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THE FAMILY TERAPONIDAE (PISCES:PERCOIDEI):
INTERRELATIONSHIPS, TAXONOMY, AND ZOOGEOGRAPHY

by

Richard P. Vari

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
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1976

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

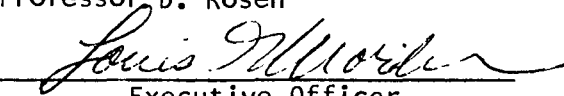
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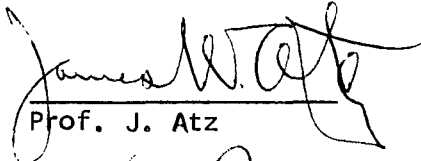
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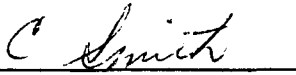

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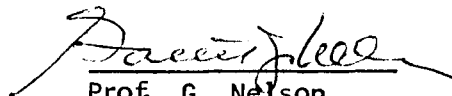
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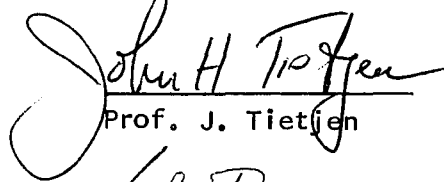
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Abstract

A revision of the family Teraponidae was carried out to determine: the monophyletic nature of the Teraponidae, the relationships of teraponids to other percoids; the relationships within the family; the recognizable species and their distinguishing characters; the distribution patterns of the family and its subunits.

Using the methods of phylogenetic and biogeographic analysis put forward by Hennig and Croizat respectively, the following results were obtained:

1) the family can be defined on the basis of derived states of the swimbladder, extrinsic swimbladder muscle, urohyal and third epibranchial.

2) the above characters fail to support the inclusion of the genera Datnioides and Pseudohelotes in the Teraponidae as suggested by Fowler. Neither these characters nor any others were found to support a hypothesis of a sister group relationship between teraponids and any other group of percoids.

3) within the family 15 monophyletic assemblages were recognized, with the relationships between them and their defining characters based on derived states of the posttemporal, tabular, dentary, maxillary, premaxillary, spinous dorsal, and vertebral osteology; forms of the extrinsic swimbladder muscle, swimbladder and intestinal patterns; and differences in body pigmentation and heights of the dorsal and anal fin sheaths.

4) these monophyletic assemblages are recognized at the generic level, with three new genera (Hannia, Lagusia, and Syncomistes) described in the work. Thirty seven species are recognized (five described for the first time) with each species described in detail and a key provided to the species of the family. Eight species recognized as distinct by some or all workers to this point are placed in synonymy and one species synonymized earlier is recognized as distinct.

5) analysis of the zoogeography of the family and its subunits revealed two major patterns:

A) a track including the costal regions of the entire Indo-west Pacific.

B) a track between the freshwaters of northern Australia and southern New Guinea.

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Introduction

The Teraponidae are a family of percoid fishes found in fresh, brackish, and marine waters of the Indo-west Pacific. Their vernacular English names of grunter, grunts, croakers and trumpeters and other names in various languages throughout their range refer to the characteristic vocalizations of the group. The grunters have challenged and perplexed taxonomists since their separation as the genus Terapon from the Holocentridae by Cuvier (1817). As noted by Cuvier and Valenciennes (1829) in their introductory discussion of the family the teraponids are "un groupe de poissons qui semble fait pour desesperer les naturalistes."

Teraponids were first distinguished as a group with Cuvier's creation of the genus Terapon in 1817 to contain two species (T. servus (= jarbua) and T. quadrilineatus) previously placed in the genus Holocentrus. In 1829 Cuvier and Valenciennes named three new genera (Helotes, Pelates, Datnia) along with fourteen new species, half of which have since been synonymized. Of these three genera, Pelates and Helotes were retained by all workers except for Bleeker (1873) who synonymized them with Terapon. Datnia, however, was generally considered to be indistinguishable from Terapon.

Since Cuvier and Valenciennes' monograph many species have

been described primarily from freshwaters of Australia and New Guinea and secondarily from rivers of the Philippines and Sulawesi (Celebes) and marine waters around Madagascar, Fiji, Southeast Asia, Japan, and Australia. With few exceptions the majority of these species were assigned to the genus Terapon.

Some ichthyologists argued, however, that the inclusion of the majority of the species in the genus Terapon obscured patterns of interrelationships within the group (Ogilby and McCulloch, 1916; Whitley, 1943; Mees, 1971). However, with only a limited amount of information available from external characters, most investigators suggested that further subdivision of the family should await additional studies, particularly of the osteology.

Other researches, nonetheless, did partition the catch-all genus Terapon. Fowler (1931) establishes a series of subgenera (Terapon, Eutherapon, Mesopristes, Rhyncopelates, and Leiopotherapon) basing most of these on shared primitive characters which failed to define monophyletic assemblages. Whitley (1943) further subdivided the genus Terapon by utilizing six previously suggested generic-level names and by creating six new ones. With his later generic descriptions (1945a, 1948b, 1955) he recognized sixteen teraponid genera. Thirteen of these Amniataba, Amphitherapon, Authistes, Bidyanus, Eutherapon, Pelsartia,

Hephaestus, Leiopotherapon, Madigania, Mesopristes, Papuservus, Scortum, and Terapon (sensu strictu) represented species or species groups previously assigned to Terapon. Helotes was divided into Helotes (sensu strictu) and Pingalla which together formed the subfamily Helotinae. The genus Pelates remained unchanged.

Teraponid taxonomy prior to this study is shown in Table 1. For several reasons that taxonomy failed to produce the intended order and clarity. Firstly, one half of the genera were monotypic; thus, for the species of these genera, the question of interrelationships had only been transferred to the generic level. Secondly, the polytypic genera were not rigorously defined on the basis of shared derived characters and some were non-monophyletic in the Hennigian sense. Finally, the generic descriptions and diagnoses of Whitley failed to deal with six nominal species (I. plumbeus, I. micracanthus, I. oxyrhynchus, I. kneri, I. elongatus, and I. lambertoni) from outside the Australia-New Guinea region. On the basis of the generic descriptions, neither these species nor those described more recently (I. brevipinnis and I. jamoerensis) could be unambiguously assigned to existing genera.

Much of the difficulty that previous workers have encountered in attempting to resolve a hypothesis of relationships in the Teraponidae was the result of the wide geo-

graphic range of the family. Marine species are found along the coasts of the Indo-west Pacific from Africa to Samoa and north to Japan and China. Throughout this range, these species also enter brackish and fresh waters. Species apparently limited to fresh-water are found on most of Australia, the southern peninsula of Sulawesi (Celebes), New Guinea and the islands of Luzon and Mindanao in the Philippines.

Because of this large range, most workers have limited their studies of the family regionally and dealt with limited numbers of species (Ogilby and McCulloch, 1916; Weber and deBeaufort, 1931; Whitley, 1943; Munro, 1967; and others). Since Cuvier and Valenciennes' monograph (1829) which discussed the few species known at that time, the only study to deal with the majority of species in the family was Fowler's (1931)- a study which depended heavily on literature information, especially for freshwater species. In both that work and others, differences in terminology and procedures among workers have caused confusion, with subsequent errors in synonymy and description of invalid species.

Besides the difficulty in resolving within-family relationships, the question of relationships of teraponids to other percoids has also been left unanswered. Teraponids have been considered to be part of the Pristipomatidae by Gunther (1859),

Kner (1868) and Klunzinger (1879); of the Lutjanidae by Boulenger (1904); and of the Haemulidae by Jordan and Everman (1902). Regan (1913) considered the group to be serranids, a suggestion followed by Bertin and Arambourg (1958). Okada (1959a) placed them in his suborder Percina along with the families Serranidae and Kuhliidae.

However, in none of these cases has the hypothesized relationship been based on derived characters shared between teraponids and the postulated nearest relatives. Neither has the monophyletic nature of the family been demonstrated by any stated and acceptable criteria.

The objectives of this study are five-fold:

- 1) to determine the monophyletic nature of the Teraponidae in the Hennigian sense. Is there evidence that the species of the group are related by common ancestry? Are there presently or have there been included in the family, species or groups of species which should be excluded?
- 2) to determine the relationships of the family to other percoid groups.
- 3) to produce theories of interrelationships within the family.
- 4) to produce a comprehensive account of the recognizable species and their distribution
- 5) to analyze the distribution patterns of the family and its various subgroups. Is there a correlation in the distribution patterns of teraponids with the generalized distribution patterns of other groups?

Methods

Systematic procedures

Relationships within the Teraponidae are evaluated using the methods of phylogenetic analysis first described in detail by Hennig (1950, 1965, 1966) and subsequently debated pro and con by Ashlock, 1972, 1974; Bock, 1973; Brundin, 1966, 1968; Cracraft, 1972; Crowson, 1970; Darlington, 1970; Mayr, 1974; Nelson, 1971, 1972; Rosen, 1974; Sneath and Sokal, 1973; and others.

In spite of the sometimes heated and persisting debate, I conclude that the Hennigian methodology best serves the purposes of this study: the elucidation of the phylogenetic relationships within the family. The two alternative methodologies presently in wide use fail to serve this purpose as well. Numerical Taxonomy, dealt with in detail by Sneath and Sokal (1973) is interested in elucidation of phenetic rather than phyletic relationships; as such it is considered inappropriate for the aims of this study. The second alternative methodology, that of "evolutionary taxonomy", is presented in greatest detail by Simpson (1961) and Mayr (1969) and attempts to introduce both phyletic and phenetic information into studies of relationships. However, neither these authors nor any other evolutionists have provided a repeatable methodology to incorporate the two kinds of information into theories of

relationship.

In using the Hennigian or cladistic methodology, certain principles are followed: taxa must be monophyletic in that they include all the descendents of a hypothetical ancestral species (this constraint not being necessary in an evolutionary taxonomic methodology). Monophyletic groups are defined on the basis of shared derived (synapomorphic) characters which are considered the only type of characters valid for the erection of a hypothesis of common ancestry. In contrast shared primitive (symplesiomorphic) characters, degrees of difference, grades, or overall resemblance are not utilized for the analysis. Species or species groups hypothesized to have had a common ancestor are termed sister groups. An apomorphic character used for the definition of a sister group pair cannot serve for the definition of taxa contained within either sister group, since it is plesiomorphic (primitive) at the level of included subtaxa.

In estimating the primitive or derived nature of various teraponid characters, two methodologies are used. The first involves a series of outgroup comparisons (e.g., the state of the character in a variety of other percoid groups) in order to determine which of the contrasting teraponid character states is of general occurrence (i.e. probably primitive). The second method utilizes information from ontogenetic character

state changes. If in two sister lineages, A and B, that share a common ancestor, the species of lineage A (but not B) undergo an ontogenetic character state change, we have two possible explanations for the distribution of the ontogenetic change.

- 1) the ontogenetic change in the character is a de novo acquisition of lineage A. As such it represents an autapomorphy uniting the species of the lineage.
- 2) the ontogenetic character state change was present in the common ancestor of lineages A and B but was subsequently lost in lineage B.

The first hypothesis makes only one assumption, the acquisition of the ontogenetic change in lineage A. The second in contrast, makes two assumptions, that of the possession of the ontogenetic change in the common ancestor of the lineages along with an assumption of its subsequent loss in lineage B. As the first hypothesis is more parsimonious, its use is preferable in attempted reconstructions of the phylogenetic history of a group. Therefore in the following analysis, it is hypothesized that the transformed state of a character in a group represents the derived condition.

Measurements and Counts

All measurements are straight-line distances made with dial calipers and recorded to the nearest tenth of a millimeter. When possible, measurements were made only on specimens that were not excessively distorted and are given as a proportion of standard length or head length. An exception used for two species is the maximum body width which is given as a proportion of the body depth. Other measurements previously used in studies on the family (postorbital head length/head length, interorbital width/head length, etc.) were abandoned after preliminary studies showed little intrafamilial variation. Proportions are presented following the procedures of the majority of previous workers on the family to facilitate comparisons. Measurements and counts were made following the procedures of Hubbs and Lagler (1958), with several exceptions discussed below. Measurements of the length of the longest spines and rays in the median fins were made to the base of the element rather than to the edge of the scaly sheath; the latter measurement results in inconsistencies both intra and interspecifically. Lateral line counts are of tubed lateral line scales counted from the origin of the lateral line at the posterior edge of the supracleithrum to the end of the hypural plate as determined by flexing the caudal fin. Other workers have counted series of scales above and below the lateral line or the number of rows of scales interrupt-

ed by a straight line drawn from the origin of the lateral line at the supracleithrum to the end of the hypural plate. Scales listed as caudal scales are pored lateral line scales posterior to the end of the hypural plate, omitting unpored scales extending beyond this. Counts of transverse scale rows above the lateral line follow the procedure of Ogilby and McCulloch (1916) and are made to the base of the dorsal fin sheath at the median dorsal spines. Scales below the lateral line are counted to the anal origin. The number of scale rows in the sheath at the base of the dorsal fin were counted under the middle of the spinous dorsal. Counts of the number of scale rows in the anal sheath were made over the posterior spine and anterior rays.

In counting dorsal and anal soft rays, the last ray which is nearly divided to its base is counted as one element rather than one and one-half or two as has been the practice of some other workers. Vertebral counts were made from radiographs and cleared alizarin stained specimens. The first two vertebrae lack pleural ribs and though difficult to count on that basis can be counted easily by their prominent neural spines. The distinction between precaudal and caudal vertebrae is made at the point of insertion of the fused proximal pterygiophores of the first and second anal spines between the hemal arches of the vertebral column. In the counts of caudal vertebrae, the terminal half-centrum supporting the parahypural and hypurals

was counted as one element.

Gill raker counts include all countable elements on the first gill arch. Where it was not feasible in smaller specimens of some species to make a nonarbitrary count of smaller gill rakers, these specimens were not included in the range for the count. Gill rakers are listed as above and below the central T-shaped gill raker which is listed separately, in contrast to earlier procedures which include it in the count of the gill rakers on the lower limb of the first arch.

Pigment patterns were recorded from preserved material of all sizes and from all available parts of a species' range. Ontogenetic pattern variation is described in detail when known. Specimens figured usually show adult coloration, with juvenile coloration, when markedly different, also figured.

All examined specimens are listed, with those individuals on which counts and measurements were made indicated by an asterisk after the catalogue number and with the range of standard lengths for these specimens. In large series, only part of which were used for counts and measurements, the number measured and the total number of specimens are noted, with the standard lengths given being those of the former.

Various characters were studied in alcohol preserved material, cleared alizarin stained specimens and articulated and disarticulated dry skeletons. Drawings of various characters were made primarily from cleared specimens using a

camera lucida. The illustrations of the osteology of Terapon
jarbua are based on a series of cleared specimens along with
radiographs and dissected materials of individuals of various
sizes.

Material of four of the new species described in this paper along with the majority of teraponid material from the Australian region that served as the basis of this study was collected by Dr. Donn E. Rosen, Dr. Gareth J. Nelson, and Mr. W. Harry Butler of the Department of Ichthyology of the American Museum of Natural History during an expedition to Western Australia and Northern Territory in 1969. This expedition was made possible by the generous financial support from Mr. James Greenway of the Department of Ornithology of the American Museum.

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Institutional Abbreviations

AM	Australian Museum, Sydney
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BM(NH)	British Museum (Natural History), London
MNHN	Museum National d'Histoire Naturelle, Paris
QM	Queensland Museum, Brisbane
RMNH	Rijksmuseum van Natuurlijke Histoire, Leiden
SU	Stanford University (now at California Academy of Sciences, San Francisco)
USNM	United States National Museum, Washington, D. C.
WAM	Western Australian Museum, Perth
ZMA	Zoologische Museum, Amsterdam

Nomenclature

Two points of nomenclature in the family, one anatomical and the other taxonomic, should be clarified at this point. The first is the question of the proper terminology for the bones of the teraponid pectoral girdle. Two of these bones vary in their exposure to the surface and have been utilized as key characters (Ogilby and McCulloch, 1916; Weber and deBeaufort, 1931; Fowler, 1931) and indicators of phylogeny by many authors. Cuvier and Valenciennes (1829) refer to these as the corocoid located slightly dorsal to the pectoral fin base and the suprascapular located above the upper opercular spine. This terminology was followed by Ogilby and McCulloch (1916), Weber (1910), Rendahl (1922) and Weber and deBeaufort (1931) in species descriptions and revisions of the group and others in various faunal studies. Trewavas (1940) in her description of Terapon adamsoni stated that in her opinion, the appropriate names for these bones should be the cleithrum and supracleithrum rather than corocoid and suprascapular. This terminology in turn was followed by Munro (1964, 1967) and Mees (1971). However, a study of the osteology of teraponids possessing the different states of these bones shows that while the ventral element originally termed the corocoid is the cleithrum as suggested by Trewavas, the

dorsal element termed the suprascapular or supracleithrum is actually the posttemporal. The actual supracleithrum is the element between the cleithrum and the posttemporal (Fig. 2).

This confusion in terminology has evidently resulted in several mistakes in species descriptions. Trewavas stated that in Terapon (=Hephaestus) adamsoni the "supracleithrum" is not exposed and notes the equivalence of this bone to the suprascapular of previous workers. However, reference to the type of the species shows that the posttemporal (suprascapular of workers before Trewavas) is exposed. The same situation appears to have occurred in Terapon habbema (=Hephaestus trimaculatus) which was described by Weber (1910) and Weber and deBeaufort (1931) as having a covered suprascapular (=posttemporal), whereas reference to the original illustration and syntypes has shown the posttemporal to be exposed and serrate. Finally, Mees (1963) states that the supracleithrum is exposed in Terapon (=Leiopteryx) aheneus. Examination of paratypes of the species shows, however, that the posttemporal though having a reduced scale covering lacks an exposed serrate edge.

The second nomenclatural question involves the proper spelling of the type genus name as Terapon or Therapon and the resultant spelling of the family name as Teraponidae or Theraponidae; a question recently discussed by Smith (1974). The ultimate derivation of the family name arises from Block's statement (1797) that among Japanese, as a consequence of the

low esteem in which it was held, Holocentrus (=Pelates) quadri-
lineatus was considered fit only for "slaves" and therefore was
termed by Europeans the "Slave fish". Although the proper
transliteration from the Greek for slave is Therapon (Woods,
1966); Cuvier (1817) both in the index (p.xi) and in the group
description (l'esclaves, p. 295) utilizes Terapon. This in-
correct spelling occurring in two widely separated sections of
the work therefore appears to be an incorrect transliteration
rather than a lapsus calami or printer's error. Since rule 32
of the International Code of Zoological Nomenclature states that
the original spelling is to be retained as the correct spelling
in the case of an incorrect transliteration, the correct type
genus name is Terapon.

This in turn is used as the stem for the formation of the
family name. During the past half-century, both Teraponidae
and Theraponidae have been used. Although Teraponidae never
achieved general acceptance, its presentation as the proper form
does predate the 1960 cut-off date for family name changes in
Article 40. Since it is based on the proper stem (Terapon)
and has a long, if inconsistent, usage, it would appear that
it is the proper form under the rules and will be used in
this revision.

Defining characters of the Teraponidae

Members of the family Teraponidae have been traditionally recognized on the basis of a series of shared characters which are, however, either primitive for percoids generally or shared with other smaller groups. Consequently, the group's monophyly in the Hennigian sense has never been demonstrated. This study, however, indicates that the species of the family share four derived characters; synapomorphies which therefore support the monophyletic nature of the group.

The first of these characters is the possession in all teraponids of a unique form of extrinsic swimbladder muscle (figs. 4 and 5). The teraponid extrinsic swimbladder muscle arises from the ventral process of the posttemporal or the rear of the skull or both. Posteriorly, it extends dorsal to Baudelot's ligament and ventral to the epipleural and pleural ribs to an attachment on the external connective tissue layer of the anteriodorsal surface of the swimbladder. This insertion is lateral to the vertebral column under the first to third pleural ribs. The extrinsic swimbladder muscles are surrounded by a thin enveloping layer of connective tissue and around that a layer of adipose tissue.

On the basis of the developmental and innervation patterns of the muscles, it appears that they are derived from the levator pectoralis muscles which in teraponids run from the posteriodorsal edge of the pterotic to the dorsomedial

edge of the supracleithrum. Ontogenetic evidence supporting this hypothesis comes from the finding that in some small individuals of Leiopotherapon unicolor (10-25 mm SL) a sharing of fibers occurs between the extrinsic swimbladder muscles and the levator pectoralis. Different individuals vary in the amount of this interconnection, but in some, the sharing is of sufficient magnitude to completely surround Baudelot's ligament which runs from the basioccipital to the cleithrum. This condition is evidently lost ontogenetically as no adult individuals have been found with the intermuscular connection.

Consistent with this hypothesis of muscle derivation is the manner of innervation of the muscle. In teraponids, the extrinsic swimbladder muscle is innervated by a branch of the first spinal nerve which also innervates the levator pectoralis. As muscles or muscle sections arising from a muscle usually retain the primitive innervation, the above similarity in innervation supports a hypothesis of the derivation of the swimbladder muscle from the levator pectoralis. In contrast, the protractor pectoralis which runs parallel to the levator pectoralis and the extrinsic swimbladder muscle and is an alternative possibility for the source of the swimbladder muscle is innervated by the vagus nerve (Winterbottom, 1974).

The presence of an extrinsic swimbladder muscle in teraponids was first described by Cuvier and Valenciennes (1829)

in Therapon servus (= Terapon jarbua) which they state has a muscular attachment between the anterior of the swimbladder and the anterior vertebrae. Although the attachment of the extrinsic swimbladder muscle to the swimbladder has been found in all species of the family; there have not been found any species or individuals with a muscle origin in the anterior vertebrae. Thus, the original description appears to be either a misinterpretation of the muscle origin or based on an anomalous specimen.

These authors also refer to elongations of the swimbladder into two anterolateral processes contacting the rear of the skull in Helotes sexlineatus (= Pelates octolineatus). This study has failed however, to find such swimbladder processes in any species of the family. In the species of the genus Pelates, the extrinsic swimbladder muscles are heavily invested on their ventral and medial surfaces with connective tissue bands. These bands are continuous with those arising from the rear of the skull and also with the connective tissue covering of the swimbladder. When viewed from the body cavity, these might have been interpreted as swimbladder diverticula.

Following these mentions of the extrinsic swimbladder muscles they do not appear to have been noted again in the family until Hardenberg (1934) illustrated the muscle form in Terapon theraps and hypothesized that they functioned as part of a sound-producing mechanism. The sonic ability

of various species was also noted by Uchida (1934), Hardenberg (1934), Scott (1962) and other workers. Schneider (1961, 1963) illustrated the extrinsic swimbladder muscles for Terapon jarbua and I. theraps; proving by extensive physiological studies the sonic function of the extrinsic swimbladder muscles. Studying the sound-producing mechanism he was able to show that the muscles serve as swimbladder vibrators with the swimbladder in turn acting as a resonator organ. The acoustical signals so produced are utilized in a variety of threat and response behaviors whose intensity and structure is a function both of age and environmental conditions. Since as noted previously the species of the family throughout its range have common names referring to their sonic ability, it seems probable that the extrinsic swimbladder muscle has a common sonic function throughout the group.

Schneider also studied ontogenetic changes in the muscle and found that the extrinsic swimbladder muscle first appears in I. jarbua by 35 mm SL. Comparisons with the juveniles of other species has shown wide variation in the appearance of the first parts of the muscle. In Leiopotherapon unicolor the muscle has been found fully developed in 18.5 mm SL individuals; in Amniataba percoides at 9 mm SL and in Hephaestus fuliginosus at 33 mm SL.

On the basis of the present information available on extrinsic swimbladder muscles, the form of the sonic muscle in

the Teraponidae appears to be unique among percoids. Extrinsic swimbladder muscles also arising on the rear of the skull or the posttemporal have been described for the Squirrelfish Holocentrus rufus (Winn and Marshall, 1963). The insertion of the muscle in this species differs, however, in being on the dorsal surface of the first three pleural ribs and contacting the swimbladder by a ligamentous band rather than being a direct attachment as in the Teraponidae. Similarly, the extrinsic swimbladder muscle in the Nassau Grouper (Epinephelus striatus (Hazlet and Winn, 1962) bears little resemblance to the teraponid condition. Dissections on other percoid groups have shown a previously undescribed extrinsic swimbladder muscle in the Pempheridae. The pempherid muscle differs from that in teraponids in having two distinct origins in some species and in attaching to the swimbladder under rather than lateral to the vertebral column.

The second character that appears to be unique to the Teraponidae is the form of the adult swimbladder. Outgroup comparisons indicate that the primitive form of percoid swimbladder is an elongate oval lacking constrictions or internal subdivisions. This hypothesis is consistent with the ontogenetic changes in teraponid swimbladders. While juvenile teraponids have an elongate, unconstricted, swimbladder (Schneider, 1963; pers. obs.) with increasing age the swimbladder develops a transverse septum approximately one-third of its total length

posteriorly. The development of this septum is followed ontogenetically by the formation of a definite trasverse swim-bladder constriction at the same point which eventually divides the swimbladder in most species into two unequal chambers connected by a short tube (figs. 4 and 5). However, in two genera within the family (Pingalla and Syncomistes) this constriction into two definite chambers is secondarily reduced. A distinct narrowing is found in the swimbladder of Syncomistes butleri at 45 mm SL forming two subchambers; though not as marked as those in other species in the family. With increasing age, this constriction becomes less pronounced so that larger specimens have only a 40% narrowing of the total swimbladder diameter and the subchambers are connected by a wide tube (fig. 6).

Within-family variation also occurs in the first appearance of the swimbladder constriction. Schneider (1963) found the constriction first appearing in Terapon jarbua at 31.5 mm SL. Examination of Leiopotherapon unicolor juveniles shows the swimbladder to be fully divided in 17.7 mm SL specimens, while in Amniatba percoides at 9.0 mm SL, there is found a partially constricted swimbladder which is totally constricted in 14.5 mm SL specimens.

In adults of the species in the family (with the exception of the groups noted above) the length of the anterior chamber is approximately one-third that of the posterior, with a rotund

form and a marked depression along its dorsomedial surface to allow a tight fit around the ventral surfaces and parapophyses of the third to fifth vertebrae. The anterior chamber has dorsolateral attachments to the posterovental surface of the sonic muscle and medial to these to the ventral surfaces of the parapophyses and proximal regions of the first three pleural ribs. These attachments to the vertebral column and ribs anchor the swimbladder against the forward pull exerted by the extrinsic swimbladder muscle resulting in vibrations of the swimbladder with consequent sound production.

The posterior swimbladder chamber is an elongate oval; tapering gradually posteriorly and ending in a rounded to distinct point. Rather than the strong connections of the anterior chamber to the vertebral column and ribs, the posterior chamber has varying degrees of loose attachments by peritoneum to the dorsolateral and dorsal body walls.

Pelates quadrilineatus has a swimbladder form that is further modified and unique to this species in the family. The posterior chamber in this species is subdivided by an additional transverse constriction which separates a small posterior section as a third swimbladder chamber.

Within both chambers of the teraponid swimbladder, macroscopically visible glandular tissue is present with the largest amounts localized in the posterovental region of the anterior

chamber and a lesser amount on the ventral surface of the posterior chamber.

The distinctive swimbladder form in teraponids was first described by Cuvier and Valenciennes (1829) for five of their nominal species . Richardson (1844) in a comparison with these descriptions stated incorrectly that Datnia caudavittata (= Amniataba caudavittatus) could be distinguished from Cuvier and Valenciennes' species in lacking a transverse swimbladder constriction. However, as in all members of the family such a constriction is actually present. More recently Juliano (1960) has described the swimbladder form in Leiopotherapon plumbeus a freshwater Philippine species.

Workers following Cuvier and Valenciennes have been inconsistent in their utilization of the divided swimbladder as a distinguishing character of the Teraponidae. Weber and deBeaufort (1931), Fowler (1931, in part), Whitley (1943) and others failed to note the presence of the swimbladder constriction in the family. Ogilby and McCulloch (1916), Day, (1878), and Günther(1859) used the character in their general family definition, with Günther further using it as a key character to differentiate teraponids from the other members of his family Pristopomatidae. However, even those workers noting the presence of the constriction failed to distinguish this character as being derived for percoids in contrast to other listed characters which were either primitive for percoids in general or shared with large numbers of other smaller groups.

Reference to available descriptions of swimbladder forms among various families in the Percoidei (Dobbin, 1941; Fange, 1953; Marshall, 1962) along with dissections in various groups has shown the swimbladder form of the species of the Teraponidae to be approached only by that of some species of the Pempheridae in which it has evidently been achieved independently (see discussion below).

The third character which is unique to the family among percoids is the form of the teraponid urohyal (Fig. 7). In teraponids the urohyal has a distinct anterodorsal ramus which articulates with the ventral edge of the first basibranchial. Ventrally the urohyal has thin lateral projections which gradually widen posteriorly. Smaller lateral processes are also present along the dorsal edge of the bone in some species. Finally, all species have a strong oblique strut running from the anterodorsal corner of the bone to its posterodorsal edge. Comparisons with the urohyals of other percoid groups using both dissected material and the extensive survey of urohyal forms of percoids by Kusaka (1974) has shown the character combinations described above for teraponids to be unique among percoids.

The fourth character that appears to be unique to the family is the form of the third pharyngobranchial (Fig 8) In all teraponid species available for the study of this character, the third pharyngobranchial has arising from its dorsomedial edge a dorsally directed process bearing two projections. The anterior pro-

jection articulates with the dorsomedial region of the dorsal process of the 2nd pharyngeal branchial. The posterior projection runs posterodorsally to the midline of the basicranium and serves for attachment of the obliquodorsalis and levators externi muscles of the dorsal gill arches.

Relationships of the Teraponidae to other percoids

Attempts to determine the closest relatives of teraponids among acanthopterygians have proved unsuccessful in this study. Two of the defining family characters (urohyal and epibranchial form) do not appear on the basis of available information to be approximated in any other acanthopterygian groups. Extrinsic swimbladder muscles arising from the rear of the skull have been reported or discovered during this study in several groups. These groups (Holocentridae, Epinephalidae, Pempheridae), however, are either parts of larger monophyletic groups having a series of apomorphic characters lacking in teraponids (see Gosline, 1966 with respect to Epinephalus and Tominaga, 1969 for Pempheris) or in the case of Holocentrus lack a series of derived characters uniting the Teraponidae to a large number of other percoid groups (lack of orbitosphenoid, and reduced number of pelvic and caudal fin rays). Thus any attempt to hypothesize a sister group relationship between any or all of these groups and the Teraponidae on the basis of common possession of the extrinsic swimbladder muscles would be less parsimonious than the assumption of the independent acquisition of the sonic

muscles in the various groups. Similarly, a hypothesis of a close relationship between those pempherids with a divided swimbladder and the Teraponidae on the basis of that character is refuted by the series of characters uniting all pempherids into a single monophyletic assemblage (Tominaga, 1968).

In addition to the above characters, the distribution of a series of other character previously examined in detail by other workers has been analysed in order to determine what information they provided on the question. Eleven families share with the Teraponidae a Pattern 10 Ramus Lateralis Aecessorius pattern (Freihofer, 1963; Johnson, 1975). All of these also possess a prominent procurrent spur (Johnson, 1975) and a bridge over the anterior vertical canal (condition unknown in the Oplegnathidae) except for the Girellidae and Nemastistidae (Haedrick, 1967). However, all of these characters appear to be plesiomorphic for percoids. As such they are not valid evidence of close relationship between or within the groups. Neither can this information be used to hypothesize that these groups are a series of plesiomorph sister groups to the rest of the percoids since plesiomorph characters may be retained in distantly related groups throughout a phylogeny. Consequently these characters also fail to clarify the phylogenetic position of the Teraponidae.

As noted previously, different workers have hypothesized

the Teraponidae to be part of the Serranidae, Lutjanidae, Pristopomatidae or Haemulonidae. Gosline (1966) pointed out that the family Teraponidae fails to conform with the characters of the Serranidae as he defined it in lacking a third opercular spine and retaining a large Baudelot's ligament and a bone enclosed neural canal along the dorsal edge of the ceratohyal. Johnson (1975) found that serranids can be further differentiated from teraponids by their lack of a procurrent spur on the lower caudal fin base. Neither has evidence been previously advanced or uncovered in the course of this study to support a hypothesis of a sister group relationship between the Teraponidae and any of the aforementioned groups.

Exclusion of the genera Datnioides and Pseudohelotes
from the Teraponidae.

Besides the species that other workers considered to be teraponids, Fowler (1931) expanded the family by adding to the Teraponidae the subfamily Datnioidinae containing two species Datnioides microlepis and D. polota. However, examination of these species has shown that they lack the four distinguishing teraponid characters discussed above, and also fail to agree with Fowler's definition of the family. Previous to Fowler and more recently, the datnioidines have been placed in the Lobotidae, a group with which they appear to be more closely related.

In addition to including the Datnioidinae in the Teraponidae, Fowler also added to the family the genus Pseudohelotes created by Capello (in Guaimares, 1881) for one species P. guntheri and placed in the Pristopomatidae (sensu Günther, 1864) which also contained the teraponids. Fowler lists the genus as a junior synonym of Helotes without discussion of either the genus or species. Although the type specimen of the species is not available for examination, the original species description is consistent with a hypothesis that the species is not a teraponid in the sense that the term was used prior to and since Fowler (1931). According to the description of P. guntheri, it has seven branchiostegal rays and one opercular spine in contrast to the six rays and two spines of the Teraponidae (sensu strictu). The name Pseudohelotes appears to be a reference to a supposed similarity in dentition between P. guntheri and Helotes (= Pelates) sexlineatus as the dentition of the latter is illustrated and contrasted to that of P. guntheri. However, examination of the tooth form in Pseudohelotes guntheri as illustrated shows it to be a truncate cone topped by a smaller recessed cone: a quite different tooth form than the tricuspidate teeth of Pelates sexlineatus.

Phylogenetic relationships in the Teraponidae

Figures 9 and 10 are cladograms representing the hypothesized relationships of genera within the family. Fifteen monophyletic groups having one to seven species and herein recognized as genera are defined in this reconstruction (assemblage 11 b is divided into two subunits, a and b, for the purposes of the discussion). For the reasons discussed above, the genera Pseudohelotes and Datnioides do not appear to be teraponids and consequently are not included in the phylogenetic analysis.

In the following preliminary discussion of the phylogeny, the groups will be discussed using the numbers that represent their cladistic sequence (increasing numbers thus coincide with decreasing universality of the apomorphic characters in the family). Avoiding the use of formal taxa avoids the confusion resulting from the hypotheses of relationship inherent in previous taxonomic definitions which differ in some manner from those presented in this work. The genera actually recognized and their numbers in the cladistic sequence are as follows:

1	<u>Leiopotherapon</u>
2	<u>Amniataba</u>
3	<u>Hannia</u>
4	<u>"Terapon"</u>
5	<u>Lagusia</u> gen. nov.
6	<u>Pelates</u>
7	<u>Terapon</u>

8	<u>Pelsartia</u>
9	<u>Rhyncopelates</u>
10	<u>Mesopristes</u>
11	<u>Hephaestus</u>
12	<u>Bidyanus</u>
13	<u>Scortum</u>
14	<u>Pingalla</u>
15	<u>Syncomistes</u> gen. nov.

The characters used in the reconstruction of the phylogeny will be discussed in order of decreasing universality of their derived states. Certain characters having multiple character states in the family will be discussed as units in advance of the overall phylogenetic analysis.

Posttemporal and tabular anatomy

The first anatomical system which shows a number of different character states among teraponids is the morphology of the posttemporal and lateral tabular bones along with their associated sensory canals. Outgroup comparisons indicate that the plesiomorph condition of these elements for percoids and consequently probably that for teraponids is that shown semidiagrammatically in figure 11. In the species with this pattern, the lateral tabular carries parts of two sensory canals, the supratemporal commissure and the otic portion of the infraorbital canal (referred to here as the otic canal), that meet at the anterior

edge of the bone. Anteriorly on the lower tabular, the otic canal contacts the rear of the pterotic sensory canal and then slants posterodorsally to communicate with the anterior opening of the posttemporal sensory canal. The part of the supratemporal commissure in the lateral tabular contacts the rear of the pterotic canal in common with the otic canal and continues posterodorsally in the upper more medial tabular bone. Together the canal sections of the lateral tabular bone form a pattern of an anteriorly pointing "V", with an apex contacting the posterior of the pterotic sensory canal. The posttemporal part of the otic sensory canal posterior to its contact with that of the lateral tabular, runs along the lateral surface of the posttemporal forming most of the lateral surface of the bone and extends posterior to the point of union of the ventral and dorsal process of the posttemporal as a distinct though small process overlapping the supracleithrum for two-thirds of the horizontal width of that bone. At its posterior terminus this process located ventral to the supracleithral-posttemporal articulation communicates with the short sensory canal of the supracleithrum which is continuous with the main trunk lateral line. In this pattern, the posttemporal sensory canal lacks any lateral openings to the surface and is overlain by an uninterrupted layer of skin and scales (sometimes partially reduced) lacking sensory pores. Species having this pattern are found in genera 1 to 5.

Three discrete derived states of parts or all of the lateral tabular-posttemporal complex and associated over

lying issues are found in genera 6 to 15. In the species of this group, in contrast to the wide anterior opening to the otic canal of the lateral tabular found in the species of genera 1 to 5, there occurs a reduced anterior aperture. Congruent with this change is a reduction in the posterodorsal slope of the otic canal in the lateral tabular or a posteroventral slope in the canal.

The species of genera 7 to 15 share a series of further modifications of the lateral tabular-posttemporal complex. The supratemporal commissure of the lateral tabular in these genera has shifted position so as to contact the midsection of the otic canal in the lateral tabular and is oriented vertically or nearly so. This results in a lateral tabular sensory canal pattern in the form of an inverted "T" (Fig. 12) (a further modification unique to a group of species in the genus Hephaestus, will be discussed below). Derived states of the posttemporal and overlying tissues congruent with the distribution of these lateral tabular changes are also found in genera 7 to 15. In these genera the posttemporal is of radically different morphology than the form in genera 1 to 6. Rather than the small posttemporal process found lateral to the supracleithrum in genera 1 to 6, the species of this group have a large plate of bone extending posteroventrally which covers both the posttemporal-supracleithral articulation and the dorsal region of the latter bone. Furthermore the posttemporal in these species terminates

posteriorly in a broad serrate edge which extends through the skin in varying degrees. Associated with this posterior elaboration of the posttemporal is an elongation of the posttemporal part of the otic sensory canal. Rather than the short unelaborated tube in genera 1 to 6, the canal in these genera is much longer and has a series of lateral openings. Finally these genera share a shift ventrally of the level of the articulation between the posttemporal and the supracleithrum. Besides these modifications in the osteology of this region, there are also found modifications of the overlying tissues. In contrast to the uninterrupted skin and scale covering found in genera 1 to 6, the species of genera 7 to 15 have a reduction in the scale covering in the posttemporal region along with the development of a series of sensory pores communicating with the lateral openings in the posttemporal part of the otic sensory canal and a protrusion of the posterior edge of the posttemporal through the skin.

The final group of posttemporal and lateral tabular modifications within the family are found in the species of subunit b of genus 11 (Hephaestus). In the species of this group, the section of the supratemporal commissure in the lateral tabular instead of being oriented postrodorsally (as in the species of genera 1 to 6) or vertically (as in the species of genera 7 to 11 and 12 to 15) has a posteroventral orientation and contacts the otic canal of the lateral tabular along the posterior edge of the bone. This results in a lateral tabular

sensory canal pattern of a posteriorly pointing "V" with an apex contacting the anterior edge of the posttemporal section of the otic canal (Fig. 13). The posttemporal in species of this group has also undergone further modifications, becoming thicker and more closely applied to the skull, with a greater reduction in scale covering. These modifications have resulted in a posttemporal form that is sufficiently different from that of other teraponids that various workers have not recognized the homology of the bone. Trewavas (1940) followed by Munro (1964, 1967) described the posttemporal in Terapon (=Hephaestus) adamsoni as being non serrate and not exposed whereas examination of the type has shown it to be both serrate and exposed. Similarly Weber (1910) and Weber and deBeaufort (1931) recorded the element as not exposed in Terapon habbemai (=Hephaestus trimaculatus) a statement found to be incorrect based on examination of part of the syntype series.

Data on the posttemporal and tabular anatomy of teraponids may be summarized as follows:

1) the primitive condition of these bones is an unelaborated posttemporal, a lateral tabular with a pattern of sensory canals communicating at the anterior edge of the bone (Fig. 11) and an uninterrupted skin and scale covering in the region. Within the family such a pattern is limited to the species of genera 1 to 5.

2) derived conditions of a reduced aperture to the lateral

tabular sensory canals and a reduced posterodorsal slope of the otic canal of this bone unite genera 6 to 15 into a monophyletic unit.

3) Genera 6 to 15 form a monophyletic unit based on the possession of an elaborate posttemporal with a serrate exposed posterior edge, an elaborate sensory canal with lateral openings, a vertical or posteriorly sloping supratemporal commissure in the lateral tabular, a ventrally shifted posttemporal-supracleithral articulation and a reduction in skin and scale covering in that region.

4) assemblage 11b (part of Hephaestus) is hypothesized to be monophyletic based on common possession of an enlarged posttemporal, a posteroventrally sloping supratemporal commissure in the lateral tabular bone and a further reduction in skin and scale covering.

Dorsal and Anal Sheath Heights

A second system having more than two states within the family is the height of the scaly sheath at the base of the dorsal and anal fins. The sheath at the base of the spinous dorsal is clearly discernable posterior to the second or third dorsal spine and surrounds the base of this and succeeding spines, forming a furrow into which the dorsal spines are partially depressible. The sheath is separated from the body

sculation in many species by a line of scaleless skin, but is less distinct in others, especially those with a reduction in dorsal spine length. In the species of genera 1 to 6 (Fig. 14) the sheath consists of only one row of scales of uniform shape and size. Species of genera 7 to 15 are characterized by the possession of two rows of scales in the basal dorsal sheath. Two states of this form of sheath are found in these genera. The species of genus 7 (Terapon) have two different sized scales in the sheath; a dorsal row of fully sized scales and a ventral one of narrower scales. This pattern approaches that of genera 8 to 15 in which there are two or more rows of fully sized scales (Fig. 15) (Syncomistes trigonicus [some specimens], S. kimberleyensis [known only from juveniles], Pingalla gilberti and P. lorentzi appear to have a secondary reduction to two irregular rows).

Parallel with this increase in the height of the dorsal fin sheath, there has occurred a similar though not as distinct increase in the height of the sheath at the spinous anal fin base. Species of genera 1 to 7 have a sheath of two or three rows while those of genera 8 to 15 have three to six rows (with the exception of Hephaestus adamsoni [genus 11b] which has two to three rows). Outgroup comparisons indicate that the lack of a dorsal and anal sheath appears to be the plesiomorphic condition in percoids. Thus the increasing sheath heights

within the family would appear to be increasingly apomorphic states. This hypothesis is supported by the finding that there is an increase in the numbers of scale rows in each fin ontogenetically.

The information on sheath heights may be summarized as follows:

1) the plesiomorph condition of the dorsal fin sheath is one row of scales as found in genera 1 to 6. That of the anal sheath is a height of 2 or 3 scales.

2) the derived condition of the dorsal sheath is two or more rows of scales found in genera 7 to 15.

3) genera 1 to 6 share both a derived dorsal sheath height (two or more rows of fully sized scales) and a derived anal sheath height (3 to 6 rows).

Intestinal patterns

In all teraponids, the stomach is large and triangular with an entrance on its anterodorsal surface into the intestine. Four intestinal patterns of increasing complexity are found within the family. The simplest of these (Fig. 16a) has only two loops. After exiting from the stomach, the intestine proceeds posterior to the rear of the body cavity where it makes a 180° turn, continues forward to a point ventral to the stomach where a second complete reversal occurs before

it runs posteriorly to the anus. In the species with this convolution pattern all of the intestinal loops are either in the median body plane or to the right of it. This is the intestinal pattern for the majority of the species in the family, being found in the adults of genera 1 to 10. It is also the juvenile pattern for the species of genera 11 to 13. In these genera (excluding 11b), however, during ontogeny there occurs an elongation and folding of the juvenile intestinal pattern to produce the more complex pattern shown in figure 16b. This pattern is derived from the simpler form by a forward infolding and elongation of the first intestinal loop and a secondary looping over on itself of the resultant intestinal segment. As a consequence of this intestinal folding and elongation, there is an ontogenetic shift from a pattern with 2 loops found in genera 1 to 10 to a pattern with 6 loops present at some point during development (genera 14 and 15 have further elaborations of this pattern, see below). Associated with this increased intestinal complexity is also a shift of the anterior loops of the intestine to the left of the median body plane.

The species of genera 14 and 15 share modifications of the above pattern. Juveniles of these genera have an intestinal convolution pattern similar to the adults of genera 11 to 13 (they probably also pass through the pattern of convolutions similar to those of genera 1 to 10, however, material of very small individuals to check this is lacking). During

development a further elaboration and elongation of the loops of the intermediate intestinal pattern results in an adult pattern shown diagrammatically in figure 16c. This pattern is derived from the juvenile pattern by a ventral shift of the first loop past the stomach and a further elongation of the anterior intestinal loops which fold back on themselves. In the species with this adult pattern, a greater percentage of the intestine is found to the left of the median body plane, with highly developed loops curling ventrally and up the left side of the stomach. The last intestinal pattern in the family, and the most complex one, is found in the species of branch 15 which undergo a further elongation and elaboration of the last discussed pattern (adult convolution pattern unknown for Syncomistes kimberleyensis which is based solely on juvenile material). This highly elongate and convoluted pattern may be related to what appears to be the main food source (filamentous algae) in the species of this genus.

On the basis of these ontogenetic changes in intestinal patterns, it is hypothesized that the intestinal patterns of genera 1 to 10 are plesiomorphic to those of genera 11 to 13, which are in turn plesiomorph with respect to those of genera 14 and 15, with the highly convoluted pattern of genus 15 being autapomorphic for the group.

Extrinsic swimbladder muscle forms

Four different forms of swimbladder muscle differing in both origin and overall shape are found in the family:

1) a cylindrical muscle with an origin limited to the ventral process of the posttemporal (Fig. 17).

2) a flattened muscle with a direct muscular attachment to the ventral process of the posttemporal and a ligamentous attachment to the pterotic (Fig. 18).

3) a flattened muscle having direct muscular attachment both to the ventral process of the posttemporal and to the ventrolateral edge of the pterotic (Fig. 19).

4) a slightly flattened muscle with an origin limited to the lateroventral edge of the pterotic (Fig. 20).

A hypothesis of the phylogenetic sequence of these muscle forms can be reconstructed on the basis of ontogenetic data.

The swimbladder muscle form found in the species of genera 1 to 6 is cylindrical, tapering slightly at both ends and with a connective tissue sheath surrounding it at its origin which is limited to the ventral process of the posttemporal (Fig. 17). Examination of a series of various size juveniles of the species of these genera has failed to reveal any ontogenetic variation in the muscle form. In contrast, each of the remaining muscle types in the family undergoes various developmental changes.

The species of genus 6 (Pelates) share the extrinsic swimbladder muscle form illustrated in figure 13. This type of muscle shares with the muscle type described above a direct muscular attachment limited to the ventral process of the posttemporal. It differs, however, in being more flattened and occupying a greater horizontal area on the posttemporal and more notably in having a second separate ligamentous origin on the rear of the skull. This second attachment is in the form of a connective tissue band arising from the medial surface of the main muscle mass and oriented away from the axis of the muscle to an attachment on the pterotic.

Ontogenetically, there occurs a change in the relative sizes of these two parts of the sonic muscle. In the smallest individuals of Pelates sexlineatus dissected, the ligamentous band is much smaller relative to the main part of the muscle than it is in the adults. This developmental change in the relative sizes of the two origins of the muscle is consistent with a hypothesis of a later phylogenetic appearance of the ligamentous origin. As such, the ligamentous tissue band is considered to be a derived character and genera 6 to 15 which share its presence of the possession of a muscle form derived from it are considered to form a monophyletic group.

Genera 7 to 15 share with the species of genus 6 an attachment of the muscle to the rear of the skull. However, the muscle in these species differ in having a direct muscular

attachment to both the pterotic and the ventral process of the posttemporal (species of genus 11b [Hephaestus, in part], lose the latter origin ontogenetically, see below). In the species of these genera, the muscles are distinctly flattened with a broad attachment along the proximal half of the ventral process of the posttemporal continuous with a direct muscular attachment to the posterior border of the pterotic (the attachment extends medially as far as the basioccipital in Rhynco- pelates oxyrhynchus (genus 9)).

In Terapon jarbua, a species with this form of sonic muscle ontogenetic changes occur from a muscular band with an origin limited to the ventral process of the posttemporal to the adult form described above. This transition is consistent with a hypothesis that the muscle form with direct origins on both the posttemporal and pterotic is apomorphic and the muscle in genera 1 to 5 is plesiomorph. Furthermore, it would appear that the muscle forms of genera 7 to 15 are derived with respect to that of branch 6 in attaching directly to the pterotic rather than by a ligamentous band and that the medial and lateral connective tissue bands found on the muscle proximally in these genera (7 to 15) are homologous with the ligamentous band and connective tissue sheath found in the muscle form of genus 6.

The remaining extrinsic swimbladder muscle form found in teraponids is limited to the species of genus 11b (Hephaestus in part). In these species, the extrinsic swimbladder muscle

in adults has an origin limited to the rear of the pterotic (Fig. 20). This contrasts with the muscles of all other species of the family which have some attachment to the ventral process of the posttemporal. This muscle form appears to be derived from that found in other species in genera 7 to 15 based on ontogenetic information. In very small individuals of Hephaestus trimaculatus, a member of this group, it has been found that there is a partial muscle origin on the ventral process of the posttemporal. This attachment is evidently lost ontogenetically as no adult specimens having this posttemporal attachment have been found in the species of this group. Such an ontogenetic shift supports a hypothesis of the muscle form in the group as apomorphic to that of the other species in genera 7 to 15 and an autapomorphy of the group.

Information on teraponid muscle forms can be summarized as follows:

1) the plesiomorph extrinsic swimbladder muscle form is a cylindrical muscle with an origin limited to the ventral process of the posttemporal. Such a muscle form is found in genera 1 to 5.

2) the derived form of extrinsic swimbladder muscle in the family has attachments to both the posttemporal and the rear of the skull at some point during ontogeny. Such a muscle form unites the species of genera 6 to 15 into a monophyletic group. Three muscle types are found with such attach-

ments in the family (in order of increasing apomorphy).

A) an extrinsic swimbladder muscle with a direct muscular attachment to the ventral process of the posttemporal and a ligamentous attachment to the pterotic.

B) an extrinsic swimbladder muscle with direct attachments to both the ventral process of the posttemporal and to the rear of the skull throughout life.

C) an extrinsic swimbladder muscle with an origin limited to the rear of the skull in adults.

Pigmentation patterns

Teraponids are noteworthy for the variety of pigmentation patterns that occur in the family both ontogenetically and interspecifically. These patterns fall into four main groups:

- 1) a vertically barred pattern
- 2) a uniform pigmentation derived from a juvenile pattern of bars.
- 3) a longitudinally striped pattern derived from a juvenile barred pattern.
- 4) a uniform pigmentation derived from a juvenile striped pattern.

Although ontogenetic information is lacking for some species (these will be discussed below), the data available does allow us to erect an hypothesis of the phylogenetic

sequence for the pigmentation patterns. The species of genera 1 to 4 for which information is available are either barred throughout life or have a juvenile pattern of vertical bars which changes to a uniform pigmentation in the adult (uniform in the sense of lacking any pattern other than a gradual lightening of the color ventrally). A transition from a barred juvenile to a uniform adult has been reported for Leiopotherapon plumbeus (Blanco and Villalobos, 1951), L. aheneus (Mees, 1971), Amniataba caudavittatus (Taylor, 1964) and has been observed in specimens of L. unicolor and Hannia greenwayi. Amniataba percoides has black bars as an adult and in A. caudavittatus a light barred pattern is retained by some individuals into adulthood. The ontogenetic changes seen here are congruent with a hypothesis that a uniform coloration is derived (apomorphic) with respect to a barred pattern.

A second pattern which appears to be directly derived from a barred pattern and apomorphic to it is that of horizontal stripes. This is the adult pattern for the species of genera 5 to 9 (with modifications in some species), and the juvenile pattern for many of the species of genera 10 to 15. A developmental shift from a juvenile barred or barred and striped pattern to an adult striped pattern has been recorded for Pelates quadrilineatus (Day, 1878), Terapon theraps (Day, 1878; Weber, 1910; pers. obs.), T. puta (1878) Rhyncopelates oxyrhynchus (Jordan and Hubbs, 1925) and has

been observed in Pelates sexlineatus. Juveniles of Terapon jarbua have a pattern of elongate disconnected pigment blotches which ontogenetically join together to form longitudinal curved bands. In many juveniles in addition to irregular horizontal connections between these pigmented areas, there are also vertical connections forming incomplete vertical bars which disappear ontogenetically. Finally as discussed in detail in the description of Pelsartia humeralis, that species has a juvenile pattern of vertical bars of irregular width which is modified into a pattern which resembles an interrupted longitudinal stripe.

The remaining type of adult pigmentation in teraponids and the one hypothesized to be most apomorphic, is a uniform adult body color derived from a striped juvenile pattern. Species having longitudinal stripes as juveniles but uniform color as adults are Mesopristes argenteus (Day, 1878; Weber and deBeaufort, 1931; pers. obs.), M. elongatus (Guichenot, 1866; Fowler, 1923; Petit, 1937 [see also discussion under the species]); M. cancellatus (Weber and deBeaufort, 1931), M. kneri (Kendall and Goldsborough, 1911), Hephaestus trimaculatus (Ogilby and McCulloch, 1916; pers. obs.), H. adamsoni (Trewavas, 1940), Pingalla gilberti (pers. obs), Syncomistes butleri (pers. obs.), and S. trigonicus (pers. obs.). Furthermore Syncomistes kimberleyensis which is presently known only from juvenile specimens has a striped pattern which probably would undergo a transition to uniform coloration as do the

other species of the genus. Hephaestus suavis is also known presently only from small specimens, but its mottled pigmentation is resolvable into a pattern of stripes and bars and it is possible that the adults of this species are uniformly colored as are the other members of its monophyletic group. Based on these ontogenetic shifts, it is hypothesized that a uniform coloration derived from stripes is apomorphic to a striped adult coloration, which in turn is derived from a more plesiomorphic barred pattern. One species with a uniform adult coloration, Hephaestus trimaculatus (genus 9b), has been found to under two transitions, from a barred to a striped and then to a uniform coloration.

There are however, a series of species which are placed in the phylogeny on the basis of other information since data on ontogenetic shifts in coloration is lacking for them, usually due to a lack of very small specimens (transitions often occurring before 30 mm SL). These include Leiopotherapon macrolepis and "Terapon" jamoerensis placed with species having uniform coloration derived directly from bars; Lagusia micracanthus a species with a striped adult pattern that is known only from limited material and with no ontogenetic information available; and Hephaestus carbo and Pingalla lorentzi whose sister species undergo a shift from a striped juvenile pattern to uniform

adult coloration. No information is available, however, for the developmental pigmentation changes in the genera 12 and 13 although the young of Bidyanus bidyanus (genus 13) and Hephaestus jenkinsi (genus 11a) has longitudinal vermiculations, with these perhaps representing remnants of horizontal stripes.

On the basis of this information on ontogenetic pigmentation changes, a hypothesis of the phylogenetic sequence of pigmentation patterns can be erected and summarized as follows:

- 1) a vertically barred pattern is plesiomorph for teraponids.
- 2) two derived patterns are found in the family apomorphic to and directly derived ontogenetically from bars:
 - A) a uniform coloration found in species of genera 1 to 4.
 - B) a striped pattern found in species of genera 5 to 9.
- 3) uniform coloration derived directly from stripes (which may in turn be preceded ontogenetically by bars) is apomorphic with respect to the striped pattern and is found in species of genera 10 to 15.

Vertebral counts

The final character analyzed with multiple character

states in the family is the number of precaudal and caudal vertebrae. As noted earlier, the distinction between these elements is made on the basis of the point that the elongate fused pterygiophore of the first and second anal spines interdigitates between the hemal arches of the spinal column. Two major differences in vertebral counts are evident in the family (Table 2); a change in the total number of vertebrae (a practically invariable count within a species) and changes in the relative number of precaudal and caudal elements for groups of species with a certain vertebral count. Most of the species in the family have 25 vertebrae with the exception of two units herein considered monophyletic. Lagusia micracanthus the only member of genus 5 has 26 vertebrae and is the only member of the family with this count. The species of genus 1b (Hephaestus trimaculatus, H. suavis, H. adamsoni, and H. carbo) have 27 vertebrae.

Lacking a definite sister group to the Teraponidae, it is not possible to know the plesiomorph vertebral count for the family with certainty. However, the majority of percoid groups previously discussed that share with the Teraponidae a series of other primitive characters have 25 vertebrae. This is a number that has been considered primitive for percoids and a hypothesis consistent with the distribution of vertebral counts and many other characters in the Teraponidae.

Variation in the relative number of precaudal and caudal elements occurs in species having 25 and 27 vertebrae. Genus

11b containing species of the genus Hephaestus is distinguished from the other members of the family by its vertebral count of 27 and other characters. Three species in this group (H. trimaculatus, H. adamsoni and H. suavis) have 11+16 vertebrae and one (H. carbo) has 10+17 vertebrae. Based on the presence of 10 precaudal vertebrae in the species of genus 11a and genus 10 which is the plesiomorph sister group to the assemblage formed by genera 11 to 15, it is considered likely that the 11+16 vertebral count represents a characters synapomorphic only for three species of Hephaestus.

Among species having 25 vertebrae, the species of genera 10 to 13 have a vertebral formula of 11+14 as does one species in genus 1 (Leiopotherapon unicolor) and one in genus 4 ("Terapon" jamoerensis). The remaining species with 25 vertebrae have a vertebral formula of 10+15. Whereas the distribution of the higher precaudal count in genera 12 to 15 is congruent with the distribution of a series of other characters considered apomorphic in this study, the increased precaudal count in L. unicolor and "T." jamoerensis appears to be a convergence. These species differ from each other in L. unicolor's lack of several derived characters uniting "T." jamoerensis to the species of genera 12 to 15. Both of these species also lack a series of apomorphic osteological (posttemporal and tabular), myological (sonic muscle), intestinal and other characters found in genera 12 to 15. Consequently it is most parsimonious to assume that the 11+14 vertebral count is a convergence.

Phylogenetic Analysis

The family Teraponidae (genera 1 to 15) as discussed in detail previously has unique forms of extrinsic swimbladder muscles, swimbladders, urohyals and third epibranchials which unite the species into a monophyletic unit (Datnioides and Pseudohelotes being excluded). The phylogenetic analysis carried out on the family has defined **fifteen** lineages herein considered genera.

Genus 1 - Leiopotherapon

In the first genus, Leiopotherapon, four species are recognized. These are L. unicolor a freshwater species distributed across most of northern Australia; L. aheneus a freshwater Western Australian species limited to the Ashburton, Robe and Fortescue rivers; L. macrolepis a previously undescribed species from the Kimberley region of Western Australia; and L. plumbeus a freshwater species limited to Luzon and Mindanao in the Philippines (see also the discussion of this species distribution under its description). All the species of genus 1 share the presence of one spine on the first proximal dorsal pterygiophore in contrast to two spines on this element in all other teraponids. This character, however, appears to be plesiomorphic on the basis of in and outgroup comparisons. An additional character shared by all four species of the genus is the insertion of the

first proximal pterygiophore between the second and third neural spines rather than between the first and second as in the majority of other teraponid groups. It is not however, presently possible to evaluate whether this condition represents an apomorphic or plesiomorphic condition for the family. Finally all species in the genus have two of the anterior proximal dorsal pterygiophores inserting between successive neural spines (Fig. 21). This character is apomorphic with respect to the primitive percoid condition of one proximal pterygiophore inserting between successive neural spines. Both this character and the posterior position of the dorsal fin appear to have arisen independently in genera 9 and 14 (see discussion on convergencies).

Genera 2 to 15

Amniataba, Hannia, "Terapon", Lagusia, Terapon,
Pelsartia, Rhyncopelates, Mesopristes, Hephaestus,
Bidyanus, Scortum, Pingalla, and Syncomistes.

Genera 2 to 15 share the common possession of two spines on the first proximal dorsal pterygiophore in contrast to the presence of one spine on the element in genus 1. Out-group comparisons and literature information (Smith and Bailey 1961) support the hypothesis that one spine on the first proximal pterygiophore is the plesiomorphic condition for percoids. Such a hypothesis is also supported by the changes

in the myology of the spine erectors and depressors associated with the first proximal dorsal pterygiophore. In the transition from one spine on this element to two, the second spine is added anterior to the original spine which retains its position with respect to the lateral strut. In such a transition, the muscles activating the new spine separate the erector of the second spine from its origin on the rear of the third predorsal. This is the situation found in the myology of species having two spines on the first proximal pterygiophore in the family. In contrast if two spines on the element was the primitive condition in teraponids, there is no reason to assume that in a transition to one spine on the element there would be a reacquisition of an attachment of the erector of the spine to the rear of the third predorsal. All of the evidence therefore points to two spines on the first proximal dorsal pterygiophore as being apomorphic and as such uniting the species of the genera with this character (2-15) into a monophyletic unit.

Processes by which an increase in the number of spines on the first proximal pterygiophore could be achieved have been discussed by Smith and Bailey (1961) who advanced three possible methods. The first a fusion between the two antero-most proximal pterygiophores into one element with two spines was rejected by these authors and is also rejected here for teraponids. In such a fusion the resultant bone

should have two full lateral struts whereas the first spine of genera with two spines on the first pterygiophore has little or no strut. In addition in such a fusion there would occur a backwards shift in the position of the dorsal origin relative to the neural spines (except if the whole fin shifted forwards), a hypothesis inconsistent with the relative positions of the dorsal fin in genus 1 vs. genera 2 to 13.

The second method discussed by Smith and Bailey for the development of two spines of the first proximal pterygiophore involves a shift backwards of the first spine to the second spine-bearing proximal pterygiophore. This results in two spines on one element and an additional predorsal. Although such a method may be how such a change occurs in other groups, it is rejected here as the method in teraponids.

On the one hand, the number of predorsals is constant at three in the family in contrast to the predicted increase to 4. On the other hand in such a shift, there should be a backwards shift of the origin of the dorsal relative to the neural spines, a shift for which there is no evidence in the Teraponidae.

The third method discussed by Smith and Bailey was a *de novo* formation of a new dorsal spine associated with the first spine-bearing pterygiophore. Although rejected by these authors as a generalized situation, it does appear to be the most likely method in this family- a hypothesis supported by the observed presence of supernumary spines as an individual

variation in the Teraponidae (in which 2 rather than 1, or 3 rather than 2 spines are present). In these individuals there is neither an increase in the number of the predorsals nor a change in the position of the fin. Rather the additional spine inserts anterior to the regular complement of spines, lacks a lateral strut and is smaller than the remaining spines, a condition comparable to that found on the first pterygiophore of genera 2 to 15.

Polychotomy: genera 2,3,4, and 5 to 15

Genera 2 to 4 (Amniataba, Hannia, and "Terapon") form an unresolved tetrachotomy with the group formed by genera 5 to 15 in that none of them shares with the species of genera 5 to 15 a derived character that they do not have in common. Neither has there been found any apomorphic characters uniting any of them into one or more monophyletic units. Consequently these genera may eventually may be shown to constitute 1 to 3 dichotomies plesiomorphic to the assemblage formed by genera 5 to 15 (such resolution being dependent in the distributions of their still undiscovered synapomorphies with each other or with the group including genera 5 to 15). In light of such uncertainties and following the systematic procedures outlined previously, each branch is recognized at the generic level. Since there is no category (supraspecific) in which one of them, the previously undescribed greenwayi, can be included, a new generic term, Hannia, has been reated to contain it.

Genus 2, Amniataba

Genus 2, Amniataba contains two species, A. percoides from the freshwaters of the northern two-third of Australia and A. caudavittatus a species found in marine, brackish, and freshwaters through northern Australia and southern New Guinea. These species are hypothesized to form a monophyletic group based on the common possession of a distinctive form of caudal mottling (see species descriptions).

Genus 3, Hannia, gen. nov.

Only one species is placed in genus 3, Hannia greenwayi, a previously undescribed form only known from the Hann River of Western Australia. The combination of a very low lateral line count and the presence of two spines on the first proximal dorsal pterygiophore serve to distinguish this species from all other members of the family.

Genus 4, "Terapon"

Genus 4 "Terapon" contains only one species "T". jamoerensis from Lake Jamoer in southern West Irian, New Guinea. For the same reasons discussed above with respect to Hannia greenwayi, "Terapon" jamoerensis must be tentatively included in a separate genus. However, rather than create a new generic name at this time, "Terapon" is retained for jamoerensis. "Terapon" in this restricted sense thus

differs from Terapon as used elsewhere in this study, and its continued use is recommended until further analysis allows the exact placement of jamoerensis as a member of its own or an existing monophyletic group.

Genera 5 to 15

Lagusia, Pelates, Terapon, Pelsartia, Rhyncopelates,
Mesopristes, Hephaestus, Bidyanus, Scortum, Pingalla,
and Syncomistes.

Genera 5 to 15 are hypothesized to be a monophyletic assemblage based on the common possession of two characters considered apomorphic for teraponids. As discussed previously all species of these groups share the presence of a striped pigmentation pattern derived from bars or a secondary pattern derived from this. This contrasts with a body pattern of vertical bars or a uniform coloration derived directly from bars found in genera 1 to 4. The presence of the striped pattern is considered apomorphic and therefore indicative of the monophyletic nature of genera 5 to 13.

Futhermore, the species of these genera share the presence of a distinctive form of blood vessel passage into the hemal canal of the third hemal arch anterior to the parahypural (Fig. 23). In genera 1 to 4, the passageway

is not enclosed ventrally, giving the appearance of a notch in the hemal arch wall. Genera 5 to 15 instead have the passageway surrounded on all sides, resulting in a distinct foramen. The condition of genera 1 to 4 (a notch in the hemal arch wall) is also present in the more anterior vertebrae and as a consequence of its general occurrence in percoids would appear plesiomorphic. The presence of a foramen in this element is therefore considered an apomorphic character and consistent with the hypothesis that genera 5 to 15 are monophyletic.

Only one species is placed in genus 5; Lagusia micracanthus, a freshwater species limited to a small area on the southern peninsula of **Sulawesi** (Celebes). As such the genus is obviously monophyletic, with L. micracanthus being distinguishable from all other species in the family in having 26 rather than 25 or 27 vertebrae.

Genera 6 to 15

Pelates, Terapon, Pelsartia, Rhyncopelates, Mesopristes
Hephaestus, Bidyanus, Scortum, Pingalla and Syncomistes

Genera 6 to 15 are hypothesized to form a monophyletic unit based on the common possession of two character states previously discussed that are considered apomorphic. The first character state being the presence of an extrinsic swimbladder muscle with both an attachment to the rear of

the skull, along with an attachment to the ventral process of the posttemporal at some point in life. This attachment to the skull is either in the form of a ligamentous tissue band attaching independently of the main muscle mass or by a direct muscle attachment to the skull (Figs. 18, 19, 20). This insertion on the rear of the skull contrast with an insertion only on the ventral process of the posttemporal as in the species of genera 1 to 5. The second modification shared by all members of genera 6 to 15 is the change in the orientation of the sensory canal of the lateral tabular so as to slope less strongly posterodorsally, along with a reduction in the anterior aperture of the sensory canals of this bone.

Genus 6, Pelates

Two species are recognized in this study as being members of Pelates. Pelates quadrilineatus (= P. quadrilineatus and P. sexlineatus of some previous workers) and Pelates sexlineatus (= Helotes sexlineatus of previous workers) share a prominent shoulder spot (may be lacking in some specimens of the former species) a character found only in these species and in a different form in Pelsartia humeralis (genus 8). Both species also have a dorsally bowed parasphenoid in the anterior orbital region, in contrast to the straight or ventrally oriented parasphenoid in other members of the family.

Genera 7 to 15

Terapon, Pelsartia, Rhyncopelates, Mesopristes,

Hephaestus, Bidyanus, Scortum, Pingalla and Syncomistes

The species placed in genera 7 to 15 are considered a monophyletic group based on the common possession of a series of previously discussed characters. All members of these genera have in common an exposed posteriorly expanded and serrate posttemporal with a lengthened posttemporal sensory canal having lateral sensory openings (Figs. 12 and 13). This condition contrast with that found in genera 1 to 6 (Fig. 11) in which the posttemporal has a small lateral process with a small sensory canal lacking lateral openings. Congruent with this change in the posttemporal form there has also occurred a reorientation of the section of the supratemporal commissure in the lateral tabular bone from a posterodorsal orientation to a vertical or posterovental orientation and a ventral shift in the point of the posttemporal-supracleithral articulation.

Major changes have also occurred in the form of the extrinsic swimbladder muscles. The species of genera 7 to 15 have a direct muscular attachment of the extrinsic swimbladder muscle to the pterotic region of the skull (Figs. 19 and 20) in addition to an attachment to the ventral process of the posttemporal at some point during development. This situation contrast with the lack in genera 1 to 6 of contact of the extrinsic swimbladder muscle with the skull or an origin on the skull by means of a band of connective tissue (Figs. 17 and 18). Finally as discussed previously all species of these genera (7 to 15) have

two or more rows of scales in the sheath at the base of the spinous dorsal fin rather than the one row found in more plesiomorph groups.

Genus 7, Terapon

Three species are included in genus 7, all of which have wide distributions in marine waters through the Indo-west Pacific. These are Terapon jarbua (considered by some previous workers to be two species; see discussion under that species), I. theraps and I. puta. They share in common a series of derived characters which serve to characterize the group as one of the most distinctive within the family. The first character is the presence in the three species of a markedly elongate lower opercular spine extending well beyond the edge of the opercular lobe. In contrast, all other species in the family possess a lower opercular spine which does not extend beyond the edge of the opercular lobe (in some juveniles of Pelates sexlineatus the spine barely extends beyond the edge of the lobe).

A second character distinguishing the species of genus 7, is a deeply emarginate spinous dorsal in which the penultimate spine is one half or less the length of the ultimate. Other teraponids have the penultimate spine longer than the ultimate or only slightly shorter. An additional character is the relative size of the dorsal and anal spines. Among those groups of teraponids having the longest dorsal spines longer than the longest dorsal ray, only in the species of the genus Terapon

does one find very short anal spines with the second spine subequal to or shorter than the third.

Two pigmentary characters also distinguish the three species of Terapon. The first of these is the presence of narrow transverse bands slanting obliquely across each lobe of the caudal fin; a condition which contrasts with a uniform or marbled pattern in the other species of the family (Amniataba caudavittatus [genus 2] also has transverse markings on each caudal lobe, but in that species they are in the form of a single wide oval blotch). All species of Terapon also share prominent dark pigmentation along the anterodorsal edge of the soft dorsal as compared with a uniform coloration or a pale margin in other members of the family.

Genera 8 to 15

Pelsartia, Rhyncopelates, Mesopristes, Hephaestus
Bidyanus, Scortum, Pingalla, and Syncomistes.

The members of genera 8 to 15 possess a sheath consisting of 2 or more rows of equally sized scales along the base of the dorsal fin. On the basis of outgroup comparisons and ontogenetic data this is considered to be derived with respect to a sheath of one or one and one-half scale rows present in genera 1 to 5. Furthermore, within branches 8 to 15, the anal sheath height is also increased, consisting of 3 to 6 rows of scales rather than the 2 or 3 rows of scales in genera 1 to 7; an increase which is also considered to be apomorphic.

Genus 8, Pelsartia

Only one species is placed in genus 8, Pelsartia humeralis a marine species from the southwestern and southern coasts of Western Australia and South Australia. This species is distinguished by its unique coloration pattern (see species description) and a distinctive upwards curl distally in the ventrolateral projections of the urohyal.

Genera 9 to 15

Rhyncopelates, Mesopristes, Hephaestus

Bidyanus, Scortum, Pingalla, and Syncomistes

The species of genera 9 to 15 share two characters. The first is the presence of a vertical or posteriorly bowed supraoccipital margin. This contrasts with the undercut anteriorly bowed edge found in the species of genera 1 to 8. On the basis of the ontogenetic shift in the species of genera 9 to 15 from an undercut to a posteriorly straight or bowed supraoccipital, the latter appears to be the derived condition in teraponids. An additional character having a distribution congruent with the above character but whose polarity cannot be determined is the form of the posterodorsal edge of the cleithrum. In all teraponids Baudelot's ligament runs from the basioccipital to the ventral portion of the supracleithrum just dorsal of the upper edge of the cleithrum. In the species of

genera 1 to 8, the cleithrum bears a bony process surrounding the ventral and posterior edges of the ligament and which forms a notch in the posterodorsal profile of the bone (Fig. 24a). The species of branches 9 to 15, however, lack the posterior process, so that the cleithrum is smooth or only slightly irregular below the passage of the ligament (Fig. 24b).

Genus 9, Rhyncopelates

Only one species is placed in genus 9; Rhyncopelates oxyrhynchus a marine species from southern China and Japan that sometimes penetrates into freshwater. R. oxyrhynchus is distinguished from the remainder of the family by its body pattern of solid and discontinuous horizontal stripes and by the very wide extrinsic swimbladder muscle which has an origin that extends in adults from the ventral process of the posttemporal to the edge of the basioccipital.

Genera 10 to 15.

Mesopristes, Hephaestus, Bidyanus, Scortum, Pingalla and
Syncomistes

The members of genera 10 to 15 possess in common a uniform adult coloration pattern which is derived directly from an ontogenetically earlier pattern of stripes (the striped pattern in turn may be derived ontogenetically from bars). Other teraponids either have a barred pattern, a uniform pattern derived directly from bars or an adult striped pattern derived

from bars. On the basis of ontogenetic shifts in coloration discussed in detail earlier, the pattern of genera 8 to 13 is considered apomorphic to the others.

Genus 10, Mesopristes

Four species are placed in genus 10, Mesopristes. Two of these, Mesopristes argenteus and M. cancellatus, have rather wide distributions in the East Indies (see also the discussion under the former species concerning reported extralimital occurrences). The remaining species are known only from limited area: M. kneri apparently is endemic to the Fiji Islands, and M. elongatus, to the eastern region of Madagascar, being the only species in the family having a distribution limited to part of the Indian Ocean.

The species of Mesopristes differ from the other species in the family in the marked difference in the degree of pronouncement of the dorsal and ventral profiles in the adults. Whereas the ventral profile of the adults is straight or nearly straight, the dorsal profile is markedly convex (Figs. 59 to 65). Associated with this difference in the comparative arches of the profiles, is a downward turning of the head anteriorly which becomes more pronounced ontogenetically. This results in a complete reorientation of the position of the tip of the snout relative to the rest of the body, with the snout shifting ventrally with respect to the median frontal plane of the body. In conjunction with this change in head position, there are two modifications of the skull. The parasphenoid in the species of

Mesopristes rather than having a horizontal or slightly anteroventral slope in and anterior to the orbital region as in other teraponids has instead a marked anteroventral orientation; being practically straight and lacking the prominent bend at the rear of the orbital region that characterizes the remainder of the family. Perhaps as a consequence of the change in the orientation of the skull, the species of the genus also have a posteriorly bowed rear supraoccipital margin, rather than the vertical or undercut margin in the other genera of the family.

The genus Mesopristes is also characterized by the possession of very strong and long anal and dorsal spines in comparison to those of other members of the family, with the longest anal spines longer than or as long as the longest anal rays. This differs from the situation in nearly all the other species of the family in which the longest anal rays are distinctly longer than the longest anal spines in the adults.

Genera 11 to 15

Hephaestus, Bidyanus, Scortum,

Pingalla and Syncomistes.

The group of species formed by genera 11 to 15 shares two characters. The first is the possession of a derived intestinal convolution pattern. In contrast to the adult

intestinal pattern found in genera 1 to 10 which has only two loops in the median body plane or to the right of it, the species of genera 11 to 15 have a more complex intestinal pattern with five loops and the anterior loops curling around the ventral surface of the stomach to the left of the median body plane (Fig. 16b) (this pattern appears to have been secondarily lost in the species of genus 11b). On the basis of the ontogenetic changes from a juvenile pattern similar to that of the adults of genera 1 to 10 to the more complex adult pattern, the latter pattern is considered apomorphic.

An additional character shared by the species of genera 11 to 15 is the common possession of a freshwater ecology. Freshwater species of teraponids have a polyphyletic distribution in the reconstruction of the phylogeny arrived at in this study. The species of genera 1 to 11 (with the exception of Amniataba caudavittatus) and 11 to 15 are freshwater, while Amniataba caudavittatus (genus 2) and the species of genera 6 to 10 are marine. Although all the species considered marine are noteworthy for their ability to penetrate into freshwaters, they do not appear to be able to reproduce there based on the limited information available (Munro, 1945; Zvjagina, 1965; Wallace, 1975).

A transition from a marine to a freshwater mode of reproduction requires a series of morphological, physiological and behavioral modifications. Therefore, the freshwater ecology and reproductive habits of the species of these

genera constitute a series of characters shared by the species of genera 11 to 15. Finally, these genera also share a decreased number of epipleural ribs from the 7 to 10 of genera 1 to 10 to 5 to 7 elements. However, it is not possible to determine the polarity of this character.

Genus 11, Hephaestus

The species of branch 11 have in common a series of characters considered apomorphic within the Teraponidae. All species have the longest dorsal spines in the adults shorter than the longest dorsal rays. This contrasts with the situation in the other species of the family (with the exception of Leiopotherapon unicolor and L. macrolepis of genus 1 and Syncomistes trigonicus of genus 15) where the longest dorsal spines are as long as or longer than the longest dorsal rays. All species of Hephaestus also share a backwards shift in the position of the insertion of the dorsal fin. Rather than an insertion of the first proximal dorsal pterygiophore between the first and second neural spines, a condition which seems to be plesiomorphic in the family, in genus 11 (and also genera 1 and 15) the first proximal pterygiophore inserts between the second and third neural spines (third and fourth in H. adamsoni) (Fig. 21). Associated with this shift in dorsal fin position is a change in the correspondence between the proximal pterygiophores of the dorsal fin and the neural spines. Rather

than the one-to-one relationships between these elements, found in most teraponids and a condition that is primitive for percoids, the species of genus 11 have two successive proximal pterygiophores inserting between successive neural spines; either the second and third or fourth and fifth neural spines (fig. 21) (with the exception of some individuals of H. roemeri).

Within the genus Hephaestus two subunits designated a and b are distinguishable. Three species are placed in genus 11a; H. fuliginosus from Northern Territory and Queensland, H. jenkinsi northwestern Australia and H. roemeri from southern West Irian. However, no derived characters have been found uniting these species into a monophyletic unit, consequently the assemblage is potentially polyphyletic. Genus 11b is however, distinguishable from the species of genus 11b in the lack of a series of derived characters that makes the latter group one of the more distinctive in the family. Four species are placed in genus 11b: Hephaestus adamsoni a poorly known species evidently limited to the waters of Lake Kutubu, southern Papua-New Guinea; H. trimaculatus (= Therapon trimaculatus and T. habbemai of previous workers) from the southern drainages of New Guinea; H. suavis known only from the Coen district of northern Queensland and H. carbo from the Gulf of Carpentaria drainages of Queensland. The four species of the genus have in common 27 vertebrae in comparison to 25 or 26 found in the remainder of

the family, an increase which as discussed earlier appears to be apomorphic. An additional character unique to these species in the family is the form of the lateral tabular and its sensory canals (tabular not examined in H. suavis which is known only from types). The supratemporal commissure and otic canals of the bone in these species join together at the posterior edge of the bone to form a pattern of a caudally directed "V" (Fig. 13). This structure contrasts with the patterns of an anteriorly pointing V or an inverted T formed by these canals in the other species of the family. Associated with this change in the lateral tabular, there has also occurred a change in the morphology of the posttemporal. In the adults of these species it is more massive, posteriorly elongate, and closely applied to the side of the head than in other groups in the family.

Finally, all species of the group (11b) have a unique form of extrinsic swimbladder muscle derived from the muscle form of the other species in genera 7 to 15 (see previous discussion; muscle form not examined in H. suavis). In this form of the sonic muscle, the origin in the adults is limited to the posteroventral edge of the pterotic. All the other muscle forms found in the species of the family differ in having at least a partial attachment to the ventral process of the posttemporal. Within the species of genus 11b, a second monophyletic unit can be distinguished by the presence of an increased number of precaudal vertebrae (11)

in Hephaestus trimaculatus, H. suavis, and H. adamsoni rather than the 10 precaudal vertebrae found in H. carbo.

Genera 12 to 15

Bidyanus, Scortum, Pingalla, and Syncomistes.

The remaining four genera (12-15) share a series of modifications of the jaws and form of the dentition that serve to distinguish groups of decreasing universality. The plesiomorph form of jaw and dentition for percoids and consequently for teraponids is that illustrated in figure 25. The conic, non-depressible, vertically directed dentition is located along the superior and to a lesser extent inner surfaces of the dentary which has a prominent symphyseal process anteroventrally. Within the Teraponidae, this is the form of jaw and dentition found in the species of genera 1 to 11 (Pelates sexlineatus, genus 6, has tricuspid teeth). The species of genera 12 to 15, however, share in common a depressible dentition and to differing levels of universality (see below) a dentary rolled laterally to varying degrees that results in the teeth pointing somewhat to distinctly laterally and the development of a prominent median dentary process. An additional apomorphic character shared by all the species of these genera is a vertebral count of 11+14, rather than the 10+15 count that characterizes the other species with 25 vertebrae (two other

species with this number of vertebrae [Leiopotherapon unicolor, and Amniataba jamoerensis] appear to have achieved this vertebral count independently).

Genus 12 Bidyanus

Two freshwater Australian species are placed in genus 12, Bidyanus bidyanus which is distributed throughout New South Wales and Victoria and B. welchi from the internal drainages of South Australia and Queensland. These species are distinctive in their overall body and head forms; having an elongate body with a long caudal peduncle and a small head which develops in adults a distinct concavity in the dorsal profile slightly posterior to the orbit. These two species also have a count of 20-25 predorsal scales to the occiput, a very high count for the family distinguishing them from all other species of the family except Terapon jarbua (genus 7) which has 19-24 predorsal scales.

Genera 13 to 15

Scortum, Pingalla and Syncomistes.

The remaining three genera in the family, 13 to 15, share a distinctively flattened depressible dentition in contrast to the conic tooth form of the remainder of the family (Pelates sexlineatus, has a tricuspidate, distally flattened dentition which is, however, non depressible and over quite different overall form). These species also share a reduction or lack of the symphyseal dentary bump and

a moderate to pronounced lateral turning of the dentary.

Genus 13, Scortum

Genus 13 is considered in this study to contain three species: Scortum parviceps from the upper Burdekin River of New South Wales, S. hillii (S. hillii+ S. ogilbyi of previous workers) of the eastern and Gulf of Carpentaria drainages of Queensland, and S. barcoo a species tentatively placed in the genus. These species share an apomorphic pattern of randomly distributed dark blotches (condition unknown in S. barcoo); the retention of vomerine teeth into the adults, a situation that also occurs in some Terapon jarbua, and a distinctive leathery flesh (condition unknown in S. barcoo). As noted above, the placement of S. barcoo is tentative as the type (only specimen collected) was not examined and the original description provides limited information. Its inclusion in the genus follows both previous taxonomic practice and the character of the retention of the vomerine teeth. However, it is possible that study of further characters not discussed in the original description may indicate that S. barcoo is more closely related to some other group in the family.

Genera 14 and 15

Pingalla and Syncomistes

The species of genera 14 and 15 form a monophyletic group based on the common possession of a series of characters

considered apomorphic for teraponids.

The species of both genera possess the more complex pattern of intestinal convolutions discussed previously (Fig. 16c) with an increase in the length and looping of the intestine and a greater percentage of the loops occurring to the left of the median body plane. Associated with this change in the morphology of the digestive system, there has also occurred a change in the dentition and jaws in these species. Species of both genera have the primitively dorsal surface of the dentary rotated laterally. This results in the dentition pointing laterally to varying degrees (Fig. 26). As a consequence of this jaw rotation, the main area of contact between the dentaries has shifted from the anterovertical edge of the symphyseal joint to a anterohorizontal point of contact, with a consequent loss in the prominent anteroventral symphyseal process. In addition to this change in the overall form of the lower jaw, these genera share a shift in the dentitional form. Rather than the slightly depressible and slightly flattened teeth of branch 13 and the conic, non-depressible teeth of genera 1 to 12, genera 14 and 15 share highly depressible, distinctly flattened teeth. Furthermore in these groups, the dentition is limited to either two rows (genus 14) or a row followed by a distinct arrow band (genus 15) in contrast to the wide tooth band found in the other species of the family.

Finally, and perhaps as a consequence of the increased

intestinal length and the consequent change in the center of gravity, there has occurred a secondary reduction in the swimbladder constriction discussed earlier (Fig. 6).

Branch 14, Pingalla

Within the monophyletic unit formed by the above characters, two species are recognized in genus 14 and three in genus 15. The two species placed in genus 14 are Pingalla gilberti from the rivers of northern Queensland and Northern Territory and P. lorentzi from the southern drainages of West Irian. These species appear to form a monophyletic unit based on the common possession of a practically non-protractile small mouth with the posterior of the maxillary strongly curved ventrally. This contrasts with the larger protractile mouth with a nearly straight maxillary in the other members of the family (mouth size also reduced in Pelates sexlineatus). These species also have only two rows of teeth in each jaw in contrast to wide bands of teeth in each jaw or a row of teeth followed internally by a narrow band that occurs in all other groups in the family.

Genus 15, Syncomistes n. gen.

Genus 15 contains three species described for the first time in this study and forming one of the more distinctive groups within the family in overall appearance. The included species are all from northern Western Australia and Northern

Territory with Syncomistes butleri having the widest distribution from the Bow River in the south to the South Alligator River in the north. The remaining species are of more limited range with S. trigonicus known from the Drysdale, Prince Regent, and Roe Rivers of the Kimberley region and S. kimberleyensis only from the Bow River.

These species share a large number of apomorphic characters unique to the group among teraponids and most of which are directly associated with modifications for eating and digestion. The adults of the species have a further elaboration of the intestinal pattern found in genus 13 involving a highly complicated pattern of intestinal convolutions and loops curling around the ventral and up the left side of the stomach.

In these species there have also occurred radical changes in the jaw form. The outward rolling of the dentary is marked, resulting in the teeth of the lower jaw pointing laterally (Fig. 28) and the main point of articulation between the dentaries shifting to the inner surface of the lower jaw with the consequent development of a prominent dorsal bump at the symphysis (Fig. 28). This bump corresponds in position to a median groove between the premaxillaries, with both the bump and groove lacking dentition. Both the presence of these structures (bump and groove) and the lack of dentition on them are characters unique to the genus and apomorphic within the family.

In addition to the presence of the median groove, there have also occurred a series of other modifications of the upper jaw. The maxillary in the species of Syncomistes is much heavier and more massive than in the other groups in the family. The ascending processes of the premaxillary are also of a distinctive shape; rather than the elongate parallel structures found in other species of the family, in the species of this genus, the ascending processes are triangular with the medial surfaces diverging from each other and being distinctly separated at their posterior tips (Fig. 27). Along with this change in the form of the ascending processes of the premaxillaries, there is also found a change in the form of the associated rostral cartilage. The condition of this structure plesiomorph for percoids and probably for teraponids based on out-group comparisons is an elongate cartilage connected to the ventral surfaces of the ascending processes of the premaxillaries by connective tissue; a condition found in genera 1 to 12.

The species of genus 15 have a highly modified rostral cartilage which is hemispherical with a concavity on its posterior surface and very loose connections to the premaxillaries (Fig. 27). In conjunction with this change in the shape of the rostral cartilage, has occurred a change in the anterior surface of the ethmoid over which the cartilage moves. Rather than an anteroventral sloping surface along which the rostral cartilage slides in the plesiomorph condition, the ethmoid in the genus Syncomistes has an anterior rounded knob. In

conjunction with the change in the form of the rostral cartilage, this results in the primary movement of the upper jaw being in a nearly vertical direction rather than the antero-posterior motion found in other species of the family.

Finally, the species of Syncomistes share with the members of genera 1 and 11 independently acquired but derived backwards shifts in the position of the origin of the dorsal fin, with the insertion of two proximal dorsal pterygiophores between two successive neural spines; both characters being considered derived as discussed previously.

Convergent characters

As would be expected in a group the size of the family Teraponidae, there occur a series of characters whose distribution is not congruent with a hypothesis of relationship based on the majority of characters. The distribution of such characters, both those that have been discussed in the course of the phylogenetic analysis and others, is shown superimposed on the arrived at phylogeny in figure 29. These characters include the changes in the relative number of pre-caudal and caudal vertebrae; increased numbers of vertebrae, shortened dorsal spines, changes in the relative positions of insertion of the dorsal fins with respect to the neural spines, flattened teeth, blotching on the dorsal and humeral spots.

In the case of flattened dentition and the humeral spots, the different conditions in the various groups having them are sufficiently distinct so as to raise questions as to the sameness of the characters (i.e., whether they are the same character at all and therefore whether they are really convergent).

However, any attempts to modify the arrived-at hypothesis of relationships to reflect some or all of these character distributions results in a still greater number of convergencies. As any reconstructed hypothesis of relationship should be maximally parsimonious in light of the available information, such changes would be unacceptable.

Comparisons with previous classifications

The hypothesis of relationships arrived at in the above reconstruction and those deduced from either Cuvier and Valenciennes' or Whitley's classification differ markedly. The division of the family into monophyletic assemblages in this work is inconsistent with the recognition of the genus Teraeon in the older usage - a usage which employed shared primitive characters. Similarly, inconsistencies exist between the conclusions of this study and those of Whitley regarding the genera Amphitherapon (as modified by Munro), Hephaestus, Nadiwania, Mesopristes, Pelates, Leiopotherapon and the subfamily Helotinae.

The genus Amphitherapon originally erected by Whitley for A. caudavittatus was expanded by Munro (1967) to include Teraeon habbema Weber (1910) which is placed as a synonym of Hephaestus trimaculatus in this work. A. caudavittatus and T. habbema are however, markedly different with the latter having a series of derived states of the tabular, posttemporal, myology and pigmentation lacking in A. caudavittatus but shared in common with the other species of Hephaestus.

Whitley placed in the genus Hephaestus another species, Teraeon welchi McCulloch and Waite, which is herein considered to be a member of the genus Bidyanus. B. welchi shares with B. bidyanus and with the species of genera 12 to 15 a series of characters lacking in Hephaestus and also lacks the derived

characters of the other species of Hephaestus.

Hunro (1964, 1967) added to the previously monotypic genus Hadigania erected by Whitley (1945a) for H. unicolor a second species M. adamsoni perhaps being misled by the previously discussed misinterpretation of the pectoral girdle osteology. However, whereas M. unicolor is considered to be a member of genus 1, Leiopotherapon, M. adamsoni shares a large series of derived characters with the other species of the genus Hephaestus (genus 11).

The genus Mesopristes as recognized in this study is limited to four species (2 of which were not considered by Whitley). Whitley also placed in the genus Terapon alligatoris Rendahl, herein considered to be a synonym of Hephaestus fuliginosus; M. jenkinsi also considered to be a member of Hephaestus in this study; and Therapon aheneus which in this reconstruction is placed in genus 1 Leiopotherapon.

The genus Leiopotherapon was erected by Fowler (1931) as a subgenus for four species lacking an exposed posttemporal and distributed in genera 1 and 2 in this study. Whitley (1943b) added to the genus a new species L. suavis which differs, however, from the species of the Fowler subgenus in having an exposed posttemporal and the possession of a series of derived states of pigmentary and osteological characters; being placed in the genus Hephaestus.

The genus Helotes originally erected by Cuvier and Valenciennes (1829) for H. sexlineatus (= Pelates sexlineatus) was expanded by Weber (1910) followed by later workers with the addition of a second species H. lorentzi based on supposed similarity in tooth form. More recently Whitley (1953) removed H. lorentzi from the genus Helotes to Pingalla along with P. gilberti a species described at the same time. However, he retained a concept of a close relationship between these three species (sexlineatus, lorentzi, and gilberti) by their separation from the rest of the family as the subfamily Helotinae. However, the tooth forms of the two genera (Helotes sensu Whitley and Cuvier and Valenciennes, and Pingalla) are quite distinct. Furthermore the species placed in Pingalla share a large series of characters supporting their placement in genus 14; characters lacking in Helotes (= Pelates) sexlineatus which is placed in genus 6.

Cuvier and Valenciennes' original (1829) concept of the genus Pelates was later modified by Weber and deBeaufort's (1931) addition to the genus of Terapon roemeri Weber (1910) based on supposed similarity in tooth arrangement. According to their concept of the genus, it was defined by triserial teeth in the upper jaw and biserial in the lower. However, none of the **species** of the genus consistently have such a pattern and the available material of Terapon (= Hephaestus)

roemeri has a band of up to six rows of teeth, with the inner rows imbedded in the flesh of the mouth and not readily visible. Finally, H. roemeri has a series of derived character states of the posttemporal, extrinsic swimbladder muscle, tabular, etc. uniting it to the monophyletic group formed by the species of Hephaestus; characters lacking, however, in Pelates.

Besides the above modifications of the genus Pelates, Fowler (1928) added to the genus another species (Terapon [Rhyncopelates] oxyrhynchus). This species, however, fails to agree with either the concept of the genus advanced by that author (see under the species description) or any other. Neither does the distribution of characters within the family support the hypothesis of a close relationship between this species and the species of Pelates.

In addition to the above modifications of the limits of various genera, there are also a series of other genera which have been placed in synonymy. These are Madigania (in genus 1), Amphitherapon (in genus 2.), Helotes (in genus 6), Authistes and Eutherapon (in genus 7), Papuservus and Archerichthys (in genus 11).

Family Teraponidae

Oblong to oblong-ovate fishes with body moderately compressed. Scales small to large; adherent; finely ctenoid; 29-100 in lateral line from origin at supracleithrum to hypural joint. Lateral line continuous; beginning at supracleithrum and following dorsal body curvature to the caudal peduncle, then running beyond hypural joint horizontally onto caudal fin. Scales of the lateral line usually smaller than surrounding scales; tubes of lateral line scales usually not reaching posterior edge of scale. Scales smallest on thoracic region, largest on anterior of body above lateral line. Scales extending onto pectoral and caudal bases. Sheath of scales at base of spinous dorsal and anal fins extending onto soft dorsal and anal.

Head moderate to large. Scales on cheeks, subopercle, opercle and nape. Top of head and snout naked. Snout moderate to elongate with the lacrimal long and overlapping the premaxillary and maxillary. Circumorbital series not covering the cheek. A subocular shelf developed in all species. Lacrimal serrate; serrations reduced with age in some forms. Preoperculum serrate; serrations more prominent in juveniles. Operculum with two spines, lower spine is stronger and longer; extending beyond edge of opercular lobe in some species. Posttemporal exposed or not; if exposed with posterior edge expanded and serrate. Supracleithrum

exposed except in one species; with a covering of skin. Cleithrum exposed; usually serrate posteriorly and with scales on side.

Mouth usually moderate; with gape oblique and protractile (gape small and not very protractile in two species and horizontal in others). Jaws usually equal or with only a slight difference in length. Teeth conic or flattened, set or depressible, with outer row enlarged and followed by a band of villiform teeth (reduced to two or three distinct rows in some forms). Dentition reduced or lacking medially in each jaw in some species. Vomer and palatines lacking dentition except in a few species. Nostrils paired; distinctly separated; with free cutaneous edges in most species.

Dorsal with 11 to 14 spines and 8 to 14 rays. Spinous dorsal arched, nearly divided by a deep notch in some species. First spine usually quite short and fifth to seventh the longest. Spinous dorsal depressible into a groove formed by basal sheath of scales. First proximal dorsal pterygiophore bearing one or two spines. Three predorsals in all species.

Anal with 3 spines and 7 to 12 rays. First anal spine shortest; either the second or the third longest. Spinous anal and anterior of soft anal depressible into basal anal sheath. First and second proximal anal pterygiophores fused. Caudal rounded, truncate or emarginate; with 17 principal rays, 15 branched. Pectoral assymmetrically pointed; 12 to

17 rays. Pelvics I-5; first ray usually longest and often filamentous. Pelvic insertion distinctly behind pectorals.

Swimbladder constricted into two or three (only in one species) chambers by transverse constrictions. Extrinsic swimbladder muscle found in all species; arising from rear of skull or posttemporal or both and inserting in anterodorsal surface of anterior swimbladder chamber. Stomach triangular. Intestine short to elongate, with pyloric caecae. Six branchiostegal rays. Pseudobranchia large. Gill rakers short to moderate; shorter than filaments; 5-18 on upper and 9-27 on lower limbs of first arch. Vertebrae 25 to 27; anteriormost pair lacking pleural ribs. Caudal with 3 epurals, 2 uroneurals, 6 independent hypurals and with hemal arches of two vertebrae anterior to urostylar vertebra autogenous.

Fishes of small to moderate maximum size (65 to 800 mm SL being range of largest individuals for different species). Found in salt, brackish and fresh waters throughout the Indo-west Pacific region.

Diagnosis: the family Teraponidae can be distinguished in having an extrinsic swimbladder muscle arising from the rear of the skull; a transversely divided swimbladder; a distinctive form of urohyal and a distinctive process of the third epibranchial.

Classification

In the classification proposed in this work, only the monophyletic groups formed by the entire family and the individual branches have been formally named (the latter at the generic level). Because the proposed cladogram contains several outstanding questions, additional hierarchic rankings were deemed undesirable. These questions include the questions of 1) the exact relationships of genera 2,3, and 4 with respect to each other and the group formed by genera 5 to 15; 2) several dichotomies defined solely on the bases of a single character; and 3) the hypothesis of a secondary loss of the advanced intestinal convolution pattern in the species of genus 9b.

Although with increasing analysis such problems should theoretically approach resolution, with a subsequent stabilization of the classification based on the most parsimonious reconstruction of relationships, the above problems might require major changes in the classification at some point in the future if every branching point were given taxonomic recognition at this time (the genera Amniataba, Hannia, and "Terapon" perhaps representing three dichotomies plesiomorphic to the group formed by genera 5 to 15). As a result of these uncertainties, I prefer to maintain a

more conservative modification of the previous taxonomy
until further study removes at least some of the major
uncertainties outlined above

Family Teraponidae

Genus Leiopotherapon Fowler, 1931Leiopotherapon plumbeus (Kner, 1865)Leiopotherapon unicolor (Günther, 1859)Leiopotherapon macrolepis n. sp.Leiopotherapon aheneus (Mees, 1963)Genus Amniataba Whitley, 1943Amniataba percoides (Günther, 1864)Amniataba caudavittatus (Richardson, 1844)Genus Hannia n. gen.Hannia greenwayi n. sp.Genus "Terapon""Terapon" jamoerensisGenus Lagusia n. gen.Lagusia micracanthus (Bleeker, 1860)Genus Pelates Cuvier and Valenciennes, 1829Pelates quadrilineatus (Block, 1790)Pelates sexlineatus (Quoy and Gaimard, 1824)Genus Terapon Cuvier, 1817Terapon jarbua (Forsk., 1775)Terapon theraps Cuvier and Valenciennes, 1829)Terapon puta Cuvier and Valenciennes, 1829Genus Pelsartia Whitley, 1943Pelsartia humeralis (Ogilby, 1899)Genus Rhyncopelates Fowler, 1931Rhyncopelates oxyrhynchus (Temminck and Schlegel 1842)Genus Mesopristes Bleeker, 1845

Mesopristes argenteus (Cuvier and Valenciennes, 1829)

Mesopristes cancellatus (Cuvier and Valenciennes, 1829)

Mesopristes kneri (Bleeker, 1873)

Mesopristes elongatus (Guichenot, 1866)

Genus Hephaestus DeVis, 1884

Hephaestus fuliginosus (Macleay, 1883)

Hephaestus roemeri (Weber, 1910)

Hephaestus jenkinsi (Whitley, 1945)

Hephaestus trimaculatus (Macleay, 1883)

Hephaestus carbo (Ogilby and McCulloch, 1916)

Hephaestus adamsoni (Trewavas, 1940)

Hephaestus suavis (Whitley, 1948)

Genus Bidyanus Whitley, 1943

Bidyanus bidyanus (Mitchell, 1838)

Bidyanus welchi (McCulloch and Waite, 1917)

Genus Scortum Whitley, 1943

Scortum parviceps (Macleay, 1884)

Scortum hillii (Castelnau, 1877)

Scortum barcoo (McCulloch and Waite, 1917)

Genus Pingalla Whitley, 1953

Pingalla lorentzi (Weber, 1910)

Pingalla gilberti Whitley, 1953

Genus Syncomistes n. gen.

Syncomistes butleri n. sp.

Syncomistes triquoicus n. sp.

Syncomistes kimberleyensis n. sp.

Key to the species of the family Teraponidae

- A) Posttemporal covered with skin and scales; not expanded posteriorly; not with a serrate edge.....B
- B) 68 or more lateral line scales; distinct black blotches on anterior of spinous dorsal; body with distinct longitudinal stripes; extrinsic swimbladder muscle with an attachment to pterotic by a ligamentous band.....C
- C) teeth tricuspidate; gill rakers on first arch 6-7+1+14-16; 80-87 lateral line scales; body depth 3.4-4.0 in SL.....Pelates sexlineatus
(Australia, East Indies, Philippines, China)
- CC) teeth lacking side cusps; gill rakers on first arch 16-18+1+22-27; 68-73 lateral line scales; body depth 2.6-3.2 in SL.....Pelates quadrilineatus
(Indo-west Pacific)
- BB) 66 or fewer lateral line scales; dorsal fin lacking prominent black blotches; if longitudinal striping is present, indistinct and species has 38-42 lateral line scales (Lagusia micracanthus); extrinsic swimbladder muscle attaching only to posttemporal.....D
- D) 60-66 lateral line scales; uniform dark silvery brown coloration....."Terapon" jamoerensis
(West Irian).

- DD) 57 or fewer lateral line scales, if lateral line greater than 52, longest dorsal spines shorter than longest dorsal rays E
- E) each caudal lobe with a prominent oblique transverse black blotch; spots randomly distributed on body.....
.....Amniataba caudavittatus
(Australia, New Guinea).
- EE) caudal lobes lacking prominent blotches.....F
- F) body with 5-8 vertical black bars, each about 2 scales wide.....Amniataba percoides
(Australia).
- FF) body without vertical black bars.....G
- G) longest dorsal spines distinctly shorter than longest dorsal rays.....H
- H) 29-33 lateral line scales; 3-5 scales above lateral line; 4-5 cheek scales.....Leiopotherapon macrolepis
n. sp.(Western Australia)
- HH) 45-57 lateral line scales; 7-9 scales above lateral line; 6-9 cheek scales.....Leiopotherapon unicolor
(Australia).
- GG) longest dorsal spines distinctly longer than longest dorsal rays.....I
- I) 13-16 gill rakers on lower limb of first arch.....J
- J) 32-38 lateral line scales; scales above lateral line 4-5.....Hannia greenwayi
n sp.(Australia)

- JJ) 43-52 lateral line scales; scales above lateral line 6-8.....Leiopotherapon plumbeus
(Philippines).
- II) 10-12 gill rakers on lower limb of first arch...K
- K) 11-12 scales above lateral line; 16 predorsal scales to occiput; 26 vertebrae..Lagusia micracanthus
(Sulawesi).
- KK) 14-15 scales above lateral line; 12-14 predorsal scales to occiput; 25 vertebrae.....Leiopotherapon aheneus (Australia)
- AA) posttemporal expanded and serrate posteriorly; exposed posteriorly; skin and scale covering reduced.....L
- L) lower opercular spine greatly developed; extending beyond edge of opercular lobe; lobes of caudal with oblique stripes; spinous dorsal with large black blotch on middle rays.....M
- M) 47-56 lateral line scales; 6-7 scales above lateral line Terapon theraps
(Indo-west Pacific)
- MM) 70 or more lateral line scales; 10-17 scales above lateral line.....N
- N) 2-4 straight longitudinal stripes along side of body, gill rakers on lower limb of first arch 18-25.....
.....Terapon puta
(Indo-west Pacific)

- NN) three downward curved longitudinal stripes along
body; gill rakers on lower limb of first arch
12-15.....Terapon jarbua
(Indo-west Pacific)
- LL) lower opercular spine not extending beyond edge of opercular
lobe. Lobes of caudal lacking oblique stripes. Spinous
dorsal lacking large black blotch.....0
- O) teeth flattened , depressible.....P
- P) mouth very small, nearly non-protractile, rear of max-
illary strongly curved ventrally; two rows of teeth in
each jaw.....Q
- Q) 48-54 lateral line scales; 13-14 dorsal spines.....
.....Pingalla lorentzi
(New Guinea)
- QQ) 35-41 lateral line scales; 11-12 dorsal spines.....
.....Pingalla gilberti
(Australia)
- PP) mouth moderate to large, more protractile; teeth in each
jaw in bands or a distinct row followed by a narrow
band; posterior of maxillary not strongly curved....R
- R) lower jaw with a dorsally directed median bump which
fits into a depression between premaxillaries (Fig. 28);
bump and depression lacking dentition.....S
- S) lower jaw triangular anteriorly on ventral aspect
(Fig. 30).....Syncomistes trigonicus
n. sp. (Australia)

- SS) lower jaw rounded anteriorly on ventral aspect
(Fig.30).....T.
- T) juveniles with 4-5 blackish body stripes, median
stripe widest; 5-7 caudal scales; 14-17
predorsal scales to occiput (see also fig. 92).
.....Syncomistes butleri
(Australia)
- TT) juveniles with 8 brownish stripes; 12-13 predorsal
scales to occiput; 3-4 caudal scales.....
.....Syncomistes kimberleyensis
(Australia)
- RR) lower jaw lacking dorsally directed bump; no marked de-
pression between premaxillaries; dentition continuous
across each jaw. Body in some individuals with irregular
blotches randomly dispersed.....U
- U) scales counted in a series above lateral line approximately
82; mouth small; cheek scales 7-8.....Scortum barcoo
(Australia)
- UU) scales counted in a series above lateral line 51-71;
mouth moderate; cheek scales 4-6.....V
- V) scales above the lateral line 11-13; scales counted in
a series above lateral line 63-71....Scortum hillii
(Australia).
- VV)scales above the lateral line 8-10; scales counted in a
series above lateral line 51-61....Scortum parviceps
(Australia)

- 00) teeth conic.....W
- W) 80-90 lateral line scales.....Pelsartia humeralis
(Australia)
- WW) 75 or fewer lateral line scales.....X
- X) lower lip continuous across ventral surface of lower
jaw (Fig. 31)..... Hephaestus jenkinsi
(Australia)
- XX) lower lip with a median gap in ventral surface of
lower jaw (Fig. 31).....Y
- Y) gill rakers on lower limb of first arch 9-12; gill
rakers on upper limb of first arch 5-6; 27 vertebrae..Z
- Z) caudal truncate; body and fins uniformly dark; 10
abdominal vertebrae.....Papuservus carbo
- ZZ) caudal emarginate; body lighter ventrally or overall;
with longitudinal stripes in smaller specimens;
fins not uniformly dark; 11 abdominal vertebrae....a
- a) 8-11 predorsal scales to occiput; 15-19 scales below
lateral line; base of caudal with three spots except
in largest specimens.....Hephaestus trimaculatus
(New Guinea)
- aa) 15-20 predorsal scales to occiput; 20-22 scales
below lateral line.....b
- b) 13-14 dorsal rays.....Hephaestus suavis
(Australia).

bb) 11-12 dorsal rays.....Hephaestus adamsoni

(New Guinea)

YY) gill rakers on lower limb of first arch 13-18; gill rakers
on upper limb of first arch 6-9 (6 rare); 25 vertebrae....c

c) predorsal scales to occiput 20-25; scales below lateral
line 24-27.....d

d) greatest body width 1.5-1.7 in body depth; scales in a
series counted above lateral line 76-79; below 71-77;
cheek scales 5-7; scales above lateral line 12-14

.....Bidyanus bidyanus

(Australia)

dd) greatest body width 1.9-2.1 in body depth; scales in
a series counted above lateral line 68-72; below 59-66;
cheek scales 7-10; scales above lateral line 10-12

..... Bidyanus welchi

(Australia)

cc) predorsal scales to occiput 13-18; scales below lateral
line 14-24.....e

e) lateral line scales 60-75; body with longitudinal stripes
throughout life; in adults solid stripes alternate with
irregular longitudinal stripes....Rhyncopelates oxyrhynchus

(Philippines, China, Japan)

ee) lateral line scales 58 or less; longitudinal stripes
present only in young, if stripes still evident in
adult, then limited to ventral half of body and with
vertical bars above them.....f

- f) dorsal rays 12-14.....g
- g) scales above lateral line 5-7; 5-6 cheek scales.....
Hephaestus roemeri
 (New Guinea)
- gg) scales above lateral line 8-10; 6-9 cheek scales.....
Hephaestus fuliginosus
 (Australia)
- ff) dorsal rays 10-11.....h
- h) 6-8 scales above lateral line.....i
- i) 4-6 cheek scales; 5-6 scales on caudal; body with dorsal
 vertical bars and ventral horizontal stripes except in
 largest specimens.....Mesopristes cancellatus
 (Indo-west Pacific)
- ii) 8-9 cheek scales; 10-12 caudal scales; horizontal body
 stripes in juveniles, lost in adults.....
Mesopristes argenteus
 (Indo-west Pacific)
- hh) 9-11 scales above lateral line.....j
- j) scales below lateral line 20-24.....Mesopristes elongatus
 (Madagascar)
- jj) scales below lateral line 18-19.....Mesopristes kneri
 (Fiji).

Genus Leiopotherapon

Leiopotherapon Fowler, 1931, p 353 (type species, Datnia plumbea Kner, by original designation (proposed as a subgenus)).

Madigania Whitley, 1945a, p. 16 (type species, Therapon unicolor Günther, by original designation).

Nomenclature: the generic name Leiopotherapon from the Greek, leios, smooth and omos, shoulder, refers to the lack of an exposed serrate posttemporal in the species of the genus. The substitution of a p for the m of omos appears to be an incorrect transliteration rather than a lapsus calami as it is used consistently by Fowler.

Dignosis: small freshwater teraponids having uniform adult coloration derived from a juvenile pattern of vertical bars (juvenile pattern unknown for Leiopotherapon macrolepis). Distinguishable from all other genera in the family in possessing only one spine on the first proximal dorsal pterygiophore (rather than the two in the other genera).

Included species: three species (unicolor, aheneus and macrolepis) are found in the freshwater drainages of Australia with the 2 latter species having limited distributions in Western

Australia overlapped by that of L. unicolor which is distributed over most of the northern two-thirds of the continent. The remaining species, L. plumbeus, is limited to the fresh waters of the Philippines (see also the discussion under this species for reported extralimital occurrences).

Remarks: Fowler (1931) erected the subgenus Leiopotherapon to contain four species from the Australia-New Guinea-Philippine region that lacked exposed serrate posttemporals. More recently Whitley (1943, 1945a) removed from the subgenus three of the species (Leiopotherapon unicolor, Amniataba percoides and A. caudavittatus) to monotypic genera. In addition he expanded the concept of the genus with his description of Leiopotherapon suavis (1948) from northern Queensland. This species, however, has an exposed serrate posttemporal and shares a series of apomorphic characters with the species of genus 11b; characters that are lacking in the species of genera 1 and 2 in which the species Fowler considered to be part of Leiopotherapon are placed in this revision

Leiopotherapon plumbeus (Kner, 1865)

Ayungin

Fig. 32

Datnia plumbea Kner, 1865, p. 48 (original description, type locality uncertain). Herre, 1930, p. 76 (Laguna de Bay, Luzon); 1934, p. 53 (Luzon); 1953, p. 432 (bibliography). Freihofner, 1963, p. 132 (RLA pattern). Johnson, 1975, p. 12 (procurrent spur).

Therapon brevipinnis Peters, 1868, p. 256 (original description, Luzon). Meyer, 1885, p. 13 (Laguna de Bay, Luzon).

Therapon brachycentrus Peters, 1869, p. 704 (on Peters, 1868).

Therapon (Datnia) brevipinnis: Bleeker, 1873, p. 384 (Luzon).

Therapon (Datnia) plumbeus: Bleeker, 1873, p. 383 (Java?, on Kner); 1873-76, p. 115 (on Kner).

Therapon (Datnia) brachycentrus; Bleeker, 1873-76, p. 115 (on Peters).

Therapon bidyanus: Meyer, 1885, p. 13 (misidentification, not Bidyanus bidyanus of Australia).

Pristopoma hasta: Seale, 1908, p. 528 (Philippine waters).

Mesopristes plumbeus: Fowler, 1918, p. 36 (Philippines); 1918, p. 63 (Philippines).

Therapon plumbeus: Fowler, 1927, p. 281 (Luzon). Weber and deBeaufort, 1931, p. 158 (Java?). Roxas and Martin, 1937, p. 139 (Philippines). Arriola and Villaluz, 1939, p. 173 (Laguna de Bay). Domantay, 1940, p. 83 (Mindanao). Blanco

and Villadolid, 1951, p. 79 (juvenile coloration).

Juliano, 1960, p. 11 (swimbladder form). Delmondo and Bastillo, 1969, p. 1 (biology). Mees, 1971, p. 221, fig. 6 (description and distribution).

Therapon argenteus: Aldaba, 1931, p. 2 (Laguna de Bay, mis-identification).

Terapon plumbeus: Fowler, 1931, p. 357 (Laguna de Bay, Santa Cruz River, Philippines; Celebes (Sulawesi)).

Mesopristes plumbea: Mane, 1934, p. 502 (spawning, food).

Nomenclature: the trivial name, plumbeus, from the Latin for lead, refers to the leaden colored of preserved specimens. A syntype of his species in the Vienna Museum has been examined by G. F. Mees and found to agree with the original species description.

Diagnosis: A species of the genus Leiopotherapon distinguishable from the other species of the genus in having the longest dorsal spine longer than the longest dorsal ray (in contrast to the situation in L. unicolor and L. macrolepis) and 13 to 16 gill rakers on the lower limb of the first gill arch (in contrast to 10 to 12 in L. aheneus).

Description: Dorsal spines XI-XIII; Dorsal rays 8-10; Anal III, 7-8; Rect. 14-15; Pel. I-5; 43-52 lateral line scales; 3-4 scales on caudal; 6-8 scales above lateral line; 13-16 scales

below lateral line; 16-20 scales predorsal to occiput; 1 row of scales in sheath at base of dorsal fin, sheath extending to fifth or sixth dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to fifth or sixth anal ray; cheek scales in 4-5 rows; gill rakers on first arch 6-8+1+13-16; vertebrae 10+15.

Reaching 160 mm SL; depth 2.5-3.1 in SL; distance from origin of dorsal fin to snout 2.2-2.6 in SL; head length 2.9-3.4 in SL; length of base of dorsal 1.9-2.1 in SL; snout length 3.1-3.8 in HL; eye width 3.2-4.1 in HL; jaw length 3.0-3.4 in HL; length of longest dorsal spine 1.75-1.9 in HL; length of longest dorsal ray 1.9-2.3 in HL; length of longest anal spine 2.0-2.4 in HL; length of longest anal ray 1.8-1.9 in HL.

This species shows considerable variation in body shape between populations. Overall it is a moderately deep bodied, compressed to slightly compressed species. Dorsal profile in compressed examples much more pronounced than ventral profile. In less compressed specimens the ventral and dorsal profiles are nearly equal. Dorsal profile slightly convex from snout to interorbital, then straight to nape; convex from nape to dorsal origin. Ventral profile nearly straight in less rotund specimens; straight to isthmus, then convex to anus in full bodied individuals. Jaws equal or the lower slightly longer. Gape oblique. Maxillary reaching to vertical through

anterior of eye; slightly beyond in very small specimens. Teeth conic, in bands, outer row enlarged. No teeth on vomer or palatines. Interorbital region with distinct ridges. Nostrils distant; separated by a distance equal to twice diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate; serrations largest along vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; slightly serrate along posterior edge; scales on side. Posttemporal not exposed; covered with skin and scales. Supracleithrum exposed.

Spinous dorsal arched; first spine very short; fourth to sixth spine longest, those following decreasing gradually in length to the ultimate. Longest dorsal spine longer than longest dorsal ray. Soft dorsal rounded. Second anal spine thickest, usually longer but sometimes same length as third; shorter than longest anal ray. Soft anal rounded. Pectorals assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest, sometimes filamentous; falling slightly short of anus. Caudal emarginate.

Coloration: overall coloration silvery. Head darker above especially anterior to orbit. Body darker above, slightly lighter ventrally with small scale markings sometimes forming longitudinal vermiculations. Spinous and soft dorsals yellowish or clear; margined with black in some specimens. Spinous anal clear. Soft anal dusky for distal two-thirds on anterior rays. Caudal dusky. Pelvics and pectorals colorless to

yellowish.

Distribution: this species appears to be limited to the freshwaters of the Philippines. It is a common member of the fauna of Laguna de Bay, a large shallow freshwater lake on Luzon (Fowler, 1918; Herre, 1930; Yapchiongco and Enriques, 1936; Mane, 1934). Within the Philippines it has also been reported from Mindanao by Domantay (1940). However, the distribution and identification of material of this species has been the source of much confusion since the original species description. The type of the species was described by Kner (1865) from an unknown locality, but was thought to be from Java. However, no further specimens were collected from that locality. As pointed out by Mees (1971), this locality report may be a labeling error. The Novara which collected the type specimen also stopped at Manila where the species are commonly sold in market and the fish may have originated there.

More recently Fowler (1931) lists a specimen of the species from Buka Buka island in the Gulf of Tomini, Sulawesi (Celebes). This is a highly unlikely locality for a species otherwise limited to the Philippines. Although the specimen bears what appears to be an original Albatross metal tag corresponding to the locality, the specimen is catalogued with a series of L. plumbeus of similar size, coloration, body form, and overall condition which were purchased in the Manila market. This makes it appear more likely that the supposed Indonesian specimen may have been part of a series that was

accidentally mislabelled.

Leiopotherapon plumbeus has furthermore been confused with both Bidyanus bidyanus a freshwater Australian species and with Mesopristes argenteus a marine form also occurring in the Philippines. Meyer (1885) lists Therapon bidyana spec. affin. from Laguna de Bay, Luzon with this identification being followed by Elera (1895) and Roxas and Martin (1937), both citing the species as Therapon bidyana. However, based on the indefinite original identification and the locality, it appears that the material was L. plumbeus which is of similar form and color. Similarly the identification of Therapon (=Mesopristes) argenteus as Laguna de Bay Ayuñgin by Aldaba (1931) is also an error for L. plumbeus.

Ecology: the spawning habits, development, and biology of this species has been extensively studied by Yapchiongco and Enriques (1936) and Mane (1934) who found that the largest individuals collected only reached 156 mm SL. Juliano (1960) studied and figured the swimbladder form in this species.

Specimens examined

Philippines: fish pond 1.5 mi west of Dangali (USNM 184815*, 2 spec., 94-108 mm); Luzon, Laguna de Bay, Los Banos (USNM 131119*, 2 spec., 59-61 mm); Luzon, Manila Market (USNM 184802*, 6 spec., 92-111 mm).

Indonesia, Sulawesi(Celebes), Gulf of Tomini, Buka Buka
Island (USNM 184803*, 1 spec., 103 mm (locality
questionable)).

Leiopotherapon unicolor (Günther, 1859)

Spangled perch

Fig. 33

Therapon unicolor Günther, 1859, p. 277 (original description, Gwydir River, New South Wales); 1867, p. 58 (Rockhampton, Fitzroy River). Schmeltz, 1869, p. 13 (Rockhampton); 1877, p. 12 (Burnett River); 1879, p. 39 (Queensland). Günther, 1880, p. 32 (Mary River, Queensland). Macleay, 1879, p. 15 (Warialda); 1881, p. 366 (copied). Pöhl, 1884, p. 27 (Queensland). Stead, 1909, p. 116 (Corella). Ogilby and McCulloch, 1916, p. 109, pl. 11, fig. 1 (Eidsvold, Rockhampton, Inkerman, Stannary Hills, Gregory River, Goondiwindi). Fowler, 1928, p. 211 (copied). McCulloch, 1934, p. 47 (New South Wales). Fletcher, 1937, p. 164 (Waroona Creek). Nichols, 1949, p. 2 (Archer River, Queensland). Grant, 1965, p. 225 (Queensland, biology). McKay, 1971, p. 13 (Millstream, Western Australia). Grant, 1972, p. 388, pl. 91 (Queensland, biology).

Therapon unicola: Kent, 1893, p. 369 (Queensland, error in spelling).

Datnia brevipinnis Steindachner, 1867, p. 309 (original description, Cape York).

Therapon truttaceus Macleay, 1881, p. 366 (original description, Endeavor River). Zeitz, 1896, p. 176 (Redbank Creek, Finke River, Palm River, Walkins Gorge).

Terapon truttaceus: Waite, 1914, p. 446 (Central Australia).

Therapon longulus Macleay, 1881, p. 367 (original description, inland from Port Darwin).

Therapon elphinstonensis DeVis, 1884b, p. 57 (original description, Lake Elphinstone).

Therapon idoneus Ogilby, 1907, p. 37 (original description, upper Condamine River, south Queensland).

Therapon unicolor: Rendahl, 1922, p. 164 (Northern Territory; Port Darwin in freshwater, Daly River). Fowler, 1931, p. 355 (Bourke, New South Wales); 1934, p. 344 (Fiji, in error). Taylor, 1964, p. 186 (Arnhem Land).

Madigania unicolor: Whitley, 1945a, p. 11 (Simpson Desert); 1947, pp. 51 and 52 (Greyian and Leichhardtian fluvi-faunulae); 1960, pp. 10 and 75, fig. (biology, distribution). Llewellyn, 1973, p. 73 (spawning, development, biology). Allen, 1975, p. 93 (Western Australia: Prince Regent Reserve).

Nomenclature: the trivial name unicolor, refers to the uniform coloration of the dried skins on which the original species description was based. The species was described from a series of skins deposited in the British Museum (Natural History).

Diagnosis: the species can be distinguished from the other members of the genus in having the longest dorsal spines shorter than the longest dorsal rays (in contrast to L. aheneus and L. plumbeus in which the longest spines

are longer than the longest rays) and 45-57 lateral line scales and 7-9 supralateral scales (in contrast to L. macrolepis which has counts of 29-32 and 3-5).

Description: Dorsal spines XI-XIII; Dorsal rays 9-12; Anal III, 7-10; Pect. 15-16; Pel. I-5; 45-57 lateral line scales; 3-6 scales on caudal; 7-9 scales above lateral line; 16-20 scales below lateral line; 15-20 predorsal scales to occiput; 1 row of scales in sheath at base of dorsal, sheath extending to second dorsal ray; 2 rows of scales in sheath at base of anal fin, sheath extending to third anal ray; cheek scales in 6-9 rows; gill rakers on first arch 5-6+1+10-12; vertebrae 11+14.

Reaching 310 mm SL; depth 2.7-3.5 in SL; distance from origin of dorsal to snout 2.2-2.5 in SL; head length 2.6-3.2 in SL; length of base of dorsal 2.0-2.4 in SL; snout length 2.9-3.9 in HL; eye width 3.6-5.8 in HL; jaw length 2.5-3.4 in HL; length of longest dorsal spine 2.8-3.5 in HL; length of longest dorsal ray 1.9-2.4 in HL; length of longest anal spine 3.0-4.1 in HL; length of longest anal ray 2.1-2.5 in HL.

Body slender; variably compressed, more rotund in young. Dorsal profile more pronounced than ventral. Dorsal profile straight from snout to nape, then slightly convex to dorsal origin. Ventral profile evenly convex from lower jaw

to anus. Jaws equal. Gape oblique. Snout elongate. Maxillary reaching to beyond vertical drawn through anterior edge of eye. Teeth strong; conic; outer row enlarged; inner villiform, in bands. No teeth on vomer or palatines. Interorbital region with ridges. Nostrils separated by a distance equal to one and one-half diameters of posterior nostril. Lacrimal with weak serrations. Preoperculum serrate; serrations largest on posterior edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate along posterior edge; scales on side. Supracleithrum covered with scales for most of its length. Posttemporal not exposed; covered with skin and scales.

Spinous dorsal arched; first spine short; third or fourth longest, those following decreasing in length to ultimate. Longest dorsal spines shorter than longest dorsal rays. Soft dorsal rounded. Anal spines short; second and third spines subequal, twice length of first. Longest anal spine shorter than longest anal ray. Soft anal rounded. Pectoral assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest; reaching one-half to two-thirds distance to anus. Caudal slightly emarginate.

Coloration: head darker above, lighter below. Lips and upper surface of snout quite dark. Cheek and opercle with randomly distributed small spots. Lower lip slightly pigmented. Body greyish, darker above; each scale with a darker edge;

intensity of scale pigmentation decreasing ventrally. Ventral scales with whitish center. Larger specimens with spots on side of cleithrum. Spinous dorsal uniformly dusky. Soft dorsal brownish with lighter margin. Spinous anal white, soft anal dusky, especially on anterior rays. Caudal dusky, especially lower lobe; white band on lower edge of ventral lobe. Pectorals and pelvics colorless.

Distribution: in freshwaters of New South Wales from level of Newcastle north, Queensland, Northern Territory, Western Australia from Murchison drainage north (Fig. 34). Two specimens examined (AMNH 8739) have a listed locality of Melbourne, Victoria; however, this appears to be an error as this locality is distinctly south of the species range. The specimens perhaps represent introduced material or were received through the Museum at Melbourne. Scott (1962) lists the species from South Australia north of 30° latitude. Although I have not found any locality records for the state, the presence of the fish in the Finke River drainage as indicated by Butler's collections and literature information makes it seem likely that the species does occur in South Australia.

This species was considered to be part of the fauna of the Fiji Islands by Whitley (1927) who listed the species in his compilation of the fishes of Fiji. In this he evidently followed Kner (1868) who described a specimen collected at Kandavu, Fiji as a member of the species. However, this is

unlikely locality for a species otherwise limited to the freshwaters of Australia. Reference to the description and figure of Kner show that the specimen is not L. unicolor, differing in overall appearance and having 4 cheek scales rather than 6-9; 39 lateral line scales rather than 45-57; and a transverse scale count of 5+1+9 rather than 7-9+1+16-20. Fowler (1928) states that he believes that the specimen was an individual of Kuhlia rupestris, a hypothesis consistent with the above information. However, more recently (1959) he includes L. unicolor in the fauna of Fiji as an introduction and citing Whitley (1927) as his source. That author, however, makes no statement on the presence of the species other than that discussed above. As such the presence of the species either naturally or as an introduction to Fiji is unsubstantiated.

L. unicolor has the largest distribution of any of the freshwater members of the family, being found in major rivers, isolated drainages and ponds throughout its range. As a consequence of its large range and presence in so many isolated drainages, there occurs a marked level of differentiation between populations; especially in general body form. Such differences arise probably from both environmental and genetic influences. However, there has not been found any reason to divide the species either on the specific or subspecific level.

Ecology: L. unicolor has been described as being able to aestivate during periods when water courses dry up (Whitley, 1959; Lake, 1966) and has been mentioned as a species dispersed in "rains of fishes". However, Llewellyn (1973) was unable to find any evidence for an aestivation ability in this species, although it was found to have a tolerance for high water temperatures (LD_{50} , 39.0°C). Their sudden appearance in previously dry water courses may be the result of emmigration of juveniles from permanent water courses during heavy rain as observed by Shipway (1947). Individuals stranded by the retreat of the sheet of water covering the countryside during such a rain may have been the source of the citation of this species in rains of fishes (Gibson, cited in Whitley, 1945a).

The reproductive habits and development of this species have been studied in great detail by Llewellyn (1973). He showed that the species commences spawning following a rise in water temperature with an increased but not necessary increase in water depth. The eggs are demersal and randomly dispersed.

This species is a resident in a variety of different water conditions, having been collected in Western Australia in hard and soft waters, both running and standing and ranging from clear to nearly opaque waters. The southern limit of the species distribution appears to be related to the intolerance of L. unicolor to temperatures below 5.3°C, with the limit of

distribution conforming well with the 4.4°C isotherm for the minimum average winter temperature.

Whitley (1945a) placed this species in a monotypic genus Madigania. However, in light of the evidence supporting its close relationship to the other species of Leiopotherapon as defined in this study, it is placed in that genus. Munro (1964) added to the genus Madigania a second species Madigania (=Hephaestus) adamsoni a freshwater New Guinea species. However, L. unicolor lacks a series of osteological, myological and intestinal apomorphic characters uniting H. adamsoni to the other species of Hephaestus. Consequently the hypothesis of a close relationship between the two species is rejected.

Specimens examined

Australia, Queensland:Gregory River (AMNH 20577*, 1 spec., 64 mm).

Australia, Western Australia:Murchison River (AMNH 35558*, 10 spec. (of 155), 41-118 mm); Gascoyne River (AMNH 35580, 38 spec.); Robe River (AMNH 35587*, 10 spec.(of 94), 45-121 mm); Fortescue River (AMNH 35577*, 6 spec.); Maitland River (AMNH 35579, 9 spec.); George River (AMNH 35582*, 10 spec. (of 406), 22-139 mm); Fortescue River, Millstream (AMNH 35534, 29 spec.); Upper Sherlock River (AMNH 35581, 93 spec.); Upper Weedi Wolli Creek (AMNH 35535, 49 spec.); Nullagine River (AMNH 35557*, 10 spec. (of 234), 24-89 mm);

Coogan River (AMNH 35540*, 14 spec., 24-112 mm); Stuart River (AMNH 35574, 81 spec.); DeGrey River (AMNH 35537, 52 spec.); Yeeda Creek (AMNH 35556, 55 spec.); Fitzroy River (AMNH 35560, 56 spec.); Meda River (AMNH 35560*, 20 spec. (of 141), 50-116 mm); Mount Hart outcamp (AMNH 35559, 48 spec.); Bell Creek (AMNH 35559, 48 spec.); Grave Creek (AMNH 35561*, 10 spec. (of 20), 40-96 mm); North Creek (AMNH 35545, 90 spec.); Gibb River (AMNH 35554, 190 spec.); Hann River, Moll Gorge (AMNH 35564, 12 spec.); Hann River (AMNH 35551*, 10 spec. (of 190), 40-113 mm); Manning Creek (AMNH 35562*, 5 spec., 35-67 mm; AMNH 35536, 45 spec.; AMNH 35563, 8 spec.); Panton River (AMNH 35547, 46 spec.); Bow River (AMNH 35548*, 10 spec. (of 34), 54-87 mm; AMNH 35544, 71 spec.); Dunbarn River (AMNH 35585, 6 spec.); Ord River 35576, 32 spec.).

Australia, Northern Territory: Moriarity Creek (AMNH 35542, 76 spec.); West Baines River (AMNH 35541, 39 spec.); Katherine River (AMNH 35553*, 10 spec. (of 25), 45-75 mm; AMNH 35538, 12 spec.); Fergusson River (AMNH 35583, 46 spec.); Mary River (AMNH 35568*, 2 spec., 72-95 mm; AMNH 35567, 12 spec.); South Alligator River (AMNH 35555, 8 spec.; AMNH 35543, 2 spec.); Barramundie Creek (AMNH 35550, 14 spec.; AMNH 35569*, 3 spec., 45-90 mm; AMNH 35584, 20 spec.); Wildman River (AMNH 35570, 2 spec.); Mary River (AMNH 35571, 4 spec.); East Mary River (AMNH 35539, 22 spec.);

Lower Daly River (AMNH 35572, 1 spec.); isolated pool, 15 mi. East of Daly River Police Station (AMNH 35568*, 10 spec., 44-100 mm); Red Lily Lagoon (AMNH 35552, 1 spec.; USNM 173655*, 4 spec., 116-184 mm); Upper Manton River (AMNH 35573, 6 spec.); Katherine River, Katherine (AMNH 20579, 1 spec.); vicinity of Finke River and Ellery Creek (AMNH 35575, 40 spec.); Ellery Creek (AMNH 35578, 23 spec.); Roper River Mission (USNM 173859, 9 spec.).

Australia; Victoria, Melbourne (AMNH 8739, 5 spec. (locality questionable)).

Leiopotherapon macrolepis n. sp.

Large scaled grunter

Fig.35

Nomenclature; the trivial name macrolepis from the Greek for large scale refers to the relatively large size of the scales in this species.

Diagnosis: a member of the genus Leiopotherapon distinguishable from the other species in the group in having 29-33 lateral line scales (in contrast to 40 or more for all other species in the group).

Description: (numbers in parentheses are numbers of examined specimens having a given count) Dorsal spines and rays XI-9(22), XI-10(42), XI-9(12), XII-10(6); Anal spines 3; rays 6(7), 7(42), 8(32), 9(1), last ray usually divided nearly to base; Pectoral with 12-15 rays; Pelvics I-5; lateral line scales from origin to hypural joint 29(18), 30(24), 31(21), 32(18), 33(1); 1-5 caudal scales; transverse series to base of sheath at median dorsal spines 3+1+8(1), 3+1+9(3), 4+1+8(7), 4+1+9(26), 4+1+10(22), 4+1+11(5), 5+1+10(3), 5+1+11(6); 12-14 predorsal scales to occiput; cheek scales in 4-5 rows, irregular, covered with a heavy layer of skin; sheath at base of spinous dorsal consisting of one row of scales, sheath extending to third or fourth dorsal ray; sheath at base of anal consisting of one or two rows of scales; sheath extending to fourth anal ray; gill rakers

on first arch 6-8+1+10-13; vertebrae 10+15.

Reaching 116 mm SL; depth 2.5-3.0 in SL; distance from origin of spinous dorsal to snout 1.95-2.3 in SL; head length 2.5-3.1 in SL; length of base of dorsal fin 2.0-2.3 in SL; snout length 2.8-3.6 in HL, getting relatively larger with increasing standard length; eye width 3.2-4.5 in HL; getting relatively smaller with increasing age; jaw length 2.6-4.0 in HL, getting relatively larger with increasing SL; length of longest dorsal spine 2.4-3.1 in SL; length of longest dorsal ray 1.9-2.7 in SL; length of longest anal spine 2.2-3.4 in SL; length of longest anal ray 1.8-2.5 in HL.

Body moderately deep, slightly compressed. Dorsal profile more pronounced than lower. Dorsal profile straight in juveniles; developing a slight concavity before orbit with age. Interorbital region nearly flat. Profile between rear of head and dorsal origin getting increasingly convex with age. Ventral profile gently curved to anus. Jaws equal. Gape oblique. Maxillary reaching to vertical through posterior nostril in young; to vertical through anterior edge of eye in adults. Each jaw with a band of fixed, conic, brown tipped teeth; outer row largest. No teeth on vomer or palatines. Nostrils well separated; distance between them equal to half the diameter of orbit. Posterior nostril set

in a depression. Neither nostril with a cutaneous flap. Lacrimal weakly serrate in some individuals. Preoperculum weakly serrate at angle. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate along posterior edge; some scales on side. Supracleithrum and posttemporal covered with skin and scales.

Spinous dorsal arched; first spine short; fourth or fifth spine longest, those following decreasing in length gradually to penultimate which is shorter than ultimate. Soft dorsal rounded. **Second** anal spine strongest; longer than third in juveniles, subequal in adults. Longest anal spine always shorter than longest anal rays. Soft anal square. Pectoral assymmetrically pointed; fourth to sixth ray longest. Pelvics inserted ahead of vertical drawn through origin of spinous dorsal; pointed; first ray longest; slightly filamentous, falling short of anus. Caudal slightly emarginate.

Coloration: head dark dorsally on snout, interorbital and nape regions, pigmentation continuing ventrally onto opercle. In adults, dark coloration also occurs on premaxillaries, maxillaries and dorsolateral surface of lower jaw. Juveniles with a darker edging to scales. Body darker overall dorsally. In adults, the overall coloration is much

darker than in juveniles, with body dorsal to level of base of pectoral fins quite dark, lacking any distinct pattern. Spinous and soft dorsal dusky, more so in adults. Soft and spinous anal dusky. Pectorals dusky, with dark pigmentation on fin base, more pronounced medially and more prominent in larger specimens. Pelvics clear in juveniles, dusky in adults. Caudal dusky, especially basally.

Distribution: this species appears to be limited to the Prince Regent Reserve region of Western Australia. Specimens were collected in the Prince Regent and Roe Rivers (Fig. 34).

Ecology: this species appears to be widely distributed in the Prince Regent and Roe Rivers in regions where the water is fresh and clear over sandstone and rock bottoms. Apparently a small species with two of the largest specimens collected (113 and 115 mm SL) being gravid females.

Specimens examined

The holotype (WAM P-25392-001), 91.5 mm SL, was obtained with rotenone by Mr. B. Wilson, August 21, 1974, in Youwanjela Creek a tributary to the Regent River, Western Australia (approx. 15°34'S, 125°25'E). Taken along with the holotype were 24 other specimens (WAM P-25040-002 and AMNH 33977 32-115 mm SL). Further paratypes were obtained with rotenone by G. R. Allen, August 18, 1974, in the upper Roe River (WAM P-25029-002, AMNH 33976 , 35 spec., 27-94 mm); by G. R. Allen and A. Chapman, Upper Roe River (approx. 15° 26'S,

125°37'E) (WAM P-25-25-002, 1 spec., 38 mm); by G. Allen August 14, 1974 in the upper Roe River (WAM P-25026-003, 5 spec., 35-53 mm); by G. R. Allen and A. Chapman, August 15, 1974 in a side channel of the Upper Roe River (WAM P-25027-003, 6 spec., 36-43 mm); by G. Allen, August 21, 1974, in Gundarara Creek, about 2 km above junction with Prince Regent River (WAM P-25025-002, 1 spec. 38 mm).

All of the above specimens were used for counts and measurements.

For the original report on the collection trip on which these specimens were collected see Allen (1975, species A).

Leiopotherapon aheneus (Mees, 1963)

Western grunter

Fig. 36

Therapon aheneus Mees, 1963, p. 2 (original description, Millstream Pool and Fortescue River, Western Australia); 1971, p. 199 (Nichol's Spring, Western Australia). McKay, 1971, p. 13 (Crossing Pool, Hammersley Gorge, Wittenoom).

Mesopristes aheneus: Whitley, 1964, p. 42. (no locality). Lake, 1971, p. 34.

Nomenclature: the trivial name aheneus from the poetic aspirated form of aeneus (Latin) for bronzy or brassy refers to the bronze life coloration of this species. The holotype is deposited in the Western Australian Museum (WAM P-5350).

Diagnosis: distinguished from the other members of the genus Leiopotherapon in having the longest dorsal spine longer than the longest dorsal ray (in contrast to the situation in L. unicolor and L. macrolepis) and in having 10-12 gill rakers on the lower limb of the first arch (in contrast to 13-16 in L. plumbeus).

Description: Dorsal spines XI-XIII; Dorsal rays 8-9; Anal III, 8-9; Pect. 13-14; Pel. I-5; 40-45 lateral line scales; 3-4 scales on caudal; 5-6 scales above lateral line;

14-15 scales below lateral line; 12-14 scales predorsal to occiput; 1 row of scales in sheath at base of dorsal fin, sheath extending to second dorsal ray; 2 rows of scales in sheath at base of anal fin, sheath extending to third or fourth anal ray; cheek scales in 4-5 rows; gill rakers on first arch 6-8+1+11-12; vertebrae 10+15.

Reaching 110 mm SL; depth 2.4-2.6 in SL; distance from origin of spinous dorsal to snout 2.1-2.3 in SL; head length 2.7-3.0 in SL; length of base of dorsal 1.9-2.0 in SL; snout length 3.1-3.9 in HL; eye width 3.2-4.0 in HL; jaw length 2.7-3.5 in HL; length of longest dorsal spine 2.1-2.4 in HL; length of longest dorsal ray 2.2-2.5 in HL; length of longest anal spine 2.3-2.7 in HL; length of longest anal ray 2.1-2.3 in HL.

Body moderately deep and moderately compressed. Dorsal profile more pronounced than ventral. Dorsal profile straight or slightly convex to nape, then convex to dorsal origin. Ventral profile slightly convex from lower lip to pelvic insertion, straight from insertion to anus. Jaws equal. Gape oblique. Maxillary reaching to vertical through anterior of eye. Teeth conic, outer row enlarged; followed by a band of smaller teeth. No teeth on vomer or palatines. Inter-orbital region with ridges. Nostrils separated by a distance equal to one-half diameter of eye. Lacrimal with 3 or 4 small serrations. Preoperculum serrate; serrations larger

on angle. Lower opercular spine stronger and longer; not extending beyond edge of opercular lobe. Posttemporal not exposed; covered with skin and scales; covering of scales reduced in some specimens. Cleithrum exposed; serrate along posterior edge; scales on side. Supracleithrum exposed.

Spinous dorsal arched; fifth spine longest, those spines following decreasing in length to ultimate. Soft dorsal rounded, longest dorsal rays shorter than longest dorsal spines. Second anal spine strongest and longest; twice length of first and slightly longer than third. Longest anal spine shorter than longest anal rays. Soft anal rounded. Pectoral assymetrically pointed; fourth ray longest. Pelvics pointed; first ray longest or equal to second; reaching three-quarters of distance to anus. Caudal emarginate.

Coloration: head dark dorsally, light ventrally. Body brown to blackish with ten to fifteen irregular longitudinal vermiculations variably present. Life coloration bronzy with vertical bars in young (Mees, 1963). Intensity of coloration varies between drainages with those from the Robe River being darker than those from other localities. Spinous and soft dorsal clear to dusky. Spinous and soft anal slightly dusky. Caudal fin darker basally; slightly dusky at edge, especially on upper lobe. Pectorals and pelvics clear to dusky.

Larger specimens more elongate than young, often approaching the body forms in some populations of L. unicolor. They can always be distinguished from that species, however, in having the longest dorsal spines longer than the longest dorsal rays.

Distribution: this species appears to have a limited distribution in Western Australia bounded by the Ashburton and Fortescue Rivers (Fig. 34). The Nelson, Butler, Rosen collection of the species in the Robe River is the first reported occurrence of the species in that drainage.

Remarks: Contrary to Whitley (1964) there is no evidence to support a hypothesis of close relationship between L. aheneus and the other species of his genus Mesopristes. All have a series of apomorphic characters (extrinsic swimbladder muscle form, posttemporal form, pigmentation patterns etc.) uniting them to the other species of genera 8 and 9; characters which are lacking in L. aheneus.

Mees (1963) in his original species description states that the suprascalupar bone is exposed. However, the posttemporal (= the suprascapular of previous authors) although having its scale covering reduced is not exposed and lacks posterior serrations.

Ecology: this species appears to be an inhabitant of clear running waters over sand and rock bottoms.

Specimens examined

Western Australia: Fortescue River (AMNH 35619*, 10 spec. (of 31), 28-71 mm; AMNH 35621*, 15 spec. (of 69), 35-86 mm); Robe River (AMNH 35620*, 10 spec. (of 32), 54-109 mm); Millstream, Millstream Bath House (WAM P-5358*, 3 spec. (paratypes), 59-70 mm).

Amniataba Whitley, 1943, p. 183 (type species Therapon percoides Gunther, by original designation).

Amphitherapon, Whitley, 1943, p. 183 (type species Datnia? caudavittata Richardson, by original designation).

Nomenclature: the generic name Amniataba, from the Latin amnis, a stream, and Ataba, an aboriginal name in Queensland for a marine teraponid, refers to the freshwater environment of the type species of the genus.

Diagnosis: freshwater and marine teraponids distributed in northern Australia-southern New Guinea. Distinguishable from other genera in the family in having two spines on the first proximal dorsal pterygiophore and lacking a foramen for exit of blood vessels from the third hemal arch anterior to the parapophyseal vertebrae, along with a mottling pattern on the caudal.

Included species: two species are placed in Amniataba, A. percoides which is distributed over the northern two-thirds of Australia in freshwater and A. caudavittatus which is distributed in marine and freshwaters of northern Australia and southern New Guinea.

Amniataba percoides (Günther, 1864)

Black striped grunter

Fig. 38

Therapon percoides Günther, 1864, p. 374 (original description, Fitzroy River near Rockhampton). Schmeltz, 1874, p. 23 (Bowen); 1877, p. 12 (Burnett River). Macleay, 1881, p. 362 (north Queensland); 1882, p. 69 (Palmer River, Gulf of Carpentaria drainages); 1882, p. 20 (Lillesmere Lagoon, Upper Burdekin). Pöhl, 1884, p. 27 (Bowen). Weber, 1895, p. 262 (Burnett River). Lucas, 1894, p. 362 (McDonnell Ranges). Zeitz, 1896, p. 177, pl. 16, fig. 1 (McDonnell Ranges). Bancroft, 1912, p. 255 (Burnett River). Ogilby and McCulloch, 1916, p. 105, pl. 10, fig. 1 (Fitzroy, Burnett, Bowen and Flinders Rivers, Eureka Creek). Mees, 1963, p. 2 (Greenough River, Western Australia). McKay, 1971, p. 13 (Millstream region, Western Australia).

Therapon fasciatus Castelnau, 1875, p. 11 (original description, Western Australia); 1876, p. 228 (west coast of Australia). Macleay, 1881, p. 363 (Swan River?, Norman River); 1882, p. 67 (Palmer River). Waite, 1894, p. 362 (Central Australia near McDonnell Ranges, Hogkinson River).

Datnia fasciata: Steindachner, 1877, p. 227 (Port Jackson, error for Queensland).

Therapon terraereginae Castelnau, 1877, p. 227 (original description, Queensland, probably Fitzroy River); 1878, p. 46 (Norman River). Macleay, 1881, p. 363 (rivers of northern Queensland); 1882, p. 69 (placed in synonymy with Therapon percoides)

Therapon spinosior DeVis, 1884a, p. 397 (original description, Queensland).

Therapon percoides: Rendahl, 1922, p. 184 (Northern Territory). Fowler, 1931, p. 353 (Queensland). Taylor, 1964, p. 188 (Arnhem Land).

Amniataba percoides: Whitley, 1943, p. 183 (northern Australia); 1960, p. 73, fig. (Queensland, Western Australia, Central Australia). Lake, 1971, p. 34, pl. 78 (northern Australia).

Amniataba percoides burnettensis Whitley, 1943, p. 183 (original description, Burnett River E on Ogilby and McCulloch, 1916)].

Amniataba percoides yorkensis Nichols, 1949, p. 3 (original description, Archer River, Coen River, Ebagoola).

Nomenclature: the trivial name percoides refers to the perch like appearance of the species. The species was described on the basis of a series of skins deposited in the British Museum (Natural History).

Diagnosis: Amniataba percoides can be distinguished on the basis of its pattern of narrow vertical bars and its lack of an oblique bar across each lobe of the caudal (in contrast to a uniform coloration or faint wide bars and an oblique bar across each caudal lobe in A. caudavittatus).

Description; Dorsal spines XIII-XIV; Dorsal rays 8-10; Anal III, 7-9; Pect. 14-16; Pel. I-5; 36-43 lateral line scales; 4-6 scales on caudal; 5-7 scales above lateral line; 13-15 scales below lateral line; 14-16 predorsal scales to occiput; 1 row of scales in sheath at base of dorsal fin, sheath extending to third or fourth dorsal ray; 2 rows of scales in sheath at base of anal fin, sheath extending to third or fourth anal ray; cheek scales in 4-5 rows; gill rakers on first arch 4-6+1+10-13; vertebrae 10+15.

Reaching 160 mm SL; depth 2.2-2.7 in SL; distance from dorsal origin to snout 2.1-2.4 in SL; head length 2.7-3.3 in SL; length of base of dorsal 1.8-2.1 in SL; snout length 2.8-3.7 in HL; eye width 2.6-3.6 in HL; jaw length 3.3-4.0 in HL; length of longest dorsal spine 1.4-1.9 in HL; length of longest dorsal ray 1.6-2.0 in HL; length of longest anal spine 1.5-2.1 in HL; length of longest anal ray 1.9-2.1 in HL.

Body moderately compressed and deep; Dorsal profile more

pronounced than ventral. Dorsal profile straight from snout to nape, then convex to dorsal origin. Ventral profile straight from tip of lower lip to isthmus; convex from isthmus to pelvic insertion, then straight to anus. Jaws equal with lips slightly fleshy, especially in larger specimens. Gape oblique. Snout slightly elongate. Maxillary reaching to vertical through posterior nostril. Teeth conic; slightly recurved; in bands, outer row enlarged. Vomer and palatines without teeth. Interorbital region with distinct ridges. Nostrils distant, separated by a distance equal to one-third of eye diameter. Lacrimal serrate. Preoperculum serrate; serrations largest on vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed. Posttemporal not exposed, covered with skin and scales.

Spinous dorsal strongly arched; first spine very short; fourth to sixth spine longest. Longest dorsal spine longer than longest dorsal rays. Spines following the longest decreasing in length gradually to penultimate which is shorter than ultimate. Soft dorsal with posterior edge straight or slightly convex. Second anal spine strong; about twice as long as first; longer than third; about as long as longest anal ray. Posterior margin of soft dorsal slightly convex.

Pectorals assymmetrically pointed; fifth ray longest.

Pelvics pointed; first and second rays subequal; reaching to anus. Caudal slightly emarginate, lobes obtusely pointed.

Coloration: young with several bands of top of head running to interorbital region. Stripes run from snout under nostrils to top of orbit and across cheek under orbit. In adults, top of head dark with stripes masked; stripes under and in front of eye variably masked; head lighter ventrally. Body light below, darker above. Scales above lateral line with darker edges. Five to seven vertical bands on side; each two scales wide. First running from nape to opercular region and cleithral serrations (this may be preceded by another faint bar); second, under fifth to seventh dorsal spines; third, under penultimate dorsal spine; fourth, under middle of soft dorsal, continuing onto fin as a basal blotch; fifth, on caudal peduncle; sixth (may be lacking), at caudal base. Spinous dorsal slightly dusky. Soft dorsal with one or two rows of dusky spots; basal blotch above fourth body bar. Spinous anal clear. Soft anal dusky with lighter border and horizontal band of pigmentation. Caudal with numerous blue spots of proximal two-thirds; forming irregular vertical bands; edges dark; lower caudal rays white. Pectorals colorless or with some slightly dusky markings. Pelvics colorless except for two outer rays which

are dusky.

Distribution: across the northern part of Australia from the Burnett River of Queensland to the Robe River of Western Australia. Collections by Nelson, Butler and Rosen have shown the species to be widely distributed throughout the northern parts of Western Australia and Northern Territory (Fig. 38). In addition Butler has collected the species at several points in the interior drainages.

Castelnau (1875) described Therapon fasciatus from the Swan River of Western Australia. This description of a species that following workers considered to be a synonym of Therapon (= Amniataba) percoides was the basis for the inclusion of the latter species in the fauna of Western Australia. Although A. percoides is indeed present in the state no further specimens have been collected south of the Robe River which is a considerable distance north of the Swan. As pointed out by Mees (1963), the specimens examined by Castelnau evidently originated on the mainland opposite the Dampier Archipelago, a region which recent collections have shown A. percoides to be plentiful.

Waite (1923) lists this species in his Fishes of South Australia without exact localities. Although I have been unable to find any specific citations of the species from that state, Bulter's collections of the species from the Finke drainage slightly north of the state border makes it seem likely that it is present in the internal drainages of

of the state.

As would be expected in a species with such a large distribution over such a diverse landscape, there are marked variations between populations of this species from different areas of Australia. Such variation was noted by Ogilby and McCulloch (1916) who provided a key distinguishing the populations of the Burnett River from those of the Fitzroy. This distinction was later formalized by Whitley (1945a) who designated the material from the Burnett as the type series of Amniataba percoides burnettensis; a subspecies he contrasted with "typical percoides" (?= A. p. percoides). More recently Nichols (1949) described a new subspecies from the Archer and Coen Rivers of northern Queensland as Therapon percoides yorkensis, failing however, to delimit what he felt were the distinguishing characters.

Although differences do occur between populations of various drainages (both those formalized by the above workers and other variations), these are overlapping and there do not appear to be any characters or character combinations unique to any population or groups of populations. Consequently, subspecific variations in this species do not appear to represent any definable naturally occurring divisions and are not recognized in this study.

Ecology: this species is an inhabitant of a variety of environments ranging from still ponds to rapidly flowing rivers. Water conditions in these ranging from slightly

brackish to fresh and clear to greenish and opaque.

Specimens examined

Australia, Queensland: Archer River, Queensland Crossing (AMNH 18544, 11 spec.); Coen River (AMNH 18545*, 6 spec., 56-73 mm); Cape York, Ebagoola (AMNH 18560, 1 spec.) (the above are paratypes of Therapon percoides yorkensis).

Australia, Western Australia: Ashburton River (AMNH 35590*, 10 spec. (of 42), 9-18 mm); Robe River (AMNH 35615, 11 spec.); Fortescue River (AMNH 35588*, 10 spec. (of 16), 47-104 mm); Maitland River (AMNH 35610, 46 spec.); George River, just below Mt. Herbert (AMNH 35595*, 12 spec., 17-38 mm); Yeeda Creek*, 2 spec., 29-33 mm); Manning Creek (AMNH 35611, 3 spec.; AMNH 35614, 10 spec.); Hann River, Moll Gorge (AMNH 35616*, 10 spec. (of 34), 35-71 mm); Bow River (AMNH 35613*, 7 spec, 40-64 mm ; AMNH 35596, 2 spec.); Ord River (AMNH 35600, 28 spec.); Dunham River (AMNH 35602, 62 spec.).

Australia, Northern Territory: Moriarty Creek (AMNH 35603, 11 spec.); Victoria River at Big Horse Creek (AMNH 33880*, 1 spec., 41 mm); Katherine River (AMNH 35607*, 10 spec. (of 67), 35-99 mm); Ferguson River (AMNH 35604*, 10 spec. (of 85), 31-73 mm); Mary River (AMNH 35591*, 5 spec. (of 34), 19-40 mm; AMNH 35606*, 1 spec., 69 mm); South Alligator River (AMNH 35612*,

15 spec., 36-115 mm; AMNH 35608, 42 spec.); Barramundie Creek (AMNH 35598, 9 spec.; AMNH 35599, 22 spec.); Lilly (Barramundie) Lagoon (AMNH 35594*, 13 spec., 40-90 mm); Jim Jim Creek (AMNH 35609, 3 spec.); Daly River (AMNH 35589, 3 spec.); isolated pool 15 mi. east of Daly River Police Station (AMNH 35601*, 9 spec., 39-58 mm); Upper Manton River (AMNH 35592, 17 spec.); Red Lily Lagoon, 9 mi. northeast of Elsey Homestead (AMNH 35593*, 2 spec., 60-96 mm); Boggy Hole, 7 mi. downstream from junction of Finke River and Ellery Creek (AMNH 35618, 34 spec.); Roper River Mission (USNM 173665, 16 spec.); Oenpelli (USNM 173666, 9 spec.).

Amniataba caudavittatus (Richardson, 1844)

Flag tailed grunter, Bar tailed grunter, Spotted perch

Fig. 42

Datnia? caudavittata Richardson, 1844-48, p. 24, pl. 18,
figs. 3-5 (original description, Western Australia,
Harvey River).

Therapon caudovittatus: Günther, 1859, p. 284 (Victoria, Cape
York, Harvey River); 1867, p. 58 (Victoria, Cape York,
Harvey River). Schmeltz, 1869, p. 13 (Port Moresby).
Castelnau, 1873, p. 129 (Western Australia). Alleyne
and Macleay, 1876, p. 270 (Port Darwin). Macleay, 1878,
p. 348 (Port Darwin). Schmeltz, 1879, p. 39 (Port MacKey).
Gunther, 1880, p. 39 (Somerset). Macleay, 1881, p. 361
(west, north and northeast coasts of Australia). McCulloch,
1912, p. 88 (Murray Island).

Therapon caudavittatus: Waite, 1900, p. 210 (west Australia).
Ogilby and McCulloch, 1916, p. 108 (Freemantle, Western
Australia, Torres Strait, Murray Island, Dutch New Guinea,
Gulf of Papua). Fowler, 1928, p. 211 (compiled).
Marshall, 1964, p. 167 (north Queensland, north and
west Australia, Torres Strait, New Guinea).

Therapon bostockii Castelnau, 1873, p. 128 (original descrip-
tion, Freemantle).

Terapon caudavittatus: Fowler, 1931, p. 354 (compiled); 1934,

p. 446 (Gulf of Papua). Taylor, 1964, p. 185, pl. 39 (Arnhem Land).

Amphitherapon caudavittatus: Whitley, 1943, p. 183 (tropical Australia, New Guinea); 1960, p. 76, fig. (Western Australia Northern Territory, Queensland, New Guinea). Munro, 1956, p. 171 (distribution); 1967, p. 324 (New Guinea). Lake, 1971, p. 34 (northern and western Australia). Grant, 1972, p. 222, pl. 38, fig. (Queensland). Bayly, 1972, p. 262 (Shark Bay, Western Australia; tolerance to hypersalinity); 1975, p. 58 (estuaries of Northern Territory and Queensland).

Nomenclature: the trivial name caudavittatus, from the Latin cauda, tail, and vittatus, striped, refers to the prominent black marks on each lobe of the caudal fin.

Diagnosis: Amniataba caudavittatus can be distinguished from the other members of the genus by the presence of large black transverse blotches on each lobe of the caudal fin; a pigmentation lacking in other species in the genus.

Description: Dorsal spines XII-XIII; Dorsal rays 8-10; Anal, III, 8-9; 46-54 lateral line scales; 4-6 scales on caudal; 7-9 scales above lateral line; 17-19 scales below lateral line; 14-17 predorsal scales to occiput; 1 row of scales in sheath at base of dorsal, sheath extending to third dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to fourth anal ray; cheek scales in 9-10 rows; gill rakers on first arch 6-8+1+12-13; vertebrae 10+15.

Reaching 200 mm SL; depth 2.4-3.1 in SL; distance from dorsal origin to snout 2.1-2.5 in SL; head length 3.0-3.7 in SL; length of base of dorsal fin 1.9-2.1 in SL; snout length 2.6-3.6 in SL; eye width 3.5-4.4 in HL; jaw length 3.1-3.7 in HL; length of longest dorsal spine 1.8-2.1 in HL; length of longest dorsal ray 1.8-2.2 in HL; length of longest anal spine 2.2-2.8 in HL; length of longest anal ray 2.3-2.7 in HL.

Body moderately deep, compressed. Dorsal profile more pronounced than ventral. Dorsal profile straight from snout to nape, then convex to dorsal origin. Ventral profile nearly straight from tip of lower lip to pelvic insertion, then straight or barely convex to anus. Upper jaw slightly longer than lower. Gape oblique. Snout elongate. Maxillary reaching to vertical through anterior edge of eye in young; falling short with age, reaching to vertical through region between nostril and eye in adults. Teeth in bands; outer row enlarged, inner series of villiform teeth. No teeth on vomer or palatines

Interorbital region with ridges. Nostrils distant, separated by a distance equal to one-half eye diameter. Lacrimal serrate. Preoperculum slightly serrate, serrations largest on angle. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal not exposed; covered with skin and scales. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal arched; first spine short; fifth longest, those following decreasing in length to ultimate. Longest dorsal spine longer than longest ray. Soft dorsal with posterior edge straight or slightly convex. Spinous anal with second spine strongest; longer than third. Second anal spine shorter than longest anal rays. Soft anal with posterior edge straight or barely convex. Pectorals assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest, filamentous, falling short of anus. Caudal emargin

Coloration: head darker above, light ventrally. Body grey on back, light ventrally; upper half with randomly dispersed spots. Some specimens of all sizes show five or six incomplete vertical bars on back running ventrally to level of pectoral fin. First runs from nape to posttemporal; second, under third to fifth dorsal spines; third, under seventh to ninth spines; fourth, under tenth to twelfth spines; fifth, under soft dorsal; sixth (may be lacking) on caudal peduncle. Spinous dorsal spotted with faint dusky on margin. Soft dorsal dusky basally and at edge, sometimes

with a median dusky band. Spinous anal slightly dusky. Soft anal dusky anteriorly. Pectorals clear to dusky. Pelvics clear. Caudal spotted basally; with a black blotch extending obliquely across each lobe.

Coloration in life: each lobe of caudal fin with a prominent black blotch, these and black tip of soft dorsal outlined by light to lemon yellow, Pectoral fin light yellow. Anal, especially spinous portion and pelvics lemon yellow to deep yellow. Spots on body and fins reddish brown (Taylor, 1964).

Distribution: this species is primarily marine but also occurs in freshwaters in Western Australia from the Perth region north, Northern Territory, Queensland, Torres Strait and the southern half of New Guinea (Fig. 38).

Ecology: little is presently known about the ecology of this species. However, in Western Australia, the species shows a tolerance for a wide variety of environments, being found in waters ranging from fresh to hypersaline (Bayly, 1972). It occurs over a variety of substrates and in association with many different types of vegetation.

Remarks: Munro (1967) added to the monotypic genus Amphitherapon, created by Whitley (1943) for A. caudavittatus, a second species A. habbema based on Therapon habbema Weber. This second species is however, a synonym of Hephaestus trimaculatus which possesses a series of apomorphic characters (extrinsic swimbladder muscle form, tabular form and others) uniting it with the other species of the genus; character

states lacking in A. caudavittatus. Consequently the hypothesis of a close relationship between A. caudavittatus and the nominal form Therapon habbema is rejected.

Specimens examined

Western Australia: Bush Bay (AMNH 35627*, 6 spec., 32-162 mm); DeGrey River (AMNH 35629*, 9 spec., 46-56 mm); Murchison River (AMNH 35631*, 1 spec., 84 mm); Northwest Cape (AMNH 35628*, 15 spec. (of 86), 25-114 mm).

Northern Territory: Casuarina Beach (AMNH 35630*, 10 spec. (of 37), 40-72 mm); Nightcliff (USNM 173668*, 4 spec., 51-62 mm); Port Langdon (USNM 173671*, 5 spec., 44-79 mm). Groote Eylandt (USNM 173672, 7 spec.); Port Bradshaw (USNM 173675, 2 spec.; USNM 173676, 1 spec.); Yirrkalla (USNM*, 6 spec., 62-174 mm).

Genus 4, Hannia, n. gen.

Nomenclature: the generic name Hannia, refers to the type locality of the type species of the genus (H. greenwayi), the Hann River of the Kimberley region of Western Australia.

Diagnosis: a freshwater teraponid with two spines on the first proximal dorsal pterygiophore, lacking adult striping and have a low lateral line count (32-38 lateral line scales).

Type species: Hannia greenwayi n. sp.

Included species: the genus Hannia contains only one species, H. greenwayi, known only from the Moll Gorge of the Hann River, Western Australia

Hannia greenwayi, n. sp.

Greenway's grunter

Fig. 39.

Nomenclature: the trivial name, greenwayi, is in honor of Mr. James Greenway of the Department of Ornithology of the American Museum of Natural History whose generous financial support made possible the expedition to Western Australia which collected the type series.

Diagnosis: as for the genus.

Description: (numbers in parentheses are numbers of examined specimens having a given count). Dorsal spines and rays XII-10(2), XII-11(1), XIII-8(1), XIII-9(22), XIII-10(73), XIII-11(1), XIV-10(1); Anal spines 3, rays 7(12), 8(88), 9(1); Pectoral fin rays 13-16; Pelvics I-5; lateral line scales from origin to hypural joint 32(1), 33(17), 34(13), 35 (13). 36(27), 38(10); 3-5 caudal scales; transverse series to base of dorsal sheath at median dorsal rays

4+1+11(29), 4+1+12(11), 4+1+13(4), 5+1+10(30), 5+1+12(20); 9-11 predorsal scales to occiput; cheek scales in 4-5 rows; 1 row of scales in sheath at base of spinous dorsal, sheath extending to fourth to sixth dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to fourth to sixth anal ray; gill rakers on first arch 6-8+1+13-16, vertebrae 10+15.

Reaching 109 mm SL; depth 2.3-2.9 in SL; distance from origin of spinous dorsal to snout 1.9-2.4 in SL; head length 2.7-3.0 in SL; length of base of dorsal 1.9-2.2 in SL; snout length 2.3-3.2 in HL; eye width 3.1-4.1 in HL, getting relatively smaller with increasing SL; jaw length 2.8-3.7 in HL, getting relatively larger with increasing SL; length of longest dorsal spine 1.8-2.1 in HL; length of longest dorsal ray 1.9-2.4 in HL; length of longest anal spine 2.0-2.7 in HL; length of longest anal ray 1.8-2.3 in HL.

Body moderately deep compressed. Dorsal and ventral profiles almost evenly arched. Interorbital region with boney ridges. Jaws equal. Lips enlarged into pads in some adults, with lower lips forming a lateral fleshy pad (Fig. 40). Gape oblique. Maxillary reaching to vertical through posterior nostril. Teeth in bands, conic, outer row enlarged. No teeth on vomer or palatines. Nostrils distant; separated by a distance equal to one-half of eye

diameter. Lacrimal with 4-6 serrations along posteroventral edge. Preoperculum serrate; serrations largest on angle. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal not exposed; covered with skin and scales. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal arched; fifth spine longest; those following decreasing in length gradually to penultimate which is slightly shorter than ultimate. Soft dorsal rounded. Second anal spine strongest; longer than third; shorter than longest anal rays. Soft anal rounded. Pectoral fin assymmetrically pointed; fifth or sixth ray longest. Pelvics pointed; first ray longest; reaching to anus. Pelvic insertion anterior to vertical drawn through dorsal origin. Caudal emarginate.

Coloration: top of head from tip of snout to insertion of first scale row is dark. A horizontal band of pigmentation runs from posterior of lacrimal around ventral and posterior borders of orbit to level of dorsal edge of eye. Another band of pigmentation runs dorsally from middle of opercle to join dark pigmentation at top of head. Overall body coloration uniform greyish, lighter below. Each scale edged with darker pigmentation; intensity of pigmentation increasing dorsally. Scales at base of dorsal fin lighter. Spinous dorsal membranes dusky along anterior edge of spines. Soft dorsal, soft and spinous anal and caudal distally dusky.

Pectorals and pelvics slightly pigmented.

Distribution: the species is presently known only from the type locality; the rapids of the Hann River at Moll Gorge (Fig.38).

Ecology: the type locality had green turbid water with a visibility of approximately one foot, over a rock and mud bottom. Water was swift flowing, in rapids.

Specimens examined

The holotype (WAM P-25380-002), 80.9 mm SL, was obtained with rotenone by G. J. Nelson, W. H. Butler, and D. E. Rosen April 28, 1969 in the rapids of the Hann River at Moll Gorge, 15 mi. northeast of the Mount House homestead, Western Australia. Taken along with the holotype were 100 paratypes (WAM P-25380-001 and AMNH 35641, 41.5-108.8 mm).

Genus 4, "Terapon"

Nomenclature: the generic name "Terapon" as discussed earlier is a retention of the original generic designation of the only contained species "Terapon" jamoerensis Mees. For reasons discussed in detail earlier, the species as part of an unresolved tetrachotomy must be included in a new genus, but rather than create a new generic name, the species is retained in "Terapon" until such time as further analysis allows its exact placement as a member of its own or an existing monophyletic group. It should be noted, however, that Terapon as used elsewhere in this study differs from "Terapon" in the restricted sense that it is used here.

Diagnosis: a freshwater teraponid from West Irian, New Guinea having two spines on the first proximal dorsal pterygiophore, having a uniform brown coloration and a relatively high lateral line count (60-66 lateral line scales).

Type species: "Terapon" jamoerensis Mees, 1971

Included species: the genus "Terapon" contains only one species, "T." jamoerensis known only from Lake Jamoer in West Irian, New Guinea.

"Therapon" jamoerensis (Mees, 1971)

Jamoer grunter

Fig. 41

Therapon jamoerensis Mees, 1971, p. 214, fig. 5 (original description, Lake Jamoer, West Irian, New Guinea).

Nomenclature: the trivial name, jamoerensis, refers to the type locality of the species, Lake Jamoer, in West Irian, Indonesia. The type is at the Rijksmuseum van Natuurlijke Histoire (RMNH 25225).

Diagnosis: as for the genus.

Description: Dorsal spines XII-XIV; Dorsal rays 10-11 Anal III, 8-9; Pect. 14-15; Pel. 1-5; 60-66 lateral line scales 4-6 scales on caudal 9-10 scales above lateral line; 20-22 scales below lateral line; 15-17 predorsal scales to occiput; 1 row of scales in sheath at base of dorsal fin, sheath extending to third to fifth dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to fifth anal ray; cheek scales in 4-5 rows; gill rakers on first arch 5-6+1+10-11; vertebrae 11+14.

Reaching 83 mm SL; depth 2.4-2.5 in SL; distance from dorsal origin to snout 2.2-2.3 in SL; head length 2.9-3.0 in SL; length of base of dorsal 1.8-1.9 in SL; snout length 3.3-3.7 in SL; eye width 3.3-3.4 in HL; jaw length 3.7-3.8 in HL; length of longest dorsal spine 1.75-1.85 in SL; length

of longest dorsal ray 2.1-2.2 in HL; length of longest anal spine 1.75-1.85 in HL; length of longest anal ray 1.95-2.1 in HL.

Body compressed, moderately deep. Dorsal profile more pronounced than ventral. Dorsal profile straight to interorbital region; slightly concave above eye, then concave to dorsal origin. Interorbital region concave with ridges strongly developed. Ventral profile straight to pelvic insertion, then slightly convex or straight from pelvic insertion to anus. Jaws equal. Snout elongate. Gape oblique. Maxillary reaching to vertical drawn through anterior edge of eye or falling slightly short. Teeth in bands; conic; outer row enlarged. No teeth on vomer or palatines. Nostrils separated by a distance equal to one and one-half times diameter of posterior nostril. Lacrimal strongly serrate; with large sensory pores. Preoperculum serrate; serrations larger on vertical edge. Lower opercular spine longer and stronger, not extending beyond edge of opercular lobe. Posttemporal not exposed; covered with skin and scales; scale covering somewhat reduced. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal arched; first and second spines short; sixth spine longest; those following decreasing gradually in length to ultimate or penultimate. Longest dorsal spine longer than longest dorsal ray. Soft dorsal rounded. Second anal spine longest and strongest; twice length of first, slightly longer than third. Longest anal rays a bit longer

than longest spine. Soft anal rounded, Pectoral fin assymmetrically pointed; fifth ray longest. Pelvics pointed; first ray longest, slightly filamentous; barely reaching to anus. Caudal emarginate.

Coloration: head brownish, darker above. Dark band of pigmentation runs across top of eye. Overall body coloration silvery-brown. Soft dorsal clear. Spinous dorsal edged with black. Anal fin slightly pigmented. Pelvics and pectorals clear to slightly pigmented. Caudal dusky.

Distribution: this species is known only from Lake Jamoer, West Irian, New Guinea. This is a small lake (diameter about 6-8 km) located in the narrow region of the the Vogelkop peninsula. The locality though closer to the northern coast of the island is part of the southern watershed (Boeseman, 1963) (Fig. 38).

Ecology: this lake is relatively shallow, with clear water, moderate vegetation and a pH of about 6. The exact habitat inhabited by the species is not known (Boeseman, 1963).

Specimens examined

Indonesia, West Irian, Lake Jamoer (RMNH 25224*, 3 spec., 65-71mm).

Genus 5, Lagusia n. gen.

Nomenclature: the generic name Lagusia, refers to the type locality of the type species of the genus (L. micracanthus), the Lagusi River on the southern peninsula of Sulawesi (Celebes).

Diagnosis: freshwater teraponids from Sulawesi having an adult coloration of longitudinal body stripes. Distinguishable from all other members of the family in having 26 vertebrae rather than 25 or 27.

Type species: Lagusia micracanthus (Bleeker, 1860)

Included species: the genus Lagusia contains only one species, L. micracanthus, having a distribution in a limited region of the southern peninsula of Sulawesi (Celebes).

Lagusia micracanthus (Bleeker, 1860)

Celebes grunter

Fig. 43

Datnia micracanthus Bleeker, 1860, p. 55 (original description, Lagusi River, Celebes (Sulawesi)).

Therapon (Datnia) micrcanthus: Bleeker, 1873, p. 388 (Lagusi River); 1876, p. 117, pl. 340 (Lagusi River).

Therapon micracanthus: Weber, 1894, p. 408 (Sulawesi: Minralang, Amparang, Tjenrama River). Weber and deBeaufort, 1931, p. 153 (Sulawesi; Minralang, Amparang, Tjenrama River). Mees, 1971, p. 218 (Sulawesi; comparisons to Therapon habbema and T. trimaculatus).

Terapon micracanthus: Fowler, 1931, p. 342 (pt.); 1934, p. 416 (pt).

Papuservus micracanthus: Munro, 1956, p. 176 (pt) (distribution).

Nomenclature: the trivial name of the species, micracanthus, appears to be derived from the Greek for short spine, but is of obscure meaning with respect to the species. Three syntypes of the species (RMNH 5632) were examined and although in poor condition, agree in all details with the original Bleeker description.

Diagnosis: as the genus Lagusia contains only one species, the distinguishing characters of L. micracanthus are the same as

those for the genus.

Description: Dorsal spines XII-XIII; Dorsal rays 8-11; Anal III, 8-9; Pect. 15; Pel. I-5; 38-42 lateral line scales; 3-5 scales on caudal; 5-6 scales above lateral line; 11-12 scales below lateral line; 16 predorsal scales to occiput; 1 row of scales in sheath at base of dorsal fin, sheath extending to sixth or seventh dorsal ray; 2 rows of scales in sheath at base of anal fin, sheath extending to sixth anal ray; cheek scales in 4 rows; gill rakers on first arch 6+1+10-11; vertebrae 10+16.

Reaching 115 mm SL; depth 2.3-2.5 in SL; distance from dorsal origin to snout 2.2-2.3; head length 2.8-3.2 in SL; length of base of dorsal 1.8-2.0 in SL; snout length 3.0-3.6 in HL; eye width 2.75-3.4 in SL; jaw length 3.3-3.6 in HL; length of longest dorsal spine 1.4-1.6 in HL; length of longest dorsal ray 1.5-1.7 in HL; length of longest anal spine 2.2 in HL; length of longest anal ray 1.6-1.7 in HL.

Body moderately deep, compressed. Dorsal profile more pronounced than ventral. Dorsal profile convex from snout to above eye; concave above orbit, then convex to dorsal origin. Ventral profile slightly convex to pelvic insertion, straight from pelvic insertion to anus. Jaws equal. Gape oblique. Snout blunt. Maxillary reaching to vertical drawn through region between posterior nostril and eye; reaching to vertical through anterior of eye in some specimens. Teeth villiform; in bands; outer row enlarged. No teeth on vomer or palatines. Interorbital region with ridges. Nostrils separated by a

distance equal to twice diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate; serrations largest on angle and vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal not exposed; covered with skin and scales. Cleithrum exposed; serrate posteriorly; lacking scales on side. Supracleithrum exposed.

Spinous dorsal arched; first spine short; fifth to seventh spine longest, those following decreasing in length to penultimate which is same length or slightly shorter than ultimate. Longest dorsal spine longer than longest dorsal ray. Soft dorsal angular posteriorly. Second and third anal spines about same length; longer than first spine and much shorter than rays. Soft anal angular. Pectorals assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest; reaching to anus. Caudal emarginate.

Coloration:(description taken from Bleeker and Weber and de-Beaufort) head darker above, light below. Body with four or five longitudinal stripes. Dusky green above, lighter below. First stripe running along base of dorsal fin; second, from nape to upper caudal peduncle; third, from upper corner of gill opening to middle of caudal peduncle; fourth, from opercle to base of caudal peduncle; fifth (sometimes lacking) from axil of pectoral to end of soft anal. Spinous dorsal clear, dusky distally. Soft dorsal with basal blotch. Spinous and soft anal yellowish. Caudal with two transverse bands on base. Lobes of caudal brown. Pectorals and pelvics yellowish.

Distribution: this species is known from a limited area on the southern peninsula of Sulawesi (Celebes): Lagusi River, Amparang River near Balangnipa, Minralang River near Tempe, and Tjenrama River near Pampanua. The species is known only from two collections, the type series from 1859 and fourteen specimens listed by Weber (1894).

Remarks: Fowler (1931, 1934) synonymized into L. micracanthus two nominal forms from New Guinea, Therapon trimaculatus and T. habbemai (both = Hephaestus trimaculatus) without explanation and without a discussion of several major differences between them. This procedure was followed by Munro (1956). Lagusia micracanthus, however, lacks a series of apomorphic character states of the posttemporal, extrinsic swimbladder muscle and other characters joining the other forms to the genus Hephaestus. Furthermore, it is quite distinct from them on the basis of coloration and scalation counts; undoubtedly representing a distinct species. Munro (1967) recognized this in reversing his previous opinion and raising all the nominal forms to their previous status.

Specimens examined

Indonesia, Sulawesi (Celebes), southern peninsula, Tjenrama
(RMNH 5632*, 3 spec., 40-82 mm (syntypes)).

Genus 6, Pelates

Pelates Cuvier and Valenciennes, 1829, p. 146 (type species Pelates quadrilineatus).

Helotes Cuvier and Valenciennes, 1829, p. 149 (type species Helotes sexlineatus, by monotypy).

Nomenclature: the generic name was not explained in the original description and is of unknown significance.

Diagnosis: Marine teraponids with an unexposed posttemporal and longitudinal body stripes. Distinguishable from the other species of the family in having an extrinsic swimbladder muscle with a direct muscular attachment to the ventral process of the posttemporal and a ligamentous attachment to the rear of the skull.

Included species: the species recognized in this study are: Pelates quadrilineatus which is distributed from the east coast of Africa east to the Australia-New Guinea region and north to China and Japan, and P. sexlineatus which is distributed through the East Indies, Australia, New Guinea and north to China.

Pelates quadrilineatus (Block, 1790)

Four lined terapon, Trumpeter perch

Fig. 44

Holocentrus quadrilineatus Block, 1790, p. 82, pl. 238, fig. 2

(original description, The Orient). Walbaum, 1792, p.

642 (on Block). Forster, 1795, p. 16. Lacépède, 1802,

pp. 339, 380 (East Indies).

Pristopoma sexlineatum Quoy and Gaimard, 1824, p. 320

(original description, shore at Sydney, Port Jackson).

Pelates sexlineatus: Cuvier and Valenciennes, 1829, p. 149

(original description, "Hawaiian Islands"?). (*). Fowler,

1931, p. 362 (compiled).

Therapon quadrilineatus Cuvier and Valenciennes, 1829, p. 134

(original description, no locality). (*).

Pelates quadrilineatus Cuvier and Valenciennes, 1829, p. 146

(original description; Port Jackson, Australia). (*).

Fowler, 1929, p. 642 (Luzon); 1931, p. 358, fig. 29

(Philippines, Borneo, Hong Kong, New South Wales, Formosa).

Weber and deBeaufort, 1931, p. 161 (East Indies, Philippines

Indo-west Pacific). Herre, 1931, p. 53 (Philippines); 1933,

p. 4 (north Borneo). Fowler, 1934, p. 446 (Port Moresby),

Job, 1940, p. 301 (feeding habits). Blegvad, 1944, p. 87,

fig. 47 (Bahrien, Iranian Gulf). Gopinath, 1946, p. 7

(larvae). Smith, 1949, p. 184 (Pondoland, Dalagoa Bay,

South Africa); 1955, p. 309 (Aldabra). Munro, 1955, p. 115

(Ceylon); 1956, p. 169 (New Guinea: Sinapa, Collingswood Bay, Buka Passage; Solomon Islands; Admiralty Islands). Okada, 1959, p. 75 (Okinawa). Fowler, 1959, p. 256 (Fiji?). Mees, 1962, p. 33 (Western Australia). Chien, 1962, p. 543, fig. 448 (Hainan Region). Freihofer, 1963, p. 132 (RLA pattern). Sanchez, 1963, p. 58, fig. 3 (Inhaca, Mozambique). Marshall, 1964, p. 167, pl. 16 (Mouton Bay, Queensland). Tortonese, 1964, p. 44 (New Guinea). Munro, 1967, p. 322 (New Guinea). Mauge, 1967, p. 101 (Tulear, Madagascar). Chan, 1968, p. 60, pl. 30 (Hong Kong). Lindberg and Krasnyukova, p. 121, fig. 165 (Japan). Grant, 1972, p. 233, pl. 38 (biology, sonic ability). FAO, 1974, TP2, fig. (distribution, fisheries). Johnson, 1975, p. 12 (procurent spur).

Therapon xanthurus Cuvier and Valenciennes, 1829, p. 129

(original description, Java).

Pelates quinquilineatus Lesson, 1831, p. 233 (original description, Port Jackson).

Helotes polytaenia Bleeker, 1854, p. 53 (original description, Sindangole, Halmahera).

Therapon cuvieri Bleeker, 1854, p. 211 (original description, Timor). (*).

Therapon (Pelates) quadrilineatus: Bleeker, 1873-76, p. 117 (East Indies, Philippines).

Therapon cuvierii: Pohl, 1884, p. 27 (Viti, Fiji; error?).

Therapon 4-lineatus Gorgoza, 1888, p. 284 (original description, Manila Bay, Cebu).

Terapon quadrilineatus: Jordan and Seale, 1907, p. 24 (Manila).
 Evermann and Seale, 1906, p. 83 (Bulan , San Fabian).
 Jordan and Starks, 1917, p. 450.

(*):further references to this nominal species can be found in Fowler, 1931, pp.358-362 for the years between the original description and 1930.

Nomenclature: the trivial name quadrilineatus from the Latin quadrus, four, and lineatus, lined, refers to the four prominent dark longitudinal lines usually present on the body of this species.

Diagnosis: this species can be distinguished from the other species of the genus in having unicuspid teeth, a gill raker count of 16-18+1+22-27, 68-73 lateral line scales, and a body depth of 2.6-3.2 (in contrast to triscupid teeth, 6-7+1+14-16 gill rakers, 80-87 scales, and a body depth of 3.4-4.0 in P. sexlineatus). The species can be separated from all members of the family in its possession of a small third chamber in the swimbladder posteriorly and the insertion of three predorsals anterior to the first neural spine.

Description: Dorsal spines XII-XIII; Dorsal rays 9-11; Anal III, 9-10; Pect. 14-16; Pel. 1-5; 68-73 lateral line scales; 5-7 scales on caudal; 9-11 scales above lateral line; 19-23 scales below lateral line; 15-17 predorsal scales to occiput; 1 row of scales in sheath at base of dorsal fin, sheath extending to fifth or sixth dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to fifth or sixth anal ray; cheek scales in 4-5 rows; gill rakers on first arch 16-18+1+22-27; vertebrae 10+15.

Reaching 200 mm SL; depth 2.6-3.2 in SL; distance from origin of dorsal to snout 2.4-3.2 in SL; head length 2.3-3.6 in SL; length of base of dorsal fin 1.7-2.0 in SL; snout length 2.7-3.1 in SL; eye width 3.2-4.2 in HL; jaw length 3.0-3.8 in HL; length of longest dorsal spine 1.5-1.75 in HL; length of longest dorsal ray 1.75-1.9 in HL; length of longest anal spine 2.2-2.5 in HL; length of longest anal ray 1.7-1.8 in HL.

Body moderately deep, compressed. Dorsal profile more pronounced than ventral. Dorsal profile slightly convex from snout to interorbital region, then straight to dorsal origin. Ventral profile convex from lower lip to pelvic insertion; straight from pelvic insertion to anus. Jaws equal. Gape oblique. Maxillary reaching to vertical through posterior nostril. Teeth in two bands in lower jaw; in three rows or a band in upper jaw; outer rows enlarged. No teeth on vomer or palatines. Interorbital region with bony ridges. Nostrils distant, separated by a distance twice diameter of posterior

nostril. Lacrimal serrate. Preoperculum evenly serrate in young, serrations larger along vertical edge with age. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe except in some juveniles. Cleithrum exposed; serrate along posterior edge; scales on side. Posttemporal not exposed; covered with skin and scales. Supracleithrum exposed.

Spinous dorsal arched; spines very long; first short, fifth to seventh spine longest, those following decreasing gradually to penultimate which is same length as ultimate. Longest dorsal spines much longer than longest dorsal rays. Soft dorsal angular with straight or emarginate border. Spinous anal spines short; first shortest; second and third subequal, shorter than longest anal rays. Soft anal border emarginate or straight. Pectoral assymmetrically pointed; fifth ray longest, Pelvics pointed; first ray longest or equal to second; reaching to anus in young, falling short with age. Caudal slightly emarginate; lobes acute.

Stripe running from snout to dorsal edge of orbit; divides in interorbital region into two stripes that are continuous with body stripes. Another stripe runs from snout over nostrils to front of orbit and from rear of orbit to lower opercular spine. A band of light pigmentation runs under orbit on cheek. In adults top of head is darker, obscuring stripes somewhat; head light ventrally. In life mouth and gill cavity are bright red (FAO, 1974). Body silvery with five horizontal black stripes

First, running under dorsal fin to anterior of soft dorsal; second, from dorsal edge of eye to posterior of soft dorsal base; third, from rear of eye to upper edge of caudal peduncle; fourth, from stripe under eye to caudal base; fifth (sometimes lacking), from below pectoral base to base of caudal peduncle. A blotch of variable intensity (sometimes lacking entirely) found posterior to nape of side of body. In larger specimens light pigmentation occurs along edge of anterior dorsal spines. Juveniles with six or seven vertical bars present in addition to the pattern of stripes retained into adulthood. First, slightly anterior to dorsal origin; second to fourth, under spinous dorsal; fifth and sixth, under soft dorsal; seventh (sometimes lacking) on caudal peduncle. Spinous dorsal with black blotch dorsally between third and seventh spines. Soft dorsal with black tips. Spinous and soft anal yellow; darker along edges. Caudal yellow with dark edge. Pectorals and pelvics yellow.

Distribution: in marine and brackish waters of Indo-west Pacific from Africa north of Natal, Madagascar, Red Sea, Arabia, Persian Gulf, India, Sri Lanka, Sumatra, Java, Borneo, Sulawesi, New Guinea, Southeast Asia, China, Philippines, Japan, Australia (Western Australia, Northern Territory, Queensland, New South Wales) (Fig. 45).

Fowler (1959) lists this species as a member of the Fiji fauna following Pöhl (1884). However, since that report there are no further records of the species from the region. As such

it appears likely that the original record was either a mis-identification or error in locality. Similarly Schmeltz (1869) appears incorrect in his description of Therapon cuvierii, a synonym of P. quadrilineatus as a member of the Fiji Fauna.

The development of this species from the postlarval stage onwards was descibed in detail by Munro (1945) based on collect-ions of early postlarvae. The spawning season in New South Wales appears to be extended; lasting from late summer well into winter.

Remarks: Cuvier and Valenciennes (1829) described several species of Pelates and Terapon which have been reduced to two nominal forms; Pelates sexlineatus and P. quadrilineatus. These were supposed to be distinguished from each other by the presence of a black blotch between the third and eighth dorsal spines and a black blotch on the anterodorsal body wall (sometimes lacking) in P. quadrilineatus; pigmentation patterns lacking in P. sexlineatus. Such a separation was retained by a variety of workers including Ogilby and McCulloch (1916) and Fowler (1931) but was not utilized by Weber and deBeaufort who recognized only one species, P. quadrilineatus.

Examination of material from throughout the Indo-west Pacific has shown that both of these pigmentation patterns vary ontogenetically and geographically without pattern throughout

the region, with complete gradations existing from total absence to dark pigmentation patterns. Thus it would appear that there is actually only one species, P. quadrilineatus.

Specimens examined

Africa, Changamu (USNM 72884, 1 spec.; USNM 72889, 1 spec.).
 Persian Gulf, Tarut bay, Saihat (USNM 148116, 5 spec.).
 Thailand (USNM 88369, 1 spec.).
 Indonesia, Borneo, Sandakan (USNM 146360*, 3 spec., 62-76 mm).
 Philippines: Manila (USNM 56307, 6 spec.); Lubang (USNM 72183*, 1 spec., 105 mm); Iloilo, Panay (USNM 106856*, 1 spec., 78 mm); Palawan (USNM 146924*, 4 spec., 31-60 mm).
 Australia, Port Jackson (USNM 59978*, 2 spec., 88-109 mm.; USNM 42028, 1 spec.; USNM 176978*, 1 spec., 100 mm).
 New Guinea: Coral Sea, at Kapa Kapa (USNM uncat., BBC 1524, 1 spec.); Trobriand Islands, Kiriwina (USNM uncat., BBC 1505*, 11 spec., 50-75 mm; BBC 1506, 6 spec.; BBC 1520*, 1 spec., 69 mm; BBC 1508, 15 spec.).
 China: Taiwan, Pescadores Islands, Peng-Hu (USNM 192540*, 1 spec., 90 mm; USNM 192865*, 3 spec., 113-118 mm); Hong Kong (USNM 6536*, 1 spec., 123 mm); Shanghai (USNM 148416*, 1 spec., 101 mm).

Pelates sexlineatus (Quoy and Gaimard, 1824)

Striped perch

Fig. 46

Terapon sexlineatus Quoy and Gaimard, 1824, p. 340, pl. 60,
fig. 1 (original description, Shark Bay, Australia).

Helotes 6 lineatus: Cuvier 1829, p. 144 (name only).

Helotes sexlineatus: Cuvier and Valenciennes, 1829, p. 149,
pl. 56 (Australia, Shark Bay). Günther, 1859, p. 285
(copied). Bleeker, 1865, p. 31 (Manila Bay). Kner, 1865,
p. 46, pl. 3, fig. 1 (Java and Manila). Castelnau, 1873,
p. 129 (Western Australia); 1878, p. 370 (Port Jackson).
Karoli, 1881, p. 153 (Singapore). Weber, 1895, p. 263
(Thursday Island). Pellegrin, 1905, p. 84 (Tonkin).
Jordan and Richardson, 1907, p. 258 (Manila). Fowler,
1918, p. 63 (Philippines). Waite, 1923, p. 120, fig.
(South Australia). Fowler, 1929, p. 642 (Melbourne,
Philippines); 1931, p. 365 (Philippines, China). Weber
and deBeaufort, 1931, p. 166, fig. 32 (East Indies, Aust-
ralia, Philippines). Herre, 1931, p. 53 (Luzon). Harden-
berg, 1938, p. 311 (Batavia [Jakarta], Singapore).
Whitley, 1953, p. 46 (assignment to subfamily Helotinae).
Munro, 1956, p. 169 (compiled). Okada, 1959, p. 75
(Okinawa). Fowler, 1959, p. 257 (Fiji, ?). Scott, 1962,
p. 215, fig. (Western Australia, New South Wales, South
Australia, Queensland). Chien, 1962, p. 538, fig. 444
(Hainan region. South China Sea). Taylor, 1964, p. 184

(Port Bradshaw, Northern Territory). Marshall, 1964, p. 167, pl. 34 (north Queensland). Munro, 1967, p. 321 (New Guinea). Chan, 1968, p. 58, pl. 29 (Hong Kong). Chen, 1969, p. 401 (Taiwan). FAO, 1974, p. TH1, fig. (fisheries, distribution).

Therapon (Helotes) sexlineatus: Bleeker, 1873-76, p. 118 (East Indies, Australia).

Helotes octolineatus Jenyns, 1842, p. 18 (original description; King George's Sound, Australia). Macleay 1881, p. 68 (after Jenyns).

? Helotes profundior De Vis, 1884, p. 397 (original description, South Australia).

? Helotes scotus Haache, 1885, p. 508 (original description, Adelaide).

Nomenclature: the trivial name, sexlineatus, from the Latin sex, six, and lineatus, lined, refers to the pattern of prominent dark longitudinal line present on the sides of the body in this species

Diagnosis: this species can be distinguished from all other

members of the family by its triscupidate teeth. Within the genus Pelates it is distinguished by the possession of 6-7+1+14-16 gill rakers on the first arch, 80-87 lateral line scales and a body depth of 3.4-4.0 (in contrast to 16-18+1+22-27 gill rakers, 68-73 lateral line scales and a body depth of 2.6-3.2 in P. quadrilineatus).

Description: Dorsal spines XI-XII; Dorsal rays 9-11; Anal III, 10-11; Pect. 15-16; Pel. I-5; 80-87 lateral line scales; 5-8 scales on caudal; 11-13 scales above lateral line; 22-24 scales below lateral line; 19-21 predorsal scales to occiput; 1 row of scales in sheath at base of dorsal fin, sheath extending to first to third dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to fourth or fifth anal ray; cheek scales in 4-5 rows; gill rakers on first arch 6-7+1+14-16; vertebrae 10+15.

Reaching 200 mm SL; depth 3.4-4.0 in SL; distance from dorsal origin to snout 2.8-3.1 in SL; head length 3.3-4.3 in SL; length of base of dorsal 1.65-1.80 in SL; snout length 3.1-3.5 in HL; eye width 3.6-4.3 in HL; jaw length 3.0-4.3 in HL; length of longest dorsal spine 1.4-1.7 in HL; length of longest dorsal ray 1.7-1.9 in HL; length of longest anal spine 2.8-3.1 in HL; length of longest anal ray, 1.6-1.9 in HL.

Body slender, elongate, only slightly compressed. Head small. Dorsal and ventral profiles evenly rounded. Dorsal profile strongly convex from snout tip to above eye,

then slightly convex to dorsal origin. Ventral profile slightly convex to pelvic insertion, then straight to anus. Jaws equal. Gape short; oblique. Snout rounded. Maxillary reaching to vertical drawn halfway between posterior nostril and anterior of eye. Teeth tricuspidate; cusps of very nearly equal size. Outer row of teeth enlarged; inner rows in bands. No teeth on vomer of palatines. Interorbital region with strong ridges. Nostrils separated by a distance equal to diameter of posterior nostril. Lacrimal serrate, serrations stronger in young. Preoperculum serrate; serrations strongest on posterior edge. Lower opercular spine longer and stronger; extending nearly to edge of opercular lobe in adults; surpassing edge in some juveniles. Cleithrum exposed; serrate along posterior edge; scales present on side (scalation reduced in some individuals). Posttemporal not exposed; covered with skin and scales. Supracleithrum exposed.

Spinous dorsal strongly arched; first spine short, fifth or sixth longest; those following decreasing in length to penultimate which is shorter than ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal emarginate. Third anal spine subequal to second; much shorter than longest anal rays. Soft anal emarginate. Pectorals assymmetrically pointed; fifth ray longest. Pelvics pointed; first ray longest or subequal to second; reaching one-half distance to anus. Caudal emarginate.

Coloration: head in young with three longitudinal stripes. First running from above upper lip across top of orbit to join third body stripe; second, from snout to anterior of eye, continuing from back of eye to join with fourth body stripe; third, from jaw across cheek to opercle. In adults the head is darker above, light below, somewhat obscuring the stripes in some individuals. Body greyish or bluish above, silvery below, with 5-8 longitudinal stripes. First running from interorbital along base of spinous dorsal (sometimes divided into two bands); second from nape to base of soft dorsal; third, contains a large spot above the upper opercular spine, from the upper edge of eye to dorsal edge of caudal peduncle; fourth, from snout to middle of caudal base; fifth, from corner of mouth to pectoral and then to caudal (lacking in smaller specimens); sixth, from base of pectoral to rear of soft anal; seventh, from below pectoral base to middle of soft anal (sixth and seventh lacking in some specimens). Spinous dorsal blackish along upper half. Soft dorsal blackish along anterior edge. Spinous and soft anal clear. Caudal with dark border and several bands of faint spots basally. Pectorals and pelvics clear.

Distribution: marine waters around Singapore, Sumatra, Java, Borneo and other islands of the East Indies, Australia (Western Australia, Northern Territory, Queensland, New South Wales and South Australia west to Adelaide), Torres Strait,

New Guinea, southeast Asia, Philippines, China (Fig. 47).
 Fowler (1959) lists this species as a member of the Fiji fauna based on citations of Therapon cuvieri and T. cuvierii from Fiji; species he evidently considered synonymous with Helotes sexlineatus (= Pelates sexlineatus). However, these actually appear to be synonyms of P. quadrilineatus. Furthermore, there are no recent reports of the species from Fijian waters. As such it would appear that Fowler was incorrect.

Specimens examined

Australia, Western Australia: Cockburn Sound, East Side (AMNH 31395*, 2 spec., 138-145 mm); Cockburn Sound, Point Peron (AMNH 31415*, 20 spec. (of 143), 45-120 mm; AMNH 35634*, 2 spec., 140-150 mm).
 Australia, Northern Territory, Port Bradshaw (USNM 173681, 9 spec.).
 Philippines, Luzon, Cavite Marker (USNM 146364*, 1 spec., 72mm).
 China, Kowloon (USNM 146365*, 2 spec., 149-174 mm).

Genus 7, Terapon

Terapon Cuvier, 1817, p. 295 (type species Holocentrus servus Block, designated by Bleeker, 1876, p. 267).

Therapon Cloquet, 1819, p. 299 (emended spelling for Terapon)

Pterapon Gray, 1835, p. 88 emendation for Terapon (type species P. trivittatus (= Terapon jarbua) by monotypy).

Authistes DeVis, 1884, p. 398 (type species, Authistes argenteus (= Terapon puta), by monotypy).

Eutherapon Fowler, 1904, p. 527 (type species, Eutherapon theraps (= Terapon theraps), by original designation).

Nomenclature: the generic name Terapon, from the Greek for slave, comes from Block's statement that these fishes were utilized by the servant classes in Japan and were consequently termed "slave fish". This spelling is an incorrect transliteration from the Greek rather than a lapsus calami and is therefore the valid form (see also discussion on the genus and family names in the Introduction).

Diagnosis: members of the genus Terapon are distinct from all others in the family in possessing an extremely elongate lower opercular spine which extends beyond the edge of the opercular lobe throughout life. The presence of parallel transverse stripes on the caudal fin lobes and a deeply emarginate spinous dorsal further distinguish the group.

Included species: three species are placed in Terapon (jarbua, theraps and puta) all being marine species that enter into brackish waters and penetrate far upstream into freshwater throughout their range. All three have extensive ranges extending from the east coasts of Africa to the New Hebrides and north to Japan. I. jarbua extends further east as far as Samoa.

Terapon jarbua (Forskål, 1775)

Crescent Perch, Tigerfish, Thorn Fish

Fig. 49

Sciaena jarbua Forskål, 1775, pp. XII, 50 (original description,

Djedda, Red Sea). Bonnaterre, 1788, p. 123 (Red Sea).

Gmelin, 1789, p. 1303 (Arabia). Walbaum, 1792, p. 318

(on Forskål). Shaw, 1803, p. 541 (Arabian Seas).

Holocentrus servus Block, 1790, p. 80, pl. 238, fig. 1

(original description, Japan). Walbaum, 1792, p. 641 (on

Block). Forster, 1795, p. 16.

Grammistes servus: Schneider, 1801, p. 185 (Japan).Holocentrus jarbua: Lacépède, 1802, pp. 329, 348, pl. 30, fig.

3 (on Forskål).

Terapon timoriensis Quoy and Gaimard, 1824, p. 341 (original

description, Coupang).

Therapon servus: Cuvier and Valenciennes, 1829, p. 125 (Timor,

Seychelles, Pondichy, Molucca, Malabar). (*). Izuka and

Matsuura, 1920, p. 150 (Kagoshima). Uchida, 1934 (sonic

ability). McCulloch, 1934, p. 47 (New South Wales). Munro,

1956, p. 169 (Trobriand Islands, D'Entrecasteaux Islands);

1967, p. 323 (New Guinea).

Pterapon trivittatus Gray, 1833-34, pl. 88, fig. 1 (copied from

Hamilton).

Therapon trivittatus: Cantor, 1849, p. 1001 (Pinang, Malay

Peninsula, Sumatra). Peters, 1868, p. 256 (Singapore).

Elera, 1895, p. 472 (Luzon, Manila Bay).

Therapon bounzetianus Hombron and Jacquinot, 1854, p. 43, pl.

4, fig. 2 (original description, no locality).

Therapon? geregar Thiollière, 1857, p. 147 (Woodlark Island).

Johnius geregar: Thiollière, 1857, p. 147 (name in synonymy).

Perca cincta: Günther, 1859, p. 279 (India, name in text).

Terapon servus: Guichenot, 1866, p. 145 (Madagascar).

Therapon jarbua: Klunzinger, 1870, p. 709 (Kosier, Red Sea).

(*). Schmidt, 1931, p. 64 (Kagoshima, Japan). Duncher and Mohr, 1931, p. 62, fig. 1 (New Pomerania, New Guinea, Admiralty Islands). Weber and deBeaufort, 1931, p. 147, fig. 5 (East Indies, Red Sea, Madagascar, Australia, New Guinea). Herre, 1931, p. 13 (New Hebrides); 1933, p. 2 (north Borneo). Pellegrin, 1933, p. 91, fig. 33 (south-east Madagascar, Seychelles). Herre, 1934, p. 53 (Philippines: Curimao, Bauang Sur, Manila, Lemery, Dumaguete, Jolo); 1936, p. 195 (Fiji, Malekula Island, New Hebrides). Hardenberg, 1936, p. 246 (Kupuas River, Borneo); 1937, p. 11 (sound production; Kumat River). Job, 1940, p. 299 (ecology, feeding habits). Blegvad, 1944, p. 87 (Iranian Gulf). Chacko, 1949, p. 32 (feeding). Smith, 1949, p. 183, fig. 101 (South Africa north of Port Alfred). Kuroda, 1951, p. 366 (Tokyo Bay, Sagumi Bay, Saguara Bay, Skikoku, Riu Kiu). Koumans, 1954, p. 224 (Morotai, Amboina). Smith, 1955, p. 309 (Aldabra). Munro, 1955, p. 116 (Gonga, Iri

bateya, Pol bateya, Ceylon). Herlad, 1956, p. 195 (territoriality in young). Imamura and Hashitani, 1957, pp. 45 and 47 (feeding). Fourmanoir, 1957, p. 89, fig. 65 (Mozambique Channel, Comoros). Okada, 1959, p. 75 (Okinawa). Raj, 1960, p. 9 (sonic ability). Schneider, 1961, p. 515 (physiology, sonic ability). Chien, 1962, p. 542, fig. 447 (Hainan region). Freihofer, 1963, p. 132 (RLA pattern). Nakamura, 1963, p. 185, fig. 137 (Japan). Sanches, 1963, p. 59, fig. 29 (Mozambique). Schneider, 1964, p. 497, (sonic ability). Imamura and Hori, 1964, p. 27 (Lake Hinuma, Japan. Tortonese, 1964, p. 43 (West Irian: Salawati, Andai; Papua: Beagle Bay, Baia Lina). Marshall, 1964, p. 166, pl. 16 (north Queensland). Talbot, 1965, p. 431 (Tutia reef, Tanganika). Okada, 1966, p. 232, fig. 215 (Japan). Mauge, 1967, p. 128 (Tulear, Madagascar). Rajan, 1968, p. 523 (Chilka Lake, India). Chan, 1968, p. 63, pl. 32 (Hong Kong). Dmitrenko and Fursa, 1969, p. 797 (Gulf of Kutch). Lindberg and Krasnyukova, 1969, p. 119, fig. 103 (Sea of Japan). Fursa, 1969, p. 102 (Seas of Hindustan). Kono and Nose, 1971, p. 169 (feeding). Fishelson, 1971, p. 128 (Red Sea, misspelled as I. jarboa). Grant, 1972, p. 222, fig. (Queensland). Kaliymurthy and Rao, 1972, p. 199 (feeding). Rahin, 1973, p. 563 (developmental morphometrics). FAO, 1974, p. T11, fig. (distribution and fisheries). Tortonese, 1975, p. 174 (Habo, Gulf of Aden). Wallace, 1975, p. 40 (distribution of larvae).

Therapon (Datnia) jarbua: Bleeker, 1873-76, p. 112 (East Indies).

Terapon jarbua: Jordan and Seale, 1905, p. 781 (Philippines: Negros).(*). Fowler, 1931, p. 330 (throughout Philippines, Kowloon, China, Samoa, Okinawa, Japan, Java, New Guinea, Queensland, Sumatra); 1931b, p. 24 (Suva, Fiji); 1934, p. 446 (Samoa, New Hebrides, Fiji, Port Moresby); 1959, p. 253 (Fiji). Whitley, 1962, p. 97 (Queensland, New South Wales). Smith, 1963, p. 13 (Seychelles). Taylor, 1964, p. 183 (Arnhem Land). Chin, 1969, p. 401 (Taiwan). Ch'en 1973, p. 19 (Taiwan). Yu and Chung, 1975, p. 15 (Taiwan).

Therapon jerbua: Sewell, 1913, p. 334 (Hinge Basin).

Holocentrus katakya Chaudhuri, 1923, p. 720 (MS name of Buchanan-Hamilton).

Stereolepis inoko Schmidt, pp. 52 and 158, fig. 7 (original description, Japan); 1933, p.103 (placed as a synonym of Therapon jarbua).

(*) further references to this species under this name can be found in Fowler, 1931, p.330 for the years between the original description and 1930.

Nomenclature: the specific name , jarbua, is a transliteration from the Arabic for a native name of the species. The type of the species is deposited in the Zoological Museum of Copenhagen (Klausewitz and Nielsen, 1965)

Diagnosis: Terapon jarbua can be distinguished from the other members of the family by its body coloration of three downwardly curved longitudinal stripes. Within the genus Terapon it can be further differentiated by having 12-15 gill rakers on the lower limb of the first arch and 70-100 lateral line scales (in contrast to 18-25 gill rakers for T. puta, and 47-56 lateral line scales for T. theraps.).

Description: Dorsal spines XI-XII; Dorsal rays 10-11; Anal III, 7-10; Pect. 13-14; Pel. I-5; 75-100 lateral line scales; 7-10 scales on caudal; 14-17 scales above lateral line; 19-24 scales below lateral line; 20-25 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal fin, sheath extending to fourth or fifth dorsal ray; scales in upper row of sheath larger than those in lower row; 3 rows of scales in sheath at base of anal fin, sheath extending to fourth or fifth anal ray; cheek scales in 6-10 rows; gill rakers on first arch 6-8+1+12-15; vertebrae 10+15.

Reaching 300 mm SL; depth 2.6-3.2 in SL; distance from dorsal origin to snout 2.2-2.8 in SL; head length 2.3-3.6 in HL; length of base of dorsal fin 1.8-2.1 in SL; snout length 3.0-3.8 in HL; eye width 3.5-5.1 in HL; jaw length 1.9-3.0 in HL; length of longest dorsal spine 1.5-2.0 in HL; length of longest dorsal ray 1.7-2.6 in HL; length of longest anal spine 2.7-3.6 in HL; length of longest anal ray 1.8-2.6 in HL.

Body moderately deep. slightly compressed. Dorsal profile

more pronounced than ventral. Dorsal profile barely convex from tip of snout to interorbital, then straight to nape; convex from nape to dorsal origin. Ventral profile nearly straight from tip of lower jaw to pelvic insertion; convex from insertion to anus. Jaws equal. Gape slightly oblique. Snout blunt. Maxillary reaching to vertical through anterior edge of eye in young, to vertical through anterior of pupil in large specimens. Teeth conic, strong, slightly recurved; outer row much enlarged. Vomerine teeth present in young; deciduous; lacking in adults. Palatines with a band of very small teeth in juveniles; smooth in adults. Interorbital region with bony ridges and arborescent patterning. Nostrils separated by a distance equal to diameter of posterior nostril. Lacrimal serrate; with 5-8 large serrations; serrations especially strong in young. Preoperculum serrate; serrations on angle strongest in juveniles; **adults** with angle serrations reduced, and serrations strongest on vertical edge. Lower opercular spine very long and strong; much longer than upper spine; extending distinctly beyond edge of opercular lobe. Posttemporal exposed; posterior edge with strong serrations. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal strongly arched, with a deep notch. First spine very short; fourth to sixth spine longest, those following decreasing in length to penultimate which is about half as long as ultimate. Longest dorsal spine much longer than long-

est dorsal ray. Soft dorsal emarginate. Anal spines short; second shorter than or equal to third. Longest anal spine much shorter than longest anal ray. Soft anal concave posteriorly. Pectorals assymetrically pointed; third or fourth ray longest. Pelvics pointed; second ray equal to or slightly longer than first; reaching to anus. Caudal emarginate.

Coloration: top of head dark from center of upper lip posteriorly; lighter on sides; whitish ventrally. Body coloration in juveniles consists of a series of disconnected spots; spots joining vertically and horizontally to give patterns of discontinuous stripes and bars. In adults body with three or four longitudinal downwardly curved stripes lacking vertical interconnections. First stripe running from in front of spinous dorsal to beginning of soft dorsal (may be divided into two slightly distinct stripes in some larger specimens); second, from occiput (quite wide anteriorly) to end of soft dorsal, reaching ventrally as far as lateral line; third, from anterior of posttemporal to middle of caudal fin; fourth (may be lacking), on abdomen from pectoral base to lower caudal peduncle. Spinous dorsal with white membranes; blackish border on upper two-thirds of membrane between third and sixth spines (lacking in specimens below 10 mm SL). Soft dorsal with first three membranes tipped with black, and fifth to seventh membranes black. Spinous anal clear. Soft anal yellowish. Caudal with a stripe on middle caudal rays that is a continuation of third body stripe. One stripe running obliquely across each caudal lobe. Tip of each

caudal lobe black. Pectorals and pelvics clear to yellowish.

Distribution: east coast of Africa from Port Alfred north, Mauritius, Madagascar, Seychelles, Comorros, Red Sea, Persian Gulf, northern shores of Indian Ocean, East Indies, Philippines, China, Japan, Australia (Western Australia north of Robe River, Northern Territory, Queensland, New South Wales [occasionally]), New Guinea, New Caledonia, New Hebrides, Fiji, and Samoa (Fig. 50). This is the only species of the family to cover the entire marine range for the family across the Indo-west Pacific (a minor gap along southern Australia); in addition it also moves considerable distances upstream in freshwater.

Ecology: as a consequence of its wide geographic range and abundance, various aspects of the biology of this species have been casually noted by different workers. However, few in-depth studies have been carried out in *T. jarbua*. Herald (1956) reported the construction of craters in the sand and establishment of territories by juveniles. He noted that the craters appeared to be juvenile characteristics and that they might serve to maintain position under tidal situations. More recently Schneider (1964) has studied the species behavior in greater detail and found that the species is gregarious between 2.0 and 5.0 cm SL, but established and defended territories at 9-15 cm SL. Acoustical signals produced by the the extrinsic swimbladder muscles play an important role in

this behavior and were found by Schneider to change both ontogenetically and in response to environmental variations.

Wallace (1975) showed that the reproduction of T. jarbua appears to be limited to a marine environment although the young and adults of this species are often found in freshwater. On the basis of literature information and stomach content analyses, this species appears to be primarily carnivorous; feeding on smaller fish and invertebrates. However, many of the examined individuals also had present in the stomach and intestinal tract masses of very large scales of various types. Comparisons of the scale sizes to the individuals from which they were removed showed that the original source would have been much larger than the specimens of T. jarbua and could not have been ingested whole. However, it is not possible to determine whether the scales were ingested during scavenging on larger dead individuals or whether T. jarbua has a partial lepidophagous food habit.

Remarks: in addition to utilizing the name Therapon or Therapon jarbua for this species, various workers have distinguished a separate eastern species Therapon servus based on Holocentrus servus described from Japan by Block. Jordan and Thompson (1912) suggested that the nominal forms T. servus and T. jarbua (described from the Arabian region by Forskal) represented distinct species separable on the basis of differences in morphometrics and meristics especially eye size and lateral line counts.

These authors considered I. servus to have a distribution around Japan, China and Australia, while I. jarbua was limited to the Indian Ocean. They also separated a third form from the East Indies, the Philippines and Samoa, though failing to define its affinities with the other forms. Their use of I. servus as a distinct species was followed by Ogilby and McCulloch (1916), McCulloch (1916), Whitley (1948) and Munro (1956) among others. However, examination of a series of specimens from throughout the family range along with literature information fails to reveal any discontinuities in any character which would serve to support the existence of two species. Consequently, there appears to be only one species, Terapon jarbua.

Specimens examined

Africa: French Somalia, Djibouti (AMNH 8174*, 1 spec., 152 mm); Changanu (USNM 72867*, 1 spec., 96 mm); Zanzibar (USNM 12640*, 2 spec., 45-90 mm); Madagascar (USNM 171062, 1 spec.).

Red Sea: (USNM 49328*, 2 spec., 98-107 mm); southern Sinai, Sharek el sheik (USNM uncat., VGS 69-32, 1 spec.).

Saudi Arabia, Damnan (USNM 147847, 1 spec.).

India: Travancore (USNM 149682, 1 spec.); Cochin (USNM 175354*, 1 spec., 85 mm).

Ceylon, Koddar Bay (USNM uncat., TI 70-331, 1 spec.).

Burma (USNM 89496, 1 spec.).

Thailand, Prachuab Kiri Khan (AMNH 52525*, 2 spec., 50-58 mm).

Sumatra (USNM 88030, 1 spec.).

Indonesia: Ceram (USNM uncat. VGS 74-3*, 1 spec., 175 mm);

Java, Djakarta (USNM 72666*, 1 spec., 107 mm); Java,

Sanarang (USNM 82101, 2 spec.); Pulau, Seribu (USNM uncat VGS

74-36, 2 spec.); Moluccas, Ambon (USNM uncat. VGS 74-22,

1 spec.; VGS 74-19, 2 spec.); Matnag Bay (USNM 184783*,

1 spec., 157 mm).

Philippines: Takao Island (USNM 72236*, 2 spec., 15-21 mm);

Zamboango (USNM 57933, 4 spec.); Mindanao, Cotabato (USNM

184781, 2 spec.)

China: Shanghai (USNM 130390, 1 spec.); Tsingtao (USNM 130360,

1 spec.); Hainan (USNM 87103, 1 spec.).

Japan: Kagoshima (USNM 75449, 1 spec.); Kobe Market (AMNH

13235*, 5 spec., 75-128 mm); RiuKiu (USNM 72011*, 1 spec.,

223 mm).

Samoa, Apia (USNM 52342*, 4 spec., 30-211 mm).

Fiji, Suva (USNM 66060*, 6 spec., 53-175 mm).

Australia, Western Australia: Fortescue River (AMNH 35622*,

1 spec., 141 mm); Yeeda Creek (AMNH 35623*, 1 spec.,

95 mm); Northwest Cape, Yardi Station (AMNH 35625*, 10

spec. (of 22), 110-131 mm.); Mandu Mandu (AMNH 35626*, 6

spec., 163-183 mm).

Australia, Northern Territory: Dinah Beach (AMNH 35624*, 6

spec., 59-81 mm.); Nightcliff (USNM 173656*, 1 spec.,

75 mm); Little Lagoon (USNM 173659*, 5 spec. (of 13),

25-61 mm); Yirrkalla (USNM 173662, 4 spec., 51-96 mm).

Australia, Queensland, One Tree Island (USNM uncat., VGS

66-9, 1 spec.

New Guinea: Trobriand Islands (USNM uncat. BBC 1512, 3 spec.);

Murnass River, 25 mi. north of Madang (USNM uncat. BBC
1485, 1 spec.).

Therapon theraps (Cuvier and Valenciennes, 1829)

Banded grunter

Figs. 450 and 51

Therapon theraps Cuvier and Valenciennes, 1829, p. 129, pl.

53 (original description, Java, Mahé). (*). Duncher and Mohr, 1931, p. 64, fig. (New Guinea), New Pomerania). Weber and deBeaufort, 1931, p. 145, figs. 1-4 (East Indies). Hardenberg, 1931, p. 128 (Sumatra, Rokan River). Herre, 1932, p. 2 (Borneo); 1934, p. 53 (Bauang Sur). Hardenberg, 1934, p. 224 (sonic muscle); 1936, p. 246 (Kapuas River, Borneo). Herre, 1940, p. 14 (India, Mergui Peninsula). Blegvad, 1944, p. 86, fig. 46 (Iranian Gulf). Smith, 1949, p. 183 (Zululand), Koumans, 1953, p. 224 (Red Sea, Menado, Bangao, Mindanao). Munro, 1955, p. 116 (Ceylon). Tortonese, 1957, p. 124 (Eritrea). Fourmanoir, 1957, p. 88 (Mozambique Channel). Okada, 1959, p. 75 (Okinawa). Khalaf, 1961, p. 77 (Iraq). Kamohara, 1962, p. 34 (Japan). Chien, 1962, p. 540, fig. 446 (Hainan). Stebbins and Kalb, 1963, (Inhaca Mozambique). Schneider, 1964, p. 167 (extrinsic swimbladder muscle). Tortonese, 1964, p. 44 (New Guinea: Baia Lina, Goodenough Island). Marshall, 1964, p. 167 (north Queensland). Zvjagina, 1965, p. 162 (development). Vien, 1968, p. 817 (biology). Chan, 1968, p. 64, pl. 33 (Hong Kong). Lindberg and Krasnyukova, 1969, p. 118, fig. 162 (distribution). Grant, 1972, p. 222 (Queensland).

FAO, 1974, TT2, fig. (fisheries, distribution). Johnson, 1975, p. 12 (procurrent spur).

Therapon obscurus Cuvier and Valenciennes, 1829, p. 135

(original description, Seas of the Indies). Cantor, 1849, p. 1002 (Pinang). Günther, 1859, p. 275 (copied). Meyer, 1885, p. 13 (north Celebes).

Therapon squalidus Cuvier and Valenciennes, 1829, p. 136

(original description, Indian Ocean, Seas of the Indies). Gunther, 1859, p. 275 (copied).

Therapon cinereus Cuvier and Valenciennes, 1829, p. 138

(original description, Seas of the Indies).

Datnia virgata Cuvier and Valenciennes, 1831, p. 480 (original description, Bengal, Bay).

Therapon rubricatus Richardson, 1842, p. 127 (original description, northwest coast of Australia).

Therapon virgatus: Günther, 1859, p. 276 (Copied from Cuvier and Valenciennes, 1831).

Perca argentea: Günther, 1859, p. 277 (India, name in text).

Therapon (Datnia) theraps: Bleeker, 1873-76, p. 113 (East Indies, Philippines). Schmeltz, 1869, p. 13 (Indian Ocean); 1874, p. 23 (China Sea). Pöhl, 1884, p. 27 (China Sea), p. 44 (Zanzibar).

Therapon nigripinnis Macleay, p. 366 (original description, Rockingham Bay).

Therapon theraps: Jordan and Seale, 1906, p. 24 (Iloilo, Philippines). Evermann and Seale, 1906, p. 83 (Bulan, Bacon).

Seale and Bean, 1907, p. 243 (Zamboango, Philippines).
 Fowler, 1931, p. 337 (Burias, Luzon, Borneo, Red Sea,
 China, Java, Sumatra); 1939, p. 390 (Sumatra). Taylor,
 1964, p. 183 (Arnhem Land). Chen, 1969, p. 401 (Taiwan)
 Ch'en, 1973, p. 19 (Taiwan).

Eutherapon theraps: Whitley, 1943, p. 168 (no locality).

Munro, 1956, p. 171 (Papua, D'Entrecasteaux Islands);
 1967, p. 322 (New Guinea).

(*). further references to this species under this name can
 be found in Fowler, 1931, p. 337 for the years between
 the original description and 1930.

Nomeclature: the trivial name, theraps, from the Greek
 for servant refers, as does the family name, to the utilization
 of members of this family as food fish by poorer segments
 of the population in many areas.

Diagnosis: a member of the genus Terapon distinguishable
 from the other species of the genus in having 47-56 lateral
 line scales and 6-8 supralateral scales (in contrast to
 more than 70 lateral line scales and 10-17 supralateral
 scales for I. jarbua and I. puta).

Description: Dorsal spines XI-XII; Dorsal rays 9-11; Anal
 III, 8-9; Pect. 14-15; Pel. I-5; 47-55 lateral line scales;
 4-5 scales on caudal; 6-8 scales above lateral line; 14-16

scales below lateral line; 12-15 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal fin, upper row consisting of larger scales, lower row irregular and scales smaller, sheath extending to between seventh and last dorsal ray; 1-2 rows of scales in sheath at base of anal fin, sheath extending across base of whole fin; cheek scales in 5-6 rows; gill rakers on first arch 6-8+1+14-16; vertebrae 10+15.

Reaching 250 mm SL; depth 2.5-3.5 in SL; distance from dorsal origin to snout 2.4-3.0 in SL; head length 2.8-3.5 in SL; length of base of dorsal fin 1.8-2.0 in SL; snout length 3.1-3.8 in HL; eye width 3.5-4.7 in HL; jaw length 3.0-3.4 in HL; length of longest dorsal spine 1.6-2.4 in HL; length of longest dorsal ray 2.2-2.5 in HL; length of longest anal spine 2.2-2.6 in HL; length of longest anal ray 1.8-2.1 in HL.

Body moderately deep, compressed. Dorsal and ventral profiles about evenly pronounced. Dorsal profile nearly straight from snout to dorsal origin in juveniles; profile slightly convex above eye in adults. Ventral profile evenly convex from tip of jaw to pelvic insertion; less convex from insertion to anus. Jaws equal. Gape oblique. Maxillary reaching to vertical through anterior edge of eye in young falling short with age. Teeth strong; conic; outer row enlarged; followed by a band of smaller teeth in each jaw. No teeth on vomer or palatines. Interorbital region with aborescent ridges. Nostrils separated by a distance equal to diameter of posterior nostril. Lacrimal strongly serrate. Preoperculum serrate; serrations larger on

on angle, especially in adults. Lower opercular spine very long and strong; extending distinctly beyond edge of opercular lobe. Cleithrum exposed; strongly serrate along posterior edge; scales on side, Posttemporal exposed; serrate along posterior edge. Supracleithrum exposed.

Spinous dorsal strongly arched; notched; spines strong. First dorsal spine very short; third to fifth spines longest, those following decreasing in length to penultimate which is half length of ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal emarginate. Anal spines short; third longest but shorter than longest anal rays. Soft anal angular with straight or emarginate border. Pectorals assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest; slightly filamentous; reaching to anus in young, falling short with age. and reaching only two-thirds of the distance Caudal emarginate.

Coloration: very small individuals with head uniformly dusky. In adults, head dark above, lighter below. Adults with a stripe running from snout to opercle and another under eye. Body with both vertical bars and horizontal stripes in young. Bars more prominent in younger individuals. Specimens at 10-15 mm SL with six dark vertical bars. First running down nape to opercle; second and third, under spinous dorsal; fourth, under soft dorsal; fifth and sixth, on caudal peduncle. In addition to bars there are also faint indications of stripes. By 25 mm SL both the stripes and bars are distinct with the unpigmented areas forming a checkerboard pattern. By 45 mm SL the bars have faded and the horizontal pattern dominates.

In adults body is dusky above, silvery below with four horizontal stripes. First stripe running under spinous dorsal to last dorsal spine; second, starts as a very wide region on nape and runs posterior as a narrow band to terminate at last few dorsal rays; third, from snout to upper caudal peduncle; fourth(may be lacking), from base of pectoral fin to middle of caudal fin base, continuing on fin as a stripe on median rays. Spinous dorsal uniformly dark in smaller juveniles; clear with a black blotch on upper membrane between third and seventh spines in adults. Soft dorsal with dark band along upper portion of rays and a horizontal band on posterior rays. Spinous anal clear. Soft anal with two dark blotches across upper and lower caudal lobes. Pectorals clear. Pelvics slightly dusky.

Distribution: east coast of Africa, Zanzibar, Red Sea, Seychelles, Madagascar, shores of India and Bay of Bengal, Ceylon, Andaman Islands, Thailand, Singapore, Sumatra, Borneo, East Indies, New Guinea, Philippines, China, Australia (Northern Territory, Queensland north of Burnett River), Torres Strait.(Fig. 52)

The coloration changes that occur ontogenetically in this species have been illustrated by Weber (1913), Weber and de-Beaufort (1931), Zvjagina (1963), and Duncker and Mohr (1931) (for caudal only). In addition Zvjagina has extensively studied and illustrated the development of this species from the egg to the adult.

Specimens examined

Africa, Kenya, Formosa Bay (USNM uncat. SOSC no. 270*, 1 spec., 87 mm).

Indonesia, Bali (AMNH 14816*, 10 spec., 50-73 mm).

Borneo: (USNM 114779*, 1 spec., 84 mm); Sandakan Bay (USNM 146359*, 1 spec., 79 mm).

Thailand, Prachuab Kiri Khan (AMNH 32526*, 2 spec., 129-139 mm).

Taiwan, Yeh, Liu (USNM uncat. Acc. 286561*, 2 spec., 27-36 mm).

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Therapon puta (Cuvier and Valenciennes, 1829)

Spiney Cheeked grunter

Fig. 53

Coilus trivittatus -Hamilton, 1822, pp. 92, 370

(Ganges mouth).

Therapon puta Cuvier and Valenciennes, 1829, p. 131 (original description, Pondicherry, Mahé). (*). Weber and deBeaufort, 1931, p. 143 (East Indies). Herre, 1933, p. 12 (Madang, New Guinea); 1933, p. 3 (north Borneo). Job, 1940, p. 296 (feeding habits). Koumans, 1947, p. 310 (Port Dickson, Malaya). Munro, 1955, p. 116 (Ceylon). Marshall, 1964, p. 167 (north Queensland). Rajan, 1968, p. 529 (feeding). Kaliyamurthy and Rao, 1972, p. 199 (feeding).

Therapon ghebul Cuvier and Valenciennes, 1829, p. 133

(original description, Red Sea). Günther, 1859, p. 281

(copied). Klunzinger, 1870, p. 708 (Kosier, Red Sea).

Therapon trivittatus Cantor, 1849, p. 1001 (original description, Sea of Penang, Singapore, Malayan Peninsula). (*).

Therapon (Datnia) trivittatus: Bleeker, 1876-77, pl. 62 (340).

fig. 2. (on Cantor).

Therapon (Datnia) puta: Bleeker, 1873-76, p. 112 (Singapore, Bintang, Banka, Java, Celebes).

Authistes argenteus DeVis, 1885, p. 398 (original description, Queensland coast).

Therapon puta: Jordan and Seale, 1906, p. 24 (Manila, Cavite).

Evermann and Seale, 1906, p. 83 (Bulan, Bacon, San Fabian). Fowler, 1931, p. 329 (Philippines, Java, India); 1934, p. 416; Taylor, 1964, p. 183 (no locality).

Authistes puta: Whitley, 1943, p. 181 (no locality). Munro, 1956, p. 170 (Tami Island); 1967, p. 322 (New Guinea). Haedrick, 1971, p. 167 (pons moultoni). Grant, 1972, p. 167 (north Queensland).

(*)further references to this species under this name for the years between the original description and 1930 can be found in Fowler, 1932, pp. 328-329.

Nomenclature: the trivial name for this species, puta, is derived from its native name, Keel-puta at Vizagapatam.

Diagnosis: I. puta can be distinguished from the other members of the genus by its body pattern of straight longitudinal stripes (in contrast to the downwardly curved stripes of I. jarbua and its high lateral line count of 70-85 (in contrast to 47-56 for I. theraps).

Description: Dorsal spines XI-XII; Dorsal rays 9-11; Anal III, 8-9; Pect. 13-15; Pel. I-5; 70-85 latera line scales; 85-95 scales counted in a series above lateral line; 4-8 scales on caudal; 10-13 scales above lateral line; 22-24 scales below lateral line; 16-20 predorsal scales to occiput; 2 rows of scales

in sheath at base of dorsal fin, upper scales larger and regular, lower row of scales smaller and irregular, sheath extending to third to sixth dorsal spine; 2 rows of scales in sheath at base of anal fin, sheath extending to fifth anal ray; cheek scales in 5-7 rows; gill rakers on first arch 7-9+1+18-24; vertebrae 10+15.

Reaching 130 mm SL; depth 3.0-4.0 in SL; distance from dorsal origin to snout 2.5-2.9 in SL; head length 2.9-3.6 in SL; length of base of dorsal 1.7-2.0 in SL; snout length 2.9-4.0 in HL; eye width 3.0-4.3 in HL; jaw length 3.1- 3.75 in HL; length of longest dorsal spine 1.45-1.6 in HL; length of longest dorsal ray 1.8-2.1 in HL; longest anal spine 2.1-2.5 in HL; longest anal ray 1.75-2.0 in HL.

Body elongate, moderately deep, compressed. Dorsal and ventral profiles about equally pronounced. Dorsal profile slightly convex from snout to nape, then straight to dorsal origin. Ventral profile straight or only slightly convex from lip to pelvic insertion, then gently convex to anus. Jaws equal. Gape horizontal. Maxillary reaching to vertical through posterior nostril. Teeth strong, outer row enlarged; inner teeth in bands, villiform. No teeth on vomer or palatines. Interorbital with distinct ridges. Nostrils distant, separated by a distance twice diameter of posterior nostril. Lacrimal strongly serrate, moreso in young. Preoperculum serrate, spines on angle very large. Lower opercular spine strong and very long, ex-

tending beyond edge of opercular lobe. Cleithrum exposed; serrate posteriorly; scales on side. Posttemporal exposed; strongly serrate along posterior edge. Supracleithrum exposed; slightly serrate posteriorly in some larger specimens.

Spinous dorsal strongly arched, deeply notched; first and second spines short; fifth or sixth spine longest; those following decreasing in length to penultimate which is one-half length of ultimate or less. Longest dorsal spines as long as or longer than longest (first) dorsal ray. Soft anal with a straight or emarginate posterior edge. Anal spines short; shorter than longest anal rays. Third anal spine longest. Soft anal with an emarginate margin. Pectoral assymmetrically pointed; third or fourth ray longest. Pelvic pointed; first ray longest; slightly filamentous, reaching to anus in young, falling short with age. Caudal emarginate.

Coloration: in young a median stripe runs from snout to interorbital where it divides in two. A stripe runs from snout to front of eye and from rear of orbit to lower opercular spine. Head darker above in adults, slightly obscuring stripes. Body greyish or brownish above with three or four straight longitudinal stripes. First running from nape to end of spinous dorsal; second, (a continuation of head stripe running above eye) to dorsal edge of caudal peduncle; third stripe to middle of caudal peduncle, continuing onto fin as median stripe; fourth (not always present), from pectoral to lower edge of

caudal peduncle. Dorsal clear or white with blackish blotch along upper edge between third or fourth and seventh or eighth spines. Soft dorsal with black blotch along top of anterior rays. Spinous and soft anal clear. Caudal with an oblique bar across upper lobe and blotch on tip; stripe on middle caudal rays continuing from body stripe; one or two bars running obliquely across lower caudal lobes. Pectoral and pelvics clear. Young with six or seven vertical bars.

Distribution: a marine species, penetrating into fresh water from the east coast of Africa north of Zanzibar, Red Sea, Arabia, Persian Gulf, Madagascar, India, Ceylon, Java, Singapore, Borneo, Philippines, New Guinea, southeast Asia, Australia (Queensland) and Torres Strait (Fig. 54).

Specimens examined

Persian Gulf: (AMNH 18383*, 1 spec., 88 mm); (USNM 147870*, 5 spec. (of 20), 70-80mm.).

Ceylon: Mullaittivu (USNM uncat. PCH 69-21*, 1 spec., 129 mm); Lunawa (USNM uncat. CCK 69-12*, 3 spec., 88-97 mm); Mannar, fish market (USNM uncat. CCK 69-21B*, 1 spec, 80 mm); Pitipana Fishery Station, Lagoon (USNM uncat. TI 70-313*, 2 spec., 57-63 mm).

Indoneasia, Java (USNM 72265*, 20 spec., 87-96 mm);

Philippines: Luzon (USNM 56274*, 20 spec., 36-54 mm); Iloilo (USNM 72250*, 1 spec., 82 mm; USNM 10297*, 10 spec. (of 40), 39-53 mm).

Genus 8, Pelsartia

Pelsartia Whitley, 1943, p. 183 (type species Therapon humeralis Ogilby, by original designation).

Nomenclature: the generic name, Pelsartia, refers to Pelsarts Island in the Houtmans Abrolhos group, Western Australia, the type locality of the type species of the genus, Pelsartia humeralis.

Diagnosis: marine teraponids having a dorsal sheath of 2 rows of fully sized scales, an exposed posttemporal and vertical bars having a wide dorsal section above a narrow ventral section. Juveniles with several series of small spots forming horizontal patterns along dorsal body surface.

Included species: one species, P. humeralis, is placed in the genus.

Pelsartia humeralis (Ogilby, 1899)

Fig. 55

Therapon humeralis Ogilby, 1899, p. 177 (original description Houtman's Abrolhos, Western Australia). Ogilby and McCulloch, 1916, p. 114 (after Ogilby, 1899). Glover, 1968, p. 792, fig. 1 (South Australia, Streaky Bay).

Terapon humeralis: Waite, 1905, p. 62, pl. 9 (Houtman's Abrolhos). Fowler, 1931, p. 344 (after Ogilby and McCulloch, 1916).

Pelsartia humeralis: Whitley, 1943, p. 183 (coast of Western Australia).

Nomenclature: the trivial name, humeralis, from the Latin humerus, shoulder, refers to the prominent "shoulder" spot in this species.

Diagnosis: characters as for the genus.

Description: Dorsal spines XII-XIII; Dorsal rays 11; Anal III, 10; Pect. 14-15; Pel. 1-5; 80-90 lateral line scales; 7 scales on caudal; 13-15 scales above lateral line; 25-26 scales below lateral line; 14 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal fin, sheath extending to third dorsal ray; 3-4 rows of scales in sheath at base of anal fin, sheath extending to third or fourth anal ray, cheek

scales in 8-9 rows; gill rakers on first arch 5-6+1+12-14; vertebrae 10+15.

Reaching 190 mm SL; depth 2.8-2.95 in SL; distance from origin of spinous dorsal to snout 2.6-2.7 in SL; head length 3.2-3.3 in SL; length of base of dorsal fin 1.8-1.9 in SL; snout length 3.0-3.1 in HL; eye width 3.6-4.3 in HL; jaw length 2.9-3.0 in HL; length of longest dorsal spine 1.5-1.8 in HL; length of longest dorsal ray 1.8-2.0 in HL; length of longest anal spine 2.0-2.3 in HL; length of longest anal ray 1.5-1.8 in HL.

Body compressed, moderately deep. Dorsal profile about as pronounced as ventral. Dorsal profile in juveniles nearly straight from snout to origin of dorsal fin. Dorsal profile in adults distinctly convex from snout to nape, then straight to dorsal origin. Ventral profile convex from lower lip to to anus, moreso in adults. Jaws equal. Gape oblique. Snout blunt in adults; more elongate in juveniles. Maxillary reaching barely to vertical through anterior edge of eye in young, falling short with age. A band of villiform teeth in each jaw, outer row distinctly larger. No teeth on vomer or palatines. Nostrils distant; separated by a distance equal to two-thirds of eye diameter. Lacrimal serrate. Preoperculum serrate; larger serrations along horizontal edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal exposed; serrate along posterior edge.

Cleithrum exposed; serrate posteriorly; scales on side, less evident in adults.

Spinous dorsal arched; fifth spine longest, those following decreasing in length to penultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal rounded. Second anal spine longest, shorter than longest anal rays. Soft anal rounded. Pectoral assymetrically pointed; fourth ray longest. Pelvic pointed; first ray longest; slightly filamentous, reaching to anus in young, falling short with age. Caudal emarginate.

Coloration: head dark above, lighter below. Dark band running from jaw across cheek. Another band running from snout to anterior of eye and from rear of orbit to opercle. Young with spots on top and sides of head. Body in young with four or five dark crossbars that are darker and broader above a horizontal line between cleithral serrations and middle of caudal peduncle. Crossbars lighter and narrower below this line. The young also have three longitudinal series of small spots on body. First running along base of dorsal fin; second from nape to top of caudal peduncle; third, from cleithrum to middle of caudal peduncle. In addition random spots of equal size are found over body. In adults longitudinal and random series of spots lacking. Ventral region of vertical crossbars lacking or very light. A longitudinal band is found along base of dorsal fin. The dorsal section of the upper part of vertical bars is lacking and very light, while ventral section of upper portion of bars are darker and elongated horizontally.

Spinous dorsal with spots. Spinous anal clear. Soft anal with dark spots distally. Caudal with random dark spots. Pelvics and pectorals clear.

Distribution: found in the marine waters of western and southern Australia from Houtman's Abrolhos in the west to Kangaroo Island in the east (Fig. 56). Over the majority of its range, it is the only member of the family.

Ecology: little is known about the life history of this species. It appears to be a common resident of weed beds in Western Australia (B. Hutchins, per. comm).

Specimens examined

Australia, Western Australia, Two Peoples Bay (AMNH 35635*,
1 spec., 95 mm).

Australia, South Australia, Kangaroo Island (USNM 177011*,
1 spec., 180 mm).

Genus 9, Rhyncopelates

Rhyncopelates Fowler, 1931, p. 363 (type species Therapon oxyrhynchus, Temminck and Schlegel, by original designation [proposed as a subgenus]).

Nomenclature: the generic name Rhyncopelates, from the Greek, rhynchos, snout and Pelates a genus of teraponids, refers to the elongate snout of the type species.

Diagnosis: marine teraponids having an elongate snout and a pigmentation pattern of alternating continuous and interrupted longitudinal stripes, a pattern unique to the genus in the family. Extrinsic swimbladder muscle in the adults having a very wide attachment across rear of skull.

Included species; only one species, R. oxyrhynchus, a marine species from the Philippines, China and Japan that also enters into freshwaters is placed in the genus.

Rhyncopelates oxyrhynchus (Temminck and Schlegel, 1842)

Blotched grunter

Fig. 57

Therapon oxyrhynchus Temminck and Schlegel, 1842, p. 16, pl.

16, fig. 3 (bays of southern Japan). Richardson, 1846, p. 239 (China and Japan). Bleeker, 1857-8, p. 2 (Kioesio). Günther, 1859, p. 281 (Japan, China). Karoli, 1881, p. 153 (Hakuri, Japan). Günther, 1883, p. 341 (Ovalau, Fiji Islands, probable error). Steindachner and Döderlein, 1884, p. 10 (Tokyo). Meyer, 1885, p. 13 (Manado, Celebes). Rutter, 1897, p. 75 (Swatow, China). Ishikawa and Matsuura, 1897, p. 55. Jordan and Snyder, 1900, p. 355 (Tokyo); 1901, p. 78 (Nagasaki, Yokohama, Shimodo). Smith and Pope, 1907, p. 475 (Kochi, Matsushima Bay). Franz, 1910, p. 46, pl. 5, fig. 31 (Yokohama). Jordan and Thompson, 1912, p. 538 (Japan and China). Izuka and Matsuura, 1920, p. 150 (Tsu, Ise). Weber and deBeaufort, 1931, p. 159 (cite Meyer, 1885). Uchida, 1934 (sonic ability). Suyehiro, 1942, p. 173 (intestinal patterns). Boseman, 1947, p. 34 (designation of type). Kuroda, 1951, p. 336 (Hokkaido, Bosiu, Tokyo Bay, Sagami Bay, Suguru Bay, Kii, Shikoku, Kiusoa). Honma, 1952, p. 145 (Japan, Echigo). Okada, 1959, p. 57 (Okinawa). Chien, 1962, p. 539, fig. 445 (Hainan region). Okada, 1966, p. 231, fig. 214 (Japan; sound production). Kamohara, 1967, p. 33, pl. 33, fig. 5 (Japan). Kananabe,

et al. 1968, p. 45 (gut contents, ecology). Kikuchi, 1968, p. 163 (Amakusa Bay, Japan). Chan, 1968, p. 62, pl. 31 (Hong Kong). Lindberg and Krasnyukova, 1969, p. 120, fig. 164 (Japan). Chan, 1969, p. 401 (Taiwan).

Therapon oxirhynchus: Elera, 1895, p. 472 (Luzon, Cavite).

Pelates oxyrhynchus: Fowler, 1928, p. 213 (compiled); 1931, p. 363 (Japan). FAO, 1974, TPI (fisheries, distribution).

Nomenclature: the trivial name oxyrhynchus, from the Greek, oxys, sharp or pointed and rhynchos, snout, refers to the elongate snout in the species. The original description of this species was based on a series of specimens from Japan. Boeseman (1947) selected Temminck and Schlegel specimen no. 95 located in the Rijksmuseum (RMNH) as the type of the species.

Diagnosis: characters as for the genus.

Description: Dorsal spines XII; Dorsal rays 9-11; Anal III, 7-9; Pect. 13-14; Pel. I-5; 60-80 lateral line scales; 5-7 scales on caudal; 10-11 scales above lateral line; 20-24 scales below lateral line; 16-18 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal fin, sheath extending to fourth or fifth dorsal ray; 3-4 rows of scales in sheath at base of anal fin, sheath extending to third or fourth anal ray; cheek scales in 7-8 rows; gill rakers on first arch 7-8+1+14-16; vertebrae 10+15.

Reaching 300 mm SL; depth 2.6-3.2 in SL; distance from dorsal origin to snout 2.2-2.6 in SL; head length 2.6-3.1 in SL; length of base of dorsal fin 1.7-2.0 in SL; snout length 2.5-3.3 in HL; eye width 3.5-5.0 in HL; jaw length 3.1-3.5 in HL; length of longest dorsal spine 2.2-2.8 in HL; length of longest dorsal ray 2.2-2.7 in HL; length of longest anal spine 2.0-2.9 in HL; length of longest anal ray 2.0-2.6 in HL.

Body moderately deep. more compressed in young. Dorsal profile more pronounced than ventral. Dorsal profile straight to slightly convex between snout and dorsal origin. Ventral profile slightly curved to pelvic insertion, then straight to anus. Jaws equal. Gape slightly oblique. Snout elongate. Maxillary reaching just beyond vertical through posterior nostril in juveniles; falling short with age and reaching to vertical drawn between nostrils. Teeth villiform, in bands, outer row much enlarged. No teeth on vomer or palatines. Interorbital region with boney ridges. Nostrils separated by a distance equal to diameter of posterior nostril; posterior nostril distant from eye. Lacrimal serrate. Lower opercular spine strong and long; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate posteriorly; scales on side. Post-temporal exposed serrate along posterior edge. Supracleithrum exposed.

Spinous dorsal arched; first spine short, third to sixth spines longest, those following decreasing in length to pen-

ultimate which is same length as ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal rounded. Second anal spine longest; shorter than longest anal rays. Soft anal rounded. Pectorals assymetrically pointed; fourth longest. Pelvics pointed; first ray longest; reaching to anus in young, falling short with age and reaching only one-half distance to anus. Caudal slightly emarginate.

Head darker above, light below. A median stripe runs from tip of snout to interorbital region where it divides into two bands which are continuous with body stripes. Other head stripes run from edge of snout underneath nostrils to upper anterior border of eye and from back of orbit across opercle. Body with four distinct stripes that vary somewhat in intensity and have a blotchy appearance. First stripe runs from posterior continuation of interorbital stripes to anterior of soft dorsal; second, from above eye to posterior of soft dorsal, continuing onto fin; third, from back of orbit to middle of caudal base; fourth from pectoral base to ventral of caudal peduncle. In addition there are two irregular bands, more prominent in adults, running between the first and second and third and fourth body stripes. These are thinner and less pigmented.

Spinous dorsal dusky basally, with a broad dusky margin. Soft dorsal with a basal band anteriorly and a continuation of second body stripe running horizontally along posterior rays.

Spinous anal clear. Soft anal with basal blotch and two horizontal stripes which are more developed in very large individuals. Caudal clear in young, with several narrow parallel stripes on each lobe in adults. Pectorals and pelvics clear to light brown.

Distribution: this species is very common in the waters of southern and eastern China, Taiwan and southern Japan (Fig. 58). The species was also reported from the Philippines (Elera, 1895). The only other indication of its presence in that region is a single specimen (USNM 183722) examined in the course of this study with a locality of the "Philippines". It therefore appears likely that the species is rare in the region with the reported specimens probably strays. Meyer (1895) also lists the species from the Celebes without further elaboration. Such a range extension is unsupported by any other collections and as such is suspect. Similarly it appears that Günther's citations (1883) of the species from Ovavilau, Fiji a locality distant from the known range of the species is also in error. Finally Fowler (1928) lists the species from India without any indication of the source of his information.

Remarks: Fowler (1928) placed Rhyncopelates oxyrhynchus in the genus Pelates along with the species P. quadrilineatus

and *P. sexlineatus*, defining the genus (1931) as being characterized by triserial upper and biserial lower teeth. However, *T. oxyrhynchus* fails to conform to this definition as it has wide tooth bands in each jaw as noted by Fowler (1931) who stated "teeth in bands... of 6 or 7 irregular series." Furthermore *R. oxyrhynchus* has a series of derived posttemporal, tabular and extrinsic swimbladder muscle character states falsifying a hypothesis of a closer relationship of the species to the genus *Pelates*.

Specimens examined

Philippines: USNM 182722*, 1 spec., 192 mm).

Japan: Kyoto Fish Institute (AMNH 34774*, 1 spec., 220 mm);

Toba Fish Market (AMNH 13147*, 1 spec., 201 mm); Mikawa bay (USNM 15253*, 1 spec, 71 mm; USNM 57733*, 2 spec., 143-150 mm); Satsuma, Akune Station (USNM 71178, 9 spec., 35-60mm); Shimizu (USNM 71179*, 2 spec., 110-125 mm); Kagoshima (USNM 71300, 2 spec.); Nagasaki (USNM 75451, 2 spec.); Miyazaki (USNM 82140*, 1 spec., 59 mm).

Genus 10, Mesopristes

Mesopristes Bleeker, 1845, p. 523 (type species, M. macracanthus [= Datnia argentea, Cuvier and Valenciennes], by original designation).

Nomenclature: the generic name is of unknown significance with respect to the species of the genus.

Diagnosis: marine teraponids that also enter into fresh water, distinguished by their very long dorsal and anal spines, with the second anal spine nearly as long as to longer than longest anal rays. Rear edge of supraoccipital bowed posteriorly. Head turned ventrally. Dorsal profile much more pronounced than ventral.

Included species: four species are included in the genus Mesopristes. Two, M. argenteus and M. cancellatus have large distributions through the East Indies and New Guinea region, while M. kneri is endemic to Fiji and M. elongatus to Madagascar.

Remarks: as discussed by Fowler (1931) the original generic name applied to the species of this genus (Datnia, Cuvier and Valenciennes, 1929, p. 138) is properly applied by tautonymy to Coius datnia Hamilton, a sparoid.

Mesopristes argenteus (Cuvier and Valenciennes, 1829)

Silver grunter

Figs. 59 and 60

Datnia argentea Cuvier and Valenciennes, 1829, p. 139, pl.

154 (original description, Java). Day, 1878, p. 71 pl.

18, fig. 7 (India?). Duncker and Mohr, 1931, p. 64.

(East Indies).

Mesopristes macracanthus Bleeker, 1845, p. 523 (original description, Java, Batavia).Datnia cancellatoides Bleeker, 1853, p. 247 (original description, Priaman, Sumatra, Amboina).

Therapon argenteus: Günther, 1859, p. 283 (Amboina). Martens, 1876, p. 386 (Luzon, Manila). Bleeker, 1873-76, pl. 326, fig. 1 (East Indies). Meyer, 1885, p. 13 (Laguna de Bay, Luzon). Gorgoza, 1888, p. 284 (Pascao). Day, 1889, p. 507 (India?). Weber, 1894, p. 407 (Amparang River, Celebes); 1913, p. 582 (Sermowai River). deBeaufort, 1913, p. 118 (west Ceram). Fowler, 1928, p. 212 (compiled). Herre and Mendoza, 1929, p. 495 (Philippines). Weber and deBeaufort, 1931, p. 150 (Philippines, East Indies). Herre, 1931, p. 121 (New Hebrides); 1936, p. 194 (freshwater, Fiji?); 1953, p. 428 (synonymy). Marshall, 1964, p. 167 (north Queensland). Mees, 1971, p. 249.

Therapon (Datnia) argenteus: Bleeker, 1873, p. 382 (East Indies) 1873-76, p. 114, pl. 339, fig. 4 (Java, Sumatra Amboina).

Ogilby and McCulloch, 1916, p. 115 (Port Moresby, Normanby Island, New Hebrides, Queensland).

Therapon nasutus Macleay, 1884, p. 258 (original description, freshwater on Normaby Island).

Therapon chalybeus Macleay, 1884, p. 259 (original description, Normanby Island).

Therapon acutirostris DeVis, 1884, p. 398 (original description, Queensland).

Terapon argenteus: Fowler, 1931, p. 347 (Philippines); 1931b, p. 24 (no locality); 1934, p. 446 (Normanby Island, Port Moresby, Teterri, Guadalcanal. Solomon Islands, New Hebrides); 1959, p. 255 (Fiji?).

Mesopristes argenteus: Whitley, 1943, p. 181 (no locality). Munro, 1956, p. 170 (Ring Ring, Bag Bag, Jacquinot Bay, New Guinea). Whitley, 1960, p. 76 (Queensland). Munro, 1967, p. 324 (New Guinea). Lake, 1971, p. 34 (Queensland). Bayly, 1975, p. 58 (estuaries of Northern Territory and Queensland).

Nomenclature: the trivial name, argenteus, from the Latin for silver, refers to the silvery overall coloration of the adults.

Diagnosis: distinguishable from the other members of the genus Mesopristes in having 6-8 scales above the lateral line (in contrast to 9-11 in M. elongatus, and M. kneri) and 8-9 cheek and 10-12 caudal scales (in contrast to 4-5 cheek and

5-6 caudal in M. cancellatus).

Description: Dorsal spines XII; Dorsal rays 10-11; Anal III, 8-9; Pect. 12-14; Pel. I-5; 52-58 lateral line scales; 10-12 scales on caudal; 6-8 scales above lateral line; 18-21 scales below lateral line; 13-16 predorsal scales to occiput; 3 rows of scales in sheath at base of dorsal fin, sheath extending to fifth or sixth dorsal ray; 4 rows of scales in sheath at base of anal fin, sheath extending across base of all rays; cheek scales in 8-9 rows; gill rakers on first arch 7-9+1+15-17; vertebrae 10+15.

Reaching 275 mm SL; depth 2.4-2.8 in SL; distance from dorsal origin to snout 2.15 to 2.4 in SL; head length 2.4-3.1 in SL; length of base of dorsal 1.7-2.0 in SL; snout length 2.5-3.2 in HL; eye width 3.3-4.3 in HL; jaw length 3.1-3.6 in HL; length of longest dorsal spine 1.4-1.9 in HL; length of longest dorsal ray 1.6-2.0 in HL; length of longest anal spine 1.4-1.9 in HL; length of longest anal ray 1.5-1.6 in HL.

Body moderately deep, distinctly compressed. Head turned ventrally anteriorly. Dorsal profile straight from snout to dorsal origin in young; in adults straight to nape, then convex to dorsal origin. Ventral profile straight from tip of lower jaw to anus; nearly horizontal, especially in adults. Upper jaw longer. Gape nearly horizontal. Lips fleshy, more so the upper. Snout elongate. Maxillary reach-

ing to vertical through anterior edge of eye; falling short with age, reaching only to vertical through posterior nostril. Teeth in bands, villiform, outer row distinctly enlarged. No teeth on vomer or palatines. Nostrils separated by a distance equal to one and one-half diameters of posterior nostril. Interorbital region with ridges, stronger in adults. Lacrimal serrate. Preoperculum serrate; serrations larger on angle and posterior edge. Lower opercular spine stronger and longer; not extending beyond opercular lobe. Posttemporal exposed; serrate along posterior edge. Cleithrum exposed; serrate along posterior edge; scales on side. Supracleithrum exposed.

Spinous dorsal strongly arched; first spine very short; fourth or fifth spine longest, those following decreasing in length to penultimate which is subequal to ultimate. Longest dorsal spine longer than longest dorsal ray. Second and third anal spines very long and strong; second longest, about twice length of first, as long as or slightly longer than longest anal ray. Soft anal angular, posterior edge concave. Pectorals pointed; fifth ray longest. Pelvics pointed; first ray longest, filamentous; reaching to anus. Caudal slightly emarginate.

Coloration: young with a brown middorsal stripe running from snout to interorbital where it divides in two. Additional head stripes run from tip of snout under nostrils to top of orbit and on cheek under eye. All head stripes continuous with body stripes. Stripes obscure in adults where head is silvery,

darker above, light below with opercular membrane dusky. Young with five longitudinal body stripes. First, curved, running below base of dorsal fin, following dorsal profile; second, slightly curved, from upper border of eye to upper border of caudal peduncle; third, straight, from rear of eye to base of caudal; fourth, from opercle to ventral border of caudal peduncle; fifth, (may be lacking) from below pectorals to anterior of soft anal. In adults body coloration is uniformly silvery, slightly darker above. Spinous and soft dorsal slightly dusky with blackish pigmentation variably present on outer edge. Spinous anal clear in young, dusky in adults. Caudal dusky. Pectorals and pelvics yellowish or dusky.

Distribution: found in marine, brackish and freshwaters of Sumatra, Java, Sulawesi, Islands of East Indies, Philippines, southern China, Queensland, New Guinea, New Hebrides and Fiji? (Fig 61). Fowler (1959) lists the species as part of the Fiji fauna and describes its presence there as a result of an introduction citing Whitley (1927) as the basis for this statement. Evidently Whitley based the locality record on Kner's description of Therapon argenteus var., a form latter described by Bleeker (1873-76) as Therapon kneri. Furthermore, Whitley made no statement about the introduction of the species to Fiji. As such there appears to be no basis for the inclusion of M. argenteus in the Fijian fauna.

Herre (1936) also reported Therapon argenteus taken in freshwater on Viti Levu Island, Fiji. Examination of the specimen has shown it to be an example of Mesopristes kneri a very similar species.

In addition to its distribution east of the Malaya-Sumatra region, Mesopristes argenteus has also been reported from India, "Cape Seas", and Madagascar. Day (1889) describes this species in his Fishes of India, noting, however, that he had never personally seen any specimens and believed its presence to be limited to stray individuals. More recently Fowler (1959) lists India as a locality for the species, failing however, to provide reference to any specific locality records.

Fowler (1931) places as a synonym of Therapon (=Meso-pristes) argenteus a nominal Madagascar species Datnia obtusirostris Guichenot. In addition Petit (1937) described a collection of supposed M. argenteus also from Madagascar. However, it appears that in both cases, the specimens in question were actually material of Mesopristes elongatus (see also discussion in description of the latter species). Finally the locality listed by both Day and Fowler for "Cape Seas" appears to be erroneous.

Specimens examined

Philippines: Luzon (USNM 146909, 1 spec.; USNM 146910, 1 spec.; USNM 146911, 1 spec.): Legaspi, Yuna River

(USNM 146914, 19 spec.); Mindanao (USNM 146912*, 1 spec., 156 mm); Nonucan River, Camp Overton (USNM 184804*, 10 spec., 85-128 mm); Leyte (USNM 184818*, 4 spec., 55-72 mm).

Indonesia, Boero Island, Uki River (USNM 146913, 2 spec.; USNM 184869*, 2 spec., 123-150 mm).

Mesopristes cancellatus (Cuvier and Valenciennes, 1829)

Tapiroid grunter

Fig.62

Datnia cancellatus Cuvier and Valenciennes, 1829, p. 144

(original description, no locality, likely from Java).

Bleeker, 1849, p.4; 1855, p. 438 (Celebes).

Therapon cancellatus: Günther, 1859, p. 276 (copied). Bleeker, 1873-76, pl. 310, fig. 4(East Indies). Meyer, 1885, p. 13 (Manado, Celebes). Weber, 1895, p. 262 (Ambon). Jordan and Richardson, , 1907, p. 258 (Mindoro). Herre, 1927, p. 303 (Lake Naujan, Mindoro). Weber and deBeaufort, 1931, p. 151, fig. 27 (East Indies , Phillipines). Herre, 1933, p. 8 (Dumaguete, Negros); 1934, p. 52 (Dumaguete); 1936, p. 194 (Auki, Malaita Island, Solomon Islands). Okada, 1959, p. 57 (Okinawa). Freihofer, 1963, p. 132 (RLA pattern). Tortonese, 1964, p. 44 (West Irian, Andai).

Datnia Rosenberghii Bleeker, 1861, p. 237 (original description, Ceram).

Therapon (Datnia) cancellatus: Peters, 1868, p. 256 (Sancar, Leyte). Bleeker, 1873-76, p. 116 (Java, Celebes, Amboina, Philippines).

Therapon (Datnia) Rosenberghii: Bleeker, 1873-76, p. 387 (Ceram).

Therapon interruptus Macleay, 1883, p. 258 (original description, freshwater of Normanby Island).

Therapon (Datnia) interruptus: Ogilby and McCulloch, 1916,
p. 114 (from type of I. interruptus).

Terapon cancellatus: Fowler, 1931, p. 345 (Philippines).

Terapon rosenbergh: Fowler, 1931, p. 347 (on Bleeker).

Mesopristes cancellatus: Munro, 1956, p. 170 (Mambare Bay);
1964, p. 175 (New Britain); 1967, p. 323.

Terpon cancellatus: Chen, 1969, p. 401 (Taiwan).

Nomenclature: the trivial name, cancellatus, from the Latin cancellus, gratings or lattice work, refers to the pattern of vertical bars and horizontal stripes on the body.

Diagnosis: a marine teraponid also entering into fresh-water. Distinguishable from the other species of Mesopristes in having 6-8 scales above lateral line (in contrast to 9-11 in M. elongatus and M. kneri) 5-6 cheek and 5-6 caudal scales (in contrast to 8-9 cheek and 10-12 caudal in M. argenteus). The body coloration of dorsal vertical bars and ventral horizontal stripes present in all but larger specimens is also unique in the family as is the development of a markedly longer, very fleshy upper lip in larger specimens.

Description: Dorsal spines XI-XII; Dorsal rays 10-11; Anal III, 8-9; Pect. 13-16; Pel. I-5; 48-58 lateral line scales; 5-6 scales on caudal; 6-8 scales above lateral line; 15-21 scales below lateral line; 14-15 predorsal scales to occiput;

2 rows of scales in sheath at base of dorsal fin, sheath extending to last dorsal ray; 4 rows of scales in sheath at base of anal fin, sheath extending to sixth anal ray; cheek scales in 4-6 rows; gill rakers on first arch 9-11+1+15-18; vertebrae 10+15.

Reaching 230 mm SL; depth 2.5-3.0 in SL; distance from dorsal origin to snout 2.1-2.5 in SL; head length 2.8-3.2 in SL; length of base of dorsal fin 1.6-1.8 in SL; snout length 2.5-3.1 in HL; eye width 3.0-5.0 in HL; jaw length 2.5-3.3 in HL; length of longest dorsal spine 1.6-2.0 in HL; length of longest dorsal ray 1.6-2.5 in HL; length of longest anal spine 1.7-2.1 in HL; length of longest anal ray 1.4-1.7 in HL.

Body deep, compressed. Head oriented ventrally anteriorly. Dorsal profile much more pronounced than ventral. Dorsal profile between snout and nape forming nearly a 45° angle with horizontal. Dorsal profile slightly convex between snout and dorsal origin. Ventral profile nearly horizontal, straight or only a bit convex from rear of isthmus to pelvic insertion. Ventral profile straight from pelvic insertion to anus. Upper jaw longer, increasingly so with age. Upper lip fleshy, forming a prominent fleshy pad with age. Maxillary reaching just posterior to vertical through anterior edge of eye in young, to vertical through anterior edge of pupil with age. Teeth conic, outer row enlarged and followed by a band of villiform teeth. No teeth on vomer or palatines. Top of head with with interorbital ridges. Nostrils separated by a distance

less than diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate with large serrations in young; serrations reduced in adults which have largest preopercular serrations on vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal exposed; serrate along posterior edge. Cleithrum exposed; posterior edge serrate; scales on side. Supracleithrum exposed.

Spinous dorsal markedly arched with strong spines; first short; fifth or sixth longest, those following decreasing gradually in length to penultimate which is about same length as but stronger than ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal with concave posterior border. Spinous anal with very strong spines; second longest, nearly as long as longest anal rays. Soft anal with posterior border straight or slightly concave. Pectorals assymmetrically pointed; third or fourth ray longest. Pelvics pointed; first ray longest, filamentous; reaching to anus or slightly beyond. Caudal emarginate.

Coloration: young with a median head band running from snout to interorbital region where it divides into two stripes that are continuous with body stripes. Top of head uniformly dark in adults. Individuals of all sizes have a pigment band running from snout to anterior of eye. Adults have an additional stripe under eye on cheek. Opercular flap dusky in adults. Body with a general overall silver coloration with three longitudinal stripes. First running from upper opercular

spine to middle of caudal base; second from serrate edge of cleithrum to ventral caudal base; third, from base of pectoral to above spinous anal. In some specimens stripes are irregular and blotchy. Dorsal to stripes there are five oblique cross bands. First running from front of spinous dorsal to posterior of posttemporal; second, third and fourth, under spinous dorsal; fifth under soft dorsal. Both stripes and bands are much less evident in larger specimens and fade into general body coloration in large specimens (Weber and deBeaufort, 1931). Spinous dorsal clear. Soft dorsal with some dusky basal marks. Spinous anal slightly pigmented between second and third spines and third spine and first ray; pigmentation continuing onto sheath. Soft anal with basal blotch on first three rays that continues onto sheath. Intensity of both spinous and soft anal coloration increasing with age. Caudal with continuation of body stripes onto base; otherwise without markings; overall coloration yellowish. Pectorals yellowish with a dark spot on base medially. Pelvics yellowish, slightly dusky on first two membranes.

Distribution: in marine, brackish and fresh waters of Java, Sulawesi, Ceram, Ambion, north and south shores of New Guinea, Philippines, Taiwan, Solomon Islands and Normanby Island (Fig. 63).

Remarks: Bleeker (1860) described a species from the East Indies, Datnia Rosenberghii, which had the same coloration

pattern as Datnia (= Mesopristes)cancellatus but differed from that species in lateral line counts and body proportions. Fowler (1931) retained these as distinct species whereas Weber and deBeaufort (1931) placed D. Rosenberghii as a synonym of Terapon cancellatus. Examination of a series of specimens of Mesopristes cancellatus and literature information has shown that the range of variation in this species overlaps the gaps in the various characters used by Bleeker to distinguish the two nominal forms. As such I will follow Weber and deBeaufort and place D. rosenbergii in synonymy with M. cancellatus.

Specimens examined.

New Guinea: (USNM 12287*, 1 spec., 157 mm).

Philippines: Mindanao, Nonucan River, Camp Overton (USNM 184776*, 4 spec., 109-158 mm); Leyte, San Roque (USNM 184774*, 3 spec., 59-6 mm; USNM 146356*, 2 spec.); Leyte, Hinunangan Bay, Malaga River (USNM 184775*, 2 spec., 82-96 mm).

Indonesia, Boero Island, Uki River (USNM 184875*, 1 spec., 205 mm).

Mesopristes elongatus (Guichenot, 1866)

Fig. 64

Datnia elongata Guichenot, 1866, p. 133 (original description, "said to be from Madagascar").

Therapon elongatus: Sauvage, 1891, p. 154, pl. 9 (description based on type).

Therapon lambertoni Fowler, 1923, p. 40 (original description, Tananarive, Madagascar).

Terapon lambertoni: Fowler, 1931, p. 350, fig. 28 (based on type).

Terapon elongatus: Fowler, 1931, p. 351 (after Guichenot).

The following also appear to be synonyms of this species:

Datnia obtusirostris Guichenot, 1866, p. 132 (original description; Madagascar).

Therapon (Datnia) argenteus: Petit, 1937, (not Mesopristes argenteus [Cuvier and Valenciennes]), p. 27 (Madagascar).

Nomenclature: the trivial name elongatus, from the Latin, ex, more, and longus, long, refers to what Guichenot believed to be the exceptionally elongate body form in this species. The type is deposited in the Museum National d'Histoire Naturelle (MNHN 4170). Though damaged, it agrees in all details with the original description except in having 14 rather than 18 pectoral rays.

Diagnosis: M. elongatus can be distinguished from the other species of the genus Mesopristes in having 9-11 scales above the lateral line (in contrast to 6-8 in M. cancellatus and M. argenteus), and 20-24 sublateral scales (in contrast to 18-19 in M. kneri), and broad stripes in young (in contrast to stripes formed of disconnected spots in M. kneri).

Description: Dorsal spines XII; Dorsal rays 10; Anal III-8, Pect. 14 (incorrectly listed as 18 in the original description); Pel. I-5; 48-50 lateral line scales; 5 scales on caudal; 9-10 scales above lateral line; 20-24 scales below lateral line; 15 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal fin, sheath extending across base of entire fin; 3-4 rows of scales in sheath at base of anal fin, sheath extending across base of entire fin; cheek scales in 4-6 rows; gill rakers on first arch 7-8+1+15-17; vertebrae 10+15.

Reaching 160 mm SL; depth 2.67-2.8 in SL; distance from origin of spinous dorsal to snout 2.4 in SL; head length 2.8-3.0 in SL; length of base of dorsal fin 2.0 in SL; snout length 3.0-3.1 in HL; eye width 3.3-3.45 in HL; jaw length 3.3 in HL; length of longest dorsal spine 1.7-1.9 in HL; length of longest dorsal ray 1.8-2.0 in HL; length of longest anal spine 1.75 in HL; length of longest anal ray 1.65-1.75 in HL.

Body compressed, moderately deep. Dorsal profile more

pronounced than ventral. Dorsal profile nearly straight from snout to origin of spinous dorsal. Ventral profile gently curved from tip of lower jaw to pelvic insertion, then straight to anus. Jaws equal. Gape oblique. Snout elongate. Maxillary reaching to vertical through posterior nostril. Teeth in villiform bands; outer row enlarged. Nostrils well separated. Preoperculum serrate; serrations largest on angle. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal exposed; posterior edge serrate. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal arched, with strong spines; first spine short; fourth or fifth longest, those following decreasing gradually in length to penultimate which is about as long as ultimate. Longest dorsal spine longer than longest dorsal rays. Posterior edge of soft dorsal concave. Anal spines strong; second longest, nearly as long as longest anal rays. Posterior edge of soft anal slightly convex. Pectoral asymmetrically pointed; fifth ray longest. Pelvics pointed; first ray longest, tip filamentous; reaching to anus in young, falling short with age.

Coloration: in young there is a median stripe running from snout to interorbital region. In addition stripes run from snout under the nostrils to orbit and under eye on cheek to opercle. Head lighter ventrally. In adults, juvenile markings are less evident; head brownish. Iris brown, lips pale.

Body in young with three longitudinal stripes. First, running along base of dorsal fin; second from posttemporal to base of soft dorsal; third, from serrate edge of cleithrum to middle of caudal base. Body dark above, light ventrally. In adults, stripes lacking. Body nearly olive lake on back and upper surfaces which are also tinged with dark grey as if indistinctly mottled. Lower surfaces and sides whitish. Spinous dorsal dusky on edge and basally. Anal spines silvery; membranes dusky basally. Caudal dusky on edge. Pectorals and pelvics yellowish

Distribution: Mesopristes elongatus was originally described on the basis of a single specimen thought to be from Madagascar. Other nominal forms from that area which are considered to be synonyms of M. elongatus, support the hypothesis. The species appears to be endemic to Madagascar.

Remarks: Since the original description of M. elongatus based only on the type, no further material has been described under that name, and the species appears to have been forgotten until Fowler (1931) gave a description based on the original. However, it would appear that two nominal species represent adults of this species and that the collection reported on by Petit (1937) as Therapon argenteus is actually M. elongatus.

Although the type of Therapon lambertoni is not available for examination, the species would appear to be based on the

adult of M. elongatus. Fowler (1923) in his description of Therapon lambertoni notes the similarity of the species to Therapon elongatus, but separated them on the basis of a more emarginate caudal in T. lambertoni, a difference in which dorsal spine was the longest (fourth or fifth), and the presence of longitudinal stripes in M. elongatus which were missing in T. lambertoni along with meristic and morphometric differences.

Most of the differences noted by Fowler are either a function of ontogenetic changes or within the expected range of variation for a species. Mesopristes elongatus is based on a single specimen of 67 mm total length, whereas T. lambertoni was based on a 158 mm total length specimen. Within such a size range in closely related species, there is a marked increase in caudal fin emargination (Rahin, 1973; Duncker and Mohr, 1931; per. obs.). Similarly in closely related species, there is an increasing ventrally turning of the head anteriorly and a change in coloration pattern from a juvenile striped pigmentation to a uniform adult coloration. The hypothesis that these forms are conspecific is also supported by the ontogenetic information provided by Petit (1937) who identified a collection of freshwater Madagascar fish as Therapon (Datnia) argenteus (= Mesopristes argenteus), an East Indies species. The young were described as having three longitudinal bands in agreement with the condition in M. elongatus (but not M. argenteus which has 4-5 stripes in young) and the adults as having a brown marbling pattern that agrees with the coloration

description for both Therapon lambertoni and Datnia obtusirostris another nominal Madagascar species. Thus it would appear that both of these latter species are synonymous with M. elongatus.

Fowler (1931) considered D. obtusirostris to be a synonym of Therapon (= Mesopristes) argenteus a species otherwise limited to east of the Malaya-Sumatra region. This appears to be in error since D. obtusirostris as described agrees with M. elongatus other than for those characters which vary ontogenetically within its close relatives (this species is based on a single 220 mm TL specimen). Furthermore Sauvage describes the type of D. obtusirostris as having 4 rows of cheek scales while M. argenteus has 7-9.

Specimens examined

Madagascar, (MNHN, 4170*, 1 spec.(holotype), 55 mm).

Mesopristes kneri (Bleeker, 1873)

Kner's grunter

Fig. 65

Therapon argenteus var. (not Cuvier and Valenciennes) Kner,
1868, p. 299, pl. 1, fig. 1 (Kandavu, Fiji).

Therapon kneri Bleeker, 1873-76, p. 111 (original description,
based on Kner 1868; Suva, Fiji). Fowler, 1928, p. 211
based on type series of Therapon maculatus).

Therapon maculatus Kendall and Goldsborough, 1911, p. 288,
pl. 4, fig. 2 (original description, Suva, Fiji).

Mesopristes plumbeus: Fowler, 1918, p. 36 (pt).

Terapon kneri: Fowler, 1931, p. 341 (Suva, Fiji); 1959, p. 259,
fig. 105 (Suva, Fiji).

Nomenclature: the trivial name, kneri, is in honor of
Rudolf Kner who first distinguished the species as Therapon
argenteus var. which served as the basis for the Bleeker descrip-
tion.

Diagnosis: a marine teraponid endemic to Fiji distinguished
from other members of the genus Mesopristes in having 9-11 supra-
lateral scales (in contrast to 6-8 in M. cancellatus and M.
argenteus), and 18-19 scales below the lateral line (in contrast
to 20-24 in M. elongatus). In addition its juvenile coloration
pattern of longitudinal stripes formed of disconnected spots is
unique in the family.

Description: Dorsal spines XII; Dorsal rays 10-11; Anal III, 8-9; Pect. 13-14; Pel. I-5; 48-51 lateral line scales; 4-6 caudal scales; 9-11 scales above lateral line; 18-19 scales below lateral line; 14-15 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal fin, sheath extending to fifth or sixth dorsal ray; 3-4 rows of scales in sheath at base of anal fin, sheath extending across base of entire fin in larger specimens, only to third or fourth anal ray in young; cheek scales in 6-7 rows; gill rakers on first arch 7-11+1+15-17; vertebrae 10+15.

Reaching 120 mm SL; depth 2.3-2.7 in SL; distance from dorsal origin to snout 2.05-2.4 in SL; head length 2.7-3.4 in SL; length of base of dorsal fin 1.75-1.9 in SL; snout length 2.75-3.5 in HL; eye width 3.1-3.7 in HL; jaw length 3.1-3.65 in HL; length of longest dorsal spine 1.4-1.8 in HL; length of longest dorsal ray 1.5-1.8 in HL; length of longest anal spine 1.4-1.8 in HL; length of longest anal ray 1.4-1.7 in HL.

Body compressed, moderately deep. Dorsal profile more pronounced than ventral. Dorsal profile a gentle curve from snout to dorsal origin in young; nearly straight in adults. Ventral profile more horizontal in adults. Jaws equal. Snout elongate. Maxillary reaching to vertical through posterior nostril. Teeth villiform, outer row enlarged; number of teeth in lower jaw reduced in median line. No teeth on vomer or palatines. Interorbital region with distinct ridges. Nostrils distant, separated by a distance equal to one and one-

half to two times diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate; serrations largest on vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal exposed; serrate along posterior edge. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal arched; first spine short; fifth spine longest, those following decreasing in length to penultimate which is about same length as ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal with posterior edge slightly convex. Second anal spine very strong and long; about twice length of first, longer than third; longer than or equal to longest anal rays. Soft anal rounded. Pectorals assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest, slightly filamentous, reaching to anus. Caudal emarginate.

Coloration: body dusky above, white ventrally; each scale with a lighter central spot. Three series of small brown spots are arranged into longitudinal patterns on side of body. First series convex, running from nape to upper caudal peduncle; second, from posttemporal to middle of caudal peduncle; third, straight, from supracleithrum to above soft anal. Longitudinal patterns lacking in larger specimens. Spinous dorsal dusky, especially along margin; membrane coloration more evident along anterior edge of spines. Soft dorsal with brown edge along upper anterior edge. Anal membranes dark; pigmentation darkest

anteriorly. Caudal clear with some spots randomly distributed on it. Pelvics very dark distally, lighter at base and along first ray. Head darker above, light ventrally.

Distribution: found in fresh and marine waters of the Fiji Islands.

Specimens examined

Fiji Islands, Suva (USNM 66061*, 1 spec. (holotype of Therapon maculatus), 99 mm; USNM 66062*, 5 spec. (paratypes of Therapon maculatus), USNM 112737*, 1 spec., 169 mm; SU (in CAS) 24935*, 1 spec., 90mm).

Genus 11, Hephaestus

Hephaestus DeVis, 1884, p. 399 (type species, Hephaestus tulliensis (=H. fuliginosus), by monotypy).

Papuservus Whitley, 1943, p. 182 (type species, Therapon trimaculatus Macleay, by original designation).

Archeria Nichols, 1949, p. 6 (type species, Archeria jamesonoides, by original designation).

Archerichthys Whitley, 1951, p. 398 (type species Archeria jamesonoides Nichols, by original designation [proposed as a subgenus]).

Nomenclature: the generic name, Hephaestus, refers to the Greek god of fire. The reference is obscure and DeVis provides no explanation.

Diagnosis: freshwater teraponids from Australia and New Guinea with an exposed posttemporal, longest dorsal spines in adults shorter than longest dorsal rays, first spine bearing proximal dorsal pterygiophore inserting between the second and third neural spines or posterior .

Remarks: within the genus a subgroup of species having a series of characters unique to them in the family can be defined (see phylogenetic discussion, genus 11b) as a monophyletic unit. The remaining species (H. jenkinsi, H. roemeri, and H. fuliginosus cannot be shown to be a monophyletic group.

Included species: seven freshwater species from New Guinea and Australia are placed in the genus Hephaestus in this study. In the species of genus 11a, two species (H. fuliginosus and H. jenkinsi) have extensive but non-overlapping distributions in the northern half of Australia, while one species (H. roemeri) is limited to the southern drainages of West Irian. Genus 9b, contains four species evenly divided between Australia and New Guinea. H. adamsoni is evidently endemic to Lake Kutuba, Papua-New Guinea; H. trimaculatus is distributed through the southern drainages of the island; H. suavis appears to be limited to the Cape York region of Australia; and H. carbo occurs in the Gregory River region of Queensland.

Whitley (1943) placed the genus Homodemus DeVis, 1884 in synonymy with Hephaestus and equated Homodemus cavifrons with Hephaestus fuliginosus. However, the latter species differs from the former in having 12-14 dorsal rays (in contrast to 16 of H. cavifrons). Furthermore, the maxillary of H. cavifrons is described as extending posterior to the vertical drawn through the posterior edge of the eye, a condition not found in any teraponid. As such it would appear that both the generic and specific synonymies are in error.

Hephaestus fuliginosus (Macleay, 1883)

Sooty grunter

Fig. 66

Therapon fuliginosus Macleay, 1883, p. 201 (original description, upper Burdekin River, Queensland). Macleay, 1884, p. 13 (upper Burdekin River). Weber, 1913, p. 585 (Burdekin-Fluss). Ogilby and McCulloch, 1916, p. 117, fig. 2 (upper Burdekin River, Tully, and Murray Rivers). Fowler, 1928, p. 212 (pt.) (upper Burdekin River). Grant, 1965, p. 223 (Queensland). Mees, 1971, p. 200 (pt) (Queensland). Grant, 1972, p. 390 (Queensland).

Hephaestus tulliensis DeVis, 1885, p. 399 (original description, Tully and Murray Rivers, Queensland).

Therapon bancrofti Ogilby and McCulloch, 1916, p. 119, pl. 11, fig. 2 (original description, Eureka Creek, Stannary Hills Queensland). McCulloch and Whitley, 1925, p. 153. Grant, 1965, p. 223 (Queensland). Mees, 1971, p. 204, figs. 2-3 (Northern Territory, Queensland). Grant, 1972, p. 390, fig. (Queensland)

Terapon alligatoris Rendahl, 1922, p. 185 (original description, South Alligator and McKinley Rivers). McCulloch, 1929, p. 161 (northwest Australia). Fowler, 1931, p. 351 (northwest Australia). Taylor, 1964, p. 185 (South Alligator River). Pethon, 1969, p. 7 (McKinley River).

Terapon Alligatoris: Dahl, 1926, p. 229 (South Alligator River).

Terapon fuliginosus: McCulloch, 1929, p. 163 (Queensland).

Fowler, 1931, p. 352 (copied).

Terapon bancrofti: McCulloch, 1929, p. 163 (Queensland). Fowler, 1931, p. 352 (copied).

Hephaestus bancrofti: Whitley, 1956, p. 41 (Australia); 1960, p. 75 (Norman and Mitchell Rivers, Queensland); 1964, p. 42 (no locality). Lake, 1971, p. 34, pl. 70 (biology, distribution).

Hephaestus fuliginosus: Whitley, 1956, p. 41 (Australia); 1960, p. 75 (Burdekin and Tully Rivers); 1964, p. 42 (no locality). Lake, 1971, p. 34, pls. 71-73 (biology, distribution).

Mesopristes alligatoris: Whitley, 1956, p. 41 (Australia); 1960, p. 76 (northwest Australia); 1964, p. 42 (no locality). Lake, 1971, p. 34 (northwest Australia).

Therapon alligatoris: Mees, 1963, p. 46 (pt)(South Alligator River and McKinley River, Northern Territory).

Nomenclature: the trivial name, fuliginosus, from the Latin word fuligo, soot, refers to the sooty coloration of the species. The lectotype and cotypes are in the Australian Museum (A.17822-4)

Diagnosis: Hephaestus fuliginosus can be distinguished from the other species in the genus in having 14-17 gill rakers on the lower limb of the first arch (in contrast to 9-11 in H. trimaculatus, H. adamsoni, H. suavis and H. carbo), an interrupted lip fold on the ventral surface of the lower jaw (in

contrast to a continuous lip fold in H. jenkinsi), 8-10 scales above lateral line and 6-9 cheek scales (in contrast to 5-7 scales above the lateral line and 5-6 cheek scales in H. roemeri).

Description: Dorsal spines XI-XII; Dorsal rays 12-14; Anal III, 8-10; Pect. 15-17; Pel. I-5; 43-51 lateral line scales; 3-7 scales on caudal; 7-10 scales above lateral line; 14-17 scales below lateral line; 13-17 predorsal scales to occiput; 2-3 rows of scales in sheath at base of dorsal fin, sheath extending to last dorsal ray; 3-4 rows of scales in sheath at base of anal fin; sheath extending to fifth to last anal ray; cheek scales in 6-9 rows; gill rakers on first arch 6-9+1+ 14-17; vertebrae 10+15.

Reaching 330 mm SL; depth 2.4-2.9 in SL; distance from origin of spinous dorsal to snout 2.2-2.45 in SL; head length 2.6-3.1 in SL; length of base of dorsal fin 1.85-2.5 in SL; snout length 2.6-3.1 in HL; eye width 3.5-5.6 in SL; jaw length 3.3-3.45 in HL; length of longest dorsal spine 2.1-3.1 in HL; length of longest dorsal ray 1.7-2.4 in HL; length of longest anal spine 2.5-3.2 in HL; length of longest anal ray 1.8-1.9 in HL.

Body moderately deep, compressed. Dorsal profile more pronounced than ventral. Dorsal profile straight from tip of snout to nape, then convex to origin of dorsal fin, convex with

age. Ventral profile nearly straight to pelvic insertion; straight from insertion to anus. Jaws equal or with upper slightly longer than lower. Gape oblique. Lips fleshy. Snout elongate. Maxillary reaching to vertical through anterior edge of eye in young, falling short with age and reaching to vertical through posterior nostril. Teeth conic, slightly recurved, in bands, outer row enlarged. No teeth on vomer or palatines. Nostrils separated by a distance ranging from one to two diameters of posterior nostril. Lacrimal serrate; serrations larger in juveniles. Preoperculum serrate; serrations larger on angle. Lower opercular spine stronger and longer; not extending beyond edge of opercular. Posttemporal exposed and serrate posteriorly. Cleithrum exposed; serrate posteriorly, scales on side. Supracleithrum exposed

Spinous dorsal arched; first spine short; fifth to seventh longest, those following decreasing in length gradually to penultimate which is same length or slightly longer than ultimate. Longest dorsal rays longer than longest dorsal spines in adults; differences less pronounced or spines longer than rays in some small individuals. Soft dorsal rounded. Spinous anal with second spine longest, relatively longer in juveniles; longest anal spine shorter than longest rays. Soft anal rounded. Pectorals assymmetrically pointed; fifth ray longest. Pelvics point-

ed; first ray longest, reaching nearly to anus in young, falling short with age.

Coloration: spines of dorsal whitish, membranes brownish with a lighter edge. Soft dorsal dusky with a basal blotch and a lighter edge. Spinous and soft anal dusky, with a lighter edge. Soft anal with a basal blotch. Caudal dusky with a lighter edge in some specimens. Pectorals grey with a dark bar across base. Pelvics dusky. Head uniformly dark above, lighter below. Body uniform purplish brown with each scale more heavily pigmented along edge. Body lighter below.

Distribution: in freshwaters of Queensland and Northern Territory from the Burdekin River of Queensland to the Daly River of Northern Territory (Fig. 67).

Ecology: H. fuliginosus is primarily a species found in rapidly flowing waters, especially along rocky sections. Lake (1971) reports that available evidence suggest that they lay small adhesive eggs after flood waters have receded. They appear to be omnivorous feeders.

Remarks: Hephaestus fuliginosus shows marked variation in head shape, lip form and coloration both ontogenetically and geographically. The coloration varies from dark brown and black to some xanthomorphic golden and silvery specimens. Variation in lip size results in some individuals developing what are commonly termed "blubber lips" with the lips form-

ing a fleshy pad. This condition which is not as pronounced in this species as in H. jenkinsi is not directly related either to the size or sex of the individual and varies from populations both in prevalence and extent.

Ogilby and McCulloch (1916) described a new species, Terapon bancrofti from Eureka Creek, Queensland which they differentiated from Therapon (=Hephaestus) fuliginosus by differences in lateral line counts and the number of scales above the lateral line. However, as pointed out by Mees (1971), when large series of material of each of the nominal forms is examined, these differences fail to separate the two forms; a finding supported by examination of collections at hand. Mees, however, retained these as distinct forms based on some differences in nostril distance and head shape, noting that additional material might prove that the differences were not as distinct as shown in his material. Examination of larger series from Queensland, Northern Territory and Western Australia has shown that there do not appear to be any discontinuities supporting the retention of the nominal forms. Consequently, Therapon bancrofti is considered to be a synonym of Hephaestus fuliginosus.

However, contrary to the conclusions of Mees, Mesopristes (=Hephaestus) jenkinsi and what were considered to be Western Australian specimens of H. fuliginosus are considered to be a distinct form, H. jenkinsi based on a lip character unique to the species (see under T. jenkinsi description).

Finally, Mees (1971) suggested that Terapon alligatoris, Rendahl was also a synonym of H. fuliginosus. Although I have not examined the type material of T. alligatoris, comparison of the original type description and specimens of H. fuliginosus from the area of the type locality shows agreement with the description. As such they are herein considered synonymous.

Weber (1913) hypothesized that his species Therapon roemeri Weber (1910) was identical with Therapon fuliginosus. This suggestion was followed by Fowler (1928, 1931) who placed it in synonymy, but not by Weber and deBeaufort (1931) who retained it as a distinct species. Although the two species are very similar, material at hand reveals differences in both the transverse scale and lateral line scale counts.

Specimens examined

Australia, Northern Territory: Katherine River, Katherine

(AMNH 32438*, 1 spec., 125 mm); Barramundie Creek (AMNH 35654*, 10 spec. (of 46), 36-53 mm); South Alligator River (AMNH 35655*, 13 spec., 33-136 mm); Mary River (AMNH 35656*, 5 spec. (of 41), 100-112 mm; AMNH 35661*, 3 spec., 41-55 mm); South Alligator River (AMNH 35657, 20 spec.); Ferguson River (AMNH 35658*, 10 spec., 28-63 mm); Barramundie Creek (AMNH 35659, 17 spec); Katherine River (AMNH 35660*, 10 spec. (of 46), 40-175 mm; WAM P-25676-001, 1 spec). Roper River (WAM P-25447-001, 1 spec.).

Australia, Queensland, Cape York Peninsula, Wenlock Crossing (AMNH 18540*, 9 spec., 61-104 mm).

Hephaestus roemeri

Römer's grunter

Fig. 68

Therapon Römeri Weber, 1910, p. 233 (original description,
Lorentz River); 1913, p. 584, fig. 35 (Lorentz River at
Van Wellskamp, Sabang, and Regen Island).

Therapon fuliginosus: Fowler, 1928, p. 212 (pt)(Lorentz River);
1931, p. 352 (pt) copied).

Pelates römeri: Weber and deBeaufort, 1931, p. 163, fig. 30
(Lorentz River); Hardenberg, 1941, p. 227 (Tanah Merah,
Digoel River).

Pelates romeri: Fowler, 1934, p. 416 (Lorentz River). Munro, 1956,
p. 169 (Lorentz River, Digoel River); 1964, p. 147 (pt)
(southwestern New Guinea); 1967, p. 320 (southwestern New
Guinea). Lake, 1971, p. 34 (northern Australia, erroneous).

Therapon roemeri: Mees, 1971, p. 212 (Lorentz River, Digoel
River; Comparisons to T. fuliginosus, T. bancrofti and
T. carbo).

Nomenclature: the trivial name, roemeri, is in honor of L.S.
A. M.von Römer, a member of the Dutch expedition to New Guin-
ea which collected the syntypic series. The syntype series
has been deposited in the Zoologische Museum of Amsterdam.

Diagnosis: a member of the genus Hephaestus distinguished from the other members of the group in having 14-18 gill rakers on the lower limb of the first arch (in contrast to 9-11 in H. trimaculatus, H. adamsoni, H. carbo, and H. suavis), a lack of an uninterrupted lip fold on the ventral surface of the lower lip (in contrast to a continuous fold in H. jenkinsi) and 5-7 scales above the lateral line and 5-6 cheek scales (in contrast to 8-10 scales above lateral line and 6-9 cheek scales in H. fuliginosus).

Description: Dorsal spines XI-XII; Dorsal rays 12-14; Anal III, 9-10; Pect. 14-16; Pel. I-5; 50-56 lateral line scales; 4-5 scales on caudal; 5-7 scales above lateral line; 16-20 scales below lateral line; 15-17 predorsal scales to occiput; 3-4 rows of scales in sheath at base of dorsal fin, sheath extending to twelfth dorsal ray; 3-5 rows of scales in sheath at base of anal fin, sheath extending to seventh anal ray; cheek scales in 5-6 rows; gill rakers on first arch 8-9+1+14-18; vertebrae 10+15.

Reaching 300 mm SL; depth 2.4-2.6 in SL; distance from origin of dorsal to snout 2.3-2.5 in SL; head length 2.9-3.3 in SL; length of base of dorsal fin 1.7-1.9 in SL; snout length 3.0-5.4 in HL; eye width 3.9-5.4 in HL; jaw length 3.1-3.5 in HL; length of longest dorsal spine 1.8-2.6 in HL; length of longest dorsal ray 1.8-2.1 in HL; length of longest anal spine 1.6-2.4 in HL; length of longest anal ray 1.6-1.8 in HL

Body moderately deep, compressed in young, less so in adults. Dorsal profile more pronounced than ventral. Dorsal profile in juveniles nearly straight from snout to dorsal origin; in adults concave above eye. Ventral profile practically straight from lower lip to pelvics; then slightly convex to anus. Jaws equal; slightly fleshy. Gape oblique. Snout elongate in young, less so in adults. Maxillary reaching to vertical through posterior nostril. Teeth conic; strong; outer row distinctly enlarged; followed by a band of smaller teeth embedded in fleshy mouth lining; outer one or two rows brown tipped, following bands colorless and difficult to see. Teeth more numerous medially. No teeth on vomer or palatines. Interorbital region smooth. Nostrils distant, separated by a distance equal to twice diameter of posterior nostril. Lacrimal with weak serrations. Preoperculum serrate; serrations largest on vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate on posterior edge; scales on side. Posttemporal exposed; serrate along posterior edge. Supracleithrum exposed.

Spinous dorsal arched; low; first spine very short; fourth to sixth spines longest, those following decreasing in penultimate which is subequal to ultimate. Longest dorsal rays longer than longest dorsal spines. Soft dorsal rounded. Anal spines long in young, relatively shorter in adults. Second spine longest; twice length of first in young, relatively longer in adults; longer and stronger than third, but shorter than

longest anal rays. Soft anal rounded. Pectorals assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest, slightly filamentous; reaching nearly to anus in young, only three-quarters of distance in adults. Caudal emarginate; lobes rounded.

Coloration: head in young specimens to 150 mm SL darker above lighter below and lacking any distinct markings. Body pale brown, darker above. Spinous dorsal clear with a dusky edge. Soft dorsal with a basal blotch and lighter edge. Spinous anal clear. Soft anal with a basal blotch and lighter edge. Pectorals and pelvics clear or very slightly dusky. Adults much darker in coloration; head, body and fins dark grey.

Distribution: in the freshwaters of southern West Irian: Lorentz and Digoel Rivers (Fig. 67).

Remarks: Fowler (1928, 1931) placed Therapon (=Hephaestus) rubrimeri as a synonym of T. fuliginosus following Weber's suggestion (1913) that these species might be identical. However, in 1934 he reversed his action, even following Weber and deBeaufort's placing of the species in the genus Pelates. Based on the material examined, the species though extremely similar and probably sister species, appear distinct. Further information may indicate, however, that they are geographical variants of one species.

Nichols (1949) created further confusion with his statement concerning a collection of H. fuliginosus from northern Queensland that "I identify this with Pelates romeri from New Guinea, and they are presumably T. bidyana as recognized elsewhere in Australia.". Whereas H. fuliginosus is indeed similar to H. romeri, it is quite distinct from Bidyanus bidyanus in many characters.

Perhaps as a result of Nichol's statement, Lake (1971) and Munro (1964) list H. romeri as a member of the northern Queensland fauna. However, this appears to be in error, since other than the above misidentification, there do not appear to be any confirmed records of the species from that region.

As noted above, Hephaestus romeri was removed to the genus Pelates by Weber and deBeaufort (1931) followed by most later workers. The genus Pelates as defined by these authors was characterized by triserial dentition in the upper jaw and biserial in the lower. However, examination of specimens of H. romeri has shown that although some individuals have what could be interpreted as irregular rows of teeth, in most, particularly the adults, the teeth are in bands. Furthermore in both cases (irregular rows and bands) there are found four or more series of teeth in each jaw, but with the posterior series colorless and difficult to locate. Neither has the evidence of this study supported the hypothesis of a close relationships between the species placed by Weber and deBeaufort in Pelates. Hephaestus romeri has a series of apomorphic

states of the posttemporal, lower tabular, extrinsic swim-bladder muscles and others that are lacking in the species placed in Pelates in this reconstruction.

Specimens examined

Indonesia, West Irian, southern drainages: Lorentz River, near Regen Island (ZMA 104731*, 1 spec. (syntype), 272 mm); Lorentz River, Bivaleiland (ZMA 104738*, 2 spec., 98-118 mm); Digoel River, near Tanah Merah (RMNH 24936*, 2 spec., 110-134 mm).

Hephaestus jenkinsi (Whitley, 1945)

Jenkins! grunter

Fig. 69

Mesopristes jenkinsi Whitley, 1945, p. 26 (original description, Ivanhoe Station; Ord River, Western Australia); 1947, p. 53 (Leichhardtian Fluvifaunula, Western Australia); 1955 p. 45, fig. 2 (Ord River); 1956, p. 41 (Australia); 1960, p. 76, fig. (northwest Australia).

Therapon alligatoris: Mees, 1963, p. 3 (pt) (Ivanhoe Station, northwest Australia).

Therapon fuliginosus: Mees, 1971, p. 200 (pt) (northwest Australia).

Therapon brevipinnis Mees, 1971, p. 209, fig. 4 (original description, Hann River, Western Australia).

Nomenclature: the trivial name, jenkinsi, is in honor of C.F.H. Jenkins, the collector of the holotype at Ivanhoe Station, Western Australia. The type (WAM 2763) is deposited at the Western Australian Museum

Diagnosis: Hephaestus jenkinsi is distinguishable from the other members of the genus in 15-18 gill rakers on the lower limb of the first arch (in contrast to 9-12 for H. trimaculatus, H. adamsoni, H. carbo, and H. suavis) and in possessing a continuous lip fold on the ventral surface of the lower jaw (in contrast to an interrupted lip fold in all other species of the family).

Description: Dorsal spines XI-XIII; Dorsal rays 11-12; Anal III, 7-8; Pect. 15-17; Pel. I-5; 46-52 lateral line scales; 4-6 scales on caudal fin; 8-10 scales above lateral line; 15-19 scales below lateral line; 13-14 predorsal scales to occiput; 2-3 rows of scales in sheath at base of dorsal fin, sheath extending to sixth to ninth dorsal ray; 3-4 rows of scales in sheath at base of anal fin, sheath extending to fifth anal ray; cheek scales in 6-9 rows; gill rakers on first arch 5-8+1+15-18; vertebrae 10+15.

Reaching 150 mm SL; depth 2.6-3.0 in SL; distance from dorsal origin to snout 2.2-2.5 in SL; head length 2.55-2.95 in SL; length of base of dorsal fin 1.9-2.15 in SL; snout length 2.7-3.1 in HL; eye width 2.7-5.6 in HL; jaw length 2.85-3.5 in HL; length of longest dorsal spine 2.9-3.5 in HL; length of longest dorsal ray 2.2-2.6 in HL; length of longest anal spine 2.3-3.0 in HL; length of longest anal ray 1.9-2.8 in HL.

Body moderately deep, slightly compressed. Dorsal profile more pronounced than ventral. Dorsal profile straight to slightly convex to dorsal origin in young, more convex in adults. Ventral profile nearly straight from lower lip to pelvic insertion in young, slightly convex in adults. Ventral profile from the pelvic insertion to anus straight. Jaws equal. Gape oblique. Lips fleshy, in some specimens developing fleshy pads curling posteriorly on both lips (Fig. 70). The lip flap on

the lower lip is continuous across the median midline. Maxillary reaching to or slightly beyond vertical drawn through posterior nostril. Teeth conic, recurved; with brown tips; outer row enlarged and followed by a villiform band. No teeth on vomer or palatines. Nostrils separated by a distance equal to one-half of eye diameter. Interorbital region smooth. Lacrimal serrate posteriorly in young, less so in adults or smooth. Preoperculum serrate; serrations larger on angle. Lower opercular spine larger or stronger; not extending beyond edge of opercular lobe. Posttemporal expanded posteriorly, exposed, serrate along posterior edge. Cleithrum exposed; posterior edge serrate; scales on side. Supracleithrum exposed.

Spinous dorsal arched; first spine short; fourth to seventh longest; those following decrease gradually in length to ultimate. Soft dorsal rays longer than longest dorsal spines. Soft dorsal rounded. Second anal spine strongest; longer than third, but shorter than longest anal rays. Soft anal rounded. Pectorals assymmetrically pointed; fourth or fifth ray longest. Pelvics pointed; first ray longest; reaching two-thirds of distance to anus. Caudal emarginate.

Coloration: head dark above, lighter below; opercular membrane darker than rest of head in many specimens. Body darker dorsally, light ventrally. Overall coloration darker in adults. Spinous dorsal dusky basally; spines lighter. Soft dorsal with

dark basal blotch and light edge; overall coloration getting darker with age. Spinous anal with dusky membranes and lighter spines. Soft anal dusky; margin lighter; dark basal blotch. Caudal dusky. Pectoral dusky; dark blotch at base. Pelvics clear to slightly dusky. The overall coloration of the species ranges from a light brown (paratypes of Therapon brevipinnis) to nearly black.

Distribution; in freshwaters of northwestern Australia from the Meda River drainage in the west to the Victoria system in the east (Fig. 67).

Ecology: this species has been collected in clear to turbid waters, both still and rapidly running over sand, mud and rock bottoms.

Remarks: this species is distinguishable from all other members of the family in its possession of an uninterrupted lip fold across the ventral surface of the lower jaw (Fig. 31). This species was first described from a single specimen collected at Ivanhoe Station on the Ord River and placed by Whitley (1945) in the genus Mesopristes evidently on the basis of its rather long second anal spine. This generic assignment is not supported by any of the available evidence as the species shares with the species of the genus Hephaestus a posterior positioning of the dorsal fin and short dorsal spines. It was put by Mees (1971) in synonymy with H. fuliginosus a species previously considered to be limited to eastern Australia. In the same

publication he also described a new Western Australian teraponid, Therapon brevipinnis from the Hann River.

Examination of Hephaestus material from Western Australia and Northern Territory has revealed the presence of two forms differing in the continuity of the lower lip fold. The form with a continuous lip fold was collected from the Victoria to Daly Rivers. Such a continuous lip fold is found in the type of Mesopristes jenkinsi (John Merrick, pers. comm) and in the paratypes of Therapon brevipinnis (pers. obs.). This information and a comparison of different sizes of Western Australian Hephaestus with the continuous lips supports the hypothesis that these nominal forms are conspecific and that T. brevipinnis is based on juveniles of Hephaestus jenkinsi.

In contrast syntypes of both Therapon fuliginosus and Therapon bancrofti have an interrupted lip fold (R. MacKay, per. comm.) in agreement with the condition in the material from the Daly River to Queensland.

On the basis of the distribution of these species, it would appear likely that the material from Western Australian localities of Mees (1971, p. 199: localities 3-6) is actually H. jenkinsi.

Material examined

Australia, Western Australia: Manning Creek (AMNH 35562*, 10 spec. (of 44), 40-124 mm; AMNH 35668, 275 spec.); Bow

River (AMNH 35663, 4 spec.; AMNH 35666*, 20 spec. (of 116), 50-110 mm). Hann River, Moll Gorge (AMNH 35664*, 15 spec. (of 196), 50-156 mm). Hann River (AMNH 35671*, 5 spec. (of 31), 47-148 mm; RMNH 26399*, 10 spec. (paratypes of Therapon brevipinnis), 35-55 mm). West Baines River (AMNH 35665, 21 spec.). Dunham River (AMNH 35667*, 10 spec. (of 112), 40-120 mm). Grave Creek, Sadler's Spring (AMNH 35669*, 1 spec., 86 mm). Meda River (AMNH 35670*, 8 spec., 60-105 mm). Drysdale River (WAM P-25409-002*, 1 spec., 100 mm).

Hephaestus trimaculatus (Macleay, 1883)

Three spot grunter

Figs. 71 and 72

Therapon trimaculatus Macleay, 1883, p. 259 (original description, Goldie River, New Guinea). Ogilby and McCulloch, 1916, p. 120, pl. 13, fig. 1 (Goldie River; Queensland?). Weber and deBeaufort, 1931, p. 157 (on Ogilby and McCulloch, 1916). Whitley, 1938, p. 228 (upper Fly River, New Guinea).

Therapon habbema Weber, 1910, p. 324 (original description, Lorentz River, New Guinea); 1913, p. 583, figs. 33-34 (Lorentz River). Regan, 1914, p. 276 (Mimika River, New Guinea). Weber and deBeaufort, 1931, p. 155, figs. 28-29 (Lorentz River, Mimika River).

Therapon micracanthus: Fowler, 1931, p. 342 (pt) (New Guinea).

Papuservus trimaculatus: Whitley, 1943, p. 182 (New Guinea); 1960, p. 77, fig. (Papua; Queensland?). Munro, 1967, p. 323 (distribution, indigenous names). Lake, 1971, p. 34 (Australia?). Berra et al, 1975, p. 320 (Laloki River, New Guinea).

Papuservus micracanthus: Munro, 1956, p. 170 (pt).

Amphitherapon habbema: Munro, 1967, p. 321

Nomenclature: the specific name, trimaculatus, from the Latin tri, three, and maculatus, spotted, refers to the three spots at the base of the caudal in smaller individuals of this species. The type series is in the Australian Museum (I.9175 and I. 13410).

Diagnosis: distinguishable from the other species of the genus Hephaestus in having three prominent spots at the base of the caudal fin in smaller specimens (unique to this species in the genus), 9-11 gill rakers on the lower limb of the first arch (in contrast to 14-18 for H. jenkinsi, H. roemeri and H. fuliginosus), 8-11 predorsal scales to the occiput (in contrast to 13 or more in all other members of the genus), and 15-19 scales below the lateral line (in contrast to 20-25 for H. adamsoni, H. carbo and H. suavis).

Description: Dorsal spines XII-XIII; Dorsal rays 10-13; Anal III, 10-11; Pect. 15-16; Pel. I-5; 46-57 lateral line scales; 3-4 scales on caudal; 7-9 scales above lateral line; 15-19 scales below lateral line; 8-11 predorsal scales to occiput; 2-3 rows of scales in sheath at base of dorsal fin, sheath extending across base of all rays in adults, nearly all in juveniles; 4-5 rows of scales in sheath at base of anal fin, sheath extending across base of whole fin except in very small juveniles; cheek scales in 6-7 rows; gill rakers on first arch 5-6+1+9-11; vertebrae 10+17.

Reaching 140 mm SL; depth 2.3-2.9 in SL; distance from dorsal origin to snout 2.1-2.4 in SL; head length 2.6-3.2 in SL; length of base of dorsal fin 1.8-2.2 in SL; snout length 2.6-3.7 in SL; eye width 2.8-5.0 in HL; jaw length 2.7-3.9 in HL; length of longest dorsal spine 2.1-2.7 in HL; length

of longest dorsal ray 1.5-2.2 in HL; length of longest anal spine 2.3-3.0 in HL; length of longest anal ray 1.8-2.0 in HL.

Body moderately deep, compressed. Dorsal profile more pronounced than ventral. Dorsal profile convex from snout to dorsal origin in young; in adults straight from snout to nape, then convex to dorsal origin. Ventral profile convex from lower lip to anus. Jaws equal. Gape slightly oblique. Snout blunt. Maxillary reaching to vertical through anterior of eye. Teeth strong, conic, outer row enlarged; followed by a band of villiform teeth. No teeth on vomer or palatines. Interorbital region smooth. Nostrils separated by a distance equal to one and one-half times diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate; serrations stronger on posterior edge, more so in juveniles. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate along posterior edge, less so in adults; scales on side. Posttemporal exposed; serrate along posterior edge. Supracleithrum exposed.

Spinous dorsal arched; first spine short; fifth to seventh spines longest, those following decreasing in length to penultimate which is shorter than or equal to ultimate. Soft dorsal with anterior rays very high; longer than longest dorsal spines; posterior edge straight. Anal spines short;

second a little longer than third; shorter than longest anal rays. Soft anal rounded. Pectoral assymmetrically pointed; fourth or fifth ray longest. Pelvics pointed; first ray longest, slightly filamentous; reaching to anus. Caudal slightly emarginate.

Coloration: young with interorbital region dark, head lighter below, with a stripe of pigmentation running from snout through eye to opercle and a second stripe on cheek under eye. In larger specimens head is very dark to midway down the cheek; lighter below, with a very dark opercular membrane. Body coloration undergoes two distinct transitions. In juveniles under 20 mm SL, there are five vertical dark bands superimposed on a pattern of longitudinal stripes, First bar runs from nape to opercle; second and third, under spinous dorsal; fourth under soft dorsal; fifth on caudal peduncle. In specimens from 25 mm SL to between 80 and 120 mm SL, the body has eight longitudinal stripes running along side. The first, from anterior of spinous dorsal to end of spinous dorsal; second, from nape to end of soft dorsal; third, from above posttemporal to upper edge of caudal peduncle; fourth, from posttemporal to a fusion on caudal peduncle with third stripe; fifth, from upper opercular spine to middle of caudal peduncle; sixth, from lower opercular spine to lower edge of caudal peduncle; seventh, from pectoral base to soft anal; eighth

(may be lacking) from under pectoral base to end of spinous anal. Stripes four through six line up with spots on the base of caudal. In larger specimens, the stripes are very indistinct or totally masked in largest. Overall coloration blackish. Spinous dorsal with a dark base and lighter edge. Soft dorsal clear with a dark spot basally in young under 30 mm SL ; dusky in adults. Spinous anal dusky with darker edge. Soft anal clear with a basal blotch in young; dusky in adults. Caudal clear in specimens under 25 mm SL; middle basal caudal spot appearing at 25 mm SL, and upper and lower spots at 30 mm SL. Caudal spots masked by overall dark body coloration in specimens above 80-100 mm SL. In larger specimens, the caudal is dusky, being darker basally. Pectoral clear. Pelvics clear to dusky.

Distribution; through the rivers of the southern half of New Guinea in both lowlands and highlands. Specimens recorded from Goldie, Lorentz, Mimika and Fly Rivers. (Fig. 73).

Remarks: Therapon trimaculatus was first described by Macleay (1883) based on material from the Goldie River in southeastern New Guinea. Weber (1910) described another nominal form, Therapon habbema from southwestern New Guinea; a species that Weber and deBeaufort (1931) differentiated from T. trimaculatus on the basis of four characters: the presence of an suprascapular that was hidden below skin and scales, a lateral line count of 54-56; a count of scales above the

lateral line of 10, and a second anal spine much longer than third for I. habbemai in contrast to an exposed posttemporal, a lateral line of 47-50, a supralateral count of 6 1/2-7 1/2, and a second spine slightly longer than third in I. trimaculatus.

An examination of a large series of Hephaestus trimaculatus from the Goldie and Fly Rivers along with a study of seven syntypes of I. habbemai has shown these presumed differences to be the result of differences in procedure or terminology or mistakes in osteological identification.

The first difference utilized by Weber and deBeaufort, the form of the posttemporal is found to be the result of a misinterpretation of the osteology of I. habbemai. Contrary to the description of Weber and deBeaufort, the posttemporal is exposed and serrate along its posterior edge (see also discussion of pectoral girdle nomenclature in introduction). The difference in the count of scales above the lateral line in turn appears to be the result of differing methodologies. Weber and Weber and deBeaufort made the count to the origin of the dorsal fin and included the scales of the dorsal sheath. In contrast Ogilby and McCulloch (1916) whose description of I. trimaculatus was used by Weber and deBeaufort for their comparisons, made the count to the median dorsal spines "excluding the dorsal sheath" (p. 101). Such a difference in procedure results in a difference of 2 or 3 scales in the supralateral scale count.

Examination of the syntypes of Therapon habbemai and material of Therapon (= Hephaestus) trimaculatus from the

region of the type locality (Goldie River) and other localities along with literature information shows no separation on the basis of scales above the lateral line. Similarly, the material shows an overlap in the lateral line counts of the nominal species (H. trimaculatus, 46-56, and I. habbemai, 54-57) along with no differences in the relative lengths of the second and third anal spines (Table 2).

Consequently there do not appear to be any valid distinctions between these forms or any other distinguishing characters. As such Therapon habbemai is considered a synonym of Hephaestus trimaculatus.

Fowler (1928) therefore was evidently correct in his synonymization of I. habbemai into I. trimaculatus though he failed to note or discuss several major differences described in the literature. Later (1931, 1934) he placed both of these forms in synonym with Therapon (= Lagusia) micracanthus a Sulawesi species; and in turn was followed in this by Munro (1956). However, L. micracanthus is quite distinct from the New Guinea forms in having fewer lateral line scales and anal rays and lacking a series of apomorphic character states uniting I. habbemai and I. trimaculatus to their monophyletic group.

Munro (1967) noted this mistake, resurrecting both I. habbemai and I. trimaculatus as distinct species and also correctly hypothesizing the close relationships of H. trimaculatus to H. suavis and H. adamsoni.

Specimens examined

New Guinea, Papua: Central District, Kubuna (AMNH 12629*,
2 spec., 61-77 mm; AMNH 14005*, 7 spec., 87-120 mm)
Central District, Laloki River (USNM 210847*, 14 spec.,
17-148 mm). Western District, Upper Fly River (AMNH
13905*, 3 spec., 99-148 mm).

Indonesia, West Irian, Lorentz River, Stream near Alkmaar
Village (ZMA 112.456*, 7 spec. (syntypes of Therapon
habbema), 94-113 mm).

Hephaestus adamsoni (Trewavas, 1940)

Adamson's grunter

Fig. 74

Therapon adamsoni Trewavas, 1940, p. 284 (original description Lake Kutubu, New Guinea). Munro, 1956, p. 170 (Lake Kutubu). Mees, 1971, p. 213 (Lake Kutubu, comparisons with T. habbema and T. trimaculatus).

Madigania adamsoni: Munro, 1964, p. 174 (Lake Kutubu); 1967, p. 324 (Lake Kutubu).

Nomenclature: the trivial name, adamsoni, is in honor of J. C. Adamson, the collector of the type series. The type series are deposited in the British Museum (Natural History).

Diagnosis: distinguishable from the other members of the genus Hephaestus in having 9-11 gill rakers on the lower limb of the first arch (in contrast to 14-18 for H. roemeri, H. fuliginosus and H. jenkinsi), 17-20 predorsal scales to occiput (vs. 8-11 in H. trimaculatus), 11-12 dorsal rays (in contrast to 13-14 for H. suavis) and a emarginate caudal (in contrast to a truncate caudal in H. carbo).

Description; Dorsal spines XII; Dorsal rays 11-12; Anal III, 9-10; Pect. 13-16; Pel. I-5; 52-56 lateral line scales; 0-2 caudal scales; 9-10 scales above lateral lone; 20-22

scales below lateral line; 17-20 predorsal scales to occiput; 2-3 rows of scales in sheath to base of dorsal fin, sheath extending to sixth to eight dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to seventh anal ray; cheek scales in 7-9 rows; gill rakers on first arch 5-6+1+9-11; vertebrae 11+16.

Reaching 215 mm SL; depth 2.5-3.2 in SL; distance from origin of dorsal to snout 2.1-2.3 in SL; head length 2.6-3.2 in SL; length of base of dorsal fin 2.0-2.3 in SL; snout length 3.2-3.5 in HL; eye width 3.5-5.6 in HL; jaw length 2.6-3.0 in HL; length of longest dorsal spine 3.2-3.8 in HL; length of longest dorsal ray 2.3-2.9 in HL; length of longest anal spine 3.7-4.0 in HL; length of longest anal ray 2.3-2.8 in HL.

Body moderately deep, slightly compressed. Dorsal profile more pronounced than ventral. Dorsal profile in young nearly straight from snout to nape; then evenly convex to dorsal origin. In adults, dorsal profile is concave in interorbital region, then convex to dorsal origin. Ventral profile convex from tip of lower jaw to pelvic insertion; then straight to anus. Jaws equal. Gape oblique. Maxillary reaching vertical through anterior edge of eye. Teeth conic; in bands; outer row enlarged. No teeth on vomer or palatines. Interorbital region smooth. Nostrils separated by a distance equal to or greater than diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate; serrations larger along vertical edge.

Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Posttemporal exposed; serrations on posterior edge. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal arched; first spine short; fourth to eighth spines longest with little differences in length, those following decreasing in length to penultimate which is shorter than or same length as ultimate. Longest dorsal spines shorter than longest dorsal rays. Anal spines short. Second anal spine strong; twice as long as first and usually longer than third which is more slender. Longest anal spine much longer than longest anal rays. Pectoral fin assymmetrically pointed; second or third ray longest. Pelvic fin pointed; second ray longest; reaching nearly to anus in young; falling short with age, reaching only one-half distance to anus. Caudal slightly emarginate.

Coloration: head dark dorsally, lighter ventrally in young. Whole head dark in adults with opercular membrane especially heavily pigmented. Young with seven or eight longitudinal dark stripes. First running along base of spinous dorsal; second, from nape to base of soft dorsal; third, from nape to upper edge of caudal peduncle; fourth, from posttemporal to a fusion with fifth stripe under soft dorsal; fifth, from upper opercular spine to middle of caudal base; sixth, from serrate edge of cleithrum to lower edge of caudal peduncle;

seventh, from pectoral base to rear of soft anal; eighth, from bottom of pectoral base to front of soft anal (lacking in many specimens). In adults, stripes are masked by overall dark body coloration. Ventral region of adults lighter than sides and back. Scales more heavily pigmented on edges. Spinous dorsal dusky. Soft dorsal dusky with pigmentation darker basally. Spinous anal dusky. Soft anal dusky; darker basally. Caudal dusky; darker at base. Pelvics and pectorals dusky in young, very dark in adults.

Distribution: this species appears to be limited to the waters of Lake Kutubu, Papua, New Guinea (Fig. 73). It is presently known from limited materials, evidently being collected only three times: 7 specimens in the type series; 1 specimen in 1939 (see material examined); and 2 specimens (204-212 mm SL) collected in 1955 (see Munro, 1964).

Remarks: this species differs from the original description in having an exposed serrate posttemporal in contrast to Trewavas' statement that the "supracleithrum" (= posttemporal is "covered with scales".

Munro (1964) placed this species in the genus Madigania erected by Whitley (1945a) for Therapon (= Leiopotherapon) unicolor, a freshwater Australian form. However, no evidence has been discovered to support a hypothesis of a close

relationship between these species. Rather Hephaestus adamsoni has a series of derived states of the posttemporal, tabular, extrinsic swimbladder muscle, pigmentation and other characters that are lacking in Leiopotherapon unicolor, but shared with the other species of Hephaestus.

Specimens examined

New Guinea; Papua, Lake Division, Lake Kutubu (AMNH 15103*, 1 spec., 134 mm; BM(NH) 1975.3.1.1.1*, 1 spec. (holotype), 127 mm; BM(NH) 1940.3.11.1-5*, 2 spec.(paratypes), 83-195 mm).

Hephaestus carbo (Ogilby and McCulloch, 1916)

Coal grunter

Fig. 75

Therapon carbo Ogilby and McCulloch, 1916, p. 116, pl. XII,
fig.1 (original description, Gregory River, Queensland).

Grant, 1965, p. 233; 1972, p. 390.

Terapon carbo: Fowler, 1931, p. 352 (on Ogilby and McCulloch)

Hephaestus carbo: Whitley, 1960, p. 75 (Carpentaria drainage
of Queensland). Lake, 1971, p. 34, pl. 69 (life coloration,
biology).

Nomenclature; the trivial name, carbo, from the Latin
carbo, coal, refers to the black coloration of the species.

Diagnosis: Hephaestus carbo can be distinguished from
the other species in the genus in having a truncate caudal
(rather than emarginate or deeply emarginate).

Description: Dorsal spines XI-XII; Dorsal rays 13-14;
Anal III, 11-12; Pect. 15-16; Pel. I-5; 56-60 lateral line
scales; 0-2 scales on caudal; 9-10 scales above lateral line;
21-23 scales below lateral line; 17-20 predorsal scales to
occiput; 3 rows of scales in sheath at base of dorsal fin,
sheath extending across base of all dorsal rays; 4-6 rows of
scales in sheath at base of anal fin, sheath extending across
base of all anal rays; cheek scales in 6-7 rows; gill rakers
on first arch 5-6+1+11-12; vertebrae 10+17.

Reaching 200 mm SL; depth 2.3-2.5 in SL; distance from dorsal origin to snout 2.3-2.4 in SL; head length 2.85-2.0 in SL; length of base of dorsal fin 1.8-2.0 in SL; snout length 2.95-3.15 in HL; eye width 4.7-5.6 in HL; jaw length 2.7-3.1 in HL; length of longest dorsal spine 2.5-3.8 in HL; length of longest dorsal ray 2.1-2.4 in HL; length of longest anal spine 2.6-3.1 in HL; length of longest anal ray 2.1-2.3 in HL.

Body deep, slightly compressed. Dorsal profile more pronounced than ventral. Dorsal profile straight from snout to nape, then distinctly convex to dorsal origin. Ventral profile convex, evenly curved from tip of lower jaw to anus. Upper jaw slightly longer. Gape oblique. Maxillary reaching to vertical through posterior nostril or barely beyond. Teeth villiform, outer row much enlarged, followed by a band of teeth. No teeth on vomer or palatines. Interorbital region smooth. Nostrils separated by a distance equal to one and one-half times diameter of posterior nostril. Lacrimal serrate; serrations very weak in large individuals. Preoperculum serrate; serrations largest on vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; weak serrations along posterior edge; scales on side. Posttemporal exposed. Supracleithrum exposed.

Spinous dorsal low, arched; first spine very short; fifth

to seventh spines longest, all of about same length, those following decreasing very gradually to penultimate which is same length or slightly longer than ultimate. Longest dorsal spine shorter than longest dorsal ray. Soft dorsal rounded. Spinous anal spines, short, stout, curved. First anal spine half as long as second which is slightly longer than third but shorter than longest anal rays. Soft anal rounded. Pectoral assymmetrically pointed; fifth or sixth ray longest. Pelvics pointed; first ray little longer than second in large specimens; slightly filamentous in young; reaching to anus or falling slightly short. Caudal rounded.

Coloration; the overall coloration of the head body and fins is a uniform blackish. Body and head speckled with gold in life (Lake, 1971). In preserved specimens scale pockets of head and body are irregularly lighter. Eye with a surface ring of black along outer edge.

Distribution: found in rivers and streams draining into the Gulf of Carpentaria and the Timor Sea (Fig.73).

Ecology: a species favoring clear, fast flowing waters. Available evidence indicates that the species lays small adhesive eggs after a flood. This usually occurs in late summer months following a monsoon. Fail to reproduce in dammed waters. Omnivorous feeders (Lake, 1971).

Specimens examined

Australia, Queensland, Gregory River (AM I-16118-004*, 4 spec., 137-160 mm).

Hephaestus suavis (Whitley, 1948)

Cichlid grunter

Fig. 76

Leiopotherapon suavis Whitley, 1948, p. 279 (original description, Coen District, North Queensland); 1951, p. 398 (assignment to the subgenus Archerichthys) fig. 6 (photograph of type). Lake, 1971, p. 34 (no locality).

Archeria jamesonoides Nichols, 1949, p. 6 (original description, Archer River at Wenlock Crossing, Cape York, Queensland).

Leiopotherapon (Archerichthys) suavis: Whitley, 1951, p. 398; 1960, p. 80, fig. (behavior).

Nomenclature: the trivial name, suavis, from the Latin suavis, pleasant or agreeable, evidently refers to the life coloration of this species. The type is preserved in the Australian Museum (AM IB-1982).

Diagnosis: Hephaestus suavis is distinguishable from the other members of the genus in having 11 gill rakers on the lower limb of the first arch (in contrast to 14 to 18 in H. fuliginosus, H. roemeri, and H. jenkinsi), an emarginate caudal (in contrast to a truncate caudal in H. carbo), 15-17 predorsal scales (in contrast to 8-11 in H. trimaculatus) and 13-14 dorsal fin rays (in contrast to 11-12 in H. adamsoni).

Description: Dorsal spines XII; Dorsal rays 13-14; Anal III, 10-11; Pect. 15-16; Pel. I-5; 52-58 lateral line scales; 1-2 scales on caudal; 10 scales above lateral line; 20 scales below lateral line; 15-17 predorsal scales to occiput; 2-3 rows of scales in sheath at base of dorsal, sheath extending to eighth to tenth dorsal ray; 3-4 rows of scales in sheath at base of anal fin, sheath extending across base of all anal rays; cheek scales in 7 rows; gill rakers on first arch 6+1+11; vertebrae 11+16.

Reaching 65 mm SL; depth 2.4-2.7; distance from origin of dorsal to snout 2.15-2.4 in SL; head length 2.8-3.0 in SL; length of base of dorsal fin 1.95-2.05 in SL; snout length 3.5-4.4 in HL; eye width 3.1-3.3 in HL; jaw length 3.1-3.6 in HL; length of longest dorsal spine 2.3-2.7 in HL; length of longest dorsal ray 2.2-2.5 in HL; length of longest anal spine 2.4-2.7 in HL; length of longest anal ray 2.2-2.5 in HL.

Body moderately deep, compressed. Dorsal and ventral profiles about equally pronounced. Dorsal profile nearly straight from snout to nape, then slightly convex to dorsal origin. Musculature in area immediately behind occiput forming a distinct bulge. Ventral profile evenly convex from lower lip to pelvic insertion; a distinct angle in profile at insertion; profile convex from pelvic insertion to anus. Jaws equal or lower projecting slightly. Gape moderately oblique. Snout elongate. Maxillary reaching to vertical through

anterior edge of eye in younger specimen, falling shorter with age. Teeth conic; outer row enlarged; inner teeth smaller and in bands. No teeth on vomer or palatines. Interorbital region smooth. Nostrils separated by a distance equal to one and one-half diameters of posterior nostril. Lacrimal serrate, less so in larger specimen. Preoperculum serrate; serrations largest on angle and vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate along posterior edge; scales on side. Posttemporal exposed; serrate along posterior edge. Supracleithrum exposed.

Spinous dorsal low, arched; first spine short, fifth to seventh spines longest, those following decreasing in length to penultimate which is shorter than or about same length as ultimate. Longest dorsal spine shorter than longest dorsal ray. Soft dorsal angular. Second anal spine longest; much longer than first; slightly longer than or subequal to third; shorter than longest anal rays. Soft anal rounded. Pectorals assymetrically pointed; fifth ray longest. Pelvics pointed; first ray longest, slightly filamentous; nearly reaching anus. Caudal truncate; lobes rounded.

Coloration: head with two pale stripes running horizontally from upper and lower edges of eye across opercle. A pale stripe runs from corner of mouth across cheek under eye.

Ground coloration in life yellowish (Whitley, 1948); pale brown in preserved specimens. Body with five to eight irregular vertical bands and 7-8 irregular horizontal stripes. First band running from nape to pectoral; second through fourth, under spinous dorsal; fifth, under intersection of spinous and soft dorsals; sixth, under soft dorsal; seventh and eighth (may be lacking). on caudal peduncle. First stripe running along base of anterior spines; second from nape to front of soft dorsal; third from nape to middle of soft dorsal; fourth, to middle of caudal peduncle; fifth to bottom of caudal peduncle; sixth, from pectoral base to middle of soft anal; seventh, from under pectoral to spinous anal; one or two faint stripes are evident ventral to these. Spinous dorsal dusky. Soft dorsal dusky; darker at base. Spinous and soft anal dusky, lighter at margin. Caudal dark basally; margin lighter. Pectoral dusky. Pelvics blackish.

Distribution: known only from two specimens, the type and the type of Archeria jamesonoides Nichols, both collected in the Coen District, Cape York, Queensland (Fig. 73)

Ecology: nothing is known about the natural activities or habitats of this species. Whitley (1948) who observed some individuals in captivity reports that they are active fish. All the fins except the spinous dorsal appear to be utilized in swimming, a trait similar to that reported by Lake (1971) for H. carbo a close relative.

Remarks: Whitley (1951) suggested that Archeria jamesonoides Nichols might be synonymous with Leiopotherapon (= Hephaestus) suavis. I have examined the types of both species and they are undoubtedly conspecific.

In his original description Whitley (1948) placed this species in the genus Leiopotherapon originally erected by Fowler (1931) as a subgenus for four species characterized by a non-exposed, non-serrate posttemporal covered by skin and scales. However, examination of the type (L. suavis) shows the species to have a posteriorly expanded, serrate posttemporal, exposed along its posterior edge with the scale covering reduced. Furthermore, H. suavis shares with the species of Hephaestus derived states of the posttemporal, tabular, extrinsic swimbladder muscle and other characters lacking in the species placed by Fowler in his subgenus Leiopotherapon. Consequently, the implied close relationship in Whitley's original generic assignation appears to have been erroneous.

Specimens examined

Australia, Queensland: Coen District (AM IB-1982*, 1 spec. (holotype of Leiopotherapon suavis), 65 mm); Cape York, Archer River, Wenlock Crossing (AMNH 18533*, 1 spec. (holotype of Archeria jamesonoides), 51 mm).

Genus 12, Bidyanus

Bidyanus Whitley, 1943, p. 182 (type species Acerina (Cernua) bidyana Mitchell, by original designation).

Nomenclature; the generic name, Bidyanus, from bidyan an aboriginal name noted by T. L. Mitchell for the type species of the genus, Bidyanus bidyanus.

Diagnosis: freshwater Australian teraponids distinguishable from all other members of the family in having depressible but unflattened teeth and 20-25 predorsal scales to the occiput.

Included species: two freshwater Australia species are placed in Bidyanus. One, B. bidyanus is distributed through New South Wales and Victoria, and B. welchi is limited to the internal drainages of Queensland and South Australia.

Bidyanus bidyanus (Mitchell, 1838)

Silver perch

Fig. 77

Acerina (Cernua) bidyana Mitchell, 1838, p. 95, pl.9 (original description, Lat. 29°9'S, river between Gwydi and McIntyre Rivers, New South Wales).

Therapon ellipticus (not of Richardson): Günther, 1859, p. 276 (Namoi River, New South Wales). Klunzinger, 1872, p. 21 (Murray River, Hobson Bay). ?Castelnau, 1873, p. 127 (Swan River, Western Australia). Klunzinger, 1879, p. 350 (Murray River, Port Philip, Hobsons Bay). ?Macleay, 1881, p. 363. ?Waite, 1900. p. 210 (Kimberley, Western Australia).

Therapon ellipticus: Waite, 1904, p. 33. Stead, 1906, p. 122, pl. 14 (New South Wales, Victoria, Queensland, South Australia, Western Australia); 1908, p. 73, pl. 42 (New South Wales).

Therapon niger Castelnau 1872, p. 59 (original description, Murray River); 1873, p. 38 (Murray River). Macleay, 1881, p. 365 (Murray River); 1884, p. 12 (note). Lucas, 1890, p. 19 (Murray River).

Therapon richardsonii Castelnau, 1872, p. 60 (original description, Murray River). Macleay, 1881, p. 362 (Murray River). Lucas, 1890, p. 19 (Murray River). Kent, 1893, p. 282 (Queensland).

Therapon richardsoni: Ramsay, 1881, p. 832 (Macquarie River).

Therapon macleayana Ramsay, 1881, p. 831 (original description, Macquarie River).

Therapon macleayanus: Lucas, 1884, p. 12 (Macquarie River).

Therapon bidyana: McCulloch, 1913, p. 359 (New South Wales).

Ogilby and McCulloch, 1916, p. 112 (Australia). Grant, 1972, p. 389, fig. (biology).

Therapon bidyana: Fowler, 1931, p. 343 (Bourke, New South Wales). Scott, 1962, p. 216, fig. (distribution).

Bidyanus bidyanus: Whitley, 1943, p. 182 (assignment to Bidyanus); 1960, p. 74, fig. (reproduction, distribution). Lake, 1967b, p. 36, (biology, distribution); 1967a, p. 137 (biology, inducement to spawning), 1971, p. 34, pls. 75-77 (biology).

Nomenclature: the trivial name bidyanus is of the same derivation as the generic name.

Diagnosis: Bidyanus bidyanus is distinguished from B. welchi the other member of the genus in having a maximum body width 1.9-2.1 in body depth (in contrast to 1.5-1.7 in B. welchi), 68-72 scales counted in a series above lateral line (in contrast to 76-79), and 59-66 below (in contrast to 71-77).

Description: Dorsal spines XII-XIII; Dorsal rays 11-13; Anal III, 7-9; Pect. 16-17; Pel. 1-5; 55-62 lateral line scales; 76-79 scales counted in a series above lateral line; 71-77 scales counted in a series below lateral line; 6-8 scales on caudal; 12-14 scales above lateral line; 24-27 scales below lateral line; 20-23 predorsal scales to occiput; 3 rows of scales in sheath at base of dorsal fin, sheath extending across base of entire fin; 3-4 rows of scales in sheath at base of anal fin, sheath extending across base of all rays; cheek scales in 7-10 rows; gill rakers on first arch 8-10+1+13-16; vertebrae 11+14.

Reaching 800 mm SL (commonly 400); depth 2.9-3.5 in SL; distance from origin of dorsal to snout 2.6-2.95 in SL; head length 3.3-3.9 in SL; length of base of dorsal fin 1.8-2.0 in SL; maximum body width 1.9-2.2 in body depth; snout length 3.1-3.7 in HL; eye width 4.4-5.3 in HL; jaw length 3.6-4.0 in HL; length of longest dorsal spine 1.8-2.1 in HL; length of longest dorsal ray 1.9-2.2 in HL; length of longest anal spine 1.6-2.1 in HL; length of longest anal ray 1.7-1.8 in HL.

Body elongate; slightly compressed in young, distinctly compressed in adults. Dorsal profile more pronounced than ventral. Dorsal profile straight from snout to nape, then convex to dorsal origin. Ventral profile convex from tip of lower jaw to pelvic insertion, then straight to anus. Jaws equal or upper slightly longer. Gape slightly oblique.

Maxillary reaching to vertical through region between posterior nostril and front of eye. Teeth conic; slightly depressible; villiform, with outer row larger and followed by an inner band. No teeth on vomer or palatines. Interorbital region smooth. Nostrils separated by a distance equal to diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate; serrations largest on posterior edge. Lower opercular spine longer and stronger; not extending beyond opercular lobe. Posttemporal exposed; serrate along posterior edge. Cleithrum exposed; serrate posteriorly, scales on side. Supracleithrum exposed.

Spinous dorsal arched; sixth or seventh spine longest, those following decreasing in length gradually to penultimate which is about same length as ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal rounded. Second anal spine strongest and longest; as long as or slightly longer than anal rays. Posterior of soft anal obliquely truncate. Pectorals pointed; fourth or fifth ray longest. Pelvics pointed; first ray longest and drawn out into a filament; reaching two-thirds of distance to anus. Caudal emarginate.

Coloration: Scott (1962) reports that the body in juveniles bears longitudinal vermiculations; with the fins being clear. In the adults, the head is dark dorsally, with heavier pigment on the opercular flap. Body is silvery with the upper surface dotted with brown; scales having a darker margin. Spinous dorsal clear. Soft dorsal slightly dusky. Spinous anal clear.

Soft anal dusky; more so basally. Caudal dusky. Pectorals clear. Pelvics clear.

Distribution: this species has been recorded from New South Wales, Victoria and South Australia, being distributed in the Darling, Murray, Gwydir, McIntyre, Murrumbidgee and Macquarie Rivers (Fig.78).

Ecology: this species achieves the largest size of any form in the family, reaching 800 mm SL and 8 kg. Lake (1967) has studied in depth the reproductive habits of the species in one of the few works of this type on the family. His results have shown that spawning is initiated by a combination of rise in water temperature to 23°C with an accompanying rise in water levels. The species releases pelagic eggs, being the only freshwater member of the family presently known to do this.

Remarks: Bidyanus bidyanus has been considered to be a member of the freshwater fauna of Western Australia based on Richardson's description (1848) of Datnia elliptica from the rivers of Western Australia; a species which following workers have considered to be a junior synonym of Therapon (=Bidyanus) bidyana. This species was reported by Castelnau from the Swan River (1873) and by Woodward (1900, 1903) from Broom on the coast of west Australia. More recently, the presence of a Western Australian population of the species has been recognized by various workers. . Whitley (1943,

1948, 1956) recognized a separate subspecies Bidyanus bidyanus ellipticus or a separate species Bidyanus elliptica. However, there are reasons to question both the existence of a population of Western Australian B. bidyanus and whether Datnia elliptica should be placed in synonymy with that species.

The presence of the species in Broom a seaside locality distant from any river appears to be a unlikely locality for a species otherwise limited to freshwater. Furthermore neither Nelson, Butler, and Rosen during their extensive collecting in Western Australia nor any other collectors in in the past three-quarters of a century have collected the species in Western Australia. The species is also totally lacking from the collection of the Western Australian Museum, Perth (B. Hutchins, per. comm.) It therefore appears likely that the Western Australian localities are erroneous, either being misidentifications of the specimens involved or incorrect locality records.

In addition, comparison of the original figure and description of the type of Datnia elliptica with the available material of Bidyanus bidyanus and B. welchi shows that D. elliptica agrees more closely with the latter. The illustration shows 10 scales above the lateral line to the base of the dorsal sheath, in agreement with the count for B. welchi (10-12) but not for B. bidyanus (12-14) and 68 scales counted in a series above the lateral line; a count which falls into the

B. welchi range (68-70) but not that of B. bidyana (71-77). Unfortunately, the type of the species (D. elliptica) appears lost and it is not possible to compare various internal characters which differentiate the species.

Bidyanus bidyanus has also been listed as a member of the Philippine fauna on the basis of identification of specimens from Laguna de Bay, Luzon as Therapon bidyana spec. affin. by Meyer (1885) followed by other workers. However, as discussed previously for Leiopotherapon plumbeus, this is probably a misidentification of that species.

Specimens examined

Australia; New South Wales, Darling River, Billabongs at Kinchega National Park (AM I-16002-005*, 3 spec., 190-230 mm); New South Wales. Bourke (USNM 42016*, 1 spec., 191 mm; USNM 42017*, 1 spec., 194 mm; USNM 47795*, 1 spec., 162 mm).

Bidyanus welchi (McCulloch and Waite, 1917)

Welch's grunter

Fig. 79

Therapon welchi McCulloch and Waite, 1917, p. 472 (original description, Cooper Creek near Innamincka, Central Australia). Waite, 1921, p. 97; 1923, pp. 117 and 119.

Terapon welchi: Scott, 1962, p. 217 (South and Central Australia).

Hephaestus welchi: Whitley, 1945, p. 10 (Andrewilla Waterhole, South Australia); 1960, p. 75 (central and south Australia). Lake, 1971, p. 34, pl. 74 (distribution, biology).

Nomenclature: the trivial name, welchi, is in honor of E. J. Welch, a member of the Burke and Wills expedition.

Diagnosis: distinguishable from B. bidyanus the only other member of the genus in having a body width 1.5-1.7 in greatest body depth (in contrast to 1.9-2.1 in B. bidyanus), 76-79 scales counted in a series above the lateral line (in contrast to 68-72), and 71-77 below (in contrast to 59-66).

Description: Dorsal spines XII; Dorsal rays 11-12; Anal 11, 8-9; Pect. 16-17; Pel. 1-5; 50-56 lateral line scales; 68-70 scales counted in a series above lateral line; 59-64 scales counted in a series below lateral line: 6-9 scales on

caudal; 10-12 scales above lateral line; 25-27 scales below lateral line; 20-25 predorsal scales to occiput; 2-3 rows of scales in sheath at base of dorsal fin, sheath extending to eighth or ninth dorsal ray; 4 rows of scales in sheath at base of anal fin, sheath extending across base of all rays; cheek scales in 5-7 rows; gill rakers on first arch 8-9+1+14-17; vertebrae 11+14.

Reaching 230 mm SL; depth 3.1-3.3 in SL; distance from dorsal origin to snout 2.8-3.1 in SL; head length 3.5-3.8 in SL; length of base of dorsal 1.8-2.0 in SL; snout length 3.1-3.3 in HL; eye width 5.0-6.6 in HL; jaw length 3.3-3.65 in HL; length of longest dorsal spine 2.1-2.5 in HL; length of longest dorsal ray 2.9-3.7 in HL; length of longest anal spine 2.0-2.3 in HL; length of longest anal ray 1.9-2.2 in HL; body width 1.9-2.1 in body depth

Body elongate, slender, slightly compressed. Dorsal and Ventral profiles evenly arched. Dorsal profile straight from snout to nape, then convex to dorsal origin. Ventral profile evenly arched to ventral insertion, then straight to anus. Upper jaw slightly longer. Gape nearly horizontal. Snout elongate. Maxillary reaching to vertical through posterior nostril. Teeth conic; slightly depressible; outer row enlarged; followed by villiform teeth in bands. No teeth on vomer or palatines. Interorbital region smooth, flat. Nostrils

separated by a distance equal to diameter of posterior nostril. Lacrimal serrate. Preoperculum serrate; serrations largest on angle. Lower opercular spine longer and stronger; reaching nearly to edge of opercular lobe. Cleithrum exposed; serrate along posterior edge; scales on side. Supracleithrum exposed. Posttemporal exposed; serrate along posterior edge.

Spinous dorsal arched; first spine very short; fifth or sixth longest, those following decreasing in length to ultimate. Longest dorsal spine longer than longest dorsal ray. Posterior edge of soft dorsal slightly convex. Second anal spine very strong; longer than third; about twice as long as first. Second anal spine as long as longest anal ray. Pectorals pointed; fifth ray longest. Pelvics pointed; first ray longest; reaching one-half distance to anus

Coloration: overall coloration yellowish or brownish, slightly darker above. Body dusky with each scale with a spot of heavier pigmentation along edge of scale pocket. On caudal peduncle, these join together in some specimens to form irregular longitudinal vermiculations. Median fins with slightly dusky membranes. Caudal dusky at base. Pelvics slightly dusky. Pectorals colorless.

Distribution; from Barcoo, Georgina and other internal drainages of western Queensland and South Australia (Fig. 78).

Remarks: Scott (1962) questioned the distinctiveness of this species from B. bidyana. Based on the material available the species appear to be distinct. However, it is possible that

these are two extremes of one species showing marked variation.

As discussed earlier (see remarks after B. bidyanus), Datnia elliptica a species placed by previous workers as a synonym of B. bidyanus appears to be equivalent to B. welchi. However, the type of D. elliptica appears lost and it is not possible to verify counts taken from the illustration with the actual specimen.

Specimens examined

Australia; Queensland, Georgina River, Parapiturie (AM

I. 16023-001*, 2 spec., 185-200); Marion Downs

(AM I-16024-001*, 1 spec., 200 mm).

Genus 13, Scortum

Scortum Whitley, 1943, p. 183 (type species Therapon parviceps Macleay, by original designation).

Nomenclature: the generic name, Scortum, Latin for leather or hide refers to the leathery texture of the flesh of members of this genus.

Diagnosis: members of the genus Scortum are distinguishable from other genera in the family in having depressible slightly flattened teeth, irregular black blotches randomly distributed over the body (condition unknown in S. barcoo), retention of vomerine teeth into the adults (also found in Terapon jarbua) and leathery textured flesh.

Included species: three species, all from the freshwaters of eastern Australia are placed in the genus Scortum. S. barcoo known only from the type comes from Cooper Creek (Barcoo Creek) in the internal drainages. S. parviceps is limited to the upper Burdekin of Queensland and S. hillii is distributed from the eastern drainages of Queensland to the Gulf or Carpentaria drainages and internal drainages.

Scortum parviceps (Macleay, 1884)

Small headed grunter

Fig. 80

Therapon parviceps Macleay, 1884, p. 201 (original description, upper Burdekin River, Queensland). Ogilby and McCulloch, 1916, p. 124, pl. XI, fig. 3 (upper Burdekin River).

Therapon parviceps: Fowler, 1931, p. 341 (after Ogilby and McCulloch).

Scortum parviceps: Whitley, 1943, p. 183 (no locality); 1960, p. 78 (upper Burdekin River). Lake, 1971, p. 34 (no locality).

Nomenclature: the trivial name, parviceps, from the Latin parvus, small, and new Latin ceps, head, refers to the relatively smaller head of this species in comparison to those of other members of the genus. The lectotype of the species is deposited in the Australian Museum (A.17847).

Diagnosis: S. parviceps can be distinguished from the other species of the genus in having 4-6 cheek scales (in contrast to 7-8 in S. barcoo), 51-61 series of scales counted above the lateral line (in contrast to 63-71 for S. hillii and 82 for S. barcoo), and 8-10 scales above the lateral line (in contrast to 11-13 for S. hillii).

Description: Dorsal spines XIII; Dorsal rays 10-11; Anal III, 9; Pect. 15-16; Pel. I-5; 49-53 lateral line scales; 3-4

scales on caudal; 8-10 scales above lateral line; 20-22 scales below lateral line; 16-20 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal, sheath extending to seventh of eighth dorsal ray; 3-4 rows of scales in sheath at base of anal, sheath extending across base of all rays; cheek scales in 4-6 rows; gill rakers on first arch 9-10+1+18-22; vertebrae 11+14.

Reaching 175 mm SL; depth 2.6-2.9 in SL; distance from origin of dorsal fin to snout 2.5-2.7 in SL; head length 3.0-3.5 in SL; length of base of dorsal fin 1.65-1.8 in SL; snout length 3.0-3.5 in HL; eye width 3.7-5.0 in HL; jaw length 3.4-3.8 in HL; length of longest dorsal spine 1.8-2.0 in HL; length of longest dorsal ray 1.8-2.0 in HL; length of longest anal spine 2.2-2.5 in HL; length of longest anal ray 1.6-1.7 in HL

Body moderately deep; compressed. Dorsal profile straight or slightly convex to nape, then straight to origin of dorsal fin. Dorsal profile much more pronounced than ventral. Ventral profile straight to isthmus; slightly convex from isthmus to insertion of pelvics, then straight from insertion to anus. Jaws equal, lower jaw slightly flattened, with teeth projecting slightly outwards. Gape horizontal. Snout elongate. Maxillary reaching to vertical through anterior of eye in young, falling short with age, reaching only to vertical through posterior nostril. Teeth slightly flattened, depressible with outer row enlarged. Young with vomerine teeth. Vomers and

palatines smooth in adults (some adults with one or two vomerine teeth). Interorbital region smooth. Nostrils separated by a distance equal to or slightly greater than diameter of posterior nostril. Lacrimal serrate in young ; serrations reduced in adults. Preoperculum serrate; serrations largest on angle. Lower opercular spine stronger and longer; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed. Posttemporal exposed; serrate along posterior edge.

Spinous dorsal arched; first spine very short; fifth or sixth spines longest, those following decreasing in length to penultimate which is approximately as long as ultimate. Longest dorsal spine longer than longest dorsal rays. Soft dorsal angular; posterior border straight. Second and third anal spines subequal; longest shorter than longest anal rays. Posterior margin of soft anal obliquely truncate or slightly convex. Pectorals assymmetrically pointed; first ray longest and slightly filamentous; reaching to anus; falling short with age. Caudal deeply emarginate.

Coloration: head darker above, light below; band of pigmentation runs from tip of snout to lower margin of eye. Opercular membranes heavily pigmented around lower opercular spine. Body darker above; with random dark blotches on sides. Edges of scales more heavily pigmented. Spinous dorsal with pigmentation more pronounced along anterior edges of spines. Soft dorsal dusky with lighter margins. Spinous and soft anal

dusky, margin much lighter. Caudal clear to dusky with a light margin. Pectorals dusky, Pelvics yellowish.

Distribution: this species appears to be limited to the upper reaches of the Burdekin River, Queensland (Fig. 81).

Specimens examined

Australia: Queensland, Burdekin River: 263 miles inland (AM

A. 13708*, 1 spec., 163 mm); (AM A. 17853*, 1 spec., 94 mm; AM A. 17854*, 1 spec., 94 mm; AM IA. 5949*, 1 spec., 175 mm).

Scortum hillii (Castelnau, 1877)

Leathery grunter

Fig. 82

Therapon hillii Castelnau, 1877, p. 226 (original description, Dawson River at Taroom). Ogilby and McCulloch, 1916, p. 121, pl. 12, fig. 2 (Dawson River, Norman River). Grant, 1965, p. 223; 1972, p. 390.

Terapon hillii: Fowler, 1931, p. 340 (after Ogilby and McCulloch).

Scortum hillii: Whitley, 1943, p. 184 (no locality); 1960, p. 78 (Dawson River). Lake, 1971, p. 34 (biology).

Scortum ogilbyi Whitley, 1951, p. 397 (original description, Norman River, Queensland); 1960, p. 78 (Norman River). Lake, 1971, p. 34 (biology).

Nomenclature: the trivial name, hillii, is in honor of Mr. Hill who was director of the Brisbane Botanical Gardens.

Diagnosis: S. hillii is distinguishable from the other species of Scortum in having 63-71 scales in a series counted above the lateral line (in contrast to 51-61 in S. parviceps and 92 in S. barcoo) and 11 to 13 scales above the lateral line (in contrast to 8-10 for S. barcoo).

Description; Dorsal spines XIII, Dorsal rays 11-13; Anal

8-10; Pect. 15-17; Pel. 1-5; 50-62 lateral line scales; 3-5 scales on caudal; 11-13 scales above lateral line; 22-28 scales below lateral line; 14-18 predorsal scales to occiput; 2 rows of scales in sheath at base of dorsal fin, sheath extending to fourth or fifth dorsal ray; 3-4 rows of scales in sheath at base of anal fin, sheath extending to seventh to tenth anal ray; cheek scales in 5-6 rows; gill rakers on first arch 8-13+1+16-26; vertebrae 11+14.

Reaching 270 mm SL; depth 2.5-3.0 in SL; distance from snout to dorsal origin 2.5-2.8 in SL; head length 3.05-3.4 in SL; length of base of dorsal fin 1.6-1.8 in SL; eye width 3.5-5.7 in HL; jaw length 3.4-4.5 in HL; length of longest dorsal spine 1.7-1.8 in HL; length of longest dorsal ray 2.1-2.2 in HL; length of longest anal spine 1.8-2.2 in HL; length of longest anal ray 1.6-1.9 in HL.

Body moderately deep, slightly compressed, more so in adults. Dorsal profile much more pronounced than ventral in juveniles, only slightly more in adults. Dorsal profile nearly straight from snout in interorbital region, concave above eyes, then convex to dorsal origin. Dorsal profile of adults straighter overall. Ventral profile straight from lower jaw to anus in young, gently curved in adults; more pronounced in larger specimens. Jaws equal. Gape oblique. Snout blunt, more so in adults. Maxillary reaching to vertical through posterior nostril or anterior of eye. Teeth partially flattened (less so than in the species of the genera Pingalla and Syncomistes), depressible; in bands with outer row enlarged. Teeth

variably present on vomers; lacking on palatines. Nostrils separated by a distance equal to diameter of posterior nostril. Lacrimal serrate; strongly in young; serrations obscure or lacking in larger individuals. Preoperculum serrate; serrations stronger on angle and vertical edge; becoming weaker with age. Lower opercular spine stronger and longer; not extending beyond edge of opercular lobe. Posttemporal exposed; posterior edge serrate. Cleithrum exposed; posterior edge serrate; serrations weaker with age: scales on side. Supracleithrum exposed.

Spinous dorsal arched; first spine short; fifth to sixth longest, those following decreasing gradually to the penultimate which is slightly shorter than ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal rounded. Second anal spine twice as long as first spine; much longer than third in juveniles, less so in adults where they may be of the same length. Soft anal rounded in young, more angular in adults. Pectoral fins assymetrically pointed; fourth or fifth rays longest. Pelvics pointed; first ray longest, slightly filamentous; reaching three-quarters of distance to anus. Caudal emarginate.

Coloration: Head darker above, light below; without any prominent markings. Body olive or greyish on back and sides. Irregular spots of varying size and position distributed over sides. Overall coloration much lighter in juveniles. Spinous dorsal uniformly dusky; lighter in young. Soft dorsal dusky with lighter edge and dark basal blotch. Caudal uniformly

dusky, darker in adults. Pectorals dusky; more heavily pigmented at base. Pelvics dusky.

Distribution: found in rivers of Queensland draining the Pacific, Gulf of Carpentaria and the internal drainages. Known from the Dawson, Norman, Saxby, Forest, and Thompson Rivers (Fig. 81).

Remarks: Whitley (1951) described a species, Scortum ogilbyi, based on the Norman River specimens of Therapon hillii used by Ogilby and McCulloch (1916) in their description of that species. The new species was distinguished from T. hillii by differences in lateral line counts and body proportions. However, based on the material that I have examined, I cannot find any basis for the continued maintenance of S. ogilbyi as a species distinct from S. hillii. The differences cited by Whitley for the distinction based on lateral line counts appear to have resulted from limited material. Based on material examined and literature information, specimens from the Dawson River (type locality of S. hillii) have 52-61 lateral line scales and those from the Norman River (type locality of S. ogilbyi) 50-55.

The other major difference cited by Whitley, differences in body depths, also do not appear to separate the populations. The supposed difference in this character appears to be the result of the fact that Whitley used for comparative purposes the original description of Therapon hillii by Castelnau (1878). However, as discussed by Ogilby and McCulloch, Castelnau's

measurements appear to have been given as proportions of total length rather than standard length, a hypothesis consistent with material examined. The remaining differences cited by Whitley, relative lengths of the second and third anal spines and extent or emargination of the caudal fin also appear to be within expected ranges of variation.

Specimens examined

Australia, Queensland: Saxby River (AM I-7942-008* (as Scortum ogilbyi), 1 spec., 95 mm); Dawson River (AM I-18013-001*, 3 spec., 225-270 mm); Thompson River (ANSP 95571*, 2 spec., 143-144 mm); Forest Home Station, Gulf of Carpentaria (ANSP 122162\$, 1 spec., 87 mm).

Scortum barcoo (McCulloch and Waite, 1917)

Barcoo grunter

Fig. 83

Therapon barcoo McCulloch and Waite, 1917, p. 474, fig. (original description, Cooper Creek, Central Australia).

Scortum barcoo: Whitley, 1943, p. 184 (no locality); 1960, p. 78 (Cooper Creek). Lake, 1971, p. 34 (no locality).

Terapon barcoo: Scott, 1962, p. 216, fig. (Cooper Creek, Central Australia).

Nomenclature: the trivial name, barcoo, refers to the type locality of the species, Barcoo or Cooper's Creek.

Diagnosis: Scortum barcoo can be distinguished from all other species in the genus in having 82 scales counted in a series above the lateral line (in contrast to 71 or fewer in S. parviceps and S. hillii).

Description: Dorsal spines XIII; Dorsal rays 12; Anal III, 8; Pect. 16; Pel. I-5; 82 scales counted in a series above lateral line to hypural base; 70 scales counted in a series below lateral line to hypural base; 12 scales above lateral line; 2 rows of scales in sheath at base of dorsal fin (from figure), sheath extending to tenth dorsal ray (from figure); 2-4 rows of scales in sheath at base of anal fin, sheath extending across base of entire fin (from figure); cheek scales in 7-8 rows.

Reaching 140 mm SL; depth 2.1 in SL; head length 3.2 in SL; snout length 3.7 in HL; eye width 4.8 in HL; length of longest dorsal spine 2.0 in HL; length of longest anal spine 2.2 in HL.

Body moderately deep compressed. Dorsal profile convex from nape to origin of dorsal; about as pronounced as ventral profile. Head almost flat above. Interorbital region flat, with boney ridges. Ventral profile straight from lower lip to pelvic insertion; then curved to anus. Jaws equal. Gape oblique. Snout pointed. Maxillary reaching to vertical through posterior nostril. Teeth minute; outer series little enlarged; subcardiform; slightly depressible. Vomer with three or four small teeth in middle. Palatines without teeth. Nostrils with free cutaneous edges separated by a distance slightly greater than diameter of posterior nostril. Lacrimal serrate posteriorly. Preoperculum serrate; largest serrations on angle. Lower opercular spine longer and stronger; not extending beyond edge of opercular flap. Posttemporal exposed; serrate along posterior edge. Cleithrum exposed; serrate; scales on side. Supracleithrum exposed.

Spinous dorsal arched; fifth spine longest, those following decreasing in length to ultimate. Longest dorsal spine longer than longest dorsal rays. Soft dorsal rounded. Second anal spine longest; shorter than longest anal rays. Soft anal rounded. Pectorals assymmetrically pointed; fifth ray longest. Pelvics inserted behind vertical through first dorsal spine;

first ray longest (from figure); reaching a little more than half distance to anus. Caudal emarginate.

Coloration: the species is known only from the type which is completely bleached.

Distribution: from Cooper (Barcoo) Creek of Central Australia (Fig. 81)

Remarks: the above description is taken from the original description and accompanying figure of McCulloch and Waite (1917). Despite the limited information available on the species and the fact that the type was not examined, there do not appear to be any other nominal species identical to S. barcoo. The species shares with the other species of Scortum a retention of vomerine teeth into adulthood and depressible dentition. Consequently, following previous procedures, this species is placed in the genus Scortum. It should be noted however, that it does share an overall resemblance to the species of the genus Pingalla especially in its small mouth with a strongly ventrally curved maxillary.

Genus 14, Pingalla

Pingalla Whitley, 1953, p. 45 (type species, Pingalla gilberti by original designation).

Nomenclature: the generic name, Pingalla, was not explained by Whitley and is of unknown significance.

Diagnosis: the genus Pingalla can be distinguished from all other groups in the family in having only two distinct rows of teeth in each jaw. In addition the combination of a very small mouth, with a strongly curved maxilla and very depressible flattened non-cuspidate teeth further separate them from all other species in the family.

Included species: two freshwater species are placed in the genus; P. gilberti from northern Australia and P. lorentzi from southern West Irian.

Remarks: Whitley (1953) in the original description of Pingalla, placed it in the subfamily Helotinae with the genus Helotes; removing one species (lorentzi) from the latter to Pingalla and describing a new species (P. gilberti). Although Whitley's assumption of a close relationship between the species of the genus Pingalla (gilberti and lorentzi) is supported by the findings of this study, the subfamily Helotinae (sensu Whitley) does not appear to be monophyletic as Helotes.

(= Pelates) sexlineatus lacks a series of apomorphic states of several characters (posttemporal, tabular, extrinsic swim-bladder muscles, dentition, and intestinal patterns) uniting the species of Pingalla and their closest relatives. Similarly, the hypothesis of a close relationship between Helotes sexlineatus (= Pelates sexlineatus) and Pingalla lorentzi as advanced by Weber's placement of the latter species in Helotes (1910) also appears to be falsified by the results of this study (see also discussion under P. lorentzi).

Pingalla lorentzi (Weber, 1910)

Lorentz's grunter

Fig. 84

Helotes lorentzi Weber, 1910, p. 326 (original description, Lorentz River, New Guinea); 1913, p. 586, fig. 36 (Lorentz River at Regen Island). Weber and deBeaufort, 1931, p. 167, fig. 31 (Lorentz River near Regen Island, Noord River, upper Digul River). Fowler, 1931, p. 365 (after Weber).

Pingalla lorentzi: Whitley, 1953, p. 46 (assigned to the sub-family Helotinae). Munro, 1956, p. 169 (distribution); 1967, p. 320 (south West Irian).

Nomenclature: the trivial name, lorentzi, is in honor of H. A. Lorentz a member of the expedition to Dutch New Guinea which collected the type series.

Diagnosis: Pingalla lorentzi can be distinguished from the other member of the genus in having 13-14 dorsal spines (in contrast to 11-12 in P. gilberti) and 48-54 lateral line scales (in contrast to 35-41 for P. gilberti).

Description: Dorsal spines XIII-XIV; Dorsal rays 11-13; Anal III, 8-9; Pect. 15; Pel. I-5; 48-54 lateral line scales; 5-6 scales on caudal; 6-7 scales above lateral line; 13-14 scales below lateral line; 11 predorsal scales to occiput;

2 irregular series of scales in sheath at base of dorsal fin, sheath extending to seventh or eighth dorsal ray; 3 rows of scales in sheath at base of anal fin, sheath extending to fifth anal ray; cheek scales in 5 rows; gill rakers on first arch 6+1+11-12; vertebrae 11+14.

Reaching 210 mm SL; depth 2.3-2.5 in SL; distance from dorsal origin to snout 2.3-2.45 in SL; head length 2.6-3.6 in SL; length of base of dorsal fin 1.6-1.8 in SL; snout length 3.1-3.2 in SL; eye width 3.6-4.5 in HL; jaw length 4.0-4.5 in HL; length of longest dorsal spine 1.7-2.0 in HL; length of longest dorsal ray 2.0-2.1 in HL; length of longest anal spine 1.7-2.0 in HL; length of longest anal ray 1.8-2.2 in HL.

Body moderately deep, compressed. Dorsal profile more pronounced than ventral. Dorsal profile straight from snout to dorsal origin. Ventral profile straight or slightly convex to pelvic insertion, then straight to anus. Jaws equal or upper slightly longer. Gape oblique. Mouth small; practically non-protractile; with posterior of maxillary strongly curved ventrally. Maxillary reaching to middle of snout, approximately to vertical through region between anterior and posterior nostrils. Teeth depressible, distinctly flattened, brown tipped. Two rows of dentition in each jaw; outer row distinctly enlarged; inner row smaller, less flattened, embedded in fleshy tissue. No teeth on vomer or palatines. Interorbital region smooth. Lacrimal serrate posteriorly. Preoperculum serrate; serrations strongest

on vertical edge. Lower opercular spine stronger and longer; not extending beyond edge of opercular lobe. Posttemporal exposed; serrate along posterior edge. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal strongly arched; first spine very short; fifth to seventh spines longest, those following decreasing in length to penultimate which is slightly longer than ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal with posterior edge straight; corners rounded. Second anal spine longest; twice as long as first spine; not as long as longest anal rays. Soft anal rounded. Pectorals assymetrically pointed; fourth ray longest. Pelvics pointed; first ray longest. slightly filamentous; reaching to anus or falling slightly short. Caudal emarginate.

Coloration: (from Weber and deBeaufort, 1931) Head dark above, lighter below. Body uniformly dark, especially along back. Scales of side and belly with a central silvery hue. Spinous and soft dorsal dusky with lighter margins. Spinous and soft anals dusky, edges light. Pectorals and pelvics dusky.

Distribution: south West Irian. Reported from the Lorentz, Noord, and Digul (Digoel) Rivers. (Fig. 85).

Remarks: this species was placed in the previously monotypic genus Helotes by Weber (1910) followed by a series of other workers, on the basis of similarity in tooth forms. However, whereas the teeth of Helotes sexlineatus (= Pelates

octolineatus) are distinctly tricuspidate, with an elongate central cusp flanked by distinct lateral cusps, the teeth of the species of Pingalla lack the distinctive side cusps, rather having lateral shoulders on each tooth. Although this is somewhat similar in overall form, a hypothesis of a close relationship between the species placed by Weber in Helotes is falsified by a series of derived states of the posttemporal, tabular, extrinsic swimbladder muscle, swimbladder, intestine and other characters uniting P. lorentzi with other groups as a monophyletic unit- character states lacking in Pelates octolineatus.

Specimens examined

Indonesia, West Irian, southern: Dogoel River near Tanah Merah (RMNH 25390*, 2 spec., 51-53 mm); Digoel River (ZMA 112.448*, 1 spec., 49 mm).

Pingalla gilberti Whitley, 1953

Gilbert's grunter

Fig. 86

Pingalla gilberti Whitley, 1953, p. 46 (original description, Gilbert River, Queensland); 1960, p. 81 (Gilbert River). Lake, 1971, p. 34, pl. 79 (Gilbert and Norman river drainages).

Nomenclature: the trivial name, gilberti, honors

John Gilbert a naturalist in Leichhardt's expedition and after whom the type locality of the species, the Gilbert River, is also named. The holotype is deposited in the Australian Museum (IB.3148).

Diagnosis: P. gilberti is distinguishable from the other member of the genus in having 11-12 dorsal spines (in contrast to 13-14 in P. lorentzi) and 35-41 lateral line scales (in contrast to 48-54 for P. lorentzi).

Description: Dorsal spines XI-XII; Dorsal rays 11-13; Anal III, 7-9; Pect. 13-17; Pel. I-5; 34-41 lateral line scales; 4-5 scales on caudal; 4-6 scales above lateral line; 10-12 scales below lateral line; 3-9 predorsal scales to occiput; 2 irregular rows of scales in sheath at base of dorsal, sheath extending to fifth or sixth dorsal ray; 3-4 rows of scales in sheath at base of anal fin; sheath extending to fifth anal ray; cheek

scales in 4 rows; gill rakers on first arch 6-7+1+11-12; vertebrae 11+14.

Reaching 65 mm SL; depth 2.4-2.9 in SL; distance from origin of spinous dorsal to snout 2.3-2.6 in SL; head length 3.0-3.25 in SL; length of base of dorsal fin 1.8-2.0 in SL; snout length 2.6-3.0 in HL; eye width 3.2-3.8 in HL; eye width 3.2-3.8 in H.; jaw length 4.1-4.4 in HL; length of longest dorsal spine 1.9-2.1 in HL; length of longest dorsal ray 2.0-2.2 in SL; length of longest anal spine 1.8-2.0 in HL; length of longest anal ray 1.95-2.1 in HL.

Body moderately deep, compressed. Dorsal profile more pronounced than ventral. Dorsal profile convex from snout to interorbital region, then straight to dorsal origin. Ventral profile curved from tip of lower jaw to pelvic insertion, straight from pelvic insertion to anus. Jaws equal or upper a bit longer. Gape oblique. Mouth small, non protractile. Posterior of maxillary strongly curved downwards; reaching to vertical through posterior nostril or falling slightly short. Snout blunt. Teeth flattened, brown, depressible, in two rows in each jaw. Outer row of teeth protruding laterally slightly. Inner row of teeth smaller, less flattened and imbedded in fleshy inner surface of mouth. Vomer and palatines without teeth. Nostrils separated by a distance twice greatest diameter of posterior nostril. Lacrimal with three or four small serrations. Preoperculum serrate; serrations largest on

angle. Lower opercular spine stronger and longer, not extending beyond edge of opercular lobe. Posttemporal exposed; serrate posteriorly. Cleithrum exposed; serrate posteriorly; scales on side. Supracleithrum exposed.

Spinous dorsal arched; first spine very short; fourth to sixth spines longest, those following decreasing gradually in length to penultimate which is shorter than ultimate. Longest dorsal spine longer than longest dorsal rays. Soft dorsal rounded. Second anal spine twice as long as first; longer and much stronger than third; shorter than longest anal rays. Pectoral fin assymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest, slightly filamentous; falling short of anus. Caudal emarginate.

Coloration: in life the eye is surrounded by pale yellow, head darker above, light below, with a band of pigmentation running from eye to snout. Opercular region dark. Body silvery in life with each scale outlined with dusky green (Whitley, 1953). Body of preserved specimens dusky above; scales with pigmented edges. Smaller specimens with two or three longitudinal stripes that are lost with age. First running from nape to base of soft dorsal; second, from nape to dorsal edge of caudal peduncle; third, from posttemporal to middle of caudal peduncle. All stripes are slightly curved upwards. Scales of dorsal sheath with marked spots of darker pigmentation. Dorsal fins pale olive in life (Whitley, 1953) dusky in preserved material and covered with black dots. Anal fin membranes

dusky, with a blackish blotch on anterior rays. Caudal dusky with lighter margin. Pectorals and pelvics yellowish in life, slightly dusky or clear in preserved specimens.

Distribution: this species is presently known only from the Gilbert and Norman Rivers of Queensland and the South Alligator River of Northern Territory (Fig. 85). The Northern Territory material is a major range extension and it would appear likely that the species is distributed in many of the stream and rivers draining into the southern and western areas of the Gulf of Carpentaria.

Remarks: Whitley in his original description of the species notes with respect to the dentition that it has "A practically single row of....incisors on jaws." Examination of available material has shown, however, that there are two distinct rows of teeth in each jaw; a condition also occurring in the type (J. Paxton, pers. comm). Whitley also states that the preorbital is entire in the type. In available specimens, however, there occur several serrations along the posteroventral edge of the bone.

Specimens examined

Australia, Northern Territory; (AM. I-16859-018*, 2 spec., 60-64 mm; AM. I-16858-018*, 2 spec, 62-65 mm); Barramundie Creek (AMNH 35638*, 14 spec., 44-51 mm); South Alligator River (AMNH 35639*, 2 spec., 55-56 mm; AMNH 35640*, 4 spec., 49-54 mm).

Genus 15, Syncomistes n. gen.

Nomenclature: the generic name, Syncomistes, is a masculine Greek noun meaning gatherer, in reference to the algae cropping habits of the members of this genus.

Diagnosis: the species of the genus Syncomistes form one of the most distinctive groups in the family in overall appearance. Characters unique to this group in the family are the presence of a highly flattened lower jaw with markedly flattened laterally pointing dentition; the presence of a unique form of rounded rostral cartilage (see phylogenetic analysis) and short but wide ascending processes of the premaxillaries. Further characters distinguishing the group are the very elaborate intestinal pattern, a secondarily reduced constriction between the swimbladder chambers and other characters.

Type species: Syncomistes butleri n. sp.

Included species: three species from the freshwaters of northwestern Australia are presently known. One of these S. butleri has a relatively widespread distribution through the region, while the other two (S. triqonicus and S. kimberleyensis) are of limited distribution. *

*, another species of this group will be described in an independent work at a later date.

Syncomistes butleri n. sp.

Butler's grunter

Figs. 87 and 88

Nomenclature; the specific name, butleri, honors Mr. W. Harry Butler, a member of the American Museum of Natural History-Australian Expedition of 1969.

Diagnosis: Syncomistes butleri can be differentiated from the other species in the genus in having a rounded lower jaw from the ventral aspect (in contrast to a triangular lower jaw in S. trigonicus [see figure 30]), 5 or 6 longitudinal body stripes in the juveniles with the median stripe the widest (in contrast to 3 irregular stripes all of the same width in juveniles of S. kimberleyensis) and relative head lengths (see figure 89).

Description: (numbers in parentheses are number of examined specimens having a given count), Dorsal spines and rays XII-11(2), XII-12 (43), XII-13(73), XII-14(9), XIII-11(4), XIII-13(2); Anal spines 3, rays 8(13), 9(100), 10(20); Pectoral rays 14-17; Pelvics I-5; lateral line scales from origin to hypural joint 47(5), 48(3), 49(12), 50(40), 51(46), 52 (10), 53(7), 54(7), 55(3); 5-7 caudal scales; transverse series to base of dorsal sheath at median dorsal spines 7+1+15(9), 7+1+16(18) 7+1+17(13), 7+1+18(6), 8+1+15(16), 8+1+16(28), 8+1+17(33),

8+1+18 (10); 14-17 predorsal scales to occiput; cheek scales in 5-7 rows; 2-3 rows of scales in sheath at base of dorsal fin, sheath extending to eighth or ninth dorsal ray; 3-5 rows of scales in sheath at base of anal fin, sheath extending to seventh to eighth anal ray; gill rakers on first arch 6-8+1+15-18; vertebrae 11+14.

Reaching 200 mm SL; depth 2.4-3.35 in SL; distance from origin of spinous dorsal to snout 2.2-2.6 in SL; head length 2.75-3.5 in SL; length of base of dorsal fin 1.7-2.2 in SL; snout length 2.4-3.0 in HL, getting relatively larger with increasing age; eye width 3.0-5.25 in HL, getting relatively smaller with increasing age; jaw length 3.0-3.8 in HL; length of longest dorsal spine 1.6-2.0 in HL; length of longest dorsal ray 1.9-2.3 in HL; length of longest anal spine 1.4-2.0 in HL; length of longest anal ray 1.5-2.0 in HL.

Body moderately deep, not very compressed. Dorsal profile more pronounced than ventral. Dorsal profile of head convex in young, getting straighter or even slightly concave with age. Ventral profile curved from lower jaw to anus. Interorbital region smooth. Jaws equal. Gape nearly horizontal. Maxillary slightly curved ventrally along posterior one third; reaching to vertical through posterior nostril. Each jaw with a large series of enlarged distally flattened, depressible teeth. Distal one third of teeth are brown tipped. Inside row of enlarged dentition is a narrow band of similar shaped smaller teeth. At symphysis of dentary there is a dorsally directed bump that fits

into a corresponding depression between the premaxillaries. Both bump and depression without teeth. Vomer and palatines without teeth. Nostrils close together, separation equal to or less than diameter of posterior nostril. Both nostrils with free cutaneous edges, posterior tubelike. Lacrimal with 3-4 weak serrations, less prominent with age. Preoperculum serrate; serrations largest on angle and vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate along posterior edge; scales on side. Supracleithrum exposed; lacking scale covering except at anterodorsal edge. Posttemporal exposed; serrate posteriorly.

Spinous dorsal arched; first spine short; fifth or sixth longest; those following decreasing gradually in length to penultimate which is same length or shorter than ultimate. Longest dorsal spines longer than longest dorsal rays. Soft dorsal rounded. Second anal spine twice as long as first; much stronger, but only slightly longer than third; shorter than longest anal rays. Soft anal angular. Pectoral assymmetrically pointed; fourth or fifth ray longest. Pelvic insertion posterior to vertical drawn through dorsal origin. Pelvics pointed; first ray longest, slightly filamentous; not reaching anus. Caudal emarginate.

Coloration: coloration of S. butleri undergoes several distinct changes during ontogeny. Juveniles of 20-40 mm SL with 5-6 longitudinal body stripes (Fig. 87). First running

along sheath at base of spinous dorsal from third dorsal spine to third or fourth ray; second, from origin of dorsal to below soft dorsal; third, from back of top of eye across posttemporal and then to posterior of soft dorsal; fourth, from back of eye across opercle to caudal base, widest stripe of all, about twice width of others; fifth, from pectoral base to rear of soft anal; sixth (indistinct and sometimes lacking) below this to spinous anal. Top of head pale except for some pigmentation along posterodorsal edge of skull. Horizontal stripe runs from rear of maxillary under eye to opercle. Opercle and subopercle with a dark blotch extending ventrally from opercular spine. Dorsal fin with membranes dusky between spines and spots of pigmentation at base of ray membranes. Caudal with a vertical bar of pigmentation at base: bar broken into two or three spots in some specimens. Membranes of spinous anal dusky. Soft anal with dark basal blotch. Membranes of pelvics dark. Pectorals colorless.

Specimens 45-75 mm SL are much darker overall. Fourth body stripe still prominent while third, fifth and sixth are less so. First and second stripe along with suborbital stripe very faint or entirely lacking. Spinous dorsal much darker. Anal blotch and pelvic coloration more pronounced. Bar at base of caudal barely discernable.

Adult specimens lacking any traces of longitudinal body stripes or caudal bar. Overall coloration uniformly dark, with edge of each scale more heavily pigmented, this pigmentation

increases dorsally. Top of head down to level of snout and top of upper lip dark, as is suborbital region. Opercle and subopercle dark below opercular spines. Spinous and soft dorsals dark, with edges lighter, especially soft dorsal. Caudal, anals and pelvics dark; first two with light margin in some specimens. Pectorals colorless.

Distribution; this species is widely distributed in Western Australia from the Bow River on the south to the South Alligator River in the north (Fig. 90).

Ecology: Syncomistes butleri has a highly developed elaborate intestine which along with its modified jaw and tooth forms are evidently adaptations for its habit of eating filamentous algae which limited gut analyses have shown to be the staple of the adults. The species is adapted to a variety of conditions. Nelson, Butler and Rosen collected it in lagoons, streams and rivers in which the current flow ranged from slight to rapid. Water conditions ranged from clear to green and turbid over a variety of bottoms.

Specimens examined

The holotype (WAM P-25385-001), 123.5 mm SL, was obtained with rotenone by W. H. Butler, G. J. Nelson, and D. E. Rosen, May 11, 1969, in Lilly (Barramundie) Lagoon near Barramundie Creek, a tributary to the South Alligator River, at the point where Barramundie Creek intersects the Oenpelli-Darwin Road, Northern Territory, Australia.

Additional paratype specimens were collected by the same

party and methods at the following localities: Barramundie Creek next to the type locality, May 12, 1969 (AMNH 35653*, 13 spec., 32-160 mm; WAM P-25388-001*, 11 spec., 55-175 mm); South Alligator River on the Pine Creek to Oenpelli Road, May 11, 1969 (AMNH 35647*, 11 spec., 58-112 mm; WAM P-25386-001*, 5 spec., 54-78 mm); main stream of Bow River at Nicholson to Wyndham Highway crossing, May 5, 1969 (AMNH*, 9 spec., 57-78 mm); main stream of Dunham River, one mile downstream of old Nicholson to Wyndham Highway crossing, May 6, 1969 (AMNH 35648*, 11 spec., 35-105 mm); main stream of Ord River below dam at crossing of Great Northern Highway, May 7, 1969 (AMNH 35650*, 2 spec., 121-139 mm); West Baines River where crossed by Great Northern Highway, May 8, 1969 (AMNH 35651*, 10 spec., 62-68 mm; WAM P-25390-001*, 3 spec., 62-69 mm); Katherine River, 3 miles downstream from Katherine, May 9, 1969 (AMNH 35649*, 10 spec., 28-212 mm; WAM P-25387-001*, 9 spec., 57-211 mm); Ferguson River where crossed by Katherine to Darwin (Stuart) Highway, May 10, 1969 (AMNH 35646*, 3 spec., 59-66 mm); main stream of Mary River on Pine Creek to Oenpelli Road, May 10, 1969 (AMNH 35652*, 2 spec., 180-118 mm); Barramundie Creek on Pine Creek to Oenpelli Road, May 11, 1969 (AMNH 35642*, 2 spec., 50-53 mm); Barramundie Creek at Oenpelli to Darwin crossing, May 12, 1969 (AMNH 35643*, 11 spec., 44-54 mm); East Mary River (Soda Creek) below Oenpelli to Darwin Road crossing, May 13, 1969 (AMNH 35645*, 10 spec., 46-59 mm; WAM P-25389-001*, 5 spec., 44-57 mm).

Syncomistes kimberleyensis n. sp.

Kimberley grunter

Fig. 91

Nomenclature: the trivial name, kimberleyensis, refers to the Kimberley region of Western Australia, where the type series of this species was collected.

Diagnosis: this species is presently known only from a limited series of juveniles which can, however, be easily separated from the juveniles of all other members of the genus. S. kimberleyensis is distinguished from other members of the genus in having a rounded lower jaw when viewed from the ventral aspect (in contrast to a triangular jaw in S. trigonicus [see Fig. 30]), and in having 8 irregular brown stripes all of the same width (in contrast to 3 stripes in S. trigonicus juveniles and 4 or 5 stripes, with the median stripe very wide, in S. butleri juveniles). Furthermore, the species can be distinguished by differences in relative head lengths (see Fig. 89).

Description: (numbers in parentheses are number of examined specimens with a given count) Dorsal spines and rays XII-11(2), XII(1); Anal spines 3, rays 8(3); Pectoral rays 14-15; Pelvics I-5; lateral line scales from origin to hypural joint 47(1), 48(2); caudal scales 3-4; transverse series to base of dorsal sheath at median dorsal spines 6+1+14(1), 6+1+15(1), 7+1+15(1); 12-13 predorsal scales to occiput; cheek scales in 4 rows; 2 irregular rows of scales in sheath at base of dorsal fin, sheath

extending to fourth or fifth dorsal ray; three rows of scales in sheath at base of anal fin, sheath extending to fourth anal ray; gill rakers on first arch 6+1+16; vertebrae 11+14.

Largest known specimen (a juvenile) 36 mm SL; depth 2.54--2.59 in SL; distance from dorsal origin to snout 2.55--2.60 in SL; head length 3.24--3.36 in SL; length of base of dorsal fin 1.95--2.0 in SL, snout length 3.08--3.3 in HL; eye width 3.5--3.9 in HL; jaw length 3.5--3.7 in HL; length of longest dorsal spine 2.05--2.20 in HL; length of longest dorsal ray 2.05--2.2 in HL; length of longest anal spine 2.15--2.34 in HL; length of longest anal ray 1.7--2.0 in HL.

Body slender, not very compressed. Dorsal profile slightly more pronounced than ventral. Dorsal profile from snout to rear of skull slightly convex; straight from rear of skull to dorsal origin. Ventral profile convex to anus. Interorbital region smooth. Upper jaw fleshy, slightly longer than lower which is flattened. Gape nearly horizontal. Maxillary reaching to vertical through posterior nostril. Each jaw with an outer series of enlarged, distally flattened brown tipped teeth oriented slightly laterally. Internal to these is a series of smaller similarly shaped teeth. Symphysis of dentary with a edentulous bump corresponding in position to a median groove between the premaxillaries which also lacks dentition. Vomer and palatines without teeth. Nostrils close together; separation equal to diameter of posterior nostril. Both nostrils with free cutaneous edges, the posterior tubelike. Lacrimal serrate;

Preoperculum with 7-8 coarse serrations in the region of the angle and with horizontal edge smooth. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate along posterior edge. Supracleithrum exposed. Posttemporal exposed; serrate along posterior edge.

Spinous dorsal arched; fourth spine longest, about same length as or slightly longer than longest dorsal ray. Spines following longest decreasing gradually in length to penultimate which is about same length as ultimate. Soft dorsal rounded. Second anal spine longest; twice length of first; slightly longer than third. Soft anal rounded. Pectorals assymmetrically pointed; fifth ray longest. Pelvics inserted posterior to vertical through dorsal origin. Pelvics pointed; first ray longest, reaching less than one-half distance to anus. Caudal slightly emarginate.

Coloration: head darker dorsally, with opercle below lower opercular spine dark. Head and body speckled with very small brown spots. Body with eight irregular wavy brown stripes running horizontally along side of body. First running from anterior of spinous dorsal to front of soft dorsal; second, below this to middle of soft dorsal; third, to top of caudal peduncle; fourth, from posttemporal along lateral line, then onto caudal base; sixth, from cleithrum to ventral edge of caudal base; seventh, below this to rear of soft anal; eighth (indistinct, sometimes lacking) running below this.

Membranes of spinous dorsal light brown, as are membranes of soft dorsal for their basal one-third. Membranes of spinous and soft anal brown with a darker blotch on middle of rays. Pelvics pigmented. Pectorals clear. Caudal with basal marks that are continuations of fourth to sixth body stripes.

Although this species is presently known only from juveniles, it is likely that the adults would be uniform as is the case with its closest relatives, S. butleri and S. trigonicus.

Distribution: known only from the type locality in the Bow River (Fig. 90).

Ecology; the species was collected in a green, murky, isolated pool over a sand and rock bottom. Based on the similarity in dentition between this species and the other members of the genus it appears probable that filamentous algae is used as the main food source in the adults.

Specimens examined

The holotype (WAM P-25383-001) 36 mm SL, was obtained with rotenone and dip net in a pool in the drying stream bed of the Bow River at the Nicholson-Wyndham Highway crossing, Western Australia, by G. J. Nelson, D. E. Rosen and W. H. Butler, May 5, 1969. Taken along with the holotype were two paratypes (AMNH 35636*, 34-35 mm).

Syncomistes trigonicus n. sp.

Triangle grunter

Figs. 92 and 93

Nomenclature: the trivial name, trigonicus, from the Latin for triangle, refers to the triangular shape of the lower jaw when viewed from a ventral aspect.

Diagnosis: a slender bodied member of the genus Syncomistes distinguished from the other members of the genus in having the lower jaw greatly flattened and with a triangular outline when viewed from the ventral aspect (in contrast to the rounded form of the jaw in S. butleri and S. kimberleyensis). Differences in relative head lengths also serve to separate this species (see Fig. 89).

Description: (numbers in parentheses are the number of examined specimens with a given count) Dorsal spines and rays XI-12(3), XII-12(6) (XI-13, reported by Allen, 1975); Anal spines 3, rays 8(8), 9(1); pectoral fins with 14-15 rays; Pelvics I-5; lateral line scales from origin to hypural joint 46(1), 47(3), 49(1), 50(1) (51 reported by Allen, 1975); caudal scales 3-6; transverse series to base of sheath at median dorsal spines 7+1+16(4); 7+1+17(1); 7+1+18(1); 8+1+15(2), 8+1+16(1); predorsal scales to occiput 14-17; cheek scales in 3-4 rows; 2 irregular rows of scales in sheath at base of dorsal fin in some specimens, 2 complete rows in others, sheath extending to fifth or sixth dorsal ray; sheath at base of anal consisting of 3 rows of scales

sheath extending to second to fourth anal ray; gill rakers on first arch 7-8+1+15-16; vertebrae 11+14.

Largest known specimen 145 mm SL; depth 3.2-3.5 in SL; distance from dorsal origin to snout 2.4-2.55 in SL; head length 3.3-3.45 in SL; length of base of dorsal fin 1.95-2.05 in SL; snout length 2.0-2.6 in HL; eye width 4.0-5.0 in HL; getting relatively smaller with increasing SL; jaw length 2.3-3.5 in HL, getting relatively larger with increasing age; longest dorsal spine 2.3-3.0 in HL; length of longest dorsal ray 2.0-2.6 in HL; length of longest anal spine 2.1-2.9 in HL; length of longest anal ray 1.8-2.1 in HL.

Body slender, only slightly compressed. Dorsal profile much more pronounced than ventral in juveniles, only slightly more in adults. Dorsal profile slightly concave behind premaxilla, convex from this point to interorbital region, then straight to dorsal origin. Interorbital region smooth. Snout distinctly pointed. Gape of mouth horizontal. Maxillary reaching to vertical drawn between nostrils. Upper jaw slightly more fleshy and longer than lower. Lower jaw triangular when viewed from ventral aspect, reduced, flattened, with teeth pointing laterally. Upper jaw with a greater number of teeth in outer row than occur in lower jaw. Each jaw with an outer row of highly depressible flattened teeth followed by a distinct narrow inner band of smaller teeth. Lower jaw with a prominent medial bump at symphysis that is oriented dorsally; bump corresponds in position to a depression between the pre-

maxillaries. Both bump and depression edentulous. No teeth on vomer or palatines. Nostrils separated by a distance equal to diameter of posterior nostril. Both nostrils with free cutaneous edges; posterior tubelike. Lacrimal with 3-4 coarse serrations. Preoperculum serrate; serrations strongest on vertical edge. Lower opercular spine longer and stronger; not extending beyond edge of opercular lobe. Cleithrum exposed; serrate along posterior edge; scales on side. Supracleithrum exposed. Posttemporal exposed; serrate along posterior edge.

Spinous dorsal arched; first spine short; fourth longest, but shorter than longest dorsal rays; spines following longest dorsal spines decreasing in length to penultimate which is shorter than ultimate. Soft dorsal rounded. Second anal spine longest; three times length of first; shorter than longest anal rays. Soft anal angular. Pelvics inserting posterior to vertical through origin of dorsal fin. Pelvics pointed; first ray longest; reaching one-half distance to anus. Pectorals assymmetrically pointed; fifth ray longest. Caudal slightly emarginate.

Coloration: juveniles with three stripes along side of body. First following base of dorsal sheath; second, running from slightly dorsal to posttemporal along lateral line and to dorsal edge of caudal peduncle; third, from supra-cleithrum to middle of caudal base. Body darker dorsally, almost white along midventral line. Anal with a basal blotch extending posteriorly on anterior rays. Caudal and dorsal

membranes dusky. All other fins clear.

Adults lacking horizontal stripes. Specimens of 90-100 mm SL darker than juveniles with each scale having a posterior band of pigmentation. Scale pigmentation increasing in intensity and extent dorsally. Coloration above midline of body approaching a uniform dark brown or black. Body coloration most intense under dorsal sheath. Posterior and ventral borders of eye surrounded by pigment band. Operculum very dark ventral to opercular spine. Anal fin with dark proximal blotch. Membranes of dorsal and caudal dusky; those of other fins clear. Specimens above 110 mm SL with a uniform dark coloration, slightly lighter ventrally. All fins, especially the median dusky.

Distribution; from the Roe, Prince Regent and Drysdale River drainages of northwestern Australia (Fig. 90).

Ecology: limited gut content studies have shown the species to feed primarily on filamentous algae. It appears to be an inhabitant of fresh clear or slightly murky waters over a variety of bottoms.

Specimens examined

The holotype (WAM P-25391-001), 93 mm SL, was obtained with rotenone by G. R. Allen, August 17, 1974, in Wyulda Creek about 2 kilometers above its junction with the Roe River, Western Australia. Taken along with the holotype was a paratype (WAM P-25028) 98 mm SL. Additional paratype materials were collected at the following localities: 2 specimens (WAM P-25026-002) 47-112 mm SL, obtained with dipnet by G. R.

Allen, August 14, 1975, in the upper Roe River, Western Australia; 1 specimen (WAM P25027-002), 130 mm SL, obtained with a sein by G. R. Allen and A. Chapman, August 15, 1975 in the upper Roe River; 4 specimens (AMNH 35637) 50-110 mm SL, obtained with rotenone by G. J. Nelson, D. E. Rosen and W. H. Butler, April 25, 1969, in Kennedy Creek a tributary to the Drysdale River. Additional material identified as this species but not seen by the author was collected at other localities in the Roe and Prince Regent Rivers (species b of Allen, 1975).

Zoogeography

The Indo-west Pacific region is an area which has been of interest to biogeographers for over a century (Sclater, 1858; Wallace, 1876; deBeaufort, 1951; Darlington, 1957; and others). In an attempt to understand the distribution of the various species and supraspecific units through this region, these authors have attempted to distinguish various faunal and floral provinces both on the scale of Weber's and Wallace's lines and on a more limited level (eg. the fluvifaunulae of Australia and New Guinea demarcated by Iredale and Whitley, 1930 and followed by other authors with modifications). However, most of these studies were concerned with the description of endemism rather than with faunal relationships and showed little concern with the general aspects of biotic history.

Most previous biogeographic analyses have been based on a hypothesis of a center of origin for single species or groups and their subsequent dispersals to other regions. Hennig (1966), for example, hypothesizes in his progression rule that ancestral forms are found at the center of a distribution of a supraspecific group. Darlington (1957, 1970) and Briggs (1974), on the other hand argue from the opposite assumption that ancestral forms are found on the periphery of a group's distribution. This hypothesis assumes that ancestral forms will be forced to the periphery by more derived forms arising at the center of origin.

However, such hypotheses and the associated aprioristic assumption of dispersal as an underlying cause of present day

distributions cannot be falsified and therefore are not testable. Also such a system does not allow us to distinguish those distributions resulting from events extrinsic to the organism. (e.g., a present day distribution resulting from a vicariance event such as continental drift) from those that are a consequence of some intrinsic quality of the organism allowing for its dispersal between two areas.

Croizat (1952, 1958, 1964), Croizat, Nelson and Rosen (1974) and Rosen (1975) reject the use of a priori assumptions of centers of origin and dispersal and instead advocate the initial use of an allopatric speciation (vicariance) model for the analysis of present distribution patterns, an approach followed here.

In such a system, one attempts to determine the limits of ancestral biotas as indicated by large scale biotic relationships between different geographic regions. This is achieved by an analysis of a series of individual distributions of various plants or animals or both. The pattern described by the sum of many individual distributions or tracks estimates the limits of an ancestral biota since subdivided by one or more vicariance events. Such a view has the advantage of not requiring that the species of each group within the ancestral biota independently acquired physiological and behavioral adaptations that are necessary for dispersal. In contrast, tracks unique to a species or group and not in agreement with the generalized tracks may represent the results of dispersals.

Analysis of the distribution of the family Teraponidae and its various subunits shows several repeated tracks of different geographic extent; two of these are marine (one being a subunit of the other) and one involves freshwater species.

The marine distribution of the Teraponidae covers most of the Indo-west Pacific with many of the species also penetrating far upstream into freshwater (the distribution of Pelates quadrilineatus in the southeastern Mediterranean appears to be a recent dispersal through the Suez Canal). Stippled areas of figure 94 represents the distribution of the entire family both marine and freshwater (the limits of this track are however, entirely defined by marine species). This track of the entire family is closely approximated by that of Terapon jarbua, with the exception of part of the southern coast of Australia from which this species is not known. Three other species in the family also have tracks which correspond in large degree with that of the family. However, all three (Pelates quadrilineatus, Terapon theraps, and T. puta) fail to extend east and south of line A in Figure 94 and the latter also does not extend south of line B. Finally the east-to-west extent of the family but not the north-to-south distribution is approximated by the genus Mesopristes which has one species (M. elongatus) in Madagascar, two species (M. argenteus and M. cancellatus) distributed through the dotted track (C) of figure 94 and one species (M. kneri) endemic to Fiji.

These six tracks, that of: 1) the entire family; 2) Terapon jarbua; 3) Pelates quadrilineatus; 4) Terapon theraps; 5) I. puta; and 6) the genus Mesopristes, form a generalized track across the entire Indo-west Pacific.

Comparison of the family track with the position of the Andesite Line in the western Pacific shows the family to be limited to the west of the line, except for I. jarbua which crosses over slightly at Samoa. The Andesite line (MacDonald, 1949; see also Springer, 1975) demarcates the division between the older continental rocks including the fragments of Gondwanaland to the west and the younger oceanic rocks of the Pacific basin. Similar agreements with the boundary have been noted by Springer (1972, 1975) for parts of some blennioid genera and by Raven and Axelrod (1972) for many plants.

Plotting the present day distribution of teraponids on a Gondwanaland reconstruction (based on information from Melville 1973; Crawford, 1974; Stauffer, 1974) shows that the family if present at that time, might have occupied the shorelines, rivers and estuaries of the parts of Gondwanaland which today form the margins of the Indian and west-Pacific oceans. Inconsistencies with this model are the presence of teraponids in the Japanese region and their absence along the coasts of Antarctica. The absence of teraponids from Antarctica, may only reflect their physiological intolerance of the present-day environmental conditions in that region. Within the Japanese biota is found an overlap between Gondwanian

(teraponids, plotosids, oryziids, synbranchids, etc.) and Laurasian (salmonids, osmerids, cyprinids, etc) biotas. From a biogeographical analysis, several possible explanations exist for this overlap: 1) a dispersal of elements of a Laurasian fauna into an originally Gondwanian fauna; 2) dispersal of elements of a Gondwanian fauna into an originally Laurasian fauna; or 3) that the region is geologically complex, being formed of parts of Gondwanaland and Laurasia with their associated faunas. The relative merits of these possibilities cannot, however, be resolved solely on the basis of teraponid distributions but must await a detailed analysis of the faunas and floras of the area. Despite this unresolved question, on the basis of available information, one might conclude that an ancient origin for the Teraponidae in the Indo-west Pacific parts of Gondwanaland should not be ruled out.

In an allopatric model of speciation, an ancestral species A is separated into at least two populations A' and A'' by some vicariance event (geographical or climatological or both) that prevents genetic interchange between them. Given a sufficiently long period of time (variable both as a function of the organisms in question and other conditions) these isolated populations might be expected to diverge. This divergence may be sufficient to prevent genetic interchange when and if the populations come into contact again. In such a model of speciation, any overlaps found between sister groups is indicative of secondary dispersal, since in the course of the speciation

event, a primary complete separation of the species or hypothetical ancestors of the groups was necessary. Such overlaps indicative of dispersal are found between Pelates (genus 6), Terapon (genus 7) and Mesopristes (genus 10) and their respective sister groups. Such dispersals may also have occurred in the genera Pelates and Terapon where wide overlap is found among their species.

A second shared track among marine teraponids is found in the region limited by Malaya, the New Hebrides and China (track C, figure 94). This entire range is covered by Pelates sexlineatus and with some gaps by Mesopristes argenteus and M. cancellatus, with the extensive overlap between these last two species also evidence of intrageneric dispersal.

The second generalized track in the Teraponidae involves sister group relationships between northern Australian and southern New Guinea freshwater species. Four such tracks are found uniting species or groups in the genera Amniataba, Hephaestus and Pingalla. The close faunal relationships between these areas have been previously remarked on and analyzed by a series of workers. Iredale and Whitley (1938), Iredale (1943) and Whitley (1943) considered the similarities sufficient to warrant the unification of the northern Australian and southern New Guinea faunas into a single Leichhardtian fluvifauna. More recently McMichael and Hiscock (1958) and Munro (1964) have distinguished the fauna of southern New Guinea as a distinct Reichian fauna. Exclusive of

teraponids, the latter authors lists 31 species representing 14 families (Pristidae, Osteoglossidae, Tachysuridae, Plotosidae, Anguillidae, Belonidae, Eleotridae, Gobiidae, Melanotaenidae, Chandidae, Apogonidae, Kurtidae, Toxotidae and Soleidae) that are shared between these two regions; of which 19 species are limited entirely to freshwater. These tracks in addition to those previously mentioned for teraponids indicate a close relationship between these faunas, and suggests that they arose from an ancestral biota divided by some vicariance event.

Examination of the geological evidence for the region shows that a likely event was the inundation of the continental shelf between Australia and New Guinea after the Pleistocene. During the Pleistocene sea levels were lowered sufficiently to expose the shelf under the Arafura Sea and Gulf of Carpentaria and it appears possible that at the time several rivers drained the combined areas of southern New Guinea and northern Australia. With increasing sea levels, the lower courses of these rivers were drowned, separating and isolating their upper reaches both north and south as independent drainages with consequent isolation of the faunas.

Within both New Guinea and Australia, no generalized tracks are evident. Evidence of dispersal is, however, found in the extensive overlap both of the various genera of freshwater teraponids and the species within these genera.

Summary

A revision of the family Teraponidae was carried out with five goals: 1, to determine the monophyletic nature of the Teraponidae; 2, to determine the relationships of teraponids to other percoids; 3, to produce theories of relationships within the family; 4, to produce an account of the species in the family and their distribution; 5, to analyze the distribution patterns of the family and its subunits.

These goals were approached using the methods of phylogenetic analysis discussed by Hennig, and the biogeographic principles proposed by Croizat.

Four apomorphic characters of all teraponids were found to be unique among percoids: 1) a transversely divided swimbladder; 2) a distinctive form of extrinsic swimbladder muscle; 3) a distinctive form of urohyal; 4) a distinctive process arising from the dorsal edge of the third epibranchial.

No hypothesis of a sister group to the teraponids among percoids could be generated on the basis of shared derived characters. Neither was evidence uncovered to support Fowler's inclusion of the genera Datnioides and Pseudohelotes in the Teraponidae.

Within the family 15 monophyletic assemblages are recognized, with the relationships between them and their defining characters based on a series of apomorphic characters and character states. These characters and the groups possessing them are:

- 1) Anatomy of the posttemporal, tabulars, and associated structures
 - A) genera 1 to 5 share an unelaborated posttemporal, a lateral tabular with the sensory canals contacting each other anteriorly, and an uninterrupted skin and scale covering over the posttemporal.
 - B) genera 6 to 15 have a derived reduction in the anterior aperture of the lateral tabular sensory canals with a reorientation of the otic part of the infraorbital canal.
 - C) genera 7 to 15 share a series of conditions of the above structures including an expanded posteriorly serrate posttemporal with an elongate sensory canal having lateral openings; a vertical or posteroventrally sloping element of the supratemporal commissure in the lateral tabular bone; a ventral shift in the supracleithral-posttemporal articulation; and a reduced scale covering over the posttemporal.
 - D) genus 1b has a further expanded posttemporal, and a posteroventrally sloping supratemporal commissural element in the lateral tabular, both conditions being considered the most apomorphic for these structures in the family.
- 2) Heights of the dorsal and anal sheaths
 - A) the hypothesized condition of the dorsal fin sheath plesiomorph for teraponids is one row of scales

and is found in genera 1 to 6. That of the anal sheath is a height of 2 or 3 scales; a condition found in genera 1 to 7.

B) the derived condition of the dorsal sheath is two scale rows of more and found in genera 7 to 15

C) genera 8 to 15 share both a derived dorsal sheath height (2 or more rows of fully sized scales) and a derived anal sheath height (3 to 6 rows).

3) Intestinal patterns

A) The plesiomorph form of the intestinal patterns in teraponids is that of two loops both located in the median body plane or to the right of it and found in genera 1 to 10 and 11 b.

B) a derived pattern with five loops and a limited amount of loops to the left of the median body plane, the pattern of genera 11 to 15 at some point in development.

C) a pattern with an elaborate intestinal pattern derived ontogenetically from B (genera 14 and 15) looping to the left of the stomach; a pattern in turn plesiomorph to a highly complex pattern of genus 15.

4) Extrinsic swimbladder muscles.

A) the plesiomorph condition of this muscle in terapon

ids appears to be a cylindrical muscle with an origin limited to the ventral process of the posttemporal. Such a muscle form is found in genera 1 to 5.

B) genera 6 to 15 share a derived form of the muscle with an attachment to both the posttemporal and the rear of the skull at some point during development. Three forms of muscle are found having this type of attachment (in order of increasing apomorphy).

a) a muscle with a direct muscular attachment to the posttemporal and a ligamentous attachment to the skull. (genus 6)

b) a muscle with a direct muscular attachment to both the posttemporal and the skull (genera 7-15)

c) a muscle with an origin limited to the rear of the skull in adults. (genus 11 b).

5) pigmentation patterns

A) a vertically barred pattern is plesiomorphic for teraponids

B) two patterns are found in the family apomorphic to and directly derived ontogenetically from bars

a) a uniform coloration of species in genera 1 to 4

b) a striped pattern of genera 5 to 9.

C) uniform coloration derived directly from stripes is apomorphic with respect to the striped pattern and found in genera 10 to 15.

6) Vertebral counts

- A) the plesiomorph vertebral formula is considered to be 10+15.
- B) two increases are found in the total number of vertebrae, a increase to 26 in Lagusia (genus 5) and to 27 in the species of genus 11b.
- C) within those species having either 25 or 27 vertebrae subgroups have an increase in the relative numbers of precaudal and caudal vertebrae:
 - a) three species in genus 1b have a formula of 11+16; a pattern considered apomorphic to the 10+17 pattern of the rest of the unit.
 - b) The species of genera 12 to 15 have an increased number of precaudal vertebrae (11), a condition considered apomorphic. Similar increases in one species in each of two other genera (1 and 2) are considered to be convergences.

7) Numbers of spines on the first proximal dorsal pterygiophore.

An increase to two spines on this element in genera 2 to 15 is considered apomorphic.

8) Form of the rear of the supraoccipital.

A posteriorly bowed or straight rear margin of the supraoccipital is considered apomorphic and found in genera 9 to 15.

9) Jaw and dentitional form

A) the plesiomorph condition of the jaw and dentition is a conic, non-depressible, vertically directed dentition located along the superior and inner surfaces of the dentary which has a prominent symphyseal process anteroventrally.

B) derived conditions of the above are

a) a flattened dentition characterizing genera 13 to 15.

b) a depressible dentition characterizing genera 12 to 15.

c) a very flattened dentition with an outward rolling of the dentary and a reduction or lack of the symphyseal process in genera 14 and 15.

d) the development of a prominent dorsally directed dentary process and modifications of the ascending processes of the premaxillary and rostral cartilages of genus 15.

10) secondary reduction in the swimbladder constriction.

In genera 14 and 15 the swimbladder constriction is hypothesized to be secondary reduced based on ontogenetic changes in the amount of the constriction.

The fifteen monophyletic assemblages are defined at the generic level in this study (Leiopotherapon, Anniataba, Lagusia, Hannia, "Terapon" (differs from the sense of Terapon [genus 7])

Pelates, Terapon, Pelsartia, Rhyncopelates, Mesopristes, Hephaestus, Bidyanus, Scortum, Pingalla, and Syncomistes) three of which (Lagusia, Hannia and Syncomistes) are described as new in this study. Thirtyseven species are recognized in this study of which five are described for the first time (Leiopotherapon macrolepis, Hannia greenwayi, Syncomistes butleri, S. trigonicus, and S. kimberleyensis). Each species is described in detail and its distribution plotted.

The following species recongized as distinct by some or all workers to this point were placed in synonymy:

Pelates sexlineatus Cuvier in P. quadrilineatus (Bloch)

Terapon servus (Block) in T. jarbua (Forskål)

Terapon rosenberghii (Bleeker) in Mesopristes cancellatus (Cuvier)

Terapon lambertoni Fowler in Mesopristes elongatus (Guichenot)

Terapon alligatoris Rendahl in Hephaestus fuliginosus (Macleay)

Terapon bancrofti Ogilby and McCulloch in Hephaestus fuliginosus (Macleay)

Terapon brevipinnis Mees in Hephaestus jenkinsi (Whitley)

Terapon habbema Weber in Hephaestus trimaculatus (Macleay)

Scortum ogilbyi Whitley in S. hillii (Castelnau)

Hephaestus jenkinsi considered by Mees to be a synonym of H. fuliginosus is herein recognized as a distinct species and Datnia elliptica Richardson which most previous workers have placed as synonym of Bidyanus bidyanus is tentatively

placed in synonymy with B. welchi.

The zoogeography of the family and its subunits were analyzed and showed five general patterns of distribution extending across all or most of the Indo-west Pacific and forming a generalized track within teraponids. Such distributions might indicate an ancient Gondwanian origin for the family during the late Mesozoic or early Tertiary, with most of the later wide geographic range of the family a consequence of continental drift.

An additional generalized track within the family occurs between the freshwaters of northern Australia and southern New Guinea, a track shared by many other groups. Such a distribution is congruent with the vicariance event that separated the two regions following the Plesitocene.

A history of dispersal among sister groups of some genera and between sister genera or groups is evidenced by the sympatry of members of the various monophyletic groups in fresh and marine waters.

Table 1. Genera of the family Theraponidae and the species assigned to them by Whitley and other workers.

Subfamily Theraponinae

Amniataba: Amniataba percoides

Amphitherapon: Amphitherapon caudavittatus, A. habbemai

Authistes: Authistes puta

Bidyanus: Bidyanus bidyanus

Eutherapon: Eutherapon theraps

Hephaestus: Hephaestus bancrofti, H. carbo, H. fuliginosus,
H. welchi.

Leiopotherapon: Leiopotherapon suavis

Madigania: Madigania unicolor, M. adamsoni

Mesopristes: Mesopristes aheneus, M. alligatoris, M. argenteus,
M. cancellatus, M. jenkinsi

Papuservus: Papuservus trimaculatus

Pelates: Pelates oxyrhynchus, P. quadrilineatus, P. sexlin-
eatus, P. roemeri

Pelsartia: Pelsartia humeralis

Scortum: Scortum barcoo, S. hillii, S. ogilbyi, S. parviceps

Terapon: Terapon jarbua

Subfamily Helotinae

Helotes: Helotes sexlineatus

Pingalla: Pingalla gilberti, P. lorentzi

The following species were not assigned to any of the above genera and remained in the genus Terapon (sensu latu)

Terapon plumbeus

Terapon micracanthus

Terapon kneri

Terapon elongatus

Terapon lambertoni

Terapon brevipinnis

Terapon jamoerensis

Table 2. Vertebral numbers in the Teraponidae

Genus	Species	Vertebral number			Vertebral formula				
		25	26	27	10+15	10+16	10+17	11+14	11+16
<u>Leiopotherapon</u>	<u>L. unicolor</u>	xx						xx	
	all others	xx			xx				
<u>Amniataba</u>	all	xx			xx				
" <u>Terapon</u> "	" <u>T.</u> <u>jamoerensis</u> "	xx						xx	
<u>Hannia</u>	<u>H. greenwayi</u>	xx			xx				
<u>Laqusia</u>	<u>L. micracanthus</u>		xx			xx			
<u>Pelates</u>	all	xx			xx				
<u>Terapon</u>	all	xx			xx				
<u>Pelsartia</u>	all	xx			xx				
<u>Rhyncopelates</u>	all	xx			xx				
<u>Mesopristes</u>	all	xx			xx				

Table 2 continued

Genus	Species	Vertebral number			Vertebral formula				
		25	26	27	10+15	10+16	10+17	11+14	11+16
<u>Hephaestus</u>	9a	xx			xx				
	<u>H. carbo</u>			xx			xx		
	all other 9b			xx					xx
<u>Bidyanus</u>	all	xx						xx	
<u>Scortum</u>	all	xx						xx	
<u>Pingalla</u>	all	xx						xx	
<u>Syncomistes</u>	all	xx						xx	

Table 3: Comparison of the relative lengths of the second and third anal spines and lateral line counts for material of Hephaestus trimaculatus and syntypes of Therapon habbema.

SL	LAS2/LAS3	LL		SL	LAS2/LAS3	LL
20.5 ¹	1.0	53	•	97.2 ⁵	1.25	54
22.5 ¹	1.0	54	•	99.4 ⁴	1.18	55
23.0 ¹	1.06	51	•	99.5 ³	1.17	46
25.3 ¹	1.03	50	•	103.7 ³	1.23	47
30.5 ¹	1.11	52	•	108.5 ³	1.29	49
60.9 ²	1.15	55	•	110.5 ³	1.24	49
73.2 ¹	1.20	50	•	114.2 ⁴	1.16	57
75.2 ¹	1.23	49	•	120.0 ³	1.18	50
76.4 ²	1.14	54	•	121.2 ⁴	1.24	55
77.8 ¹	1.18	47	•	123.6 ⁴	1.25	55
79.2 ¹	1.19	47	•	124.5 ¹	1.17	49
82.0 ¹	1.18	51	•	128.0 ⁵	1.16	53
82.4 ¹	1.27	49	•	139.3 ⁴	1.19	54
83.2 ¹	1.25	50	•	142.8 ⁴	1.24	53
86.4 ¹	1.25	50	•	147.3 ⁵	1.21	57
86.8 ³	1.15	46	•			
93.0 ³	1.20	46	•			
93.8 ⁴	1.21	54	•			

1, USNM 210847; 2, AMNH 12629; 3, WMNH 14005; 4, ZMA 112.456

(syntypes of Therapon habbema); 5, AMNH 13905.

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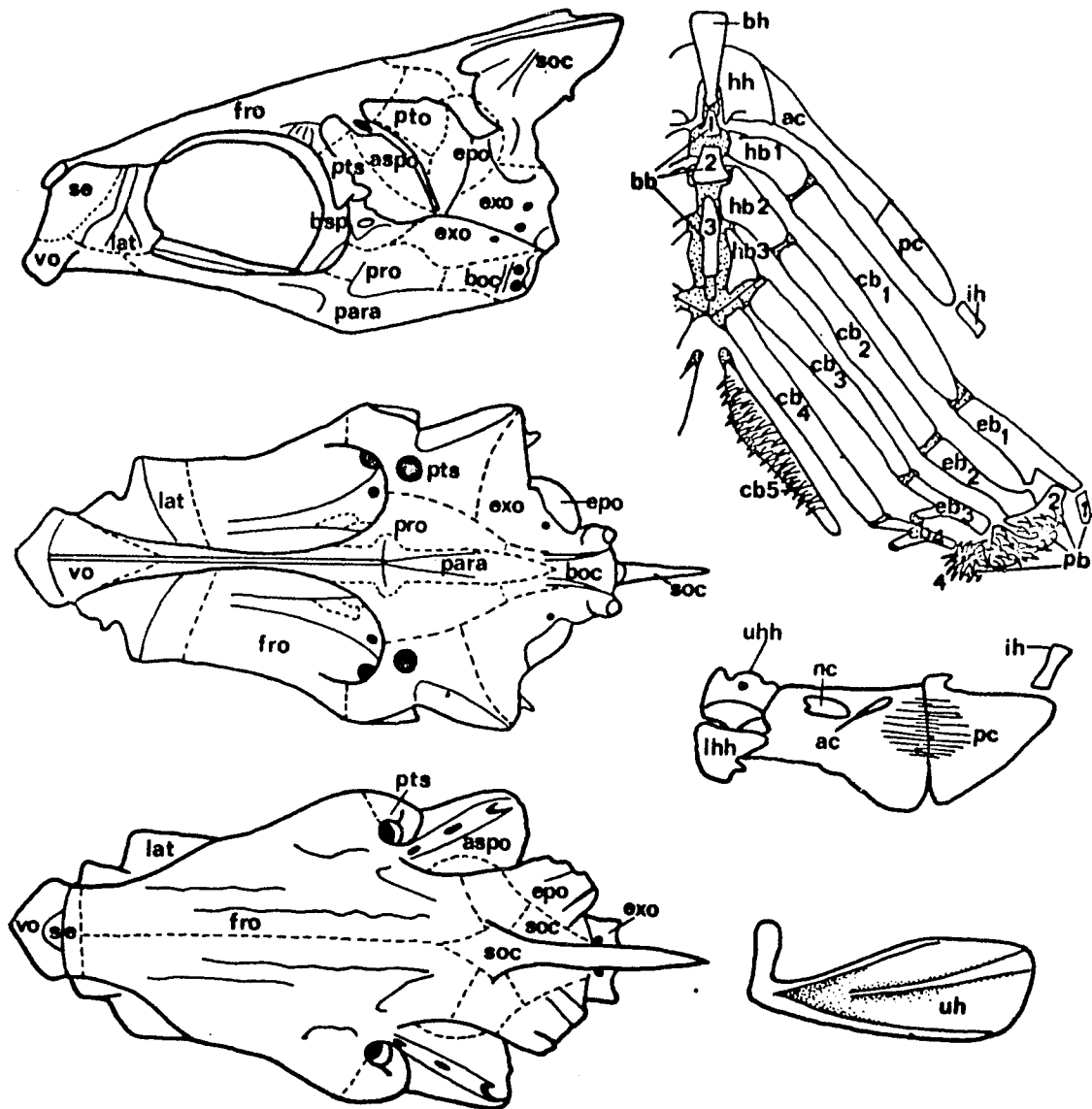


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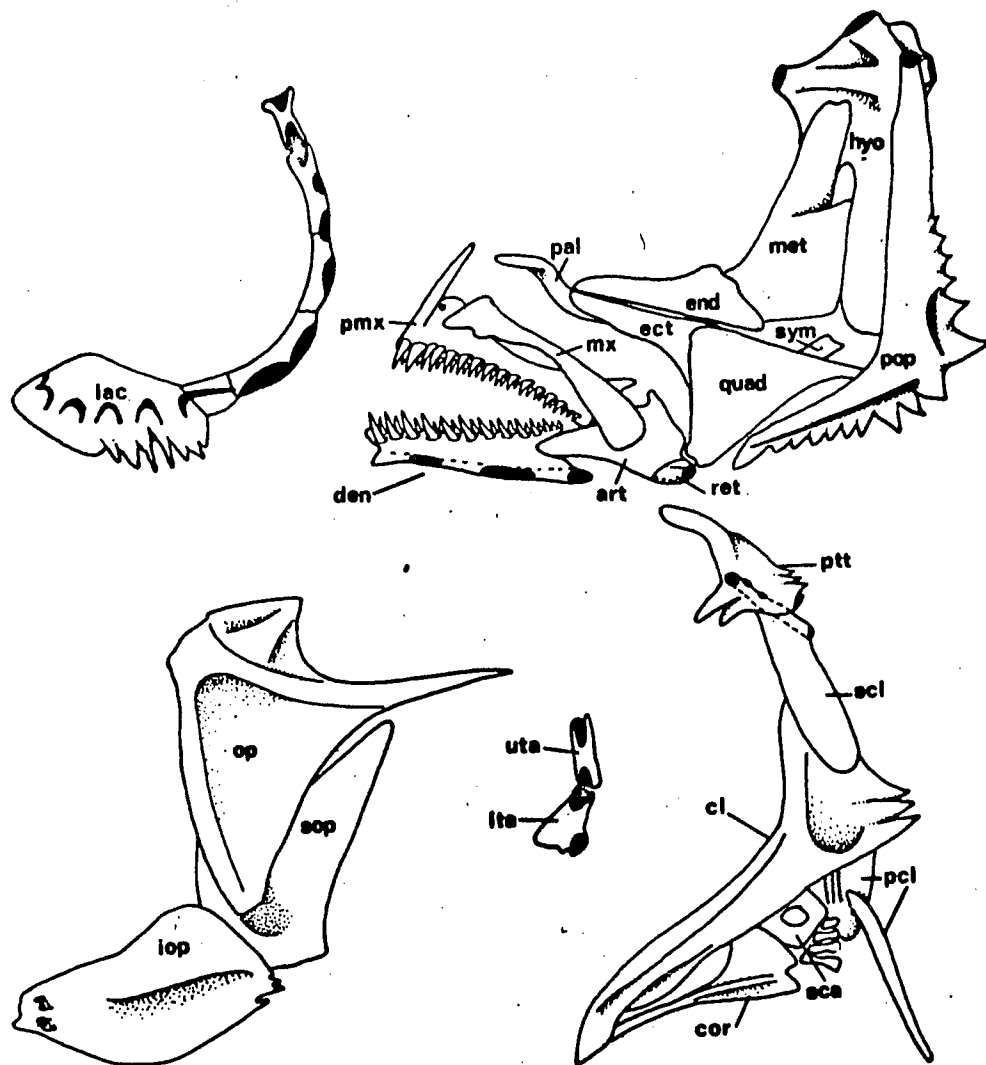


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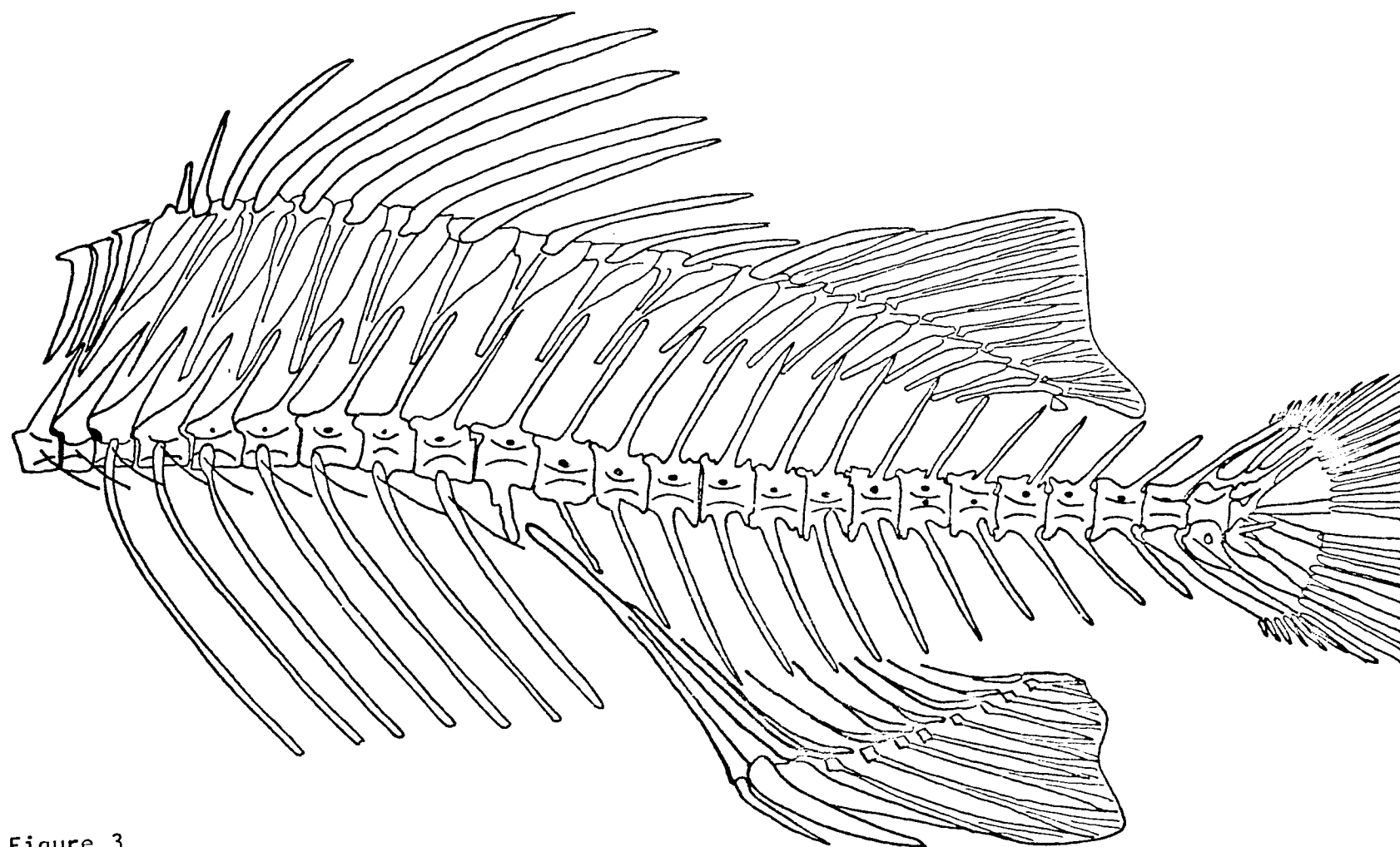
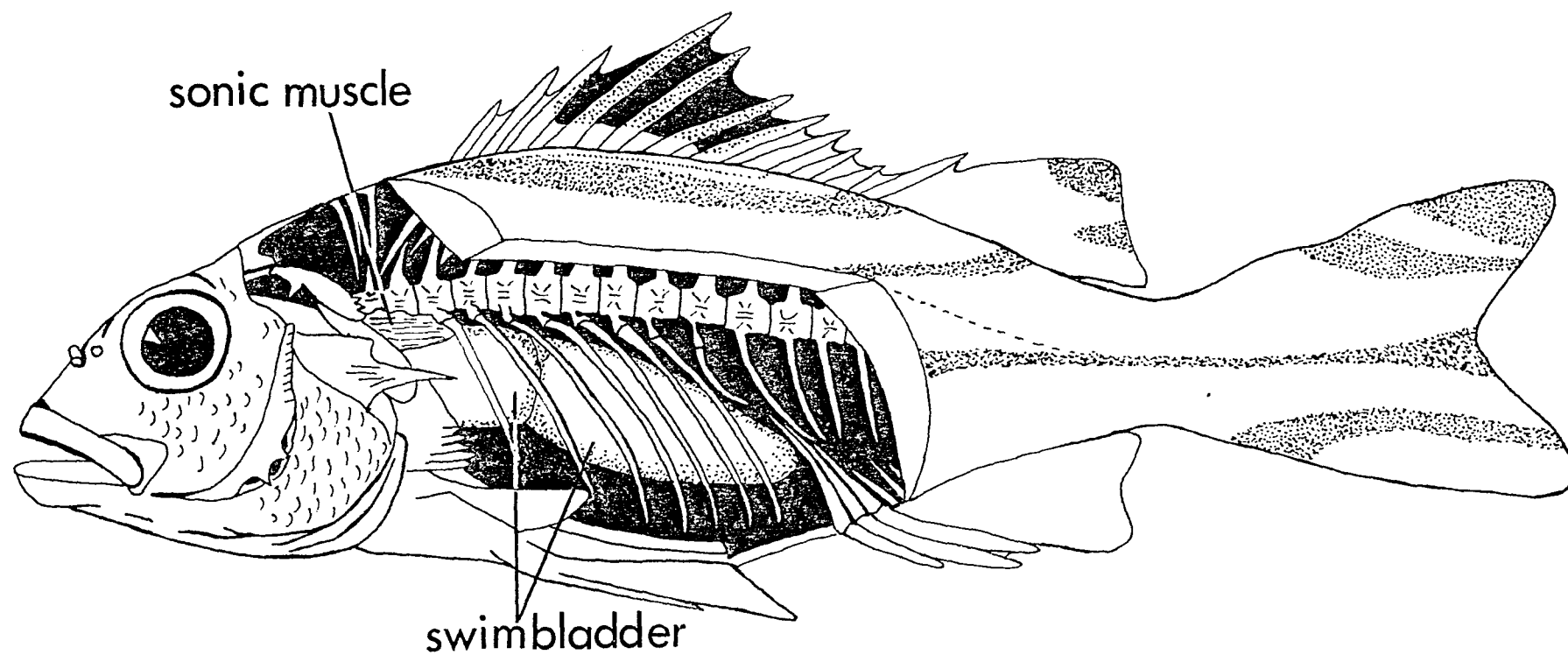


Figure 3



396

Figure 4

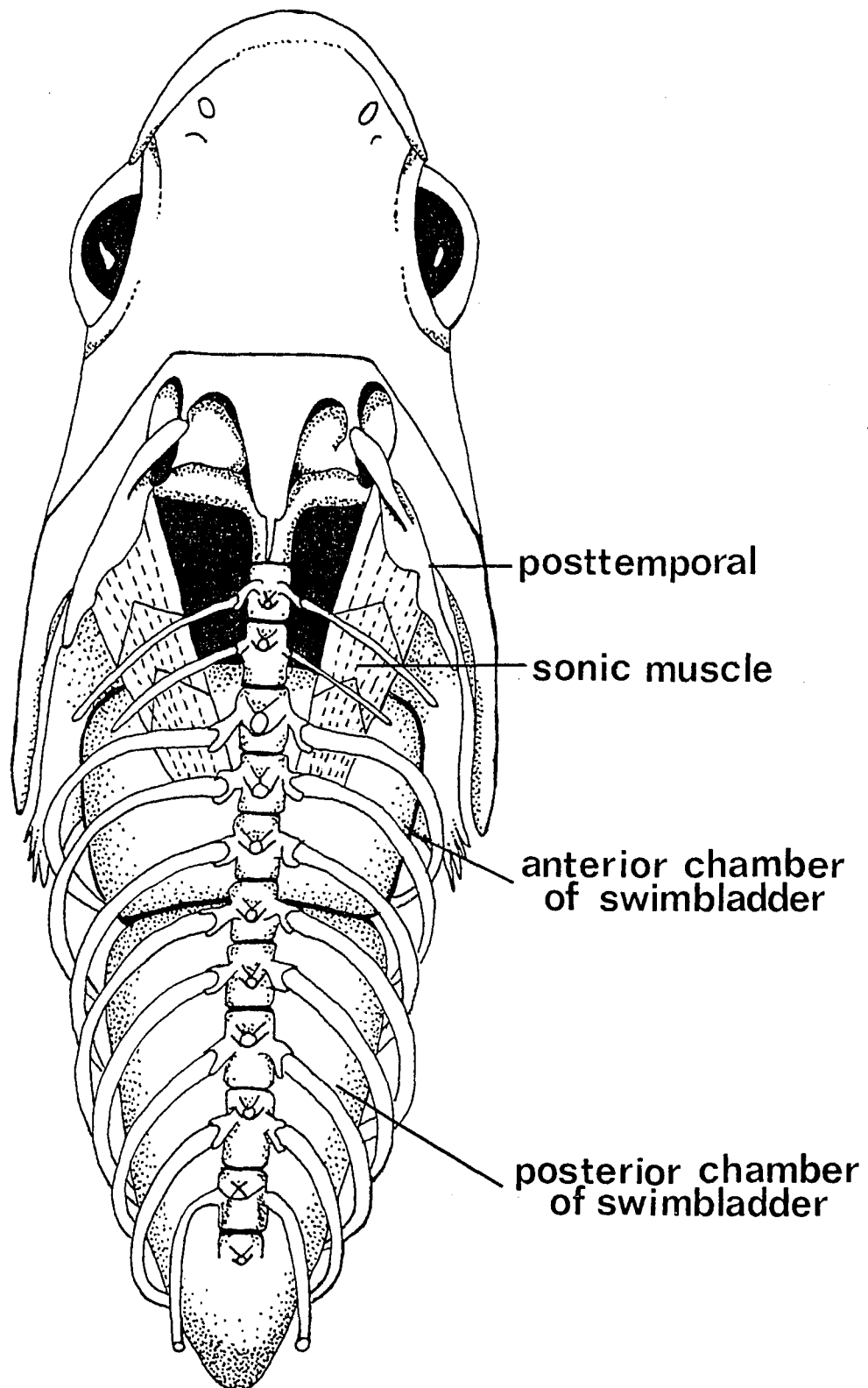


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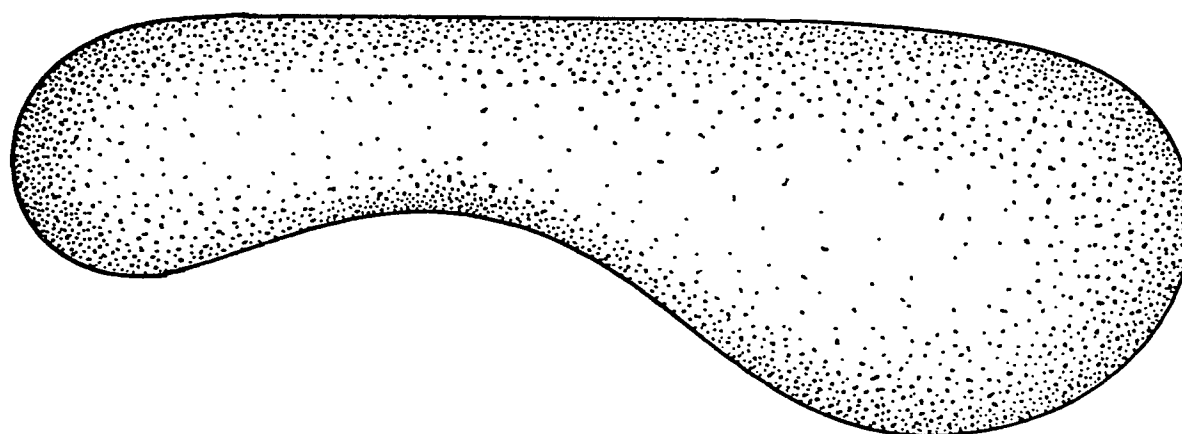


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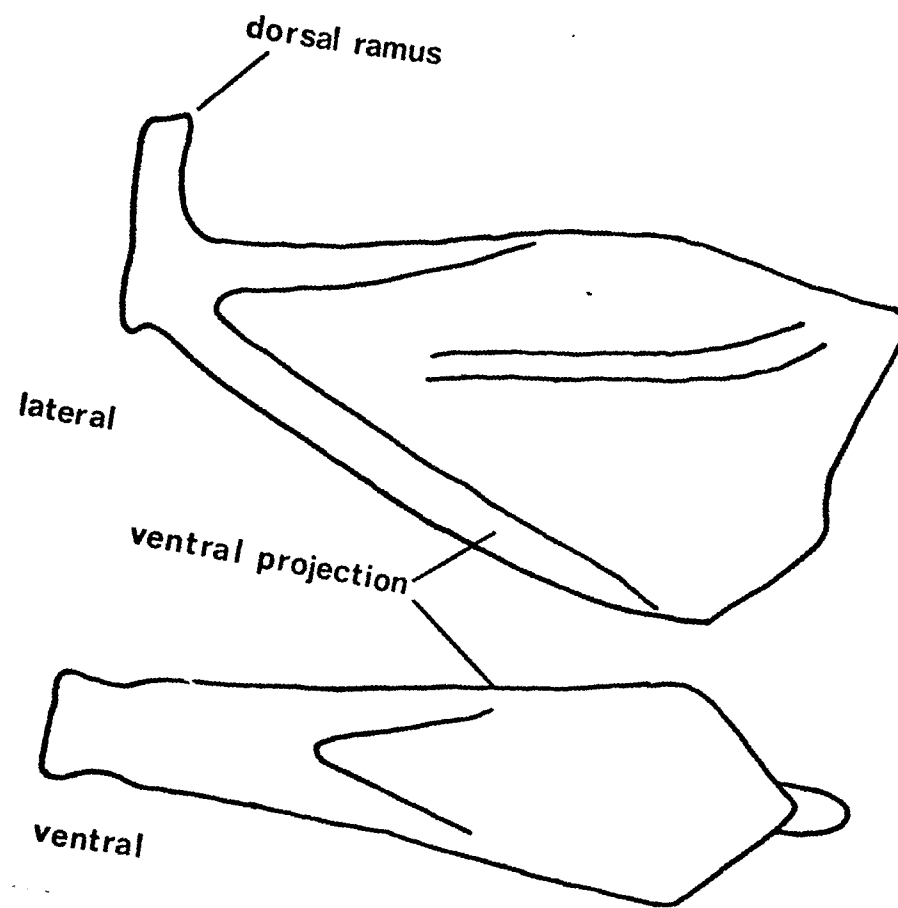


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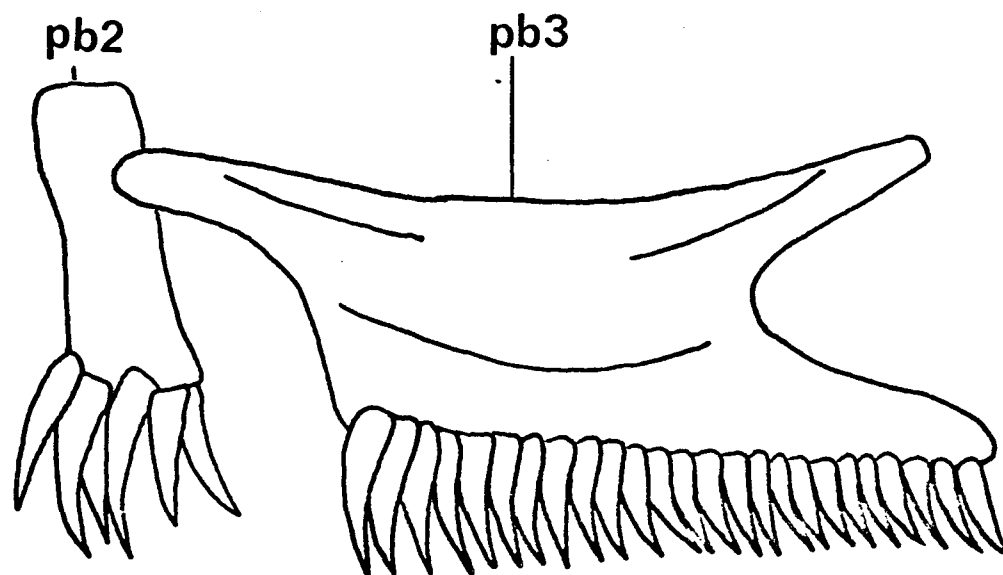


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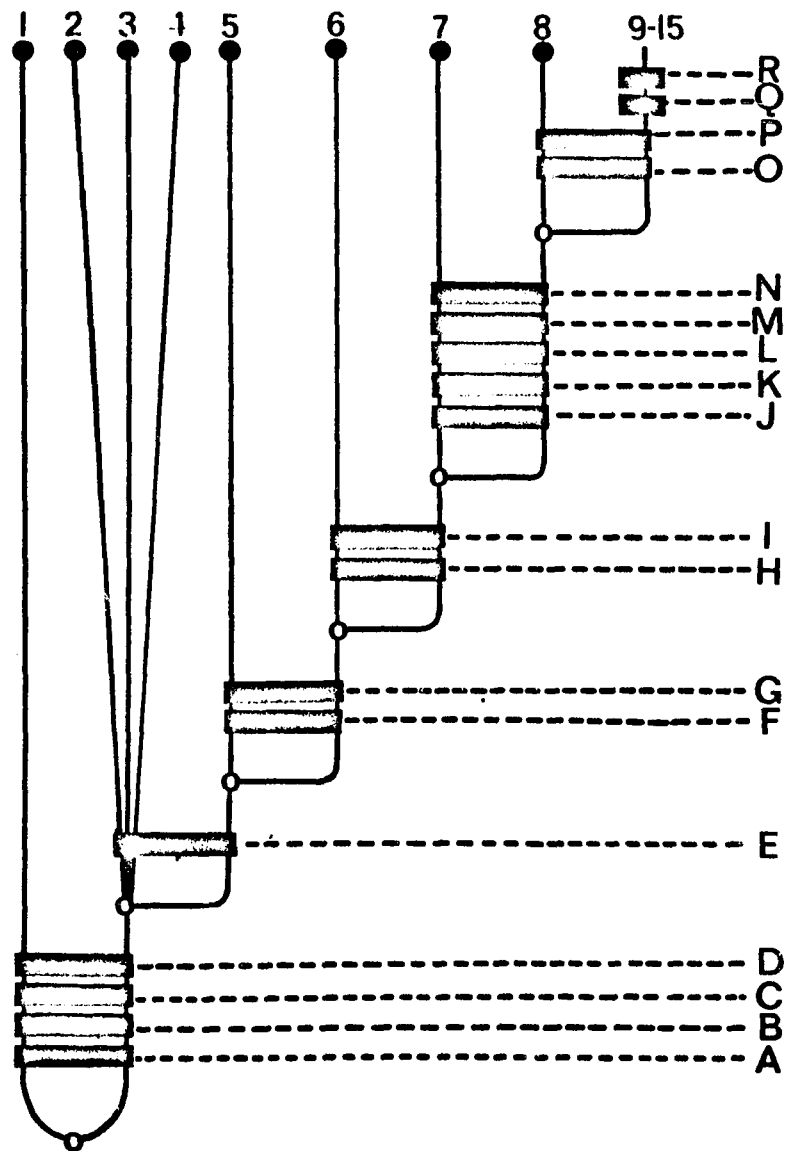


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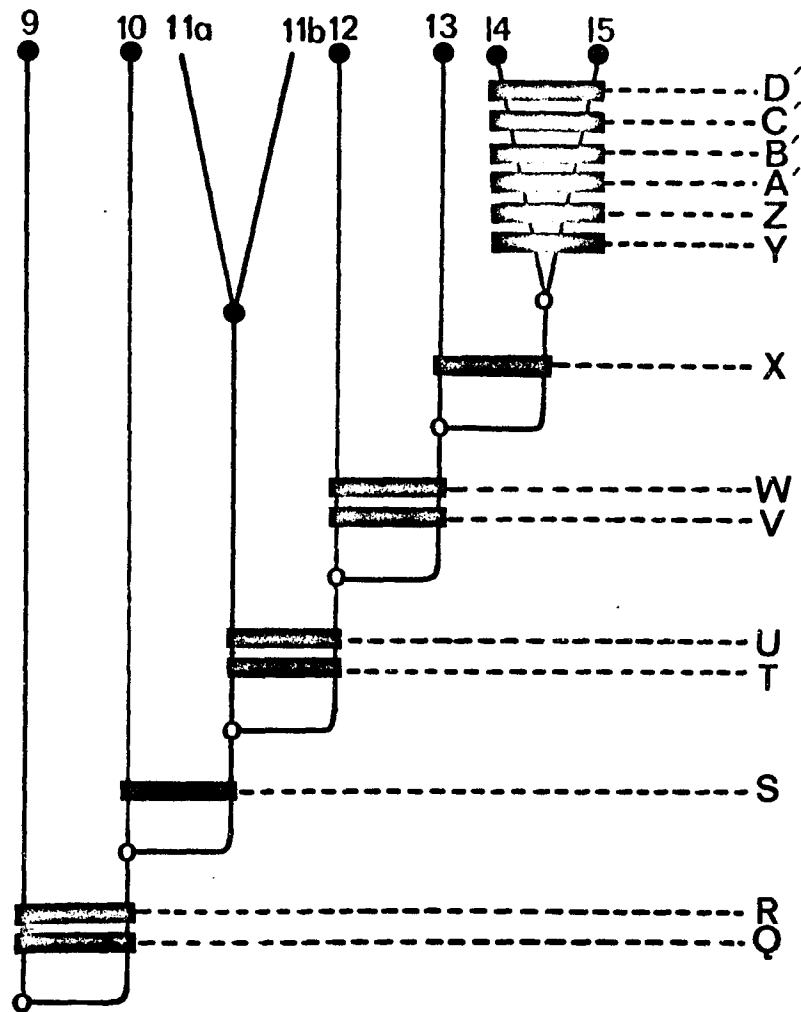


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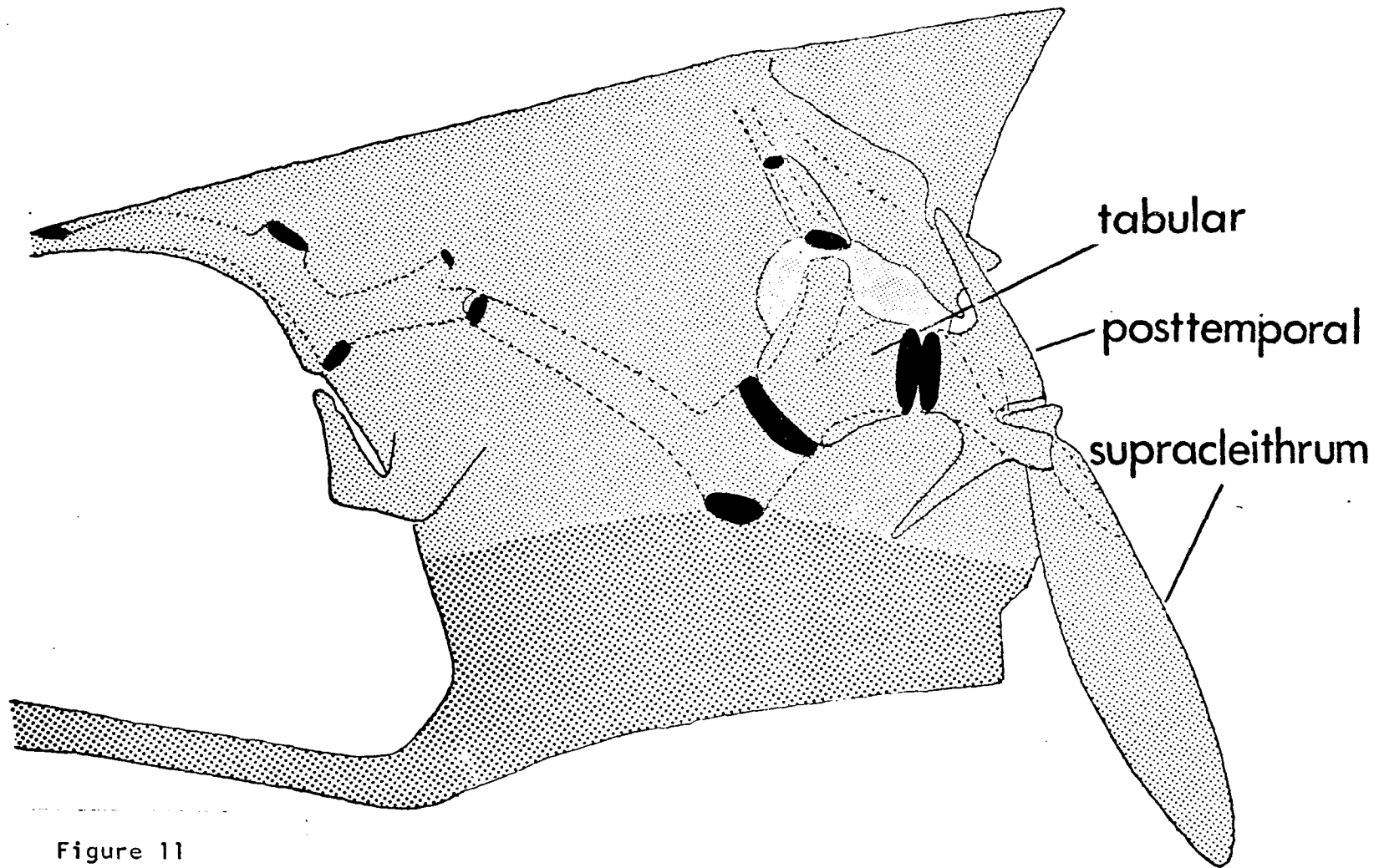
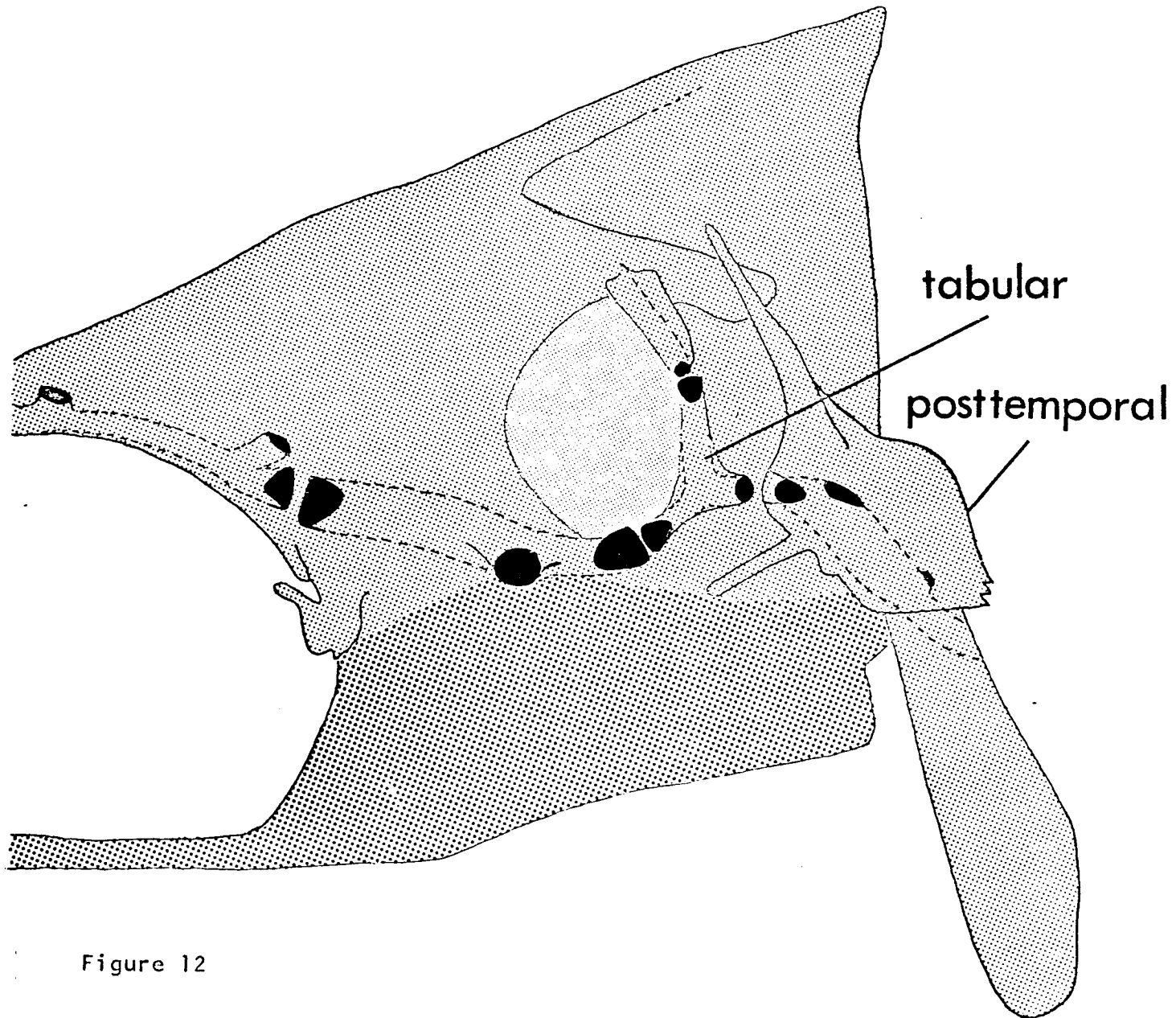
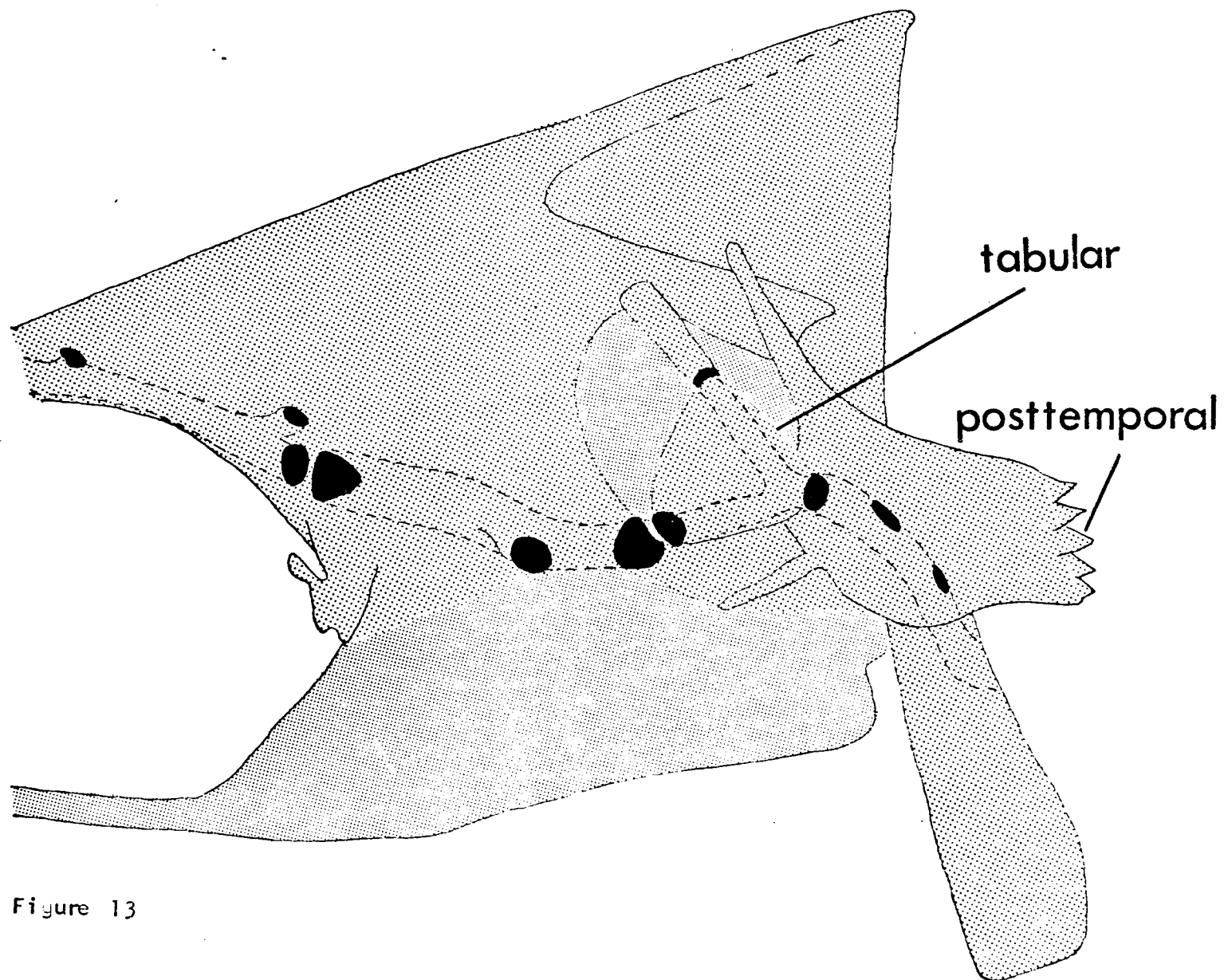


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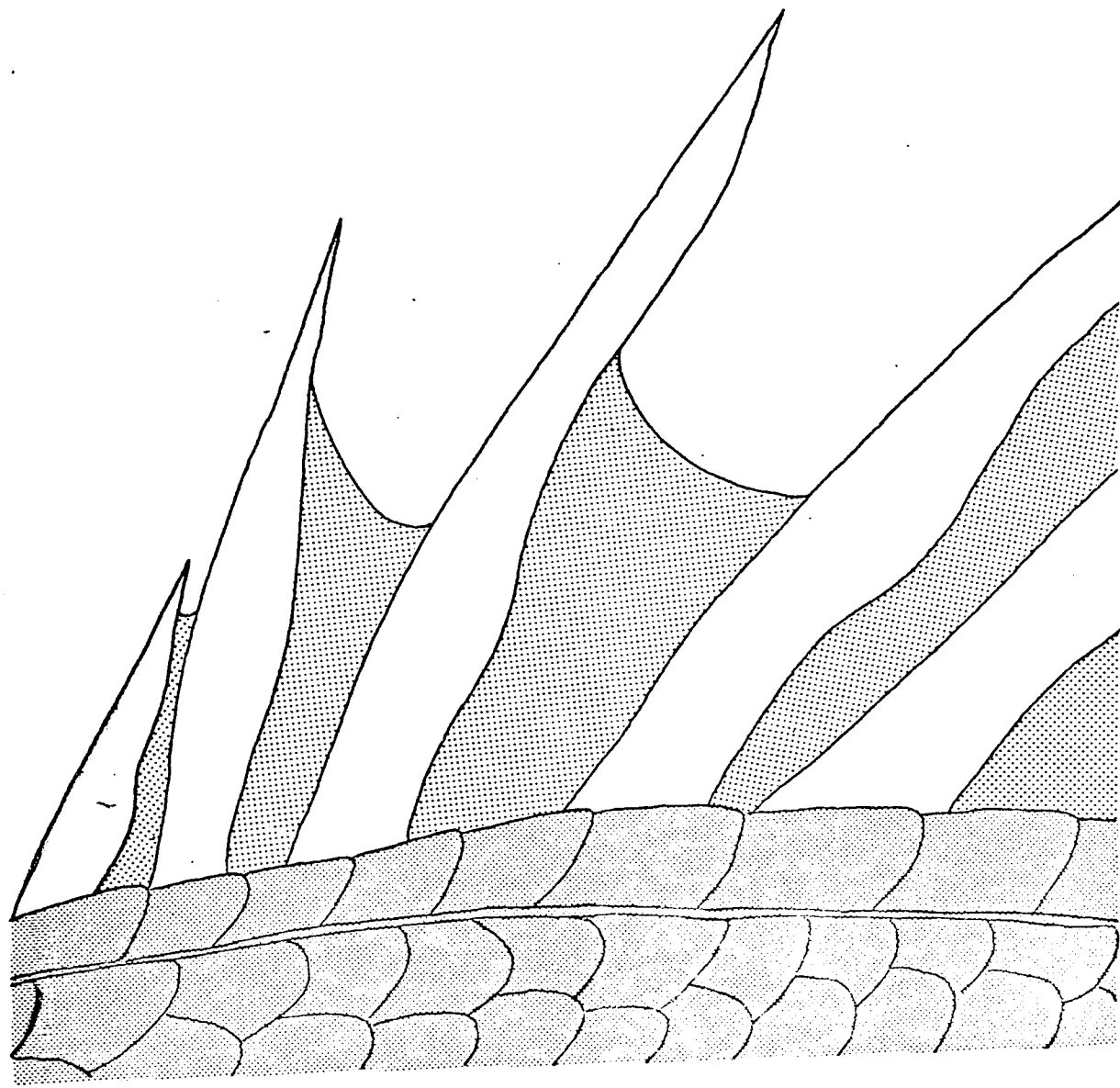
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Figure 12



1405

Figure 13



basal sheath

Figure 14

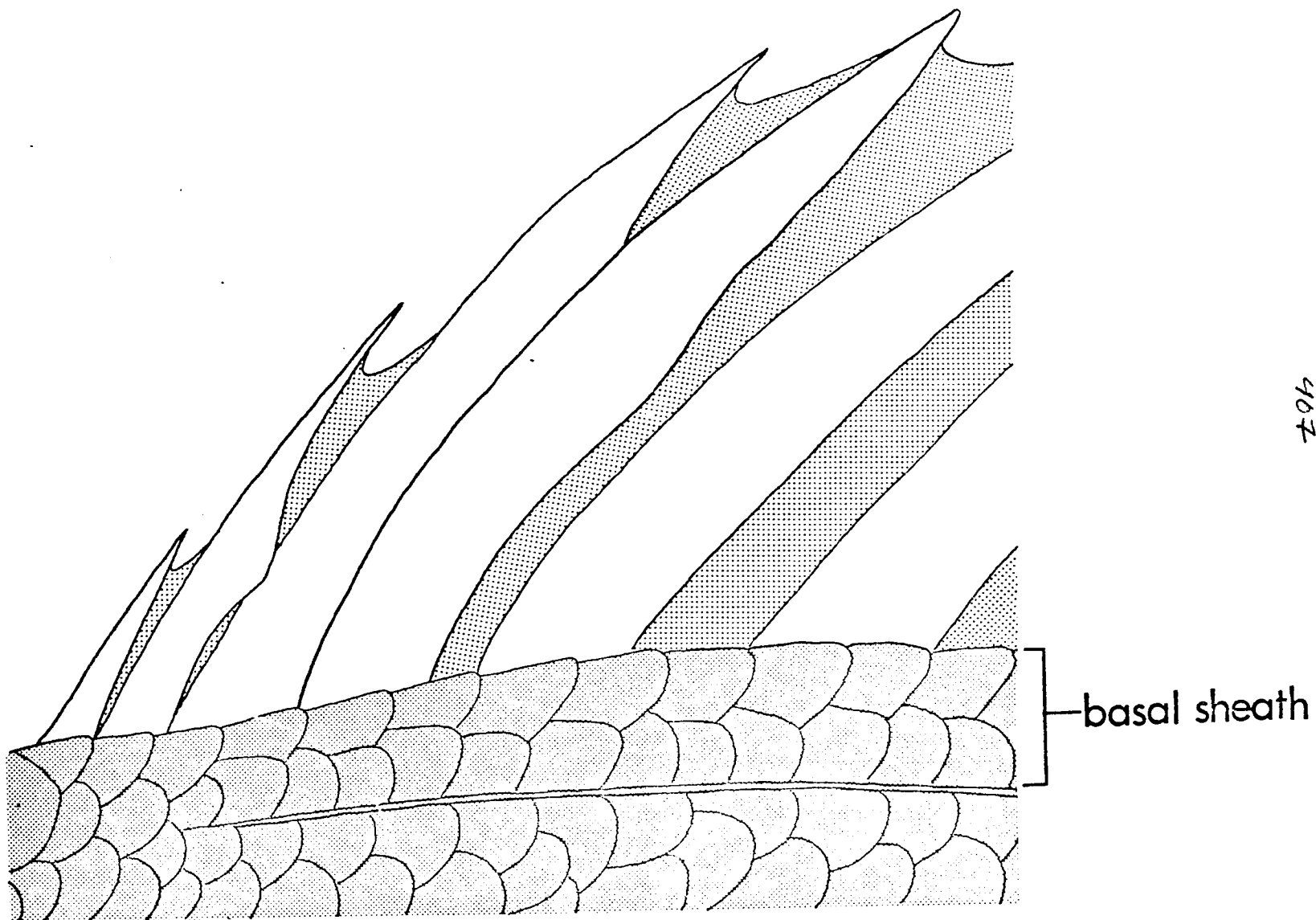


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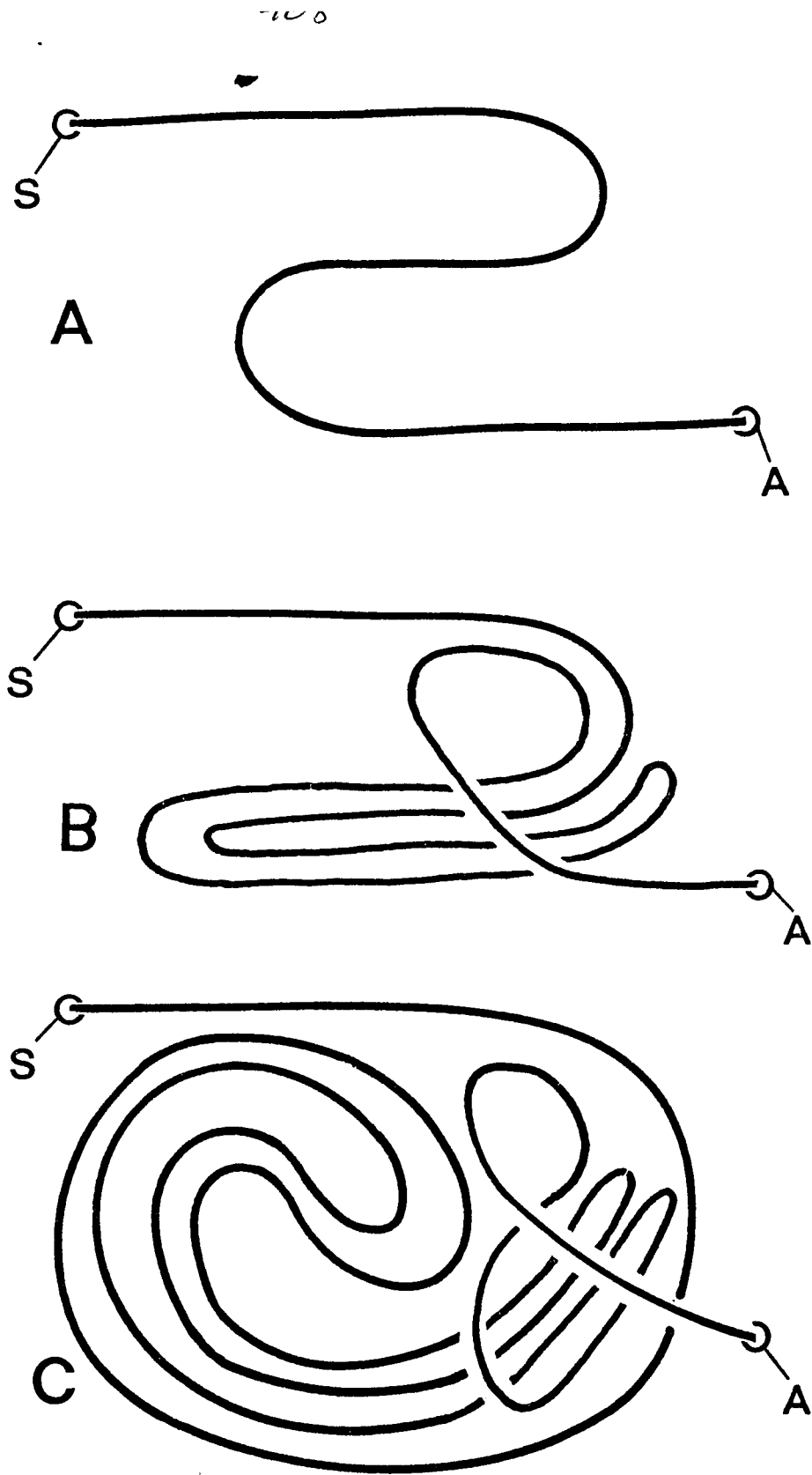


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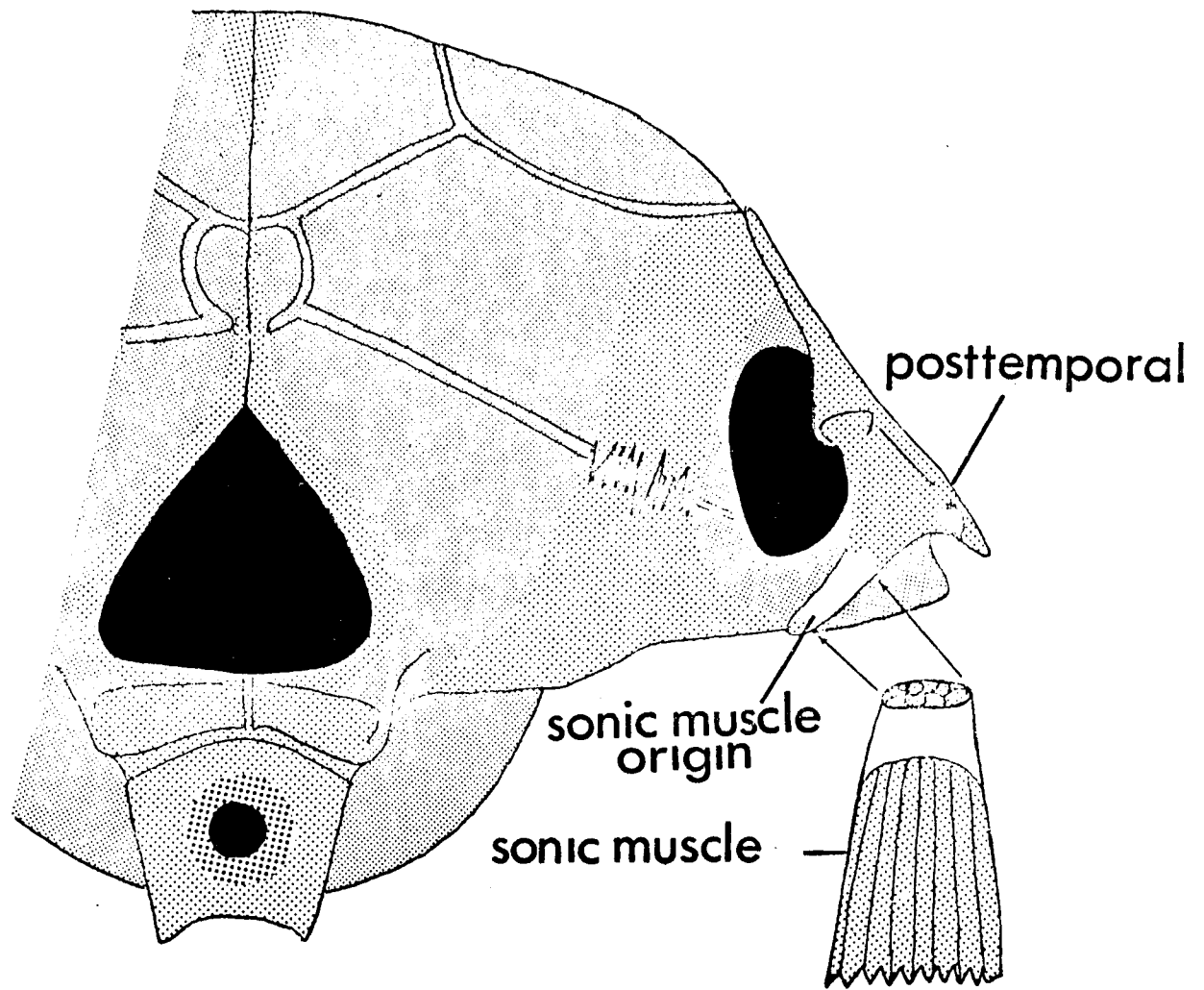


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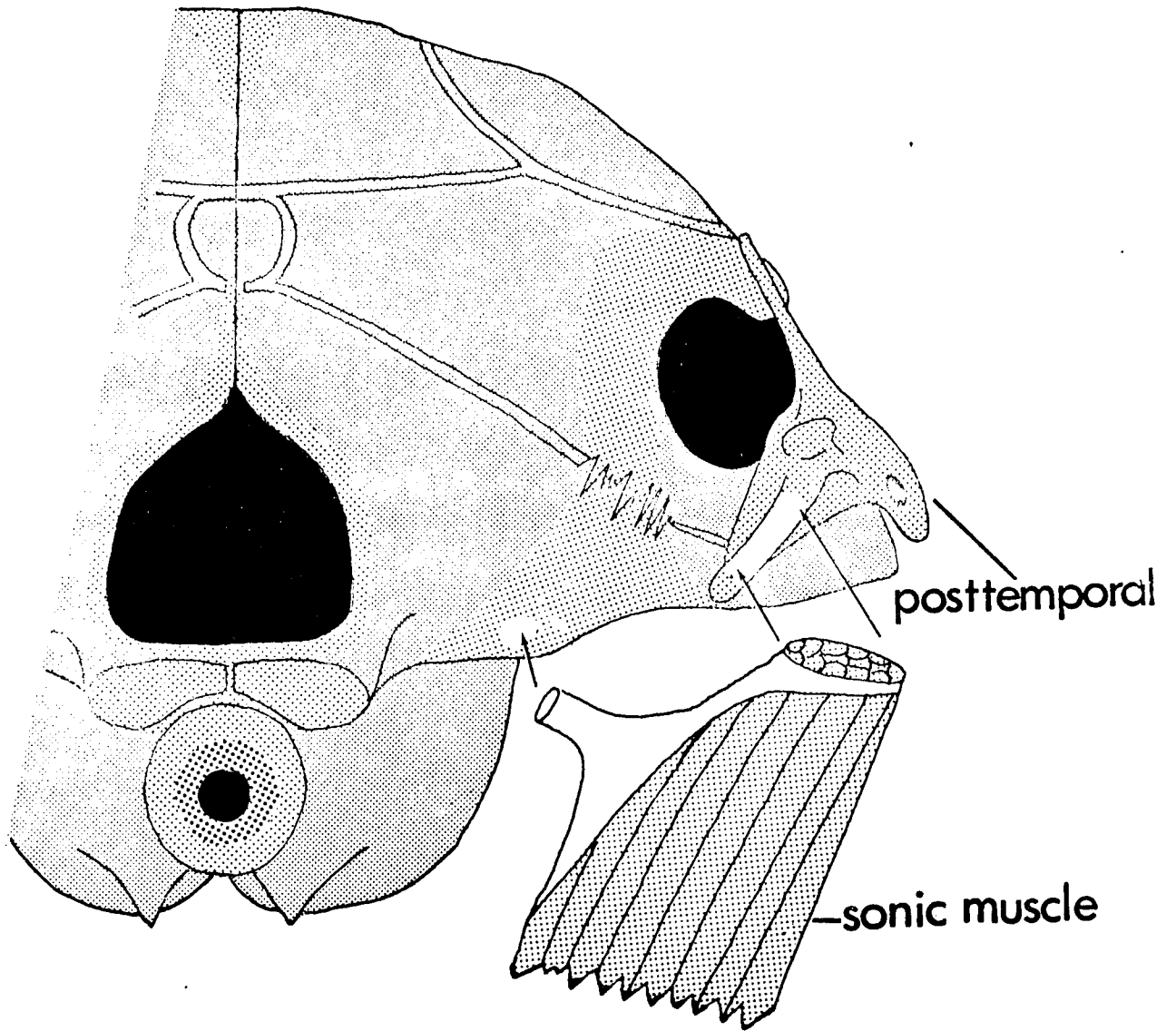


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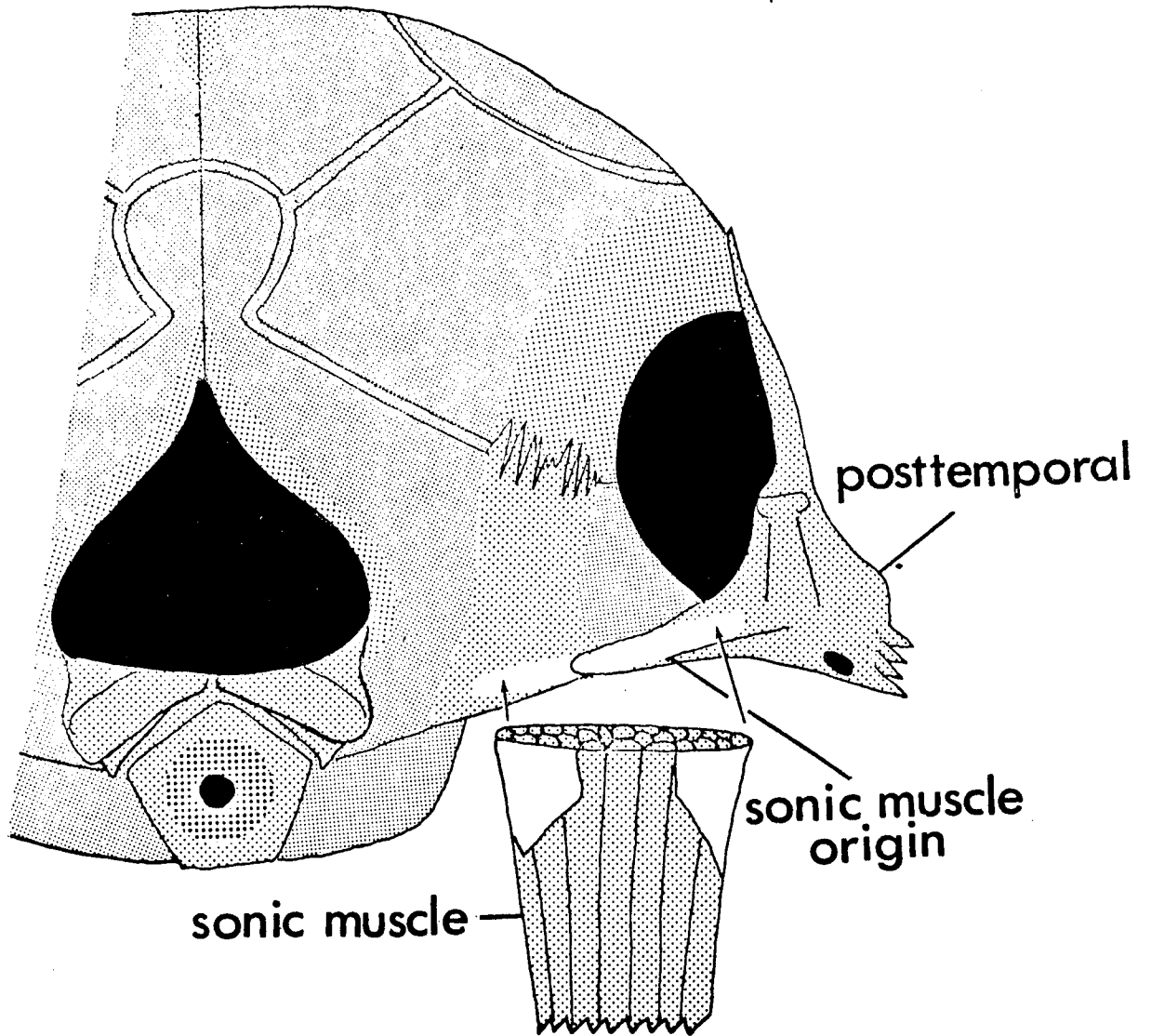


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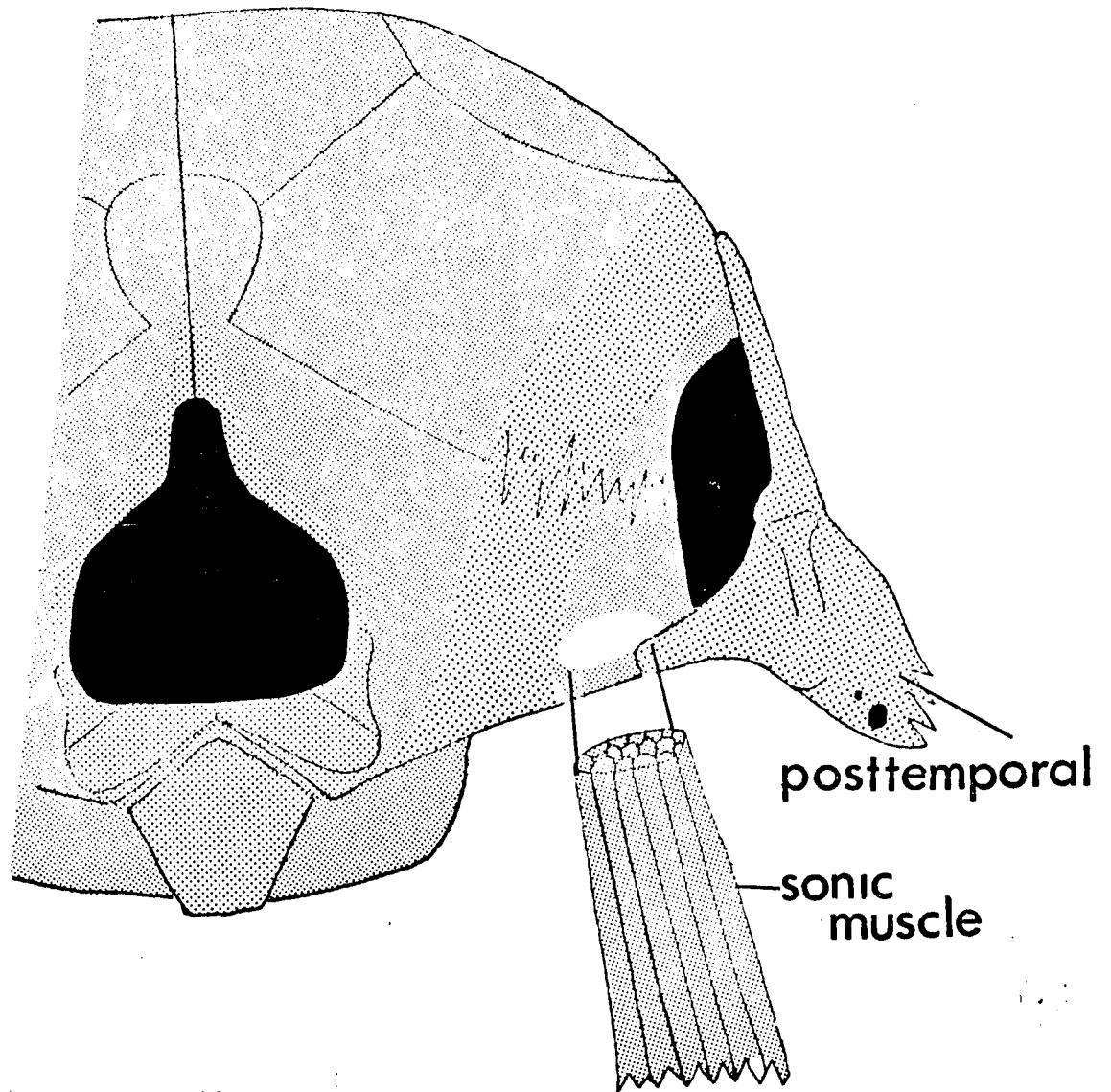
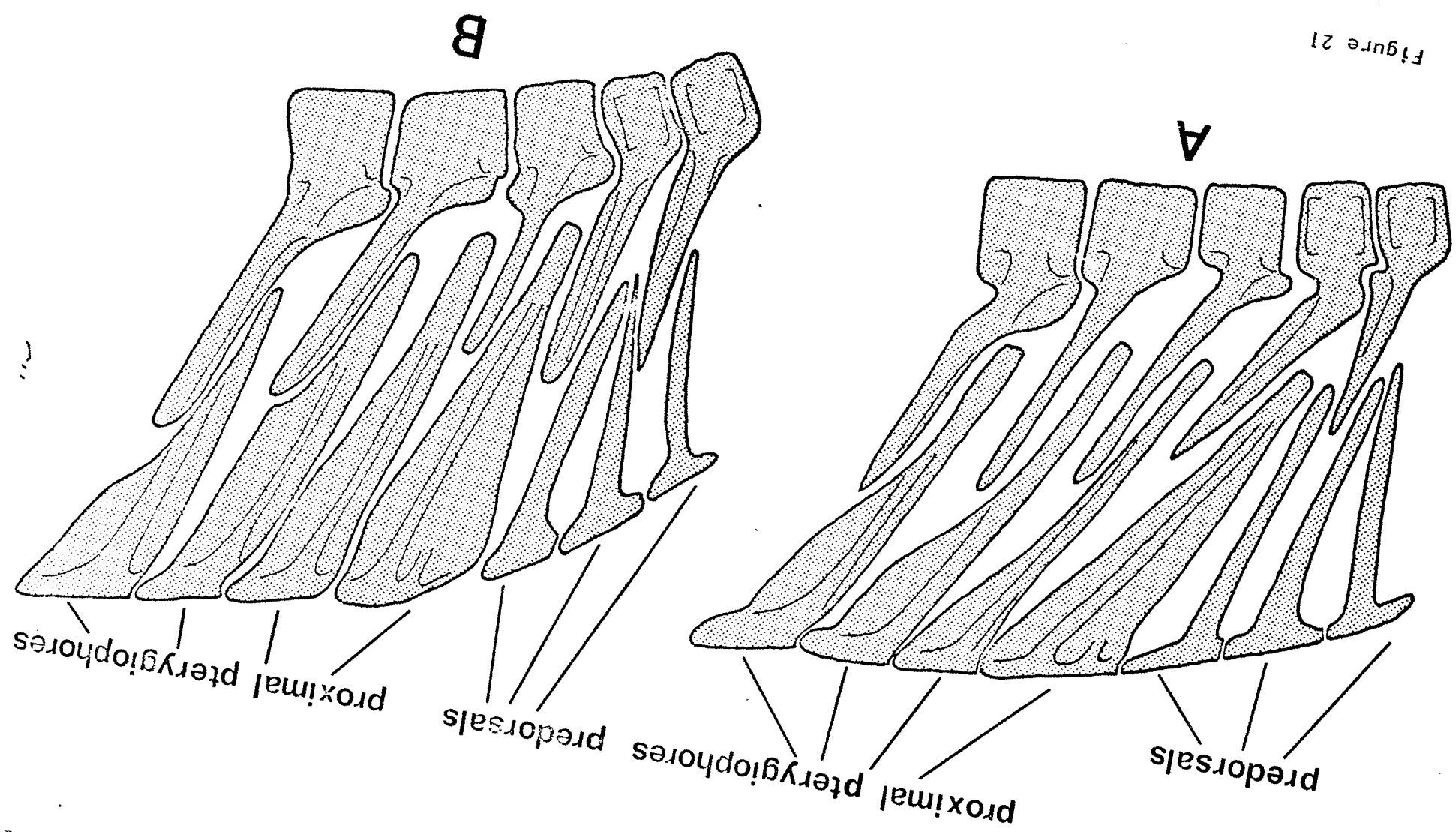


Figure 20

Figure 21



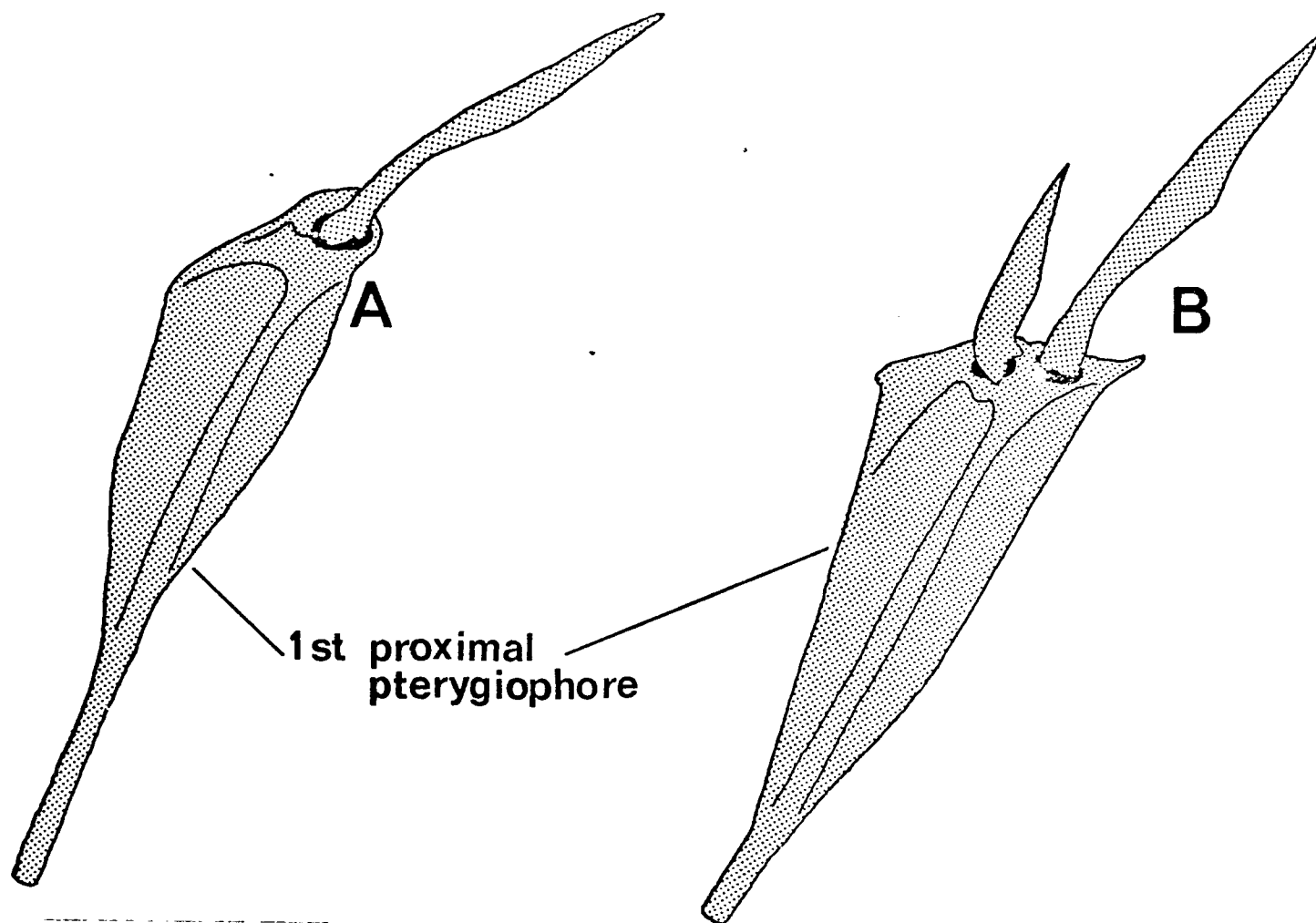
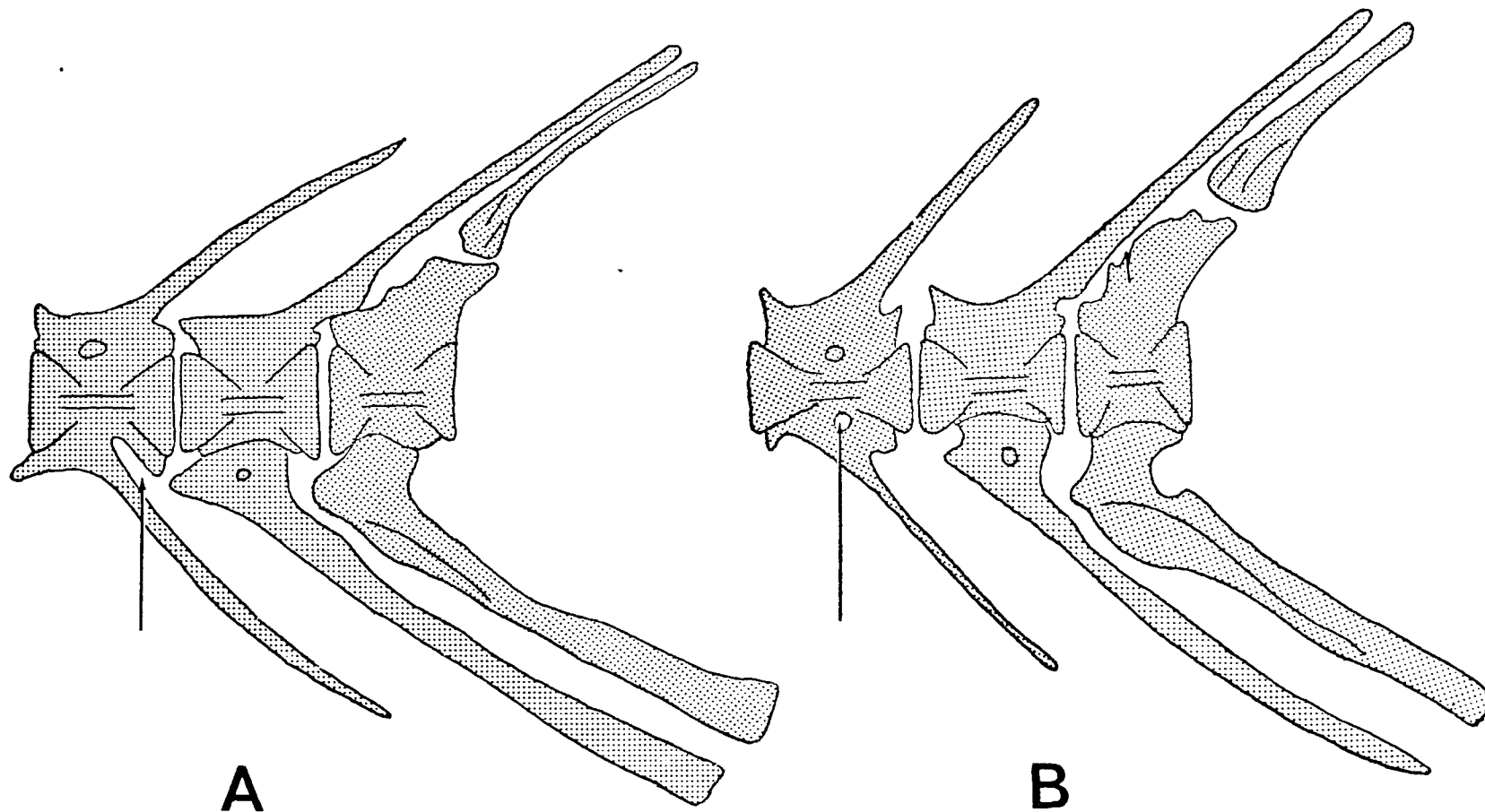
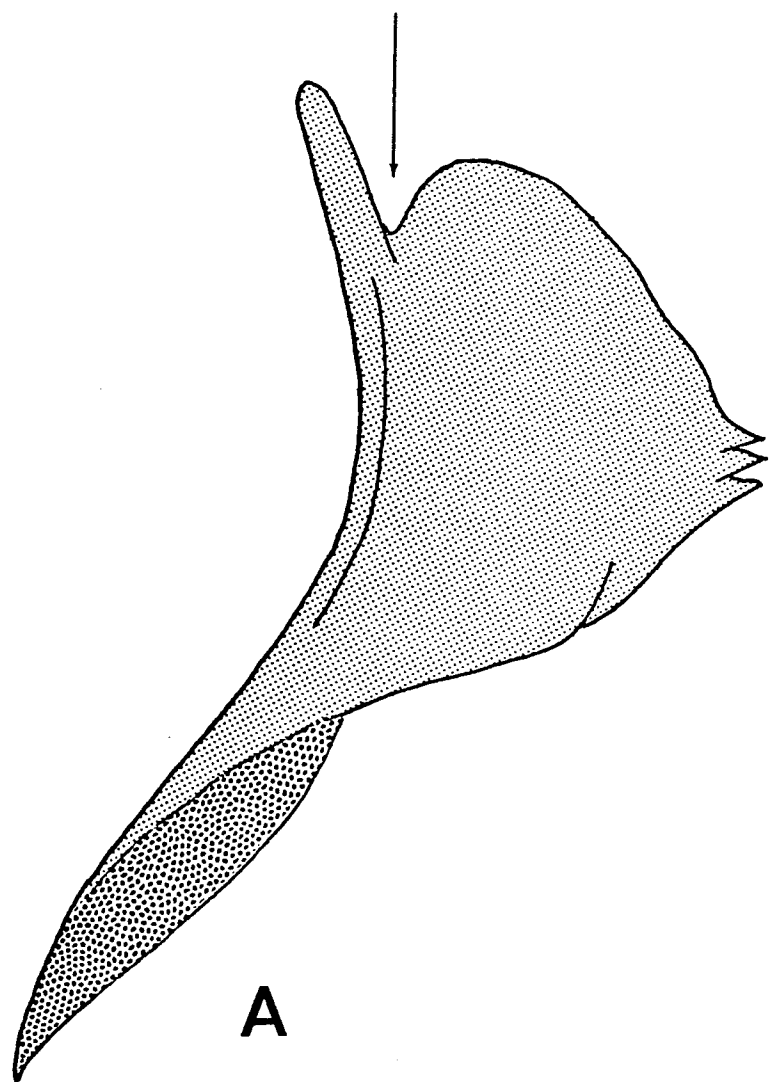


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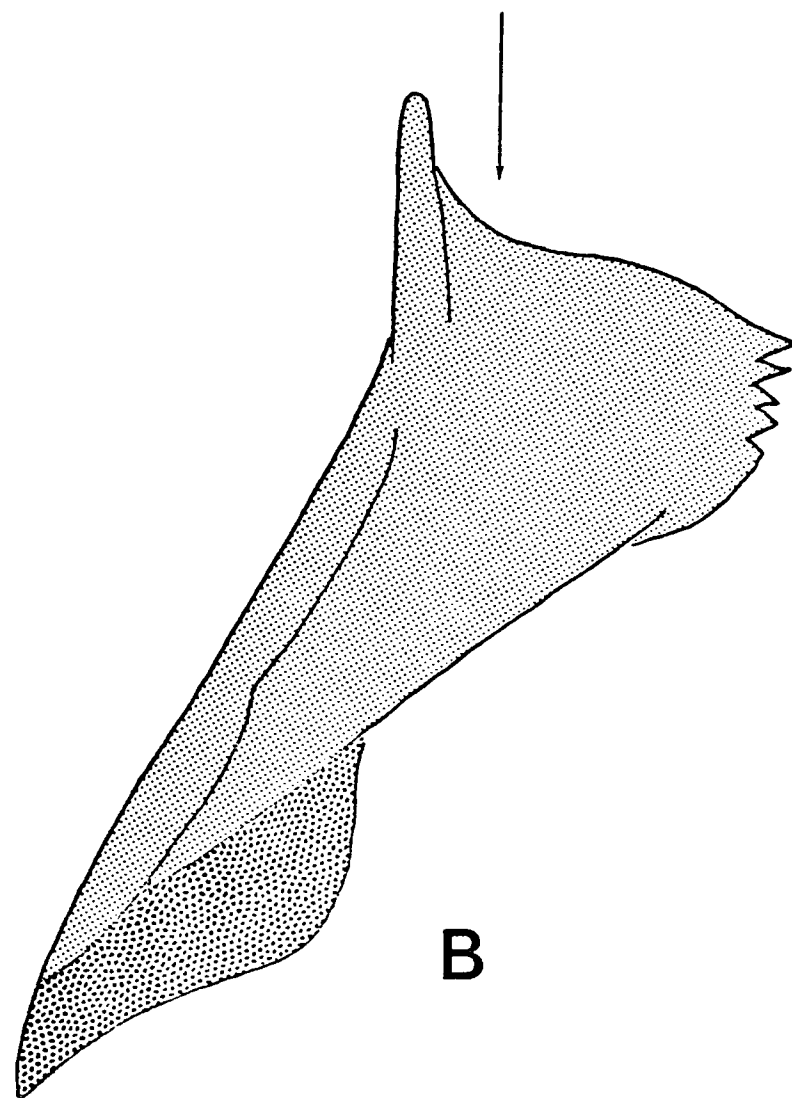


412

Figure 23



A



B

416

Figure 24

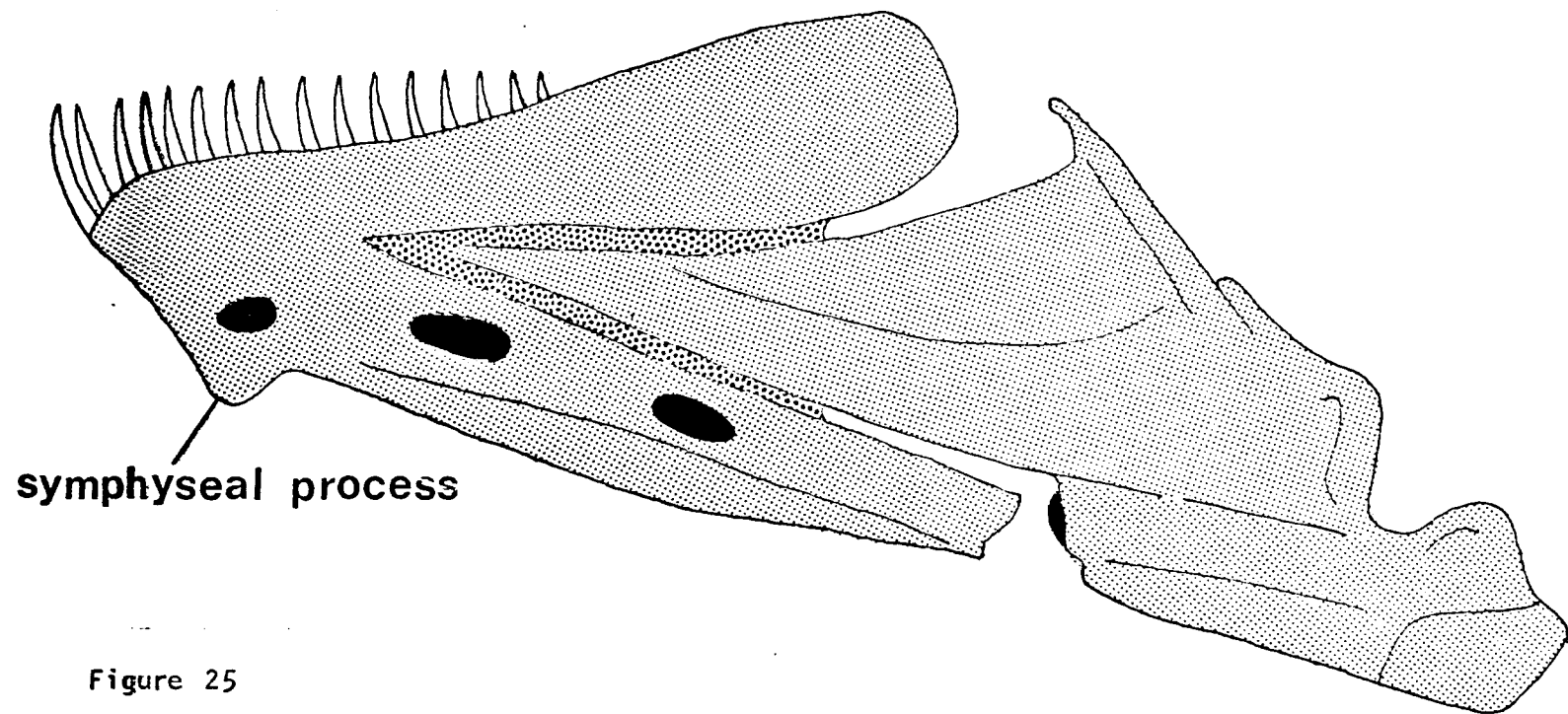


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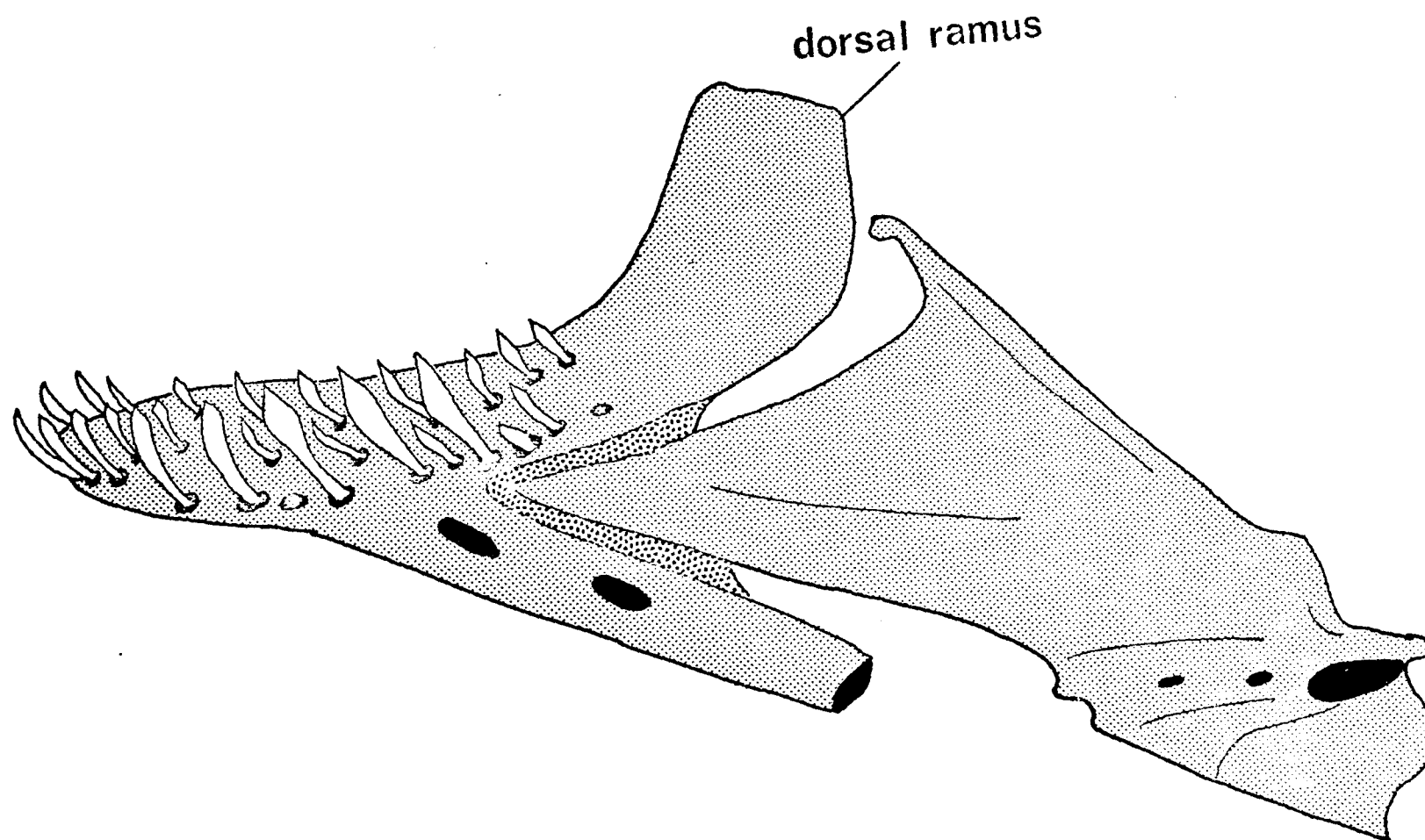


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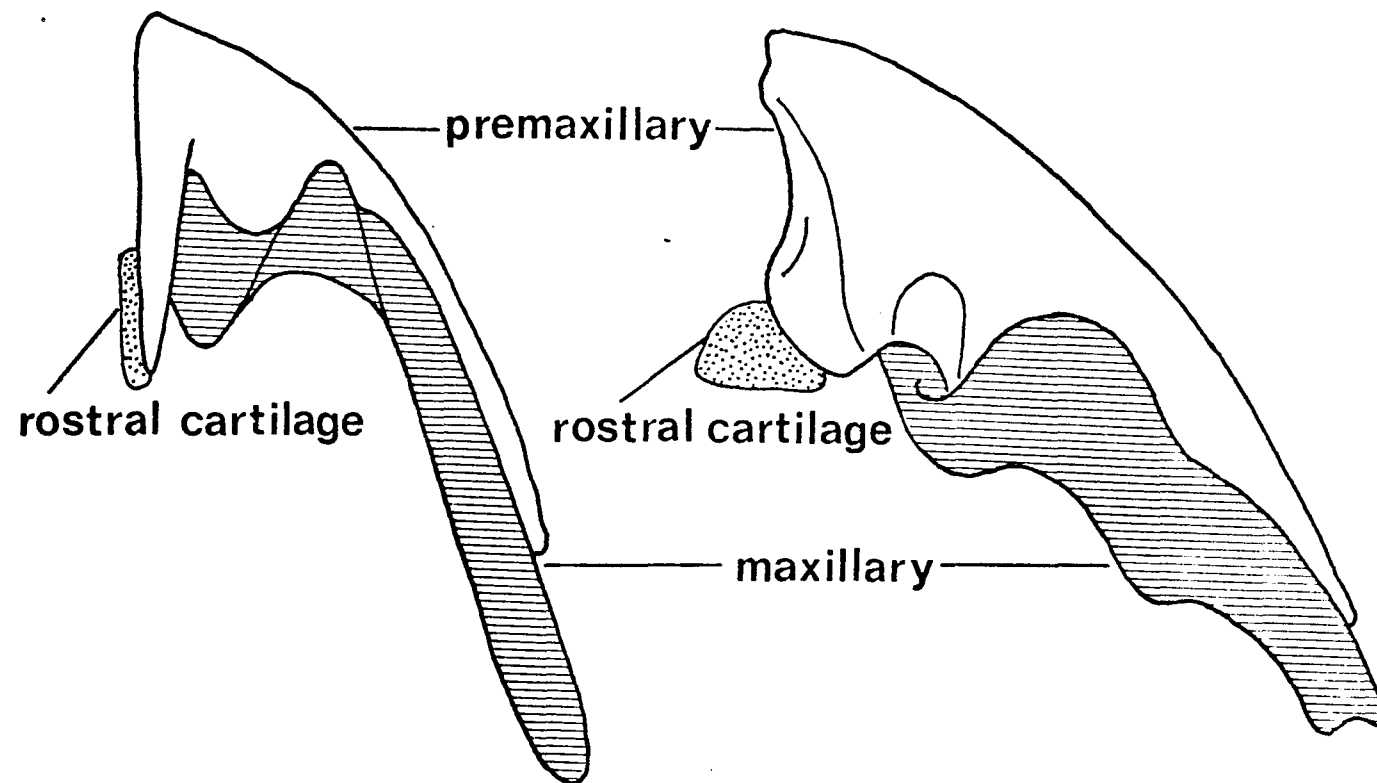


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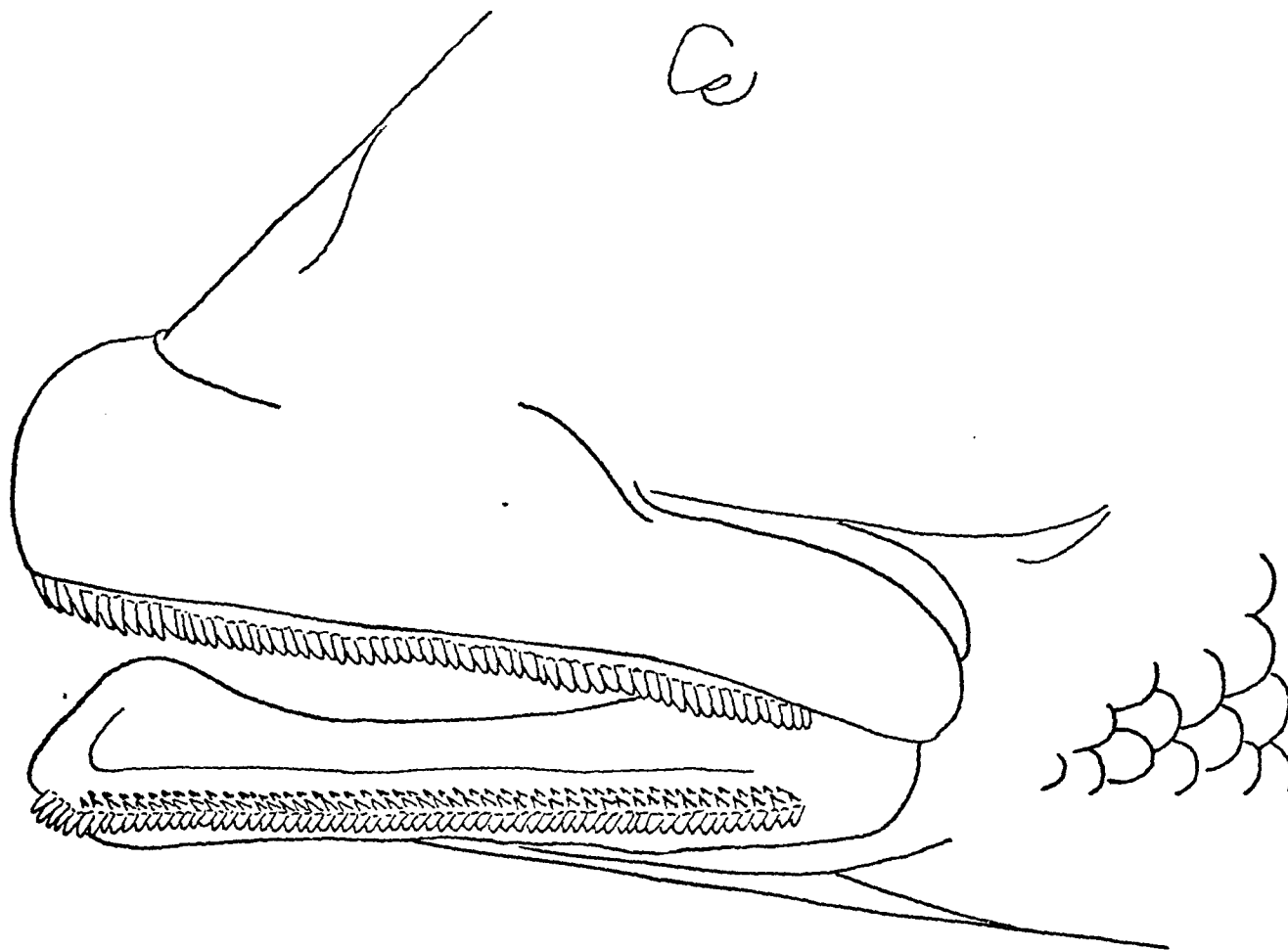
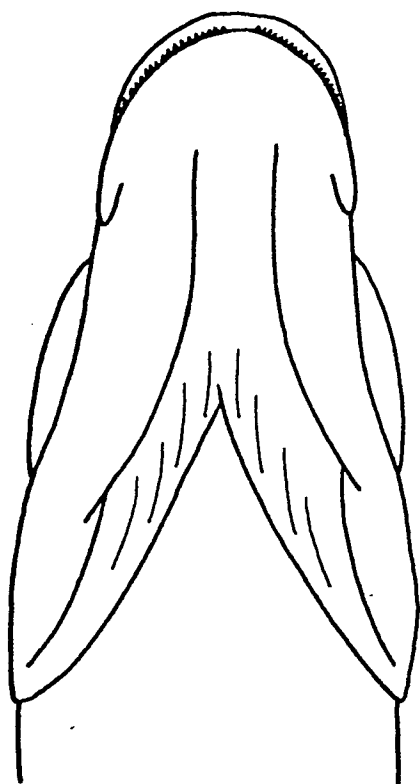


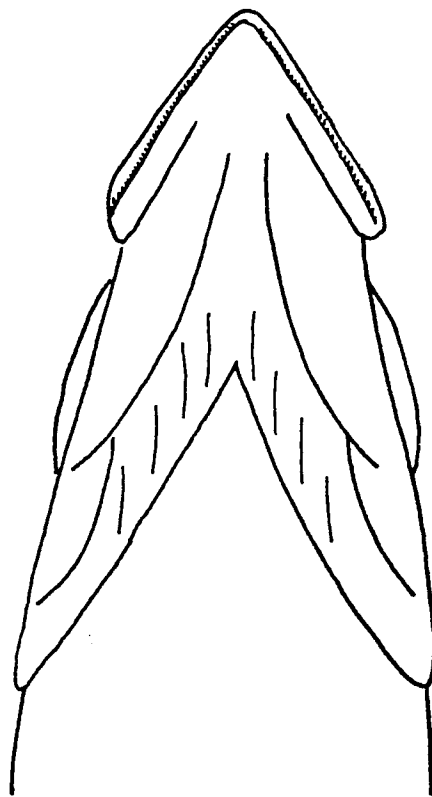
Figure 28



704

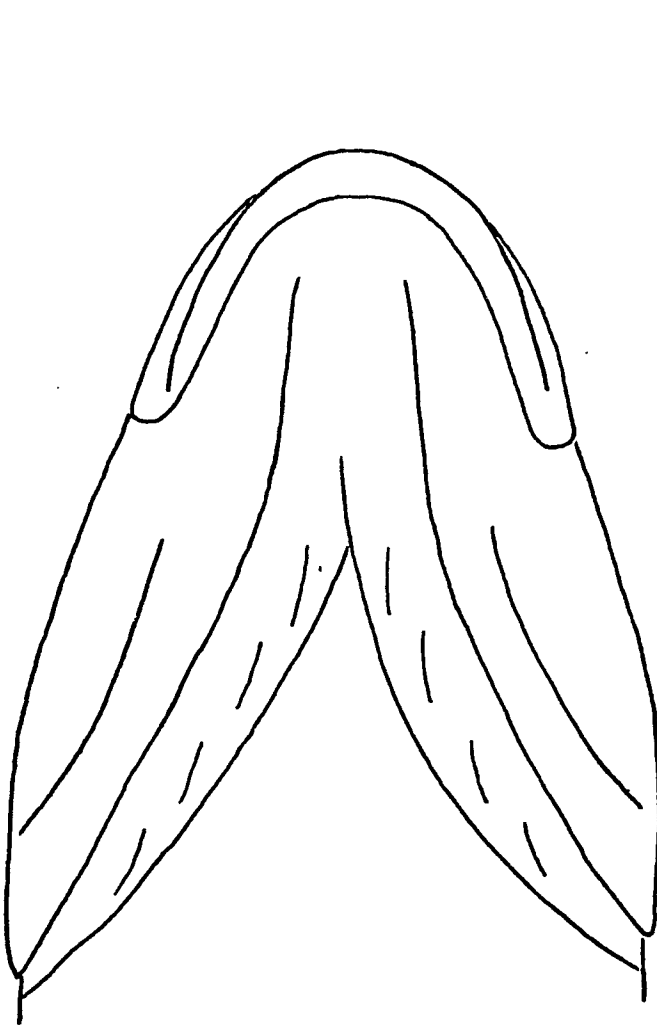


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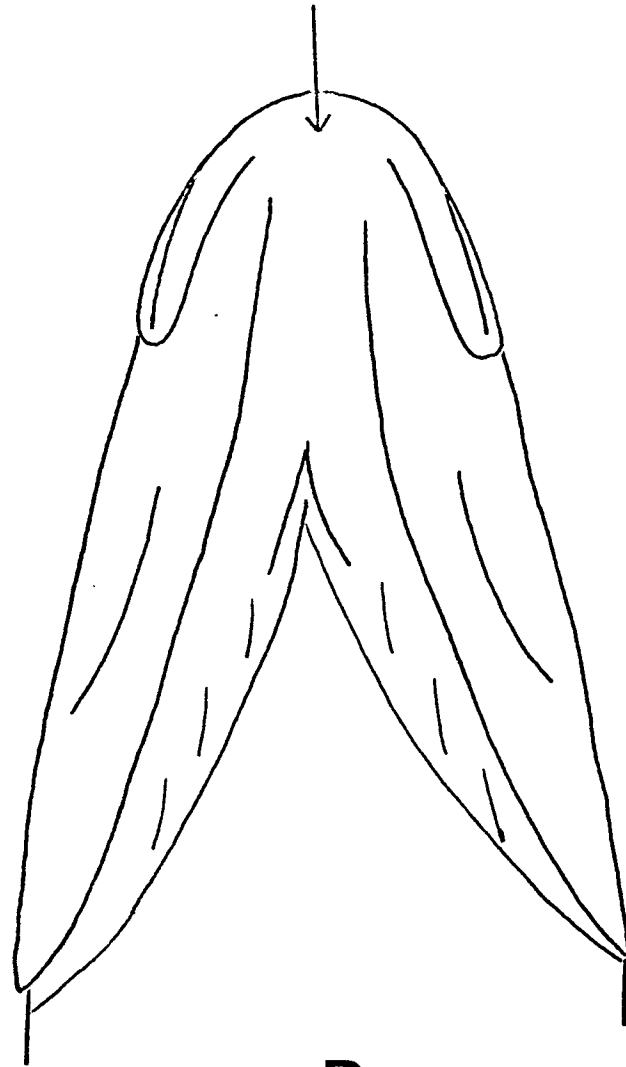


B

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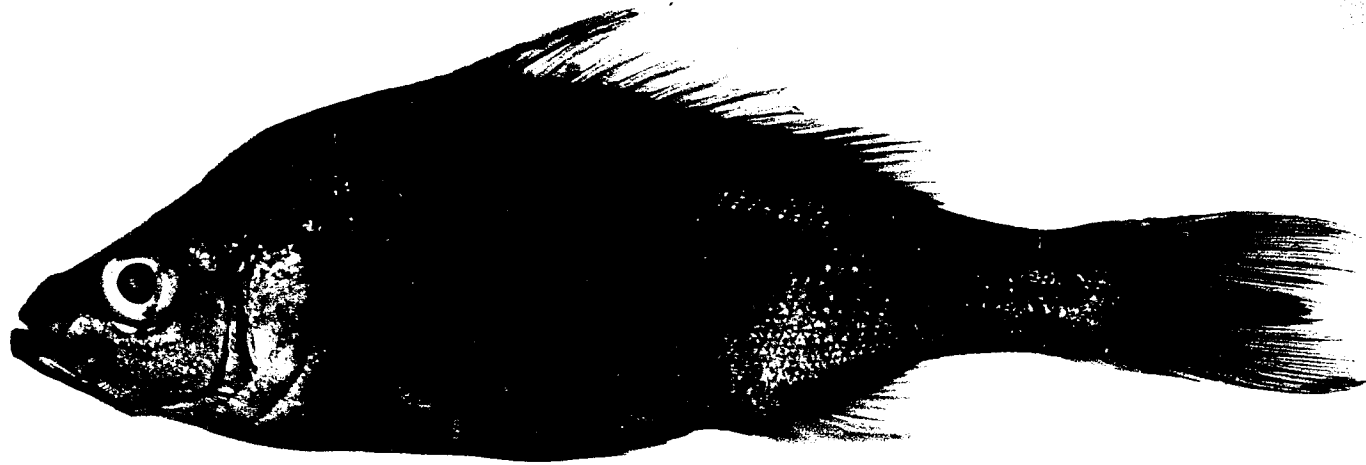


A



B

Figure 31



424

Figure 32



425

Figure 33

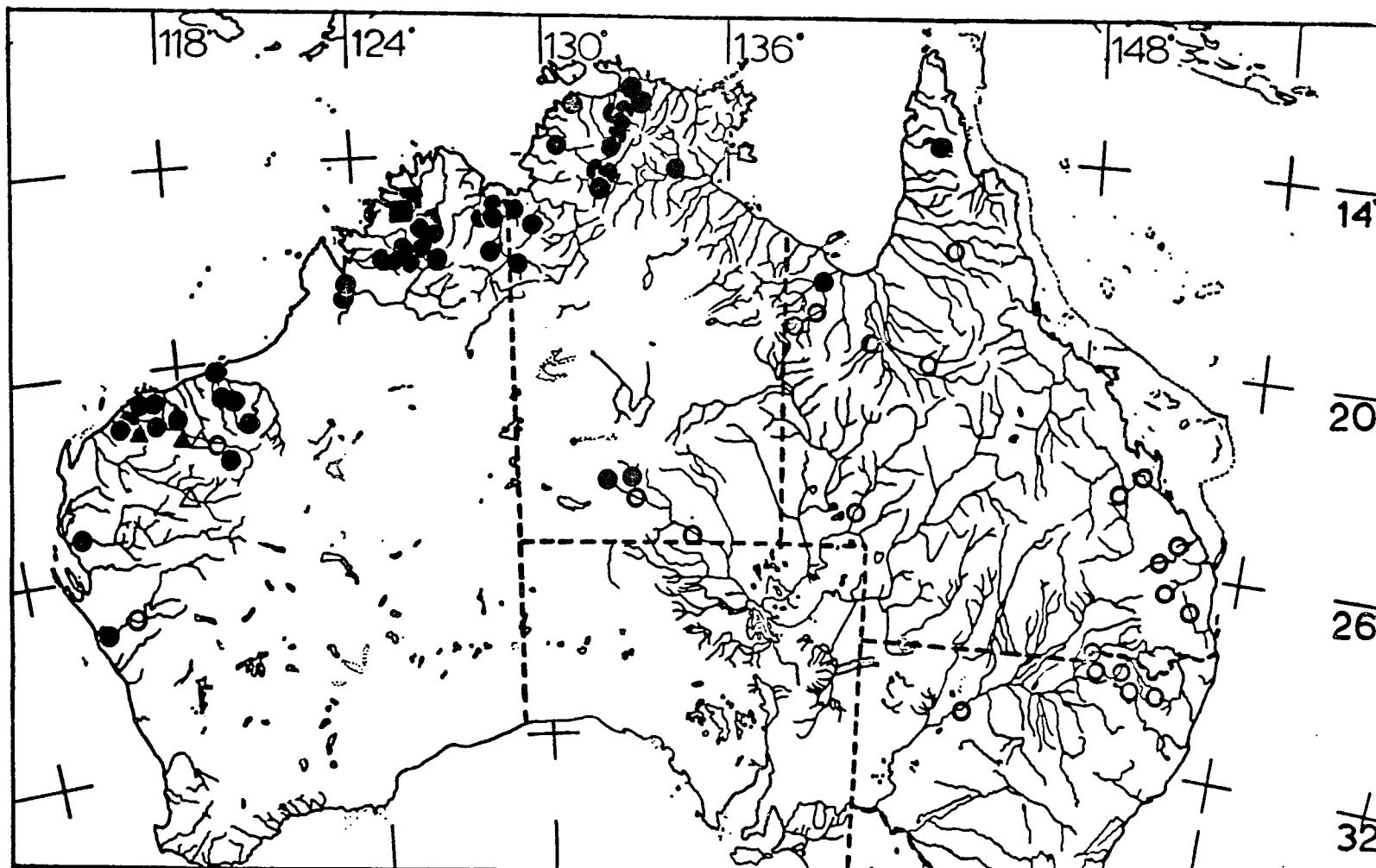


Figure 34



427

Figure 35

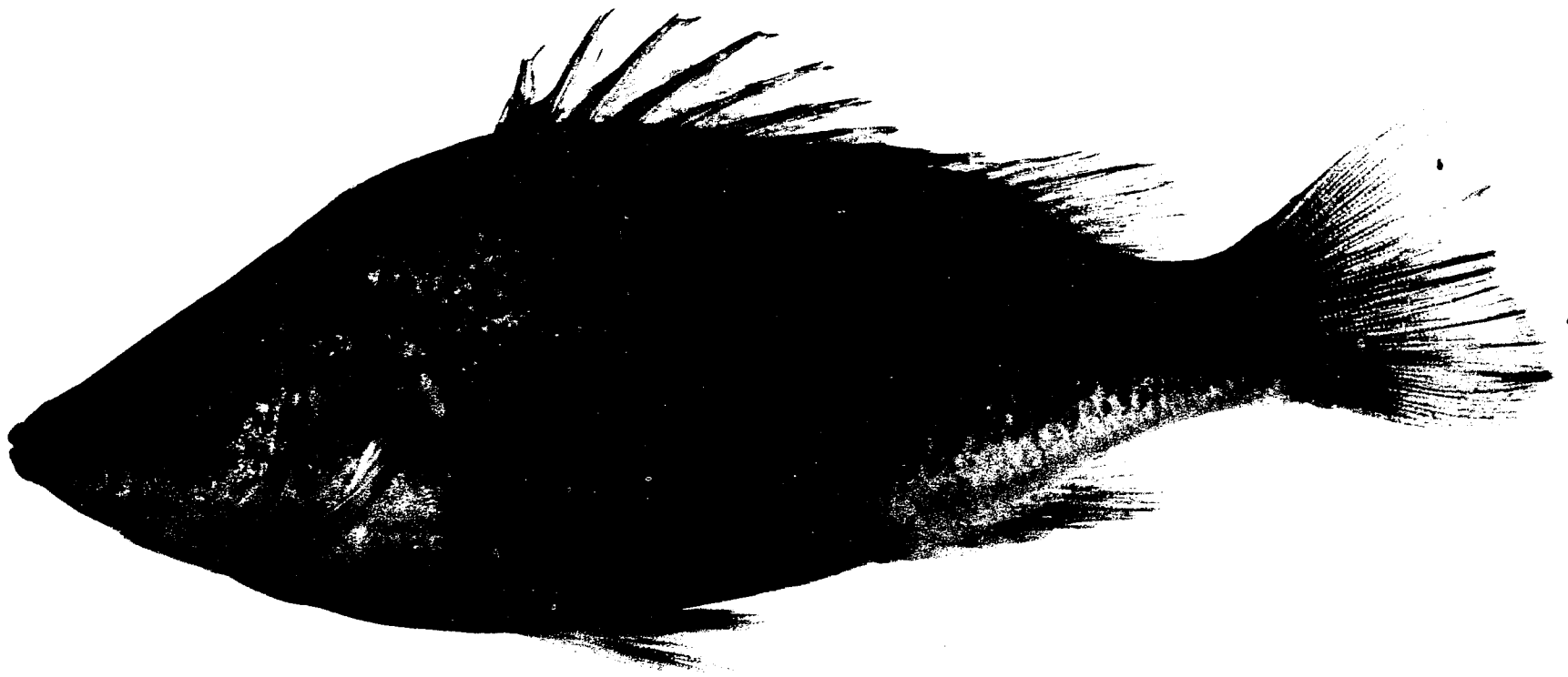
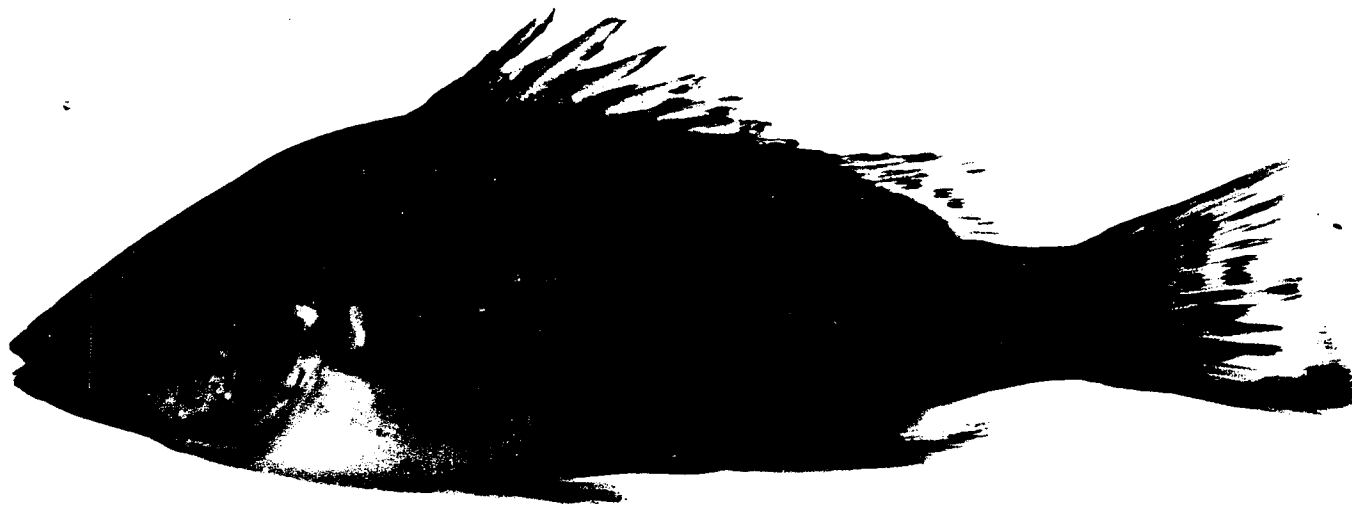


Figure 36



429

Figure 37

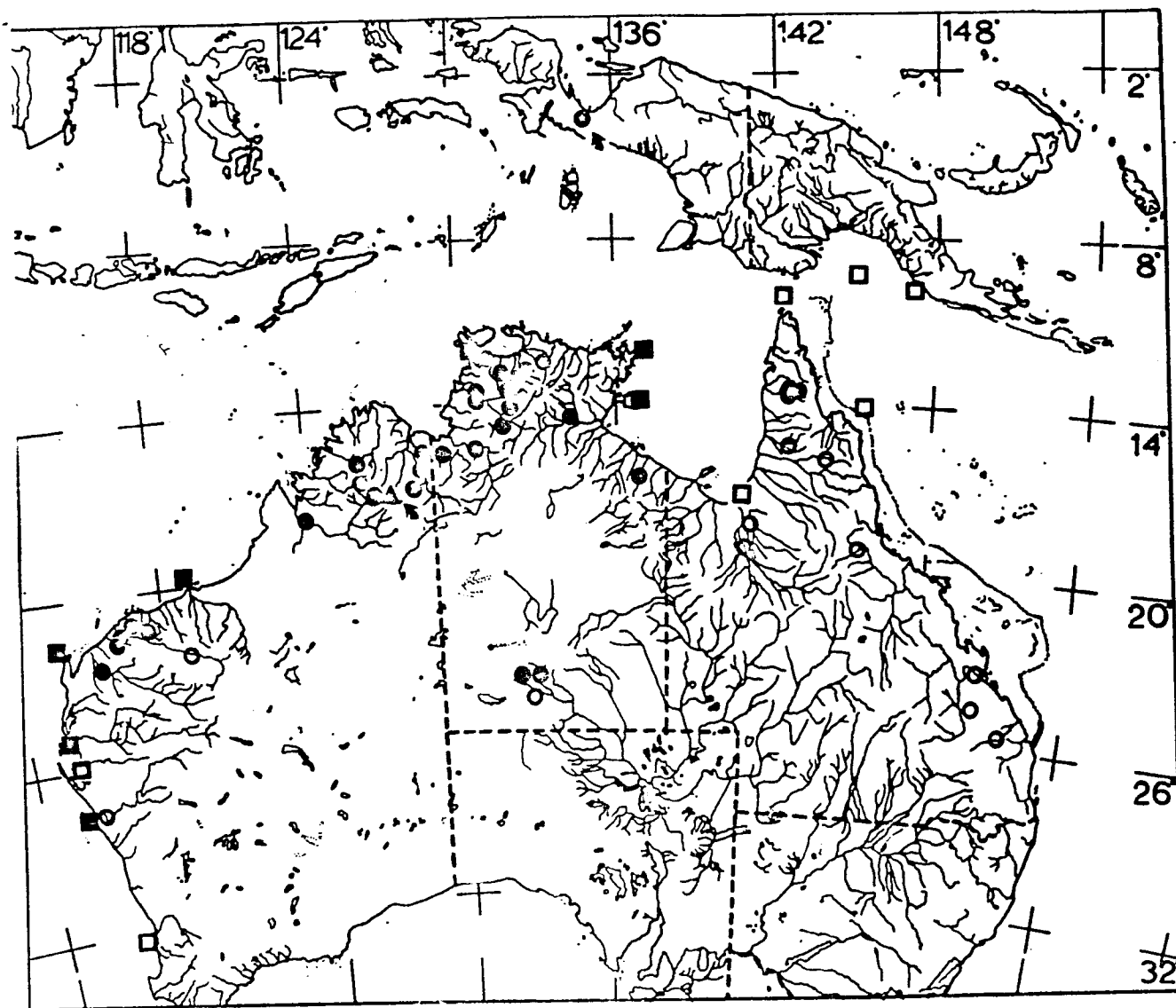
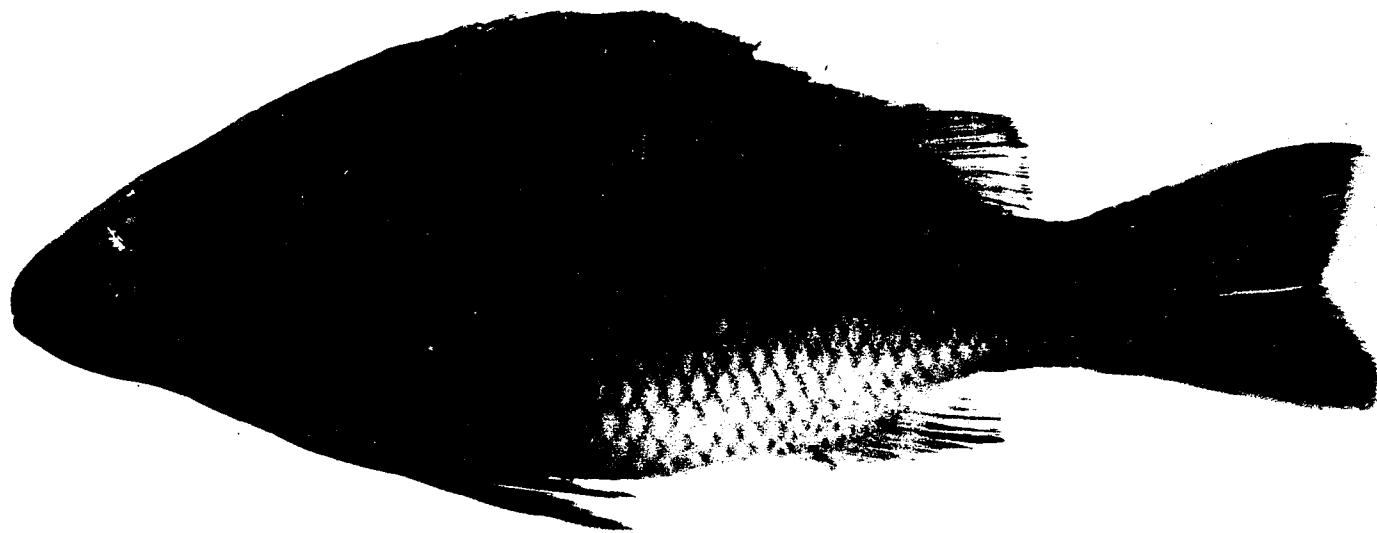


Figure 38



431

Figure 39

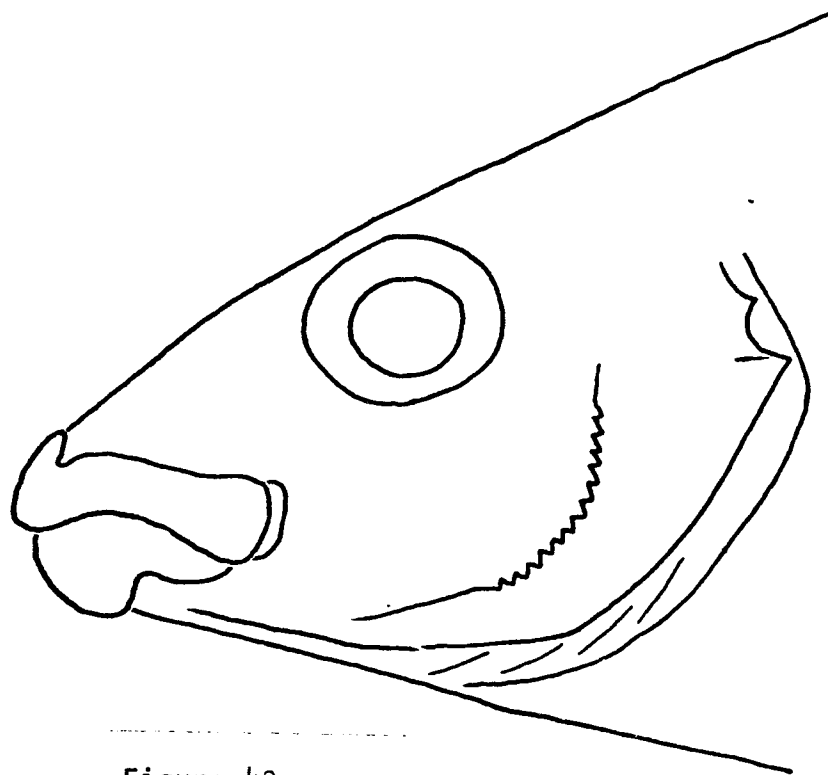
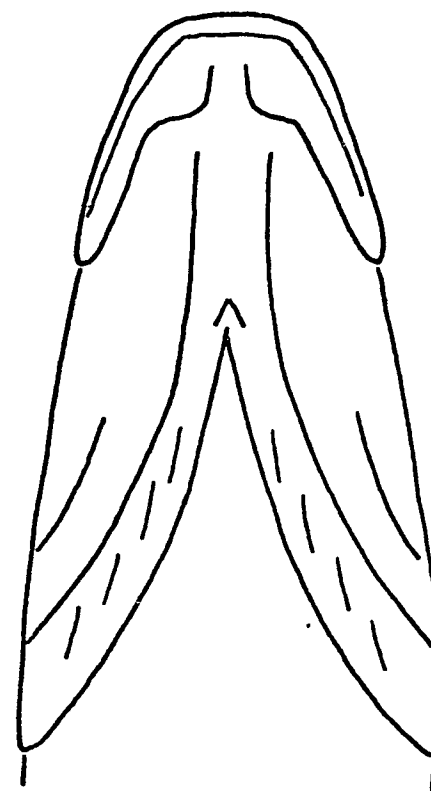


Figure 40





433

Figure 41

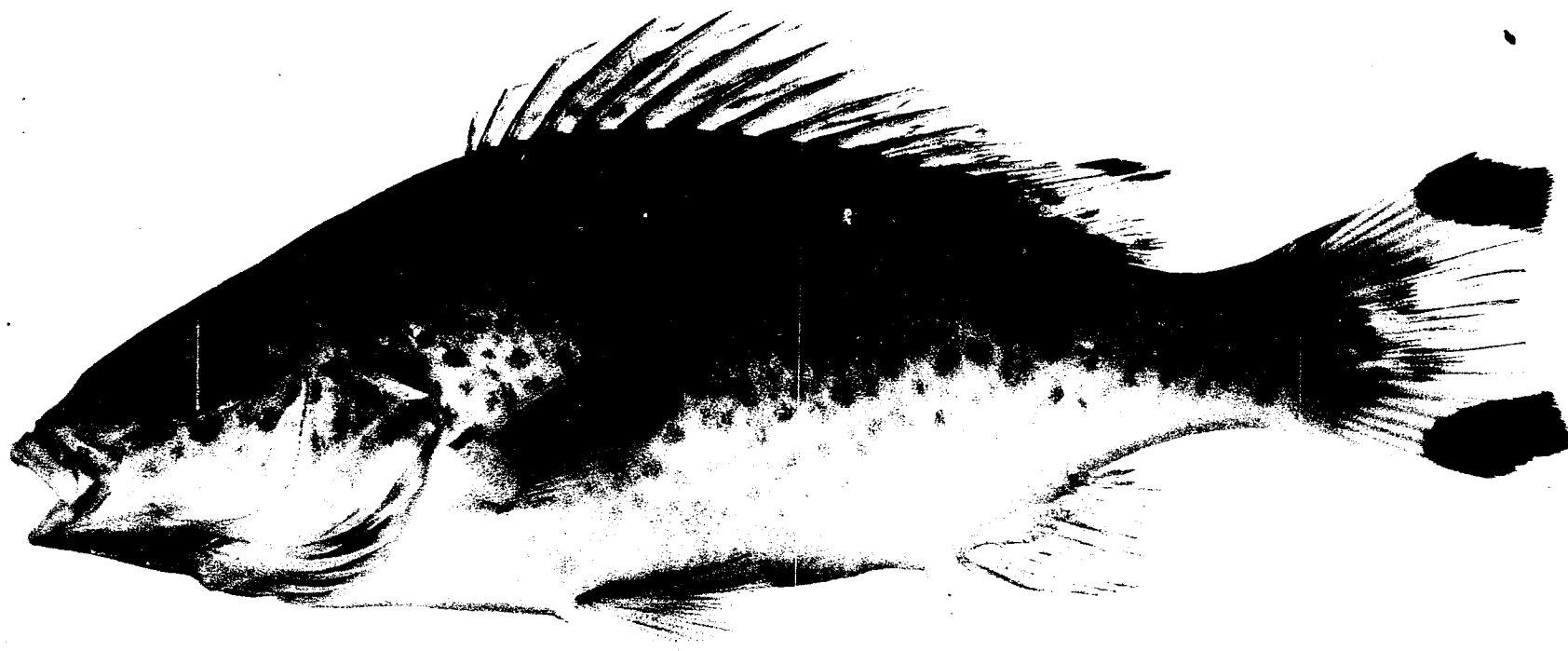
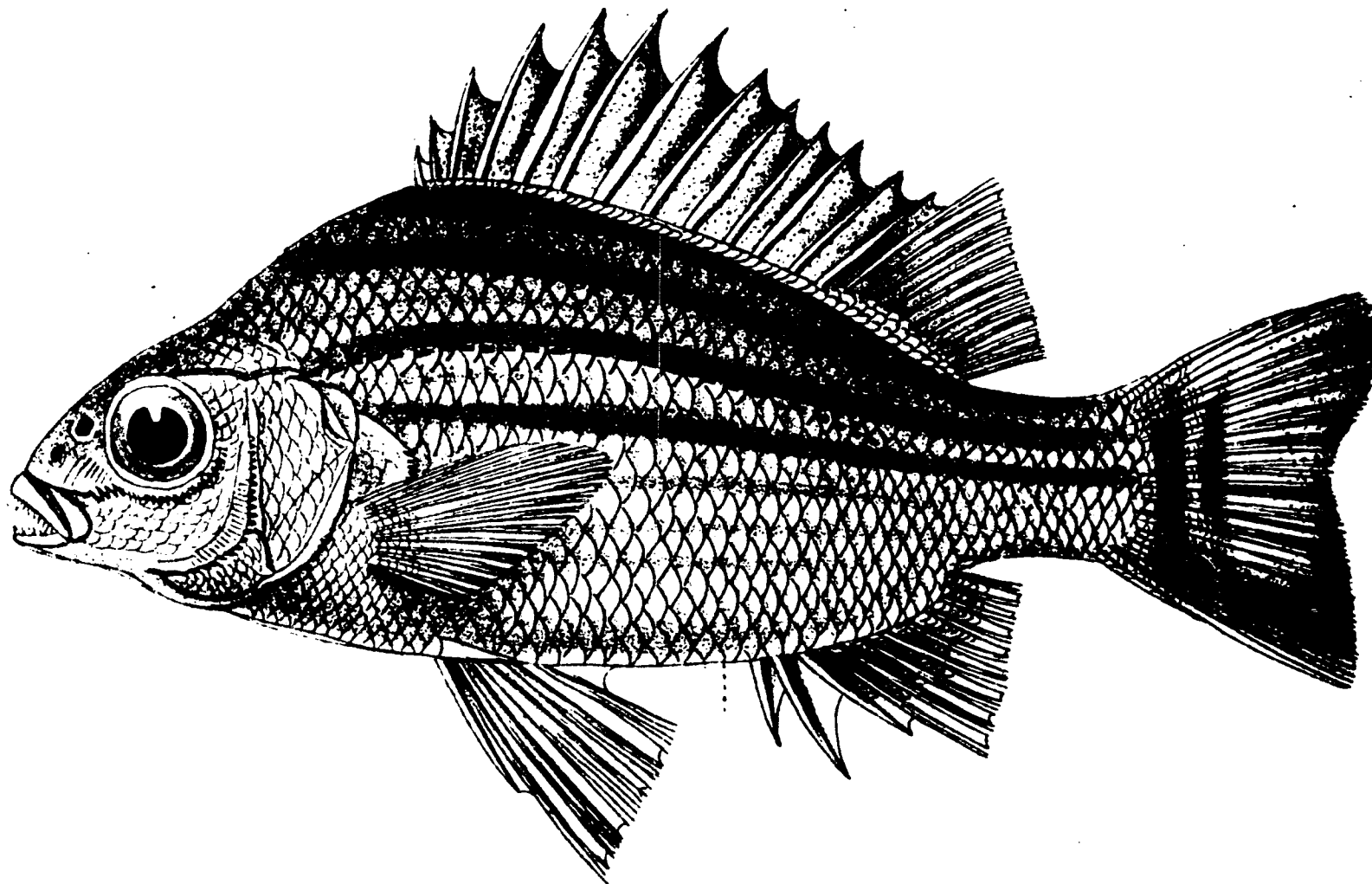


Figure 42



435

Figure 43

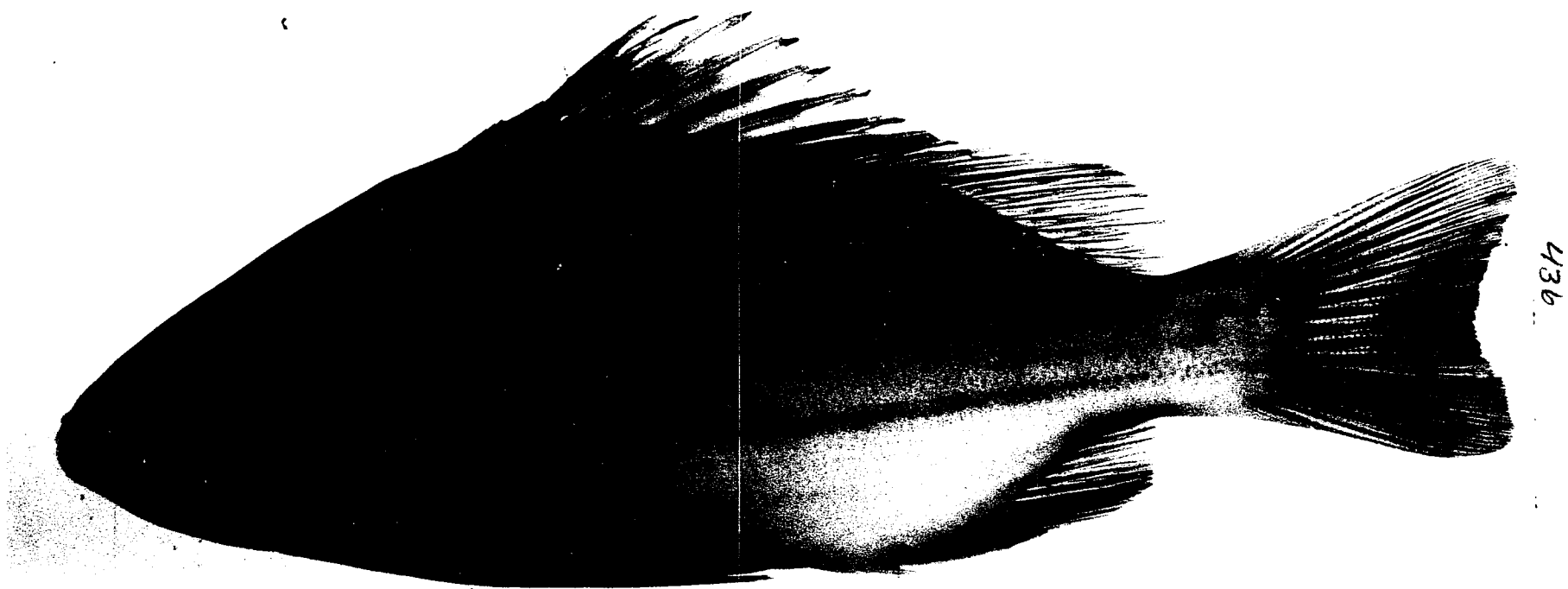


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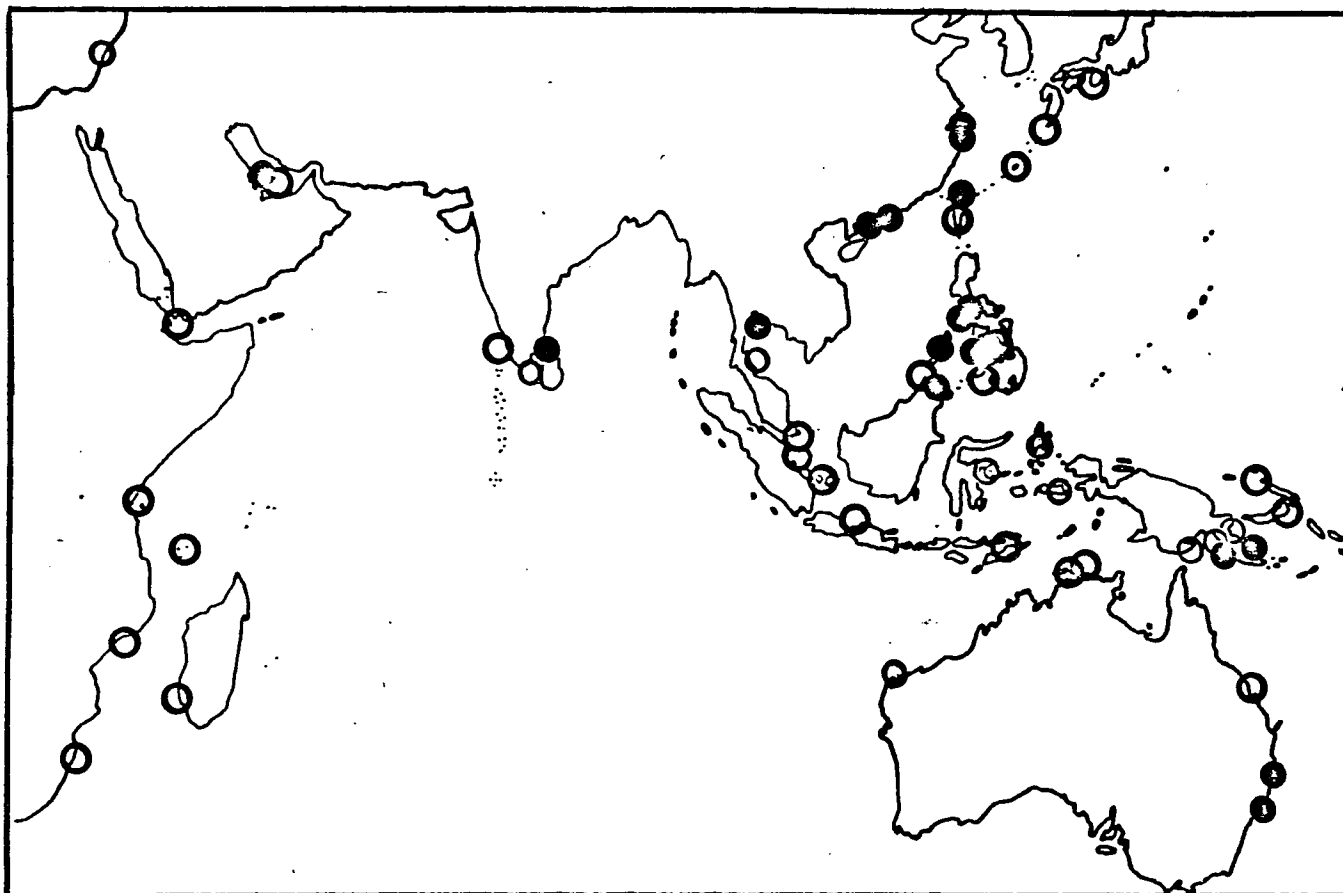
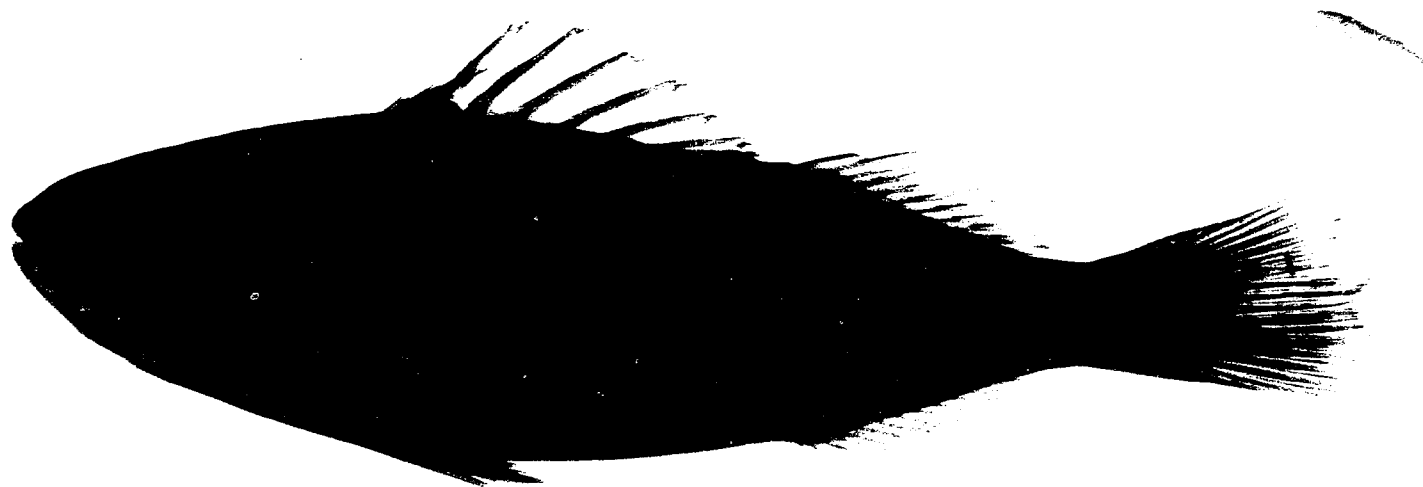
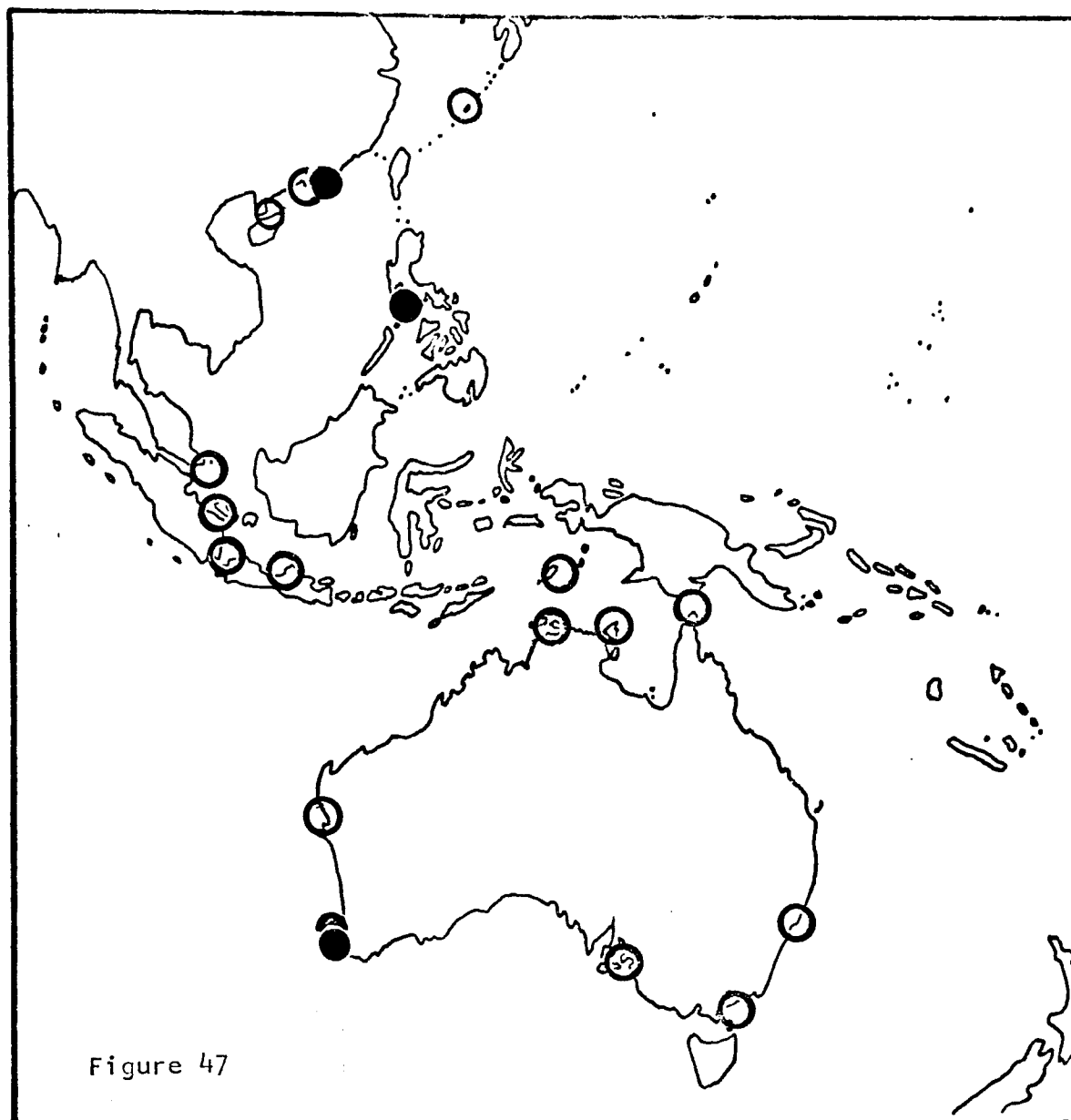


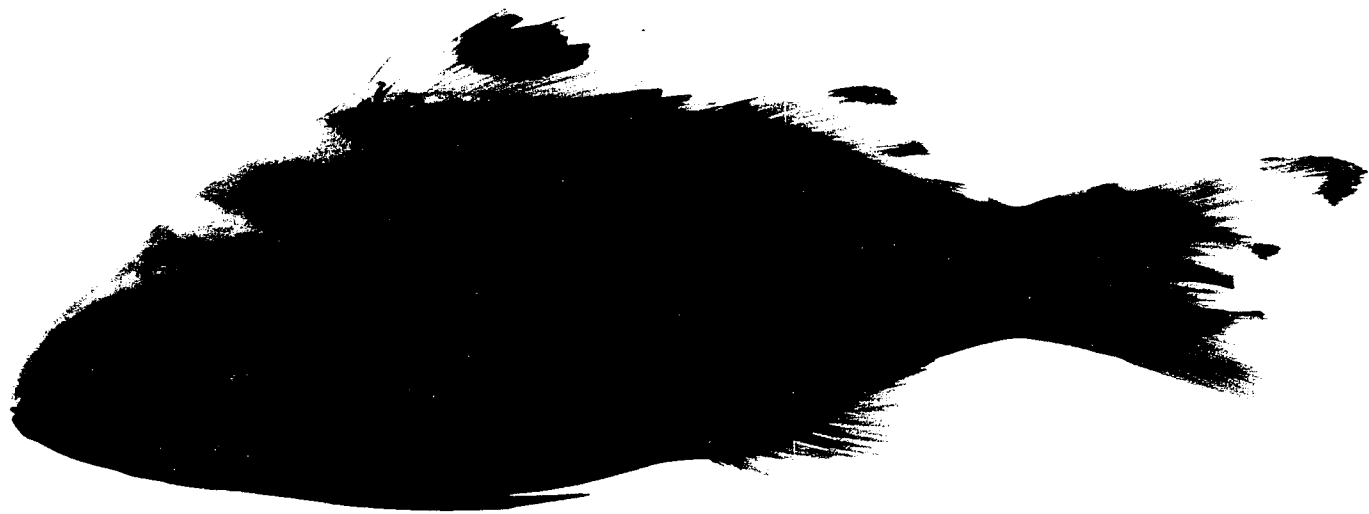
Figure 45



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Figure 46





440

Figure 48

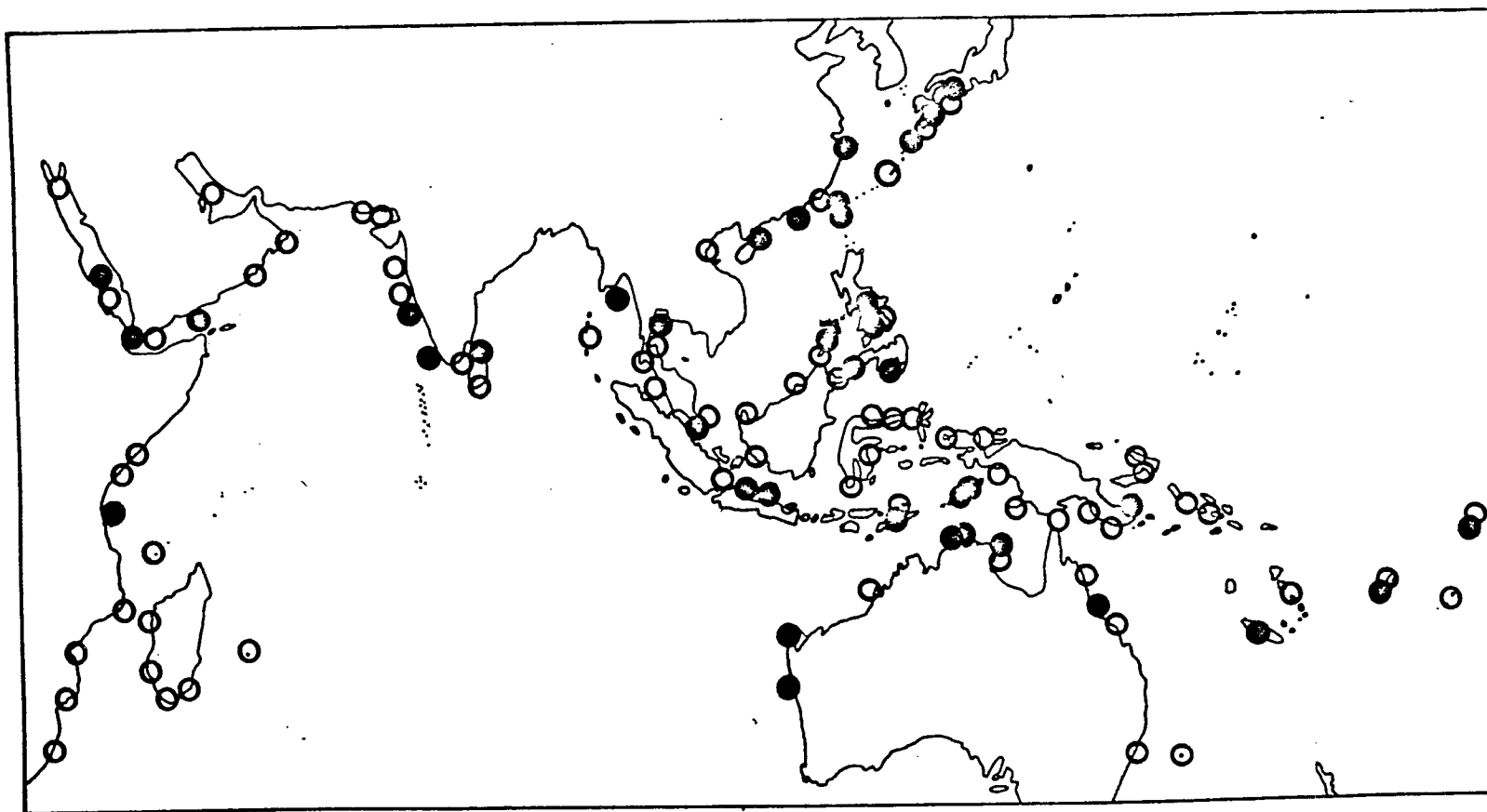
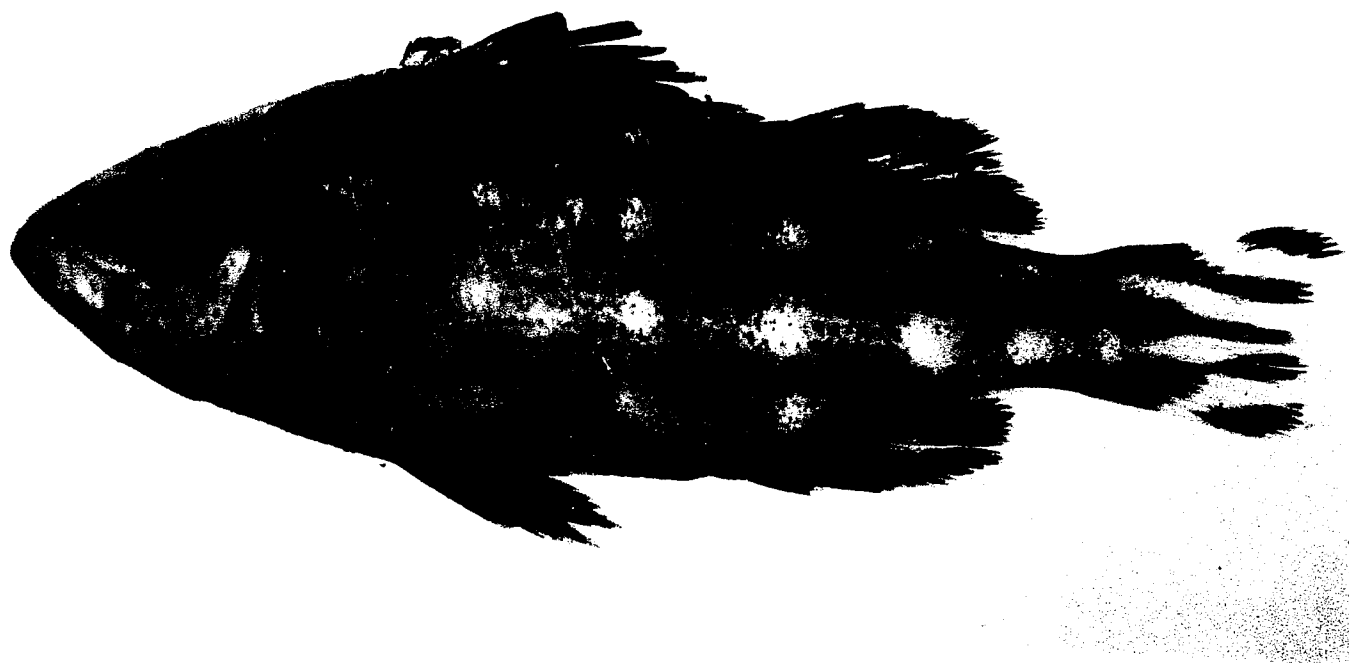


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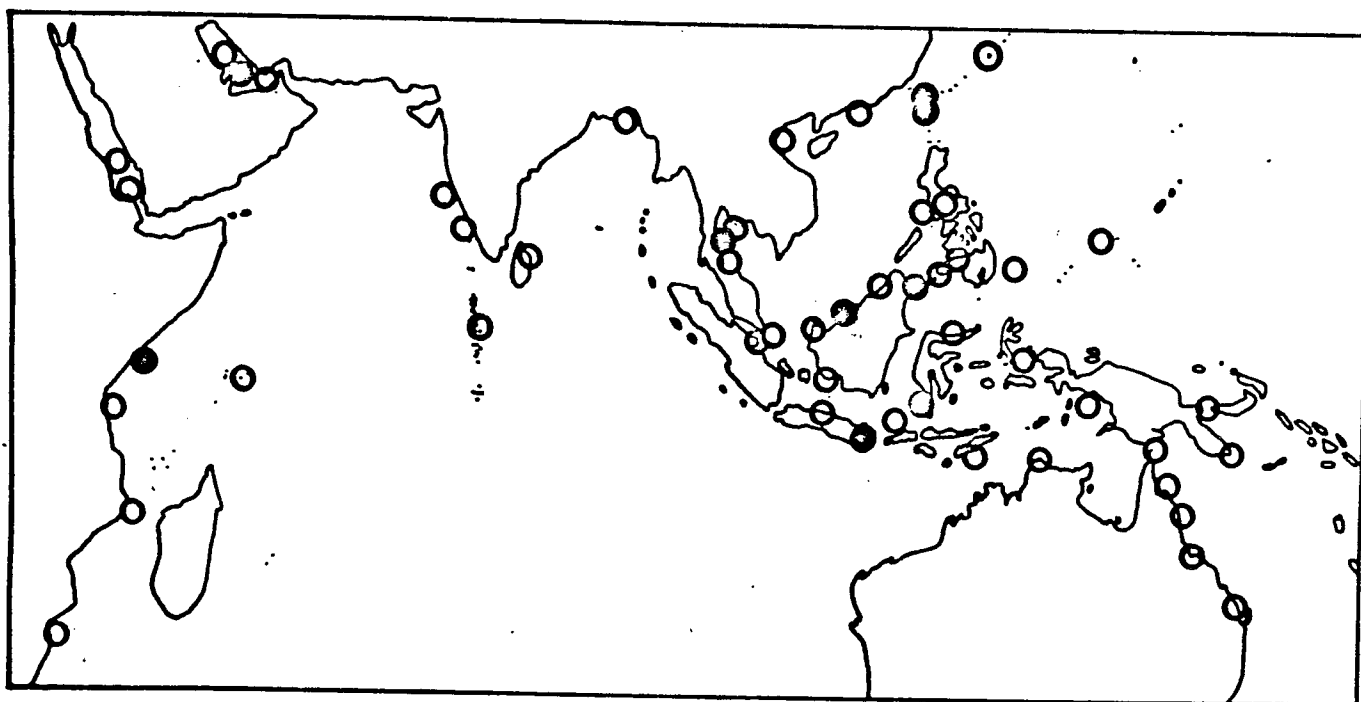
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Figure 50



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Figure 51



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Figure 52

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Figure 53

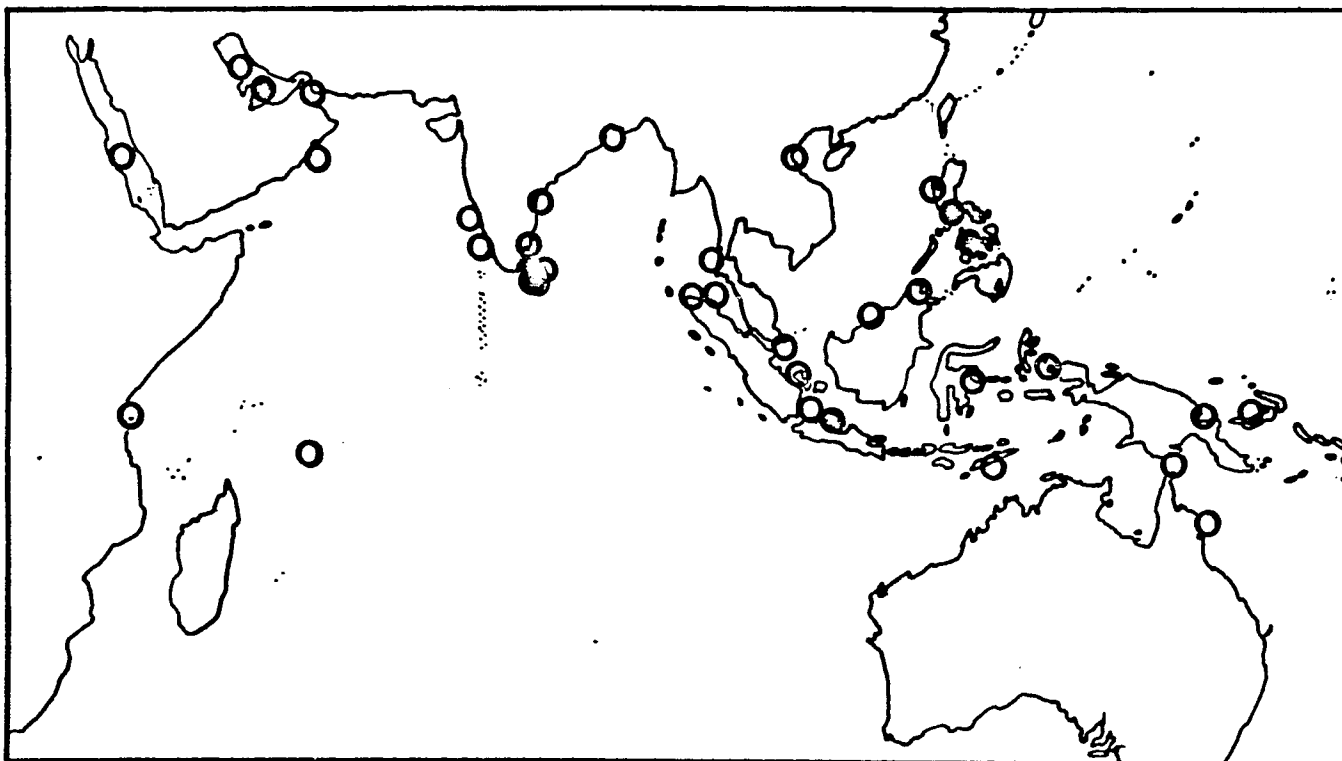
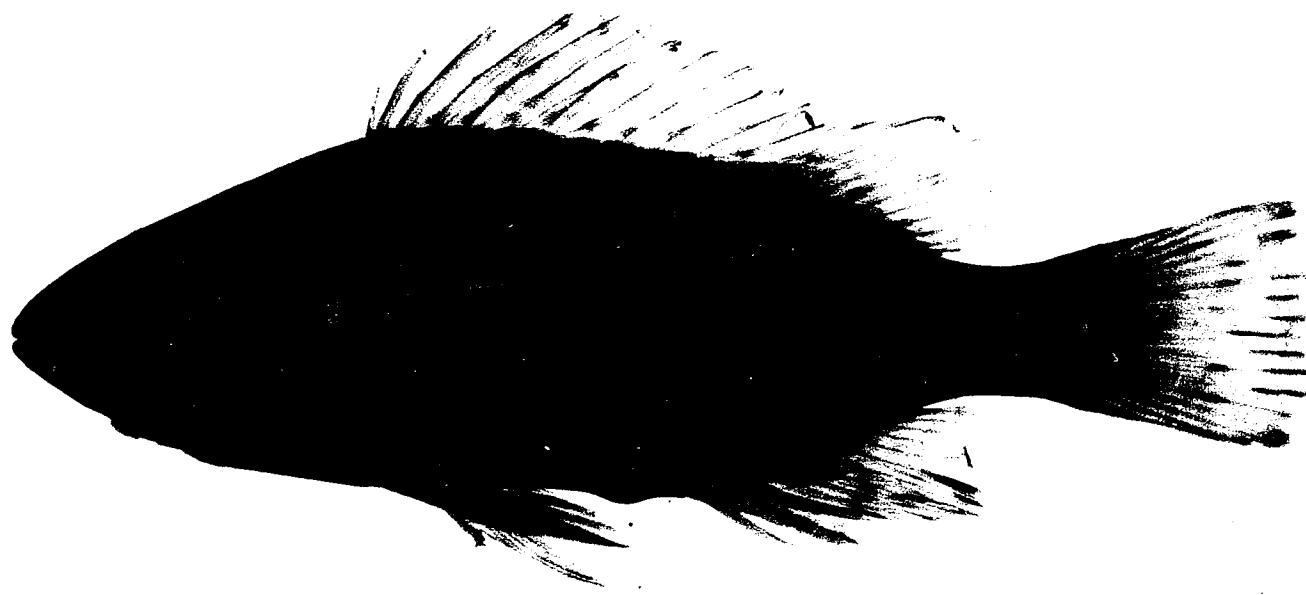
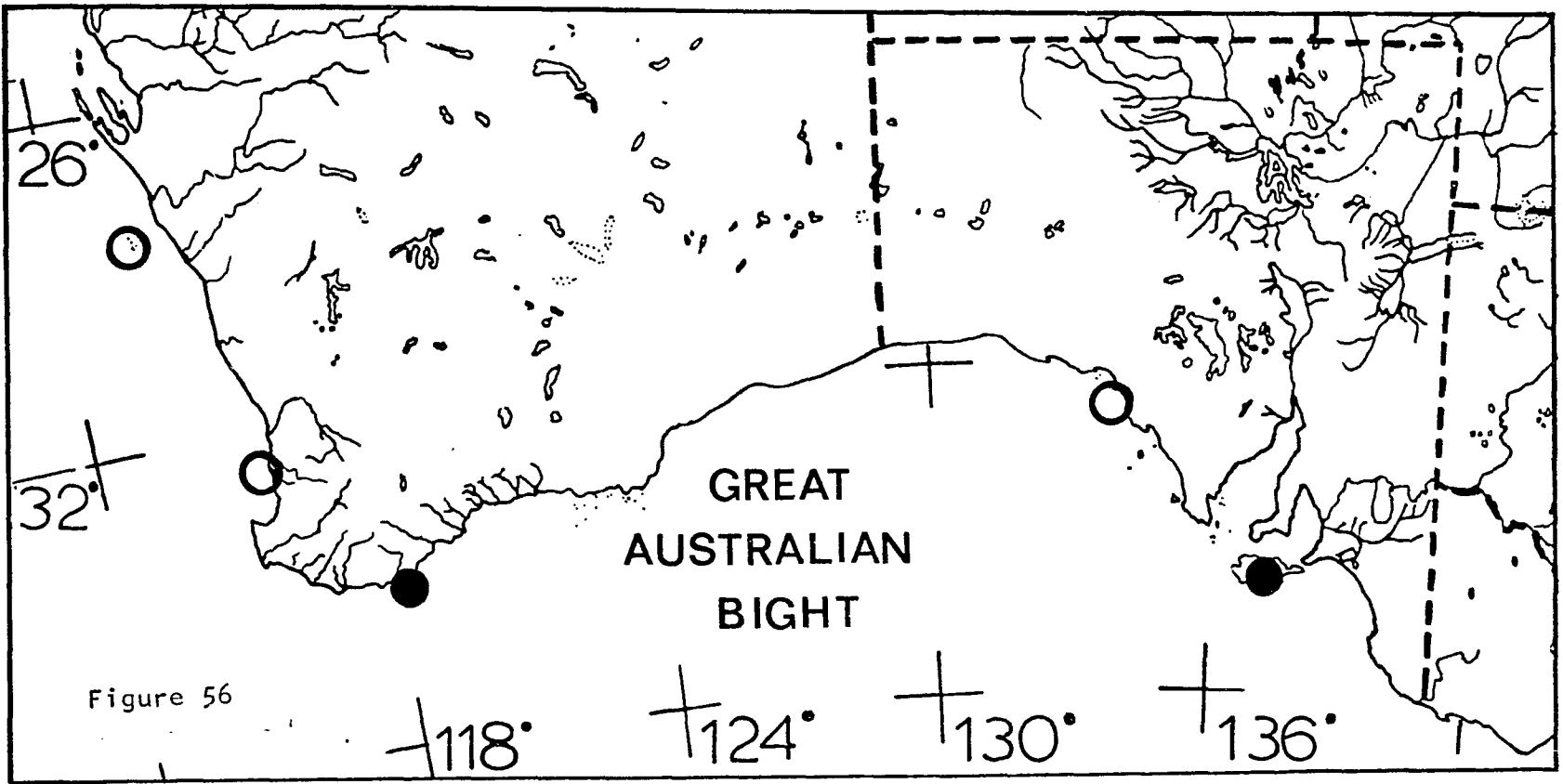


Figure 54



447

Figure 55



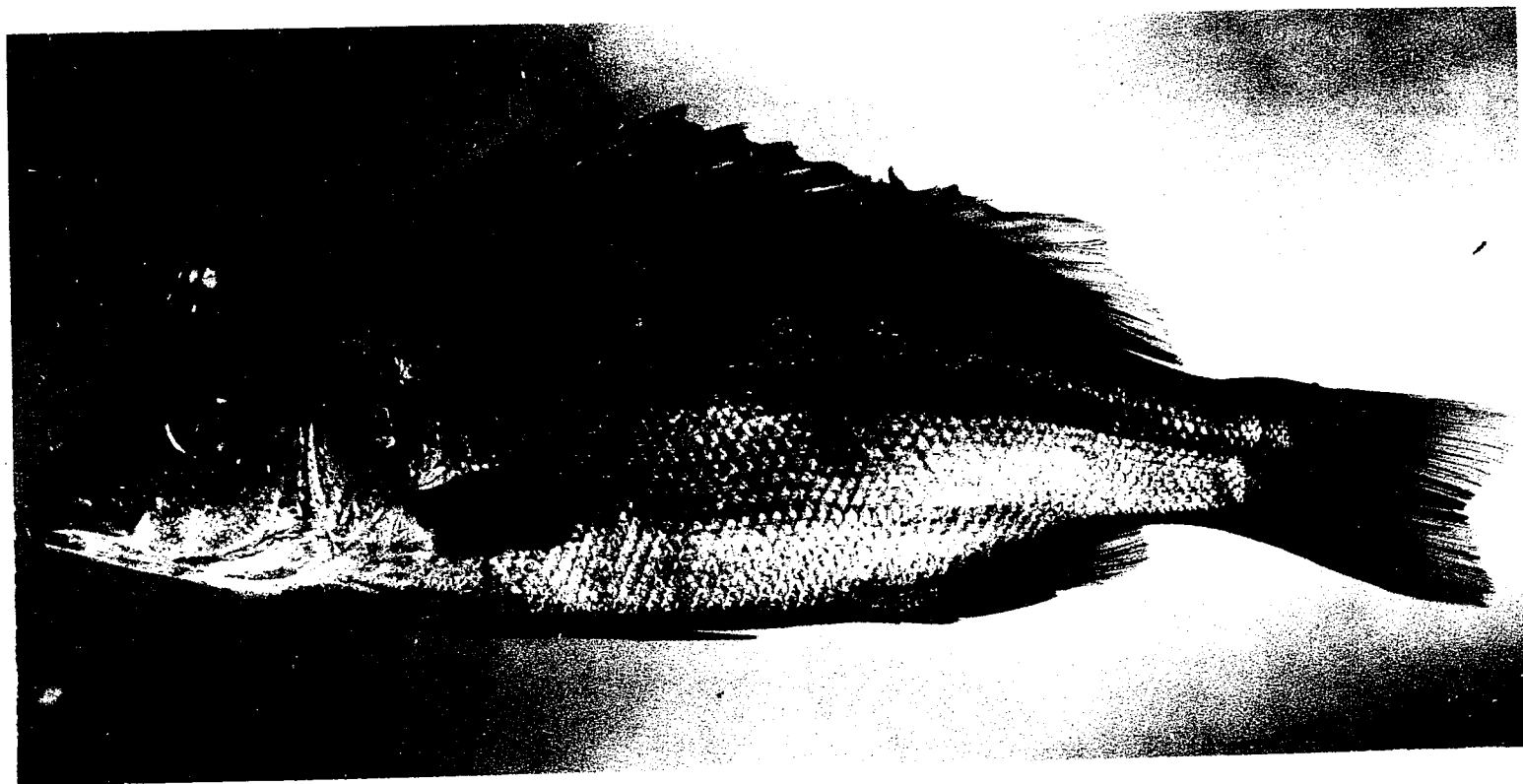


Figure 57

6777

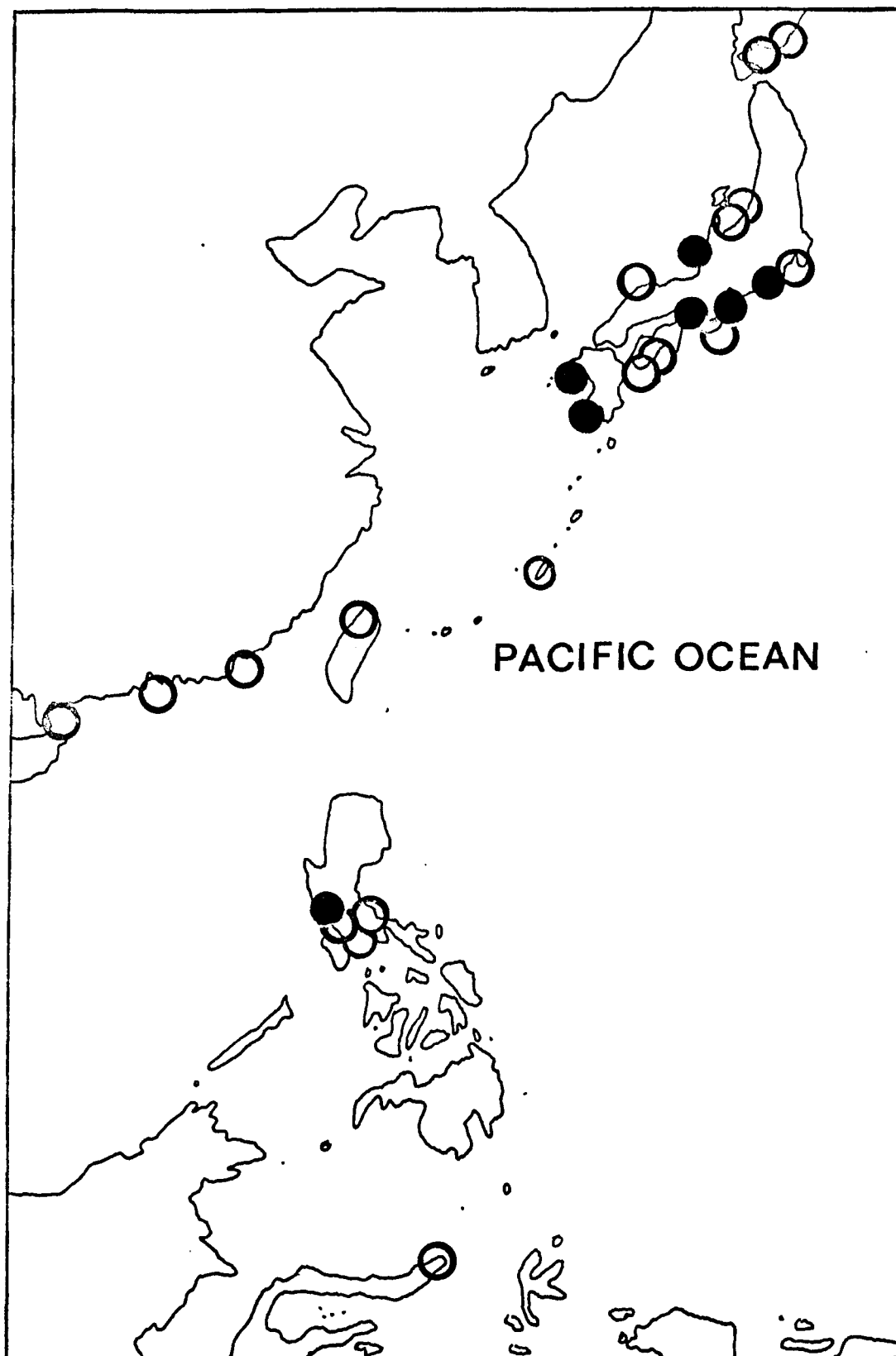


Figure 58

451

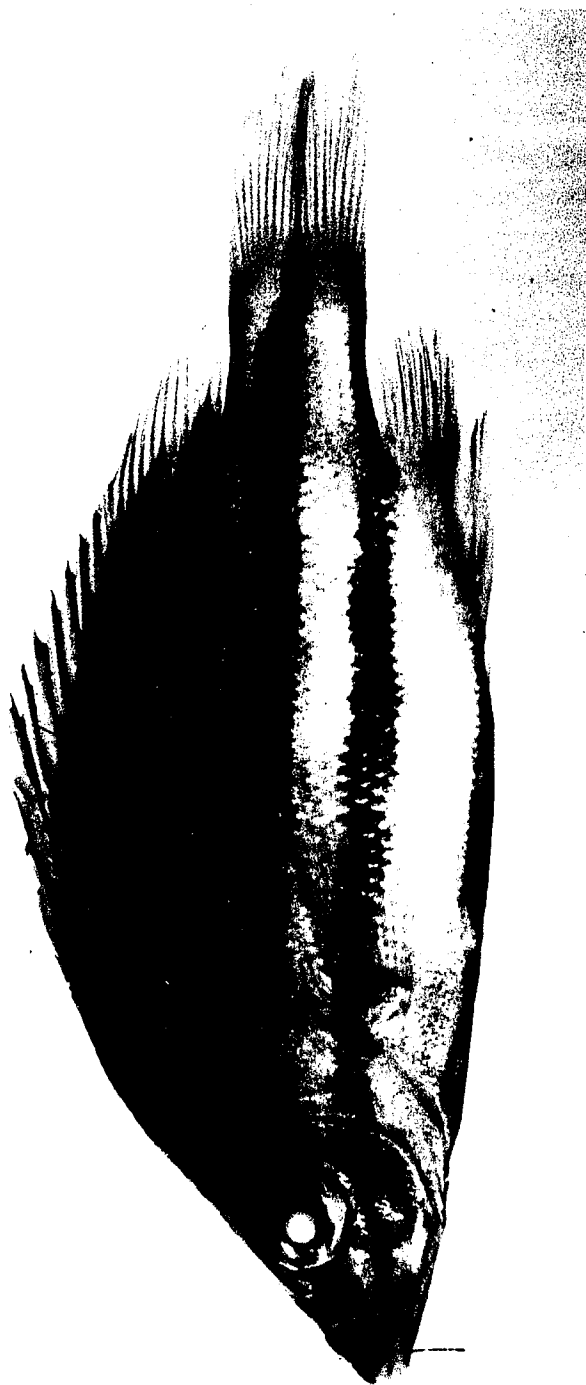
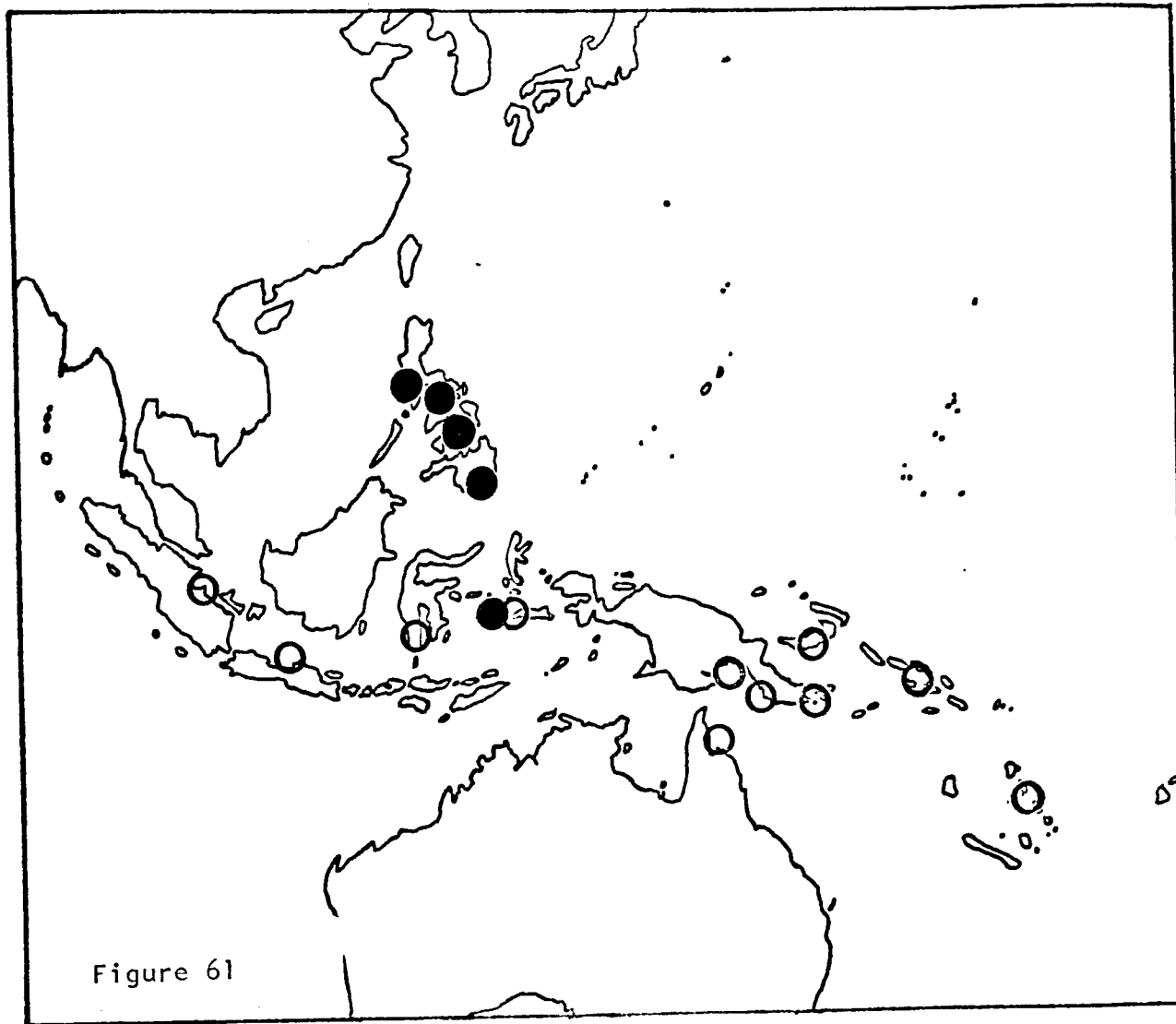


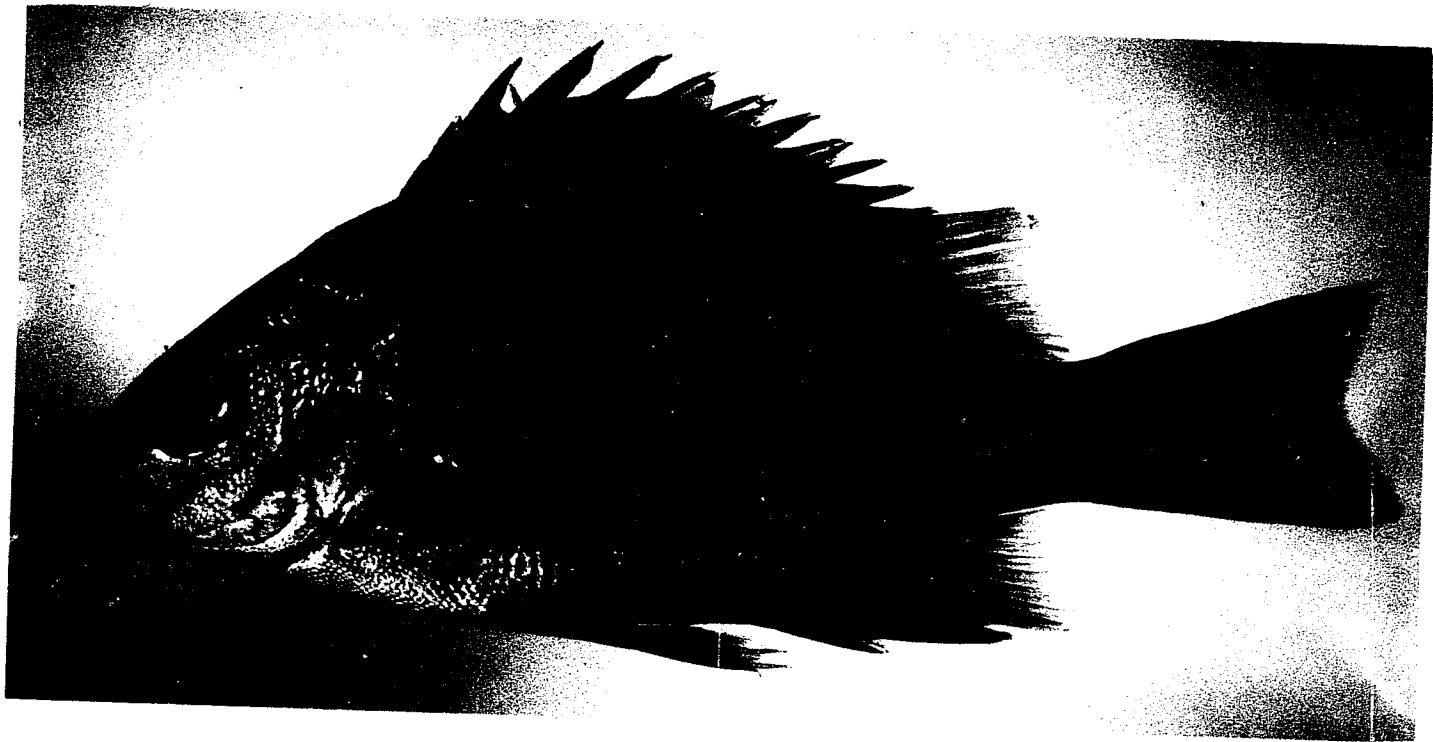
Figure 59

452



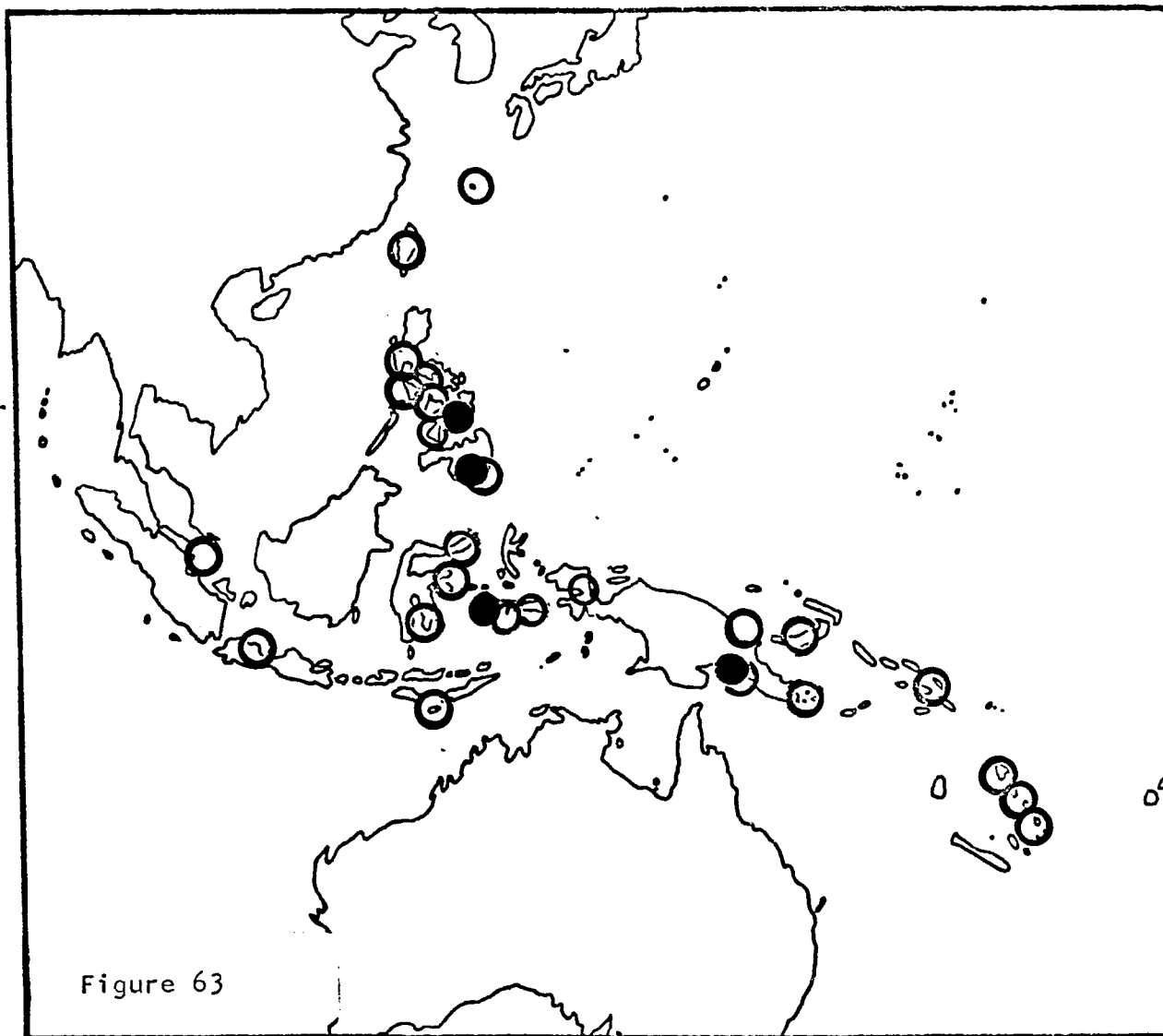
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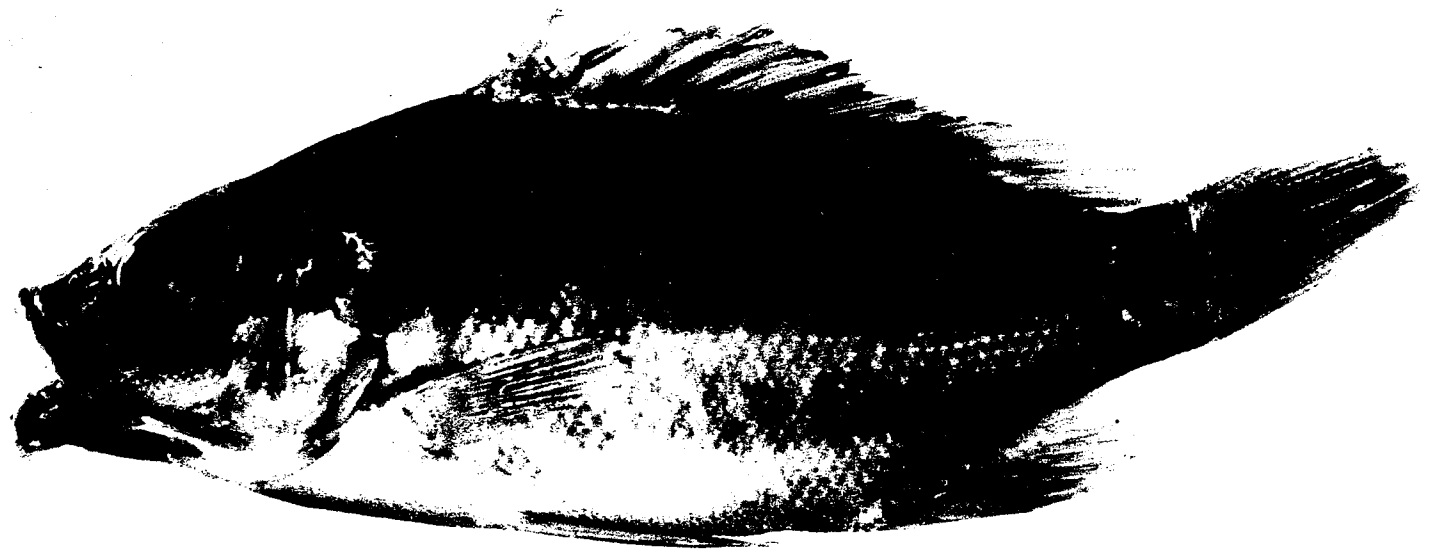




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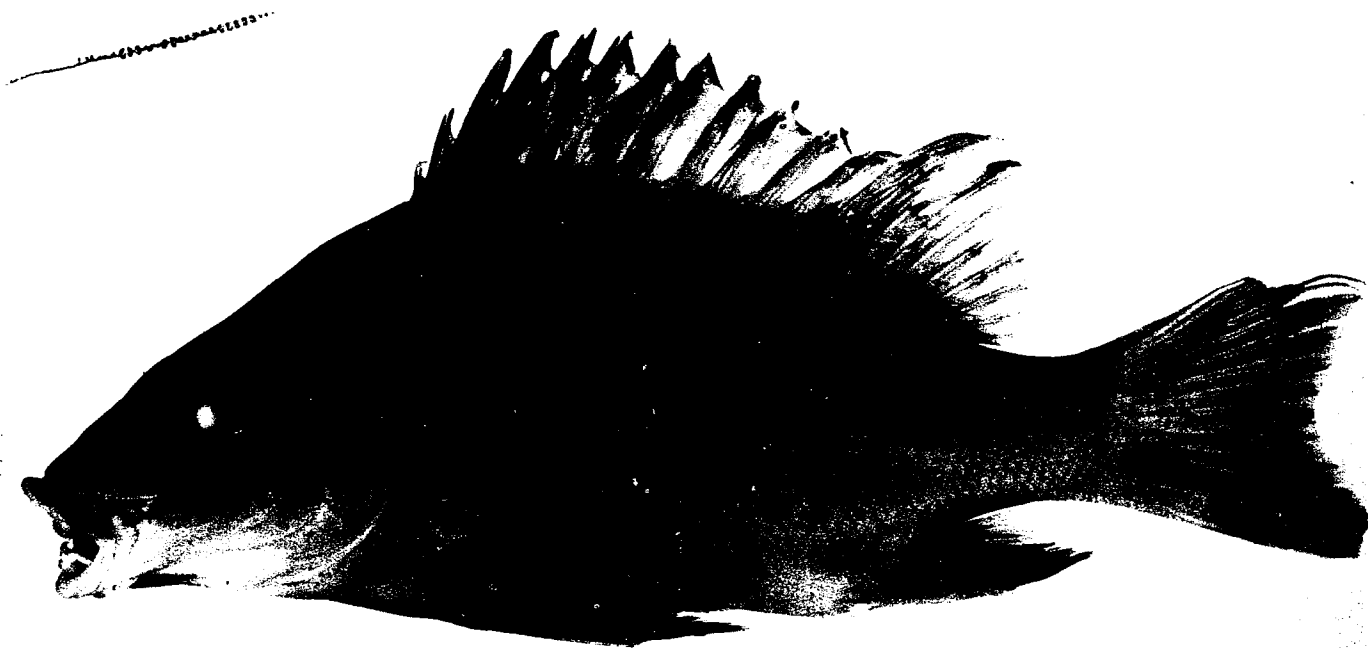
Figure 62





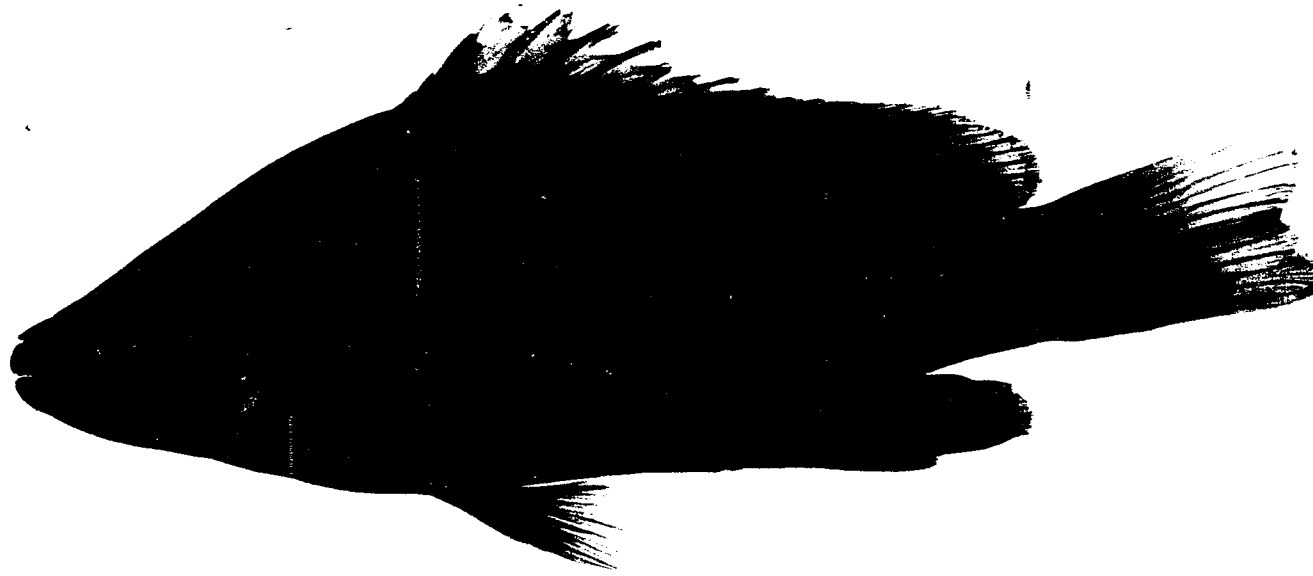
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Figure 64



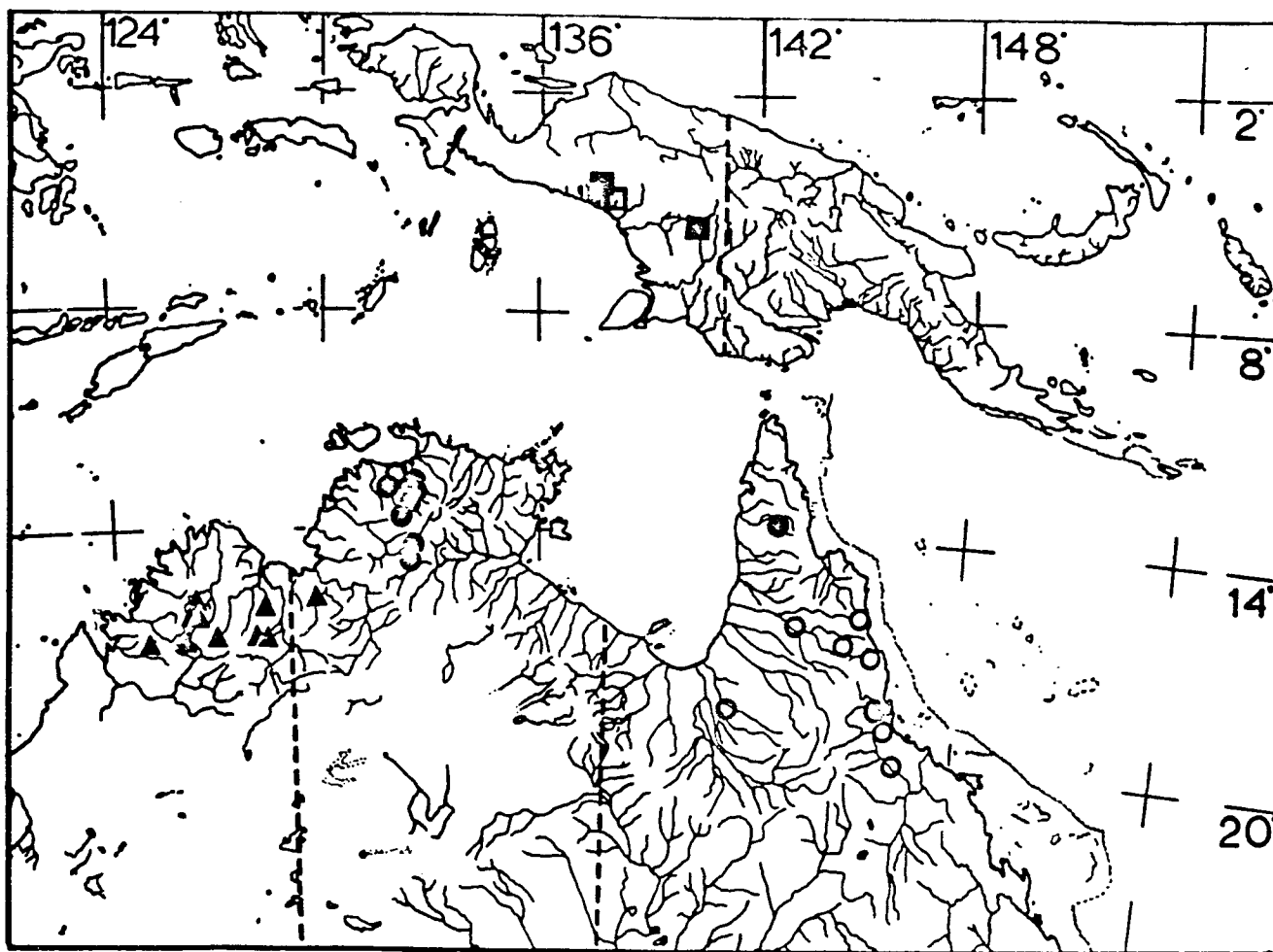
457

Figure 65



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Figure 66



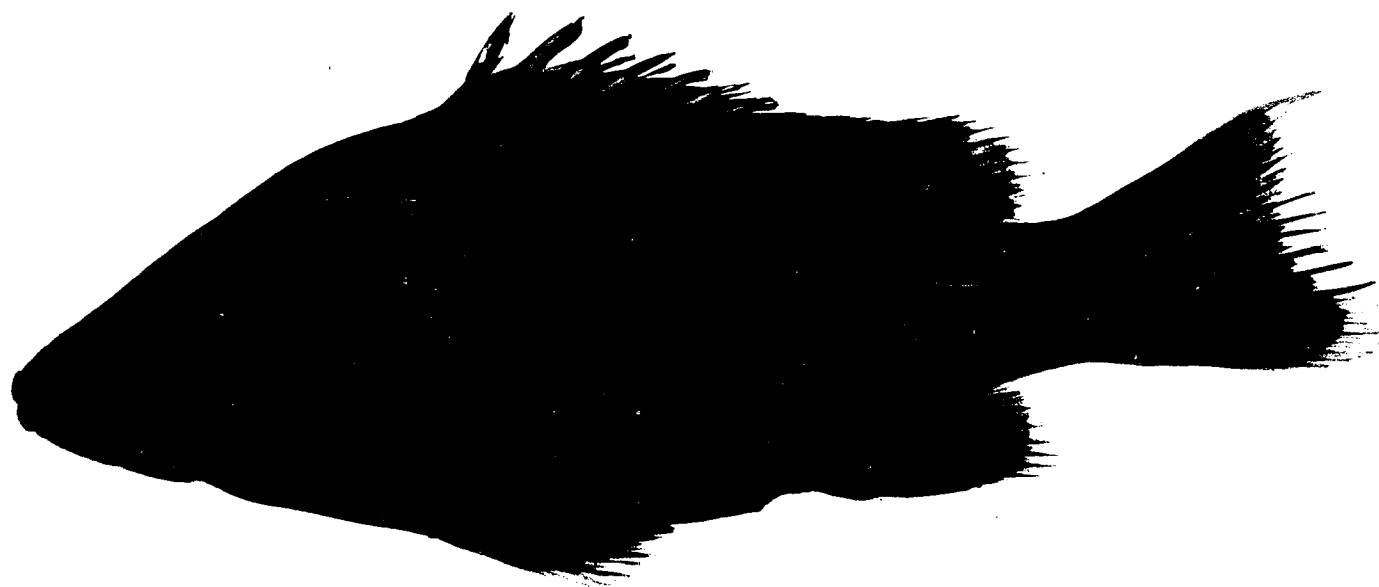
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Figure 67

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Figure 60



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Figure 69

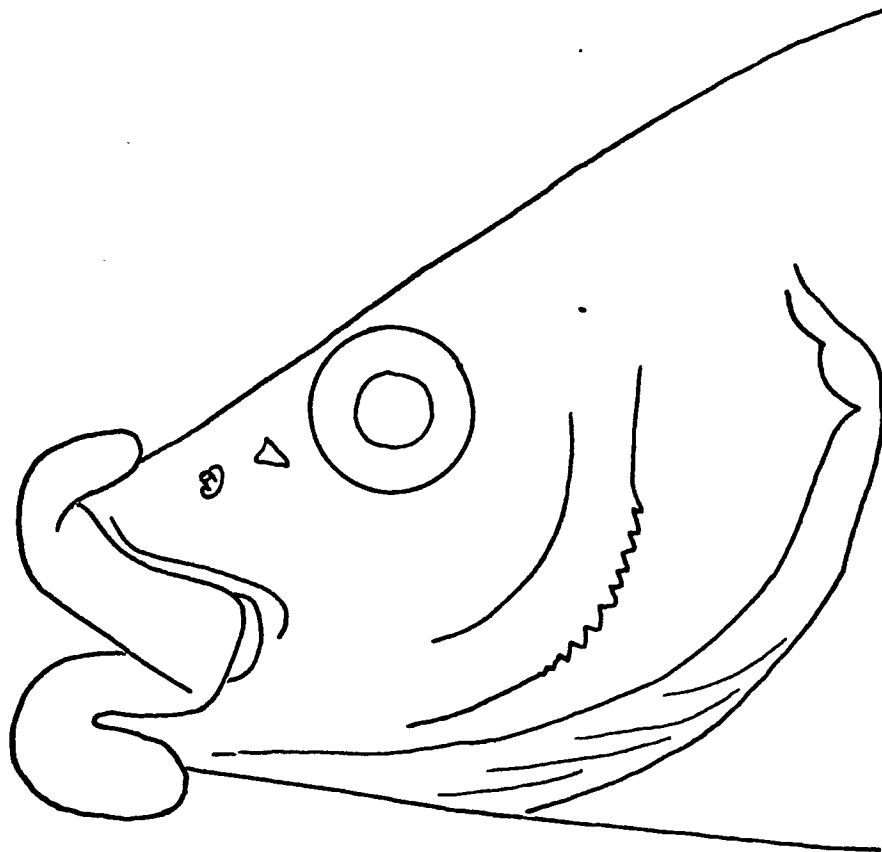
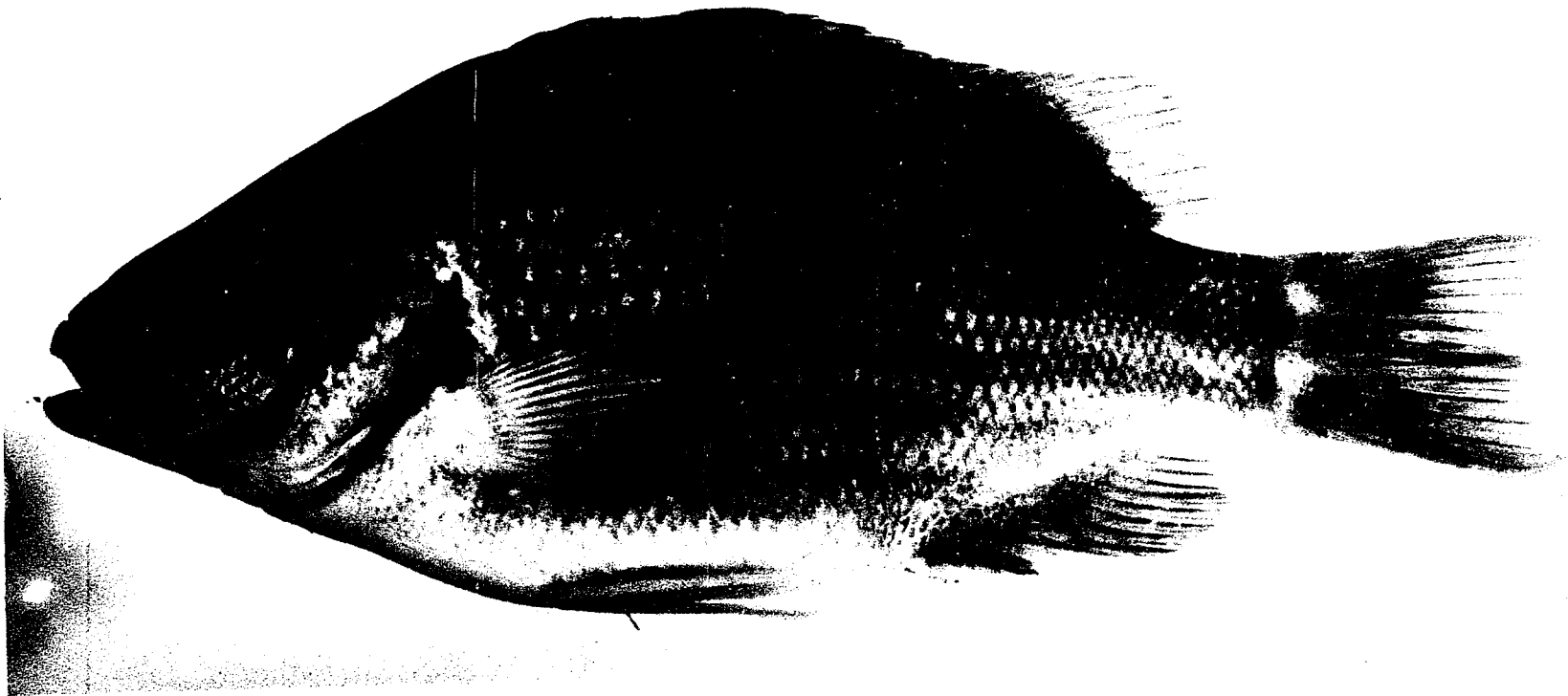


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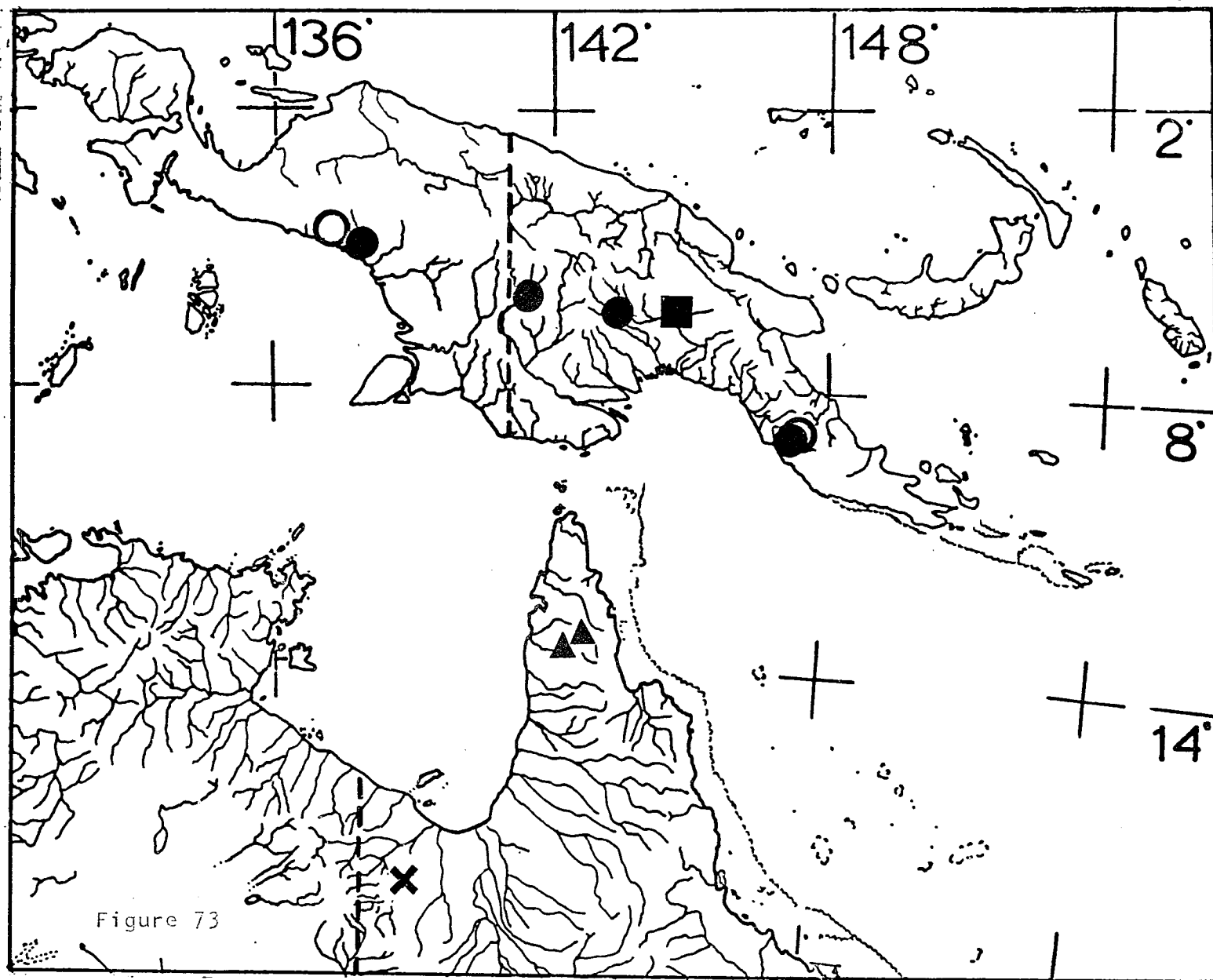
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Figure 71



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Figure 72



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Figure 74

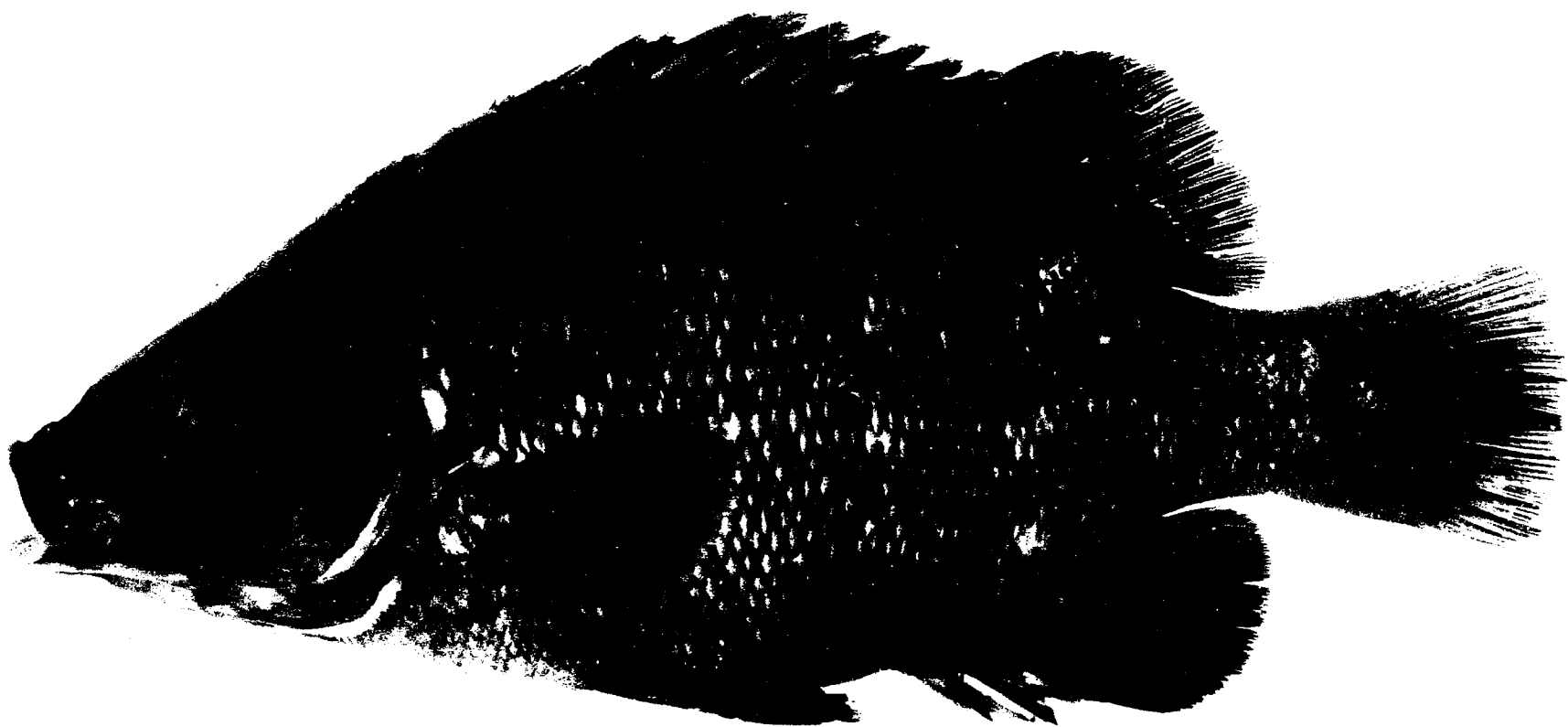
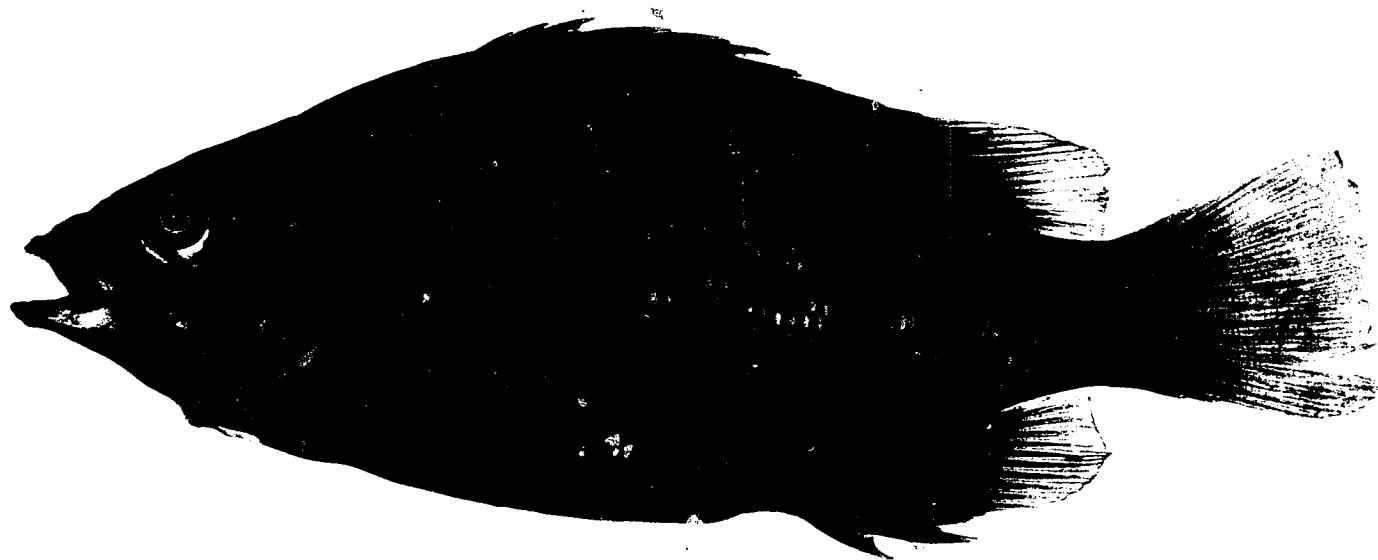


Figure 75



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Figure 76

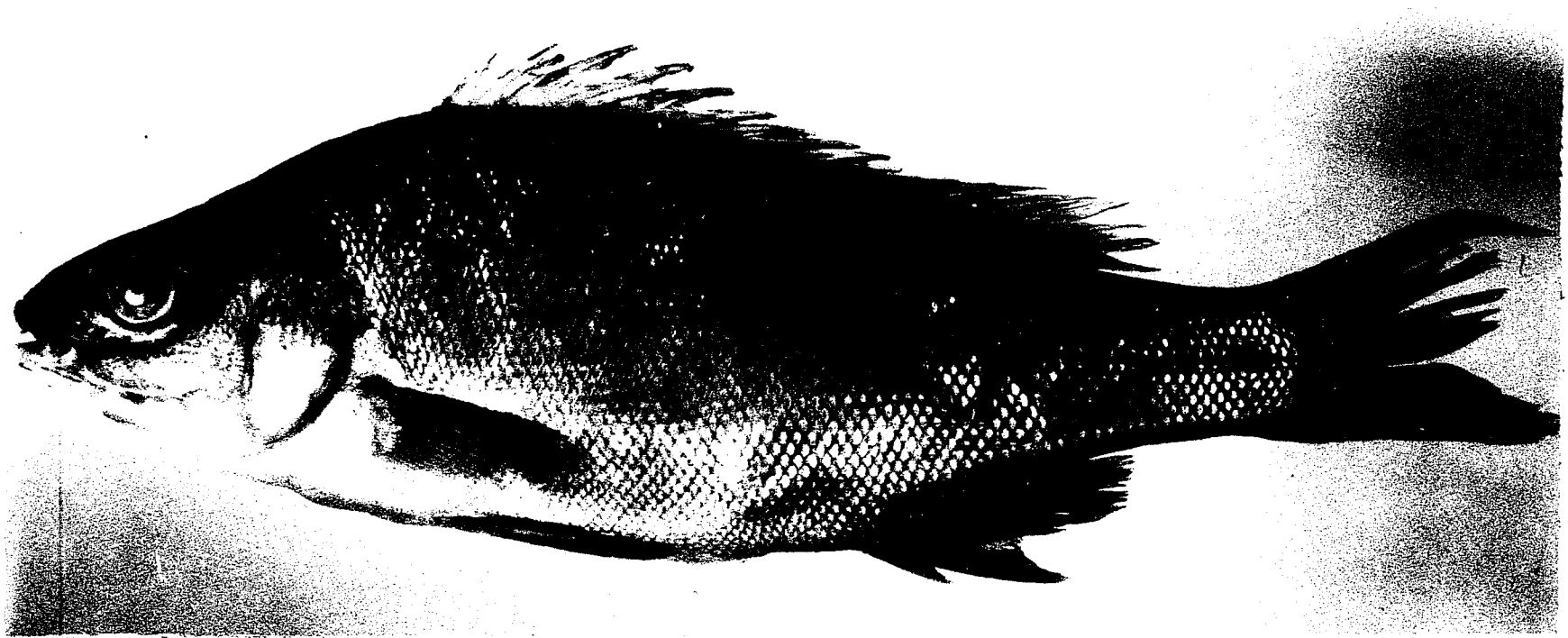
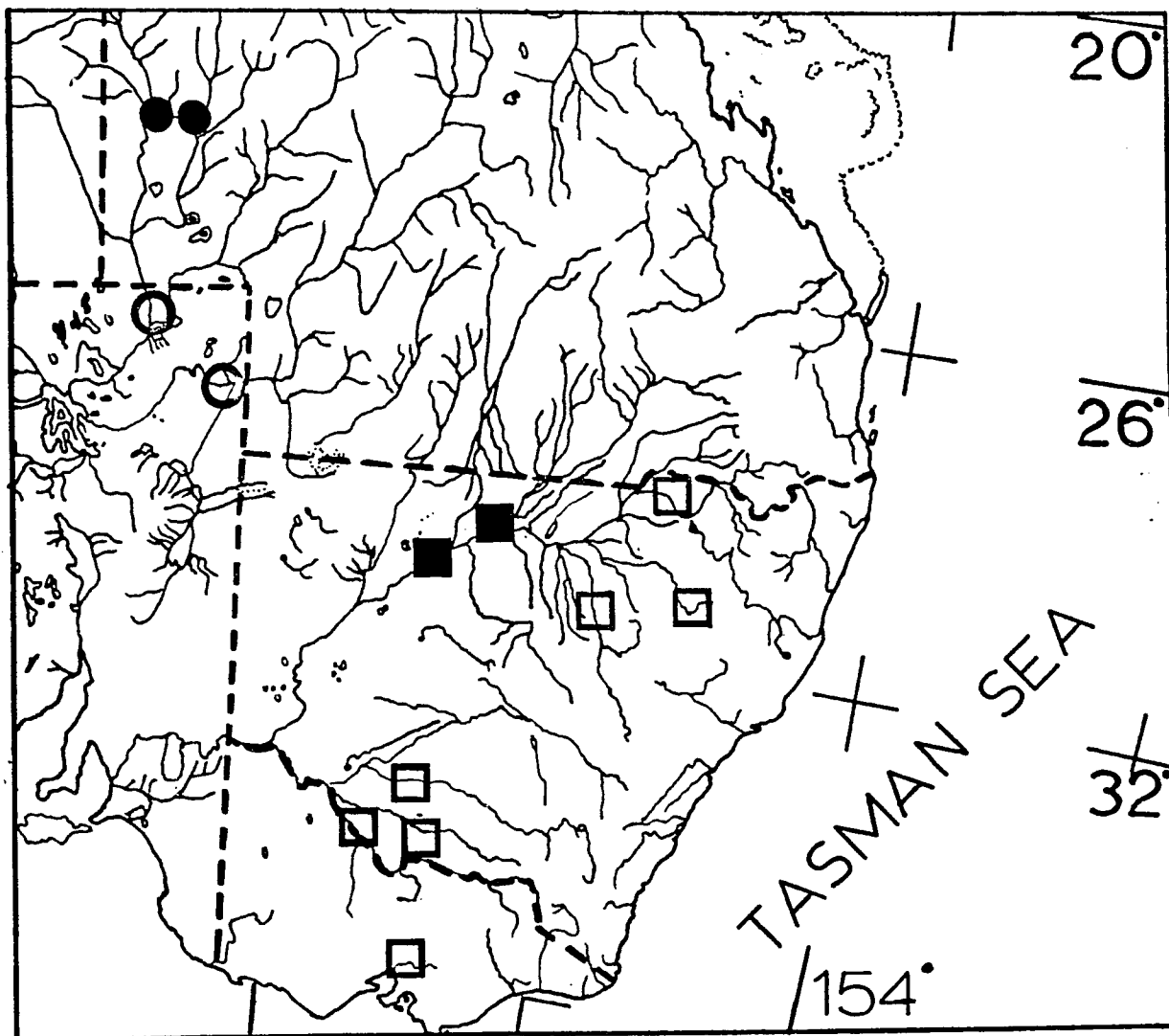
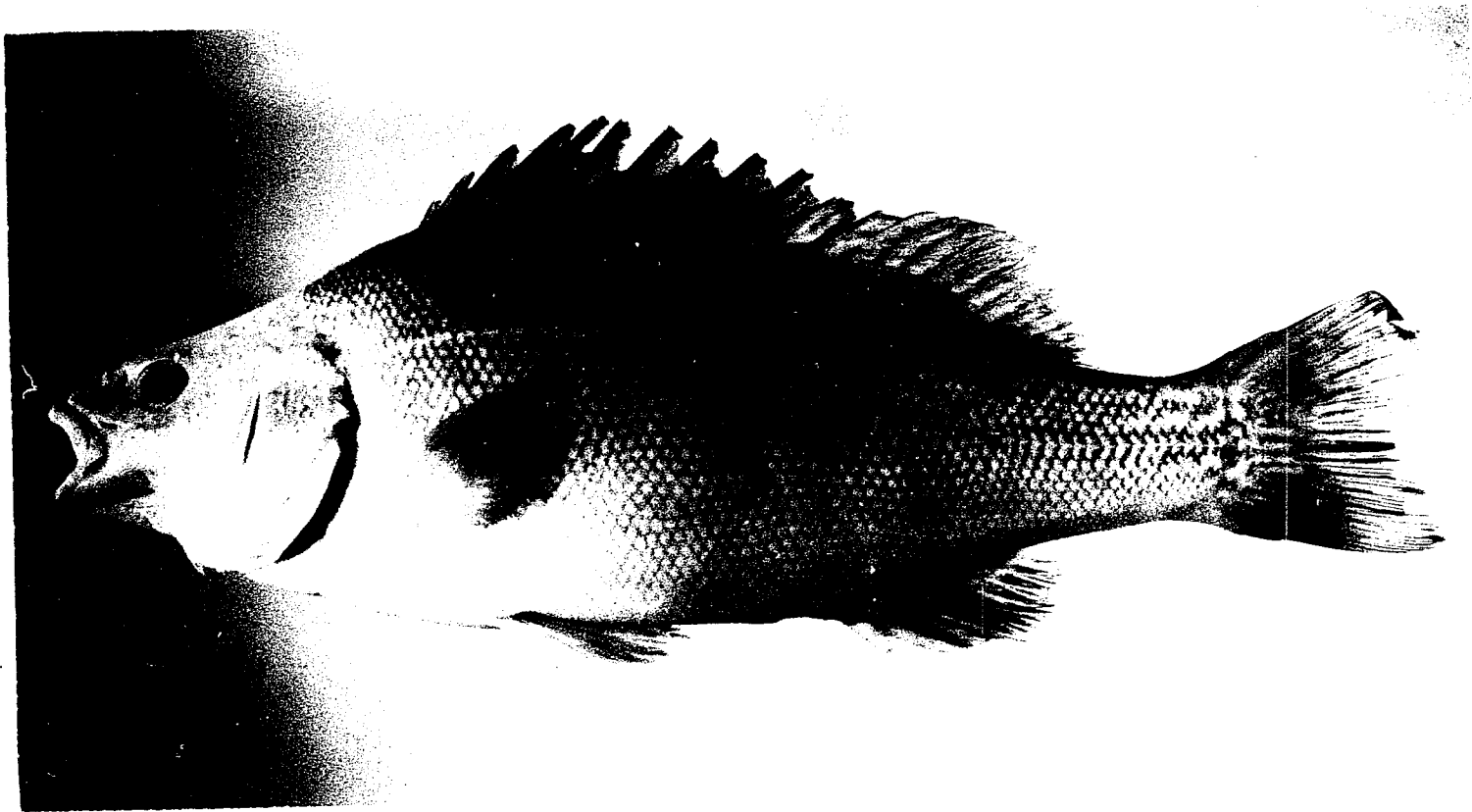


Figure 77



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Figure 78



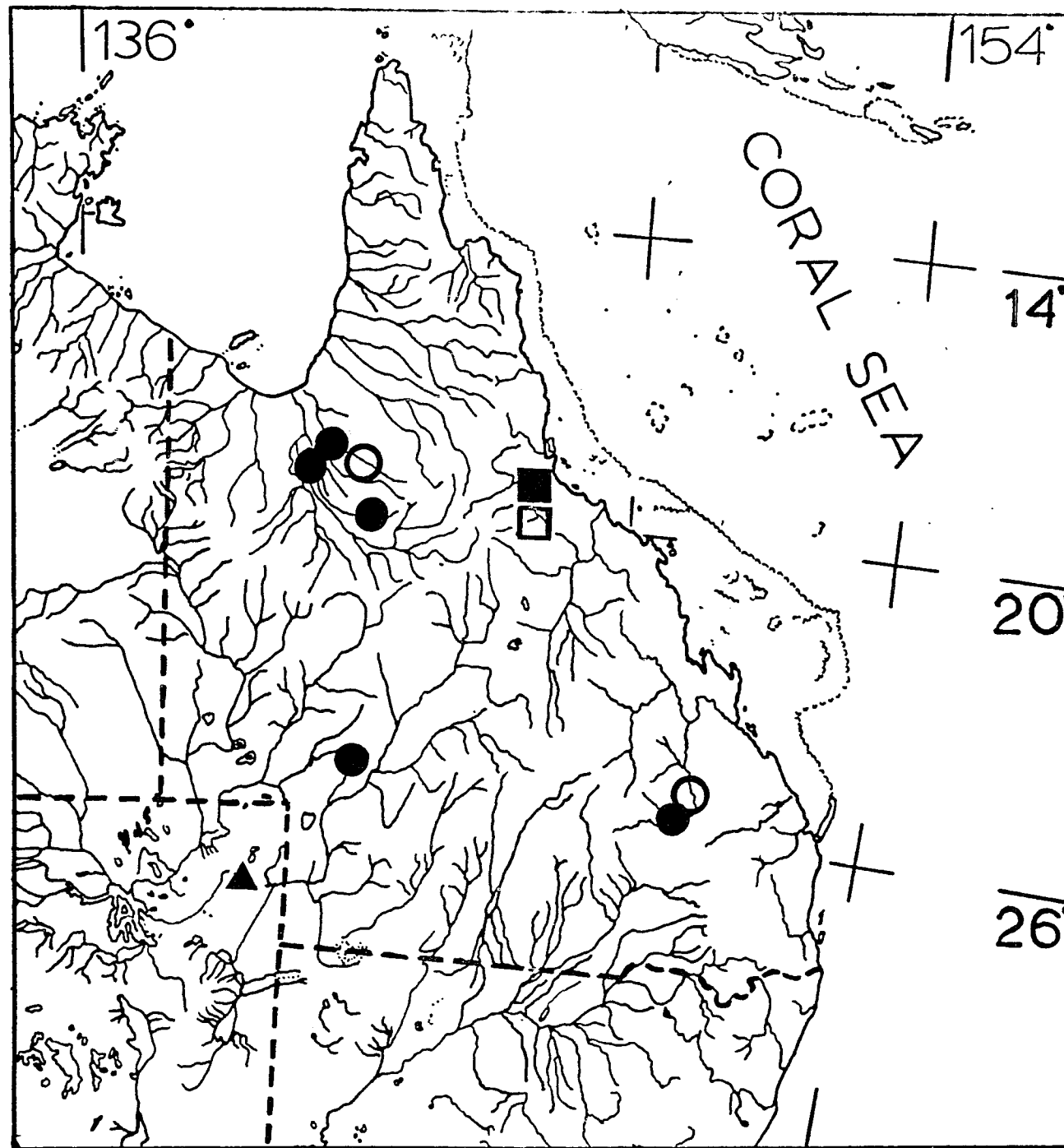
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Figure 79

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Figure 80



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Figure 81

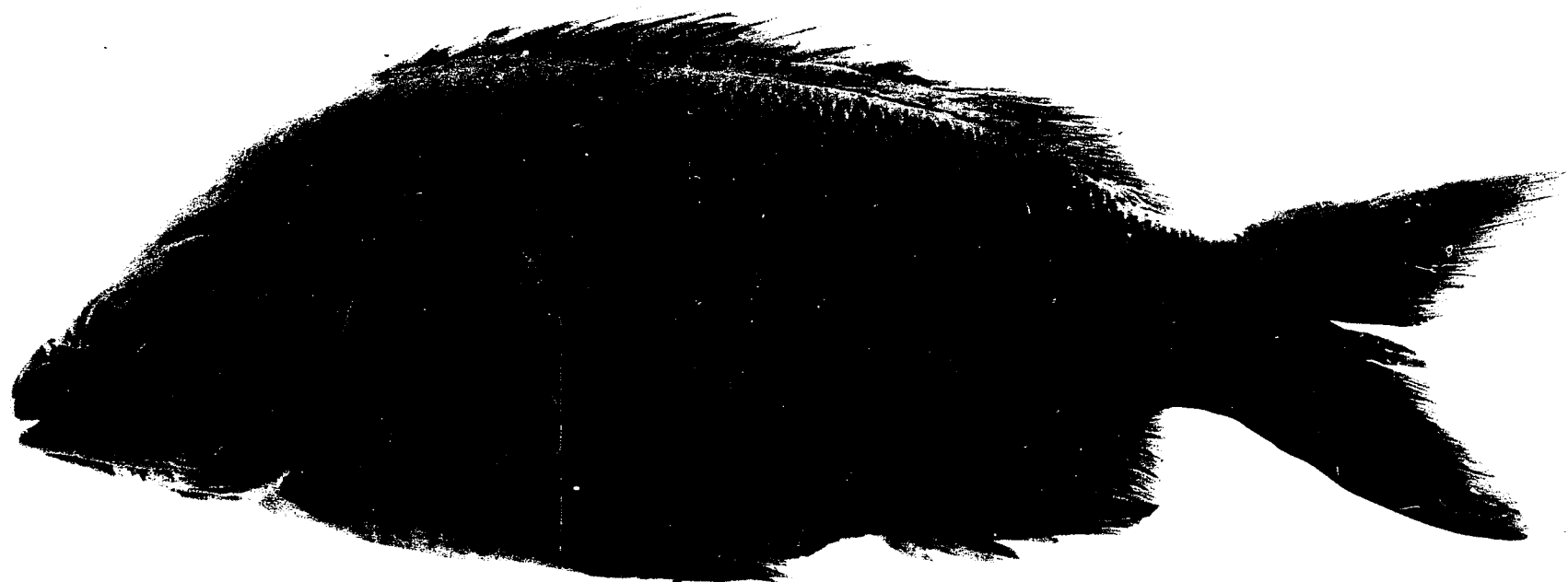
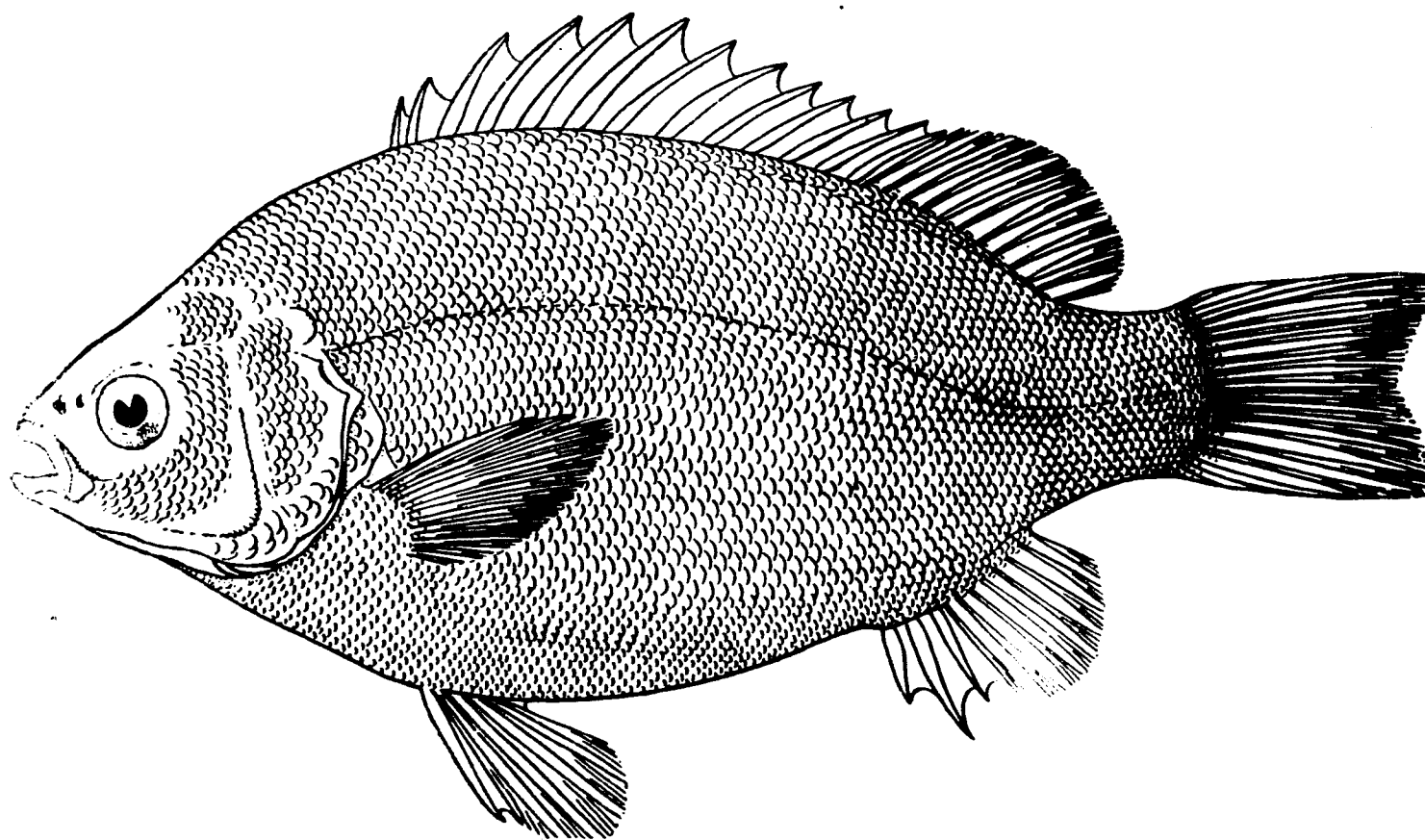
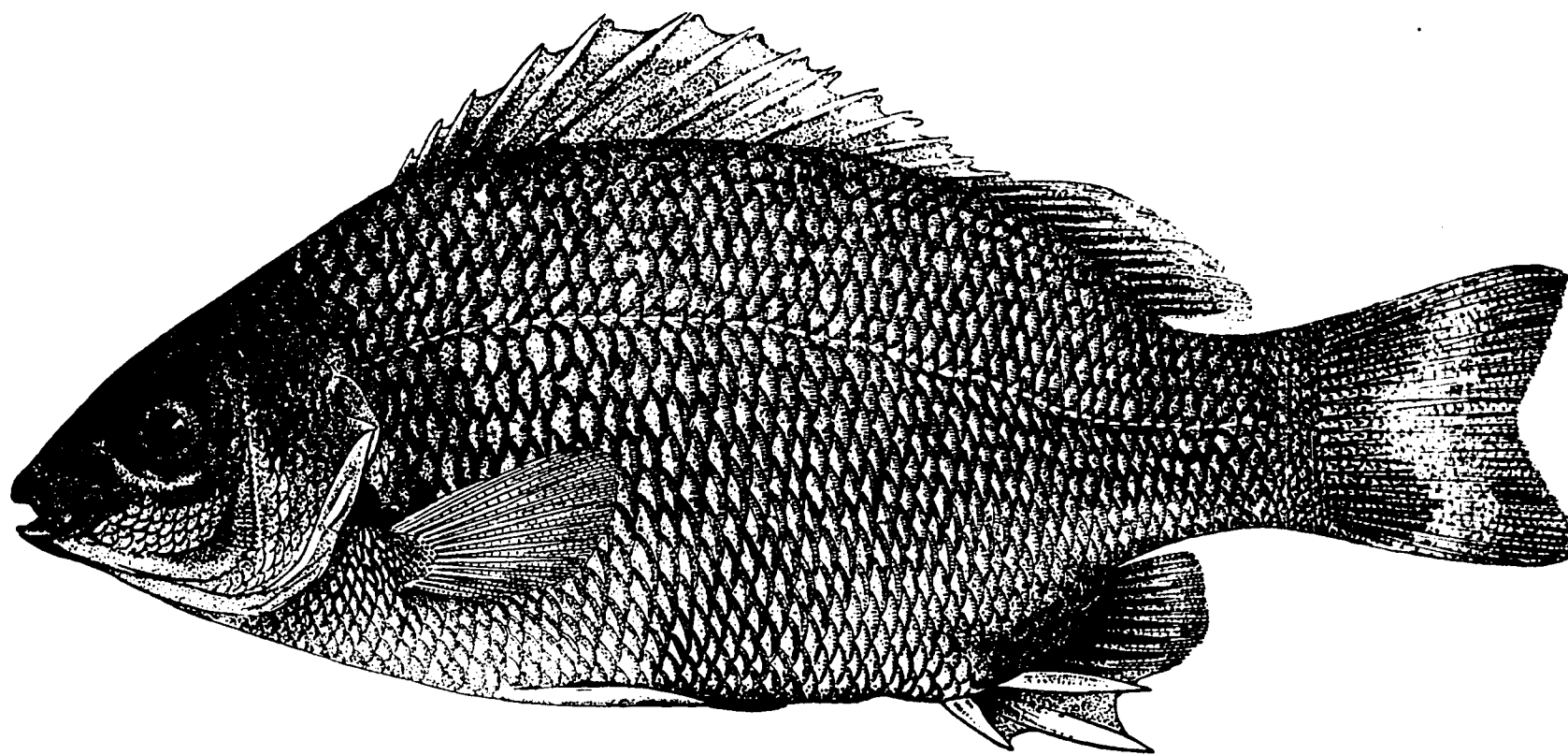


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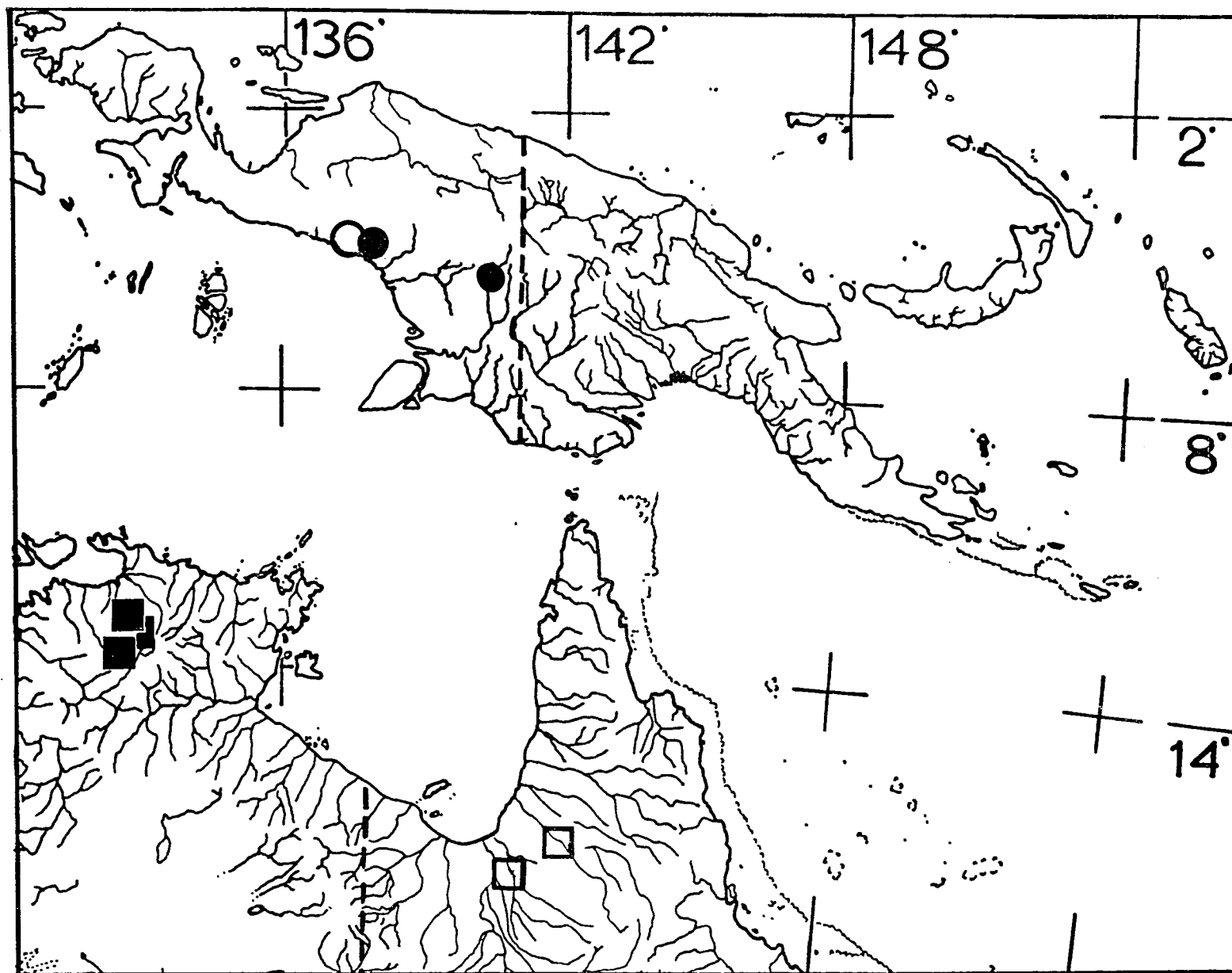
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Figure 83



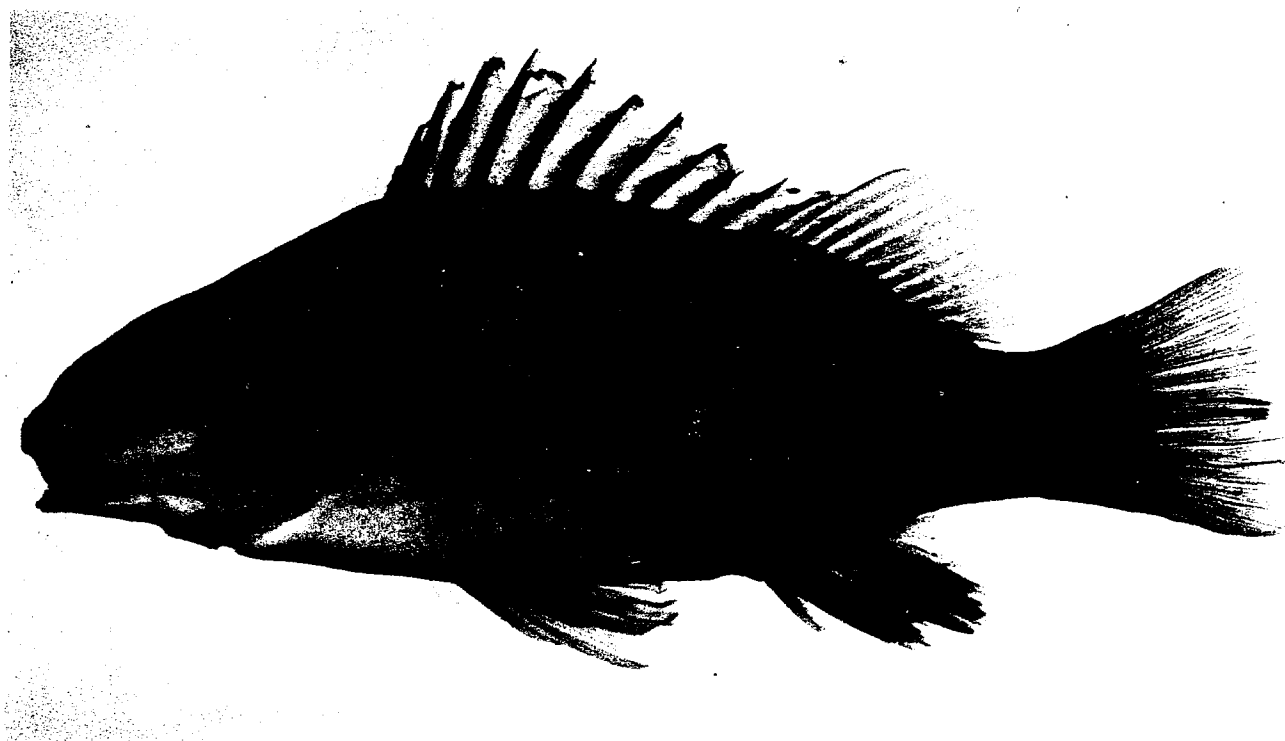
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Figure 84



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Figure 85



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Figure 86



6512

Figure 37

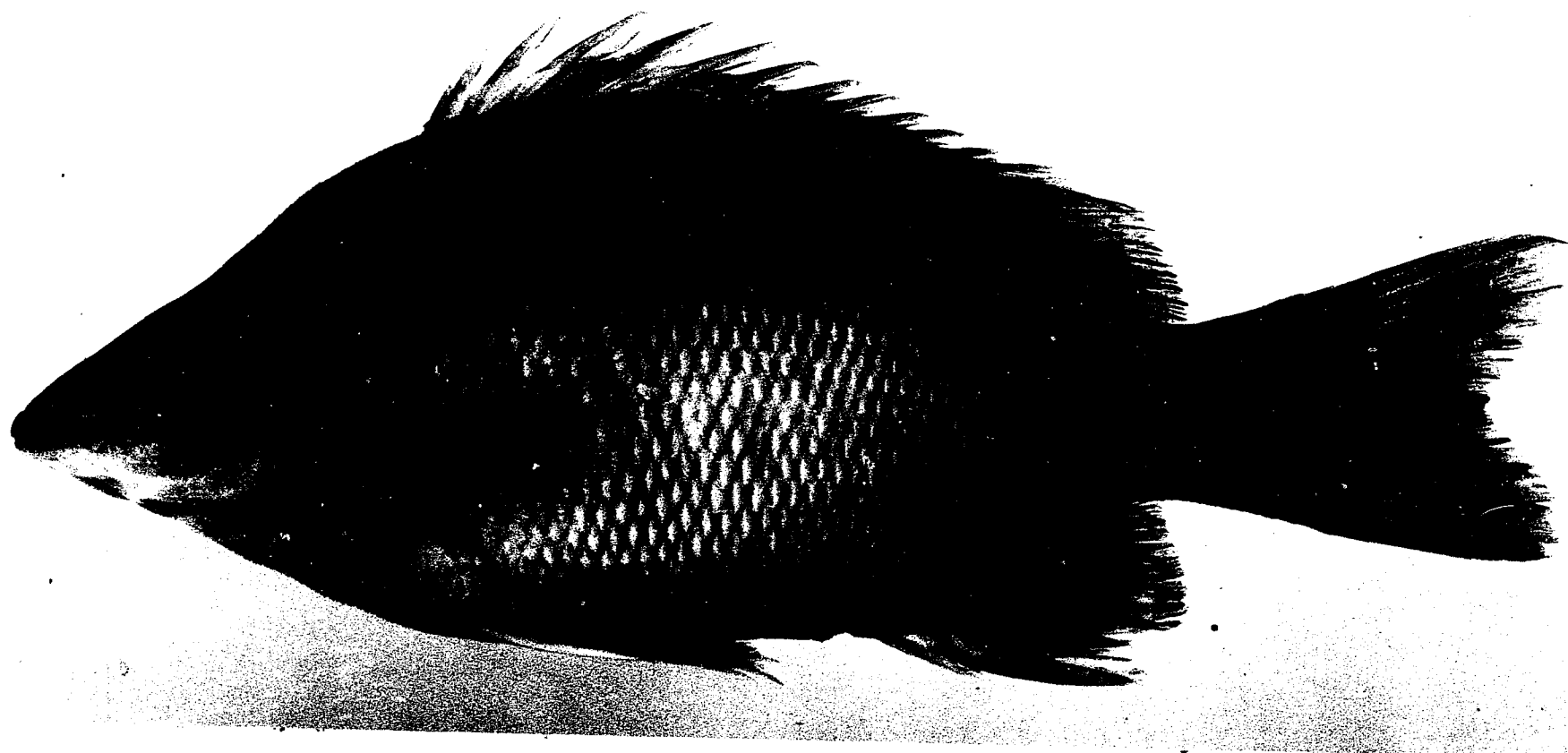
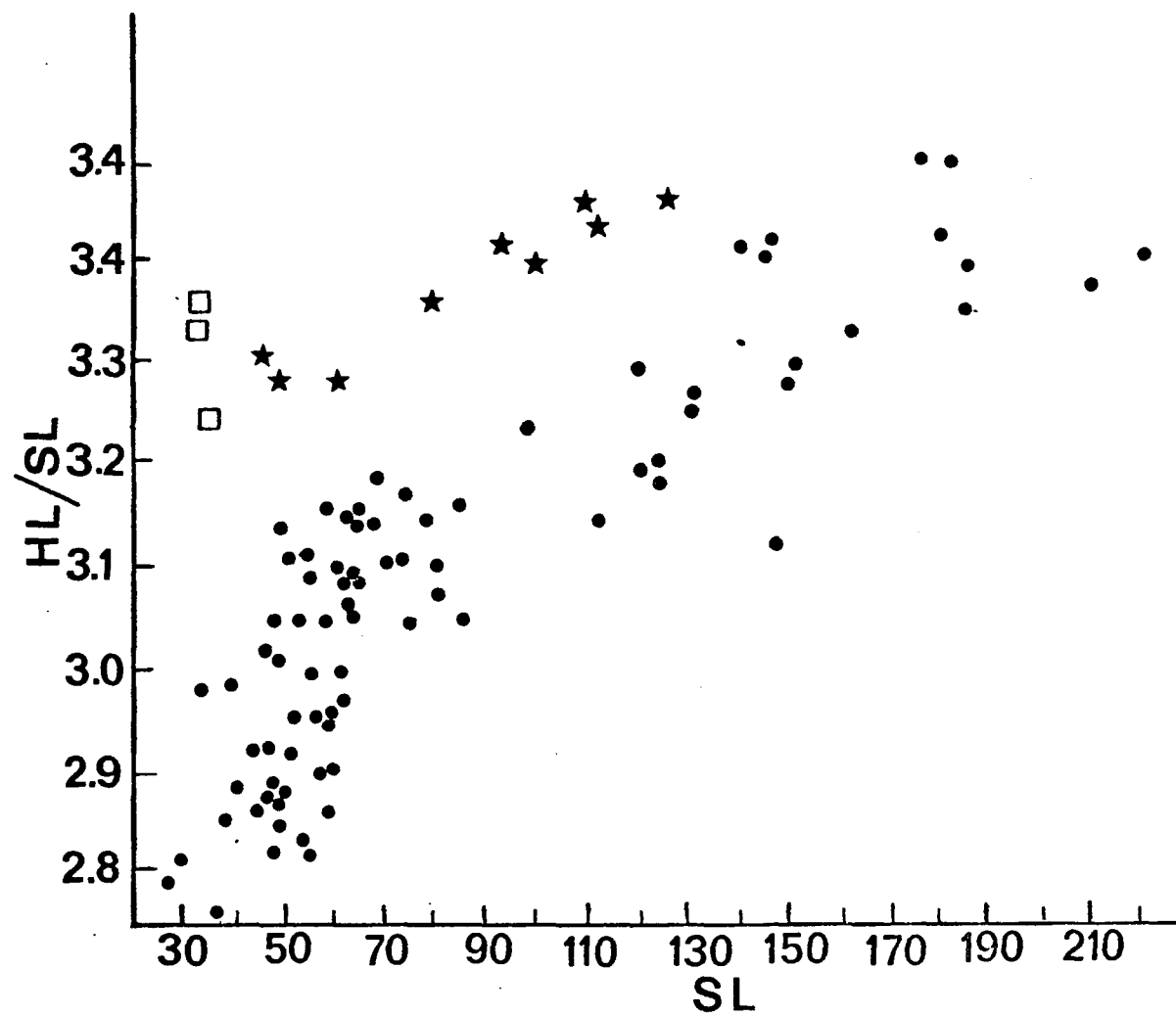


Figure 88



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Figure 89

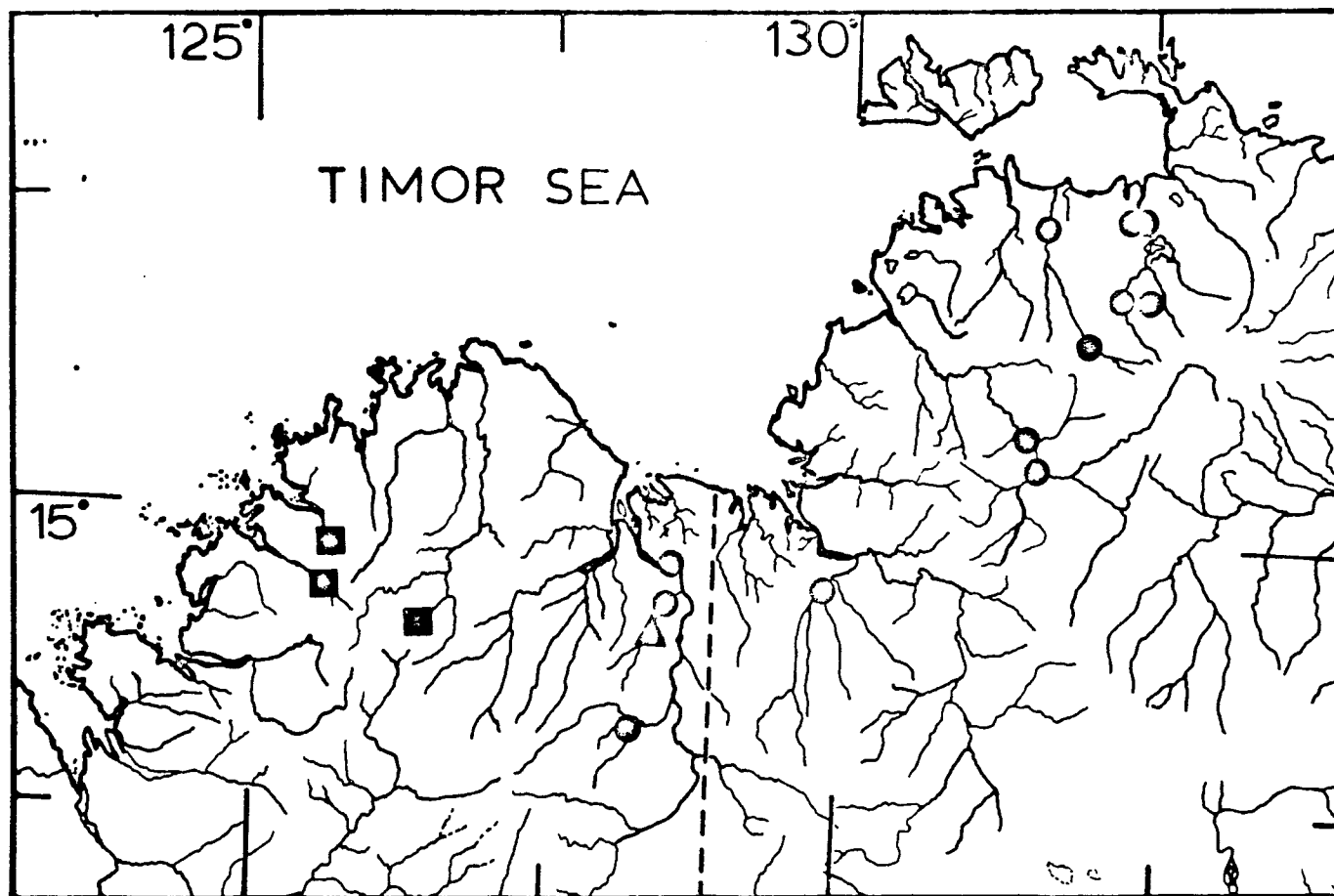
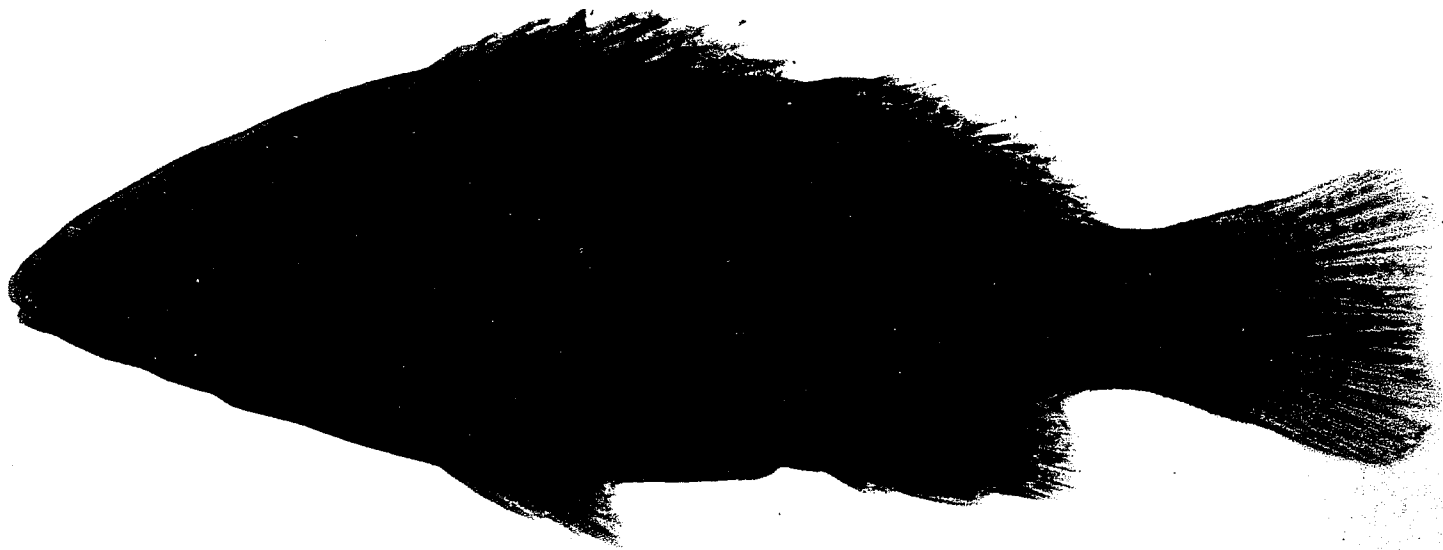


Figure 90



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Figure 91



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Figure 92



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Figure 93

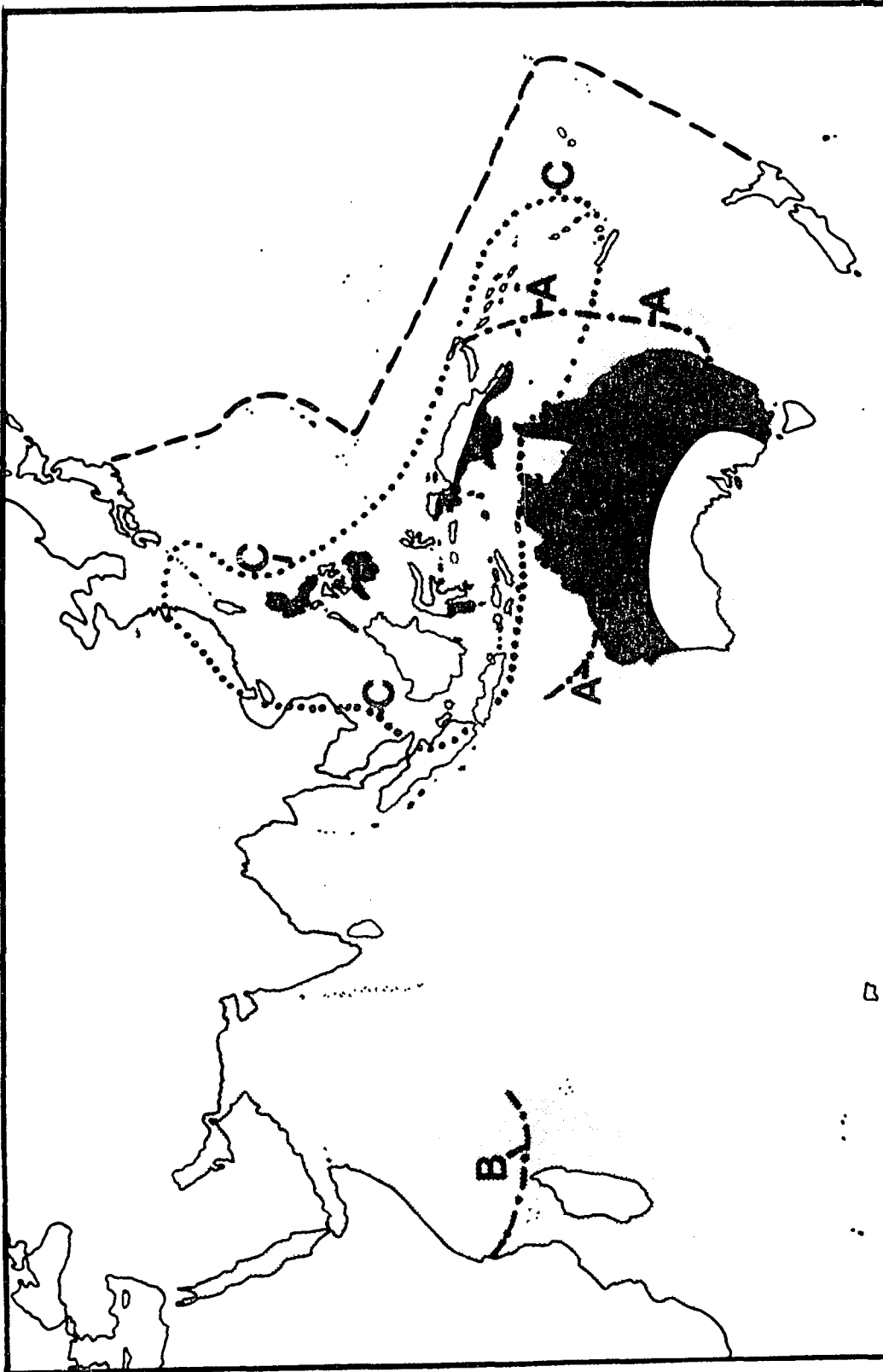


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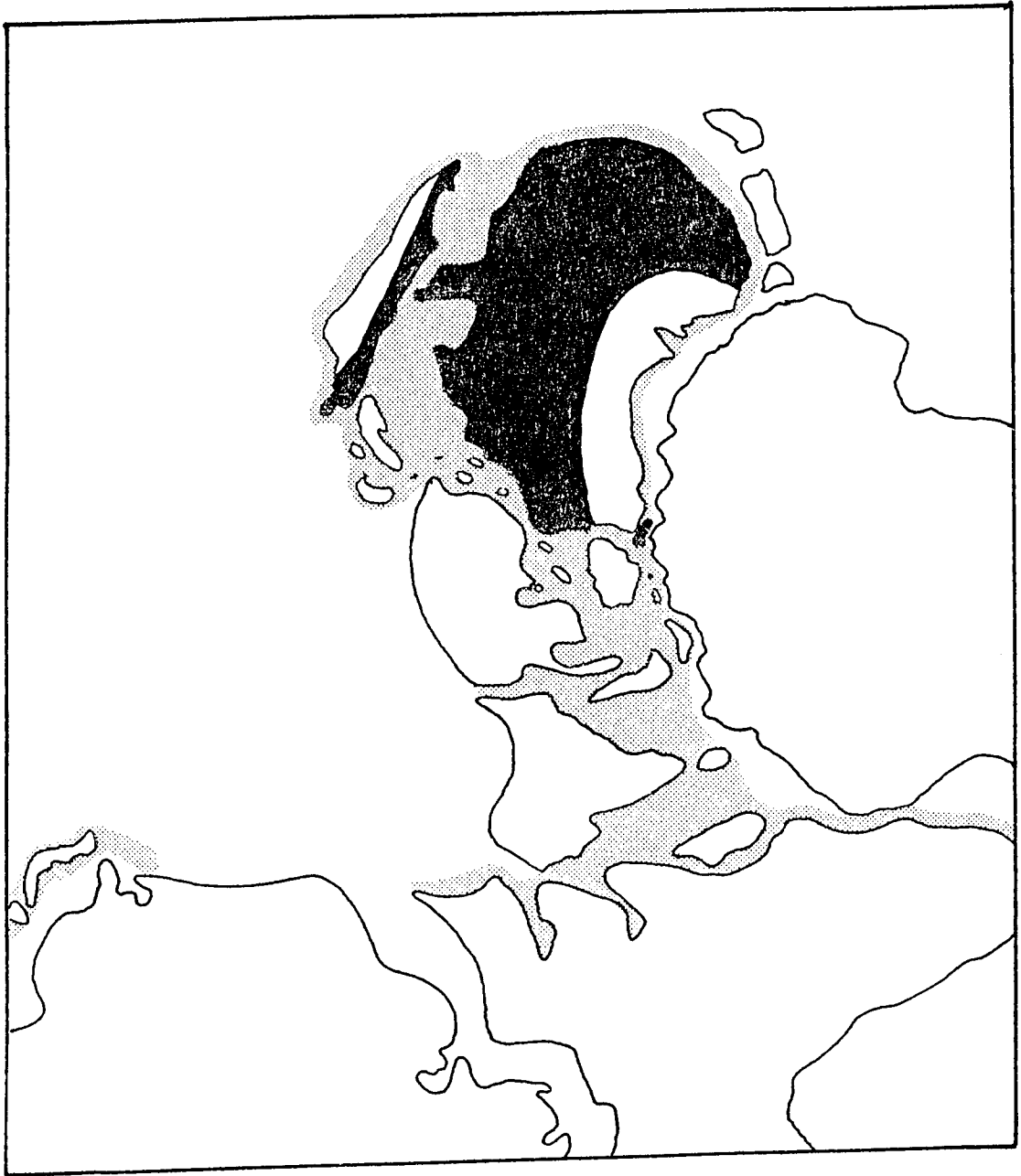


Figure 25