A5.—Fin rays, all species of *Nannobrachium*.

Group	Dorsal								Anal									
Species	12	13	14	15	16	17	18	19	14	15	16	17	18	19	20	21	22	23
Regale																		
N. regale				13	12							5	17	3				
N. ritteri			17	7	1								12	13				
N. idostigma		12	13								1	1	15	6	2			
N. fernae	7	19	4							1	8	15	6					
N. bristori			12	10							1	5	14	2				
Cuprarium																		
N. cuprarium					1	20	3	1				1	16	6	2			
N. lineatum					9	30	11							1	25	22	1	1
Atlantic					3	19	6								11	16		
Indo-Pacific					6	11	5							1	14	6	1	1
Isaacsi																		
N. isaacsi			2	16	6							3	14	7	1			
Nigrum																		
N. nigrum	3	24	2	2					1	3	16	5	6					
N. atrum	1	16	17	1								1	5	22	5	1		
N. gibbsi		9	12	4								2	10	11	2			
N. indicum		10	18	1							6	18	5					
Achirus																		
N. achirus	7	43	24	4						1	1	34	37	5				
N. phyllisae		5	7	7	2							2	11	6	2			
N. wisneri		17	8								1	6	15	3				
N. hawaiiensis	1	13	7	4						1	2	11	10	1				
N. crypticum	1	20	6	2						1	5	15	7	1				

TABLE A6.—Luminous caudal gland scales, all species of *Nannobrachium*.

Group	Supracaudal						Infracaudal										
Species	1	2	3	4	5	6	i	ii	2	3	4	5	6	7	8	9	10
Regale																	
N. regale			8	15	2		13	3			1	6	15	2			
N. ritteri		7	18									1	12	12			
N. idostigma	1	12	8						1	18	4						
N. fernae			7	17	6									1	11	10	1
N. bristori		4	9	1			3			6	5	3					
Cuprarium																	
N. cuprarium		7	18				1				23	2					
N. lineatum		9	24	7		1	1	2		6	19	13	5				
Atlantic		8	14	3			6	1		6	9	5	5				
Indo-Pacific		1	10	4		1	5	1			10	8					
Isaacsi																	
N. isaacsi		5	9	2	1		5				2	4	9	1			
Nigrum																	
N. nigrum		8	15	1			2			5	23	1					
N. atrum		1	13	11	3		13	2		1	6	17	8				
N. gibbsi		8	11	3			3			4	8	6	4				
N. indicum	1	16	8				3		1	25	1	1					
Achirus																	
N. achirus		4	34	6			21						8	22	16	2	
N. phyllisae		3	9	2			6					6	10	1			
N. wisneri		5	12				1						4	12	3	2	
N. hawaiiensis		5	15				2				17	5					
N. crypticum		2	11	3			2				10	7	5				

TABLE A7.—Lateral line organs, all species of *Nannobrachium*.

Group Species	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Regale																
N. regale									6	11	5	2				
N. ritteri							1	3	14	6						
N. idostigma			7	11	5											
N. fernae									6	8						
N. bristori							17	5								
Cuprarium																
N. cuprarium				8	14											
N. lineatum									8	24	19	4	2	2	2	2
Atlantic			2?						6	16	11					
Indo-Pacific									2	8	8	4	2	2	2	2
Isaacsi																
N. isaacsi						6	14	4								
Nigrum																
N. nigrum				7	13	3										
N. atrum					1?	1?		6	36	57	12					
N. gibbsi			2?		10	7	3		2?							
N. indicum	1	9	7	2												
Achirus																
N. achirus						1	9	20	25	5						
N. phyllisae						9	10									
N. wisneri						2	18	24	7							
N. hawaiiensis				5	14	4										
N. crypticum				1	7	1										

TABLE A8.—Vertebrae, all species of *Nannobrachium*.

Group	Precaudal						Caudal										Total												
Species	14	15	16	17	18	19	17	18	19	20	21	22	23	24	25	26	32	33	34	35	36	37	38	39	40	41	42	43	44
Regale																													
N. regale			17							1	8	8									1	8	8						
N. ritteri		1	11								9	3									1	8	3						
N. idostigma	8	4						7	5								4	7	1										
N. fernae			13								4	8	1									4	8	1					
N. bristori		1	8							2	4	2	1								2	4	3						
Cuprarium																													
N. cuprarium	1	12	2					6	9								1	3	11										
N. lineatum	1	1	15	20	4	3					1	13	24	3	2	1						1	5	16	16	2	2	1	1
Atlantic			12	2							1	5	8									1	4	8	1				
Indo-Pacific	1	1	3	18	4	3						8	16	3	2	1							1	8	15	2	2	1	1
Isaacsi																													
N. isaacsi		12								3	9									3	9								
Nigrum																													
N. nigrum	10	118	13					16	81	36	8							12	88	34	5	2							
N. atrum		3	35							1	16	18	3								1	18	17	2					
N. gibbsi		5	54	3						2	45	15									2	47	13						
N. indicum	6	13					2	9	8								2	15	2										
Achirus																													
N. achirus		1	10	4						3	9	3									2	8	5						
N. phyllisae		11								2	9									2	9								
N. wisneri		2	12							2	10	2									3	10	1						
N. hawaiiensis	1	16	1					3	15										3	15									
N. crypticum	12	67	2					13	59	25	1							11	68	19	1								

TABLE A9.—Regale group: Modal characters with extremes in parentheses.

Character	*N. regale*	*N. ritteri*	*N. idostigma*	*N. fernae*	*N. bristori*
Gill rakers	4+10, total 14; (3–5)+ (9–11), total (13–15)	4+10, total 14; (4–5)+ (9–11), total (13–15)	4+11, total 15; (4) + (10–12), total (14–16)	4+12, total 16; (4–5)+ (11–13), total (15–18)	4–5+11, total 15–16; (4–5)+(10–12), total (14–17)
Tooth patches, 2nd gill arch (lower limb)	8 (8–9)	8 (7–8)	8 (8–9)	9 (8–9½)	9 (7½–9½)
AO photophores	6–7+7–8, total 14–15; (5–8) + (7–9), total (12–15)	7+8–9, total 15; (6–8) + (8–9), total (15–16)	5–6+6, total 11–12; (5–6)+ (6–8), total (10–14)	6+8–9, total 14–15; (5–7)+(8–9), total (13–16)	6+7, total 13; (5–7)+ (6–8), total (13–14)
Dorsal-fin rays	15–16 (15–16)	14 (14–16)	13–14 (13–14)	13 (12–14)	14–15 (14–15)
Anal-fin rays	18 (17–19)	18–19 (18–19)	18 (16–20)	17 (15–18)	18 (16–19)
Supracaudal/infracaudal gland scales	4/i+6 (3–5)/(o–ii) + (4–7)	3/6–7 (2–3)/(5–7)	2–3/3 (1–3)/(2–4)	4/8–9 (3–5)/(7–10)	3/3–4 (2–4)/(o–i) + (3–5)
Lateral line organs	38 (37–40)	37 (35–38)	32 (31–33)	37–38 (37–38)	35 (35–36)
Vertebrae	16+21–22, total 37–38; (16)+(20–22), total (36–38)	16+21, total 37; (15–16)+ (21–22), total (36–38)	14+18–19, total 33; (14–15)+(18–19), total (32–34)	16+22, total 38; (16) + (21–23), total (37–39)	16+21, total 37–38; (15–16)+(20–23), total (36–38)
SAO_1 position	above VO_{2-3} interspace	above, or slightly before vertical from, VO_3	above VO_{3-4} interspace	above VO_3	above, or slightly before vertical from, VO_3
SAO_2 position relative to VO_4 and AOa_1	closer to VO_4	above AOa_1	above, or slightly behind vertical from, AOa_1	slightly closer to VO_4	midway, often closer to AOa_1
SAO_3 position	above, or before vertical from, AOa_1	above AOa_{1-2} interspace	above AOa_2	above AOa_1	above, or slightly behind vertical from, AOa_1
VLO relative to lateral line and pelvic-fin base	slightly above midway between	approximately midway between	slightly above midway between	slightly above midway between	closer to LL; 2–3 photophore diameters below LL
Pol position relative to adipose-fin base	below middle to end of base	before origin	below origin	before origin	below origin

TABLE A10.—Cuprarium group and *N. isaacsi*: Modal characters with extremes in parentheses.

Character	*N. cuprarium*	*N. lineatum* Atlantic	*N. lineatum* Indo-Pacific	*N. isaacsi*
Gill rakers	5+12, total 17; (5) + (11–13), total (16–18)	5+13, total 18; (5–6)+(12–14), total (17–19)	5+12, total 17; (4–6) + (11–13), total (16–19)	5+13–14, total 18–19; (5–6) + (12–15), total (17–21)
Tooth patches, 2nd gill arch (lower limb)	9 (8–10)	10 (9½–10½)	9 (8–9)	10 (9–10)
AO photophores	6+5, total 11; (5–6)+(5–6), total (10–11)	7–8+7–8, total 14–15; (7–9)+(6–9), total (14–16)	7–8+7–8, total 15–16; (7–9)+(7–9), total (15–17)	6+8, total 14; (5–7)+ (7–8), total (13–14)
Dorsal-fin rays	17 (16–19)	17 (16–18)	17 (16–18)	15 (14–16)
Anal-fin rays	18 (17–20)	20–21 (20–23)	20 (19–22)	18–19 (17–20)
Supracaudal/infracaudal gland scales	3/4 (2–3)/(o–ii) +(4–5)	3/i+3–4 (2–4)/(o–ii) +(3–6)	3/i+4–5 (2–6)/(o–ii) +(4–5)	2–3/i+6 (2–5)/(o–i) +(4–7)
Lateral line organs	33 (32–33)	38–39 (37–39)	38–39 (37–44)	35 (34–36)
Vertebrae	15+19, total 34; (14–16) + (18–19), total (32–34)	16+22–23, total 38–39; (16–17) + (21–23), total (37–40)	17+23, total 40; (14–19) + (22–26), total (38–44)	15+21, total 36; (15)+ (20–21), total (35–36)

TABLE A11.—Achirus group: Modal characters with extremes in parentheses.

Character	*N. achirus*	*N. phyllisae*	*N. wisneri*	*N. hawaiiensis*	*N. crypticum*
Gill rakers	5–6+13, total 18–19; (5–7)+(11–15), total (16–21)	5+12, total 17; (4–6)+(11–13), total (15–18)	4+11–12, total 15–16; (4–5)+(11–12), total (15–17)	4+11, total 15; (4)+(11–12), total (15–16)	4+10, total 14; (4)+(8–11), total (12–15)
Tooth patches, 2nd gill arch (lower limb)	10 (9–12)	9 (8–10)	9 (8–10)	9 (8½–10)	8 (7½–8)
AO photophores	7+8, total 15; (6–8)+(7–9), total (14–16)	7+7, total 14; (6–8)+(6–7), total (13–14)	7+7–8, total 14–15; (5–8)+(7–9), total (13–16)	5–6+6–7, total 12; (5–6)+(6–7), total (11–13)	5–6+5–6, total 11–12; (5–7)+(5–7), total (10–13)
Dorsal-fin rays	14–15 (13–16)	15–16 (14–17)	14–15 (14–15)	14–15 (13–16)	13–14 (12–15)
Anal-fin rays	17–18 (15–19)	18–19 (17–20)	18 (16–19)	17–18 (15–19)	17 (15–19)
Supracaudal/infracaudal gland scales	3/i+7–8; (2–4)/(o–i)+(6–9)	3/i+5–6; (2–4)/(o–i)+(5–7)	3/7; (2–3)/(o–i)+(6–9)	3/4; (2–3)/(o–i)+(4–5)	3/4–5; (2–4)/(o–i)+(4–6)
Lateral line organs	36–37 (34–38)	34–35 (34–35)	35–36 (34–37)	33 (32–34)	33 (32–34)
Vertebrae	16+21, total 37; (15–17)+(20–22), total (36–38)	15+21, total 36; (15)+(20–21), total (35–36)	16+21, total 37; (15–16)+(20–22), total (36–38)	15+20, total 35; (14–16)+(19–20), total (34–35)	15+19–20, total 34–35; (14–16)+(18–21), total (33–36)
Size at loss of pectoral fins	approximately 40–60 mm; at 60–80 mm, often only a single, short, bony ray visible externally	approximately 30–40 mm	approximately 20–30 mm (perhaps shortly after transformation from postlarval stage)	approximately 20 mm (at transformation from postlarval stage)	remain externally visible in largest specimens available (>90 mm)
Condition of pectoral fins in adults	normally not visible but atrophied rays can be found if skin is abraded or dissected away	as in *N. achirus* but rays are not so well developed at comparable sizes	no trace of pectoral rays buried in skin or of actinosts	as in *N. wisneri*	rays thick and stiff; atrophied and pointing downward
Maximum size of specimens	approximately 150 mm	approximately as in *N. achirus*	approximately 90 mm	approximately 80 mm	approximately 100 mm

Appendix Tables 12 to 14: Explanation

The following tables will help to identify specimens through the use of a series of measurements to distinguish between pairs of species. The pairs of species are primarily those within a species group, but they also may include selected pairs of species from different species groups when the species are likely to co-occur and are morphologically similar. To use a table effectively it is necessary to have some idea of the identification of the specimen at hand, usually by having identified it to one of two possibilities through use of a key. Turning to the table for that species group, the intersection of the column and row with the two species names will give 4 or 5 quotients (Q) for which 8 or 10 measurements are needed. Once the measurements have been obtained and the necessary division operation done to produce the quotients, these must be multiplied by the proper function (F) following each quotient. These S values (either positive or negative values) are then added arithmetically and the final value compared with the Discriminant Value (D.V.) given at the bottom of the box. An obtained value will be larger than the D.V. for one species and smaller than the D.V. for the other species in almost all cases. A few specimens, probably only 1 or 2% (certainly less than 5% of the total number measured), for pairs of species that are morphologically the most similar, have been found to give an obtained value on the "wrong" side of the D.V. Thus, this technique is not infallible, but it is merely another aid to the identification of these morphologically similar species. The abbreviations for the measurements are as follows.

AFB	Anal-fin base length
CPD	Caudal peduncle depth
CPL	Caudal peduncle length
DFB	Dorsal-fin base length
ED	Eye diameter
HD	Head depth
HL	Head length
IGEL	Infracaudal gland, extreme length
IGS	Infracaudal gland, solid length
PADL	Post adipose length
PANL	Preanal length
PDD	Predorsal depth
PDL	Predorsal length
PAL	Pelvic to anal length
SGEL	Supracaudal gland, extreme length
SGS	Supracaudal gland, solid length
SL	Standard length
SOL	Snout to orbit length
UJL	Upper-jaw length

Table A12.—Discrimination values for distinguishing between pairs of species in the the Nigrum group, *N. crypticum*, and *N. bristori* using mensuristics.

	N. atrum		*N. indicum*		*N. gibbsi*		*N. crypticum*		*N. bristori*	
N. nigrum	Q	F	Q	F	Q	F	Q	F	Q	F
	AFB/DFB	4.28593	AFB/IGS	2.08827	AFB/DFB	-3.89030	AFB/DFB	-3.35558	UJL/SGS	0.86869
	HD/IGEL	-1.19300	HL/PAL	1.13370	UJL/SGS	-0.99254	AFB/HD	-2.21707	CPL/ED	0.75745
	IGS/ED	0.89838	DFB/IGEL	-1.01640	IGS/ED	-0.92298	PDD/ED	0.61417	HL/CPL	2.59523
	PADL/SOL	0.23386	DFB/CPD	-0.72363	PAL/SOL	-0.46925	PAL/PDD	-1.14351	PAL/SOL	0.37720
	PDL/IGS	0.24946	CPL/ED	-0.25337	HL/CPL	-1.28531	CPD/IGS	-1.05418	PANL/UJL	-0.89206
	D.V.	7.78873	D.V.	3.26593	D.V.	-13.29711	D.V.	-8.47545	D.V.	8.92823
	smaller	*N. nigrum*	smaller	*N. nigrum*	smaller	*N. gibbsi*	smaller	*N. crypticum*	smaller	*N. nigrum*
	larger	*N. atrum*	larger	*N. indicum*	larger	*N. nigrum*	larger	*N. nigrum*	larger	*N. bristori*
N. atrum			Q	F	Q	F	Q	F	Q	F
			HD/IGS	1.86732	UJL/SGS	-1.18561	SGS/SOL	-2.13589	HL/SGEL	-0.32564
			PAL/SOL	-0.38165	PADL/SOL	0.40997	PDD/ED	-0.49630	AFB/DFB	3.32936
			CPL/ED	-0.17701	CPD/SOL	-1.69868	HL/IGEL	0.87878	PANL/UJL	0.87400
			AFB/DFB	-0.89949	PAL/AFB	-3.18750	PDL/IGS	-0.85661	SGS/SOL	0.65417
					SOL/CPL	-11.20595	CPL/IGS	0.99615	PDL/PDD	0.27120
			D.V.	0.19798	D.V.	-9.21298	D.V.	-3.72048	D.V.	7.59093
			smaller	*N. atrum*	smaller	*N. gibbsi*	smaller	*N. atrum*	smaller	*N. bristori*
			larger	*N. indicum*	larger	*N. atrum*	larger	*N. crypticum*	larger	*N. atrum*
N. indicum					Q	F	Q	F	Q	F
					IGS/ED	0.66631	AFB/HD	4.47627	CPL/ED	0.52034
					PAL/SOL	0.73910	PAL/CPD	1.78978	PANL/UJL	-2.17561
					UJL/SGS	0.54443	DFB/IGS	-1.03005	PAL/PDD	4.08840
					AFB/IGS	-0.93585	CPL/PADL	3.51764	PDL/PDD	-1.29621
					PADL/UJL	-1.98869	PDD/SGEL	0.36772	DFB/CPD	1.25132
					D.V.	0.69912	D.V.	12.26213	D.V.	-0.73524
					smaller	*N. indicum*	smaller	*N. indicum*	smaller	*N. indicum*
					larger	*N. gibbsi*	larger	*N. crypticum*	larger	*N. bristori*
N. gibbsi							Q	F	Q	F
							CPL/ED	0.77066	AFB/DFB	-4.09715
							CPD/SOL	2.20488	IGS/ED	-0.71268
							PADL/UJL	-5.02667	DFB/CPD	1.76053
							DFB/CPD	-1.69377	HD/PADL	4.53729
							AFB/IGS	-0.47258	CPL/HD	1.34807
							D.V.	-2.90258	D.V.	2.57128
							smaller	*N. crypticum*	smaller	*N. gibbsi*
							larger	*N. gibbsi*	larger	*N. bristori*
N. crypticum									Q	F
									AFB/DFB	3.91133
									HD/SGEL	-0.43594
									CPL/ED	-0.40748
									PANL/UJL	1.63635
									DFB/CPD	1.39928
									D.V.	9.62238
									smaller	*N. bristori*
									larger	*N. crypticum*

TABLE A13.—Discrimination values for distinguishing between pairs of species in the Regale group using mensuristics.

	N. fernae		*N. idostigma*		*N. ritteri*		*N. bristori*	
N. regale	Q	F	Q	F	Q	F	Q	F
	CPL/PDD	1.64874	PDD/ED	0.76872	CPL/DFB	-1.23393	CPL/PDD	-1.32559
	CPL/IGS	-0.52919	CPL/UJL	-2.23421	PAL/CPD	1.05236	DFB/IGEL	-1.52353
	AFB/DFB	1.04425	PAL/AFB	2.84570	PDD/ED	0.65627	CPD/IGEL	1.98750
	PDD/ED	-0.41708	PDL/IGS	-0.78810	IGS/SOL	-0.57912	CPL/HD	-3.37848
	PANL/PDD	-0.42235	HL/IGS	1.02779	AFB/SGEL	-0.27820	HD/CPL	-5.34372
	D.V.	0.24495	D.V.	1.05008	D.V.	-0.53493	D.V.	-11.24901
	smaller	*N. regale*	smaller	*N. idostigma*	smaller	*N. ritteri*	smaller	*N. regale*
	larger	*N. fernae*	larger	*N. regale*	larger	*N. regale*	larger	*N. bristori*
N. fernae			Q	F	Q	F	Q	F
			DFB/IGS	-0.41033	CPD/IGS	3.25855	UJL/IGS	-0.45499
			IGEL/SOL	0.43772	HL/PAL	0.72940	DFB/CPD	-0.66417
			PDD/SOL	-0.50203	CPL/PDD	-0.50966	PANL/HD	-0.21376
			PANL/PDD	-0.29133	IGS/SOL	-0.11169	CPL/ED	-0.24343
			PAL/AFB	0.72811			IGS/ED	0.31994
			D.V.	-1.44158	D.V.	2.12710	D.V.	-2.82233
			smaller	*N. idostigma*	smaller	*N. fernae*	smaller	*N. bristori*
			larger	*N. fernae*	larger	*N. ritteri*	larger	*N. fernae*
N. idostigma					Q	F	Q	F
					PDL/IGS	-0.17142	DFB/CPD	2.38627
					DFB/CFD	-1.15595	PAL/AFB	0.88424
					SGS/SOL	-1.73156	PADL/UJL	-3.24499
					IGEL/SOL	0.72796	PAL/SOL	0.95396
					UJL/SGS	-0.28382	HD/IGS	0.54833
					D.V.	-4.04154	D.V.	6.06414
					smaller	*N. idostigma*	smaller	*N. idostigma*
					larger	*N. ritteri*	larger	*N. bristori*
N. ritteri							Q	F
							DFB/CPD	-0.94309
							AFB/IGS	-0.54981
							PAL/SOL	-0.32171
							UJL/CPD	-0.57795
							DFB/SGEL	0.15878
							D.V.	-4.28522
							smaller	*N. bristori*
							larger	*N. ritteri*

Table A14.—Discrimination values for distinguishing between pairs of species in the Achirus group using mensuristics.

	N. phyllisae		*N. wisneri*		*N. hawaiiensis*		*N. crypticum*	
N. achirus	Q	F	Q	F	Q	F	Q	F
	HL/IGS	-0.80310	CPL/UJL	-0.12577	UJL/IGEL	-0.90177	UJL/IGS	0.74155
	HD/PADL	-3.11239	PDL/PDD	3.27854	PAL/CPD	-0.66011	CPL/PADL	-1.59650
	PDD/ED	-0.48372	PANL/PDD	-2.63273	PADL/UJL	-1.66174	IGL/SOL	-0.38564
	PAL/UJL	2.92181	PANL/HD	1.05501	UJL/IGS	-0.81765	PADL/SOL	0.25917
	DFB/CPL	-2.38989	HL/CPL	3.25726	PANL/UJL	0.43230	PANL/CPD	0.12926
	D.V.	-4.43272	D.V.	8.63552	D.V.	-3.60037	D.V.	0.69611
	smaller	*N. phyllisae*	smaller	*N. achirus*	smaller	*N. hawaiiensis*	smaller	*N. achirus*
	larger	*N. achirus*	larger	*N. wisneri*	larger	*N. achirus*	larger	*N. crypticum*
N. phyllisae			Q	F	Q	F	Q	F
			HD/IGS	-1.36357	PAL/CPD	-1.21320	IGS/ED	-0.53283
			PAL/DFB	1.89473	CPL/IGS	-0.23369	PADL/PDD	1.23626
			HD/PADL	2.55588	PADL/PDD	-0.64120	AFB/DFB	1.47062
			PDD/ED	-0.44454	IGS/ED	0.42933	HD/CPL	-9.24936
			AFB/DFB	1.44285	HL/CPL	1.08317	CPL/HD	-3.95183
			D.V.	-1.53048	D.V.	-0.97351	D.V.	-9.77993
			smaller	*N. phyllisae*	smaller	*N. hawaiiensis*	smaller	*N. phyllisae*
			larger	*N. wisneri*	larger	*N. phyllisae*	larger	*N. crypticum*
N. wisneri					Q	F	Q	F
					UJL/IGS	0.97169	IGS/SOL	1.11068
					PAL/CPD	0.78232	PADL/SOL	-0.31937
					PADL/UJL	1.69386	SGS/SOL	-1.16377
					IGS/SOL	-0.27714	HL/SGEL	-0.31007
					CPL/AFB	0.88427	PDL/IGS	0.15734
					D.V.	4.81378	D.V.	-0.68881
					smaller	*N. wisneri*	smaller	*N. crypticum*
					larger	*N. hawaiiensis*	larger	*N. wisneri*
N. hawaiiensis							Q	F
							HD/PADL	5.35289
							IGS/SOL	0.81532
							AFB/DFB	-1.82957
							PANL/UJL	-1.36786
							PDL/PDD	0.48222
							D.V.	0.94892
							smaller	*N. crypticum*
							larger	*N. hawaiiensis*

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