

THE TERAPON PERCHES (PERCOIDEI,
TERAPONIDAE). A CLADISTIC ANALYSIS
AND TAXONOMIC REVISION

RICHARD P. VARI

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AND TAXONOMIC REVISION

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ABSTRACT

The family Teraponidae was revised to determine: the monophyletic nature of the family; the relationships of teraponids to other perciform fishes; the relationships within the family; the recognizable species and their distinguishing characters; and the distribution patterns of the family and its subunits.

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

(1) The Teraponidae can be defined on the basis of derived states of the swimbladder, extrinsic swimbladder muscle, urohyal, and third pharyngobranchial. These 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 in the Percoidei.

(2) Within the family 15 monophyletic assemblages were recognized, with the relationships between them and their defining characters based on derived states of posttemporal, tabular, dentary, maxillary, premaxillary, spinous dorsal,

and vertebral osteology; forms of the extrinsic swimbladder muscle; swimbladder and intestinal patterns; and differences in pigmentation and heights of the dorsal and anal fin sheaths.

(3) These monophyletic assemblages are recognized at the generic level; and three new genera (*Hannia*, *Lagusia*, and *Syncomistes*) are described. Thirty-seven species are recognized of which five (*Leiopotherapon macrolepis*, *Hannia greenwayi*, *Syncomistes butleri*, *Syncomistes trigonicus*, and *Syncomistes kimberleyensis*) are described for the first time. Each species is described in detail and a key is provided to the species of the family. Eight species recognized as distinct by some or all workers to this point are placed in synonymy, one species synonymized previously is recognized as distinct, and the previous synonymizations of two nominal forms are tentatively modified.

(4) Track analysis of the zoogeography of the family and its subunits revealed two major patterns: a track including the coastal regions of the entire Indo-west Pacific and a track between the fresh waters of northern Australia and southern New Guinea. The significance of these tracks in light of various geological events in the region is discussed.

INTRODUCTION

The Teraponidae, a family of perciform fishes, are 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. In his introductory discussion of the family, Cuvier (1829) said the teraponids are "un groupe de poissons qui semble fait pour désespérer les naturalistes."

Teraponids were first distinguished as a group when Cuvier created the genus *Terapon* in 1817 to contain two species (*T. servus* and *T. quadri-lineatus*) previously placed in the genus *Holocentrus*. Cuvier (1829) erected three new genera (*Helotes*, *Pelates*, and *Datnia*) to contain a series

of species most of which were described at the same time. Of these genera *Datnia* was generally considered to be indistinguishable from *Terapon* by most following workers, whereas *Pelates* and *Helotes* were retained as distinct except by Bleeker (1873) who synonymized them into *Terapon*.

Since Cuvier's monograph, many species have been described from the fresh waters 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 species were assigned to the genus *Terapon*; a procedure claimed by some workers as obscuring the patterns of interrelationships within the family (Ogilby and McCulloch, 1916; Whitley, 1943; Mees, 1971). However, with only a limited amount of informa-

tion available from external characters, most investigators suggested that further subdivision of the family should await future studies, particularly of the osteology.

Other researchers, nonetheless, did partition the catch-all genus *Terapon*. Fowler (1931) established a series of subgenera (*Eutherapon*, *Leiopotherapon*, *Mesopristes*, *Rhyncopelates*, and *Terapon*) 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 erected generic-level names and creating six new ones. With later generic descriptions (1945a, 1948b, 1955) he recognized 16 teraponid genera. Thirteen of these (*Amniataba*, *Amphitherapon*, *Authistes*, *Bidyanus*, *Eutherapon*, *Hephaestus*, *Leiopotherapon*, *Madigania*, *Mesopristes*, *Pelsartia*, *Papuservus*, *Scortum*, and *Terapon* (*sensu stricto*)) represented species or species groups previously assigned to *Terapon*. *Helotes* was divided by Whitley into *Helotes* (*sensu stricto*) and *Pingalla*, with these two genera forming

the subfamily Helotinae. The genus *Pelates* remained unchanged.

Teraponid taxonomy prior to the present 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 in this system 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, Whitley's generic descriptions and diagnoses failed to deal with six nominal species (*T. plumbeus*, *T. micracanthus*, *T. oxyrhynchus*, *T. kneri*, *T. elongatus*, and *T. lambertoni*) from outside the Australia-New Guinea region. On the basis of his generic descriptions neither these species nor those described more recently (*T. brevipinnis* and *T. jamoerensis*) could be unambiguously assigned to existing genera.

Much of the difficulty that previous workers

TABLE 1
Genera of the Family Teraponidae and the Species Assigned to Them
by Whitley and Other Workers^a

| SUBFAMILY TERAPONINAE | |
|-------------------------|---|
| <i>Amniataba</i> : | <i>Amniataba percoides</i> |
| <i>Amphitherapon</i> : | <i>Amphitherapon caudavittatus</i> , <i>A. habbema</i> |
| <i>Authistes</i> : | <i>Authistes puta</i> |
| <i>Bidyanus</i> : | <i>Bidyanus bidyanus</i> |
| <i>Eutherapon</i> : | <i>Eutherapon theraps</i> |
| <i>Hephaestus</i> : | <i>Hephaestus bancrofti</i> , <i>H. carbo</i> , <i>H. fuliginosus</i> , <i>H. welchi</i> |
| <i>Leiopotherapon</i> : | <i>Leiopotherapon suavis</i> |
| <i>Madigania</i> : | <i>Madigania unicolor</i> , <i>M. adamsoni</i> |
| <i>Mesopristes</i> : | <i>Mesopristes aheneus</i> , <i>M. alligatoris</i> , <i>M. argenteus</i> , <i>M. jenkinsi</i> , <i>M. cancellatus</i> |
| <i>Papuservus</i> : | <i>Papuservus trimaculatus</i> |
| <i>Pelates</i> : | <i>Pelates oxyrhynchus</i> , <i>P. quadrilineatus</i> , <i>P. sexlineatus</i> , <i>P. roemeri</i> |
| <i>Pelsartia</i> : | <i>Pelsartia humeralis</i> |
| <i>Scortum</i> : | <i>Scortum barcoo</i> , <i>S. hillii</i> , <i>S. ogilbyi</i> , <i>S. parviceps</i> |
| <i>Terapon</i> : | <i>Terapon jarbua</i> , <i>T. servus</i> |
| SUBFAMILY HELOTINAE | |
| <i>Helotes</i> : | <i>Helotes sexlineatus</i> |
| <i>Pingalla</i> : | <i>Pingalla gilberti</i> , <i>P. lorentzi</i> |

^aThe following species were not assigned to any of the above genera and remained in the genus *Terapon* (*sensu lato*): *Terapon plumbeus*, *T. kneri*, *T. micracanthus*, *T. elongatus*, *T. lambertoni*, *T. brevipinnis*, *T. jamoerensis*.

have encountered in attempting to resolve a hypothesis of relationships within the Teraponidae was a consequence of difficulties arising from the wide geographic range of the family. Marine species are found along the coasts of the Indo-west Pacific from Africa to Samoa and enter into brackish and fresh waters throughout this range. Species apparently limited to fresh water are found through the northern two-thirds of Australia, southern New Guinea, the southern peninsula of Sulawesi (Celebes) and the islands of Luzon and Mindanao in the Philippines.

Because of this widespread range, and the poor information available for many nominal species, most workers have limited their studies regionally and, consequently, have dealt with a limited number of species (Ogilby and McCulloch, 1916; Weber and deBeaufort, 1931; Whitley, 1943; Munro, 1967; and others). Since Cuvier's monograph, the only study dealing with the majority of the members of the family was Fowler's (1931)—a study that depended heavily on literature information, especially for fresh-water species. In both Fowler's study and other works, differences in terminology and procedures between workers have caused confusion, with subsequent error in synonymy and descriptions of invalid species.

Besides the difficulty in resolving within-family relationships, the question of relationships of teraponids to other perciform fishes had also been left unresolved. Teraponids have been considered to be a part of the *Pristopomatidae* by

Günther (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 the present study are fivefold:

- (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 perciform 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.

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 descendants 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 the included subtaxa.

In estimating the plesiomorphic or apomorphic (derived) nature of various teraponid characters, two methodologies are used. The first involves a series of outgroup comparisons (determination of the state of the character in a variety of other perciform 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.

As discussed by Nelson (1973), 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 transformation two possible hypotheses exist as an explanation of the distribution of the ontogenetic change: (1) the ontogenetic character transformation is acquired in lineage A; (2) the ontogenetic character transformation was present in the common ancestor of lineages A and B but was subsequently lost in lineage B.

The first hypothesis makes one assumption, the acquisition of the ontogenetic transformation in lineage A. The second, in contrast, makes two assumptions, that of the possession of the ontogenetic change by 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 an attempted reconstruction of phylogenies. Therefore in the following analysis, it is hypothesized that the transformed state of character within a group represents the apomorphic 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 (SL) or head length (HL). 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. To facilitate comparisons, proportions are presented following the procedures of the majority of previous workers on the family.

Measurements and counts were made in general following the procedures of Hubbs and Lagler (1958) (exceptions are discussed below). 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 resulting in inconsistencies both intra- and inter-specifically. 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 counted along the lateral line either above or below it or the number of rows of scales interrupted by the 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 posterior to 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 and stained specimens. The first two vertebrae lack pleural ribs but can be

easily counted by their prominent neural spines. The distinction between precaudal and caudal vertebrae is where the fused proximal pterygiophores of the first and second anal spines insert between the hemal arches. In counts of caudal vertebrae, the terminal half-centrum supporting the parahypural and hypurals was counted as one element.

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

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 if available.

Specimens examined are listed for each species, with those individuals from which counts and measurements were taken indicated by an asterisk after the catalogue number, including their range of standard lengths. In large series, only part of which were used for counts and measurements, both the total specimens and the number measured are noted, with the standard lengths given being those of the latter.

Various characters were studied in alcohol preserved material, cleared and stained specimens, and articulated and disarticulated dry skeletons. Drawings of various characters were made primarily from cleared and stained specimens using a camera lucida. The illustrations of the osteology of *Terapon jarbua* are based on a series of cleared and stained specimens along with radiographs and dissected materials of individuals of various sizes.

Unless otherwise noted for the species, ecological information presented is based on information taken from the field notes of the American Museum-Australian expedition in Western Australia and Northern Territory.

Vernacular English names for the species of the family are taken primarily from Smith (1949),

Munro (1967), Lake (1971), and Grant (1972). Vernacular names in various other languages for the species of the group are not usually presented but can be found in Weber and deBeaufort (1931), Herre (1953), Chan (1968), and other regional surveys.

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ABBREVIATIONS

AM, Australian Museum, Sydney
 AMNH, the 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 Historie, Leiden
 SU, Stanford University (at California Academy of Sciences)
 UMMZ, University of Michigan, Museum of Zoology, Ann Arbor
 USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 WAM, Western Australian Museum, Perth
 ZMA, Zoölogisch Museum, Amsterdam

ABBREVIATIONS IN FIGURES

ac, anterior ceratohyal
 art, articular
 aspo, autosphenotic
 bb₁₋₃, basibranchials
 bh, basihyal
 bsd, basal sheath of dorsal
 bsp, basisphenoid
 cb₁₋₅, ceratobranchial
 cor, corocoid
 den, dentary
 drd, dorsal ramus of dentary
 dru, dorsal ramus of urohyal
 eb₁₋₄, epibranchials

ect, ectopterygoid
 end, endopterygoid
 epo, epiotic
 esm, extrinsic swimbladder muscle
 esmo, extrinsic swimbladder muscle origin
 exo, exoccipital
 fro, frontal
 hb₁₋₃, hypobranchial
 hyo, hyomandibular
 ih, interhyal
 iop, interopercle
 lac, lacrimal
 lat, lateral ethmoid
 lhh, lower hypohyal
 lta, lateral tabular
 met, metapterygoid
 mta, medial tabular
 mx, maxilla
 op, opercle
 ot, otic sensory canal
 pa, parietal
 pal, palatine
 pas, parasphenoid
 pc, posterior ceratohyal
 pcl, postcleithra
 pd, predorsal
 ph₁₋₄, pharyngobranchial
 pmx, premaxilla
 pop, preopercle
 pro, prootic
 pto, pterotic
 pts, pterosphenoid
 ptt, posttemporal
 quad, quadrate
 rc, rostral cartilage
 ret, retroarticular
 sca, scapular
 scl, supracleithrum
 se, supraethmoid
 soc, supraoccipital
 sop, subopercle
 spd, symphyseal process of dentary
 sym, symplectic
 stc, supratemporal commissure
 uh, urohyal
 uhh, upper hypohyal
 vo, vomer
 vpu, ventrolateral projection of urohyal

NOMENCLATURE

Two points of nomenclature in the family, one anatomical and the other taxonomic, should be clarified. The first is the question of the terminology applied to the parts of the teraponid

pectoral girdle. Two pectoral girdle bones vary in the extent of their development and exposure to the surface and have been utilized as key characters and indicators of phylogenetic relationships by many authors (Ogilby and McCulloch, 1916; Weber and deBeaufort, 1931; Fowler, 1931; and others). Cuvier (1829) referred to the bone visible slightly dorsal to the pectoral fin base as the corocoid and that exposed in some species above the upper opercular spine as the suprascapular. This terminology was followed by Weber (1910), Ogilby and McCulloch (1916), Rendahl (1922) and Weber and deBeaufort (1931) in studies of the group and species descriptions and by other workers in faunal studies.

Trewavas (1940) stated in her description of *Terapon* (=Hephaestus) *adamsoni* that the appropriate names for these bones were the cleithrum and supracleithrum rather than corocoid and suprascapular. Her terminology was in turn followed by Munro (1964, 1967) and Mees (1971). A study of the different states of the teraponid pectoral girdle bones shows, however, that whereas the ventral element termed the corocoid by Cuvier is actually the cleithrum as suggested by Trewavas, the dorsal element termed the suprascapular or supracleithrum is actually the posttemporal. The actual supracleithrum is an elongate element with a normal relationship between the cleithrum and posttemporal (fig. 2).

This confused terminology has resulted in errors in several original descriptions. Trewavas (1940) stated that in *Terapon* (=Hephaestus) *adamsoni*, the "supracleithrum" is not exposed and equated this bone to the suprascapular of previous workers. However, reference to the holotype of the species shows the posttemporal (=suprascapular of workers before Trewavas) to be exposed and serrate. The same situation occurred in *Terapon habbema* (=Hephaestus *trimaculatus*) described by Weber (1910) followed by Weber and deBeaufort (1931) as having a covered suprascapular (=posttemporal). The original illustration and study of part of the syntype series show, however, that the posttemporal is exposed and serrate. Finally, Mees (1963) stated that the supracleithrum is exposed in *Terapon* (=Leiopotherapon) *aheneus*. Examination of paratypes of this species shows, however, that the posttemporal, though having a reduced scale covering, lacks an exposed, serrate, expanded edge.

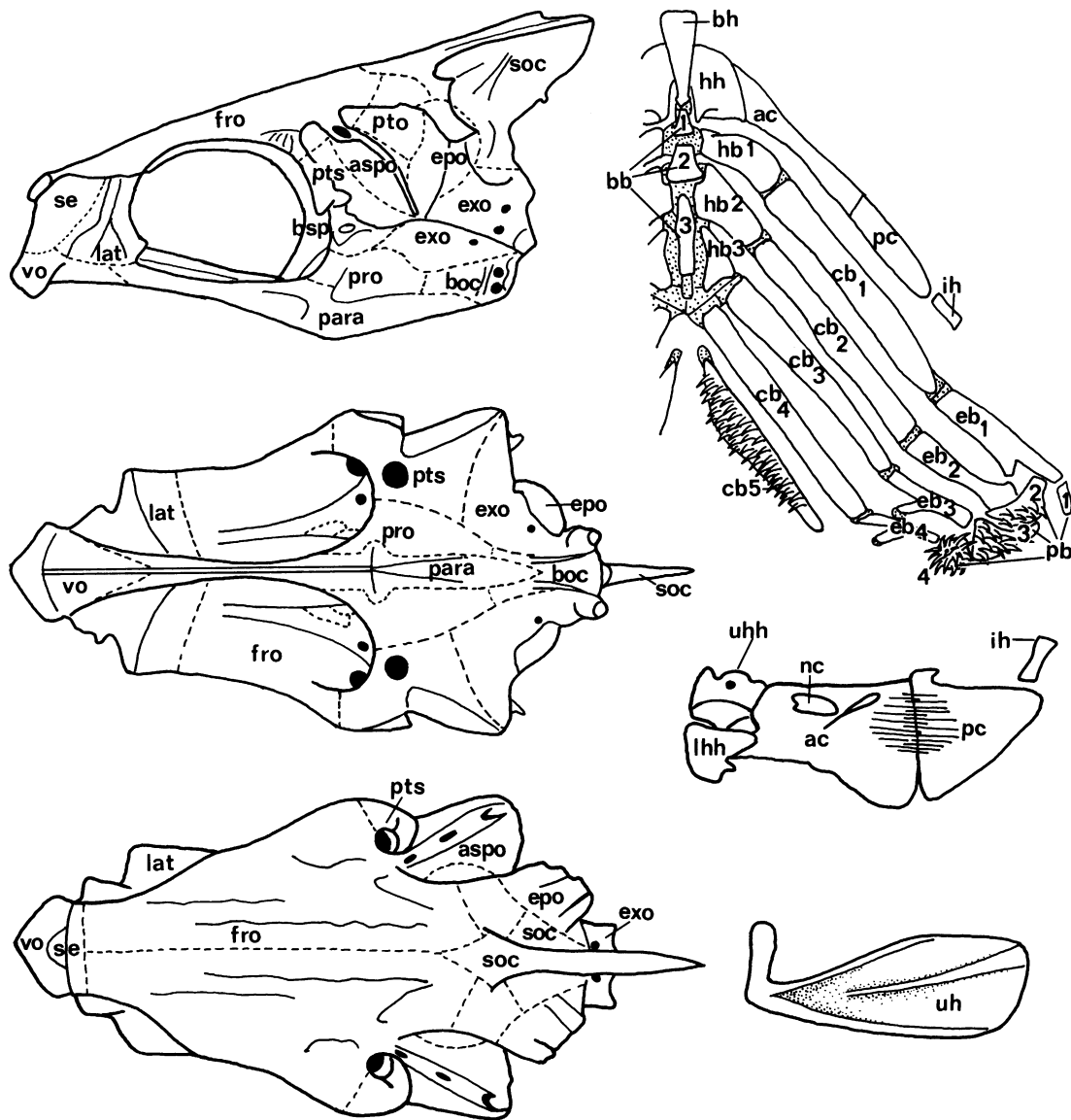


FIG. 1. Osteology of *Terapon jarbua*; skull and branchial apparatus.

The second nomenclatural question involves the proper spelling of the type genus name for the family, whether *Terapon* or *Therapon*, and whether the family name is Teraponidae or Theraponidae; questions recently discussed by Smith (1974). The type genus name is derived from Bloch's statement (1797) that as a conse-

quence of the low esteem in which it was held among the Japanese, *Holocentrus* (= *Pelates*) *quadrilineatus* was considered fit only for "slaves" and was therefore termed by Europeans the "slave-fish" (l'esclaves).

Although the proper transliteration from the Greek for slave is *Therapon* (Woods, 1966);

Cuvier (1817), both in the index and in the group description, utilized *Terapon*. This consistent, though incorrect, spelling occurring in two widely separated sections of the work would therefore appear to be an incorrect transliteration rather than a repeated *lapsus calami*. 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 must be *Terapon*.

Terapon in turn should be the stem for the

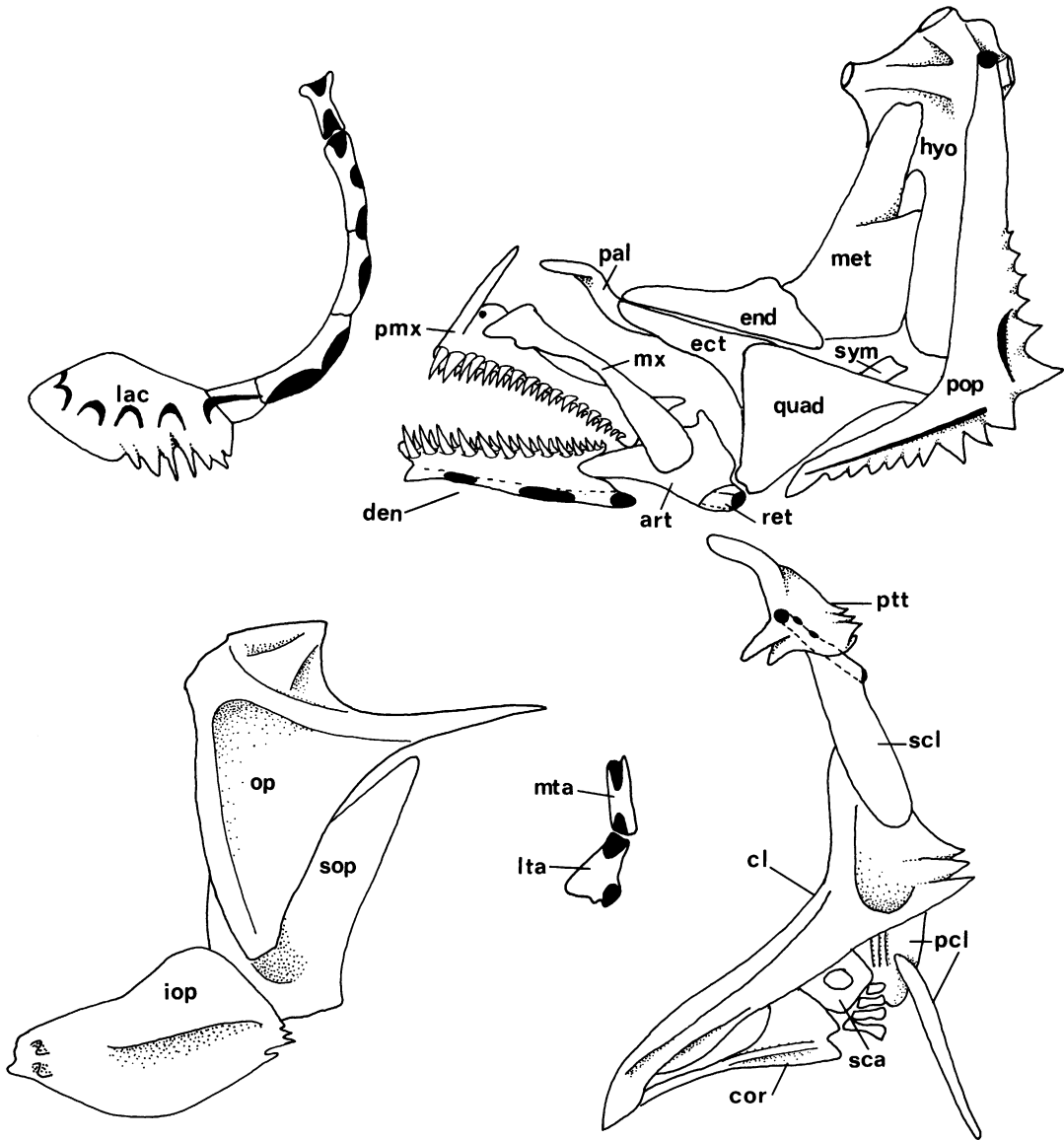


FIG. 2. Osteology of *Terapon jarbua*; jaw suspensorium, opercular series, and pectoral girdle.

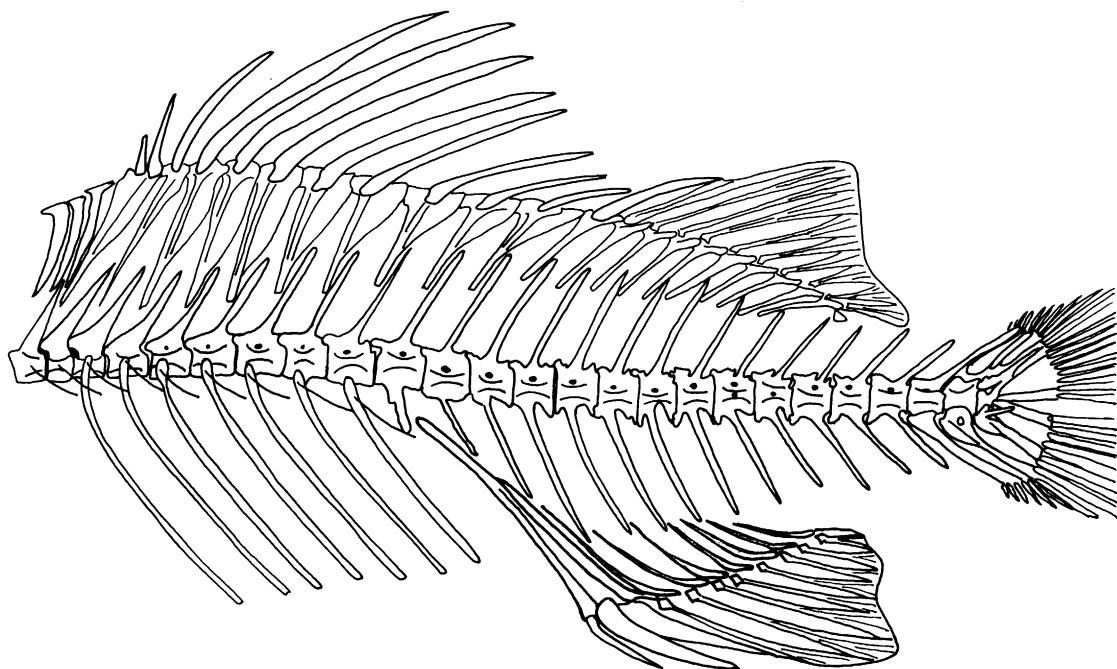


FIG. 3. Osteology of *Terapon jarbua*; axial skeleton.

formation of the family name. During the past half-century, both Teraponidae and Theraponidae have been used by various workers. Teraponidae, however, is based on the correct type genus name spelling. Along with the fact that its presentation as the proper form of the family name

predates the 1960 cut-off date for family name changes in Article 40 and its long if inconsistent usage, it would therefore appear to be proper under the rules and will be used throughout this revision.

DEFINING CHARACTERS OF THE TERAPONIDAE

Members of the family Teraponidae form a distinctive group of perciform fishes that have been traditionally defined on the basis of a series of shared characters which are, however, either primitive for members of the suborder Percoidei in general or shared with smaller groups within it. Consequently, the monophyly of the group in the Hennigian sense, that is a hypothesis of common ancestry based on shared derived characters, has never been demonstrated. This study indicates, however, that the species of the family (as defined here) share four derived characters; synapomorphies that therefore support the hy-

pothesis of the monophyletic nature of the group.

The first of these characters is a unique form of extrinsic swimbladder muscle present with some variations in all members of the family. This extrinsic swimbladder muscle arises from the posterior surface of the ventral process of the posttemporal or the rear of the skull or both. From this origin, it extends posteriorly under the expaxial muscles, dorsal to Baudelot's ligament and ventral to the epipleural and pleural ribs to an insertion on the external connective tissue layer of the anterodorsal surface of the swim-

bladder. This insertion is distinctly lateral to the vertebral column and 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 extrinsic swimbladder muscles, it appears that they are derived from the levator pectoralis muscles which in teraponids run from the posterodorsal edge of the pterotic to the dorsomedial edge of the supracleithrum. This hypothesis is supported by the ontogenetic changes in the extrinsic swimbladder muscle which in some small individuals of *Leiopotherapon unicolor* (10-25 mm. SL) shares fibers with the levator pectoralis. When present, the amount of interconnection varies, with the sharing being of sufficient magnitude in some individuals to completely surround Baudelot's ligament. This interconnection is evidently lost with age as no adults have been found possessing it.

Consistent with this hypothesis of the derivation of the extrinsic swimbladder muscle from the levator pectoralis is its mode of innervation. In teraponids, the extrinsic swimbladder muscle is innervated by a branch of the first spinal nerve (Schneider, 1964; personal observ.), a nerve which also innervates the levator pectoralis. As muscles or muscle sections derived from them are

with few exceptions innervated by the same nerves or nerve elements through a phylogenetic lineage (Romer, 1970), the above similarity in innervation supports a hypothesis of the derivation of the extrinsic swimbladder muscles of teraponids from the levator pectoralis. In contrast, the protractor pectoralis, which runs parallel to the levator pectoralis and the extrinsic swimbladder muscle and as such is a good alternative source of the latter, is innervated by the vagus nerve (Winterbottom, 1974).

The presence of an extrinsic swimbladder muscle in teraponids was first described by Cuvier (1829) for *Therapon servus* (= *Therapon jarbua*) which he stated had a muscular attachment between the anterior chamber of the swimbladder and the anterior vertebrae. Although an attachment of the extrinsic swimbladder muscle to the anterior of the swimbladder is consistently found in all species of the family, there have not been discovered any species or individuals with an extrinsic swimbladder muscle arising from the anterior vertebrae. Thus Cuvier's original description appears either to be a misinterpretation of the origin of the muscle or based on an anomalous individual.

This author also refers to anterolateral elongations of the swimbladder in *Helotes* (= *Pelates*) *sexlineatus* that form two processes contacting the rear of the skull. This study has failed,

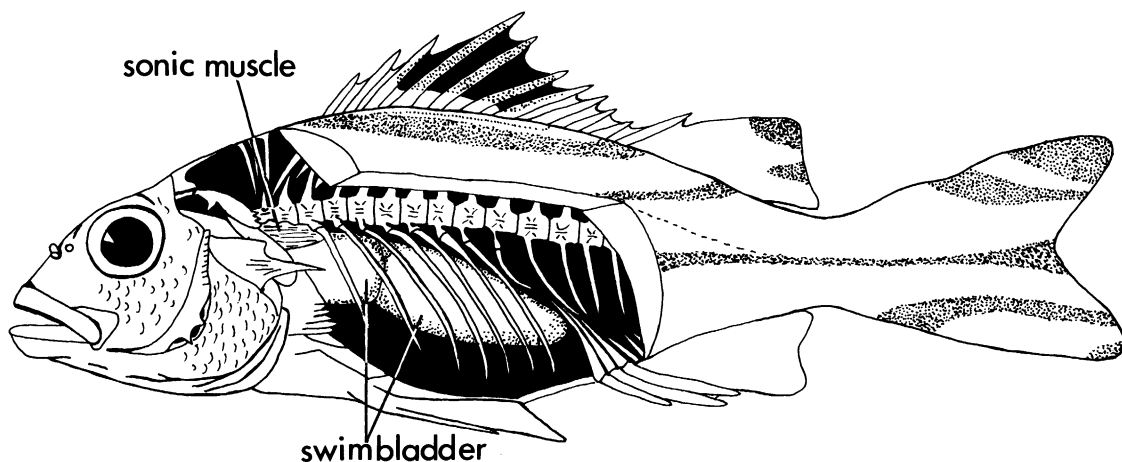


FIG. 4. Lateral cutaway view of *Therapon jarbua*, showing the extrinsic swimbladder muscle and swimbladder form (after Schneider, 1964).

however, to find any such processes in any species of the family. However, the extrinsic swimbladder muscles of the species of the genus *Pelates* (as defined herein) have connective tissue bands on their ventral and medial surfaces. These bands, which are continuous with those arising from the rear of the skull and the connective tissue covering of the swimbladder, might be interpreted as swimbladder diverticula when viewed from the body cavity.

Following these references to the extrinsic swimbladder muscles, they do not appear to have been noted again for the family until Hardenberg (1934) illustrated the muscle form for *Terapon theraps* and hypothesized that they functioned as part of a sound-producing mechanism. Schneider (1961, 1964) illustrated the extrinsic swimbladder muscles for *Terapon jarbua* and *T. theraps* and proved their sonic function by extensive physiological studies. His studies of the sound-producing mechanism showed that the muscles serve as vibrators of the swimbladder which in turn acts as a resonator organ.

Acoustical signals produced by this system are utilized in a variety of threat and response behaviors whose intensity and structure were shown by Schneider to be a function of both age and environmental conditions. Since the sonic ability of many species has been repeatedly noted (Uchida, 1934; Dorai, 1960; Scott, 1962; and others), it is probable that the extrinsic swimbladder muscle in all teraponids has a common sonic function.

Schneider also studied the ontogeny of the extrinsic swimbladder muscle which he found first appears in *Terapon jarbua* by 35 mm. SL. Comparisons with the juveniles of other teraponids have shown wide variation in the development of the muscle. In *Leiopotherapon unicolor* the muscle is fully developed in some 18.5 mm. SL individuals; in *Amniataba percooides* at 9 mm. SL; and in *Hephaestus fuliginosus* at 33 mm. SL.

More recently Eichelberg (1976) has studied the fine structure of the extrinsic swimbladder muscles and found it to reflect the very high rate of contraction noted by Schneider; a rate which is one of the most rapidly operating among vertebrate muscles.

On the basis of information presently available on extrinsic swimbladder muscles in the Perciformes, the form of the muscles in the

Teraponidae would appear to be unique. Within the Perciformes, extrinsic swimbladder muscles have been previously described in the Serranidae (*Epinephalus striatus*; Hazlett and Winn, 1962) and discovered in the Pempheridae (*Pempheris* spp.) during the course of comparative studies associated with this work.

The extrinsic swimbladder muscle in *Epinephalus striatus* differs from that of teraponids in position, a lack of an attachment to the skull, an attachment to the ribs and appears to be derived from the epaxial muscles. The pempherid extrinsic swimbladder muscle which is quite similar to that of teraponids also extends from the skull to an insertion on the anterodorsal surface of the swimbladder. This sonic muscle differs from that in teraponids, however, in a more dorsal origin on the skull and a more medial insertion on the swimbladder.

A second defining derived character of teraponids is the adult swimbladder form. Outgroup comparisons in and out of the Perciformes indicate that the plesiomorph swimbladder form in the Percoidei is an elongate oval lacking constrictions or internal subdivisions; a hypothesis consistent with the ontogenetic changes in teraponid swimbladders. Juvenile teraponids have an elongate unconstricted, ovoid swimbladder (Schneider, 1964, fig. 24; personal observ.) which develops a transverse septum ontogenetically at a point approximately one-third of its total length posteriorly. The formation of this septum is followed by the development of a definite transverse swimbladder constriction at the same point; a constriction which eventually divides the swimbladder in most teraponids into two unequal chambers connected by a short narrow tube (figs. 4 and 5). However, in two genera within the family (*Pingalla* and *Syncomistes*) this constriction is secondarily reduced. The swimbladder of *Syncomistes butleri* is distinctly constricted at 45 mm. SL. This constriction partially subdivides the swimbladder into two subchambers which are not however, as marked as those of other groups of teraponids. With increasing age, this constriction is secondarily reduced, with larger specimens having only a 40 percent reduction of the swimbladder diameter at the point of maximum constriction. This results in two subchambers connected by a wide tube (fig. 6).

Within family variation also occurs in the

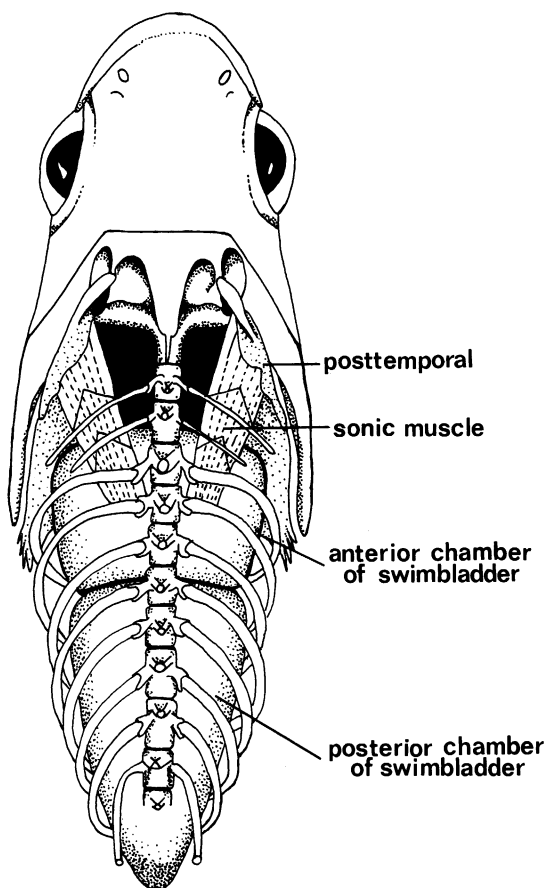


FIG. 5. Dorsal cutaway view of *Terapon jarbua*, showing the extrinsic swimbladder muscle and swimbladder form (after Schneider, 1964).

development of the swimbladder constriction. Schneider (1964) found the swimbladder constriction in *Terapon jarbua* at 31.5 mm. SL. Examination of juveniles of *Leiopotherapon unicolor* shows the swimbladder to be fully divided in 17.7 mm. SL specimens and in *Amniataba percoides* the swimbladder is partially constricted at 9 mm. SL and totally constricted at 14.5 mm. SL.

In adult teraponids the length of the anterior swimbladder chamber is approximately one-third that of the posterior, with a rotund form and a marked dorsomedial depression which allows a close fit to the ventral surfaces and parapophyses of the third to fifth vertebrae. The anterior

swimbladder chamber has dorsomedial attachments to the posteroventral surface of the extrinsic swimbladder muscles and medial to these to the ventral surfaces of the parapophyses and proximal sections of the first three pleural ribs. These attachments anchor the swimbladder during contractions of the extrinsic swimbladder muscles, resulting in the creation of a tension and consequent vibration in the swimbladder and associated sound production.

The posterior swimbladder chamber is an elongate oval that gradually tapers posteriorly and ends in a rounded to distinct point. The posterior swimbladder chamber has varying degrees of loose attachments by peritoneum to the dorsolateral and dorsal body walls which contrasts with the strong connections of the anterior chamber to the vertebral column and ribs.

Macroscopically visible glandular tissue is present in both chambers of the teraponid swimbladder with the largest amounts localized on the posteroventral region of the anterior chamber and a lesser amount on the ventral surface of the posterior chamber.

Within the family, one species, *Pelates quadrilineatus*, has a further derived autapomorphic swimbladder form. The posterior chamber in this species has a second transverse constriction which separates off a small posterior section resulting in a trichambered swimbladder.

The distinctive teraponid swimbladder form was first described by Cuvier (1829) for five of his nominal species. Later, Richardson (1844) in his description of *Dania caudavittata* (= *Amniataba caudavittatus*) described the swimbladder form in that species as undivided, a character that he used to distinguish the species from other teraponids. However, the constriction is present in this species as in all other teraponids. More recently Juliano (1960) described the swimblad-

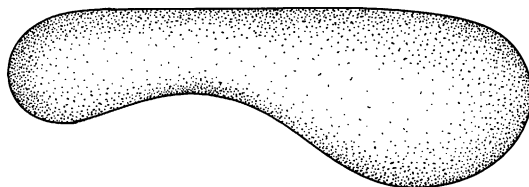


FIG. 6. Right lateral view of the swimbladder form in *Syncomistes butleri*.

der form in *Leiopotherapon plumbeus*, a freshwater Philippine species.

Workers since Cuvier 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 swimbladder constriction in their family diagnoses. Ogilby and McCulloch (1916), Day (1878), and Günther (1859) used the character in their general definitions of the family, with Günther further utilizing it as a key character differentiating teraponids from other groups in his family Pristopomatidae. However, even those workers who noted the presence of the swimbladder constriction failed to distinguish this as a derived character for teraponids among perciform fishes in contrast to the other listed characters which were either primitive for Perciformes in general or shared with other smaller groups.

Reference to available literature information on swimbladder forms in the Percoidei (Dobbin, 1941; Fänge, 1953; Marshall, 1962) and dissections in various groups have found the swimbladder form in the Teraponidae to be approached only by that of some species in the Pempheridae which also have a transversely divided swimbladder (personal observ.). However, it is most parsimonious to assume that this has been independently achieved in teraponids and pempherids (see discussion below).

The third character which is unique to the Teraponidae in the Percoidei is the form of the teraponid urohyal (fig. 7). In teraponids the urohyal has a distinct anterodorsal ramus which articulates dorsally with the ventral edge of the first basibranchial. Ventrally the urohyal has thin lateral projections which gradually widen posteriorly. Smaller lateral projections 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 groups using both dissected materials and the extensive survey of urohyal forms by Kusaka (1974) has shown the character combinations described above for teraponids to be unique in the Percoidei.

The fourth character that appears to be unique to the family is the form of the third

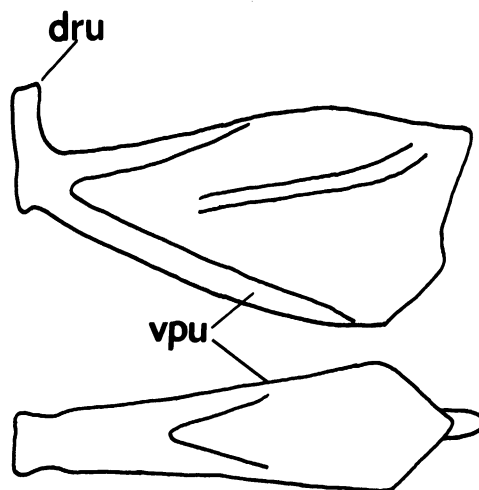


FIG. 7. Right lateral and ventral views of the urohyal of *Terapon jarbua*.

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 projection articulates with the dorsomedial region of the dorsal process of the second pharyngobranchial. The posterior projection runs posterodorsally to the midline of the basicranium and serves for the attachment of dorsal gill arch muscles. Although available information is limited, neither literature descriptions nor comparative studies undertaken during this study have revealed any comparable processes in the Percoidei.

RELATIONSHIPS OF THE TERAPONIDAE TO OTHER PERCIFORMES

Attempts to determine the closest relatives of teraponids among perciform fishes have proved unsuccessful in this study. On the basis of available information, two of the defining family characters (urohyal and pharyngobranchial form) do not appear to be approximated in any other group. Extrinsic swimbladder muscles arising from the rear of the skull have been reported or discovered during this study in several acanthopterygian groups. These groups (Holocentridae, Epinephalinae, and 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* lacking a series of derived characters uniting the Teraponidae to the Perciformes (absence 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 the common possession of the extrinsic swimbladder muscles would be less parsimonious than the assumption of the independent acquisition of the muscles in the various groups. Similarly, a hypothesis of a sister-group relationship between those pempherids with a transversely divided swimbladder and the Teraponidae on the basis of swimbladder form is refuted by the series of characters uniting all pempherids into a single monophyletic assemblage (see Tominaga, 1968).

The distribution of a series of other characters previously examined in detail by other workers have been analyzed in order to determine what information they could provide on the question of teraponid relationships. Eleven families share with the Teraponidae a Pattern 10 Ramus Lateralis Accessorius 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 Nemastistiidae (Haedrick, 1967). However, all of these characters appear to be plesiomorphic in the Percoidei. As such they are

not valid evidence of close relationships between or within the groups. Neither can this information be used to hypothesize that these are a series of plesiomorph sister groups to the other families of the Percoidei since plesiomorph characters may be retained in distantly related groups throughout a phylogeny. Consequently, these characters 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, Pristipomatidae, or Haemulonidae. Gosline (1966) pointed out that the family Teraponidae fails to conform with the characters of the Serranidae as defined in that work in its lack of a third opercular spine and retention of 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 distinguished from teraponids by their lack of a prominent spur on the lower caudal fin base. In summary, neither evidence previously advanced nor any uncovered in the course of this study supports a hypothesis of a sister-group relationship based on shared apomorphic characters between the Teraponidae and any of the aforementioned groups.

EXCLUSION OF THE GENERA *DATNIOIDES* AND *PSEUDOHELOTES* FROM THE TERAPONIDAE

In addition to the species workers before him considered to be teraponids, Fowler (1931) expanded the family by including in it the subfamily Datnioidinae containing two species *Datnioides microlepis* and *D. polota* (= *quadrifasciatus*). However, examination of these species has shown that they fail to agree with Fowler's definition of the family and lack the distinguishing teraponid characters previously discussed. Prior to and since Fowler, the datnioidines have been placed in the Lobotidae (Weber and deBeaufort, 1936; Lindberg, 1971), a group to which they appear to be more closely related.

At the same time of his inclusion of the Datnioidinae in the Teraponidae, Fowler also placed a monotypic genus, *Pseudohelotes*, as a synonym of *Helotes*. This genus created by Capello (in Pereira-Guimarães, 1881) was added

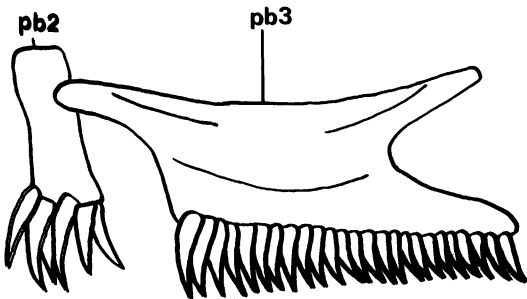


FIG. 8. Median view of the second and third pharyngobranchials in *Terapon jarbua*.

to *Helotes* without a discussion of either the genus or the type species, *P. guntheri*. Although the type specimen of the species is not available for examination, on the basis of the original description, it would appear that *P. guntheri* is not a teraponid in the sense that the term was used prior to and since Fowler. 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 stricto*). The name *Pseudohelotes* appears to be a reference to a supposed similarity in dentition between *P. guntheri* and *Helotes* (= *Pelates*) *sexlineatus* as the teeth of the two species are illustrated and compared. However, examination of the tooth form of *Pseudohelotes guntheri* as illustrated shows it to have the form of a truncate cone topped by a smaller recessed cone; a form quite different from the tricuspidate teeth of *Pelates sexlineatus*.

PHYLOGENETIC RELATIONSHIPS IN THE FAMILY TERAPONIDAE

The methodologies and procedures used in the reconstruction of a hypothetical series of relationships in the Teraponidae have been discussed in detail previously. A cladogram representing the hypothesized relationships within the family is presented in figure 9. Fifteen monophyletic groups having one to seven species and herein recognized as genera are defined in this reconstruction (for the purposes of the discussion, assemblage 11 is subdivided into units a and b). For reasons discussed above, the genera *Pseudohelotes* and *Datnioides*, which lack the apomorphic characters distinguishing the Teraponidae, are not included in the following phylogenetic analysis.

The following phylogenetic analysis is divided into two major parts. In the first, characters having multiple character states within the family are discussed as units, with a description of each state, its distribution and the basis for its hypothesized polarity. In the second part of the analysis all the character states used in the reconstruction of the phylogeny are discussed in order of their decreasing universality of the apomorphic states.

In the following discussion of the phylogenetic reconstruction, the subgroups have been assigned numbers (1-15, see fig. 9) representing their cladistic sequence, with the most plesiomorph sister group being one (increasing numbers thus coincide with decreasing universality of the apomorphic characters in the family). Avoiding the use of formal taxa at this point avoids the

confusion resulting from the hypotheses of relationship inherent in previous taxonomic definitions which differ from those presented in this work and also eliminates the necessity for a repeated reference by the reader to the exact sequence of formal taxa, a sequence whose precision is necessary for an understanding of the reconstruction.

The genera actually recognized and their numbers in the cladistic sequence are as follows:

- 1-*Leiopotherapon*
- 2-*Amniataba*
- 3-*Hannia*, new genus
- 4-"*Terapon*"
- 5-*Lagusia*, new genus
- 6-*Pelates*
- 7-*Terapon*
- 8-*Pelsartia*
- 9-*Rhyncopelates*
- 10-*Mesopristes*
- 11-*Hephaestus*
- 12-*Bidyanus*
- 13-*Scortum*
- 14-*Pingalla*
- 15-*Syncomistes*, new genus

CHARACTER ANALYSIS

Posttemporal and Tabular Anatomy. The first anatomical system to be discussed in which a number of different character states are present in the Teraponidae 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 Perciformes and consequently probably for teraponids is that shown semidiagrammatically in figure 10. In this pattern, the supratemporal commissure and the otic portion of the infraorbital canal (referred to hereafter as the otic canal) meet and open in common 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 bone and extends posterior to the point of union of the ventral and dorsal process of the posttemporal as a small distinct process overlapping the supracleithrum for two-thirds of the horizontal width of that bone. At its posterior terminus this process, which is situated ventral to the supracleithral-posttemporal articulation, communicates with the short sensory canal of the supracleithrum, a canal that in turn is continuous with the main trunk lateral line. In this pattern, the posttemporal sensory canal lacks any lateral openings to the surface and is overlaid by an uninterrupted layer of skin and scales (the latter sometimes partially reduced) lacking sensory pores. Species having this pattern are found in genera 1 to 5.

Three discrete derived states of parts or of all the lateral tabular-posttemporal and associated overlying tissues are found in genera 6 to 15. In the species of the genera of this group there occurs a reduced anterior aperture to the otic canal of the lateral tabular in contrast to the wide anterior opening found in the species of genera 1 to 5. Congruent with this change in the aperture is a reduction in the posterodorsal slope

of the otic canal in the lateral tabular to a more nearly horizontal or a posteroventral slope.

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. 11; a further modification of this sensory canal pattern, unique to a group of species in the genus *Hephaestus*, is discussed below). Congruent with the distribution of these derived states of the lateral tabular in genera 7 to 15 are derived states of the posttemporal and overlying tissues. These genera share a posttemporal of radically different morphology from 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 these genera have a large plate of bone that extends posteroventrally to cover both the posttemporal-supracleithral articulation and the dorsal region of the latter bone. Furthermore the posttemporal in the species of these genera terminates posteriorly in a broad serrate edge that extends through the skin to 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 genera 7 to 15 is much longer and also has a series of lateral openings. These genera (7 to 15) also share a ventral shift in the level of the articulation between the posttemporal and the supracleithrum.

Associated with these modifications in osteology are changes in the overlying tissues. In contrast to the uninterrupted skin and scale covering over the lateral tabular and posttemporal found in genera 1 to 6, the species of genera 7 to 15 have a reduction in the scalation, the development of a series of sensory pores that communicate with the lateral openings of the posttemporal part of the otic sensory canal and a protrusion of the posterior edge of the posttemporal through the skin.

The remaining posttemporal and lateral tabu-

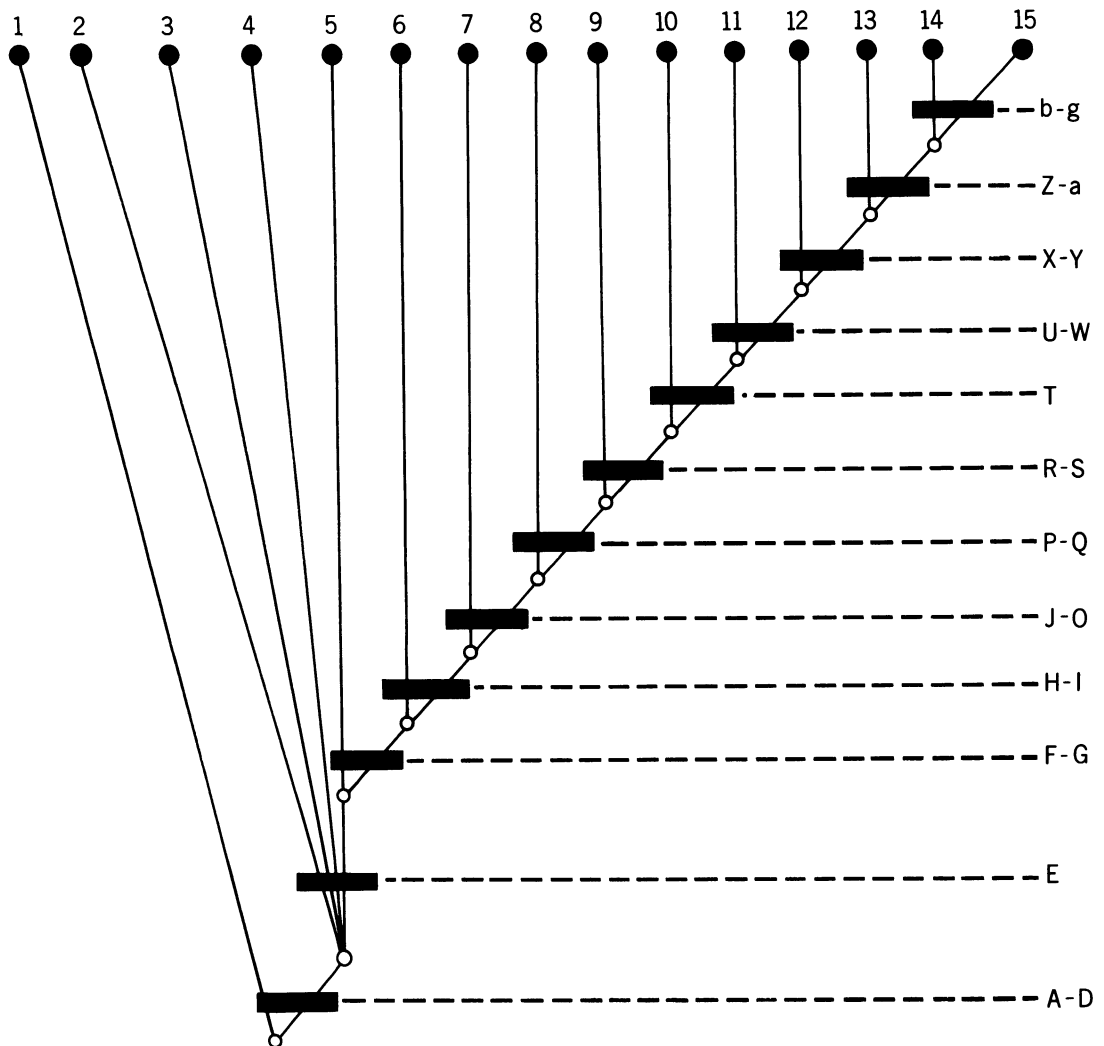


FIG. 9. Cladogram of the most parsimonious hypothesis of relationships in the family Teraponidae based on 33 synapomorphies. Apomorphic characters defining the genera (1 to 15) are discussed in the text. Taxa (solid circles): 1, *Leiopotherapon*; 2, *Amniataba*; 3, *Hannia*; 4, "*Terapon*"; 5, *Lagusia*; 6, *Pelates*; 7, *Terapon*; 8, *Pelsartia*; 9, *Rhyncopelates*; 10, *Mesopristes*; 11, *Hephaestus*; 12, *Bidyanus*; 13, *Scortum*; 14, *Pingalla*; 15, *Syncomistes*. Synapomorphies: A, extrinsic swimbladder muscle; B, transversely divided swimbladder; C, third pharyngobranchial process; D, urohyal form; E, two spines on first proximal dorsal pterygiophore; F, longitudinally striped body pigmentation or a pattern derived from it; G, foramen in third preparaphypural hemal arch; H, extrinsic swimbladder muscle with an origin on rear of skull; I, reduction in anterior aperture of lateral tabular sensory canals, posterodorsal slope of otic canal in lateral tabular reduced; J, extrinsic swimbladder muscle with a direct origin on rear of skull; K, expanded serrate posttemporal, ventral shift in posttemporal-supracleithral articulation; L, lengthening of posttemporal sensory canal with development of lateral openings; M, vertical orientation of portion of supratemporal commissure in lateral tabular; N, reduction in scale covering over posttemporal with development of sensory pores; O, two or more rows of scales in basal dorsal sheath; P, two or more rows of full-sized scales in basal dorsal sheath; Q, three

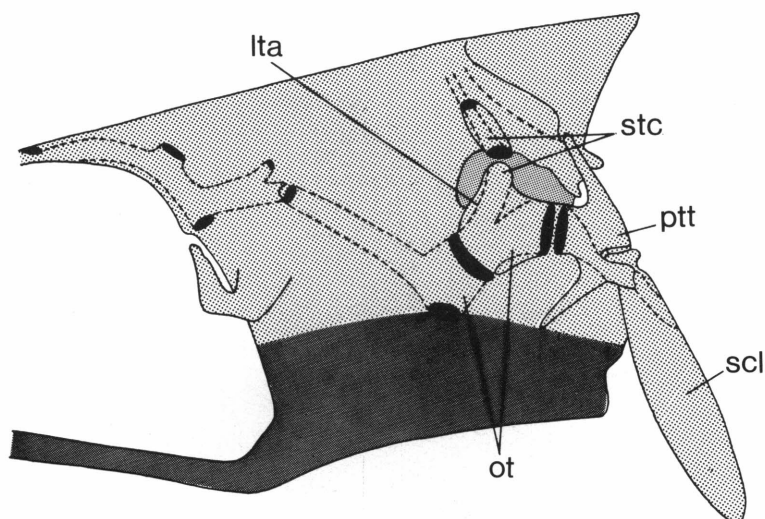


FIG. 10. Diagrammatic drawing of lateral tabular, posttemporal, and supracleithrum in *Leiopotherapon unicolor*.

lar modifications within the family are found in the species placed in 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 postero-dorsally (as in genera 1 to 6) or vertically (as in genera 7 to 11a and 12 to 15) is oriented posteroventrally and contacts the otic canal of the lateral tabular at the posterior edge of the bone. This results in a lateral tabular sensory canal pattern of a posteriorly pointing "V" with the apex contacting the anterior edge of the posttemporal part of the otic canal (fig. 12). The posttemporal in species of this group has 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 sufficiently different from that of other teraponids that various workers have not properly

homologized the bone. Trewavas (1940) followed by Munro (1964, 1967) described the posttemporal in *Terapon* (= *Hephaestus*) *adamsoni* as nonserrate and not exposed, whereas examination of the holotype has shown the posttemporal to be both serrate and exposed. Similarly Weber (1910) and Weber and deBeaufort (1931) described the posttemporal of *Terapon habbema* (= *Hephaestus trimaculatus*) as not exposed, a statement found to be incorrect based on the examination of syntypes.

Data on the posttemporal and tabular anatomy of teraponids may be summarized as follows: (1) The primitive condition of these bones in the family is an unelaborated posttemporal, a lateral tabular with sensory canals in contact at the anterior edge of the bone (fig. 10) overlaid by 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

to six rows of scales in basal anal sheath; R, posterior vertical edge of supraoccipital straight or posteriorly bowed; S, cleithrum lacking a deep posterodorsal notch (polarity undetermined); T, uniform adult body coloration; U, intestinal pattern with six loops, anterior loops to the left of the median body plane; V, freshwater ecology; W, decreased number of epipleural ribs (polarity undetermined); X, depressible dentition; Y, 11+14 vertebral formula; Z, flattened teeth; a, reduced symphyseal dentary process; b, highly complex intestinal convolution pattern with large amount of looping to left of median body plane; c, outward rotation of dentary; d, lack of symphyseal dentary process; e, highly depressible and flattened teeth; f, reduction to two distinct rows of teeth or to a row and a narrow distinct band in each jaw; g, swimbladder constriction secondarily reduced.

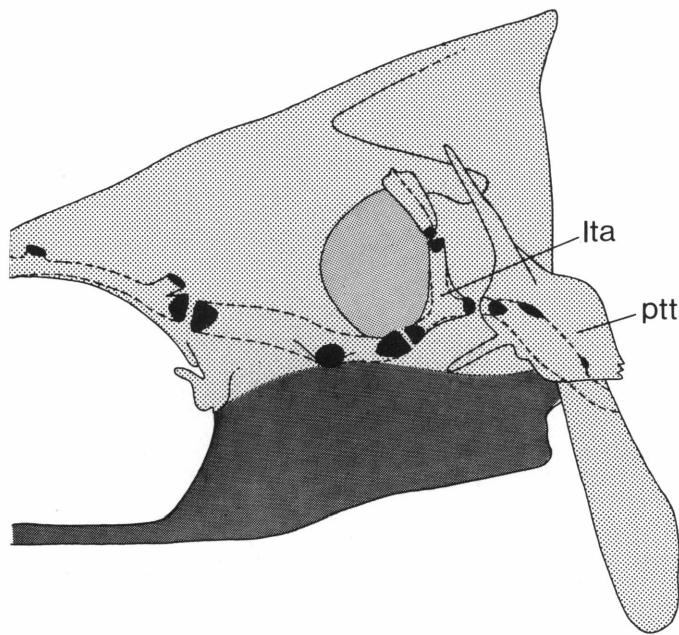


FIG. 11. Diagrammatic drawing of lateral tabular, posttemporal, and supracleithrum in *Terapon jarbua*.

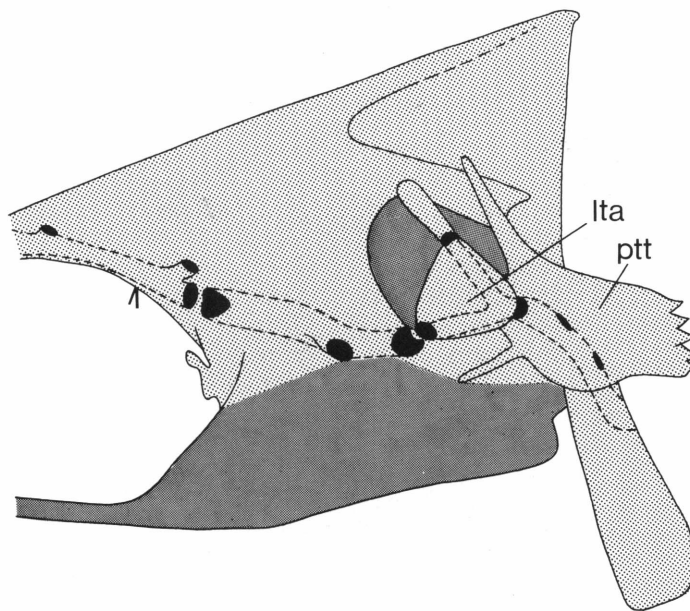


FIG. 12. Diagrammatic drawing of lateral tabular, posttemporal, and supracleithrum in *Hephaestus trimaculatus*.

conditions of a reduced anterior 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 group; (3) genera 7 to 15 form a monophyletic unit based on the common possession of an expanded 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 the overlying region; (4) assemblage 11b (*Hephaestus* in part) is hypothesized to be monophyletic based on possession of a further 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 with several character states within the family is the height of the scaly sheath at the base of the dorsal and anal fins. The scaly sheath at the base of the spinous dorsal is clearly

discernible posterior to the second or third dorsal spines and surrounds the base of this and succeeding spines, forming a furrow into which the heteracanth dorsal spines are partially depressible. In many species the sheath is separated from the body scalation by a distinct line of scaleless skin, but is less distinct in other species, particularly those with a reduction in the relative dorsal spine lengths. In the species of genera 1 to 6 (fig. 13) the dorsal sheath consists of only one row of uniformly shaped and sized scales. In contrast the species of genera 7 to 15 possess two rows of scales in the basal dorsal sheath with two states of this sheath type found in these genera. In genus 7 (*Terapon*) the sheath consists of two rows of different sized scales; a dorsal row of fully sized scales and a ventral row of vertically narrower scales. This pattern is intermediate to that of genera 8 to 15 in which the dorsal fin sheath consists of two or more rows of fully sized scales (fig. 14). (*Syncomistes trigonicus* [some specimens], *S. kimberleyensis* [known only from juveniles], *Pingalla gilberti*, and *P. lorentzi* within these genera appear to have a

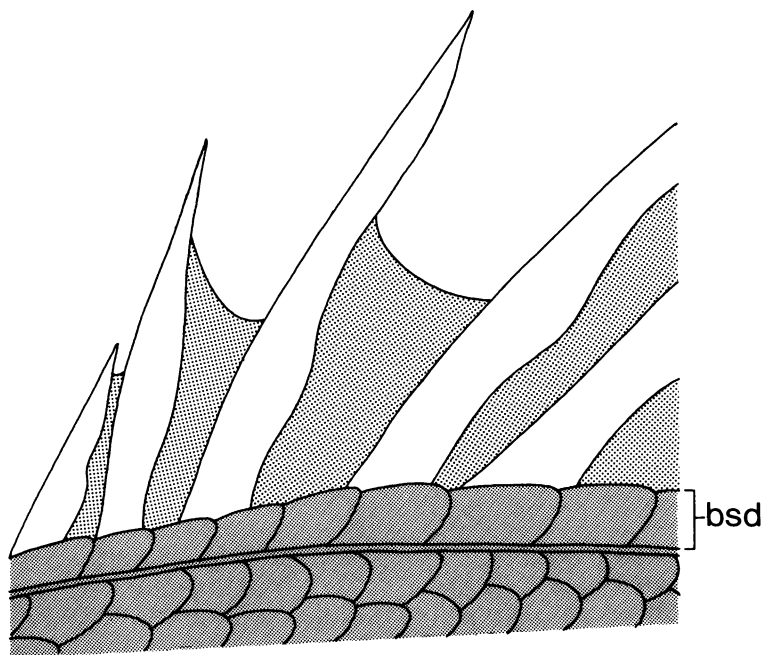


FIG. 13. Diagrammatic illustration of lateral view of the basal dorsal sheath in genera 1 to 6.

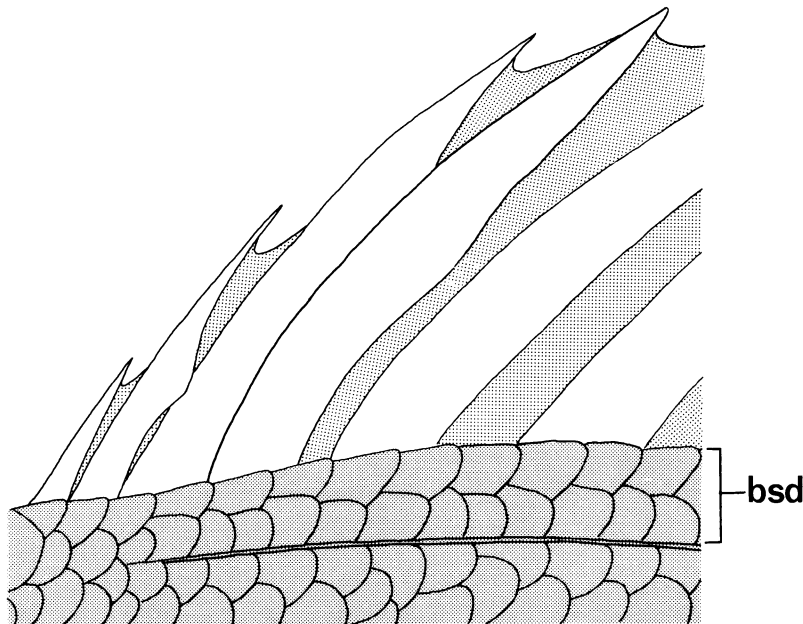


FIG. 14. Diagrammatic illustration of lateral view of the basal dorsal sheath in genera 7 to 15.

secondary reduction of the dorsal fin sheath to two irregular rows.)

Congruent with this increased dorsal fin sheath height is a similar though not so distinct an increase in the height of the sheath at the base of the spinous anal fin. The species of genera 1 to 7 have an anal sheath of two or three rows, whereas those of genera 8 to 15 have three to six rows (with the exception of *Hephaestus adamsoni* [genus 11b] which has two or three rows). Outgroup comparisons indicate that the lack of dorsal and anal fin sheaths is the plesiomorph condition for the Percoidei. Thus the increasing sheath heights within the family would appear to be increasingly apomorphic states, a hypothesis supported by the ontogenetic increase in the number of scale rows for many species.

The information on dorsal and anal sheath heights in the Teraponidae 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 and that of the anal fin sheath is two or three rows of scales as found in genera 1 to 7; (2) the derived condition of the dorsal sheath is two or more rows of scales found in genera 7 to 15; (3) genera 8 to 15 share both a

derived anal sheath height of three to six scale rows and a derived dorsal sheath height of two or more rows of fully sized scales.

Intestinal Patterns. Within the family Teraponidae four intestinal patterns of increasing complexity occur, being evidently related to the various diets of members of the family. The simplest intestinal convolution pattern consists of only two loops (fig. 15A). From the stomach, the intestine proceeds posterior to the rear of the body cavity where it makes a complete turn, then continues forward to a point ventral to the stomach where a second complete reversal in direction occurs after which it runs posteriorly to the anus. In the species with this convolution pattern all intestinal loops are either in the median body plane or to the right of it. The above intestinal pattern occurs in the adults of the majority of species in the family, being the adult convolution pattern of the species of genera 1 to 10. It is also the juvenile pattern for the species of genera 11 to 13. Ontogenetically in the species of these genera (excluding 11b) there occurs an elongation and folding of the juvenile intestinal pattern to produce the more complex pattern shown diagrammatically in figure 15B.

This pattern is derived from the juvenile pattern by a forward infolding and elongation of the first intestinal loop and a secondary folding over on itself of the resultant intestinal segment. As a consequence of this intestinal elongation and folding, there is an ontogenetic shift in the convolution pattern from the two loops found in genera 1 to 10 to six loops present at some point in development in genera 11 to 15 (genera 14 and 15 undergo a further ontogenetic shift, see below). Associated with this increased convolution is a shift of the anterior intestinal loops around the ventral surface of the stomach to the left of the median body plane which contrasts with the simpler pattern described above in which such looping to the left side of the body is lacking.

The species of genera 14 and 15 have further modifications of the second intestinal pattern. Juveniles of the species in these genera have an intestinal convolution pattern similar to that of the adults of genera 11 to 13 (probably also passing through the pattern of convolutions similar to those of genera 1 to 10 earlier in ontogeny). During development a further elaboration of the intestinal pattern results in a pattern shown diagrammatically in figure 15C. This pattern is derived from the juvenile pattern of these species (the adult pattern of species of genera 11 to 13) by a ventral shift of the first loop after the stomach and a further elongation of the anterior intestinal loops which fold back on themselves. Species with this adult pattern have highly developed loops curling around the ventral and left sides of the stomach and a greater percentage of the intestine to the left of the median body plane than in any other species in the family. The final and most complex intestinal pattern in the family is autapomorphic to the species of genus 15 (*Syncomistes*) which undergo a further elongation and elaboration of the above pattern (the adult convolution pattern for *Syncomistes kimberleyensis*, which is known only from juvenile material, is unknown). This highly elongate and convoluted pattern may be an adaption for the digestion of filamentous algae, the main food of the species in this genus.

Data on intestinal patterns in teraponids can be summarized as follows: (1) The plesiomorph adult intestinal pattern is one of two loops both to the right of or in the median body plane and

occurs in genera 1 to 10; (2) a pattern of six loops or a pattern derived from it and with looping to the left of the median plane is apomorphic with respect to the above and occurs in genera 11 to 15; (3) a further elaboration of this last pattern characterized by a greater number of loops and increased looping around the ventral surface of the stomach characterizes genera 14 and 15, with genus 15 having a highly developed pattern unique to it in the family.

Extrinsic Swimbladder Muscle Forms. Four different forms of swimbladder muscle differing in both origin and overall shape are found in the

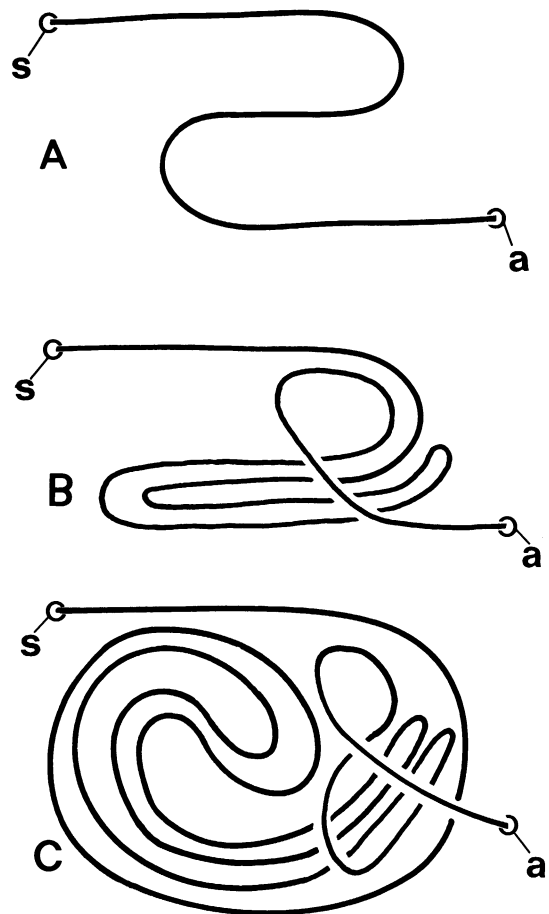


FIG. 15. Diagrammatic illustration of the major intestinal convolution patterns in the Teraponidae. A, pattern of genera 1 to 10 and 11b; B, pattern of genera 11a, 12 and 13; C, pattern of genera 14 and 15; a, anus; s, stomach.

family: (1) A cylindrical muscle with an origin limited to the ventral process of the posttemporal (fig. 16); (2) a flattened muscle with a direct muscular attachment to the ventral process of the posttemporal and a ligamentous attachment to the pterotic (fig. 17); (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. 18); (4) a slightly flattened muscle with an origin limited to the lateroventral edge of the pterotic (fig. 19). 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. 16). 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 17. As in the muscle form of genera 1 to 5,

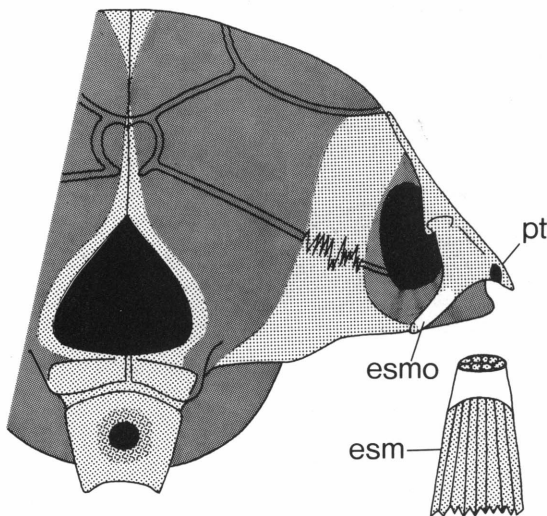


FIG. 16. Diagrammatic view of the rear of the skull, showing extrinsic swimbladder muscle form and origin in genera 1 to 5.

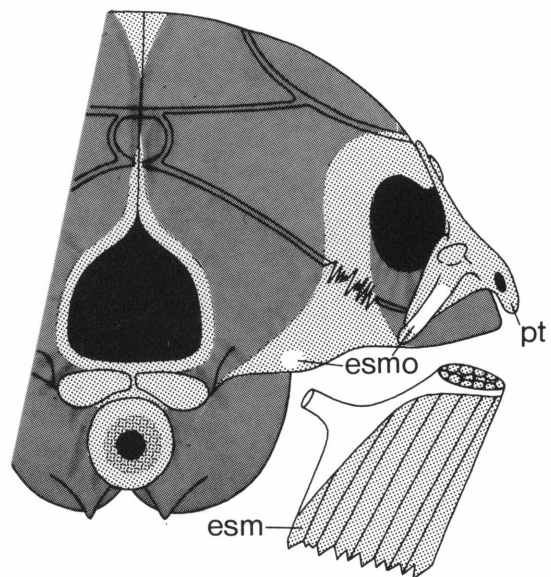


FIG. 17. Diagrammatic view of the rear of the skull, showing extrinsic swimbladder muscle form and origin in genus 6.

this muscle has a direct muscular attachment limited to the ventral process of the posttemporal; an origin which differs, however, in having a broader horizontal area on the posttemporal. More notably, this form of extrinsic swimbladder muscle has an additional separate ligamentous origin on the rear of the skull. This second origin is in the form of a connective tissue band arising from the rear of the skull and joining the main muscle mass on its medial surface.

Ontogenetically in this form of the extrinsic swimbladder muscle there occurs a change in the relative sizes of the main muscle mass and the ligamentous band. In smaller specimens of *Pelates sexlineatus*, the ligamentous band is much smaller relative to the main part of the muscle than in the adult condition. Such a developmental change in the relative sizes of the two muscle origins is consistent with a hypothesis of a later developmental and consequently phylogenetic appearance of the ligamentous origin. As such, the ligamentous tissue band is considered to be a derived character state of the extrinsic swimbladder muscle and genera 6 to 15 which share the presence of this muscle form or a 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 extrinsic swimbladder muscle to the rear of the skull. However, the muscle in the species of these genera differs from that in genus 6 in having a direct muscular attachment to both the rear of the skull and the ventral process of the posttemporal (species of genus 11b [*Hephaestus* in part] lose the latter origin, see below). The extrinsic swimbladder muscles in the species of these genera are distinctly flattened with a broad attachment along the proximal half of the ventral process of the posttemporal and the posterior border of the pterotic (the muscle origin extends medially as far as the basioccipital in *Rhyncopelates oxyrhynchus* [genus 9]).

Among species with this form of extrinsic swimbladder muscle, an ontogenetic transition from a muscular band with an origin limited to the ventral process of the posttemporal to the adult muscle form described above occurs in *Terapon jarbua* (genus 7). This transition is consistent with a hypothesis that an extrinsic swimbladder muscle with a direct muscular origin on

both the posttemporal and pterotic is apomorphic with respect to the muscle form in genera 1 to 5 (origin limited to posttemporal). 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 rear of the skull, rather than arising by way of a ligamentous band, and that the proximal medial and lateral connective tissue bands found on the extrinsic swimbladder muscles in these genera (7 to 15) are homologous with the ligamentous band and proximal connective tissue sheath found in the muscle form of genus 6 (the latter also occurring in genera 1 to 5).

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 the adults has an origin limited to the rear of the skull (fig. 19). This origin contrasts with that of the muscles of all other species of the family which have at least a partial attachment to the ventral process of the posttemporal. Based on ontogenetic information, this muscle form ap-

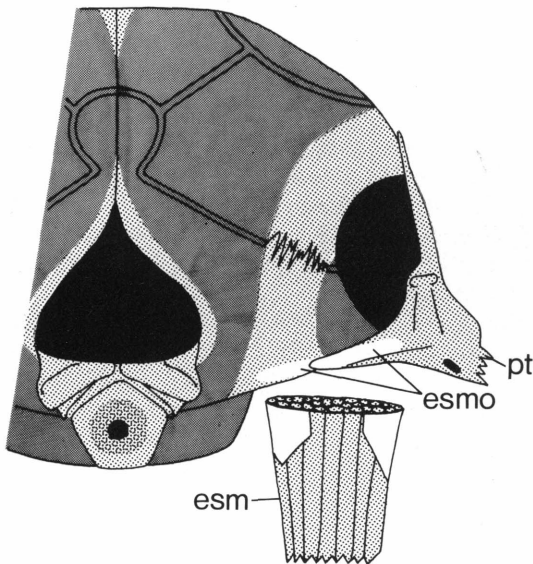


FIG. 18. Diagrammatic view of the rear of the skull, showing extrinsic swimbladder muscle form and origin in genera 7 to 11a, and 12 to 15.

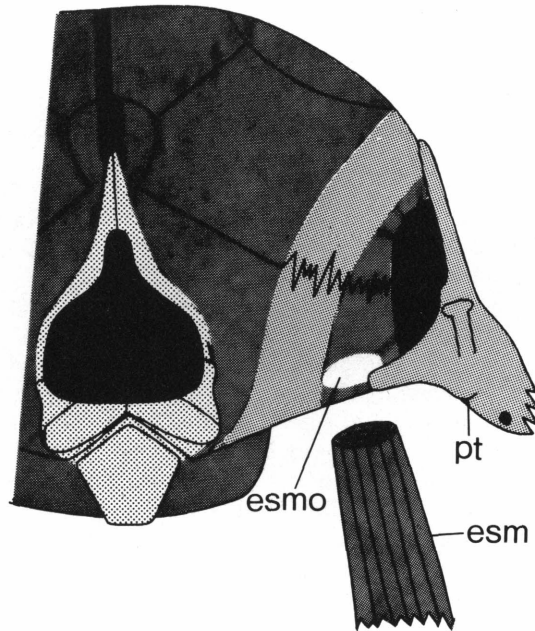


FIG. 19. Diagrammatic view of the rear of the skull, showing extrinsic swimbladder muscle form and origin in genus 11b.

pears to be derived from that found in the other species in genera 7 to 15. In very small individuals of *Hephaestus trimaculatus*, there has been found a partial origin of the muscle on the ventral process of the posttemporal; an attachment which is lost ontogenetically as no adults have been found with this condition. Such an ontogenetic shift is congruent with a hypothesis that the muscle form of genus 11b is apomorphic to that of the other species of genera 7 to 15 and an autapomorphy of the group.

Information on teraponid extrinsic swimbladder muscle forms is summarized below:

(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 is found in genera 1 to 5.

(2) Derived forms of extrinsic swimbladder muscles in the family have attachments to both the posttemporal and the rear of the skull at some point during ontogeny. The possession of such muscle forms unites the species of genera 6 to 15 into a monophyletic group. Within these genera three distinct muscle types are found with such an origin (in order of increasing apomorphy):

(A) An extrinsic swimbladder muscle with a direct muscular origin on the ventral process of the posttemporal and a ligamentous origin on the rear of the skull. Such a muscle form is found in genus 6.

(B) An extrinsic swimbladder muscle with a direct origin from both the ventral process of the posttemporal and the rear of the skull throughout life. Found in genera 7 to 11a and 12 to 15.

(C) Extrinsic swimbladder muscles with an origin limited to the rear of the skull in adults. Autapomorphic to genus 11b.

Pigmentation Patterns. Teraponids are noteworthy for the variety of pigmentation patterns that occur in the family both ontogenetically and interspecifically. Studies have shown these patterns to fall into four main groups: (1) A vertically barred pattern; (2) a uniform pigmentation derived from a vertically barred pattern; (3) a longitudinally striped pattern derived from a barred pattern; (4) a uniform pigmentation derived from a striped pattern.

Although ontogenetic information is lacking for some species (to be discussed below), the data presently available does allow us to erect a

hypothesis of the phylogenetic sequence of 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 converts to a uniform pigmentation in the adult (uniform in lacking any marked pattern). A transition from barred juveniles to uniform adult coloration occurs in *Leiopotherapon plumbeus* (Blanco and Villoid, 1951), *L. aheneus* (Mees, 1971), *Amniataba caudavittatus* (Taylor 1964), *Leiopotherapon unicolor* (personal observ.) and *Hannia greenwayi* (personal observ.). However, the variation that exists in the pigmentation forms among these species having this kind of uniform adult pigmentation is sufficient to make the character somewhat ambiguous (e.g., whether the pattern of spots superimposed on a uniform ground coloration in *Amniataba caudavittatus* should be considered uniform). Furthermore, lacking a definite sister group to the Teraponidae, it is not presently possible to determine whether the transition from a juvenile barred coloration to a uniform adult pigmentation is plesiomorphic for the Teraponidae, with the presence of bars in the adults of *Amniataba percoides* and some *A. caudavittatus* a secondary reversal, or if the pigmentation of the latter species is plesiomorphic in the Teraponidae with the uniform coloration of the remaining species in genera 1 to 4 derived.

A second pigmentation pattern in teraponids directly derived from and hypothesized to be apomorphic to a barred pattern is that of horizontal stripes. Horizontal stripes are the adult pigmentation for the species of genera 5 to 9 (modified in some species), and the juvenile pigmentation pattern for many of the species of genera 10 to 15. A developmental shift from juvenile bars or bars and stripes to adult stripes has been recorded for *Pelates quadrilineatus* (Day, 1878), *Terapon theraps* (Day, 1878; Weber 1910; personal observ.), *Terapon puta* (Day, 1878) and has been observed in *Pelates sexlineatus*. *Terapon jarbua*, which has a juvenile pattern of elongate disconnected pigment blotches that join together ontogenetically to form curved bands, also has in the juveniles irregular vertical connections forming incomplete vertical bars; connections that are lost with age. Finally, *Pelsartia humeralis* has a juvenile pattern of verti-

cal bars that is modified ontogenetically into an interrupted longitudinal stripe.

The remaining type of adult pigmentation in the Teraponidae is a uniform adult body coloration derived from a striped juvenile pattern, a coloration found in genera 10 to 15. Species having juvenile stripes but uniform adult coloration are *Mesopristes argenteus* (Day, 1878; Weber and deBeaufort, 1931), *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), *Pingalla gilberti* (personal observ.), *Syncomistes butleri* (personal observ.), and *S. trigonicus* (personal observ.). Furthermore, *Syncomistes kimberleyensis*, known only from juveniles, has a striped pattern and probably undergoes a transition to uniform coloration, as in its sister species, as would *Hemphaestus suavis*, a species also known only from small specimens with stripes and bars but whose sister species are uniform.

Based on these ontogenetic shifts, it is hypothesized that a uniform adult coloration derived from stripes is apomorphic with respect to a striped adult coloration. The latter in turn is considered to be derived from a more plesiomorphic barred pattern. One species uniform as an adult, *Hephaestus trimaculatus* (genus 11), undergoes both transitions, from a barred to a striped pattern and then to a uniform coloration.

For certain species, however, information is lacking on the ontogenetic pigmentation changes, if any, that occur in juveniles. Until such time as information becomes available for those species, their ontogenetic pigmentation shifts are assumed to be congruent with those of other species having congruent distributions of apomorphic states of other characters.

Species so placed include *Leiopotherapon macrolepis* and "*Terapon*" *jamoerensis* placed with species having uniform coloration directly derived from bars; *Lagusia micracanthus* which is striped as an adult; *Hephaestus carbo* and *Pingalla lorentzi* whose sister species undergo a shift from a striped juvenile to uniform adult coloration, and the species of genera 11a, 12, and 13 (the young of *Hephaestus jenkinsi* [genus 11a] and *Bidyanus bidyanus* [genus 13] have partial longitudinal vermiculations).

On the basis of the above information, the phylogenetic sequence of the pigmentation patterns can be hypothesized and summarized as follows:

- (1) A vertically barred pattern is plesiomorphic for teraponids.
- (2) Two patterns directly derived ontogenetically from bars are found in the family:
 - (A) A uniform coloration found in species of genera 1 to 4 (with the exception of *Anmiataba percoides* and some individuals of *A. caudavittatus*). However, it is not presently possible to determine whether this is apomorphic within the Teraponidae due to a lack of a definite sister group to the family.
 - (B) A striped pattern found in genera 5 to 9; a pigmentation considered apomorphic with respect to bars.
- (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 with multiple character states in the family analyzed at this point is the number of precaudal and caudal vertebrae. As discussed in the Materials and Methods section, the distinction between precaudal and caudal vertebrae is made on the basis of the point of interdigitation of the fused pterygiophores of the first and second anal spines between the hemal arches of the spinal column. Table 2 illustrates the major differences in vertebral counts in the family; a change in the total number of vertebrae (an invariate number within a species, with rare exceptions) and within groups with a vertebral count, changes in the relative number of precaudal and caudal vertebrae. The majority of species have 25 vertebrae with the exception of two units considered monophyletic in this study: *Lagusia micracanthus*, the only member of genus 5, has 26 vertebrae, a count unique to this species in the family; and the species of genus 11b (*Hephaestus suavis*, *H. trimaculatus*, *H. adamsoni*, and *H. carbo*) have 27 vertebrae.

Lacking a definite sister group to the Teraponidae, it is not possible to know the plesiomorphic vertebral count for the family with certainty. However, a 10+15 vertebral formula (or the

TABLE 2
Vertebral numbers in the Teraponidae

| Genus | Species | Vertebrae | Vertebral Formula | | | | |
|-------------------------|--------------------|-----------|-------------------|-------|-------|-------|-------|
| | | | 10+15 | 10+16 | 10+17 | 11+14 | 11+16 |
| <i>Leiopotherapon</i> | <i>L. unicolor</i> | 25 | — | — | — | X | — |
| | all others | 25 | X | — | — | — | — |
| <i>Amniataba</i> | all | 25 | X | — | — | — | — |
| " <i>Terapon</i> " | all | 25 | — | — | — | X | — |
| <i>Hannia</i> | all | 25 | X | — | — | — | — |
| <i>Lagusia</i> | all | 26 | — | X | — | — | — |
| <i>Pelates</i> | all | 25 | X | — | — | — | — |
| <i>Pelsartia</i> | all | 25 | X | — | — | — | — |
| <i>Rhyncopelates</i> | all | 25 | X | — | — | — | — |
| <i>Mesopristes</i> | all | 25 | X | — | — | — | — |
| <i>Hephaestus</i> (11a) | all | 25 | X | — | — | — | — |
| <i>Hephaestus</i> (11b) | <i>H. carbo</i> | 27 | — | — | X | — | — |
| | all other 11b | 27 | — | — | — | — | X |
| <i>Bidyanus</i> | all | 25 | — | — | — | X | — |
| <i>Scortum</i> | all | 25 | — | — | — | X | — |
| <i>Pingalla</i> | all | 25 | — | — | — | X | — |
| <i>Syncomistes</i> | all | 25 | — | — | — | X | — |

similar 10+14 formula) has been considered by various authors (e.g., Gosline, 1966; Haedrich, 1967) to be a basal perciform vertebral count. This hypothesis is consistent with both the distribution of vertebral counts in the Teraponidae and the distribution of the other characters in the group.

Variation in the relative number of precaudal and caudal elements occurs both in groups of species having 25 vertebrae and those with 27. Genus 11b (*Hephaestus* in part) is distinguished from all other members of the family by its vertebral count of 27 among other apomorphic character states. Three species in this group (*Hephaestus trimaculatus*, *H. adamsoni*, and *H. suavis*) have 11+16 vertebrae and one (*H. carbo*) has 10+17 vertebrae. On the basis of the presence of 10 precaudal vertebrae in the outgroups-genus 11a and genus 10 which is the plesiomorph sister group to the assemblage formed by genera 11 to 15, it is most parsimonious to hypothesize the 11+16 vertebral count as synapomorphic for these three species of *Hephaestus*.

Among the species having 25 vertebrae, the majority have a 10+15 vertebral formula with the exception of the species of genera 12 to 15 which have a 11+14 vertebral formula as does

one species in genus 1 (*Leiopotherapon unicolor*) and one in genus 4 ("*Terapon*" *jamoerensis*). If the previously advanced hypothesis of a 10+15 vertebral count being plesiomorph among perciform fishes is correct, then the 11+14 count found in these species is apomorphic. However, whereas the higher caudal count in genera 12 to 15 is congruent with a series of character states considered apomorphic in this study, the increased precaudal counts of *Leiopotherapon unicolor* and "*Terapon*" *jamoerensis* appear to be convergent with each other and with the species of genera 12 to 15. These species differ from each other in the lack in *L. unicolor* of several derived characters uniting "*T.*" *jamoerensis* to the other species of genera 2 to 15. Both of these species in turn lack a series of apomorphic osteological, myological, intestinal, pigmentary and other characters found in genera 12 to 15. Consequently, it is most parsimonious to assume that the 11+14 vertebral count is convergent within the family.

PHYLOGENETIC ANALYSIS

The family Teraponidae (genera 1 to 15) as discussed in detail previously has unique forms of

the extrinsic swimbladder muscle, swimbladder, urohyals, and third pharyngobranchial that support the hypothesis of the monophyletic nature of the group (*Datnioides* and *Pseudohelotes* are excluded for the reasons discussed previously). The phylogenetic analysis carried out within the family has defined 15 lineages herein considered genera (see fig. 9). The relationships between these lineages and the characters defining them are discussed in detail below.

GENUS 1, *LEIOPOTHERAPON*

Four species are recognized in genus 1, *Leiopotherapon*: *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.

All species of genus 1 have 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 for teraponids on the basis of both in- and outgroup comparisons (see discussion of this character under genus 2, *Amniataba*). An additional character shared by all four species of the genus is the insertion of the first proximal dorsal pterygiophore between the second and third neural spines rather than between the first and second as in the majority of other teraponid genera. However, as a consequence of the lack of a definite sister group to the Teraponidae, it is not 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. 20). Such an insertion is apomorphic with respect to the primitive perciform condition of one proximal pterygiophore inserting between successive neural spines and as such supports the hypothesis of the monophyletic nature of the genus *Leiopotherapon*. Both this character and the insertion of the dorsal fin in a posterior position with respect to

the neural spines appear to have risen independently in genera 11 and 15 (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 one spine on this element in species of genus 1. Outgroup comparisons and literature information (Smith and Bailey, 1961) support the hypothesis that one spine on the first proximal dorsal pterygiophore is the plesiomorph condition among perciforms. Such a hypothesis is also supported by the changes in the myology of the spine erectors and depressors associated with the spines of the first proximal dorsal pterygiophore. In the transition from one to two spines on this element, the second spine is added anterior to the original spine which retains its position relative to the lateral strut. In such a transition, the muscles activating the *de novo* spine would separate the erector of the second spine (the plesiomorphic first spine) from an origin on the rear of the third predorsal, with the origin shifting to the first proximal dorsal pterygiophore, the condition in various teraponid species examined in genera 2 to 15. In contrast, if the polarity of the transition were actually the opposite, then one would expect the erectors of the first spine (the plesiomorph second spine in such a system) to be limited to the first proximal dorsal pterygiophore, a condition not occurring in genus 1. Thus, two spines on the first proximal dorsal pterygiophore is considered apomorphic, uniting the species of genera 2 to 15 into a monophyletic unit.

Three processes by which an increase in spines on the first proximal dorsal pterygiophore could be achieved were discussed by Smith and Bailey (1961). The first, a fusion between the two primitively antermost proximal dorsal pterygiophores into a single element bearing two spines, was rejected by those authors and is also rejected here as a mechanism in the Teraponidae. In such a fusion, the resultant first proximal dorsal pterygiophore would have two full lateral struts,

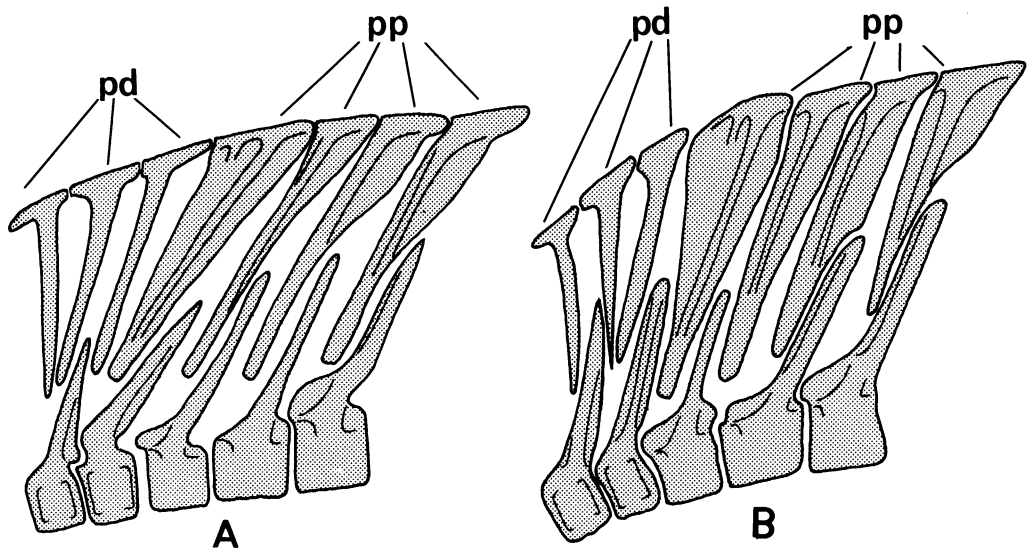


FIG. 20. Diagrammatic drawing, showing relationships between predorsals, anterior proximal pterygiophores and anterior neural spines in teraponids. A, pattern of genera 2 to 10 and 12 to 14; B, pattern of genera 1, 11, and 15 (*Hephaestus adamsoni* [genus 11b] has a further backward shift in the dorsal fin position).

whereas the first spine on the first proximal pterygiophore of teraponids with two spines on the element lacks or has a small strut associated with it. Furthermore, in such a fusion there would occur a backward shift in the position of the dorsal origin relative to the neural spines (unless the more complicated forward shift of the entire fin takes place); a hypothesis inconsistent with the relative positions of the dorsal fin in genus 1 contrasted to genera 2 to 15.

The second method discussed by Smith and Bailey for the development of two spines on the first proximal dorsal pterygiophore involves a backward shift of the first spine to the second spine-bearing proximal pterygiophore resulting in two spines on the second element and an additional predorsal. Although such a shift may occur in other groups, it is rejected as a mechanism in the teraponids for several reasons. First, the number of predorsals is constant in the family at three in contrast to the increase to four predicted under the above mechanism. Second, in such a shift, there would be a backward shift of the dorsal origin relative to the neural spines; a shift that is not evident in the Teraponidae.

The third method discussed by Smith and Bailey was a *de novo* formation of a new dorsal pterygiophore. Although rejected by these authors as a generalized method, it appears to be the mechanism among teraponids. This hypothesis is supported by the observed presence of supernumerary spines as an individual variation in the Teraponidae (in which two rather than one, or three rather than two spines are present). In these individuals, as predicted by a model of *de novo* spine formation, there is neither an increase in the number of 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 associated with the first spine of the first proximal pterygiophores 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 be shown to constitute 1 to 3 dichotomies plesiomorphic to the assemblage formed by genera 5 to 15 (such resolution being dependent on 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 group is recognized at a generic level. The numbering of these genera (2 to 4) is arbitrary and as such does not indicate any hypothesized relationship between these genera or between any one of them and the rest of the family. Since there is no supraspecific category in which one of them, the previously undescribed *greenwayi*, can be placed, a new generic term, *Hannia*, has been created to contain it.

GENUS 2, *AMNIATABA*

Two species are placed in genus 2, *Amniataba*: *A. percoides*, a common species of the fresh waters of the northern two-thirds of Australia,

and *A. caudavittatus*, found in marine, brackish, and fresh waters of northern and western Australia and southern New Guinea. These species are hypothesized to form a monophyletic group on the basis of their common possession of a distinctive form of caudal mottling (see figs. 36 and 38). In addition the retention of vertical bars in *A. percoides* and some individuals of *A. caudavittatus* may represent a further apomorphic character uniting these species (see discussion on coloration shifts in the family).

GENUS 3, *HANNIA*, NEW GENUS

Hannia contains one species, *Hannia greenwayi*, in this reconstruction. This previously undescribed form is known only from the type locality in the Hann River of Western Australia. A combination of very low lateral line counts and the presence of two spines on the first proximal dorsal pterygiophore serves to distinguish this species in the family.

GENUS 4, "TERAPON"

Genus 4, "Terapon" contains one species, "T". *jamoerensis* from Lake Jamoer in southern

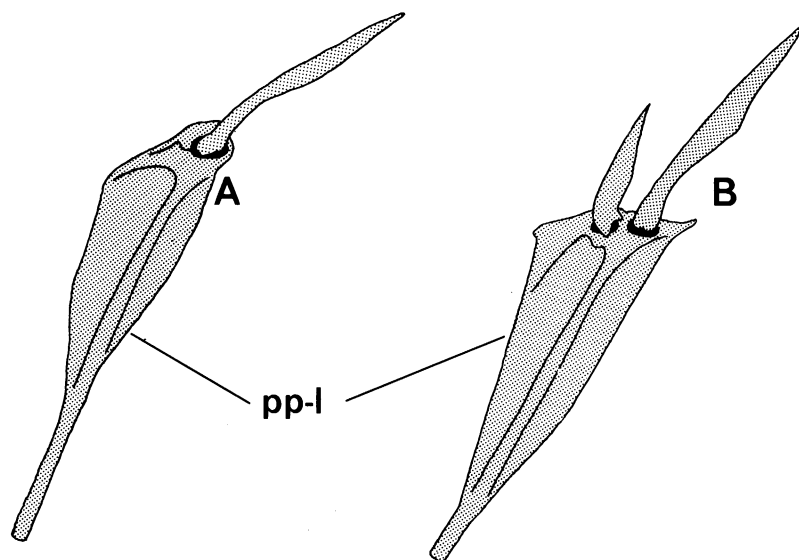


FIG. 21. Diagrammatic drawing of the first proximal dorsal pterygiophore and associated spines in the family. A, condition in genus 1; B, condition in genera 2 to 15.

West Irian, New Guinea. For the reasons discussed previously 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*, but in this restricted sense 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 genera share a striped pigmentation pattern derived from bars or a pattern secondarily derived from stripes. This contrasts with a body pigmentation of vertical bars or uniform coloration derived directly from a barred pattern as found in genera 1 to 4. The presence of a adult striped pattern is therefore

considered apomorphic within the Teraponidae and indicative of the monophyletic nature of the group formed by genera 5 to 15.

In addition the species of these genera share the presence of a distinctive passage for blood vessels in the hemal canal of the third hemal arch anterior to the paraphypural (fig. 22). In genera 1 to 4, the passageway is not enclosed, resulting in a notch in the hemal arch wall. Genera 5 to 15 instead have an enclosed passageway forming a distinct foramen. The condition of the blood passageways in 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 perciformes would appear to be plesiomorphic. The presence of a foramen in this element is therefore considered apomorphic, supporting the hypothesis of the monophyly of the group formed by genera 5 to 15.

GENUS 5, *LAGUSIA*, NEW GENUS

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

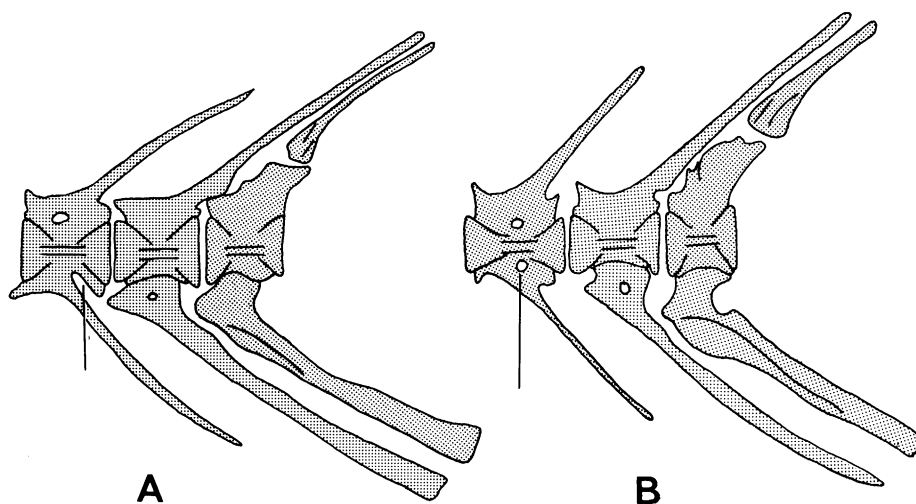


FIG. 22. Diagrammatic drawing of the hemal arches and blood vessel passages of the third preparahypural hemal arches. A, condition in genera 1 to 4; B, condition in genera 5 to 15.

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 previously discussed character states considered apomorphic within the Teraponidae. The first state is the presence of an extrinsic swimbladder muscle with origins both on the rear of the skull and the ventral process of the posttemporal at some point during life. The origin on the skull is either in the form of a ligamentous tissue band attaching independent of the main muscle mass or by a direct muscle attachment (figs. 17-19). This origin on the rear of the skull contrasts with an origin solely from the ventral process of the posttemporal that occurs 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 position of the otic sensory canal in the lateral tabular from a strongly posterodorsal slope to a horizontal or posteroventral slope, along with a reduction in the anterior aperture to the sensory canals of this bone.

GENUS 6, *PELATES*

In this study two species are recognized as members of *Pelates*: *Pelates quadrilineatus* (= *P. quadrilineatus* + *P. sexlineatus* of some previous authors) and *Pelates sexlineatus* (= *Helotes sexlineatus* of previous authors). These species share a prominent shoulder blotch (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). These species also have in common a parasphenoid which is dorsally bowed in the anterior orbital region, in contrast to the straight or ventrally bowed parasphenoid in other species of the family.

Genera 7 to 15: *Terapon*, *Pelsartia*,
Rhyncopelates, *Mesopristes*, *Hephaestus*,
Bidyanus, *Scortum*, *Pingalla* and *Syncomistes*

The common possession of a series of previously discussed characters unite the species placed in genera 7 to 15 into a monophyletic

group. All members of these genera possess a posteriorly expanded and serrate posttemporal that extends through the skin and bears a lengthened posttemporal sensory canal having lateral sensory openings (figs. 11, 12). This condition of the posttemporal contrasts with that found in genera 1 to 6 (fig. 10) in which the unexposed posttemporal has a small lateral process carrying a short sensory canal lacking lateral openings. Congruent with this change in posttemporal form is a reorientation of the section of the supratemporal commissure in the lateral tabular bone from a posterodorsal orientation to a vertical or posteroventral orientation (figs. 11, 12) and a ventral shift in the level of the posttemporal-supracleithral articulation.

The species of these genera also have markedly different extrinsic swimbladder muscles. The species of genera 7 to 15 have a direct muscular origin of the extrinsic swimbladder muscle on the rear of the skull (figs. 18, 19) in addition to the plesiomorph attachment of the extrinsic swimbladder muscle to the ventral process of the posttemporal at some point during development. Such a sonic muscle origin contrasts with the lack of contact of the extrinsic swimbladder muscle with the skull or a partial origin on the skull by means of a band of connective tissue in genera 1 to 6 (figs. 16, 17). Finally, as previously discussed, all species of these genera (7 to 15) have two or more rows of scales in the basal sheath 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* (subdivided by some workers into two species; see the discussion under that species), *T. theraps* and *T. puta*. These species share a series of derived states of various characters which distinguish them as one of the more distinctive groups in the family. The three species share strong, markedly elongate, lower opercular spines that extend well beyond the edge of the opercular lobe. In contrast in adults of other species in the family the lower opercular spine falls short of

or barely reaches the edge of the opercular lobe (some juveniles of *Pelates sexlineatus* have an opercular spine that barely extends beyond the edge of the opercular lobe).

A second character autapomorphic to 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. In other teraponids the penultimate spine is longer than, equal to, or not markedly shorter than, the ultimate. Furthermore among those groups of teraponids with the longest dorsal spines longer than the longest dorsal rays, only the species in *Terapon* have very short anal spines with the second spine subequal to or shorter than the third.

An autapomorphic pigmentary character also distinguishes the species of *Terapon*. All species of the genus have in common narrow oblique transverse bands across each lobe of the caudal fin, a condition that contrasts with the uniform or marbled pattern of most other species in 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).

Genera 8 to 15: *Pelsartia*, *Rhyncopelates*,
Mesopristes, *Hephaestus*, *Bidyanus*, *Scortum*,
Pingalla, and *Syncomistes*

The members of genera 8 to 15 possess a basal dorsal sheath consisting of two or more rows of equally sized scales. On the basis of outgroup comparisons and ontogenetic data this sheath height is considered to be derived with respect to the sheath of one or one and one-half scale rows present in genera 1 to 5. Furthermore, genera 8 to 15 have in common a basal anal sheath of three to six rows of scales rather than the two or three rows of scales in genera 1 to 7; an increase that is also considered to be apomorphic.

GENUS 8, *PELSARTIA*

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 can be distinguished by its unique coloration pattern (see the species description) and a distinctive distal up-

ward curl in the ventrolateral projections of the urohyal which contrast with the straight or slightly downward curling on these processes in other teraponids.

Genera 9 to 15: *Rhyncopelates*, *Mesopristes*,
Hephaestus, *Bidyanus*, *Scortum*, *Pingalla*,
and *Syncomistes*

Two characters are shared by and distinguish the members of genera 9 to 15. The first is an apomorphic state of the form of the posteromedian edge of the supraoccipital. In the species of genera 9 to 15, this section of the bone is either vertically straight or posteriorly bowed in contrast with the anteriorly undercut edge found in the species of genera 1 to 8. In the species of genera 9 to 15 there is an ontogenetic shift from an anteriorly undercut to a posteriorly straight or bowed supraoccipital. Thus the latter condition appears to be derived in teraponids and an apomorphy uniting genera 9 to 15 into a monophyletic group. An additional character having a distribution congruent with the above character but whose polarity cannot be presently determined is the form of the posterodorsal edge of the cleithrum. In all teraponids Baudelot's ligament runs from the basioccipital to the ventral edge of the supracleithrum just dorsal of the upper edge of the cleithrum. In the species examined in genera 1 to 8, the cleithrum has a bony process forming a notch in the posterodorsal profile of the bone and surrounding the ventral and posterior edges of the ligament at its contact with the supracleithrum (fig. 23A). Species of genera 9 to 15, however, lack the posterior process with the posterior edge of the cleithrum being either smooth or only slightly irregular below the ligament (fig. 23B).

GENUS 9, *RHYNCOPELATES*

One species is placed in genus 9, *Rhyncopelates oxyrhynchus* a marine species from southern China, Japan, and the Philippines that also penetrates into freshwater. *Rhyncopelates oxyrhynchus* is distinguished from the remainder of the family by its body pigmentation pattern of alternating solid and discontinuous horizontal stripes and by the very wide origin of the extrinsic swimbladder muscle which extends in adults

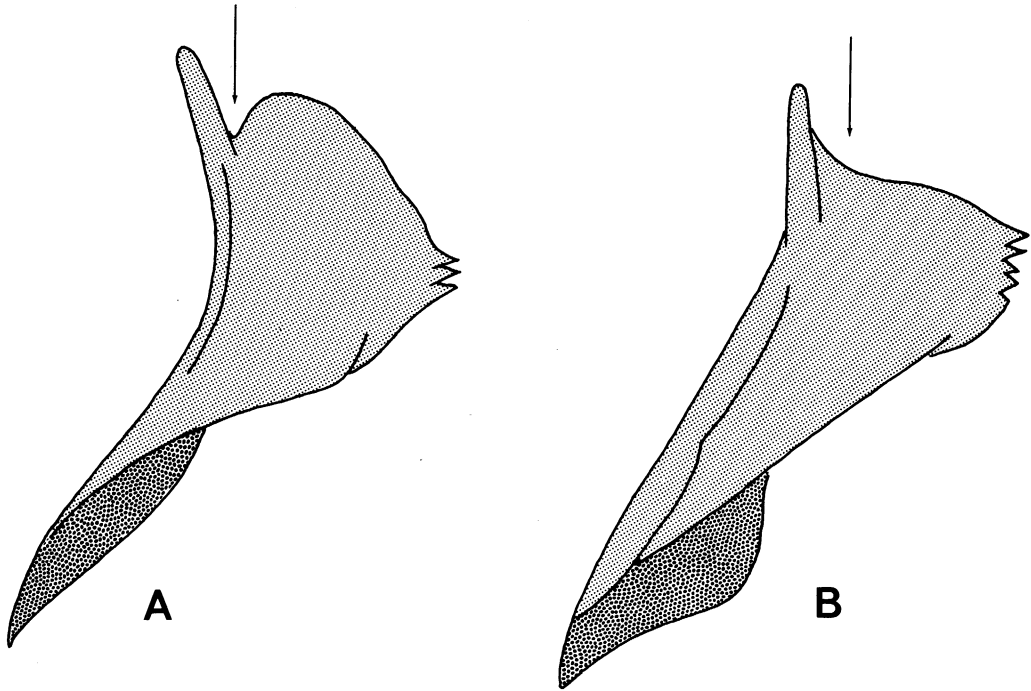


FIG. 23. Diagrammatic illustration of the cleithral forms in teraponids. A, form in genera 1 to 8; B, form in genera 9 to 15.

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 species of genera 10 to 15 share a uniform adult coloration pattern directly derived from an ontogenetically and phylogenetically earlier pattern of horizontal stripes (the striped pattern in turn may be ontogenetically derived from bars). Such an adult uniform coloration contrasts with the pigmentation of other teraponids that have either a barred pattern, a uniform pattern derived directly from bars, or an adult striped pattern derived from bars. On the basis of the ontogenetic pigmentation shifts discussed in detail earlier, the uniform adult coloration pattern of genera 10 to 15 is considered apomorphic to the other patterns and supports the hypothesis of the monophyletic nature of the group formed by these genera.

GENUS 10, *MESOPRISTES*

Four species are placed in genus 10, *Mesopristes*. Two of these, *Mesopristes argenteus* and *M. cancellatus*, are widely distributed through the East Indies (see also the discussion under the former concerning reported extralimital occurrences). The remaining species have limited ranges, with *M. kneri* apparently endemic to Fiji and *M. elongatus* to Madagascar; being the only member of the family with a distribution limited to part of the Indian Ocean.

The species of *Mesopristes* differ from the other genera of the family in the marked difference in the degree of pronouncement of the dorsal and ventral adult profiles. Whereas the dorsal profile of the adults of this genus is markedly convex, the ventral profile is straight or only moderately convex (see figs. 58, 61, and 64). Contributing to this difference in the comparative arches of the profiles is a ventral shift of the anterior of the head; a change which becomes

more pronounced ontogenetically. This shift results in a reorientation ventrally of the position of the tip of the snout with respect to the median frontal plane of the body. In conjunction with this change in head orientation are two modifications of the skull. The parasphenoid in the species of *Mesopristes* has a marked anteroventral orientation rather than the horizontal or slightly anteroventral slope in and anterior to the orbital region in other teraponids. The parasphenoid in these species is also distinctive in being practically straight and lacking the prominent bend at the rear of the orbital region that characterizes the remainder of the family. Perhaps as an adaptation to the change in skull orientation, the species of the genus also have a posteriorly bowed rear supraoccipital margin, rather than the vertical or undercut margin in other genera of the family.

Mesopristes is also characterized by the possession of very strong and long dorsal spines relative to the situation in other members of the family, with the longest anal spines nearly as long as to longer than the longest anal rays. This differs from nearly all other members 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 in genera 11 to 15 share two characters considered apomorphic in this study. The first is the possession of a previously discussed derived intestinal convolution pattern. In contrast to the adult intestinal pattern in genera 1 to 10, which has two loops in the median body plane or to the right of it, the species of genera 11 to 15 share a complex pattern with six or more loops with the anterior loops curling around the ventral surface of the stomach to the left of the median body plane (fig. 15B) (this pattern appears to have been secondarily lost in the species of genus 11b). On the basis of ontogenetic transitions from a juvenile convolution pattern similar to that of the adults of genera 1 to 10 to this more complex pattern, the latter is considered apomorphic and uniting the species of genera 11 to 15.

A second character shared by the species of genera 11 to 15 is the common possession of a freshwater ecology. Fresh water teraponids have a polyphyletic distribution in the phylogeny reconstructed in this study. The species of genera 1 to 5 (with the exception of *Amniataba caudavittatus*) and 11 to 15 are fresh water, whereas *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 fresh waters, on the basis of the limited information available (Munro, 1945; Zvjagina, 1965; Wallace, 1975) they do not appear to reproduce there.

As any transition between reproduction in marine and fresh waters (or the reverse) requires a series of morphological, physiological, and behavioral modifications, the freshwater ecology and reproductive habits of the species of genera 11 to 15 constitute a series of characters shared by these genera. These characters, it must be noted, however, have a polyphyletic distribution in the family and have not been studied in detail.

Finally, these genera (11 to 15) also share a decrease to 5 to 7 epipleural ribs from the 7 to 10 elements of genera 1 to 10. On the basis of available information, however, it is not possible to determine the polarity of this transition.

GENUS 11, *HEPHAESTUS*

The species of branch 11 share several characters considered apomorphic within the Teraponidae. In the adults of all species the longest dorsal spines are shorter than the longest dorsal rays. This situation contrasts with that in all other species in the family (with the exception of *Leiopotherapon unicolor* and *L. macrolepis* of genus 1 and *Syncomistes trigonicus* of genus 15) in which the longest dorsal spines are as long as or longer than the longest dorsal rays.

The species of this genus also have in common a change in the correspondence between the proximal pterygiophores of the dorsal fin and the neural spines. Rather than the one-to-one relationship between these elements found in most teraponids, a condition primitive for perciformes, the species of genus 11 have two proximal dorsal pterygiophores inserting between either the second and third or the third and fourth neural

spines (with the exception of some individuals of *H. roemeri*) (fig. 20). This transition which is considered apomorphic within the Teraponidae appears to have arisen independently in genera 1 and 15 (see discussion of convergencies).

All species of *Hephaestus* also share a backward shift in the position of the insertion of the dorsal fin relative to the situation in most teraponids. In genus 11 (and also genera 1 and 15) rather than an insertion of the first proximal pterygiophore between the first and second neural spines, the proximal pterygiophore inserts between the second and third neural spines (third and fourth in *H. adamsoni*) (fig. 20). Lacking a sister group to the Teraponidae it is not possible, however, to determine the polarity of this transition.

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* from 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, perhaps being one to three plesiomorph sister groups to genus 11b. Genus 11a is, however, distinguishable from genus 11b in the lack of a series of derived characters that makes the latter genus one of the more distinctive within the family. Four species are placed in genus 11b: *Hephaestus adamsoni* endemic to Lake Kutubu, Papua-New Guinea, *H. trimaculatus* (= *Terapon trimaculatus* + *T. habbemai* of previous authors) from southern New Guinea, *H. suavis* from Cape York, Queensland, and *H. carbo* from the Gregory River region of Queensland. The four species of this group have in common 27 vertebrae in contrast to the 25 or 26 found in the remainder of the family, an increase that, as discussed previously, appears to be apomorphic within the family. In addition, the forms of the lateral tabular sensory canals and posttemporal in these species are unique in the family. The supratemporal commissure and otic canals of the lateral tabular in these species open in common at the posterior edge of the bone to form a pattern of a caudally directed "V" (fig. 12) which contrasts with the patterns of an anteriorly pointing "V"

or an inverted "T" formed by these canals in other species of the family. In the adults of these species the posttemporal differs in being more massive, posteriorly elongate and closely applied to the side of the head than in other groups in the family.

Finally, all species of genus 11b have a unique form of extrinsic swimbladder muscle apomorphic to and ontogenetically derived from the muscle form present in the other species in genera 7 to 15 (see previous discussion). The origin of the muscle in the adults of genus 11b is limited to the posteroventral edge of the rear of the skull, a condition which differs from that of the extrinsic swimbladder muscle forms in the other species of the family in which there is at least a partial attachment to the ventral process of the posttemporal.

Within the species of genus 11b, a less universal 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 plesiomorph count of 10 precaudal vertebrae found in *H. carbo*.

Genera 12 to 15: *Bidyanus*, *Scortum*, *Pingalla*, and *Syncomistes*

The remaining four genera (12 to 15) in the family share a series of modifications of the jaws and dentition form that serve to distinguish groups of decreasing universality. Based on out-group comparisons, the plesiomorph form of jaw and dentition for teraponids is that illustrated diagrammatically in figure 24. The conic, non-depressible, vertically directed dentition is situated 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 jaw and dentition form 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 a depressible dentition, and to differing degrees of universality (see below), a dentary rolled laterally to varying extents that results in the teeth pointing somewhat to distinctly laterally and the development of a prominent dorsally directed median dentary process. An additional apomor-

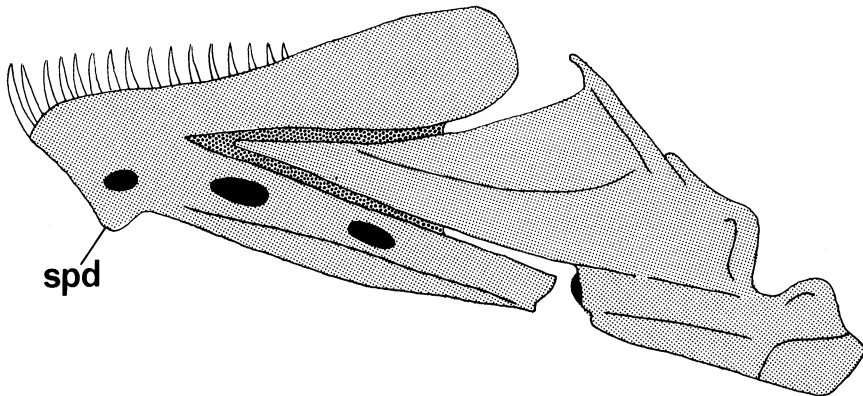


FIG. 24. Plesiomorph jaw form and tooth position in teraponids (form in *Leiopotherapon unicolor*).

phic character shared by all 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 (as discussed previously two other species with this vertebral number, *Leiopotherapon unicolor* and "*Terapon*" *ja-moerensis*, appear to have achieved it 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 *Bidyanus welchi* from the internal drainages of South Australia and Queensland. Within the family these species can be distinguished by their overall body and head forms; having an elongate body with a long caudal peduncle and a small head, which in adults develops a distinctly concave dorsal profile slightly posterior to the orbit. These two species also have 20-25 predorsal scales to the occiput, a very high count for the family, which distinguishes them from all other species except *Terapon jarbua* (genus 7) which has 19-24 predorsal scales.

Genera 13 to 15: *Scortum*, *Pingalla*, and *Syncomistes*

The remaining genera in the family (13 to 15) share a distinctively flattened depressible dentition which contrasts with the conic tooth form of the remainder of the family (the tricuspidate,

distally flattened dentition of *Pelates sexlineatus* [genus 6] is nondepressible and of 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 to contain three species in this study; *Scortum parviceps* from the Burdekin River, New South Wales; *S. hillii* (*Scortum hillii* and *S. ogilbyi* of previous workers) from the eastern and Gulf of Carpentaria drainages of Queensland, and *S. barcoo* from Barcoo (Cooper's) Creek, a species that is tentatively placed in the genus. These species share an apomorphic pattern of randomly distributed dark body blotches (condition unknown in *S. barcoo*); the retention of vomerine teeth into the adults, a situation also found in some individuals of *Terapon jarbua*; and a distinctive leathery-textured flesh (condition unknown in *S. barcoo*). As noted above, the placement of *S. barcoo* is tentative as the type (the only known specimen) was not examined and the original description provides limited information. Its inclusion in the genus is based both on the retention of vomerine teeth into adulthood and follows previous taxonomic practice. However, it is possible that examination of characters not discussed in the original description may indicate that its affinities are with another group within the family.

Genera 14 and 15: *Pingalla* and *Syncomistes*

The species of genera 14 and 15 are considered to be a monophyletic group based on the common possession of a series of characters considered apomorphic for teraponids.

Both genera share the previously discussed complex pattern of intestinal convolutions having both 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 (fig. 15C). Associated with this change in the morphology of the digestive system in these species is a change in their dentition and jaws. In both genera the primitively dorsal surface of the dentary has rotated outward resulting in the dentition pointing laterally to varying degrees (fig. 25). As a consequence of this rotation the main area of contact between the dentaries has shifted from the anterovertical edge of the symphyseal joint to an anterohorizontal point of contact with a consequent reduction in the prominent anteroventral symphyseal process. Along with this change in the overall form of the lower jaw, these genera also share a shift in dentitional form. Rather than the slightly depressible and flattened teeth of genus 13, the

nonflattened depressible teeth of genus 12, or the conic nondepressible teeth of genera 1 to 12, the species of genera 14 and 15 share highly depressible, distinctly flattened teeth. Furthermore in these groups the dentition is reduced either to two rows of teeth (genus 14) or a tooth row followed by a distinct narrow band of teeth (genus 15); conditions which contrast with the wide tooth band found in all other species in 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 extent of the transverse swimbladder constriction as was discussed previously (see fig. 6).

Within the monophyletic unit formed by the above characters are placed five species, two recognized in genus 14, *Pingalla*, and three in genus 15, *Syncomistes*.

GENUS 14, *PINGALLA*

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 New Guinea. These

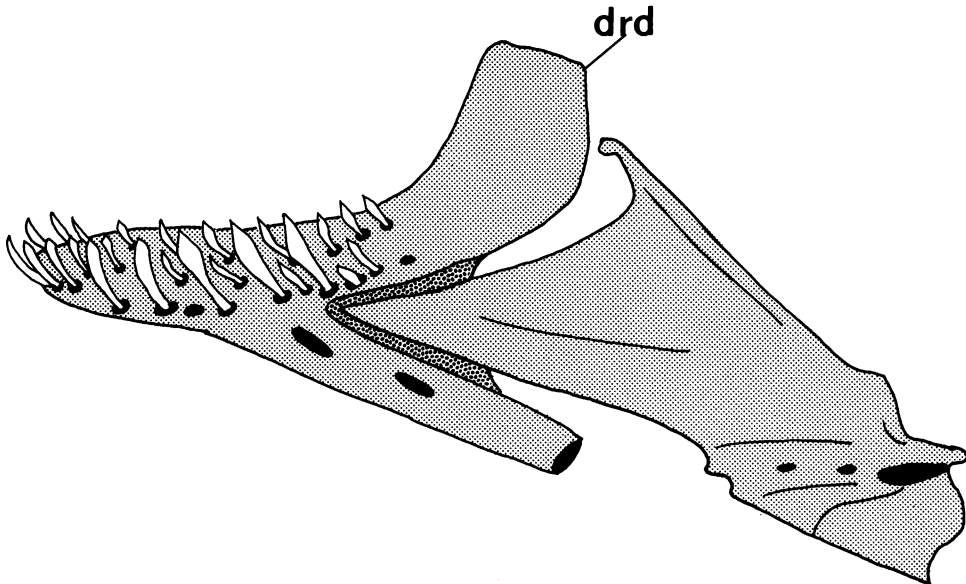


FIG. 25. Jaw form and tooth position in *Syncomistes butleri*.

species form a monophyletic unit based on the common possession of a practically nonprotractile small mouth with the posterior of the maxillary strongly curved ventrally in contrast to the larger protractile mouth with a nearly straight maxillary that occurs in other members of the family (the mouth size is also reduced in *Pelates sexlineatus*, genus 5). These species also have only two distinct rows of teeth in each jaw, a character autapomorphic to the genus within the family.

GENUS 15, *SYNCOMISTES*, NEW GENUS

Genus 15, *Syncomistes*, contains three species described for the first time here and forms 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 a wide distribution from the Bow River to the South Alligator River, *S. trigonicus* being known from the Drysdale, Prince Regent, and Roe rivers of the Kimberley region and *S. kimberleyensis* having been collected only in the Bow River.

These species share a large series of apomorphic characters unique to the group among teraponids and primarily associated with modifications for ingestion and digestion. The adults of the species of this genus have a further elaboration of the intestinal pattern found in genus 14 to form a highly complicated pattern of intestinal convolutions and loops curling around the ventral and up the left side of the stomach; a pattern autapomorphic to the genus in the family.

These species also share radical changes in the form of the jaw. The dentary is markedly rolled outward resulting in the dentition of the lower jaw pointing laterally (fig. 27) and a shift in the main point of articulation between the dentaries from the anterior edge of the jaw to the antero-medial surface with the consequent development of a prominent dorsally directed bump at the dental symphysis (fig. 27). This bump conforms in form to and inserts into a median groove between the premaxillaries, with both the bump and groove being edentulous. Both of these

structures (bump and groove) and the lack of median dentition on them are characters autapomorphic to the genus within the family. In addition to the development of a median groove between the premaxillaries there have also occurred a series of other upper jaw modifications. The maxillary in the species of this genus are broader and heavier than the condition found in the species of any other genera in the family. The premaxillaries are of a distinctive shape with the ascending processes being triangular and with the medial surfaces of the ascending processes diverging from each other and being distinctly separated at their tips. This condition contrasts with the elongate parallel ascending processes found in the other species of the family (fig. 26). Along with this change in the form of the ascending processes is a change in the form of the rostral cartilage and its attachment to the ascending process. The plesiomorph condition of the rostral cartilage among perciformes and probably for teraponids is an elongate cartilage tightly attached to the ventral surfaces of the ascending processes by connective tissue; a condition found in genera 1 to 14.

The species of genus 15 have a highly modified hemispherical rostral cartilage with a concavity on its posterior surface and loose connections to the premaxillaries (fig. 26). Associated with this change in rostral cartilage shape is a change in the part of the anterior surface of the ethmoid which contacts the posterior concavity on the rostral cartilage. Rather than an antero-ventrally sloping surface along which the rostral cartilage slides primitively, the ethmoid in the genus *Syncomistes* bears a rounded anterior knob. Along with the posteriorly concave surface of the rostral cartilage this functional complex (cartilage and ethmoid knob) forms a sliding joint that allows a more vertical movement of the upper jaw than occurs in the species of genera 1 to 14.

The species of *Syncomistes* share with the members of genera 1 and 11 an independently acquired backward shift in the origin of the dorsal fin relative to the neural spines; a transition whose polarity is presently undetermined as a consequence of a lack of a definite sister group to the Teraponidae. The species of *Syncomistes*

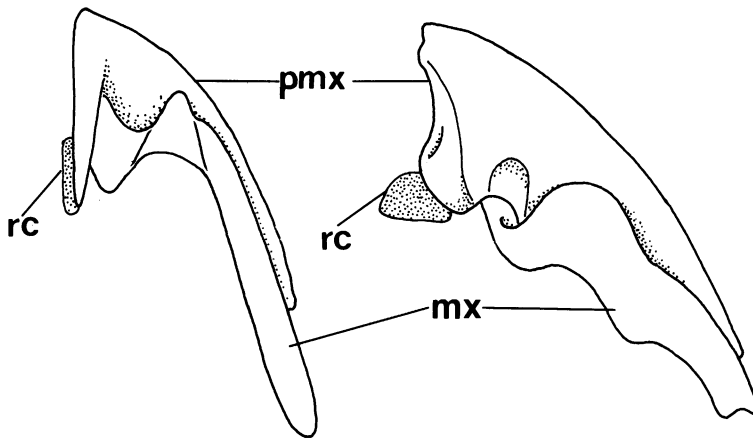


FIG. 26. Dorsal view of the premaxillaries, maxillaries, and rostral cartilages in teraponids. A, form in genera 1 to 14 (*Terapon jarbua* shown); B, form in genus 15, *Syncomistes* (*S. butleri* shown).

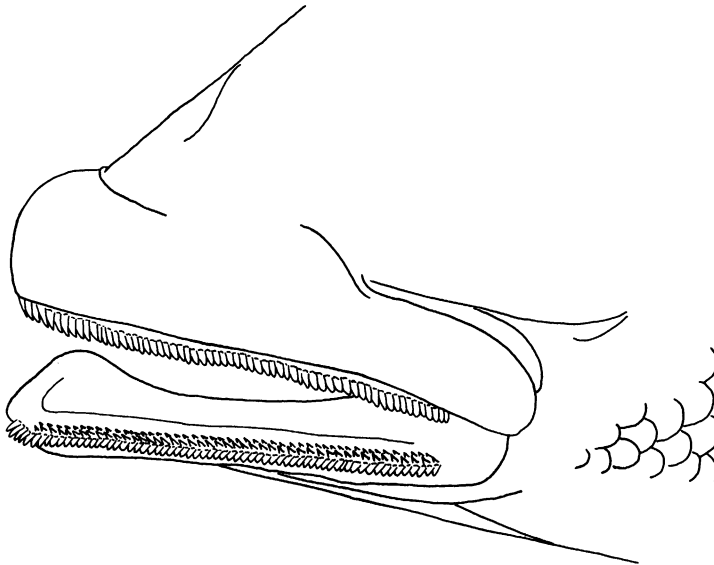


FIG. 27. Lateral view of the head of *Syncomistes trigonicus*, showing the laterally directed lower jaw dentition, reduced height of the rotated lower jaw and medial dentary bump. WAM P-25391-001, 93 mm. SL.

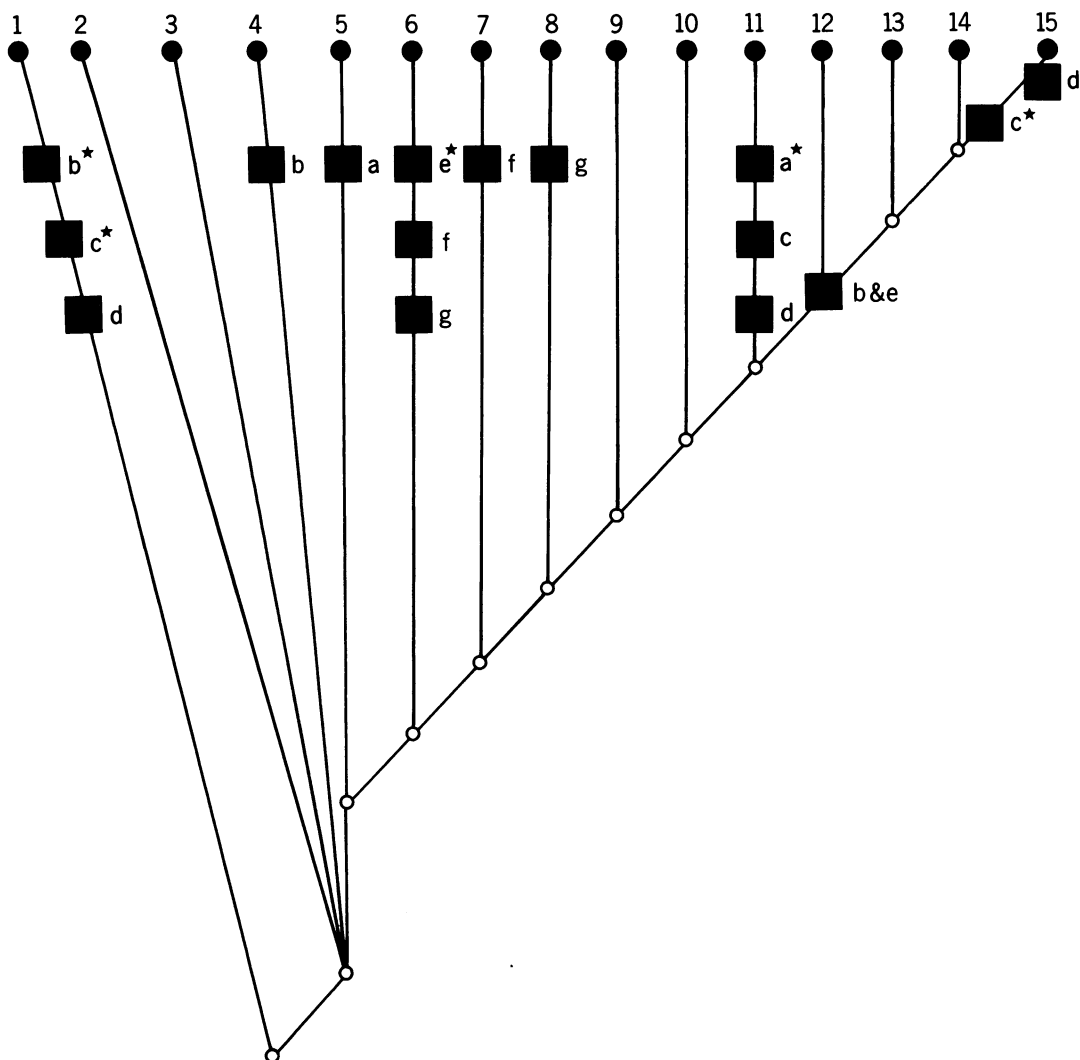


FIG. 28. Cladogram of the most parsimonious hypothesis of relationships of the genera of the family with a superimposed distribution of characters considered convergent in teraponids. Taxa (solid circles, see figure 9 for key) (starred characters are found in only some members of the indicated genus): A, increased vertebral number; B, increased precaudal vertebrae; C, longest dorsal spine shorter than longest dorsal rays; D, posterior origin of dorsal fin with respect to neural spines, two proximal dorsal pterygiophores inserting between successive neural spines; E, flattened teeth; F, spinous dorsal with black blotching on edge; G, humeral spot.

also have in common and share with the species of genera 1 to 11 an insertion of two proximal dorsal pterygiophores between successive neural spines, a character considered apomorphic within the family (see discussion under genus 1).

HYPOTHEZED CONVERGENT CHARACTERS

As would be expected within a group of its size, in the Teraponidae there occur a series of characters whose distribution is not congruent with the most parsimonious hypothesis of relationship based on the sum of characters examined. Such characters are consequently considered to be convergent within the family. The distribution of these characters among teraponids is shown superimposed on the arrived-at cladogram of the most parsimonious phylogeny (fig. 28). These characters include the changes in the relative numbers of precaudal and caudal vertebrae, increased numbers of vertebrae, relative shortening of the dorsal spines, changes in the relative position of the dorsal fin insertion with respect to the neural spines, flattened teeth, humeral spots, blotching on the dorsal fins, and uniform coloration derived from bars.

In the cases of flattened dentition and humeral spots, the different conditions in the groups having them are sufficient 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).

Regardless of any resolution of these questions, any attempts to modify the arrived-at hypothesis of relationships shown in figure 9 to reflect some or all of these character distributions results in a still greater number of convergencies. As any reconstructed hypothesis of relationships 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 this study differs markedly from that inherent in

Cuvier's and Whitley's classifications. The division of the family into monophyletic assemblages in this work is inconsistent with the recognition of the genus *Terapon* (*sensu lato*) in the older usage—a usage that employed shared primitive characters and whose included species have a polyphyletic distribution in this reconstruction. Similarly, inconsistencies exist between the conclusions of this study and those of Whitley regarding the genera *Amphitherapon* (as modified by Munro), *Hephaestus*, *Madigania*, *Mesopristes*, *Pelates*, *Leiopotherapon*, and the subfamily Helotinae.

The genus *Amphitherapon* originally erected by Whitley for *A. caudavittatus* was expanded by Munro (1967) to include *Terapon habbemai* Weber (1910), considered a synonym of *Hephaestus trimaculatus* in this work. *Amphitherapon caudavittatus* and *T. habbemai*, however, differ markedly, with the latter having a series of derived states of osteological, myological, and pigmentary characters lacking in *A. caudavittatus* but shared in common with the other species of *Hephaestus*.

Whitley also placed in the genus *Hephaestus* a second species, *Terapon welchi* McCulloch and Waite (1917), herein considered to be a member of the genus *Bidyanus*. *Bidyanus 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 species considered members of *Hephaestus* in the present study.

Munro (1964) added *Terapon* (= *Hephaestus*) *adamsoni* to the previously monotypic genus *Madigania* erected by Whitley (1945a) for *Madigania* (= *Leiopotherapon*) *unicolor*. However, whereas the characters studied in this work indicate the relationships of *L. unicolor* to be with genus 1 (*Leiopotherapon*), they show *H. adamsoni* to share a series of derived characters with genus 11 (*Hephaestus*).

In contrast to Whitley's wider concept of the genus, *Mesopristes* as recognized in this study is limited to four species, two of which were not considered by Whitley. Besides the species placed in the genus in this study, Whitley's genus included three other species: *Terapon alligatoris* placed as a synonym of *Hephaestus fuliginosus* in

this study, *Hephaestus jenkinsi*, and *Leiopotherapon aheneus*. On the basis of the characters discussed in detail in the phylogenetic reconstruction, these species have closer relationships with other monophyletic groups in the family outside of *Mesopristes*.

The genus *Leiopotherapon*, originally erected as a subgenus by Fowler (1931) for four species characterized by the lack of an exposed posttemporal, was expanded with Whitley's addition (1948b) of a new species, *L. suavis*. This species placed in the genus *Hephaestus* in this work differs from those of Fowler's subgenus in having an exposed, serrate posttemporal and in a series of derived states of pigmentary, osteological, and myological characters.

The genus *Helotes* originally erected by Cuvier (1829) for *Helotes* (= *Pelates*) *sexlineatus* was expanded by Weber (1910) and later workers by the addition of a second species, *H. lorentzi*, based on supposed similarity in tooth form. More recently Whitley (1953) removed *H. lorentzi* to *Pingalla* which also contains *P. gilberti* a species described at that time. However, in his placement of these species (*sexlineatus*, *lorentzi*, and *gilberti*) as a separate subfamily *Helotinae* he retained the concept of a close relationship between *Helotes* and *Pingalla*. However, the tooth forms of the two genera (*Helotes* [sensu Cuvier and Whitley] and *Pingalla*) are quite distinct as discussed earlier. Furthermore, the species of *Pingalla* share a large series of characters supporting their placement in genus 14; characters lacking in *Helotes* (= *Pelates*) *sexlineatus* of genus 6.

Cuvier's original concept (1829) of the genus *Pelates* was modified with Weber and deBeaufort's addition (1931) of *Terapon roemeri* Weber (1910) to the genus based on supposed similarity in tooth arrangement. According to their concept, *Pelates* 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 states of the posttemporal, extrinsic swimbladder muscle, lateral tabular, etc., uniting it to the monophyletic group of the species of *Hephaestus*; characters lacking, however, in *Pelates*.

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

In addition to the above modifications of the limits of various genera, there are also a series of genera that have been placed in synonymy. These are *Madigania* (in *Leiopotherapon*), *Amphitherapon* (in *Amniataba*), *Helotes* (in *Pelates*), *Authistes* and *Eutherapon* (in *Terapon*), *Papuservus*, and *Archerichthys* (in *Hephaestus*).

SYSTEMATIC ACCOUNTS

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 onto caudal fin. Tubes of lateral line

scales usually not reaching edge of scales. 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 to various degrees onto soft dorsal and anal.

Head moderate to large (2.5-4.3 in SL). Scales on cheeks, subopercle, opercle, and nape. Top of head and snout naked. Snout moderate to elongate, with lacrimal long and overlapping the premaxillary and maxillary slightly. Circumorbital series not covering cheek. A subocular shelf developed in all species. Preoperculum serrate; serrations more prominent in juveniles. Lacrimal serrate; serrations reduced with age in some species. Operculum with two spines, lower spine longer and stronger; 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 equal or with 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 edentulous except in a few species. Nostrils paired; distinctly separated; with free cutaneous edges in most species.

Dorsal fin 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 longest. Spinous dorsal depressible into a groove formed by a basal sheath of scales. First proximal dorsal pterygiophore bearing one or two spines. Three predorsals in all species.

Anal fin with 3 spines and 7 to 12 rays. First anal spine shortest; either second or 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 rays branched. Pectoral fin asymmetrically pointed; 12 to 17 rays. Pelvic fins I-5; first ray usually longest and often filamentous. Pelvic fins inserted 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 on 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; five to 18 on upper and nine to 27 on lower limb of first arch. Vertebrae 25 to 27; two anteriormost lacking pleural ribs. Caudal with three epurals, two uroneurals, six 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 the range of largest individuals for the species). Inhabitants of salt, brackish, and fresh waters throughout the Indo-west Pacific region.

Diagnosis. Among perciform fishes the family Teraponidae can be distinguished in having an extrinsic swimbladder muscle arising from the rear of the skull or the posttemporal or both and inserting directly on the anterodorsal surface of the anterior chamber of the swimbladder; a transversely divided swimbladder; a distinctive form of urohyal and a distinctive process of the third pharyngobranchial.

CLASSIFICATION OF THE FAMILY TERAPONIDAE

In the classification proposed herein, only the monophyletic groups consisting of 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 at this time. These questions include: (1) the exact relationships of

genera 2, 3, and 4 both with respect to each other and with the unit formed by genera 5 to 15; (2) several dichotomies defined solely on the basis of a single character; and (3) the hypothesis of a secondary loss in the species of genus 11b of the apomorphic intestinal convolution pattern defining genera 11 to 15 as a monophyletic group.

With increasing analysis, both of the characters used in this study and others, such problems should theoretically approach resolution, with a subsequent stabilization of the classification based on the most parsimonious reconstruction

of relationships. However, the above problems might necessitate major changes in classification at some future date if every branching point were given taxonomic recognition at this time following a traditional Hennigian procedure (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 existing taxonomy until such time that further study removes at least some of the major uncertainties outlined above.

Family Teraponidae

Genus *Leiopotherapon* Fowler, 1931

Leiopotherapon plumbeus (Kner, 1865)

Leiopotherapon unicolor (Günther, 1859)

Leiopotherapon macrolepis, new species

Leiopotherapon aheneus (Mees, 1963)

Genus *Amniataba* Whitley, 1943

Amniataba percoides (Günther, 1864)

Amniataba caudavittatus (Richardson, 1844)

Genus *Hannia*, new genus

Hannia greenwayi, new species

Genus "*Terapon*"

"Terapon" jamoerensis Mees, 1971

Genus *Lagusia*, new genus

Lagusia micracanthus (Bleeker, 1860)

Genus *Pelates* Cuvier, 1829

Pelates quadrilineatus (Block, 1790)

Pelates sexlineatus (Quoy and Gaimard, 1824)

Genus *Terapon* Cuvier, 1817

Terapon jarbua (Forskål, 1775)

Terapon theraps Cuvier, 1829

Terapon puta Cuvier, 1829

Genus *Pelsartia* Whitley, 1943

Pelsartia humeralis (Ogilby, 1899)

Genus *Rhyncopelates* Fowler, 1931

Rhyncopelates oxyrhynchus (Temminck and Schlegel, 1824)

Genus *Mesopristes* Bleeker, 1845

Mesopristes argenteus (Cuvier, 1829)

Mesopristes cancellatus (Cuvier, 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*, new genus
Syncomistes butleri, new species
Syncomistes trigonicus, new species
Syncomistes kimberleyensis, new species

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) 66 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 rear of skull by a ligamentous band . . . C
 C) teeth tricuspidate; 6-7+1+14-16 gill rakers on first arch; 76-87 lateral line scales; body depth 3.4-4.0 in SL . . . *Pelates sexlineatus* . . . (Australia, East Indies, Philippines, China)
 CC) teeth lacking side cusps; 16-18+1+22-27 gill rakers on first arch; 66-75 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 indistinct longitudinal striping is present, the 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 brown silvery coloration . . . "*Terapon*" *jamoerensis* (New Guinea)
 DD) 57 or fewer lateral line scales, if more than 52 scales in lateral line, then the longest dorsal spines are shorter than longest dorsal rays . . . E
 E) each caudal lobe with a prominent oblique transverse black blotch; small spots randomly distributed on body . . . *Amniataba caudavittatus* . . . (Australia, southern 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*, new species . . . (Western Australia)
 HH) 45-57 lateral line scales; 7-9 scales above lateral line; 6-9 cheek scales . . . *Leiopotherapon unicolor* . . . (Australia)
 GG) longest dorsal spine 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; 4-5 scales above lateral line . . . *Hannia greenwayi*, new species (Western Australia)

- JJ) 43-56 lateral line scales; 6-8 scales above lateral line *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* (Western 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) 46-56 lateral scales; 6-8 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, 18-24 gill rakers on lower limb of first gill arch *Terapon puta* (Indo-west Pacific)
- NN) three downward curved longitudinal stripes along body; 12-15 gill rakers on lower limb of first arch *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 O
- O) teeth flattened, depressible P
- P) mouth small, nearly nonprotractile, rear of maxillary strongly curved ventrally; two rows of teeth in each jaw Q
- Q) 48-54 lateral line scales; 13-14 dorsal spines . *Pingalla lorentzi* . (southern New Guinea)
- QQ) 35-41 lateral line scales; 11-12 dorsal spines . . *Pingalla gilberti* . . (northern Australia)
- PP) mouth moderate to large, 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. 27); bump and depression lacking dentition S
- S) lower jaw triangular anteriorly from ventral aspect (fig. 29). *Syncomistes trigonicus*, new species. (Western Australia)
- SS) lower jaw rounded from ventral aspect (fig. 29). T
- T) juveniles with 4-5 blackish body stripes, median stripe widest; 5-7 caudal scales; 14-17 predorsal scales to occiput *Syncomistes butleri*, new species (Western Australia)
- TT) juveniles with 8 brownish stripes; 12-13 predorsal scales to occiput; 3-4 caudal scales *Syncomistes kimberleyensis*, new species (Western Australia)
- RR) lower jaw lacking dorsally directed median bump, no marked depression between premaxillaries; dentition continuous across each jaw. Body in some individuals with irregular randomly dispersed blotches U
- U) approximately 82 scales counted in a series above lateral line; 7-8 cheek scales *Scortum barcoo* (eastern Australia)
- UU) scales counted in a series above lateral line 51-71; 4-6 cheek scales V
- V) 11-13 scales above lateral line; 63-71 scales counted in a series above lateral line. *Scortum hillii* (eastern Australia)
- VV) 8-10 scales above lateral line; 51-61 scales counted in a series above lateral line. *Scortum parviceps*. (eastern Australia)
- OO) teeth conic. W
- W) 80-90 lateral line scales, prominent humeral spot, vertical bars variably present. *Pelsartia humeralis* (southwestern and southern Australia)
- WW) 75 or fewer lateral line scales. X
- X) lower lip with a continuous ventral lip fold (fig. 30). *Hephaestus jenkinsi* (Western Australia)
- XX) lower lip with a median ventral gap in lip fold (fig. 30). Y
- Y) 9-12 gill rakers on lower limb of first arch; 5-6 gill rakers on upper limb of first arch, 27 vertebrae Z
- Z) caudal truncate; body and fins uniformly dark; 10 abdominal vertebrae.

- *Hephaestus carbo* (northern Australia)
- 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 distinct spots except in largest specimens.
- *Hephaestus trimaculatus* (southern New Guinea)
- aa) 15-20 predorsal scales to occiput; 20-22 scales below lateral line. b
- b) 13-14 dorsal rays. *Hephaestus suavis* (Cape York, Australia)
- bb) 11-12 dorsal rays. *Hephaestus adamsoni* (Lake Kutubu, New Guinea)
- YY) 13-18 gill rakers on lower limb of first arch; 6-9 on upper limb of first arch (6 rare); 25 vertebrae c
- c) 20-25 predorsal scales to occiput; 24-27 scales below lateral line. d
- d) greatest body width 1.9-2.1 in body depth; 76-79 scales in a series counted above lateral line; 71-77 below; 7-10 cheek scales; 12-14 scales above lateral line. *Bidyanus bidyanus* ... (eastern Australia)
- dd) greatest body width 1.5-1.7 in body depth; 68-72 scales in a series counted above lateral line; 59-66 below; 5-7 cheek scales; 10-12 scales above lateral line. *Bidyanus welchi* ... (eastern Australia)
- cc) 13-18 predorsal scales to occiput; 14-24 scales below lateral line. e
- e) 60-75 lateral line scales; body with longitudinal stripes throughout life; in adults solid stripes alternate with irregular longitudinal stripes *Rhynocopelates oxyrhynchus* (Philippines, China, Japan)
- ee) 58 or fewer lateral line scales; longitudinal stripes present only in young, if stripes are still evident in some adults, then they are limited to the ventral half of body and with vertical bars above them. f
- f) dorsal rays 12-14. g
- g) 5-7 scales above lateral line; 5-6 cheek scales.
- *Hephaestus roemeri* (southern New Guinea)
- gg) 8-10 scales above lateral line; 6-9 cheek scales.
- *Hephaestus fuliginosus* (northern Australia)
- ff) 10-11 dorsal rays. 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 larger adults
Mesopristes cancellatus . . (East Indies, New Guinea, China, Solomons, Philippines, New Hebrides)
- ii) 8-9 cheek scales; 10-12 caudal scales; horizontal body stripes in juveniles, lost in adults *Mesopristes argenteus*
(East Indies, New Guinea, China, Solomons, Philippines, New Hebrides)
- hh) 9-11 scales above lateral line j
- j) 20-24 scales below lateral line *Mesopristes elonatus*
(Madagascar)
- jj) 18-19 scales below lateral line . . *Mesopristes kneri* . . (Fiji)

GENUS 1, *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 *Leiopothera-*

pon from the Greek, *leios*, smooth; *omos*, shoulder, and *Therapon*, a genus of the family refers to the lack of an exposed serrate post-temporal in the species of the family. The substitution of a p for the m of *omos* appears to be an incorrect transliteration.

Diagnosis. Members of the genus are distinguishable from all other species of the family in possessing only one spine on the first proximal

dorsal pterygiophore (in contrast to the two of all other teraponids).

Included Species. Three species (*unicolor*, *aheneus*, and *macrolepis*) are found in the fresh waters of Australia, with the last two 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. *Leiopotherapon plumbeus*, the fourth member of the group, is limited to the fresh waters of the Philippines (see also the discussion of this species for reported extralimital occurrences).

Remarks. Fowler (1931) erected the subgenus *Leiopotherapon* to contain four species from Australia, New Guinea, and the Philippines that lacked exposed serrate posttemporals. More recently Whitley (1943, 1945a) removed three of the species (*Leiopotherapon unicolor*, *Amniataba percoides* and *A. caudavittatus*) to monotypic genera. He also expanded *Leiopotherapon* with his description of *L. 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 (*Hephaestus*), characters lacking in genera 1 and 2 in which the species Fowler considered to be part of *Leiopotherapon* are placed in this work. Consequently, the hypothesis of close relationship inherent in Whitley's addition of *L. suavis* to the genus is rejected in this revision.

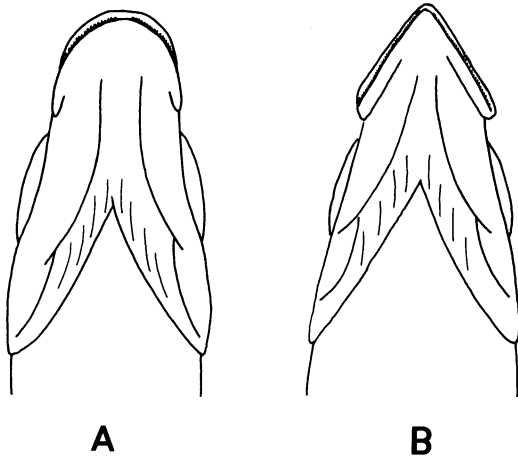


FIG. 29. Ventral views of the heads of *Syncomistes butleri* (A), and *S. trigonicus* (B), showing differences in the shape of the lower jaw.

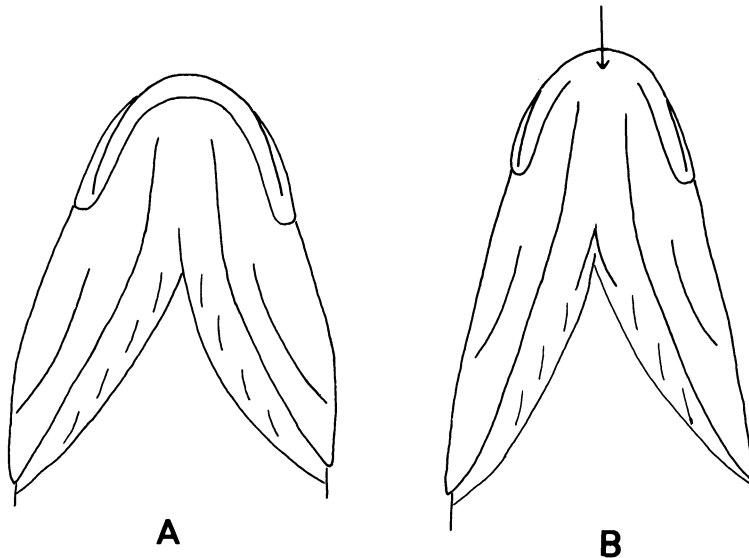


FIG. 30. Ventral views of the head of *Hephaestus jenkinsi* (A) and *H. fuliginosus* (B), showing the median gap in the lip fold of the latter.

Leiopotherapon plumbeus (Kner, 1865)

Ayuñgin

Figure 31

- 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). Freihofer, 1963, p. 132 (RLA pattern). Johnson, 1975, p. 12 (procurent spur).
- Therapon brevispinis* 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) brevispinis*: Bleeker, 1873, p. 384 (Luzon).
- Therapon (Datnia) plumbeus*: Bleeker, 1873, p. 383 (Java?, on Kner); 1873-1876, p. 115 (on Kner).
- Therapon (Datnia) brachycentrus*: Bleeker, 1873-1876, 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 morphology). 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, misidentification).

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

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

Nomenclature. The trivial name, *plumbeus*, from the Latin for lead, evidently refers to the leaden coloration of preserved specimens. A syntype of the species from the Vienna Museum was examined by G. F. Mees and found to agree with the original description.

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

Description. Dorsal spines XI-XIII; dorsal rays 8-10; anal III, 7-9; pectorals 14-15; pelvics 1-5; 43-56 lateral line scales; 2-6 scales on caudal; 6-8 scales above lateral line; 13-17 scales below lateral line; 13-19 predorsal scales to occiput; one row of scales in sheath at base of dorsal fin, sheath extending to third to sixth dorsal ray; 2-3 rows of scales in sheath at base of anal fin, sheath extending to third to fifth 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;

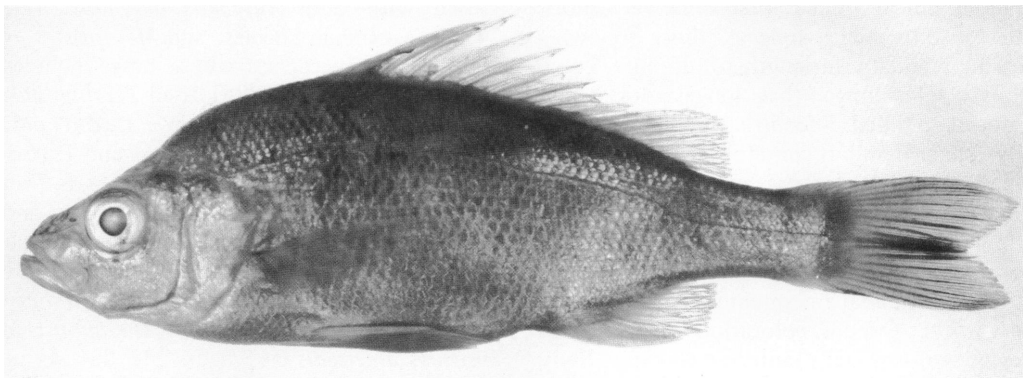


FIG. 31. *Leiopotherapon plumbeus*, USNM 184802, 116 mm. SL.

distance from origin of dorsal fin to snout 2.2-2.7 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 3.0-4.3 in HL; jaw length 3.0-3.8 in HL; length of longest dorsal spine 1.4-1.9 in HL; length of longest dorsal ray 1.6-2.3 in HL; length of longest anal spine 1.7-2.4 in HL; length of longest anal ray 1.7-2.1 in HL.

This species shows some variation in overall body shape between populations. It is a moderately deep bodied, compressed to slightly compressed species. Dorsal profile in members of more compressed populations 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 and then convex to anus in full-bodied individuals. Jaws equal or lower one 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. Post-temporal not exposed; covered with skin and scales. Supracleithrum exposed.

Spinous dorsal arched; first spine very short; fourth to sixth spines longest, those following decreasing gradually in length to ultimate. Longest dorsal spine longer than longest dorsal ray. Soft dorsal rounded. Second anal spine thickest, usually longer than but sometimes same length as third; shorter than longest anal ray. Soft anal rounded. Pectorals asymmetrically 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 dark above, slightly lighter ventrally, with scale markings sometimes forming longitudinal vermic-

ulations. 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. *Leiopotherapon plumbeus* is a common member of the fauna of Laguna de Bay, a large shallow lake on Luzon (Fowler, 1918; Herre, 1930; Mane, 1934; Yapchiongco and Enriques, 1936) and also has been reported from Mindanao (Domantay, 1940). However, confusion has surrounded the identification and distribution of this species since its description. The species was described by Kner (1865) based on material from an unknown locality, but thought to be from Java. No further material of the species has been collected from Java and the locality may represent a labelling error. As pointed out by Mees (1971) the "Novara" which collected the type series stopped at Manila where the species is commonly sold and from which the specimens probably originated.

More recently Fowler (1931) listed a specimen of *L. plumbeus* from Buka Buka Island in the Gulf of Tomini, Sulawesi (Celebes); a highly unlikely locality for this species. Although the specimen bears an "Albatross" tag corresponding to that locality, it is bottled with a series of *L. plumbeus* of similar size, coloration, body form, and overall condition purchased in the Manila market by the same expedition. Therefore, it appears that the supposed Indonesian specimen may have been a mislabelled member of a Philippine series.

Leiopotherapon plumbeus has also been confused with both *Bidyanus bidyanus*, a freshwater Australian species, and *Mesopristes argenteus*, a marine species whose range includes the Philippines. Meyer (1885) listed *Terapon bidyana* sp. aff. from Laguna de Bay, Luzon and was followed in this by Elera (1895) and Roxas and Martin (1937) who cited the species as *Terapon bidyana*. However, based on the locality and the indefinite original identification, it is probable that the material was *L. plumbeus*, which is close to the overall form and coloration of *B. bidyana*. Similarly the identification of *Therapon* (= *Mesopristes*) *argenteus* as Laguna de Bay Aynunigin by Aldaba (1931) is also a misidentification of *L. plumbeus*.

Ecology. The spawning habits, development, and biology of this species have been extensively studied by Mane (1934) and Yaphiongco and Enriques (1936) who found the largest individuals collected reached 156 mm. SL. Juliano (1960) studied the swimbladder morphology in this species.

Specimens Examined

Philippines: fish pond 1.5 mi. west of Dangali (USNM 184815*, 2, 94-108 mm.); Luzon, Laguna de Bay, Los Banos (USNM 131119*, 2, 59-61 mm.; UMMZ 100254*, 17, 44-98 mm.); Luzon, Manila Market (USNM 184802*, 6, 92-111 mm.); Luzon (BM(NH) 1872.10.18.9*, 1, 158 mm.).

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

Leiopotherapon unicolor (Günther, 1859)

Spangled perch

Figure 32

Therapon unicolor Günther, 1859, p. 277 (original description, Mosquito Creek, 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 (compiled). McCulloch, 1934, p. 47 (New South Wales). Fletcher, 1937, p. 164 (Waroon 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).

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

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

Therapon elphinstonensis De Vis, 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 fluvifaunulae); 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: BMNH 1846.3.24.4 specimen measured by Günther, 1846.8.16.2-3, and 1853.1.14.12-15).

Diagnosis. A member of the genus *Leiopotherapon* distinguishable 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; pectorals 15-16; pelvics 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; one row of scales in sheath at base of dorsal, sheath extending to second dorsal ray; two 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

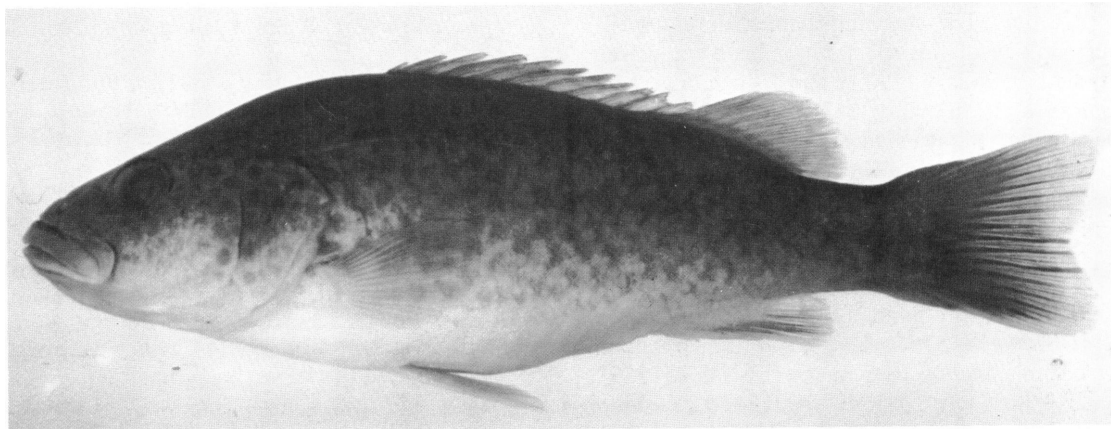


FIG. 32. *Leipothorapon unicolor*, AMNH 35540, 112 mm. SL.

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 asymmetrically 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 grayish, 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 fresh waters of New South Wales from Newcastle north, Queensland, Northern Territory, Western Australia from Murchison drainage north (fig. 33). Two specimens examined (AMNH 8739) have a locality of Melbourne, Victoria. This locality appears to be an error as it is distinctly south of the other records for the species.

Scott (1962) listed *L. unicolor* from South Australia north of 30 degrees latitude. Although I have been unable to find any locality records for the species in 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 it also occurs in South Australia, at least in the interior drainages.

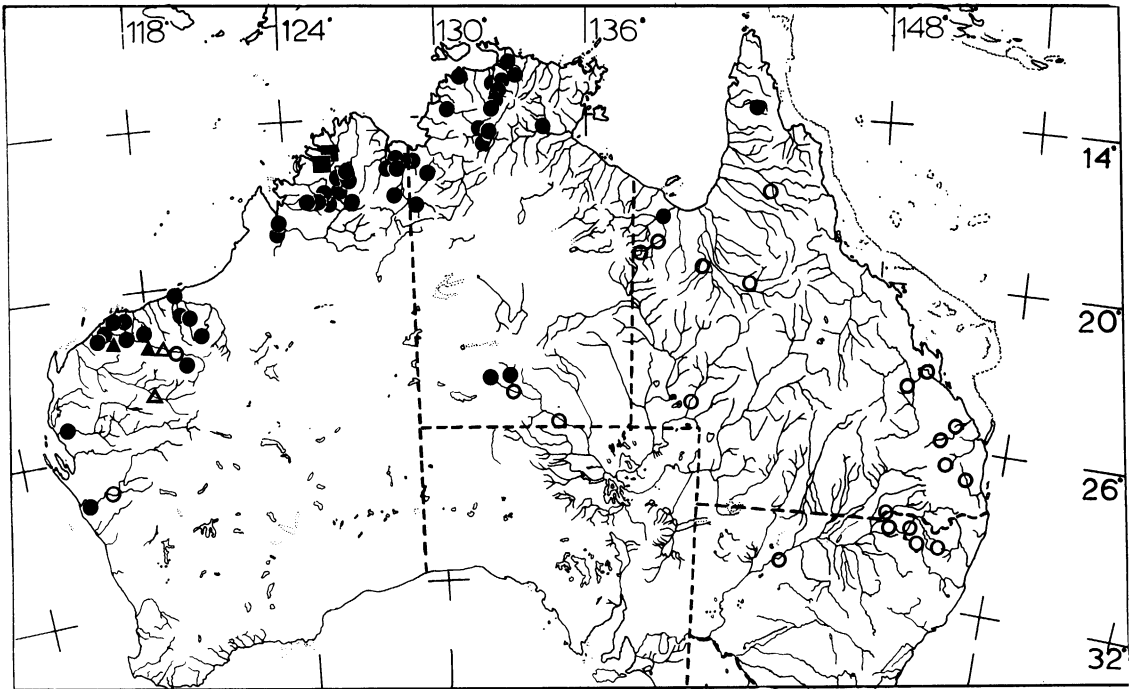
Leipothorapon unicolor was considered to be

part of the fauna of the Fiji Islands by Whitley (1927) who evidently followed Kner's (1868) description of a specimen collected at Kandavu, Fiji as a member of the species. This is, however, an unlikely locality for a species otherwise limited to the fresh waters of Australia. Reference to Kner's description and figure shows that the specimen differs from *L. unicolor* in overall appearance and in having 4 cheek scales rather than 6 to 9; 39 lateral line scales rather than 45 to 57 and a transverse scale count of 5+1+9 rather than 7-9+1+16-20. Fowler (1928) believed the specimen to be an individual of *Kuhlia rupestris*, a hypothesis consistent with the above information. More recently, however, he listed *L. unicolor* as an introduction in the Fiji fauna, citing Whitley (1927) as his source although that author made no such statement. Therefore, the distribution of *L. unicolor* in Fiji either naturally or as an introduction appears unsubstantiated.

Leiopotherapon unicolor has the largest dis-

tribution of any freshwater teraponid, occurring in major rivers, isolated drainages, and ponds throughout the northern two-thirds of Australia. Associated with this large range there occurs a marked level of variation between populations, especially in overall body form. Despite these interpopulational differences, there has not been found any basis for a subdivision of *L. unicolor* either at the specific or subspecific level.

Ecology. *Leiopotherapon unicolor* has been cited as having the ability to aestivate when water courses dry up (Whitley, 1959; Lake, 1966) and as being dispersed in "rains of fishes." Although Llewellyn (1973) found the species able to tolerate high water temperatures (LD₅₀, 39.0°C.), he was unable to find evidence for any ability to aestivate. The sudden appearance of the species in previously dry water courses probably results from the observed emigration of juveniles from permanent water courses during heavy rains (Shipway, 1947). In turn, individuals



22

FIG. 33. Distribution records for the species of the genus *Leiopotherapon* (those of *L. plumbeus* from the Philippines not shown), *L. unicolor* (circles), *L. macrolepis* (squares), and *L. aheneus* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

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, in Whitley, 1945a).

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

Leiopotherapon unicolor is resident in a variety of water conditions, and has been collected in Western Australia in hard and soft waters, both running and standing and ranging from clear to nearly opaque. The southern limit of the species distribution appears to be related to its intolerance to water temperatures below 5.3°C., with the limit of distribution conforming well with the 4.4°C. isotherm for the minimum average winter temperature.

Remarks. Whitley (1945a) placed this species in its monotypic genus *Madigania*. Evidence uncovered during this study, however, supports its close relationship to the species of the genus *Leiopotherapon* as defined here and it is consequently 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 apomorphic osteological, myological, and intestinal characters uniting *H. adamsoni* to the other species of *Hephaestus*. Consequently, the hypothesis of a close relationship between the two species inherent in Munro's classification is herein rejected.

Specimens Examined

- Australia, Queensland: Gregory River (AMNH 20577*, 1, 64 mm.).
- Australia, Western Australia: Murchison River (AMNH 35558*, 10 [of 155], 41-118 mm.); Gascoyne River (AMNH 35580, 38); Robe River (AMNH 35587*, 10 [of 94], 45-121 mm.); Fortescue River (AMNH 35577*, 6); Maitland River (AMNH 35579, 9); George River (AMNH 35582*, 10 [of 406], 22-139 mm.); Fortescue River, Millstream (AMNH 35534, 29); Upper Sherlock River (AMNH 35581, 93); Upper Weedi Wolli Creek (AMNH 35535, 49); Nullagine River (AMNH 35557*, 10 [of 234], 24-89 mm.); Coogan River (AMNH 35540*, 14, 24-112 mm.); Stuart River (AMNH 35574, 81); DeGrey River (AMNH 35537, 52); Yeeda Creek (AMNH 35556, 55); Fitzroy River (AMNH 35560, 56); Meda River (AMNH 35560*, 20 [of 141]), 50-116 mm.); Mount Hart outcamp (AMNH 35559, 48); Bell Creek (AMNH 35559, 48); Grave Creek (AMNH 35561*, 10 [of 20], 40-96 mm.); North Creek (AMNH 35545, 90); Gibb River (AMNH 35554, 190); Hann River, Moll Gorge (AMNH 35564, 12); Hann River (AMNH 35551*, 10 [of 190], 40-113 mm.); Manning Creek (AMNH 35562*, 5, 35-67 mm.); AMNH 35536, 45; AMNH 35563, 8); Panton River (AMNH 35547, 46); Bow River (AMNH 35548*, 10 [of 34], 54-87 mm.); AMNH 35544, 71); Dunbarn River (AMNH 35585, 6); Ord River (AMNH 35576, 32.)
- Australia, Northern Territory: Moriarity Creek (AMNH 35542, 76); West Baines River (AMNH 35541, 39); Katherine River (AMNH 35553*, 10 [of 25], 45-75 mm.; AMNH 35538, 12); Fergusson River (AMNH 35583, 46); Mary River (AMNH 35568*, 2, 72-95 mm.; AMNH 35567, 12); South Alligator River (AMNH 35555, 8; AMNH 35543, 2); Barramundie Creek (AMNH 35550, 14; AMNH 35569*, 3, 45-90 mm.; AMNH 35584, 20); Wildman River (AMNH 35570, 2); Mary River (AMNH 35571, 4); east Mary River (AMNH 35539, 22); Lower Daly River (AMNH 35572, 1); isolated pool, 15 mi. east of Daly River Police Station (AMNH 35568*, 10, 44-100 mm.); Red Lily Lagoon (AMNH 35552, 1; USNM 173655*, 4, 116-184 mm.); Upper Manton River (AMNH 35573, 6); Katherine River, Katherine (AMNH 20579, 1); vicinity of Finke River and Ellery Creek (AMNH 35575, 40); Ellery Creek (AMNH 35578, 23); Roper River Mission (USNM 173859, 9).
- Australia; Victoria, Melbourne (AMNH 8739, 5 (locality questionable)).
- Australia; New South Wales: Head of Mosquito

Creek near Darling Downs (BM[NH]) 1846.3.24.4, 1; 1846.8.12.2-3, 3); Gwydir River (BM[NH] 1853.1.11.12-15, 5) (all syntypes).

***Leiopotherapon macrolepis*, new species**

Large scaled grunter

Figure 34

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 in having 29-33 lateral line scales (in contrast to 40 or more for all other members in the group).

Description. (Numbers in parentheses are of examined specimens having a given count.) Dorsal spines and rays XI-9(22), XI-10(42), XII-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 1-2 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 HL; length of longest dorsal ray 1.9-2.7 in HL; length of longest anal spine 2.2-3.4 in HL; 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

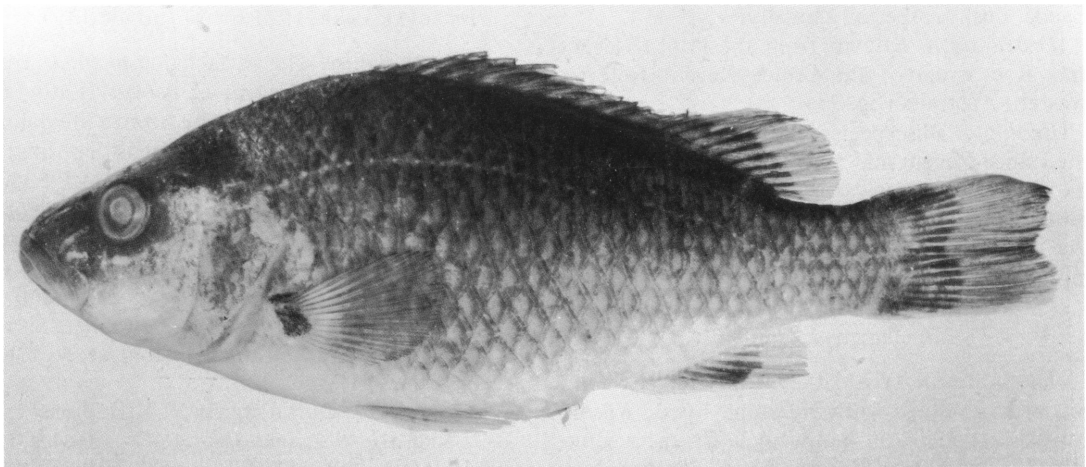


FIG. 34. *Leiopotherapon macrolepis*, holotype, WAM P-25389-001, 91.5 mm. SL.

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 asymmetrically 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 and lacking any distinct patterning. Spinous and soft dorsals 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. Known from the Prince Regent and Roe rivers of the Prince Regent Reserve, Western Australia (fig. 33).

Ecology. This species is widely distributed in the Prince Regent and Roe rivers 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 (Allen, 1975).

Specimens Examined

The holotype (WAM P-25392-001), 91.5 mm. SL, was obtained with rotenone by B. Wilson, August 21, 1974, in Youwanjela Creek, a tributary to the Prince 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). More paratypes were obtained with rotenone by G. R. Allen, August 18, 1974, in the upper Roe River (WAM P-25029-002 and AMNH 33976, 35, 27-94 mm. SL); by G. R. Allen and A. Chapman, in the upper Roe River (approx. lat. 15°26'S, long. 125°37'E) (WAM P-25-25-002, 1, 38 mm.); by G. Allen, August 14, 1974 in the upper Roe River (WAM P-25026-003, 5, 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, 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, 38 mm.).

All 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

Figure 35

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 (no locality).

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. A member of the genus *Leiopotherapon* distinguishable 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; pectorals 13-14; pelvics I-5; 40-45 lateral line scales; 3-4 scales on caudal; 5-6 scales above lateral line; 14-15 scales below lat-

eral line; 12-14 predorsal scales to occiput; one row of scales in sheath at base of dorsal fin, sheath extending to second dorsal ray; two 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. Interorbital region with ridges. Nostrils separated by a distance equal to one-half diameter of eye. Lacri-

mal with three or four 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 asymmetrically 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 10 to 15 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,

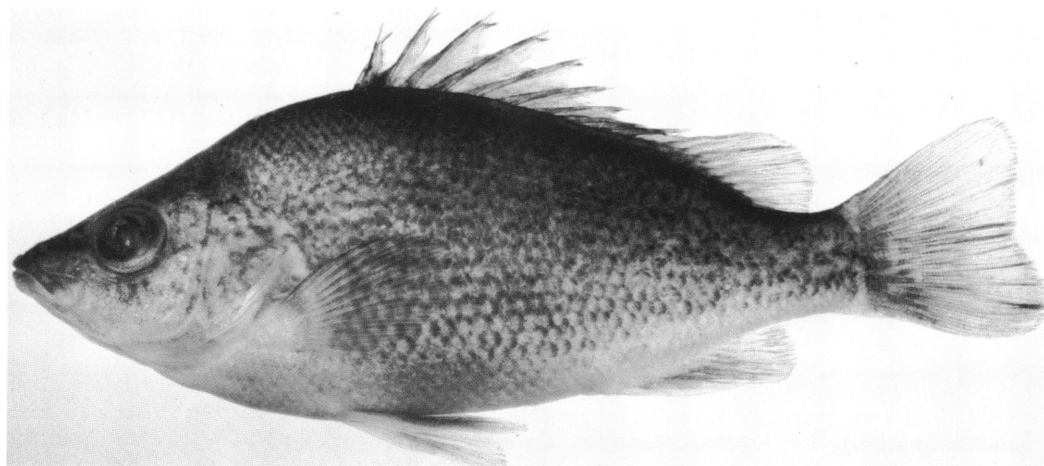


FIG. 35. *Leiopotherapon aheneus*, AMNH 35621, 64 mm. SL.

especially on upper lobe. Pectorals and pelvics clear to dusky. Adults elongate, often approaching the body forms of some populations of *L. unicolor*, from which they can always be distinguished, however, in having the longest dorsal spines longer than the longest dorsal rays.

Distribution. This species has a limited distribution in Western Australia bounded by the Ashburton and Fortescue rivers (fig. 33). 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), who placed the species in the genus *Mesopristes*, evidence of this study supports the placement of this species in *Leiopotherapon*. All the other species of the genus *Mesopristes* (*sensu* Whitley) share a series of apomorphic states of the extrinsic swimbladder muscle, posttemporal form, pigmentation patterns and other characters lacking in *L. aheneus*.

Mees (1963) in the original species description stated that the suprascapular bone is exposed in *L. aheneus*. However, the posttemporal (= suprascapular of previous authors) although having a reduced scale covering is not expanded, serrate, or exposed.

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

GENUS 2, *AMNIATABA*

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

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

Nomenclature. The generic name, *Amniataba*, from *amnīs*, Latin for stream, and *Ataba*, a Queensland aboriginal name for a marine tera-

ponid, refers to the freshwater habitat of the type species of the genus.

Diagnosis. Distinguishable from other members of the family in having two spines on the first proximal dorsal pterygiophore, a distinctive caudal mottling pattern and lacking a foramen for exit of blood vessels from the third hemal arch anterior to the parahypural vertebrae.

Included Species. Two species are placed in the genus *Amniataba* in this study; *A. percoides* which is distributed in fresh water across the northern two-thirds of Australia and *A. caudavittatus* which is distributed in marine and fresh waters of northern Australia and southern New Guinea.

Amniataba percoides (Günther, 1864)

Black striped grunter

Figure 36

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, Hodgkinson River).

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

Therapon terrae-reginae 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).

Terapon 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, figure (Queensland, Western Australia, Central Australia). Lake, 1971, p. 34, pl. 78 (northern Australia).

Amniataba percoides burnettensis Whitley, 1943, p. 183 (original description, Burnett River [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 perchlike appearance of the species. The syntypes are deposited in the British Museum (Natural History) (BM[NH] 1864.10.9.1-2).

Diagnosis. *Amniataba percoides* can be distinguished from the adults of all other species in the family by its pattern of narrow, black vertical bars. Within the genus, it is distinguished further by its lack of an oblique bar across each lobe of the caudal and the lack of body spots (in contrast to the presence of each of these pigmentation patterns in *A. caudavittatus*).

Description. Dorsal spines XIII-XIV; dorsal rays 8-10; anal III, 7-9; pectorals 14-16; pelvics 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; two 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 SL; 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

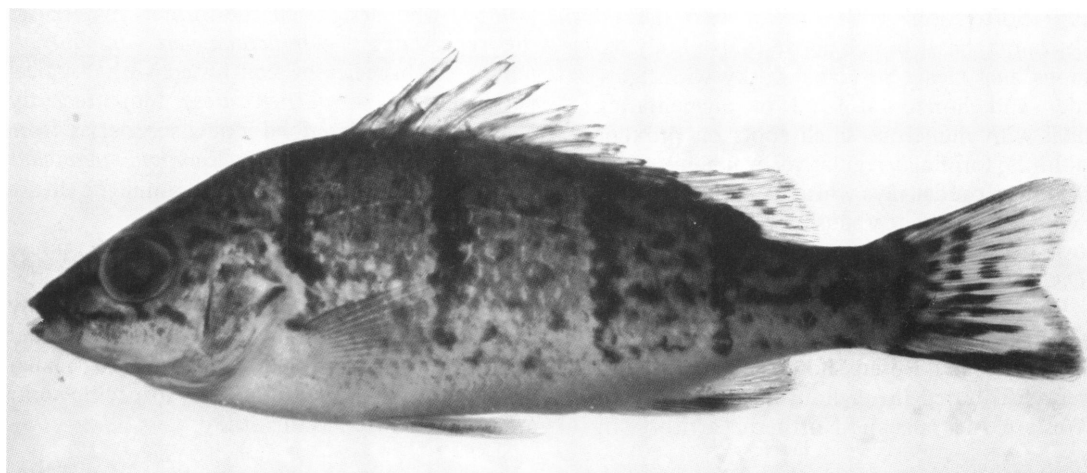


FIG. 36. *Amniataba percoides*, AMNH 35615, 68 mm. SL.

side. Supracleithrum exposed. Posttemporal not exposed, covered with skin and scales.

Spinous dorsal strongly arched; first spine very short; fourth to sixth spines 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 asymmetrically pointed; fifth ray longest. Pelvics pointed; first and second rays longest; reaching to anus. Caudal slightly emarginate, lobes obtusely pointed.

Coloration. Young with several dorsal head stripes running to interorbital region. Additional stripes run from tip of snout to top of orbit and under orbit across cheek. In adults, top of head darker with stripes variably masked; stripes under and in front of eye variably masked; head lighter ventrally. Body dark above, lighter below. Scales above lateral line with darker edges. Five to seven vertical black bands on side; each about 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 soft dorsal 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 small spots on proximal two-thirds; forming irregular vertical bands; edges dark; lower caudal rays white. Pectorals colorless or with some slightly dusky markings. Pelvics colorless except outer rays that are dusky.

Distribution. Across northern Australia from the Burnett River of Queensland to the Robe River of Western Australia. Collections by Nelson, Butler, and Rosen show the species to be widely distributed throughout the northern parts of Western Australia and Northern Territory (fig. 37).

Castelnau (1875) described a new species, *Terapon fasciatus*, from the Swan River of West-

ern Australia. This description of a species that following workers considered a synonym of *Terapon* (= *Amniataba*) *percoides* was the basis for the inclusion of the latter species in the Western Australian fauna. Although *A. percoides* is indeed present in the state, no further specimens have been collected in the past century south of the Robe River, a considerable distance north of the Swan. As pointed out by Mees (1963), the specimens examined by Castelnau probably originated on the mainland opposite the Dampier Archipelago, a region where *A. percoides* is plentiful.

Waite (1923) listed this species for South Australia without exact localities. Although I have not found citations of the species from that state, Butler'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 South Australia.

Ecology. This species is an inhabitant of a variety of environments ranging from still ponds to rapidly flowing rivers. It is found in water conditions ranging from slightly brackish to fresh and from clear to greenish and opaque.

Remarks. There occur marked variations between populations of *Amiataba percoides* as would be expected of a species having a distribution over great distances and a diverse landscape. This variation was noted by Ogilby and McCulloch (1916) in a key distinguishing populations from the Burnett and Fitzroy rivers. This distinction was later formalized by Whitley (1945a) who designated the Burnett material 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 northern Queensland as *Terapon percoides yorkensis*, failing, however, to delimit its distinguishing characters.

Although differences do occur between populations of *Amniataba percoides* (both those formalized by the above subspecies and many others) there have not been found any consistent differences subdividing the species into smaller units. Consequently the above subspecific units are not recognized in this study.

Specimens Examined

Australia, Queensland: Archer River, Queensland

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

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

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

35606*, 1, 69 mm.); South Alligator River (AMNH 35612*, 15, 36-115 mm.); AMNH 35608, 42); Barramundie Creek (AMNH 35598, 9; AMNH 35599, 22); Lilly (Barramundie) Lagoon (AMNH 35594*, 13, 40-90 mm.); Jim Jim Creek (AMNH 35609, 3); Daly River (AMNH 35589, 3); isolated pool 15 mi. east of Daly River Police Station (AMNH 35601*, 9, 39-58 mm.); Upper Manton River (AMNH 35592, 17); Red Lily Lagoon, 9 mi. northeast of Elsey Homestead (AMNH 35593*, 2, 60-96 mm.); Boggy Hole, 7 mi. downstream from junction of Finke River and Ellery Creek (AMNH 35618, 34); Roper River Mission (USNM 173665, 16); Oenpelli (USNM 173666, 9).

Amniataba caudavittatus (Richardson, 1844)

Flag tailed grunter, Bar tailed grunter,

Spotted perch

Figure 38

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

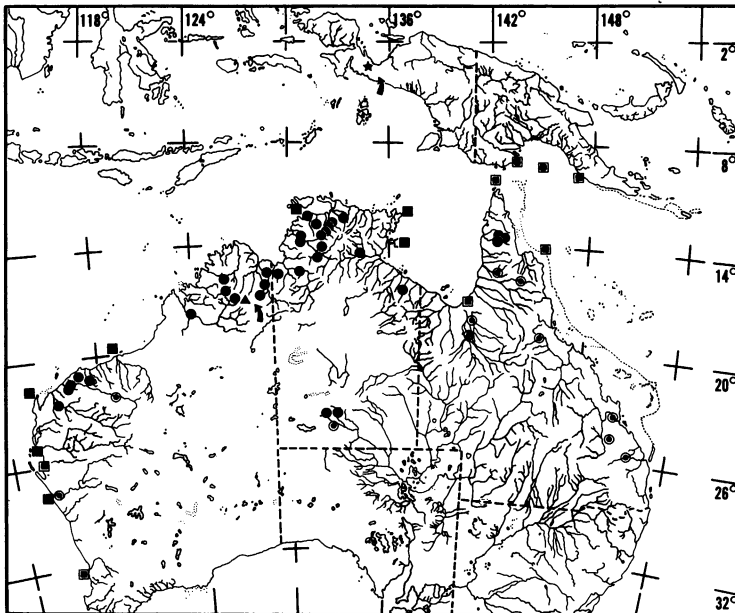


FIG. 37. Distribution records for the species of genera 2, 3, and 4. *Amniataba percoides* (circles), *A. caudavittatus* (squares), *Hannia greenwayi* (triangle, indicated by arrow), and "*Terapon*" *jamoerensis* (star indicated by arrow). Solid symbols represent specimens examined, patterned symbols are additional literature records.

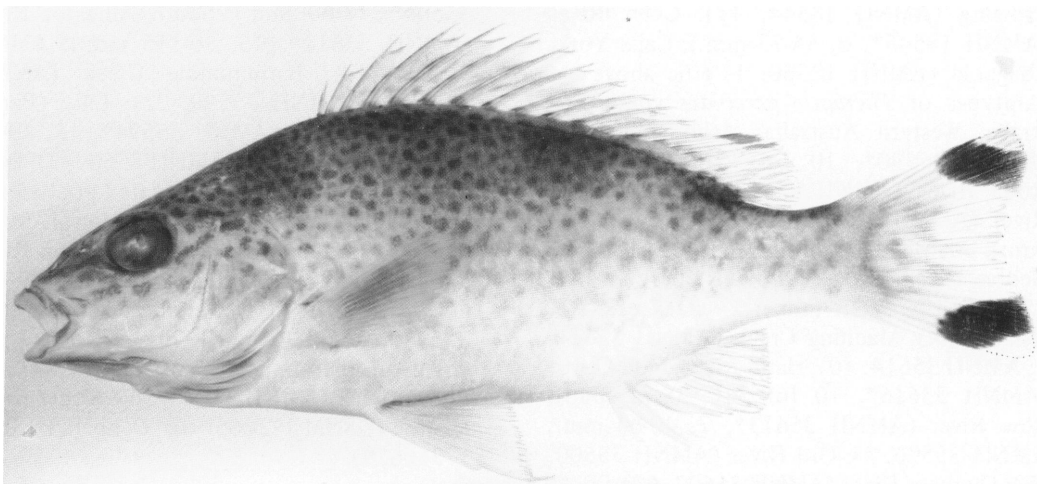


FIG. 38. *Amniataba caudavittatus*, AMNH 35627, 110 mm. SL.

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). Günther, 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). Kailola, 1975, p. 100 (New Guinea: Bristow Island, Thomson and Jerai Bays).

Therapon bostockii Castelnau, 1873, p. 128 (original description, Freemantle).

Therapon 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 hypersaline waters); 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 transverse black blotches across each lobe of the caudal fin in this species. The species was described from a series of skins now in the British Museum (Natural History) (BM[NH] 1844.12.15.44-46).

Diagnosis. *Amniataba caudavittatus* is distinguishable by its possession of large transverse black blotches across each lobe of the caudal fin (in contrast to a mottled caudal lacking these blotches in *A. percoides*).

Description. Dorsal spines XII-XIII; dorsal rays 8-10; anal, III, 8-9; pectorals 13-17; pelvics I-5; 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; one 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 HL; 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 asymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest, filamentous, falling short of anus. Caudal emarginate.

Coloration. Head darker above, light ventrally. Body gray 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.

Life Coloration. Each caudal lobe with a prominent black blotch; blotches 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 fresh waters of Western Australia from Perth north, Northern Territory, Queensland, Torres Strait and the southern half of New Guinea (fig. 37).

Ecology. In Western Australia, *A. caudavittatus* was found in waters ranging from fresh to hypersaline (Bayly, 1972), over a variety of substrates and in association with many different types of vegetation.

Remarks. Munro (1967) added a second species *A. habbema* (= *Hephaestus trimaculatus*), to the previously monotypic genus *Amphitherapon* erected by Whitley (1943) for *A. caudavittatus*. The added species, however, possesses a series of apomorphic characters (extrinsic swimbladder muscle form, tabular form, and others) uniting it with the other species of the genus *Hephaestus*, character states lacking in *A. caudavittatus*. Consequently the hypothesis of a close relationship between *A. caudavittatus* and the nominal form *Terapon habbema* is rejected.

Specimens Examined

Western Australia: Bush Bay (AMNH 35627*, 6, 32-162 mm.); DeGrey River (AMNH 35629*, 9, 46-56 mm.); Murchison River (AMNH 35631*, 1, 84 mm.); Northwest Cape (AMNH 35628*, 15 [of 86], 25-114 mm.). Northern Territory: Casuarina Beach (AMNH 35630*, 10 [of 37], 40-72 mm.); Nightcliff (USNM 173668*, 4, 51-62 mm.); Port Langdon (USNM 173671*, 5, 44-79 mm.). Groote Eylandt (USNM 173672, 7); Port Bradshaw

(USNM 173675, 2; USNM 173676, 1); Yirr-kalla (USNM*, 6, 62-174 mm.).

GENUS 3, *HANNIA*, NEW GENUS

Nomenclature. The generic name *Hannia* refers to the type locality of the type species of the genus, 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 vertical striping and a distinct foramen for the exit of blood vessels from the third hemal arch anterior to the parahypural vertebrae and having 32-38 lateral line scales.

Type Species. *Hannia greenwayi*, new species.

Included Species. The genus *Hannia* contains only one species, *H. greenwayi* of Western Australia.

***Hannia greenwayi*, new species**

Greenway's grunter

Figure 39

Nomenclature. The trivial name, *greenwayi*, is in honor of Mr. James C. Greenway, Jr., of the Department of Ornithology, the American Museum of Natural History, whose generous financial support made possible the American Museum-Australian expedition to Western Australia that 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(18), 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; one 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. Inter-

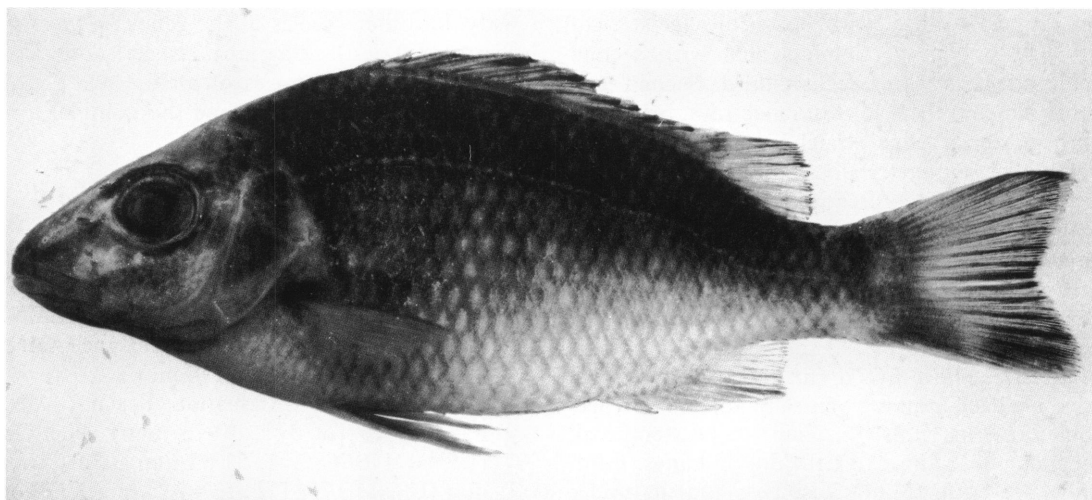


FIG. 39. *Hannia greenwayi*, holotype, WAM P-25380-002, 80.9 mm. SL.

orbital region with bony 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 asymmetrically 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 grayish, 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 1 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

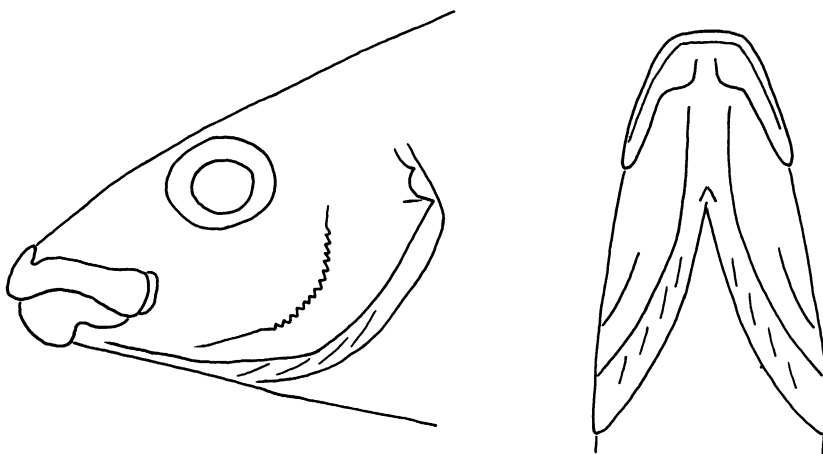


FIG. 40. Drawing of the lateral and ventral views of the "blubber" lip condition found in some individuals of *Hannia greenwayi*.

generic designation of the only contained species "*Terapon*" *jamoerensis* Mees. For reasons already detailed 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, Indonesia having two spines on the first proximal dorsal pterygiophore, a uniform brown coloration and a relatively high lateral line count (60-66 lateral line scales).

Included Species. The genus "*Terapon*" contains one species, "*T.*" *jamoerensis*, known only from Lake Jamoer in West Irian.

"*Terapon*" *jamoerensis* (Mees, 1971)

Jamoer grunter

Figure 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 Historie (RMNH 25225).

Diagnosis. As for the genus.

Description. Dorsal spines XII-XIV; dorsal rays 10-11; anal III, 8-9; pectorals 14-15; pelvics I-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; one 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 HL; 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 HL; 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 convex 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. Nos-

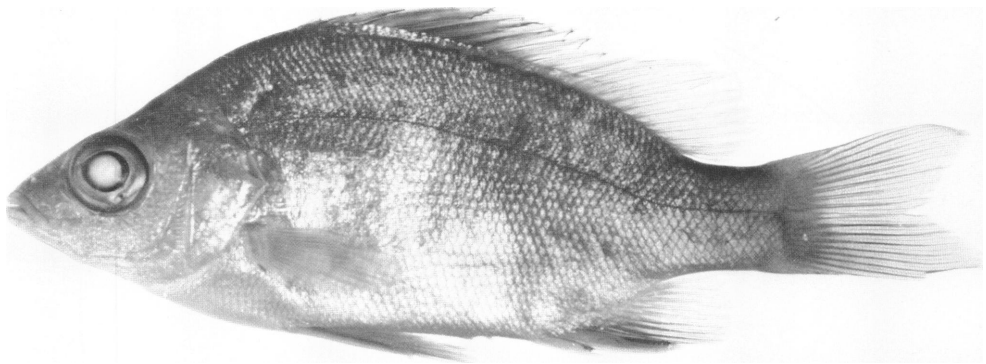


FIG. 41. "*Terapon*" *jamoerensis*, paratype, RMNH 35224, 65 mm. SL.

trils 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 asymmetrically 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 running 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; a small lake (diameter 6-8 km.) in the narrow region of the Vogelkop peninsula (fig. 38). This locality though closer to the northern coast of the island is actually part of the southern watershed (Boeseman, 1963).

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

Specimens Examined

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

GENUS 5, *LAGUSIA*, NEW GENUS

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

Diagnosis. Freshwater teraponids distinguish-

able 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 one species, *L. micracanthus* from Sulawesi.

Lagusia micracanthus (Bleeker, 1860)

Celebes grunter

Figure 42

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

Therapon (Datnia) micracanthus: 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*).

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

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

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

Diagnosis. Characters as for the genus.

Description. Dorsal spines XII-XIII; dorsal rays 8-11; anal III, 8-9; pectorals 15; pelvics 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; one row of scales in sheath at base of dorsal fin, sheath extending to sixth or seventh dorsal ray; two rows of scales in sheath at base of anal fin, sheath extending to sixth anal ray; cheek scales in four 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 in SL; 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 HL; jaw length 3.3-3.6 in

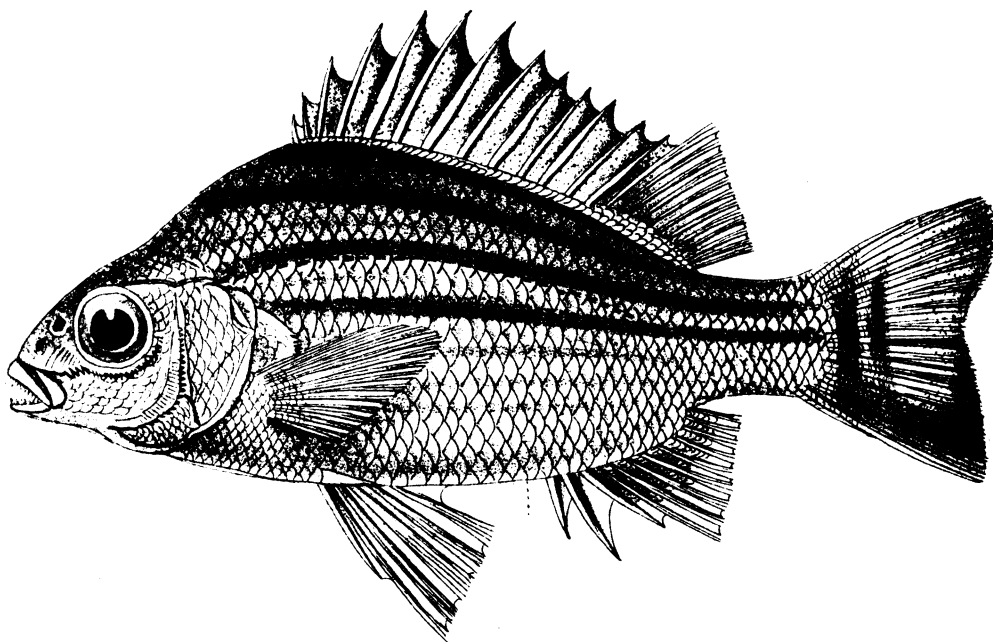


FIG. 42. *Lagusia micracanthus*, from Bleeker, 1873, pl. 340.

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 decreas-

ing 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 asymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest; reaching to anus. Caudal emarginate.

Coloration. Description taken from Bleeker (1860), and Weber and deBeaufort (1931). 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,

Minralang River, and Tjenrama River. It has only been collected twice, the type series in 1859 and the specimens listed by Weber (1894).

Remarks. Fowler (1931, 1934) followed by Munro (1956) synonymized two nominal New Guinea species, *Terapon trimaculatus* and *T. habbemai*, into *Lagusia micracanthus*. However, *L. micracanthus* lacks apomorphic states of the posttemporal, extrinsic swimbladder muscle and other characters found in the New Guinea species; characters placing them in *Hephaestus*. It is furthermore quite distinct from them on the basis of coloration and scalation; undoubtedly representing a distinct and not closely related species, a situation noted by Munro (1967).

Specimens Examined

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

GENUS 6, *PELATES*

Pelates Cuvier, 1829, p. 146 (*Pelates quadrilineatus* Cuvier¹).

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

Nomenclature. The generic name is of unknown significance.

Diagnosis. Marine teraponids with an unexposed, non-serrate posttemporal, and longitudinal body stripes. Distinguishable in having a direct muscular attachment of the extrinsic swimbladder muscle to the ventral process of the posttemporal and a ligamentous attachment of the muscle to the rear of the skull.

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

Pelates quadrilineatus (Bloch, 1790)

Four-lined terapon, Trumpeter perch

Figure 43

Holocentrus quadrilineatus Bloch, 1790, p. 82,

pl. 238, fig. 2 (original description, The Orient). Walbaum, 1792, p. 642 (on Bloch). Forster, 1795, p. 16. Lacépède, 1802, pp. 339, 380 (East Indies).

Pristopoma sexlineatus Quoy and Gaimard, 1824, p. 320 (original description, shore at Sydney, Port Jackson).

Pelates sexlineatus: Cuvier, 1829, p. 149 (original description, "Hawaiian Islands," in error).² Fowler, 1931, p. 362 (compiled).

Therapon quadrilineatus Cuvier, 1829, p. 134 (original description, no locality).² Kailola, 1975, p. 101 (New Guinea: Fairfax Harbor, Manus Island, Bristow Island).

Pelates quadrilineatus Cuvier, 1829, p. 146 (original description, Port Jackson, Australia).² 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 (Bahrein, Iranian Gulf). Gopinath, 1946, p. 7 (larvae). Smith, 1949, p. 184 (Pomdoland, Dalagao Bay, South Africa); 1955, p. 209 (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, in error?). Mees, 1962, p. 33 (Western Australia). Chien, 1962, p. 543, fig. 448 (Hainan region). Freihof, 1963, p. 132 (RLA pattern). Sanchez, 1963, p. 58, fig. 3 (Inhaca, Mozambique). Marshall, 1964, p. 167, pl. 16 (Mouton Bay, Queensland). Tortones, 1964, p. 44 (New Guinea). Munro, 1967, p. 322 (New Guinea). Maugé, 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 (procurrent spur).

Therapon xanthurus Cuvier, 1829, p. 135 (original description, Java).

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

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

¹Jordan (1917) listed this species as the type of the genus. I am unable to determine the basis for this designation.

²Further references to this nominal species can be found in Fowler, 1931, pp. 358-362 for the years between the original description and 1930.

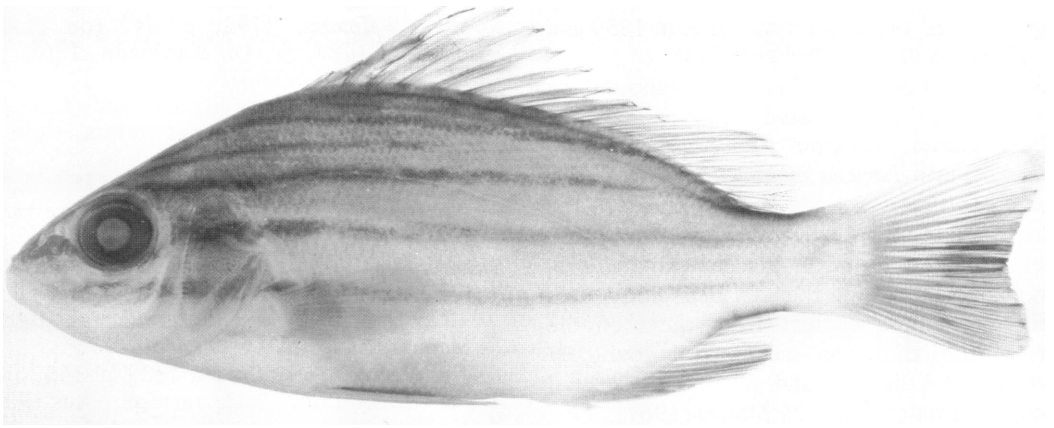


FIG. 43. *Pelates quadrilineatus*, USNM uncat., BBC 1508, 70 mm. SL.

Therapon cuvieri Bleeker, 1854, p. 211 (original description, Timor¹).

Therapon (Pelates) quadrilineatus: Bleeker, 1873-1876, p. 117 (East Indies, Philippines).

Therapon cuvierii: Pöhl, 1884, p. 27 (Viti, Fiji; in 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 (Ceylon, Formosa, Philippines, Queensland).

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 is distinguished from all members of the family by its tri-chambered swimbladder and three predorsals inserting anterior to the first neural spine (in contrast to a bichambered swimbladder and at most two predorsals in all other members of the family). Within the genus it can be distinguished by its unicuspid teeth, 16-18+1+22-27 gill rakers and 66-75 lateral line scales (in contrast to tricuspid teeth, 6-7+1+14-16 gill rakers and 76-87 lateral line scales in *P. sexlineatus*).

Description. Dorsal spines XII-XIII; dorsal rays 9-11; anal III, 9-10; pectorals 13-16; pelvics

I-5; 66-75 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; one 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 HL; 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 1.7-2.0 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 opercu-

¹See footnote 2, page 249.

lar 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 spines 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 asymmetrically 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.

Stripe running from snout to dorsal edge of orbit; dividing in interorbital region into two stripes 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 pigmentation under orbit. In adults top of head 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 spinous dorsal 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 on side of body posterior to nape. In larger individuals light pigmentation occurs along edge of anterior dorsal spines. Juveniles with six or seven vertical bars present in addition to striped pattern. 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 dusky edges. Pectorals and pelvics yellowish.

Distribution. In marine and brackish waters of Indo-west Pacific: Africa north of Natal, Mada-

gascar, 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. 44).

Fowler (1959) listed this species from Fiji following Pöhl (1884). However, since Pöhl there have been no further collections of the species from that region. As such it is likely that the original record was either an error in identification or locality. Similarly Schmeltz (1869) appears incorrect in his identification of material from Fiji as *Terapon cuvierii*, a species considered a synonym of *P. quadrilineatus*.

Ecology. The development of this species from the postlarval stages onward has been described in detail by Munro (1945) who found an extended spawning season in New South Wales lasting from late summer well into winter.

Remarks. Cuvier (1829) described four species of *Pelates* and *Terapon*, which have since been reduced to two nominal forms: *Pelates sexlineatus* and *P. quadrilineatus*. These species were distinguished from each other by the presence in *P. quadrilineatus* of black blotches between the third and eighth dorsal spines and on the antero-dorsal body wall (the latter sometimes lacking); pigmentation lacking in *P. sexlineatus*. These nominal forms were retained as distinct species by a variety of workers including Ogilby and McCulloch (1916) and Fowler (1931) but not by Weber and deBeaufort (1931) who recognized only *P. quadrilineatus*.

Examination of material of *Pelates* from throughout the Indo-west Pacific has shown that these pigmentation patterns vary in intensity ontogenetically and geographically throughout the region, with complete gradation from dark pigmentation to its total absence. It would therefore appear that there is actually only one variable species, *P. quadrilineatus*.

Specimens Examined

Africa: Changamu (USNM 72884, 1; USNM 72889, 1); Madagascar, Tulear (UMMZ 185976, 1, UMMZ 185648, 1).
Persian Gulf, Tarut Bay, Siyat (USNM 148116, 5).
Thailand (USNM 88369, 1).

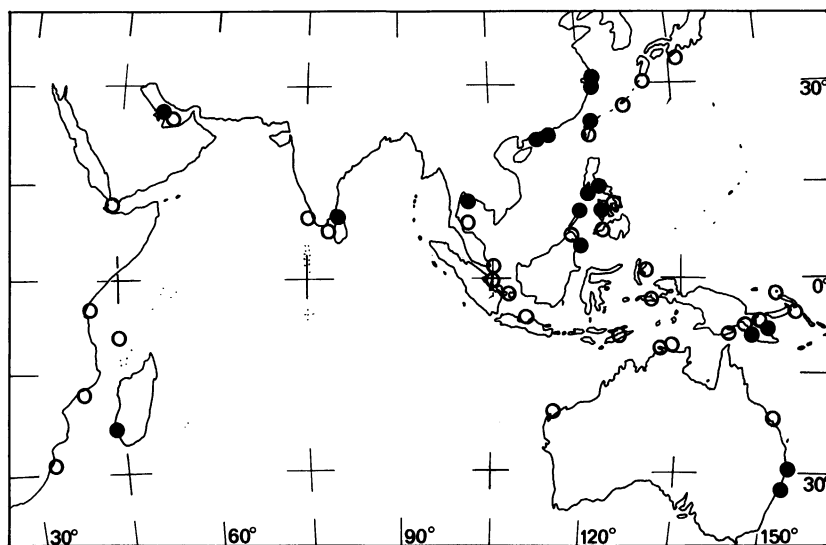


FIG. 44. Distribution records for *Pelates quadrilineatus*. Solid symbols represent specimens examined, open symbols are additional literature records.

Indonesia, Borneo, Sandakan (USNM 146360*, 3, 62-76 mm.).

Philippines: Manila (USNM 56307, 6); Lubang (USNM 72183*, 1, 105 mm.); Iloilo, Panay (USNM 106856*, 1, 78 mm.); Palawan (USNM 146924*, 4, 31-60 mm.); Culion (UMMZ 100379*, 1, 86 mm.).

Australia, Port Jackson (USNM 59978*, 2, 88-109 mm.; USNM 42048, 1; USNM 176978*, 1, 100 mm.).

New Guinea: Coral Sea at Kapa Kapa (USNM uncat., BBC 1524, 1); Trobriand Islands, Kiriwana (USNM uncat., BBC 1505*, 11, 50-75 mm.; BBC 1506, 6; BBC 1520*, 1, 69 mm.; BBC 1508, 15).

China: Taiwan, Pescadores Islands, Peng-Hu (USNM 192540*, 1, 90 mm.; USNM 192865*, 3, 113-118 mm.); Hong Kong (USNM 6536*, 1, 123 mm.); Shanghai (USNM 148416*, 1, 101 mm.).

Pelates sexlineatus (Quoy and Gaimard, 1824)

Striped perch

Figure 45

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 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, Australia, Philippines). Herre, 1931, p. 53 (Luzon). Hardenberg, 1938, p. 311 (Batavia [Djakarta], 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).
Kailola, 1975, p. 98 (Gulf of Papua, Dago Island, Bristow Island).

Therapon (Helotes) sexlineatus: Bleeker, 1873-1876, 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 lines present along the sides of the body in the 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, 76-87 lateral line scales and a body depth of 3.4-4.0 (in contrast to 16-18+1+22-27) gill rakers, 66-75 lateral line scales and a body depth of 2.6-3.2 in *P. quadri-lineatus*).

Description. Dorsal spines XI-XII; dorsal rays 9-11; anal III, 9-11; pectorals 15-16; pelvics I-5; 76-87 lateral line scales; 5-8 scales on caudal; 11-13 scales above lateral line; 22-24 scales below lateral line; 16-21 predorsal scales to occiput; one 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 2.6-3.1 in HL; length of longest anal ray 1.6-2.1 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 triscupidate; cusps of very nearly equal size. Outer row of teeth enlarged; inner rows in bands. No teeth on vomer or 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

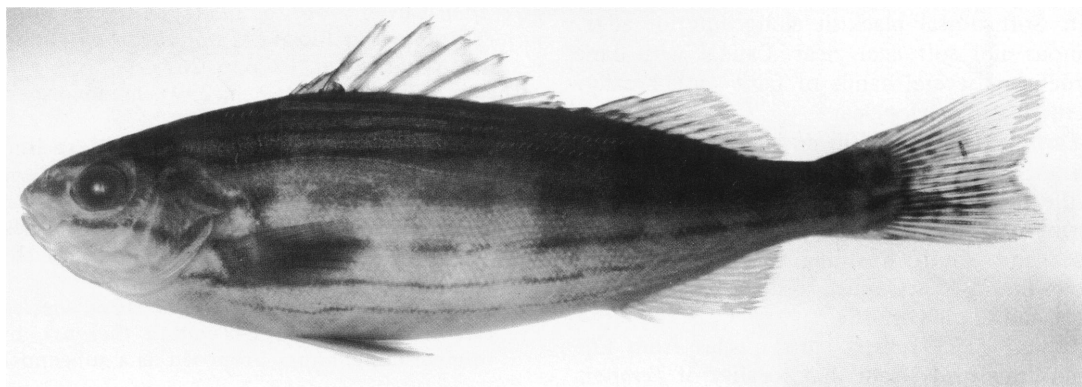


FIG. 45. *Pelates sexlineatus*, AMNH 31415, 115 mm. SL.

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 asymmetrically 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 grayish 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. Found in marine waters of 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, and China (fig. 46).

Fowler (1959) listed this species from Fiji based on records from that locality of *Terapon cuvieri*. However, these records of a species that he evidently considered to be a synonym of *P.*

sexlineatus have not been supported by more recent collections. As such it would appear that the presence of *P. sexlineatus* around Fiji, an area distant from confirmed records, would be unsubstantiated.

Helotes octolineatus, described by Jenyns (1842) from Western Australia, was differentiated by him from *Helotes* (= *Pelates*) *sexlineatus* by a greater number of body stripes and a lower anal ray count. However, no difference exists between the nominal species in the number of stripes, and an examination of the holotype of *H. octolineatus* shows the reduced anal ray count to be a consequence of a malformed anal fin.

Specimens Examined

Australia, Western Australia: Cockburn Sound, east side (AMNH 31395*, 2, 138-145 mm.); Cockburn Sound, Point Peron (AMNH 31415*, 20 [of 143], 45-120 mm.; AMNH 35634*, 2, 140-150 mm.); King George's Sound (BM[NH] 1917.7.14.41 [type of *Helotes octolineatus*]).
Australia, Northern Territory, Port Bradshaw (USNM 173681, 9).
Philippines, Luzon, Cavite Market (USNM 146364*, 1, 72 mm.).
China, Kowloon (USNM 146365*, 2, 149-174 mm.).
Indonesia; Java, Batavia (UMMZ 182780*, 1, 90 mm.).

GENUS 7, *TERAPON*

Terapon Cuvier, 1817, p. 295 (type species *Holocentrus servus* Bloch (= *Terapon jarbua*), designated by Bleeker, 1876, p. 267).

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

Pterapon Gray, 1835, p. 88 (emended spelling 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, proposed as a subgenus).

Nomenclature. The generic name, *Terapon*, Greek for slave, comes from Bloch's statement

that these fishes were utilized primarily by the servant classes in Japan and were consequently termed "slave fish." The spelling is an incorrect transliteration rather than a *lapsus calami* and is therefore valid (see also the discussion on the genus and family names in the Introduction).

Diagnosis. Members of the genus *Terapon* are distinguishable from the other species 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 entering into brackish and fresh waters throughout their range. All have extensive ranges extending from the east coast of Africa to the New Hebrides and north to Japan, with *T. jarbua* extending east to Samoa.

Terapon jarbua (Forskål, 1775)

Crescent perch, Tigerfish, Thornfish

Figure 47

- Sciaena jarbua* Forskål, 1775, pp. XII, 50 (original description, Djedda, Red Sea). Bonnatere, 1788, p. 123 (Red Sea). Gmelin, 1789, p. 1303 (Arabia). Walbaum, 1792, p. 318 (on Forskål). Shaw, 1790, p. 541 (Arabian Seas). *Holocentrus servus* Bloch, 1790, p. 80, pl. 238, fig. (original description, Japan). Walbaum, 1792, p. 641 (on Bloch). 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). *Terapon servus*: Cuvier, 1829, p. 125 (Timor, Seychelles, Pondichery, Moluca, Malabar).¹ 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, figure 1 (copied from Hamilton). *Terapon trivittatus*: Cantor, 1849, p. 1001

¹Further references to this nominal species can be found in Fowler, 1931, p. 330 for the years between the original description and 1930.

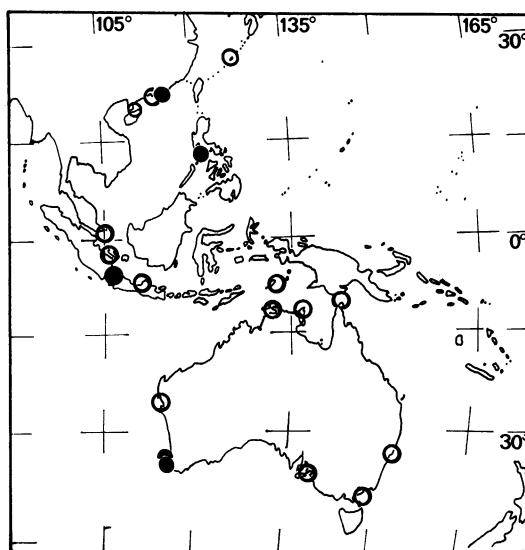


FIG. 46. Distribution records for *Pelates sexlineatus*. Solid symbols represent specimens examined, open symbols are additional literature records.

- (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).² 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 (southeast Madagascar, Seychelles). Herre, 1934, p. 53 (Philippines: Curimao, Bauang Sur, Manila, Lemery, Duma-

² See footnote 1, this page.

- guete, Jolo); 1936, p. 195 (Fiji, Malekula Island, New Hebrides). Hardenberg, 1936, p. 246 (Kapuas 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, Sagurara 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). Herald, 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). Dorai, 1960, p. 9 (sonic ability). Schneider, 1961, p. 515 (physiology, sonic ability). Chien, 1962, p. 542, fig. 447 (Hainan region). Freihofner, 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, Tanganyika). Okada, 1966, p. 232, fig. 215 (Japan). Maugé, 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 *T. jarboa*). Grant, 1972, p. 222, fig. (Queensland). Kaliymurthy and Rao, 1972, p. 199 (feeding). Rahin, 1973, p. 563 (developmental morphometrics). FAO, 1974, p. TT1, figure (distribution and fisheries). Tortonese, 1975, p. 174 (Habo, Gulf of Aden). Wallace, 1975, p. 40 (distribution of larvae). Kailola, 1975, p. 100 (New Guinea: Port Moresby, Kerema Bay, Dargo Island, Fairfax Harbor, Orokelo Bay, Manus Island, Kairiru Island). Eichelberg, 1976, p. 453 (fine structure of extrinsic swimbladder muscle).
- Therapon (Datnia) jarbua*: Bleeker, 1873-1876, p. 112 (East Indies).
- Therapon jarbua*: Jordan and Seale, 1905, p. 781 (Philippines: Negros).¹ 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). Chen, 1973, p. 19 (Taiwan). Yu and Chung, 1975, p. 15 (Taiwan).
- Therapon jarbua*: Sewell, 1913, p. 334 (Hinge Basin).
- Holocentrus katakya* Chaudhuri, 1923, p. 720 (MS name of Hamilton).
- Stereolepis inoko* Schmidt, pp. 52 and 158, fig. 7 (original description, Japan); 1933, p. 103 (placed as a synonym of *Therapon jarbua*).
- 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.** *Therapon jarbua* can be distinguished from all other members of the family by its body coloration of three downwardly curved longitudinal stripes. Within the genus *Therapon* it can be differentiated by having 12-15 gill rakers on lower limb of first arch, 70-100 lateral line scales (in contrast to 18-24 gill rakers for *T. puta*, and 46-56 lateral line scales for *T. theraps*).
- Description.** Dorsal spines XI-XII; dorsal rays 9-11; anal III, 7-10; pectorals 13-14; pelvics I-5; 75-100 lateral line scales; 7-10 scales on caudal; 13-17 scales above lateral line; 19-24 scales below lateral line; 18-25 predorsal scales to occiput; two 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; three 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 2.5-3.2 in SL; distance from dorsal origin to snout 2.2-2.9 in SL; head length 2.3-3.6 in SL; length of base of dorsal fin 1.8-2.1 in SL; snout length 3.0-3.8 in
- ¹ Further references to this nominal species can be found in Fowler, 1931, p. 330 for the years between the original description and 1930.

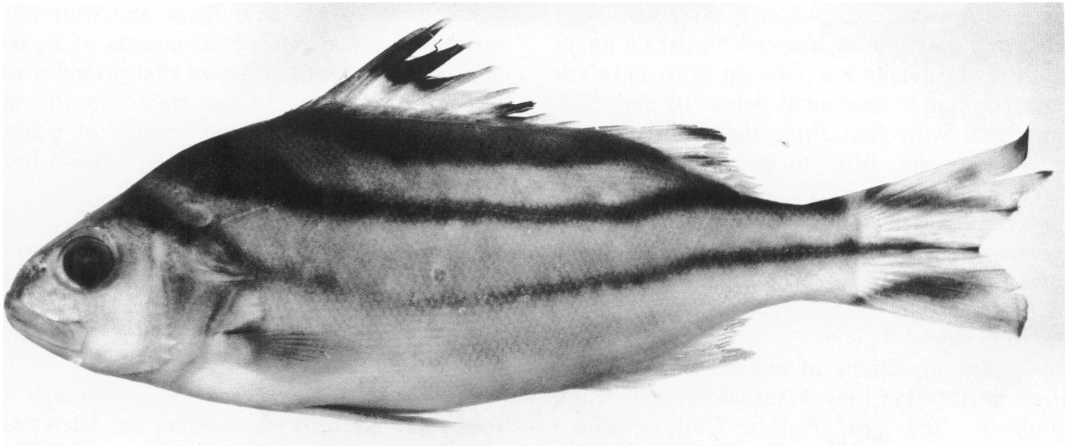


FIG. 47. *Terapon jarbua*, AMNH 35622, 141 mm. SL.

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 longest 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 asymmetrically 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 longitudinally 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 dusky.

Distribution. Coasts of east Africa from Port Alfred north, Mauritius, Madagascar, Seychelles, Comoros, 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. 48). This is the only species of the family to cover the entire marine range for the family across the Indo-west Pacific (with a minor gap along southern Australia); in addition it also moves considerable distances upstream into fresh water.

Ecology. Although there have not been any in-depth studies of the biology of *T. jarbua*, as a

consequence of its abundance and wide range, various workers have noted aspects of its ecology. Herald (1956) reported that juveniles were territorial and constructed craters in the sand perhaps as an aid to maintenance of position under tidal conditions. Schneider (1964) found *T. jarbua* to be gregarious between 2 and 5 cm. SL, but territorial between 9 and 15 cm. SL. Acoustical signals produced by the extrinsic swimbladder muscles were shown by this worker to be important in communication and to change both ontogenetically and in response to environmental variations.

Wallace (1975) reported that although the young and adults of this species are often found in fresh water, the reproduction of *T. jarbua* appears to be limited to marine waters.

Literature information and stomach content analyses show this species to be primarily carnivorous, feeding on smaller fish and invertebrates. However, many of the individuals examined had masses of scales present in the stomach and intestinal tract. Although the scales were obviously from individuals larger than that in which they were found, it is not possible to determine whether the scales were ingested during scavenging or whether *T. jarbua* has a partial lepidophagous food habit.

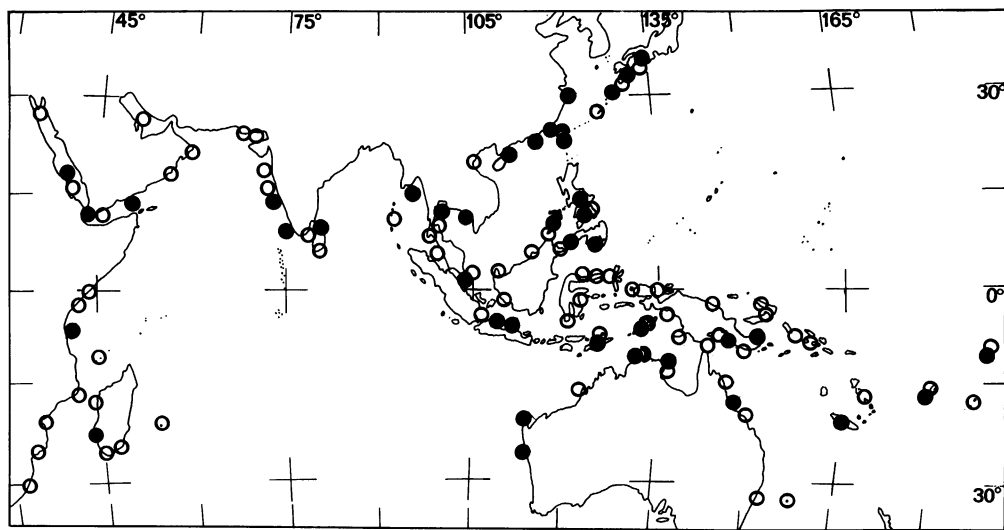


FIG. 48. Distribution records for *Terapon jarbua*. Solid symbols represent specimens examined, open symbols are additional literature records.

Remarks. Rather than recognizing only a single species (*T. jarbua*) with an Indo-west Pacific distribution, various workers have distinguished a separate eastern species, *Terapon servus* based on *Holocentrus servus* which was described by Block from Japan. Jordan and Thompson (1912) suggested that the nominal forms *T. servus* and *T. jarbua* (the latter described from the Arabian region by Forskål) represented distinct species separable on the basis of differences in morphometrics and meristics, particularly eye size and lateral line counts. These authors considered *T. servus* to be distributed around Japan, China, and Australia, with *T. jarbua* limited to the Indian Ocean. They also recognized a third form from the East Indies, the Philippines, and Samoa, but failed to define its affinities with the other two nominal forms. Their retention of *T. servus* as a distinct species was followed by Ogilby and McCulloch (1916), McCulloch (1916), Whitley (1948) and Munro (1956) among others. However, neither examination of specimens from throughout the Indo-west Pacific nor literature information reveals any discontinuities that support the existence of two species. Consequently, a single Indo-west Pacific species, *Terapon jarbua*, is recognized in this study.

Specimens Examined

- Africa: French Somalia, Djibouti (AMNH 8174*, 1, 152 mm.); Changamu (USNM 72867*, 1, 96 mm.); Zanzibar (USNM 12640*, 2, 45-90 mm.).
- Madagascar: (USNM 171062, 1); Tulear (UMMZ 185855*, 2, 70-101 mm.; UMMZ 185424*, 2 [of 17], 22-25 mm.; UMMZ 185965, 11).
- Red Sea: (USNM 49328*, 2, 98-107 mm.); southern Sinai, Sharm al Sheik (USNM uncat., VGS 69-32, 1).
- Saudi Arabia, Damnan (USNM 147847, 1).
- India: Travancore (USNM 149682, 1); Cochin (USNM 175354*, 1, 85 mm.).
- Ceylon, Koddery Bay (USNM uncat., TI 70-331, 1).
- Burma (USNM 89496, 1).
- Thailand, Prachuab Kiri Khan (AMNH 52525*, 2, 50-58 mm.; UMMZ 181157*, 2, 148-166 mm.; UMMZ 191093, 2; UMMZ 191331, 1).
- Cambodia, Kaskapik (UMMZ 181214*, 1, 107 mm.).
- Sumatra (USNM 88030, 1).
- Indonesia: Ceram (USNM uncat. VGS 74-3*, 1, 175 mm.); Java, Djakarta (USNM 72666*, 1, 107 mm.); Java, Sanarang (USNM 82101, 2); Pulau, Seribu (USNM uncat. VGS 74-36, 2); Moluccas, Ambon (USNM uncat. VGS 74-22, 1; VGS 74-19, 2); Matnag Bay (USNM 184783*, 1, 157 mm.).
- Philippines: Takao Island (USNM 72236*, 2, 15-21 mm.); Zamboango (USNM 57933, 4); Mindanao, Cotabato (USNM 184781, 2).
- China: Shanghai (USNM 130390, 1); Tsingtao (USNM 130360, 1); Hainan (USNM 87103, 1); Swatow (UMMZ 70350, 1).
- Japan: Kagoshima (USNM 75449, 1); Kobe Market (AMNH 13235*, 5, 75-128 mm.); Riu Kiu (USNM 72011*, 1, 223 mm.); Nagoya (UMMZ 142706*, 6, 51-81 mm.).
- Samoa, Apia (USNM 52342*, 4, 30-211 mm.).
- Fiji, Suva (USNM 66060*, 6, 53-175 mm.).
- Australia, Western Australia: Fortescue River (AMNH 35622*, 1, 141 mm.); Yeeda Creek (AMNH 35623*, 1, 95 mm.); Northwest Cape, Yardi Station (AMNH 35625*, 10 [of 22], 110-131 mm.); Mandu Mandu (AMNH 35626*, 6, 163-183 mm.).
- Australia, Northern Territory: Dinah Beach (AMNH 35624*, 6, 59-81 mm.); Nightcliff (USNM 173656*, 1, 75 mm.); Little Lagoon (USNM 173659*, 5 [of 13], 25-61 mm.); Yirrkalla (USNM 173662*, 4, 51-96 mm.).
- Australia, Queensland, One Tree Island (USNM uncat., VGS 66-9, 1).
- New Guinea: Trobriand Islands (USNM uncat. BBC 1512, 3); Murnass River, 25 mi. north of Madang (USNM uncat. BBC 1485, 1).

Terapon theraps (Cuvier, 1829)

Banded grunter

Figures 49, 50

Therapon theraps Cuvier, 1829, p. 129, pl. 53 (original description, Java, Mahé).¹ 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).

¹Further references to this nominal species can be found in Fowler, 1931, pp. 337-339 for the years between the original description and 1930.

- 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, Mindano), Munro, 1955, p. 116 (Ceylon). Tortonese, 1957, p. 124 (Eritrea). Fourmanoir, 1957, p. 88 (Mozambique Channel). Okada, 1959, p. 75 (Okinawa). Khalaf, 1951, p. 77 (Iraq). Kamohara, 1962, p. 34 (Japan). Chien 1962, p. 540, figure 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, (procurement spur). Kailola, 1975, p. 101 (New Guinea: Hall Sound, Yule Island, Vari Vari Island, Orokelo Bay, Fairfax Harbor).
- Therapon transversus* Cuvier, 1829, p. 137 (original description, Malabar).
- Therapon obscurus* Cuvier, 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, 1829, p. 136 (original description, Indian Ocean, Seas of the Indies). Günther, 1859, p. 275 (copied).
- Therapon cinereus* Cuvier, 1829, p. 138 (original description, Seas of the Indies).
- Datnia virgata* Cuvier, 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, 1831).
- Perca argentea*: Günther, 1859, p. 277 (India, name in text).
- Therapon (Datnia) theraps*: Bleeker, 1873-1876, 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). Evermann and Seale, 1906, p. 83 (Philippines: 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). Chen, 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).
- Nomenclature.** 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 the poorer segments of the population in many areas.
- Diagnosis.** A member of the genus *Therapon* distinguishable in having 46-56 lateral line scales and 6-8 supralateral scales (in contrast to more than 70 lateral line scales and 10-17 supralateral scales for *T. jarbua* and *T. puta*).
- Description.** Dorsal spines XI-XII; dorsal rays 9-11; anal III, 7-9; pectorals 14-15; pelvics I-5; 46-56 lateral line scales; 4-8 scales on caudal; 6-8 scales above lateral line; 14-16 scales below lateral line; 12-18 predorsal scales to occiput; two rows of scales in sheath at base of dorsal fin, upper row of scales larger, 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+14-17; vertebrae 10+15.
- Reaching 250 mm. SL; depth 2.4-3.5 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 3.0-4.0 in HL; length of longest dorsal spine 1.6-2.4 in HL; length of longest dorsal ray 2.1-2.5 in HL; length of longest anal spine 2.1-2.6 in HL; length of longest anal ray 1.8-2.5 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

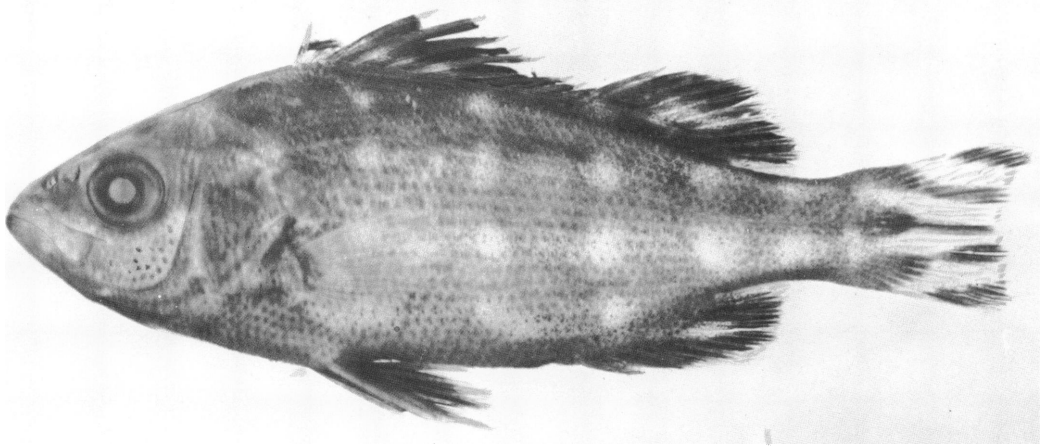


FIG. 49. *Terapon theraps*, juvenile, USNM 286561, 36 mm. SL.

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 arborescent ridges. Nostrils separated by a distance equal to diameter of posterior nostril. Lacrimal strongly serrate. Preoperculum serrate; serrations larger 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 asymmetrically 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 dusky above, silvery below with four horizontal stripes. First 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 black blotch. Caudal lobes with two bars, upper with black tip. Pectorals clear. Pelvics slightly dusky.

Distribution. Coasts of east Africa, Zanzibar,

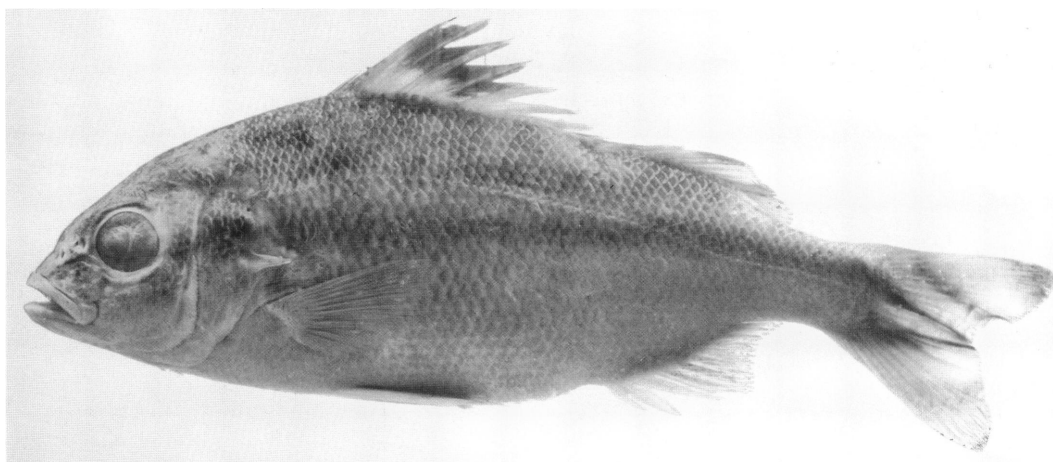


FIG. 50. *Therapon theraps*, adult, AMNH 32526, 139 mm. SL.

Red Sea, Seychelles, Madagascar, India, Bay of Bengal, Sri Lanka, Andaman Islands, Thailand, Singapore, Sumatra, Borneo, East Indies, New Guinea, Philippines, China, Australia (Northern Territory, Queensland north of Burnett River) (fig. 51).

Ecology. Zvjagina (1963) has studied and illustrated the development of this species from the egg to the adult.

Remarks. This species undergoes marked ontogenetic coloration changes which have resulted in various life stages being described as distinct species and which are illustrated by Weber (1913), Weber and deBeaufort (1931), Zvjagina (1963), and Duncher and Mohr (1931) (for caudal only).

Specimens Examined

Africa, Kenya, Formosa Bay (USNM uncat. SOSC no. 270*, 1, 87 mm.).
 Indonesia: Bali (AMNH 14816*, 10, 50-73 mm.); Java, Batavia (UMMZ 176758*, 5 [of 14], 48-132 mm.).
 Borneo: (USNM 114779*, 1, 85 mm.); Sandakan Bay (USNM 146359*, 1, 79 mm.).
 Thailand, Prachuab Kiri Khan (AMNH 32526*, 2, 129-139 mm.; UMMZ 191166*, 1, 113 mm.; UMMZ 191427*, 3, 72-75 mm.; UMMZ 191240*, 3, 117-133 mm.).
 China: Taiwan, Yeh (USNM 286561*, 2, 129-139 mm.); Fukien (UMMZ 185252*, 1,

75 mm.); Swatow (UMMZ 70430*, 2, 32-53 mm.).

Therapon puta (Cuvier, 1829)

Spiny cheeked grunter

Figure 52

Keelputa Russell, 1803, p. 19, pl. 126 (Vizagapatam).

Coius trivittatus Hamilton, 1822, pp. 92 and 370 (Ganges mouth).

Therapon puta Cuvier, 1829, p. 131 (original description, on Russell, 1803; Pondicherry, Mahé).¹ 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). Kailola, 1975, p. 101 (New Guinea).

Therapon ghebul Cuvier, 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).¹

¹Further references to this nominal species can be found in Fowler (1931) pp. 328-329 for the years between the original description and 1930.

Therapon (Datnia) trivittatus: 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 (Madang, New Guinea). 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).

Nomenclature. The trivial name *puta* is de-

rived from its native name, Keel-puta, at Vizagapatam.

Diagnosis. A member of the genus *Therapon* distinguishable in its body pattern of straight longitudinal stripes (in contrast to downwardly curved stripes of *T. jarbua*) and lateral line count of 70-85 (in contrast to 46-56 for *T. theraps*).

Description. Dorsal spines XI-XII; dorsal rays 9-11; anal III, 8-9; pectorals 13-15; pelvics I-5; 70-85 lateral line scales; 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; two rows of scales in

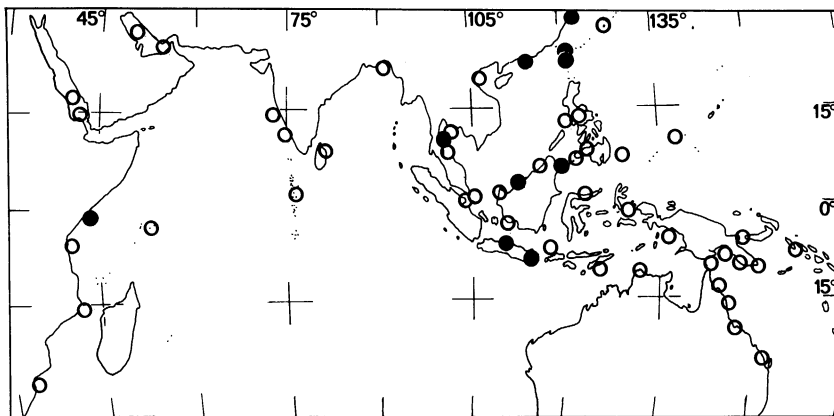


FIG. 51. Distribution records for *Therapon theraps*. Solid symbols represent specimens examined, open symbols are additional literature records.

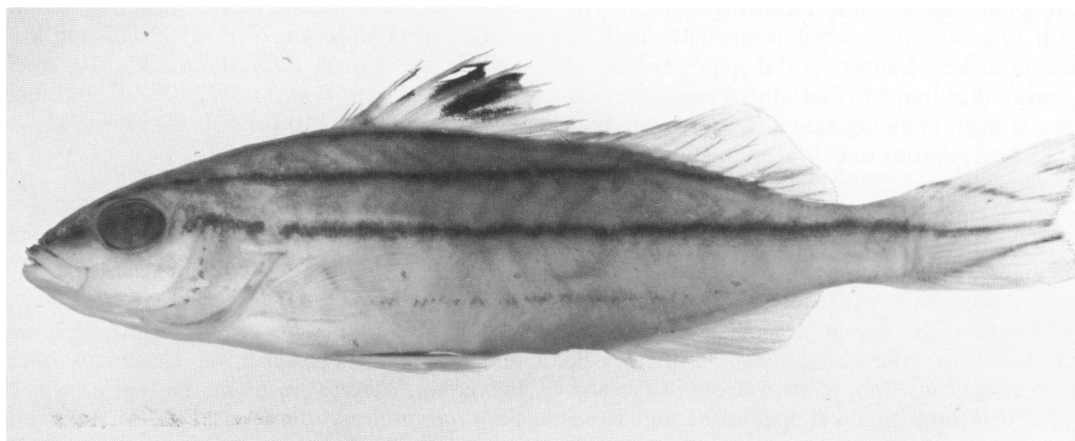


FIG. 52. *Therapon puta*, USNM 147876, 89 mm. SL.

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 1.8-2.4 in HL; longest anal spine 2.1-2.9 in HL; longest anal ray 1.75-2.5 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, more so in young. Preoperculum serrate, spines on angle very large. Lower opercular spine strong and very long, extending 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 asymmetrically 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 grayish 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 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 at tip; middle caudal rays with stripe; one or two bars running obliquely across lower caudal lobe. Pectorals and pelvics clear. Young with six or seven vertical bars.

Distribution. A marine species that enters into brackish and fresh waters. Found along coasts of Africa north of Zanzibar, Red Sea, Arabia, Persian Gulf, Madagascar, India, Ceylon, Java, Singapore, Borneo, Philippines, New Guinea, southeast Asia, and Australia (Queensland) (fig. 53).

Specimens Examined

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

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

Indonesia: Java (USNM 72265*, 20, 87-96 mm.); Batavia (UMMZ 182785*, 2, 99-103 mm.).

Philippines: Luzon (USNM 56274*, 20, 36-54 mm.); Iloilo (USNM 72250*, 1, 82 mm.; USNM 10297*, 10 [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*.

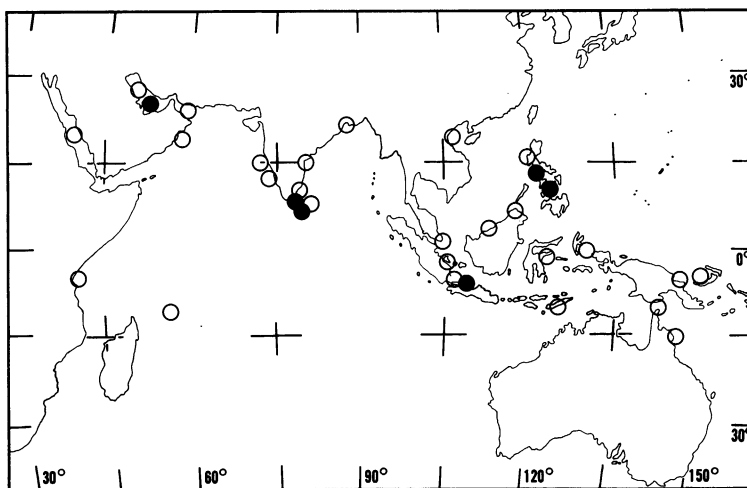


FIG. 53. Distribution records for *Terapon puta*. Solid symbols represent specimens examined, open symbols are additional literature records.

Diagnosis. Marine teraponids having a dorsal sheath of two 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)

Figure 54

Terapon 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; pectorals 14-15; pelvics I-5;

80-90 lateral line scales; seven scales on caudal; 13-15 scales above lateral line; 25-26 scales below lateral line; 14 predorsal scales to occiput; two 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 anus, more so 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,

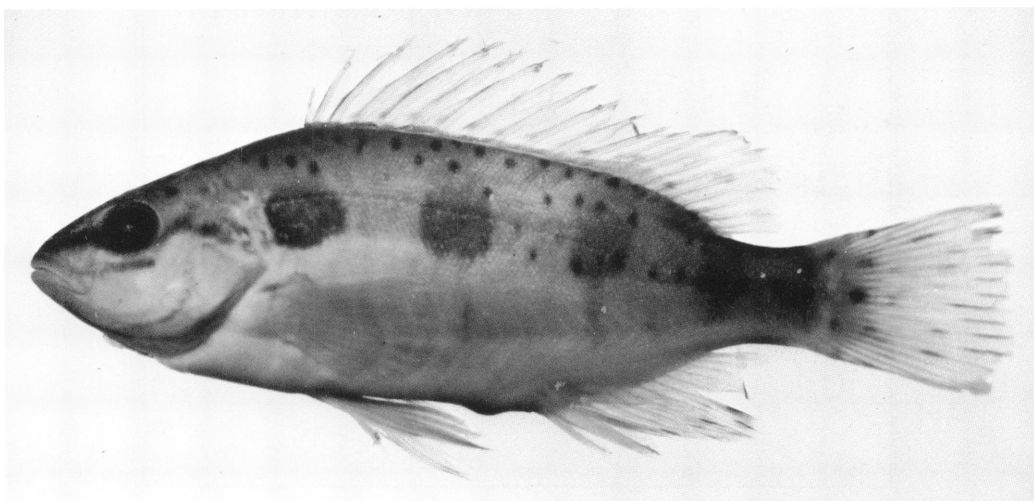


FIG. 54. *Pelsartia humeralis*, AMNH 35635, 97 mm. SL.

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 asymmetrically 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 is 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. 55). 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 (J. B. Hutchins, personal commun.).

Specimens Examined

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

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

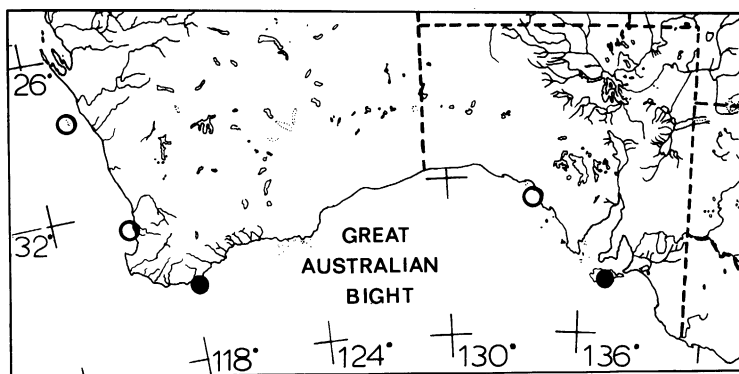


FIG. 55. Distribution records for *Pelsartia humeralis*. Solid symbols represent specimens examined, open circles are additional literature records or from personal communications.

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 fresh waters is placed in the genus.

Rhyncopelates oxyrhynchus (Temminck and Schlegel, 1842)

Blotched grunter

Figure 56

Therapon oxyrhynchus Temminck and Schlegel, 1842, p. 16, pl. 16, fig. 3 (original description, bays of southern Japan). Richardson, 1846, p. 239 (China and Japan). Bleeker, 1858, p. 2 (Kioesio). Günther, 1859, p. 281 (Japan, China). Karoli, 1881, p. 153 (Hakuri, Japan). Günther, 1880, p. 34 (Ovalau, Fiji Islands,

probable error). Steindachner and Döderlein, 1884, p. 10 (Tokyo). Meyer, 1885, p. 13 (Manado, Celebes). Rutter, 1897, p. 75 (Swatow, China). Isikawa 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 (China and Japan). Izuka and Matsuura, 1920, p. 150 (Tsu, Ise). Weber and deBeaufort, 1931, p. 159 (after Meyer, 1885). Uchida, 1934 (sonic ability). Suyehiro, 1942, p. 173 (intestinal patterns). Boeseman, 1947, p. 34 (designation of type). Kuroda, 1951, p. 336 (Hokkaido, Bosiu, Tokyo Bay, Sagami Bay, Surugu Bay, Kii, Shikoku, Kiusoa). Honma, 1952, p. 145 (Echigo, Japan). 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, TP1 (fisheries, distribution).

Nomenclature. The trivial name *oxyrhynchus*, from the Greek, *oxys*, sharp or pointed and *rhynchos*, snout, refers to the elongate snout in

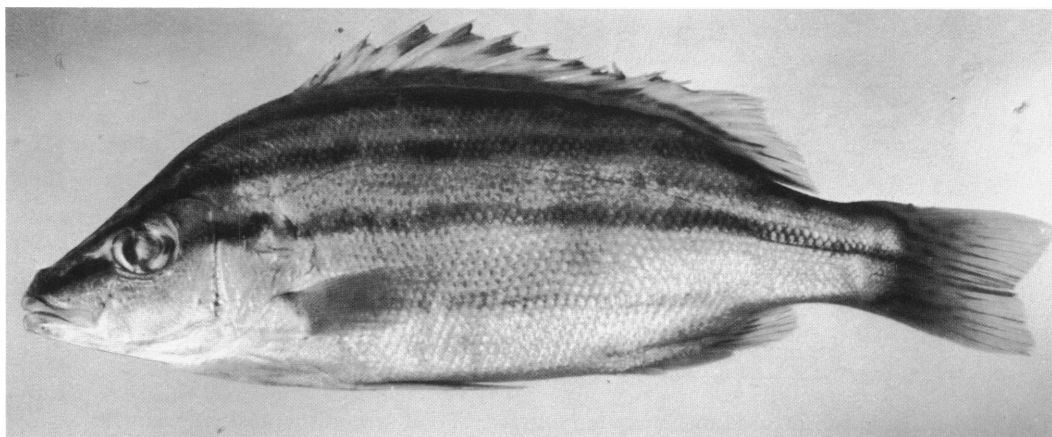


FIG. 56. *Rhyncopelates oxyrhynchus*, USNM 57735, 158 mm. SL.

the species. The original description of this species was based on a series of specimens from Japan of which Boeseman (1947) selected Temminck and Schlegel specimen no. 95 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; pectorals 13-14; pelvics I-5; 58-80 lateral line scales; 5-7 scales on caudal; 10-11 scales above lateral line; 20-24 scales below lateral line; 16-20 predorsal scales to occiput; two 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 2.6-3.3 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 1.8-2.8 in HL; length of longest dorsal ray 1.8-2.7 in HL; length of longest anal spine 2.0-2.9 in HL; length of longest anal ray 1.8-2.6 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 bony 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. Posttemporal exposed; serrate along posterior edge. Supracleithrum exposed.

Spinous dorsal arched; first spine short, third to sixth spines longest, those following decreasing in length to penultimate, 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 asymmetrically 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. *Rhyncoelates oxyrhynchus* is common in the waters of southern and eastern China, Taiwan, and southern Japan (fig. 57). The species also appears to be a rare member of the Philippine fauna. It has previously been reported from that region by Elera (1895) and a single specimen examined in the course of this study (USNM 183722) also has a locality of the Philippines. Meyer (1885) listed the species from the Celebes without further elaboration. Such a range extension is unsupported by further collections and as such is suspect.

Günther's citation of this species from the Ovalau, Fiji (1880) a locality distant from the known range of the species, would appear to be in error as would Fowler's listing of the species from India (1928).

Remarks. Fowler (1928) placed *Rhyncoelates 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, *R. oxyrhynchus* fails to conform to this definition as it has wide tooth bands in each jaw as noted by Fowler (1931) who stated "teeth small, in bands of 6 or 7 irregular series." Furthermore *R. oxyrhynchus* has a series of apomorphic posttemporal, tabular, extrinsic

swimbladder muscle characters etc., shared with a series of other species but not with those of the other species of the genus *Pelates* (*sensu* Fowler). Consequently, the hypothesis of a close relationship between *R. oxyrhynchus* and these other species is rejected in this study.

Specimens Examined

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

Japan: Kyoto Fish Institute (AMNH 34774*, 1, 220 mm.); Toba Fish Market (AMNH 13147*, 1, 201 mm.; UMMZ 142699*, 2, 67-133 mm.); Mikawa Bay (USNM 15253*, 1, 71 mm.; USNM 57733*, 2, 143-150 mm.); Satsuma, Akune Station (USNM 71178*, 9, 35-60 mm.); Shimizu (USNM 71179*, 2,

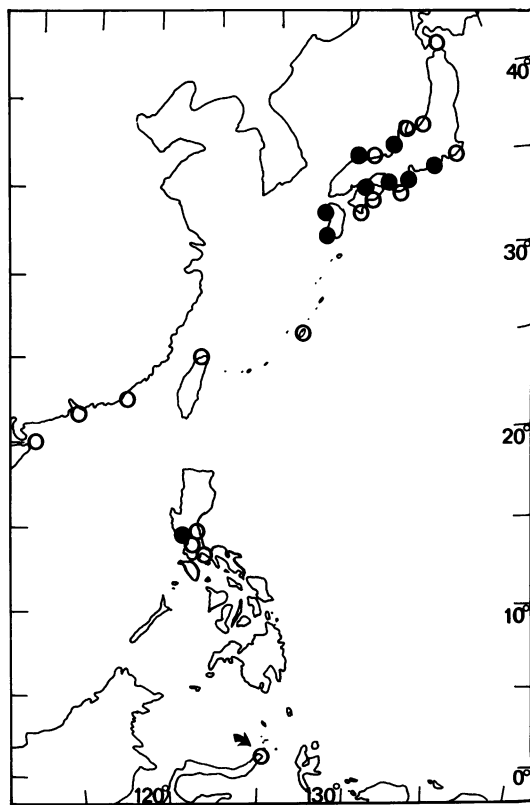


FIG. 57. Distribution records for *Rhyncoelates oxyrhynchus*. Solid symbols represent specimens examined, open symbols are additional literature records.

110-125 mm.); Kagoshima (USNM 71300, 2); Nagasaki (USNM 75451, 2); Miyazaki (USNM 82140*, 1, 59 mm.); Miyazu (UMMZ 182840*, 1, 89 mm.); UMMZ 182724, 1); Suruga Bay (UMMZ 182839*, 1, 122 mm.); UMMZ 182772*, 4, 116-176 mm.); Sagami Bay (UMMZ 182776*, 1, 131 mm.); UMMZ 182778, 1); Makumi (UMMZ 182779, 1); Hamada (UMMZ 182773, 1); Hajoza-gatu (UMMZ 182777, 1); Lake Mikata (UMMZ 142683, 1).

GENUS 10, *MESOPRISTES*

Mesopristes Bleeker, 1845, p. 523 (type species, *M. macracanthus* [= *Datnia argentea*, Cuvier] by monotypy).

Nomenclature. The generic name is of unknown significance.

Diagnosis. Marine teraponids 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 of supraoccipital bowed posteriorly. Anterior of 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, whereas *M. kneri* is endemic to Fiji and *M. elongatus* to Madagascar.

Remarks. As discussed by Fowler (1931) the original generic name applied to some of the species of this genus—*Datnia* (Cuvier, 1829, p. 138)—is properly applied by tautonymy to *Coius datnia* Hamilton, a sparoid.

Mesopristes argenteus (Cuvier, 1829)

Silver grunter

Figures 58, 59

Datnia argentea Cuvier, 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).

Datnia cancellatoides Bleeker, 1845, p. 523 (original description, Priaman, Sumatra, Amboina).

Therapon argenteus: Günther, 1859, p. 283 (Am-

boina). Martens, 1876, p. 386 (Luzon, Manila). Bleeker, 1873-1876, pl. 326, fig. 1 (East Indies). Meyer, 1885, p. 13 (Laguna de Bay, Luzon). Gorgoza, 1888, p. 284 (Pascaso). Day, 1889, p. 507 (India?). Weber, 1894, p. 407 (Amparang River, Celebes (Sulawesi)); 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 (Fiji, error for *M. kneri*); 1953, p. 428 (synonymy). Marshall, 1964, p. 167 (north Queensland). Mees, 1971, p. 249. Kailola, 1975, p. 100 (New Guinea: Gazelle Peninsula, Bougainville).

Therapon (Datnia) argenteus: Bleeker, 1873, p. 382 (East Indies); 1873-1876, 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, fresh water on Normanby Island).

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

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

Therapon argenteus: Fowler, 1931, p. 347 (Philippines); 1931b, p. 24 (no locality); 1934, p. 446 (Normanby Island, Port Moresby, Teterrri, 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; pectorals 12-14; pelvics 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; three rows of scales in sheath at base of dorsal fin, sheath extending to fifth or sixth dorsal ray; four 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 2.15-2.4 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 reaching 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 diameter 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 pedun-

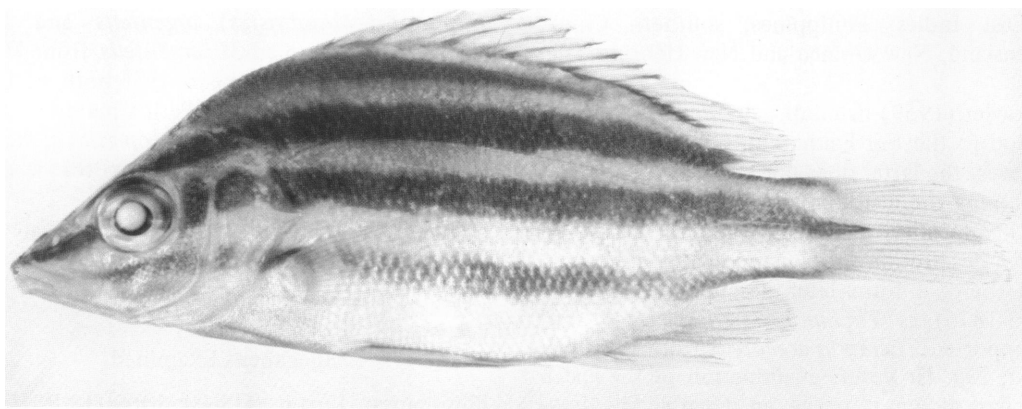


FIG. 58. *Mesopristes argenteus*, juvenile, USNM 184818, 60 mm. SL.

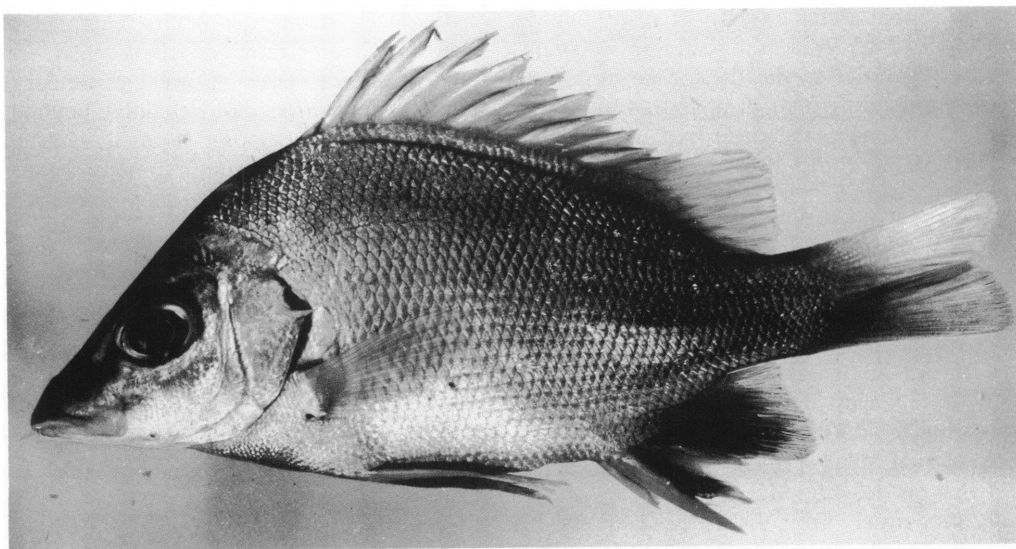


FIG. 59. *Mesopristes argenteus*, adult, USNM 184804, 100 mm. SL.

cle; 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 fresh waters of Sumatra, Java, Sulawesi, islands of East Indies, Philippines, southern China, Queensland, New Guinea and New Hebrides (fig. 60).

Fowler (1959) listed *M. argenteus* as an introduction to the Fiji Fauna citing Whitley (1927). However, the latter does not make any statement concerning the introduction of the species to Fiji and his locality record is evidently based on Kner's description of *Therapon argenteus* var. from there; a form later described by Bleeker (1873-1876) as *Therapon kneri*. Herre (1936) also reported *Therapon argenteus* from Viti Levu Island, Fiji. However, examination of the specimen has shown it to be an example of *Mesopristes kneri*. Consequently, the inclusion of *M. argenteus* in the Fijian fauna appears to be erroneous.

Mesopristes argenteus has also been reported from India, "Cape Seas," and Madagascar. Day (1889) listed this species from India, noting, however, that he had not personally seen any specimens and believed its presence to be limited to stray individuals. More recently Fowler (1959) listed India as a locality for the species failing, however, to provide any specific locality records. Therefore, the distribution of *M. argenteus* in the Indian region appears questionable.

Fowler (1931) placed *Datnia obtusirostris* Guichenot from Madagascar as a synonym of *Therapon* (= *Mesopristes*) *argenteus* and Petit (1937) also described *M. argenteus* from Madagascar. However, it appears that both of these cases (*D. obtusirostris* and Petit's material) actually represent specimens of *Mesopristes elongatus* (see remarks under that species for a more detailed explanation).

Finally, the locality of "Cape Seas" listed by both Day and Fowler appears to be unsubstantiated.

Specimens Examined

Philippines: Luzon (USNM 146909, 1; USNM 146910, 1; USNM 146911, 1); Legaspi, Yuna River (USNM 146914, 19); Mindanao (USNM 146912*, 1, 156 mm.); Nonucan River, Camp

Overton (USNM 184804*, 10, 85-128 mm.);
Leyte (USNM 184818*, 4, 55-72 mm.).
Indonesia, Boero Island, Uki River (USNM
146913, 2; USNM 184869*, 2, 123-150
mm.).

Mesopristes cancellatus (Cuvier, 1829)

Tapiroid grunter

Figure 61

Datnia cancellatus Cuvier, 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, 1873-1876, 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, Philippines). Herre, 1933, p. 8 (Dumaguete, Negros); 1934, p. 52 (Dumaguete); 1936 p. 194 (Auki, Malaita Island; Solomon Islands). Okada, 1959, p. 57 (Okinawa). Freihofner, 1963, p. 132 (RLA pattern). Tortonese, 1964, p. 44 (West Irian, Andai). Kailola, 1975, p. 100 (New Guinea:

Gazelle Peninsula, Sambogo River, Bougainville, Buna).

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

Therapon (Datnia) cancellatus: Peters, 1868, p. 256 (Sancar, Leyte). Bleeker, 1873-1876, p. 116 (Java, Celebes, Amboina, Philippines).

Therapon (Datnia) Rosenberghii: Bleeker, 1873-1876, p. 387 (Ceram).

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

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

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

Terapon rosenberghii: 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*, grating or lattice work,

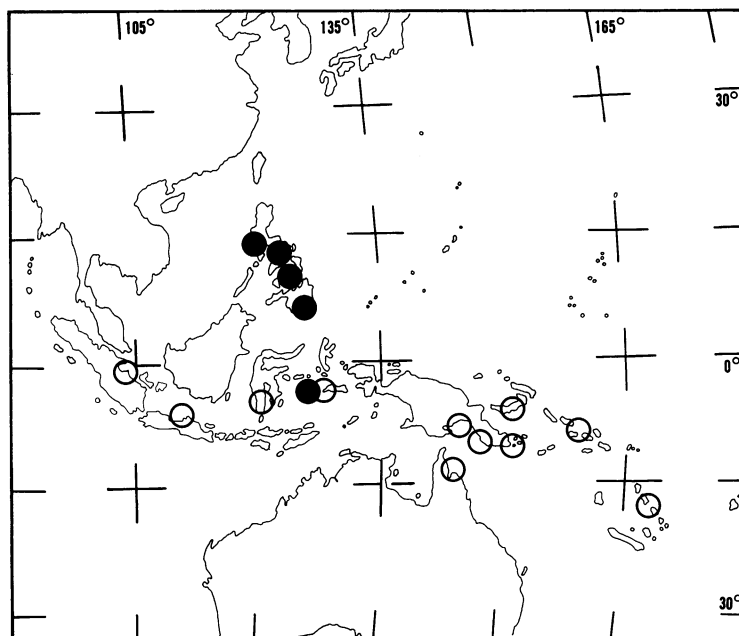


FIG. 60. Distribution records for *Mesopristes argenteus*. Solid symbols represent specimens examined, open symbols are additional literature records.

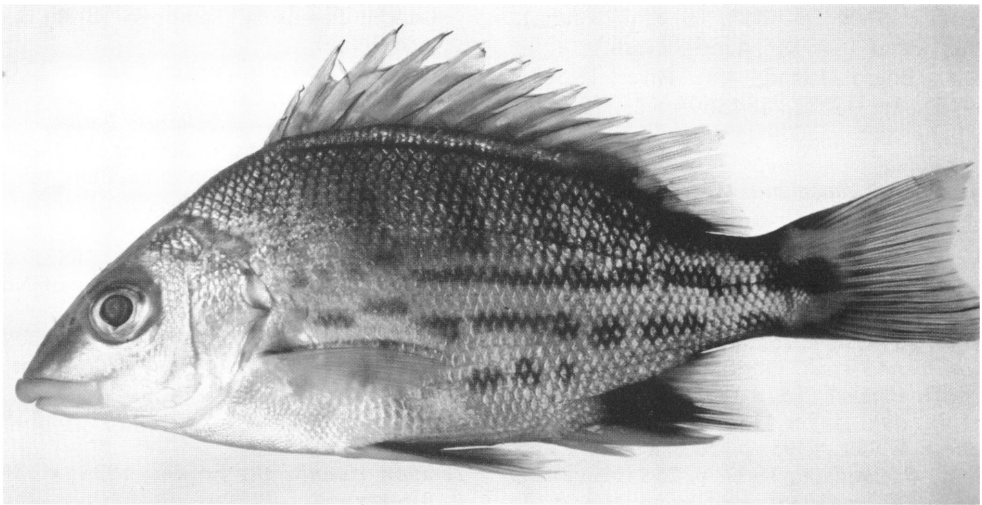


FIG. 61. *Mesopristes cancellatus*, USNM 184775, 100 mm. SL.

refers to the pattern of vertical bars and horizontal stripes on the body.

Diagnosis. A member of the genus *Mesopristes* distinguishable from the other members of the family by its body coloration of dorsal vertical bars and ventral horizontal stripes occurring in all but larger specimens and a markedly longer, very fleshy upper lip in larger specimens. Within the genus it is further distinguishable in having 6-8 scales above the lateral line (in contrast to 9-11 in *M. elongatus* and *M. kneri*), 4-5 cheek and 5-6 caudal scales (in contrast to 8-9 cheek and 10-12 caudal in *M. argenteus*).

Description. Dorsal spines XI-XII; dorsal rays 10-11; anal III, 8-9; pectorals 13-16; pelvics 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; two rows of scales in sheath at base of dorsal fin, sheath extending to last dorsal ray; four 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+15-8; 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 degree 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 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 asymmetrically 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 irreg-

ular 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. 62).

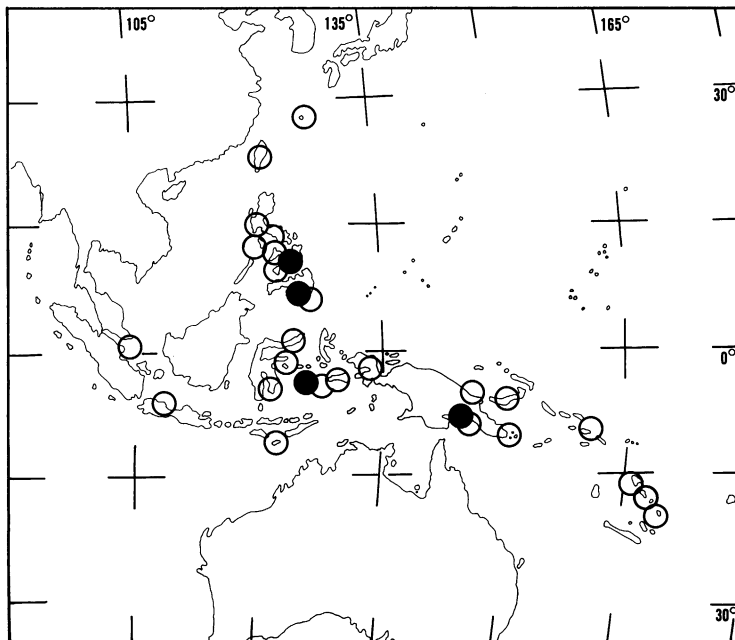


FIG. 62. Distribution records for *Mesopristes cancellatus*. Solid symbols represent specimens examined, open symbols are additional literature records.

Remarks. Bleeker (1860) described a species from the East Indies, *Datnia Rosenberghii*, which had the same coloration as *Datnia* (= *Mesopristes*) *cancellatus* but differed 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*. However, material of *Mesopristes cancellatus* and literature information shows the range of variation in the characters used by Bleeker to distinguish the two nominal forms overlaps the gaps between these nominal forms. Therefore, I follow Weber and deBeaufort and place *D. rosenberghii* in synonymy with *M. cancellatus*.

Specimens Examined

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

Philippines: Mindanao, Nonucan River, Camp Overton (USNM 1847762*, 4, 109-158 mm.); Leyte, San Roque (USNM 184774*, 3, 59-66 mm.; USNM 146356*, 2); Leyte, Hinunangan Bay, Malaga River (USNM 184775*, 2, 82-96 mm.); Dumaguete (UMMZ 100292*, 1, 116 mm.).

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

Mesopristes elongatus (Guichenot, 1866)

Figure 63

Datnia elongata Guichenot, 1866, p. 133 (original description, Madagascar).

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

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

Therapon lambertoni: Fowler, 1931, p. 350, fig. 28 (based on Fowler, 1923).

Therapon elongatus: Fowler, 1931, p. 351 (after Guichenot, 1866).

The following also appear to be synonyms of this species:

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

Therapon obtusirostris: Sauvage, 1891, p. 155, pl. 28, fig. 5 (Madagascar, based on type of *Datnia obtusirostris*).

Therapon (*Datnia*) *argenteus*: Petit, 1937, p. 27 (not *Datnia argentea* (= *Mesopristes argenteus*) Cuvier, 1829) (misidentification, Madagascar).

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

Diagnosis. A member of the genus *Mesopristes* distinguishable in having 9-11 scales above the lateral line (in contrast to six to eight in *M. cancellatus* and *M. argenteus*), 20-24 scales below the lateral line and broad continuous stripes in juveniles (in contrast to 18-19 scales below the lateral line and stripes formed of disconnected spots in *M. kneri*).

Description. Dorsal spines XII; dorsal rays 10; anal III-8; pectorals 14 (incorrectly listed as 18 in the original description); pelvics I-5; 48-50 lateral line scales; five scales on caudal; 9-10 scales above lateral line; 20-24 scales below lateral line; 15 predorsal scales to occiput; two 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 2.7-2.8 in SL; distance from origin of spinous dorsal to snout 2.3-2.5 in SL; head length 2.8-3.0 in SL; length of base of dorsal fin 2.0-2.1 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 ex-

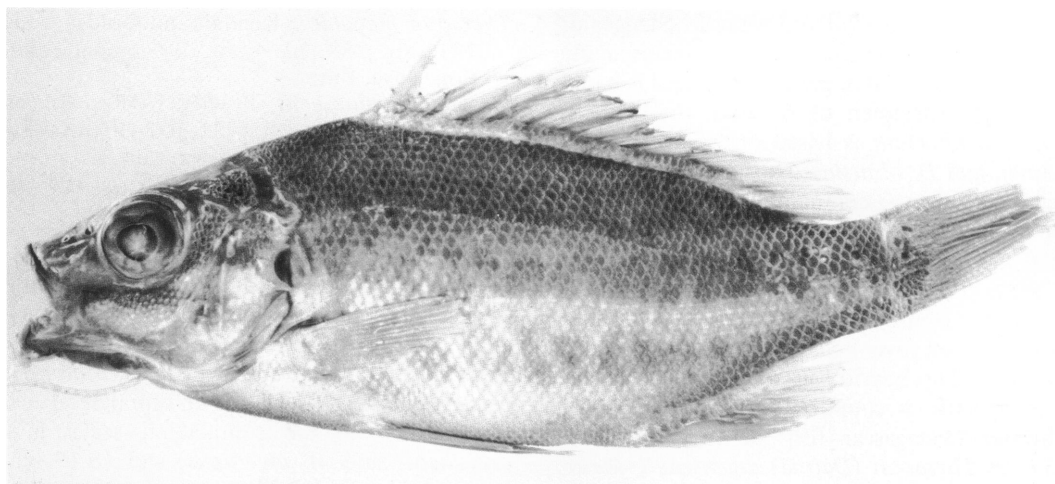


FIG. 63. *Mesopristes elongatus*, holotype, MNHN 4170, 55 mm. SL.

posed; 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 black on back; upper surfaces are tinged with dark gray 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* appears to be endemic to Madagascar.

Remarks. Since the original description of *Mesopristes elongatus* based on a single specimen, no further material of this species has been described. Available evidence indicates, however, that two other nominal species from Madagascar (*Datnia obtusirostris* and *Terapon lambertoni*) are based on adults of this species and that a collection reported on by Petit (1937) as *Terapon argenteus* is actually *M. elongatus*.

Fowler (1923) described a species from Madagascar, *Terapon lambertoni*, from a single specimen. Although noting the similarity of his species to *M. elongatus*, he separated them on the basis of differences in the extent of caudal emargination, which dorsal spine (fourth or fifth) was longest, general head shape and the presence of longitudinal stripes in *M. elongatus*, which are lacking in *T. lambertoni*, and several meristic and morphometric differences. In this he paralleled the differences found between *M. elongatus* and *D. obtusirostris* Guichenot (1866).

Although the types (and only specimens) of *T. lambertoni* and *D. obtusirostris* were not available for examination the differences between these species and *M. elongatus* as presented in the original descriptions appear to be

either a consequence of ontogenetic changes or fall within the expected range of intraspecific variation. Whereas *Mesopristes elongatus* is based on a single specimen of 67 mm. total length (TL), *T. lambertoni* is based on a 158 mm. TL specimen and *D. obtusirostris* on a 220 mm. TL specimen. Over a comparable range in other teraponids, there occurs a marked increase in the caudal fin emargination (Rahin, 1973; Duncher and Mohr, 1931; personal observ.), an increase in the ventral turning of the head anteriorly, and a transition from juvenile stripes to uniform adult coloration. The hypothesis that all these forms are conspecific is supported by a collection of freshwater Madagascar fish identified by Petit (1937) as *Therapon (Datnia) argenteus* (= *Mesopristes argenteus*). In that collection, the young had three longitudinal body stripes as in *M. elongatus* (but not *M. argenteus* which has 4-5 stripes in the young), whereas adults have a brown marbling pattern that agrees with that of both *Therapon lambertoni* and *Datnia* (= *Therapon*) *obtusirostris*. Thus it would appear that both of these species are probably adults of *M. elongatus*.

Fowler (1931) considered *Datnia obtusirostris* to be a synonym of *Therapon* (= *Mesopristes*) *argenteus*, which is otherwise limited to east of the Malaya-Sumatra region. This synonymization appears to be in error since *D. obtusirostris* agrees with *M. elongatus* as described above. Furthermore Sauvage described the type of *D. obtusirostris* as having four rows of cheek scales in agreement with *M. elongatus* but not *M. argenteus* which has 7-9.

Specimens Examined

Madagascar (MNHN, 4170*, 1 (holotype of *Datnia elongata*), 55 mm.).

Mesopristes kneri (Bleeker, 1873)

Kner's grunter

Figure 64

Therapon argenteus var. (not *T. argenteus* Cuvier, 1829) Kner, 1868, p. 299, pl. 1, fig. 1 (Kandavu, Fiji).

Therapon kneri Bleeker, 1873-1876, p. 111 (original description, based on Kner, 1868, 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.).

Therapon kneri: Fowler, 1931, p. 341 (Suva, Fiji); 1959, p. 259, fig. 105 (Suva, Fiji).

Therapon argenteus: Herre, 1936, p. 194 (Fiji, misidentification).

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 description.

Diagnosis. A member of the genus *Mesopristes* distinguishable in having 9-11 supralateral scales (in contrast to 6-8 supralateral scales 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 of longitudinal stripes formed of disconnected spots is unique in the family.

Description. Dorsal spines XII; dorsal rays 10-11; anal III, 8-9; pectorals 13-14; pelvics I-5; 48-53 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; two 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

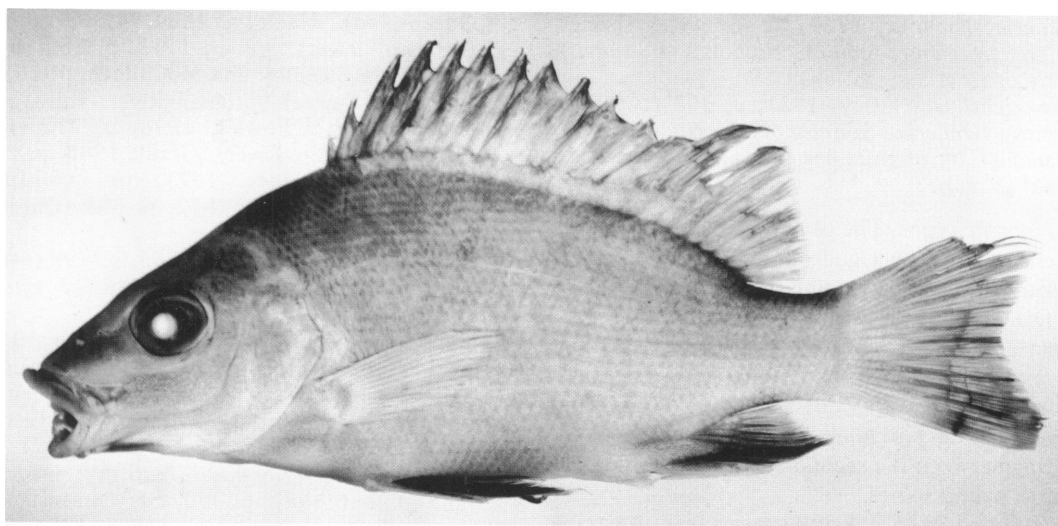


FIG. 64. *Mesopristes kneri*, SU 24935, 90 mm. SL.

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 asymmetrically 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. Fresh and marine waters of the Fiji Islands.

Specimens Examined

Fiji Islands: Suva (USNM 66061*, 1 (holotype of *Therapon maculatus*), 99 mm.; USNM 66062*, 5 (paratypes of *Therapon maculatus*), 34-68 mm.; USNM 112737*, 1, 169 mm.; SU 24935*, 1, 90 mm.); Viti Levu (BM[NH] 1879.6.20.3*, 1, 152 mm.).

GENUS 11, *HEPHAESTUS*

Hephaestus DeVis, 1884, p. 399 (type species, *Hephaestus tulliensis* DeVis (= *H. fuliginosus*), by monotypy).

Papuservus Whitley, 1943, p. 132 (type species, *Therapon trimaculatus* Macleay, by original designation).

Archeria Nichols, 1949, p. 6 (type species, *Archeria jamesonoides*, Nichols (= *H. suavis*), by original designation).

Archerichthys Whitley, 1951, p. 398 (type species *Archeria jamesonoides* Nichols (= *H. suavis*), by original designation (proposed as a subgenus)).

Nomenclature. The generic name, *Hephaestus*, refers to the Greek god of fire. The reference is obscure and is not explained by DeVis.

Diagnosis. Freshwater teraponids from Australia and New Guinea with set conic dentition, an exposed posttemporal, longest dorsal spines shorter than longest dorsal rays in adults, first spine bearing proximal dorsal pterygiophore inserting between the second and third or third and fourth neural spines.

Included Species. Seven species from Australia and New Guinea are placed in *Hephaestus* in the present study. As discussed in the phylogenetic analysis, two subgroups (a and b) are definable in this genus. In 11a, two species (*H. fuliginosus* and *H. jenkinsi*) have extensive nonoverlapping distributions in northern Australia and one species (*H. roemeri*) occurs in the southern drainages of West Iran. Genus 11b contains four species: *H. adamsoni*, an endemic to Lake Kutubu, Papua-New Guinea; *H. trimaculatus* distributed through the southern drainages of the island of New Guinea; *H. suavis* from Cape York, Australia; and *H. carbo* from the Gregory River region of Queensland.¹

Remarks. Whitley (1943) placed the genus *Homodemus* DeVis (1884) in synonymy with *Hephaestus*, equating *Homodemus cavifrons* with *Hephaestus fuliginosus*. However, *Homodemus cavifrons* has 16 dorsal rays (in contrast to 12-14 in *Hephaestus fuliginosus*) and is described as having a maxillary that extends past the vertical drawn through the posterior edge of the eye; a condition not found in any teraponid. As such, it appears that both the generic and specific synonymy of Whitley are incorrect.

Hephaestus fuliginosus (Macleay, 1883)

Sooty grunter

Figure 65

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).

Therapon 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).

Therapon Alligatoris: Dahl, 1926, p. 229 (South Alligator River).

Therapon fuliginosus: McCulloch, 1929, p. 163 (Queensland). Fowler, 1931, p. 352 (copied).

Therapon 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

¹ Another species of this group will be described in an independent work at a later date.

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; pectorals 15-17; pelvics 1-5; 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 lobe. 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 asymmetrically pointed; fifth ray longest. Pelvics pointed; 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.

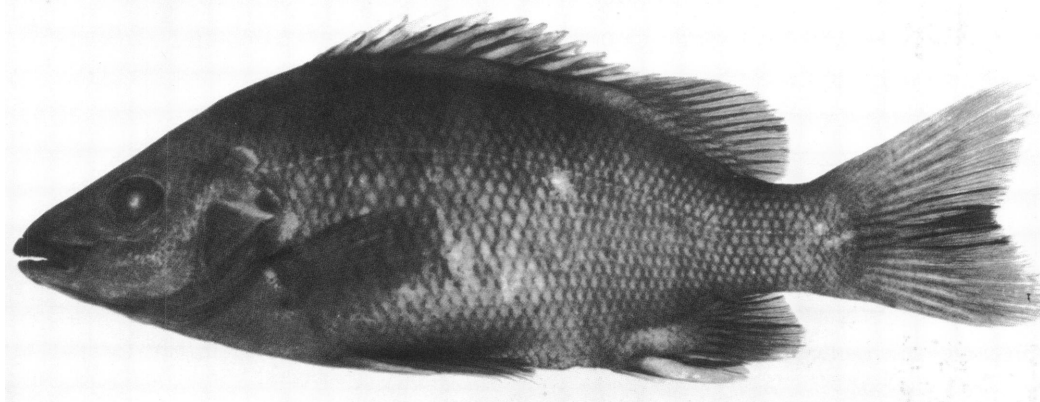


FIG. 65. *Hephaestus fuliginosus*, AMNH 35660, 100 mm. SL.

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 gray 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 ventrally.

Distribution. Fresh waters of Queensland and Northern Territory from the Burdekin River of Queensland to the Daly River of Northern Territory (fig. 66).

Ecology. *Hephaestus fuliginosus* is primarily a species of rapidly flowing waters particularly along rocky bottoms. Lake (1971) reported that available evidence indicates they lay small adhesive eggs after flood waters have receded and are omnivorous feeders.

Remarks. *Hephaestus fuliginosus* shows marked variation in overall head shape, lip form and coloration both ontogenetically and geographically. Its coloration varies from dark brown and black to some xanthomorphic golden and silvery individuals. The variation in lip size ranges from the slightly fleshy lips of some individuals to what are termed "blubber lips" in which the lips form a fleshy pad. This condition is not so pronounced as that in *H. jenkinsi* and does not appear to be related to either the size or sex of the individual and varies in populations both in prevalence and development.

Ogilby and McCulloch (1916) described a new species, *Terapon bancrofti*, that they differentiated from *Terapon* (= *Hephaestus*) *fuliginosus* in the number of scales counted in a series below the lateral line. However, as discussed by Mees (1971), in large series of these nominal forms, overlaps occur in these scale counts; a finding supported by material at hand. Mees, nonetheless, retained these forms as distinct based on differences in distance between the nostrils and head shape, noting, however, that additional study might show them to be conspecific. Examination of large series of *Hephaestus* material from Queensland, Northern Territory, and Western Australia failed to uncover any differences supporting the retention of the nominal forms. Consequently, *Terapon bancrofti* is herein considered to be a synonym of *Hephaestus fuliginosus*.

Contrary to the conclusions of Mees (1971), *Mesopristes* (= *Hephaestus*) *jenkinsi* and what were considered by him to be Western Australian populations of *H. fuliginosus* are considered in this work to be a distinct species, *H. jenkinsi*, on the basis of a lip character unique to that species in the family (see *H. jenkinsi* description).

Finally, Mees also suggested that *Terapon alligatoris* Rendahl was a synonym of *T. bancrofti* Ogilby and McCulloch, in this study considered a synonym of *H. fuliginosus*. Although I

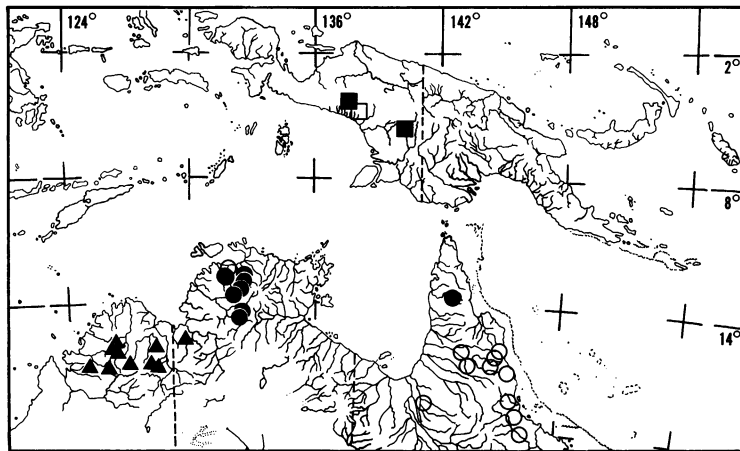


FIG. 66. Distribution records for the species of the genus *Hephaestus* in part (genus 11a), *H. fuliginosus* (circles), *H. roemeri* (squares), and *H. jenkinsi* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

have not been able to examine the type material of *T. alligatoris*, examination of specimens of *H. fuliginosus* from the area of the type locality of *T. alligatoris* shows them to agree with the original description of the latter species. As such, *T. alligatoris* is also recognized herein as a synonym of *H. fuliginosus*.

Weber (1913) hypothesized that his species *Terapon roemeri* Weber (1910) was identical with *Terapon 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 in *Pelates*. Although the species are similar, material examined has shown differences in transverse and lateral line counts. Therefore these species are retained as distinct at this time.

Specimens Examined

Australia, Northern Territory: Katherine River, Katherine (AMNH 32438*, 1, 125 mm.); Barramundie Creek (AMNH 35654*, 10 [of 46], 36-53 mm.); South Alligator River (AMNH 35655*, 13, 33-136 mm.); Mary River (AMNH 35656*, 5 [of 41], 100-112 mm.; AMNH 35661*, 3, 41-55 mm.); South Alligator River (AMNH 35657, 20); Ferguson River (AMNH 35658*, 10, 28-63 mm.); Barramundie Creek (AMNH 35659, 17); Katherine River (AMNH 35660*, 10 [of 46], 40-175 mm.); WAM P-25676-001, 1); Roper River (WAM P-25447-001, 1).

Australia, Queensland, Cape York Peninsula, Wenlock Crossing (AMNH 18540*, 9, 61-104 mm.).

Hephaestus roemeri

Römer's grunter

Figure 67

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 roemeri: 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 Guinea that collected the syntypic series. The syntype series has been deposited in the Zoölogisch Museum of Amsterdam.

Diagnosis. A member of the genus *Hephaestus* distinguishable 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 (in contrast to its presence in *H. jenkinsi*), 5-7 scales above the lateral line and 5-6 cheek scales (in contrast to 8-10 scales above the lateral line and 6-9 cheek scales in *H. fuliginosus*).

Description. Dorsal spines XI-XII; dorsal rays 12-14; anal III, 9-10; pectorals 14-16; pelvics 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

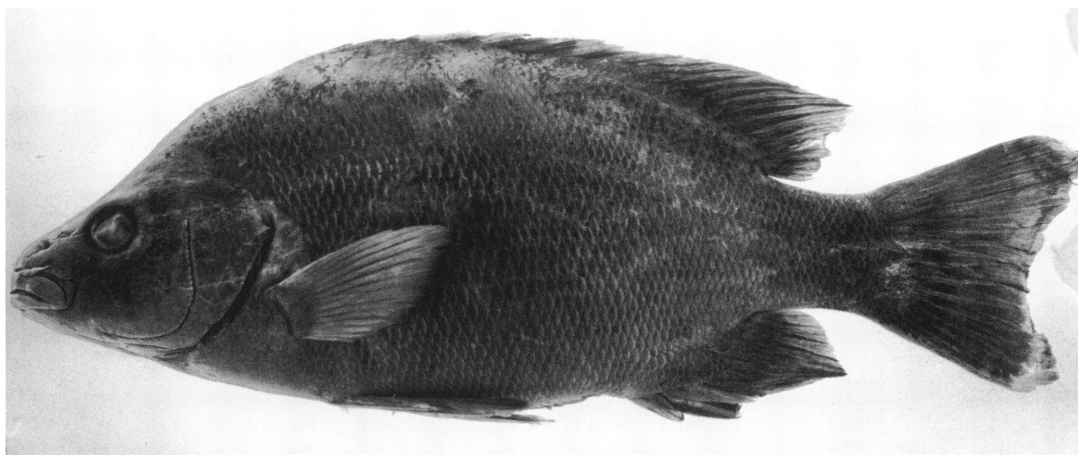


FIG. 67. *Hephaestus roemerii*, syntype, ZMA 104.731, 272 mm. SL.

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 to 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 asymmetrically 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 dark above, lighter below and lacking any distinct markings. Body 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 gray.

Distribution. In the fresh waters of southern West Irian, Indonesia: Lorentz and Digoel rivers (fig. 66).

Remarks. Fowler (1928, 1931) placed *Tetrapon* (= *Hephaestus*) *roemerii* as a synonym of *H. fuliginosus* in accordance with Weber's suggestion (1913) that these were conspecific. In 1934, however, he reversed his action, resurrected the species and followed Weber and deBeaufort in placing it in the genus *Pelates*. Material examined has shown *H. fuliginosus* and *H. roemerii* to be extremely similar but distinct. However, further collections may show them to be geographical variants of a single species.

As noted above, *Hephaestus roemerii* was placed in the genus *Pelates* by Weber and deBeaufort (1931) followed by most later workers. These authors defined the genus *Pelates* as characterized by triserial dentition in the upper jaw and biserial in the lower. Examination of specimens of *H. roemerii* shows that although some individuals have very irregular rows of teeth, in

most the teeth are in bands. Furthermore, in both cases (irregular rows or bands) there are four or more series in each jaw, with the posterior series colorless and difficult to locate. Neither does the evidence of this study support a hypothesis of a monophyletic relationship for the species placed in the genus *Pelates* by Weber and deBeaufort.

Nichols (1949) confused the question of the species distribution and relationships further 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." However, whereas *H. fuliginosus* is indeed similar to *H. romeri*, both are distinct from *Terapon* (= *Bidyanus*) *bidyanus* in many characters and no evidence exists to support the presence of *H. romeri* in Australia.

Perhaps as a consequence of Nichols' statement, Munro (1964) and Lake (1971) listed *H. romeri* as a member of the northern Queensland fauna.

Specimens Examined

Indonesia, West Irian: Lorentz River near Regen Island (ZMA 104731*, 1 [syntype], 272 mm.); Lorentz River, Bivaleiland (ZMA 104738*, 2, 98-118 mm.); Digoel River near Tanah Merah (RMNH 24936*, 2, 110-134 mm.).

Hephaestus jenkinsi (Whitley, 1945)

Jenkins' grunter

Figure 68

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. The type (WAM 2763) is deposited at the Western Australian Museum.

Diagnosis. *Hephaestus jenkinsi* can be distinguished from all other species in the family in its possession of an uninterrupted lip fold across the ventral surface of the lower jaw (fig. 30). Within the genus *Hephaestus*, it is further distinguishable in having 15-18 gill rakers on the lower limb of the first arch (in contrast to 9-11 for *H. trimaculatus*, *H. adamsoni*, *H. carbo*, and *H. suavis*).

Description. Dorsal spines XI-XIII; dorsal rays 11-12; anal III, 7-8; pectorals 15-17; pelvics 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 or 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. 69). 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

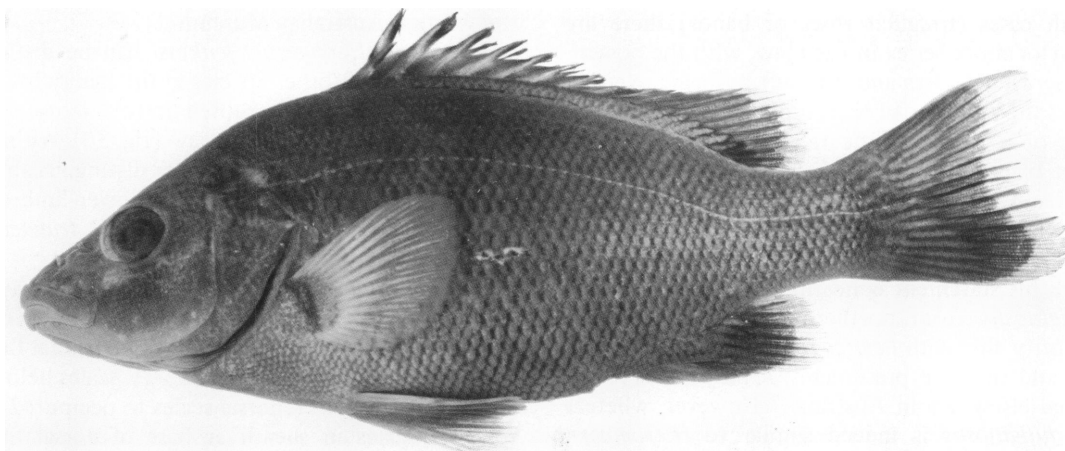


FIG. 68. *Hephaestus jenkinsi*, AMNH 35670, 105 mm. SL.

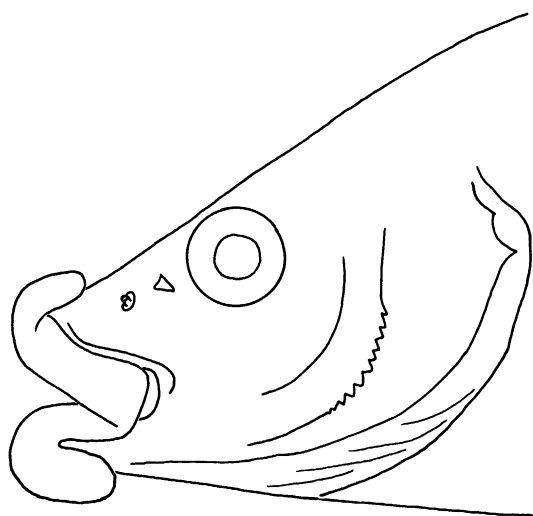


FIG. 69. Drawing of the "blubber" lip condition found in some individuals of *Hephaestus jenkinsi*.

on angle. Lower opercular spine larger and 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 asymmetrically 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 dusky, with spines lighter. 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 fresh waters of northwestern Australia from the Meda River in the west to the Victoria in the east (fig. 66).

Ecology. This species has been collected in clear to turbid waters, both still and rapidly running and over sand, mud, and rock bottoms.

Remarks. *Mesopristes jenkinsi* was first described from a single specimen collected at Ivanhoe Station and placed in the genus *Mesopristes* by Whitley (1945) evidently on the basis of its

rather long anal spine. This generic assignment is not supported by the evidence of this study and the species shares with the other species of the genus *Hephaestus* the defining characters of the genus.

Mees (1971) considered *H. jenkinsi* to be a synonym of *H. fuliginosus*, a species considered previous to that work to be limited to eastern Australia. However, this synonymization appears incorrect in that *H. jenkinsi* has a continuous lower lip fold (from type, personal commun., J. Merrick) (fig. 30), a condition not found in either *Hephaestus fuliginosus* or *H. bancrofti*, the other Australian members of genus 11a (from lectotype of *T. bancrofti* and paralectotype of *T. fuliginosus*; R. McKay, personal commun.).

Mees in the same paper described a new

species, *Terapon brevipinnis*, based on juvenile specimens. He believed that this species was most closely related to *T. bancrofti*, but distinguishable from it in the relative lengths of the longest dorsal spine and ray. *Terapon brevipinnis*, however, shares with *Hephaestus jenkinsi* a continuous lower lip fold, a character unique in the family (from paratypes of *T. brevipinnis*, personal observ.). Comparisons of the relative lengths of the longest dorsal spines and rays for the paratypes of *T. brevipinnis*, collections of *H. jenkinsi* and the holotype of *H. jenkinsi* fail to reveal any discontinuities between these forms (fig. 70). *Terapon brevipinnis* would therefore appear to be indistinguishable from and based on the young of *Hephaestus jenkinsi*.

Examination of *Hephaestus* material from

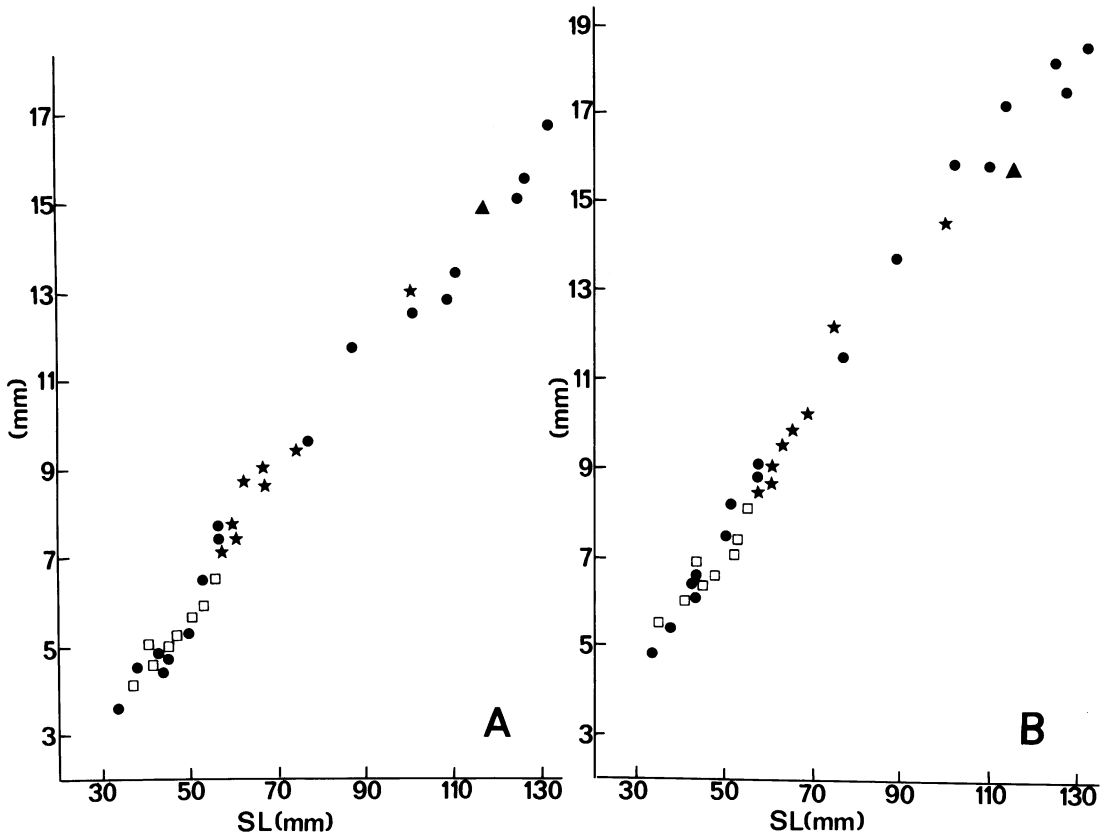


FIG. 70. Graph of lengths of longest dorsal spines and rays plotted against standard length for *Hephaestus jenkinsi* material and paratypes of *Terapon brevipinnis*. A, length of longest dorsal spines plotted against standard length; B, length of longest dorsal rays plotted against standard length; holotype of *Mesopristes jenkinsi* (triangle, data from Whitley, 1945); paratypes of *Terapon brevipinnis* (squares), *H. jenkinsi* (circles) (AMNH 35671); *H. jenkinsi* (stars) (AMNH 35670).

Western Australia and Northern Territory has shown *H. jenkinsi* to be the only member of the genus occurring between the Victoria and Daly rivers. Based on this information, it would appear likely that the material listed by Mees (1971) as Western Australian *Therapon fuliginosus* (p. 199, localities 3 to 6) is actually *H. jenkinsi*.

Specimens Examined

Australia, Western Australia: Manning Creek (AMNH 35562, 10 [of 44], 40-124 mm.; AMNH 35668, 275); Bow River (AMNH 35663, 4; AMNH 35666*, 20 [of 116], 50-110 mm.). Hann River, Moll Gorge (AMNH 35664*, 15 [of 196], 50-156 mm.). Hann River (AMNH 35671*, 5 [of 31], 47-148 mm.; RMNH 26399*, 10 (paratypes of *Therapon brevipinnis*), 35-55 mm.). West Baines River (AMNH 35665, 21). Dunham River (AMNH 35667*, 10 [of 112], 40-120 mm.). Grave Creek, Sadler's Spring (AMNH 35669*, 1, 86 mm.). Meda River (AMNH 35670*, 8, 60-105 mm.). Drysdale River (WAM P-25409-002*, 1, 100 mm.).

Hephaestus trimaculatus (Macleay, 1883)

Three spot grunter
Figures 71, 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). Kailola, 1975, p. 102 (New Guinea: Brown and Laloki rivers). *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). *Terapon 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, Moore and Reynolds, 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. A member of the genus *Hephaestus* distinguishable in having three prominent spots at the base of the caudal fin (a unique pigmentation within 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; pectorals 15-16; pelvics 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 entire 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 HL; 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 asymmetrically pointed; fourth or fifth ray longest. Pelvics pointed; first ray longest, slightly filamentous; reaching to anus. Caudal slightly emarginate.

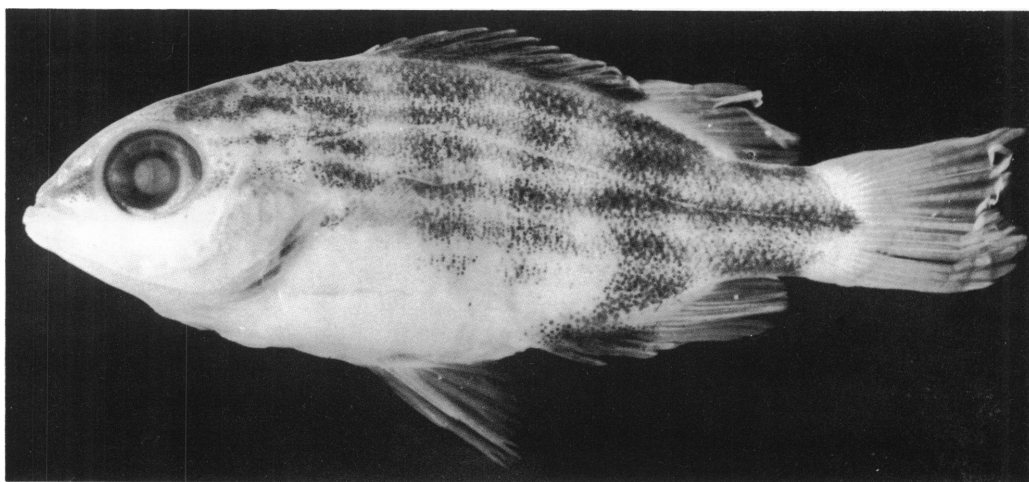


FIG. 71. *Hephaestus trimaculatus*, juvenile, USNM 210487, 22 mm. SL.



FIG. 72. *Hephaestus trimaculatus*, adult, USNM 210487, 130 mm. SL.

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 4 to 6 line up with spots

on the caudal base. In large specimens, stripes are indistinct or totally masked. 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. Rivers of New Guinea in both lowlands and highlands: Goldie, Lorentz, Mimika, Brown, Fly, and Laloki rivers (fig. 73).

Remarks. *Terapon* (= *Hephaestus*) *trimaculatus* was first described by Macleay (1883) from the Goldie River in southeastern New Guinea. Weber (1910) described another nominal species, *Terapon habbema* from southwestern New Guinea. Weber and de Beaufort (1931) differentiated this species from *T. trimaculatus* by the presence in *T. habbema* of a suprascapular (=posttemporal)

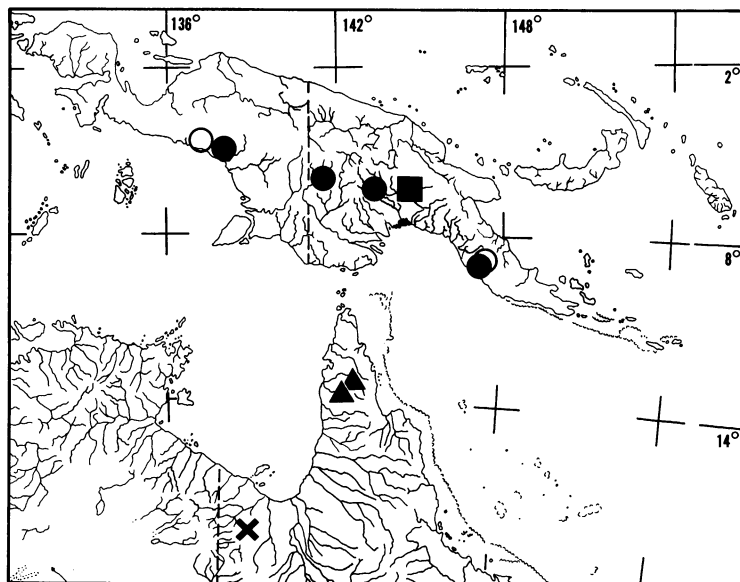


FIG. 73. Distribution records for the species of the genus *Hephaestus* in part (genus 11b), *H. trimaculatus* (circles), *H. adamsoni* (square), *H. suavis* (triangle), and *H. carbo* (cross). Solid symbols represent specimens examined, open symbols are additional literature records.

hidden below skin and scales, 54-56 lateral line scales; 10 scales above the lateral line and a second anal spine much longer than the third in contrast to *T. trimaculatus*, which has an exposed serrate posttemporal, 47-50 lateral line scales, 6 1/2-7 1/2 scales above the lateral line and a second anal spine slightly longer than the third.

However, examination of *Hephaestus trimaculatus* material from various Papua-New Guinea localities and seven syntypes of *T. habbema* has shown these presumed differences to result from limited sample size, procedural differences, or osteological misidentifications.

The difference in the form of the suprascapular (=posttemporal) cited by Weber and deBeaufort is a consequence of a misinterpretation of the osteology of *T. habbema*. Contrary to their description of the element as hidden beneath skin and scales, the posttemporal is exposed and serrate as in *H. trimaculatus*. The difference noted in the scales above the lateral line results from differing methods of taking the count. Weber (1910) and Weber and deBeaufort (1931) made this count to the dorsal fin origin, includ-

ing the dorsal sheath scales. However, these authors used as a basis of comparison Ogilby and McCulloch's (1916) description of *T. trimaculatus*. In that work, counts of scales above the lateral line were made to the median dorsal spines "excluding the dorsal sheath" (Ogilby and McCulloch, 1916; p. 101). Such differences in procedure result in a difference of two to four scales in the supralateral scale count; a difference overlapping that distinguishing the species according to Weber and deBeaufort.

Examination of the syntypes of *Therapon habbema* and material of *Hephaestus trimaculatus* from various Papua-New Guinea localities including the type locality region and literature information shows no separation between these nominal forms on the basis of scales above the lateral line. Similarly the material examined shows an overlap in the lateral line scale counts and relative lengths of the second and third anal spines between the nominal forms (table 3).

Consequently, the characters utilized by Weber and deBeaufort do not discriminate between the nominal forms, nor has any other distinguishing character been uncovered in the course of the

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*

| Standard length | LAS2/LAS3 ^a | Lateral line | Standard length | LAS2/LAS3 | Lateral line |
|-------------------|------------------------|--------------|--------------------|-----------|--------------|
| 20.5 ^b | 1.0 | 53 | 93.8 ^e | 1.21 | 54 |
| 22.5 ^b | 1.0 | 54 | 97.2 ^f | 1.25 | 55 |
| 23.0 ^b | 1.06 | 51 | 99.4 ^e | 1.18 | 55 |
| 25.3 ^b | 1.03 | 50 | 99.5 ^d | 1.17 | 46 |
| 30.5 ^b | 1.11 | 52 | 103.7 ^d | 1.23 | 47 |
| 60.9 ^c | 1.15 | 55 | 108.5 ^d | 1.29 | 49 |
| 73.2 ^b | 1.20 | 50 | 110.5 ^d | 1.24 | 49 |
| 75.2 ^b | 1.23 | 49 | 114.2 ^e | 1.16 | 57 |
| 76.4 ^c | 1.15 | 54 | 120.0 ^d | 1.18 | 50 |
| 77.8 ^b | 1.18 | 47 | 121.2 ^e | 1.24 | 55 |
| 79.2 ^b | 1.19 | 47 | 123.6 ^e | 1.25 | 55 |
| 82.0 ^b | 1.18 | 51 | 124.5 ^b | 1.17 | 49 |
| 82.4 ^b | 1.27 | 49 | 128.0 ^f | 1.16 | 53 |
| 83.2 ^b | 1.25 | 50 | 139.3 ^e | 1.19 | 54 |
| 86.4 ^d | 1.25 | 50 | 142.8 ^e | 1.24 | 53 |
| 86.8 ^d | 1.15 | 46 | 147.3 ^f | 1.21 | 57 |
| 93.0 ^d | 1.20 | 46 | — | — | — |

^aLength of anal spine 2/ Length of anal spine 3; ^b USNM 210847; ^c AMNH 12629; ^d AMNH 14005; ^e ZMA 112-456 (syntypes of *Therapon habbema*); ^f AMNH 13905

study. As such *Terapon habbema* is placed in synonymy with *Hephaestus trimaculatus*.

Fowler (1928) was therefore evidently correct in his synonymization of *T. habbema* into *T. trimaculatus*, although he failed to note or discuss the supposed major differences between these forms as described. Later however, he placed both these species as synonyms of *Terapon* (= *Lagusia*) *micracanthus*, a Sulawesi species; being followed in this by Munro (1956). However, *L. micracanthus* is distinct from the New Guinea forms in lateral line scale counts, anal ray counts, and in lacking a series of apomorphic character states found in *Terapon habbema* and *Hephaestus trimaculatus*.

Munro (1967) noted this mistake and recognized all three species as distinct and hypothesized a close relationship of *H. trimaculatus* to *H. suavis* and *H. adamsoni*, a hypothesis supported by the findings of this study.

Specimens Examined

New Guinea, Papua: Central District, Kubuna (AMNH 12629*, 2, 61-77 mm.; AMNH 14005*, 7, 87-120 mm.). Central District, Laloki River (USNM 210847*, 14, 17-148 mm.). Western District, Upper Fly River (AMNH 13905*, 3, 99-148 mm.).

Indonesia, West Irian: Lorentz River, stream near Alkmaar Village (ZMA 112.456*, 7 (syntypes of *Therapon habbema*), 94-113 mm.), (BM[NH] 1913.12.15.9, 1); Mimika River (BM[NH] 1913.12.9.214, 1).

Hephaestus adamsoni (Trewavas, 1940)

Adamson's grunter

Figure 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*). Kailola, 1975, p. 100 (Lake Kutubu).

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 is deposited in the British Museum (Natural History) (see Specimens Examined).

Diagnosis. A member of the genus *Hephaestus* distinguishable 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 (in contrast to 8-11 in *H. trimaculatus*), 11-12 dorsal rays (in contrast to 13-14 in *H. suavis*), and an emarginate caudal (in contrast to a truncate caudal in *H. carbo*).

Description. Dorsal spines XII; dorsal rays 10-12; anal III, 9-10; pectorals 13-16; pelvics I-5; 52-56 lateral line scales; 0-2 caudal scales; 8-10 scales above lateral line; 20-22 scales below lateral line; 17-20 predorsal scales to occiput; 2-3 rows of scales in sheath at base of dorsal fin, sheath extending to sixth to eighth 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 3.2-4.8 in HL; length of longest dorsal ray 2.3-2.9 in HL; length of longest anal spine 3.0-4.0 in HL; length of longest anal ray 2.1-2.8 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

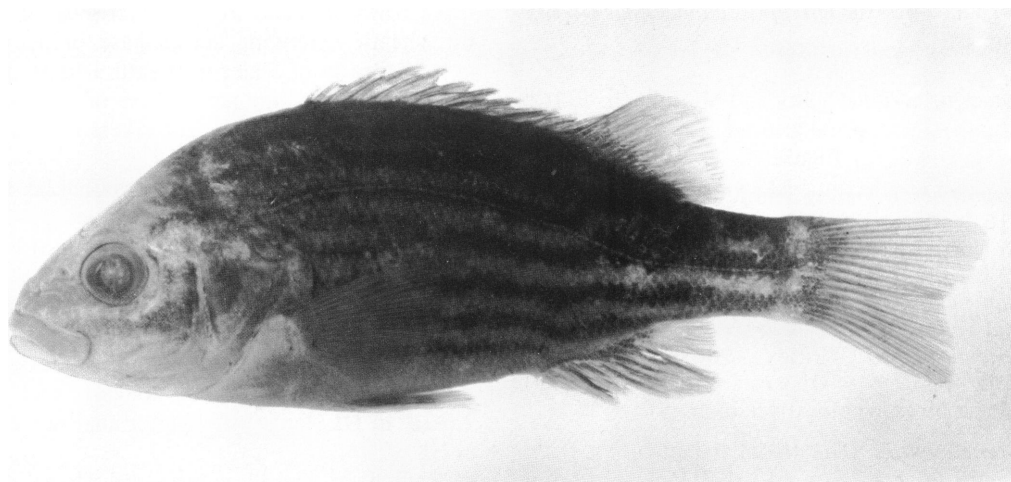


FIG. 74. *Hephaestus adamsoni*, paratype, BM(NH) 1940.3.11.15, 83 mm. SL.

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 asymmetrically 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 (lacking in many specimens) from below pectoral base to front of soft anal. 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 endemic to Lake Kutubu, Papua-New Guinea (fig. 73) and is known from limited collections.

Remarks. Examination of the type of *Terapon* (= *Hephaestus*) *adamsoni* shows it to differ from the original description in having an exposed serrate posttemporal in contrast to Trewavas's statement that the "supracleithrum" (=posttemporal) is "covered with scales."

Munro (1964) placed *H. adamsoni* in the genus *Madigania* erected by Whitley (1945a) for *Madigania* (= *Leiopotherapon*) *unicolor*, a freshwater Australian species. However, the evidence of this study does not support the hypothesis of a close relationship between these species inherent in that classification. Rather, *Hephaestus adamsoni* shares with the other species of *Hephaestus* a series of derived states of the posttemporal, tabular, extrinsic swimbladder muscle, pigmentation and other characters lacking in *Leiopotherapon unicolor*.

Specimens Examined

New Guinea; Papua, Lake Division, Lake Kutubu (AMNH 15103*, 1, 134 mm.; BM(NH) 1975.3.1.1.1*, 1 (holotype of *Terapon adamsoni*), 127 mm.; BM(NH) 1940.3.11.1-5*,

6 (paratypes of *Therapon adamsoni*), 64-195 mm.).

Hephaestus carbo (Ogilby and McCulloch, 1916)

Coal grunter

Figure 75

Therapon carbo Ogilby and McCulloch, 1916, p. 116, pl. 12, fig. 1 (original description, Gregory River, Queensland). Grant, 1965, p. 233; 1972, pl. 390.

Terapon carbo: Fowler, 1931, p. 352 (on Ogilby and McCulloch).

Hephaestus carbo: Whitley, 1960, p. 75 (Carpentaria drainages of Queensland). Lake, 1971, p. 34, pl. 69 (life coloration, biology).

Nomenclature. The trivial name, *carbo*, from the Latin for coal, refers to the black coloration of the species.

Diagnosis. *Hephaestus carbo* is unique in the family in its vertebral formula of 10+17 (see table 2) and can be further distinguished within the genus by its truncate caudal (rather than the slightly to deeply emarginate caudal of the other species).

Description. Dorsal spines XI-XII; dorsal rays 13-14; anal III, 11-12; pectorals 15-16; pelvics 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;

three 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 2.85-3.0 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 2.5-2.8 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

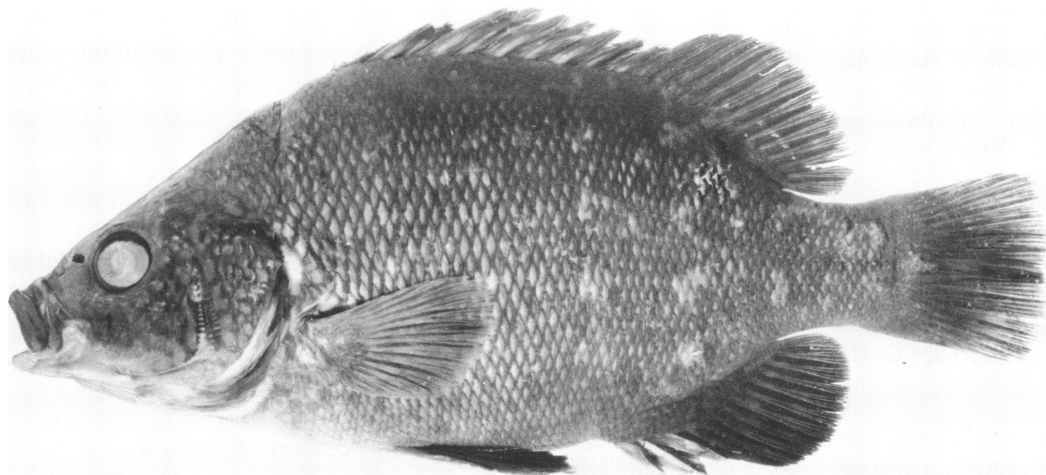


FIG. 75. *Hephaestus carbo*, AM I.16118-004, 137 mm. SL.

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. Post-temporal 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. All 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 asymmetrically 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, 137-160 mm.).

Hephaestus suavis (Whitley, 1948)

Cichlid grunter

Figure 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 (origi-

nal 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 for 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*), a slightly 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; pectorals 15-16; pelvics 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 ante-

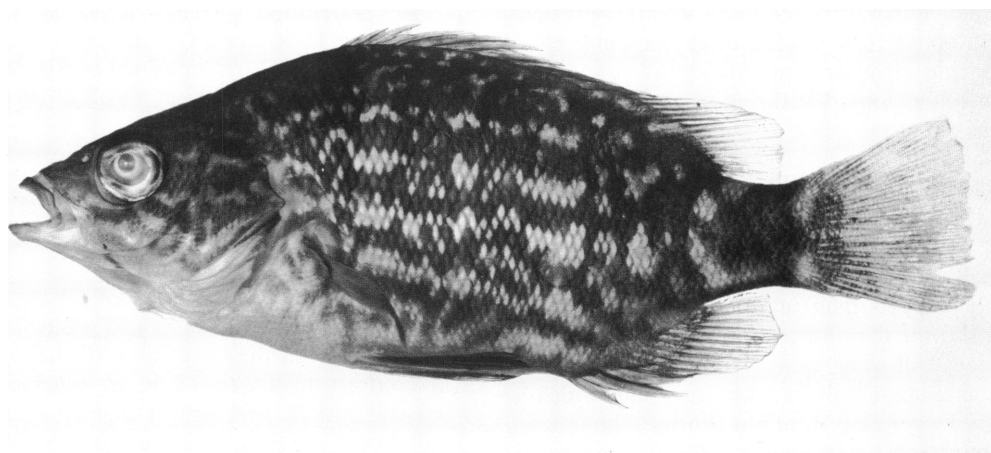


FIG. 76. *Hephaestus suavis*, holotype, AM IB-1983, 65 mm. SL.

rior edge of eye in younger specimens, falling short 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 asymmetrically pointed; fifth ray longest. Pelvics pointed; first ray longest, slightly filamentous; nearly reaching anus. Caudal slightly emarginate; 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 yellowish in life (Whitley, 1948); pale brown in preserved specimens. Body with five to eight

irregular vertical bands and seven to eight 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 of the species and the type of *Archeria jamesonoides* Nichols, both collected in the Coen District, Cape York, Queensland (fig. 73).

Ecology. No information is available on the natural activities or habitat of this species. Whitley reported it to be very active in captivity. It shares with *H. carbo* a utilization of all fins except the spinous dorsal for swimming (Lake, 1971).

Remarks. Whitley (1951) suggested that *Archeria jamesonoides* was a junior synonym of *Leio-*

potherapon (=Hephaestus) *suavis*. Examination of the types of both species has shown them to be indeed conspecific.

In his original description, Whitley (1948) placed this species in *Leiopotherapon*, originally proposed by Fowler (1931) as a subgenus for four species characterized by nonexposed, non-serrate posttemporals. However, *Leiopotherapon* (=Hephaestus) *suavis* in contrast has an exposed, posteriorly expanded and serrate posttemporal. Furthermore, it shares with the other *Hephaestus* species derived states of the posttemporal, tabular, extrinsic swimbladder muscle, and other characters lacking in the species of Fowler's subgenus. Consequently, the close relationship implied in Whitley's original generic assignment appears to be erroneous.

Hephaestus suavis is very similar to another Queensland species, *H. carbo*, which is, however, only known from much larger specimens. Although *H. suavis* may be based on juveniles of the latter species, the differences found between the specimens of these nominal species (vertebral formula, relative jaw length, relative distance from origin of dorsal to snout, and extent of caudal emargination) are such that I prefer to maintain the species as distinct at this time.

Specimens Examined

Australia, Queensland: Coen District (AM IB-1982*, 1 (holotype of *Leiopotherapon suavis*, 65 mm.); Cape York, Archer River, Wenlock Crossing (AMNH 18533*, 1 (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*, is 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 Australian

species are placed in *Bidyanus*. One, *B. bidyanus*, distributed through New South Wales and Victoria, and *B. welchi*, limited to the internal drainages of Queensland and South Australia.

Bidyanus bidyanus (Mitchell, 1838)

Silver perch

Figure 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, 1976b, p. 36 (biology, distribution); 1967a, p. 137

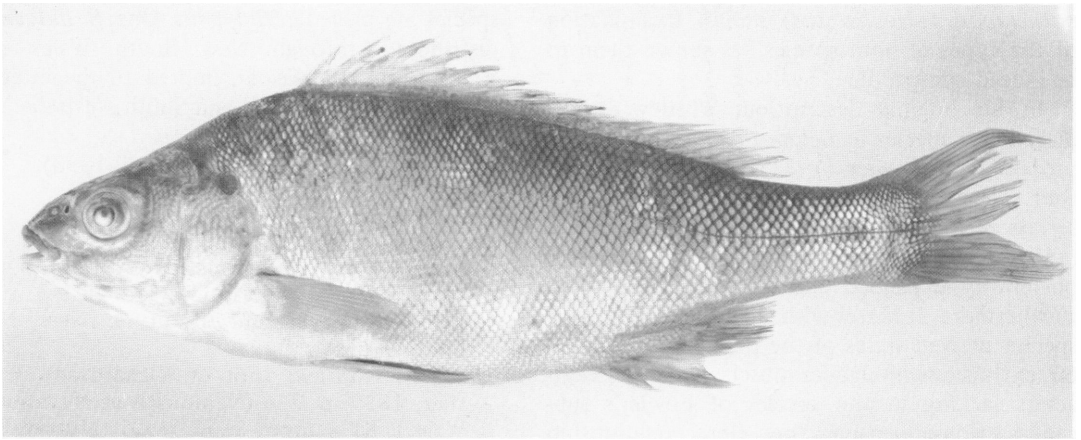


FIG. 77. *Bidyanus bidyanus*, USNM 42017, 195 mm. SL.

(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*), 76-79 scales counted in a series above lateral line (in contrast to 68-72), and 71-77 below (in contrast to 59-66).

Description. Dorsal spines XII-XIII; dorsal rays 11-13; anal III, 7-9; pectorals 16-17; pelvics I-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; three 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 1.9-2.1 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 longest 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) reported that the body in juveniles bears longitudinal vermiculations; with the fins being clear. In the adults, the head is dark dorsally, with heavier pigmentation 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. New South Wales, Victoria, and South Australia: Darling, Murray, Gwydir, McIntyre, Murrumbidgee and Macquarie rivers (fig. 78).

Ecology. This species achieves the largest size of any species in the family, reaching 800 mm. SL and 8 kg. Lake (1967) has studied the reproductive habits of the species in depth. His results show that spawning is initiated by a combination of a rise in water temperature and water levels. The species releases pelagic eggs,

being the only freshwater member of the family known to do so.

Remarks. *Bidyanus bidyanus* has been considered to be a part of the freshwater fauna of Western Australia based on Richardson's description (1848) from the rivers of Western Australia of *Datnia elliptica*, a species that following workers considered to be a junior synonym of *Therapon* (= *Bidyanus*) *bidyana*. The species was later reported by Castelnau from the Swan River (1873) and by Woodward (1900, 1903) from Broom on the west coast of Australia. More recently Whitley (1948, 1956) recognized a separate western Australian subspecies (*Bidyanus bidyanus ellipticus*) or a separate species (*Bidyanus ellipticus*) for this nominal species. However, both the existence of a Western Australian population of *Bidyanus* and the synonymy of *Datnia elliptica* with *B. bidyanus* are questionable.

Neither Nelson, Butler, and Rosen during their extensive collecting in Western Australia nor any other collectors in the past three-quarters of a century have obtained the species in

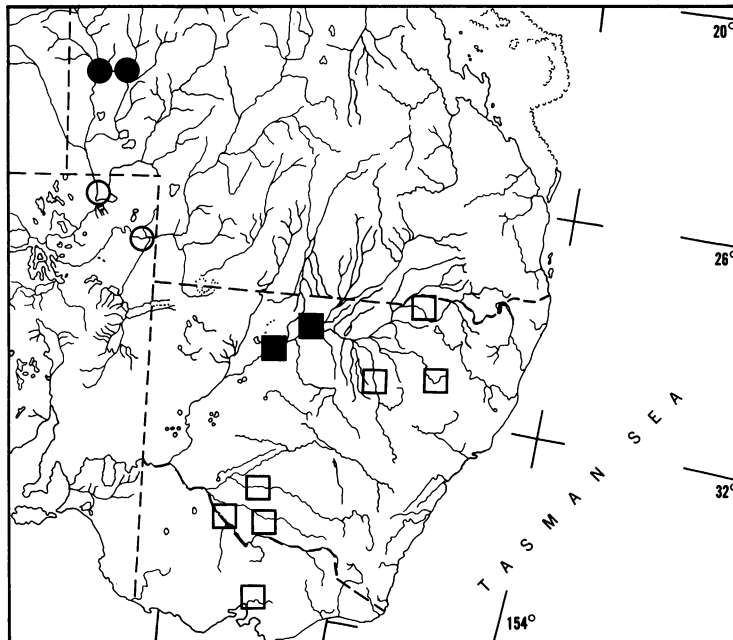


FIG. 78. Distribution records for the species of the genus *Bidyanus*, *B. bidyanus* (squares), and *B. welchi* (circles). Solid symbols represent specimens examined, open symbols are additional literature records.

Western Australia, and *Bidyanus* material is totally lacking from the collection of the Western Australian Museum (J. B. Hutchins, personal commun.). In addition, the presence of *Bidyanus bidyanus* in Broom, a seaside locality distant from any river, is unlikely for a species known only from fresh water. Consequently, it appears likely that the Western Australian localities are erroneous, either being misidentifications or incorrect locality records.

A comparison of the original figure and description of *Datnia elliptica* with the available material of *Bidyanus bidyanus* and *B. welchi* shows *D. elliptica* to agree more closely with the latter contrary to its placement by most previous authors. Richardson's figure shows 10 scales above the lateral line to the base of dorsal sheath, in agreement with *B. welchi* (10-12 scales) but not that for *B. bidyanus* (12-14 scales) and 68 scales in a series above the lateral line, a count that also falls into the *B. welchi* range. Unfortunately, the type of *D. elliptica* appears to be lost (P. H. Greenwood, personal commun.) and it is therefore not possible to examine it for the various internal characters that differentiate the species.

Bidyanus bidyanus has also been considered to be part of the Philippine fauna based on the identification of specimens from Laguna de Bay, Luzon as *Terapon bidyana* sp. affin. by Meyer (1885) followed by other workers. However, as discussed previously, this is probably a misidentification for *Leiopotherapon plumbeus* (see Remarks for that species).

Specimens Examined

Australia, New South Wales: Darling River, Kinchega National Park (AM I-16002-005*, 3, 190-230 mm.); Bourke (USNM 42016*, 1, 191 mm.; USNM 42017*, 1, 194 mm.; USNM 47795*, 1, 162 mm.); (BM(NH) 1871.3.29.11-13.3).

Bidyanus welchi (McCulloch and Waite, 1917)

Welch's grunter

Figure 79

Terapon 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 (Andriwilla Waterhole, South Australia); 1960, p. 75 (central and south Australia). Lake, 1971, p. 34, pl. 74 (distribution, biology).

The following species may also be a synonym of this species:

Datnia elliptica Richardson, 1844, p. 118, pl. 52, figures 4-8 (original description, Rivers in Western Australia?).

Nomenclature. The trivial name, *welchi*, is in honor of E. J. Welch, a member of the Burke and Wills expedition.

Diagnosis. Distinguishable from *Bidyanus bidyanus* in having a body width 1.5-1.7 in body depth (in contrast to 1.9-2.1 in *B. bidyanus*), 68-72 scales counted in a series above the lateral line and 59-66 counted below (in contrast to 76-79 above and 71-77 below in *B. bidyanus*).

Description. Dorsal spines XII; dorsal rays 11-12; anal III, 8-9; pectorals 16-17; pelvics I-5; 50-56 lateral line scales; 68-72 scales counted in a series above lateral line; 59-66 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 1.5-1.65 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

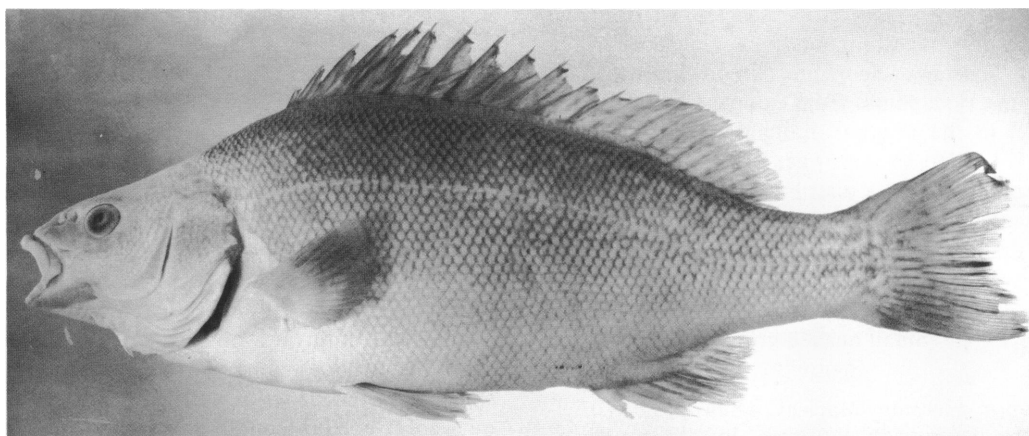


FIG. 79. *Bidyanus welchi*, AM I.16023-001, 200 mm. SL.

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, 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 distinc-

tiveness of this species from *B. bidyana*. Based on the material available the species appear to be distinct. However, it is possible that these nominal forms are the extremes of a single variable species.

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*.

Specimens Examined

Australia; Queensland, Georgina River, Parapituri (AM I. 16023-001*, 2, 185-200 mm.); Marion Downs (AM I-16024-001*, 1, 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 *Therapon jarbua*), and leathery textured flesh.

Included Species. Three species, all from the fresh waters of eastern Australia, are placed in the genus *Scortum*. *Scortum barcoo* known only from the type comes from Cooper Creek (Barcoo Creek) in the internal drainages. *Scortum parviceps* is limited to the upper Burdekin of Queensland and *S. hillii* is distributed from the eastern drainages of Queensland to the Gulf of Carpentaria drainages and internal drainages.

Scortum parviceps (Macleay, 1884)

Small headed grunter

Figure 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).

Terapon 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. *Scortum 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; pectorals 15-16; pelvics 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; two rows of scales in sheath at base of dorsal, sheath extending to seventh or 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 outward. 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 asymmetrically 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 pro-

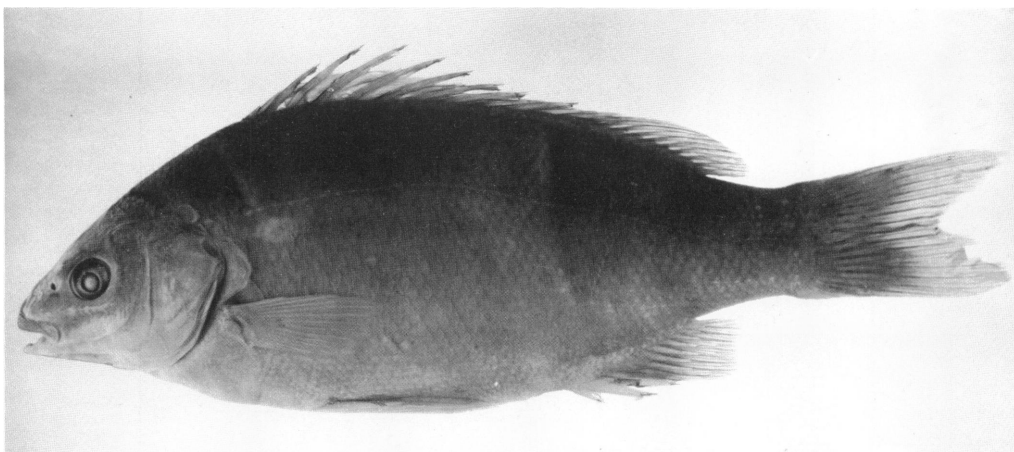


FIG. 80. *Scortum parviceps*, AM IA.5949, 175 mm. SL.

nounced 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, 163 mm.); (AM A. 17853*, 1, 94 mm.; AM A. 17854*, 1, 94 mm.; AM IA. 5949*, 1, 175 mm.).

Scortum hillii (Castelnau, 1877)

Leathery grunter

Figure 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.

Therapon 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. *Scortum 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 82 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 III, 8-10; pectorals 15-17; pelvics I-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 3.05-3.5 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 1.7-2.4 in HL; length of longest dorsal ray 2.1-2.5 in HL; length of longest anal spine 1.8-2.2 in HL; length of longest anal ray 1.6-2.1 in HL.

Body moderately deep, slightly compressed, more so in adults. Dorsal profile much more

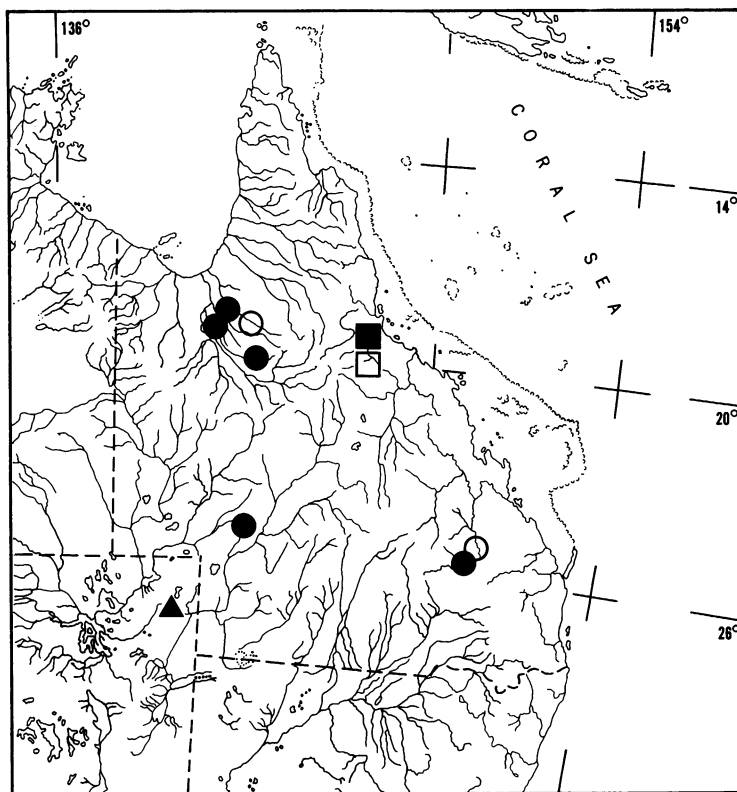


FIG. 81. Distribution records for the species of the genus *Scortum*, *S. parviceps* (squares), *S. hillii* (circles) and *S. barcoo* (triangle). Solid symbols represent material examined, open symbols are additional literature records.

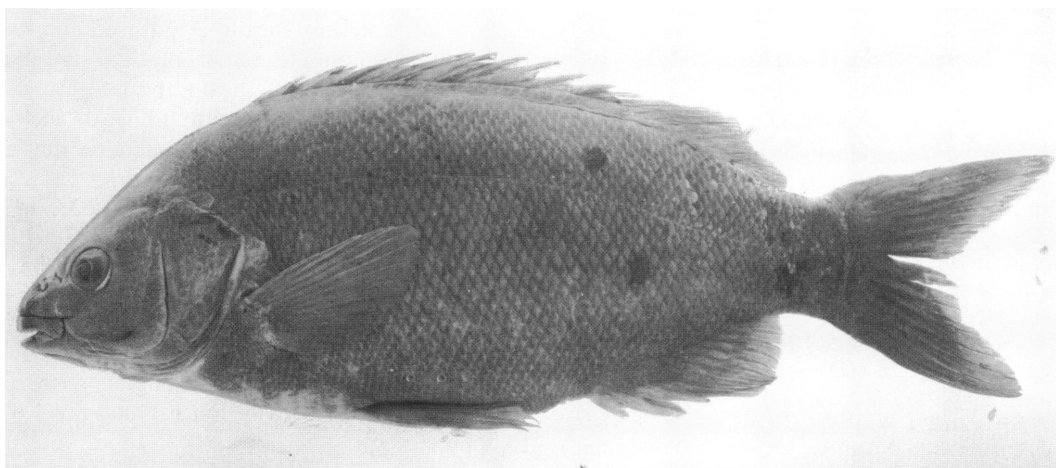


FIG. 82. *Scortum hillii*, AM I.19013-001, 240 mm. SL.

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 or 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 asymmetrically 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 grayish 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. Rivers of Queensland draining into 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 new species, *Scortum ogilbyi*, based on specimens of *Terapon hillii* from the Norman River used by Ogilby and McCulloch (1916) in their redescription of the latter species. Whitley distinguished the new species from *T. hillii* by lateral line counts and body proportions. Based on material examined, however, the continued maintenance of *S. ogilbyi* as a distinct species does not appear to be justified. Contrary to the lateral line count differences cited by Whitley, the material examined and literature information shows an overlap for the nominal forms with specimens from the Dawson River (type locality of *S. hillii*) having 52-61 lateral line scales and those from the Norman River region (type locality of *S. ogilbyi*) having 50-55 scales.

The second major difference cited by Whitley, a difference in the body depth, appears to be a result of differing methodologies. Whitley used the original description of *Terapon hillii* by Castelnau (1878) as a basis of comparison with his new species. However, as discussed by Ogilby and McCulloch (1916) Castelnau's depth measurements appear to have been proportions of total rather than standard length; a hypothesis consistent with material examined. Finally, the remaining differences cited by Whitley—the relative lengths of the second and third anal spines and the extent of emargination of the caudal fin—also appear to fall within expected ranges of variation of teraponid species.

Specimens Examined

Australia, Queensland: Saxby River (AM I-7942-008* (as *Scortum ogilbyi*), 1, 95 mm.); Dawson River (AM I-18013-001*, 3, 225-270 mm.); Thompson River (ANSP 95571*, 2, 143-144 mm.); Forest Home Station, Gulf of Carpentaria (ANSP 122162*, 1, 87 mm.); Peak Downs (BM[NH] 1876.3.29.1*, 1, 265 mm.).

Scortum barcoo (McCulloch and Waite, 1917)

Barcoo grunter

Figure 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; pectorals 16; pelvics 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; two rows of scales in sheath at base of dorsal fin (from fig.), sheath extending to tenth dorsal ray (from fig.); 2-4 rows of scales in sheath at base of anal fin, sheath extending across base of entire fin (from fig.); 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 bony 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

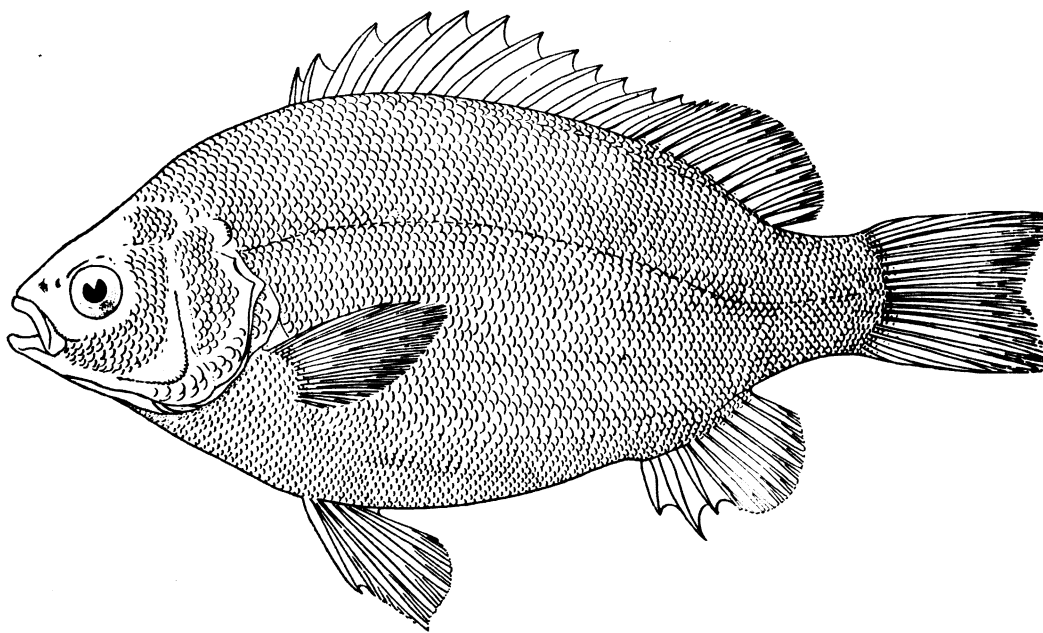


FIG. 83. *Scortum barcoo*, from Scott, 1962.

rays. Soft dorsal rounded. Second anal spine longest; shorter than longest anal rays. Soft anal rounded. Pectorals asymmetrically pointed; fifth ray longest. Pelvics inserted behind vertical through first dorsal spine; first ray longest (from fig.); 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. Since the type and only specimen of the species was not available for examination, the above description is taken from the original description and figure of McCulloch and Waite (1917). Despite the limited information available, *S. barcoo* is placed in the genus *Scortum* following previous practice and on the basis of its retention of vomerine teeth into adulthood and its depressible teeth, traits shared with other *Scortum* species. However, it should be noted that it bears an overall resemblance to the species of the genus *Pingalla*, especially in its small mouth with a strongly curved maxillary.

GENUS 14, *PINGALLA*

Pingalla Whitley, 1953, p. 45 (type species, *Pingalla gilberti* Whitley, 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 in having only two distinct rows of teeth in each jaw (in contrast to a band of teeth or a row of teeth followed by a distinct band in all other groups in the family). In addition the combination of a very small mouth, a strongly curved maxilla and very flattened noncuspidate teeth further separates it from all other species in the family.

Included Species. Two freshwater species are placed in the genus: *P. gilberti* from Northern Territory and Queensland in Australia and *P. lorentzi* from southern New Guinea.

Remarks. Whitley (1953), in his original description of *Pingalla*, placed it in the subfamily Helotinae along with the genus *Helotes*; removing one species (*lorentzi*) from the latter to *Pingalla* along with *P. gilberti*, which was described at the

same time. 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 since *Helotes* (= *Pelates*) *sexlineatus* lacks apomorphic states of many characters (posttemporal, tabular, extrinsic swimbladder muscle, dentition, intestinal patterns, etc.) uniting the species of *Pingalla* and their closest relatives. Similarly, the hypothesis of a close relationship between *Helotes* (= *Pelates*) *sexlineatus* and *Pingalla lorentzi* inherent in Weber's placement of the latter in *Helotes* (1910) also is falsified by the results of this study (see also the discussion under *P. lorentzi*).

Pingalla lorentzi (Weber, 1910)

Lorentz's grunter

Figure 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, Digul River). Fowler, 1931, p. 356 (after Weber). Kailola, 1975, p. 98 (New Guinea: Lake Murray, Morehead, Kiunga).

Pingalla lorentzi: Whitley, 1953, p. 46 (assigned to the subfamily 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 that collected the type series.

Diagnosis. *Pingalla lorentzi* can be distinguished from the other member of the genus in having 13 or 14 dorsal spines and 48-54 lateral line scales (in contrast to 11 or 12 spines and 35-41 scales for *P. gilberti*).

Description. Dorsal spines XIII-XIV; dorsal rays 11-13; anal III, 8-9; pectorals 15; pelvics 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; two irregular series of scales in sheath at base of dorsal fin, sheath extending to seventh or eighth dorsal ray; three rows of scales in sheath at base of anal fin, sheath extending to fifth anal ray; cheek scales in

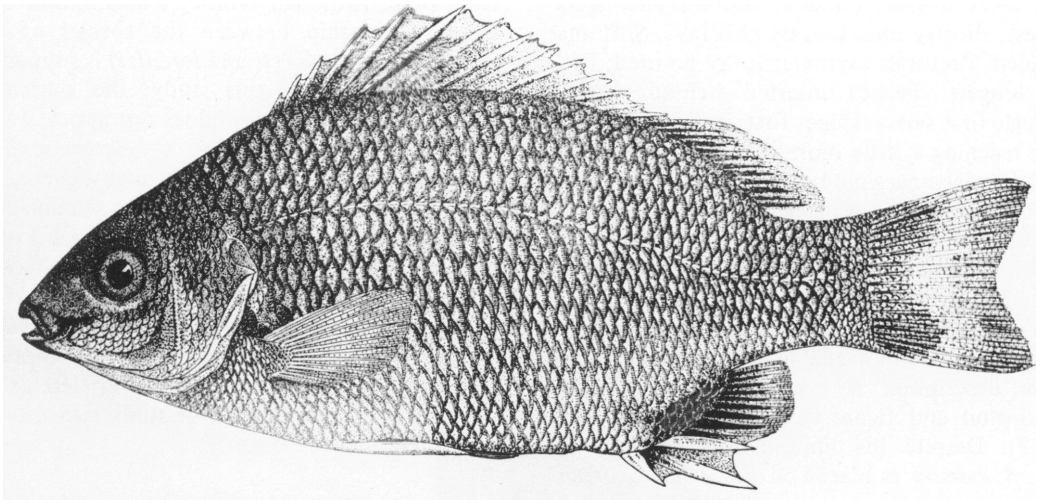


FIG. 84. *Pingalla lorentzi*, from Weber, 1913.

five 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 nonprotractile; 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 spine 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 asymmetrically pointed; fourth ray longest. Pelvics pointed; first ray longest; slightly filamentous; reaching to anus or falling slightly short. Caudal emarginate.

Coloration. (Taken from Weber and deBeaufort, 1931). Head dark above, lighter ventrally. 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. Drainages of southern New Guinea: Lorentz, Noord, Digoel and Moorehead Rivers, Lake Murray, and Kiunga (fig. 85).

Remarks. *Pingalla lorentzi* was placed in the previously monotypic genus *Helotes* by Weber (1910) primarily on the basis of the similarity in the overall tooth forms between the species. However, whereas the teeth of *Helotes* (= *Pelates*)

sexlineatus are distinctly tricuspidate, with a slightly longer central cusp flanked by distinct lateral cusps, the teeth of the *Pingalla* species are more elongate with lateral shoulders rather than distinctive side cusps. Although these two tooth forms are somewhat similar in overall form, a hypothesis of the monophyletic relationship of the species of *Helotes* (*sensu* Weber) is falsified by a series of derived states of the posttemporal, tabular, extrinsic swimbladder muscle, swimbladder form, intestinal patterns and other characters found in *P. lorentzi*—character states lacking in *Pelates sexlineatus*.

Specimens Examined

Indonesia, West Irian: Digoel River near Tanah Merah (RMNH 25390*, 2, 51-53 mm.); Digoel River (ZMA 112.448*, 1, 49 mm.).

Pingalla gilberti Whitley, 1953

Gilbert's grunter

Figure 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 rivers).

Nomenclature. The trivial name, *gilberti*, honors John Gilbert, a naturalist in Leichhardt's expedition after whom the type locality of the species, the Gilbert River, is also named. The holotype is deposited in the Australian Museum (AM IB.3148).

Diagnosis. *Pingalla gilberti* is distinguishable from the other member of the genus, *P. lorentzi*, in having 11-12 dorsal spines (in contrast to 13-14) and 35-41 lateral line scales (in contrast to 48-54).

Description. Dorsal spines XI-XII; dorsal rays 11-13; anal III, 7-9; pectorals 13-17; pelvics I-5; 34-41 lateral line scales; 4-5 scales on caudal; 4-6 scales above lateral line; 10-12 scales below lateral line; 8-9 predorsal scales to occiput; two 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 four 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 to 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;

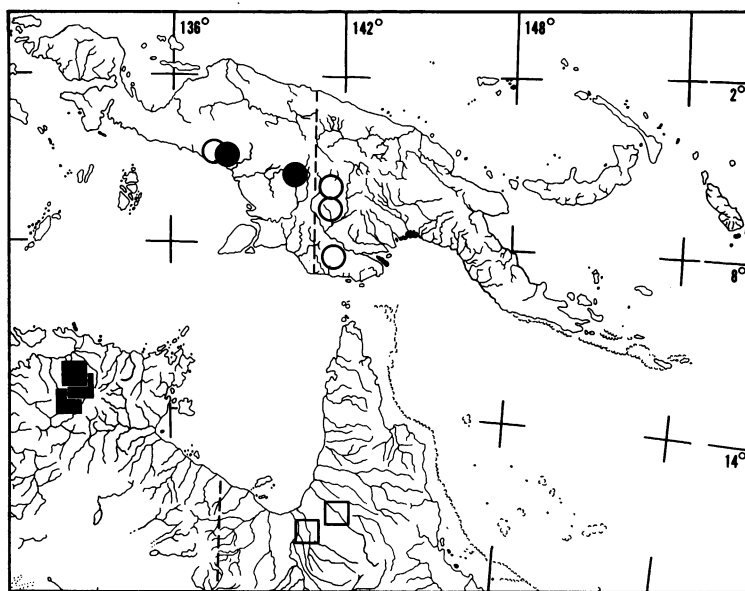


FIG. 85. Distribution records for the species of the genus *Pingalla*, *P. lorentzi* (circles) and *P. gilberti* (squares). Solid symbols represent specimens examined, open symbols are additional literature records.

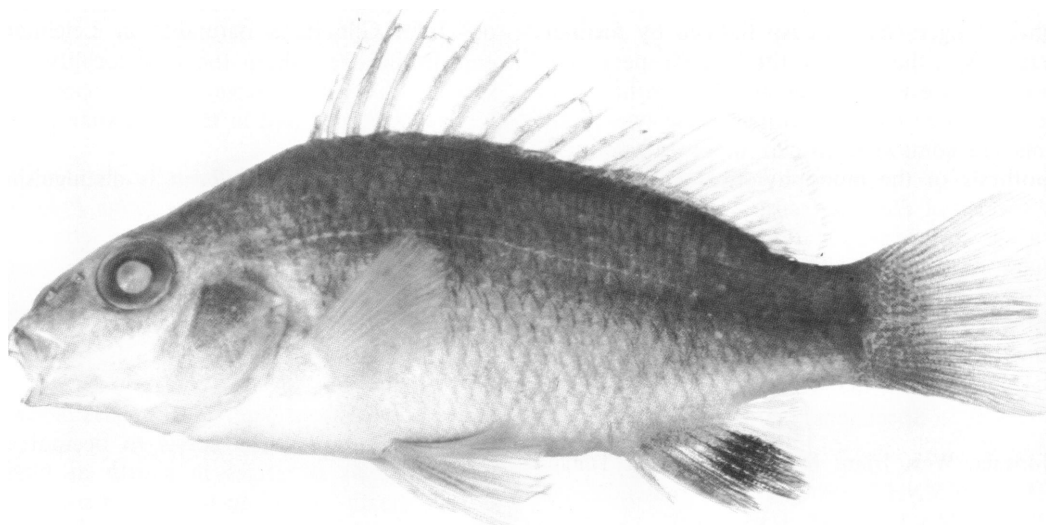


FIG. 86. *Pingalla gilberti*, AM I.16859-018, 64 mm. SL.

eye width 3.2-3.8 in HL; jaw length 4.1-4.4 in HL; length of longest dorsal spine 1.6-1.9 in HL; length of longest dorsal ray 1.8-2.0 in SL; length of longest anal spine 1.7-1.9 in HL; length of longest anal ray 1.6-1.8 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, nonprotractile. Posterior of maxillary strongly curved downward, 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 embedded 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 asymmetrically 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 light-

er margin. Pectorals and pelvics yellowish in life, slightly dusky or clear in preserved specimens.

Distribution. Gilbert and Norman rivers of Queensland and the South Alligator River of Northern Territory (fig. 85). The Northern Territory material represents a major range extension for the species and it is likely that the species also occurs in the intervening freshwater drainages.

Remarks. Whitley in his original description of *Pingalla gilberti* described its dentition as "a practically single row of . . . incisors on jaws." In contrast, however, material examined and the holotype (J. Paxton, personal commun.) have two distinct rows of teeth in each jaw. Whitley also stated that the preorbital is entire, whereas available material bears several serrations along the posteroventral edge of the bone.

Specimens Examined

Australia, Northern Territory (AM. I-16859-018*, 2, 60-64 mm.; AM. I-16858-018*, 2, 62-65 mm.); Barramundie Creek (AMNH 35638*, 14, 44-51 mm.); South Alligator River (AMNH 35639*, 2, 55-56 mm.; AMNH 35640*, 4, 49-54 mm.).

GENUS 15, *SYNCOMISTES*, NEW GENUS

Nomenclature. The generic name, *Syncomistes*, a masculine Greek noun meaning gath-

erer, refers to the algae-cropping habits of the members of this genus.

Diagnosis. The species of *Syncomistes* are one of the most distinctive groups in the family in overall appearance. Characters unique to this genus are the presence of a highly flattened lower jaw with markedly laterally pointing dentition; the arrangement of the teeth in an enlarged outer row and a narrow inner series; the presence of a unique form of rostral cartilage; the form of the ascending processes of the premaxillaries; a very elaborate intestinal pattern and other characters (see phylogenetic analysis for details).

Type Species. *Syncomistes butleri*, new species.

Included Species. Three freshwater species from northwestern Australia are described. One, *S. butleri*, is relatively widespread throughout the region and the others (*S. trigonicus* and *S. kimberleyensis*) are of limited distribution.¹

Syncomistes butleri, new species

Butler's grunter

Figures 87, 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 distinguished in having a rounded lower jaw from a ventral aspect (in contrast to a triangular jaw in

¹Another species of this genus will be described in an independent work at a later date.

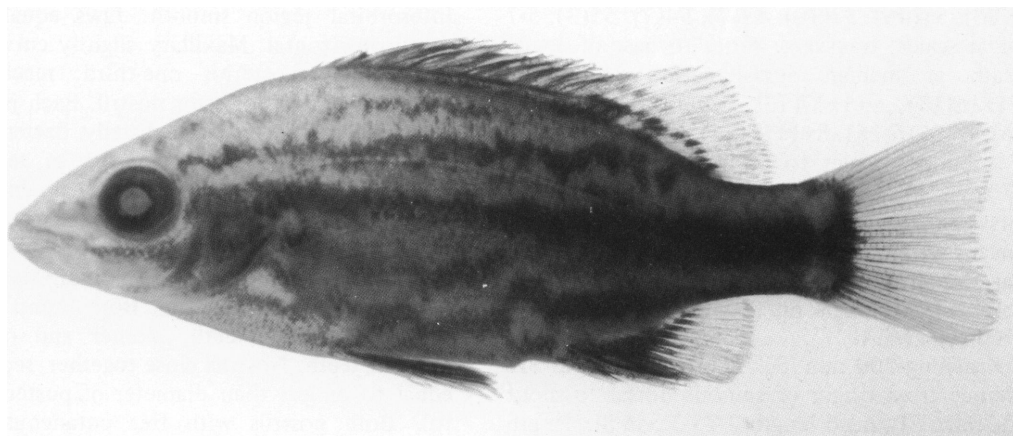


FIG. 87. *Syncomistes butleri*, juvenile, AMNH 35649, 28 mm. SL.

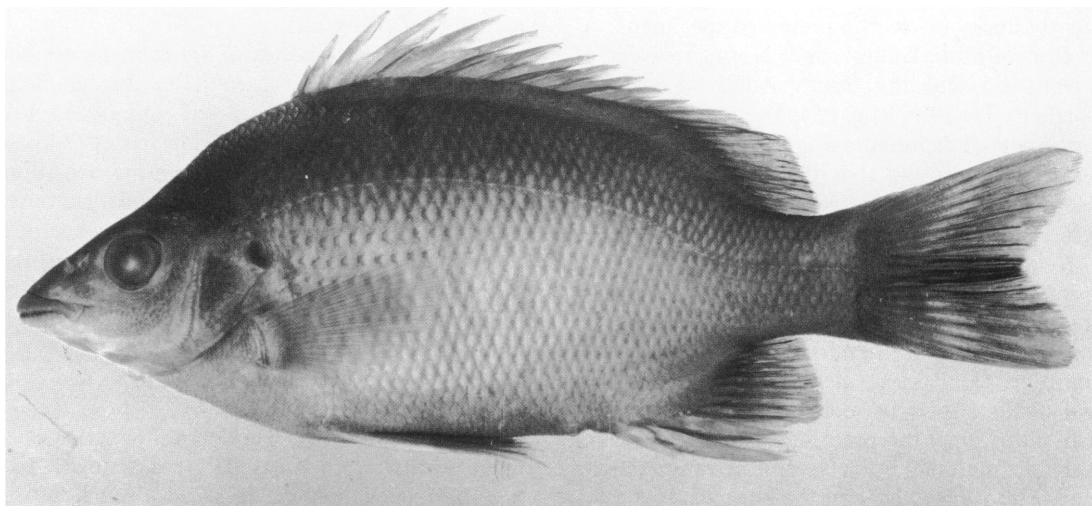


FIG. 88. *Syncomistes butleri*, holotype, WAM P-25385-001, 124 mm. SL.

S. trigonicus [see fig. 30]), five or six longitudinal stripes in the juveniles with the median stripe distinctly wider (in contrast to eight irregular stripes of equal width in juveniles of *S. kimberleyensis* and three in juveniles of *S. trigonicus*) and in relative head lengths (see fig. 89).

Description. (Numbers in parentheses are 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 or 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, becoming relatively larger with increasing age; eye width 3.0-5.25 in HL, becoming 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, becoming 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 serra-

tions, 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. Post-temporal 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 asymmetrically 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 running 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, whereas 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

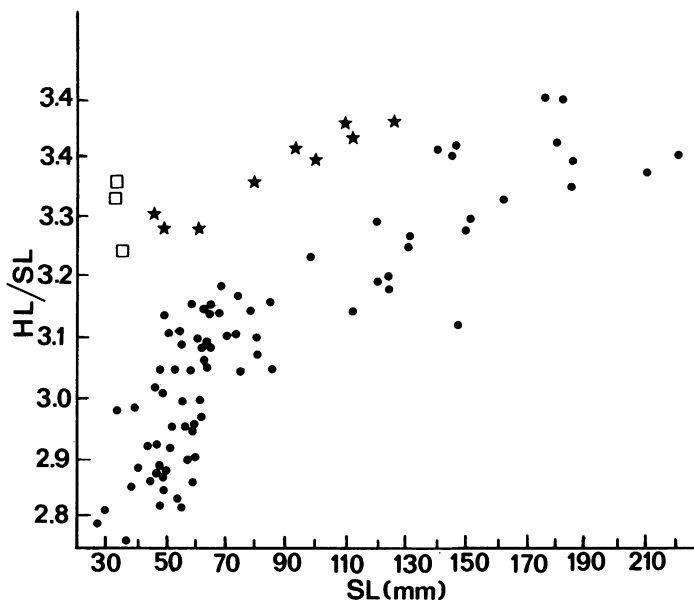


FIG. 89. Graph of head length/standard length plotted against standard length for the species of the genus *Syncomistes*; *S. butleri* (circles), *S. kimberleyensis* (squares), and *S. trigonicus* (stars).

more pronounced. Bar at base of caudal barely discernible.

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 lower lip dark, as is suborbital region. Opercle and subopercle dark below opercular spines. Spinous and soft dorsals dark, with lighter edges, especially in soft dorsal. Caudal, anals, and pelvics dark; first two with light margins in some individuals. Pectorals colorless.

Distribution. Western Australia from the Bow to the South Alligator rivers (fig. 90).

Ecology. *Syncomistes butleri* has an elaborate intestinal pattern and highly modified jaws and teeth that appear to be adaptations for eating filamentous algae, the staple diet of the adults (based on stomach content analyses). The species has been collected in lagoons, streams, and rivers

in which the current flow ranged from slight to rapid. Water conditions of its habitats 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, 32-160 mm.; WAM P-25388-001*, 11, 55-175 mm.); South Alligator River on the Pine Creek to

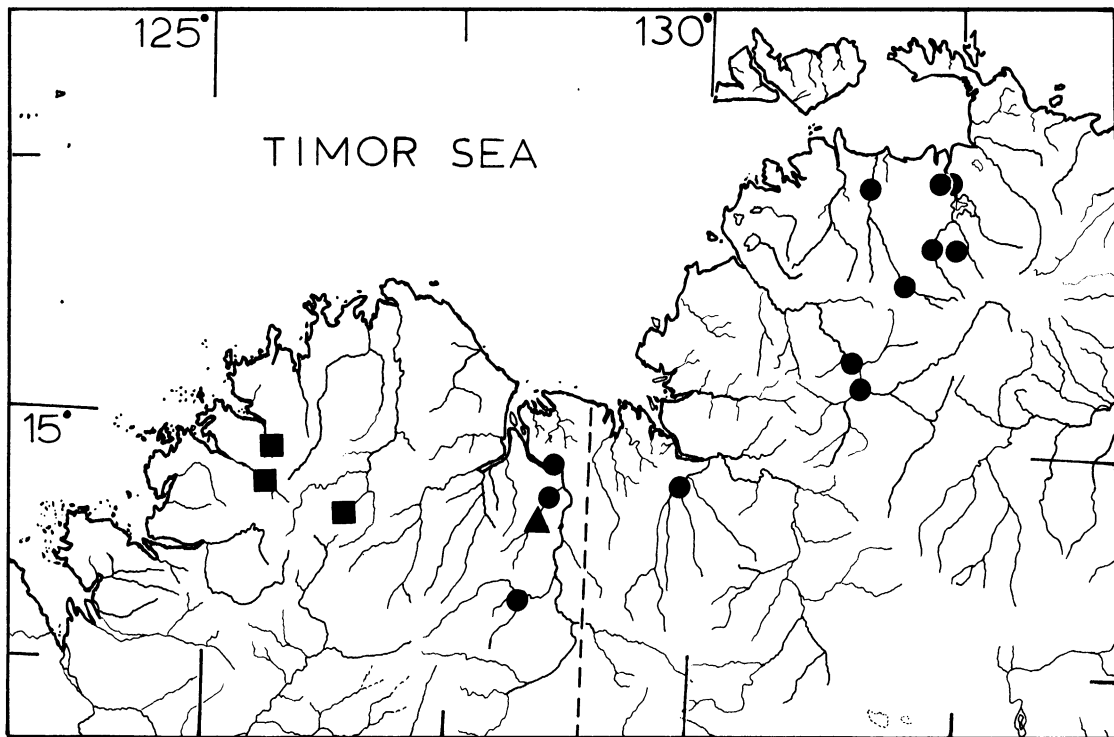


FIG. 90. Distribution records for the species of the genus *Syncomistes* based on material examined, *S. butleri* (circles), *S. trigonicus* (squares) and *S. kimberleyensis* (triangle).

Oenpelli Road, May 11, 1969 (AMNH 35647*, 11, 58-112 mm.; WAM P-25386-001*, 5, 54-78 mm.); main stream of Bow River at Nicholson to Wyndham Highway crossing, May 5, 1969 (AMNH 35644*, 9, 57-78 mm.); main stream of Dunham River, one mi. downstream of old Nicholson to Wyndham Highway crossing, May 6, 1969 (AMNH 35648*, 11, 35-105 mm.); main stream of Ord River below dam at crossing of Great Northern Highway, May 7, 1969 (AMNH 35650*, 2, 121-139 mm.); West Baines River where crossed by Great Northern Highway, May 8, 1969 (AMNH 35651*, 10, 62-68 mm.; WAM P-25390-001*, 8, 62-69 mm.); Katherine River, 8 mi. downstream from Katherine, May 9, 1969 (AMNH 35649*, 10, 28-212 mm.; WAM P-25387-001*, 9, 57-211 mm.); Ferguson River where crossed by Katherine to Darwin (Stuart) Highway, May 10, 1969 (AMNH 35646*, 3, 59-66 mm.); main stream of Mary River on Pine Creek to Oenpelli Road, May 10, 1969 (AMNH 35652*, 2, 108-118 mm.); Barramundie Creek on Pine Creek to Oenpelli Road, May 11, 1969 (AMNH 35642*, 2, 50-53 mm.); Barramundie Creek at Oenpelli to Darwin crossing, May 12, 1969 (AMNH 35643*, 11, 44-54 mm.); East Mary River (Soda Creek) below Oenpelli to Darwin Road crossing, May 13, 1969 (AMNH 35645*, 10, 46-59 mm.; WAM P-25389-001*, 5, 44-57 mm.); Ord River, Stockyard Pools (WAM P-21536, 1); Drysdale River (WAM P-25427-003, 1).

***Syncomistes kimberleyensis*, new species**

Kimberley grunter

Figure 91

Nomenclature. The trivial name, *kimberleyensis*, refers to the type region of the species, the Kimberley region of Western Australia.

Diagnosis. This species, which is presently known only from juveniles, is, however, easily distinguished from the juveniles of the other members of the genus. *Syncomistes kimberleyensis* is distinguished in having a lower jaw which appears rounded when viewed from a ventral aspect (in contrast to a triangular jaw in *S. trigonicus* (see fig. 30)), and in having eight irregular brown body stripes, all of equal width (in contrast to three stripes in *S. trigonicus* juveniles; and four or five stripes with the median much wider in *S. butleri* juveniles). Differences in its relative head length also distinguish this species (see fig. 89).

Description. (Numbers in parentheses are of examined specimens with a given count.) Dorsal spines and rays XII-11(2), XII-12(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

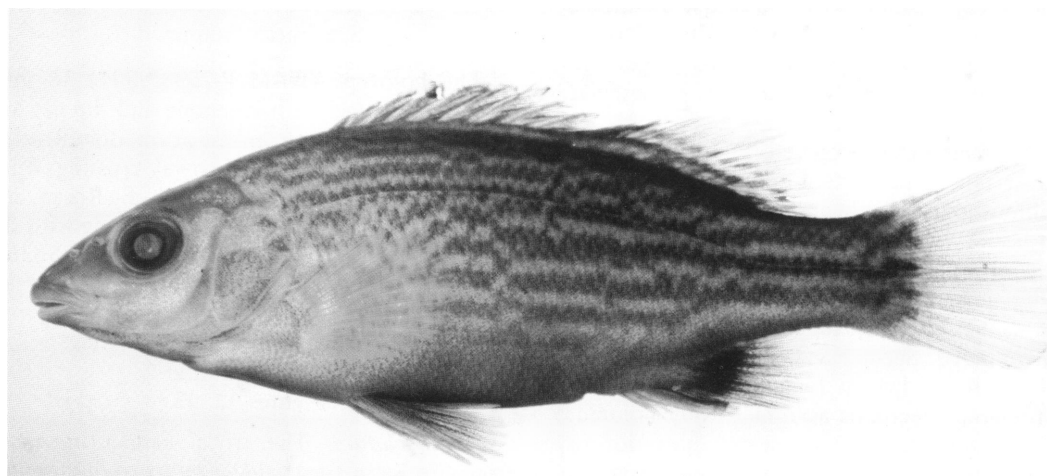


FIG. 91. *Syncomistes kimberleyensis*, holotype, WAM P-25383-001, 36 mm. SL.

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 2.05-2.3 in HL; length of longest dorsal ray 2.05-2.3 in HL; length of longest anal spine 2.15-2.35 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 that 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 asymmetrically 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 streambed 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, new species

Triangle grunter
Figures 92, 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 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(3), 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; two irregular rows of scales in sheath at base of dorsal fin in some specimens, two complete rows in others, sheath extending to fifth or sixth dorsal ray; sheath at base of anal consisting of three rows of scales, sheath extending to second to fourth anal rays; 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 2.8-3.5 in HL, becoming 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 premaxillaries, convex from that 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 and lower jaws with an equal number of teeth in outer row of jaw. Each jaw with an outer row of highly depressible flattened teeth followed by a distinct narrow band of smaller teeth. Lower jaw with a prominent medial dorsally oriented bump at symphysis; bump corresponds in position to a depression between the premaxillaries. 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; anterior tube-like. Lacrimal with 3-4 coarse serrations. Preoperculum serrate; serrations strongest on vertical

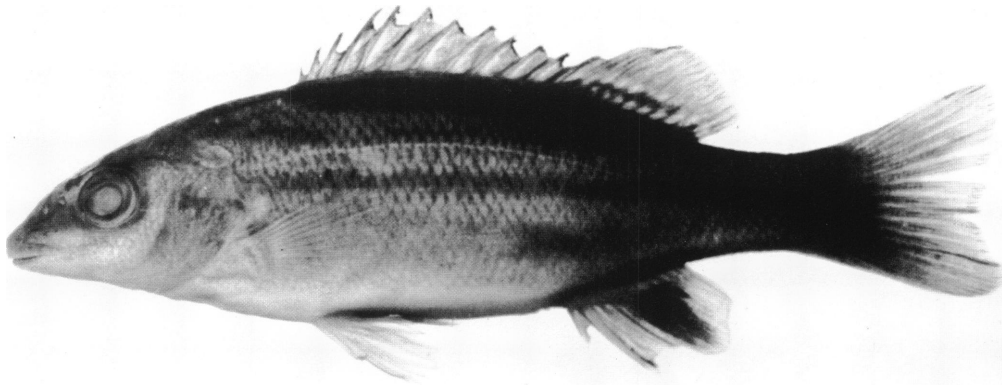


FIG. 92. *Syncomistes trigonicus*, juvenile, WAM P-25026-002, 47 mm. SL.

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 asymmetrically 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 supracleithrum 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 km. above its junction with the Roe River, Western Australia. Taken along with the holotype was a paratype (WAM P-25028-006), 98 mm. SL. Additional paratype materials were collected at the following localities: two specimens (WAM P-25026-002) 47-112 mm. SL, obtained with dip net by G. R. Allen, August 14, 1975, in the upper Roe River, Western Australia; 1 (WAM P-25027-002), 130 mm. SL, obtained with a seine by G. R. Allen and A. Chapman, August 15,

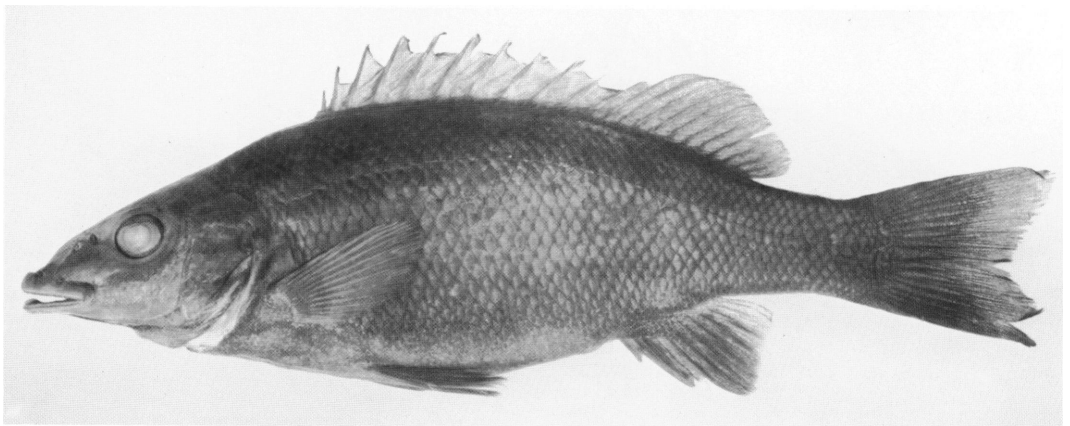


FIG. 93. *Syncomistes trigonicus*, adult, WAM P-25026-002, 112 mm. SL.

1975 in the upper Roe River; 4 (AMNH 35637), 50-100 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 me was collected at other localities in the Roe and Prince Regent rivers (species B of Allen, 1975).

ZOOGEOGRAPHY

The Indo-west Pacific through which the Teraponidae are distributed is a region that has long interested biogeographers (Sclater, 1858; Wallace, 1876; deBeaufort, 1951; Darlington, 1957; and others). In an attempt to understand the distribution of specific and supraspecific units through the region, these authors have attempted to distinguish faunal and floral provinces both on the scale of Weber's and Wallace's lines and on more limited levels (e.g., the fluvifaunulae of Australia and New Guinea demarcated by Iredale and Whitley, 1938, and followed with modifications by other authors). However, these studies were primarily concerned with the description of endemism rather than faunal relationships and showed little concern with the general aspects of biotic history.

Most previous biographic analyses have been based on a center-of-origin hypothesis for species or groups and their subsequent dispersals to other regions. Hennig (1966) in his progression rule hypothesizes that ancestral forms are found at the center of the 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 the distribution of a group. 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 their associated aprioristic assumption of dispersal as an underlying cause of present-day distributions cannot be falsified and therefore are not testable. Also such systems do 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-day 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 methodology has the advantage of not requiring the independent acquisition of the necessary physiological and behavioral adaptations for dispersal in each of the species of the groups within the ancestral biota. In contrast, tracks unique to species or groups and not in agreement with the generalized tracks may represent the results of dispersals.

An analysis of the distribution of the family Teraponidae and its subunits cannot of course constitute a definitive analysis of an ancestral biota but does show 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 (the occurrence of *Pelates quadrilineatus* in the southwestern Mediterranean appears to be a recent dispersal through the Suez Canal). Stippled areas of figure 94 represent the marine distributions of the entire family and black land masses the regions in which freshwater teraponids occur. The track of the entire family is closely approximated by *Terapon jarbua* with the exception of its absence from a part of the southern coast of

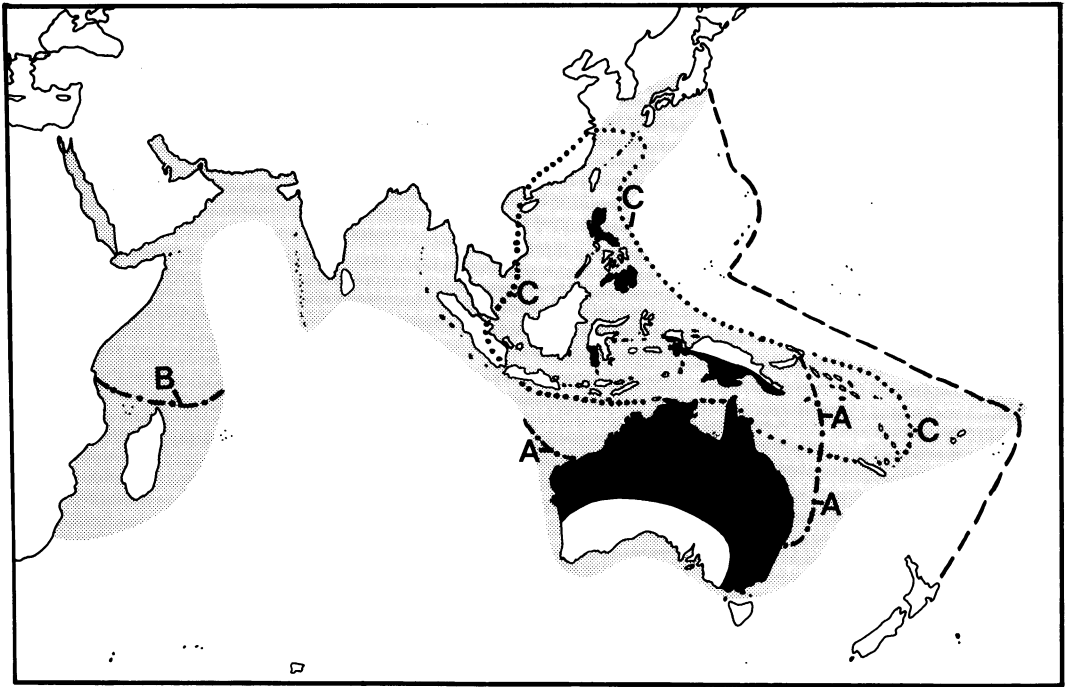


FIG. 94. Distribution and major tracks in the family Teraponidae. Shaded areas delimit the distributions of the marine species of the family, black regions are areas of distribution of freshwater species in Australia, New Guinea, the Philippines and Sulawesi. Line A demarks the southern and eastern limits in the Australian region of *Terapon theraps*, *T. puta*, and *Pelates quadrilineatus*. Line B is the southern limit of the distribution of *T. puta* in the African region. Line C is the track with variations of *Pelates sexlineatus*, *Mesopristes argenteus*, and *M. cancellatus*. The dashed line in the western Pacific is the approximate locality of the Andesite Line.

Australia. Three other species in the family also have tracks that 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 of figure 94 and the latter also does not extend south of line B. Finally, the east-to-west range of the family but not its north-to-south extent is approximated by the genus *Mesopristes* which has one species (*M. elongatus*) in Madagascar, two species (*M. argenteus* and *M. cancellatus*) distributed through 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) *Terapon puta*, and (6) the genus *Mesopristes*—form with some variations a generalized track across the Indo-west Pacific.

Comparison of the limits of the family track with the position of the Andesite Line in the western Pacific shows the family distribution to occur entirely to the west of the line, except for *Terapon jarbua* which crosses it at Samoa. The Andesite Line (MacDonald, 1949) 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 distributional agreements with the boundary have been noted by Springer (1972) and Springer and Gomon (1975) for parts of some blennioid genera; by Smith-Vaniz (1976) for many species and the majority of endemic species in the Nemophini (Blenniidae); by Raven and Axelrod (1972) for many plants, and occurs in the gizzard shads of the tribe Anodontostomatini (Nelson and Rothman, 1973).

Although the exact relative positions of various land masses in Indo-Asiatic Gondwanaland is still the subject of considerable debate (see Melville, 1973; Crawford, 1974; Stauffer, 1974) a comparison of present-day teraponid distributions with Gondwanaland reconstructions shows that if the family were present at that time, it 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 the latter, however, 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 biotas (teraponids, plotosids [Jordon, Tanaka, and Snyder, 1913], adrianichthyoids [Rosen, 1964], synbranchids [Rosen and Greenwood, 1976], etc.) and Laurasian ones (osmerids [McAllister, 1963], salmonids [Rosen, 1974], cyprinids [Myers, 1951], etc.). 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) a dispersal of elements of a Gondwanian fauna into an originally Laurasian fauna, and (3) that the region is geologically complex, being formed of parts of Gondwana land and Laurasia and 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 of the Teraponidae in the Indo-west Pacific parts of Gondwanaland should not be ruled out.

In an allopatric speciation model, an ancestral species A is separated into at least two populations A' and A'' by some vicariance event (geographical, climatological, biological, or other) 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. When and if the

populations become sympatric again this divergence may be sufficient to prevent genetic interchange. In such a model of speciation, any overlaps 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) among marine groups and their respective sister groups. Such dispersals may also have occurred within the genera *Pelates* and *Terapon*, which have wide overlaps among their species.

A second shared track among marine teraponids is found in the region limited by Malaya, the New Hebrides, and China (fig. 94, track C). This track delimits the average of the main distributions of *Pelates sexlineatus*, *Mesopristes argenteus*, and *M. cancellatus*, with the extensive overlap between the last two species also evidence of intrageneric dispersal.

The second generalized track in the Teraponidae involves a series of sister-group relationships between northern Australian and southern New Guinean freshwater species. Tracks uniting species or groups in these areas are found in the genera *Amniataba*, *Hephaestus*, and *Pingalla*. The close faunal relationships between these areas have been remarked on previously 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 Guinean faunas into a single Leichhardtian fluvifaunulae. More recently McMichael and Hiscock (1958) and Munro (1964) have distinguished the fauna of southern New Guinea as a distinct Reichian fauna. In addition the large extent of floral similarity between these regions has been noted by Hoogland (1972), that of amphibians and reptiles by Tyler (1972), and that of birds and mammals by Schoode and Calaby (1972).

Exclusive of the Teraponidae, Munro (1964) listed 31 species representing 14 families (Pristidae, Osteoglossidae, Gobiidae, Melanotaeniidae, Tachysuridae, Plotosidae, Anguillidae, Belonidae, Eleotridae, Chandidae, Apongonidae, Kurtidae, Toxotidae, and Soleidae) that are shared between

these regions, of which 19 are limited entirely to fresh water. These tracks, in addition to those previously mentioned for teraponids, and the faunal and floral similarities listed above, indicate a close relationship between these biotas and suggest that they arose from an ancestral biota subdivided by some vicariance event.

Examination of the geological evidence for the Australia-New Guinea region shows that such a vicariance event may be the result of either or both of two geological events. The first is a vicariance event resulting from the division and drift of the parts of Gondwanaland now inhibited by teraponids; a hypothesis previously noted as a possible vicariance event associated with the present distribution of marine teraponids. The second is a vicariance event resulting from the inundation of the continental shelf between Aus-

tralia and New Guinea during Tertiary interglacial periods. During the Pleistocene, for example, sea levels were lowered sufficiently to expose the continental shelf under the Arafura Sea and Torres Strait (Doutch, 1972) and it is possible that during that period 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.

No generalized tracks within the Teraponidae are evident in either New Guinea or Australia. Evidence of dispersal is, however, found in the extensive overlap both of the various genera of freshwater teraponids and of the species within these genera.

S U M M A R Y

A revision of the Teraponidae was carried out with five goals: to determine the monophyletic nature of the family, to determine the relationships of teraponids to other perciform fishes, to produce theories of interrelationships within the family, to produce an account of the species in the family and their distribution, 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 were found distinguishing the family: (1) a transversely divided swimbladder; (2) an extrinsic swimbladder muscle; (3) the urohyal form, and (4) a distinctive process arising from the third pharyngobranchial.

No hypothesis of a sister group to the teraponids among perciform fishes 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 monophyly supported by a series of apomorphic characters. The char-

acters supporting the hypothesized interrelationships and the groups possessing them are:

- (1) Anatomy of the posttemporal, lateral tabular, and associated structures.
 - (A) genera 1 to 5 share an unelaborated posttemporal, a lateral tabular with an anterior common opening to the sensory canals, and an uninterrupted skin and scale covering in the region.
 - (B) genera 6 to 15 have a derived reduction of the anterior aperture to 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 derived 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 11b has a further expanded posttemporal and a posteroventrally sloping supratemporal commissural element in the lateral tabular. Both conditions

are considered the most apomorphic for these structures in the family.

- (2) Height of the dorsal and anal sheaths
 - (A) the hypothesized plesiomorph dorsal fin sheath for teraponids is one row of scales, a condition found in genera 1 to 6. That of the anal sheath is two or three scale rows, a condition found in genera 1 to 7.
 - (B) the derived dorsal sheath condition of two scale rows occurs in genera 7 to 15.
 - (C) genera 8 to 15 share both a derived dorsal sheath height of two or more rows of full-sized scales and a derived anal sheath height of three to six rows.
- (3) Intestinal patterns.
 - (A) the plesiomorph form of teraponid intestinal pattern is two loops in or to the right of the median body plane; a condition found in genera 1 to 10 and 11b.
 - (B) a derived pattern with six loops and a limited amount of looping to the left of the median body plane is apomorphic with respect to the above and occurs in genera 11 to 15 (with the exception of genus 11b) at some point during development.
 - (C) a pattern with an elaborate intestinal pattern and marked looping to the left of the stomach is derived ontogenetically from B and occurs in genera 14 and 15 at some point in ontogeny. This pattern in turn is plesiomorphic to the highly complex pattern of genus 15.
- (4) Extrinsic swimbladder muscles.
 - (A) a cylindrical extrinsic swimbladder muscle with an origin limited to the ventral process of the posttemporal is plesiomorphic for teraponids. Such a muscle form is found in genera 1 to 5.
 - (B) genera 6 to 15 share derived forms of the extrinsic swimbladder muscle having an origin both on the posttemporal and the rear of the skull at some point during development. Three forms of muscles occur with this type of origin (in order of increasing apomorphy):
 - (a) a muscle with a direct muscular origin on the posttemporal and a ligamentous origin on the skull (genus 6).
 - (b) a muscle with a direct muscular attachment to both the posttemporal and to the rear of the skull (genera 7 to 11a and 12 to 15).
 - (c) a muscle with an origin limited to the rear of the skull in adults (genus 11b).
- (5) Pigmentation patterns.
 - (A) a vertically barred pattern is plesiomorphic for teraponids.
 - (B) two patterns occur in the family apomorphic to and directly derived ontogenetically from bars:
 - (a) the uniform coloration of species in genera 1 to 4.
 - (b) the striped pattern of species in genera 5 to 9.
 - (C) uniform coloration derived directly from stripes is apomorphic with respect to the striped pattern and is found in the species of genera 10 to 15.
- (6) Vertebral counts.
 - (A) the plesiomorph teraponid vertebral formula is considered to be 10+15.
 - (B) apomorphic increases in the number of vertebrae to 26 occur in *Lagusia* (genus 5) and to 27 in the species of genus 11b.
 - (C) within those groups with 25 or 27 vertebrae occur subgroups characterized by a change in the relative numbers of precaudal and caudal vertebrae:
 - (a) three species in genus 11b have 11+16 vertebrae, a count considered apomorphic to the 10+17 pattern of the rest of the unit.
 - (b) the species of genera 12 to 15 share an apomorphic increased number of precaudal vertebrae (11). Similar increases in one species in both genera 1 and 4 are considered convergent.
- (7) Numbers of spines on the first proximal dorsal pterygiophore.

An increase to two spines on this element in genera 2 to 15 (from the one spine of genus 1) is considered apomorphic.
- (8) Form of the supraoccipital.

A posteriorly bowed or straight rear margin of the supraoccipital is considered apomorphic and occurs in genera 9 to 15.
- (9) Jaw and dentition.
 - (A) the plesiomorph condition of the jaw and dentition for teraponids is a conic,

- nondepressible, vertically directed dentition located along the superior and inner surfaces of the dentary which has a prominent dentary symphyseal process anteroventrally.
- (B) derived conditions of the above are:
- (a) a depressible dentition characterizing genera 12 to 15.
 - (b) a flattened dentition characterizing genera 13 to 15.
 - (c) a highly flattened dentition with an outward rolling of the dentary and a lack of the symphyseal process occurring in genera 14 and 15.
 - (d) a prominent dorsally directed median process and modifications of the ascending processes of the premaxillary and rostral cartilages characterizing genus 15.
- (10) In genera 14 and 15 the swimbladder constriction is hypothesized to be secondarily reduced based on ontogenetic changes in the extent of the constriction.

The 15 monophyletic assemblages in the family are defined at the generic level in this study (*Leiopotherapon*, *Amniataba*, *Lagusia*, *Hannia*, "Terapon" (differs from *Terapon* in the strict sense), *Pelates*, *Terapon*, *Pelsartia*, *Rhyncopelates*, *Mesopristes*, *Hephaestus*, *Bidyanus*, *Scortum*, *Pingalla*, and *Syncomistes*). Three of these (*Lagusia*, *Hannia*, and *Syncomistes*) are described as new in this study. Thirty-seven species are recognized 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 presented.

The following species recognized as distinct by some or all workers to this point were placed in synonymy:

Pelates sexlineatus Cuvier in *Pelates quadrilineatus* (Bloch)

Terapon servus (Bloch) in *Terapon jarbua* (Forskål)

Terapon rosenberghii (Bleeker) in *Mesopristes cancellatus* Cuvier.

Terapon lambertoni Fowler in *Mesopristes elongatus* (Guichenot)

Terapon alligatoris Rendahl in *Hephaestus fuliginosus* (Macleay)

Terapon brevipinnis Mees in *Hephaestus jenkinsi* (Whitley)

Terapon habbema Weber in *Hephaestus trimaculatus* (Macleay)

Scortum ogilbyi Whitley in *Scortum hillii* (Castelnau)

Hephaestus jenkinsi considered to be a synonym of *H. fuliginosus* by Mees, is herein recognized as a distinct species. *Datnia elliptica* Richardson, which most previous workers have placed as a synonym of *Bidyanus bidyanus*, is tentatively placed in synonymy with *B. welchi*. *Datnia obtusirostris* placed by Fowler as a synonym of *Mesopristes argenteus* is tentatively placed as a synonym of *Mesopristes elongatus*.

The zoogeography of the family and its subunits were analyzed and showed five patterns of distribution extending across most or all of the Indo-west Pacific, forming a generalized track within teraponids. A more limited track through the East Indies was shared by several marine species. Such distributions might indicate an ancient Gondwanian origin for the family with most of the present wide geographic range of the family a consequence of continental drift.

An additional generalized track within the family occurs between the fresh waters of northern Australia and southern New Guinea, a track shared by many other groups. Such a distribution is congruent both with ancient events of continental fragmentation and with a separation of the regions following late Tertiary fluctuations in sea levels.

A history of dispersal among sister groups in 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.

ADDENDUM

Recently three specimens relevant to conclusions reached in this study have been found

in the collections of the British Museum (Natural History).

The description of *Scortum barcoo* in the present paper was based on the original by McCulloch and Waite (1917) since the only known specimen, the holotype, was not available for examination. As a consequence, the generic assignment remained somewhat tentative (see discussion under the species). However, I found that a specimen identified as *Terapon ellipticus* (BM[NH] 1905.10.31.57) was actually a second specimen of *Scortum barcoo*. This specimen shows that the species possesses characters congruent with its assignment to *Scortum* as defined herein (see Phylogenetic Analysis), thereby confirming the earlier tentative placement.

A short description of this specimen follows:

Dorsal spines XIII; dorsal rays 12; anal III, 8; pectoral rays 16 including a very short ventral-most element; pelvis I-5; 65 tubed lateral line scales from supracleithrum to hypural joint; 68 series of scales below and 76 series above lateral line to hypural joint; transverse series 12+1+26; six cheek scales; 21 predorsal scales to occiput, sheath extending to eighth dorsal ray; four rows of scales in sheath at base of anal fin, sheath extending to third anal ray; vertebrae 12+13, a count unique to this species in the family and further derived with respect to the apomorphic 11+14 count of genera 12 to 15; gill rakers on first arch 12+1+26.

142 mm. SL; head length 3.35 in SL; greatest body depth 2.34 in SL; length of base of dorsal fin 1.65 in SL; distance from origin of spinous dorsal to snout 2.50 in SL; snout length 3.4 in HL; eye width 5.0 in HL; jaw length 3.54 in HL; length of longest dorsal spine 2.07 in HL; length of longest dorsal ray 2.36 in HL; length of longest anal spine 2.1 in SL; length of longest anal ray 2.29 in HL.

Vomer with five firmly attached teeth. Outer row of jaw teeth slightly flattened distally, depressible; followed by an inner band of smaller teeth. Lower jaw rotated slightly laterally.

Other characters as given under the species description in the text.

Coloration. Overall coloration golden, darker dorsally. Fins yellowish, with dark chromatophores randomly distributed over their surfaces.

Distribution. This specimen is part of a series collected in Washburton and Cooper's creeks "100 miles east of Lake Eyre, South Australia."

Although it is not known which drainage this specimen originated from, it is notable that Cooper's Creek is the type locality for the species.

Two other examined specimens are relevant to questions on distribution raised earlier. Under remarks on the distribution of *Rhyncopelates oxyrhynchus*, I note that apparently erroneous locality records for this species from Ovalau, Fiji, and Manado, Celebes (Sulawesi) were made by Günther (1880) and Meyer (1885), respectively. The "Challenger" specimen on which the Günther record is based (BM[NH] 1879.5.14.147) is actually an individual of *Mesopristes kneri*, a Fiji endemic. A specimen collected by Meyer at Manado and identified by him as *Terapon oxyrhynchus* (BM[NH] 1871.7.20.111) is actually a juvenile *Mesopristes argenteus*. Whether this specimen was the sole basis for Meyer's citation of *Terapon* (= *Rhyncopelates*) *oxyrhynchus* from the Celebes cannot be determined. However, the misidentification casts further doubt on the presence of *R. oxyrhynchus* in the Celebes, a region from which it has not been otherwise reported.

Mees and Kailola (1977) have recently published a review of the freshwater New Guinea teraponids, including five new species. These authors place all their new species in the genus *Terapon* (*sensu lato*). However, under the classification adopted in this study, these species are assignable to three different genera.

Terapon lacustris described from the Fly River region is very similar to "*Terapon*" *jamoerensis*, a species known from five specimens collected more than 400 miles to the west of the range of *T. lacustris*. The similarity between these nominal forms is such that the authors state "This species (*T. lacustris*) is very close to *T. jamoerensis*, of which eventually it may be regarded as a subspecies." The principal differences cited between the nominal forms are eye size and the lack of a silvery shine on the flanks of *T. lacustris*. The latter character, however, varies both with water condition and method of preservation (personal observ.). If *T. lacustris* does prove to represent a distinct species, it is undoubtedly the sister species of "*Terapon*" *jamoerensis* and assignable to the genus "*Terapon*" as defined in this work.

The second species, *Terapon affinis*, described

by Mees and Kailola is, as noted, very similar to *Amniataba percoides* from which it differs slightly in scale count. As such it would appear to be the sister species of *Amniataba percoides* and assignable to *Amniataba*. A specimen of this species lent me by Dr. Mees has 26 vertebrae in contrast to the 25 found in all other *Amniataba* species and some *A. affinis* (see Mees and Kailola, 1977, table 3). A decision as to whether this specimen is anomalous or *A. affinis* is characterized by a variable vertebral count awaits the examination of further material.

The three remaining new species (*Terapon raymondi*, *T. transmontanous*, and *T. obtusifrons*) all have 27 vertebrae, a count unique among teraponids to a group of species in *Hephaestus* (subunit b). In addition, these species all share the possession of dorsal spines equal to or shorter than the longest dorsal rays, a character common to all *Hephaestus* species.

I have only seen material of *Terapon transmontanous* of these three new species. Examination of a specimen from the type series lent me by Dr. Mees and of a series collected by Dr. Diane Kershaw (Queen Mary College, University of London) in the Markham River (a new easterly record for the species), has shown this species to possess the characters common to the species placed in subunit b of *Hephaestus* (see Phylogenetic Analysis for a discussion of the characters). The two other species would also appear to belong to the same monophyletic group. *Terapon obtusifrons* is very similar to *T. transmontanous* from which it differs slightly in body proportions. *Terapon raymondi* in turn is very similar to *Hephaestus suavis*, a species also assigned to subunit b of *Hephaestus* in this revision. In light of these similarities and the aforementioned vertebral and fin characters, it appears that these three species (*transmontanous*, *raymondi*, and *obtusifrons*) belong in the genus *Hephaestus* as defined in this work.

Mees and Kailola (1977) also discussed several points concerning previously described species, phylogenetic characters and nomenclature which require comment. They retain as distinct the nominal forms *Terapon trimaculatus* and *T. habbema* recognized as a single species, *Hephaestus trimaculatus*, in the present study. As discussed earlier, an examination of a large

series of the nominal species shows the supposed differences in scalation to be a consequence of limited material. This conclusion is further supported by the examination of a specimen of nominal *Terapon habbema* from the Lorentz River, West Irian, whose counts fall within the range of eastern *H. trimaculatus*. Furthermore, the cited differences in width of the body stripes appear to be a function of age. These stripes widen ontogenetically until they eventually merge into a uniform dark dorsal coloration. Consequently, I see no reason to modify my previous synonymization of *Terapon habbema* into *Hephaestus trimaculatus*.

Mees and Kailola (1977) discount the supra-cleithrum (a misidentification for the post-temporal, see discussion in Introduction) as a significant character in the understanding of teraponid interrelationships. This comment appears to be a consequence of their emphasis on the variations in the extent of serration along the posterior edge of the bone, rather than a consideration of the morphology of the entire element. As noted under the discussion of posttemporal form, the element differs radically between those species in which it has been considered exposed or nonexposed, with these two condition readily differentiable.

These authors also raise the nomenclatural question of the availability of the generic name *Mesopristes*. They state that it cannot be available since in its original use by Bleeker (1845) it was a *nomen nudum*. However, an examination of the rules of the International Code of Zoological Nomenclature fails to reveal any such prohibition. Indeed, Mayr (1969) in his discussion of the concept, specifically discourages any reference to a *nomen nudum* since this may make it available. The question is then one of the equivalence of *Mesopristes* Bleeker, 1845. This question would appear to have been resolved by Bleeker (1873) who synonymized the genus into *Datnia* Cuvier, 1829 (a genus not available in teraponids, see discussion under *Mesopristes* in text) at the same time that he synonymized *Mesopristes macracanthus* Bleeker, 1845 into *Datnia argentea* Cuvier, 1829, the type species of that genus. Mees and Kailola stated that this use of the name by Bleeker (1873) is the usage that must

be validated. However, the cited rule (11d) refers to a name first published as a synonym, a situation that does not apply in this case since the 1873 synonymy is predated by the original 1845 *nomen nudum*. *Mesopristes* of Bleeker, 1845 was in turn validated by Fowler (1931) and Whitley (1943) who utilized it as an available name (as a subgenus and genus, respectively), with the original date (1845) and authorship (Bleeker). Thus *Mesopristes* Bleeker, 1845 appears to be available, and I see no reason to erect a new generic name for the hypothesized monophyletic group recognized as the genus *Mesopristes* in this revision.

Finally, the reader's attention is drawn to the new range extension for *Terapon* (= *Hephaestus*) *fuliginosus* on New Guinea, and the variable

increased number of 27 to 29 vertebrae reported in *Hephaestus adamsoni* by these authors. The latter is autapomorphic for the species in the family and further derived with respect to the apomorphic count of 27 vertebrae found in the other species of subunit b of *Hephaestus*.

One additional paper presently in press and dealing with a hypothesis advanced in this paper has recently been brought to my attention. Under my discussion of the ecology of *Terapon jarbua*, I noted that it might be partially lepidophagous. Dr. S. J. M. Blaber of the University of Natal and Mr. A. K. Whitfield (personal commun.) inform me that they have a paper in press dealing with the behavioral, nutritional, and evolutionary aspects of the lepidophagous habits in this species.

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