Records of the Australian Museum (1989) Supplement 11. ISBN 0 7305 6374 X

A Taxonomic Revision and Cladistic Analysis of the Oxudercine Gobies (Gobiidae: Oxudercinae)

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ABSTRACT. The gobiid subfamily Oxudercinae was revised to assess the monophyletic nature of the subfamily; the intergeneric relationships within the subfamily; the relationships of oxudercines to other gobiid genera; the recognisable species and their distinguishing characters; and the distribution patterns of the subfamily and component taxa. The following results were obtained: (1) The Oxudercinae can be defined on the basis of derived states of certain neurocranial bones and muscles, eye position, nasal flap morphology, the palatine-ectopterygoid arrangement, reduction in size of the premaxillae ascending processes, and in having a single anal fin pterygiophore anterior to the first hemal spine. (2) Within the subfamily, one undefined and nine monophyletic terminal assemblages are recognised, with relationships amongst them based on derived states of various morphological features. These assemblages are recognised at the generic level and one new genus *(Zappa)* is described; a key to the genera is provided. Thirty four species are recognised of which one *(Boleophthalmus birdsongi)* is described for the first time. Each species is described in detail and a key is provided for each genus. (3) Two monophyletic assemblages (one comprising three genera, the other seven) are recognised at the tribal level. Defining characters for each tribe are provided and illustrated. (4) Biogeographic analysis indicated that nine of the ten genera are distributed in an area bounded by the Arabian Gulf to the west, southern Japan to the north, northern Australia to the south, and Papua New Guinea to the east. The remaining genus, *Periophthalmus,* overlaps and exceeds the above limits, ranging from west Africa eastward to Samoa. Species-specific correlations linking *Periophthalmus* with mangrove distributions are discussed.

Contents

The Oxudercinae, a subfamily of gobiid fishes, are found in soft bottom intertidal areas and mangrove swamps of the Indo-west Pacific (*sensu* Springer, 1982), with one representative in tropical west Africa. All oxudercines are at least occasional burrow dwellers and several genera can be referred to the vernacular name of mudskippers which describes their habits on exposed littoral surfaces.

Historically, the taxon has been treated as a monotypic family (Oxudercidae) of uncertain affinity. Springer (1978) exposed the gobiid nature of the type genus *(Oxuderces)* and species *(O. dentatus)* and stated that although the Oxudercidae is a junior synonym of the Gobiidae, the name has priority over the closely related Apocrypteinae, Boleophthalminae and Periophthalminae. Hoese (1984) defined the characters that unite the included genera of the Oxudercinae.

Oxudercine gobies, especially *Boleophthalmus* and *Periophthalmus,* have been the subject of numerous morphological, physiological and natural history studies. Petit (1922) described burrow construction by *Periophthalmus koelreuteri* (=*argentilineatus* or *kalolo*). Harms (1929) described differences in associations among several species of *Periophthalmus* and Eggert (1929 a,b; 1935) recognised morphological differences among these and other species. Schöttle (1931) described aspects of morphology and physiology in ten mudskipper species and compared them to other gobioids. Hora (1935) studied the physiology of air-breathing fishes including several oxudercines. Lele & Kulkarni (1938, 1939) described the skeleton of *Periophthalmus barbarus* (= *kalolo*). Harris (1960) studied locomotion in *Periophthalmus koelreuteri* (= *barbarus*). Stebbins & Kalk (1961) reported on nesting, locomotion and thermal tolerance in the east African *Periophthalmus sobrinus* (= *argentilineatus* or *kalolo*). Gordon *et al.* (1965, 1968, 1978) studied physiological aspects of terrestriality in *Periophthalmus sobrinus* (= *argentilineatus* or *kalolo*) and *Periophthalmus cantonensis* (= *modestus*). Teal & Carey (1967) examined respiratory adaptations in *Periophthalmus sobrinus* (= *argentilineatus* or *kalolo*) from Madagascar. Macnae (1968) provided information on the natural history of several mudskippers. Graham (1971) reported on aerial visual modifications in *Periophthalmus* and respiratory adaptations (1976) in several oxudercines. Nursall (1974, 1981) analysed inter- and intraspecific aggression in four sympatric species of *Periophthalmus.* Sponder & Lauder (1981) examined feeding mechanics of *Periophthalmus koelreuteri* (= *barbarus*) by cineradiographic analysis. The thermal ecology of *Periophthalmus koelreuteri* (= *waltoni*) and *Boleophthalmus boddarti* (= *dussumieri*) was studied by Tytler & Vaughan (1983). Unfortunately, in most of the above studies, the inexactness of the group's taxonomy caused invalid specific names to be used. Consequently, it is difficult to associate the data and experimental results with a particular species. This is especially true for *Periophthalmus,* the species of which have been notoriously difficult to identify (Macnae, 1968; Nursall, 1974). In fact, Smith (1959:219) stated "...the precise diagnosis of species in this almost circumtropical genus is difficult, for it involves either the recognition of a multitude of intergrading forms, or the lumping of most in one highly polymorphous form." *Periophthalmus,* the most amphibious and best known oxudercine, has long fascinated ichthyologists. The first published account of *Periophthalmus* I can confirm is Vlaming (1701) and the first published figure appeared in Ruysch (1718). Valentijn (1726) and Prevost (1747) were also pre-Linnaean works that figured *Periophthalmus.* Linnaeus described the first species of *Periophthalmus (Gobius barbarus)* in 1766 and the first oxudercine in 1758. Subsequent authors have described more than 100 nominal oxudercine species and subspecies.

The most important post-Linnaean works pertaining to the taxonomy and systematics of oxudercines are the following: Pallas (1770) described and figured two oxudercines; Bloch & Schneider (1801) coined *Periophthalmus* and described three new oxudercines; Hamilton (1822) described five new oxudercines and figured three of them; Valenciennes (1837) erected two genera and described nine new species; Bleeker (1874) erected four genera and proposed three supergeneric taxa to include the then known genera of oxudercines; Day (1876) described and figured four new species; Eggert (1935) described eight new species and 13 subspecies of *Periophthalmus;* Koumans (1941, 1953) assembled all then known oxudercine genera into two subfamilies and provided keys to genera and species; Springer (1978) reviewed the classificatory history of the Oxudercidae (= Oxudercinae); and Hoese (1984) presented uniting characters for the Oxudercinae.

Much of the nomenclatural disruption within the Oxudercinae has been due to confusion surrounding the validity and/or identity of species described by early workers such as Osbeck (1757, 1765, 1771), Linnaeus (1758, 1766), Pallas (1770), Bloch & Schneider (1801) and Hamilton (1822). In most instances, type material of these authors was not saved or is not extant. In fact, of the 103 nominal species and subspecies of Oxudercinae, there was type material for only 45 of them.

The objectives of this study are (1) to define the Oxudercinae using derived characters, (2) to revise and define the genera of Oxudercinae, (3) to provide characters for reorganising the included species, (4) to list synonyms for all valid forms, (5) to provide and analyse distributional and ecological data, and (6) to hypothesise intrarelationships of the Oxudercinae. Specimens were examined at or obtained from the following institutions (abbreviations in parentheses): University of Alabama, University (ALA); American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); Academy of Natural Sciences, Philadelphia (ANSP); British Museum (Natural History), London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS-SU); Laboratoire d'ichthyologie, Courrendlin, Switzerland (CMK); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Museum of Natural History, Los Angeles (LACM); The Crown Prince's Palace, Tokyo (LICPP); Harvard University, Cambridge (MCZ); Museum National d'Histoire Naturelle, Paris (MNHN); Museo Civico di Storia Naturale di Genova, Genova (MSNG); Naturhistorika Riksmuseet, Stockholm (NHRM); Naturhistorisches Museum Basel, Basel (NMBA); Northern Territory Museum of Arts & Sciences, Darwin (NTM); Queensland Museum, Brisbane (QM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Royal Ontario Museum, Toronto (ROM); J.L.B. Smith Institute of Ichthyology, Grahamstown (RUSI); Texas A&M University, College Station (TCWC); University of Alberta, Edmonton (UAMZ); University of Michigan, Ann Arbor (UMMZ); National Museum of Natural History, Washington (USNM); Western Australian Museum, Perth (WAM); Universiteit van Amsterdam, Amsterdam (ZMA); Universität Humboldt, Berlin (ZMB); Kobenhavns Universitet, Copenhagen (ZMUC); Zoological Survey of India, West Bengal (ZSI); and University of Tokyo, Tokyo (ZUMT).

Methods

Measurements. All measurements are straight-line distances made with dial calipers and recorded to the nearest tenth of a millimeter. All fish lengths given are standard lengths (SL); standard lengths of specimens in material examined sections are listed to the nearest mm. Methods of measurement follow Hubbs & Lagler (1964) except for the following: body depth = vertical distance from anal spine base to second dorsal fin base; head length = distance from anterior tip of upper lip to dorsoposterior attachment of opercular membrane; head depth = vertical head depth at posterior margin of preopercle; head width = distance between posterior margins of preoperculae; and height of pectoral fin base = vertical distance between dorsal and ventral insertions of pectoral fin.

Counts. The first element of the anal and second dorsal fins may be a soft spine or a segmented ray. Counts of anal and second dorsal fins do not differentiate between spines and rays. The last two rays of each of these fins are very close together, share the ultimate pterygiophore, and, as in common practice, counted as a single element. (Springer, 1978 and 1983 appears to be the most recent worker who counted the last two rays separately.) Pectoral fin rays were counted on both right and left sides of the body and tabulated as separate counts. The count of scales in a longitudinal series was begun at the dorsoposterior attachment of the opercular membrane, continued on a posteroventral diagonal to the tip of the pectoral fin, and then in a straight line along the midline of the body to the posterior edge of the hypural plate, determined externally. Scales on the caudal fin were tabulated separately. Transverse scale counts were taken from the second dorsal fin origin ventroposteriorly to the anal fin base (TRDB), from the anal fin origin dorsoanteriorly to the first dorsal fin base (TRF), and from the anal fin origin dorsoposteriorly to the second dorsal fin base (TRB). Predorsal scales are those that extend just anterior to the first dorsal spine to just posterior to the interorbital region and were counted in a straight line. Gill raker counts were made on the outer face of the first arch and include the raker (if present) at the angle of the arch plus those on the lower limb of the arch. The vertebral count is separated into precaudal and caudal counts, the latter including the terminal vertebral element; counts were taken from radiographs and cleared and stained material. The methods of Birdsong *et al.* (1988) were used in describing the relationship between the spinous dorsal fin pterygiophores and the underlying vertebrae. On many oxudercines, pigment bands or blotches mark the dorsal surface. These bands or blotches are perpendicular to the fin base, appear saddle like, and are counted anterior to posterior.

Morphometrics. The following proportional measurements were expressed as a percent of SL: head length, D1-base length, D2-base length, anal fin base length, body depth, head depth, head width, least depth of caudal peduncle, caudal fin length, pectoral fin length, pectoral fin height, and predorsal length.

Statistical procedure. Specimens were initially sorted according to morphological features. Counts and measurements were then made to determine if significant differences existed. Univariate and multivariate procedures were performed on an IBM XT using the SYSTAT statistical package. Principal components analysis (PCA) was employed in multivariate comparisons using the covariance matrix. Before comparison by PCA, raw morphometric data were log transformed because the equation log (x/y)=log x - log y is a linear function of log x and log y whereas x/y is not a linear function of x and y.

Osteological preparations. Specimens were cleared with trypsin enzyme solution, stained for cartilage with alcian blue and for bone with alizarin red S according to methods described in Taylor & Van Dyke (1985).

Systematic procedures. Inter-relationships among taxa were made by the phylogenetic comparative biology method (Hennig, 1966) as outlined by Eldredge & Cracraft (1980) and Wiley (1981). The method of character analysis was outgroup comparison (Maddison *et al.*, 1984; Wiley, 1981). When character conflicts occurred, i.e. incongruities in polarity interpretation among different characters, the principle of parsimony (Farris, 1982) was invoked to choose among alternative hypotheses of character polarity. For instance, if the ingroup possesses character states A and B and the outgroup possesses A, then character state A is considered the plesiomorphic condition. The inter-relationships among taxa are displayed as a cladogram.

D.L. Swofford's PAUP (Phylogenetic Analysis Using Parsimony), version 2.4 run on an IBM XT, was used to obtain the most parsimonious phylogenetic hypothesis. The methods of Fink & Fink (1986) were employed for this procedure. Reductive and innovative specialisations were treated as equally likely to occur, as were reversals and independent acquisitions. A posteriori arguments for reversal and independent acquisitions were hypothesised based on the results of the PAUP-derived cladogram.

Presentation of material lists. All specimens examined are listed in the material examined section and grouped by major geographic areas. The total number of specimens and size range follow each catalog number. Data referring to type specimens, including those pertaining to synonyms, are listed by specific name and type category.

Systematic Accounts

Oxudercinae Günther, 1861

Oxudercidae Günther, 1861 (includes *Oxuderces*).
Periophthalmini Bleeker, 1874 (includes *Euchoristopus*, *Periophthalmus* and *Periophthalmodon*).
Apocrypteini Bleeker, 1874 (includes *Apocryptes*, *Apocryptodon*, *Boleophthalmus*, *Parapocryptes*, *Pseudapocryptes* and *Scartelaos*).
Periophthalmidae Jordan, 1923 (includes *Apocryptes*, *Boleophthalmus*, *Boleops*, *Euchoristopus*, *Periophthalmodon*, *Periophthalmus* and *Scartelaos*).
Periophthalminae Koumans, 1953 (includes *Periophthalmodon* and *Periophthalmus*).
Apocrypteinae Koumans, 1953 (includes *Apocryptichthys*, *Apocryptodon*, *Boleophthalmus*, *Parapocryptes*, *Pseudapocryptes* and *Scartelaos*).

Type genus. *Oxuderces* Eydoux & Souleyet, 1848.

Diagnosis. Elongate gobiid fishes, posteriorly compressed. Scales very small to large, cycloid, few to as many as 275 in a longitudinal series; predorsal scales 0-113. Head small to moderate (15-34% SL). Eyes located dorsally. Gape moderate to wide. Teeth caninoid, obtusely pointed, or bifid; uniserial in both jaws (except in *Periophthalmodon* which has 2 rows in upper jaw); a pair of recurved canine teeth internal to lower jaw symphysis (except in *Oxuderces dentatus*, *Periophthalmodon* and *Periophthalmus*). Tongue adnate. Spinous dorsal fin with 4-17 spines and 10-33 second dorsal fin elements. Anal fin with 9-31 elements. Pectoral fin rays 11-25. Pelvic fin I,5. Vertebrae 10 + 15 + terminal vertebral element = 26. Branchiostegals 5. Epurals 2. Fishes of small to moderate size inhabiting mangrove and mudflat areas from west coast of Africa eastward to Samoa.

Key to the Genera of Oxudercinae

(Accounts are presented alphabetically by genus and species)

1. Lower eyelid (dermal cup) absent.......................................2
—— Lower eyelid (dermal cup) present.......................................7
2. Spinous dorsal fin with 5 spines.......................................3
—— Spinous dorsal fin with 6 spines.......................................5

3. Second dorsal fin with 23 or fewer total elements; anal fin with 23 or fewer total elements .... *Apocryptes*

—— Second dorsal fin with 27 or more total elements; anal fin with 26 or more total elements........ 4

4. Second dorsal fin 27-30; caudal fin length usually more than 23% SL; head length greater than 22% SL........ *Zappa* n.gen.

—— Second dorsal fin I, 28-32; caudal fin length 23% SL or less; head length less than 22% SL........ *Pseudapocryptes*

5. Second dorsal fin with 24 or fewer total elements, modally fewer; anal fin with 23 or fewer total elements; longitudinal scale count fewer than 60........ *Apocryptodon*

—— Second dorsal fin with 24 or more total elements, modally more; anal fin with 24 or more total elements, modally more; longitudinal scale count typically more than 60........ 6

6. No prominent canine tooth lateral to upper jaw symphysis; head length 24% SL or less; second dorsal fin base typically 45% SL or greater; caudal fin length 19% SL or greater........ *Parapocryptes*

—— Prominent canine tooth (about twice as long as others) on each side of upper jaw symphysis; head length 24% SL or greater; second dorsal fin base 45% SL or less; caudal fin length 19% SL or less........ *Oxuderces*

7. Two canine teeth internal to lower jaw symphysis; anal fin base and second dorsal fin base 34% SL or greater........ 8

—— No canine teeth internal to lower jaw symphysis; anal fin base and second dorsal fin base 27% SL or less........ 9

8. Barbels present on underside of head........ *Scartelaos*

—— No barbels on underside of head........ *Boleophthalmus*

9. A single row of teeth in upper jaw........ *Periophthalmus*

—— Two rows of teeth in upper jaw........ *Periophthalmodon*

Apocryptes

Fig. 1, Tables 1-8

Apocryptes Valenciennes *in* Cuvier & Valenciennes, 1837: 142 (type species *Apocryptes bato* Valenciennes, 1837 [= *Gobius bato* Hamilton 1822], subsequent designation by Bleeker, 1874: 327).
?*Gobileptes* Swainson, 1839: 183 (no type species ever designated).

Included species. A single species *(Apocryptes bato)* distributed from India to Burma.

Diagnosis. *Apocryptes* is unique amongst oxudercines in possessing small, cycloid scales on the snout. Only two species of *Periophthalmodon,* amongst the other oxudercines, possess snout scales. Of the *Periophthalmodon* species that possess snout scales, the scales are approximately five times as large as those in *Apocryptes*.

Description. Spinous dorsal fin V; second dorsal fin I, 20-22 (dorsal fins connected by membrane basally); spinous dorsal fin pterygiophore formula: 3-1221*0 (sixth pterygiophore lacking associated spine); first 4 interspinous spaces about equal; fourth spine is longest fin element; second dorsal fin base terminates within 3 scales of dorsal procurrent rays; appressed second dorsal fin overlaps procurrent rays.

Anal fin I, 19-23; insertion of last ray slightly posterior to a vertical with last ray of second dorsal fin; anal fin base terminates within 3 scales of ventral procurrent rays; appressed anal fin overlaps procurrent rays.

Pectoral fin 20-25, ventralmost rays shortest, medial rays longest.

Pelvic fin I,5, united by membrane with fin of opposite side; frenum well developed. Caudal fin lanceolate, with 17

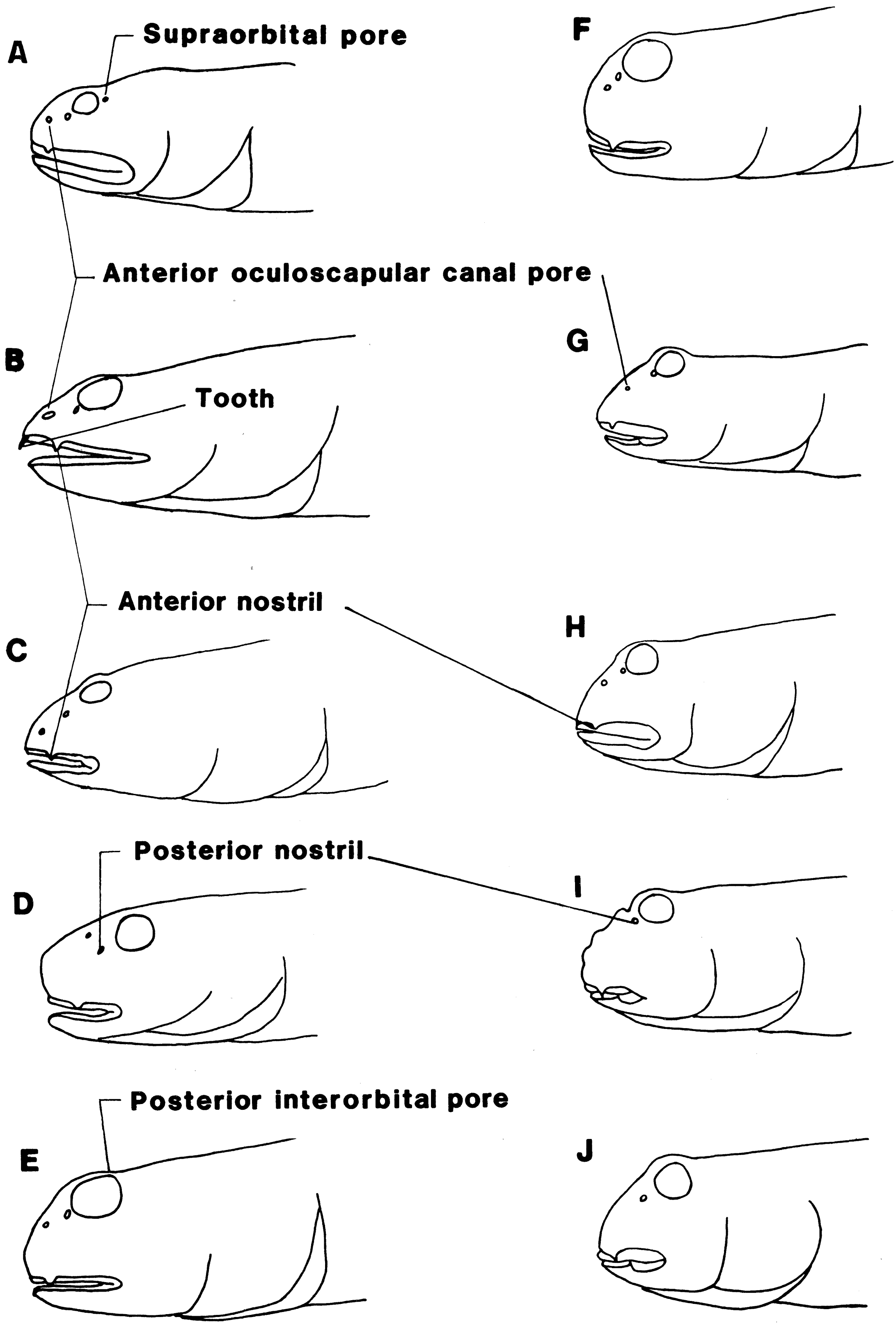

Fig.1. Cephalic sensory and nasal pores (left side) of the Oxudercinae: A, *Apocryptodon;* B, *Oxuderces;* C, *Parapocryptes;* D, *Apocryptes;* E, *Pseudapocryptes;* F, *Zappa;* G, *Scartelaos;* H, *Boleophthalmus;* I, *Periophthalmodon;* J, *Periophthalmus.*

segmented rays, 15-16 of which are branched; 8 dorsal procurrent rays, 7 ventral rays.

Scales cycloid, covering most of body except for isthmus; largest scales posteriorly, smallest embedded in snout; scale series irregular, difficult to count accurately; longitudinal scale count 93-143 (mean = 121.2); TRF 26-46 (mean = 36.2); TRB 25-40 (mean = 32.3); TRDB 29-50 (mean = 35.7). Gill opening restricted, extending from dorsalmost point of pectoral fin base to just slightly ventral to terminus of pectoral fin base.

Teeth in both jaws in a single row; 14-44 (mean = 27.8) teeth in upper jaw, most bifid, the rest caninoid; 18-36 (mean = 26.8) teeth in lower jaw, most bifid, the rest caninoid; 1 large, recurved, canine tooth on each side of symphysis internal to anterior margin of lower jaw. Specimens equal to or greater than 100 mm SL tend to have mostly caninoid teeth.

Gape moderate, posterior tip of maxilla extending to a vertical slightly posterior to midpoint of eye; head bluntly rounded not noticeably depressed; anterior nostril at the tip of a pendulous flap overlapping upper jaw laterally.

Single pore posteriorly in interorbital space; anterior oculoscapular canal pore anteromedial to eye, ventrolateral to this pore is posterior nostril. Cutaneous papillae and sensory pore system not otherwise visible.

Ventral portion of first gill arch with 4-5 gill rakers; gill filaments feather like.

Etymology. The name *Apocryptes* is presumably derived from the Latin, *apo,* attached, and *crypta,* subterranean passage, alluding to their fossorial habit; masculine gender.

Nomenclature. *Apocryptes* has been the subject of much nomenclatural confusion (see Springer, 1978). The following complex and tortuous history of the name is intended to clarify rather than cause any further nomenclatural disruption.

The first appearances of *Apocryptes* that I can find are in the combinations *Apocryptes chinensis* and *As. cantonensis* included as junior synonyms in Linnaeus (1758); *As. cantonensis* is listed as a synonym of *Gobius niger* (p.263) whereas *As. chinensis* is as a synonym of *G. pectinirostris* (p.264). Linnaeus referenced *As. cantonensis* and *As. chinensis* to Osbeck (1757, *As. chinensis* on p.130, *As. cantonensis* on p.131). Pehr Osbeck (1757), a student of Linnaeus', published a detailed faunistic and floral report on his travels to China. This original work was in Swedish and subsequently was translated and published in both German (1765) and English (1771). [The Swedish version was unavailable to me.]

As Osbeck's original publication is pre-Linnaean, it has no taxonomic standing. However, several authors have referred to Osbeck's supposed usage of *Apocryptes* in his 1765 and/or 1771 editions: Valenciennes (1837) cited pages 170 and 171 of the German edition; Richardson (1845) cited pages 200 and 201 of the English edition; Günther (1861) cited pages 170 and 171 of the German edition and pages 200 and 201 of the English edition; and Jordan (1917:17) cited page 130 of the German edition. Neither Koumans (1953), nor Springer (1978), nor I could find any mention of *Apocryptes* in either the German or English editions. However, in the German edition, *Gobius pectinirostris* is mentioned on page 170 and *G. niger* on page 171, whereas, in the English edition, *Gobius pectinirostris* appears on page 200, *G. niger* on page 201. It is stated, furthermore, in the editor's preface to the English edition that Osbeck reviewed and made changes in the German translation (upon which the English version is based). Therefore, I assume that even if Osbeck used *Apocryptes* (which I cannot verify) in his 1757 version, he adopted Linnaeus' nomenclature and changed his *Apocryptes chinensis* to *Gobius pectinirostris* Linnaeus and *As. cantonensis* to *G. niger* Linnaeus in the translated editions. Consequently, I can find no evidence of the availability of *Apocryptes* before Valenciennes (1837).

Bleeker (1874) designated *Gobius bato* as the type species for *Apocryptes* Valenciennes. Bleeker probably made this selection because *As. bato* was the first species listed under the generic heading *Apocryptes* in Valenciennes (1837). Valenciennes also included *Gobius pectinirostris* Linnaeus in his *Apocryptes,* but this placement, I suspect, was based on the inadequate description of *Gobius pectinirostris* provided by Linnaeus. Valenciennes' meristic data for *G. pectinirostris* closely parallel those given by Linnaeus (except Valenciennes gave the total for both pelvic fins instead of just one as Linnaeus did), and Valenciennes probably had very little idea to which species *G. pectinirostris* referred.

Bleeker (1874) considered *Gobileptes* Swainson a junior synonym of *Apocryptes.* Based on the limited information given for *Gobileptes* by Swainson (1839), it is difficult to imagine why Bleeker did this. Swainson did not list a type species for *Gobileptes* and mentioned only that *Gobileptes* possesses a lanceolate caudal fin and large scales, two characters found in several groups of gobies, but not occurring in combination in any oxudercine genus. Jordan (1919) surmised *Gobileptes* might refer to *Oligolepis acutipennis.*

Apocryptes bato (Hamilton)

Figs 2-3; Tables 9-16

Gobius bato Hamilton, 1822: 40, pl. 37, fig. 10 (type locality, Ganges Delta, India).
Apocryptes bato.-Valenciennes *in* Cuvier & Valenciennes, 1837: 143 (new combination).
Apocryptes batoides Day, 1876: 301, pl. 66, fig. 3 (type locality Moulmein, Burma).

Material examined. 27 specimens from 3 general localities; size range 46-141): INDIA: AMS B.8205, 1:102; ANSP 123143, 2:88-91; BMNH 1889.2.1:3467-71, 3: 78-102; BMNH 1889.2.1:3472, 1:134; SU 34758, 3: 46-141; SU 34759, 1:93; ZMA 100.115, 1:64. BANGLADESH: UMMZ 187890, 9:69-118. BURMA: SU 33798, 6:87-116.

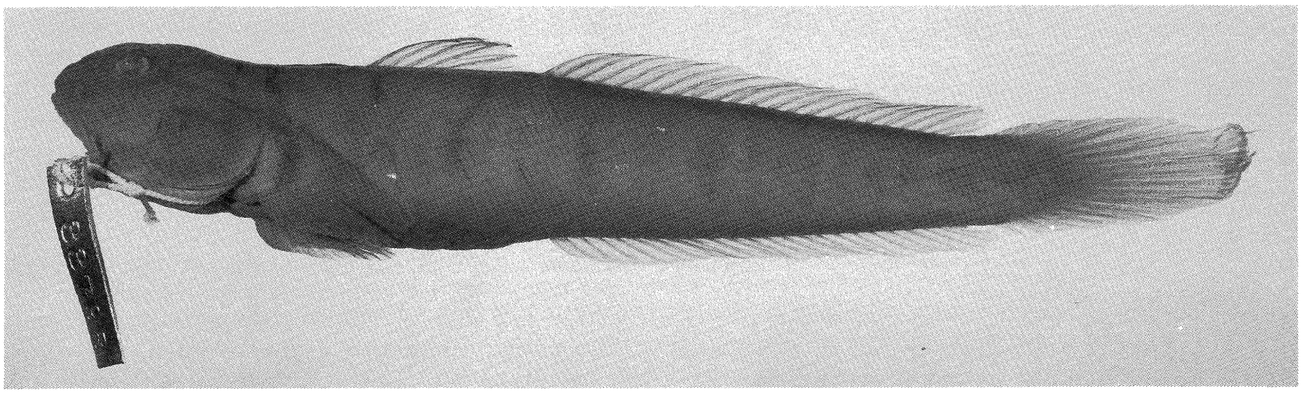

Fig.2. *Apocryptes bato,* SU 33798, 90 mm SL, Ganges Delta, India.

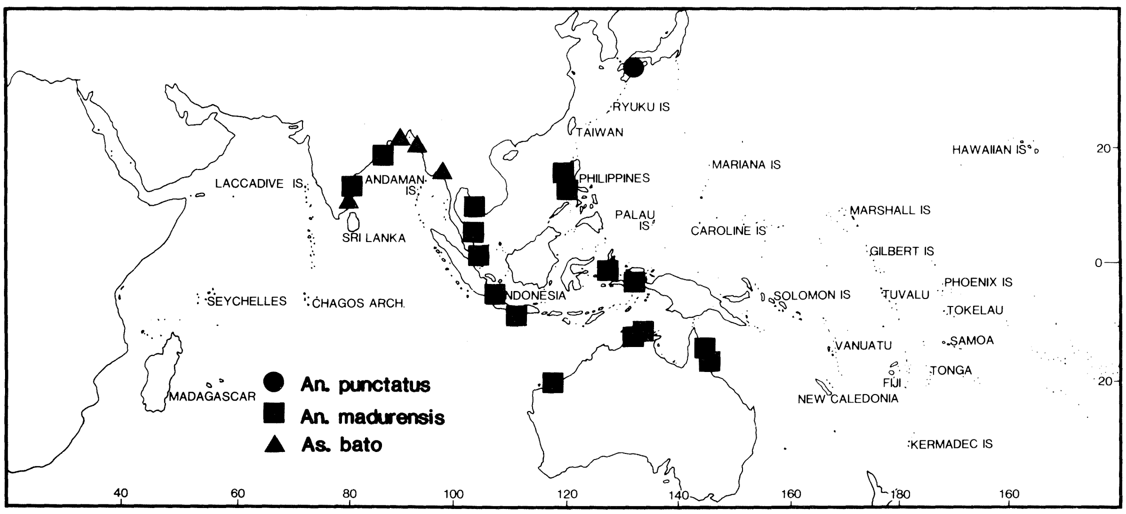

Fig.3. Known localities of *Apocryptes bato, Apocryptodon madurensis* and *An. punctatus* based on examined material.

Diagnosis. Total elements in D2 21-23 (mean = 22.0); total elements in anal fin 20-24 (mean = 22.1); head length 21.9-23.9% SL (mean = 22.7%); in some preserved specimens, 6-7 vertical narrow, brown bars along sides, anteriormost coursing from dorsum through pectoral base; caudal fin length 22.6-32.9% SL (mean = 28.2%).

Colouration. No colour notes or photographs available of live or freshly dead individuals. In the original description, Hamilton (1822:40) stated, "The body is slippery, above of a pale green colour, with numerous black dots, and beneath white, with a silvery gloss on the sides."

Ground colour of preserved specimens yellow brown to brown; some specimens with 6-7 narrow, vertical, brown bars along sides, anteriormost extends across pectoral base, second at spinous dorsal fin origin, third at about fifth dorsal fin spine, fourth at base of third or fourth second dorsal fin ray, fifth at base of eighth or ninth ray, and sixth at base of 14th or 15th ray. Some of these bars may be discontinuous and, in some instances, dusky blotches replace bars.

Distribution. Burrows within tidal limits of river deltas from the east coast of India to Burma. Fowler (1962) reported *As. bato* from Hong Kong but did not list any specimens, therefore, this record is unsubstantiated.

Remarks. Type material for Hamilton's species was not saved (Hora, 1934). However, Hamilton's figure of *Gobius bato* is sufficiently accurate to allow positive identification. Hamilton does not show any vertical bands on his figure, but Day's (1876, pl. 64, fig. 6) figure of the species does. Type material of *Apocryptes batoides* Day from Burma was not available (and may no longer exist). One specimen (BMNH 1889.2.1:3472) collected in Madras and identified by F. Day as *As. batoides* is a very large specimen (134 mm SL) of *As. bato.* This specimen lacks bifid teeth in the jaws, the only character used by Day (1876) to distinguish *batoides* from *bato.* I suggest bifid teeth are replaced ontogenetically by caninoid ones and this may be a manifestation of ecological partitioning.

Etymology. The trivial name, *bato*, refers to the local Indian name for this fish, bhato (Hora, 1934).

Apocryptodon

Fig. 1; Tables 1-8

Apocryptodon Bleeker, 1874: 327 (type species, *Apocryptes madurensis* Bleeker, 1849, by original designation.)

Included species. Two species are assigned to *Apocryptodon, An. madurensis* and *An. punctatus.* The former is known from the east coast of India to the Philippines and northern Australia, the latter is endemic to Japan.

Diagnosis. This genus is unique among oxudercines in possessing posteriorly directed lamina on the parapophyses of the fourth vertebra and in possessing a supraorbital pore.

Description. Spinous dorsal fin VI; second dorsal fin I, 20-23 (dorsal fins connected by basal membrane); spinous dorsal fin pterygiophore formula: 3-12210; base of sixth spine almost midway between base of fifth spine and origin of second dorsal fin; first four interspinous spaces about equal; little or no elongation of spines with the fourth spine typically the longest fin element; second dorsal fin base terminates within two scales of dorsal procurrent rays; appressed second dorsal fin overlaps procurrent rays.

Anal fin 21-23; insertion of last ray at a vertical to last ray of the second dorsal fin; anal fin base extends within two scales of ventral procurrent rays; appressed anal fin overlaps procurrent rays.

Pectoral fin 17-24, ventralmost rays shortest, medial rays longest.

Pelvic fin I, 5, united by membrane with fin of opposite side; frenum well developed.

Caudal fin slightly elongate, with 17 segmented rays, 15 of them branched; dorsal and ventral procurrent rays typically seven.

Scales cycloid covering most of body except for tip of snout, interorbital region, ventral surface of head, and pectoral fin bases; largest scales posteriorly, smallest scales embedded on superior surface of head; scale rows irregular, difficult to count with accuracy; longitudinal scale count 47-58; TRF 13-18; TRB 13-17; TRDB 13-19; predorsal scales 19-33.

Gill opening restricted, extending from a point equal to dorsalmost aspect of pectoral fin base to just slightly ventral to terminus of pectoral fin base. Isthmus broad.

Teeth in both jaws in a single, discontinuous row; 15-30 caninoid teeth in upper jaw with bluntly rounded tips, those medial larger and overlapping lower jaw (one specimen with bifid teeth); 22-49 compressed teeth in lower jaw, most bifid, anteriormost area lacking teeth; one, large, recurved, canine tooth on each side of symphysis internal to anterior margin of lower jaw.

Gape wide, posterior tip of maxilla extending to a point posterior to a vertical from posterior margin of eye; anterior nostril at the tip of a pendulous flap that overlaps a portion of the upper jaw.

A large, anterior oculoscapular canal pore about midway between eye and upper jaw; posterior nostril large and anteroventral to eye; posterior pore in interorbital region typically lacking except for a single specimen; supraorbital pore posterolateral to eye and connected by canal to interorbital region; a small crest on posterior midline of nape.

Ventral portion of first gill arch without gill rakers, only rudimentary bumps; gill filaments extremely feather like.

Etymology. From the Latin suffix *odon,* toothed, and *Apocryptes,* another genus in the subfamily, in reference to the prominent teeth, and superficial similarity to *Apocryptes;* masculine gender.

Key to the Species of *Apocryptodon*

1. Three or four, vertical, brown bars on sides (Japan)................................... *An. punctatus* Tomiyama

—— No bars on body, only roundish blotches eastern Indian Ocean to western Pacific) .... *An. madurensis* (Bleeker)

Apocryptodon madurensis (Bleeker)

Pl. 1A; Figs 3-4; Tables 9-10

Apocryptes madurensis Bleeker, 1849: 35 (type locality, Java).
Apocrytpes glyphisodon Bleeker, 1849: 36 (type locality, Jakarta).
Apocryptes bleekeri Day, 1876: 300, pl. 54, fig. 3 (type locality, Madras).
Apocryptodon montalboni Herre, 1927: 277, pl. 22, fig. 2 (type locality, Iloilo, Philippines).
Apocryptodon sealei Herre, 1927: 278 (type locality, Manila).
Apocryptodon taylori Herre, 1927: 279, pl. 22, fig. 3 (type locality, Tablas, Philippines).
Apocryptodon malcolmi Smith, 1932: 47 (type locality, Thailand).
Apocryptodon lomboyi Ablan, 1940: 373, pl. 1 (type locality, Dagupan, Philippines).
Apocryptodon madurensis.-Koumans, 1943: 254 (new combination).

Material examined. (369 specimens from eight general localities; size range 11-71): INDIA: AMS B.7501, syntype of *Apocryptes bleekeri* Day, 54; BMNH 1889.2.1.3460-1, possible syntypes of *Apocryptes bleekeri* Day, 2:55-58; USNM 276552, 1:56. THAILAND: ANSP (uncatalogued), 1:60; CAS 27443, 15:33-52; USNM 90323, holotype of *Apocryptodon malcolmi* Smith, 58. SINGAPORE: SU 30338, 1:50. INDONESIA: RMNH 4520 (syntypes), 3: 48-71; RMNH 4765, syntypes of *Apocryptes glyphisodon,* 12:46-52; USNM 246616, 1:50; USNM 276001, 1:43. PHILIPPINES: CAS 52045, 1:61; USNM

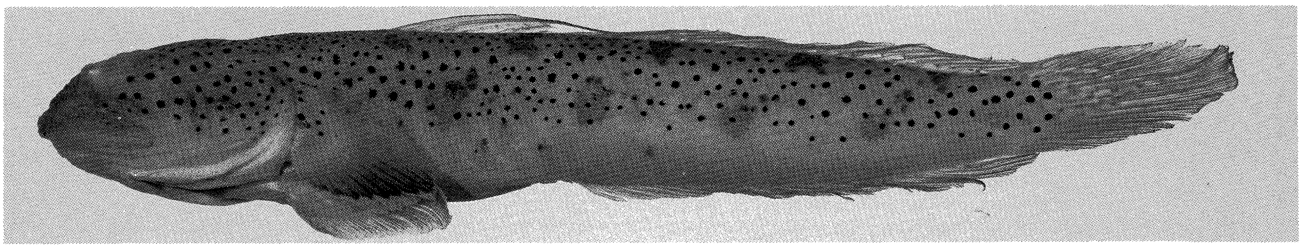

Fig.4. *Apocryptodon madurensis,* NTM S.10649, 51 mm SL, Northern Territory, Australia.

99874, 29:52-64; USNM 160933, 2:62; USNM 160934, 1:62; ZMB 7637, 1:55. AUSTRALIA: Northern Territory: AMNH 41557, 6:20-40; AMS I.23943-001, 5:14-32; NTM S.10020-005, 2:31-42; NTM S.10429-001, 53: 14-51; NTM S.10469-013, 4:16-18; NTM S.10553-011, 44:18-43; NTM S.10649-016, 35:17-53; NTM S.10649-017, 2: 25-38; NTM S.10727-006, 12:19-35; NTM S.10802-008, 15: 15-28; NTM S.11242-013, 40: 11-43; NTM S.11506-020, 46:12-35. Queensland: AMS. I.22040-013, 3:41-43; AMS I.23259-006, 8:33-50; AMS I.23265-007, 2:44-48; AMS I.23313-004, 4:35-47. Western Australia: NTM S.10802-008, 15:15-28.

Diagnosis. Five, brown, roundish blotches along the lateral midline; predorsal scales 19-27 (mean = 23.4).

Colouration (based on a photograph of a freshly dead specimen, AMS I.25516, from Port Hedland, Western Australia). Ground colour whitish; numerous, small, black spots on head and trunk, a broken, black stripe infraorbitally to edge of gill cover; 5, large, greenish brown blotches midlaterally - the first ventral to D1 terminus, 3 ventral to D2, the fifth on caudal peduncle; 5 greenish brown blotches on dorsum that are smaller than those midlaterally - first at D1 origin, second at D1 terminus, third and fourth at D2 base, and fifth at D2 terminus; D1 with black margin, remainder of fin immaculate; D2 with columns of 1-4, small, black spots on inter-radial membranes with some rays dusky; caudal fin with some short, broken, brown lines and a black ventral margin; anal fin distally blackened with a few, small, black spots posteriorly; pectoral fin with small, black spots proximally, a black band inframarginally, and a white margin; pelvic fin dusky.

Ground colour in preservative light or dark brown; head and trunk typically covered with small, black and/or brown spots (one lot from Australia, AMNH 41557, lacks these spots); 5 large, brown blotches along lateral midline, one ventral to D1, 3 ventral to D2, and 1 on caudal peduncle; on dorsal surface, eight, brown, saddle-like blotches - 3 cross midline of nape, 1 at D1 origin, 1 across D1 terminus, and 3 across D2; irregular black and brown, wavy, vertical bands on caudal fin; first D1 spine black in recently preserved material, remainder of fin transparent; inter-radial portion of D2 slightly dusky with small, black streaks at bases; anal fin dusky; ventral third of pectoral fin blackened with pale margin; pelvic fin transparent, sometimes with dusky margin.

Distribution. Specimens of *Apocryptodon madurensis* were examined from eastern India, Thailand, Singapore, Indonesia, northern Australia, and the Philippines.

Remarks. Bleeker's type material of *Apocryptodon glyphisodon* and *An. madurensis* is in poor condition. Thus, it is impossible to determine if differences once existed that warranted separate recognition; there are no significant meristic or morphometric differences. Bleeker's (1849) key (pp. 35-36) separated *An. glyphisodon* from *An. madurensis* on tooth number (26-30 upper jaw teeth, 60 lower jaw teeth in *An. madurensis* versus 16 upper, 24 lower in *An. glyphisodon*). Tooth counts varied between 14-22 (mean= 18.2) in the upper jaw and 22-29 (mean = 25.8) in the lower jaw in the *An. glyphisodon* types, and between 22-31 (mean = 25.7) upper and 1-52 (mean = 25.3) lower in the *An. madurensis* type material. As Koumans (1953) noted, teeth in *Apocryptodon* are variable in number and type, and easily lost. Therefore, I follow Koumans (1953) in synonymising *An. glyphisodon* with *An. madurensis.*

The types of *Apocryptodon lomboyi, An. montalboni, An. sealei* and *An. taylori* were destroyed during World War II. Based on the original description and/or figures each is considered synonymous with *An. madurensis.*

D.F. Hoese and H.K. Larson (personal communication) believe two species of *Apocryptodon* inhabit northern Australia. They contend that specimens without small, black spots represent a different species; I do not concur. I found no significant meristic or morphometric differences between specimens with small, black spots and those without. Specimens with varying degrees of black spot retention were also evident. Therefore, I believe the lack of small, black spots may represent an ecological manifestation. Based on my definition of *An. madurensis,* only that species is found in northern Australia.

Etymology. The trivial name, *madurensis,* refers to the type locality of the species, Madura Island, Java, Indonesia.

Apocryptodon punctatus Tomiyama

Pl. 1B; Figs 3, 5; Tables 9-16

Apocryptodon punctatus Tomiyama, 1934: 332, figs 4, 5

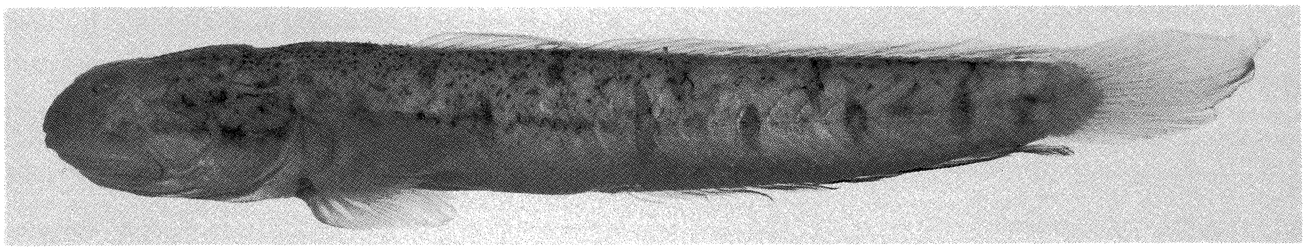

Fig.5. *Apocryptodon punctatus,* LICPP 1969128, 62 mm SL, Japan.

(type locality, Kyushu, Japan).

Material examined. (9 specimens from one general locality; size range 61-67): JAPAN: LICPP 1968128, 2: 63-67; ZUMT 17694-696, 3:49-52; ZUMT 17700-702, 3:49-53; ZUMT 26306 (holotype), male, 61.

Diagnosis. 3 or 4 vertical, narrow, brown bars along the sides; predorsal scales 22-33 (mean = 27.9).

Colouration (based on a photograph of a 59 mm SL specimen in Masuda *et al.* 1984: 257, fig. C, identified as *Apocryptodon madurensis,* reproduced herein as Pl. 1B). Greenish dorsally, silver ventrally, these areas demarcated anteriorly by a longitudinal line coursing from below eye, across cheek and opercle, above pectoral base, and ending below fourth D2 element; 5 short, narrow, black bars midlaterally, first ventral to fourth D1 spine, second ventral to fifth D2 element, third ventral to 13th D2 element, fourth ventral to the 18th D2 element, and the fifth on caudal peduncle; many scattered small, black spots from midlateral region to dorsal midline; lateral edges of 5 midline bars evident (described in more detail below); dorsal fins mostly transparent; small, dusky markings basally on D2; caudal fin with an orange tint dorsally, blackened ventrally; anal fin mostly transparent with posterior elements distally blackened; pelvic fin mostly transparent, rays proximally orange; pectoral fin with orange tint proximally and slight blackening inframarginally along ventral edge.

Ground colour in preservative light brown; all spots, bars and lines brown; portion of midlateral line remains; 6 midlateral markings, anteriormost a large blotch ventral to third and fourth dorsal spines, next 4 markings short, narrow bars in the following sequence - one at fourth D2 element, one at ninth, one at 14th, and one at 20th, posteriormost marking a blotch on caudal peduncle; many scattered, small spots dorsally; in a dorsal view, 3 bars cross midline of nape, another across D1, one just anterior to D2 origin, one at sixth element of D2, one at 12th D2 element, and the last at 21st; dorsal, caudal and pelvic fins transparent; anal fin elements distally dusky; pectoral fin mostly transparent, narrow, dusky band inframarginally along ventral edge.

Distribution. This species lives in burrows made by the crustacean *Alpheus* at river mouths in mainland Japan (Dotsu, 1961). All records of *Apocryptodon punctatus* are from Japan.

Remarks. Subsequent to his original description, Tomiyama (1936) synonymised his *Apocryptodon punctatus* with *An. bleekeri* (= *An. madurensis*). The distinctive colour pattern of *An. punctatus* is sufficient divergence from that of *An. madurensis* to warrant specific recognition.

Etymology. The trivial name, *punctatus,* is from the Latin *punctum,* bar or spot, in reference to the lateral markings on this species.

Boleophthalmus

Fig. 1; Tables 1-8

Boleophthalmus Valenciennes *in* Cuvier & Valenciennes, 1837: 198 (type species *Boleophthalmus boddarti* Valenciennes, 1837 [= *Gobius boddarti* Pallas, 1770], subsequent designation by Bleeker, 1874: 328).

Included species. The genus comprises four described species (*B. boddarti, B. caeruleomaculatus, B. dussumieri* and *B. pectinirostris*) and one undescribed species.

Diagnosis. Distinguishable from other oxudercine genera by the greatly thickened epidermis of the head and nape and in possessing a rectangular piece of cartilage spanning the width of the pelvic girdle.

Description. Spinous dorsal fin V; second dorsal fin 24-28 or I, 23-25, first element typically segmented and unbranched but occasionally segmented and branched; dorsal fins not connected by membrane; spinous dorsal fin pterygiophore formula: 3-1221*0, sixth pterygiophore lacking associated spine; in most species, spines elongated into filaments, third or fourth spine longest; 4 interspinous spaces about equal; second dorsal fin base terminates within 3 scales of caudal fin; appressed second dorsal fin overlaps caudal fin.

Anal fin 24-27 or I, 23-25, first element typically segmented and unbranched; insertion of last ray at a vertical to that of the last ray of the second dorsal fin; height of anal fin less than half that of second dorsal fin; appressed anal fin barely overlaps ventral procurrent rays.

Pectoral fin 16-21, middle rays longest.

Pelvic fin I, 5, united by membrane with fin of opposite side; frenum well developed.

Caudal fin lanceolate, with 17 segmented rays, 15 of them branched, ventral rays thickened; dorsal procurrent rays 3-6, typically 5, ventrally 2-5, typically 4.

Scales cycloid, covering entire body except for snout and chin (all scales on anterior one third of body beneath a thick epidermal layer, probably an anti-dessication feature related to semi-terrestrial life); largest scales posteriorly; scale rows irregular, difficult to count with accuracy; longitudinal scale count 61-185; TRF 19-43; TRB 18-38; TRDB 18-46; predorsal scales 25-60.

Gill opening restricted, extending from the distalmost point of pectoral fin base to just slightly ventral to terminus of pectoral fin base.

Teeth in both jaws in a single row; 31-79 caninoid teeth in upper jaw with bluntly rounded tips, the 6 most medial teeth much larger and overlapping lower jaw when mouth closed; 31-81 highly compressed and unusually shaped (notched) teeth in lower jaw in all but one species (Fig. 6a); medial area of lower jaw lacking teeth; 1 recurved, canine tooth on each side of symphysis internal to anterior margin of lower jaw.

Gape relatively large, posterior tip of maxilla extending to a vertical from posterior margin of eye; anterior nostril at tip of a pendulous flap overlying lateral portion of upper jaw.

Dermal cup covering ventral half of eye; posterior nostril just anterior to eye; anterior oculoscapular canal pore about one third the distance towards upper lip from eye.

Ventral portion of first gill arch without gill rakers, only rudimentary bumps; gill filaments feather like.

Etymology. The generic name, *Boleophthalmus,* is from the Greek *bole,* dart or arrow, and *ophthalm,* eye; masculine gender.

Key to the Species of *Boleophthalmus*

1. Second dorsal fin modally with 27-28 total elements; anal fin modally with 26-27 total elements........2

—— Second dorsal fin modally with 24-26 total elements; anal fin modally with 24-25 total elements........3

2. Caudal fin length usually greater than 22% SL; head length usually less than 26% SL; length of second dorsal fin base almost always less than 45% SL. (Arabian Gulf to Bombay)........*B. dussumieri* (Valenciennes)

—— Caudal fin length usually less than 22% SL; head length greater than or equal to 27% SL; length of second dorsal fin base often greater than 45% SL. (Western Australia north to Gulf of Carpentaria)........*B. caeruleomaculatus* McCulloch & Waite

3. First D2 element usually spinous; longitudinal scale count fewer than 80; 5-7 prominent, dusky bars inclined anteriorly from dorsum, occasionally extending well below midline. (Bombay to Sabah)........*B. boddarti* (Pallas)

—— First D2 element usually a segmented ray; longitudinal scale count more than 80, usually more than 90; if dusky bars present, never extending ventrally below lateral midline........4

4. Predorsal scales usually fewer than 40; lower jaw teeth notched. (Taiwan to Japan)........*B. pectinirostris* (Linnaeus)

—— Predorsal scales usually more than 40; lower jaw teeth lacking notch. (Northern Territory, Australia)........*B. birdsongi* n.sp.

Boleophthalmus birdsongi n.sp.

Pl. 1C; Figs 6-8; Tables 9-16

Type material. HOLOTYPE: AMS I.18394-002, male, 94 mm SL, mouth of Liverpool River, Arnhem Land, N.T., 12°10'S, 134°09'E, collected by D. Grace, 28 Jan. 1975. PARATYPES: AMS I.24685-012, 1 female 76 mm SL, Darwin, N.T.; NTM S.11362-032, 2 males 98-100 mm SL, 3 females 74-108 mm SL, northeast of Darbilla Creek, Milingimbi, N.T., collected from a mud and log habitat at a depth of 0-2 m by H. Larson and P. Horner, 24 July 1984; NTM S.10421-001, 2:108-110, East Arm of Darwin Harbour at mouth of Elizabeth River, Darwin, N.T., collected by H. Larson and R. Hanley using ratshot while fish were feeding on riverbank, 29 Mar. 1982; NTM S.10694-006, 2:66-90, collected at Gunn Point north of Shoal Bay, N.T., collected from a mangrove habitat over sandy mud at a depth of 0-1 m by H. Larson and R. Williams, 20 Sept. 1982; USNM 289283, 1 female 68 mm SL, creek on north-east side of Milingimbi Island, N.T., collected at a depth of 0-2 m by H. Larson and P. Horner, 25 July 1984; USNM 289284, 1 male 100 mm SL, 5 females 56-66 mm SL, northern bank of Norman River between Karumba and Karumba Point, N.T., collected at a depth of 0-1 m by G. and M. Hardy, 6 July 1980.

Other material examined. (21 specimens from one general locality; size range 30-111): NORTHERN TERRITORY: AMS I.24689-002, 1:68; NTM S.239, 1:66; NTM S.440, 1:79; NTM S.10418-001, 1:111; NTM S.11097-001, 1:98; NTM S.11362-033, 5:46-53; NTM S.11364-016, 11:30-91.

Diagnosis. Total elements in D2 23-25 (mean = 24.1); caudal fin length 17.9-24.6% SL (mean = 20.7%); head length 26.6-31.1% SL (mean= 28.9%); length of D2 base

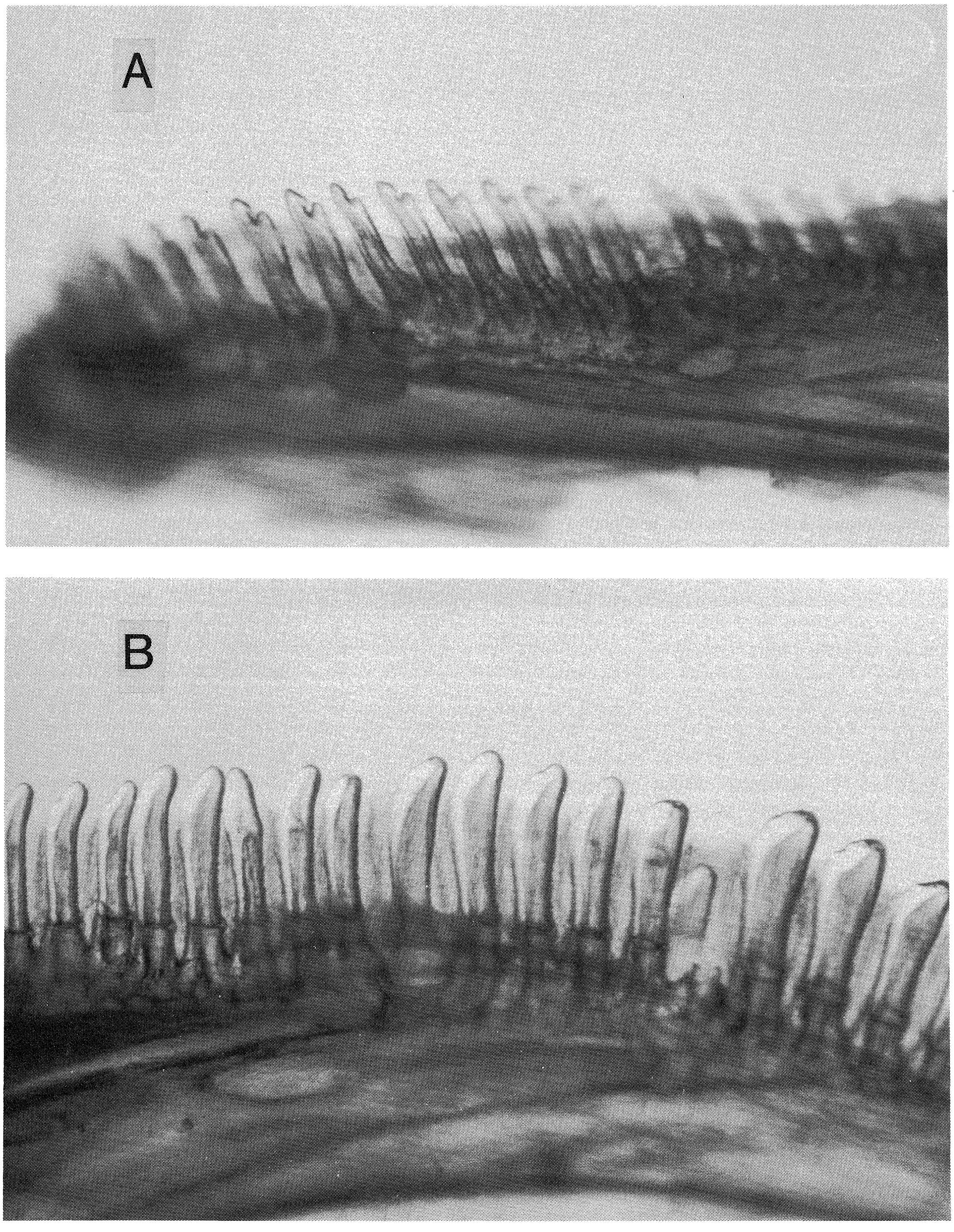

Fig.6. A, Dorsolateral view of left lower jaw teeth in four species of *Boleophthalmus*. B, Dorsal view of left lower jaw teeth of *Boleophthalmus birdsongi*.

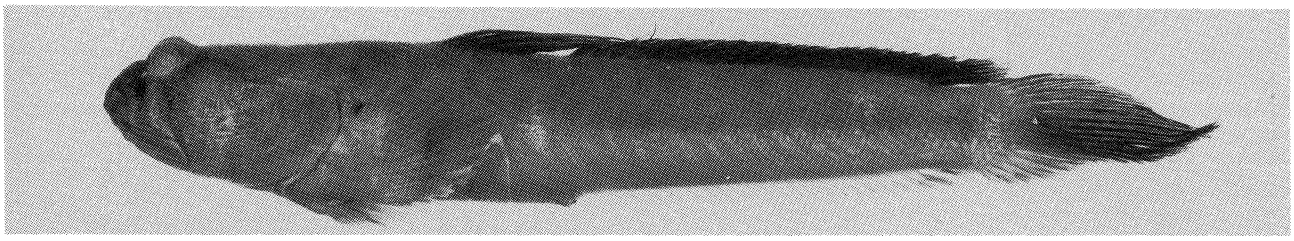

Fig.7. *Boleophthalmus birdsongi,* AMS I.18394-002, 94 mm SL, holotype, Northern Territory, Australia.

38.2-43.5% (mean = 41.5%); first D2 element usually segmented and unbranched; longitudinal scale count 89-111 (mean = 103.1); predorsal scales 38-60 (mean = 46.3); lower jaw teeth atypical for *Boleophthalmus,* notch lacking, teeth more rounded than congeners (Fig. 6b).

Description. Counts and measurements for holotype given first followed by the range in parentheses: first dorsal fin spines V; total elements in second dorsal fin 24 (23-25); total elements in anal fin 23 (22-24); pectoral fin rays (right side) 19 (17-20); pectoral fin rays (left side) 19 (17-20); predorsal scales 51 (38-60); TRF 33 (27-43); TRB 26 (26-36); TRDB 34 (29-43); longitudinal scales 100 (89-111); upper jaw teeth 49 (35-56); lower jaw teeth 51 (39-57).

Head length 27.8% SL (26.6-31.1%); head depth 14.6% SL (14.3-16.8%); head width 14.7% SL (14.7-20.9%); length of D1 base 13.0% SL (9.8-13.0%); length of D2 base 42.3% SL (38.2-43.5%); length of anal fin base 38.6% SL (34.5-42.7%); caudal fin length 21.2% SL (17.9-24.6%); body depth 14.9% SL (14.0-17.8%); least depth of caudal peduncle 9.7% SL (8.1-9.7%); pectoral fin length 17.4% SL (17.4-22.1%); pelvic fin length 14.1% SL (11.9-15.5%).

Head cylindrical, about as wide as deep. Body compressed. Mouth subterminal. Jaws extend posteriorly to a vertical point equivalent to the posterior eye margin. Interorbital region very narrow with a small pore posteriorly. Anterior nostril at tip of pendulous flap of skin overhanging upper jaw. Posterior nostril a simple pore close to anterior eye margin. Anterior oculoscapular canal pore about one half eye diameter anterior to posterior nostril. Gill opening somewhat restricted, extending the height of pectoral fin base. A small pocket of skin at dorsal edge of pectoral fin base. Third and fourth dorsal spines elongate, the fourth is longest. Pectoral fin slightly pointed, pointed tip reaching a vertical point slightly posterior to terminus of D1. Caudal fin slightly elongate. Pelvic fins connected by a strong frenum; medial rays longest.

No vomerine or palatine teeth. 2-3 upper jaw teeth on either side of symphysis twice as long as those posterior. Lower jaw teeth subequal and compressed.

Cycloid scales on nape and body. Preoperculum, operculum and isthmus lacking scales.

Comparisons to congeners: *Boleophthalmus birdsongi* is the only species in the genus with a longitudinal stripe coursing along the lateral midline. Additionally, the lower jaw teeth of *B. birdsongi* lack the distinctive notch found in all other members of the genus. Known thus far only from northern Australia, *B. birdsongi* is much paler in background colouration than its only other congener from Australia, *B. caeruleomaculatus.* Also, *B. birdsongi* differs from *B. caeruleomaculatus* in usually having fewer second dorsal and anal fin elements.

Colouration (based on a photograph of a fresh, 76 mm SL, female specimen, AMS I.24685-012, from Darwin, N.T., see Pl. 1C). Most of head and dorsal half of body brown, ventral half of body yellow white with ventral surface of head yellow; a wide, black stripe along lateral midline from gill cover to caudal peduncle; extending dorsally from this black stripe are several blotches and stripes, partially covered by the pectoral fin are 2 blotches, with 1 stripe between D1 and D2 and 4 beneath D2 (D.F. Hoese informed me these stripes and/or blotches are only seen in females); D1 blackened proximally, whitish distally; D2 proximally white with a wide, black stripe in middle of fin, and distally off white; caudal fin greyish black; anal fin proximally black, distally white; pelvic fins dusky; pectoral fin base dusky with numerous small, white spots, fin rays slightly dusky; numerous white spots on gill cover, few on cheek.

Ground colour of preserved specimens typically greyish black, some specimens brown; black stripe present on some adult males and females but not all; some specimens with greyish blotches and/or stripes on dorsum; others lack any sort of markings on sides; D1 largely blackened; D2 with a black or brown stripe in middle of fin; caudal fin dusky with a medial black streak; anal and pelvic fins transparent; pectoral fin rays dusky; no white spots on head or pectoral fin base.

Distribution. Known only from mudflat areas in the Northern Territory, Australia where it is sympatric with *Boleophthalmus caeruleomaculatus.*

Etymology. The trivial name is in honor of Ray S. Birdsong for his contributions towards a better understanding of gobioid osteology and systematics.

Boleophthalmus boddarti (Pallas)

Pl. 1D; Figs 8-10; Tables 9-16

Gobius boddarti Pallas, 1770: 11, pl. 2, figs 4-5 (type locality, Indian Ocean).

Gobius striatus Bloch & Schneider, 1801: 71, pl. 16 (type

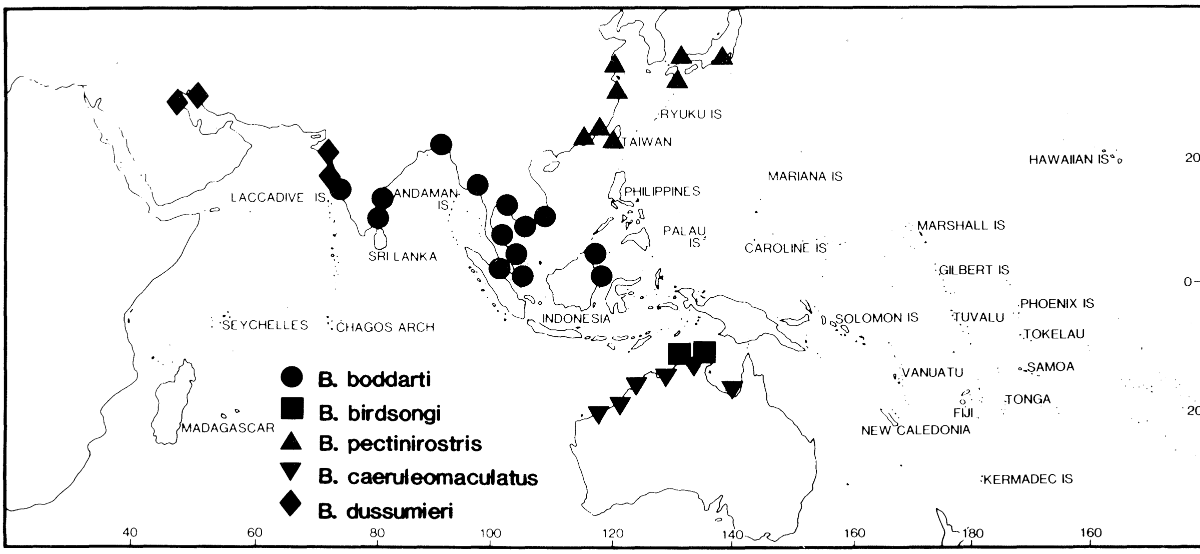

Fig.8. Known localities of *Boleophthalmus* based on examined material.

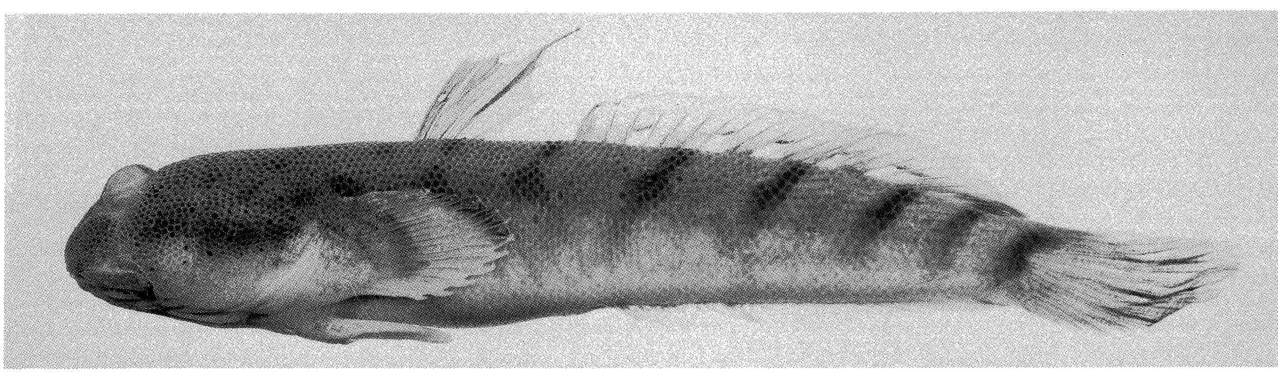

Fig.9. *Boleophthalmus boddarti,* FMNH uncatalogued, 45 mm SL, Malaysia.

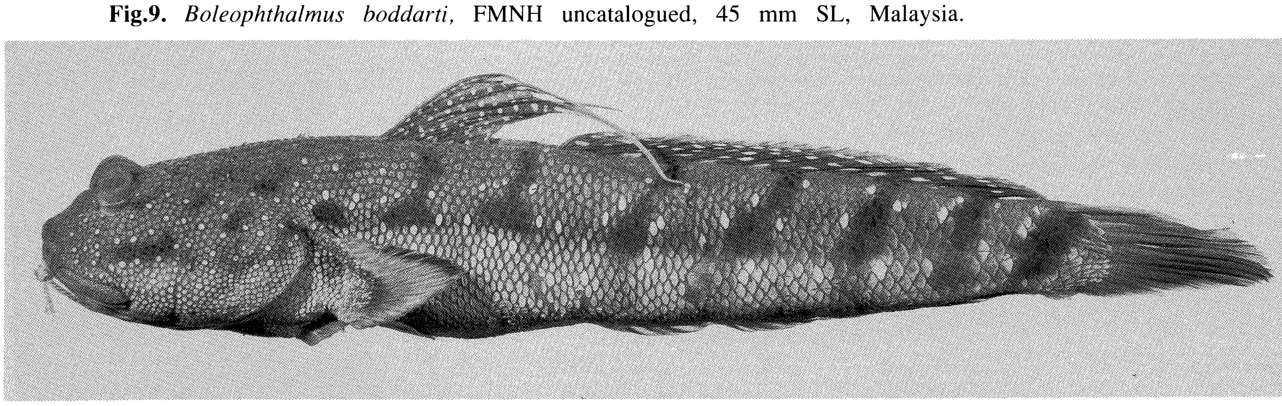

Fig.10. *Boleophthalmus boddarti,* SU 34761, 97 mm SL, India.

locality, Tranquebar, India).
Gobius plinianus Hamilton, 1822: 45, pl. 35, fig. 13 (type locality, Ganges Delta, India).
Boleophthalmus boddarti.-Valenciennes *in* Cuvier & Valenciennes, 1837: 199 (new combination).
Boleophthalmus inornatus Blyth, 1861: 148 (type locality, Tenasserim, India).
Boleophthalmus sculptus Günther, 1861: 104 (type locality, India).
Apocryptes punctatus Day, 1867: 941 (type locality, Madras, India).

Material examined. (103 specimens from seven general localities; size range 39-135): INDIA: ANSP 77540, 1:87; ANSP 85017, 4:83-98; BMNH (uncatalogued), holotype of *Boleophthalmus sculptus* Günther, 83; SU 34761, 15:64-116; USNM 279310, 1:112; USNM 279311, 2:48-65; USNM 279312, 1:89; USNM 279314, 1:89; USNM 279315, 4:39-63; USNM 279316, 1:138; USNM 280240, 1:134; USNM 280480,

1:76; ZMB 2145, 1:128. BURMA: MSNG 15244, 2: 89-94. THAILAND: AMNH 14505, 1:102; AMS I.21034-006, 18:69-103; ANSP 59998, 1:100; ANSP 59999-02, 4: 98-125; ANSP 62878-89, 12:100-126; ANSP 62892-94, 3:69-79; ANSP 62890-91, 2:104-113; LICPP 1970187, 2:84-90; USNM 103353, 1:121; USNM 181861, 4: 79-117. MALAYSIA: USNM 278429, 1:145; USNM 278444, 3:46-48; VIETNAM: ANSP 77237, 1:88. SINGAPORE: SU 33141, 1:107; ZMA 110.042, 2:107-112. SABAH: ANSP 17285, 2:50-63; USNM 139351-52, 9: 61-99.

Diagnosis. Total elements in D2 24-26 (mean = 24.5); caudal fin length 17.9-23.3% SL (mean = 19.9%); head length 25.0-30.4% SL (mean = 27.0%); length of D2 base 40.2-46.4% SL (mean = 43.4%); first D2 element usually unsegmented and unbranched; longitudinal scale count 61-79 (mean = 71.4); predorsal scales 25-35 (mean = 29.2); lower jaw teeth notched.

Colouration (based on a painting by H. Ito of a specimen, USNM 139351-2, from Sabah). Head and dorsal half of body grey brown, ventral half of body greenish white; head and trunk with white speckles; dark brown line from anterior nostril to dorsal tip of operculum; brown spots on head and nape; 7 dark brown, saddle like, diagonal bars inclined anteriorly from dorsum - 1 at D1, 5 beneath D2 and 1 on caudal peduncle; D1 greenish blue with bluish tips and covered with blue-white spots; D2 dusky with small, white spots and white margin; caudal fin grey blue except proximally yellow with a white ventral margin; anal fin transparent except for a black stripe inframarginally; pectoral fin yellow distally, dark brown proximally with a brown margin and numerous small, white spots on base and on proximal portion of fin rays; pelvic fin yellow proximally, blue distally.

Ground colour of preserved specimens tan to brown; ventroposterior portion of lower jaw blackened; white or chocolate brown spots and brown bars retained on many specimens, lost on others; dorsal fins bluish brown with white spots; caudal fin brown; inframarginal dusky band on anal fin retained, remainder of fin light brown; pelvic and pectoral fins brownish with a dark brown, dorsal margin on the pectoral fin in some specimens and numerous, small, white spots on pectoral fin base; venter whitish.

From my field observations in Malaysia, the spinous dorsal fin of *B. boddarti* can be one of three types. The most common of these is discussed above. The second type is one that is entirely yellow; only some subadults exhibit this type. The third type is displayed only by some adult females: D1 is more rectangular than the typical adult D1, and in addition to the small bluish white spots there are two, large, black spots distally either anterior or posterior to the third spine. The significance of the various D1 types was not evident to me.

Distribution. The west coast of India to Sabah. *Boleophthalmus boddarti* is apparently sympatric with *B. dussumieri* in the vicinity of Bombay.

Remarks. Type material of *Gobius boddarti* Pallas is not extant (A. Andriashev, in literature); the original description and figure were sufficient to affix identity. Type material of the following is also not extant (with authority in parentheses): *Gobius striatus* Bloch & Schneider (H.J. Paepke, personal communication); *Gobius plinianus* Hamilton (Hora, 1934); *Boleophthalmus inornatus* Blyth (J. Chambers, personal communication); the original description and/or figure most closely allies each with *B. boddarti*. *Apocryptes punctatus* Day is considered synonymous with *B. boddarti* based on the original description; type material could not be located.

Ecological and behavioural observations of *B. boddarti* were reported by Macnae (1968) and Murdy (1986).

Etymology. The trivial name, *boddarti,* honors Dr Pierre Boddaert, who collected material for the original description. Although the spellings of the trivial name and Dr Boddaert differ, I would recommend that an emendation be rejected.

Boleophthalmus caeruleomaculatus McCulloch & Waite

Figs 8, 11; Tables 9-16

Boleophthalmus caeruleomaculatus McCulloch & Waite, 1918: 79, pl. 8, fig. 1 (type locality, Adelaide River, N.T., Australia).

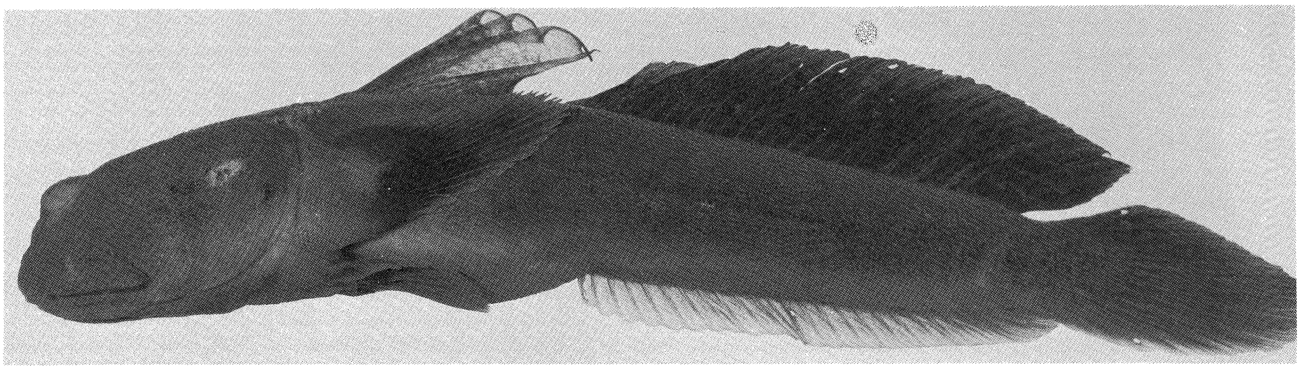

Fig.11. *Boleophthalmus caeruleomaculatus,* NTM S.10727-001, 94 mm SL, Northern Territory, Australia.

Material examined. (67 specimens from three general localities; size range 19-162): AUSTRALIA: Western Australia: AMS IB.2836, 1:107; AMS IB.2839-40, 2:107-108; WAM P.4853, 1:152; WAM P.9418, 2:112-119; WAM P.9426, 1:69. Northern Territory: AMNH 41558, 39:19-42; AMS I.14325 (paratype), 165; AMS I.18393-001, 1:162; AMS I.21219-001, 2:41-62; AMS IB.2844, 1:36; AMS IB.2847, 2:42-43; AMS IB.2849, 1:46; AMS IB.2850, 1:37; NTM S.10149-001, 1:41; NTM S.10528-001, 1:72; NTM S.10727-001, 4: 94-161; NTM S.11362-030, 1:153. Queensland: AMS I.21319-001, 1:112; QM I.10891, 4:117-124.

Diagnosis. Total elements in D2 24-28 (mean = 27.0); caudal fin length 18.5-22.7% SL (mean = 20.4%); head length 27.0-29.8% SL (mean = 28.0%); length of D2 base 43.2-47.9% SL (mean = 45.0%); first D2 element usually segmented and unbranched; longitudinal scale count 90-136 (mean = 119.0); predorsal scales 30-53 (mean = 40.4); lower jaw teeth notched.

Colouration. No colour notes or photographs of live or freshly dead individuals available.

Ground colour of preserved specimens brown to gray; numerous, small, dusky spots on cheeks, operculae, nape and dorsal to pectoral fins; proximal three quarters of D1 dusky with some whitish mottling, distal one quarter transparent with dusky margin; D2 dark brown to black with columns of 6-8, blue or brown dash marks on inter-radial membranes; caudal fin black or dark brown with blue or brown spots in dorsalmost inter-radial membranes; anal fin basally dusky, distally pale; pelvic and pectoral fins black or brown. Specimens less than 50 mm SL lack the fin pigment mentioned above.

Distribution. Western Australia north to Gulf of Carpentaria. *Boleophthalmus caeruleomaculatus* is sympatric with *B. birdsongi* in northern Australia.

Remarks. Two specimens from Broome, Western Australia (WAM P.9418-19) differ slightly from the above colour description and in the diagnostic morphometrics. In colouration, these specimens most closely resemble the original colour description of McCulloch & Waite (1918) in having numerous, white spots on the head and body, D2 possessing columns of 6-8, white spots, and the caudal fin also with white spots. Morphometrically, these specimens have a caudal fin length 20.9-22.7% SL (versus mean = 20.2% for others) and length of second dorsal fin base 42.2-43.2% SL (versus mean = 45.2%). In all other characters and descriptive features, these specimens agree with *B. caeruleomaculatus*.

Etymology. The trivial name, *caeruleomaculatus*, is from the Latin *caeruleus*, sky blue, and *macula*, spot, in reference to the markings on the trunk scales.

Boleophthalmus dussumieri Valenciennes

Pl. 1E; Figs 8, 12; Tables 9-16

Boleophthalmus dussumieri Valenciennes *in* Cuvier & Valenciennes, 1837: 207, fig. 354 (type locality, Bombay, India).

Boleophthalmus dentatus Valenciennes *in* Cuvier & Valenciennes, 1837: 208, fig. 355 (type locality, Bombay, India).

Boleophthalmus chamiri Holly, 1929a: 64 (type locality, Strait of Hormuz).

Material examined (70 specimens from eight localities; size range 52-139): IRAQ: ANSP 83333, 1:128. IRAN: USNM 196374, 1:124. ARABIAN GULF: USNM 196293, 1:93. KUWAIT: BPBM 30528, 5:95-104. PAKISTAN: AMS B.8006, 1:139; AMS I.21217-002, 1:70; LACM 38125-6, 1:125; LACM 38126-15, 1:122; LACM 38129-55, 1:77; LACM 38132-28, 1:83; LACM 38137-3, 17:52-109; LACM 38137-4, 6:51-103; LACM 38141-6, 1:50; LACM 38301-4, 4:25-69; LACM 38302-2, 8: 43-100; LACM 38303-1, 4:50-81; LACM 38308-5, 1:72. INDIA: ANSP 100161, 4:78-131; ANSP 122437, 4: 93-107; ANSP 123100, 2:113; BMNH 1889.2.1:3511, 1:81; MNHN A.1468 (holotype), male, 115; MNHN 1475, syntypes of *Boleophthalmus dentatus* Valenciennes, 3: 115-122.

Diagnosis. Total elements in D2 24-28 (mean = 26.8); caudal fin length 21.9-25.5% SL (mean = 23.6%); head length 23.6-28.7% SL (mean = 25.8%); length of D2 base 42.2-44.7% SL (mean = 43.6%); first D2 element usually unsegmented and unbranched; longitudinal scale count 103-185 (mean = 146.2); predorsal scales 48-56 (mean = 52.6); lower jaw teeth notched.

Colouration (based on a photograph of a freshly dead, 104 mm SL male from Kuwait, BPBM 30528). Head and trunk light blue; 3 greenish brown blotches on nape, 3

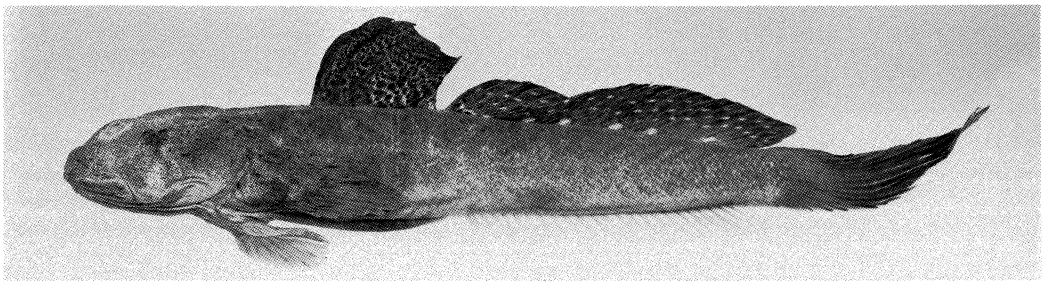

Fig.12. *Boleophthalmus dussumieri*, BPBM 30528, 89 mm SL, Kuwait.

similar blotches at D1 base, and 2 at D2 base anteriorly; small, green spots on opercle, pectoral base, and just dorsal to pectoral fin; brown orbital rim; D1 with greenish spots basally and with wavy, white lines and bluish spots throughout; D2 with columns of 2 or 3 (mostly 3) white spots on inter-radial membranes; basally on D2, large white spots on inter-radial membranes 7, 10, 14, 17 and 22; wavy, white line curving basally across first 5 D2 elements and membranes; distal margins of D2 inter-radial membranes mostly black, some white; caudal fin bluish proximally and blackish distally; anal fin transparent; pectoral fin bluish; pelvic fin whitish.

Ground colour of preserved specimens light to dark brown; dorsal blotches and spots on head no longer visible; occasionally with spots on pectoral fin base; D1 mostly dusky with small, bluish spots, occasionally white streaks present; D2 dusky with white spots similar to above; caudal fin dusky; anal, pelvic and pectoral fins transparent.

Distribution. Arabian Gulf to west coast of India. In the vicinity of Bombay, *Boleophthalmus dussumieri* is sympatric with *B. boddarti*.

Remarks. The holotype of *Boleophthalmus chamiri* Holly (NMW 13804) was not available to me. Based on the original description and subsequent figure (Holly, 1929b), it is synonymous with *B. dussumieri*.

Etymology. Named in honor of Mssr Dussumier who collected material for the original description.

Boleophthalmus pectinirostris (Linnaeus)

Pl.1F; Figs 8, 13-14; Tables 9-16

Gobius pectinirostris Linnaeus, 1758: 264 (type locality, Canton).
Apocryptes pectinirostris.-Valenciennes *in* Cuvier & Valenciennes, 1837: 150 (new combination).
Boleophthalmus pectinirostris.-Richardson, 1845: 209 (new combination).
Apocryptes polyophthalmus Günther, 1867: 117 (type locality, China).

Material examined (112 specimens from five general localities; size range 38-155): SABAH: USNM 139356, 1:71. TAIWAN: BMNH 1909.4.28:20, 1:108; NTM S.11173-001, 2:142-145; SU 18282, 2:104-109; SU 182811, 3:72-80; USNM 179158, 4:82-90; USNM 276535, 3:97-103. HONG KONG: ANSP 76626, 3:97-110; SU 27990, 9:98-104; SU 32820, 1:93; SU 39613, 6:74-81. CHINA: AMNH 17768, 1:65; AMNH 35865, 24:38-78; ANSP 77010, 2:72-73; ANSP 95624, 2:61-65; ANSP 123267, 4:75-83; BMNH 1867.2.23:11-12, 1:101; BMNH 1927.1.5:6, 1:79; SU 25481, 2:81-94; SU 28187, 4:46-58; SU 30254, 3:62-70; SU 34029, 3:60-63; SU 56340, 6: 101-107; USNM 85844, 2:76-144; USNM 86377, 5: 48-77 JAPAN: AMNH 34928, 1:141; AMS IB.961, 3: 99-102; AMS I.20360-001, 5:114-155; ANSP 126301, 1:147; SU 6589, 2:109-115; SU 6620, 2:111-137; USNM 49887, 1:110. Additionally one lot (USNM 12567, 3: 112-122) marked only as "East Indies".

Diagnosis. Total elements in D2 23-26 (mean = 24.8); caudal fin length 18.3-22.2% SL (mean = 20.2%); head length 24.3-28.0% SL (mean = 26.0%); length of D2 base 41.5-46.1% SL (mean = 43.4%); first D2 element usually segmented and branched; longitudinal scale count 84-123 (mean = 104.1); predorsal scales 26-48 (mean = 33.9); lower jaw teeth notched.

Colouration (based upon a photograph of a 130 mm SL individual in Masuda *et al.*, 1984:257, fig.D, reproduced herein as Pl. 1F). Background colour greenish grey; numerous small, white spots on head; few widely separated, larger white spots on body; numerous small, white spots on greenish grey D1 in combination with a few slightly larger, black spots with 5 large, white spots basally on fin; D2 greenish grey with columns of 6-8 white spots or dashes on membranes, basally on fin 3 black spots each sandwiched by large white spots; caudal fin greenish grey with numerous, small white spots; anal fin with orange tint proximally, distally transparent; pelvic fin dusky; pectoral fin proximally bluish with small dusky spots and distally dusky.

Ground colour of preserved specimens off white to tan or brown; dorsal and caudal fins bluish, all others light brown; spotting pattern described above for head, body and fins retained except body spots sometimes lost; some specimens show remnants of 1-4 diagonal bands directed anteriorly from dorsum on posterior part of body; some specimens with large, dark brown spots on head.

Distribution. Taiwan, China and Japan. A lot

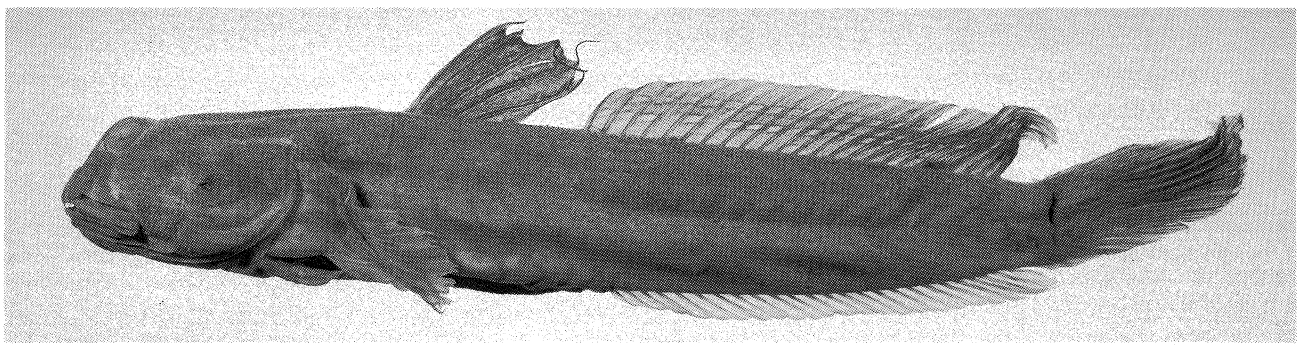

Fig.13. *Boleophthalmus pectinirostris*, AMNH 35865, 77 mm SL, Foochow, China.

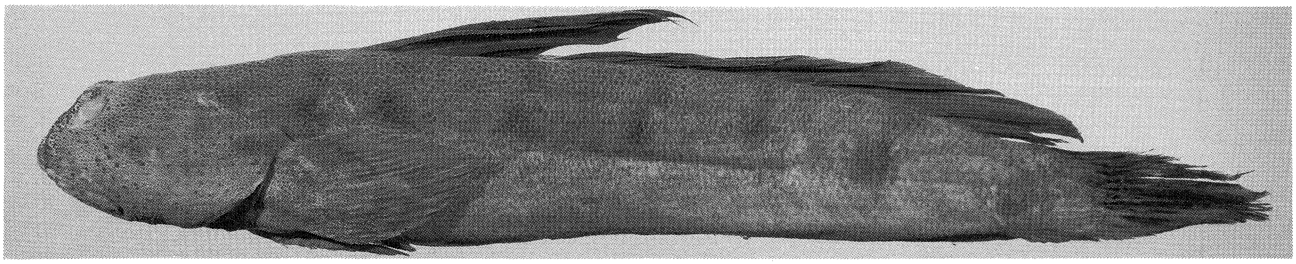

Fig.14. *Boleophthalmus pectinirostris,* NTM S.11173-001, 143 mm SL, Taiwan.

reportedly from Sabah (USNM 139356) represents the only record of *B. pectinirostris* from south of 20°N, thus, the locality reliability is questioned considering the distribution of conspecifics.

Remarks. *Gobius pectinirostris* was described from Magnus Lagerstrom's fish collection containing many, possibly all, of the specimens collected by Pehr Osbeck which is why Linnaeus (1758:264) cited both "Chin. Lagerstr." and "Osbeck iter.". Linnaeus' description of *Gobius pectinirostris* contained only some fin ray counts, which were derived from an earlier publication (Linnaeus, 1754, on Lagerstrom's Chinese fish collections), some branchiostegal and fin ray counts attributed to Osbeck, and the following (translated in its entirety): "lower jaw teeth horizontal". The fin ray counts and nature of the teeth are characteristic of several genera of oxudercines. This 1758 description of *G. pectinirostris* is inadequate and has, consequently, led to confusion regarding the proper assignment of this species. The first description was probably in J.L. Odhelius' "dissertation" *S. N. A Specimen Academicum, sistens Chinensia Lagerstromiana* (1754:25), written by Linnaeus and defended by Odhelius. The subsequent reprint of this work (Linnaeus, 1759) includes a figure (p. 260, fig. 3). A probable type (L.S. 106 according to Fernholm & Wheeler, 1983) is at the Zoological Institute of the University of Uppsala and was examined for me by A. Wheeler.

Etymology. The trivial name, *pectinirostris,* is presumably from *pecten,* Latin for comb, and *rostrum,* Latin for snout.

Oxuderces

Fig. 1; Tables 1-8

Oxuderces Eydoux & Souleyet, 1848: 182 (type species, *Oxuderces dentatus* Eydoux & Souleyet, 1848 by original designation).
Apocryptichthys Day, 1876: 302, pl. 17, fig. 7 (type species, *Apocryptichthys cantoris* Day, 1876 by original designation).

Included species. Two species (*dentatus* and *wirzi*) are found in mudflat areas, the former from Indo-Malaya to China and the latter from Australia and New Guinea.

Diagnosis. The genus is unique amongst the subfamily in possessing a fang-like, canine tooth on each side of the premaxillary symphysis, in having the anterior ceratohyal lengthened posterior to insertion of the fourth branchiostegal, and in its anteriorly depressed head.

Description. Spinous dorsal fin VI; second dorsal fin 24-31 (dorsal fins connected basally by membrane); spinous dorsal fin pterygiophore formula: 3-12210; base of sixth spine positioned about midway between bases of fifth spine and first ray of second dorsal fin; interspinous spaces 3 and 4 about equal and larger than 1 and 2 that are also about equal to each other; fourth or fifth spine is longest fin element; spinous dorsal fin about same height as second dorsal fin; large, blue or black ocellus posteriorly on second dorsal fin.

Anal fin 24-30, all rays segmented and branched; insertion of terminal anal fin ray slightly anterior to a vertical from insertion of terminal second dorsal fin ray.

Pectoral fin 20-25, medial rays longest.

Pelvic fin I,5, joined by membrane with fin of opposite side to form cup; frenum well developed.

Caudal fin lanceolate, with 17 segmented rays, 15 or 17 of them branched; 1-6 dorsal procurrent rays and 1-5 ventral procurrent rays.

Scales cycloid, extending from anterior portion of caudal fin to axil of pectoral fin in some, to orbit in others; no scales on snout or isthmus; largest scales posteriorly; longitudinal scale count 59-88; TRF 17-26; TRB 16-25; TRDB 19-25; predorsal scales 0-44.

Gill opening restricted, extending from a point anterior to pelvic fin base to a horizontal with fifth ventralmost pectoral fin ray.

Teeth in a single row in both jaws; 15-40 teeth in upper jaw along with one enlarged and very prominent canine tooth lateral to the symphysis; lower jaw with 12-49 teeth; teeth in lower jaw slightly larger than those of upper jaw; recurved canine tooth on each side of symphysis internal to anterior margin of lower jaw in one species.

Gape large; posterior tip of maxilla reaching well beyond a vertical with posterior margin of eye; anterior nostril at tip of pendulous flap that overlies upper jaw.

No membrane (dermal cup) covering ventral portion of eye; anterior to each eye is posterior nostril; anterior oculoscapular pore anteromedial to posterior nostril; single, large interorbital pore. No cutaneous papillae system.

Eight rudimentary gill rakers on ventral limb; gill filaments feather like.

Etymology. The generic name *Oxuderces* is from the Greek, *oxyderkes,* sharp sighted, referring to the prominent eyes; masculine gender.

Key to the Species of *Oxuderces*

1. Second dorsal fin with 24-27 total elements; second dorsal and anal fins not connected to caudal fin.(India, Malaysia, Thailand, Indonesia, Macao, China)...........*O. dentatus* Eydoux & Souleyet

—— Second dorsal fin with 29-31 total elements; second dorsal and anal fins connected to caudal fin. (Papua New Guinea, Australia)..*O. wirzi* (Koumans)

Oxuderces dentatus Eydoux & Souleyet

Pl. 1G; Figs 15-16; Tables 9-16

Oxuderces dentatus Eydoux & Souleyet, 1848: 182 (type locality, Macao).
Apocryptes nexipinnis Cantor, 1850: 1170 (type locality, Sea of Penang).
Apocryptichthys cantoris Day, 1876: 302, pl. 17, fig. 7 (type locality, Madras).
Apocryptichthys sericus Herre, 1927: 264, pl. 21, fig. 1 (type locality, Amoy, China).
Apocryptichthys pelligrini Wu, 1931: 48, fig. 8 (type locality, Chinese coast).
Apocryptichthys livingstoni Fowler, 1935: 162, figs 131, 132 (type locality, Paknam, Thailand).

Material examined. (51 specimens from 5 general localities; size range 22-93): INDIA: AMS B.8336, 1:46. MALAYSIA: FMNH (uncatalogued), 11:22-44; USNM 279359, 27:22-49. THAILAND: ANSP 63091, holotype of *Apocryptichthys livingstoni* Fowler, 73; USNM 119547, 1:68. JAVA, INDONESIA: BMNH 1932.6.20:18, 1:70. MACAO: MNHN A.1822 (holotype), female, 75; SU 61139, 1:76. CHINA: SU 25524, 1:65; USNM 85846, 2: 80-82; USNM 86378, 2:57-67; USNM 86954, 2:81-93.

Diagnosis. Total D2 elements 24-27 (mean = 25.9); total anal fin elements 24-26 (mean = 25.5); second dorsal and anal fins unattached to caudal fin; 15 branched caudal fin rays; predorsal scales 22 or fewer, often lacking; no canine teeth internal to symphysis of lower jaw; teeth in both jaws caninoid with blunt tips, none bilobed; pore situated in middle of interorbital region; basihyal spatulate.

Colouration (based on a freshly dead, 44 mm SL specimen from Malaysia, FMNH uncatalogued). Head and trunk greyish blue; 7 greyish blue spots along lateral midline starting at a point equal to origin of first dorsal fin and ending at a point equal to about 75% of the length of D2; a suffusion of shiny, bluish scales on posterior half of trunk; 6 dusky, saddle-like blotches on dorsum starting at terminus of D1 with 4 across the base of D2 and 1 on caudal peduncle; D1 translucent; D2 translucent except for a thin, faint dusky stripe through the median part of fin and a large, black ocellus near distal tips of last 4 rays; caudal, anal and pelvic fins translucent; pectoral fin translucent but with a large, dusky blotch on upper base; nape with dusky reticulations; anterior nostril with a black anterior margin; venter shiny white.

Ground colour of preserved specimens light brown or grey. Older material typically completely faded. In recently preserved material, 5-7 midlateral dusky spots; large, dusky blotch on pectoral base; posterior portion of upper jaw and anterior nostril blackened; no markings on fins except for a remnant of the dusky blotch distally on the posteriormost second dorsal fin rays.

Based on Chatterjee (1981), a preserved specimen from India was light violet with brown spots on the sides of head. Wu (1931) mentioned that his Chinese specimen had a bluish throat and abdomen with a black line on the upper lip. Herre (1927) mentioned seven or eight dorsal crossbands posteriorly on his Chinese material.

Ecology. *Oxuderces dentatus* inhabits intertidal mudflats, living within the muddy benthos. During low tide in Malaysia, I observed subadults slithering through the muddy sediment with just a thin surface film of water above them through which they would occasionally poke their heads. They are frequently associated with subadult *Scartelaos.*

Distribution. Shallow mudflats in India, Malaysia, Thailand, Indonesia, Macao and China.

Remarks. All synonyms, except for *Apocryptes nexipinnis,* were first determined by Springer (1978). Wu (1931) and Springer (1978) drew attention to a possible affinity between *As. nexipinnis* and *Oxuderces.* Although

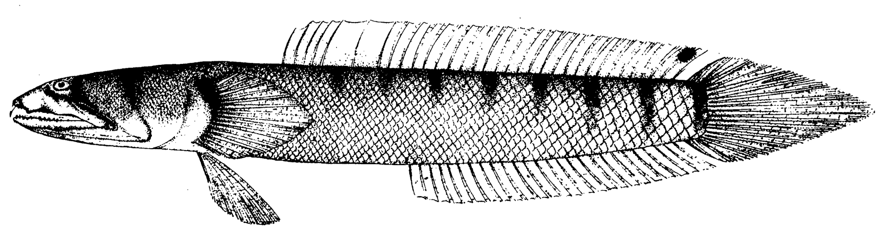

Fig.15. *Apocryptichthys sericus* (= *Oxuderces dentatus*) after Herre (1927).

no type material of *A. nexipinnis* was examined (types exist only as skins at the BMNH and are too fragile to be lent), it is possible to assign *A. nexipinnis* as a junior synonym of *O. dentatus* based on the original description.

Etymology. The trivial name, *dentatus,* from the Latin for toothed in reference to the prominent canine teeth of the upper jaw.

Oxuderces wirzi (Koumans)

Figs 16-17; Tables 9-16

Apocryptodon wirzi Koumans, 1938: 26 (type locality, Papua New Guinea).

Material examined. (33 specimens from 2 general localities; size range 24-105): PAPUA NEW GUINEA: NHB 4218 (holotype), female, 74. AUSTRALIA: AMS IB.7146, 1:98; AMS I.15552-017, 1:47; AMS I.15557-229, 2: 99-103; AMS I.21220-004, 1:67; AMS I.21816-002, 4: 58-69; AMS I.23943-007, 4:57-64; NTM S.10020-007, 1:24; NTM S.10076-001, 1:51; NTM S.10078-002, 1:67; NTM S.10649-001, 2:82-87; NTM S.10727-002, 12: 28-85; QM I.10631, 1:69; QM I.20682, 1:105.

Diagnosis. Total D2 elements 29-31 (mean = 29.9); total anal fin elements 27-30 (mean = 28.9); second dorsal and anal fins basally connected with caudal fin; 17 branched caudal rays; predorsal scales 26-44 (mean = 32.9); 2 recurved, canine teeth internal to symphysis of lower jaw; bifid teeth usually present in lower jaw, sometimes in both jaws; pore situated posteriorly in interorbital region; basihyal bifid.

Colouration. No colour notes or photographs of live or freshly dead individuals available. Helen Larson (in literature) stated that *Oxuderces wirzi* has yellow jaws and a peacock-blue ocellus on the second dorsal fin when live.

Ground colour of recently preserved specimens yellowish brown ventrally, greenish brown dorsally; midlaterally, a discontinuous blue-grey band which curves ventrally at posterior quarter of D2 and continues onto caudal fin base; dorsal portion of trunk with small, brown spots; 4-7 large, dark blue markings on cheeks and operculae; dark blue bar or spots on pectoral base; prominent dark blue ocellus distally on posteriormost 2-3 rays of D2, same region of anal fin with a slight duskiness; posterior third of D2 with dusky mottling; pectoral fins occasionally with small, dusky spots ventrally; except as noted above, all fins transparent; juveniles have 8-10 dusky bars on dorsal region of trunk, 3-4 bars occasionally observed posteriorly on adults.

Distribution. Mud and sand bottoms at river mouths in northern Australia and Papua New Guinea.

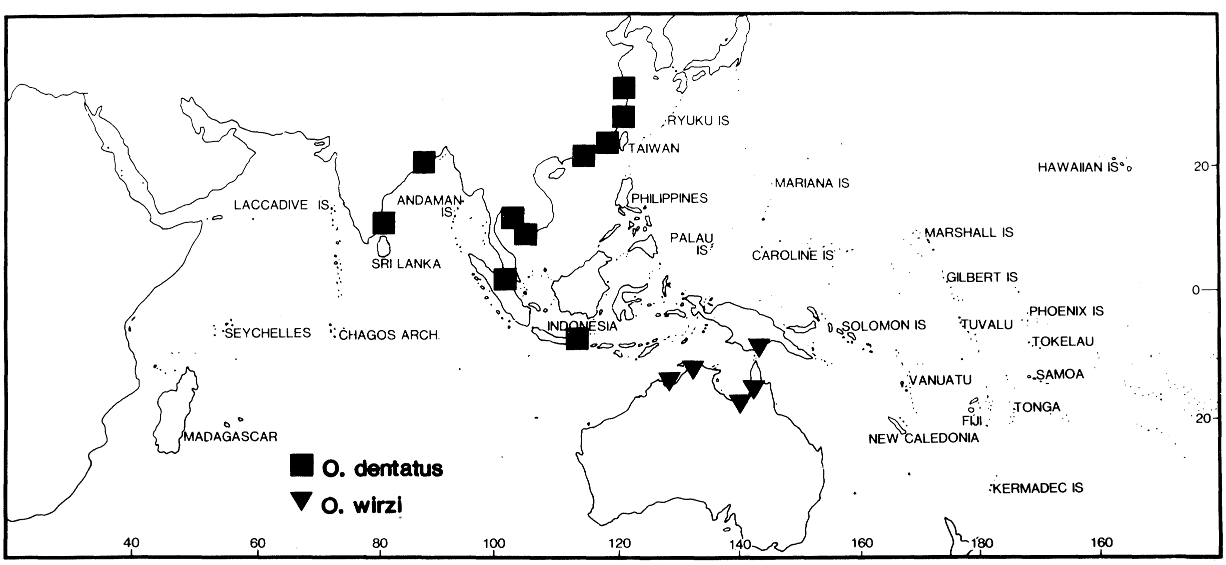

Fig.16. Known localities of *Oxuderces* based on examined material.

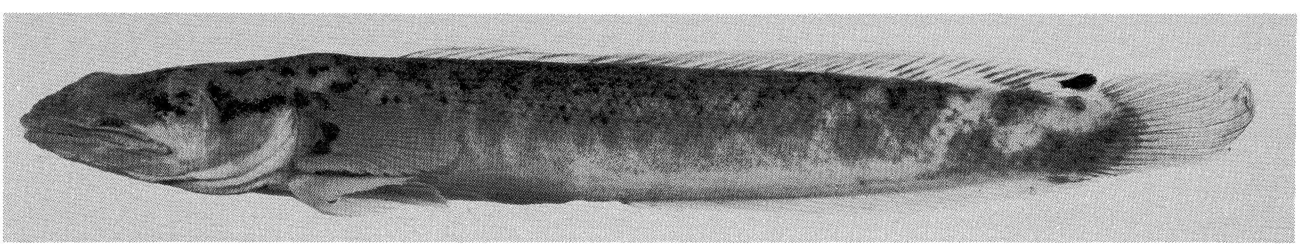

Fig.17. *Oxuderces wirzi,* NTM S.10727-002, 77 mm SL, Northern Territory, Australia.

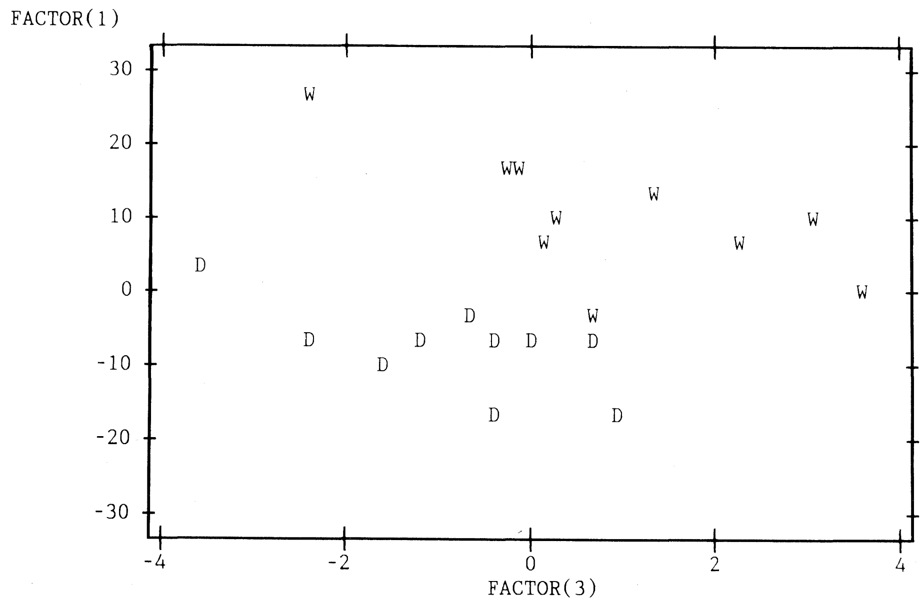

Fig.18. PCA discriminating *Oxuderces dentatus* (D) from *O. wirzi* (W) based on characters listed in text.

Remarks. Based on independent group t-tests, significant differences exist at the p=.05 level between *Oxuderces dentatus* and *O. wirzi* in the following meristic and morphometric features: in second dorsal and anal fin elements, in upper and lower jaw tooth counts, in lengths of spinous and second dorsal fin bases, and in length of anal fin base. These differences are expressed graphically by PCA (Fig. 18).

Etymology. The trivial name, *wirzi,* is in honor of Dr P. Wirz who collected the holotype.

Parapocryptes

Fig. 1; Tables 1-8

Parapocryptes Bleeker, 1874: 299 (type species *Apocryptes macrolepis* Bleeker, 1851a, by original designation).

Included species. Two species (*Parapocryptes rictuosus* and *Pa. serperaster*) are found in mudflat areas, the former along the east coast of India and the latter from the Ganges Delta to China.

Diagnosis. The genus is unique amongst oxudercines in possessing a greatly expanded distal head of the fourth epibranchial.

Description. Spinous dorsal fin VI; second dorsal fin I, 25-28 (dorsal fins typically connected by a basal membrane); spinous dorsal fin pterygiophore formula: 3-12210, occasional variant with only 5 first dorsal fin spines and formula of 3-11210; second dorsal fin base terminates within 2 scales of caudal fin; appressed second dorsal fin overlaps dorsal procurrent rays; height of both dorsal fins moderate, spinous dorsal fin slightly higher than second dorsal fin.

Anal fin 25-29; insertion of last ray at a vertical with insertion of last ray of second dorsal fin; anal fin base terminates within 2 scales of caudal fin; appressed anal fin overlapping ventral procurrent rays; height of anal fin approximately equal to that of second dorsal fin.

Pectoral fin 19-23, medial rays longest. Pelvic fin I,5, united by membrane with fin of opposite side; frenum well developed.

Caudal fin lanceolate, with 17 segmented rays, 15 of them branched; dorsal procurrent rays 5-6, ventrally 4-5.

Scales cycloid, covering practically whole body except for snout and most of ventral surface of head; scale rows irregular, difficult to count with precision; longitudinal scale count 62-94; TRF 16-26; TRB 15-26; TRDB 17-23; predorsal scales 23-38. Gill opening slightly more than length of pectoral fin base both dorsally and ventrally.

Teeth in both jaws in a single row; 23-56 caninoid teeth in upper jaw with bluntly rounded tips; 4-6 anteriormost teeth largest, but only slightly overlapping lower jaw, if at all and not prominent when jaws closed; posterior teeth small and extend to rictus; 23-44 subequal caninoid teeth in lower jaw, anterior symphyseal area lacking teeth; 1 recurved, canine tooth on each side of symphysis internal to anterior margin of lower jaw.

Gape moderate, posterior tip of maxilla extending to a point equal to a vertical from posterior margin of eye; anterior nostril at tip of pendulous flap overlapping upper jaw laterally.

No membrane (dermal cup) covering ventral half of eye; posterior nostril just anterior to eye margin; anterior oculoscapular pore anteromedial to posterior nostril, about one half eye diameter from margin of upper lip; posterior pore(s) either a single pore posteriorly in interorbital region or 2 pores located on either side of nape anteriorly. Cutaneous papillae system greatly reduced.

Ventral portion of first gill arch without gill rakers; gill filaments feather like.

Etymology. The generic name, *Parapocryptes,* is from the Latin *par,* equal manner, and *Apocryptes,* another genus in the subfamily, in reference to these fishes being very similar; masculine gender.

Key to the Species of *Parapocryptes*

1. In most specimens, floor of mouth and tongue with many small, black flecks; 2 small pores anteriorly on nape; caudal fin extemely long, usually greater than 27% SL; longitudinal scale count more than 80; body depth less than 12% SL. (east coast of India)..*Pa. rictuosus* (Valenciennes)

—— No black pigment inside mouth; a single, large pore posteriorly in interorbital region; caudal fin not greatly lengthened, caudal fin length usually less than 26% SL; longitudinal scale count typically fewer than 80; body depth typically greater than 12% SL. (Ganges Delta eastward to China and Indonesia)..*Pa. serperaster* (Richardson)

Parapocryptes rictuosus (Valenciennes)

Figs 19-20; Tables 9-16

Apocryptes rictuosus Valenciennes *in* Cuvier & Valenciennes, 1837: 151 (type locality, Pondichery, India).

Material examined. (7 specimens from 3 localities; size range 52-106): INDIA: Bengal: AMS B.8356, 1:55. Madras: USNM 279317, 2:52-78; Pondicherry: MNHN A.1444 (paratypes), 3:79-98; MNHN A.1445 (holotype), male, 106.

Diagnosis. In most specimens, floor of mouth and tongue with many black flecks; 2 small pores anteriorly on nape; caudal fin extremely long, caudal fin length 26.6-32.5% SL (mean = 30.1); longitudinal scale count 81-94 (mean = 87.7); body depth 8.3-11.6% SL (mean = 9.8%); head depth 8.9-11.5% SL (mean = 9.9%); head width 8.3-11.2% SL (mean = 9.5%); TRF 16-19 (mean = 17.4); TRB 16-20 (mean = 17.8); predorsal scales 32-40 (mean = 35.9).

Colouration. No colour notes or photographs available of live or freshly dead individuals.

Ground colour of preserved specimens brown, paler

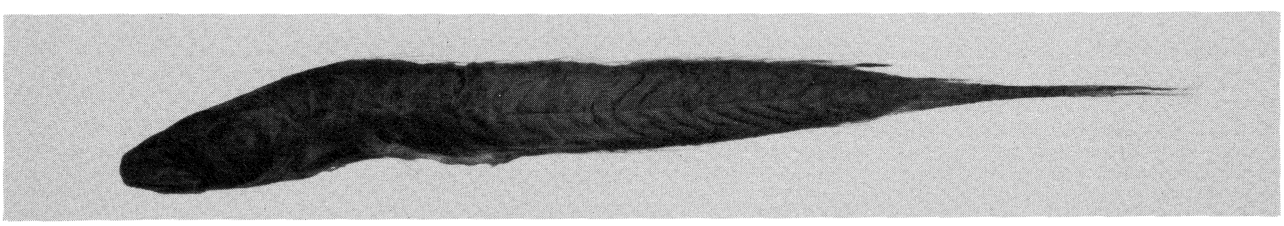

Fig.19. *Parapocryptes rictuosus,* AMS B.8356, 55 mm SL, India.

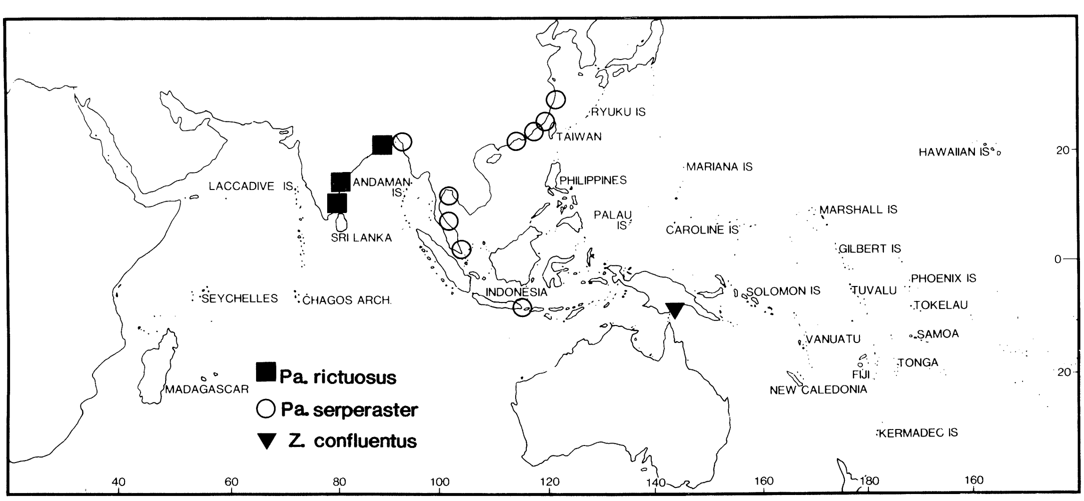

Fig.20. Known localities of *Parapocryptes rictuosus, Pa. serperaster* and *Zappa confluentus* based on examined material.

ventrally than dorsally; no markings on head or trunk except for small, brown spots on pectoral base; remnant of a dusky blotch posterodorsally on D2; faint brown bands proximally on caudal fin; other fins translucent.

Distribution. This species is only known from the east coast of India. In the Ganges Delta, *Pa. rictuosus* is sympatric with *Pa. serperaster*. No information available on habitat preference.

Etymology. The trivial name, *rictuosus,* is from the Latin *rictus,* open mouth, and *osus,* having the nature of, referring to the wide gape.

Parapocryptes serperaster (Richardson)

Figs 20-21; Tables 9-16

Apocryptes serperaster Richardson, 1845: 206 (type locality, Macao).
Apocryptes henlei Bleeker, 1849: 37 (type locality, Surabaya, Java).
Apocryptes macrolepis Bleeker, 1851a: 66 (type locality, Bandjermassing, Kalimantan, Indonesia).
Parapocryptes cantonensis Herre 1932: 441 (type locality, Canton).
Boleophthalmus smithi Fowler 1934: 160 (type locality, Bangkok).

Material examined. (150 specimens from 6 general localities; size range 35-173): INDIA: SU 3477, 1:116. THAILAND: ANSP 60020, holotype of *Boleophthalmus smithi* Fowler, 148; ANSP 60023, 1:103; ANSP 62962-10, 49:47-163; ANSP 63011-14, 4:59-82; ANSP 63015-18, 4:67-83; ANSP 63019, 1:138; USNM 103364, 1:159; USNM 119621, 1:62; USNM 119622, 2:72-140; USNM 119623, 2:137-149; USNM 119624, 1:72; USNM 119625, 4:76-101; USNM 119626, 2:97-105; USNM 119627, 1:134; USNM 119628, 3:51-89; USNM 119989-90, 5:89-173. SINGAPORE: SU 33148, 1:35. INDONESIA: RMNH 4547, syntypes of *Apocryptes henlei* Bleeker, 2:92-109. CHINA: AMNH 13626, 2:52-63; AMNH 17793, 5:41-79; AMNH 18590, 15:73-81; AMNH 35868, 4:80-104; BMNH 1965.8.12:51 (holotype), male, 115; SU 4718, 4:76-97; SU 25721, holotype of *Parapocryptes cantonensis* Herre, 91; SU 25722, paratypes of *Parapocryptes cantonensis* Herre, 10:70-89; SU 30263, 5:58-76; UMMZ 167382, 1:90; USNM 117791, 1:53; USNM 130436, 8:81-123. MACAO: CAS 51207, 2:94-104; SU 61279, 5:63-98.

Diagnosis. No black pigment inside mouth; a single large pore posteriorly in interorbital region; caudal fin not greatly lengthened, caudal fin length 19.4-26.7% SL (mean = 23.0); longitudinal scale count 62-81 (mean = 71.9); body depth 10.5-16.5% SL (mean = 13.9%); head depth 9.8-14.4% SL (mean = 11.8%); head width 9.9-14.4% SL (mean = 11.9%); TRF 20-26 (mean = 22.2); TRB 15-26 (mean = 20.5); predorsal scales 23-38 (mean = 31.4).

Colouration (based on a photograph of an aquarium specimen appearing in Hunziker, 1985). Background colour greenish yellow; 5 large, midlateral, longitudinally ovoid, brown spots, anteriormost ventral to D1, posteriormost on caudal peduncle; 5 dark brown, saddle-like blotches on dorsum - first at D1 origin, second between D1 and D2, third and fourth at D2 base and fifth at D2 terminus; D1 and D2 basally yellow, elements proximally green with transparent membranes; caudal fin dusky with a yellow dorsal and ventral margin; anal fin hyaline; pectoral fin base with some small red spots, proximally yellow with red and yellow ventroposterior margin; pelvic fin yellow.

Ground colour of preserved specimens pale brown; midlateral spots retained, however, not as large as figured by Bleeker (1983); additionally, brown spot dorsal to pectoral base; 4-5 bands crossing mid-dorsal region, 1 or 2 cross D1 base, 3 cross D2 base and occasionally connect to midlateral spots; nape and sides of head with irregular, brown blotches and/or lines; small, brown spots on pectoral base; black distal margin on D1; distal half of D1 and D2 dusky; caudal fin dusky, blackish ventrally; anal fin blackish posteriorly; pelvic fins translucent; pectoral fins medially dusky.

Distribution. Ganges Delta eastward to China and Indonesia. Herre (1953) reported a specimen from the northwest coast of Luzon, Philippines and Koumans (1953) reported specimens from the Andaman Islands and Sri Lanka; specimens upon which these reports are based were not located.

Remarks. Koumans (1953) reported that type material of *Apocryptes macrolepis* Bleeker was lost; this was confirmed by M. van Oijen (personal communication) of RMNH. The original description and figure of *As. macrolepis* are sufficient to synonymise it with *Parapocryptes serperaster.* Although Koumans (1953) recognised *As. henlei* as a distinct species, he indicated doubt that the diagnostic differences cited (D1 membrane reaching base of D2 versus not reaching and body with blotches versus without) were of specific value. I do not

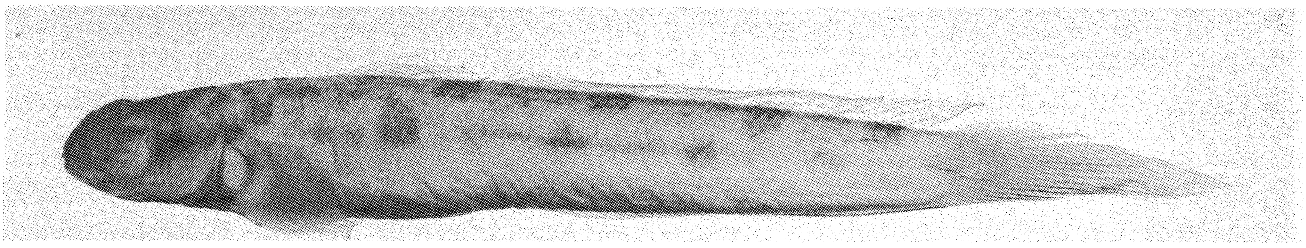

Fig.21. *Parapocryptes serperaster,* SU 61279, 73 mm SL, Hong Kong.

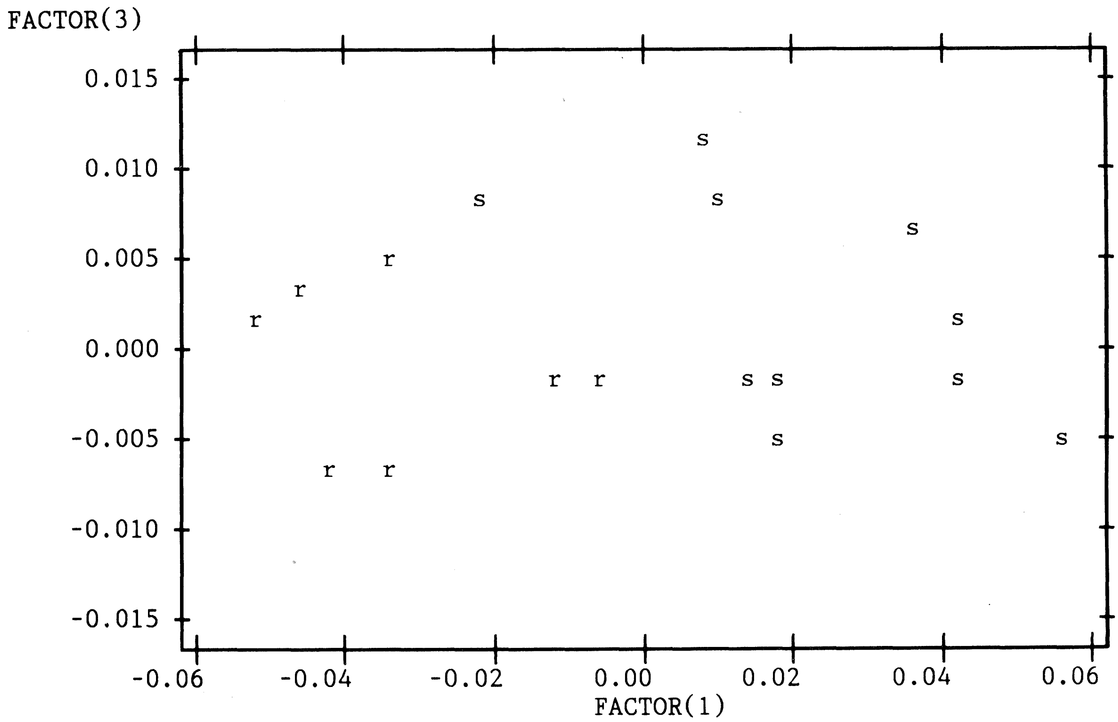

Fig.22. PCA discriminating *Pa. serperaster* (s) from *Pa. rictuosus* (r) based on characters listed in text.

believe Koumans' characters warrant recognition at the species level, because the former seems insignificant and the latter may be a preservation artifact. Therefore, I synonymise *As. henlei* with *Pa. serperaster*.

Based on independent group t-tests, significant differences exist at the p=.05 level between *Pa. rictuosus* and *Pa. serperaster* in the following meristic and morphometric characters: longitudinal scale count, predorsal scales, upper and lower jaw teeth, TRF, head width, body depth, head depth and least depth of caudal peduncle. These differences are expressed graphically by PCA (Fig. 22).

Etymology. The trivial name, *serperaster,* is from the Latin *serpo,* creeping, and *rastrum,* splints, an allusion to this fish's movement on the mudflat.

Periophthalmodon

Fig. 1; Tables 1-8

Periophthalmodon Bleeker, 1874: 326 (type species *Periophthalmus schlosseri* Valenciennes, 1837 [= *Gobius schlosseri* Pallas, 1770] by original designation).

Included species. Three species are placed in *Periophthalmodon: Pn. freycineti* from northern Australia, eastern Indonesia, and the Philippines; *Pn. schlosseri* from Thailand, Strait of Malacca, Java, Sarawak and Kalimantan; and *Pn. septemradiatus* from the Bay of Bengal, Gulf of Thailand, and Sarawak.

Diagnosis. This genus is unique among oxudercines in possessing two rows of teeth in the upper jaw, and in having a black stripe (brown in preservative) coursing posteriorly from the eye to the caudal peduncle.

Description. Spinous dorsal fin IV-XV; second dorsal fin I, 10-13 or 11-14; dorsal fins not connected by membrane; spinous dorsal fin pterygiophore formula variable but always with 3 or 4 pterygiophores in the fourth interneural space (Table 25); second dorsal fin terminates within 9 scales of caudal fin; appressed second dorsal fin not reaching caudal fin.

Anal fin I, 9-13 or 10-12; insertion of last ray at a vertical with insertion of last ray of second dorsal fin; anal fin spine very small; anal fin base terminates within 12 scales of caudal fin; appressed anal fin far short of reaching caudal fin; height of anal fin about one third that of second dorsal fin.

Pectoral fin 12-19, medial rays longest.

Pelvic fin I, 5, united by membrane with fin of opposite side, frenum well developed.

Caudal fin elongate and rounded, with 14-17 segmented rays, 13-15 of them branched; dorsal procurrent rays 6-9, ventrally 9-10.

Scales cycloid, covering whole body except for isthmus or snout in some species; scales large and firm, and in nearly regular rows that extend onto caudal fin;

longitudinal scale count 47-57; TRF 12-17; TRB 12-16; TRDB 11-15; predorsal scales 16-26. Gill opening restricted; extending from a point slightly ventral to ventral terminus of pectoral fin base to about three quarters of length of pectoral fin base; additional flap of skin on gill cover along its posterior surface.

Teeth in upper jaw in 2 rows, 1 row of 16-35 caninoid teeth spans entire jaw with 4 anteriormost enlarged canine teeth, internal to this row is a second row of 3-11 very small caninoid teeth; 16-26 stout canine teeth in single row of lower jaw, lower jaw teeth larger than all but the largest canine teeth of upper jaw; no large, recurved, canine teeth internal to symphysis of lower jaw.

Gape moderate, posterior tip of maxilla extending to a point slightly anterior to a vertical from posterior margin of eye; anterior portions of upper and lower lip internally papillose, upper lip more so; posterior portion of upper lip expanded such that rictus is covered even when mouth is slightly agape; when jaws closed, upper lip completely covers teeth of both jaws; fold of skin overlying most of upper lip, on each side of this fold is the anterior nostril at the tip of a pendulous flap.

Eyes erectile, dermal cup at base of eye; fleshy ridge located anterior to eyes across midline; posterior nostril not prominent, located just anterior to eye at posterolateral portion of fleshy ridge; no pores on head.

Ventral portion of first gill arch with 5 or fewer rudimentary gill rakers; gill filaments thread like.

Etymology. The generic name, *Periophthalmodon,* is from the Latin suffix, *odon,* toothed, and *Periophthalmus,* another genus in the subfamily, in reference to the prominent teeth and superficial similarity of the two genera; masculine gender.

Key to the Species of *Periophthalmodon*

1. Pectoral fin rays typically 13 or 14, rarely 12 or 15; isthmus completely scaled; pelvic fins separate. (Ganges Delta, Burma, Thailand, Sarawak)....................*Pn. septemradiatus* (Hamilton)

— Pectoral fin rays typically 15-17; isthmus lacking scales; pelvic fins completely united into a disk...2

2. Spinous dorsal fin IV, rarely V; length of D1 base less than 10% SL. (northern Australia, Timor, Halmahera, Philippines) ....*Pn. freycineti* (Valenciennes)

— Spinous dorsal fin modally VIII-IX, rarely VI or VII; length of D1 base greater than 10% SL. (Thailand, Malaysia, western Indonesia)................................*Pn. schlosseri* (Pallas)

Periophthalmodon freycineti (Valenciennes)

Figs 23-25; Tables 17-25

Periophthalmus freycineti Valenciennes *in* Cuvier & Valenciennes, 1837: 197 (type locality, Timor).
Periophthalmus australis Castelnau, 1876: 22 (type locality, Queensland, Australia).
Periophthalmodon schlosseri freycineti.-Eggert, 1935: 50 (new combination).
Periophthalmus weberi Eggert, 1935: 56 (type locality, Lorentz River, Irian Jaya, Indonesia), in part.

Material examined. (39 specimens from 6 localities; size range 74-210): BURMA: AMS IB.7480, 3:125-168. PHILIPPINES: USNM 102663, 2:84-88. INDONESIA: Halmahera: USNM 243430, 1:124; USNM 243431, 1:128; USNM 243453, 1:92; USNM 243454, 2:135-145; USNM 268460, 5:126-181; USNM 269246, 1:153. Irian Jaya: ZMA 112.942, syntypes of *Periophthalmus weberi* Eggert, 5:117-173. AUSTRALIA: Northern Territory: NTM S.10422-001, 1:185; NTM S.10426-001, 3: 173-212; NTM S.11171-001, 1:200. Queensland: AMS IA.7526, 1:210; ANSP 81565, 1:144; ANSP 122409, 1:169; CAS 46524, 1:195; QM I.10831, 3:181-184; ROM 38686, 2:165-198; UAMZ 6523, 1:77; UAMZ 6524, 2:74-77. Western Australia: WAM P.24252, 1:201.

Diagnosis. Pectoral fin rays 15-17 (mean = 16.0); spinous dorsal fin IV-V (mean = 4.1); length of D1 base 5.0-8.1% SL (mean = 6.3%); pelvic fins with frenum and completely united; isthmus lacking scales; snout completely scaled; dorsal fins not contiguous in adult males.

Colouration (based on a photograph of a freshly collected female, 165 mm SL, from Queensland, Australia, ROM 38686). Most of head and body bluish black with numerous white spots, venter white; D1 brown with white margin; D2 dusky brown with whitish margin; caudal fin blackish; anal fin white; pectoral fin bluish black dorsoposteriorly, brown ventroposteriorly; pelvic fin yellowish brown.

Ground colour of preserved specimens slate grey or brown laterally and dorsally, whitish ventrally; typically, no markings on head or body; 2 specimens from the Philippines (USNM 102663) have numerous white spots on the head and body as well as a brown stripe coursing from the orbit posteriorly to the caudal peduncle; 1 specimen

Fig.23. *Periophthalmodon freycineti,* UAMZ 6524, 79 mm SL, Queensland, Australia.

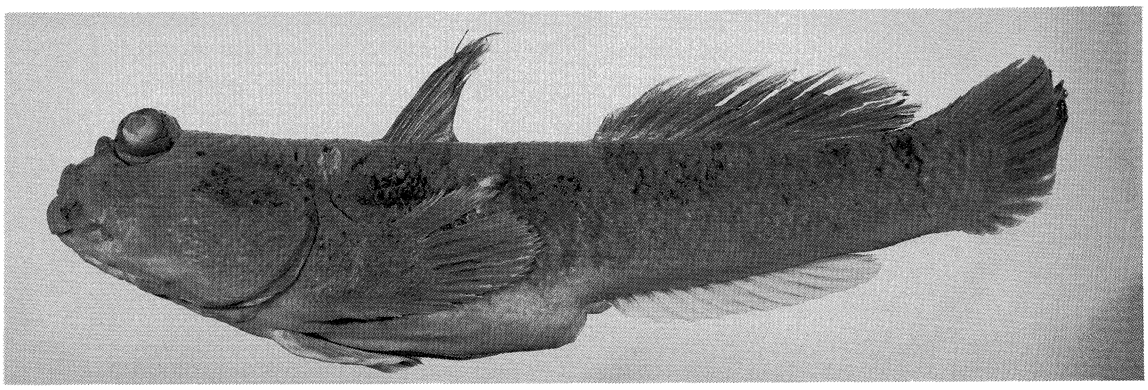

Fig.24. *Periophthalmodon freycineti,* ROM 38686, 171 mm SL, Queensland, Australia.

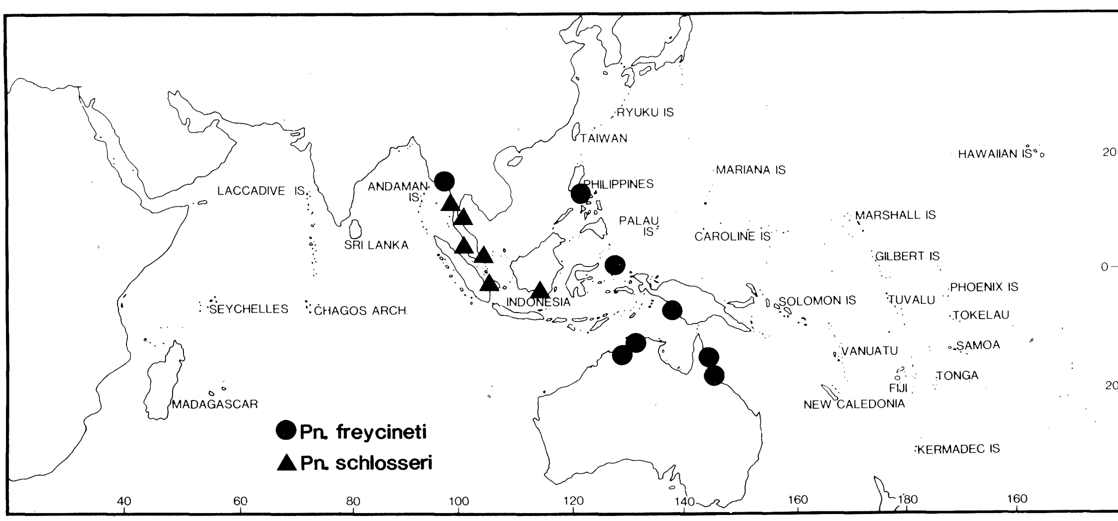

Fig.25. Known localities of *Periophthalmodon freycineti* and *Pn. schlosseri* based on examined material.

from Queensland (UAMZ 6524) showed remnants of 5, saddle-like, brown blotches dorsally, the first across D1 base, the second just anterior to D2 origin, the third and fourth across D2 base and the fifth across the caudal peduncle; in all specimens, D1 and D2 blackish with a whitish margin, caudal fin black, anal and pelvic fins flesh coloured, pectoral fins dusky.

Distribution. Specimens were examined from the Philippines, eastern Indonesia, and northern Queensland. Additionally, one lot (AMS IB. 7480) has a stated locality of Burma that I believe questionable. My data indicate that *Periophthalmodon freycineti* is not sympatric with its congener except if these supposed Burmese specimens are considered.

Remarks. Type material of *Periophthalmus freycineti* Valenciennes and *Ps. australis* Castelnau is not at MNHN and is presumed lost (M.L. Bauchot, in literature). Identification was made based on diagnostic features stated in the original descriptions.

In his description of *Periophthalmus weberi,* Eggert (1935:56) lists 19 specimens in his material examined section. Of the two lots of syntypes I examined, ZMA 112.942 (five total specimens) is assignable to *Periophthalmodon freycineti* whereas ZMA 112.939 (five total specimens) is *Periophthalmus weberi* and is discussed in that species account.

Specimens smaller than 74 mm SL were not available. A behavioral and/or ecological basis, or collecting bias may account for this absence. For instance, small specimens and large individuals may occupy different habitats as they do in *Pn. schlosseri*.

Etymology. The trivial name, *freycineti*, is in honor of Captain Freycinet who collected material for the original description.

Periophthalmodon schlosseri (Pallas)

Pl. 1H; Figs 25-26; Tables 17-25

Gobius schlosseri Pallas, 1770: 5, figs 1-4, pl. 1 (type locality, Ambon, Indonesia).
Periophthalmus ruber Bloch & Schneider, 1801: 64 (type locality, Tranquebar, India).
Periophthalmus schlosseri.-Bloch & Schneider, 1801: 64 (new combination).
Periophthalmodon schlosseri.-Bleeker, 1874: 327 (new combination).
Periophthalmus phya Johnstone, 1903: 296, fig. 1 (type locality, Jambu, Malaysia).
Periophthalmodon schlosseri argentiventralis Eggert, 1935: 49 (type locality, Jakarta, Indonesia).

Material examined. (65 specimens from 8 general localities; size range 40-210): THAILAND: Andaman Sea: ZMUC P.781612-26, 4:79-117. Gulf of Thailand: ANSP 62862, 2:164-166; CAS 46487, 9:176-199; CAS 57428, 13:94-210; LICPP 1966118, 1:107; USNM 103363, 1:165; USNM 181863, 1:184. SINGAPORE: NMBA 1920, 1:181; NMBA 1921, 1:182; SU 24060, 1:152. BORNEO: ANSP 122563, 4:123-168. INDONESIA: Kalimantan: USNM 22970, 3: 95-144; USNM 41959, 5:141-203; USNM 161010-11, 6:106-153. Sumatra: ANSP 77288, 5:183-195; ZMB 2269, 2: 143-189. MALAYSIA: Peninsular: CAS 34246, 2:161-173; FMNH (uncatalogued), 1:159; USNM 280385, 1:40; USNM 278462, 2:90-170. Sarawak: SU 33142, 3: 134-142: USNM 35728, 3:104-197.

Diagnosis. Pectoral fin rays 16-19 (mean = 17.0); spinous dorsal fin VI-IX (mean = 8.0); length of D1 base 10.3-16.7% SL (mean = 13.9); pelvic fins with frenum and completely united; isthmus lacking scales; snout completely scaled; dorsal fins not contiguous in adult males.

Colouration (based on a fresh male specimen, 159 mm SL, from Malaysia, FMNH uncatalogued). Head and trunk greenish brown; black stripe coursing from eye posteriorly across dorsal opercular edge, continuing dorsal to pectoral fin and terminating ventral to D2; 6 broad, dusky, saddle-like dorsal bars, first just anterior to D1, second across D1 base, third between D1 and D2, fourth and fifth across D2 base, and sixth across caudal peduncle; numerous white speckles on snout, cheek, opercle and trunk; D1 orange brown with pale margin; D2 dusky with median black stripe; caudal fin blackish; anal fin hyaline; pectoral fin greenish brown with some white speckles on dorsalmost rays; pelvic fins hyaline.

Ground colour of preserved specimens brown or slate grey dorsally and laterally, whitish or tan ventrally; wide, brown stripe coursing posteriorly from orbit and terminating near caudal peduncle, this stripe only seen in some specimens; silvery white speckles on snout, cheek, opercle and trunk but only in some specimens; dorsal fins blackish or dusky brown with pale margins; caudal fin blackish or dusky; 1 specimen from Thailand (USNM 181863) with anal fin blackish posteriorly.

Distribution. Specimens were examined from Thailand, Malaysia, Singapore, Indonesia and Sarawak; *Periophthalmodon schlosseri* is sympatric with *Pn. septemradiatus* in Thailand and Sarawak. Bloch & Schneider (1801) stated China as a locality for *Pn. schlosseri;* I have been unable to confirm this.

Remarks. Type material of *Gobius schlosseri* (Pallas) no longer exists (A.P. Andriashev, in literature). Identity was based on diagnostic features given in the original description and figure. Although not specified by Pallas (1770), both Gmelin (1789) and Shaw (1803) list Ambon as the type locality for *Pn. schlosseri*. Ambon is more than 10° eastward of other known occurrences of *Pn. schlosseri* and would appear to place *Pn. schlosseri* within the range of *Pn. freycineti*. Distribution limits for both species are unclear.

Type material of *Periophthalmus ruber* Bloch & Schneider does exist (ZMB 2143) and was examined for me by H.J. Paepke. *Ps. ruber* has united pelvic fins, two rows of teeth in the upper jaw, six spines in the first dorsal fin, an anal fin length equal to 20.6% SL, and is 216 mm SL. Based on these features, I concur with Eggert (1935) and Koumans (1953) in synonymising *Ps. ruber* with

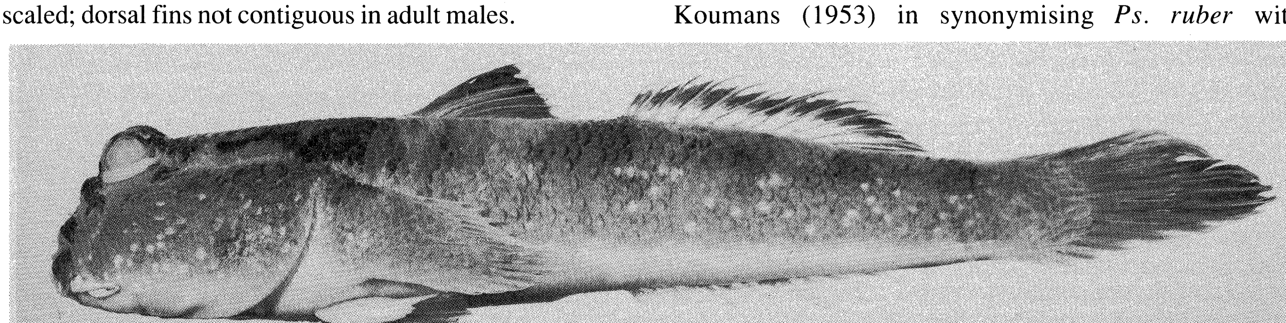

Fig.26. *Periophthalmodon schlosseri,* USNM 278462, 90 mm SL, Malaysia.

Pn. schlosseri. Bloch and Schneider listed Tranquebar as the type locality for *Ps. ruber*. This would appear to be in error, much the same as for *Ps. papilio* Bloch & Schneider (= *Ps. barbarus*) which was also listed from Tranquebar but is a west African endemic.

Type material for *Periophthalmus phya* Johnstone could not be located, however, the description and figure clearly indicate it as being equivalent to *Pn. schlosseri.*

All material of *Pn. schlosseri argentiventralis* Eggert (1935) was deposited at Universität Tübingen and destroyed during World War II (G. Mickoleit, in literature). Eggert's description is sufficient to ally his subspecies with *Pn. schlosseri.*

Macnae (1968) and Murdy (1986) provided ecological and behavioural observations of *Pn. schlosseri.*

Etymology. The trivial name, *schlosseri,* honors J.A. Schlosser who collected material for the original description.

Periophthalmodon septemradiatus (Hamilton)

Figs 27-28; Tables 17-25

Gobius septemradiatus Hamilton, 1822: 46 (type locality, near Ganges Delta).
Gobius tredecemradiatus Hamilton, 1822: 48 (type locality, near Ganges Delta).
Periophthalmus borneensis Bleeker, 1851b: 11 (type locality, Banjermassing, Kalimantan).

Material examined. (27 specimens from 4 general localities; size range 42-86): INDIA: SU 40076, 6:41-62; SU 69059, neotype, male, 60. BURMA: AMS I. 25898-001, 1:58; BMNH 1880.12.1:39-49, 3:42-56. THAILAND: MCZ 13304, 2:53-75; MCZ 56360, 4:57-76; USNM 11932, 2:53-64; USNM 179815, 2:50-53. SARAWAK: USNM (uncatalogued), 4:74-86. JAPAN (questionable locality): ANSP 11026-7, 2:55-57.

Diagnosis. Pectoral fin rays 12-15 (mean = 13.6); spinous dorsal fin IV-XV (mean = 10.4); length of D1 base 3.2-17.9% SL (mean = 12.3%); pelvic fins lack frenum and separate to fin bases; isthmus completely scaled; snout lacking scales; dorsal fins contiguous in adult males.

Colouration. No colour notes or photographs of live or freshly dead individuals available.

Ground colour of preserved specimens brown laterally, off white to tan on venter and dorsum; wide, brown stripe coursing posteriorly from orbit, passing dorsal to pectoral base and midlateral area, and terminating on caudal peduncle; on some specimens, brown stripe interrupted, replaced by brown blotches; in some specimens, cheek and opercle with brown spots and head scales with brown edges; in females, all fins pale; in males, D1 dark brown with a pale margin, D2 pale brown with pale margin, caudal fin

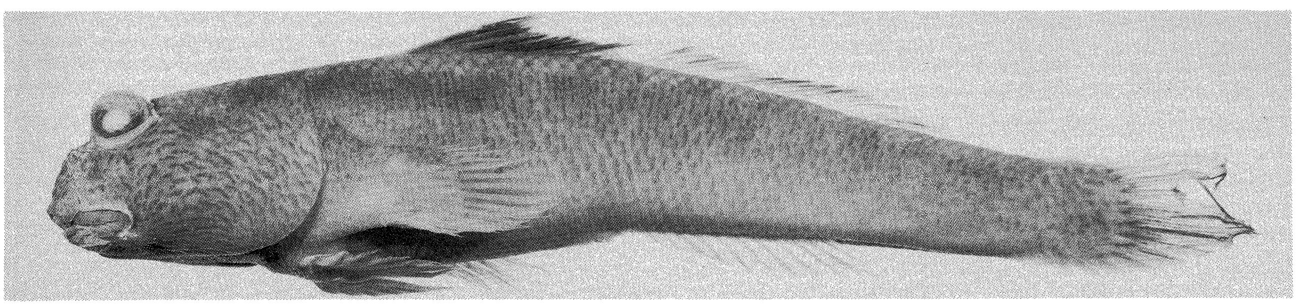

Fig.27. *Periophthalmodon septemradiatus,* MCZ 13304, 76 mm SL, Thailand.

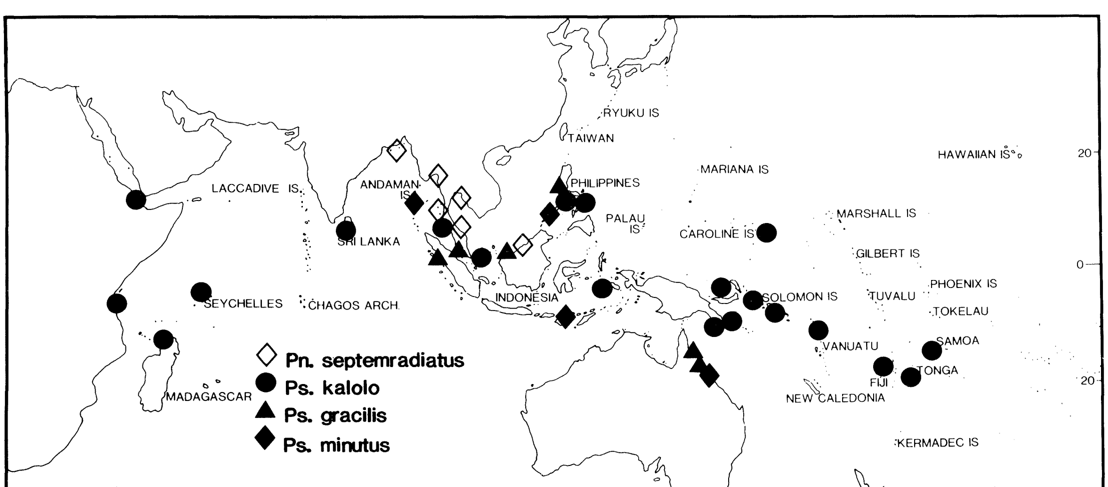

Fig.28. Known localities of *Periophthalmus gracilis, Ps. kalolo, Ps. minutus* and *Periophthalmodon septemradiatus* based on examined material.

with brown stripe medially, anal, pelvic and pectoral fins transparent.

Distribution. Specimens were examined from the northeast coast of India, Burma, Thailand and Sarawak. Additionally, one lot of *Pn. septemradiatus* (ANSP 11026-7) has a stated locality of Japan. Given the distribution of the other material and that no specimens have been reported from Japan (Masuda *et al.*, 1984), the locality of this lot is seriously questioned. *Pn. septemradiatus* is sympatric with *Pn. schlosseri* in Thailand and Sarawak.

Remarks. Hamilton's type material of *Gobius septemradiatus* and *G. tredecemradiatus* do not exist (Hora, 1934). The original descriptions were not diagnostic and confusion has surrounded the proper assignment of these names historically. Hora (1934) considered Hamilton's *G. septemradiatus* and *G. tredecemradiatus* as synonyms of *Periophthalmodon schlosseri*. Both Eggert (1935) and Koumans (1953) considered *G. septemradiatus* synonymous with *Pn. schlosseri* and listed *G. tredecemradiatus* as a separate species. Given the incomplete description of *G. septemradiatus* and the fact that I have not examined any specimens of *Pn. schlosseri* from the Ganges Delta or anywhere else in India, I consider *G. septemradiatus* and *G. tredecemradiatus* as synonyms of one another with *G. septemradiatus* as senior synonym. Additionally, I deem it appropriate to designate a neotype (SU 40076). The neotype is from Uttarbhag, Lower Bengal, an area five miles from where Hamilton obtained many of his fishes (Hora, 1934).

Type material of *Periophthalmus borneensis* Bleeker could not be located at RMNH (M.J.P. van Oijen, in literature) or at BMNH (J. Chambers, in literature); it is synonymised with *Pn. septemradiatus* based on the described number of pectoral fin rays, longitudinal scale count and size of the specimens. Eggert (1935) listed *Ps. borneensis* as a subspecies of his *Pn. tredecemradiatus*.

A pronounced sexual dimorphism exists in *Periophthalmodon septemradiatus*. Adult males possess from 10-16 spines in D1, the first of which is elongate, and the membrane of D1 terminates near or is attached to the origin of D2. Adult females have a poorly developed D1 possessing 5-10 rudimentary spines with D2 reduced. A similar phenomenon is found in *Periophthalmus weberi*. Additionally, *Pn. septemradiatus* shares with *Ps. weberi* a heavily scaled isthmus, scales extending from the pelvic fins almost to the chin (only found in large *Ps. weberi*), contiguous dorsal fins in adult males and an elongate first dorsal spine in adult males (the latter character also being found in *Ps. malaccensis* and *Ps. novemradiatus*). Morphologically, these two species are extremely similar, differentiated on the number of tooth rows in the upper jaw (2 in *Pn. septemradiatus* versus 1 in *Ps. weberi*) and in the arrangement of cheek scales (diagonal in *Pn. septemradiatus* versus vertical in *Ps. weberi*).

Etymology. The trivial name, *septemradiatus,* is from the Latin *septem,* seven, and *radiatus,* rayed, referring to the number of elements in the first dorsal fin.

Periophthalmus

Fig. 1; Tables 1-8

Periophthalmus Bloch & Schneider, 1801: 63 (type species *Periophthalmus papilio* Bloch & Schneider [= *Gobius barbarus* Linnaeus], subsequent designation by Bleeker, 1874: 326).

Euchoristopus Gill, 1863: 271 (type species *Gobius koelreuteri* Pallas [= *Gobius barbarus* Linnaeus] by original designation).

Included species. Twelve species are assigned to *Periophthalmus: Ps. argentilineatus, Ps. barbarus, Ps. chrysospilos, Ps. gracilis, Ps. kalolo, Ps. malaccensis, Ps. minutus, Ps. modestus, Ps. novaeguineaensis, Ps. novemradiatus, Ps. waltoni* and *Ps. weberi.*

Diagnosis. Members of the genus are as yet undefined by a synapomorphy. However, they are characterised by the following features (which may or may not be shared with non-congeners: possession of compressed, convex posterior extensions on the neural and hemal spines of caudal vertebrae 8-13; pelvic fins only partially united or totally separate (except in *Ps. chrysospilos*); and in possessing 16 or fewer (typically 12-14) pectoral fin rays. Additionally, species of *Periophthalmus* live in association with both the mangal and mudflat ecosystems, and are the most amphibious of any oxudercine.

Description. Spinous dorsal fin IV-XVII; second dorsal fin I, 9-13; spinous dorsal fin pterygiophore formula variable but always with 3 or 4 pterygiophores inserted within the fourth interneural space (Table 25); second dorsal fin base relatively short, terminating within a distance of 14-16 scales of caudal fin; appressed second dorsal fin reaching within 6-8 scales of caudal fin.

Anal fin I, 8-13 and typically unbranched; insertion of last ray of anal fin slightly anterior to a vertical with insertion of last ray of second dorsal fin; height of anal fin moderate but less than second dorsal fin; anal fin spine much reduced; appressed anal fin terminates well short of caudal fin.

Pectoral fin 11-16, ventralmost 2-6 rays apically branched with segmentations close together.

Pelvic fin I, 5; frenum present or absent depending on species; basal membrane uniting fins present or absent depending on species.

Caudal fin with 17 segmented rays, 12-15 of them branched, ventralmost rays thickened distally with segmentations close together; dorsal procurrent rays 5-10; ventrally 6-10.

Scales cycloid, covering entire body except for snout, isthmus and interorbital region in most species; largest scales posteriorly, becoming very small on head and ventrum; scales in regular rows and extend onto caudal fin; longitudinal scale count 46-121; TRF 12-32; TRB 11-30; TRDB 12-34; predorsal scales 18-40.

Teeth in both jaws in a single row; 13-39 caninoid teeth in upper jaw, those anteriorly typically larger and pointed; 11-39 caninoid teeth in lower jaw, those anterior typically larger and pointed; no canine teethinternal to symphysis of lower jaw.

Gape moderate, posterior tip of maxilla extending to a point equal to a vertical from middle of eye; anterior portions of upper and lower lip internally papillose, roof of mouth with 2 large papillae; posteriorly, near tip of maxilla, upper lip expanded into a large fold that joins a similar fold of lower lip at rictus, this fold completely covers posterior portion of jaws even when agape; anterior portion of upper lip completely overlaps upper and lower jaw teeth when mouth closed; overlying upper lip is an additional sheath of skin, on each side of this sheath is a pendulous flap with the anterior nostril at its tip, this flap extends ventrally below lower jaw when jaws are closed.

Eyes erectile, dermal cup covering ventral portion of eye; fleshy ridge located anterior to eyes in midline; posterior nostril not prominent, located anterolaterally to eye at lateral edge of a fleshy ridge; no pores on head.

Ventral portion of first gill arch with 4-5 gill rakers; gill filaments short and thread like.

Remarks. In naming *Euchoristopus,* Gill (1863) created confusion over the designation of the type species due to an apparent error in the paper. *Gobius koelreuteri* was indicated as the type of *Euchoristopus,* but under a section headed *Periophthalmus, koelreuteri* is designated as type species (therefore implying it is the type species of *Periophthalmus*). From the description and key, it appears that the usage of *Periophthalmus* is in error in the heading.

Etymology. The generic name, *Periophthalmus,* is from the Greek, *peri,* around, and *ophthalm,* eye, in reference to the prominent, dorsally-placed eyes that appear to provide a broad range of vision; masculine gender.

Key to the Species of *Periophthalmus*

1. Frenum uniting pelvic spines either prominent or vestigial, if vestigial, visible without magnification....................2

—— No pelvic frenum or, if present, visible only with magnification....................8

2. Innermost pelvic fin rays of both fins joined by membrane for entire length to form a disk (India to Indonesia)....................*Ps. chrysospilos* Bleeker

—— Innermost pelvic fin rays of both fins not joined by membrane for entire length, no disk present....................3

3. Spinous dorsal fin with numerous white or black spots....................4

—— Spinous dorsal fin with few or no spots....................6

4. Pelvic frenum prominent; D1 typically X or fewer; longitudinal scale count typically fewer than 70; head width typically less than 17% SL....................5

—— Pelvic frenum vestigial; D1 XI or more; longitudinal scale count typically more than 70; head width 17% SL or greater. (East Africa to Oceania)....................*Ps. kalolo* Lesson

5. Pelvic fin length 13% SL or less; length of anal fin base typically 20% SL or greater; length of D2 base 22% SL or greater; total D2 elements 13-14; total anal fin elements 12-14; longitudinal scale count more than 60; D1 with black spots. (India to the Philippines)....................*Ps. novemradiatus* (Hamilton)

—— Pelvic fin length 13% SL or greater; length of anal fin base usually 20% SL or less; length of D2 base usually 22% SL or less; total D2 elements 11-12; total anal fin elements 11-12; longitudinal scale count usually fewer than 60; D1 with white spots. (Indonesia and the Philippines)....................*Ps. malaccensis* Eggert

6. Longitudinal scale count usually more than 80; in freshly preserved adults, only 1 dusky stripe on D2 (either black or brown)....................7

—— Longitudinal scale count fewer than 80; in freshly preserved adults, 2 solid black stripes on D2. (Papua New Guinea and Australia)....................*Ps. novaeguineaensis* Eggert

7. Total D2 elements 13 or more; longitudinal scale count 90 or more; length of D2 base usually 24% SL or greater. (Pakistan and Arabian Gulf)..*Ps. waltoni* Koumans

—— Total D2 elements usually 13 or fewer; longitudinal scale count usually fewer than 90; length of D2 base 24% SL or less. (Hong Kong, Korea, Japan)............................*Ps. modestus* Cantor

8. D1 and D2 contiguous in adult males, D1 greatly reduced in females, barely perceptible in some; D2 lacking stripes. (Papua New Guinea and Australia)...........Ps. *weberi* Eggert

—— D1 and D2 not contiguous but may be close together in males and females, D1 not reduced in females; D2 with single dusky stripe..9

9. D1 with white or black spots; longitudinal scale count usually fewer than 90...................................10

—— D1 lacking spots or occasionally with a few white spots posteriorly; longitudinal scale count usually more than 90. (tropical west Africa)...*Ps. barbarus* (Linnaeus)

10. D1 rounded with prominent black spot posteriorly; D1 usually X or fewer. (Malaysia, Indonesia, Australia, Philippines)...*Ps. gracilis* Eggert

—— D1 pointed and lacking black spot posteriorly; D1 usually more than X..11

11. D1 with prominent black stripe inframarginally; ventral peritoneum densely black; longitudinal scale count usually 75 or more. (western Indian Ocean to Oceania) ....*Ps. argentilineatus* Valenciennes

—— D1 with light-brown stripe inframarginally; ventral peritoneum lightly pigmented medially; longitudinal scale count usually fewer than 75. (Andaman Islands, Thailand, Indonesia, Australia, Philippines)...*Ps. minutus* Eggert

Periophthalmus argentilineatus Valenciennes

Pl. 2A; Figs 29, 32; Tables 17-25

Periophthalmus argentilineatus Valenciennes *in* Cuvier & Valenciennes, 1837: 191 (type localities, Irian Jaya and Moluccas, Indonesia).
Periophthalmus dipus Bleeker, 1854: 320 (type localities, Java and Sumatra, Indonesia).
Euchoristopus kalolo regius Whitley, 1931: 326 (type locality, northwestern Australia).
Periophthalmus vulgaris vulgaris Eggert, 1935: 81, pls 6-7, figs 23-28 (type locality, Buru, Moluccas, Indonesia).
Periophthalmus vulgaris notatus Eggert, 1935: 83, pl. 7, fig. 29 (type locality, Sungei, Malaysia).
Periophthalmus vulgaris regius.-Eggert, 1935: 84, pl. 7, fig. 30 (new combination).
Periophthalmus vulgaris ceylonensis Eggert, 1935: 85 (type locality, Sri Lanka).
Periophthalmus dipus parvus Eggert, 1935: 88, pl. 8, fig. 32 (type locality, Belawan, Sumatra, Indonesia).
Periophthalmus dipus angustiformis Eggert, 1935: 89, fig. 14 (type locality, Flores, Java, Indonesia).
Periophthalmus argentilineatus striopunctatus Eggert, 1935: 94, pl. 9, fig. 36 (type locality, Balikpapan, Kalimantan, Indonesia).
Periophthalmus sobrinus Eggert, 1935: 95, pl. 9, figs 37-38 (type locality, southwestern Red Sea).

Material examined. (937 specimens from 32 localities; size range 16-93): SOUTH AFRICA: Natal: ANSP 55228, 1:70; ANSP 77881, 9:55-73. East Cape: RUSI 12060, 1:72. TANZANIA: USNM 72869, 40:48-57; ZUMC P.781043-46, 4:53-65. KENYA: Mombasa: ANSP 100169, 3:46-61; USNM 278289, 4:56-64; USNM 278290, 17: 50-66; SOMALIA: MSNG 23257, possible syntypes of *Periophthalmus sobrinus* Eggert, 2:58-63. ERITREA: Arafali: MSNG 7892, possible syntype of *Periophthalmus sobrinus* Eggert, 59. SEYCHELLES: Mahe': USNM 267222, 3:29-59. MADAGASCAR: AMNH 11698, 3:54-55; USNM 279320, 3:40-56. PAKISTAN: Sind: LACM 38137-2, 3:16-39. BURMA: MNHN 1402, 4:37-43; MNHN B.2915, 1:31; MNHN B.2916, 1:40. SRI LANKA: USNM 278317, 4:19-21; USNM 279146, 31:16-40. THAILAND: USNM 119629, 2:45-47; USNM 119630, 1:52; USNM 119631, 1:71; USNM 279334, 57:27-65. MALAYSIA: Sabah: ANSP 72195-7, 3:33-46. Sarawak: MCZ 64689, 4:47-51. INDONESIA: Irian Jaya: USNM 123801, 2:37-45; USNM 278296, 31:14-42. Java and Sumatra: RMNH 4593, includes 10 possible syntypes of *Periophthalmus dipus* Bleeker, 19:41-64. Java: MNHN A.1500 (paralectotype), female, 45; MNHN A.1501 (paralectotype), male, 58. Lesser Sunda Islands: NTM

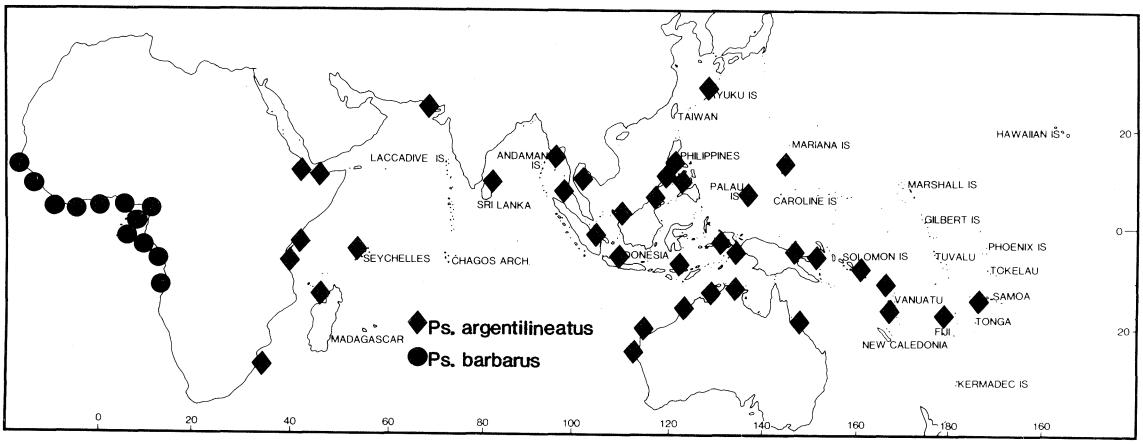

Fig.29. Known localities of *Periophthalmus argentilineatus* and *Ps. barbarus* based on examined material.

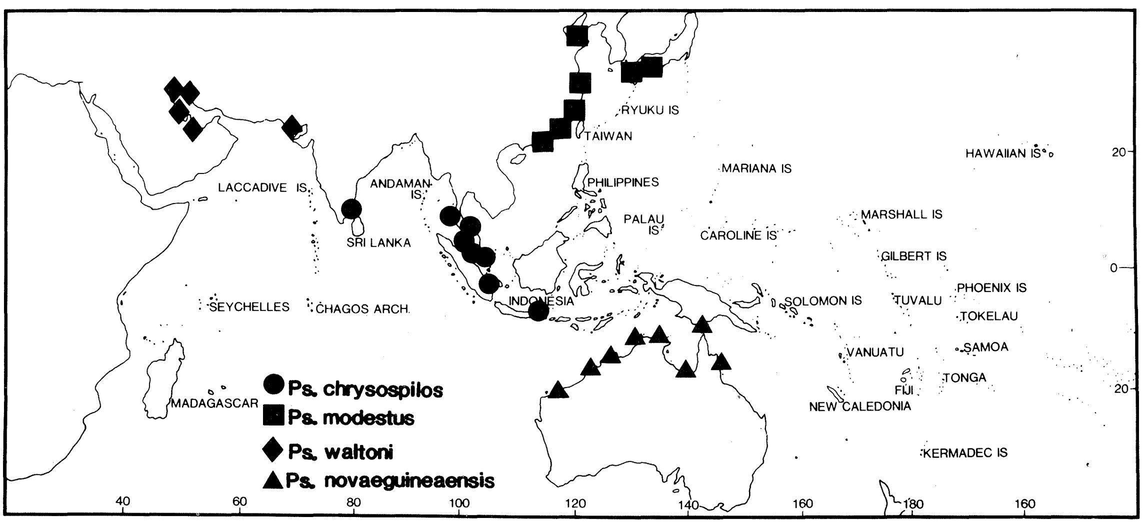

Fig.30. Known localities of *Periophthalmus chrysospilos, Ps. modestus, Ps. novaeguineaensis* and *Ps. waltoni* based on examined material.

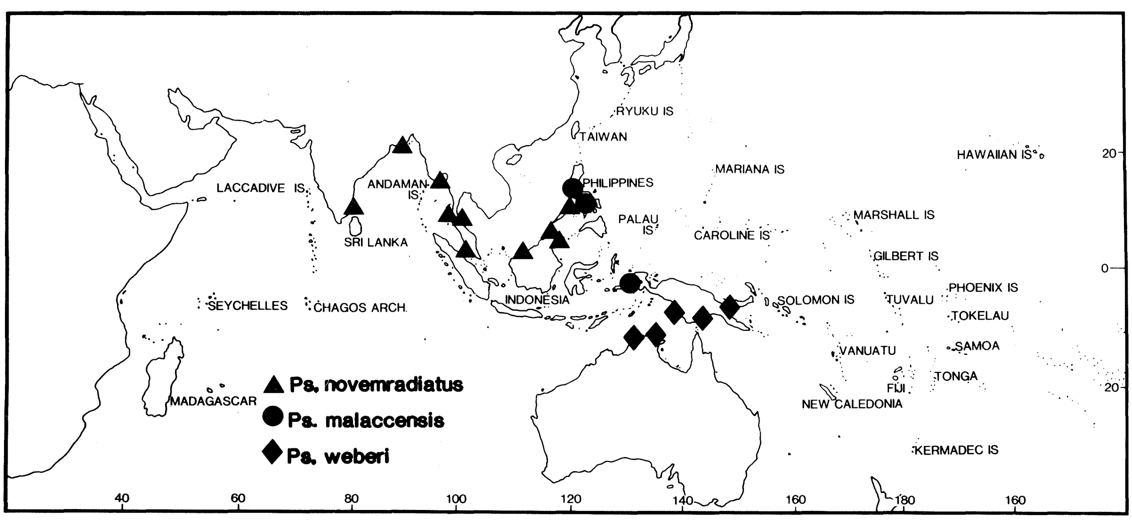

Fig.31. Known localities of *Periophthalmus malaccensis, Ps. novemradiatus* and *Ps. weberi* based on examined material.

S.10688-008, 1:52; NTM S.11125-026, 11:16-52; USNM 243152, 3:60-68; USNM 243155, 2:42-55; USNM 243439, 1:50; USNM 243438, 1:59; ZMA 110.947, 1:49; ZMA 113.218, in part, possible syntype of *Periophthalmus dipus angustiformis* Eggert, 71. Moluccas: MNHN A.1499 (lectotype), male, 54; USNM 243440, 2:56-60; USNM 246614, 6:39-49; USNM 268452, 1:85; USNM 268454, 1:52; USNM 268455, 1:56; USNM 278291, 1:51; ZMA 113.703, paratypes of *Periophthalmus vulgaris vulgaris* Eggert, 12:49-64. Sumatra: CMK 4548, 1:39; CMK (uncatalogued), 1:56; CMK (uncatalogued), 1:53. PAPUA NEW GUINEA: AMNH 16683, 5:38-82; USNM 260936, 3:42-52; USNM 278322, 5:49-87; USNM 278313, 7:17-67; USNM 278320, 1:62; USNM 278323, 3:61-66; USNM 278365, 1:60; USNM 278366, 9:46-83; USNM 278367, 2:16-17; USNM 279011, 8:40-72; WAM P.27412-005, 3:45-83; ZMA 103.055, 1:57; ZUMC P.7881473-77, 5:50-64. AUSTRALIA: Northern Territory: NTM S.10408-001, 13:19-39; NTM S.10413-001, 9: 47-53; NTM S.10416-001, 11:39-60; NTM S.10439-003, 2:32-37; NTM S.10452-003, 36:19-90; USNM 278316, 2:50-60; USNM 278319, 1:34; USNM 278324, 1:36; USNM 278325, 1:38; USNM 279145, 11:41-81. Queensland: MCZ 28285, 7:43-84; ROM 38436, 2:51-59; ROM 38814, 1:32; UAMZ 6503, 1:49; UAMZ 6504, 1:56; UAMZ 6506, 1:56; UAMZ 6507, 1:43; UAMZ 6508, 1:48; UAMZ 6509, 1:36; UAMZ 6518, 2:58-72; UAMZ 6519, 2:67; UAMZ 6522 5:37-68; USNM 279014, 1:75; WAM P.27780-007, 1:56. Western Australia: AMS I.14140, holotype of *Euchoristopus kalolo regius* Whitley, 73; WAM P.23218-9, 2:23-68; WAM P.8227-8254, 28:37-67; WAM P.9430-33, 4:51-64; WAM P.25118-003, 5:35-56. PHILIPPINES: ANSP 100168, 8: 45-62; SU 38592, 1:70; USNM 52035, 8:27-62; USNM 78094, 7:28-37; USNM 106734, 1:38; USNM 123375, 2:29-34; USNM 133166, 3:31-39; USNM 133167, 1:37; USNM 150523, 1:35; USNM 150920, 14:37-54; USNM 161014, 6:51-69; USNM 243150, 1:46; USNM 243151, 146:32-57; USNM 243154, 1:44; USNM 243156, 18: 29-51; USNM 261690, 75:32-53; USNM 262025, 1:53; USNM 278474, 2:48-51; USNM 278286, 1:55; USNM 278285, 31:33-57; USNM 278288, 13:31-45. JAPAN: Okinawa: USNM 132790, 1:39; USNM 278321, 4:43-59. PALAU: CAS 57427, 5:58-62. YAP: BPBM 10529, 1:63. SOLOMON ISLANDS: SU 14898, 2:43-55; USNM 123447, 1:51; USNM 144297, 5:23-64. SANTA CRUZ ISLANDS: USNM 278295, 4:42-52. VANUATU: USNM 226561, 1:93. FIJI: ANSP 84765, 2:57-60; ANSP 87037, 1:48; ANSP 91476, 2:55-56; BPBM 14623, 1:51; ROM 38296, 1:41; ROM 45393, 2:48-51; ROM 45415, 2:22-25; ROM 45447, 6: 43-56; USNM 256565, 1:52; USNM 278368, 6:35-61; USNM 279332, 4:31-48. MARIANAS: Guam: AMNH 27028, 3:45-65. SAMOA: USNM 52214, 7:50-58; USNM 76267, 1:42; USNM 126283, 4:40-53; USNM 279007, 3:42-52.

Diagnosis. Pelvic fins lacking frenum; little or no membrane uniting medialmost pelvic rays; D1 height moderate, its margin usually convex, occasionally straight, with a black stripe inframarginally and numerous small, white spots posteriorly on fin, no elongate spines; D2 with single, dusky stripe mesially; dorsal fins not connected by membrane; D1 with 11-16 spines (mean = 13.9); longitudinal scale count 64-100 (mean = 81.1); head width 14.3-22.6% SL (mean = 18.7%); pelvic fin length 11.3-15.2% SL (mean = 13.2%); length of anal fin base 14.0-19.4% SL (mean = 16.8%); length of D2 base 17.6-23.7% SL (mean = 20.8%); total D2 elements 10-13 (mean = 12.0) total anal fin elements 9-12 (mean = 11.0); TRDB 18-26 (mean = 20.8).

Colouration (based on a photograph of a freshly dead, 51 mm SL specimen from Fiji, BPBM 14623, see Pl. 2A). Background colouration on sides and dorsum brown, silvery white ventrally; nape and dorsal half of head dark brown, ventral half of head and pectoral base silvery white; many small, white spots on head, a few on trunk; trunk with many narrow, short silvery bars ventrally and 3-4 dark brown, saddle-like blotches posterodorsally; D1 suffused with red and with a wide black stripe extending length of fin inframarginally; distal margin pale, about 24 small, white spots on posterior two thirds of fin; D2 margin red with wide black stripe through middle of fin, basally pale; caudal fin with many brownish red spots on fin rays; anal and pectoral fins pale; pelvic fin whitish. Ground colour in preservative dark brown; white spots on head and trunk only in a few specimens; 6-8 dark brown, saddle-like blotches dorsally on many specimens along with narrow, silver bars ventrally; D1 brown basally with scattered small, white spots on a brown background proximally, a black stripe inframarginally, margin pale; D2 brownish with a dark brown stripe in middle of fin; caudal fin with brown spots on fin rays; pectoral fins dusky; anal and pelvic fins off white; ventral peritoneum densely black.

Distribution. Brackish mangrove and nipa palm areas from the Southern Red Sea and east coast of Africa

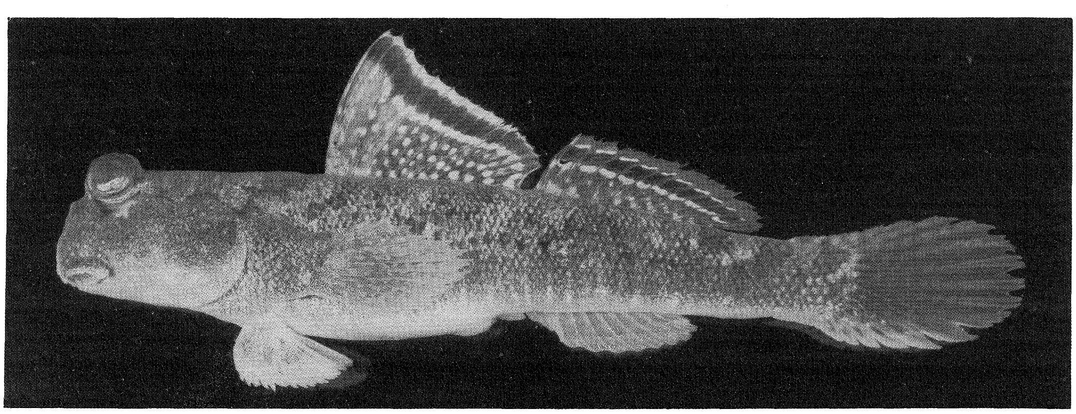

Fig.32. *Periophthalmus argentilineatus,* 60 mm SL, Ambon, Indonesia. (Photo by J.E. Randall).

eastward to Japan and Oceania. *Periophthalmus argentilineatus* is syntopic with *Ps. kalolo* in several localities; it is syntopic with *Ps. gracilis, Ps. minutus, Ps. novaeguineaensis* and *Pn. freycineti* in Queensland.

Remarks. Dr G. Mickoleit informed me that type material of *Periophthalmus argentilineatus striopunctatus* Eggert, *Ps. dipus parvus* Eggert, and *Ps. vulgaris notatus* Eggert was deposited at Universität Tübingen and destroyed during World War II; these taxa are synonymised based on published accounts and illustrations. Type material of *Periophthalmus vulgaris ceylonensis* might have been deposited at the Zoological Institute of the University of Jena, GDR (W. Klausewitz, in literature). Although I have not examined Eggert's type material, I consider *Ps. vulgaris ceylonensis* equivalent to *Ps. argentilineatus* based on the original description of *Ps. vulgaris ceylonensis.* As indicated by Koumans (1953:213), type material of *Ps. dipus angustiformis* Eggert (ZMA 113.218) comprises two specimens and two species: one is a 78 mm SL, male specimen of *Ps. minutus* and the other (72 mm SL, female) is *Ps. argentilineatus.* As the latter specimen was figured in Eggert (1935, fig. 14), I choose to recognise *Ps. d. angustiformis* as a synonym of *Ps. argentilineatus.* Putative syntypes of *Periophthalmus melanotaeniatus* (RMNH 1966), a *nomen nudum* treated by Koumans (1953) as a synonym of *Ps. dipus,* were examined and found equivalent to *Ps. argentilineatus.* I hereby designate MNHN A.1499 lectotype and MNHN A.1500 and 1501 paralectotypes of *Periophthalmus argentilineatus* Valenciennes. Variation in colour, shape and size of the first dorsal fin is common. Eggert (1935) accorded some variants species or subspecies recognition but I do not believe this variation conforms very well to geographic boundaries or population limits. All individuals in a region or even in the same lot do not necessarily possess the same type of D1. All species of *Periophthalmus* (and many other oxudercines) use their D1 for communication purposes (i.e. territorial signals, courtship displays) rather than swimming. I believe this variation in shape, size and colour is more a result of ontogenetic and behavioural factors than specific differences, and reflects an individual's stage of development. Nursall (1974, 1981) studied community structure of four syntopic species of *Periophthalmus* in Queensland. He reported both intra- and interspecific aggression with fin displays being one way of expressing this aggression. Of the species he observed, *Ps. vulgaris* (= *argentilineatus*) had the most intense fin-signalling system. At different development stages, individual *Ps. argentilineatus* use their D1 to convey different messages. Therefore, lability in D1 form should be expected in collections representing a broad size range.

Etymology. The trivial name, *argentilineatus,* is from the Latin *argentum*, silver, and *lineatus,* lined, in reference to the vertical, silver lines on the ventral portion of the body.

Periophthalmus barbarus (Linnaeus)

Figs 29, 33; Tables 17-25

Gobius barbarus Linnaeus, 1766: 450 (type locality, unknown).
Gobius koelreuteri Pallas, 1770: 8, pl. 2, figs 1-3 (type locality, unknown).
Periophthalmus papilio Bloch & Schneider, 1801: 63, fig. 14 (type locality, Tranquebar, India).
Periophthalmus gabonicus Dumerile, 1858: 250, pl. 22, fig. 4 (type locality, Gabon).
Periophthalmus erythronemus Guichenot in Dumerile, 1858: 250, pl. 22, fig. 5 (type locality, Senegal).

Material examined (124 specimens from 14 localities; size range 15-147): SENEGAL: MNHN A.1082, 1:87; MNHN 1965-523, 1:94; MNHN 1975-55, 4:46-77; MNHN 6241, holotype of *Periophthalmus erythronemus* Guichenot, 59. GUINEA BISSAU: MSNG 42497, 2:95-109. SIERRA LEONE: ALA 1078.01, 40:45-92; ALA 737.01, 9:66-92. LIBERIA: AMNH 32777 (neotype), 1:121; USNM 179692, 2:67; USNM 193811, 1:83. IVORY COAST: NMB 5641-5645, 5:62-72. GHANA: SU 63043, 1:70. NIGERIA: ROM 5492, 2:82-100; ROM 9153, 5:48-115; USNM 88575, 1:137; ZMA 115.624, 1:118. BIOKO: ZMUC P.78896, 1:89. CAMEROON: MNHN 1978-728, 1:88; ZMUC P.781343, 2:14-21; ZMUC P.781505-13, 9: 31-100. GABON: MNHN 6240, syntypes of *Periophthalmus gabonicus* Dumerile, 3:56-68; MNHN 1924-127/130, 4:85-95. SAO TOME: ZMUC P.781493, 1:101. CONGO: MNHN 37-118, 1:142; MNHN 1884-7, 2:126; MNHN 1926-216/217, 2:78-94; MNHN 1967-418/420, 13:15-112; MNHN 1967-905, 5:88-108. CABINDA: ZMB 19862, 1:147. ANGOLA: MNHN 1923-52, 1:50; ZMA 113.721, 1:90.

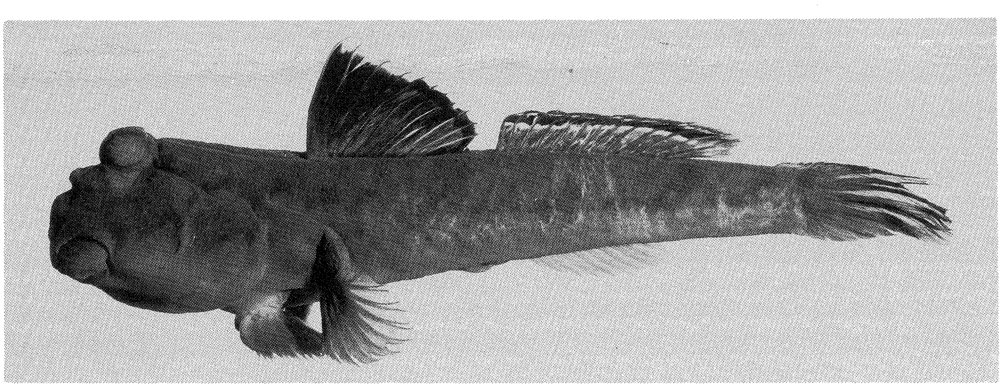

Fig.33. Neotype of *Periophthalmus barbarus,* AMNH 32777, 121 mm SL, Liberia.

Diagnosis. No frenum uniting pelvic fins; large adult size, approaching 150 mm SL; D1 height moderate, its margin straight with a blackish stripe inframarginally and, occasionally, with a few white spots posteriorly (spots often lacking), no elongate spines; D2 with single dusky stripe mesially; dorsal fins not connected by membrane; D1 with 10-14 spines (mean = 11.5); longitudinal scale count 86-107 (mean = 96.6); head width 15.4-21.8% SL (mean = 18.1%); pelvic fin length 14.2-16.0% SL (mean = 14.9%); length of anal fin base 14.1-17.7% SL (mean = 15.5%); length of D2 base 20.9-24.1% SL (mean = 22.7%); total D2 elements 11-14 (mean = 12.9); total anal fin elements 9-11 (mean = 9.9); TRDB 20-34 (mean = 25.5).

Colouration. No colour notes or photographs of live or freshly dead individuals available. In preservative, ground colour brown, venter yellow; remnants of brown blotches on head and dorsum in some specimens; D1 with thin, pale margin, blackish band inframarginally with a broken white line proximal to this black band, remainder of fin grey or brown; first spine of D1 grey to white and slightly elongate in some specimens; some specimens with a few white spots basally on posterior portion of D1; D2 with a brownish margin, inframarginally a black or brown stripe is sandwiched by 2 thin, whitish lines, proximally grey or brown; caudal fin rays sometimes with a series of brown spots, otherwise dusky brown; anal fin whitish; pelvic and pectoral fins slightly dusky.

Distribution. I examined specimens from Senegal to Angola (approximately 15°N to 15°S).

Remarks. Type material of the following no longer exists: *Gobius barbarus* Linnaeus (A. Wheeler, in literature), *G. koelreuteri* Pallas (A.P. Andriashev, in literature), and *Periophthalmus papilio* (H.J. Paepke, in literature). The proper assignment of *G. barbarus* was difficult given the very brief desciption provided by Linnaeus coupled with the lack of locality information. However, very similar wording to Linnaeus' 1766 description also appeared as a heading or introduction to Koelreuter's detailed and much more extensive 1763 paper in which he described and figured a mudskipper. Koelreuter did not assign a binomen to his goby and stated that the locality was unknown. Koelreuter did, however, provide sufficient information to equate his specimen with the west African *Periophthalmus*. I believe Linnaeus' *Gobius barbarus* is simply a binomen for Koelreuter's described but unnamed mudskipper. Pallas (1770) dedicated his mudskipper description to Koelreuter and even cited Koelreuter's 1763 paper. Pallas' description and figure were based on a different specimen than the one Koelreuter used, and, curiously, Pallas also stated that the locality of his specimen was unknown. Bloch & Schneider's (1801) description and figure of *Periophthalmus papilio* is clearly the west African *Periophthalmus,* however, the stated locality is Tranquebar, India. Valenciennes (1837:191) was first to comment on this discrepancy with the concluding statement, "But one knows how much to challenge Bloch's assertions on these localities." Because of the confusion surrounding *Gobius barbarus* Linnaeus, I hereby designate a 121 mm SL female specimen from Liberia (AMNH 32777) as neotype for *Periophthalmus barbarus.*

Etymology. The trivial name, *barbarus,* is from the Greek *barbaros,* foreign, possibly alluding to the unusual nature of this mudskipper in relation to other gobies.

Periophthalmus chrysospilos Bleeker

Pl. 2B; Figs 30, 34; Tables 17-25

Periophthalmus chrysospilos Bleeker, 1852: 728 (type locality, Banka Island, Indonesia).

Material examined. (110 specimens from 8 localities; size range 16-129): INDIA: Madras: USNM 279015, 2:123-129; USNM 279309, 1:58. THAILAND: Andaman Sea: CAS 57429, 1:66; ZUMC P.78616-18, 3:40-65. Gulf of Thailand: USNM 244031, 1:60. MALAYSIA: Muar: FMNH (uncatalogued), 23:16-61; FMNH (uncatalogued), 8:34-54; USNM 278428, 29: 20-58; USNM 279331, 7:51-63; USNM 278435, 21: 21-57. Penang: USNM 151130, 8:24-33. SINGAPORE: LICPP 1966114, 1:93. INDONESIA: Banka Island: RMNH 4760 (syntypes), 2:75-76. JAVA SEA: MCZ 33228, 1:80; ZMUC P.781480-81, 2:56-67.

Diagnosis. Pelvic fins totally united into a rounded disk; D1 tall, its margin straight, no stripes or spots on fin, first two spines elongate in males, only first spine elongate in females, first spine in males relatively longer than first spine in females; D2 with dusky stripe mesially; dorsal fins

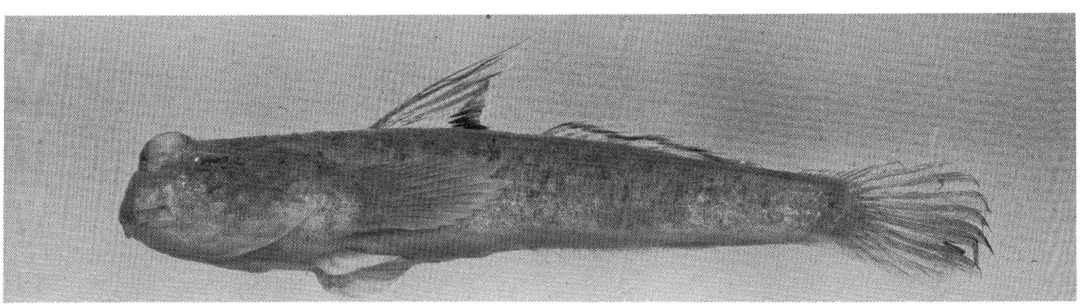

Fig.34. *Periophthalmus chrysospilos,* USNM 278428, 58 mm SL, Malaysia.

not connected by membrane; D1 with 7-10 spines (mean = 8.7); longitudinal scale count 64-77 (mean = 70.7); head width 12.6-21.8% SL (mean = 17.3%); pelvic fin length 12.4-16.8% SL (mean = 14.3%); length of anal fin base 16.7-20.6% SL (mean = 18.5%); length of D2 base 16.3-24.3% SL (mean = 21.2%); total D2 elements 12-13 (mean = 12.5); total anal fin elements 11-13 (mean = 11.7); TRDB 15-19 (mean = 17.0).

Colouration (based on photographs of a freshly dead male, 61 mm SL, and female, 63 mm SL, from the west coast of Malaysia, USNM 279331, see Pl. 2B). Background colouration pale or dark grey; head and trunk with multitudinous orange spots, orange spots also ventrally on gill cover, prepelvic area, and chin; on trunk, orange spots from pectoral base to caudal peduncle; on male specimen, background duskier than on female; a few, diagonal, dusky bands on dorsum in both male and female; first and second dorsal spines in male bright orange, only first spine is orange in female; in both males and females, posteriormost four spines orange for three quarters of length, then black for distal one quarter; interspinous membranes basally orange; distal area of interspinous membrane of spines III-VII black with white margin; distal area of interspinous membrane of spines I-III dusky; distal margin of D2 red with a black stripe in middle of fin; most of caudal fin dusky, distal portion pale; anal fin transparent; pectoral fin inter-radial membrane dusky, rays transparent; pelvic fins white.

Ground colour in preservative varying from tan to dark grey or brown, one specimen with many white speckles; no orange spots retained on head or trunk; D1 totally or just distally blackened; black stripe in D2 retained in some specimens; caudal fin sometimes dusky; other fins whitish.

Distribution. Brackish mangrove and nipa palm areas from the east coast of India to Gulf of Thailand and Java Sea.

Remarks. Macnae (1968), Polunin (1972) and Murdy (1986) provided information on the behavior and ecology of *Periophthalmus chrysospilos*.

Etymology. The trivial name, *chrysospilos*, from the Greek *chryso*, gold, and *spilos*, spot, refers to the scattered pigment on the head and trunk.

Periophthalmus gracilis Eggert

Pl. 2C; Figs 28, 35; Tables 17-25

Periophthalmus gracilis Eggert, 1935: 79, pl. 6, fig. 22 (type locality, Java and Sumatra, Indonesia).

Material examined. (52 specimens from 5 localities; size range 19-45): SUMATRA, INDONESIA: ZMA 113.722, 9:32-40. MALAYSIA: Peninsular: USNM 279365, 1:27. Sarawak: MCZ 64530, 4:25-32. LUZON, PHILIPPINES: USNM 278473, 2:35-36. QUEENSLAND, AUSTRALIA: ROM 38399, 4:19-42; ROM 38767, 4:29-42; ROM 38840, 1:38; UAMZ 6511, 6:26-45; UAMZ 6512, 4: 21-34; UAMZ 6520, 11:36-43; UAMZ 6522, 6:43-45.

Diagnosis. No pelvic frenum, or if present, only visible with magnification; pelvic fins totally separate; D1 short and rounded, brown inframarginal stripe terminating into a prominent black spot, no elongate spines; D2 with single dusky stripe mesially; dorsal fins not connected by membrane; D1 with 9-11 spines (mean = 9.4); longitudinal scale count 52-70 (mean = 59.2); head width 14.2-19.3% SL (mean = 17.1%); pelvic fin length 11.7-15.1% SL (mean = 12.8%); length of anal fin base 17.8-21.1% SL (mean = 19.3%); length of D2 base 18.8-21.3% SL (mean = 20.0%); total D2 elements 12-13 (mean = 12.1); total anal fin elements 11-12 (mean = 11.9); TRDB 14-20 (mean = 17.1).

Colouration (based on a photograph of a freshly dead, 27 mm SL specimen from Peninsular Malaysia, USNM 279365, see Pl. 2C). Background colouration on sides and dorsum light brown, venter white; head and body with 7 anteriorly directed, diagonal, brown bars: 2 on head, 1 between D1 and D2, 2 beneath D2, and 2 on caudal peduncle; small, brown spot on midline of snout near upper jaw, another ventral to D1 and 1 ventral to D1 origin; D1 short with a broad, brown stripe that terminates posteriorly into a large, black spot; D1 margin immaculate, basal portions of D1 spines II-VI yellowish; D1 interspinous membranes brown mesially along basal portion of fin; distal tips of D2 elements dusky yellow, a narrow, brown stripe mesially with brown spots on elements basally; a series of 2-6 brown spots on caudal fin elements; pectoral fin elements with brown spots; anal and pelvic fins immaculate.

Ground colour in preservative light brown over most of body, venter white or yellow; head lacking spots, 4-6 small, white spots posteroventrally on trunk; 9 saddle-like blotches on dorsum: first across nape; second anterior to D1 origin; third across base of D1; fourth at D1 terminus; fifth at D2 origin; sixth across base of D2; seventh at D2 terminus; eighth across caudal peduncle; and ninth at caudal fin origin; D1 mostly brown with a pale margin, a line of white spots at middle and base of fin, prominent, black blotch covering most or all of posterior four spines; D2 with pale margin, brown stripe inframarginally, scattered brown spots proximally; caudal fin rays with numerous, brown spots; anal fin immaculate; pectoral fin rays with brown spots; pelvic fins immaculate.

Distribution. Specimens were examined from Indonesia, Malaysia, Australia, and the Philippines. In Peninsular Malaysia, *Periophthalmus gracilis* is syntopic with *Ps. novemradiatus;* in Queensland, *Ps. gracilis* is syntopic with *Ps. argentilineatus, Ps. minutus, Ps. novaguineaensis* and *Pn. freycineti*.

Remarks. Type material deposited at Universität Tübingen is lost (G. Mickoleit, in literature) as is that at MSNG (G. Arboco, in literature). Assignment was made based on the original description and figure. Nursall (1974, 1981) provided ecological and behavioural information on *Periophthalmus gracilis*.

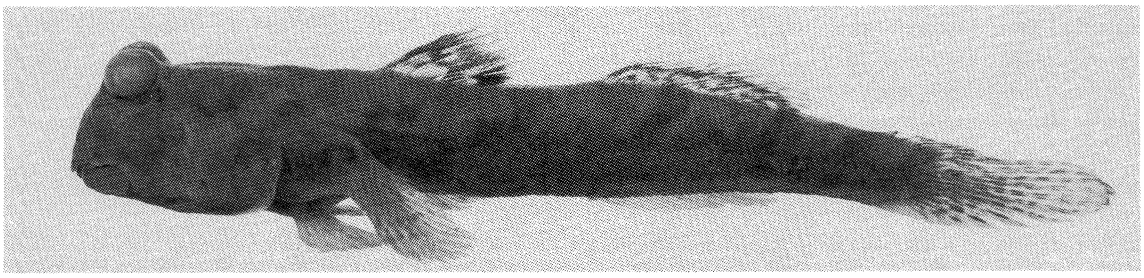

Fig.35. *Periophthalmus gracilis,* UAMZ 6511, 45 mm SL, Queensland, Australia.

Etymology. The trivial name, *gracilis,* is Latin for slender referring to the thinness of this species.

Periophthalmus kalolo Lesson

Pl. 2D; Figs 28, 36-37; Tables 17-25

Periophthalmus kalolo Lesson, 1830: 146 (type locality, Waigiou, Irian Jaya, Indonesia).
Periophthalmus kallopterus Bleeker, 1853: 342 (type locality, Ambon, Indonesia).
Periophthalmus fuscatus Blyth, 1858: 271 (type locality, Andaman Islands).
Periophthalmus harmsi Eggert, 1929a: 398 (type locality, Java, Indonesia).
Periophthalmus koelreuteri albostriatus Eggert, 1935: 73, fig. 10 (type locality, Java, Indonesia).
Periophthalmus koelreuteri velox Eggert, 1935: 75 (type locality, Java, Indonesia).
Periophthalmus koelreuteri kalolo.-Eggert, 1935: 76, fig. 11, pl. 5, figs 19-20 (new combination).
Periophthalmus koelreuteri africanus Eggert, 1935: 78, pl. 5, fig. 21 (type locality, Dar es Salaam, Tanzania).
Euchoristopus kalolo.-Whitley, 1953: 127 (new combination).
Periophthalmus musgravei Whitley, 1961: 69 (type locality, Misima, Papua New Guinea).

Material examined. (182 specimens from 14 localities; size range 15-141): DJIBOUTI: Khor Anghar: BPBM 21553, 2:60-95. TANZANIA: Dar es Salaam: ZMB 18364, holotype of *Periophthalmus koelreuteri africanus* Eggert, 62. MADAGASCAR: Nosy-Be': USNM 278372, 2:46-80; USNM 278373, 1:72. SEYCHELLES: USNM 278300, 1:60. SRI LANKA: ZMUC P.78742-3, 2:89-95; ZMUC P.78745, 1:102; ZMUC P.78748, 1:80. THAILAND: Phuket: USNM 279143, 24:43-98. ST. BARBE ISLAND (EAST OF SINGAPORE): USNM 49273, 1:141. MOLUCCAS: Ambon: RMNH 4754, syntypes of *Periophthalmus kallopterus* Bleeker, 2:68-103; USNM 278297, 7:41-64; USNM 278299, 2:40-48. Tandjung Tala: USNM 210948, 2:59-81. PAPUA NEW GUINEA: USNM 30663, 2:58-70; USNM 279008, 1:28; USNM (uncatalogued), 1:22. PHILIPPINES: Calatagan: USNM (uncatalogued) 1:67. Cebu: ROM 51596, 5:27-66; USNM 148598, 2:32-48. Himohan: USNM 123362, 1:86. NEGROS: USNM (uncatalogued) 1:15; USNM (uncatalogued) 1:69; USNM (uncatalogued) 25:46-91; USNM 249848, 14:47-98. Palawan: USNM 200244, 7: 66-94; USNM 279890, 4:58-84. Ticao: USNM 72179, 1:67. ADMIRALTY ISLANDS: USNM 143628, 1:69. PAPUA NEW GUINEA: AMS IA.5868, holotype and paratypes of *Periophthalmus musgravei* Whitley, 5:77-96. SANTA CRUZ ISLANDS: USNM 278469, 1:87. PONAPE, MICRONESIA: USNM 65978, 2:80-89; USNM 233019, 8:21-68; USNM 233133, 1:21; USNM 233265, 2:51-58; USNM 233266, 2:36-64. SOLOMONS: USNM 260510, 1:90; USNM 278469, 1:83; USNM 279186, 1:72. FIJI: Kandavu: USNM 238856, 25:19-81; Viti Levu: ROM 45392, 8: 24-59; USNM 241796, 4:24-36. TONGA: USNM 278301, 5:16-77. AMERICAN SAMOA: USNM 278475, 1:50; USNM 278476, 2:48-56; USNM 278477, 5:68-83; USNM 283226, 3:46-74.

Diagnosis. Frenum of pelvic fins vestigial, but visible macroscopically; pelvic fins united by membrane for about one half their length; D1 height moderate, its margin rounded, black stripe inframarginally with numerous white spots proximally, no elongate spines; D2 with single dusky stripe inframarginally; dorsal fins not connected by membrane; D1 with 11-15 spines (mean = 12.9); longitudinal scale count 66-86 (mean = 74.6); head width 16.5-22.5% SL (mean = 19.7%); pelvic fin length 13.1-15.4% SL (mean = 14.5%); length of anal fin base 15.9-18.7% SL (mean = 17.6%); length of D2 base 18.5-23.8% SL (mean = 20.9%); total D2 elements 12-13 (mean = 12.3); total anal fin elements 11-12 (mean = 11.6); TRDB 18-22 (mean = 20.2).

Colouration (based on a photograph of freshly dead, 95 mm SL specimen from Djibouti, BPBM 21553, see Pl.2D). Background colour greyish; head with numerous white spots anteroventrally, irregularly-shaped black blotches dorsoposteriorly; trunk with scattered black flecks; 3 faint-brown, saddle-like blotches dorsally, first at D1 terminus, second at midpoint of D2, and third at D2 terminus; D1 margin white with prominent black stripe inframarginally, proximally grey with many white spots, tips of I-II reddish; D2 margin red, a wide, black stripe sandwiched between narrow, white lines inframarginally, proximally grey with white spots; caudal fin rays with dusky spots; anal fin immaculate; pectoral fin dusky with greyish spots on fin rays; pelvic fin dusky. Ground colour in preservative brownish grey; white spots on head in some but not all specimens; trunk with scattered black spots; D1 mostly grey, margin pale, black stripe inframarginally, pale spots proximally; D2 pale distally except for black stripe inframarginally, black spots proximally; caudal fin rays with black blotches; anal fin immaculate; pectoral and pelvic fins dusky, rays with black blotches.

Distribution. *Periophthalmus kalolo* is distributed from

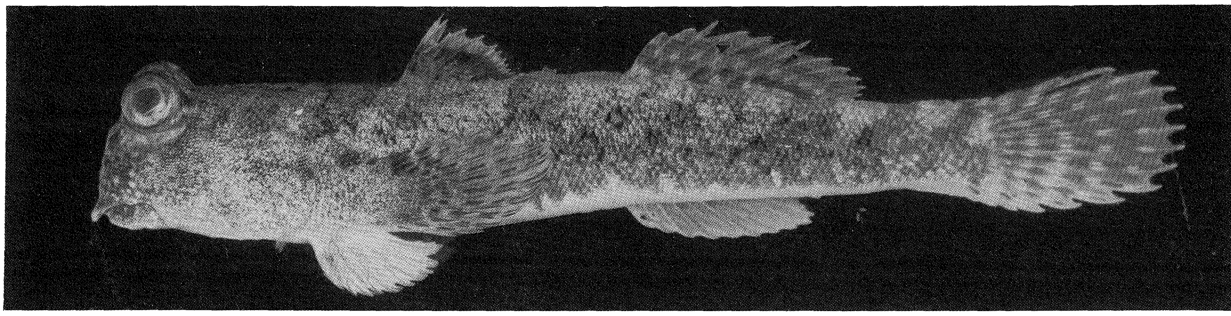

Fig.36. *Periophthalmus kalolo,* BPBM 19276, 43 mm SL, Poka Ambon, Indonesia.

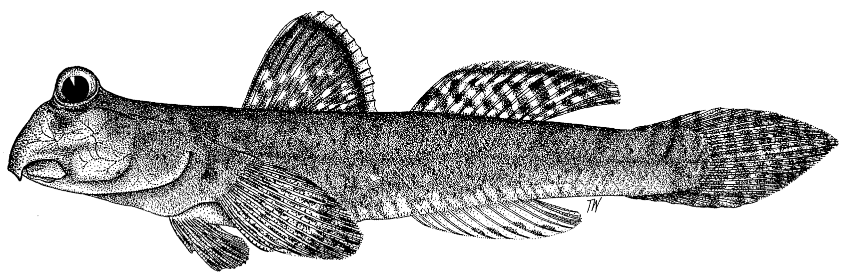

Fig.37. *Periophthalmus kalolo,* USNM 283226, 75 mm SL, American Samoa. (Drawing by Thosaporn Wongratana).

east Africa to Samoa. *Ps. kalolo* is syntopic with *Ps. argentilineatus* at several localities.

Remarks. Type material of *Periophthalmus kalolo* Lesson is not at MNHN (M.L. Bauchot, in literature) and is presumed lost. Diagnostic features were included in the original description and, thus, identification can be made. Type material of *Periophthalmus fuscatus* Blyth is not at BMNH (J. Chambers, in literature) and that of *Ps. harmsi* Eggert, *Ps. koelreuteri albostriatus* Eggert and *Ps. k. velox* Eggert was deposited at Universität Tübingen and destroyed during World War II (G. Mickoleit, in literature). I based synonymies on the original descriptions and/or figures. Ontogenetic variation occurs in the size and shape of the first dorsal fin. In specimens 60 mm SL or less, D1 is greatly rounded and its height is about equal to that of D2. At 60 mm SL or greater, D1 is only slightly rounded and its height is about 1.5-2 times that of D2.

Etymology. The trivial name, *kalolo,* is the native name for this species (Lesson, 1830).

Periophthalmus malaccensis Eggert

Figs 31, 38; Tables 17-25

Periophthalmus malaccensis Eggert, 1935: 62, figs 3-4 (type locality, Singapore).

Material examined. (32 specimens from 2 general localities; size range 48-90): INDONESIA: Moluccas: USNM 268451, 1:81. PHILIPPINES: Iloilo: USNM 148591, 25:56-84. Mariveles: USNM 112908, 6:48-90.

Diagnosis. Pelvic frenum prominent; pelvic fins partially united by basal membrane; D1 height moderate, its margin slightly rounded, a brown stripe inframarginally with numerous white spots proximally, first spine elongate; D2 with single dusky stripe mesially; dorsal fins not connected by membrane; D1 with 9-10 spines (mean = 9.8); longitudinal scale count 47-61 (mean = 54); head width 14.3-19.5% SL (mean = 16.6%); pelvic fin length 13.6-16.1% SL (mean = 14.5%); length of anal fin base 15.4-20.6% SL (mean = 17.7%); length of D2 base 17.0-23.2% SL (mean = 19.8%); total D2 elements 11-12 (mean = 11.6); total anal fin elements 11-12 (mean = 11.3); TRDB 14-17 (mean = 15.7).

Colouration. No colour notes or photographs of live or freshly dead individuals available. Ground colour in preservative light to dark brown; head with many tiny, white spots ventrally; in most specimens, trunk with 8 prominent, saddle-like blotches dorsally - first anterior to D1 origin; second across D1 base, third at D1 terminus; fourth at D2 origin; fifth across D2 base; sixth at D2 terminus; seventh at origin of dorsal procurrent rays, and eighth at caudal fin base; D1 margin white, dark brown stripe inframarginally with a transparent stripe immediately ventral, remainder of fin light brown with numerous, small, white spots; D2 margin light brown, dark brown stripe sandwiched between 2 narrow transparent stripes inframarginally, remainder of fin light brown with a few white spots; caudal fin membranes with dusky spots throughout; anal fin with narrow, white margin, remainder black; pectoral fin membranes dusky, rays mostly transparent; pelvic fins with narrow, white margins, remainder black.

Distribution. Although the type locality is Singapore, specimens were available only from Indonesia and the Philippines.

Remarks. Type material was deposited at Universität

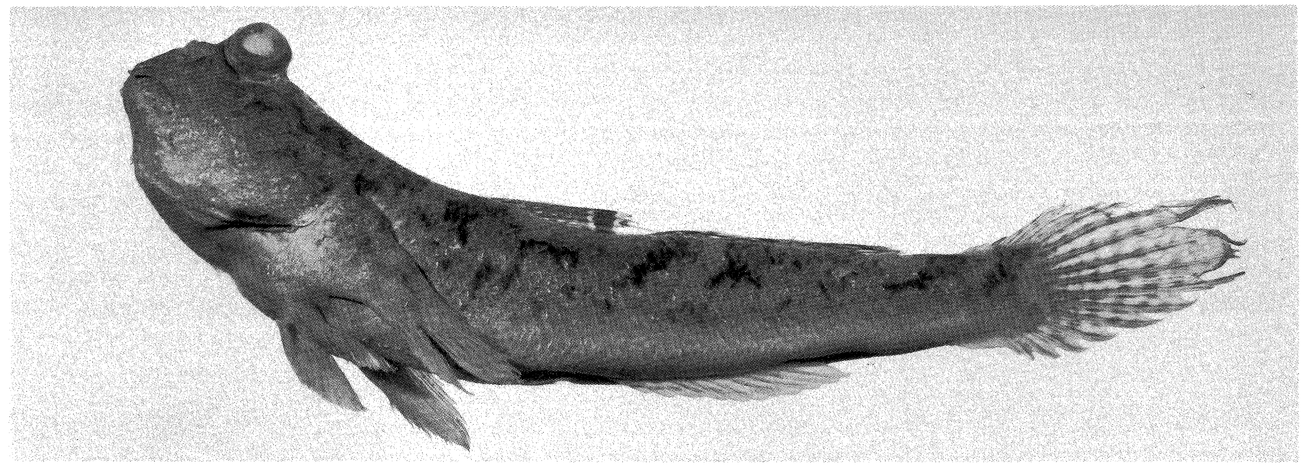

Fig.38. *Periophthalmus malaccensis,* USNM 148591, 64 mm SL, Philippines.

Tübingen and destroyed during World War II (G. Mickoleit, in literature). Based on the original description and figures, the above specimens are assignable to *Periophthalmus malaccensis*.

Etymology. The trivial name, *malaccensis,* refers to the body of water (Strait of Malacca) that adjoins the type locality.

Periophthalmus minutus Eggert

Figs 28, 39; Tables 17-25

Periophthalmus minutus Eggert, 1935: 90, figs 15-16, pl. 8, fig. 33 (type locality Deli River, Belawan, Sumatra, Indonesia).

Material examined. (33 specimens from 5 localities, size range 18-78): ANDAMAN ISLANDS: SU 36161, 2:42-46; SU 37162, 6:38-47. THAILAND: Phuket: ZMUC P.781595-96, 2:40-43. INDONESIA: Java: ZMA 113.218, in part, 1:78. AUSTRALIA: Queensland: UAMZ 6502, 1:55; UAMZ 6513, 1:57; UAMZ 6514, 5:48-62; UAMZ 6515, 1:42; UAMZ 6516, 1:52; UAMZ 6517, 3:54-55; UAMZ 6522, 7:18-55. PHILIPPINES: Palawan: USNM 136683, 3:49-68.

Diagnosis. Pelvic frenum lacking or only visible with magnification; membrane uniting medial rays of pelvic fin slight to moderate; D1 height moderate, its margin straight to slightly convex, a brown stripe mesially and many white spots proximally, no elongate spines; D2 with single dusky stripe mesially; dorsal fins not connected by membrane; D1 with 10-17 spines (mean = 12.5); longitudinal scale count 62-78 (mean = 69.8); head width 14.2-18.9% SL (mean = 17.1%); pelvic fin length 11.6-14.8% SL (mean = 12.8%); length of anal fin base 15.7-19.3% SL (mean = 17.7%); length of D2 base 20.1-22.7% SL (mean = 21.3%); total D2 elements 11-13 (mean = 11.9); total anal fin elements 11-12 (mean = 11.4); TRDB 16-19 (mean = 17.5).

Colouration (based on a photograph of a freshly dead specimen from Queensland, Australia). Background dark brown except for white venter; 6 black, saddle-like blotches dorsally, first anterior to D1, second across D1 base, third at D1 terminus, fourth across D2 base; fifth at D2 terminus and sixth at origin of dorsal procurrent rays; D1 mostly red with numerous white spots proximally, fin margin white; D2 margin red, white inframarginally with a brown stripe in middle of fin, a few, black spots basally on D2 rays; caudal fin dusky mesially, ventral and dorsal rays with black spots; anal fin immaculate; pectoral and pelvic fins off white.

Ground colour in preservative khaki; saddle-like dorsal blotches only faint; D1 light brown with transparent margin and white spots; D2 transparent except for brown stripe in middle of fin and few, brown spots basally on rays; caudal, anal, pectoral and pelvic fins as above; ventral peritoneum lightly pigmented medially.

Distribution. Specimens were available from the Andaman Islands, Thailand, Java, Queensland and the Philippines. Based on Nursall (1981), *Periophthalmus minutus* is syntopic with *Ps. argentilineatus, Ps. gracilis, Ps. novaeguineaensis* and *Pn. freycineti* in Queensland. [The "red-fin" *Periophthalmus* of Nursall (1981) is *Ps. minutus.*]

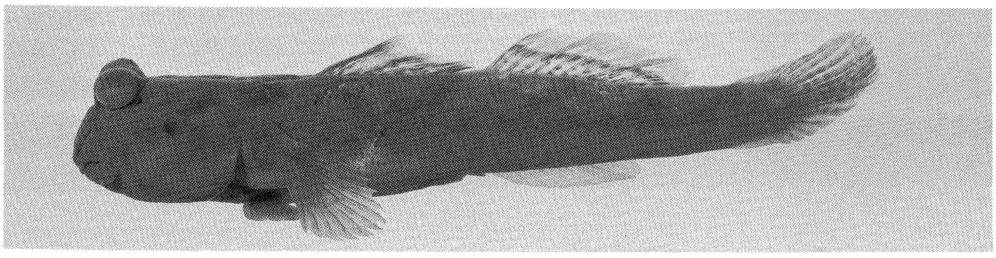

Fig.39. *Periophthalmus minutus,* UAMZ 6514, 58 mm SL, Queensland, Australia.

Remarks. Type material of *Periophthalmus minutus* was deposited at the Universität Tübingen and destroyed during World War II (G. Mickoleit, in literature); identification was based on the original description and figures. Koumans (1953:213) considered *Ps. minutus* the juvenile form of *Ps. dipus* (= *Ps. argentilineatus*). *Periophthalmus minutus* differs morphologically from *Ps. argentilineatus* most markedly in the shape and colouration of D1 and in peritoneal pigmentation. Based on J.R. Nursall's unpublished and published (1974 and 1981) behavioural observations, *Ps. minutus* differs significantly from *Ps. argentilineatus*: *Ps. argentilineatus* is dominant to *Ps. minutus* when they are brought together; *Ps. argentilineatus* is active near the water's edge whereas *Ps. minutus* lives in two-chimneyed burrows 15-25 m from the low water mark; *Ps. minutus* is not as active as *Ps. argentilineatus* and spends much of the time in its burrow, head poking out; in an aquarium, the activity level of *Ps. minutus* is much reduced compared to *Ps. argentilineatus*. Refer to Nursall (1981) for more detailed information.

Etymology. The trivial name, *minutus,* is Latin for small.

Periophthalmus modestus Cantor

Pl. 2E; Figs 30, 40; Tables 17-25

Periophthalmus modestus Cantor, 1842: 484 (type locality Chusan, China).

Material examined. (88 specimens from 4 localities; size range 30-65): HONG KONG: SU 61102, 63:30-62. CHINA: AMNH 43017, 8:44-64; ANSP 91009, 1:44; ANSP 97871, 1:56; USNM 86000, 1:52; USNM 86376, 1:44; USNM 86408, 1:39; USNM 86467, 1:68; USNM 86468, 1:65; USNM 148440, 1:61. KOREA: USNM 37976, 2:49-54. JAPAN: MCZ 25486, 2:59-62: MCZ 25488, 2: 56-64; ROM 39867, 3:59-65.

Diagnosis. Pelvic fins united anteriorly by a moderate to strong frenum; medial rays united by a membrane for about half their length; D1 height moderate, its margin rounded, a dusky stripe inframarginally and no spots on fin, no elongate spines; D2 with single dusky stripe inframarginally; dorsal fins not connected by membrane; D1 with 10-17 spines (mean = 13.1); longitudinal scale count 75-100 (mean = 85.3); head width 14.1-19.8% SL (mean = 17.1%); pelvic fin length 11.5-14.6% SL (mean = 13.0%); length of anal fin base 16.1-22.2% SL (mean = 19.8%); length of D2 base 19.8-24.1% SL (mean = 22.7%); total D2 elements 12-14 (mean = 12.6); total anal fin elements 11-13 (mean= 12.3); TRDB 19-29 (mean = 24.1).

Colouration (based on a photograph of a fresh specimen in Masuda *et al.,* 1984:257, fig. A, identified as *Periophthalmus cantonensis,* reproduced herein as Pl. 2E).

Ground colour grey; tiny, whitish spots on head; several small, black spots mid-laterally; 7 irregular, brownish saddle-like blotches on dorsum, first anterior to D1, second and third below D1, fourth and fifth beneath D2, sixth on caudal peduncle, and seventh at caudal fin base; D1 mostly grey with whitish margin, a grey-black stripe inframarginally; D2 with transparent margin, inframarginally a greyish stripe, ventral to this stripe is a whitish one with grey spots basally on fin rays; caudal fin greyish; anal fin off white; pelvic fins whitish; pectoral fins grey. In preservative, ground colour brownish; tiny, white spots on head; several small, brown spots midlaterally; blotches on dorsum brown, not retained in some specimens; D1 mostly brown with whitish margin; inframarginally on D2 a brown stripe with faded brown spots basally on fin rays; caudal fin brownish with dark brown area in middle of fin; anal and pelvic fins whitish; pectoral fins yellow brown with small, dusky spots proximally.

Distribution. Hong Kong northward to Korea and southern Japan.

Remarks. *Periophthalmus modestus* Cantor has frequently been referred to as *Ps. cantonensis* (Osbeck). As explained in the section under *Apocryptes,* Osbeck's *cantonensis* is pre-Linnaean and has no standing. Type material of *Periophthalmus modestus* is not deposited at BMNH (J. Chambers, in literature) and was not located at other museums; identification was made based on the original description. Akihito *in* Masuda *et al.* (1984) stated that *Ps. modestus* inhabits brackish waters and moves briskly on land preying on small animals.

Etymology. The trivial name, *modestus,* is from the

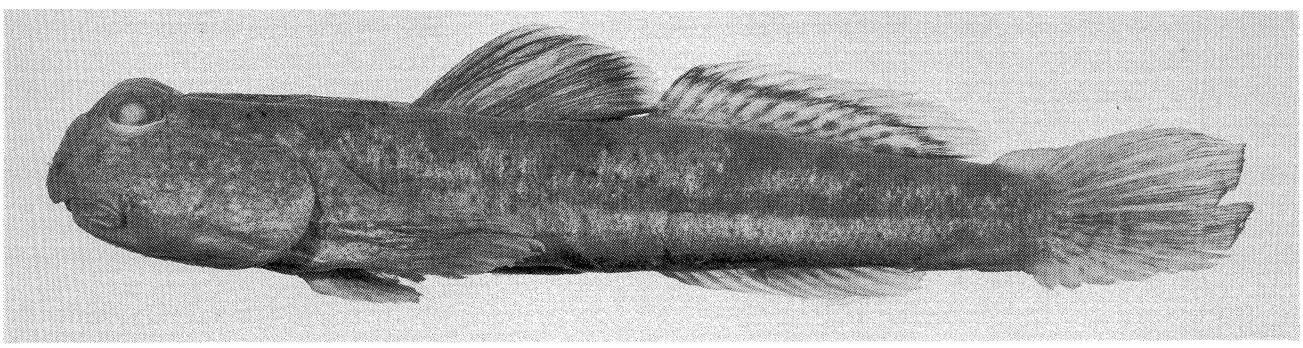

Fig.40. *Periophthalmus modestus,* MCZ 25486, 58 mm SL, Japan.

Latin, for modest perhaps referring to the lack of striking colouration.

Periophthalmus novaeguineaensis Eggert

Pl. 2F; Figs 30, 41; Tables 17-25

Periophthalmus cantonensis novae-guineaensis Eggert, 1935: 61, fig. 2, pl. 3, fig. 12 (type locality, Meruake, Irian Jaya, Indonesia).
Periophthalmus expeditionium Whitley, 1953: 127, fig. 2 (type locality, Gulf of Carpentaria, Queensland).

Material examined. (263 specimens from 4 localities; size range 12-71): AUSTRALIA: Western Australia: AMNH 41561, 14:25-66; AMNH 41562, 8: 12-50; NTM S.10802-006, 2:15-39; WAM P.25035-002, 4:32-47; WAM P.254472-001, 1:71; WAM P.25668-009, 5:39-47; WAM P.26198-001, 1:70; WAM P.27367-001, 2:35-45. Northern Territory: BPBM 30932, 6:40-62; NTM S.462, 1:34; NTM S.10408-002, 5:15-32; NTM S.10410-003, 4:47-48; NTM S.10418-004, 13:32-71; NTM S.10421-002, 1:62; NTM S.10426-002, 17:32-41; 10429-025, 5:17-39; NTM S.10472-018, 19:18-44; NTM S.10554-001, 48:22-47; NTM S.10649-007, 13:13-26; NTM S.10694-001, 41:32-65; NTM S.10718-056, 1:29; NTM S.10989-002, 2:16-20; NTM S.11114-002, 5:28-34; NTM S.11360-015, 7:28-40; USNM 279010, 9:37-49. Queensland: AMS I.6195, holotype of *Periophthalmus expeditionium* Whitley, 41; ANSP 89838, 3:42-59; MCZ 38530, 1:51; ROM 38832, 1:60; UAMZ 6522, 2:43-69. INDONESIA: ZMA 112.466 (lectotype), female, 42; ZMA 112.945 (paralectotypes), 21:32-46.

Diagnosis. Pelvic fins with a strong frenum; medially, pelvic fins partially united by membrane for at least one half their length; D1 height moderate, its margin rounded, no spots or stripes on fin, no elongate spines; D2 with 2 dusky stripes mesially; dorsal fins not connected by membrane; D1 with 5-13 spines (mean = 9.1); longitudinal scale count 54-78 (mean = 68.6); head width 15.1-20.2% SL (mean = 17.3%); pelvic fin length 10.9-14.5% SL (mean = 12.4%); length of anal fin base 16.8-21.9% SL (mean = 19.3%); length of D2 base 18.8-26.8% SL (mean = 22.8%); total D2 elements 12-14 (mean = 12.9); total anal fin elements 11-13 (mean = 12.1); TRDB 15-21 (mean = 18.0).

Colouration (based on a photograph of a freshly dead, 58 mm SL female from the Northern Territory, Australia, BPBM 30932, see Pl. 2F). Background colour whitish grey; head and trunk with both black and golden-yellow spots; 3 large, black, saddle-like blotches posterodorsally, 1 beneath the midpoint of D2, 1 at terminus of D2, and the third near the origin of dorsal procurrent rays; D1 membrane blackish with some reddish orange tint, spines whitish, most of distal margin white, remainder black; D2 with 2 solid black stripes sandwiching a white stripe, distal margin whitish, a broken, black line basally on fin; caudal fin slightly dusky; pectoral fin grey proximally, whitish distally; anal and pelvic fins whitish.

Ground colour in preservative light brown; head and trunk with a few dark-brown spots; 5 brown, saddle-like blotches on dorsum - first anterior to D1 origin, second at D1 terminus, third across middle of D2 base, fourth at D2 terminus, and fifth on caudal peduncle; D1 dusky; D2 with 2 solid black stripes distally and 1 broken black line proximally; caudal fin with many dusky spots; pectoral fin dusky proximally, hyaline distally; anal and pelvic fins immaculate.

Distribution. Specimens were examined from Port Hedland to Townsville in Australia and from southern Irian Jaya, Indonesia. In the Townsville area, *Ps. novaeguineaensis* is syntopic with *Ps. gracilis, Ps. argentilineatus, Ps. minutus* and *Pn. freycineti* (Nursall, 1981).

Remarks. The syntypic series (ZMA 112.945) contained specimens in various states of preservation; it appears that specimens may have been added to this lot. I have designated a female syntype (42 mm SL) as lectotype, now cataloged as ZMA 112.466.

Etymology. The trivial name, *novaeguineaensis*, refers to the type locality which is part of New Guinea.

Periophthalmus novemradiatus (Hamilton)

Pl. 2G; Figs 31, 42; Tables 17-25

Gobius novemradiatus Hamilton, 1822: 47, pl. 2, fig. 14 (type locality, vicinity of Calcutta).
Periophthalmus novemradiatus.-Valenciennes *in* Cuvier & Valenciennes, 1837: 148 (new combination).
Periophthalmus pearsei Eggert, 1935: 57, pl. 3, fig. 10 (type locality, Port Canning, India).

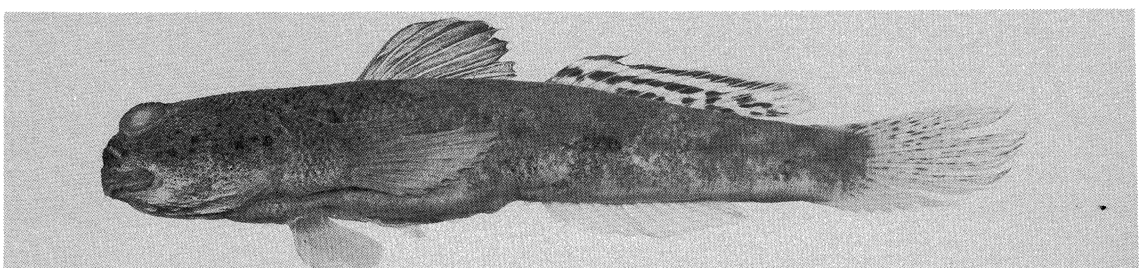

Fig.41. *Periophthalmus novaeguineaensis,* ROM 38832, 61 mm SL, Queensland, Australia.

Periophthalmus variablilis variabilis Eggert, 1935: 64, fig. 5, pl. 3, fig. 13 (type locality, Java, Indonesia).
Periophthalmus variabilis sumatranus Eggert, 1935: 65, fig. 6, pl. 4, figs 14-15 (type locality, Belawan, Sumatra, Indonesia).
Periophthalmus variablilis asiaticus Eggert, 1935: 66, fig. 7 (type locality, Paknam, Thailand).
Periophthalmus variabilis tidemani Eggert, 1935: 67, fig. 8 (type locality, Halmahera, Moluccas, Indonesia).

Material examined. (63 specimens from 9 localities; size range 33-64): INDIA: Madras: USNM 279159, 1:53. Uttarbhag: SU 34776, 5:43-51; SU 69060 (neotype), 49. BURMA: MNHN 1402, 4:37-43. MALAYSIA: Peninsular: FMNH (uncatalogued), 15:33-64; USNM 279318, 5: 42-62; ZMA 113.702, 2:42-52. Sabah: USNM 139372, 2:42-59; USNM 278470, 1:51. Sarawak: MCZ 54404, 10:24-53. THAILAND: Paknam: USNM 222971, 1:49. Phuket: ZMUC P.781597-611, 14:28-62. PHILIPPINES: Mariveles: USNM 278471, 1:57.

Diagnosis. Pelvic fins with prominent frenum; inner rays of pelvic fins united for only one quarter or less of their length; D1 height moderate, its margin straight to slightly rounded, no stripes on fin but with reddish orange spots in life, black spots in preservative, first spine longest, occasionally elongate; D1 with 9-11 spines (mean = 9.3); longitudinal scale count 61-76 (mean = 67.8); head width 13.2-18.6% SL (mean = 15.9%); pelvic fin length 11.3-13.3% SL (mean = 12.3%); length of anal fin base 19.1-24.0% SL (mean = 22.3%); length of D2 base 21.9-25.9% SL (mean = 24.1%); total D2 elements 13-14 (mean = 13.1); total anal fin elements 12-14 (mean = 13.7); TRDB 15-21 (mean = 18.5).

Colouration (based on a photograph of a freshly dead, 52 mm SL female specimen from Peninsular Malaysia, USNM 279318, see Pl. 2G). Ground colour of dorsal half of body brown, ventral half whitish; ventroposterior edge of gill cover blackened; head and trunk with numerous, black spots, spots larger on trunk; a thin, black bar directed anteroventrally from orbit; 8 black, saddle-like blotches on dorsum - first anterior to D1, second across middle of D1 base, third at D1 terminus, fourth and fifth across D2 base, sixth at D2 terminus, seventh on caudal peduncle, and eighth at caudal fin base; D1 with pale margin, greyish black stripe inframarginally, reddish orange spots on a white background proximally and a reddish tint on the first 3 interspinous membranes; tips of D1 spines black, first spine blackened on distal half; D2 with yellow margin, a white stripe distal to a black stripe inframarginally, and reddish orange spots on inter-radial membranes basally; caudal fin dusky mesially with dusky brown spots on rays, distal portion of rays bright orange; anal fin distally yellow, proximally off white; pectoral fin suffused with orange; pelvic fin whitish. Ground colour in preservative light or dark brown dorsally, whitish ventrally; 8 brown, saddle-like dorsal blotches as above in most specimens; some scattered brown spots on head and trunk; ventral margin of gill cover blackened in many specimens; D1 with a pale margin and black stripe inframarginally with either large, black spots on a pale membrane throughout proximal portion of fin or with membrane dusky anteriorly and black spots posteriorly on pale membrane; D2 margin pale, inframarginally with black stripe, dusky spots basally on inter-radial membranes; caudal fin rays dusky with black spots; anal fin immaculate; pectoral fin rays dusky; pelvic fin membrane dusky, rays hyaline.

Distribution. Specimens were examined from the east coast of India, Burma, Thailand, Malaysia and the Philippines.

Remarks. Type material of *Gobius novemradiatus* Hamilton was not saved (Hora, 1934). Eggert's type material of *Periophthalmus pearsei* and *Ps. variabilis* (and subspecies thereof) was most probably deposited at Universität Tübingen and destroyed during World War II. Hora (1934) synonymised *G. novemradiatus* with *Periophthalmus* (= *Periophthalmodon*) *schlosseri*. Eggert (1935) was confused about the placement of *G. novemradiatus* and did not include it in his key but did include a brief account. Koumans (1941, 1953) did not mention *G. novemradiatus*. Based primarily on Hamilton's figure, I recognise *G. novemradiatus* as a distinct species and designate a male specimen, 49 mm SL, SU 69060, as neotype. The neotype was collected from Uttarbhag in the Ganges Delta, an area near where Hamilton collected the material for his description (Hora, 1934).

Etymology. The trivial name, *novemradiatus*, from the Latin *novem*, nine and *radius*, rays, refers to the typical condition of nine spines in the first dorsal fin.

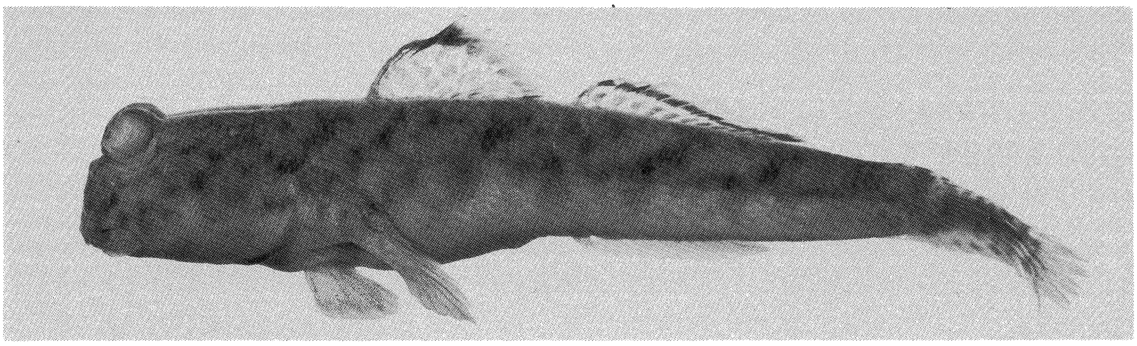

Fig.42. *Periophthalmus novemradiatus,* USNM 279318, 52 mm SL, Malaysia.

Periophthalmus waltoni Koumans

Pl. 2H; Figs 30, 43; Tables 17-25

Periophthalmus waltoni Koumans, 1941: 288 (type localities, Iraq and Pakistan).

Material examined. (19 specimens from 4 localities; size range 55-123): IRAN: USNM 196295, 2:57-68. KUWAIT: BPBM 30527, 4:68-105; USNM 279330, 3: 55-99. BAHRAIN: ZMUC (uncatalogued), 4:69-89. PAKISTAN: LACM 38142-2, 1:101; LACM 38303-2, 1:78; ROM 40109, 2:99-123; ROM 40110, 2:74-79.

Diagnosis. Moderate to strong frenum uniting pelvic fins; medially, pelvic fins united for about one half their length; D1 height moderate, its margin slightly rounded, no stripe on fin with only a few white spots posteriorly, no elongate spines; D2 with single dusky stripe inframarginally; dorsal fins not connected by membrane; D1 with 10-13 spines (mean = 12.0); longitudinal scale count 91-121 (mean = 103.4); head width 13.7-21.9% SL (mean = 17.0%); pelvic fin length 11.8-13.9% SL (mean = 12.8%); length of anal fin base 16.2-21.0% SL (mean = 19.0%); length of D2 base 23.2-27.2% SL (mean = 24.8%); total D2 elements 13-14 (mean = 13.8); total anal fin elements 11-12 (mean = 11.8); TRDB 21-28 (mean = 25.1).

Colouration (based on a photograph of a freshly dead, 90 mm SL specimen from Kuwait, BPBM 30527, see Pl. 2H). Background colour of head and trunk grey; small white spots and a few dusky blotches on cheek and gill cover; series of 7 irregular, black blotches along dorsum; ventral to D1 are 8 short, diagonal, black bars; D1 light grey with a yellowish margin between I-VIII; small black area inframarginally between I-VII; 2 small, white spots basally on posterior third of D1; D2 margin transparent, inframarginally a black stripe dorsal to a white stripe, grey stripe basally; 3 black blotches on caudal peduncle; caudal fin brownish grey; anal and pelvic fins blackish brown with pale margin; pectoral fin greyish with whitish margin; curving brown stripe proximally on dorsal half of pectoral fin. In preservative, ground colour grey; remnants of white spots on head; large dark grey blotches along sides in some specimens; silvery bars ventral to D1 in some specimens; dusky blotches on dorsum in some specimens; D1 grey with blackish inframarginal region anteriorly; 4 stripes on D2, distalmost light grey, below which in succession black, white, dark grey; caudal and anal fins grey; pelvic fins blackish on dorsal surface, dusky ventrally; pectoral fins grey with curved brown stripe proximally on some specimens.

Distribution. Mudflat areas from the Arabian Gulf to Pakistan.

Remarks. Koumans (1941) based his description of *Periophthalmus waltoni* on four specimens that were deposited at the Zoological Survey of India (ZSI). A.G.K. Menon (in literature) could not locate the specimens at ZSI in Calcutta and fears they are lost.

Etymology. The trivial name, *waltoni*, honors H.J. Walton who collected material for the original description.

Periophthalmus weberi Eggert

Pl. 3A; Figs 31, 44-45; Tables 17-25

Periophthalmus weberi Eggert, 1935: 55, pl. 2, figs 6-7 (type localities, Noord and Lorentz Rivers, Irian Jaya, Indonesia).

Material examined. (18 specimens from 3 localities, size range 38-71): AUSTRALIA: NORTHERN TERRITORY: AMNH 41563, 6:57-71; USNM 278472, 2:38-60. PAPUA NEW GUINEA: USNM 217304, 1:44; USNM 279193, 1:38; WAM P.27815-011, 3:46-58. INDONESIA: IRIAN JAYA: ZMA 112.939 (paralectotypes), 4:60-67; ZMA 119.465 (lectotype), male, 71.

Diagnosis. Pelvic frenum lacking or only visible with magnification; in males, D1 height moderate, its margin almost straight, no stripe on fin only a few pale blue spots in life, white spots in preservative, all spines extend beyond membrane and first spine more than twice as long as others, dorsal fins contiguous, connected by membrane; in females, D1 negligible, represented by only a few short spines; D2 in both sexes lacking stripes; D1 with 4-16 spines (mean = 9.9); longitudinal scale count 46-52 (mean = 50.1); head width 15.4-19.4% SL (mean = 17.4%); pelvic fin length 15.0-17.1% SL (mean = 15.7%); length of anal fin base 14.2-18.5% SL (mean = 16.5%); length of D2 base 20.6-26.8% SL

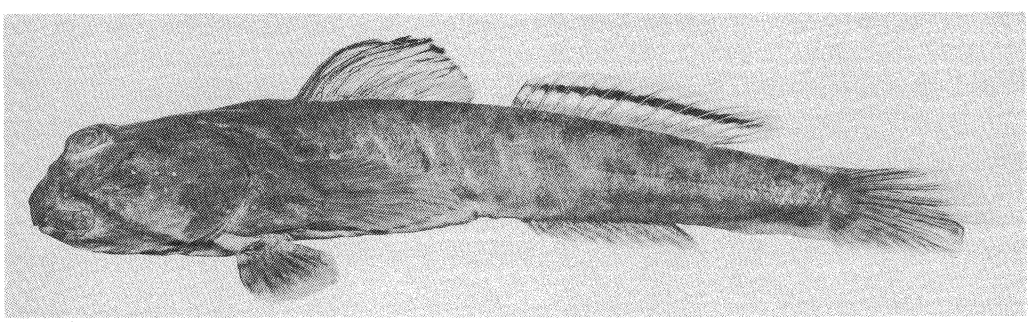

Fig.43. *Periophthalmus waltoni,* BPBM 30527, 90 mm SL, Kuwait.

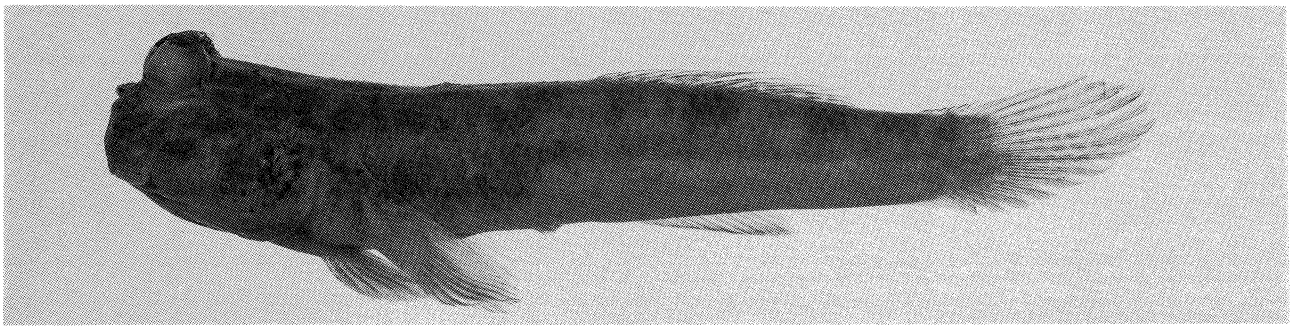

Fig.44. *Periophthalmus weberi,* WAM P.27815-011, 47 mm SL, female, Papua New Guinea.

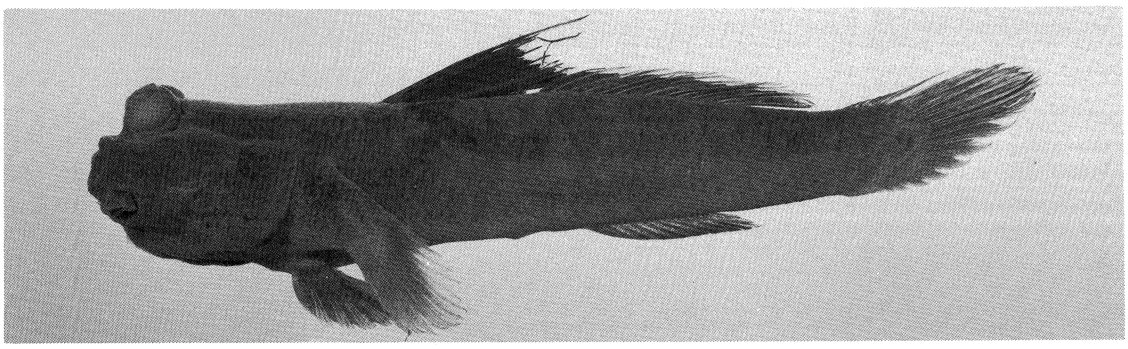

Fig.45. *Periophthalmus weberi,* WAM P.27815-011, 58 mm SL, male, Papua New Guinea.

(mean = 24.5%); total D2 elements 11-14 (mean = 13.1); total anal fin elements 9-12 (mean = 10.9); TRDB 12-17 (mean = 14.0).

Colouration (based on a photograph of freshly dead, 58 mm SL, male specimen from the Oriomo River, Papua New Guinea, WAM P.27815-011, see Pl. 3A). Background colouration bluish grey; no spots or stripes on head and trunk; D1 black with small, pale blue spots on interspinous membranes; all D1 spines grey, however, first dorsal spine mostly grey but whitish distally; margin of D1 light blue; D2 dark brown except for pale margin; caudal fin light brown dorsally, dark brown ventrally; anal fin distally blackened with transparent margin and black speckles on a hyaline background proximally; pelvic fin blackish grey on dorsal surface, dusky ventrally with transparent margin. Colouration of same specimen in preservative: background colour brown, darker brown dorsally than ventrally; remnants of 2 saddle-like blotches posterodorsally, one at D2 terminus and the other at caudal peduncle; D1 and D2 black except for transparent margins; caudal fin brownish black; anal fin distally blackened with proximal portion speckled with black; pectoral and pelvic fins mostly brown with distal tips whitish. A 47 mm SL female specimen from the same lot had a light brown background colour with 6 brown, saddle-like blotches on dorsum -- first anterior to D1 origin, second between D1 and D2; third at D2 origin; fourth at D2 midpoint, fifth at D2 terminus, and sixth at caudal peduncle. In other colour respects, it is similar to the male specimen described above except for the greatly reduced D1.

Distribution. The distribution of *Periophthalmus weberi* is restricted to northern Australia, Irian Jaya and Papua New Guinea. Chatterjee & Siddiqi (1975) reported *Ps. weberi* from the Ganges Delta, however, I suspect their specimen might be referable to *Periophthalmodon septemradiatus*, the only other oxudercine species exhibiting marked sexual dimorphism in D1 shape.

Remarks. Of the 18 specimens listed in Eggert's type series, ten (in two lots) were available to me. Five of these are in ZMA 112.939, two of which are in far better condition than the other three (it appears they were preserved in a different manner). Of the two good specimens, one male and one female, I designate the male (71 mm SL) as lectotype, now catalogued as ZMA 119.465. The other five specimens (ZMA 112.942) are referable to *Periophthalmodon freycineti* rather than *Periophthalmus weberi*.

Etymology. The trivial name, *weberi*, honors Max Weber who published many works on fishes in the New Guinea-Australia region.

Pseudapocryptes

Fig. 1; Tables 1-8

Pseudapocryptes Bleeker, 1874: 299 (type species *Apocryptes lanceolatus* Cantor, 1850 [= *Eleotris lanceolata* Bloch & Schneider, 1801] by original designation).

Included species. Two species (*P. borneensis* and *P. lanceolatus*) known from mudflats in Singapore and

Kalimantan, the latter also found in Java, South Vietnam, Thailand, Malaysia, Burma and the east coast of India.

Diagnosis. *Pseudapocryptes* is unique amongst oxudercines in possessing 150 or more scales in a longitudinal series.

Description. Spinous dorsal fin V; second dorsal fin I, 28-32, dorsal fins connected by membrane basally; spinous dorsal fin pterygiophore formula: 3-1221*0, sixth pterygiophore lacking an associated spine; fifth spine longest; second dorsal fin base terminates within 5 scales of caudal fin; appressed second dorsal fin overlaps dorsal procurrent rays. Anal fin I, 26-30, first element occasionally with 1 or 2 segments but always unbranched; insertion of last ray slightly posterior to a vertical with insertion of last ray of second dorsal fin; height of anal fin less than that of second dorsal fin; appressed anal fin partly overlapping caudal fin. Pectoral fin 17-21, lanceolate. Pelvic fin I,5, united by membrane with fin of opposite side; frenum well developed. Caudal fin lanceolate, with 17 segmented rays, 15-16 of which are branched; dorsal procurrent rays 7-8, ventral procurrent rays 6-7. Scales cycloid and small, covering most of body except for snout and most of ventral surface of head, approximately 30 rows of prepelvic scales; lateral scales extending to midpoint of caudal fin; longitudinal scale count 150-275; TRF 31-63; TRB 31-59; TRDB 34-58; predorsal scales 56-113. Gill opening slightly more than length of pectoral fin base both dorsally and ventrally.

Teeth in both jaws in a single row; 17-45 caninoid teeth in upper jaw with bluntly rounded tips, 6-12 anteriormost teeth longest and overlap lower jaw when mouth closed, posterior teeth about half the size of those anteriorly; 12-26 caninoid teeth with bluntly rounded tips in lower jaw, all visible when mouth is closed, longest tooth of lower jaw approximately equal to that of upper jaw; 1 recurved, canine tooth on each side of symphysis internal to anterior margin of lower jaw.

Gape moderate, posterior tip of maxilla extending to a point almost equal to a vertical with posterior margin of eye; anterior nostril at the tip of a pendulous flap overlapping upper jaw laterally.

No membrane (dermal cup) covering ventral half of eye; posterior nostril directly anterior to anterior eye margin; anterior oculoscapular canal pore about one half eye diameter anteromedial to eye; small ridge on nape.

Ventral portion of first gill arch with 7 short, rounded gill-rakers; gill filaments feather like.

Etymology. The generic name, *Pseudapocryptes*, is from the Latin *pseud*, false, and *Apocryptes*, another genus in the subfamily, in reference to the similarity of these fishes; masculine gender.

Key to the Species of *Pseudapocryptes*

1. Anal fin with 27-29 total elements; body depth more than 14% SL; head length 20% SL or greater; head depth 11% SL or greater; pectoral fin length 13% SL or greater; pelvic fin length 12% SL or greater; many small, brown spots on body. (Singapore and Kalimantan)..*P. borneensis* (Bleeker)

—— Anal fin with 28-31 total elements; body depth less than 14% SL; head length typically less than 20% SL; head depth typically less than 10% SL; pectoral fin length 13% SL or less; pelvic fin length 12% SL or less; few small, brown spots, if any, on body. (east coast of India to South Vietnam and Indonesia)...........................
....*P. lanceolatus* (Bloch & Schneider)

Pseudapocryptes borneensis (Bleeker)

Figs 46-47; Tables 9-16

Apocryptes borneensis Bleeker, 1855: 421 (type locality, Bandjermassing, Kalimantan, Indonesia).
Pseudapocryptes borneensis.-Koumans, 1953: 247 (new combination).

Material examined. (6 specimens from a single locality; size range 67-100): SINGAPORE: SU 30370, 6: 67-100, all gravid females.

Diagnosis. Anal fin with 27-29 total elements (mean = 28.4); body depth 14.3-15.9% SL (mean = 15.1%); head length 20.0-21.9% SL (mean = 20.6%); head depth 11.1-13.1% SL (mean = 12.1%); pectoral fin length 13.1-16.6% SL (mean = 15.0%); pelvic fin length 12.3-13.8% SL (mean = 13.2%); many small, brown spots on head and trunk.

Colouration (based on an illustration in Bleeker 1983, pl. 440, fig. 3). Background colour green dorsally, greyish ventrally; numerous, black spots of small to moderate size on head, trunk and pectoral fin base; D1 posteriorly brown, anteriorly yellow except for brownish basal portion between I-II; D2 with columns of small, black spots on membrane, membrane proximally yellow, distally whitish; caudal fin proximally yellow, distally dusky with many small, black spots on rays; anal fin with yellowish elements, membrane whitish; pectoral fin rays yellow or dusky, membrane white; pelvic fin yellow.

Ground colour in preservative brown or tan; all

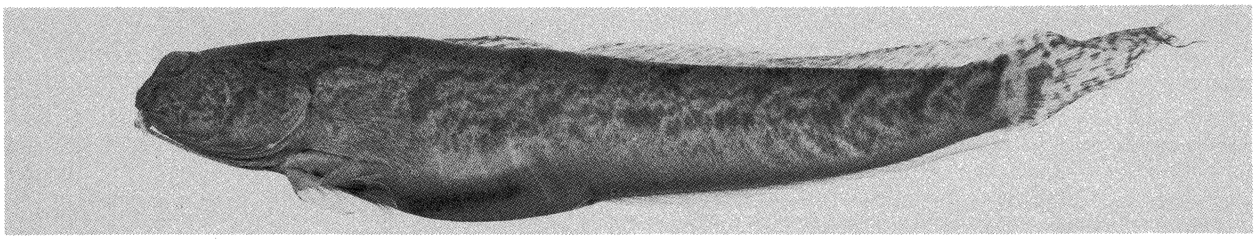

Fig.46. *Pseudapocryptes borneensis*, SU 30370, 72 mm SL, Singapore.

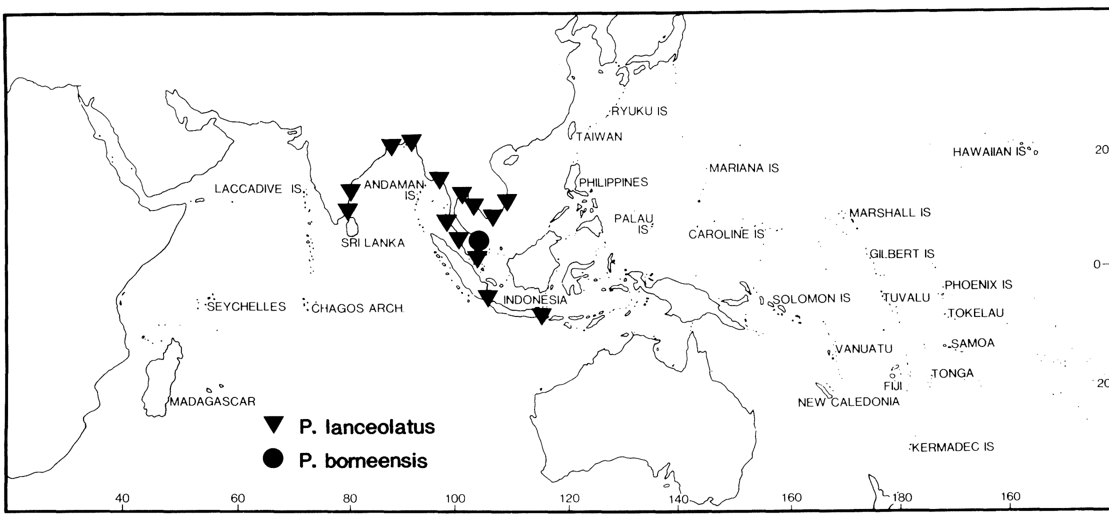

Fig.47. Known localities of examined material of *Pseudapocryptes*.

6 specimens available to me (SU 30370) possess many small, brown spots dorsal to the lateral midline in addition to 6-7 brown, diagonal, saddle-like blotches dorsally (but not as bold as those in *P. lanceolatus*), first at D1 origin, last at caudal fin base; brown diagonal stripe at posterior margin of preopercle and across cheek; dorsal fins with small, brown spots on elements; caudal fin yellowish with numerous brown spots on rays and a brown, vertical line proximally; pectoral, anal and pelvic fins yellow.

Distribution. Specimens were available from Singapore only. Given that the type locality is Bandjermassing, Kalimantan, *P. borneensis* is sympatric with *P. lanceolatus* there.

Remarks. Type material of *Apocryptes borneensis* is lost (M. van Oijen, in literature). Koumans (1953), based solely on Bleeker's description, retained *A. borneensis* as a distinct species and placed it in *Pseudapocryptes*. Koumans mentioned, however, that *P. borneensis* may represent juvenile *P. lanceolatus* due to Bleeker's description being based on specimens 60-112 mm (presumably total length). Subsequently, a figure of *P. borneensis* (Bleeker, 1983:pl.440, fig.3) was published that superficially is quite different from *P. lanceolatus*: numerous small, black flecks are scattered on the body, D1 is partially dusky, and the brown, saddle-like dorsal blotches are lacking. Although I have not examined any specimens which perfectly match Bleeker's figure, the figure of *P. borneensis* does show a degree of similarity to the specimens from Singapore (SU 30370) described above. Therefore, I am recognising SU 30370 as distinct from *P. lanceolatus* and tentatively identify the lot as *P. borneensis*. However, I think it prudent to postpone neotype designation for *P. borneensis* until specimens can be examined from the type locality.

Etymology. The trivial name, *borneensis*, refers to the type locality (Borneo).

Pseudapocryptes lanceolatus (Bloch & Schneider)

Pl.3B; Figs 47-48; Tables 9-16

Eleotris lanceolata Bloch & Schneider, 1801: 67, fig. 15 [listed as *E. lanceolatus*] (type locality, Tranquebar, India).
Gobius changua Hamilton, 1822: 41, pl. 5, fig. 10 (type locality, Ganges River, India).
Apocryptes dentatus Valenciennes *in* Cuvier & Valenciennes, 1837: 148 (type locality, Bay of Bengal).
Apocryptes lanceolatus.-Cantor, 1850: 1169 (new combination).
Pseudapocryptes lanceolatus.-Bleeker, 1874: 328 (new combination).
Boleophthalmus taylori Fowler, 1934: 159, fig. 128 (type locality, Bangkok, Thailand).
Apocryptodon edwardi Fowler, 1937: 257 (substitute

name for *Boleophthalmus taylori*, a secondary homonyn of *Apocryptodon taylori* Herre).

Material examined. (168 specimens from 8 general localities; size range 30-187 mm): INDIA: AMNH 1529, 2:100-103; AMS B.8034, 1:127; AMS B.8044, 2:138-139; MNHN A.1370, syntypes of *Apocryptes dentatus* Valenciennes, 2:124-139; SU 34777, 13:75-122; SU 40014, 4:129-141; SU 40081, 30:30-106; USNM 279313, 2:126-141; USNM 279321 (neotype), female, 136; USNM 279345, 1:51. BURMA: ANSP 77018, 4: 62-102; MSNG 15243, 2:87-99; NRM MAL/ 1934.087.3503, 7:45-83; NRM MAL/1934.457.3505, 4:107-125; NRM MAL/1934.484.3502, 12:71-111; NRM MAL/1935.229.3507, 3:68-70; NRM MAL/ 1935.359.3506, 4:100-114; USNM 44730, 1:115; USNM 89497, 1:77. MALAYSIA: USNM 151131, 3:41-43. SINGAPORE: ANSP 152740, 2:51-55. THAILAND: ANSP 60019, holotype of *Boleophthalmus taylori* Fowler, 157; ANSP 63020-22, 3:134-181; CAS 14120, 40:132-166; USNM 119636, 1:187; USNM 11987-88, 4:142-162; USNM 119991, 1:169; USNM 181862, 1:152. SOUTH VIETNAM: CAS 29363, 4:102-123; LICPP 1971270, 2: 98-105; USNM 47987, 1:138. INDONESIA: Java: AMNH 17532, 1:131; SU 62730, 4:54-121; ZMA 108.056, 2: 130-139. Kalimantan: AMNH 17286, 2:50-75.

Diagnosis. Anal fin with 28-31 total elements (mean = 29.3); body depth 9.9-13.6% SL (mean = 11.4%); head length 14.8-22.0% SL (mean = 17.7%); head depth 7.8-11.4% SL (mean = 9.3%); pectoral fin length 10.4-13.4% SL (mean = 11.9); pelvic fin length 9.0-11.5% SL (mean = 10.6%); few brown spots, if any, on body.

Colouration (based on an illustration in Bleeker 1983, pl. 440, fig. 4). Background colour greenish brown dorsally, yellow brown ventrally; 6 black, diagonal, saddle-like blotches dorsally, first located at D2 origin, the last at caudal fin base; dorsal fin elements slightly yellowish brown proximally with no stripes or spots; caudal fin yellowish with more than 12 wavy, vertical, brown, broken lines; anal and pectoral fins yellowish; pelvic fin proximally yellow, distally white.

Ground colour of preserved specimens tan or dark brown dorsally, yellow brown ventrally; specimens preserved for 50 years or more occasionally silvery white; 6-8 brown, diagonal bars coursing from the dorsal midline to lateral midline or slightly beyond, the first at D1 terminus, the last at caudal fin base; large brown spot on caudal peduncle in most specimens; brown bar coursing anteroventrally from eye to upper jaw; brown lines from eye to upper jaw on snout; small brown spots and irregular markings on cheeks, operculae and nape; all markings mentioned above more prominent in specimens less than 100 mm SL; dorsal fins dusky, sometimes with small brown spots on elements; all other fins, except caudal, essentially translucent; caudal fin with many brown spots arranged in irregular columns, slightly curved or wavy lines, and, occasionally, with a brown spot dorsally at base.

Distribution. Mudflats from the east coast of India to South Vietnam, Kalimantan and Java. Hora (1937) stated that *Pseudapocryptes* occupied deep burrows in spring tide pools during rainy season and retired to burrows in water five to six feet deep in dry season. Although I examined no specimens from China, Wu (1931), Koumans (1953) and Fowler (1962) recorded *P. lanceolatus* from there. Doubtful records include Japan (Tomiyama, 1936 and Koumans, 1953), and Tahiti (Koumans, 1953).

Remarks. Based on the original description (Bloch & Schneider, 1801), the identity of *Eleotris lanceolata* is uncertain. Type material is lost (H.J. Paepke, in literature) leaving only the original description and figure on which to base an opinion. The original figure (pl. 15) is quite detailed and indicates a number of what should be diagnostic features. However, a melding of two genera (*Parapocryptes* and *Pseudapocryptes*) seems apparent from the figure. Characteristic of *Pseudapocryptes* are the following from Bloch & Schneider's pl. 15: D1 V; D2 32 or 33; anal fin 30; and black bands on the caudal fin. The following characters from the figure would seem to refer best to *Parapocryptes*: longitudinal scale count slightly more than 70, head shape, colour pattern of body, and lack of prominent upper jaw teeth. Because of this confusion, I designate USNM 279321, female, 136 mm SL, from Madras as neotype of *Pseudapocryptes lanceolatus*. The selection of neotype was made from as near the type locality as possible. Type material of *Gobius changua* was not saved (Hora, 1934). Valenciennes (1837) first drew attention to the similarity between Hamilton's figure of *G. changua* and Bloch & Schneider's *Eleotris lanceolata*. Günther (1861) was the first to synonymise the two based on Hamilton's description and figure.

Etymology. The trivial name, *lanceolatus*, is from the Latin for elongate in reference to its shape.

Fig.48. *Pseudapocryptes lanceolatus*, SU 34777, 97 mm SL, India.

Scartelaos Swainson

Fig. 1; Tables 1-8

Scartelaos Swainson, 1839: 279 (type species *Boleophthalmus viridis* Valenciennes *in* Cuvier & Valenciennes, 1837 [= *Boleophthalmus histophorus* Valenciennes *in* Cuvier & Valenciennes, 1837], subsequent designation by Bleeker, 1874: 328.

Boleops Gill, 1863: 271 (type species *Boleophthalmus aucupatorius* Richardson, 1845 by original description).

Diagnosis. The only genus in the subfamily possessing barbels on the ventral surface of the head.

Description. Spinous dorsal fin V; second dorsal fin 23-27 or I, 25-27, first element of second dorsal fin typically segmented and unbranched, dorsal fins unconnected by membrane; spinous dorsal fin pterygiophore formula 3-1221*0, sixth pterygiophore lacking an associated spine; spinous dorsal fin base short, 5.0-10.5% SL; first 4 interspinous spaces about equal; second to fourth spine often filamentous; second dorsal fin attached to caudal fin in all but one species.

Anal fin 24-27 or I, 24-25, first element of second dorsal fin typically segmented and unbranched; anal fin attached basally to caudal fin in all but one species.

Pectoral fin 18-22.

Pelvic fin I,5, united by membrane with fin of opposite side; frenum well developed.

Caudal fin lanceolate with 17 segmented rays, 15 of which are branched; dorsal procurrent rays 1-4 (typically 2-3), ventrally 0-3 (typically 1-2).

Scales cycloid and very small, partially embedded, located only on posterior half of body, difficult to see without forced air and impossible to detect without magnification; scales in no discernible pattern, approximately 90-100 in a longitudinal series.

Teeth in both jaws in a single discontinuous row; 19-37 caninoid teeth in upper jaw with bluntly pointed tips, 10 most medial overlapping lower jaw and about twice the size of those laterally; 17-47 caninoid teeth in lower jaw, anteriormost teeth approximately subequal but much smaller than the anterior teeth in upper jaw; posteriorly on each side of the lower jaw are 8, tiny teeth set farther back from jaw edge than others; anterior symphyseal area lacking teeth; 1 large, recurved, canine tooth on each side of symphysis internal to anterior margin of lower jaw.

Gape moderate, posterior tip of maxilla reaching a vertical from posterior margin of eye; large, fleshy upper lip overlain by flap of skin which covers most of upper jaw, on each side of this flap is the anterior nostril represented by a flaccid, fleshy tube; 6-12 short barbels ventrally on each side of head near posterior curve of lower jaw.

Dermal cup present; posterior nostril anterolateral to eye; anterior oculoscapular canal pore about midway between posterior nostril and upper lip.

Ventral portion of first gill arch with 4-5 gill rakers; gill filaments thread like.

Etymology. The generic name, *Scartelaos*, is presumably from *scarto*, Greek for leaper and, *laos*, Greek for stone, or possibly *laus*, Latin for fame. *Scartelaos* has been spelled *Scartolaus* by some authors according to Norman (1966). Masculine gender. Swainson (1839) listed three species in his new genus *Scartelaos*, all species supposedly attributable to Hamilton (1822): *viridis, chrysophthalmus* and *calliurus*. Only *Gobius viridis* is attributable to Hamilton (1822); the trivial names *calliurus* and *chrysophthalmus* listed by Swainson as appearing in Hamilton's book, do not. Swainson correctly lists *G. viridis* as fig. 12 on pl. 32 of Hamilton (1822); however, Swainson's *calliurus* (listed as fig. 10, pl. 5) is *Gobius changua* Hamilton and *chrysophthalmus* (listed as fig. 10, pl. 37) is *Gobius bato* Hamilton. *Gobius changua* and *G. bato* are treated in my study under *Pseudapocryptes* and *Apocryptes* respectively. The authority of the trivial names *calliurus* and *chrysophthalmus* is unclear; I consider these names *nomina nuda*. Bleeker (1874) designated *Gobius viridis* Hamilton 1822 as the type species for *Scartelaos*. Subsequently, Whitley (1933), Koumans (1953) and Fowler (1962) drew attention to the homonym *Gobius viridis* Otto, 1821. Based on the International Code, Article 59(a), Whitehead & Joysey (1967) asserted that *Gobius viridis* Hamilton (1822) should be permanently rejected because of its standing as a junior primary homonym. Whitehead & Joysey (1967) designated *Boleophthalmus histophorus* Valenciennes, 1837 as the replacement name for *G. viridis*.

Key to the Species of *Scartelaos*

1. Single, prominent barbel on ventral midline near symphysis of lower jaw; upper jaw teeth usually fewer than 30. (Pakistan to Japan and Australia).............*S. histophorus* (Valenciennes)

—— Fleshy mounds but no barbel on ventral midline near symphysis of lower jaw; upper jaw teeth usually more than 30..2

2. 15-18 vertical, brown bars on trunk; large, black spots basally on posterior half of second dorsal fin. (Arabian Gulf to Pakistan)..*S. tenuis* (Day)

—— No brown bars on trunk nor large, black spots on fin..3

3. Head depth less than 13% SL; caudal fin length greater than 22% SL; length of D1 base greater than 9% SL; D2 and anal fins connected by membrane to caudal fin; 3 horizontal, brown lines posteriorly on D2. (Andaman Islands)................................. *S. cantoris* (Day)

—— Head depth greater than 13% SL; caudal fin length less than 20% SL; length of D1 base less than 9% SL; D2 and anal fins not connected by membrane to caudal fin; no brown lines on D2. (China)... *S. gigas* Chu & Wu

Scartelaos cantoris (Day)

Figs 49-50; Tables 9-16

Apocryptes cantoris Day, 1871: 693 (type locality, Andaman Islands).
Apocryptichthys cantoris.-Day, 1876: 302 (in part, pl. 62, fig. 7 does not pertain to this species), new combination.
Boleophthalmus glaucus Day, 1876: 306, pl. 65, fig. 3 (type locality, Andaman Islands).
Boleophthalmus cantoris.-Springer, 1978: 9, fig. 6 (designation of lectotype and new combination).

Material examined. (3 specimens from a single locality; size range 64-119): ANDAMAN ISLANDS: AMS B.8121, probable syntype of *Boleophthalmus glaucus* Day, 119; BMNH 1870.5.18.23 (lectotype), 64; RMNH 2009, syntype of *Boleophthalmus glaucus* Day, 69.

Diagnosis. No barbel on ventral midline near symphysis of lower jaw; upper jaw teeth 25-37 (mean = 30.7); head depth 10.4-12.5% SL (mean = 11.3%); caudal fin length 22.5-27.2% SL (mean = 24.3%); length of D1 base 9.1-10.5% SL (mean = 9.6%); 5-10 narrow, pale, vertical bars on body anterior to D2 origin; no large, black spots but 3 horizontal, brown-black lines basally on D2, most distinct posteriorly; D2 and anal fins connected by membrane to caudal fin.

Colouration. No colour notes or photographs of live or freshly dead individuals available.

Ground colour in preservative pale brown; many scattered, small, brown-black spots on nape, cheek, gill cover, and pectoral base; 5-10 narrow, pale, vertical bars on body anterior to D2; D1 mostly pale except for duskiness between I-II and at tip of second spine; D2 pale except for 3 longitudinal, brown-black lines beginning at sixth element and extending to last ray, lines more prominent posteriorly; caudal fin dusky medially; anal and pelvic fins off white; pectoral fin rays slightly dusky; remnants of 2-3 brownish bars crossing nape; many tiny, brown spots covering body, spots only visible with magnification.

Distribution. Known only from the Andaman Islands.

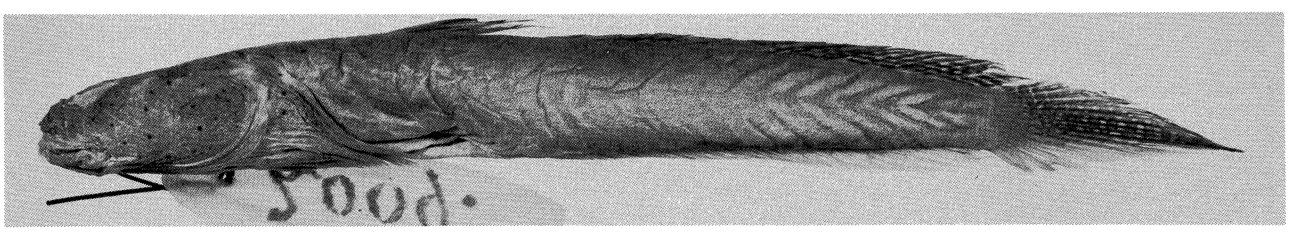

Fig.49. *Scartelaos cantoris*, RMNH 2009, 70 mm SL, Andaman Islands.

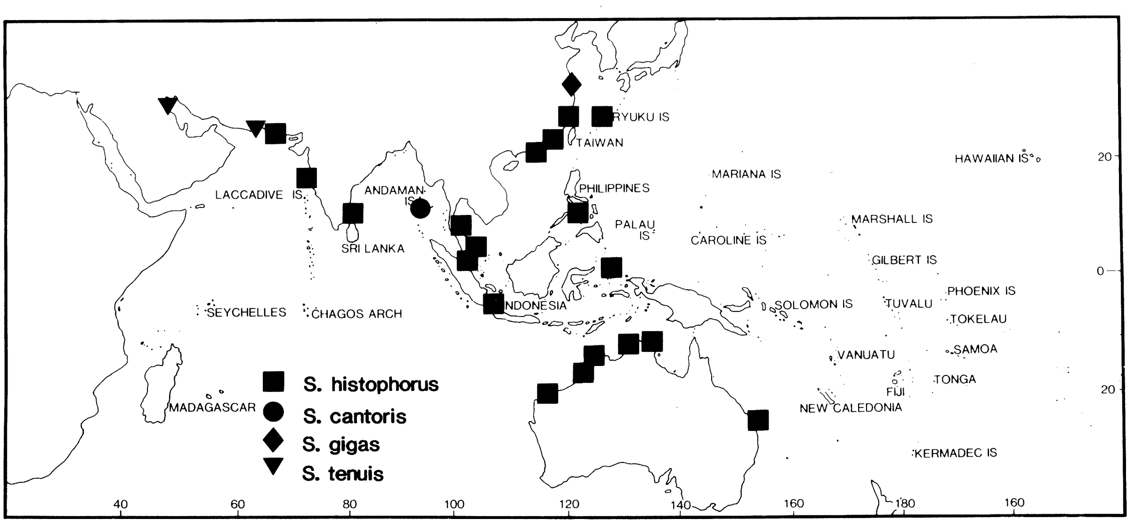

Fig.50. Known localities of examined material of *Scartelaos*.

Remarks. Even though he misassigned it to *Boleophthalmus*, Springer (1978) designated the lectotype (BMNH 1870.5.18.23), provided a valuable historical review, and redescribed *Scartelaos cantoris*.

Etymology. The trivial name, *cantoris*, is presumably a patronym for T. Cantor, a British naturalist, who collected and published on fishes in Asia.

Scartelaos gigas Chu & Wu

Figs 50, 52; Tables 9-16

Scartelaos gigas Chu & Wu *in* Chu, 1963: 437, fig. 333 (type locality, China).

Material examined. USNM 148438, male, 172 mm SL, collected June, 1882, Shanghai, China. (This was the only available specimen.)

Diagnosis. No barbel on ventral midline near symphysis of lower jaw; upper jaw teeth 37; head depth 13.1% SL; caudal fin length 18.5% SL; length of D1 base 5.0% SL; no vertical bars on body; no large, black spots or stripes basally on posterior half of D2; D2 and anal fins not connected by membrane to caudal fin.

Colouration. No colour notes or photographs of live or freshly dead individuals available.

Ground colour tan; numerous, tiny, brown spots on nape, trunk, D2 and caudal fin; D1 pale on ventral half, dorsally dusky except for whitish membrane between II-III; distal margin of D2 blackish; anal, pelvic and pectoral fin pale tan.

Distribution. Only available specimen collected in Shanghai, China; habitat unknown.

Remarks. Chu & Wu (1963) based their description on two specimens now deposited at the Shanghai Fishery Institute and collected from Zhejiang Province: the holotype (156 mm, No. 43717) collected at Ta Chen Island in the Fall of 1958 and the paratype (146 mm, No. 59-0049) collected at Kan Men on 22 October 1959. Although I have not examined these types, the original figure and description of *Scartelaos gigas* is sufficiently detailed to ally my specimen with those of Chu & Wu.

Etymology. The trivial name, *gigas*, is Greek for giant.

Scartelaos histophorus (Valenciennes)

Pl. 3C; Figs 50-51; Tables 9-16

Gobius viridis Hamilton, 1822: 42, pl. 32, fig. 12 (type locality, Ganges River, India), a primary homonym of *G. viridis* Otto, 1821.
Boleophthalmus histophorus Valenciennes *in* Cuvier & Valenciennes, 1837: 210 (type locality, Bombay, India).
Boleophthalmus sinicus Valenciennes *in* Cuvier & Valenciennes, 1837: 215 (type locality, Canton, China).
Boleophthalmus chinensis Valenciennes *in* Cuvier & Valenciennes, 1837: 215 (type locality, Canton, China).
Bolephthalmus aucupatorius Richardson, 1845: 208 (type locality, China Seas).
Boleophthalmus campylostomus Richardson, 1845: 209 (type locality, Canton, China).
Apocryptes macrophthalmus Castelnau, 1873: 87 (type locality, northern Australia).
Gobiosoma guttulatum Macleay, 1878: 357, pl, 9, fig. 6

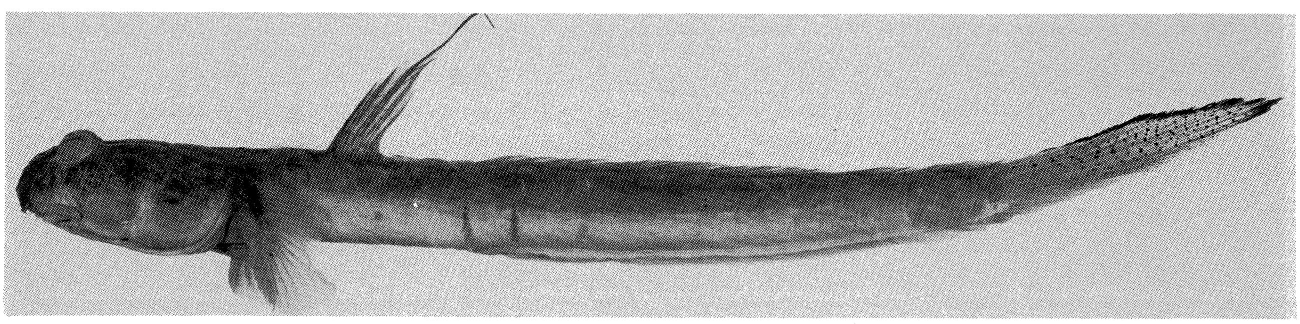

Fig.51. *Scartelaos histophorus*, NTM 10727-003, 109 mm SL, Northern Territory, Australia.

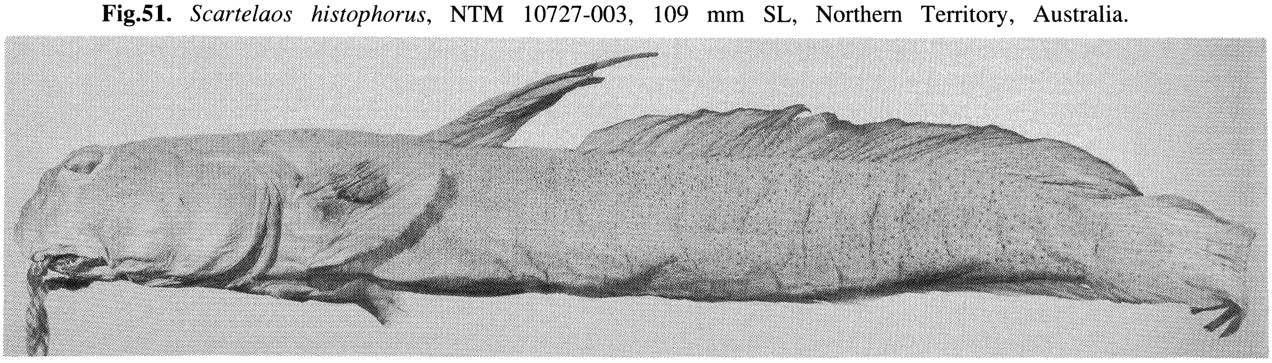

Fig.52. *Scartelaos gigas*, USNM 148438, 172 mm SL, China.

(type locality, Port Darwin, Northern Territory, Australia).

Gobiosoma punctularum De Vis, 1884: 445 (type locality, South Seas).

Boleophthalmus novaeguinea Hase, 1914: 535, fig. 8 (type locality, New Guinea).

Material examined. (248 specimens from 15 localities; size range 14-105): PAKISTAN: LACM 38137-1, 2:66; LACM 38141-3, 8:51-60; LACM 38301-2, 2:58-65. INDIA: Bombay: MNHN A.1477 (syntypes), 2:99-105; MNHN A.1478 (syntypes), 3:81-103. Madras: USNM 279160, 2:68-98. THAILAND: ANSP 63090, 1:79; CAS 56341, 3:92-99. MALAYSIA: USNM 278437, 2:25-45. INDONESIA: USNM 243432, 5:60-84; USNM 243433, 38:49-98; ZMA 113.003, 8:61-94. SOUTH SEA ISLANDS: QM I.103, syntypes of *Gobiosoma punctularum* De Vis, 2:37-41. BORNEO: MSNG 12706, 1:79. AUSTRALIA: Western Australia: BMNH 1933.8.14:16, 1:68; NTM S.10802-009, 17:15-33; WAM P.9420-23, 4:71-100; WAM P.27368-002, 4:33-71. Northern Territory: AMS I.16396-001, syntypes of *Gobiosoma guttulatum* Macleay, 8:54-90; AMS I.21221-002, 1:95; NTM S.10084-001, 1:88; NTM S.10110-001, 1:65; NTM S.10151-001, 1:90; NTM S.10309-001, 1:62; NTM S.10413-003, 3:19-50; NTM S.10418-002, 14:31-97; NTM S.10529-001, 1:93; NTM S.10649-008, 17:16-29; NTM S.10727-003, 15: 49-97; QM I.20313, 1:58; QM I.20314, 1:73; USNM (uncatalogued), 5:26-36. Queensland: AMS I.22036-003, 9:14-80; AMS I.23943-009, 2:34-51; QM I.2706-10, 4: 68-87. PHILIPPINES: SU 63617, 4:86-92; USNM 51992, 1:77; USNM 102537, 2:90-92; USNM 112846, 14:66-83; USNM 135685, 3:82-86; USNM 148592, 6:59-86. MACAO: ANSP 77059, 1:80. CHINA: AMNH 35819, 22:61-81; ANSP 29826, 1:71; BMNH 1965.8.12:52-53, holotype of *Boleophthalmus aucupatorius* Richardson, 50; BMNH 1917.7.14:89 (labelled as "type" of *Boleophthalmus campylostomus* Richardson), 69. JAPAN: LICPP 1984043, 2:57-62.

Diagnosis. Prominent barbel on ventral midline near symphysis of lower jaw; upper jaw teeth 19-31 (mean = 24.7); head depth 10.1-12.4% SL (mean = 11.2%); caudal fin length 18.5-25.1% SL (mean = 22.2%); length of D1 base 5.7-7.5% SL (mean = 6.4%); 4-7 vertical, narrow, bluish grey bars on trunk; no large, black spots or stripes basally on posterior half of D2; D2 and anal fins connected by membrane to caudal fin.

Colouration (based on a photograph of an 89 mm SL specimen appearing in Masuda *et al.*, 1984:257, fig. E, identified as *Scartelaos viridis*, reproduced herein as Pl. 3C). Greenish grey dorsally, pale blue ventrally; cheek with a few, small, bluish spots; trunk with scattered bluish spots; 7 greenish, narrow, vertical bars on trunk, prominent against pale blue background, anteriormost immediately dorsal to genital papilla, second bar dorsal to second anal fin element, third bar dorsal to 5th element, fourth dorsal to 9th element, fifth dorsal to 14th element, sixth dorsal to 17th, and seventh dorsal to 21st anal fin element; bluish spot between fourth and fifth vertical bars; spinous dorsal fin greenish grey; second dorsal fin dusky with randomly arranged small blue spots; bluish spots on caudal fin typically forming 3-5 narrow, vertical lines, dorsoposterior margin black; anal fin transparent; pectoral and pelvic fins dusky; blue spots on pectoral fin and base.

Ground colour of preserved specimens slate grey or brown dorsal to lateral midline and white or tan ventrally; pigment patterns similar to that described above however some specimens no longer retain trunk bars. Juveniles typically lack trunk bars and fin spots.

Distribution. Mud and sandflats along bay shores from Pakistan to Japan and Australia.

Remarks. Type material of *Gobius viridis* was not saved (Hora, 1934), that of *Apocryptes macrophthalmus* is not at MNHN (M.L. Bauchot, in literature) or the Museum of Victoria (M.F. Gomon, in literature), and that of *Boleophthalmus novaeguinea* could not be located at museums in Tübingen, Frankfurt, or Berlin. All of the above are assignable to *Scartelaos histophorus* based on original descriptions and/or figures. Both *Boleophthalmus sinicus* Valenciennes and *B. chinensis* Valenciennes were described from Chinese paintings. The descriptions were brief, no type specimens designated, and the artist's name was not given. Consequently, it is difficult to assign these names even to the proper genus. Koumans (1953) tentatively assigned both species as junior synonyms of *Scartelaos viridis* (= *S. histophorus*); I have no reason to alter this assignment. Macnae (1968) and Murdy (1986) reported ecological and behavioral observations of *S. histophorus*.

Etymology. The trivial name, *histophorus*, is presumably from the Greek *histos*, upright web-beam of a loom, and *phoras*, to bear.

Scartelaos tenuis (Day)

Figs 50, 53; Tables 9-16

Boleophthalmus tenuis Day, 1876: 305, pl. 65, fig.1 (type locality, Karachi, Pakistan).

Material examined. (28 specimens from 3 localities; size range 55-125): ARABIAN GULF: USNM 196244, 1:103. KUWAIT: BMNH 1981.3.19:15-17, 3:93-98. PAKISTAN: AMS B.7618 (lectotype), 117; AMS B.8037 (paralectotype), 122; BMNH 1889.2.1:3482, 6:98-125; LACM 38141-2, 15:55-83; USNM 171789, 1:105.

Diagnosis. No barbel on ventral midline near symphysis of lower jaw; upper jaw teeth 31-37 (mean = 32.8); head depth 9.5-10.8% SL (mean = 10.2%); caudal fin length 21.7-26.3% SL (mean = 23.0%); length of D1 base 5.6-8.3% SL (mean = 7.1%); 15-18 vertical, brown bars on trunk; large, black spots basally on posterior half of second dorsal fin; D2 and anal fins not connected by membrane to caudal fin.

Colouration (based on a photograph of a 142 mm SL individual from Kuwait appearing in Kuronuma & Abe, 1972, pl. 16). Background colour of head and trunk light grey; head with dark grey mottling dorsally; trunk with at least 6 blackish grey blotches posteriorly that appear to be continuations of D2 blotches; D1 blackened distally, proximally grey; D2 mostly grey with a black distal margin and white stripe inframarginally, at least 5 greyish blotches posteriorly; caudal fin dusky throughout with some orange spots, dorsal and distal margin black, white stripe inframarginally along dorsal edge, ventral portion of fin faintly orange; anal and pelvic fins yellowish; pectoral fin grey with small, dusky spots.

Ground colour of preserved specimens brownish; 15-18 vertical, brown bars on trunk, anteriormost ventral to D1 origin, posteriormost on caudal peduncle; numerous, brown spots on nape and smaller, brown spots on cheeks, operculae, pectoral bases and fins; D1 pale basally, black distally except for white spot between I-III; D2 speckled with tiny, dusky spots, dorsoposterior margin black; 4-5 large, black spots basally on posterior half of D2; dorsoposterior margin of caudal fin black, medially dusky except for small, white spots with black centers; anal and pelvic fins transparent. Some preserved specimens do not retain the trunk pigment patterns.

Distribution. Mud and sand flats from Arabian Gulf to Pakistan. Collections made by Camm Swift near Korangi Creek, Sind, Pakistan indicate *Scartelaos tenuis* and *S. histophorus* are syntopic. This area may represent the south-easternmost limit of *S. tenuis* and north-westernmost limit of *S. histophorus*.

Remarks. Day's syntypes are hereby designated as lectotype (AMS B.7618) and paralectotype (AMS B.8037).

Etymology. The trivial name, *tenuis*, is Latin for thin, in reference to the slender shape of this fish.

Zappa n.gen.

Figs 20, 54; Tables 1-8

Included species. The genus contains one species, *Z. confluentus*, from Papua New Guinea.

Diagnosis. Distinguishable from all other members of the subfamily in having the first spinous dorsal fin pterygiophore bent posteriorly at a point three quarters along its length to extend horizontally over tip of fourth neural spine.

Description. Spinous dorsal fin V; second dorsal fin 27-30, dorsal fins connected by membrane; spinous dorsal fin pterygiophore formula: 3-1221*0, sixth pterygiophore lacking an associated spine; fifth spine longest; 4 interspinous spaces about equal; second dorsal fin connected to caudal fin.

Anal fin 26-28; insertion of last ray at a vertical to that of the last ray of the second dorsal fin; height of anal fin equal to that of second dorsal fin; anal fin connected to caudal fin.

Pectoral fin 18-21, medial rays longest.

Pelvic fin I, 5, united by membrane with fin of opposite side; frenum well developed.

Caudal fin lanceolate, with 17 segmented rays, 15 of them branched; dorsal procurrent rays 4-5, ventral procurrent rays 3-4.

Scales embedded, small and cycloid, difficult to discern and impossible to count with accuracy. Roberts (1978) claimed there were 140-180 longitudinal scales and 100 predorsal scales; I find far fewer scales. Longitudinal scale series does not extend anterior to a vertical point roughly equivalent to the origin of the second dorsal fin and scale numbers do not exceed 80 or 90. Contrary to Roberts, I find the predorsal area, snout, cheeks and gill covers scaleless. I agree with Roberts that the prepelvic area and pectoral bases are scaleless but did find some scales on the ventral surface of the abdomen.

Gill opening extending length of pectoral fin base, slightly more ventrally.

Teeth in both jaws in a single row; 35-48 caninoid teeth with bluntly rounded tips in upper jaw, 2 on either side of midline long and overlapping lower jaw when mouth is closed; posterior teeth in upper jaw about half the size of those anteriorly; 19-22 compressed teeth with bluntly rounded tips in lower jaw, all visible when mouth is closed; longest tooth of lower jaw much shorter than longest tooth of upper jaw, but all lower jaw teeth larger than posterior teeth in upper jaw; 1 large, recurved, canine tooth on each side of symphysis internal to anterior margin of lower jaw.

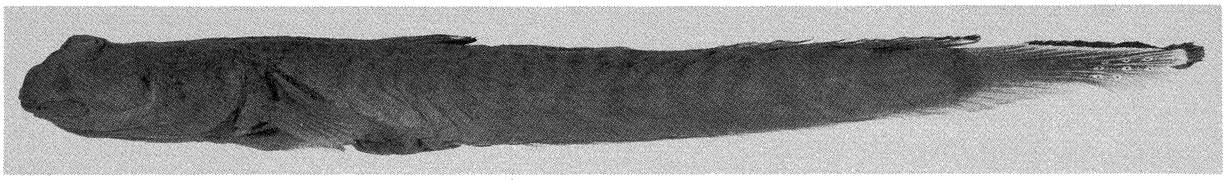

Fig.53. *Scartelaos tenuis*, LACM 38141-2, 73 mm SL, Pakistan.

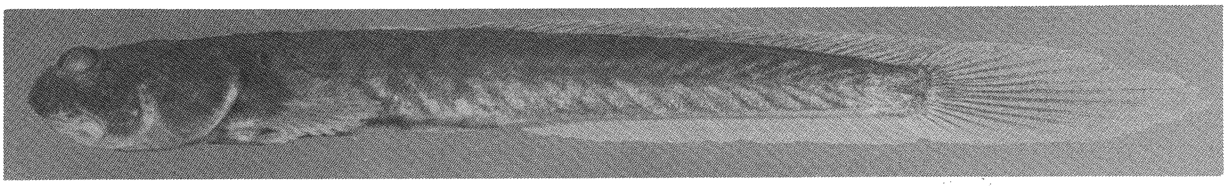

Fig.54. Holotype of *Zappa confluentus*, USNM 217952, 35 mm SL, Papua New Guinea.

Gape moderate, posterior tip of maxilla extending to a point almost equal to a vertical with posterior eye margin; anterior nostril at tip of a pendulous flap overlapping lateral portions of upper jaw.

No membrane (dermal cup) covering ventral half of eye; posterior interorbital pore present; posterior nostril with short flap and located directly anterior to eye margin; slightly anterior to posterior nasal opening is anterior oculoscapular canal pore.

Ventral portion of first gill arch with 4 gill rakers, 3 of which are rudimentary; gill filaments feather like.

Etymology. The generic name is in honour of Frank Zappa for his articulate and sagacious defense of the First Amendment of the U.S. Constitution. Masculine gender.

Zappa confluentus (Roberts)

Fig. 54

Pseudapocryptes confluentus Roberts, 1978: 68, fig. 39 (type locality, Fly River, Papua New Guinea).

Material examined. (17 specimens from one locality; size range 15-44): PAPUA NEW GUINEA: USNM 217305 (paratype), 44; USNM 217306 (paratypes), 15: 15-38; USNM 217952 (holotype), 35.

Diagnosis. Total D2 elements 27-30 (mean = 28.1); caudal fin length 21.4-27.9% SL (mean = 25.0); head length 22.0-25.7% SL (mean = 23.9%).

Colouration. Roberts (1978) provided the following colour description of preserved specimens that he maintained was similar in all or almost all respects to that in life: "body more or less uniformly dark brownish dorsally and laterally; side of abdomen with about 6 oblique dark bands; ventral surface of head and abdomen pale (not purple or blood red in life); all fins hyaline." I cannot add anything to this description except that none of the specimens I examined (which are the same ones that Roberts originally collected) retained the lateral oblique bands.

Distribution. *Zappa confluentus* is known only from the type locality - lower Fly River at Madiri, about 74 km upriver from Toro Pass, Papua New Guinea. Roberts (1978) observed hundreds of individuals on an exposed mudflat flipping about but never on their pelvic fins in an upright position.

Etymology. The trivial name, *confluentus*, is from the Latin referring to the membranous connection of the dorsal and anal fins with the caudal fins.

Defining Characters of the Oxudercinae

In this section, the procedure of Weitzman & Fink (1985) is followed: apomorphies are numbered sequentially so that they can be identified on the cladogram (Fig. 55) and under each number a morphological description of the

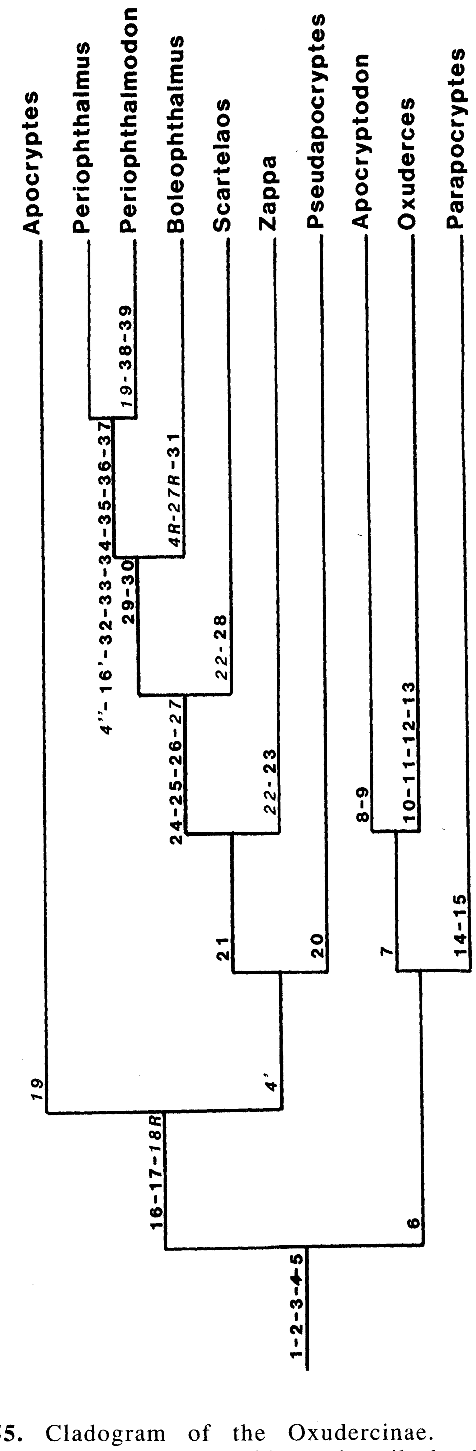

Fig. 55. Cladogram of the Oxudercinae. Numbers correspond to apomorphies described in text. Homoplasious characters are italicised and reversals are indicated by "R". All other characters are unique and unreversed.

apomorphy is followed by description of the character as found in outgroup comparison. Members of the Oxudercinae form a distinctive group of gobiid fishes that have only been formally united recently (Hoese, 1984). Characters used by Hoese to ally the oxudercines are: a single pterygiophore preceding anterior to the first hemal spine; lateral process of sphenotic large and not in contact with eye; eyes displaced forward and upward; tongue fused to floor of mouth; teeth flattened; second dorsal fin usually long based; and two epurals. Only the first three of the above characters can be considered synapomorphies of the Oxudercinae, all other features are shared with at least one other group of gobiid fishes. Diagnostic features of the Oxudercinae that corroborate the hypothesis that the inclusive taxa (*Apocryptes, Apocryptodon, Boleophthalmus, Oxuderces, Parapocryptes, Periophthalmodon, Periophthalmus, Pseudapocryptes, Scartelaos* and *Zappa*) are more closely related to each other than to any other gobiids are:

1. Complex character involving displacement of the eyes anterodorsally, elongation of the frontals, shift in location of the sphenotics such that they are no longer in contact with the eye, and rearrangement of adductor mandibulae complex such that it also originates from the frontal as well as the sphenotic and preopercular bones (Fig. 56).

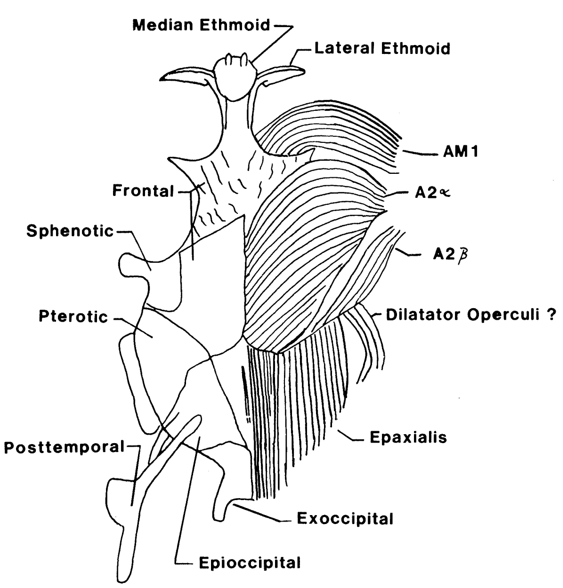

Fig.56. *Oxuderces dentatus*, dorsal view of the cranium, musculature removed from the left side.

In most other gobiids and gobioids, the eyes are situated laterally and do not extend appreciably above the interorbital region; the frontals are not elongate or enlarged; the sphenotic is in contact with eye or orbit; and no portion of the adductor mandibulae complex originates from the frontal bone (Fig. 57). In amblyopine gobies, the frontals are slightly elongate but not to the extent shown in the Oxudercinae. Some could argue that the various morphological changes in Character 1 were independent of each other. However, I feel strongly that these structural changes were interdependent and that to list them individually would be misleading. Even though all aspects of this complex may not have evolved simaltaneously, they probably do not reflect separate evolutionary events. For example, hypertrophy of the head musculature probably occurred soon after the elongation of the frontals.

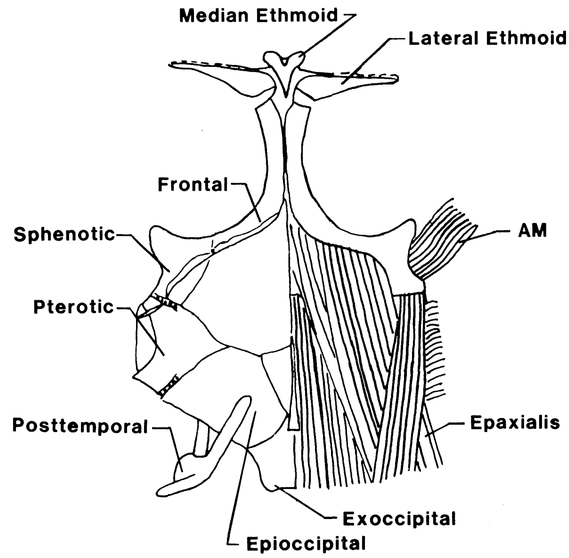

Fig.57. *Evorthodus lyricus* dorsal view of the cranium, muscles removed from the left side.

2. Anterior nostril at tip of pendulous flap that overlaps the upper jaw (Fig. 58).

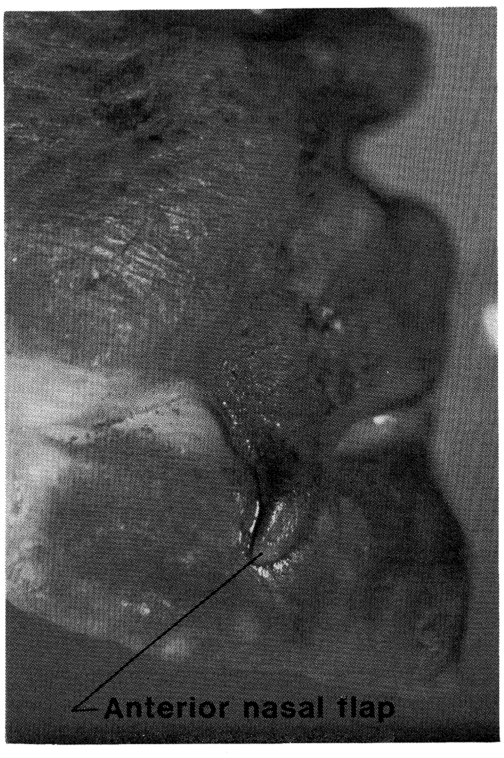

Fig.58. *Periophthalmodon freycineti*, lateral view of snout, right side.

In most other gobiids and gobioids, the anterior nostril is at the end of a short tube located near the upper jaw (Fig. 59). According to D.F. Hoese (in literature), *Mugilogobius* has a short nasal flap overlapping the upper jaw, and some eleotridids also possess a nasal flap. However, none of the above exhibit the same condition possessed by oxudercines.

3. The ventroposterior process of palatine greatly reduced such that there is little or no overlap with the ectopterygoid (Fig. 60).

In most other gobiids and gobioids, the palatine possesses a large process directed ventroposteriorly that overlaps and sometimes is joined to the ectopterygoid (Fig. 61). In the two amblyopine genera examined (*Brachyamblyopus* and *Trypauchen*), the ventroposteriorly directed process is reduced but not to the extent shown in oxudercines. This process and the ectopterygoid are closely applied and the ectopterygoid is moderately expanded for most of its length. Both *Brachyamblyopus* and *Trypauchen* have the same or similar spinous dorsal fin pterygiophore formula (DF of Birdsong *et al*., 1988) to the Oxudercinae (3-12210 in *Brachyamblyopus*, 3-1221 in *Trypauchen*) but both have more than 16 caudal vertebrae and thus differ from the Oxudercinae, and are therefore excluded.

4. Ascending processes of premaxillae greatly reduced and oriented vertically (Fig. 62).

In the vast majority of other gobioids, the ascending processes of the premaxillae are moderate to well developed and, typically, terminate dorsoposteriorly at or near the median ethmoid. At least two xenisthmid genera (*Tyson* and *Xenisthmus*) lack any vestige of the ascending

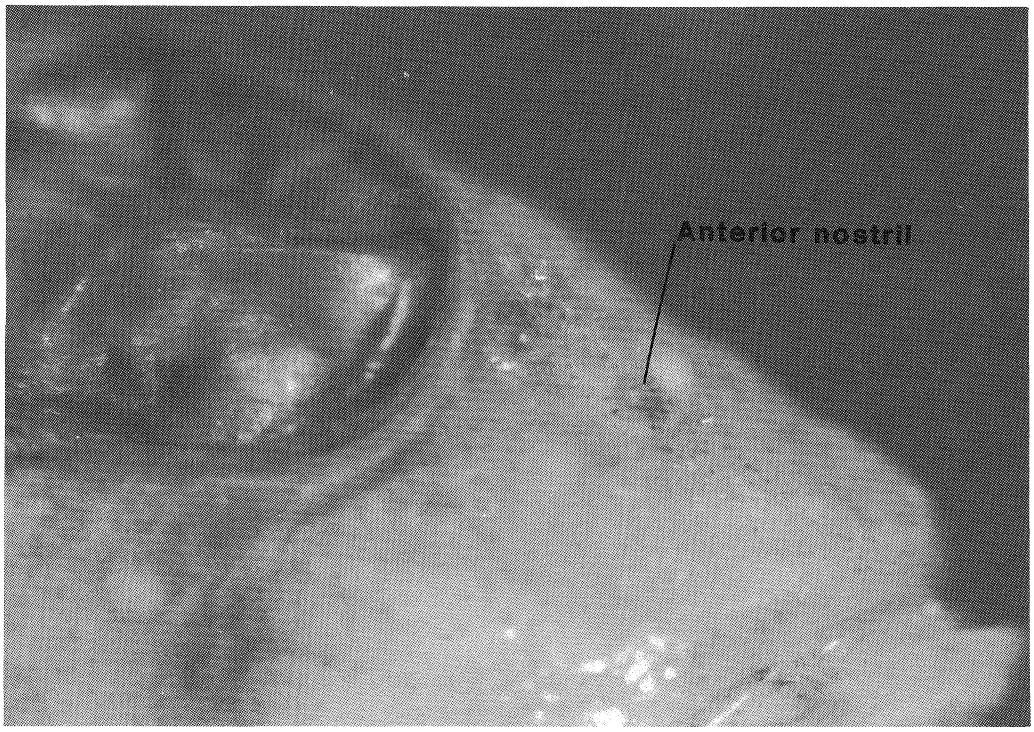

Fig.59. *Gnatholepis* sp., lateral view of snout, right side.

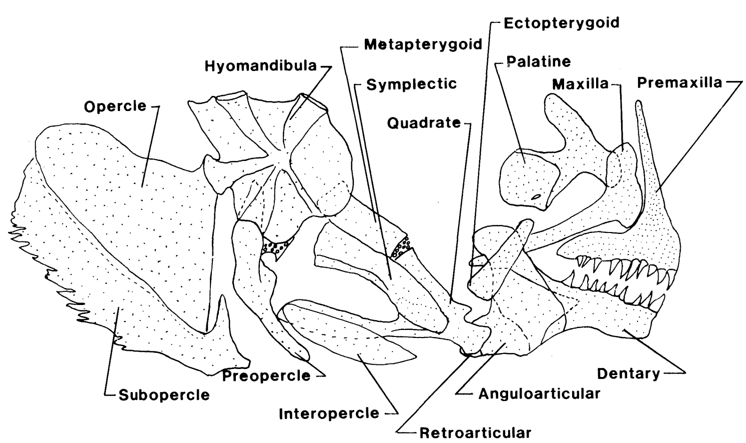

Fig.60. *Periophthalmus kalolo*, internal view of left suspensorium and jaws.

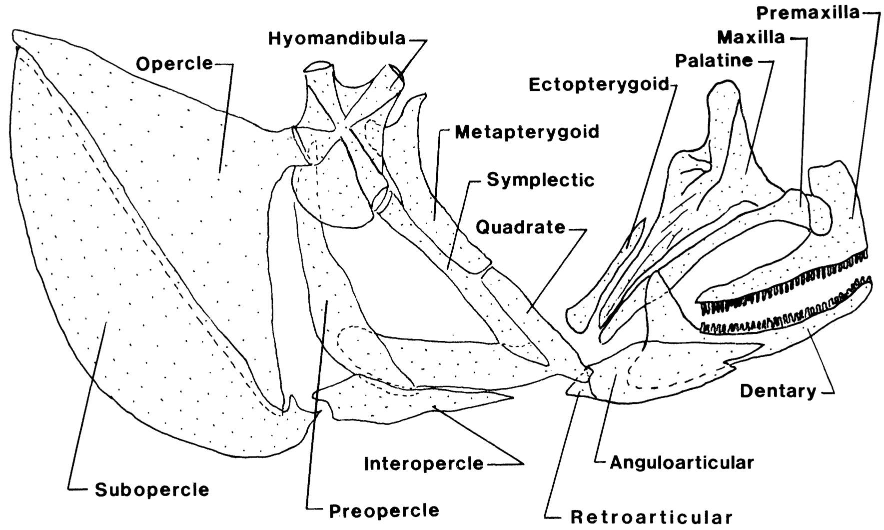

Fig.61. *Evorthodus lyricus*, internal view of left suspensorium and jaws.

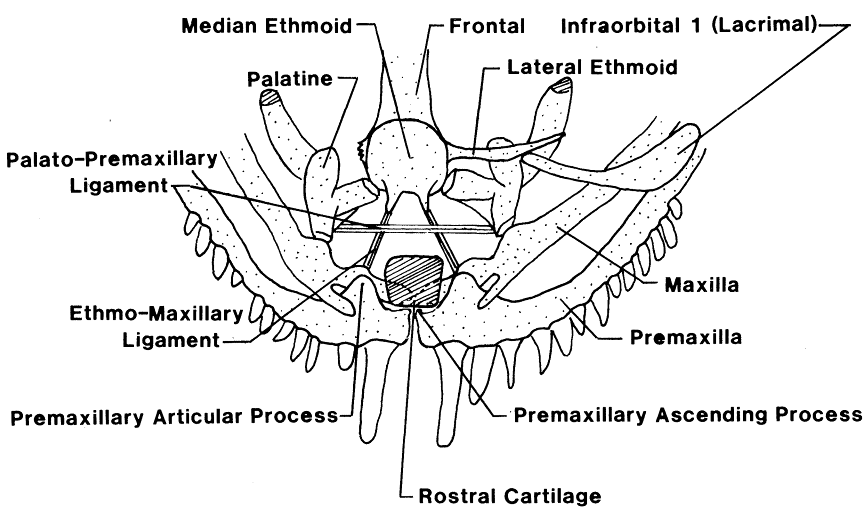

Fig.62. *Oxuderces dentatus*, dorsoanterior view of snout region (frontals, maxillae and premaxillae truncated posteriorly; lateral ethmoid and infraorbital 1 removed from right side).

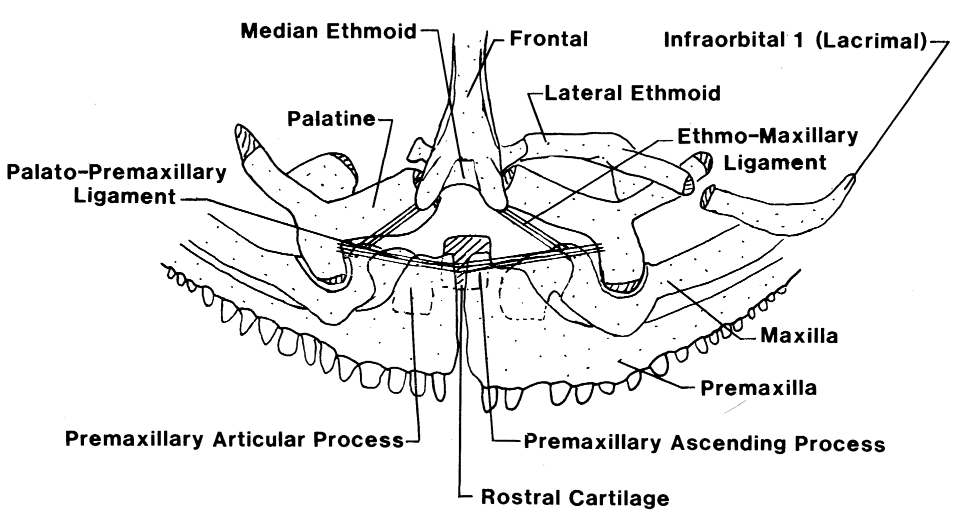

Fig.63. *Pseudapocryptes lanceolatus*, dorsoanterior view of snout region (frontals, maxillae and premaxillae truncated posteriorly; lateral ethmoid and infraorbital 1 removed from right side).

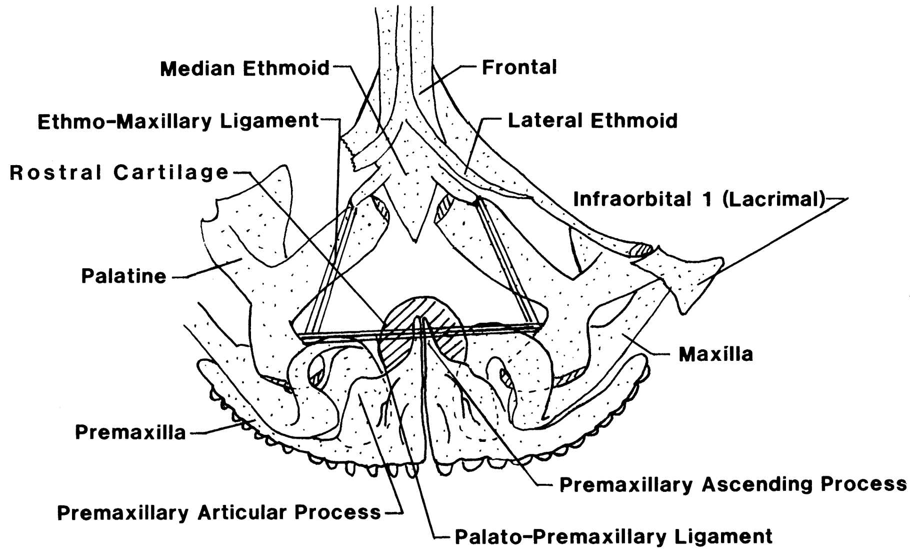

Fig.64. *Periophthalmus kalolo*, dorsoanterior view of snout region (frontals, left palatine, maxillae and premaxillae truncated posteriorly; lateral ethmoid and infraorbital 1 removed from right side).

processes (Springer, 1983). Within the Oxudercinae, significant reduction in size and orientation of the ascending processes of the premaxillae is found in *Apocryptes, Apocryptodon, Boleophthalmus, Oxuderces* and *Parapocryptes*. Moderately developed ascending processes are present in *Pseudapocryptes, Scartelaos* and *Zappa*, whereas in *Periophthalmodon* and *Periophthalmus*, the ascending processes are well developed. Based on other character distributions and the PAUP-generated cladogram, it is most parsimonious to assume that the transformation from less (Character 4, Figure 62) to moderate (Character 4', Figure 63) to well-developed (Character 4", Figure 64) ascending processes is a reversal.

Additionally, in those genera possessing character state 4, the palato-premaxillary ligament arises adjacent to the maxillary head of palatine and inserts on its mate without connection to the premaxillary ascending processes. The palato-premaxillary ligament attaches to the rostral cartilage by connective tissue (Fig. 62, connective tissue not indicated).

In other gobiids and gobioids, the palato-premaxillary ligament crosses and attaches to the ascending processes of the premaxillae and does not attach to the rostral cartilage. This generalised condition is also found in *Pseudapocryptes, Scartelaos, Zappa, Periophthalmodon* and *Periophthalmus* and, based on other character distributions as above, must be considered a reversal (Fig. 64).

5. Single pterygiophore anterior to first hemal spine (Fig. 65).

In most other gobiids and gobioids, at least two pterygiophores are anterior to the first hemal spine (Fig. 66). Birdsong *et al.* (1988) found a single pterygiophore anterior to the first hemal spine consistently in only the following gobioid taxa: *Discordipinna, Kelloggella* and the Ptereleotrinae. *Discordipinna*, a small goby inhabiting Indo-west Pacific coral reef areas, has the unique specialisation of four pterygiophores inserting in the third interneural space (versus one in the Oxudercinae) and a single epural (versus two in Oxudercinae). *Kelloggella*, another small Indo-west Pacific goby, has a DF = 3-22110 (versus 3-12210 in Oxudercinae), a vertebral count of 11 + 15 = 26 (versus 10 + 16 = 26 in Oxudercinae), and a single epural (versus two in Oxudercinae). The Ptereleotrinae, a circumtropical subfamily of the Microdesmidae according to Hoese (1984), has a DF = 3-22110 or 3-32010 (versus 3-12210) and a single epural (versus two). Based on the above character distributions, the most parsimonious hypothesis is that the condition of having only a single anal fin pterygiophore anterior to the first hemal spine evolved independently within several gobioid groups.

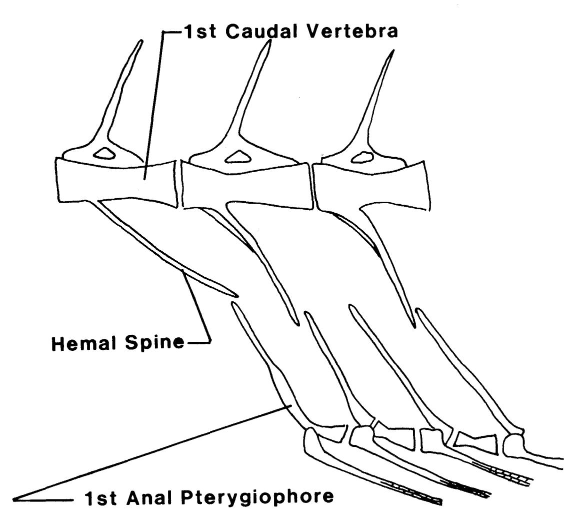

Fig.65. *Parapocryptes serperaster*, lateral view from left side of interdigitation between anterior anal fin pterygiophores and hemal spines.

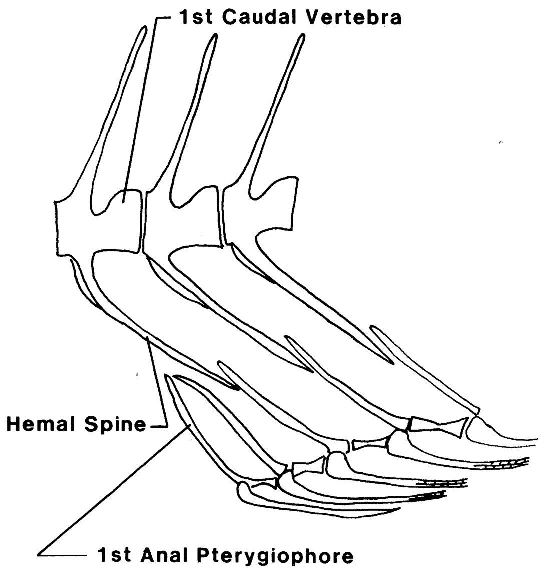

Fig.66. *Evorthodus lyricus*, lateral view from left side of interdigitation between anal fin pterygiophores and hemal spines.

Relationships of the Oxudercinae to Other Groups of Gobiidae

Attempts to hypothesise a sister-group relationship between the Oxudercinae and another gobiid group have been moderately successful. Three of the five defining characters of the Oxudercinae are unique within the Gobioidei and not approximated by any other group.

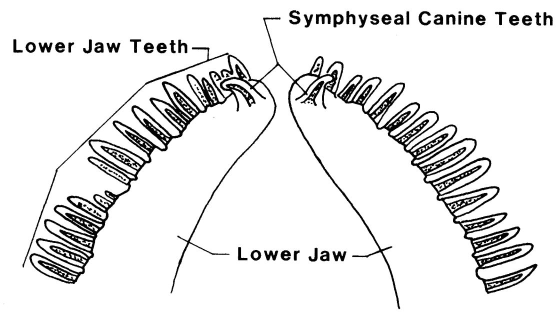

Fig.67. *Boleophthalmus boddarti*, dorsal view of lower jaw.

Character 3 (ectopterygoid-palatine articulation) is approximated in at least two amblyopine genera. The fifth oxudercine synapomorphy (single pterygiophore anterior to the first hemal spine) is found consistently in only two other gobiid genera and one other gobioid subfamily. However, other character distributions in these taxa dispute a close relationship to the Oxudercinae (see preceding section).

Based on Birdsong *et al.* (1988) and using unpolarised features of the axial skeleton, potential sister groups were identified and assessed. The Oxudercinae possess the following axial skeletal features: vertebral number of 10 + 16 = 26; two epurals; and, in eight of the ten genera, six spinous dorsal fin pterygiophores arranged in the DF of 3-12210 (several oxudercine genera lack an associated spine with the sixth pterygiophore). Using vertebral and

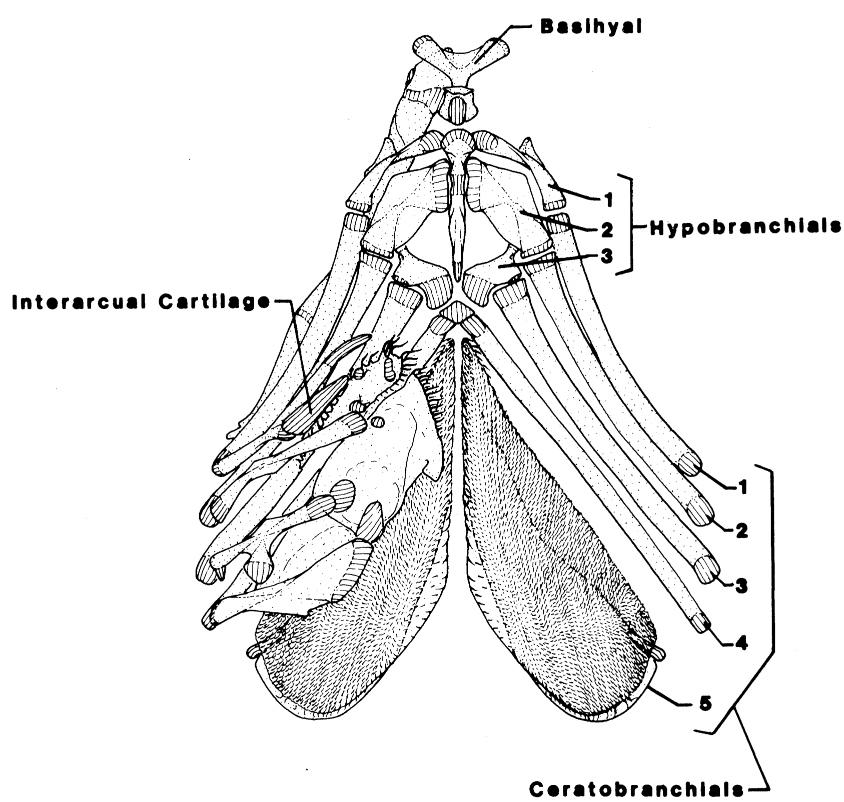

Fig.68. *Parapocryptes serperaster*, dorsal view of gill arches and basihyal.

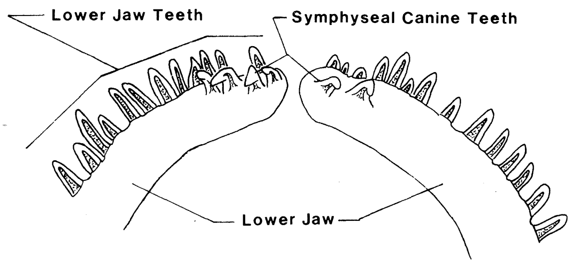

Fig.69. *Evorthodus lyricus*, dorsal view of lower jaw.

epural numbers, and pterygiophore formulae, two groups listed in Birdsong *et al.* (1988) were equivalent to or approximated the same set of characters in the Oxudercinae. The Gobionellus Group (nine genera) and the Sicydium Group (eight genera) share with the oxudercines the same vertebral number (10 + 16 = 26) and DF (3-12210). The Gobionellus Group shares with the Oxudercinae the same number of epurals (two) and many genera have lanceolate caudal fins much like several genera of oxudercines. Additionally, the Gobionellus Group is typically found in soft bottom, estuarine habitats not too dissimilar from that of oxudercines. The Sicydium Group, although differing in epural number (one versus two), shares with the Oxudercinae a single row of teeth in both jaws, an unusual if not unique feature in the suborder.

Amongst the Gobionellus and Sicydium Group members sampled (Gobionellus Group - *Ctenogobius, Gnatholepis, Mugilogobius, Oxyurichthys*; Sicydium Group - *Evorthodus, Sicydium, Stiphodon*), *Evorthodus* most closely approximates several character states shared by many of the oxudercine genera. Within the Oxudercinae, eight of the ten genera possess two, large, recurved canine teeth internal to the symphysis of the lower jaw (Fig. 67) and deeply concave, large, lattice-like fifth ceratobranchials, and infrapharygobranchials to which the epibranchials articulate dorsally rather than laterally (Fig. 68); *Evorthodus* approximates the condition in the eight oxudercine genera that possess these features. Male *Evorthodus* possess two or more small, recurved canine teeth internal to the symphysis of the lower jaw (Fig. 69) and both sexes possess large, concave branchial tooth apparati to which the epibranchials attach dorsally (Fig. 70). In the oxudercines that possess the large, concave branchial-toothplate apparati, the fourth infrapharyngobranchial is typically larger than the third (Fig. 68); in *Evorthodus* however, the third is larger than the fourth (Fig. 70). Additionally, *Evorthodus* shares with *Apocryptodon, Oxuderces* and *Parapocryptes* the derived state of having the retractor dorsalis muscle coursing through the ribs and inserting on some portion of the fourth vertebra (Fig. 71). In *Evorthodus lyricus,* the retractor dorsalis inserts laterally along the fourth neural spine with a slip of muscle also attaching to the fifth neural spine. In *Oxuderces dentatus*, the retractor dorsalis originates on the posteriorly expanded fourth neural spine whereas in *O. wirzi* it attaches to the parapophyses of the fourth vertebra. In *Apocryptodon madurensis*, laminar extensions of the parapophyses of the fourth vertebra (see character 8) are the point of attachment for the retractor dorsalis. *Parapocryptes*

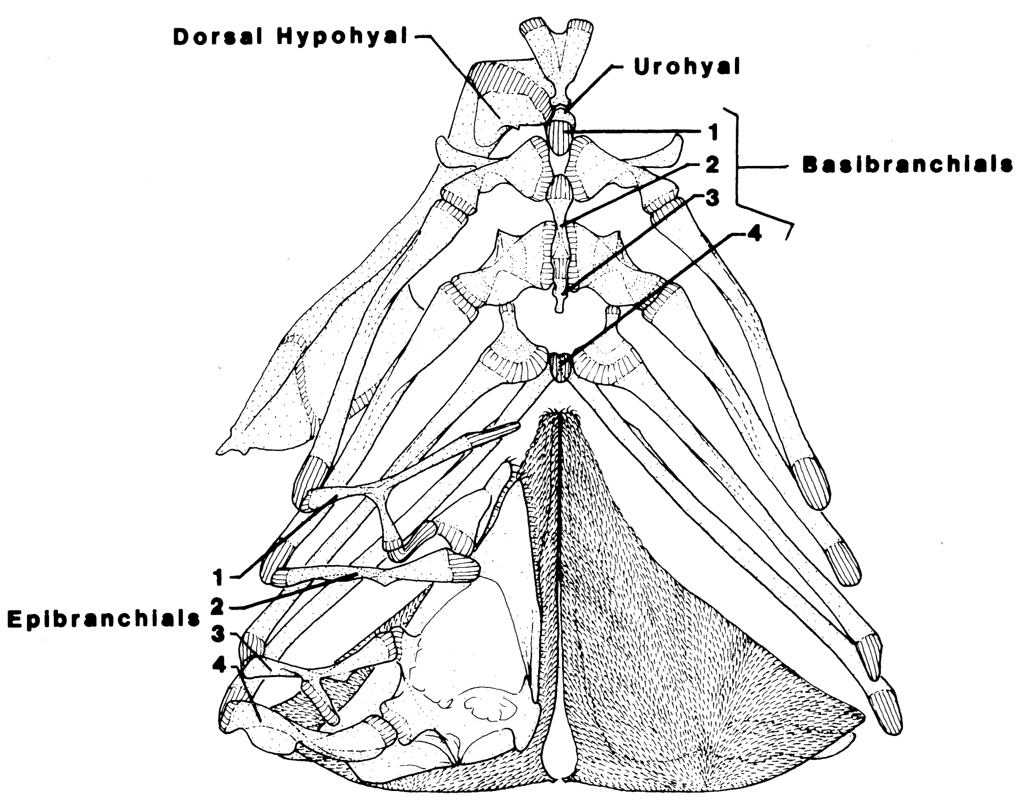

Fig.70. *Evorthodus lyricus*, dorsal view of gill arches and basihyal.

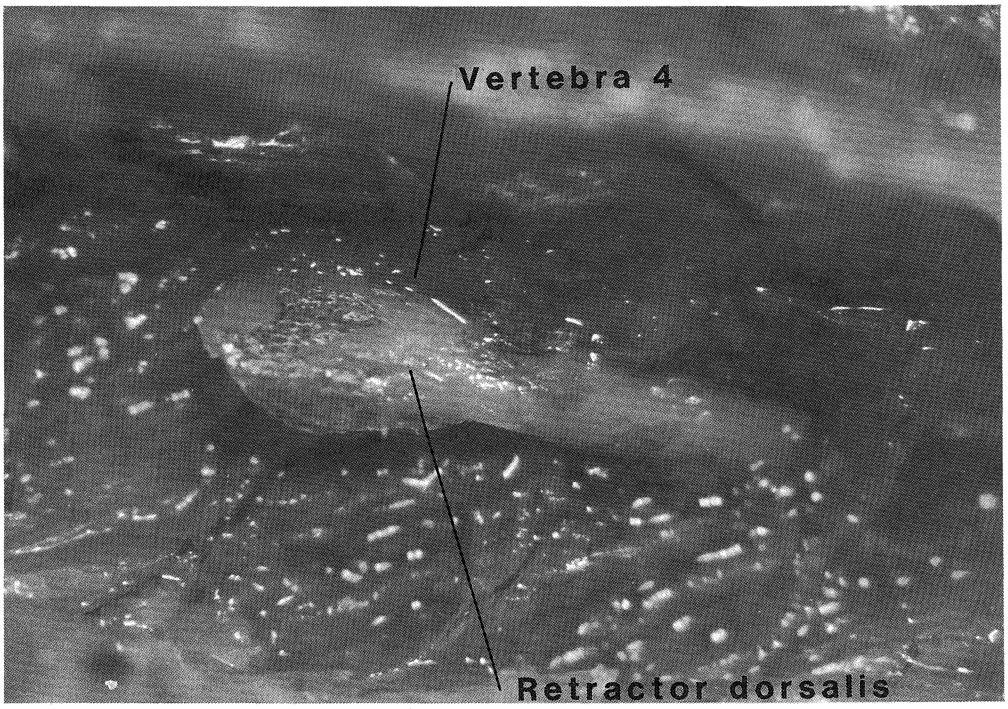

Fig.71. *Apocryptodon madurensis*, dorsolateral view of retractor dorsalis from right side.

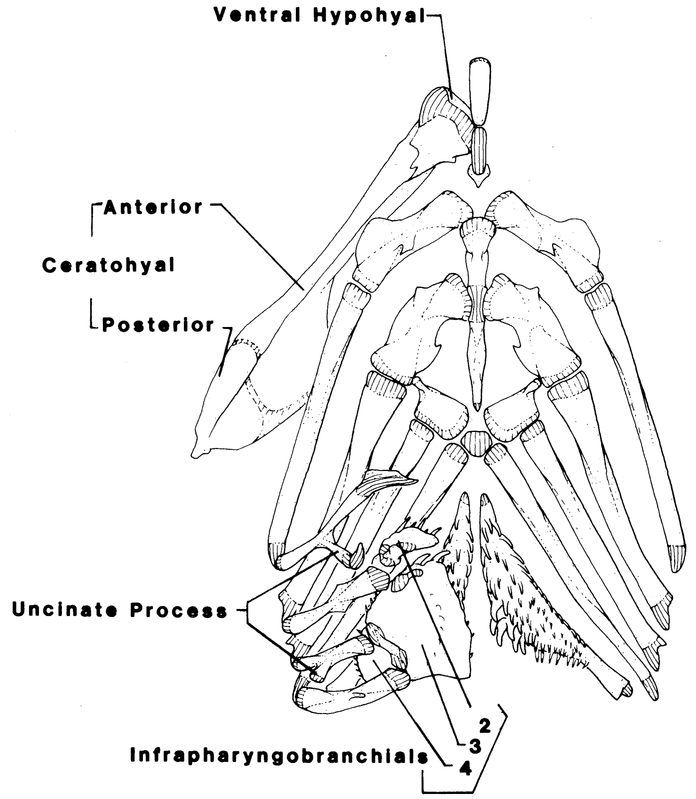

Fig.72. *Periophthalmus kalolo*, dorsal view of gill arches and basihyal.

serperaster has rounded, lateral extensions of the parapophyses of the fourth vertebra that serve as the attachment site for the retractor dorsalis (see character 15). In all other oxudercines, the retractor dorsalis originates on some portion of the third vertebra. This condition needs a more thorough survey within the Gobioidei in order to better assess polarity. R.S. Birdsong informed me that in two eleotridid genera (*Butis* and *Eleotris*), the retractor dorsalis originates on the third vertebra whereas an origin on the second or third vertebra is the typical condition in percoids (G.D. Johnson, personal communication). I am assuming, therefore, that an origin of the retractor dorsalis on the fourth vertebra is the derived condition. Based on the three characters above, I am hypothesising a close (possibly sister-group) relationship between *Evorthodus* and the Oxudercinae.

It is possible that convergence is responsible for the similarity in branchial arch structure and jaw dentition between *Evorthodus* and eight of the ten Oxudercine genera. These fishes live in soft bottom (typically muddy) estuarine areas and ingest a great deal of substrate when feeding. The large surface area and lattice-like structure of the fifth ceratobranchials and infrapharygobranchials must aid in straining the substrate whereas the recurved canine teeth internal to the symphysis of the lower jaw may aid in burrow digging and/or be related to feeding. These two apomorphic features might be necessary for the successful exploitation of the environment. The two oxudercine genera lacking these features (*Periophthalmodon* and *Periophthalmus*) are also soft bottom inhabitants but strictly carnivorous much like most gobioids. By parsimony, however, their lack of two canine teeth internal to the symphysis of the lower jaw and possession of more typical gobioid branchial toothplate apparati (Fig. 72) are considered reversals and, therefore, derived states. One species of *Oxuderces* (*O. dentatus*) possesses lattice-like branchial apparati but, like *Periophthalmodon* and *Periophthalmus*, has lost the internal symphyseal canine teeth of the lower jaw.

In summary, the above evidence supports a close (possibly sister-group) relationship between *Evorthodus* and the Oxudercinae. A broader survey of mud-dwelling, omnivorous gobies is necessary to assess the uniqueness of the symphyseal canine teeth, branchial toothplate apparati, and placement of the retractor dorsalis. For the purposes of this study, *Evorthodus* was used as the principal (first) outgroup with additional outgroups being other members of the Sicydium Group (*Stiphodon, Sicydium*), Gobionellus Group (*Gnatholepis, Ctenogobius, Mugilogobius* and *Oxyurichthys*), Trypauchen Group (*Trypauchen*), Taenioides Group (*Brachyamblyopus*), and the lone member of the Gobioides Group (*Gobioides*). *Evorthodus* and the other outgroups examined, possess, except where noted, the more generalised condition of the characters that define the Oxudercinae. Additionally, *Periophthalmus* and *Periophthalmodon* share three primitive states for oxudercines - well-developed premaxillary ascending processes, absence of symphyseal canine teeth, and generalised shape and structure of the fifth ceratobranchial. The other eight oxudercine genera share the opposite states of these characters as three congruent synapomorphies. However, based on the most parsimonious presentation of relationships as determined by PAUP, the primitive states for the three characters mentioned above are considered reversals.

Phylogenetic Hypotheses and Classification of the Oxudercinae

The methodologies and procedure used in the reconstruction of a hypothetical series of relationships in the Oxudercinae have been discussed in detail previously. Characters 1 to 5 define the subfamily, characters 6 to 39 distinguish taxa within the subfamily.

6. Dorsoposteriorly in the lip of the lower jaw of *Apocryptodon, Oxuderces* and *Parapocryptes*, a series of 6 to 8 finger-like projections originate from a rigid but still flexible L-shaped structure that attaches posteriorly at the terminus of the maxilla and inserts anterolaterally on the dentary (Fig. 73). This L-shaped structure conforms to the description of an unnamed ligament in Birdsong (1975:150), the maxillodentary ligament in Springer (1983:14), and the maxillo-mandibularis ligament in Van Dobben (1937). Contained within the ligament and its dorsal projections is a cellular matrix that appears to provide additional support to this portion of the lip.

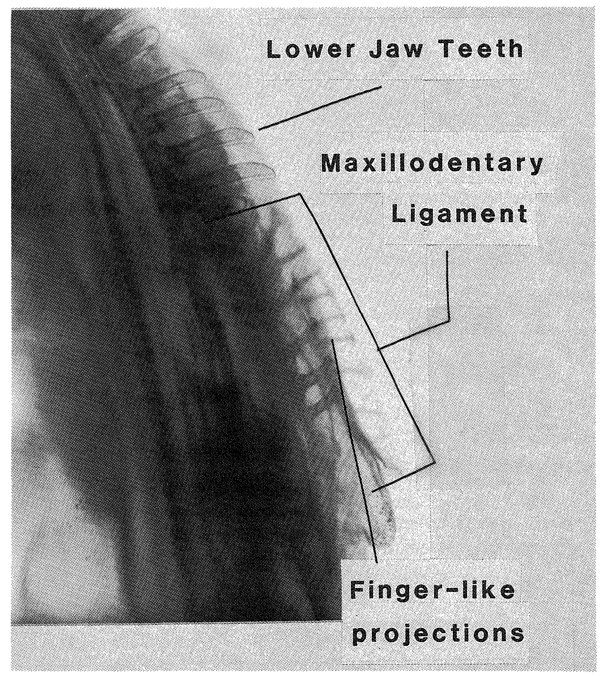

Fig.73. *Oxuderces dentatus*, ventrolateral view of lower jaw from left side.

The maxillodentary ligament was found in all gobioids examined, however, shapes and lengths of the ligament varied greatly. Possible homologues of the ligament were observed by G.D. Johnson in representatives of other Perciformes, Beryciformes and Myctophiformes. In no other specimens examined, however, were finger-like dorsal projections observed.

7. In *Apocryptodon* and *Oxuderces*, the epaxialis muscle attaches anteriorly at the frontal and epioccipital junction (Fig. 56).

In the outgroups and other oxudercines, the epaxialis attaches to the postorbital region of the frontal bone (Fig. 57).

8. In *Apocryptodon*, the parapophyses of the fourth vertebra possess posterodorsally-directed laminar extensions (Fig. 74).

A similar condition has not been observed in the outgroups, other oxudercines, or any other gobioid examined. The retractor dorsalis muscle is attached to this flexible structure, additional functions, if any, are unknown.

9. In *Apocryptodon*, a supraorbital pore (sensory canal pore E of Akihito *et al.*, 1984) is present (Fig. 1).

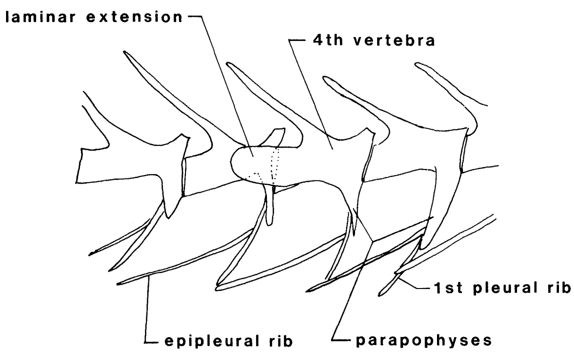

Fig.74. *Apocryptodon madurensis*, dorsolateral view of parapophyseal extension on right side.

Gobionellus and *Sicydium* group members lack a supraorbital pore but possess an infraorbital pore (sensory canal pore F of Akihito *et al.*, 1984) that opens to the surface at the junction of the frontal and sphenotic troughs which form part of the cephalic sensory pore system. In the Trypauchen, Taenioides and Gobioides Groups, the frontal and sphenotic troughs are absent as are infra- and supraorbital pores. In all oxudercines, frontal and sphenotic troughs are absent as are infraorbital pores, and only *Apocryptodon* possesses a supraorbital pore. Supraorbital pores are present in many other other gobioids, however, so I assume that supraorbital pores have either been derived or lost several times within the suborder.

10. In *Oxuderces* there is an extremely wide gape with the jaws terminating well posterior to orbit. Thus, the angle between the metapterygoid-symplectic-quadrate strut and the anguloarticular is 90° or less when the mouth is closed (Fig. 75).

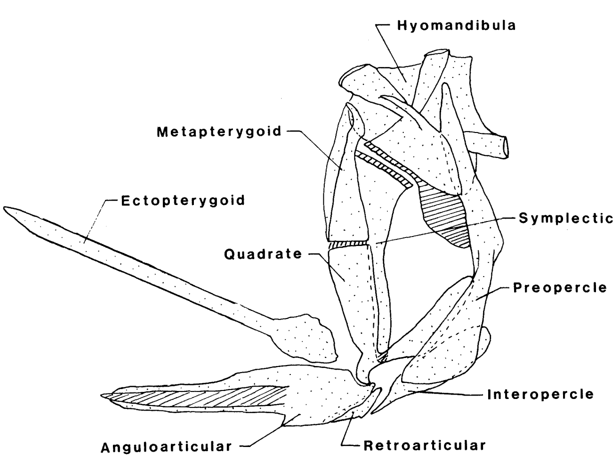

Fig.75. *Oxuderces dentatus*, lateral view of suspensorium and ectopterygoid of left side.

In the outgroups and other oxudercines, the gape is moderate, the jaws terminating slightly posterior to, at, or slightly anterior to the orbit with the angle between the metapterygoid-symplectic-quadrate strut and the anguloarticular greater than or equal to 90°, typically greater (Figs 60-61). The gobiine genera *Quietula* and *Gillichthys* of the eastern Pacific also possess wide gapes; independent derivation would appear to account for this based on other character distributions.

11. In *Oxuderces*, the upper jaw has an anteriorly-directed but ventrally curving tooth (fang-like canine tooth) on each side of the premaxillary symphysis (Fig. 76).

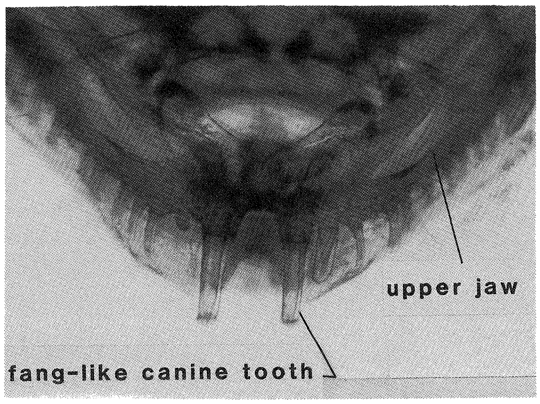

Fig.76. *Oxuderces dentatus*, dorsoanterior view of snout region.

In the outgroups and other oxudercines, there is no similar feature. Several oxudercine genera possess large canine teeth in the upper jaw (*Periophthalmus*, *Periophthalmodon* and *Pseudapocryptes*) but none show the same orientation and relative size.

12. In *Oxuderces*, the anterior ceratohyal is lengthened posterior to the insertion of the fourth branchiostegal (Fig. 77).

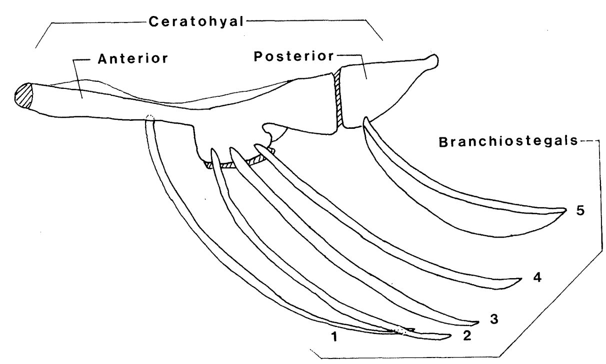

Fig.77. *Oxuderces dentatus*, lateral view of left hyoid arch rotated about 45° counterclockwise.

In the outgroups and other oxudercines, the symphysis between the anterior and posterior ceratohyals is almost immediately posterior to the insertion of the fourth branchiostegal (Fig. 78).

13. In *Oxuderces*, the head is depressed anteriorly (Fig. 1).

In the outgroups and other oxudercines, the head is slightly rounded anteriorly and compressed (Fig. 1).

14. In *Parapocryptes*, the head of the fourth epibranchial is expanded (Fig. 68).

In the outgroups and other oxudercines, the head of the fourth epibranchial is moderate to narrow (Fig. 70).

15. In *Parapocryptes*, the parapophyses of the fourth vertebra are expanded laterally such that a rounded, anterior concavity exists with the retractor dorsalis muscle

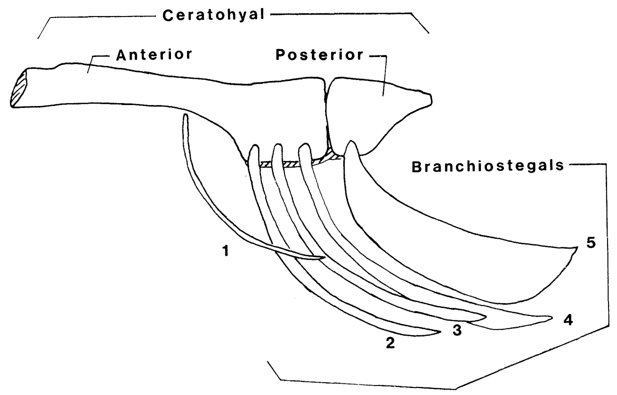

Fig.78. *Periophthalmus kalolo*, lateral view of left hyoid arch rotated about 45° counterclockwise.

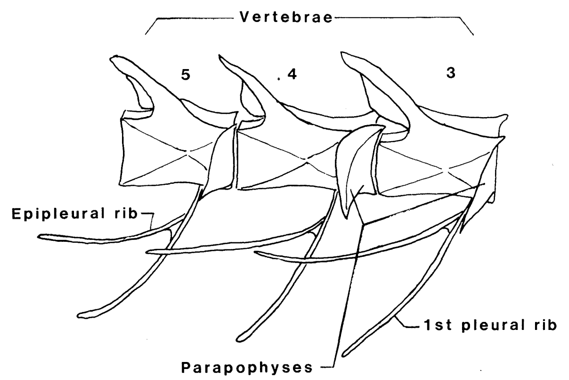

Fig.79. *Parapocryptes serperaster*, dorsolateral view of portion of vertebral column and associated structures.

originating from this concavity (Fig. 79).

In the outgroups and in all but one oxudercine genus (*Apocryptodon*), there is no similar structure. *Apocryptodon* possesses posterior extensions of the parapophyses of the fourth vertebra (see character 8).

16. *Apocryptes, Boleophthalmus, Periophthalmodon, Periophthalmus, Pseudapocryptes, Scartelaos* and *Zappa*, have a dorsal fin pterygiophore formula of 3-1221*0, the asterisk indicating the last pterygiophore has no associated spine (Fig. 80b).

There is no equivalent of this formula among any of the 200+ gobioid genera sampled by Birdsong *et al.* (1988). It is considered unique and a transformation from the formula 3-12210.

In the outgroups and all but two oxudercine genera, two pterygiophores insert in the fourth interneural space. The condition of having three or four pterygiophores within the fourth interneural space (16') is unique to *Periophthalmodon* and *Periophthalmus* (Birdsong *et al.*, 1988) and represents a transformation of character 16 caused by an anterior shift of one or more pterygiophores. The posterior distal process of each pterygiophore is reduced thereby allowing a tighter grouping of elements.

Species of *Periophthalmodon* and *Periophthalmus* are variable in pterygiophore pattern (see Table 25). An evolutionary scenario to explain this phenomenon is presented in Figure 81.

17. *Apocryptes, Boleophthalmus, Periophthalmodon, Periophthalmus, Pseudapocryptes, Scartelaos* and *Zappa* accomplish air-breathing by means of gills as well as by having modified buccopharyngeal and opercular epithelium for air-breathing and/or having the ability to cutaneously respire in air.

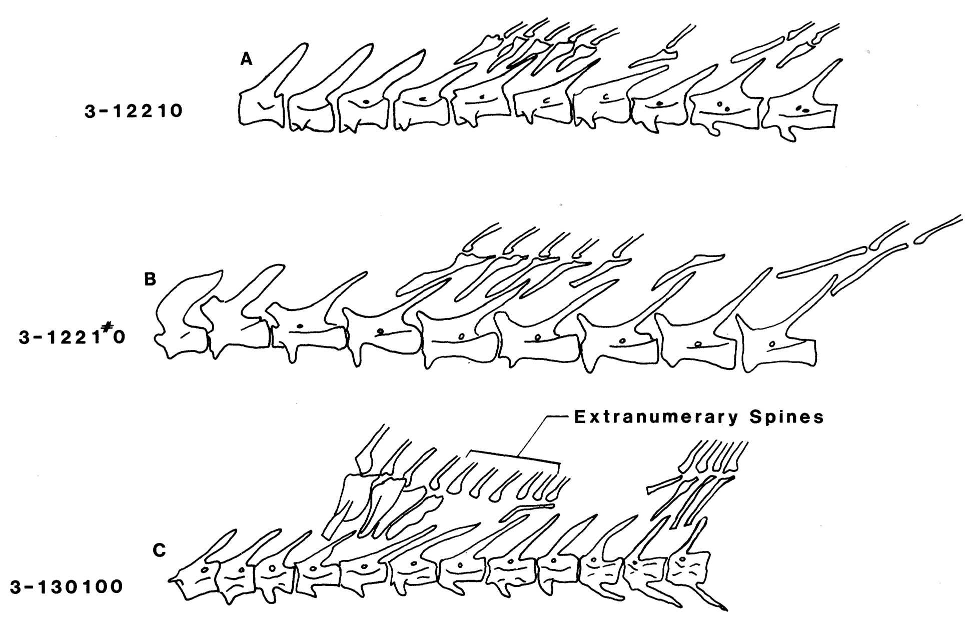

Fig.80. Representative pterygiophore patterns in the Oxudercinae: A, *Apocryptodon, Oxuderces, Parapocryptes*; B, *Apocryptes, Boleophthalmus, Pseudapocryptes, Scartelaos, Zappa*; C, several species of *Periophthalmus*.

Morphological specialisations that allow for three modes of air-breathing (gills, buccopharyngeal-opercular or cutaneous) in the oxudercine genera *Periophthalmus, Periophthalmodon, Boleophthalmus* and *Scartelaos* are well documented (Schöttle, 1931; Gordon *et al*., 1968; Macnae, 1968). *Apocryptes* and *Pseudapocryptes* utilise both their gills and increased vascularisation in the buccopharyngeal and opercular regions to breathe aerially (Hora, 1937); air-breathing in *Apocryptes* and *Pseudapocryptes* may be restricted to periods of prolonged drought or anoxia. *Zappa* was collected on an exposed muddy surface (Roberts, 1978) and I assume it has at least limited air-breathing ability by means of gills and increased vascularisation in the buccopharyngeal-opercular areas; morphological adaptations for such have not been studied.

Amongst non-oxudercine gobiid fishes, only *Gobionellus saggitula* (see Graham, 1976) has been shown to have the ability to respire aerially by means of gills. Because of other character distributions found in *G. saggitula*, this ability is assumed to have evolved independently at least twice in the Gobiidae. *Gobionellus saggitula* also has the inferred capability, based on vascularised skin, to respire cutaneously in air. Cutaneous respiration amongst gobiids is known only in four oxudercine genera (*Boleophthalmus, Periophthalmodon, Periophthalmus* and *Scartelaos*) and *G. saggitula.* Aerial respiration by gills and cutaneous respiration in air is known in the non-gobioid, marine families Blenniidae, Clinidae, Gobiesocidae and Megalopidae (see Table 1 in Graham, 1976). Increased vascularisation in the walls of the buccal and pharyngeal cavities and the inside of the operculum is a common structural adaptation for aerial respiration in some gobies, one blenny (*Entomacrodus nigricans*) and one clingfish (*Sicyases sanguineus*) (see Table 1 in Graham, 1976). In species that have been studied, vascularisation in these tissues has occurred through increased branching and spreading of existing blood vessels (for references, see Graham, 1976). The non-oxudercine gobies that exhibit this morphological and physiological specialisation are *Taeniodes rubicundus, Gillichthys mirabilis, G. seta* and *Quietula guaymasiae* (Graham, 1976). Because of other character distributions found in the above non-oxudercine gobies, this specialisation is assumed to have evolved independently several times in the Gobiidae as well as in at least two other non-gobioid families.

To summarise, air-breathing in fishes can be accomplished in at least three ways: 1. air-breathing with gills; 2. air-breathing with modified buccopharyngeal and opercular epithelium; and 3. cutaneous respiration in air. Six oxudercine genera are reported to have the ability to respire aerially by gills, one oxudercine genus (*Zappa*) is assumed to have this ability based on the original description (Roberts, 1978). Only one other non-oxudercine goby (*Gobionellus saggitula*) is reported to have the ability to respire aerially with gills. The homology of this character amongst oxudercines that possess it is by no means assured but is assumed based on the infrequency of its occurrence amongst gobiids. Further detailed investigation of the respiratory morphology and physiology of oxudercine gobies is necessary to clearly establish homology. However, character 17 correlates in a parsimony analysis with character 16 and thus may be of significance.

18. In *Apocryptes, Boleophthalmus, Periophthalmodon, Periophthalmus, Pseudapocryptes, Scartelaos* and *Zappa*, the origin of retractor dorsalis is on some portion of the third vertebra.

In *Evorthodus, Apocryptodon, Oxuderces* and *Parapocryptes*, the origin of the retractor dorsalis is on the fourth vertebra, an hypothesised derived condition in

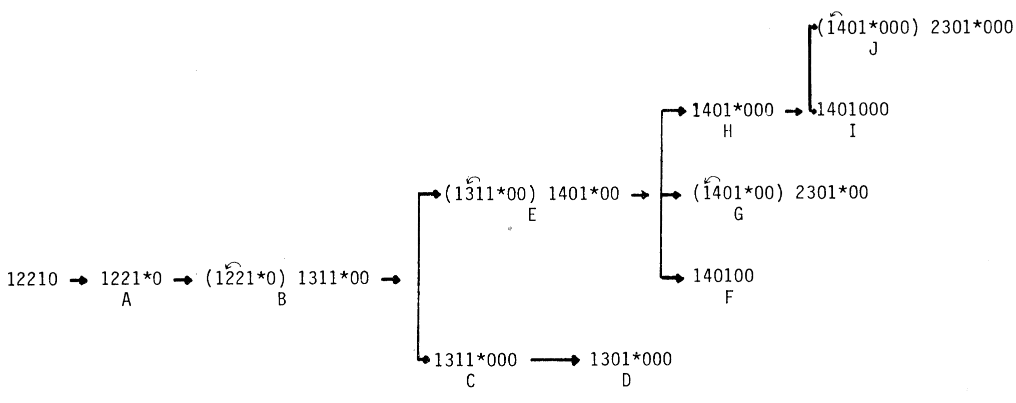

Fig.81. Hypothetical scenario accounting for the various pterygiophore patterns in *Periophthalmodon* and *Periophthalmus*, patterns in parentheses represent a transitional state: A, loss of sixth spine causing sixth pterygiophore to be disassociated from a spine; B, a pterygiophore in fifth interneural space shifts anteriorly one interneural space accompanied by a posterior shift of the second dorsal fin one space; C, a posterior shift of the second dorsal fin one space; D, loss of pterygiophore in the fifth interneural space; E, a pterygiophore in fifth interneural space shifts anteriorly one space; F, sixth pterygiophore is reassociated with a spine; G, a pterygiophore in the fourth interneural space shifts anteriorly one space; H, first pterygiophore of second dorsal fin shifts posteriorly such that it inserts in the same interneural space as the second D2 pterygiophore; I, sixth pterygiophore is reassociated with a spine; and J, a pterygiophore in the fourth interneural space shifts anteriorly one space.

gobioids (see discussion of similarities between *Evorthodus* and the Oxudercinae.) The most parsimonious explanation for the condition in other oxudercines of having the shift in the origin of the retractor dorsalis from the fourth to the third vertebra is that a character reversal has occurred.

19. In *Apocryptes*, small, cycloid scales cover the snout.

Gobionellus and Sicydium group members possess mostly ctenoid scales (some have cycloid scales anteriorly on the trunk), but in none is the snout scaled. The Gobioides group has only cycloid scales with the nape partially scaled, no other part of the head is scaled. In the Trypauchen and Taenioides Groups, the trunk possesses cycloid scales whereas the head is largely scaleless. (At this time, the polarity between cycloid and ctenoid scales cannot be determined.) Within the Oxudercinae, only *Apocryptes* and *Periophthalmodon* have scales (cycloid) on the snout, however, the scales of *Periophthalmodon* are much larger in a relative sense. Based on other character distributions, this condition is assumed to have been independently derived in these genera.

20. In *Pseudapocryptes*, there are 150 or more longitudinal scales.

No outgroup possesses near this number of longitudinal scales and only *Pseudapocryptes* amongst the oxudercines consistently possesses at least this many (mean = 209, see Table 4). One specimen of *Boleophthalmus dussumieri* possessed 185 longitudinal scales, however, the mean for the species is 146 (see Table 12).

21. *Boleophthalmus, Periophthalmodon, Periophthalmus, Scartelaos* and *Zappa* have the ability to survive for short periods out of water.

None of the outgroups has been reported to possess this capabilility. Of the five oxudercine genera that exhibit this ability, I observed four of them in this mode (*Boleophthalmus, Periophthalmodon, Periophthalmus* and *Scartelaos*, see Murdy, 1986) and the fifth (*Zappa*) has only been collected on land (Roberts, 1978). No other oxudercine has ever been reported out of water although *Pseudapocryptes* can survive periods of drought in deep burrows containing little or no water (Hora, 1937). Only one other non-oxudercine goby (*Gillichthys mirabilis*) has been reported to occasionally be completely out of water (Graham, 1976). Due to other character distributions, *Gillichthys* is not considered closely related to the Oxudercinae and, thus, the ability to survive for short periods out of water has evolved independently at least twice in gobioids.

This character is, of course, related to air-breathing (see character 17). As with air-breathing, homology is questionable. However, as this specialisation is infrequently encountered in fishes, is innovative and complex, an hypothesis of homology is proposed.

22. In *Scartelaos* and *Zappa*, the scales are reduced in size and lost anteriorly on trunk and head.

Other oxudercines are heavily scaled on the head and body with small (*Pseudapocryptes*) to large (*Periophthalmodon*) cycloid scales (see Table 4). Although small sized, the scales of *Pseudapocryptes* are still visible macroscopically, countable and larger than those found on *Scartelaos* and *Zappa*. The interpretation of events as indicated on the cladogram (Fig. 55) assumes a parallel reduction in *Scartelaos* and *Zappa*. This requires two evolutionary events or steps. Another two step interpretation entails reducing the scalation and then redeveloping the scales. As there is no parsimony argument, either interpretation is valid. However, I believe parallelism to be biologically more probable than reversal so that is why the parallel evolution scenario is presented on the cladogram.

23. In *Zappa*, the short portion of the first pterygiophore that is bent posteriorly at a point three quarters along its length extends horizontally over the tip of the fourth neural spine (Fig. 82).

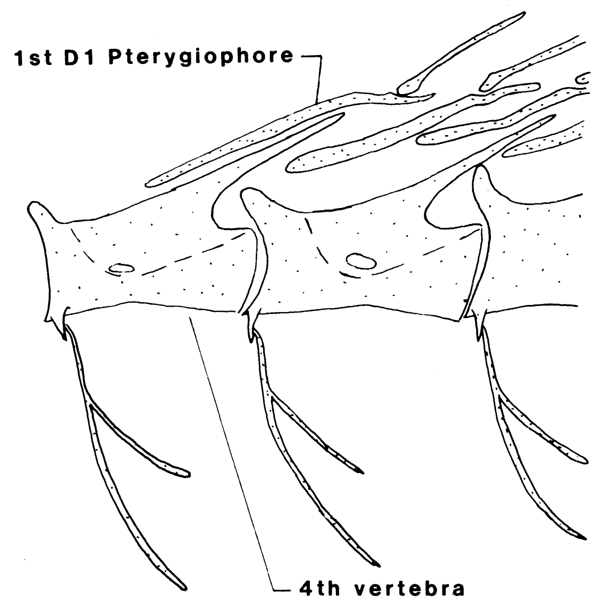

Fig.82. *Zappa confluentus*, left lateral view of the interdigitation between the first few spinous dorsal fin pterygiophores and neural spines.

In the Gobionellus and Sicydium groups, the entire first pterygiophore-spine complex is typically contained with the limits of the third interneural space (Fig. 83). In *Brachyamblyopus, Ctenotrypauchen, Gobioides* and other oxudercines, the first spine is typically anterior to the fourth neural spine (if the terminus of the neural spine were extended by an invisible line, Fig. 84). The very distal portion of the pterygiophore may extend posterior to the neural spine but there is no portion of the pterygiophore coursing horizontally dorsal to the neural spine.

24. *Boleophthalmus, Periophthalmodon, Periophthalmus* and *Scartelaos* exhibit truly amphibious behavior. Some portion of the daily cycle involves terrestriality. This is an extension of character 21.

This ability is not encountered often in fishes (Graham, 1976). None of the outgroups have been reported to have terrestriality as part of their daily regimen. According to Graham (1976), only one other gobiid (*Gillichthys mirabilis*) is at least occasionally amphibious (see characters 17 and

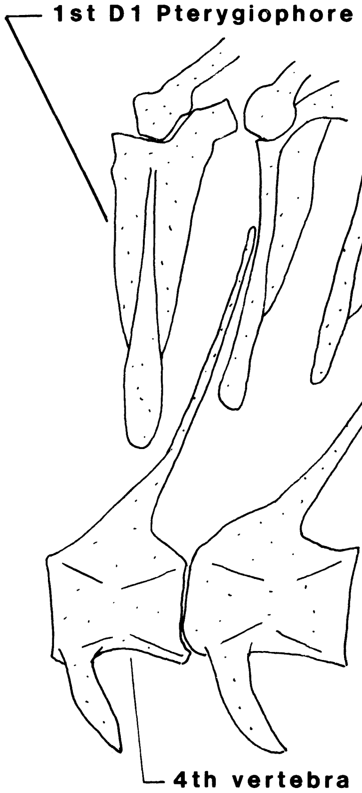

Fig.83. *Gnatholepis* sp., left lateral view of the interdigitation between the first few spinous dorsal fin pterygiophores and neural spines.

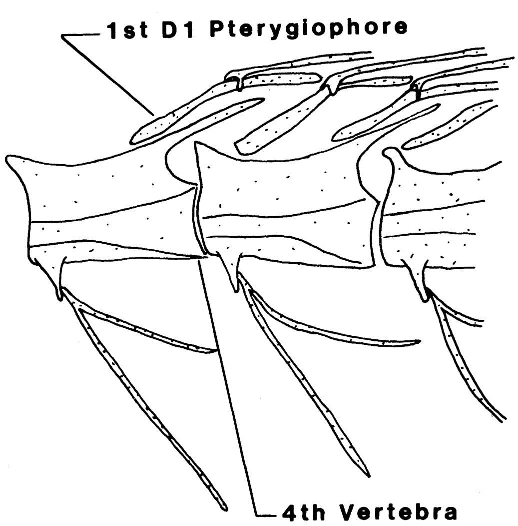

Fig.84. *Gobioides peruanus*, left lateral view of the interdigitation between the first few spinous dorsal fin pterygiophores and neural spines.

21). Four oxudercine genera (*Boleophthalmus, Periophthalmodon, Periophthalmus* and *Scartelaos*) are fully terrestrial for some portion of the daily cycle. *Zappa* is not considered to be truly amphibious based on the account of Roberts (1978); although collected from an exposed muddy surface, he stated the fishes were flipping from side-to-side and never upright on their pelvic fins. Such behavior is not consistent with that of the amphibious fishes cited above (see Macnae, 1968 and Murdy, 1986).

Any activity that is under the potential control of the animal can be used as a character. Here again, homology is not clear-cut and difficult to test. This complex and unusual character correlates with other synapomorphies (characters 25 and 26), and, thus, an hypothesis of homology is proposed.

25. In *Boleophthalmus, Periophthalmodon, Periophthalmus* and *Scartelaos*, the dorsal fins are not connected by membrane.

In the outgroups and other oxudercines, the first and second dorsal fins are connected either fully or basally by membrane.

26. In *Boleophthalmus, Periophthalmodon, Periophthalmus* and *Scartelaos*, a dermal cup is attached to the ventral half of the eye and serves as a reservoir of water for moistening the eye surface when the eyes are retracted (Fig. 85).

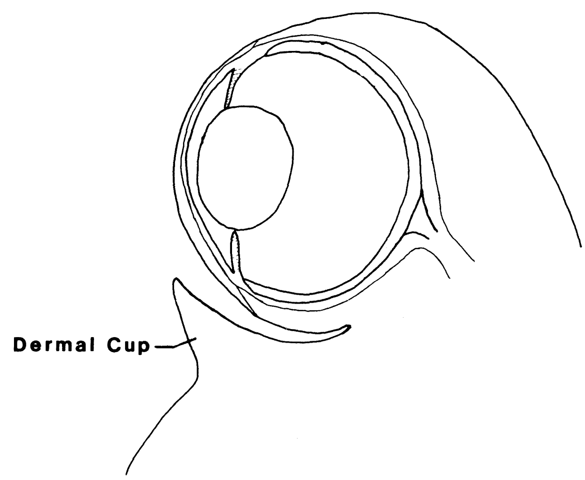

Fig.85. Cross-section through mudskipper eye (from Graham, 1971).

This structure is unique to *Boleophthalmus, Periophthalmodon, Periophthalmus* and *Scartelaos* within the Gobioidei and may be unique in fishes.

27. In *Periophthalmodon, Periophthalmus* and *Scartelaos*, the metapterygoid terminates well short of the hyomandibular condyle that articulates with the sphenotic (Fig.60).

In the outgroups and other oxudercines, the metapterygoid terminates almost adjacent to the hyomandibular-sphenotic junction (Figs 61 and 75).

28. In *Scartelaos*, a series of short barbels follow the jaw line ventrally on the head (Fig. 86).

Within the limits of this study, this feature is unique to *Scartelaos*; it was not observed in any of the outgroups or any other oxudercine. The gobiine (*sensu* Hoese, 1984) genera *Gobiopsis* and *Barbuligobius* also possess barbels on the ventral surface of the head. Based on other character distributions, these two genera are not considered closely related to the oxudercines and, thus, it is most parsimonious to assume this feature has evolved at least twice in the Gobiidae.

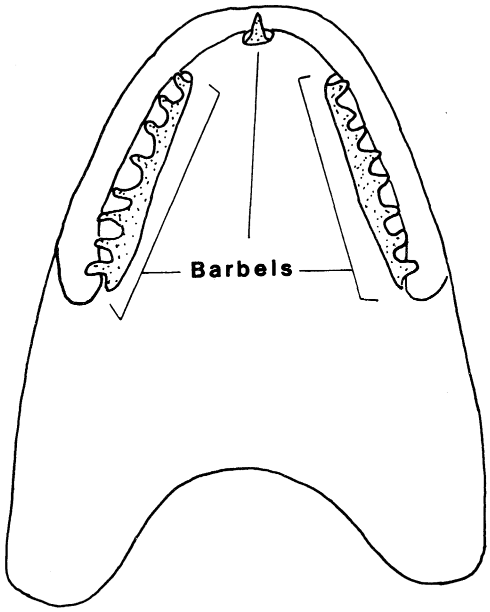

Fig.86. *Scartelaos histophorus*, ventral view of isthmus and lower jaw.

29. In *Boleophthalmus, Periophthalmodon* and *Periophthalmus,* the abductor superficialis muscle of the pectoral fin is divided into two sections (I and II of Grenholm, 1923). This presumably allows for greater control and flexibility of the limb during terrestrial forays (Fig. 87).

In the outgroups and other oxudercines, the abductor superficialis muscle is fan shaped and not divided into two parts (Fig. 88).

30. In *Boleophthalmus, Periophthalmodon* and *Periophthalmus*, the neurocranial cavity is enlarged anteriorly, and the frontal bones forming the interorbital bridge are greatly curved and overlap the ethmoid bones (Fig. 89).

In the outgroups and other oxudercines, the anterior portion of the neurocranial cavity is not enlarged and the frontal bones are only slightly curved anteriorly (Fig. 90).

31. In *Boleophthalmus*, a rectangular cartilage spans the width of the pelvic girdle just anterior to the processes to which the spines are connected (Fig. 91); it connects ligamentously to the cleithrum and possibly aids in stabilisation and/or constriction of the pelvic disk.

In the outgroups and other oxudercines, thin ligaments

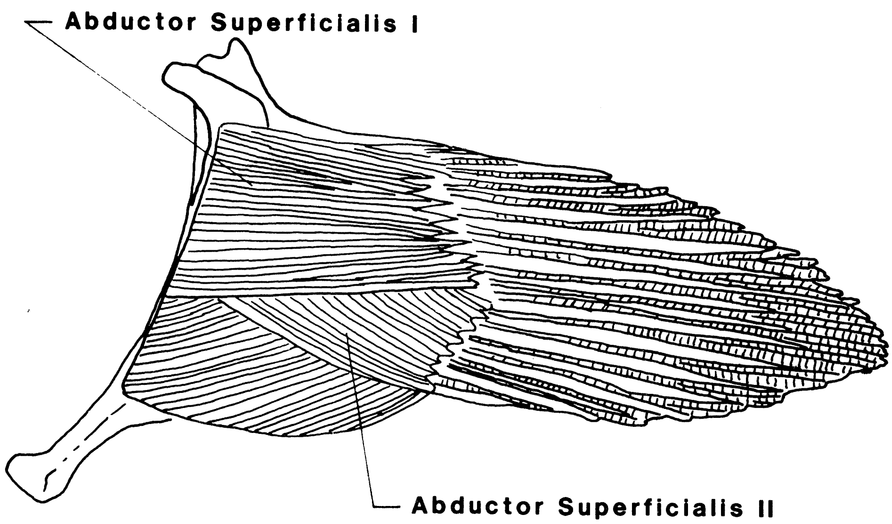

Fig.87. *Periophthalmodon schosseri*, left lateral view of pectoral fin musculature.

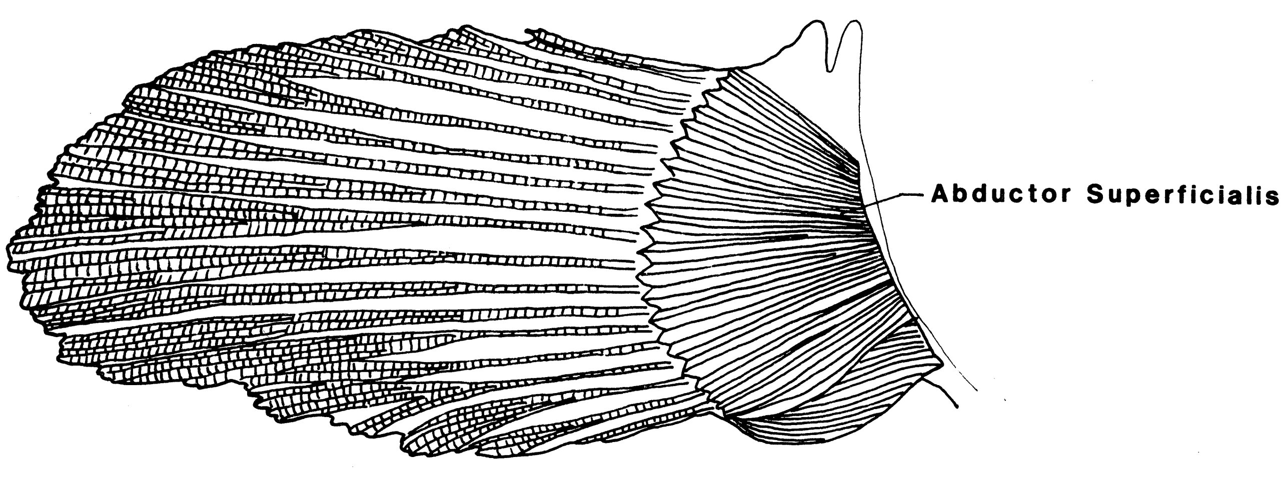

Fig.88. *Scartelaos histophorus*, right lateral view of pectoral fin musculature.

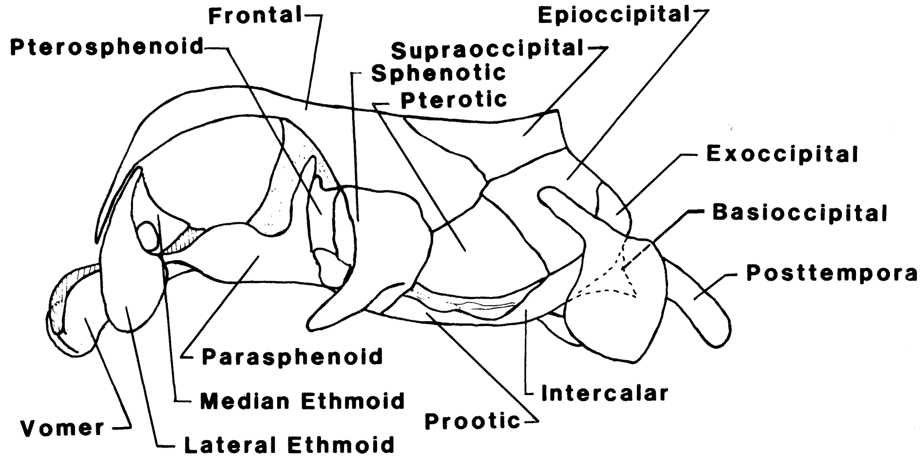

Fig.89. *Periophthalmus kalolo*, left lateral view of neurocranium.

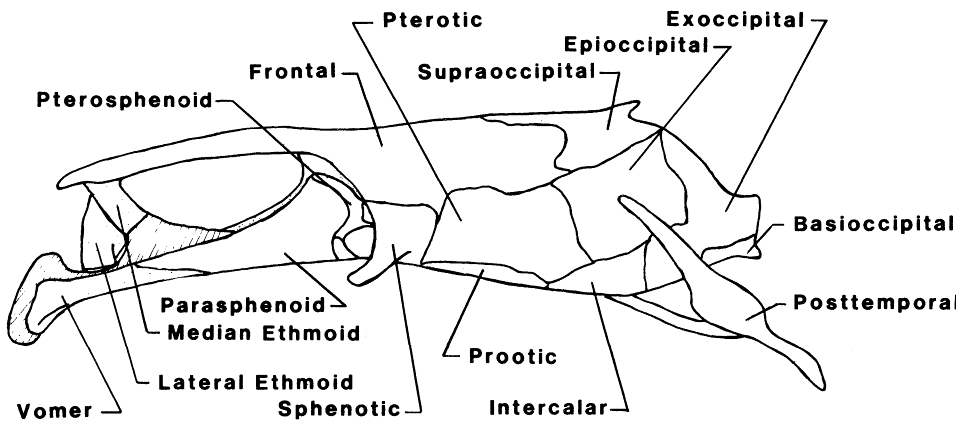

Fig.90. *Scartelaos histophorus*, left lateral view of neurocranium.

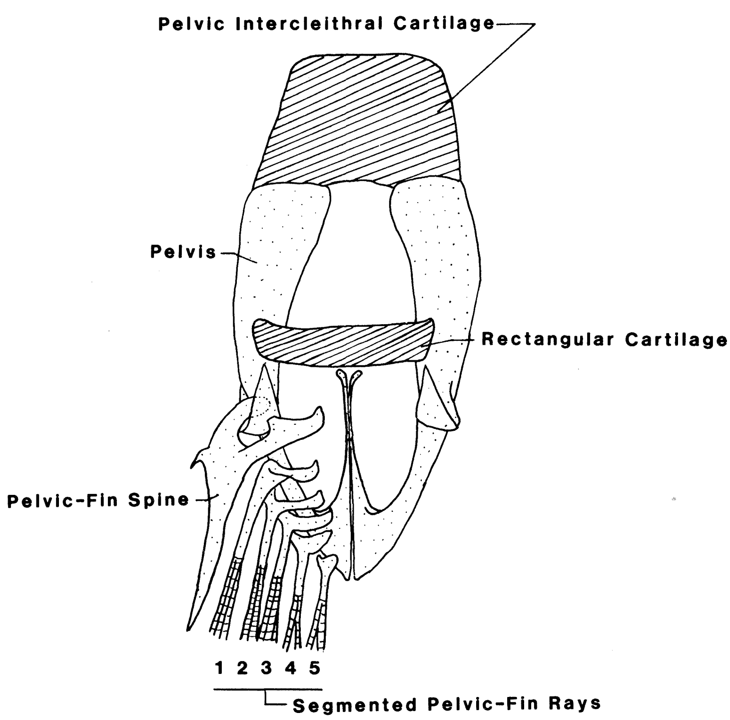

Fig.91. *Boleophthalmus boddarti*, ventral view of pelvis (pelvic fin elements removed from left side).

are in this same area but nothing approximating this cartilage is present.

32. In *Periophthalmodon* and *Periophthalmus*, the dorsal ramus of urohyal is displaced posteriorly so that it is situated ventroposteriorly to basibranchial 1 (Fig. 92).

In the outgroups and other oxudercines, the dorsal ramus of the urohyal is situated just ventral to basibranchial 1 such that basibranchial 1 appears to be resting on the concave surface of the dorsal ramus of the urohyal (Fig. 93).

33. In *Periophthalmodon* and *Periophthalmus*, the foramen of the internal carotid artery is situated adjacent to the facial foramen (Fig. 94).

In most outgroups, most other oxudercines, and other

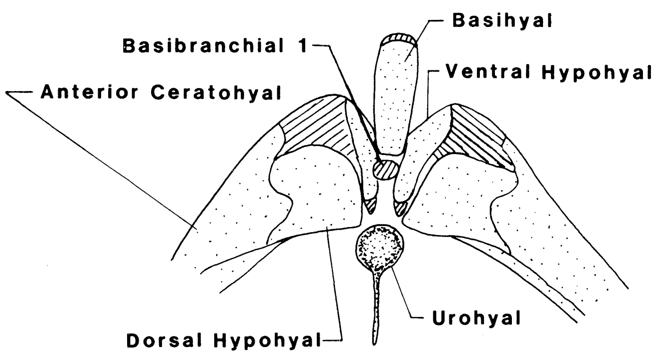

Fig.92. *Periophthalmus kalolo*, dorsal view of basihyal and anterior gill arches.

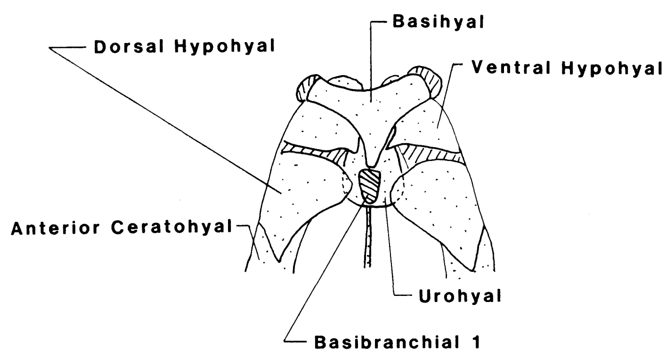

Fig.93. *Parapocryptes serperaster*, dorsal view of basihyal and anterior gill arches.

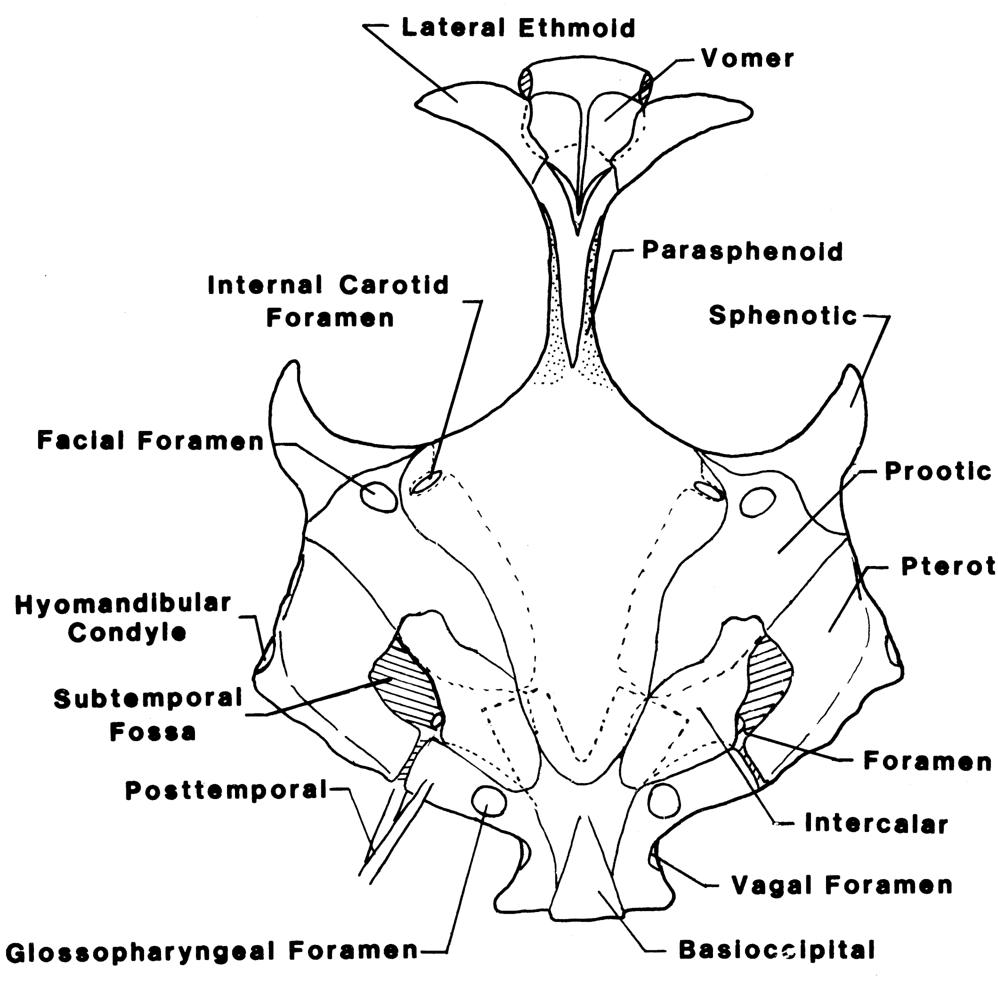

Fig.94. *Periophthalmus kalolo*, ventral view of neurocranium (post-temporal removed from left side).

gobioids, the internal carotid foramen is located near the base of the anterior strut of the parasphenoid. In *Boleophthalmus* and *Sicydium*, the foramen of the internal carotid is located about midway between the base of the parasphenoid strut and the facial foramen (Fig. 95).

34. In *Periophthalmodon* and *Periophthalmus*, extranumerary spines are present in the first dorsal fin (Fig. 80c). These spines lack associated pterygiophores. Birdsong (1975) hypothesised that the extranumerary spines supply additional support to an erect fin in an air environment.

In the outgroups and other oxudercines, all dorsal fin spines have an associated pterygiophore. The possession of extranumerary spines is unique within the Gobioidei

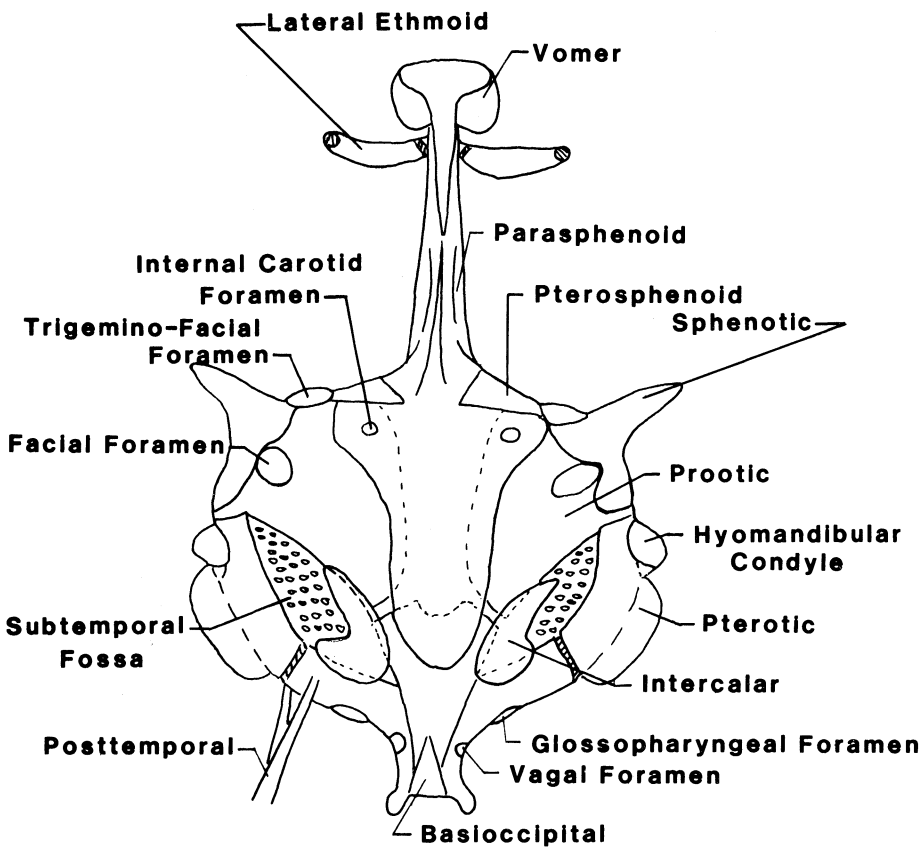

Fig.95. *Boleophthalmus boddarti*, ventral view of neurocranium (post-temporal removed from left side).

Fig.96. *Periophthalmodon freycineti*, ventral view of the upper jaw.

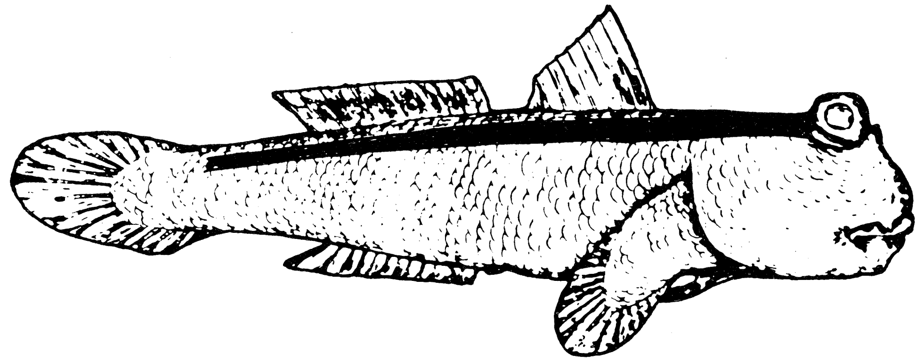

Fig.97. *Periophthalmodon schlosseri*, right lateral view (adapted from Johnstone, 1903).

(Birdsong *et al.*, 1988).

35. In *Periophthalmodon* and *Periophthalmus*, the basihyal is narrow and lacks an expanded tip (Fig. 92).

In *Evorthodus* and all but one outgroup, and in all other oxudercines, the basihyal is either broadly spatulate or bifid (Table 16). The outgroup exception is *Sicydium*, in which the basihyal is narrow as above.

36. In *Periophthalmodon* and *Periophthalmus*, the first D2 pterygiophore inserts posterior to the 9th or 10th neural spine (Table 26, Fig. 80c).

In the outgroups and other oxudercines the first pterygiophore of D2 inserts posterior to the 8th neural spine which is the typical gobiid condition (Fig. 80a,b).

37. In *Periophthalmodon* and *Periophthalmus*, the anterior oculoscapular canal pore is absent (Fig. 1).

In the outgroups and other oxudercines, the anterior oculoscapular canal pore is present. It is also present in a number of other gobiid genera, thus the absence or loss of the pore appears derived. I am cautioned by Hecht & Edwards (1977) statement that absent characters cannot be compared and, thus, homology is not testable. However, this loss character correlates a parsimony analysis with unrelated, but innovative synapomorphies (characters 32-36) and, thus, appears meaningful.

38. In *Periophthalmodon*, a second, short row of stout canine teeth (4-8 teeth) is internal to the first row of teeth in the upper jaw (Fig. 96).

The outgroups *Gobionellus* and *Gnatholepis* have more than two rows of teeth in the upper jaw, however, the condition in these two genera does not appear homologous to that above because of the shape and positioning of the teeth. The outgroups *Evorthodus, Gobioides, Oxyurichthys* and *Sicydium* have a single row of teeth in the upper jaw as do all other oxudercines. I interpret the presence of a second, short row of stout canine teeth in the upper jaw as a *de novo* acquisition rather than a reversal to a more generalised condition.

39. In *Periophthalmodon*, a broad, black stripe (brown in preservative) courses posteriorly from the eye and terminates near the tail (Fig. 97). This stripe has been observed in *Pn. schlosseri* to be displayed only in times of aggression or stress.

Nothing approximating this feature is found in the outgroups or any other oxudercine, whereas a longitudinal stripe is found in preserved specimens of all three *Periophthalmodon* species.

Discussion

The monophyly of the Oxudercinae is supported by synapomorphies (characters 1 to 5) that are either reductive or loss characters or innovative features. All oxudercine genera, except *Periophthalmus*, are defined by at least one synapomorphy. Although I cannot now propose a synapomorphy for *Periophthalmus*, both *Periophthalmus* and *Periophthalmodon* are retained due to their widespread and historical usage and because I believe it useful to recognise the innovative features (characters 38 to 39) of *freycineti, schlosseri* and *septemradiatus* at the generic level. I am hopeful that further study will eventually deduce a defining character for *Periophthalmus*.

In most instances, characters necessary to deduce intrageneric relationships were not identified; two genera (*Apocryptes* and *Zappa*) are monotypic whereas, four genera (*Apocryptodon, Oxuderces, Parapocryptes* and *Pseudapocryptes*), are bitypic. In the remaining genera, with one exception, sufficient numbers of characters to hypothesise relationships were not identified. *Periophthalmodon freycineti* and *P. schlosseri* are considered sister-species based on the synapomorphic feature of large, adult size (frequently exceeding 200 mm SL). Other such relationships are not so clear and await further investigation.

Hypothesised intergeneric relationships (Fig. 55), based upon ingroup synapomorphies parsimoniously arranged by PAUP, differ from those of Günther (1861), Bleeker (1874) and Koumans (1953). Günther's Oxudercidae was erected solely for *Oxuderces dentatus*; he placed the remaining genera treated here in the Gobiidae (see Springer, 1978 for elaboration). Bleeker coined Apocrypteini, which included his Apocryptei and Boleophthalmi. Apocryptei comprised *Apocryptodon, Apocryptes, Parapocryptes* and *Pseudapocryptes* whereas Boleophthalmi consisted of *Boleophthalmus* and *Scartelaos*. Additionally, Bleeker erected the Periophthalmini to include *Euchoristopus, Periophthalmodon* and *Periophthalmus*. Koumans essentially followed Bleeker's classification but used the subfamilial group-names Apocrypteinae and Periophthalminae.

Based on evidence presented here, *Apocryptodon, Oxuderces* and *Parapocryptes* represent one monophyletic subset of the Oxudercinae with *Apocryptes, Boleophthalmus, Periophthalmodon, Periophthalmus, Pseudapocryptes, Scartelaos* and *Zappa* forming another. Bleeker's groupings all appear to be subsumed in the latter subset with the group-name Periophthalmini having page priority. Therefore, Periophthalmini is the tribal group-name for the monophyletic unit comprising *Apocryptes, Boleophthalmus, Periophthalmodon, Periophthalmus, Pseudapocryptes, Scartelaos* and *Zappa* whereas the Oxudercini comprises *Apocryptodon, Oxuderces* and *Parapocryptes.*

Family Gobiidae
- Subfamily Oxudercinae
  - Tribe Oxudercini
    - Genus *Parapocryptes* Bleeker, 1874
      - *Parapocryptes rictuosus* (Valenciennes, 1837)
      - *Parapocryptes serperaster* (Richardson, 1845)
    - Genus *Apocryptodon* Bleeker, 1874
      - *Apocryptodon madurensis* (Bleeker, 1849)
      - *Apocryptodon punctatus* Tomiyama, 1934
    - Genus *Oxuderces* Eydoux & Souleyet, 1848
      - *Oxuderces dentatus* Eydoux & Souleyet, 1848
      - *Oxuderces wirzi* (Koumans, 1938)
  - Tribe Periophthalmini
    - Genus *Apocryptes* Valenciennes, 1837
      - *Apocryptes bato* (Hamilton, 1822)
    - Genus *Pseudapocryptes* Bleeker, 1874
      - *Pseudapocryptes borneensis* (Bleeker, 1855)
      - *Pseudapocryptes lanceolatus* (Bloch & Schneider, 1801)
    - Genus *Zappa* n.gen.
      - *Zappa confluentus* (Roberts, 1978)
    - Genus *Scartelaos* Swainson, 1839
      - *Scartelaos cantoris* (Day, 1871)
      - *Scartelaos gigas* Chu & Wu, 1963
      - *Scartelaos histophorus* (Valenciennes, 1837)
      - *Scartelaos tenuis* (Day, 1876)
    - Genus *Boleophthalmus* Valenciennes, 1837
      - *Boleophthalmus birdsongi* n.sp.
      - *Boleophthalmus boddarti* (Pallas, 1770)
      - *Boleophthalmus caeruleomaculatus* McCulloch & Waite, 1918
      - *Boleophthalmus dussumieri* Valenciennes, 1837
      - *Boleophthalmus pectinirostris* (Linnaeus, 1758)
    - Genus *Periophthalmodon* Bleeker, 1874
      - *Periophthalmodon freycineti* (Valenciennes, 1837)
      - *Periophthalmodon schlosseri* (Pallas, 1770)
      - *Periophthalmodon septemradiatus* (Hamilton, 1822)
    - Genus *Periophthalmus* Bloch & Schneider, 1801
      - *Periophthalmus argentilineatus* Valenciennes, 1837
      - *Periophthalmus barbarus* (Linnaeus, 1766)
      - *Periophthalmus chrysospilos* Bleeker, 1852
      - *Periophthalmus gracilis* Eggert, 1935
      - *Periophthalmus kalolo* Lesson, 1830
      - *Periophthalmus malaccensis* Eggert, 1935
      - *Periophthalmus minutus* Eggert, 1935
      - *Periophthalmus modestus* Cantor, 1842
      - *Periophthalmus novaeguineaensis* Eggert, 1935
      - *Periophthalmus novemradiatus* (Hamilton, 1822)
      - *Periophthalmus waltoni* Koumans, 1941
      - *Periophthalmus weberi* Eggert, 1935

Biogeography

Although it is possible to discuss the distribution of oxudercine gobies in general terms, precise information for most species is often lacking and our present knowledge is often deficient in significant detail.

Oxudercines are typically associated with soft bottom habitats, many are burrowers. *Periophthalmus* utilises the mesozone (*sensu* Tomlinson, 1986) of the mangrove community (hereafter referred to as mangal), however, the remaining oxudercine genera are largely restricted to the seaward zone that is oftentimes simply a soft, muddy tidal flat nearly or totally devoid of mangroves. This seaward zone is flooded at all high tides and exposed to some degree at low tide. Consequently, the distribution of non-*Periophthalmus* oxudercines is probably limited to availability of suitable mudflat habitat. I have not located any literature dealing with the distribution of broad, shallow mudflats in the Indo-west Pacific but their distribution may closely resemble the distribution of non-*Periophthalmus* oxudercines that is: northwest Arabian Gulf (48°E longitude); eastward and southward to Queensland, Australia (20°S latitude, 150°E longitude); and northward to the Ariake Sea, Japan (33°N latitude). Mudflats are difficult areas to reach and even more difficult to work in, thus, the above limits may be extended by future collecting efforts.

In assessing the distribution of non-*Periophthalmus* oxudercines, only two genera (*Boleophthalmus, Scartelaos*) are found west of the southern tip of India and from there extend as far west as the Arabian Gulf. *Apocryptodon, Boleophthalmus* and *Scartelaos* extend as far north as the southern part of Japan and these three genera plus *Oxuderces* and *Periophthalmodon* reach as far south as northern Australia.

Many oxudercines are endemic to relatively restricted geographic areas. The three oxudercine species found throughout the Arabian Gulf and as far south as either Bombay or Karachi (*Boleophthalmus dussumieri, Periophthalmus waltoni* and *Scartelaos tenuis*) are endemic to that region. The west African *Periophthalmus, Ps. barbarus*, is found only on that coast. One oxudercine from Japan (*Apocryptodon punctatus*) is endemic there, whereas *Ps. modestus* is only found in northern China, Japan and Korea. In northern Australia two species of *Boleophthalmus, B. birdsongi* and *B. caeruleomaculatus*, are endemic, whereas *Oxuderces wirzi* is known only from southern Papua New Guinea and northern Australia.

Scartelaos cantoris is known only from the Andamans, whereas *S. gigas* is known only from northern China. *Zappa confluentus* is known only from a single locality in Papua New Guinea.

I recognise seven divisional associations of oxudercines in the Indo-west Pacific and west Africa based on maximal endemism (Fig. 98). Two divisions lack endemic elements, the remaining five have endemism rates equal to or greater than 50%. My conceptualisation is a modification of that of Macnae (1968:223, fig. 74) which was based on mangrove distribution patterns.

(i) *West Africa (Senegal to Angola).* One endemic species, *Periophthalmus barbarus.* Although known in other groups of fishes (Springer, 1982), no other gobioid genus has both an Indo-west Pacific distribution with representation in west Africa and nowhere else. Elaboration on this distribution is provided below.

(ii) *East Africa (southern Red Sea to south Africa).* Two widely distributed species, no endemics. Elaboration on this distribution is provided below.

(iii) *Arabian Gulf (Iraq to Bombay).* Six species, three of which are endemic. The non-endemics (*Boleophthalmus boddarti, Periophthalmus argentilineatus* and *Scartelaos histophorus*) are not known farther north than Pakistan (and *B. boddarti* does not range farther north than Bombay); they have not been reported from the Arabian Gulf (Kuronuma & Abe, 1972). Although the Arabian Gulf is not considered an area of high endemism (Relyea, 1981), by enlarging the faunal boundaries to include the Gulf of Oman to Bombay, a higher rate of endemism may be achieved.

At least two blenniids (*Ecsenius pulcher, Omobranchus mekranensus*) are endemic to this enlarged division (V.G. Springer, personal communication). As the west coast of India south of Bombay and the southern end of the Arabian Peninsula are largely devoid of mangrove (Macnae, 1968), we might also assume that extensive, shallow mudflats are also lacking. Therefore, the Arabian Gulf oxudercine fauna may have been isolated for a lengthy period, possibly since India collided with Asia (early-middle Eocene according to Audley-Charles *et al.*, 1981). The three non-endemic species found at the southern end of the division may be recent dispersalists from the east coast of India or the three endemics could be dispersing southward. Either alternative would account for the areas of sympatry.

(iv) *Indo-Malaya (west coast of India to Borneo including Java and Vietnam).* 17 species, nine of which are endemic. The west coast of India south of Bombay is largely lacking in suitable habitat for oxudercines. Oxudercines are not known or reported from the Laccadives or Maldives. From the east coast of India to Borneo, plentiful, suitable habitat exists and oxudercines exhibit their greatest diversity. Nine of the ten oxudercine genera are found in this division, with two of them (*Apocryptes* and *Pseudapocryptes*) endemic. The southeastern edge of this division represents Wallace's Line except that it does not include the Philippines which I have allied with the Australia/New Guinea division. Additionally, it is not possible to associate Sulawesi with any division because oxudercines have not been reported from there.

(v) *Australia/New Guinea (including Timor, the Moluccas and the Philippines).* 12 species of which seven species including one monotypic genus are endemic. The placement of the Philippines in this division is problematic. Aligning the Philippines with this division is based solely on the distribution of two species, *Periophthalmodon freycineti* and *Periophthalmus malaccensis*; the inclusion of the Philippines in this division makes these two species endemics. Some authorities believe, and evidence suggests, that Philippine affinities, both biological and geological, are with Indo-Malaya rather than Australia/ New Guinea (Audley-Charles, 1981; Earl of Cranbrook,

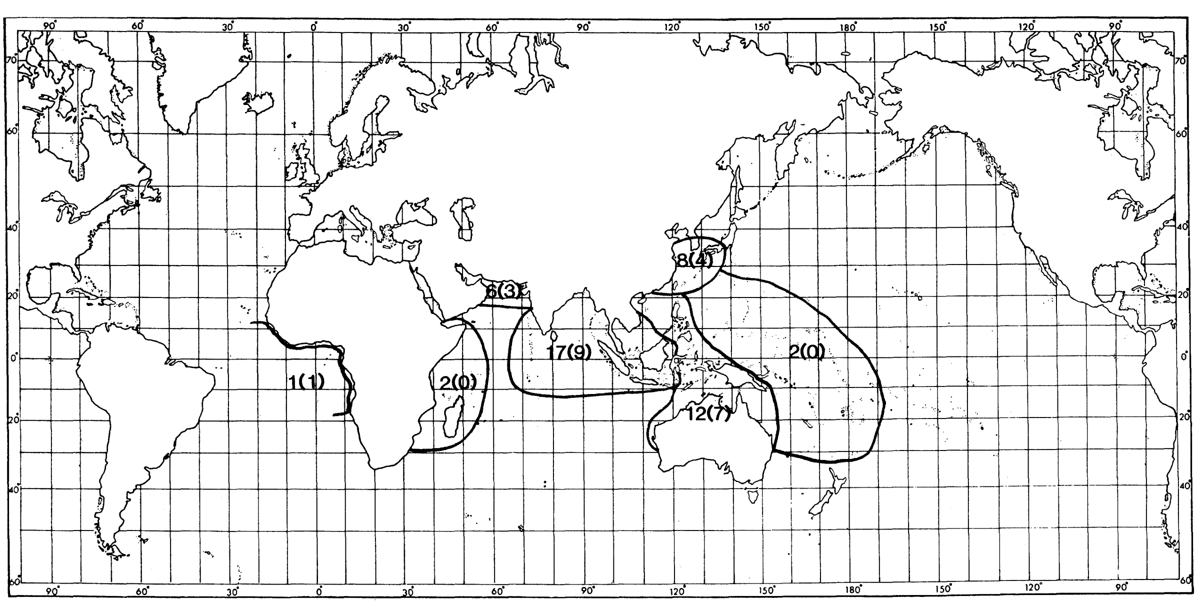

Fig.98. Subdivisions of the Indo-west Pacific and west coast of Africa based on maximal oxudercine endemism. The first number indicates oxudercine species diversity in that subdivision followed by the number of subdivional oxudercine endemics in parentheses.

1981). However, Vari (1978) demonstrated that the distribution of the freshwater species of the family Terapontidae was limited to the Philippines-Sulawesi-New Guinea-Australia area. There are only three non-*Periophthalmus* oxudercines (*Apocryptodon madurensis, Pn. freycineti* and *Scartelaos histophorus*) in the Philippines.

(vi) *China Sea (China and Taiwan northward to southern Korea and Japan).* Eight species, four of which are endemic. Macnae (1968) included the Philippines in this division. As mentioned above, the Philippines are associated, albeit loosely, with Australia/New Guinea.

(vii) *Oceania (approximate Pacific Plate margin eastward to Samoa).* Two species, neither of which is endemic. The indigenous species (*Periophthalmus argentilineatus* and *Ps. kalolo*) are widely distributed throughout this division. Further discussion is given below.

Two sister-species distributions are worthy of note: *Oxuderces dentatus* and *O. wirzi* (Fig. 16), and *Periophthalmodon freycineti* and *Pn. schlosseri* (Fig. 25). In each sister-species pair, one member is found in southern New Guinea and northern Australia (Sahul Shelf) whereas the other member is more widely distributed in Indo-Malaya (Sunda Shelf). A similar but not identical distribution pattern is known for the mangrove species *Aegialites annulata* and *A. rotundifolia* (Chapman 1976: fig. 87). *Oxuderces dentatus* ranges from northern China to southern India with extension onto the eastern end of Java. *O. wirzi* is known only from northern Australia and southern New Guinea. Representatives of the genus are not yet known from Borneo, Sulawesi, Timor, Halmahera or the Philippines (Fig. 16).

Periophthalmodon freycineti is known from the Philippines southward to Halmahera, New Guinea and northern Australia. (One lot from Burma is known but I seriously question its locality reliability). The material from which the original description of *Pn. freycineti* was based came from Timor. *Periophthalmodon schlosseri* is known from the Andaman Sea, Strait of Malacca, Sumatra and southern Borneo. Representatives of the genus are not yet known from Sulawesi.

The segregation of the geminate species of *Oxuderces* conforms well to Wallace's Line, a demarcation that would place *O. dentatus* in the Oriental zoogeographic region (Sunda Shelf) and *O. wirzi* in the Australian region (Sahul Shelf) (regions based on Bond, 1979). Using Wallace's Line as a model for predicting distributions, we would expect that *O. wirzi* would be found in Timor, Halmahera and Sulawesi, whereas *O. dentatus* would be present in Borneo and the Philippines. [Although originally proposed for freshwater and terrestrial species, Wallace's Line (1863) may be applicable to oxudercines as well as they are typically associated with reduced salinity conditions of river mouths.] Examples supporting the influence of Wallace's Line on the distribution and evolution of inshore fishes are provided by Winterbottom *et al.* (1984) and Woodland (1986).

The occurrence of *Periophthalmodon freycineti* in the Philippines belies a distribution congruent with either Wallace's Line or the Sahul Shelf but is in accordance with Huxley's (1868) Line, a possible *lapsus calami* which associated the Philippines with all territory east of Wallace's Line. Thus, Huxley's Line would demarcate an area equivalent to my Australia/New Guinea division (see above).

Except for the Philippine representatives of *Pn. freycineti, Pn. freycineti* and *O. wirzi* are found only on Gondwanic elements whereas *Pn. schlosseri* and *O. dentatus* are exclusively Laurasic (Audley-Charles, 1981). Does this imply that these species, which are still sufficiently alike to be considered congeneric, have none the less been separated since late Cretaceous and have independently ridden the Laurasian and Gondwanan plates to arrive vicariously at their present locations of comparative proximity? I don't think so. What it does mean, I think, is that sometime after the collision of Australia/New Guinea and Asia (about 5-15 million years ago according to Audley-Charles *et al.*, 1981), a vicariant event (possibly sea level fluctuations) caused both *Oxuderces* and *Periophthalmodon* to speciate. Audley-Charles (1981) considered the eastern part of Sulawesi (= Celebes) Gondwanic, the western portion Laurasic; the discovery of *Oxuderces* and/or *Periophthalmodon* on Sulawesi would be most informative. Additionally, as I have examined only one lot (2 specimens) of *Pn. freycineti* from the Philippines, it would be useful to reconfirm its presence there.

Periophthalmus is much more widely distributed than the rest of the Oxudercinae being found from Samoa westward to east Africa with one species along the west African coast (Fig. 29). The distribution of *Periophthalmus* appears more closely linked to mangal rather than mudflat distributions and this mangal association of *Periophthalmus* is probably not fortuitous. Unfortunately, little is known about possible species-specific associations between *Periophthalmus* and mangroves. This topic merits further study and may have symbiotic implications. Sufficient information is known about several *Periophthalmus*/mangal distributions to be worthy of mention.

Mangrove Diversity and Distribution Patterns

Mangrove evolved at least as early as the Cretaceous (Raven & Axelrod, 1974). McCoy & Heck (1976:204) suggested a pan-Tethyan mangrove distribution and cited Cretaceous fossil evidence in Europe, east Africa, and Borneo. Subsequently, in the Eocene-Oligocene-Miocene fossil record, mangroves were recorded from the Pacific coast of South America eastward to the Caribbean, Africa, Europe, India, Borneo and New Guinea (McCoy & Heck, 1976:fig. 2).

Evolutionary diversification resulted, in part, from the closure of the east-west Tethyan passageway caused by Africa/Arabia adjoining Asia in the late Cretaceous/early Eocene. Consequently, the present distribution of mangroves in the New World is considered relictual (Tomlinson, 1986:55). All five species of west African mangrove trees listed by Tomlinson (1986:42) are found in the Americas, none is found on the east African coast or anywhere else in the Indo-west Pacific (*sensu* Springer, 1982). Thus, west African mangrove affinities are clearly with the New World (Chapman, 1976; Tomlinson, 1986).

The Old World mangrove flora (not including west Africa) is more speciose than the New World (60 versus 10, Chapman, 1976) and extends from east Africa to Samoa and Tonga (15°E to 165°W).

Periophthalmus Diversity and Distribution Patterns and Co-occurrence with Mangal

The diversity and distribution of *Periophthalmus* can be segregated into two components: west Africa (one species) and Indo-west Pacific (11 species). The endemic west African species (*Periophthalmus barbarus*) ranges from Senegal to Angola, which parallels the distribution of mangal. Since the opening of the Atlantic, the cold waters of the Cape of Good Hope have been an effective barrier to mangrove migration (Chapman, 1976; Tomlinson, 1986), we can probably assume the same for *Periophthalmus*. If we assume *Ps. barbarus* was derived from the diverse *Periophthalmus* fauna of the Indo-west Pacific region and did not cross the African continent (although very small land barriers are probably traversable), then *Ps. barbarus* probably represents a relict from an original Tethyan stock. *Periophthalmus barbarus* may have been separated from congeners since late Cretaceous/early Eocene and could possibly help corroborate Winterbottom's (1985) hypothesis on Cretaceous origins of many perciform fishes. I am unaware, however, of any *Periophthalmus* fossils that would support or refute this idea.

Why are there no *Periophthalmus* in the New World since the west African *Periophthalmus* is associated with some of the same mangrove species found in the Americas? Other gobioid genera have circumtropical distributions (i.e. *Eleotris, Awaous*), why not *Periophthalmus*, especially since suitable habitat is available? Even if we assume that *Periophthalmus* and mangrove had pan-Tethyan distributions, their occurrences may not have been contemporaneous. An ancestral *Periophthalmus* may have never reached South America before it separated from Africa, whereas mangrove could have dispersed across a sizeable water barrier to reach the New World. The dispersal capability of *Periophthalmus* is not known but they certainly are not adept swimmers. Long-distance dispersal by water seems unlikely. Of course, we cannot discount or test the former existence and subsequent extinction of *Periophthalmus* in the Americas (unless fossil evidence is discovered). Also, evolutionary rates probably differ. Mangroves possibly have a slower rate than *Periophthalmus* which could account for the conspecificity of west African with New World mangroves.

The north coast of Africa lacks mangroves, probably due to the aridity of the region. In the Red Sea, a single species of mangrove (*Avicennia marina*) extends from Djubal (southern tip of Sinai Peninsula) as far south as Massawa (Chapman, 1976). I have not examined any specimens nor do I know of any records of *Periophthalmus* along the north coast of Africa or in the Red Sea north of Massawa. Along the east African coastline from south of Massawa to Durban are sporadic concentrations of *A. marina, Bruguiera gymnorrhiza, Rhizophora mucronata* and five other species of mangrove. Two widespread species of *Periophthalmus* (*Ps. argentilineatus* and *Ps. kalolo*) also occur along the east coast of Africa.

Periophthalmus argentilineatus and *Ps. kalolo* are found from the southern Red Sea and east Africa eastward across Indo-Malaya, Australia and the Philippines, and on to Samoa (30°E to 165°W). Additionally, *Ps. kalolo* is also known from Tonga. Similarly, three species of mangrove (*A. marina, B. gymnorrhiza* and *R. mucronata*) are found from 30°E to 165°E with *A. marina* and *B. gymnorrhiza* extending farther eastward to 180°E and *B. gymnorrhiza* even as far as Tonga and Samoa (165°W) (Tomlinson, 1986). The taxonomy of the *Rhizophora* species in Fiji, Tonga and Samoa is unsettled; Chapman (1976) stated *R. mucronata* and the variety *selala* of *R. mucronata* were present whereas Tomlinson (1986) listed only the variety *selala* from 165°E to 180°E and *R. samoensis* from 180°E to 165°W. Many other mangrove species range from 30°E to 165°W but no species has a continuous distribution such as the three listed above. No mangroves or *Periophthalmus* are found east of 165°W.

The high diversity of *Periophthalmus* (12 species) in comparison to other oxudercines (no other non-*Periophthalmus* oxudercine genus has more than five species) may be related to mangal diversity. That *Periophthalmus* is, at the very least, a facultative mangal associate is obvious. Less obvious is the possible species-species correlation between *Periophthalmus* and mangrove. Only a detailed survey of *Periophthalmus* and mangrove, locality by locality, can adequately address this issue. Additionally, other mangal associates such as crabs, shrimps and molluscs could be incorporated in such a study to assess the degree to which mangroves affect and influence animal distributions.

ACKNOWLEDGMENTS. Numerous individuals aided this study in the loan and exchange of specimens, collections, habitat data or in other diverse ways. For their contributions I am grateful: T. Abe, A.C. Alcala, G.R. Allen, G. Arboco, M.L. Bauchot, M. Boeseman, J. Chambers, W.N. Eschmeyer, N. Feinberg, C.J. Ferraris, Jr., A.G. Gerberich, M.S. Gordon, D.F. Hoese, R.E. Hunziker, B. Jayne, J.W. Johnson, W. Klausewitz, M. Kottelat, H.K. Larson, J.D. McEachran, K. Meguro, G. Mickoleit, P.J. Miller, H.K. Mok, D.W. Nelson, J. Nielsen, H. Njissen, J.R. Nursall, H.J. Paepke, T.W. Pietsch, K. Rema-Devi, J.E. Randall, T.R. Roberts, J.A. Siegel, W.F. Smith-Vaniz, W.C. Starnes, C. Stocker, M.J.P. van Oijen, H.K. Voris, S.H. Weitzman, A. Wheeler, J.T. Williams, R. Winterbottom and T. Wongratana.

Figures 68, 70 and 71 were drawn by B. Griswold. G.R. Allen, D.F. Hoese, B. Jayne, J.R. Nursall, J.E. Randall and R. Winterbottom graciously provided color transparencies and/or black and white negatives of both *in situ* and recently captured specimens. A.G. Gerberich, J.A. Louton, W.C. Starnes and J.T. Williams provided computer expertise.

Portions of early drafts were laboured through and constructively criticised by R.S. Birdsong, D.F. Hoese, G.D. Johnson, V.G. Springer and R. Winterbottom. Special thanks are due to Drs Johnson and Springer for their patient toleration of curiosities during the course of my two-year fellowship period at the USNM.

Support for this research was partially provided in the form of a Research Grant-in-Aid from Sigma Xi, the Scientific Research Society and a National Science Foundation Postdoctoral Fellowship (Grant BSR-8411087). Travel to Malaysia was made possible by an National Science Foundation grant to Dr H.K. Voris (INT-8305817).

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Accepted 14 July 1988

Table 1. Ranges, means and standard deviations of dorsal and anal fin elements.

Genus		Spinous dorsal fin			Second dorsal fin (total elements)			Anal fin (total elements)		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Apocryptes	10	5.0	5	0.000	22.0	21-23	0.667	22.1	20-24	1.101
Apocryptodon	18	6.0	6	0.000	22.7	21-24	1.018	22.2	21-23	0.878
Boleophthalmus	72	5.0	5	0.000	25.3	23-28	1.151	25.0	22-27	1.066
Oxuderces	20	6.0	6	0.000	27.9	24-31	2.222	27.2	24-30	1.908
Parapocryptes	17	5.9	5-6	0.243	27.3	26-29	0.849	26.8	25-29	0.951
Periophthalmodon	32	7.7	4-15	3.524	12.8	11-14	0.622	12.0	10-14	1.031
Periophthalmus	140	11.2	4-17	3.250	12.5	10-14	1.000	11.6	9-14	1.250
Pseudapocryptes	17	5.0	5	0.000	31.2	29-33	0.970	29.1	27-31	0.899
Scartelaos	24	5.0	5	0.000	26.1	23-28	1.116	25.3	24-27	0.847
Zappa	7	5.0	5	0.000	28.1	27-30	1.069	27.3	26-28	0.951

Table 2. Ranges, means and standard deviations of counts for pectoral fin rays and predorsal scales.

Genus		Pectoral fin rays (right side)			Pectoral fin rays (left side)			Predorsal Scales		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Apocryptes	10	22.4	20-25	1.578	22.2	20-25	1.874	53.5	44-63	6.835
Apocryptodon	18	21.7	17-23	1.353	22.1	18-24	1.353	25.7	19-33	3.773
Boleophthalmus	72	19.1	17-21	0.900	19.2	16-21	1.017	37.8	25-60	6.375
Oxuderces	20	22.4	20-24	1.334	22.4	20-25	1.314	34.9	22-44	6.851
Parapocryptes	17	20.8	20-23	0.928	20.6	19-22	0.795	33.3	23-40	3.989
Periophthalmodon	32	15.4	12-19	1.625	15.2	12-18	1.674	21.4	16-26	2.697
Periophthalmus	140	13.2	11-16	1.250	13.1	11-16	1.250	27.7	18-40	5.500
Pseudapocryptes	17	19.2	17-21	1.091	19.5	18-21	0.869	75.9	56-113	14.217
Scartelaos	24	20.0	18-22	0.908	20.2	18-22	1.274	-	-	-
Zappa	7	19.6	18-21	0.976	19.6	19-20	0.535	-	-	-

Table 3. Ranges, means and standard deviations of counts for transverse scales: transverse scales from anal fin origin dorsoanteriorly (TRF); transverse scales from anal fin origin dorsoposteriorly (TRB); and transverse scales from origin of second dorsal fin ventroposteriorly (TRDB).

Genus		TRF			TRB			TRDB		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Apocryptes	10	36.2	26-46	6.844	32.3	25-40	5.334	35.7	29-50	6.550
Apocryptodon	18	15.9	13-18	1.415	14.6	13-17	1.042	15.9	13-19	1.608
Boleophthalmus	66	29.9	19-43	4.951	27.2	18-38	4.655	30.4	18-46	5.244
Oxuderces	20	21.2	17-26	2.681	19.2	16-25	2.159	21.5	19-25	1.916
Parapocryptes	17	20.2	16-26	3.148	19.4	15-26	2.887	20.8	17-23	1.620
Periophthalmodon	32	14.4	12-17	1.385	13.5	12-16	1.047	13.2	11-15	1.194
Periophthalmus	140	20.3	12-32	4.750	18.7	11-30	4.750	19.6	12-34	5.500
Pseudapocryptes	17	40.1	31-63	8.400	40.1	31-59	7.035	44.5	34-58	6.866
Scartelaos	-	-	-	-	-	-	-	-	-	-
Zappa	-	-	-	-	-	-	-	-	-	-

Table 4. Ranges, means and standard deviations of counts for longitudinal scales, and upper and lower jaw teeth. Number of upper jaw teeth indicated for *Periophthalmodon* is for the outer row only.

Genus		Longitudinal scales			Upper jaw teeth			Lower jaw teeth		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Apocryptes	10	121.2	93-143	19.263	27.8	14-44	9.987	26.8	18-36	5.453
Apocryptodon	18	52.1	47-58	4.013	21.9	15-30	3.857	31.4	22-49	7.056
Boleophthalmus	72	101.9	61-185	22.465	51.7	24-79	10.572	55.7	30-81	11.665
Oxuderces	20	68.8	59-88	8.284	28.2	15-40	6.438	27.0	12-49	10.083
Parapocryptes	17	78.4	62-94	9.532	42.1	23-56	10.078	31.9	23-44	6.408
Periophthalmodon	32	51.0	47-57	2.747	24.0	16-35	4.348	21.4	16-26	2.312
Periophthalmus	140	67.0	46-121	18.750	23.5	14-39	6.250	21.7	11-39	7.000
Pseudapocryptes	17	208.8	150-275	42.103	28.1	17-45	7.889	17.7	12-26	3.754
Scartelaos	24	-	-	-	29.3	19-37	5.435	35.4	17-47	7.064
Zappa	7	-	-	-	40.7	35-48	4.680	20.0	19-22	1.155

Table 5. Ranges, means and measurements of head length, head depth and head width expressed as a percentage of standard length.

Genus		Head Length		Head Depth		Head Width	
	N	mean	range	mean	range	mean	range
Apocryptes	10	22.7	21.9-23.9	14.0	12.5-15.1	15.1	12.1-17.3
Apocryptodon	18	26.1	23.2-28.6	13.5	11.6-15.4	15.4	13.0-18.6
Boleophthalmus	72	27.0	23.6-31.1	15.1	12.6-17.3	15.7	12.0-20.9
Oxuderces	20	26.0	23.3-28.2	11.4	9.6-12.9	13.3	10.5-16.0
Parapocryptes	17	20.4	18.3-23.9	11.0	8.9-14.4	10.9	8.3-14.4
Periophthalmodon	32	29.2	25.9-33.6	18.2	16.0-20.8	16.4	13.3-20.9
Periophthalmus	140	27.5	24.2-31.1	17.3	14.3-23.8	17.5	12.6-22.6
Pseudapocryptes	17	18.5	14.8-22.0	10.1	7.8-13.1	10.0	6.9-13.4
Scartelaos	24	24.5	21.2-27.7	10.9	9.5-13.1	13.2	9.9-17.7
Zappa	7	23.9	22.1-25.7	11.7	10.3-13.7	14.2	11.4-18.5

Table 6. Ranges and means of measurements of length of spinous dorsal fin base, length of second dorsal fin base, and length of anal fin base expressed as a percentage of standard length.

Genus		D1 base		D2 base		Anal base	
	N	mean	range	mean	range	mean	range
Apocryptes	10	7.9	7.1-8.9	44.1	41.4-46.9	41.9	39.8-45.4
Apocryptodon	18	12.5	11.1-14.7	42.5	40.6-44.9	38.6	33.8-41.0
Boleophthalmus	72	13.3	9.8-18.9	43.4	38.2-47.9	39.4	34.5-43.3
Oxuderces	20	12.6	11.6-14.3	43.2	40.0-47.2	40.0	38.2-42.6
Parapocryptes	17	12.6	11.6-14.5	48.4	43.5-51.3	45.1	42.1-47.9
Periophthalmodon	32	10.9	3.2-17.9	22.9	20.1-27.0	20.2	16.0-23.6
Periophthalmus	140	19.3	2.9-27.6	22.1	16.3-27.2	18.3	14.0-24.0
Pseudapocryptes	17	7.1	6.2-7.7	47.7	42.8-52.0	45.3	40.5-48.1
Scartelaos	24	7.0	5.0-10.5	49.1	44.3-54.7	44.2	39.1-48.6
Zappa	7	6.9	4.7-9.5	46.5	43.9-50.1	42.5	40.2-45.6

Table 7. Ranges and means of measurements of caudal fin length (CFL), body depth and least depth of caudal peduncle (LDP), all expressed as a percentage of standard length.

Genus		CFL		Body depth		LDP	
	N	mean	range	mean	range	mean	range
Apocryptes	10	28.2	22.6-32.9	15.7	14.6-17.6	8.9	8.2-9.5
Apocryptodon	18	19.9	15.2-23.0	14.6	12.2-17.4	8.7	7.8-10.3
Boleophthalmus	72	20.8	17.9-25.5	15.7	12.1-18.4	8.8	7.4-9.8
Oxuderces	20	17.2	14.8-19.4	12.7	10.3-14.2	7.4	6.6-8.2
Parapocryptes	17	25.9	19.4-32.5	12.2	8.3-16.5	7.2	5.0-9.2
Periophthalmodon	32	19.4	13.1-23.3	16.3	14.0-18.8	10.6	9.4-12.9
Periophthalmus	140	19.3	14.4-23.6	14.9	11.6-18.4	9.3	7.4-11.4
Pseudapocryptes	17	20.3	16.1-23.4	12.5	9.9-15.9	7.2	5.7-8.3
Scartelaos	24	22.6	18.5-27.2	10.3	8.2-13.0	6.1	5.2-8.0
Zappa	7	25.0	21.4-27.9	9.8	9.3-11.3	6.1	5.2-7.3

Table 8. Ranges and means of measurements of pectoral fin length and pelvic fin length in percent of standard length.

Genus		Pectoral fin length		Pelvic fin length	
	N	mean	range	mean	range
Apocryptes	10	16.2	14.2-17.9	13.8	12.7-15.3
Apocryptodon	18	17.1	14.7-19.9	16.2	14.6-19.2
Boleophthalmus	72	19.5	14.9-27.6	14.6	11.4-18.2
Oxuderces	18	15.7	13.9-18.0	14.7	12.4-16.6
Parapocryptes	17	14.7	11.8-16.7	14.5	12.0-18.2
Periophthalmodon	32	25.4	22.1-29.2	15.8	14.0-18.7
Periophthalmus	140	26.3	21.4-34.7	13.5	10.9-17.1
Pseudapocryptes	17	12.8	10.4-16.6	11.3	9.0-13.8
Scartelaos	24	15.4	12.2-18.6	12.6	10.8-15.4
Zappa	7	14.9	13.4-15.8	13.5	12.4-14.4

Table 9. Ranges, means and standard deviations of counts of dorsal and anal fin rays for species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.*

Genus		Spinous dorsal fin			Second dorsal fin (total elements)			Anal fin (total elements)		
	N	mean	range	sd	mean	range	sd	mean	range	sd
As. bato	10	5	5	0.000	22.0	21-23	0.667	22.1	20-24	1.101
An. madurensis	9	6	6	0.000	22.3	21-24	1.000	21.7	21-23	0.972
An. punctatus	9	6	6	0.000	23.1	22-24	0.928	22.7	22-23	0.500
B. birdsongi	10	5	5	0.000	24.1	23-25	0.568	23.2	22-24	0.789
B. boddarti	20	5	5	0.000	24.5	24-26	0.605	24.5	24-26	0.596
B. caeruleomaculatus	11	5	5	0.000	27.0	24-28	1.522	26.4	24-27	1.467
B. dussumieri	11	5	5	0.000	26.8	24-28	1.401	25.6	24-27	1.027
B. pectinirostris	20	5	5	0.000	24.8	23-26	0.851	24.3	23-25	0.657
O. dentatus	10	6	6	0.000	25.9	24-27	0.994	25.5	24-26	0.707
O. wirzi	10	6	6	0.000	29.9	29-31	0.738	28.9	27-30	0.876
Pa. rictuosus	7	5.9	5-6	0.378	26.9	26-28	0.690	26.4	26-27	0.535
Pa. serperaster	10	6	6	0.000	27.6	26-29	0.843	27.1	25-29	1.101
Ps. borneensis	5	5	5	0.000	31.0	31	0.000	28.4	27-29	0.894
Ps. lanceolatus	12	5	5	0.000	31.3	29-33	1.155	29.3	28-31	0.778
S. cantoris	3	5	5	0.000	25.0	23-26	1.732	24.3	24-25	0.577
S. gigas	1	5	5	0.000	24	24	0.000	24	24	0.000
S. histophorus	10	5	5	0.000	25.9	25-27	0.738	25.5	24-27	0.972
S. tenuis	10	5	5	0.000	26.9	26-28	0.568	25.4	25-26	0.516
Z. confluentus	7	5	5	0.000	28.1	27-30	1.069	27.3	26-28	0.951

Table 10. Ranges, means and standard deviations of counts for pectoral fin rays and predorsal scales for species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.*

Genus		Pectoral fin rays (right side)			Pectoral fin rays (left side)			Predorsal scales		
	N	mean	range	sd	mean	range	sd	mean	range	sd
As. bato	10	22.4	20-25	1.578	22.2	20-25	1.874	53.5	44-63	6.835
An. madurensis	9	21.8	21-23	0.833	22.5	22-23	0.500	23.4	19-27	2.833
An. punctatus	9	21.7	17-23	1.871	21.7	18-24	1.803	27.9	22-33	3.333
B. birdsongi	10	18.8	17-20	0.919	18.7	17-20	0.823	46.3	38-60	6.945
B. boddarti	20	19.4	17-20	0.813	19.7	18-21	0.733	29.2	25-35	2.519
B. caeruleomaculatus	11	19.6	17-21	1.120	19.8	18-21	1.033	40.4	30-53	8.503
B. dussumieri	11	18.5	17-20	0.934	18.8	16-20	1.328	52.6	48-56	2.764
B. pectinirostris	20	18.9	18-20	0.642	18.8	18-20	0.696	33.9	26-48	6.299
O. dentatus	10	21.4	20-24	1.165	21.9	20-24	1.101	4.2	0-22	9.500
O. wirzi	10	23.4	23-24	0.516	22.9	20-25	1.370	36.2	26-44	5.640
Pa. rictuosus	7	21.1	20-23	1.345	20.7	19-22	1.113	35.9	32-40	2.619
Pa. serperaster	10	20.6	20-21	0.458	20.5	20-21	0.527	31.4	23-38	3.777
Ps. borneensis	5	19.6	18-21	1.140	20.0	19-21	0.707	70.4	60-80	8.503
Ps. lanceolatus	12	19.1	17-21	1.084	19.3	18-21	0.863	78.2	56-113	15.759
S. cantoris	3	19.0	18-20	1.000	19.0	18-20	1.000	-	-	-
S. gigas	1	20	20	0.000	22	22	0.000	-	-	-
S. histophorus	10	19.9	19-21	0.876	20.2	18-22	1.317	-	-	-
S. tenuis	10	20.5	20-22	0.707	20.3	18-22	1.160	-	-	-
Z. confluentus	7	19.6	18-21	0.976	19.6	19-20	0.535	-	-	-

Table 11. Ranges, means and standard deviations of counts for transverse scales: transverse scales from anal fin origin dorsoanteriorly (TRF); transverse scales from anal fin origin dorsoposteriorly (TRB); and transverse scales from origin of second dorsal fin ventroposteriorly (TRDB) for species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.*

Genus		TRF			TRB			TRDB		
	N	mean	range	sd	mean	range	sd	mean	range	sd
As. bato	10	36.2	26-46	6.844	32.3	25-40	5.334	35.7	29-50	6.550
An. madurensis	9	16.0	13-18	1.664	14.8	13-17	1.202	15.8	13-18	1.929
An. punctatus	9	15.8	14-18	1.202	14.3	13-16	0.866	16.0	15-19	1.323
B. birdsongi	10	33.8	27-43	5.224	29.3	26-36	3.561	34.6	29-43	4.326
B. boddarti	20	23.1	19-27	2.350	20.8	18-23	1.446	22.4	18-27	2.280
B. caeruleomaculatus	11	35.0	30-41	4.062	31.2	24-35	4.550	34.8	27-40	4.868
B. dussumieri	11	35.6	31-42	3.412	32.3	28-38	3.378	37.8	30-46	4.354
B. pectinirostris	20	30.6	22-39	4.796	29.0	23-36	3.692	31.4	22-37	3.789
O. dentatus	10	21.2	18-26	3.011	19.0	16-25	2.404	22.4	19-25	2.066
O. wirzi	10	21.1	17-25	2.470	19.3	16-23	2.000	20.7	19-23	1.334
Pa. rictuosus	7	17.4	16-19	1.239	17.8	16-20	1.461	20.1	18-21	1.029
Pa. serperaster	10	22.2	20-26	2.486	20.5	15-26	3.171	21.3	17-23	1.829
Ps. borneensis	5	42.2	35-52	7.085	41.0	36-46	4.000	46.6	40-53	4.827
Ps. lanceolatus	12	39.2	31-63	9.024	39.8	31-59	8.103	43.7	34-58	7.572
S. cantoris	3	-	-	-	-	-	-	-	-	-
S. gigas	1	-	-	-	-	-	-	-	-	-
S. histophorus	10	-	-	-	-	-	-	-	-	-
S. tenuis	10	-	-	-	-	-	-	-	-	-
Z. confluentus	7	-	-	-	-	-	-	-	-	-

Table 12. Ranges, means and standard deviations of counts for longitudinal scales, and upper and lower jaw teeth for species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.*

Genus		Longitudinal scales			Upper jaw teeth			Lower jaw teeth		
	N	mean	range	sd	mean	range	sd	mean	range	sd
As. bato	10	121.2	93-143	19.263	27.8	14-44	9.987	26.8	18-36	5.453
An. madurensis	9	50.0	47-57	3.428	21.6	15-30	4.558	33.1	22-49	9.466
An. punctatus	9	54.2	49-58	3.528	22.3	18-27	3.240	29.7	25-34	3.082
B. birdsongi	10	103.1	89-111	7.520	48.2	35-56	6.197	47.2	39-57	6.303
B. boddarti	20	71.4	61-79	5.471	55.8	37-72	7.495	62.1	49-74	7.702
B. caeruleomaculatus	11	119.0	90-136	19.723	54.0	36-70	12.304	62.0	32-81	14.484
B. dussumieri	11	146.2	103-185	23.800	54.2	39-76	11.663	60.3	43-71	9.921
B. pectinirostris	20	104.1	84-123	11.069	48.4	31-79	10.378	48.1	31-64	8.127
O. dentatus	10	63.2	59-66	2.658	25.3	15-35	5.513	19.4	12-28	4.987
O. wirzi	10	74.3	61-88	8.327	31.2	18-40	6.125	34.7	25-49	7.704
Pa. rictuosus	7	87.7	81-94	3.968	34.6	23-51	9.467	35.9	27-44	6.203
Pa. serperaster	10	71.9	62-81	6.118	47.3	37-56	6.832	29.2	23-39	5.203
Ps. borneensis	5	192.0	159-214	20.236	32.0	23-41	6.819	18.6	15-23	3.209
Ps. lanceolatus	12	215.8	150-275	47.419	26.5	17-45	7.994	17.3	12-26	4.030
S. cantoris	3	-	-	-	30.7	25-37	6.028	41.7	39-46	3.786
S. gigas	1	-	-	-	37	37	0.000	36	36	0.000
S. histophorus	10	-	-	-	24.7	19-31	4.111	31.5	17-42	8.059
S. tenuis	10	-	-	-	32.8	31-37	2.486	37.3	31-47	5.034
Z. confluentus	7	-	-	-	40.7	35-48	4.680	20.0	19-22	1.155

Table 13. Ranges and means of measurements of head length, head depth and head width expressed as a percentage of standard length for species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.*

Genus		Head Length		Head Depth		Head Width	
	N	mean	range	mean	range	mean	range
As. bato	10	22.7	21.9-23.9	14.0	12.5-15.1	15.1	12.1-17.3
An. madurensis	9	26.1	24.4-28.1	14.3	13.3-15.4	16.2	13.6-18.6
An. punctatus	9	26.1	23.2-28.6	12.8	11.6-13.7	14.6	13.0-16.3
B. birdsongi	10	28.9	26.6-31.1	15.6	14.3-16.8	17.7	14.7-20.9
B. boddarti	20	27.0	25.0-30.4	16.0	15.0-17.0	16.6	14.2-20.6
B. caeruleomaculatus	11	28.0	27.0-29.8	15.6	14.3-17.3	14.4	12.4-17.3
B. dussumieri	11	25.8	23.6-28.7	13.4	12.6-15.2	13.6	12.0-17.9
B. pectinirostris	20	26.0	24.3-28.0	14.7	13.5-15.9	15.6	13.0-17.9
O. dentatus	10	26.2	24.1-27.5	11.6	9.9-12.6	13.2	10.5-16.0
O. wirzi	10	25.8	23.3-28.2	11.2	9.6-12.9	13.4	10.9-15.3
Pa. rictuosus	7	20.8	18.5-23.5	9.9	8.9-11.5	9.5	8.3-11.2
Pa. serperaster	10	20.2	18.3-23.9	11.8	9.8-14.4	11.9	9.9-14.4
Ps. borneensis	5	20.6	20.0-21.9	12.1	11.1-13.1	12.6	12.0-13.4
Ps. lanceolatus	12	17.7	14.8-22.0	9.3	7.8-11.4	8.9	6.9-11.0
S. cantoris	3	25.1	24.8-25.5	11.3	10.4-12.5	13.8	12.4-16.2
S. gigas	1	24.1	24.1	13.1	13.1	14.7	14.7
S. histophorus	10	24.8	21.2-27.7	11.2	10.1-12.4	13.2	9.9-17.7
S. tenuis	10	24.0	23.3-25.1	10.2	9.5-10.8	13.0	11.7-14.6
Z. confluentus	7	23.9	22.1-25.7	11.7	10.3-13.7	14.2	11.4-18.5

Table 14. Ranges and means of measurements of length of spinous dorsal fin base, length of second dorsal fin base, and length of anal fin base expressed as a percentage of standard length for species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.*

Genus		D1 base		D2 base		Anal base	
	N	mean	range	mean	range	mean	range
As. bato	10	7.9	7.1-8.9	44.1	41.4-46.9	41.9	39.8-45.4
An. madurensis	9	12.8	11.1-14.7	42.8	41.1-44.9	39.8	38.2-41.0
An. punctatus	9	12.2	11.4-13.8	42.1	40.6-44.6	37.3	33.8-40.8
B. birdsongi	10	11.2	9.8-13.0	41.5	38.2-43.5	38.3	34.5-42.7
B. boddarti	20	11.5	9.9-13.1	43.4	40.2-46.4	40.2	38.1-42.4
B. caeruleomaculatus	11	16.2	12.6-18.9	45.0	43.2-47.9	40.1	36.2-43.3
B. dussumieri	11	17.4	16.4-18.5	43.6	42.2-44.7	39.0	35.8-41.3
B. pectinirostris	20	12.3	9.9-14.3	43.4	41.5-46.1	38.9	36.6-40.9
O. dentatus	10	12.2	11.6-13.7	42.1	40.0-44.4	39.2	38.5-41.0
O. wirzi	10	13.1	12.4-14.3	44.3	41.1-47.2	40.8	38.2-42.6
Pa. rictuosus	7	12.6	11.6-13.5	49.2	48.0-50.3	45.1	42.9-47.3
Pa. serperaster	10	12.6	11.8-14.5	47.8	43.5-51.3	45.1	42.1-47.9
Ps. borneensis	5	7.4	6.8-7.6	46.0	44.0-47.6	43.9	43.2-45.0
Ps. lanceolatus	12	7.0	6.2-7.7	48.4	42.8-52.0	45.9	40.5-48.1
S. cantoris	3	9.6	9.1-10.5	48.4	44.3-54.7	43.4	42.0-46.2
S. gigas	1	5.0	5.0	45.4	45.4	39.1	39.1
S. histophorus	10	6.4	5.7-7.5	48.5	46.6-50.5	45.9	41.0-48.6
S. tenuis	10	7.1	5.6-8.3	50.2	48.1-51.9	43.4	40.3-45.4
Z. confluentus	7	6.9	4.7-9.5	46.5	43.9-50.1	42.5	40.2-45.6

Table 15. Ranges and means of measurements of caudal fin length (CFL), body depth and least depth of caudal peduncle (LDP), all expressed as a percentage of standard length, for species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.*

Genus		CFL		Body depth		LDP	
	N	mean	range	mean	range	mean	range
As. bato	10	28.2	22.6-32.9	15.7	14.6-17.6	8.9	8.2-9.5
An. madurensis	9	19.5	17.2-21.9	15.7	13.2-17.4	9.0	7.8-10.3
An. punctatus	9	20.3	18.2-23.0	13.4	12.2-14.1	8.4	7.8-9.8
B. birdsongi	10	20.7	17.9-24.6	15.3	14.0-17.8	9.0	8.1-9.7
B. boddarti	20	19.9	17.9-23.3	17.0	14.5-18.4	9.2	8.3-9.8
B. caeruleomaculatus	11	20.4	18.5-22.7	15.4	12.1-17.0	8.7	7.5-9.3
B. dussumieri	11	23.6	21.9-25.5	14.4	13.3-15.4	8.1	7.4-8.6
B. pectinirostris	20	20.2	18.3-22.2	15.2	12.2-17.6	8.7	7.8-9.3
O. dentatus	10	17.1	15.1-19.4	13.0	10.3-14.2	7.3	6.6-7.8
O. wirzi	10	17.3	14.8-19.1	12.3	11.0-12.8	7.6	6.6-8.2
Pa. rictuosus	7	30.1	26.6-32.5	9.8	8.3-11.6	6.0	5.0-6.9
Pa. serperaster	10	23.0	19.4-26.7	13.9	10.5-16.5	8.1	7.2-9.2
Ps. borneensis	5	19.9	17.2-23.4	15.1	14.3-15.9	7.9	7.6-8.1
Ps. lanceolatus	12	20.5	16.1-23.4	11.4	9.9-13.6	6.9	5.7-8.3
S. cantoris	3	24.3	22.5-27.2	11.7	10.6-12.6	6.6	6.4-6.8
S. gigas	1	18.5	18.5	13.0	13.0	8.0	8.0
S. histophorus	10	22.2	18.5-25.1	10.9	9.6-12.7	5.9	5.2-6.7
S. tenuis	10	23.0	21.7-26.3	9.1	8.2-9.7	6.1	5.5-6.5
Z. confluentus	7	25.0	21.4-27.9	9.8	9.3-11.3	6.1	5.2-7.3

Table 16. Ranges and means of measurements of pectoral fin length and pelvic fin length expressed as a percentage of standard length for the species of *Apocryptes (As.), Apocryptodon (An.), Boleophthalmus, Oxuderces, Parapocryptes (Pa.), Pseudapocryptes (Ps.), Scartelaos* and *Zappa.* The type of basihyal for each species is also provided.

Genus		Pectoral fin length		Pelvic fin length		Basihyal type
	N	mean	range	mean	range	
As. bato	10	16.2	14.2-17.9	13.8	12.7-15.3	spatulate
An. madurensis	9	17.3	16.0-18.9	15.8	14.6-17.4	bifid
An. punctatus	9	16.8	14.7-19.9	16.6	14.8-19.2	unknown
B. birdsongi	10	19.7	17.4-22.1	14.4	11.9-15.5	bifid
B. boddarti	20	19.1	16.5-22.1	14.6	12.8-16.3	bifid
B. caeruleomaculatus	11	23.6	20.9-27.6	16.7	15.6-18.2	bifid
B. dussumieri	11	17.4	14.9-19.8	13.0	11.4-15.7	bifid
B. pectinirostris	20	18.8	16.0-22.3	14.2	13.4-15.2	bifid
O. dentatus	10	15.4	13.9-16.6	14.9	13.4-16.2	spatulate
O. wirzi	10	16.0	14.6-18.0	14.5	12.4-16.6	bifid
Pa. rictuosus	7	13.8	11.8-16.0	14.3	12.0-16.0	unknown
Pa. serperaster	10	15.3	12.9-16.7	14.7	12.2-18.2	bifid
Ps. borneensis	5	15.0	13.1-16.6	13.2	12.3-13.8	unknown
Ps. lanceolatus	12	11.9	10.4-13.4	10.6	9.0-11.5	spatulate
S. cantoris	3	16.8	15.2-18.2	12.7	12.4-12.9	unknown
S. gigas	1	15.1	15.1	13.5	13.5	unknown
S. histophorus	10	15.7	12.2-18.6	13.4	10.9-15.4	spatulate
S. tenuis	10	14.7	13.3-16.4	11.6	10.8-12.8	spatulate
Z. confluentus	7	14.9	13.4-15.8	13.5	12.4-14.4	spatulate

Table 17. Ranges, means and standard deviations of counts of dorsal and anal fin rays for species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*.

Genus		Spinous dorsal fin			Second dorsal fin (total elements)			Anal fin (total elements)		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Pn. freycineti	10	4.1	4-5	0.316	12.7	12-13	0.483	12.6	11-13	0.699
Pn. schlosseri	10	8.0	7-9	0.816	12.7	12-13	0.483	12.7	12-14	0.675
Pn. septemradiatus	12	10.4	4-15	3.801	12.8	11-14	0.835	11.0	10-12	0.603
Ps. argentilineatus	20	13.9	11-16	1.861	12.0	10-13	0.725	11.0	9-12	0.686
Ps. barbarus	11	11.5	10-14	1.128	12.9	11-14	1.136	9.9	9-11	0.701
Ps. chrysospilos	10	8.7	7-10	1.059	12.5	12-13	0.527	11.7	11-13	0.675
Ps. gracilis	10	9.4	9-11	0.699	12.1	12-13	0.316	11.9	11-12	0.316
Ps. kalolo	10	12.9	11-15	1.101	12.3	12-13	0.483	11.6	11-12	0.516
Ps. malaccensis	10	9.8	9-10	0.422	11.6	11-12	0.516	11.3	11-12	0.483
Ps. minutus	11	12.5	10-17	1.968	11.9	11-13	0.539	11.4	11-12	0.505
Ps. modestus	12	13.1	10-17	1.881	12.6	12-14	0.669	12.3	11-13	0.622
Ps. novaeguineaensis	16	9.1	5-13	2.335	12.9	12-14	0.574	12.1	11-13	0.443
Ps. novemradiatus	10	9.3	9-11	0.675	13.1	13-14	0.316	13.7	12-14	0.675
Ps. waltoni	10	12.0	10-13	1.054	13.8	13-14	0.422	11.8	11-12	0.422
Ps. weberi	10	9.9	4-16	3.900	13.1	11-14	1.197	10.9	9-12	0.994

Table 18. Ranges, means and standard deviations of counts for pectoral fin rays and predorsal scales for species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*.

Genus		Pectoral fin rays (right side)			Pectoral fin rays (left side)			Predorsal scales		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Pn. freycineti	10	16.0	15-17	0.667	15.4	13-16	0.966	20.1	17-21	1.287
Pn. schlosseri	10	17.0	16-19	0.816	17.0	16-18	0.667	24.0	20-26	2.160
Pn. septemradiatus	12	13.7	12-15	0.778	13.5	12-15	0.798	20.3	16-23	0.798
Ps. argentilineatus	20	12.8	12-14	0.550	12.6	11-14	0.826	29.1	22-37	4.621
Ps. barbarus	11	13.1	12-14	0.539	13.3	13-14	0.467	31.7	28-36	2.803
Ps. chrysospilos	10	14.7	13-16	1.160	14.7	14-16	0.675	28.5	24-32	2.991
Ps. gracilis	10	12.2	11-13	0.632	12.6	11-14	0.843	22.2	19-24	1.814
Ps. kalolo	10	12.9	12-14	0.568	12.7	12-13	0.483	33.6	27-40	4.402
Ps. malaccensis	10	12.6	12-13	0.516	12.4	11-13	0.699	23.0	21-24	1.054
Ps. minutus	11	12.2	11-14	0.786	12.1	11-13	0.539	25.7	21-30	2.832
Ps. modestus	12	13.8	13-16	0.866	13.7	11-15	1.155	29.8	25-35	2.832
Ps. novaeguineaensis	16	13.8	13-15	0.683	13.3	12-14	0.790	27.2	23-34	2.949
Ps. novemradiatus	10	12.9	11-14	0.876	13.0	12-14	0.471	24.5	20-28	2.415
Ps. waltoni	10	14.7	14-15	0.483	14.5	13-15	0.850	32.7	27-37	3.302
Ps. weberi	10	13.4	12-16	1.075	13.2	12-14	0.632	22.2	18-24	1.874

Table 19. Ranges, means and standard deviations of counts for transverse scales: transverse scales from anal fin origin dorsoanteriorly (TRF); transverse scales from anal fin origin dorsoposteriorly (TRB); and transverse scales from origin of second dorsal fin ventroposteriorly (TRDB) for species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*.

Genus		TRF			TRB			TRDB		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Pn. freycineti	10	14.2	12-16	1.476	13.7	13-15	0.675	12.7	11-14	1.059
Pn. schlosseri	10	15.4	14-17	1.174	14.0	13-16	1.247	14.1	12-15	0.994
Pn. septemradiatus	12	13.7	12-16	0.985	12.9	12-15	0.900	12.8	11-15	1.055
Ps. argentilineatus	20	21.2	16-27	2.876	19.2	15-24	2.254	20.8	18-26	2.359
Ps. barbarus	11	27.5	23-31	2.945	24.2	20-30	3.371	25.5	20-34	3.959
Ps. chrysospilos	10	18.7	16-22	2.111	16.7	14-19	1.494	17.0	15-19	1.247
Ps. gracilis	10	18.3	17-19	0.823	17.8	16-20	1.135	17.1	14-20	1.729
Ps. kalolo	10	21.6	18-28	3.098	20.0	18-24	2.211	20.2	18-22	1.476
Ps. malaccensis	10	15.8	13-19	2.044	15.2	13-17	1.317	15.7	14-17	0.823
Ps. minutus	11	18.0	16-21	1.612	16.8	14-19	1.537	17.5	16-19	1.440
Ps. modestus	12	23.5	19-27	2.505	21.6	19-27	2.392	24.1	19-29	2.429
Ps. novaeguineaensis	16	18.1	16-21	1.731	17.1	15-20	1.962	18.0	15-21	1.966
Ps. novemradiatus	10	18.8	16-23	2.658	17.9	15-21	1.853	18.5	15-21	1.900
Ps. waltoni	10	27.3	24-32	2.830	23.7	20-26	2.263	25.1	21-28	2.424
Ps. weberi	10	14.8	12-18	1.751	13.4	11-19	2.366	14.0	12-17	1.633

Table 20. Ranges, means, and standard deviations of counts for longitudinal scales, and upper and lower jaw teeth for species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*. Number of upper jaw teeth indicated for *Periophthalmodon* is for the outer row only.

Genus		Longitudinal scales			Upper jaw teeth			Lower jaw teeth		
	N	mean	range	sd	mean	range	sd	mean	range	sd
Pn. freycineti	10	50.5	48-53	1.716	24.5	16-32	4.453	20.7	18-25	2.669
Pn. schlosseri	10	53.0	47-57	3.300	23.0	18-28	3.682	20.6	16-23	2.066
Pn. septemradiatus	12	49.8	47-53	2.904	24.4	18-35	4.963	22.7	20-26	1.723
Ps. argentilineatus	20	81.1	64-100	9.339	19.5	13-26	3.687	18.9	12-25	3.986
Ps. barbarus	11	96.6	86-107	7.646	20.4	14-25	3.499	17.0	11-21	2.757
Ps. chrysospilos	10	70.7	64-77	4.373	27.2	18-36	6.033	24.5	14-35	7.412
Ps. gracilis	10	59.2	52-70	6.143	22.1	14-28	4.909	22.8	15-29	4.442
Ps. kalolo	10	74.6	66-86	6.518	18.8	13-25	3.360	16.1	11-23	3.446
Ps. malaccensis	10	54.0	47-61	3.887	23.9	21-28	2.885	22.0	19-25	1.764
Ps. minutus	11	69.8	62-78	5.056	21.1	17-25	3.048	21.4	16-27	3.233
Ps. modestus	12	85.3	75-100	6.746	25.1	21-30	2.429	25.5	21-30	2.782
Ps. novaeguineaensis	16	68.6	54-78	7.429	27.8	16-39	6.557	26.4	19-39	5.440
Ps. novemradiatus	10	67.8	61-76	5.673	29.0	23-35	3.651	27.1	23-33	3.143
Ps. waltoni	10	103.4	91-121	9.430	25.7	19-28	2.908	19.8	17-23	1.932
Ps. weberi	10	50.1	46-52	2.025	23.2	16-28	3.882	18.9	17-22	1.663

Table 21. Ranges and means of measurements of head length, head depth and head width expressed as a percentage of standard length for species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*.

Genus		Head Length		Head Depth		Head Width	
	N	mean	range	mean	range	mean	range
Pn. freycineti	10	30.4	27.4-33.6	18.8	16.9-20.8	17.4	14.3-19.8
Pn. schlosseri	10	29.7	28.2-31.2	18.3	16.9-18.8	16.7	13.8-20.9
Pn. septemradiatus	12	27.8	25.9-31.0	17.7	16.0-19.7	15.4	13.3-18.7
Ps. argentilineatus	20	26.7	25.3-28.7	17.5	15.8-19.3	18.7	14.3-22.6
Ps. barbarus	11	28.3	26.1-31.1	19.2	16.8-23.8	18.1	15.4-21.8
Ps. chrysospilos	10	28.3	26.1-30.1	17.6	14.6-20.6	17.3	12.6-21.8
Ps. gracilis	10	26.0	24.2-27.1	16.3	15.0-17.1	17.1	14.2-19.3
Ps. kalolo	10	28.3	26.3-30.2	18.0	16.5-20.2	19.7	16.5-22.5
Ps. malaccensis	10	28.2	24.4-29.8	18.1	16.4-19.7	16.6	14.3-19.5
Ps. minutus	11	26.8	25.4-27.9	17.7	15.7-19.2	17.1	14.2-18.9
Ps. modestus	12	26.8	25.4-28.3	16.3	14.9-17.7	17.1	14.1-19.8
Ps. novaeguineaensis	16	27.2	25.5-29.4	16.5	15.1-17.8	17.3	15.1-20.2
Ps. novemradiatus	10	26.9	25.9-28.3	16.1	14.8-18.0	15.9	13.2-18.6
Ps. waltoni	10	29.2	27.5-30.9	16.3	14.3-17.9	17.0	13.7-21.9
Ps. weberi	10	28.0	26.8-29.6	18.1	17.4-19.4	17.4	15.4-19.4

Table 22. Ranges and means of measurements of length of spinous dorsal fin base, length of second dorsal fin base, and length of anal fin base expressed as a percentage of standard length for species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*.

Genus		D1 base		D2 base		Anal base	
	N	mean	range	mean	range	mean	range
Pn. freycineti	10	6.3	5.0-8.1	22.4	20.4-23.8	22.4	21.2-23.6
Pn. schlosseri	10	13.9	10.3-16.7	22.3	21.5-23.4	21.2	19.9-23.2
Pn. septemradiatus	12	12.3	3.2-17.9	23.9	20.1-27.0	17.6	16.0-18.9
Ps. argentilineatus	20	22.2	15.9-27.4	20.8	17.6-23.7	16.8	14.0-19.4
Ps. barbarus	11	16.3	14.2-18.2	22.7	20.9-24.1	15.5	14.1-17.7
Ps. chrysospilos	10	17.6	14.8-21.0	21.2	16.3-24.3	18.5	16.7-20.6
Ps. gracilis	10	14.8	13.2-18.5	20.0	18.8-21.3	19.3	17.8-21.1
Ps. kalolo	10	19.7	16.9-22.6	20.9	18.5-23.8	17.6	15.9-18.7
Ps. malaccensis	10	21.0	18.4-23.0	19.8	17.0-23.2	17.7	15.4-20.6
Ps. minutus	11	20.9	18.6-24.9	21.3	20.1-22.7	17.7	15.7-19.3
Ps. modestus	12	21.8	19.9-24.5	22.7	19.8-24.1	19.8	16.1-22.2
Ps. novaeguineaensis	16	17.6	8.2-22.9	22.8	18.8-26.8	19.3	16.8-21.9
Ps. novemradiatus	10	20.6	18.9-22.5	24.1	21.9-25.9	22.3	19.1-24.0
Ps. waltoni	10	21.8	19.1-27.6	24.8	23.2-27.2	19.0	16.2-21.0
Ps. weberi	10	14.4	2.9-24.4	24.5	20.6-26.8	16.5	14.2-18.5

Table 23. Ranges and means of measurements of caudal fin length (CFL), body depth and least depth of caudal peduncle (LDP), all expressed as a percentage of standard length) for species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*.

Genus		CFL		Body depth		LDP	
	N	mean	range	mean	range	mean	range
Pn. freycineti	10	20.4	17.4-23.3	16.6	15.4-18.8	11.0	10.1-12.9
Pn. schlosseri	10	19.5	18.5-21.8	15.8	14.7-17.1	10.2	9.4-11.0
Pn. septemradiatus	12	18.5	13.1-21.4	16.4	14.0-18.4	10.5	9.5-11.3
Ps. argentilineatus	20	18.2	14.4-21.4	14.9	12.8-17.3	9.5	7.9-11.1
Ps. barbarus	11	20.3	17.5-22.8	15.7	14.5-18.1	9.6	8.5-10.8
Ps. chrysospilos	10	19.7	18.0-21.2	15.4	12.8-18.4	9.3	7.4-10.7
Ps. gracilis	10	19.2	17.7-20.5	13.8	12.8-15.2	8.9	8.4-10.1
Ps. kalolo	10	20.2	15.1-22.8	15.0	14.2-15.9	9.7	9.1-10.1
Ps. malaccensis	10	21.3	19.5-23.6	15.7	14.5-16.9	9.8	8.8-10.9
Ps. minutus	11	17.3	15.6-20.1	14.8	13.6-17.5	9.2	8.8-11.1
Ps. modestus	12	18.1	16.0-20.3	15.0	14.3-16.1	9.3	8.2-10.5
Ps. novaeguineaensis	16	18.9	16.0-22.7	14.4	12.2-16.1	9.0	7.7-9.9
Ps. novemradiatus	10	18.8	16.6-20.8	14.6	12.3-15.7	8.9	7.4-9.5
Ps. waltoni	10	18.5	16.4-19.8	13.0	11.6-14.3	8.3	7.6-9.8
Ps. weberi	10	19.7	16.9-23.4	16.2	14.3-17.7	10.7	9.6-11.4

Table 24. Ranges and means of measurements of pectoral fin length, pelvic fin length and pectoral fin height expressed as a percentage of standard length for the species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*.

Genus		Pectoral fin length		Pelvic fin length		Pectoral fin height	
	N	mean	range	mean	range	mean	range
Pn. freycineti	10	25.8	23.8-29.2	16.2	14.6-18.7	12.1	10.3-14.4
Pn. schlosseri	10	24.9	22.2-27.3	15.9	14.0-17.1	12.1	11.0-13.1
Pn. septemradiatus	12	25.4	22.1-28.2	15.5	14.3-16.8	11.2	9.6-12.1
Ps. argentilineatus	20	26.9	23.9-29.7	13.2	11.3-15.2	10.8	9.8-11.9
Ps. barbarus	11	26.4	21.4-34.7	14.9	14.2-16.0	-	-
Ps. chrysospilos	10	26.7	24.6-29.0	14.3	12.4-16.8	11.3	9.4-13.9
Ps. gracilis	10	25.2	23.6-27.7	12.8	11.7-15.1	9.5	7.8-10.3
Ps. kalolo	10	28.0	24.6-30.2	14.5	13.1-15.4	10.5	9.7-11.7
Ps. malaccensis	10	26.6	25.1-28.5	14.5	13.6-16.1	10.7	8.7-12.1
Ps. minutus	11	26.3	23.8-28.5	12.8	11.6-14.8	9.7	8.2-11.3
Ps. modestus	12	25.8	22.8-28.3	13.0	11.5-14.6	10.7	8.6-12.1
Ps. novaeguineaensis	16	26.4	24.2-29.7	12.4	10.9-14.5	10.3	9.0-12.4
Ps. novemradiatus	10	24.8	22.7-27.7	12.3	11.3-13.3	10.8	10.1-11.4
Ps. waltoni	10	26.4	24.7-27.9	12.8	11.8-13.9	10.5	9.5-11.5
Ps. weberi	10	25.0	23.4-26.2	15.7	15.0-17.1	10.4	8.4-11.7

Table 25. Distribution of spinous dorsal-fin pterygiophore formulae (DF) within species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*. Modal and variant formulae are given followed by frequency of occurrence (in parentheses). An asterisk indicates that the preceding pterygiophore does not have an attached spine. The first pterygiophore in all species inserts posterior to the third neural spine.

Species	Mode 1	Mode 2	Variants
Ps. modestus	1311*00 (7)	1301*000 (3)	
Ps. novemradiatus	131100 (8)	1311*00 (2)	140100 (1)
Ps. malaccensis	1311*000 (15)		1401*000 (1)
Ps. argentilineatus	1301*000 (15)		
Ps. gracilis	1301*000 (5)	1301*0000 (2)	13001*000 (1)
Ps. kalolo	1301*000 (6)	1311*000 (2)	1401*000 (1)
Ps. minutus	1301*000 (5)		1401*000 (1)
Ps. novaeguineaensis	1301*000 (6)	1300000 (2)	13001*00(1); 1301000 (1)
Ps. weberi	1401*00 (5)		1311*00 (1); 2301*00 (1)
Pn. septemradiatus	2301*00 (7)	1401*00 (3)	
Ps. barbarus	230100 (9)		
Ps. chrysospilos	1401*000 (12)	1401*00 (6); 2301*00 (5); 2301*000 (5)	
Pn. freycineti	1401*000 (4)		2301*000(1);1301*000 (1); 1301*1*00(1); 2301*1*00 (1)
Pn. schlosseri	1401000 (7)		140100 (1)
Ps. waltoni	2301*000 (5)		3201*000 (1)

Table 26. Variation in placement of the first two pterygiophores of the second dorsal fin in species of *Periophthalmodon (Pn.)* and *Periophthalmus (Ps.)*. The first number listed is the frequency of occurrence followed by a number in parentheses that indicates whether one or two pterygiophores insert in that particular interneural space.

Species	Interneural Space	
	9th	10th
Ps. modestus	3 (1)	3 (1)
Ps. novemradiatus	10 (1)	1 (1)
Ps. malaccensis		16 (1)
Ps. argentilineatus		15 (1)
Ps. gracilis		7 (1), 1 (2)
Ps. kalolo		3 (1)
Ps. minutus		5 (1)
Ps. novaeguineaensis		10 (1)
Ps. weberi	6 (1), 1 (2)	
Pn. septemradiatus	6 (2), 3 (1)	
Ps. barbarus	8 (1)	
Ps. chrysospilos	6 (1), 3 (2)	16 (2), 4 (1)
Pn. freycineti		6 (2)
Pn. schlosseri		8 (2)
Ps. waltoni		10 (2)

Appendix

The following list represents the cleared and stained material used in this study. Specimen preparation and institutional abbreviations are listed in the "Methods and Materials" section.

Apocryptes bato: removed from UMMZ 187890, 1(96); removed from SU 33798, 1(100).

Apocryptodon madurensis: CAS 27444, 1; removed from NTM S.10649-016, 3(43-50); USNM 99874, 3(56-61).

Awaous sp.: TCWC 3267.1, 1(42).

Boleophthalmus birdsongi: removed from NTM S.11364-016, 3(47-59).

Boleophthalmus boddarti: removed from ANSP 62878-89, 3(100-119); USNM 278444, 3(46-48).

Boleophthalmus caeruleomaculatus: removed from AMNH 41558, 3(28-34).

Boleophthalmus dussumieri: removed from LACM 38137-3, 3(62-85).

Boleophthalmus pectinirostris: USNM 192933, 3(75-82); USNM (uncatalogued), 1(97).

Brachyamblyopus sp.: USNM 243403, 3(49-64).

Ctenotrypauchen microcephalus: USNM (uncatalogued), 1(49).

Evorthodus lyricus: TCWC 3283.1, 2(46-52).

Gnatholepis sp.: TCWC 3267.2, 3(36-40).

Gobioides peruanus: removed from WCS 1558, 5(32-34).

Gobionellus boleosoma: TCWC 3266.1, 3(36-56).

Mugilogobius sp.: TCWC 3268.1, 2(28-28).

Oxuderces dentatus: FMNH (uncatalogued), 3(21-38); USNM 86954, 1(93).

Oxuderces wirzi: removed from NTM S.10727-002, 3(69-70).

Oxyurichthys tentacularis: TCWC 3281.1, 2(76-80).

Parapocryptes serperaster: removed from AMNH 18590, 3(71-79); removed from ANSP 62962-10, 3(59-94); removed from SU 61279, 1(63); USNM 119987-88, 1(129); USNM (uncatalogued), 1(93).

Periophthalmodon freycineti: removed from UAMZ 6524, 1(72); USNM 268460, 1(126).

Periophthalmodon schlosseri: removed from CAS 57428, 1(115); USNM 278438, (113); USNM 280385, 1(40).

Periophthalmus argentilineatus: USNM 278285, 3(41-47).

Periophthalmus barbarus: removed from ALA 1078.01, 3(57-71).

Periophthalmus chrysospilos: USNM 278304, 2(35-36).

Periophthalmus gracilis: removed from UAMZ 6520, 1(43).

Periophthalmus kalolo: removed from ROM 51596, 1(53); TCWC 3261.2, 1(48); USNM (uncatalogued), 3(25-51).

Periophthalmus minutus: removed from UAMZ 6514, 2(48-58).

Periophthalmus novaeguineaensis: removed from UAMZ 6522, 2(44-55).

Periophthalmus novemradiatus: USNM 279159, 1(51); USNM (uncatalogued), 3(43-50).

Periophthalmus weberi: removed from AMNH 41563, 2(58-60).

Pseudapocryptes lanceolatus: CAS 14121, 2; removed from SU 40081, 3(44-54); USNM 279313, 1(49); USNM 279353, 1(40); USNM (uncatalogued), 3(46-54).

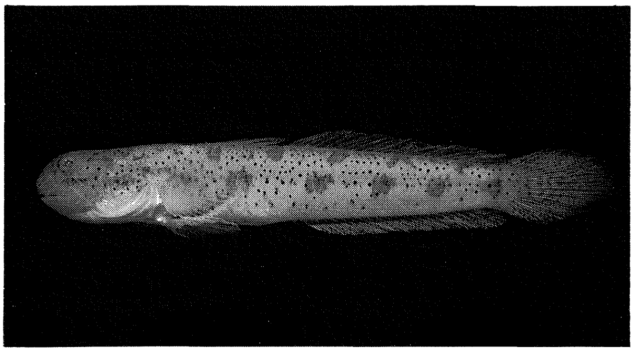
Scartelaos histophorus: removed from AMNH 35819, 3(65-71); removed from NTM S.10727-003, 3(56-70); USNM 243433, 3(55-80); USNM 278437, 2(25-45); USNM (uncatalogued), 1(32).

Scartelaos tenuis: removed from LACM 38141-2, 3(59-69).

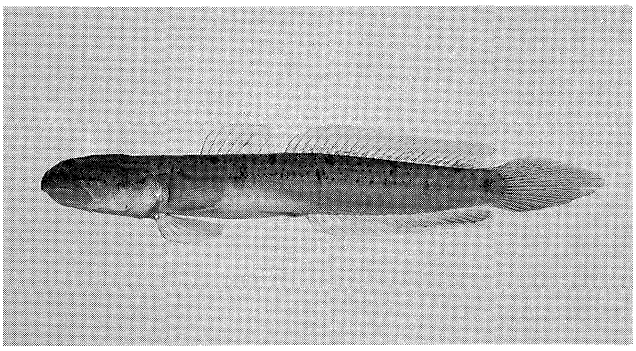
Sicydium salvani: removed from WCS 1564, 2(31-49).

Stiphodon elegans: CAS 27426, 1.

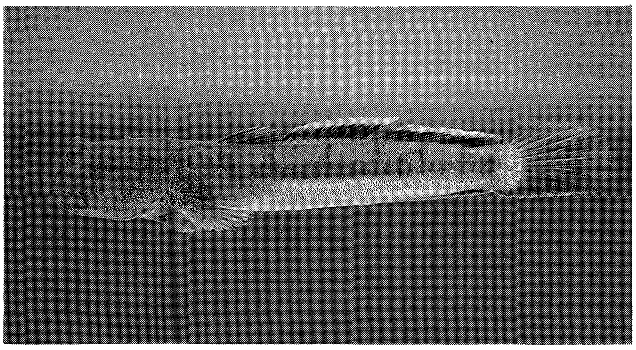
Zappa confluentus: USNM 217306, 2(25-32).



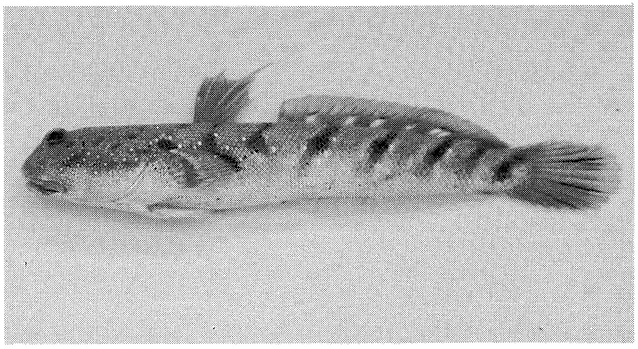
1A. *Apocryptodon madurensis*, AMS I.22040-013, Kewara Beach, Queensland (D.F. Hoese).



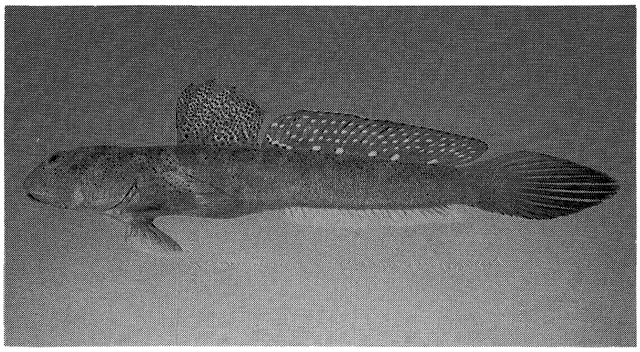
1B. *Apocryptodon punctatus*, 58 mm SL, Japan (H. Masuda).



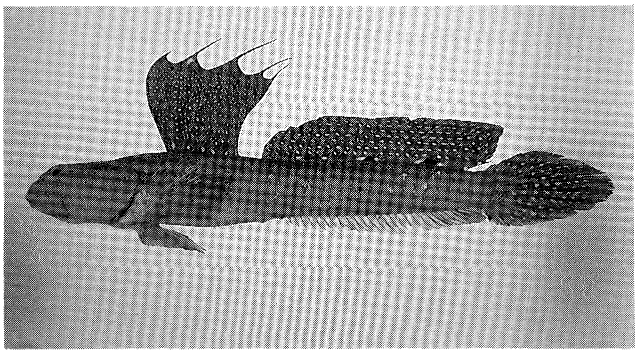
1C. *Boleophthalmus birdsongi*, AMS I.24685-012, 76 mm SL, Darwin (D.F. Hoese).



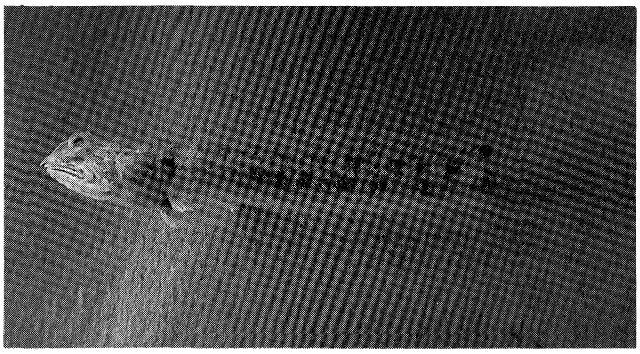
1D. *Boleophthalmus boddarti*, FMNH uncatalogued, Malaysia (B. Jayne).



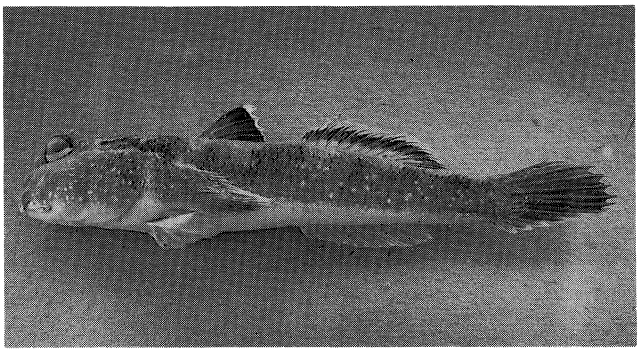
1E. *Boleophthalmus dussumieri*, BPBM 30528, 89 mm SL, Kuwait (J.E. Randall).



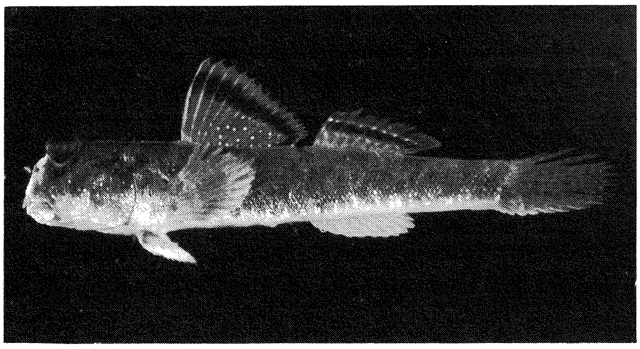
1F. *Boleophthalmus pectinirostris*, 130 mm SL, Japan (H. Masuda).



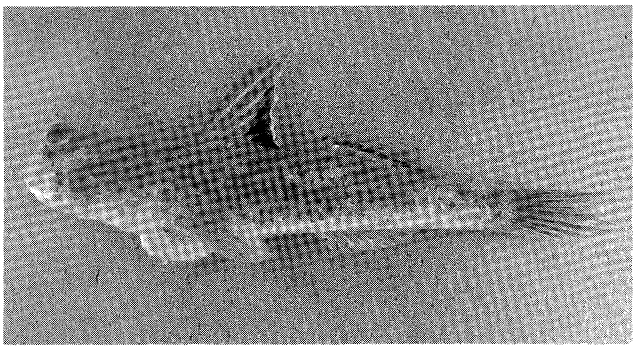
1G. *Oxuderces dentatus*, USNM 279359, 44 mm SL, Malaysia (E.O Murdy).



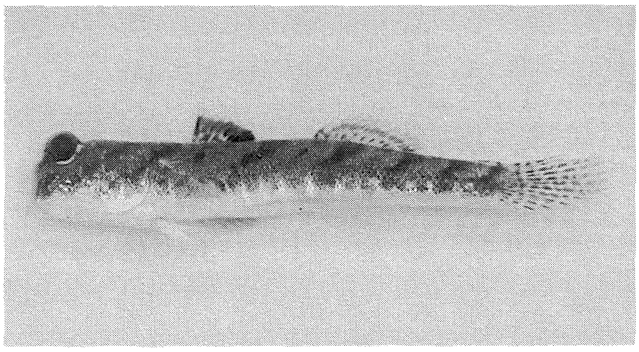
1H. *Periophthalmodon schlosseri*, USNM 278462, 91 mm SL (E.O. Murdy).



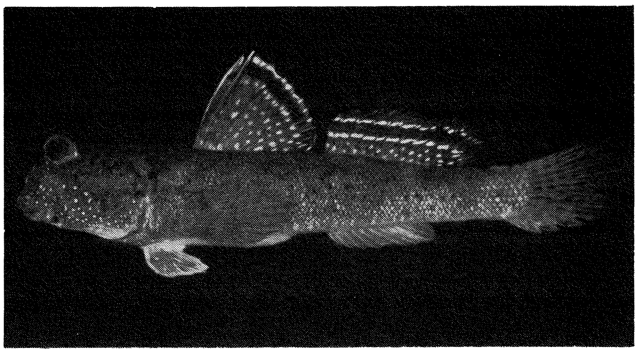
2A. *Periophthalmus argentilineatus*, BPBM 14623, 51 mm SL, Fiji (J.E. Randall).



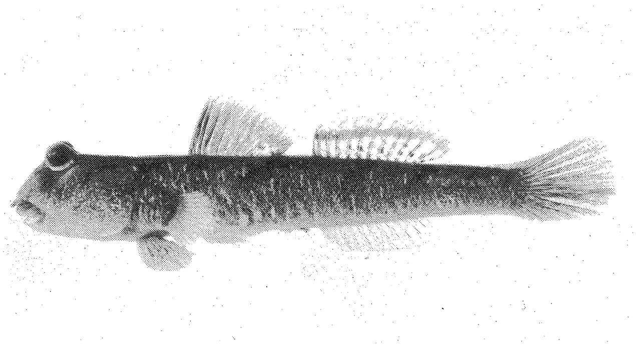
2B. *Periophthalmus chrysospilos*, USNM 279331, 61 mm SL, Malaysia (E.O. Murdy).



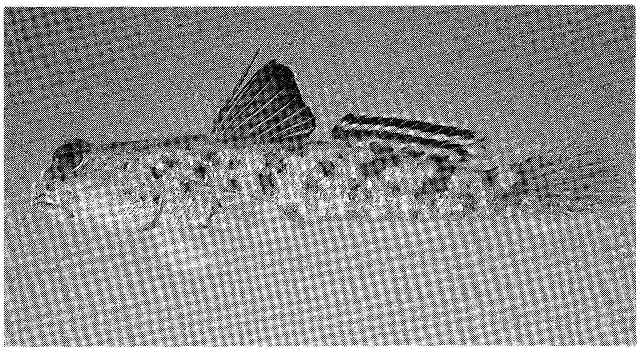
2C. *Periophthalmus gracilis*, USNM 279365, 27 mm SL, Malaysia (B. Jayne).



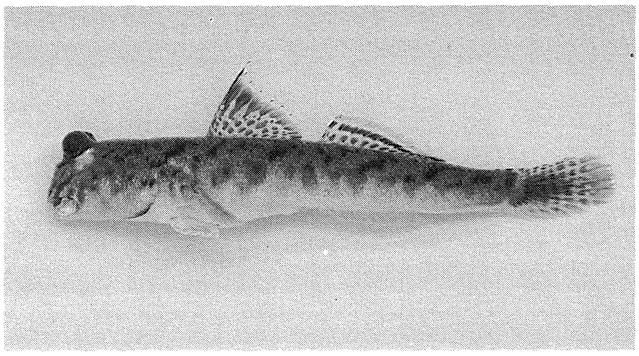
2D. *Periophthalmus kalolo*, BPBM 21553, 95 mm SL, Djibouti (J.E. Randall).



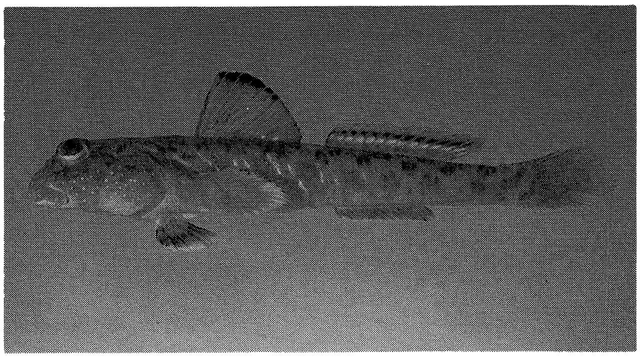
2E. *Periophthalmus modestus*, 70 mm SL, Japan (H. Masuda).



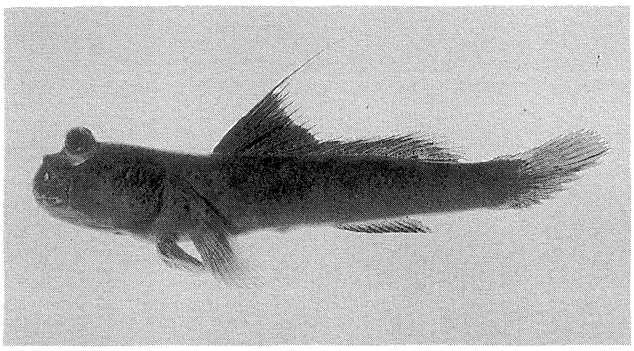
2F. *Periophthalmus novaeguineaensis*, BPBM 30932, 58 mm SL, Northern Territory (J.E. Randall).



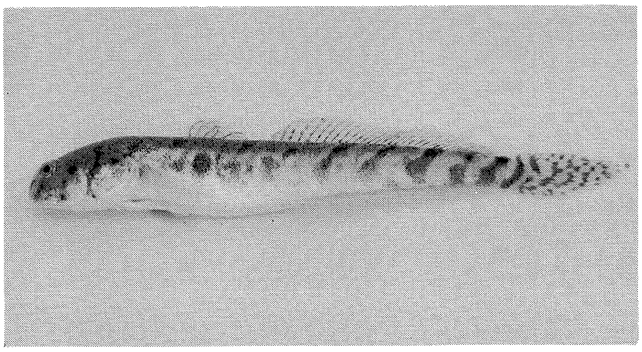
2G. *Periophthalmus novemradiatus*, USNM 279318, 52 mm SL, Malaysia (B. Jayne).



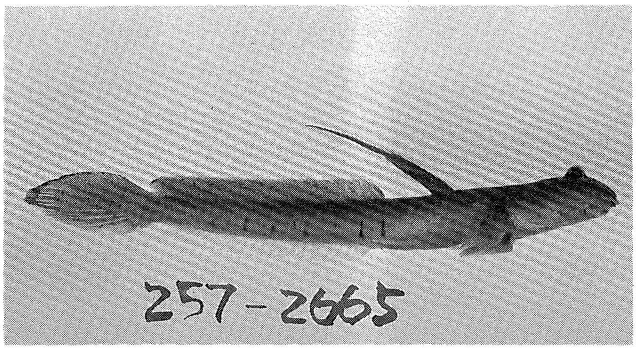
2H. *Periophthalmus waltoni*, BPBM 30527, 98 mm SL, Kuwait (J.E. Randall).



3A. *Periophthalmus weberi*, WAM P.27815-011, 58 mm SL, Papua New Guinea (G.R. Allen).



3B. *Pseudopocryptes lanceolatus*, FMNH uncatalogued, Malaysia (B. Jayne).



3C. *Scartelaos histophorus*, 89 mm SL, Japan (H. Masuda).