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Pseudomugil reticulatus, (Pisces: Pseudomugilidae) a review of the species originally described from a single specimen, from Vogelkop Peninsula, Irian Jaya with further evaluation of the systematics of Atherinoidea

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Abstract:
Pseudomugil reticulatus, hitherto only known from a single specimen from Vogelkop Peninsula, Irian Jaya is redescribed on the basis of selected specimens collected in the environs of Timika and Tembagapura, (approx. 4° 23'S 136° 53'E) Irian Jaya. Examination of a large number of specimens allows for a much more accurate description of meristics, morphometrics, coloration, and sexual dimorphism. Osteological study of *P. reticulatus* provides a clear cut diagnosis of the species. Although the present study does not contradict the hypothesized systematic position of Pseudomugilidae, it suggests that Telmatherinidae, Pseudomugilidae and Melanotaeniidae may form a transformation series. The latest definition of the family Pseudomugilidae and the genus *Pseudomugil* are given.

Zusammenfassung:
Pseudomugil reticulatus, bislang nur in einem Exemplar von der Vogelkop Penisula, Irian Jaya bekannt, wird an hand ausgewählter Exemplare aus der Umgebung von Timika and Tembagapura, (ca. 4°23'S 136°53'O), Irian Java, wiederbeschrieben. Die Untersuchung einer größeren Anzahl von Exemplaren erlaubt eine viel genauere Beschreibung von Meristik, Morphometrie, Farbkleid und Sexualdimorphismus. Osteologische Untersuchungen an *P. reticulatus* liefern eine klar umrissene Diagnose der Art. Obgleich die vorliegende Arbeit der hypothetischen Position der Familie Pseudomugilidae nicht widerspricht, legt sie nahe, daß Telmatherinidae, Pseudomugilidae und Melanotaeniidae eine Transformationsserie bilden könnten. Die neueste Definition der Familie Pseudomugilidae und der Gattung *Pseudomugil* wird gegeben.

Résumé:
Pseudomugil reticulatus, connu par un unique spécimen de la péninsule de Vogelkop, Irian Jaya, est redécrit d'après un choix d'individus collectés dans les environs de Timika et Tembagapura (approx. 4°23'S, 136°53'E), Irian Jaya. L'examen d'un grand nombre de spécimens permet de définir avec plus de précision les données méristiques et morphométriques, la coloration et le dimorphisme sexuel. L'ostéologie permet une diagnose sans ambiguïté de *P. reticulatus.* L'étude ne remet pas en question la position systématique supposée des Pseudomugilidae, elle suggère néanmoins que les Telmatherinidae, les Pseudomugilidae et les Melanotaeniidae forment une série évolutive. De nouvelles définitions sont données pour la famille des Pseudomugilidae et pour le genre *Pseudomugil.*

Riassunto:
Pseudomugil reticulatus, noto in precedenza per un unico esemplare proveniente dalla Penisola di Vogelkop (Irian Java, Indonesia), viene ridescritto sulla base di esemplari collezionati nei pressi di Timika e Tembagapura (all'incirca 4°23' lat.S, 136°53' long.E), in Irian Jaya. L'esame di un gran numero di individui consente un'analisi particolarmente acurata dei dati morfometrici, della colorazione e del dimorfismo sessuale. Lo studio osteologico di *P. reticulatus* fornisce una precisa diagnosi della specie. Anche se l'indagine non contraddice la posizione sistematica ipotizzata per gli Pseudomugilidae, essa suggerisce che Telmatherinidae, Pseudomugilidae e Melanotaeniidae possano costituire una serie contigua. Viene data una definizione aggiornata della famiglia Pseudomugilidae e del genere *Pseudomugil.*

Introduction

Members of the family Pseudomugilidae, or blue-eyes, are small (rarely exceeding 60 mm SL) but colourful fishes which are restricted to Australia, the island of New Guinea and some small islands in the vicinity of the latter. The fish occur both in fresh, brackish waters, and occasionally in more saline waters of mangrove swamps (eg *P. signifer, P. majusculus, P. inconspicuus,* and *P. cyanodorsalis)*. A revision of the family by Saeed *et al.* listed 12 known species in 1989. Another species placed into a new subfamily of blue-eyes, Scaturiginichthyinae, was added to the list by Ivantsoff *et al.* in 1991. Recent expeditions to Irian Jaya by G. R. Allen have yielded additional specimens of *P. reticulatus,* previously described from a single specimen, as well as at least one other species which will require a description in the very near future.

Blue-eyes have recently been attracting much attention because of their relationships to Atherinidae, Telmatherinidae, Melanotaeniidae and Phallostethidae (Allen, 1980; Parenti, 1984; Ivantsoff *et al,.* 1987; Saeed *et al.,* 1994 and Dyer and Chernoff, 1996). The present study suggests that *Pseudomugil* spp. show greater variability in their morphology than known pre-viously, which allows for better evaluation of their relationships to other atherinomorph groups. Possibly some of the atherinomorph representatives may form a transformation series. However, at this time, no evidence at hand suggests that Pseudomugilidae are not indistinct.

Methods

Procedures for measuring and counting are based on those used by Saeed *et al.* (1989). Fin spine counts other than in the first dorsal fin have been omitted since their numbers are constant when present. Clearing and staining procedures used herein are described in Aarn and Ivantsoff (1996). Illustrations are based on specimens disarticulated to show the suspensorium, jaws, opercle, hyobranchial apparatus, cranium, and the pectoral and pelvic girdles. Cranial and pectoral girdle musculature (Fig. 8) was exposed by removal of the surface structures. Drawings were made (by Aarn and M.A.S.) with the help of a *camera lucida* mounted on a Wild dissecting microscope. Terminology and descriptions of the bones follow Saeed *et al.* (1989) and those of the muscles follow Winterbottom (1973).

Fig. 1. Map of Irian Jaya showing collecting site.

Materials

The fish were collected by G.R.A. during an expedition to Irian Jaya in 1995. One of the more intensive collecting areas, with many sample sites, was located 15-20 km north of Timika and in the vicinity of Tembagapura (Fig. 1). The following collection stations yielded specimens of *P. reticulatus*:

Station 17. Tributary of Iweka River, 16km NW of Timika (4°23.5'S 136°49.3'E). Collected with seine by G. R. Allen, S. Renyaan and D. Norris, July 31, 1995. WAM P31057-004 26 (20-30 mm SL). 5 specimens measured and counted; 2 specimens cleared and stained.

Station 20. Tributary of Iweka River, 16km NW of Timika (4°23.5'S 136°49.3'E). Collected with seine by G. R. Allen and D. Norris, August 1, 1995. Specimens unregistered 29 (20.3-24.7 mm SL). 14 specimens measured and counted; 4 specimens cleared and stained; all osteological drawings based on these specimens.

Station 27. Tributary of Kopi River, 17km N of Timika (4°25.7'S 136°57.0'E). Collected with seine by G. R. Allen and D. Norris, August 2, 1995. WAM P31055-004 34 (20-30 mm SL). 5 specimens measured and counted; 2 specimens cleared and stained.

Station 28. Tributary of Kopi River, 17km N of Timika (4°25.0'S 136°57.0'E). Collected with seine by G. R. Allen and D. Norris, August 2, 1995. Specimens unregistered 36 (20.4-33.5 mm SL). 2 specimens measured and counted; 2 specimens cleared and stained.

Station 31. Tributary of Iweka River, 15km NW of Timika (4°24.0'S 136°49.0'E). Collected with rotenone powder (0.5kg) by G. R. Allen, S. Renyaan and D. Norris, August 3, 1995. Specimens unregistered 27 (20.4-29.6). 1 specimen measured and counted; 2 specimens cleared and stained.

Description

Family Pseudomugilidae

Diagnosis. An atherinomorph family restricted to the estuaries and freshwaters of Australia and the island of New Guinea. With truncated rostrum, lacking mesethmoid, ethmomaxillary ligament arising from dorsal facet of lateral ethmoid; articular and dentary coronoid processes elevated, approximately equal; rostral infraorbital series consisting of one element, the lacrimal; cleithrum dorsal enclosure reduced, dorsal postcleithrum absent, axialpectoral (Baudelot's) ligament absent, supracleithrum reduced; hypural fan of fused dorsal and fused ventral plates; principle caudal ray count reduced.

Fig. 2a. *Pseudomugil reticulatus,* male, Timika, Eweka River (Station 20), approximately 27mm SL.

Fig. 2b. *P. reticulatus,* female, Timika, Eweka River (Station 19), approximately 25mm SL.

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Genus *Pseudomugil* Kner, 1865

Type species: *Pseudomugil signifer* Kner, 1865.

Diagnosis. Lacking the articularmaxillary ligament; pelvic fin elements I 5.

Pseudomugil reticulatus Allen and Ivantsoff, 1986. Vogelkop blue-eye (Fig.2a & 2b).

General description

External morphology

Small, laterally compressed fish, not exceeding 30mm in SL. Mouth subvertical and small but not greatly restricted by labial ligament; lower jaw protruding slightly beyond premaxilla. Jaws oblique. Teeth numerous on jaws near symphysis, small and pointed. Later-

Table 1. Measurements and counts based on 27 specimens of *Pseudomugil reticulatus.* Measurements are expressed as proportions of Standard Length (SL), Head and Eye. Abbreviations: **Pec. L**: length of pectoral fin; **H max**: greatest body depth; **Width max**: greatest body width; **H min**: least body depth; **Pec-anus**: distance between dorsal origin of pectoral and anus; **Sn**: vertical through tip of snout from where following measurements are taken: **Sn-OD1**: snout and origin of first dorsal fin; **Sn-OD2**: snout and origin of second dorsal fin; **Sn-OV**: snout and origin of ventral fin; **Sn-TV**: snout and tips of ventrals; **Sn-OA**: snout and origin of anal fin; **Sn-TA**: snout and origin of last anal ray. **Premax. Process**: dorsal process of premaxilla. In other attributes, the position of fins relative to each other is indicated by the number of scales in front (+) or behind (-) each other.

IN SL	MEAN	SD	RANGE
Head	3.7	0.20	3.2-4.3
Pec. L.	5.9	0.48	5.1-7.4
H max.	3.9	0.19	3.5-4.3
Width Max.	6.8	0.51	5.9-8.4
H. Min.	7.5	0.49	6.4-9.1
Pec-anus	4.0	0.36	3.3-4.9
Sn-OD1	2.2	0.08	2.0-2.3
Sn-OD2	1.6	0.04	1.5-1.7
Sn-OV	2.4	0.11	2.2-2.6
Sn-TV	1.8	0.05	1.6-1.9
Sn-OA	1.8	0.05	1.7-1.9
Sn-TA	1.3	0.04	1.3-1.9
IN HEAD			
Eye	2.8	0.22	2.4-3.2
Interorbital	2.7	0.14	2.3-3.1
Postorbital	2.2	0.53	2.2-2.7
Caudal peduncle	1.0	0.6	0.9-1.2

IN EYE	MEAN	SD	RANGE
Snout	1.8	0.25	1.4-2.2
Premaxilla	1.4	0.40	1.1-1.8
Premax. process	3.7	0.90	2.2-5.6
MERISTICS			
Midlateral scales	28.7	0.70	27-30
Transverse rows	6.4	0.46	6-7
Predorsal scales	11.9	0.73	11-14
Interdorsal scales	3.0	0.73	2-4
Vertebral count	32.1	0.79	30-33
First Dorsal fin	5.4	0.72	4-7
Second Dorsal	8.0	0.60	7-10
Anal fin	11.1	0.85	9-13
Pectoral fin	10.2	0.56	9-11
Gill rakers	9.2	0.81	8-11
OTHER ATTRIBUTES			
Anus position	2.6	0.76	1.5-4
OD1 to TV	2.7	0.80	2-5
OD1 to T.Pec.	- 1.2	0.71	0.5-2
OV to T.Pec.	1.2	0.79	0-3.5

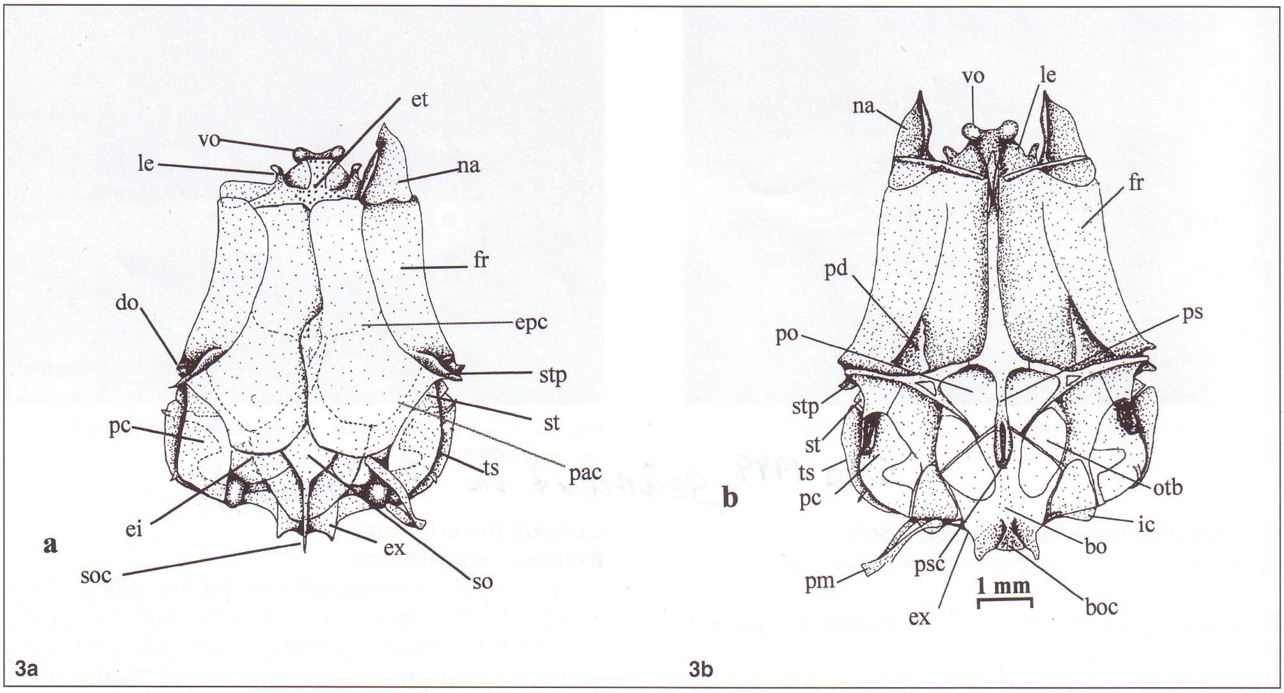


Fig. 3a. *Pseudomugil reticulatus*, Station 20, 23.2 mm SL. Cranium in: **a.** dorsal aspect; **b.** ventral aspect. Abbreviations: **bo,** basioccipital; **boc,** basioccipital condyle; **do,** dermosphenoid; **ei,** epiotic; **et,** ethmoid cartilage; **ex,** exoccipital; **fr,** frontal; **ic,** intercalar; **le,** lateral ethmoid; **na,** nasal; **otb,** otic bulla; **pac,** parietal cartilage; **pc,** pterotic; **pd,** pterosphenoid; **pm,** posttemporal; **po,** prootic; **ps,** parasphenoid; **psc,** parasphenoid caudal foramen; **so,** supraoccipital; **soc,** supraoccipital crest; **st,** sphenotic; **stp,** sphenotic postorbital process; **ts,** temporal shelf; **vo,** vomer. Heavy stippling: cartilage; dotted lines: obscured structures. **Fig**
3b: *P: reticulatus;* Station 20; 23:2 mm SL. Cranium in ventral aspect. Abbreviarions see Fig: 3a.

al premaxillary teeth larger, hooked, pointed and distinctly noticeable. Premaxilla notched and thus narrow in mid region. Dorsal process of premaxilla relatively long (Table 1) and spatulate. Anterior half of maxilla wide, narrowing to less than half width in distal half. Free edge of dentary elevated obliquely distally, anterior half with pungent villiform teeth. Other bones in mouth edentulous. Pelvic girdles attached to 3rd, 4th or 5th rib. Principal caudal rays 8+7 (detailed osteology presented below). Gill rakers on lower gill arch 8-10, shorter than diameter of pupil, sometimes leaf-like in shape. Transverse scale rows 6-7, predorsal scales 11-14, midlateral scales 27-30. Body scales cycloid, dorsoventrally elongated; circuli complete and obvious. Pointed axillary scale at lateral origin of ventral fins. Small scales covering preopercle and two large scales on dorsum of head. Sensory pits on dorsum of head large. Origin of first dorsal fin usually in front of vertical through tips of ventrals; origin of ventrals in front of vertical through pectoral tips. Spine present in anal fin but not second dorsal. Sexual dimorphism obvious, first three spines of first dorsal fin in males often extended as filaments, ventral fins extending beyond origin of anal fin. Dorsal and ventral fins of female shorter.

Colour

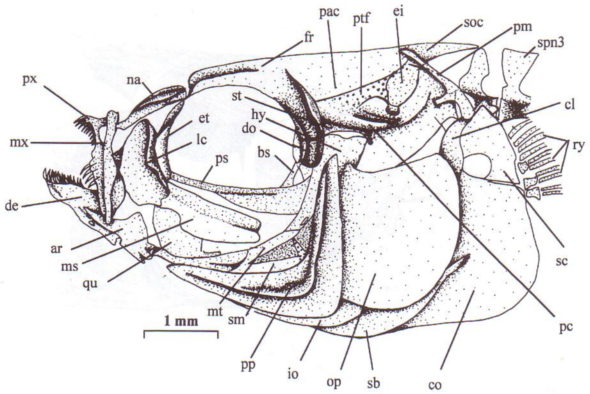
Live body colour in males light brown; abdomen and swim bladder region silvery. Upper half of first dorsal and anterior half of second dorsal, edge of anal fin, brick red. Dorsal and ventral contour posterior to 2nd dorsal and anal fins edged with similar red. Upper and lower third of caudal also red. Head with red tinge, ventral fins pink. Eyes intensely blue. Edges of some scales on abdomen contoured with black. Females possibly similar in coloration. Female specimens photographed (Fig. 2b., freshly dead) showing stronger reticular pattern and with yellow fins (similar in colour as described by Allen and Ivantsoff in 1986). Colour in alcohol as previously described (Allen and Ivantsoff, 1986) *viz.* body colour yellow brown, edges of scales outlined with chromatophores, fins whitish, transparent or translucent, edges of rays and spines peppered with chromatophores.

Habitat

Habitat variable, from clear water (in some cases heavily stained with tannin) running swiftly over mud, gravel and sand, to slow-flowing water over similar terrain. In all cases, aquatic vegetation sparse or absent. Water temperature about 26-27°C; pH always slightly above neutral (7.1-7.6).

Musculoskeletal anatomy

Cranium (Figs 3,4). Vomer edentulous, elongate. Vomerine condyles, contacting submaxillary menisci, directed rostrolaterally. Ligament to mesopterygoid



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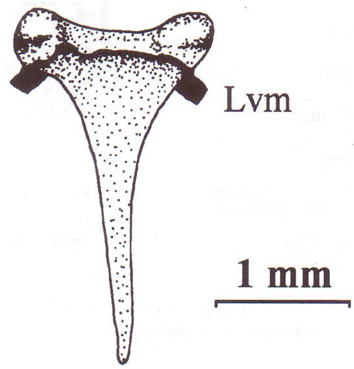

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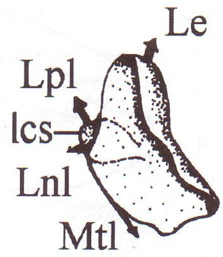

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Fig. 4. *Pseudomugil reticulatus,* Station 20, 23.2 mm SL. Head and pectoral girdle (hyobranchial apparatus removed). Abbreviations: **ar**, articular; **bs**, basisphenoid; **cl**, cleithrum; **co**, coracoid; **de**, dentary, **do**, dermosphenoid; **ei**, epiotic; **en**, epineural; **et**, ethmoid cartilage; **fr**, frontal; **hy**, hyomandibula; **io**, interopercle; **lc**, lacrimal; **le**, lateral ethmoid; **ms**, mesopterygoid; **mt**, metapterygoid; **mx**, maxilla; **na**, nasal; **op**, opercle; **pc**, pterotic; **po**, prootic; **pp**, preopercle; **ps**, parasphenoid; **ptf**, posttemporal fossa; **px**, premaxilla; **qu**, quadrate; **re**, epineural; **rp**, pleural rib; **ry,** fin ray; **sb,** subopercle; **sc**, scapula; **sm,** symplectic; **soc**, supraoccipital crest; **spn**, vertebral neural process; **st**, sphenotic; **vp,** ventral postcleithrum. Stippling: cartilage.
Fig. 5. *Pseudomugil reticulatus,* Station 20, 23.2 mm SL. Vomer in dorsal aspect. Abbreviation: **Lvm**, ligament between vomer and mesopterygoid. Stippling: cartilage.
Fig. 6. *Pseudomugil reticulatus,* Station 20, 23.2 mm SL. Lacrimal in lateral aspect. Abbreviations: **lcs**, lacrimal subnasal shelf; **Lel**, ethmolacrimal ligament; **Lnl**, nasolacrimal ligament; **Lpl**, ligament between palatine and lacrimal; **Mtl**, tendon of m. adductor mandibulae to lacrimal. Dotted lines: obscured structures.

arising bilaterally just caudal to condyles (Fig. 5). Parasphenoid narrow, coursing from rostral angle, dorsal to vomer, through interorbital plane, giving truncated alae to contact rostroventral margin of prootics, terminating with caudal fossa, ventral to basioccipital. Basisphenoid belophragm broad, contacting dorsal surface of parasphenoid; basisphenoid meningosts extending bilaterally to rostral margin of prootics.

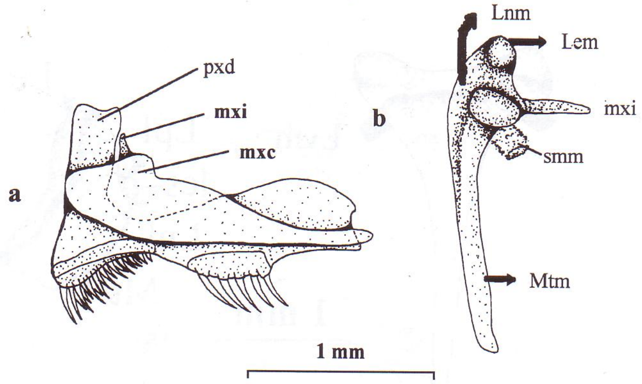
Ethmoid cartilage narrow, coursing from rostral angle above vomer to caudal angle beneath frontal fontanel, forming rostral interorbital septum. Lateral ethmoids separated by ethmoid cartilage. Lateral ethmoid rostromedial angle truncated, at level of transverse plane through rostrolateral angle. Rostrolateral angle dorsally giving ethmolacrimal ligament (Fig. 6), ventrally forming condyle articulating with lacrimal. Rostral cartilage discoidal, loosely attached to dorsal surface of ethmoid cartilage.

Nasals widely separated by rostral fossa. Nasal compact, falcate overlying lateral ethmoid, dorsal surface bearing neurosensory canal, caudal margin contacting frontal. Nasal rostral angle giving strong nasomaxillary ligament to rostral aspect of maxilla (Fig. 7), and small nasolacrimal ligament (Fig. 6) to rostral margin of lacrimal. Nasal ventromedian process receiving small nasopalatine ligament from apex of palatine. Frontals forming roof of cranial vault and orbit, overlying adjacent skeletal elements Frontal irregular, extending from rostromedian fontanel, dorsal to ethmoid cartilage, to caudal margin contacting supraoccipital and epiotic. Frontal median lamina slightly domed, demarcated from supraorbital (lateral) lamina by shallow sulcus. Caudal angle of sulcus developed as neurosensory crest, continuous with dermosphenoid. Supraoccipital forming caudodorsal cranial vault, underlying caudal portion of frontals, between epiotics. Supraoccipital rostral process contacting epiphyseal cartilage (Fig. 3a); caudally, supraoccipital crest extending to level of second intervertebral articulation.

Epiphyseal cartilage oriented transversely, at level of rostral angle of neurosensory crest (Fig. 3). Parietal cartilage oriented obliquely, between sphenotic and epiotic.

Sphenotic at caudal margin of orbit, giving origin to major portion qof m. delator operculi (Fig. 8). Postorbital process directed ventrolaterally, giving origin to m. levator arcus palatini. Pterotic at caudolateral angle of cranium, ventral surface bearing prominent caudoventrally-directed facet for hyomandibula (Fig. 3). Pterotic periphery developed as fragile temporal shelf, ventrally giving origin to m. levator operculi. Posttemporal fossa bounded by sphenotic rostrally, parietal cartilage and frontal dorsally, pterotic ventrally and epiotic caudally (Fig. 4).

Epiotic approximately deltoid, with prominent vertical ridge receiving posttemporal dorsal ramus and epaxial musculature. Exoccipital about foramen magnum, articulating with first vertebra. Intercalar in pit at caudolateral angle of exoccipital. Basioccipital forming caudoventral cranial vault, with occipital condyle for articulation with first vertebral centrum, ventrally form-



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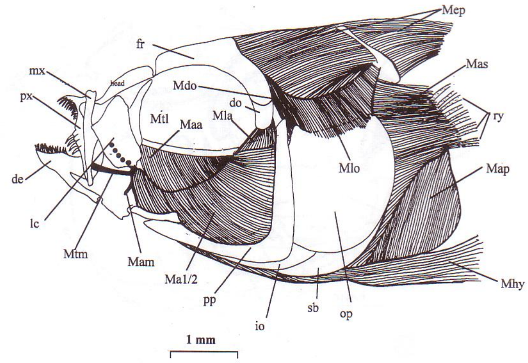

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Fig. 7a, b. *Pseudomugil reticulatus,* Station 20, 23.2 mm SL. Upper jaw. **a.** maxilla and premaxilla in lateral aspect; **b.** maxilla in dorsal aspect. Abbreviations: **Lem,** ethmomaxillary ligament; **Lnm**, nasomaxillary ligament; **Mtm**, tendon of m. adductor mandibulae to maxilla; **mxc**, maxilla condyle; **mxi**, maxilla internal ramus; **pxd**, premaxilla dorsal process; **smm**, submaxillary meniscus. Stippling: cartilage.
Fig. 8. *Pseudomugil reticulatus*, Station 20, 23.2 mm SL. Superficial musculature of head and pectoral region. Abbreviations: **de**, dentary; **do**, dermosphenoid; **fr**, frontal; **io**, interopercle; **lc**, lacrimal; Ma1/2, m. adductor mandibulae, A1and A2 sections; **Maa,** m. adductor arcus palatini; **Mam**, m. adductor mandibulae, mandibular branch; **Map**, m. deep pectoral abductor; **Mas**, m. superficial pectoral abductor. **Mdo**, m. delator operculi; **Mep**, epaxial musculature; **Mhy**, hypaxial musculature; **Mla**, m. levator arcus palatini; **Mlo**, m. levator operculi; **Mtl**, tendon of m. adductor mandibulae to lacrimal; **Mtm**, tendon of m. adductor mandibulae to maxilla; **mx**, maxilla; **op**, opercle; **orb**, orbit; **ry**, fin ray; **sb**, subopercle. Dotted lines: obscured structures; dashed lines: muscles.

ing major portion of bilateral otic bullae. Prootic irregular, rostrolateral angle contacting pterosphenoid, laterally contacting sphenotic and pterotic, caudally contacting basioccipital. Synchondrosis between prootics in median plane dorsal to parasphenoid caudal process. Pterosphenoid narrow, on ventral surface of frontal, medial margin concave, contacting rostrolateral margin of prootic, forming partial septum between orbit and cranial vault.

Jaws. Upper jaw protrusible. Maxilla with tubiform internal process (Fig. 7b), deep to rostral cartilage, and truncated external process receiving ethmomaxillary ligament. Maxillary dorsomedian margin, just caudal to internal process, bearing condyle contacting elongate meniscus. Maxilla tapering caudally, resting in slight depression of premaxilla external face, receiving tendon from m. adductor mandibulae. Premaxilla dorsal process elongate (Figs 5a, 6), loosely attached to rostral cartilage. Premaxilla somewhat curved (in horizontal plane), ventral margin with prominent notch, lateral to symphyseal region. Small teeth present on alveolar surface from symphyseal margin to base of dentary coronoid process, premaxilla caudal angle edentulous.

Dentary angular, ventral surface bearing rostroventral prominence. Dentary dorsal margin dentigerous from symphysis to base of coronoid process, few large caniniform teeth opposite premaxilla notch (Fig. 4). Coronoid process elevated, slightly taller than articular. Articular elevated, giving minute mandibular branch of m. adductor mandibulae, caudally forming trochlear groove to receive quadrate tubercle. Mandibular cartilage from inner face of dentary, coursing along rostral process of articular. Supraangular bone small, enveloping mandibular cartilage medial to articular. Retroarticular small, at caudoventral angle of articular. Mandibular neurosensory canal open, from external face of dentary to retroarticular. Labial ligament coursing along dentary, above canal.

Suspensorium. (Fig. 9, together with opercular series). Comprising palatoquadrate assemblage, mesopterygoid, symplectic, metapterygoid, preopercle and hyomandibula (all edentulous).

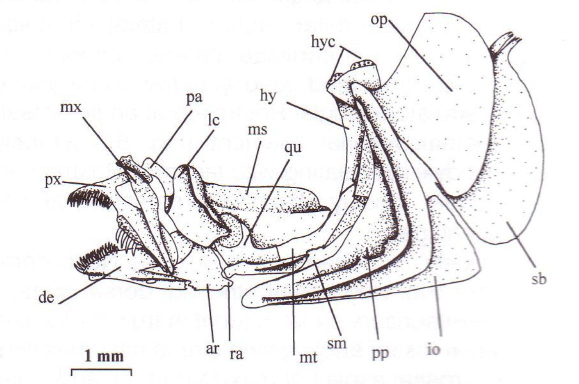

Fig. 9. *Pseudomugil reticulatus,* Station 20, 23.2 mm SL. Suspensorium. Abbreviations: **ar**, articular; **de**, dentary; **io**, interopercle; **hy**, hyomandibula; **hyc**, hyomandibula condyle; **lc**, lacrimal; **ms**, mesopterygoid; **mt**, metapterygoid; **mx,** maxilla; **op,** opercle; **pa**, palatine; **pp**, preopercle; **px**, premaxilla; **qu**, quadrate; **ra**, retroarticular; **sb**, subopercle; **sm**, symplectic. Heavy stippling: cartilage.

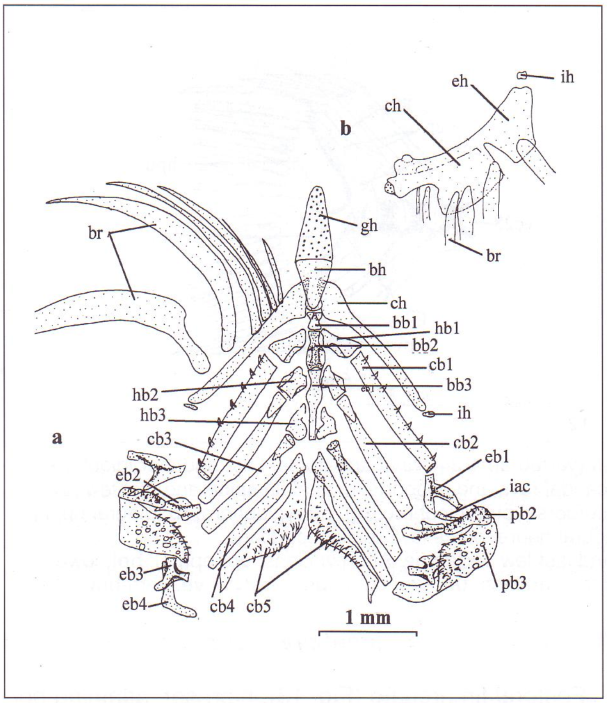

Fig. 10. *Pseudomugil reticulatus,* Station 20, 23.2 mm SL. Hyobranchial apparatus in; **a.** dorsal aspect; **b.** detail, hyoid bar. Abbreviations: **bb**, basibranchial; **bc**, basibranchial cartilage; **bh**, basihyal; **br**, branchiostegal; **cb**, ceratobranchial; **ch**, ceratohyal; **dh**, dorsal hypohyal; **eb**, epibranchial; **ebr**, epibranchial rostral process; **ebu**, epibranchial uncinate process; **eh**, epihyal; **gh**, glossohyal; **gr**, gill raker; **hb**, hypobranchial; **iac**, interarcual cartilage; **ih**, interhyal; **Lih**, interhyal ligament; **pb**, pharyngobranchial; **pbt**, pharyngobranchial toothplate; **tp**, toothpatch; **uh**, urohyal; **vh**, ventral hypohyal. Stippling: cartilage.

Palatine compact, cartilaginous rostral process directed dorsad above maxillary condyle, caudal border contacting mesopterygoid (dorsally) and quadrate (ventrally). Palatine rostral process attached to lacrimal subnasal shelf by palatolacrimal ligament, and to nasal. Quadrate with discoidal dorsal lamina, ventral lamina folded over preopercle, and rostral tubercle contacting articular. Mesopterygoid narrow, at ventrolateral rim of orbit. Metapterygoid narrow, contacting quadrate rostrally, hyomandibula caudally, fused to symplectic ventrally. Symplectic tubiform. Ectopterygoid absent.

Hyomandibula irregular, dorsal angle bearing articular cartilage, small rostroventral ramus contacting symplectic, ventral angle cartilaginous, receiving interhyal ligament. Hyomandibula medial face bearing caudally-directed tubercle. Preopercle rightangular, forming canal open ventrally and caudally, rostral angle giving strong ligament to retroarticular.

Opercular series. Comprising interopercle, opercle and subopercle.

Interopercle deltoid, lying deep to preopercle, caudodorsal margin with shallow notch for partial attachment of interhyal ligament. Opercle dorsal margin oblique, m. delator operculi attaching to medial and lateral faces of dorsal margin. Rostrodorsal angle forming process for attachment of m. levator operculi. Medial face of opercle giving rise to rostrally-directed process, bearing glenoid fossa for hyomandibula tubercle. Opercle caudal border convex. Subopercle lacrimiform, bearing stout rostrodorsal process.

Circumorbital series. Comprising lacrimal (Figs. 4 & 6) and dermosphenoid.

Lacrimal vertical axis elongate, caudal margin concave adjacent to lateral ethmoid condyle (Fig. 4). Medial face bearing short subnasal shelf, rostral margin receiving tendon from m. adductor mandibulae (Fig. 6). Lateral face with vertical neurosensory canal. Dermosphenoid short, attached to rostral face of sphenotic postorbital process (Fig. 4).

Hyobranchial apparatus (Fig. 10): Comprising median unpaired glossohyal cartilage, basihyal, (3) basibranchials and urohyal, bilaterally paired dorsal and ventral hypohyals, ceratohyal, epihyal, (6) branchiostegals, interhyal, (3) hypobranchials, (5) ceratobranchials, (4) epibranchials and (3) pharyngobranchials, with associated toothplates (Fig. 10a).

Glosohyal fused to basihyal, both elongate. Basihyal contacting dorsal hypohyals bilaterally, and small first basibranchial caudally. First and second basibranchials contacting first hypobranchials, second and elongate third basibranchial contacting second hypobranchials, third hypobranchials encircling caudal angle of third basibranchial. Basibranchial series terminating in small cartilaginous nodule, dorsal to atrophied ventrally-directed cartilage pedicle.

Urohyal deep, with paired rostral condyles, prominent rostrodorsal spine, ventral canal and caudodorsal alae. Dorsal hypohyal hemispherical, ventral hypohyal somewhat discoid, hyoid bar (ceratohyal and epihyal) contacting articular processes of 6 branchiostegals (Fig. 10b). Epihyal caudodorsal margin giving rise to interhyal ligament, containing ossified sesamoid, attaching to suspensorium.

First hypobranchial angular, large; second hypobranchial compact; third hypobranchial narrow, arcuate. Ceratobranchials elongate, first bearing 8-9 compact gill-rakers, fifth ceratobranchial broad, supporting lower pharyngeal toothplate. First epibranchial, contacting small ossified pharyngobranchial, with small uncinate process contacting spherical interarcual cartilage, contacting dorsal apex of deltoid second pharyngobranchial. Second and third epibranchials irregular, contacting third pharyngobranchial, above large upper third pharyngeal toothplate. Fourth epibranchial large, ventral face of distal angle supporting small fourth upper pharyngeal toothplate.

Vertebrae and ribs. (Fig. 11). Total vertebrae 30-33, precaudal 15-17, epineurals on all precaudal, and (in some specimens) first caudal, vertebrae. First 2

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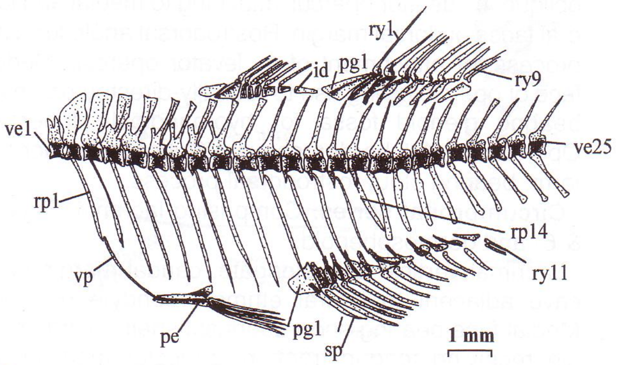

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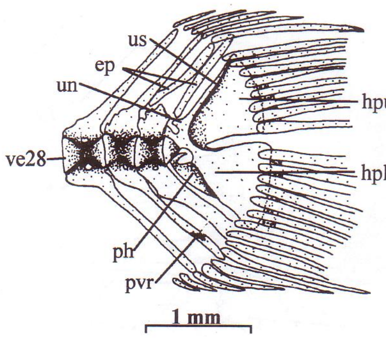


Fig. 11. *Pseudomugil reticulatus*, Station 20, 21.1 mm SL. Axial skeleton (vertebrae 1-24), anal and dorsal fins (and pterygiophores). Fins and supports: a, first dorsal fin and supports; b, second dorsal fin caudal rays and supports; c, anal fin spine and first few rays, and supports; d, anal fin caudal rays and supports. Abbreviations: **id**, interdorsal pterygiophore; **pg**, pterygiophore; **rp**, pleural rib; **ry**, fin ray; **sp**, fin spine; **sy**, fin stay; **veh**, vertebral haemal spine; **ven**, vertebral neural process. Stippling: cartilage.

Fig. 12. *Pseudomugil reticulatus*, Station 20, 23.2 mm SL. Caudal fin and last few vertebrae. Abbreviations: **ep**, epural; **hpl**, lower hypural plate; **hpu**, upper hypural plate; **ph**, parhypural; **pvr**, preural ventral cartilage; **un**, uroneural; **us**, urostyle; **ve**, vertebra. Stippling: cartilage.

vertebrae with small neural processes, subsequent 5-6 vertebrae with well-developed neural plates, becoming reduced to neural spines in distal vertebrae, penultimate vertebra lacking neural process (Fig. 11). Pleural ribs resting on caudal aspect of parapophyses, from third to fourteenth-sixteenth vertebrae. Parapophyses developed as haemal arches in first caudal vertebra, as haemal spines in subsequent vertebrae, greatly expanded in penultimate vertebra.

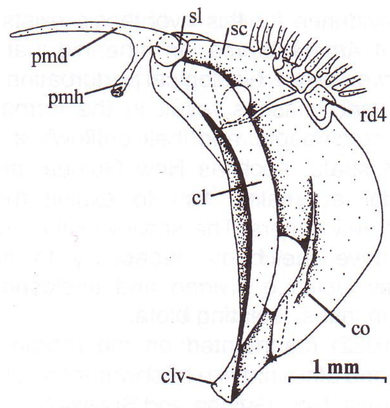
Two epurals above penultimate vertebra. Small uroneural fused to cranial aspect of urostyle. Terminal hemivertebra fused to urostyle. Hypural fan of fused upper hypural plate, fused to caudal aspect of urostyle, and fused lower hypural plate, fused to parhypural. Preural ventral radial cartilage (may become ossified - Fig. 12) cranial to penultimate vertebral haemal spine.

Fins and girdles. First dorsal fin originating at level of transverse plane through vertebra 10. First dorsal supported by arcade of shallow pterygiophores. Interdorsal pterygiophores variable: 2 fully-formed plates (Fig. 11), vestigial ossifications, or no skeletal material may be present. Second dorsal fin originating at level of transverse plane though vertebra 16 (caudal limit of visceral cavity), supported by plate-like pterygiophores. Anal originating at level of vertebra 12/13, cranial to distal angles of 4/5 pleural ribs. First anal pterygiophore expanded cranially, subsequent pterygiophores becoming slender. Cranial pterygiophore of anal and first dorsal fins supporting 2 elements, of second dorsal fin supporting one element. Subsequent elements supported individually on single pterygiophore - except last 2 elements of second dorsal and anal fins, supported on single dorsal or anal pterygiophore, respectively.

Pectoral fin arcuate (Fig. 13), high-set, attaining horizontal plane through vertebral centra, extending rostroventrally to ventral midline at level of transverse plane through pterotic hyomandibular facet. Cleithrum cranial border everted laterally to form trough, open caudally, giving origin to m. superficial abductor (Fig. 5). Cleithrum dorsal process (enclosure) not developed. M. protractor pectoralis inserting high on rostral margin of cleithrum.

Scapula triangular, foramen small. First (dorsal) proximal radial fused to, second radial fully supported at, third radial partially supported at, scapula caudal margin (Fig. 13). Coracoid irregular, fully supporting fourth radial. Supracleithrum small, discoidal to reniform, in pit on dorsal angle of cleithrum. Axialpectoral ligament absent. Posttemporal with elongate dorsal ramus and short horizontal ramus, posttemporal base attached to supracleithrum. Dorsal postcleithrum absent. Ventral post cleithrum elongate, on cranial aspect of first rib. M. superficial pectoral abductor on dorsal portion of fin, fibres near-horizontal, m. deep pectoral abductor below fourth radial, fibres vertical-oblique.

Pelvic fin spanning 2-3 intercostal spaces (Fig. 11), rounded caudolateral process attached ligamentously to fourth (sometimes third or fifth) rib. Pelvic medial lamina reduced (Fig. 14), medial process overlapping that of contralateral pelvic girdle, lacking cranial spine. M. abductor superficialis pelvicus small, originating on midventral fibrous raphe. M. arrector ventralis pelvicus originating cranial to abductor, inserting on base of pelvic spine. M. arrector dorsalis pelvicus coursing lateral to ventral arrector, pelvic central part produced as ventral crest separating arrector muscles near their insertions.



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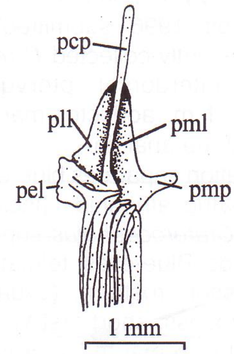

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Fig. 13. *Pseudomugil reticulatus*, Station 20, 23.2 mm SL. Pectoral fin and posttemporal. Abbreviations: **cl**, cleithrum; **clv**, cleithrum ventral process; **co**, coracoid; pmd, posttemporal dorsal ramus; pmh, posttemporal horizontal ramus; **rd**, proximal radial; **sc**, scapula; **sl**, supracleithrum. Stippling: cartilage; dotted lines: obscured structures.

Fig. 14. *Pseudomugil reticulatus*, Station 20, 23.2 mm SL. Pelvic girdle in ventral aspect. Abbreviations: **pcp**, pelvic central part; **pel**, pelvic lateral process; **pll**, pelvic lateral plate; **pml**, pelvic medial plate; **pmp**, pelvic medial process.

Remarks on the systematic position of *Pseudomugil*

Since Kner (1865) described *Pseudomugil signifer* and suggested the erection of a new family, the status and relationships of the blue-eyes has remained uncertain. Restriction to the estuarine and freshwaters of Australia, New Guinea and Irian Jaya suggests that blue-eyes form a "natural group". Despite variability in mouth-parts, morphological adaptations for small body-size suggest similarity within the clade.

Allen (1980) reported some osteological details of *Pseudomugil* spp. and the closely-related *Popondetta* (= *Popondichthys*). The high-set pectoral fin was considered a blue-eye apomorphy. Blue-eyes and rainbowfish constituted Melanotaeniidae, with 3 defining characteristics: sexual dimorphism, a "distinctive premaxillary shape" (2 somewhat inconsistent apomorphies) and an apomorphic pelvic modification: the pelvic fins attaching to the ventral body wall by a fine membrane, enclosing an asquamate area cranial to the anus. Blue-eyes were considered pleisiomorphic to the 6 other melanotaeniid genera. Pungent fin spines were considered a synapomorphy of *Melanotaenia, Chilatherina* and *Glossolepis* (which also develop near-discoidal adult bodies).

Saeed *et al.* (1989) revised the blue-eyes, reinvoking the family Pseudomugilidae and diagnosing it with 3 characters: absence of mesethmoid, reduction of rostral infraorbital series to one element (2 apomorphies) and "articular as high as dentary" (inconsistent). Pseudomugilinae (*Pseudomugil* spp., the 2 nominal *Popondichthys* spp. returned to the former genus) was diagnosed with 4 characters: absence of articular-maxillary ligament and maxilla external process (2 apomorphies); and a reduced intercalar, and elongate first epibranchial uncinate process (2 inconsistent characters). Kiunginae (*Kiunga ballochi)* was diagnosed with 8 characters: an apparently autapomorphic suite (maxilla articulating with lateral ethmoid via submaxillary meniscus, vomerine condyle absent), 2 apomorphies (first dorsal fin vestigial, "keel-like structure present between pelvic and anal fins" ie. persistent juvenile fin-fold), and further unreliable "characters".

Ivantsoff *et al.* (1991) described *Scaturiginichthys vermeilipinnis* and placed it in a third blue-eye subfamily, Scaturiginichthyinae, diagnosed with 2 apomorphies (5 branchiostegal rays, low-set pectoral fin) and 2 characters shared with some pseudomugilines.

Saeed & Ivantsoff (1991) described *Kalyptatherina* (type species *Pseudomugil helodes* Ivantsoff & Allen), extending the range of telmatherinids to east of Wallace's line, and suggesting that this fish was "potentially sympatric" with pseudomugilids.

Saeed *et al.*(1994) analysed 7 atherinoidean families, and on the basis of 9 character states placed pseudomugilids closest to phallostethids, the most apomorphic groups. In this analysis, melanotaeniids and bedotiids were considered plesiomorphic.

Dyer & Chernoff (1996) analysed Atheriniformes (ie. Old World atherinoideans and New World atherinopsoideans) using 83 variably-weighted characters. Pseudomugilini (blue-eyes - defined with 10 apomorphies) was grouped with Telmatherinini, in Pseudomugilinae (with 7 synapomorphies). Pseudomugilinae plus Bedotiinae and Melanotaeninae comprised Melanotaeniidae (with 6 apomorphies), one of 6 families in Atheriniformes. This was the first formal alignment of the 3 deep-bodied, largely freshwater atherinoidean clades.Analysing either Atherinoidea or Atheriniformes is a huge task, requiring careful examination of adequate representatives of each clade. Subsequent investigations may be facilitated by more, diverse, specimens and the benefit of hindsight.

Studies of the anatomy of the monotypic melanotaeniid genera *Cairnsichthys, Iriatherina* and *Rhadinocentrus* (Aarn & Ivantsoff, 1996, submitted) will provide useful data. Here, recently-collected *P. reticulatus* displayed (variable) interdorsal pterygiophores, a mandibular branch of m. adductor mandibulae, and cranial positioning of the anal fin.

The pelvic modification separates blue-eyes and rainbowfish from sympatric atherinids (including *Atherinomorus* spp. and *Craterocephalus* spp.) and neighbouring telmatherinids. Blue-eyes, telmatherinids and atherinids have a short rostrum, (usually) elongate premaxilla dorsal process, short first vertebral neural spine and short first proximal radial of first dorsal fin. Blue-eyes and *Kalyptatherina* lack a notch in the lacrimal posterior border and a pelvic ventral spinous process (present in atherinids and other telmatherinids), but share with telmatherinids a similar body-shape, distinctive first anal pterygiophore, and absence of a second dorsal fin spine.

Phallostethids are a well-defined group (Parenti, 1989) - some of the characters shared with pseudomugilids (absence of mesethmoid and axialpectoral ligament; reduction of temporal neurosensory canals, intercalar, rostral infraorbital series, uncinate process of first epibranchial, fourth upper pharyngeal toothplate, interdorsal pterygiophores, dorsal cleithrum and supracleithrum; extensive fusion of hypurals) may be independently-derived adaptations of diminutive fishes. Other traits variously distributed in smaller atherinoideans (including the 3 monotypic melanotaeniid genera) include absence of basisphenoid, ectopterygoid, rostral process of hyomandibula and metapterygoid; reduction of first dorsal fin, branchiostegals, caudal fin rays, and dentition; and non-ossification of interhyal sesamoid and first pharyngobranchial.

Phenetic variability within a species (eg. the interdorsal pterygiophores of *Pseudomugil reticulatus*, the occasional fusion between the parhypural and lower hypural plate, and presence of the mesethmoid in *P. signifer*, fusion of second and third rostral inrafraorbitals in *Glossolepis* spp.) suggests that there is a genetic capacity (undergoing incomplete repression) to produce a structure, and may provide evidence of that species' relationships. In fish, there is substantial evidence that environmental factors influence genetically-coded traits. For example, asquamation in hot pools (*Aphanius* spp. - Villwock, 1976), reduction of the pelvic fin in shallow pools (*Scaturiginichthys* - Ivantsoff *et al.*, 1991), small size at maturity of *Tilapia* spp. cultured in crowded pools, and optic degeneration in cavernicolous fish. The theory of natural selection confers a reproductive advantage to the individual(s) best able to respond to any novel environmental factor(s). Repression, without deletion, of genetic material may occur.

It is presupposed here that extant atherinoideans derived from marine ancestors with a "complete" skeleton, which entered estuarine, even freshwater, habitats. Some evidence for this hypothesis exists in the distribution of *Atherinosoma*, an atherinid that enters freshwater (two words). Geological perturbations causing uplift of land masses result in the formation of hydrological catchments, and their outflows. In recent geographical strata, such as New Guinea, possibilities arose for euryhaline fish to exploit the food resources of new waters. The shallower the pool, the more diminutive the body necessary to survive. Concomitantly, uplifting divided and enclosed some basins to form lakes, isolating biota.

Beaufort (1922) commented on the morphological similarity among atherinid-like freshwater fish of Madagascar, Australia, New Guinea and Sulawesi. Saeed *et al.* (1994) gave some support to this observation, noting the long rostrum bearing an enlarged mesethmoid, the elongate first vertebral neural spine and dorsal pterygiophores, common to bedotiids and melanotaeniids, considering these characters plesiomorphic. Dyer & Chernoff (1996) formalised the relationship between the 3 above groups and pseudomugilines. Increased body depth, and placement of the origin of the anal fin cranial to at least 3 pleural ribs, were 2 (of 6) proposed melanotaeniid apomorphies.

From field observations, Beaufort (1922) postulated the features of adaptive evolution of *Chilatherina* and *Melanotaenia*. Algal fodder available in newly-formed lakes probably fuelled the evolutionary drive. To harvest an abundant crop of filamentous algae, nipping the strands would be adequate, but when overgrazed, an effective ingestive action would be to rasp the base of the crop using a fixed polydentate implement, such as the non-protrusile premaxilla of some melanotaeniids. Herbivorous fish require a longer digestive tract than omnivores. One way of increasing the volume of the visceral cavity, without excessively increasing drag while swimming, is to elongate the dorsoventral body profile. Also, Alexander (1967) suggested that deep-bodied fish can manoeuvre most efficiently amongst vegetation at the edge of lakes (and are less apparent to aerial predators). Development of a narrow, deep body (with elongate vertebral neural processes, pterygiophores and ribs) required cranial repositioning of the anal and dorsal fins, to maintain the optimal centre of gravity.

There is evidence for transformation series within each of telmatherinids, blue-eyes and melanotaeniids. The telmatherinids *Tominanga, Telmatherina, Kalyptatherina,* and the blue-eye *Pseudomugil signifer*, have, in common with *Craterocephalus* spp., an expanded first anal pterygiophore ("anal plate") situated ventral to the caudal limit of the visceral cavity, the tip of the caudal 1-3 pleural ribs being caudal to the transverse plane through the base of the anal spine. In *P. reticulatus and P. furcatus,* there are 4-5 ribs distal to the anal origin. Within Melanotaeniidae, *Cairnsichthys* and *Rhadinocentrus,* 6-8 ribs are caudal to the anal origin; in *Iriatherina,* 8 ribs are caudal to the anal origin: in *Chilatherina* and *Melanotaenia,* 10 ribs are caudal to the anal origin, and the second dorsal fin origin is cranial to the transverse plane through the caudal limit of the visceral cavity. In *Glossolepis,* the anal fin origin lies cranial to 11-12 ribs, the second dorsal fin origin is also cranial to the caudal visceral cavity, while the fish has a leaf-like profile, with marked bilateral compression.

Interestingly, in *Bedotia* and *Rheocles*, the anal origin is cranial to 6 ribs. However, the Indian Ocean has separated Madagascar from Australia for at least 60 Ma, during which time extant atherinomorph groups probably arose, and may have evolved convergently. While a number of characters are shared between bedotiids and melanotaeniids, particularly *Cairnsichthys* (Aarn & Ivantsoff, submitted) the biogeographic disjunction and a number of unshared characters suggests that, at best, these forms are related to common atherinid-like stock.

Figure 15 presents a summary of this discussion in the form of a cladistic analysis of the relationships of *Pseudomugil.*

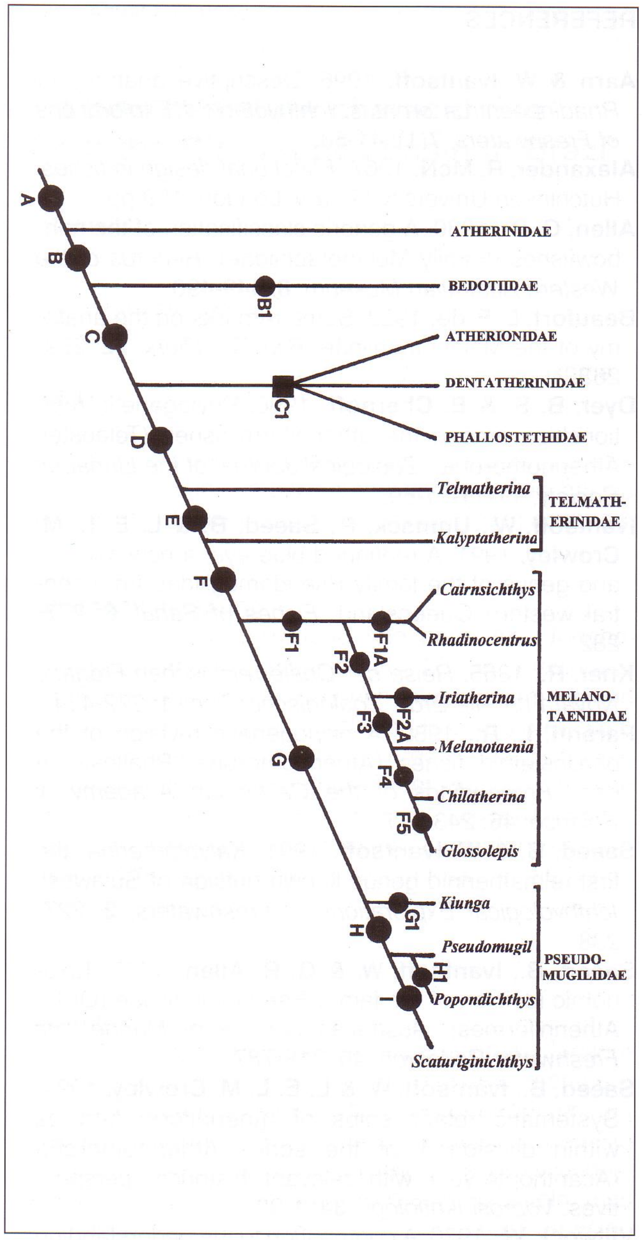

Fig. 15. Analysis of *Pseudomugil* and near relatives (Phallostethidae/Dentatherinidae/Atherionidae not evaluated - Node C1).
Node A: rostrum short; mandibular canal enclosed; rostral infraorbital series of 3 elements; lacrimal caudal border notched; pelvic ventral spinous process; dorsal postcleithrum large, ventral postcleithrum laminar; 5+ interdorsal pterygiophores; pelvic fin attached at, or posterior to, fourth pleural rib; flexible spine in anal fin; first anal pterygiophore enlarged, anal fin originating behind level of visceral cavity, body tubiform;
Node B: ventral postcleithrum narrow; Node B1: Presence in freshwaters of Madagascar; rostrum elongate, upper jaw not protrusible; rostral infraorbital series of 2 elements; first anal pterygiophore reduced, anal fin originating cranial to 6 pleural ribs, deep body;
Node C: mandibular canal open; Node C1: not evaluated;
Node D: presence in waters of Sulawesi and Irian Jaya; dorsal postcleithrum reduced; spine of second dorsal fin absent; pelvic fins close together; distinctive "plate-like" first anal pterygiophore, anal fin originating cranial to 1-3 ribs, body deep and narrow;
Node E: lacrimal caudal notch and pelvic ventral spinous process absent;
Node F: presence in waters of Irian Jaya, New Guinea and Australia; interpelvic area modified; large caniniform teeth present on premaxilla;
Node F1: rostrum elongate, upper jaw not protrusible, first anal pterygiophore reduced, anal fin originating cranial to 6-8 pleural ribs;
Node F1A: mandibular canal partially enclosed, posttemporal neurosensory canal absent; ethmomaxillary ligament absent; 1-2 interdorsal pterygiophores;
Node F2: strong spines present in dorsal and anal fins; Node F2A: metapterygoid absent;
Node F3: very tall cranial vertebral neural plates; aged fish discoidal; pelvic fin attached to third pleural rib; anal fin originating cranial to 10 ribs;
Node F4: presence in freshwaters of northern Irian Jaya & New Guinea; Node F4A: jaws elongate, almost without curvature, many rows of teeth on premaxilla; Node
F5: mouth small, body extremely bilaterally compressed, pelvic fins very close, anal fin originating cranial to 11/12 ribs;
Node G: mesethmoid, ectopterygoid, dorsal postcleithrum and axialpectoral ligament absent; reduction of rostral infraorbital series, cleithrum caudodorsal process, interdorsal pterygiophores and caudal fin elements; upper and lower hypural plates each fully fused;
Node G1: maxilla articulating with lateral ethmoid, vomerine condyle absent; vestigial first dorsal fin; ventral keel;
Node H: articularmaxillary ligament absent; supracleithrum discoid-reniform;
Node H1: presence in freshwaters of northern New Guinea;
Node I: reduction of branchiostegals and pelvic fin.

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