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New Series, No. 12

FISHES OF THE FAMILIES EVERMANNELLIDAE AND SCOPELARCHIDAE: SYSTEMATICS, MORPHOLOGY, INTERRELATIONSHIPS, AND ZOOGEOGRAPHY

ROBERT KARL JOHNSON

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ABSTRACT

The alepisauroid family Evermannellidae contains seven species arranged in three genera. Diagnostic characters for the recognition of species and genera include meristic and morphometric characters, conformation of the eye, number and arrangement of laterosensory pores and associated structures, osteological features, pigment patterns, gut morphology, larval morphology and pigmentation, and the presence or absence of luminous tissue. Evermannellids are relatively large-bodied, mesopelagic predators, not known to exhibt diel vertical migration, and, based on rarity of representation (of adults) in collections, are probably often successful at net avoidance. Although the principal prey of most evermannellid species appears to be fish, species in the genus *Coccorella* may frequently concentrate on squid. Evermannellids exhibit a highly peculiar tripartite division of the tail musculature that may relate to the need for maintaining position in the water column and for achieving short but rapid bursts of speed during prey capture. Luminous tissue occurs in the species of *Coccorella*. The tubular eyes of *Evermannella* spp. and scopelarchid species, although very similar in morphology and no doubt in function, have probably evolved independently. Examination of a large number of characters based on external morphology, larval morphology, osteology, and myology fails to confirm sister-group relationship for the Evermannellidae and Scopelarchidae. Although evermannellids appear to be most closely related to other alepisauroids, particularly to the Alepisauridae and Omosudidae, available evidence suggests that scopelarchids are members of a chlorophthalmoid lineage, not closely related to the alepisauroids. Within the Evermannellidae, *Odontostomops* is regarded as the sister group of *Coccorella* + *Evermannella*. Each evermannellid genus can be well defined, largely in terms of autapomorphous features. Evermannellids occur throughout the tropical and subtropical Atlantic, Indian, and Pacific Oceans, including (one species) the Mediterranean Sea, but no evermannellid occurs in polar seas. *Coccorella* contains two species: *C. atlantica*, a subtropical species occurring in all three oceans, and *C. atrata*, a tropical species limited to the Indian and Pacific Oceans. *Evermannella* contains four species: *E. ahlstromi*, endemic to ecotonal areas in the eastern tropical Pacific; *E. balbo*, largely restricted to relatively cool and/or productive areas in the Atlantic, Indian, and Pacific Oceans; *E. indica*, a tropical-subtropical species that is widely distributed in all three oceans; and *E. megalops*, endemic to central-water areas in the South Pacific. *Odontostomops* is monotypic, *O. normalops* is a tropical-subtropical species that is widely distributed in all three oceans. New material is reported for 15 (of 17) scopelarchid species, adding substantially to our knowledge of the distribution of several of these species. The distribution of evermannellid and scopelarchid species, taken singly and in combination, is examined for agreement with patterns ex-

hibited by other midwater organisms, with patterns of possible environmental correlates of distribution, and, to a lesser extent, with data bearing on the historical components of open-ocean species assemblages.

INTRODUCTION

The family Evermannellidae, the saber-toothed fishes, occurs in midwater throughout the tropical and subtropical ocean. Despite the widespread distribution of evermannellids, the family has until now remained poorly known, largely a result of lack of material. I recognize seven species of evermannellids arranged in three genera: *Coccorella*, *Evermannella*, and *Odontostomops*. It has long been supposed that the closest relatives of the evermannellids are to be found among the Scopelarchidae, the pearl-eyed fishes, a suggestion based largely on the occurrence of tubular-eyed forms in both groups. The present study was prompted by the supposed sister-group status of these two families; it seemed an ideal opportunity to compare patterns of distribution and variation between two morphologically and perhaps ecologically similar open-ocean families.

This study has the following objectives: (1) recognition and definition of extant evermannellid species and genera, (2) description of patterns of variation in widely distributed evermannellid species, (3) assemblage of all available morphological and ecological data bearing on the natural history of evermannellid species, (4) based on examination of considerable additional material, to update my revision of the Scopelarchidae (Johnson, 1974c), (5) to make detailed comparisons of the distributions of evermannellid and scopelarchid species with possible physical, chemical, and biological correlates of distribution and to compare observed patterns with those exhibited by other midwater organisms, (6) on the basis of study of all available characters, external morphology, larval morphology, osteology, etc., to produce the best-possible hypothesis of interrelationships among evermannellid species, (7) to attempt a synthesis of phylogenetic and zoogeographic information leading to accounts of the evolutionary zoogeography of the two groups, (8) by examining other iniomous (*sensu* Gosline et al., 1966) taxa, to assemble and assess evidence bearing on the hypothesis of sister-group relationship for the Evermannellidae and Scopelarchidae.

Species of scopelarchids recognized are those included in Johnson (1974c). That work was based on some 2,102 specimens from 1,122 lots. Since that time I have had the opportunity to examine an additional 1,549 specimens from 717 lots.

My account of the Evermannellidae is based on 2,763 specimens from 1,270 lots. The listing of nominal species and genera below summarizes the taxonomic conclusions of this study. Names are listed in chronological order of their appearance in the literature, with the original combination on the left and the currently recognized combination (if different from the original) on the right.

Coccorella Roule 1929

Type species: *Coccorella atrata* (Alcock 1893)

Odontostomus atratus Alcock 1893	= *Coccorella atrata* (Alcock)
Evermannella atrata atlantica Parr 1928	= *Coccorella atlantica* (Parr)
Odontostomops braueri Rofen 1963	= *Coccorella atrata* (Alcock)

Evermannella Fowler 1901

Type species: *Evermannella balbo* (Risso 1820)

Scopelus balbo Risso 1820	= *Evermannella balbo* (Risso)
Odontostomus hyalinus Cocco 1838	= *Evermannella balbo* (Risso)
Evermannella indica Brauer 1906	
Evermannella indica melanoderma Parr 1928	= *Evermannella indica* Brauer
Odontostomus balbo atlanticus Borodin 1931	= *Evermannella indica* Brauer
Evermannella borodini Whitley 1958	= *Evermannella indica* Brauer
Evermannella sicaria Rofen 1963	= *Evermannella balbo* (Risso)
Evermannella ahlstromi Johnson & Glodek 1975	
Evermannella megalops Johnson & Glodek 1975	

Odontostomops Fowler 1934

Type species: *Odontostomops normalops* (Parr 1928)

Evermannella normalops Parr 1928	= *Odontostomops normalops* (Parr)

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Last, but by no means least, thanks to my wife, Pat, who aided me in preparation of the manuscript, typed the final draft, helped read various stages of proof, and who puts up with me.

METHODS

Descriptions.—In the descriptions of the various taxa of evermannellids I have attempted to avoid redundancy by including characters common to all members of a taxon only in the description of that taxon. Except where otherwise noted, all drawings are by the author.

Material Examined.—The following abbreviations are used in reference to material examined:

AMS — Australian Museum, Sydney; material listed by ship, cruise, and station number.

CAS — California Academy of Sciences, San Francisco; material listed either by CAS or SU (Stanford University) catalogue number.

FMNH — Field Museum of Natural History, Chicago; material listed by FMNH catalogue number.

FSBC — Florida State Department of Natural Resources, St. Petersburg; material listed by FSBC catalogue number.

IOAN — Institute of Oceanography, Academy of Sciences of the U.S.S.R., Moscow; material listed by ship and station number:

- AK — R/V *Akademik Kurchatov*
- B — R/V *Baikal*
- V — R/V *Vityaz*

ISH — Institut für Seefischerei, Bundesforschungsanstalt für Fischerei, Hamburg; material listed by ISH catalogue number or by ship and station number:

- WH — FFS *Walther Herwig*

LACM — Natural History Museum of Los Angeles County, Los Angeles; material listed by LACM catalogue number.

MCZ — Museum of Comparative Zoology, Harvard University, Cambridge; material listed by MCZ catalogue number or by ship, cruise, and station number:

- AB — R/V *Anton Bruun*

NIO — Institute of Oceanographic Sciences, Wormley, Godalming, Surrey, U.K.; material listed by ship and station number:

- DY — R/S *Discovery*

NMFS(H) — National Marine Fisheries Service, Honolulu; material listed by ship and station number:

- HMS — R/V *Hugh M. Smith*
- JRM — R/V *John R. Manning*

NMFS(LJ) — National Marine Fisheries Service, La Jolla; material listed by ship and station number:

- J — R/V *David Starr Jordan*
- TC — R/V *Townsend Cromwell*

ORSTOM Office de la Recherche Scientifique et Technique Outre-mer, Noumea, New Caledonia; material listed by name of ship, cruise, and station number or by date of capture.

SAM South African Museum, Capetown; material listed by SAM catalogue number.

SIO Scripps Institution of Oceanography, University of California at San Diego, La Jolla; material listed by SIO catalogue number.

SOSC Smithsonian Oceanographic Sorting Center, Smithsonian Institution, Washington, D.C.: all SOSC material will be permanently deposited at either Field Museum of Natural History or the National Museum of Natural History; material listed by ship, cruise, and station number:

AB	R/V *Anton Bruun*
DES	USNS *De Steiguer*
ELT	USNS *Eltanin*
J	R/V *David Starr Jordan*
TV	R/V *Te Vega*
UND	R/V *Undaunted*

UH Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe; all UH material is or will be deposited in several permanent institutional collections; material listed by date of capture (year/month/station number) or by ship, cruise, and station number:

TC	R/V *Townsend Cromwell*

UMML Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami; material listed by UMML catalogue number.

USC University of Southern California, Los Angeles; material listed by ship, cruise, and station number:

ELT	USNS *Eltanin*

USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C.; material listed as follows: (1) USNM catalogue number; (2) ACRE, Ocean Acre Expeditions, material listed by cruise and station number (see Gibbs, Roper, et al., 1971; Gibbs & Roper, 1971); (3) MED, Mediterranean Biological Studies Expeditions, material listed by cruise and station number (see Goodyear et al., 1972); (4) uncatalogued material listed by ship, cruise, and station number:

AB	R/V *Anton Bruun*
ELT	USNS *Eltanin*
ORE	R/V *Oregon*
TV	R/V *Te Vega*
UND	R/V *Undaunted*

WHOI Woods Hole Oceanographic Institution, Woods Hole, Mass.; most of this material has been or will be deposited in the Museum of Comparative Zoology, Harvard University; material listed by Richard H. Backus (RHB) station number.

ZIZM Zoological Institute and Zoological Museum, Hamburg; material listed by IOES or RBF catalogue number.

ZMUC Zoological Museum of the University of Copenhagen, Copenhagen; material listed by *Dana* (D) station numbers. A number of vessels were involved in the collection of this material, notably the M/S *Dana I* and R/S *Dana II* (see Schmidt, 1929, Jesperson & Tåning, 1934).

The list of material examined includes only the institutional catalogue or station number and the number of specimens examined corresponding to each lot. Complete capture and locality data may be obtained upon motivated request from the respective institutions or from the author. Material listed under the heading "additional larval and juvenile material" represents specimens for which standard lengths were not recorded.

Most specimens were taken in non-closing net hauls with the following types of gear: Isaacs-Kidd Midwater Trawl (IKMT, 3-m diameter unless otherwise specified); CMBT 1600 Midwater Trawl (ISH *Walther Herwig* collections); and the conical nets used by the Dana Expeditions (S150, S200, E300, etc., see *Dana*, Rep. No. 1 [1934] p. 18).

Counts and Measurements.—Unless specified below, methods of taking counts and measurements follow those given by Hubbs & Lagler (1958, pp. 19–26) and Johnson (1974c, pp. 6–7). The last rays of the dorsal and anal fins are divided completely to the base and in each case were counted as one. All vertebral centra were counted, including the compound stegural element. A free second ural centrum is present in all evermannellids (presumed for *Evermannella megalops*) but could not be distinguished in radiographs and is not included in vertebral counts. Vertebral counts were made from radiographs and from cleared and stained specimens.

Lengths are given as the standard length (SL) in millimeters. Measurements were made to 0.1 mm with 180-mm dial calipers or needle-point dividers except for those measurements less than 3 mm, which were taken to 0.01 mm using an ocular micrometer on a Wild M5 microscope. All measurements were taken in a straight-line point-to-point fashion.

In all, 29 measurements were made on each selected specimen. Those measurements listed below are either undefined in or taken differently than methods used in Hubbs & Lagler (1958) or Johnson (1974c).

Body depth at anal-fin origin = vertical distance between base of anteriormost anal-fin ray and dorsal margin of body.

Adipose fin: distance from dorsal-fin base = distance between base of posteriormost dorsal-fin ray and origin of adipose fin; distance from snout = distance from tip of snout to origin of adipose fin.

Head length = distance from tip of snout to posteroventral margin of opercle. Postorbital head length = distance from posteriormost margin of orbit to posteroventral margin of opercle.

Eye diameter, horizontal and vertical = in each case the greatest fleshy diameter of eye.

Longest tooth, dentary and palatine = in each case the longest straight-line distance from base to distal tip.

Interorbital width = least transverse distance between dorsolateral ridge of

each frontal bone; dorsolateral ridge of each frontal bone forming lateral margin of frontal bone in interorbital region.

Cephalic Laterosensory Pores.—The cephalic laterosensory system is well developed in evermannellids and is composed of characteristic series of large to very large pores and numerous sensory papillae (especially in *Coccorella* and *Odontostomops*). The number and arrangement of pores in certain of these series are of diagnostic value in separating certain species. I have (more or less arbitrarily) divided the cephalic laterosensory system as found in evermannellids into six major series.

SNOUT-PAD SERIES.—A group of seven to 11 pores piercing the snout-pad. The snout-pad is defined as the flattened dorsoanterior surface of the head lying between the anterior nostril and orbit and medial to the posterior nostrils. The snout-pad encloses the nasal bones and overlies the dermethmoid. The snout-pad forms a membranous roof extending from the interorbital area of the frontals to the anterior margins of the nasal bones. An extensive laterosensory canal system underlies the snout-pad. This system is divided anteriorly by the nasal bones and a median membranous septum, but the two canals thus formed share a common pore posteriorly (the posterior snout-pad pore) at about the point each canal enters the respective (left and right) frontal bone.

The snout-pad series includes up to five separately identifiable pores or pore series (fig. 1).

Nasal pores (PSN): two pores, one on each side, piercing the moderately to strongly truncate anterior wall of the snout-pad, and each lying dorsomedial to the respective tubular anterior nostril. Each nasal pore providing direct access to the hollow, trough-like lumen of the respective nasal bone.

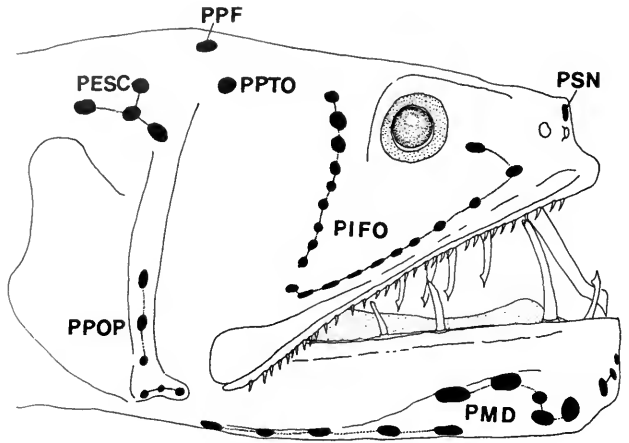
Anterior snout-pad pores (PSA): four pores arranged transversely across snout-pad at about posterior borders of nasal bones, lying on or slightly posterior to a transverse line through the center of each posterior nostril. PSA pores subequal in size, or the two lateral pores slightly larger than the two medial pores.

Medial snout-pad pores (PSM): if present, two pores each slightly lateral to dorsal midline, one on each side, about midway between anterior snout-pad pores and posterior snout-pad pore.

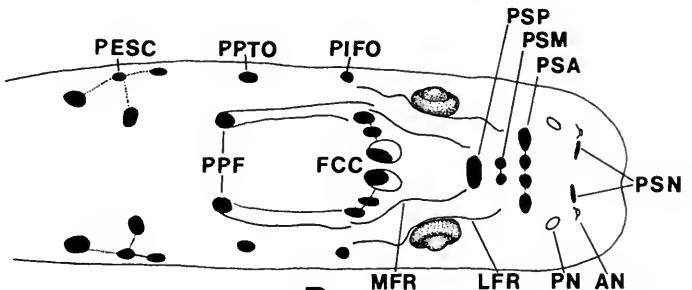
Posterior snout-pad pore (PSP): a single pore centered at dorsal midline between or just behind anterior terminus of dorsomedial ridge of each frontal bone (fig. 1), just anterior to or over anterior portion of interorbital region of frontals.

Lateral snout-pad pores (PSL): if present, two pores, one on each side, anterolateral to PSP pore. Only three species, *Coccorella atlantica*, *C. atrata*, and *Evermannella balbo*, have the full complement of 11 snout-pad pores (table 1).

MANDIBULAR SERIES (PMD).—A series of 12 to 14 pores arranged in four groups on the ventrolateral and anterolateral surfaces of the articular and dentary of each side (fig. 1). Five pores along ventrolateral margin of articular, subequal in size, posteriormost pore of series at posteroventral corner of lower jaw. Four to six pores (table 1) on lateral face of dentary, the posteriormost directly over anterior pore of articular series. Counts for this group are variable, sometimes differing between left and right sides of a single specimen. The counts given are the maximum number of large pores observed. A number of much smaller pores (especially common in larger adults) may or may not be present in this area. Two pores ventrally on anterolateral face of dentary. One


PPF
PESC
PPTO
PSN
PIFO
PPOP
PMD

A


PESC
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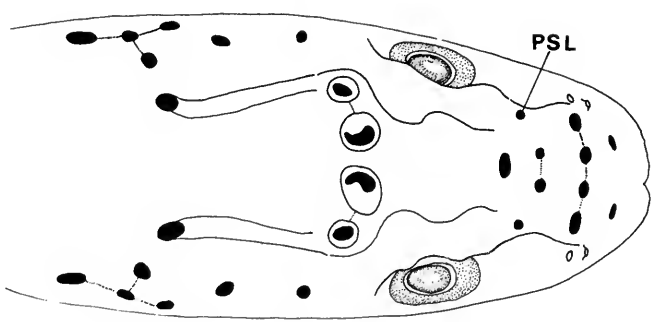
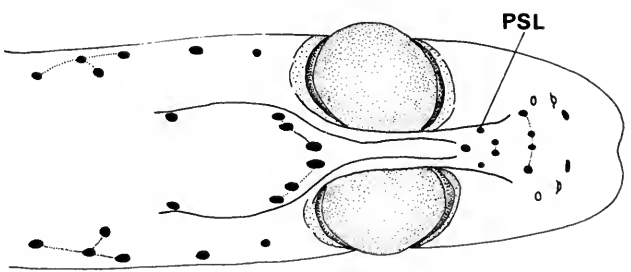

PSL

C


PSL

D

pore closely adjacent and lateral to protruding vertical ridge marking dentary symphysis (*Coccorella, Odontostomops*) or at ventrolateral margin of a vertically elongate fossa centered on dentary symphysis (*Evermannella*).

PREOPERCULAR SERIES (PPOP).—Typically a series of six pores over each preopercle, three pores arranged vertically over ventral portion of troughlike main shaft of preopercle and three pores arranged in the rough form of a triangle over ventral plate of preopercle. Membrane over preopercle in *Evermannella* extremely delicate, and counts of the preopercular series in species of *Evermannella* difficult or impossible to obtain in the material available (table 1).

TEMPORAL SERIES.—A series of five pores (fig. 1) connecting the infraorbital, preopercular, and lateral line laterosensory canals.

Pterotic pore (PPTO): a single pore centered over canal-like portion of pterotic and anterolateral to posterior frontal pore.

Extrascapular pores (PESC): four pores, one at each corner and one at center of lateral edge of the roughly triangle-shaped extrascapular bone. Anteriormost pore marking junction of temporal canal (from pterotic) and preoperculomandibular canal (from preopercle). Medialmost pore marking terminus of the short supratemporal canal. Posteriormost pore at the point where temporal canal passes to the lateral line system via posttemporal and supracleithrum.

FRONTAL SERIES.—Two well-defined pore series (fig. 1) over postorbital region of frontal bones.

Posterofrontal pore (PPF): two pores, one on each side marking posterior terminus of the short posterofrontal canal that runs along the posterior continuation of the dorsomedial ridge of each frontal. Posterofrontal pore of each side almost directly posterior to the respective lateralmost pore of frontal canal commissure and just anterior to articulation of frontal and parietal bones.

Frontal canal commissure (FCC): a series of four [two on each side (*Coccorella atrata*)] or six [three on each side (all other evermannellid species)] pores directly posterior to interorbital region of each frontal and forming a transverse connection between infraorbital series of each side (see Gosline et al., 1966, pp. 3–4, fig. 2). A very small percentage of the specimens of *Coccorella* have an asymmetric 2 + 3 or 3 + 2 (left + right) FCC pore count, and a detailed discussion of these abnormal specimens is provided following the description of *Coccorella*.

INFRAORBITAL SERIES (PIFO).—A series of small pores arranged in two limbs corresponding to the first and second and to the third through eighth infraorbitals, respectively (fig. 1), with pores of the two series separated by a slight but noticeable gap at the ventroposterior corner of the infraorbital series

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Opposite:

FIG. 1. Cephalic laterosensory pores in three species of evermannellids. **A, B,** *Odontostomops normalops,* SIO 72-316, 76.5. **C,** *Coccorella atrata,* SIO 70-346, 85.4. **D,** *Evermannella balbo,* ZMUC uncatalogued, from Mediterranean Sea, 75.2. **Pore abbreviations:** Snout-pad series: PSN=nasal pore; PSA=anterior snout-pad pores; PSM=medial snout-pad pores; PSP=posterior snout-pad pore; PSL=lateral snout-pad pores. Mandibular series: PMD. Preopercular series: PPOP. Temporal series: PPTO=pterotic pore; PESC=extrascapular pores. Frontal series: PPF=postero-frontal pore; FCC=frontal canal commissure. Infraorbital series: PIFO. **Other abbreviations:** AN=anterior nostril; PN=posterior nostril; LFR=lateral frontal ridge (interorbital region); MFR=medial frontal ridge (interorbital region).

TABLE 1. Number of pores in six series of the cephalic laterosensory system in evermannellids. See text and Figure 1 for definition and location of the pore series.

Pore series	*Coccorella*		*Evermannella*				*Odontostomops*
	atrata	*atlantica*	*ahlstromi*	*balbo*	*indica*	*megalops*	*normalops*
SNOUT-PAD SERIES							
PSN	2	2	2	2	2	2	2
PSA	4	4	4	4	4	4	4
PSM	2	2	2	2	2	0	2
PSP	1	1	1	1	1	1	1
PSL	2	2	0	2	0	0	0
MANDIBULAR SERIES							
PMD	5+6+2+1	5+6+2+1	5+4+2+1	5+6+2+1	5+5+2+1	5+4+2+1	5+5+2+1
PREOPERCULAR SERIES							
PPOP	3+3	?3+3	?3+3	?	?	?3+3	3+3
TEMPORAL SERIES							
PPTO	1	1	1	1	1	1	1
PESC	4	4	4	4	4	4	4
FRONTAL SERIES							
PPF	1	1	1	1	1	1	1
FFC	2+2	3+3	3+3	3+3	3+3	3+3	3+3
INFRAORBITAL SERIES							
PIFO	13–14+9	13–14+9	9+5	14+10	11–12+8	8–9+5	11+9

(fig. 1). Counts for the infraorbital series (table 1) are given as number of anterior pores + number of posterior pores. Infraorbital pores difficult or impossible to count in numerous specimens (true for all species) due to damage.

Osteology.—Osteological studies were based on trypsin-prepared cleared and stained material processed following the method of Taylor (1967). The procedure used in studying the prepared material closely followed that of Paxton (1972). Drawings of skeletal elements were done by the author, using a camera lucida attachment on a Wild M5 microscope. Unless otherwise noted, terminology employed for skeletal elements follows that of Johnson & Cohen (1974) and Johnson (1974c). Terminology employed for muscles follows that of Winterbottom (1974).

SYSTEMATICS

Systematic Position of the Evermannellidae

Reviews of the recent history of attempts at classifying "iniomous" fishes may be found in Gosline et al., 1966; Goody, 1969; Rosen & Patterson, 1969; Gosline, 1971; Paxton, 1972; Johnson, 1974c; Marshall & Staiger, 1975; Zehren, 1975; Bertelsen et al., 1976; Sulak, 1977. The only recent classification of iniomous fishes widely divergent from that presented by Gosline et al., 1966, is that of Rosen, 1973. Rosen removed the families Myctophidae and Neoscopelidae from the group of iniomous fishes to form a much restricted order Myctophiformes. The remaining inioms (to which Rosen added the Giganturidae) were placed in a new order, Aulopiformes, with two suborders: Aulopoidei (Aulopidae, Bathysauridae, Bathypteroidae, Ipnopidae, Chlorophthalmidae, Notosudidae) and Alepisauroidei. The Alepisauroidei was further divided into two superfamilies: Synodontoidea (Giganturidae, Harpadontidae, Synodontidae) and Alepisauroidea (Alepisauridae, Anotopteridae, Evermannellidae, Omosudidae, Paralepididae, Scopelarchidae). The placement of the synodontids, harpadontids, and giganturids with the alepisauroids is unique to Rosen's scheme among recent classifications of this group. To some extent that placement is corroborated by evidence discussed in a subsequent section of the present paper.

I regard as open the question of aulopiform vs. myctophiform (*sensu* Rosen, 1973) interrelationships and herein adopt the old and presumably now neutral term Iniomi to refer to that assemblage of taxa treated by Gosline et al., 1966. Families treated herein are those recognized by Gosline et al., 1966, and most subsequent authors, with the following exceptions and changes:

(1) The Giganturidae, allied by Rosen (1973) with the synodontoids, is not treated in this paper.

(2) The family Pseudotrichonotidae described by Yoshino & Araga (in Masuda et al., 1975), based on a new genus and species, *Pseudotrichonotus altivelis*, known from one station off Izu Peninsula, Japan, was allied by the authors with the Myctophiformes. A number of characters reported for this species (which I have not had the opportunity to examine) strongly suggest that the authors incorrectly allied it with iniomous fishes (see table 9): 17 principle caudal-fin rays (vs. 19 in all inioms); six branchiostegal rays (vs. seven or more in all inioms [except n = 6 reported for one specimen of *Diogenichthys atlanticus* (Myctophidae) by Moser & Ahlstrom (1970, p. 9)]); seven pelvic-fin rays (vs. eight or more in all other inioms except the myctophids *Notolychnus valdiviae* [n = 6, Wisner 1976, p.

144], *Gonichthys* ["very rarely," n = 7, Nafpaktitis et al. 1977, p. 86], and the ipnopid *Bathymicrops brevianalis* [n = 7, Nielsen 1966, p. 64]).

(3) Sulak (1977) offers well-reasoned arguments for the recognition of only three families of benthic inioms—no pelagic genera are included in his study—Aulopidae (*Aulopus, Hime*), Chlorophthalmidae (*Bathymicrops, Bathypterois, Bathysauropsis, Bathytyphlops, Chlorophthalmus, Ipnops, Parasudis*), Synodontidae (*Bathysaurus, Harpadon, Saurida, Synodus, Trachinocephalus*). Other than allying *Saurida* with *Harpadon* and bathypteroids with ipnopids, Sulak's scheme of classification does not differ markedly from that of Gosline et al. (1966) except with respect to whether a given set of relationships should be recognized by award of familial or subfamilial rank. I recognize the following benthic iniomous families: Aulopidae (*Aulopus, Hime*), Bathysauridae (*Bathysaurus*), Chlorophthalmidae (*Bathysauropsis, Chlorophthalmus, Parasudis*), Harpadontidae (*Harpadon, Saurida*), Ipnopidae (*Bathymicrops, Bathypterois,*[1] *Bathytyphlops, Ipnops*), Synodontidae (*Synodus, Trachinocephalus*).

Virtually all authors offering any opinion have suggested that the Scopelarchidae and Evermannellidae are closely related (Gregory & Conrad, 1936, pp. 33–34; Marshall, 1955, p. 331; Gosline et al., 1966, p. 17). Rofen (1966d, p. 516) felt that the evermannellids were more closely related to the Omosudidae than to the Scopelarchidae, which he (Rofen, 1966e, p. 570) felt to be "the most distinct family among the alepisauroids." Johnson (1974c, pp. 210–211) reviewed a limited number of characters and came to the conclusion that there existed no good evidence to suggest a closer relationship between these two families than between the Scopelarchidae and any other alepisauroid family. In a subsequent section of this paper (Interrelationships) I review available evidence bearing on the hypothesis that the Evermannellidae and Scopelarchidae are each other's closest relatives and that these two families form a monophyletic group.

Family EVERMANNELLIDAE

Type-Genus.—*Evermannella* Fowler 1901, p. 211 (original diagnosis of Evermannellidae, replacement for Odontostomidae Gill 1896, based on *Odontostomus* Cocco 1838, preoccupied by *Odontostomus* Beck 1837 [Mollusca]).

Diagnosis.—Alepisauroids, with an externally visible tripartite division of the posterior main trunk musculature, musculature of tail divided into three distinct regions with epaxial and hypaxial musculature separated by a midlateral band of muscle tissue centered and arranged longitudinally on the vertebral column. Normal scales lacking on head and body. Anteriormost tooth on each palatine bone an enormous barbed or saber-like (unbarbed) fang, easily the largest tooth present on each side. Eyes large and tubular in *Evermannella;* moderately large and semitubular in *Coccorella;* and small, nontubular, and directed laterad in *Odontostomops.* Basihyal much reduced, only partially ossified, lacking teeth. Teeth absent over first three basibranchials. Parietal bones invariably present, not separated by supraoccipital, meeting medially. Three postcleithra. One extrascapular. Posttemporal unforked. Coracoid not greatly expanded. Pectoral-fin insertion ventrolateral, near ventral contour of body. Infraorbitals eight. First precaudal centrum complete. Two supraneurals. Second ural centrum invariably present and free. One epural. Larvae with three (*Evermannella,*

[1]Sulak (1977) accords the species assigned to *Benthosaurus* subgeneric status within *Bathypterois.*

Coccorella) or 12 or more (*Odontostomops*) peritoneal pigment sections. Peritoneal pigment sections unpaired.

Description.—Dorsal-fin rays 10 to 13. Anal-fin rays 26 to 37. Pectoral-fin rays 11 to 13. Pelvic-fin rays nine. Caudal-fin rays (principal rays) 1 + 9 + 8 + 1 (counting from dorsal, the inner 17 rays branched). Branchiostegal rays eight. Vertebrae 45 to 54.

Body short to moderately elongate, deep, reaching (*Coccorella atlantica*) 184.5 mm SL. Body strongly compressed, essentially ribbon-like posteriorly. Normal scales lacking on body and head. Skin smooth, delicate, and easily torn. Lateral line single, extending from upper edge of gill cover posteriorly to a point that varies according to species (details of lateral line structure are provided by Rofen, 1966d). Dermal keels lacking on caudal peduncle. Intermuscular bones present.

Musculature of tail divided into three distinct regions with the epaxial and hypaxial musculature separated by a midlateral band of muscle centered and arranged longitudinally on the vertebral column (fig. 8). Medial muscle band (lateralis superficialis, see section on Size and Habits below) essentially covering caudal skeleton posteriorly and tapering anteriorly, becoming indistinguishable in external view over a point between vent and anal-fin origin (depending upon species).

Anus distinctly anterior to anal-fin origin, slightly ahead of, at, slightly posterior to, or distinctly posterior to a point midway between pelvic-fin insertion and anal-fin origin (varying with species). Stomach very large, heavily muscularized, extending to a point over or just posterior to pelvic-fin bases.

Pigmentation varying (interspecifically and in some cases intraspecifically) from nearly unpigmented specimens with few or no evident melanophores, to individuals with some to numerous large stellate melanophores and numerous smaller, scattered melanophores, to individuals essentially covered with uniform brownish black pigment. No concentration of pigment into bars, stripes, or conspicuous markings. Peritoneum black.

Luminous tissue present in *Coccorella atrata*, probably present in *C. atlantica*, possibly present in *Evermannella*, presumed absent in *Odontostomops*. Swimbladder lacking. Synchronous hermaphrodites with functional ovotestis.

Head relatively large and massive, especially so in species of *Coccorella*. Frontals extremely large, occupying most of dorsal roof of skull. Low keels present on frontal bones. Parietals invariably present, overlying anterior and anterolateral margins of supraoccipital and meeting in midline. Basisphenoid present or absent. No antorbital. Supraorbital large and elongate, except *Odontostomops* where it is lacking. No direct articulation between palatine and maxillary.

Snout rounded anteriorly but with a distinct indentation at premaxillary symphysis. Anterior nostril tubular, subequal to posterior nostril in diameter. Anterior nostril on each side lying lateral and adjacent to nasal pore in anterior wall of snout pad. Posterior nostril directly posterior to anterior nostril and lying on a longitudinal line connecting anterior nostril and center of lens of eye. Cephalic laterosensory system (fig. 1) well developed, with numerous pores and sensory papillae. Dentary symphysis marked by a vertically elongate fossa (*Evermannella*) or by a distinct and protruding ridge (*Coccorella, Odontostomops*).

Eyes small to very large; nontubular, semitubular, or tubular (fig. 3). Interorbital space varying from extremely narrow, interorbital width considerably less than eye diameter (tubular-eyed species), to quite broad, interorbital width con-

siderably exceeding eye diameter. A roughly elliptical lens pad present in tubular-eyed species. No sclerotic bones. Infraorbitals small and membranous, numbering eight, partially overlying posterior margin of eye.

Opercular bones membranous. Opercle much larger than subopercle in size. Branchiostegal membranes free from isthmus, united by a small membrane anteriorly, at or slightly posterior to a vertical through anterior margin of eye. Left branchiostegal membrane distinctly overlapping right branchiostegal membrane. Gills four. Gill rakers absent, represented by minute gill teeth developing on small nodules of bone, each nodule supporting one to several teeth. Gill teeth limited to ceratobranchial of second gill arch in all species (except for two species in which the largest gill tooth plate lies astride the articulation of ceratobranchial and hypobranchial of second gill arch). Pseudobranchiae large and well developed, with four to 16 filaments (varying with both species and size of individual).

Gape large. Lower jaw relatively deep and massive, not arched. Maxillary excluded from gape, never bearing teeth. A single large supramaxillary. Teeth present on premaxillaries, dentaries, vomer, and palatines. Teeth on premaxillary small, uniserial, retrorse anteriorly but typically straight posteriorly. All evermannellid species with an edentulous area on anterior premaxillary at anterolateral corner of snout. Dentary teeth barbed and biserial (*Evermannella, Odontostomops*) or unbarbed and uniserial (*Coccorella*). Vomer with two small teeth, one on each side, although in numerous specimens (true for all species), only one laterally positioned tooth is present, its counterpart either failing to develop or (more probable) lost. Palatine teeth uniserial, decreasing in length from anterior to posterior. Anteriormost palatine tooth (on each side) an enormous barbed (*Evermannella, Odontostomops*) or saber-like (unbarbed) (*Coccorella*) fang, easily the largest tooth occurring in evermannellids. Lingual teeth lacking. Basihyal much reduced, neither basihyal nor first three basibranchials bearing teeth. A fourth basibranchial toothplate bearing six to nine small conical teeth is unique to *Evermannella balbo*.

Fins soft-rayed. Dorsal fin with rays relatively short, second or third dorsal-fin ray typically the longest, and with base relatively short. Middle of dorsal-fin base anterior to a vertical through middle of standard length. A well-developed dorsal adipose fin invariably present, inserted over posterior one-third of anal-fin base. Anal-fin base short to elongate, distinctly longer than head. Anal-fin origin posterior to a vertical through middle of standard length. Caudal fin deeply forked, lobes equal in length, with well-developed adjacent procurrent caudal rays. Pelvic fins abdominal, inserted under anterior one-half of dorsal-fin base. Pectoral-fin insertion just above ventral contour of body, line of insertion of pectoral-fin rays rather more horizontal than vertical. Angle between horizontal axis of body and axis of pectoral-fin insertion = 15° to 20° (Marshall, 1955).

Content and Range.—I recognize seven species of evermannellids distributed among three genera (*Coccorella, Evermannella,* and *Odontostomops*). The Evermannellidae is a warm-water group, circumglobal in distribution (fig. 2). Poleward distribution limits for the family roughly coincide with the north and south subtropical convergence areas. Although at least one species (*Evermannella balbo*) occurs within the Transition Zone (see McGowan, 1971) of the South Pacific, no evermannellid species is known to occur in subarctic, subantarctic, or antarctic waters. All three genera occur in all three oceans. An artificial key to the seven species of evermannellids is given on page 101.

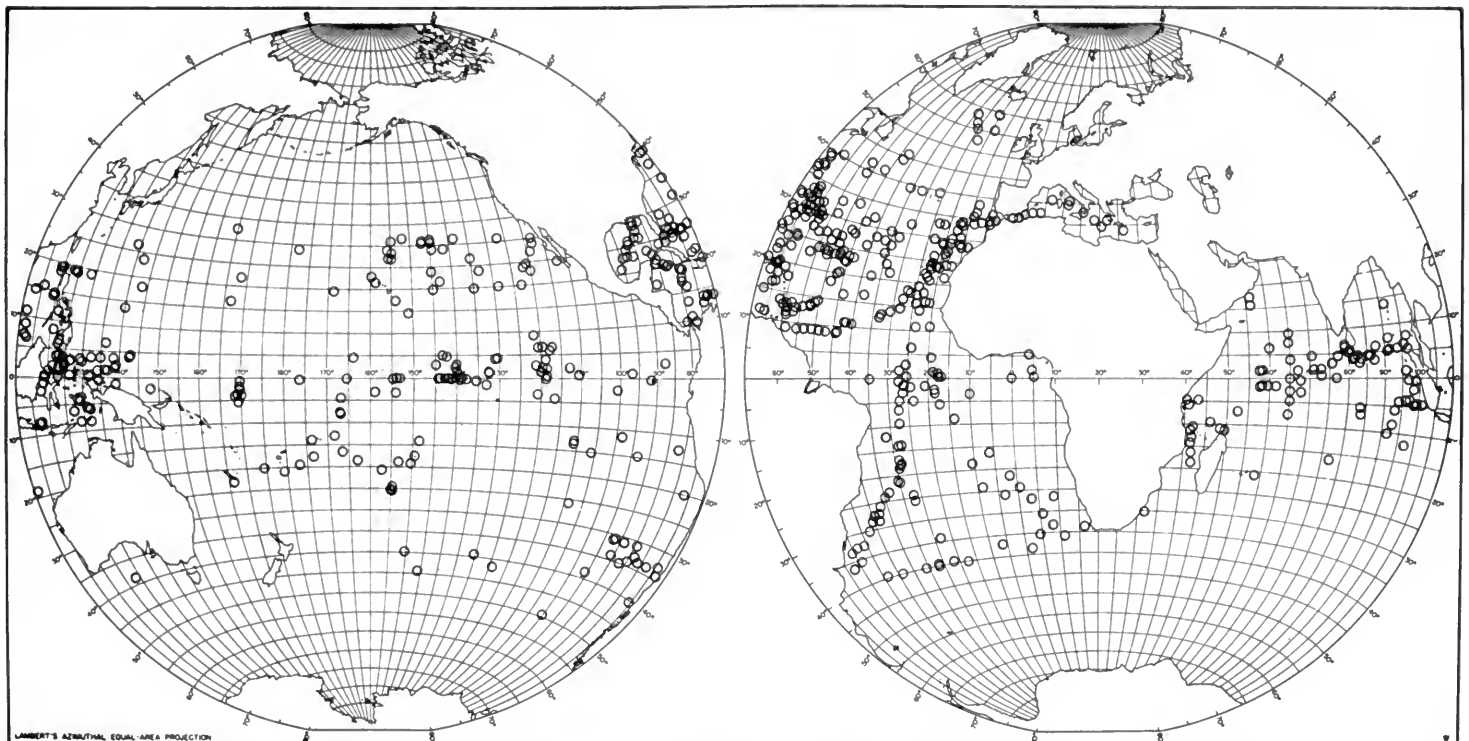

FIG. 2. Distribution of the family Evermannellidae. All genera and species included, but numerous overlapping or closely adjacent points omitted.

Diagnostic Characters.—Among alepisauroids, the evermannellids are most readily distinguished by the following combination of characters: (1) an externally visible tripartite division of the tail musculature with the epaxial and hypaxial muscles separated by a midlateral band of muscle tissue (the lateralis superficialis, see section on Size and Habits below); (2) the lack of normal scales on the head or body; (3) the greatly reduced basihyal that lacks teeth; (4) the lack of teeth over the first three basibranchials; (5) the restriction of gill teeth to the ceratobranchial of the second gill arch; (6) the short-based dorsal fin with 10 to 13 rays; (7) the presence of tubular or semitubular eyes in six of the seven species; (8) the lack of external keels on the body; (9) the development of enormous barbed or unbarbed fangs on each palatine; and (10) the relatively massive head, massive lower jaw, and deep body.

Characters considered to be diagnostic at the generic and specific level among evermannellids are indicated in the next several pages. This is followed by an account of what little is known of the biology of evermannellid species.

MERISTIC CHARACTERS.—Meristic characters useful in distinguishing evermannellid species include counts of the following elements: dorsal-fin rays, anal-fin rays, and vertebrae. Counts of pectoral-fin rays (11 to 13), pelvic-fin rays (invariably nine), and branchiostegal rays (invariably eight) do not differ between species.

Tables 2 and 3 allow comparison of meristic characters between all seven evermannellid species. In several cases counts of anal-fin rays and number of vertebrae are or appear to be geographically variable within species. These species are indicated in Table 3, and geographic variation within species is documented and discussed in the appropriate species accounts.

MORPHOMETRIC CHARACTERS.—In all, 29 measurements of various body proportions were taken from a representative sample over the geographic and the available size range for each species. Only post-metamorphic juveniles and adults were included. Only characters relating directly to differences in eye

TABLE 2. Comparison of meristic characters in evermannellids.

	A. Dorsal-fin rays					
Species	10	11	12	13	N	Mean ± 95% limits
C. atlantica	—	9	97	3	109	11.94±.063
C. atrata	1	32	48	1	82	11.60±.119
E. ahlstromi	5	72	1	—	78	10.95±.620
E. balbo	—	—	83	2	85	12.02±.033
E. indica	—	—	209	6	215	12.03±.022
E. megalops	1	8	1	—	10	11.00±.337
O. normalops	—	4	77	2	83	11.98±.059

	B. Pectoral-fin rays				C. Pelvic-fin	D. Branchiostegal
Species	11	12	13	N	rays = 9	rays = 8
C. atlantica	—	30	1	31	29	27
C. atrata	1	14	—	15	14	15
E. ahlstromi	—	13	—	13	10	10
E. balbo	—	37	—	37	25	24
E. indica	1	52	—	53	42	35
E. megalops	—	6	—	6	6	5
O. normalops	4	59	1	64	39	29

TABLE 3. Comparison of meristic characters in evermannellids. The VAR column indicates whether significant geographic variation in counts is (+) or is not (0) found for the indicated species. Additional tables documenting geographic variation in those species indicated are presented in the appropriate species accounts.

E. Anal-fin rays

Species	26	27	28	29	30	31	32	33	34	35	36	37	N	Mean ± 95% limits	VAR
C. atlantica	1	18	79	11	1	—	—	—	—	—	—	—	110	27.94±.110	+
C. atrata	—	29	40	10	—	—	—	—	—	—	—	—	79	27.76±.149	0
E. ahlstromi	—	—	—	12	18	19	5	—	—	—	—	—	54	30.31±.254	0
E. balbo	—	—	—	—	—	—	—	10	64	53	28	2	157	34.67±.139	+
E. indica	—	5	114	124	83	10	—	—	—	—	—	—	337	28.94±.094	+
E. megalops	—	—	—	4	3	1	—	—	—	—	—	—	8	29.62±.622	0
O. normalops	—	—	—	—	1	16	44	55	12	4	—	—	132	32.55±.163	+

F. Vertebrae

Species	45	46	47	48	49	50	51	52	53	54	N	Mean ± 95% limits	VAR
C. atlantica	—	—	—	8	20	2	—	—	—	—	30	48.80±.206	0
C. atrata	2	14	5	—	—	—	—	—	—	—	21	46.14±.261	0
E. ahlstromi	—	—	5	11	5	—	—	—	—	—	21	48.00±.322	0
E. balbo	—	—	—	—	—	—	—	21	28	6	55	52.73±.176	+
E. indica	—	—	—	5	13	36	24	7	—	—	85	50.18±.214	+
E. megalops	—	—	—	1	2	1	—	—	—	—	4	49.00±1.30	0
O. normalops	—	—	—	1	2	14	7	1	—	—	25	50.20±.337	+

morphology (i.e., non-tubular, semitubular, tubular) and to the tremendously elongate anteriormost palatine tooth in *Coccorella* differed between genera (table 4). The range of values for the other measurements overlapped significantly or completely in comparisons between genera. Values for some of these morphometric characters were useful in separating species, as indicated in the species accounts below, but I have not included tables comparing these characters between species at this point.

OSTEOLOGICAL CHARACTERS.—For the most part there exists little interspecific variation in skeletal features between evermannellids. Those structures that do exhibit interspecific variation have been most useful in distinguishing and defining genera. Examples include a vertically elongate fossa centered on the dentary symphysis (fig. 11) unique to *Evermannella;* a lack of barbed palatine or dentary teeth (fig. 11) unique to *Coccorella;* and a posterior prolongation of the ethmoid cartilage unique to *Coccorella.* A subsequent section of this paper is devoted to osteological studies.

LATEROSENSORY SYSTEM.—Although evermannellid species are quite similar to one another in the arrangement of major series of cephalic laterosensory pores (fig. 1), the presence or absence of certain pores is useful in distinguishing some species (table 1). *Evermannella megalops* is unique in lacking PSM pores, probably attributable to the tremendous expansion of the eyes and foreshortening of the snout that typify this species. Only three species, *Coccorella atlantica, C. atrata,* and *Evermannella balbo,* possess PSL pores. *Coccorella atrata* is unique in typically having only four pores in the frontal canal commissure.

Evermannellids lack normal scales, but most evermannellid species do possess a series of membranous, non-ossified shieldlike structures segmentally arranged

TABLE 4. Comparison of selected morphometric characters between evermannellid species and genera. Values expressed as thousandths of the SL and given as the range and mean.

A. Comparison between species

Character	CA	CI	EA	EB	EI	EM	ON
HEYE	40–65	47–65	67–81	52–72	49–93	74–85	27–42
	53	55	72	62	69	81	33
VEYE	42–76	54–70	69–87	59–81	60–97	86–110	28–40
	56	61	79	70	79	95	34
IO	32–47	47–61	17–26	9–19	8–20	4–17	36–52
	38	54	21	13	11	8	41
LPAL	71–96	80–100	46–69	54–69	48–73	61–69	53–69
	84	90	54	61	62	67	61

B. Comparison between genera (ranges only)

Character	*Coccorella*	*Evermannella*	*Odontostomops*
HEYE	40–65	49–93	27–42
VEYE	42–76	59–110	28–40
IO	32–61	4–26	36–52
LPAL	71–100	46–73	53–69

KEY: HEYE=horizontal eye diameter; VEYE=vertical eye diameter; IO=interorbital width; LPAL=longest palatine tooth; CA=*Coccorella atlantica* (n=37 [36.0–184.5]); CI=*C. atrata* (n=24 [38.3–104.6]); EA=*Evermannella ahlstromi* (n=10 [38.2–67.9]); EB=*E. balbo* (39 [39.6–149.2]); EI=*E. indica* (n=82 [30.0–119.0]); EM=*E. megalops* (n=5 [32.5–66.0]); ON=*Odontostomops normalops* (n=25 [36.5–122.0]).

along the lateral line. These structures may represent highly modified scale derivatives. Their structure is illustrated in Rofen (1966d, p. 523). Due to the segmental arrangement of these shields, it is usually possible to determine the number of lateral line segments even when damage to the specimen has resulted in destruction and removal of most of the shield. The three genera of evermannellids differ in the maximum posterior extent of the lateral line and in the maximum number of lateral line segments. In *Odontostomops* the lateral line may reach a vertical through the middle of the anal-fin base and is composed of up to 43 segments. In *Coccorella* the lateral line may reach a point over the anterior one-third of the anal-fin base and is composed of up to 34 segments.

In *Evermannella balbo* and *E. indica* the lateral line does not reach posterior to a vertical through a point just posterior to the pelvic-fin base and contains no more than 18 segments. In *E. megalops* the lateral line is probably represented by three or four pairs of sensory (presumably) papillae just posterior to the (externally visible) posterior margin of the supracleithrum, each pair dorsally and ventrally arranged around a midlateral line and connected at their bases by a common fold of skin. No shieldlike structures have been observed in *E. megalops*. In *E. ahlstromi* the lateral line is apparently lacking.

EYE MORPHOLOGY.—The three genera of evermannellids may be readily distinguished by the gross morphology of the eye and associated structures (fig. 3). In *Odontostomops* the eye is "normal" in appearance, small, lateral in position, and is directed laterally. There is no lens pad. (The structure termed the lens pad throughout this paper corresponds to the "pearl organ" of scopelarchids [see Johnson, 1974c, p. 28]. For reasons discussed in a subsequent section on vision, I have followed N. A. Locket in abandoning the term pearl organ.) The aperture in the adipose eyelid is considerably less than the lens of the eye in diameter. The interorbital region of the frontals (fig. 9) is quite broad, and consequently the interorbital width is relatively large (3.6% to 5.2% SL). In *Coccorella* the eye is moderately large, semitubular, and directed dorsolaterally. A distinct lens pad is present in fully metamorphosed specimens less than about 70 mm SL but tends to become indistinct in larger adults. The aperture in the adipose eyelid is only slightly greater than the lens of the eye in diameter. The interorbital region of the frontals is quite broad (fig. 9) and consequently the interorbital width is relatively large (3.2% to 6.1% SL). In *Evermannella* the eye is moderately to greatly enlarged, tubular, directed nearly straight upward, and slightly dorsoanteriad. A distinct and elliptical lens pad is present in all post-metamorphic individuals. The aperture in the adipose eyelid distinctly exceeds the lens of the eye in diameter. The interorbital region of the frontals is extremely constricted (fig. 9), and consequently the interorbital width is small (0.4% to 2.6% SL). Further comments on the eye morphology of evermannellids are offered in a subsequent section on vision.

GUT MORPHOLOGY.—*Coccorella* is unique among evermannellids and possibly among teleosts in the possession of a pyloric caecum that extends into the head. This and other aspects of the gut morphology and diet of evermannellid species are discussed in Wassersug & Johnson (1976) and below.

LUMINOUS TISSUE.—Luminous tissue is at present known to occur only in *Coccorella atrata*, although it seems certain that luminous tissue is present in *C. atlantica*. It is possible that luminous tissue is present in *Evermannella*, and luminous tissue is probably absent in *Odontostomops*. A subsequent section

summarizes available knowledge concerning luminous tissue in the Evermannellidae.

PIGMENTATION.—Four of the seven species of evermannellids—*C. atlantica, C. atrata, O. normalops, E. megalops*—are highly melanistic, with pigmentation consisting of a rather uniform dark brown over head, body, and fin membranes. Individual adults of *C. atrata* may bear numerous, discretely visible, moderately large melanophores on the paired and median fins, resulting in a spotted appearance. In no species is the pigmentation concentrated into distinct stripes, bars, or conspicuous markings. Most of the species exhibit brassy iridescent areas on the flanks, cheeks, and beneath the eyes—these areas are most conspicuous in the two species of *Coccorella* and in *E. megalops*.

In three of the species of *Evermannella—E. ahlstromi, E. balbo, E. indica*—the pigmentation tends to be much more mottled, with numerous, variably sized (some very large) melanophores on a light brown (in alcohol) ground color over the body and with pigment concentrations on the occiput, cheeks, gill covers, snout, and anterior lower jaw. Both *E. balbo* and *E. indica* exhibit variation in the development of pigmentation, with individuals ranging from nearly unpigmented specimens with a nearly uniform light brown ground color and very few or no visible melanophores, to highly melanistic specimens, essentially covered with brown-black pigmentation. Individuals at either extreme of pigment development occur throughout the range of both species. The degree to which this variation in intensity of pigmentation occurs on an individual basis is unknown.

LARVAL CHARACTERS.—In evermannellids metamorphosis is gradual. Adult characteristics are acquired essentially one by one, but this for the most part occurs during early growth (to 30 mm SL). The result is that specimens larger than about 30 mm SL are essentially miniature adults and can be distinguished on the basis of characters given in the Key to the Species (p. 101).

Several larval characters are very useful in assigning specimens to genera and in defining evermannellid genera. These are listed in the descriptive material to follow. Smaller larvae (less than 10 mm SL) of congeneric species are very similar and, in the absence of development of diagnostic characters (e.g., ossification of dorsal- and anal-fin rays), are either unidentifiable or identifiable on the basis of locality of capture. In this study I adopted the latter procedure only in cases where there existed reasonably good evidence for sole occupation of an area by one species of a given genus—this is actually the rule rather than the exception among evermannellid species.

The following characters are of value in attempts to identify evermannellid larvae:

(1) Peritoneal Pigment Sections.—In all adult evermannellids the gut is completely enclosed by a uniform tube of dark brown to black (in alcohol) peritoneal pigment. In larval specimens this peritoneal pigment develops in

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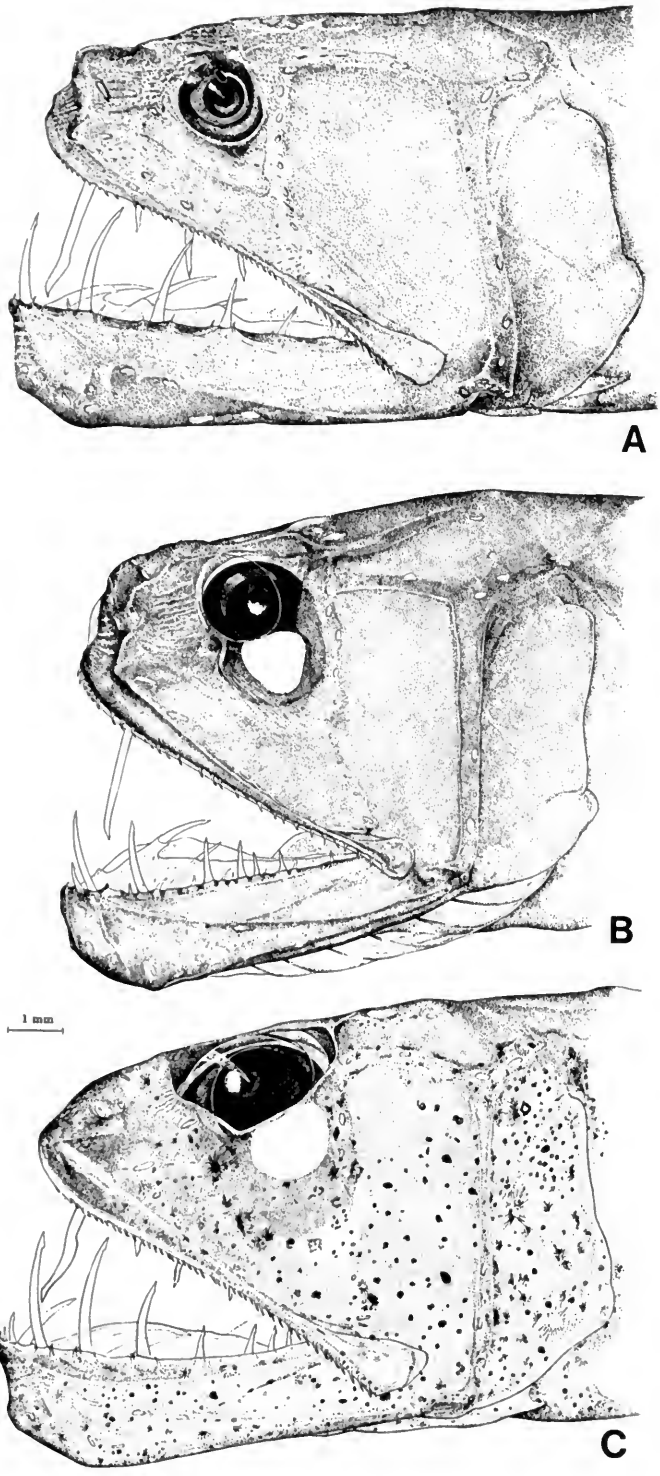
Opposite:

FIG. 3. Eye morphology: side views of head of three evermannellid species. **A,** *Odontostomops normalops,* USNM 108305, 100.4 mm SL. **B,** *Coccorella atlantica* (holotype of *Evermannella atrata atlantica* Parr), BOC 2141, 40.6 mm SL. **C,** *Evermannella indica,* FMNH 49864, 77.3 mm SL. (All from drawings by E. M. Soule in Rofen, 1966d.)


A
B
1 mm
C

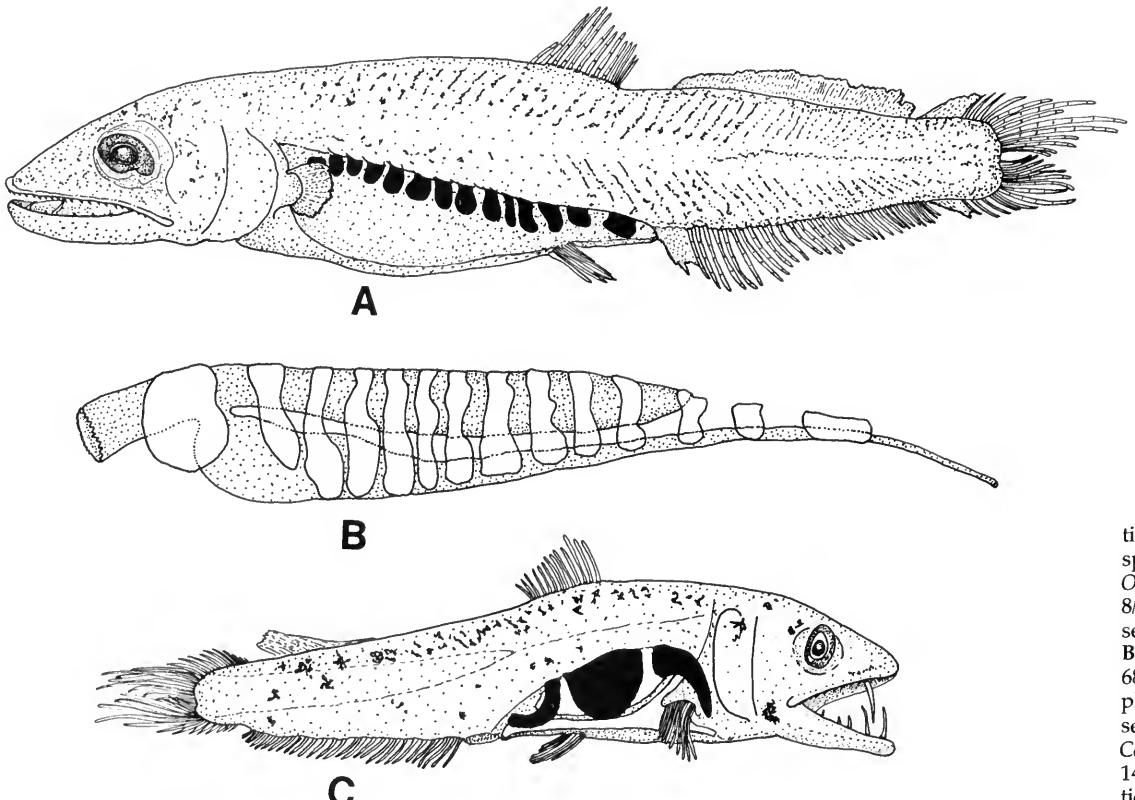


FIG. 4. Peritoneal pigment sections in larval specimens of two species of evermannellids. **A,** *Odontostomops normalops*, UH 73/8/38, 10.5 (peritoneal pigment sections shown in solid black). **B,** *Odontostomops normalops*, SIO 68-535, 25.6 (part of gut [stippled] and peritoneal pigment sections [solid white] only). **C,** *Coccorella atlantica*, RHB 2951, 14.0 (peritoneal pigment sections shown in solid black).

discrete sections, and the number of sections is useful in identifying genera (fig. 4). In *Odontostomops* there are always 12 or more peritoneal pigment sections (typically 13 to 15). In *Coccorella* and *Evermannella* there are invariably three peritoneal pigment sections. In no evermannellid species are peritoneal pigment sections paired as is true for some scopelarchids (Johnson, 1974c, p. 23). The peritoneal pigment sections in evermannellids form a canopy-like continuous sheet over the dorsal and dorsolateral margins of the gut in small larvae and expand ventrad with growth. In specimens larger than 35 to 45 mm SL the peritoneal pigment sections coalesce to form the complete pigment tube enclosing the gut characteristic of adults.

(2) Meristic Characters.—Counts of fin rays do not differ between larval and adult specimens. The posteriormost myotomal segments of the epaxial and hypaxial trunk musculature are extremely difficult or impossible to count due to the interposition of the midlateral band of trunk muscle, and no attempt was made to distinguish larvae on the basis of counts of myotomes.

(3) Gut Morphology.—Larvae of *Coccorella* are distinguished by the unique possession of a pyloric caecum that expands anteriad with growth and enters the head in larger larvae, juveniles, and adults. The pyloric caecum is visible as a short, blind, budlike sac on the ventroanterior margin of the intestine in the smallest known larvae of *Coccorella*. A detailed and illustrated account of the structure and development of this remarkable organ is presented by Wassersug & Johnson, 1976. *Evermannella* and *Odontostomops* lack a pyloric caecum.

In all evermannellid genera the stomach forms a heavily muscularized blind sac (fig. 4). The stomach expands posteriad with larval growth, reaching its full extension (to a vertical just behind the pelvic-fin base) in specimens exceeding 20 to 25 mm SL.

(4) Pigmentation.—Accessory pigment spots or areas characteristic of certain scopelarchid species (Johnson, 1974c, pp. 22–23) are lacking in evermannellid larvae. The major pattern of body pigmentation in evermannellid larvae occurs in two phases, a larval phase (fig. 5) and a juvenile phase (figs. 6, 7), with a gradual transition between the phases. In smaller larvae (less than 12 to 15 mm SL) the most prominent body pigmentation consists of a pattern of pigment bands arranged along the myosepta. Typically these bands are arranged in groups with the intervening myosepta unpigmented, resulting in a characteristic barred appearance (fig. 5; see also Schmidt, 1918, figs. 21–23). In larvae larger than 12 to 15 mm SL the pigmentation characteristic of adults begins to appear. In *Odontostomops* the juvenile phase is characterized by the development of numerous fine melanophores generally distributed over the head and body (figs. 6, 7). In *Evermannella* the juvenile phase is typically characterized by the development of three rows of very large melanophores, each row associated with one of the three main divisions of trunk musculature (figs. 6, 7; see also Rofen, 1966d, fig. 201). In *Coccorella* the juvenile phase coloration (figs. 6, 7) tends to be intermediate in state between that of *Evermannella* and *Odontostomops;* the developing melanophores tend to be much larger and more prominent than those of *Odontostomops,* but they are smaller, much more numerous, and not arranged in rows as in *Evermannella*. Body pigmentation in larvae and juveniles larger than 25 to 30 mm SL is similar to that in the adults (fig. 7). Development of adult pigmentation in evermannellid larvae is associated with the disappearance

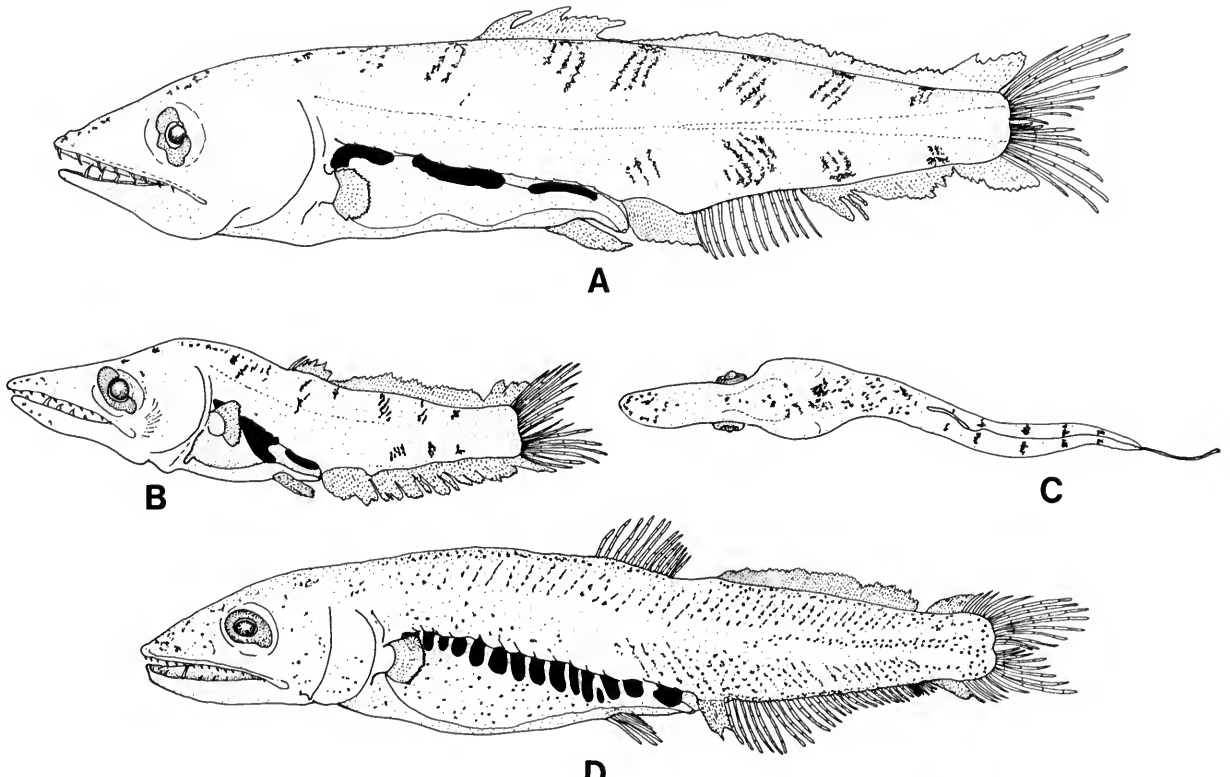


FIG. 5. Larvae of three species of evermannellids. **A,** *Evermannella balbo,* D 3533 III, 10.8; **B, C,** *Coccorella atlantica,* RHB 2960, 6.3; **D,** *Odontostomops normalops,* UH 73/8/38, 10.5.

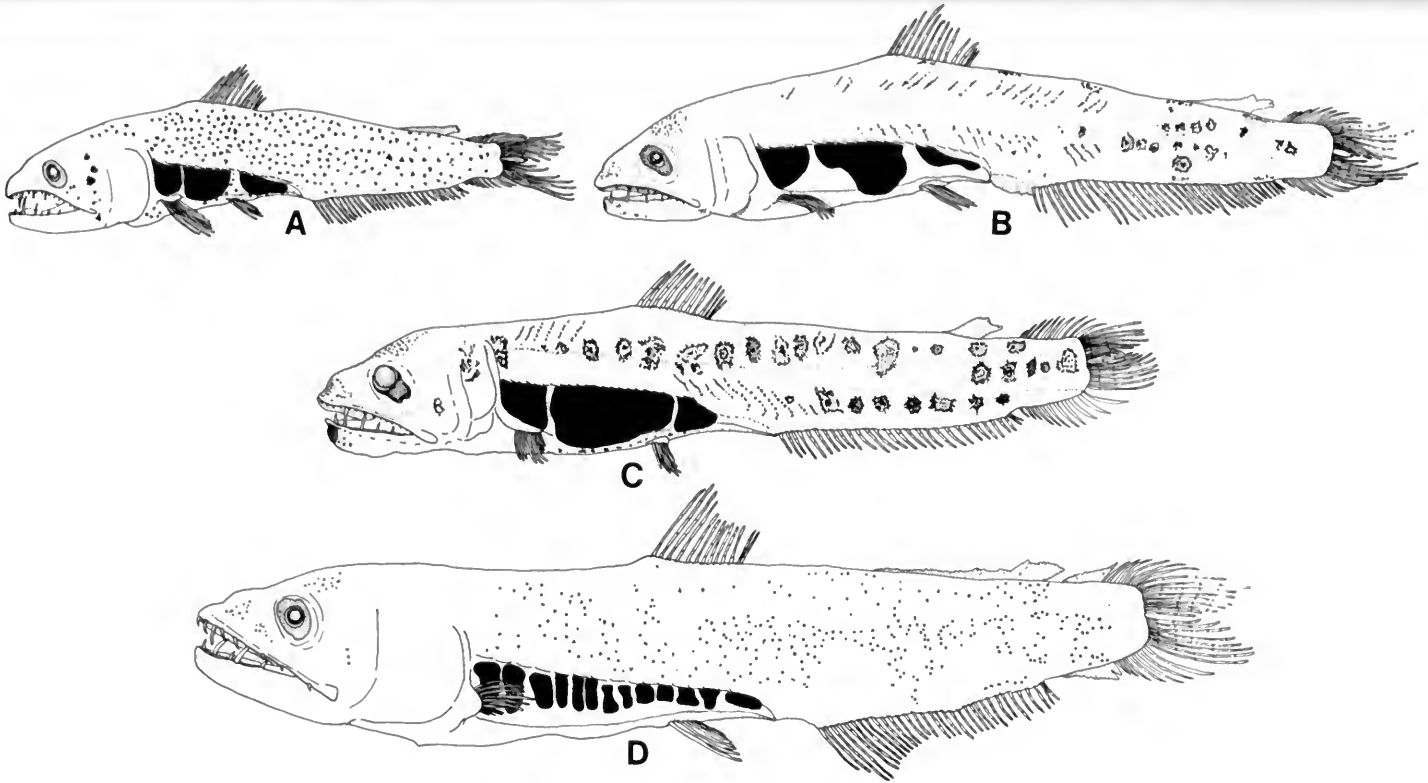


FIG. 6. Larvae of four species of evermannellids. **A,** *Coccorella atrata,* V 5278, 15.6; **B,** *Evermannella balbo,* RHB 1041, 22.8; **C,** *Evermannella megalops,* SIO 70-121, 24.1; **D,** *Odontostomops normalops,* D 3752 II, 14.1.

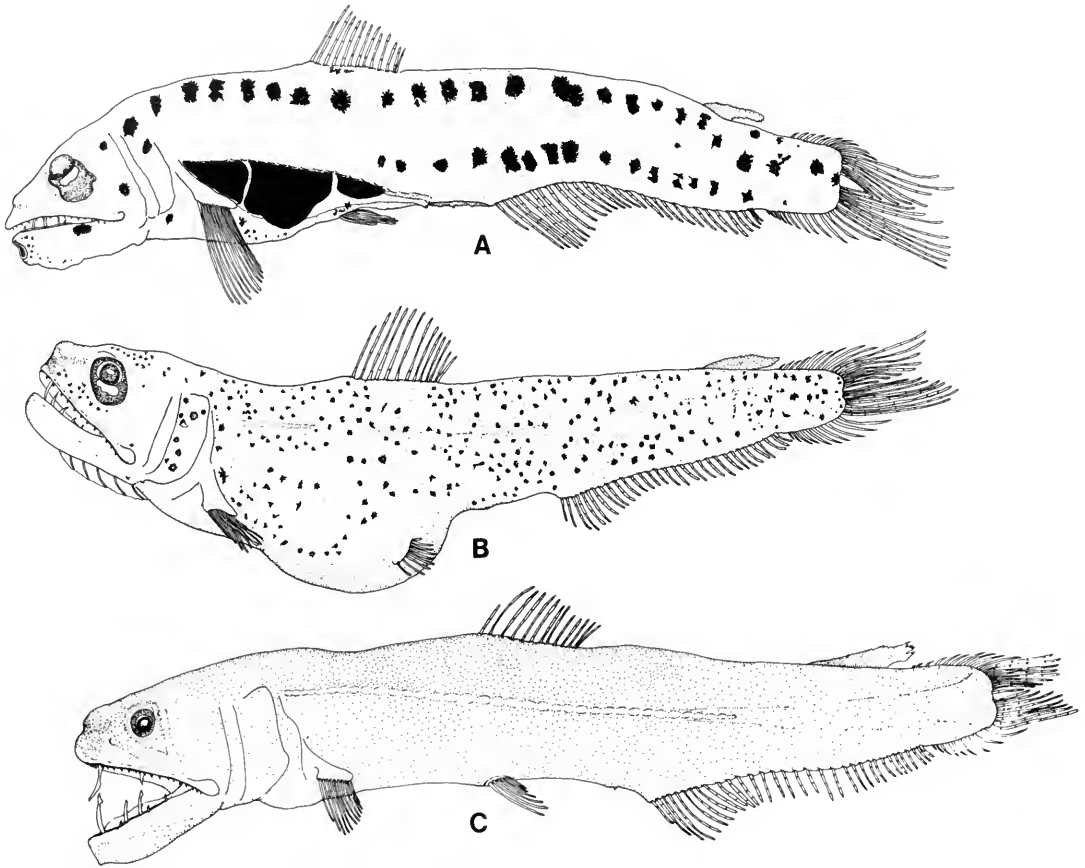


FIG. 7. Larvae and juvenile of three species of evermannellids. **A,** *Evermannella indica*, ORSTOM CY III-5, 28.0; **B,** *Coccorella atlantica*, UH 71/6/4, 26.1; **C,** *Odontostomops normalops*, SIO 61-588, 30.0.

of the pigment bands arranged along the myosepta characteristic of the larval phase.

(5) Metamorphosis.—In all evermannellid larvae the onset of metamorphosis is signaled by the development of juvenile phase pigmentation. In no evermannellid is metamorphosis characterized by radical and rapid changes in morphology such as seen in larvae of the scopelarchid genus *Benthalbella* (Johnson, 1974c, pp. 68–70). For those scopelarchid species whose larvae exhibit more than one peritoneal pigment section, Johnson (1974c, p. 131) defined metamorphosis as complete when the anterior and posterior sections had fused to form one sheath of pigment. If this definition were applied to evermannellid larvae, only those individuals larger than about 35 mm SL (*Coccorella, Evermannella*) or 45 mm SL (*Odontostomops*) would be termed postmetamorphic. However, in all evermannellid species, individuals larger than 25 to 30 mm SL are (except for fusion of the peritoneal pigment sections) essentially miniature adults and can be distinguished readily on the basis of adult characters (e.g., eye morphology, presence or absence of dentary fossa, posterior extent of the lateral line, arrangement of cephalic laterosensory pores, dentition, pigmentation, and meristic and morphometric characters). For this reason I have used a somewhat arbitrary dividing line by terming specimens less than 30 mm SL larvae; specimens equal to or greater than 30 mm SL are termed juveniles and adults.

Aspects of the Biology of Evermannellids

Sampling Difficulties.—Evermannellids, particularly adults, are relatively rare in collections. In a series of 1,600 tows to all depths and generally of four to five hours' duration, the Bermuda Oceanographic Expeditions of the New York Zoological Society captured evermannellids in only 35 tows, and only four tows contained more than one specimen (Rofen, 1966d, p. 516). On the Antipodes Expedition (Scripps Institution of Oceanography, 1970, see Johnson & Barnett [1975, p. 292]), using a 10-ft IKMT and fishing in a stepped-trawl with slow-oblique-tow-between-steps hauling plan (28 tows total, each generally of five to 10 hours' duration), only 13 evermannellids were taken (four larvae, nine juveniles and adults), and these 13 were taken in eight of the 28 tows. These 13 specimens did include all four evermannellid species known to occur in the Philippine and South China seas.

Part of the Antipodes results might be explained in terms of gear-related sampling bias. In the Antipodes material only one tow resulted in the capture of more than one specimen of a given species, and that haul (Antipodes 4–27) contained two specimens of *Coccorella atrata*. By comparison, numerous single tows taken by the R/S *Dana* using a very different type of net (Jesperson & Tåning, 1934) contained more than 40 larval and small juvenile specimens of a single species. The use of fine-mesh nets on the Antipodes Expedition might well have increased the total capture of evermannellid specimens.

Nonetheless, the results for the Evermannellidae appear to parallel those for the scopelarchids and for other alepisauroid fishes (summarized by Johnson, 1974c, pp. 24–25) and suggest that evermannellids, at least the larger adults, are often successful net-avoiders. This has already been suggested by Rofen (1966d, p. 515). This seems to be strongly corroborated by the success at capturing large evermannellid specimens of ichthyologists of the Institute für Seefischerei, Hamburg, aboard the FRS *Walther Herwig*. The very large, commercial, midwater

trawl frequently used aboard the *Walther Herwig* (Krefft, 1974) has resulted in the capture of the largest known specimens of *Coccorella atlantica* and *Evermannella balbo* and the largest known Atlantic specimen of *Evermannella indica*. Most of the larger specimens of the four evermannellid species known from the Atlantic have been taken by efforts aboard the *Walther Herwig*. In the Atlantic *E. balbo* is known from 59 specimens exceeding 90.0 mm SL, and 52 of these were taken by the *Walther Herwig*. Comparable figures for Atlantic specimens of other species are as follows: *C. atlantica* (30 specimens exceeding 90.0 mm, 24 of them taken by the *Walther Herwig*), *E. indica* (11 specimens exceeding 90.0 mm, eight from *Walther Herwig*), *Odontostomops normalops* (19 specimens exceeding 90.0 mm, 12 from *Walther Herwig*). These results can best be explained in terms of frequently successful net avoidance by evermannellid species in the case of smaller nets.

Size and Habits—All evermannellids are oceanic and mesopelagic in habitat. Evermannellids reach a relatively large size for midwater fishes. Size records for the family include the following: *C. atlantica*, 184.5 mm; *E. balbo*, 168.5 mm; *E. indica*, 127.2 mm; *O. normalops*, 123.1 mm; *C. atrata*, 104.6 mm; *E. ahlstromi*, 70.0 mm; *E. megalops;* 68.1 mm (*E. megalops* is known from only five specimens larger than 50 mm SL).

No systematic analysis of the gut contents of evermannellids was attempted, because the majority of specimens examined contained no recognizable material in the stomach or intestine. All specimens examined that did contain identifiable gut contents had fed on either fish or squid. The contents included midwater fishes of the families Gonostomatidae (*Cyclothone*), Photichthyidae Weitzman 1974 (*Vinciguerria nimbaria* [Jordan & Williams], *Vinciguerria lucetia* Garman), Myctophidae (*Diaphus* among other genera), Paralepididae, and Evermannellidae (*E. indica,* see below). Most of the specimens of *Coccorella* spp. that contained identifiable gut contents had fed on squid, although midwater fishes were found in the stomachs of some specimens. This sketchy information on diet at least agrees with the few previously published accounts: Alcock & MacGilchrist (1905, plate 37, fig. 2) illustrated a specimen of *C. atrata* from the Andaman Sea whose stomach was greatly distended with a large squid; Parr (1928, p. 164) reported that the 51.6-mm holotype of *O. normalops* contained a myctophid 30.3 mm SL; Marshall (1955, p. 330) notes the existence of a specimen of *E. indica* in the *Discovery* collections with a gonostomatid fish folded up in its stomach, the length of the prey exceeding the length of the abdomen of the predator; Rofen (1966d, p. 535) reported the known gut contents of evermannellid specimens as including mesopelagic fishes and squid; Kotthaus (1967, p. 83) tentatively identified *Vinciguerria* from an Indian Ocean specimen of *E. indica*. Collard (1970, p. 350) reports that the gut contents of a single specimen of "*Evermannella* sp." from the Santa Catalina Basin (33° 20′ N, 118° 42′ W) off southern California consisted of "fish." This specimen, the only known record of the family from off California (fig. 2), could be either *Evermannella ahlstromi* or *E. indica*. Collard did not indicate where the specimen was deposited, and I have not seen it.

Among the alepisauroids, the evermannellids, along with *Alepisaurus*, *Anotopterus*, and *Omosudis*, are well-known swallowers, with greatly distensible foreguts. A detailed account of the gut structure of evermannellids is provided by Wassersug & Johnson (1976). In evermannellids, scopelarchids (Johnson, 1974c), and other alepisauroids (e.g., Rofen, 1966b, p. 478), the only identifiable food items recovered have been found in the thick-walled heavily muscularized

stomach, not in the thin-walled intestine. The function of the enlarged, saclike stomach of alepisauroids and scopelarchids is thought to be related to the ability of many of these fishes to ingest and store (during digestion) very large food particles, and, once the prey is ingested, the stomach morphology may represent a specific adaptation for extraction of all possible nourishment from ingested food items (Johnson, 1974c; Wassersug & Johnson, 1976).

Among evermannellid species the largest ingested particles have been found in specimens of *Coccorella* spp. Whether the peculiar specializations found in *Coccorella*—the remarkable pyloric caecum, the lack of barbed palatine and dentary fangs, and the exceptional length of the palatine fangs—represent adaptations related to this swallowing ability and/or to the apparent tendency for *Coccorella* spp. to feed on squid (as opposed to fish) is unknown.

There exists very little information on possible predators of evermannellid species. Fourmanoir (1969, p. 56) reports the recovery of *Coccorella atrata* from the gut of *Alepisaurus ferox,* and I have taken a 16.5-mm specimen of *E. indica* in the stomach of a 26.1-mm specimen of *C. atlantica* (UH 71/6/4, fig. 7B).

The vast majority of evermannellid specimens has been taken in open net hauls. This, combined with the relative rarity of evermannellids in collections, results in there being very little information on the vertical distribution of evermannellid species. For all species, the great majority of larval specimens has been taken in the upper 100 m, but only the larvae of three species (*Evermannella balbo, E. indica, Odontostomops normalops*) have been commonly taken in hauls to 50 m or less. Most adult evermannellids were taken in hauls to between 400 and 800 m, but adults of all species (excluding *E. megalops*) have been commonly taken in hauls to between 100 and 400 m. If anything, the available information suggests that larval evermannellids occur at shallower depths than the adults (this is generally true for all midwater fishes) and that the adults occupy a wide vertical range in the upper 1,000 m.

Among the characters most readily distinguishing the evermannellids from other alepisauroids is the externally visible tripartite division of the tail musculature (fig. 8A), with the epaxial and hypaxial muscles separated by a midlateral band of muscle centered and arranged longitudinally on the vertebral column. The medial muscle band corresponds to the lateralis superficialis subdivision of the body musculature described by Winterbottom (1974, p. 295). The lateralis superficialis is composed largely or exclusively of red muscle (myoglobin-rich striated muscle), the epaxialis and hypaxialis are largely composed of white muscle (for distinctions in structure and physiology between red and white muscle see Barets, 1961, p. 92; Prosser, 1973, p. 749). Barets (1961), in an extensive study of the swimming muscles of fishes, proposed two categories corresponding to function, "lent et rapide" (i.e., slow and fast), with the red-muscle lateralis superficialis largely forming the slow system, the (deeper) white-muscle epaxialis and hypaxialis, the fast. It is believed that red muscle is adapted for slower, aerobic, long-term, continuous output; white muscle for shorter term, anaerobic, but higher amplitude bursts of power output (Bone, 1966; Hudson, 1973; Rosenblatt & Johnson, 1976; Mosse, 1978). Extensive development of red muscle is associated with a need for continuous swimming (e.g., Barets, 1961; Rayner & Keenan, 1967; Alexander,1969).

Typically in teleosts the lateralis superficialis is narrow and poorly developed anteriorly but larger posteriorly. Fibers of the lateralis superficialis may be dis-

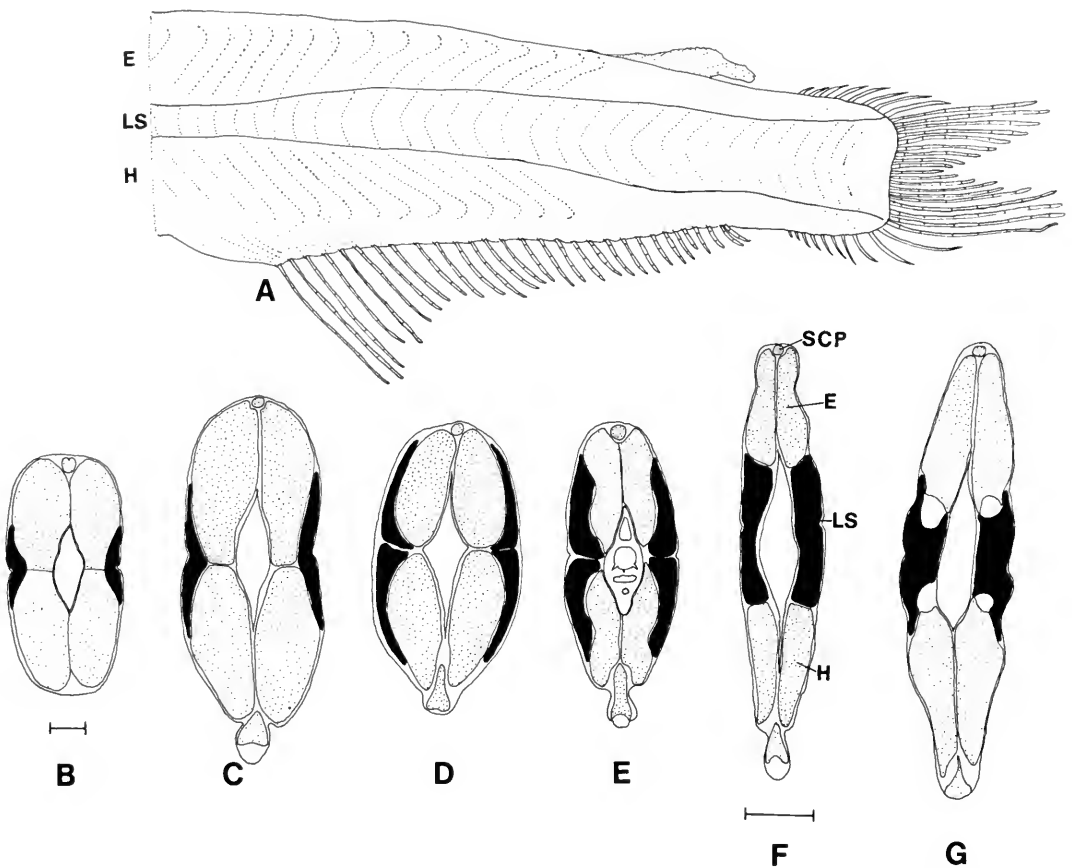


FIG. 8. Body musculature of tail region in evermannellids, other alepisauroids, scopelarchids, and chlorophthalmids. **A,** Lateral view of tail region (skin removed) in *Evermannella indica,* FMNH 82736, 96.5 mm. **B–G,** Diagrammatic representations of cross-sections through tail region. Suspected red muscle tissue indicated by solid black areas, suspected white muscle tissue is indicated by stippled areas. Abbreviations: SCP=supracarinalis posterior; E=epaxialis; LS=lateralis superficialis; H=hypaxialis. The bracketed line (**B, F**) indicates 2.00 mm; the scale indicated for **B** also applies to **D;** the scale indicated for **F** also applies to **C, E,** and **G. B,** *Parasudis truculentus,* FMNH 88723, 170.5 mm; **C,** *Scopelarchus analis,* FMNH 88146, 90.2 mm; **D,** *Omosudis lowei,* FMNH 84778, 200.0 mm; **E,** *Paralepis* sp., FMNH 85332, 120.5 mm; **F,** *Coccorella atrata,* FMNH 85321, 85.4 mm; **G,** *Odontostomops normalops,* FMNH 88171, 106.8 mm.

tinguished from the underlying epaxialis and hypaxialis in both texture (the fibers are narrower in diameter) and color. In alcohol-preservation the fibers of the lateralis superficialis appear lighter in color than those of the epaxialis and hypaxialis (in species I have examined), but in life they tend to be distinctly red. The large lateralis superficialis of evermannellids is apparently bright red in life (R. McGinnis, pers. comm., based on observation of freshly captured material of *E. ahlstromi*).

The lateralis superficialis is enormously well developed in many mesopelagic fishes (Marshall, 1971, p. 78), and this is apparently true for all alepisauroids (fig. 8). In all examined alepisauroids the lateralis superficialis tapers anteriorly, resembling the condition illustrated by Winterbottom (1974, figs. 53, 54). Subsequent discussion is restricted to the body musculature posterior to the anal-fin origin.

The lateralis superficialis in *Parasudis truculentus* (Goode & Bean) (Chlorophthalmidae), a bottom-dwelling species that feeds in "midwater" (Mead, 1966e, p. 183), is similar in position and size to that normal for teleosts (Barets, 1961; Winterbottom, 1974)—a narrow, midlateral sheath, considerably less massive than the underlying epaxialis and hypaxialis (fig. 8B). In the scopelarchids (species examined: *Scopelarchus analis* (Brauer), FMNH 88146, 90.2 mm; *Benthabella infans* Zugmayer, FMNH 79702, 134.0 mm) the lateralis superficialis is proportionately somewhat larger than that of *Parasudis* but otherwise is similar in arrangement (fig. 8C). In alepisauroids other than evermannellids (species examined: *Alepisaurus* sp. [Alepisauridae], FMNH 83657, 35.5 mm; *Anotopterus pharao* Zugmayer [Anotopteridae], SIO uncat., 350 mm; *Omosudis lowei* Guenther [Omosudidae], FMNH 84778, 200.0 mm; *Paralepis* sp. [Paralepididae], FMNH 85322, 120.5 mm) the lateralis superficialis is enormously well developed, occupying most of the lateral surfaces of the body in the tail region (fig. 8D, E; see also Marshall's [1971, fig. 34a] illustration of the red muscle system in the Antarctic paralepidid *Notolepis coatsi* Dollo).

In the evermannellids (species examined: *Coccorella atrata*, FMNH 85321, 85.4 mm; *Evermannella indica*, FMNH 82736, 96.5 mm; *Odontostomops normalops*, FMNH 88171, 106.8 mm) the arrangement of the well-developed lateralis superficialis is quite different from that seen in other alepisauroids in that in the tail region the epaxialis and hypaxialis muscles do not extend beneath the lateralis superficialis (fig. 8F, G). Thus, the apparent tripartite division of the tail musculature visible on external view (fig. 8A) actually reflects the underlying structure.

Marshall (1971, pp. 77–79) summarizes the available information on the distribution of red and white muscle tissue in midwater fishes, noting that for the mesopelagic species examined by him the proportion of red to white is significantly larger than normal in teleosts. Apparently the greater development of red muscle tissue in midwater species is associated with the problem of maintaining position in the water column faced by many mesopelagic species. Many midwater fishes (including all alepisauroids) have no swimbladder and, despite reductions in the degree of bone ossification, loss or reduction of scales, and other adaptations directed toward decreasing overall specific gravity, remain negatively buoyant (Marshall, 1955; Denton & Marshall, 1958). The result is a need for continuous, if low-velocity, swimming if position in the water column is to be maintained. It is this sustained but relatively low-level activity for which red muscle tissue is well adapted (Barets, 1961; Rayner & Keenan, 1967; Alexan-

der, 1969; Marshall, 1971; Prosser, 1973). Although no histological examination of the lateralis superficialis in evermannellids has been made, it seems very likely (based on work on other teleosts, see Barets, 1961; Winterbottom, 1974) that this muscle is composed primarily of red muscle fibers. The great development of this muscle in evermannellids provides additional support (for evermannellids) for the contention of Gosline et al. (1966, p. 10) that ". . . alepisauroids . . . have a hovering and darting, pike-like way of securing their food." If true, it seems likely that the red muscle lateralis superficialis is largely used to maintain position in the water column, the white muscle hypaxialis and epaxialis to provide short but powerful bursts of speed needed in the capture of food and avoidance of predators (see Hudson, 1973). According to Marshall (1954, pp. 325–328), alepisauroids are partly characterized by a hydroplane-like configuration of the pectoral fins. A key component in this configuration is the low angle (said to be 15°–20° in *E. balbo*) between the horizontal axis of the body and the axis of the pectoral-fin insertion. This low setting and relatively large size of the pectoral fins combined with the joint action of the caudal and anal fins provide, in Marshall's (1954) view, requisite lift. The rich development of red muscle tissue might provide the basis for continuous power output. Both lift and continuous power output are required components of the mechanism envisioned as allowing maintenance of position in the water column.

Reproduction.—The evermannellids (and all other alepisauroid fishes) are synchronous hermaphrodites with a functional ovotestis similar to that described for certain alepisauroid and other iniomous fishes (Mead, 1960; Mead et al., 1964; Nielsen, 1966, Gosline et al., 1966; Johnson, 1974c; Bertelsen et al., 1976; Herring, 1977).

Luminescence.—The first description of luminous tissue in an evermannellid is provided by Herring (1977). Herring discovered and described luminous tissue in *Coccorella atrata,* based on living and preserved material. The following account (for *C. atrata*) is abstracted from Herring's paper. The light produced is a weak blue glow along the ventral midline. All luminous areas are part of the ventral wall of the intestine (intestinal organs) or part of the ventral wall of the entire length of the pyloric caecum (isthmus organ). The three intestinal areas are as follows: median ventral organ, extending anteriad from just anterior to the pelvic-fin base to a point about three-fourths the distance to the pectoral-fin base; post-pelvic organ, just behind the pelvic-fin base; anal organ, just anterior to the anus. Each of these organs is indicated by a reflective, silvery-colored (in alcohol) streak or patch in ventral midline situated ventrally to a translucent line or patch in the otherwise heavily pigmented peritoneum. The dense pigmentation of the skin of the ventral abdominal body wall is interrupted in the region of these reflective streaks such that the skin is translucent except for a number of large but scattered melanophores. An elaborate concentric reflector system (with a ventral aperture permitting exit of light) is associated with the isthmial organ. There is no reflector system associated with the intestinal organs. The downwelling light shines through and must be diffused by the ventral musculature, particularly in the case of the isthmus organ. The light-producing system is intrinsic, the light is nonbacterial in orgin.

I have reexamined material representing all evermannellid species in an attempt to determine the presence or absence of possible luminous tissue. *Coccorella atlantica* possesses midventral reflective streaks and patches in exactly the

same positions as those of *C. atrata*, and, with *C. atrata*, shares the unique possession of a pyloric caecum extending into the head. It seems very safe to assume that *C. atlantica* is also luminous.

Herring (1977) tested freshly caught species of *Odontostomops normalops* and *Evermannella* sp. (almost certainly *E. indica*) and failed to demonstrate any luminescent capability, either on simple exposure of the ventral gut wall or on application of dilute hydrogen peroxide. Herring reports that *O. normalops* lacks any reflective streaks, but that *Evermannella* sp. does show an ill-defined reflecting organ ventrally. Herring's examination of alcohol-preserved material of *O. normalops* and *E. indica* failed to demonstrate the presence of luminous tissue.

My reexamination of material of all evermannellid species confirmed Herring's results for *O. normalops*—there are no reflective streaks nor any other indication on gross examination that luminous tissue is present. However, in all four species of *Evermannella* there are narrow but well-defined reflective streaks, one on each side of the ventral midline, extending from the pelvic-fin base to just before the anus. These streaks are most visible in my material of *E. megalops*. The streaks diverge under the pelvic-fin base and disappear or become much less distinct anterior to the pelvic-fin base. The arrangement is vaguely reminiscent of the luminous organs of the paralepidid genus *Lestrolepis* (Rofen, 1966a, p. 371), although no discrete ducts are involved and the reflective streaks in *Evermannella* are best-developed posterior to the pelvic-fin base. On cross examination these reflective streaks in *Evermannella* appear similar to the unpaired and discretely distributed intestinal organs of *Coccorella*. The question of whether they are or are not indicative of luminous tissue in *Evermannella* awaits histological examination.

Although Herring (1977) did not propose any functions for the ventral luminous tissue of *Coccorella*, it seems that the best available explanation is that widely put forward for midwater fishes with ventral concentrations of luminous organs, viz., that the light produced matches the background of downwelling sunlight, breaking up the silhouette and tending to render the fish less visible to predators lower in the water column (Clarke, 1963; Babcock, 1970; Lawry, 1974). This function has been all but proved for mesopelagic squid (Young & Roper, 1976, 1977; Young, 1977), for *Sergestes similis* (Crustacea, Sergestidae, see Warner et al., 1979), and, by analogy, for midwater fishes. Marshall (1971) offers possible objections to this theory in the case of certain species.

Vision.—Of all the remarkable characters of evermannellids and scopelarchids, that which has provoked the widest interest in these fishes is the development of tubular eyes. All scopelarchid species possess fully developed tubular eyes directed straight upward or dorsoanteriad (three species). The gross external features of eye morphology in evermannellids have already been described (fig. 3).

The eyes and details of eye morphology of *Coccorella atrata* and *Evermannella indica* are illustrated in Brauer (1908) and Munk (1966), and for the scopelarchids *Scopelarchus analis* and *Benthalbella infans* (*Neoscopelarchoides* sp. of Munk, 1966, p. 32) by Brauer (1908), Munk (1966), and Locket (1970, 1971). A number of the main features of the tubular eyes of both *Evermannella indica* and *Scopelarchus analis* are at least superficially similar. The visual axes are parallel and directed dorsad (and slightly anteriad in *Evermannella*). The retinal cup is roughly tube-shaped (in *S. analis* the retinal cups flare out ventrally and hence increase in

diameter from the pupillary margin to the floor of the eye). The bottom of the tube is formed by the main retina, whereas an accessory retina forms the medial wall of the tube. Locket (1971) has shown that the main retina in *S. analis* is actually divided into anterior and posterior portions in terms of histological structure, containing, respectively, non-grouped and grouped rods. The pupil is tilted such that the medial margin is distinctly more dorsal to the main retina than the lateral margin. The lens pad (= "pearl organ" of Johnson, 1974c, p. 28) is nearly centered on the lateral dorsal margin of the pupil. Locket (pers. comm.) has objected to my use of the term pearl organ to describe the glistening white oval-shaped tissue centered at the lateral pupillary margin and characteristic of the tubular-eyed species of evermannellids and scopelarchids. Locket points out that the term lens pad (based on Brauer's [1908, p. 218] "Linsenpolster oder Linsenkissen") was coined by Munk (1966, p. 32) and used by Merrett et al. (1973) as well as Locket (1970, 1971). Locket's objections are based not only on priority of usage but also on function. The lens pad in scopelarchids (confirmed for *B. infans* by Locket, for *B. dentata* by myself) is transparent in life, possibly as Locket (1970) has suggested, serving as a light guide, picking up light from almost beneath the fish (within 20° of the vertical below the fish) and guiding the light to the lens and thence to the dorsalmost part of the accessory retina. Thus the use of the term pearl organ, based on an artifact of preservation, implying as it does opacity, obscures the probable function of this organ. I follow Locket's suggestion in this paper, abandoning pearl organ in favor of lens pad.

The first detailed anatomical description of the eye in evermannellids is provided by Brauer (1908). Brauer was aware of three evermannellid species, *Coccorella atrata*, *Evermannella balbo*, and *E. indica*, and was able to make detailed histological studies of the eyes of *C. atrata* and *E. indica*. Brauer (1908, p. 192) expresses surprise at the difference in eye structure between *C. atrata* and the two species of *Evermannella*, particularly that in *C. atrata* the visual axis is more lateral than dorsal, and the aperture in the palpebral fold is much smaller (the palpebral fold [Munk, 1966] is termed the adipose eyelid by Rofen [1966d] and elsewhere in the present paper). Brauer's figures (cf. plate 35 fig. 15 vs. plate 38 fig. 4) clearly show the difference in structure between the semitubular eye of *Coccorella* and the fully tubular eye of *Evermannella*. Munk (1966) has provided additional information on the eye of *Evermannella indica*. It is unfortunate that no one has studied in detail the eye morphology of *Odontostomops normalops*. Such a study is sorely needed if the sequence suggested below is to be confirmed.

Munk's (1966, p. 44) description of the ontogenetic development of tubular eyes in conjunction with Brauer's (1908) detailed descriptions and illustrations of the eyes of *Coccorella* and *Evermannella* allow further comment on the possible phylogenetic development of the tubular eyes in *Evermannella*. The typical morphology of the tubular eye develops gradually from a laterally directed eye in the larvae of tubular-eyed species. The sequence of events is illustrated by Contino (1931) for the sternoptychid *Argyropelecus hemigymnus;* Merrett et al. (1973), for the scopelarchid *Benthalbella infans;* and Brauer (1908), for the scopelarchid *Scopelarchus analis*. In the course of development of the tubular eye the following events occur: (1) the lens and pupil are displaced dorsally, and (2) the main retina is developed from that part of the larval retina located ventrad to the optic papilla and mainly from the lower temporal quarter. The latter is brought about through a rotation around a vertical axis of the retinal cup during growth.

Munk (1966, p. 45) viewed the non-tubular eye of *Omosudis lowei* Guenther (Omosudidae) as nearly ideal in structure for a hypothetical precursor of the tubular eye of *Evermannella*. He shows (Munk, 1966, fig. 11) that the course of the choroid fissure in *Omosudis* indicates that the broad ventral portion of the retina in that species corresponds to the lower temporal quarter of the retina in other teleosts, with the displacement of the choroid fissure possibly accomplished by rotation of the optic cup around the anterior-posterior axis. Thus the broad ventral portion of the retina in *Omosudis* is located in that exact part of the retina from which the main retina of *Evermannella indica* (and certain other tubular-eyed species listed by Munk, 1966, p. 44) develops.

Munk (1966) points out additional similarities between the eye morphology of *Omosudis lowei* and *Evermannella indica* that suggest that the eye structure of *O. lowei* may represent more than an idealized precursor of the eye structure of evermannellids. Munk (1965) showed that *Omosudis lowei* possesses an almost pure cone retina, with a very small number of irregularly distributed typical teleost rods and a broad, ventrally located, rod-free area. Virtually all other midwater fishes have pure rod retinae (Munk, 1966; Marshall, 1971)—the shift to scotopic vision might be expected in the dimly lit mesopelagic environment (Goldsmith, 1973). The only other known exception is *Evermannella indica*, which (Munk, 1966) believes to have a retina composed of rods that are in fact highly modified cones. Munk (1966, p. 50) lists four characters of the rodlike cells of *E. indica* that he believes indicate the derivation of these cells from cones—normal teleost rods (present in small numbers in *Omosudis*) are lacking in *Evermannella*. A final point of similarity in eye structure between *Omosudis* and the evermannellids is the development of the adipose eyelid (palpebral fold). In large specimens of *O. lowei* the adipose eyelid encloses the entire eye except for a round aperture dorsolaterally (Rofen, 1966b, fig. 166), in shape and position similar to that found in *Coccorella* spp. (fig. 3). All three genera of evermannellids have such an adipose eyelid with the aperture very small in *Odontostomops*, very large in *Evermannella*, and intermediate in size in *Coccorella* (fig. 3). If, as Munk (1966) suggests, the eye of *Omosudis lowei* represents an ideal precursor for the tubular eye of *Evermannella*, the nontubular eye of *Odontostomops* and the semitubular eye of *Coccorella* represent logically ideal stages in the development of tubular eyes in this family.

The tubular eye represents an adaptation to the dim lighting of the mesopelagic and has been independently evolved in a number of midwater groups (Marshall, 1971, pp. 42–43). Thoughts on the functional significance of tubular eyes are summarized in Munk (1966), Marshall (1971), and Locket (1970, 1971). Tubular eyes are modified such that a relatively large lens is associated with a proportionally small area of main retina. This arrangement allows an enlarged (but not brighter) image on the main retina. The parallel visual axes enlarge the binocular field, resulting in greater sensitivity and a better judgment of distance. The advantages of these improvements to an inhabitant of the poorly lit mesopelagic, particularly in the case of active predators, are clear enough.

Munk (1966) discards the suggestion (e.g., Walls, 1942) that the division of the retina into main and accessory regions implies that tubular eyes are bifocal, the accessory retina used for the perception of distant objects, the main retina used for the perception of nearby objects. Munk goes to some length to show that no

sharp image can be formed on the accessory retina and concludes that the advantages of the tubular eye (in terms of enlarged image and binocularity) have been at the expense of optical adjustment of the accessory retina. Locket (1970), in discussing the tubular eye of scopelarchids, has pointed out that the most important difference in probable function between the accessory and main retinae lies not in optical adjustment but in field of view—the two main retinae covering a rather restricted binocular field dorsad and slightly anteriad, the accessory retinae covering two much wider monocular fields at the sides (made wider by the presence of the lens pad, if Locket's suggested function for this organ proves true). Locket (1970) goes on to suggest that an object to one side of the fish forms a blurred image on the accessory retina (which may be constructed such that its best response is to movement), stimulating the fish to turn toward the object and swim beneath it. The image would thereby be transferred to the sharply focused binocular field. The division of the main retina into anterior and posterior regions with non-grouped and grouped rods, respectively (see Locket, 1971, for a detailed discussion), represents a possible compromise between sensitivity (possibly higher in the posterior portion) and acuity (higher in the anterior portion). Thus the sequence implied by Locket (1970) is that the accessory retina is used for first location of an object (and in this is aided by the lens pad), that the function of the grouped-rod portion of the main retina is to allow homing-in on the object, and that the visual acuity provided by the anterior non-grouped main retina allows an accurate strike. Locket admits this to be conjectural but in accord with available morphological evidence (see also Merrett et al., 1973, p. 44).

The limiting light threshold for vision in midwater fishes with well-developed eyes is thought to be on the order of 3×10^{-10} $\mu W/cm^2$ (Clarke & Denton, 1962), some 10 to 100 times more sensitive than the eyes of epipelagic fishes (see Brett, 1957; Denton & Warren, 1957; Munz, 1971). A number of authors have used this value to estimate the greatest depth at which midwater fishes should be able to detect diel changes in light intensity (among the estimates: 1,000 to 1,100 m [Sargasso Sea, Clarke & Denton, 1962]; 700 to 1,300 m [Indian Ocean, Clarke & Kelly, 1964]). Marshall (1971) places the average of the various available estimates at about 1,000 m for very clear oceanic waters. Virtually all estimates are well below the probable depth range of maximum abundance for all evermannellid species.

OSTEOLOGY

Only five papers have dealt with osteological characters of the Evermannellidae. Regan (1911) presented a very brief description of some of the skeletal features of *Evermannella balbo*. Parr (1929) studied the osteology of *Coccorella atlantica* and *Evermannella indica*. The works of Rofen (1966d), McAllister (1968), and Rosen (1973) considered a limited number of characters. My studies of the osteology of evermannellids are based on six of the seven species (*Evermannella megalops* had to be excluded due to lack of material) and all three genera. When compared with the considerable variation in skeletal morphology exhibited by scopelarchid species (Johnson, 1974c), evermannellids are very similar to one another in osteological features, and the description below is based on *Evermannella balbo* except as indicated. Following the account of skeletal features in the Evermannellidae is a limited comparison of the Evermannellidae with its sup-

posed sister group, the Scopelarchidae, and with other alepisauroid and myctophoid fishes.

The terminology I have employed for the various skeletal structures closely follows that used for the Scopelarchidae (Johnson, 1974c) and for the Chiasmodontidae (Johnson & Cohen, 1974). A listing of abbreviations used in the figures and tables is presented as Table 5, and a listing of cleared and stained material examined is presented as Table 7.

Cranium

In evermannellids the ethmoid cartilage and 16 bones, 10 paired and six median, form the cranium (fig. 9). The bones include the following: basioccipital (BOC), basisphenoid (BAS), dermethmoid (DEM), epiotics (EPO), exoccipitals (EXO), frontals (FR), lateral ethmoids (LEM), opisthotics (OPO), parietals (P),

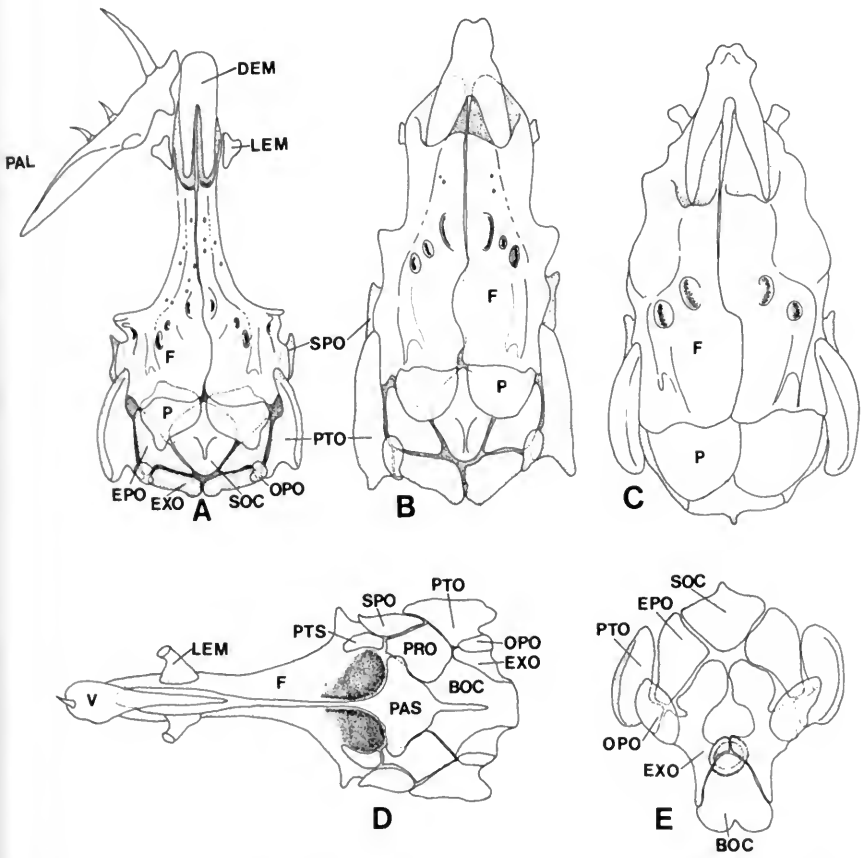


Fig. 9. Cranium of Evermannellidae. **A**, Dorsal view of cranium of *Evermannella balbo*, ISH 546/73, 94.6 mm. Left palatine bone left in place. **B**, Dorsal view of cranium of *Odontostomops normalops*, ISH 2220/71, 111.5 mm. **C**, Dorsal view of cranium of *Coccorella atrata*, SIO 68-533, 99.6 mm. **D**, Ventral view of cranium of *E. balbo*, ISH 546/73, 94.6 mm. **E**, Posterior view (diagrammatic) of cranium of *Coccorella atrata*, 99.6 mm.

TABLE 5. Abbreviations used in tables and figures in osteological account of iniomous fishes.

AN	angular
AO	antorbital
AR	articular
BB	basibranchial
BH	basihyal
BOC	basioccipital
CB	ceratobranchial
CH	ceratohyal
CL	cleithrum
CMN	coronomeckelian
COR	coracoid
CT	conical tooth
D	dentary
DEM	dermethmoid
DHH	dorsal hypohyal
DPCL	dorsal postcleithrum
DR	distal radial
EB	epibranchial
EC	epicentral rib
ECP	ectopterygoid
EH	epihyal
EN	epineural rib
EP	epural
EPO	epiotic
EPR	epipleural rib
ESC	extrascapular
EXO	exoccipital
F	frontal
FR	fin ray
GT	gill tooth
HB	hypobranchial
HYOM	hyomandibular
HYP	hypural
IH	interhyal
IO	infraorbital
IOP	interopercle
LEM	lateral ethmoid
MC	Meckel's cartilage
MCP	midcleithral process
MPCL	medial postcleithrum
MR	medial radial
MSP	mesopterygoid
MTP	metapterygoid
MX	maxillary
NA	nasal
OP	opercle
OPO	opisthotic
P	parietal
PAL	palatine
PAS	parasphenoid
PB	pharyngobranchial
PCL	postcleithrum
PH	parhypural
PL	posterior lamina (CL)
PLR	pleural rib
PMX	premaxillary
POP	preopercle
PR	proximal radial
PRO	prootic
PT	posttemporal
PTO	pterotic
PTS	pterosphenoid
PU	preural centrum
Q	quadrate
R	radial
S	sympletic
SC	scapula
SCL	supracleithrum
SMX	supramaxillary
SN	supraneural
SO	supraorbital
SOC	supraoccipital
SOP	subopercle
SPO	sphenotic
ST	stegural
TP	tooth plate
U	ural centrum
UH	urohyal
UN	uroneural
V	vomer
VHH	ventral hypohyal
VPCL	ventral postcleithrum

parasphenoid (PAS), prootics (PRO), pterosphenoids (PTS), pterotics (PTO), supraoccipital (SOC), sphenotics (SPO), and vomer (V).

Ethmoid Region.—Ethmoid region consisting of central mass of ethmoid cartilage, paired lateral ethmoid bones, and dermethmoid. Ethmoid cartilage single, covered dorsally over almost entire length by dermethmoid and by frontals (which lie between ethmoid cartilage and dermethmoid over posterior two-thirds of length of ethmoid cartilage). Ethmoid cartilage projecting anteriorly slightly beyond anterior terminus of dermethmoid. Ethmoid cartilage separating dermethmoid from vomer and parasphenoid. Ethmoid cartilage in both species of *Coccorella* considerably expanded posteriorly, forming an orbital septum between the eyes, and extending to or nearly to midline in posterior wall of orbit. Ethmoid cartilage in *Evermannella* and *Odontostomops* not extending into orbit and not forming an orbital septum. Dermethmoid thin in cross-section but elongate, with two posteriorly directed projections overlying respective (right and left) anterior sheetlike portions of frontal bones (fig. 9). Ascending head of each premaxillary bone bound to dermethmoid by a mass of connective tissue. Lateral ethmoids prominent, thin, sheetlike bones completely enclosing a cartilaginous core, forming a major point of abutment of dorsal margins of palatine.

Vomer.—Vomer an elongate sheathlike bone. Head of vomer lying ventral to ethmoid cartilage and bearing one tooth on each side, although in most specimens only one tooth (right or left) is present—the other tooth is apparently lost. Palatine bone of each side articulating with and strongly connected to vomer. Vomer with a posteriorly tapering shaft resting in an elongate shallow fossa on anteroventral surface of parasphenoid.

Frontals.—Frontals the largest, most complex bones of dorsal skull roof. Frontals meeting tightly in midlongitudinal line posteriorly but not fusing, frontals closely adjacent but not directly articulating anteriorly. In *Evermannella* (fig. 9A) each frontal is divided among three main portions: an anterior troughlike sheet, a tubular interorbital area, and an expanded posterior plate. Anterior troughlike area overlying posterior two-thirds of ethmoid cartilage and supporting (dorsally) posterior projection of dermethmoid on each side. Tubelike interorbital area markedly constricted and narrow in the tubular-eyed species belonging to *Evermannella*. Tubelike area opening anteriorly on troughlike frontal plate, posteriorly through pores of frontal commissural canal, and posterolaterally at junction of supraorbital, pterotic, and infraorbital cephalic laterosensory canals. Interorbital area of frontals in *Odontostomops* and *Coccorella* somewhat but not markedly narrower than posterior plate (fig. 9B, C). Posteriorly, frontals forming a thin sheet of bone occupying most of dorsal surface of cranial vault and partly overlying parietals posteriorly. Posterior frontal plate articulating posterolaterally with pterotics, anterolaterally with sphenotics, and anteriorly with pterosphenoids.

Parietals—Although most definitions of the Evermannellidae (Parr, 1929, Gosline et al., 1966; Rofen, 1966d; Johnson, 1974c [following Parr, 1929]) have stated that the parietals are indistinguishably fused with the frontals, this is not true for any evermannellid species examined by me. Parietals present as thin platelike bones, which rather than being separated by supraoccipital in midline in fact overlap anterior and anterolateral margins of supraoccipital and thus meet in midline. Parietals overlain by frontals anteriorly and overlay anteromedial margin of epiotics posterolaterally. Posteriorly, parietals with a dorsally directed

ridge that articulates with and serves as a continuation of a similar ridge on epiotics—and the anterior somatic musculature thus inserts on both epiotics and parietals, although the major insertion is on the epiotics.

Supraoccipital.—Supraoccipital a large oblong bone centered at posterodorsal margin of cranium. There is no supraoccipital spine, but there is a strongly developed, short, blunt knob of bone at center of supraoccipital. Supraoccipital overlain anteriorly and anterolaterally by parietals, articulating with epiotics posterolaterally and separated from exoccipitals posteriorly and ventrally by an area of cartilage.

Epiotics.—Epiotics relatively large, rounded bones contributing significantly to posterior wall of cranial vault (fig. 9) but largely excluded from dorsal wall of cranial vault. Epiotics overlain by parietals anteriorly, articulating with supraoccipital medially, with exoccipitals posteriorly, and with pterotics laterally within the posttemporal fossae. Dorsal projection of posttemporal connected to epiotics via a strong ligament.

Exoccipitals.—Exoccipitals forming the major portion of posterior wall of cranium. Exoccipitals articulating with each other above foramen magnum, which they completely enclose. Exoccipitals articulating dorsolaterally with epiotics, laterally with pterotics, and ventrally with basioccipital. Exoccipital partially overlain by opisthotic at common junction of exoccipital, epiotic, and pterotic on each side. Joint between exoccipitals and supraoccipital interrupted by an area of cartilage. Exoccipitals and basioccipital combining to form a bowl-shaped, centrum-like posterior face that serves as a point of articulation (through dense fibrous connective tissue) for first vertebral centrum. Each exoccipital extending anteriad on ventral surface of cranium between pterotic and basioccipital and meeting the prootic.

Opisthotics (=Intercalars).—Opisthotics lying astride common junction between exoccipital, epiotic, and pterotic on each side. A ligament connecting opisthotic to posttemporal is present on each side. An anteroventral projection of opisthotic lies astride pterotic-exoccipital joint but does not reach prootic.

Basioccipital.—Basioccipital forming posterior portion of cranial floor. Basioccipital meeting prootics and parasphenoid anteriorly and exoccipitals laterally and dorsally, forming, with exoccipitals, articulatory surface for attachment of vertebral column.

Pterotics.—Pterotics forming posterolateral corner of skull roof, articulating anteriorly with sphenotics and frontals, medially with epiotics, posteriorly and ventrally with exoccipitals and opisthotics, and anteroventrally with prootics. Junction of epiotics and pterotics within posttemporal fossae on each side. Dorsal troughlike surface of pterotic carrying temporal cephalic laterosensory canal from frontal to extrascapular. A shallow troughlike depression in pterotic receiving posterior head of hyomandibular.

Sphenotics (Autosphenotics).—Sphenotics forming lateral margin of posterodorsal orbit at anterolateral corner of cranial vault and largely overlain by lateral margin of frontals. Sphenotics meeting pterotic posteriorly, prootic ventrally, and pterosphenoids anteromedially within the orbit. Dermosphenotic (eighth infraorbital) connected to anterior margin of sphenotic and frontal, not overlying sphenotic. Sphenotic receiving and supporting anterior head of hyomandibular.

Prootics.—Prootics extensive, forming most of posteroventral wall of orbit.

Each prootic meeting its fellow in midline, dorsal to the myodome. Each prootic meeting parasphenoid ventrally, basioccipital and exoccipital posteriorly, and pterosphenoid, sphenotic, and pterotic dorsally.

Basisphenoid.—Basisphenoid (not illustrated) a narrow splintlike bone overlying articulation of prootics in midline of ventroposterior wall of orbit and with basisphenoid pedicel articulating with parasphenoid in ventral midline. Basisphenoid lacking in *Odontostomops*.

Parasphenoid.—Parasphenoid elongate, forming much of ventral contour of cranium. Parasphenoid lying between ethmoid cartilage and vomer anteriorly. Posteriorly two dorsolateral wings of parasphenoid meet with prootics. Parasphenoid articulates with and partly overlies basioccipital in ventral midline of skull.

Pterosphenoids.—Pterosphenoids forming bony posterior wall of orbit dorsal to prootics and meeting frontals dorsally, sphenotic laterally, and prootics ventrally. Pterosphenoids expanded medially in *Coccorella atrata,* nearly meeting in midline of posterior wall of orbit. Pterosphenoids not extended medially and widely separated in other evermannellid species.

Otoliths.—Due to a lack of fresh material, no detailed study of otoliths in evermannellids was possible. In cleared and stained material examined by me the sagittae are large and quite evident. An otolith of *Evermannella indica* is pictured in Kotthaus (1967).

Superficial Dermal Bones

This section includes descriptions of the superficial dermal bones of the snout and orbital region. Included are the following bones: infraorbitals (IO, IO-1 to 8), nasals (NA), and supraorbitals (SO). The tubular-eyed Scopelarchidae invariably possess two sclerotic bones on each side, but no evermannellid possesses sclerotic bones.

Nasals.—Nasal bones thin, troughlike elements, one on each side of snout above dermethmoid and just anterior to anterior margin of frontals. Two pores in posterolateral wall of each nasal marking presence of supraorbital laterosensory canal, received by nasals from frontals.

Supraorbitals.—Supraorbitals elongate, strutlike, slightly expanded ventrally, and noticeably expanded dorsally (fig. 10). Supraorbitals connected via loose connective tissue to anterodorsal margin of first infraorbital ventrally. Supraorbital abutting on and connected to dorsolateral frontal ridge dorsally and overlying anterior margin of lateral ethmoid medially. Supraorbital apparently lacking in *Odontostomops*.

Infraorbitals.—Evermannellids possess eight infraorbital bones on each side, including the lachrymal (IO-1) and dermosphenotic (IO-8). All carry in turn a segment of the infraorbital laterosensory canal. Infraorbital-1, an elongate oblong platelike element with a raised shelf of bone along dorsolateral margin (fig. 10). One to three pores, varying by species, piercing IO-1. Infraorbital-1 the largest and IO-2 the next largest infraorbital elements; IO-2 basically triangular in shape, with apex directed posteroventrally (fig. 10), except in *Odontostomops normalops* in which all members of infraorbital series are only partially ossified and are irregular in outline. Infraorbital-2 forming posteroventral corner of in-

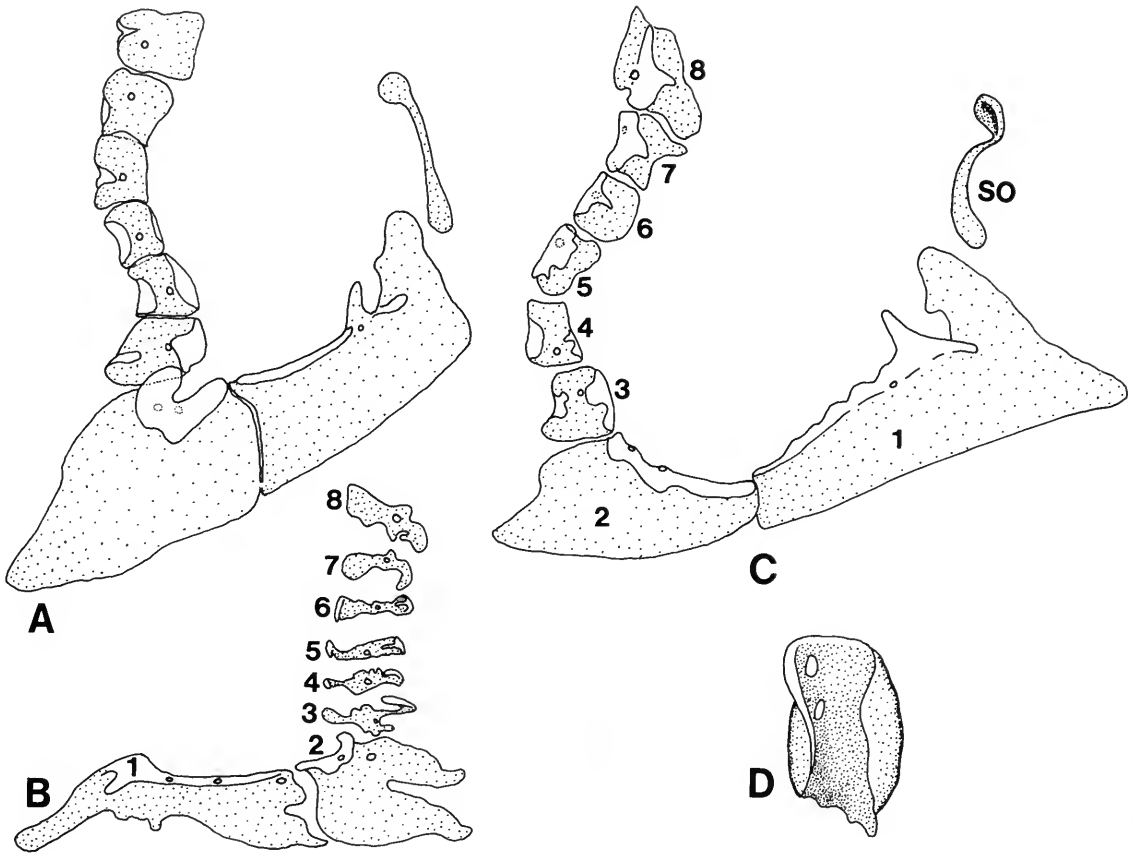


FIG. 10. Superficial dermal bones of the snout and orbital regions in evermannellids. **A,** Infraorbital series in *Coccorella atrata,* SIO 68-533, 99.6 mm. **B,** Infraorbital series in *Odontostomops normalops,* ISH 2220/71, 111.5 mm. **C,** Infraorbital series in *Evermannella indica,* UH 70/12/31, 108.8 mm. **D,** Nasal bone in *E. indica* as above.

fraorbital series. Infraorbital-3 to -8 basically similar in outline, with a central plate pierced by a single pore and with anterior and/or posterior margins curved laterally into bony ridges.

Mandibular Arch

The mandibular arch consists of the upper and lower jaws. Paired elements of the mandibular arch include the following bones: premaxillaries (PMX), maxillaries (MX), supramaxillaries (SMX), dentaries (D), articulars (AR), angulars (AN), Meckel's cartilages (MC), and coronomeckelian bones (CMN).

Upper Jaw—Premaxillaries.—Each premaxillary an elongate, very narrow and thin dentigerous bone, tapering to a point posteriorly (fig. 11A). Premaxillary and maxillary largely separated anteriorly, but premaxillary largely overlain by maxillary posteriorly. Premaxillary and maxillary sharply curving medially and dorsally at anterolateral corner of snout. Premaxillary expanded anteriorly into a bladelike ascending process. A triangular cartilaginous element (here termed the rostral cartilage) attached to but not fused with each premaxillary ascending process. The stout interpremaxillary ligament is largely attached to the rostral cartilage of each side. A short but stout ligament connects the rostral cartilage and maxillary on each side. Premaxillary teeth small, uniserial, retrorse anteriorly but typically straight posteriorly. All evermannellid species with an edentulous area on anterior premaxillary centered at the point where premaxillary turns sharply mediad.

Upper Jaw—Maxillaries.—Each maxillary an elongate, thin, and narrow bone similar in shape to the premaxillary over most of its length. Anteriorly the maxillary ends in four articulating processes (fig. 11): a dorsoposterior process connected via a strong ligament to the palatine, a medially directed dorsoanterior process connected via a ligament with the rostral cartilage, and two ventrally directed processes, one lying lateral and the other medial to the base of the ascending process of the premaxillary.

Upper Jaw—Supramaxillaries.—One supramaxillary. Supramaxillary rather large, one-third to one-fourth of maxillary length, deep and bladelike posteriorly, narrow and spikelike anteriorly.

Lower Jaw—Dentaries.—Dentaries the largest and most complex bones of the lower jaw. Dentaries consisting of a dorsal dentigerous ridge and posterolateral and anteroventral sheets of bone (fig. 11). When viewed medially, the anteroventral sheet curves abruptly laterad at its dorsal margin, forming a narrow, slightly oblique platform on which rests the anterodorsal process of the articular and the anterior portion of Meckel's cartilage. This platform ends at the ventral margin of the posterolateral sheet of bone. In *Evermannella* and *Odontostomops* dentary teeth partially biserial with four or fewer smaller fangs anteriorly, and these followed by 10 or fewer large barbed fangs (largest in length anteriorly and decreasing in length posteriorly), with the larger fangs bordered anterolaterally by six or fewer smaller teeth. In *Coccorella* dentary teeth uniserial, and none of the fangs are barbed (fig. 11E). A row of partially ossified replacement teeth occurring medially to row of fangs. Preoperculomandibular sensory canal partially encased in bone on anterolateral face of dentary. A distinct oval fossa (fig. 11F) at dentary symphysis in all species of *Evermannella* and lacking in *Coccorella* and *Odontostomops*.

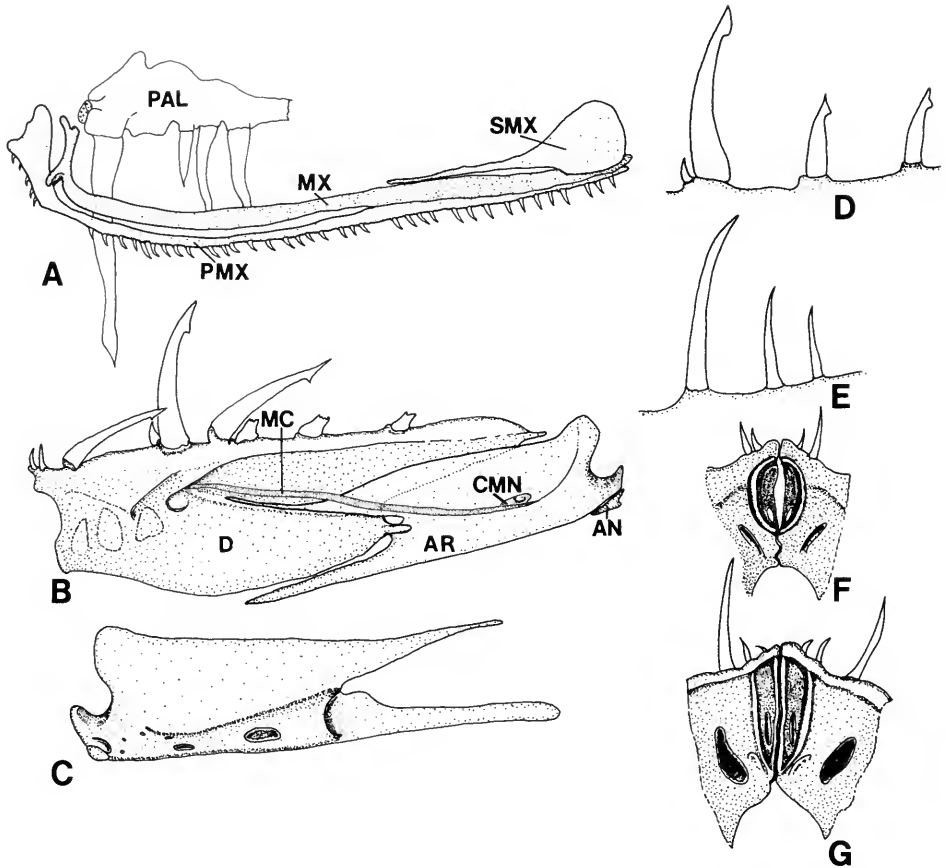


FIG. 11. Mandibular arch in evermannellids. **A,** Upper jaw, left lateral view, *Evermannella balbo,* ISH 546/73, 93.1 mm. **B,** Lower jaw, left medial view, *E. balbo,* ISH 546/73, 94.6 mm. **C,** Lower jaw, articular and angular, right lateral view, *Odontostomops normalops,* ISH 2220/71, 111.5 mm. **D,** Dentary teeth, left lateral view, *Evermannella indica,* UH 71/3/9, 104.5 mm. **E,** Dentary teeth, left lateral view, *Coccorella atrata,* SIO 68-533, 99.6 mm. **F,** Dentary symphysis, view from anterior, *Evermannella balbo,* ISH 546/73, 94.6 mm. **G,** Dentary symphysis, view from anterior, *Odontostomops normalops,* ISH 2220/71, 111.5 mm.

Lower Jaw—Articulars.—Articulars forming posterior two-fifths of lower jaw. Each articular divided into dorsal and ventral portions by the elongate bar of Meckel's cartilage (fig. 11B). Ventral portion tubular posteriorly, completely encasing the articular portion of the preoperculomandibular sensory canal in bone, and bladelike anteriorly. A dorsoposterior projection, the retroarticular process, supporting the articulation of the quadrate and receiving the preoperculomandibular sensory canal from the preopercle. Dorsal to the articulation of the quadrate, a dorsal process of the articular is connected via strong ligaments to the distal end of the maxillary and posterior terminus of the dentary. Articular and dentary articulating anteriorly in a complex pattern of overlapping projections (fig. 11B).

Lower Jaw—Angulars (Retroarticulars).—Each angular a small, irregularly shaped bone on ventromedial surface of articular and at posteroventral corner of lower jaw. Angular connected via a ligament to interopercle.

Lower Jaw—Coronomeckelian Bones (Sesamoid Articulars).—Each coronomeckelian bone a small, flattened, nodular element lying lateral to Meckel's cartilage, just anterior to retroarticular region of articular, and on the approximately horizontal line separating the dorsal and ventral portions of the articular. A strong ligament connecting coronomeckelian bone with pars mandibularis of adductor mandibulae muscle.

Palatine Arch

The palatine arch includes the ectopterygoid (ECP), mesopterygoid (MSP), metapterygoid (MTP), and palatine (PAL) (fig. 12A). Elements of the palatine arch are essentially identical in size and shape in all evermannellid species. Only the palatines bear teeth.

Metapterygoids.—Each metapterygoid inserted between ventral shaft of hyomandibular (which is partially overlapped by the metapterygoid), dorsal border of quadrate, and posterior border of mesopterygoid. Mesopterygoid and metapterygoid not overlapping in *Evermannella* and *Odontostomops*, but in *Coccorella*, metapterygoid overlapping medial surface of mesopterygoid. Metapterygoid large and well ossified, except in *Odontostomops* in which the metapterygoid is membranous and only partly ossified, forming a major brace between the hyoid and palatine arches.

Mesopterygoids.—Each mesopterygoid bladelike, membranous, poorly ossified at dorsal and posterior margins, tapering to a splintlike process anteriorly, and entirely supported by dorsal surface of ectopterygoid.

Ectopterygoids.—Each ectopterygoid an elongate, strong, strutlike bone partially hollowed to form a troughlike surface on posterior and dorsal surface. This concave surface receiving anterior margin of quadrate ventrally and supporting the mesopterygoid dorsally. Splintlike posterior portion of palatine attached to anteroventral surface of ectopterygoid. Ectopterygoid splintlike anteriorly, lying along dorsal margin of palatine for nearly one-half the length of palatine.

Palatines.—Each palatine an elongate, massive, dentigerous bone, forming (with the dentary) the principal bite of evermannellid species. Palatine teeth uniserial, decreasing in length from anterior to posterior, with replacement teeth forming medially to the active row. Palatine teeth rather loosely attached, all but the posteriormost teeth depressible. Anteriormost palatine teeth remarkably

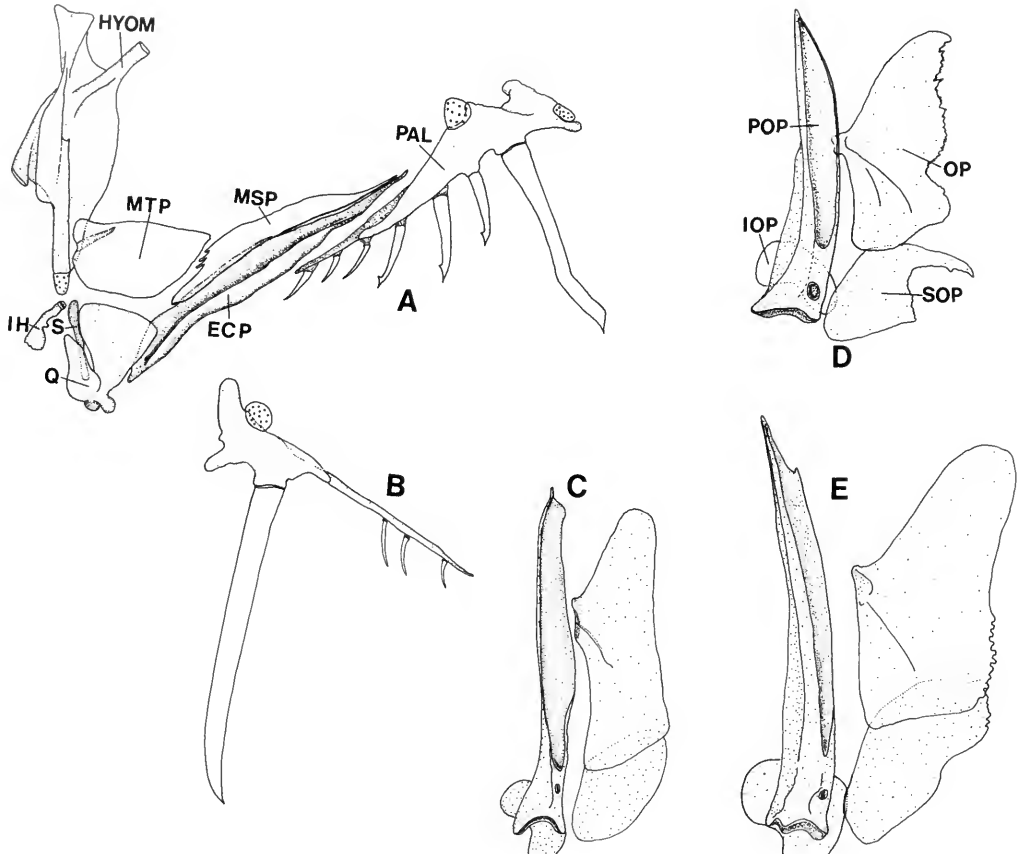


FIG. 12. Palatine arch, opercular apparatus, and part of hyoid arch in evermannellid species. **A,** Palatine arch and part of hyoid arch in *Evermannella balbo,* ISH 546/73, 102.0 mm. **B,** Palatine bone in *Coccorella atrata,* SIO 68-533, 99.6 mm. **C–E,** Opercular apparatus in three evermannellid species: **C,** *Coccorella atlantica,* SIO 68-476, 76.0 mm; **D,** *Odontostomops normalops,* UH 70/7/1, 86.6 mm; **E,** *Evermannella balbo,* ISH 546/73, 102.0 mm.

enormous barbed (except *Coccorella*) fangs and are by far the largest teeth occurring in evermannellids. In *Coccorella* the anteriormost palatine fangs are enormously large (the palatine fangs in *Coccorella* are the largest teeth relative to body length found in evermannellids: longest palatine tooth 7.1% to 10.0% SL in *Coccorella* cf. 4.6% to 7.3% in other evermannellid species) but are unbarbed (fig. 12B). A dorsal cartilaginous head of the palatine articulates with and is connected to the lateral ethmoid. Anterior to this head, connecting with the lateral ethmoid, is an ascending process articulating directly with the ethmoid cartilage. A concave anteroventral articular surface connecting with and attached to a convex dorsolateral articular surface of vomer.

Contrary to the statement of Gosline et al. (1966, p. 3), I find no anterior process of the palatine directed upward and laterally to *overlap* the proximal end of the maxillary in any evermannellid species. Gosline et al. (1966) supposed that such a connection was typical for myctophiform fishes. Johnson (1974c, p. 42) reports a modified version of this condition in scopelarchids. In evermannellids, however, although the posterodorsal process of the maxillary is connected (via a ligament) to a short anterolateral process of the palatine, there is no direct articulation.

Opercular Apparatus

Bones of the opercular apparatus include the interopercle (IOP), preopercle (POP), opercle (OP), and subopercle (SOP) of each side (fig. 12C–E).

Opercles.—Each opercle a thin, membranous bone, incompletely ossified at ventroposterior margin, typically resulting in a serrate margin. A disc-shaped articulatory apparatus at about center of anterior margin at the point where opercle is connected to posterior arm of hyomandibular. A bony ridge directed ventroposteriad from articulatory disc. Opercle considerably larger than subopercle in all evermannellid species. Opercle essentially rectangular in outline, except at anterodorsal margin where anterodorsal border of opercle is directed at a sharp diagonal from posterodorsal corner of opercle to just above articulatory disc. This arrangement results in a large, roughly triangular area bordered but not covered by preopercle, extrascapular, supracleithrum, and opercle. Directly beneath the skin covering this area is the large levator operculi muscle (see Winterbottom, 1974) that inserts on and covers most of the dorsomedial surface of the opercle. Dorsoposterior corner of opercle overlying and supported by lateral face of supracleithrum. Anterior margins of opercle and subopercle closely adjacent to posterior margin of preopercle except for dorsoanterior margin of opercle.

Subopercles.—Each subopercle a thin, membranous bone, incompletely ossified posteriorly, typically resulting in a serrate posterior margin. Dorsal portion of subopercle overlain by and attached to opercle. Subopercle partly overlying and connected to posterior border of interopercle. Pectoral insertion in all evermannellids at or below a horizontal line through center of subopercle.

Interopercles.—Each interopercle bladelike and membranous, roughly V-shaped, with one limb directed dorsoventrally, the other limb anteriorly. A bony thickening at center of interopercle marking origin of a very strong ligament connecting interopercle to angular. A strong ligament connecting medial face of interopercle to interhyal. Lateral face of interopercle connected via loose connective tissue to ventral portions of preopercle and quadrate.

Preopercles.—Each preopercle vertically elongate, somewhat expanded ventrally, carrying preopercular section of preoperculomandibular laterosensory canal. Preopercle supported by hyomandibular dorsally and posteroventral process of quadrate ventrally. Sensory canal carried in a troughlike structure made up of dorsal three-fourths of preopercle, entering into a short, bony canal ventrally and emerging onto a slightly expanded ventral plate from which the canal passes to retroarticular portion of articular.

Hyoid Arch

The hyoid arch includes the following elements: basihyal (BH), basihyal toothplate (BHTP), branchiostegal rays (BRR), ceratohyal (CH), dorsal hypohyal (DHH), epihyal (EH), hyomandibular (HYOM), interhyal (IH), quadrate (Q), symplectic (S), urohyal (UH), and ventral hypohyal (VHH). All but the basihyal, basihyal toothplate, and urohyal are paired.

Hyomandibulars.—Each hyomandibular with two stiff, flattened rods of bone dorsally, anterior rod articulating with sphenotic, posterior rod with pterotic (fig. 13E—G). A thin sheet of bone connecting ventral portions of these two rods. Hyomandibular with two stiff, flattened rods ventrally, a ventral shaft articulating (through cartilage) with interhyal and symplectic, and a posteroventral shaft articulating with and supporting opercle. A stout ridge of bone extending vertically along lateral face of main dorsoventral axis closely connecting with and supporting preopercle. A thin sheet of bone extending anteriorly, underlying and supporting dorsoposterior corner of metapterygoid.

Symplectics.—Each symplectic an elongate, well-ossified splint, articulating with medial face of posteroventral process of quadrate. Level of hyomandibular-symplectic joint about the same as the level of quadrate-metapterygoid joint.

Quadrate.—Each quadrate lying ventral to metapterygoid and composed of the usual three main parts: body, posteroventral process, and articular head. Body delta-shaped, articulating dorsally through a synchondral joint with metapterygoid and fitting anteriorly into a shallow, troughlike depression formed by posterior surface of ectopterygoid. Posteroventral process large, well ossified, receiving preopercle on posteroventral face and symplectic on anterodorsal face. Articular head with two strong condyles, one lateral and one medial, separated by a concave surface and fitting convex articulatory surface of retroarticular process of articular.

Interhyals.—Each interhyal rodlike dorsally and flattened, rounded, and somewhat expanded ventrally (except *Coccorella* in which symplectic is rodlike over entire length, with no portion distinctly expanded). Interhyal bound to hyomandibular-symplectic joint dorsally and to posterior articular facet of epihyal ventrally. A bony protuberance at about midlength of interhyal marks interhyal insertion of interoperculo-interhyal ligament.

Epihyals.—Epihyal stout, wedge-shaped, articulating via synchondral joint with ceratohyal. Epihyal equal to or greater than ceratohyal in length in *Evermannella* but less than ceratohyal in length in *Coccorella* and *Odontostomops*.

Ceratohyals.—Ceratohyal similar to epihyal in shape, articulating anteriorly with hypohyals. There is no ceratohyal foramen.

Hypohyals.—A dorsal hypohyal and slightly larger ventral hypohyal immediately anterior to each ceratohyal. A ventroanterior knob on ventral

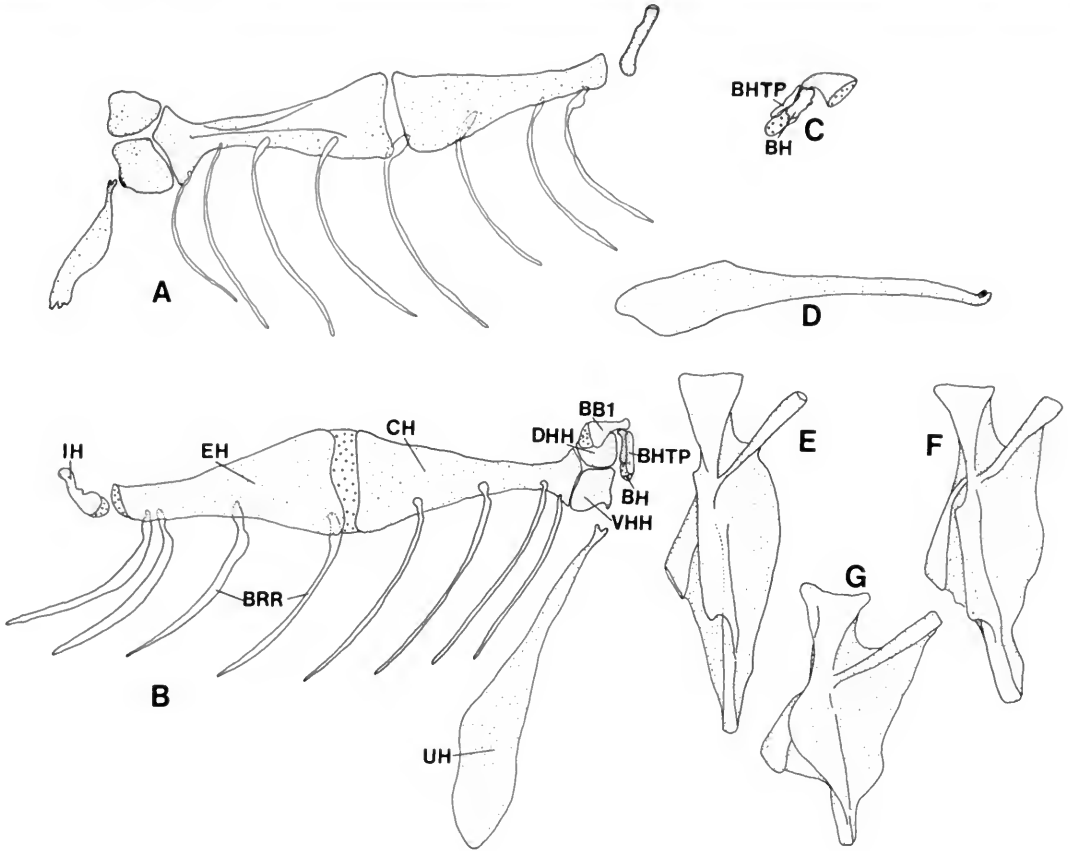


FIG. 13. Hyoid arch (partial) in Evermannellidae. **A,** *Coccorella atrata,* SIO 68-533, 99.6 mm. **B,** *Evermannella balbo,* ISH 546/73, 102.0 mm. **C,** Basihyal, basihyal tooth plate, and first basibranchial in *Coccorella atlantica,* UH 71/3/8, 93.3 mm. **D,** Urohyal in *Evermannella indica,* UH 70/9/24, 99.8 mm. **E–G,** Hyomandibula in three evermannellid species: **E,** *Coccorella atrata,* SIO 68-533, 99.6 mm; **F,** *Evermannella indica,* UH 70/9/24, 99.8 mm; **G,** *Odontostomops normalops,* ISH 2220/71, 111.5 mm.

hypohyal connected via a strong ligament to corresponding (right or left) fork of anterior projection of urohyal.

Branchiostegal Rays.—Eight branchiostegal rays on each side. Branchiostegal rays acinaciform and distributed in the 4 + 4 pattern described by McAllister (1968), with four external epihyal branchiostegal rays and four ventral or internal ceratohyal branchiostegal rays. Epihyal branchiostegal rays with a flattened, much expanded head (lacking on ceratohyal branchiostegal rays, which are rodlike dorsally). The anteriormost epihyal branchiostegal ray inserts at the ceratohyal-epihyal joint in *Coccorella* and *Odontostomops* and posterior to this joint in *Evermannella*.

Urohyal.—Urohyal short (*Coccorella atrata*) to elongate (*Evermannella indica*), much less than ceratohyal in length in *C. atrata*, about equal to ceratohyal in length in *C. atlantica*, and distinctly greater than ceratohyal in length in *Odontostomops* and *Evermannella*. Urohyal bladelike posteriorly, with posterior margin irregularly ossified or not ossified (*O. normalops*). A rodlike structure anteriorly, divided into right and left projections, as in a yoke, each projection connected via a ligament to corresponding ventral hypohyal.

Basihyal.—Basihyal much reduced in evermannellids, a rodlike structure connected via a hingelike joint to anterior margin of first basibranchial and via ligaments on each side to each dorsal hypohyal. Basihyal only half ossified, cartilaginous anteriorly. A distinct basihyal toothplate covering dorsal and dorsolateral margins of basihyal except in *Coccorella atlantica* (basihyal toothplate over only posterior two-thirds of basihyal) and *C. atrata* (basihyal toothplate apparently lost). No basihyal teeth.

Branchial Arches

Endoskeletal components of the branchial arches include the following: basibranchials (BB), ceratobranchials (CB), epibranchials (EB), hypobranchials (HB), and infrapharyngobranchials herein referred to as pharyngobranchials (PB) (fig. 14). Dermal elements associated with these bones include nodules or plates supporting two types of dentition: gill teeth (GT) vs. conical teeth (CT). Gill toothplates, developed as small nodules of bone supporting one to several small teeth in a uniserial row, occur on the second ceratobranchial and are limited to this bone, except in *Evermannella balbo* and *E. indica* in which the largest gill toothplate lies astride the articulation of the ceratobranchial and hypobranchial of the second arch (fig. 15E). Conical teeth, so-called to distinguish the larger single-based teeth of the gill arches from the gill teeth, are invariably present on pharyngobranchials 3 and 5 and are present or absent (table 6) on ceratobranchial 5, epibranchial 3, and pharyngobranchial 4. A toothplate of the fourth basibranchial (i.e., over the cartilaginous third basibranchial copula, see Nelson, 1969a) is unique to *Evermannella balbo* among evermannellids (fig. 14C). All conical teeth are no doubt associated with dermal toothplates that may (CB5, EB3, PB3) or may not (PB4, PB5) be fused with their respective endoskeletal elements.

Basibranchial Series.—Lingual teeth lacking in all evermannellid species. A single dermal toothplate overlying first basibranchial, indistinguishably fused with second basibranchial, and overlying anterior one-half or more of third basibranchial (fig. 14). Compound second basibranchial element easily the longest member of basibranchial series, with the result that the distance between

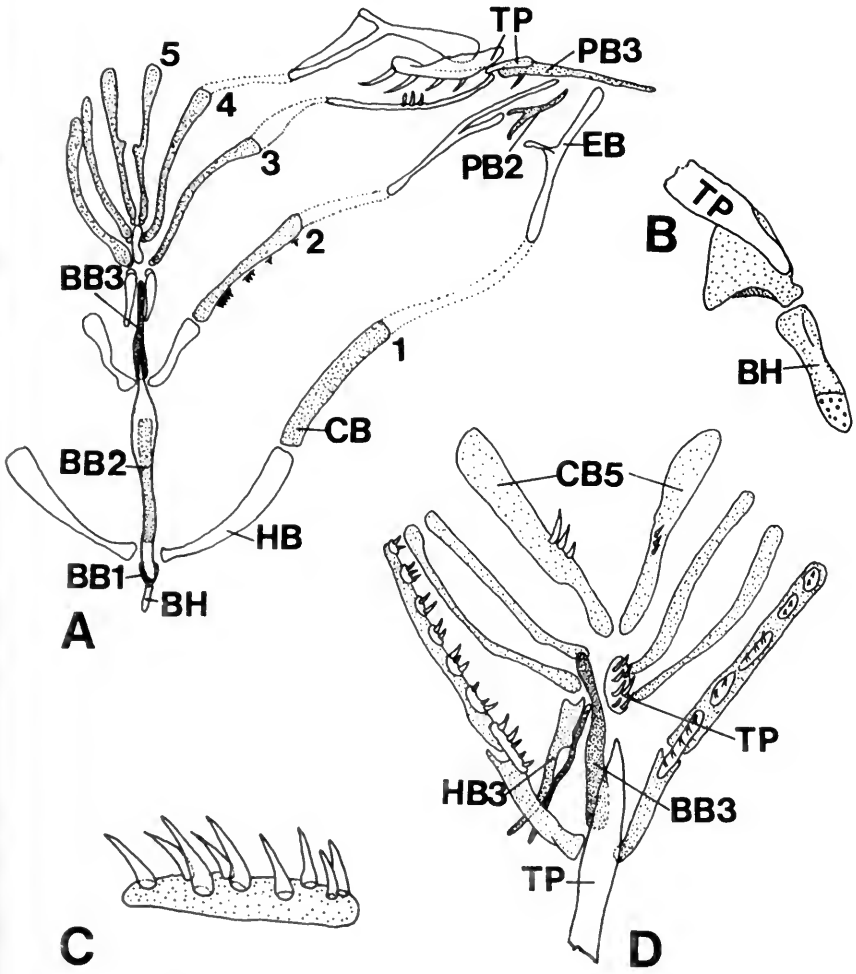


FIG. 14. Branchial arch elements in Evermannellidae. **A**, Branchial arch elements in *Coccorella atrata*, SIO 68-533, 99.6 mm. **B**, Basihyal and first basibranchial in *C. atrata* as above. **C**, Tooth plate of third basibranchial copula in *Evermannella balbo*, ISH 546/73, 102.0 mm. **D**, Posteroventral branchial arch elements in *E. balbo* as above.

ventral portions of first and second arches is noticeably greater than the distance between ventral portions of any succeeding pair of gill arches. A cartilaginous area, apparently single and median, lying posterior to third basibranchial and representing third copula of basibranchial series. This element receiving cartilaginous articular heads of fourth and fifth ceratobranchials. In *Evermannella balbo* a fourth basibranchial toothplate, bearing a patch of six to nine conical teeth, lies embedded in the skin over this cartilaginous element (fig. 14C).

Hypobranchials.—There are three paired hypobranchials corresponding to the first three gill arches, decreasing in length from the anterior pair to the posterior pair. Hypobranchials 1 and 2 articulating through cartilage with cartilaginous

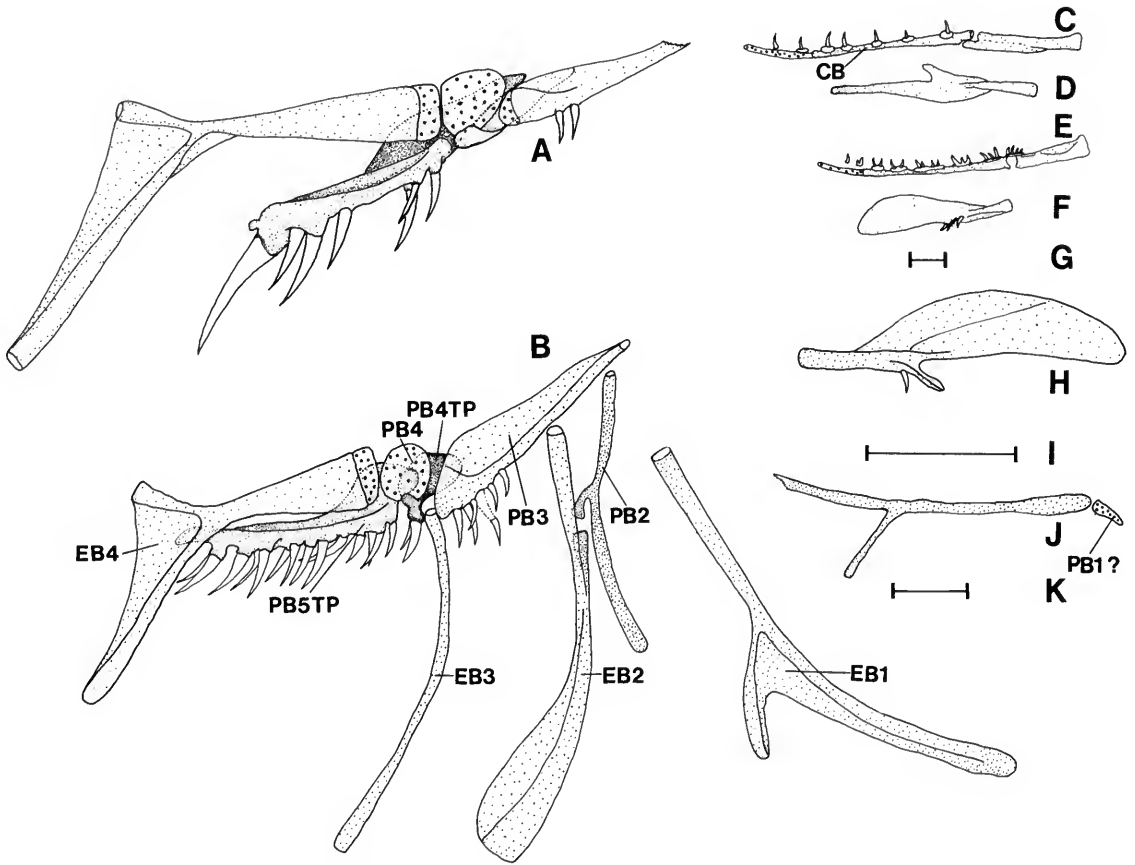


FIG. 15. Branchial arch elements in Evermannellidae. **A, B,** Dorsal branchial arch elements: **A,** *Coccorella atrata,* SIO 68-533, 99.6 mm; **B,** *Evermannella indica,* UH 70/12/31, 108.8 mm. **C,** Ceratobranchial and hypobranchial of second arch in *Coccorella atlantica,* UH 71/3/8, 93.3 mm. **D,** Fifth ceratobranchial in *C. atlantica,* UH 71/3/8, 93.3 mm. **E,** Ceratobranchial and hypobranchial of second arch in *Evermannella balbo,* ISH 546/73, 94.6 mm. **F,** Fifth ceratobranchial in *E. balbo,* ISH 546/73, 94.6 mm. **G,** Scale for drawings **C, D, E,** and **F;** indicated length = 1 mm. **H,** Fifth ceratobranchial in *Odontostomops normalops,* ISH 2270/71, 111.5 mm. **I,** Scale for drawing **H;** indicated length = 1 mm. **J,** Portion of first epibranchial and putative first pharyngobranchial in *Odontostomops normalops,* ISH 2270/71, 111.5 mm. **K,** Scale for drawing **J;** indicated length = 1 mm.

TABLE 6. Distribution of branchial teeth in evermannellids. Abbreviations for branchial arch elements given in text.

	Species						
Branchial arch element	**1**	**2**	**3**	**4**	**5**	**6**	**7**
GT/CB2	+	+	+	+	+	+	+
GT/HB2	0	0	0	+	+	?	0
CT/PB5	+	+	+	+	+	+	+
CT/PB4	+	0	+	+	+	?	+
CT/PB3	+	+	+	+	+	+	+
CT/EB3	+	+	0	+	0	?	0
CT/CB5	0	0	0	+	0	0	+
CT/BB4 tooth plate	0	0	0	+	0	0	0

KEY: +=present, 0=absent, ?=unknown, 1=*Coccorella atlantica*, 2=*C. atrata*, 3=*Evermannella ahlstromi*, 4=*E. balbo*, 5=*E. indica*, 6=*E. megalops*, 7=*Odontostomops normalops*, GT=gill teeth, CT=conical teeth.

areas between basibranchials 1 and 2 and 2 and 3, respectively, beneath the single basibranchial toothplate. Articulation of first two pairs of hypobranchials complete in that hypobranchial of each side articulates (through cartilage) with its fellow of the opposite side medially and with corresponding basibranchial element anteriorly. Third hypobranchials closely attached to third basibranchial and parallel it along half or more of its length. Third hypobranchial converging anteroventrally with its fellow, and the two tightly bound together beneath third basibranchial. Posteriorly, third hypobranchial of each side articulating (through cartilage) with third ceratobranchial laterally and third basibranchial copula medially.

Ceratobranchials.—There are five paired ceratobranchials, with the first four essentially identical in shape and articulating dorsally through a considerable length of cartilage with corresponding epibranchials. Fifth ceratobranchial (lower pharyngeal), no doubt a compound bone, a rod-shaped element bearing a distinct medially directed flange at about midlength. Fifth ceratobranchial edentulous, except in *Odontostomops normalops* and *Evermannella balbo* where one (*O. normalops*) to several (*E. balbo*) conical teeth are present on lateral flange.

Epibranchials.—There are four paired epibranchials. Epibranchials of first gill arch an elongate Y-shaped bone connecting dorsally through a ligament to anterior end of third pharyngobranchial. A rodlike projection (uncinate process of Rosen, 1973) at midlength connects posteriorly through a ligament to ventroanterior fork of second pharyngobranchial. Epibranchial of second arch elongate and with a distinct keel over ventral one-half of length in *Evermannella* (keel poorly developed in *Coccorella* and *Odontostomops*). A short, forklike anterior projection articulating with ventroposterior limb of second pharyngobranchial. A markedly elongate projection (= uncinate process) extending dorsomedially and attaching second epibranchial to third pharyngobranchial at about the middle of the latter bone.

Epibranchial of third arch elongate, unkeeled, rodlike, connecting dorsally to posterior edge of third pharyngobranchial, between the third and fourth pharyngobranchial toothplates. Several evermannellid species (table 6) possess conical teeth occurring at about midlength on third epibranchial.

Epibranchial of fourth arch a stout, Y-shaped bone. A dorsoposterior projection at about midlength of fourth epibranchial forming short leg of the "Y," and the longer limbs of the "Y" connect respectively with fourth ceratobranchial ventrally and fourth pharyngobranchial dorsally. A distinct keel present on ventral limb. Fourth epibranchial connecting (through cartilage) with cartilaginous fourth pharyngobranchial and for the most part not closely associated with the large fifth pharyngobranchial toothplate.

Pharyngobranchials.—There are three (or questionably four) paired pharyngobranchials. First (suspensory) pharyngobranchial absent or, if present, reduced to an exceedingly minute nodule of cartilage. This element is both difficult to see and to distinguish from cartilaginous dorsal terminus of first epibranchial. Rosen (1973, fig. 12) illustrates a first pharyngobranchial in a specimen identified as *Evermannella* sp. Although I have seen what appears to be a separate cartilaginous element dorsal to first epibranchial in several evermannellid species (*Evermannella balbo, E. indica, Odontostomops normalops*), such an element is not discernible in the other species examined, nor is it ever ossified, nor is it as large as Rosen's figure indicates.

Second pharyngobranchial an edentate, Y-shaped bone, with longest limb connecting dorsally with third pharyngobranchial, an anteroventral limb connecting through a ligament to first epibranchial, and a posteroventral limb articulating with second epibranchial.

Third pharyngobranchial easily the largest pharyngobranchial bone and providing the principal dorsal support for the gill arches. Conical teeth invariably present on third pharyngobranchial but in no evermannellid species are they as large or as numerous as conical teeth on fifth pharyngobranchial toothplate. Conical teeth of third pharyngobranchial limited to posterior one-fourth of ventral surface of that bone.

A cartilaginous fourth pharyngobranchial and an associated but separate fourth pharyngobranchial toothplate present in all evermannellid species. Fourth pharyngobranchial articulating posteriorly with fourth epibranchial and anteriorly with third pharyngobranchial. Toothplate of fourth pharyngobranchial narrow but well ossified in all evermannellids, roughly trough-shaped, enclosing (ventral) surface of fourth pharyngobranchial. Fourth pharyngobranchial toothplate provided with strong conical teeth except in *Coccorella atrata* in which the toothplate is present but edentate.

There exists no identifiable fifth pharyngobranchial, but the toothplate of the fifth pharyngobranchial (see Nelson, 1969a) is by far the largest pharyngobranchial toothplate and bears the largest and most numerous conical teeth of any gill arch element. Rosen (1973, p. 407) apparently did not see the fourth pharyngobranchial toothplate in his evermannellid material and thereby misidentified the fifth toothplate as the fourth (Rosen, 1973, pp. 407, 435). A dorsomedially directed flange from anterior terminus of fifth toothplate closely paralleling a similar projection on fourth toothplate and thus partially encloses (ventrally) anterior end of fourth epibranchial and posterior portion of fourth pharyngobranchial.

Vertebrae, Supraneurals, Intermuscular Bones, and Caudal Skeleton

Vertebrae.—The number of vertebrae varies between 45 and 54 (table 3). Point of separation between precaudal and caudal vertebrae taken as the first centrum,

with a complete haemal arch being termed first caudal vertebra. This point could not be determined in radiographs. For cleared and stained material the following precaudal + caudal vertebral counts were obtained: *Coccorella atlantica* (16 + 34), *C. atrata* (16 + 31), *Evermannella balbo* (17 + 36), *E. indica* (17 + 33), *Odontostomops normalops* (16 + 33). These counts include the fused first preural plus first ural element ($PU_1 + U_1$) but do not include the second ural element (U_2).

All centra large, amphicoelous, pierced centrally by a large notochord canal. First precaudal centrum complete. Neural arch elements on all centra as deep as or deeper than spool-shaped centrum. Neural arch prezygapophyses and postzygapophyses well developed, rigidly interlocking, and strengthening the vertebral column.

Neural spines present on all centra, but those of first three centra unfused distally. Each precaudal centrum bearing bilateral large ventrolaterally directed parapophyses. Most precaudal parapophyses articulating with and providing support for an epipleural and a pleural (ventral) rib. First (anteriormost) precaudal centrum lacking both pleural and epipleural ribs. Second precaudal centrum bearing an epipleural rib but lacking a pleural rib. Parapophyses of eleventh precaudal centrum prolonged ventrally as spinelike processes, with parapophyses of succeeding precaudal centra sequentially longer than those on preceding centra. Sequence terminated with distal fusion of these processes on first caudal vertebra.

Intermuscular Bones and Ribs.—First precaudal centrum bearing epineural (EN) and epicentral (EC) intermuscular bones (fig. 16). Second centrum bearing only an epipleural (EPR) rib. Succeeding precaudal centra bearing an epipleural and a pleural (PLR) rib. Additional intermuscular bones absent. Caudal vertebrae lacking intermuscular bones, except that first caudal vertebra may or may not bear an epipleural rib.

Supraneurals.—Supraneurals (SN) invariably two, the first inserted between neural arch elements of first precaudal vertebra, the second between neural arch elements of third precaudal vertebra.

Caudal Skeleton.—The six autogenous hypurals (HYP 1 to 6) and the autogenous parhypural (PH) support the 1 + 9 + 8 + 1 (counting from dorsalmost ray) principal caudal rays. The sixth (dorsalmost) hypural is greatly reduced to a very small wedge-shaped element (fig. 16E). First preural centrum (PU_1), first ural centrum (U_1), and first pair of uroneurals (UN_1) fused into a single bone—the stegural (ST) of Monod (1968). The first uroneurals are fused with the stegural ventrally but are separate distally (fig. 16G). Thin bladelike second uroneurals (UN_2) attached to but not fused with dorsoposterior lateral faces of respective (right or left) first uroneurals. Stegural supporting the parhypural and first two hypurals. Third hypural inserted between second hypural, stegural, and ventral margin of second ural centrum. Second ural centrum (U_2) invariably present and free in all evermannellids, inserted behind and partly between the separate uroneural wings of stegural. Second ural centrum expanded and centrum-like ventrally but rodlike dorsally (fig. 16I). A marked notch in posterior border of second ural centrum receiving and supporting fourth hypural. Fifth hypural inserted between fourth hypural and uroneural portion of stegural. Sixth hypural much reduced, a wedge-shaped bony nodule attached to posterodorsal margin of fifth hypural. Only one epural (EP) present in evermannellids—an oblong platelike element situated dorsally between stegural and neural spine of third preural vertebra. Neural spine of second preural vertebra represented by a

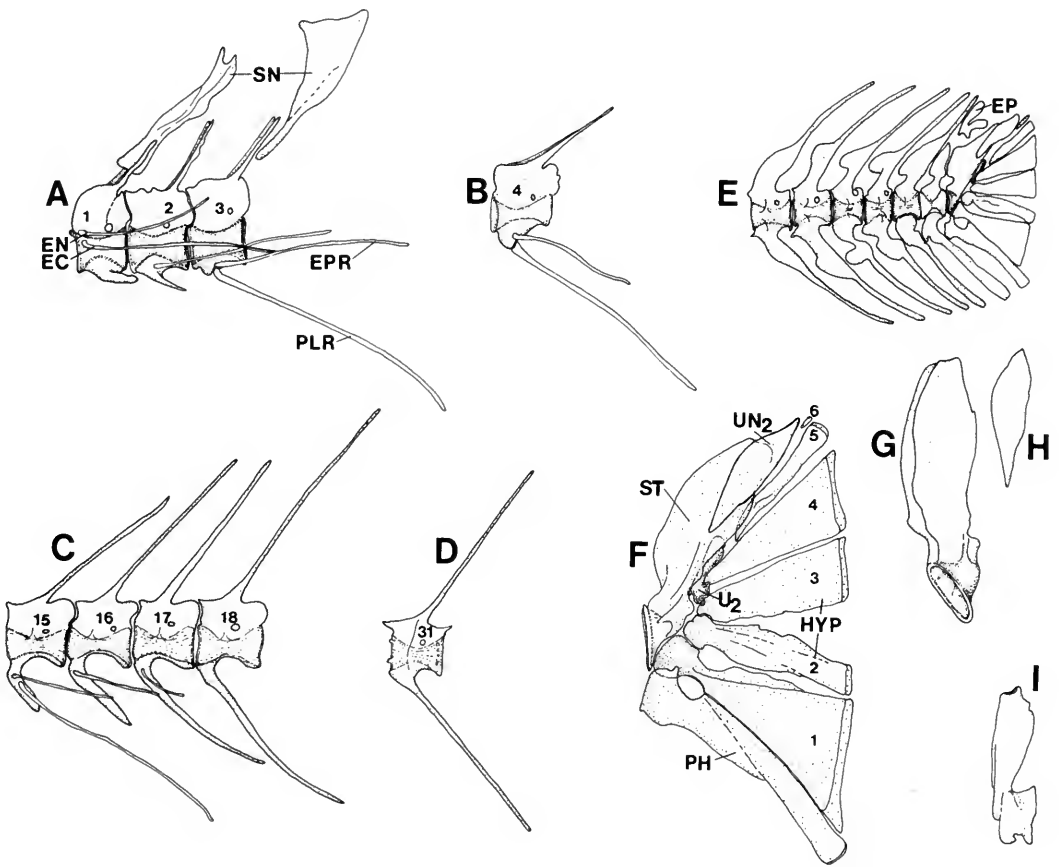


FIG. 16. Vertebrae, supraneurals, intermuscular bones, and caudal skeleton in *Coccorella atlantica* (**A–E**), UH 71/3/8, 93.3 mm SL; and *Evermannella indica* (**F–I**), UH 70/12/31, 108.8 mm SL. **A,** Precaudal vertebrae 1 to 3; **B,** precaudal vertebra 4; **C,** precaudal vertebrae 15 to 16, caudal vertebrae 1 to 2 (numbered 17 to 18); **D,** caudal vertebra 19 (=31st vertebra numbered from first precaudal); **E,** caudal skeleton; **F,** caudal skeleton; **G,** stegural; **H,** second uroneural; **I,** second ural centrum.

broad spatulate projection, tapering to a point distally, and about one-half the length of preceding neural arch and spine elements.

Dorsal Fin

Evermannellids exhibit a range of 10 to 13 dorsal-fin rays (table 2). Last dorsal-fin ray divided completely to base and counted as one element. Number of pterygiophores equal to number of fin rays (FR), but whereas the greatly expanded first (anteriormost) pterygiophore supports the first two dorsal-fin rays (fig. 17), the last two pterygiophores support the posteriormost divided ray. First pterygiophore consisting of an elongate bladelike proximal radial (PR) that is enormously expanded ventrally and two distal radials (DR) supporting the first two dorsal-fin rays. First pterygiophore inserted over seventh through tenth precaudal vertebrae in *Coccorella atlantica*. All distal radials consisting of a spherical central cartilage, with two hemispherical bony capsules providing the articulatory surface. Second pterygiophore consisting of an elongate proximal radial and a single distal radial, providing support for third dorsal-fin ray. Succeeding pterygiophores composed of proximal, medial (MR), and distal radials except for the terminal pterygiophore that consists of a single proximal radial. A single distal radial and the last two pterygiophores supporting the posteriormost dorsal-fin ray.

Anal Fin

Anal-fin rays 26 to 37 (table 3). Posteriormost anal-fin ray divided completely to base and counted as one element. Number of pterygiophores one less than the number of anal-fin rays—first (anteriormost) pterygiophore supporting first two anal-fin rays, final pterygiophore supporting terminal divided anal-fin ray. Anteriormost pterygiophore consisting of an elongate, rodlike proximal radial, inserting between haemal spines of 19th to 20th to 21st to 22nd vertebrae, depending upon the species, and two distal radials supporting first two anal-fin rays. Second pterygiophore consisting of proximal and distal radials only, supporting third anal-fin ray. Third and successive (fourth and successive in *Coccorella atlantica*) pterygiophores consisting of proximal, medial, and distal radials. Final two or three distal radials lacking ossified bony caps.

Pectoral Girdle

The dermal elements of the pectoral girdle include the posttemporal (PT), supracleithrum (SCL), cleithrum (CL), and three postcleithra (PCL)—dorsal (DPCL), medial (MPCL), and ventral (VPCL). Endochondral elements include the scapula (SC) and coracoid (COR). One extrascapular (ESC) is associated with but not part of the pectoral girdle.

In evermannellids the insertion of the pectoral fin lies just above the ventral contour of the body, and the line of insertion of the pectoral-fin rays is rather more horizontal than vertical. Marshall (1955) gives 15° to 20° as the value of the angle between the horizontal axis of the body and the axis of the pectoral-fin insertion in *Evermannella balbo*.

Posttemporal.—Posttemporal unforked, consisting of two portions: (1) a rodlike dorsal articulating process and (2) a slightly expanded ventral bladelike area (fig. 18). Dorsal process of posttemporal converging medially with its fellow of

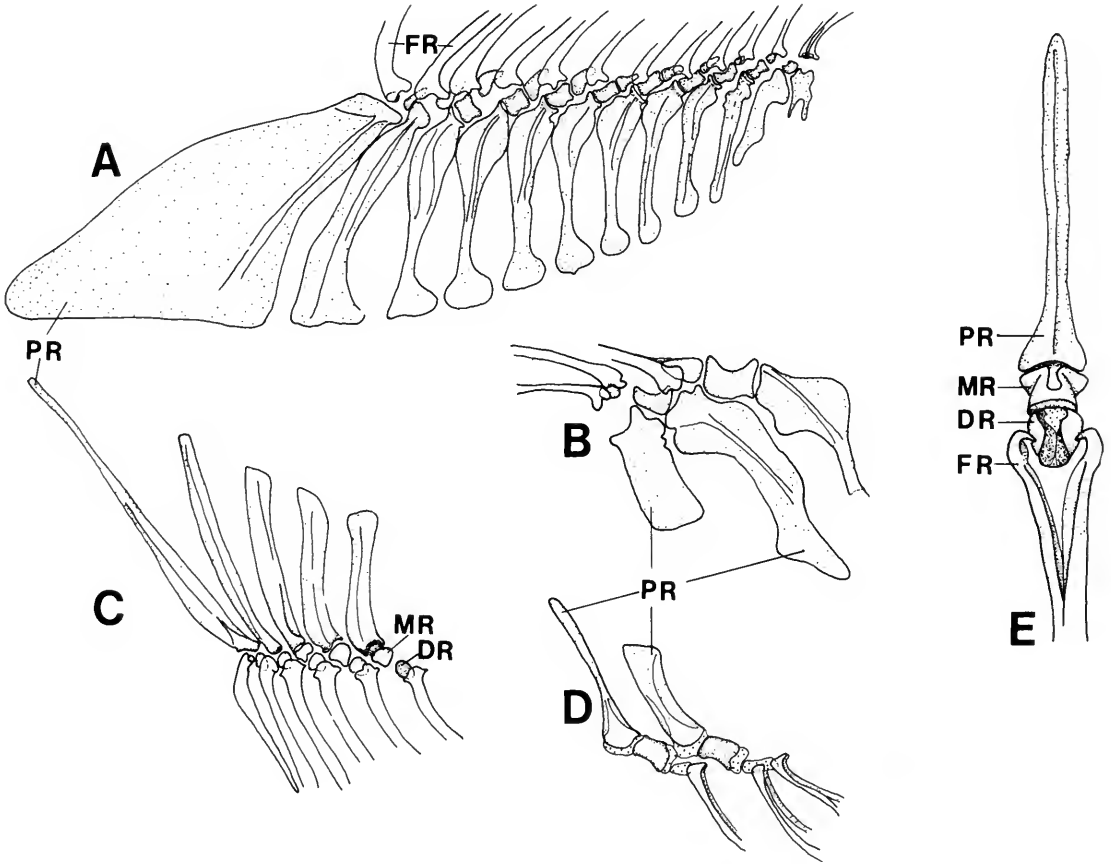


FIG. 17. Dorsal (**A, B**) and anal (**C–E**) fins in *Coccorella atlantica*, UH 71/3/8, 93.3 mm SL (**A**) and *Evermannella indica*, UH 70/12/31, 108.8 mm SL (**B–E**). **A,** Dorsal fin, left lateral view; **B,** dorsal fin, posteriormost fin rays, right lateral view; **C,** anal fin, anteriormost fin rays, left lateral view; **D,** anal fin, posteriormost fin rays, left lateral view; **E,** anal fin, fourth pterygiophore, posterodorsal view.

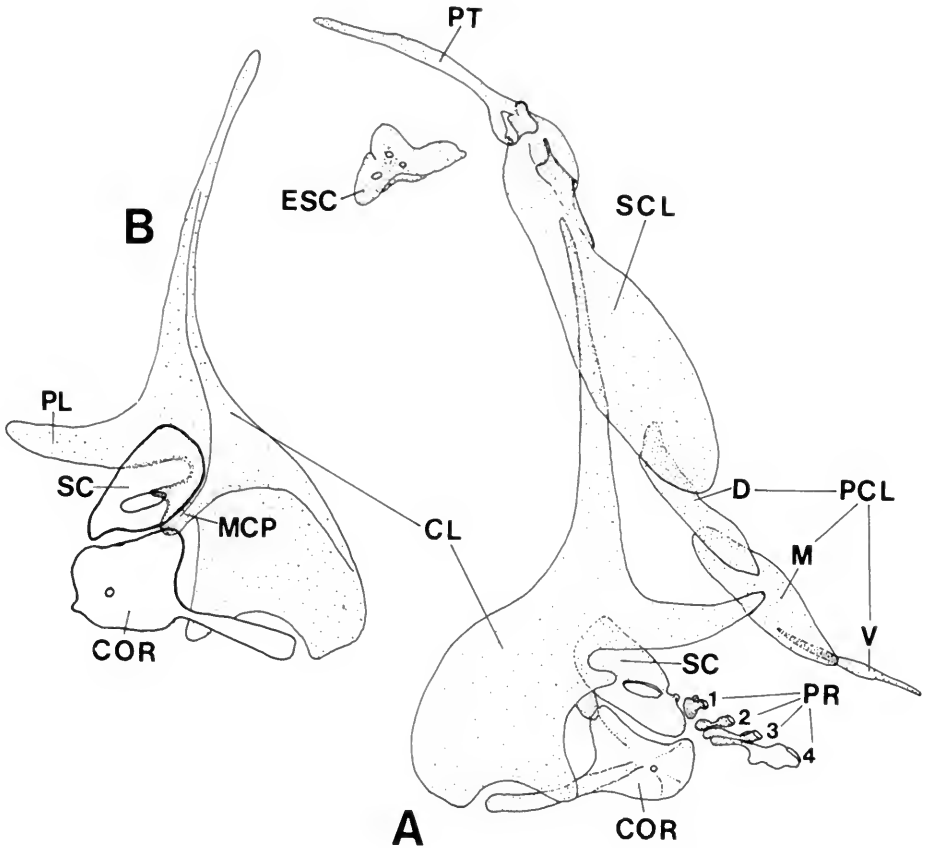


FIG. 18. Pectoral girdle in *Evermannella balbo*, ISH 546/73, 102.0 mm SL. **A**, Pectoral girdle, left lateral view; **B**, portion of left pectoral girdle, right medial view, showing cleithrum (shaded), scapula, and coracoid (both unshaded).

the opposite side and loosely connected to the epiotic. Ventral bladelike area partially covering and loosely connected to dorsal tip of supracleithrum. Typically a raised tubelike bony process present on posttemporal and encasing laterosensory canal which posttemporal receives from extrascapular and passes to supracleithrum. A strongly developed nodular bony process near anteromedial margin of posttemporal marking insertion of strong posttemporal-opisthotic ligament.

Extrascapular.—Only one extrascapular on each side present in evermannellid species. Extrascapular Y-shaped, partly troughlike, pierced by three pores, one pore in each limb of the Y. Three branches of the laterosensory system meet at the extrascapular, the temporal branch from the pterotic, a supratemporal branch from over the posterior portion of the cranium, and the main lateral line canal.

Supracleithrum.—Supracleithrum an elongate, nearly straight, flattened, oblong bone, slightly tapering dorsally and expanded and rounded ventrally. Supracleithrum overlying and loosely attached to rodlike dorsal process of cleithrum. Dorsal postcleithrum attached to supratemporal medially. A raised tubelike bony process passes the laterosensory canal from the posttemporal to the lateral line. Rofen (1966d, p. 512) states that no bony processes on the posttemporal or supracleithrum are associated with the lateral line in evermannellids. This statement is in error. There is invariably just such a process on the supracleithrum and typically such a process on the posttemporal (apparently absent in *Coccorella atrata*).

Cleithrum.—Cleithrum the largest and most complex element of the pectoral girdle. Main shaft of cleithrum strongly arched, ending dorsally in a rodlike shaft lying medial to and attached loosely to the supracleithrum. A posteriorly directed process, the posterior lamina (PL) may (*Evermannella, Odontostomops*) or may not (*Coccorella*) overlap the lateral face of the medial postcleithrum. Ventrally, the main shaft of the cleithrum curving sharply anteriad and slightly mediad, converging with its fellow of the opposite side. A medial shelf, the midcleithral process (MCP, fig. 18B), projecting posteriorly from main shaft and articulating dorsally with scapula and ventrally with coracoid.

Scapula.—Scapula roughly oval in outline, articulating dorsally, anteriorly, and laterally with cleithrum, and ventrally with coracoid. A saddle-shaped raised bony process supporting the enlarged dorsalmost pectoral-fin ray. Scapula providing support for first (dorsalmost) proximal pectoral radial. Scapular foramen large, an elongate oval lying nearly in center of scapula.

Coracoid.—Coracoid an expanded bony sheet, rounded concavely at anterior margin and convexly at posterior margin, narrowing to a bony rodlike process anteroventrally and connected to ventral tip of cleithrum. Coracoid overlying and strongly connected to posterior margin of midcleithral process. Coracocleithral fenestra moderately large but not readily visible in lateral view. A distinct coracoid foramen present. A cartilaginous ridge along posterodorsal margin of coracoid supporting second, third, and fourth proximal pectoral radials.

Postcleithra.—Three postcleithra—here termed dorsal, medial, and ventral. Each postcleithrum membranous, bladelike, ovoid, distinctly longer than wide. Ventral postcleithrum especially narrow and splintlike. Dorsal postcleithrum attached to medial face of supracleithrum. Each succeeding (medial, ventral) postcleithrum attached to medial face of preceding (from dorsal) postcleithrum.

Rofen (1966d, p. 512) illustrates only two postcleithra for a specimen of *Evermannella indica*, but I find three postcleithra in my material of *E. indica*, as in all evermannellid species.

Pectoral Radials.—The four proximal pectoral radials (PR) are roughly hourglass-shaped. Dorsalmost radial the smallest, with successively ventral radials sequentially larger. Distal radials unossified, one such distal radial associated with each pectoral-fin ray except no distal radial is associated with the first pectoral-fin ray. It seems likely that the distal radial of the first pectoral-fin ray is both ossified and fused with the medial half of the enlarged first ray. Pectoral-fin rays 11 to 13 (table 2).

Pelvic Girdle

Pelvic bones paired, flattened, elongate, lying in ventral plane of abdominal body wall, neither reaching to nor connected with pectoral girdle (fig. 19). Anterior region of each pelvic bone a thick lateral strut supporting a thin, narrow, medial bony shelf. Pelvic bones converging in midline anteriorly but are only

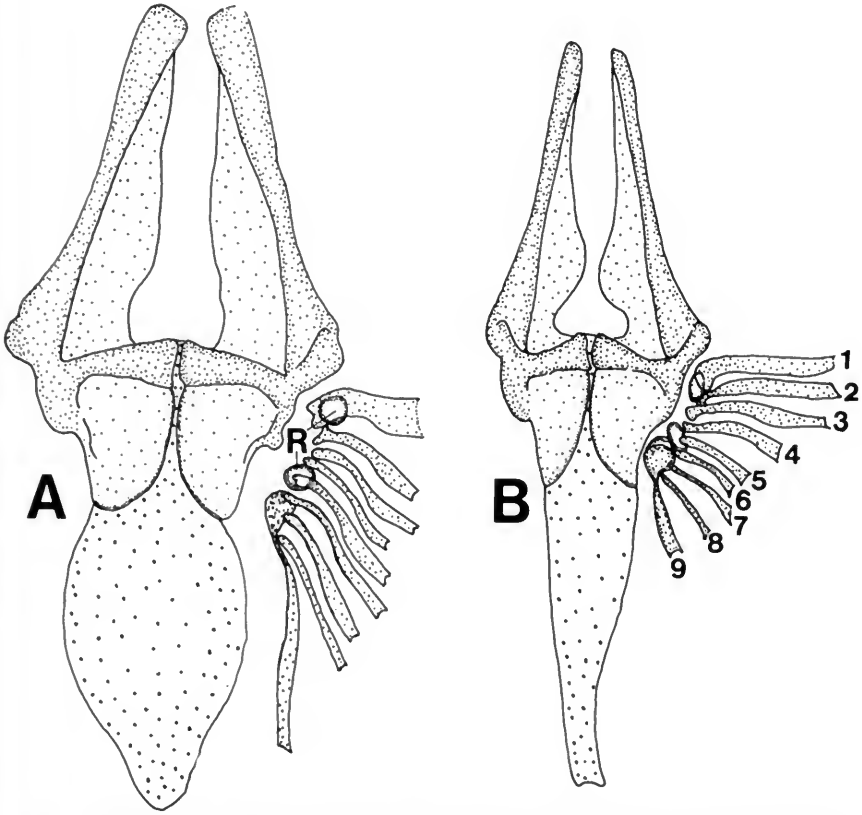


Fig. 19. Pelvic girdle of evermannellids. **A**, Pelvic girdle, ventral view, *Coccorella atlantica*, UH 71/3/8, 93.3 mm SL. **B**, Pelvic girdle, ventral view, *Evermannella indica*, UH 70/12/31, 108.8 mm SL.

loosely connected. Posteriorly, pelvic bones consisting of two regions: (1) a lateral expanded ridge of bone providing support for the nine movable pelvic-fin rays and (2) a medial area of two very thin, bony lamellae encasing a cartilaginous plate. Cartilaginous plate of each side coalescing indistinguishably with its fellow in midline, forming a single common plate. Pelvic cartilaginous plate extending posteriad far behind ossified region of pelvic girdle—posterior extension up to two-thirds the length of ossified region of pelvic girdle (fig. 19). A thickened area of bone, forming a bony strut extending medially from the region of insertion of first pelvic-fin ray on each side, with strut from each side nearly meeting in midline.

Pelvic-fin rays numbered in order from lateral (anterior) to medial (posterior). Two bony or cartilaginous radials (R, fig. 19A) associated with pelvic-fin rays, the first between expanded bases of stout first pelvic-fin ray, the second (which may be partly ossified or entirely cartilaginous) between bases of fourth to sixth pelvic-fin rays. Seventh and eighth pelvic-fin rays supported ventrally by expanded base of ninth pelvic-fin ray. Gosline (1961, pp. 20, 21) points out that this expanded base is a compound element formed by fusion of the fin-ray base with the innermost radial. There is no curved splint of bone along the outer surface of the upper half of the first pelvic-fin ray as in *Solivomer* (Neoscopelidae, Gosline, 1961, p. 18) and most myctophids (Paxton, 1972, p. 32).

INTERRELATIONSHIPS

In attempting to infer relationships among evermannellid species and between the family Evermannellidae and other iniomous families, I have applied the same methods of phylogenetic reasoning used in my earlier (Johnson, 1974c, pp. 199–220) study of the scopelarchids. Two fundamental difficulties characterize the following discussion. The first is that evermannellid genera as defined herein are distinctly monothetic (Mayr, 1969), for the most part defined by autapomorphous (Brundin, 1966) character states. Such uniquely diagnostic, presumably derivative features reinforce the concept of monophyly in the case of each evermannellid genus but do not aid the attempt to infer relationships among all evermannellid species. The second difficulty pertains to the attempt to determine relationships among iniomous families—it is that the survey of iniomous taxa for many (seemingly) critical characters is woefully incomplete.

Catalogue of Characters and Character States

The list of characters compiled below is used for two purposes: (1) to summarize all available information relevant to the assessment of interrelationships among evermannellid species; and (2) as a basis for my discussion of the hypothesis (e.g., Gosline et al., 1966, p. 17) of the sister-group relationship between evermannellids and scopelarchids. The complete character state by OTU matrix is presented as Table 8, excluding characters for which states could not be adequately defined and those characters used solely in the attempt to infer relationships among evermannellid species. Characters catalogued below were selected specifically for the attempt to study scopelarchid/evermannellid relationships. Many other characters could have been included and will have to be included in any thoroughgoing study of interrelationships among iniomous taxa.

To avoid confusion in nomenclature and terminology, I list below the working classification of iniomous fishes adopted in this paper. The groupings adopted herein are for the most part those traditional among ichthyologists, but also reflect results of recent work on iniomous taxa, including the present paper:

Aulopoidei: Aulopidae (*Aulopus* + *Hime*)
Myctophoidei: Myctophidae, Neoscopelidae
Chlorophthalmoidei: Chlorophthalmidae (*Bathysauropsis* + *Chloropthalmus* + *Parasudis*), Ipnopidae (including Bathypteroidae), Notosudidae, Scopelarchidae
Synodontoidei: Bathysauridae, Harpadontidae (*Harpadon* + *Saurida*), Synodontidae (*Synodus* + *Trachinocephalus*)
Alepisauroidei: Alepisauridae, Anotopteridae, Evermannellidae, Omosudidae, Paralepididae.

This working classification assumes the monophyly not only of the 15 family-level OTU's separately listed but also each of the five groups accorded subordinal status and of the Iniomi itself. The character catalogue presented below is the basis for my discussion of the evidence for and against these hypotheses of monophyly and intergroup relationships implicit in this classification. Groupings proposed by other authors are referenced in the text by the author's (authors') initial in parentheses, e.g., Aulopiformes(R) refers to the order Aulopiformes as proposed by Rosen (1973). Only two papers, Gosline et al., 1966 ("G"), and Rosen, 1973 ("R"), are cited in this fashion.

In addition to material examined personally (table 7), statements regarding character states exhibited by various iniomous taxa are based (1) on previous studies of interrelationship among some or all of these taxa (Harry, 1952; Marshall, 1955; Gosline et al., 1966; Goody, 1969; Rosen & Patterson, 1969; Paxton, 1972; Rosen, 1973; Johnson, 1974c; Marshall & Staiger, 1975; Zehren, 1975; Sulak, 1977); (2) on morphological data (Gregory, 1933; Marshall, 1960; Monod, 1968; Nelson, 1969a; Okiyama, 1974); and, in addition to the above, (3) on data presented for particular taxa, such as Alepisauridae (Regan, 1911; Gibbs & Wilimovsky, 1966; Rofen, 1966b); Anotopteridae (Rofen, 1966c); Aulopidae (Mead, 1966a); Bathysauridae (Mead, 1966b); Chlorophthalmidae (Tåning, 1918; Mead, 1966e; Ahlstrom, 1971); Evermannellidae (Herring, 1977); Harpadontidae (Gibbs, 1959; Anderson et al., 1966); Ipnopidae (Regan, 1911; Mead, 1966c,d; Nielsen, 1966; Theisen, 1966); Myctophidae (Jollie, 1954; Moser & Ahlstrom, 1970, 1972; Nafpaktitis et al., 1977); Neoscopelidae (Butler & Ahlstrom, 1976; Nafpaktitis, 1977); Notosudidae (Bertelsen et al., 1976); Omosudidae (Parr, 1929; Rofen, 1966b); Paralepididae (Harry, 1953; Rofen, 1966a); Synodontidae (Gibbs, 1959; Anderson et al., 1966).

In the following catalogue of characters, states believed to be primitive are all identified with a "0"; states believed to be derived are designated by positive integers. Derived states recognized exclusively for evermannellid species are identified by the prefix "E." In attempting to determine "derivativeness" I follow criteria established by Marx & Rabb (1972, pp. 5, 6), relying most heavily on the following criteria: (1) uniqueness and (2) relative abundance. Assignment of character states to OTU's in Table 8 was based in part on the assumption that possession by one or more representatives of a particular OTU of a state considered primitive indicates (except where contrary evidence can be cited) the primi-

TABLE 7. Listing of cleared and stained material.

Anotopteridae	
Anotopterus pharao	SIO 62-775, 1 (182.0)
Aulopidae	
Hime japonica	FMNH 71831, 1 (162.5)
Chlorophthalmidae	
Chlorophthalmus agassizi	FMNH 67116, 1 (100.2)
Chlorophthalmus agassizi	FMNH 67131, 1 (80.2)
Chlorophthalmus brasiliensis	FMNH 67135, 1 (99.5)
Parasudis truculentus	FMNH 67150, 1 (120.2)
Parasudis truculentus	FMNH 67156, 1 (87.5)
Evermannellidae	
Coccorella atlantica	SIO 68-476, 1 (76.0)
Coccorella atlantica	UH 71-3-8, 1 (93.3)
Coccorella atrata	SIO 68-533, 1 (99.6)
Evermannella ahlstromi	LACM 30413, 2 (55.2–56.1)
Evermannella balbo	ISH 546/73, 4 (93.1–102.0)
Evermannella indica	FMNH 49876, 1 (73.5)
Evermannella indica	UH 70-9-24, 1 (99.8)
Evermannella indica	UH 70-12-31, 1 (108.8)
Evermannella indica	UH 71-3-9, 1 (104.5)
Odontostomops normalops	ISH 2270/71, 1 (111.5)
Odontostomops normalops	SIO 68-447, 1 (78.7)
Odontostomops normalops	UH 70-7-1, 1 (86.6)
Harpodontidae	
Harpodon nehereus	FMNH 80818, 2 (126.9–159.5)
Harpodon squamosus	FMNH 80828, 2 (116.1–118.5)
Saurida brasiliensis	FMNH 64810, 1 (84.0)
Saurida brasiliensis	FMNH 76945, 1 (93.1)
Myctophidae	
Myctophum nitidulum	FMNH 59974, 1 (68.9)
Neoscopelidae	
Neoscopelus microchir	FMNH 66741, 1 (77.0)
Notosudidae	
Scopelosaurus sp.	RHB 2902, 2 (71.1–74.6)
Scopelosaurus sp.	SIO 70-326, 1 (73.0)
Omosudidae	
Omosudis lowei	SIO 60-229, 1 (105.0)
Paralepididae	
Macroparalepis sp.	FMNH 49988, 1 (190.0)
Notolepis sp.	SIO 64-554, 1 (132.1)
Paralepis sp.	SIO 61-39, 1 (103.0)
Scopelarchidae	
Benthalbella dentata	SIO 63-379, 1 (118.0)
Benthalbella dentata	SIO 70-19, 1 (203.0)
Benthalbella elongata	USC-E 1392, 1 (126.1)
Benthalbella infans	UH 70-9-15, 1 (95.6)
Benthalbella macropinna	USC-E 1671, 1 (113.5)
Rosenblattichthys alatus	SIO, uncat., CATO II, tow 143, 1 (77.5)
Rosenblattichthys volucris	LACM 9806, 1 (103.5)
Scopelarchoides danae	SIO 61-584, 1 (89.1)
Scopelarchoides danae	SIO 69-20, 1 (63.3)
Scopelarchoides nicholsi	SIO 65-243, 1 (103.2)
Scopelarchoides signifer	ORSTOM CY V-2, 1 (104.6)
Scopelarchoides signifer	SIO 68-534, 1 (70.0)
Scopelarchus analis	UH 70-9-12, 1 (95.0)
Scopelarchus guentheri	SIO 69-21, 1 (112.4)
Scopelarchus michaelsarsi	UH 70-9-9, 1 (68.0)
Synodontidae	
Synodus intermedius	FMNH 62029, 1 (108.2)
Trachinocephalus myops	FMNH 45392, 1 (81.1)

tiveness of that state for that OTU. This simplifying assumption was necessary due to inadequacy of survey for many characters for certain speciose families (e.g., Myctophidae, Paralepididae) and also to lack of material of seemingly critical taxa (e.g., *Bathysauropsis, Bathysaurus*).

1. Eye Morphology.—Among iniomous fishes the evermannellids (except *Odontostomops*) and scopelarchids are unique in possessing dorsally directed tubular eyes. Anteriorly directed tubular eyes are present in giganturids, a group included by Rosen (1973) among aulopiform(R) fishes but not treated in this paper. Dorsally directed semitubular eyes are present in *Protomyctophum* (*Hierops*) spp. (Myctophidae, see Wisner, 1976, p. 18).

(A) States Recognized for Iniomous Fishes

(0) = Eyes not tubular.

(1) = Eyes tubular, directed dorsad, large to extremely large, provided with a transparent (in life) lens pad, with division of the retina into an optically adjusted main retina and a nonadjusted accessory retina.

It should be emphasized that state (0) incorporates (artifically) an enormous range of variation in eye morphology, from *Aulopus* to *Chlorophthalmus* to *Ipnops*. It should also be noted that the family Scopelarchidae is unique in that all species exhibit state (1).

Fundamental to my interpretation of evermannellid interrelationships, whether among evermannellid species or between iniomous families, is my belief that the semitubular or tubular eyes of *Coccorella* and *Evermannella*, respectively, represent synapomorphous features, indicating sister-group relationship for these two genera and implying convergent and independent acquisition of tubular eyes by the Evermannellidae and Scopelarchidae. Marshall (1971, p. 42) lists 11 mesopelagic families (including the scopelarchids and evermannellids) that have ". . . independently acquired . . . tubular eyes, each fully stopped by a relatively large lens, and with the two main axes virtually parallel."

My belief that the "normal" laterally directed eyes of *Odontostomops normalops* represent the primitive state for this character in the family Evermannellidae is based on the intuitively appealing notion that reversal from the tubular-eyed state[2] to the "normal" laterally directed state is less likely than the presumably sequential acquisition of binocularity implied by relationships postulated herein. Evidence is needed to support this notion. Such evidence as exists is found in Munk's (1965, 1966) work on the ocular morphology of *Omosudis* and certain evermannellids and scopelarchids. Munk (1966) lists the following points of similarity between the nontubular eyes of *Omosudis* and the fully tubular eyes of *Evermannella:* (1) retina composed almost entirely of cones (*Omosudis*) or highly modified cones (*Evermannella*)[3]; (2) presence in *Omosudis* (as in all evermannellids) of an adipose eyelid pierced by a small (*Odontostomops*) to moderately sized (*Omosudis, Coccorella*) to large (*Evermannella*) pore; (3) correspondence in position between ventral portion of retina in *Omosudis* vs. main retina of *Evermannella*. As

[2]With concomitant changes in skull morphology (fig. 9); number and arrangement of cephalic laterosensory pores (fig. 1, table 1); development of the lens pad; increased size of aperture in the adipose eyelid; and, presumably (see discussion of "Vision" in preceding section), in behavior relating to detection and capture of prey (see Marshall, 1971, p. 44).

[3]Scopelarchids possess the pure-rod retina typical for midwater fishes (see Munk, 1966; Marshall, 1971).

TABLE 8. Character state by OTU matrix for 15 groups of iniomous fishes. Characters and character states are defined and discussed in the text. States considered primitive are denoted by "0"; states considered derived are denoted by positive integers; states presumed for inadequately known taxa are prefixed "?."

	Groups														
Character	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**
1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
3	2	0	0	2	2	2	2	2	2	2	2	2	2	2	2
4	0	0	0	0	0	0	0	0	0	0	0	3	3	3	3
5	0	0	0	0	0	0	0	0	0	0	0	0	5	5	4
6	0	0	0	6	6	6	6	0	0	6	6	6	6	6	6
8	0	7	7	7	0	0	0	9	9	8	8	?8	7	8	8
11	0	0	0	0	0	0	0	0	0	0	0	0	10	10	0
12	0	12	12	11	11	11	11	0	0	0	11	11	11	11	11
13	0	14	13	0	0	0	0	0	0	0	0	15	0	0	0
15	0	0	0	0	16	0	?0	0	0	?0	0	16	16	16	0
16	0	0	?0	0	0	0	?0	0	0	?0	17	17	?17	17	17
19	0	18	0	0	0	0	?0	0	0	?0	18	18	?18	18	18
20	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	?0	0	0	?0	20	20	20	20	20
22	0	21	21	0	0	0	?0	0	0	?0	0	21	21	21	0
23	0	0	0	22	0	0	?0	0	0	?0	23	0	?23	23	23
24	0	0	0	0	0	0	0	0	0	0	24	24	0	0	0
25	0	0	0	0	0	0	0	25	27	26	0	0	0	0	0
29	0	0	0	0	28	0	0	28	28	28	28	28	28	28	28

30	0	0	0	0	0	0	0	0	0	0	0	29	0	29	29
31	0	30	30	0	0	0	0	0	30	?0	0	30	30	0	0
32	0	0	0	0	0	0	31	31	0	?0	31	31	31	31	31
33	0	0	0	0	0	0	0	0	0	?0	0	32	0	0	0
34	0	0	33	0	0	0	0	0	33	?0	0	33	33	33	0
35	0	35	35	0	0	0	0	34	34	0	34	34	34	34	34
37	0	0	0	36	0	36	?0	0	0	?0	36	36	36	36	36
38	0	0	0	0	0	0	0	0	0	?0	0	37	37	37	37
39	0	0	38	0	0	0	?0	0	0	?0	0	0	0	0	0
40	0	39	0	0	39	39	39	0	0	0	0	0	0	0	0
41	0	0	0	40	0	0	40	0	0	0	40	40	?40	40	40
43	0	0	0	0	0	0	0	0	0	0	0	42	42	42	0
44	0	0	43	0	43	0	0	0	0	?0	0	0	43	0	0
45	0	0	0	0	0	0	0	44	44	0	0	44	44	44	44
46	0	0	0	0	0	0	0	0	0	0	0	0	45	45	0
47	0	0	0	0	46	0	0	0	0	0	0	0	0	0	46
49	0	47	47	0	0	0	0	0	0	0	0	0	0	0	0

KEY to groups (completely defined in text): 01=Aulopidae, 02=Neoscopelidae, 03=Myctophidae, 04=Notosudidae, 05=Scopelarchidae, 06=Chlorophthalmidae, 07=Ipnopidae, 08=Harpadontidae, 09=Synodontidae, 10=Bathysauridae, 11=Paralepididae, 12=Anotopteridae, 13=Alepisauridae, 14=Omosudidae, 15=Evermannellidae.

noted above (section on "Vision"), a critical detailed histological study of the eye of *Odontostomops* is lacking.

If Munk's (1965, 1966) interpretations are correct, the nontubular eye of *Odontostomops* and the semitubular eye of *Coccorella* represent logically ideal stages in the development of the fully tubular eyes of *Evermannella*. This by no means implies that I regard the extant species *Omosudis lowei* as directly ancestral to the evermannellids. I regard trends in certain other characters (e.g., narrowing of the interorbital region of the frontals, increase in size of aperture in adipose eyelid, development of distinct lens pad, etc.) as functionally related to the development of tubular eyes and list them in the definition of character states to follow. Three states of character 1 are recognized for species of evermannellids (fig. 3).

(B) States Recognized for Evermannellid Species

(0) = Eyes "normal," directed laterally, relatively small (horizontal eye diameter 2.7% to 4.2% SL, vertical eye diameter 2.8% to 4.0% SL), lacking lens pad, diameter of aperture in adipose eyelid less than diameter of lens, interorbital relatively broad (3.6% to 5.2% SL).

(E1) = Eyes semitubular, directed dorsolaterally, relatively large (horizontal eye diameter 4.0% to 6.5% SL, vertical eye diameter 4.2% to 7.6% SL), lens pad present in postmetamorphic specimens less than ca. 70 mm SL (becoming indistinct in larger adults), diameter of aperture in adipose eyelid only slightly greater than diameter of lens, interorbital relatively broad (3.2% to 6.1% SL).

(E2) = Eyes tubular, directed dorsad and slightly anteriad, large to extremely large (horizontal eye diameter 4.9% to 9.3% SL, vertical eye diameter 5.9% to 11.0% SL), lens pad present in all postmetamorphic individuals, diameter of aperture in adipose eyelid considerably broader than diameter of lens, interorbital narrow to extremely narrow (0.4% to 2.6% SL).

Hypothesized character-state sequence: 0 → E1 → E2

2. Lateral Division of Musculature—Evermannellids are apparently unique among iniomous fishes in possessing a complete, externally visible, tripartite division of the tail musculature such that the epaxialis and hypaxialis muscle masses are completely separated by an enlarged lateralis superficialis muscle (fig. 8; see discussion under Size and Habits). Due to inadequate survey for states of this character among iniomous fishes, I choose not to formally define states of character 2 in this paper.

3. Swimbladder.—According to Marshall (1954, p. 323; 1960, p. 54) and Marshall & Staiger (1975, p. 110), the only iniomous fishes retaining a swimbladder are the neoscopelids *Neoscopelus* and *Solivomer* and the lantern fishes (Myctophidae).[4] The absence of a swimbladder, clearly a derivative feature, is thus characteristic of aulopiform(R) fishes.

Rosen (1973, p. 452) states that the swimbladder and gas glands of neoscopelids and myctophids are of the advanced "acanthopterygian type," thus supposedly bolstering his argument for inclusion of his Myctophiformes(R) with

[4]Anderson et al. (1966, p. 31) state that the swimbladder is "small or absent" in synodontids(G) but provide neither details nor documentation.

"higher" neoteleosts (Paracanthopterygii + Acanthopterygii). Information presented by Marshall (1960, pp. 54, 55) and Marshall & Staiger (1975, p. 109) raises doubts about the "advanced" nature of the swimbladder of neoscopelids. For the time being two states of character 3 are recognized for iniomous fishes. There is no variation in this character among evermannellids (which lack a swimbladder).

(A) States Recognized for Iniomous Fishes

(0) = Swimbladder present.
(2) = Swimbladder absent.

4. Squammation.—Four iniomous families (Alepisauridae, Anotopteridae, Evermannellidae, and Omosudidae) have completely lost all body scales. Among paralepidids, only members of the Tribe Paralepidini possess body scales. Primitively, at least, in all other iniomous families the body and postorbital regions of the head are covered with scales. Rosen (1973, p. 506) argues that the presence of ctenoid scales in some myctophids (four species of *Myctophum* [Nafpaktitis et al., 1977], *Notoscopelus japonicus* [Tanaka, 1908] [see Nafpaktitis, 1975]) distinguishes the Myctophiformes(R) from the Aulopiformes(R) and allies the former with higher neoteleosts (Paracanthopterygii + Acanthopterygii). The possession of ctenoid scales by species in other iniomous families (including the Aulopidae [Mead, 1966a, p. 20], Chlorophthalmidae [Mead, 1966e, p. 162], and the Cretaceous Sardinioididae [Goody, 1969, p. 160]) offers little support for Rosen's conclusion.

Given the strong possibility for convergent reduction or loss of body scales among the five alepisauroid families listed, the possession of "normal" cycloid scales distributed over the entire body in scopelarchids (not to mention myctophids and notosudids) as in benthonic inioms leads me to recognize two states of character 4 among iniomous fishes.

(A) States Recognized for Iniomous Fishes

(0) = Body and (typically) postorbital regions of head bearing scales.
(3) = Scales or scalelike structures absent or, if present, limited entirely to association with the lateral line.

5. Lateral Line Scales—Distinctive lateral line scales that are highly modified relative to adjacent body scales are found in representatives of many iniomous families. Typically, such scales are larger than the adjacent body scales and each (except the posteriormost) consists of a bony plate, pierced by a central pore, the latter covered or partly so by a bony shelf or tympanum (see Johnson, 1974c, p. 15). Among scopelarchids, the shape and size of these components differs between species such that in combination the lateral-line-scale conformation is distinctive for each known scopelarchid species (Johnson, 1974c, p. 21). Marshall & Staiger (1975) conducted a limited survey of lateral line scale and associated laterosensory organ morphology among iniomous families. They conclude that an "aulopoid" lineage, comprised of the families Aulopidae, Chlorophthalmidae, Neoscopelidae, and Ipnopidae (including Bathypteroidae), can be distinguished by the presence of free-ending laterosensory organs on the lateral line scales. These organs are innervated by bilateral nerves emerging from the main lateral line nerve (see Marshall & Staiger, 1975, p. 109). Such a system is probably also present in the Scopelarchidae and Paralepididae and may be present, in

highly modified form, in the Evermannellidae. It is certainly lacking in the Alepisauridae and Omosudidae (which lack lateral line scales), is probably lacking in the Anotopteridae (see Rofen, 1966c, p. 506), and, according to Marshall & Staiger (1975, p. 109), free-ending organs on the trunk and tail are absent in *Bathysaurus*, synodontids, harpadontids, and myctophids. Based on the taxonomic distribution of such organs, I suspect that the presence of these free-ending, lateral-line-scale-associated organs is primitive for iniomous fishes. This is the reverse of the character-state sequence implied by the discussion of Marshall & Staiger. I have not, however, conducted an adequate survey for the presence or absence of such organs among iniomous fishes and choose not to distinguish character states relating to their presence at this time.

The total lack of scales or ossified, scalelike structures associated with the lateral line (in all included species) is apparently unique to three iniomous families (Alepisauridae, Evermannellidae, Omosudidae). State (4) represents a possible morphological intermediate between state (0) and state (5), and thus three states of character 5 are tentatively recognized among iniomous fishes.

(A) States Recognized for Iniomous Fishes

(0) = Scales or ossified scalelike structures associated with the lateral line.

(4) = Scales absent; a series of membranous, nonossified, shieldlike structures (see Rofen, 1966d, p. 523) segmentally arranged along the lateral line.

(5) = No scales or scalelike structures are associated with the lateral line (which is present, at least in young stages; Rofen, 1966b, p. 467; Gibbs & Wilimovsky, 1966, p. 483).

Hypothesized character-state sequence: 0 → 4 → 5

Evermannellids lack normal scales, but most evermannellid species have a series of membranous, nonossified shieldlike structures segmentally arranged along the lateral line. The three genera of evermannellids differ in the *maximum* observed posterior extent of lateral line segments and in the *maximum* observed number of lateral line segments (both features vary ontogenetically). State (E3) represents a possible morphological intermediate between state (0) and (E4).

(B) States Recognized for Evermannellid Species

(0) = Lateral line present, extending (maximally) to a vertical through middle of anal-fin base and composed of up to 43 segments.

(E3) = Lateral line present, extending (maximally) to a vertical through anterior one-third of anal-fin base and composed of 34 or fewer segments (34 or fewer in *Coccorella atlantica;* 30 or fewer in *C. atrata*).

(E4) = Lateral line present or (possibly) absent (*Evermannella ahlstromi*), extending (maximally) to a vertical through a point just posterior to pelvic-fin base and containing no more than 18 segments.

Hypothesized character-state sequence: 0 → E3 → E4

6. Mode of Reproduction.—Gonochorism is presumably the primitive mode of reproduction among iniomous fishes and is found in aulopids (Mead, 1966a), synodontids and harpadontids (Sulak, 1977), neoscopelids (Nafpaktitis, 1977), and myctophids (Nafpaktitis et al., 1977). Synchronous hermaphroditism is universal among the abyssal-benthic families Bathysauridae (Gosline et al., 1966), Ipnopidae (Mead et al., 1964; Mead, 1966b; Nielsen, 1966; Sulak, 1977) and

among the Chlorophthalmidae (Mead, 1966e), Scopelarchidae, and the alepisauroids (Johnson, 1974c). If Sulak's (1977) interpretation of the relationships of *Bathysaurus* is correct, the monoecious state characterizing this genus may have been acquired independently. Two states of character 6 are recognized among iniomous fishes. All evermannellids are synchronous hermaphrodites (Herring, 1977).

(A) States Recognized for Iniomous Fishes

(0) = Species are dioecious.
(6) = Species are monoecious.

7. Pyloric Caecum.—Pyloric caeca are present in chlorophthalmids (including *Bathysauropsis*), ipnopids, and notosudids (Nielsen, 1966; Bertelsen et al., 1976; Sulak, 1977). Most other iniomous families have been inadequately surveyed for this character. As far as is known (Wassersug & Johnson, 1976), pyloric caeca are absent in scopelarchids and in all alepisauroids except species in the genus *Coccorella*. Thus, although the presence of pyloric caeca may (or may not, see Qureshi, 1966, for comments on the "plasticity" of pyloric caeca among teleosts) be primitive for iniomous fishes, the presence of a pyloric caecum is here presumed to be derivative for evermannellids. This conclusion is reinforced by the fact that the pyloric caecum in *Coccorella* (Wassersug & Johnson, 1976; Herring, 1977) exhibits a conformation that may be unique among teleosts.

(B) States Recognized for Evermannellid Species

(0) = Pyloric caeca absent.
(E5) = A single pyloric caecum present as a narrow elongate structure extending into the head and easily visible in the floor of the orobranchial cavity as a distinct tubelike structure beneath the basibranchial series.

8. Peritoneal Pigment Sections.—I believe it likely that the development of discrete peritoneal pigment sections (see section on Larval Characters, fig. 4; Johnson, 1974c, pp. 23, 24; Okiyama, 1974, pp. 618–620) in larval inioms will prove of great importance to the satisfactory definition of myctophiform or aulopiform (*sensu* Rosen, 1973) fishes. The pigment sections are striking features of the larval morphology of most aulopiform(R) fishes, and this is certainly true for both evermannellids and scopelarchids. The function of these pigment sections is unknown—Okiyama (1974, p. 619) suggests a possible correlation with the loss of the swimbladder.

A single dorsomedial section is found in larval aulopids (*Hime* only, see Okiyama, 1974, p. 610), chlorophthalmids (Tåning, 1918; Ahlstrom, 1971), ipnopids (*Bathytyphlops*, see Okiyama, 1972), and (primitively) scopelarchids (Johnson, 1974c, pp. 206, 207). Multiple (three or more, serially arranged, paired or unpaired) peritoneal pigment sections occur in aulopids (*Aulopus*, see Okiyama, 1974, p. 611), bathysaurids (Johnson, 1974b), synodontids and harpadontids (Gibbs, 1959; Anderson et al., 1966; Okiyama, 1974), paralepidids (Rofen, 1966a), *Omosudis* (Rofen, 1966b), and evermannellids (state unknown in *Anotopterus*). Larvae of certain scopelarchids (*Scopelarchoides danae, S. nicholsi, Scopelarchus* spp.) exhibit three peritoneal pigment sections, but it seems certain that the unique unpaired and paired conformation of these sections is autapomorphous for this scopelarchid lineage only (see Johnson, 1974c, pp. 23,

206). The peritoneal pigment sections are paired in the harpadontids and synodontids (Anderson et al., 1966; Okiyama, 1974, pers. obs.) but single (connected dorsomedially over the gut, see fig. 4) in the others. If, as Rosen (1973, pp. 438–441) suggests, giganturids are allied with synodontoids, they (giganturids) are unique among synodontoids in apparently lacking any peritoneal pigment sections (Tucker, 1954). Discrete peritoneal pigment sections are lacking in notosudids (Bertelsen et al., 1976), at least some ipnopids (Okiyama, 1974, p. 614), and in all known neoscopelid and myctophid larvae (Moser & Ahlstrom, 1970, 1972; Okiyama, 1974; Yefremenko, 1977). Whether the ". . . elliptical shield of melanophores [lying] above the developing gas bladder . . ." in such forms as *Scopelopsis multipunctatus* (quotation from Moser & Ahlstrom, 1972, p. 547) is homologous to aulopiform(R) peritoneal pigment sections is unknown, but here the presumption is that it is not. According to Rofen (1966b), peritoneal pigment sections in larvae of *Alepisaurus* are lacking or indistinct. I examined larvae of *Alepisaurus* taken off Hawaii and found no discrete peritoneal pigment sections, although I found ample pigmentation completely enclosing the gut in larger larvae and junveniles (as in adults, see Gibbs 1960).

Based on the above information and following Okiyama (1974), I regard the presence of a single, dorsomedial peritoneal pigment section as primitive for iniomous fishes.

(A) States Recognized for Iniomous Fishes

(7) = Peritoneal pigment sections absent.
(0) = A single, dorsomedial peritoneal pigment section.
(8) = Multiple (3 or more), serially arranged, *unpaired* peritoneal pigment sections.
(9) = Multiple (3 or more), serially arranged, *paired* peritoneal pigment sections.

Hypothesized character-state sequence: 7 ← 0 → 8 → 9 (*Alepisaurus*)

Three peritoneal pigment sections are found in larvae of *Coccorella* and *Evermannella* (figs. 4–7), *Omosudis* (Rofen, 1966b, p. 472), and the paralepidine barracudina *Paralepis atlantica*, characterized by Rofen (1966a, p. 238) as ". . . the most primitive species in the Paralepididae." Larvae of *Odontostomops normalops* exhibit 12 or more unpaired peritoneal pigment sections—a state regarded herein as autapomorphous.

(B) States Recognized for Evermannellid Species

(0) = Larvae with three unpaired peritoneal pigment sections.
(E6) = Larvae with 12 or more unpaired peritoneal pigment sections.

9. Accessory Pigment Spots or Areas.—Johnson (1974c, p. 207) notes the presence of deep-lying pigment spots or areas in larval chlorophthalmids, paralepidids, and scopelarchids. Such accessory pigment spots or areas occur widely in larval inioms (aulopids, alepisaurids, myctophids, ?neoscopelids, notosudids, and synodontoids) and are of great diagnostic value at the species level for some groups (e.g., Gibbs, 1959; Moser & Ahlstrom, 1972; Anderson et al., 1966; Johnson, 1974c). Discrete accessory pigment spots or areas, such as

described by Johnson (1974c) for some scopelarchid species are lacking in evermannellids, *Omosudis*, and at least some ipnopids (*Bathytyphlops*, see Okiyama, 1972). Evermannellids have a distinctive larval-phase pigmentation described above (see Larval Characters). The survey of iniomous larvae is by no means complete enough to justify recognition of character states at this time, but I believe that the presence and conformation of accessory pigment spots and areas will (when known) provide valuable systematic information not only at the species but also at higher-category levels.

10. Juvenile-Phase Pigmentation.—The major pattern of body pigmentation in evermannellid larvae occurs in two phases—a larval phase (fig. 5) and a juvenile phase (figs. 6, 7)—with a gradual transition between the two phases (see Larval Characters). The juvenile-phase pigmentation of *Evermannella* larvae is characterized by the development of three rows of very large melanophores, each row associated with one of the three main divisions of the tail musculature. I regard the fixation of this pattern in *Evermannella* as indicative of relationship between the four species comprising this genus. The juvenile-phase pigmentation in *Odontostomops* (figs. 6, 7) is characterized by the development of numerous fine melanophores generally distributed over the head and body. The juvenile-phase pigmentation in *Coccorella* (figs, 6, 7) is intermediate in state, with larger, more prominent melanophores than seen in *Odontostomops*, but the developing melanophores are smaller, much more numerous, and not arranged in rows as in *Evermannella*. For the present I recognize two states of character 10 among evermannellids.

(B) States Recognized for Evermannellid Species

(E7) = Juvenile-phase pigmentation characterized by the development of three distinct rows of very large melanophores, each row associated with one of the three main divisions of the tail musculature (figs. 6–8).

(0) = Juvenile-phase pigmentation not as described above.

11. Stomach Pigmentation in Juveniles.—According to Wassersug & Johnson (1976, p. 280), juveniles of *Alepisaurus* and *Omosudis* differ from scopelarchids and other alepisauroids in two aspects of gut morphology: (1) the stomach is thin-walled and balloon-like, not the heavily muscularized sac characteristic of scopelarchids and other alepisauroids, (2) the stomach wall is densely pigmented, and this pigment appears before or coincident with but independent from the development of peritoneal pigment sections (such sections are present in *Omosudis*, apparently absent in *Alepisaurus*). Wassersug & Johnson examined only juvenile (less than 100 mm SL) specimens of *Alepisaurus* and *Omosudis*. Gibbs (1960, p. 4) describes the stomach in adult *Alepisaurus brevirostris* as follows, "Stomach black, highly distensible, forming a long blind sac." According to Gibbs' description, the pigmentation of the stomach is distinct from the well-developed peritoneal pigmentation. Wassersug & Johnson (1976) conducted a limited survey of other iniomous fishes (*Chlorophthalmus, Parasudis, Harpadon*) and report a stomach/pigment conformation similar to that seen in scopelarchids and alepisauroids other than *Alepisaurus* and *Omosudis* (i.e., thick-walled, heavily-muscularized, unpigmented). State (10), described below, is apparently unique to *Alepisaurus* and *Omosudis*, although my survey of iniomous taxa for this character is far from thorough.

(A) States Recognized for Iniomous Fishes

(10) = Stomach large, a highly distensible blind sac, thin-walled, not heavily muscularized; stomach wall densely pigmented, the pigmentation appearing (in ontogeny) independent of any peritoneal pigmentation.

(0) = Stomach/pigment conformation not as described above.

MERISTIC CHARACTERS: VARIATION AMONG INIOMOUS FISHES

Values for meristic characters differ strikingly between various iniomous families (table 9) and are of great value in writing diagnoses for individual families. For the most part, however, intrafamilial variation results in extensive overlap between families, making difficult or impossible the meaningful definition of separate character states and the determination of character-state sequence. In certain cases, where both state and probable sequence can be determined (e.g., the unique lack of a dorsal fin in *Anotopterus*, the uniquely high dorsal-fin ray count in alepisaurids), the derived states are evident autapomorphies, of no readily discernible value to the attempt to infer relationship among iniomous families. The same statement can probably be made in the case of the very low dorsal-fin ray count exhibited by scopelarchids (table 9), although this distinction is masked to some extent by overlap.

12. Number and Distribution of Branchiostegal Rays.—McAllister (1968, pp. 89, 90) recognizes three character states among iniomous fishes with respect to number and distribution of branchiostegal rays. My redefinition of these states includes data presented in Table 9.

(A) States Recognized for Iniomous Fishes

(0) = Branchiostegal rays numerous (12 or more), lacking the 4 + X pattern (McAllister, 1968), with 6 to 9 branchiostegal rays on the epihyal (see Rosen & Patterson, 1969, p. 452).

(11) = Branchiostegal rays fewer (7 to 14, usually 8 to 10), with the 4 + X pattern, with 3 to 5 (usually 4) branchiostegal rays on the epihyal (see Rosen & Patterson, 1969, p. 452).

(12) = Branchiostegal rays fewer (6 to 12, usually 7 to 11), with the 4 + X pattern, but with only two branchiostegal rays on the epihyal (see Paxton, 1972, p. 25).

Hypothesized character-state sequence: 0 → 11 → 12

Sulak (1977, pp. 53, 54) states that a high number of branchiostegal rays is primitive for iniomous fishes. Paxton (1972, p. 56) notes that the presence of only two branchiostegal rays on the epihyal is an advanced neoteleost characteristic distinguishing the myctophids and neoscopelids from all other inioms.

All evermannellids have eight branchiostegal rays. The anteriormost epihyal branchiostegal inserts at the ceratohyal-epihyal joint in *Coccorella* and *Odontostomops* and posterior to this joint in *Evermannella* (fig. 13).

13. Number of Vertebrae.—Vertebral number is quite variable among iniomous fishes (reported range 28 to 121, table 9).[5] In the definition of character

[5]The reported extreme is ca. 186 vertebrae in *Polymerichthys nagurai* Uyeno, 1967 (Polymerichthyidae), a species known from one specimen from the Middle Miocene Tubozawa Formation of Japan. Uyeno (1967) allied *Polymerichthys* with *Anotopterus* princi-

TABLE 9. Comparison of selected meristic characters among iniomous fishes. Values given are ranges of values reported for the various groups.

Group	Dorsal	Anal	Pectoral	Pelvic	Caudal	Branchiostegal rays	Vertebrae
1	14–21	8–13	11–14	9	19	14–17	41–53
2	11–13	10–14	14–19	8	19	8–11	29–35
3	10–26	12–27	0–22[1]	8[2]	19	6–12[3]	28–45[4]
4	9–14	16–21	10–15	9	19	10[5]	43–67[6]
5	5–10	17–39	18–28	9	19	8	40–65
6	9–13	7–11	15–18	9	19	7–10	38–49
7	10	9	15–16	9	19	8	38
8	11	11	23–24	8	?19	9	58
9	8–16	7–19	10–21	7–9	19	10–14	49–80
10	9–14	9–14	11–14	9	19	13–17	49–56
11	10–14	14–16	11–13	8	19	12–18	56–61
12	15–18	11–14	15–17	8	19	8–12	50–63
13	8–12	20–34	9–17	9	19	8	60–90[7]
14	7–14	19–50	10–13	9–10	19	8	75–121
15	12–16	21–24	13–15	9	19	8	53–60
16	0	14–16	12–15	9–11	19	8	78–83
17	39–48	13–18	12–16	8–10	19	7[8]	50
18	9–12	14–16	11–13	8	19	8	39–41
19	10–13	26–37	11–13	9	19	8	45–54

KEY: Listed below are groups (corresponding to the group numbers in the left column) and references consulted in compiling meristic data for each group. (1) Aulopidae—Mead, 1966a; Rosen, 1971; Masuda et al., 1975; Sulak, 1977; (2) Neoscopelidae—Nafpaktitis, 1977; (3) Myctophidae—Paxton, 1972; Nafpaktitis, et al., 1977; (4) Notosudidae—Bertelsen et al., 1976; (5) Scopelarchidae—Johnson, 1974c; (6) *Chlorophthalmus*—Mead, 1966e; McAllister, 1968; Rosen, 1971; Sulak, 1977; (7) *Parasudis*—Mead, 1966e; (8) *Bathysauropsis*—Mead, 1966e; Sulak, 1977; (9) Ipnopidae (including Bathypteroidae)—Mead, 1966c, 1966d; McAllister, 1968; Rosen, 1971; Sulak, 1977; (10) *Saurida* and *Harpadon*—Anderson et al., 1966; Rosen, 1971; Sulak, 1977; (11) *Synodus* and *Trachinocephalus*—Anderson et al., 1966; Sulak, 1977; (12) *Bathysaurus*—Guenther, 1887; Mead, 1966b; Rosen, 1971; Johnson, 1974b; Sulak, 1977; (13) Paralepididae, Paralepidini—Rofen, 1966a; (14) Paralepididae, Lestidiini—Rofen, 1966a; (15) Paralepididae, Sudinae—Rofen, 1966a; (16) Anotopteridae—Rofen, 1966c; (17) Alepisauridae—Gibbs & Wilimovsky, 1966; (18) Omosudidae—Rofen, 1966b; (19) Evermannellidae—present study.

[1]Values of 10 to 17 are typical. [2]Except *Notolychnus* with 6 and *Gonichthys* which may have 7. [3]Values of 7 to 11 are typical. [4]Values of 30 to 40 are typical. [5]Range reported: 3–4 + 4–6. [6]Count includes first preural + first ural compound element. [7]Fossil species with as few as 45 (Harry, 1953; Rofen, 1966a). [8]Pers. obs.

states below I have followed techniques devised by Marx & Rabb (1972, pp. 54–62) for the analysis of continuous meristic characters. Due to enormous variation in number of species per taxon for the groups as listed in Table 9, I chose to apply the techniques of Marx & Rabb first to Paxton's (1972, p. 33) data for myctophid genera (reported range: 28–45). "Spans" of seven vertebrae or less characterized 90% of the myctophid genera, and 22 of 31 myctophid genera fall into the interval 35 to 41 vertebrae defined through a lower limit of 28 and a span of seven. Using this basis (span = 7, lower limit = 28), all iniomous taxa were assigned to one of four character states.

(A) States Recognized for Iniomous Fishes

Number of vertebrae:
(14) = 28 to 34
(13) = 35 to 41
(0) = 42 to 62
(15) = 63 to 121

Hypothesized character-state sequence: 14 ← 13 ← 0 → 15

Most iniomous families (all but two: Anotopteridae, Neoscopelidae) have some or all members that exhibit state (0) (see below and table 9), and on this basis I believe 42 to 62 vertebrae to be the primitive state. Due to large intrafamilial variation in some groups, e.g., Notosudidae (reported range: 43–67), Scopelarchidae (reported range: 40–65), Paralepididae (reported range: 53–121), there exists little basis for subdivision of states (0) or (15) at this time. The following notes explain the assignment of states to certain taxa in Table 8.

The character state (0) assigned to the Chlorophthalmidae is based on the total reported range of variation (38 to 58) for this family (including *Bathysauropsis*, *Chlorophthalmus*, and *Parasudis*). The high number of vertebrae (58) in *Bathysauropsis* parallels an apparent trend toward a higher number of vertebrae in ipnopids (49 to 80). The character state (13) assigned to the Myctophidae is based on the fact that 26 of 31 myctophid genera exhibit this state (22 genera) or a state intermediate between states (13) and (14) (four genera). None of the four genera (*Diogenichthys*, *Lepidophanes*, *Notolychnus*, *Triphoturus*) exhibiting state (14) or the single genus (*Gymnoscopelus* + *Nasolychnus*—regarded by Paxton, 1972, as only subgenerically distinct) exhibiting state (0) is noted by Paxton (1972) as basal or primitive within the family. Because only one genus, *Gymnoscopelus*, exhibits state (0), this is regarded as a reversal. Within the Ipnopidae, *Bathypterois* (reported range = 49–61) and *Ipnops* (reported range = 55–61) exhibit state (0), the genera *Bathymicrops* (reported range = 65–80, 65 to 69 in *B. regis*, 76 to 80 in *B. brevianalis*) and *Bathytyphlops* (62–67) exhibit state (15). It may well be that state (15) should be assigned to the Paralepididae—the low number of vertebrae in *Sudis* (reported range: 53–60) plus knowledge of fossil paralepidids with as few as 45 vertebrae (Rofen, 1966a, p. 208) resulted in the assignment of state (0) to this family.

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pally on the basis of similarities in the shape of the body and head and in the morphology of the palatine teeth. *Polymerichthys* differs from *Anotopterus* in having a well-developed, enormously elongate dorsal fin (300–350 dorsal-fin rays) and a much restricted, "almost vestigial" caudal fin. The apparently extinct Polymerichthyidae is not treated elsewhere in this paper.

There is an undoubted trend toward a greater number of vertebrae among some benthonic (ipnopids, synodontoids) and pelagic (e.g., Anotopteridae, Paralepididae) lineages. Evolution in the Scopelarchidae has apparently featured trends toward a higher number of vertebrae in the line leading to *Benthalbella* and a lower number of vertebrae in the line leading to *Scopelarchus* (Johnson, 1974c). The neoscopelids and myctophids are largely distinct from other iniomous fishes in having fewer vertebrae.

14. Frontal/Dermethmoid Contact.—Evermannellids differ strikingly from scopelarchids in the configuration of the frontal/dermethmoid contact zone. In evermannellids the dermethmoid exhibits two posteriorly directed projections (fig. 9) overlying the respective (right and left) anterior sheetlike portions of the frontals. In scopelarchids the anterior end of the frontals overlies the dermethmoid (Johnson, 1974c, p. 35). The state in *Omosudis* is like that in evermannellids. The state in *Alepisaurus* is unknown. Apparently other inioms are similar to scopelarchids with respect to this character (see Goody, 1969, p. 205; Bertelsen et al., 1976, p. 8), but the survey is too incomplete to justify formal recognition of character states and assignment of states to taxa at this time.

15. Parietals.—Evermannellids were said to be closely related to scopelarchids because parietal bones were said to be lacking in the two families ("parietals fused with frontals," see Gosline et al., 1966, p. 17). Actually this state is true for neither group. The parietals are present and do meet in midline (or very nearly so) in all evermannellids (fig. 9). Parietals are present but widely separated in most scopelarchids (Johnson, 1974c, p. 31). The presence of parietal bones that are in contact in dorsal midline is primitive for iniomous fishes (Goody, 1969; Sulak, 1977).

(A) States Recognized for Iniomous Fishes

(0) = Parietals present and in contact (or nearly so) in dorsal midline.
(16) = Parietals absent or when present are widely separated, not in contact in dorsal midline.

16. Attachment of Dermosphenotic.—In evermannellids the dermosphenotic (IO-8, fig. 10) is attached to the lateral face of the autosphenotic. In scopelarchids, as (apparently) in most iniomous fishes, the dermosphenotic overlies (is dorsal to) the autosphenotic.

(A) States Recognized for Iniomous Fishes

(0) = Dermosphenotic overlies (is dorsal to) the autosphenotic.
(17) = Dermosphenotic is attached to lateral or anterolateral face of autosphenotic.

17. Basisphenoid.—A basisphenoid bone is present in *Aulopus*, the Cretaceous *Sardinioides*, *Chlorophthalmus*, *Saurida*, *Omosudis*, and the presence of this bone is primitive for iniomous fishes (Goody, 1969). The bone has been lost, apparently independently, in a number of iniomous families (including all scopelarchids). Among evermannellids a narrow, splintlike basisphenoid is present in *Coccorella* and *Evermannella* but apparently absent in *Odontostomops*.

(B) States Recognized for Evermannellid Species

(0) = Basisphenoid present.
(E8) = Basisphenoid absent.

18. Orbitosphenoid and Ethmoid Cartilage—An orbitosphenoid bone is present in *Aulopus* and the Cretaceous *Sardinioides* and is apparently a primitive feature for iniomous fishes (Goody, 1969). I am unable to confirm the presence of an orbitosphenoid in any other extant iniom (neither scopelarchids nor evermannellids have it, but Regan [1911, p. 124] reports its presence in some synodontoids). Due to incompleteness of the survey of iniomous taxa for this character, I choose not to define formal states at this time.

A presumably neomorphous feature characteristic of the evermannellid genus *Coccorella* is a considerable rearward expansion of the ethmoid cartilage described in the states recognized below.

(B) States Recognized for Evermannellid Species

(0) = Ethmoid cartilage not entering orbit, not forming an orbital septum.
(E9) = Ethmoid cartilage considerably expanded posteriorly, forming an orbital septum between the eyes, extending to or nearly to midline in posterior wall of orbit.

19. Sclerotic Bones.—All scopelarchids possess two sclerotic bones (anterior and posterior), which are embedded in and which strengthen the tubular eye. Sclerotic bones are also present in aulopids (*Hime*), *Chlorophthalmus*, *Parasudis*, notosudids, and at least certain synodontoids (e.g., *Saurida*). Sclerotic bones are absent in evermannellids, and, as far as is known, in all other iniomous fishes. The presence of such elements in all three benthonic "lineages" (Sulak, 1977) suggests the presence of sclerotics may be primitive for iniomous fishes. Harder (1975, p. 345) notes the widespread (if sporadic) occurrence of scleral ossifications and suggests that presence or absence is a function of eye size. It may be worthwhile to note that the eyes of *Evermannella* spp. are (relative to body size) no smaller than those of scopelarchids, yet *Evermannella* spp. lack scleral ossifications.

(A) States Recognized for Iniomous Fishes

(0) = Sclerotic bones present.
(18) = Sclerotic bones absent.

20. Subocular Shelf.—According to Paxton (1972, p. 10), a subocular shelf extends medially from IO-3, IO-4, and usually IO-5 in all myctophids. The presence of a subocular shelf is an advanced neoteleost (acanthopterygian not paracanthopterygian) character (Smith & Bailey, 1962; Rosen & Patterson, 1969; Rosen, 1973; Zehren, 1975). A subocular shelf is not found in any other iniomous fish (including neoscopelids). Among other teleosts, a subocular shelf is known only from the osteoglossomorph genus *Notopteris* (Rosen & Patterson, 1969, p. 379).

(A) States Recognized for Iniomous Fishes

(0) = Subocular shelf absent.
(19) = Subocular shelf present.

21. Antorbitals—Reviews of the morphology of infraorbital bones in teleosts are provided by Smith & Bailey (1962), Gosline (1965), and Nelson (1969b). Nelson (1969b, pp. 2, 3) regards the presence of an antorbital followed by six infraorbitals as the primitive pattern for most or all major teleost groups, including iniomous fishes. Antorbitals are present in representatives of most iniomous families, including the basal scopelarchid genera *Scopelarchoides* and

Rosenblattichthys, as well as *Benthalbella macropinna* (Johnson, 1974c), but antorbitals apparently are lacking in all alepisauroid families. Paxton (1972, p. 9) describes an antorbital/nasal configuration unique to myctophids among iniomous fishes.

(A) States Recognized for Iniomous Fishes

(0) = Antorbitals present.
(20) = Antorbitals absent.

22. Supraorbitals.—In evermannellids the elements herein termed supraorbitals are elongate, strutlike bones (fig. 10), slightly expanded ventrally and noticeably expanded dorsally. These elements are termed supraorbitals (rather than antorbitals) because of their close abutment on and attachment to the dorsolateral ridge of the frontal (on each side). Supraorbitals have been lost, apparently in most cases independently, in many iniomous lineages, including the evermannellid genus *Odontostomops* and all scopelarchid genera except *Rosenblattichthys* (Johnson, 1974c, p. 36).

(A) States Recognized for Iniomous Fishes

(0) = Supraorbitals present.
(21) = Supraorbitals absent.

23. Infraorbital Series.—Most iniomous fishes, including aulopids, chlorophthalmids, myctophids, neoscopelids, and scopelarchids, have six infraorbitals—the primitive state for most or all major teleost groups (Nelson, 1969b). Notosudids apparently have seven infraorbitals (Bertelsen et al., 1976). Evermannellids, *Omosudis*, and paralepidids have eight infraorbitals.

(A) States Recognized for Iniomous Fishes

Number of infraorbitals:
(0) = 6
(22) = 7
(23) = 8

Hypothesized character-state sequence: (22) ← (0) → (23)

24. Premaxillary Fenestra.—Rosen (1973, p. 450) notes the presence of a peculiar fenestrated premaxilla in the Cretaceous fossil genera *Enchodus*, *Palaeolychus*, and *Eurypholis* (see Goody, 1969, p. 104). Rosen states that a premaxillary fenestra is present in and characteristic of the extant alepisauroid families Paralepididae (see Rofen, 1966a, p. 232), Omosudidae, and Alepisauridae. The fenestra is unquestionably present in paralepidids[6] and in *Anotopterus* (Goody, 1969, p. 171). According to Goody (1969, p. 172), the fenestra is not present in *Alepisaurus*, and I am unable to confirm its presence in *Omosudis*. It is absent in evermannellids and other iniomous fishes.

(A) States Recognized for Iniomous Fishes

(0) = Premaxillary unfenestrated.
(24) = Premaxillary fenestrated.

25. Modification of Maxilla.—According to Goody (1969), the following features of the upper jaw, as seen in *Aulopus* and the Cretaceous *Sardinioides*, are primitive for myctophiform fishes: (1) presence of two supramaxillae (in extant

[6]According to Harry (1953, p. 225), *Sudis* is unique among paralepidids in lacking a fenestrated premaxilla.

forms true only of aulopids and *Saurida*, in the latter the two supramaxillae are extremely reduced, see Sulak, 1977, p. 55), (2) maxilla long and narrow except posteriorly where it is dilated, (3) premaxilla with ascending and articular processes (see Rosen & Patterson, 1969, p. 457) and a very long alveolar arm. Sulak (1977) recognizes three "natural" groupings of benthonic inioms—the Aulopidae, a synodontoid lineage, and a chlorophthalmoid lineage. The chlorophthalmoid lineage (Chlorophthalmidae + Ipnopidae) is said (Sulak, 1977, p. 54) to have retained a more primitive configuration of the upper jaw, with a prominent maxilla that is dilated (deepened) and free posteriorly and a single elongate supramaxilla. According to Sulak, the synodontoid lineage (*Saurida* + *Harpodon*, *Bathysaurus*, *Synodus* + *Trachinocephalus*) is characterized by an upper jaw dominated by a strong premaxilla, with the maxilla reduced and variously modified (usually partly or wholly adherent to the premaxilla). These modifications were recognized by Sulak (1977) and in the present paper as three separate and presumably autapomorphic character states respectively defining the three main synodontoid lineages.

(A) States Recognized for Iniomous Fishes

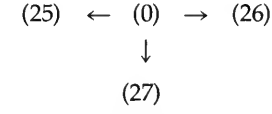
(25) = Maxilla separated into anterior and posterior portions; the posterior portion reduced to a thin, adherent lamina along the posterior half of the premaxilla; the anterior portion consisting of the isolated head of the maxilla, which lies between the palatine and premaxilla and retains its original articulating functions (*Saurida*, *Harpadon*—see Sulak, 1977, p. 55).

(26) = Maxilla undivided, present only as a short (less than 10% of premaxillary length in length), slender rudiment lying between the palatine and premaxillary heads (*Bathysaurus*—see Sulak, 1977, p. 58).

(27) = Maxilla undivided, about equal to premaxilla in length but reduced to a simple lamina that is closely adherent to the premaxilla and lacks a free articulating head anteriorly or a free and dilated expansion posteriorly (*Synodus* + *Trachinocephalus*—see Sulak, 1977, p. 58).

(0) = Maxilla not as described above.

Hypothesized character-state sequence:



It should be noted that state (0) includes additional states to be recognized in some future study of iniomous relationships, these states ranging from the basal (for inioms) configuration of upper jaw bones seen in aulopids, chlorophthalmids, neoscopelids, and scopelarchids (Rosen & Patterson, 1969; Johnson, 1974c) to highly derived states such as seen in *Anotopterus* (see Goody, 1969, p. 171) and *Omosudis*, in which the anterior maxilla is present as an extremely narrow, threadlike structure, lacking articulating processes. Incompleteness of information precludes subdivision of state (0) at this time.

26. Dentary Fossa.—The genus *Evermannella* is uniquely characterized among evermannellids, and, apparently, among iniomous fishes, by the presence of a vertically elongate fossa at the dentary symphysis. This fossa (fig. 11)

contains the anteriormost mandibular cephalic laterosensory pore of each side and also contains two to four vertically oriented rows of laterosensory papillae. The exact function—presumably sensory—of this structure is unknown. In *Odontostomops* and *Coccorella* an externally visible ridge marks the line of the dentary symphysis.

(B) States Recognized for Evermannellid Species

Dentary fossa (as described above):

(0) = Absent.
(E10) = Present.

27. Jaw and Palatine Teeth.—A character supposedly separating alepisauroids(G) from myctophoids(G) are uniserial premaxillary teeth in alepisauroids (true in all cases) vs. arranged in more than one row in myctophoids. The problem—as pointed out by Gosline et al. (1966, p. 8)—is separation of similarity due to relationship from similarity due to convergence. In some families in which premaxillary teeth usually occur in bands, there exist representatives with uniserial premaxillary teeth, e.g., *Parasudis* among the chlorophthalmids, the genera *Centrobranchus, Diogenichthys,* and *Gonichthys* among the myctophids (Gosline et al., 1966; Paxton, 1972).

In *Odontostomops* and *Evermannella,* as in all scopelarchids, the dentary teeth are arranged in two series, with an outer series of smaller teeth and an inner series of large, barbed fangs (Johnson, 1974c, p. 39). The arrangement of dentary teeth in two or more series occurs widely among iniomous fishes and is therefore taken as primitive. In *Odontostomops* and *Evermannella,* as in all scopelarchids, as well as many other inioms, at least the largest dentary and palatine teeth are barbed (fig. 11). Barbed teeth are present in some or all representatives of the following: Aulopidae, Myctophidae, Notosudidae, Paralepididae, synodontoids. Barbed teeth are absent in *Anotopterus, Alepisaurus,* and *Omosudis.*

In *Coccorella* neither dentary nor palatine teeth are barbed, the saber-like palatine fangs are greatly enlarged, and the dentary teeth are uniserial. I believe that in combination this suite of characters defines a derived state unique to *Coccorella* among evermannellids—a state possibly related to differences in prey and prey-capture style between *Coccorella* and other evermannellids (see Size and Habits).

(B) States Recognized for Evermannellid Species

(0) = Dentary teeth arranged in two series; at least some dentary and palatine fangs barbed; longest palatine tooth = 4.6% to 7.3% SL.
(E11) = Dentary teeth uniserial; dentary and palatine fangs not barbed but saber-like; longest palatine tooth = 7.1% to 10.0% SL.

28. Basihyal.—Scopelarchids and evermannellids differ strikingly in the development and configuration of the basihyal, basihyal toothplate, and basihyal dentition. In scopelarchids the basihyal is well ossified, the basihyal toothplate is (apparently) indistinguishably fused with the basihyal, and large, hooked basihyal teeth are present in all species (Johnson, 1974c, p. 48). In evermannellids the basihyal is much reduced (fig. 14), consisting of a rodlike structure that is only half-ossified (cartilaginous anteriorly) and is connected via a hingelike joint to the anterior margin of the first basibranchial. A distinct but edentate basihyal toothplate covers the basihyal except in *Coccorella* (see below).

A toothed basihyal is presumably primitive for iniomous fishes (Nelson, 1969a; Zehren, 1975) and occurs in aulopids, paralepidids, and all scopelarchids. More typical (apparently) for extant inioms is the presence of a basihyal (that is often cartilaginous or at least partly so) and an edentate basihyal toothplate (true for chlorophthalmids, myctophids, neoscopelids, notosudids, evermannellids). Both basihyal and basihyal toothplate are apparently lacking in *Anotopterus* and *Omosudis* (state unknown for *Alepisaurus*). I choose not to define formal states of character 28 for iniomous fishes at this time for two reasons: (1) the survey of iniomous taxa is insufficient for this character, and (2) the problem of how to treat groups such as chlorophthalmids (*Chlorophthalmus, Parasudis*) in which partly hooked and strongly developed basihyal teeth are present in larvae and juveniles (Rosen, 1971; pers. obs.) but are lost in adults.

The species of *Coccorella* differ from other evermannellids in the reduction (*C. atlantica*) or loss (*C. atrata*) of the basihyal toothplate as described in character states defined below. State (E12) is regarded as logically intermediate between states (0) and (E13).

(B) States Recognized for Evermannellid Species

(0) = Basihyal toothplate covers dorsal and dorsolateral margins of basihyal.

(E12) = Basihyal toothplate reduced, covering only posterior two-thirds of dorsal margin of basihyal.

(E13) = Basihyal toothplate absent.

Hypothesized character-state sequence: (0) → (E12) → (E13)

29. Gill Rakers.—Normal lath- or bladelike gill rakers occur in aulopids, chlorophthalmids, ipnopids, neoscopelids, notosudids, and most myctophids (all but *Centrobranchus*, Paxton, 1972, p. 24). Said by Sulak (1977, p. 53) to partly characterize the synodontoid lineage is modification of gill rakers into clusters of short gill teeth—a state that also characterizes the Paralepididae (Rofen, 1966a, p. 218) and Alepisauridae (Gibbs & Wilimovsky, 1966, p. 485: "Gill rakers with tufts of depressible filaments."). *Anotopterus* lacks both gill rakers and gill teeth (except for conical teeth limited to the fifth pharyngobranchial toothplate). In *Omosudis* the gill rakers are reduced to fixed individual short gill teeth (Rofen, 1966b, p. 463). In scopelarchids gill tooth plates replace gill rakers—the plates expanding with growth to form flattened plates of bone bearing one to many small teeth arranged in one to three rows on the dorsal margin of the plate. Similar gill tooth plates in evermannellids support one to several small teeth arranged uniserially, with gill teeth limited to the second gill arch. The possibility of convergent loss of lathlike gill rakers is discussed by Gosline et al. (1966, p. 12).

(A) States Recognized for Iniomous Fishes

(0) = "Normal" lath- or bladelike gill rakers present.

(28) = "Normal" lath- or bladelike gill rakers absent.

30. Distribution of Gill Teeth.—Evermannellids are apparently unique among inioms in the restriction of gill teeth (for the distinction between "gill teeth" vs. "conical teeth" see section on Branchial Arches above) to the ceratobranchial of the second gill arch. Other iniomous groups exhibiting a restricted distribution of gill teeth include *Anotopterus* (which lacks gill teeth) and *Omosudis* (in which gill teeth are restricted to the first and second arches). In at least some

representatives of all other iniomous families either gill rakers or gill teeth (or both) are found on all four gill arches (HB1 to 3, CB1 to 4 [in most, 1 to 5], EB1 to 4 [1 to 3 in scopelarchids and notosudids]).

(A) States Recognized for Iniomous Fishes

(0) = Gill rakers or gill teeth (or both) present on gill arches one to three (or on all four gill arches).

(29) = Gill rakers absent; gill teeth (if present) lacking on third and fourth gill arches.

UPPER BRANCHIAL TOOTHPLATES

Rosen (1973, pp. 406, 435) distinguishes (in part) his "alepisauroid" (= synodontoids + giganturids + alepisauroids) lineage from aulopoids(R) by listing the following characters as supposedly advanced features shared by alepisauroids(R):

(A) Loss of an independent fifth upper pharyngeal toothplate (PB5TP) with concomitant great enlargement of the fourth upper pharyngeal toothplate (PB4TP; the fourth pharyngobranchial [PB4] is cartilaginous in all iniomous fishes).

(B) Loss of the second upper pharyngeal toothplate (PB2TP).

(C) Loss of the third epibranchial toothplate (EB3TP).

(D) Frequent loss or reduction of the third upper pharyngeal toothplate (PB3TP).

(E) Confinement of the muscle retractor arcuum branchialum (RAB) to the PB4, the PB4TP, the PB5TP (see discussion of character 31 below), and (in some cases) to the distal half of the fourth epibranchial (EB4).

(F) Presence of relatively few fanglike teeth on the remaining (branchial) toothplates.

(G) "Alepisauroids exhibit an exaggeration of the principal epibranchial and pharyngobranchial specializations of aulopoids. All of the elements are greatly attenuated, seemingly in relation to the development of a very long jaw with an oblique suspensorium" (Rosen, 1973, p. 435).

(H) "The teeth of alepisauroids, both on the pharyngobranchials and on the jaws and palate, are much larger and fewer than those of aulopoids. They are often notched distally or bear scalpel-like tips" (Rosen, 1973, pp. 435, 436).

Feature (F) is actually true for virtually all inioms (one prominent exception being the scopelarchids in which some species have remarkably large teeth over the basibranchials). Feature (G) apparently relates to the marked prolongation of the uncinate process of the second epibranchial (EB2) discussed below (character 39). Feature (H) is only partly true, fewer and larger teeth are found in alepisauroids but not synodontoids (where, as Rosen, 1973, p. 436, points out, the state tends to be intermediate), and the dental configuration of alepisauroids is likely related to the common predaceous feeding mode of these fishes. Barbed teeth are neither unique to nor characteristic of all alepisauroids (see character 27). Features (A) through (E) are discussed in the following paragraphs.

31. Fourth and Fifth Upper Pharyngeal Toothplates.—Rosen (1973) considers the loss of an independent PB5TP (with concomitant enlargement of the PB4TP) to be characteristic of alepisauroid(R) fishes. In fact this supposed advanced feature is probably true of no iniomous fish. In scopelarchids, evermannellids, and most other inioms the fifth toothplate (see Nelson, 1969a, pp. 488–

490, for a discussion of the possible homologies of this element) is the most prominent (in terms of size of the toothplate, number of teeth, and size of teeth) and in some cases is the largest upper pharyngeal element (although in most inioms the PB3 is the largest upper pharyngeal element). Rosen (1973, p. 407) obviously did not see the small and easily missed PB4TP in his specimen of *Evermannella* sp. (a PB4TP is present in all evermannellids) and, as a result, identified the large PB5TP as the fourth. In evermannellids the PB4TP is quite small (fig. 15) and in one species (*Coccorella atrata*) is edentate (also true for *Notolepis* among the paralepidids). Although the PB4TP is somewhat larger (relative to the PB5TP) in scopelarchids (Johnson, 1974c, p. 49), the PB5TP is the largest and most prominent upper pharyngeal toothplate. Only one upper pharyngeal toothplate (either PB4TP or PB5TP or possibly a compound element) is present in this position in neoscopelids, myctophids, some synodontoids (*Synodus* and *Trachinocephalus*), *Anotopterus*, and *Alepisaurus*. In all of these cases I suspect that the single element present is the PB5TP—this based (a) on the trend toward reduction of the PB4TP as exhibited by evermannellids and certain paralepidids (e.g., *Paralepis*, *Notolepis*), and (b) on the relative size of the PB4TP vs. PB5TP in iniomous families that have both. Rosen (1973, pp. 453, 454, 506) argues that reduction of the posterior upper pharyngeal dentition (relative to the PB3TP) is an advanced feature separating myctophids and neoscopelids from other inioms and allying the Myctophiformes with higher neoteleosts. Yet Paxton (1972, p. 26), while noting that the PB3TP is larger than the "PB4TP" in most myctophids, states "However in *Protomyctophum*, *Hierops*, all *Electrona* (except *E. rissoi*), most *Diaphus*, and *Notolychnus*, the fourth [here interpreted as the fifth toothplate] is equal in size or larger than the third." Paxton (1972, p. 28) also notes that the ". . . fourth [here called fifth] . . . bears the largest and most posterior teeth in the oral cavity." I interpret these features as retention of the basal iniom state by the myctophid taxa listed and note that *Protomyctophum* is said (Paxton 1972, p. 63) ". . . to approach the most primitive adult condition in the tribe Myctophini and family."

(A) States Recognized for Iniomous Fishes

(0) = Both PB4TP and PB5TP are present.
(30) = Only one upper pharyngeal toothplate present in this position (here assumed to be the PB5TP).

Coccorella atrata is unique among evermannellids in that the PB4TP is edentate.

(B) States Recognized for Evermannellid Species

(0) = The PB4TP bears teeth.
(E14) = PB4TP is edentate.

32. Second Upper Pharyngeal Toothplate.—A PB2TP occurs in aulopids, chlorophthalmids, myctophids, neoscopelids, notosudids, some synodontoids (*Synodus*, see Rosen, 1973, p. 404), and scopelarchids (*Benthalbella elongata*, *B. infans*, *B. macropinna*, *Scopelarchoides signifer*). No alepisauroid is known to have a PB2TP (several gill toothplates are present on the PB2 of the specimen of *Notolepis* examined by me).

(A) States Recognized for Iniomous Fishes

Conical teeth on PB2 are
(0) = Present.
(31) = Absent.

33. Third Upper Pharyngeal Toothplate.—An advanced feature supposedly characteristic of alepisauroids (R) is, according to Rosen 1973 (p. 435), the reduction or loss of the PB3TP. With respect to loss, the actual distribution of this state is rather monotonous among inioms (true only for *Anotopterus;* and certain paralepids [Rosen, 1973, p. 408]; among paralepidid genera I have examined a PB3TP is present in *Paralepis* and *Notolopis* but not *Macroparalepis*).

(A) States Recognized for Iniomous Fishes

Conical teeth on PB3 are
(0) = Present.
(32) = Absent.

34. Third Epibranchial Toothplate.—Rosen (1973, p. 435) states that an advanced feature characteristic of alepisauroids is reduction or loss of the EB3TP. The EB3TP is absent in myctophids, some synodontoids (*Synodus*, see Rosen, 1973, p. 404), some paralepidids (*Notolepis, Macroparalepis* but not *Paralepis*), *Alepisaurus* (Rosen, 1973, p. 405), *Anotopterus*, and *Omosudis*.

(A) States Recognized for Iniomous Fishes

Conical teeth on EB3 are
(0) = Present.
(33) = Absent.

35. M. Retractor Arcuum Branchialum.—Rosen (1973, pp. 399, 400) argues that the presence of the muscle retractor arcuum branchialum (RAB) divides the Euteleostei into two major groups. Those with the RAB (Stomiatiformes + Aulopiformes + Myctophiformes + Paracanthopterygii + Acanthopterygii) are collectively termed neoteleosts. Winterbottom (1974, pp. 256–258) reviewed the literature on this muscle, termed by Winterbottom the m. retractor dorsalis, and noted that there exists some question concerning the uniqueness of this feature to neoteleosts, but he tentatively accepted Rosen's conclusion.

According to Rosen (1973), the RAB is always paired, the anterior end inserts on dorsal gill arch elements, and, in most cases, the posterior end originates directly or via a tendon from the first to sixteenth vertebrae. The RAB's are believed to assist in swallowing. I have not surveyed iniomous fishes with respect to configuration of the RAB, and the following account follows Rosen (1973).

(A) States Recognized for Iniomous Fishes

(0) = RAB undivided, a flat sheet of muscle inserting on distal half of EB4, the cartilaginous PB4, and along the posterior ventromedial edge of the PB3 (Rosen, 1973, p. 400).
(34)[7] = RAB undivided, confined to the PB4, associated toothplates (PB4TP if present, PB5TP), and, in some, distal half of EB4 (Rosen, 1973, p. 406).

[7]For most of the species to which Rosen assigns state (34), Rosen terms the element herein called PB5TP as the PB4TP. Rosen's illustrations suggest that state (34) occurs in *Synodus* (p. 404), *Harpadon* (p. 405), *Alepisaurus* (p. 405), *Anotopterus* (p. 406), *Evermannella* (p. 407), *Lestrolepis* (p. 408), and *Paralepis* (p. 408). State (34) also occurs in giganturids (p. 409) and stomiatoids (pp. 409, 410). Rosen's illustration for *Scopelarchoides* (p. 407) suggests that state (0) occurs in scopelarchids—a conclusion in agreement with other results presented in this paper (see below). The state for *Omosudis* (p. 406) appears to be somewhat intermediate between states (0) and (34), but closer to the latter.

(35) = RAB divided, with distinct medial (the smaller, inserting on PB3) and lateral (the larger, inserting on PB4 and associated toothplate, here assumed to be PB5TP) bundles (see Rosen, 1973, pp. 453–455).

Hypothesized character-state sequence: (34) ← (0) → (35)

36. Fifth Ceratobranchial Toothplate.—Conical teeth occur on the fifth ceratobranchial (fig. 14D) in all iniomous families except the Anotopteridae. Among evermannellids, however, conical teeth occur on the fifth ceratobranchial only in *Odontostomops normalops* and *Evermannella balbo*.

(B) States Recognized for Evermannellid Species

Conical teeth on fifth ceratobranchial are

(0) = Present.

(E15) = Absent.

37. Basibranchial Dentition.—The presence of teeth over the ossified basibranchials (BB 1 to 3, fig. 14) is widespread in primitive teleosts (Nelson, 1969a) and regarded as primitive for iniomous fishes. A number of iniomous families have lost basibranchial dentition (although not the toothplate), and this includes all alepisauroids.[8] Among scopelarchids, *Rosenblattichthys*, *Scopelarchus*, and two species of *Scopelarchoides* (*S. danae*, *S. nicolsi*) exhibit strongly developed, hooked teeth arranged uniserially above at least the first two basibranchials (Johnson, 1974c, p. 48).

(A) States Recognized for Iniomous Fishes

A tooth-bearing toothplate dorsal to the ossified basibranchials (BB 1 to 3) is

(0) = Present.

(36) = Absent.

38. First Pharyngobranchial.—The dorsal support of the first epibranchial (EB1) is through a first or suspensory pharyngobranchial (PB1) in most iniomous families (Johnson, 1974c, pp. 49, 201). In three families (Anotopteridae, Evermannellidae, Omosudidae) there is no PB1, and the EB1 attaches directly (through a ligament) to the anterior end of the third pharyngobranchial (PB3, fig. 14). In *Alepisaurus* (Rosen, 1973, p. 405) as in one scopelarchid lineage (that including the genus *Scopelarchus*, Johnson, 1974c, p. 51) there is no PB1, and support for the EB1 is provided by the second pharyngobranchial (PB2), which in turn attaches (ligamentously) to the anterior end of PB3.

(A) States Recognized for Iniomous Fishes

A suspensory pharyngobranchial (PB1) is

(0) = Present.

(37) = Absent.

Myctophids are to my knowledge unique among iniomous fishes in possession (= ? retention) of a PB1TP (Paxton, 1972, p. 25).

39. Uncinate Process of Second Epibranchial.—Rosen (1972, 1973) discusses the apparent diagnostic value of a markedly elongate uncinate process on the second epibranchial in the recognition of aulopiform(R) fishes. According to

[8]In *Evermannella balbo* (fig. 14) and certain paralepidids (*Paralepis*, *Notolepis*, but not *Macroparalepis*) a fourth basibranchial toothplate (or toothplates) lies embedded in the skin over the cartilaginous element representing the third copula (Nelson, 1969a) of the basibranchial series.

Rosen, all iniomous fishes (excepting the Myctophidae, Neoscopelidae, and Paralepididae) have such a "notably elongate" uncinate process, except (presumably rare) cases where secondarily reduced, and this modification of the second epibranchial is unique to aulopiform(R) fishes. Apparently primitive for euteleosts (Rosen, 1973, pp. 401, 402) is the presence of two dorsal articulating heads or processes on the first three epibranchials (EB1 to 3). The anterior process articulates with its respective pharyngobranchial (PB1 to 3), and the posterior (uncinate) process with its respective succeeding pharyngobranchial (PB2 to 4). Whereas the EB1 typically retains both processes, according to Rosen (1973, pp. 402, 403), the uncinate processes of EB2 and EB3 are ". . . lost, greatly modified or reoriented . . . in the more advanced euteleosteans." In inioms the marked elongation of the EB2 uncinate process is apparently associated with reorientation of the pharyngobranchials and enlargement of the PB3 (both advanced characters helping to define Rosen's "Section Eurypterygii") and especially with an elongation and lateral extension of the PB2 (Rosen, 1973, p. 402).

Although the EB2 uncinate process is indeed markedly elongate in most inioms (fig. 14; see also Rosen, 1973, pp. 403–408), there is variation among iniomous fishes in relative length of this process. The question remains—how does one quantitatively define "notably elongate"? Rosen (1973, p. 404) provides a possible test in his figure caption for *Bathypterois atricolor*, a species in which the ". . . uncinate process on [EB2 is] also apparently secondarily reduced judging from its failure to contact PB3." This suggests that states for character 39 can be defined as follows:

(A) States Recognized for Iniomous Fishes

(0) = EB2 uncinate process extremely elongate, extending to a point dorsomedial to dorsolateral border of the PB3 (e.g., Rosen, 1973, text-fig. 7)

(38) = EB2 uncinate process not as elongate, not extending to a point dorsomedial to dorsolateral border of PB3 (e.g., Rosen, 1973, text-fig. 6).

Application of this test results in assignment of state (0) to all iniomous families except the Myctophidae. I find, for my material, that certain paralepidids (*Paralepis, Notolepis*) exhibit state (0), in that the (cartilaginous) dorsal terminus of EB2 extends to a point over the PB3. Other paralepidids (*Macroparalepis*) may exhibit state (38), the EB2 uncinate process not reaching a point dorsomedial to the dorsolateral border of the PB3. Both the specimen of *Neoscopelus microchir* in my material and *N. macrolepidotus* as illustrated in Rosen (1973, p. 454) apparently exhibit state (0)—contrary to Rosen's comments (p. 455). My interpretation of the EB2 morphology in *Neoscopelus* is that the anterior articulating process has been reduced, and the uncinate process has retained the configuration typical for inioms. Diagrams presented by Paxton (1972, p. 25) and Rosen (1973, p. 453) suggest that myctophids may have taken the opposite tack, so to speak, retaining the anterior process (which articulates with the PB2) but losing (or showing reduction of) the uncinate process.

Note that Rosen's (1973) discussion is concerned with relationships among all neoteleosts, whereas my discussion is limited to inioms. Thus, the markedly elongate EB2 uncinate process is regarded by Rosen as an advanced feature of aulopiform fishes (relative to other euteleosts) and is regarded by me as a state

primitive for inioms (relative to iniomous taxa in which the process is secondarily reduced). Whether the state typifying myctophids represents retention of the basal euteleost configuration (as suggested by Rosen) or secondary reduction of the configuration typical for inioms is unknown—I argue that the latter hypothesis cannot be rejected on the basis of information presented by Rosen.

40. Attachment of First Centrum.—Gosline et al. (1966, p. 8) note that in neoscopelids (*Neoscopelus, Scopelengys, Solivomer*) as well as chlorophthalmids, there is a gap in ossification between the skull and the first vertebral centrum. This gap is said to attain its greatest extent in *Solivomer*—where it is nearly equal to the width of the two centra following the gap. The gap is filled by a rubbery membrane (= ? coat of notochord), and the whole structure may represent development of the intervertebral disk between the skull and first centrum. Such a gap also occurs in ipnopids and is said by Sulak (1977, p. 54) to characterize a "chlorophthalmid lineage" among iniomous fishes. Rosen & Patterson (1969) argue that the peculiar cervical joint (i.e., the gap in ossification) of chlorophthalmids and neoscopelids indicates relationship between the two groups and state (contrary to Gosline et al., 1966; and Sulak, 1977) that this peculiar joint is ". . . present in a somewhat simpler form in aulopids" (it is not evident in *Hime*). Johnson (1974c, p. 206) reports that scopelarchids possess the unossified gap of chlorophthalmids and neoscopelids—the first vertebra is a half-centrum attached to the rear of the skull through a tube of fibrous tissue, the length of this tube equal to or greater than the length of the first centrum. An extremely clear illustration (x-radiograph) of this gap in an adult *Benthalbella infans* is provided by Merrett et al. (1973, p. 17). They (Merrett et al., 1973, pp. 42–44) suggest that in scopelarchids the presence of the gap is related to feeding style, ". . . during active feeding, prey located above is struck at by a rapid, upwards arching of the predorsal region, with the flexible unossified section of the vertebral column allowing an extra backward bending of the head and hence a widening of the gape." In notosudids (Bertelsen et al., 1976, p. 8) there is a very slight gap in ossification—the gap filled by a short, rubbery tube—but the first centrum is not shorter than succeeding centra. In evermannellids as in all other inioms (including myctophids) there is no gap in ossification between the first centrum and the skull, and the first vertebra includes a full amphicoelous centrum (fig. 16A).

(A) States Recognized for Iniomous Fishes

Gap in ossification between skull and first centrum with reduction in size of first centrum relative to succeeding centra as described above is

(0) = Absent.

(39) = Present.

41. Supraneurals.—Rosen (1973, p. 450) states that a trend toward the reduction or loss of supraneurals is characteristic of alepisauroids(R). Goody (1969, p. 220) regards the presence of three or four supraneurals, as seen in *Aulopus* and the Cretaceous *Sardinioides*, as primitive for iniomous fishes. All scopelarchids have three supraneurals (also true for chlorophthalmids, including *Bathysauropsis; Bathysaurus* and certain other synodontoids [*Saurida, Harpadon, Trachinocephalus*], and apparently also for myctophids [Jollie, 1954, p. 92]). Four supraneurals are present in the *Neoscopelus microchir* specimen in my material. Ipnopids have one or two supraneurals (Sulak, 1977). Evermannellids have two

supraneurals (fig. 16A), and this is apparently true for most paralepidids. Only a single supraneural is present in notosudids and *Omosudis*. Rofen (1966c, p. 499) indicates three supraneurals in *Anotopterus*, but I believe these to be expanded neural arch elements and find no supraneurals in my material. The state in *Alepisaurus* is unknown.

(A) States Recognized for Iniomous Fishes

The number of supraneurals is
(0) = 3 or 4
(40) = 0, 1, or 2

42. Intermuscular Bones.—Intermuscular bones are well developed in all evermannellid and scopelarchid species (contrary to Marshall, 1954, p. 331; Gosline et al., 1966, p. 11), and, apparently, in most (or all) inioms, including aulopids and the Cretaceous *Sardinioides* (Goody, 1969). The alepisauroid families Alepisauridae, Anotopteridae, Omosudidae, and Paralepididae (some genera) are characterized by an enormous proliferation (in both number of elements and length of individual elements) of intermuscular bones (see Marshall, 1954, pp. 329, 330). The survey of iniomous groups with respect to configuration of intermuscular bones is too incomplete to allow formal recognition of character states at this time.

43. Number of Hypurals.—Rosen (1973, pp. 422–432) provides a detailed description of major patterns in the variation of caudal-skeleton morphology among euteleosts and characterizes (pp. 423, 424) the basal configuration for iniomous fishes. Typical for inioms (and many other euteleost groups) is the presence of six hypurals, and this is true for all extant inioms except certain synodontoids (*Synodus foetens* [HYP=5], Rosen, 1973, p. 427; *Trachinocephalus myops* [HYP=5], Rosen, 1973, p. 428; *Harpadon nehereus* [HYP=5], Rosen, 1973, p. 428; but not *Saurida brasiliensis* [HYP=6] or *Synodus synodus* [HYP=6], see Sulak, 1977, p. 56), some paralepidids (HYP=5, e.g., *Paralepis*, see Rosen, 1973, p. 429), and the families Anotopteridae, Alepisauridae, and Omosudidae (HYP = 5 in each case).

In most inioms the dorsalmost hypural, HYP-6, is by far the smallest hypural element. Based on this fact plus the size of hypural elements remaining in those inioms with HYP=5, it appears that the typical pathway of reduction has been loss of HYP-6. The only exception appears to be certain paralepidids (*Paralepis*, *Notolepis*) in which it seems clear that reduction (in number of hypurals) has been through fusion of HYP-1 and HYP-2 (the articular heads apparently remain distinct, see Rosen, 1973, p. 429). This fusion is not present in all paralepidids (e.g., *Macroparalepis*, HYP=6).

(A) States Recognized for Iniomous Fishes

Number of hypurals is
(0) = 6.
(41) = 5, resulting from fusion of HYP 1 + 2.
(42) = 5, resulting from loss of HYP 6.

Hypothesized character-state sequence: (42) ← (0) → (41)

44. Second Ural Centrum.—According to Goody (1969) and Rosen (1973), the basal configuration of the caudal skeleton in iniomous fishes includes fusion of the first preural (PU-1) and ural (U-1) centra but retention (as a terminal

half-centrum) of a free second ural centrum (U-2). Only three iniomous families lack representatives with a free U-2 centrum (Alepisauridae, Myctophidae, Scopelarchidae: see Paxton, 1972; Rosen, 1973; Johnson, 1974c).

(A) States Recognized for Iniomous Fishes

A free U-2 centrum is
(0) = Present.
(43) = Absent.

Rosen (1973, p. 438) states, "Although in synodontids the second ural centrum is free as in aulopoids, this centrum is consolidated with the preceding compound centrum in other alepisauroids." This statement is true only for *Alepisaurus* and the scopelarchids among alepisauroid(R) fishes.

45. Number of Epurals.—In *Aulopus* and the Cretaceous *Nematonotus* there are three epurals (Rosen & Patterson, 1969), and the distribution of this state (table 8) suggests that possession of three epurals is primitive for iniomous fishes. In scopelarchids there are three epurals in all species except *Benthalbella dentata*, which has two. All evermannellids have only a single epural (fig. 16E). In representatives of a number of lineages (ipnopids, synodontoids, alepisauroids) the number of epurals has been reduced (EP=2 in *Alepisaurus, Harpadon, Ipnops, Omosudis* [the posterior epurals are fused distally], *Saurida;* EP=1 in *Anotopterus, Bathymicrops, Synodus, Trachinocephalus*).

(A) States Recognized for Iniomous Fishes

Number of epurals is
(0) = 3.
(44) = 1 or 2.

46. Fleshy Midlateral Keel.—An adipose lateral keel, a raised, midlateral, dermal ridge arranged longitudinally, is apparently unique among inioms to two families. In *Omosudis* (Rofen, 1966b, p. 468) the keel is essentially limited to the caudal peduncle. In *Alepisaurus* (Gibbs & Wilimovsky, 1966, pp. 490, 492), the keel is present midlaterally along the caudal one-third to one-half of the body.

(A) States Recognized for Iniomous Fishes

An adipose midlateral keel as described above is
(0) = Absent.
(45) = Present.

47. Posttemporal.—Scopelarchids (Johnson, 1974c, pp. 57, 58) and evermannellids (fig. 18) are unique among inioms in that the posttemporal is unforked. In both families the posttemporal of each side consists of a rodlike dorsal articulating process, which is connected to the epiotic, and a ventral bladelike area from which a strong ligament extends to the opisthotic. In all other inioms (e.g., Paxton, 1972, p. 28) there is also a ventral rod or spikelike process (of the posttemporal) directed toward and strongly connected to the opisthotic.

(A) States Recognized for Iniomous Fishes

The posttemporal is
(0) = Forked.
(46) = Unforked.

48. Pectoral Girdle.—According to Marshall (1954, pp. 325–328), a key character tending to separate alepisauroid(G) from myctophoid(G) fishes involves the setting of the pectoral fin as measured by the angle between the horizontal axis of the body and the axis of the pectoral fin (bases). In most alepisauroids(G) this angle is less than 45°, and the fin tends to be low on the body and is rather hydroplane-like in configuration. In myctophoids(G) the fin is set higher on the body, and the angle of inclination tends to be steeper, generally greater than 45°. Marshall relates the hydroplane-like conformation in alepisauroids(G), which lack a swimbladder, to problems involved in maintaining position in the water column (and in part to problems involved in maneuvering). Marshall relates the relatively steep pectoral angle in myctophids to the presence of a swimbladder, tending to free the pectorals for use in braking and maneuvering. I am unwilling to use the angle of pectoral-fin insertion as a systematic character because, as Marshall's data (p. 327) on *Gonostoma denudatum* (has functional swimbladder, pectoral angle = 45° to 50°) vs. *Gonostoma bathyphilum* (no swimbladder, pectoral angle = 20° to 25°) shows, the possibility for convergence (among mesopelagics with no swimbladder) is great.

Scopelarchids and evermannellids differ in the number of extrascapulars (scopelarchids have two [or, possibly, in the case of *Rosenblattichthys volucris*, three]; evermannellids have one [fig. 18]) and postcleithra (scopelarchids have two widely separated postcleithra; evermannellids have three postcleithra connected in sequence [fig. 18]). The number of extrascapulars in other inioms varies from one (*Aulopus*, *Chlorophthalmus*, neoscopelids, notosudids, paralepidids, *Anotopterus*, *Omosudis*) to two (*Parasudis*, some synodontoids [*Synodus*], myctophids). The number of postcleithra in other iniomous fishes varies from one (some ipnopids [*Ipnops*, *Bathymicrops*], *Anotopterus*) to two (some ipnopids [*Bathytyphlops*], myctophids, neoscopelids, notosudids, *Omosudis*), to three (aulopids, chlorophthalmids, *Bathysauropsis*, certain synodontoids [*Bathysaurus*, *Saurida*], paralepidids). In both cases the available data is far too meager relative to the observed variation to allow formal recognition of character states at this time.

49. Luminous tissue.—Rosen (1973, p. 505) lists two derived character states as unique (autapomorphic) to his Myctophiformes: (1) presence of an ethmoid crest and (2) presence of photophores. Rosen does not elaborate on the "ethmoid crest," nor can I. Photophores are of course not unique to the Myctophiformes(R), occurring widely in elasmobranch and teleost as well as invertebrate groups. More to the point, I note (1) the development of a myctophiform(R)-like photophore (isthmial organ) in the paralepidid *Lestidium bigelowi* (Graae, 1967), and (2) Bolin (1966, pp. 192, 193) notes that the arrangement and (more importantly) structure of photophores in *Neoscopelus* (the only neoscopelid genus whose members possess photophores) are ". . . markedly different [in] character [from those of myctophids]." In *Neoscopelus* the photogenic tissue and enveloping black pigment is largely restricted to the posterior end of the organ, the anterior portion is a simple, flaring sheet of reflective guanine (overlain by translucent tissue) and lacking definite anterior limits, and the overlying scales are not modified into lenses (cf., Myctophidae, see Nafpaktitis et al., 1977, pp. 15–18). Despite these differences, the consensus of opinion, based on external morphology, osteology, and larval morphology (Fraser-

Brunner, 1949; Moser & Ahlstrom, 1970; Paxton, 1972; Rosen, 1973; but not Marshall & Staiger, 1975), indicates sister-group relationship for the myctophids and neoscopelids. Following this consensus, I recognize two states of character 49 for iniomous fishes:

(A) States Recognized for Iniomous Fishes

(0) = Photophores absent.
(47) = Photophores present.

Note that in assigning state (47) to the neoscopelids (table 8), I am following the preliminary discussion of interrelationships among neoscopelids provided by Nafpaktitis (1977, p. 3). Thus the presence of photophores is here hypothesized to be primitive for this family.

Among other iniomous families, only certain paralepidids (Rofen, 1966a; Graae, 1967), scopelarchids (Merrett et al., 1973; Johnson, 1974c), and the evermannellid genus *Coccorella* (Herring, 1977) are known to be luminous. Evidence suggests that the presence of luminous organs in *Coccorella* is synapomorphous (a state which may be shared with species of *Evermannella*, see section on Luminescence).

(B) States Recognized for Evermannellid Species

(0) = Luminous tissue absent.
(E16) = Luminous tissue present, associated with ventral wall of intestine ("intestinal organs") or pyloric caecum ("isthmus organ," see Herring, 1977).

50. PSM Cephalic Laterosensory Pores.—*Evermannella megalops* is unique among evermannellid species in lacking the medial snout-pad pores (PSM, fig. 1; see Johnson & Glodek, 1975, p. 721). This feature is probably related to the tremendous expansion of the eyes and foreshortening of the snout in this species (Johnson & Glodek, 1975).

(B) States Recognized for Evermannellid Species

PSM cephalic laterosensory pores are
(0) = Present.
(E17) = Absent.

51. Number of Dorsal-Fin Rays in Evermannellid Species.—Almost without overlap the genus *Evermannella* can be divided on the basis of number of dorsal-fin rays (table 2): 10 to 11 in *E. ahlstromi* (one specimen of 78 with 12 rays) and *E. megalops* (one specimen of 10 with 12 rays) vs. 12 to 13 in *E. balbo* and *E. indica* (no exceptions). I regard the state in *E. ahlstromi* and *E. megalops* as derived for the following reasons: (1) In *Odontostomops normalops* and *Coccorella atlantica* the great majority of specimens (92% and 95%, respectively) have 12 or 13 dorsal-fin rays; only in *Coccorella atrata* is there substantial overlap (40% with 10 or 11, 60% with 12 or 13 rays, table 2); (2) within *Evermannella*, the state exhibited by *E. ahlstromi* and *E. megalops* apparently correlates with derived states in other characters (lateral line segments lacking [character 5], lack of PSM pores in *E. megalops* [character 51], and hypertrophy of gill filaments in *E. ahlstromi* [fig. 29]).

(B) States Recognized for Evermannellid Species

Modal number of dorsal-fin rays is
(0) = 12 or 13.
(E18) = 10 or 11.

Interrelationships Among Iniomous Fishes

Most attempts at finding derivative character states monothetically defining the Iniomi have failed. The problem is well summarized in Gosline et al. (1966, p. 5): "Though there is apparently no one feature that will separate all iniomous from all isospondylous fishes, this is hardly surprising in two such large and varied groups, groups which are . . . an expression of very early teleost ("explosive") evolution. . . ." Again, as stated by Rosen & Patterson (1969, pp. 452, 453): "What we find is a mosaic of primitive and advanced features, the first lost and the second acquired in different lineages in a pattern that can be disentangled in a number of ways depending upon the weight attached to various characters. . . ." Most "definitions" of the Myctophiformes (e.g., Gosline et al., 1966; Goody, 1969; Gosline, 1971) have involved listings of character states that are shared with certain salmoniform groups and/or are primitive for neoteleosts. Such listings are not useful in demonstrating the monophyletic origin of the Iniomi.

Rosen (1973, pp. 505–510) argues for the monophyly of an aulopiform(R) group containing all iniomous families except the Myctophidae and Neoscopelidae. The latter families constitute in Rosen's classification a monophyletic and much restricted order Myctophiformes(R), the supposed sister-group of "higher" neoteleosts (Paracanthopterygii + Acanthopterygii). As noted by Zehren (1975, p. 213), the aulopiforms(R) exhibit a number of specialized characters also occurring in the myctophiformes(R), Paracanthopterygii and Acanthopterygii, arguing for the monophyletic origin of the entire assemblage but not adding to Rosen's arguments for the monophyly of his Aulopiformes.

Rosen (1973, p. 403) regards the presence of a notably elongate EB2 uncinate process as uniquely diagnostic of his aulopiform group, but, as indicated in my discussion of character 39, I regard as open to question the exclusion of the Myctophidae + Neoscopelidae from the aulopiform(R) group on the basis of this character. An additional character, not considered by Rosen (1973), involves the presence and conformation of peritoneal pigment sections in larvae (character 8). Discrete peritoneal pigment sections are characteristic of the larvae of iniomous fishes (excepting apparently the families Myctophidae, Neoscopelidae, Notosudidae) and may prove diagnostic for the group—unfortunately adequate knowledge of larval morphology in other major neoteleost groups is lacking.

Rosen (1973, p. 505) lists two features as autapomorphic for his Myctophiformes: (1) presence of photophores, (2) presence of an ethmoid crest, but elaborates on neither feature (see discussion of character 49). Other character states listed by Rosen (1973, p. 506) are said to separate the Aulopiformes(R) vs. Myctophiformes(R) and are said to be shared by the latter with the Paracanthopterygii + Acanthopterygii. Zehren (1975, p. 214) agrees with Rosen's conclusions but notes that the evidence provided by Rosen's listing of characters might

well be taken to suggest ". . . that myctophids are more closely related to paracanthopterygians and acanthopterygians than to neoscopelids."

For purposes of exploring relationships between the evermannellids and scopelarchids, I herein adopt the view traditional among ichthyologists (e.g., Gosline et al., 1966; Goody, 1969; Marshall & Staiger, 1975), viz., that the Iniomi constitutes a monophyletic assemblage. I note, however, that myctophids and neoscopelids differ strikingly from other iniomous fishes in several seemingly trenchant characters. It may well be that thoroughgoing study of this group of fishes will corroborate Rosen's classification.

Based on the assumption of monophyly of the Iniomi, I have prepared a dendrogram (fig. 20) illustrating the distribution of derived character states among five possible major groups of iniomous fishes distributed among three perceived lineages. Evidence presented in support of these groupings is based on the foregoing character catalogue. Evidence for two of the groups (myctophoids, alepisauroids) appears substantial, but the remaining groups are not well supported. This study makes no pretense at producing a formal classification of iniomous fishes, an effort awaiting a more comprehensive survey than presented here. My object in the discussion to follow is twofold: (1) to summarize the preceding catalogue of characters and character states in terms of distribution of derived character states among iniomous taxa and (2) to examine the available evidence in support of (or against) the supposed sister-group relationship between evermannellids and scopelarchids.

Of the three perceived "lineages"—aulopoids, myctophoids + chlorophthalmoids, synodontoids + alepisauroids—there exists, to my knowledge, no basis for asserting closer relationship among any two relative to the third. A central problem is illustrated by the fact that of 36 characters for which states were defined for iniomous taxa, the aulopids exhibit a derived state only in character 3 (2, absence of a swimbladder—a state shared with all iniomous taxa except the myctophoids). Rearrangement of the tree to include the aulopids but to exclude the myctophoids conflicts with character 12 (number of branchiostegal rays)—the result, for the time being, is an impasse. Adding to the difficulty is evident diversity within the Aulopidae, illustrated by the divergence between *Aulopus* and *Hime* in character 8 (peritoneal pigment section single in *Hime;* multiple sections present in *Aulopus*), diversity that can only be interpreted after a much-needed revisionary study of this family is completed.

As noted above, of the remaining groups and lineages, the best-supported groups, in terms of number of synapomorphic features (fig. 20, table 10), are the alepisauroids and myctophoids. The five families herein postulated to represent a chlorophthalmoid + myctophoid lineage group together primarily on the basis of symplesiomorphy. Only a single derived state in character 12 (11, number of branchiostegal rays) provides evidence for the grouping suggested, and that state is shared with the alepisauroids.

The myctophoids (Myctophidae, Neoscopelidae) share derived states of characters 8 (7, lack of peritoneal pigment sections), 12 (12, number and arrangement of branchiostegal rays), 13 (13, number of vertebrae), 22 (21, lack of supraorbital bones), 31 (30, loss of PB4TP), 35 (35, division and insertion of RAB muscle), and 49 (47, possession of photophores). The myctophoids differ from all other iniomous fishes in the symplesiomorphic state of character 3 (possession of a swimbladder). Additional derived states shared by myctophoids as listed by

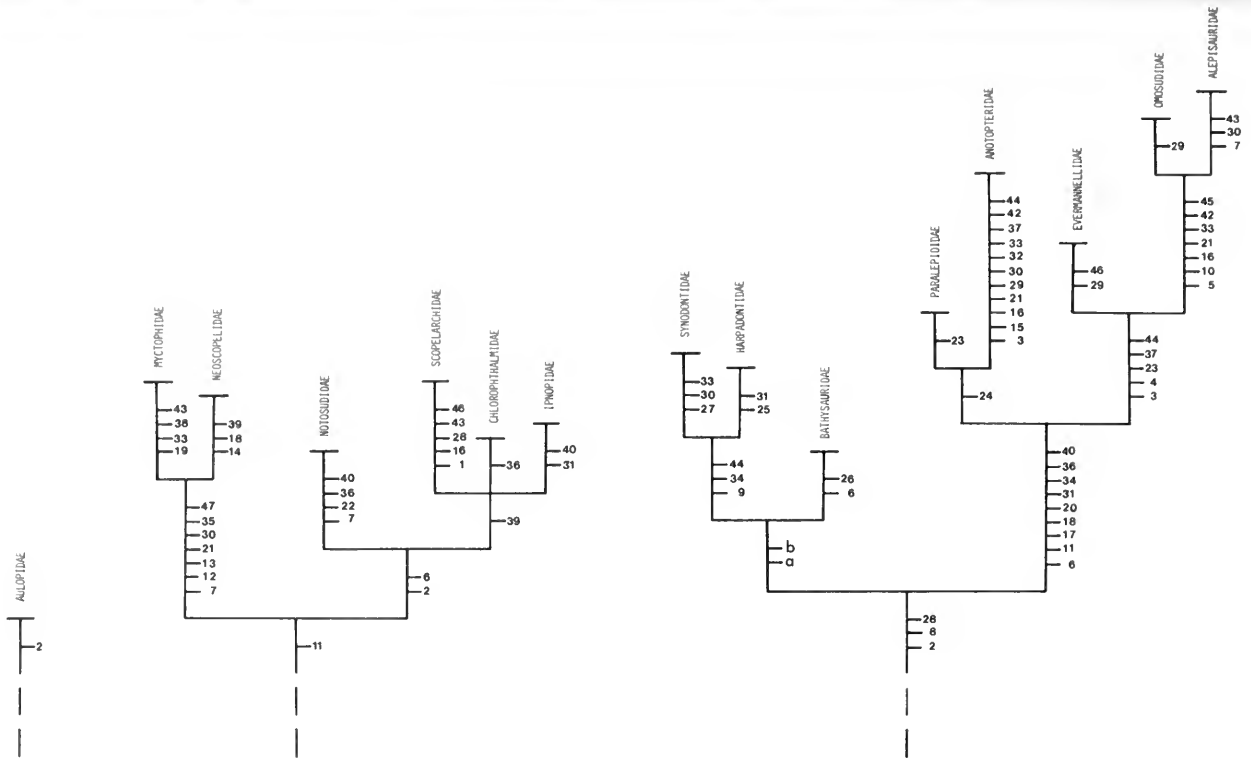


FIG. 20. Representation of possible interrelationships among iniomous fishes presented to summarize the distribution of derived character states (integers) defined and discussed in the text. Note that certain states have been presumed for certain inadequately known taxa (based on data in Table 8; see text for additional explanation).

TABLE 10. Number of derived character states *shared* by iniomous taxa (based on data presented in Table 8, Figure 20, and discussed in the text).

	Groups														
Groups	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**
01	—	0	0	1	1	1	1	1	1	1	1	1	1	1	1
02	—	—	8	2	2	2	2	0	1	0	2	4	5	3	2
03	—	—	—	2	2	1	1	0	2	0	1	4	6	3	1
04	—	—	—	—	3	4	4	1	1	2	6	5	6	5	5
05	—	—	—	—	—	4	4	2	2	3	4	5	6	5	5
06	—	—	—	—	—	—	4	1	1	2	5	4	4	4	4
07	—	—	—	—	—	—	—	2	1	2	5	5	5	5	5
08	—	—	—	—	—	—	—	—	6	3	5	6	6	6	6
09	—	—	—	—	—	—	—	—	—	3	4	7	7	6	5
10	—	—	—	—	—	—	—	—	—	—	4	4	4	4	4
11	—	—	—	—	—	—	—	—	—	—	—	13	13	13	13
12	—	—	—	—	—	—	—	—	—	—	—	—	20	20	16
13	—	—	—	—	—	—	—	—	—	—	—	—	—	24	17
14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18

KEY: 01=Aulopidae, 02=Neoscopelidae, 03=Myctophidae, 04=Notosudidae, 05=Scopelarchidae, 06=Chlorophthalmidae, 07=Ipnopidae, 08=Harpadontidae, 09=Synodontidae, 10=Bathysauridae, 11=Paralepididae, 12=Anotopteridae, 13=Alepisauridae, 14=Omosudidae, 15=Evermannellidae.

Rosen (1973) include: (1) formation of a hinge between PB4TP (=? PB5TP) and the PB3TP; and (2) formation of a hinge joint between the EB2TP and PB2TP. Other derived states listed by Rosen (1973) in his characterization of the Myctophiformes(R) are not shared by the Myctophidae + Neoscopelidae and/or are not unique to myctophoids among iniomous fishes.

The four families (Notosudidae, Scopelarchidae, Chlorophthalmidae, Ipnopidae) constituting the supposed chlorophthalmoid group (fig. 20) share derived states in two characters: 3 (2, lack of a swimbladder) and 6 (6, synchronous hermaphroditism). Both states occur widely among iniomous fishes. A single derived state in character 40 (39, gap in ossification between first centrum and skull) links the scopelarchids + chlorophthalmids + ipnopids—this state also occurs in neoscopelids.

All members of the family Scopelarchidae exhibit derived states in nine characters (table 8, fig. 20):

1 (1, possession of tubular eyes)
3 (2, lack of a swimbladder)
6 (6, synchronous hermaphroditism)
12 (11, reduced number of branchiostegal rays)
15 (16, separation of parietals by supraoccipital)
29 (28, lack of normal, lathlike gill rakers)
40 (39, gap in ossification between first centrum and skull)
44 (43, no free second ural centrum)
47 (46, posttemporal unforked)

Derived states in three characters (3, 6, 12) occur widely among iniomous taxa. Derived states in two characters (15, 44) occur rarely and sporadically among iniomous taxa. A single derived state (character 29) is shared with members of the synodontoid + alepisauroid lineage. A single derived state (character 40) is shared with three families in the myctophoid + chlorophthalmoid lineage. A single derived state (character 47) is unique to scopelarchids and evermannellids among iniomous taxa. A single derived state (character 1) is unique to the Scopelarchidae and the genus *Evermannella* among iniomous fishes.

Characteristic of *all* members of the alepisauroid group but *not* the Scopelarchidae are derived states in eight characters:

8 (8, multiple peritoneal pigment sections)
16 (17, lateral attachment of the dermosphenotic)
19 (18, loss of sclerotic bones)
21 (20, loss of antorbital bones)
32 (31, loss of PB2TP)
35 (34, restricted insertion of RAB muscle)
37 (36, loss of basibranchial dentition)
41 (40, reduction in number of supraneurals)

Characteristic of the Evermannellidae + Alepisauridae + Omosudidae but not the Scopelarchidae are derived states of an additional five characters:

4 (3, loss of body scales)
5 (4, loss of lateral line scales)
23 (23, possession of eight infraorbital bones)
38 (37, loss of PB1)
45 (44, reduction in number of epurals)

On the basis of the large number of derived character states shared by the evermannellids with some or all alepisauroids but not with the scopelarchids, I am unable to confirm the supposition (see Gosline et al., 1966) of sister-group relationship between these two families. I believe that the Scopelarchidae must be excluded from the alepisauroid group, and, on the basis of distribution of derived states of three characters—8 (number of peritoneal pigment sections), 12 (number of branchiostegal rays), 40 (gap in ossification between first centrum and skull)—would argue that the Scopelarchidae be excluded from the synodontoid + alepisauroid lineage and instead be allied with the chlorophthalmoid group. Note that linkage of the scopelarchids with the chlorophthalmoids is based largely on symplesiomorphy and must be confirmed with additional study. If this suggested scheme of relationship is true, two striking similarities between the scopelarchids and evermannellids, viz., the presence of tubular eyes (scopelarchids + the genus *Evermannella*) and the unforked posttemporal (unique to these two families among inioms), must be regarded as convergences.

I know of no characters suggesting that any two of the Scopelarchidae + Chlorophthalmidae + Ipnopidae are more closely related than is either to the third. Much has been made of the morphological intermediacy of *Bathysauropsis* between the chlorophthalmids and ipnopids (Mead, 1966e; Sulak, 1977). However, there exist similarities in larval morphology (size at metamorphosis, peritoneal pigmentation, presence of accessory pigment spots, presence of hooked basihyal teeth) between chlorophthalmids and scopelarchids that also suggest relationship (Johnson, 1974c). It is tempting to speculate that from a benthic stock evolution in this lineage has resulted in three independent radiations (myctophoids, notosudids, scopelarchids) with pelagic (or pseudopelagic) representatives and with evolution in one lineage involving increasing adaptation to abyssal depths (see Marshall & Staiger, 1975).

Derived states of three characters—3 (2, lack of a swimbladder), 8 (8, multiple peritoneal pigment sections), 29 (28, lack of "normal" lathlike gill rakers)—are shared by members of the synodontoid + alepisauroid lineage. Of these, the occurrence of multiple (three or more), serially arranged, paired or unpaired peritoneal pigment sections is unique to members of this lineage and *Aulopus* (but not *Hime*, see discussion of character 8).

I know of no derived character states monothetically defining the synodontoid group (Bathysauridae + Harpadontidae + Synodontidae), but follow Sulak (1977) in assuming the monophyly of the group. A peculiarity shared by all synodontoids is a striking reduction of the maxilla (character 25), although structural details of reduction differ markedly between the three groups. I tentatively follow Sulak (1977) who argues that parallel reduction of the maxilla suggests relationship (state "A," fig. 20). Marshall & Staiger (1975) argue for the monophyly of the synodontoid lineage (as proposed here) on the basis of lack of free-ending nerve organs on the trunk and tail (state "B," fig. 20).

Derived states of three characters—8 (9, presence of multiple, serially arranged, paired peritoneal pigment sections), 35 (34, restricted insertion of RAB muscle), 45 (44, reduction in number of epurals)—suggest relationship between harpadontids and synodontids (fig. 20). If all three family-level groupings (Bathysauridae, Harpadontidae, Synodontidae) are to be combined in one family, as suggested by Sulak (1977), the available evidence, especially the unique (for inioms) conformation of the peritoneal pigment sections in larval harpadon-

tids + synodontids, indicates a different arrangement of subfamilies than that proposed by Sulak, *viz.* Bathysaurinae vs. Synodontinae (including as tribes Harpadontini and Synodontini).

Characteristic of all members of the alepisauroid group (fig. 20) is the unique (in combination) possession of derived states of nine characters (table 8):

6 (6, synchronous hermaphroditism)
12 (11, reduced number of branchiostegal rays)
16 (17, lateral attachment of dermosphenotic)
19 (18, absence of sclerotic bones)
21 (20, lack of antorbital bones)
32 (31, lack of PB2TP)
35 (34, restricted insertion of RAB muscle)
37 (36, lack of teeth on toothplate over basibranchials 1 to 3)
41 (40, reduced number of supraneurals)

The placement of *Anotopterus* with the paralepidids (fig. 20) violates strict application of parsimony. Of 12 derived states exhibited by *Anotopterus* and not shared with all alepisauroids, only a single derived state—character 24 (24, fenestrated premaxilla)—is shared exclusively with paralepidids. Derived states in two characters are shared only with some (but not all) representatives of other iniomous taxa:

character 13 (15, number of vertebrae, n = 78–83; a state shared only with certain ipnopids and paralepidine and lestidiine paralepidids; see table 9);
character 33 (32, lack of conical teeth on PB3, a state otherwise known only from certain paralepidids among iniomous fishes—among paralepidids I have examined conical teeth are present on the PB3 in *Paralepis* and *Notolepis* but not *Macroparalepis;* see also Rosen, 1973, p. 408).

Derived states of nine characters are shared with some (n = 6; characters 15, 22, 30, 31, 34, 43) or all (n = 3; characters 4, 38, 45) members of the triad Alepisauridae + Evermannellidae + Omosudidae (fig. 20, table 8):

4 (3, loss of body scales)
15 (16, separation of parietals by supraoccipital)
22 (21, lack of supraorbital bones)
30 (29, restricted distribution of gill teeth)
31 (30, lack of PB4TP)
34 (33, lack of EB3TP)
38 (37, lack of PB1)
43 (42, loss of HYP-6)
45 (44, reduction in number of epurals)

In grouping *Anotopterus* with the paralepidids I follow Rofen (1966c, p. 508):

> It [*Anotopterus*] is most closely related to the Paralepididae in many fundamental features. If it were not for the unique absence of the dorsal fin . . . this group would more naturally be a subfamily of the Paralepididae. In general form of the head and body, the nonossified prolongation of the lower jaw . . . and the peculiar lateral-line structure, *Anotopterus* is close to, or the same as, the more elongate paralepidids of the genera *Stemonosudis* and *Macroparalepis.* In the evolutionary pattern of alepisauroid fishes, *Anotopterus* is an extreme specialized end-point of the paralepidid line.

If this view is correct, it will eventually be necessary to either divide the family Paralepididae or incorporate in it the family Anotopteridae. Prerequisite to such

action and needed to confirm the position of *Anotopterus* among the alepisauroids is a thoroughgoing study of interrelationships among the paralepidids.

Linking the families Evermannellidae + Alepisauridae + Omosudidae are derived states of five characters (fig. 20, table 8):

4 (3, lack of body scales)
5 (4, lack of ossified lateral line scales)
23 (23, possession of eight infraorbital bones on each side)
38 (37, lack of PB1)
45 (44, reduced number of epurals)

Rofen (1966d, p. 516) believed the evermannellids to be most closely related to *Omosudis*, a view partly corroborated in the present study.

Linking the families Alepisauridae and Omosudidae are derived states of seven characters (fig. 20, table 8):

5 (5, lack of scales or scalelike structures associated with the lateral line)
11 (10, stomach pigmentation in juveniles)
15 (16, separation of parietals by supraoccipital)
22 (21, lack of supraorbital bones)
34 (33, lack of EB3TP)
43 (42, loss of HYP-6)
46 (45, presence of an adipose lateral keel)

Rofen (1966b, pp. 473–478) emphasized similarities between the larvae of *Alepisaurus* and *Omosudis* and postulated the close relationship of these two families.

Interrelationships Among Evermannellid Species

Of 36 characters for which states are defined in the foregoing catalogue, evermannellids exhibit derived states in 19 characters (table 8), none of them unique to, but in combination defining, this family. An apparently autapomorphic feature shared by all evermannellids is the striking lateral tripartite division of the tail musculature (character 2). With respect to osteological features, there exists little variation among evermannellid species. Within the family, the three genera (fig. 21) are readily and largely distinguished through autapomorphic features unique to each genus (table 11).

Odontostomops is specialized in having 12 or more serially arranged peritoneal pigment sections (8, E6). It agrees with certain other iniomous taxa (not other evermannellids) in derived states of two characters: 17 (E8, lack of basisphenoid), and 22 (21, lack of supraorbital bones).

The genus *Coccorella* exhibits autapomorphous states in four characters: 7 (E5, pyloric caecum present and extending into orobranchial cavity), 18 (E9, ethmoid cartilage considerably expanded posteriorly), 27 (E11, arrangement and conformation of dentary and palatine teeth), 49 (E16, presence of luminous tissue). *Coccorella* differs from other evermannellids in the reduction (*C. atlantica*) or loss (*C. atrata*) of the basihyal toothplate (character 28, states E12 and E13). *Coccorella* agrees with *Anotopterus* and all evermannellids except *Odontostomops normalops* and *Evermannella balbo* in lacking conical teeth on the fifth ceratobranchial (character 36, state E15).

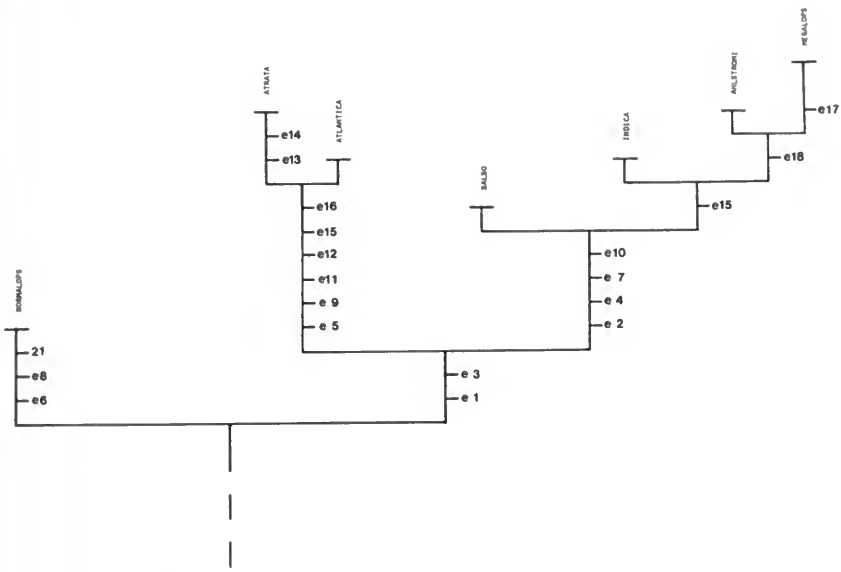


FIG. 21. Representation of proposed relationships among evermannellid species, based on characters discussed in the text and data presented in Table 11. Integers indicate derived character states possessed by taxa above indicated point in dendrogram (states defined solely for evermannellid species are prefixed "E").

Derived states in two characters link *Coccorella* with *Evermannella* (fig. 21, table 11): 1 (E1, eyes semitubular or [*Evermannella*] tubular) and 5 (E3, reduced maximum number of lateral line segments).

The genus *Evermannella* exhibits autapomorphous states in two characters: 10 (E7, unique pattern of juvenile-phase pigmentation), 26 (E10, presence of vertically elongate fossa at dentary symphysis). Species of *Evermannella* and the family Scopelarchidae are unique among iniomous fishes in possessing dorsally directed fully tubular eyes (character 1). Species of *Evermannella* exhibit further reduction in the maximum number of lateral-line segments (character 5).

The triad *Evermannella indica* + *E. ahlstromi* + *E. megalops* is linked by one derived character state (character 36, state E15, lack of teeth on fifth ceratobranchial—a state also shared with *Coccorella* spp.). A single derived state (character 51, state E18, number of dorsal-fin rays) arguably links *E. ahlstromi* and *E. megalops*. Given the restricted distribution of these two species, *E. ahlstromi* to ecotonal areas in the eastern tropical Pacific, *E. megalops* to the central-gyral area of the South Pacific (see section on Zoogeography and Evolution), convergence may well be the explanation for the apparent linkage.

EVERMANNELLIDAE: Species Accounts

Artificial Key to the Species of Evermannellidae (juveniles and adults, 25 mm SL and larger)

1A. Eyes "normal" and lateral in position, not tubular, directed laterally (fig. 3); aperture in adipose eyelid much less than lens in diameter (anteriormost palatine fang and at

TABLE 11. Character state by OTU matrix for seven species of Evermannellidae. Characters and character states are defined and discussed in the text. States considered primitive denoted by "0," states considered derived are denoted by positive integers, states presumed for inadequately known taxa indicated by "?."

	Species						
Character	**01**	**02**	**03**	**04**	**05**	**06**	**07**
1	0	E1	E1	E2	E2	E2	E2
5	0	E3	E3	E4	E4	E4	E4
7	0	E5	E5	0	0	0	0
8	E6	0	0	0	0	0	0
10	0	0	0	E7	E7	E7	E7
17	E8	0	0	0	0	0	?0
18	0	E9	E9	0	0	0	?0
22	21	0	0	0	0	0	?0
26	0	0	0	E10	E10	E10	E10'
27	0	E11	E11	0	0	0	0
28	0	E12	E13	0	0	0	?0
31	0	0	E14	0	0	0	0
36	0	E15	E15	0	E15	E15	E15
49	0	E16	E16	0	0	0	0
50	0	0	0	0	0	0	E17
51	0	0	0	0	0	E18	E18

KEY: 01=*Odontostomops normalops*, 02=*Coccorella atlantica*, 03=*Coccorella atrata*, 04=*Evermannella balbo*, 05=*Evermannella indica*, 06=*Evermannella ahlstromi*, 07=*Evermannella megalops*.

least some dentary teeth barbed; no fossa centered on dentary symphysis; no pyloric caecum) ..... *Odontostomops normalops* (Parr 1928), Atlantic, Indian, and Pacific Oceans.

1B. Eyes semitubular or tubular, directed dorsolaterally or dorsally (fig. 3); aperture in adipose eyelid slightly to markedly greater than lens of eye in diameter 2A

2A. Eyes semitubular, directed dorsolaterally; aperture in adipose eyelid only slightly greater than diameter of lens; jaw teeth nonbarbed (figs. 3, 11); anteriormost palatine tooth an enormous saber-like fang, 7.1% to 10.0% SL; no fossa centered on dentary symphysis; pyloric caecum present and extending into head, easily visible in floor of orobranchial cavity as a distinct black-pigment-enclosed tubelike structure beneath basibranchial series 3A

2B. Eyes tubular, directed dorsally (slightly dorsoanteriad); aperture in adipose eyelid considerably exceeding lens in diameter; anteriormost palatine fang (4.6% to 7.3% SL) and at least some dentary fangs distinctly barbed; a vertically elongate fossa centered on dentary symphysis; no pyloric caecum 4A

3A. Vertebrae 48 to 50; interorbital width 3.2% to 4.7% SL; typically 6 pores, 3 + 3, in frontal canal commissure (fig. 1; in 243 specimens examined, 238 with 6 pores, 3 with 5 pores [3 + 2], 2 with 4 pores [2 + 2]) ..... *Coccorella atlantica* (Parr 1928), central water areas of Atlantic, Indian, and Pacific Oceans.

3B. Vertebrae 45 to 47; interorbital width 4.7% to 6.1% SL; typically 4 pores, 2 + 2, in frontal canal commissure (fig. 1; in 123 specimens examined, 122 with 4 pores, 1 with 5 pores [2 + 3]) ..... *Coccorella atrata* (Alcock 1893), equatorial areas of Indian and Pacific Oceans.

4A. Anal-fin rays 33 to 37; vertebrae 52 to 54 ..... *Evermannella balbo* (Risso 1820), Atlantic Ocean (incl. Mediterranean Sea, southwestern Indian Ocean, transition regions of eastern and central South Pacific Ocean).

4B. Anal-fin rays 27 to 32; vertebrae 48 to 52 ..... 5A

5A. Gill filaments elongate, noticeably projecting beyond posterior and ventroposterior margins of gill covers and nearly reaching pectoral-fin insertion; body depth at anal-fin origin 17.3% to 20.0% SL (dorsal-fin rays 10 to 12, typically 11, 1 of 78 specimens with 12 rays) ..... *Evermannella ahlstromi* Johnson & Glodek 1975, eastern Pacific Ocean.

5B. Gill filaments not projecting beyond margins of gill covers; body depth at anal-fin origin 13.5% to 17.1% SL 6A

6A. Dorsal-fin rays 10 to 12, typically 11, 1 of 10 specimens with 12 rays; snout-pad pore formula = 2 + 4 + 0 + 1 + 0 (fig. 1); interorbital width extremely narrow, 0.28 to 0.55 mm in 5 specimens (32.5 to 66.0) .... *Evermannella megalops* Johnson & Glodek 1975, central South Pacific Ocean.

6B. Dorsal-fin rays 12 to 13, 209 specimens of 215 counted with 12 rays; snout-pad pore formula = 2 + 4 + 2 + 1 + 0 (fig. 1); interorbital width narrow but somewhat greater, 0.55 to 0.97 mm in 37 specimens (24.4 to 116.9) ..... *Evermannella indica* Brauer 1906, Atlantic, Indian, and Pacific Oceans.

Coccorella Roule 1929

Coccorella Roule 1929, p. 11 (original description, type-species by original designation, *Odontostomus atratus* Alcock 1893).

Type-Species.—*Coccorella atrata* (Alcock, 1893).

Diagnosis—Evermannellids with eyes semitubular, directed dorsolaterally. Horizontal eye diameter about equal to interorbital width. Aperture in adipose eyelid only slightly greater than lens of eye in diameter. A distinct, elliptical lens

pad present in all fully metamorphosed specimens less than about 70 mm SL, becoming indistinct in larger adults. Teeth on jaws and palatines not barbed. Anteriormost palatine tooth an enormous saber-like fang, 7.1% to 10.0% SL. Dentary teeth uniserial. No fossa centered on dentary symphysis. Body deep to extremely deep, body depth at anal-fin origin 14.4% to 21.0% SL. A single, narrow but elongate pyloric caecum present and extending into head, easily visible in floor of orobranchial cavity as a distinct black-pigment-enclosed tubelike structure beneath basibranchial series. Ethmoid cartilage expanded posteriorly into orbit, forming an orbital septum between eyes and reaching to or nearly to posterior wall of orbit. Basisphenoid present. Luminous tissue present. Larvae with three peritoneal pigment sections.

Description.—Dorsal-fin rays 10 to 13. Anal-fin rays 26 to 30. Pectoral-fin rays 11 to 13. Vertebrae 45 to 50.

Body moderately elongate, deep, strongly compressed. Anus at or posterior to a point midway between pelvic-fin insertion and anal-fin origin. Lateral line extending to a point over anterior one-third of anal-fin base and composed of 34 or fewer segments.

Head large and massive. Head width subequal to body width. Head depth equal to or somewhat greater than body depth (except specimens containing very large, ingested food particles). Snout high, truncate, sharply angular, dropping almost vertically (in lateral view) from anterior margin of snout pad to premaxillary border.

Eyes large, semitubular, directed dorsolaterally. Horizontal eye diameter 4.0% to 6.5% SL, vertical diameter 4.2% to 7.6% SL. Fleshy eye diameter slightly less than snout length. Pupil broader than lens. A roughly elliptical lens pad centered on dorsal margin of lateral face of pigmented eye cup in fully metamorphosed juveniles and small adults but tending to become indistinct in larger adults.

Dentary symphysis marked by a distinctly protruding, vertically oriented ridge and lacking any central, vertically elongate fossa. Branchiostegal membranes free from isthmus, united by a small membrane anteriorly, at a vertical through anterior margin of pupil, slightly posterior to a vertical through anterior margin of eye.

Gill filaments dense, matlike, relatively elongate but not protruding beyond margins of gill covers. Pseudobranchiae with filaments nearly as long as longest gill filaments. Number of pseudobranch elements: *C. atlantica* (N=11, 48.7 to 146.2), 8 to 10; *C. atrata* (N=10, 46.3 to 104.6), 8 to 10. Number of pseudobranch elements slightly higher in larger specimens.

Dorsal fin relatively short based, 9.9% to 13.1% SL. Middle of dorsal-fin base distinctly anterior to a vertical at middle of standard length. Pelvic-fin insertion under anterior one-half of dorsal-fin base. Appressed pelvic fins reaching to or nearly to anus in best-preserved specimens but not reaching to anal-fin origin. Pectoral fins distinctly exceeding pelvic fins in length. Appressed pectoral fins nearly reaching pelvic-fin insertion and distinctly reaching a point posterior to a vertical through one-half of distance from pectoral-fin insertion to pelvic-fin insertion in best-preserved specimens. Anal-fin base relatively short, 23.3% to 31.3% SL.

Discussion.—I recognize two species of *Coccorella* (fig. 22), *C. atlantica*, distributed in central water areas of the Atlantic, Indian, and Pacific Oceans, and *C. atrata*, distributed in equatorial water areas of the Indian and Pacific Oceans. The

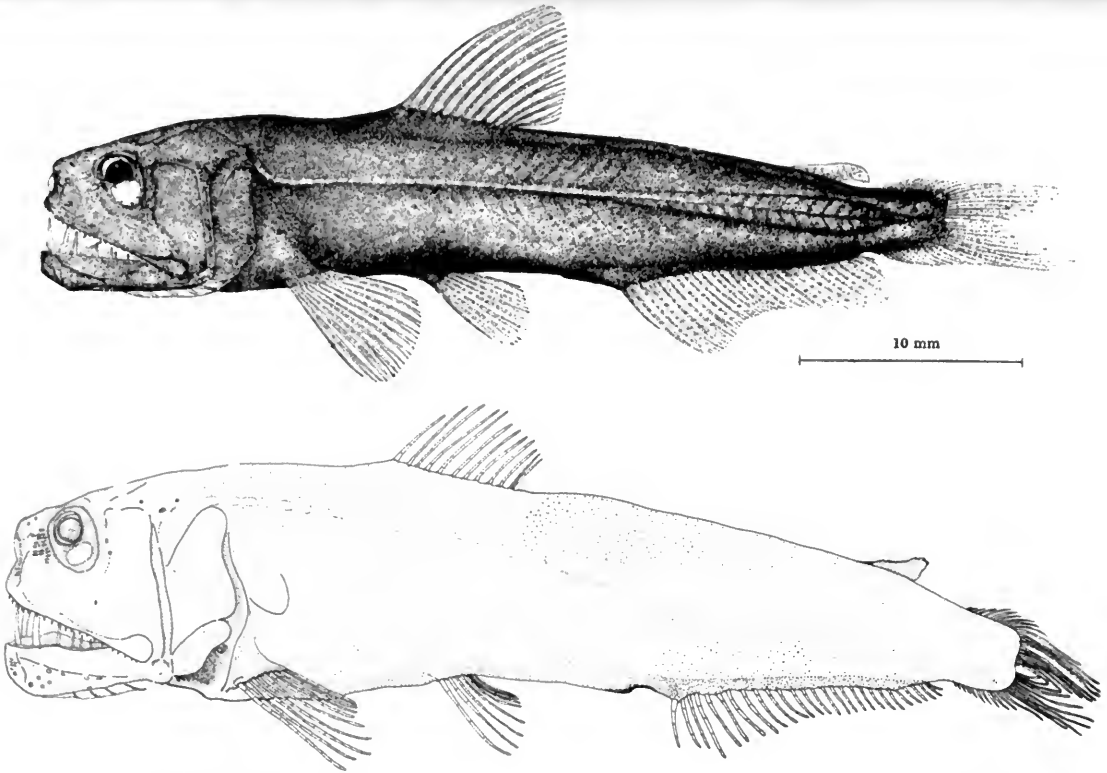


FIG. 22. The species of *Coccorella*. **Above,** *Coccorella atlantica,* 40.6 mm SL, Bingh. Oceanogr. Coll. 2141, lectotype of *Evermannella atrata atlantica* Parr 1928, after Rofen, 1966d, p. 531 (drawing by E. M. Soule). **Below,** *Coccorella atrata,* 79.5 mm SL, SIO 70-346.

two species can be distinguished on the basis of characters provided in the key on page 101 and by additional characters cited in the following discussion.

Rofen (1966d, p. 528) recognized only one species of *Coccorella*, *C. atrata* (Alcock), sinking in synonymy the supposed Atlantic subspecies *C. atrata atlantica* (Parr) (recognized by some authors as a full species). Among the most interesting taxonomic problems posed by the Evermannellidae has been to find characters separating the two species of *Coccorella* recognized herein, *C. atlantica* and *C. atrata*. The problem was the direct result of the discovery of an apparently ideal external and qualitative character separating the two forms—the number of pores in the frontal canal commissure (FCC) of the cephalic laterosensory system. In the vast majority (238 of 243) of specimens examined, the form herein recognized as *C. atlantica* has six pores in the frontal canal commissure, i.e., FCC=3 + 3 (fig. 23). Virtually all specimens (122 of 123) of the form herein recognized as *C. atrata* have four pores in the frontal canal commissure, i.e., FCC=2 + 2 (fig. 23). Parr's (1928, p. 167, fig. 40B) illustration shows the FCC=3 + 3 pattern in one of the syntypes of *C. atlantica*. Alcock's description and illustrations (Alcock, 1893, p. 182; Alcock, 1899, p. 167; Alcock & McArdle, 1900, plate 33, fig. 3; Alcock & MacGilchrist, 1905, plate 37, fig. 2) do not indicate the state of this character in Alcock's specimens of *C. atrata*. The FCC=2 + 2 pattern of *C. atrata* is shown in Brauer's (1906, plate 10, fig. 4) illustration of a specimen from 04° 05.1′ S, 73° 24.1′ E. Evidence presented below shows that Alcock's specimens from the Andaman Sea and Bay of Bengal may be associated with specimens of *Coccorella* exhibiting the FCC=2 + 2 pore pattern. The number of pores in the frontal canal commissure may be determined in all intact specimens exceeding 25 mm SL. Use of this one character to assign specimens to one or the other of the two species resulted in a nearly classic picture of *C. atlantica* as a biantitropical, central water species in all three oceans and *C. atrata* as an equatorial species limited to the Indian and Pacific oceans (fig. 24). All specimens from the Indian Ocean north of 10° S exhibit the 2 + 2 pore pattern, and thus this pattern may be associated with *C. atrata*.

The problem in using the number of pores in the frontal canal commissure as a character separating the two species arose from the discovery of four specimens in which the state of the head pore character was intermediate, i.e., FCC=2 + 3 (fig. 23). I later discovered two additional specimens exhibiting the FCC=2 + 2 pattern characteristic of *C. atrata* but agreeing in all other respects with specimens of *C. atlantica*. These six specimens, listed below, are hereafter termed "intermediate" specimens. The specimens are referred to in the following account and in the figures by the specimen numbers assigned below.

(1) ZMUC, D 3714 I, South China Sea, 15° 22′ N, 155° 20′ E, 1 (100.0). FCC=2 + 3 (left + right).
(2) ISH 1362/71, South Atlantic Ocean, 35° 32′ S, 10° 36′ E, 1 (109.0). FCC=3 + 2.
(3) ISH 1173/71, South Atlantic Ocean, 37° 08′ S, 05° 23′ W, 1 (77.5). FCC=3 + 2.
(4) ISH 847/71, South Atlantic Ocean, 39° 55′ S, 26° 02′ W, 1 (59.1). FC=3 + 2.
(5) ISH 1521/71, South Atlantic Ocean, 30° 04′ S, 05° 22′ E, 1 (141.5). FCC=2 + 2.
(6) WHOI, AB 13-23, eastern South Pacific Ocean, 33° 49 to 48′ S, 90° 07 to 19′ W, 1 (57.2). FCC=2 + 2.

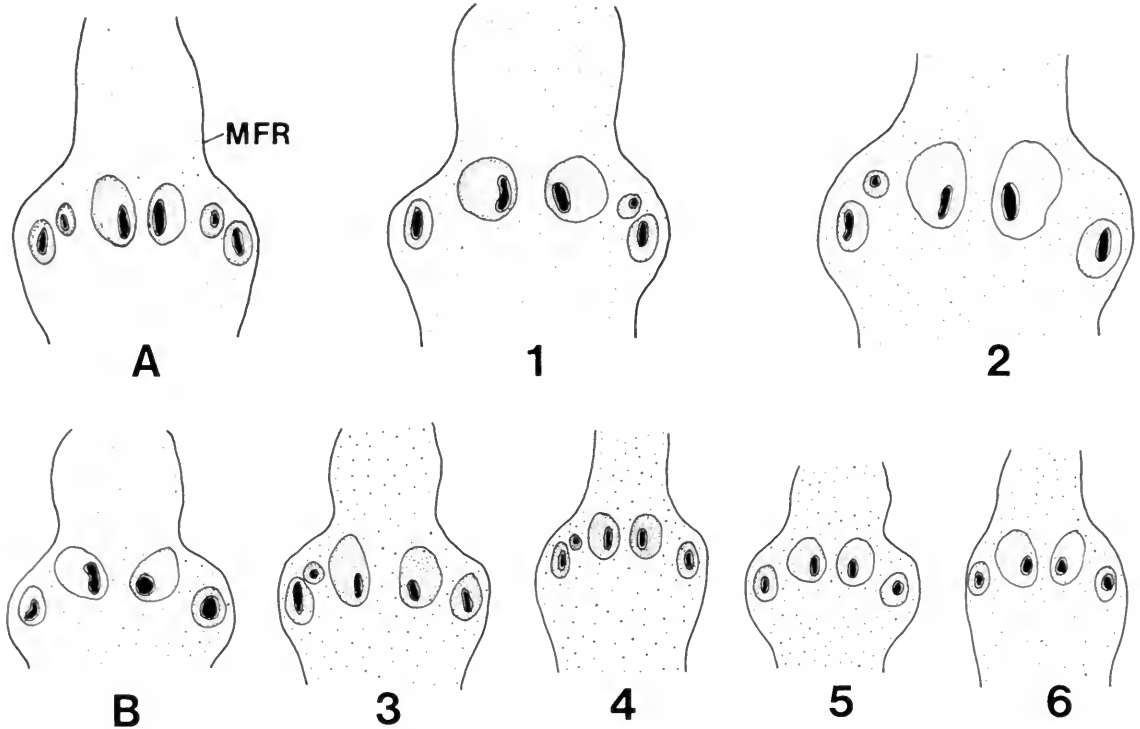


FIG. 23. Frontal canal commissure in *Coccorella*. See Figure 1 for location of frontal canal commissure and text for explanation of term "intermediate specimens." MFR=medial frontal ridge. **A**, *Coccorella atlantica*, UH 74/5/15, 82.2 mm; **B**, *Coccorella atrata*, SIO 70-346, 80.0 mm. **1–6**, "Intermediate specimens": **1**, ZMUC, D 3714 I, 100.0 mm; **2**, ISH 1362/71, 109.0 mm; **3**, ISH 1173/71, 77.5 mm; **4**, ISH 847/71, 59.1 mm; **5**, ISH 1521/71, 141.5 mm; **6**, WHOI, AB 13-23, 57.2 mm.

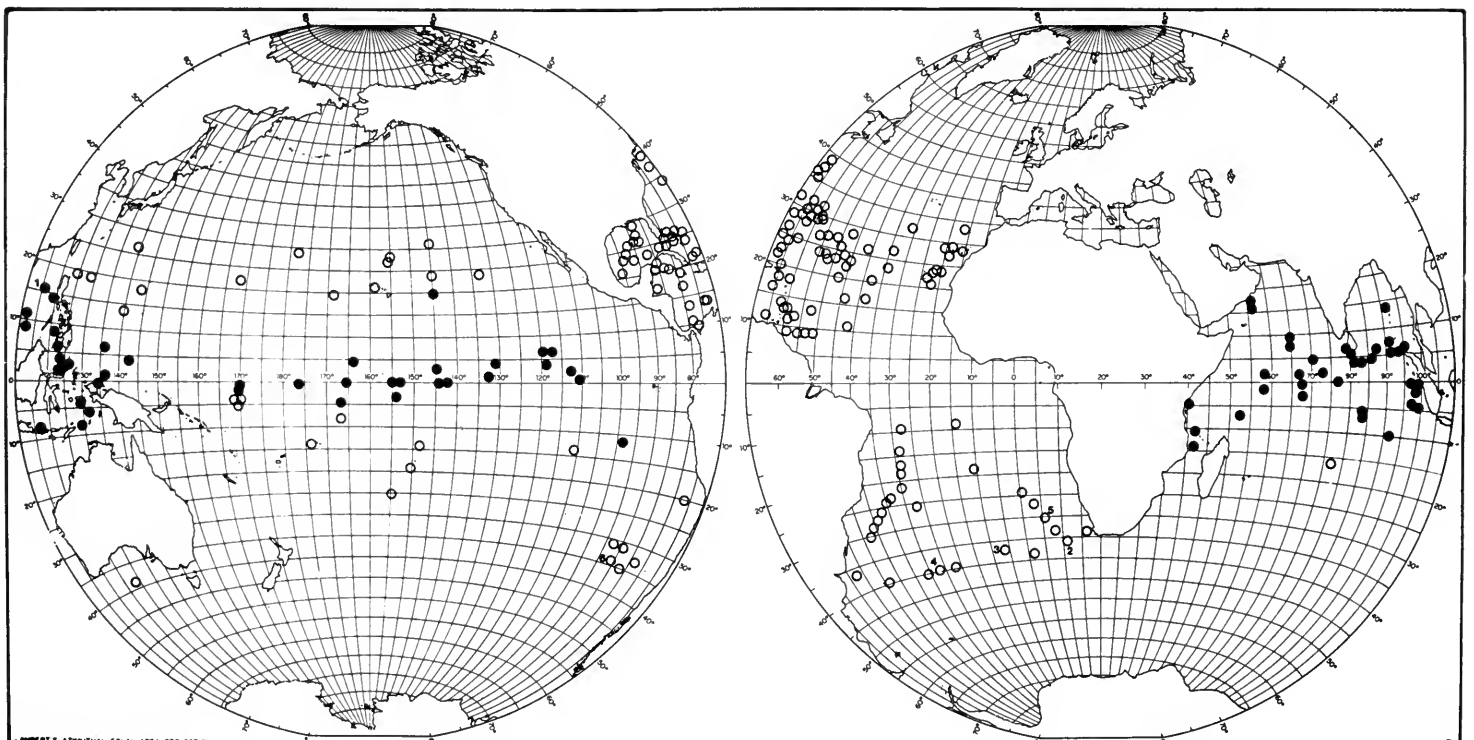


FIG. 24. Distribution of *Coccorella atlantica* (open symbols) and *Coccorella atrata* (closed symbols). Numerals indicate capture sites for the six specimens designated in the text as possible intermediates.

These six specimens of 360 total specimens of both species examined for this character could not be identified on the basis of number of pores in the frontal canal commissure. The two resulting problems were (1) to discover additional characters separating the two species and (2) to explain the abnormal FCC pore pattern in the six intermediate specimens. Two plausible explanations are (1) that the six intermediate specimens represent hybrids or (2) that the abnormal pore pattern in these six specimens was teratological in origin.

The two species do not differ in external meristic characters (tables 2, 3), in pigmentation, in gut morphology (Wassersug & Johnson, 1976), in dentition, nor in any readily recognizable qualitative feature other than head pore pattern. The two species differ without overlap in number of vertebrae (table 12): specimens with FCC=3 + 3 and assigned to *C. atlantica* have 48 to 50 vertebrae, specimens with FCC=2 + 2 and assigned to *C. atrata* have 45 to 47 vertebrae. This distinction remains true throughout the range of each form. The six intermediate specimens are not intermediate in number of vertebrae (table 12), specimen (1) agreeing with *C. atrata*, specimens (2 to 6) agreeing with *C. atlantica*. The capture site of each of the intermediates similarly agrees with this assignment, specimen (1) taken within the known range of *C. atrata*, specimens (2 to 6) taken within the known range of *C. atlantica* (fig. 24). It is interesting, if probably coincidental, that specimen (1) has the FCC=2 + 3 (left + right), whereas specimens (2, 3, 4) have the FCC=3 + 2 (left + right). The apparent bimodal distribution of number of vertebrae in the intermediate specimens favors the hypothesis that the abnormal FCC pore pattern in these specimens is of teratological rather than hybrid origin. Additional attempts to confirm this tentative conclusion were based on morphometric characters.

TABLE 12. Number of vertebrae in species of *Coccorella*. Geographic areas as defined in Figure 26.

Species and geographic area	No. of vertebrae						
	45	46	47	48	49	50	N
C. atrata							
ION	1	5	2	—	—	—	8
IWP	1	7	—	—	—	—	8
CEP	—	2	3	—	—	—	5
C. atlantica							
NA	—	—	—	3	6	—	9
SA	—	—	—	2	6	—	8
IOS	—	—	—	1	1	—	2
NP	—	—	—	2	2	—	4
SP	—	—	—	—	5	2	7
C. atrata (totals)	2	14	5	—	—	—	21
C. atlantica (totals)	—	—	—	8	20	2	30
Intermediates							
1	—	X	—	—	—	—	
2	—	—	—	—	X	—	
3	—	—	—	—	X	—	
4	—	—	—	—	X	—	
5	—	—	—	X	—	—	
6	—	—	—	—	X	—	

TABLE 13. Comparison of values for five morphometric characters (and range of SL) between North Atlantic (NA) specimens of *Coccorella atlantica* and northern Indian Ocean (ION) specimens of *C. atrata*.

Character	*Coccorella atlantica* from NA (N=20)	*Coccorella atrata* from ION (N=17)
	A. RANGE OF VALUES	
SL (mm)	34.0–142.7	36.2–104.6
BDAO	149–174	171–203
ADC	108–133	122–141
PD	416–448	394–429
POHL	133–157	147–183
IO	32–39	47–61
	B. MEAN ± 95% LIMITS	
BDAO	161.65±3.03	<180.47±3.74
ADC	121.35±3.13	<133.65±2.83
PD	428.10±4.40	>411.94±4.96
POHL	144.25±2.76	<166.24±4.44
IO	35.95±1.07	< 52.59±1.61

KEY: BDAO=body depth at anal-fin origin; ADC=distance from adipose-fin base to bases of midcaudal rays; PD=distance from snout to dorsal-fin origin; POHL=postorbital head length; IO=interorbital width.

In my attempt to find morphometric characters useful in separating *C. atlantica* and *C. atrata*, I first compared results for 20 specimens assigned to *C. atlantica* from the North Atlantic with results for 17 specimens assigned to *C. atrata* from the northern Indian Ocean. Of the 29 measurements per specimen (see Methods), values for five characters (table 13) sufficiently differed between the two species to be of possible value in separating the two forms. Only one of these characters, interorbital width, showed separation without overlap (table 13), and this separation held throughout subsequent study (fig. 25). The interorbital width is 3.2% to 4.7% SL in *C. atlantica* vs. 4.7% to 6.1% SL in *C. atrata*.

If the intermediate specimens are hybrids, they might be expected to show intermediate values of these five morphometric characters. If true, then each of the six intermediates should exhibit an intermediate value of a combined character index based on all five characters. The combined character index for each specimen was computed as the sum of a standard score for each character for each specimen. The standard score was constructed by adjusting the value for each character for each specimen relative to a mean value of 100 for each character for all specimens of *C. atlantica* from the North Atlantic Ocean. The standard score and the combined character index were computed as follows:

$$(1)\ Y_{i,j} = (X_{i,j}/SL_j) \times 1{,}000$$

where $X_{i,j}$ represents the original measurement (in mm) for character i on specimen j, SL_j is the standard length (in mm) of specimen j, and $Y_{i,j}$ is the raw measurement expressed in thousandths of the standard length.

$$(2)\ M_i = (\Sigma_j\ Y_{i,j}) / N_i$$

where N_i is the number (=20) of North Atlantic specimens of *C. atlantica* measured for each character, and M_i is the mean value for each character for these specimens.

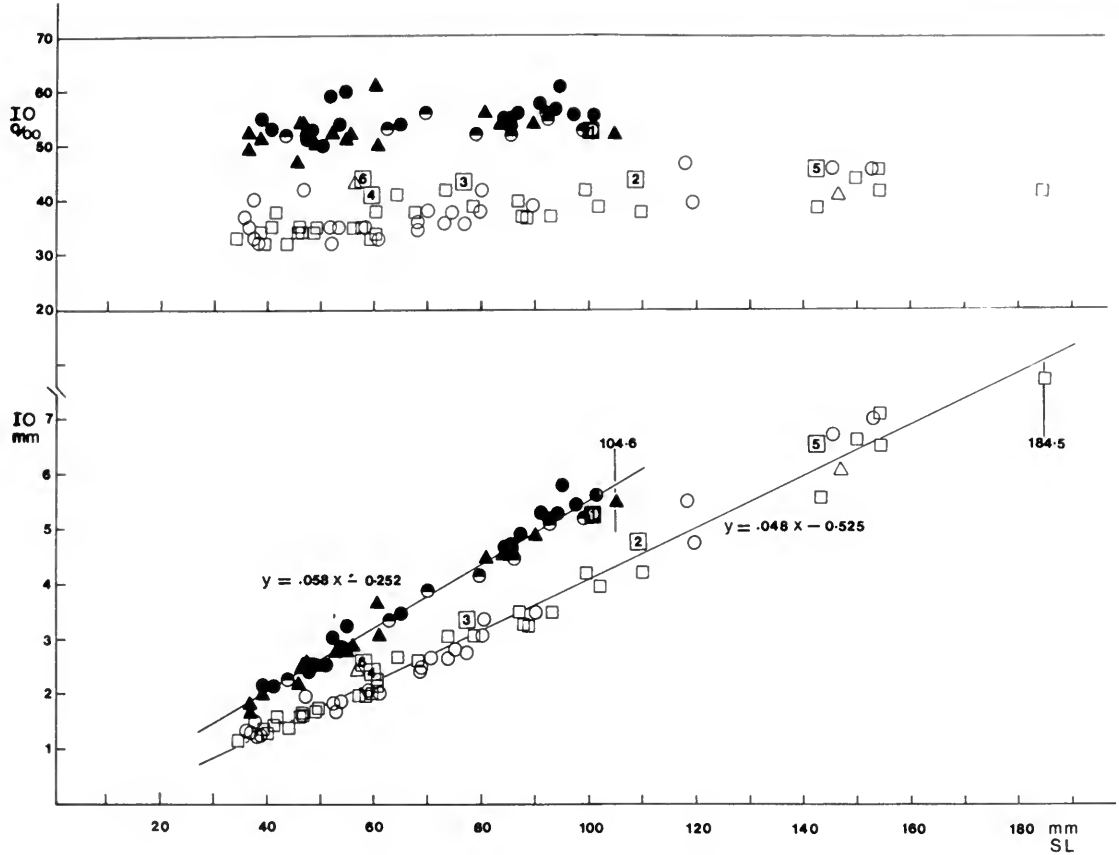


FIG. 25. Interorbital width plotted against standard length (abscissa) for specimens of *Coccorella*. **Upper:** Interorbital width expressed as thousandths of the standard length (ordinate). **Lower:** Interorbital width in mm (ordinate). Geographic areas as defined in Figure 26. SYMBOLS: *Coccorella atlantica* (open symbols)—□ = NA, SA; △ = IOS; ○ = NP, SP. *C. atrata* (closed symbols)—▲ = ION; ◓ = IWP; ● = CEP. Intermediates denoted by symbols enclosing numerals.

$$(3)\ Z_{i,j} = (Y_{i,j}/M_i) \times 100$$

where $Z_{i,j}$ is the standard score for each character for each specimen.

$$(4)\ CI_j = Z_{1,j} + Z_{2,j} + (-Z_{3,j}) + Z_{4,j} + Z_{5,j}$$

where Z_1 is the standard score for each specimen for body depth at anal-fin origin, Z_2 corresponds to distance from adipose-fin base to bases of midcaudal rays, Z_3 corresponds to distance from snout to dorsal-fin origin, Z_4 corresponds to postorbital head length, Z_5 corresponds to interorbital width, and CI_j is the combined character index for each specimen.

Combined character indices were determined for 62 specimens assigned to *C. atlantica*, 44 specimens assigned to *C. atrata*, and the six intermediate specimens. The specimens were chosen from throughout the range of each species (figs. 24, 26) and represented the full size range (by 10-mm increments) of post-metamorphic juveniles and adults available from each of the eight subareas of the total range of *Coccorella* (*C. atlantica:* North Atlantic, 20 [34.0–142.7]; South Atlantic, 12 [40.8–184.5]; southern Indian Ocean, 2 [56.2–146.2]; North Pacific, 11 [37.2–79.6]; South Pacific, 17 [35.5–152.5]; *C. atrata:* northern Indian Ocean, 17 [36.2–104.6]; insular western Pacific, 11 [43.2–98.6]; equatorial Pacific, 16 [38.7–100.9]).

A plot (fig. 27) of the combined character indices for the 68 specimens included in the analysis shows a clear separation between the two species and also shows that the six intermediates do not tend to group between the two modes but rather agree with the results for number of vertebrae and the distributional data in allowing the clear assignment of specimen (1) to *C. atrata* and specimens (2 to 6) to *C. atlantica*.

Application of multivariate techniques to this problem yielded virtually identical results. Canonical analysis of the data was performed using the program BMD 07M (Dixon, 1968). In each case the previously determined groups were identical to those used for the character index comparison (fig. 27), with the following exceptions: (1) data for the two Indian Ocean specimens of *C. atlantica* were combined with data for the South Atlantic specimens of this species in one group; (2) in the first run of the data, values for the intermediate specimens were not included (fig. 28A); (3) in the second run, values for the intermediate specimens were included with data for the geographically most adjacent group (i.e., specimen (1) was included with IWP [fig. 28B], specimens (2, 3, 4, 5) with SA, specimen (6) with SP); (4) in the third run, values for the intermediate specimens were included as one separate group—the purpose of this being to test whether or not the analysis accepted the six intermediates as one group. Although the data for each character for each specimen were entered as ratios, i.e., expressed as thousandths of the standard length, at least part of the objection to this procedure is countered by my effort to equally represent in the data all size classes (by 10-mm increments) for each area for each species (table 14). Obviously this was not possible for specimens exceeding 104.6 mm SL (the length of the largest known individual of *C. atrata*). The results of this analysis, based on the five characters (table 13) included in the combined character index analysis, compare favorably with results for vertebral number and for the character index analysis, i.e., intermediate specimen (1) clusters with *C. atrata*, intermediate specimens (2 to 6) cluster with *C. atlantica* (fig. 28C). I have run the same analysis using 20 of the 29 morphometric characters (excluding those showing obvious

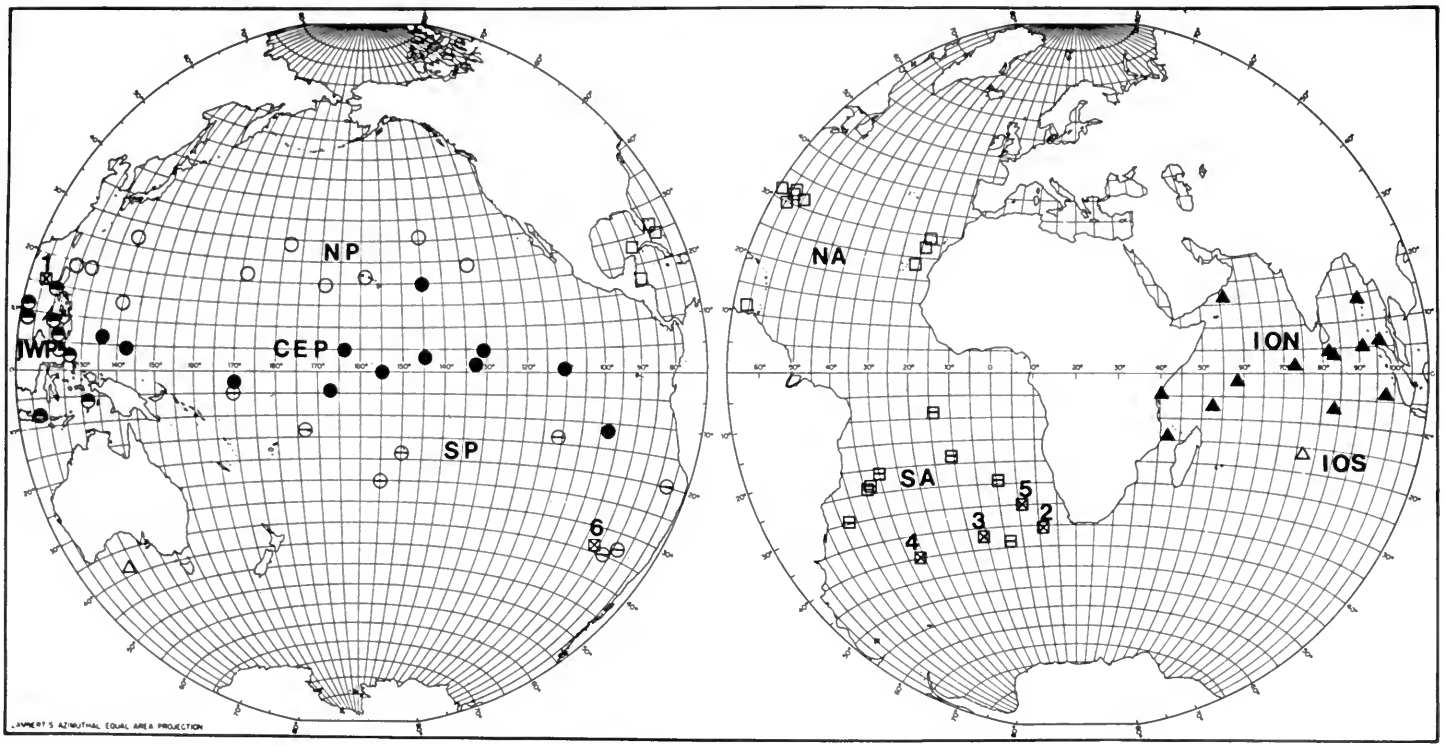


FIG. 26. Geographic distribution of specimens of *Coccorella* used in morphometric analyses. SYMBOLS: *C. atlantica*—□ = NA; ⊟ = SA; △ = IOS; ○ = NP; ⊖ = SP. *C. atrata*—▲ = ION; ◓ = IWP; ● = CEP; ⊠ = intermediates.

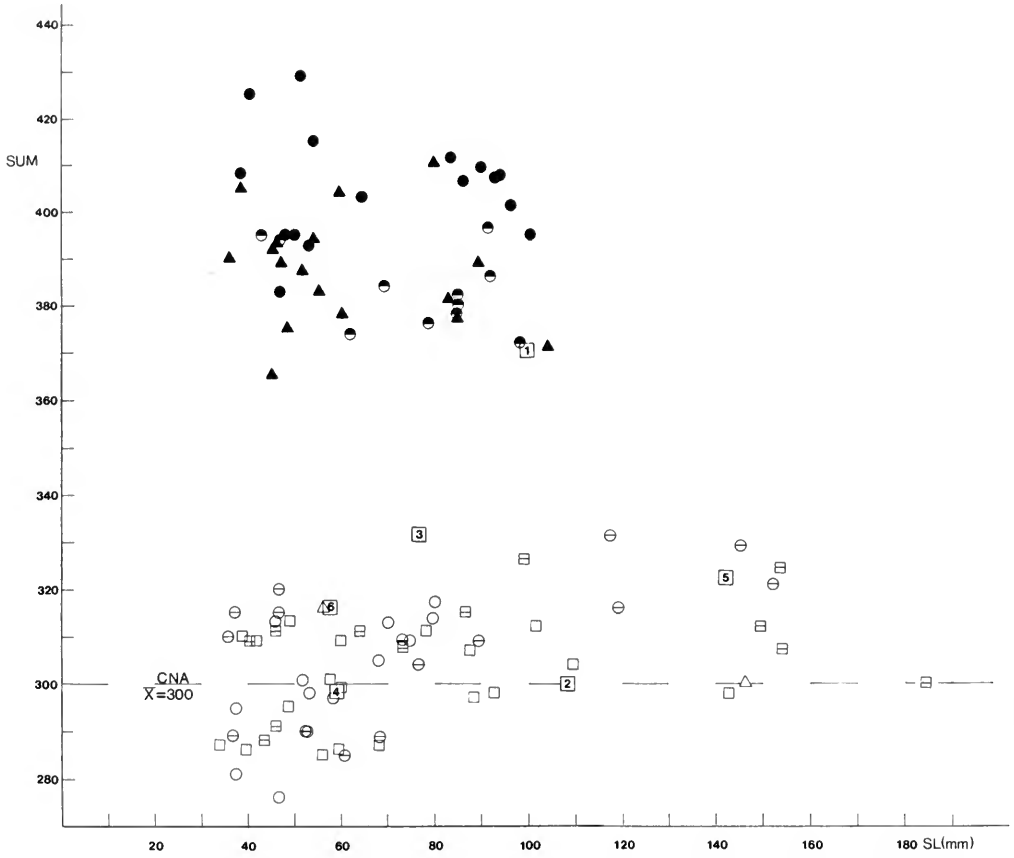


FIG. 27. Combined character index (ordinate) plotted against standard length (abscissa) for 68 specimens of *Coccorella*. See text for derivation of values of combined character index. Geographic areas as defined in Figure 26. SYMBOLS: *Coccorella atlantica* (open symbols)—□ = NA; ⊟ = SA; △ = IOS; ○ = NP; ⊖ = SP. *Coccorella atrata* (closed symbols)—▲ = ION; ◓ = IWP; ● = CEP. Intermediates denoted by symbols enclosing numerals.

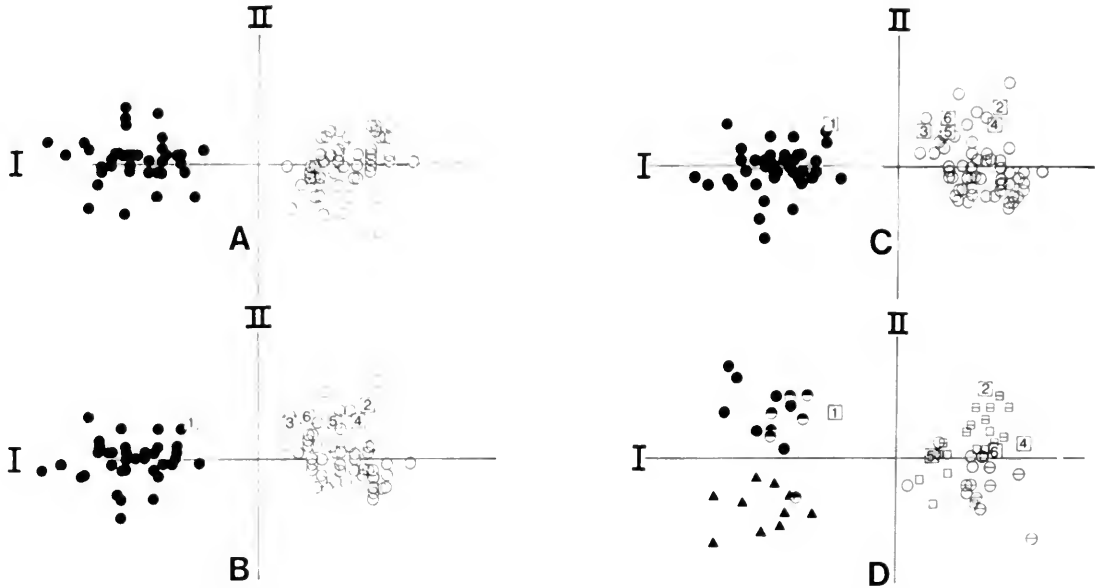


FIG. 28. Canonical variate analysis of morphometric characters in *Coccorella*. Only the first two canonical variates are plotted. Geographic areas are those defined in Figure 26 and in each case included the following: *C. atlantica* (open symbols)—NA, SA + IOS, NP, SP; *C. atrata* (closed symbols)—ION, IWP, CEP. Intermediate specimens denoted by symbols enclosing numerals. Due to considerable overlap, the geographic subareas are not distinguished in **A, B,** or **C,** and some overlapping or closely adjacent points have been omitted. See text for additional explanation. **A,** Based on five measurements and seven groups, intermediate specimens excluded from the analysis. **B,** Based on five measurements and seven groups, with data for each intermediate specimen included with that group geographically closest to the site of capture of each intermediate. **C,** Based on five measurements and eight groups, with all six intermediates included as one separate group. **D,** Based on 20 measurements and eight groups, with five of the intermediates included as one separate group. SYMBOLS: *C. atlantica* (open symbols)—□ = NA; ⊟ = SA + IOS; ○ = NP; ⊖ = SP. *C. atrata* (closed symbols)—▲ = ION; ◓ = IWP; ● = CEP.

TABLE 14. Representation by size class (10-mm increments) of specimens of *Coccorella* in canonical analysis of five morphometric characters. Geographic areas as defined in Figure 26. See text for additional explanation.

Size class (mm)	Geographic areas							
	C. atlantica				*C. atrata*			
	NA	SA + IOS	NP	SP	ION	IWP	CEP	Intermediates (all specimens)
	No. of Specimens							
30.0–39.9	3	0	2	3	2	0	1	0
40.0–49.9	3	4	1	3	5	2	3	0
50.0–59.9	3	1	3	2	3	0	4	2
60.0–69.9	4	1	2	1	2	2	1	0
70.0–79.9	1	1	3	2	0	1	0	1
80.0–89.9	2	1	0	2	4	3	2	0
90.0–99.9	1	1	0	0	0	3	4	0
100.0–109.9	2	0	0	0	1	0	1	2
= > 110.0	1	5	0	4	0	0	0	1
Totals	20	14	11	17	17	11	16	6

allometric growth) for 37 specimens of *C. atlantica*, 24 specimens of *C. atrata*, five of the six intermediates (it was impossible to determine values for certain characters in specimen (3) due to damage to the specimen), and from throughout the geographic range and over the post-metamorphic size range of *Coccorella*. Results for this analysis (fig. 28D) are virtually identical with results based on the five selected characters.

I believe that the conclusions to be drawn from these results are (1) that there exist two discretely recognizable species of *Coccorella*, *C. atlantica* and *C. atrata*, and (2) that the six intermediate specimens do not represent hybrids and that the abnormal state of the frontal canal commissure in each is probably the result of a developmental accident.

Two additional points derived from this study of *Coccorella* seem worthy of mention at this point:

(1) *Coccorella atlantica*, the central water species, apparently grows to nearly twice the size of *C. atrata*, the species found in more productive equatorial waters (figs. 24, 25). The largest known specimen of *C. atlantica* is 184.5 mm SL, whereas the largest known specimen of *C. atrata* is 104.6 mm SL. Ebeling (1962, pp. 145-147) discusses at some length the apparent trend among species of *Melamphaes* for areas of lower biological productivity to be occupied by smaller-bodied species (viz., "dwarf" species of the *M. simus* group). Certainly no evidence for such "dwarfing" of central water species is to be found in comparing *C. atlantica* with *C. atrata;* in fact the reverse appears to be true. Dr. Gerhard Krefft (in a letter) cites evidence that in the circumtropical, mesopelagic gonostomatid *Diplophos taenia* (see Johnson & Barnett, 1972, 1975) populations in areas of higher productivity are smaller-bodied than those in areas of lower productivity. Krefft found that specimens from the relatively productive equatorial Atlantic area (ca. 20° N to 07° S at about 20° W) represented a "dwarf" form, sexually mature at less than 100 mm SL. Specimens from the central South Atlantic (ca. 20° to 40° S), an area of relatively low biological productivity, included

"giants," reaching 265 mm in SL and not attaining sexual maturity until a size of 150 mm SL or larger. Thus, what appears to be true between species in *Coccorella* may be true between populations in *Diplophos*, i.e., populations or species found in the areas of lowest productivity attain the largest adult body sizes. In general this trend, if true, parallels the conclusion offered by Ebeling & Cailliet (1974) that forms inhabiting zones of lower food availability tend to have larger bodies with consequently larger mouths, allowing the capture and ingestion of a wide range of food particle sizes.

(2) The difference in vertebral counts between *C. atlantica* (48 to 50) vs. *C. atrata* (45 to 47) parallels the results of Johnson & Barnett (1972, 1975), who showed that populations of widely ranging species inhabiting areas of lower productivity tend to exhibit higher values of longitudinal meristic characters than populations inhabiting areas of higher productivity. The results for *C. atlantica* and *C. atrata* suggest, at least, that this trend may also prove true for comparisons between closely related species.

Coccorella atlantica (Parr 1928), Figure 22

Evermannella atrata atlantica Parr 1928, p. 166 (original description, seven syntypes from off the Bahamas); Parr, 1929, p. 21 (osteology); Parr, 1930, p. 154 (synonymy); Grey, 1955, p. 284 (report of two specimens taken off Bermuda, one of these specimens later reidentified as *Evermannella indica* by Rofen, 1966d, p. 536).

Coccorella atlantica Wassersug & Johnson 1976, p. 273 (gut morphology, illustration of larval and juvenile specimens, records from Atlantic, Indian, and Pacific oceans); Herring, 1977, p. 306 (name only).

Coccorella atrata Rofen 1966d, p. 528 (not *Coccorella atrata* Alcock 1893, description, records from western North Atlantic); Johnson, 1974c, p. 30 (not *Coccorella atrata* Alcock 1893, record from central North Pacific).

Coccorella atrata atlantica Roule 1929, p. 11 (original description, not based on *Evermannella atrata atlantica* Parr 1928, type from eastern North Atlantic).

Evermannella atlantica Beebe 1937, p. 205 (record from off Bermuda).

Odontostomops sp. A, Schmidt 1918, p. 33 (illustration of 9-mm specimen from western North Atlantic, records from North Atlantic Ocean).

Lectotype.—Bingham Oceanographic Collection No. 2141, 1 (40.6). Western North Atlantic, 23° 58′ N, 77° 26′ W (7,000 ft wire), Nov. 2–3, 1927. Parr (1928, p. 166) based his description of *Evermannella atrata atlantica* on seven specimens from five collections. Of this series of syntypes the specimen herein designated as the lectotype was the largest and the specimen labeled as the holotype by Parr (see Rofen, 1966d, p. 528).

Diagnosis.—A species of *Coccorella* with 48 to 50 vertebrae, typically (238 of 243 specimens examined for this character) with six pores, 3 + 3, in the frontal canal commissure of the cephalic laterosensory system (fig. 23) and interorbital width = 3.2% to 4.7% SL. Detailed comparisons of the two species of *Coccorella* are given above, following the description of the genus.

Description.—Values for meristic characters are presented in Tables 2 and 3.

PROPORTIONAL DIMENSIONS: Based on 37 (36.0–184.5 mm SL) specimens from throughout the range of the species. Expressed as thousandths of the SL and given as the mean and range (values in parentheses).

Body: depth at anal-fin origin, 163 (144–191). Caudal peduncle: least depth, 74 (60–87); length, 94 (77–105). Adipose fin: distance to midcaudal rays, 122 (108–141); distance to dorsal-fin base, 338 (306–365). Anal fin: length of base, 256

(233–283). Dorsal fin: length of base, 113 (99–132); dorsal-fin origin to anal-fin origin (distance between verticals), 260 (232–287); end of dorsal-fin base to base of midcaudal rays, 501 (472–527). Pelvic-fin insertion to anal-fin origin: 217 (193–239). Pectoral-fin insertion to pelvic-fin insertion: 204 (164–247). Anus to anal-fin origin: 63 (27–104). Distance from snout to: anus, 610 (558–673); dorsal-fin origin, 432 (414–459); adipose fin, 839 (800–864); anal-fin origin, 665 (631–707); pectoral-fin insertion, 258 (234–287); pelvic-fin insertion, 451 (418–501); anterior margin of eye (=snout length), 59 (51–69). Head length: 222 (196–243). Postorbital head length: 142 (122–157). Eye: horizontal diameter, 53 (40–65); vertical diameter, 56 (42–76). Upper jaw length: 172 (157–184). Lower jaw length: 171 (151–188). Longest dentary tooth: 52 (41–63). Longest palatine tooth: 84 (71–96). Interorbital width (based on 62 [34.0–184.5 mm SL] specimens): 38 (32–47).

BODY: Body moderately elongate, largest known specimen 184.5 mm SL (Atlantic Ocean, ISH 1436/68). Body moderately deep, body depth at anal-fin origin, 14.4% to 19.1% SL. Anus distinctly posterior to a point midway between pelvic-fin insertion and anal-fin origin. Lateral line extending to a point over anterior one-third of anal-fin base and composed of 34 or fewer segments. About eight pairs of sensory (presumably) papillae along dorsal margin of body anterior to dorsal-fin origin.

CEPHALIC LATEROSENSORY PORES: Snout-pad pore formula: 2 + 4 + 2 + 1 + 2. Mandibular pore formula: 5 + 6 + 2 + 1. Preopercular pores: ? 3 + 3. Temporal pores: PPTO = 1, PESC = 4. Frontal pores: PPF = 1. Frontal canal commissure: 3 + 3 (in 238 of 243 specimens examined, a discussion of the five specimens assigned to *C. atlantica* and not agreeing in this character is given above). Infraorbital pores: 13 or 14 + 9. Numerous sensory (presumably) papillae distributed over occiput, interorbital region, snout, cheeks, and anterior lower jaw.

MOUTH: Upper jaw extending to or nearly to anterior margin of preopercle, well past a vertical through posterior margin of eye. Lower jaw projecting anteriorly very slightly beyond snout.

Tooth counts given below are based on 11 (48.7–146.2 mm SL) specimens. Premaxillary teeth small, retrorse, uniserial, numbering 29 to 55 in the 11 specimens counted. Dentary with two smaller fangs anteriorly near symphysis followed by nine to 17 unbarbed larger fangs arranged uniserially. The largest fangs occur anteriorly. Vomer with one small tooth on each side, but in numerous specimens only a single, laterally positioned tooth is present, its counterpart probably being lost. Anteriormost palatine tooth an enormous, unbarbed, saber-like fang, easily the largest tooth on each side, noticeably exceeding the snout length in length. Anteriormost palatine fang separated from posterior palatine teeth by a distinct gap. Posterior palatine teeth numbering six to nine in the 11 specimens counted. Number of premaxillary, dentary, and palatine teeth higher in larger specimens.

COLOR: Color in alcohol a dark brown over head, body, and fins, without any distinct concentration into stripes, bars, or markings. In well-preserved specimens a brassy green, iridescent layer is present along flanks, beneath eyes, and on cheeks. In fully metamorphosed specimens less than 60 mm SL a distinct and typically elliptical lens pad is present. In larger specimens there is no distinct lens pad as in *Evermannella*, but an opaque (presumably transparent in life),

glistening tissue centered beneath the lens is probably similar in function. Midventral areas of body anterior to anal-fin origin with especially dense pigmentation except for areas of luminous tissue (see above). Peritoneum dense black.

Discussion.—Rofen (1963, p. 2; 1966d, p. 536) synonymized *Evermannella atrata atlantica* Parr 1928 with *Coccorella atrata* (Alcock); stated that the range of *C. atrata* included the North Atlantic Ocean, Bay of Bengal, and Andaman Sea; and described *Odontostomops braueri* based on Brauer's (1906, pp. 136, 137, plate 10, figs. 3, 4) description and illustrations of a specimen Brauer identified as *Evermannella atrata* (Alcock). As I have shown, there are two clearly separable species of *Coccorella,* and the species occurring in the North Atlantic (*C. atlantica*) is not conspecific with the species occurring in the northern Indian Ocean (*C. atrata*). Because Rofen's description of *C. atrata* is based on nine specimens from the North Atlantic, including four syntypes of *E. atrata atlantica* and five specimens from off Bermuda, it is clear that these specimens in fact belong to *C. atlantica*. This is confirmed by reading Rofen's (1966d, pp. 529–534, figs. 194, 195) excellent description of his specimens and by my reexamination of the Bermuda specimens now deposited at Field Museum of Natural History. Further, because Brauer's (1906) specimen possessed a semitubular eye, huge but unbarbed fangs on the palatine bone, and other characters diagnostic for *Coccorella* (Brauer 1906, pp. 136, 137, plate 10, figs. 3, 4); was taken well within the known Indian Ocean range of *C. atrata* (it was taken at 04° 5.1′ S, 73° 24.1′ E, cf. fig. 24), and exhibits 2 + 2 pores in the frontal canal commissure (Brauer, 1906, plate 10, fig. 4). I assign *Odontostomops braueri* Rofen to the synonymy of *Coccorella atrata* (Alcock).

Geographic Variation.—Although mean values for number of anal-fin rays are higher (table 15) in Pacific samples of *C. atlantica* than in Atlantic samples, the differences between mean values for Pacific vs. Atlantic specimens are not statistically significant ($p > .05$). Thus, the question of whether there exists geographic variation in this character awaits resolution based on additional material.

Distribution.—*Coccorella atlantica* is known from central water areas of the Atlantic, Indian, and Pacific oceans (fig. 24). Only two specimens from two lots are known from the Indian Ocean (IOAN, V 4603, 16° 05′ S, 76° 16′ E, 1 (56.0); SOSC, ELT 35-2271, 38° 12′–06.2′ S, 128° 01.0′ to 127° 57.5′ E, 1 [146.5]). The distribution of *C. atlantica* and *C. atrata* is compared above, and the distribution of *C. atlantica* is compared with that of other central water species in a subsequent section of this paper.

Larvae and small juveniles (to 30 mm SL) of *C. atlantica* have been taken commonly in the upper 125 m, but very few records are from hauls to depths less than 50 m. Most adults (greater than 50 mm SL) were taken in hauls to depths exceeding 500 m, but both juveniles and adults have been taken on numerous

TABLE 15. Geographic variation in number of anal-fin rays in *Coccorella atlantica.*

Area	No. of anal-fin rays					N	Mean ± 95% limits
	26	27	28	29	30		
North Atlantic	—	9	44	2	—	55	27.87±.117
South Atlantic	1	5	11	—	—	17	27.59±.318
Indian	—	1	1	—	—	2	27.50
North Pacific	—	1	13	4	1	19	28.26±.315
South Pacific	—	2	10	5	—	17	28.18±.327

occasions in hauls to between 100 and 400 m. Larvae and small juveniles have been taken throughout the year.

Material Examined.—A total of 403 (6.2–184.5 mm SL) specimens from 269 collections.

ATLANTIC OCEAN. A total of 344 (6.2–184.5 mm SL) specimens from 218 collections. FMNH: 49985 (1), 49987 (1), 66096 (2), 78579 (1). IOAN: AK 826 (1). ISH: 86/66 (1), 186/66 (2), 230/66 (2), 676/66 (1), 702/66 (1), 722/66 (1), 766/66 (1), 786/66 (1), 824/66 (1), 1168/68 (1), 1281/68 (2), 1318/68 (1), 1350/68 (1), 1369/68 (1), 1436/68 (1), 2127/68 (1), 628/71 (1), 802/71 (1), 847/71 (1), 919/71 (2), 1106/71 (2), 1135/71 (1), 1173/71 (1), 1227/71 (1), 1362/71 (1), 1431/71 (1), 1436/68 (1), 1521/71 (1), 1562/71 (2), 1613/71 (1), 1632/71 (1), 1986/71 (2), 2034/71 (1), 2884/71 (1), 2939/71 (3). SIO: 63-552 (1). UMML: 9047 (2), 11832 (2), 11875 (1), 14897 (1), 15903 (1), 15906 (1), 17784 (1), 18355 (1), 22987 (1), 24178 (2), 26439 (1), 26452 (1), 27278 (1), 27728 (1), 27906 (1), 29435 (1), 29456 (1). USNM, UNCAT.: ORE 3219 (1), ORE 4569 (1), UND 1966-3, 17 (1); USNM, ACRE: 1-4A (1), 1-31 (1), 4-30 A-D (1), 7-13 (1), 8-2 (1), 8-3 (2), 10-15m (1), 11-10c (1), 12-18A (1), 12-53 (1), 12-56 (1), 12-63 (2), 12-64 (1), 12-67 (1), 12-69 (3), 12-70 (3), 12-72 (2), 12-79 (1), 12-81 (2), 12-83 (1). WHOI, RHB: 867 (2), 873 (1), 910 (1), 1101 (2), 1112 (1), 1261 (2), 1263 (7), 1264 (2), 1271 (1), 1274 (7), 1281 (5), 1282 (3), 1287 (1), 1289 (1), 1290 (23), 1291 (2), 1294 (2), 1297 (2), 1300 (1), 1302 (1), 1307 (2), 1308 (1), 1309 (1), 1310 (3), 1313 (2), 1428 (1), 1441 (1), 1505 (12), 1509 (7), 1713 (3), 1716 (1), 1718 (1), 1728 (1), 1731 (1), 1737 (4), 2024 (1), 2093 (1), 2100 (1), 2111 (1), 2904 (1), 2908 (1), 2913 (1), 2917 (1), 2926 (1), 2945 (1), 2946 (2), 2948 (1), 2951 (2), 2956 (1), 2957 (2), 2960 (2), 2962 (1), 2965 (2), 2976 (1), 2985 (2), 2990 (1), 2993 (1), 3003 (2), 3014 (1), 3015 (1), 3017 (1), 3018 (2), 3021 (1), 3104 (2), 3105 (1), AEJ 008 (1). ZIZM: RBF #32 (1). ZMUC: D 859 (1), D 1041 (1), D 1043 (1), D 1180 (1), D 1182 II (1), D 1183 VIII (3), D 1190 I (1), D 1238 I (1), D 1256 II (1), D 1339 II (1), D 1342 VIII (1), D 4014 IV (1).

Additional larvae and juvenile material from the Atlantic Ocean. CAS: CAS 14857 (4), SU 57717 (1). USNM, ACRE: 3-13 (1), 3-14 (1), 10-38N (2), 12-1B (1), 12-13B (2), 12-13C (4), 12-13M (1), 12-14B (1), 12-14M (1), 12-34M (2), 12-36B (1). ZMUC: D 839 (1), D 842 (1), D 845 (3), D 855 XVII (3), D 855 XVIII (1), D 856 VII (1), D 857,150 mwo (2), D 857,200 mwo (1), D 863 (2), D 864 (1), D 865 (1), D 944 (2), D947,300 mwo (1), D 947,400 mwo (1), D 947,1000 mwo (1), D 948 (1), D 949 (1), D 1157 V (1), D 1185 IX (1), D 1186 VII (1), D 1189 VII (1), D 1195 II (3), D 1217 V (1), D 1218 II (1), D 1228 II (4), D 1229 II (1), D 1230 IV (1), D 1231 II (1), D 1239 II (1), D 1239 IV (1), D 1239 VI (1), D 1241 VII (2), D 1242 IX (2), D 1242 XV (1), D 1243 III (4), D 1253 II (1), D 1261 II (1), D 1267 IV (1), D 1283 X (1), D 1285 III (1), D 1322 IX (1), D 1323 VIII (2), D 1323 XIV (1), D 1327 II (1), D 1332 XV (1), D 1335 V (1).

INDIAN OCEAN. A total of two (56.0–146.5 mm SL) specimens from two collections. IOAN: V 4603 (1). SOSC: ELT 35-2271 (1).

PACIFIC OCEAN. A total of 57 (15.7–175.0 mm SL) specimens from 49 collections. IOAN: AK 236 (1), V 6033 (1), V 6493 (3). NMFS (LJ): J 24.133 (1), J 24.145 (1), J 31.145 (1). ORSTOM: CY III-18 (1), CY VI-16 (2). SIO: 61-47 (1), 64-482 (1), 68-442 (1), 68-490 (1), 69-341 (1), 69-354 (1), 70-102 (1), 70-110 (1), 70-121 (1), 70-311 (1), 70-331 (1), 70-336 (1), 71-297 (1), 71-301 (1), 71-310 (1), 72-9 (1), 72-24 (2), 72-304 (1), 72-305 (1), 72-308 (1), 72-316 (1), 72-321 (1), 73-322 (1), 76-121 (1), 76-133 (2), 76-134 (1), 76-147 (1). UH: 70-7-25 (2), 71-3-8 (1), 71-6-4 (1), 71-6-17 (1), 71-6-22 (1), 71-9-4 (1). USNM: 201187 (1), 208109 (1). WHOI: AB 13-23 (1), AB 13-28 (2), AB 13-30 (2). ZMUC: D 3588 II (1).

Additional larvae and juvenile material from the Pacific Ocean. ZMUC: D 3570 IV (1), D 3585 III (1).

Coccorrella atrata (Alcock 1893), Figure 22

Odontostomus atratus Alcock, 1893, p. 182 (original description, type from Bay of Bengal); Alcock, 1896, p. 333 (name only, after Alcock, 1893); Alcock, 1899, p. 167 (description of specimens from Bay of Bengal and Andaman Sea); Alcock & McArdle, 1900, plate 33, fig. 3 (illustration of specimen from Bay of Bengal); Alcock & MacGilchrist, 1905, plate 37, fig. 2 (illustration of specimen from Andaman Sea); Garman, 1899, p. 402 (name only, after Alcock, 1893); Schmidt, 1918, p. 33 (name only, after Alcock, 1893).

Coccorella atrata Wassersug & Johnson 1976, p. 273 (description of gut morphology, records from Indian and Pacific oceans); Herring, 1977, p. 297 (first report of luminous tissue in *C. atrata*, records from Banda and Halmahera seas).

Evermannella atrata Brauer 1906, p. 136 (record from southern Indian Ocean); Brauer, 1908, p. 192 (description of morphology of eye); Fowler, 1901, p. 212 (synonymy); Marshall, 1954, p. 142 (illustration of specimen from Andaman Sea, after Alcock & MacGilchrist, 1905); Marshall, 1955, p. 323 (swimbladder absent).

Evermannella atrata atrata Parr 1928, p. 163 (name only, after Alcock, 1893).

Odontostomops braueri Rofen 1963, p. 2 (original description, based on Brauer's [1906, p. 136, plate 10, figs. 3, 4] description of a specimen from 04° 05′ 08″ S, 73° 24′ 08″ E); Rofen, 1966d, p. 520 (listed in key to species of *Odontostomops*).

Holotype.—Ca. 89 mm (3.5 inches). RIMS *Investigator*, Bay of Bengal, 573 fathoms. Deposited in Indian Museum, Calcutta.

Diagnosis.—A species of *Coccorella* with 45 to 47 vertebrae; typically (122 of 123 specimens examined for this character) four pores, 2 + 2, in the frontal canal commissure of the cephalic laterosensory system (fig. 23); and interorbital width = 4.7% to 6.1% SL. Detailed comparisons of the two species of *Coccorella* are given above, following the description of the genus.

Description.—Values for meristic characters are presented in Tables 2 and 3.

PROPORTIONAL DIMENSIONS: Based on 24 (38.3–104.6 mm SL) specimens from throughout the range of the species. Expressed as thousandths of the SL and given as the mean and range (values in parentheses).

Body: depth at dorsal origin, 186 (171–210). Caudal peduncle: least depth, 85 (76–99); length, 96 (85–108). Adipose fin: distance to midcaudal rays, 134 (122–151); distance to dorsal-fin base, 331 (309–358). Anal fin: length of base, 268 (247–313). Dorsal fin: length of base, 122 (107–131); dorsal-fin origin to anal-fin origin (distance between verticals), 268 (244–290); end of dorsal-fin base to bases of midcaudal rays, 513 (480–551). Pelvic-fin insertion to anal-fin origin: 218 (190–260). Pectoral-fin insertion to pelvic-fin insertion: 187 (151–230). Anus to anal-fin origin: 57 (41–79). Distance from snout to: anus, 612 (556–655); dorsal-fin origin, 418 (392–445); adipose-fin, 827 (805–862); anal-fin origin, 661 (596–694); pectoral-fin insertion, 275 (240–309); pelvic-fin insertion, 450 (403–493); anterior margin of eye (=snout length), 62 (56–70). Head length: 242 (225–261). Postorbital head length: 166 (147–183). Eye: horizontal diameter, 55 (47–65); vertical diameter, 61 (54–70). Upper jaw length, 176 (164–193). Lower jaw length: 173 (163–185). Longest dentary tooth: 57 (50–63). Longest palatine tooth: 90 (80–100). Interorbital width (based on 44 [36.2–104.6] specimens): 54 (47–61).

BODY: Body moderately elongate, largest known specimen 104.6 mm SL (Indian Ocean, ZMUC D 3951 I). Body deep, body depth at dorsal origin 17.1% to 21.0% SL, the deepest of any evermannellid species. Anus at or slightly posterior to a point midway between pelvic-fin insertion and anal-fin origin. Lateral line extending to a point over anterior one-third of anal-fin base and composed of 30 or fewer segments. About eight pairs of sensory (presumably) papillae along dorsal margin of body, lateral (left and right) to middorsal contour between occiput and dorsal-fin origin. These palps are often difficult to see or missing, presumably due to damage during capture.

CEPHALIC LATEROSENSORY PORES: Snout-pad pore formula: 2 + 4 + 2 + 1 + 2. Mandibular pore formula: 5 + 6 + 2 + 1. Preopercular pores: 3 + 3. Temporal pores: PPTO = 1, PESC = 4. Frontal pores: PPF = 1; frontal canal commissure typically 2 + 2 (in 122 of 123 specimens examined for this character, a discussion of the single specimen assigned to *C. atrata* and not agreeing in this character is given above). Infraorbital pores: 13 or 14 + 9 or 10. Numerous

sensory (presumably) papillae distributed over occiput, interorbital region, snout, cheeks, and anterior lower jaw.

MOUTH: Upper jaw extending to or nearly to anterior margin of preopercle, well past a vertical through posterior margin of eye. Lower jaw projecting anteriorly very slightly beyond snout.

Tooth counts given below are based on 10 (46.3–104.6 mm SL) specimens. Premaxillary teeth small, retrorse, uniserial, numbering 25 to 37 in the 11 specimens counted. Dentary with two smaller fangs anteriorly near symphysis followed by nine to 16 unbarbed fangs arranged uniserially. Largest fangs positioned anteriorly. Vomer with one small tooth per side, but in numerous specimens only a single, laterally positioned tooth is present, its counterpart probably being lost. Anteriormost palatine tooth an enormous, unbarbed, saber-like fang, easily the largest tooth on each side, noticeably exceeding the snout length in length. Anteriormost palatine fang in *C. atrata,* 8.0% to 10.0% SL, on a proportional basis the largest fang occurring in any evermannellid species. Anteriormost palatine fang separated from posterior palatine teeth by a distinct gap. Posterior palatine teeth numbering four to eight in the 11 specimens counted. Number of premaxillary and dentary teeth higher in larger specimens.

COLOR: Color in alcohol a dark brown over head and body, without any distinct concentration into stripes, bars, or markings. In many (but not all) larger adult specimens median and paired fins with numerous moderately sized, discretely separated melanophores resulting in a spotted appearance. This pattern is shown quite clearly in Brauer's (1906, plate 10, fig. 3) illustration of *C. atrata.* In well-preserved specimens a brassy green, iridescent layer along flanks, beneath eyes, and on cheeks. In fully metamorphosed specimens less than 70 mm SL a distinct and typically elliptical lens pad is present. In larger specimens the lens pad is indistinct, but an opaque (presumably transparent in life) glistening tissue centered beneath the lens is probably similar in function. Midventral areas of body anterior to anal-fin origin with especially dense pigmentation except for areas of luminous tissue (see above). Peritoneum dense black.

Distribution.—Coccorella atrata is limited to equatorial areas of the Indian and Pacific oceans (fig. 24). In the Indian Ocean *C. atrata* is limited to the area of Indian Ocean Equatorial Water. In the Pacific Ocean *C. atrata* occurs throughout the semi-isolated seas of the Indo-Malayan Archipelago but in the central Pacific is limited to a relatively narrow band along the equator. Only one specimen (NMFS(LJ) J 20.145, 20° N, 145° W, 1 [93.6]) has been taken well poleward from the equator in the central Pacific. This specimen is in all respects a typical example of *C. atrata,* and I have no explanation for this apparently anomalous record. Although the range of *C. atrata* extends well into the eastern tropical Pacific (easternmost Pacific records: NMFS(LJ) J 65-76, 11° 27′ S, 97° 59′ W, 1 [97.0]; S1O 52-338, 00° 17.7 to 42.0′ N, 110° 26.0 to 12.1′ W, 1 [40.5]), it does not extend to the American mainland nor does *C. atrata* occur in the main areas of the oxygen-minimum layer in the eastern Pacific. The distributions of *C. atlantica* and *C. atrata* are compared above, and the distribution of *C. atrata* is compared with other equatorial midwater species in a subsequent section of this paper.

Larvae and small juveniles (to 30 mm SL) have most commonly been taken in hauls to between 100 and 300 m. Larvae, small juveniles, and adults have been taken in the upper 80 m, but I have found no records for this species from hauls limited to the upper 50 m. Most large adults (greater than 50 mm SL) were taken

in hauls to depths exceeding 300 m, but both juveniles and adults have been taken on numerous occasions in hauls to between 100 and 300 m. Larvae and small juveniles have been taken throughout the year.

Material Examined.—A total of 149 (10.5–104.6 mm SL) specimens from 91 collections.

INDIAN OCEAN. A total of 71 (16.0–104.6 mm SL) specimens from 42 collections. IOAN: B-6 (3), B-7 (5), V 4631 (1), V 4953 (1), V 4957 (1), V 5207 (1), V 5255 (1), V 5277 (1), V 5278 (1). NIO: DY 5353 (1), DY 5359 (2), DY 5395 (2), DY 5399 (5), DY 5413 (4), DY 5420 (2). MCZ: AB 6-332B (1), AB 6-333B (1). SOSC: TV Cr 5, stn. 193 (1). SIO: 71-71 (1). ZMUC: D 3815 VI (1), D 3817 III (2), D 3827 I (1), D 3856 I (1), D 3902 II (2), D 3904 III (4), D 3907 II (1), D 3908 I (1), D 3908 II (1), D 3908 III (1), D 3909 III (1), D 3912 I (1), D 3916 I (1), D 3925 I (1), D 3944 I (1), D 3951 I (1).

Additional larvae and juvenile material from the Indian Ocean. ZMUC: D 3821 III (3), D 3831 I (1), D 3903 III (3), D 3906 IV (1), D 3907 III (3), D 3910 II (2), D 3914 III (2).

PACIFIC OCEAN. A total of 78 (10.5–100.9 mm SL) specimens from 49 collections. AMS: Alpha Helix 1974 stn. 24 (JP75-24) (1). IOAN: V 5117 (3), V 5139 (1), V 6429 (8). NMFS (LJ): J 20-145 (1), J 57-112 (1), J 65-76 (1), J 77-28 (1), J 77-115 (1). ORSTOM: CA II-103 (1), CA III-135 (1), CA III-145 (1), CY IV-10 (1), CY V-6 (1). SIO: 52-338 (1), 60-219 (1), 60-225 (1), 61-540 (1), 61-584 (1), 61-588 (1), 68-533 (2), 68-534 (1), 68-535 (1), 69-19 (1), 70-346 (2), 73-104 (1), 73-120 (1), 73-108 (4), 73-169 (1). UH: TC 47-57 (1), TC 47-58 (10), TC 47-60 (1), TC 47-61 (1), TC 47-68 (3), TC 47-69 (3). USNM: ELT 31-11A (RHG 67-43) (1). ZMUC: D 3676 VI (1), D 3683 I (1), D 3683 VII (2), D 3714 I (1), D 3738 I (1), D 3788 I (1), D 3800 I (1).

Additional larvae and juvenile material from the Pacific Ocean. ZMUC: D 3676 VIII (1), D 3753 II (2), D 3755 II (1), D 3782 III (1), D 3789 VIII (1), D 3800 IV (1).

Evermannella Fowler 1901

Evermannella Fowler 1901, p. 211 (original description; replacement name for *Odontostomus* Cocco 1838, preoccupied by *Odontostomus* Beck 1837 (Mollusca); type-species by original designation *Odontostomus hyalinus* Cocco 1838, a junior synonym of *Scopelus balbo* Risso 1820).

Odontostomus Cocco 1838, p. 192 (original description; type-species by original designation *Odontostomus hyalinus* Cocco 1838).

Type Species.—*Evermannella balbo* (Risso 1820).

Diagnosis.—Evermannellids with tubular eyes directed dorsad and slightly anteriad. Horizontal eye diameter much broader than interorbital width, ratio of horizontal eye diameter to interorbital width exceeding 3.00. Aperture in adipose eyelid distinctly broader than lens of eye. A distinct, elliptical lens pad present in all post-metamorphic specimens. At least some dentary and palatine teeth barbed. Anteriormost palatine tooth a large, barbed fang, 4.6% to 7.3% SL. Dentary teeth biserial. A large vertically elongate fossa centered on dentary symphysis. Body relatively shallow to extremely deep, body depth at anal-fin origin 13.6% to 20.0% SL. No pyloric caecum. Ethmoid cartilage not expanded posteriorly into orbit, not forming an orbital septum. Basisphenoid present. Luminous tissue may be present. Larvae with three peritoneal pigment sections.

Description.—Dorsal-fin rays 10 to 13. Anal-fin rays 27 to 37. Pectoral-fin rays 11 to 12. Vertebrae 47 to 54.

Body short to relatively elongate, relatively shallow to quite deep, strongly compressed. Anus slightly anterior to, at, or slightly posterior to a vertical midway between pelvic-fin insertion and anal-fin origin. Lateral line either lacking (in available material) or relatively short, not extending posterior to a vertical just behind pelvic-fin base and composed of 18 or fewer segments.

Head moderately large, head depth and width subequal to body depth and width. Snout relatively low, rounded, or moderately truncate. Eyes large to extremely large, distinctly tubular, typically directed somewhat dorsoanteriad. Horizontal diameter of eye 5.2% to 9.3% SL, vertical diameter 5.9% to 11.0% SL. Fleshy eye diameter varying from being subequal to considerably exceeding snout length. Diameter of aperture in adipose eyelid considerably exceeding diameter of lens. Pupil distinctly broader than lens. A roughly elliptical lens pad centered on dorsal margin of lateral face of pigmented eye cup, with major axis normal to visual axis of eye.

Dentary symphysis with a well-marked, vertically elongate fossa containing anteriormost mandibular cephalic laterosensory pore on each side and also containing two to four vertically oriented rows of laterosensory papillae. Branchiostegal membranes free from isthmus, united by a small membrane anteriorly, at, or slightly anterior to a vertical through anterior margin of eye.

Gill filaments elongate and narrow but not extending beyond posterior and ventral margins of gill covers except in *E. ahlstromi*, where gill filaments are exceptionally dense and elongate, forming a matlike surface that extends beyond posterior and posteroventral margins of gill covers and that nearly reaches the pectoral-fin insertion. Pseudobranchiae with filaments nearly as long as longest gill filaments. Number of pseudobranch elements: *E. ahlstromi* (N=5, 38.5 to 67.9) 7 to 10; *E. balbo* (N=8, 62.5 to 139.1) 10 to 16; *E. indica* (N=12, 46.0 to 102.0) 9 to 13; *E. megalops* (N=2, 65.6 to 66.0) 8 to 9. Pseudobranch counts tending to be higher in larger specimens (presumed for *E. megalops*).

Dorsal fin relatively short based, 9.1% to 12.0% SL. Middle of dorsal-fin base distinctly anterior to a vertical at middle of standard length. Pelvic-fin insertion anterior to a vertical through middle of dorsal-fin base but not anterior to a vertical through dorsal-fin origin. Appressed pelvic fins reaching to or slightly past anus in best-preserved specimens but not reaching anal-fin origin. Pectoral fins distinctly exceeding pelvic fins in length. Appressed pectoral fins reaching to or distinctly past a vertical through a point midway between pectoral-fin insertion and pelvic-fin insertion but not reaching pelvic-fin insertion. Anal-fin base relatively short to quite elongate, 25.0% to 34.3% SL.

Content.—I recognize four species of *Evermannella* (fig. 29): *E. ahlstromi*, restricted to the eastern Pacific Ocean; *E. balbo*, for the most part restricted to relatively cool and productive areas of the Atlantic (including the Mediterranean Sea), Indian, and Pacific oceans; *E. indica*, nearly circumtropical in distribution; and *E. megalops*, restricted to central water areas of the South Pacific Ocean. The four species may be distinguished on the basis of characters provided in the Key on page 101 and by additional characters cited below.

Evermannella balbo differs from its three congeners in the following characters: number of anal-fin rays 33 to 37 vs. 27 to 32; number of vertebrae 52 to 54 vs. 48 to 52; fourth basibranchial toothplate present vs. absent; snout-pad pore formula = 2 + 4 + 2 + 1 + 2 vs. 2 + 4 + 2 + 1 + 0 (*E. ahlstromi*, *E. indica*) or 2 + 4 + 0 + 1 + 0 (*E. megalops*). *Evermannella balbo* differs from *E. ahlstromi* and *E. megalops* in having a modally higher number of dorsal-fin rays, 12 to 13 (83 of 85 counted with 12 rays) vs. 10 to 12 in *E. ahlstromi* (one of 78 counted with 12 rays) and 10 to 12 in *E. megalops* (one of 10 counted with 12 rays). *Evermannella balbo* differs from *E. ahlstromi* and *E. megalops* in typical values for the following morphometric characters: caudal peduncle depth, 6.3% to 8.3% SL ($\bar{x}$ = 7.1% ± .18) vs. 8.5%

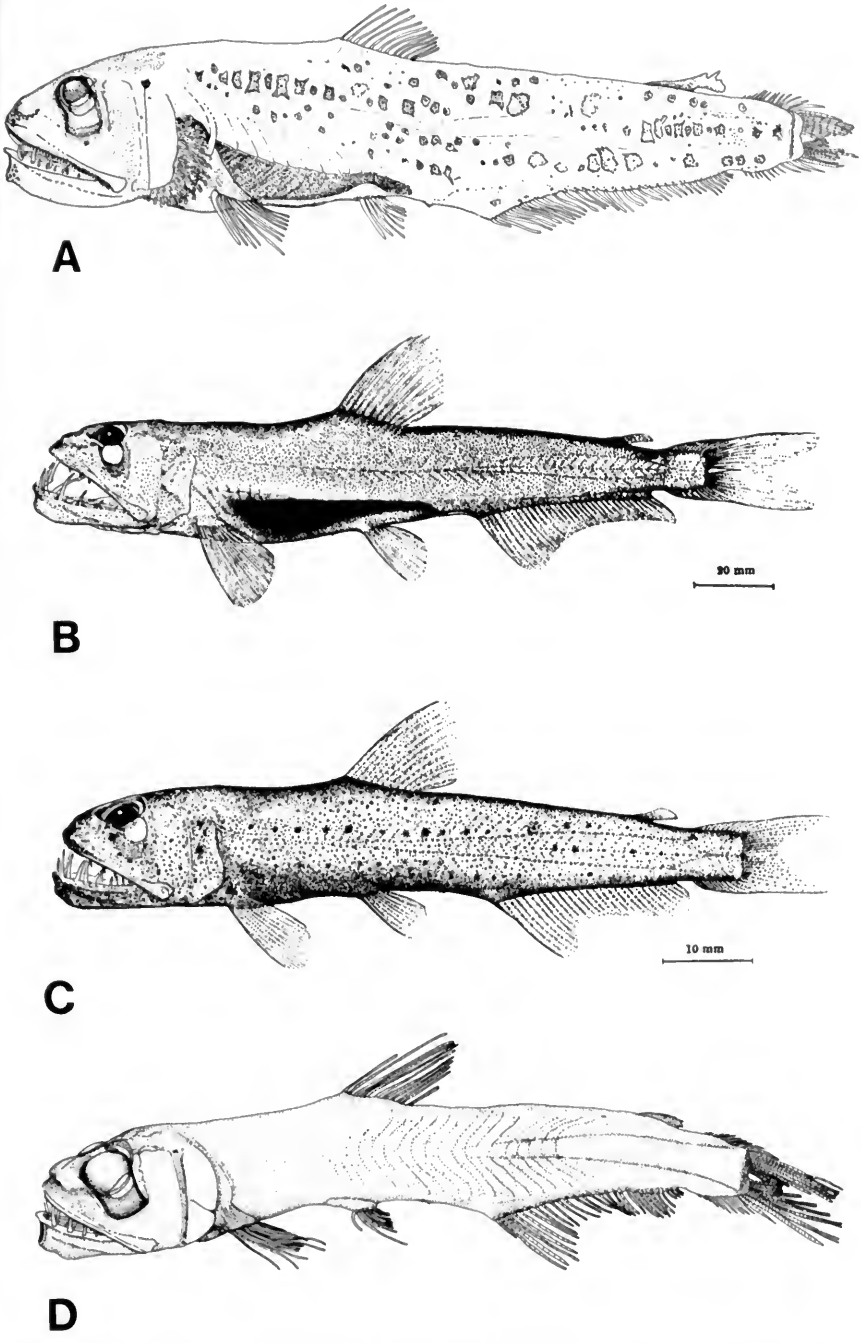


FIG. 29. The species of *Evermannella*. **A**, *Evermannella ahlstromi*, holotype, USNM 211302, 63.1 mm SL; **B**, *Evermannella balbo*, MNHN 98-1105, 171 mm SL; **C**, *Evermannella indica*, FMNH 49864, 77.3 mm SL; **D**, *Evermannella megalops*, holotype, SIO 72-305, 65.6 mm SL. (**A** and **D** from Johnson & Glodek, 1975, drawings by R. K. Johnson; **B** and **C** from Rofen, 1966d, drawings by E. M. Soule.)

to 10.5% SL ($\bar{x}$ = 9.5% ± .40) in *E. ahlstromi* and 8.2% to 9.5% SL ($\bar{x}$ = 8.7% ± .64) in *E. megalops;* distance from adipose-fin base to bases of midcaudal-fin rays, 10.6% to 12.5% SL ($\bar{x}$ = 11.7% ± .19) vs. 13.8% to 15.5% SL ($\bar{x}$ = 14.6% ± .39) in *E. ahlstromi* and 13.9% to 15.7% SL ($\bar{x}$ = 14.6% ± .93) in *E. megalops. Evermannella balbo* differs from *E. megalops* in typical values for the following morphometric characters: caudal peduncle length, 8.4% to 10.1% SL vs. 10.2% to 12.3% SL; distance from pelvic-fin insertion to anal-fin origin, 14.6% to 19.3% SL ($\bar{x}$ = 17.4% ± .40) vs. 18.7% to 21.5% SL ($\bar{x}$ = 20.1 ± 1.53).

Evermannella ahlstromi differs from its three congeners in having very elongate gill filaments that project beyond the margins of the gill covers and nearly reach the pectoral-fin insertion. *Evermannella ahlstromi* may be distinguished from *E. indica* and *E. megalops* on the basis of additional characters discussed in detail by Johnson & Glodek (1975, pp. 724, 725).

Evermannella indica is the most generalized species of *Evermannella* in the sense that it lacks the distinctive features uniquely and respectively defining its three congeners. It is thus not possible to provide a monothetic diagnosis of *E. indica.*

Evermannella megalops differs from its three congeners, and indeed from all other evermannellids, in having quite enormously enlarged eyes: horizontal eye diameter 7.4% to 8.5% SL ($\bar{x}$ = 8.1) vs. 6.7% to 8.1% SL ($\bar{x}$ = 7.2) in *E. ahlstromi,* 5.2% to 7.2% SL ($\bar{x}$ = 6.2) in *E. balbo,* and 4.9% to 9.3% SL ($\bar{x}$ = 6.9) in *E. indica;* vertical eye diameter 8.6% to 11.0% SL ($\bar{x}$ = 9.5) vs. 6.9% to 8.7% SL ($\bar{x}$ = 7.9) in *E. ahlstromi,* 5.9% to 8.1% SL ($\bar{x}$ = 7.0) in *E. balbo,* and 6.0% to 9.7% SL ($\bar{x}$ = 7.9) in *E. indica.* In *E. megalops* the interorbital width actually decreases with growth over the known size range (to 66.0 mm, see Johnson & Glodek, 1975, p. 724) and for juvenile and young adult specimens (based on five specimens, 32.5–66.0 mm SL) is equal to or less than 0.55 mm, both proportionately and absolutely the least of any evermannellid species. *Evermannella megalops* further differs from its three congeners in having a snout-pad pore formula = 2 + 4 + 0 + 1 + 0. *Evermannella megalops* may be distinguished from *E. ahlstromi* and *E. indica* on the basis of additional characters discussed in detail by Johnson & Glodek (1975, pp. 724–725).

Evermannella ahlstromi Johnson & Glodek 1975, Figure 29

Evermannella ahlstromi Johnson & Glodek 1975, pp. 716–721 (original description based on 84 specimens from eastern Pacific Ocean).

Holotype.—63.1 mm SL. USNM 211302. Eastern equatorial Pacific, 00° 41′ S, 91° 36 to 38′ W, IKMT, 0–390 m, 26 May 1966.

Diagnosis.—A species of *Evermannella* with 10 to 12 dorsal-fin rays (only one specimen of 78 counted with 12 dorsal-fin rays), 29 to 32 anal-fin rays, and 47 to 49 vertebrae. Snout-pad pore formula = 2 + 4 + 2 + 1 + 0. Gill filaments notably elongate, projecting beyond gill covers both posteriorly and ventrally. Detailed comparisons of *E. ahlstromi* with other species of *Evermannella* are given above, following the description of the genus.

Description.—Values for meristic characters are presented in Tables 2 and 3 and in the original description (Johnson & Glodek, 1975). Although substantial additional material of *E. ahlstromi* has come to hand, my study of this material has not resulted in data requiring meaningful alteration of the original description. Therefore, a full description of *E. ahlstromi* is not presented here. Only those characters not listed in the original description are given below.

PROPORTIONAL DIMENSIONS.—Based on 10 specimens (38.2–67.9 mm SL) from throughout the range of the species. Expressed as thousandths of the SL and given as the mean and range (values in parentheses).

Interorbital width, 21 (17 to 26).

CEPHALIC LATEROSENSORY PORES.—Snout-pad pore formula: 2 + 4 + 2 + 1 + 0. Mandibular pore formula: 5 + 4 + 2 + 1. Preopercular pores: ? 3 + 3, about 6. Temporal pores: PPTO = 1, PESC = 4. Frontal pores: PPF = 1. Frontal canal commissure = 3 + 3. Infraorbital pores: about 9 + 5.

Distribution.—Evermannella ahlstromi is limited to the eastern Pacific Ocean (fig. 30). It is known from the Transition Region off Baja California, the regions of transition between Pacific Equatorial Water and central waters of the North and South Pacific, and from a constricted zone along the equator from 155° W to near the American mainland. The distribution of *E. ahlstromi* as well as other eastern Pacific endemics is discussed in considerably greater detail in a subsequent section of this paper.

No specimens of *E. ahlstromi* have been taken in discrete-depth sampling devices. Larvae and small juveniles (to 30 mm SL) have commonly been taken in the upper 100 m, but most adults have been taken in hauls to depths exceeding 400 m. Larvae and small juveniles have been taken throughout the year, specifically in September, November, January, February, March, and May.

Material Examined.—The original description of *E. ahlstromi* (Johnson & Glodek, 1975) was based on 84 (17.7–70.0 mm SL) specimens from 34 collections. These are not listed here. An additional 37 (20.7–65.1 mm SL) specimens from 19 collections have come to hand.

PACIFIC OCEAN. IOAN: V 5090 (2). NMFS (LJ): J 57-123 (1), J 60-42 (1), J 77-38 (3), J 77-86 (1), J 77-92 (1), J 77-109 (2), J 77-138 (1), TC 51-37 (3), TC 51-70 (1), TC 51-78 (1), TC 51-87 (1). SIO: 60-229 (1), 73-20 (2), 73-171 (1). ZMUC: D 3556 II (1), D 3556 IV (2), D 3561 IV (3), D 3561 IX (9).

Evermannella balbo (Risso 1820), Figure 29

Scopelus balbo Risso 1820, p. 268 (original description, from Mediterranean Sea).

Evermannella balbo, Fowler 1901, p. 211 (synonymy); Rofen 1966d, p. 553 (description, references not given here, records from Atlantic Ocean and Mediterranean Sea); Goodyear, Zahuranec, et al. 1972, p. 149 (records from Mediterranean Sea, discussion of vertical distribution and seasonal distribution of young stages); Karrer 1973, p. 149 (record from South Atlantic Ocean); Johnson & Glodek 1975, p. 274 (comparison with *Evermannella ahlstromi* and *E. megalops,* record from Mediterranean Sea); Wassersug & Johnson 1976, p. 276 (gut morphology, record from North Atlantic Ocean).

Evermannella hyalina, Regan 1911, p. 130 (osteology, figure of pectoral girdle).

Evermannella sicaria Rofen 1963, p. 1 (original description, eight types from off Bermuda); Johnson & Glodek 1975, p. 729 (list two paratypes from off Bermuda).

Evermannella spp., Johnson & Glodek 1975, p. 729 (records from Atlantic and Pacific oceans).

Odontostomus balbo, Müller 1844, p. 185 (*Scopelus balbo* Risso placed in *Odontostomus,* cf. *O. hyalinus* Cocco).

Odontostoma hyalinus Doderlein 1878–79, p. 54 (name only).

Odontostomus hyalinus Cocco 1838, p. 192 (original description from Mediterranean Sea).

Holotype.—MNHN nr. B 1034, Paris.

Diagnosis.—A species of *Evermannella* with 12 or 13 dorsal-fin rays (97.6% of 85 specimens counted had 12 dorsal-fin rays), 33 to 37 anal-fin rays, and 52 to 54 vertebrae. Snout-pad pore formula = 2 + 4 + 2 + 1 + 2. Gill filaments not projecting beyond gill covers. Detailed comparisons of *E. balbo* with other species of *Evermannella* are given above, following the description of the genus.

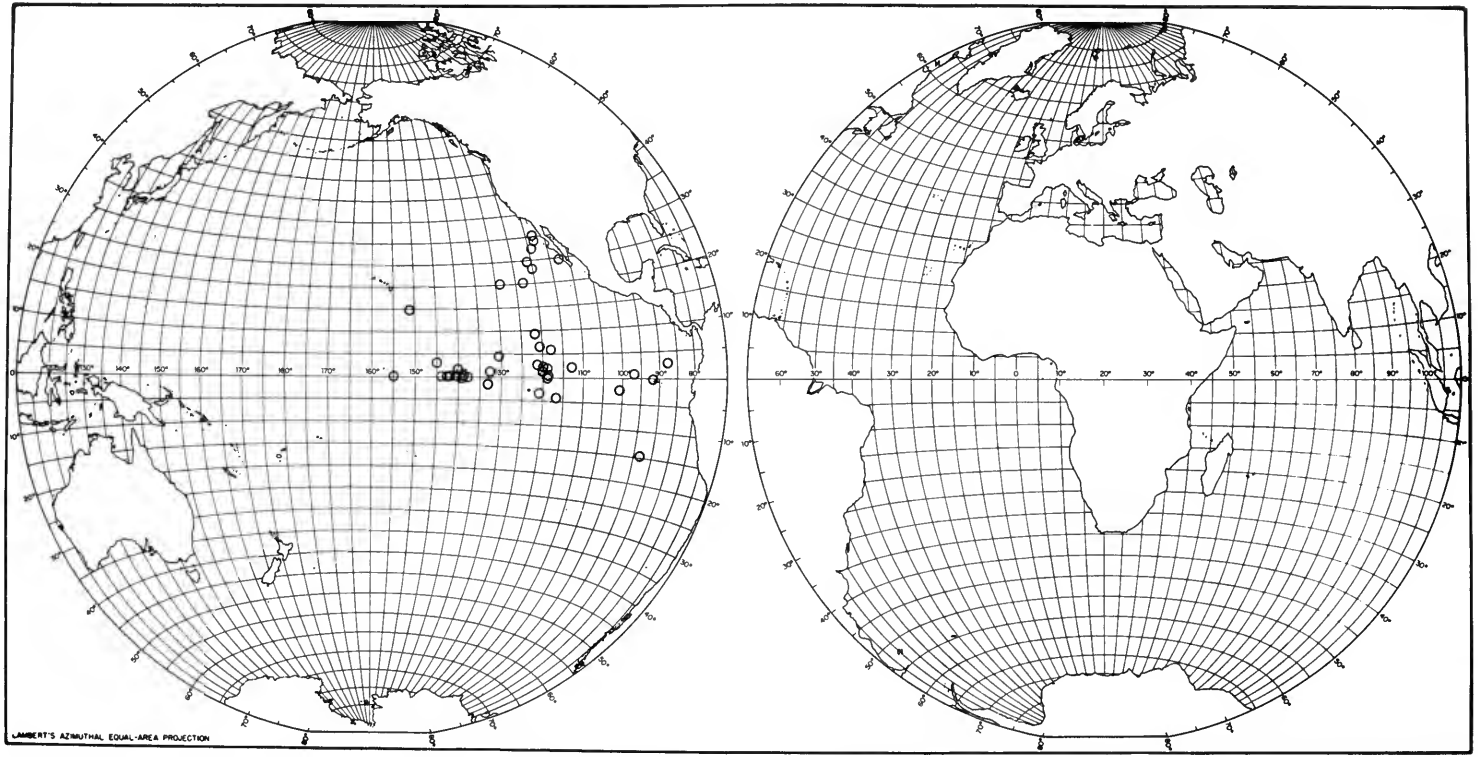


FIG. 30. Distribution of *Evermannella ahlstromi*.

Description.—Values for meristic characters are presented in Tables 2 and 3.

PROPORTIONAL DIMENSIONS.—Based on 39 (39.6–149.2 mm SL) specimens from throughout the range of the species. Expressed in thousandths of the SL and given as the mean and range (values in parentheses).

Body depth at anal origin: 158 (145–181). Caudal peduncle: least depth, 71 (63–83); length, 92 (84–101). Adipose fin: distance to midcaudal rays, 117 (106–125); distance to dorsal-fin base, 338 (321–363). Anal fin: length of base, 295 (266–333). Dorsal fin: length of base, 103 (93–110); dorsal-fin origin to anal-fin origin (distance between verticals), 199 (170–218); end of dorsal-fin base to base of midcaudal rays, 488 (468–502). Pelvic-fin insertion to anal-fin origin: 174 (146–193). Pectoral-fin insertion to pelvic-fin insertion: 210 (169–252). Anus to anal-fin origin: 82 (59–101). Distance from snout to anus: 550 (519–601); dorsal-fin origin, 438 (406–460); adipose fin, 849 (825–874); anal-fin origin, 629 (585–657); pectoral-fin insertion, 254 (231–286); pelvic-fin insertion, 457 (431–481); anterior margin of eye (= snout length), 58 (51–65). Head length: 229 (209–250). Postorbital head length: 127 (117–139). Eye: horizontal diameter, 62 (52–72); vertical diameter, 70 (59–81). Upper jaw length: 175 (161–195). Lower jaw length: 174 (163–201). Longest dentary tooth: 54 (46–63). Longest palatine tooth: 61 (54–69). Interorbital width: 13 (9–19).

BODY.—Body moderately elongate, largest known specimen 168.5 mm SL (Atlantic Ocean: ISH 1750/68). Body moderately deep, body depth at anal origin 14.5% to 18.1% SL. Anus at or slightly posterior to a point midway between pelvic-fin insertion and anal-fin origin. Lateral line not extending beyond a vertical just posterior to pelvic-fin base and composed of 18 or fewer segments.

CEPHALIC LATEROSENSORY PORES.—Snout-pad pore formula: 2 + 4 + 2 + 1 + 2. Mandibular pore formula: 5 + 6 + 2 + 1. Preopercular pores: not countable in any specimen examined by me. Temporal pores: PPTO = 1, PESC = 4. Frontal pores: PPF = 1; frontal canal commissure = 3 + 3. Interorbital pores: not countable in any specimen examined by me but approximately 14 + 10.

MOUTH.—Upper jaw extending to or nearly to anterior margin of preopercle, well past a vertical through posterior margin of eye. Lower jaw projecting anteriorly very slightly beyond snout.

Premaxillary teeth small, retrorse, uniserial, numbering 33 to 62 in seven (62.5–139.1 mm SL) specimens counted. Dentary with two smaller fangs anteriorly near symphysis, followed by a row of five to nine large barbed fangs, with these bordered anterolaterally by a row of two to four smaller teeth. Dentary tooth counts based on eight (62.5–139.1 mm SL) specimens. Large, dentary fangs the longest anteriorly and decreasing in length posteriorly. Vomer probably with one small tooth on each side, but in numerous specimens only a single, laterally postitioned tooth is present, its counterpart either failing to develop or lost. Anteriormost palatine tooth an enormous, barbed fang, easily the largest tooth on each side. Each such fang with a peculiar elbow-shaped bend near distal terminus, at which point tooth angles forward and ventrally and ends in a triangular point. Palatine teeth numbering six to nine. Palatine tooth counts based on eight (62.5–139.1 mm SL) specimens. Number of premaxillary and palatine teeth higher in larger specimens. Teeth lacking on basihyal and over first three basibranchials, but a fourth basibranchial toothplate, bearing a patch of six to nine small, conical teeth, overlies the third (cartilaginous) copula of the basibranchial series (fig. 14c).

COLOR.—Color in alcohol typically a light brown, with numerous, variably sized melanophores distributed over body and head. Melanophores on body arranged in seven to 13 irregular rows, with arrangement in recognizable rows most prominent on body posterior to dorsal-fin base. Variation in pigmentation ranges from nearly unpigmented specimens, with no melanophores or very few and extremely punctate melanophores visible, to highly melanistic specimens essentially covered with brownish black pigment. Individuals at either extreme of pigment development apparently occur throughout the range of *E. balbo*. Head lightly pigmented, with pigment concentrations on occiput, cheek, gill covers, snout, and anterior lower jaw. All fins with pigment present at fin-ray bases and finely scattered on rays and membranes. Midventral region between pectoral- and pelvic-fin bases with especially dense pigmentation in most specimens. Peritoneum black.

Discussion.—Rofen (1963, 1966d) based his description of *Evermannella sicaria* on eight (19.6–32.7 mm SL) specimens, all from the vicinity of Bermuda. Rofen's description leaves no doubt that the eight specimens in question belong to *Evermannella*, and the very high anal-fin ray counts (35 to 36) limit the need for comparison to *E. balbo*. The key characters supposedly distinguishing *E. sicaria* from *E. balbo* were said to be as follows (Rofen 1966d, pp. 537, 538): "lens very large, directed dorsally, appreciably larger than width of interorbital; no longitudinal rows of large dark spots on sides of head and body," (*E. balbo*) vs. "lens moderate in size, directed dorsolaterally, smaller than width of interorbital; 4–7 rows of large dark spots on sides of head and body," (*E. sicaria*). Additional characters said to separate the two species included (Rofen, 1966d, p. 554): eye diameter into head length, 3.7 to 4.5 (*E. balbo*) vs. 5.3 to 5.8 (*E. sicaria*); lens diameter into eye diameter, 1.4 to 1.5 (*E. balbo*) vs. 1.6 to 1.9 (*E. sicaria*); interorbital width into head length, 11.8 to 18.4 (*E. balbo*) vs. 5.7 to 9.1 (*E. sicaria*); peritoneum black (*E. balbo*) vs. light (*E. sicaria*). All but one of these supposed differences are in fact ontogenetic in origin. The states supposedly defining *E. sicaria*, viz. smaller eye diameter, smaller lens diameter, relatively wider interorbital diameter, are typical of smaller juveniles not only of *E. balbo* but of all species of *Evermannella*. The states supposedly defining *E. balbo* are typical of larger juveniles not only of *E. balbo* but of all species of *Evermannella*. Rofen's (1966d) study material of *E. sicaria* consisted of eight small juveniles (19.6–32.7 mm SL) with values reported for three (28.9, 30.1, and 32.7 mm SL) specimens. Rofen's study material of *E. balbo* consisted of four (21.4, 28.6, 37.1, and 171 mm SL) specimens with values reported only for the latter three. The one character purportedly separating the two forms that is not strictly explainable in terms of ontogenetic variation is the presence or absence of rows of melanophores along the sides of the head and body. The presence or absence of such melanophores and particularly the tendency for melanophores on the body to be arranged in rows is variable in juvenile and adult specimens of *E. balbo*, as discussed above. I have examined 837 specimens of *E. balbo* from 178 collections, including six paratypes of *E. sicaria*. I can see no basis for recognizing two species on the basis of characters used by Rofen or indeed on the basis of any other characters, and I conclude that *E. sicaria* and *E. balbo* are conspecific.

It might be mentioned at this point that the key to known western North Atlantic postlarval evermannellids provided by Rofen (1966d, p. 515) suffers from much the same problem as Rofen's description of *E. sicaria* as distinct from

E. balbo, i.e., most of the supposed differences are in fact ontogenetically variable. Thus this key, at least in part, is more useful in separating growth stages than in separating species.

Geographic Variation.—Schmidt (1918) recorded 72 specimens of *E. balbo* taken by Danish collecting efforts in the North Atlantic (33 specimens) and Mediterranean Sea (39 specimens). Schmidt found no discernible geographic variation in counts of dorsal-fin rays or anal-fin rays but reports (1918, p. 31) apparent geographic variation in numbers of vertebrae. Schmidt found that specimens from the Mediterranean tended to have more vertebrae ($\bar{x}$ = 52.4, range = 52 to 53, based on five specimens) than specimens from the North Atlantic ($\bar{x}$ = 51.7, range = 50 to 53, based on nine specimens). Examples of species exhibiting meristic (and morphometric) differences between North Atlantic and Mediterranean "populations" are cited by Nafpaktitis (1975, p. 83).

I have examined values of meristic characters for material of *E. balbo* from throughout the range of the species. For purposes of comparison I have (somewhat arbitrarily) divided the range of the species (fig. 32) into five subareas: CNA, includes all North Atlantic specimens taken north of 40° N and also includes all North Atlantic specimens taken north of 30° N *and* west of 25° W; MED, includes all specimens taken in the Mediterranean Sea; ENA, includes all North Atlantic specimens taken south of 30° N, all North Atlantic specimens taken south of 40° N *and* east of 25° W, and all South Atlantic specimens taken north of 05° S; CSA, includes all South Atlantic specimens taken south of 05° S; SP, includes all specimens taken in the South Pacific Ocean. I find geographic variation in values for two meristic characters: number of anal-fin rays and number of vertebrae (table 16).

My results for numbers of vertebrae disagree with the results of Schmidt (1918) in two respects: (1) Schmidt found a range in vertebral counts of 50 to 53 for specimens of *E. balbo*, I find a range of 52 to 54; (2) I find no evidence that specimens from the Mediterranean tend to exhibit higher vertebral counts (table 16). The apparent difference between CSA specimens (six of six specimens with 54 vertebrae) and specimens from other areas (49 of 49 specimens with 52 or 53

TABLE 16. Geographic variation in certain meristic characters in *Evermannella balbo*.

	A. No. of anal-fin rays						
Geographic area	**33**	**34**	**35**	**36**	**37**	**N**	**$\bar{x}$ ± 95% limits**
CNA	—	13	28	12	—	53	35.0±0.19
MED	4	9	2	1	—	16	34.0±0.43
ENA	3	17	3	—	—	23	34.0±0.23
CSA	—	4	10	15	2	31	35.5±0.30
SP	3	21	10	—	—	34	34.2±0.21

	B. No. of vertebrae				
Geographic area	**52**	**53**	**54**	**N**	**$\bar{x}$ ± 95% limits**
CNA, ENA	11	18	—	29	52.6±0.19
MED	4	2	—	6	52.3±0.54
CSA	—	—	6	6	54.0
SP	6	8	—	14	52.6±0.30

KEY to geographic areas (defined in the text): CNA=central North Atlantic, MED=Mediterranean Sea, ENA=eastern North Atlantic and equatorial Atlantic, CSA=central South Atlantic, SP=South Pacific.

vertebrae) needs confirmation on the basis of additional material. Only three specimens from the ENA area were suitable for radiography—the counts for these three (52, 52, 53) suggested no difference between CNA and ENA specimens, but this too needs to be tested on the basis of additional material.

The most interesting geographic variation in meristic character values seen in my study of *E. balbo* was in numbers of anal-fin rays (table 16). Values for specimens from two of the areas (CNA, CSA) are significantly higher than values for specimens from each of the three remaining areas (MED, ENA, SP). Among the environmental features known to affect meristic characters in fishes (see Barlow, 1961; Fowler, 1970), the most obvious feature to invoke in attempting to explain this pattern would be temperature were it not for values for specimens from the South Pacific, a cold water area (Sverdrup et al., 1942, chart III). Johnson & Barnett (1975) report an inverse correlation between central values of meristic characters and three measures of biological productivity for five species of midwater fishes. It seems certain that average productivity conditions throughout most of the area defined by the records of *E. balbo* categorized as CNA or CSA are lower than average productivity conditions for the other areas (especially the areas ENA and SP, see Cushing, 1971). Thus, it might be suggested that the pattern of meristic variation exhibited by *E. balbo* parallels that for the species discussed by Johnson & Barnett (1975). This certainly needs confirmation on the basis of study of additional specimens. I know of no other character in *E. balbo* exhibiting discernible geographic variation.

Distribution.—Evermannella balbo is known from the Atlantic, Indian, and Pacific oceans (figs. 31, 32), but only one specimen is known from the Indian Ocean (SAM 23612, 29° 52′ S, 31° 36′ E; IKMT: 0-500 m; 25–26 February 1963; 1 [57.6]). *Evermannella balbo* is the only evermannellid known to occur in the Mediterranean Sea. It occurs throughout the Mediterranean Sea (fig. 32) and has been recorded from the Aegean Sea (Schmidt, 1918, p. 35). *Evermannella balbo* occurs throughout the North Atlantic from 59° 49.6′ N (at 20° 22.9′ W, DY 7709, 1 [109.0]) to about 30° N. South of 30° N, *E. balbo* is limited to the eastern North Atlantic. *Evermannella balbo* occurs in the equatorial Atlantic and Gulf of Guinea. *Evermannella balbo* is known from throughout the South Atlantic between (roughly) 25° S and 40° S. *Evermannella balbo* is unknown from the South Atlantic between roughly 05° S and 25° S. The distribution of South Atlantic capture records for evermannellid species (fig. 31) suggests that *E. balbo* may well be absent from the western and central South Atlantic between these latitudes, but the absence of *E. balbo* from the Benguela Current area of the eastern South Atlantic is, I believe, questionable, and can only be resolved with additional sampling effort and study. In the central and eastern South Pacific, the distribution of *E. balbo* agrees very well with the distribution of the Transition Zone fauna discussed by McGowan (1971).

Schmidt (1918) discusses the North Atlantic distribution of *E. balbo* based on material obtained by Danish collecting efforts. Schmidt (1918, p. 35) discusses the apparent "replacement" of *E. balbo* by other evermannellid species in the western subtropical North Atlantic. My data (fig. 31) confirm the basic pattern discussed by Schmidt except that north of 30° N, *E. balbo* occurs throughout the North Atlantic (to roughly 60° N). A chart (fig. 31) comparing the distribution of *E. balbo* with all other evermannellid species suggests that throughout a large part of its range, *E. balbo* co-occurs with no other evermannellid species.

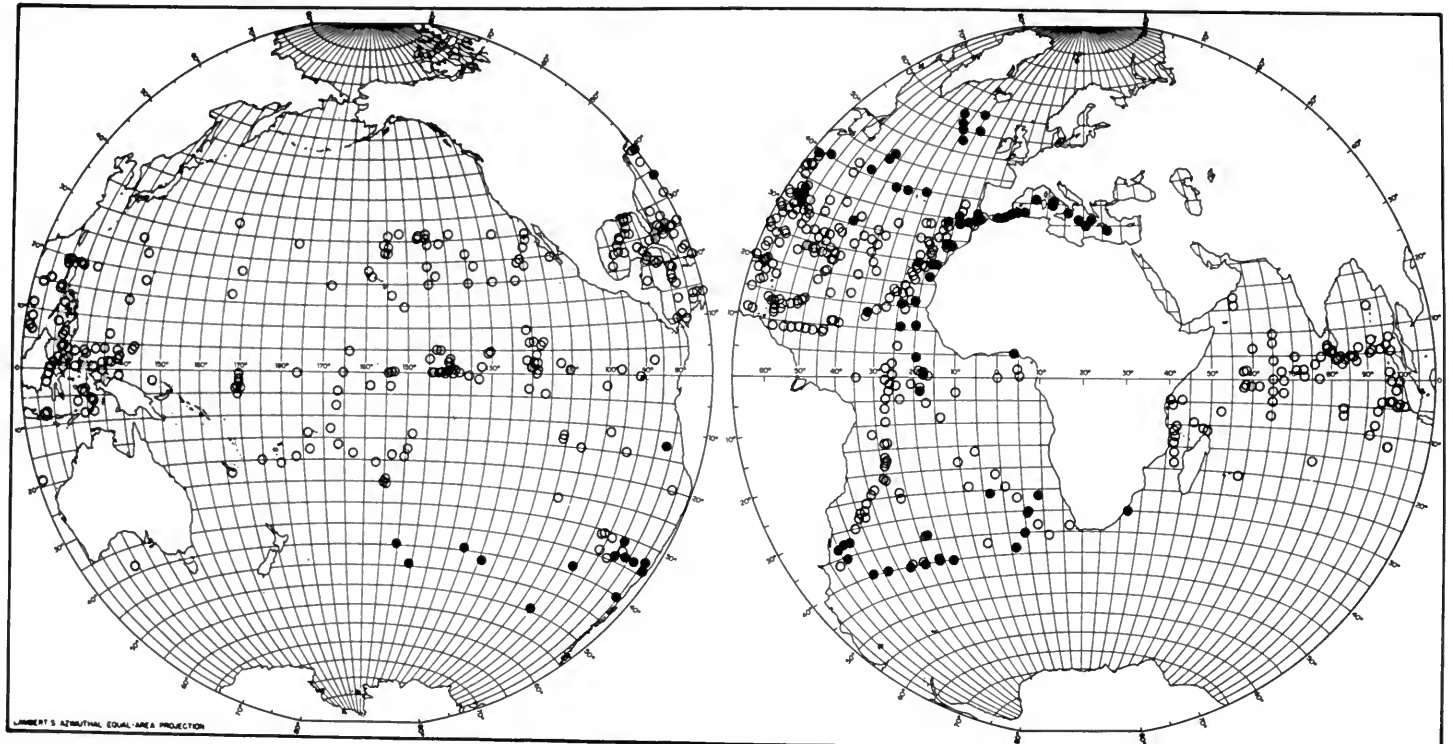


FIG. 31. Distribution of *Evermannella balbo* (solid circles) and other evermannellid species (all records, open circles).

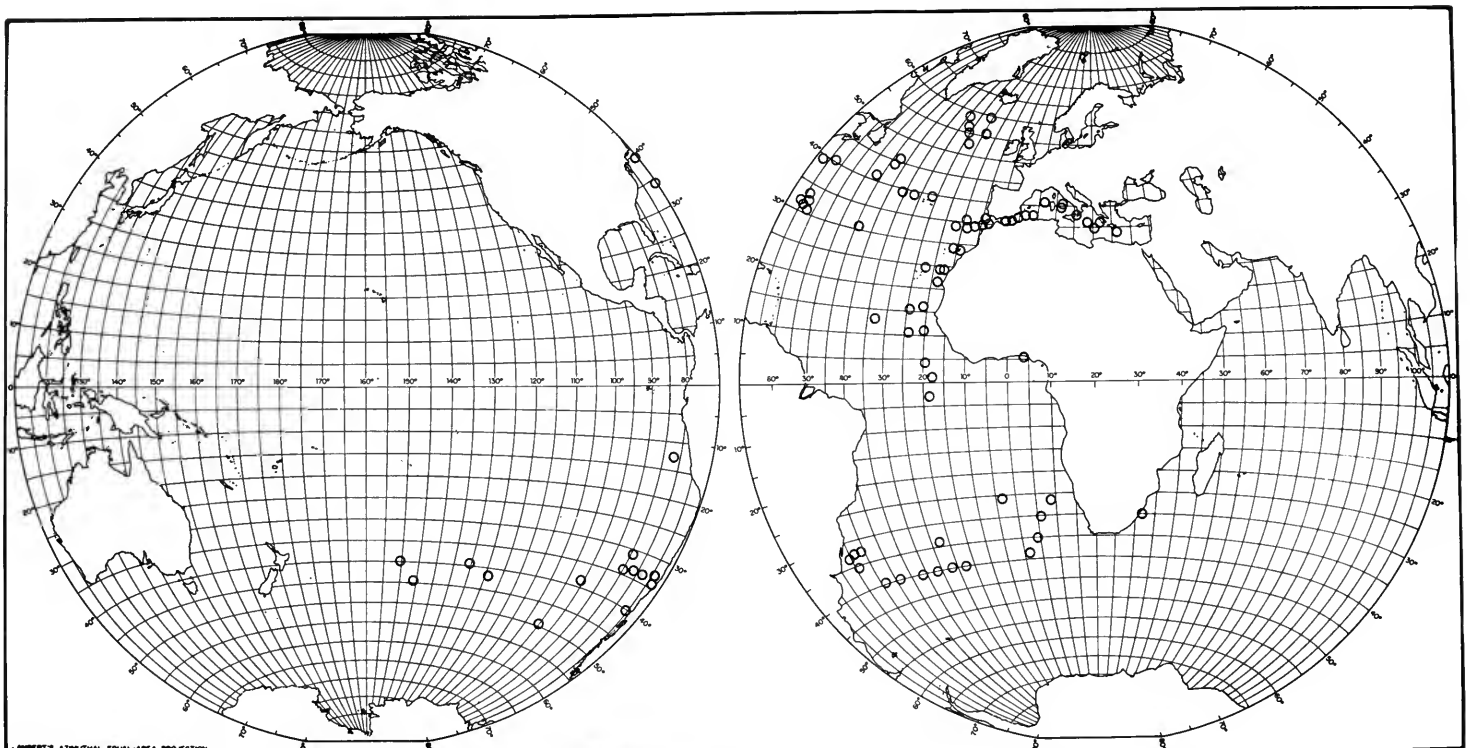


FIG. 32. Distribution of *Evermannella balbo*.

Schmidt (1918) notes two points concerning the capture of postlarval *E. balbo* represented in his material: (1) a great majority of the smallest postlarval specimens were taken with only 25 mwo, i.e., very near the surface, whereas the larger postlarvae were taken at greater depths, (2) young stages of *E. balbo* were taken (in the Mediterranean) almost exclusively in July, August, and September. Schmidt tentatively concludes that *E. balbo* is a summer-spawning species in the Mediterranean. He (Schmidt, 1918, p. 36) contrasts his results for *E. balbo* with the results for two other species occurring in the Mediterranean—*Argentina sphyraena* Linnaeus and *Nansenia oblita* (Facciola)—both of which he found to be winter-spawners in the Mediterranean. Schmidt's data suggest that *E. balbo* is a more southerly form in the North Atlantic than either *A. sphyraena* or *N. oblita*, and he thus explains the co-occurrence of these three species in the Mediterranean on the basis of timing of spawning to seasonal changes in surface temperatures in the Mediterranean. My data tend to blur this neat picture—*E. balbo* occurs much farther north in the North Atlantic than Schmidt had supposed (to 59° 49.6′ N, fig. 32), and in the North Atlantic larvae and small juveniles of *E. balbo* have been taken in every month except December, January, and February. Larvae and small juveniles of *E. balbo* have been taken in January and February in the South Pacific and South Atlantic, respectively. In line with Schmidt's suggestion, however, it may be of interest to note that whereas *E. balbo* is known as far north as 59° 49.6′ N, the most northerly records (north of 45° N) are only of large (greater than 87 mm SL) adults. The most northerly record for a young specimen is from 44° 07 to 13′ N, 44° 09 to 11′ W (RHB 1024, 1 (20.8), 10 September 1964). If it is indeed true that adults occur far to the north of the northerly limit for occurrences of larval and postlarval stages (and thus presumably far to the north of the northern limit of spawning), this differential distribution of young and adult stages would be unique to *E. balbo* among evermannellids and scopelarchids (with the possible exception of the Antarctic scopelarchid species *Benthalbella elongata* and *B. macropinna*, see Johnson, 1974c, p. 228). Additional data will be required to test this suggestion.

Goodyear, Zahuranec, et al. (1972) discuss the capture of six specimens taken with discrete-depth sampling devices in the Mediterranean in 1970. Specimens of *E. balbo* were taken at four of the five localities sampled, excluding only the westernmost sampling area (Goodyear, Gibbs, et al., 1972). The depth records for the six specimens, arranged by size, follow: 15 mm (200 m, night), 21 mm (600 m, day), 24 mm (700 to 500 m, day), 32 mm (200 m, day), 44 mm (325 to 250 m, night), 87 mm (200 m, night). The authors conclude "these catches suggest, if anything, that this species may occupy a wide vertical range during the daytime, and, perhaps, also at night."

Larvae and small juveniles (to 30 mm SL) of *E. balbo* have commonly been taken in the upper 100 m and, in numerous cases, in the upper 50 m. Most adults have been taken in hauls to depths greater than 400 m, but adults have been taken on a number of occasions in hauls to between 100 and 300 m. Most of the shallower records (less than 300 m) for larger adults (greater than 55 mm SL) are from the eastern South Pacific.

Material Examined.—A total of 834 (10.6–168.5 mm SL) specimens from 177 collections.

ATLANTIC OCEAN: A total of 796 (10.6–168.5 mm SL) specimens from 152 collections. FMNH: 49850 (2) paratypes of *E. sicaria* Rofen, 63114 (2). ISH: 371/66 (1), 914/66 (1), 1628/68

(1), 1750/68 (1), 627/71 (2), 665/71 (1), 801/71 (2), 846/71 (1), 918/71 (1), 947/71 (1), 1135/71 (1), 1520/71 (1), 2220/71 (1), 2285/71 (1), 2442/71 (1), 454/73 (5), 485/73 (2), 546/73 (32), 699/73 (2). MCZ: 42380 (2). NIO: DY 5797 (3), DY 5798 (1), DY 5801 (1), DY 7036 (1), DY 7709 (1), DY 7824 (1). UMML: 19986 (1). USNM: 40054 (1). USNM, ACRE: 3-4 (2), 3-5 (2), 3-6 (2), 6-16 B (1), 7-19 (1), 10-36 A (1), 10-38 N (2), 12-6 A (1), 12-15 B (1), 12-53 (1), 12-71 (1), 12-83 (3). USNM, MED: 1-14 M (2), 2-2 P (3), 2-5 B (1), 2-18 Z (1), 2-19 A (1), 3-4 M (1), 3-9 P (2), 3-18 P (2), 4-18 (1), 5-2 B (1), 5-2 M (2). WHOI, RHB: 473 (1), 474 (1), 482 (2), 486 (1), 1018 (2), 1024 (1), 1028 (2), 1041 (1), 1045 (5), 1046 (4), 1438 (3), 1503 (1), 1940 (2), 2006 (1), 2059 (1), 2066 (1), 2070 (1), 2217 (3), 2234 (1), 2263 (1), 2406 (1), 2407 (1), 2416 (1), 2417 (1), 2418 (1), 2621 (1). ZMUC: Uncat., no data, from Mediterranean Sea (1), 1107 I (3), 1163 III (3), 1342 III (1).

Additional larvae and juvenile material from the Atlantic Ocean. CAS, SU: 57689 (1) paratype of *E. sicaria* (= P), 57690 (1) P, 57691 (1) P, 57692 (1), 57693 (1) P, 57718 (1), 57720 (1). USNM, ACRE: 3-2 (1), 3-8 (1), 10-4 B (1). ZMUC: Texas 528 (5), Dana 830 (2), D 857 (1), D 1107 I (2), D 1107 V (4), 1107 VI (2), D 1107 VII (1), D 1107 XI (2), D 1108 I (1), D 1120 II (1), D 1122 I (40), D 1122 II (31), D 1122 III (21), D 1122 IV (7), D 1122 V (22), D 1122 VI (2), D 1122 VII (58), D 1123 I (4), D 1123 II (51), D 1123 III (34), D 1123 IV (13), D 1123 V (2), D 1124 I (9), D 1124 II (48), D 1124 III (44), D 1124 IV (46), D 1126 III (1), D 1130 III (4), D 1141 I (1), D 1141 VI (1), D 1141 XI (1), D 1141 XVI (8), D 1141 XVII (6), D 1229 I (18), D 1363 II (1), D 3523 III (1), D 3527 I (1), D 3528 II (1), D 3533 I (1), D 3533 II (1), D 3533 III (25), D 3534 I (6), D 3535 I (1), D 3535 III (26), D 3536 I (16), D 3979 II (4), D 3979 III (1), D 4008 I (1), D 4009 I (1), D 4009 III (13), D 4009 VIII (1), D 4017 VIII (1), D 4066 III (14), D 4066 IV (6), D 4070 VII + XI (2), D 4070 VIII + XII (2), D 4070 X + XIV (8), D 4070 XVI (1), D 4070 XX (2).

INDIAN OCEAN: A total of one (57.6 mm SL) specimen from one collection. SAM: 23612 (1).

PACIFIC OCEAN: A total of 37 (26.4–115.0 mm SL) specimens from 24 collections. IOAN: AK 229 (1). LACM: 11078 (1), 11243 (1), 11250 (1), 11284 (1), 11297 (1). SIO: 65-665 (1), 65-667 (1). SOSC: ELT 25-303 (1), ELT 25-338 (1). USNM: 208085 (1). WHOI: AB 13-2 (1), AB 13-3 (1), AB 13-4 (2), AB 13-7 (1), AB 13-17 (1), AB 13-19 (6), AB 13-23 (1), AB 13-24 (1), AB 13-30 (2), AB 13-48 (1), AB 13-50 (7), AB 13-51 (1), AB 13-52 (1).

Evermannella indica Brauer 1906, Figure 29

Evermannella indica Brauer 1906, p. 135 (original description, three syntypes from Indian Ocean); Rofen 1966d, p. 544 (description, references not given here, records from Atlantic Ocean and Banda Sea); Johnson 1974c, p. 30 (osteology, records from Atlantic and Pacific oceans); Johnson & Glodek 1975; p. 724 (comparison with *Evermannella ahlstromi* and *E. megalops*, records from Atlantic, Indian, and Pacific oceans); Wassersug & Johnson 1976, p. 276 (gut morphology, record from Pacific Ocean). Herring 1977, p. 306 (name only).

Evermannella indica indica, Parr 1928, p. 164 (name only, in key to species of *Evermannella*).

Evermannella indica melanoderma Parr 1928, p. 170 (original description, two syntypes from off Bermuda).

Evermannella borodini Whitley 1958, p. 32 (original description, new name proposed for *Odontostomus balbo atlanticus* Borodin 1931, preoccupied by *Evermannella atrata atlantica* Parr 1928).

Evermannella melanoderma, Beebe, 1937, p. 205 (name after Parr 1928, records from off Bermuda).

Odontostomus balbo atlanticus Borodin 1931, p. 78 (original description, holotype from off Bermuda).

Syntypes.—A total of three, the largest 32.5 mm (Brauer 1906, p. 136). VALDIVIA station 182, Indian Ocean, 10° 08.0′ S, 97° 14.2′ E; VALDIVIA station 231, Indian Ocean, 03° 24.1′ S, 58° 38.0′ E; VALDIVIA station 239, Indian Ocean, 05° 42.1′ S, 43° 36.1′ E. Syntypes presumably deposited in Museum für Naturkunde, East Berlin, D. D. R.

Diagnosis.—A species of *Evermannella* with 12 or 13 dorsal-fin rays (97.2% of 215 specimens counted had 12 dorsal-fin rays), 27 to 31 anal-fin rays, and 48 to

52 vertebrae. Snout-pad pore formula = 2 + 4 + 2 + 1 + 0. Gill filaments not projecting beyond gill covers. Detailed comparisons of *E. indica* with other species of *Evermannella* are given above, following the description of the genus.

Description.—Values for meristic characters are presented in Tables 2 and 3.

PROPORTIONAL DIMENSIONS.—Based on 82 (30.0–119.0 mm SL) specimens from throughout the range of the species. Expressed as thousandths of the SL and given as the mean and range (values in parentheses).

Body: depth at anal-fin origin, 155 (136–173). Caudal peduncle: least depth, 83 (69–97); length, 104 (87–121). Adipose fin: distance to midcaudal rays, 138 (109–162); distance to dorsal-fin base, 324 (291–387). Anal fin: length of base, 282 (250–309). Dorsal fin: length of base 109 (97–120); dorsal-fin origin to anal-fin origin (distance between verticals), 226 (201–263); end of dorsal-fin base to base of midcaudal rays, 493 (451–536). Pelvic-fin insertion to anal-fin origin: 192 (151–224). Pectoral-fin insertion to pelvic-fin insertion: 207 (162–263). Anus to anal-fin origin: 88 (42–136). Distance from snout to: anus, 558 (469–607); dorsal-fin origin, 421 (383–464); adipose fin, 831 (800–880); anal-fin origin, 641 (601–672); pectoral-fin insertion, 269 (233–317); pelvic-fin insertion, 455 (408–511); anterior margin of eye (= snout length), 70 (57–85). Head length: 249 (216–265). Postorbital head length: 118 (91–140). Eye: horizontal diameter, 69 (49–93); vertical diameter, 79 (60–97). Upper jaw length: 186 (170–209). Lower jaw length: 191 (169–225). Longest dentary tooth: 58 (43–70). Longest palatine tooth: 62 (48–73). Interorbital width: 11 (8–20).

BODY.—Body moderately elongate, largest known specimen 127.2 mm SL (Pacific Ocean: SIO 70-314). Body moderately deep, body depth at anal origin 13.6% to 17.3% SL. Anus at or slightly posterior to a point midway between pelvic-fin insertion and anal-fin origin. Lateral line not extending beyond a point above pelvic-fin base and composed of 16 or fewer segments.

CEPHALIC LATEROSENSORY PORES.—Snout-pad pore formula: 2 + 4 + 2 + 1 + 0. Mandibular pore formula: 5 + 5 + 2 + 1. Preopercular pores: not countable in any specimen examined by me. Temporal pores: PPTO = 1, PESC = 4. Frontal pores: PPF = 1; frontal canal commissure = 3 + 3. Infraorbital pores: about 11 or 12 + 8.

MOUTH.—Upper jaw extending to or nearly to anterior margin of preopercle, well past a vertical through posterior margin of eye. Lower jaw projecting anteriorly very slightly beyond snout.

Premaxillary teeth small, retrorse, uniserial, numbering 34 to 52 in 12 (46.0–102.0 mm SL) specimens counted. Dentary with one or two smaller fangs anteriorly near symphysis, followed by a row of five to 10 large barbed fangs, with these bordered anterolaterally by a row of three to four smaller teeth. Dentary tooth counts based on 13 (46.0–102.0 mm SL) specimens. Largest dentary fangs the longest anteriorly and decreasing in length posteriorly. Vomer probably with one small tooth on each side, but in numerous specimens only one laterally positioned tooth is present, its counterpart either failing to develop or lost. Anteriormost palatine tooth an enormous barbed fang, easily the largest tooth on each side. Each such fang with a peculiar elbow-shaped bend near distal terminus, at which point tooth angles forward and downward, ending in a triangular point. Palatine teeth numbering six to 10 in 13 specimens (46.0 to 102.0) counted. Number of premaxillary, dentary, and palatine teeth distinctly higher in larger specimens. Lingual teeth lacking.

COLOR.—Color in alcohol a light brown with numerous, variably sized melanophores irregularly distributed over head and body. A brassy iridescent coloration overlying dermal pigmentation on cheeks and flanks, evident in best-preserved specimens. No marked concentration of pigment into bars, stripes, patches, or the like on either body or head. *Evermannella indica* exhibits marked individual variation in intensity of pigmentation, with individuals varying from pale-colored specimens with very sparse pigmentation to specimens essentially covered with brownish black pigmentation. Individuals at both extremes of color variation occur throughout the range of the species. Head lightly pigmented, with pigment concentrations on occiput, cheek, gill covers, snout, and anterior lower jaw. All fins with pigment present at fin-ray bases and finely scattered on rays and membranes. Peritoneum dense black.

Geographic Variation.—In both *Evermannella indica* and *Odontostomops normalops* there is significant and interesting geographic variation in number of anal-fin rays. The pattern of variation in both species appears to be similar, and therefore data for both species is presented here.

Evermannella indica and *O. normalops* have the broadest distributions of any evermannellid species. Both species occur in central and equatorial waters of the Atlantic, Indian, and Pacific oceans (figs. 34, 37). Neither species occurs in the Mediterranean Sea, and both are largely or entirely excluded from most of the area of eastern Pacific Equatorial Water.

In both species counts of anal-fin rays are lowest in the Atlantic, intermediate in the Indian, and highest in the Pacific Ocean (table 17). In the case of *E. indica* differences between mean values of anal-fin ray counts for specimens from each of the three oceans are statistically significant ($p < .05$) for all three possible comparisons. In the case of *O. normalops* the mean value for Atlantic specimens is significantly lower than those for specimens from the Indian Ocean and Pacific Ocean, but the difference between mean values for Indian and Pacific Ocean specimens is not statistically significant.

Values for vertebral counts in *O. normalops* apparently parallel the results for numbers of anal-fin rays, with lowest values in the Atlantic, highest values in the Pacific, and intermediate values in the Indian Ocean (table 18). This trend is not seen in results for *E. indica* (table 18), although values for Pacific Ocean specimens are again the highest. No other meristic character in either species was found to exhibit discernible geographic variation.

In the case of *E. indica* enough material was available that I was able to examine geographic variation in anal-fin ray counts on a within-ocean as well as a between-ocean basis. It was necessary to divide the range of *E. indica* into a number of subareas such that comparisons between areas could be made. I chose nine subareas for detailed study. These subareas are indicated in Figure 33 and were given the following designations: western North Atlantic (WNA), eastern North Atlantic (ENA), equatorial Atlantic (EQA), central South Atlantic (CSA), Indian Ocean (IOC), western equatorial Pacific (WEP), central equatorial Pacific (CEP), central North Pacific (CNP), and central South Pacific (CSP).

These areas were chosen to meet the following criteria: (1) enough material of *E. indica* was available from each subarea to make possible meaningful between-area comparisons of anal-fin ray counts; (2) the subareas chosen taken as a whole covered most of the range of *E. indica* (compare figs. 33 and 34); (3) boundaries between the subareas corresponded more or less closely with distri-

TABLE 17. Anal-fin ray counts in *Evermannella indica* and *Odontostomops normalops*.

Area	27	28	29	30	31	32	33	34	35	N	Mean ± 95% limits
						E. indica					
Atlantic	5	98	52	4	—	—	—	—	—	159	28.4±.09
Indian	—	7	27	14	2	—	—	—	—	50	29.2±.21
Pacific	—	9	46	65	8	—	—	—	—	128	29.6±.13
						O. normalops					
Atlantic	—	—	—	1	15	24	17	—	—	57	32.0±.21
Indian	—	—	—	—	—	5	6	1	—	12	32.7±.41
Pacific	—	—	—	—	1	15	32	11	4	63	33.0+.22

TABLE 18. Vertebral counts in *Evermannella indica* and *Odontostomops normalops*.

Area	48	49	50	51	52	N	Mean ± 95% limits
				E. indica			
Atlantic	—	6	21	4	—	31	49.9±.21
Indian	5	6	3	—	—	14	48.9±.45
Pacific	—	1	12	20	7	40	50.8±.24
				O. normalops			
Atlantic	1	2	6	—	—	9	49.6±.56
Indian	—	—	4	—	—	4	50.0
Pacific	—	—	4	7	1	12	50.8±.40

butional boundaries for one or more species of midwater fish as reported in the literature; and (4) the subareas chosen represented a broad range of open ocean habitats with respect to physical and biological features and particularly with respect to measures of biological productivity.

The fit of the subareas chosen with respect to criterion (3) is variable. The faunal distinctiveness of the central gyral areas in the North and South Pacific is reasonably well documented (e.g., McGowan, 1971; Barnett, 1975; Johnson & Glodek, 1975). Other areas were delineated more arbitrarily, e.g., it seems likely that the Indian Ocean should be divided into at least two subareas, but lack of material of *E. indica* from the Indian Ocean, particularly from south of 10° S, precluded such a division.

Criterion (4) was included because of the findings of Johnson & Barnett (1972, 1975) that at least some midwater species exhibit geographic variation in values for meristic characters that may best be related to variation in measures of biological productivity. I expected that the results for *E. indica* would parallel the results for *Diplophos taenia* Guenther, *Vinciguerria nimbaria* (Jordan & Williams), and the other species studied by Johnson & Barnett (1975). That is, I expected values for anal-fin ray counts in *E. indica* to be lowest in areas of highest productivity, highest in areas of lowest productivity, and intermediate in areas of intermediate productivity. This did not prove to be the case.

In *E. indica* anal-fin ray counts (table 19) are lowest in the western North Atlantic, highest in the central North Pacific, and the highly significant tau value ([table 19], $tau_8 = +0.893$, $p < .01$, tau is Kendall's rank-correlation coefficient [see Tate & Clelland, 1957]) indicates that mean values for anal-fin ray counts increase sequentially, i.e., clinally, around the world from the western North Atlantic to the central North Pacific.

Two additional points should be noted. The result obtained would not be different if the value for specimens from the central South Pacific were used in place of the value for specimens from the central North Pacific (table 19). One might question the order of geographic proximity used in Table 19, viz., 6—WEP, 7—CEP, 8—CNP. At least part of the WEP subarea (viz., the South China Sea) is geographically closer to part of the CNP subarea (viz., the Philippine Sea) than to any portion of the CEP subarea (fig. 33). It might therefore be argued that the order of geographic proximity should read: 6—WEP, 7—CNP, 8—CEP. However, the results of Johnson & Barnett (1975), McGowan (1971), Brinton (1975), and the distribution of such forms as the two species of *Coccorella* (see above) suggest that the ordering used (6—WEP, 7—CEP, 8—CNP) is

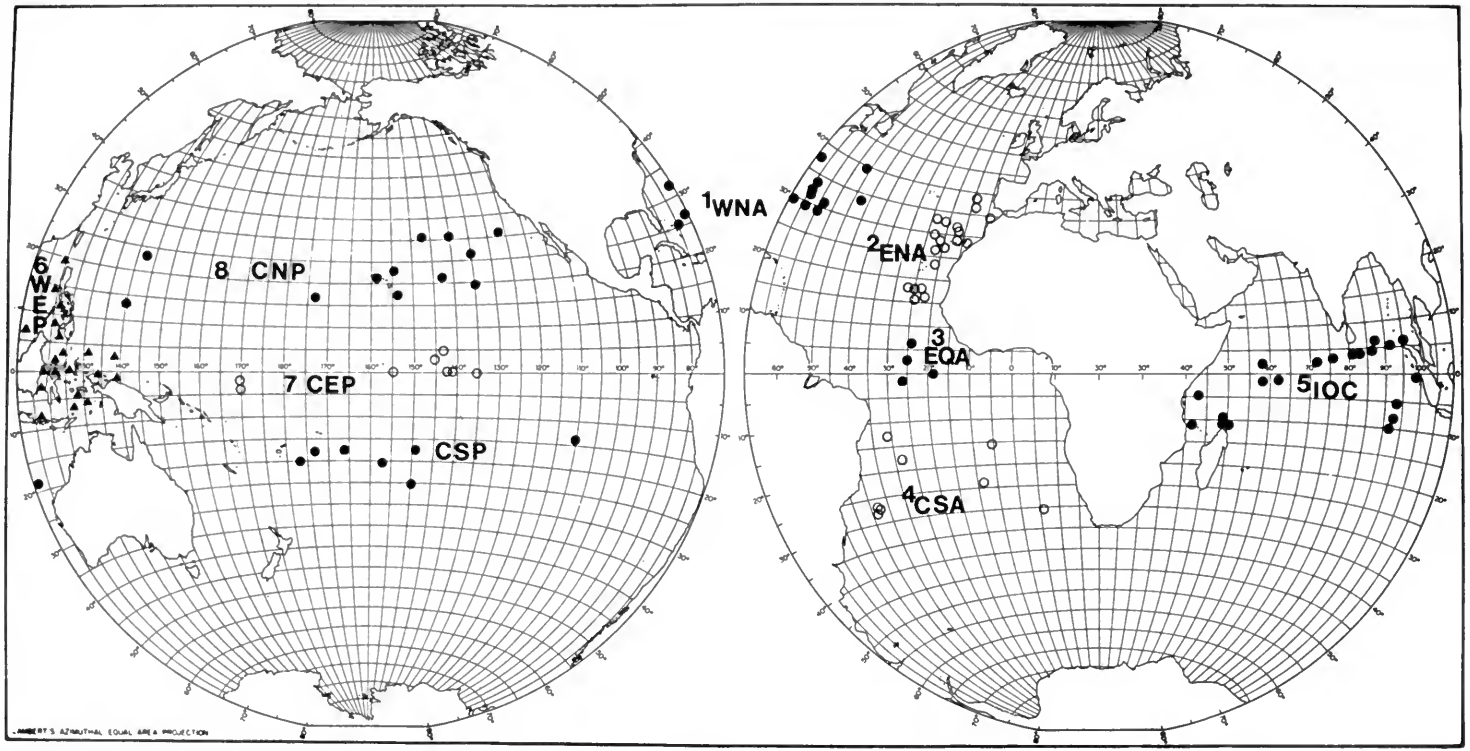


FIG. 33. Geographic subareas chosen for study of variation in numbers of anal-fin rays in *Evermannella indica*. Symbols show actual capture localities for specimens of *E. indica* included in the study. Subarea designations: WNA = western North Atlantic; ENA = eastern North Atlantic; EQA = equatorial Atlantic; CSA = central South Atlantic; IOC = Indian Ocean; WEP = western equatorial Pacific; CEP = central equatorial Pacific; CNP = central North Pacific; CSP = central South Pacific. See text for additional explanation.

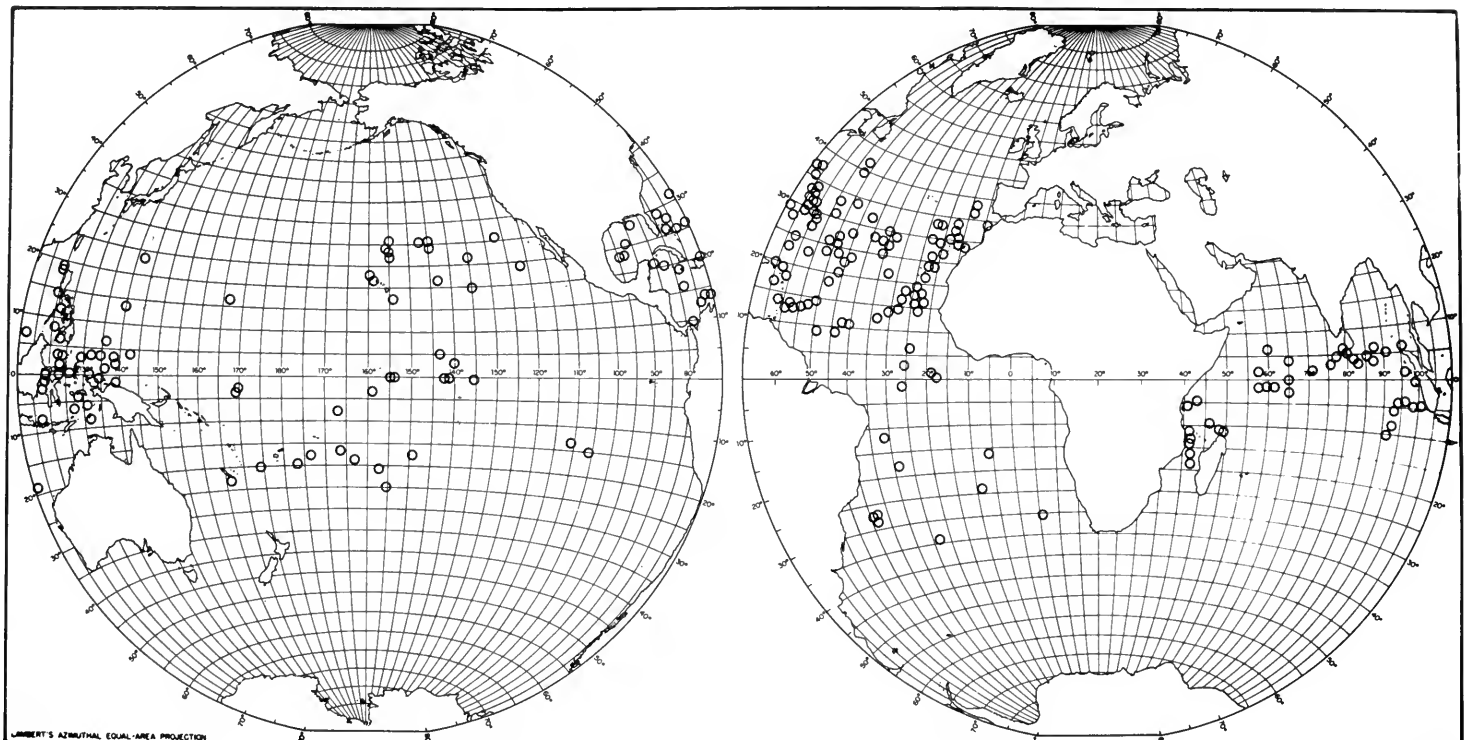


FIG. 34. Distribution of *Evermannella indica*.

TABLE 19. Anal-fin ray counts in *Evermannella indica*. Subarea abbreviations and location of subareas given in Figure 33. See text for further explanation.

Subarea	27	28	29	30	31	N	Mean ± 95% limits	Rank of mean	Rank of distance
WNA	4	73	26	2	—	105	28.2±.11	1	1
ENA	1	23	14	—	—	38	28.3±.18	2	2
EQA	—	1	6	1	—	8	29.0±.45	3.5	3
CSA	—	1	6	1	—	8	29.0±.45	3.5	4
IOC	—	7	27	14	2	50	29.2±.21	6	5
WEP	—	5	22	6	1	34	29.1±.23	5	6
CEP	—	2	4	9	—	15	29.5±.41	7	7
CNP	—	2	15	42	7	66	29.8±.16	8	8
								$tau_s = +0.893$ $p < .01$	
CSP	—	—	5	8	—	13	29.6±.31	—	—

biologically more meaningful in that interchange between populations in the two equatorial areas is more likely than interchange between populations in either equatorial area with the population(s) in the North Pacific central gyral area.

These results for *E. indica* remain unexplained. I know of no physical, chemical, or biological feature of the open ocean environment to which this sequential around-the-world clinal variation in *E. indica* might be related. I am unaware of any other midwater species that exhibits variation in meristic counts that parallels the variation observed in *E. indica* (and *O. normalops*). I believe that additional study of variation in *E. indica* could provide us with clues to the population structure of wide-ranging midwater species and possibly to the level of interchange between such populations. The problem that remains is lack of material.

Distribution.—*Evermannella indica* is a nearly circumglobal warm-water species found in central and equatorial waters of all three oceans (fig. 34). With the possible exception of *Odontostomops normalops* (fig. 37), *E. indica* has the broadest geographic distribution of any evermannellid species. *Evermannella indica* appears to be replaced by its closely related congeners, *E. ahlstromi* and *E. megalops*, in portions of Pacific Equatorial Water and in much of the central gyral area of the South Pacific, respectively (figs. 30, 35).

Larvae and small juveniles (to 30 mm SL) of *E. indica* have commonly been taken in the upper 100 m and, on a number of occasions, in the upper 50 m. Gibbs & Roper (1971, p. 127) report the capture of juvenile specimens of *E. indica* between 200 and 400 m at the Ocean Acre site near 32° N, 64° W. Most adults were taken in hauls to depths exceeding 400 m and for the most part in hauls to depths between 500 and 800 m. However, adults have been taken on a number of occasions in the upper 200 m and on several occasions in the upper 100 m. Larvae and small junveniles have been taken in all months of the year.

Material Examined.—A total of 986 (9.0–127.2 mm SL) specimens from 483 collections.

ATLANTIC OCEAN: A total of 564 (9.0–116.9 mm SL) specimens from 261 collections. FMNH: 49846 (1), 49847 (1), 49864 (1), 49873 (1), 49876 (1), 49883 (1), 49984 (1), 49986 (1), 66088 (1). ISH: 152/66 (1), 476/66 (3), 523/66 (2), 524/66 (1), 589/66 (1), 202/67 (1), 330/68 (1), 531/68 (1), 1168/68 (1), 1349/68 (1), 1484/71 (1), 2286/71 (2), 2836/71 (3), 2981/71 (1), W.H. 506/71 (1). MCZ: 32280 (1). NIO: DY 3700 (1), DY 4258 (1), DY 4947 (1), DY 4949 (1), DY 6411 (1), DY 7036 (2), DY 7089-13 (1), DY 7089-53 (1), DY 7802 (1), DY 7836-2 (1). SIO: 64-443 (1). UMML: 16557 (1), 18628 (1), 23638 (1), 24161 (1), 24329 (1), 24360 (2), 27581 (2). USNM, ACRE: 1-4B (1), 1-4C (1), 1-8 C+D (1), 1-11B (2), 1-16C (1), 1-18B (1), 1-19A (3), 3-3 (1), 3-10 (1), 3-13 (3), 4-3C (1), 4-5A (1), 4-5B (2), 4-10B (1), 4-10C (2), 4-11B (1), 4-21D (1), 7-12 (2), 7-15 (2), 7-16 (2), 7-17 (1), 7-18 (1), 7-19 (4), 8-2 (1), 8-3 (1), 9-27 (1), 10-1N (1), 11-13C (1), 12-2M (1), 12-5M (1), 12-9C (1), 12-12B (1), 12-12C (1), 12-12M (1), 12-15C (1), 12-18A (3), 12-20M (1), 12-22B (1), 12-22M (1), 12-26A (2), 12-26C (2), 12-32A (9),12-32B (18), 12-32C (4), 12-33M (1), 12-34C (2), 12-35B (1), 12-36A (3), 12-36B (1), 12-55 (4), 12-61 (3), 12-61N (1), 12-70 (6), 12-72 (3), 12-72N (1), 12-74 (3), 12-80 (2), 12-83 (1), 12-84 (1), 12-88 (1), 13-05B (1), 13-08B (1), 13-15B (1). WHOI, RHB collection numbers: 1013 (1), 1054 (1), 1108 (1), 1119 (1), 1127 (1), 1257 (1), 1258 (1), 1263 (2), 1266 (1), 1267 (1), 1277 (17), 1289 (4), 1297 (3), 1298 (1), 1302 (1), 1423 (1), 1435 (2), 1505 (2), 1509 (7), 1510 (2), 1515 (1), 1733 (1), 2005 (1), 2006 (2), 2018 (2), 2020 (1), 2027 (1), 2031 (2), 2066 (2), 2067 (1), 2069 (1), 2082 (1), 2090 (1), 2109 (1), 2118 (1), 2218 (1), 2265 (1), 2295 (1), 2906 (3), 2908 (1), 2909 (1), 2910 (1), 2912 (2), 2923 (2), 2924 (3), 2925 (1), 2927 (2), 2928 (3), 2929 (1), 2930 (3), 2931 (2), 2938 (1), 2939 (1), 2944 (1), 2966 (1), 2967 (1), 2972 (1), 2973 (1), 2976 (1), 2980 (1), 2987 (1), 2988 (1), 2990 (2), 2993 (1), 3000 (1), 3015 (1), 3102 (3), 3104 (1), A & J 015 (1). ZIZM: RBF 122 (1). ZMUC: D 855 III (1), D 855 XXI (1), D 858 (1), D 883 (1), D 891 (3), D 1016 IV (2), D 1148 I (3), D 1153 (2), D 1153 I (3), D 1153 VI (2), D 1161 IV (2), D 1162 II (2), D 1163 III (2), D 1166 IV (1), D 1185 VIII (1), D 1185 XI (1), D 1240 I (2), D 1365 IX (2), D 4180 II (1).

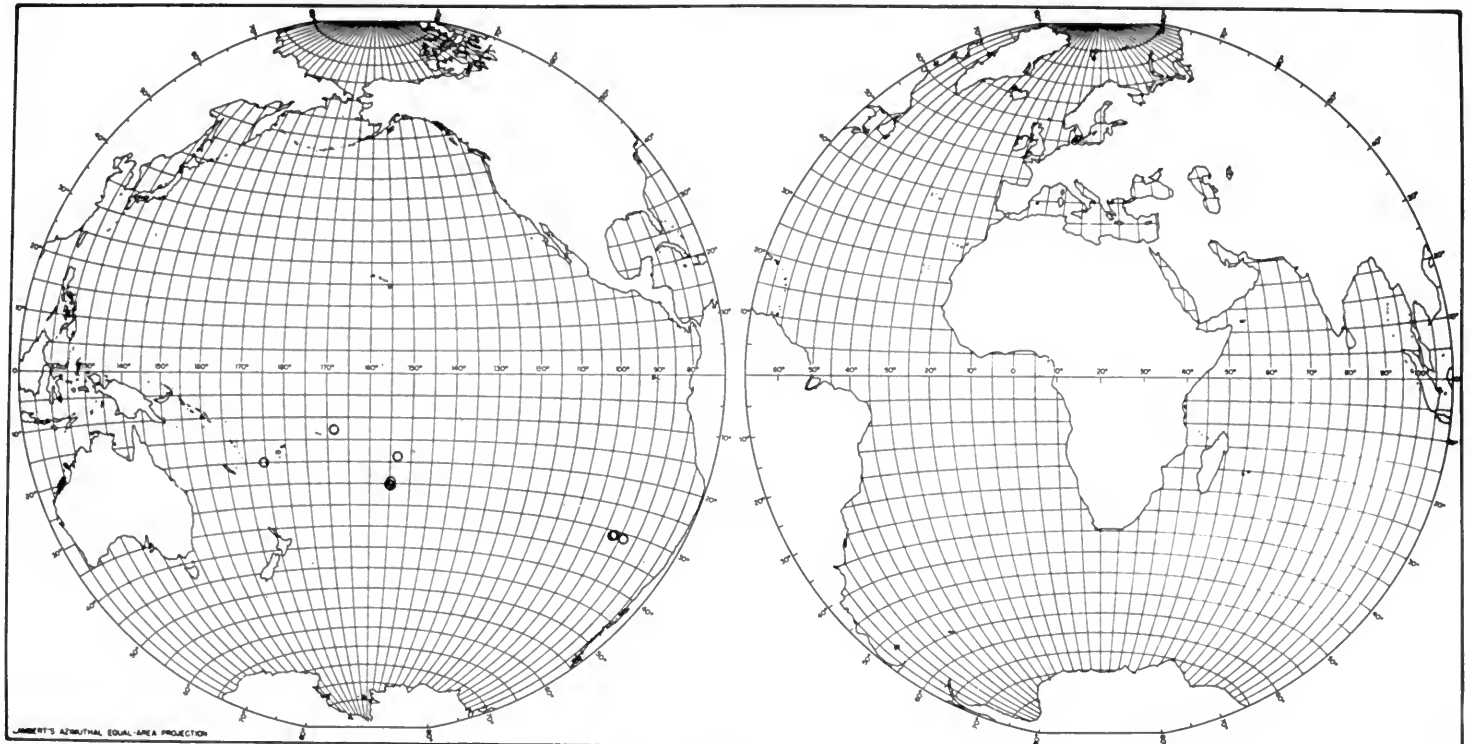


FIG. 35. Distribution of *Evermannella megalops*.

Additional larval and juvenile material from Atlantic Ocean: CAS, SU catalogue numbers: 57694 (1), 57696 (1), 57698 (2), 57699 (2), 57700 (1), 57701 (1), 57703 (2), 57704 (1), 57705 (1), 57706 (1), 57707 (1), 57708 (1), 57709 (1), 57710 (1), 57711 (1), 57712 (1), 57713 (1), 57714 (2), 57715 (1), 57716 (1), 57719 (1), 57721 (1), 57725 (1), 57726 (1), 57727 (1), 57892 (1), 57893 (1). USNM, ACRE: 3-5 (1), 3-13 (9)?, 4-25 (1)?, 7-14 (1), 12-24M (1), 12-34C (1)?, 12-35C (1)?. ZMUC: D 837 (1), D 842 (1), D 844 (7), D 849 (3), D 855 II (1), D 855 XVIII (1), D 856 VIII (2), D 857 (3), D 862 (7), D 864 (8), D 865 (4), D 882 (14), D 926 (7), D 934 (3), D 935 (1), D 941 (1), D 944 (2), D 945 (3), D 947 (3), D 1053 V (1), D 1142 IX (1), D 1155 I (2), D 1155 II (3), D 1157 II (1), D 1183 XIV (1), D 1216 II (1), D 1218 III (1), D 1242 III (1), D 1269 VII (1), D 1320 III (1), D 1362 IV (1), D 3538 I (52), D 3541 I (49).

INDIAN OCEAN: A total of 142 (12.8–97.1 mm SL) specimens from 62 collections. IOAN: B 6 (1), V 5177 (1), V 5207 (1), V 5290 (1). NIO: DY 5413 (1), DY 5420 (1). MCZ: MCZ 49182 (1), MCZ 50993 (3), MCZ 50996 (1), AB 3-147 (1), AB 6-335A (1), AB 6-337A (1). ZIZM: IOES No. 39 (1). ZMUC: D 3821 I (1), D 3828 V (1), D 3850 I (1), D 3851 I (2), D 3902 II (2), D 3904 III (2), D 3906 III (4), D 3906 IV (3), D 3907 II (1), D 3907 III (3), D 3908 I (1), D 3908 II (7), D 3908 III (1), D 3915 III (2), D 3917 VIII (1), D 3920 VIII (1), D 3931 II (1), D 3933 III (2), D 3933 IV (1), D 3935 I (1), D 3947 I (3), D 3949 I (1), D 3949 II (1).

Additional larvae and juvenile material from the Indian Ocean. ZMUC: D 3828 XI (1), D 3849 I (2), D 3851 II (4), D 3851 III (6), D 3852 I (2), D 3852 II (5), D 3852 III (1), D 3853 I (3), D 3856 II (8), D 3856 III (6), D 3872 I+II (1), D 3906 IV (3), D 3907 I (1), D 3907 III (2), D 3910 II (1), D 3912 III (4), D 3914 III (3), D 3934 II+VII+XII (1), D 3935 I (1), D 3937 I (4), D 3937 II (2), D 3941 I (1), D 3943 I (1), D 3951 I (1), D 3953 I (2), D 3955 I (1).

PACIFIC OCEAN: A total of 280 (9.6–127.2 mm SL) specimens from 160 collections. FMNH: 80405 (1), 80406 (2). IOAN: V 3786 (1), V 4494 (1), V 5117 (1), V 6429 (6), V 6469 (2), V 6490 (1), V 6493 (1). NMFS: J 20.135 (1). J 22.143 (2), J 27.135 (1), J 31.127 (1), J 31.145 (1). ORSTOM: CA II-70 (1), CA III-121 (1), CA IV-3 (1), CY II-15 (5), CY II-14 (1), CY IV-10 (1), CY VI-12 (1). SIO: 60-206 (2), 60-239 (1), 60-249 (1), 69-341 (2), 69-344 (3), 70-103 (1), 70-314 (1), 70-345 (1), 70-346 (1), 71-301 (1), 71-305 (2), 71-310 (1), 72-14 (1), 72-16 (2), 72-17 (1), 72-18 (2), 72-23 (1), 72-314 (1), 73-147 (1), 73-148 (2), 73-149 (1), 73-159 (1), 73-161 (1), 73-170 (2), 73-171 (1), 73-325 (1), 73-326 (1), 73-328 (1), 73-330 (1), 73-334 (1), 73-336 (1), 73-338 (1), 75-631 (1), 75-632 (1), 76-14 (1), 76-144 (1). UH: 69/9/11 (1), 69/11/1 (3), 69/11/3 (4), 69/11/6 (1), 70/7/14 (1), 70/7/16 (1), 70/7/22 (1), 70/7/26 (1), 70/7/28 (1), 70/9/4 (2), 70/9/9 (1), 70/9/11 (1), 70/9/12 (2), 70/9/13 (2), 70/9/14 (2), 70/9/20 (1), 70/9/24 (1), 70/9/28 (1), 70/12/7 (1), 70/12/9 (2), 70/12/13 (1), 70/12/31 (1), 71/2/7 (1), 71/3/3 (1), 71/3/4 (1), 71/3/9 (1), 71/6/9 (1), 71/6/10 (5), 71/6/11 (1), 71/6/14 (2), 71/6/14 (1), 71/6/20 (1), 71/6/22 (2), 71/6/28 (2), 71/6/31 (1), 71/6/34 (1), 71/9/8 (1), 71/10/7 (1), 71/10/8 (1), 73/8/15 (1), 73/8/19 (1), 73/8/21 (1), 73/8/27 (1), 73/8/30 (1), 73/8/31 (2), 73/9/13 (1), TC 47-57 (1), TC 47-68 (4), TC 47-69 (3), TC 52-52 (1). USNM: USNM 201694 (1). ELT: 31-11A (2), 31-21A (3), 31-22A (5). ZMUC: D 3576 I (1), D 3578 II (1), D 3581 I (1), D 3585 VIII (2), D 3602 VIII (1), D 3676 II (2), D 3677 I (1), D 3678 III (1), D 3678 V (1), D 3681 II (1), D 3683 IV (1), D 3684 III (1), D 3689 I (2), D 3689 VIII (1), D 3731 XIII (1), D 3734 I (1), D 3738 III (2), D 3739 VI (2), D 3746 II (1), D 3751 II (4), D 3755 II (1), D 3768 IV (1), D 3768 V (1), D 3789 II (1), D 3789 VIII (2), D 3795 III (1), D 3797 III (1), D 3800 II (1).

Additional larval and juvenile material from the Pacific Ocean. ZMUC: D 3563 III (2), D 3580 IX (1), D 3581 II (1), D 3613 II (1), D 3678 VIII (1), D 3683 VIII (2), D 3689 V (1), D 3715 III (1), D 3738 II (1), D 3745 III (2), D 3746 II (1), D 3749 III (8), D 3752 II (6), D 3753 II (2), D 3768 VI (37), D 3768 VII (4), D 3768 IX (1), D 3775 I (2), D 3795 III (1), D 3797 III (5), D 4799 (1).

Evermannella megalops Johnson & Glodek 1975, Figure 29

Evermannella megalops Johnson & Glodek 1975, pp. 721–723 (original description based on 10 specimens from the South Pacific Ocean).

Evermannella indica, Craddock & Mead 1970, p. 3.26 (not of Brauer, 1906; in part, specimens from offshore stations, R/V *Anton Bruun* stations 13-26, 13-28, 13-30).

Holotype.—65.6 mm SL, SIO 72-305, central South Pacific, 25° 05.3′ to 08.5′ S, 154° 54.5′ to 155° 12.5′ W, IKMT, 3,000 mwo, 27 July 1972.

Diagnosis.—A species of *Evermannella* with 10 to 12 dorsal-fin rays (eight of 10 specimens counted with 11 dorsal-fin rays), 29 to 31 anal-fin rays, and 48 to 50

vertebrae. Snout-pad pore formula = 2 + 4 + 0 + 1 + 0. Gill filaments not projecting beyond gill covers. Detailed comparisons of *E. megalops* with other species of *Evermannella* are given above, following the description of the genus.

Description.—Values for meristic characters are presented in Tables 2 and 3 and in the original description (Johnson & Glodek, 1975). Only six additional specimens of *E. megalops* have come to hand, and the description of this species is not repeated here. The following constitutes an addition to the original description.

PROPORTIONAL DIMENSIONS.—Expressed as thousandths of the SL and based on five specimens, 32.5, 58.0, 61.0, 65.6, 66.0 with values listed in that order.

Interorbital width, 17, 7, 6, 4, 5.

CEPHALIC LATEROSENSORY PORES.—Snout-pad pore formula: 2 + 4 + 0 + 1 + 0. Mandibular pore formula: 5 + 4 + 2 + 1. Preopercular pores: about 4. Temporal pores: PPTO = 1, PESC = 4. Frontal pores: PPF = 1; frontal canal commissure = 3 + 3. Infraorbital pores: 8 or 9 + 5.

Distribution.—*Evermannella megalops* is restricted to the central South Pacific (fig. 35). The distribution of *E. megalops* as well as other central gyral endemic species in the Pacific Ocean is discussed in considerable detail in a subsequent section of this paper.

No specimens of *E. megalops* have been taken in discrete-depth sampling devices. Only four larvae and small juveniles (to 30 mm SL) from four collections are known. These were taken in March (1), August (1), and October (2).

Material Examined.—The original description of *E. megalops* (Johnson & Glodek, 1975) was based on 10 (22.1–66.0 mm SL) specimens from nine collections. These are not listed here. An additional six (29.8–68.1 mm SL) specimens from four collections have come to hand.

PACIFIC OCEAN: SIO: 72-305 (1), 76-122 (1). ZMUC: D 3577 IX (1), D 3602 IV (3).

Odontostomops Fowler 1934

Odontostomops Fowler 1934, p. 322 (original diagnosis as a subgenus of *Evermanella*, type-species by original designation *Evermannella* [*Odontostomops*] *normalops* [Parr 1928]).

Type-Species.—*Odontostomops normalops* (Parr 1928).

Diagnosis.—Evermannellids with "normal," nontubular eyes, directed laterad. Horizontal eye diameter distinctly less than interorbital width. Aperture in adipose eyelid much smaller than lens of eye in diameter. No lens pad. At least some dentary and palatine teeth barbed. Anteriormost palatine tooth a large fang, 5.3% to 6.9% SL. Dentary teeth biserial. No fossa centered on dentary symphysis. Body relatively shallow, body depth at anal-fin origin 13.5% to 17.0% SL. No pyloric caecum. Ethmoid cartilage not expanded posteriorly into orbit, not forming an orbital septum. Basisphenoid absent. Luminous tissue absent. Larvae with 12 or more peritoneal pigment sections.

Description.—Dorsal-fin rays 11 to 13. Anal-fin rays 30 to 35. Pectoral-fin rays 11 to 13. Vertebrae 48 to 52.

Body moderately elongate, relatively shallow, strongly compressed, Anus distinctly posterior to a point midway between pelvic-fin insertion and anal-fin origin. Lateral line extending to a vertical through middle of anal-fin base and composed of up to 43 segments.

Head moderately large, head depth and width subequal to body depth and width. Snout relatively high and distinctly truncate.

Eyes small, rounded, lateral in position, not tubular, and directed laterad. Horizontal diameter of eye 2.7% to 4.2% SL, vertical diameter 2.8% to 4.0% SL. Fleshy eye diameter distinctly less than snout length. Diameter of aperture in adipose eyelid much less than diameter of lens. Pupil broader than lens. Lens pad absent.

Dentary symphysis marked by a distinctly protruding ridge and lacking any vertically elongate fossa. Branchiostegal membranes free from isthmus, united by a small membrane anteriorly, at or just posterior to a vertical through anterior margin of eye. Gill filaments elongate and narrow, typically extending to or nearly to margin of gill covers but not projecting beyond margin of gill covers. Pseudobranchiae with filaments distinctly shorter than longest gill filaments, numbering four to seven in seven (37.2–118.7 mm SL) specimens counted. Number of pseudobranch elements tending to be higher in larger specimens.

Dorsal fin relatively short based, 9.0% to 11.5% SL. Middle of dorsal-fin base just anterior to a vertical through middle of standard length. Pelvic-fin insertion under anterior one-third of dorsal-fin base. Appressed pelvic fins reaching to or nearly to anus in best-preserved specimens but not reaching anal-fin origin. Pectoral fins distinctly exceeding pelvic fins in length. Appressed pectoral fins reaching to or nearly to a vertical through a point midway between pectoral-fin insertion and pelvic-fin insertion but not reaching pelvic-fin insertion. Anal-fin base relatively elongate, 27.3% to 30.4% SL.

Content.—*Odontostomops* is monotypic, and the single species, *O. normalops* (fig. 36), is nearly circumtropical in distribution.

Odontostomops normalops (Parr 1928), Figure 36

Evermannella normalops Parr 1928, p. 164 (original description, holotype from western North Atlantic); Parr 1930, p. 154 (name only).

Evermannella (*Odontostomops*) *normalops* Fowler 1934, p. 322 (diagnosis of subgenus *Odontostomops* Fowler, type-species = *Evermannella normalops* Parr).

Odontostomops normalops Rofen 1966d, p. 520 (description, records from western North Atlantic); Johnson 1974c, p. 30 (record from North Pacific Ocean); Wassersug & Johnson 1976, p. 276 (gut morphology, record from North Pacific Ocean); Herring 1977, p. 306 (lack of luminous tissue, cf., *Coccorella atrata* Alcock).

Holotype.—Bingham Oceanographic Collection No. 2143; 51.6 mm SL. PAWNEE station 23 (third expedition), western North Atlantic, 24° 29′ N, 77° 29′ W (8,000 ft wire out). 14 March 1927.

Diagnosis.—As for the genus.

Description.—Values for meristic characters are presented in Tables 2 and 3.

PROPORTIONAL DIMENSIONS: Based on 25 (36.5–122.0 mm SL) specimens from throughout the range of the species. Expressed as thousandths of the standard length and given as the mean and range (values in parentheses).

Body: depth at anal-fin origin, 145 (135–170). Caudal peduncle: least depth, 72 (63–82); length, 95 (84–104). Adipose fin: distance to midcaudal rays, 122 (113–134); distance to dorsal-fin base, 315 (291–356). Anal fin: length of base, 287 (273–304). Dorsal fin: length of base, 99 (90–115); dorsal-fin origin to anal-fin origin (distance between verticals), 193 (164–216); end of dorsal-fin base to base of midcaudal rays, 480 (464–505). Pelvic-fin insertion to anal-fin origin: 180 (151–206). Pectoral-fin insertion to pelvic-fin insertion: 209 (179–267). Anus to

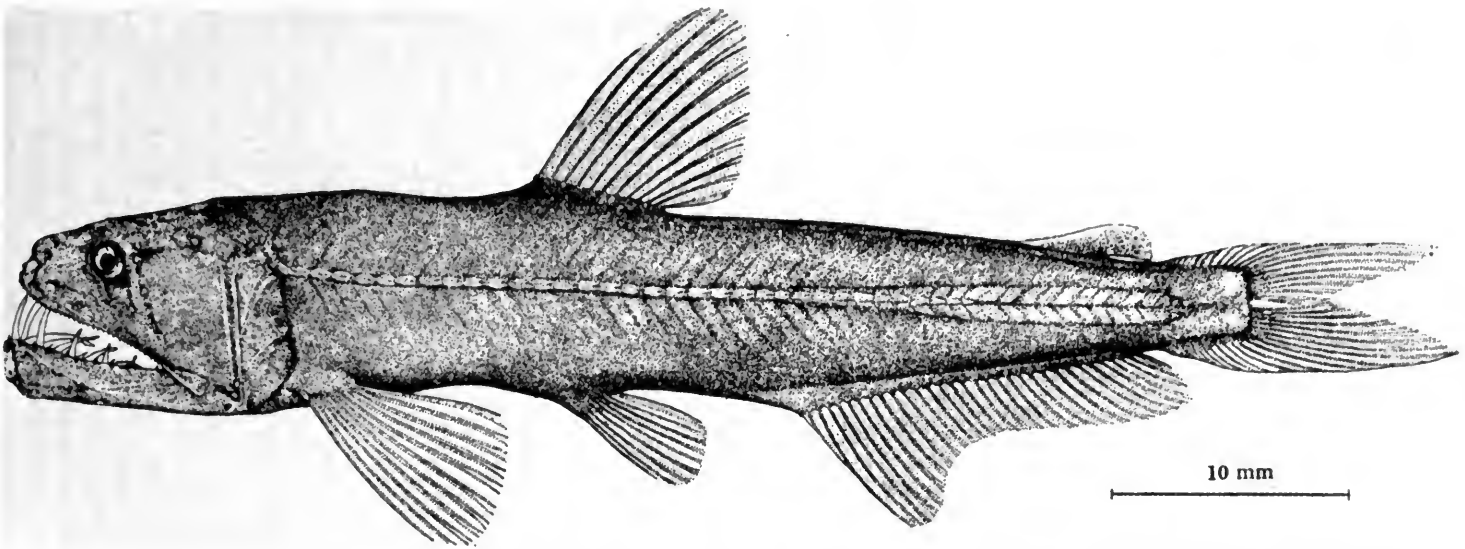


FIG. 36. *Odontostomops normalops* (Parr, 1928), holotype, Bingh. Oceanogr. Coll. 2143, 51.6 mm SL (after Rofen, 1966d; drawing by E. M. Soule).

anal-fin origin: 52 (41–68). Distance from snout to: anus, 586 (554–614); dorsal-fin origin, 451 (433–491); adipose fin, 844 (817–878); anal-fin origin, 629 (576–659); pectoral-fin insertion, 259 (231–285); pelvic-fin insertion, 455 (409–490); anterior margin of eye (=snout length), 60 (52–71). Head length: 221 (197–247). Postorbital head length: 141 (113–167). Eye: horizontal diameter, 33 (27–42); vertical diameter, 34 (28–40). Upper jaw length: 166 (149–182). Lower jaw length: 161 (144–178). Longest dentary tooth: 52 (45–60). Longest palatine tooth: 61 (53–69). Interorbital width: 41 (36–52).

BODY: Body moderately elongate, largest known specimen 123.1 mm SL (Atlantic Ocean: IOAN AK 998). Body relatively shallow, body depth at anal-fin origin 13.5% to 17.0% SL. Anus posterior to a point midway between pelvic-fin insertion and anal-fin origin. Ratio of distance from pelvic-fin insertion to anus over distance from pelvic-fin insertion to anal-fin origin = 0.73 to 0.80 in 12 (37.2–118.7 mm SL) specimens measured (from Atlantic [n=8], Indian [n=2], and Pacific [n=2] oceans). Lateral line extending to a vertical through middle of anal-fin base and composed of up to 43 segments.

CEPHALIC LATEROSENSORY PORES: Snout-pad pore formula: 2 + 4 + 2 + 1 + 0. Mandibular pore formula: 5 + 5 + 2 + 1. Preopercular pores: 3 + 3. Temporal pores: PPTO = 1, PESC = 4. Frontal pores: PPF = 1; frontal canal commissure = 3 + 3. Infraorbital pores: about 11 + 9.

MOUTH: Upper jaw extending nearly to anterior margin of preopercle, well past a vertical through posterior margin of eye. Lower jaw projecting anteriorly very slightly beyond snout.

Premaxillary teeth small, retrorse, uniserial, numbering 34 to 51 in eight (37.2–118.7 mm SL) specimens counted. Dentary with one or two smaller fangs anteriorly near symphysis, followed by a row of five to seven large, barbed fangs, with these bordered laterally by a row of four to nine smaller teeth. Dentary tooth counts based on eight (37.2–118.7 mm SL) specimens. Largest dentary fangs the longest anteriorly and decreasing in length posteriorly. Vomer probably with one small tooth on each side, but in the majority of specimens only one laterally positioned tooth is present, its counterpart either failing to develop or lost. Anteriormost palatine tooth an enormous, barbed fang, easily the largest tooth on each side. Each such fang with a peculiar elbow-shaped bend near distal terminus, at which point tooth angles forward and downward, ending in a triangular point. Palatine teeth numbering five to seven in eight (37.2–118.7 mm SL) specimens counted. Number of premaxillary teeth distinctly higher in larger specimens. Lingual teeth lacking.

COLOR: Color in alcohol a solid dark brown over head, body, and fins. A brassy, iridescent coloration overlying head and flanks, evident in best-preserved specimens. No marked concentration of pigment into bars, stripes, patches, or the like on either head or body. Peritoneum black.

Geographic Variation.—Odontostomops normalops exhibits geographic variation in number of anal-fin rays and number of vertebrae (tables 17, 18). The pattern of variation observed—with counts lowest in the Atlantic, intermediate in the Indian, and highest in the Pacific Ocean—apparently parallels that seen in results for *Evermannella indica*. Results for both species are discussed under *E. indica*.

Distribution.—Odontostomops normalops is nearly circumglobal in tropical and subtropical waters, occurring in central and equatorial waters in the Atlantic, Indian, and Pacific oceans (fig. 37). *Odontostomops normalops*, however, is appar-

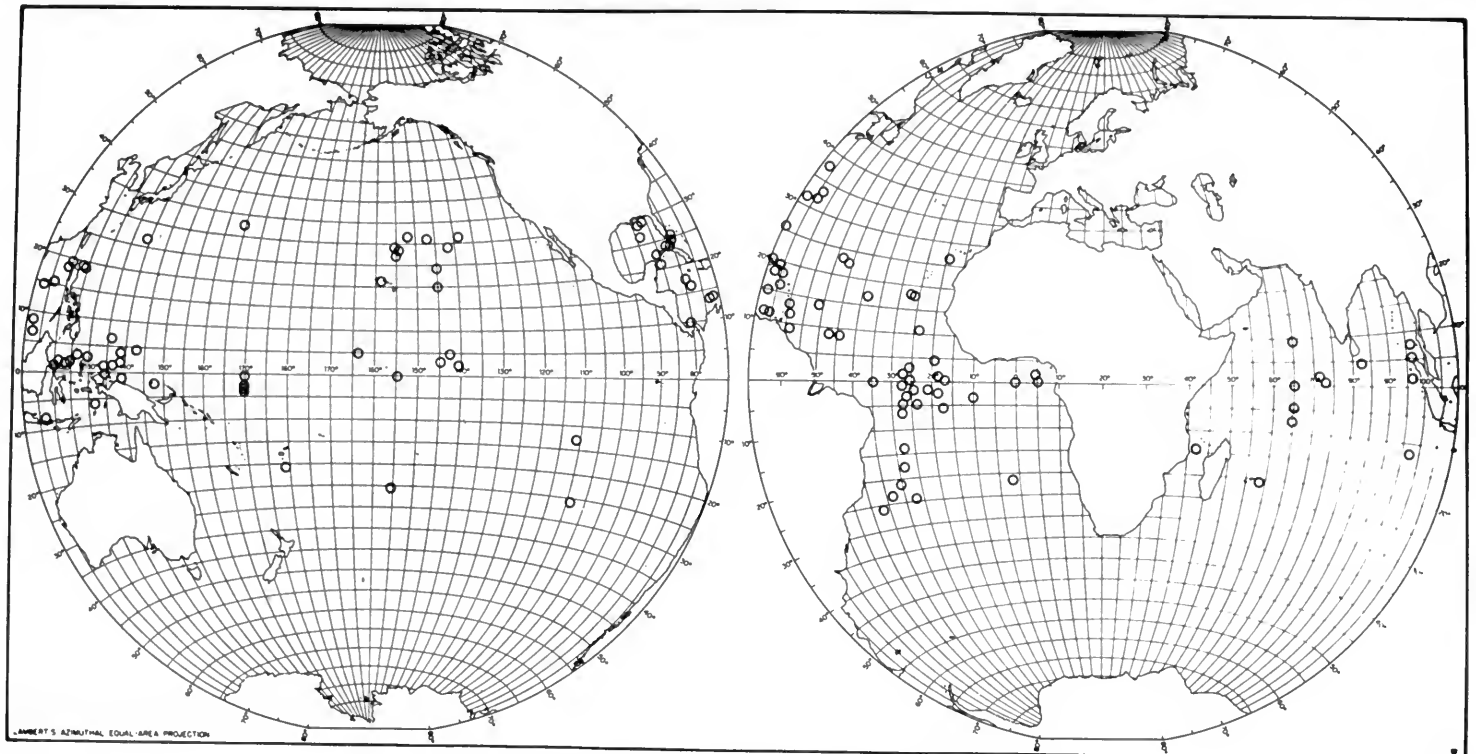


FIG. 37. Distribution of *Odontostomops normalops*.

ently excluded from much of the North Atlantic range of *Evermannella balbo* (compare figs. 32 and 37), including the Mediterranean Sea, and is also apparently excluded from the eastern Pacific.

Larvae and small juveniles (to 30 mm SL) of *O. normalops* have commonly been taken in the upper 100 m, and, on a number of occasions, in the upper 50 m. Most adults (greater than 50 mm SL) were taken in hauls to depths exceeding 400 m, but adults have been taken on a number of occasions in hauls to between 100 and 400 m. Larvae and small juveniles have been taken throughout the year.

Material Examined.—A total of 254 (9.0–123.1 mm SL) specimens from 184 collections.

ATLANTIC OCEAN. A total of 115 (9.0–123.1 mm SL) specimens from 78 collections. FMNH: 66087 (4), 71704 (1). FSBC: 2985 (1). IOAN: AK 820 (1), AK 991 (1), AK 998 (1). ISH: 371/66 (1), 523/66 (3), 722/66 (1), 286/68 (1), 825/68 (3), 895/68 (1), 947/68 (1), 1024/68 (1), 1139/68 (1), 1219/68 (2), 1282/68 (1), 1318/68 (3), 1684/71 (1), 2087/71 (2), 2220/71 (2), 2286/71 (3), 2390/71 (1). NIO: DY 7089-53 (4), DY 7836-3 (1). UMML: 14811 (1), 15960 (1), 17333 (2), 17584 (1), 20002 (1), 20006 (1), 22999 (1), 23903 (1), 26442 (1). USNM: 108305 (1). ACRE: 3-4 (1), 4-10D (1), 9-31 (1), 12-14M (1), 12-22C (1). WHOI, RHB: 970 (1), 971 (1), 975 (1), 1100 (1), 1107 (1), 1252 (1), 1253 (8), 1255 (1), 1258 (1), 1263 (3), 1277 (3), 1281 (1), 1290 (1), 1308 (1), 1315 (3), 1506 (3), 2294 (1), 2295 (4), 2296 (2), 2300 (1), 2918 (1), 2941 (1), 2958 (1), 2965 (1), 2979 (1), 2992 (1), 3010 (1), 3056 (1). ZMUC: D 1171 XII (1), D 1189 I (1), D 1225 II (1), D 1230 VI (1), D 3999 II (1).

Additional larvae and juvenile material from the Atlantic Ocean. ZMUC: D 1189 III (1), D 1231 II (1), D 1260 II (1), D 1269 IX (1), D 1270 II (1).

INDIAN OCEAN. A total of 19 (21.9–118.7 mm SL) specimens from 15 collections. IOAN: V 4953 (1). MCZ: AB 3 AE-17d (1), AB 6-332B (2), AB 6-337A (1), AB 6-339A (1). SIO: 69-22 (1). ZMUC: D 3828 V (2), D 3847 V (1), D 3904 III (2), D 3908 III (1), D 3917 VIII (1), D 3951 I (1).

Additional larvae and juvenile material from the Indian Ocean. ZMUC: D 3907 III (2), D 3916 III (1), D 3951 II (1).

PACIFIC OCEAN. A total of 120 (10.5–112.5 mm SL) specimens from 91 collections. FMNH: 80403 (1), 80404 (1). IOAN: V 23 (1), V 3700 (1), V 6429 (3 May 1971) (5), V 6429 (5 May 1971) (3), V 6429 (7 May 1971) (1), V 6437 (2), V 6469 (1). NMFS(LJ): J 20.145 (2), J 24.145 (1), J 31.139 (1). ORSTOM: CY II-14 (1), CY V-21 (1), CY VI-11(1). SIO: 51-375 (1), 60-134 (1), 60-236 (1), 60-239 (2), 61-576 (2), 61-588 (1), 68-535 (1), 69-341 (1), 69-345 (1), 70-311 (1), 70-336 (1), 70-340 (1), 70-343 (1), 70-345 (1), 71-294 (1), 71-296 (1), 71-297 (2), 71-309 (1), 71-310 (1), 72-9 (2), 72-15 (1), 72-22 (1), 72-23 (1), 72-316 (1), 73-147 (1), 73-149 (2), 73-151 (1), 73-165 (3), 73-166 (1), 73-170 (1), 73-325 (1), 73-329 (1), 73-331 (1), 73-336 (1); SIO uncat., 76-6 (1). UH: 69/11/1 (5), 61/11/2 (1), 69/11/6 (1), 70/7/1 (1), 70/12/9 (1), 70/12/31 (1), 70/12/34 (1), 71/3/10 (1), 71/6/1 (1), 71/6/14 (1), 71/6/20 (1), 71/6/21 (2), 71/6/22 (3), 71/6/31 (1), 73/8/38 (1), TC 47-68 (1), TC 47-69 (2), TC 52-63 (1). USNM: 201691 (1). ZMUC: D 3676 I (1), D 3682 II (1), D 3689 II (1), D 3689 VII (1), D 3714 III (1), D 3714 XI (1), D 3740 II (6), D 3751 VI (1), D 3788 I (1).

Additional larvae and juvenile material from the Pacific Ocean. ZMUC: D 3676 III (1), D 3745 II (1), D 3752 II (1), D 3753 I (1), D 3753 II (1), D 3766 XIII (2), D 3773 I (1), D 3789 VIII (1), D 3789 IX (1), D 3791 II (1), D 3792 II (1), D 3800 II (1).

SCOPELARCHIDAE: Species Accounts

The alepisauroid family Scopelarchidae contains 17 species arranged in four genera. The family is worldwide in distribution (fig. 38) except that no scopelarchid occurs in the Arctic Ocean or in the Mediterranean Sea. My revision of the family (Johnson, 1974c) was based on 2,102 specimens from 1,122 collections. Since publication of that revision, I have examined an additional 1,557 scopelarchid specimens from 714 collections and from throughout the geographic range of the family. This new material represents all known scopelarchid species except *Scopelarchoides kreffti* and *Scopelarchus stephensi*. The new material adds sub-

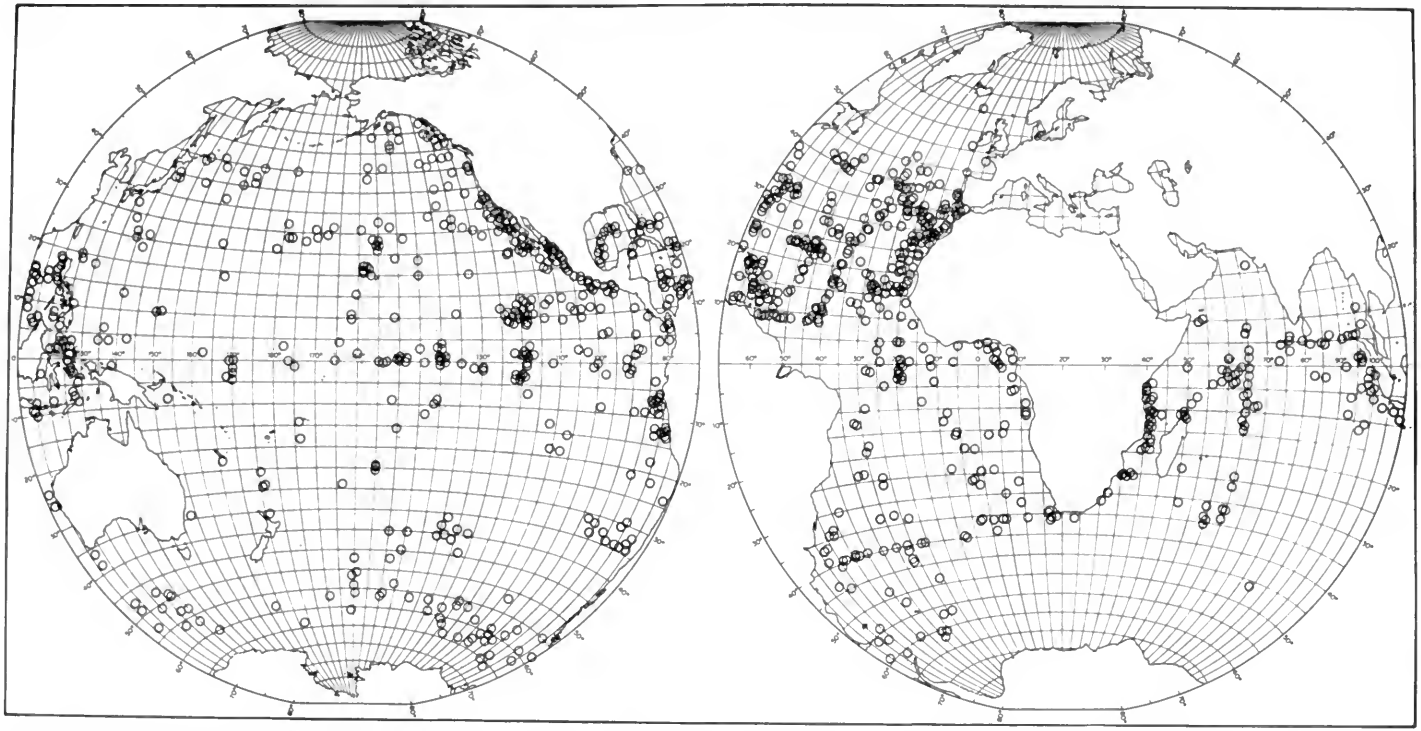


FIG. 38. Distribution of the family Scopelarchidae. All genera and species are plotted, but numerous overlapping or closely adjacent points omitted.

stantially to our knowledge of several scopelarchid species and confirms distributional patterns discussed in Johnson (1974c). In this section I present additions to the revision of the Scopelarchidae necessitated by study of this new material.

Benthalbella Zugmayer 1911

Benthalbella dentata (Chapman, 1939)

Distribution.—*Benthalbella dentata* is limited to the Pacific Subarctic and Transition Region areas of the North Pacific Ocean (Johnson, 1974c, p. 70, fig. 19).

Material Examined.—Johnson (1974c, pp. 70, 235) lists 127 (20.0–203.0 mm SL) specimens from 108 collections. An additional 17 (29.0–193.5 mm SL) specimens from 11 collections are listed here.

PACIFIC OCEAN: FMNH: 71698 (1), 71699 (1). SOSC: DES 5-T3-B (1), DES 5-T3-C (1), DES 5-T6-A (3), DES 5-T6-B (4), DES 5-T7-D (2), DES 5-T8-B (1), DES 5-T8-D (1), DES 6-T2-A (1), DES 6-T13-A (1).

Benthalbella elongata (Norman) 1937

Distribution.—*Benthalbella elongata* is an Antarctic species known only from south of the Subtropical Convergence (Johnson, 1974c, p. 76, fig. 21).

Material Examined.—Johnson (1974c, p. 76) lists 68 (33.0–234.0 mm SL) specimens from 48 collections. An additional four (98.5–192.5 mm SL) specimens from four collections are listed here.

ATLANTIC OCEAN: IOAN: AK 883 (1), AK 907 (1), AK 923 (1), AK 942 (1).

Benthalbella infans Zugmayer 1911

Johnson (1974c, p. 82) reports that specimens of *B. infans* from the central North Pacific exhibit higher anal-fin ray counts than specimens from other geographic areas. This report is corroborated by results for the additional material reported here. Anal-fin ray counts for specimens from the central North Pacific are significantly higher than for specimens from any other area (table 20). The lack of significant difference between counts for areas A, B, and C (table 20) suggests that the pattern of variation in *B. infans* is different from the pattern in *Evermannella indica* and *Odontostomops normalops* (see above).

Johnson & Barnett (1975, pp. 293, 294) present limited evidence for the existence of two separable populations of the photichthyid *Vinciguerria nimbaria* (Jordan & Williams) in the insular west Pacific (specifically the South China Sea) vs. the central North Pacific. The data for *B. infans* presented here partially parallel those for *V. nimbaria* to the extent of suggesting the distinctness of the North Pacific central gyral population of *B. infans*. This suggestion needs further confirmation based on additional material and characters and particularly requires the examination of additional adult material of *B. infans* from the central North Pacific.

Distribution.—*Benthalbella infans* is a nearly cosmopolitan warm-water species (fig. 39) inhabiting central and equatorial water mass areas of all three oceans. *Benthalbella infans* does not occur in the Transition Region areas of the North or South Pacific nor does it occur in the eastern portion of Pacific Equatorial Water. *Benthalbella infans* occurs almost throughout the area of North Atlantic Central Water, is known from the Caribbean Sea, but has apparently not been taken in the Gulf of Mexico.

TABLE 20. Comparison of values for anal-fin ray counts for specimens of *Benthalbella infans* from the Atlantic, Indian, and Pacific oceans.

Area	20	21	22	23	24	25	26	N	Mean ± 95% limits
A. North Atlantic + Caribbean	3	12	4	—	2	3	—	24	21.79±.670
B. South Atlantic, Indian Ocean, insular west Pacific, western and central equatorial Pacific	2	9	4	3	3	1	—	22	21.95±.619
C. Central South Pacific	2	1	3	1	—	—	—	7	21.43±1.049
D. Central North Pacific	—	—	1	1	1	7	2	12	24.67±.734

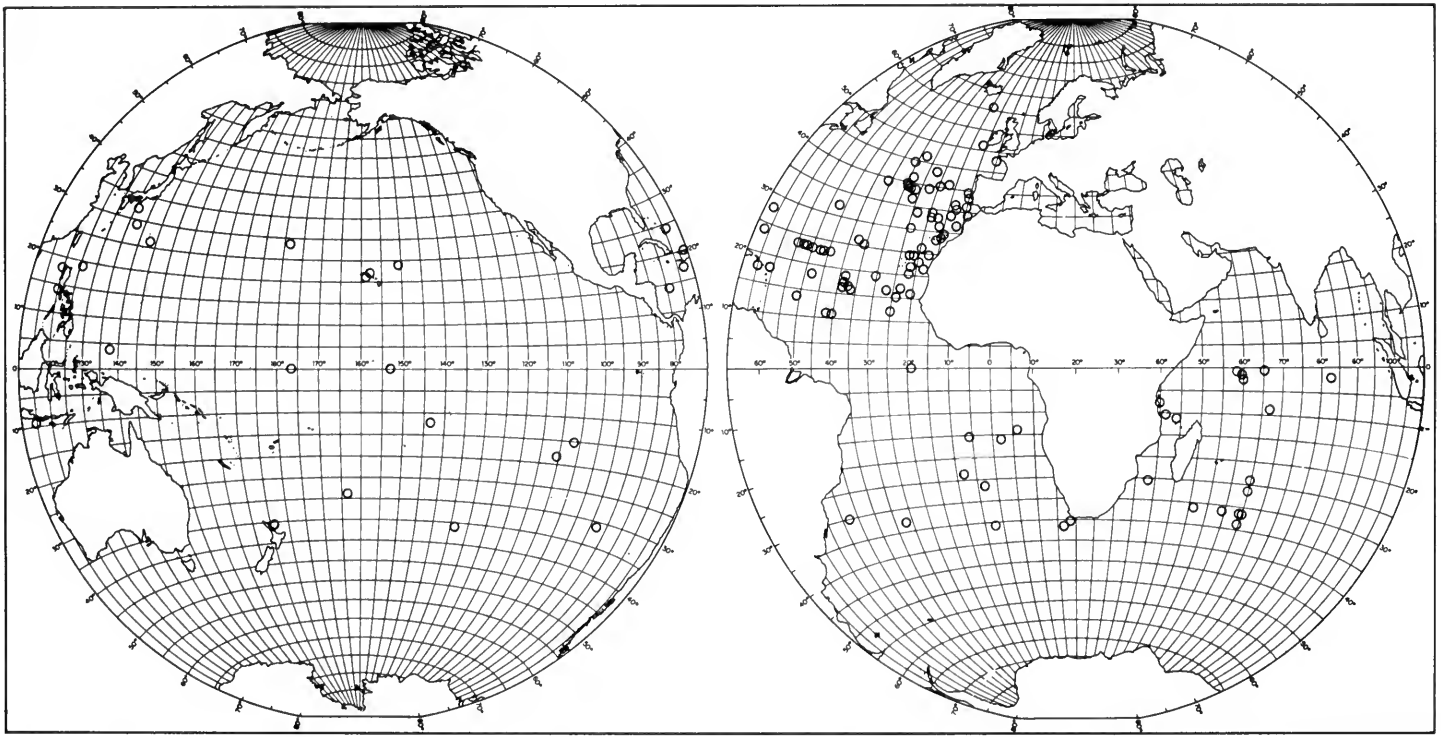


FIG. 39. Distribution of *Benthalbella infans*.

Material Examined.—Johnson (1974c, pp. 84, 235) lists 93 (6.6–137.4 mm SL) specimens from 64 collections. An additional 90 (12.2–124.4 mm SL) specimens from 54 collections are listed here.

ATLANTIC OCEAN: WHOI, RHB: 807 (1), 1037 (1), 1038 (12), 1046 (1), 1411 (3), 1721 (1), 1730 (1), 1886 (1), 1911 (1), 2025 (2), 2026 (1), 2032 (1), 2058 (1), 2070 (1), 2080 (6), 2087 (1), 2097 (1), 2116 (1), 2216 (1), 2229 (1), 2245 (1), 2264 (1), 2265 (1), 2274 (11), 2278 (1), 2531 (1), 2555 (2), 2565 (1), 2601 (1), 2900 (1), 2915 (1), 2917 (2), 2918 (2), 2923 (1), 2926 (1), 2979 (1), 2988 (1), 2998 (1), 3004 (2), 3005 (2), 3010 (3), 3014 (1), 3015 (1), 3017 (1), 3018 (1), 3020 (1). INDIAN OCEAN: SOSC: AB 3-6 (1), AB 3-13 (1), AB 6-348A (1), AB 6-349A (1), AB 6-351C + 352A (1). PACIFIC OCEAN: IOAN: V 25 (1). UH: 70/7/24 (1), TC 52-52 (1).

Benthalbella linguidens (Mead & Böhlke) 1953

Distribution.—*Benthalbella linguidens* is known only from the subarctic North Pacific, north of 39° 21′ N, from off northern Japan to off Oregon (Johnson, 1974c, p. 87, fig. 19).

Material Examined.—Johnson (1974c, pp. 88, 235) lists 22 specimens (40.6–221.0 mm SL) from 12 collections. One additional specimen (82.1 mm SL) is reported here.

PACIFIC OCEAN: IOAN: V 3605 (1).

Benthalbella macropinna Bussing & Bussing 1966

Distribution.—*Bethalbella macropinna* is an Antarctic species occurring throughout subantarctic and antarctic waters in the Antarctic Circumpolar Current (Johnson, 1974c, p. 94, fig. 28).

Material Examined.—Johnson (1974c, p. 94) lists 63 (29.1–233.5 mm SL) specimens from 47 collections. An additional 15 (52.8–240.0 mm SL) specimens from 11 collections are listed here.

ATLANTIC OCEAN: IOAN: AK 844 (3), AK 845 (1), AK 850 (1), AK 855 (2), AK 856 (2), AK 886 (1), AK 936 (1), AK 942 (1), AK 949 (1), AK 960 (1). WHOI, RHB: 2250 (1).

Rosenblattichthys Johnson 1974

Rosenblattichthys alatus (Fourmanoir) 1970

The account of *R. alatus* in Johnson (1974c, pp. 97–103) was based on 26 specimens from 24 collections. The discovery of substantial additional material of *R. hubbsi* Johnson 1974 (see below), allowed elucidation of characters useful in separating larval material of *R. alatus* from that of *R. hubbsi*. Using this new information, I reexamined specimens and/or recorded character data for material of *R. alatus*. A number of the specimens previously identified as *R. alatus* are in fact *R. hubbsi*—SIO: 70-310 (1), 71-295 (1), 72-9 (1); ZMUC: D 3932 VII (1), D 3932 VIII (1), D 3964 II (2). The following specimens are now tentatively identified as *R. hubbsi*—ZMUC: D 3927 II (1), D 3928 I (1), D 3929 I (1). I have also examined new material of *R. alatus*, six specimens from six collections. This new material and the changes in identification of the above specimens force me to partially modify my previous description of *R. alatus* and to substantially modify the zoogeographic account for this species.

Description.—Only necessary changes in my previous description (Johnson, 1974c) of *R. alatus* are included in the following account. Meristic characters: anal-fin rays 20 to 22, pectoral-fin rays 23 to 26 (table 21). Development: smallest known larva (D 3893 I, 11.1 mm SL) with only pectoral- and caudal-fin rays fully

TABLE 21. Comparison of values for meristic characters in three species of *Rosenblattichthys*.

A. Anal-fin rays

Species	20	21	22	23	24	25	N	Mean ± 95% limits
alatus	1	3	7	—	—	—	11	21.5±.46
hubbsi	—	—	—	4	13	2	19	23.9±.27
volucris	—	2	8	22	8	—	40	22.9±.25

B. Pectoral-fin rays

Species	21	22	23	24	25	26	N	Mean ± 95% limits
alatus	—	—	3	1	3	4	11	24.7±.85
hubbsi	4	16	3	—	—	—	23	22.0±.24
volucris	—	—	2	11	19	8	40	24.8±.26

differentiated and with the following accessory pigment spots or areas developed: DA, CA, PA, IA (see Johnson, 1974c, pp, 96, 101, for explanation of accessory pigment spots). The following accessory pigment spots or areas are present in all known larger larvae (14.6 mm SL and larger): DA, CA, PA, AA.

Distribution.—*Rosenblattichthys alatus* is known from a total of 25 (11.1–93.9 mm SL) specimens (including the holotype and two additional specimens reported by Fourmanoir [1971] but not examined by me) from the Indian and Pacific oceans (fig. 40). *Rosenblattichthys alatus* is not known from the Atlantic Ocean. The distributions of *R. alatus* and *R. hubbsi* (fig. 40) as now known are mutually exclusive: *R. hubbsi* in central waters of the North and South Atlantic, Indian, and North Pacific oceans; *R. alatus* in equatorial waters of the Indian and Pacific oceans, insular west Pacific, and (based on one [80.1 mm SL] specimen) central water in the South Pacific Ocean. Except for the absence of *R. hubbsi* from the central gyral area of the South Pacific, the distribution of these two species of *Rosenblattichthys* is quite reminiscent of the distributions of *Coccorella atlantica* and *C. atrata* (see above).

Material Examined.—The following listing includes all valid records of *R. alatus* for specimens I have examined. A total of 22 (11.1–93.9 mm SL) specimens from 21 collections.

INDIAN OCEAN: A total of 14 (11.1–53.5 mm SL) specimens from 13 collections. MCZ: AB 6-339A (1), AB 6-340B (1). USNM: AB 6-340A (1). WHOI: AB 6-335 (1). ZMUC: D 3814 I (1), D 3893 I (1), D 3902 III (1), D 3903 II (1), D 3906 III (1), D 3921 III (2), D 3921 V (1), D 3921 VIII (1), D 3925 IV (1). PACIFIC OCEAN: A total of eight (19.5–93.9 mm SL) specimens from eight collections. IOAN: V 4494 (1), V 6429 (3 May 1971) (1), V 6429 (5 May 1971) (1). ORSTOM: MARURU 18A (1). SIO: 60-130 (1), 70-343 (1), 70-344 (1), 72-317 (1).

Rosenblattichthys hubbsi Johnson 1974

Rosenblattichthys hubbsi was described from one adult specimen (144.5 mm SL) from the equatorial South Atlantic (Johnson 1974a, 1974c). Three additional larval specimens (*Dana* 1288 II, 1 [23.1 mm SL]; SIO 69-26, 2 [18.8—22.1 mm SL]) from the Atlantic and Indian oceans, respectively, were tentatively identified as this species by Johnson (1974c, p. 106). Included in the large number of additional scopelarchid specimens examined since publication of my revision of this family are 42 larval and juvenile specimens of *R. hubbsi* from all three oceans. This material resulted in confirmation of my identification of the three larval

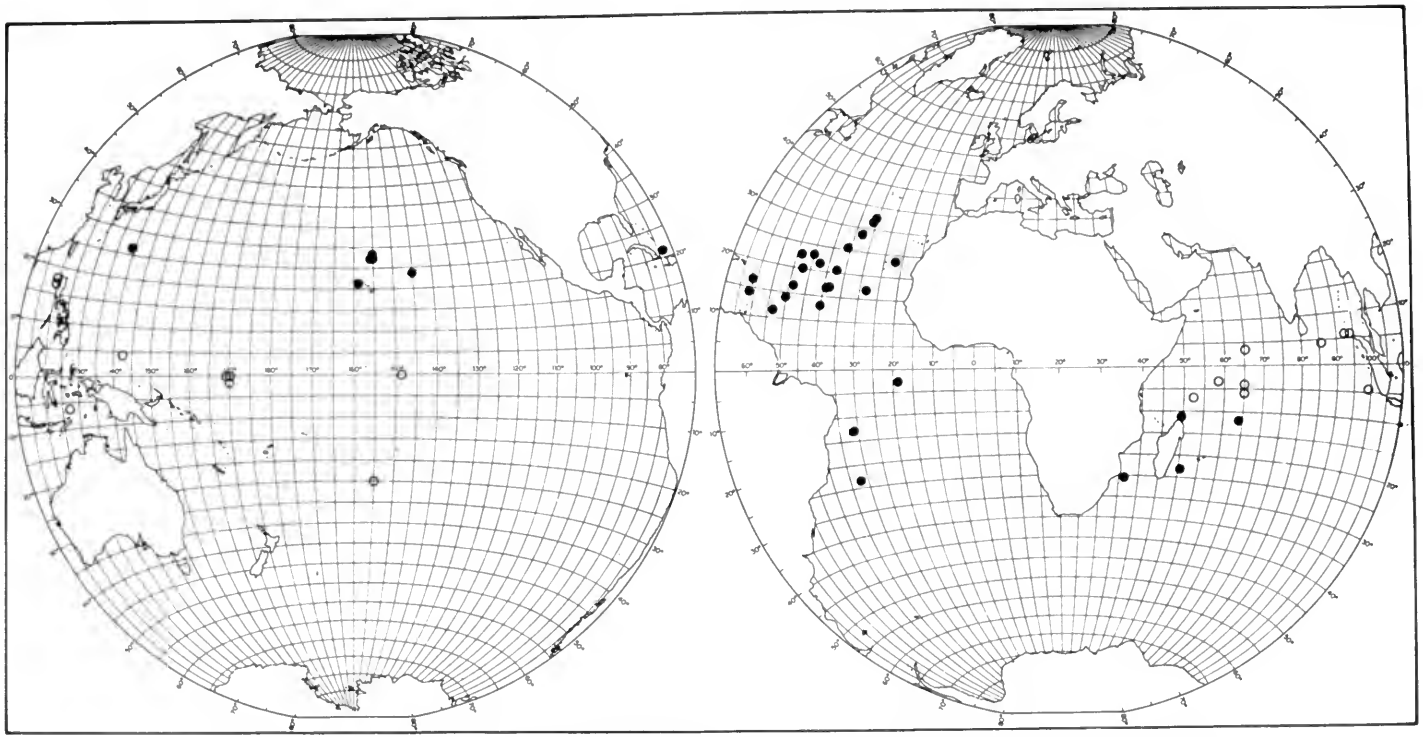


FIG. 40. Distribution of two species of *Rosenblattichthys: R. alatus* (open circles) and *R. hubbsi* (closed circles).

TABLE 22. Comparison of values for meristic characters for specimens of *Rosenblattichthys hubbsi* from the Atlantic, Indian, and Pacific oceans.

	A. Anal-fin rays				
Area	**23**	**24**	**25**	**N**	**Mean ± 95% limits**
Atlantic	3	6	—	9	23.7±.38
Indian	1	2	—	3	23.7
Pacific	—	5	2	7	24.3±.45
	B. Pectoral-fin rays				
Area	**21**	**22**	**23**	**N**	**Mean ± 95% limits**
Atlantic	4	7	1	12	21.8±.39
Indian	—	2	1	3	22.3
Pacific	—	7	1	8	22.1±.30

specimens listed above and allows me to expand the description of *R. hubbsi* to include larval and juvenile specimens.

Meristic Characters.—Counts based on a total of 23 specimens from all three oceans: dorsal-fin rays 8 or 9 (usually 9); anal-fin rays 23 to 25; pectoral-fin rays 21 to 23. *Rosenblattichthys hubbsi* has more anal-fin rays and fewer pectoral-fin rays than either *R. alatus* or *R. volucris* (table 21), but there is significant overlap in the case of *R. hubbsi* and *R. volucris*. Specimens of *R. hubbsi* from the Atlantic Ocean appear to have fewer anal-fin rays (and possibly fewer pectoral-fin rays) than specimens from the Pacific Ocean (table 22). This is similar to the pattern described above for *Evermannella indica* and *Odontostomops normalops*. However, the differences between the mean values for anal-fin ray counts and pectoral-fin ray counts given in Table 22 are not statistically significant, and the possibility of inter-ocean differences in these counts for *R. hubbsi* needs to be confirmed on the basis of additional material.

Description.—Description is based on larval and juvenile specimens.

RECOGNITION.—Larvae of *R. hubbsi* (fig. 41) are distinguished by the following combination of characters: dorsal-fin rays 8 or 9, anal-fin rays 23 to 25, pectoral-fin rays 21 to 23; head remarkably large in smaller larvae, head length in larvae up to 30 mm exceeding 30% SL; pectoral fins precocious, very prominent, and elongate in smaller larvae, ossification of pectoral-fin rays preceding ossification of rays of all other fins; unique combination of two accessory pigment spots or areas, one middorsal appearing over posterior one-third of anal-fin base (DA) and one appearing as an oblong dash at fork of caudal fin (CA) on each side of body. Larvae of *R. hubbsi* larger than 12 to 15 mm SL may easily be distinguished from those of *R. alatus* and *R. volucris* in having only two accessory pigment spots or areas rather than five or seven, respectively, accessory pigment spots or areas. Larvae and juveniles of *R. hubbsi* larger than 20 to 25 mm SL possess dermal pigmentation on the body (described below); such pigmentation is lacking in larvae and juveniles of *R. alatus*.

FINS.—In smallest known specimen (RHB 3011, 9.2 mm), pectoral-fin rays essentially fully differentiated, caudal-fin rays partially differentiated, rays of remaining fins unformed. Pectoral fins precocious, appearing very early in development, prolonged, and remarkably prominent in smaller larvae. Light pigmentation on pectoral-fin rays in larvae 12 to 15 mm in length and larger. Pigment at bases and/or on rays of all fins in juveniles. Pelvic fins appearing

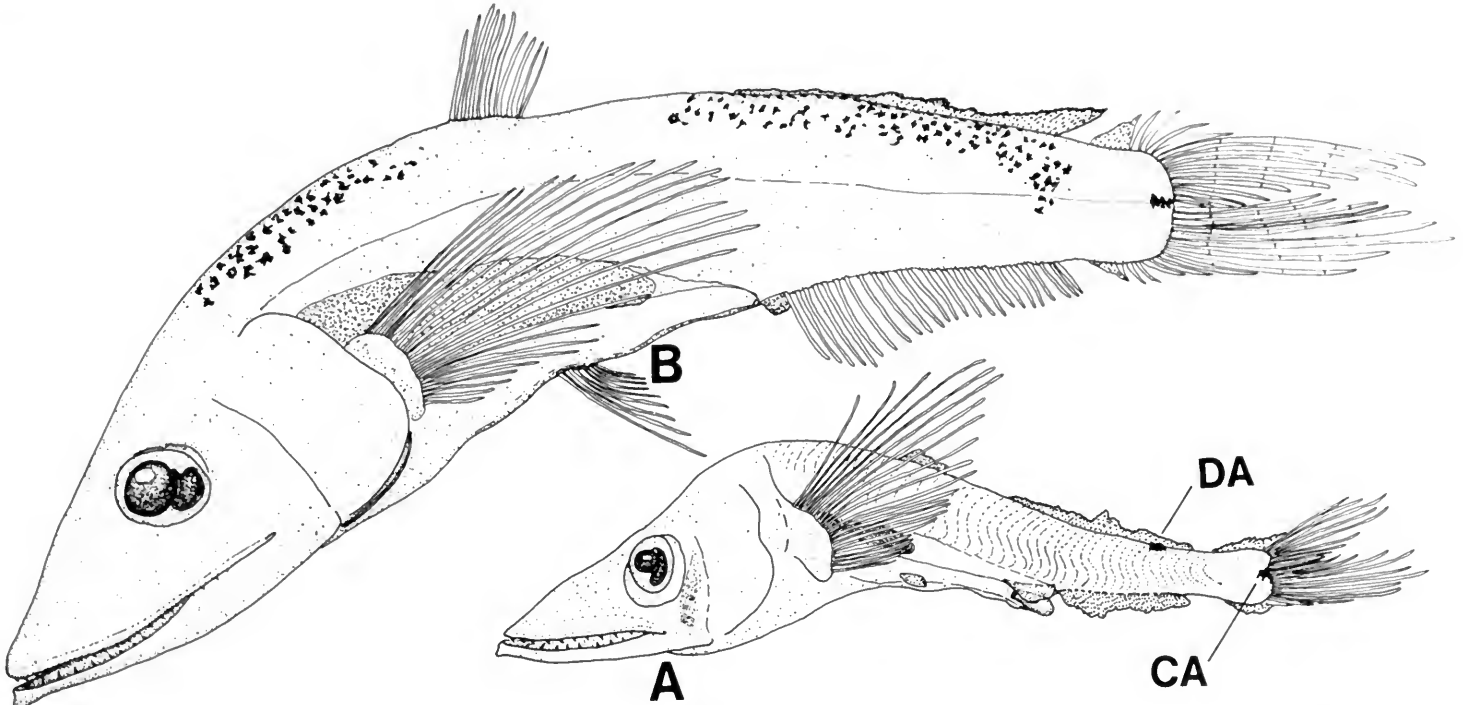


FIG. 41. *Rosenblattichthys hubbsi*, larvae, (**A**) 14.1 mm SL, central North Pacific, SIO 72-14; (**B**) 24.9 mm SL, central North Atlantic, RHB 2910.

midlaterally, dorsal to level of gut, and beneath developing dorsal-fin base. Pelvic-fin insertion beneath dorsal-fin base in larger larvae and slightly in advance of dorsal-fin origin in juveniles larger than 30 to 35 mm SL. Ventral adipose fin never exceeding one-third of pelvic-anal distance, reduced to a thin triangular flap in larvae larger than 18 mm, absent in juveniles. Dorsal adipose fin remaining elongate, to over anterior anal-fin rays, in largest larvae. All fin rays ossified in specimens exceeding 18 to 20 mm. Order of fin ray ossification: pectoral, caudal, dorsal, anal, pelvic.

PERITONEAL PIGMENT SECTIONS.—Only one peritoneal pigment section. Peritoneal pigment section present in smallest known larvae (9.2 mm) as a thin, dark brown, transverse sheet above gut and medial to pectoral-fin base. Peritoneal pigment section expanding posteriad during subsequent growth and forming a canopy above gut prior to laterad expansion, forming a complete tube of pigmentation around gut. Posteriad expansion of and enclosure of gut by peritoneal pigment section complete in specimens 30 to 35 mm SL and larger. Completion of peritoneal pigment tube around gut taken arbitrarily as basis for classifying specimens as larvae or as juveniles.

ACCESSORY PIGMENT SPOTS OR AREAS.—A maximum of two accessory pigment spots or areas (fig. 41): DA and CA. Both pigment spots absent in smallest known larvae (9.2 mm). All known larger larvae, to about 28 mm SL maximum, have both DA and CA pigment spots. The DA appearing over posterior one-third of anal-fin base, middorsally, well anterior to posterior terminus of dorsal adipose-fin base. The CA appearing as a single spot, group of spots, or oblong dash of pigment over bases of middle caudal-fin rays. Appearance of dermal pigmentation (see below) results in masking DA, making DA indiscernible in specimens larger than 28 to 30 mm SL. The CA becoming indiscernible in specimens 35 to 40 mm SL and larger.

DERMAL PIGMENTATION.—Dermal pigmentation (see Johnson, 1974c, pp. 20–23) present in larvae larger than 20 to 25 mm SL. Two areas of dermal pigmentation appear at about the same time, one middorsally above pectoral-fin base, the other associated with and just posterior to DA pigment spot. Dermal pigmentation on epaxial portion of body appearing to spread posteriorly and anteriorly, respectively, from these two initial areas, with the last epaxial area of body to develop dermal pigmentation being that area immediately ventral to dorsal-fin base. Epaxial dermal pigmentation essentially complete in juveniles 30 to 35 mm and larger. Dermal pigmentation on hypaxial portion of body first appearing on caudal peduncle, immediately ventral to horizontal septum and centered on a vertical through a point immediately posterior to adipose-fin base. Hypaxial pigmentation on body appearing (in successively larger larvae) to spread anteriorly from this area and still incompletely developed in largest known juvenile (SIO 72-9, 63.9 mm SL). Juveniles with a distinctive band of dark pigment along dorsolateral margin of lower jaw.

GUT.—Post-pelvic gut length exceeding pelvic-anal distance in smaller larvae, forming a partial loop outside of normal limits of abdominal cavity (fig. 41), and attached to ventral adipose fin. Gut with essentially adult proportions—anus immediately in advance of anal-fin origin—in larger larvae and juveniles. In smaller larvae stomach visible only as a short blind sac protruding from posterodorsal margin of gut between pectoral-fin bases. Stomach expanding posteriad with growth, reaching to just before anus in largest juvenile.

METAMORPHOSIS.—As is true for other species of *Rosenblattichthys*, *R. hubbsi* exhibits gradual metamorphosis, with changes leading to adult morphology occurring over a wide size range. These changes include at least the following: resorption of ventral adipose fin, decrease in length of base of dorsal adipose fin, extensive posteriad expansion of peritoneal pigment section and stomach, development of distinctive dermal pigmentation of juveniles, and invasion of abdominal body wall by musculature. Based on material I have examined, these processes begin in specimens 18 to 20 mm in size and are not complete in any of the juvenile specimens.

Distribution.—*Rosenblattichthys hubbsi* is now known from 47 specimens from the Atlantic, Indian, and Pacific oceans (fig. 40). *Rosenblattichthys hubbsi* occurs in the North and South Atlantic central, Indian Ocean central, and North Pacific central-water-mass areas.

Larvae of *R. hubbsi* have been taken throughout the year in hauls to depths as shallow as 60 m. The holotype remains the only known adult specimen.

Material Examined.—A total of 46 (9.2–63.9 mm SL) specimens from 38 collections plus the 144.5 mm SL holotype, ISH 2219/71.

ATLANTIC OCEAN: A total of 28 (9.2–41.3 mm SL) specimens from 23 collections. WHOI, RHB collection numbers: 954 (1), 1423 (2), 1431 (1), 2028 (1), 2084 (2), 2103 (1), 2903 (1), 2904 (1), 2906 (1), 2910 (1), 2913 (1), 2914 (1), 2917 (1), 2918 (2), 2922 (1), 2981 (1), 2983 (1), 2989 (1), 2997 (1), 3011 (2). ZMUC: D 1243 III (1), D 1285 III (2), D 1288 II (1). INDIAN OCEAN: A total of seven (10.0–27.2 mm SL) specimens from five collections. SIO: 69-26 (2). SOSC: AB 6-343A (1). ZMUC: D 3932 VII (1), D 3932 VIII (1), D 3964 II (2). PACIFIC OCEAN: A total of 11 (12.6–63.9 mm SL) specimens from 10 collections. NMFS (LJ): cruise 7205, station 24.145 (1). SIO: 70-310 (1), 71-295 (1), 72-9 (2), 72-14 (1), 73-329 (1), UH: 71/2/9 (1), 71/6/17 (1), 71/6/23 (1), 71/6/27 (1).

The following specimens are tentatively assigned to *R. hubbsi* on the basis of capture location. They are too small for positive identification. Localities for these specimens are not plotted on Figure 40. INDIAN OCEAN: ZMUC, D 3927 II, 1 (9.0), 10° 55′ S, 50° 15′ E; D 3928 I, 1 (12.1), 11° 20′ S, 50° 10′ E; D 3929 I, 1 (10.5), 12° 11′ S, 50° 18′ E.

Rosenblattichthys volucris (Rofen, 1966)

On the basis of counts and other information presented, the three specimens recorded as *Scopelarchus* sp. by Parin et al. (1973)—IOAN: B 92 (1), B 124 (1), B 125 (1)—are assigned to *R. volucris*.

Distribution.—*Rosenblattichthys volucris* is confined to the eastern half of the Pacific Ocean (fig. 42). It is known from the Transition Region off California and off Chile and from a relatively narrow zone along the equator from near the American mainland to 161° 52.5′ to 51.5′ W. A detailed discussion of the zoogeography of scopelarchids and evermannellids inhabiting the eastern portion of the Pacific Equatorial Water Mass region is presented in a subsequent section of this paper.

Material Examined.—Johnson (1974c, p. 116) lists 108 (5.9–103.5 mm SL) specimens from 71 collections. An additional 64 (4.7–81.3 mm SL) specimens from 35 collections are listed here.

PACIFIC OCEAN: CAS: 63778 (1). IOAN: B 74 (2). NMFS (LJ): J 60-71 (1), J 65-41 (1), J 65-118 (1), J 77-86 (1), J 77-92 (1), J 77-127 (1), J 77-138 (1), J 77-142 (1), TC 51-31 (1), TC 51-37 (1), TC 51-55 (1), TC 51-65 (1), TC 51-66 (1). SIO: 72-171 (1), 74-28 (2), 74-40 (1), 74-41 (2). SOSC: AB 16-618D (1), AB 16-622 A (1), DES 1-T7-C (1), DES 1-T14-D (1), DES 2-T1-C (1), DES 2-T1-D (1), DES 4-T13-C (1), DES 4-T13-D (1), DES 4-T14-B (1), DES 4-T14-C (1), DES 4-T16-D (1), DES 5-T7-D (1), UND 46-50 (1). ZMUC: D 3556 II (1), D 3556 III (3), D 3556 VI (25).

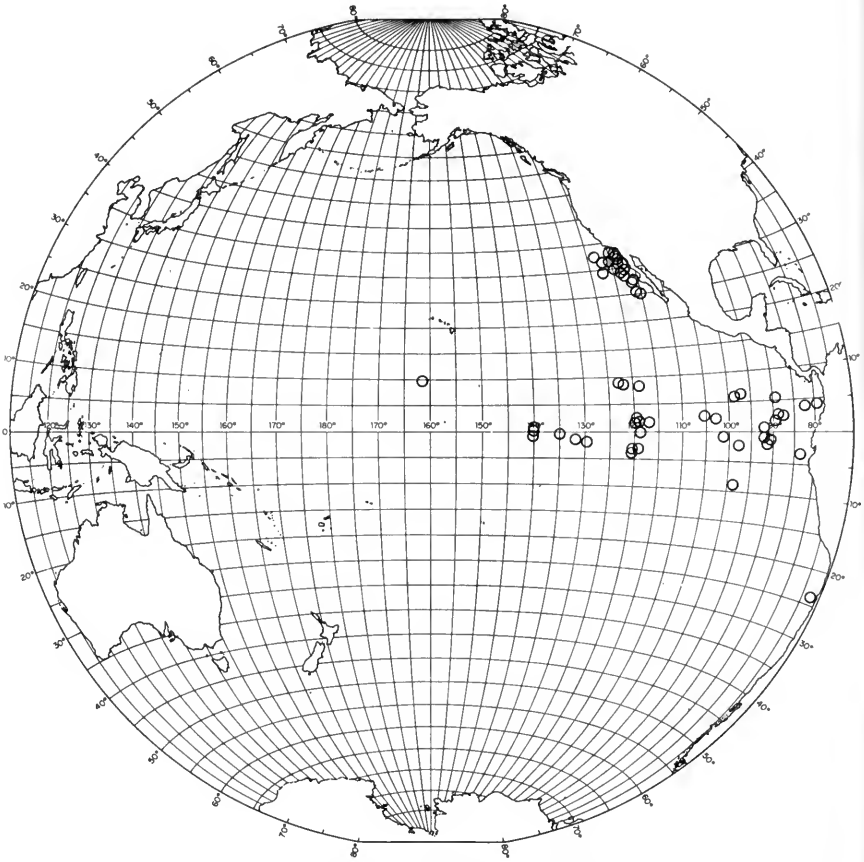


FIG. 42. Distribution of *Rosenblattichthys volucris*.

Scopelarchoides Parr 1929

Scopelarchoides climax Johnson 1974

Scopelarchoides climax was described from a total of nine (18.6–99.3 mm SL) specimens from seven collections, all from the vicinity of 24.5° to 25° S, ca. 155° W, in the central South Pacific. Only one additional specimen has come to hand: ORSTOM, Sillage sta. No. 6, south Tuamotu Islands, 22° S, 139° W, IKMT, 220 m, December 1977, 97.8 mm SL. This specimen is the second known adult of *S. climax*, and meristic and morphometric data for it are presented below. Meristic characters: dorsal-fin rays 8, anal-fin rays 27, pectoral-fin rays 25, lateral line scales ca. 52. Proportional dimensions, expressed as thousandths of the SL: Body: depth at dorsal-fin origin, 148. Caudal peduncle: least depth, 74; length, 102. Adipose fin: distance to midcaudal rays, 204; length of base, 49. Anal fin: length of base, 286. Dorsal fin: length of base, 44; dorsal-fin origin to anal-fin origin (distance between verticals), 254; end of dorsal-fin base to bases of midcaudal rays, 602. Pectoral-fin insertion to pelvic-fin insertion, 134. Anus to anal-fin origin, 52. Distance from snout to: dorsal-fin origin, 367; anal-fin origin, 627; pectoral insertion, 242; pelvic insertion, 373; orbit, 69. Head length, 231. Postor-

bital head length, 80. Orbit: horizontal diameter, 94; vertical diameter, 97. Interorbital width, 10. Upper jaw length, 176. Lower jaw length, 195. Longest dentary tooth, 29. In meristics, morphometrics, and all other examined characters, including the presence of a distinctive black cap of melanophores at the dorsal margin of the lens pad and the distribution of pigment on the head, body, and fins, the ORSTOM specimen agrees well with Johnson's (1974c) description of the holotype. Barnett (1975) lists *S. climax* as endemic to the central-gyral area of the South Pacific.

Scopelarchoides danae Johnson 1974

Distribution.—*Scopelarchoides danae* is a wide-ranging tropical species occurring in all three oceans (fig. 43). *Scopelarchoides danae* is known from both sides of the Atlantic, as far as 41° 31′ to 33′ N (RHB 1010, 1 [21.0], specimen taken in a station in the direct path of the Gulf Stream) and from the Caribbean Sea, Gulf of Mexico, and Gulf of Guinea. The only South Atlantic records for *S. danae* are within 06° of the equator, near the African mainland. *Scopelarchoides danae* occurs throughout the Indian Ocean and insular western Pacific. In the Pacific Ocean *S. danae* is known from only two adult specimens and one larval specimen: ORSTOM, Coriolis P 1-6, 1 (113.6), 22° 03′ S, 165° 58.0′ E, near New Caledonia; ORSTOM, Caride V-20A, 1 (86.1), 09° 54′ S, 141° 53′ W (not 141° 33′ W as listed by Johnson, 1974c, p. 133), near the Marquesas; ZMUC, D 3567 I, 1 (17.4), 09° 06′ S, 140° 21.5′ W, near the Marquesas. Most captures of *S. danae* have been near continental or insular land masses. *Scopelarchoides danae* has not been captured and probably does not occur in the central gyral areas of the Pacific away from island chains, nor does *S. danae* occur in the eastern Pacific.

Material Examined.—Johnson (1974c, pp. 133, 235) lists 230 (6.5–121.2 mm SL) specimens from 104 collections. An additional 119 (10.0–107.5 mm SL) specimens from 57 collections are listed here.

ATLANTIC OCEAN: WHOI, RHB: 1010 (1), 1104 (2), 1251 (3), 1253 (1), 1259 (2), 1262 (1), 1266 (1), 1274 (20), 1275 (2), 1278 (1), 1282 (4), 1283 (1), 1289 (1), 1312 (1), 1315 (2), 1506 (3), 2288 (2), 2289 (6), 2290 (1), 2291 (2), 2929 (2), 2938 (1), 2942 (2), 2943 (1), 2945 (1), 2947 (2), 2948 (2), 2949 (3), 2950 (1), 2952 (2), 2953 (2), 2955 (5), 2956 (5), 2957 (1), 2960 (1), 2961 (1), 2962 (2), 2963 (2), 2964 (1), 2966 (2), 2972 (1), 2979 (2), 2984 (1), 3050 (1), 3053 (1). ZMUC: D 1188 III (1), D 1228 II (1), D 1230 III (1), D 1285 III (1), D 3545 V (1), D 3546 II (2), D 3547 I (3). INDIAN OCEAN: IOAN: V 4618 (1). MCZ: AB 6-340B (2); O. Nographer, station J 20-12 (1). PACIFIC OCEAN: ZMUC: D 3687 III (1), D 3712 III (1).

Scopelarchoides kreffti Johnson 1972

Distribution.—*Scopelarchoides kreffti* is known only from the 10 (52.8–187.5 mm SL) specimens from five collections listed in Johnson (1974c, p. 136). All specimens were taken in the South Atlantic Ocean between 34° and 41° S, and 48° to 07° W (Johnson, 1974c, p. 136, fig. 41).

Scopelarchoides nicholsi Parr 1929

Parin et al. (1973, p. 125) list 14 (27–119 mm SL) specimens from the eastern tropical Pacific.

Brewer (1973, p. 19) lists an additional 18 (25–106 mm SL) specimens from the Gulf of California and eastern tropical Pacific.

Distribution.—*Scopelarchoides nicholsi* is restricted to the eastern Pacific Ocean in those areas of Pacific Equatorial Water exhibiting the greatest development of a subsurface layer of poorly oxygenated water (fig. 44). A detailed account of the

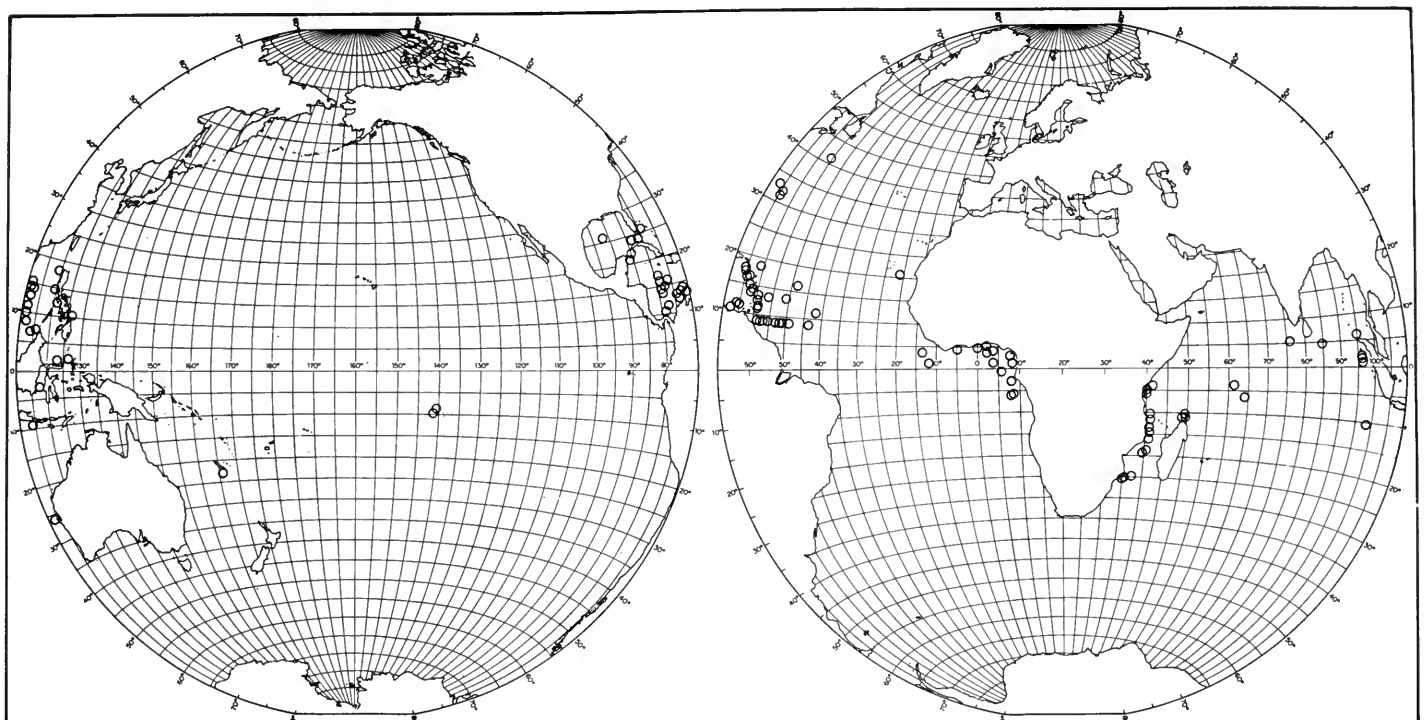


FIG. 43. Distribution of *Scopelarchoides danae*.

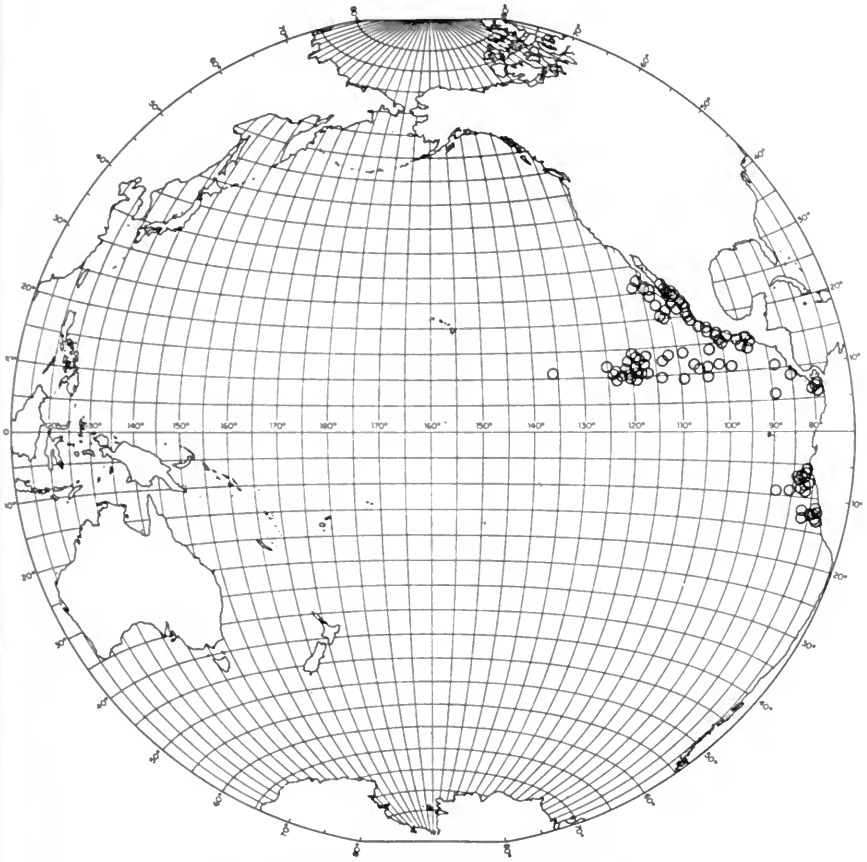


FIG. 44. Distribution of *Scopelarchoides nicholsi*.

distribution of *S. nicholsi* is included in the discussion of the zoogeography of scopelarchids and evermannellids inhabiting the eastern portion of Pacific Equatorial Water in a subsequent section of this paper.

Material Examined.—Johnson (1974c, pp. 144, 145) lists 241 (8.1–115.5 mm SL) specimens from 100 collections. An additional 106 (5.2–111.0 mm SL) specimens from 51 collections are listed here.

PACIFIC OCEAN: IOAN: AK 229 (1), AK 276 (1), AK 282A (1), AK 291 (1), AK 300 (1). NMFS(LJ): J 57-1 (2), J 57-6 (1), J 57-12 (1), J 57-18 (4), J 57-24 (3), J 57-41 (1), J 57-47 (7), J 57-50 (2), J 57-52 (2), J 57-132 (1), J 57-134 (2), J 57-136 (1), J 60-170 (4), J 77-3 (2), J 77-142 (1), J 77-144 (3), J 77-157 (4), J 77-161 (2), J 77-168 (1), J 77-176 (1), J 77-180 (1). SOSC: AB 16-650R (5), AB 16-655D (2), AB 16-655F (1), AB 16-656A (4), AB 16-656F (4), AB 16-656O (1), AB 16-656Q (1); ARGO 11-48 (1); ALAMINOS 14-213 (1), J 12-260 (1), J 12-268 (2), J 30-128 (1), J 30-167 (1), J 50-146 (1), J 50-162 (1), J 60-183 (2), UND 46-118 (1); WASHINGTON 45-23 (1), 45-46 (1), 46-11 (1). UMML: 24511 (1), 24530 (1), 28005 (1). ZMUC: D 3548 V (4), D 3548 VII (15).

Scopelarchoides signifer Johnson 1974

Distribution.—*Scopelarchoides signifer* is limited to the Indian and Pacific oceans (fig. 45). *Scopelarchoides signifer* occurs throughout the Indian Ocean and the

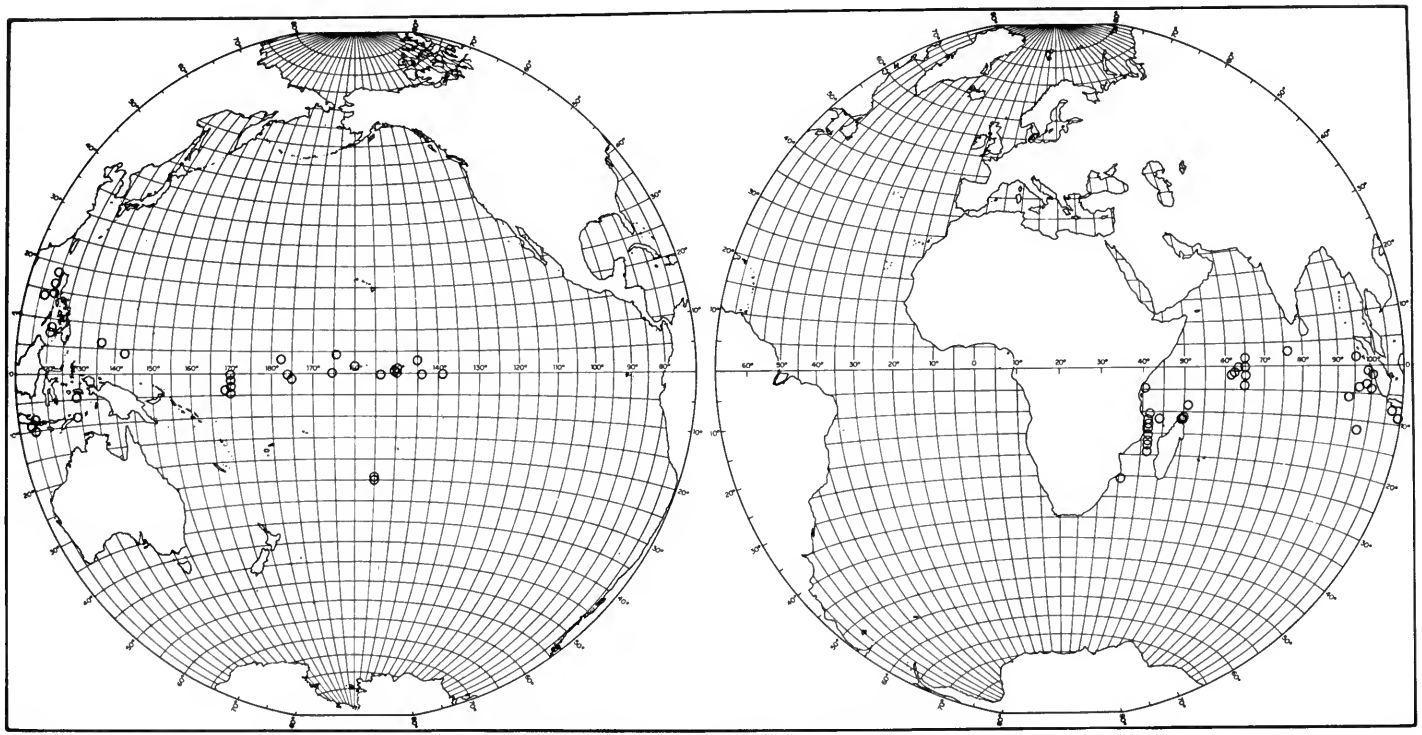


FIG. 45. Distribution of *Scopelarchoides signifer*.

semi-isolated seas of the Indo-Malayan Archipelago. Most records in the Pacific are from a relatively narrow band along the equator. *Scopelarchoides signifer* does not occur in the central North Pacific but is known from 10 larvae taken near 24.5° to 25° S, 155° W, in the central South Pacific.

Material Examined.—Johnson (1974c, p. 152) lists 208 (4.8–104.6 mm SL) specimens from 76 collections. An additional 27 (10.0–78.0 mm SL) specimens from 15 collections are listed here.

INDIAN OCEAN: SOSC: AB 6-336B (1), AB 6-337A (1), AB 6-338A (1), TV 4-171 (2). PACIFIC OCEAN: SOSC: ELT 30-2102 (2). UH: TC 47-69 (1). IOAN: V 5117, 21-22 October 1961 (2), V 5117, 22 October 1961 (1), V 5139 (2), V 6033 (1), V 6429, 3 May 1971 (5), V 6429, 5 May 1971 (4), V 6469 (1), V 6490, 25 June 1971 (2), V 6490, 26 June 1971 (1).

Scopelarchus Alcock 1896

Scopelarchus analis (Brauer, 1902)

Distribution.—*Scopelarchus analis* is a circumglobal warm-water species occurring throughout the North and South Atlantic, Indian Ocean, and insular western Pacific. In the Pacific Ocean virtually all records of *S. analis* are from central water areas of the North and South Pacific. *Scopelarchus analis* is known from the Transition Region off California and Baja California, but it is not known from the Transition Region off Chile. *Scopelarchus analis* appears to be largely excluded from the area of Pacific Equatorial Water (fig. 46).

Material Examined.—Johnson (1974c, pp. 170 to 173) lists 602 (6.0–126.3 mm SL) specimens from 275 collections. An additional 815 (6.2–98.5 mm SL) specimens from 290 collections are listed here.

ATLANTIC OCEAN: IOAN: AK 820 (1), 826 (1), 829 (1), 1009 (1). UMML: 19993 (1), 20003 (1), 20010 (1), 22843 (1), 22971 (1), 24179 (3), 24300 (1), 24575 (1), 24720 (1), 26326 (6). USNM: 113298 (2), 196068 (1); ACRE 4-5B (1). WHOI, RHB: 801 (3), 803 (1), 805 (1), 970 (1), 1013 (1), 1018 (1), 1023 (1), 1046 (1), 1047 (10), 1107 (1), 1200 (1), 1254 (3), 1257 (2), 1258 (1), 1267 (1), 1281 (2), 1297 (13), 1305 (2), 1314 (2), 1315 (1), 1423 (1), 1427 (2), 1431 (2), 1438 (5), 1441 (1), 1505 (2), 1509 (5), 1511 (1), 1520 (1), 1718 (2), 1721 (1), 1728 (7), 1729 (2), 1730 (1), 1733 (1), 1735 (1), 1736 (3), 1737 (9), 1869 (1), 1873 (2), 1884 (1), 1888 (8), 1889 (6), 1890 (10), 1891 (2), 1892 (3), 1893 (12), 1894 (5), 1895 (12), 1896 (10), 1897 (3), 1898 (1), 1899 (3), 1900 (4), 1901 (2), 1902 (9), 1903 (2), 1904 (2), 1906 (2), 1907 (2), 1908 (5), 1911 (1), 1914 (3), 1921 (1), 1923 (1), 1928 (1), 1929 (2), 1934 (3), 1935 (2), 2000 (20), 2001 (27), 2002 (6),2003 (3), 2004 (26), 2005 (3), 2006 (6), 2007 (44), 2008 (8), 2011 (8), 2012 (1), 2013 (3), 2014 (4), 2015 (8), 2016 (3), 2017 (1), 2020 (1), 2021 (8), 2027 (2), 2029 (2), 2034 (1), 2037 (5), 2042 (1), 2043 (1), 2045 (1), 2046 (1), 2050 (2), 2055 (1), 2059 (1), 2061 (2), 2065 (1), 2066 (3), 2071 (6), 2082 (1), 2086 (1), 2090 (3), 2095 (6), 2100 (2), 2101 (1), 2105 (2), 2109 (1), 2111 (8), 2112 (9), 2114 (1), 2117 (5), 2118 (15), 2213 (2), 2216 (1), 2218 (1), 2225 (1), 2226 (2), 2230 (1), 2231 (1), 2234 (4), 2235 (6), 2236 (2), 2245 (1), 2248 (1), 2255 (5), 2262 (1), 2263 (1), 2265 (1), 2266 (4), 2776 (2), 2278 (1), 2281 (4), 2282 (3), 2285 (2), 2286 (6), 2288 (1), 2289 (2), 2295 (2), 2546 (1), 2549 (2), 2551 (1), 2553 (3), 2556 (2), 2560 (1), 2562 (1), 2565 (2), 2901 (5), 2904 (1), 2906 (4), 2907 (1), 2908 (1), 2909 (1), 2912 (1), 2914 (2), 2917 (2), 2918 (1), 2919 (3), 2921 (2), 2922 (3), 2923 (3), 2924 (3), 2925 (11), 2928 (2), 2935 (1), 2948 (1), 2950 (1), 2961 (1), 2969 (1), 2971 (1), 2973 (1), 2978 (1), 2979 (1), 2986 (1), 2988 (2), 2991 (1), 2992 (1), 2993 (4), 2995 (2), 2996 (2), 2997 (2), 2999 (2), 3000 (1), 3002 (1), 3005 (1), 3008 (2), 3009 (1), 3012 (2), 3014 (1), 3015 (2), 3018 (1), 3019 (2), 3102 (1), 3103 (2), 3106 (1), 3110 (1), 3112 (1), 3117 (1), 3120 (2), 3124 (1). ZMUC: D 1228 II (4), D 1230 III (2), D 1324 V (1), D 1330 (1), D 3515 V (2), D 3515 VIII (1), D 3534 II (5), D 3536 I (1). INDIAN OCEAN: IOAN: V 5220 (3). SOSC: AB 3-14 (9/9/63) (1), AB 3-14 (9-10/9/63) (1), AB 6-344A (1), AB 6-351D (2). PACIFIC OCEAN: IOAN: B 74 (1), V 4261 (1), V 6429 (1971): 3 May (6), 5 May (2), 6 May (1); V 6469 (1971): 2 June (1), 5 June (1); V 6490 (1); V 6493 (1971): 5 July (1), 5-6 July (1). SIO: 70-314 (1), 70-329 (1). SOSC: R/V WASHINGTON: 75-137 (2). UH: 70/7/24 (1), 70/12/7 (2), 70/12/9 (1), 71/2/2 (8), 71/2/3 (1), 71/2/6 (3), 71/2/8 (1), 71/2/9 (4), 71/2/12 (1), 71/3/1 (3), 71/3/8 (2), 71/3/11 (1), 71/6/2 (1), 71/6/5 (3),

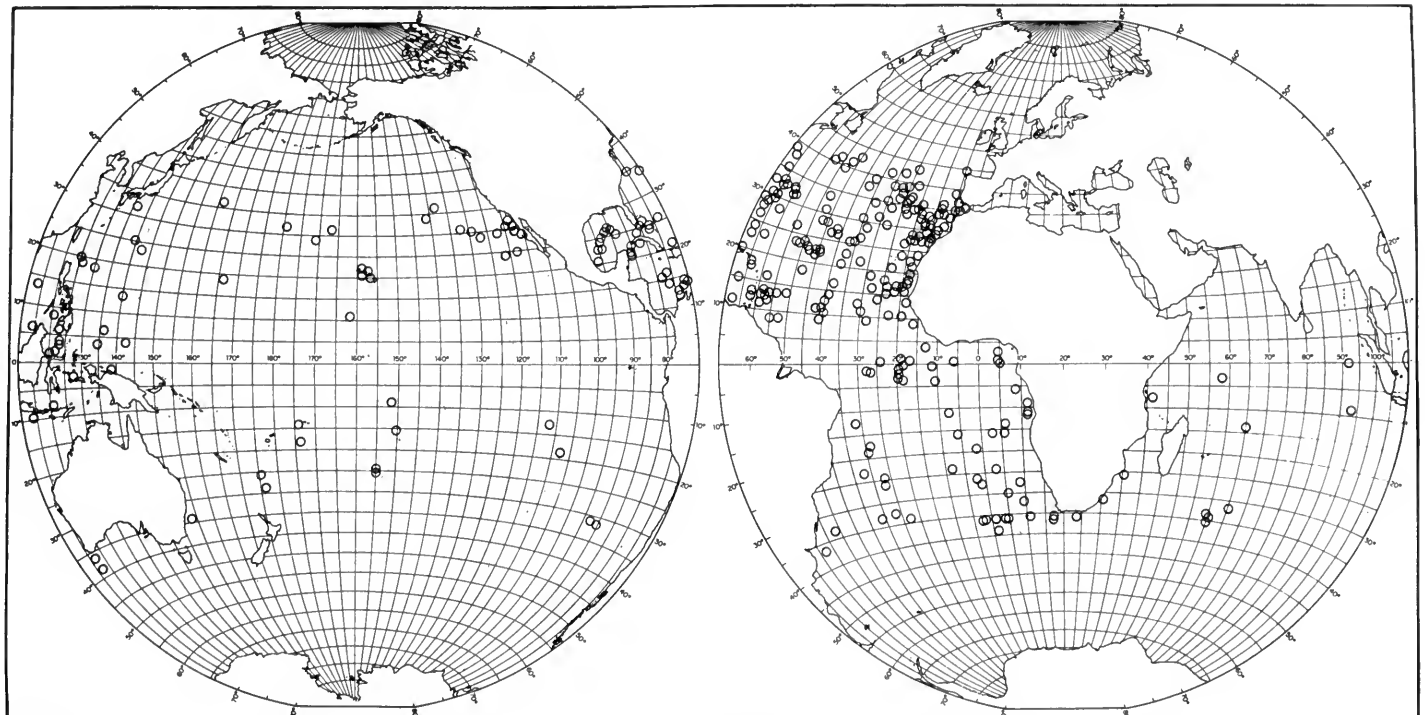


FIG. 46. Distribution of *Scopelarchus analis*.

71/6/11 (1), 71/6/13 (2), 71/6/16 (5), 71/6/17 (6), 71/6/20 (1), 71/6/21 (1), 71/6/28 (1), 71/6/31 (3), 71/6/34 (1), 71/9/4 (1), 71/9/6 (4), 71/9/8 (3), 71/10/1 (1), 71/10/2 (2), 71/10/3 (2), 71/10/4 (3), 71/10/5 (8), 71/10/6 (10), 71/10/7 (1), 71/10/8 (8), TC 52-59 (1). ZMUC: D 3659 III (2), D 3683 III (1), D 3718 II (1). SOSC: DES 4-T3-B (1), DES 4-T4-D (1), DES 4-T13-D (1), DES 4-T14-A (1), DES 4-T14-D (1), DES 4-T15-D (1), DES 4-T16-B (1)

Scopelarchus guentheri Alcock 1896

Distribution.—*Scopelarchus guentheri* is a circumglobal warm-water species occurring in all three oceans (fig. 47). In the North Atlantic *S. guentheri* is known only from the Caribbean Sea and from in or south of the boundary area between North Atlantic Central Water and South Atlantic Central Water. *Scopelarchus guentheri* probably occurs throughout the South Atlantic, Indian Ocean, and insular western Pacific. *Scopelarchus guentheri* apparently occurs throughout the warm-water Pacific, but there exists evidence suggesting that it is more abundant in areas peripheral to the central gyral areas and along the equator and less abundant within the central portions of the Pacific central gyral areas (see discussion below and Johnson, 1974c, pp. 229–231).

Material Examined.—Johnson (1974c, pp. 182, 183) lists 205 (7.0–119.0 mm SL) specimens from 121 collections. An additional 143 (10.5–115.0 mm SL) specimens from 79 collections are listed here.

ATLANTIC OCEAN: IOAN: AK 991 (1). UMML: 29326 (1). WHOI, RHB: 801 (1), 2056 (1), 2075 (1), 2076 (1), 2077 (6), 2078 (1), 2081 (1), 2920 (1), 2923 (1), 2924 (2), 2925 (5), 2927 (2), 2928 (2), 2929 (10), 2930 (5), 2931 (2), 2932 (1), 2933 (1), 2934 (4), 2935 (1), 2936 (1), 2938 (1), 2945 (1), 2946 (1), 2949 (1), 2951 (3), 2952 (2), 2954 (1), 2956 (1), 2996 (7). INDIAN OCEAN: IOAN: B 7 (1), V 4562 (1), V 4618 (1), V 4623 (1), V 4638 (1), V 4796 (2), V 4940 (1), V 5247 (1). MCZ: AB 6-333B (1), AB 6-340B (1). SIO: uncat., 24 February 1971 (1). SOSC: AB 3-5 (1), AB 3-6 (1), AB 6-333A (1), AB 6-340B (8), AB 6-341B (1), AB 6-342A (3), AB 6-344A (1). PACIFIC OCEAN: IOAN: V 3658 (1), V 4291 (1), V 5086 (1), V 5094 (1), V 5139 (1), V 5153 (1), V 6493 (2). NMFS (LJ): J 60-42 (1), J 77-38 (1), J 77-129 (1), J 20.145 (2), J 31.135 (1), J 7205 (130.90) (2), TC 51-53 (3), TC 51-37 (2), TC 51-66 (1), TC 51-74 (1), TC 51-81 (1). SIO: 73-139 (9), 73-142 (2), 73-166 (1), 74-40 (1). SOSC: J 60-56 (1); R/V WASHINGTON: 45-133 (1), 75-73 (1). UH: 70/6/4 (1), 71/2/14 (1), 71/6/22 (2), 71/10/6 (1).

Scopelarchus michaelsarsi Koefoed 1955

Distribution.—*Scopelarchus michaelsarsi* is a tropical-subtropical species occurring in all three oceans (fig. 48). *Scopelarchus michaelsarsi* is now known from the eastern North Atlantic, but most Atlantic records for this species are from the western or central North Atlantic. *Scopelarchus michaelsarsi* apparently does not occur in the eastern Pacific—all Pacific records for this species are west of 150° W.

Material Examined.—Johnson (1974c, p. 192) lists 69 (12.0–101.5 mm SL) specimens from 53 collections. An additional 106 (8.5–70.0 mm SL) specimens from 64 collections are listed here.

ATLANTIC OCEAN: WHOI, RHB: 801 (1), 1051 (1), 1101 (1), 1293 (1), 1294 (9), 1297 (4), 1307 (4), 1309 (1), 1728 (2), 1729 (1), 1733 (2), 1737 (10), 2015 (2), 2076 (1), 2082 (1), 2111 (2), 2113 (1), 2903 (1), 2906 (1), 2909 (1), 2911 (1), 2913 (1), 2919 (1), 2921 (1), 2924 (1), 2925 (2), 2926 (2), 2929 (1), 2932 (2), 2933 (2), 2936 (1), 2938 (2), 2939 (1), 2943 (1), 2944 (1), 2945 (1), 2949 (1), 2989 (1), 2991 (1), 2994 (1), 2996 (1), 3002 (1), 3007 (1), 3009 (1), 3010 (1), 3014 (1), 3018 (2), 3019 (1). INDIAN OCEAN: SOSC: AB 6-340B (4), TV 5-190 (2). PACIFIC OCEAN: IOAN: V 5117 (1), V 6469 (1). UH: 70/6/4 (1), 71/2/8 (2), 71/6/1 (1), 71/6/18 (1), 71/6/22 (1), 71/6/28 (1), 71/6/30 (1), 71/6/31 (2). ZMUC: D 3680 VII (1), D 3712 III (2), D 3788 I (1).

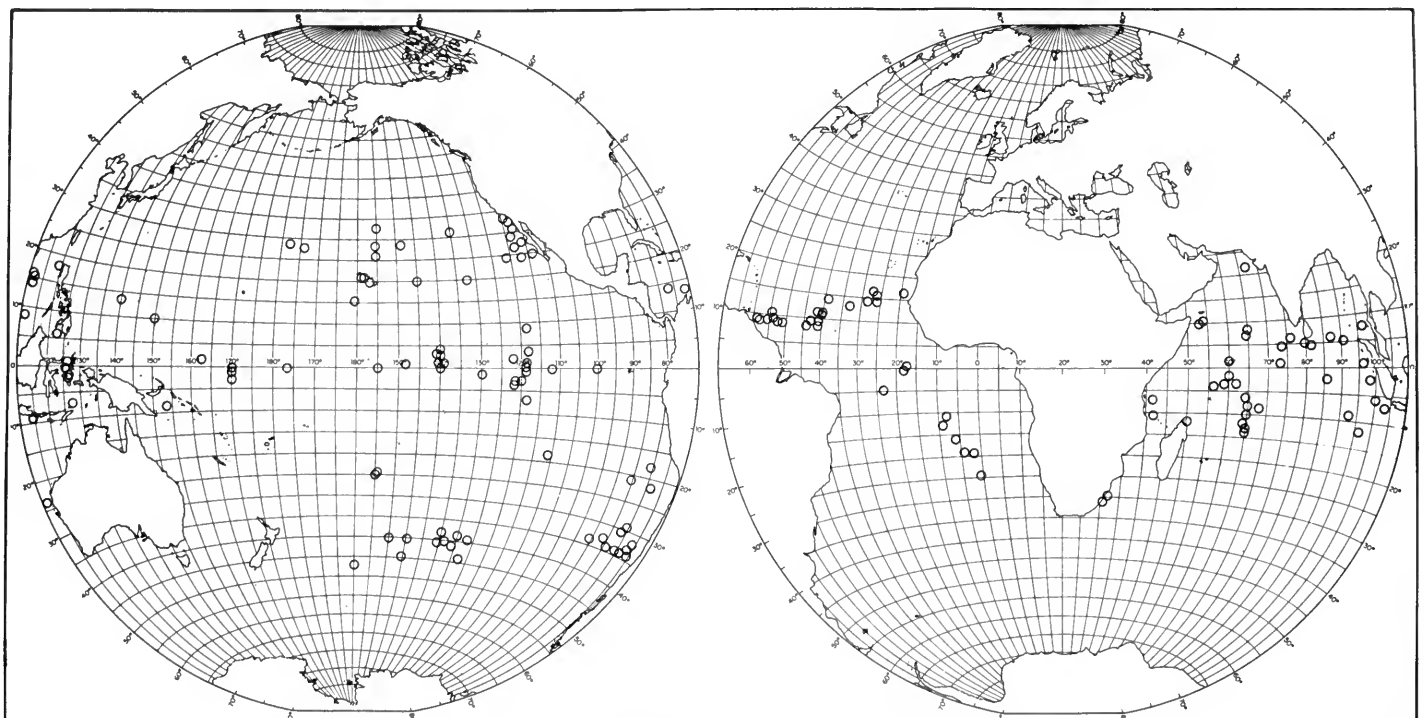


FIG. 47. Distribution of *Scopelarchus guentheri*.

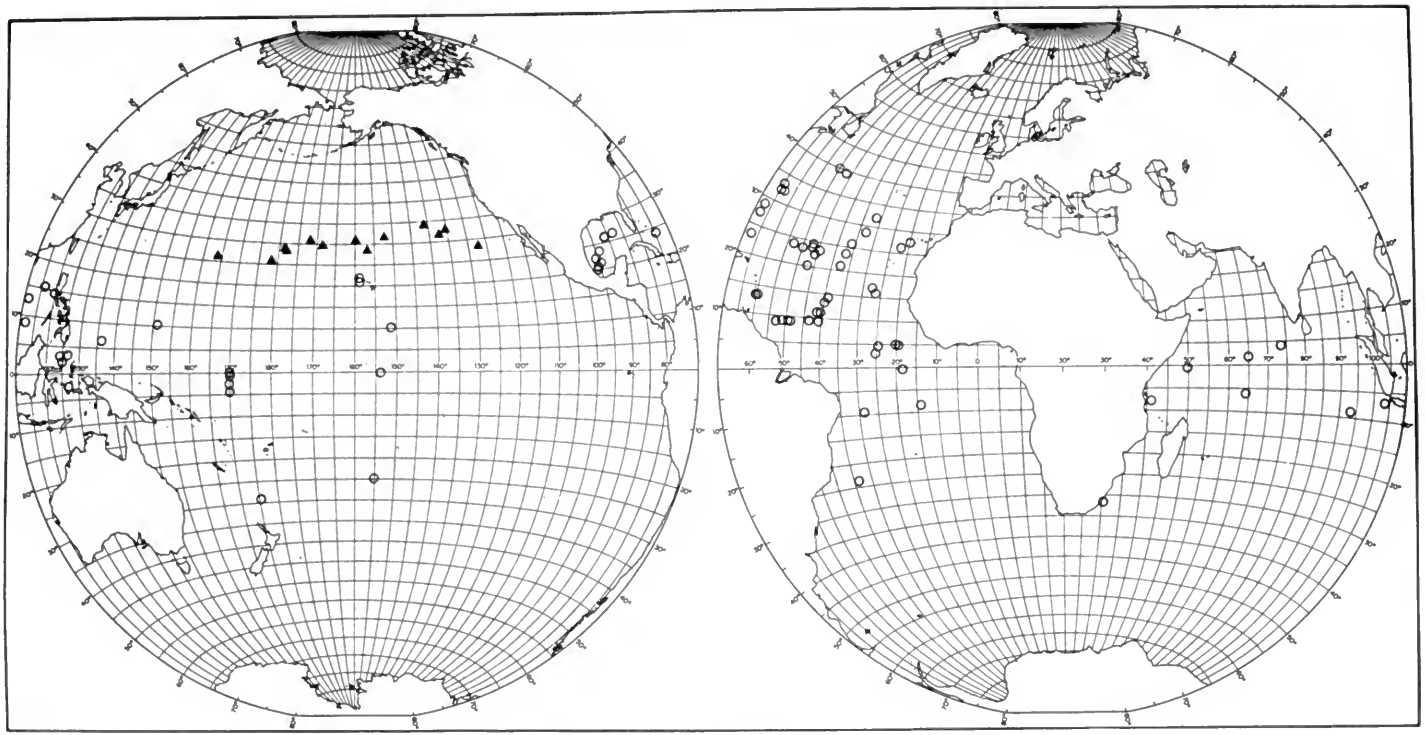


FIG. 48. Distribution of two species of *Scopelarchus: S. michaelsarsi* (open circles) and *S. stephensi* (solid triangles).

Scopelarchus stephensi Johnson 1974

Distribution.—Scopelarchus stephensi is endemic to the central gyral area of the North Pacific Ocean (Johnson, 1974c, p. 198, fig. 58). Johnson (1974c, pp. 198, 235) lists 27 (14.8–62.0 mm SL) specimens from 13 collections. No additional material has come to hand. For purposes of comparison with *S. michaelsarsi*, the distribution of *S. stephensi*, as known, is replotted on Figure 48.

ZOOGEOGRAPHY AND EVOLUTION

Zoogeography is and has been plagued by two major problems: (1) an overwhelmingly large but frequently spotty, discontinuous, and questionable data base and (2) an all too common lack of agreement among zoogeographers on the general concept, purpose, and best methodology for distributional studies (e.g., Briggs, 1974a; Brundin, 1972a; Croizat et al., 1974; Darlington, 1970). Common to all zoogeographic studies is a basic question: Why does this animal species occur *here* and not *elsewhere?*

Cohen (1973) describes two distinct approaches in attempts to answer this question: ecological zoogeography vs. historical zoogeography. Ecological zoogeography is concerned with fitting animal distribution patterns to the distribution of environmental parameters. The parameters studied may be physical, chemical, or biological in nature, but the underlying assumption is one of ecological association. The scale of study may range from populations and single species to communities and faunas, but the underlying belief is that individual and recurrent distributional patterns exhibited by the organisms parallel and are causally related to the distribution of important environmental parameters.

Historical zoogeography is concerned with fitting the present-day distribution of species in a monophyletic lineage to the presumed evolutionary history of that lineage. This is at base a group-oriented approach that depends upon prior systematic and phylogenetic study of the taxon in question. The unifying factor is the deduced interrelationship of the constituent species of a taxon. The species themselves may occupy quite different kinds of habitats and belong to strikingly distinct ecological assemblages. Comparison of patterns exhibited by similarly studied taxa may lead the historical zoogeographer to put forward broad propositions concerning the history of large faunal units.

Differences between the two approaches might partially be characterized as a difference in the scale of study—the scale of the *here* and the *elsewhere* (Ball, 1975, p. 408). Ecological zoogeography is largely concerned with studies at the scale of local species assemblages in the here and now. Historical zoogeography typically has a broader spatial and temporal scale and is concerned with the world distribution of single taxa and the deduced history of recognizable general distribution patterns. In practice the results of the two approaches appear very different (see Banarescu, 1975, pp. 6–9, for additional comments on "causal" zoogeography), and these differences have led one prominent historical zoogeographer to exclude ecological zoogeography from the discipline of zoogeography (Briggs, 1974a, p. 5).

In recent years there have been at least three distinct and competitive approaches to historical zoogeography. The "traditional" school, typified by Matthew (1915), Darlington (1957, 1965, 1970), and Briggs (1974a, 1974b), can be characterized as the center-of-origin/dispersal approach to historical zoogeo-

graphic analysis. The essence of this approach is the search for evolutionary centers, the centers of origin, in which competitively dominant species evolve. Rules for finding such centers are listed in Ebeling (1962, p. 148). Competitively superior species (equivalent to "dominant" species and usually equivalent to most recently evolved species) are seen by this school as arising in the centers of origin and, by virtue of their competitive superiority, spreading out (via dispersal) from the centers, replacing and extinguishing or forcing into relictual distributions earlier-evolved species. A very clear example of this approach to zoogeographic explanation is Gibbs' (1969) account of the distributional history of *Stomias*, discussed below. A corollary of this approach is the hypothesis that within a monophyletic lineage the more primitive species (roughly combining the notions of earlier-evolved and plesiomorph [*sensu* Hennig, 1966a] species) will be found in areas geographically (or ecologically) peripheral to the evolutionary centers; the more advanced species will be found in the areas of the evolutionary centers.

A second school, typified by Hennig (1966a, 1966b), Brundin (1966, 1972a, 1972b), and Nelson (1969b), can be characterized as the cladistic approach to historical zoogeographic analysis. This approach is dependent upon a prior phylogenetic analysis of the group being studied, and that analysis must be performed utilizing cladistic methodologies (Hennig, 1966a; Brundin, 1966). Given the results of this analysis and the knowledge of the present-day distribution of species in the group, the method in essence is an effort to determine the simplest possible (fewest dispersal events) direct correspondence between present-day distribution of species and the sister-group relationships of species within the group. That is, the inferred distributional history is based on the deduced interrelationships of members of the group studied. An obvious corollary of this approach is stated by Brundin (1972b, p. 2): ". . . [a] fundamental biogeographical principle [is] that the primitive group at least primarily is closer to the area once occupied by the ancestral species than the comparatively derivative sister group."

A third school, typified by Croizat et al. (1974), Nelson (1974), and Rosen (1975), can be characterized as the generalized-track/vicariance approach to historical zoogeographic analysis. The essence of this method was described by Croizat et al. (1974, pp. 265, 266): "If a given type of geographical distribution (individual track) recurs in group after group of organisms, the region delineated by the coincident distributions (generalized track) becomes statistically and, therefore, geographically significant . . . ." In the view of this school complexity in distributional patterns has been introduced by a continuing temporal sequence of vicariance events (i.e., subdivision of ancestral biotas as a result of changing geography) and by subsequent dispersal modifying (in the case of some groups) earlier vicariant patterns. Thus, in general, vicariant events have led to geographic division and differentiation of biotas and the multiplication of numbers of species, whereas dispersal events have resulted in sympatry and the possibility of interspecific interactions (with the possible concomitants of competitive exclusion, ecological differentiation, and extinction). Dispersal events are recognized as having occurred and indeed may be (hypothetically) called upon when all else fails in explaining the distribution of exceptional species, but dispersal is viewed as difficult to interpret and not of overriding importance in explaining the distribution of complex biotas (see McDowall, 1978, for an exten-

sive criticism of this viewpoint). This school rejects the notion of a center of origin as an essential initial premise and therefore takes no firm position on the question of where we should expect to find earlier-evolved and later-evolved species relative to such centers (cf., Nelson, 1969b vs. Nelson, 1974). Ball (1975), Platnick & Nelson (1978), and Rosen (1978) explore the possibilities for combining the cladistic and generalized-track/vicariance approaches to zoogeography (for a recent overview, see Ferris, 1980). Due to seemingly mutually exclusive initial assumptions and hypotheses, no one has yet suggested an acceptable combination of the center-of-origin/dispersal school with either of the other two schools.

Most attempts at explaining distribution patterns exhibited by open ocean organisms have been couched in ecological, not historical, terms. Attempts at explaining the distribution of species of a given midwater group with respect to the deduced evolutionary history of that group for the most part suffer from an incomplete or inadequately documented knowledge of relationships between the species studied and/or an incomplete knowledge of the distribution of various included species. An additional difficulty is that some of the most exhaustive studies of the relationship between groups of midwater fishes, e.g., Paxton (1972) on myctophids, Baird & Eckhardt (1972) on sternoptychids, Weitzman (1967, 1974) on various stomiatoids, Pietsch (1974) on oneirodids, among others, deal with interrelationships of higher taxa (rank of genus or higher) and are for the most part inapplicable to open ocean zoogeographic studies. This inapplicability stems from the fact that higher taxa of midwater organisms occurring in the warm-water ocean are typically cosmopolitan or nearly so within the approximate limits of 40° N to 40° S. Thus, as McGowan (1971, p. 11) has emphasized, it is studies at the species and subspecific level that are of greatest importance for interpreting distributional patterns exhibited by open-ocean organisms.

Of those attempts that have been made to interpret present-day distributions of midwater fish species in terms of presumed evolutionary history, most have been phrased more or less vaguely in terms of the center-of-origin/dispersal approach to zoogeographic explanation (e.g., Fraser-Brunner 1949; Bolin, 1959; Ebeling, 1962; Gibbs, 1969; Johnson, 1974c; Bertelsen et al., 1976). Typifying this approach is Gibbs' (1969) account of the evolutionary history of *Stomias*. In this view the history of *Stomias* is a running competitive battle for possession of the more productive areas of the world ocean. The most recently evolved species of *Stomias*, those in the *S. boa* group, are regarded as having proven competitively superior ("dominant" *sensu* Briggs, 1974a, p. 254) to species in the earlier-evolved *S. brevibarbatus*, *S. colubrinus*, and *S. nebulosus* species groups. Thus the competitive superiority of species in the *S. boa* group has forced species in the older groups into relictual distributions in unfavorable or specialized environments—examples given include areas with marked oxygen-minimum layers in the Atlantic and Pacific, central gyral areas, and near-shore areas. Gibbs (1969, p. 20) believes that the competitive pressure on *S. danae* may have been (and is) so severe that ". . . *S. danae* may even be on the verge of extinction."

To my knowledge no one has yet attempted direct application of the cladistic methodology to a distributional study of any midwater fish group. Application of an essential part of the generalized-track/vicariance approach, viz., the determination of generalized tracks (although not referred to in existing literature by

that name), has become increasingly common in studies of distribution patterns of open-ocean organisms. In fact the recognition of concordant restriction (= generalized tracks) of species to a given subarea of the world ocean is at present the only widely available method for recognizing distinct assemblages of open-ocean species. Such assemblages are fully the open-ocean equivalent of the "biotas" of Croizat et al. (1974), but the study of such assemblages by workers on the open-ocean fauna has been entirely ecological in orientation. Aside from more or less vague references to the possible effects of closure of the Tethys Seaway on the distribution of certain midwater organisms (e.g., Andriashev, 1962; Brinton, 1962; Crane, 1966; Gibbs, 1969; Goodyear, 1970; Judkins, 1972), there has been, for fairly obvious reasons, no attempt to explain the present-day distribution of such assemblages in terms of subdivision (vicariation) of ancestral assemblages (see Croizat et al., 1974).

Most attempts to explain distribution patterns exhibited by open-ocean organisms have involved the ecological approach to zoogeographic analysis. Even the few attempts to explain present-day distribution patterns in terms of an inferred history of those patterns commonly have been based on presumed historical changes in the distribution of important environmental parameters, e.g., Brinton's (1962, pp. 245–252) explanation of the origin of biantitropical distributions or McGowan's (1971, p. 53) belief that the development of present-day distributional patterns must be explained in part in terms of ". . . ancient circulation systems and water-mass structures."

A large number of physical, chemical, and biological parameters have been used, singly or in combination, to explain the observed distributions of various species or groups of species (summary outlines of such attempts are provided by Brinton, 1962; Ebeling, 1962; Johnson & Brinton, 1963; Ebeling, 1967; Ebeling et al., 1970; Parin, 1970; Baird, 1971; McGowan, 1971, 1974; Johnson, 1974c; Badcock & Merrett, 1976, 1977, among others). Included among these factors are the following:

CURRENTS: Including confinement of indigenous populations by gyral systems and the boundary effects of convergences and divergences: Bruun, 1958; Wisner, 1959; Ebeling, 1962; Reid, 1962; Wickett, 1967; Frost, 1969; McGinnis, 1974; and Reid, 1977.

TEMPERATURE: Brinton, 1962; Nafpaktitis, 1968; Backus et al., 1969; Parin, 1970; and Briggs, 1974a.

DENSITY: Pickford, 1946.

OXYGEN: Gibbs & Hurwitz, 1967; Longhurst, 1967; and Johnson & Glodek, 1975.

BIOLOGICAL PRODUCTIVITY: Bogorov, 1958; Ebeling, 1962; Backus et al., 1965; Roper, 1969; Baird et al., 1973; Briggs, 1974a; Fleminger & Hulsemann, 1974; and Pietsch, 1974.

WATER MASSES: Brinton, 1962; Johnson & Brinton, 1963; Ebeling, 1962, 1967; Backus et al., 1965; Ebeling et al., 1970; McGowan, 1971, 1974; Wormuth, 1971; Kobayashi, 1973; McGowan & Williams, 1973; and Bertelsen et al., 1976.

Although the water-mass hypothesis (see below) is implicitly a multifactorial approach (Ebeling, 1962), there have also been explicit attempts at using multivariate techniques to assess the relative importance of various environmental features on the distribution of midwater fish species (Ebeling et al., 1970; Ebeling et al., 1971).

Since the early 1960's, the leading paradigm in open ocean zoogeographic studies has been the so-called "water-mass hypothesis"—the association of the distributional boundaries of oceanic fish species with water-mass boundaries (see Sverdrup et al., 1942, and Ebeling, 1962, for discussions of water-mass identification, properties, and distribution). The distributional limits and/or areas of maximum abundance (e.g., Craddock & Mead, 1970; McGowan, 1971; Barnett, 1975) have been shown to conform closely with the area underlain by a given water mass or water masses. The result has been that in recent years virtually all open-ocean zoogeographers have compared the distributions of their organisms to water-mass boundaries and have discussed oceanic zoogeography in terms of water-mass regions (see Johnson, 1974c, pp. 221, 222, for a representative list of papers utilizing, in part, the water-mass hypothesis). Most comparisons have been made with respect to the upper water masses (Ebeling, 1962, p. 145), but the distributions of certain species have been associated with the distribution of the deeper intermediate or even deep water masses (e.g., Ebeling, 1975).

Opposition has arisen to the water-mass hypothesis. For example, Briggs (1974a, pp. 335–338), in reviewing a limited (and highly selective) sample of the open-ocean literature, rejects (p. 338) the water-mass hypothesis and opts for temperature as *the* single factor most critically influencing the shape of open-ocean distribution patterns. Briggs (1974a, p. 337) bases an important part of his argument on the work of Parin (1970) but fails to note Parin's (1970, p. 128) emphasis on the important distributional distinctions between what Parin refers to as "planktonic" vs. "nektonic" fishes. Most opposition to the water-mass hypothesis stems from the belief that it is too simplistic (Johnson, 1974c, p. 222), that patterns of midwater fish distribution are too numerous and too complex to be explainable solely in terms of water-mass distribution (e.g., Backus et al., 1970; Baird, 1971; Hartman & Clarke, 1975; Jahn & Backus, 1976). Fit with respect to the water-mass hypothesis unquestionably varies by ocean, being worst for the Atlantic (Backus et al., 1970; Krefft, 1974; Fasham & Angel, 1975; Backus et al., 1977) and best for the Pacific (e.g., McGowan, 1971, 1974; McGowan & Williams, 1973). There is growing evidence that other factors, e.g., productivity (Roper, 1969; Pietsch, 1974), dissolved oxygen (Johnson & Glodek, 1975), temperature/light effects (e.g., Paxton, 1967; Badcock & Merrett, 1977), may be associated with substantial departures of the distributions of individual species or groups of species from concordance with water-mass regions.

There exists in the open-ocean literature a growing emphasis on comparing the distribution of individual species with the distribution of other oceanic species and then comparing the distribution of concordantly restricted assemblages of species with the distribution of selected environmental features (e.g., Parin, 1970; McGowan, 1971, 1974; Johnson & Glodek, 1975). The recognition of the species assemblages uses the same methods as the determination of generalized tracks as described by Croizat et al. (1974). The generalized tracks or "recurrent" patterns (Fager & McGowan, 1963) thus determined are apparently both relatively few in number, are repeated from one taxonomic group to another, and are repeated virtually irrespective of trophic level or guild. McGowan (1971, 1974, 1977) has summarized the available information on discernible generalized tracks, which he refers to as "ecosystems," in the Pacific Ocean. His suggestion is that the concordance in distribution of oceanic species from many taxonomically distinct groups, the recurrent assemblages of oceanic

species, indicates the great importance of biological interaction in determining the major patterns of distribution of oceanic species.

Maintenance of these recurrent distributional patterns is seen not only in terms of those processes that maintain the shape of water-mass patterns (McGowan, 1971, p. 50) but also in terms of evolutionary co-adaptation (McGowan, 1974, p. 16). The perceived character and structure of these "community-ecosystems" is summarized by McGowan (1972, pp. 16–23; 1977, p. 425).

The definition, identification, and study of communities in the open ocean is an exceedingly complex problem (see Angel, 1977). The scale of study represented in the literature varies from fine, e.g., the "community" of organisms represented in *Alepisaurus* stomachs described by Haedrich & Nielsen (1966), to medium, e.g., the offshore middepth vs. offshore deep "communities" of Ebeling et al., 1971, to the very broadscale "community-ecosystems" discussed by McGowan (1971, 1974) and his students (e.g., Barnett, 1975; Shulenberger, 1977). Adding to the complexity are the very real quantitative and qualitative differences in basic processes between ecosystems (McGowan, 1974; McGowan & Williams, 1973) and between "ecosystem" assemblages vs. "ecotonal" assemblages (McGowan, 1974, 1977). There exist well-reasoned arguments that deny the reality of communities as discrete and coherent natural units formed by species bound together by co-adaptation (Whittaker & Woodwell, 1972). Krefft (1974, pp. 233, 234) argues ". . . actually each species develops its own specific [distribution] pattern, depending on biotic and abiotic environmental factors as well as its distributional history . . . however, in spite of the diversity of specific patterns, the threads of the web join to form larger patterns, which characterize well-defined faunal communities."

No attempt is made in this paper to resolve conflicts in concept and definition of oceanic communities, but an attempt is made to discuss observed distribution patterns in terms relevant to these conflicts. In the remainder of this chapter I have three major purposes:

1) To discuss, where possible, the distributions of evermannellid and scopelarchid species with reference to recognizable recurrent distributional patterns of open-ocean species. Because of the relative abundance of evidence, particular attention is paid to discussion of species occurring in either the eastern tropical Pacific or in central gyral areas of the North and South Pacific.

2) To discuss the categories of evidence that, as Barnett (1975) has argued, at least some of these generalized tracks, these oceanic "ecosystems" (*sensu* McGowan, 1977), broadly correspond to the concept of biologically accommodated communities in which interspecific interactions are more important in the regulation of community structure than variation in physical and chemical parameters of the environment.

3) To support my belief that study of open-ocean systems may lead to partial resolution, at least, of the seemingly wide gap in purpose, methodology, and results separating historical from ecological approaches to zoogeography.

Distribution-Pattern Categories

There exist numerous schemes for describing and categorizing distributional patterns exhibited by midwater fishes. Four commonly used bases for dividing

observed distributional patterns are discussed in this paper: (1) division by inshore vs. offshore association; (2) division into "cold-water" vs. "warm-water" areas; (3) division by ocean basin (i.e., Atlantic, Indian, Pacific); and (4) division with respect to water mass regions. Table 23 summarizes the distribution of evermannellid and scopelarchid species with respect to these broad distributional categories.

TABLE 23. Classification of distributional patterns exhibited by evermannellid and scopelarchid species in terms of broad distributional patterns discussed in text. Information given in parentheses gives geographic and water mass region information.

I. "Cold-water" species

Evermannellidae (0/7)
Scopelarchidae (5/17)
Benthalbella dentata (North Pacific: Pacific Subarctic and Transition Region)
Benthalbella elongata (Southern Ocean: Subantarctic and Antarctic)
Benthalbella linguidens (North Pacific: Transition Region)
Benthalbella macropinna (Southern Ocean: Subantarctic and Antarctic)
Scopelarchoides kreffti (Southern Ocean: known only from South Atlantic but presumed circumglobal in southern Transition Region)

II. "Warm-water" species

A. SPECIES LIMITED TO A SINGLE OCEAN BASIN

Evermannellidae (2/7)
Evermannella ahlstromi (Pacific: most records from eastern Pacific Equatorial)
Evermannella megalops (Pacific: Eastern and Western South Pacific Central)
Scopelarchidae (4/17)
Rosenblattichthys volucris (Pacific: most records from eastern Pacific Equatorial)
Scopelarchoides climax (Pacific: Eastern and [presumably] Western South Pacific Central)
Scopelarchoides nicholsi (Pacific: most records from eastern Pacific Equatorial)
Scopelarchus stephensi (Pacific: Eastern and Western North Pacific Central)

B. SPECIES LIMITED TO TWO OCEAN BASINS

Evermannellidae (1/7)
Coccorella atrata (Indian and Pacific: most records from Indian Equatorial or Pacific Equatorial)
Scopelarchidae (2/17)
Rosenblattichthys alatus (Indian and Pacific: most records from Indian Equatorial or Pacific Equatorial)
Scopelarchoides signifer (Indian and Pacific: most records from Indian Equatorial or Pacific Equatorial)

C. SPECIES OCCURRING IN THREE OCEAN BASINS

Evermannellidae (4/7)
Coccorella atlantica (subtropical in all three oceans)
Evermannella balbo (cooler more productive parts of North and South Atlantic; Mediterranean Sea; presumed to be circumglobal in southern Transition Region)
Evermannella indica (tropical-subtropical in all three oceans)
Odontostomops normalops (tropical-subtropical in all three oceans)
Scopelarchidae (6/17)
Benthalbella infans (tropical-subtropical in all three oceans)
Rosenblattichthys hubbsi (subtropical in all three oceans, not known from South Pacific)
Scopelarchoides danae (tropical in all three oceans)
Scopelarchus analis (tropical-subtropical in all three oceans)
Scopelarchus guentheri (largely tropical in Atlantic, tropical-subtropical in Indian and Pacific oceans)
Scopelarchus michaelsarsi (tropical-subtropical in all three oceans)

A major problem in discussing distributional patterns exhibited by evermannellid and scopelarchid species is that there exists no adequate picture of vertical distribution for any of the 24 species. Although available information, largely from open-net hauls, suggests the expected (e.g., Vinogradov, 1970, p. 93) vertical segregation of life history stages, with small larvae occurring high in the water column (except, possibly, *Benthalbella dentata*, see Johnson, 1974c, p. 70), for the adults of most species the available information suggests only a widespread vertical distribution in the upper 1,000 m.

(1) Division by Inshore/Offshore Association.—A number of groups of midwater organisms contain species or groups of species that are largely neritic, closely associated with inshore waters near continental or insular land masses. Such species may spend their entire life cycles in inshore waters or may be pelagic as larvae and juveniles and "pseudo-oceanic" (Bertelsen et al., 1976, p. 101) or bottom-associated as adults. Apparently representative of such land-associated forms are the myctophids *Benthosema panamense* (Wisner, 1976); *Diaphus taaningi* (Nafpaktitis, 1968); *Diaphus adenomus* (Nafpaktitis et al., 1977); *Diaphus coeruleus*, *D. garmani*, and *D. watasei* (Nafpaktitis, 1978); the neoscopelids *Neoscopelus* and probably *Solivomer* (Nafpaktitis, 1977); the melamphaid *Melamphaes acanthomus* (Ebeling, 1962); the sternoptychid (*sensu* Weitzman, 1974) genera *Argyripnus* (Struhsaker, 1973) and *Polyipnus* (Baird, 1971); a substantial number of notosudid species (Bertelsen et al., 1976); and a number of euphausiid species (Brinton, 1962). All evermannellid and scopelarchid species are pelagic and oceanic. Despite an apparent association of *Scopelarchoides danae* with insular and continental land masses (fig. 43, and see account of *S. danae* above), all specimens, larvae, juveniles, and adults, have been taken with pelagic gear.

(2) Division into "Cold-Water" vs. "Warm-Water" Areas.—A major division in the distribution of open-ocean organisms is between the "cold-water" vs. "warm-water" faunal areas (Ekman, 1967, pp. 324, 325). Dividing lines correspond with the North (Pacific only) and South Subtropical Convergences (Deacon, 1963; Alverson et al., 1964; McGowan & Williams, 1973), ca. 40° N and 40° S except in eastern-boundary-current areas (fig. 49). Included in the southern cold-water area are the regions of Subantarctic and Antarctic Water in the Southern Ocean. Included in the northern cold-water area is the region of Pacific Subarctic Water (Sverdrup et al., 1942, p. 740). A number of "cold-water" species enter hydrologically intermediate but biologically distinctive "Transition Regions" in the eastern-boundary-current areas of the North and South Pacific (e.g., Brinton, 1962; Lavenberg & Ebeling, 1967; Craddock & Mead, 1970; Ebeling et al., 1970; McGowan, 1971). The "Transition Region" fauna of the eastern South Pacific (e.g., Craddock & Mead, 1970) at least in part is included in or coincides with the "Subtropical Convergence" or "Transition-Zone" faunas of Brinton (1962, p. 202), Gibbs (1968, p. 3), and McGowan (1971, p. 44). The distinctiveness of the southern cold-water fauna is documented in Andriashev (1962), Brinton (1962), David (1962), Bussing (1965), Gibbs (1968), Parin (1970), Briggs (1974a), and Backus et al. (1977), among others. The distinctive North Pacific boreal fauna is documented in Brinton (1962), Ebeling (1967), McGowan (1971, 1974), and McGowan & Williams (1973). There is no distinct boreal fauna in the North Atlantic (e.g., Backus et al., 1977).

In this paper a species is assigned to the category "cold-water species" if the known range of adults does not enter the region of any central or equatorial

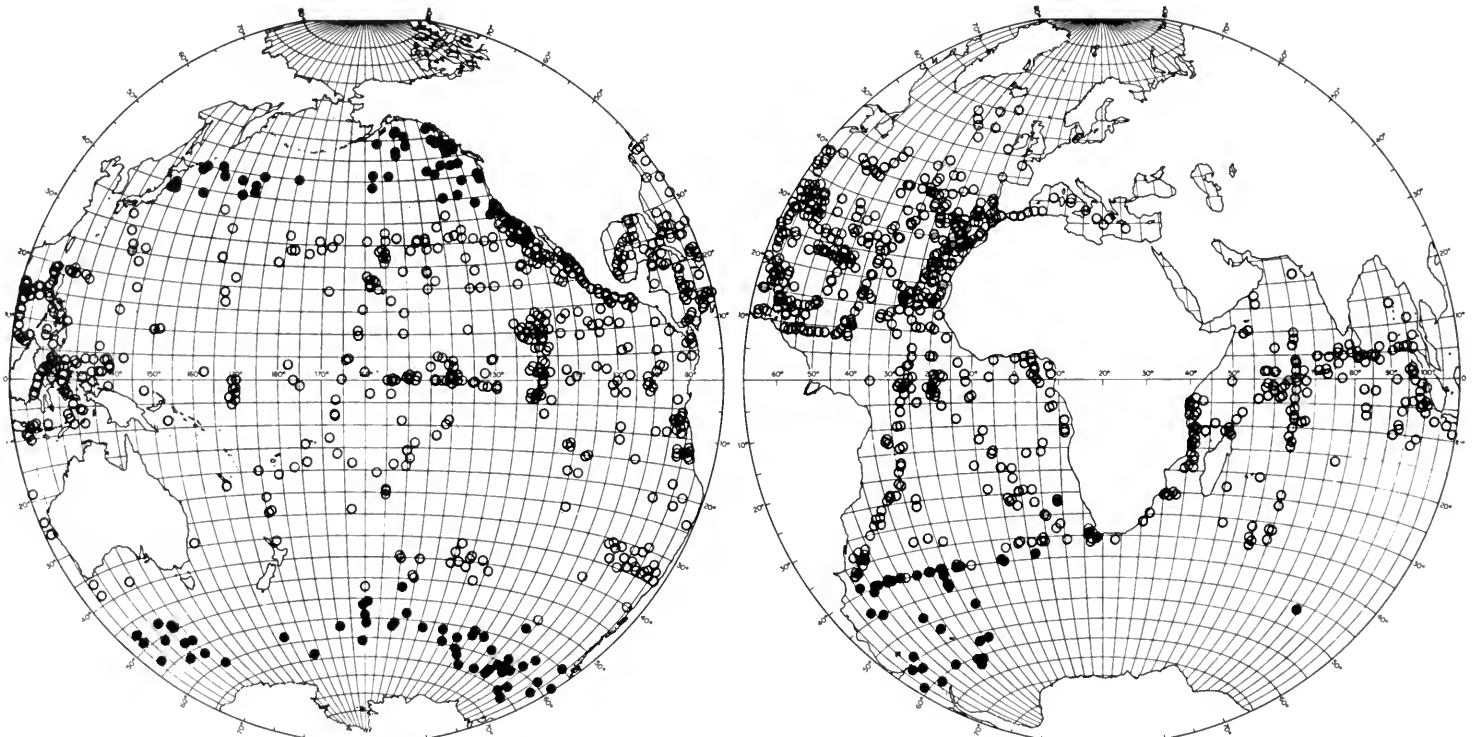


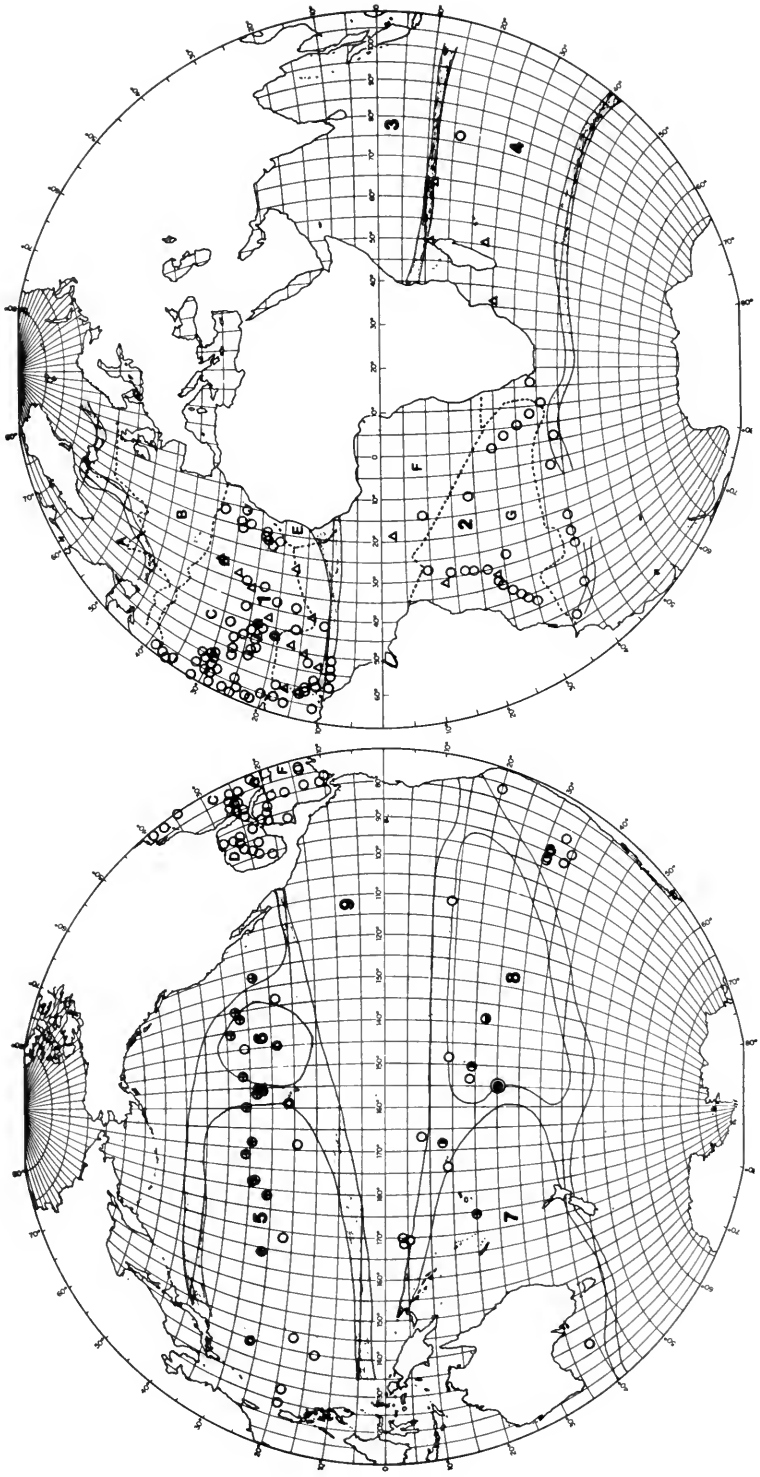
FIG. 49. "Cold-water" vs. "warm-water" faunal areas. Composite distribution of 19 warm-water (open circles) and five cold-water (closed circles) species of evermannellids and scopelarchids. See Table 23 for listing of species. Numerous closely adjacent or overlapping records omitted as are a number of records for *Benthalbella dentata* in the Transition Region off southern California and northern Baja California.

water mass. Five scopelarchid species apparently meet this definition (table 23), and I have nothing to add to the discussion of these species presented by Johnson (1974c). Three of the 19 warm-water species (*Coccorella atlantica*, fig. 24, *Evermannella balbo*, fig. 32, and *Scopelarchus guentheri*, fig. 47) occur in the Transition Region of the Southern Ocean but, in each case, most records are from warm-water areas. The possible existence of a separable Subtropical-Convergence-region population of *Scopelarchus guentheri* is discussed by Kashkin (1977) in relationship to McGinnis' (1974) study of circulation in the Pacific Subantarctic sector of the Southern Ocean.

(3) Division by Ocean Basin.—Despite the continuity of the world ocean, there are geographic barriers, more or less effective, to panmixis among widely distributed warm-water oceanic species. Most notably these barriers include the American, African, and Indonesian-Australian land masses. Brinton (1975) provides extensive discussion of the four possible "barrier/pathways" in the tropical and subtropical ocean: (1) the Indo-Australian Archipelago, (2) the tip of South Africa, (3) southern Australia, and (4) the tip of South America. Briggs (1960, 1974a) has argued that the so-called East-Pacific Barrier may be effective for many surface and midwater pelagic species. Isolation of populations among ocean basins is known for a number of midwater species, both invertebrates and fishes (e.g., Gibbs, 1968; Mauchline & Fisher, 1969; and see data for *Coccorella atlantica*, above, fig. 24).

Fleminger & Hulsemann (1973), in discussing the distributions of a number of warm-water copepod species, argue that one might expect greater provincialism (separation of populations and species) in equatorial rather than central water forms. Their evidence (Fleminger & Hulsemann, 1973, 1974) indicates that tropical (=equatorial) copepods tend to be restricted to either (1) the Atlantic, (2) Indian Ocean and (at least) western portion of Pacific Ocean, and (3) eastern tropical Pacific. Judkins (1978) shows that the largely equatorial distributions of pelagic decapod shrimp in the *Sergestes edwardsii* group agree well with Fleminger & Hulsemann's predictions. Among the species of evermannellids and scopelarchids largely restricted to equatorial waters (table 23), one species, *Scopelarchoides danae*, occurs in all three ocean basins. Three species (*Coccorella atrata*, *Rosenblattichthys alatus*, and *Scopelarchoides signifer*) occur only in the Indian and Pacific oceans, and only one of these, *C. atrata*, reaches the eastern tropical Pacific. Among the 24 species in the Evermannellidae and Scopelarchidae, only three warm-water species are limited to two of the three ocean basins, all three are largely equatorial in distribution, and none occurs in the Atlantic. This agrees with the predictions of Fleminger & Hulsemann. There appear to be very few warm-water oceanic species limited to two ocean basins in which one member of the pair is the Atlantic, but there exist a fair number of oceanic species limited to the Indo-Pacific area.[9] Gibbs & Craddock (1973, p. 159)

[9]A number of warm-water species known from the Atlantic and only one other ocean are known from very few specimens from one or both members of the pair, e.g., *Rondeletia bicolor* (Paxton, 1974), *Bolinichthys distofax*, *Diaphus adenomus*, *D. dumerilii*, and *Lampanyctus photonotus* (Nafpaktitis et al., 1977). Others are poorly understood taxonomically, e.g., *Lampadena urophaos atlanticus* vs. *L. u. urophaos* (Nafpaktitis et al., 1977). Other species, particularly those that are subtropical (*sensu* Backus et al., 1977) in the Atlantic and Pacific oceans, may well occur but yet have not been captured in the poorly sampled central water area of the southern Indian Ocean, e.g., *Hygophum reinhardti* and *Diaphus anderseni* (Nafpaktitis et al., 1977). There do, however, appear to be some warm-water species that are



Opposite:

FIG. 50. Distribution of evermannellid and scopelarchid species exhibiting subtropical distribution patterns. SYMBOLS: ○ = *Coccorella atlantica;* ◑ = *Evermannella megalops;* △ = *Rosenblattichthys hubbsi;* ◒ = *Scopelarchoides climax;* ⊕ = *Scopelarchus stephensi;* ◉ = overlapping records for *C. atlantica, S. climax,* and *E. megalops.* Shaded bands denote areas transitional between water-mass regions (after Sverdrup et al., 1942): 1 = North Atlantic central; 2 = South Atlantic central; 3 = Indian equatorial; 4 = Indian central; 5 = western North Pacific central; 6 = eastern North Pacific central; 7 = western South Pacific central; 8 = eastern South Pacific central; 9 = Pacific equatorial. Dashed lines indicate boundaries (approx.) between areas recognized as mesopelagic faunal regions by Backus et al., 1977: A = Atlantic Subarctic Region; B = North Atlantic Temperate Region; C = North Atlantic Subtropical Region; D = Gulf of Mexico Region; E = Mauritanian Upwelling Region; F = Atlantic Tropical Region; G = South Atlantic Subtropical Region.

argue for isolation of the Pacific Ocean population of *Eustomias trewavasae* from populations in the Atlantic and Indian oceans. Because *E. trewavasae* is limited to the zone of the southern Subtropical Convergence, these results are in agreement with those of Fleminger & Hulsemann. I believe that the possible round-the-world cline discussed above for *Evermannella indica* is similarly related, at least in part, to geographic barriers to dispersal and gene flow. Further discussion of distribution patterns with respect to ocean basins is combined with an account of distribution with respect to water-mass regions.

(4) Division with Respect to Water-Mass Regions.—For the warm-water areas of the ocean, it is heuristically useful to distinguish two major categories of distribution exhibited by mid-depth oceanic species (e.g., Brinton, 1962; Ebeling, 1962, 1967; Johnson & Brinton, 1963; Johnson, 1974c):

1. Species relatively restricted in distribution, limited to one ocean basin, and limited to all or part of one water-mass region[10] or limited to the region of two adjacent and physically and biologically similar water masses. Among the 19 warm-water species of evermannellids and scopelarchids, six species (table 23), all limited to the Pacific, fit in this category.

2. Species more widespread, with distributions crossing water-mass boundaries, typically in two or more ocean basins, and exhibiting varying approaches toward warm-water cosmopolitanism (no evermannellid or scopelarchid is cosmopolitan in the warm-water ocean). Ebeling (1967) discusses two subcategories among widely distributed species to which I add a third.

   a. Subtropical or central-water species[11] (fig. 50)—species for the most part associated with (or restricted to) the central water-mass regions within the large, subtropical anticyclones of the Atlantic, Indian, and Pacific oceans. Two species treated in this paper, *Coccorella atlantica* (fig. 24) and *Rosenblattichthys hubbsi* (fig. 40), fit this subcategory.

   b. Tropical or equatorial species (fig. 51)—species for the most part associated with (or restricted to) the equatorial water-mass regions of the Indian and Pacific oceans and/or to a relatively productive equatorial zone in the Atlantic

exceptional in occurring in the Atlantic and in either the Indian or Pacific Ocean (but not both), e.g., *Bolinichthys indicus, Diaphus termophilus,* and *Symbolophorus rufinus* (Nafpaktitis et al., 1977).

[10]Refers to geographic area underlain by a principal upper water mass as depicted by Sverdrup et al., 1942, p. 740.

[11]Termed "central-tropical" species by Ebeling, 1967.

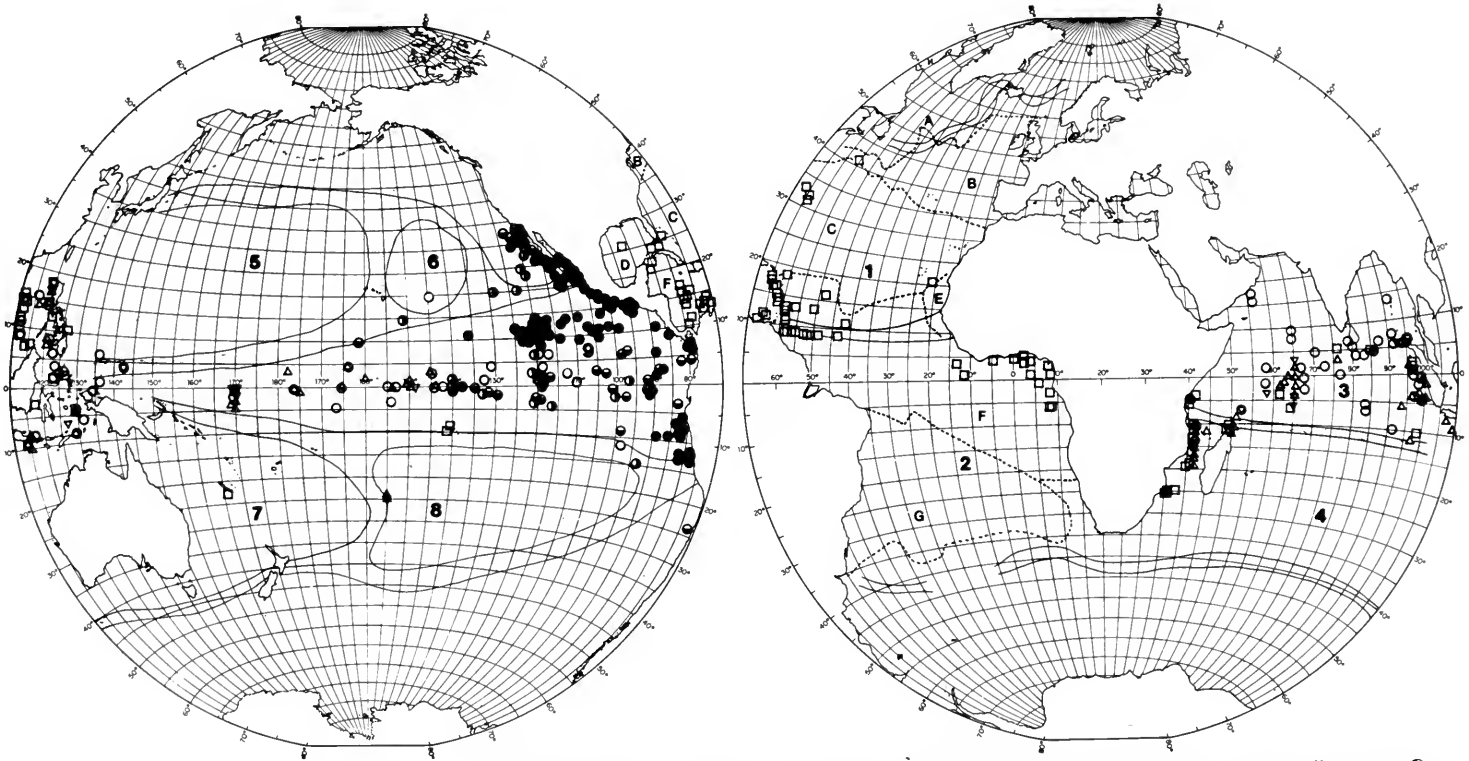


FIG. 51. Distribution of evermannellid and scopelarchid species exhibiting tropical distribution patterns. SYMBOLS: ○ = *Coccorella atrata*; ◐ = *Evermannella ahlstromi*; ▽ = *Rosenblattichthys alatus*; ◒ = *Rosenblattichthys volucris*; □ = *Scopelarchoides danae*; ● = *Scopelarchoides nicholsi*; △ = *Scopelarchoides signifer*. Other symbols as in Figure 50.

Ocean (more or less congruent with the "Atlantic Tropical Region" of Backus et al., 1977). Equatorial species can occur in one, two, or all three ocean basins. Four species treated herein, *Coccorella atrata* (fig. 24), *Rosenblattichthys alatus* (fig. 40), *Scopelarchoides danae* (fig. 43), and *Scopelarchoides signifer* (fig. 45), apparently fit this subcategory. Note that this listing does not include the three equatorial species endemic to the eastern tropical Pacific (table 23).

c. Tropical-subtropical species (fig. 52)—species broadly distributed in tropical and subtropical waters, occurring in both central and equatorial water-mass regions (not necessarily throughout a given water-mass region nor in equal abundance over all regions), and (typically) in all three ocean basins. Six species treated herein fit this subcategory: *Evermannella indica* (fig. 34), *Odontostomops normalops* (fig. 37), *Benthalbella infans* (fig. 39), *Scopelarchus analis* (fig. 46), *S. guentheri* (fig. 47), and *S. michaelsarsi* (fig. 48).

It is possible the availability of more complete distributional information would increase the number of categories deemed useful for descriptive purposes—Backus et al. (1977) recognize nine major distributional categories to describe the zoogeography of Atlantic myctophid species. However, none of the 19 warm-water species treated herein exhibits a known distribution exactly coincident with any other species (some approach this, e.g., *Evermannella ahlstromi* cf. *Rosenblattichthys volucris*), and I believe that the number of descriptively useful categories is both finite and relatively small. It is certain that one "warm-water" species, *Evermannella balbo* (fig. 53), fits none of the above categories. Peculiarities in the distribution of *E. balbo* are discussed in the regional accounts presented below.

Distribution of Evermannellid and Scopelarchid Species: Regional Accounts

Atlantic Ocean

Ten of the 19 warm-water species of evermannellids and scopelarchids occur in the Atlantic Ocean (table 23). None of these species is restricted to the Atlantic. Recent papers contributing to our knowledge of distribution patterns exhibited by midwater fishes in the Atlantic Ocean include Tortonese (1960), Ebeling (1962), Backus et al. (1965, 1969, 1970, 1977), Harrison (1967), Nafpaktitis (1968), Briggs (1970), Gibbs & Roper (1971), Gibbs, et al. (1971), Rass (1971), Goodyear, Gibbs, et al. (1972), Krefft (1974), Badcock & Merrett (1976, 1977), Parin & Golovan (1976), Backus & Craddock (1977), and Nafpaktitis et al. (1977).

A number of authors have proposed systems for division of the Atlantic Ocean into open-ocean zoogeographic regions or provinces (e.g., Ebeling, 1967; Ekman, 1967; Backus et al., 1970, 1977; Parin, 1970; Baird, 1971; Briggs, 1974a; Krefft, 1974). The following discussion is largely in terms of zoogeographic systems proposed by Krefft (1974) and Backus et al. (1977, hereafter abbreviated to *B*)—the most recent and by far the most synoptic studies of Atlantic Ocean midwater fish distributions.

Krefft (1974) divides the Atlantic midwater fish fauna among four major geographic assemblages or distribution patterns. Each of these major groups is further divided into two or more subgroups. The main features of Krefft's classification parallel those in the system proposed by *B*, and I have attempted a

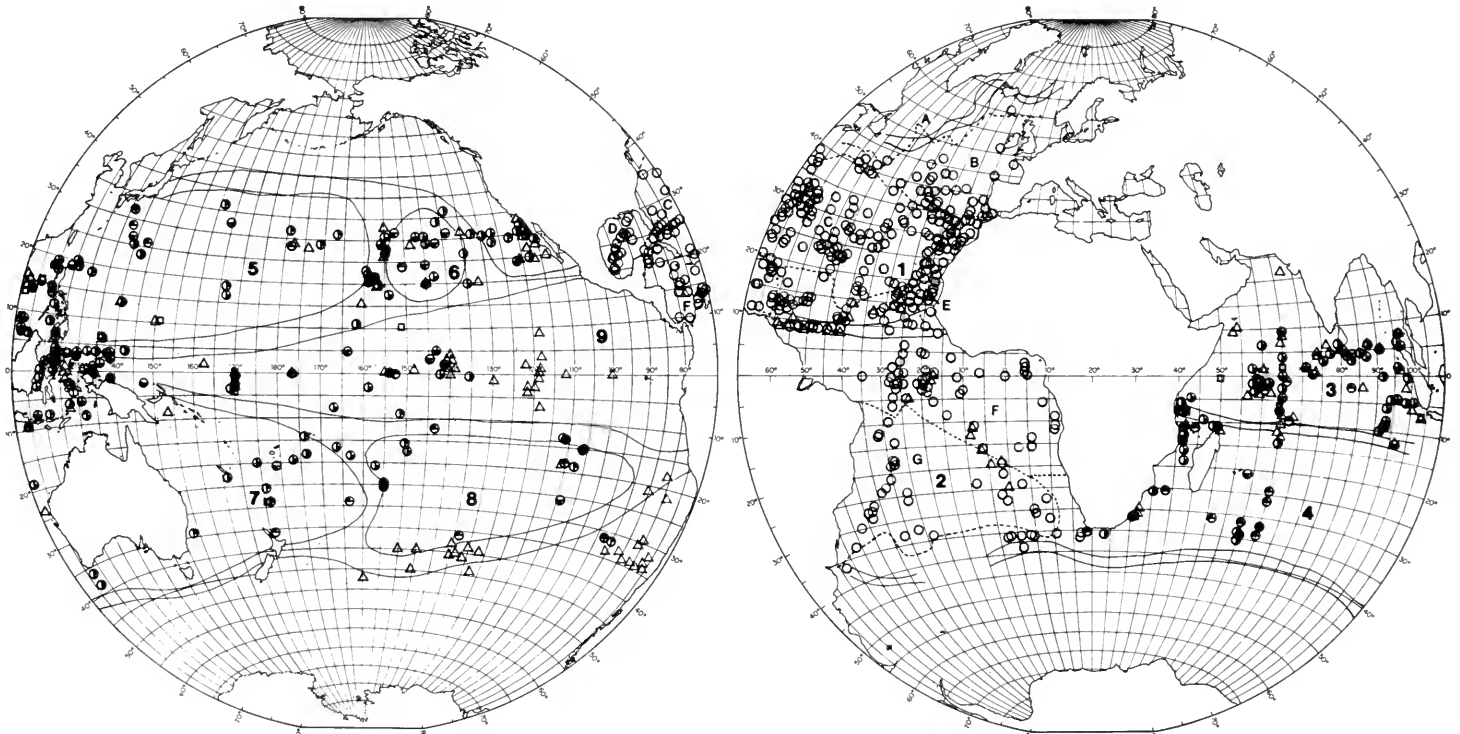


FIG. 52. Distribution of evermannellid and scopelarchid species exhibiting tropical-subtropical distribution patterns. SYMBOLS: ◓ = *Benthalbella infans*; ◒ = *Evermannella indica*; ◓ = *Odontostomops normalops*; ◔ = *Scopelarchus analis*; △ = *Scopelarchus guentheri*; □ = *Scopelarchus michaelsarsi*. Due to a large number of overlapping or closely adjacent records, only records for *Scopelarchus guentheri* are discretely indicated for the Atlantic; records for all other species are represented by an open circle. Other symbols as in Figure 50.

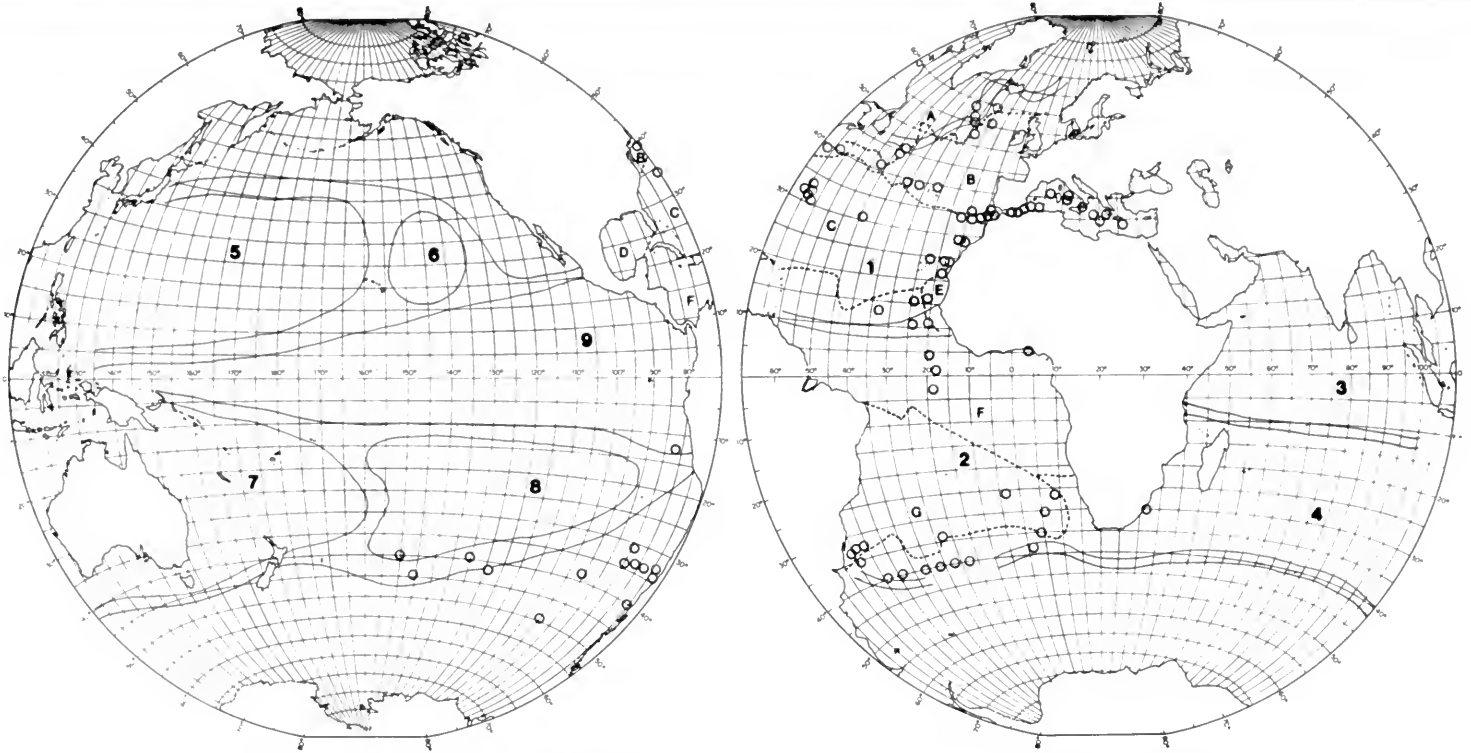


FIG. 53. Distribution of *Evermannella balbo* relative to faunal and water-mass regions. Symbols as in Figure 50.

rough listing of corresponding components (table 24). The listing does not include "bathypelagic" or "pseudo-oceanic" groups.

The system of Atlantic Ocean zoogeographic regions and provinces proposed by *B*, based on the study of more than 280,000 myctophid specimens (and an unstated number of specimens of other midwater fish groups) representing more than 105 myctophid species from more than 1,500 stations, represents by far the most thorough, synoptic distributional study of any midwater fish group in any ocean basin. The system includes seven zoogeographic regions (Atlantic Subarctic, North Atlantic Temperate, North Atlantic Subtropical, Gulf of Mexico, Mauritanian Upwelling, Atlantic Tropical, and South Atlantic Subtropical) and incorporates all but the southernmost warm-water Atlantic. Four of the regions (*B*, pp. 270, 271) are subdivided into two or more provinces (a total of 23 provinces). Nine "distribution patterns" (*B*, pp. 272, 273) exhibited by Atlantic myctophids are described in terms of these regions and provinces or parts or combinations thereof. The system provides a powerful tool for describing distribution patterns exhibited by Atlantic midwater organisms, and I have attempted below to describe the Atlantic distributions of 10 evermannellid and scopelarchid species largely in terms of this system.

Despite its usefulness, I believe that a careful reading of *B* with its companion paper by Nafpaktitis et al. (1977, hereafter referred to as *N*) reveals a number of inconsistent applications of the system and perhaps failings. These are briefly outlined in the following paragraphs.

To be noted first is the fact that neither restriction nor endemism of any species is prerequisite to the recognition of a zoogeographic region, province, or, for that matter, distribution pattern. Of the 82 myctophid species listed (*B*, p. 267), only one, *Lampadena pontifex*, is said to be limited to one region, the Mauritanian Upwelling, and (*N*, p. 182) "apparently limited to the southern province of that region" (this despite the fact that the distribution chart presented for this species [*N*, p. 181] shows records from the northern province and the adjacent Guinean Province of the Atlantic Tropical Region). No other myctophid species listed is endemic or restricted to any zoogeographic region or province.[12] Very few species are restricted to the indicated geographic area of the distribution pattern to which they are assigned.

It is not my belief that absolute restriction is the *sine qua non* for inclusion or exclusion of any species in a given part of any system of zoogeographic regions, provinces, or distribution patterns. The case for relative abundance as a component of faunal description and differentiation has been made (e.g., Craddock & Mead, 1970, p. 342) and needs no elaboration here. But it seems to me that *B* have gone too far, that their system, at least as presented, comes dangerously close to ignoring the value of restriction and endemism to our understanding of open-ocean species assemblages (see below under Pacific central-water species). There are several problems thereby introduced.

First, there is the real difficulty in fitting distribution patterns exhibited by groups such as the evermannellids and scopelarchids (and indeed most midwater fish groups) into a zoogeographic system based largely on geographic differences in relative abundance. The samples do not exist that would allow

[12]Mention is also made (*N*, p. 78; *B*, p. 284) of an undescribed *Symbolophorus* sp. also endemic to the Mauritanian Upwelling Region.

TABLE 24. Comparison of systems of distribution patterns recognized for Atlantic midwater fishes by Backus et al. (1977) and Krefft (1974). Species indicated as representative of named patterns by *both* sources are listed (page reference to distribution chart in Nafpaktitis et al., 1977, given in parentheses).

Backus et al., 1977	Krefft, 1974	Representative species (Myctophidae only)
"NORTHERN PATTERNS"	I. NORTHERN-TEMPERATE GROUP	
(1) Subpolar-temperate	Boreal	*Benthosema glaciale* (51)[1]
(2) Temperate (3) Temperate-semisubtropical	Temperate-subtropical	*Sybolophorus veranyi* (77)[2] *Ceratoscopelus maderensis* (243)[1]
(4) Subtropical	II. SUBTROPICAL GROUP	
Bipolar subtropical	Biantitropical subtropical	*Diaphus effulgens* (148)
Northern subtropical	Northern subtropical	*Lampadena urophaos atlantica* (177)
Southern subtropical[3]	Southern subtropical[3]	
	III. TROPICAL GROUP	
(5) Tropical-subtropical	Broadly tropical	*Ceratoscopelus warmingii* (246)
(6) Tropical-semisubtropical	—	—
(7) Tropical	Tropical	*Myctophum asperum* (69)
—	Agulhas pattern[4]	—
(8) Mauritanian Upwelling	Special pattern[5]	*Lampadena pontifex* (181)
	IV. SOUTHERN GROUP	
—	Subtropical convergence pattern	—
—	West wind drift pattern	—
—	Broadly Antarctic	—
—	Bipolar	—
(9) Eastern	—	—

[1]Also taken in Mauritanian Upwelling Region.

[2]Specimens assigned to this species from Mauritanian Upwelling probably represent a distinct, undescribed species (Krefft, 1974; Nafpaktitis et al., 1977).

[3]Example: *Diaphus anderseni* (Nafpaktitis et al., 1977, p. 171). Examples listed by Krefft (1974, p. 230) include two myctophid species not treated in Nafpaktitis et al. (1977): *Myctophum phengodes* and *Scopelopsis multipunctatus*.

[4]Tropical Indian Ocean species carried around Cape into South Atlantic by Agulhas Current; see Krefft (1974, pp. 231, 232) for listing of examples.

[5]Krefft (1974, p. 231) recognizes a number of "special" categories of distribution patterns, some of which correspond to patterns recognized by Backus et al. (1977). For example, Krefft notes the restriction of *Lampadena pontifex* and an undescribed *Symbolophorus* species to an area around the Cape Verdes and refers to these species as "pseudo-oceanic" (=land-associated). The restricted distribution of these same two forms constitutes an important part of the justification for recognition of a distinct Mauritanian Upwelling Region by Backus et al., 1977.

meaningful abundance comparisons on a geographic basis for most midwater fish groups for most areas of the world ocean.

Second, there is the possibility that exclusion (from consideration) of some distributional records as "waifs" or "expatriates," a course invited and practiced in *B* and *N*, may prove seriously misleading (e.g., compare O'Day & Nafpaktitis, 1967, with Karnella & Gibbs, 1977).

Third, the system as applied by *B* has resulted in what seems to me to be remarkable inconsistencies. For example, *Lepidophanes guentheri* (*N*, pp. 226–228), said to be a "tropical" species (*N*, p. 228; *B*, p. 274), was in fact taken in abundance not only throughout the Atlantic Tropical Region but also in the North Atlantic Subtropical, South Atlantic Subtropical, Gulf of Mexico, Mauritanian Upwelling, and even the western North Atlantic Temperate Region (*N*, p. 227; also see authors' comments [*N*, p. 228] on the distribution of this species). It seems to me that a system that includes *Lepidophanes guentheri* (*N*, p. 227) and *Diaphus vanhoeffeni* (*N*, p. 156) as examples of the *same* distribution pattern ("tropical") requires substantial modification. The same objection, i.e., apparent nonobjectivity in the assignment of a given species to one pattern or another, seems more or less appropriate in the cases of *Notolychnus valdiviae* (*N*, p. 94), *Lobianchia dofleini* (*N*, p. 98), *Diaphus dumerilii* (*N*, p. 115), *D. lucidus* (*N*, p. 139), *D. perspicillatus* (*N*, p. 145), *Lampanyctus alatus* (*N*, p. 225), and a number of other species. In fairness, there are also species showing moderate to strong restriction to the distribution patterns assigned them, e.g., *Protomyctophum arcticum* (*N*, p. 32), *Lampadena urophaos atlantica* (*N*, p. 177), *L. speculigera* (*N*, p. 179), and *Notoscopelus elongatus* (*N*, p. 254).

Fourth, but possibly first in importance, is a conceptual problem implicit in the zoogeographic system proposed by *B*. Two core elements of this system include the authors' concept of a **pelagic region:** "From the variety of overlapping distribution patterns, it follows that each pelagic region is faunally distinct with its characteristic assemblage of species whose numbers are in characteristic proportion, its characteristic diversity, and so on" (Backus et al., 1970, p. 196); and a **faunal boundary:** "By faunal boundary we mean a narrow zone across which there is a relatively rapid change from one constituency of species, or one fauna, to another. . . . A principal goal of this zoogeographic system has *been to describe the way in which the ocean changes physically at those places in which it changes faunally*" (*B*, p. 269; italics theirs). It appears that the authors are so preoccupied with describing oceanographically separable regions and provinces that the primary purpose of the exercise, i.e., the recognition of different faunas, is sometimes lost. This seems to me to be implicit in the authors' need to set up a dual system of zoogeographic regions and provinces vs. distribution-pattern areas. It is explicit in the authors' own description of how they came to propose the "Azores-Britain Province"—a province whose "boundaries are determined by the boundaries of its neighbors" (*B*, p. 280). Where is the faunal evidence for the distinctness of this province?

I believe that the only widely applicable method for the recognition of oceanic species assemblages lies in the discovery of species (or populations) exhibiting concordantly restricted distributions—a method employed to good advantage in studies of the Pacific (see below). The first step is the discovery of "recurrent" (*sensu* Fager & McGowan, 1963) distribution patterns. The second step is the study of hydrographic and biological parameters that might define faunal

boundaries separating such patterns. I believe that, to some extent, *B* have reversed these steps, and, to that extent, their zoogeographic system is lacking. I conclude by affirming the great utility of their system for describing the distribution of individual species—their system provides a precisely defined set of geographic and oceanographic adjectives. It may well be that the main features of the system of Atlantic mesopelagic zoogeography proposed by *B* will be confirmed, but, in my opinion, that confirmation is not to be found in *B*.

The 10 evermannellid and scopelarchid species occurring in the Atlantic exhibit distributions comparable to the following patterns described by *B* for myctophids: subtropical (2/10), tropical-subtropical (5/10), tropical (2/10), ? eastern (1/10).

Subtropical Species.—*Coccorella atlantica* (fig. 24; 218 Atlantic Ocean records) closely fits the definition of subtropical or central-water species given above, occurring in and essentially restricted to central water-mass areas of the Atlantic, Indian, and Pacific oceans. In the Atlantic, except for a considerable number of records from the Lesser Antillean and Caribbean provinces of the Atlantic Tropical Region and from the Gulf of Mexico Region, *C. atlantica* fits well the subtropical distribution pattern as depicted and described by *B* (pp. 272, 280–283) for 13 mesopelagic, myctophid species. The distribution of *C. atlantica* is similar to the distributions of *Hygophum reinhardtii* (*N*, p. 41), *H. taaningi* (*N*, p. 49, North Atlantic only), *Lampanyctus cuprarius* (*N*, p. 198), and *L. lineatus* (*N*, p. 200, North Atlantic only). All four myctophid species also occur in the western Tropical provinces and the Gulf of Mexico.

Rosenblattichthys hubbsi is known from 22 Atlantic Ocean collections (fig. 40). Except for the site of capture of the holotype (02° 27′ S, 19° 00′ W) and a number of records from the Lesser Antillean Province, the known distribution of *R. hubbsi* appears to best agree with the subtropical pattern. Most Atlantic records for *R. hubbsi* are from the North and South North African Subtropical Sea provinces of the North Atlantic Subtropical Region (*B*, p. 270), with only a single record from either Sargasso Sea Province. I am unable to find another example of a subtropical midwater species similar to *R. hubbsi* in apparent relative restriction to the eastern subtropics in the North Atlantic. *B* (p. 287) cite *Pollichthys mauli* (a photichthyid) and *Melamphaes pumilus* (a melamphaid) as examples of species ". . . common in the Sargasso Sea and rare in the North African Subtropical Sea." In the Indian and North Pacific oceans, *R. hubbsi* is, as far as is known, restricted to central-water areas.

Tropical-Subtropical Species.—Five evermannellid and scopelarchid species exhibit distributions comparable to the tropical-subtropical pattern as described and depicted for 18 mesopelagic myctophid species (*B*, pp. 273, 283, 284). All five are also known from central and equatorial water-mass areas in the Indian and Pacific oceans. *Scopelarchus michaelsarsi* (fig. 48; 74 Atlantic Ocean records), *Evermannella indica* (fig. 34; 261 Atlantic Ocean records), and *Odontostomops normalops* (fig. 37; 78 Atlantic Ocean records) show fairly close restriction to the Tropical and North and South Subtropical regions as depicted by *B* (p. 270). All three species occur in the Gulf of Mexico, but *S. michaelsarsi* has not been taken in the Caribbean Sea. Of these three, only *Odontostomops normalops* has been taken in the Gulf of Guinea, and, although all three are known from the eastern subtropical North Atlantic, none of them has been taken in the region of the Mauritanian Upwelling. *Odontostomops normalops* is known from very few rec-

ords in the eastern subtropical North Atlantic, and, as noted above, the range of *O. normalops* is essentially complementary to that of *Evermannella balbo* (fig. 32). Examples of somewhat similar pairings are provided by *Diaphus mollis* (*N*, p. 160) vs. *D. rafinesquii* (*N*, p. 158) and by *Scopelogadus mizolepis mizolepis* vs. *S. beanii* (Ebeling & Weed, 1963, p. 41).

In the Atlantic Ocean, *Scopelarchus analis* (fig. 46; 416 Atlantic Ocean records) and *Benthalbella infans* (fig. 39; 72 Atlantic Ocean records) are widely distributed in tropical and subtropical waters (although there are few records for *B. infans* from the Caribbean Sea and none from the Gulf of Mexico). Both species have also been taken commonly in temperate waters, especially in the North Atlantic Temperate region (*B*, p. 270). The myctophids *Benthosema suborbitale* (*N*, p. 55), *Diogenichthys atlanticus* (*N*, p. 58), *Myctophum nitidulum* (*N*, p. 67), *Gonichthys cocco* (*N*, p. 88), *Notolychnus valdiviae* (*N*, p. 94), *Lobianchia gemellari* (*N*, p. 101), *Diaphus mollis* (*N*, p. 160), *Lampanyctus photonotus* (*N*, p. 213), *Ceratoscopelus warmingii* (*N*, p. 246), and *Notoscopelus resplendens* (*N*, p. 252) are all examples of species classed by *B* as tropical-subtropical which, similar to *Scopelarchus analis* and *Benthalbella infans*, were commonly taken in at least parts of the south and/or north Temperate regions in the Atlantic in addition to the tropics and subtropics. A similar distribution pattern is exhibited by *Lepidophanes guentheri* (*N*, p. 227), a species classed by *B* (p. 274) as tropical.

Odontostomops normalops, *Scopelarchus analis*, and *Benthalbella infans* have all been taken in the Mediterranean Outflow Province (*B*, p. 270), but none of them is known from the Mediterranean. As Merrett et al. (1973) have pointed out, the overwhelming majority of captures of *Benthalbella infans* in the North Atlantic are from the eastern sector (temperate and subtropical). Both *Scopelarchus analis* and *Benthalbella infans* have been taken in the Mauritanian Upwelling Region.

Benthalbella infans holds the northernmost distributional record (61° 04′ N, 14° 39′ W; *Petr Lebedev*, sta. 98) of any scopelarchid or evermannellid (*Evermannella balbo* is second—the northernmost record for this species is 59° 49.6′ N, 20° 22.9′ W). *B* (p. 274) consider the mesopelagic habitat to extend from near the surface to about 700 or 800 m. The limited data for *B. infans* presented by Merrett et al. (1973) and Johnson (1974c) suggest that the daytime depth stratum occupied by most juveniles and adults may be deeper than 800 m, making *B. infans* a bathypelagic species as the term is used by *B*. However, there are nighttime records of large adults in the upper 200 m (possibly suggesting diel vertical migration), and Merrett et al. (1973) give the overall depth range (day) as 90 to 1,500 m (night = upper 100 to 900 m). Distributional records for *Scopelarchus analis* and *Benthalbella infans* provide good evidence for continuity of distribution around the Cape of Good Hope (cf. figs. 39, 46), suggesting that, for these species, Africa does not completely isolate the Atlantic from Indian Ocean populations (for additional discussion of "the South African Barrier" see Brinton, 1975, pp. 146, 147).

Tropical Species.—Two scopelarchid species, *Scopelarchoides danae* and *Scopelarchus guentheri*, exhibit Atlantic distributions comparable to the "tropical pattern" described by *B* (pp. 273, 283) for 18 mesopelagic myctophid species.

Virtually all Atlantic records for *S. danae* (fig. 43; 109 Atlantic Ocean records) are from the Atlantic Tropical Region as defined by *B* (pp. 270, 271), with the majority of records from either the Gulf of Guinea or the Lesser Antilles/Caribbean Provinces. Exceptions include one record from the Gulf of Mexico,

one record from Slope Water, one record from the Mauritanian Upwelling, and a number of records from the Sargasso Sea and Straits of Florida provinces of the North Atlantic Subtropical Region. In the Indian and Pacific oceans, *S. danae* has been taken in both equatorial and central water-mass areas, but the distribution of *S. danae* is largely equatorial, with most records from near continental and insular land masses. Aside from the apparent association with relatively nearshore areas, the Atlantic distribution of *S. danae* is similar to that of the myctophids *Myctophum asperum* (*N*, p. 69), *M. obtusirostre* (*N*, p. 72), *Diaphus luetkeni* (*N*, p. 133), and *Lampanyctus tenuiformes* (*N*, p. 220) as well as the decapod crustacean *Sergestes edwardsii* (Judkins, 1978, p. 13).

Scopelarchus guentheri (fig. 47; 45 Atlantic Ocean records) is widespread in tropical, subtropical, and even temperate waters in the Indian and especially in the Pacific Ocean, but it is essentially limited to the Atlantic Tropical Region in the Atlantic. *Scopelarchus guentheri* is all but excluded from the region of the North Atlantic Central Water Mass. The Atlantic distributions of *Scopelarchus guentheri* and *Coccorella atlantica* are largely complementary, providing a nearly perfect example of the contrast between central (=subtropical) vs. equatorial (=tropical) distribution patterns (fig. 54). The most glaring discrepancy in this contrast is the large number of records of *C. atlantica* from the Gulf of Mexico and Caribbean and Lesser Antilles provinces—*S. guentheri* is virtually unknown (two Caribbean Sea records only) from these areas. At least two myctophid species, classed as subtropical by *B* (p. 274), resemble *C. atlantica* in distribution, having been commonly taken in the Gulf of Mexico, Caribbean, and Lesser Antilles provinces but not in the Amazonian or Guinean provinces: *Hygophum taaningi* (*N*, p. 49, North Atlantic only) and *Lampanyctus cuprarius* (*N*, p. 198). Pietsch (1974, p. 93) notes the value of the 14° C isotherm at 200 m (as depicted by Schroeder, 1963) in indicating the boundary between North Atlantic vs. South Atlantic Central Water. Addition of a line indicating the position of this isotherm (fig. 54) gives good separation between the North Atlantic distributions of *C. atlantica* and *S. guentheri*. This, in connection with other distributional evidence cited above, might suggest that part or all of the "Lesser Antilles Province" should be placed in the North Atlantic Subtropical rather than Atlantic Tropical Region. I have discussed limited evidence suggesting that in the Pacific *S. guentheri* is, relative to its congeners, partly excluded from central water-mass areas (Johnson, 1974c; see discussion of Pacific central-water species below). *Scopelarchus guentheri* is apparently more abundant (in the Pacific) in the more productive waters peripheral to the central regions of the subtropical anticyclones. Thus, it is surprising to note that in the Atlantic *S. guentheri* has yet to be taken in the Gulf of Guinea and far eastern South Atlantic, areas of relatively high productivity, and that *S. analis* (fig. 46) has been taken in those areas.

Eastern Species.—The distribution of *Evermannella balbo* (fig. 53; 152 Atlantic Ocean records) may be comparable with the "eastern pattern" described by *B* (pp. 273, 274, 284, 285) for two mesopelagic myctophid species: *Electrona risso* (*N*, p. 34, known from widely scattered records in the Indian and Pacific oceans) and *Diaphus holti* (*N*, p. 163, known only from the Atlantic). *Evermannella balbo* is known from both the eastern and western Mediterranean and is the only evermannellid or scopelarchid occurring in that sea. *Evermannella balbo* has been taken in the Atlantic Subarctic (to 59° 49.6′ N), North Atlantic Temperate, and the cooler and more productive portions of the North Atlantic Subtropical, At-

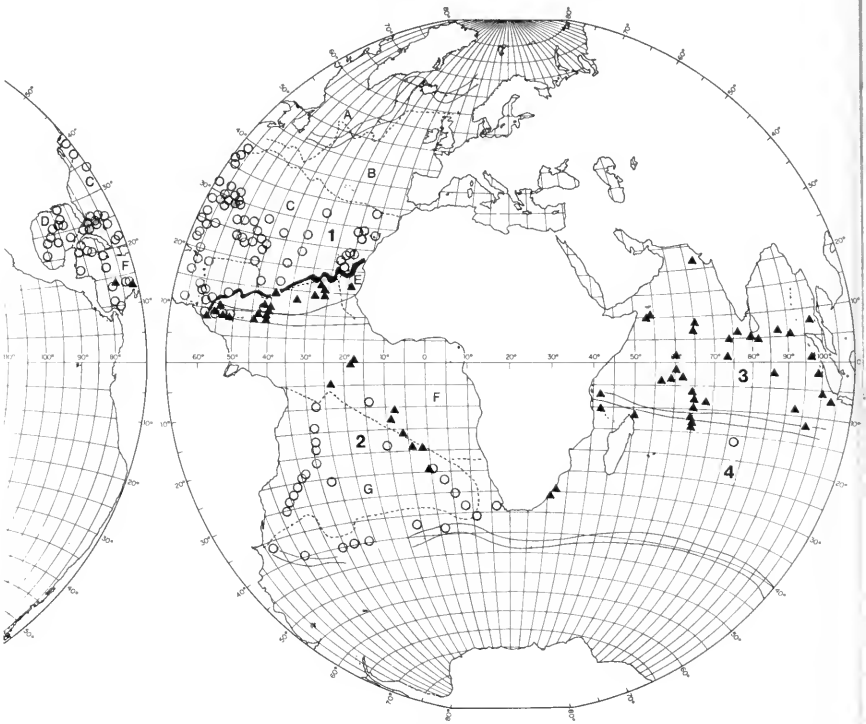


FIG. 54. Atlantic and Indian Ocean distributions of *Coccorella atlantica* (open symbols) and *Scopelarchus guentheri* (closed symbols). Shown for the Atlantic are the approximate boundaries of seven pelagic faunal regions recognized by Backus et al., 1977: A = Atlantic Subarctic Region; B = North Atlantic Temperate Region; C = North Atlantic Subtropical Region; D = Gulf of Mexico Region; E = Mauritanian Upwelling; F = Atlantic Tropical Region; G = South Atlantic Subtropical Region. Open bands show approximate boundaries (after Sverdrup et al., 1942) between the major upper water masses: 1 = North Atlantic Central; 2 = South Atlantic Central, 3 = Indian Ocean Equatorial; 4 = Indian Ocean Central. Heavy black band denotes position of 14° C isotherm at 200 m (after Schroeder, 1963).

lantic Tropical, and South Atlantic Subtropical regions. *Evermannella balbo* is known from only one record in the Indian Ocean but has been widely taken in the southern Transition Region (see McGowan, 1971, p. 44) of the Pacific Ocean, and *E. balbo* is probably circumglobal in the Subtropical Convergence Region of the Southern Ocean.

Evermannella balbo thus illustrates the "east-west effect" described by *B* (p. 285), who characterize the waters on the eastern side of the Atlantic as generally ". . . cooler, . . . fresher, denser, lower in dissolved oxygen, higher in dissolved inorganic phosphorus, and more productive than waters to the west." In the eastern North Atlantic *E. balbo* is known from the Mediterranean, Mediterranean Outflow, far eastern North African Subtropical Sea, Mauritanian Upwelling, and Guinea provinces (*B*, p. 270, 271). In the western North Atlantic *E. balbo* is known from the western Temperate provinces (including Slope Water) and the northern Sargasso Sea, a pattern recognized as distinctive by Backus et al. (1970)

and Jahn & Backus (1976). Backus et al. (1969) described the faunal differences between the northern and southern Sargasso Sea at the apparent boundary region (ca. 27° N at 70° 20′ W) largely in terms of primary productivity and vertical distribution of temperature. Species agreeing with *E. balbo* in western North Atlantic distribution include *Lampanyctus crocodilus* (*N*, p. 208, a "temperate-semisubtropical" species limited to the North Atlantic), *Lampanyctus pusillus* (*N*, p. 222), *Lobianchia dofleini* (*N*, p. 98), *Stomias boa ferox* (Gibbs, 1969, p. 15), and the decapod crustacean *Sergestes arcticus* (Judkins, 1972, p. 166). *Lampanyctus pusillus*, *S. boa ferox*, and *S. arcticus* agree in distribution with *E. balbo* in occurring (or presumably so) circumglobally in the Southern Ocean but differ in apparent exclusion from the Atlantic Tropical Region. The distribution of *E. balbo* is similar to that depicted by Ebeling & Weed, 1963, p. 39, for *Scopelogadus beanii* (except that the latter is apparently unrecorded from the Mediterranean or eastern South Pacific). The distribution of *E. balbo* and *Lobianchia dofleini* is virtually congruent. *Lobianchia dofleini* is said to occur circumglobally in the neighborhood of the southern Subtropical Convergence (*N*, p. 98), and it is likely that this is true of *E. balbo*. *Lobianchia dofleini* is classed by *B* (p. 274) as a "temperate-semisubtropical" species, a distribution pattern described for eight mesopelagic, myctophid species. In the main features of its North Atlantic distribution *E. balbo* agrees moderately to very well with the myctophid species assigned to this pattern. Nonetheless, I have retained my assignment of *E. balbo* to the "eastern" pattern because I believe that *E. balbo* well illustrates the east-west polarity discussed by *B* (pp. 284, 285) and particularly so when the distribution of *E. balbo* is compared with that of other evermannellid species (fig. 31). Thus, the distribution of *E balbo* in boreal, temperate, subtropical, and tropical waters can be associated largely with the cooler and more productive areas of the Atlantic and southern Indian and Pacific oceans.

Indian Ocean

Thirteen of the 19 warm-water species of evermannellids and scopelarchids occur in the Indian Ocean (table 23). None of these species is restricted to the Indian Ocean. Recent papers contributing to our knowledge of distribution patterns exhibited by midwater organisms in the Indian Ocean include Ebeling (1962, 1967), Ebeling & Weed (1963), Baker (1965), Gibbs & Hurwitz (1967), Kotthaus (1967), Aron & Goodyear (1969), Mauchline & Fisher (1969), Nafpaktitis & Nafpaktitis (1969), Parin (1970), Bradbury et al. (1971), Brinton & Gopalakrishnan (1973), Cohen (1973), Fleminger & Hulsemann (1973), and Nafpaktitis (1978).

Survey efforts in the Indian Ocean have resulted in an extremely uneven distribution of sampling effort (e.g., Dietrich, 1973), with most attention having been given to the northern and far-western regions. A huge gap in sampling effort for midwater fishes is present in the southern and southeastern Indian Ocean as reflected by Figure 49 and clearly shown in Nafpaktitis (1978, p. 3). The gap in sampling effort results in considerable uncertainty concerning subtropical (=central-water area) distribution patterns in the Indian Ocean—an uncertainty reflected in the following distribution accounts.

A valuable summary of the oceanography of the Indian Ocean is provided by Wyrtki (1973). In the tropical and subtropical Indian Ocean two major and distinct circulation systems are recognizable: the unique monsoon gyre that

changes seasonally and the southern hemisphere subtropical, anticyclonic gyre. Dividing the monsoon gyre (="tropical" or "equatorial-water" area) from the subtropical gyre (="subtropical" or "central-water" area) is a prominent "hydro-chemical front" (Wyrtki, 1973, pp. 23–25) at ca. 10° S. Identified by a horizontal salinity minimum that stretches from Sumatra to Africa, this front separates the low-nutrient, high-oxygen water of the south from the nutrient-rich, oxygen-poor water of the north. Although identifiable in the vertical and horizontal distribution of a number of parameters, the front is perhaps most dramatically delineated by the distribution of dissolved oxygen (Wyrtki, 1973, p. 24). Most authors who have dealt with open-ocean distribution patterns in the Indian Ocean have explicitly or implicitly recognized the importance of this frontal zone, marking as it does the division between Indian Equatorial and Indian Central Water-Mass areas (e.g., Ebeling, 1962, 1967; Cohen, 1973; Brinton & Gopalakrishnan, 1973; Nafpaktitis, 1978).

It is clear, however, that distribution patterns exhibited by Indian Ocean mid-water organisms are more numerous than a simple "equatorial" vs. "central." Brinton & Gopalakrishnan (1973) recognize (for euphausiids) five major, zonally distributed boundary regions, at 10° N, 0°, 10° S, 25° to 30° S, and 40° to 45° S. The boundary at 10° N corresponds roughly to the extent of the main subsurface low-oxygen waters of the northern Indian Ocean (see below). The boundary at the equator is said (Brinton & Gopalakrishnan, 1973, p. 379) to correspond with the southern edge of the North Equatorial Current (NE Monsoon). The boundary at 10° S is the prominent hydrochemical front discussed above. There is no specific hydrographical feature identified by Brinton & Gopalakrishnan (1973, p. 381) with the boundary at 25° to 30° S, but a number of euphausiid species apparently find the northern or southern end-points of their range within this latitudinal zone. The boundary at 40° to 45° S is identifiable with the Subtropical Convergence zone—the boundary between subtropical and subantarctic waters in all oceans. There is sufficient information to allow discussion of the Indian Ocean distributions of evermannellid and scopelarchid species with respect to three of these boundary regions—those at 10° N, 10° S, and at the Subtropical Convergence.

Brinton & Gopalakrishnan (1973) also report on meridional features of euphausiid distribution in the Indian Ocean, particularly the extensive north to south ranges of coastal forms and the far southerly occurrences of tropical and subtropical species in the region of the Agulhas Current system (tropical species range as far as 33° S, tropical-subtropical species as far as 38° S). Wyrtki (1973) notes the lack of a well-developed eastern boundary current (see Wooster & Reid, 1963) in the southern Indian Ocean. A western boundary current, the Agulhas Current, is by far the strongest component of the subtropical gyral, with core velocities up to 2 m/sec and large transport values south of 10° to 12° S (Wyrtki, 1973; Pearce, 1977). Nafpaktitis (1978) notes the southward extension (to 20° to 25° S and beyond) of equatorial (=tropical) myctophid species in the Agulhas Current. Whether directly (Nafpaktitis, 1978, p. 84) or indirectly (Wyrtki, 1973, p. 30), the Agulhas Current system provides a basis for transport of Indian Ocean water and midwater species into the eastern South Atlantic (Krefft, 1974, pp. 231, 232). A very clear example of the "Agulhas Pattern" can be seen in Brinton's (1975, p. 98) depiction of the distribution of *Euphausia diomedeae*. In the far-western Indian Ocean the southern distributional end-

points of six evermannellid and scopelarchid species are possibly or probably related to the Agulhas system. The six species are: *Coccorella atrata* (fig. 24), *Evermannella indica* (fig. 34), *Scopelarchoides danae* (fig. 43), *S. signifer* (fig. 45), *Scopelarchus guentheri* (fig. 47), and *S. michaelsarsi* (fig. 48). This conclusion seems particularly well supported for three species that are largely equatorial in distribution, viz., *Coccorella atrata, Scopelarchoides danae,* and *S. signifer.*

Bradbury et al. (1971, pp. 423–436) suggest a possible east-west polarity in the distribution of certain Indian Ocean species, i.e., some species limited to the east, others occurring only in the west. The cruise track and sampling regime (Bradbury et al., 1971, pp. 411, 436) providing the samples on which this conclusion was based seem to me to be largely inappropriate to detecting such a polarity even if the suggestion is valid. Nonetheless, east-west polarity in the Indian Ocean may well occur as Nafpaktitis (1978, p. 84) has suggested for a number of myctophid species. No evermannellid or scopelarchid species shows any evidence of such eastern or western limitation in the Indian Ocean.

Transition Region Species.—No warm-water species of evermannellid or scopelarchid is actually recorded from the Subtropical Convergence Region of the southern Indian Ocean. The most probable candidate, *Evermannella balbo,* is known from a single Indian Ocean specimen taken in the Agulhas Current system at 29° 52′ S, 31° 36′ E. Based on the distribution of *E. balbo* in the South Atlantic and South Pacific (fig. 53), it seems likely that *E. balbo* will be found to occur throughout the southern Indian Ocean in the Subtropical Convergence Region. I also predict the occurrence in this region of two additional species: *Coccorella atlantica* (fig. 24) and *Scopelarchus guentheri* (fig. 47).

Subtropical (=Central-Water) Species.—Two species, *Coccorella atlantica* (fig. 24) and *Rosenblattichthys hubbsi* (fig. 40), are known in the Indian Ocean only from the region of the Central Water Mass (Sverdrup et al., 1942, p. 740), south of 10° S. *Coccorella atlantica* is known from only two specimens from two collections in the Indian Ocean—one record from 16° 05′ S at 76° 16′ E; the other from the South Australian Basin (ca. 38° S, 128° E). *Rosenblattichthys hubbsi* is known from only seven Indian Ocean specimens, all larvae or small juveniles, representing five Indian Ocean records. Both *C. atlantica* and *R. hubbsi* are replaced by closely related congeners, *C. atrata* and *R. alatus,* respectively, in the Equatorial Water-Mass area of the Indian Ocean, north of 10° S. *Coccorella atlantica* and *R. hubbsi* are essentially limited to central-water areas in the Atlantic and Pacific oceans. A similar equatorial vs. central distributional contrast is exhibited by the lantern fishes *Diogenichthys panurgus* vs. *D. atlanticus* (Nafpaktitis & Nafpaktitis, 1969, p. 15).

Cohen (1973, p. 462) tallied distributional information for a number of midwater fish groups occurring in the Indian Ocean. He (p. 462) reports that for 50 myctophid species surveyed, 18 species appear to be restricted to the region of the Equatorial Water Mass, six are restricted to the region of the Central Water Mass, eight occur in (at least parts of) both areas, 11 occur in central and subantarctic water, five are restricted to the subantarctic, and two are broadly distributed, ranging from the Arabian Sea to the subantarctic.

Tropical-Subtropical Species.—Three species are broadly distributed in Equatorial and Central Water-Mass areas of the Indian Ocean: *Odontostomops normalops* (fig. 37; 15 Indian Ocean records: 09° 36′ N to 20° 47.9′ S), *Benthalbella infans* (fig. 39; 24 Indian Ocean records: 00° 14′ S to 34° S), and *Scopelarchus analis* (fig. 46; 16

Indian Ocean records: 00° 01′ N to 38° 53.2′ to 58.5′ S). All three species are tropical-subtropical in the Atlantic and Pacific Oceans. A fourth species, *Scopelarchus guentheri*, is also broadly distributed in the warm-water Indian Ocean (fig. 47), but the account of this species is reserved for the section dealing with species occurring north of 10° N (see below). Extremely limited evidence suggests that *B. infans* and *S. analis* may agree with the tropical-subtropical euphausiids *Euphausia brevis* and *Thysanopoda subaequalis* (Brinton & Gopalakrishnan, 1973, pp. 366, 376) in sharing the equator as the (approximate) northern limit of distribution in the Indian Ocean. Midwater fish species showing a similar distribution in the Indian Ocean include the lantern fishes *Benthosema suborbitale* and *Lampanyctus alatus* (Nafpaktitis & Nafpaktitis, 1969, pp. 11, 56). *Odontostomops normalops* agrees with many tropical-subtropical and tropical euphausiid species in not occurring north of ca. 10° N (Brinton & Gopalakrishnan, 1973).

Tropical (=Equatorial) Species.—Five species are largely or entirely restricted to the region of the Equatorial Water Mass in the Indian Ocean: *Evermannella indica* (fig. 34; 62 Indian Ocean records), *Rosenblattichthys alatus* (fig. 40; 13 Indian Ocean records), *Scopelarchoides danae* (fig. 43; 34 Indian Ocean records), *S. signifer* (fig. 45; 48 Indian Ocean records), and *Scopelarchus michaelsarsi* (fig. 48; 8 Indian Ocean records). *Rosenblattichthys alatus* and *Scopelarchoides signifer* are limited to the Indian and Pacific Oceans, the other three species occur as well in the Atlantic Ocean. All five species agree with most Indian Ocean equatorial midwater species, including the majority of species of *Diaphus* (Nafpaktitis, 1978), in showing restriction (or near restriction) to the zone between 10° N and 10° S except for southerly range extensions in the Agulhas Current system. One additional species, *Coccorella atrata*, is restricted to the Equatorial Water-Mass Region of the Indian Ocean but also occurs north of 10° N (see below).

Rosenblattichthys alatus, Scopelarchoides danae, and *S. signifer* are (on the basis of known captures) essentially restricted to equatorial or tropical waters throughout their respective ranges. *Evermannella indica* and *Scopelarchus michaelsarsi* are tropical-subtropical species in both the Atlantic and Pacific oceans. It is quite possible that the apparent restriction of the latter two species to the Equatorial Water-Mass Region in the Indian Ocean is an artifact of sampling effort.

Species Occurring North of 10° N.—Two species are known from north of 10° N in the Indian Ocean: *Coccorella atrata* (fig. 24; 42 Indian Ocean records) and *Scopelarchus guentheri* (fig. 47; 54 Indian Ocean records). *Coccorella atrata,* known only from the Indian and Pacific oceans, is essentially restricted to tropical or equatorial waters throughout its range. In the Atlantic *S. guentheri* is essentially restricted to the Atlantic Tropical Region (Backus et al., 1977, p. 270), but *S. guentheri* is widely distributed in equatorial, central, and Transition Region waters in the Pacific and (probably) Indian oceans. The majority of Indian Ocean records for both species are from the zone between 10° N and 10° S, a result that may partly reflect sampling effort.

The northern Indian Ocean including the semi-enclosed basins of the Arabian Sea and Bay of Bengal, an area strongly influenced by the seasonal monsoon systems, is characterized by strong regional upwelling systems, high nutrient levels, high productivity, and a marked oxygen minimum layer (Vinogradov & Voronina, 1962; Gibbs & Hurwitz, 1967; Kinzer, 1969; Wyrtki, 1971; Brinton & Gopalakrishnan, 1973; Currie et al., 1973; McGill, 1973). The horizontal and

vertical extent of the oxygen minimum layer is depicted in a number of charts presented by Wyrtki (1971). If the oxygen minimum layer is defined as subsurface waters in which dissolved oxygen values are ≦ 1.0 ml/L, the layer is more than 1,000 m thick in parts of the Arabian Sea, with values less than 0.1 ml/L occurring vertically over an extent of several hundred meters in some areas (e.g., Wyrtki, 1971, p. 441). A similarly striking if somewhat less pronounced oxygen minimum layer is present throughout the Bay of Bengal (e.g., Wyrtki, 1971, p. 413).

Gibbs & Hurwitz (1967) found the southern limit of occurrence of *Chauliodus pammelas*, a species endemic to the low-oxygen area, to be at about 05° S in the Arabian Sea. This latitude was stated (Gibbs & Hurwitz, 1967, p. 802) to closely correspond with the southern extension of the 1.0 ml/L isopleth in the upper 200 m (compare Gibbs & Hurwitz, 1967, fig. 1, with Wyrtki, 1971, p. 78). South of 05° N, *C. pammelas* is replaced by the broadly distributed *Chauliodus sloani*. The two species apparently overlap in the zone 05° to 10° N. A parallel distribution pattern is described by Goodyear & Gibbs (1969) for *Astronesthes lamellosus* (endemic to Arabian Sea and Bay of Bengal) vs. *A. cyaneus* (10° N to 10° S in Indian Ocean, 25° N to 15° S in Pacific Ocean). Other midwater species apparently endemic to the low-oxygen area of the northern Indian Ocean include the lantern fishes *Diaphus arabicus* and *D. lobatus* (Nafpaktitis, 1978) as well as decapod crustacean *Sergestes semisses* (Judkins, 1978).

Of those evermannellid and scopelarchid species occurring in the Indian Ocean Equatorial Water-Mass Region, two, *Benthalbella infans* and *Scopelarchus analis*, are not known from north of the equator (i.e., not north of 00° 01′ N). Six species, *Evermannella indica*, *Odontostomops normalops*, *Rosenblattichthys alatus*, *Scopelarchoides danae*, *S. signifer*, *Scopelarchus michaelsarsi*, are known from north of the equator but find the northernmost limit of their distribution in the Indian Ocean somewhere in the zone of 05° to 10° N, in parallel with the results cited above for *Chauliodus sloani*. It seems likely that this northern end-point is associated, at least in part, with the extent of the northern Indian Ocean low-oxygen area. Goodyear & Gibbs (1969, p. 128) note the paucity of stomiatoid species in the Arabian Sea: "Perhaps six species in the families Chauliodontidae, Stomiatidae, Melanostomiatidae, and Malacosteidae occur there, and only one of these, *Stomias affinis*, has not speciated to some degree. By contrast, approximately 50 species in these same families are found in the adjacent Equatorial or Central waters of the Indian Ocean." They (Goodyear & Gibbs, 1969) relate this, at least in part, to the presence of the marked oxygen minimum layer in the northern Indian Ocean.

Coccorella atrata and *Scopelarchus guentheri*, the only species in their respective families known to occur in the low-oxygen area of the Indian Ocean, are likewise the only broadly distributed (two or three ocean) species in these families to occur in the eastern tropical Pacific, another area characterized by a strongly developed oxygen minimum layer. As will be noted below, however, the eastern tropical Pacific distribution of these two species is restricted to a rather narrow latitudinal zone along the equator.

Kashkin (1977) has recently shown that relative to material taken elsewhere, specimens of *Scopelarchus guentheri* taken north of 04° N in the Indian Ocean have longer gill filaments ("first-order" filaments—measured at two different points on the second gill arch), a feature assuredly associated with the distribu-

tion of *S. guentheri* in the oxygen-minimum area of the northern Indian Ocean. Gibbs & Hurwitz (1967) note that *Chauliodus pammelas* may be distinguished from *C. sloani* in possessing longer gill filaments with longer, thinner, and more numerous lamellae. Goodyear & Gibbs (1969) state that *Astronesthes lamellosus*, endemic to the low-oxygen area of the northern Indian Ocean, has, relative to other species in the *A. cyaneus* species group, longer gill filaments and larger gill lamellae. Additional putative examples of adaptive changes in gill filament morphology relative to inhabitation of low-oxygen areas are given in the discussion of species occurring in the eastern tropical Pacific in a subsequent section.

Pacific Ocean

All 19 warm-water species of evermannellids and scopelarchids occur in the Pacific Ocean, and six species are endemic to either central or eastern equatorial water-mass regions in the Pacific (table 23). Recent papers contributing to our knowledge of distribution patterns exhibited by midwater organisms in the Pacific Ocean include: Aron (1959, 1962), Bieri (1959), Parin (1961, 1970, 1971, 1976), Brinton (1962, 1975), Ebeling (1962, 1967), King & Iverson (1962), Fager & McGowan (1963), Johnson & Brinton (1963), Pearcy (1964), Alvarino (1965), Bussing (1965), Berry & Perkins (1966), Crane (1966), Grandperrin & Rivaton (1966), Lavenberg & Fitch (1966), Lavenberg & Ebeling (1967), Paxton (1967), Fitch & Lavenberg (1968), Mauchline & Fisher (1969), Craddock & Mead (1970), Ebeling et al. (1970, 1971), Ahlstrom (1971, 1972), McGowan (1971, 1974, 1977), Judkins (1972, 1978), Robison (1972), Brewer (1973), Clarke (1973, 1974), Kobayashi (1973), McGowan & Williams (1973), Brown (1974), Johnson (1974c), Hartman & Clarke (1975), Johnson & Glodek (1975), Clarke & Wagner (1976), and Wisner (1976).

It is certain that the best fit to the "water-mass hypothesis" (see above) is exhibited by certain midwater species occurring in the Pacific Ocean, and this fit is most strikingly evident in species limited to particular subregions of the Pacific (e.g., Johnson, 1974c, p. 223; Pietsch, 1974, p. 91). Thus, unlike the largely zonal systems of zoogeographic regions proposed for the Atlantic (e.g., Backus et al., 1977) and Indian (e.g., Brinton & Gopalakrishnan, 1973) oceans, the most recent attempts to describe faunal regions in the Pacific have been couched almost entirely in terms of water-mass regions.

Ebeling (1962, 1967) constructs a scheme of faunal boundaries, regions, and subregions associated with water-mass boundaries and based on the distributions (as known at that time) of 135 meso- and bathypelagic fish species. For the Pacific, Ebeling (1967, p. 603) recognizes four "Primary Zoogeographical Regions," viz.: (1) Circumcentral-tropical (divided into Atlantic Central vs. Indo-Pacific, with the latter further divided into North Pacific Central, South Pacific Central, Indonesian, and Indian, as "tertiary" or "quaternary" zoogeographic regions), (2) eastern Pacific Equatorial, (3) North Pacific Subarctic and Transitional, and (4) Subantarctic. Note that in Ebeling's system there are only two recognized "Primary" warm-water regions—circumcentral (combining central and western equatorial) vs. eastern equatorial.

Brinton (1962) plotted the known distributions of 59 euphausiid species in the Pacific Ocean. For those species occurring mainly above 500 to 700 m (termed "epipelagic species"), Brinton (pp. 199–212) recognizes four major categories of

distribution in relation to Pacific water-mass regions inhabited and (partly) characterized by distinct groups of euphausiid species: (1) Pacific Subarctic, Subantarctic; (2) Transition Zone, North vs. South; (3) Central, North vs. South; (4) Equatorial, East vs. West. Also recognized are various composites of these basic distributional patterns.

McGowan (1971, 1974, 1977) and his colleagues and students (e.g., McGowan & Williams, 1973; Barnett, 1975; Shulenberger, 1977) have marshalled substantial evidence to support a scheme of major oceanic biotic provinces in the North and South Pacific. The method of constructing charts of these provinces (McGowan, 1971, pp. 14–46; McGowan, 1974, pp. 10, 11) is that also used in determination of "generalized tracks" (see above). The patterns recognized (McGowan, 1974, pp. 14, 15; McGowan, 1977, p. 426) include: Subarctic and Subantarctic; North and South Transition Zones; North and South Central; Equatorial; Eastern Tropical Pacific; Warm-Water Cosmopolitan. Also recognized (McGowan, 1974, p. 12) is the existence of endemic species of macrozooplankton and fishes in the California Current (Brinton, 1962; Ebeling, 1962, 1967; Lavenberg & Ebeling, 1967; Ebeling et al., 1970) and Peru Current (Bussing, 1965; Craddock & Mead, 1970) systems. McGowan (1977) distinguishes between the major faunal provinces, the "ecosystems" of his zoogeographic scheme, and the rather broad areas of transition, the "ecotones," separating the provinces. The provinces are seen as ". . . *in situ* regulated ecosystems," the ecotones as ". . . regulated by both *in situ* processes and large-scale and variable horizontal advection." Further mention of this distinction is included in subsequent sections.

Species Occurring in Austral-Asian Seas.—Brinton (1975) reviews the distribution of oceanic species (especially euphausiids) in the Austral-Asian seaway region: ". . . the only existing low-latitude interocean pathway for pelagic organisms." Brinton notes that various of these enclosed or semi-enclosed basins harbor populations of oceanic species that may be transient or resident, widespread or endemic. Although there exist species of oceanic invertebrates (e.g., Brinton, 1962, 1975) as well as fishes (e.g., Johnson, 1970) endemic to portions of the Austral-Asian seaway region, this is true of no evermannellid or scopelarchid. Of 12 warm-water species (excluding *Evermannella balbo*) occurring in the Indian and Pacific oceans, two species (*Coccorella atlantica* and *Rosenblattichthys hubbsi*), both limited to central water areas in the Indian and Pacific oceans, are apparently excluded from the seaway region. All 10 species occurring in (at least part of) the Austral-Asian seaway are either tropical (n=4: *Coccorella atrata, Rosenblattichthys alatus, Scopelarchoides danae, S. signifer*) or tropical-subtropical (n=6: *Evermannella indica, Odontostomops normalops, Benthalbella infans, Scopelarchus analis, S. guentheri, S. michaelsarsi*) in distribution. These results essentially parallel those of Brinton (1975, pp. 77, 80–141) for euphausiids: of those euphausiid species occurring in more than one ocean basin, tropical (=equatorial) and tropical-subtropical species generally occur in (at least part of) the Austral-Asian seaway region; subtropical (=central) species are largely excluded from the region (exceptions include putative expatriates recorded during the Northeast Monsoon season, see Brinton, 1975, p. 45). None of the three species (*Evermannella megalops, Scopelarchoides climax, Scopelarchus stephensi*) endemic to central water areas in the Pacific has been recorded from the seaway region.

Transition Region Species.—Narrow to rather broad Transition Regions (= Transition Zones) separate or border the three major water-mass regions in the

North Pacific (subarctic vs. "central" vs. equatorial) and in the South Pacific (subantarctic vs. "central" vs. equatorial). These Transition Regions are characterized by intermediate and geographically variable (especially in eastern-boundary-current areas) hydrography (Sverdrup et al., 1942; Brinton, 1962; Johnson & Brinton, 1963; McGowan, 1971, 1977; McGowan & Williams, 1973). As would be expected, the fauna of each Transition Region is also, to a greater or lesser extent, intermediate, with elements representing faunas in each of the bordered water-mass regions but with the presence or absence and abundance of these forms a function of geographic position and advection (see Wickett, 1967). This is nowhere better exemplified than by the "borderland fauna" of the California Current system in the Transition Region off southern California and northern Baja California. Here is encountered a mixed fauna, with elements representing faunas in the Pacific subarctic, central, and equatorial water-mass regions as well as a small, but distinct, endemic component (Lavenberg & Ebeling, 1967; Paxton, 1967; Ebeling et al., 1970, 1971). McGowan (1977, p. 425) has described the resulting "ecotonal" fauna as follows: "ecotones . . . where species which evolved in radically different habitats with very different selection pressures, are mixed together; allochthonous flora, fauna, nutrients and biomass are constantly added through large-scale lateral mixing processes."

Faunally as well as oceanographically it is possible to divide the Transition Region in the North Pacific into two subregions: "oceanic" vs. "eastern boundary current." The oceanic subregion, centered at about 40° N, extends east to west across the entire North Pacific from off Japan to off Oregon and is superimposed on the boundary zone between the central and subarctic water-mass regions (McGowan & Williams, 1973). A boundary between the oceanic and eastern boundary current subregions can be meaningfully drawn to coincide with the boundary between the lower-zone Transitional Domain vs. California Undercurrent Domain as depicted by Alverson et al. (1964, p. 167; based on Dodimead et al., 1963). This places proper emphasis on the importance of poleward intrusion of equatorial water (see Wooster & Reid, 1963, pp. 273–275) in determining faunal composition in the eastern boundary current subregion. It is not, to my knowledge, possible to draw a sharp boundary between oceanic vs. eastern boundary current subregions in the Transition Region of the South Pacific. Nonetheless, there exists ample oceanographic and faunal evidence indicating analogy with the system in the north (e.g., Bussing, 1965; Craddock & Mead, 1970).

Among species treated herein, only the two cold-water scopelarchid species *Benthalbella dentata* and *B. linguidens* occur in the oceanic subregion of the North Pacific Transition Region (see Johnson, 1974c, p. 69). Based on admittedly limited evidence, *B. linguidens* may be restricted in distribution to the oceanic subregion. *Benthalbella dentata* occurs in both the oceanic and eastern boundary current subregions of the Transition Region as well as in (at least) the Alaska gyre area of the Pacific subarctic. Both species are endemic to the North Pacific.

Five warm-water species (table 23) occur in the eastern boundary current subregion of the North Pacific Transition Region: Subtropical (=central) species: none; tropical-subtropical species: *Scopelarchus analis* (fig. 46), *S. guentheri* (fig. 47); eastern equatorial species: *Evermannella ahlstromi* (fig. 30), *Rosenblattichthys volucris* (fig. 42), and *Scopelarchoides nicholsi* (fig. 44). All but *Scopelarchoides nicholsi* find their northernmost distributional limit in the California Current

System between 30° and 35° N. *Scopelarchoides nicholsi* is not known north of the vicinity of Cedros Island (ca. 27° N).

Eight warm-water species (table 23) occur in the Transition Region of the South Pacific. *Evermannella balbo* (fig. 53; 24 Pacific Ocean records) is restricted in the Pacific Ocean (and, presumably, in the Indian Ocean) to the southern Transition Region. In the Pacific *E. balbo* occurs in both the oceanic and eastern boundary current subregions. Likewise occurring in both subregions is the tropical-subtropical species *Scopelarchus guentheri* (fig. 47). Based on its occurrence in the South Atlantic, it seems likely that *Coccorella atlantica* (fig. 24), a central-water species, will be found in both subregions in the South Pacific. *Coccorella atlantica* is not known from east of 130° W in the North Pacific. Known only from the westernmost edge (west of 90° W at ca. 30° S) of the eastern boundary current subregion are the tropical-subtropical species *Benthalbella infans* (fig. 39) and *Scopelarchus analis* (fig. 46) as well as the south central water endemic *Evermannella megalops* (fig. 35). Two eastern equatorial species, *Rosenblattichthys volucris* (fig. 42) and *Scopelarchoides nicholsi* (fig. 44), are known from the eastern boundary current subregion of the South Pacific Transition Region.

Subtropical Species.—Two broadly distributed subtropical species (table 23), *Coccorella atlantica* (fig. 24; 49 Pacific Ocean records) and *Rosenblattichthys hubbsi* (fig. 40; 10 Pacific Ocean records), appear to be essentially restricted to central water areas in the Pacific Ocean. The biantitropical *C. atlantica* occurs throughout central water areas in the North and South Pacific. *Rosenblattichthys hubbsi* is, as far as is known, limited to the North Pacific. *Coccorella atlantica* is replaced by its congener *C. atrata* (fig. 24) in the Pacific Equatorial Water-Mass Region as well as throughout the area of the Austral-Asian seaway. One record of *C. atlantica* from south of Australia suggests the possibility of interchange between the Indian Ocean and South Pacific Ocean populations.

Rosenblattichthys hubbsi is replaced by its congener *R. alatus* in the equatorial Pacific, in the Austral-Asian seaway region, and, based on one (80.1 mm SL) specimen (SIO 72-317, 25° 16.0′ to 24° 57.0′ S, 155° 29.7′ to 06.7′ W, 4–5 August 1972), may also be replaced by *R. alatus* in the central South Pacific. Three species, *Evermannella megalops*, *Scopelarchoides climax*, and *Scopelarchus stephensi*, are endemic to central water areas (either north or south) in the Pacific. Discussion of the distributions of these three species with additional comments on the Pacific central water faunas is deferred to a subsequent section on central-gyral species.

Tropical-Subtropical Species.—Six warm-water species (table 23) are broadly distributed throughout part or all of central, (western) equatorial, and Austral-Asian seaway areas in the Pacific: *Evermannella indica* (fig. 34; 160 Pacific Ocean records), *Odontostomops normalops* (fig. 37; 91 Pacific Ocean records), *Benthalbella infans* (fig. 39; 23 Pacific Ocean records), *Scopelarchus analis* (fig. 46; 133 Pacific Ocean records), and *S. michaelsarsi* (fig. 48; 35 Pacific Ocean records). As is true for a number of widely distributed tropical-subtropical euphausiid species (Brinton, 1975), four of these six species (*E. indica*, *O. normalops*, *B. infans*, *S. michaelsarsi*) are excluded from the eastern Pacific, including both eastern boundary current and eastern equatorial areas. *Scopelarchus analis*, a species all but excluded from any part of the Pacific Equatorial Water-Mass Region, occurs in the Transition Region of the North Pacific in waters off southern California and northern Baja California but is excluded from the eastern tropical Pacific and is

unknown from the Transition Region of the South Pacific. *Scopelarchus guentheri* occurs in the North Pacific Transition Region in waters off southern California and northern Baja California, in the eastern tropical Pacific, and probably throughout the South Pacific Transition Region. If a "generalized track" (fig. 52) is constructed (Croizat et al., 1974) based on the Pacific Ocean distributions of the six tropical-subtropical species listed above, the area enclosed by that track fits well McGowan's (1974, p. 15) depiction of the area occupied by the "warm-water cosmopolite fauna." Discussion of this "fauna" is deferred to the section below on central-gyral species.

Tropical Species.—Seven warm-water species (table 23) are largely restricted to the Pacific Equatorial Water-Mass Region in the Pacific Ocean. Three of these, *Evermannella ahlstromi*, *Rosenblattichthys volucris*, and *Scopelarchoides nicholsi*, are endemic to the eastern Pacific, and discussion of their distributions is deferred to the following section. Four species, none of them endemic to the Pacific, are largely restricted in the Pacific to western and central portions of the Pacific Equatorial Water-Mass Region and/or to the Austral-Asian Seaway region: *Coccorella atrata* (fig. 24; 49 Pacific Ocean records), *Rosenblattichthys alatus* (fig. 40; nine Pacific Ocean records, including the holotype), *Scopelarchoides danae* (fig. 43; 18 Pacific Ocean records), and *S. signifer* (fig. 45; 43 Pacific Ocean records).

The existence of separable assemblages of mesopelagic species within the area of Pacific Equatorial Water is well established (Brinton, 1962, 1975; Ebeling, 1962, 1967; McGowan, 1971, 1974; Barnett, 1975). The sharp contrast in faunal composition between a western + central vs. eastern equatorial assemblage of mesopelagic species is noted by Hartmann & Clarke (1975). Species occurring in abundance in equatorial waters of the western and central Pacific are typically not endemic to the Pacific but occur in the Indian Ocean and (in some cases) the Atlantic as well. The lack of species endemic to central + western areas of the Pacific Equatorial Water-Mass Region led Ebeling (1967) to include this area in his very large (Atlantic, Indian, and Pacific) circumcentral zoogeographic region. Ebeling recognized the eastern equatorial area as a distinct and coordinate primary zoogeographic region. McGowan (1971, 1974, 1977) and his associates (e.g., Barnett, 1975), concerned largely with distributional patterns within the Pacific Ocean basin, recognize the assemblage of species within the western + central area of Pacific Equatorial Water as representing a distinct and separate faunal region, or, using their terminology, "ecosystem," coordinate with other warm-water ecosystems in North and South Pacific central waters as well as in the eastern tropical Pacific. Fleminger & Hulsemann (1973) argue that three main equatorial oceanic zoogeographic regions exist: Atlantic, Indian Ocean and west + central Pacific, and eastern tropical Pacific.

The distribution of *Scopelarchoides danae* is the least well known of any evermannellid or scopelarchid inhabiting the tropical Pacific. Fifteen of the 18 Pacific Ocean records are from areas of the Austral-Asian seaway. Only three records (and three specimens), one from near New Caledonia and two from near the Marquesas, are known from the Pacific Basin east of 130° E. The distribution of the barracudina *Lestrolepis intermedia* (Poey) (see Rofen, 1966a, p. 380) is similar to that of *S. danae* (fig. 43) and, perhaps, particularly so in its Pacific distribution.

Except for one (presumably waif) record from 20° N, 145° W, in the region of Eastern North Pacific Central Water, *Coccorella atrata* is limited, in the western and central Pacific, to the equatorial water-mass area. *Coccorella atrata* is one of

two broadly distributed species (the other is *Scopelarchus guentheri*) to occur in the equatorial eastern Pacific east of 135° W. *Coccorella atrata, Rosenblattichthys alatus,* and *Scopelarchoides signifer* are the only evermannellid or scopelarchid species (table 23) to be limited to the Indian + Pacific oceans. As noted above, it is apparently no coincidence that all three are also largely restricted to equatorial water-mass areas.

The Pacific distributions of *Rosenblattichthys alatus* and *Scopelarchoides signifer* are virtually congruent and differ from that of *Coccorella atrata* in only one possibly significant respect—both *S. signifer* and *R. alatus* are known from central water in the South Pacific; *C. atrata* is not. All central South Pacific records for *R. alatus* (n=1) and *S. signifer* (n=4) are from the vicinity of ca. 24.5° to 25° S, 155° W, near the Tubuai Archipelago. This is at the southeastern edge of an area depicted by Ebeling (1962, p. 146) as exhibiting enhanced (local) productivity related to the presence of island chains. Ebeling (1962, p. 145) states, "In the South Pacific large concentrations of bathypelagic fishes around island chains and submerged ridges reflect the relatively high productivity of these areas." It is possible that future captures will reveal that the distribution of *R. alatus* and *S. signifer* in the central South Pacific is in each case related to this "island effect" and is thus analogous to the above-mentioned apparent association of the distribution of *Scopelarchoides danae* with nearness to continental and insular land masses. South Pacific captures for *Stomias affinis* (Gibbs, 1969), a species whose worldwide distribution is virtually congruent with the composite range of *S. danae* and *S. signifer,* as well as captures of *Astronesthes cyaneus* (Goodyear & Gibbs, 1969) might be cited to support this notion. In the North Pacific, persistent captures of equatorial species near the Hawaiian Islands might be related to elevated productivity around the islands (Clarke, 1973, 1974; Barnett, 1975).

Species Occurring in the Eastern Tropical Pacific.—Three evermannellid and scopelarchid species are endemic to the eastern Pacific: *Evermannella ahlstromi* (fig. 30; 53 records), *Rosenblattichthys volucris* (fig. 42; 106 records), and *Scopelarchoides nicholsi* (fig. 44; 151 records). *Evermannella ahlstromi* is limited to those eastern Pacific areas that are "ecotonal" in the sense of McGowan (1977), areas oceanographically and faunally intermediate between the major eastern Pacific faunal-province centers as indicated by McGowan (1974). Specifically, *E. ahlstromi* has been taken in the North Pacific Transition Region off Baja California, along the regions of transition between Pacific Equatorial Water and the central water masses of the North and South Pacific, and in a constricted zone along the equator from ca. 155° W to near the American mainland. *Evermannella ahlstromi* replaces the nearly circumtropical *E. indica* in the eastern tropical Pacific east of about 135° W, but the two species overlap in distribution and have been taken in the same net haul (five occasions) between 155° and 135° W. The distribution of *Rosenblattichthys volucris* is virtually congruent (fig. 55) with that of *E. ahlstromi,* differing only in that *R. volucris* has been taken further north (numerous records between 30° and 35° N), west (to 161° 52.5′–51.5′ W), and south (Transition Region off Chile).

The distribution of *Scopelarchoides nicholsi* is disjunct, with a northern area extending from ca. 27° N to 09°–05° N and west to or beyond 136° W, and a southern area extending from 06° S to 12°–13° S and west to ca. 89° W (fig. 44). The area of disjunction is roughly centered on the equator, and in the area of disjunction occur *E. ahlstromi* and *R. volucris,* as well as the tropical-subtropical

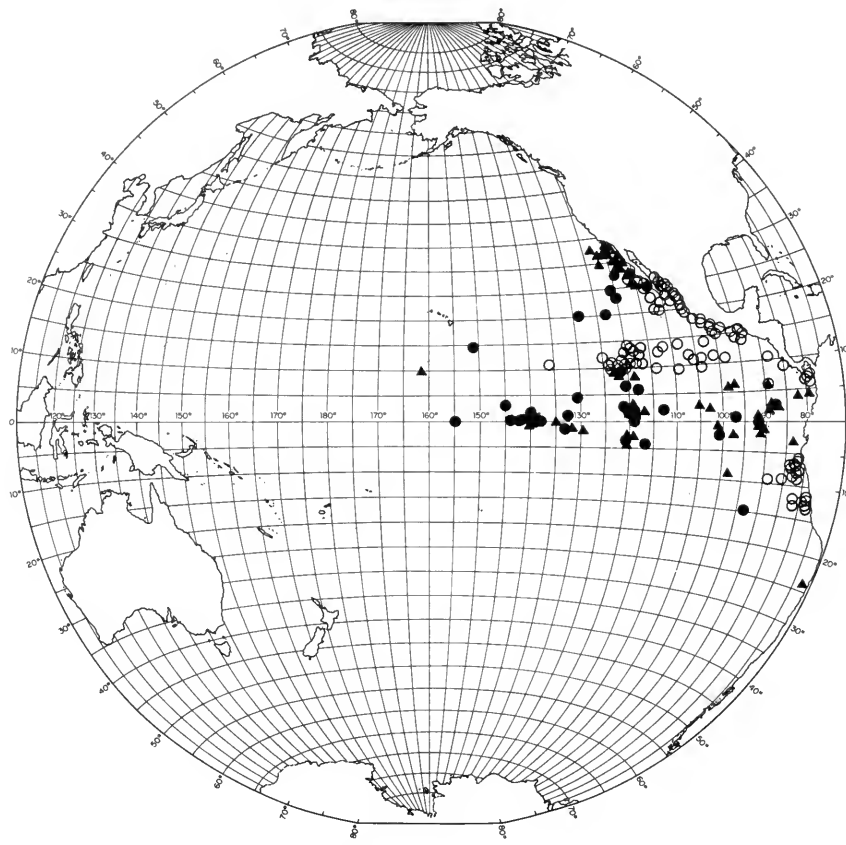


FIG. 55. Distribution of *Evermannella ahlstromi* (solid circles), *Rosenblattichthys volucris* (solid triangles), and *Scopelarchoides nicholsi* (open circles) in the eastern Pacific.

species *Scopelarchus guentheri* and the tropical species *Coccorella atrata* (figs. 24, 47)—the only other scopelarchid and evermannellid, respectively, known from the eastern tropical Pacific. No other evermannellid or scopelarchid species is found within most of the area of occurrence of *S. nicholsi* (Johnson, 1974c; Johnson & Glodek, 1975).

The eastern tropical Pacific (ETP) is a large, roughly wedge-shaped area, for the most part bounded by the North and South Equatorial Currents (see Wyrtki, 1965). Circulation in this area is largely zonal and dominated by the equatorial currents, the North Equatorial Countercurrent, and the Equatorial Undercurrent. The ETP is unique hydrographically and is largely independent of the major subtropical anticyclonic gyrals of the North and South Pacific.

The ETP is characterized by a very distinctive assemblage of mesopelagic species, both invertebrates and fishes, with many endemic to this area (e.g., Bertelsen, 1951; Bieri, 1959; Morrow, 1961; Brinton, 1962; Ebeling, 1962, 1967; Barnett & Gibbs, 1968; Gibbs, 1969; McGowan, 1971, 1974; Wormuth, 1971; Johnson, 1974c; Johnson & Glodek, 1975; Judkins, 1978). There is increasing

evidence that in many cases species occurring in, but not endemic to, the ETP are represented in the ETP by distinct and separable populations (e.g., Brinton, 1962; Ebeling & Weed, 1963; Johnson & Cohen, 1974; Johnson & Barnett, 1975).

The distinctiveness of the ETP fauna has been recognized by numerous authors, including Ebeling (1962, 1967), who classed the ETP as one of four primary zoogeographic regions in the warm-water ocean, and more recently by McGowan (1971, 1974, 1977), who recognized the ETP as one of eight pelagic "ecosystems" in the Pacific. Ahlstrom (1972) provides a review of significant papers dealing with adult oceanic fishes occurring in the ETP and has himself (e.g., Ahlstrom, 1971, 1972) made major contributions to our knowledge of the distribution and abundance of species represented in the ichthyoplankton over this broad area. More recent papers dealing with the oceanic fish fauna of the ETP include those by Robison (1972) and Brewer (1973), as well as numerous works dealing with specific groups of fishes.

A number of prominent features of the oceanic environment of the ETP have no doubt contributed to the distinctness of its fauna. These include the zonal, seasonally variable, and (below the shallow thermocline) relatively sluggish circulation; intense vertical and horizontal gradients in temperature, dissolved oxygen, and other features; the subsurface, *in situ* formation of Pacific Equatorial Water (resulting from the mixing of subtropical subsurface water spreading from the Undercurrent with Intermediate Water of Antarctic or North Pacific Origin); the permanent shallow thermocline and consequently shallow mixed layer; widespread regional upwelling; and important divergence systems at the equator and at the boundary between the North Equatorial Current and the North Equatorial Countercurrent (see Wooster & Cromwell, 1958; Wyrtki, 1966, 1967; Tsuchiya, 1968, 1974). Associated with these features are relatively large concentrations of inorganic nutrients in near-surface waters and very high values of biological productivity and zooplankton standing stocks over most of the ETP (Holmes et al., 1957; Brandhorst, 1958; Reid, 1962; Blackburn et al., 1970; Koblentz-Mishke et al., 1970; Cushing, 1971). Important physical, chemical, and biological features of the ETP as determined by the multivessel *Eastropac* expeditions (1967, 1968) are depicted in the multivolume *Eastropac Atlases* (Love, 1971, 1972a, 1972b, 1973).

A very prominent feature of the ETP midwater environment is the development of a markedly hypoxic, thick, and widespread oxygen minimum layer, herein defined as waters containing less than 1.0 ml/L of dissolved oxygen. The extent of this layer has been charted by Brandhorst (1959), Austin (1960), and Wyrtki (1966, 1967), among others. The layer is more than 1,200 m thick off Mexico and more than 800 m thick off Peru (fig. 56). Values less than 0.1 ml/L are present vertically through several hundred meters in the core of the oxygen minimum, and the concentration of dissolved oxygen may fall below the limits of detectability (less than 0.05 ml/L), but no hydrogen sulfide has been detected in midwaters of the ETP.

The oxygen minimum extends into the upper 100 m over broad areas of the ETP (fig. 56). The oxygen minimum extends at least as far west as 170° E (Tsuchiya, 1968), and core values of less than 0.1 ml/L extend at least as far west as 172° W (Austin, 1960), although beyond 104° W the oxygen minimum layer is markedly restricted latitudinally (see Austin, 1960; Tsuchiya, 1968). The oxygen minimum layer in the ETP is the largest, markedly hypoxic volume of water

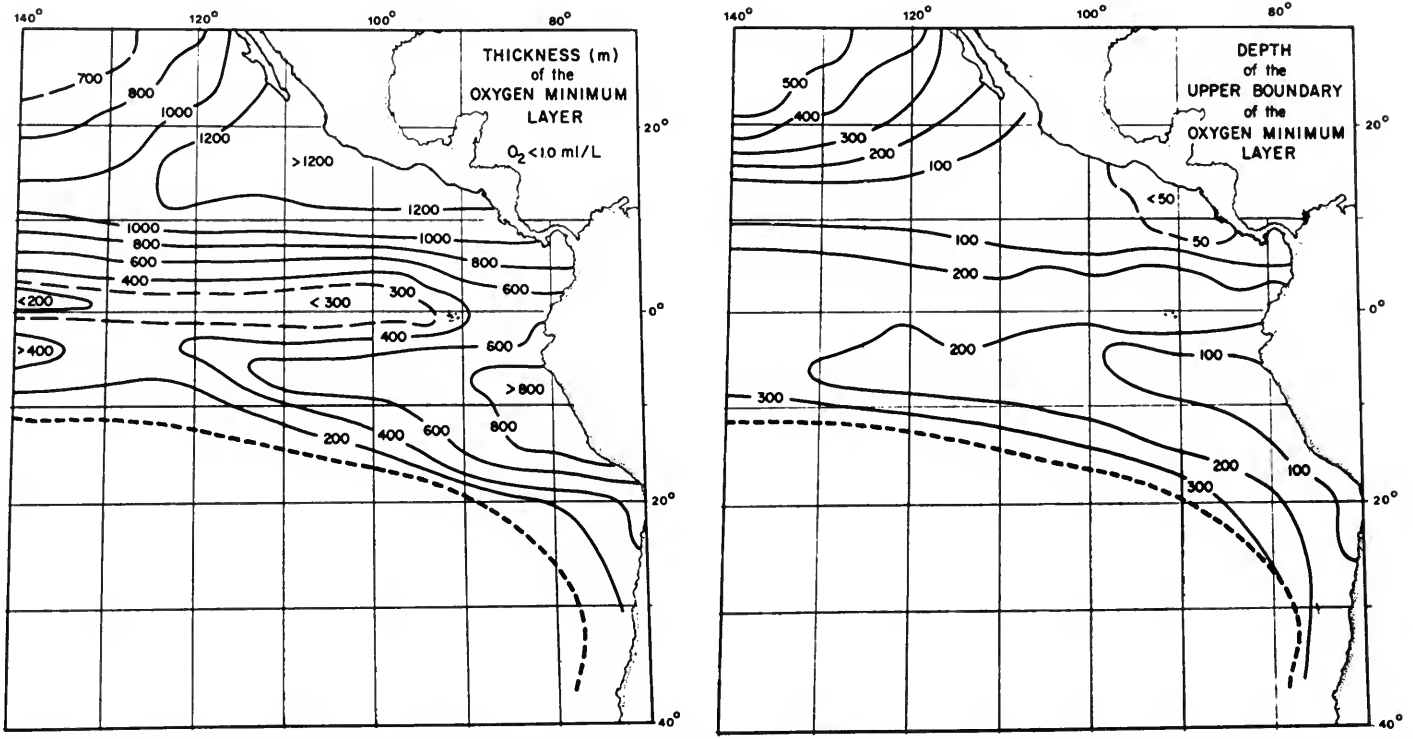


FIG. 56. Extent of the oxygen minimum layer in the eastern tropical Pacific. **Left,** Thickness of the oxygen minimum layer charted for those areas in which dissolved oxygen content in the oxygen minimum layer is less than 1.00 ml/L (from Wyrtki, 1966). **Right,** Depth of the upper boundary of the oxygen minimum layer as given by the surface where dissolved oxygen = 1.00 ml/L (from Wyrtki, 1967).

found in the open waters of the ocean. Richards (1957), Wyrtki (1962), and Packard et al. (1977) provide reviews of the physical and biological processes resulting in the formation of marked oxygen minima, and Wyrtki (1966, 1967) provides detailed information on the origin and extent of the oxygen minimum in the ETP. Aspects of the oceanography and biology of the ETP low-oxygen area may be compared with other low-oxygen areas in the world oceans through examination of papers by Vinogradov & Voronina, 1962; Gibbs & Hurwitz, 1967; Kinzer, 1969; Wilson, 1972; Baird et al., 1973, 1974, 1975; Pugh, 1973; Baird & Wilson, 1977; and Ingham et al., 1977, among others.

Species endemic to the ETP typically exhibit more or less "wedge-shaped" distributions as shown for the myctophids *Gonichthys tenuiculus* and *Diogenichthys laternatus* (fig. 57), with broad to very broad latitudinal ranges in the eastern portion of the ETP which taper rapidly to the west. The broadness of the eastern portion of the distribution of such species is typically due to poleward range extensions associated with subsurface intrusions of Pacific Equatorial Water into the Transition Regions of the North and South Pacific (Reid et al., 1958; Brinton, 1962, 1975; Ebeling, 1962, 1967; Bussing, 1965; Lavenberg & Ebeling, 1967; Paxton, 1967; Craddock & Mead, 1970; Ebeling et al., 1970, 1971; Fleminger & Hulsemann, 1973; Johnson, 1974c; McGowan, 1974, 1977; Johnson & Glodek, 1975; Wisner, 1976; Judkins, 1978).

The boundary between the western + central (see previous section) vs. ETP equatorial species assemblages in the main appears to reflect two prominent oceanographic features of the ETP: (1) the extent of the main oxygen minimum areas, from which western species are in nearly all cases excluded, and (2) the zonal character of the circulation. As Brinton (1962) has shown, euphausiid species occurring in the western and central Equatorial Pacific vary in the extent to which they enter the ETP area, some not occurring to the east of ca. 140° W, others extending to or nearly to 90° W, and still others extending to or nearly to the American mainland. This may be related to differing abilities to respire in poorly oxygenated waters (Teal & Carey, 1967; Childress, 1968, 1971) or to competition with ETP species, or both. This contrast has also been observed for midwater fish species. For example, six species (*Evermannella indica*, fig. 34; *Odontostomops normalops*, fig. 37; *Benthalbella infans*, fig. 39; *Rosenblattichthys alatus*, fig. 40; *Scopelarchoides signifer*, fig. 45; *Scopelarchus michaelsarsi*, fig. 48) that are widespread in equatorial waters of the Indian Ocean and western + central Pacific apparently do not occur in the ETP east of ca. 135° W. Other species, e.g., *Scopelarchus guentheri* (fig. 47) and *Coccorella atrata* (fig. 24), extend much farther into the ETP.

The eastward extension of western species and the westward extension of ETP species seem to follow nearly zonal lines that must be associated with the equatorial currents and countercurrents. The penetration of the ETP east of about 140° W by western species is largely within the zone of the Equatorial Undercurrent and the North Equatorial Countercurrent. The westward extension of ETP species is largely associated with the North Equatorial Current and, to a lesser extent, with the South Equatorial Current. This is suggested by the results (fig. 58) of a study of *Vinciguerria nimbaria*, a nearly circumtropical species that is largely replaced by its closely related congener, *V. lucetia*, in the ETP (Johnson & Feltes, in prep.). Brinton (1962) presents a number of similar examples for euphausiid species—the most striking of these is his (Brinton, 1962, pp. 178–190) analysis of the distribution of the "forms" of *Stylocheiron affine*.

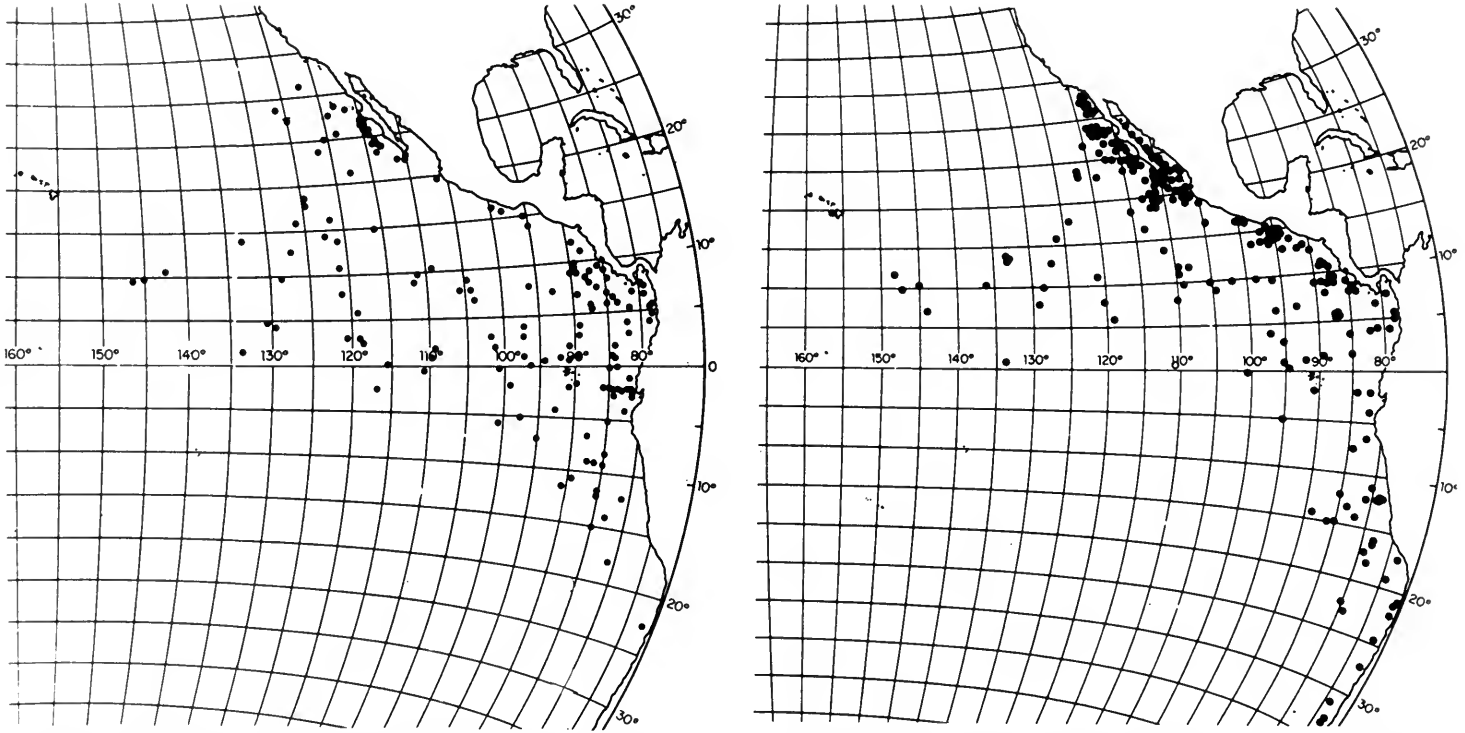


FIG. 57. Distribution of two myctophid species endemic to the eastern tropical Pacific (both from Wisner, 1976). **Left,** *Gonichthys tenuiculus;* **right,** *Diogenichthys laternatus.*

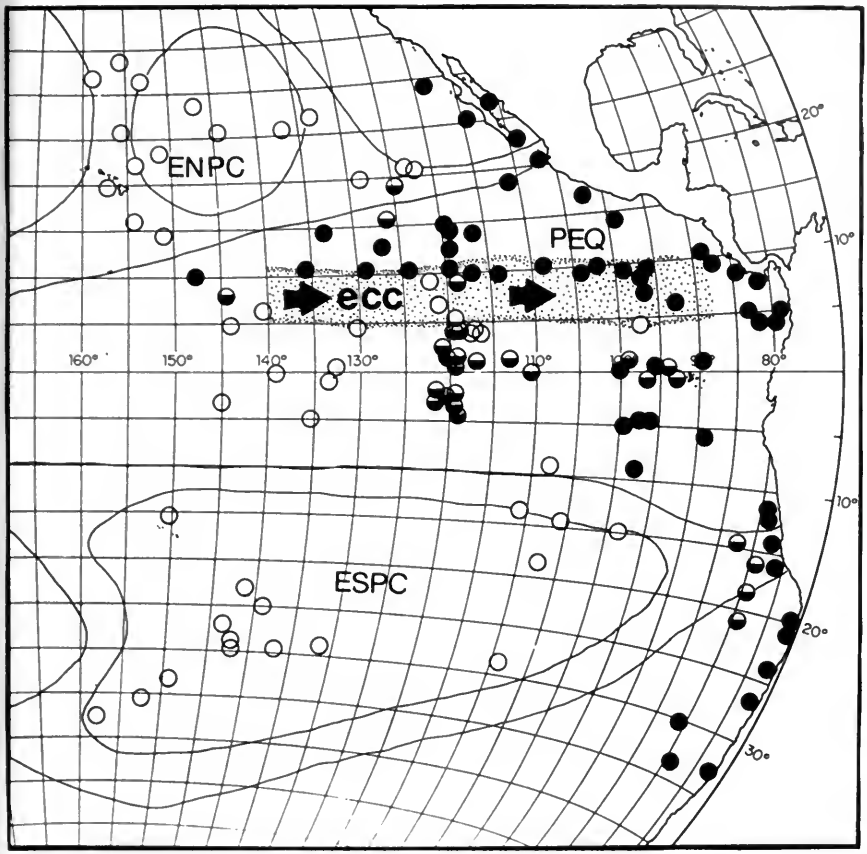


FIG. 58. Distribution of two species of *Vinciguerria* in the eastern tropical Pacific. SYMBOLS: ○ = *V. nimbaria;* ● = *V. lucetia;* ◒ = stations at which both species were taken in the same net haul. (Data from Johnson & Feltes, in prep.) Areas transitional between water-mass regions indicated as bands: ENPC = Eastern North Pacific Central; ESPC = Eastern South Pacific Central; PEQ = Pacific Equatorial (after Sverdrup et al., 1942). Zone of North Equatorial Countercurrent (ecc) in October (after Wyrtki, 1966) shown by stippled band for area between 140° W to ca. 90° W.

The composite distribution of the three evermannellid and scopelarchid species endemic to the ETP (fig. 55) coincides with the "wedge-shaped" distribution pattern exhibited by a number of ETP endemics (cf., figs. 57, 58). It differs strikingly in the division of the ETP, apparently without overlap, into two disjunct areas occupied by *Scopelarchoides nicholsi* vs. areas peripheral to and dividing the range of *S. nicholsi,* these areas occupied by *Evermannella ahlstromi* and *Rosenblattichthys volucris.* Examination of physical, chemical, and biological features of the ETP led Johnson (1974c) and Johnson & Glodek (1975) to conclude that the distributions of these three species correlate strongly (either positively or negatively) with the distribution of the core areas of the oxygen minimum. The basis for this conclusion can be shown by plotting the distributions of these three species against charts depicting the areas of extent of the main ETP oxygen

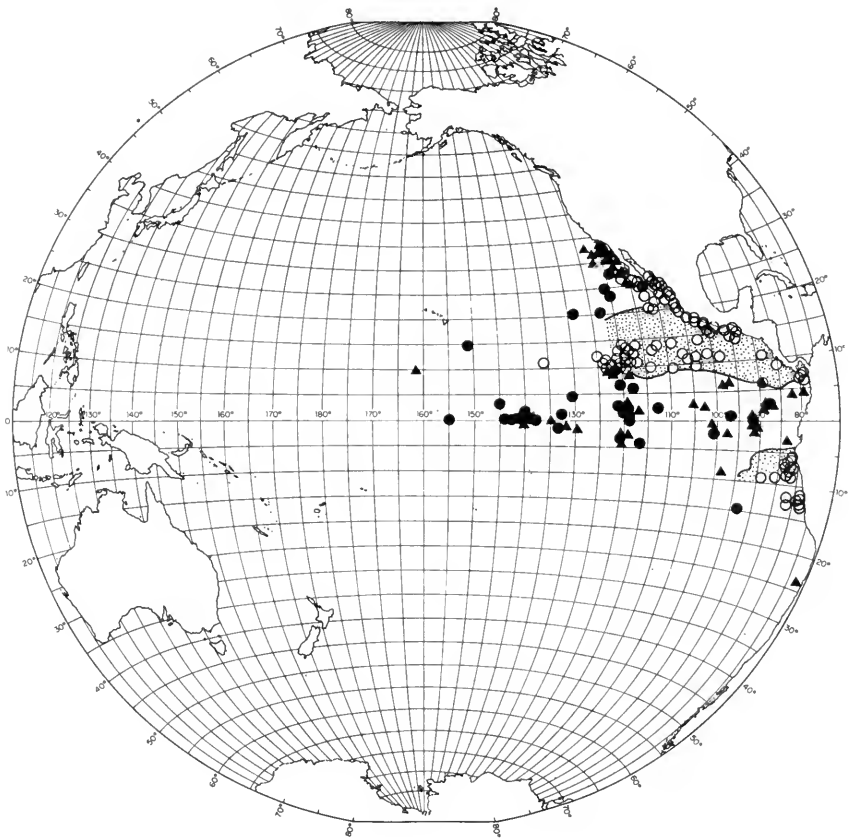


FIG. 59. Distribution of *Evermannella ahlstromi* (solid circles), *Rosenblattichthys volucris* (solid triangles), and *Scopelarchoides nicholsi* (open circles) relative to those areas delineated by Brandhorst (1959) as showing the greatest development of an oxygen minimum layer in the ETP (stippled areas).

minimum areas prepared by Brandhorst (1959; fig. 59), Austin (1960; fig. 60), and Wyrtki (1967; fig. 61). The distributions of these three midwater species, *S. nicholsi* within the main low-oxygen areas, *E. ahlstromi* and *R. volucris* on the periphery of these areas and most strikingly in the equatorial zone of disjunction, strongly suggested the correlation of distribution with subsurface oxygen concentration. No other factor known to be causally related to patterns of midwater distribution, not temperature, not biological productivity, not circulation, clearly divides the ETP in a pattern coincident with the distribution pattern exhibited by these three species.

Publication of the *Eastropac Atlases* (Love, 1971, 1972a, 1972b, 1973) allows more detailed examination of the main features of the ETP oxygen minimum and comparison of these features with the distributions of ETP evermannellids and scopelarchids. I have prepared a series of charts (figs. 62–67) based on the *Eastropac Atlases*, showing the vertical distribution of dissolved oxygen in the upper 1,000 m along six north to south transects at 126° W, 119° W, 112° W, 98°

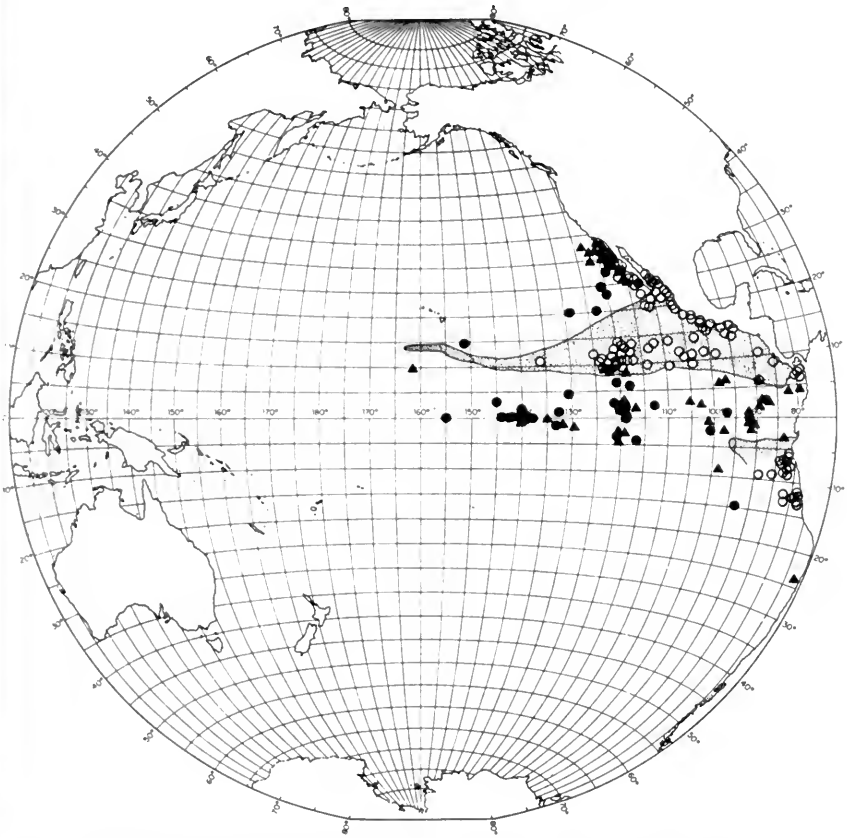


FIG. 60. Distribution of *Evermannella ahlstromi* (solid circles), *Rosenblattichthys volucris* (solid triangles), and *Scopelarchoides nicholsi* (open circles) relative to those areas in the ETP indicated by Austin (1960) as showing the greatest development of an oxygen minimum layer (stippled areas).

W, 85° W, and 82° W. Only three isopleths are shown: 2.00 ml/L, 1.00 ml/L, and 0.25 ml/L. The main features visible on the first five sections are: (1) a narrow but prominent troughing of oxygen isopleths centered at the equator—the result of extensive vertical mixing in the upper 300 m associated with the equatorial divergence and Equatorial Undercurrent; (2) a prominent troughing of oxygen isopleths centered at 04° to 07° N and related to the convergence system at the southern boundary of the countercurrent; and (3) a coincident and marked ascent and descent of the 1.00 ml/L isopleth between 05° and 10° N; this feature is indicated by an arrow on the charts.

Charts prepared by Tsuchiya (1968) and Wyrtki (1967) show two main areas of the oxygen minimum in the ETP, one to the north, the other to the south of the equator (fig. 61). Low-oxygen water (less than 0.5 ml/L) in the South Pacific extends to at least 142° W between 02° and 04° S. The main oxygen minimum of the equatorial South Pacific is visible on all *Eastropac* charts (figs. 62–67) but is most evident in the transects at 85° W and 82° W.

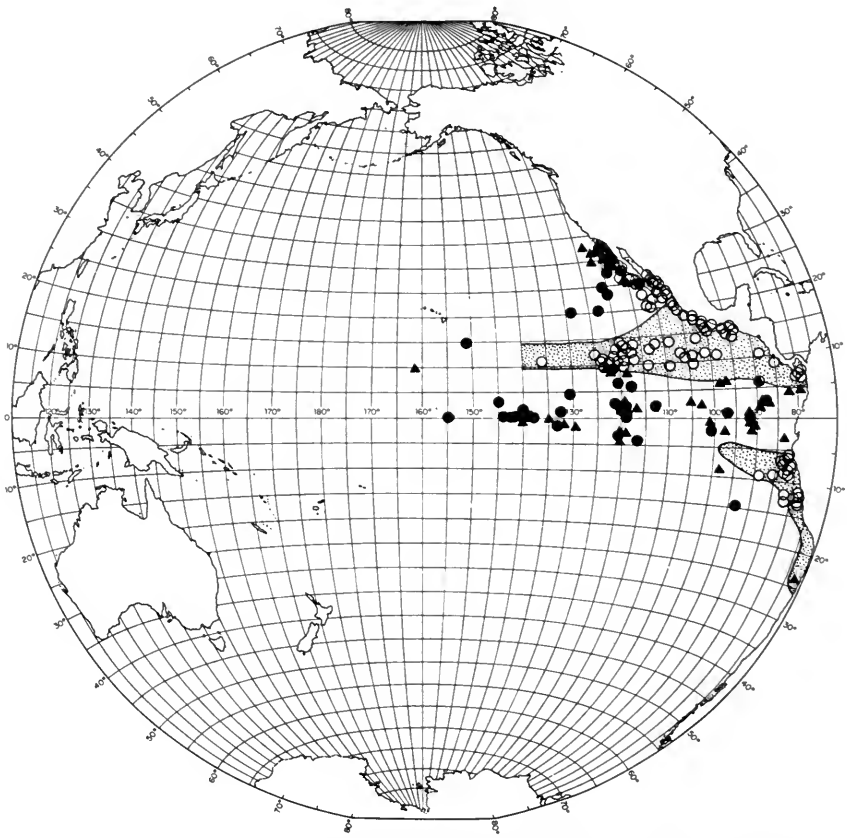


FIG. 61. Distribution of *Evermannella ahlstromi* (solid circles), *Rosenblattichthys volucris* (solid triangles), and *Scopelarchoides nicholsi* (open circles) relative to those areas of the ETP in which the 1.00-ml/L dissolved oxygen isopleth lies at or shallower than 100 m (dissolved oxygen plot from Wyrtki, 1967).

Examination of the *Eastropac* charts shows that the two main areas of the oxygen minimum are roughly indexed by the depth of the 1.00 ml/L isopleth. Wyrtki (1967) used the depth of this isopleth to show the horizontal extent of the main ETP low-oxygen areas (fig. 56). It appears that the depth of this isopleth serves as a rough boundary marker between the distribution of *Scopelarchoides nicholsi* vs. the distributions of *Evermannella ahlstromi* and *Rosenblattichthys volucris* (fig. 61).

Despite marked seasonal variation in the position, width, and strength of the North Equatorial Countercurrent (Wyrtki, 1965, 1966, 1967; Tsuchiya, 1974), the location of the southern boundary of the main northern oxygen minimum area appears to be relatively stable. This is shown by charts (from the *Eastropac Atlases*) of the vertical distribution of the 1.00 ml/L isopleth over one full year, shown for 119° W (fig. 68) and for 98° W (fig. 69). Data for the months shown (especially February to April vs. August to October) should represent yearly extremes.

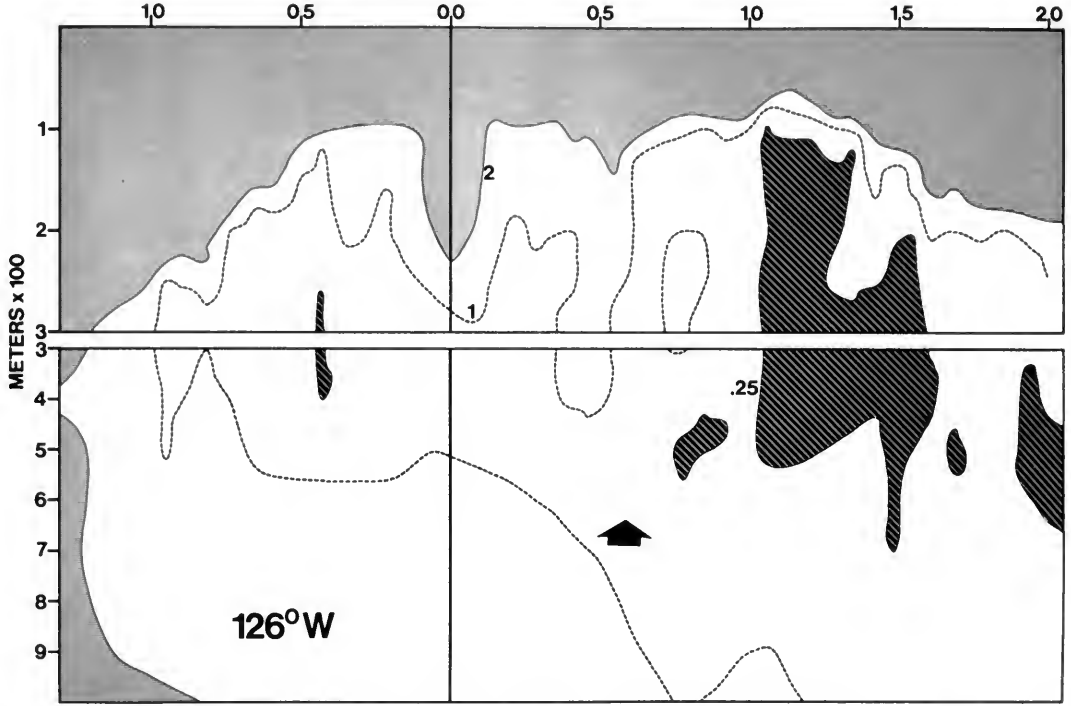


FIG. 62. Vertical distribution of dissolved oxygen (ml/L) along 126° W, 9 February to 2 March 1967. Only the 0.25-, 1.00-, and 2.00-ml/L isopleths are plotted (simplified from Love, 1972b, fig. 11-O_2-v5). Horizontal axis (figs. 62–69) indicates distance (degrees of latitude) north or south of the equator (vertical line labeled "00").

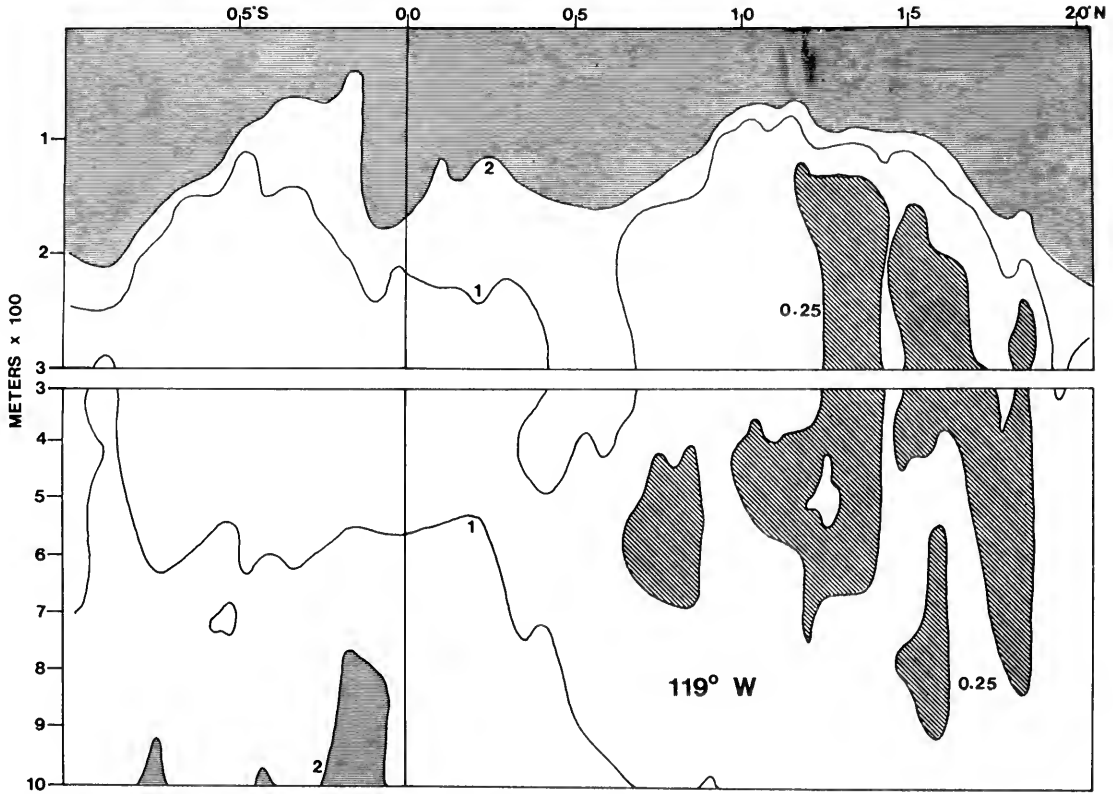


FIG. 63. Vertical distribution of dissolved oxygen (ml/L) along 119° W, 7–21 August 1967. Only the 0.25-, 1.00-, and 2.00-ml/L isopleths are plotted (simplified from Love, 1972b, fig. 45-O_2-v1).

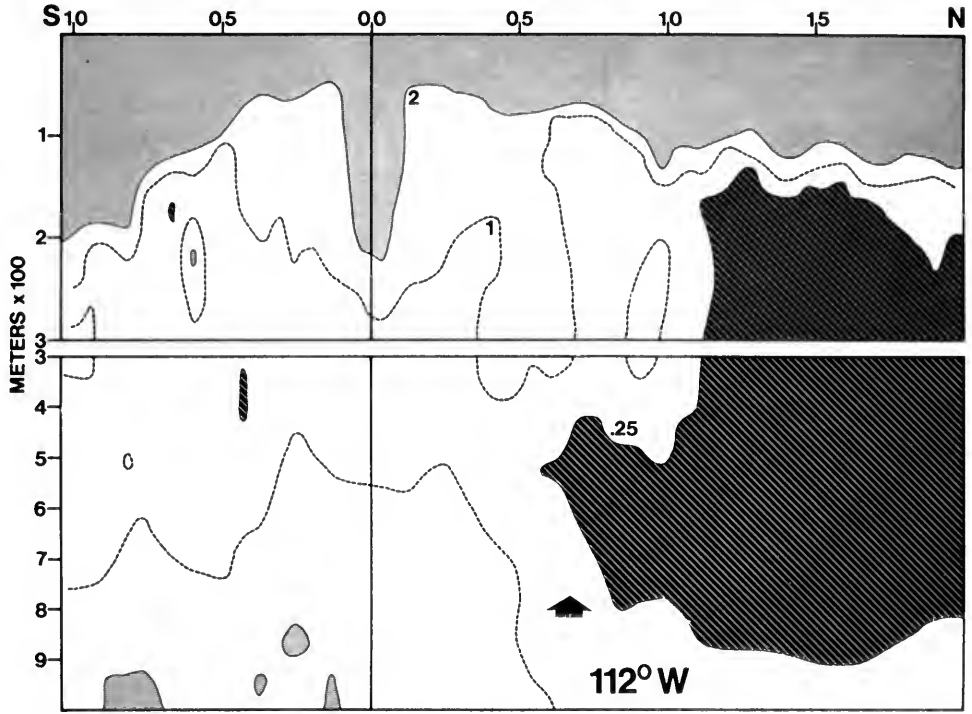


FIG. 64. Vertical distribution of dissolved oxygen along 112° W, 9–21 March 1967. Only the 0.25-, 1.00-, and 2.00-ml/L isopleths are plotted (simplified from Love, 1972a, fig. 12-O_2-v6).

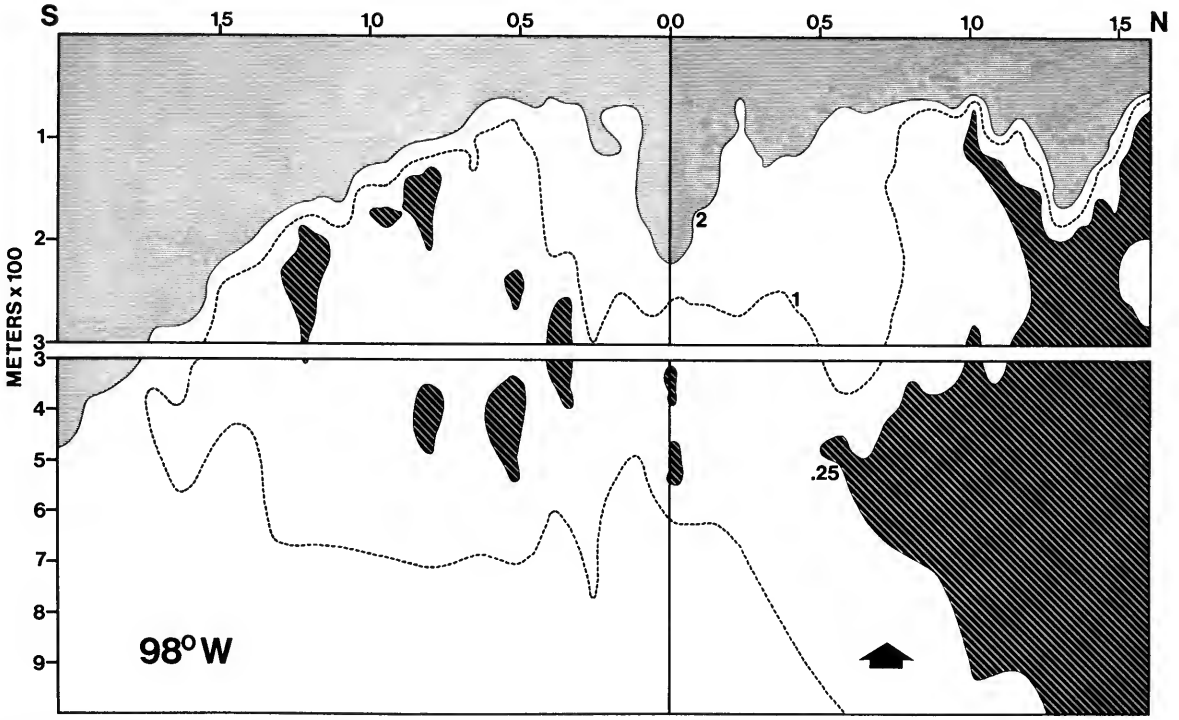


FIG. 65. Vertical distribution of dissolved oxygen (ml/L) along 98° W, 23 February to 8 March 1967. Only the 0.25-, 1.00-, and 2.00-ml/L isopleths are plotted (simplified from Love, 1972a, fig. 13-O_2-v4).

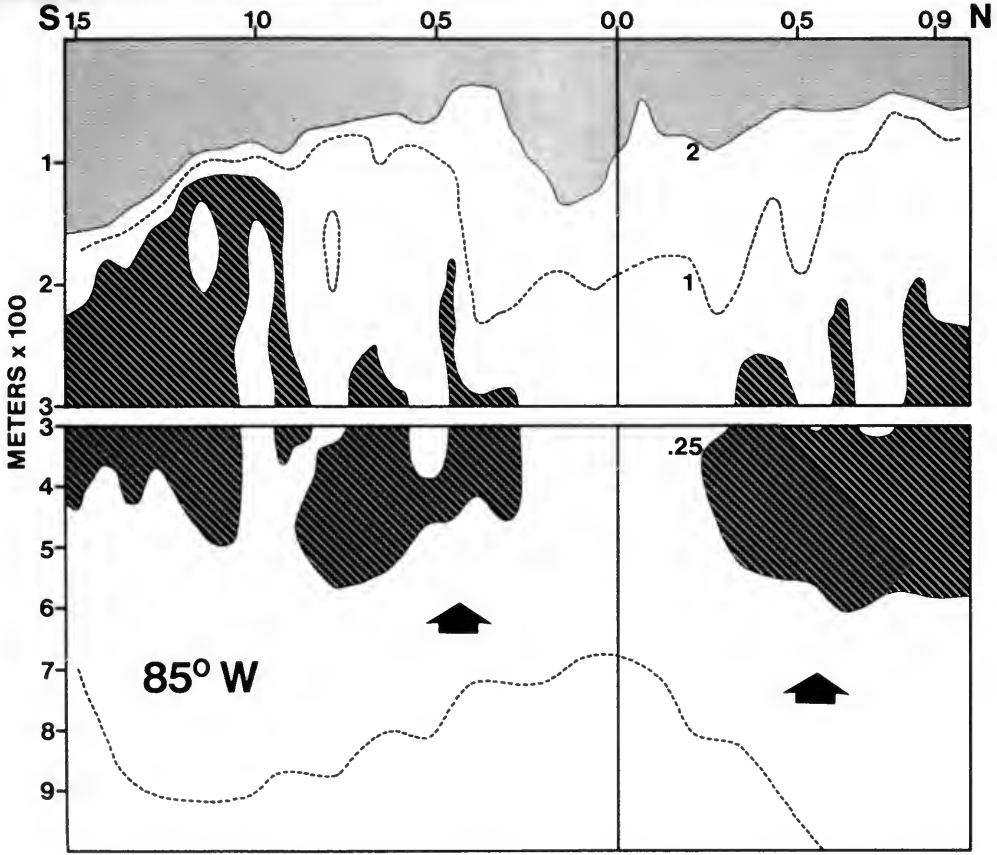


FIG. 66. Vertical distribution of dissolved oxygen (ml/L) along 85° W, 19–28 August 1967. Only the 0.25-, 1.00-, and 2.00-ml/L isopleths are plotted (simplified from Love, 1972b, fig. 47-O_2-v8).

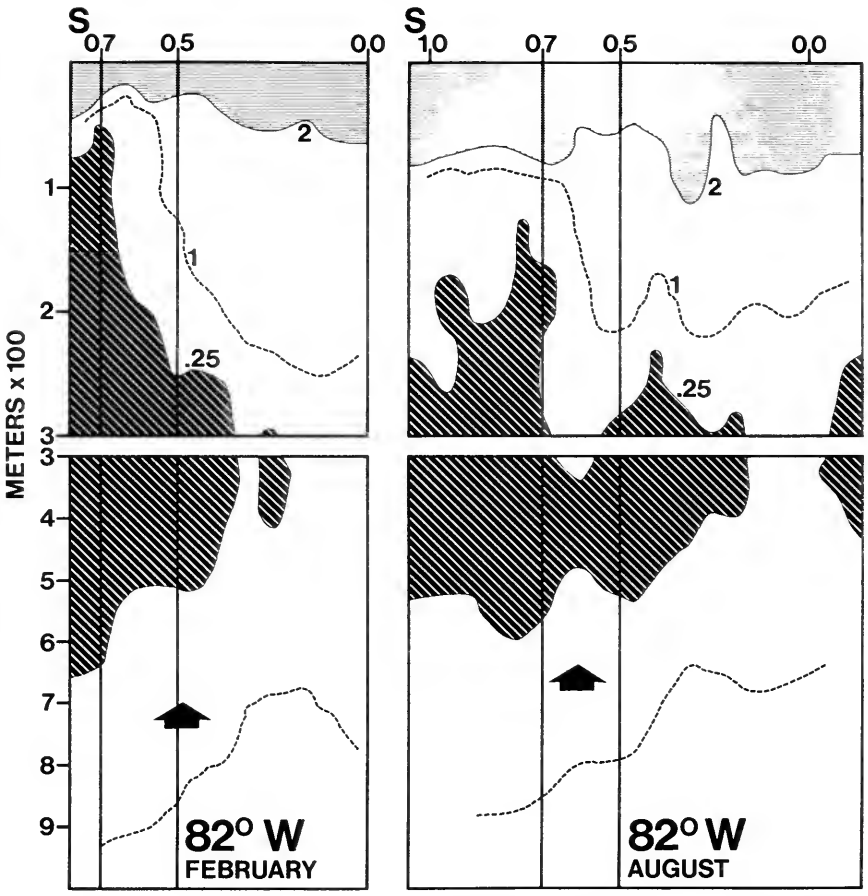


FIG. 67. Vertical distribution of dissolved oxygen (ml/L) along 82° W, 9–11 February 1967 (left) and 6–12 August 1967 (right). Only the 0.25-, 1.00-, and 2.00-ml/L isopleths are plotted (simplified from Love, 1972a, fig. 14-O_2-v10; and Love, 1972b, fig. 47-O_2-v4).

Coincident with this southern boundary of the main northern oxygen minimum, there is an apparent distributional boundary between ETP evermannellid and scopelarchid species at ca. 07° to 10° N between ca. 140° W and the American mainland. To the north of this boundary, in the northern core of low-oxygen water, occurs *S. nicholsi*. To the south, in the zone of the North Equatorial Countercurrent and along the equator, occur the ETP-endemics, *E. ahlstromi* and *R. volucris*, as well as the more broadly distributed *C. atrata* and *S. guentheri*. The boundary, as suggested by available distributional records, is very sharp, as indicated by the north-south distribution of captures of these five species in the vicinity of 120° W (fig. 70). The records presented, based largely on material taken during *Eastropac* cruises, also suggest that the boundary is seasonally stable in that the specimens were taken throughout the year.

Based on data presented by Brinton (1962, 1975), McGowan (1971), Hartmann & Clarke (1975), Wisner (1976), Johnson & Feltes (in prep.), and in the present

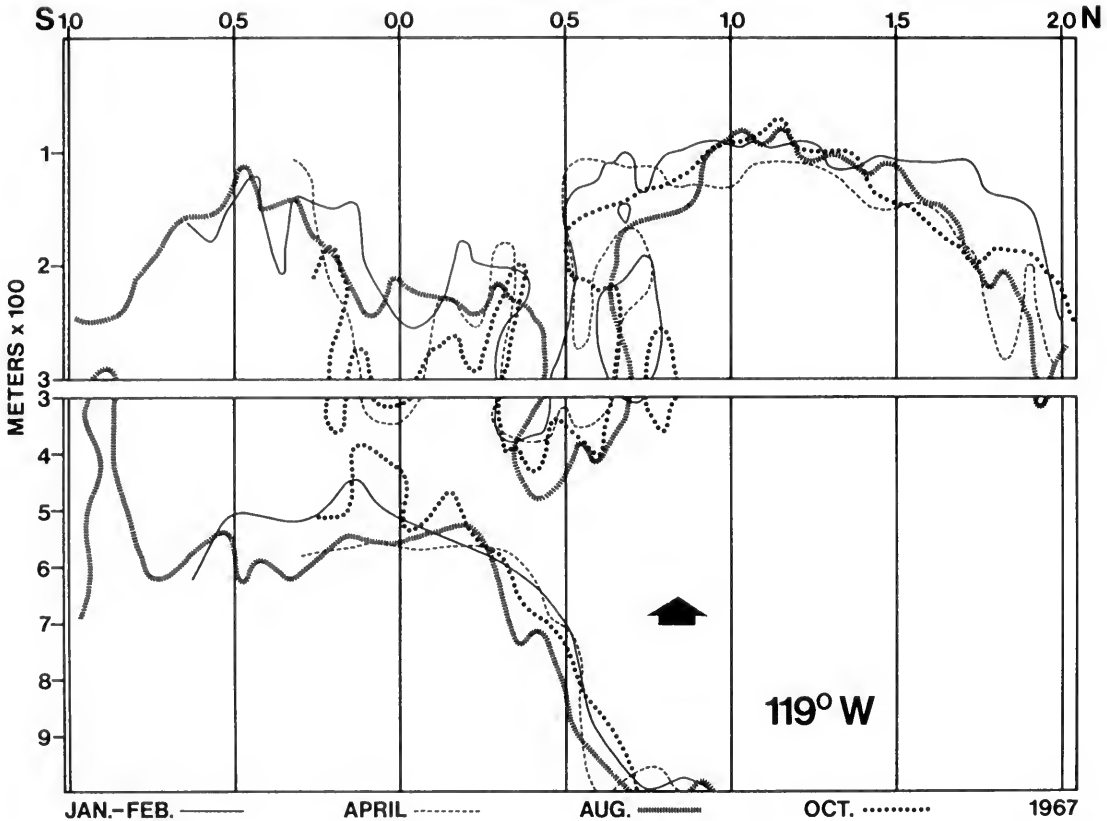


FIG. 68. Vertical distribution of dissolved oxygen (ml/L) in the vicinity of 119° W, 28 January to 9 February 1967 (119° W); 13–21 April 1967 (119° 20′ W); 7–21 August 1967 (119° W); 20–29 October 1967 (119° 10′ W). Only the 1.00-ml/L isopleth is plotted (simplified from Love, 1972a, fig. 11-O_2-v1; Love, 1971, fig. 20-O_2-v1; Love, 1972b, fig. 45-O_2-v1; Love, 1973, fig. 50-O_2-v1).

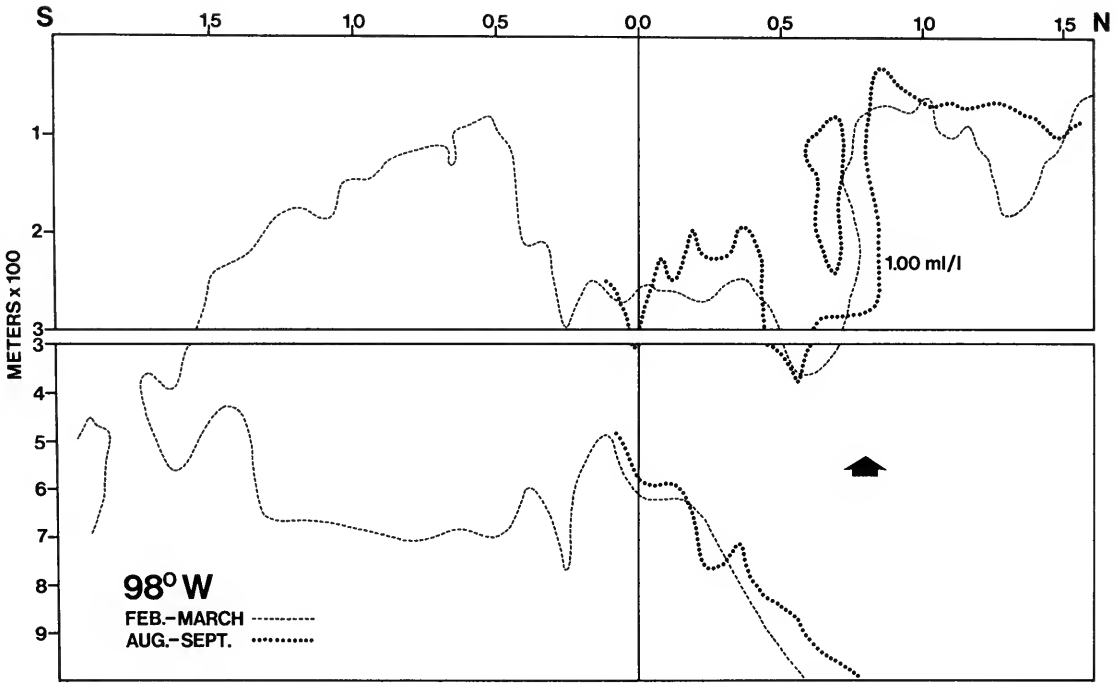


FIG. 69. Vertical distribution of dissolved oxygen (ml/L) along 98° W, 23 February to 8 March 1967 and 31 August to 6 September 1967. Only the 1.00-ml/L isopleth is plotted (simplified from Love, 1972a, fig. 13-O_2-v4; Love, 1972b, fig. 46-O_2-v3).

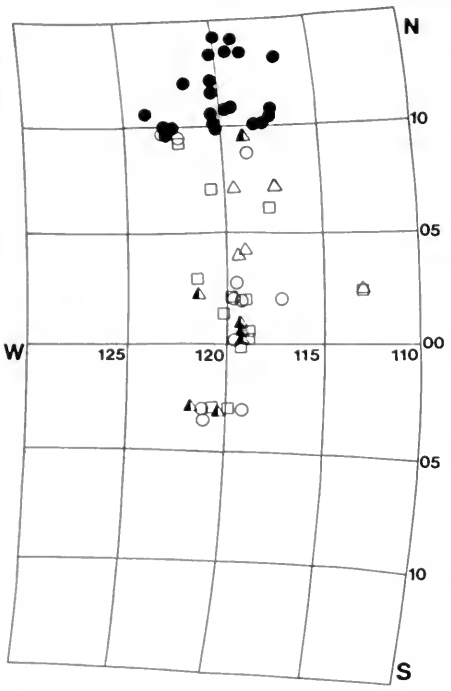


FIG. 70. Distribution of five species of evermannellids and scopelarchids in the vicinity of 15° S to 15° N, ca. 120° W. ● = *Scopelarchoides nicholsi*; △ = *Coccorella atrata*; □ = *Evermannella ahlstromi*; ○ = *Rosenblattichthys volucris*; ◭ = *Scopelarchus guentheri*.

work, it appears that this boundary separates two quite distinctive assemblages. I predict that the assemblage north of the boundary will be found to be mainly (particularly in terms of abundance of individuals) comprised of species endemic to the ETP and associated with the ETP main low-oxygen areas. The assemblage south of the boundary probably contains a much more heterogeneous fauna, consisting of a mixture of species occurring widely in the central + western equatorial Pacific, species limited to the ETP but largely or entirely excluded from the main low-oxygen areas, and species limited to and widespread in the ETP. Predicted ecological properties of the assemblage associated with low-oxygen water are those listed by McGowan (1977), applying to "ecosystem" assemblages, centered largely around greater "predictability" (both geographically and temporally) when compared with "ecotonal" assemblages. Relevant to the two assemblages discussed here is the prediction that the assemblage north of the boundary should, relative to the assemblage south of the boundary, exhibit less site-to-site variability with respect to diversity, rank-abundance of species, length of the species list, and other community parameters. The samples do not exist to permit testing of these predictions.

I believe that the boundary and the patterns of distribution exhibited in the ETP by evermannellid and scopelarchid species are intimately and causally related to the subsurface distribution of dissolved oxygen. This interpretation is supported by: (1) the apparent seasonal stability of the boundary (as suggested by data collected along ca. 120° W) despite marked seasonal shifts in the strength of the North Equatorial Countercurrent; (2) the close correspondence between

the distributions of three ETP endemics and the geographic extent of the main oxygen minimum areas in the ETP, *S. nicholsi* within the main low-oxygen areas, *E. ahlstromi* and *R. volucris* in areas peripheral to or dividing the main low-oxygen areas; and (3) the lack of correspondence between the distribution of these species and the ETP-distribution of any other factor, physical or biological, known to be causally related to observed patterns of distribution among mid-water organisms.

Supporting this interpretation is the fact that *Scopelarchoides nicholsi* exhibits an apparent morphological correlate of its distribution in oxygen-poor waters of the ETP. The gill filaments of this species are the longest of any scopelarchid, projecting beyond the gill covers and overlapping the pectoral-fin base. This remarkable extension of the gill filaments beyond the gill covers is unique to *S. nicholsi* among scopelarchids (Johnson, 1974c). This gill filament prolongation and presumably enhancement of gill surface area surely reflects adaptation to low oxygen concentrations in the environment of this species.

Ebeling & Weed (1963) have shown that eastern Pacific representatives of two broadly distributed melamphaid species, *Scopelogadus mizolepis* and *Poromitra megalops*, have notably more gill surface area than specimens from elsewhere. They relate this to the marked ETP oxygen minimum layer. The ETP searsiid species characteristically exhibit longer gill filaments than western equatorial species (R. H. Rosenblatt, pers. comm.). A similar trend has been reported for eastern Pacific species of *Cyclothone* (Dewitt, 1972; Kobayashi, 1973). These results parallel those cited above for species occurring in the low-oxygen area of the northern Indian Ocean. A partial review of the respiratory physiology of fishes occurring in ETP low-oxygen areas is provided by Douglas et al. (1976) (see also Teal & Carey, 1967; Childress, 1968, 1971).

The ETP fauna is characterized by a large proportion of endemic species. With respect to the origin(s) of this fauna, we can only surmise with Brinton (1975) that these origins are related to ". . . contraction and fragmentation of once continuous ranges across the [tropics] . . . ." The existence of closely related or virtually indistinguishable species pairs may be cited as evidence for either trans-Pacific (e.g., Ebeling, 1962; Ebeling & Weed, 1963; Brinton, 1975; Judkins, 1978) or transisthmian (e.g., Crane, 1966; Gibbs, 1969; Goodyear, 1970) vicariant and/or dispersal events contributing to ETP faunal history. A fundamental problem is that we know very little about phylogenetic relationships among mesopelagics at the species level, and this is true for ETP species. Without such knowledge, further discussion could only be speculation.

The Pacific Central-Gyral Species.—Three evermannellid and scopelarchid species are endemic to central water-mass areas in the North or South Pacific: *Evermannella megalops* (fig. 35; 13 records), *Scopelarchoides climax* (eight records), and *Scopelarchus stephensi* (fig. 48; 13 records). Two species, *Coccorella atlantica* (fig. 24) and *Rosenblattichthys hubbsi* (fig. 40), are essentially limited in the Pacific, as elsewhere, to central water areas.

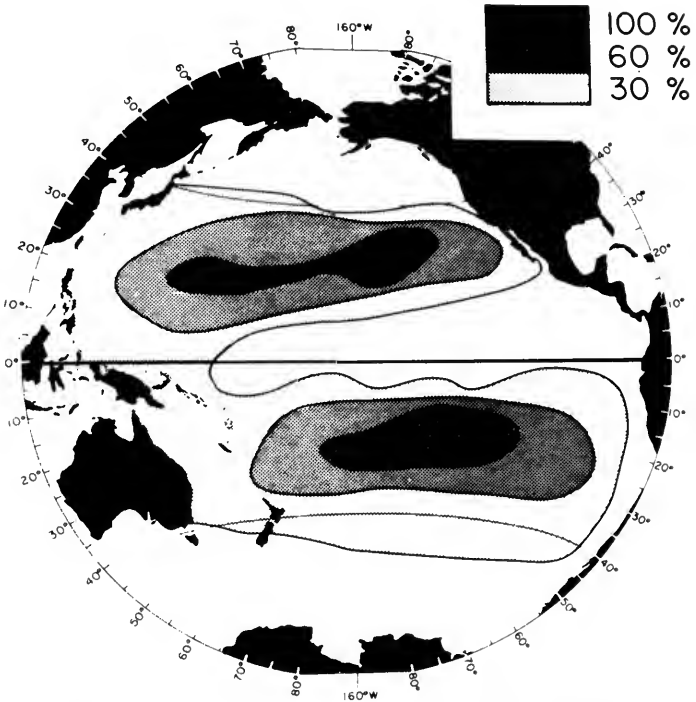
Johnson & Glodek (1975) present evidence for distinct central water species assemblages in the North and South Pacific. Endemic to the central portions of the Western and Eastern North Pacific Central Water area are the following species (fig. 71): *Sagitta pseudoserratodentata* (Chaetognatha, see Bieri, 1959; Alvarino, 1965), *Scopelarchus stephensi*, *Centrobranchus brevirostris* (Myctophidae, see Becker, 1966; Wisner, 1976). Johnson & Glodek (1975) originally supposed that

Bolinichthys distofax (Johnson, 1975) was a member of this group, but subsequent records (Nafpaktitis et al., 1977) have shown this species to occur in central water areas of the South Pacific and Atlantic. The Pacific distributions of *Rosenblattichthys hubbsi* and the euphausiid *Euphausia hemigibba* (see Brinton, 1962, 1975; Mauchline & Fisher, 1969) correspond well with the distributions of the North Pacific central-gyral endemics. Barnett (1975, p. 28) lists seven additional midwater fish species as probable endemics to the North Pacific central water area.

A counterpart assemblage (fig. 71) is found in central water areas of the South Pacific. Known endemics (Johnson & Glodek, 1975) include *Evermannella megalops, Scopelarchoides climax, Gonostoma longipinnis* (Gonostomatidae, see Mukhacheva, 1972; Johnson & Glodek, 1975), *Bathophilus abarbatus* (Melanostomiatidae, Barnett & Gibbs, 1968), and the euphausiid *Euphausia gibba* (Brinton, 1962, 1975; Mauchline & Fisher, 1969). Barnett (1975, p. 28) lists one additional midwater fish species as a probable South Pacific central water endemic.

That the two assemblages (north vs. south) are distinct is clearly shown by Barnett's (1975) data, with evident differences in species present or absent as well as marked (and consistent) differences in rank-abundances among the top 23 shared species (Barnett, 1975, p. 20). According to Barnett (1975), about half of the total species for both areas are shared between the north and the south. Those species shared include widely distributed tropical-subtropical species (such as the six scopelarchid and evermannellid species assigned to this category, table 23) as well as biantitropical subtropical species such as *Coccorella atlantica* and the following euphausiid species: *Euphausia brevis, Euphausia mutica, Nematoscelis atlantica, Stylocheiron suhmiii,* and *Thysanopoda obtusifrons* (see Brinton, 1962, 1975; Mauchline & Fisher, 1969; Brinton & Gopalakrishnan, 1973).

The two major features of wind-driven circulation within the warm-water Pacific are the immense subtropical anticyclones. Four major upper water masses are circumscribed by this gyral circulation (Sverdrup et al., 1942). In recent years McGowan (1971, 1974, 1977) and his students and colleagues (e.g., McGowan & Williams, 1973; Barnett, 1975; Shulenberger, 1977) have conducted extensive studies of the communities of pelagic organisms found in the central regions of the central water-mass areas of the North and South Pacific. In exhaustive reviews of the hydrography and biological oceanography of the central-gyral areas these authors have emphasized the following properties (among others) as essential determinants of the character and organization of these central-water "ecosystems" (see McGowan, 1977; McGowan & Hayward, 1978): (1) they are large and essentially homogeneous laterally in the distribution of biologically important properties; (2) they are geologically old (Arrhenius, 1963; Riedel & Funnell, 1964); (3) they are semiclosed systems, isolated from significant lateral advection by the gyral circulation enclosing them, but mixing (of faunas and water) does occur along their margins; (4) they are extremely stable, tuned to climate not weather, regulated largely by *in situ*, not large-scale, advective processes, and are relatively undisturbed; (5) they are highly oligotrophic, with yearly productivity values averaging less than 40 $gC/m^2/yr$ and correspondingly low zooplankton standing stocks (Reid, 1962; Cushing, 1971), both largely a function of very low nutrient levels in the eutrophic zone related to a water column structure that features great stability, very low rates of vertical mixing, and generalized downwelling (Reid, 1962; Cushing, 1971; Gregg et al.,



ESTIMATED PERCENT OF CENTRAL FAUNA PRESENT

1973; McGowan, 1974; McGowan & Hayward, 1978). Additional detailed studies at one central-gyral site (28° N, 155° W) are listed by Shulenberger (1977). Barnett (1975) argues, primarily on the basis of limited distributional evidence, for a two-gyre (northeast vs. northwest) system in the central North Pacific. The evidence is by no means complete—the area of the postulated Northwest Gyre is very poorly sampled—and no further discussion of the supposed two-gyre system in the north is offered in this paper.

The geographic area occupied by the central-gyral species assemblages described above (fig. 71) agrees well with the geographic extent of the central regions of the subtropical gyrals as indicated by surface currents (Sverdrup et al., 1942; Reid, 1962; Knox, 1970), transport (Sverdrup et al., 1942; Warren, 1970), temperature distribution with depth (Brinton, 1962), and the distribution of the Pacific central water masses (Sverdrup et al., 1942, Brinton, 1962; see figs. 71, 72). There is also very strong agreement between the area occupied by the central-gyral species assemblages and the central portions of the subtropical gyrals as indicated by minimum values for three commonly employed measures of food supply: net primary production (see Fleming & Laevastu as redrawn in Ebeling, 1962, p. 146; Koblentz-Mishke et al., 1970, and as redrawn by Cushing in Zeitschel & Gerlach, 1973; inside-back-cover sheets), zooplankton stock, and phosphate-phosphorus concentration (see Reid, 1962).

A preliminary conclusion is that there exist distinct assemblages of pelagic species in central water areas in the North and in the South Pacific and that these assemblages are comprised of species jointly and concordantly restricted to the areas of lowest food availability. An appealing hypothesis is that these assemblages owe their existence and organization to the low productivity conditions. I believe that any test of this hypothesis will require input involving four different categories of evidence: (1) the significance of endemism and joint restriction; (2) the significance of replacement (populations and species) within the context of species-assemblage areas; (3) the fit of wide-ranging species; (4) the significance of phyletic analyses for interpretation of the biological meaning of oceanic species assemblages. Each category is considered in turn in the paragraphs to follow.

(1) The Significance of Endemism and Joint Restriction.—Because higher taxa (rank of genus and higher) of mesopelagic organisms are commonly cosmopolitan (or nearly so) in the warm-water ocean, the open-ocean zoogeographer

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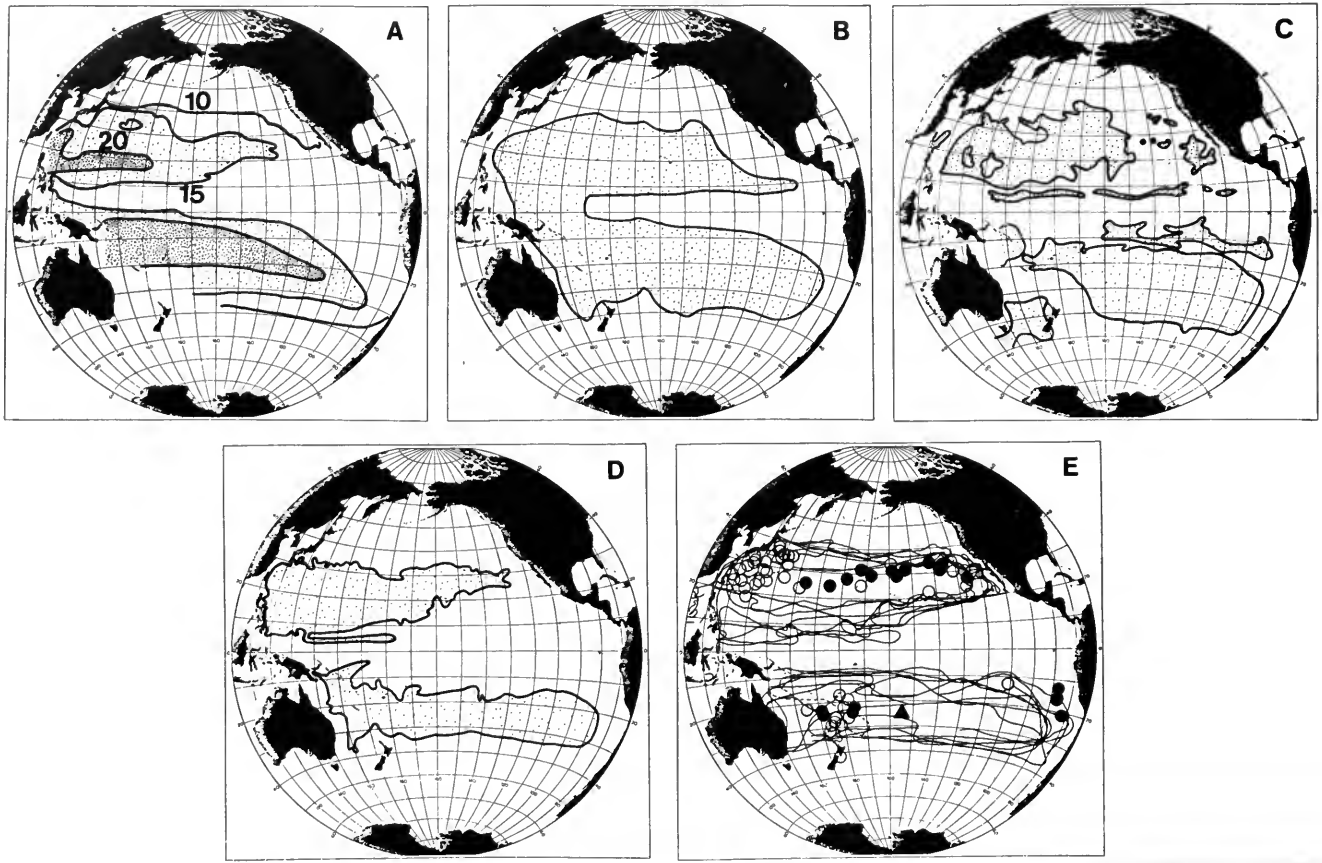
Opposite:

FIG. 71. Pacific central-water species assemblage areas. **Left,** Pacific distributions of six midwater fish species: North Pacific—*Scopelarchus stephensi* (solid circles), *Centrobranchus brevirostris* (open circles); South Pacific—*Evermannella megalops* (solid triangles), *Gonostoma longipinnis* (solid circles), *Scopelarchoides climax* (open square), *Bathophilus abarbatus* (open circles). Large triangle at 25° S, 155° W indicates overlapping capture records for *Evermannella megalops* and *Scopelarchoides climax*. Also indicated are the distributions of *Sagitta pseudoserratodentata* (after Bieri, 1959), seven euphausiid species (listed in text, after Brinton, 1962), and *Stylocheiron affine* "central form" (after Brinton, 1962). The midwater fish records are indicated by discrete symbols. The distributional limits of the oceanic invertebrates are indicated by range boundary lines. **Right,** Limits of the Pacific central-water provinces (north vs. south) according to McGowan (1974), showing the estimated percentage of the central fauna present. In the core areas of the faunal provinces, 100% of the species forming the faunal group are present (from McGowan, 1974).


A
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E

largely works with the distribution of species in attempts to define faunal units. As Barnett (1975, pp. 13, 14) points out, definition of such units should include not only presence or absence of a given species in an area, but also the relative abundance of common species, since, in Barnett's words ". . . the relative importance of a species . . . may differ in different parts of its range . . . [and] a consistent shift observable over time in the rank of a given species from one area to another must reflect some change in its role in the community . . . ."

Nonetheless, the nature of open-ocean data (for many and probably most groups) results in the fact that the only widely applicable method for the recognition of open-ocean species assemblages lies in the discovery of concordance in relatively restricted distributions of species from a variety of taxonomic groups and trophic levels. Such restriction is the basis for subsequent discussion. I believe that the extent to which McGowan's (1971, 1974, 1977) Pacific Ocean "ecosystems" correspond to the Atlantic "faunal regions and provinces" recognized by Backus et al. (1977, see discussion under Atlantic Ocean in a preceding section) will largely be resolved in terms of the importance of joint and concordant species restriction to the meaningful definition of such faunal units.

(2) The Significance of Replacement.—McGowan (1971, 1974, 1977) argues that organized, highly evolved communities (prime exemplars of which should be those in the central gyral areas of the Pacific) should consist of species that have undergone a long period of evolutionary co-adaptation. Many competitive interactions should already have taken place in such "biologically accommodated" communities (see Barnett, 1975, pp. 92, 93), leaving us to study the results of that competition. We might expect that species have co-evolved so as to minimize competitive interactions; consequently, functionally similar species should tend not to co-occur. This segregation may occur vertically (e.g., Clarke, 1973) or geographically (e.g., Fager & McGowan, 1963; Hartmann & Clarke, 1975). If the central gyral species assemblages in the Pacific represent discrete natural units, whether they be termed communities or ecosystems or faunal regions, we should expect to find species and populations being replaced in the context of (i.e., at the boundaries between) such units. I recognize that ecological replacement can and does take place without respect to taxonomic relationship, but I believe that the best evidence for such replacement that can currently be cited for open-ocean systems is provided by the allopatry of closely related congeners.

Scopelarchus stephensi is the sister-species of *S. michaelsarsi* (Johnson, 1974c, p. 201). In the area of the central gyral assemblage of the North Pacific (figs. 48, 71) *S. stephensi* replaces *S. michaelsarsi*, an otherwise widely distributed tropical-

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Opposite:

FIG. 72. Correlates of the distribution of Pacific central-gyral species. **A,** Distribution of 10°-, 15°-, and 20°-C isotherms contoured at 200 m in the Pacific Ocean (after Brinton, 1962). **B,** Area of minimum net primary production in the Pacific Ocean; contour encloses area in which production is estimated at or below 50 $gC/m^2/yr$ (Fleming & Laevastu redrawn in Ebeling, 1962). **C,** Areas of minimum zooplankton volume (at or below 25 ppb by volume in approximately the upper 150 m) in the Pacific Ocean (after Reid, 1962). **D,** Areas of minimum phosphate-phosphorus concentration (at or below 25 g-at/L contoured at 100 m) in the Pacific Ocean (after Reid, 1962). **E,** Pacific central-water species assemblage areas, as in Figure 71.

subtropical species occurring in all three oceans. A similar replacement of a broadly distributed species by a closely related congener endemic to one of the two central gyral species assemblage areas apparently occurs in the cases of *Centrobranchus choerocephalus* vs. *C. brevirostris* (Becker, 1966; Wisner, 1976; Naftpaktitis et al., 1977), *Gonostoma elongatum* vs. *G. longipinnis* (Mukhacheva, 1972; Johnson & Glodek, 1975), and *Evermannella indica* vs. *E. megalops* (these two species have broadly overlapping distributions north of ca. 20° S, figs, 34, 35; nothing is known regarding their relative abundance). I predict that additional examples will be found as the relationships of additional mesopelagic groups containing central gyral species are worked out.

(3) The Fit of Wide-Ranging Species.—A fundamental problem in attempting to understand the biological significance of discretely recognizable open-ocean species assemblages involves fitting broadly distributed species to the developing zoogeographic scheme. Of 19 warm-water evermannellid and scopelarchid species (table 23), only six species are restricted to postulated species assemblage areas (either eastern tropical Pacific or central water), the remainder are more broadly distributed in two or more ocean basins. This is by no means atypical. It led Ebeling (1967) to recognize a vast "Circumcentral-Tropical Primary Zoogeographic Region," incorporating all oceanic warm-water areas except the Mediterranean and eastern tropical Pacific. McGowan (1974, p. 15) recognized a supposedly distinct Pacific warm-water cosmopolite "fauna." The core area indicated for this "fauna" overlaps core areas of at least five more-restricted "faunas," thereby raising severe conceptual problems involving the meaning of faunal regions. Barnett (1975, pp. 36, 37) discusses a number of possible categories for understanding the fit of broadly distributed species to a scheme of open-ocean zoogeography based largely on species relatively (and jointly) restricted in distribution. Two of these categories, explicit or implicit in Barnett's discussion, are singled out for additional comment.

(A) Differential Abundance Patterns

In addition to the five euphausiid species biantitropical in the Pacific (see above), Brinton (1962, 1975) shows that 25 euphausiid species occur in at least the western portion of the Pacific Equatorial Water-Mass area as well as in North and South Pacific central water areas. Taken together, the distributions of these 25 species show several salient features: (1) none is endemic to the Pacific; (2) a plot (fig. 73) of the distributional limits of a representative 13 of these 25 species shows marked nonconcordance when compared with the remarkably concordant distributions (fig. 71) of those species limited to the central water areas; (3) probably more significant is an apparent marked difference between the two groups (widespread vs. central) in pattern of abundance. Eight of the broadly distributed species, five of the central gyral species, and the "Central Form" of *Stylocheiron affine* were sufficiently well known that Brinton (1962) was able to plot areas of maximum abundance within the range of each. I have compiled Brinton's data and illustrate (fig. 73) the **overlap** of areas of maximum abundance. The comparison suggests that the eight widely distributed species tend to group together (in terms of maximum abundance) in areas peripheral to the central gyral areas and in particular tend to group together along the equator. Those forms limited to central water areas tend to group together in the central

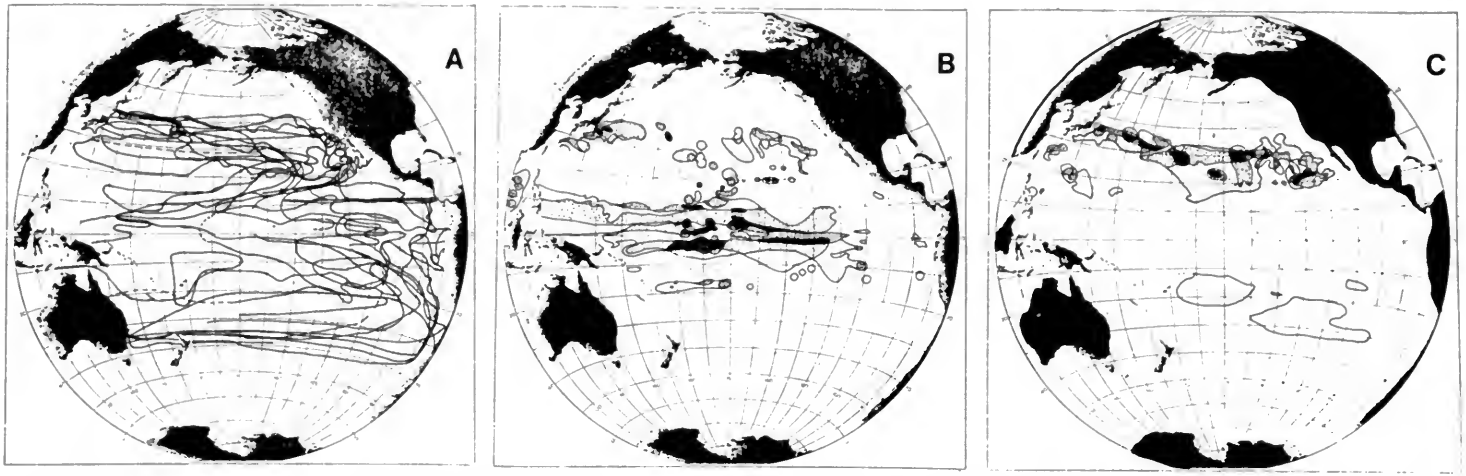

FIG. 73. Comparison of broadly distributed vs. central-gyral euphausiid species in the Pacific Ocean (all figures based on data presented by Brinton, 1962). **A,** Distribution (range limits) of 13 warm-water euphausiid species in the Pacific. The 13 species were selected from 25 euphausiids occurring in both central and equatorial water-mass areas in the Pacific, but excluding species that also occurred in polar waters and bathypelagic species (species plotted: *Euphausia tenera, Nematobrachion sexspinosus, Nematoscelis microps, N. tenella, Stylocheiron microphthalma, S. robustum, Thysanopoda aequalis, T. cristata, T. monacantha, T. orientalis, T. pectinata, T. subaequalis, T. tricuspidata*). **B,** Areas of overlap of areas of maximum abundance of eight euphausiid species widespread in central and equatorial waters. The intensity of the shading indicates whether two (unshaded), three (stippled), or four (black) or more species overlap in maximum abundance. See text for additional explanation (species included: *Euphausia tenera, Nematobrachion sexspinosus, Nematoscelis microps, N. tenella, Stylocheiron microphthalma, Thysanopoda tricuspidata, Stylocheiron carinatum, S. abbreviatum*). **C,** Areas of overlap of areas of maximum abundance of five euphausiid species essentially limited to central-water areas in the Pacific (species included: *Euphausia brevis, E. hemigibba, E. mutica, Nematoscelis atlantica, Stylocheiron suhmii*) and for *Stylocheiron affine* "central form."

portions of the central gyrals. Barnett (1975, pp. 36, 37) offers evidence for the converse distribution pattern: broadly distributed species more abundant within the central gyrals but occurring (in reduced numbers) along the equator (see also McGowan, 1971, p. 17; Hartmann & Clarke, 1975, p. 637).

Whittaker & Woodwell (1972) argue that if two species of similar niche and habitat requirements occur within a definable area, competition may be reduced by niche divergence, allowing broadly overlapping distributions, or by habitat differentiation, resulting in a separation of areas of maximum abundance along a given environmental gradient. I believe that if the apparently sharp and concordant difference between areas of maximum abundance suggested by data for the euphausiid species is both true and occurs more commonly than is now known to be the case, this difference supports the notion of the central gyral species assemblages as discrete natural units by in effect arguing for species replacement in the context of these units.

(B) The Population Structure of Broadly Distributed Species

A markedly different but complementary hypothesis is that widely distributed species are comprised of separable, genetically distinct populations, the differences reflecting adaptation, and that replacement of these populations occurs at the boundaries of species assemblage areas. There is (at present) no direct evidence supporting this hypothesis, and such indirect evidence as exists is marred by our inability to distinguish ecophenotypic effects from differences related to genetic divergence (e.g., Brinton, 1962, pp. 178–190; 1975, p. 210).

This problem is mirrored in studies of variation in meristic characters among populations of broadly distributed midwater fish species conducted by Johnson & Barnett (1972, 1975). They selected the material to be studied from the broadest possible range of warm-water oceanic habitats, from the richly productive eastern tropical Pacific and Gulf of Guinea to the highly oligotrophic Sargasso Sea and central gyral areas of the North Pacific. They found that for the species and areas studied, central values of the meristic characters considered were correlated negatively and quite significantly with various measures of food supply but were not correlated with temperature, salinity, or any other factor known to be causally associated with meristic character variation in fishes. They (Johnson & Barnett, 1975) then hypothesized that the meristic variation observed reflects and is the result of adaptation of egg size, fecundity, and larval size to differing productivity conditions. In this scheme selection is thought to favor the production of fewer, larger larvae in oligotrophic areas where the danger of larval starvation is greatest, and to favor higher fecundity (with the concomitants of smaller eggs and larvae) in areas of higher productivity where the danger of larval starvation may be lessened.

Relevant to the present discussion is the hypothesis that the meristic variation observed reflects genetically distinct allopatric populations of broadly distributed midwater fish species in different areas and that the distribution of such populations will be found congruent with areas defined in terms of assemblages of distributionally restricted species. If true, the consequences upon our interpretation of open-ocean distribution patterns would be far reaching.

(a) It would negate the apparent and largely unexplained distinction between species widely distributed in the warm-water ocean vs. species more restricted

in distribution. The division of wide-ranging polytypic species into allopatric populations restricted to faunal regions is consonant with the recognition of such regions based on concordantly restricted, rather narrow-ranging species. Such infraspecific populations, congruent in distribution with narrowly ranging endemics, may be adapted to biological and/or physical features whose values are distinctive for a particular region. Such features, e.g., variation in food supply, may differ markedly between regions (see McGowan, 1971; Johnson & Barnett, 1975).

(b) It would allow us to envision a continuum in open-ocean distributional patterns, a continuum related (at least in part) to gradients in food supply, a continuum from tropical species largely restricted to more productive areas in the warm-water ocean, to tropical-subtropical species most abundant in higher productivity areas peripheral to central areas of the subtropical anticyclones, to widespread species with distinct central vs. equatorial populations or widespread species distinctly most abundant within the central gyral areas, to subtropical species restricted to the oligotrophic central gyral areas. Interpretation of such a continuum will depend largely on input from the fourth and last major category of evidence: input from phylogenetic studies.

(4) The Significance of Phyletic Analyses.—Three assumptions are prerequisite to the discussion of the possible effects of input from phyletic analyses upon our understanding of the biological meaning of the Pacific central gyral species assemblages:

(a) Central water areas in the Pacific are very old. The proto-Pacific must have been largest just prior to the breakup of Pangaea, some 180 million years BP (Rosen, 1974) and has been shrinking ever since (e.g., Dietz & Holden, 1970).[13] It is the geography of the central gyral areas that in large measure contributes toward their distinctive oligotrophic environment (e.g., Eppley et al., 1973). It seems likely that these properties have typified these Pacific central gyral areas throughout a vast expanse of time (Gordon, 1973; McGowan, 1974).

(b) The midwater fish faunas of the central gyral areas are not as old as the central gyral areas. If the Pacific central gyral areas are as old as is believed, their midwater fish faunas are far younger, in all likelihood no older than upper Cretaceous or early Tertiary age (see Romer, 1966; Goody, 1969; Rosen, 1973).

(c) It seems likely that the present midwater fish fauna has its roots in ancient faunas of the tropical continental shelf (Andriashev, 1953; Marshall, 1963; Parin, 1970). In Marshall's (1963, p. 189) words:

> . . . the earlier colonizers [of the deep sea] lived in the more productive parts of the ocean . . . those parts most resembling the environments of their shallow-water ancestors . . . [first to be colonized] would be the waters over the upper reaches of the continental slope and those in the equatorial oceanic regions . . . [the last warm-water habitat to be colonized would be] the great central gyres.

I believe that continued study may result in evidence that in the open ocean the "community" (for which also read species assemblage in the sense of central gyral species assemblages) functions as a unit of evolution. To be accepted, this notion must meet at least two criteria: (1) that populations and/or closely related species replace each other in the context of "community" boundaries and (2) that evolutionary changes leading to the multiplication of species tend to occur with

[13]Shields (1979) argues for a much more recent (Jurassic) origin of the Pacific.

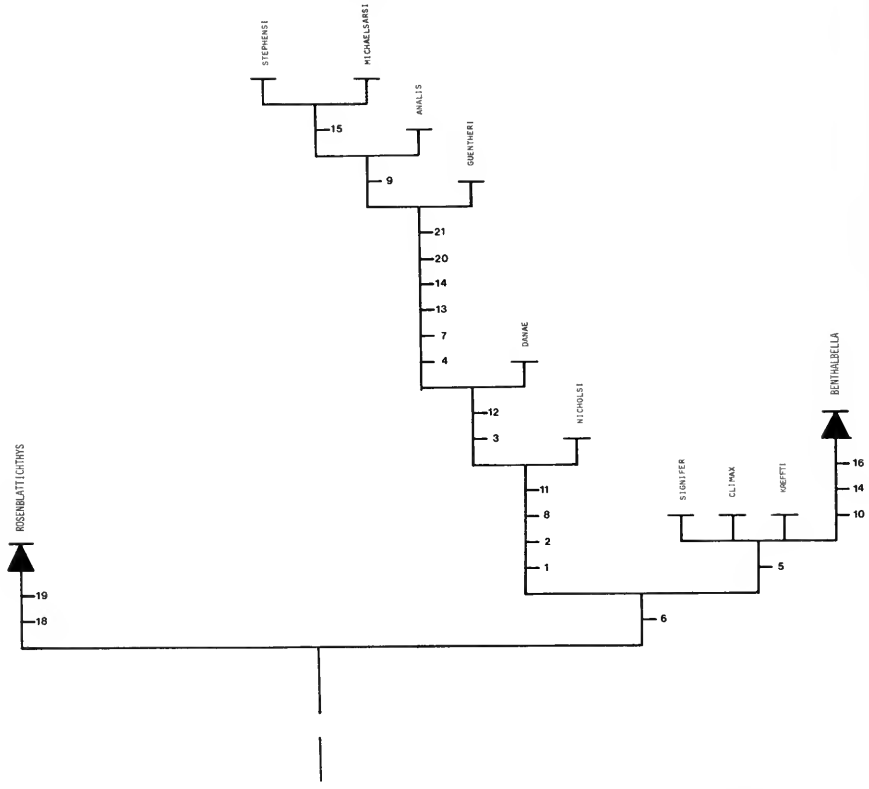

FIG. 74. Sister-group relationships among scopelarchid taxa comprising the lineage containing *Scopelarchus*. Integers represent derived character states defined in Johnson (1974c, pp. 200–210). See text for additional explanation.

respect to boundaries between such "communities." The first of these criteria, as discussed previously, is probably testable. The second may not be directly testable, but the discovery that species endemic to the Pacific central gyral areas are the most derivative members of the monophyletic lineages to which they belong would, given the three assumptions listed above, lend support to the notion of separation of populations (by unknown mechanisms) with subsequent divergence within the context of species assemblage (or "community") units. Evolution within the scopelarchid lineage including *Scopelarchus* appears to support these ideas.

My view of the relationships of scopelarchid species and the substantial evidence for the monophyly of the lineage including *Scopelarchus* (fig. 74) are presented in Johnson (1974c, pp. 199–220).

Scopelarchoides signifer, *S. nicholsi*, and *S. danae* inhabit relatively productive nearshore and/or divergence areas in the tropical ocean, *S. signifer* in the Indo-Pacific, *S. nicholsi* in the eastern tropical Pacific. *Scopelarchoides danae*, the sister group of the genus *Scopelarchus*, is found in all three oceans but has been most

commonly taken in relatively productive areas near continental and insular land masses. It does not occur in central waters in the Pacific.

Scopelarchus guentheri is a circumglobal warm-water species, virtually excluded from North Atlantic central water but extending from the equatorial Atlantic to the eastern tropical Pacific. In the Pacific *S. guentheri* is apparently most abundant in areas peripheral to the oligotrophic central regions of the subtropical anticyclones, this statement based on admittedly limited catch/effort information (see Johnson, 1974c, pp. 229–231). It thus appears that *Scopelarchus guentheri* is largely replaced by its three congeners within the central portions of the Pacific central gyral areas.

Scopelarchus analis, a circumglobal, tropical-subtropical species, is essentially biantitropical in central water areas in the North and South Pacific and all but excluded from the area of Pacific Equatorial Water. The distribution of *Scopelarchus michaelsarsi* is largely similar to that of *S. analis*. Although *S. michaelsarsi* is not known from west of ca. 150° W in the Pacific, it is known from western and central sites within the Pacific Equatorial Water-Mass area. *Scopelarchus michaelsarsi* is apparently replaced by *S. stephensi* in the area of the central gyral species assemblage of the North Pacific.

This monophyletic lineage thus seems to reflect an evolutionary sequence involving greater and greater adaptation to low-productivity conditions, a sequence incorporating species limited to or more abundant in more productive areas around the oligotrophic centers of the Pacific subtropical gyrals, to species most abundant in or limited to (in the Pacific) the central gyral areas, to a species endemic to one of the central gyral species assemblage areas in the Pacific and one of the two most derivative warm-water species in the family. It is tantalizing to note possible parallels, i.e., derivative species in central water, "primitive" species in more productive tropical nearshore areas or divergence areas (e.g., Ebeling, 1962, p. 31; Gibbs, 1969, pp. 21, 22; Baird, 1971, pp. 104, 105), and frustrating to note that relationships in neither these nor other midwater groups are sufficiently well worked out to allow continuation of this discussion. Among the keys to understanding the biological meaning of open-ocean species assemblages will be further synoptic systematic studies of groups, studies that involve analysis of phylogenetic relationships between species. As I have attempted to suggest in the preceding pages, among the rewards of such study will be insight into the common meeting ground between ecological and historical approaches to zoogeography.

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