TAXONOMY, PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHY OF THE DEEP-SEA HATCHETFISH GENUS *POLYIPNUS* (STOMIIFORMES: STERNOPTYCHIDAE)

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A thesis submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

Department of Biology
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ABSTRACT

The tropical to subtropical mesopelagic fish genus *Polyipnus* (family Sternoptychidae) is the subject of a taxonomic, phylogenetic, and biogeographic study. Examination of specimens from most of the major collections leads to recognition of 29 species in the genus. A key is provided. New species are described from the South China Sea, off the northwestern coast of Australia, the Andaman Sea (eastern Indian Ocean), the western Indian Ocean off Kenya, and the tropical western North Atlantic.

A study of phylogenetic relationships, based on mainly osteology and photophores, results in a well-resolved phylogeny. Instances of unresolved branching order are due to homoplasy and/or lack of osteological observations for rare species. Reductive homoplastic characters, such as small body size (within the *omphus* species group) and low photophore number (*P. fraseri*) are paedomorphic and likely derived. Monophyly of the genus and 4 species groups is indicated; the infrastructure of the genus is organized on the basis of these groups. Species that were previously members of the *laternatus* species complex do not constitute a monophyletic group and are placed in the *asteroides* and *omphus* species groups with their closest relatives. The remaining *meteori* and *spinosus* species groups contain species previously referred to the *asteroides* and *spinosus* complexes.

Cladograms formed the framework for a vicariance biogeographic analysis. The history of the genus dates to pre-Miocene times (prior to 25 million years ago) when a widespread Tethyan ancestral biota existed. A chronological series of tectonic/climatic vicariant events is proposed which accounts for much of the observed endemism in the genus. The *asteroides* species group appears to be the only *Polyipnus* group that was present in the Atlantic as well as the Indo-Pacific in the early Miocene. Final closure of Tethys in the Mediterranean region, later in the Miocene, caused subdivision of a species ancestral to all Atlantic species and possibly a single species in the western Indian Ocean. Subdivision of an ancestral deep-sea fauna in the Indo-Pacific was effected by the early Miocene collision of the Australian and Asian Plates and subsequent tectonic activity which cut off deep water circulation between the eastern Indian Ocean and the western Pacific. Later in the Miocene, circulation between the South China Sea and the adjacent southern Sulu Basin was disrupted, possibly causing vicariance in three *Polyipnus* species groups.

ACKNOWLEDGEMENTS

Many people have assisted me in this study. Foremost, I thank my supervisor Dr. Richard L. Haedrich, Ocean Sciences Centre, Memorial University of Newfoundland, for his interest, encouragement and unflinching support. I thank the other members of my supervisory committee, Dr. Ian R. Ball and Dr. David Larson, for their significant contributions. The efforts of Dr. Roy Knoechel, Graduate Officer and Dr. Alan Whittick, Acting Head, Department of Biology, towards production of this thesis are much appreciated. I also acknowledge Dr. Stanley H. Weitzman, Smithsonian Institution, Washington, D.C., for helpful correspondence and discussions pertaining to phylogenetic analysis and evolutionary relationships of stomiiform fishes. I thank Christine Campbell, Donald Clark, Jean-Marc Gagnon, Hugh Griffith, Terry Hedderson, Greg Klassen, Dave Methven, Randy and Rich Mooi, Malcolm Telford and H. Todd Wareham for their parts in manuscript reviews and discussions.

For making collections and facilities freely accessible during my trips abroad I'm indebted to Dr. William Eschmeyer (California Academy of Sciences, San Francisco, California), Dr. Karsten E. Hartel (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts), Dr. Robert Lavenberg (Los Angeles County Museum of Natural History), Mr. Nigel R. Merrett (Institute of Oceanographic Sciences,

Surrey, U.K.), Drs. J. Nielsen and E. Bertelsen, Zoologisk Museum, Copenhagen, Denmark, Dr. Alex Peden (Royal British Columbia Museum, Victoria, B.C.), Dr. Richard H. Rosenblatt (Scripps Institution of Oceanography, La Jolla, California), Dr. Alwyne Wheeler [British Museum (Natural History), London, U.K.], Dr. Stanley H. Weitzman (National Museum of Natural History, Washington, D.C.) and Dr. Richard Winterbottom (Royal Ontario Museum, Toronto, Ontario). I also thank Dr. Raymond R. Wilson, Jr. for an invitation to take part in a collecting trip to the New England continental slope on board R/V Oceanus (Woods Hole Oceanographic Institution).

Specimens were generously donated for this study by H. Kishimoto (Institute of Oceanic Research and Development, Tokai University, Shimizu, Japan), N.V. Parin (P.P. Shirshov Institute of Oceanology, Moscow, U.S.S.R.) and K.J. Sulak (Huntsman Marine Laboratory, St. Andrew's, New Brunswick).

I thank the personnel and their respective museums or institutions (abbreviations defined in text, pages 11-13) that were involved in the processing of specimen loans: M.E. Anderson (CAS), A.P. Andriashev (ZIL), M.-L. Bauchot (MNHN), P. Bourret (ORSTOM, Délégation Océan Indien, La Réunion, France), D. Catania (CAS), B. Chernoff (FMNH), O. Crimmen (BMNH), W. Eschmeyer (CAS), M.N. Feinberg (AMNH), L. van Guelpen (ARC), K.E. Hartel (MCZ), E. Holm (ROM), G.W. Hughes (BCPM), J.B. Hutchins (WAM), K. Kawaguchi (ORIT), S.L.

Jewett (USNM), P. Lambert (BCPM), K. Matsuura (NSMT), J. Mauchline (Dunstaffnage Marine Research Laboratory, Argyll, Scotland), M. McGrouther (AMS), N.R. Merrett (IOS, BMNH), B.C. Mundy (NMFSH), J.G. Nielsen (ZMUC), O. Okamura (BSKU), N.V. Parin (IOAN), J.R. Paxton (AMS), S.J. Raredon (USNM), C.B. Renaud (NMC), J. Roberts (J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa), R.H. Rosenblatt (SIO), P.H. Schalk (ZMA), J.A. Seigel (LACM), M.P. Seki (BPBM), K. Smith (WAM), A.Y. Suzumoto (BPBM), H.J. Walker, Jr. (SIO), A. Wheeler (BMNH), H. Wilkens (ZMA), S.H. Weitzman (USNM), J.T. Williams (USNM), R. Winterbottom (ROM) and R. Witbaard (ZMA).

I thank Roy Ficken for his skillfull work as Department of Biology photographer, and Heather Roche and Ada O'Reilly, Ocean Sciences Centre, for administrative work in support of my program. I'm grateful to Dr. Ali Aksu, Department of Earth Sciences, Memorial University of Newfoundland, for access to the Picker X-Ray device and to Brian Sears for technical assistance. Permission for reproduction of the illustrations of _P_. _elongatus_ and _P_. _parini_ was granted by John Wiley and Sons, New York.

This research was funded through Natural Sciences and Engineering Research Council of Canada operating grant number 330068 to Dr. R.L. Haedrich. Personal support was gratefully received through this grant, and in the form of a Memorial University of Newfoundland Bursary.

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INTRODUCTION

This is an account of the systematics and biogeography of the tropical to subtropical mesopelagic fish genus Polyipnus, family Sternoptychidae. This moderately speciose genus has been reviewed twice over the last thirty years (Schultz, 1961; Baird, 1971) and presently contains about 20 species. In this study I review collections from about 30 institutions. This material forms the basis of a revised taxonomy, including descriptions of new species, and analyses of phylogenetic relationships and historical biogeography. The style of the thesis is that of a systematic monograph.

The 'INTRODUCTION' and 'MATERIALS AND METHODS' chapters are subdivided under the subject areas taxonomy, phylogenetic relationships and biogeography. The layout of the 'TAXONOMIC REVISION' chapter is traditional, with a diagnosis of the genus, a key to the species, brief definitions of species groups and detailed accounts of the species. Comparative remarks in that chapter are confined to similarities, as an aid to identification. The ensuing chapter, 'PHYLOGENETIC RELATIONSHIPS', is a clade by clade catalogue of shared, derived characters with a general discussion of relationships. The last analytical chapter is entitled, 'BIOGEOGRAPHY'. It describes general distribution patterns of the species groups and provides an analysis of historical biogeography in the vicariance paradigm. The report finishes with a short chapter of 'CONCLUSIONS'. Format generally follows that of monographs published in *Smithsonian Contributions to Zoology* except in the 'REFERENCES' where the authors' names are not placed on a separate line.

Taxonomy

The family Sternoptychidae, order Stomiiformes, is a group of small luminescent fishes, inhabiting mesopelagic to bathypelagic realms. Beginning with Günther (1864), there has been much debate concerning which genera should be placed in this family. Baird (1971) provided an explicit definition for the Sternoptychidae and restricted it to the deep-bodied forms, or hatchetfish, of the genera *Argyopelecus* Cocco, *Sternoptyx* Hermann and *Polyipnus* Günther. Usage of the family name was expanded by Weitzman (1974; 1986a) to include *Araiophos* Grey, *Argyripnus* Gilbert and Cramer, *Danaphos* Bruun, *Maurolicus* Cocco, *Sonoda*, *Thorophos* Bruun and *Valenciennellus* Jordon and Evermann on the basis that these 10 genera constituted a monophyletic group. The subgroup of three hatchetfish genera is also monophyletic (Weitzman, 1974) but is now referred to the tribe Sternoptychini (Baird, 1986; Weitzman, 1986b).

The genus Polyipnus was erected by Günther (1887) to accommodate the single specimen of P. spinosus, captured by bottom trawling near the Philippines by H.M.S. Challenger. Günther recognized that his specimen had certain affinities with the other hatchetfish genera, Argyropelecus Cocco and Sternoptyx Hermann, but noted some important distinctions. Diagnostic features were the multispinose posttemporal bone and the large number of posterior ventral (=AC) photophores.

The next Polyipnus species described was P. laternatus Garman, 1899 from the North Atlantic Ocean. This species was distinguished by the single posttemporal spine (compared with 3 in P. spinosus) and the absence of spinelike denticles originating on the ventral photophore scales. The two species both had 10 abdominal photophores with the associated heavy scales forming a ventral bony keel.

Shortly after the turn of the century three species similar to Polyipnus spinosus from the Pacific Ocean were described: P. stereope Jordan and Starks, 1904, Sagami Bay, Japan, P. nuttingi, Hawaiian Islands, and P. tridentifer McCulloch, 1914, Great Australian Bight. Polyipnus fraseri Fowler, 1934 from off the Philippines was the next to be described and, although it shared many unusual features with P. spinosus and allies which are not present in P. laternatus, a new subgenus, Acanthopolyipnus, was designated. Fowler's enigmatic species has been synonymized with P. tridentifer and P. spinosus in two relatively recent reviews (Baird, 1971 and Borodulina, 1979, respectively) but Harold (1990b) has resurrected *P. fraseri*, arguing that some of the problematical characters are paedomorphic and not aberrant.

Schultz (1938) provided the first review of the genus, and described 3 new species, *Polyipnus asteroides* (western North Atlantic Ocean), *P. unispinus* and *P. triphanos* (both Philippines). In 1961 Schultz revised the genus again, adding the new species *P. matsubarai* (Japan), *P. polli* (eastern South Atlantic Ocean), *P. indicus* (off the east coast of southern Africa) and *P. japonicus* (Japan).

Baird (1971) described 5 new species: *Polyipnus omphus* (western Indian and central Pacific oceans), *P. aquavitus* (Tasman and Banda seas), *P. kiwiensis* and *P. ruggeri* (off New Zealand) and *P. oluolus* (Marshall Is.). Baird (1971:81-82) was the first to offer detailed comments on relationships among *Polyipnus* species. The genus was subdivided into the *asteroides*, *laternatus* and *spinosus* species complexes. The former two groups were thought to be most closely related on the basis of posttemporal structure, body shape, photophore pattern and dentition. Within the *P. spinosus* complex Baird recognized the *P. indicus* subgroup with 1 or 2 posttemporal spines and low anal (=AC[B]) photophore number and the *P. spinosus* subgroup with 3 posttemporal spines and relatively high anal photophore number.

Of the three species complexes established by Baird (1971), only the Polyipnus spinosus complex has attracted much systematic investigation. Borodulina (1979) reviewed the P. spinosus subgroup, describing 3 new species: P. parini (western Pacific Ocean), P. elongatus (Coral Sea) and P. spinifer (off the Philippines and Japan). Later she added P. inermis, a new species from the Sala-y-Gomez Ridge, eastern South Pacific Ocean (Borodulina, 1981). This was the first record of a Polyipnus species from the eastern Pacific. More recently, a new species in the P. spinosus complex, Polyipnus paxtoni Harold, 1989, has been described. Harold (1989) presented evidence for monophyly of the spinosus complex but recommended that further subdivisions of the complex should not be recognized until phylogenetic relationships are better understood.

Recent additions to the other two species complexes recognized by Baird (1971) have also been proposed. Harold (1990a) described a new 'miniature' (sensu Weitzman and Vari, 1988) species, most similar to P. unispinus, from the South China Sea. The new species P. danae Harold, 1990 was provisionally assigned to the laternatus species complex (sensu Baird, 1971) with the caveat that homoplasy obscured interrelationships. In addition, there is a new species described in the asteroides species complex from Suruga Bay, Japan (Aizawa, in press). This species is thought to be most similar to P. triphanos of the Indo-Australian Archipelago.

In the present revision, a total of 29 species are recognized, including descriptions of 5 that are new. New illustrations are provided for certain species that are redescribed. This was done to facilitate identification and, for species for which type specimens are in very poor condition (e.g. P. oluolus Baird, 1971), to pictorially present important features.

Phylogenetic Relationships

Baird (1971) was the first to propose relationships among groups of Polyipnus species, although the genus had been previously reviewed (Schultz, 1938; 1961). Members of the spinosus species complex were considered most primitive on the basis of generalized axial and caudal osteology. The remaining asteroides and laternatus complexes were thought to be most closely related, having similar body form, posttemporals, photophore configuration and dentition. Some of the characters identified by Baird are not derived with regard to Polyipnus and as such are not regarded here as evidence of most recent common ancestry.

I adopt the methods of phylogenetic systematics (Hennig, 1966; Wiley, 1981) or "cladistics", an analytical framework in which only shared-advanced or derived characters (synapomorphies) are evidence of common ancestry or monophyly. Only monophyletic groups are recognized as valid taxa. Shared-primitive or plesiomorphic characters (symplesiomorphies) are the result of common ancestry at a higher or more inclusive level of relationship. In this study I analyze a suite of morphological characters and propose phylogenetic relationships for the 29 *Polyipnus* species. *Polyipnus* new species MS Aizawa is not included.

Biogeography

Baird (1971) described the patterns of distribution in *Polyipnus* as "land-oriented". The feeding ecology of these species, related to various unusual aspects of skull and jaw morphology, was thought to be specialized and somehow tied to coastal areas of elevated productivity. Baird also drew a parallel between this pattern and those of *Melamphaes* species (Melamphaeidae) (Ebeling, 1962) and various shorefish species. Matsui and Rosenblatt (1987) considered the association between mesopelagic fishes of the family Platytroctidae and continental slope or other high relief features of the sea floor as analogous to distribution in *Polyipnus*, *Melamphaes*, the stomiids *Stomias nebulosus* (see Gibbs, 1969) and *Astronesthes macropogon* (see Goodyear and Gibbs, 1969) and the scopelarchid *Scopelarchoides danae* (see Johnson, 1982).

Polyipnus species, however, have a much shallower depth distribution than do these other deep-sea taxa and generally have much more restrictive geographical ranges (Baird, 1971). Most of the species are restricted to island groups, minor sea basins or sections of semi-enclosed continental slope whereas the other forms are usually associated with vast, occasionally disjunct, regions of elevated productivity. It is hypothesized here that much of the observed endemism in *Polyipnus* is due to geophysical remodelling of the ocean areas or their enclosing features, and their oceanographic interconnections.

Croizat (1964) analyzed the patterns of geographic distribution of organisms and believed them to result largely from the geological/climatological breakup or vicariism of widespread ancestral biotas. His main analytical tool was the track, a line drawn on a map connecting the areas occupied by members of a given taxon. The track has been regarded as an estimate of the distribution of the common ancestor (Rosen, 1975). When tracks of different groups of organisms coincide they form a generalized track which is an indication of common history. Craw (1988a, b) and Page (1987) are among the few to apply Croizat's methods ("panbiogeography"); except for the track concept, the elements of Croizat's panbiogeography have been dismissed by contemporary biogeographers (Humphries and Parenti, 1986; Nelson and Platnick, 1981; Seberg, 1986).

Vicariant processes impose hierarchical structure on distribution through phylogeny. The framework of vicariance explanations should reflect this by expressing the relationships among geographical areas in terms of the phylogenetic relationships among the groups of inhabiting organisms. Area cladograms fulfill this requirement and are simply constructed by replacing the names of taxa at the tips of the branches of a cladogram with the areas occupied. Hennig (1966) and Brundin (1966) originally applied area cladograms to biogeography ("phylogenetic biogeography") but distribution was explained by dispersal or progression of derived forms away from primitive forms at a center of origin. This, and other methods that explain distribution patterns in terms of essentially random dispersal rarely lead to a testable explanation (Ball, 1976).

The more general methods of vicariance cladistics (in the broad sense of Humphries et al., 1988) draw on the concept that replication of branching patterns in the studied area cladograms increases the likelihood that the contributing taxa were affected by the same biogeographic factors (Wiley, 1988a, b). An explanation so formulated is at least potentially falsifiable.

Sets of area cladograms are usually not congruent. The unique elements may be due to extinctions, dispersal events, primitive absence, systematic or distributional errors or lack of common history. Component Analysis (Humphries and

Parenti, 1986; Nelson and Platnick, 1981; Zandee and Roos, 1987) and co-speciation or Brooks Parsimony Analysis (Brooks, 1981, 1985, 1990; Wiley, 1988a, b) are two computational techniques that have been developed for interpretation of incongruence. Parsimony Analysis was chosen for the present study because it uses the distributional/phylogenetic data in their raw form and does not create taxa for groups that are not represented in one or more areas. Furthermore, the necessity to identify "natural" sets of areas of endemism (Wiley, 1981) is relaxed and left for *a posteriori* determination (Wiley, 1988b).

That vicariance methods are applicable to biogeography of oceanic fishes has been suggested by Fink and Fink (1986), Johnson (1982) and Nelson (1986). Ho (1990) provided an explanation of distribution patterns of the hakes (*Merluccius*, family Merlucciidae) and their parasites; a move toward corroborated explanation. In the present analysis I extract distributional characters from the proposed phylogenetic relationships among several *Polyipnus* species groups and combine these to generate a hypothetical sequence of events leading to the observed patterns. I also present a chronology of geophysical events affecting the oceanic areas and attempt to date the vicariant events by comparison with the topology of the biogeographic hypothesis.

MATERIALS AND METHODS

Specimen Sources

Specimens were made available for this study from museums and institutions around the world. Material of all described taxa, including often the holotype, were examined as indicated in the individual species accounts. The only specimen of Polyipnus n. sp. MS Aizawa was not available for study and therefore is not treated in detail in this revision. The names and standard abbreviations (according to Leviton et al., 1985) of these institutions are:

AMNH	American Museum of Natural History, New York, New York, U.S.A.
AMS	Australian Museum, Sydney, Australia
ARC	Atlantic Reference Centre, St. Andrew's, New Brunswick, Canada
ASH	donated collections (to be deposited)
BCPM	Royal British Columbia Museum, Victoria, B.C., Canada
BMNH	The Natural History Museum, London, England
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
BSKU	Kochi University, Kochi City, Japan
CAS	California Academy of Sciences, San Francisco, California, U.S.A.

FAKU	Kyoto University, Kyoto, Japan
FMNH	Field Museum of Natural History, Chicago, Illinois, U.S.A.
IOAN	Academy of Sciences, Institute of Oceanology, Moscow, U.S.S.R
IOS	Institute of Oceanographic Sciences, Godalming, Surrey, England
KMMA	Koninklijk Museum voor Midden-Afrika (Musée Royal du Congo Belge): not listed by Leviton et al. (1985)
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MMSU	Moscow State University, Moscow, U.S.S.R
MNHN	Museum National d'Histoire Naturelle, Paris, France
NMC	National Museums of Canada, National Museum of Natural History, Ottawa, Ontario, Canada
NMNZ	National Museum of New Zealand, Wellington, New Zealand
NMFSH	National Marine Fisheries Service, Honolulu, Hawaii, U.S.A.
NSMT	National Science Museum, Tokyo, Japan
ORIT	University of Tokyo, Ocean Research Institute, Tokyo, Japan

ROM	Royal Ontario Museum, Toronto, Ontario, Canada
SIO	Scripps Institution of Oceanography, University of California, San Diego, California, U.S.A.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
WAM	Western Australian Museum, Perth, Western Australia, Australia
ZIL	Academy of Sciences, Zoological Institute, Leningrad, U.S.S.R.
ZMA	Universiteit van Amsterdam, Zoologisch Museum, Amsterdam, Netherlands
ZMH	Universitat Hamburg, Zoologisches Institut und Museum, Hamburg, Germany (FDR)
ZMUC	Zoologisk Museum, Copenhagen, Denmark

Specimens studied are listed by museum catalogue number in the MATERIAL EXAMINED section of each species account. Collection data, consisting of number of specimens, size range in mm standard length, latitude and longitude, depth of tow, sounding depth (S.D.), vessel, local time and date are given when available. In some cases, only the length of the wire in mwo (meters of wire out) was available and is provided in place of the depth(s) towed.

Descriptive Methods

Over the last 30 years a set of unique terms and abbreviations has been used to refer to the various photophores of the deep-bodied sternoptychids (e.g. Schultz, 1961; Baird, 1971). Weitzman (1974) synonymized such terms with those in common use for all other stomiatoid (=stomiiform) fishes, although he was uncertain as to the equivalents of supra-anal (SAN) and lateral (L) photophores. Badcock (1984) used the new terminology in a key to the hatchetfishes of the eastern Atlantic but this appears to be the only application.

In regard to counts and terminology pertaining to photophore clusters, I follow Ahlstrom et al. (1984) and Weitzman (1986). Letters in square brackets refer to discrete parts of a group. Counts in parentheses indicate the number of photophores in a common gland. Individual photophores are referred to by number, counting from the anterior. For example, 1+(2) indicates 1 isolated photophore immediately anterior to 2 that are united.

To facilitate outgroup comparisons in phylogenetic analysis I apply Weitzman's system of photophore terminology to the hatchetfishes (Figure 1) (the superceded terms of Schultz, 1961 are given in parentheses): AC, ventral and extending from anal-fin origin to caudal-fin base, subdivided into AC[A] (='supra-anal'), AC[B] (='anal') and AC[C]

(='subcaudal'); BR, photophores on branchiostegal membranes; OP, photophores associated with the opercular bones; ORB, photophores associated with the orbit; OV, flank photophores between operculum and pelvic-fin base, subdivided into anterior OV[A] (='suprapectoral') and posterior OV[B] (='supra-abdominal'); VAV, ventral photophores between the pelvic- and anal-fin origins (='preanal').

Anatomical and ontogenetic studies made indicate that supra-anal photophores should be treated as an anterior part of the AC cluster (AC[A]). Five discrete arrangements of AC[A] photophores occur in Polyipnus (Figure 2). In some species these photophores appear continuous with the AC[B] section (Fig. 2A) but these occur in the same muscle segments relative to the anal-fin origin and develop by the same sequence as do the other four discrete arrangements (Figures 2B, C, D, E). Since the structure of the first anal-fin pterygiophore is unique among Polyipnus species it is concluded that the five AC[A] forms should be regarded as homologues. The homology of the L (='lateral') photophore of Polyipnus remains uncertain and therefore the unique term is retained. Other important photophore terminology relates to the presence (Fig. 3A, C) or absence (Figure 3B) of denticles on the scales that cover the photophores and whether the AC[C] photophores are separated by broad gaps (Figure 3D), although united as a single gland, or compact (Figure 3E).

A bilaterally symmetrical bony structure (dorsal blade) is usually present at the leading edge of the dorsal fin (Figure 1). This blade is an external projection of two fused pterygiophores and possibly a supraneural (Weitzman, 1974). A pair of ventrolaterally-directed spines which originate on the first anal-fin pterygiophore (AFPS) is present in some species (Figure 1). There has also been some confusion in the literature concerning terminology for spines and spinelike extensions of scales. I follow Schultz (1961) in using "spine" for processes of internal skeletal elements and "denticle" for those originating on scales.

All species of Polyipnus have between one and three posttemporal spines of various sizes and configurations (Figs. 1 and 4). The most complex arrangement is shown in Figure 4A in which there are dorsal (d), median (m) and ventral (v) spines. Some species have reduced ventral and median posttemporal spines (e.g. P. paxtoni), which could be confused with serrations. These spines are distal projections of ossified rods that originate near the structural base of the dorsal posttemporal spine. Serrations are confined to the edges of bony structures. The two-spined configuration (Figure 4B) has long dorsal and short basal (b) spines. The simplest arrangement, shown in Figure 4C in a modified elongate form, is the unispinous posttemporal. Some unispinous species have an anterodorsal barb at the base of the posttemporal spine. There are various spines located at the preopercular angle, occurring in up to three positions. The ventral preopercular spine (VPS) is always the longest in *Polyipnus* and is either free of the distal lamella (Figure 5A) or embedded within it (Figure 5B). A large, free posterior preopercular spine (PPS, Figure 5A) is present in one species (*P. fraseri*) and a dorsal spine (DPS, Figure 5A) is variously reduced or absent.

There is interspecific variation in the form of the longitudinal parietal keel. This structure is in some species a continuous serrated blade (Figure 5C) and in others variously differentiated but often with the posterior section modified as a pair of opposed medial spines (Figure 5D).

Most *Polyipnus* species have a saddle of dark pigment (Figure 1) with a diagnostic pattern of ventral undulations. There is usually a fingerlike lateral projection extending ventrally immediately anterior to the dorsal blade. There may also be a notchlike dorsal deflection of the pigment margin below the dorsal-fin origin (predorsal pigment notch) and/or below the insertion (postdorsal pigment notch).

Unless indicated otherwise, determinations of morphometric and meristic characters were made following Hubbs and Lagler (1958). All fish lengths are standard lengths. The total number of fin rays is given. Vertebral counts are the total number and determined from X-radiographs. Values of meristic characters (excluding photophores) for holotypes are given in parentheses. Head length is the distance from the tip of the snout to the most distant location on the operculum;

orbit length is the diameter of the orbit in the horizontal plane; body depth is always the maximum; caudal-peduncle depth is the minimum; caudal-peduncle length is the distance from the posterior anal-fin ray to the structural base of the central caudal-fin ray; predorsal length is the distance from the origin of the dorsal fin to the tip of the snout; dorsal-fin length and anal-fin length are basal lengths; preanal, predorsal and preventral are the distance from the tip of the snout to the anterior anal-fin, dorsal-fin and pectoral-fin rays, respectively; postdorsal and postanal lengths are the distance from the origins of the dorsal and anal fins, respectively, to the end of the vertebral column. AC[C] length is the length of that photophore cluster at the ventral body margin. AC[B]-[C] length is the minimum distance between the AC[B] and AC[C] photophore clusters.

The generic revision is based on external observations with the exception of vertebral counts which were determined from X-radiographs.

Phylogenetic Methods

OUTGROUP COMPARISON.-According to Weitzman's (1974) phylogenetic analysis, a clade consisting of Sternoptyx and Argyropelecus is the sister group to Polyipnus. These "hatchetfish" genera are the sister group to a clade comprising Argyripnus and Sonoda. This well corroborated set of relationships forms the framework for establishing the polarity (plesiomorphic/apomorphic status) of characters within Polyipnus by the method of outgroup comparison (Wiley, 1981; Watrous and Wheeler, 1981). Of the latter clade, Argyripnus atlanticus Maul and Argyripnus sp. (A. aff. ephippiatus Gilbert and Cramer) were cleared and stained but no representatives of any Sonoda species were available for study. I refer to Weitzman's (1974) descriptions and illustrations exclusively for Sonoda, Araiophos and Thorophos and also include text and figure references where appropriate for the other outgroup genera. Of the remaining sternoptychid genera, Danaphos, Valenciennellus and Maurolicus were examined histologically as a means of checking polarities established within the five-taxon system described above. The most probable ingroup (within Polyipnus) character polarities will usually be established by examining the first two outgroup branches (Maddison et al., 1984). Characters for which there were no comparable structures in the designated outgroup genera were polarized by the method of functional outgroup/functional ingroup comparison (Watrous and Wheeler, 1981; Mooi, 1989).

ANALYTICAL TECHNIQUES.-The phylogenetic analysis was done manually using a computer graphic aid (Maclade software by W.

Maddison) on an Apple MacIntosh Plus microcomputer. A more powerful branch-swapping algorithm was available through PAUP (Phylogenetic Analysis Using Parsimony, version 2.4 by D.L. Swofford) and was used later to check previous results and to search for any shorter (more parsimonious) topologies. The MULPARS option with GLOBAL branch-swapping was used to find the most parsimonious trees. The most parsimonious cladogram, or the one that is most highly corroborated by synapomorphies, is an estimate of phylogenetic relationships. The number of character state changes implied by the most-parsimonious cladogram and a value for CI, the consistency index (Farris and Kluge, 1969), are provided. The latter is calculated by dividing the theoretical minimum number of steps of character state change required (no homoplasy) by the number of steps implied by the estimated cladogram. Values of CI vary from 0 to 1, where the maximum indicates that the character distributions are fully consistent with the cladogram (no homoplasy).

Of the recognized Polyipnus species, 23 were sufficiently common in collections to allow clearing and staining. Since data were missing for the 6 "rare" species (P. bruuni n. sp., P. fraseri Fowler, 1934, P. oluolus Baird, 1971, P. ovatus n. sp., P. parini Borodulina, 1979, P. spinosus Günther, 1887) these taxa were excluded from the initial phylogenetic analysis. After arriving at a cladogram for the 23 "common" species, the others were added on the basis of external synapomorphies, a method which is analogous to the treatment of organisms known only from fossils (see Patterson, 1981). In the cladogram figures of Polyipnus relationships, the rare species are joined to the underlying branching pattern by a broken line to indicate uncertainty.

CHARACTERS.-The characters studied included both external and internal structures. The former includes general body shape and size, photophore configuration and ornamentation/spination of various bony structures. Internal structures were mainly osteological and were visualized to some extent by X-radiography and by bulk histology. The methods of Dingerkus and Uhler (1977) (with refixation according to Potthoff, 1984) are standard in ichthyology for preparation of the stained skeleton. Simplified, the method involves staining for cartilage with alcian blue, digesting muscle and other connective tissue to transparency in a trypsin solution followed by counter-staining for bone in alizarin red S. Pigments are removed in a dilute potassium hydroxide/hydrogen peroxide solution. The resulting preparation is stored in glycerine.

Dissections to expose various joints and other underlying structures were made following clearing and staining. The procedure described by Weitzman (1974) was followed to isolate the suspensorium on the right side, the pectoral girdle and posttemporal on the right side, the branchial basket with the pharyngobranchial bones of the right side and the hyoid arch of the left side.

Only the characters used in phylogenetic analysis are described in this report. General osteology of _Polyipnus_ was covered in detail by Weitzman (1974). Synapomorphies are numbered sequentially and described in the 'PHYLOGENETICS RELATIONSHIPS' chapter. In some cases the character number has a suffix which indicates that the character is homoplastic or inconsistent. These suffixes which follow the system of Fink (1985) are outlined below.

c: The character maps onto another branch of the cladogram and is separated from the present occurrence by at least one branch (convergence).
r: The character reverses at a lower level of generality.
R: The character is in its reversed state.
Rr: The character is in its reversed state and reverses again at a lower level of generality.
R1: The character has reversed twice to a condition resembling the original derived state.

SPECIMENS CLEARED AND STAINED.-Representatives of _Polyipnus_ species and outgroup taxa which were cleared and stained, and their museum catalogue numbers, are listed below. Station data for _Polyipnus_ species listed here are provided in the accounts ('TAXONOMIC REVISION' chapter).

Polyipnus aquavitus Baird, 1971: AMS I.19761-029 (1), 29.0 mm; AMS I.19762-002 (1), 23.4 mm; AMS I.20316-005 (1), 29.0 mm; LACM 44493 (1), 28.1 mm.

P. asper n. sp.: USNM 304746 (2), 47.0 and 50.0 mm.

P. asteroides Schultz, 1938: CAS 61110 (1), 58.0 mm; USNM 295951 (1), 53.9 mm.

P. clarus n. sp.: ASH 89034 (1), 27.0 mm; MCZ 66696 (1), 22.0 mm; USNM 304745 (2 paratypes), 40.3 and 44.0 mm.

P. danae Harold, 1990: ZMUC P208577 (1 paratype), 24.8 mm.

P. elongatus Borodulina, 1979: AMS I.21795-007 (2), 63.0 and 65.0 mm.

P. indicus Schultz, 1961: ASH 88021 (2), 50.0 and 53.6 mm.

P. inermis Borodulina, 1981: ASH 88253 (2), 48.9 and 49.4 mm.

P. kiwiensis Baird, 1971: AMS I.15984-002 (1), 48.6 mm; AMS I.17861-001 (1), 84.0 mm.

P. laternatus Garman, 1899: MCZ 40575 (1), 33.0 mm; USNM 298924 (1), 43.9 mm.

P. matsubarai Schultz, 1961: ASH 88192 (1), 39.0 mm; NSMT P.12415 (1), 32.0 mm.

P. meteori Kotthaus, 1967: IOS uncat., R/V Discovery, Sta. 5415 (2), 15.7 and 29.6 mm; ZMUC P206931 (1), 37.6 mm.

P. nuttingi Gilbert, 1905: BPBM 23790 (1), 53.3 mm; BPBM 24892 (1), 39.9 mm.

P. omphus Baird, 1971: ZMUC P206933 (1), 48.0 mm; ZMUC P207116 (1), 40.0 mm.

P. *paxtoni* Harold, 1989: AMS I.25825-002 (1 paratype), 42.7 mm.

P. *polli* Schultz, 1961: MCZ 66699 (2), 21.0 and 21.4 mm; MCZ 66693 (7), 15.5-28.1 mm; ZMUC P206955 (1), 30.1 mm.

P. *ruggeri* Baird, 1971: AMS I.20305-009 (1), 37.0 mm; ZMUC P206957 (1), 19.6 mm; ZMUC P207118 (1), 50.3 mm.

P. *soelae* n. sp.: AMS I.22808-028 (2), 37.3 and 39.2 mm; AMS I.23425-011 (2), 46.0 and 60.0 mm; AMS I.22817-014 (1), 59.0 mm.

P. *spinifer* Borodulina, 1979: CAS 34854 (1), 49.0 mm; NSMT P.6768 (1), 38.0 mm; ZMUC P206960 (1), 66.9 mm.

P. *stereope* Jordan and Starks, 1904: NSMT P.6772 (1), 37.0 mm; NSMT P.6773 (1), 38.5 mm.

P. *tridentifer* McCulloch, 1914: AMS I.18711-014 (1), 58.0 mm.

P. *triphanos* Schultz, 1938: CAS 56034 (1), 27.4 mm; ZMUC P206963 (1), 30.4 mm.

P. *unispinus* Schultz, 1938: AMS I.19292-008 (1), 28.0 mm; ZMUC P207119 (1), 30.4 mm.

Argyropelecus *aculeatus* Cuvier and Valenciennes, 1849: ASH uncat., R/V *Gadus* Cr. 62 (1), 43.0 mm, R/V *Knorr* Cr. 118 (2), 13.0 and 19.0 mm; CAS uncat. (1), 75.0 mm.

A. *affinis* Garman, 1899: IOS uncat., R/V Discovery Sta. 7803 (1), 35.0 mm; MCZ 66647 (1), 35.0 mm; MCZ 66648 (2), 19.5 and 47.0 mm.

A. gigas Norman, 1930: MCZ 66658 (1), 57.0 mm; MCZ 66661 (1), 29.0 mm.

A. hemigymnus Cocco, 1829: LACM 11075-1 (1), 32.0 mm; MCZ 66655 (1), 37.0 mm; MCZ 66656 (1), 26.0 mm; MCZ 66657 (1), 35.0 mm; SMBA uncat. (4), 13.6, 19.0, 29.0, 36.0.

A. lychnus Garman, 1899: LACM 33587-18 (2), 24.5 and 38.0 mm.

A. olfersi (Cuvier, 1829): BCPM uncat. (2), 17.0 and 60.0 mm.

A. sladeni Norman, 1930: MCZ 66651 (1), 34.0 mm; MCZ 66667 (1), 35.0 mm; MCZ 66669 (1), 13.0 mm; IOS uncat., R/V Discovery Sta. 7824 (1), 52.0 mm.

Argyripnus atlanticus Maul, 1952: FMNH 65693 (1), 55.6 mm; FMNH 71735 (1), 56.4 mm; IOS uncat., R/V *Discovery* Sta. 6374 (1), 44 mm.

Argyripnus sp.: MNHN uncat., Philippines (1), 87.4 mm.

Danaphos oculatus (Garman, 1899): CAS 62347 (1), 31.5 mm.

Maurolicus muelleri (Gmelin, 1788): MCZ 66690 (2), 46.7 and 51.0 mm.

Sternoptyx diaphana Hermann, 1781: ASH uncat., R/V *Gadus* Cr. 51 (2), 31.9 and 34.7 mm.

S. obscura Garman, 1899: MCZ 66702 (1), 19.0 mm.

S. pseudodiaphana Borodulina, 1977: LACM 11293-17 (2), 25.6 and 37.3 mm.

S. pseudobscura Baird, 1971: ORIT 2115 (1), 41.1 mm.

Valenciennellus tripunctulatus (Esmark, 1871): MCZ 66692 (2), 21.8 and 24.9 mm.

Biogeographic Methods

AREA CLADOGRAMS.-Cladograms depicting phylogenetic relationships among Polyipnus species were converted to working hypotheses of area relationship by including the names of the areas inhabited. Distribution patterns within indicated monophyletic subgroups of the genus were compared and those with elements in common were combined to form a general vicariance explanation. This was accomplished using the algorithmic approach, Brooks Parsimony Analysis (Wiley, 1988a, b; Brooks, 1990). Distribution of taxa outside of the set of common areas were explained tentatively in terms of their respective cladograms.

CONSTRUCTION OF A GENERAL AREA CLADOGRAM.-Brooks Parsimony Analysis (henceforth BPA) is analogous to phylogenetic analysis of taxa and implemented by the same algorithm. In BPA the "taxa" are the areas and the "characters" the species inhabiting them. Biogeographic characters were encoded into a binary area-by-taxon matrix (matrix provided in Appendix 1) for a set of 11 Indo-Pacific areas. Widespread taxa were coded as present in each of the subareas in which they occur. Abbreviations and definitions for areas as they appear in the cladograms are defined in Appendix 2. The nodes or branch points of the contributing cladograms are interpreted as hypothetical ancestral species and coded into the matrix to preserve all of the hierarchical relationships. Widespread taxa are coded as present in all geographic areas occupied, a treatment which is referred to Assumption 0 (Zandee and Roos, 1987); the original cladogram is the best estimate of the phylogeny. A wide distribution becomes compartmentalized and the subareas can be explained in the context of the final area cladogram by dispersal or failure to respond to a vicariant event (see Brooks, 1990). For areas that are "missing" in one or more of the contributing cladograms terminal taxa are coded as absent (0) in the area-by-species matrix. Their ancestors or nodes are coded as missing data (9) so that absence in that area has no weight in the assessment of tree topologies (Wiley, 1988b).

The analysis was done using PAUP (Phylogenetic Analysis Using Parsimony, D.L. Swofford, 1985) software on the Memorial University of Newfoundland main UNIX computer with the options: characters ordered, global branch-swapping, MULPARS and CONFILE (following Mayden, 1988). Characters were polarized using a zero vector for the outgroup (Wiley, 1988b). Multiple most-parsimonious cladograms were saved using the CONFILE option and a Strict consensus tree was computed using the program CONTREE (written by D.L.

Swofford). The consensus diagram which combines the elements in common to all input cladograms indicates the relationship among the areas which is most highly corroborated by the original data. A measure of consistency is provided (CI) which varies from 0 to 1 where a value of 1.0 indicates that the characters are fully consistent with the cladogram.

Distributional characters (species or inferred ancestors) were mapped onto the consensus tree and form the basis of the proposed history of Polyipnus species in the Indo-Australian region. Species were not incorporated into this analysis if their occupied area was unique among Polyipnus clades. Computationally there is no advantage to including these taxa because doing so would only generate missing areas for the remaining clades. Tentative explanations for these unique patterns precede the results and discussion of the BPA.

A NOTE ON TERMINOLOGY.-The term endemic is used to describe a species distribution if it is restricted to a single ocean basin, a partially enclosed system of interconnected basins, a section of coastline or an island group. Dating of events is given in Ma (millions of years ago).

DISCLAIMER.-Under the provisions of the International Code of Zoological Nomenclature (Articles 8 and 9), any actions taken in this document regarding nomenclature of Polyipnus is not to be regarded validly published or issued for permanent scientific record.

TAXONOMIC REVISION

Genus Polyipnus Günther, 1887

Polyipnus Günther, 1887:170 [type species Polyipnus spinosus Günther, 1887 by monotypy].-Fowler, 1936:240.-Schultz, 1938:135; 1961:620.-Baird, 1971:79.

Acanthopolyipnus (subgenus) Fowler, 1934:257 [type species Polyipnus fraseri Fowler, 1934 by monotypy].

DIAGNOSIS.-Body deep (42.4-76.7 % SL) and compressed. Eyes large (orbit length 11.1-23.0 % SL) and laterally positioned. Photophores: PV (10), OV[A] (2)+1, OV[B] 1+1+1, L 1 and highly elevated, AC variable among species, never originating anterior of anal-fin origin: AC[A] 0, 1+(2), (3) or 1+1+1, AC[B] (4-14), AC[C] (4). Dorsal blade unique and diminutive, with bilateral dorsolaterally to posterodorsally directed spines. One to three posttemporal spines present. Frontal bones with one transverse and two longitudinal external keels. Extensive posteriorly directed shelflike epiotic processes. Ceratohyal relatively short and with a longitudinal blade dorsally. Urohyal large and expanded. Distal radials of dorsal and anal fins mainly cartilagenous but with rounded ossified lateral plates.

DESCRIPTION.-Maximum body size about 100 mm SL. D 10-16. A 11-20. P 11-16. V 6/7. C 8+9. GR 3-8+7-16 = 11-30.

Vertebrae 31-36. (Frequency distributions of meristic characters: dorsal-fin rays, Table 1; anal-fin rays, Table 2; pectoral-fin rays, Table 3; AC[B] photophores, Table 4; vertebrae, Table 5; gill rakers on first gill arch, Table 6). Body compressed. Anterior body profile broadly elliptical to subrectangular. Flank scales diaphanous, sheetlike, frequently deciduous. Modified scales covering photophores, in many species with denticles laterally and/or ventrally. Frontal with a longitudinal keel usually adjoining and appearing continuous with parietal keel. Additional keels extending anterolaterally from parietal onto frontal, the 2 frontal keels connected by a transverse keel. Margins of dentary and premaxillary with 2 or 3 rows of minute conical to recurved teeth. Maxillary teeth smaller, much more widely spaced than other jaw teeth and essentially excluded from gape. Palatine teeth present or absent. Vomerine dentition various.

Posttemporal limbs elongate and with 1 to 3 posteriorly-directed spines at angle. Ventral limb of posttemporal fused with supracleithrum. Cleithrum with a fanlike pectoral shield which has evenly distributed along its ventral margin 1 to 3 rows of minute spines. Cleithrum terminates anteroventrally in a bipartite 'preabdominal' spine (terminology of Schultz, 1961). Preopercle usually with 2 spines at angle. Ventral preopercular spine largest and of various shapes and attitudes. Dorsal preopercular spine usually very short and indistinct. A third, posterior, preopercular spine occurs in one species (P. fraseri Fowler, 1934). Pelvic skeleton with paired iliac ('postabdominal' of Schultz, 1961) spines. First anal-fin proximal radial with medial and expanded lateral lamellae, some species with paired spines originating on the ventral surface of this modified pterygiophore.

Photophores: IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1. L 1. The following elements of the IC photophore series have (in many species) denticles originating on the covering scales: PV (10). VAV (5). AC[A] 1+(2), (3), 1+1+1 or 0 (AC[A] photophores absent in P. fraseri), AC[B] (4-14), AC[C] (4).

Dorsal dark pigment saddle present; ventral margin with various projections and undulations frequently diagnostic of species. Melanic pigment also associated with dorsal and lateral surfaces of head, photophore tissues, fin bases and body-trunk myosepta.

REMARKS.-Baird (1971:79) in his diagnosis of the genus listed 4 postabdominal spines as characteristic of Polyipnus. Whether applying the terminology of Schultz (1961) or Baird (1971) there are only 2 postabdominal (iliac) spines in all species. This must be an editorial error unless Baird was including as postabdominal the paired 'preanal' spines that originate on the first anal-fin pterygiophore in several *Polyipnus* species (e.g. *P. asteroides* Schultz, 1938, *P. laternatus* Garman, 1899).

Among putative shared derived characters listed by Weitzman (1974) that support monophyly of the 3 hatchetfish genera, *Polyipnus*, *Argyropelecus* and *Sternoptyx*, is the lack of an antorbital bone. Most *Polyipnus* species recognized here do have an antorbital although in many cases (esp. *spinosus* species group) it is highly reduced. In his morphological study of *Polyipnus* Weitzman (1974) examined one of these species (*P. tridentifer* McCulloch, 1914 from the Philippines = *P. spinifer* Borodulina, 1979) and three others in which this bone is reduced or likely absent. The significance of finding an antorbital bone in *Polyipnus* is in corroboration of the sister group relationship of *Sternoptyx* and *Argyropelecus* proposed by Weitzman (1974) on the basis of other characters. Loss of the antorbital should now be viewed as derived at that level.

Baird (1971) recognized 16 *Polyipnus* species in 3 species complexes (*P. spinosus* Günther, 1887, *P. asteroides* Schultz, 1938 and *P. laternatus* Garman, 1899 complexes). Including the contributions of Borodulina (1979; 1981), Harold (1989; 1990a) there are 29 species recognized here. Although the species of Baird's *spinosus* complex probably constitute a monophyletic group, it is no longer constructive to recognize the other complexes based on phylogenetic analysis (pages 204-262). In the following classification the composition of four monophyletic species groups is given. Schultz (1961) used the term "complex" with reference to Polyipnus originally to indicate uncertainty about delimitation of species (especially P. spinosus and P. stereope). The change from "species complex" to "species group" terminology is made to make the distinction that the contained species are closely related, not that there is confusion about their taxonomy. The derived characters in support of these groups and the relationships among their contained species is provided in a brief definition with the accounts of the species and in greater detail in the 'PHYLOGENETIC RELATIONSHIPS' chapter.

Polyipnus Günther, 1887
  P. meteori species group
    P. kiwiensis Baird, 1971
    P. matsubarai Schultz, 1961
    P. meteori Kotthaus, 1967
    P. ovatus new species
    P. ruggeri Baird, 1971
  P. asteroides species group
    P. asteroides Schultz, 1938
    P. bruuni new species
    P. clarus new species
    P. laternatus Garman, 1899
    P. polli Schultz, 1961

  - *P*. *triphanos* Schultz, 1938 complex
- *P*. *omphus* species group
  - *P*. *aquavitus* Baird, 1971
  - *P*. *danae* Harold, 1990
  - *P*. *omphus* Baird, 1971
  - *P*. *unispinus* Schultz, 1938
- *P*. *spinosus* species group
  - *P*. *asper* new species
  - *P*. *elongatus* Borodulina, 1979
  - *P*. *fraseri* Fowler, 1934
  - *P*. *indicus* Schultz, 1961
  - *P*. *inermis* Borodulina, 1981
  - *P*. *nuttingi* Gilbert, 1905
  - *P*. *oluolus* Baird, 1971
  - *P*. *parini* Borodulina, 1979
  - *P*. *paxtoni* Harold, 1989
  - *P*. *soelae* new species
  - *P*. *spinifer* Borodulina, 1979
  - *P*. *spinosus* Günther, 1887 (type species)
  - *P*. *stereope* Jordan and Starks, 1904
  - *P*. *tridentifer* McCulloch, 1914

Key to the Species of *Polyipnus*

1A. Posttemporal bone with serrate external keels and 2 or 3 posteriorly-directed spines; ventral margins of PV photophore scales (abdominal keel) with numerous denticles 2

1B. Posttemporal bone with smooth external keels and a single posteriorly-directed spine; ventral margins of PV scales smooth (except *P*. *unispinus* which has minute denticles) 15

2A. Ventral margin of PV photophore scales rectangular and finely denticulate; one or two lateral dark pigment projections present 3

2B. Ventral margin of PV photophore scales with triangular extensions, each with one or two denticles at apex; lateral dark pigment projections absent .... *P*. *oluolus* Baird, 1971 (Marshall Islands)

3A. AC[B] photophores 7-13 (specimens > 20 mm SL); one lateral dark pigment projection 4

3B. AC[B] photophores 4 (specimens > 20 mm SL); two lateral dark pigment projections .... *P. fraseri* Fowler, 1934 (Philippine Sea)

4A. Ventral posttemporal spine relatively large, its length greater than or equal to half of the length of dorsal spine; posttemporal spines always 3 5

4B. Ventral or basal posttemporal spine short, length less than half of the length of dorsal spine; posttemporal spines 2 or 3 11

5A. Posttemporal spines subequal, tridentlike 6

5B. Posttemporal spines of various lengths, dorsal and ventral spines longest, median much shorter than ventral spine 8

6A. Gap separating AC[B] and AC[C] photophore clusters about equal to length of AC[C] cluster; lateral dark pigment projection long, reaching lateral midline; ventral surface of AC[C] photophore scales smooth, without denticles 7

6B. Gap separating AC[B] and AC[C] photophore clusters about equal to width of one AC[C] photophore; lateral dark pigment projection short, not reaching midline; ventral surface of AC[C] photophore scales denticulate .... P. tridentifer McCulloch, 1914 (Great Australian Bight)

7A. VAV and AC[B] photophore scales smooth, without denticles; AC[B] photophores 8 or 9; gill rakers 23-26 .... P. inermis Borodulina, 1981 (Sala-y-Gomez Ridge, eastern South Pacific)

7B. VAV and anterior AC[B] photophore scales denticulate; AC[B] photophores 10; gill rakers 28 (holotype) or 30 .... P. parini Borodulina, 1979 (western Pacific)

8A. AC[C] photophores separated by distinct gaps; AC[B] photophores 11-14; lateral pigment projection short and triangular; caudal peduncle elongate, longer than deep 9

8B. AC[C] photophores compact, not separated by distinct gaps; AC[B] photophores 9-11; lateral pigment projection tapered ventrally, approaching but not reaching lateral midline; caudal peduncle deep, about as deep as long 10

9A. Anterior AC[B] photophore scales each with 3-6 denticles; ventral and ventrolateral keels of dentary serrate .... _P_. _spinifer_ Borodulina, 1979
(South China Sea to Japanese Archipelago)

9B. Anterior AC[B] photophore scales smooth or with at most a single denticle; ventrolateral keel of dentary smooth, nonserrate .... _P_. _soelae_ new species
(eastern Indian Ocean and Indonesia)

10A. Gill rakers 24-28; anal photophores 9-11 ....
.... _P_. _stereope_ Jordan and Starks, 1904
(Japanese Archipelago)

10B. Gill rakers 19-23; anal photophores 10-12
.... _P_. _spinosus_ Günther, 1887
(eastern Indonesia)

11A. Long, broad lateral dark pigment projection extending ventrally at least to lateral midline; anal rays 15-18; anal photophores 7-12 12

11B. Lateral dark pigment projection approaches but does not reach lateral midline; anal-fin rays 18 or 19;

AC[B] photophores 13 or 14 .... P. elongatus Borodulina, 1979 (Coral Sea)

12A. AC[B] photophores 7-10; posttemporal usually with 2 spines, 1 long dorsal and 1 much shorter basal spine; AC[B] photophore scales smooth or with 1-3 denticles per scale 13

12B. AC[B] photophores 11-12, occasionally 10; posttemporal with 3 spines, 1 long dorsal with subequal medial and ventral spines; AC[B] photophore scales each with more than 3 long denticles originating on lateral scale flanges .... P. paxtoni Harold, 1989 (Coral Sea)

13A. AC[C] photophore scales denticulate; dorsal posttemporal spine long, length at least twice dorsal blade height; lateral dark pigment projection extends ventrally no further than level of centre of orbit 14

13B. AC[C] photophore scales smooth, without denticles; dorsal posttemporal spine short, length about equal to dorsal blade height; lateral dark pigment projection extends ventrally beyond level of centre of orbit .... P. nuttingi Gilbert, 1905 (Hawaiian Islands)

14A. Longitudinal parietal keel evenly serrate and continuous with frontal keel; AC[B] photophore scales smooth, without denticles; palatine teeth present .... P. indicus Schultz, 1961 (western Indian Ocean)

14B. Longitudinal parietal keel discontinuous, posterior region forming 2 minute conical spines directed towards anterior and posterior; AC[B] photophore scales each with 1 to 3 denticles (specimens over 40 mm SL); palatine teeth absent .... P. asper new species (Andaman Sea, eastern Indian Ocean)

15A. Ventral preopercular spine prominent, tapered; AC[B] photophores 9-13 (specimens over 25 mm SL) and without a conspicuous step between photophores #3 and #4; posttemporal spine long and needlelike 16

15B. Ventral preopercular spine reduced and imbedded within ventral lamella of preopercle; AC[B] photophores 7-10 and with a conspicous step between #3 and #4; posttemporal spine short and stout, expanded basally 20

16A. Gill rakers 16-21; posttemporal spine of moderate length (5.7-10.7 % SL), extending posteriorly about half way to dorsal blade; AC[C] photophores in contact or separated by gaps less than the diameter of 1 photophore; body size moderate, reaching at least 45 mm SL 17

16B. Gill rakers 11-15; posttemporal spine highly elongate (10.0-16.1 % SL), extending posteriorly to or beyond dorsal blade origin; AC[C] photophores separated by gaps greater than diameter of 1 photophore; miniature species, not known to exceed 35 mm SL 18

17A. AC[A] photophores elevated relative to AC[B] #1 by a distance greater than twice the diameter of 1 photophore; AC[A] #1 located ventrally to #2; OV[B] photophores arranged in a 'V' configuration; caudal peduncle profile rectangular, slightly expanded posteriorly; lateral dark pigment projection short, tapered and not bordered posteriorly by a lightly pigmented stripe .... _P_. _laternatus_ Garman, 1899

(tropical western Atlantic)

17B. AC[A] photophores elevated relative to AC[B] #1 by a distance less than the diameter of 1 photophore; AC[A] #1 at about same elevation as or dorsally of AC[A] #2; OV[B] photophores arranged in an anteriorly-inclined straight line; caudal peduncle profile tapered posteriorly; lateral pigment projection short but ventral termination blunt, and bordered posteriorly by a narrow, anterodorsally-arced lightly pigmented stripe .... P. omphus Baird, 1971 (equatorial Indo-Pacific)

18A. Gill rakers 13-15; lateral pigment projection short, hemispherical; caudal peduncle rectangular, compressed .... P. aquavitus Baird, 1971 (eastern Indonesia, Coral and Tasman Seas)

18B. Gill rakers 11 or 12; lateral pigment projection short and triangular or absent; caudal peduncle highly elongate, rodlike 19

19A. Ventral margins of PV photophore scales with minute denticles; AC[B] photophores 9-10, posterior 4-6 not visibly interconnected; ventral margin of pigment saddle parallel to dorsal surface of body, without projections or undulations ... P. unispinus Schultz, 1938 (Indonesia, Coral and Tasman Seas)

19B. Ventral margins of PV photophore scales smooth, without denticles; AC[B] photophores 11 or 12, only posterior 1 or 2 photophores at most not visibly interconnected; ventral margin of dorsum pigment with a minute broad triangular lateral pigment projection ventral to dorsal blade origin .... P. danae Harold, 1990 (South China Sea)

20A. AC[A] photophore #2 slightly ventral to and not connected to #3; 1 or 2 rows of large, recurved teeth present on posteromedial shaft of vomer 26

20B. AC[A] photophore #2 similarly elevated and connected to #3 in a common gland; no teeth present on posteromedial shaft of vomer 21

21A. Anal-fin pterygiophore spines present; gill rakers 19-24 22

21B. Anal-fin pterygiophore spines absent; gill rakers 14-20 24

22A. OV[B] photophores in a 'V' configuration; anal-fin base highly convex, with pterygiophores extending noticeably beyond ventral margins of AC[B] photophores; AC[B] 7/8 .... P. polli Schultz, 1961

(tropical eastern Atlantic)

22B. OV[B] photophores in an anteriorly-inclined straight line or #2 and #3 at same elevation with #1 located dorsally; anal-fin base nearly straight, pterygiophores not extending noticeably beyond ventral margins of AC[B] photophores; AC[B] 8-10 23

23A. Lateral pigment projection long and tapered, extending ventrally to lateral midline; overall pigmentation very dark, body-trunk myosepta with heavy concentrations of dark pigment; anal-fin pterygiophore spines short and ventrally expanded; AC[A] #3 elevation (relative to AC[B] #1) 6.9-7.9 % SL; gill rakers 20-24 .... P. asteroides Schultz, 1938

(Caribbean Sea and off Greater Antilles)

23B. Lateral pigment projection short and triangular, extending ventrally less than half way to lateral midline; overall pigmentation pale, body-trunk myosepta diffusely delineated with dark pigment; anal-fin pterygiophore spines long and needlelike; AC[A] #1 elevation (relative to AC[B] #1) 4.9-6.6 % SL; gill rakers 19-21 .... P. clarus new species

(tropical western Atlantic)

24A. Ventral margin of dark dorsomedian pigment from caudal peduncle to dorsal-fin origin parallel to dorsal surface of body; AC[A] photophores in a horizontal straight line and united as a common gland .... _P_. _bruuni_ new species
(western Indian Ocean, off Kenya)

24B. Ventral margin of dark dorsomedian pigment arched dorsally ventral to dorsal-fin insertion; AC[A] photophore #1 ventrally displaced relative to #2 by a distance greater than the diameter of one AC[A] photophore 25

25A. Gill rakers 14-19; dorsal-fin rays 11/12; lateral pigment projection short, extending ventrally no more than half way to lateral midline .... _P_. _triphanos_ Schultz, 1938
(South China Sea, Indonesia and Coral Sea)

25B. Gill rakers 20; dorsal-fin rays 13; lateral pigment projection long and broad, extending ventrally to lateral midline .... _P_. aff. _triphanos_ Schultz, 1938
(eastern Indian Ocean, off Sumatra)

26A. Gill rakers 22-24; lateral pigment projection very narrow, its width ventrally less than the diameter of

L photophore .... <u>P</u>. <u>matsubarai</u> Schultz, 1961 (Japanese Archipelago, Northwest Pacific Basin)

26B. Gill rakers 13-18; lateral pigment projection broad, its width ventrally greater than the diameter of L photophore 27

27A. Lateral pigment projection reduced or absent; OV[B] photophores arranged in a horizontal line .... <u>P</u>. <u>ruggeri</u> Baird, 1971 (Tasman Sea)

27B. Lateral pigment projection well-developed and extending ventrally at least to lateral midline; OV[B] photophores variously arranged but never in a horizontal line 28

28A. Ventral margin of pigment saddle with an abrupt postdorsal notch; lateral pigment projection ventrally tapered; indistinct dorsal step between photophores AC[B] #3 and #4; posttemporal spine with a pronounced anterodorsal barb .... <u>P</u>. <u>meteori</u> Kotthaus, 1967 (equatorial Indo-Pacific)

28B. Ventral margin of pigment saddle with broad postdorsal notch; lateral pigment projection terminating bluntly near lateral midline; pronounced dorsal step between photophores AC[B] #3 and #4; posttemporal spine anterodorsal surface without a barb 29

29A. Anal-fin rays 15-17; pectoral-fin rays 15-16; lateral ridges of preopercle smooth, nonserrate .... _P_. _kiwiensis_ Baird, 1971
(Tasman Sea and off New Zealand)

29B. Anal-fin rays 18; pectoral-fin rays 14; lateral keels of preopercle with shallow serrations around angle .... _P_. _ovatus_ new species
(South China Sea off the Philippines)

Polyipnus _meteori_ species group

DEFINITION.-Large fanglike teeth present on posteromedial shaft of vomer. Premaxillary ascending process broadly triangular. Symphyseal process of dentary truncate. Iliac spine of pelvic skeleton shorter than ischial process. Dorsal limb of posttemporal finely serrate. See 'PHYLOGENETIC RELATIONSHIPS', page 208.

Five species of the Indo-Pacific region: P. kiwiensis, P. matsubarai, P. meteori, P. ovatus and P. ruggeri.

Polyipnus kiwiensis Baird, 1971

FIGURE 10

Polyipnus kiwiensis Baird, 1971:103-104 [holotype fig. 79].-Paxton et al., 1989:192 [part, specimens from northwest Australian shelf questionably identified as P. kiwiensis].-Harold, 1990b:515.

DIAGNOSIS.-Gill rakers 16-18. Anal-fin rays 15-17. Pectoral-fin rays 15/16. Lateral pigment projection long and broad, usually reaching lateral midline. One short posttemporal spine present (length 3.9-5.4 % SL). Anal-fin pterygiophore spines and photophore scale denticles absent. AC[A] photophores separate, #2 and #3 conspicuously elevated relative to first AC[B]. AC[B] 8-10. AC[C] photophores compact, not separated by gaps. Teeth present on posteromedial vomerine process. Anteroventral ramus of preopercle smooth, nonserrate.

DESCRIPTION.-Maximum adult body size 82.0 mm SL. D (12) 11-12. A (17) 15-17. P 15-16. V 7. GR (17) 5/6+11/12 = 16-18. Vertebrae (34) 33. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin ovate, acutely tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, slightly elongate. Scales diaphanous, cresentic laterally, round and crowded dorsally. External bony ridges and keels of skull nonserrate except as noted below. Ventral margin of dentary slightly convex. Margins of dentary and premaxillary with long recurved teeth. Maxillary teeth recurved but much shorter than other jaw teeth. Palatine with a row of 3-6 large conical teeth. Anterolateral processes of vomer each with a small patch of 2 or 3 recurved fanglike teeth. Two to five recurved fanglike teeth present on posteromedial process of vomer. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel terminates posteriorly in a conical spine. Dorsal and ventral arms of posttemporal obtusely divergent and support a short (3.9-5.4 % SL) spine. Ventral margin of pectoral shield bears 14-21 minute triangular spines. Preopercle with two spine: ventral spine straight and short (1.4-1.9 % SL), ventrally directed, embedded entirely within ventral lamella except for terminus; dorsal spine reduced (represented only by abrupt angle in proximal preopercular keel). Dorsal blade smooth anterodorsally, and apically depressed with two rounded triangular spines, one per side, directed posterodorsally. Anal-fin pterygiophore spines absent. Adipose-fin base of moderate length, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 36.5-38.4, orbit length 14.6-16.4, body depth 64.6-67.7, caudal-peduncle depth 10.9-11.7, caudal-peduncle length 13.7-15.4, dorsal-fin length 21.1-23.4, anal-fin length 25.1-27.3, preanal length 73.0-76.1, predorsal length 58.3-63.7, preventral length 65.7-67.9, postdorsal length 55.4-58.9, postanal length 38.7-40.9, AC[C] length 6.7-7.7, AC[B]-[C] length 3.0-3.5.

Ventral margins of all photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in a "V" configuration but with #1 elevated dorsally, less than the diameter of one photophore, relative to #3. PV (10). L 1. VAV (5). AC[A] 1+1+1, not united in a common gland, increasing in elevation from anterior to posterior and #2 and #3 usually proximal to one another. AC[B] (10, according to illustration of holotype in Baird, 1971: fig. 79; 8-9), with a dorsal step between #3 and #4. AC[C] (4), compact.

Dark pigment saddle with abrupt predorsal and broad postdorsal notches. Lateral pigment projection long and tapered, termination rounded and ventral to lateral midline. Dark pigment also present in association with glandular and ventral nonglandular photophore tissues, dorsal and dorsolateral regions of head, anterior dorsal-fin and outer caudal-fin rays, external surface of dentary, scale pockets and delineating body-trunk myosepta. Isolated melanophores present in association with body-trunk myosepta.

SIMILAR SPECIES.- *Polyipnus kiwiensis* most closely resembles *P. ovatus*, both of which have a long lateral pigment projection with a rounded terminus and a very broad postdorsal pigment notch. The present species is distinguished from *P. ovatus* by nonserrate preopercular ridges, low number of gill rakers (15-17 as compared with 18) and anal-fin rays (15-17 as compared with 18), and higher pectoral-fin ray counts (15/16 as compared with 14). The pattern of pigmentation is also similar to *P. triphanos*, *P.* aff. *triphanos* and *Polyipnus* n. sp. MS Aizawa; *P. kiwiensis* is distinguished by the 1+1+1 AC[A] photophore configuration [as compared with 1+(2)] and presence of posteromedial vomerine teeth.

DISTRIBUTION.-*Polyipnus kiwiensis* is restricted to the Tasman Sea off the southeast coast of Australia and continental slope areas of New Zealand (Figure 11). A disjunct population of this species has been reported off the northwest coast of Australia (Paxton et al., 1989). Specimens from that area are referred to *P.* aff. *kiwiensis*.

REMARKS.-This species was originally thought by Baird (1971) to be endemic to the New Zealand slope. The range is here expanded to encompass both east and west sides of the Tasman Sea. Specimens from the northwest Australian shelf (*P.* aff. *kiwiensis*; WAM P28071-001) differ in some meristic character values from the Tasman Sea population. Further study may reveal there to be an undescribed species here but this apparent differentiation is, for the present, best regarded as geographic variation.

MATERIAL EXAMINED.-Holotype: NMNZ 4802 (1, 59.5 mm), 36°50'S 176°10'E, R/V *Tui*, 26 Sep 1962 (not seen).

Non-types: AMS I.15984-002 (1, 48.6 mm), 34°43'S 151°12'E, 0-357 m, R/V *Kapala*, field no. K71-11-04, -2225 h, 06 Jul 1971. AMS I.24496 (1, 73.6 mm), 35°01'S 151°06'E, 0-412 m, R/V *Kapala*, field no. K77-22-08, 1 Dec 1977. AMS I.17863 (1, 82.0 mm), 33°12'S 152°16'E, 0-366 m, R/V *Kapala*, field no. KP72-06-15, 0600-0830 h, 1 Nov 1972. AMS I.19855 (1, 79.4 mm), 33°42'S 151°12'E, (0-) 448-461 m, R/V *Kapala*, field no. K76-29-01, -1430 h, 20 Dec 1976. AMS I.17861-001 (1, 73.8 mm), 33°34'S 151°59'E, 0-411 m, R/V *Kapala*, field no. KP72-06-13, 1940-2230 h, 31 Oct 1972. AMS I.17864-003 (1, 77.3 mm), 34°01'S 152°31'E, 0-366 m, R/V *Kapala*, field no. K72-06-17, 1200-1430 h, 01 Nov 1972. AMS I.24501-004 (1, 60.3 mm), 35°39'S 150°42'E, (0-) 252-351 m, R/V *Kapala*, field no. K77-02-09, 06 Apr 1977. WAM P28071-001 (7, 54.0-72.0 mm), about 18°08'S 118°13'E, 90 km. off Rowley Shoals, (0-) 350-354 m, 17 Aug 1983.

Polyipnus matsubarai Schultz, 1961

FIGURE 9

Polyipnus matsubarai Schultz, 1961:641-642 [holotype fig. 17]; 1964:267.-Baird, 1971:101-102 [fig. 77].-Kubota et al. 1984:43-50 [fig. 1].-Fujii, 1984:47 [pl. 49N].-Harold 1990a:1114; 1990b:515.

Polyipnus japonicus Schultz, 1961:643 [holotype fig. 19]; 1964:268.

Polyipnus asteroides.-Matsubara, 1941:2; 1950:192.

DIAGNOSIS.-Gill rakers 22-24. Lateral pigment projection long and very narrow, extending ventrally of lateral midline. One short posttemporal spine present (length 2.9-6.0 % SL). Anal-fin pterygiophore spines and photophore scale denticles absent. AC[A] photophores separate, #2 and #3 conspicuously elevated relative to first AC[B]. AC[B] 8-9. AC[C] photophores compact, not separated by gaps. Teeth present on posteromedial vomerine process.

DESCRIPTION.-Maximum adult body size 96.7 mm SL. D (13) 12-13. A (17) 16-17. P (12/13) 12-14. V 7. GR 6/7+15/16 = 22-24. Vertebrae (33) 33. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin round, acutely tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, highly elongate. Body flank scales diaphanous. External bony ridges and keels of skull nonserrate except as noted below. Ventral margin of dentary slightly convex. Margins of dentary and premaxillary with long recurved teeth. Maxillary teeth shorter, conical. Three of four conical teeth on palatine. Anterolateral processes of vomer each with a broad patch of 4 or 5 conical teeth. Four to six recurved teeth present on posteromedial process of vomer. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel which terminates posteriorly in a short conical spine. Dorsal and ventral arms of posttemporal obtusely divergent and support a short (2.9-6.0 % SL) needlelike spine. Dorsal arm of postemporal serrate. Ventral margin of pectoral shield bears 12-21 minute triangular spines. Preopercle with two spines: ventral spine posteroventrally directed, recurved, short (1.4-2.9 % SL), embedded entirely within ventral lamella except for terminus; dorsal spine reduced (represented only by abrupt angle in proximal preopercular keel). Dorsal blade smooth anterodorsally, and apically depressed with two triangular spines, one per side, directed posterodorsally. Anal-fin pterygiophore spines absent. Adipose-fin base long, occupying about three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 30.4-32.3, orbit length 14.3-15.5, body depth 57.7-63.3, caudal-peduncle depth 9.9-12.9, caudal-peduncle length 14.3-16.2, dorsal-fin length 24.4-25.6, anal-fin length 26.2-29.7, preanal length 64.6-69.0, predorsal length 53.5-58.5, preventral length 58.7-63.5, postdorsal length 54.0-59.7, postanal length 40.5-45.8, AC[C] length 5.8-7.6, AC[B]-[C] length 5.1-5.6.

Ventral margins of photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (3). OV[B] (3), arrangement variable but #1 always dorsally elevated relative to #2 and #3. PV (10). L 1. VAV (5). AC[A] 1+1+1, each isolated, not united in a common gland, increasing in elevation incrementally from anterior to posterior. AC[B] (9, 8-9), with a dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with abrupt predorsal and broad postdorsal notches. Lateral pigment projection long and very narrow, terminating ventrally of lateral midline. Dark pigment also present in association with glandular photophore tissues, posterodorsal region of head, bases of dorsal-fin rays, and delineating body-trunk myosepta.

SIMILAR SPECIES.-Of the members of the _meteori_ species group species _P_. _matsubarai_ most closely resembles _P_. _meteori_ in pigmentation both having a very long narrow lateral band of dark pigment. The postdorsal pigment notch is broad in _P_. _matsubarai_, however, and not abrupt. _Polyipnus_ _matsubarai_ is distinguished from all other members of the species group by its high gill raker counts (22-24 as compared with 13-18, total range.

DISTRIBUTION.-Polyipnus matsubarai is known mainly from the Japanese Archipelago, especially the Suruga Bay area where it is often caught by commercial shrimp trawls (Kubota et al., 1984). Captures have also been made in the Philippine Sea and eastward in the Northwest Pacific Basin near the Hawaiian-Emperor Seamounts (Figure 7). Bathymetric range is generally shallow; about 80 to 130 m, according to Kubota et al., 1984.

Other Polyipnus species occuring in the area are P. spinifer and P. stereope (both P. spinosus species group) and Polyipnus n. sp. MS Aizawa (probably P. asteroides species group).

REMARKS.-The holotype of P. japonicus Schultz, 1961 was re-examined during the present study and it appears to be a juvenile or subadult of P. matsubarai. The very low number of AC[B] photophores (4) which Schultz believed was an indication of close relationship with P. fraseri is expected in small Polyipnus (Harold, 1990b). Baird (1971: 101) listed P. japonicus as a junior synonym of P. matsubarai but did not comment.

Schultz (1961:641), who described P. matsubarai, discussed the species in terms of differences from P. asteroides (Atlantic Ocean), which at the time appeared to be the most similar of the nominal species. It is now recognized that P. matsubarai is a northerly representative of the Indo-Pacific P. meteori species group.

MATERIAL EXAMINED.-Holotype: USNM 179793 (1, 64.0 mm), Kumanonada, Japan, no exact data.

Paratypes: USNM 179794 (1, 51.5 mm) and FAKU cat. no. unknown (3, 45.0-59.0 mm), same data as holotype (FAKU specimens not seen).

Other Material: ASH 88192 (2, 39.0-42.6 mm), Suruga Bay, Japan, no exact data. IOAN uncat. (6, 52.3-66.5 mm), 37°27'N 160°00'E, 260-0 m, R/V Mys Tikhiy Sta. 41, 21 May 1979. NMC 79-0009 (1, 96.7 mm), Kyushu-Palau Seamount region, approx. 600 km east of Okinawa (about 23°N 135°E). NMC 79-0006 (1, 84.1 mm), same data as NMC 79-0009. NMFSH P-1002 (1, 67.7 mm), 29°47.7'N 179°03.8'E, R/V Townshend Cromwell Cr. 87-04, Sta. 102, 25 Aug 1987. NSMT P12415 (1, 25.2 mm), off Yui, Suruga Bay, Japan (about 35°00'N 138°15'E, 2 May 1970. ORIT 2581 (1, 41.4 mm) and ORIT 2582 (1, 39.5 mm), Suruga Bay, Japan (about 35°N 138°E), 13 Apr 1967. SIO H53-367-10A (1, 12.3 mm), Kii Strait, Japan, no exact data (P. japonicus Schultz, 1961, holotype). ZMUC P206927 (1, 19.0 mm), 25°11'N 122°35'E, 600 mwo, R/V Dana Sta. 3722 II, 2250-2350 h, 29 May 1929. ZMUC P206926 (1, 33.0 mm), 25°11'N 122°35'E, 1000 mwo, R/V Dana Sta. 3722 I, 2250-2350 h, 29 May 1929.

Polyipnus meteori Kotthaus, 1967

FIGURE 6

Polyipnus meteori Kotthaus, 1967:26-27 [holotype fig. 44; holotype x-radiograph fig. 45; otoliths fig. 46].-Baird, 1971:104; 1986:257.-Harold 1990a:1114; 1990b:515.

DIAGNOSIS.-Gill rakers 13-18. Lateral pigment projection long and very narrow, extending ventrally of lateral midline. Abrupt archlike deflection of dorsum pigment ventral margin dorsal to AC[A] photophores. One short posttemporal spine present (length 2.5-6.6 % SL). Anal-fin pterygiophore spines and photophore scale denticles absent. AC[A] photophores separate, #2 and #3 conspicuously elevated relative to first AC[B]. AC[B] 7-9. AC[C] photophores compact, not separated by gaps. Teeth present on posteromedial vomerine process.

DESCRIPTION.-Maximum adult body size 54.6 mm SL. D (12) 11-12. A (16) 16-17. P (15) 13-15. V (6) 6-7. GR 4/5+9-13 = (15/13) 14-18. Vertebrae (33) 33. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin broadly elliptical, moderately tapered posteriorly as far as anterior margin of AC[C] photophore cluster. Profile of caudal peduncle rectangular, elongate. Body flank scales diaphanous, sheetlike. External bony ridges and keels of skull smooth and nonserrate, except as noted below. Ventral margin of dentary slightly convex. Margins of dentary and premaxillary with minute recurved teeth. Maxillary teeth shorter, conical. Three to five conical teeth on palatine. Anterolateral processes of vomer each with a patch of 2 to 4 conical teeth. Four to six large recurved teeth present on posteromedial process of vomer. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel terminates posteriorly in a short conical spine. Dorsal and ventral arms of posttemporal obtusely divergent and support a short (2.5-6.6 % SL) spine. Dorsal arm of postemporal serrate. Ventral margin of pectoral shield bears 10-14 minute conical spines. Preopercle with two spines: ventral spine posteroventrally directed, recurved, short (2.0-5.5 % SL), embedded entirely within ventral lamella except for terminus; dorsal spine reduced (represented only by abrupt angle in proximal preopercular keel). Dorsal blade short-based, smooth anterodorsally, terminating posteriorly with two triangular spines, one per side, directed posterodorsally. Adipose-fin base long, occupying more than three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 30.8-36.6, orbit length 13.2-20.1, body depth 54.6-68.6, caudal-peduncle depth 11.7-14.0, caudal-peduncle length 13.6-17.4, dorsal-fin length 21.5-23.2, anal-fin length 28.1-31.3, preanal length 65.4-74.1, predorsal length 51.5-58.1, preventral length 58.7-72.4, postdorsal length 53.1-56.8, postanal length 43.7-48.0, AC[C] length 5.9-7.5, AC[B]-[C] length 4.9-6.7.

Ventral margins of photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, arrangement variable but #1 always dorsally elevated relative to #2 and #3, commonly in a "V" arrangement. PV (10). L 1. VAV (5). AC[A] 1+1+1, each isolated, not united in a common gland, increasing in elevation incrementally from anterior to posterior. AC[B] (9; 7-9), with a dorsal step #3 and #4. AC[C] (4), not separated by gaps.

Dark pigment saddle with abrupt predorsal and postdorsal notches. Postdorsal notch reaches dorsum in some specimens. Lateral pigment projection long and tapered, terminating ventrally of lateral midline. Dark pigment also present in association with glandular photophore tissues, posterodorsal region of head, bases of caudal- and dorsal-fin rays, ventral surface of AC[B] photophore cluster, and delineating body-trunk myosepta in two concentric lines.

SIMILAR SPECIES.-Of the members of the meteori species group P. meteori most closely resembles P. matsubarai with regard to body shape and extent of lateral pigmentation but is distinguished by lower gill raker counts (13-18 compared with 22-24) and the presence of an abrupt postdorsal pigment notch. Such a pigmentation pattern is also present in *P. ruggeri* but this species has a highly reduced lateral pigment projection and an unusual convex abdominal profile.

DISTRIBUTION.-*Polyipnus meteori* is more widely distributed longitudinally than any other species in the genus. It was originally known from a single station in the western Indian Ocean off Madagascar but is reported here from the Indo-Malayan Archipelago and as far east as the Line Islands (central Pacific) thus spanning more than 170 degrees of longitutude (Figure 7). *Polyipnus meteori* appears to be restricted to the equatorial region (no captures at latitude greater than 15°). This species has been collected by discrete-depth sampling gear (i.e. RMT-8 net) in Indonesia and the results show that it occurs between 250 and 320 m and between 100 and 290 m at night. The only capture known with certainty to have been made during daylight hours was an open tow to 650 m.

The distribution of *P. meteori* as presently understood is disjunctive. The more likely cause is insufficient collecting effort in the gap areas. Numerous collections in the Indonesian Archipelago show overlap between the range of this wide-ranging species and *P. ovatus*, *P. triphanos*, *P. omphus*, *P. danae*, *P. aquavitus*, *P. unispinus*, *P. danae*, *P. soelae*, *P. spinifer* and *P. spinosus*.

REMARKS.-One specimen is here tentatively referred to P. aff. meteori (ZMUC P206930, Java Trench off Sumatra) because of atypical morphometric values and photophore arrangements. Although this specimen possibly represents an undescribed species it is not treated formally here, expecting that material in better condition will eventually be collected (ZMUC P206930 is decalcified and has been badly damaged by fungal infestation).

MATERIAL EXAMINED.-Holotype: ZMH 4887 (1, 37.0 mm), 02°54'S 58°02'E to 02°46'S 57°59.5'E, 0-450 m, R/V Meteor Sta. 170, 2345-0054 h, 30-31 Jan 1965.

Other Material: IOAN uncat. (1, 44.1 mm), 05°18'N 125°50'E, 200-0 m, R/V Vityaz Cr. 57, Sta. 7227, 0212-0312 h, 24 Feb 1975. IOAN uncat. (1, 66.0 mm), 01°43'S 143°04'E, 0-500 m, R/V Vityaz Cr. 50, Sta. 7321, 6 Apr 1975. IOAN uncat. (1, 60.5 mm), 05°15'N 124°05'E to 05°20'N 124°02'E, 0-500 m, R/V Vityaz Cr. 57, Sta. 7231, 2320-0020 h, 25-26 Feb 1975. IOS uncat. (2, 15.7-29.6 mm), 00°03'N 58°03.3'E to 00°32.1'N 58°04'E, 1200 mwo, R.R.S. Discovery Sta. 5415, 2030-0242 h, 1965. LACM 36143- uncat. (1, 50.8 mm), 04°43'S 129°36'E, 0-1000 m, R/V Alpha-Helix Sta. 108, 0020-0445 h, 8 May 1975. LACM 36063- uncat. (1, 24.8 mm), 00°0.6'S 128°46.3'E, 250-320 m, R/V Alpha-Helix Sta. 140, 0203-0310 h, 20 May 1975. LACM 36054- uncat. (2, 21.1-22.6 mm), 04°49.5'S 129°55'E, 0-650 m, R/V Alpha-Helix Sta. 76, 0955-1247 h, 27 Apr 1975. MCZ 64694 (1, 18.6 mm), 04°56'S

152°26'E, R/V Lady Basten, 23 May 1981. SIO 61-541-10 (1, 29.0 mm), 05°01'S 127°57'E, Naga Expedition, 25 Apr 1961. USNM 256965 (1, 21.3 mm), 09°54'S 150°03'W to 09°46'S 150°02'W, 0-300 m, R/V Wecoma, Norpax Expedition field no. 77-12-5, 5 Dec 1977. ZMUC P206928 (1, 54.6 mm), 12°44'N 110°45'E, 1000 mwo, R/V Dana Sta. 3712 I, 1420-1620 h, 18 May 1929. ZMUC P206929 (2, 12.8-22.6 mm), 03°55'N 134°30'E, 600 mwo, R/V Dana Sta. 3749 II, 0320-0520 h, 11 Jul 1929. ZMUC P206930 (1, 64.1 mm), 00°51.5'S 99°24.5'E, 1000 mwo, R/V Dana Sta. 3821 I, 0400-0600 h, 14 Sep 1929. ZMUC P206931 (1, 37.6 mm), 11°33'S 41°44'E, 1000 mwo, R/V Dana Sta. 3949 I, 1915-2045 h, 6 Jan 1930. ZMUC uncat. (1, 20.4 mm), 14°16'S 41°48'E, 600 mwo, R/V Dana Sta. 3951 II, 1900-2030 h, 7 Jan 1930. ZMUC uncat. (2, 17.7-21.1 mm), 07°53'S 116°18'E, 600 mwo, R/V Dana Sta. 3800 I, 1925-2125 h, 13 Aug 1929. ZMUC uncat. (1, 15.7 mm), 05°18'N 90°55'E, 2500 mwo, R/V Dana Sta. 3904 III, 1745-1945 h, 18 Nov 1929.

Polyipnus ovatus new species

FIGURE 12

DIAGNOSIS.-Gill rakers 18. Anal-fin rays 18, Pectoral-fin rays 14. Lateral pigment projection long and broad, usually reaching lateral midline. One short posttemporal spine present (length 4.4 % SL). Anal-fin pterygiophore spines and photophore scale denticles absent. AC[A] photophores separate, #2 and #3 conspicuously elevated relative to first AC[B]. AC[B] (9). AC[C] photophores compact, not separated by gaps. Teeth present on posteromedial vomerine process. Anteroventral ramus of preopercle serrate.

DESCRIPTION OF HOLOTYPE.-Maximum adult body size: 47.0 mm SL. D (12). A (18). P (14). V (6). GR (5+13=18). Vertebrae (33). Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin ovate, acutely tapered posteriorly as far as AC[C] photophore cluster. Profile of caudal peduncle rectangular, short. Scales diaphanous, deciduous (only remaining body scales on anterior dorsum), round. Ventral margin of dentary smooth, nonserrate, and slightly convex. Margins of dentary and premaxillary with long recurved teeth. Maxillary with shorter conical teeth. Three conical palatine teeth in a medial row. Anterolateral processes of vomer each with a patch of 2 or 3 recurved teeth. Five recurved fanglike teeth on posteromedial process of vomer in 2 medial rows. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel terminates anteriorly and posteriorly in spines, anterior spine more than twice the length of posterior spine. Dorsal and ventral limbs of posttemporal nonserrate, obtusely divergent and support a short (4.4 % SL) dorsally-concave spine. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 12 or 13 minute triangular spines. Preopercle with two spines: ventral spine straight and short (2.4 % SL), ventrally directed, embedded entirely within ventral lamella except conical terminus; dorsal spine short (slightly longer than preopercular serration), triangular, bladelike. Preopercular external ridges smooth except for the presence of a single prominent serration immediately anterior of preopercular angle. Dorsal blade smooth and obtusely convex anterodorsally, apically depressed with two rounded triangular spines, one per side, directed posterodorsally. Anal-fin pterygiophore spines absent. Adipose fin base moderately long, occupying about two thirds of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

<u>Morphometric</u> <u>characters</u> (% SL): Head length 35.1, orbit length 14.6, body depth 60.0, caudal-peduncle depth 10.0, caudal-peduncle length 14.1, dorsal-fin length 20.4, anal-fin length 27.2, preanal length 70.2, predorsal length 58.5, preventral length 63.0, postdorsal length 53.2, postanal length 41.7, AC[C] length 6.1, AC[B]-[C] length 3.8.

Ventral margins of photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1). OV[A] (2)+1. OV[B] 1+1+1, in a "V" configuration but with #1 elevated dorsally a distance greater than diameter of one photophore, relative to #3. PV (10). L 1. VAV (5). AC[A] 1+1+1, separate, not united in a common gland, increasing in elevation from anterior to posterior and #2 and #3 proximal to one another. AC[B] (9), with a dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with abrupt predorsal and broad postdorsal notches. Long, broad, tapered lateral projection of dark pigment present that terminates ventrally of lateral midline dorsal to OV[B] photophores. Dark pigment also present in association with photophore tissues, dorsal and dorsolateral regions of head, dorsal- and caudal-fin ray bases, and delineating body-trunk myosepta. Isolated melanophores in association with body-trunk myosepta and their intersections with lateral midline.

SIMILAR SPECIES.-*Polyipnus ovatus* and *P. kiwiensis* are most similar with regard to body shape and pigmentation pattern but clearly distinguished by fin-ray counts; *P. ovatus*: A 18, P 14, V 6 compared with *P. kiwiensis*: A 15-17, P. 15/16, V 7. The pattern of pigmentation is also similar to *P. triphanos* and *Polyipnus* n. sp. MS Aizawa (*asteroides* species group), species which differ from *P. ovatus* in vomerine dentition and AC[A] photophore arrangment.

DISTRIBUTION.-The holotype was collected in Pagapas Bay, west coast of the Philippine Islands (Figure 11). The depth of capture (194-209 m) is relatively shallow for the genus but since this was a night sample it may result from vertical migration.

Polyipnus ovatus is one of several species now known from the South China Sea (also P. spinifer, P. danae, P. meteori and P. triphanos). Polyipnus kiwiensis, the most closely related species to P. ovatus, occurs in the Tasman Sea with a geographic variant off northwestern Australia.

REMARKS.-The holotype is remarkably similar in body shape to material here ascribed to P. kiwiensis. However, there are exclusive meristic characters (6 pelvic-fin rays is otherwise unknown in the meteori species group) as well as presence of preopercular serrations as distinguishing features. The presence or absence of serrations on certain bones in Polyipnus species is a conservative diagnostic character on the basis of this survey of the genus.

ETYMOLOGY.-The trivial name ovatus is a Latin adjective meaning oval, referring to the general body shape.

MATERIAL EXAMINED.-Holotype: CAS 33347 (1, 47.0 mm), Pagapas Bay, Philippine Islands (about 13°N 121°E), 194-209 m, 0355-0435 h, 21 Jul 1966.

Polyipnus ruggeri Baird, 1971

FIGURE 8

Polyipnus ruggeri Baird, 1971:102-103 [fig. 78].-Paxton et al., 1989:192.-Harold, 1990a, b [photophores].

DIAGNOSIS.-Gill rakers 17 or 18. Lateral pigment projection highly reduced, saddlelike. Abrupt archlike deflection of dorsum pigment ventral margin dorsal to AC[A] photophores. One short posttemporal spine present (length 1.5-3.8 % SL). Anal-fin pterygiophore spines and photophore scale denticles absent. AC[A] photophores separate, #2 and #3 conspicuously elevated relative to first AC[B]. AC[B] 8/9. AC[C] photophores compact, not separated by gaps. OV[B] photophores in a horizontal line or with #1 and #3 slightly elevated. Teeth present on posteromedial vomerine process.

DESCRIPTION.-Moderate to large adult size, largest specimen examined 65.5 mm SL. D (12) 12. A (17) 16-18. P (15) 14-15. V 6-7. GR 5+12/13 = (18) 17-18. Vertebrae (33). Body laterally compressed. Very deep in abdominal area; ventral margin of abdominal keel from photophore PV #4 to #10 convex. Body profile anterior of dorsal blade and pelvic fin broadly elliptical, tapered posteriorly as far as caudal peduncle at about a 45° angle. Profile of caudal peduncle rectangular, elongate. Body flank scales diaphanous, sheetlike, much deeper than long, posterior margin nearly vertical. Ventral margin of dentary slightly convex. Margins of dentary and premaxillary with long recurved teeth. Maxillary teeth shorter, conical. One row of 3 to 8 conical teeth on palatine. Anterolateral processes of vomer each with a patch of 2 to 4 conical teeth. Three to nine large recurved teeth in one or two medial rows present on posteromedial process of vomer. Frontal keel finely serrate and extending to, and overlapping, parietal keel. Parietal keel finely serrate and terminates posteriorly in a minute conical spine. Dorsal and ventral limbs of posttemporal obtusely divergent and support a short (1.5-3.8 % SL), triangular, dorsally-concave spine. Small barb present on anterodorsal surface of posttemporal spine. Ventral limb of posttemporal smooth, dorsal arm serrate. Lateral ridges of preopercle and cleithrum smooth; ventral margin of pectoral shield bears 10-20 minute conical spines. Preopercle with two spines: ventral spine posteroventrally directed, slightly recurved, short (1.7-3.0 % SL), embedded entirely within ventral lamella; dorsal spine reduced (represented only by abrupt angle in proximal preopercular keel). Dorsal blade short-based, smooth anterodorsally, terminating posteriorly with two rounded triangular spines, one per side, directed posterodorsally. Anal-fin pterygiophore spines absent. Adipose fin base long, occupying about two thirds of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 30.7-31.0, orbit length 14.7-16.2, body depth 67.2-69.5, caudal-peduncle depth 11.7-12.9, caudal-peduncle length 15.6-18.7, dorsal-fin length 21.8-24.4, anal-fin length 30.1-31.3, preanal length 66.0-75.6, predorsal length 57.6-58.5, preventral length 59.9-71.4, postdorsal length

51.4-55.4, postanal length 46.6-47.9, AC[C] length 6.6-7.9, AC[B]-[C] length 5.7-6.7.

Ventral margins of photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in a horizontal to anteriorly inclined straight line. PV (10). L 1. VAV (5). AC 1+1+1, separate, not united in a common gland, increasing in elevation incrementally from anterior to posterior. AC[A] (9, 8-9), with a dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with abrupt predorsal and postdorsal notches, the latter reaching the dorsum in some specimens. Lateral pigment projection very short or absent. Dark pigment also present in association with photophore tissues, dorsal, dorsolateral, and ventral regions of head, lower jaw, anterior rays of dorsal fin and membranes of caudal-fin ray bases, base of dorsal fin, ventral surface of central PV photophores, flank scale pockets, and delineating body-trunk myosepta in two concentric lines, with heavier pigment concentrations at intersections of myosepta and lateral midline. Silvery reflective pigment covering much of flank (especially photophores), cheek and opercular areas.

SIMILAR SPECIES.-*Polyipnus* *ruggeri* most closely resembles *P*. *meteori* and *P*. *matsubarai* in some body proportions, meristic character values, pigmentation and posttemporal morphology. Low gill raker counts distinguish this species from P. matsubarai (17/18 as compared with 22-24). Polyipnus meteori differs in its very long lateral pigment projection and elevated first OV[B] photophore. The near horizontal row of OV[B] photophores distinguishes P. ruggeri from all other members of the genus.

DISTRIBUTION.-Polyipnus ruggeri was originally known only from the eastern Tasman Sea and other New Zealand slope areas but material is reported here which extends its range westward to include the southeast coast of Australia (Figure 7). This species may occur as deep as 500 m but it has also been taken above 100 m in one night tow (AMS I.20312).

Other species occurring in the region are P. kiwiensis, P. aquavitus, P. unispinus and possibly P. parini.

REMARKS.-Polyipnus ruggeri is a member of the monophyletic P. meteori species group. Phylogenetic analysis (see 'PHYLOGENETIC RELATIONSHIPS', page 208) indicates that P. ruggeri and P. meteori are most closely related. One other member of this species group, P. kiwiensis, occurs in the Tasman Sea but is distantly related to P. ruggeri.

Polyipnus ruggeri has two external characters that are unique: reduced lateral pigment projection and OV[B] photophores nearly in a horizontal line. The OV[B] configuration resembles the condition in other sternoptychid genera (e.g. Argyropelecus, Argyripnus) but the first and last elements in P. ruggeri are dorsal to the second by a very small distance; this situation is not known to occur outside Polyipnus.

MATERIAL EXAMINED.-Holotype: NMNZ (DMNZ) 4670 (1, 46.8 mm), 31°57'S 177°38'E, R/V Tui, 24 Jul 1962 (not seen).

Other Material: AMS I.20066 (1, 49.1 mm), 35°36'S 150°55'E, 0-650 m, R/V Kapala, 1905-2250 h, 27 Oct 1977. AMS I.27166 (1, 65.5 mm), 33°04'S 158°59'E, 0-457 m, R/V Cook, 0100-0250 h, 1 Aug 1987. AMS I.21372 (1, 27.1 mm), 33°12'S 152°47'E, 0-750 m, R/V Kapala, 1215-1630 h, 29 Nov 1979. AMS I.20312 (1, 22.4 mm), 33°17'S 152°31'E, 0-100 m, R/V Kapala, 2345-0115 h, 13 Dec 1977. USNM 298919 (1, 16.3 mm), 35°18'S 170°30'E to 35°14'S 170°28'E, R/V Eltanin Cr. 31, Sta. 27, field no. RHG 67-77, 16 Dec 1967. ZMUC P207118 (1, 50.3 mm), 34°20'S 152°46'E, 1000 mwo, R/V Dana Sta. 3659 I, 0430-0530 h, 17 Feb 1929.

Polyipnus asteroides species group

DEFINITION.-Second and third AC[A] photophores united in a common gland (first photophore isolated except in P. bruuni which has all three united). Maxillary and premaxillary bones densely pitted. Dorsal process of maxillary extending to medial terminus of the bone. Anterior ceratohyal with arched bladelike process on dorsal surface. See 'PHYLOGENETIC RELATIONSHIPS', page 213.

Six species of the Atlantic Ocean, Indian Ocean or the

Indo-Pacific region: P. asteroides, P. bruuni, P. clarus, P. laternatus, P. polli and P. triphanos.

Polyipnus asteroides Schultz, 1938

FIGURE 17

Polyipnus asteroides Schultz, 1938:138-140 [holotype fig. 44]; 1961:640-641 [part, table 6]; 1964:267, 269-270 [part, holotype fig. 70].-Baird, 1971:99-101 [part, fig. 76 is P. clarus].-Weitzman, 1974:344.-Harold, 1990a:1114.

Polyipnus laternatus.-Jespersen, 1934:15.

DIAGNOSIS.-Gill rakers 20-24. Lateral pigment projection tapered and long, extending ventrally to lateral midline. Overall pigmentation very dark. Posttemporal spine single, short (1.7-3.0 % SL). Anal-fin pterygiophore spine basally expanded. Photophore scale denticles absent. Second and third AC[A] photophores united and highly elevated (6.9-7.9 % SL) relative to first AC[B] photophore.

DESCRIPTION.-Maximum adult body size 75.4 mm SL (this study). D (14) 12-16. A (16) 16-17. P (14) 14-15. V 7. GR 7/8+13-16 = (24) 20-24. Laterally compressed, deep-bodied. Body profile anterior of dorsal blade and pelvic fin subrectangular, abruptly tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate. Flank scales deciduous, very few remaining on specimens examined. Ventral margin of dentary entire and with slight convexity. Margins of dentary and premaxillary with long, recurved teeth. Maxillary with minute, conical teeth. One medial row of 4 to 6 recurved teeth on palatine. Anterolateral processes of vomer each with a patch of 3 to 6 conical teeth. No teeth present on posteromedial process of vomer. Posterior half of frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Dorsal and ventral limbs of posttemporal nonserrate, obtusely divergent, and support a short (1.7-3.0 % SL), needlelike spine without a posteriorly-directed basal barb. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 15-23 minute, conical spines. Vertical ramus of preopercle smooth, nonserrate, anteroventral ramus with 3 or 4 broad serrations. Preopercle with two spines: ventral spine short (1.5-1.6 % SL), slightly recurved, embedded entirely within distal lamella of preopercle; dorsal spine minute (slightly longer than one preopercular serration), triangular, directed anteroventrally. Dorsal blade nonserrate, apically depressed, and with two acutely-tapered triangular spines, one per side, directed posteriorly. First anal-fin pterygiophore bears two long, basally expanded ventroanteriorly-directed spines (one per side). Adipose fin base long, occupying about three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 30.0-35.3, orbit length 13.4-16.2, body depth 61.1-66.7, caudal-peduncle depth 10.3-10.9, caudal-peduncle length 13.7-17.8, dorsal-fin length 24.1-30.8, anal-fin length 27.7-31.5, preanal length 69.6-79.5, predorsal length 52.0-56.5, preventral length 66.8-76.3, postdorsal length 48.5-58.8, postanal length 43.4-47.6, AC[C] length 5.3-6.9, AC[B]-[C] length 3.6-4.5.

Ventral margins of photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, arrangement variable, usually with #2 and #3 at level of posterior VAV photophore and the first dorsally elevated, but occasionally in an anteriorly-inclined straight line. PV (10). L 1. VAV (5). AC[A] 1+(2), #1 isolated, located posterodorsally to VAV #5, #2 and #3 posterodorsally to #1 and united in a common gland (AC[A] #3 elevation relative to AC[B] #1 6.9-7.9 % SL). AC[B] (9; 8-10), with a conspicuous dorsal step between #3 and #4. SC=AC[B] (4).

Very darkly pigmented overall. Dark pigment saddle with an abrupt predorsal notch. Postdorsal notch or arch absent, giving a basically straight ventral pigment margin from the position of the dorsal-fin origin to the caudal peduncle.

Lateral pigment projection narrow and tapered ventrally, approaching and in some specimens reaching lateral midline. Dark pigment also associated with photophores, dorsal surface of head, bases of dorsal-fin and caudal-fin rays, and body trunk myosepta.

SIMILAR SPECIES.-*Polyipnus asteroides* is most similar to *P. clarus* with regard to photophore patterns and meristic characters. The present species, however, has a deeper body, frequently higher gill raker counts, basally expanded and shorter ventroanteriorly directed anal-fin pterygiophore spines, and much darker pigmentation overall. The shape and size of the lateral pigment projection is most similar to that of *P. matsubarai* of the western Pacific, a member of the *meteori* species group. Also see 'SIMILAR SPECIES' section for *P. clarus*.

DISTRIBUTION.-*Polyipnus asteroides* has been collected through much of the Caribbean Sea in the vicinity of the continental slope of South America and off Puerto Rico (Figure 18). This species is much more restricted in geographic distribution than the new subdivided species *P. clarus*. Bathymetric records suggest that *P. asteroides* may be a deep-dwelling species, occurring to about 500 or 600 m.

The geographic range of *P. asteroides* overlaps extensively with *P. clarus* (Caribbean Sea) but since they do not appear together in collections they probably occupy different geographic and bathymetric positions within the region. There is also major range overlap with *P. laternatus* which is also restricted to the tropical to subtropical western Atlantic Ocean.

REMARKS.-The account of *P. asteroides* given by Schultz (1961) included much material here referred to *P. clarus*. Baird (1971) accepted Schultz's treatment and used a specimen of the new species (*P. clarus*) to illustrate *P. asteroides* in his review of the genus. The only published illustration of the species seems to be that of the holotype (Schultz, 1938: fig. 44; 1964: fig. 70).

In addition to the type material listed here, Schultz (1938) designated one other paratype (USNM 96131 [1, 20.0 mm], Lesser Antilles, 0-300 m, R/V *Grampus* Sta. 10482, 23 Mar 1917), reportedly in very poor condition. The specimen is no longer listed in the USNM catalog and may be lost.

MATERIAL EXAMINED.-*Holotype*: USNM 102979 (1, 39.5 mm), 18°29'45"N 65°25'50"W to 18°35'30"N 65°23'54"W, 370-740 m, First Johnson-Smithsonian Deep-sea Expedition, Sta. 81, 26 Feb 1933.

Paratypes: USNM 102978 (4, 26.0-39.5 mm), 18°32'54"N 65°23'42W to 18°32'15"N 65°18'45"W, 462-492 m, First Johnson-Smithsonian Deep-sea Expedition, Sta. 83, 26 Feb 1933.

Other Material: CAS 32467 (1, 44.0 mm), 09°03'N 81°18'W, (0-) 370-407 m, R/V *Oregon* Sta. 3598. CAS 61110 (6, 54.3-64.5 mm), 18°31'N 65°40'W, 500-555 m, R/V *Oregon*

_II_, Sta. 46060, 1800-1900 h, 15 Aug 1987. CAS 61111 (3, 42.2-54.9 mm), 18°31'12"N 65°40'36"W, 518-444 m, R/V _Oregon II_, Sta. 46061, 1955-2040 h, 15 Aug 1987. USNM 295951 (3, 49.4-75.4 mm), 11°53'N 69°28'W, 426 m, R/V _Oregon_, Cr. 87, 29 Sep 1963. USNM 298949 (1, 66.3 mm), 09°12'N 81°11'W, 0-611 m, R/V _Oregon II_ Cr. 22, Sta. 11227, 28 Oct 1970. USNM 179049 (22, 39.3-66.6 mm), 09°03'N 81°22'W, (0-) 370-407 m, R/V _Oregon_ Sta. 3598, 31 May 1962. USNM 298940 (10, 66.7-81.3 mm), 11°25'N 73°56'W, (0-) 440 m, R/V _Oregon_ II Cr. 22, Sta. 11252, 10 Nov 1970. USNM 203280 (3, 47.2-53.5 mm), 12°01'N 61°53.5'W, (0-) 389 m, R/V _Oregon II_ Cr. 15, Sta. 10906, 08 Feb 1970. USNM 190472 (10, 36.8-50.5 mm), 18°12'N 67°42'W, (0-) 481 m, R/V _Oregon_ Sta. 2645, no other data. USNM 298945 (1, 61.8 mm), 11°12'N 74°24'W, R/V _Oregon II_ Sta. 11284, 16 Nov 1970. USNM 298936 (3, about 60-75.9 mm), 10°00'N 76°10'W, (0-) 555 m, R/V _Oregon II_ Cr. 22, Sta. 11244, 06 Nov 1970. USNM uncat., acc. no. 289062 (5, 70.8-77.8 mm), 11°12'N 74°21'W, (0-) 444 m, R/V _Oregon II_ Sta. 10267, 03 Dec 1968. USNM uncat., acc. no. 261501 (2, 60.6-68.3 mm), 20°42'N 73°38'W, (0-) 666 m, R/V _Oregon_ Sta. 5417, 24 May 1965. USNM uncat., acc. no. 254315 (4, 38.6-61.5 mm), 11°09.5'N 74°24.5'W, (0-) 315-333 m, R/V _Oregon_ Sta. 4838, 16 May 1964. USNM uncat. (2, 40.9-56.2 mm), same data as previous entry.

Polyipnus bruuni new species

FIGURE 15

DIAGNOSIS.-Gill rakers 19. Lateral pigment projection broad, tapered, reaching ventrally about half way to lateral midline. One short posttemporal spine present (length 3.8 % SL). Anal-fin pterygiophore spines and photophore scale denticles absent. AC[A] (3), in a horizontal line and united in a common gland, highly elevated relative to first AC[B]. AC[B] (7). AC[C] photophores compact, not separated by gaps. No teeth on posteromedial vomerine process.

DESCRIPTION OF HOLOTYPE.-Known only from the holotype (19.5 mm SL). D (12). A (15). P (14). V (6). GR (6+13)=(19). Vertebrae (13+20)=(33). Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin elliptical and deep, tapered posteriorly as far as caudal peduncle at about 30°. Profile of caudal peduncle rectangular, elongate. Flank scales diaphanous, deciduous with few remaining in holotype. Ventral margin of dentary entire and slightly convex. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary with shorter, conical teeth. Four conical palatine teeth. Anterolateral processes of vomer each with a patch of 6 conical teeth. No teeth present on posteromedial process of vomer. Frontal keel smooth, extending posteriorly to, and overlapping, parietal keel. Parietal keel nonserrate but terminating posteriorly in a short posteriorly-directed spine. Dorsal and ventral limbs of posttemporal, obtusely divergent, and support a short (3.8 % SL) posteriorly-directed spine. Dorsal limb of posttemporal with two spinelike serrations, ventral limb smooth. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 7 triangular spines. Vertical and anteroventral rami of preopercle smooth, nonserrate. Preopercle with a short (2.1 % SL) ventral spine only, which is embedded within distal lamella of preopercle. Dorsal blade short-based, nonserrate, and terminating posteriorly with two acutely triangular posterodorsally-directed spines (one per side). Anal-fin pterygiophore spines absent. Adipose-fin base long, occupying more than three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 41.0, orbit length 17.6, body depth 63.9, caudal-peduncle depth 12.4, caudal-peduncle length 18.0, dorsal-fin length 20.5, anal-fin length 22.5, preanal length 74.6, predorsal length 54.9, preventral length 73.8, postdorsal length 54.1, postanal length 39.3, AC[C] length 7.8, AC[B]-[C] length 5.4.

Ventral margins of photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in a "V" configuration. PV (10). L 1. VAV (5). AC[A] (3), united in a horizontal, linear cluster. AC[B]

(7), with a dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with a short predorsal notch and a short, triangular lateral projection. Postdorsal pigment notch appears to be absent. Dark pigment also present in association with photophore tissues, dorsolateral surface of head, base of dorsal-fin rays, dentary and delineating anterior body-trunk myosepta (epidermis and pigment are missing posteriorly in the holotype).

SIMILAR SPECIES.-Polyipnus bruuni is most similar to P. triphanos, the only members of the asteroides species group lacking anal-fin pterygiophore spines. These two species further differ from other members of the group by the low dorsal-fin ray count (12 or fewer as compared with 13 or more) with the exception of Polyipnus laternatus which is quite variable (12-15). Polyipnus bruuni is distinguished from all other Polyipnus species by its unique AC[A] photophore configuration (3 united).

DISTRIBUTION.-The P. bruuni holotype was collected by open tow to 240 m in the equatorial western Indian Ocean (Figure 14). The collection label reads "off Madagascar" but the geographical position given is actually more than 10 latitude degrees north of Madagascar and immediately off the coast of Kenya (Somali Basin margin).

The western Indian Ocean has not been well-sampled in the continental slope areas where Polyipnus species are most likely to be encountered. Polyipnus indicus, P. omphus, and

P. meteori are the only other species known to occur in the region.

REMARKS.-Although the holotype of P. bruuni is very small (19.5 mm SL) it appears to have most features that are characteristic of adults other closely-related species. I suspect that the slightly low AC[B] photophore count (7), however, reflects an early developmental stage. Photophores of that cluster usually appear at body sizes of up to 25 mm SL (Harold, 1990b). There are also potential difficulties in making critical morphometric comparisons between the P. bruuni holotype and larger individuals of other species because of allometry. The species can be diagnosed, however, on the basis of a qualitative character; no other species has 3 united AC[A] photophores.

ETYMOLOGY.-Named for the vessel R/V Anton Bruun, from which the holotype was collected during the International Indian Ocean Expeditions.

MATERIAL EXAMINED.-Holotype: USNM 298923 (1, 19.5 mm), 02°56'S 40°28'E, 0-240 m, R/V Anton Bruun Cr. 8 (International Indian Ocean Expedition), Sta. 421G, 8 Nov 1964.

Polyipnus clarus new species

FIGURE 19

Polyipnus asteroides.-Schultz, 1961:621, 640-641 [part]; 1964:267, 269-270 [part, fig. 70 is P. asteroides holotype].-Scott, 1965:1303-1305 [fig. 1].-Baird, 1971:99-101 [part, fig. 76 only].-Musick, 1973:173.-Markle et al., 1980:52.-Scott and Scott, 1988:172 [unnumbered illustration].-Harold, 1990b:515.

Polyipnus laternatus.-Jespersen, 1934:15.-Fowler, 1936:1206-1207 [part].

Polyipnus sp. A.-Harold and Clark, in prep.

DIAGNOSIS.-Gill rakers 19-21. Lateral pigment projection triangular and short, extending ventrally about half way to lateral midline. Overall pigmentation very pale. Posttemporal spine single, short (2.4-3.1 % SL). Anal-fin pterygiophore spines needlelike, not noticeably expanded basally. Photophore scale denticles absent. Second and third AC[A] photophores united and highly elevated (4.9-6.6 % SL) relative to first AC[B] photophore.

DESCRIPTION.-Maximum adult body size 60 mm SL. D (15) 15-16. A (16) 16-17. P (14) 13-15. V 7. GR 5-7+13-15 = (21) 19-21. Vert. (32) 32/33. Body laterally compressed, profile anterior of dorsal blade and pelvic fin broadly elliptical, abruptly tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate. Flank scales deciduous, very few remaining on specimens examined. Ventral margin of dentary entire and slightly convex. Margins of dentary, premaxillary and maxillary with minute, recurved teeth. One medial row of 5 or 6 conical teeth on palatine. Anterolateral processes of vomer each with a patch of 4 or 5 conical teeth. No teeth present on posteromedial process of vomer. Frontal and parietal keels serrate. Frontal keel extending from to, and overlapping, parietal keel. Dorsal and ventral limbs of posttemporal nonserrate and support a short (2.4-3.1 % SL) dorsally-curved spine which bears on its anterodorsal surface a minute posteriorly-directed barb. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 6-9 conical spines. Vertical ramus of preopercle smooth, nonserrate, anteroventral ramus with 4 or 5 serrations. Preopercle with two spines: ventral spine straight, short (0.9-2.2 % SL), except for terminus embedded entirely within distal lamella, and directed ventrally; dorsal spine minute (slightly longer than one preopercular serration). Dorsal blade smooth or with 1 serration on anterodorsal surface, and with two triangular spines, one per side, directed dorsolaterally. First anal-fin pterygiophore bears two long (1.1-2.0 % SL), needlelike spines (one per side), ventrolaterally-directed. Adipose fin base short, occupying about one quarter of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 28.6-34.4, orbit length 13.4-16.1, body depth 58.1-64.9, caudal-peduncle depth 9.6-11.2, caudal-peduncle length 12.2-15.4, dorsal-fin length 26.0-28.7, anal-fin length 28.0-29.0, preanal length 72.3-78.9, predorsal length 50.0-52.8, preventral length 68.1-77.1, postdorsal length 50.4-53.1, postanal length 40.1-44.7, AC[C] length 5.5-6.5, AC[B]-[C] length 4.1-5.2.

Ventral margins of all photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, arrangement variable but usually with #2 and #3 at level of posterior VAV photophore and the first dorsally elevated. PV (10). L 1. VAV (5). AC[A] 1+(2), #1 isolated, located posterodorsally to VAV #5, AC[A] #2 and #3 posterodorsally to #1 and united in a common gland. AC[B] (10/9; 8-10), with a dorsal step in arrangment between #3 and #4. AC[C] (4).

General pigmentation pale brown in preservative. Pigment saddle, ventrally, with a predorsal notch and a short, triangular lateral projection extending about half way to lateral midline. Dark pigment also present in association with glandular photophore tissues, posterodorsal region of head, bases of dorsal-fin rays, and delineating body trunk myosepta.

SIMILAR SPECIES.-Five species have the distinctive AC[A] photophore arrangement 1+(2). Of these, P. clarus and P. asteroides are quite similar and are distinguished on the basis of pigmentation, relative body depth, size and shape of the anal-fin pterygiophore spine, and gill raker counts. Another distinguishing character is the relative distance between the posterior AC[A] and the anterior AC[B] photophores which is 4.9-6.6 % SL in P. clarus as compared with 6.9-7.9 % SL in P. asteroides sensu stricto. Polyipnus polli is distinguished from P. clarus by its posteriorly placed dorsal fin, higher dorsal-fin ray and gill raker counts, and unique sinusoidal anal-fin base. Polyipnus laternatus has much longer posttemporal spines (5.7-8.6 % SL) than any of the aforementioned species (1.7-3.8 % SL total range). In contrast to P. clarus, Polyipnus triphanos has low gill raker counts and lacks anal-fin pterygiophore spines.

DISTRIBUTION.-Polyipnus clarus has been collected through much of the Gulf of Mexico and the Caribbean Sea, and in the Gulf Stream as far north as the Scotian Shelf (Scott, 1965: "P. asteroides" = P. clarus) (Figure 18). Polyipnus clarus appears to be most common between 300 and 400 m depth. This species has been collected by bottom trawl to 833 m but this record may result from fishing off the bottom. There is one record of a capture by midwater trawl at a maximum depth of 39 m - time of day for this sample is not known.

The geographic range of *P. clarus* overlaps with that of *P. asteroides* in the Caribbean Sea. The collections examined in this study suggest that the two species probably occur at different depths. There are no known records of these two species being caught in the same tow. There is also range overlap between *P. clarus* and *P. laternatus* which also occurs through the Caribbean and Gulf of Mexico.

REMARKS.-*P. clarus* populations were considered conspecific with *P. asteroides* by previous investigators. In fact, intraspecific variation other than typical dispersion of meristic characters for *P. asteroides* sensu lato has never been reported. Specimens of the new species were the basis of illustrations of *P. asteroides* in Schultz (1961: fig. 16) and Baird (1971: fig. 76), the two most recent revisions, and consequently problems in routine identification have not been encountered. Moreover, the original species *P. asteroides* of Schultz (1938) is highly restricted in geographical distribution (Caribbean Sea, Greater Antilles) and has been caught on very few occasions. Detailed studies of pigmentation pattern, morphometric characters and micromorphology show that these are separate and quite distinct species.

ETYMOLOGY.-The trivial name *clarus* is a Latin adjective meaning bright or distinct, referring to the very light pigmentation of P. clarus in comparison to P. asteroides with which it has been confused.

MATERIAL EXAMINED.-Holotype: USNM 273283 (1, 43.6 mm), 33°59'N 76°05'W, 0-409 m, R/V Oregon II, Cr. 9, Sta. 11761, 1 Feb 1972.

Paratypes: AMNH 76178 (10, 38.5-54.4 mm), 33°59'N 76°05'W, R/V Oregon II Sta. 11761, 01 Feb 1972. FMNH 66633 (1, 25.4 mm), 29°04'N 87°37'W, R/V Oregon Sta. 3258, 28 Apr 1961. MCZ 66694 (2, 24.7-27.1 mm), 22°22'N 95°20'W, 385-435 m, R/V Chain, Cr. 60, 18 Jun 1966. USNM 304745 (18, 31.3-45.7 mm), same data as holotype. ZMUC uncat. (1, 25.9 mm), 13°47'N 61°26'W, 2500 mwo, R/V Dana Sta. 1183 III.

Other Material: AMNH 37337 (1, 23.8 mm), 38°59'N 72°48'W, (0-) 311 m, R/V Albatross IV, Sta. 26, 0808 h, 26 Sp 1974. AMNH 37336 (1, 27.0 mm), 39°48.5'N 71°48'W, (0-) 229 m, vessel unknown, 06 Mar 1975. ASH 89034 (3, 23.3-41.2 mm), 34°25'00"N 75°39'45"W, 0-348 m, 14 Feb 1969. CAS 18718 (1, 22.0 mm), 28°58'N 88°00'W, R/V Oregon, 1953. MCZ 66695 (1, 41.9 mm), 11°30'N 65°19'W, (0-) 1500 m, R/V Atlantis II, 11 Dec 1973. MCZ 66698 (1, 38.6 mm), 34°38'N 75°36'W, 0-270 m, R/V Oceanus, 21 Feb 1979. MCZ 66696 (2, 26.0-30.9 mm), 34°38'N 75°36'W, 250-200 m, R/V Oceanus, 21 Feb 1979. CAS (SU) 17430 (3, 37.3-40.8 mm), 29°42'00"N 88°25'30"W, 0-39 m, 14 Feb 1951. SIO 70-365 (7, 12.0-15.2 mm), 09°40'N 79°08'W, 0-225 m, field no. JEM 70-54, 8 Oct 1970. USNM 298941 (39, 30.2-46.5 mm), 29°17'N 86°36'W, (0-) 370 m, R/V Oregon II

Cr. 15, Sta. 10906, 08 Feb 1970. USNM 261627 (6, 34.4-50.3 mm), 29°17'N 86°36'W, (0-) 370 m, R/V *Oregon II* Cr. 15, Sta. 10906, 08 Feb 1970. USNM 302437 (2, 26.2-27.5 mm), 39°55'N 69°54'W, (0-) 622 m, R/V *Albatross IV* Cr. 8809, Sta. 159, 29 Sep 1988. USNM 302436 (2, 23.5-27.3 mm), 37°49'N 74°06'W, (0-) 312-410 m, R/V *Albatross IV* Cr. 8809, Sta. 15, 14 Sep 1988. USNM 186016 (5, 28.5-31.4 mm), 27°40'N 94°48'W, (0-) 509 m, R/V *Oregon* Sta. 1506, 06 May 1956. USNM 190468 (1, 22.6 mm), 29°05'N 88°09'W, (0-) 833 m), R/V *Oregon* Sta. 2507, 20 May 1959. USNM 186022 (3, 36.1-48.5 mm), south of Mobile, Alabama, R/V *Oregon* Sta. 1282, no exact data. USNM 298946 (1, 54.9 mm), 11°23'N 74°16'W, 0-463 m, R/V *Oregon II* Cr. 22, Sta. 11251, 10 Nov 1970. USNM uncat. (1, 23.0 mm), 27°42'N 94°26'W, (0-) 370 m, R/V *Oregon* II Cr. 89, Sta. 4616, 20 Jan 1964. USNM uncat., acc. no. 254315 (6, 21.8-42.7 mm), 27°46'N 94°13'W, (0-) 370 m, R/V *Oregon* Sta. 4614, 20 Jan 1964. USNM uncat., acc. no. 261501 (1, 40.3 mm), 28°58.5'N 79°57.0'W, (0-) 407-416 m, R/V *Oregon* Sta. 5250, 19 Feb 1965. USNM uncat., acc. no. 225026 (4, 37.0-44.1 mm), 27°03'N 96°16'W, (0-) 389 m, R/V *Oregon* Sta. 1093, 04 Jun 1954. USNM uncat., acc. no. 261501 (3, 32.5-37.5 mm), 29°04.5'N 80°01.0'W, R/V *Oregon* Sta. 5259, 17 Feb 1965. USNM uncat., acc. no. 261501 (1, 37.9 mm), 29°34'N 79°57'W, (0-) 648 m, R/V *Oregon* Sta. 5748, 19 Nov 1965.

Polyipnus laternatus Garman, 1899

FIGURE 20

Polyipnus laternatus Garman, 1899:238.-Norman, 1930:305 [part, fig. 14 is P. polli].-Fowler, 1936:1206-1207 [part].-Parr, 1937:55 [fig. 22].-Schultz, 1938:142-143; 1961:639; 1964:267, 270-271 [fig. 71].-Baird, 1971:92-94 [fig. 70].-Weitzman, 1974:344 [fig. 10].-Harold, 1990a:1114; 1990b:515.

Polyipnus spinosus.-Brauer, 1906:121 [part].-Rivero, 1936:56.

DIAGNOSIS.-Gill rakers 16-19. Lateral pigment projection short, tapered, reaching about half way to lateral midline. Posttemporal spine: single, length moderate (5.7-8.6 % SL). Anal-fin pterygiophore spines long, needle-like. Photophore scale denticles absent. AC[A] photophores 1+(2) or 1+1+1, #3 highly elevated relative to first AC[B]. AC[B] 11-13. AC[C] photophores compact, not separated by broad gaps.

DESCRIPTION.-Body size small to moderate, largest examined 43.9 mm SL. D (15) 12-15. A (15) 15-18. P 12-14. V 6-7. GR 4-6+11-14 = (18) 16-19. Vertebrae (34) 32-33. Body laterally compressed. Body profile excluding caudal peduncle elliptical. Profile of caudal peduncle rectangular, elongate. Flank scales diaphanous, deciduous. Ventral margin of dentary entire and slightly convex. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary teeth shorter, conical. One medial row of 5 to 8 conical teeth on palatine. Anterolateral processes of vomer each with a patch of 4 to 8 conical, slightly recurved teeth. No teeth present on posteromedial process of vomer. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Dorsal and ventral arms of posttemporal nonserrate and support a single moderately long (5.7-8.6 % SL) spine which bears on its anterodorsal surface a minute posteriorly-directed barb. Lateral ridges of cleithrum and preopercle smooth, nonserrate. Ventral margin of pectoral shield bears 7-11 minute conical spines. Preopercle with two spines: ventral spine straight, short (1.6-2.2 % SL), directed ventrally; dorsal spine minute, bladelike, triangular. Dorsal blade long-based, apically depressed, anterodorsal surface smooth, terminating posteriorly in two (one per side) triangular posterodorsally-directed spines. First anal-fin pterygiophore bears two long ventrolaterally-directed spines (one per side). Adipose-fin base of moderate length, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 30.4-35.9, orbit length 14.7-18.3, body depth 55.0-63.2, caudal-peduncle depth 9.3-11.7, caudal-peduncle length 14.7-19.0, dorsal-fin length 22.7-25.9, anal-fin length 23.7-30.1, preanal length 66.5-73.8, predorsal length 52.5-57.6, preventral length 59.2-69.4, postdorsal length 51.2-55.8, postanal length 39.3-47.9, AC[C] length 7.1-8.3, AC[B]-[C] length 2.2-5.6.

Ventral margins of all photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in a shallow "V" configuration. PV (10). L 1. VAV (5). AC[A] 1+(2), rarely 1+1+1, all in close proximity but #1 positioned ventrally of #2 by a distance equal to its diameter, #3 highly elevated relative to AC[B] #1. AC[B] (11; 11-13), with a slight dorsal step between #3 and #4. AC[C] (4), compact, not separated by broad gaps.

Dark pigment saddle with a short, abrupt predorsal notch and a short, rounded lateral projection. Dark pigment also present in association with glandular photophore tissues, dorsal and dorsolateral regions of head, between bases of dorsal-fin rays, and delineating body trunk myosepta. Isolated large melanophores present in association with myosepta.

SIMILAR SPECIES.-Polyipnus laternatus, P. clarus, P. asteroides, P. polli, P. omphus, P. unispinus, and P. aquavitus are the only members of the genus with first anal-fin pterygiophore spines. These spines are useful in identification, being visible in specimens as small as 10 mm

SL. *Polyipnus laternatus* is distinguished from *P. clarus*, *P. asteroides* and *P. polli* by higher AC[B] photophore counts (11-13 compared with a total range of 7-10 for the other 3 species) and longer posttemporal spines. *Polyipnus laternatus* is separated from *P. unispinus* and *P. aquavitus* (both of the *omphus* species group) on the basis of its higher gill raker counts (16-22 as compared with 11-12 and 13-15, resp.) and highly elevated AC[A] photophores. With regard to body shape, AC[B] photophore number and configuration, and posttemporal spine morphology *P. laternatus* is most similar to *P. omphus*; *P. laternatus* is distinguished by its elevated AC[A] photophores with #2 and #3 usually united, OV[B] photophores in a "V" configuration as opposed to an anteriorly-inclined straight line, and AC[B] photophores 11-13 compared with 10-12.

DISTRIBUTION.-*Polyipnus laternatus* has been collected throughout the Caribbean Sea (type locality off Barbados) and Gulf of Mexico with some captures in the Gulf Stream as far north as Cape Hatteras (Figure 21). Few data on vertical distribution are available. Schultz (1964:271) gives a bathymetric range of 240 to 1200 fm (about 444-2220 m) but these figures were presumably derived from the maximum depth fished by open tows. Collections examined in the present study indicate a range of about 370 to 500 m.

The geographic range of *P. laternatus* overlaps to a large extent with that of *P. asteroides* and *P. clarus* but data are insufficient to detect any interspecific differences in bathymetric range. In one instance P. laternatus and P. asteroides were collected in the same tow (depth 0-666 m, USNM uncat., R/V Oregon Sta. 5417) but there is no way of determining at which depths the specimens were taken.

REMARKS.-Baird (1971) delimited the P. laternatus species complex, consisting additionally of P. omphus, P. unispinus and P. aquavitus. Polyipnus danae was tentatively ascribed to this group on the basis of such features as elongate posttemporal spines and high AC[B] photophore counts (Harold, 1990a). Phylogenetic evidence presented elsewhere ('PHYLOGENETIC RELATIONSHIPS' chapter) shows that P. laternatus is more closely related to the P. asteroides species group than to any of the aforementioned.

According to the specimens examined, the range for total gill raker count is 16 to 19 with 18 in the holotype. Schultz (1961) reported a range of 18 to 22 which was based on more material. The entire observed plus reported range is given here but until some of the higher values are verified they should not be used as key characters. I also draw attention to MCZ 40576 which was listed as representative of P. asteroides (sensu lato) by Schultz (1961).

MATERIAL EXAMINED.-Holotype: MCZ 27945 (1, 37.6 mm), off Barbados, (0-) 409 m, R/V Blake, dredge no. 280.

Other Material: MCZ 40570 (1, 35.0 mm), 23°10'N

79°35'W, (0-) 481 m, R/V Atlantis Sta. 3434, 01 May 1939. MCZ 40572 (3, 31.7-34.5 mm), 22°38'N 78°25'W, (0-) 435 m, R/V Atlantis Sta. 3405, 28 Apr 1939. MCZ 50573 (2, 34.4-34.6 mm), 22°37'N 78°23.5'W, (0-) 298 m, R/V Atlantis Sta. 3404, 28 Apr 1939. MCZ 40574 (1, 40.1 mm), 23°23'N 79°17'W, (0-) 463 m, R/V Atlantis Sta. 2985, 12 Mar 1938. MCZ 40575 (2, 31.1-33.0 mm), 22°48'N 78°51'W, (0-) 352-426 m, R/V Atlantis Sta. 2981D, 10 Mar 1938. MCZ 40576 (14, 18.7-22.0 mm), 22°53.5'N 79°08'W, (0-) 463 m, R/V Atlantis Sta. 3424, 30 Apr 1939. MCZ 40577 (1, 26.2 mm), 22°48'N 78°48'W, (0-) 416 m, R/V Atlantis Sta. 2981, 10 Mar 1938. MCZ 40578 (1, 34.2 mm), 22°33'N 78°10'W, (0-) 435 m, R/V Atlantis Sta. 3387, 26 Apr 1939. MCZ 40579 (2, 20.9-23.0 mm), 22°53.5'N 79°10.0'W, (0-) 463 m, R/V Atlantis Sta. 3425, 30 Apr 1939. MCZ 40580 (1, 23.0 mm), 22°07'N 81°08.5'W, (0-) 500 m, R/V Atlantis Sta. 2960, 18 Feb 1938. MCZ 40582 (1, 34.0 mm), 21°50'N 83°45'W, (0-) 2183-2220 m, R/V Atlantis Sta. 2956, 13 Feb 1938. USNM 17950 (17, 29.6-36.7 mm), 12°23'N 82°29'W, (0-) 370 m, R/V Oregon Sta. 3610, 02 Jun 1962. USNM 298237 (2, 38.5-44.0 mm), 10°00'N 76°10'W, R/V Oregon II Cr. 22, Sta. 11244, 06 Nov 1970. USNM 298924 (12, 32.4-43.9 mm), 14°56'N 81°10'W, R/V Oregon II, Cr. 22, Sta. 11221, 26 Oct 1970. USNM uncat. (1, 41.5 mm), 20°42'N 73°38'W, (0-) 666 m, R/V Oregon Sta. 5417, 24 May 1965.

Polyipnus polli Schultz, 1961

FIGURE 16

Polyipnus polli Schultz, 1961:635 [holotype fig. 13]; 1964:267, 271-272 [fig. 72].-Baird, 1971:98-99; 1986:257-258 [fig. 75.10].-Harold, 1990a:1114.

Polyipnus laternatus.-Norman, 1930:305 [fig. 14].-Fraser-Brunner, 1931:218.-Fowler, 1936:1206-1207 [part].-Poll, 1953:65.-Marshall, 1960:22.

DIAGNOSIS.-Gill rakers 20-23. Lateral pigment projection triangular and short, extending ventrally about half way to lateral midline. Postttemporal spine single, short (2.9-3.8 % SL). Anal-fin pterygiophore spines long and needlelike. Photophore scale denticles absent. Second and third AC[A] photophores united and highly elevated (6.9-7.9 % SL) relative to first AC[B] photophore. AC[B] (7-8). AC[C] compact, without conspicuous gaps. Anal-fin base sinusoidal, highly convex posteriorly.

DESCRIPTION.-Maximum adult body size moderate, not exceeding 50 mm SL. D (16) 14-16. A (15) 15-17. P (13) 13-14. V 7. GR 6/7+14-16 = (20) 20-23. Body laterally compressed. Body profile, excluding caudal peduncle, elliptical, anal-fin base sinusoidal, highly convex posteriorly and digitate with distal portions of pterygiophores extended beyond ventral body margin. Profile of caudal peduncle rectangular, relatively deep. Flank scales diaphanous, sheetlike, and deciduous. Ventral margin of dentary slightly convex and smooth. Dentary and premaxillary teeth long and recurved, maxillary teeth shorter, conical and stout. One patch of 1 to 3 conical teeth on palatine. Anterolateral processes of vomer each with a patch of 1 to 3 conical teeth. No teeth present on posteromedial process of vomer. Posterior region of frontal keel and entire parietal keel finely serrate. Frontal keel extending to, and overlapping, parietal keel. Dorsal and ventral limbs of posttemporal nonserrate, obtusely divergent and support a short (2.9-3.8 % SL) slender, dorsally-curved spine which bears on its anterodorsal surface a minute posteriorly-directed barb. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 2-5 minute triangular spines. Vertical ramus of preopercle smooth, nonserrate, anteroventral ramus deeply and broadly serrate. Preopercle with two spines: ventral spine straight, short (1.6-2.1 % SL), except for terminus embedded entirely within distal lamella, and directed posteroventrally; dorsal spine minute (about the size of one preopercular serration). Dorsal blade without serrations, and terminating posteriorly in two acute triangular spines, one per side, directed posterodorally. First anal-fin pterygiophore bears two long narrow ventrolaterally-directed spines (one per side). Adipose fin base short, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 34.3-39.9, orbit length 15.6-16.9, body depth 64.9-70.8, caudal-peduncle depth 11.6-13.0, caudal-peduncle length 12.5-13.6, dorsal-fin length 26.8-29.9, anal-fin length 26.5-29.2, preanal length 76.1-85.5, predorsal length 55.1-63.5, preventral length 68.8-82.6, postdorsal length 47.5-50.8, postanal length 38.9-42.5, AC[C] length 5.3-5.6, AC[B]-[C] length 4.0-5.0.

Ventral margins of all photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, usually in a "V" configuration but with #1 elevated slightly with respect to #3. PV (10). L 1. VAV (5). AC[A] 1+(2), #1 isolated, located posterodorsally to VAV #5, #2 and #3 posterodorsally to #1 and united in a common gland. AC[B] (7; 7-8), with a conspicuous dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with a predorsal notch and a short, triangular lateral projection, reaching about half way to the lateral midline. Postdorsal pigment notch absent (ventral margin of pigment essentially straight from caudal peduncle to position of dorsal-fin. Dark pigment also present in association with photophore tissues, dorsal and lateral surfaces of head, bases and membranes of all fins including adipose fin, body flank scale pockets, and delineating body trunk myosepta.

SIMILAR SPECIES.-Polyipnus polli is most similar to P. asteroides, P. clarus and P. laternatus, the four members of the asteroides species group with anal-fin pterygiophore spines. Of these species P. clarus is most similar to P. polli, both having short triangular lateral pigment projections and long, needlelike anal-fin pterygiophore spines. Polyipnus polli is distinguished from P. clarus by the posterior position of the dorsal fin (predorsal length 55.1-63.5 as compared with 50.0-52.8 % SL, respectively) and from all other Polyipnus species by the unique sinusoidal anal-fin base.

DISTRIBUTION.-Polyipnus polli is restricted to the eastern tropical to subtropical Atlantic Ocean from the Gulf of Guinea and Benguelan Upwelling region northwards to the Mauritanian Upwelling region (Figure 14). This species has been taken above 200 m depth at night.

REMARKS.-In the original description Schultz (1961: 636, table 6) indicates that one third of the type specimens have 6 and the remaining have 7 AC[B] photophores. The size range of the series is 17.0-26.0 mm SL and from ontogenetic studies of these photophores (Harold, 1990b) it is likely that 1 or 2 more photophores would have developed. According to the material examined in the present study a count of 6 AC[B] photophores would only be expected in juveniles or subadults of P. polli.

MATERIAL EXAMINED.-Holotype: KMMA 95092 (1, 22.0 mm), 06°08'S 11°24'E, 350-380 m, (not seen).

Paratypes: USNM 179878 (1, 26.0 mm), 11°53'S 15°26'E, 480-510 m, Belgium Oceanographic Expedition, field no. 8674, 18 Dec 1948.

Other Material: BMNH 1930.1.12.458-467 (10, 16.0-33.0 mm), 13°25'N 18°22'W, 0-900 m, R/V *Discovery*. BMNH uncat. (3, 10.6-12.0 mm), 05°54'S 11°19'E, R/V *Discovery* Sta. 276. MCZ 41581 (1, 17.5 mm), about 02°S 17°W, R/V Chain Sta. 311, 2135-2345 h, 11 Nov 1961. MCZ 66699 (5, 15.0-25.6 mm), 20°07'N 18°15'W, 190-200 (-0) m, R/V *Atlantis II*, 0020-0200 h, 12 Nov 1970. MCZ 66700 (2, 18.2-21.1 mm), 20°16'N 18°15'W to 20°13'N 18°153'W, 0-500-0 m, R/V *Atlantis II* Cr. 59, 2135-2220 h, 11 Nov 1970. MCZ uncat. (27, 11.4-30.5 mm), 16°22'N 21°43'W to 16°23'N 21°50'W, (0-) 230-250 (-0) m, R/V *Atlantis II* Cr. 59, field no. RHB 2062, 0255-0450 h, 15 Nov 1970. MCZ uncat. (3, 30.8-40.2 mm), 12°51'S 08°15'E to 12°47'S 08°22'E, (0-) 390-400 (-0) m, R/V *Atlantis II* Cr. 60, field no. RHB 2279, 2020-2300 h, 03 Jun 1971. MNHN 1962-733 (1, 16.8 mm), 06°42'S 09°06'E, 1100 mwo, R/V *Ombango* Cr. 14, Sta. 339, 1935 h, 11 Mar 1961. MNHN 1962-725 (1, 17.5 mm), 07°00'S 06°55'E, 1100 mwo, R/V *Ombango* Cr. 14, Sta. 319, 2330 h, 26 Feb 1961. MNHN 1962-722 (1, 37.2 mm), 05°30'S 10°10'E, 1200 mwo, R/V *Ombango* Cr. 14, Sta. 316, 2210 h, 24 Feb 1961. ZMUC P206955 (6, 25.4-32.1 mm), 17°24'N 22°57'W, 305-293 m, R/V *Walter*

Herwig Sta. 498 II, 17 Apr 1971. ZMUC uncat. (2, 30.1-34.5 mm), 17°55'N 24°55'W, 1000 mwo, R/V Dana Sta. 1159. ZMUC uncat. (4, 4.0-33.0 mm), 18°22'N 18°14'W, 1000 mwo, R/V Dana Sta. 4007 I, 0315-0515 h, 15 Mar 1930. ZMUC uncat. (6, 19.0-25.0 mm), 00°31'S 11°02'W, 1000 mwo, R/V Dana Sta. 4000 I, 0230-0430 h, 04 Mar 1930. ZMUC uncat. (3, 9.0-13.0 mm), 18°22'N 18°14'W, 1000 mwo, R/V Dana Sta. 4007 XI, 0700-0900 h, 15 Mar 1930. ZMUC uncat. (1, 15.0 mm), 08°26'N 15°11'W, 600 mwo, R/V Dana Sta. 4003 VIII, 1845-2045 h, 09 Mar 1930.

Polyipnus triphanos Schultz, 1938 complex

FIGURE 13

Polyipnus triphanos Schultz, 1938:140 [holotype fig. 45]; 1961:140 [holotype fig. 15].-Baird, 1971:97-98 [fig. 74, reproduction of Schultz, 1938: fig. 45].-Fujii, 1984:47 [pl.49].-Harold, 1990a:1114; 1990b:515.-Aizawa, in press.

DIAGNOSIS.-Gill rakers 14-19. Lateral pigment projection tapered and short, reaching ventrally about half way to lateral midline. One short posttemporal spine present (length 2.4-4.0 % SL). Anal-fin pterygiophore spines and photophore scale denticles absent. AC[A] 1+(2), second and third photophores united and highly elevated relative to first AC[A] and AC[B]. AC[B] (8-10). AC[C] photophores compact, not separated by gaps. No teeth on posteromedial vomerine process.

DESCRIPTION.-Small to moderate body size, largest examined 47.3 mm SL. D 11-12. A 15-18. P 13-14. V 7. Vert. (33). GR 4-6+10-13 = (15) 14-19. Laterally compressed, deep-bodied. Body profile, excluding caudal peduncle, elliptical with greatest body depth at dorsal-fin origin. Caudal peduncle short and subrectangular. Flank scales diaphanous, sheetlike and deciduous. Ventral margin of dentary entire and slightly convex. Margins of dentary and premaxillary with minute recurved teeth. Maxillary teeth smaller, conical. One medial row of 4 to 6 recurved teeth on palatine. Anterior region of vomer with 4 to 5 medial rows of 4 to 6 conical teeth each. No teeth present on posteromedial process of vomer. Frontal keel smooth, nonserrate. Parietal keel discontinuous; nonserrate anteriorly and differentiated posteriorly into 2 conical spines directed towards anterior and posterior. Frontal keel extending to, and overlapping, parietal keel. Dorsal and ventral limbs of posttemporal nonserrate, obtusely divergent, and supporting a short (2.4-4.0 % SL), needlelike spine. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 4-15 minute conical spines. Rami of preopercle smooth, nonserrate. Preopercle with one ventral short spine (1.9-4.7 % SL), embedded within distal lamella, conical terminus emergent and directed posteroventrally. Dorsal preopercular spine represented only by acute angle in proximal bony lamella. Dorsal blade long-based, smooth and nonserrate, apically depressed, and terminating posteriorly with two triangular spines, one per side, directed dorsolaterally. Anal-fin pterygiophore spines absent. Adipose fin long-based, occupying about three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 27.8-34.5, orbit length 11.1-16.2, body depth 55.9-64.6, caudal-peduncle depth 10.0-14.0, caudal-peduncle length 12.4-15.3, dorsal-fin length 16.0-21.6, anal-fin length 24.2-30.8, preanal length 66.0-79.4, predorsal length 50.7-59.6, preventral length 63.6-76.7, postdorsal length 45.9-60.1, postanal length 38.5-44.7, AC[C] length 5.8-9.8, AC[B]-[C] length 0.9-4.5.

Ventral margins of all photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in a "V" configuration but with #1 elevated dorsally about the diameter of one OV[B] photophore in relation to #3. PV (10). L 1. VAV (5). AC 1+(2), #1 isolated, located posterodorsally to VAV #5, #2 and #3 united in a common gland and highly elevated relative to first AC[A] and AC[B]. AC[B] (8/9; 8-10), with a dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with an abrupt predorsal notch and a gradual postdorsal arch. Lateral dark pigment projection varying from triangular and short to broad and long, approaching lateral midline. Dark pigment also present on photophore glands, nonglandular ventrolateral margins of photophores, dorsal surface of head, between bases of dorsal- and anal-fin rays, and delineating in two concentric lines the body trunk myosepta.

SIMILAR SPECIES.-Polyipnus triphanos is most similar to P. asteroides, P. clarus, P. laternatus and P. polli. These species all have the 1+(2) AC[A] photophore arrangement which, except for P. bruuni [AC[A] (3)], is characteristic of the P. asteroides species group. Some specimens of P. kiwiensis have the posterior two AC[A] photophores in very close proximity but they are not joined. Polyipnus triphanos is the only one of the species with AC[A] 1+(2) that lacks anal-fin pterygiophore spines and has a postdorsal deflection of the pigment saddle margin. This species is further distinguished by gill raker count: 13-18 in P. triphanos as compared with 20-24, 19-21 and 20-22 in P. asteroides and P. clarus and P. polli, respectively. Gill raker counts in P. triphanos overlap with those of P. laternatus (16-22) but it is clearly distinguished by low AC[B] photophore number (7-10 vs. 10-13), a short posttemporal spine (2.4-4.0 vs. 5.7-8.6 % SL) and an absence of anal-fin pterygiophore spines.

DISTRIBUTION.-*Polyipnus triphanos* occurs around the Philippine Islands and Taiwan in the South China Sea and southward through the Sulu, Celebes and Banda Seas and into the western Coral Sea (one record) (Figure 14). There are unverified reports of this species from the western Indian Ocean (Baird, in prep.) and the Japanese Archipelago (Fujii, 1984).

Discrete-depth samples taken by Rectangular Midwater Trawl (RMT-8; R/V *Snellius-II*) in the Banda Sea indicate that *P. triphanos* occurs between 100 and 300 meters at night. A sample from the Philippines (CAS 34899) shows *P. triphanos* occurring above 250 m during daylight hours. Extensive sampling by R/V *Alpha Helix* in the Banda Sea (Southeast Asian Bioluminescence Expedition, 1975) was negative for *P. triphanos*, although other *Polyipnus* species were taken, suggesting extreme patchiness, migratory behavior, annual life cycle or extreme interannual variation in population size.

REMARKS.-*Polyipnus triphanos* is quite variable with regard to a number of meristic, pigmentation and photophore characters. Of special note is variation in the lateral pigment projection, which usually varies very little in *Polyipnus* species. However, from the few samples containing more than one specimen pigmentation patterns appear to be "fixed" within *P. triphanos* populations. There are also meristic and dentition characters which also appear to vary geographically. A systematic analysis based on more material may reveal that there are several species divisable from that recognized here as P. triphanos complex. One specimen in particular (ZMUC uncat., 24.8 mm, R/V Dana Sta. 3881 I) from the Java Trench is very likely a representative of an undescribed species, but is referred to P. aff. triphanos pending capture of additional material.

MATERIAL EXAMINED.-Holotype: USNM 103027 (1, 20.4 mm), 13°35'30"N 121°48'E, (0-) 333 m, R/V Albatross Sta. 5368, 23 Feb 1909.

Paratypes: USNM 103028 (2, 17.6-21.0 mm), 08°37'45"N 124°36'45"E, (0-) 494 fms, R/V Albatross Sta. 5500, 4 Aug 1909.

Other Material: AMS I.25816-008 (1, 40.3 mm), 17°59'S 147°07'E to 17°55'S 147°05'E, 0-300 m, 2130-2230 h, R/V Soela, field no. SO 1/86/49, 13 Jan 1986. AMS I.24316-004 (1, 43.8 mm), 00°04'S 97°55'E to 10°04'S 122°43'E, no exact data. AMS I.24338-001 (1, 47.3 mm), 08°30'S 117°46'E, 150-280 m, field no. TGT 1660-1682, Jul 1981. CAS 56034 (10, 17.9-30.6 mm), 22°23'N 120°25'E, 18 Nov 1983. CAS 34899 (1, 40.4 mm), Batangas Bay, Philippines (about 14°N 121°E), (0-) 222-248 m, 0905-1000 h, 9 Aug 1966. IOAN uncat. (1, 39.0 mm), 01°43'S 143°04'E, 0-500 m, R/V Vityaz Cr. 50, Sta. 7321, 6 Apr 1975. IOAN uncat. (1, 29.3 mm), 05°37'S 130°50'S to 05°36'S 130°51'E, 100-0 m, R/V Vityaz Cr. 57, Sta. 7263, 2315-0000 h, 19-20 Mar 1975. SIO 77-167 (1, 37.5

mm), 17°40'N 119°55'E, 3000 mwo. SIO 77-184 (1, 26.8 mm), 05°21.2'S 133°34.7'E, 0-1500 m, Indopac VII Expedition, 19 Sep 1976. ZMUC P206962 (1, 28.9 mm), 13°32'N 121°21'E, 600 mwo, R/V *Dana* Sta. 3733 II, 0250-0450 h, 26 Jun 1929. ZMUC P206963 (2, 26.5-30.4 mm), 09°17'N 123°58'E, 600 mwo, R/V *Dana* Sta. 3736 VI, 2140-2340 h, 28 Jun 1929. ZMUC uncat. (1, 24.8 mm), 01°19'S 100°12'E, 500 mwo, R/V *Dana* Sta. 3881 I, 2345-0145 h, 29 Oct 1929.

Polyipnus omphus species group

DEFINITION.-Dorsal blade with secondary, ventrolateral processes. No overlap between ossified parts of ectopterygoid and palatine. Anal-fin pterygiophore spines present, except in *P. danae*. More than 10 AC[B] photophores. Dorsal step between AC[B] photophores #3 and #4 small, inconspicuous. Anterior medial lamella of first anal-fin pterygiophore absent. First branchiostegal ray of posterior ceratohyal narrow, not bladelike. See 'PHYLOGENETIC RELATIONSHIPS', page 221.

Four species of the equatorial Indian and Pacific Oceans and the Indo-Pacific region: *P. aquavitus*, *P. danae*, *P. omphus* and *P. unispinus*.

Polyipnus aquavitus Baird, 1971

FIGURE 23

Polyipnus aquavitus Baird, 1971:96-97 [holotype fig. 72].-Schalk, 1988:31-32.-Paxton et al. 1989:192.-Harold, 1990a:1114; 1990b:515.

DIAGNOSIS.-Gill rakers 13/14. Lateral pigment projection short, hemispherical. Posttemporal spine: single, elongate (10.0-15.1 % SL). Anal-fin pterygiophore spines long, needlelike. Photophore scale denticles absent. AC[B] photophores 9-11. AC[C] photophores separated by broad gaps.

DESCRIPTION.-Miniature species, maximum adult body size 35.3 mm SL. D (13) 12-14. A (15) 14-16. P 12-14. V 7. GR 4-5+9-10 = (13) 13-15. Vert. (35) 31-35. Anterior region of body laterally compressed. Body profile subrectangular anteriorly, with dorsal and ventral surfaces nearly parallel from horizontal position of orbit to dorsal blade and iliac spines ventrally, tapered posteriorly as far as anal-fin insertion. Caudal peduncle compressed and elongate. Flank scales diaphanous and deciduous. External bony keels and ridges of head smooth, nonserrate. Ventral margin of dentary slightly convex. Margins of dentary, premaxilla and maxilla with minute, recurved teeth. Conical teeth in one or two medial rows on palatine and 7 or 8 medial rows in a transverse patch in anterior region of vomer. No teeth present on posteromedial process of vomer. Frontal keel long, extending to, and overlapping, parietal keel. Dorsal and ventral arms of posttemporal nonserrate and support a long (10.0-15.1 % SL) tapered spine which bears on its anterodorsal surface a posteriorly directed barb. Ventral margin of pectoral shield bears 7-13 minute conical spines. Preopercle with two spines: ventral spine long (2.1-5.5 % SL) and directed posteroventrally; dorsal spine short (about 1/5 the length of ventral spine). Dorsal blade nonserrate and with two broadly tapered spines, one per side, directed dorsolaterally. First anal-fin pterygiophore bears two long ventrolaterally-directed spines (one per side). Adipose fin present, its base occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 28.6-36.4, orbit length 12.7-17.7, body depth 46.2-63.3, caudal-peduncle depth 9.0-10.8, caudal-peduncle length 15.8-21.1, dorsal-fin length 19.3-22.3, anal-fin length 20.5-25.3, preanal length 65.7-79.7, predorsal length 48.8-54.4, preventral length 59.6-79.2, postdorsal length 46.7-53.5, postanal length 38.7-43.1, AC[C] length 9.6-10.9, AC[B]-[C] length 2.3-4.0.

Ventral margins of all photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line.

PV (10). L 1. VAV (5). AC[A] 1+1+1, separate (not united in a common gland), in an anteriorly-inclined straight line. AC[B] (10;9-11). AC[C] (4), separated by gaps greater than diameter of 1 photophore.

Dark pigment saddle with a short, narrow predorsal notch only. Lateral pigment projection rounded and very short, extending very slightly beyond adjacent ventral pigment margin. Dark pigment also present in association with glandular photophore tissues, posterodorsal region of head, and delineating body trunk myosepta.

SIMILAR SPECIES.-<u>Polyipnus</u> <u>aquavitus</u> is most similar to <u>P</u>. <u>unispinus</u> and <u>P</u>. <u>danae</u>, two other miniature species (standard length less than 40 mm). <u>Polyipnus</u> <u>aquavitus</u> is distinguished from both by gill raker counts (13-15 compared with 11/12) and a rectangular as compared with a long, rodlike caudal peduncle. Also see Similar Species for <u>P</u>. <u>danae</u>.

DISTRIBUTION.-<u>Polyipnus</u> <u>aquavitus</u> has been collected off the east coast of Australia (Coral and Tasman Seas), New Caledonia, New Hebrides, various sites in the South Fiji Basin, and Indonesia (Celebes, Banda, Halmahera, Sulu seas) (Figure 24). This species was thought by Baird (1971) to be disjunct from the Tasman to the Banda Sea but additional collections reported here indicate a broad continuous geographic range.

<u>Polyipnus</u> <u>aquavitus</u> has been captured at depths above

50 m at night (Sulu Sea only), but according to other data from discrete-depth sampling (RMT-8 net) the bathymetric range is about 350 to 1100 m during the day and 90 to 500 m at night. The 1100 m value is the maximum depth fished by an oblique tow that finished at 450 m. Specimens were also collected by the same gear between 1000 and 1400 m but the presence of P. aquavitus in the shallower sample which preceded suggests at least a possibility of sample contamination. Polyipnus aquavitus has been taken in discrete-depth tows with P. unispinus or P. triphanos in Indonesia indicating very little or no bathymetric separation between these species in that region.

REMARKS.-Populations in the seas of Indonesia (e.g. Banda Sea) appear to be characterized by a slightly deeper body. There are, however, no detectable meristic differences among the populations of P. aquavitus. The observed morphometric differences may be a result of differential growth rates, since the Banda Sea is known to be an area of intense upwelling and elevated productivity (Van der Spoel and Schalk, 1988) and the Coral and Tasman Seas are not.

MATERIAL EXAMINED.-Holotype: ZMUC P20969 (1, 34.0 mm), 33°42'S 155°51'E, 1500 mwo, R/V Galathea Sta. 551, 2000 h (start), 13 Nov 1951.

Paratypes: ZMUC P20970-P20981 (11, 15.0-31.0 mm), same data as holotype. MCZ 46526 (2, 21.9-31.5 mm), same data.

Other Material: AMS I.19762-002 (3, 22.3-35.3 mm), 22°03'S 167°44'E, 0-800 m, R/V *Kimbla*, 1830-2345 h, 13 May 1971. AMS I.16494-004 (1, 24.2 mm), 34°08'S 152°13'E, 0-600 m, R/V *Kapala*, 2000-2230 h, 31 Oct 1972. AMS I.20316-005 (3, 21.4-36.6 mm), 34°20'S 151°56'E, 0-900 m, R/V *Kapala* 2050-0030 h, 14 Dec 1977. AMS I.19761-029 (10, 11.0-34.4 mm), 19°55'S 170°00'E, 0-550 m, R/V *Kimbla* field no. K4/71-8, 0315-0545 h, 12 May 1971. AMS I.20310-017 (3, 18.6-21.7 mm), 33°23'S 152°37'E, 0-625 m, R/V *Kapala*, 1545-1900 h, 13 Dec 1977. AMS I.16492-008 (3, 12.5-15.0 mm), 34°11'S 152°10'E, 0-250 m, R/V *Kapala*, 2255-0145 h, 25 Mar 1971. IOAN uncat. (2, 18.8-22.6 mm), 02°36'S 147°35'E, 800-0 m, R/V *Vityaz* Cr. 50, Sta. 6437, 14 May 1971. IOAN uncat. (1, 31.2 mm), 05°34'S 130°48'E, 1500-0 m, R/V *Vityaz* Cr. 57, Sta. 7261, 19 Mar 1975. Additional records provided in Appendix 4.

Polyipnus danae Harold, 1990

FIGURE 25

Polyipnus danae Harold, 1990a:1112-1114 [holotype fig. 1].

DIAGNOSIS.-Gill rakers 11/12. Lateral pigment projection indistinct, triangular. Posttemporal spine single, elongate (10.0-13.7 % SL). Anal-fin pterygiophore spines and photophore denticles absent. AC[B] photophores 11 or 12. AC[C] photophores separated by broad gaps. Caudal peduncle highly elongate, rodlike.

DESCRIPTION.-Miniature species, maximum adult body size 27.5 mm. D (13) 11-13. A (15) 15-18. P (13) 11-13. V (6) 6. GR 3/4+8/9 = (11) 11-12. Vert. (36). Anterior region of body laterally compressed. Body profile subrectangular anteriorly, with dorsal and ventral surfaces nearly parallel from horizontal position of orbit to dorsal blade and iliac spines ventrally, tapered posteriorly as far as anal-fin insertion. Caudal peduncle cylindrical and elongate (about one fifth of standard length). Flank scales diaphanous and deciduous. External keels and ridges of head smooth, nonserrate. Ventral margin of dentary convex and smooth. Premaxillary, maxillary and dentary with minute, conical teeth. One or two conical palatine teeth present. Anterior region of vomer with small, conical teeth in 4 to 6 medial rows in a transverse patch, posteromedial process without teeth. Longitudinal keel of frontal extending to, and overlapping, that of parietal. Long (10.5-13.7 % SL) spine present on posttemporal bone reaching posteriorly at least to origin of dorsal blade, with a posteriorly directed barb on anterodorsal surface. Ventral margin of pectoral shield with 2 or 3 concentric rows of 7 to 13 minute conical spines. Two preopercular spines present: ventral spine long (3.6-4.7 % SL), needlelike, ventrally directed; dorsal spine short (less than one fifth length of ventral spine), conical, directed ventrolaterally. Dorsal blade long-based (greatest dimension in anterior-posterior axis), with two posterodorsally directed, needlelike spines (one per side). Anal-fin pterygiophore spines absent. Adipose fin base occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 26.5-33.5, orbit length 13.9-15.8, body depth 42.4-50.2, caudal-peduncle depth 9.0-10.0, caudal-peduncle length 16.1-21.0, dorsal-fin length 15.7-19.1, anal-fin length 20.2-24.3, preanal length 67.3-74.0, predorsal length 45.6-50.3, preventral length 64.1-70.9, postdorsal length 43.3-50.7, postanal length 38.2-43.3, AC[C] length 9.1-12.4, AC[B]-[C] length 4.0-6.6.

Ventral margins of photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10). L 1. VAV (5). AC[A] 1+1+1, separate (not united in a common gland), in an anteriorly-inclined line. AC[B] (12; 11-12). AC[C] (4), separated by broad gaps (greater than or equal to diameter of 1 photophore).

Dark pigment saddle without notches, the ventral margin appearing straight over the length of the body trunk except for the very short and inconspicuous, triangular lateral projection. Flank, ventral to pigment saddle, silvery and reflective (especially in holotype). Myosepta of posterior body trunk outlined with melanic pigment.

SIMILAR SPECIES.-*Polyipnus danae* most closely resembles *P. unispinus* and *P. aquavitus*. These three species have relatively long posttemporal spines (10.5-13.7, 10.5-16.4, 10.1-16.6 % SL, respectively) compared with *P. omphus* (5.7-10.0 % SL) and *P. laternatus* (5.7-8.5 % SL), two other rather similar species. The *P. danae* - *P. unispinus* - *P. aquavitus* group is further characterized by small body size (less than 40 mm SL, and attaining sexual maturity at less than 30 mm), and very low gill raker counts (11-12; 11-12; 13-15, respectively, compared with *P. omphus*, 17-21, and *P. laternatus*, 16-22). *Polyipnus danae* is distinguished from all of the aforementioned by the lack of external anal-fin pterygiophore spines.

DISTRIBUTION.-*Polyipnus danae* is known only from two collections made off the Philippine Islands in the South China Sea, during the 1928-30 DANA Expedition (Figure 26). The specimens were trawled with 2,000 and 1,000 m wire (holotype and paratypes, respectively), indicating that this species occurs at some level between the surface and a maximum depth of about 700 m. The geographic positions of the collecting stations suggest that *P. danae*, like many other *Polyipnus*, may be associated with the continental slope.

The area around the Philippines is particularly rich in

Polyipnus species but only P. danae, P. triphanos Schultz, 1938, P. spinifer Borodulina, 1979, P. ovatus and P. meteori Kotthaus, 1967 are known from collecting stations within the South China Sea.

REMARKS.-The P. laternatus complex, consisting of P. laternatus, P. omphus, P. aquavitus, and P. unispinus was delimited by Baird, 1971 on the basis of single long posttemporal spines, a relatively high number of anal photophores, the first supra-anal (=AC[A]) photophore at the level of the second or dorsally, and elongate body shape. Pending completion of phylogenetic analysis, P. danae was provisionally placed by Harold (1990a) in this group. The analysis has shown that of these five species, all except P. laternatus together constitute a monophyletic group. A new group, the P. omphus species group is recognized here which excludes P. laternatus.

In an unpublished report (Søgaard, 1975) listed the specimens now recognized as P. danae as P. aquavitus. Although these two species are similar in pigmentation and scale denticulation, P. danae is much more similar to P. unispinus with which it shares the lowest gill raker counts in the genus (11-12) and a unique rodlike caudal peduncle. Polyipnus danae shares an unusual character (reduced anal-fin pterygiophore spines) with many Polyipnus species but not with the remaining members of the P. omphus species group.

MATERIAL EXAMINED.-Holotype: ZMUC P206919 (1 male, 26.5 mm), 19°18.5'N, 120°13'E, 2000 mwo, R/V Dana Sta. 3716 III, 1400-1600 h, 22 May 1929.

Paratypes: ZMUC P206920 (1, 24.2 mm), ZMUC P208577 (1, 24.8 mm), ZMUC P208578 (1, 27.3 mm), ZMUC P208579 (1, 25.4 mm), ZMUC P208580 (1, about 26 mm), ZMUC P208581 (1, about 30 mm), 20°03.5'N, 120°50.0'E, 1000 mwo, R/V Dana Sta. 3729 I, 2015-2215 h, 14 Jun 1929.

Polyipnus omphus Baird, 1971

FIGURE 22

Polyipnus omphus Baird, 1971:94-96 [fig. 71].-Harold, 1990a:1114; 1990b:515.

Polyipnus laternatus.-Kobayashi, 1963:179.-Kotthaus, 1967:26 [fig. 41; otoliths, figs. 42 and 43].

DIAGNOSIS.-Gill rakers 17-21. Lateral pigment projection broad-based, triangular, reaching about half way to lateral midline; elongate curvilinear lightly pigmented area immediately posterior of projection. Posttemporal spine: single, length moderate (5.9-10.7 % SL). Anal-fin pterygiophore spines long, needlelike. Photophore scale denticles absent. AC[A] photophores 1+1+1, in a horizontal or slightly inclined line, #3 slightly elevated relative to first AC[B]. AC[B] 10-12. AC[C] photophores compact, separated by gaps approaching the diameter of 1 photophore.

DESCRIPTION.-Body size up to about 56 mm SL. D (14) 14-15. A (16) 16-18. P 13-14. V 6-7. GR 5-6+12-15 = (19) 17-21. Vertebrae (33) 33-34. Body laterally compressed. Body profile anterior of dorsal blade elliptical, relatively shallow, tapered posteriorly at about a 30° angle as far as caudal peduncle. Profile of caudal peduncle subrectangular, slightly tapered posteriorly. Flank scales diaphanous, sheetlike, deciduous. Ventral margin of dentary slightly convex and with minute widely-spaced serrations. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary teeth much shorter, conical. One medial row of 3 to 8 conical teeth on palatine. Anterolateral processes of vomer each with a patch of 2 to 8 conical teeth. No teeth present on posteromedial process of vomer. Frontal keel margin smooth, nonserrate. Parietal keel finely serrate and with a minute anteriorly-directed spine at its intersection with frontal keel. Dorsal and ventral limbs of posttemporal smooth, nonserrate and support a single moderately long (5.9-10.7 % SL) spine which bears on its anterodorsal surface a minute posteriorly-directed barb. Lateral ridges of cleithrum, nonserrate; ventral margin of pectoral shield bears 8-14 minute, triangular spines. Preopercular lateral ridges nonserrate. Preopercle with two spines: ventral spine straight, short (1.7-2.7 % SL) and directed ventrally;

dorsal spine minute, bladelike, triangular. Dorsal blade long-based, apically depressed, anterodorsal surface smooth, terminating posteriorly in 2 (one per side) triangular dorsolaterally-directed spines. First anal-fin pterygiophore bears two long ventrolaterally-directed spines (one per side). Adipose fin base short, occupying less than one third of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 27.5-34.3, orbit length 13.6-16.1, body depth 51.1-57.1, caudal-peduncle depth 9.4-10.7, caudal-peduncle length 13.0-17.7, dorsal-fin length 19.8-25.3, anal-fin length 26.5-29.0, preanal length 66.7-79.3, predorsal length 49.6-55.7, preventral length 59.8-76.3, postdorsal length 49.0-54.3, postanal length 39.5-47.1, AC[C] length 6.7-9.5, AC[B]-[C] length 2.0-4.8.

Ventral margins of all photophore scales smooth, without denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10). L 1. VAV (5). AC[A] 1+1+1, separate (not united in a common gland), arranged in a horizontal to slightly inclined straight line. AC[B] (11; 10-12), with a slight dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with a long, narrow predorsal notch, curved slightly towards the anterior. Lateral pigment projection broad-based, triangular and extending about half way to lateral midline. Dark pigment also present in association with photophore tissues, dorsolateral region of head, between bases of dorsal-fin rays, base of pectoral fin, and delineating body trunk myosepta with heaviest concentration at midline.

SIMILAR SPECIES.-*Polyipnus omphus* most closely resembles *P. laternatus* with which it shares moderately long posttemporal spines, presence of anal-fin pterygiophore spines and high gill raker counts. Like other members of the *omphus* species group, *P. omphus* always has three isolated AC[A] photophores that appear as an anterior continuation of the AC[B] cluster. In *P. laternatus* the posterior two of these photophores are usually joined and markedly disjunct from the AC[B] elements. *Polyipnus omphus* is distinguished from other members of the *omphus* group by the much shorter posttemporal spine (5.9-10.7 as compared with 10.0-16.1 % SL total range) and much higher gill raker counts (17-21 compared with 11-15 total range).

DISTRIBUTION.-Originally known from the western Indian Ocean (including type locality) and the central Pacific (Baird, 1971). New material reported here suggests that *P. omphus* is an equatorial species of Indonesia and the western Pacific in addition to the western Indian Ocean (Figure 21). There are no records from the central or eastern Indian Ocean and parts of the western Pacific; such range gaps could represent real disjunction or collection artifacts.

REMARKS.-Although not specifically designated by Baird (1971: 94-96) in his description of P. omphus the 35.1 mm specimen taken with the holotype at R/V Discovery Sta. 5509 is assumed to be a valid paratype. It is labelled as such in the collection of the Museum of Comparative Zoology, Harvard University.

Baird (1971) stated that the specimen he examined from the central Pacific Ocean (SIO 60-236-10) was "slightly different phenotypically" from Indian Ocean material. Additional collections from Indonesia and the central Pacific examined here indicate that any morphometric or meristic distinctiveness of the SIO specimen is probably due more to a small sample size than any geographic trend or disjunction in morphological variation.

MATERIAL EXAMINED.-Holotype: BMNH 1970.7.30.1 (1, 43.0 mm), 11°26.8'S (not 11°21'S as reported by Baird, 1971: 94) 48°58.2'E, (0-) 200 m, R/V Discovery Sta. 5509, 21 Aug 1964.

Paratype: MCZ 46525 (1, 35.1 mm), same data as holotype.

Other Material: IOAN uncat. (1, 33.6 mm), 05°14'S 41°51'E, 1000-0 m, R/V Vityaz Cr. 31, Sta. 4688, 2054-2145 h, 17 Mar 1960. IOAN uncat. (1, 41.1 mm), 01°15'S 142°46'E, 1000-0 m, R/V Vityaz Cr. 57, Sta. 7318, 1975. IOAN uncat. (2, 31.6-35.5 mm), 00°01'S 175°56'W to 00°03'S 176°07'W, 5428-0 m, R/V Vityaz Cr. 34, Sta. 5139, 1145-1205 h, 09 Nov 1961. MCZ 64696 (1, 44.3 mm), 05°25'S 152°38'E, 2380 mwo, R/V Lady Basten, field no. GRH 1012, 20 May 1981. MCZ 64695 (1, 55.9 mm), 06°25'S 152°09'E, 2380 mwo, R/V Lady Basten, field no. GRH 1011, 20 May 1981. SIO 60-236-10 (1, 28.4 mm), 02°31.3'N 140°39.3'W to 02°31.3'N 141°08'W, R/V Tethys, 4 Jul 1960. SIO 68-534-10 (1, 33.6 mm), 00°00'S 165°42.5'W to 00°03.7'N 165°46'W, 11-12 Aug 1968. USNM 265967 (1, 33.2 mm), 00°52'N 153°02'W to 00°58'N 153°02'W, 0-360 m, R/V Gyre, NORPAX-79 Expedition, field no. 79-5-12, 2323-0110 h, 23-24 May 1979. ZMH 4886 (2, 18.1-32.9 mm), 02°06.5'N 57°54'E, R/V Meteor Transect 19, Sta. 179, 1540-1640 h, 2 Feb 1965. ZMUC P206932 (1, 19.5 mm), 01°15'N 136°07'E, 1000 mwo, R/V Dana Sta. 3753 I, 0320-0520 h, 14 Jul 1929. ZMUC P206933 (1, 51.0 mm), 04°38'S 126°51'E, 1500 mwo, R/V Dana Sta. 3786 VI, 2345-0030 h, 8-9 Aug 1929. ZMUC P206934 (1, 45.3 mm), 01°24'S 138°42'E, 1200 mwo, R/V Dana Sta. 3767 V, 0230-0430 h, 24 Jul 1929. ZMUC P207116 (1, 40.0 mm), 01°13'S 138°42'E, 1000 mwo, R/V Dana Sta. 3766 XIII, 0300-0530 h, 23 Jul 1929.

Polyipnus unispinus Schultz, 1938

FIGURE 27

Polyipnus unispinus Schultz, 1938:137-138,142 [fig. 43, holotype]; 1961:643-644 [fig. 20, holotype].-Baird, 1971:97 [fig. 73, holotype].-Harold, 1990a:1114;

1990b:515.

Polyipnus sp..-Weitzman, 1974:344 [USNM 203345].

DIAGNOSIS.-Gill rakers 11/12. Ventral margin of dorsomedian pigment essentially straight from pectoral girdle to cudal peduncle. Posttemporal spine: single, elongate (10.5-16.1 % SL). Anal-fin pterygiophore spines long, needlelike. Minute denticles restricted to ventral surface of PV photophore scales. AC[A] 1+1+1, not connected to but appearing continuous with AC[B] cluster. AC[B] photophores 9-10, posterior 3 to 5 appearing isolated and not interconnected. AC[C] photophores united but separated by broad gaps.

DESCRIPTION.-Miniature species, maximum adult body size 35.2 mm SL. D (12) 11-13. A (14) 13-15. P (12) 12-13. V (7) 6-7. GR 4+7/8 = (12) 11-12. Vert. 35/36. Body laterally compressed, profile excluding caudal peduncle excentric elliptical. Caudal peduncle highly elongate, rodlike (as in P. danae). Flank scales diaphanous and sheetlike, highly elongate dorsoventrally. Ventral margin of dentary slightly convex and with broad, shallow serrations. Margin of dentary with minute, recurved teeth. Premaxillary teeth about half as long as dentary teeth. Maxillary teeth smaller smaller, conical. One or two conical teeth present on palatine. Anterior region of vomer with minute conical teeth in 4 to 6 medial rows radiating from anteromedial margin. No teeth present on posteromedial process of vomer. Frontal keel with broad, shallow serrations and extending to, and overlapping, parietal keel. Dorsal and ventral limbs of posttemporal nonserrate, diverging at about a 90° angle and supporting a long (10.5-16.1 % SL) slender spine which bears on its anterodorsal surface a posteriorly directed barb. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 7-13 minute conical spines. Lateral ridges of preopercle serrate, two spines present at angle: ventral spine long, (4.0-7.0 % SL), straight and directed ventrolaterally; dorsal spine short, its length about 1/10 that of ventral spine. Dorsal blade long-based, occupying more than half of dorsum between base of posttemporal spine and dorsal-fin origin, anterodorsal surface smooth, nonserrate and terminating posteriorly with two long needlelike spines, one per side, directed posterodorsally. First anal-fin pterygiophore bears two long ventrolaterally-directed spines (one per side). Adipose-fin base short, occupying between one third and one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

<u>Morphometric</u> <u>characters</u> (% SL): Head length 28.6-34.2, orbit length 13.5-16.5, body depth 46.7-51.0, caudal-peduncle depth 8.8-10.2, caudal-peduncle length 17.9-22.5, dorsal-fin length 16.7-20.3, anal-fin length 16.9-23.3, preanal length 65.9-70.8, predorsal length

58.4-63.2, preventral length 58.5-66.7, postdorsal length 43.4-46.6, postanal length 36.8-41.9, AC[C] length 10.5-11.2, AC[B]-[C] length 1.0-2.8.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins with minute denticles. L 1. VAV (5). AC[A] 1+1+1, separate (not united as a cluster), in anteriorly-inclined straight line or with #1 and #2 adjacent and elevated relative to #3; not connected to first AC[B]. AC[B] (9; 9-10), the posterior 3 to 5 photophores appearing isolated and not interconnected by lumena. AC[C] (4), widely spread, separated by spaces greater than diameter of 1 photophore.

Dark pigment saddle without notches or a lateral projection. Some specimens have a slight ventral deflection of the pigment margin in the position of the lateral projection in other species. Within pigment saddle scale pockets accentuated by heavy concentrations of melanic pigment. Dark pigment also present in association with photophore tissues, dorsal and dorsolateral regions of head, between bases of anal- and dorsal-fin rays, covering base of caudal fin, and delineating body trunk myosepta with 2 diffuse bands. Lateral midline at intersections with myosepta accentuated by large melanophores, giving the general appearance of a narrow stripe.

SIMILAR SPECIES.-Polyipnus unispinus is most similar to P. danae and P. aquavitus. These three miniature species do not exceed 40 mm, have single, long, slender posttemporal spines and reduced numbers of gill rakers (11-15). The former two species are closest, both having highly elongate, rodlike caudal peduncles and 11 or 12 gill rakers. Polyipnus unispinus is distinguished from P. danae by the presence of anal-fin pterygiophore spines and PV photophore scale denticles. It is distinguished from all congenerics by the lack of a lateral pigment projection. Polyipnus unispinus is the only species outside of the P. spinosus species group with photophore scale denticles. These last two characters can be used effectively for identification of specimens as small as 10 mm SL.

DISTRIBUTION.-Polyipnus unispinus occurs in the Java Trench, Timor, Halmahera, Sulu and Celebes Seas, the New Britain Trench (off the Solomon Islands), southeastward to New Caledonia and with a few captures to the north of New Zealand (Figure 26). This species has not been collected in the South China Sea (adjacent to the Sulu Sea). Collections from Indonesia made with discrete-depth sampling gear indicate a bathymetric range of 300-500 m by day, however, one night sample from the Sulu Sea (R/V Alpha Helix Sta. 177, 1975) shows P. unispinus within 50 m of the surface. This suggests that either significant vertical migration takes place or that the species has a shallow depth distribution in the Sulu Sea (Harold, in prep.). Anomolous shallow depth distributions for many deep-sea taxa, including sternoptychids, in the nearby Banda Sea have been reported by van der Spoel and Schalk (1988).

REMARKS.-The presence of minute denticles on the ventral surfaces of the PV photophore scales which also occurs throughout the *spinosus* species group is not regarded here as an indication of close relationship. The position of *P. unispinus* within the *P. omphus* species group is well corroborated (see 'PHYLOGENETIC RELATIONSHIPS' chapter). It therefore seems likely that denticles on the PV photophore scales have arisen in this species independently of such structures in the other group.

MATERIAL EXAMINED.-*Holotype*: USNM 103353 (1, 20.5 mm), 13°22'22"N 124°00'48"E, (0-) 703 m, R/V *Albatross* Sta. 5451, 5 Jun 1909.

Paratypes: USNM 103029 (5, 16.0-19.0 mm), same data as holotype.

Other Material: AMS I.19287-003 (2, 27.1-28.8 mm), 08°50'S 129°57'E, 0-1000 m, 0355-0750 h, R/V *Alpha Helix* Sta. 17, field no. JP 75-17, 20 Mar 1975. AMS I.19284-007 (1, 35.2 mm), 04°39'S 129°54'E, 0-2000 m, 2215-0530 h, R/V *Alpha Helix* Sta. 23, field no. JP 75-22, 26 Mar 1975. AMS I.19292-007 (5, 25.4-30.4 mm), 08°50'S 129°43'E, 0-550 m, 0855-1350 h, R/V *Alpha Helix* Sta. 18, field no. JP 75-18, 20 Mar 1975. IOAN uncat. (1, 33.2 mm), 05°49'N 152°53'E to

05°45'N 152°43'E, 1050-0 m, R/V Vityaz Cr. 25, Sta. 3655, 21 Aug 1957. IOAN uncat. (1, 31.0 mm), 05°34'S 130°48'E, 1500-0 m, R/V Vityaz Cr. 57, Sta. 7261, 19 Mar 1975. IOAN uncat. (2, 28.4-29.8 mm), 29°52'S 168°48'E to 29°49'S 168°53'E, 500-0 m, R/V Dmitry Mendeleev Cr. 16, Sta. 1261, 04 Jan 1976. IOAN uncat. (9, 21.2-33.9 mm), 02°36'S 147°35'E, 800-0 m, R/V Vityaz Cr. 50, Sta. 6437, 14 May 1971. LACM 44481 (18, 16.0-32.0 mm), 04°43.7'S 129°00'E, 420-500 m, R/V Alpha Helix Sta. 69, 0200-0300 h, 18 Apr 1975. LACM 38588 (4, 20.0-30.0 mm), 04°57.0'S 130°08.0'E, 350-550 m, R/V Alpha Helix Sta. 92, 1500-1600 h, 5 May 1975. LACM 44503 (1, 33.0 mm), 08°41.0'N 121°19.3'E, 0-50 m, R/V Alpha Helix Sta. 177, 2320-0012 h, 4 Jun 1975. LACM 44469 (3, 32.0-35.0 mm), 04°53.5'S 129°54.0'E, 480-680 m, R/V Alpha Helix Sta. 50, 14 Apr 1975. LACM 44481 (2, 33.0-35.0 mm), 04°54.8'S 129°47.0'E, 500-600 m, R/V Alpha Helix Sta. 62, 17 Apr 1975. LACM 44486 (4, 16.0-29.0 mm), 04°56.0'S 129°36.0'E, 500-600 m, R/V Alpha Helix Sta. 62, 17 Apr 1975. MCZ 64702 (1, 36.0 mm), 12°38'S 148°55'E, 3240 mwo, R/V Lady Basten, field no. GRH 1046, 02 Dec 1982. MCZ 64703 (1, 28.9 mm), 07°19'S 151°11'E, (0-) 1250 m, R/V Lady Basten, field no. GRH 1058, 30 Jan 1982. MCZ 64706 (5, 27.5-33.2 mm), 04°46'S 152°39'E, 0-800 m, R/V Lady Basten, field no. GRH 1063, 06-07 Feb 1982. MCZ 89816 (1, 24.4 mm), 06°14'S 151°50'E, 2376 mwo, R/V Lady Basten, 18 May 1981. MCZ 89817 (2, 31.9-34.5 mm), 06°12'S 152°11'E, 2388 mwo, R/V Lady

Basten, 19 May 1981. MCZ 89818 (1, 25.6 mm), 05°37'S 152°38'E, R/V *Lady Basten*, 21 May 1981. MCZ 89822 (1, 29.9 mm), 06°54'S 152°06'E, 2380 mwo, R/V *Lady Basten*, 23 May 1981. SIO 61-31-108 (1, 31.6 mm), 11°56.7'S 115°22.2'E to 12°15'S 115°30.1'E, 0-2000 m, R/V *Monsoon*, MT no. 3, 29-30 Oct 1964. ZMUC P206964 (1, 21.4 mm), 05°31'S 131°01'E, R/V *Galathea* Sta. 494. ZMUC P206965 (2, 21.5-34.3 mm), 01°20'S 138°42'E, 2000 mwo, R/V *Dana* Sta. 3768 V, 1340-1640 h, 24 Jul 1929. ZMUC P207119 (1, 30.4 mm), 01°20'S 138°42'E, 2000 mwo, R/V *Dana* Sta. 3768 V, 1340-1640 h, 24 Jul 1929.

Polyipnus spinosus **species group**

DEFINITION.-Ventral preopercular spine long and scythelike. PV photophore scales denticulate. Serrations present on ventral margin of dentary, posttemporal limbs, lateral surfaces of preopercle and dorsal blade. Posttemporal with two or three spines. Anterior medial lamella of first dorsal-fin pterygiophore absent. Ectopterygoid elongate, distinctly arced and with a medial ridge. Secondary frontal keel not extending to parietal. Posterior shelf of epiotic with cuplike fossa. Fifth ceratobranchial with short, densely packed teeth. Antorbital bone minute, transversely elongate. See 'PHYLOGENETIC RELATIONSHIPS', page 232.

Fourteen species endemic to various oceanic areas from the western Indian Ocean through the Indo-Pacific region and east to the Hawaiian Islands and the East Pacific Rise: *P. asper*, *P. elongatus*, *P. fraseri*, *P. indicus*, *P. inermis*, *P. nuttingi*, *P. oluolus*, *P. parini*, *P. paxtoni*, *P. soelae*, *P. spinifer*, *P. spinosus*, *P. stereope*, *P. tridentifer*.

Polyipnus asper new species

FIGURE 32

DIAGNOSIS.-Gill rakers 17-20. Lateral pigment projection tapered and long, approaching but not reaching lateral midline. Two posttemporal spines: dorsal spine long (5.7-12.2 % SL), basal spine length less than half of that of dorsal spine. Anal-fin pterygiophore spines absent. Photophore scale denticles restricted to PV, VAV, AC[B] and AC[C] clusters. AC[A] photophores grade into AC[B]. AC[B] 8-10. AC[C] photophores compact, not separated by conspicuous gaps.

DESCRIPTION.-Moderate-sized species, maximum adult body size 62.1 mm SL. D (13) 12-13. A (16) 15-17. P (13) 12-13. V (7) 6-7. GR (6+13) 5-6+12-14 = (19) 17-20. Vert. (33) 33. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin subrectangular, slightly tapered anteriorly, acutely tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate in anterior-posterior axis. Flank scales diaphanous and deciduous, very few remaining on specimens examined. Ventral margin of dentary slightly convex and with two serrate keels. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary teeth shorter, conical. Palatine teeth absent. Anterior region of vomer with 16-20 medial rows of minute conical teeth in a transverse patch. No teeth present on posteromedial process of vomer. Frontal and parietal medial keels serrate, overlapping but not forming a continuous frontal-parietal keel. Parietal keel discontinuous; anterior region keel-like, posterior region with 2 conical spines in the medial plane, directed anteriorly and posteriorly. Dorsal and ventral limbs of posttemporal acutely divergent, with 2 parallel serrate ridges and supporting 2 spines: dorsal spine serrate, long (5.7-12.2 % SL), and curved dorsally; ventral spine short (usually less than half of the length of the dorsal spine), nonserrate, ventrolaterally directed. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 5-11 conical spines. Vertical and anteroventral rami of preopercle each with 2 parallel deeply serrate lateral ridges. Preopercle with two spines: ventral spine long (2.4-6.6 % SL), anteriorly curved, directed anteroventrally; dorsal spine short (not longer than one preopercular serration), directed laterally. Dorsal blade smooth or with a single spine-like serration, exposed length and height about equal, terminating posterodorsally as 2 conical dorsolaterally-directed spines (one per side). Anal-fin pterygiophore spines absent. Adipose-fin base moderately long, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 31.2-39.4, orbit length 13.7-18.4, body depth 58.8-68.0, caudal-peduncle depth 9.6-12.9, caudal-peduncle length 13.2-20.0, dorsal-fin length 19.2-25.7, anal-fin length 21.9-25.6, preanal length 67.8-76.0, predorsal length 56.2-62.1, preventral length 63.2-74.8, postdorsal length 49.5-61.9, postanal length 37.9-42.9, AC[C] length 6.7-9.1, AC[B]-[C] length 1.9-3.5.

Ventral margins of photophore scales smooth, except PV, VAV, and AC[C] which have numerous denticles, and AC[B] which have 1 to 3 denticles per scale. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10). L 1. VAV (5). AC[A] 1+1+1, #1 and #2 isolated, but aligned with #3 and first three AC[B]. AC[A] #3 united with AC[B] forming a continuous gland: AC[A] photophores appear to grade into AC[B]. AC[B] (?; 8-10), with dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with predorsal notch and moderately long lateral pigment projection tapering toward but but not reaching lateral midline. Dark pigment also present in association with glandular photophore tissues, posterodorsal region of head, opercle, lateral surface of dentary, between bases of dorsal-fin rays, and diffusely delineating body-trunk myosepta.

SIMILAR SPECIES.-Four species of the *P*. *spinosus* species group have posttemporals with 2 spines: *P*. *asper*, *P*. *indicus*, *P*. *nuttingi*, and *P*. *oluolus*. *Polyipnus* *asper* most closely resembles *P*. *indicus* in overall body form, photophore patterns and fin-ray counts. The present species is distinguished from *P*. *indicus* by the presence of denticles on scales of the AC[B] photophore cluster and two opposed medial spines representing the modified posterior region of the parietal keel. Two other species, *P*. *parini* and *P*. *inermis*, have body shapes and photophore complements that are similar to those of *P*. *asper* but they have 3 posttemporal spines and a broad gap separating the third and fourth AC[B] photophores.

DISTRIBUTION.-*Polyipnus* *asper* is known from one R/V *Anton* *Bruun* and one R/V *Akademik* *Knipovich* station off the west coast of the Malay Peninsula in the Andaman Sea (Figure 29). These collections were made 3 years apart at approximately the same position. The maximum depth of capture for the type series is 384 m.

REMARKS.-*Polyipnus asper* is probably more widely distributed in the eastern Indian Ocean but has gone undetected because of low sampling density in the region. Most expeditions (e.g. R/V *Dana*, 1928-1930) made very few collections and only along a single west-east line which passed to the south of Sumatra. In that area several other *Polyipnus* taxa have been collected albeit not members of the *P. spinosus* species group (i.e. *P. meteori*, *P.* aff. *triphanos*, *P. unispinus*). Numerous collections made off the northwest coast of Australia have yielded *P.* aff. *kiwiensis* and large numbers of a new species, *P. soelae*.

Günther (1887) listed a reference to *P. spinosus* from the Bay of Bengal and although such a western occurrence of that species cannot be ruled out the species referred to is more likely to have been *P. asper*.

ETYMOLOGY.-The trivial name *asper* is a Latin adjective meaning rough, referring to the presence of denticles on the AC[B] photophore scales.

MATERIAL EXAMINED.-*Holotype:* USNM 273282 (1, 62.1 mm), 10°39'N 46°35'E, 0-384 m, R/V *Anton Bruun*, Cr. 1 (International Indian Ocean Expedition), Sta. 23, 24 Mar 1963.

Paratypes: USNM 304746 (30, 28.0-54.9 mm), same data as holotype. IOAN uncat. (15, 26.5-58.0 mm), 10°42.4'N 96°43.7'E, R/V *Akademik Knipovich* Sta. 452, 11 Mar 1966.

Polyipnus elongatus Borodulina, 1979

FIGURE 42

Polyipnus elongatus Borodulina, 1979:8-9 [holotype fig. 5].-Harold, 1989:874-875; 1990b:515.-Paxton et al., 1989:192.

DIAGNOSIS.-Gill rakers 22-24. Lateral pigment projection tapered and long, approaching but not reaching lateral midline. Three posttemporal spines: dorsal long (9.0-10.1 % SL), median and ventral spines subequal, about 1/4 length of dorsal spine. Anal-fin pterygiophore spine absent. Photophore scale denticles restricted to PV and VAV clusters. AC[A] photophores grade into AC[B]. AC[B] 13 or 14. AC[C] photophores separated by conspicuous gaps.

DESCRIPTION.-Adult body size moderate to large, maximum about 70 mm SL. D (13) 13-14. A (19) 17-20. P (13) 12-13. V 7. GR 7+15/16 = (23) 22-24 (24 from Borodulina, 1979). Vertebrae (35) 35. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin subrectangular, gradually tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate. Flank scales deciduous, diaphanous. Ventral margin of dentary slightly convex and with 2 parallel, serrate bony keels. Margins of dentary and premaxillary with long, recurved teeth. Maxillary with minute, recurved teeth. Palatine usually without teeth, occasionally a single conical tooth is present. Anterior region of vomer with a transverse patch conical teeth in about 8 rows radiating from anterior margin of bone. No teeth present on posteromedial process of vomer. Frontal and parietal keels serrate. Frontal keel long, extending to, and overlapping, parietal keel. Parietal keel discontinuous; posterior region of keel with 2 minute conical spines, directed anteriorly and posteriorly. Dorsal and ventral arms of posttemporal with 2 parallel, serrate bony keels. Posttemporal arms acutely divergent, and supporting 3 spines: dorsal spine long (9.0-10.1 % SL), bladelike, posteriorly directed, with lateral margins and medial ridge serrate; median and ventral spines short (less than or equal to one quarter of the length of dorsal spine), and directed posterolaterally. Lateral ridges of cleithrum smooth, nonserrate, except ventral margin of pectoral shield which bears 14-19 short, recurved spines. Lateral ridges of vertical and anteroventral rami of preopercle with widely-spaced, abrupt, spinelike serrations. Preopercle with two spines: ventral spine long (5.9-7.3 % SL), with a medial keel-like ridge, anteriorly arced, axis directed ventrally; dorsal spine minute (slightly longer than one preopercular serration), recurved, directed anteroventrally. Dorsal blade short-based, anterodorsal surface deeply serrate, with two conical spines, one per side, directed posterodorsally. Anal-fin pterygiophore spines absent. Adipose fin base long, occupying between one half and three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

<u>Morphometric</u> <u>characters</u> (% SL): Head length 32.9-34.0, orbit length 14.9-17.7, body depth 58.3-59.9, caudal-peduncle depth 10.8, caudal-peduncle length 14.9-15.5, dorsal-fin length 19.3-22.3, anal-fin length 22.6-34.2, preanal length 65.1-67.4, predorsal length 55.1-58.4, preventral length 59.0-62.3, postdorsal length 57.0-57.4, postanal length 36.0-46.4, AC[C] length 7.2-8.0, AC[B]-[C] length 1.2-1.4.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins of scales with spinelike denticles. L 1. VAV (5), ventral margins of scales denticulate. AC[A] 1+(2), in an anteriorly-inclined straight line: #1 isolated, not connected to #2 by a lumen; #2 and #3 connected to each other and to AC[B], appearing as a continuous glandular photophore cluster. AC[B] (14; 13-14), with an indistinct dorsal step between #3 and #4. AC[C] (4), conspicuous gaps separating each photophore, modified scales not present in specimens examined but scales reported to be without "spines" (= denticles) by Borodulina (1979:8).

Dark pigment saddle with predorsal notch and a long lateral projection, strongly tapered ventrally, approaching but not reaching lateral midline. Dark pigment also present in association with glandular photophore tissues, nonglandular ventrolateral margins of photophores, dorsal surface of head, and delineating body trunk myosepta.

SIMILAR SPECIES.- Polyipnus elongatus bears some similarity to P. spinosus sensu stricto with regard to pigmentation and, superficially, the spines of the posttemporal bone. Polyipnus elongatus is most similar to P. paxtoni, particularly with respect to photophore patterns, pigmentation and posttemporal spine configuration. These two species are the only members of the genus with two highly reduced, subequal median and ventral posttemporal spines. Polyipnus elongatus differs in its higher AC[B] photophore counts and lack of denticles throughout the AC cluster. Also see 'SIMILAR SPECIES' section for P. paxtoni.

DISTRIBUTION.-Polyipnus elongatus has been collected only in the western Coral Sea, off the east coast of Queensland, Australia (Figure 43). Available records suggest that this species occurs above 440 m.

The range of P. elongatus probably overlaps with P. paxtoni and P. triphanos and possibly P. unispinus and P. aquavitus.

REMARKS.-According to Borodulina (1979:9), P. elongatus is most similar to P. spinosus. However, the material that she listed and described for the latter species had denticulate AC[C] photophore scales, a feature which is not evident in the holotype of P. spinosus, other material reported here or by Bourret (1985). The specimens mistaken for P. spinosus by Borodulina have been examined and are attributed to a new species, P. soelae.

MATERIAL EXAMINED.-Holotype: ZIL 43999 (1, 59.0 mm), 19°15.6'S 150°27.5'E, (0-) 440 m, R/V Lira, 14 Jun 1968 (x-radiograph only).

Paratypes: ZIL 44001 (1, 51.0 mm), same data as holotype (x-radiograph examined only).

Other Material: AMS I.21795-007 (5, 54.6-68.8 mm), 28°03'S 154°04'E, (0-) 731 m, 0650 h, R/V Kapala, field no. K78-23-08, 6 Nov 1978. AMS I.20518-005 (2), 28°02'S 153°59'E, (0-) 548 m, R/V Kapala, field no. K78-09-05, 0735-0835 h, 02 Jun 1978 (not seen; apparently lost).

Polyipnus fraseri Fowler, 1934

FIGURE 38

Polyipnus fraseri Fowler, 1934:257-258.-Parr, 1937:55.-Schultz, 1938:142, 145; 1961:642; 1964:267.-Yamamoto, 1982:327.-Fujii, 1984:47 [pl. 49L].-Harold, 1989:874-875; 1990b:509-515 [holotype fig. 2].

Polyipnus tridentifer.-Baird, 1971:86 [part, incorrect subsequent spelling and year in synonymy: *Polyipnus frazeri* Fowler, 1933].

Polyipnus spinosis [sic].-Borodulina 1979:7-8 [part, incorrect subsequent spelling of *Polyipnus spinosus*].

DIAGNOSIS.-Gill rakers 19/20. Two dark lateral pigment projections on flank, anterior projection broad with a rounded termination ventral of lateral midline, posterior projection short and tapered. Three posttemporal spines: dorsal spine highly elongate (15.2-23.0 % SL), median and ventral spines about half of the length of dorsal spine. Unique posterior preopercular spine. Anal-fin pterygiophore spines absent. Eye relatively large, orbit length about one quarter of standard length. PV, VAV, AC[B] and AC[C] photophore scales with numerous denticles. AC[A] photophores absent. AC[B] (4). AC[C] photophores without isolating gaps. Large space between AC[B] and AC[C] photophore clusters (8.7-11.9 % SL).

DESCRIPTION.-Adult body size small to moderate, largest specimen 40.4 mm. D (10) 10. A (11) 12. P (14) 14. V (7) 6. GR 6/7+13 = (20) 19. Body deep, compressed, anterior body profile round. Caudal peduncle extremely narrow. Head relatively large. Flank scales diaphanous, deciduous. Ventral margin of dentary smooth, without serration. Margins of dentary and premaxillary with minute recurved teeth, maxillary teeth shorter and conical. Palatine teeth absent. Anterior region of vomer with a transverse patch of 12 or 13 medial rows of minute conical teeth, no teeth present on posteromedial process. Longitudinal frontal keel smooth, extending to and overlapping a reduced parietal keel. Posttemporal dorsal limb smooth, lateral ridge of ventral limb deeply serrate. Dorsal and ventral arms joined by broad web-like ossification, producing extensive armored shield between occiput and dorsal fin origin. Three posttemporal spines: dorsal element longest (15.2-23.0 % SL), reaching beyond dorsal-fin origin, ventral and median spines about half length of dorsal spine. Ventral posttemporal spine curving slightly towards anterior, median spine curved dorsally. Lateral ridges of cleithrum smooth; pectoral shield with many short conical spines over entire surface and a group of about six such spines present on lateral prominence adjacent to pectoral fin base. Dorsal and anteroventral rami of preopercle deeply serrate. Two preopercular spines: ventral spine long (9.7-11.7 % SL) and narrow; posterior spine unique, posteriorly directed, length about 4.5 % SL. Dorsal preopercular spine absent. Dorsal blade not visible externally. Anal-fin ptergiophore spines absent. Adipose fin base of moderate length, occupying about half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 38.0-43.0, orbit length 18.0-23.0, body depth 65.8-72.8, caudal-peduncle depth 11.3-12.7, caudal-peduncle length 21.0-22.2, dorsal-fin length 15.3-17.3, anal-fin length 14.3-16.6, preanal length 70.5-71.0, predorsal length 58.7-62.7, preventral length 67.1-71.0, postdorsal length 48.8-53.4, postanal length 32.1-38.1, AC[C] length 5.3-6.3, AC[B]-[C] length 8.7-11.9.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, stepped dorsally in approximately equal increments from anterior to posterior. PV (10), ventral and lateral margins of scales with numerous denticles. L 1. VAV (5), ventral margins of scales denticulate. AC[A] photophores absent. AC[B] (4; 4), with numerous minute denticles. AC[C] (4), denticulate, compact.

Dark pigment saddle extending posteriorly as far as midpoint of dorsal fin; without ventral notches. Two lateral projections: anterior projection long and broad, terminating bluntly at level of photophore OV[A] #3, posterior projection shorter, tapered, originating immediately posterior of anterior projection. Isolated melanophores located on preopercle, dorsal-fin base, caudal peduncle and posterior midline.

SIMILAR SPECIES.-*Polyipnus fraseri* is a member of the *P. spinosus* species group, characterized in part by the presence of a multispinose (2 or 3 spines) posttemporal. Arrangement and shape of posttemporal spines in *P. fraseri* is most similar to that of *P. spinifer*, *P. soelae*, *P. spinosus* and *P. stereope*, all of which have large dorsal and prominent, but much shorter, basal spines. *Polyipnus fraseri* is distinguished from these and all other species by the presence of a unique posterior preopercular spine, absence of AC[A] photophores, and only 4 AC[B] photophores at standard length over 20 mm.

DISTRIBUTION.-This species has been collected at two stations; off the east coast of the Philippines and in the central Philippine Sea near the Kyushu-Palau Ridge (Figure 37). Maximum depth of capture of the holotype is about 1000 m but the second specimen was taken above 340 m which is closer to the bathymetric ranges of other species.

The geographic ranges of *P. triphanos*, *P. unispinus*, *P. spinifer* and *P. matsubarai* may overlap with that of *P. fraseri*.

REMARKS.-Capture of a second specimen has contributed to the recognition of *Polyipnus fraseri* as a distinct species (Harold, 1990b). The present redescription reiterates morphological and ontogenetic evidence which also lead to this conclusion. Usually only a juvenile (up to about 15 mm SL) would have as few as 4 AC[B] photophores.

Appearance of new photophores usually occurs at body sizes up to 30 mm SL (lowest AC[B] count in other species at that standard length is 7). Rate of photophore budding is probably quite low in P. oluolus as well (6 AC[B] photophores at 26.9 mm SL, only known specimen). The largest individual of another species with no AC[A] photophores is 16.9 mm SL (P. ruggeri). With so much interspecific and ontogenetic variation in photophore number, and only one specimen known, Baird (1971) and Borodulina (1979) believed they were taking a conservative approach in synonymizing P. fraseri with P. tridentifer and P. spinosus, respectively.

Relative size of various elements of the skull are also atypical and seem to be correlated with enlargement of the eye. As percentages of standard length, P. fraseri has an orbital length of 18.0 to 23.0, 13.6 to 19.0 in other species at SL less than 25 mm, and 10.8 to 17.2 in other species at SL greater than 25 mm.

MATERIAL EXAMINED.-Holotype: USNM 92324 (1, 40.4 mm SL), 12°56'24"N 124°25'24"E, (0-) 1032 m, R/V Albatross Sta. D5476, 24 Jun 1909.

Other Material: BSKU 29353 (1, 32.4 mm SL), 26°46.01'N 135°19.00'E, 322-340 m, 17 Dec 1979.

Polyipnus indicus Schultz, 1961

FIGURE 31

Polyipnus indicus Schultz, 1961:645-646 [holotype fig. 22]; 1964:268.-Baird, 1971:91-92 [fig. 68]; 1986:25 [fig. 75.8].-Harold, 1989:874-875; 1990b:515.

Polyipnus nuttingi.-Norman, 1939:20 [part].

?Polyipnus spinosus.-Reimer, 1985:225 [parasites].

DIAGNOSIS.-Gill rakers 19-21. Lateral pigment projection tapered and long, usually reaching lateral midline. Two posttemporal spines: dorsal spine long (6.9-13.1 % SL), basal spine length less than half of that of dorsal spine. Anal-fin pterygiophore spines absent. Photophore scale denticles restricted to PV, VAV and AC[C] clusters. AC[A] photophores grade into AC[B]. AC[B] 7-9. AC[C] photophores compact, not separated by conspicuous gaps.

DESCRIPTION.-Adult body size moderate, reaching more than 60 mm SL. D (14) 12-14. A (16) 15-16. P (13) 12-14. V 7. GR (7+13) 5-7+13-16 = (20) 19-21. Vert. 32-33. Body laterally compressed, profile anterior of dorsal blade and pelvic fin broadly elliptical, abruptly tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate. Flank scales diaphanous and deciduous, very few remaining on specimens examined. Ventral margin of dentary slightly convex and with two deeply serrate keels. Margins of dentary, premaxillary and maxillary with minute, recurved teeth. Palatine teeth absent. Anterior region of vomer with a transverse patch of minute conical teeth in medial rows. No teeth present on posteromedial process of vomer. Frontal and parietal medial ridges serrate, overlapping, and forming a continuous keel. Parietal keel terminates posteriorly with a minute spine. Dorsal and ventral limbs of posttemporal serrate, acutely divergent, and supporting 2 (rarely 3) spines: dorsal spine serrate, long (6.9-13.1 % SL), and curved dorsally; ventral spine short, nonserrate, laterally directed. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 8-14 triangular spines. Vertical and anteroventral arms of preopercle with 2 parallel deeply serrate external ridges. Preopercle with two spines: ventral spine long (4.4-6.0 % SL), anteriorly curved, directed anteroventrally; dorsal spine minute (slightly longer than one preopercular serration), directed anteroventrally. Dorsal blade smooth or with 1 serration on anterodorsal surface, short-based, terminating dorsally as 2 triangular spines (one per side). Anal-fin pterygiophore spines absent. Adipose-fin base of moderate length, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters: (% SL): Head length 31.3-34.7, orbit length 13.0-17.8, body depth 58.4-65.4, caudal-peduncle depth 10.0-12.4, caudal-peduncle length 14.0-16.6, dorsal-fin length 21.1-26.0, anal-fin length, 20.5-24.1 preanal length 68.8-74.4, predorsal length 57.3-62.1, preventral length 63.1-68.4, postdorsal length 48.7-55.8, postanal length 36.2-41.3, AC[C] length 5.5-6.8, AC[B]-[C] length 4.2-5.6.

Ventral margins of photophore scales smooth, except PV, VAV and AC[C] which have numerous denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10). L 1. VAV (5). AC[A] 1+1+1, #1 and #2 isolated, but aligned with #3 and first three AC[B]. AC[A] #3 united with AC[B] #1 forming a continuous gland. AC[B] (8; 7-9), with a dorsal step between #3 and #4. SC=AC[C] (4).

Dark pigment saddle with predorsal notch and long lateral projection, usually reaching midline. Dark pigment also present in association with glandular photophore tissues, posterodorsal region of head, bases of dorsal-fin rays, and delineating body trunk myosepta.

SIMILAR SPECIES.-*Polyipnus indicus* is most similar to *P. nuttingi*, *P. oluolus* and, especially, *P. asper*. These four are the only species in *Polyipnus* with two posttemporal spines. Of these, only *P. indicus* and *P. asper* have denticulate AC[C] photophore scales. *Polyipnus indicus*, unlike P. asper, has a simple, blade-like parietal keel (not differentiated posteriorly into 2 spines) and lacks AC[B] photophore scale denticles. In addition, Polyipnus indicus frequently has more gill rakers than P. asper (19-21 compared with 17-20).

DISTRIBUTION.-Polyipnus indicus is restricted to the western Indian Ocean off the east coast of Africa from Natal in the south and as far north as the Gulf of Aden (Figure 29). To the east, this species has been taken frequently off the north coast of Madagascar. Catch data indicate a bathymetric range of about 480 to 660 m but due to the use of open-tow gear these ranges should be viewed as maximum values.

REMARKS.-Polyipnus indicus is the only representative of the P. spinosus species group which occurs in the western Indian Ocean. Any references to P. spinosus (e.g. Reimer, 1985) or other members of the group from this region are probably P. indicus. Baird (1971:90) refers to questionable records of P. spinosus from off peninsular India but concluded that they were likely P. tridentifer (sensu lato, = P. spinifer). Polyipnus spinifer has never been taken in the Indian Ocean and these records are more likely to represent P. soelae, P. indicus or P. asper.

MATERIAL EXAMINED.-Holotype: BMNH 1939.5.24.403 (1, 37.0 mm), Zanzibar area (about 06°S 41°E), (0-) 640-658 m, John Murray Expedition 1933-34, Sta. 115.

Paratypes: BMNH 1939.5.24.404 (1, 38.2 mm) and USNM 179897 (1, 46.2 mm), same data as holotype.

Other Material: ARC 8909384 (4, 52.0-63.0 mm), 12°27'N 48°20'W, (0-) 470-480 m, R/V Vityaz Cr. 17, Sta. 2608, 14 Nov 1988. ASH 88281 (5, 53.6-62.3 mm), 21°12.8'S 35°41.8'E to 21°16.6'S 35°41.3E, 480-500 m, R/V Vityaz Sta. 2622, 0215-0418 h, 26 Dec 1988. CAS 66558 (4, 46.0-57.0 mm), 12°26'06"S 48°20'12"E to 12°24'54"S 48°21'12"E, R/V Vityaz Sta. 2608. IOAN uncat. (15, 34.3-48.7 mm), 25°30.4'S 35°08'E to 25°34.2S 35°01.5'E, (0-) 570-500 m, R/V Vityaz Cr. 17, Sta. 2631, 1342-1500 h, 23 Nov 1988. IOAN uncat. (25, 33.7-42.0 mm), 12°17.5'N 53°14.5'E to 12°17.5'N 53°06.5'E, (0-) 364-384 m, R/V Vityaz Cr. 17, Sta. 2566, 1330-1426 h, 28 Oct 1988. MNHN 1988-1322, -1326, -1327 and -1328 (1, 48.6 mm; 1, 42.6 mm; 1, 49.8 mm; 1, 41.2 mm), 12°28'S 48°12'E, (0-) 605 m, R/V Le Vauban Sta. 21, 1972. USNM 293986 (3, 42.6-45.1 mm), 12°01'00"N 51°16'36"E, 375-393 m, R/V Beinta, Cr. 20, Sta. 18, 12 Mar 1987. USNM 301277 (5, 23.3-30.7 mm), 11°57'30"N 51°07'30"E, 366m, R/V Beinta, Cr. 20, haul 11, field no. GJS 152, 11 Mar 1987. ZMUC P206973 (1, 13.0 mm), 01°37'N 44°52'E, R/V Meteor, S. nr. 21, Sta. 141, no other data. ZMUC P206922 (10, 31.0-47.0 mm), 29°55'S 31°20'E, (0-) 425-430 m, R/V Galathea Sta. 196, no other data. ZMUC P206924 (5, 38.0-49.0 mm), 25°20'S 35°17'E, (0-) 590 m, R/V Galathea, Sta. 202, no other data.

Polyipnus inermis Borodulina, 1981

FIGURE 35

Polyipnus inermis Borodulina, 1981:122-124 [holotype fig. 1].-Harold, 1989:874-875; 1990b:515.

DIAGNOSIS.-Gill rakers 23-26. Lateral pigment projection tapered and long, terminating bluntly at or near lateral midline. Posttemporal spines 3, subequal, tridentlike: dorsal spine (8.0-9.0 % SL). Anal-fin pterygiophore spine absent. Photophore scale denticles weak, restricted to PV cluster. AC[A] photophores grade into AC[B]. AC[B] 8-10, with a gap about equal to the width of one photophore between #3 and #4. AC[C] photophores compact.

DESCRIPTION.-Maximum adult body size 63.5 mm SL. D (12) 12-13. A (16) 16/17. P (14) 14-15. V 7. GR 6-8+16-17 = (24) 23-26 (25 and 26 values reported by Borodulina, 1981). Vertebrae (34). Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin broadly elliptical, abruptly tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate. Flank scales cresentic and deciduous. Ventral margin of dentary slightly convex and with two finely serrate keels. Margins of dentary and premaxillary with minute, recurved teeth; maxillary teeth smaller and conical. Palatine teeth absent. Anterior region of vomer with a transverse patch of 12 to 15 medial rows of minute conical teeth. No teeth present on posteromedial process of vomer. Frontal and parietal longitudinal keels serrate, overlapping. Parietal keel discontinuous, terminating posteriorly with two conical spines directed anteriorly and posteriorly. Posttemporal dorsal limb smooth, nonserrate, ventral limb (including supracleithrum) serrate, limbs acutely divergent, and supporting 3 long posterolaterally-directed subequal spines: dorsal spine length about 8.0-9.0 % SL, median and ventral spines slightly shorter. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 10-12 triangular spines. Vertical and anteroventral rami of preopercle each with two parallel deeply serrate lateral ridges. Preopercle with two spines: ventral spine long (6.8-7.8 % SL), curved distally toward anterior, axis directed ventrally; dorsal spine minute (slightly longer than one preopercular serration), triangular and bladelike, directed posteroventrally. Dorsal blade short-based, smooth anterodorsal surface, terminating dorsally in 2 triangular, dorsolaterally-directed spines (one per side). Anal-fin pterygiophore spines absent. Adipose-fin base long, occupying about three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 36.0-39.7, orbit length 17.2-17.3, body depth 58.1-63.1, caudal-peduncle depth 10.3, caudal-peduncle length 15.5-17.7, dorsal-fin length 18.3-23.3, anal-fin length 20.5-23.2, preanal length 68.5-71.8, predorsal length 54.6-55.4, preventral length 65.1-69.1, postdorsal length 50.1-55.1, postanal length 39.5-39.7, AC[C] length 5.1-6.2, AC[B]-[C] length 5.6-6.2.

Ventral margins of photophore scales smooth, except PV cluster which is sparsely and weakly denticulate. Photophore counts: IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10). L 1. VAV (5). AC[A] 1+1+1, #1 and #2 isolated, but aligned with #3 and first three AC[B]. AC[A] #3 united with AC[B] #1, forming a continuous gland. AC[B] (8; 8-10), with a dorsal step and a broad gap about equal to the width of one photophore between #3 and #4.

Dark pigment saddle with a predorsal notch and a long and tapered lateral projection that terminates bluntly at or near lateral midline. Dark pigment also present in association with photophore tissues, posterodorsal region of head, lateral surface of dentary, bases of dorsal-, pectoral- and caudal-fin rays, posterior margins of flank scales, and delineating body-trunk myosepta with two concentric lines.

SIMILAR SPECIES.-Polyipnus inermis is one of several species in the genus that have 3 subequal posttemporal spines. The others are P. parini and P. tridentifer. In some instances the spine configuration of P. spinifer, P. soelae and P. stereope may approach this condition but the median spine is always noticeably shorter than the dorsal. In contrast to these posttemporal characters, the presence of a dorsal step between the third and fourth AC[B] photophores is similar to P. oluolus, P. nuttingi, P. indicus and P. asper (of the spinosus species group). Polyipnus inermis and P. parini are most similar, sharing a unique gap (about equal to the width of one photophore) between photophores #3 and #4 of the AC[B] cluster. Polyipnus inermis is distinguished from P. parini by a lack denticles on the scales of the VAV photophores and lower gill raker counts (23-26 compared with 28 or 30, respectively).

DISTRIBUTION.-Polyipnus inermis has been collected only at several stations in the vicinity of the Sala-y-Gomez Submarine Ridge, eastern South Pacific Ocean (Figure 34). Available data indicate that P. inermis occurs above 420 m, and possibly as deep as 575 m.

REMARKS.-Borodulina (1981:124) stated that P. inermis is "closest" to P. parini but provided no comparisons with other species. These two species, however, possess a unique gap in the AC[B] photophore cluster. Apparent reduction of PV photophore scale denticles in P. inermis is unusual for members of the spinosus group. Another peculiarity is the extensive horizontal predorsal surface of the body; this predorsal area is convex in other species.

MATERIAL EXAMINED.-Holotype: MMSU P-15413 (1, 39.0 mm), 25°01'S 88°27'W, 535-575 m, R/V Ikhtiandr trawl no. 54, (x-radiograph only).

Paratypes: IOAN uncat. (5, 40.0-63.5 mm), same data as holotype (not seen).

Other Material: ASH 88253 (3, 48.9-49.4 mm), 24°58'S 88°29'W, (0-) 562-545 m, R/V Professor Shtokman Sta. 1965, 30 Apr 1987. IOAN uncat. (15, 38.3-50.6 mm), same data as previous entry. IOAN uncat. (3, 49.2-56.2 mm), 25°25'S 86°32'W, 420-0 m, R/V Ikhthyander Cr. 5, trawl 57, 31 Oct 1979. IOAN uncat. (2, 37.9-43.0 mm), 25°03.4'S 88°38.1'E, 545-0 m, R/V Gerakl, 1350 h, 04 Nov 1975.

Polyipnus nuttingi Gilbert, 1905

FIGURE 30

Polyipnus nuttingi.-Jordan and Starks, 1904:581 [text reference to P. nuttingi MS Gilbert].

Polyipnus nuttingi Gilbert, 1905:609-610 [holotype pl. 73].-Schultz, 1938:142, 145.-Norman, 1939:20.-Schultz, 1961:645 [fig. 21]; 1964:268.-Baird, 1971:92 [fig. 69].-Harold, 1989:874-875; 1990b:515.

DIAGNOSIS.-Gill rakers 20-24. Lateral pigment projection tapered and long, usually reaching ventrally of lateral midline. Two posttemporal spines: dorsal spine moderately long (5.5-7.0 % SL), deeply serrate margins; basal spine highly reduced, inconspicuous. Anal-fin pterygiophore spines absent. Photophore scale denticles restricted to PV and VAV clusters. AC[A] photophores grade into AC[B]. AC[B] 7-9. AC[C] photophores compact, not separated by conspicuous gaps. Frontal-parietal keel continuous and evenly serrate.

DESCRIPTION.-Maximum adult body size moderate to large, up to 83.0 mm SL (holotype). D (13) 12-13. A (17) 16-17. P (13) 12-14. V 7. GR 6-8+14-16 = (22) 20-24. Vert. 33/34. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin broadly elliptical, acutely tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle elongate, rectangular. Flank scales diaphanous, sheetlike, ovate dorsoventrally. Ventral margin of dentary slightly convex and deeply serrate. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary teeth slightly shorter and recurved. Palatine with randomly distributed minute conical teeth. Anterior region of vomer with 8 to 14 medial rows of conical teeth. No teeth present on posteromedial process of vomer. Frontal and parietal medial keels serrate, overlapping, and forming a continuous keel. Parietal keel terminates posteriorly with a minute conical spine. Dorsal and ventral limbs of posttemporal deeply serrate, acutely divergent, and supporting 2 spines:

dorsal spine longest (5.5-7.0 % SL), with serrate margins and curved dorsally; ventral spine short (less than one quarter of length of dorsal spine), nonserrate, laterally directed. Lateral ridges of cleithrum smooth; anterior ventral margin of pectoral shield bears 4-8 minute conical spines. Vertical and anteroventral rami of preopercle with single deeply serrate lateral ridges. Preopercle with two spines: ventral spine longest (2.1-2.7 % SL) but short in comparison with other species of the P. spinosus species group, anterolaterally curved, axis directed ventrally; dorsal spine minute (length about equal to that of one preopercular serration), triangular, directed posteroventrally. Dorsal blade smooth or with 1 serration on anterodorsal bladelike surfaces, short-based, terminating posteriorly in 2 triangular spines (one per side) directed dorsolaterally. Anal-fin pterygiophore spines absent. Adipose fin base long, occupying about three quarters of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 31.9-36.0, orbit length 13.9-18.9, body depth 62.4-65.0, caudal-peduncle depth 10.6-12.4, caudal-peduncle length 16.8-18.5, dorsal-fin length 23.4-24.1, anal-fin length 24.5-25.1, preanal length 69.1-70.9, predorsal length 54.4-57.7, preventral length 65.4-65.8, postdorsal length

52.6-53.9, postanal length 39.0-43.3, AC[C] length 5.2-5.5, AC[B]-[C] length 5.2-7.9.

Ventral margins of photophore scales smooth, except PV which are finely denticulate and VAV which are either smooth or with blunt denticles. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10). L 1. VAV (5). AC[A] 1+1+1, #1 and #2 isolated, but aligned with #3 and first three AC[B]. AC[A] #3 united with AC[B] cluster, forming a continuous gland. AC[B] (8; 7-9), with a pronounced dorsal step between #3 and #4. AC[C] (4).

Dark pigment saddle with a predorsal notch immediately posterior to extremely long lateral projection which extends ventrally to about level of third OV[A] photophore. Dark pigment also present in association with photophore tissues, opercular bones, bases of anal-, caudal- and dorsal-fin rays, and diffusely delineating body-trunk myosepta.

SIMILAR SPECIES.-Polyipnus nuttingi is similar to P. indicus, P. asper, and P. oluolus which all have a large serrate dorsal posttemporal spine with a single minute basal secondary spine. This contrasts with Baird's (1971:92) description in which the secondary spine in P. nuttingi was not distinguished from adjacent serrations. Polyipnus nuttingi and P. oluolus are the only two species of the above that lack denticles on the AC[C] photophore scales. Polyipnus nuttingi is distinguished from P. oluolus by the long pigment projection (P. oluolous appears to lack a lateral pigment projection), higher numbers of AC[B] photophores (7-9 as compared with 6), and a much shorter dorsal posttemporal spine (5.5-7.0 as compared with 17.0 % SL).

DISTRIBUTION.-*Polyipnus nuttingi* is restricted to the continental slope and channel areas of the Hawaiian Islands (Figure 29) at depths of about 400 to 570 m.
Although this is the only representative of the genus occurring in the Hawaiian Islands several species (*P. omphus*, *P. meteori*, and *P. matsubarai*) that have broad ranges may also occur in the area.

REMARKS.-According to Schultz (1961) the collection of "cotypes" listed below as paratypes (USNM 51693) is an amalgamation of specimens taken at a number of R/V *Albatross* stations and consequently no precise locality can be given. Each specimen has a numbered tag but their significance is not known. Gilbert (1905:610) lists localities descriptively and trawling depths for the contributing collections which are repeated below. One additional R/V Albatross collection (AMNH) which was received by the American Museum of Natural History in 1907 appears to come from the original set of collections and may be a paratype. The specimen was sent to AMNH on exchange from the Smithsonian Institution (USNM) but neither the details of the transaction nor the exact source of the specimen are known.

MATERIAL EXAMINED.-Holotype: USNM 51599 (1, 83.0 mm), entrance to Pailolo Channel between Molokai and Maui, Hawaiian Islands (about 21°N 156°40'W), 550-566 m, R/V *Albatross* Sta. 4088, no exact data.

Paratypes: USNM 51693 (29, 33.5-69.5 mm), Hawaiian Islands, total depth range sampled 400-599 m, R/V *Albatross*, Sta. 3867 (Pailolo Channel, 525-537 m), 3920 (off southeast coast of Oahu, 490-518 m), 4088 (approach to Pailolo Channel, 550-566 m), 4089 (same, 550-562 m), 4090 (same, 562-570 m), 4091 (same, 566-570 m), 4097 (same, 529-? m), 4121 (off the northwest coast of Oahu, 400-464 m), 4134 (off Kauai, 416-599 m).

Other Material: AMNH 3548 (1, 55.5 mm), Hawaiian Islands, R/V *Albatross*, no exact data. BPBM 24892 (3, 28.3-39.9 mm), 21°07'N 156°21'W, 0-470 m, R/V *Townsend Cromwell* Cr. 66, Sta. 4, 10 Sep 1975. BPBM 23779 (2, 47.1-48.5 mm), 21°08'N 156°21'W, 463-485 m, R/V *Townsend Cromwell* Cr. 35, Sta. 16, 1 Apr 1968. BPBM 23790 (7, 47.6-60.5 mm), 21°15'N 156°26'W, 512-545 m, R/V *Townsend Cromwell* Cr. 35, Sta. 23, 5 Apr 1968. BPBM 24005 (7, 38.1-55.5 mm), 21°02'N 157°49'W, 512-576 m, R/V *Townsend Cromwell* Cr. 36, Sta. 30, 6 May 1968.

Polyipnus _oluolus_ Baird, 1971

FIGURE 28

Polyipnus _oluolus_ Baird, 1971:90-91 [holotype, fig. 67].-Harold, 1989:874-875; 1990b:515.

DIAGNOSIS.-Gill rakers 19. Lateral pigment projection absent, diffuse dark pigment dorsally. Two posttemporal spines: dorsal spine long (13.8 % SL), lateral margins deeply serrate, basal spine highly reduced, in conspicuous. Anal-fin pterygiophore spines absent. PV photophore scales with extensive triangular ventral margins with 1 or 2 denticles at apices. AC[A] photophores all separate and increase in elevation incrementally from anterior to posterior. AC[B] 6. AC[C] photophores compact, not separated by conspicuous gaps.

DESCRIPTION OF HOLOTYPE.-Known only from holotype, 33.0 mm SL. D (14). A (14). P (13). V (6). GR (19). Body laterally compressed. Body profile anterior of dorsal-fin insertion subrectangular. Caudal peduncle short and narrow, slightly tapered posteriorly. Flank scales diaphanous, sheetlike. Ventral margin of dentary slightly convex and serrate. Margin of dentary with minute, recurved teeth. Premaxillary and maxillary teeth shorter, conical. Palatine teeth absent. Anterior region of vomer with a transverse patch of about 24 medial rows of recurved teeth. No teeth present on posteromedial process of vomer. Frontal and parietal longitudinal keels serrate, overlapping, and forming a continuous keel. Dorsal and ventral limbs of posttemporal with two and one serrate prominent ridges respectively, limbs acutely divergent, and supporting 2 spines: dorsal spine serrate, long (13.8 % SL), straight, posteriorly directed; ventral spine short, nonserrate, laterally directed, dorsally curved. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 4 conical spines which decrease in length from anterior to posterior. Preopercular bones missing in specimen, fleshy sheathes present. Dorsal blade smooth, short-based, terminating posteriorly as 2 triangular dorsolaterally-directed spines (one per side). Anal-fin pterygiophore spines absent. Adipose-fin base of moderate length, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

<u>Morphometric</u> <u>characters</u> (% SL): Head length 42.8, orbit length 22.0, body depth 94.1, caudal-peduncle depth 13.4, caudal-peduncle length 17.8, dorsal-fin length 28.0, anal-fin length 25.6, preanal length 81.0, predorsal length 74.7, preventral length 88.5, postdorsal length 54.3, postanal length 41.3, AC[C] length 6.8, AC[B]-[C] length 3.9.

Ventral margins of photophore scales smooth, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, #2 and #3 adjacent and at an elevation ventral to #1. PV (10), ventral margins triangular and with 1 or 2 denticles at apices. L 1. VAV (5), with extensive blade-like ventral margins. AC[A] 1+1+1, isolated, not united in a common gland, increasing in elevation from anterior to posterior, #3 located proximal to first AC[B]. AC[B] (3)+1+1+1, with a dorsal step between #3 and #4, #1-#3 united in a common gland only. AC[C] (4), with extensive bladelike ventral margins.

Pigment saddle not evident in only specimen. Diffuse dark pigment over entire body flank with greatest concentration along trunk myosepta. Dark pigment also present in association with glandular photophore tissues. Baird (1971:91) states "pigment somewhat darker dorsally" and does not describe a lateral pigment projection as is found in all other species in the genus except _P_. _unispinus_.

SIMILAR SPECIES.-_Polyipnus_ _oluolus_, _P_. _indicus_, _P_. _asper_ and _P_. _nuttingi_ are the only members of the genus with two posttemporal spines. The basal spine in _P_. _indicus_ and _P_. _asper_ is conspicuous whereas in _P_. _oluolus_ and _P_. _nuttingi_ it is very small and partially concealed by a field of deep spinelike serrations. The holotype has only 14 anal-fin rays which contrasts with a total range of 15 to 17 for the other three species.

The feature that distinguishes *P. oluolus* from all other members of the *spinosus* species group is the lack of connection between the posteriormost AC[A] photophore and the anteriormost of the AC[B] photophores. *Polyipnus oluolus* is also the only species with triangular bladelike extensions of the ventral margins of the PV photophore scales. Some specimens of *P. nuttingi* have PV #9 and #10 scale morphology similar to that of *P. oluolus* but the remaining scales have the rectangular form.

DISTRIBUTION.-The holotype was collected off the Marshall Islands, depth of capture not known (Figure 29). No other *Polyipnus* have been reported from this island group.

REMARKS.-*Polyipnus oluolus* is known only from the holotype which is in very poor condition. The drawing of the holotype (Figure 29) is partially a reconstruction and includes many features that were overlooked in the original illustration of Baird (1971: fig. 67). In addition, the body shape has been restored and the pectoral fin shown in its correct position.

MATERIAL EXAMINED.-*Holotype:* USNM 204390 (1, 26.9 mm), 11°18'N 162°06'E, R/V *Hugh M. Smith* Cr. 37, Sta. 43, 9 Dec 1956.

Polyipnus parini Borodulina, 1979

FIGURE 33

Polyipnus parini Borodulina, 1979:4-6 [holotype fig. 3]; 1981:124.-Fujii, 1984:47 [pl. 49I].-Harold, 1989:874-875; 1990b:515.

Polyipnus cf. parini.-Borodulina, 1979:4-6.

DIAGNOSIS.-Gill rakers 28 or 30. Lateral pigment projection tapered and long, terminating at or near lateral midline. Posttemporal spines 3, subequal, trident-like: dorsal spine long (9.6-12.6 % SL). Anal-fin pterygiophore spine absent. Photophore scale denticles, restricted to PV, VAV and AC[B] clusters. AC[A] photophores grade into AC[B]. AC[B] 10-11, with a gap about equal to the width of one photophore between #3 and #4. AC[C] photophores compact.

DESCRIPTION.-Maximum adult body size 61.0 mm SL (holotype). D (13) 12. A (17) 17. P (14) 16. V (7). GR (28) 30. Vertebrae (35) 35. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin broadly elliptical, tapered posteriorly as far as caudal peduncle at about a 45° angle. Profile of caudal peduncle rectangular, elongate. Flank scales diaphanous and sheetlike. Ventral margin of dentary convex, finely serrate. Dentary and premaxillary teeth minute, recurved; maxillary teeth smaller, conical. Frontal and parietal longitudinal keels serrate and overlapping. Parietal keel discontinuous; posterior region with 2 opposed minute conical spines, directed anteriorly and posteriorly. Dorsal and ventral limbs of posttemporal serrate, acutely divergent, and supporting 3 long posterolaterally-directed subequal spines: dorsal spine length 9.6-12.6 % SL, median and ventral spines slightly shorter. Lateral ridges of cleithrum smooth; ventral margin of pectoral shield bears 6-17 minute, conical spines. Vertical and anteroventral rami of preopercle smooth or with 1 spinelike serration. Preopercle with two spines: ventral spine long (7.1-10.3 % SL), curved anteriorly with axis directed ventrally; dorsal spine minute, triangular and bladelike, directed ventrolaterally. Dorsal blade short-based, exposed basal length slightly greater than height, anterodorsal surface finely serrate, terminating dorsally in 2 triangular, dorsolaterally-directed spines (one per side). Anal-fin pterygiophore spines absent. Adipose fin base long, occupying about two thirds of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 31.8-35.7, orbit length 15.6-17.7, body depth 53.9-56.6, caudal-peduncle depth 10.6-11.0, caudal-peduncle length 13.6-16.3, dorsal-fin length 19.4-20.5, anal-fin length 23.0-24.3, preanal length 66.2-70.8, predorsal length 53.6-55.0, preventral length 61.0-66.9, postdorsal length

53.4-53.8, postanal length 36.9-38.5, AC[C] length 5.6, AC[B]-[C] length 4.8.

Ventral margins of photophore scales smooth, except as noted below. Photophore counts: IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), denticulate. L 1. VAV (5), deticulate. AC[A] 1+1+1, separate, not united in a common gland, aligned with first three AC[B] photophores. AC[A] #3 united with AC[B] #1 forming a continuous gland. AC[B] (10; 11), with a dorsal step and a broad gap about equal to the width of one photophore between #3 and #4; AC[B] scales #2 and #3 each with a single denticle (holotype). AC[C] (4).

Saddle of dark pigment present and with a predorsal notch and a lateral projection that tapers ventrally, terminating bluntly at or near the lateral midline. Dark pigment also present in association with photophore tissues, dorsal and dorsolateral regions of head, bases of dorsal, anal and caudal fins, and delineating body-trunk myosepta.

SIMILAR SPECIES.-*Polyipnus parini* is most similar to *P. inermis*. These two species have tridentlike posttemporal spine groups and a unique broad gap between photophores #3 and #4 of the AC[B] cluster. *Polyipnus parini* has a greater number of gill rakers on the first arch than *P. inermis* (28/30 as compared with 23-26). Generally *P. parini* is much more "spiny", with serrated posttemporal keels and denticles on VAV and AC[B] photophore scales. See 'SIMILAR SPECIES' section for *P. inermis*.

DISTRIBUTION.-The geographical distribution of *P. parini* is very poorly known. In the original description Borodulina (1979:4) says that the holotype was given to the USSR Academy of Sciences with some specimens of *P. matsubarai*. The collection was not labelled but A.S. Sokolvskiy, who donated the specimens conveyed that "they were caught at different times in the 'zone of the Kuroshio Current'" (20-43°N 138-152°E). Aizawa (pers. comm.) is of the opinion that *P. parini* has never been collected near Japan. Nevertheless, a tentative collecting locality is given in Figure 34 which follows the original description (Borodulina, 1979: fig. 2). The only other reported capture of this species (*P.* cf. *parini*, Borodulina, 1979:5) is in the Tasman Sea off the North Island of New Zealand. Therefore, in the presence of these sparse and ambiguous data, *P. parini* is here considered a western Pacific species.

REMARKS.-Unfortunately, neither of the specimens of *P. parini* were available for direct study. Comments made here are derived from the original description with its illustration (Borodulina, 1979) and x-radiographs of both specimens.

On the basis of morphology the "juvenile" small specimen (ZIL 43998, 28.0 mm SL) referred to *P.* cf. *parini* by Borodulina (1979: 4-6) is not distinguishable from the holotype. From her discussion it appears that the source of doubt regarding the identification of this juvenile specimen was the "considerable separation" of the collecting localities. Geographical occurrence should not be used in forming taxonomic decisions concerning specific status, especially when the type locality is not known. This specimen, therefore, is treated here as a valid representative of _P_. _parini_.

The diagnosis and description provided by Borodulina (1979) are in one aspect contradictory. In the diagnosis the "anal" (AC[B]) photophores are described as being without "spiny scales" but in the description such spines (=denticles) are present albeit restricted to photophores #2 and #3 of the cluster.

MATERIAL EXAMINED.-_Holotype_: ZIL 43997 (1, 61.0 mm), Kuroshio Current area?, no other data (x-radiograph only).

Other Material: ZIL 43998 (1, 28.0), 33°16'S 171°59'E, depth unknown, R/V _Vityaz_ Sta. 3842, 20 Jan 1958 (x-radiograph only).

Polyipnus paxtoni Harold, 1989

FIGURE 36

Polyipnus paxtoni Harold, 1989:871-876 [holotype fig. 1].

DIAGNOSIS.-Gill rakers 23 or 24. Lateral projection of dark pigment tapered and long, reaching lateral midline. Three posttemporal spines present, dorsal spine longest (9.6-11.6 % SL), median and ventral spines subequal (about 1/4 to 1/2 of the length of dorsal spine). Numerous denticles originating on scales of PV, VAV, AC[B], AC[C] and occasionally AC[A] #3 photophores. AC[B] 10-12. AC[C] photophores not separated by gaps.

DESCRIPTION.-Maximum adult body size moderate, up to 49.3 mm SL. D (12) 11-13. A (17) 15-18. P (12) 12/13. V (7) 7. GR 7/8+16/17 = (23) 23/24. Highly compressed laterally. Body profile anterior of dorsal-fin origin broadly elliptical, tapering posteriorly at about a 45° angle. Caudal peduncle elongate, rectangular. Flank scales diaphanous, deciduous. Ventral margin of dentary with 2 parallel serrate keels. Premaxillary, maxillary and dentary teeth minute, recurved. Palatine teeth absent. Anterior region of vomer with transverse patch of 10 to 14 medial rows of minute conical teeth; posteromedial region of vomer without teeth. Frontal and parietal longitudinal keels serrate; frontal keel extending to, and overlapping, parietal keel. Parietal keel differentiated posteriorly into 2 conical medial spines, directed anteriorly and posteriorly. Dorsal and ventral limbs of posttemporal serrate and support three spines; dorsal spine longest (9.6-11.6 % SL), serrate over anterodorsal surface, median and ventral spines subequal, short (2.9-5.2 and 1.8-5.0 % SL resp.). Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield with 18-22 minute conical spines. Preopercle with 2 spines; ventral spine long (6.3-6.7 % SL), ventrally directed with slight anterior curve; dorsal spine minute, similar in size to preopercular serrations, and directed dorsolaterally; external ridges of preopercle deeply and broadly serrate. Dorsal blade with up to four serrations on anterodorsal and terminating posteriorly with 2 triangular spines, one per side, directed posterolaterally. Anal-fin pterygiophore spines absent. Adipose-fin base long, occupying about 2/3 of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

<u>Morphometric</u> <u>characters</u> (% SL): Head length 31.6-37.7, orbit length 14.2-16.5, body depth 59.6-68.3, caudal-peduncle depth 9.5-11.1, caudal-peduncle length 11.3-15.4, dorsal-fin length 16.1-19.3, anal-fin length 20.9-25.2, preanal length 68.0-74.8, predorsal length 56.0-60.0, preventral length 63.7-71.4, postdorsal length 44.2-52.8, postanal length 34.6-39.5, AC[C] length 6.1-8.0,

AC[B]-[C] length 2.2-3.9.

Ventral margins of photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. SAB=OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins of scales with numerous denticles. L 1. VAV (5), denticulate. AC[A] 1+1+1, in a straight line, #3 united with AC[B] #1, forming a continuous gland. AC[A] #3 frequently with denticulate ventral margin. AC[B] (11; 10-12), with an indistinct dorsal step between #3 and #4; most scales with five or more denticles ventrolaterally, often originating on diagonal scale flange. AC[C] (4), without isolating gaps, scales with ventral lamellae extending beyond lateral outline and numerous denticles. AC [1+1+1](10-12)+(4).

Dark pigment saddle with a short, triangular predorsal notch. Lateral projection of moderate length, approaching but not reaching midline. Dark pigment also present in association with dorsal and dorsolateral surfaces of head, unpaired fin bases, photophores and delineating body trunk myosepta.

SIMILAR SPECIES.-All species of the P. _spinosus_ species group have 3 posttemporal spines except _P_. _nuttingi_, _P_. _asper_ and _P_. _oluolus_, which have one large dorsal and one small ventral spine with a series of associated deep spinelike serrations, and _P_. _indicus_ which usually has two and occasionally three spines. _Polyipnus_ _paxtoni_ differs from P. indicus, P. oluolus, P. tridentifer, P. stereope, P. spinosus, P. elongatus, P. soelae and P. inermis, in having denticles over most scales of the AN photophore cluster. Denticles are present in the AC[B] cluster of P. parini, but are apparently restricted to the second and third scales. Polyipnus tridentifer and P. soelae may in large specimens have a single weak denticle on some of the AC[B] photophore scales. Polyipnus fraseri, has numerous denticles on all AC[B] photophore scales but there are only four organs in the cluster. Polyipnus paxtoni is similar to P. spinifer, in denticulation but differs in having equidimensional ventral and median posttemporal spines, a long, tapered lateral dark pigment bar that reaches the lateral midline and usually 11 (10-12) AN photophores (11-13 in P. spinifer). One other species, P. asper, has denticulate AC[B] photophores but unlike P. paxtoni has 2 posttemporal spines and 8-10 AC[B] photophores. Polyipnus paxtoni is similar to P. elongatus with regard to pigmentation and posttemporal morphology.

DISTRIBUTION.-Polyipnus paxtoni is known only from two R/V Soela stations in the Coral Sea, off the north-east coast of Queensland, Australia, at about 18° S latitude, 147° E longitude (Figure 37). The specimens were taken between the surface and a depth of 300 m at night.

The geographic range of P. paxtoni appears to overlap to some degree that of P. elongatus, P. triphanos, and possibly P. aquavitus. On the basis of the few captures, P.

paxtoni and *P. elongatus* are endemic to the Coral Sea but may not occupy the same geographic or bathymetric areas within the region. Numerous trawl samples from other parts of the Coral Sea that contained other *Polyipnus* species (*P. aquavitus* and *P. unispinus*) indicate that *P. paxtoni* (and *P. elongatus*) may be restricted to the western Coral Sea off Queensland.

REMARKS.-*Polyipnus paxtoni* is a recent addition to the genus (Harold, 1989). Posttemporal morphology is quite similar to that of *P. elongatus*. The rudimentary median and ventral posttemporal spines in both species are virtually concealed by adjacent spinelike serrations. Unlike serrations, the spines originate medially at the base of the dorsal spine and are joined by an ossified sheet. In spite of posttemporal similarities, *P. paxtoni* and *P. elongatus* are very distinct with regard to scale denticulation, various fin-ray and photophore meristic characters and body shape.

MATERIAL EXAMINED.-*Holotype*: AMS I.25825-009 (1, 42.5 mm), 18°01'S 147°07'E to 17°59'S 147°05'E, 0-300 m, R/V *Soela*, field no. SO 1/86/49, 2130-2230 h, 16 Jan 1986.

Paratypes: AMS I.25825-002 (7, 41.8-49.3 mm), same data as holotype.-AMS I.25816-006(3, 41.6-46.3 mm), 17°59'S, 147°07'E to 17°55'S, 147°05'E; 0-300 m, R/V *Soela*, field no. SO 1/86/31, 2130-2230 h, 13 Jan 1986.

Polyipnus _soelae_ new species

FIGURE 46

Polyipnus _spinosus_.-Borodulina, 1979:7-9 [part].-Paxton et al., 1989:192 [part].

Polyipnus _spinosis_ [sic].-Borodulina, 1979:7 [incorrect subsequent spelling of _P_. _spinosus_].

Polyipnus _spinifer_.-Harold, 1990b [part, AMS I.22808-028 and I.22817-014].

DIAGNOSIS.-Gill rakers 20-23. Lateral pigment projection short and triangular, reaching about half way to lateral midline, without dorsal deflections of pigment margin posterior of projection. Three posttemporal spines: dorsal spine longest (7.4-16.9 % SL), median spine shortest and ventral spine intermediate and with a slight anterior arc. Anal-fin pterygiophore spines absent. Photophore scale denticles mainly restricted to PV, VAV and AC[C] clusters but AC[B] scales may have a single weak denticle in specimens over 50 mm SL. AC[A] photophores grade into AC[B]. AC[B] 11-14. AC[C] photophores separated by conspicuous gaps. Dorsal blade length and height about equal.

DESCRIPTION.-Maximum adult body size moderate, up to 60.3 mm SL. D (13) 12-14. A (16) 15-17. P (13) 12-13. V (7) 7. GR 5-7+13-16 = (21) 20-23. Vertebrae (34) 33-35. Laterally compressed. Body profile anterior of dorsal blade and pelvic fin deep and broadly elliptical, tapered posteriorly as far as caudal peduncle at about a 45° angle. Caudal peduncle rectangular, highly elongate. Flank scales diaphanous, sheetlike, ovoid and elongate dorsoventrally. Ventral margin of dentary slightly convex and with two parallel serrated keels. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary with smaller, conical teeth. Anterior region of vomer with a transverse patch of 12 to 16 medial rows of minute conical teeth. No teeth present on posteromedial process of vomer. Two or three conical teeth in a medial row on palatine. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel discontinuous; posterior region with 2 minute conical spines, directed anteriorly and posteriorly. Dorsal limb of posttemporal with two serrate keels. Ventral limb of posttemporal with two serrated lateral keels. Posttemporal limbs acutely divergent, and supporting three posterolaterally-directed spines: dorsal spine longest (7.4-16.9 % SL), ventral spine shorter (3.3-6.7 % SL), median spine less than one half of the length of the dorsal spine. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 6-13 minute conical spines. Vertical and anteroventral rami of preopercle each with 2 parallel lateral ridges, ventral ridge of anteroventral ramus usually with 1 to 3 serrations. Preopercle with two spines: ventral spine long (7.1-12.3 %

SL), slightly curved distally toward anterior and axis of spine directed ventrally; dorsal spine minute (slightly longer than one preopercular serration), conical and directed ventrolaterally. Dorsal blade short-based, exposed length and height about equal, anterodorsal surface blade-like with 1 or 2 deep spine-like serrations, terminating posteriorly in two elongate conical spines, one per side, directed dorsolaterally. Anal-fin pterygiophore spines absent. Adipose fin base of moderate length, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 30.1-30.8, orbit length 13.1-18.8, body depth 56.7-64.9, caudal-peduncle depth 9.3-12.8, caudal-peduncle length 15.1-22.3, dorsal-fin length 17.4-23.3, anal-fin length 20.3-27.0, preanal length 65.0-75.5, predorsal length 52.5-65.2, preventral length 58.6-74.6, postdorsal length 49.7-63.0, postanal length 36.6-48.7, AC[C] length 7.4-11.5, AC[B]-[C] length 0.2-2.3.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins of scales with numerous denticles. L 1. VAV (5), ventral margins of scales denticulate. AC[A] 1+1+1, in a straight line and appearing continuous with AC[B] cluster, AC[A] #1 and #2 isolated, not connected to each other or to #3 by a lumen; #3 connected to AC[B] forming a continuous gland. AC[B] (11; 11-14), with an indistinct dorsal step between #3 and #4; nondenticulate ventral scale margins except in large specimens (> 50 mm SL) which may have one weak denticle per scale. AC[C] (4), scales with ventral lamellae extending beyond lateral outline and numerous but often weak denticles.

Dark pigment saddle present: predorsal and postdorsal notches generally absent, but minute predorsal inflection of pigment margin occasionally present. Lateral projection short, triangular, ventrally-tapered and extending about half way to the lateral midline. Dark pigment also present in association with photophore tissues, lateral and dorsolateral surfaces of head including opercle and subopercle, between bases of anal- and dorsal-fin rays and diffusely delineating body trunk myosepta. Generally flank appears unpigmented and contrasts sharply the dorsal region of the body. All specimens of the AMS collections exhibit silvery and reflective pigments on the flank.

SIMILAR SPECIES.-*Polyipnus soelae* is most similar to *P. spinifer* and *P. tridentifer*; distinguished from *P. spinifer* mainly by a lack of denticles on the AC[B] photophore scales and from *P. tridentifer* by its reduced median and ventral posttemporal spines. See also 'SIMILAR SPECIES' section for *P. spinifer* and *P. tridentifer*.

DISTRIBUTION.-*Polyipnus soelae* occurs off the northwest coast of Australia (Indian Ocean) and in the Timor, western Arafura, Celebes, and Madura Seas of Indonesia (Figure 43). Questionable references to *P. spinosus* from peninsular India in Baird (1971) may represent *P. soelae* or *P. asper*. The bathymetric range is about 520 m maximally and probably above 300 m.

The geographic range of *P. soelae* does not appear to overlap with either of the most closely related species *P. spinifer* (Philippine and Japanese Archipelagos) and *P. tridentifer* (Great Australian Bight). There is, however, possible overlap with *P. spinosus* to the south of the Philippines. More distantly related congenerics (not members of the *P. spinosus* species group) occurring within the range of *P. soelae* include *P. meteori*, *P.* aff. *kiwiensis*, *P. triphanos*, *P. unispinus*, *P. aquavitus*, and *P. omphus*.

REMARKS.-Although *P. soelae* is nearly identical in its most obvious external features to *P. spinifer* it has been misidentified as *P. spinosus* in the literature (Borodulina, 1979:7-8; Paxton et al., 1989:192). The redescription of *P. spinosus* provided by Borodulina (1979) was based upon erroneously identified Russian collections of "*P. spinosus*" (=*P. soelae*) and not the holotype. In her key to the species of the "*P. spinosus* subgroup", the type species *P. spinosus* sensu stricto cannot be identified. The description and key indicate that the subcaudal photophores (=photophore scales) of P. spinosus are "spinous" (=denticulate) but it is not true of the holotype (pers. obs.; Bourret, 1985) or of the additional specimen reported here. Also see Remarks section for Polyipnus spinosus.

ETYMOLOGY.-Named for the Australian vessel R/V Soela from which many specimens of P. soelae were collected.

MATERIAL EXAMINED.-Holotype: AMS I.22808-028 (1, 54.8 mm), 17°59'N 118°17'E, (0-) 404-420 m, 0550-1400 h, R/V Soela, field no. SO 2-82-17,18, 3 Apr 1982.

Paratypes: AMS I.22808-[028] (29 of 30 from AMS I.22808-028, 38.5-52.1 mm), same data as holotype. AMS I.22817-014 (30, 49.6-60.1 mm), 18°06'S 117°45'E, (0-) 492-520 m, 0555-1450 h, R/V Soela, field no. SO-2-82-31,32,33,34, 7-10 Apr 1982. IOAN uncat. (15, 41.4-50.2 mm), 09°06'S 131°15'E, 0-340 m, R/V Vityaz, trawl 37.1, 26 May 1967.

Other Material: AMS I.23423-001 (5, 38.3-50.7 mm), 18°01'S 118°23'E, 0-376 m, R/V Soela, 1 Aug 1982. AMS I.23425-011 (8, 40.4-43.0 mm), 18°46'S 117°00'E, 0-400 m, R/V Soela, 1 Aug 1982. FMNH 52447 (1, 46.7 mm), 07°15'S 115°15.6'E, R/V Siboga Sta. 12, 14 Mar 1899. IOAN uncat. (7, 29.5-43.2 mm), 09°05'S 131°22'E, 0-316 m, R/V Akademik Berg, 19 Jul 1967. IOAN uncat. (1, 47.7 mm), 09°00'S 130°39.8'E, 445-520 m, R/V Akademik Berg, 30 Oct 1968. USNM 135537 (5, 49.2-57.6 mm), 00°07'30"N 127°29'E, R/V Albatross Sta. D5626, 29 Nov 1909. WAM P26209-010 (3, 46.0-53.0 mm), 18°18'S 118°08'E, 297-330 m, R/V Courageous, 20 May 1978. WAM P27612-004 (3, 25.0-28.0 mm), 18°33'S 121°01'E, R/V Courageous, trawl 49-1086, 19 May 1979. WAM P28057-007 (2, 50.0-53.0 mm), 18°05'S 118°06'E, (0-) 432 m, 17 Aug 1983.

Polyipnus spinifer Borodulina, 1979

FIGURE 45

Polyipnus spinifer Borodulina, 1979:6-7 [holotype fig. 4].-Fujii, 1984:47 [pl. 49J].-Bourret, 1985:59-61.-Harold, 1989:871-876; 1990b:515 [part].

Polyipnus tridentifer.-Schultz, 1961:646-647 [part].-Baird, 1971:86-88 [fig. 64, part].-Weitzman, 1974:345.

Polyipnus spinosus.-Schultz, 1938:143-144 [part].-Matsubara, 1950:187-197 [fig. 2; fig. 4A, photophore scale denticles, part].-Okada and Suzuki, 1956:296-302 [fig. 1, part].

DIAGNOSIS.-Gill rakers 19-25. Lateral pigment projection short and triangular, reaching about half way to lateral midline; without dorsal deflections of pigment margin posterior of projection. Three posttemporal spines: dorsal spine longest (9.3-16.8 % SL), median spine shortest and ventral spine intermediate and with a slight anterior arc. Anal-fin pterygiophore spines absent. Photophore scale denticles restricted to PV, VAV, AC[B] and AC[C] clusters. AC[A] photophores grade into AC[B]. AC[B] 11-13. AC[C] photophores separated by conspicuous gaps.

DESCRIPTION.-Maximum adult body size moderate, up to 52.1 mm SL, reported to 60.0 mm (Borodulina, 1979:6). D (13) 12-14. A (16) 15-18. P (13) 12-14. V (7) 7. GR 6-8+13-16 = 19-24 (21-25 for type series, Borodulina, 1979). Vertebrae (34) 33-35. Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin deep and broadly elliptical, tapered posteriorly as far as caudal peduncle at about a 45° angle. Caudal peduncle rectangular, highly elongate. Flank scales diaphanous, sheetlike, ovoid and elongate dorsoventrally. Ventral margin of dentary slightly convex and with 2 parallel serrated keels. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary with shorter, conical teeth. Anterior region of vomer with a transverse patch of 14 to 24 medial rows of minute conical teeth. No teeth present on posteromedial process of vomer. Three to six conical teeth in a medial row on palatine. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel discontinuous; posterior region with 2 minute conical spines, directed anteriorly and posteriorly. Dorsal limb of posttemporal with two ridges, the dorsalmost serrate; ventral limb with two serrate lateral ridges. Posttemporal limbs acutely divergent, and support 3 posterolaterally-directed spines: dorsal spine longest (9.3-16.8 % SL), ventral spine shorter (4.4-7.6 % SL), median spine shortest, less than one half of the length of the dorsal spine. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 13-17 minute conical spines. Vertical and anteroventral rami of preopercle each with 2 parallel ridges (all serrate except ventral keel of anteroventral limb). Preopercle with two spines: ventral spine long (4.8-11.4 % SL), straight and directed ventrally; dorsal spine minute (slightly longer than one preopercular serration), three faceted and directed posterolaterally. Dorsal blade short-based, exposed length and height about equal, anterodorsal surface with one to five prominent serrations, terminating posteriorly in two triangular spines, one per side, directed dorsolaterally. Anal-fin pterygiophore spines absent. Adipose fin base moderate, occupying about one half to two thirds of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 29.8-34.1, orbit length 13.3-16.8, body depth 58.6-62.3, caudal-peduncle depth 9.6-12.0, caudal-peduncle length 14.0-19.3, dorsal-fin length 19.6-23.3, anal-fin length 23.0-27.0, preanal length 64.5-71.9, predorsal length 53.5-58.3, preventral length 61.3-70.5, postdorsal length 48.5-54.9, postanal length 37.5-45.9, AC[C] length 8.2-9.8, AC[B]-[C] length 0.5-2.1.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins of scales with spine-like denticles. L 1. VAV (5), ventral margins of scales denticulate. AC[A] 1+1+1, in a straight line and appearing continuous with AC[B] photophores: #1 and #2 isolated, not connected to each other or to #3 but the latter connected to first AC[B] forming a continuous gland; AC[A] #3 frequently with denticulate ventral margin. AC[B] (12; 11-13), with an indistinct dorsal step between #3 and #4; most scales with five or more denticles. AC[C] (4), scales with ventral lamellae extending beyond lateral outline and numerous denticles.

Dark pigment saddle with nearly straight ventral margin except for short, triangular, ventrally-tapered lateral projection that extends about half way to the lateral midline; predorsal notch absent or reduced, postdorsal notch absent. Dark pigment also present in association with photophore tissues, dorsum-scale pockets, lateral and dorsolateral surfaces of head, including opercle and subopercle, between bases of anal-, caudal- dorsal-fin rays and diffusely delineating trunk myosepta. Scattered melanophores within dorsomedian body of dark pigment.

SIMILAR SPECIES.-_Polyipnus_ _spinifer_ is most similar to

P. tridentifer and *P. soelae*, and bears some resemblance also to *P. inermis*, *P. parini*, *P. spinosus*, *P. stereope*. These species have in common 3 large subequal posttemporal spines. Of these, only *P. spinifer*, *P. soelae* and *P. tridentifer* have denticulate AC[C] photophore scales. *Polyipnus spinifer* differs from the latter two species by the presence of multiple denticles on scales of the AC[B] photophores.

DISTRIBUTION.-*Polyipnus spinifer* is known from Suruga Bay, Japan, the East China Sea and off the Philippines in the South China and Sulu seas (Figure 43). The bathymetric range is generally about 220 m to 380 m but specimens have been taken above 150 m in Suruga Bay, Japan.

To the south of the Philippines, the geographic range of *P. spinifer* meets and possibly overlaps that of *P. soelae* and *P. spinosus* of the members of the *spinosus* group. The range clearly overlaps that of *P. stereope* around the Japanese Archipelago. Other species possibly occurring within the range of *P. spinifer* include *P. fraseri*, *P. matsubarai*, *P. meteori*, *P. ovatus*, *P. triphanos*, *P. danae* and *P. unispinus*.

REMARKS.-Populations of *P. spinifer* (East China Sea and Philippines) have in the past been considered to be *P. tridentifer* (Baird, 1971; Schultz, 1961) or *P. spinosus* (Schultz, 1938; Matsubara, 1950; Okada and Suzuki, 1956). Borodulina (1979) established that these northern populations are distinct at the species level from P. tridentifer (Great Australian Bight). Specimens from Indonesia and off the northwest coast of Australia are nearly indistinguishable from P. spinifer but have in the past been referred to P. spinosus (Borodulina, 1979: 7). Such specimens are here described as a new species, P. soelae. See Remarks section for P. soelae and P. tridentifer.

MATERIAL EXAMINED.-Holotype: ZIL 43996 (1, 59.0 mm), 35°41'N 128°05'E, (0-) 449 m, R/V Vityaz Sta. 3540, 1 Oct 1955 (not available for direct study; x-radiograph provided by A.P. Andriashev, ZIL).

Paratypes: ZIL 43995 (4, 45.0-51.0 mm), East China Sea, R/V Raduga, Trawl 177, 5 May, 1968, no exact data (x-radiographs only).

Other Material: AMS I.B4604 (1, 52.1 mm), 10°38'N 124°13'E, (0-) 704 m, R/V Albatross Sta. D5409. AMS I.B4605 (1, 48.2 mm), same data. AMS I.B4606 (1, 44.8 mm), same data. ORIT 2551, 2554, 2557-2568 (14, 38.4-49.0 mm), Suruga Bay, Japan, 0-150 m, R/V Shou-jin Maru, 1 May, 1973. CAS 32254 (1, 58.0 mm), off Shikoku, Kimino-Neda, Japan, R/V Herre, 1936-37 Expedition, no exact data. CAS 34854 (6, 48.6-51.5 mm), Balayan Bay, Luzon Island, Philippines, 222-248 m, 0905-1000 h. IOAN uncat. (1, 51.0 mm), 30°50'N 127°49'E to 30°48'N 127°46'E, 150-0 m, R/V Vityaz Cr. 22, Sta. 3541, 0042-0153 h, 02 Nov 1955. MNHN 1984-375 (2, 50.0-54.0 mm), 13°07.7'N 122°39.1'E, (0-) 299-320 m, R/V Musorstom II Sta. 26, 1200-1300 h, 23 Nov 1980. MNHN 1984-377 (1, 60.0 mm), 13°38.4'N 121°44.1'E, (0-) 425-416 m, R/V Musorstom II Sta. 49, 2037-2137 h, 26 Nov 1980. MNHN 1984-378 (17, 34.0-58.0 mm), 13°59.3'N 120°16.4'E, (0-) 170-187 m, R/V Musorstom II Sta. 51, 1225-1306 h, 27 Nov 1980. USNM 103036 (2, 47.6-49.1 mm), 13°38'15"N 121°48'15"E, (0-) 357 m, R/V Albatross Sta. D.5221, 24 Apr 1908. USNM 103044 (1, 38.5 mm), 13°46'45"N 121°35'08"E, (0-) 333 m, R/V Albatross Sta. D.5374, 02 Mar 1909. USNM 135514 (4, 45.0-56.3 mm), 09°11'N 123°23'E, (0-) 470 m, R/V Albatross Sta.5537, 19 Aug 1909. USNM 135523 (4, 44.9-47.0 mm), 21°36'N 117°27'E, (0-) 426 m, R/V Albatross Sta. D.5317, 05 Nov 1908. USNM 135525 (1, 36.9 mm), 13°49'12"N 121°36'09"E, (0-) 278 m, R/V Albatross Sta. 5372, 24 Feb 1909. USNM 135528 (11, 30.9-54.8 mm), 13°46'45"N 121°35'08"E, (0-) 333 m, R/V Albatross Sta. D.5374, 02 Mar 1909. USNM 135535 (39, 39.3-56.4 mm), 13°41'N 120°47'05"E, (0-) 370 m, R/V Albatross Sta. D.5116, 20 Jan 1908. USNM 135536 (18, 58.9-44.5 mm), 09°15'45"N 123°22'00"E, (0-) 516 m, R/V Albatross Sta. 5536, 19 Aug 1909. USNM 289176 (3, 22.9-25.6 mm), 32°33'30"N 128°20'00", 0-383 m, R/V Albatross Sta. 4898, 10 Aug 1906. ZMUC C.N. 3 (1, 54.0 mm), off Bonomisaki, Japan, (0-) 407 m, R/V Hyatori Moru, no exact data.

Polyipnus spinosus Günther, 1887

FIGURE 39

Polyipnus spinosus Günther, 1887:170 [holotype pl. 5, fig. 1B].-Goode and Bean, 1896:128 [pl. 39, fig. 148].-Garman, 1899:238.-Gilbert, 1905:609-610.-McCulloch, 1914:89.-Fowler, 1936:240-241 [part].-Parr, 1937:55.-Schultz, 1938:142-144 [part].-Matsubara, 1950:188-192 [part, fig. 2 is P. spinifer Borodulina, 1979].-Okada and Susuki, 1956:296-302 [part].-Baird, 1971:89-90.-Borodulina, 1979:7 [part, P. spinosus Günther, 1887 in synonymy; remaining description refers to P. soelae n. sp.].-Bourret, 1985:59-61.-Paxton et al., 1989:192 [part].-Harold, 1989:874-875; 1990b:515.

Polyipnus spinosus spinosus.-Schultz, 1961:647-649 [holotype fig. 24]; 1964:268.

Polyipnus spinosis [sic].-Borodulina, 1979:7 [incorrect subsequent spelling].-Yamamoto, 1982:41.

DIAGNOSIS.-Gill rakers 19-21. Lateral pigment projection tapered and moderately long, approaching but not reaching lateral midline. Three posttemporal spines: dorsal longest (8.4-9.5 % SL), median spine shortest, ventral spine intermediate, both less than or equal to half of length of the dorsal spine. Anal-fin pterygiophore spines absent.

Photophore scale denticles restricted to PV and VAV clusters. AC[A] photophores grade into AC[B]. AC[B] (9-11). AC[C] photophores compact. Palatine teeth absent. Caudal peduncle deep and slightly tapered posteriorly.

DESCRIPTION.-Maximum adult body size moderate, up to 85 mm SL, according to Bourret (1985). D (12) 12-14. A (15) 15-17. P (14) 12-13. V 7. GR 5/6+13 = (19/18) 19-21 (20 and 21 according to Bourret, 1985: 59). Vertebrae (32) 32/33 (33 according to Bourret, 1985). Body laterally compressed. Body profile anterior of dorsal blade and pelvic fin broadly elliptical, acutely tapered posteriorly as far as caudal peduncle. Caudal peduncle deep, slightly tapered posteriorly. Flank scales diaphanous and cresentic. Ventral margin of dentary slightly convex and serrate. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary with smaller, conical teeth. Anterior region of vomer with a transverse patch of about 8 medial rows of conical teeth. No teeth present on palatine or posteromedial process of vomer. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel discontinuous; posterior region with 2 opposed conical spines, directed anteriorly and posteriorly. Dorsal and ventral limbs of posttemporal serrate, acutely divergent, and supporting 3 spines: dorsal spine longest (8.4-9.5 % SL), with lateral margins serrate; median spine shortest, ventral spine intermediate (less than one half of the length of dorsal spine) and directed ventrolaterally. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 5-8 minute conical spines. Rami of preopercle with widely-spaced serrations. Preopercle with two spines: ventral spine longest (6.8-10.3 % SL), slightly curved anteriorly, main axis directed ventrally; dorsal spine minute (slightly longer than one preopercular serration), directed ventrolaterally. Dorsal blade short-based, anterodorsal surface nonserrate, terminating posteriorly in two triangular spines, one per side, directed dorsolaterally. Anal-fin pterygiophore spines absent. Adipose fin base of moderate length, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 34.5-36.6, orbit length 14.0-18.3, body depth 65.6-70.6, caudal-peduncle depth 12.7-14.9, caudal-peduncle length 18.3-18.8, dorsal-fin length 21.6-21.7, anal-fin length 24.1-26.0, preanal length 72.8-73.8, predorsal length 57.5-62.1, preventral length 69.3-72.3, postdorsal length 47.7-54.0, postanal length 42.6-43.4, AC[C] length 7.8-8.5, AC[B]-[C] length 2.1-2.5.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins of scales with numerous denticles. L 1. VAV (5), ventral margins of scales denticulate. AC[A] 1+1+1, in an anteriorly-inclined straight line: #1 and #2 isolated, not visibly connected to each other or to #3 by a lumen; #3 connected to AC[B] forming a continuous gland. AC[B] (10), with an indistinct dorsal step between #3 and #4. AC[C] (4), scales with extensive flangelike ventral margins extending beyond ventral profile but without denticles.

Dark pigment saddle with a short predorsal notch; ventral margin of saddle straight from predorsal notch to caudal peduncle. Lateral pigment projection short, ventrally-tapered, not reaching lateral midline. Dark pigment also present in association with photophore tissues, lateral and dorsolateral surfaces of head, and outlining flank scales (not trunk myosepta as in most species).

SIMILAR SPECIES.-*Polyipnus spinosus* is similar to *P. stereope*, *P. spinifer*, *P. soelae*, *P. tridentifer*, *P. parini*, *P. inermis*, and *P. fraseri* with regard to posttemporal morphology (all have 3 large posteriorly-directed spines). Other species that have 3 posttemporal spines have reduced equidimensional ventral and median spines (*P. paxtoni* and *P. elongatus*). *Polyipnus spinosus* is distinguished from *P. tridentifer*, *P. spinifer*, *P. soelae* and *P. fraseri* by its lack of denticles on the ventral margins of the AC[C] photophore scales and from *P. parini* and *P. inermis* by the lack of a large gap between photophores AC[B] #3 and #4.

Polyipnus spinosus is most similar to *P. stereope* in body shape and pigmentation pattern, however the former has fewer gill rakers (18-21, as compared with 22-28 in *P. stereope*) and lacks palatine teeth.

DISTRIBUTION.-*Polyipnus spinosus* is known from the Celebes and Halmahera seas and from around the Philippine Islands (Figure 40). Schultz (1961) also listed the Bay of Bengal and the east coast of Africa as part of the geographic range but this cannot be verified. The USNM collections that Schultz (1961:648) refers to have been lost through loan transactions. I suspect that material from the African coast is *P. indicus* and from the Bay of Bengal either *P. spinosus* or *P. asper*.

Schultz (1961) gives a bathymetric range of 185 to 561 m but being based on open tows the 561 m should be regarded as a maximum possible, not an actual depth of capture. The holotype was taken between the surface and 472 m and data from one discrete-depth sample examined here (R/V *Alpha Helix* Sta. 128) gives a range of 350-390 m.

There is range overlap between *P. spinosus* and *P. soelae*, *P. meteori*, *P. triphanos*, *P. aquavitus*, *P. unispinus* and possibly *P. omphus*. *Polyipnus spinosus* was taken in the same tow as *P. aquavitus* at R/V Alpha Helix Sta. 128.

REMARKS.-The most similar species to *P. spinosus* and one that has been thought synonymous by some investigators (e.g. Matsubara, 1950) is *P. stereope*. Schultz (1961) recognized both forms but only as subspecies of P. spinosus (i.e. P. spinosus spinosus and P. spinosus stereope). Baird (1971) recognized these similar but distinct forms as species and they are treated as such here.

In her account of P. spinosus, Borodulina (1979:7) notes that two important diagnostic features are a long and narrow caudal peduncle and "spinous" (=denticulate) scales on the subcaudal (=AC[C]) photophores. Neither of these features are found in the holotype or the other specimen examined here (LACM 36062). Re-examination of some of the specimens ascribed to P. spinosus by Borodulina has shown them to be representatives of another species (P. soelae n. sp.), closely related to P. spinifer and P. tridentifer.

MATERIAL EXAMINED.-Holotype: BMNH 1987.12.7.159 (1, 45 mm), 06°47'N 122°28'E, (0-) 472 m, R/V Challenger Sta. 200, 28 Oct 1874.

Other Material: LACM 36062 (1, 23.5 mm), 00°13.5'S 128°23.7'E, 350-390 m, R/V Alpha Helix Sta. 128, 0249-0349 h, 18 May 1975.

Polyipnus stereope Jordan and Starks, 1904

FIGURE 41

Polyipnus stereope Jordan and Starks, 1904:581 [holotype pl. 2, fig. 3].-Gilbert, 1905:609-610.-McCulloch, 1914:89.-Okada and Suzuki, 1956:296-302.-Borodulina, 1979:7.-Fujii, 1984:47 [pl. 49K].-Bourret, 1985:59-61.-Harold, 1989:871-876; 1990b:515.

Polyipnus spinosus.-Schultz, 1938:143-144 [part].-Matsubara, 1950:189 [part].

Polyipnus spinosus stereope.-Schultz, 1961:649 [holotype fig. 25]; 1964:268.

Polyipnus sterope [sic].-Schultz, 1961:636,637 [table 6].-Baird, 1971:88-89 [incorrect subsequent spelling].

DIAGNOSIS.-Gill rakers 22-28. Lateral pigment projection highly tapered and moderately long, approaching but not reaching lateral midline. Three posttemporal spines: dorsal longest (8.5-8.8 % SL), median spine shortest, ventral spine intermediate, both less than or equal to half of length of the dorsal spine. Anal-fin pterygiophore spines absent. Photophore scale denticles restricted to PV and VAV clusters. AC[A] photophores grade into AC[B]. AC[B] (9-11). AC[C] photophores compact. Three or four palatine teeth. Caudal peduncle stout, about as deep as long, slightly tapered posteriorly.

DESCRIPTION.-Maximum adult body size moderate, up to 51.7 mm SL (holotype). D 13-14. A 15-16. P 13-16. V 7. GR 7-10 + 15-18 = (23) 22-28. Vertebrae (33) 33. Body laterally compressed, profile anterior of dorsal blade and pelvic fin deep and rounded, tapered posteriorly as far as caudal-fin ray bases. Caudal peduncle stout, about as deep as long. Flank scales deciduous and diaphanous. Ventral margin of dentary slightly convex and with 2 parallel deeply serrated keels. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary with smaller, conical teeth. Anterior region of vomer with a transverse patch of 6 to 10 medial rows of minute conical teeth. No teeth present on posteromedial process of vomer. Palatine with a patch of 3 or 4 minute conical teeth. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel discontinuous; posterior region with 2 opposed minute conical spines, directed anteriorly and posteriorly. Dorsal limb of posttemporal with a deeply serrated ridge, ventral limb with two such ridges. Posttemporal limbs acutely divergent, and supporting 3 posterolaterally-directed spines: dorsal spine longest (8.5-8.8 % SL), with basal margins serrate; ventral spine slightly shorter, median spine less than one half of the length of the dorsal spine. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears

8-10 minute conical spines. Rami of preopercle each with 2 parallel serrated ridges. Preopercle with two spines: ventral spine long (6.2-6.3 % SL), scythe-like, slightly curved anteriorly and main axis directed ventrally, dorsal spine minute (slightly longer than one preopercular serration), directed ventrolaterally. Dorsal blade short-based, anterodorsal surface nonserrate, terminating posteriorly in two triangular spines, one per side, directed dorsolaterally. Anal-fin pterygiophore spines absent. Adipose fin base of moderate length, occupying about one half of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 30.8-32.3, orbit length 14.0-15.2, body depth 62.9-66.5, caudal-peduncle depth 12.9-13.0, caudal-peduncle length 16.2-16.5, dorsal-fin length 21.2-22.9, anal-fin length 24.1-24.3, preanal length 69.9-72.4, predorsal length 57.9-59.0, preventral length 65.5-68.2, postdorsal length 53.1-53.2, postanal length 39.1-40.4, AC[C] length 7.0-7.6, AC[B]-[C] length 0.6-0.9.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins of scales with spinelike denticles. L 1. VAV (5), ventral margins of scales denticulate. AC[A] 1+1+1, in an anteriorly-inclined straight line: #1 and #2 isolated, not connected to each other or to #3 by a lumen; #3 connected to first AC[B] forming a continuous gland. AC[B] (10; 9-11), with an indistinct dorsal step between #3 and #4. AC[C] (4), scales without extensive flangelike ventral margins extending beyond ventral profile.

Dark pigment saddle with predorsal notch, ventral margin straight from notch to caudal peduncle. Pigment projection tapered, terminating sharply about half way to lateral midline. Dark pigment also present on photophore tissues, lateral and dorsolateral surfaces of head and dorsal scale pockets, and delineating body trunk myosepta.

SIMILAR SPECIES.-Polyipnus stereope is most similar to P. spinosus with regard to most meristic characters and body shape. These are the only Polyipnus species with a deep, posteriorly-tapered caudal peduncle. These species also have nondenticulate scales covering the AC[B] and AC[C] photophores. The only other species with this combination is P. inermis which is otherwise distinguished by a large step and a break in the AC[B] photophores, body shape and posttemporal features. Polyipnus stereope is distinguished from P. spinosus on the basis of larger number of gill rakers (22-28 as compared with 19-21) and presence of palatine teeth.

DISTRIBUTION.-Polyipnus stereope is restricted to the seas around Japan: East China Sea and Suruga and Sagami Bays

(Figure 40) at depths of about 150 to 280 m.

The geographic range of P. stereope overlaps with that of P. spinifer (P. spinosus species group), P. matsubarai (P. meteori species group) and Polyipnus n. sp. MS Aizawa.

REMARKS.-Polyipnus stereope is most closely related to the Indonesian species P. spinosus, both regarded by Schultz (1961) as subspecies of P. spinosus. This affinity was indicated by robust body and caudal peduncle as well as the relatively short posttemporal spine[s]. Although regarded here as distinct species (following Baird, 1971), Schultz's proposal of close affinity is supported (see 'PHYLOGENETIC RELATIONSHIPS' chapter). The caudal peduncle of P. stereope appears deeper than that of P. spinosus, although this is not born out by the morphometric measurements (12.9-13.0 as compared with 12.7-14.9 % SL). The fact that the peduncle of P. stereope is more acutely tapered and consequently deeper anterior of the point of measurement explains this discrepancy. The marked taper and stoutness of the caudal peduncle in P. stereope clearly distinguishes this species.

MATERIAL EXAMINED.-Holotype: USNM 051451 (1, 51.7 mm), Sagami Bay, Japan (about 35°00'N 139°30'E), (0-) 283 m, R/V Albatross Sta. 3698, 5 May 1900.

Paratypes: USNM 177895 (1, 24.2 mm), same data as holotype.

Other Material: NSMT P.6773 (1, 38.5 mm), Suruga Bay, Japan (about 35°00'N 138°30'E), no exact data. ORIT 2519

(1, 47.5 mm), 34°51.1'N 138°22.6'E, 0-150 m, 0425-0445 h, 29 May 1971.

Polyipnus tridentifer McCulloch, 1914

FIGURE 44

Polyipnus tridentifer McCulloch, 1914:87-89; 1929:51.-Schultz, 1961:646-647 [fig. 23, part].-Baird, 1971:86-88 [part].-Borodulina, 1979:3-4.-Paxton et al., 1989:192.-Harold, 1989:871-876; 1990b:515.

Polyipnus spinosus.-Schultz, 1938:143-144 [part].-Matsubara, 1950:189 [part].

Polyipnus trigentifer [sic].-Okada and Suzuki, 1956:296-302 [incorrect subsequent spelling].

DIAGNOSIS.-Gill rakers 19-25. Lateral pigment projection short and triangular, reaching about half way to lateral midline, without dorsal deflections of pigment margin posterior of projection. Three large subequal posttemporal spines: dorsal spine length (7.4-13.7 % SL). Anal-fin pterygiophore spines absent. Photophore scale denticles mainly restricted to PV, VAV and AC[C] clusters but AC[B] scales may have a single weak denticle in specimens over 50 mm SL. AC[A] photophores grade into AC[B]. AC[B] 11-14. AC[C] photophores separated by conspicuous gaps.

DESCRIPTION.-Maximum adult body size moderate to large, up to 71.6 mm SL (paralectotype), reported to 93.0 mm (McCulloch, 1914:89). D 13-14. A 17-18. P 12-13. V 7. GR 6-8+13-17 = 19-25. Vertebrae 34-35. Body laterally compressed, anterior of dorsal blade and pelvic fin deep and broadly elliptical, tapered posteriorly at about a 45° angle as far as caudal peduncle. Caudal peduncle rectangular, highly elongate. Flank scales deciduous and diaphanous, sheet-like. Ventral margin of dentary slightly convex and with 2 parallel serrated keels. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary with smaller, conical teeth. Anterior region of vomer with a transverse patch of 8 to 10 medial rows of minute conical teeth. No teeth present on posteromedial process of vomer. One or two minute conical palatine teeth present. Frontal and parietal keels serrate. Frontal keel extending to, and overlapping, parietal keel. Parietal keel discontinuous; posterior region with 2 minute opposed conical spines, directed anteriorly and posteriorly. Dorsal and ventral limbs of posttemporal each with two parallel, deeply serrated ridges, limbs acutely divergent, and supporting 3 posterolaterally-directed spines: dorsal spine longest (7.4-13.7 % SL), ventral spine slightly shorter (7.8-9.8 % SL), median spine about equal in length to ventral spine. Lateral ridges of cleithrum smooth, nonserrate; ventral margin of pectoral shield bears 12-17 minute conical spines. Rami of preopercle with 2 parallel ridges (all serrate except distal ridge of anteroventral ramus). Preopercle with two spines: ventral spine long (5.1-7.5 % SL), very slightly curved anteriorly and main axis directed ventrally; dorsal spine minute (slightly longer than one preopercular serration) and blade-like, directed ventrolaterally. Dorsal blade short-based, exposed length and height about equal, anterodorsal surface with one or two prominent serrations, terminating posteriorly in two triangular spines, one per side, directed dorsolaterally. Anal-fin pterygiophore spines absent. Adipose fin base short, occupying about one third of the distance between dorsal-fin insertion and anterior dorsal procurrent caudal-fin ray.

Morphometric characters (% SL): Head length 32.9-33.9, orbit length 15.1-16.8, body depth 58.2-60.8, caudal-peduncle depth 9.2-10.4, caudal-peduncle length 15.1-18.4, dorsal-fin length 21.6-23.9, anal-fin length 22.2-27.7, preanal length 65.0-66.3, predorsal length 55.0-57.3, preventral length 61.6-62.8, postdorsal length 49.5-56.5, postanal length 39.3-44.8, AC[C] length 8.3-9.5, AC[B]-[C] length 0.5-1.7.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. IP (6). BR (6). ORB 1+1. OP 1+1. OV[A] (2)+1. OV[B] 1+1+1, in an anteriorly-inclined straight line. PV (10), ventral margins of scales with spinelike denticles. L 1. VAV (5), ventral margins of scales denticulate. AC[A] 1+1+1, in a straight line and appearing continuous with photophores of AC[B] cluster: #1 and #2 isolated, not connected to each other or to #3; #3 connected to first AC[B], forming a continuous gland. AC[B] (11-14), with an indistinct dorsal step between #3 and #4, usually not ornamented but large specimens may have a single small denticle on each of the first four scales of the cluster. AC[C] (4), scales with ventral lamellae extending beyond lateral outline and numerous denticles.

Dark pigment saddle with a short, triangular, ventrally-tapered dark pigment projection extending about half way to midline. Predorsal notch absent or inconspicuous. Dark pigment also present in association with photophore tissues, lateral and dorsolateral surfaces of head, between bases of dorsal-fin rays and diffusely delineating trunk myosepta. Scattered melanophores within the body of dark dorsomedian pigment.

SIMILAR SPECIES.-Polyipnus tridentifer is most similar to P. spinifer and P. soelae. These three species have similar counts for fin rays and AC[B] photophores. Saddle pigmentation is similar in the absence or reduction of the predorsal notch. Also common to this trio of species is a long very narrow caudal peduncle, large gaps between AC[C] photophores and only a very minute gap between the AC[B] and

AC[C] clusters. Polyipnus tridentifer is distinguished from these other 2 species by a lack of palatine teeth and usually shorter dorsal posttemporal and ventral preopercular spines.

DISTRIBUTION.-Polyipnus tridentifer was described originally from material collected in the Great Australian Bight (McCulloch, 1914). Although some authors (e.g. Matsubara, 1950; Baird, 1971) reported specimens from the Japanese and Philippine Archipelagoes, Borodulina, 1979 has shown that P. tridentifer is probably endemic to the seas off southern Australia (Figure 43). Bathymetric data (from open bottom trawls) indicate only that the species occurs above 650 m.

No other Polyipnus species are known from the Great Australian Bight although P. kiwiensis, P. ruggeri, P. aquavitus, P. unispinus and P. parini occur to the east in the Tasman Sea vicinity and P. soelae off the northwestern coast of Australia.

REMARKS.-There has been much confusion associated with treatments of P. tridentifer. Many species of the P. spinosus species group have 3 large subequal posttemporal spines but this and P. soelae are the only ones with nondenticulate (note exceptions in description) AC[B] and denticulate AC[B] photophore clusters. Denticulation and pigmentation in P. soelae are very similar but median and ventral posttemporal spines are reduced.

MATERIAL EXAMINED.-Lectotype: AMS E.3543 (1, 72.0 mm), Great Australian Bight (about 35°S 130°E), (0-) 822 m, R/V *Endeavour*, 14 May 1913.

Paralectotypes: AMS E.3543 (1, 46.9 mm), same data as lectotype. AMS E.3542 (3, 67.5-71.6 mm), same data as lectotype.

Other Material: AMS E.5687 (1, 67.6 mm), "no exact data", registered 1933. AMS I.18711-014 (7, 48.3-69.3 mm), 33°28.7'S 127°15'E to 33°31.7'S 127°19'E, (0-) 640-650 m, 1000-1400 h, R/V *Dmitry Mendeleev*, field no. DM 1372, 28 Feb 1976. ZIL 39034 (6 of 9, 29.8-51.5 mm), "no exact data", (x-radiographs only).

PHYLOGENETIC RELATIONSHIPS

The phylogenetic analysis resulted in a cladogram of 179 character state changes in length with a CI (consistency index) value of 0.68. Using the Bootstrapping option of PAUP, four species groups were determined to be valid clades with greater than 80 % confidence. Branching order within three of these groups is generally unambiguous. However, in the _spinosus_ group, the Branch and Bound procedure of PAUP identified 11 cladograms only 1 step longer than the shortest tree and 62 that were only 2 steps longer. This result stems from the relatively small number of characters which apply to this group and their inconsistency. The latter is attributed to character convergence, reduction and other sources of error in proposing homology. The exact relationships of species within the _spinosus_ group are therefore not highly corroborated.

The shortest or most-parsimonious tree was selected as the most probable hypothesis of relationships. Uncertainty in branching order concerns the 'basal' members of the _spinosus_ group. These possible variations in topology do not affect the analytical biogeography which extracts information from the terminal _P_. _paxtoni_ to _tridentifer_ clade. Instances of homoplasy are discussed in the Character Analysis and in the discussions of monophyly of _Polyipnus_ and the four species groups. The original cladogram for 29 species is subdivided into five less-inclusive diagrams.

Character Analysis

Clade A: Polyipnus

FIGURE 47

1. The epiotic has an extensive shelflike posterior process which forms the point of attachment for the dorsal limb of the posttemporal (e.g. P. meteori, Figure 48).

Such processes are absent in all other sternoptychids.

2. The length of the anterior ceratohyal (=ceratohyal) is less than half that of the posterior ceratohyal (=epihyal) (e.g. P. meteori, Figure 49A). Weitzman (1974) stated that in combination with the presence of a winglike blade on the dorsal surface of the anterior ceratohyal the shortness of this bone is likely synapomorphous of Polyipnus species. However, this very deep blade appears to be a synapomorphy of the asteroides species group (character 31). The dimensions of the anterior ceratohyal in general are somewhat similar to those of Argyropelecus and Sternoptyx and this character is therefore a questionable autapomorphy of Polyipnus.

The length of the anterior ceratohyal is more than twice that of the posterior ceratohyal in all other sternoptychid genera.

3 (r). The urohyal is very large and dorsoventrally

expanded (e.g. *P. meteori*, Figure 49A). This bone is relatively small in *P. inermis*, as is the case in *Argyropelecus*. In the context of the most-parsimonious cladogram, however, this situation is best viewed as a result of secondary reduction and not plesiomorphy.

The urohyal is relatively small and not greatly expanded in other sternoptychids.

4 (r). Within the AC[B] photophore cluster there is a steplike increase in elevation immediately posterior to the third photophore (Figures 2C and E). There is considerable interspecific variation with regard to the conspicuousness of this condition. In *P. fraseri* there does not appear to be a step which is probably a reductive feature.

5 and 6. The distal radials of the anal (5) and dorsal fin (6) are mainly cartilaginous but there are circular perichondral ossified plates on the lateral surfaces.

No other sternoptychid has such distal radial ossifications although similar plates are present in the remaining stomiiform families Gonostomatidae, Photichthyidae and Stomiidae (sensu Fink, 1985).

Clade B: *P. meteori* + *P. asteroides* species groups

FIGURE 47

7. The urohyal has a convex posterior margin (e.g. *P. meteori* and *P. asteroides*, Figures 49A and B, resp.).

The urohyal of other *Polyipnus* species, *Argyripnus* and *Sonoda* has its posterior margin incised to various degrees. In *Sternoptyx* and *Argyropelecus* this bone has a very deeply incised posterior margin, giving the dorsal and ventral limbs a winglike appearance.

8 and 9. The second (8) and third (9) AC[A] photophores are highly displaced dorsally relative to the first AC[B] (Figures 2C, D and E).

These photophores, when present, are at or near the elevation of the first AC[B] in all other *Polyipnus* species. The AC[A] photophores of *Polyipnus* are probably homologous with parts of the VAV+AC[A] cluster of *Argyripnus* and *Sonoda* which are not dorsally displaced. On the basis of morphological evidence, homology of *Polyipnus* AC[A] with the single AC[A] photophore in *Sternoptyx* is uncertain because of metameric differences. In the context of the cladogram it is more parsimonious to interpret the dorsal displacement of the AC[A] photophores in *Polyipnus* and *Sternoptyx* as independently derived.

10 (r). The ventral preopercular spine is largely or entirely embedded within the distal lamella of the preopercle (Figure 5B). Although this character is interpreted as derived at the level of clade B, it is reversed in *P. laternatus*. In this species the spine is quite short but its terminus extends well beyond the margin of the bone and resembles the condition in the *P. omphus* species group.

A free ventral preopercular spine is present in all other *Polyipnus* species (Figure 5A), and in *Argyropelecus* and *Sternoptyx*. No other stomiiforms have such spines.

11. The OV[B] photophores are arranged in a "V" configuration although the relative elevations of the first and third elements vary widely in the clade (e.g *P. matsubarai*, Figure 8). In *P. ruggeri* these photophores all approach the horizontal plane although the first and third are usually slightly elevated (Figure 12).

In most other sternoptychids, these photophores are in a horizontal or slightly inclined straight line. Some possible exceptions are *P. fraseri* (*spinosus* species group) and *Polyipnus* n. sp. MS Aizawa (probably *asteroides* species group) in which the anterior or posterior OV[B] photophore is highly elevated.

Clade C: *P. meteori* species group

P. kiwiensis, *P. ovatus*, *P. matsubarai*,
P. meteori, *P. ruggeri*

FIGURES 47 AND 51

12. One or two medial rows of large fanglike teeth are present on an elongate posterior process of the vomer (e.g. *P. meteori*, Figure 48).

Such teeth are absent in other sternoptychids.

13 (state 2). The ectopterygoid is elongate, narrow and curved (e.g. *P. meteori*, Figure 48).

This bone is broad and triangular in the *asteroides* species group (e.g. *P. asteroides*, Weitzman, 1974:356, fig. 30), *P. omphus* within *Polyipnus*, and in all other sternoptychids except *Argyropelecus* and *Sternoptyx*. In these two genera the ectopterygoid is triangular but moderately elongate.

14. Bladelike medial processes of the posterior dorsal surface of the symplectic are inconspicuous (reduced) (e.g. *P. meteori*, Figure 48).

These blades, which apparently contribute to the anchoring of the metapterygoid, are well-developed in all other *Polyipnus* species but absent in the remaining sternoptychids. The presence of such structures in *Polyipnus* is derived but with secondary reduction in the *meteori* species group.

15. The ascending process of the premaxillary is short and broadly triangular (e.g. *P*. *ruggeri*, Figure 50A).

All other *Polyipnus* species (e.g. *P*. *omphus* and *P*. *clarus*, Figure 50B and C, resp.), *Argyropelecus* and *Argyripnus* have elongate processes. In *Sternoptyx* the premaxillary lacks ascending processes, likely an independent derivation.

16 (c). Absence of a diagonal ridge on the lateral face of the preopercular angle.

This ridge is well-defined or even prominent in other *Polyipnus* species but absent in the remaining sternoptychid genera. Polarity was established by functional outgroup comparison.

17. The symphyseal process of the dentary is truncate, without conspicuous ventral extension (e.g. *P*. *ruggeri*, Figure 50A).

The dentary symphysis is broadly triangular in all other *Polyipnus* species (e.g. *P*. *omphus*, Figure 50B) except *P*. *laternatus*, *P*. *asteroides*, *P*. *clarus* (Figure 50C) and *P*.

polli in which it is elongate and narrow. In *Argyropelecus*, *Sternoptyx* and *Argyripnus* the process is triangular.

18 (c). The iliac spine is very short, its length much less than that of the ischial process. Similar conditions occur in *P. laternatus* and *Argyropelecus* species which are tentatively interpreted as convergences.

The iliac spine is about equal in length to or longer than the ischial process in other *Polyipnus* species. Comparisons with other outgroups are not possible because of extreme modification in *Sternoptyx* and a lack of iliac spines in other stomiiform genera.

19. The bony ridge of the dorsal limb of the posttemporal is finely serrate.

Such serrations are absent in all other *Polyipnus* species, *Argyropelecus*, *Sternoptyx* and other sternoptychid genera. Coarse serrations are present on the dorsal limb in most species of the *spinosus* species group but are much coarser and probably independently derived.

Clade D: *P. matsubarai* to *P. ruggeri*

FIGURE 51

20. Middle radial cartilage of anterior anal-fin

pterygiophores are deeply dissected into three separate elements (e.g. *P. meteori*, Figure 52A). These cartilages are enveloped by secondary articular heads.

In other *Polyipnus* species (e.g. *P. unispinus*, Figure 52B) and other sternoptychid genera there are occasionally two cartilages, but in most cases there is just one continuous element.

21. The basisphenoid is very narrow and not particularly expanded basally (e.g. *P. meteori*, Figure 48).

Although outgroup comparisons are somewhat ambiguous, the most parsimonious interpretation of this character is apomorphy within *Polyipnus*. The basisphenoid is lacking in *Argyropelecus*, narrow in *Sternoptyx* but quite broad and basally expanded in *Argyripnus*.

22. The basisphenoid posteriorly-directed 'spine' is short (e.g. *P. meteori*, Figure 48).

In all other *Polyipnus* species, *Sternoptyx* and *Argyripnus* this spinelike process is long and in some cases extends well beyond the anterior margin of the ascending limb of the parasphenoid.

23. The tooth patch associated with the pharyngobranchial of the third branchial arch includes the medial surface of the articular head and at least part of

the shaft (e.g. *P. meteori*, Figure 54A).

In all other *Polyipnus* species except *P. triphanos* (which lacks such teeth), and *Argyripnus* the teeth are restricted to the medial surface of the articular head. In *P. triphanos* and *Argyropelecus* there are no teeth associated with this bone. The third and fourth pharyngobranchials, which are toothed in *Sternoptyx*, are fused making homology of the teeth uncertain. Teeth are not present on the shaft of this composite element.

Clade E: *P. meteori*, *P. ruggeri*

FIGURE 51

24. The ventral margin of the dorsomedian body of dark pigment has an abrupt dorsal notch near the horizontal position of the AC[A] photophores (*P. meteori* and *P. ruggeri*, Figures 10 and 12, resp.).

In other *Polyipnus* species, *Argyropelecus* and *Argyripnus* this region of the pigment margin is either raised in a broad, shallow arc or is essentially straight as in *Maurolicus muelleri* and *P. unispinus*. Such a body of dark pigment is not present in other sternoptychids.

25. The supraoccipital has a medial posteriorly-directed rodlike process (e.g. *P. meteori*,

Figure 48).

In other members of the genus there is either a medial bladelike process or no process at all. This character was polarized by functional outgroup comparison since there are no equivalent structures outside *Polyipnus*.

26. Hypurals one and two are not fused (e.g. *P. meteori*, Figure 55). Although a similar condition exists in *Argyropelecus affinis* and *A. gigas* this is parsimoniously interpreted as convergent.

Hypurals one and two are fused in other *Polyipnus* and the remaining sternoptychid genera.

Clade F: *Polyipnus asteroides* species group
P. triphanos, *P. bruuni*, *P. laternatus*,
P. polli, *P. asteroides*, *P. clarus*
FIGURES 47 AND 56

27 (c?). The second and third AC[A] photophores are united in a common gland (Figures 2C and E). One species in the group, *P. laternatus*, is polymorphic, occasionally having these photophores separate albeit in close proximity to one another.

In other species of *Polyipnus* (except *P. fraseri* which lacks AC[A] photophores) these light organs are not united.

In some species (e.g. P. kiwiensis) they are so close to one another that they appear united; dissection is needed to reveal the lack of a connecting lumen. In Argyropelecus, AC[A] photophores are absent and in Sternoptyx there appears to be one. Argyripnus and Sonoda have numerous united photophores in a horizontal line that may be, in part (serially), homologous to AC[A] of Polyipnus. With the extreme dorsal displacement of AC[A] photophores in Polyipnus, however, it is not clear that united elements necessarily represent the plesiomorphic condition. It is more parsimonious to interpret the gland in Polyipnus as derived.

28. The maxillary bone is densely pitted (e.g. P. clarus, Figure 50C). Slight pitting is present in P. stereope, P. unispinus, Argyropelecus and Sternoptyx but does not approach the condition in the asteroides species group.

Pitting of the maxillary is absent in all other Polyipnus species (e.g. P. ruggeri and P. omphus, Figures 50A and B, resp.) and the remaining sternoptychid genera.

29. The premaxillary is densely pitted in a manner similar to the maxillary (e.g. P. clarus, Figure 50C).

In other sternoptychids this bone is at most only slightly pitted (e.g. P. ruggeri and P. omphus, Figures 50A and B, resp.).

30. The dorsal lamellar process of the maxillary is low and extends to the medial terminus of the bone (e.g. *P. clarus*, Figure 50C).

In other sternoptychids this process, if present, terminates well before the medial terminus (e.g. *P. ruggeri* and *P. omphus*, Figures 50A and B).

31 (state 1). The dorsal bladelike process of the anterior ceratohyal is very deep with an arched profile and extends the entire length of the bone (e.g. *P. asteroides*, Figure 49B).

In other *Polyipnus* species, *Sternoptyx* and *Argyropelecus* this blade is low with a flattened profile (e.g. *P. meteori*, Figure 49A), and is restricted to the anterior region of the bone. Other sternoptychid genera lack such a blade.

Clade G: *P. bruuni* to *P. clarus*

FIGURE 56

32. The ventral process of the dentary symphysis is elongate (e.g. *P. clarus*, Figure 50C).

This process is truncate in the *Polyipnus meteori* species group (e.g. *P. ruggeri*, Figure 50A) and broadly triangular in the remaining *Polyipnus* species (e.g. *P. omphus*, Figure 50B), and in *Sternoptyx*, *Argyropelecus* and *Argyripnus*.

Clade H: *P.* laternatus to *P. clarus*

FIGURE 56

33 (c). A paired ventrally-directed external spine is present on the ventral surface of the first anal-fin proximal radial. Similar spines are also present in the *P. omphus* species group (e.g. *P. unispinus*, Figure 52B), presumably through convergence. Paired spines are also present in *Sternoptyx* but these are highly modified (Weitzman, 1974:448, fig. 112) and probably convergent with those of *Polyipnus*. If the spines in *Polyipnus* are homologous with those of *Sternoptyx*, then a large number of instances of loss within *Polyipnus* would have to be postulated.

Such spines are lacking in other *Polyipnus* species and the remaining sternoptychids.

34 (c). The pharyngobranchial of the second branchial arch has a long uncinate process (e.g. *P. clarus*, Figure 54B). A somewhat similar condition exists in other

sternoptychid genera, especially Argyropelecus, Argyripnus and Maurolicus (Weitzman, 1974:409, fig. 76). The form of this bone in clade H is therefore tentatively regarded convergent with the latter although on morphological grounds it appears primitive.

This bone is simple and rodlike or with a very short uncinate process in other Polyipnus species (e.g. P. meteori, Figure 54A) and in Sternoptyx.

Clade I: P. polli to P. clarus

FIGURE 56

35. The primary longitudinal keel of the frontal has serrations restricted to the posterior half of its margin.

Other sternoptychids have this keel variously smooth or serrate over the entire margin.

36 (c). The lateral ridge of the anterior ramus of the preopercle has several broad serrations. This condition appears to be convergent with similar serrations in P. unispinus and the P. spinosus species group.

All other Polyipnus species do not have serrations in this position. Of the other sternoptychids only Sternoptyx species (variable among species) have serrate anterior preopercular rami.

37 (c). The shafts of the proximal radials posterior to the anal-fin hiatus are cylindrical. This character is convergent with similar radials in clade N (*P. danae* plus *P. unispinus*).

In all remaining *Polyipnus* species, *Argyripnus* and *Sonoda megalophthalma* (Weitzman, 1974:417, fig. 82), the shafts are proximally expanded in the medial plane. Cylindrical radial shafts occur in *Argyropelecus*, *Sternoptyx* and *Maurolicus* which likely represents the primitive condition for the Sternoptychidae. With respect to the phylogenetic reconstruction presented here expanded radial shafts are regarded primitive within *Polyipnus*.

Clade J: *P. asteroides*, *P. clarus*

FIGURE 56

38. The paired lamellar processes of the dorsal blade extend only about one half of the distance from their posterior origins to the anterior margin of the medial process (e.g. *P. clarus*, Figure 57).

All other *Polyipnus* species, except *P. fraseri* which lacks an external dorsal blade, have these lamellar processes occupying the entire anterior-posterior axis of the pterygiophore (e.g. *P. danae* and *P. soelae*, Figures 58 and 59, resp.). Comparisons to outgroups with dorsal blades outside Polyipnus are not possible since the blades of Argyropelecus and Sternoptyx are unpaired medial structures.

Clade K: P. omphus + P. spinosus species groups

FIGURE 47

39. The posttemporal spine, or dorsal posttemporal spine in species with more than one spine, is very long (at least 10 % SL) (e.g. P. danae and P. inermis, Figures 24 and 35, resp.). The spine of P. laternatus (Figure 18) approaches this condition, especially resembling that of P. omphus (Figure 26), but is probably convergent.

All other Polyipnus species have a short posttemporal spine, usually much less than 10 % SL (e.g. P. meteori, Figures 10 and 48). These spines are short (Argyropelecus), rudimentary (Sternoptyx) or lacking in other sternoptychids.

40. The dorsal lamellar process of the maxillary is erect and tabular, its sides being nearly vertical (e.g. P. omphus, Figure 50B).

This process has low relief with sloping sides in all other Polyipnus species (e.g. P. ruggeri and P. clarus, Figure 50A and C, resp.), Argyropelecus, Sternoptyx and Argyripnus.

41. The articular process of the coracoid for the attachment of the mesocoracoid is short (e.g. P. soelae, Figure 60A).

In all other Polyipnus species (e.g. P. clarus, Figure 61) and remaining sternoptychids this process is elongate with the point at which the two bones meet well above the surrounding surface of the coracoid.

31 (state 2). The dorsal winglike blade of the anterior ceratohyal is of moderate depth and mainly restricted to the anterior region of the bone (e.g. P. soelae, Figure 49C).

This blade is very deep (derived in asteroides species group) (e.g. P. asteroides, Figure 49B) or very low in the meteori species group (e.g. P. meteori, Figure 49A), Argyropelecus and Sternoptyx (see Weitzman, 1974:405, figs. 73 and 74). Such blades do not occur in other sternoptychids.

43. The posteriorly-directed lateral process of the coracoid is narrow and terminates sharply (e.g. P. soelae, Figure 60A).

This process is broad and its posterior termination rounded in other Polyipnus species (e.g. P. clarus, Figure 61; P. asteroides, Weitzman, 1974:440, fig. 102) and either rounded or vertical in other sternoptychids.

Clade L: *P. omphus* species group

P. omphus, *P. aquavitus*, *P. unispinus*, *P. danae*

FIGURES 47 AND 62

44. The lamellar processes of the dorsal blade are double, having secondary parallel ventrolateral elements (e.g. *P. danae*, Figure 58).

No other *Polyipnus* species (e.g. *P. clarus* and *P. soelae*, Figures 57 and 59, resp.) or sternoptychid genus has such structures.

45. The ossified portions of the ectopterygoid and palatine bones do not overlap. Contact of these bones occurs between the ossified dorsal termination of the ectopterygoid and the cartilaginous ventroposterior region of the palatine.

In all other *Polyipnus* species (e.g. *P. meteori*, Figure 48; *P. asteroides*, Weitzman 1974:356, fig. 30), *Argyropelecus*, *Sternoptyx* and *Argyripnus* the ossified part of the palatine overlies the dorsoanterior extremity of the ectopterygoid.

33 (cr). Anal-fin pterygiophore spines are present (e.g. *P. unispinus*, Figure 52B). These spines are apparently independently derived with regard to those of the *P. asteroides* species group (*P. laternatus*, *P. asteroides*, *P.*

polli and *P. clarus* only). Within the *P. omphus* species group the spines are lost in *P. danae*. Somewhat similar spines are also present in *Sternoptyx* but their extreme modification defies direct comparison with those of the *P. asteroides* and *P. omphus* species groups.

Other sternoptychids lack such spines.

47 (cr). In adults there are 10 or more photophores in the AC[B] cluster: reversed in *P. fraseri*. This character is convergent with similar proliferation in *P. laternatus* and clade U within the *P. spinosus* species group.

In other *Polyipnus* species, *Argyropelecus*, *Sternoptyx*, *Argyripnus* and *Sonoda* there are fewer than 10 AC[B] photophores. Other sternoptychids (e.g. *Valenciennellus* and *Danaphos*) have at most 3 united AC[B] elements.

48 (c). The dorsal step between AC[B] photophores #3 and #4 is indistinct (e.g. *P. omphus* and *P. unispinus*, Figures 26 and 27, resp.). Similar conditions in *P. laternatus* (Figure 18) and clade U of the *P. spinosus* species group (e.g. *P. soelae*, Figure 41) probably represent convergences. Such elevation of the posterior AC[B] photophores is perfectly correlated with proliferation of AC[B] number as described in character 47 above.

Other *Polyipnus* species have a distinct dorsal step between the third and fourth AC[B] photophores (e.g. *P.*

meteori, P. asteroides and P. asper, Figures 10, 13 and 28, resp.). Outgroup comparisons are ambiguous because of questionable homology of specific AC[B] photophores among ingroup and outgroup taxa. There may not be a photophore in any outgroup genus that is equivalent to AC[B] #4 of Polyipnus. However, the character can be polarized on the basis of parsimony.

49 (r). The paired anterolateral processes of the first anal-fin pterygiophore descend smoothly to the distal head (e.g. P. unispinus, Figure 52B). This condition also occurs in Sternoptyx but is convergent in the context of the cladogram. A reversed condition appears to be present in P. danae of this clade.

These structures are angular and dorsolaterally produced, to varying degrees, in the remaining Polyipnus species, and in Argyropelecus (Weitzman, 1974:419, fig. 84), Argyripnus and Danaphos.

50 (cRr). The first branchiostegal ray of the posterior ceratohyal is narrow. This character reverses in P. aquavitus where the branchiostegal ray is expanded and bladelike. Polyipnus triphanos (P. asteroides species group) also has a narrow branchiostegal ray in this position, and this is interpreted as a convergence.

This branchiostegal ray is expanded and bladelike in other Polyipnus species, Argyropelecus lychnus species complex (sensu Baird, 1971), the other sternoptychid genera examined and Thorophos euryops according to Weitzman (1974:402, fig. 67).

Clade M: P. aquavitus to P. danae

FIGURE 62

51. Photophores of the AC[C] cluster are separated by very broad gaps, often greater than the diameter of one of these photophores (Figure 3D; e.g. P. aquavitus, Figure 22). In clade Y there is a similar condition (e.g. P. soelae, Figure 41) but the gaps are narrower and heavily ossified scales are associated with each organ. In terms of the cladogram these should be regarded as convergent. Outside Polyipnus one further possible instance of convergence occurs in the Argyropelecus affinis species complex (sensu Baird, 1971) (see Weitzman, 1974:336, fig. 11). In this case, however, the OV, VAV, and all AC photophores are widely spaced, likely a derived condition itself.

Photophores of the AC[C] cluster are compact (Figure 3E) and frequently in contact with one another in other Polyipnus species (e.g. P. meteori, Figure 10) and the remaining sternoptychids that have a cluster in this position (Sternoptyx, Argyropelecus lychnus species complex, *A*. *hemigymnus*, *Argyripnus*, *Sonoda*, *Danaphos*, *Valenciennellus*, *Maurolicus* and *Araiophos*).

52. The longitudinal keel of the parietal has a smooth margin. This may also be true of *Argyripnus* but homology is uncertain.

Such parietal keels are serrate to varying degrees in all other *Polyipnus* species, *Argryopelecus* and *Sternoptyx*.

53. The paired perichondral ossifications on the distal radials of the anal-fin are small.

These plates are relatively large in all remaining *Polyipnus* species but absent in other sternoptychids. In *P*. *aquavitus*, *P*. *unispinus* and *P*. *danae* this character is most parsimoniously regarded apomorphic.

54. The distal radial cartilages of the anterior (excluding the first two) anal-fin pterygiophores are approximately equidimensional with a circular to triangular profile (e.g. *P*. *unispinus*, Figure 52B).

Other *Polyipnus* species and the remaining sternoptychids examined have these radials elongate in the anterior-posterior axis and with an acute triangular profile (e.g. *P*. *meteori*, Figure 52A).

55. The paired spines of the dorsal blade are long and

needlelike (e.g. P. danae, Figure 58).

Other Polyipnus species have much shorter, flattened spines (e.g. P. clarus and P. soelae, Figures 57 and 59, resp.). Uniqueness of the dorsal blade of Polyipnus makes outgroup comparisons to other genera inappropriate.

13 (state 3). The ectopterygoid is very short, broad and anteriorly truncate.

The ectopterygoid is long and triangular in P. omphus, the P. asteroides species group (Weitzman, 1974:356, fig. 30) and other sternoptychids (e.g. Argyripnus atlanticus, Weitzman, 1974:354, fig. 27). Other forms of the ectopterygoid are independently derived for the P. meteori (clade C) and P. spinosus (clade O) species groups.

57. The dorsal preopercular spine is simple in structure but relatively large. This spine is also elongate in P. nuttingi and P. indicus of the P. spinosus species group but does not approach the relative size that occurs in clade M.

Other Polyipnus species either lack this spine or it is very short with its length about equal to that of a preopercular serration. A dorsal preopercular spine is present, but modified, in Argyropelecus. These spines do not occur in other sternoptychids.

58. Small body size, not exceeding 40 mm SL. Although body size is not a reliable character for reconstructing relationships, size reduction in clade M is congruent with the above synapomorphies. *Argyropelecus hemigymnus* appears to have independently undergone evolutionary size reduction.

All other *Polyipnus* species, *Sternoptyx*, *Argyripnus*, *Sonoda* and all *Argyropelecus* species except *A. hemigymnus* attain body sizes in excess of 40 mm.

59 (r). The anterior margin of the ascending limb of the parasphenoid extends anteriorly of the posterior extremity of the basisphenoid-parasphenoid articulation. In the context of the cladogram this character is reversed in *P. danae* to a condition resembling that of the outgroups.

In all other *Polyipnus* species (e.g. *P. meteori*, Figure 48) and other sternoptychids, except *Argyropelecus* in which the basisphenoid is lacking, the anterior margin of the parasphenoid is posterior of the basisphenoid (e.g. *Argyripnus* and *Sternoptyx*, Weitzman, 1974:354, 359, figs. 27 and 34, resp.).

Clade N: *P. danae*, *P. unispinus*

FIGURE 62

60. The caudal peduncle is very long and rodlike. This

feature is unique to *P. danae* and *P. unispinus* (Figures 24 and 27, resp.) although in *P. aquavitus* there is some elongation in relation to other deep-bodied sternoptychids.

61. The ventral process of the retroarticular is produced as a long spine.

This process is somewhat spinelike albeit very short in some other *Polyipnus* species (e.g. *P. aquavitus*, *P. inermis* and *P. indicus*). Remaining *Polyipnus* species (e.g. *P. asteroides*, Weitzman, 1974:356, fig. 30) and other sternoptychids (e.g. *Argyripnus*, *Sonoda*, *Argyropelecus* and *Sternoptyx*, Weitzman, 1974: figs. 27, 28, 32 and 34) have a rounded conical retroarticular process.

62. The medial lamellae on the shafts of the anal-fin proximal radials (excluding the first pterygiophore) are restricted to the distal one half of the bone and are somewhat teardrop-shaped overall in lateral view (e.g. *P. unispinus*, Figure 52B).

In other *Polyipnus* species (e.g. *P. meteori* and *P. soelae*, Figures 52A and 53, resp.), *Argyropelecus*, *Sternoptyx* and *Argyripnus* these lamellae extend at least to the vicinity of the proximal tip of the bone (e.g. *Argyropelecus aculeatus*, Weitzman, 1974:419, fig. 84).

63. The shaft of the dorsal blade pterygiophore inserts

fewer than six vertebrae anterior of the first anal-fin pterygiophore. The only sternoptychid examined with this feature was *Argyripnus* sp. from the Philippines.

In all other *Polyipnus* species, *Argyropelecus*, *Sternoptyx* and *Argyripnus atlanticus* the dorsal blade inserts at least six vertebrae anterior to the anal fin origin.

64 and 65. The dorsal blade (64) and the dorsal blade shaft (65) are enlarged in comparison with the head and the shaft of the second pterygiophore (e.g. *P. danae*, Figure 58).

In other *Polyipnus* species the blade is relatively small and the shaft is similar in length and diameter to the second pterygiophore (e.g. *P. clarus* and *P. soelae*, Figures 57 and 59, resp.). The dorsal blades of *Argyropelecus* and *Sternoptyx* are very different in structure from that of *Polyipnus* and direct comparisons of dimensions may be misleading for outgroup comparison. In all likelihood the dorsal blades of *Argyropelecus* and *Sternoptyx*, which together form a clade (Weitzman, 1974), have undergone enlargement independent of *P. danae* and *P. unispinus*.

66. The perichondral ossifications of the dorsal-fin distal radials are very small (e.g. *P. danae*, Figure 58).

These plates are relatively large in other *Polyipnus* species (e.g. *P. clarus* and *P. soelae*, Figure 57 and 59, resp.) but absent in other sternoptychid genera. Polarity was established by functional outgroup comparison.

67 (c). The secondary longitudinal keel of the frontal is discontinuous, its margin descending to the surface of the surrounding bone (e.g. *P. unispinus*, Figure 63).

This keel is continuous in all other *Polyipnus* species, except *P. nuttingi* in which it is lacking. In *Argyripnus* there is a continuous keel but its structure is somewhat unusual and may not be homologous with that of *Polyipnus*. Other sternoptychids lack this keel.

68. The dorsal and ventral hypohyals are very small and separated by a broad field of cartilage.

In the remaining *Polyipnus* species and the other sternoptychid genera the dorsal and ventral hypohyals are large, approaching or even contacting one another (e.g. *P. meteori*, *P. asteroides* and *P. soelae*, Figures 49A, B and C, resp.).

69 (c). The medial lamellae of the pectoral fin radials are highly reduced. A similar condition occurs in *P. polli*, probably as a convergence.

Such lamellae are well-developed in all other *Polyipnus* species (e.g. *P. soelae* and *P. clarus*, Figures 60A and 61, resp.), Argyropelecus and Argyripnus but altogether lacking in Sternoptyx. In the latter genus the lack of these lamellae is more likely a result of convergence than primitive absence.

70. The fifth ceratobranchial has long, sparse teeth in a patch at the proximal end of the bone (e.g. P. unispinus, Figure 64A).

Long, sparse teeth are present in other Polyipnus species (except the P. spinosus species group), Argyropelecus, Sternoptyx and Argyripnus but they are distributed along most of the proximal half of the bone. In the Polyipnus spinosus species group the tooth patch occupies the proximal one half of the ceratobranchial but the teeth themselves are very short and densely packed.

71 (c). The tooth plates of the fifth ceratobranchial are absent (e.g. P. unispinus, Figure 64A). This is also true of P. triphanos and Sternoptyx, conditions which are here interpreted as convergent.

These tooth plates are present in all other Polyipnus species (e.g. P. soelae, Figure 64B), Argyropelecus, Argyripnus and Sonoda (Weitzman, 1974:410, fig. 77).

Clade O: P. spinosus species group

P. oluolus, P. nuttingi, P. indicus, P. asper, P. inermis,
P. parini, P. paxtoni, P. elongatus, P. fraseri,
P. stereope, P. spinosus, P. spinifer, P. soelae,
P. tridentifer

FIGURES 47 AND 65

72. The ventral preopercular spine is ventrally-directed, very long and scythelike, with some degree of anterior arc (Figure 5A).

Other Polyipnus species have either a reduced spine (asteroides and meteori species groups, not including P. laternatus) or a short relatively weak conical spine (P. omphus species group and P. laternatus). These spines are of moderate length in Argyropelecus and Sternoptyx but do not approach the size and configuration of the spinosus species group. Preopercular spines do not occur in other sternoptychids.

73 (c?). The ventral margins of the PV photophore scales have strong denticles (fused cteni) which extend distally from prominent ridgelike radii (Figure 3A and C). In P. inermis these denticles are present but weak as in other photophore clusters of that species. Outside the P. spinosus species group PV scale denticles are present in P.

unispinus but these structures are minute and lack radii and may not be homologues. In *Argyropelecus sladeni* there are PV scale denticles in some individuals from the Pacific Ocean. This trait may also have arisen independently.

All other members of *Polyipnus* and *Argyropelecus* lack PV scale denticles (Figure 3B). No other sternoptychid has denticulate scales covering the PV photophores.

74 (c?). The ventral margin of the dentary is deeply serrate. *Polyipnus omphus* (*P. omphus* species group) also has serrations but these are minute scallops and not comparable with those in the *spinosus* species group.

All other *Polyipnus* species and the remaining sternoptychid genera have dentaries with a smooth ventral margin.

75. The ventral limb of the posttemporal, which is fused with the supracleithrum (Weitzman, 1974), is serrate.

In other sternoptychids, regardless of whether the supracleithrum is fused to the posttemporal (remaining *Polyipnus* species and *Argyropelecus*) or is a separate element (other genera) the ventral limb is smooth and without serration.

76. The posterior process of the posttemporal bone has more than one spine. These spines have rodlike bases

originating at and radiating from the posterior process. They are unlike associated serrations which are restricted to ridges and flangelike margins of the bone (Harold, 1989:873, fig. 2.) (Figure 4A and B).

All other *Polyipnus* species (Figure 4C), *Argyropelecus* and *Sternoptyx* have to various degrees of development single posttemporal spines. Other sternoptychids lack posttemporal spines.

77. The shaft of the first proximal radial of the dorsal fin does not have an anterior medial lamella (e.g. *P. soelae*, Figure 59).

Such lamellae are present in all other *Polyipnus* species (e.g. *P. clarus* and *P. danae*, Figures 57 and 58, resp.), *Argyropelecus*, *Sternoptyx*, *Argyripnus* and *Maurolicus*.

13 (state 1). The ectopterygoid is elongate and very narrow. This condition is one of three forms of ectopterygoid in *Polyipnus* which, according to this reconstruction, are possibly independently derived.

The ectopterygoid is broad and triangular throughout the *asteroides* species group (e.g. *P. asteroides*, Weitzman, 1974:356, fig. 30), and in *P. omphus*, *Argyropelecus*, *Sternoptyx*, *Argyripnus* and, according to Weitzman (1974), *Sonoda*.

79. The ectopterygoid has a medial ridge or keel which describes a broad arc.

This ridge is deflected through an acute angle dorsally in the remaining _Polyipnus_ species (e.g. _P_. _meteori_, Figure 47), _Argyropelecus_, _Sternoptyx_ and _Argyripnus_.

80. The frontal bone has a lateral secondary longitudinal keel which does not extend posteriorly to the secondary parietal keel.

In all other _Polyipnus_ species (e.g. _P_. _unispinus_, Figure 63) and in _Argyripnus_ such a frontal keel extends posteriorly and is continuous with the secondary parietal keel. These keels do not appear to occur in other sternoptychids.

81. The posterior shelf of the epiotic is modified into a cuplike fossa into which the dorsal limb of the posttemporal articulates.

Other sternoptychids lack such fossae.

82. Along the proximal one half of the ceratobranchial of the fifth gill arch there is a patch of densely packed short teeth (e.g. _P_. _soelae_, Figure 64B).

Other sternoptychids have sparse, long teeth on this bone (e.g. _P_. _unispinus_, Figure 64A).

83. The dorsal limb of the posttemporal bone has deep spinelike serrations (Figure 4A). Outside the *spinosus* species group weak serrations are present in the *meteori* species group. However, the ridges on which these serrations originate differ in their structure and tend to support a hypothesis of independent derivation (see character 19, page 211).

Such serrations are absent in all other sternoptychids. Polarity was established by functional outgroup comparison.

36 (state 1) and 85 (c). The anterior (36) and the dorsal (85) rami of the preopercle have deep spinelike serrations. The anterior ramus has several weak serrations in *P*. *unispinus*, *P*. *polli*, *P*. *asteroides*, *P*. *clarus* and some *Sternoptyx* species. Weak serrations of the dorsal ramus occur in *P*. *unispinus*, *Argyropelecus* and *Sternoptyx*. It is likely that the deep serrations of the *spinosus* species group represent an apomorphic condition.

These serrations are absent in all other *Polyipnus* species and the remaining sternoptychids.

86 (c) (state 2). The antorbital is a minute transversely elongate element (e.g. *P*. *stereope*, Figure 66C). A somewhat similar ossification also occurs in *P*. *danae* but not other members of the *P*. *omphus* species group.

The antorbital is well-developed and equidimensional to dorsoventrally elongate in *P. omphus*, *P. meteori* species group (e.g. *P. meteori*, Figure 66A), *Argyripnus*, *Danaphos* and *Maurolicus* but absent in the *P. asteroides* species group (e.g. *P. asteroides*, Figure 66B), *P. unispinus*, *P. aquavitus*, *Sternoptyx* and *Argyropelecus*.

87 (r). The anterodorsal surface of the dorsal blade is to varying degrees serrate (e.g. *P. soelae*, Figure 59). *Polyipnus inermis* is the only member of the *spinosus* species group that lacks this feature.

All other *Polyipnus* species have a nonserrate dorsal blade (e.g. *P. clarus* and *P. danae*, Figures 57 and 58, resp.). Dorsal blades in *Argyropelecus* and *Sternoptyx* are usually serrate but they are not structurally comparable to those in *Polyipnus*. In *Polyipnus* the presence of serrations is parsimoniously interpreted as derived.

88 (r). An absence of palatine teeth is probably derived for clade O but reverses to presence at a lower level of generality (clade WY).

Other sternoptychids have palatine teeth.

Clade P: *P. nuttingi* to *P. tridentifer*

FIGURE 65

89. The third AC[A] photophore is united with the anteriormost AC[B] photophore forming a continuous gland (Figure 2A; e.g. *P. indicus*, Figure 34).

In all other *Polyipnus* species the third AC[C] photophore is not joined to the first AC[B] element (Figures 2B to E; e.g. *P. oluolus*, Figure 38). A single AC[A] photophore is present in *Sternoptyx* and is not joined to the AC[B] cluster. The VAV/AC[A] photophores of *Argyripnus* and *Sonoda* are separated from the AC[B] by a broad gap.

90. The scales of the VAV photophores are denticulate. These structures are present but very weak in *P. inermis* which has various reductions of scale denticles and spinous processes.

Other sternoptychids with VAV-covering scales (*Polyipnus* and *Argyropelecus*) except *A. sladeni* from the Pacific Ocean do not have denticles in this position.

Clade Q: P. indicus to P. tridentifer

FIGURE 65

There are four derived characters in support of clade Q that are not ubiquitous. The weakness of this evidence is expressed in the cladogram by a broken line indicating an alternate topology.

91 (r). The ventral margin of the angular is minutely serrate in all clade Q species except P. inermis.

Other sternoptychids have a smooth angular.

92 (r). The point of insertion on the maxillary for the ventral extremity of the premaxillary is angular to deeply incised. This character is reversed in P. fraseri which has a rounded insertion point.

In other Polyipnus species, Argyropelecus, Sternoptyx and Argyripnus this insertion point is rounded or with a shallow concave incision. There is considerable intraspecific variation in the outgroups but deep sculpting as described above is restricted to clade Q.

93 (r). The scales of the AC[C] photophores are denticulate. This character appears to have been lost in

clade T (P. inermis plus P. parini), P. elongatus and clade X (P. stereope plus P. spinosus). Similar denticles also occur in Argyropelecus aculeatus and sporadically in A. sladeni populations from the Pacific Ocean.

Other sternoptychids lack denticulate AC[C] photophore scales.

94 (r). The lateral ridge of the dentary is serrate. This character reverses to nonserrate in P. inermis and clade Z (P. soelae plus P. tridentifer).

Other sternoptychids lack these serrations.

Clade R: P. asper to P. tridentifer

FIGURE 65

95. The posteriormost region of the primary keel of the parietal is modified into two minute opposed medial spines (PKS in Figure 5D).

This keel in other Polyipnus species is continuous (e.g. P. unispinus, Figure 63) or with a central hiatus, and in Sternoptyx, Argyropelecus and Argyripnus it is continuous.

96 (r). Denticles are present on AC[B] scales. Although this character is interpreted as derived for clade R there

are three instances of putative loss: P. inermis, P. elongatus, clade X (P. stereope plus P. spinosus).

Other sternoptychids lack denticulate AC[B] photophore scales.

Clade S: P. inermis to P. tridentifer

FIGURE 65

97. Three spines originate on the posterior process of the posttemporal bone (Figures 4A; e.g. P. fraseri, Figure 32). Although the median and ventral spines are in some species very short and indistinct there are always three spines.

In the remaining members of the P. spinosus species group there are two spines (Figure 4B) although in some cases (e.g. P. nuttingi) there are many deep spinelike serrations on the posterior process of the posttemporal. Single posttemporal spines characterize the remaining Polyipnus species, Argyropelecus and Sternoptyx.

Clade T: P. inermis, P. parini

FIGURE 65

98. A broad gap, about equal to the diameter of one

photophore, is present between the third and fourth photophores of the AC[B] cluster (e.g. P. inermis, Figure 35).

Disjunction of the AC[B] photophores is unknown in other sternoptychids with clearly equivalent light organs (i.e. remaining Polyipnus species, Argyropelecus, Argyripnus and Sonoda). In Sternoptyx there are only three AC[B] photophores.

99 (c). In species with three posttemporal spines the ventral element is very long, at least one half of the length of the dorsal spine. This condition occurs possibly as a convergence in clade W (P. fraseri to P. tridentifer). Alternatively the long ventral spine is derived lower in the tree (clade S) and independently reduced in P. paxtoni and P. elongatus. However, the latter hypothesis requires an additional step and on the basis of parsimony is not preferred.

In other Polyipnus species with multispinose posttemporals the ventral/basal spine is short and resembles very closely those of P. paxtoni and P. elongatus.

93 (R). The AC[C] photophore scales are not denticulate. See clade Q (P. indicus to P. tridentifer) derived characters for comments.

Clade U: *P. paxtoni* to *P. tridentifer*

FIGURE 65

100. The articular heads of the posterior two dorsal-fin proximal radials are fused at some point and, in some cases, reduced (e.g. *P. soelae*, Figure 59).

In other sternoptychids these radials are separate elements.

47 (c). Ten or more united photophores are present in the AC[B] cluster (e.g. *P. paxtoni*, Figure 40). In *P. fraseri* (Figure 32), however, there are only 4 AC[B] photophores which is considered a paedomorphic and secondarily derived character (Harold, 1990b). In addition, proliferation of these photophores occurs in *P. laternatus* and in the *P. omphus* species group as convergences. Two outgroup genera, *Maurolicus* and *Sonoda* (but not its sister group *Argyripnus*), also have relatively high AC[B] counts that probably represent secondary derivations.

Other sternoptychids have fewer than 10 AC[B] photophores.

48 (c). The dorsal step between the third and fourth AC[B] photophores is not pronounced (e.g. *P. paxtoni*, Figure 40). This apparently reductive character also occurs in *P. laternatus* and the *P. omphus* species group as convergences.

Other Polyipnus species have a pronounced step in this position (e.g. P. meteori, Figure 10), a unique condition but probably not synapomorphous in view of the number of conflicting derived characters. In this case polarity was determined by functional outgroup comparison, not by explicit comparison to designated outgroup genera.

Clade V: P. elongatus to P. tridentifer

FIGURE 65

101. The anterior angle of the pectoral shield is deflected laterally as a spinous process (e.g P. soelae, Figure 60B).

Other sternoptychids with a pectoral shield (remaining Polyipnus species and Argyropelecus) do not have spinous processes.

102. The bladelike process on the dorsal surface of the anterior ceratohyal is low and restricted to the anterior region of the bone and has a concave anterior margin (e.g. P. soelae, Figure 49C).

The plesiomorphic condition, a low rounded process without anterior concavity, occurs in other Polyipnus species except the asteroides and meteori species groups as well as Sternoptyx and Argyropelecus. Such processes are lacking in other sternoptychids.

103 (c?). The lateral surface of the parahypural is minutely spinose. A somewhat similar but likely independently derived condition occurs in P. nuttingi and in the Argyropelecus lychnus species complex.

Other sternoptychids lack parahypural spines.

Clade W: P. fraseri to P. tridentifer

FIGURE 65

104. The ventral posttemporal spine is slightly curved towards the anterior (Figure 4A).

In other Polyipnus species with multispinose posttemporals this spine is essentially straight or with slight dorsal curvature. Other sternoptpychids lack ventral posttemporal spines.

99 (c). In Polyipnus species with three posttemporal spines the ventral element is very long, at least one half of the length of the dorsal spine (Figure 4A). A similar condition occurs in clade T (P. inermis, P. parini) which is probably convergent.

Clade WY: *P. stereope* to *P. tridentifer*

FIGURE 65

There are no ubiquitous unreversed synapomorphies at this level and therefore node WY "collapses" into an unresolved trichotomy at node W.

88 (R1). Teeth are present on the palatine bone. Some specimens of *P. tridentifer* lack these teeth but McCulloch (1914:87) noted the presence of one or two small teeth on the anterior end of the palatine in the type series. Since this a reversed character it is considered weak evidence of monophyly of clade WY which is accordingly shown rooted by a broken line in the cladogram.

Most sternoptychids have palatine teeth and their loss appears to be derived at the level of clade O ("base" of the *spinosus* species group) thus yielding the absence of such teeth as plesiomorphic within this species group.

Clade X: *P. stereope*, *P. spinosus*

FIGURE 65

106. The caudal peduncle is very deep and stout with a slight posterior taper (Figures 43 and 45). The caudal peduncle of *Polyipnus omphus* also has a slight posterior

taper (Figure 26) but it is much shallower and overall the shape does not compare well with that of clade X.

All remaining *Polyipnus* species and other sternoptychids have variously elongate caudal peduncles with dorsal and ventral surfaces essentially parallel (e.g. *P. tridentifer*, Figure 46).

96 (cR). The scales of the AC[B] photophores do not have denticles. See clade T (*P. inermis*, *P. parini*) derived characters for further comments.

93 (cR). The scales of the AC[C] photophores do not have denticles. See clade T (*P. inermis*, *P. parini*) derived characters for further comments.

Clade Y: *P. spinifer* to *P. tridentifer*

FIGURE 65

107. The predorsal pigment notch is indistinct, appearing only as a very slight inflection of the ventral margin of the dorsum pigment (Figures 41, 42 and 46).

All other *Polyipnus* species have to varying degrees a raised area in this position (e.g. *P. inermis*, Figure 35) except *P. unispinus* which has an essentially straight pigment margin along the entire length of the body (Figure

27). A raised area of the pigment margin occurs in *Argyropelecus* suggesting that this pattern of pigmentation is likely plesiomorphic within *Polyipnus*.

108. The photophores of the AC[C] cluster are separated by spaces which are less than or equal in width to the diameter of one photophore. A similar dispersion of the AC[C] photophores occurs in the miniature species *P*. *aquavitus*, *P*. *unispinus* and *P*. *danae* of the *P*. *omphus* species group which is probably convergent with the clade Y arrangement. In the *Argyropelecus* *affinis* complex, a general spreading apart of OV, VAV and AC photophores occurs but is probably also a nonhomology.

Other sternoptychids with comparable AC[C] clusters (remaining *Polyipnus* species, *Sternoptyx*, *Argyropelecus*, *Argyripnus*, *Sonoda*, *Danaphos*, *Valenciennellus* and *Maurolicus*) have these photophores either in contact or close proximity.

109 (cR). The two epurals are separate basally but distally fused. One distantly-related species, *P*. *aquavitus*, has similar epural fusion. The distribution of epural fusion in the genus is odd and suspect as an indicator of relationship. *Polyipnus* *nuttingi*, *P*. *inermis*, *P*. *indicus*, *P*. *asper*, *P*. *paxtoni*, *P*. *elongatus* and *P*. *stereope* (all members of the *spinosus* species group), and *P*. *unispinus*, of the

omphus species group, have completely fused epurals while in all remaining species (e.g. *P. meteori*, Figure 55) for which cleared and stained preparations were available the epurals are separate.

Complete fusion of the epurals appears to be plesiomorphic within the *P. spinosus* species group yielding the partial fusion in clade Y as a derived but reversed condition.

In other sternoptychids the epural is a single or fused ossification as in *Argyropelecus* and *Sternoptyx* or single and cartilaginous as in *Sonoda* (Weitzman, 1974:427, fig. 93) and *Maurolicus muelleri*.

Clade Z: *P. soelae*, *P. tridentifer*

FIGURE 65

110. The ventral margins of the anterior AC[B] photophore scales have at most a single denticle. The parsimonious interpretation of this character indicates that the presence of a single denticle is a reduced derived feature.

Other *Polyipnus* species have either numerous or no AC[B] scale denticles. Such denticles are lacking in other sternoptychid genera.

94 (cR). The lateral ridge of the dentary is smooth and not serrated.

Other members of the *P. spinosus* species group except *P. inermis* have serrations in this position. In *P. inermis* the lack of such serration is probably convergent with clade Z. No other sternoptychid has this ridge serrated and therefore character 94 is considered a reversed synapomorphy.

Monophyly of Polyipnus and Four Species Groups: A Discussion

POLYIPNUS.-Weitzman (1974), in a study of the intergeneric relationships of sternoptychid fishes, listed features that were thought to be unique to *Polyipnus*. Weitzman examined only four species but his characters appear to be valid autapomorphies on the basis of the present expanded set of taxa.

a) shelflike posterior processes of the epiotic (character 1, this study)
b) relatively short anterior ceratohyal (character 2)
c) large dorsoventrally expanded urohyal (character 3)
d) reduction of the centrumlike facet of the basioccipital
e) large sagitta, much deeper than long
f) club-shaped cartilaginous and bony palatine

g) unique long upper jaw ligaments coupled with very long ascending process of the premaxillary

h) arrangement and configuration of the supraethmoid, lateral ethmoids and vomer associated with a highly modified arrangement of the ethmoid region

i) short dentary with a relatively deep middle area.

In this study preservation of sagittae has precluded an adequate appraisal of e) above. Length of the ascending process of the premaxillary as described in g) above actually varies within *Polyipnus*. Elongation of the ascending process which is also characteristic of *Argyropelecus* appears to be plesiomorphic within *Polyipnus*. The broad triangular form of the premaxillary ascending process of the *P. meteori* species group (clade C, character 15) is, therefore, apomorphic.

Among new characters in support of monophyly of *Polyipnus* is the presence of a steplike increase in elevation of the fourth relative to the third AC[B] photophore (character 4). This step, while indistinct in about half of the species (e.g. *P. paxtoni*), is present in all forms except *P. fraseri*. In the latter species these photophores are considerably reduced in size and the step may as a result be obscured. Another possibility is that the four AC[B] photophores in *P. fraseri* are actually equivalent to the third AC[A] followed by the first three AC[B] photophores as they occur in the other species. In either case, since the developmental program for these photophores in _P_. _fraseri_ has been highly modified through heterochrony (Harold, 1990b), the steplike feature that was likely present in the common ancestor of clade W (see Figure 47) has probably also been affected.

The disrupted configuration of the three OV[B] photophores appears to be unique in _Polyipnus_. Within the genus there are several arrangements that in some cases define clades, but common to all is the dorsal displacement of at least one of the three OV[B] elements. In addition, the L or lateral photophore is positionally unique and should be considered autapomorphous. Weitzman (1974:461, table 1) indicated that the L photophore is synonymous with anterior VAL in other stomiatoids (=stomiiforms). This is true in as far as the L is located slightly posterior of a vertical line through the base of the pelvic fin but the following morphological evidence suggests that it may be derived from the posterior OV[B] photophores. Typically in stomiiforms the PV and OV photophores are arranged in vertical pairs, with one of each per axial segment. This is not true, however, of the posteriormost PV photophore in _Polyipnus_. That photophore is crowded together with the penultimate PV organ and there is no corresponding fourth OV[B] photophore dorsally. That is, however, approximately the position of the L photophore. Further evidence of derivation of the L from the OV[B] comes from the outgroups. *Sonoda* and *Argyripnus* both have four and *Argyropelecus* six OV[B] photophores, suggesting that in all likelihood the common ancestor of all recognized *Polyipnus* species had a minimum of four.

Another putative apomorphy of *Polyipnus* is the presence of paired perichondral ossifications associated with the distal radials of the anal and dorsal fins (characters 5 and 6, resp.). Such ossifications do not occur in other sternoptychid genera (see Weitzman, 1974) but are widespread in other stomiiform families (Weitzman, 1974; Fink and Weitzman, 1982; Fink, 1985). In view of Weitzman's (1974) highly corroborated phylogeny of the Sternoptychidae (sensu lato) it is unlikely that these structures in *Polyipnus* on the one hand and the remaining stomiiforms on the other, are homologues.

P. *METEORI* AND *P*. *ASTEROIDES* SPECIES GROUPS.-Seven rather similar species were referred to the *asteroides* species complex by Baird (1971) and these comprise much of clade B (*meteori* plus *asteroides* species groups). I add to this group *Polyipnus* *ovatus*, *P*. *bruuni* and *P*. *clarus* which are new species and *P*. *laternatus* is moved from another previously recognized group. This latter species was thought by Baird on the basis of body shape and size, posttemporal spine length, photophore configuration and dentition to be most closely related to P. omphus, P. unispinus and P. aquavitus (collectively the P. laternatus species complex sensu Baird, 1971). Of these characters, body shape and size do not differ significantly between the two groups. Polyipnus laternatus is a relatively stout-bodied species that reaches sizes comparable to P. omphus and members of the meteori and asteroides species groups. Concerning dentition, the arrangement in P. laternatus is plesiomorphic and resembles that of both groups. The posttemporal spine is slightly longer than in other clade B species but does not reach 10 % SL as it does in the P. omphus species group. This latter character and the large number (up to 13) of AC[B] photophores with an indistinct step between the third and fourth photophores appear to be convergent in the context of the most parsimonious hypothesis of relationships. Contrary to Baird's conclusions one aspect of photophore configuration, dorsal displacement of AC[A] photophores (characters 8 and 9), supports the hypothesis that P. laternatus is more closely related to members of the meteori and asteroides species groups than to the omphus species group.

Monophyly of clade B is also supported by extreme expansion of the urohyal which has a convex posterior margin (character 7) and the "V" configuration of the OV[B] photophores (character 11). The presence of a reduced ventral preopercular spine (character 10) unites all of these species except *P. laternatus* which has a short but well-developed spine.

Baird (1971) initially recognized but did not name the *meteori* species group. He did, however, treat it as a distinctive subgroup of his *asteroides* species complex characterized by elongation and dentition of the posterior process of the vomer and a unique configuration of AC[A] photophores. The *meteori* species group (clade C) is clearly monophyletic. In addition to synapomorphic vomerine dentition described above (character 12) this relationship is supported by unique ectopterygoid shape (character 13), reduction of the dorsal lamellar processes of the symplectic (character 14), a broadly triangular premaxillary ascending process (character 15), reduction of the diagonal ridge in the preopercular angle (character 16), truncation of the dentary symphyseal process (character 17), a short iliac spine (character 18) and fine serration of the dorsal limb of the posttemporal (character 19). The AC[A] photophore configuration mentioned by Baird (1971) is distinctive but not derived at this level.

According to Baird (1971), the species here referred to the *asteroides* species group (in its original form consisting only of *P. asteroides*, *P. polli* and *P. triphanos*) formed a "dichotomy" with the *meteori* species group members. He did not discuss relationships in detail, indicating the differences between the two groups in an artificial dichotomous key. The unifying characters given by Baird are absence of teeth on the posterior vomerine shaft, dorsal displacement of the second supra-anal (=AC[A]) photophore relative to the third and a "symmetrical" arrangement of supra-abdominal (=OV[B]) photophores. The vomerine dentition character is plesiomorphic and not a useful indicator of relationship. Dorsal displacement of the second AC[A] photophore is, in fact, a condition which occurs throughout the genus except for the *meteori* species group. Symmetry of OV[B] configuration exhibits too much intraspecific variation to be of any use at this level. However, a new shared derived character which concerns the AC[A] photophores is the uniting of the second and third organs in a common gland (character 27). Other supporting characters are dense pitting of the maxillary (character 28) and premaxillary (character 29), shape of the dorsal process of the maxillary (character 30) and the presence of a deep bladelike process on the dorsal surface of the anterior ceratohyal (character 31).

P. *OMPHUS* AND *P*. *SPINOSUS* SPECIES GROUPS.-A close phylogenetic relationship has not previously been postulated for the members of the *omphus* and *spinosus* species groups (i.e. clade K). Baird (1971) suggested that the species here referred to the *P*. *omphus* species group ("P. *laternatus* species complex", including *P*. *laternatus* but not the recently described P. danae Harold, 1990) were most closely related to the P. asteroides species complex on the basis of "similar otoliths" and unspecified osteological resemblances. He further stated that the P. spinosus complex appeared primitive with regard to axial and caudal osteology. Baird's opinions were formed on the basis of overall similarity and are not regarded here as evidence of close evolutionary relationship.

Clade K is an assemblage of 18 species exhibiting a broad array of forms ranging from miniature, weakly ornamented species (e.g. P. danae) to relatively large, spinose forms (e.g. P. tridentifer). This apparently heterogeneous group is united by the following shared derived characters:

a) extreme elongation of the (dorsal) posttemporal spine (at least 10 % SL) (character 39)
b) a tabular process on the dorsomedial surface of the maxillary (character 40)
c) a short coracoid process articulating with the mesocoracoid (character 41)
d) moderate depth and anterior restriction of the dorsal winglike blade of the anterior ceratohyal (character 31)
e) narrow and acute termination of the posteriorly-directed lateral process of the coracoid.

Within clade K there are two major monophyletic subgroups, the *omphus* species group (clade L) and the *spinosus* species group (clade O). The *omphus* species group is essentially the *laternatus* complex of Baird (1971) without *P*. *laternatus*, as discussed above. Seven apomorphies were found for clade L but many of these (characters 46 to 50, incl.) are convergent with other subgroups of *Polyipnus* or are reversed within this clade (characters 33 and 50) and therefore should not be considered reliable evidence of common ancestry. However, the four contained species do share a unique dorsal blade structure (character 44) and a lack of overlap of the ossified portions of the ectopterygoid and palatine bones.

Within clade L *P*. *omphus* is the sister group of the remaining three miniature (sensu Weitzman and Vari, 1988) species *P*. *aquavitus*, *P*. *unispinus* and *P*. *danae* (collectively clade M). None of these three species exceeds 40 mm SL (character 58) and, based on the small number of specimens that were examined internally, they all attain sexual maturity by about 25 mm SL. In the context of the cladogram such size reduction as well as body elongation is probably the result of heterochronic change (sensu Fink, 1981, 1982, 1988; Kluge, 1988) in the common ancestor which resulted in paedomorphosis. Some of the other derived features of these miniature species may also be paedomorphic. The photophores of the AC[C] cluster are separated by broad gaps (character 51), a condition that could result through retardation of growth of the light organs themselves leaving relatively large areas of intervening glandular tissue. The perichondral ossifications of the anal-fin distal radials are reduced in size (character 53) and the radials themselves are spherical, both considered to be juvenile or larval features.

The P. spinosus species group, referred to by Baird (1971), Borodulina (1979) and Harold (1989) as the spinosus species complex, is a clade of 14 Indo-Pacific species. The six species comprising the spinosus complex defined by Baird (1971) were originally united on the basis of 8 characters.

a) "greater development of the posttemporal spine complex", which I interpret to mean more than one spine present (character 76)
b) otolith structure (attributed by Baird, 1971 to Weitzman, pers. comm.)
c) presence of four hypural elements (i.e. hypurals 3 through 6 separate)
d) ventral surface of the dentary serrate (character 74)
e) "spine-bearing" abdominal keel plates (i.e. PV photophore scales denticulate; character 73)
f) second and third preterminal neural spines wedge-shaped
g) "extension of the cleithrum below the pectoral fin relatively more broadened"

h) reduction of the anal-fin pterygiophore hiatus

Of these characters, a, d and e (characters 76, 74 and 73, resp.) appear to be valid synapomorphies of the much larger (14 species) <u>spinosus</u> species group recognized here. Characters c, f, g and h exhibit too much variation within and among species to be interpreted at this level. Adequately preserved otoliths were not available for study so appraisal of b above is not possible.

Among new characters found that support monophyly of the <u>spinosus</u> species group are ventral preopercular spine shape (character 72), ventral limb of the posttemporal serrate (character 75), lack of an anterior medial lamella on the first proximal radial of the dorsal fin (character 77), elongate and very narrow ectopterygoid (character 13), broadly arced ectopterygoid medial ridge (character 79), secondary lateral frontal keel disjunction (character 80), modification of the posterior shelf of the epiotic into a cuplike fossa (character 81) and presence of numerous minute densely-packed teeth on the ceratobranchial of the fifth branchial arch (character 82).

Baird (1971) suggested that there were two distinct lineages within his <u>spinosus</u> complex on the basis of posttemporal morphology. One of these groups, with three posttemporal spines, was referred to as the <u>spinosus</u> subgroup by Borodulina (1979) and the remaining species, which according to Baird were characterized by "peculiar reductions" of these spines, were subsequently named the *indicus* subgroup (consisting of *P. oluolus*, *P. nuttingi*, *P. indicus*, and by Baird's criterion, *P. asper*). According to present analysis, the *indicus* subgroup is not monophyletic but the *spinosus* subgroup is (Clade S, *P. inermis* to *P. tridentifer*). *Polyipnus oluolus* of the "*indicus* subgroup" is the sister group of the remaining 13 species in the *spinosus* species group.

BIOGEOGRAPHY

The four Polyipnus species groups have broadly overlapping patterns of distribution. These patterns were examined to determine which, if any, common elements are likely to be due to shared biogeographic history. Possible explanations for unique aspects of distribution (e.g. extinction or dispersal) were also generated. Before proceeding to the analysis of historical relationships the generalized distributions and derived area cladograms are described and illustrated below for each of the species groups.

Geographic Distribution of Species Groups

P. METEORI SPECIES GROUP.-These species are confined to various ocean basins of Japan-Indo-Australia except P. meteori which occurs in the equatorial region from the western Indian Ocean eastward to the central Pacific (Figure 67). There are gaps in the distribution of P. meteori but these are more likely the result of inadequate sampling than actual disjunction. Two species, P. ruggeri and P. kiwiensis, both occur in the Tasman Sea, but are restricted to the slope areas off southeast Australia and New Zealand (see Appendix 3, Figure A-1 for locations of basins and other oceanic areas of the Indo-Pacific region). Specimens reported as P. kiwiensis by Paxton et al. (1989) from off the northeast coast of Australia (P. aff. kiwiensis) have been examined; they differ in several meristic characters from the Tasman Sea material. P. ovatus, a new species that is very similar to P. kiwiensis, has been recorded from a single locality in the South China Sea. Polyipnus matsubarai is the sole representative of the group from the Japanese Archipelago. It has an extensive range which reaches eastward nearly to the Hawaiian Emperor seamount chain.

P. ASTEROIDES SPECIES GROUP.-This is the only group with representatives in the Atlantic Ocean (Figure 68). One of these species, P. laternatus, was previously (Baird, 1971) thought more closely related to the species here placed in the Indo-Pacific omphus species group. The geographic ranges of P. laternatus and P. clarus are essentially congruent, both occurring throughout the Caribbean Sea, Gulf of Mexico and parts of the Gulf Stream system. Polyipnus clarus has been collected several times off the Scotian Shelf, but P. laternatus is not known to occur north of Cape Hatteras. Polyipnus asteroides, in its present restricted sense, occurs only in the Caribbean Sea and off Puerto Rico. The ranges of these three western Atlantic species overlap in the Caribbean area. The fourth Atlantic species, P. polli, is known only from the tropical eastern Atlantic near the coast of Africa in and between the Mauritanian and Benguelan Upwelling regions. Polyipnus *bruuni* is known from a single capture in the western Indian Ocean. *Polyipnus triphanos*, which may be a complex of closely related species, has been collected throughout much of Indonesia and adjacent areas. One unusual specimen from off Sumatra (*P*. aff. *triphanos*) may represent an undescribed species.

P. *OMPHUS* SPECIES GROUP.-There are one widespread although disjunctive Indo-Pacific species, *P*. *omphus*, and three Indo-Australian species in this group (Figure 69). *Polyipnus aquavitus* and *P*. *unispinus* have broadly congruent ranges which include most basins from the Tasman Sea north through the South Fiji Basin, parts of the Coral Sea, off New Guinea and through most of the eastern Indonesian basins, but not north of Palawan (northern margin of the Sulu Sea). The fourth species, *P*. *danae*, has been captured at two localities off the northwest coast of the Philippines in the South China Sea.

P. *SPINOSUS* SPECIES GROUP.-This is the largest species group, containing 14 mainly locally endemic forms through the Indo-Pacific region (Figure 70). From the Pacific Plate, *P*. *oluolus* is known from just a single capture from the Marshall Islands and *P*. *nuttingi* has been collected in large numbers off the Hawaiian Islands. *Polyipnus inermis*, from the Sala-y-Gomez Ridge (East Pacific Rise), is the only member of the genus from the eastern Pacific. In the western

Pacific the only verified record of *P. parini* is from the Tasman Sea, off New Zealand. There is a questionable record of the latter from the Kuroshio Current off Japan. Three species are apparently endemic to areas close to the Australian continent: *P. tridentifer* from the Great Australian Bight and *P. paxtoni* and *P. elongatus* from the Coral Sea off the east coast of Queensland. *Polyipnus soelae* occurs off the northwest coast of Australia and northwards through eastern Indonesia. *Polyipnus spinosus* is restricted to eastern Indonesia, but there are only a small number of verified records. Only one member of the *spinosus* species group, *P. spinifer*, has been collected in the South China Sea. This species also occurs as far north as the East China Sea and off the east coast of Japan where its range overlaps with that of the endemic *P. stereope*. *Polyipnus fraseri* is known from off the east coast of the Philippines and in the vicinity of the Kyushu-Palau Ridge, Philippine Sea. The two remaining members of the *spinosus* group are Indian Ocean species: *P. asper* occurs off the west coast of the Malay Peninsula in the Andaman Sea and *P. indicus* occurs off the east coast of Africa from the Natal area north to the Gulf of Aden.

Historical Biogeography

It is hypothesized that an ancestral Polyipnus assemblage occurred throughout the tropical Atlantic and Indo-Pacific regions in the early to middle Tertiary and various subsequent events have led to subdivision of oceanic areas and thereby allopatric speciation. Interconnection of oceanic areas by currents is assumed to be one of the major factors in the maintenance of genetic contact among populations of Polyipnus species. Breakdown of circulation patterns therefore may result in allopatric/parapatric speciation.

Prior to the late Oligocene (30-25 Ma), cosmopolitanism was maintained among many warm water marine organisms by a continuous circumglobal equatorial current (Herman, 1979). The overall distribution pattern of Polyipnus species appears Tethyan and probably resulted from their association with this current. This widespread Tertiary biota has been fragmented by a series of events over time relating mainly to plate tectonics and climatic modification. Only one of four Polyipnus lineages, the asteroides species group, was likely present in western Tethys (Mediterranean area), according to fossil evidence (Steurbaut, 1984). The remaining three groups have been restricted to the Indian and Pacific Oceans since their origins. Historical explanations for distribution patterns are developed below and tentatively dated by comparison with geology and paleoceanography.

AREA CLADOGRAMS.-The cladograms depicting phylogenetic relationships among the species also serve as area cladograms by including the inhabited areas with the species names (*meteori* sp. grp., Figure 51; *asteroides* sp. grp., Figure 56; *omphus* sp. grp., Figure 62; *spinosus* sp. grp., Figure 65). For example, in Figure 65 node Y implies a vicariant event that subdivided the range of species ancestral to the *P*. *spinifer*-*tridentifer* clade. That species occurred in an area consisting of the South China Sea plus the Japanese Archipelago on the one hand and eastern Indonesia plus the northwest coast of Australia plus the Great Australian Bight on the other.

Unique vicariant patterns with respect to *Polyipnus* are discussed below under ATLANTIC/INDO-PACIFIC PATTERN and INDIAN/PACIFIC OCEAN PATTERN. The remaining information, encompassing the *omphus* and *meteori* species groups and the *P*. *paxtoni*-*tridentifer* clade of the *spinosus* group are combined in a vicariance explanation under the subheading INDO-AUSTRALIAN PATTERN.

ATLANTIC/INDO-PACIFIC PATTERN.-The area cladogram for the *P*. *asteroides* species group (Figure 56) suggests a degree of historical independence from the remaining *Polyipnus* groups. Biogeographic inferences for this species group must be tentative because of a lack of area cladograms for other taxonomic groups and uncertainty about the interrelationships of Polyipnus bruuni.

The four Atlantic species share a unique common ancestor and the group is coordinate with P. bruuni of the western Indian Ocean. Together, these five species form the sister group of P. triphanos of the Indo-Australian region. Although the Atlantic deep water fauna is generally regarded most ancient (van der Spoel and Heyman, 1983) this does not appear to be the case with the P. asteroides group.

The most likely explanation is that there was a widespread equatorial Tethyan ancestor of the asteroides species group. Vicariant speciation of P. triphanos in the Indo-Australian region was the result of diminished equatorial flow following contact between the Australian Plate and the eastern part of the Asian Plate at about 22 to 20 Ma (Coleman, 1980; Edwards, 1975). The pattern would then result if a common ancestor of the P. bruuni-clarus clade existed throughout Tethys and was divided into western (Atlantic) and eastern (western Indian Ocean) parts later in the Miocene. Gibbs (1969) proposed such an event in his explanation of the distribution patterns of the tropical bathypelagic fishes Stomias brevibarbatus and S. danae (family Stomiidae). A recent analysis of phylogenetic relationships (Fink and Fink, 1986) has shown these two species to be descendants of a most recent common ancestor. Fossil evidence indicates that a warmwater deep-sea fauna of various stomiiform fishes, including Polyipnus, was present over continental Europe between late Oligocene and Miocene times (Jerzmańska, 1960; Steurbaut, 1984). Herman (1979) and Berggren and Hollister (1977) suggest that oceanic subdivision was occurring as early as 15 Ma as a result of the collision between Africa and Eurasia, with extreme division by 7 to 5 Ma as a consequence of lowered sea levels.

The apparent Tethyan pattern of the asteroides species group may alternatively be the result of invasion of the Atlantic by the ancestor of the P. laternatus-clarus clade after closure of Tethys when warmer oceanic conditions existed south of Africa. These conditions may have existed as late as 5 Ma when there was a major global cooling event (Herman, 1979; Hoddell and Kennett, 1986). This explanation, however, tends to conflict with the above fossil evidence which indicates the presence of possible ancestral species to the north of Africa in the Miocene.

Explaining the distributional/phylogenetic pattern of the Atlantic species is complicated by range overlap in the Caribbean/Gulf of Mexico area which could be a result of sympatric speciation events and/or range expansion and contraction during Plio-Pleistocene glacial epochs. The P. polli-clarus clade exhibits an east-west vicariant pattern which may be the result of diminished equatorial flow in the Atlantic following the emergence of the Panamanian isthmus in the Pliocene (3.5-3.0 Ma, Rosenblatt and Waples, 1986;

Harold and Telford, 1990). Separation of the Caribbean Sea from the Atlantic deep water at about this time (Pierrot-Bults and van der Spoel, 1979) was probably followed by disruption of equatorial flow. Restriction of the Caribbean by this mechanism caused peripheral isolation of part of the *P. clarus-asteroides* ancestor, with subsequent differentiation producing the species here recognized as *P. asteroides*.

INDIAN/PACIFIC OCEAN PATTERN.-The taxon/area cladogram for the *spinosus* species group (Figure 65) shows the least derived species to be *P. oluolus* (Marshall Islands) and *P. nuttingi* (Hawaiian Islands), both of the Pacific Plate. Geologically, these are the most ancient areas of the Indo-Pacific region inhabited by *Polyipnus* species. These and many other volcanic edifices of the region were formed during a late Cretaceous (70-60 Ma) episode of intense vulcanism (Springer, 1982; Schlanger and Premoli-Silva, 1981). The Hawaiian and Marshall island groups are to some degree geological and biogeographical relicts as a result of many of the other edifices formed at that time subsiding to depths unsuitable for shallow and moderately deep-living marine organisms. Invasion of biotas to the newly formed island groups would therefore have been possible by diffusion and not necessarily by long distance quantum dispersal. It is otherwise very difficult to explain the presence of forms like *Polyipnus* species that appear to have short lived larval stages.

Springer (1982) and Rotondo et al. (1981) invoked an "island migration" hypothesis to explain certain elements of Hawaiian endemism. There is geological evidence that the island group has been conveyed to the north, away from other island groups, causing vicariance in the shorefish fauna. This process probably has contributed to the large distance between *P. nuttingi* and its sister group, the *P. indicus*-*tridentifer* clade and could be a causal vicariant mechanism.

Polyipnus indicus of the western Indian Ocean is the sister group to the remaining Indo-Australian clade S (Figure 65). The range of this species is correlated with the path of the Agulhas Current. The western Indian Ocean is distinct, being an area of concentrated endemism in marine fishes (Cohen, 1973) but as is likely the case for *P. indicus* a component of this endemism is related to historical factors. The Indian subcontinent broke free from its southerly attachment to Gondwanaland by about 140-100 Ma (Coleman, 1980) and by the early Tertiary (about 60 Ma) had divided the Indian Ocean into west and east basin areas (Springer, 1988; Hocutt, 1987). By late Oligocene (25 Ma), westerly equatorial flow in the eastern Indian Ocean was diverted to the south (Berggren, 1982). The Australian Plate was located well to the south of eastern Asia, and consequently the eastern Indian Ocean and remained connected by an equatorial current to the Pacific Ocean (Edwards, 1975).

The approach of the Australian continent to east Asia in the early Miocene (22-21 Ma; Coleman, 1980, Edwards, 1975) coincided with an episode of Antarctic ice buildup (Herman, 1986) and concomitant sea level drop. These events led to extreme reduction of equatorial flow south of the Indo-Malayan Archipelago and constriction of equatorial flow between the eastern Indian Ocean and the western Pacific. These conditions persist to the present (Haedrich and Judkins, 1979). The result was subdivision of the ancestor of the P. asper-tridentifer clade (Clade R, Figure 65). A similar pattern, and here suggested as corroborative is found in the pontellid copepods. The Lapidocera pectinata species group, reported by Fleminger (1986) and Fleminger et al. (1982), has an eastern Indian Ocean species that is the sister group of the remaining Indo-Australian clade.

The sister group to the P. paxtoni-tridentifer clade consists of P. inermis and P. parini (Clade T, Figure 65). The distributions of these species suggests an east-west event in the Pacific. The distribution of P. parini is poorly known and here it is treated only as a western Pacific form. Polyipnus inermis, on the other hand, appears to be an endemic in the Sala-y-Gomez area of the East Pacific Rise. The ocean bottom around Sala-y-Gomez is dated at only about 9 Ma, according to Springer (1982), which is not consistent with the approximate ages placed on the P. paxtoni-tridentifer and other more derived clades (see analysis below). One possible explanation is that P. inermis or its ancestral species has occurred over this topographic part of the East Pacific Rise for much longer than 9 Ma, and the older sections of sea floor have been conveyed away from the ridge by sea floor spreading. Another possibility is that an ancestral species of P. inermis dispersed eastwards from the Indo-Pacific region. In terms of the biogeographic model of the Indo-Australian region presented below it seems most likely that a widespread ancestral biota included the Sala-y-Gomez area. The fact that closely-related Polyipnus species are not known from the central equatorial or South Pacific may be due to extinction or errors in distributional information.

INDO-AUSTRALIAN PATTERNS.-Among the meteori, omphus and spinosus species groups of Polyipnus there are replicated patterns of distribution in this region. A computational vicariance approach (Parsimony Analysis: Wiley 1988a, b; Brooks, 1990) is adopted here to identify which, if any, of these patterns are the result of common historical factors.

The area cladogram for the meteori species group (Figure 51) shows that relationships are fully resolved for just the terminal 3-species clade. The species of this group have quite restrictive geographic ranges with the exception of P. meteori. This species is probably a widespread equatorial Indo-Pacific form with a number of range disjunctions. This derived species is the sister group of the Tasman Sea endemic *P. ruggeri*. The areas occupied by *P. matsubarai*, *P. meteori* and *P. ruggeri*, and their implied common ancestors (nodes D and E) were incorporated into the Parsimony Analysis. Relationships of *P. kiwiensis* and *P. ovatus* are not well-resolved and therefore were not analysed, although possible implications of their distributions are discussed.

Phylogenetic relationships of the *omphus* species group are fully resolved (Figure 62). Three of the four species have relatively broad distributions, two of which are essentially congruent (*P. aquavitus* and *P. unispinus*; Indo-East Australian pattern). *P. danae*, the sister species of *Polyipnus unispinus*, occurs directly to the north in the South China Sea. All four of these species and their implied common ancestors (nodes L, M and N) were analysed.

The area cladogram for the *spinosus* species group is depicted in Figure 65. Generally, the members of this group have quite restricted geographic ranges. Nonetheless, those of *P. indicus*, *P. spinifer* and *P. soelae* span 30 or more degrees of latitude. Of the 14 species, only those of clade U (*P. paxtoni* through *P. tridentifer*) were encoded for the analysis. The remaining species occur outside the region under consideration and have unique distribution patterns with regard to *Polyipnus*.

The Parsimony Analysis resulted in 15 equally parsimonious area cladograms with a length of 35 steps and a consistency index (CI) of 0.743. Following the procedure of

Mayden (1988), a consensus tree was computed to determine which branching patterns are common to the 15 cladograms (Figure 71). This branching pattern is interpreted as a hypothesis of the relative timing of vicariant events. Biogeographic events will be interpreted _a posteriori_ in the context of this topology.

All of the areas are hypothesized to have been occupied by ancestral species to the _P. elongatus-tridentifer_ clade and the _P. paxtoni-tridentifer_ clade (Node 1, Figure 71, Table 7). The exceptions are the Equatorial Indian (EQ. INDIAN OC.) and western Pacific Ocean (EQ. W. PAC.) areas (Node 4) where there are no modern representatives of _Polyipnus_. Among possible explanations are extinction, primitive absence and presence of species not yet collected.

With the meeting of the Asian and Australian Plates, the Tasman and Coral seas became part of a suitable tropical regime for warm water organisms. According to Coleman (1980) the Tasman Sea area was more than 40 latitude degrees south of its present position, and therefore much colder, in the early Eocene (prior to 56 Ma). The fossil record shows that two species of _Polyipnus_ (_P. plebeius_ Grenfell, 1984 and _Polyipnus_ sp.) occurred along with other members of a marginally tropical deep-sea fish fauna off New Zealand in the early Miocene (Grenfell, 1984) but no earlier records exist. The Tasman Sea and the Great Australian Bight were likely invaded by ancestral _Polyipnus_ species following climatic amelioration and long after formation of the basins themselves (late Cretaceous to early Paleocene, Coleman, 1980).

By 20 Ma the New Guinea area of the Australian Plate was impinging on eastern Indonesian arcs (Coleman, 1980). Tectonic uplift and drop in sea level due to polar ice buildup led to reduced marine connections among the many basins of the Indo-Australian region. Shoaling of the New Guinea-Australia area at this time cut off deep water connections between the Coral Sea and the eastern Indonesia area to the west of New Guinea (e.g. Banda, Arafura, Timor, Celebes seas). This event led to the geographic subdivision of the ancestor of the P. paxtoni/elongatus-tridentifer clade.

Polyipnus paxtoni and P. elongatus are both endemics in the western Coral Sea off the coast of Queensland. They are phylogenetically placed on adjacent branches of the original cladogram (Figure 65). This is not a vicariant pattern but speciation may have proceeded via bathymetric isolation or "deep allopatry" (White, 1987). Oxygen minimum layers have been shown to strongly influence the distributions of an array of deep sea organisms (Brinton and Gopalakrishnan, 1973; Cohen, 1973; Marshall, 1979; Rao, 1979). Little is known of the depth distribution of P. paxtoni and P. elongatus, but intensification of anoxic layers in the Miocene (White, 1987) would have occurred at about the right time to explain this somewhat "basal" speciation.

Two other co-occurring Indo-Australian species, Polyipnus unispinus and P. aquavitus, are placed on adjacent branches of their cladogram (P. omphus species group, Figure 62). This is analogous to the P. paxtoni/elongatus pattern and may be the result of a similar mechanism. Such an explanation for the omphus group is also speculative and is not consistent with the broadly overlapping bathymetric ranges of the descendant species P. unispinus and P. aquavitus.

All areas except the western Coral Sea (CORAL SEA (W)) were occupied by a species ancestral to the P. fraseri-tridentifer clade (Node 2). No such ancestral species is postulated to have occurred in the two equatorial areas, as discussed above. The level of Node 2 is unresolved with regard to four branches but nevertheless indicates the presence of a widespread ancestral biota in these basin areas. There is insufficient information in the model to hypothesize the order of fragmentation of the Philippine Sea (PHILIPP. SEA), the Great Australian Bight (GRT. AUSTR. BGT.), the Japanese Archipelago (JAPAN. ARCH.), and all Node 3 areas which encompass the central basins of the Indo-Australian region plus the two equatorial oceanic areas. There is limited evidence, in the form of the implied distribution of the ancestor of the P. matsubarai-ruggeri clade, that the Japanese Archipelago area may have been more recently connected to the Indo-Australian basins than was the Philippine Sea or the Great Australian Bight. That the oceanic areas from the Japanese Archipelago, the South China

Sea and southeastward to the Coral Sea have been more recently connected is corroborated by phylogeny and distribution of copepods of the stenothermic warmwater Labidocera pectinata species group (Fleminger, 1986; Fleminger et al., 1982). I infer from Fleminger's (1986) cladogram that a common ancestor of six descendant species which occur around the Japanese Archipelago, in the East and South China seas, off Sumatra, off western New Guinea, in the Arafura Sea and in the Coral Sea has undergone vicariant speciation in these areas. Unless there have been extinctions in the Philippine Sea and the Great Australian Bight these warmwater forms have never been present there.

Node 5 implies a large central region of historically united areas consisting of the South China Sea (S. CHINA SEA), northwestern Australian coast (NW. AUSTR.), eastern Indonesia (E. INDONESIA), the eastern Coral Sea (CORAL SEA (E)) and the Tasman Sea (TASMAN SEA). These areas were occupied by ancestral species of the P. aquavitus-danae clade, the P. unispinus-danae clade and to some extent by the P. spinifer-tridentifer clade.

The distributions of P. kiwiensis, P. aff. kiwiensis and P. ovatus of the meteori species group, which were not part of the formal analysis, are also relevant to Node 5. Polyipnus ovatus has been collected only in the South China Sea and may be endemic. Interrelationships of these taxa are not yet resolved but they are most similar to one another. If they do constitute a monophyletic group then an additional instance of vicariance between the South China Sea and southerly Indo-Australian areas is inferred.

The _P_. _spinifer_-_tridentifer_ clade is not represented in the Coral Sea (CORAL SEA (E)) or the Tasman Sea. This absence is interpreted as derived in this reconstruction and likely the result of extinction. Distribution of the ancestor of the _P_. _spinifer_-_tridentifer_ clade is also inconsistent regarding its inferred presence in the Great Australian Bight and the Japanese Archipelago. _A posteriori_ interpretation of this pattern indicates that _P_. _spinifer_ is primitively absent in the Japanese Archipelago and has reached there by northward dispersal/diffusion from the South China Sea. An ancestor of _P_. _tridentifer_ reached the Great Australian Bight also by dispersal and subsequently underwent speciation there (Type II speciation of Wiley and Mayden, 1985). Such dispersal is consistent with the hypothesis that the south coast of Australia was not suitable for these tropical/subtropical forms until relatively recent times.

By the middle to late Miocene the configuration of land and intervening seas of the Indo-Australian region was virtually as it is today, with the exception of the amount of continental area. An event of apparent major biogeographic importance did affect the Philippine/South China Sea area. At this time the Philippine Islands were not wholly formed and consisted mainly of an island arc. A broad deep water channel existed between there and Borneo to the southwest, an area now occupied by the island of Palawan. A section of southern China, the North Palawan Continental Terrane, was rifted free in the middle Oligocene and began drifting eastward through the South China Sea (Holloway, 1982; McCabe and Cole, 1989). In the late Miocene this exotic terrane collided with the Philippine arc resulting in a geologically composite group of islands (Audley-Charles, 1981) and closure of most deep-water circulation between the South China Sea and the Sulu Sea immediately to the south. The effect of the closure on deep-sea and probably some shallow water organisms was probably magnified by the return of world glaciation and sea level drops of 40 to 60 m between 7 and 5 Ma (Herman, 1986; Hoddell and Kennett, 1986). This event appears to explain vicariant patterns in the omphus, and possibly the meteori and spinosus species groups.

The South China Sea and adjacent basins constitutes a biotically distinctive area, with endemic species in a variety of other deep-sea fish groups; e.g. Himantolophidae, Lophiiformes (Bertelsen and Krefft, 1988), Monognathidae, Anguilliformes (Bertelsen and Nielsen, 1987) and Stomiidae, Stomiiformes (Gibbs et al., 1983). When phylogenies for these other groups become available it will be possible to test the hypothesis that a vicariant event between the Philippines and Borneo led to the subdivision of a deep-sea fauna that existed in the South China Basin and extended southwards into the Sulu Sea and southwards through many of the basins of eastern Indonesia (E. INDONESIA), the northwest coast of Australia (NW. AUSTR), the eastern Coral Sea (CORAL SEA (E)) and the Tasman Sea (TASMAN SEA). A common history for the latter four areas (Node 6) is supported by distribution patterns of *P. unispinus*, *P. aquavitus* and the ancestor of the *P. soelae-tridentifer* clade.

Eastern Indonesia and northwestern Australian areas are historically united by the presence of the descendant species *P. soelae* (Node 7). These closely juxtaposed areas probably maintain a degree of biotic similarity through the action of fluctuating equatorial counterflow (see van der Spoel and Schalk, 1988) which would tend to disperse the young stages of pelagic organisms.

Pleistocene glaciation also resulted in significant drops in sea level as well as in temperature. Fleminger (1986) hypothesized that this climatic event caused large scale extinctions of equatorial stenotherms in Wallacea (the interocean area of eastern Indonesia) in addition to vicariance. He suggested that a significant barrier to dispersal north of Australia was the result of reduced temperature and circulation. Changing sea level undoubtedly affected distribution in *Polyipnus*, but due to a lack of phylogenetic resolution this cannot be tested. Evidence of differentiation in *P. kiwiensis* between the Tasman Sea and off the northwest coast of Australia could be a result of such Pleistocene vicariance.

In the present model of Polyipnus biogeography, major vicariant patterns are largely congruent with events that predate the Pleistocene by several million years. Remodelling of distribution patterns undoubtedly has taken place during each of the post-Miocene glacial episodes. Fleminger (1986) inferred from sea level drop and equatorial sea temperature decrease that there was large-scale extinction of deep-water taxa in Wallacea. Occurrence of the endemic P. spinosus suggests that some refuges may have been present. Some of the more widely distributed species, such as P. meteori, P. aquavitus and P. unispinus, either sustained populations in refugia or recolonized the region from the unaffected parts of their ranges.

According to BPA, most of the oceanic areas of the Indo-Autralian region have associated with them uniquely derived characters or autapomorphies (listed in Table 7 by area). Autapomorphies in Parsimony Analysis imply the presence of species that have evolved in situ. Areas with such species are considered areas most likely to exhibit endemism in other groups of organisms. The implied presence of the ancestor of the P. stereope-spinosus clade in eastern Indonesia and the Japanese Archipelago leads to a different conclusion, regarding P. stereope. In the context of the consensus diagram (Figure 71) dispersal of such an ancestral species to the Japanese Archipelago with subsequent speciation of P. stereope (Type II speciation mode of Wiley and Mayden, 1985) is a more likely explanation than extinction of the ancestor in all remaining Node 2 areas following vicariant speciation.

One other apparently inconsistent aspect of this model is the occurrence of P. omphus in the equatorial Indian, western Pacific and eastern Indonesian areas but not in other Node 3 areas (i.e. South China Sea, northwestern Australia, eastern Coral Sea and the Tasman Sea). These areas are "missing" as a result of primitive absence or, as is quite possible with rarely-encountered oceanic organisms, collecting artifacts.

CONCLUSIONS

A morphological survey of *Polyipnus* specimens from about 30 major museum collection leads to the recognition of seven new species, bringing the total number in the genus to 29. Two recently described species, *P. paxtoni* Harold, 1989 and *P. danae* Harold, 1990, are included in the review of the genus.

Four monophyletic species groups are defined, following the criterion for recognition of taxa in phylogenetic systematics (Hennig, 1966; Wiley, 1981). The *P. meteori* species group consists of 5 species of which *P. ovatus* from the South China Sea is new. New material representing *P. meteori* expands the range eastward from the western Indian Ocean to include the Indo-Malayan Archipelago and the central equatorial Pacific. There are also new records of *P. matsubarai* (Japanese Archipelago and the northwestern Pacific), *P. ruggeri* (Tasman Sea) and *P. kiwiensis* (Tasman Sea); a population of the latter off the northwest coast of Australia originally reported by Paxton et al. (1989) shows slight differences from Tasman Sea representatives and is here referred to as *P.* aff. *kiwiensis*.

In the *P. asteroides* species group there are 6 species, including 2 that are new (*P. clarus* and *P. bruuni*) and *P. laternatus* (western North Atlantic) which is moved from the *laternatus* complex of Baird (1971). *Polyipnus asteroides*, previously considered a widely distributed western Atlantic species (Schultz, 1961, 1964; Baird, 1971), is restricted to the Caribbean Sea and the Greater Antilles. Almost all material previously referred to P. asteroides is attributed to P. clarus, a new species which occurs from the Caribbean through the Gulf of Mexico and the Gulf Stream as far north as the Scotian Shelf. New records of P. polli from the tropical eastern Atlantic are reported; its range now extends northwards from the Benguelan to the Mauritanian Upwelling regions. Polyipnus bruuni is described from a single specimen from the western Indian Ocean. New records of P. triphanos indicate that this highly variable species is widely distributed in the Indo-Australian region. Further study, based on more material, may reveal the presence of more than one species in this complex.

The P. omphus species group consists of 3 species previously of the laternatus complex (Baird, 1971) and one recently described species from the South China Sea (P. danae). New records show the range of P. omphus to include the Indo-Malayan region, in addition to the Indian and Pacific Oceans as reported by Baird (1971). The ranges of P. unispinus and P. aquavitus are nearly congruent and include many of the basins from south of the Philippines to the Tasman Sea.

The P. spinosus species group, consisting of species attributed to the spinosus species complex (Baird, 1971; Borodulina, 1979), now includes 14 species. Polyipnus asper (Andaman Sea) and P. soelae (Indo-West Australia) are new, *P. paxtoni* Harold 1989 (Coral Sea) was recently described as a member of the *spinosus* complex and *P. fraseri* (Philippine Sea) was resurrected by Harold (1990b). The status of the remaining species are affected very little by this revision. These species tend to have restrictive geographic distributions: *P. elongatus* (Coral Sea), *P. inermis* (Sala-y-Gomez Ridge, southeastern Pacific), *P. nuttingi* (Hawaiian Islands), *P. oluolus* (Marshall Islands), *P. parini* (western Pacific), *P. spinifer* (South China Sea to Japanese Archipelago), *P. spinosus* (eastern Indonesia) and *P. stereope* (Japanese Archipelago). The range of *P. indicus*, previously restricted to the southeast coast of Africa, is here expanded northward as far as the Gulf of Aden.

Cleared and stained specimens for 23 species were studied and a suite of morphological characters was delimited for cladistic analysis. Relationships were reconstructed using the outgroup comparison method of polarizing characters. The six species that could not be studied histologically were fitted to the initial cladogram using external synapomorphies.

Monophyly of the genus and 4 species groups was indicated by uniquely derived characters, although one or more inconsistent or homoplastic characters were present at many levels. In particular, reductions in spines, scale denticles, AC photophore elevations and counts, and body size were noted. Such reductive characters may be paedomorphic and derived. In a study of sternoptychid relationships, Weitzman (1974) proposed a series of apomorphies of Polyipnus. These were based only on P. aquavitus, P. asteroides, P. laternatus and P. tridentifer. The present expanded study of the genus largely corroborates Weitzman's findings and adds some new characters.

Baird (1971) divided the genus into species complexes. These were based on overall similarity and not uniquely derived features. The four species groups recognized in the present study are based on shared derived osteological and photophore characters. Many external characters were interpreted, resulting in a well-resolved phylogeny which even included species for which internal osteological characters were not available. Baird's (1971) asteroides and spinosus species complexes were found generally to be monophyletic, but P. laternatus appears to be more closely related to members of the asteroides species group (a subgroup of Baird's asteroides complex) than to the omphus species group (the remaining members of Baird's laternatus complex).

The patterns of endemism in Polyipnus are of particular biogeographic interest in the tropical Indo-Pacific. An explanation of these patterns was a major goal of this study. A vicariance approach (Wiley, 1988a, b) to historical biogeography was adopted. Such a study requires a hypothesis of phylogenetic relationships (sensu Hennig, 1966) as the framework for proposing a sequence of events which led to subdivision of geographic areas, and resultant vicariant speciation.

Area cladograms constructed from taxon cladograms for each of the species groups were compared and, where possible, the shared elements of branching patterns were combined to form a general explanation of vicariance in the Indo-Australian region. A computational technique (Brooks Parsimony Analysis, Wiley, 1988a, b; Brooks, 1990) was used to generate a consensus of the area cladograms for the omphus and meteori species groups, and the P. paxtoni-tridentifer clade of the spinosus group. Historical inferences were also drawn from the asteroides species group and the lower branches of the spinosus group cladogram, taxa which do not have endemic species in the Indo-Australian region.

The four Polyipnus species groups have broadly overlapping generalized distributions, a reflection of widespread ancestral forms in the early to middle Tertiary.

Ancestors of the asteroides species group were widespread in western and eastern Tethys, from the Caribbean area to Indonesia. Subdivision and vicariant speciation was effected by a chronological series of events causing diminished equatorial current flow in the early Miocene, the late Miocene and the early Pliocene. These events were the collision of the Australian and Asian Plates, closure of Tethys in the Mediterranean area and the emergence of the Panamanian isthmus.

Ancestral forms to the spinosus species group were present in the proto-Indian Ocean and eastwards onto the Pacific Plate possibly as early as the Paleocene (60 Ma). This rather early date is inferred from subdivision of the Indian Ocean into eastern and western basins during the traversal of the Indian subcontinent. Diversion of equatorial flow southwards by this obstruction, however, was still occurring in the late Oligocene (about 25 Ma), placing a minimum age on the event.

A sequence of tectonic/climatological events beginning in the early Miocene (20 to 25 Ma) caused vicariant speciation in the Indo-Australian region. Closure of the seaway between the forming Indo-Malayan Archipelago and the Australian Plate isolated the eastern Indian Ocean from Indo-Australian basins. Lowered sea levels effectively cut off connections between the Coral Sea and the Indo-Australian area. In the latter region widespread north-south ancestral ranges were maintained until the late Miocene when deep water circulation between the South China Sea and the Sulu Sea was disrupted by arrival from South China of the North Palawan Continental Terrane. This accounts for the presence there of South China Sea endemics in Polyipnus and possibly in other groups of deep-sea fishes and zooplankton.

This analysis suggests that peripheral areas like the Great Australian Bight, and possibly the Japanese Archipelago, were too cold in pre-Miocene times to have supported Polyipnus species and were later invaded by ancestral forms.

Generality of vicariant mechanisms proposed here are largely corroborated by phylogenetic/distributional patterns from other taxonomic groups, but such data are still of limited availability and occasionally unreliable. One goal for future research will be to establish phylogenies for other groups of fishes in order to test the hypotheses presented here.

TABLE 1.-Frequency distribution of number of dorsal fin rays in the species of *Polyipnus*.

	Number of Dorsal Fin Rays						
Species	10	11	12	13	14	15	16
kiwiensis			5				
aff. *kiwiensis*		5	2				
matsubarai			7	2			
meteori		4	14				
ovatus			1				
ruggeri			4				
asteroides				1	10	5	1
bruuni			1				
clarus					3	10	3
laternatus[c]			4	10	11	1	
polli					1	10	1
triphanos		12	16				
aff. *triphanos*				1			
aquavitus			17	20	2		
danae		1	1	3			
omphus					8	3	
unispinus		3	12	2			
asper			15	14			
elongatus				4	1		
fraseri	2						
indicus			1	10	4		
inermis			6	X[a]			
nuttingi			2	19	4		
oluolus					1		
parini			1	1			
paxtoni		2	6	3			
soelae			11	15			
spinifer			6	19	2		
spinosus			1	1			
spinosus[c]			1	15	4	1	
stereope				6[c]			
tridentifer				9	9		

Literature values from: a Borodulina, 1981; b Baird, 1971; c Schultz, 1961; d Borodulina, 1979; e Schultz, 1938

TABLE 2.-Frequency distribution of number of anal fin rays in the species of *Polyipnus*.

	Number of Anal Fin Rays									
Species	11	12	13	14	15	16	17	18	19	20
kiwiensis					1	2	2			
aff. *kiwiensis*						1	6			
matsubarai							10			
meteori						8	7			
ovatus								1		
ruggeri							3	1		
asteroides						10	7			
bruuni					1					
clarus						9	8			
laternatus^c					2	15	9	1		
polli						8	4			
triphanos					1	3	7	4		
aff. *triphanos*								1		
aquavitus				2	19	5				
danae				1	1	2		1		
omphus						3	5	1		
unispinus			8	7	1					
asper					21	7	1			
elongatus							1	1	2	1
fraseri	1	1								
indicus					8	7				
inermis^a						5	1			
nuttingi					10	13	2			
oluolus				1						
parini							2			
paxtoni					2	1	6	2		
soelae					12	12	2			
spinifer					6	15	5	2		
spinosus					2					
spinosus^c				2	11	5	4			
stereope				2	4					
tridentifer^d						7	15	2		

a, b, c, d, e defined in Table 1

TABLE 3.-Frequency distribution of number of pectoral fin rays in the species of *Polyipnus*.

Species	11	12	13	14	15	16
	Number of Pectoral Fin Rays					
kiwiensis					3	1
aff. *kiwiensis*			1	4	2	
matsubarai		1	4	4		
meteori				11	3	
ovatus				1		
ruggeri				4		
asteroides				12	3	
bruuni				1		
clarus			2	10	2	
laternatus[c]		1	6	10		
polli			9			
triphanos			6	7		
aff. *triphanos*				1		
aquavitus		17	6	1		
danae	3	2	2			
omphus			2	9		
unispinus		8	6			
asper		15	13			
elongatus		1	4			
fraseri				2		
indicus		2	6	7		
inermis[e]				4	4	
nuttingi		3	9	2		
oluolus			1			
parini				1		1
paxtoni			4	7		
soelae		8	19			
spinifer			19	9		
spinosus			1	1		
spinosus[c]			6	5	1	
stereope[c]			6	16	14	1
tridentifer		4	19	1		

a, b, c, d, e defined in Table 1

TABLE 4.-Frequency distribution of number of AC[B] photophores in the species of *Polyipnus* (specimens > 25 mm SL except *bruuni* holotype).

	Number of AC[B] Photophores										
Species	4	5	6	7	8	9	10	11	12	13	14
kiwiensis					1	6	X[b]				
aff. *kiwiensis*						7					
matsubarai					1	9					
meteori			1	5	2						
ovatus						1					
ruggeri					3	1					
asteroides					1	15	1				
bruuni				1							
clarus					2	13	2				
laternatus[c]							1	17	10	3	
polli				10	2						
triphanos				1	3	9	3				
aff. *triphanos*					1						
aquavitus						5	13	1			
danae								3	4		
omphus							3	4	1		
unispinus					4[e]	7	5				
asper						21	8				
elongatus										3	2
fraseri	2										
indicus					14	4					
inermis[a]					4	3	1				
nuttingi				1	22	6					
oluolus			1								
parini							1	1			
paxtoni							2	8	1		
soelae								11	12	3	
spinifer								8	13	5	
spinosus							2				
spinosus[c]						3	14	2			
stereope						2	5	1			
tridentifer[d]							1	12	24	23	3

a, b, c, d, e defined in Table 1

TABLE 5.-Frequency distribution of number of vertebrae in the species of *Polyipnus*.

	Number of Vertebrae						
Species	30	31	32	33	34	35	36
kiwiensis			X[b]	2	X[b]		
matsubarai				5			
meteori				5			
ovatus				1			
ruggeri				1			
asteroides			2				
bruuni				1			
clarus		2	2	2			
laternatus[c]			3	1			
polli			1	1			
triphanos		1		6			
aff. *triphanos*				1			
aquavitus		1		1	3	1	
danae							2
omphus				2	2		
unispinus[c]						1	9
asper				2			
elongatus						2	
fraseri		1	1				
indicus				3	1		
inermis					1		
nuttingi[c]				24	3		
oluolus				1			
parini					2		
paxtoni				1	2	1	
soelae				2	2		
spinifer				2	3		
spinosus			1	1			
spinosus[c]				8	1		
stereope[c]				3			
tridentifer[d]					4	1	

d, c, d defined in Table 1

TABLE 6. Frequency distribution of the number of gill rakers on the first branchial arch for *Polyipnus* species.

Species	Number of Gill Rakers																			
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
kiwiensis					1	3	1													
aff. *kiwiensis*					5	2														
matsubarai												6	1	2						
meteori			1	2	1	1	7	1												
ovatus								1												
ruggeri							2	2												
asteroides										1	2	1	7	4						
bruuni								1												
clarus									6	6	8									
laternatus						1	5	4	8	1[c]	2[c]	1[c]								
polli										6	4	2								
triphanos			1	4	12	6	1	4												
aff. *triphanos*										1										
aquavitus		1	5	28	2															
danae		3	4																	
omphus							1	3	4	2	1									
unispinus	15	2																		
asper							6	11	9	2										
elongatus												1	2	1						
fraseri									1	1										
indicus									2	7	1									
inermis													4	2	X[a]	X[a]				
nuttingi										1	3	9	11	3						
oluolus									1											
parini																		1		1
paxtoni													4	2						
soelae										10	7	7	2							
spinifer									1	2	3	5	13	2						
spinosus								1	1											
spinosus[c]							4	8	3											
stereope											1	1								
stereope[c]											1	6	8	11	5	6	3			
tridentifer[d]									1	4	14	13	1							

a, c, d defined in Table 1

TABLE 7.-Summary of biogeographic inferences drawn from consensus area cladogram of Indo-Pacific oceanic areas, Figure 71. Species names joined by hyphens indicate common ancestors of clades as implied by original cladograms (Figures 51, 56, 62 and 65). Letters in parentheses indicate inconsistency, as defined for homoplastic characters in phylogenetic analysis.

Node/Oceanic Area		Inference
1		*P. elongatus*-*tridentifer* ancestor
		P. paxtoni-*tridentifer* ancestor
2	(r)	*P. fraseri*-*tridentifer* ancestor
3	(r)	*P. meteori*-*ruggeri* ancestor
		P. omphus species group ancestor
	(c)	*P. matsubarai*-*ruggeri* ancestor
4	(R)	extinction of *P. paxtoni*-*tridentifer* ancestor
5		*P. aquavitus*-*danae* ancestor
		P. unispinus-*danae* ancestor
	(R)	extinction of *P. omphus*
	(rc)	*P. spinifer*-*tridentifer* ancestor
6		*P. unispinus*
	(r)	*P. aquavitus*
	(c)	*P. soelae*-*tridentifer* ancestor
7		*P. soelae*
8	(R)	extinction of *P. spinifer*-*tridentifer* ancestor
	(R)	extinction of *P. meteori*-*ruggeri* ancestor
TASMAN SEA		*P. ruggeri*
GRT. AUSTR. BGT.		*P. tridentifer*
	(c)	dispersal of *P. soelae*-*tridentifer* ancestor
E. INDONESIA		*P. spinosus*
	(c)	*P. spinosus*-*stereope* ancestor
	(l)	reinvasion of *P. omphus*
NW. AUSTR.	(r)	*P. aquavitus* extinction or not collected
S. CHINA SEA		*P. danae*
	(c)	*P. spinifer*
JAPAN ARCH.		*P. matsubarai*
		P. stereope
	(c)	*P. spinifer*
	(c)	*P. stereope*-*spinosus* ancestor
	(c)	*P. spinifer*-*tridentifer* ancestor
CORAL SEA (W)		*P. paxtoni*
		P. elongatus
CORAL SEA (E)	(r)	extinction of *P. meteori*-*ruggeri* ancestor
PHILIPP. SEA		*P. fraseri*

FIGURE 1.-Photophores and other external features of Polyipnus species, left side. AFPS, anal-fin pterygiophore spine. Photophore terminology: AC, ventral and extending from anal-fin origin to caudal-fin base, subdivided into AC[A] (='supra-anal'), AC[B] (='anal') and AC[C] (='subcaudal'); BR, photophores on branchiostegal membranes; OP, photophores associated with the opercular bones; ORB, photophores associated with the orbit; OV, flank photophores between operculum and pelvic-fin base, subdivided into anterior OV[A] (='suprapectoral') and posterior OV[B] (='supra-abdominal'); VAV, ventral photophores between the pelvic- and anal-fin origins (='preanal')..

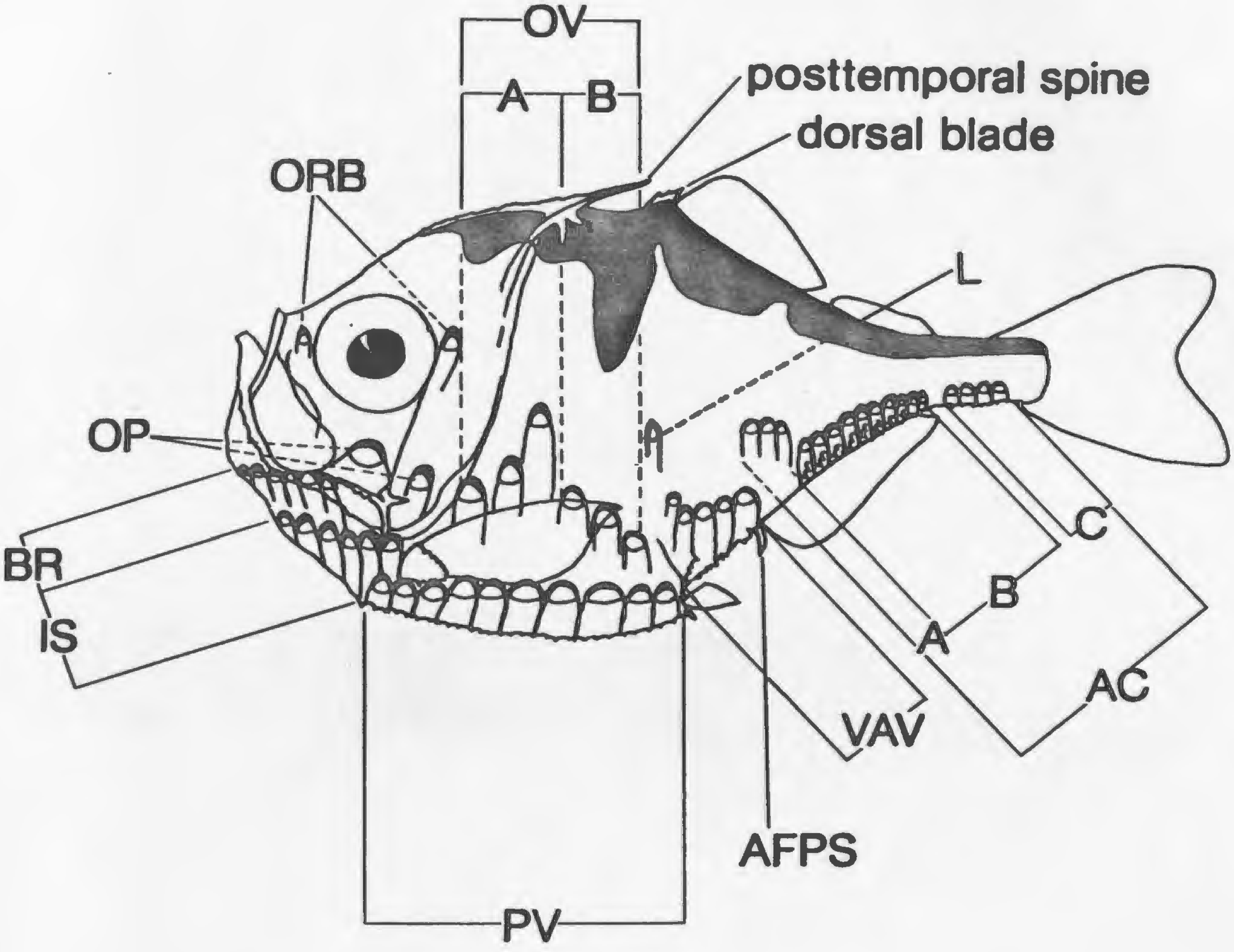

OV
A
B
posttemporal spine
dorsal blade
ORB
L
OP
BR
IS
C
B
A
AC
VAV
AFPS
PV

FIGURE 2.-Configurations of AC[A] photophores and their topographical relationships to AC[B], left side: A, AC[A] 1+1+1, horizontal with third joined to first AC[B] (e.g. *P. indicus*); B, AC[A] 1+1+1, horizontal with third not joined to AC[B] (e.g. *P. omphus*); C, 1+(2) with second and third united and highly elevated (e.g. *P. asteroides*); D, 1+1+1, increasing in elevation anterior to posterior, third highly elevated relative to first AC[B] (e.g. *P. meteori*); E, AC[A] (3), horizontal and united but not joined to first AC[B] (e.g. *P. bruuni*).

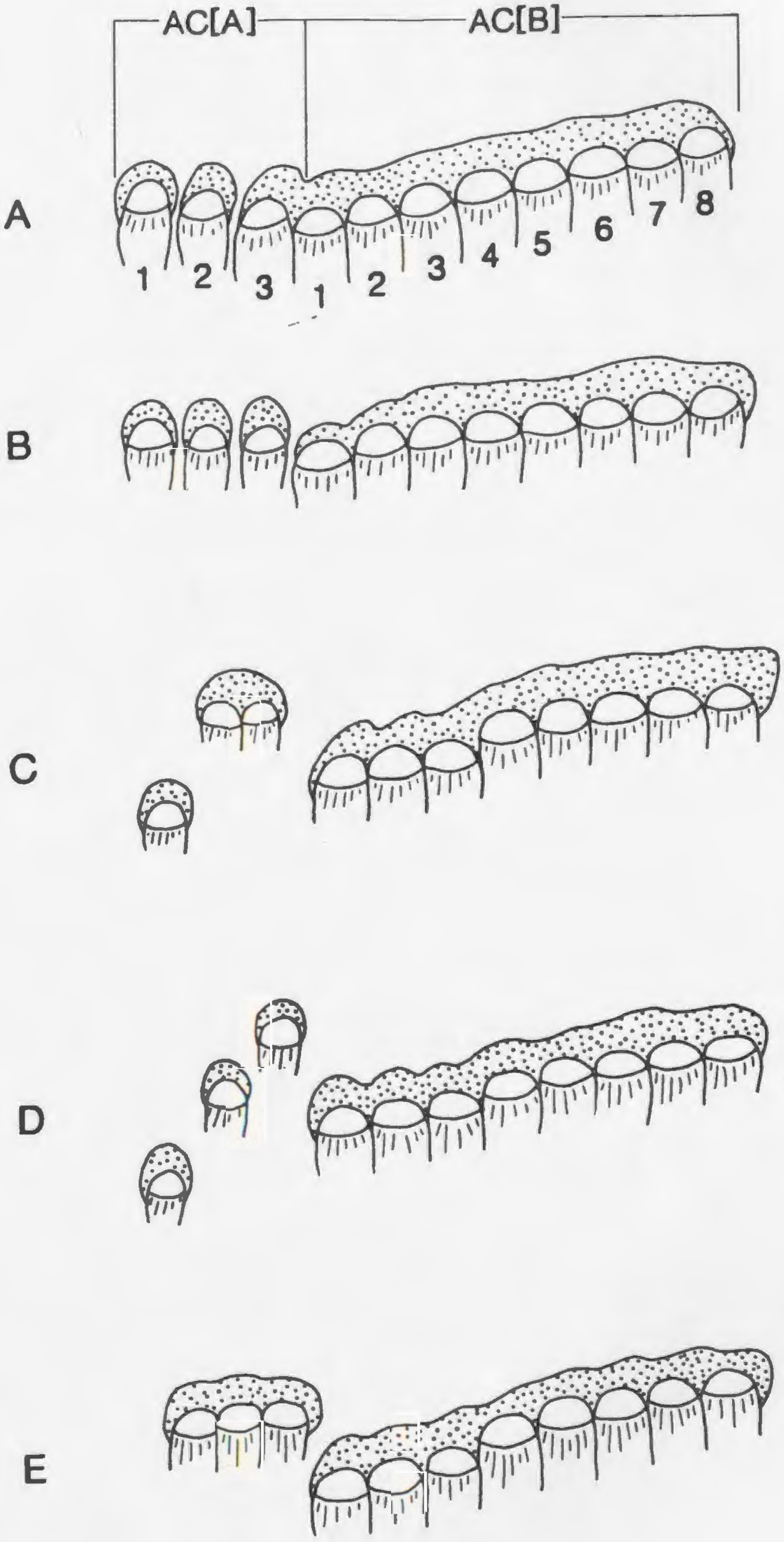

AC[A]
AC[B]
A
1
2
3
1
2
3
4
5
6
7
8
B
C
D
E

FIGURE 3.-Photophore denticulation and spacing, left side: A, ventral margin with numerous denticles; B, ventral margin smooth, nondenticulate; C, ventral margin with triangular margin and apical denticle(s); D, photophores separated by broad gaps; E, photophores compact, not separated by broad gaps.

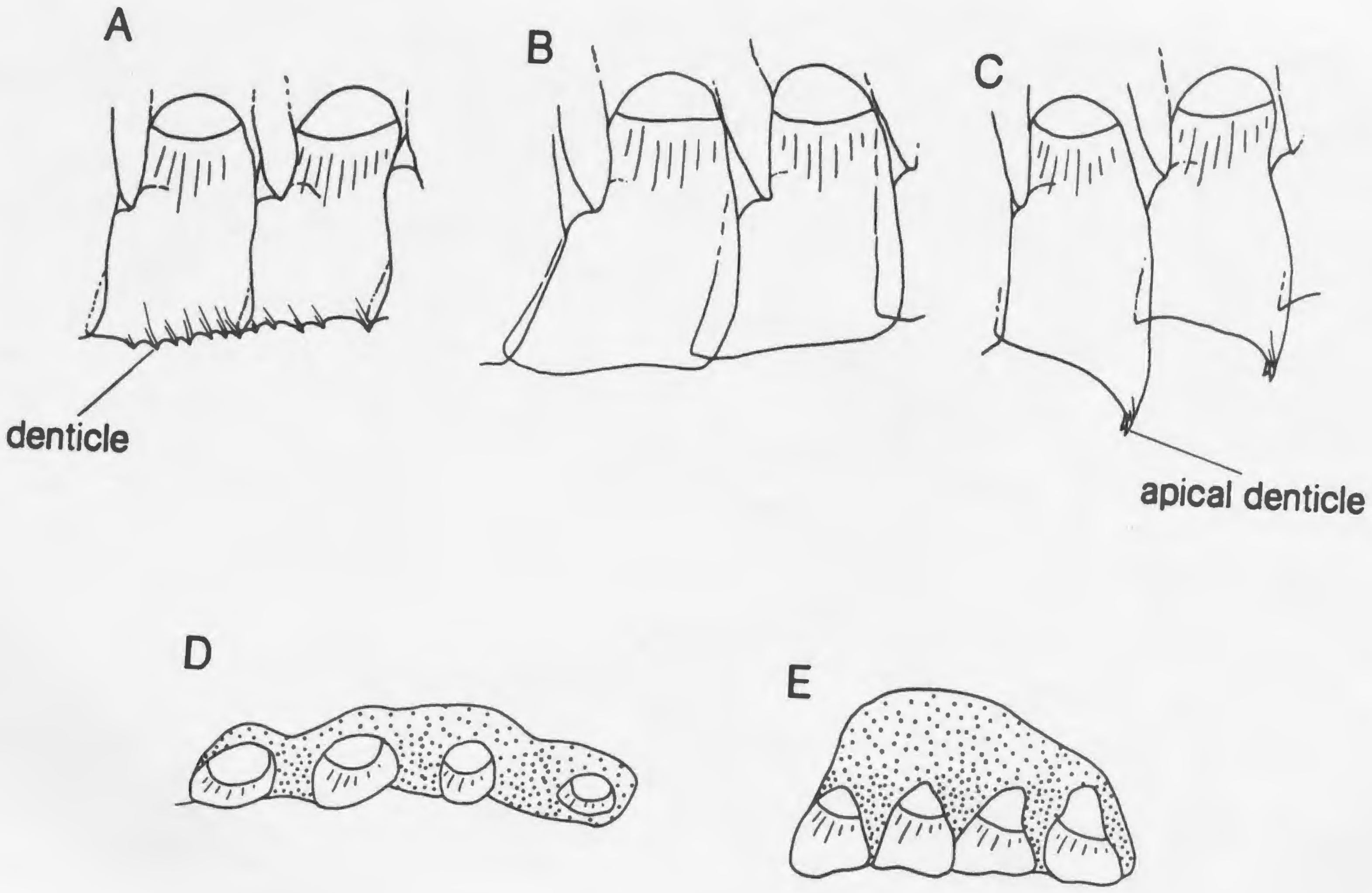

A
B
C
denticle
apical denticle
D
E

FIGURE 4.-Posttemporal spine configurations and terminology, left side: A, three spines, d=dorsal, m=median, v=ventral; B, two spines, b=basal; C, single spine with anterodorsal barb.

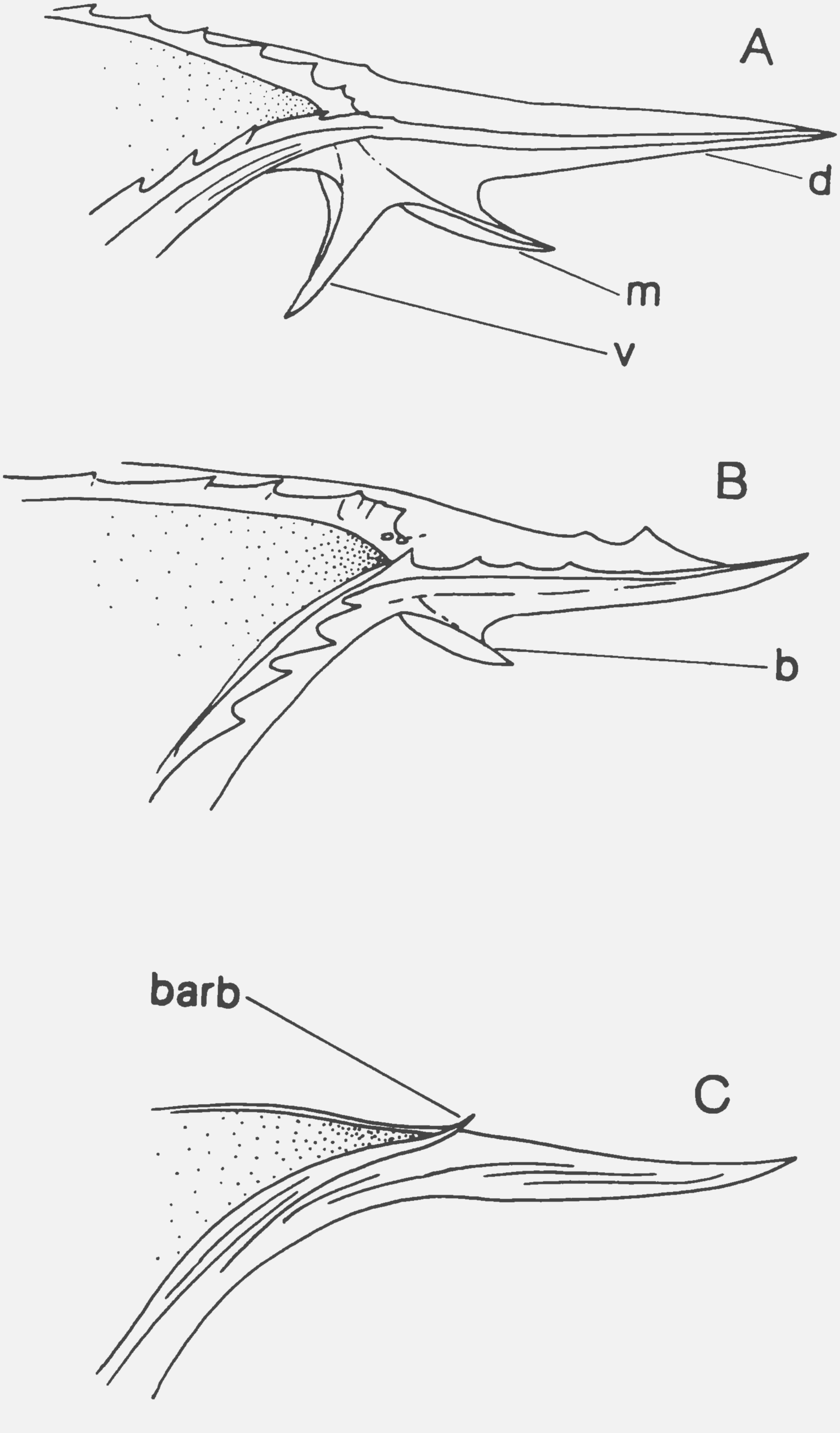

A
d
m
v
B
b
barb
C

FIGURE 5.-Terminology of preoperculum and associated spines and external longitudinal keels of frontal and parietal bones, left side: A, free ventral preopercular spine. Preopercular spines: VPS=ventral, PPS=posterior, DPS=dorsal; B, VPS reduced and embedded within distal lamella of preopercle; C, longitudinal parietal keel continuous with frontal keel: PLFK=primary longitudinal frontal keel, LPK=longitudinal parietal keel; D, LPK discontinuous, differentiated posteriorly as two opposed medial spines: PKS=parietal keel spines.

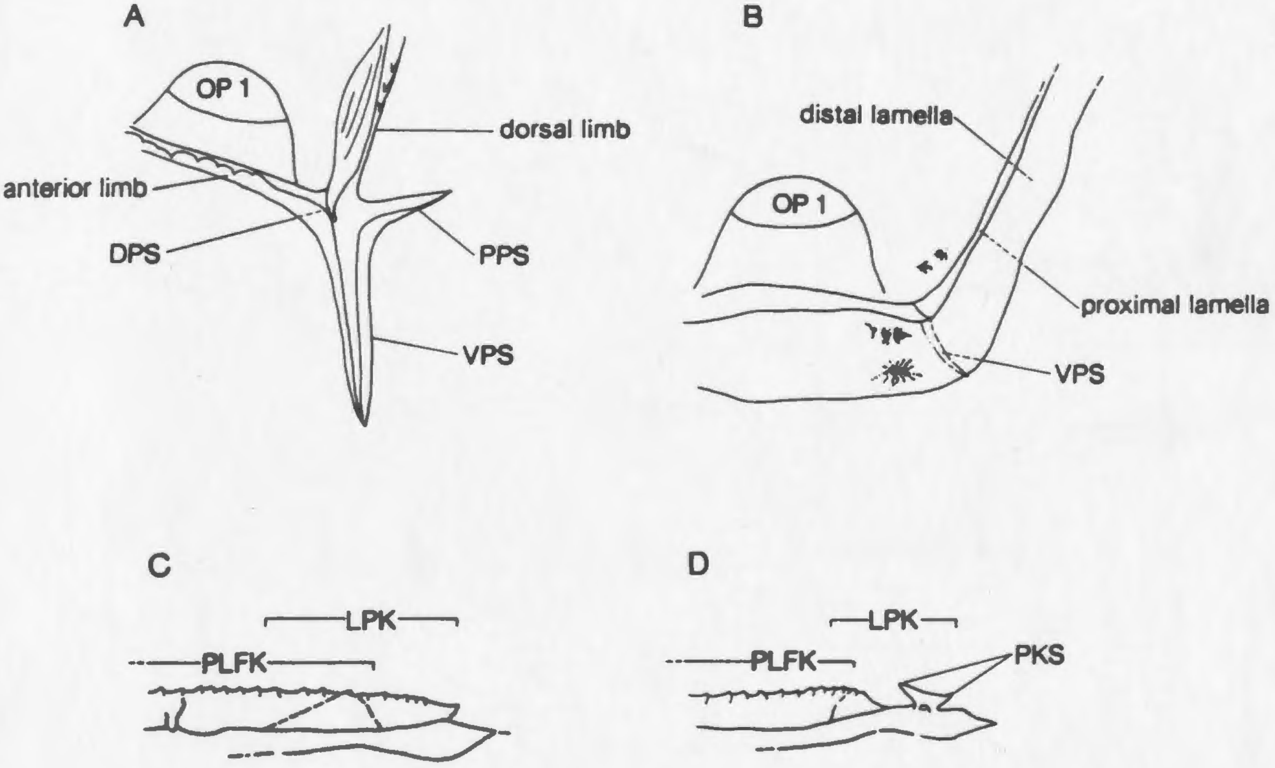

A
OP 1
dorsal limb
anterior limb
DPS
PPS
VPS
B
distal lamella
OP 1
proximal lamella
VPS
C
LPK
PLFK
D
LPK
PLFK
PKS

FIGURE 6.-*Polyipnus* *kiwiensis*, AMS I.24501-004, 60.3 mm.

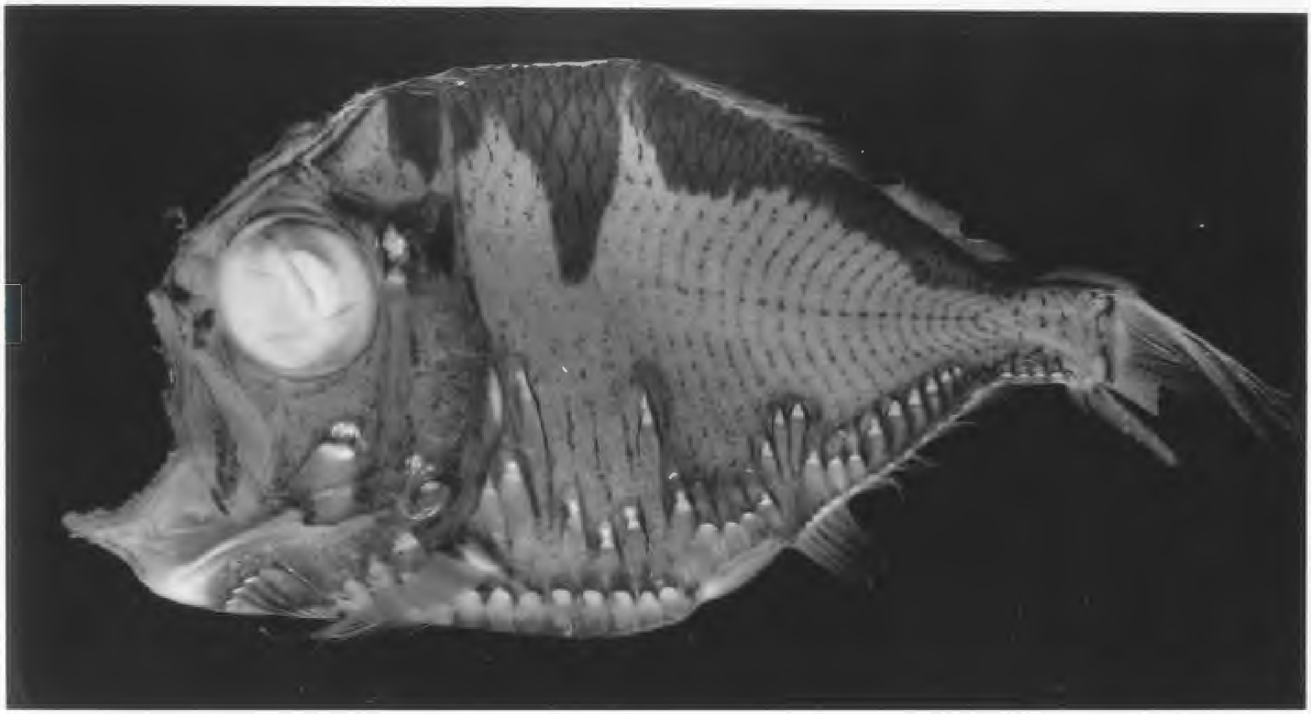


FIGURE 7.-Collection station localities for *P*. *kiwiensis*, *P*. aff. *kiwiensis* and *P*. *ovatus*, *P*. *meteori* species group.

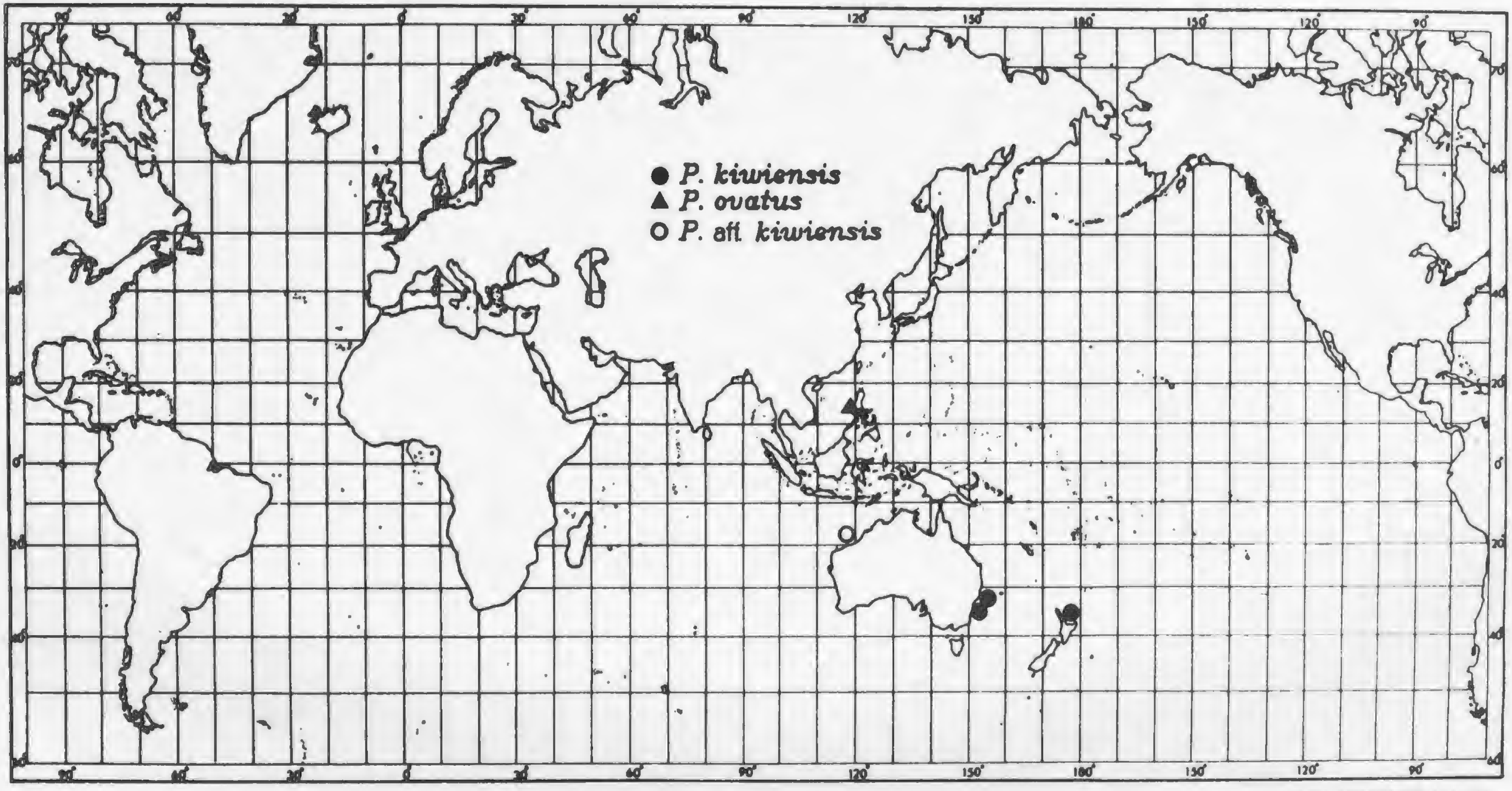

● P. kiwiensis
▲ P. ovatus
○ P. aff. kiwiensis
90°
60°
30°
0°
30°
60°
90°
120°
150°
180°
150°
120°
90°

FIGURE 8.-*Polyipnus matsubarai*, ASH 88192, 42.6 mm.

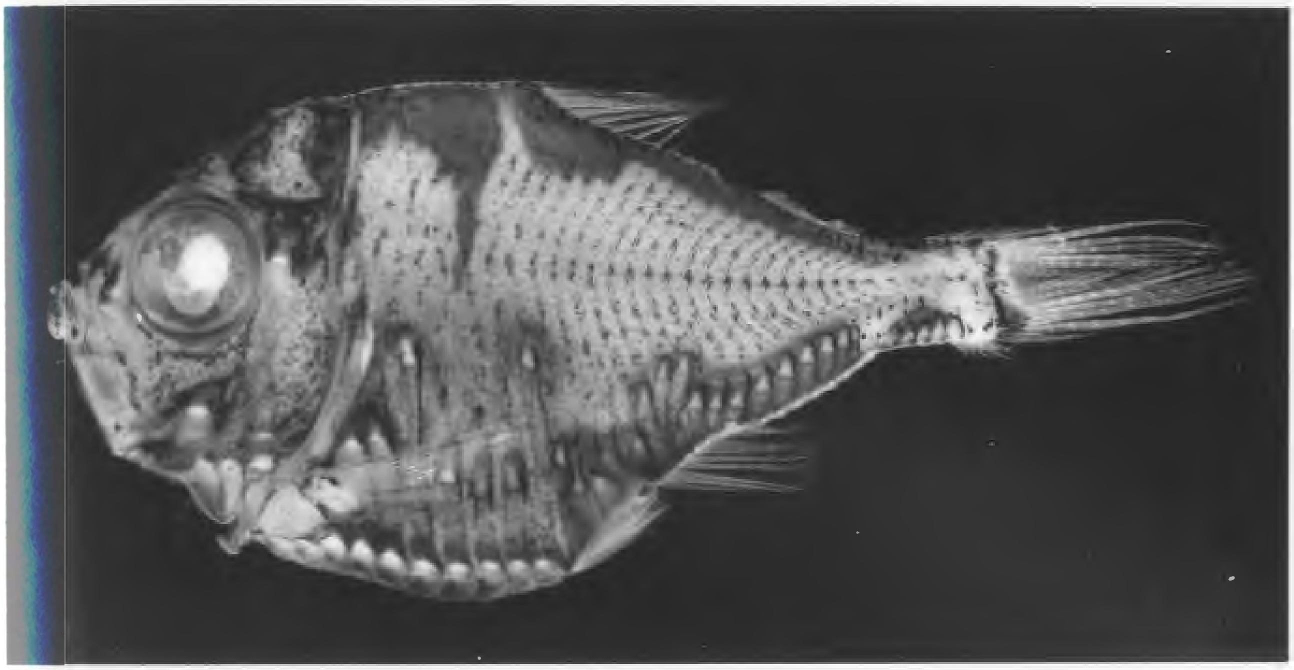


FIGURE 9.-Collection station localities for *P*. *meteori*, *P*. *ruggeri* and *P*. *matsubarai*, *P*. *meteori* species group.

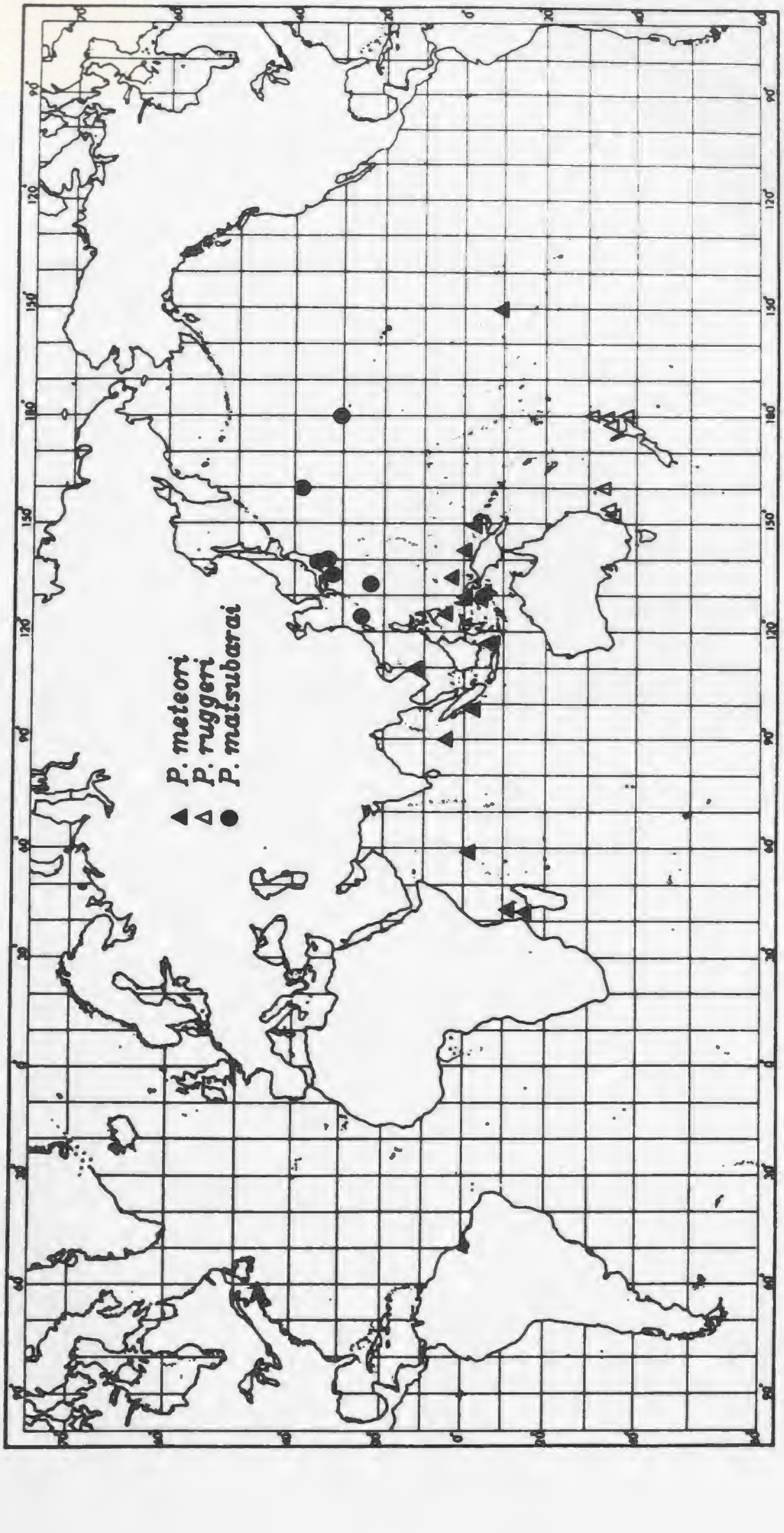

▲ P. meteori
△ P. ruggeri
● P. matsubarai

FIGURE 10.-*Polyipnus meteori*, LACM uncat., R/V *Alpha Helix* Sta. 108, 52.0 mm.

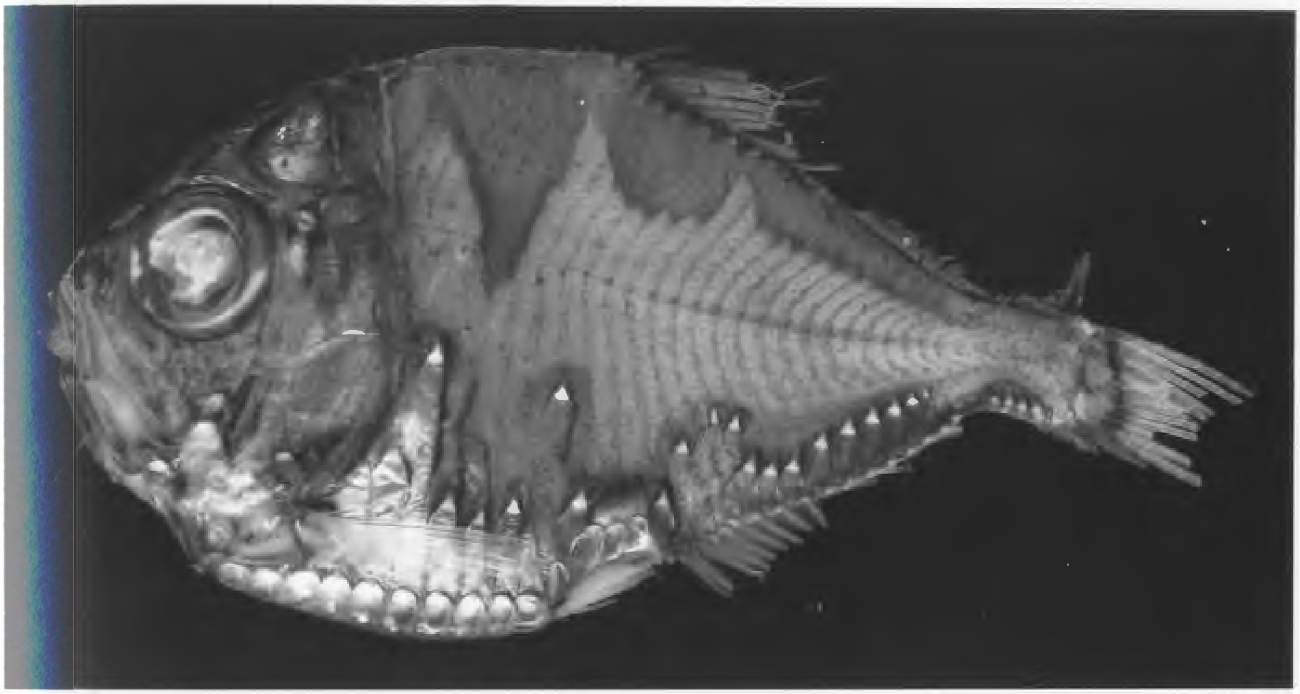


FIGURE 11.-*Polyipnus ovatus*, holotype, CAS 33347, 47.0 mm.

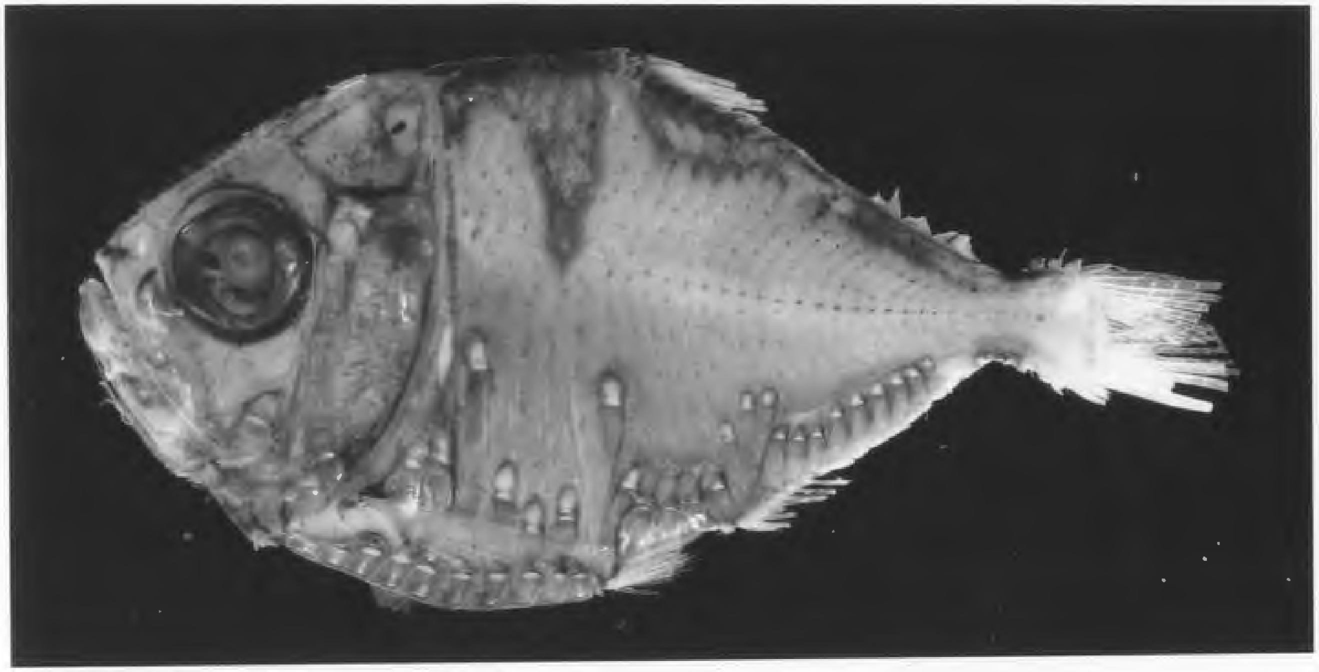


FIGURE 12.-*Polyipnus* *ruggeri*, AMS I.20066-014, 49.1 mm.

FIGURE 13.-*Polyipnus* *asteroides*, CAS 61111, 48.6 mm.

FIGURE 14.-Collection station localities for *P. asteroides* and *P. clarus*, *P. asteroides* species group.

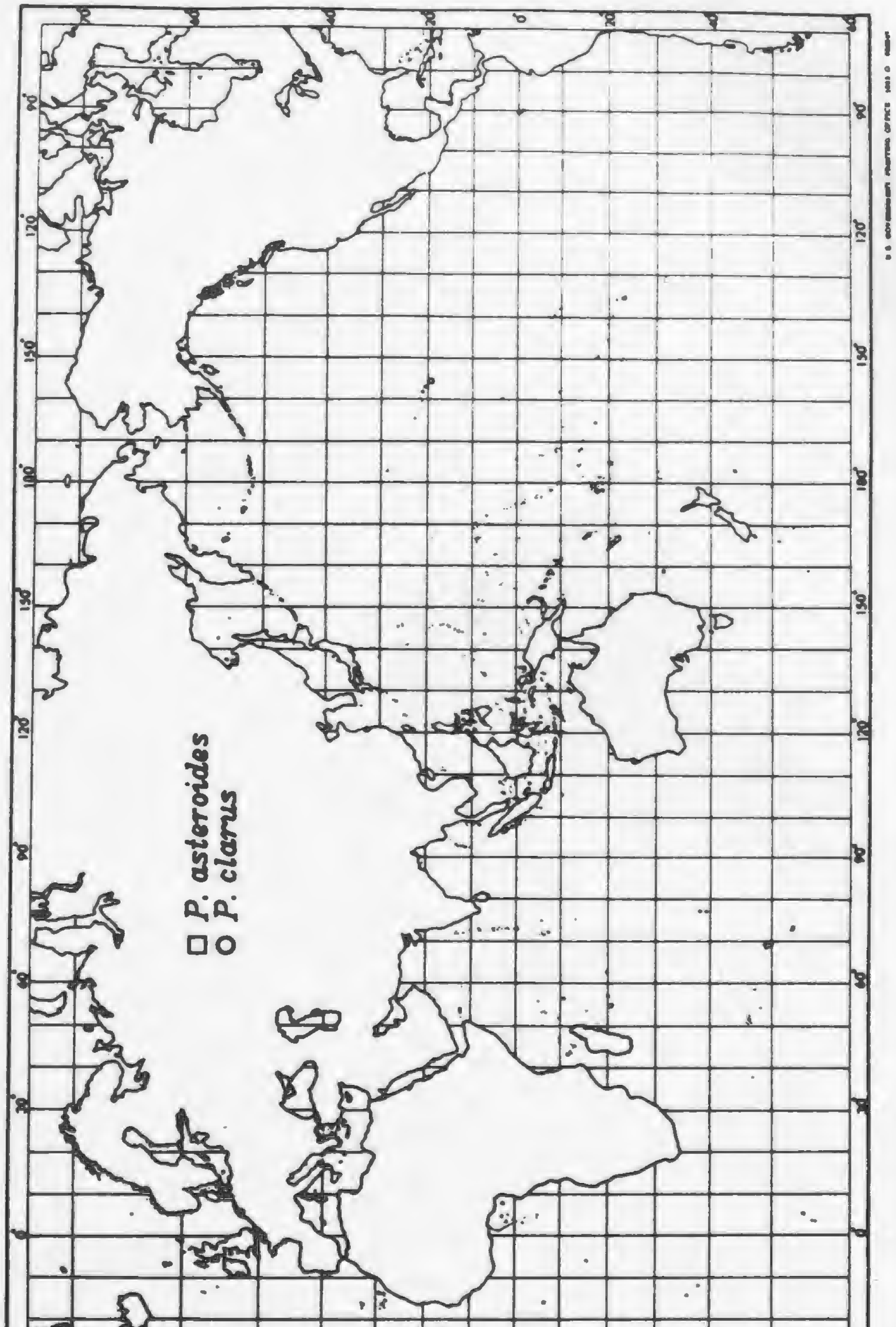

□ P. asteroides
○ P. clarus

FIGURE 15.-*Polyipnus bruuni*, holotype, USNM 298923, 19.5 mm.

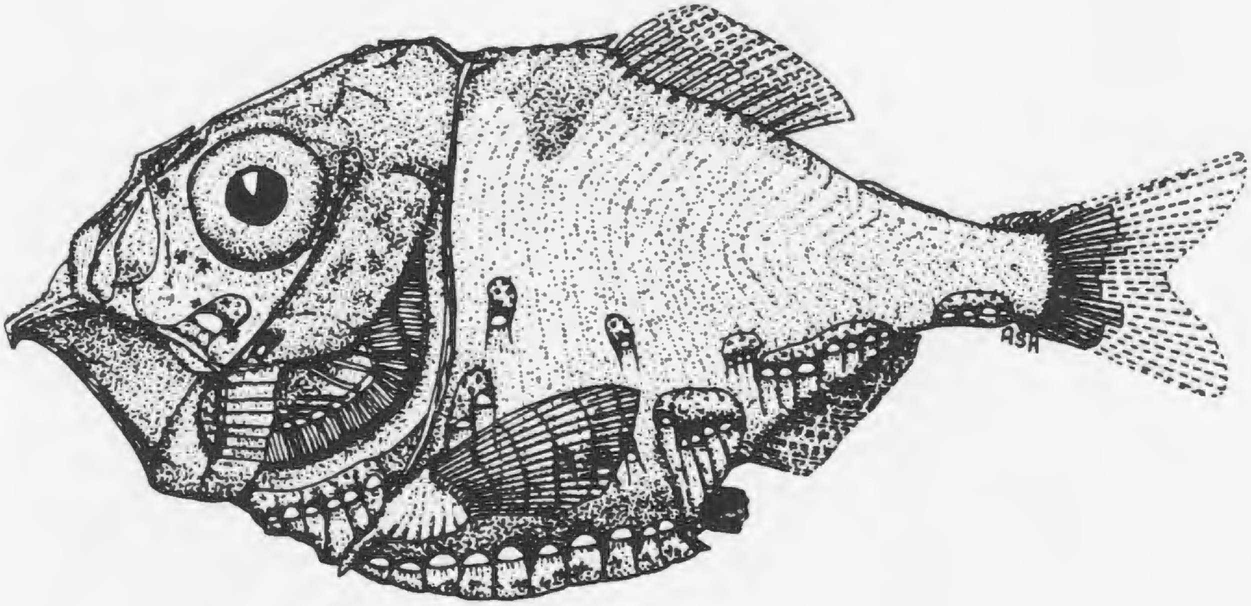

ASH

FIGURE 16.-Collection station localities for *P*. *triphanos*, *P*. aff. *triphanos*, *P*. *polli* and *P*. *bruuni*, *P*. *asteroides* species group.

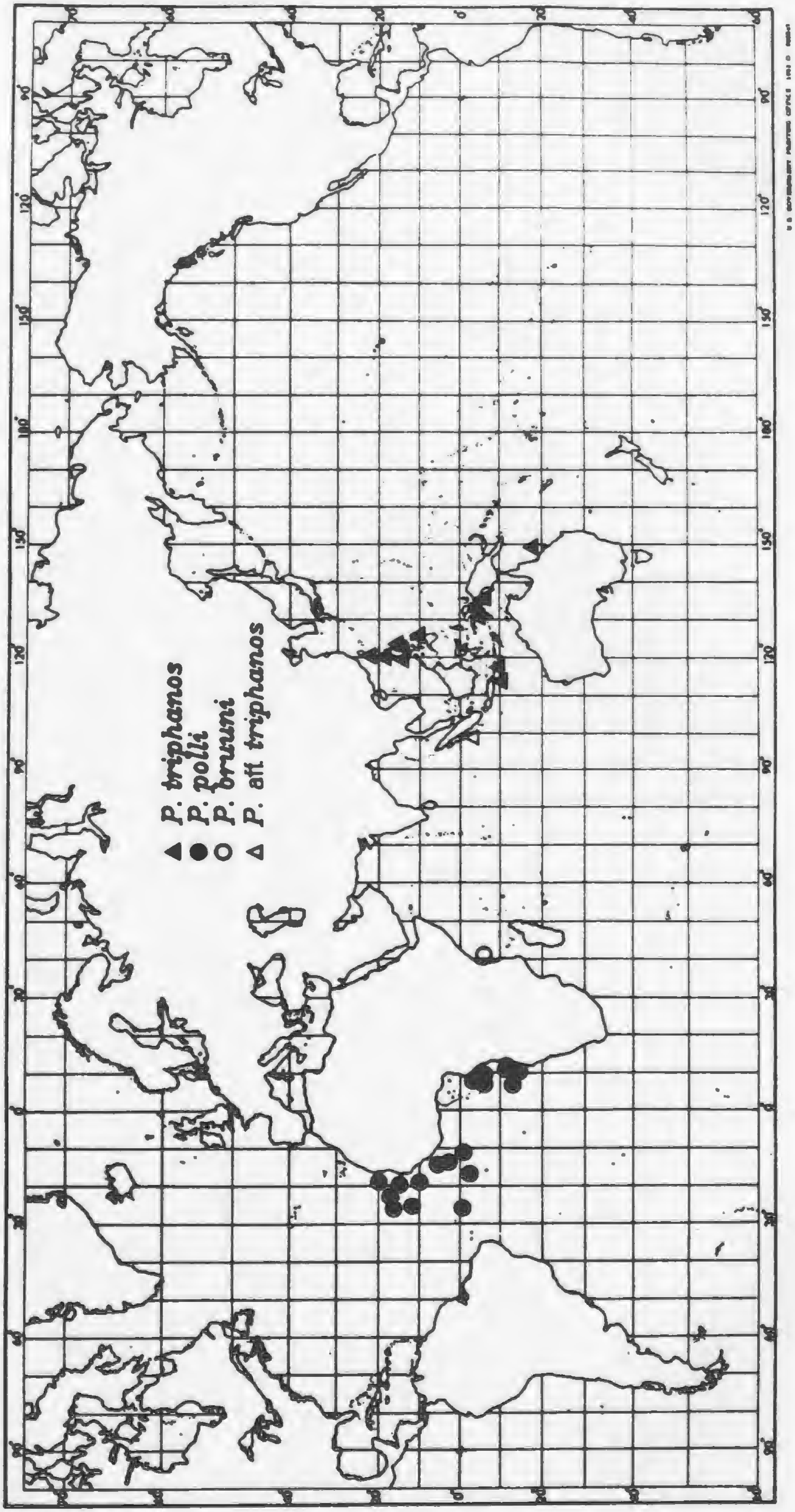

▲ P. triphanos
● P. pollii
○ P. bruuni
△ P. aff triphanos

FIGURE 17.-*Polyipnus clarus*, holotype, USNM 273283, 43.6 mm.

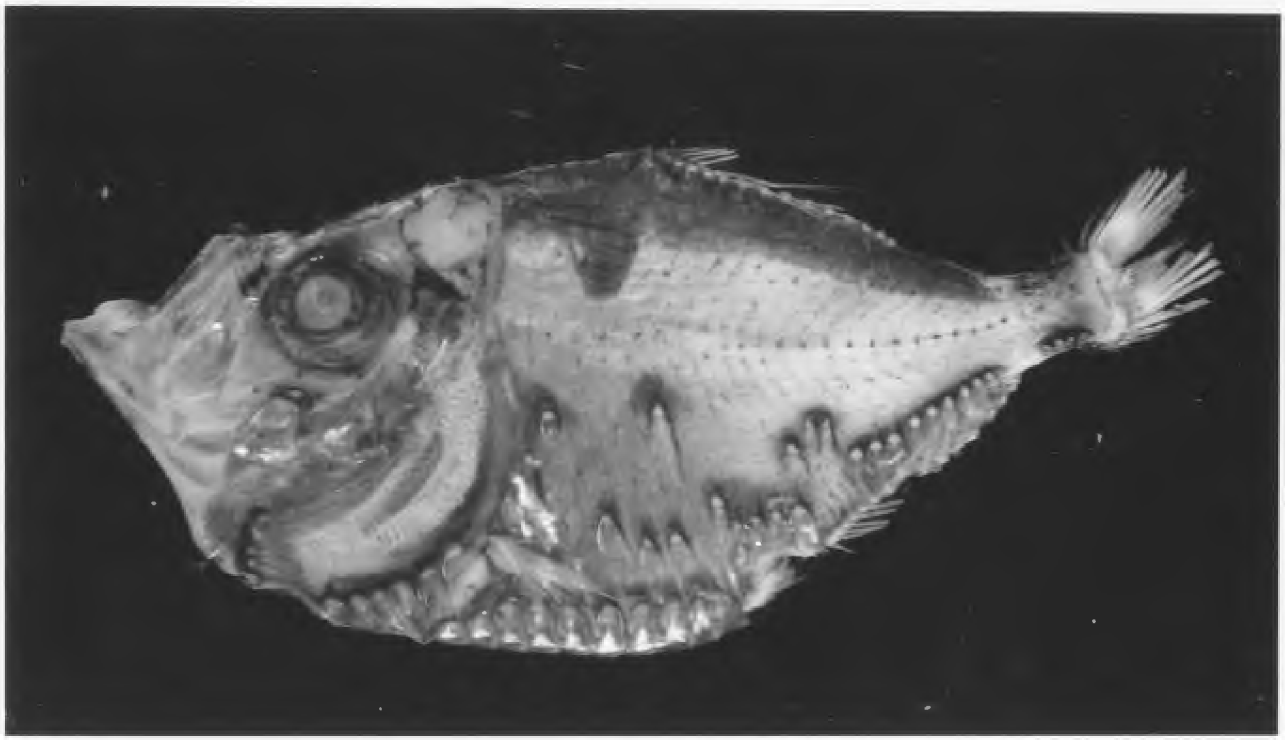


FIGURE 18.-*Polyipnus laternatus*, MCZ 40575, 31.1 mm.

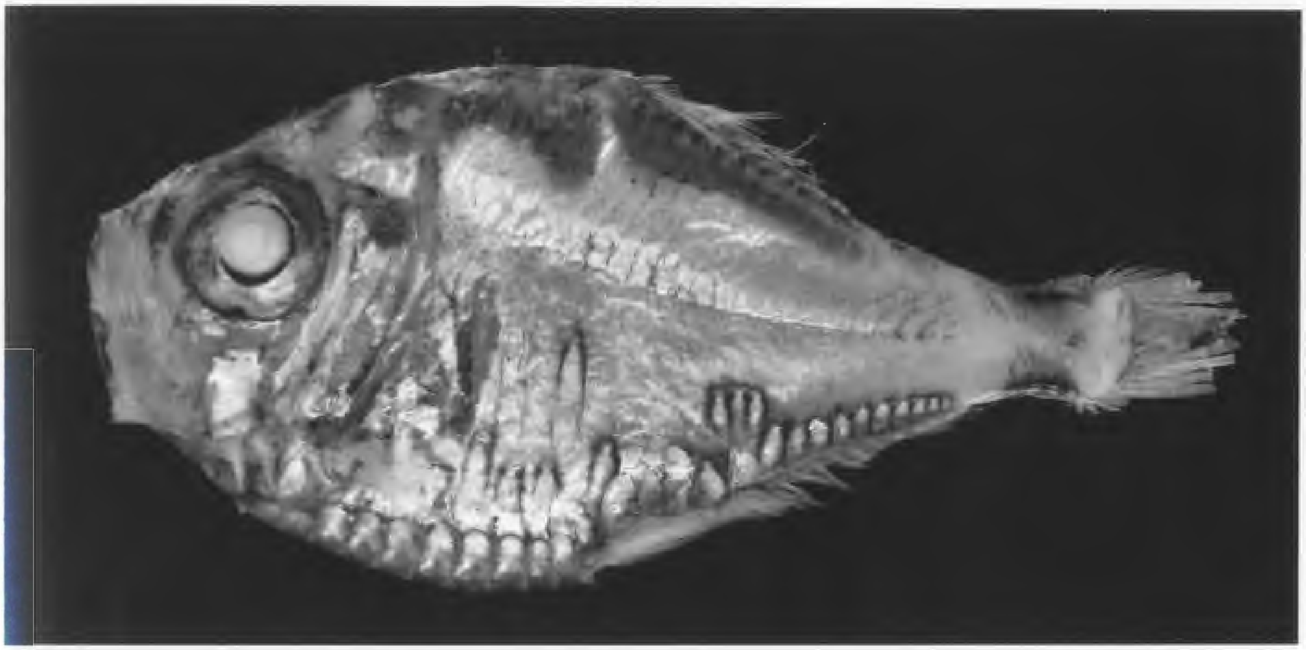


FIGURE 19.-*Polyipnus polli*, ZMUC uncat., R/V *Dana* Sta. 1159, 30.1 mm.

FIGURE 20.-*Polyipnus triphanos*, CAS 34899, 40.4 mm.

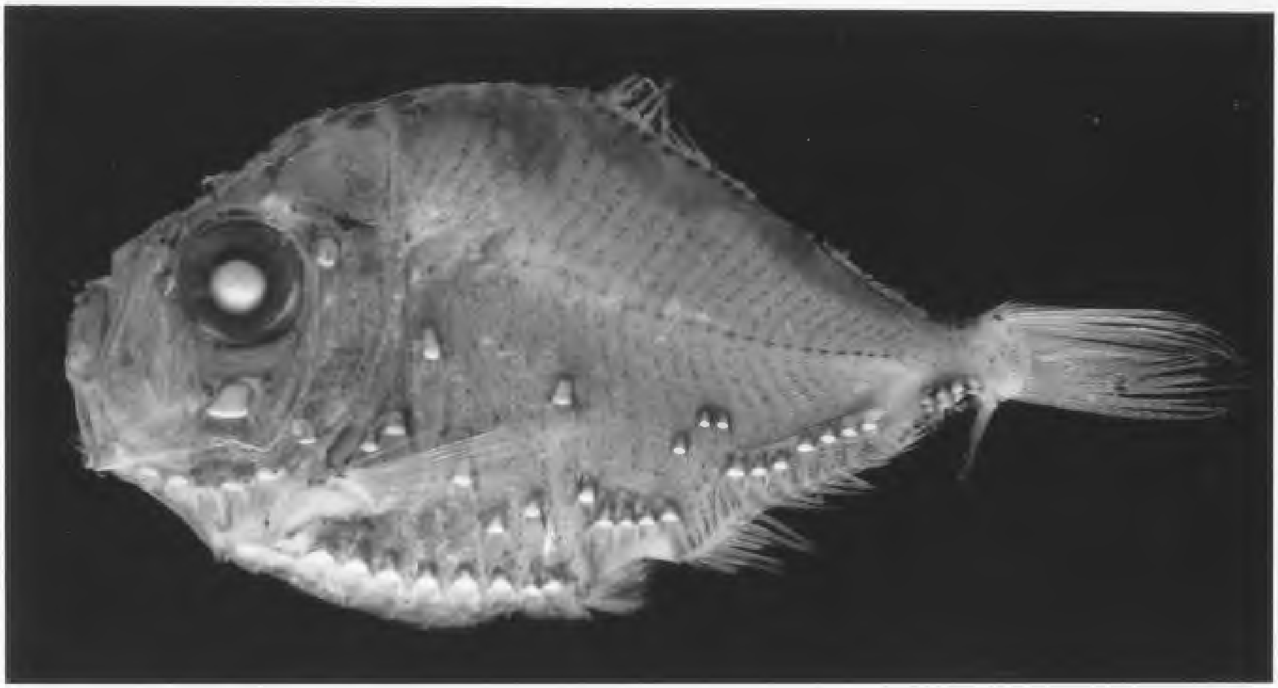


FIGURE 21.-Collection station localities for *P. omphus* (*P. omphus* species group) and *P. laternatus* (*P. asteroides* species group).

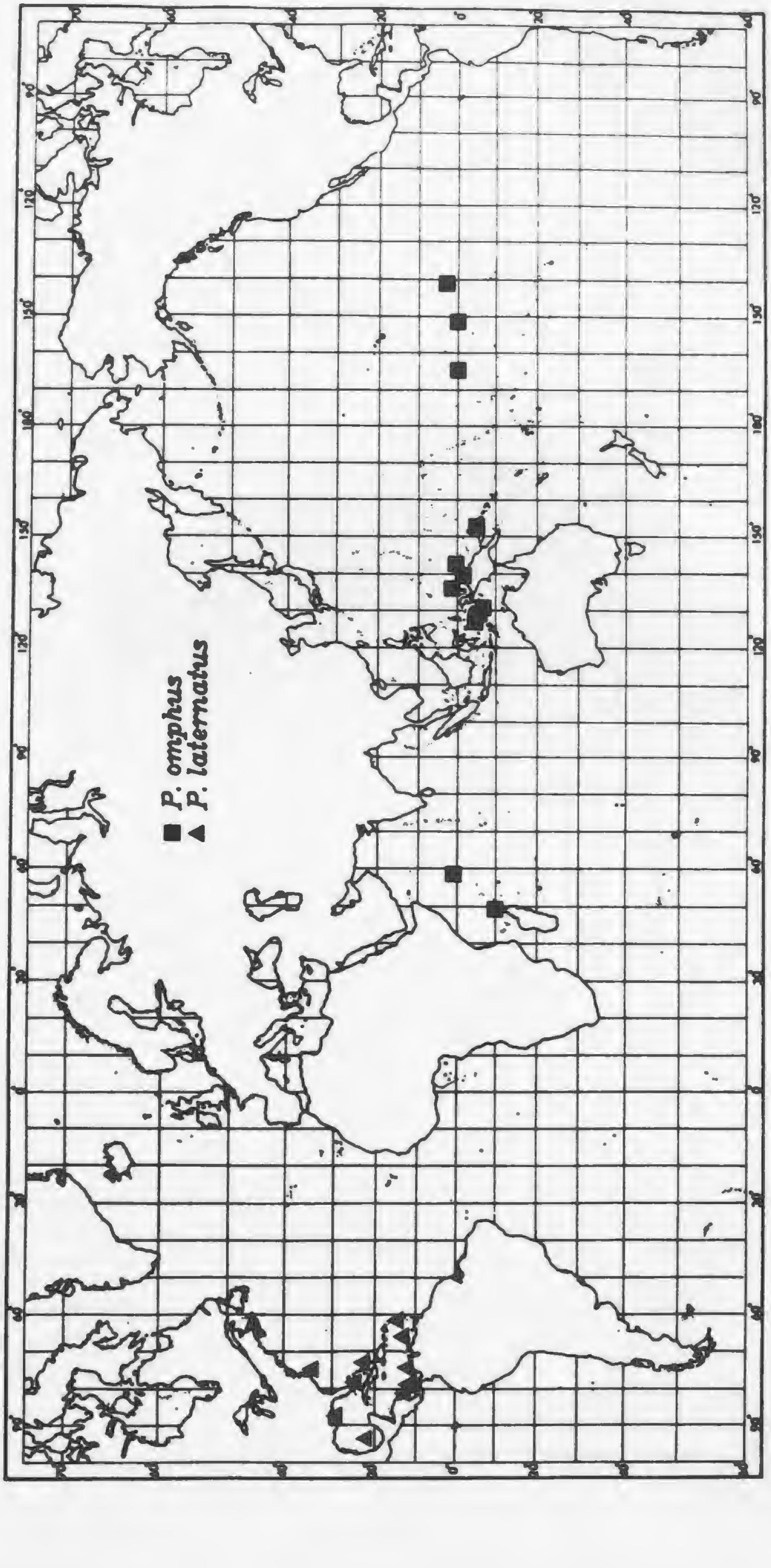

■ P. omphus
▲ P. laternatus
90
120
150
180
150
120
90
60
30
0
30
60
90
60
30
0
30
60

FIGURE 22.-*Polyipnus aquavitus*, AMS I.19762-002, 35.3 mm.

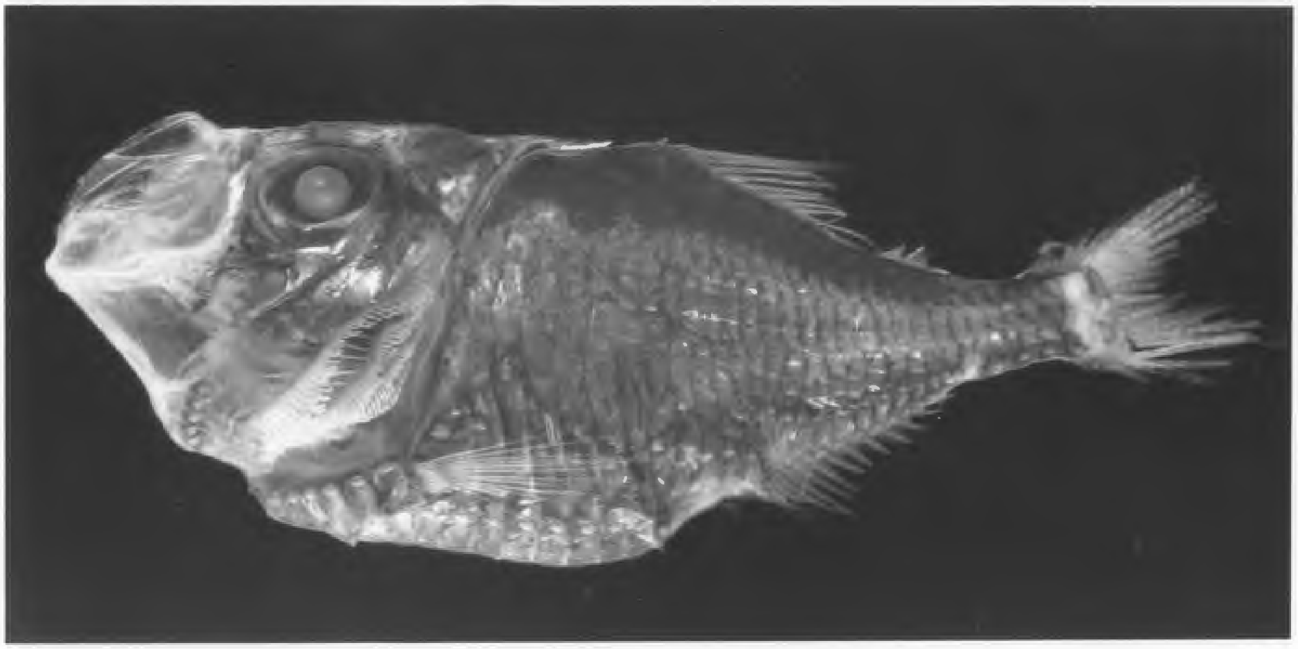


FIGURE 23.-Collection station localities for *P*. *aquavitus*, *P*. *omphus* species group.

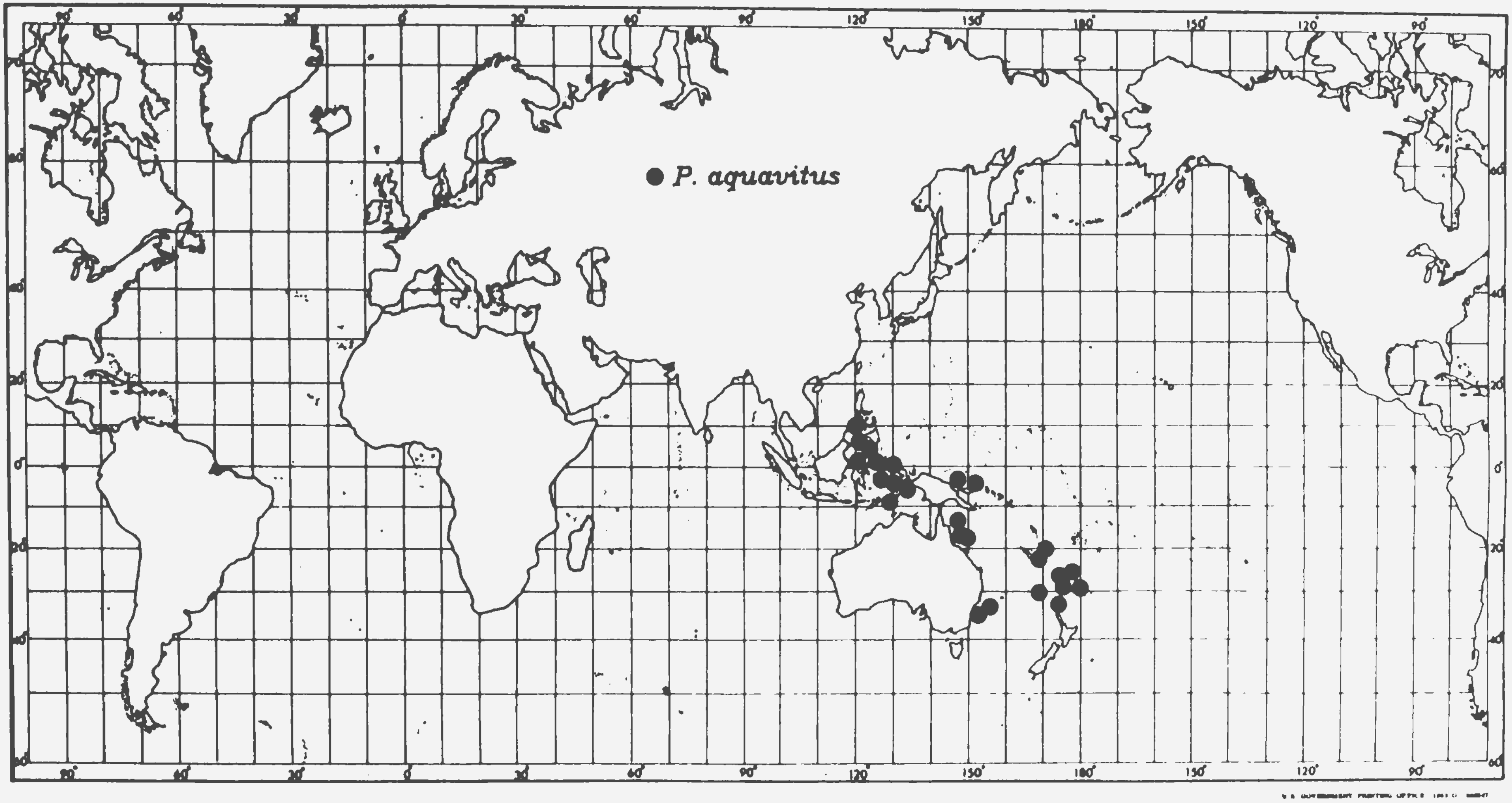

● P. aquavitus
90°
60°
30°
0°
30°
60°
90°
120°
150°
180°
150°
120°
90°
60
40
20
0°
20
40
60

FIGURE 24.-Polyipnus danae, paratype, ZMUC P208578, 27.3 mm.

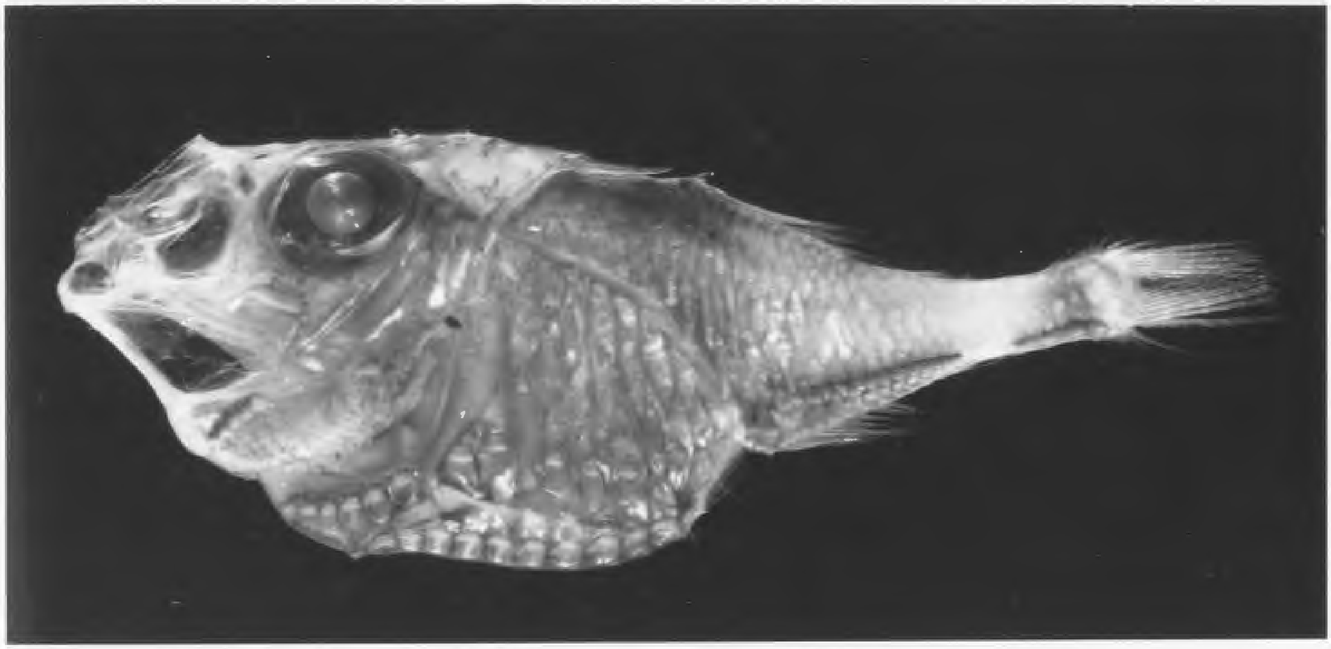


FIGURE 25.-Collection station localities for *P*. *danae* and *P*. *unispinus*, *P*. *omphus* species group.

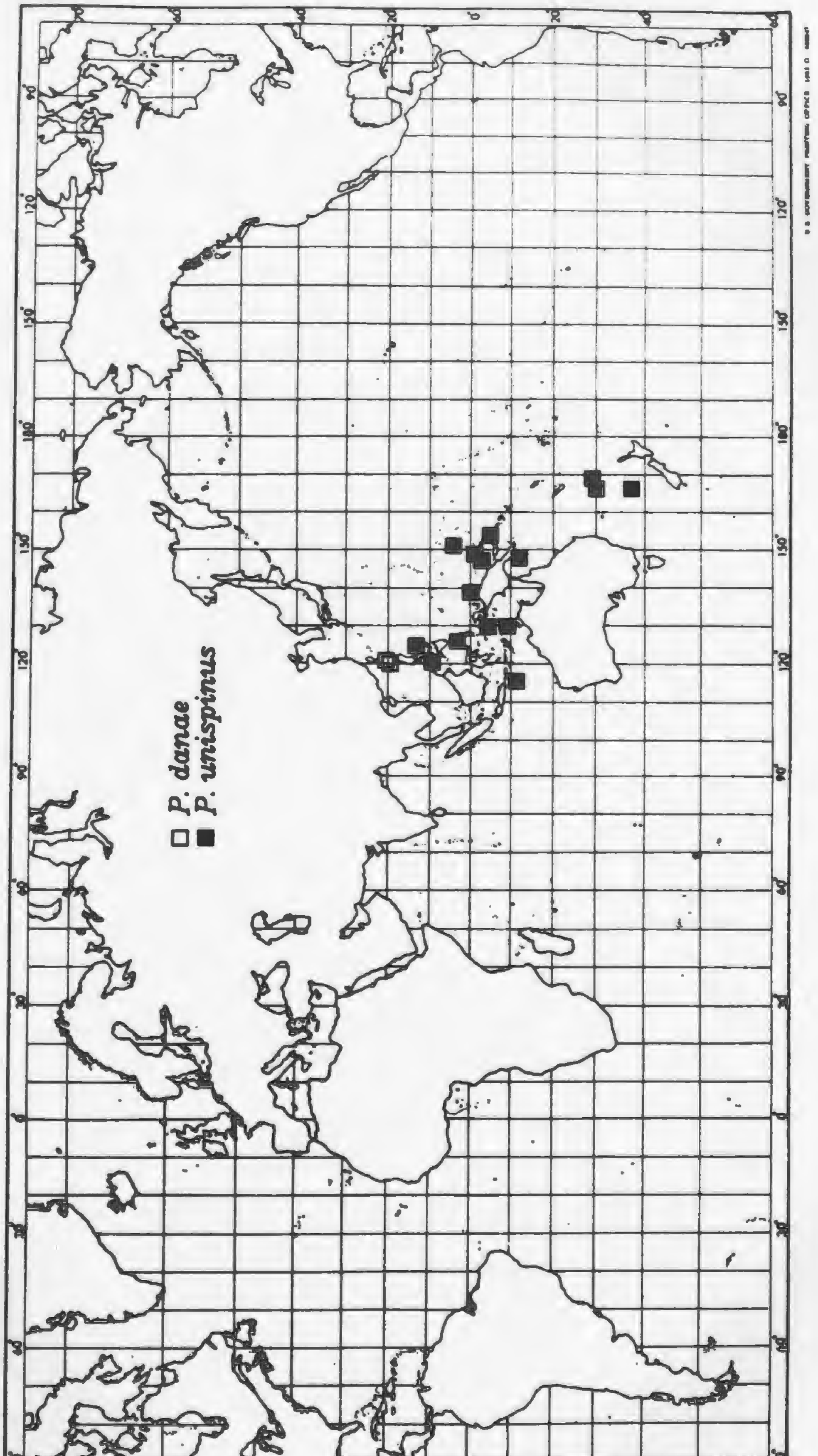

□ *P. danae*
■ *P. unispinus*

FIGURE 26.-Polyipnus omphus, ZMH 4886, 32.9 mm.

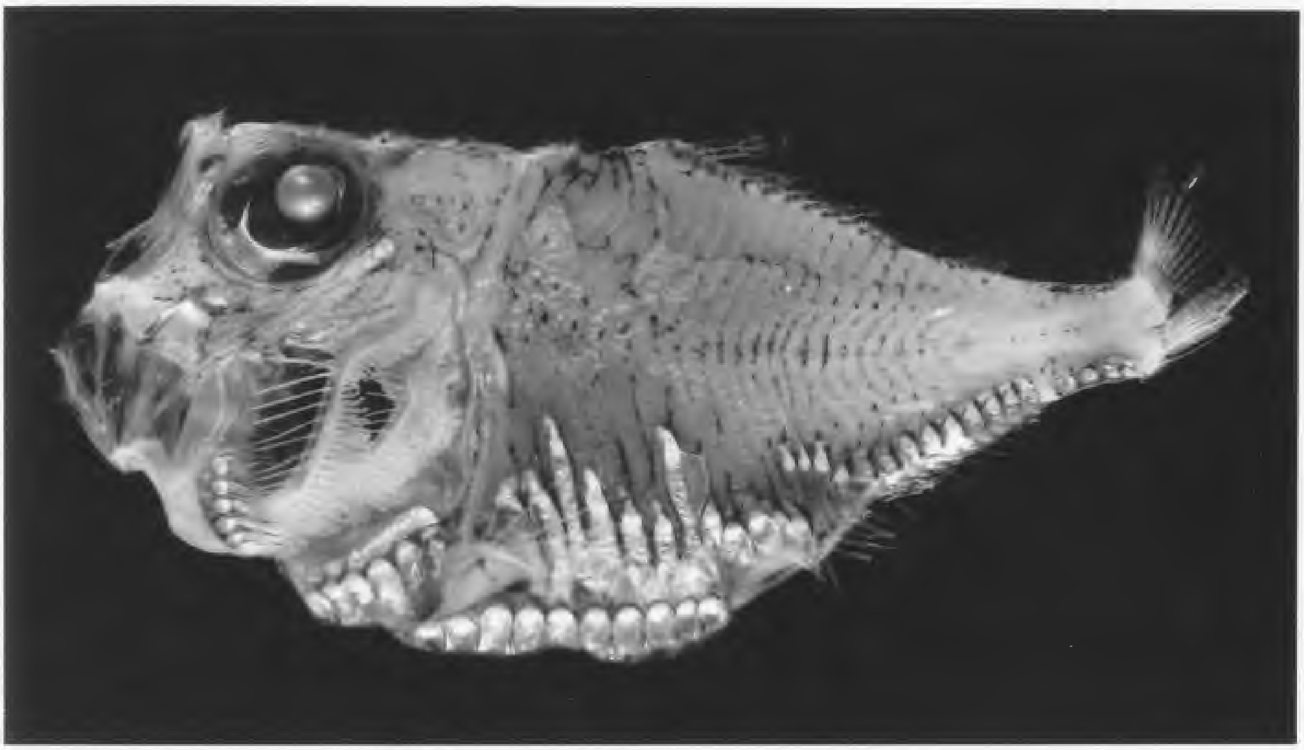


FIGURE 27.-*Polyipnus unispinus*, AMS I.19287-003, 27.1 mm.

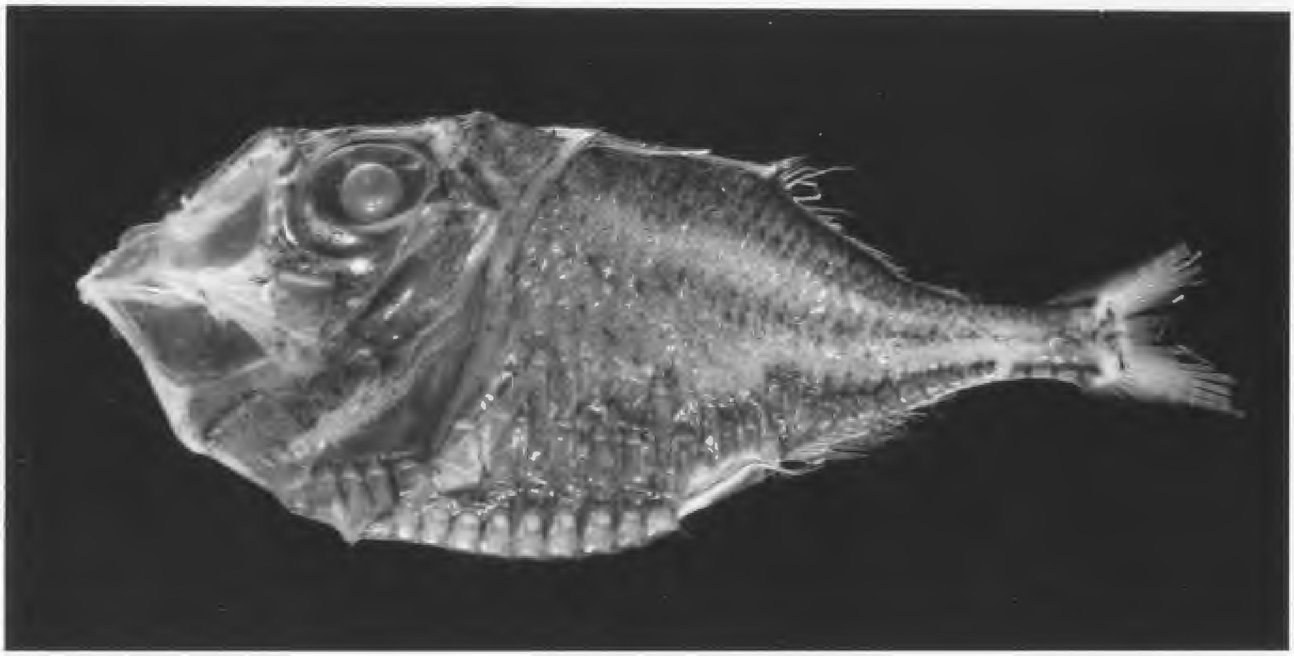


FIGURE 28.-*Polyipnus asper*, holotype, USNM 273282, 62.1 mm.

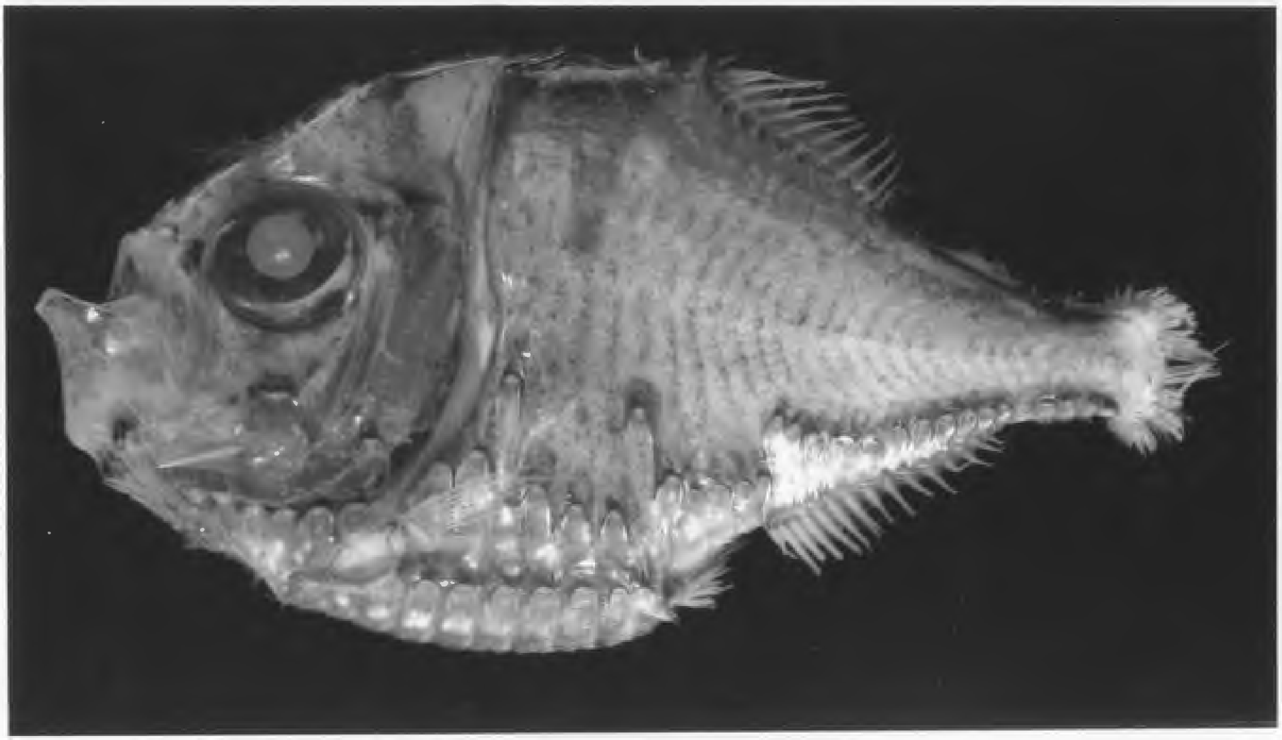


FIGURE 29.-Collection station localities for *P*. *indicus*, *P*. *nuttingi*, *P*. *oluolus* and *P*. *asper*, *P*. *spinosus* species group.

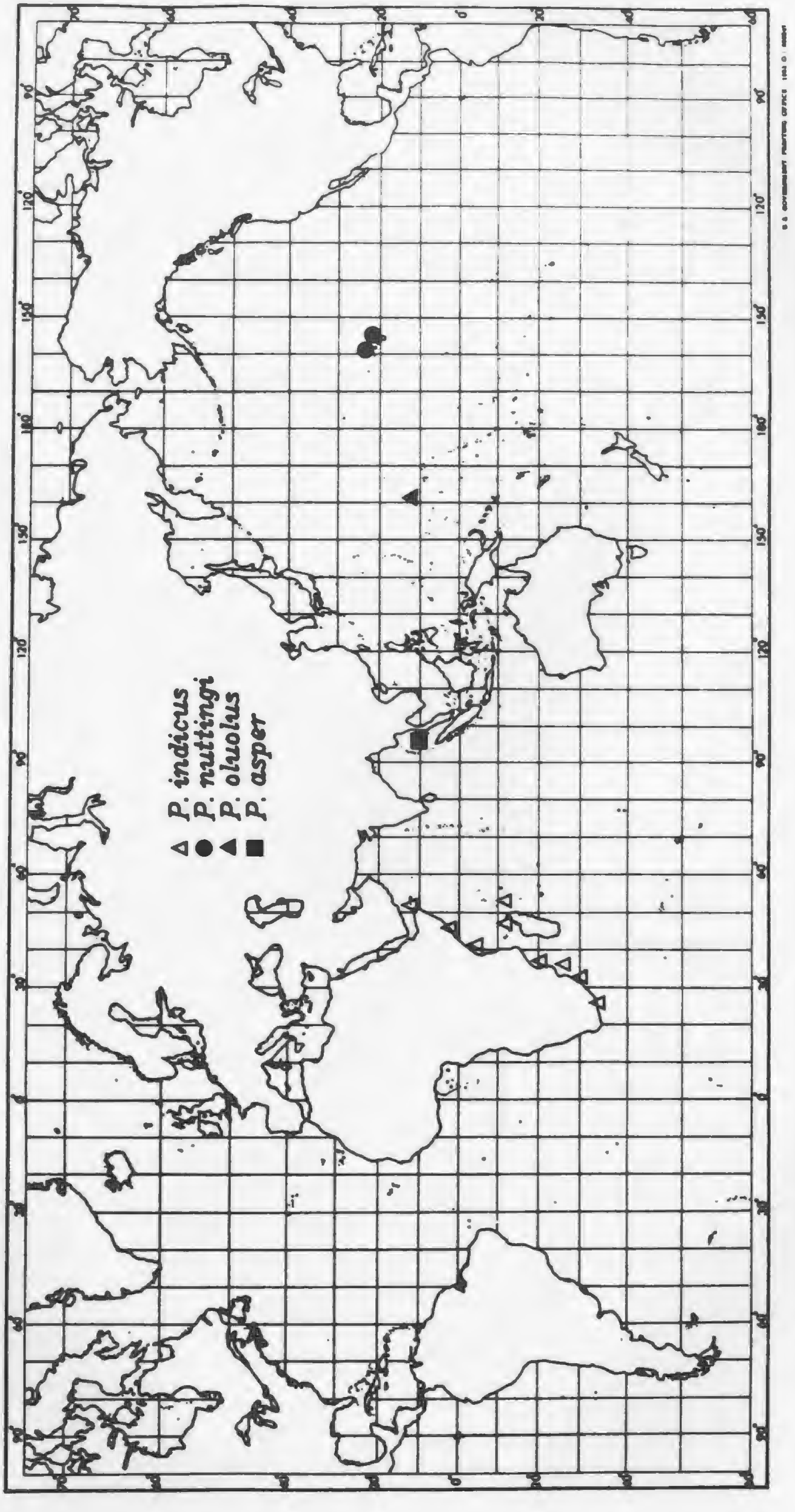

△ P. indicus
● P. nuttingi
▲ P. oluolus
■ P. asper
90°
120°
150°
180°
150°
120°
90°
60°
30°
0°
30°
60°
90°
U.S. GOVERNMENT PRINTING OFFICE

FIGURE 30.-*Polyipnus elongatus*, holotype, ZIL 43999, 59.0 mm. After Borodulina (1979).

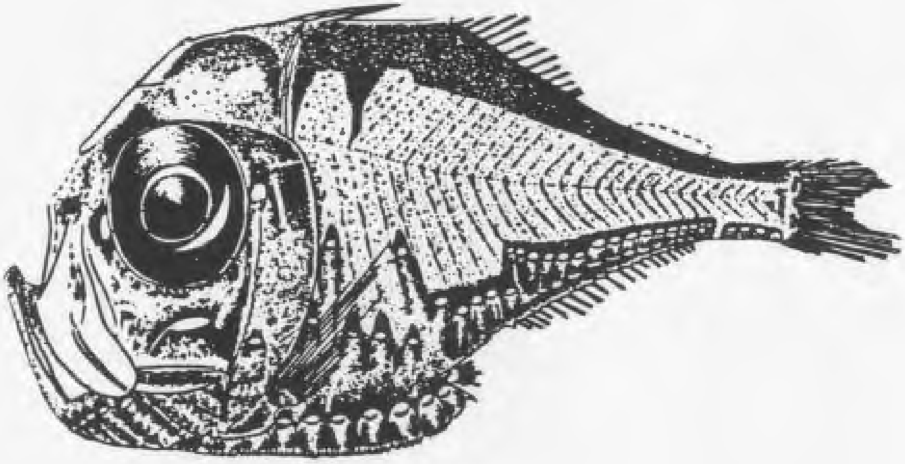


FIGURE 31.-Collection station localities for *P. tridentifer*, *P. spinifer*, *P. soelae* and *P. elongatus*, *P. spinosus* species group.

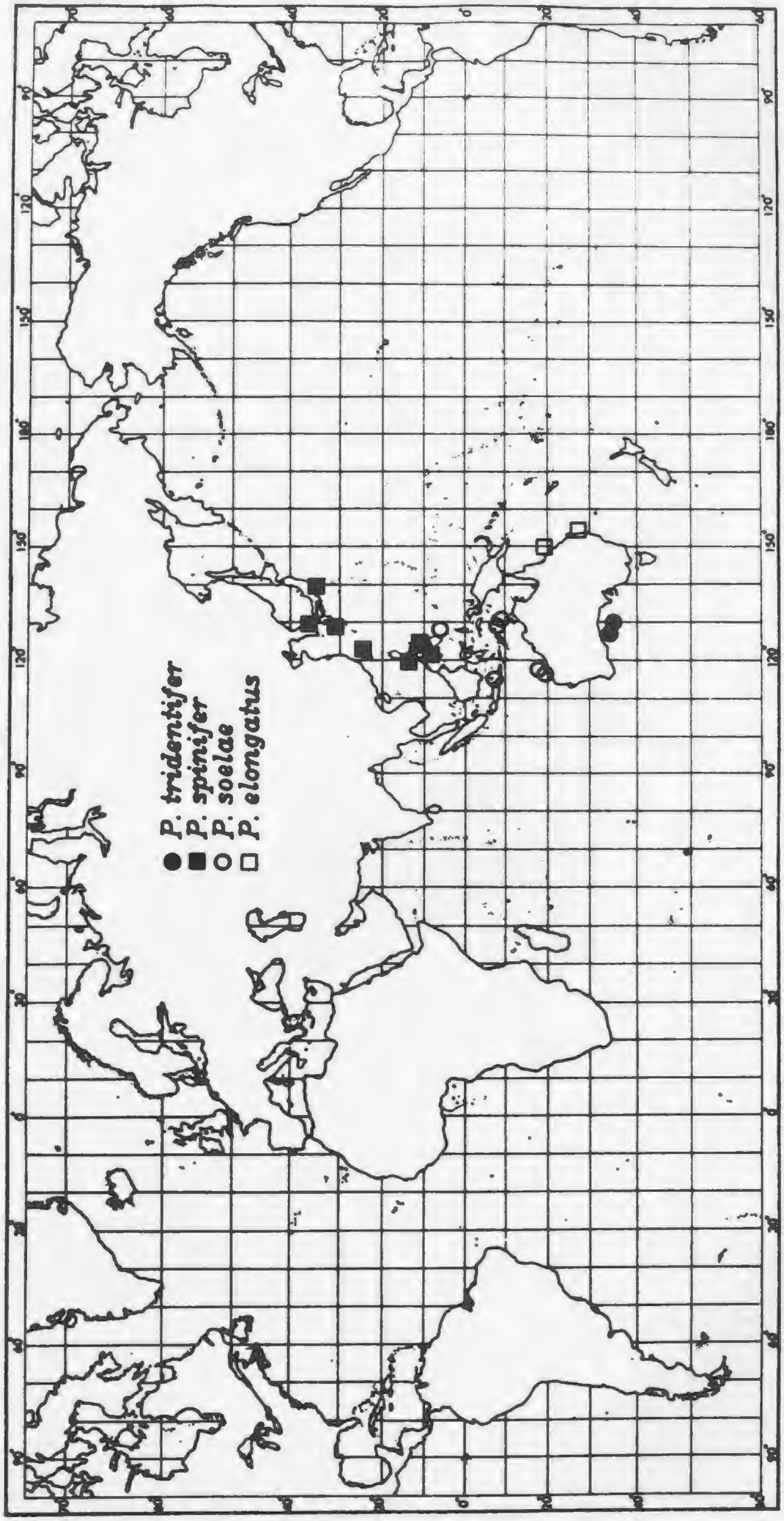

● P. tridentifer
■ P. spinifer
○ P. soelae
□ P. elongatus

FIGURE 32.-Polyipnus fraseri, holotype, USNM 92324, 40.4 mm.

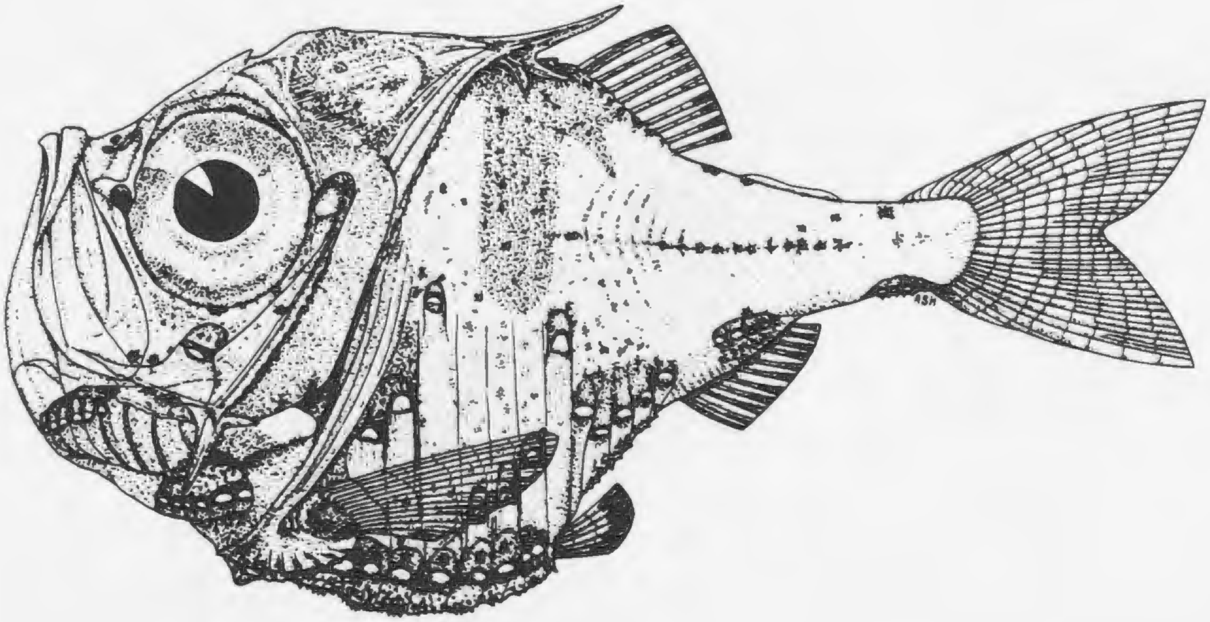

ASH

FIGURE 33.-Collection station localities for *P. paxtoni* and *P. fraseri*, *P. spinosus* species group.

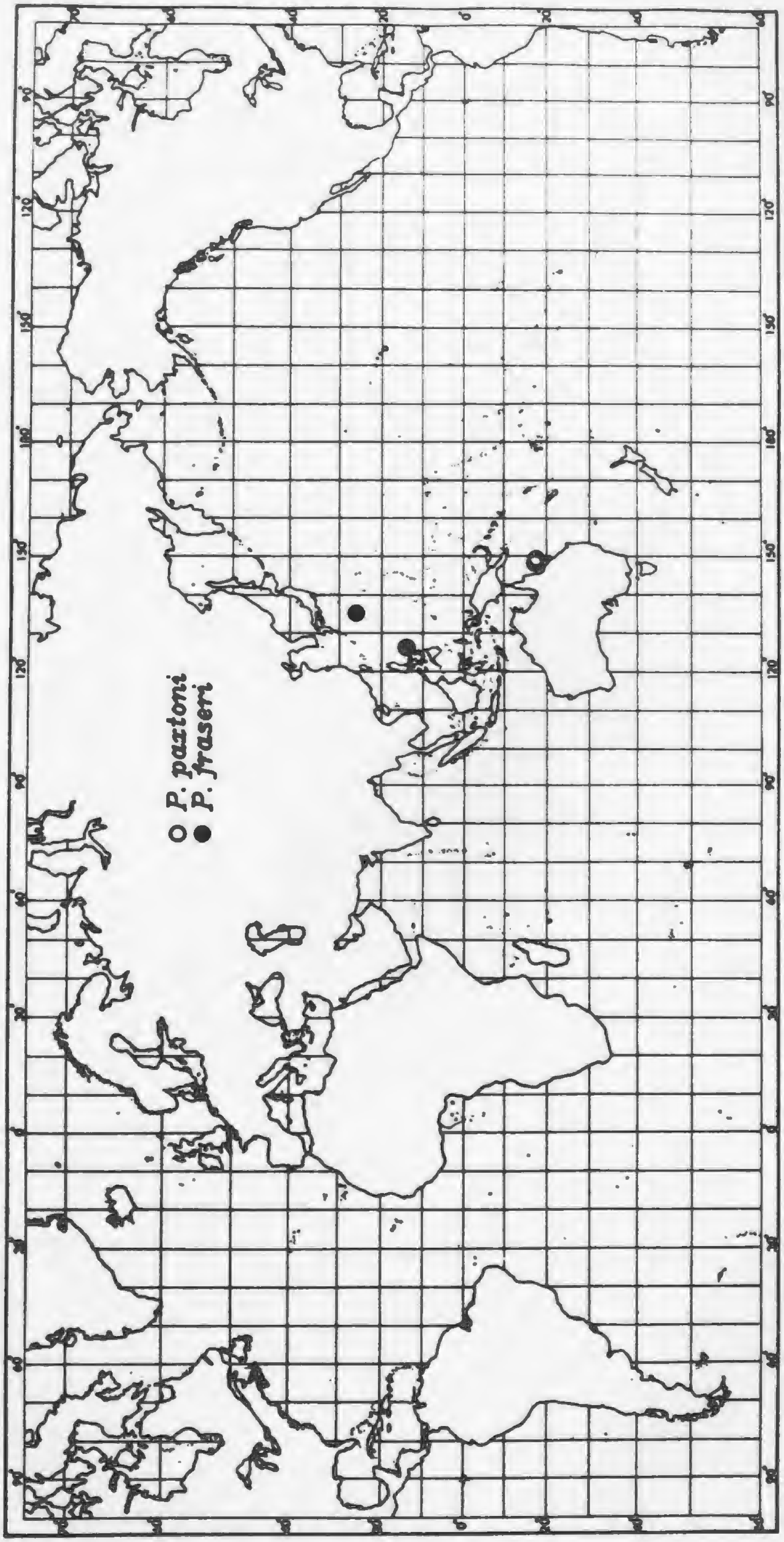

○ P. paxtoni
● P. fraseri

FIGURE 34.-*Polyipnus indicus*, ASH 88281, 62.3 mm.

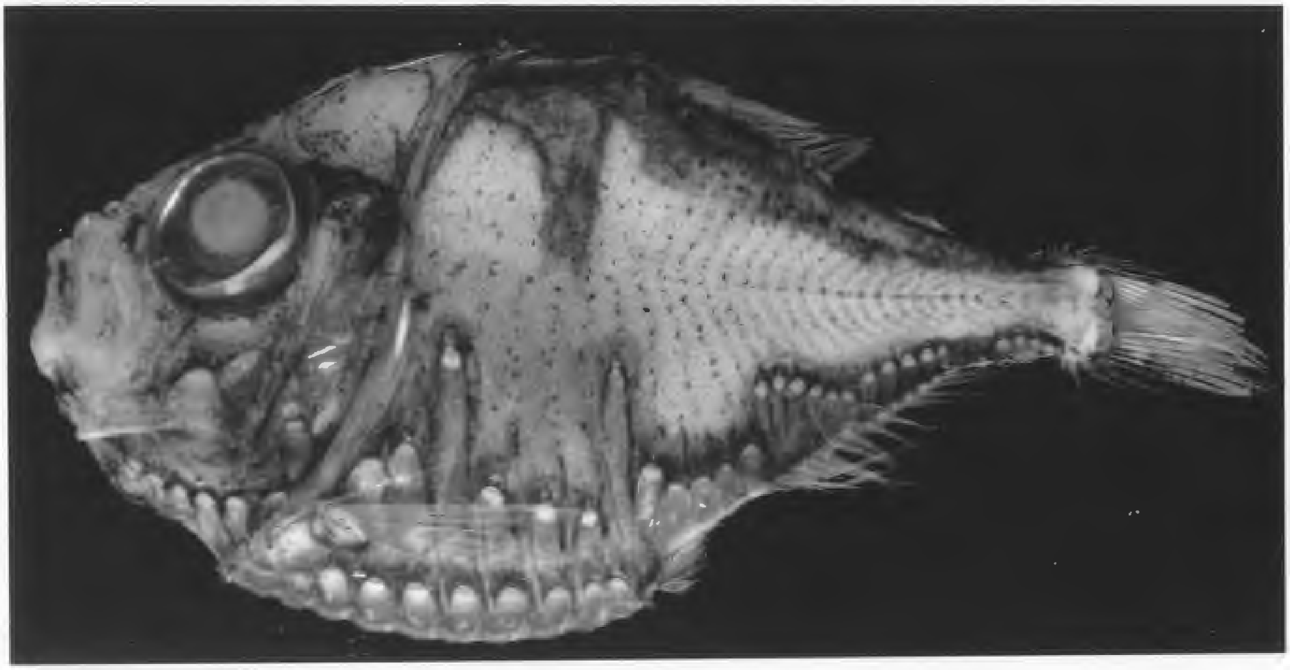


FIGURE 35.-*Polyipnus inermis*, IOAN uncat., R/V *Prof. Shtokman*, Cr. 18, Sta. 1965, 51.5 mm.

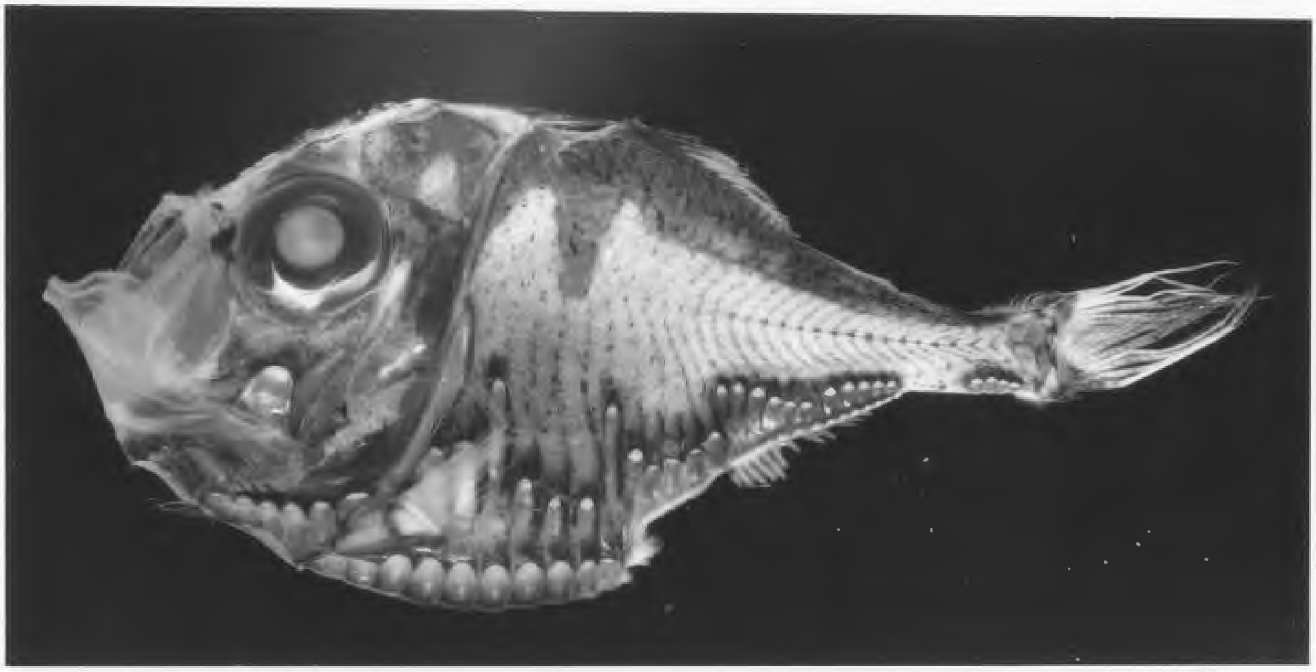


FIGURE 36.-Collection station localities for *P*. *inermis*, *P*. *parini* and *P*. cf. *parini*, *P*. *spinosus* species group.

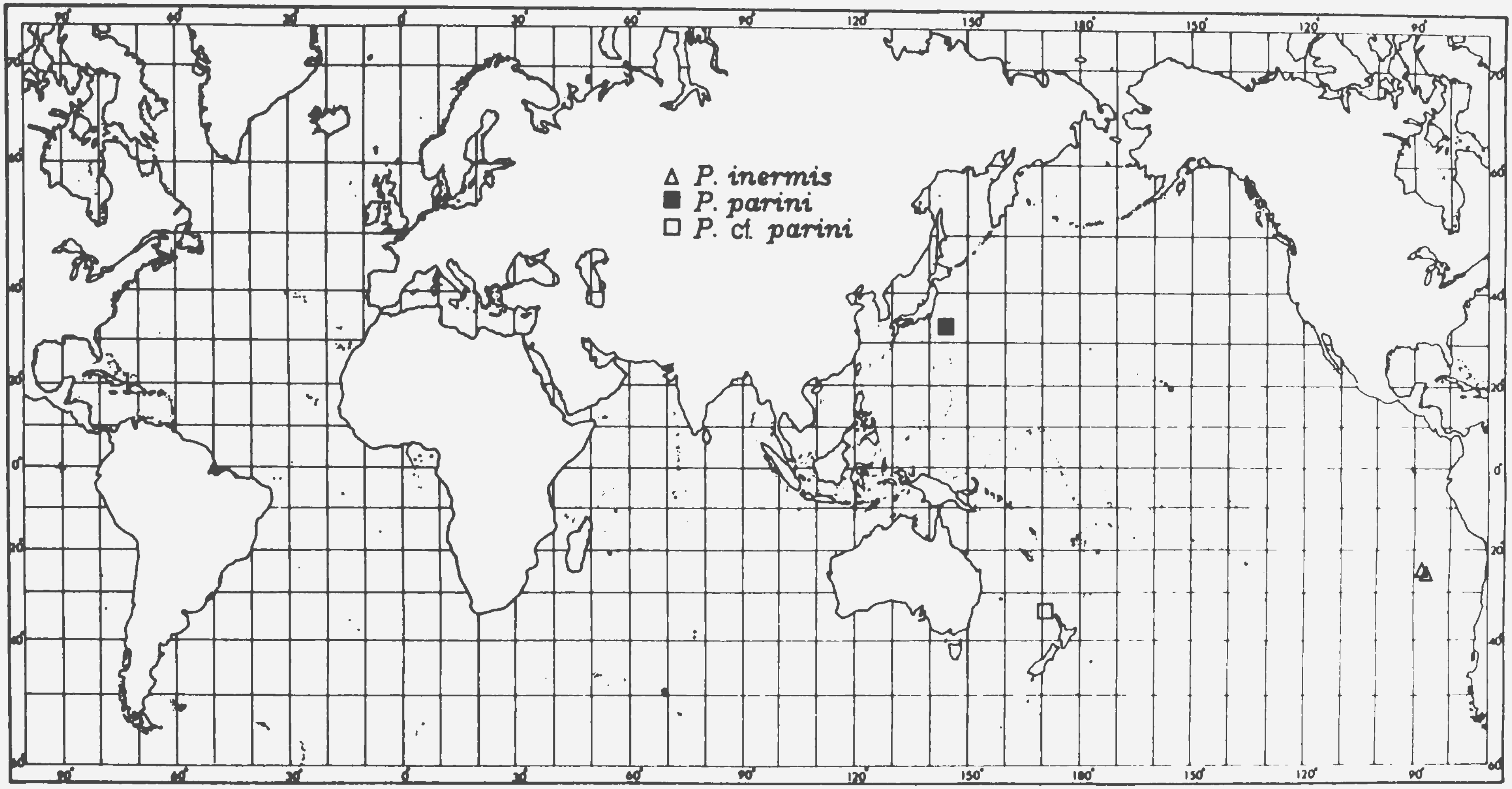

△ P. inermis
■ P. parini
□ P. cf. parini
90°
60°
30°
0°
30°
60°
90°
120°
150°
180°
150°
120°
90°
60
40
20
0°
20
40
60

FIGURE 37.-*Polyipnus nuttingi*, BPBM 24892, 37.9 mm.

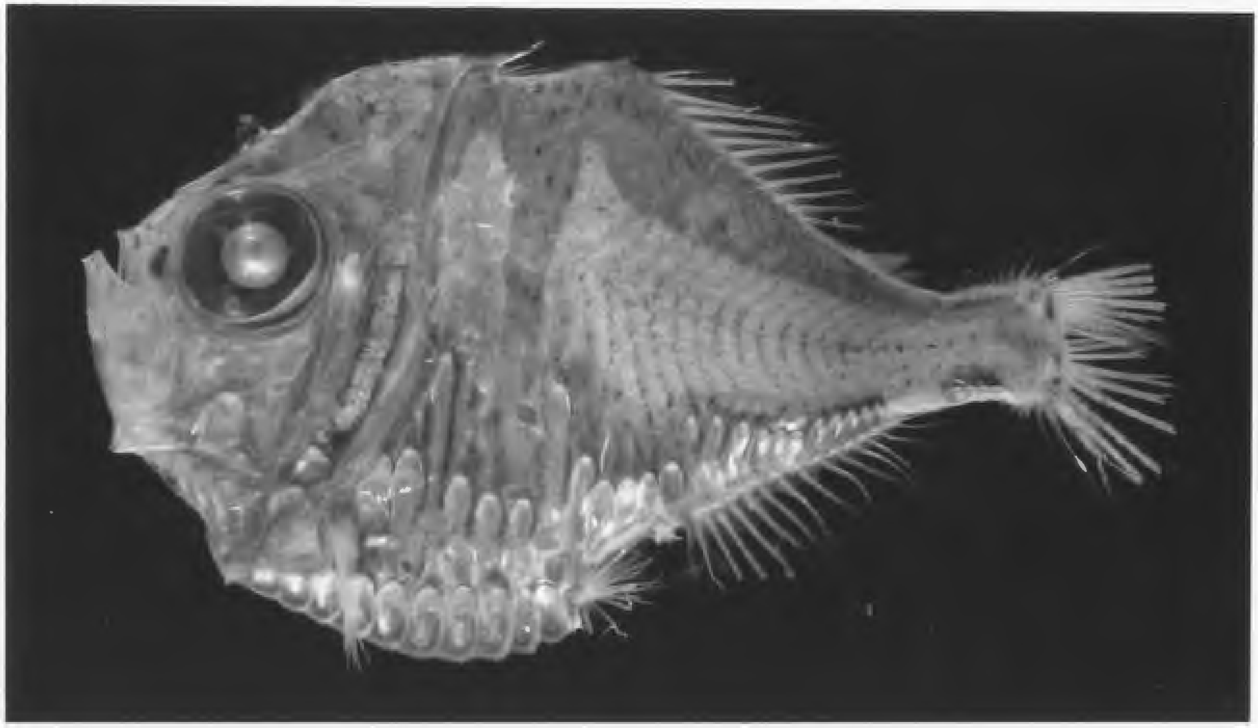


FIGURE 38.-*Polyipnus* *oluolus*, holotype, USNM 204390, 32.9 mm.

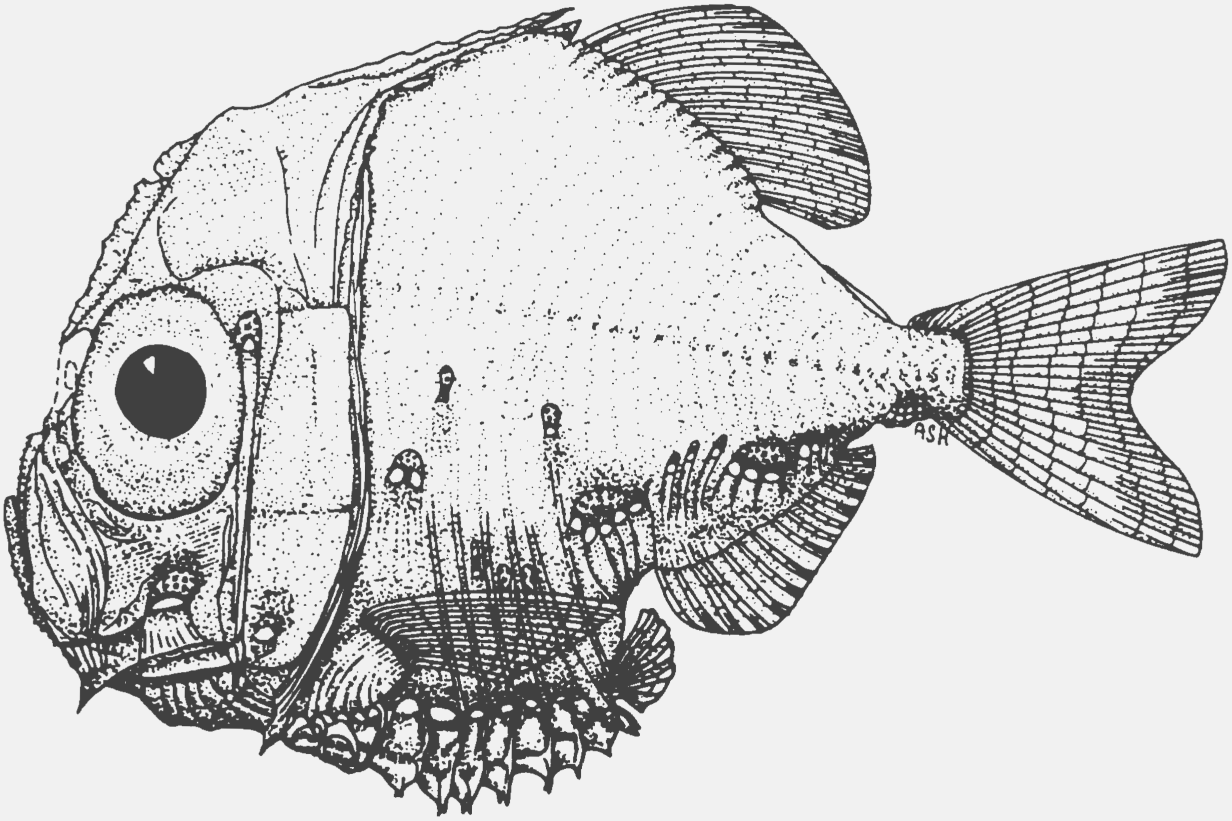

ASH

FIGURE 39.-Polyipnus parini, holotype, ZIL 43997, 61.0 mm. After Borodulina (1979).

3 -

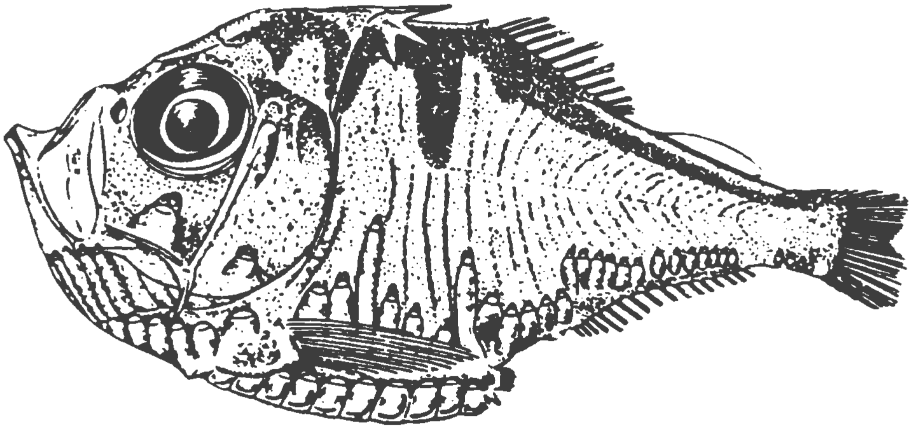


FIGURE 40.-*Polyipnus paxtoni*, paratype, AMS I.25825-002, 45.1 mm.

FIGURE 41.-*Polyipnus soelae*, holotype, AMS I.22808-028, 54.8 mm.

FIGURE 42.-*Polyipnus spinifer*, ORIT 2565, 38.7 mm.

FIGURE 43.-*Polyipnus spinosus*, holotype, BMNH 1987.12.7.159. After Günther (1887).

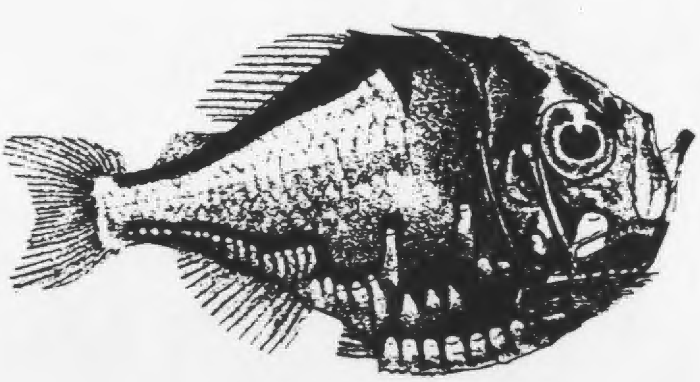


FIGURE 44.-Collection station localities for *P*. *stereope* and *P*. *spinosus*, *P*. *spinosus* species group.

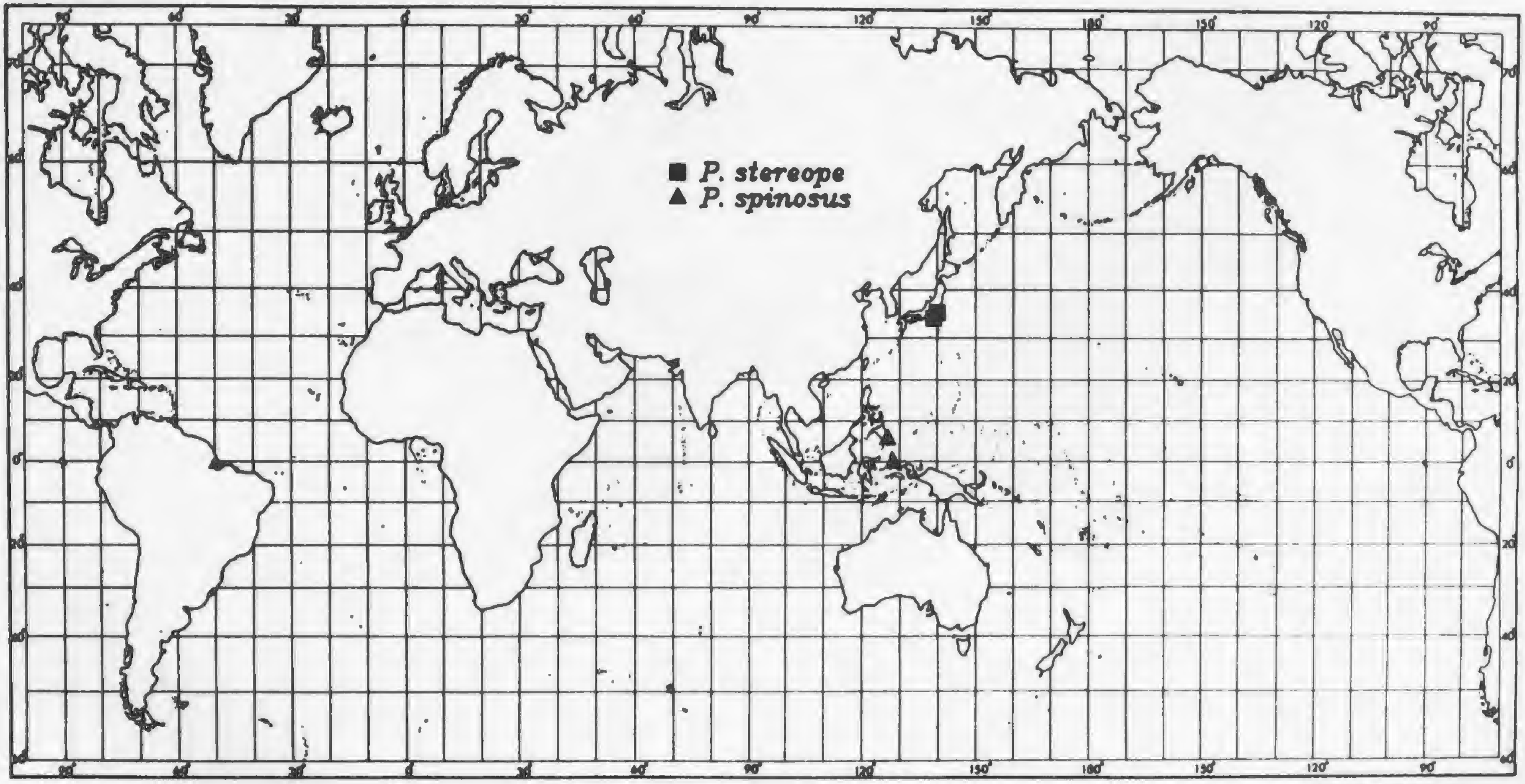

■ P. stereope
▲ P. spinosus

FIGURE 45.-*Polyipnus stereope*, ORIT 2519, 47.5 mm.

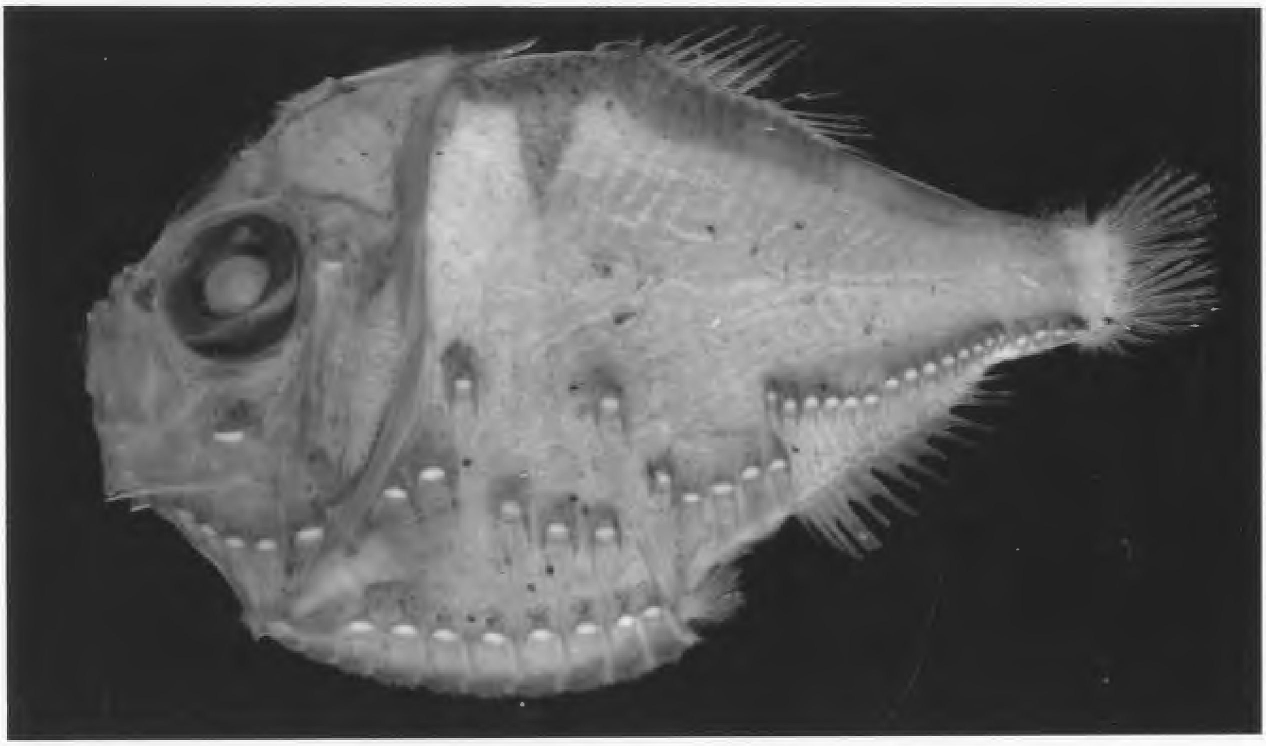


FIGURE 46.-*Polyipnus tridentifer*, paralectotype, AMS E.3542, 46.9 mm.

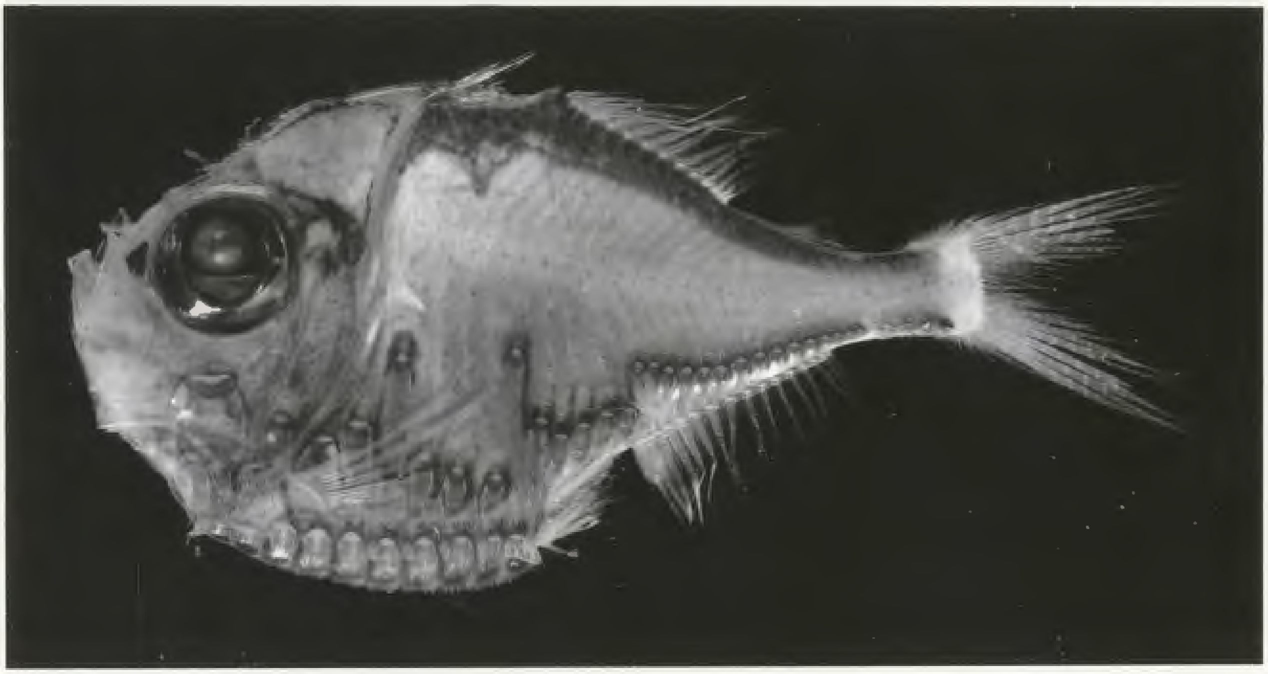


FIGURE 47.-Cladogram of the genus *Polyipnus* through species group levels. Derived characters marked on branches of diagram. States of multi-state characters given in parentheses. Total number of character state changes implied by the tree for inconsistent characters indicated by superscript tick marks.

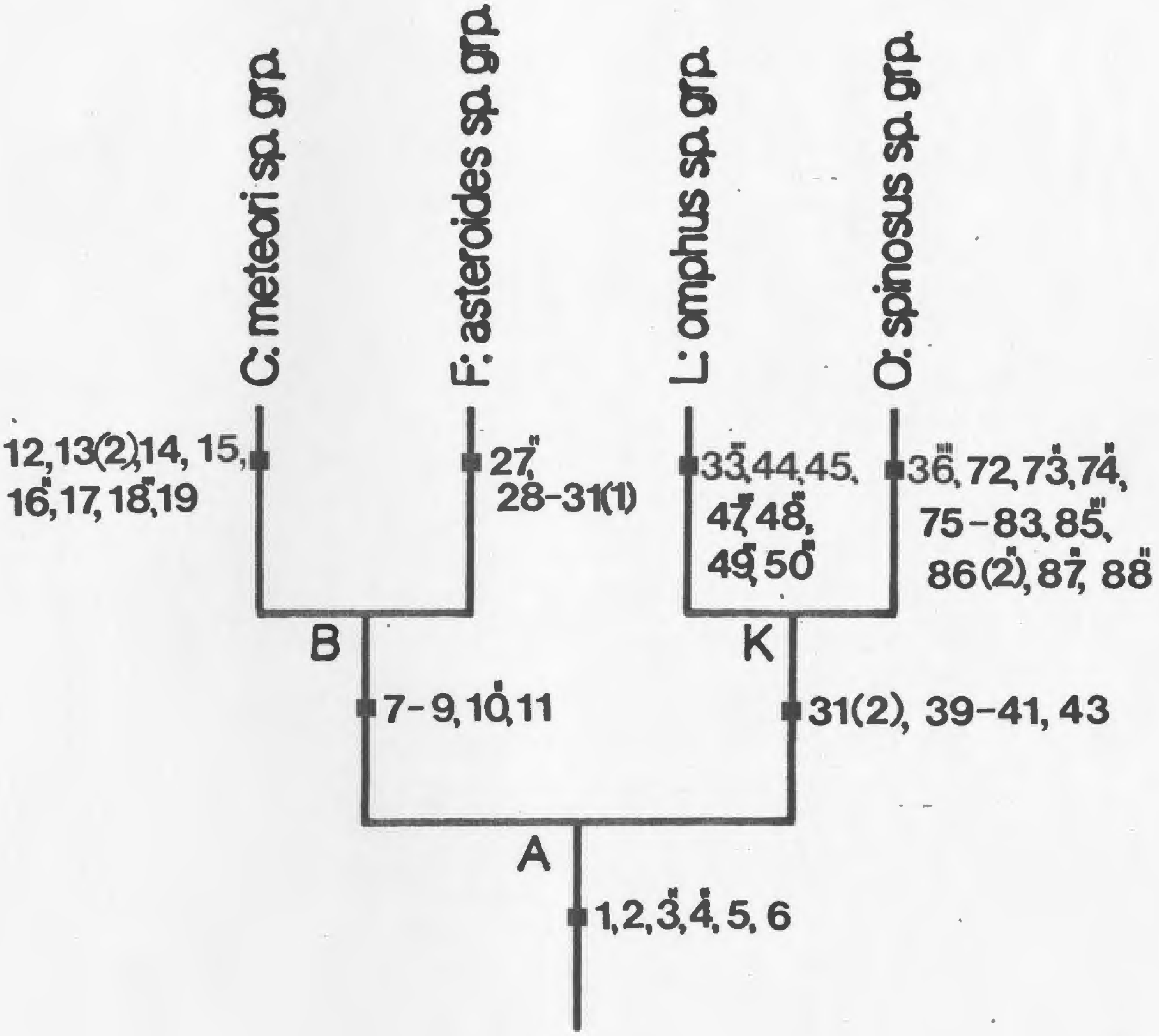

C: meteori sp. grp.
F: asteroides sp. grp.
L: omphus sp. grp.
O: spinosus sp. grp.
12, 13(2), 14, 15, 16″, 17, 18‴, 19
27″, 28-31(1)
33‴, 44, 45, 47″, 48″, 49″, 50″
36⁗, 72, 73″, 74″, 75-83, 85‴, 86(2″), 87″, 88″
B
K
7-9, 10′, 11
31(2), 39-41, 43
A
1, 2, 3″, 4″, 5, 6

FIGURE 48.-Cranium, right side, lateral view and bones of the lateral and ventral regions of the head, left side, medial view: Polyipnus meteori, ZMUC P206931, 37.6 mm.

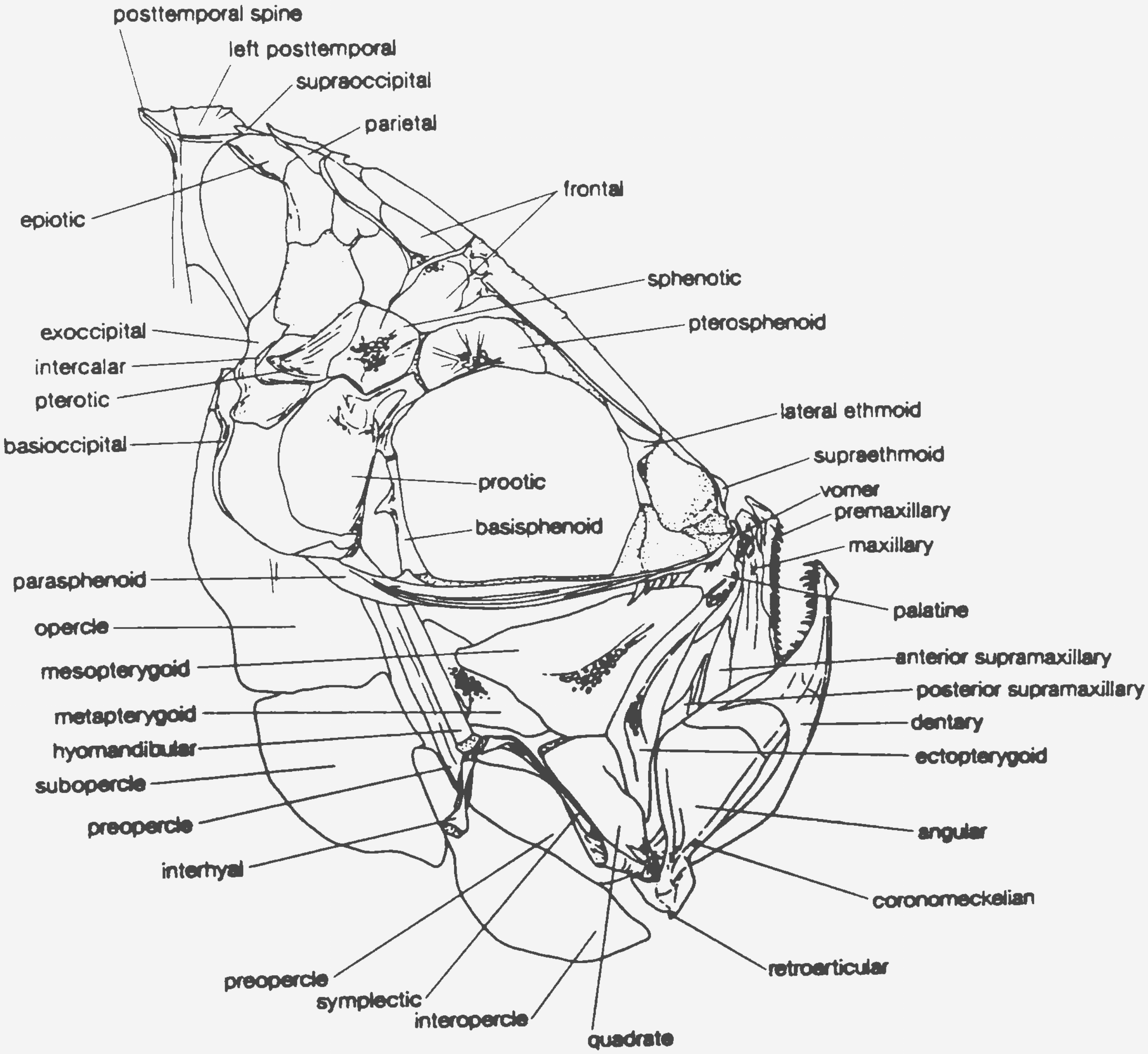

posttemporal spine
left posttemporal
supraoccipital
parietal
frontal
epiotic
sphenotic
pterosphenoid
exoccipital
intercalar
pterotic
lateral ethmoid
basioccipital
supraethmoid
prootic
vomer
premaxillary
basisphenoid
maxillary
parasphenoid
palatine
opercle
anterior supramaxillary
mesopterygoid
posterior supramaxillary
metapterygoid
dentary
hyomandibular
ectopterygoid
subopercle
preopercle
angular
interhyal
coronomeckelian
retroarticular
preopercle
symplectic
interopercle
quadrate

FIGURE 49.-Hyoid arch, right side lateral view (branchiostegal rays included only in C): A, *P*. *meteori*, ZMUC P206931, 37.6 mm; B, *P*. *asteroides*, CAS 61110, 58.0 mm; C, *P*. *soelae*, AMS I.23425-011, 46.0 mm.

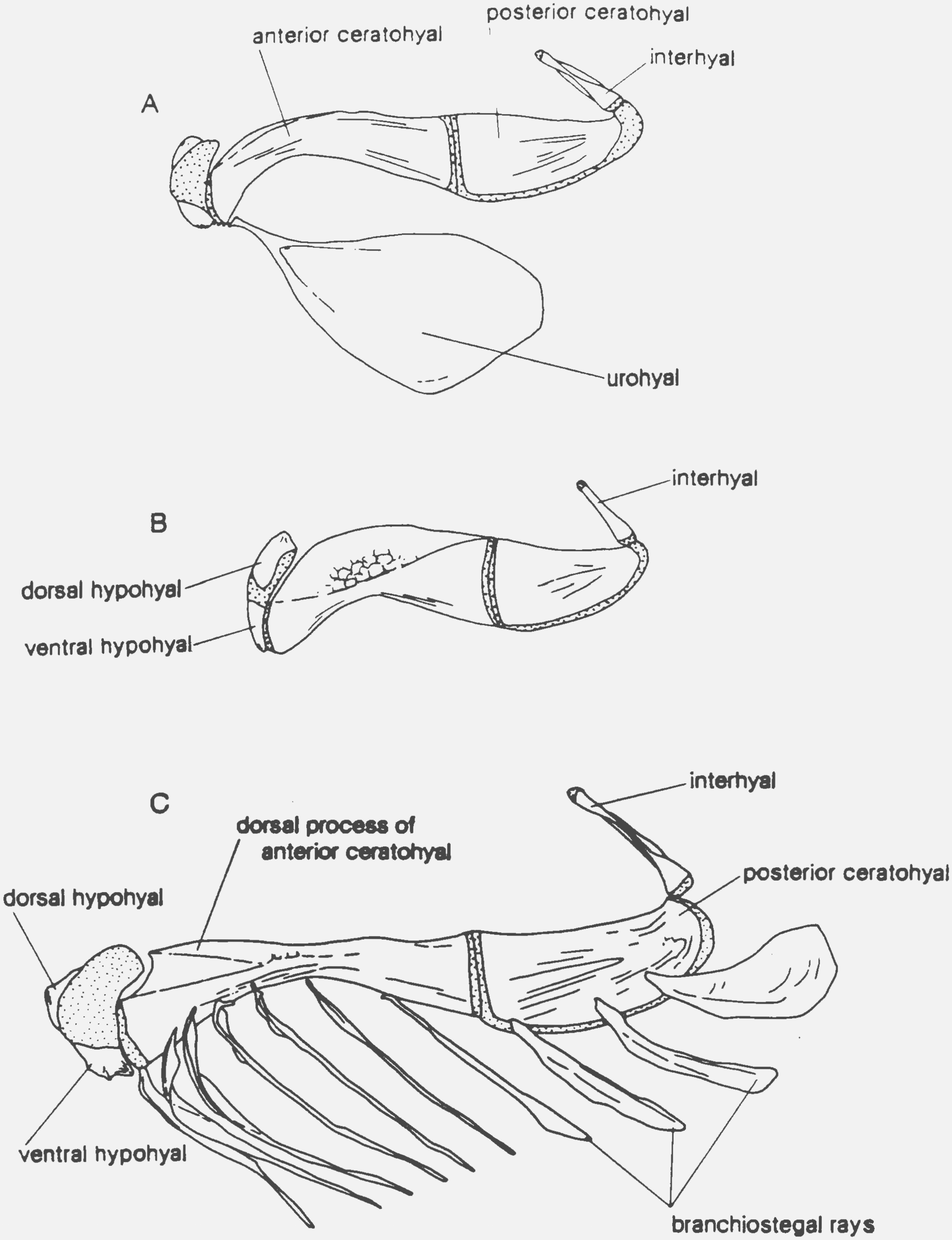

A
posterior ceratohyal
anterior ceratohyal
interhyal
urohyal
B
interhyal
dorsal hypohyal
ventral hypohyal
C
interhyal
dorsal process of anterior ceratohyal
posterior ceratohyal
dorsal hypohyal
ventral hypohyal
branchiostegal rays

FIGURE 50.-Medial terminations of the premaxillary, maxillary and dentary, right side, lateral view: A, *P. ruggeri*, AMS I.20305-009, 37.0 mm; B, *P. omphus*, ZMUC P206933, 48.0 mm; C, *P. clarus*, USNM 304745, 44.0 mm.

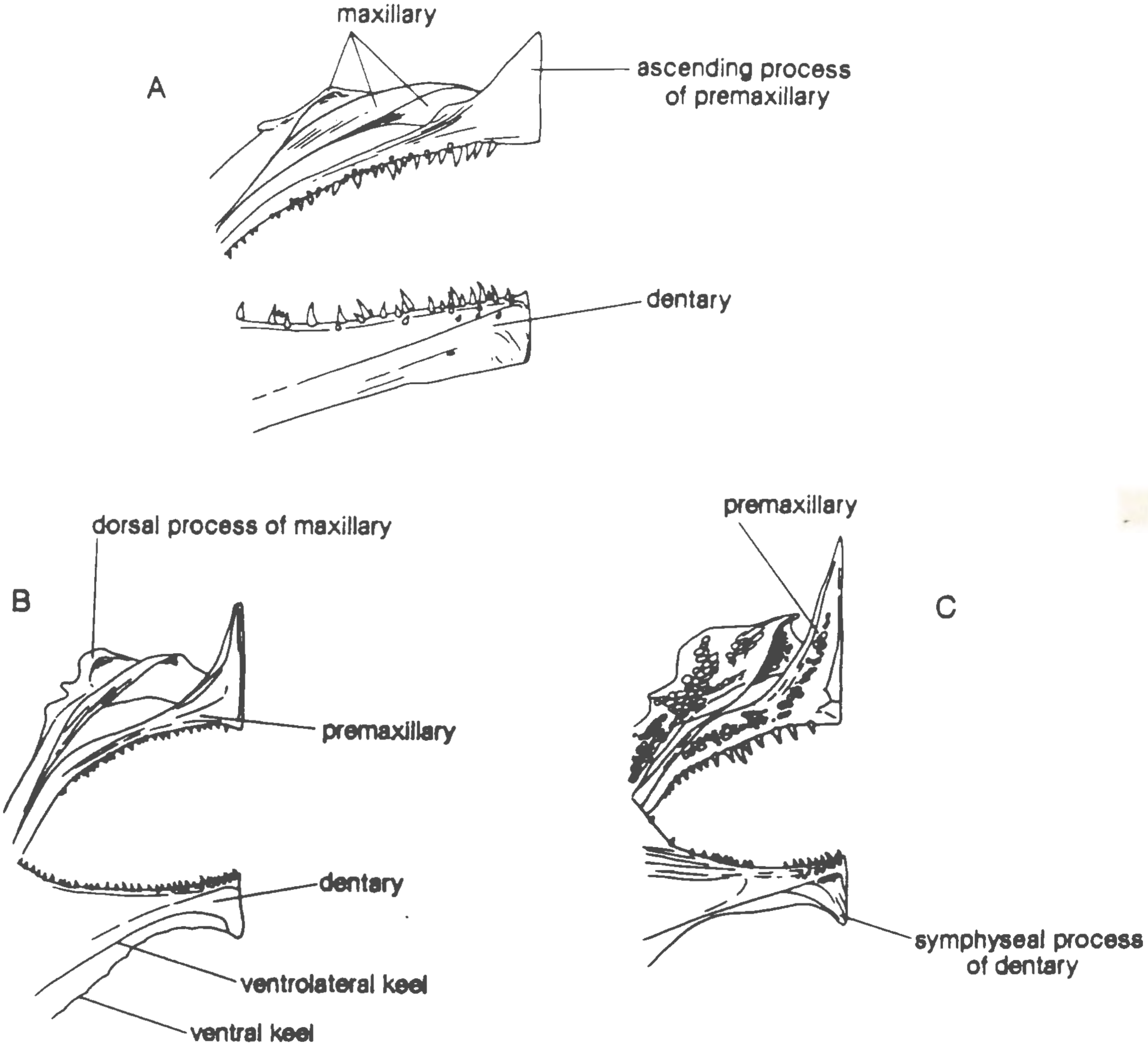

A
maxillary
ascending process of premaxillary
dentary
dorsal process of maxillary
B
premaxillary
dentary
ventrolateral keel
ventral keel
premaxillary
C
symphyseal process of dentary

FIGURE 51.-Cladogram of the P. meteori species group. EQ. INDO-PAC., equatorial Indo-Pacific west to Africa and east to Line Islands; JAPAN., Japanese Archipelago; NW. AUSTR., northwest Australian coast; NW. PAC. OC., northwestern Pacific Ocean; CHINA SEA, South China Sea. Derived characters marked on branches of diagram. States of multi-state characters given in parentheses. Total number of character state changes implied by the tree for inconsistent characters indicated by superscript tick marks.

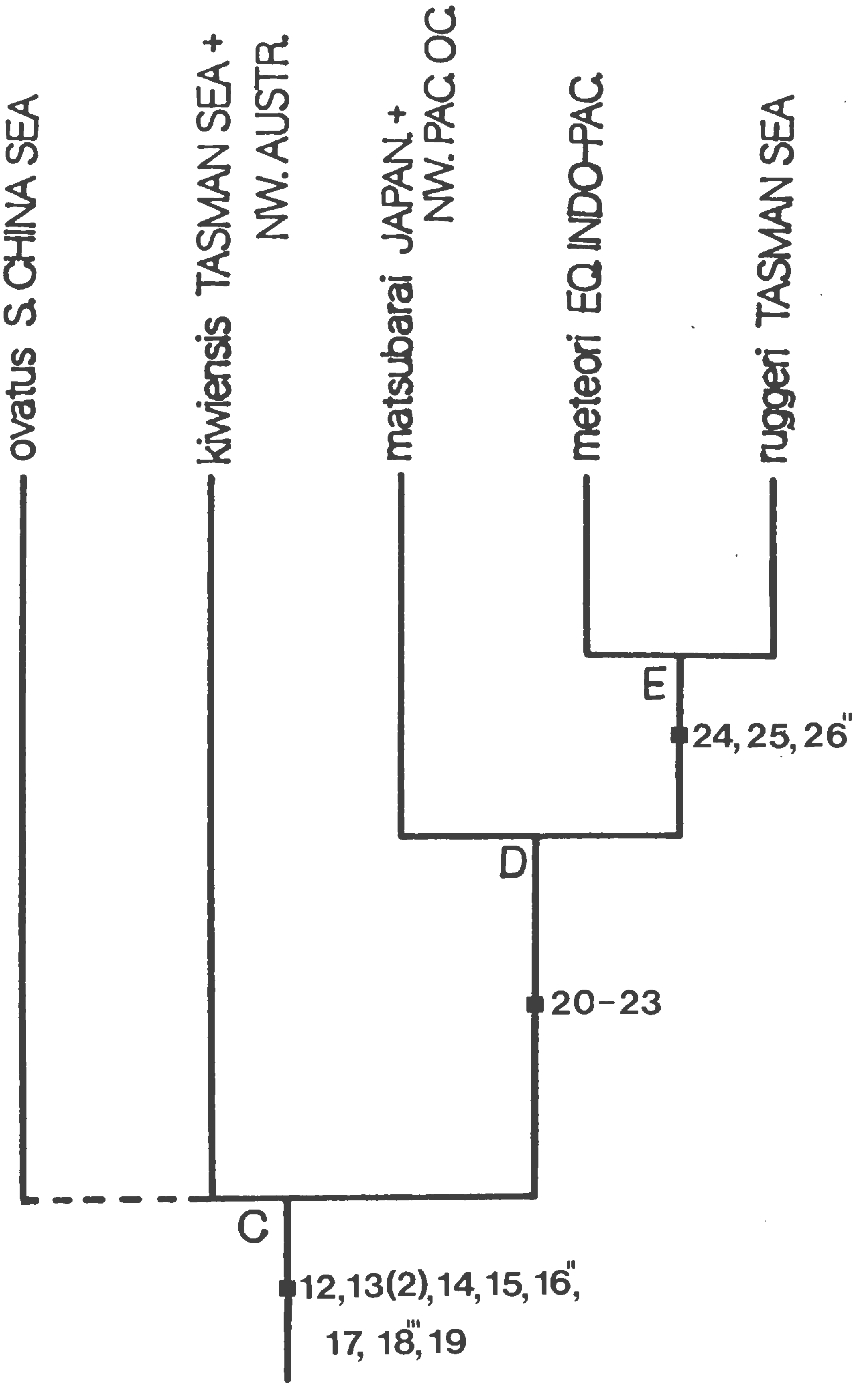
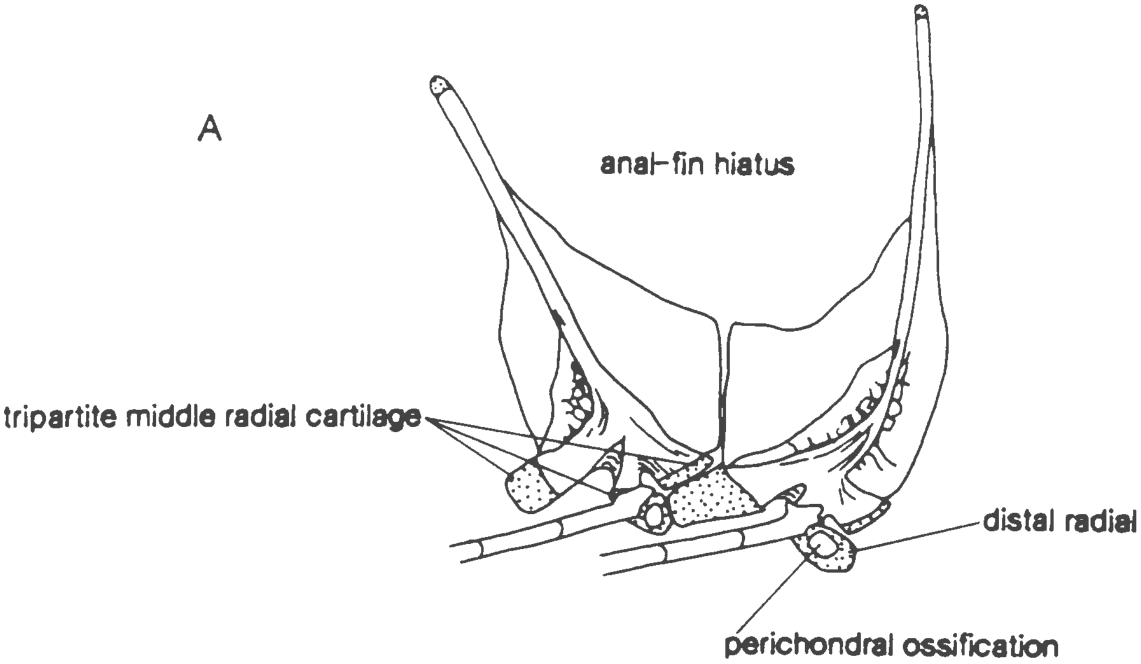

ovatus S. CHINA SEA
kiwiensis TASMAN SEA + NW. AUSTR.
matsubarai JAPAN. + NW. PAC. OC.
meteori EQ. INDO-PAC.
ruggeri TASMAN SEA
E
24, 25, 26"
D
20-23
C
12, 13(2), 14, 15, 16",
17, 18"', 19

FIGURE 52.-Anal-fin pterygiophores, right side, lateral view: A, hiatus pterygiophores, P. meteori, ZMUC P206931, 37.6 mm; B, anterior four pterygiophores, P. unispinus, AMS I.19292-008, 28.0 mm.


A
anal-fin hiatus
tripartite middle radial cartilage
distal radial
perichondral ossification

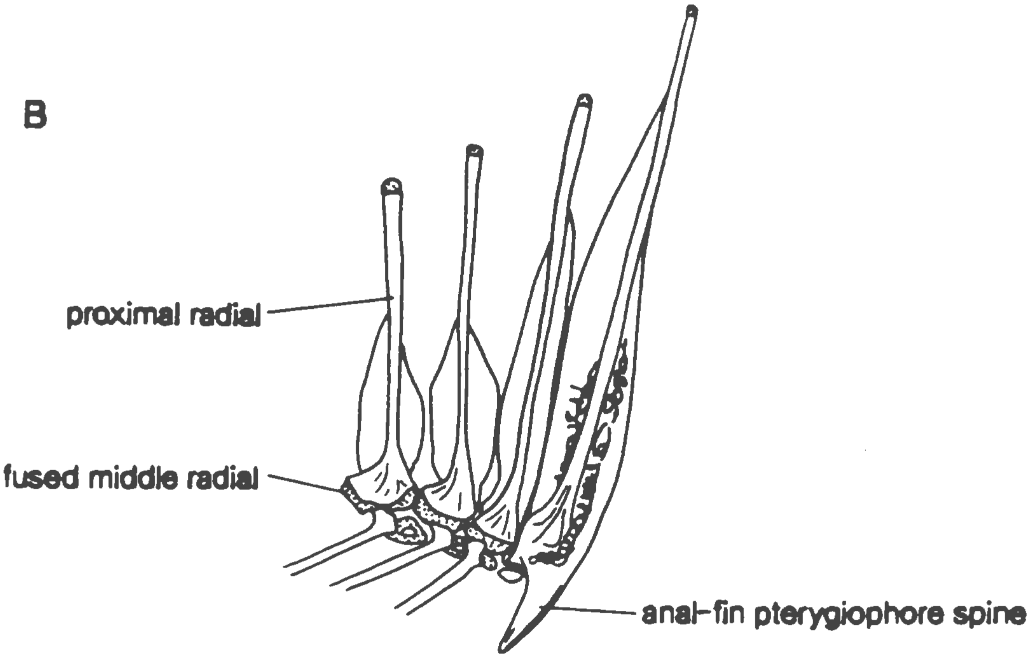

B
proximal radial
fused middle radial
anal-fin pterygiophore spine

FIGURE 53.-Anal-fin pterygiophores, right side, lateral view: Polyipnus soelae, AMS I.23425-011, 46.0 mm.

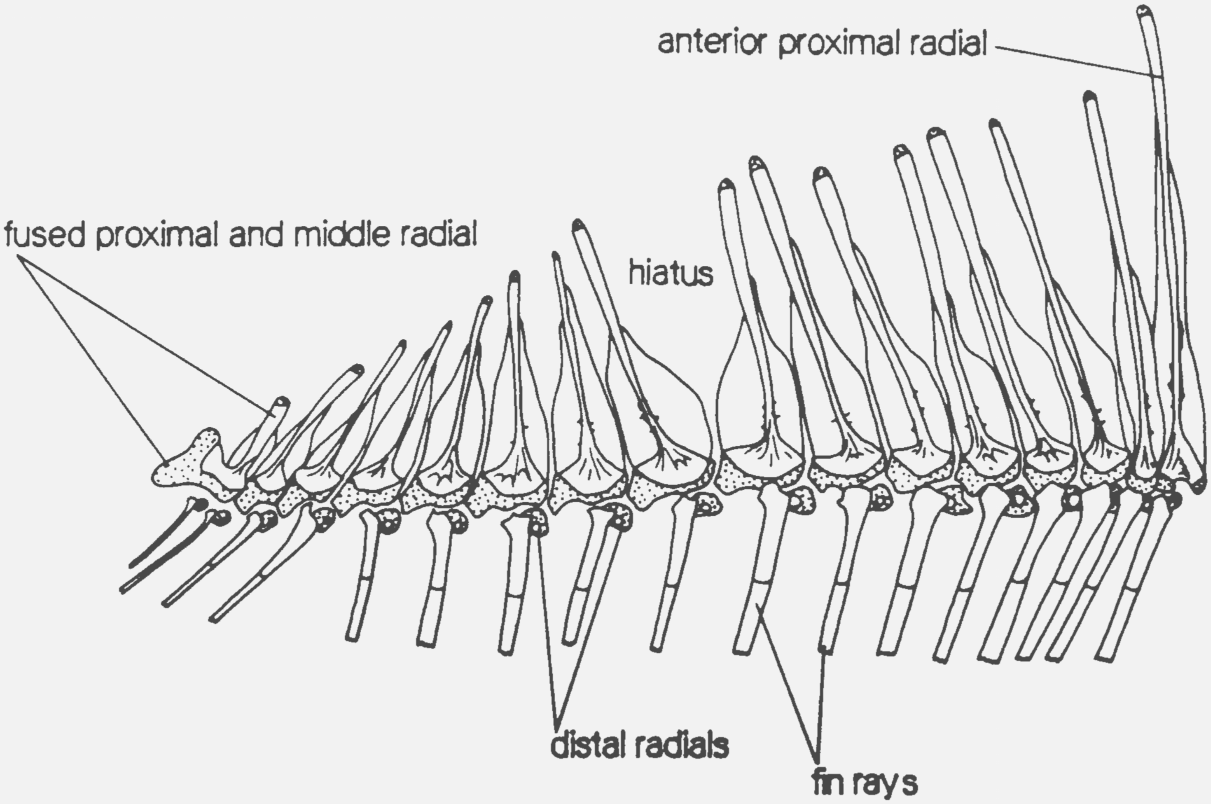

anterior proximal radial
fused proximal and middle radial
hiatus
distal radials
fin rays

FIGURE 54.-Pharyngobranchial bones, right side, medial view: A, *Polyipnus meteori*, ZMUC P206931, 37.6 mm; B, *P. clarus*, USNM 304745, 44.0 mm.

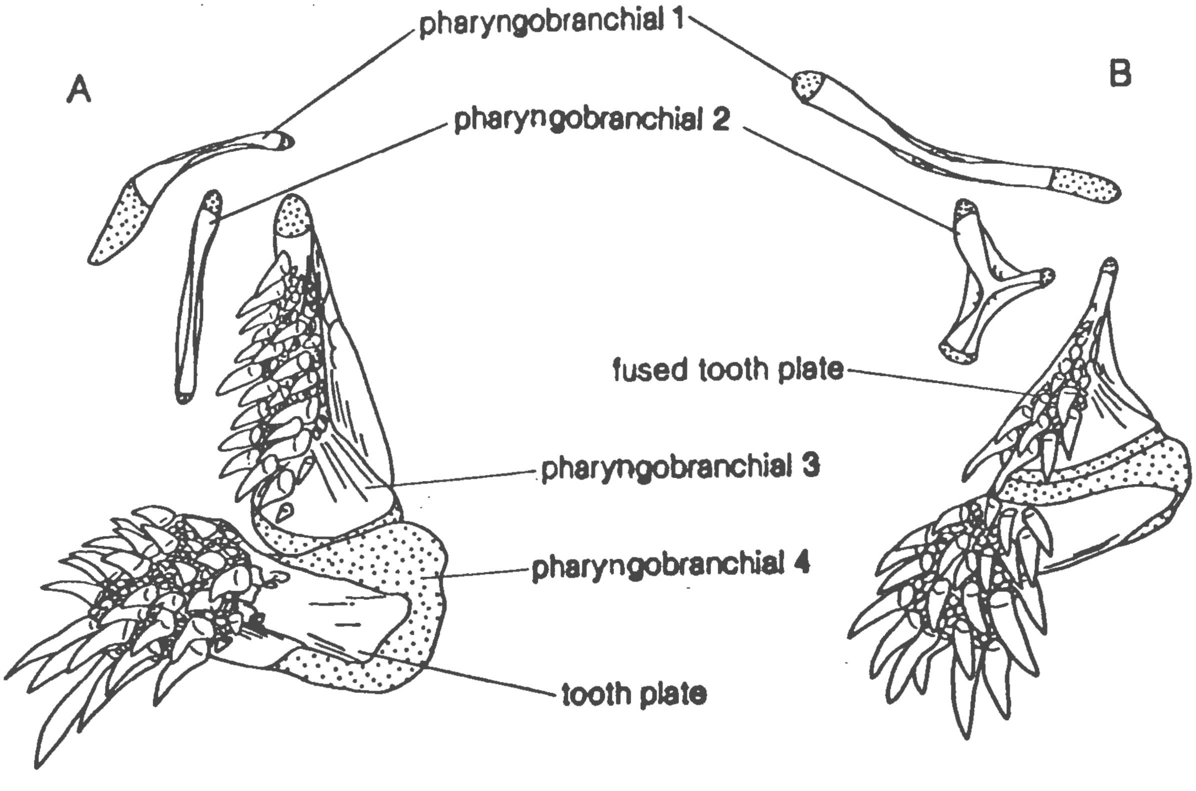

A
B
pharyngobranchial 1
pharyngobranchial 2
fused tooth plate
pharyngobranchial 3
pharyngobranchial 4
tooth plate

FIGURE 55.-Caudal skeleton, right side, lateral view: Polyipnus meteori, ZMUC P206931, 37.6 mm.

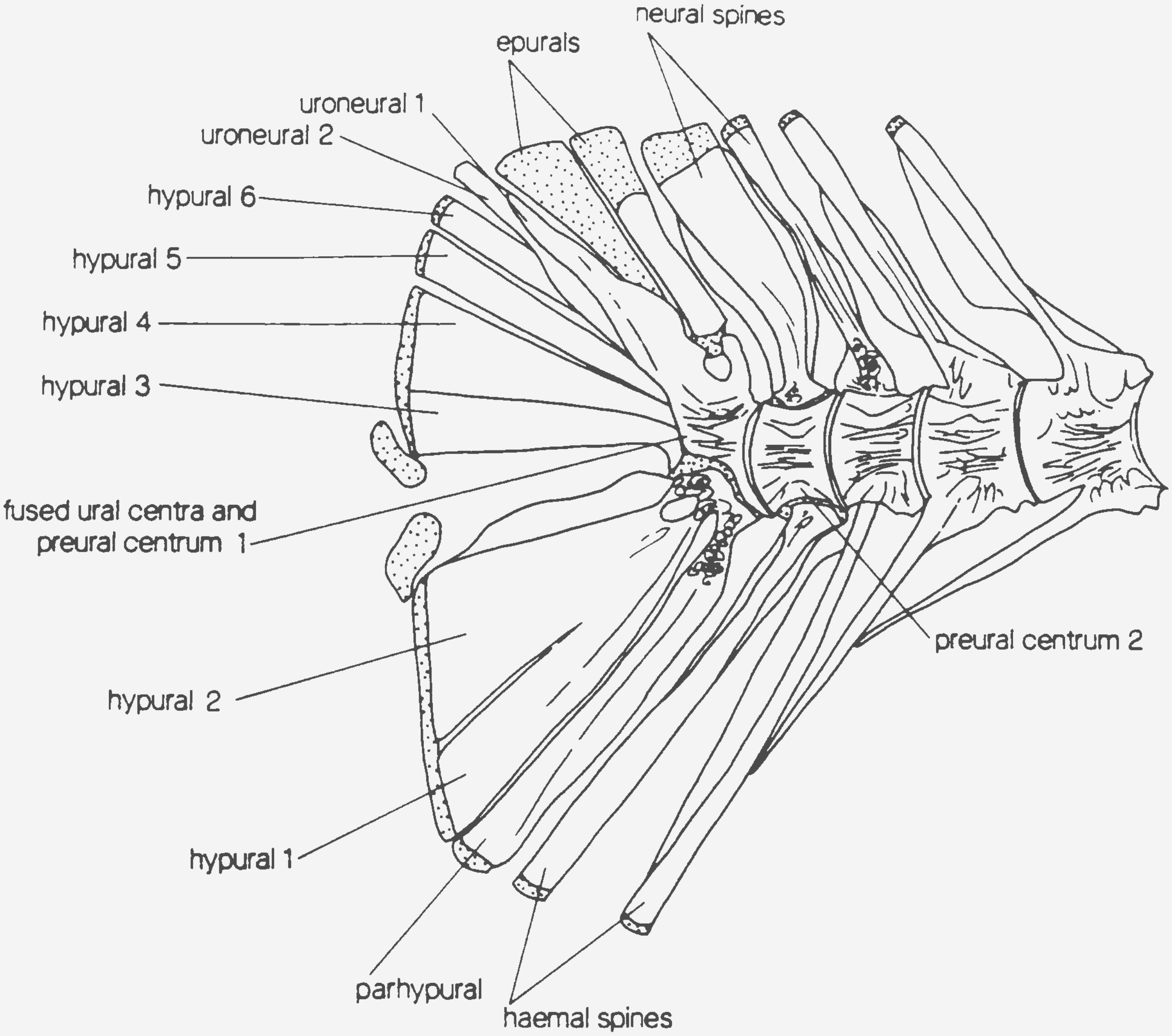

neural spines
epurals
uroneural 1
uroneural 2
hypural 6
hypural 5
hypural 4
hypural 3
fused ural centra and preural centrum 1
preural centrum 2
hypural 2
hypural 1
parhypural
haemal spines

FIGURE 56.-Cladogram of the *Polyipnus asteroides* species group. CARIBB. SEA, Caribbean Sea; E. ATL. OC., tropical/subtropical eastern Atlantic Ocean; INDO-AUSTR., Indo-Australian; W. ATL. OC., tropical/subtropical western Atlantic Ocean; W. INDIAN OC., western Indian Ocean. Derived characters marked on branches of diagram. States of multi-state characters given in parentheses. Total number of character state changes implied by the tree for inconsistent characters indicated by superscript tick marks.

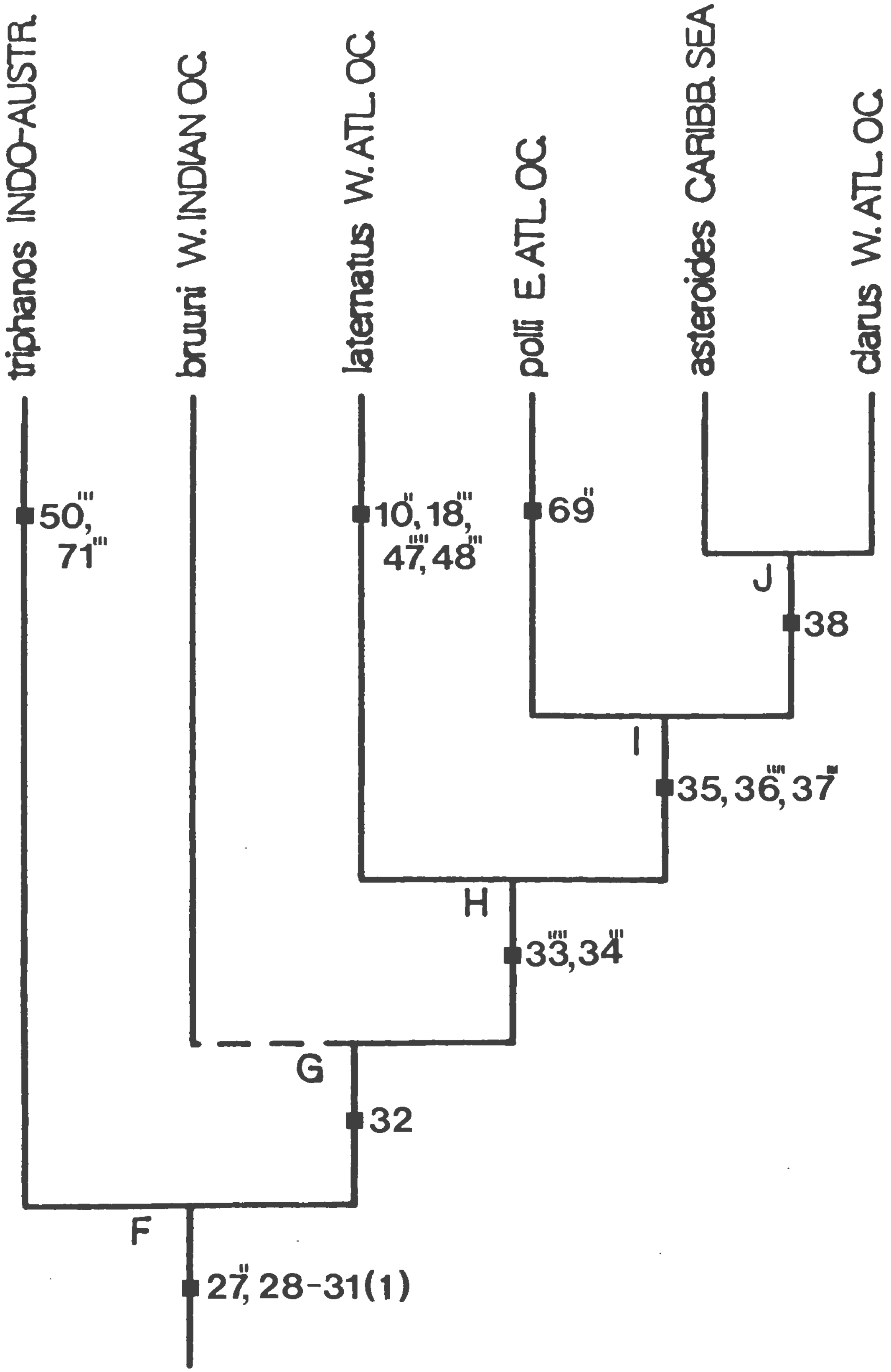

triphanos INDO-AUSTR.
bruuni W. INDIAN OC.
laternatus W. ATL. OC.
polli E. ATL. OC.
asteroides CARIBB. SEA
clarus W. ATL. OC.
50''', 71'''
10'', 18''', 47'''', 48'''
69''
J
38
I
35, 36'''', 37''
H
33'''', 34'''
G
32
F
27'', 28-31(1)

FIGURE 57.-Three anterior dorsal-fin pterygiophores, including dorsal blade, right side, lateral view: *Polyipnus clarus*, USNM 304745, 44.0 mm.

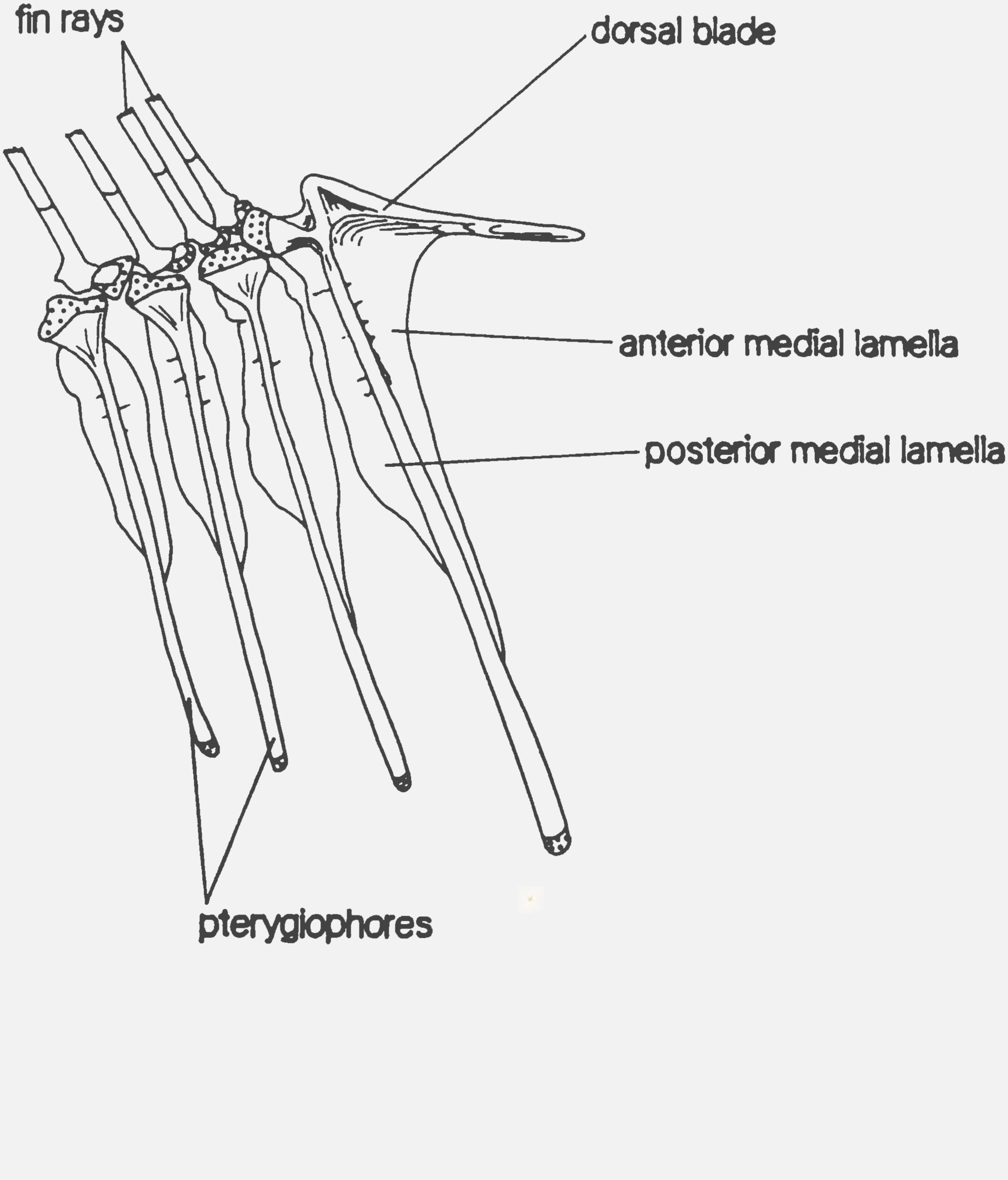

fin rays
dorsal blade
anterior medial lamella
posterior medial lamella
pterygiophores

FIGURE 58.-Two anterior dorsal-fin pterygiophores, including dorsal blade, right side, lateral view: Polyipnus danae, ZMUC P208577, 24.8 mm.

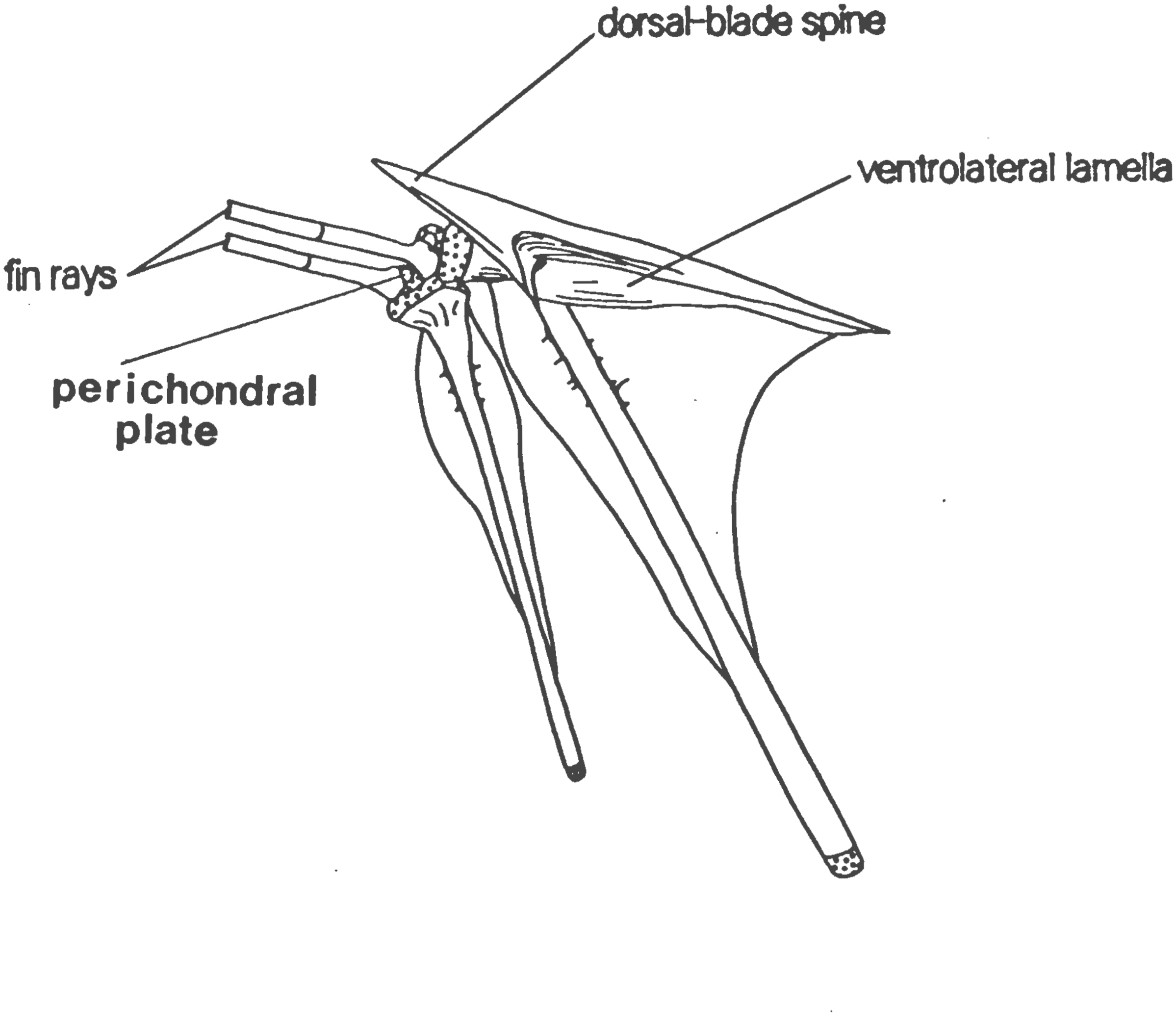

dorsal-blade spine
ventrolateral lamella
fin rays
perichondral plate

FIGURE 59.-Dorsal blade and dorsal-fin pterygiophores, right side, lateral view: Polyipnus soelae, AMS I.23425-011, 46.0 mm.

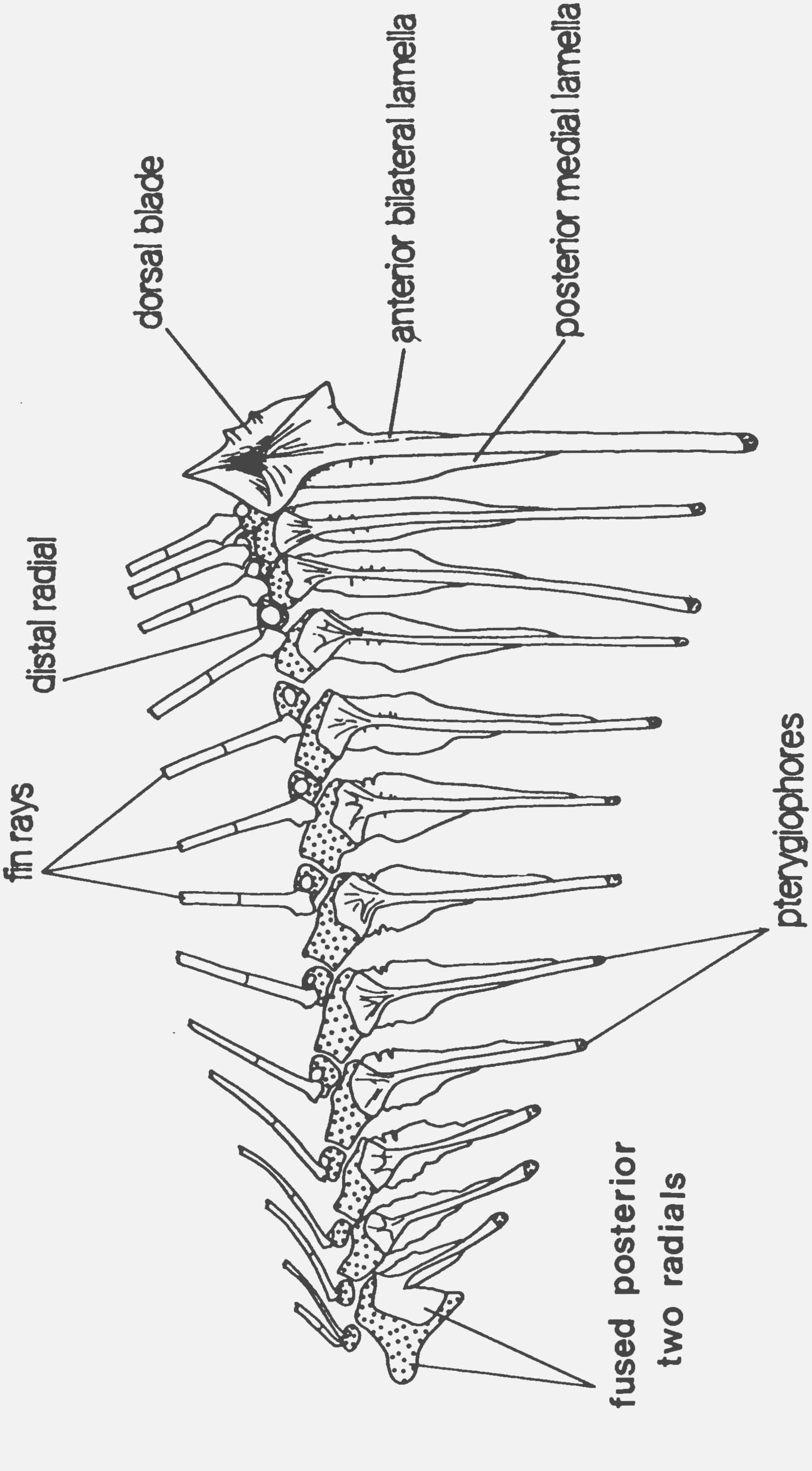
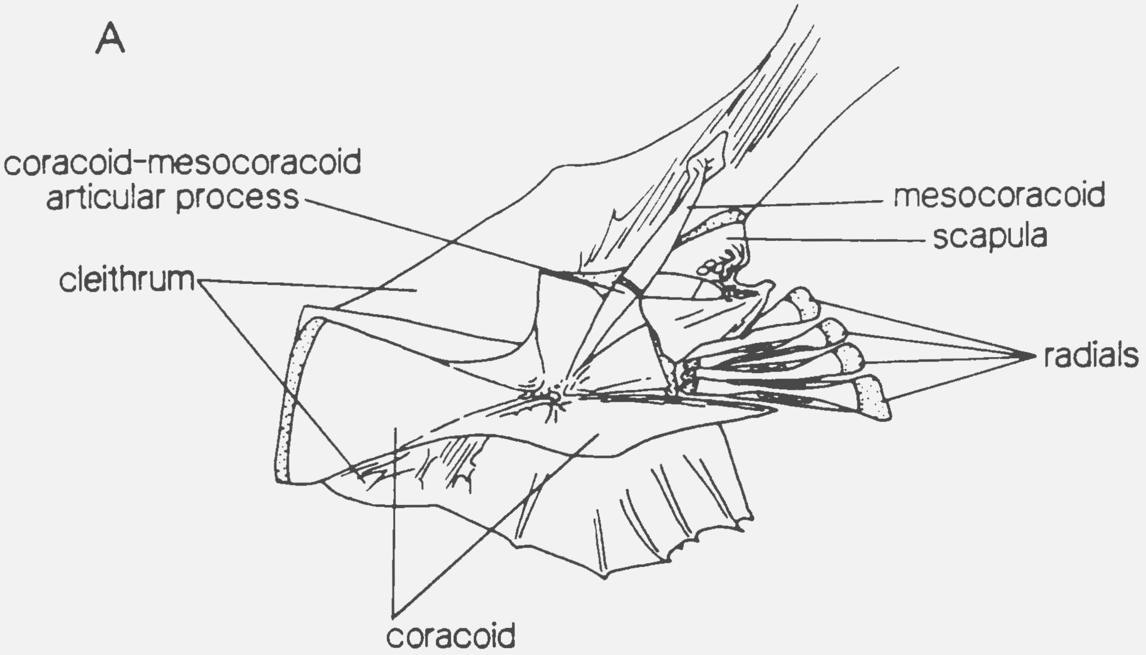

dorsal blade
anterior bilateral lamella
posterior medial lamella
distal radial
fin rays
pterygiophores
fused posterior two radials

FIGURE 60.-Ventral region of pectoral girdle, right side, Polyipnus soelae, AMS I.23425-011, 46.0 mm: A, medial view; B, lateral view.


A
coracoid-mesocoracoid
articular process
mesocoracoid
scapula
cleithrum
radials
coracoid

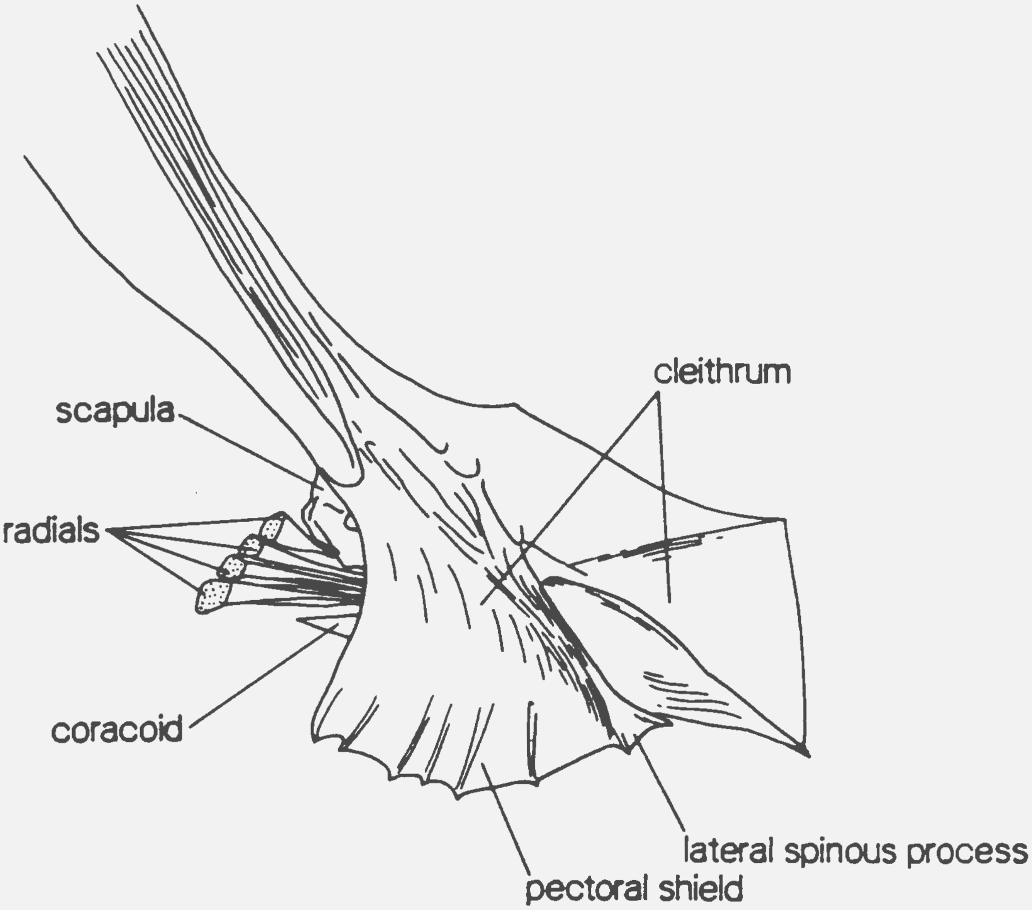

B
cleithrum
scapula
radials
coracoid
lateral spinous process
pectoral shield

FIGURE 61.-Ventral region of pectoral girdle, right side, medial view: *Polyipnus clarus*, USNM 304745, 44.0 mm.

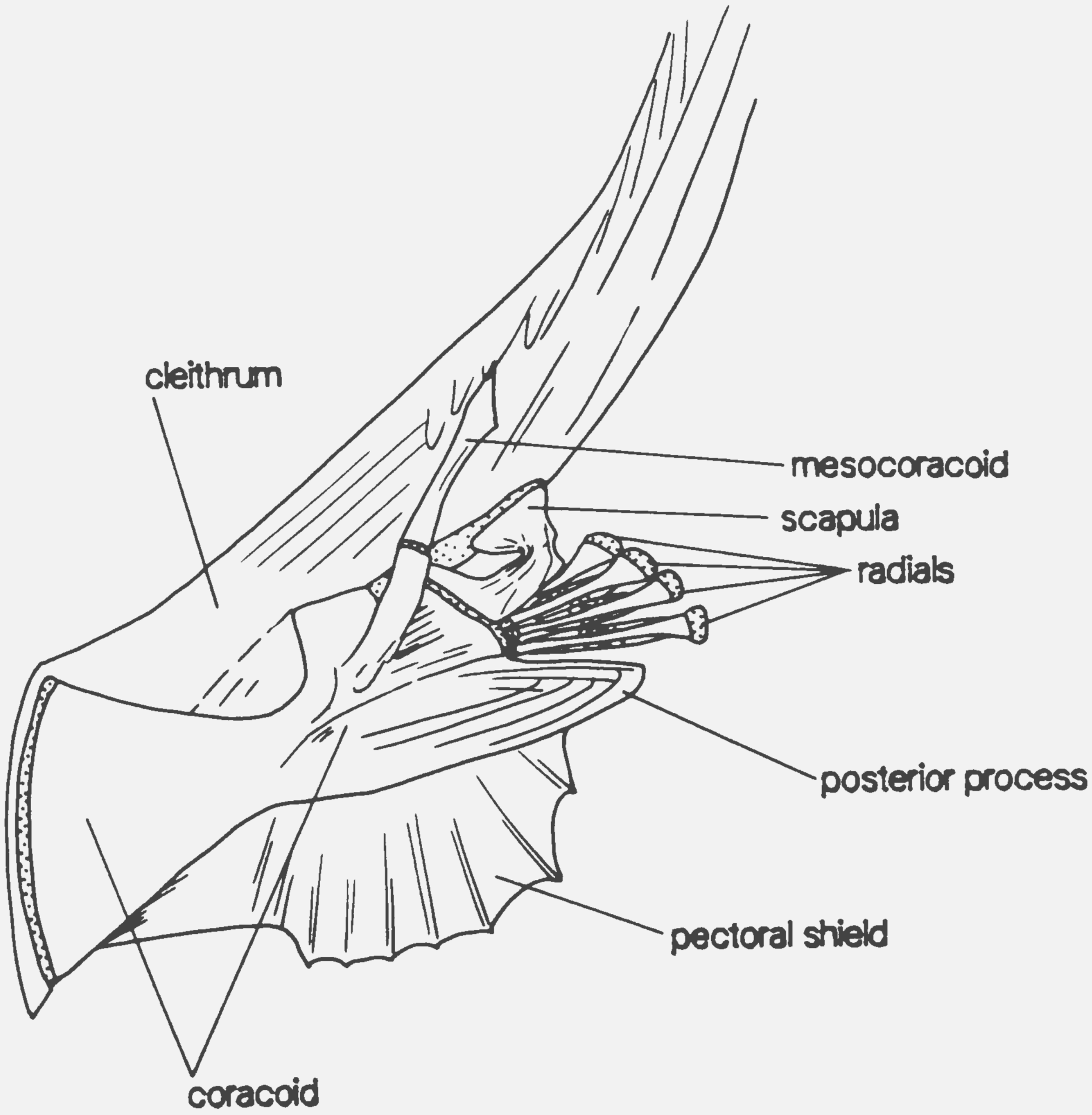

cleithrum
mesocoracoid
scapula
radials
posterior process
pectoral shield
coracoid

FIGURE 62.-Cladogram of the *Polyipnus omphus* species group. INDO-E. AUSTR., Indo-East Australian; EQ. INDO-PAC, equatorial Indo-Pacific, west to Africa and east to central Pacific; S. CHINA SEA, South China Sea. Derived characters marked on branches of diagram. States of multi-state characters given in parentheses. Total number of character state changes implied by the tree for inconsistent characters indicated by superscript tick marks.

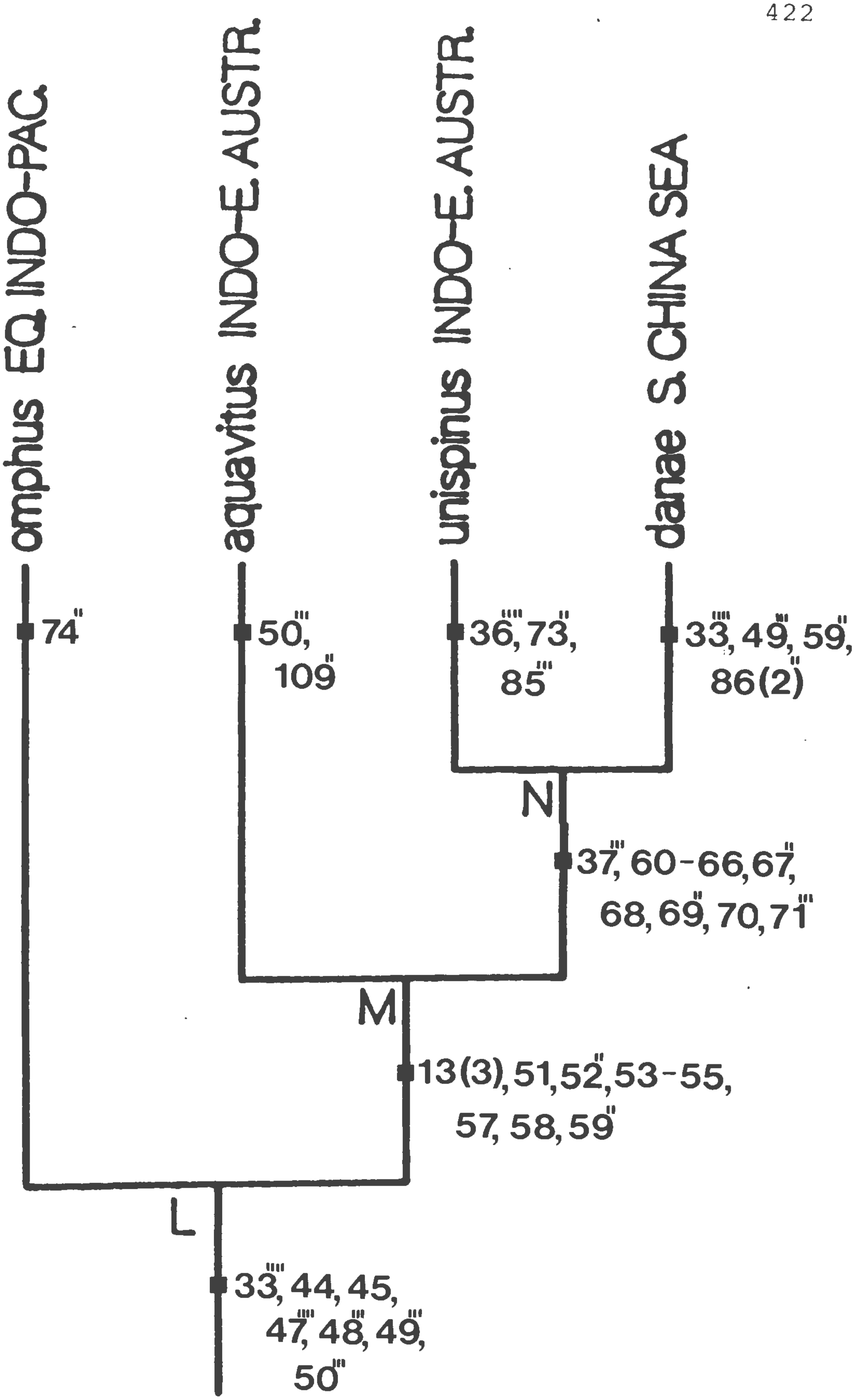

omphus EQ. INDO-PAC.
aquavitus INDO-E. AUSTR.
unispinus INDO-E. AUSTR.
danae S. CHINA SEA
74''
50''', 109''
36'''', 73'', 85'''
33'''', 49'', 59'', 86(2'')
N
37''', 60-66, 67'', 68, 69'', 70, 71'''
M
13(3), 51, 52'', 53-55, 57, 58, 59''
L
33'''', 44, 45, 47'''', 48''', 49''', 50''

FIGURE 63.-Frontal and parietal, right side, lateral view: *Polyipnus unispinus*, AMS I.19292-008, 28.0 mm.

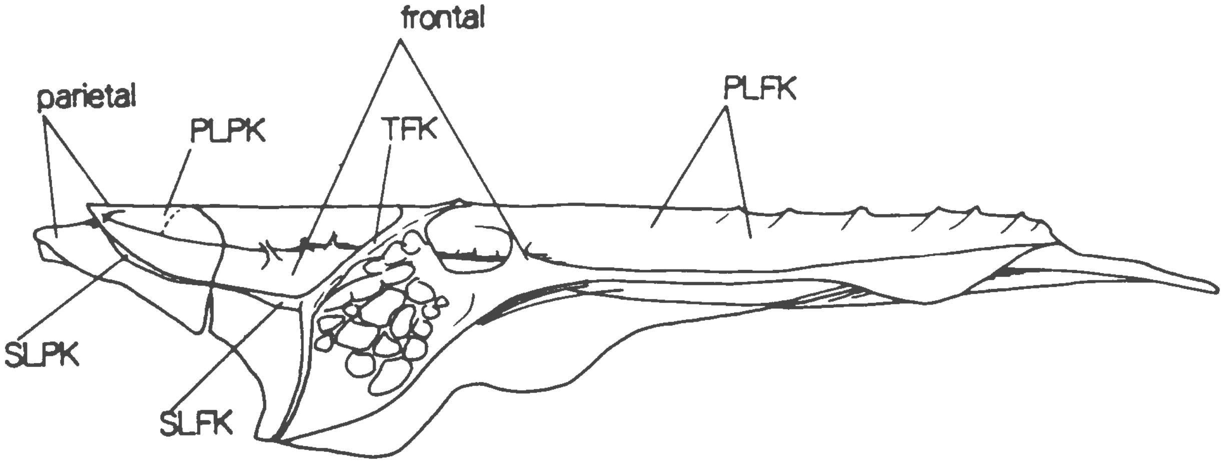

frontal
parietal
PLPK
TFK
PLFK
SLPK
SLFK

FIGURE 64.-Ceratobranchial of the fifth gill arch, left side, dorsal view: A, *Polyipnus unispinus*, AMS I.19292-008, 28.0 mm; B, *P. soelae*, AMS I.23425-011, 46.0 mm.

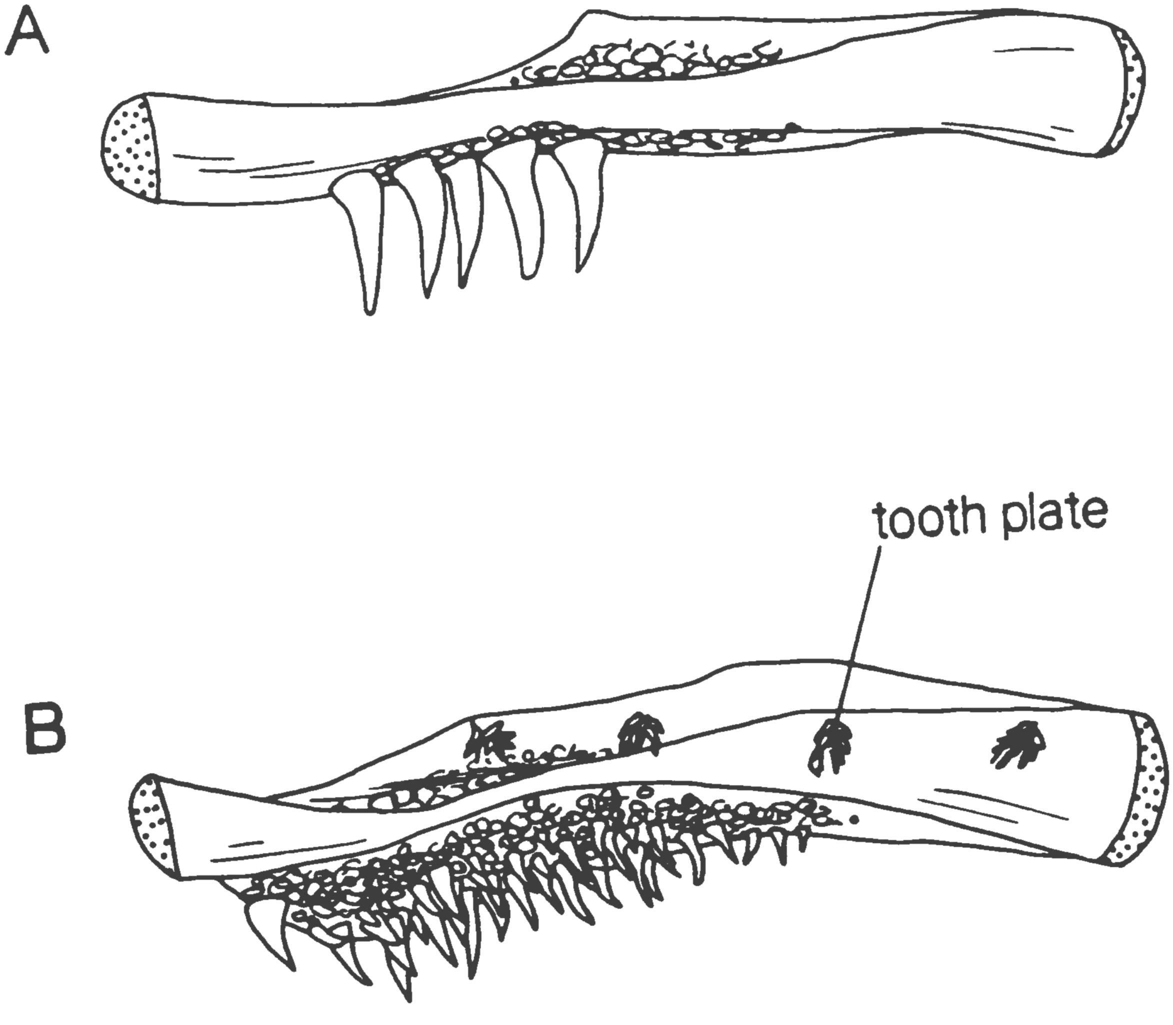

A
B
tooth plate

FIGURE 65.-Cladogram of the _Polyipnus_ _spinosus_ species group. CORAL SEA (W), western Coral Sea, off Queensland; E. INDIAN OC., eastern Indian Ocean, Andaman Sea; E. INDONESIA, eastern Indonesia, excluding northwestern Australian coast and South China Sea; GR. AUSTR. BGT., Great Australian Bight; JAPAN., Japanese Archipelago; NW. AUSTR., northwestern Australian coast; PHILIPP. SEA, Philippine Sea; SE. PAC. OC., southeastern Pacific Ocean, Sala-y-Gomez; W. INDIAN OC., western Indian Ocean off Africa; W. PAC. OC., western Pacific Ocean (off Japan and in Tasman Sea). Derived characters marked on branches of diagram. States of multi-state characters given in parentheses. Total number of character state changes implied by the tree for inconsistent characters indicated by superscript tick marks.

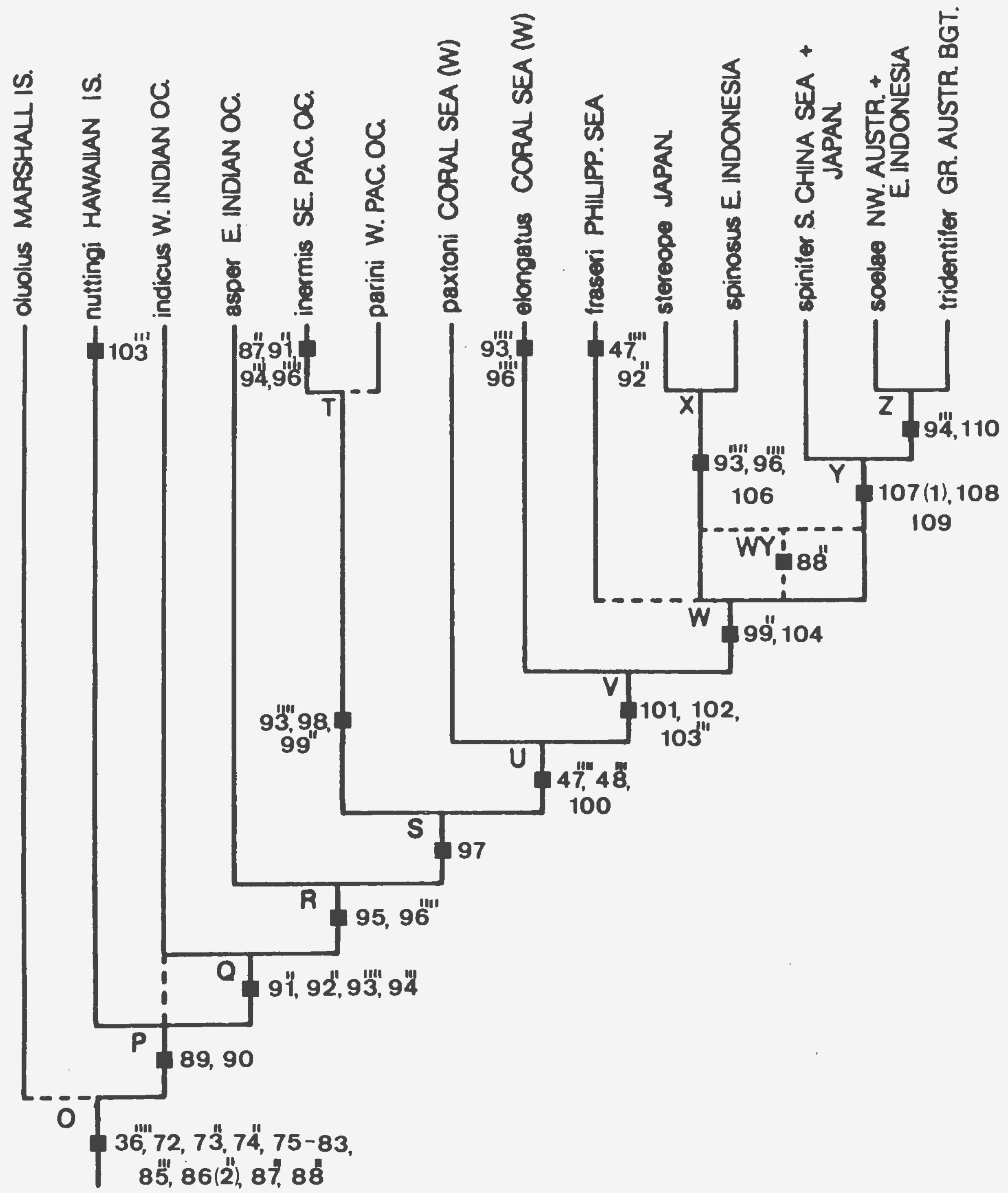
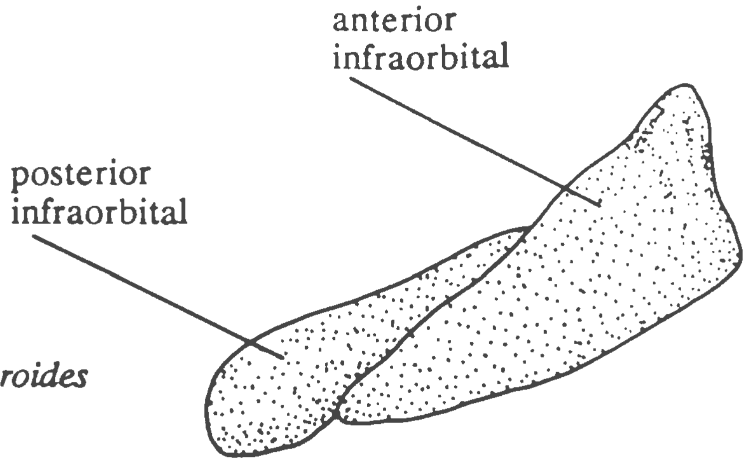
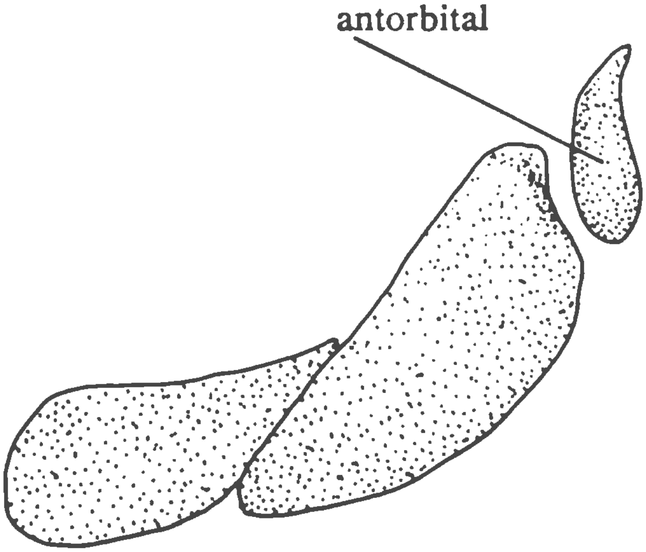

oluolus MARSHALL IS.
nuttingi HAWAIIAN IS.
indicus W. INDIAN OC.
asper E. INDIAN OC.
inermis SE. PAC. OC.
parini W. PAC. OC.
paxtoni CORAL SEA (W)
elongatus CORAL SEA (W)
fraseri PHILIPP. SEA
stereope JAPAN.
spinosus E. INDONESIA
spinifer S. CHINA SEA + JAPAN.
soelae NW. AUSTR. + E. INDONESIA
tridentifer GR. AUSTR. BGT.
103''
87'', 91'', 94'', 96''''
93'''', 96''''
47'''', 92''
T
X
Z
94''', 110
93'''', 96'''', 106
Y
107 (1), 108 109
WY
88''
W
99'', 104
V
101, 102, 103'''
93'''', 98, 99''
U
47'''', 48''', 100
S
97
R
95, 96''''
Q
91'', 92'', 93'''', 94''
P
89, 90
O
36'''', 72, 73'', 74'', 75-83, 85''', 86(2), 87'', 88''

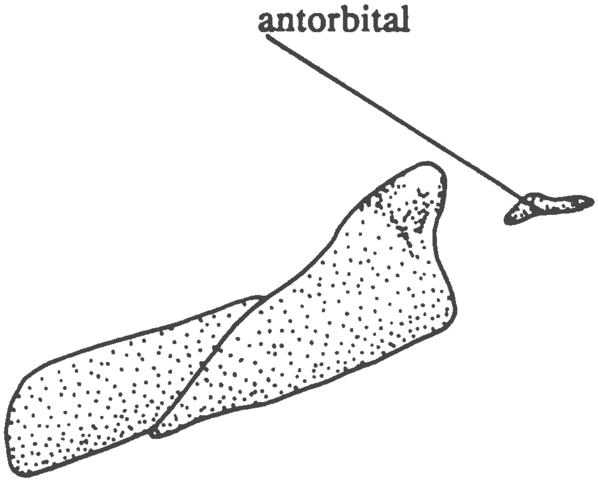
FIGURE 66.-Configuration of orbital bones, right side, lateral view: A, *Polyipnus meteori*, ZMUC P206931, 37.6 mm; B, *P. asteroides*, CAS 61110, 58.0 mm; C, *P. stereope*, NSMT P.6772, 37.0 mm.



A *Polyipnus asteroides*

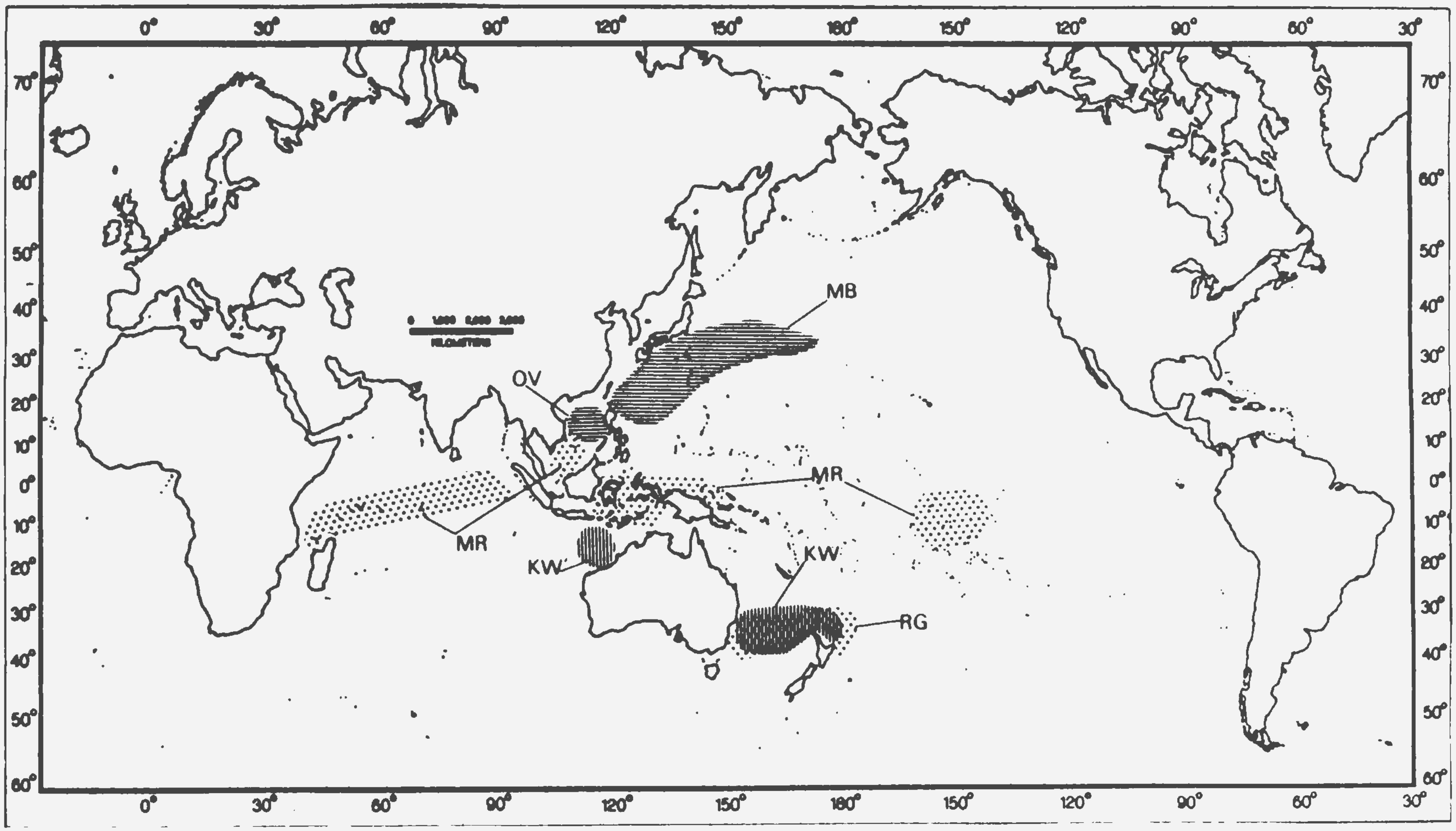


B *Polyipnus meteori*



C *Polyipnus stereope*

FIGURE 67.-Generalized distribution of the *P*. *meteori* species group. KW, *P*. *kiwiensis*; KW´, *P*. aff. *kiwiensis*; MB, *P*. *matsubarai*; MR, *P*. *meteori*; OV, *P*. *ovatus*; RG, *P*. *ruggeri*.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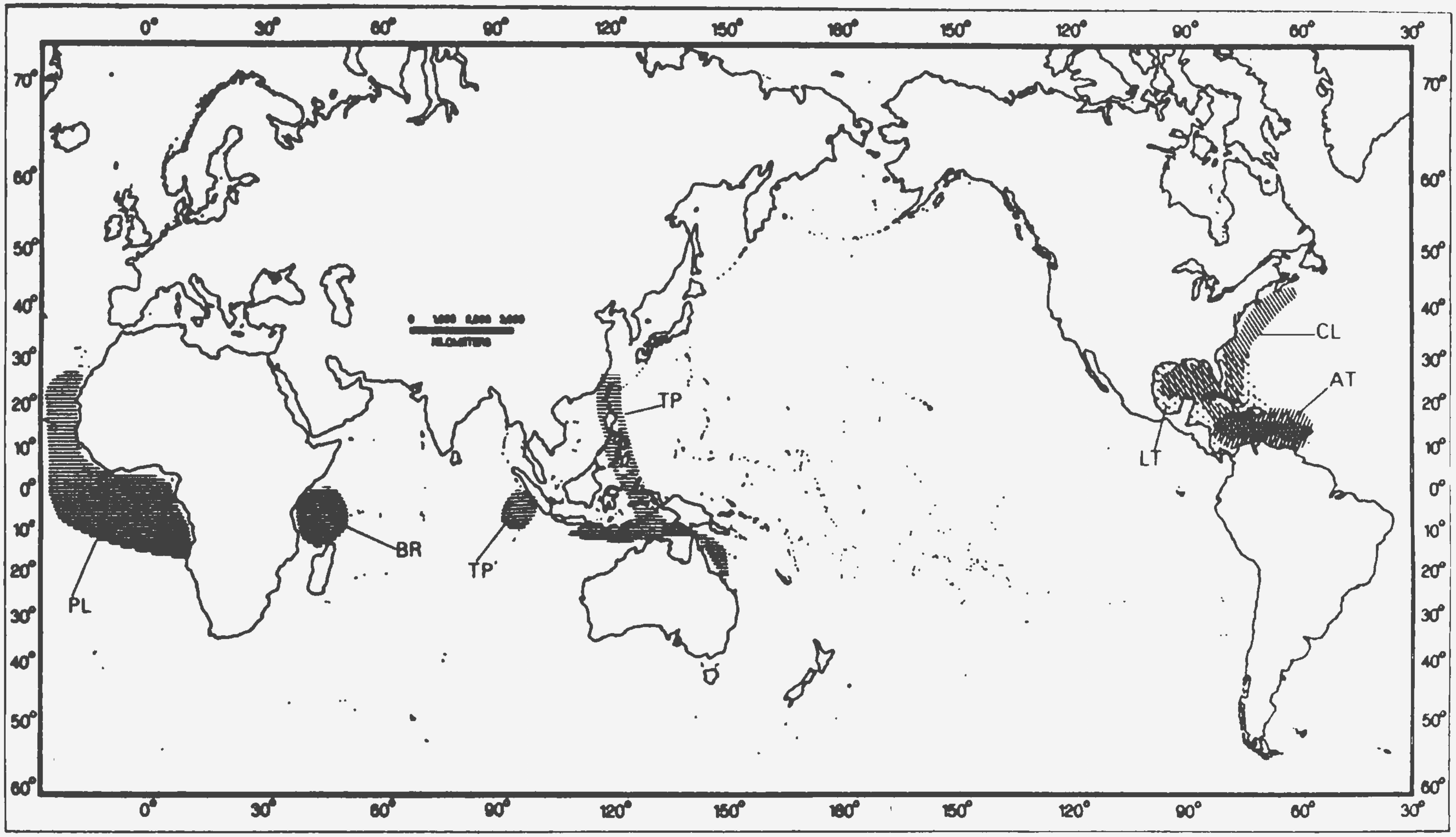
KILOMETERS
MB
OV
MR
MR
KW
KW
RG

FIGURE 68.-Generalized distribution of the *P*. *asteroides* species group. AT, *P*. *asteroides*; BR, *P*. *bruuni*; CL, *P*. *clarus*; LT, *P*. *laternatus*; PL, *P*. *polli*; TP, *P*. *triphanos*; TP´, *P*. aff. *triphanos*.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KILOMETERS
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TP
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FIGURE 69.-Generalized distribution of the *P. omphus* species group.. AQ, *P. aquavitus*; DN, *P. danae*; OM, *P. omphus*; UN, *P. unispinus*.

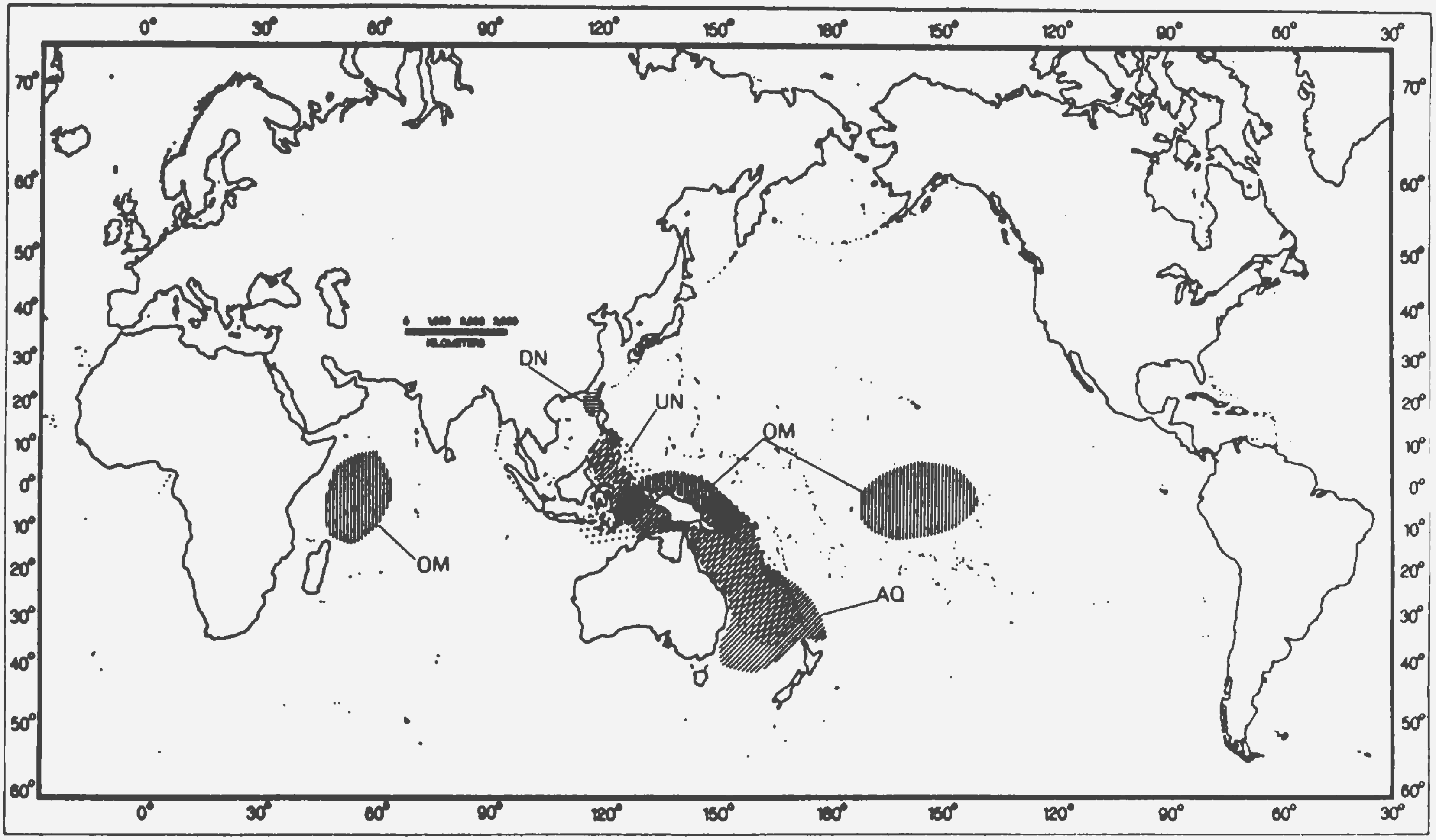
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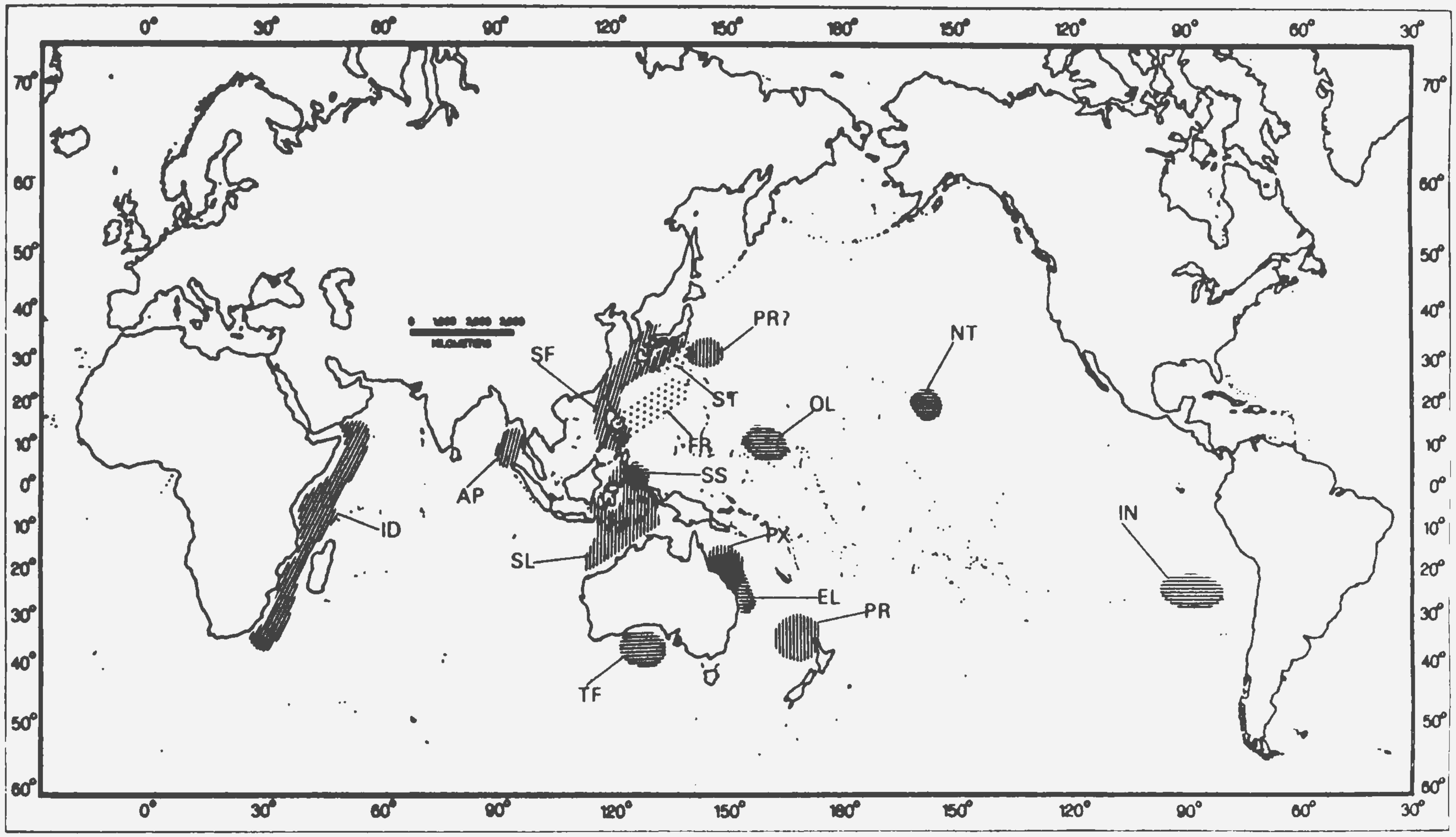
FIGURE 70.-Generalized distribution of the *P*. *spinosus* species group. AP, *P*. *asper*; EL, *P*. *elongatus*; FR, *P*. *fraseri*; ID, *P*. *indicus*; IN, *P*. *inermis*; NT, *P*. *nuttingi*; OL, *P*. *oluolus*; PR, *P*. *parini*; PX, *P*. *paxtoni*; SF, *P*. *spinifer*; SL, *P*. *soelae*; SS, *P*. *spinosus*; ST, *P*. *stereope*; TF, *P*. *tridentifer*.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APPENDIX 1

Binary matrix of distributional characters used in Brooks Parsimony Analysis. Missing areas coded as '9'.

AREAS	TAXA
TASMAN	00111011011100099
AUSTRBGT	00099000099900111
INDONNOR	01011111011101011
INDONSW	01011001011101011
SOCHINA	01011000111110001
JAPAN	10001000099910001
EQINDIAN	01011100000100099
EQPACIF	01011100000100099
CORALSEA	00000011011100099
OUTGROUP	00000000000000000

APPENDIX 2

Abbreviations and definitions of geographic areas.

Areas used in Parsimony Analysis and cladograms

CORAL SEA (E)	Coral Sea, not including coastal Queensland
CORAL SEA (W)	Coral Sea, coastal Queensland only
E. INDONESIA	eastern Indonesia: Sulu to Timor seas and vicinity
EQ. INDIAN OC.	Equatorial Indian Ocean
EQ. INDO-PAC.	Equatorial Indo-Pacific region (Equatorial Indian plus Pacific Ocean areas
GR. AUSTR. BGT.	Great Australian Bight
INDO-E. AUSTR.	Indo-East Australia: eastern Indonesia and eastern Coral Sea
JAPAN.	Japanese Archipelago
PHILIPP. SEA	Philippine Sea
S. CHINA SEA	South China Sea
TASMAN SEA	Tasman Sea, Australian and New Zealand coasts only

Areas not used in Parsimony Analysis

CARIBB. SEA	Caribbean Sea and Greater Antilles
E. ATL. OC.	tropical/subtropical eastern Atlantic Ocean

E. INDIAN OC.	Andaman Sea, eastern Indian Ocean
EQ. INDIAN OC.	equatorial Indian Ocean
EQ. PAC. OC.	equatorial western and central Pacific Ocean
HAWAIIAN IS.	Hawaiian Islands
INDO-AUSTR.	Indo-Australia: northwest Australia, eastern Indonesia and western Coral Sea
MARSHALL IS.	Marshall Islands
NW. AUSTR.	continental slope of northwestern Australia
NW. PAC. OC.	northwestern Pacific Ocean
SE. PAC. OC.	Sala-y-Gomez Ridge, southeastern Pacific Ocean
W. ATL. OC.	tropical/subtropical western Atlantic Ocean
W. INDIAN OC.	Agulhas region, western Indian Ocean
W. PAC. OC.	western Pacific Ocean

APPENDIX 3

TABLE A-1.-Tow and sounding depths for collections of 13 _Polyipnus_ species. Institutional code and station number provided for uncatalogued collections. R/V _Dana_ represented in table by D.

Species	Catalogue No.	Tow Depth	Sounding Depth (m)
kiwiensis	AMS I.15984-002	0-357 m	390
	AMS I.17863	0-366 m	360
	AMS I.19855	448-461 m	448-460
	AMS I.17861-001	0-411 m	405
	AMS I.17864	0-366 m	360
meteori	ZMUC P206928	1000 mwo	2700
	ZMUC P206929	600 mwo	4700
	ZMUC P206930	1000 mwo	1565
	ZMUC P206931	1000 mwo	1890
	ZMUC (D Sta. 3951 II)	600 mwo	2380
	ZMUC (D Sta. 3800 I)	600 mwo	1500
ruggeri	AMS I.20066	0-650 m	2000
	AMS I.27166	0-457 m	4072
	AMS I.21372	0-750 m	1500
	AMS I.20312	0-100 m	1800
	ZMUC P207118	1000 mwo	4775
polli	ZMUC (D Sta. 4007 I)	1000 mwo	2675
	ZMUC (D Sta. 4000 I)	1000 mwo	3760
	ZMUC (D Sta. 4007 XI)	1000 mwo	2425
	ZMUC (D Sta. 4003 VIII)	600 mwo	3210
triphanos	AMS I.25816-008	0-300 m	300
	AMS I.24338-001	150-280 m	150-280
	ZMUC P206962	600 mwo	450
	ZMUC P206963	600 mwo	1770
	ZMUC (D Sta. 3881 I)	500 mwo	540
aquavitus	AMS I.19762-002	0-800 m	2300
	AMS I.20316-005	0-900 m	3700
	AMS I.19761-029	0-550 m	2000
	AMS I.20310-017	0-625 m	2900
	AMS I.16492-008	0-250 m	1350-1400
	ZMUC P206916	1000 mwo	3660
	ZMUC P206907	1000 mwo	3190
danae	ZMUC P206919	2000 mwo	3225
	ZMUC P206920	1000 mwo	2150
omphus	ZMUC P206932	1000 mwo	4000
	ZMUC P206933	1500 mwo	1010
	ZMUC P206934	1200 mwo	2080
	ZMUC P207116	1000 mwo	3160
unispinus	AMS I.19287-003	0-1000 m	1937-2101
	AMS I.19284-007	0-2000 m	3654
	AMS I.19292-007	0-550 m	900-1100

continued ...

TABLE A-1 continued:

Species	Catalogue No.	Tow Depth	Sounding Depth (m)
unispinus	ZMUC P207119	2000 mwo	3040
	ZMUC P206965	2000 mwo	3040
elongatus	AMS I.21795-007	731 m	731
	AMS I.20518-005	548 m	548
paxtoni	AMS I.25825-009	0-300 m	300
	AMS I.25816-006	0-300 m	300
soelae	AMS I.22808-028	404-420 m	404-420
	AMS I.22817-014	492-520 m	492-520
	AMS I.23423-001	0-376 m	376
	AMS I.23425-011	0-400 m	400
tridentifer	AMS I.18711-014	640-650 m	640-650

APPENDIX 4

Additional collections of Polyipnus aquavitus examined.

Other Material: IOAN uncat. (3, 18.4-24.5 mm), 29°52'S 168°48'E to 29°49'S 168°53'E, 500-0 m, R/V Dmitry Mendeleev Cr. 16, Sta. 1261, 04 Jan 1976. LACM 44481 (4, 23.0-31.0 mm), 04°43.7'S 129°00'E, 420-500 m, R/V Alpha Helix Sta. 69, 0200-0300 h, 18 Apr 1975. LACM 38588 (2, 21.0-26.0 mm), 04°57.0'S 130°08.0'E, 350-550 m, R/V Alpha Helix Sta. 92, 1500-1600 h, 5 May 1975. LACM 36074 (3, 22.0-25.0 mm), 00°32.0'S 129°08.3'E, 450-1100 m, R/V Alpha Helix Sta. 120, 1125-1325 h, 16 May 1975. LACM 36075 (1, 23.0 mm), 00°41.7'S 128°55.7'E, 1000-1400 m, R/V Alpha Helix Sta. 121, 1730-1930 h, 16 May 1975. LACM 36062 (8, 16.0-31.0 mm), 00°13.5'S 128°23.7'E, 350-390 m, R/V Alpha Helix Sta. 128, 0249-0349 h, 18 May 1975. LACM 44503 (2, 31.0-32.0 mm), 08°41.0'N 121°19.3'E, 0-50 m, R/V Alpha Helix Sta. 177, 2320-0012 h, 4 Jun 1975. LACM 36040 (5, 14.0-21.0 mm), 02°45.3'S 127°55.1'E, 0-2000 m, R/V Alpha Helix Sta. 27, 0150-0800 h, 1 Apr 1975. LACM 44493 (17, 21.2-30.4 mm), 00°9.4'S 128°33.2'E, 420-500 m, R/V Alpha Helix Sta. 131, 1130-1230 h, 18 May 1975. SIO 84-15 (1, 34.0 mm), 34°27'S 151°38'E to 34°20'S 151°40'E, 23 May 1978. MCZ 89815 (1, 29.5 mm), 14°28'S 147°14'E, 1820 mwo, R/V Lady Basten, 04 Dec 1981. SIO 69-19-10 (1, 23.4 mm), 06°00.5'N 122°35.6'E, 21 Apr 1968. SIO 77-184 (2, 27.0-27.1

mm), 05°21.2'S 133°34.7'E, 0-1500 m, 19 Sep 1976. USNM 298928 (1, 12.8 mm), 26°21'S 177°39'E to 26°26'S 177°26'E, R/V Eltanin Sta. 31-24A, 13 Dec 1967. USNM 298927 (2, 7.6-15.4 mm), 33°20'S 172°57'E to 32°23'S 172°49'E, R/V Eltanin Sta. 31-26A, 15 Dec 1967. USNM 298925 (9, 10.6-18.4 mm), 29°08'S 175°28'E to 29°14'S 175°25'E, R/V Eltanin Sta. 31-25A, 14 Dec 1967. ZMA uncat. (16, 12.8-31.0 mm), 06°32.8'S 133°02.8'E, 109-299 m, R/V Snellius-II, Cr. 321, Leg 8, Sta. 69-2, 2206-2306 h, 20 Feb 1985. ZMUC P206916 (1, 26.0 mm), 01°42'N 124°29'E, 1000 mwo, R/V Dana Sta. 3682 I, 2120-2320 h, 29 Mar 1929. ZMUC P206906 (1, 40.0 mm), 27°21'S 175°11'E, 1000 mwo, R/V Dana Sta. 3623 I, 2005-2105 h, 09 Dec 1928. ZMUC P206907 (1, 30.0 mm), 29°40'S 170°34'E, 1000 mwo, R/V Dana Sta. 3625 I, 2005-2105 h, 11 Dec 1928.

APPENDIX 5

Character data matrix for phylogenetic analysis of <u>Polyipnus</u> species, including three outgroups. Format compatible with PAUP version 3.0i. Missing data coded as '?'.

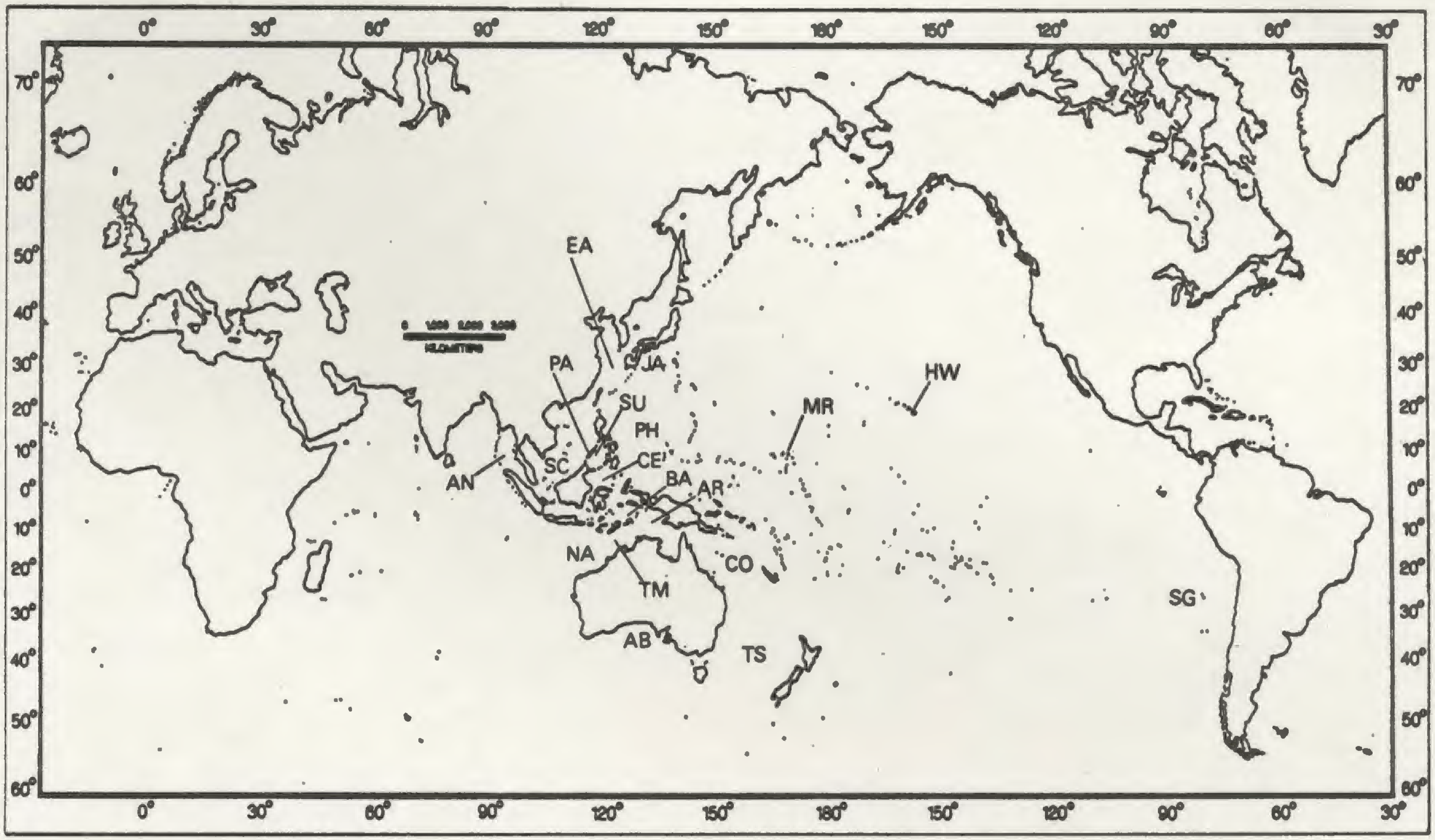
```
Argyripnus       000000000?  000?010?00  0000001000  ?001000??0  0?000?0?00  0100???000  00100010
00 00000?0?00  000?01?100  000000?0?0  000??00000  0000000000  000
Sternoptyx       000?000??0  000??10?00  000?00?000  0010011?00  0?000?0?10  0000???000  00000000
?0 1000000?0?  000?10?100  00000000?0  000??00000  1111111111  111
Argyropelecus    0000000??0  000?010100  ??0001?000  0001001?00  0?000?0?00  0000??0000  00000000
00 0000000?0?  000?10?1?0  00100000?0  001??00000  1111111111  111
ruggeri          1111111111  1121111111  1111110000  0000000000  0?000?0000  00000?0000  00000000
00 0000000?00  000?010100  00000000?0  000??00000  1111111100  000
meteori          1111111111  1121111111  1111110000  0000000000  0?000?0000  00000?0000  00000000
00 0000000?00  000?010100  00000000?0  000??00000  1111111100  000
matsubarai       1111111111  1121111111  1110000000  0000000000  0?000?0000  00000?0000  00000000
00 0000000?00  000?010100  00000000?0  000??00000  1111111100  000
kiwiensis        1111111111  1121111110  0000000000  0000000000  0?000?0000  00000?0000  00000000
00 0000000?00  000?010100  00000000?0  000??00000  1111111100  000
triphanos        1111111111  1000000000  0000001111  1000000000  0?000?0001  00000?0000  00000000
00 1000000?00  000?000100  00000000?0  000??00000  1111111100  000
laternatus       1111111110  1000000100  0000001111  1111000000  0?000?1100  00000?0000  00000000
00 0000000?00  000?000100  00000000?0  000??00000  1111111100  000
asteroides       1111111111  1000000000  0000001111  1111111100  0?000?0000  00000?0000  00000000
00 0000000?00  000?000100  00000000?0  000??00000  1111111100  000
clarus           1111111111  1000000000  0000001111  1111111100  0?000?0000  00000?0000  00000000
00 0000000?00  000?000100  00000000?0  000??00000  1111111100  000
polli            1111111111  1000000000  0000001111  1111111000  0?000?0000  00000?0000  00000000
10 0000000?00  000?000100  00000000?0  000??00000  1111111100  000
danae            1111110000  0030000000  0000000000  2000001011  1?111?1101  11111?1101  11111111
11 1000000?00  000?020100  00000000?0  000??00000  1111111100  000
unispinus        1111110000  0030000000  0000000000  2010011011  1?111?1111  11111?1111  11111111
11 1010000?00  000?1?0100  00000000?0  000??02000  1111111100  000
aquavitus        1111110000  0030000000  0000000000  2010000011  1?111?1110  11111?1110  00000000
00 0000000?00  000?0?0100  00000000?0  000??00010  1111111100  000
omphus           1111110000  0000000000  0000000000  2010000011  1?111?1111  00000?0000  00000000
00 0001000?00  000?010100  00000000?0  000??00000  1111111100  000
inermis          1101110000  0010000000  0000000000  2000010011  1?100?0000  00000?0000  00000000
00 0111111?11  111?120011  0100101110  0000?00000  1111111100  000
nuttingi         1111110000  0010000000  0000000000  2000010011  1?100?0000  00000?0000  000000?0
00 0111111?11  111?121011  0000000000  0010?00000  1111111100  000
indicus          1111110000  0010000000  0000000000  2000010011  1?100?0000  00000?0000  00000000
00 0111111?11  111?121011  1111000000  0000?00000  1111111100  000
asper            1111110000  0010000000  0000000000  2000010011  1?100?0000  00000?0000  00000000
00 0111111?11  111?121011  1111110000  0000?00000  1111111100  000
paxtoni          1111110000  0010000000  0000000000  2000010011  1?100?1100  00000?0000  00000000
00 0111111?11  111?121011  1111111001  0000?00000  1111111100  000
elongatus        1111110000  0010000000  0000000000  2000010011  1?100?1100  00000?0000  00000000
00 0111111?11  111?121011  1101101001  1110?00000  1111111100  000
stereope         1111110000  0010000000  0000000000  2000010011  1?100?1100  00000?0000  00000000
00 0111111?11  111?121111  1101101011  1111?10000  1111111100  000
spinifer         1111110000  0010000000  0000000000  2000010011  1?100?1100  00000?0000  00000000
00 0111111?11  111?121111  1111111011  1111?01110  1111111100  000
soelae           1111110000  0010000000  0000000000  2000010011  1?100?1100  00000?0000  00000000
00 0111111?11  111?121111  1110111011  1111?01111  1111111100  000
tridentifer      1111110000  0010000000  0000000000  2000010011  1?100?1100  00000?0000  00000000
00 0111111?11  111?121111  1110111011  1111?01111  1111111100  000
ovatus           1111???111  11??11111?  ???0??0000  ?00?00?000  ???0??00??  00??0?00?0  0?000?0?
?? ?000000??0  0?0?0?0100  00000000??  0????000?0  ?111?1?10?  0??
bruuni           1111???111  10??00000?  ???0??1111  ?10?00?000  ???0??00??  00??0?0??0  0?000?0?
?? ?000000??0  0?0?0?0100  00000000??  0????000?0  ?111?1?10?  0??
```

```
oluolus         1111???110  00??00000?  ???0??0000  ?00?01?011  ???0??00??  00??0?0??0  0?000?0?
?? ??11111??1  1?1?1?1000  000000000?  0??0?000?0  ?111?1?10?  0??
parini          1111???000  00??00000?  ???0??0000  ?00?01?011  ???0??00??  00??0?00?0  0?000?0?
?? ?111111??1  1?1?1?1011  110111111?  0??0?000?0  ?111?1?10?  0??
fraseri         1110?????0  ?0??00000?  ???0???000  ?00?01??11  ??????01??  00????00?0  0?000?0?
?? ?111111??1  1?1?1??0?1  1011?1101?  1??1?000?0  ?111?1?10?  0??
spinosus        1111???000  00??00000?  ???0??0000  ?00?012011  ???0??11??  00??0?00?0  0?000?0?
?? ?111111??1  1?1?1?1111  110110101?  1??1?100?0  ?111?1?10?  0??
```

APPENDIX 6

Map identifying oceanic areas and associated land forms of the Indo-Pacific region (Figure A-1).

FIGURE A-1.-Indo-Pacific oceanic and land areas. AB, Great Australian Bight; AN, Andaman Sea; AR, Arafura Sea; BA, Banda Sea; CE, Celebes Sea; CO, Coral Sea; EA, East China Sea; HW, Hawaiian Islands; JA, Japanese Archipelago; MR, Marshall Islands; NA, northwestern Australian coast; PA, Palawan; PH, Philippine Sea; SC, South China Sea; SG, Sala-y-Gomez Ridge; SU, Sulu Sea; TM, Timor Sea; TS, Tasman Sea.


0° 30° 60° 90° 120° 150° 180° 150° 120° 90° 60° 30°
70° 60° 50° 40° 30° 20° 10° 0° 10° 20° 30° 40° 50° 60°
0 1,000 2,000 3,000
KILOMETERS
EA
JA
PA
SU
PH
SC
CE
AN
BA
AR
NA
TM
CO
AB
TS
MR
HW
SG