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A GENERIC CLASSIFICATION OF THE RAINBOWFISHES (FAMILY MELANOTAENIIDAE)

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ABSTRACT

A generic classification of the rainbowfishes (Melanotaeniidae) of Australia-New Guinea is proposed. The family is considered to be a probable sister group of the Atherinidae. An important character state which is apparently apomorphic among the Melanotaeniidae is the presence of a modified inter-pelvic region consisting of a membrane between the innermost pelvic ray and abdomen which forms a scaleless, V-shaped enclosure containing the uro-genital openings. The following eight genera are recognised, including two which are described as new: *Cairnsichthys,* new genus; *Chilatherina* Regan; *Glossolepis* Weber; *Iriatherina* Meinken; *Melanotaenia* Peters; *Popondetta,* new genus; *Psuedomugil* Kner; and *Rhadinocentrus* Regan. *Centratherina* Regan, previously recognised as a distinct genus, is placed in the synonymy of *Chilatherina.* Each genus is diagnosed or described and illustrations which show important anatomical features are included. A key to the genera of melanotaeniids and freshwater atherinids of Australia-New Guinea is presented. The genus *Quirichthys,* whose familial affinity was previously in doubt, is placed in the Atherinidae. A list of the nominal species of Melanotaeniidae and their present allocation is given in tabular form.

INTRODUCTION

The rainbowfishes (Melanotaeniidae) of northern Australia and New Guinea comprise a group of approximately 45 species, all of relatively small size (usually under 14 cm TL), which inhabit freshwater streams, lakes, and swamps. They are generally recognised as having evolved from a marine atherinid ancestor and share many anatomical similarities with the members of that family. Indeed, many previous authors (including Regan 1914; Jordon & Hubbs 1919; Weber & de Beaufort 1922; Fowler 1928; and Taylor 1964) have included the rainbowfishes as a subfamily within the Atherinidae. However, Munro (1964, 1967), and Rosen (1964) suggested that on the basis of certain morphological features the rainbowfishes should be accorded separate family status. This view was also shared by Greenwood *et al.* (1966) in their provisional classification of living teleost fishes.

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Since 1974 the present author has become greatly involved with the study of rainbowfish taxonomy. During this period extensive collections of melanotaeniids and other freshwater fishes were procured from Western Australia, Northern Territory, Queensland, New South Wales, and Papua-New Guinea. In addition, rainbowfish collections were studied in major museums of Australia, Europe, and America. This paper is the first of a series which will encompass the respective melanotaeniid faunas of Australia and New Guinea. The primary purpose of the present work is to define the generic relationships within the family, which until now have been poorly understood. As a result of this investigation two genera (*Pseudomugil* and *Iriatherina*) previously considered to be atherinids are re-assigned to the Melanotaeniidae. Evidence is also presented which confirms the separation of this group from the Atherinidae. The following eight genera are recognised: *Cairnsichthys,* new genus; *Chilatherina* Regan; *Glossolepis* Weber; *Iriatherina* Meinken; *Melanotaenia* Peters; *Popondetta,* new genus; *Pseudomugil* Kner; and *Rhadinocentrus* Regan.

MATERIALS AND METHODS

Specimens of melanotaeniids and other freshwater fishes were procured on seven field expeditions to northern Australia and Papua-New Guinea between August 1974 and October 1979. Approximately 6000 specimens of rainbowfishes were obtained representing 23 species and eight genera. This material, now deposited at the Western Australian Museum, formed the basis for this study, but was also supplemented by valuable collections made in northern Australia by Drs D.R. Rosen and J.P. Beumer, and in New Guinea by Drs M. Boeseman and T. Roberts. Most of the melanotaeniid holdings at the following institutions were also examined (abbreviations which appear in parentheses are used in the subsequent text): American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); British Museum of Natural History, London; California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago; Museum National d'Histoire Naturelle, Paris; Rijksmuseum van Natuurlijke Histoire, Leiden (RMNH); United States National Museum of Natural History, Washington, D.C. (USNM); Western Australian Museum, Perth (WAM); and Zoologisch Museum, Amsterdam (ZMA).

Approximately 75 specimens, representing all the known genera of melanotaeniids and several atherinids were cleared in KOH and stained with Alizarin Red-S. These were stored in 100% glycerin and studied with the use of a dissecting microscope. Illustrations of certain bones were obtained by photo microscopy or were made with the aid of the Wild drawing attachment on the M-5 dissecting microscope.

Outgroup comparisons were made on approximately 400 specimens of Australian atherinids deposited in the WAM collection belonging to the follow-

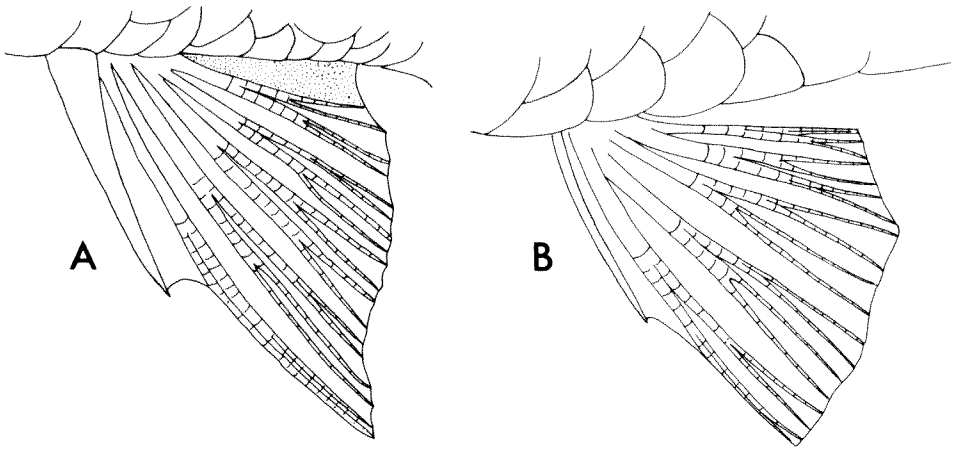

Fig. 1—Pelvic fins of melanotaeniids (A) and atherinids (B). The stippled area represents the membrane which connects the innermost ray and the abdomen.

ing genera: *Allanetta, Atherinosoma, Craterocephalus, Hypoatherina, Pranesus,* and *Quirichthys.* In addition, several loan specimens of *Bedotia* from Madagascar and *Telmatherina* from the Celebes were obtained from CAS and ZMA respectively.

Relationships within the Melanotaeniidae were evaluated using the methods of phylogenetic analysis described by Hennig (1966).

DEFINITION OF CHARACTERS

Selected characters which are used to define inter- and intra-familial relationships are briefly discussed below. A given character or character state was judged to be plesiomorphic (primitive) or apomorphic (derived) primarily on the basis of outgroup comparisons with the Atherinidae, which is considered to be the sister group of the Melanotaeniidae (see discussion section). This analysis should be regarded as provisional because mainly Australian atherinids were examined.

Inter-pelvic modification (Figs. 1-2)—Melanotaeniids possess an apparent unique external modification of the area between the pelvic fins consisting of a naked V-shaped enclosure containing the uro-genital openings. The enclosure is formed by a membranous attachment between the innermost pelvic ray and the abdomen with the uro-genital pores positioned near the open end of the V. This condition is considered to be apomorphic in comparison with the typical atherinid state which lacks membranes and has the uro-genital openings surrounded by scales. The function of this modification is not known, but it is probably related to reproductive activities.

A general survey of teleosts in the WAM collection revealed that the major-

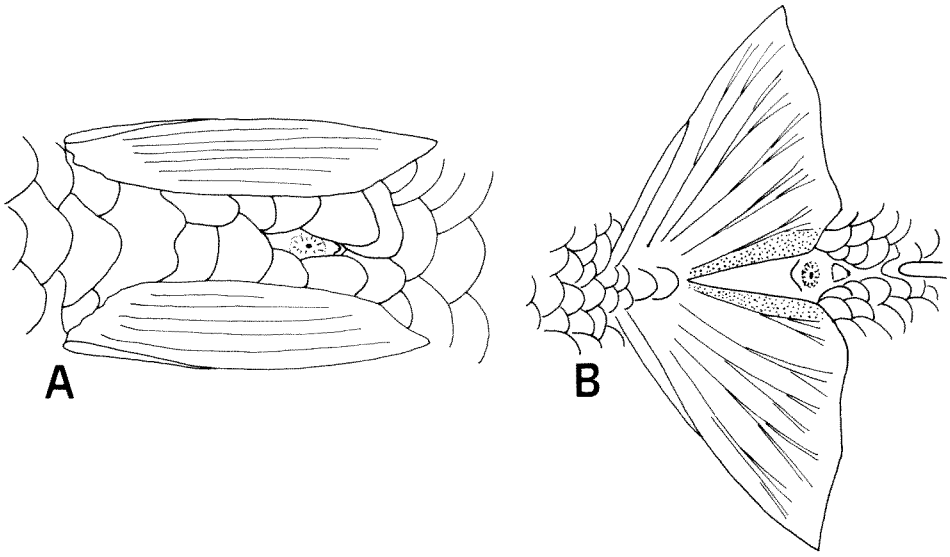

Fig. 2—Ventral view of pelvic regions of atherinids (A. *Pranesus* sp.) and melanotaeniids (B. *Melanotaenia* sp.)). The stippled area represents the membrane which connects the innermost ray and the abdomen.

ity of sub-perciform level groups lack the membrane which binds the pelvic fin to the abdomen, therefore reinforcing the apomorphic status of this membrane. However, a partial membrane is present in scorpaenids and a number of higher groups such as some serranids, grammistids, pseudogrammids, apogonids, carangids, lutjanids, kyphosids, lethrinids, pomacentrids, acanthurids, and mugilids. A very well developed membrane is found in several groups including priacanthids, kuhliids, pomatomids, toxotids, and the freshwater apogonid genus *Glossamia*. In addition, Patten (pers. comm.) has informed me that a partial membrane is present at the base of the pelvic fin in some specimens of the Australian freshwater atherinid *Quirichthys*, in most American atherinids, and in *Bedotia* a freshwater atherinoid from Madagascar. However, in all the abovementioned groups, the overall inter-pelvic area does not resemble the modified condition of melanotaeniids. In non-atherinoid fishes which display membrane development the uro-genital aperatures are generally situated well behind the inter-pelvic area.

Caudal skeleton—The overall morphology of the caudal skeleton of melanotaeniids and atherinids is very similar (**Figs. 3-5**). The main difference involves the lowermost hypural element (parahypural) which is fused to the lower hypural plate in most melanotaeniids (except *Cairnsichthys* and *Pseudomugil*) and autogenous in the Atherinidae. The latter condition is considered to be pleisiomorphic.

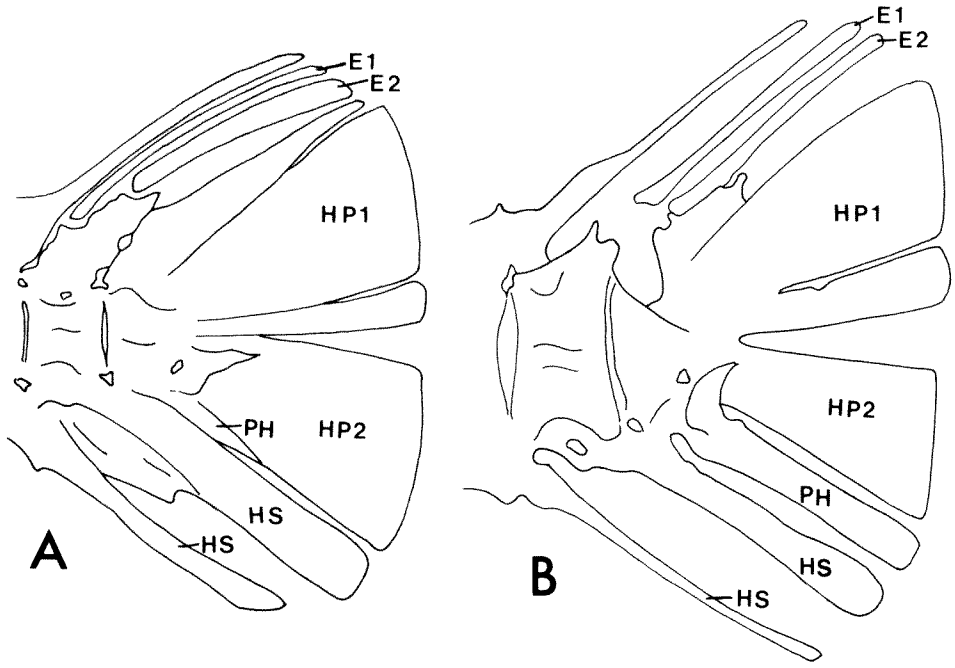

Fig. 3—Caudal skeletons of *Glossolepis incisus* (A, Melanotaeniidae) and *Atherinosoma* sp. (B, Atherinidae). Symbols are as follows: E1 and E2 = epurals; HP1 and HP2 = fused hypural elements representing upper and lower hypural plates respectively; PH = parahypural; HS = hemal spine.

Premaxillary shape and dentition—Melanotaeniids are characterised by a relatively short median ascending process on the premaxillary (**Fig. 6**). Furthermore, this bone usually supports a liberal number of conical to caniniform teeth, frequently extending outside of the mouth onto the lips (**Figs. 7-9**). Most Australian atherinids have a relatively elongate median process and lack external teeth of the melanotaeniid type (except in *Quirichthys*, **Fig. 6L**, and the marine genus *Atherion*). According to Patten (pers. comm.) basal autherinoids such as the Notocheirinae, *Atherion* and the most primitive atherinines possess a short premaxillary process and therefore this state is considered to be primitive. However, it is possible that the melanotaeniid condition has been secondarily derived from a marine ancestor possessing an elongate premaxillary, which as mentioned previously is typical of recent Australian atherinids.

Vomerine and palatine dentition—The presence of tiny conical teeth on the vomer and palatine bones (**Fig. 9**) is provisionally considered to be an apomorphic character. However, I have not examined a sufficient number of atherinids. The detection of this condition in small specimens is facilitated by dissection after clearing and staining.

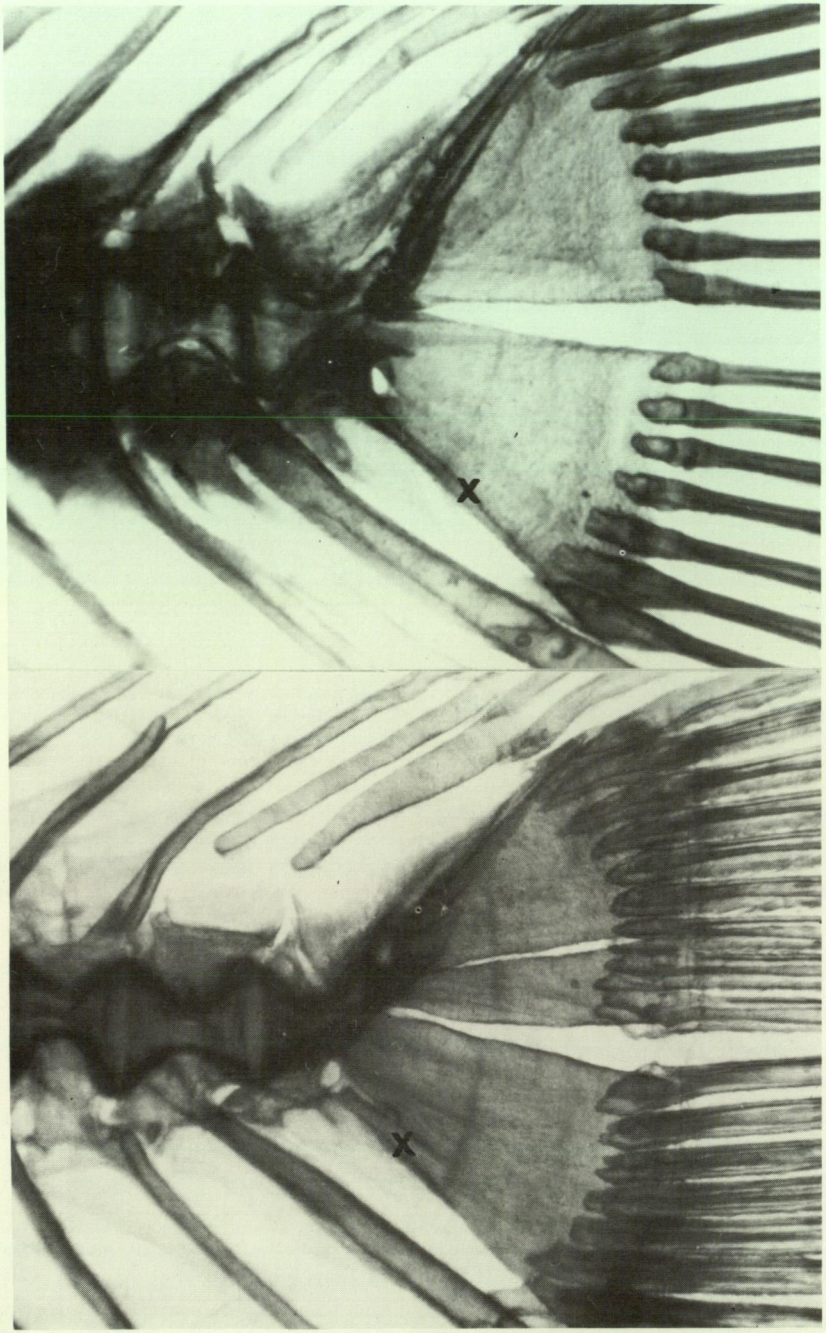

Fig. 4—Caudal skeletons of selected melanotaeniids: (upper) *Rhadinocentrus ornatus;* (lower) *Iriatherina werneri.* The fused parahypural is indicated by the symbol "X."

Fig. 5—Caudal skeletons of selected atherinids: (upper) *Hypoatherina barnesi;* (lower) *Quirichthys stramineus.* The autogenous parahypural is indicated by the symbol "X."

Fin-rays—Several characters or character states pertaining to fin-rays were useful in defining the various genera. These include: (1) presence or absence of stout spines at the beginning of the pelvic, anal, and both dorsal fins; (2) the presence or absence of segmentation of the first ray of the second dorsal fin in species lacking a stout spine in this position; (3) the number of unbranched rays in the second dorsal and anal fins; (4) the number of branched rays in the

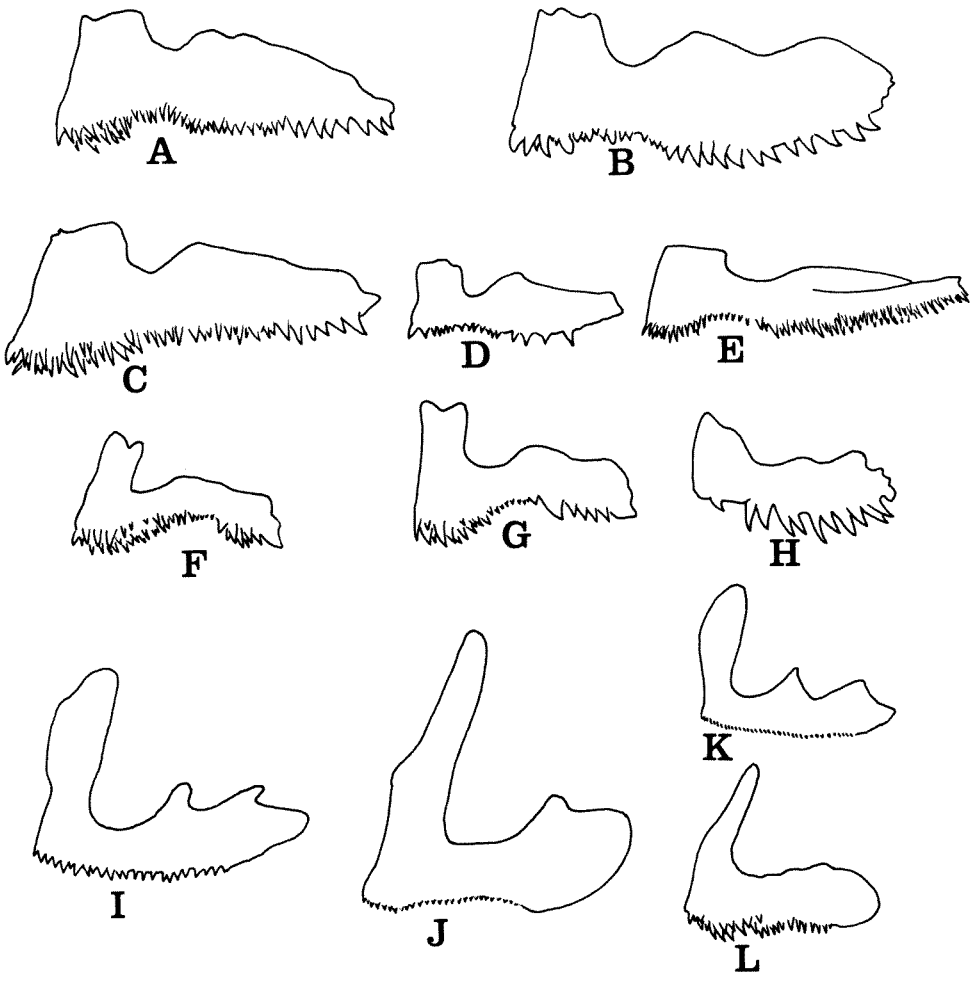

Fig. 6—Premaxillary bones of melanotaeniid (A-H) and selected atherinid genera (I-L) shown at equal magnification except H and J which are twice the scale of the others: (A) *Melanotaenia splendida*, 53 mm SL; (B) *Glossolepis incisus*, 74 mm SL; (C) *Chilatherina sentaniensis*, 67 mm SL; (D) *Rhadinocentrus ornatus*, 43 mm SL; (E) *Cairnsichthys rhombosomoides*, 48 mm SL; (F) *Popondetta furcatus*, 43 mm SL; (G) *Pseudomugil signifer*, 41 mm SL; (H) *Iriatherina werneri*, 33 mm SL; (I) *Atherinosoma presbyteroides*, 53 mm SL; (J) *Craterocephalus pauciradiatus*, 30 mm SL: (K) *Hypoatherina barnesi*, 43 mm SL: (L) *Quirichthys stramineus*, 40 mm SL.

caudal fin; and (5) the soft anal fin-ray count. The presence of stout spines, lack of segmentation in the first ray of the second dorsal fin, presence of several unbranched rays in the second dorsal and anal fins, a branched caudal fin-ray count of less than 15 and soft anal fin-ray count of more than 15 were all considered to be apomorphic character states.

Inter-dorsal pterygiophores—The number of non-supportive pterygiophores between the two dorsal fins is 2 or 3 in most melanotaeniids (**Fig. 22A**), except in *Pseudomugil* and *Popondetta* these elements are either lacking or represented by a rudiment. These character states are provisionally considered to be apomorphic compared to the atherinid condition in which there are gen-

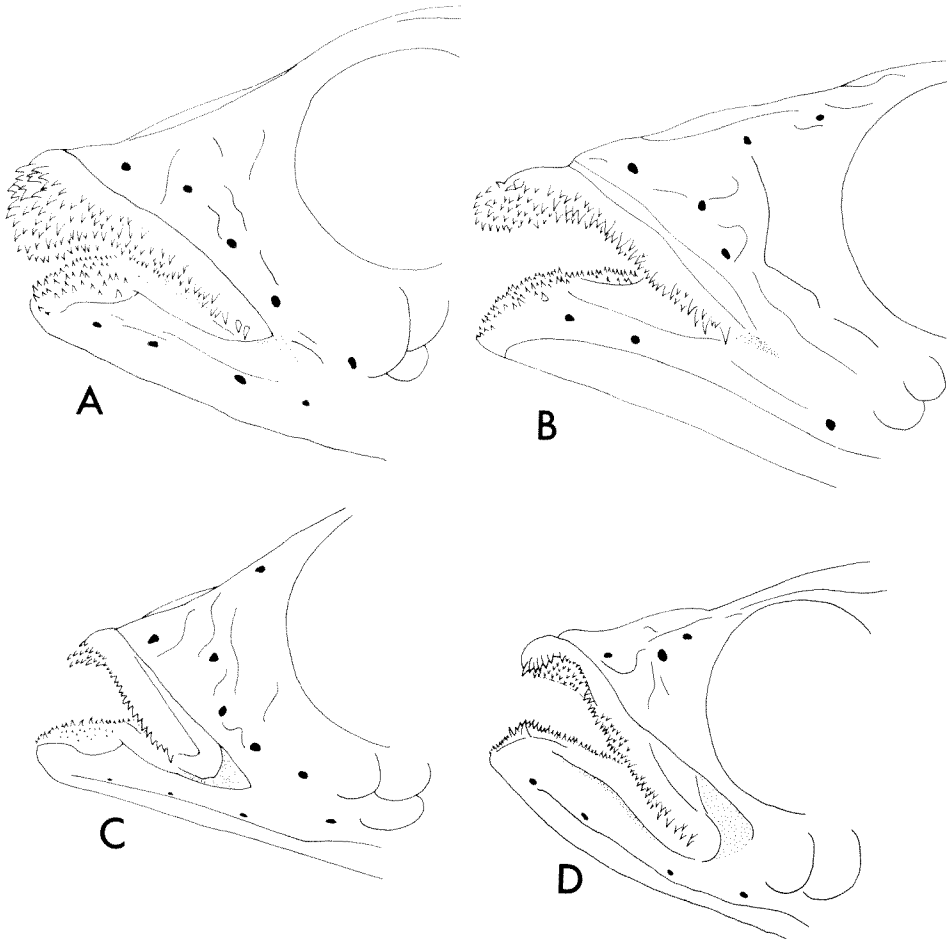

Fig. 7—Snout region of certain melanotaeniids showing external dentition: (A) *Chilatherina crassispinosa*, 82 mm SL; (B) *Chilatherina sentaniensis*, 77 mm SL; (C) *Glossolepis wanamensis*, 70 mm SL; (D) *Cairnsichthys rhombosomoides*, 54 mm SL.

erally more than four elements. However, my comparison with atherinids was limited to the Australian genera.

Pelvic girdle—The general shape of the pelvic girdle is extremely variable among melanotaeniid and atherinid genera (**Fig. 10**). Most genera possess finger-like projections anteriorly and posteriorly at the ventral mid-line, but

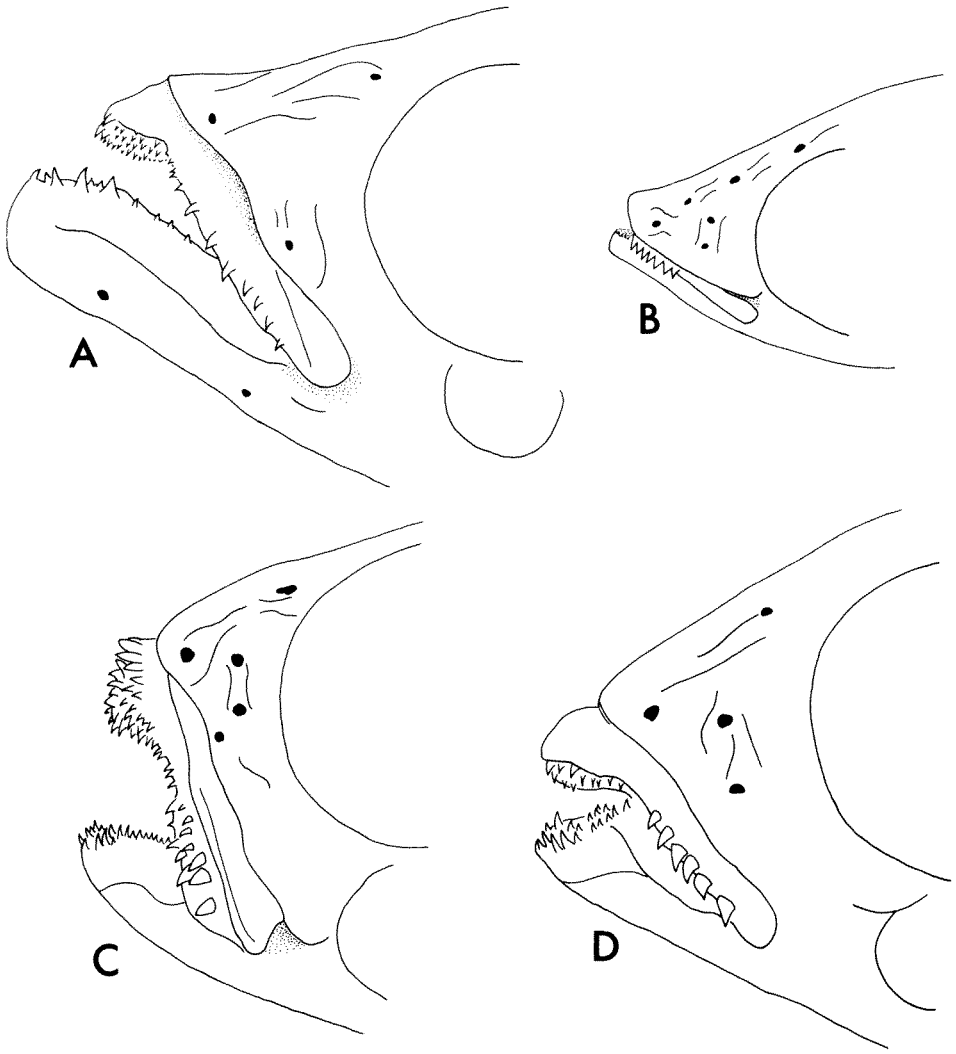

Fig. 8—Snout region of certain melanotaeniids showing external dentition: (A) *Rhadinocentrus ornatus*, 48 mm SL; (B) *Iriatherina werneri*, 19 mm SL; (C) *Popondetta furcatus*, 43 mm SL; (D) *Pseudomugil signifer*, 41 mm SL.

two melanotaeniid genera lack the anterior projections (**Fig. 10F & H**). Generally, the lateral "wings" of melanotaeniids are better developed than in atherinids. There is also variation in the muscular attachment or 'anchoring' of the lateral 'wing' to the pleural ribs; in melanotaeniids the attachment is with the

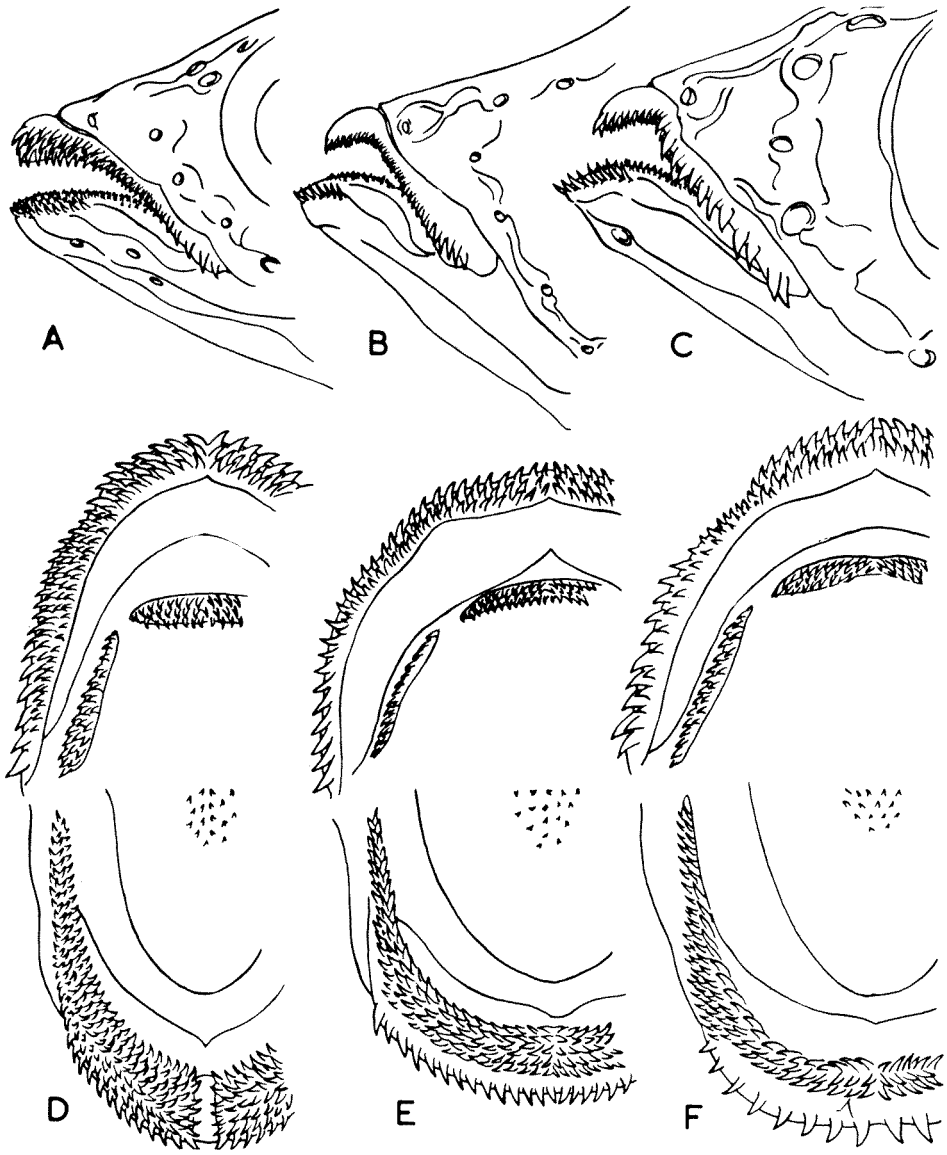

Fig. 9—Dentition of the genus *Melanotaenia*: (A & D) *M. affinis*, 98 mm TL; (B & E) *M. splendida rubrostriata*, 142 mm TL; (C & F) *M. splendida splendida*, 96 mm TL (drawings from Munro, 1964).

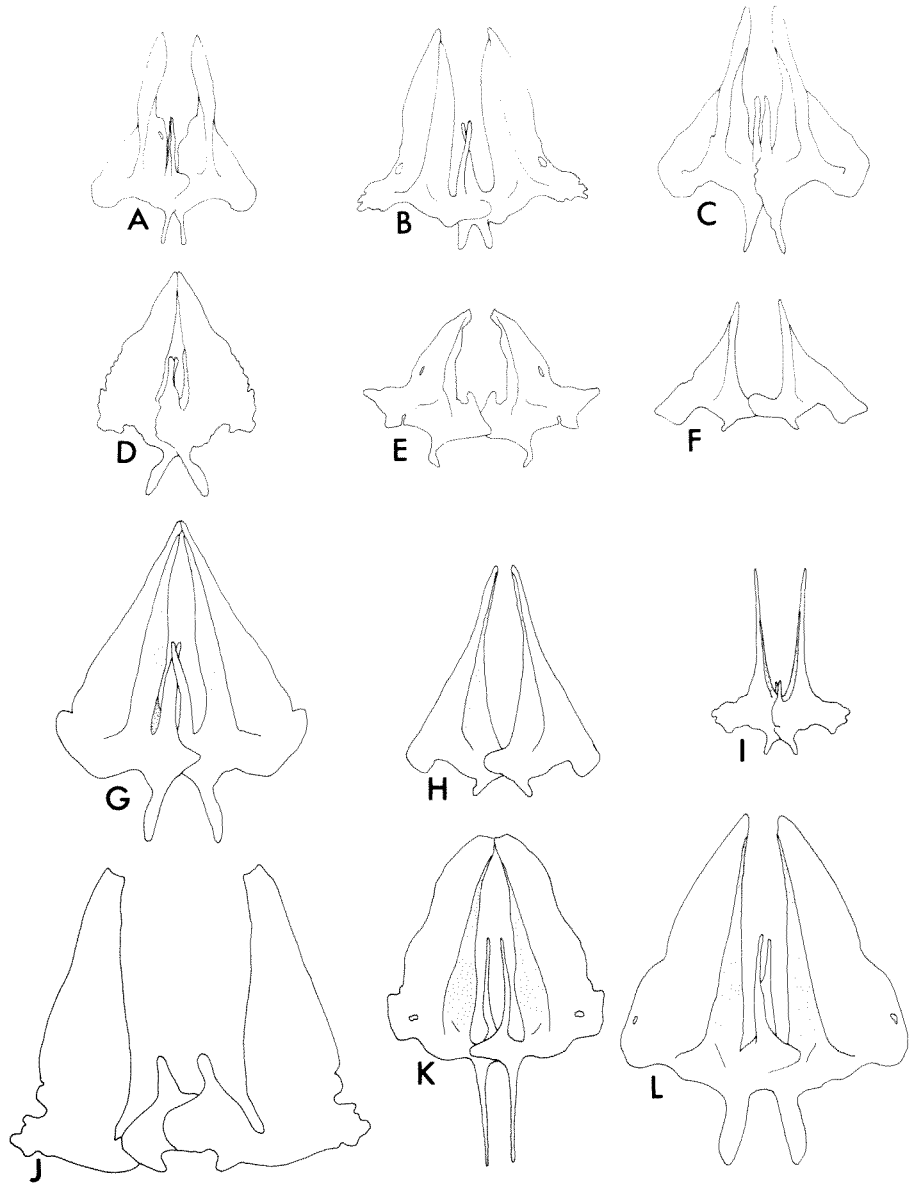

Fig. 10—Ventral view of pelvic girdles of melanotaeniid (A-I) and selected atherinid genera (J-L) shown at equal magnification except D which is half the scale of the others: (A) *Melanotaenia exquisita*, 42 mm SL; (B) *Melanotaenia* sp. (Lake Eacham, Queensland), 52 mm SL; (C) *Chilatherina crassispinosa*, 42 mm SL; (D) *Glossolepis incisus*, 74 mm SL; (E) *Rhadinocentrus ornatus*, 41 mm SL; (F) *Cairnsichthys rhombosomoides*, 32 mm SL; (G) *Pseudomugil signifer*, 41 mm SL; (H) *Popondetta furcatus*, 40 mm SL; (I) *Iriatherina werneri*, 30 mm SL; (J) *Atherinosoma presbyteroides*, 53 mm SL; (K) *Hypoatherina barnesi*, 43 mm SL; (L) *Quirichthys stramineus*, 40 mm SL.

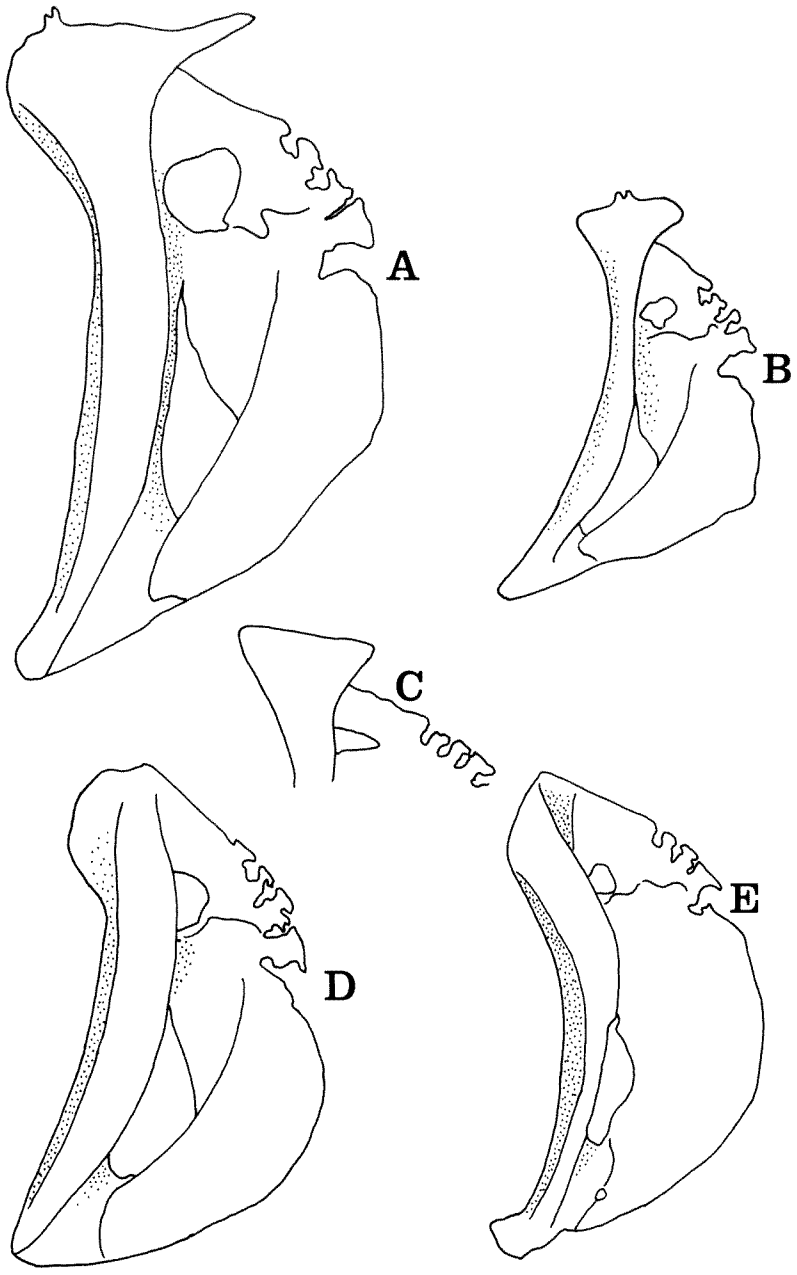

Fig. 11—Lateral view of left pectoral girdle of selected melanotaeniids: (A) *Melanotaenia splendida*, 53 mm SL; (B) *Rhadinocentrus ornatus*, 37 mm SL; (C) *Iriatherina werneri*, 33 mm SL; (D) *Pseudomugil signifer*, 41 mm SL; (E) *Popondetta furcatus*, 38 mm SL.

second, third, or fourth rib, whereas in the Australian atherinid genera examined the fourth or fifth ribs were involved. The lack or reduction of anterior projections at the ventral mid-line, presence of well-developed lateral 'wings' and their attachment to the second or third pleural rib are provisionally considered to be apomorphic character states, pending further study of a wider range of atherinid genera.

Pectoral girdle—Atherinids and some melanotaeniid genera possess a well-developed posteriorly directed process on the dorsal head of the cleithrum (**Fig. 11**). The presence of this feature in only the more advanced melanotaeniid groups is therefore difficult to interpret, but may represent a form of secondary convergence. The majority of melanotaeniids have a reduced process or this feature is lacking.

Scalation—A count of eight or less horizontal scale rows at the level of the anal fin origin is provisionally considered to be plesiomorphic and is found in three melanotaeniid genera and most Australian atherinids. Most melanotaeniids possess a probable apomorphic condition consisting of 10 to 18 rows. The scale margins are generally cycloid or slightly crenulate in both atherinids and melanotaeniids, except in the genus *Glossolepis,* a member of the latter group which exhibits a specialised condition characterised by prominent crenulations (**Fig. 12**). In addition, two melanotaeniid genera, *Popondetta* and *Cairnsichthys,* lack well-developed radii, another feature considered to be apomorphic within the melanotaeniidae.

Gill-rakers—There is a trend towards an increased gill raker count in the more advanced melanotaeniids. Counts for the various genera range from 8 to 25 rakers on the lower limb of the first gill arch. A similar range of counts is found in Australian atherinids.

Vertebrae—Total vertebral counts in melanotaeniids usually range from 27 to 38, which is considered to be an apomorphic character state compared to the atherinid condition in which there are usually more than 38 vertebrae. However, this vertebral count trend is reversed within the Melanotaeniidae as the most advanced genera possess the highest counts (i.e., usually 34-38).

Otolith morphology—Approximately 100 melanotaeniid otoliths were analysed. Generic differences appear to be associated mainly with overall shape (**Fig. 13**), but there is a great deal of variation, even within species. No atherinid otoliths were examined and therefore no attempt has been made to ascertain specialisation trends.

FAMILY MELANOTAENIIDAE

(type genus: *Melanotaenia* Gill, 1862)

Diagnosis: Small, laterally compressed fishes, oblong to slender in shape; head more or less pointed; top of snout and interorbital region flattened; eye relatively large. Mouth opening moderate or small, usually not extending

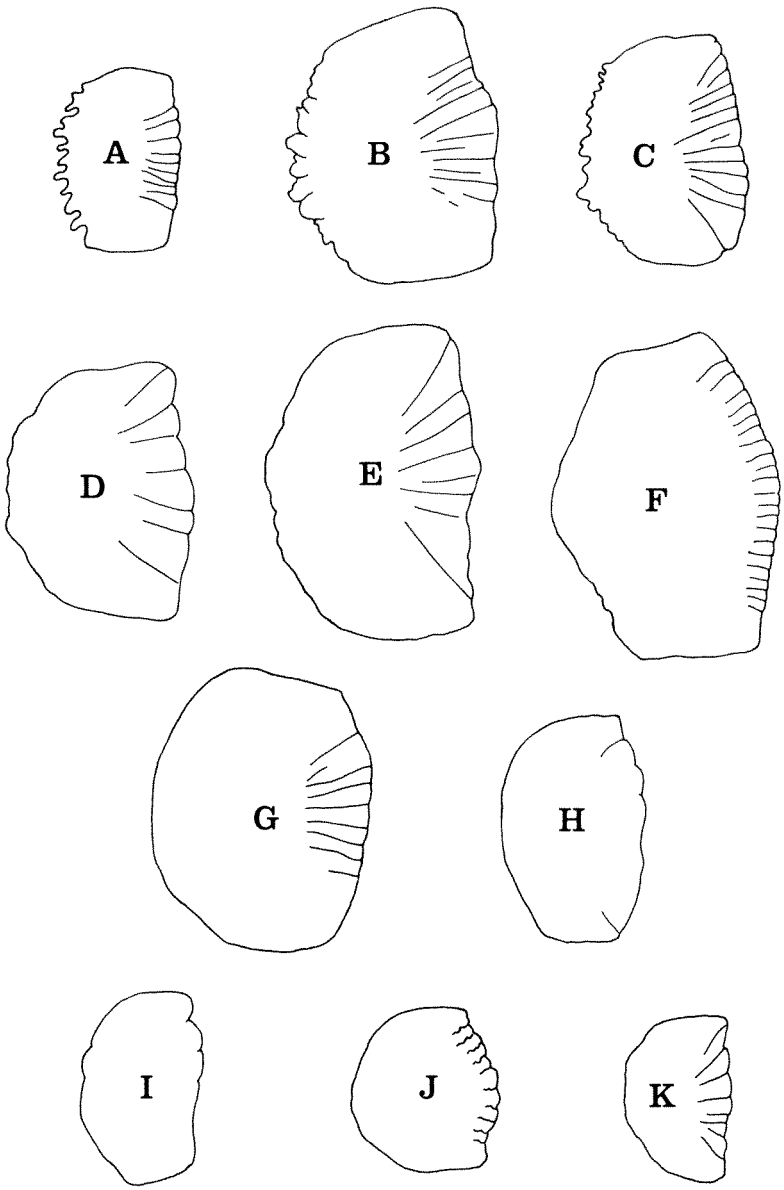

Fig. 12—Scales of selected melanotaeniids taken from the approximate same position of each fish, three rows directly below origin of first dorsal spine. (A) *Glossolepis incisus*, 79 mm SL; (B) *G. multisquamatus*, 87 mm SL; (C) *G. wanamenis*, 78 mm SL; (D) *Chilatherina crassispinosa*, 85 mm SL; (E) *C. lorentzi*, 89 mm SL; (F) *Melanotaenia splendida*, 80 mm SL; (G) *Rhadinocentrus ornatus*, 48 mm SL; (H) *Cairnsichthys rhombosomoides*, 66 mm SL; (I) *Popondetta furcatus*, 43 mm SL; (J) *Iriatherina werneri*, 30 mm SL; (K) *Pseudomugil signifer*, 41 mm SL. All scales shown at equal magnification, except G and H which are twice the scale of the others.

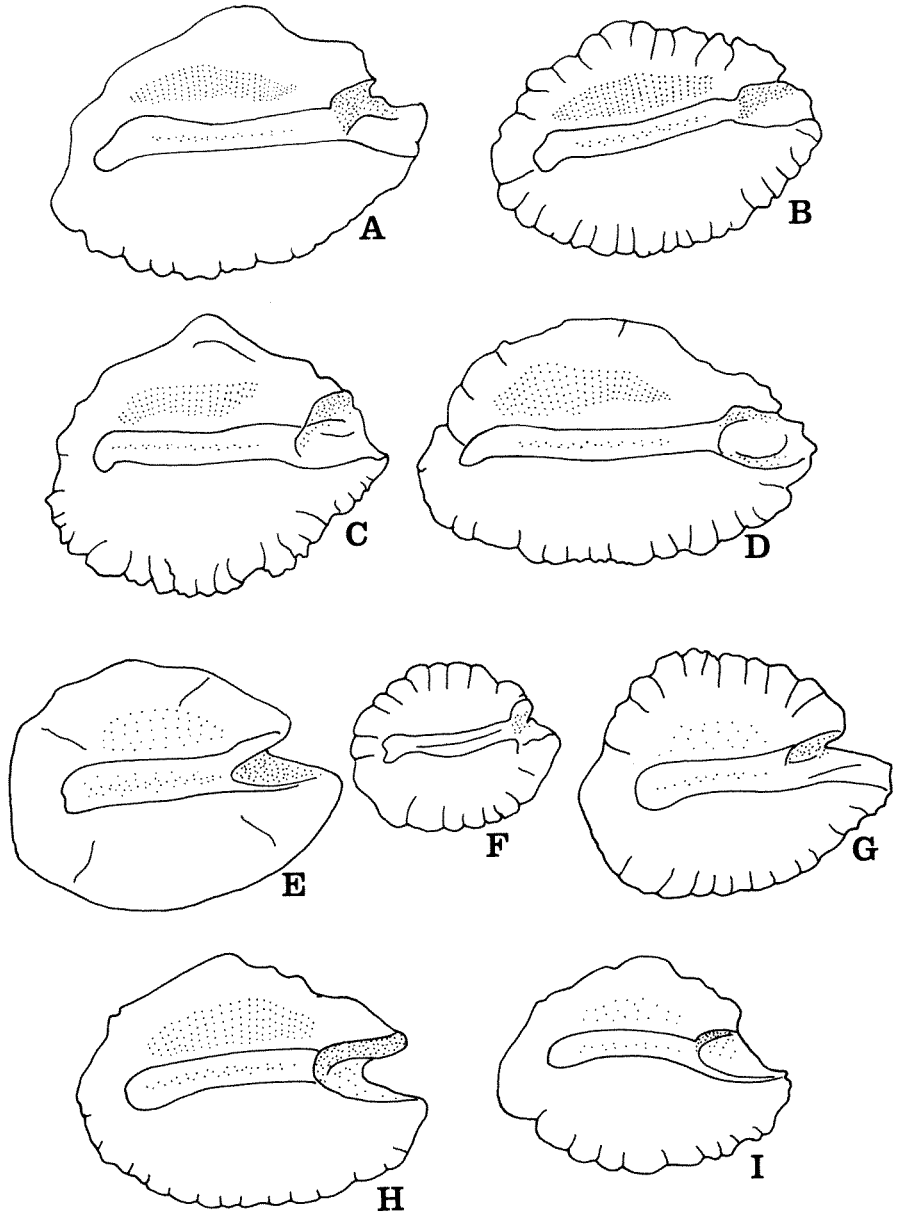

Fig. 13—Sagittal otoliths from left side of certain melanotaeniids: (A) *Melanotaenia trifasciata*, 73 mm SL; (B) *M. goldiei*, 64 mm SL; (C) *Glossolepis wanamensis*, 74 mm SL; (D) *Chilatherina lorentzi*, 79 mm SL; (E) *Rhadinocentrus ornatus*, 48 mm SL; (F) *Cairnsichthys rhombosomoides*, 46 m SL; (G) *Popondetta furcatus*, 39 mm SL; (H) *Pseudomugil signifer*, 41 mm SL; (I) *Iriatherina werneri*, 31 mm SL. Otoliths A-D and F shown at equal magnification; E and G-I are twice the scale of the others.

beyond level of anterior edge of eye; lips frequently thickened and often bearing one or more rows of teeth; premaxillaries bordering the mouth opening, nearly straight, gently curved, or with an abrupt bend between the anterior horizontal portion and lateral part; ascending median process or premaxillary relatively short; maxillaries rod-like, visible or not when mouth is closed; jaw teeth conical to caniniform, usually arranged in several rows, often extending outside of mouth onto lips; teeth on vomer, palatines, and tongue present or absent; two dorsal fins present; first dorsal fin usually composed of 3 to 7 spines, the first of which is often several times larger in diameter than the others, second dorsal fin composed of 6 to 22 rays, the first a stout spine in some genera; anal fin with 10 to 30 rays, the first a stout spine in some genera; pelvic fins composed of one spine and 5 soft rays; innermost pelvic ray attached to abdomen by membrane along its entire length; inter-pelvic region naked between pelvic axillary scale cluster and anus; preopercle, opercle, and body covered with scales, horizontal rows on body at level of anal fin origin 6 to about 18, vertical rows from upper corner of gill opening to caudal fin base about 28 to 60; hind margin of scales smooth to deeply crenulate; lateral line absent or represented by shallow pits on some scales; a few weakly developed rakers on upper limb and about 8 to 30 rakers on lower limb of first gill arch; vertebrae 27 to 38; lowermost element of hypural (para-hypural) fused to lower hypural plate in most genera; inter-dorsal pterygiophores 0-3 (rarely 4).

Remarks: The most useful character for separating the Melanotaeniidae from the closely related Atherinidae is the possession of a membrane between the full length of the innermost pelvic ray and the abdomen (**Fig. 1**) which forms a V-shaped enclosure or furrow around the naked inter-pelvic area (**Fig. 2**). The membrane is frequently damaged in preserved specimens. Great care must be exercised when extending the fin with a probe while searching for this feature as the membrane is easily split. The pelvic fins of Australian atherinids are generally set wider apart than those of melanotaeniids and the pelvic girdle of the former group is larger in relation to size. The posterior finger-like projections at the ventral mid-line of the girdle (**Fig. 10**) are readily visible in cleared and stained atherinids, but are hidden by the over-lying pelvic fins in melanotaeniids. The premaxillary shape and associated dentition of melanotaeniids is also very distinctive (**Fig. 6**), although a few atherinids have some teeth outside the mouth (for example, *Atherion* and *Quirichthys*) or a reduced ascending process (for example, *Pranesus* and *Atherion*). Another difference between these groups is the presence of pronounced secondary sexual characteristics among most melanotaeniids, usually manifested in the brighter colours and more elongate dorsal, anal, and pelvic fin rays of mature males. Most atherinids, on the contrary, exhibit little or no sexual dimorphisim.

Rosén (1964), in comparing atherinoid caudal skeletons, stated that atherinids had an autogenous parahypural (**Fig. 5**) and two epurals, whereas melanotaeniids have the parahypural fused to the other hypural elements and possess

a single epural. However, the present study indicates that the parahypural is autogenous in two melanotaeniid genera, *Pseudomugil* and *Cairnsichthys,* and the presence of two epurals is common in most members of the family (**Fig. 4**).

The following key will serve to distinguish the genera of Melanotaeniidae and sympatric freshwater atherinids.

Key to the Genera of Melanotaeniidae and Freshwater Atherinidae of N. Australia and New Guinea

1a. Innermost pelvic ray not attached to abdomen by membrane (**Fig. 1B**); scales present on abdomen between pelvic base and anus (**Fig. 2A**) (Family ATHERINIDAE) 2

1b. Innermost pelvic ray attached to abdomen by membrane (**Fig. 1A**); scales absent on abdomen between pelvic base and anus (**Fig. 2B**) (Family MELANOTAENIIDAE) 3

2a. No conical teeth on lips outside of mouth; first dorsal fin never taller than second dorsal fin (N. Australia and New Guinea ..... *Craterocephalus*

2b. Conical teeth present on lips outside of mouth; first dorsal fin of males significantly taller than second dorsal fin (N. Australia) ..... *Quirichthys*

3a. No rigid fin spines present, all rays slender and flexible 4

3b. Some rigid fin spines present, usually at beginning of first dorsal (except in *Iriatherina*), second dorsal, anal, and pelvic fins 7

4a. Total anal fin rays usually 9-13; anal fin usually originates on posterior half of body (caudal fin excluded) (N. and E. Australia and New Guinea) ..... *Pseudomugil*

4b. Total anal fin rays usually 17-21; anal fin usually originates on anterior half of body 5

5a. Pores in interorbital region well-developed and conspicuous; a large scale covering much of interorbital; first dorsal fin originating well in advance of level of first anal ray; first dorsal fin of males elongate and filamentous, extending as far as fifth ray of second dorsal fin when depressed; middle caudal rays dark (vicinity of Popondetta, New Guinea). *Popondetta,* n.gen.

5b. Pores in interorbital region very small and inconspicuous; no large scale covering most of interorbital; first dorsal fin originating slightly behind to slightly ahead of level of first anal ray; first dorsal fin of males not elongate and filamentous; middle caudal rays not contrasted with remainder of fin (Australia) 6

6a. Lower jaw prominant (**Fig. 8A**); exposed lateral part of premaxillary with a single row of 15 or less widely separated teeth (**Fig. 8A**); horizontal scale rows at level of anal fin origin 8 or 9 (S. Queensland and N. New South Wales) .. *Rhadinocentrus*

6b. Jaws about equal (**Fig. 7D**); exposed lateral part of premaxillary with numerous teeth arranged in several rows (**Fig. 7D**); horizontal scale rows at level of anal fin origin 10 or 11 (N. Queensland) ..... *Cairnsichthys,* n.gen.

7a. A stout, rigid spine present at beginning of first dorsal fin; soft anal fin rays 15-30; first few rays of second dorsal and anal fins not produced into elongate filaments; exposed teeth on premaxillary numerous and well-developed (**Figs. 7A & B, & 9**) 8

7b. All spines of first dorsal fin relatively soft and flexible; soft anal fin rays 11 or 12; first few rays of 2nd dorsal and anal fins produced into elongate filaments in adult males; exposed premaxillary teeth restricted to a single row of about 7-8 enlarged canines (**Fig. 7B**) (S. New Guinea and Cape York Peninsula) ..... *Iriatherina*

8a. Scale margins deeply crenulate (**Fig. 12, A-C**); vertical scale rows from upper edge of gill opening to caudal fin base 37-60 (N. New Guinea) ..... *Glossolepis*

8b. Scale margins smooth or with only shallow crenulations (**Fig. 12, D-F**); vertical scale rows from upper edge of gill opening to caudal fin base 29-44 9

9a. Premaxillaries with an abrupt bend between anterior horizontal portion and lateral portion (**Fig. 9**) (Australia-New Guinea ..... *Melanotaenia*

9b. Premaxillaries without an abrupt bend between anterior horizontal portion and lateral portion (**Fig. 23**) (N. New Guinea ..... *Chilatherina*

Genus *Pseudomugil*
(Fig. 14)

Pseudomugil Kner, 1865: 275 (type species, *Pseudomugil signifer* Kner, 1865, by monotypy).

Diagnosis–Relatively elongate, laterally compressed body; greatest body depth 3.4 to 5.0 in standard length; premaxillaries with a distinct bend between the anterior horizontal portion and lateral part; jaw teeth conical to caniniform, with or without one or more rows extending outside of mouth;

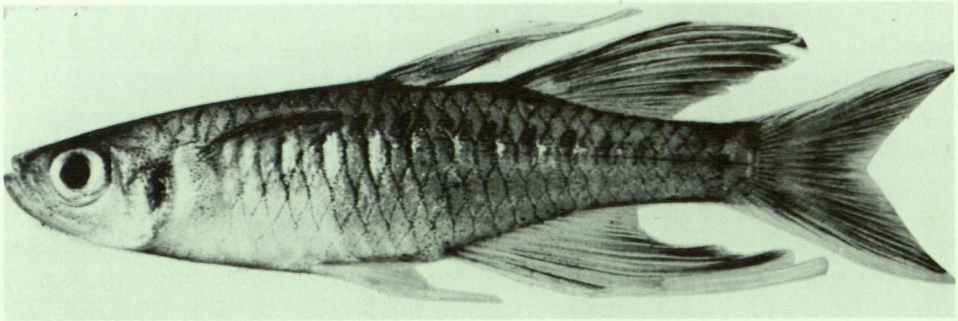

Fig. 14—*Pseudomugil signifer*, male, 40 mm SL, Saltwater Creek, Cape York Peninsula, Australia.

vomer and palatines toothless; inter-dorsal pterygiophores absent; first dorsal fin consisting of 3 to 5 slender, flexible spines; second dorsal fin composed of 6 to 12 segmented rays; anal fin with or without slender, flexible spine, and 8 to 12 segmented rays; anal fin originates on posterior half of body; all soft, segmented fin rays usually branched except first ray of second dorsal and anal fins; branched caudal rays 9 to 14; parahypural autogenous; pelvic girdle with well-developed finger-like projections anteriorly at ventral mid-line; lateral 'wing' of pelvic girdle anchored to fourth pleural rib; dorsal head of cleithrum without posteriorly directed projection; scales cycloid with well-developed radii, horizontal rows on body at level of anal fin 6 to 8, vertical rows from upper corner of gill opening to caudal fin base 27 to 30; gill rakers on lower limb of first gill arch 8 to 11; vertebrae 27 to 32; sexual dimorphism characterised by more elongate rays in first dorsal, second dorsal, anal, and pelvic fins of males.

Remarks—*Pseudomugil* contains six known species and perhaps three or more undescribed forms. The distribution includes coastal fresh and brackish water of New South Wales and Queensland, Arnhem Land (Northern Territory), southern New Guinea, and the Aru Islands.

Popondetta gen. nov.
(Fig. 15)

Type species, *Pseudomugil furcatus* Nichols, 1955: 2.

Description—A genus of Melanotaeniidae with the following combination of characters: relatively elongate, laterally compressed body; greatest body depth 3.4 to 4.4 in standard length; premaxillaries with a distinct bend between the anterior horizontal portion and lateral part; jaw teeth conical to caniniform, several rows extending outside of mouth; vomer and palatines

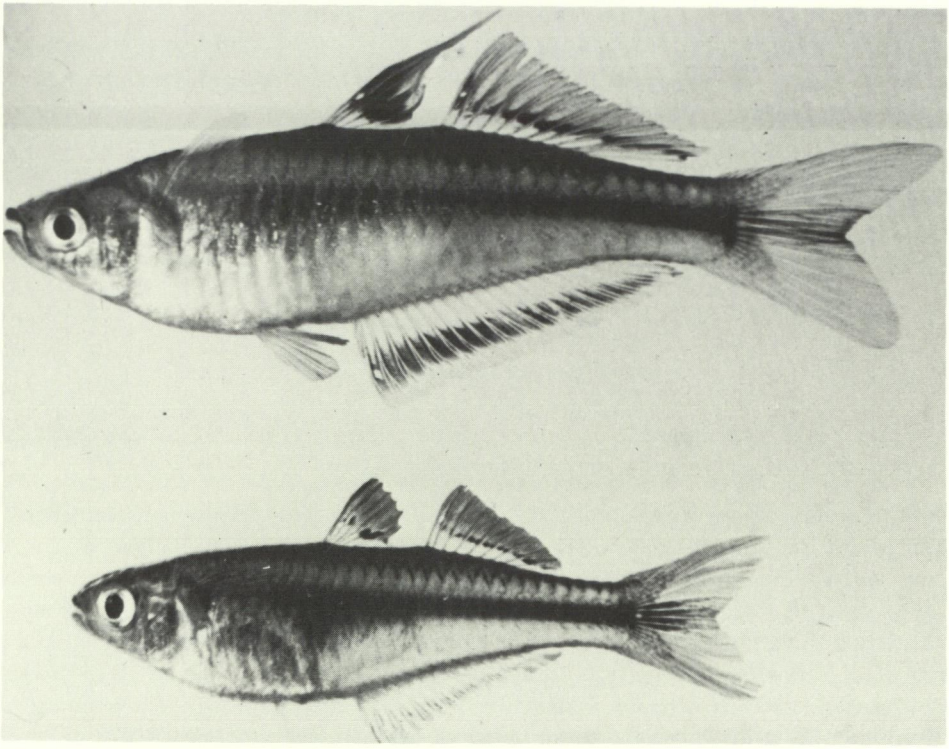

Fig. 15—*Popondetta furcatus,* male (top), 39 mm SL, and female, 33 mm SL, Auga Creek, near Popondetta, Papua New Guinea.

toothless; usually a single, rudimentary inter-dorsal pterygiophore; first dorsal fin consisting of 5 to 8 slender, flexible spines; second dorsal fin composed of 10 to 12 segmented rays; anal fin with a slender, flexible spine and 16 to 20 segmented rays; anal fin originates on anterior half of body; all soft, segmented fin rays usually branched except first ray of second dorsal fin and second ray of anal fin, branched caudal rays 9 to 12; parahypural fused to lower hypural plate; pelvic girdle without anterior projections at ventral mid-line; lateral 'wing' of pelvic girdle anchored to fourth pleural rib; dorsal head of cleithrum without posteriorly directed projection; scales cycloid with radii absent or poorly developed; horizontal rows on body at level of anal fin 6 to 8, vertical rows from upper corner of gill opening to caudal fin base 29 to 33; gill rakers on lower limb of first gill arch 8 to 10; vertebrae 32; sexual dimorphism characterised by more elongate rays in first dorsal fin and posteriormost part of second dorsal fin of males.

Remarks—This genus contains a single known species, *furcata,* which was originally described as a species of *Pseudomugil* by Nichols (1955). This species

differs from *Pseudomugil,* however, on the basis of the following characters: (1) presence of 16 to 20 soft anal rays (8 to 12 in *Pseudomugil*); (2) pelvic girdle without anterior projections at ventral mid-line (**Fig. 10H**); and (3) absence of distinct scale radii (**Fig. 12I**). *Popondetta* and *Pseudomugil* are clearly monophyletic. Their relationship is outlined in detail under the discussion section.

The genus is named after the town of Popondetta (approximately 8°45′S, 148°15′E), as the distribution of the type species is confined to the vicinity of this location. The gender is considered to be feminine.

Genus *Rhadinocentrus*
(Fig. 16)

Rhadinocentrus Regan, 1914: 280 (type species, *Rhadinocentrus ornatus* Regan, 1914, by original designation).

Diagnosis—Moderately elongate, laterally compressed body; greatest body depth 3.5 to 4.0 in standard length; premaxillaries with a more or less distinct bend between the anterior horizontal portion and lateral part; jaw teeth conical to caniniform, one or more rows extending outside of mouth; vomer and palatines toothless; inter-dorsal pterygiophores 2 or 3; first dorsal fin consisting of 3 to 5 slender, flexible spines; second dorsal fin composed of 11 to 15 segmented rays (first ray occasionally unsegmented); anal fin with a slender, flexible spine and 18 to 22 segmented rays; anal fin originates on anterior half of body; usually only last few dorsal and anal rays branched; branched caudal rays 10 to 13; parahypural fused to lower hypural plate; pelvic girdle with anterior finger-like projections at ventral mid-line; lateral 'wing' of pelvic girdle anchored to second or third pleural rib; dorsal head of cleithrum with moderately developed, posteriorly directed projection; scales cycloid with well-developed radii, horizontal rows on body at level of anal fin 8 or 9, vertical rows from upper corner of gill opening to caudal fin base 31 to 37; gill rakers on

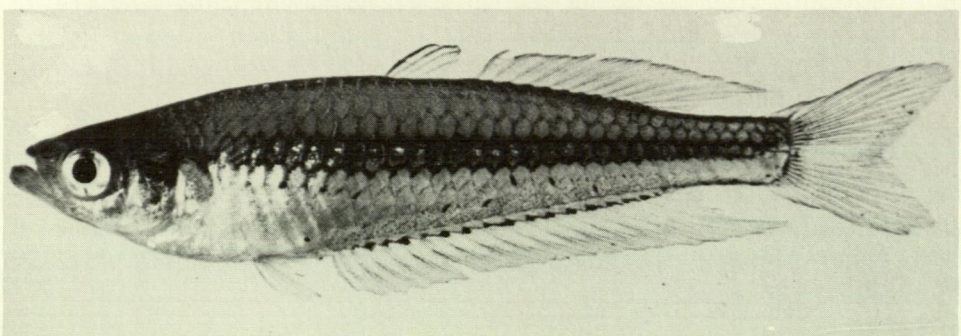

Fig. 16—*Rhadinocentrus ornatus,* male, 43 mm SL, small creek near Lake Cooroiba, S. Queensland, Australia.

lower limb of first gill arch 11 or 12; vertebrae usually 35; sexual dimorphism characterised by more elongate rays in second dorsal and anal fins of males.

Remarks—*Rhadinocentrus* contains a single species, *R. ornatus,* confined to coastal areas of northern New South Wales and southern Queensland, Australia. A second species, *rhombosomoides* was also described as a member of this genus by Nichols & Raven (1928), but the present study indicates it is deserving of separate generic status. It is placed in *Cairnsichthys,* which is herein described as new.

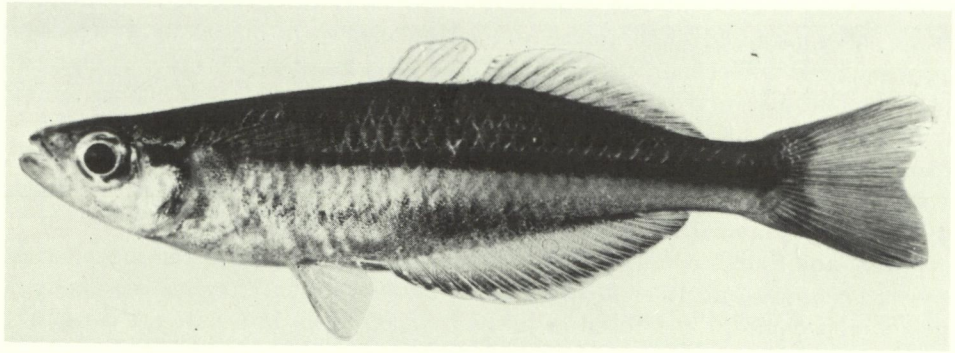

Fig. 17—*Cairnsichthys rhombosomoides,* male, 48 mm SL, Harvey Creek, near Cairns, N. Queensland, Australia.

Cairnsichthys gen. nov.
(Fig. 17)

Type species, *Rhadinocentrus rhombosomoides* Nichols & Raven, 1928: 1.

Description—A genus of Melanotaeniidae with the following combination of characters: relatively elongate, laterally compressed body; greatest body depth 3.3 to 4.4 in standard length; premaxillaries with a distinct bend between the horizontal anterior portion and lateral part; jaw teeth conical to caniniform, several rows extending outside of mouth; vomer and palatines toothless; inter-dorsal pterygiophores 2 or 3; first dorsal fin consisting of 5 or 6 slender, flexible spines, second dorsal fin composed of 14 segmented rays (except first ray sometimes unsegmented or with very weak segmentation visible only under high magnification); anal fin with a slender, flexible spine and 18 to 20 segmented rays; anal fin originates on anterior half of body; all soft, segmented rays branched except first 2 or 3 rays of second dorsal fin and first 6 or 7 rays of anal fin; branched caudal rays 13 or 14; parahypural autogenous; pelvic girdle without anterior projections at ventral mid-line; lateral 'wing' of pelvic

girdle anchored to fourth pleural rib; dorsal head of cleithrum with moderately developed posterior projection; scales cycloid with well-developed radii, horizontal rows on body at level of anal fin 10 or 11, vertical rows from upper edge of gill opening to caudal fin base 36 to 38; gill rakers on lower limb of first gill arch 10 to 12; vertebrae 36 or 37; sexual differences slight, related mainly to fin colouration.

Remarks—The type species, *rhombosomoides,* was placed in *Rhadinocentrus* by Nichols & Raven (1928), but they stated "This fish is quite unlike the type of *Rhadinocentrus, R. ornatus* Regan." Likewise, Munro (1958) questioned the inclusion of this species in *Rhadinocentrus.* The present study indicates there are several significant differences between *R. ornatus* and *'Rhadinocentrus' rhombosomoides;* therefore the latter species is placed in a separate genus. These differences include: (1) scale radii absent or weakly developed in *rhombosomoides,* and well-developed in *ornatus* (**Figs. 12G & H**); (2) no denticulations on margin of otolith of *ornatus,* and well-developed denticulations in *rhombosomoides* (**Figs. 13E & F**); (3) no anterior projections of pelvic girdle at ventral mid-line of *rhombosomoides,* and projections present in *ornatus* (**Figs. 10E & F**); (4) lateral 'wing' of pelvic girdle anchored to second or third rib in *ornatus,* and fourth rib of *rhombosomoides;* (5) usually 8 or 9 horizontal scale rows in *ornatus,* and 10 or 11 in *rhombosomoides;* (6) parahypural autogenous in *rhombosomoides* and fused to lower hypural plate in *ornatus* (**Fig. 4**); (7) vertebrae 35 in *ornatus* and 36 or 37 in *rhombosomoides;* (8) external teeth on edge of lateral portion of premaxillary low in number, arranged in a single row in *ornatus* (**Fig. 8A**), and numerous arranged in several rows in *rhombosomoides* (**Fig. 7D**); and (9) lower jaw of *ornatus* with definite protrusion (**Fig. 8A**) and that of *rhombosomoides* nearly equal with upper jaw (**Fig. 7D**).

The genus is named *Cairnsichthys* with reference to the city of Cairns, Queensland. *C. rhombosomoides,* the only known member of the genus, is confined to relatively few streams in the vicinity of Cairns. The gender is considered to be masculine.

Genus *Iriatherina*
(Fig. 18)

Iriatherina Meinken, 1974: pages not numbered (type species, *Iriatherina werneri* Meinken, 1974, by original designation).

Diagnosis—Relatively elongate, laterally compressed body; greatest body depth 4.6 to 5.6 in standard length; premaxillaries with a more or less distinct bend between the anterior horizontal portion and lateral part; jaw teeth conical to coniniform, one or more rows extending outside of mouth; vomer and palatines toothless; inter-dorsal pterygiophores 2 or 3; first dorsal fin consist-

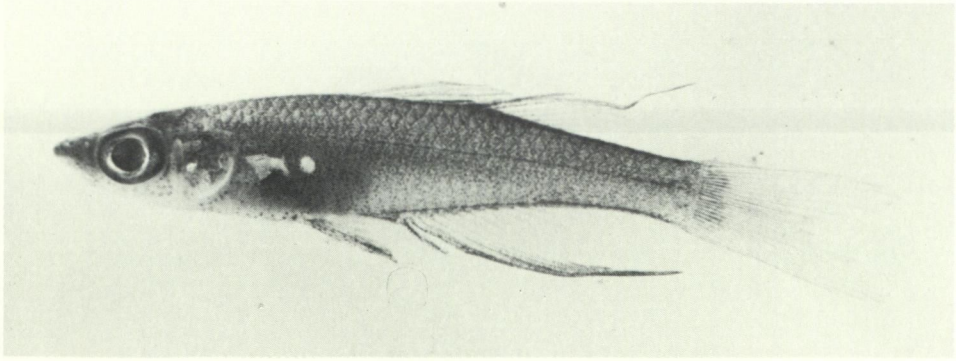

Fig. 18—*Iriatherina werneri,* male, 19 mm SL, Jardine River, Cape York Peninsula, Australia.

ing of 6 to 9 slender flexible spines; second dorsal fin with a stiff spine and 7 segemented rays; anal fin with a stiff spine and 10 to 12 segmented rays; anal fin originates on anterior half of body; only last 3 to 4 rays of second dorsal fin and last 3 to 8 rays of anal fin branched; branched caudal rays 11 to 13; parahypural fused to lower hypural plate; pelvic girdle with anterior finger-like projections at ventral mid-line; lateral 'wing' of pelvic girdle anchored to third pleural rib; dorsal head of cleithrum with moderately developed, posteriorly directed projection; scales cycloid with well-developed radii, horizontal rows on body at level of anal fin origin usually 9 or 10, vertical rows from upper corner of gill opening to caudal fin base 30 or 31; gill rakers on lower limb of first gill arch 11 to 13; vertebrae 32 or 33; sexual dimorphism characterised by extremely elongate rays at beginning of anal and second dorsal fins of males.

Remarks—*Iriatherina* contains a single species, which is confined to the tip of Cape York Peninsula, Australia and south-central New Guinea between the Merauke and Fly River systems (Allen and Hoese, in press).

Genus *Melanotaenia*
(Figs. 19 & 20)

Melanotaenia Gill, 1862: 280 (type species, *Atherina nigrans* Richardson, 1843, by original designation).

Nematocentris Peters, 1866: 516 (type species, *Nematocentris splendida* Peters, 1866, by monotypy).

Strabo Kner and Steindachner, 1867: 372 (type species, *Strabo nigrofasciatus* Kner & Steindachner, 1867, by monotypy).

Zantecla Castelnau, 1873: 88 (type species, *Zantecla pusilla* Castelnau, 1873, by monotypy).

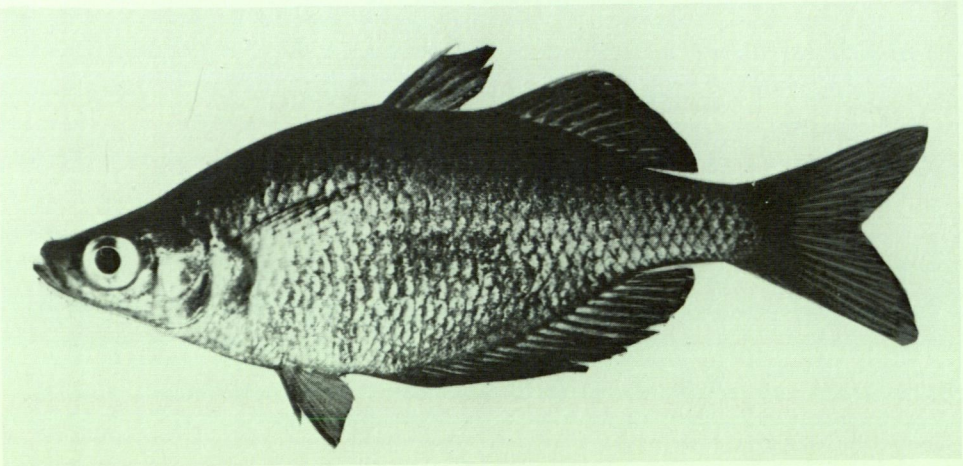

Fig. 19—*Melanotaenia goldiei,* male (top), 65 mm SL and female, 57 mm SL, Laloki River, Papua New Guinea.

Aida Castelnau, 1875: 10 (type species, *Aida inornata* Castelnau, 1875, by monotypy).

Neoatherina Castelnau, 1875: 31 (type species, *Neoatherina australis* Castelnau, 1875, by monotypy).

Aristeus Castelnau, 1878: 141 (type species, *Aristeus fitzroyensis* Castelnau, 1878, by subsequent designation of Jordan & Hubbs, 1919: 24).

Rhombatractus Gill, 1894: 709 (substitute name for *Aristeus* Castelnau, 1878, preoccupied by *Aristeus* Duvernoy, a crustacean genus).

Anisocentrus Regan, 1914: 281 (type species, *Nematocentrus rubrostriatus* Ramsay & Ogilby, 1886, by original designation).

Rhombosoma Regan, 1914: 283 (type species, *Nematocentrus novaeguineae* Ramsay & Ogilby, 1886, by subsequent designation of Jordan & Hubbs, 1919: 23).

Amneris Whitley, 1935a: 37 (type species, *Nematocentrus rubrostriatus* Ramsay & Ogilby, 1886, by original designation).

Aidapora Whitley, 1935b: 224 (type species, *Aidapora carteri* Whitley, 1935, by original designation).

Charisella Fowler, 1939: 90 (type species, *Charisella fredericki* Fowler, 1939, by original designation).

Diagnosis—Oblong, laterally compressed body; body depth generally increasing with age, particularly in males; body depth 1.9 to 4.9 in standard length; premaxillaries with an abrupt bend between the anterior horizontal portion and lateral part; jaw teeth conical to caniniform, several rows extending outside of mouth; teeth present on vomer and palatines; inter-dorsal pterygiophores 2 or 3 (rarely 4); first dorsal fin with a stout spine and 3 to 6 slender

flexible spines; second dorsal fin with a stout spine and 7 to 22 segmented rays; anal fin with a stout spine and 15 to 28 segmented rays; anal fin originates on anterior half of body; all soft segmented fin rays usually branched except first soft ray of anal and second dorsal fins; branched caudal rays usually 15; parahypural fused to lower hypural plate; pelvic girdle with well-developed finger-like projections anteriorly at ventral mid-line; lateral 'wing' of pelvic girdle anchored to third pleural rib; dorsal head of cleithrum with well-developed posteriorly directed projection; scales cycloid to slightly crenulate with well-developed radii, horizontal rows on body at level of anal fin origin 7 to 13, vertical rows from upper corner of gill opening to caudal fin base 29 to 40, gill rakers on lower limb of first gill arch usually 13 to 15; vertebrae 32 to 37; sexual dimorphism characterised by deeper body and more elongate posterior dorsal and anal fin rays in males.

Remarks—A number of mainly monotypic generic names were introduced for the members of this group between 1862 and 1894 (see synonymy above). The proliferation of names during this period was evidently due to poor descriptions in the literature and lack of communication between widely scattered researchers. The first serious revisionary attempt of the melanotaeniids was undertaken by Regan (1914) in his account of a collection of freshwater fishes from Dutch New Guinea. He recognised seven genera, including *Melanotaenia, Anisocentrus,* and *Rhombosoma.* Regan stated that the latter two genera closely resembled *Melanotaenia,* but differed in the degree of expansion of the posterior section of the premaxillary and the disposition of the jaw teeth (*Anisocentrus* with outer row teeth of lower jaw enlarged and separated from inner band by a space; *Rhombosoma* without enlarged outer row teeth; *Melanotaenia* with enlarged outer row teeth, but without space between inner band). This separation was accepted by Weber & de Beaufort (1922), although with some modification. They replaced Regan's *Rhombosoma* with the name *Rhombatractus* which had been proposed by Gill (1894) as a substitute name for *Aristeus* Castelnau. Weber and de Beaufort separated the two genera on the basis of the dentition on the lips outside the mouth (present in *Rhombatractus,* absent in *Melanotaenia*) and the extent of the mouth opening (reaching level of eye in *Rhombatractus* and not reaching in *Melanotaenia*). They did not recognise Regan's *Anisocentrus,* stating that Ramsay & Ogilby's (1886) description of *Nematocentrus rubrostriatus,* the type species, was insufficient for determining its correct generic position.

Munro (1964), likewise recognised two genera based principally on dentition. He maintained *Melanotaenia* for species having thick lips and a dense patch of teeth on the lower jaw which is separated by an edentulous suture at the symphysis (**Figs. 9, A & D**). This group included species placed in *Rhombatractus* by Weber and de Beaufort, with Munro basing this nomenclatural change on an examination of the type of *Atherina nigrans* Richardson, the type species for *Melanotaenia.* Munro ressurected *Nematocentrus* Peters for species

having thin lips, lacking the edentulous median suture on the lower jaw, and possessing an outer row of enlarged teeth on the lower jaw separated from the inner teeth by a space (**Figs. 9B, C, E & F**). This group corresponds with *Anisocentrus* Regan and *Melanotaenia* (non Gill) of Weber & de Beaufort (1922). More recently, Allen (1978) placed *Nematocentrus* in the synonymy of *Melanotaenia,* noting that the dentition arrangement was variable with specimens frequently possessing intermediate patterns or more rarely with both patterns present in a single species. This character was also found to be unreliable in juvenile and sub-adult specimens. In addition, no other differences were detected to support the separation of two genera.

The monotypic *Amneris* and *Aidapora* described by Whitley (1935a & b) were based on differences in the size of mouth, dentition, body shape, and colour. However, the species involved do not differ significantly from other *Melanotaenia.*

Four of Fowler's five paratypes of *Charisella* were examined and I have determined these as small (18-22 mm SL) juveniles of *Melanotaenia goldiei.* They agree well in every respect with similar sized specimens of *M. goldiei* recently collected in the Port Moresby District.

Melanotaenia is the largest genus in the family containing approximately 22 known species, which are distributed over a wide area of Australia and New Guinea, including the Aru Islands and Waigeo Island.

Genus *Glossolepis*
(Fig. 20)

Glossolepis Weber, 1908: 241 (type species, *Glossolepis incisus* Weber, by monotypy).

Diagnosis—Oblong, laterally compressed body; body depth generally increasing with age, particularly in males; body depth 1.9 to 3.1 in standard length; premaxillaries with an abrupt bend between the anterior horizontal portion and lateral part; jaw teeth conical to caniniform, with curved tips, several rows extending outside of mouth; a single row of enlarged teeth on exposed lateral edge of premaxillary; teeth present on vomer and palatines; inter-dorsal pterygiophores 2 or 3 (rarely 4); first dorsal fin with a stout spine and 4 to 6 slender flexible spines; second dorsal fin with a stout spine and 9 to 12 segmented rays; anal fin with a stout spine and 18 to 23 segmented rays; anal fin originates on anterior half of body; all soft segmented fin rays usually branched except first soft ray of anal and second dorsal fins; branched caudal rays usually 15; parahypural fused to lower hypural plate; pelvic girdle with well-developed finger-like projections anteriorly at ventral mid-line; lateral 'wing' of pelvic girdle anchored to third pleural rib; dorsal head of cleithrum with well-developed posteriorly directed projection; scales deeply crenulate with well-developed

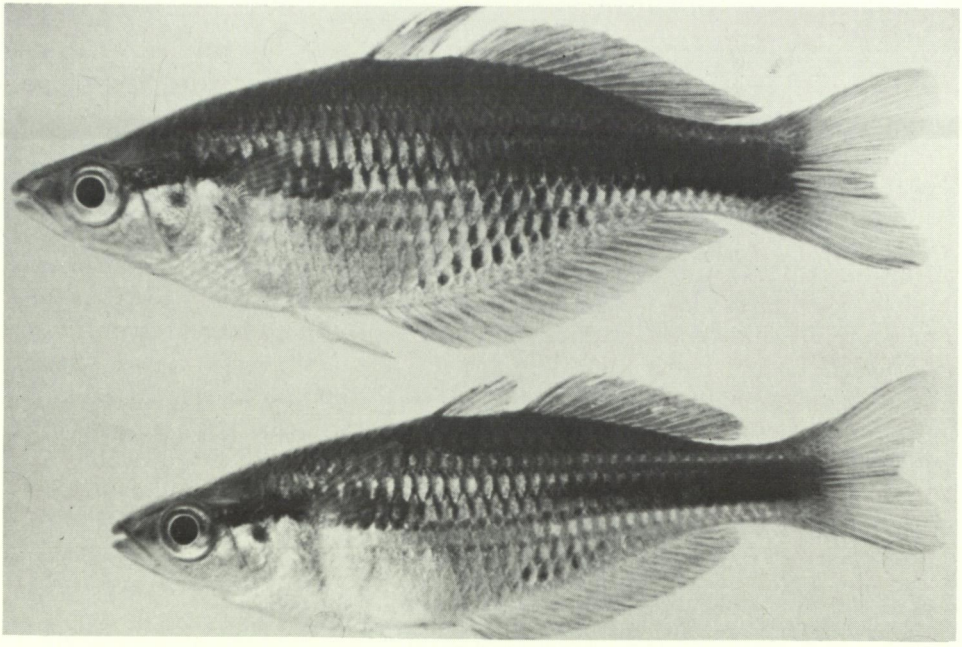

Fig. 20—*Glossolepis wanamensis*, male, 70 mm SL, Lake Wanam, near Lae, Papua New Guinea.

radii, horizontal rows on body at level of anal fin origin 12 to 17, vertical rows from upper corner of gill opening to caudal fin base 36 to 60, gill rakers on lower limb of first gill arch usually 19 to 32; vertebrae 27 or 28; sexual dimorphism characterised by deeper body and more elongate middle dorsal and anal fin rays in males.

Remarks—*Glossolepis* appears to be a specialised offshot of *Melanotaenia*. The two genera are similar in overall morphology, but *Glossolepis* differs by having distinctly crenulate scale margins, the middle dorsal and anal rays elongated in males instead of the posterior rays, a distinct head profile, particularly in adult males, characterised by a steep forehead and pointed snout, and the lateral wing of the premaxillary typically with a single row of enlarged teeth which are exposed when the mouth is closed.

Weber & de Beaufort (1922) separated this genus from other melanotaeniids on the basis of an irregular scale arrangement (i.e., scales not in uniform parallel rows) and the smaller size and crenulations of the scales. At that time *G. incisus* Weber was the only known member of the genus. Three additional species are now included and the irregular small scales are diagnostic only from *G. incisus* (see Allen & Kailola 1979).

The four known species are restricted to northern New Guinea between the Markham and Mamberamo River systems.

Genus *Chilatherina*
(Fig. 21)

Chilatherina Regan, 1914: 282 (type species, *Rhombatractus fasciatus* Weber, 1913, by subsequent designation of Jordon and Hubbs, 1919: 22).
Centratherina Regan, 1914: 283 (type species, *Rhombatractus crassispinosus* Weber, 1913, by original designation).

Diagnosis—Oblong, laterally compressed body; body depth generally increasing with age, particularly in males; greatest body depth 2.3 to 5.4 in standard length; premaxillaries more or less straight, without abrupt bend between the anterior horizontal portion and lateral part; jaw teeth conical to caniniform, several rows extending outside of mouth; teeth present on vomer and palatines; inter-dorsal pterygiophores 2 or 3; first dorsal fin with a stout spine (rarely 2 stout spines) and 2 to 5 slender flexible spines; second dorsal fin with a stout spine and 8 to 17 segmented rays; anal fin with a stout spine and 20 to 30 segmented rays; anal fin originates on anterior half of body; all soft segmented fin rays usually branched except first soft ray of anal and second

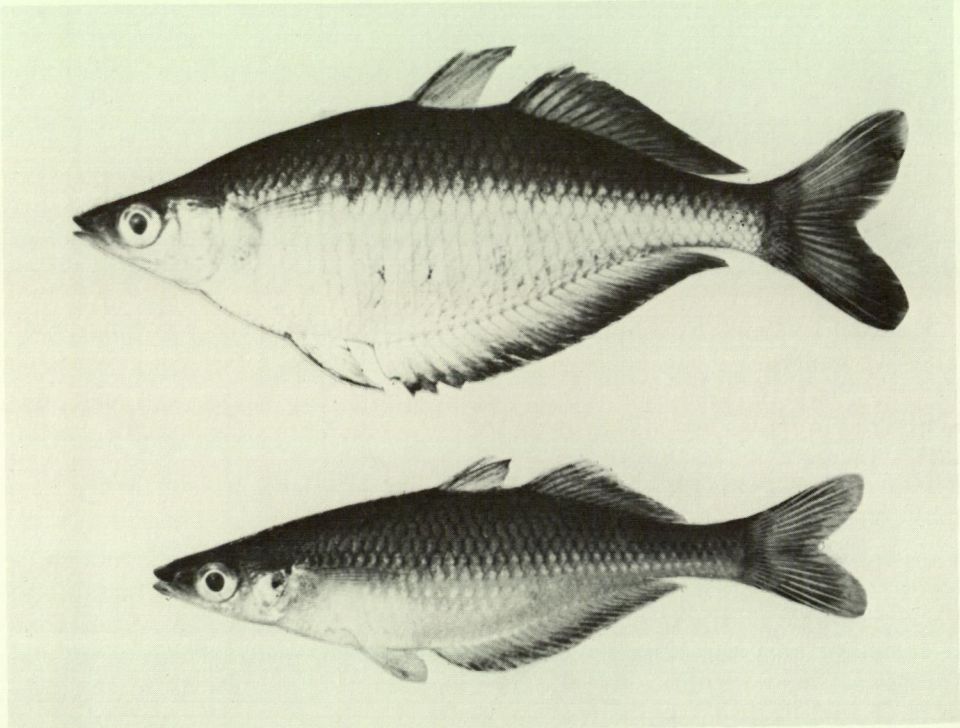

Fig. 21—*Chilatherina lorentzi,* male (top), 78 mm SL and female, 65 mm SL, Lake Wanam, near Lae, Papua New Guinea.

dorsal fin; branched caudal rays usually 15; parahypural fused to lower hypural plate; pelvic girdle with well-developed finger-like projections anteriorly at ventral mid-line; lateral 'wing' of pelvic girdle anchored to third pleural rib; head of cleithrum with well-developed posteriorly directed projection; scales cycloid to slightly crenulate with well-developed radii, horizontal

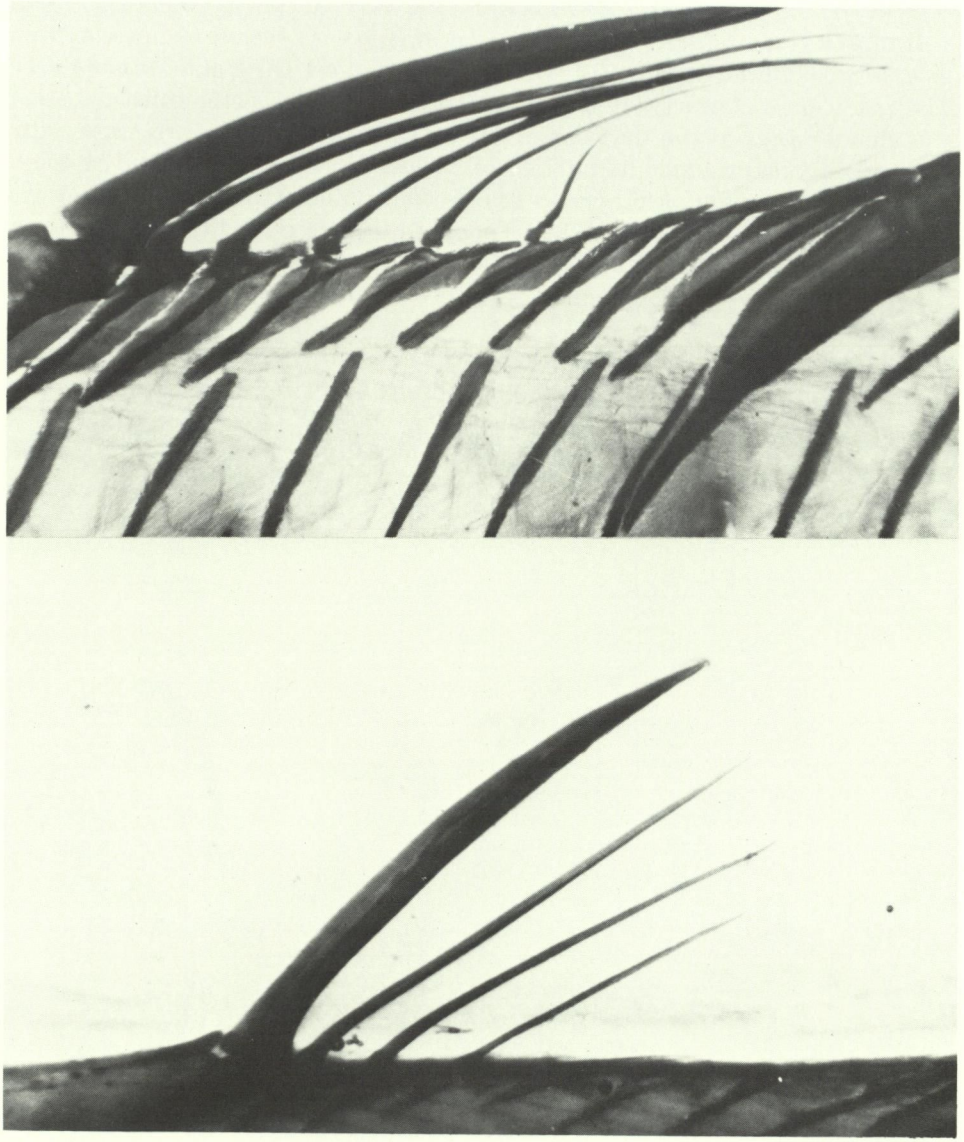

Fig. 22—First dorsal fin of *Chilatherina:* (top) *C. sentaniensis,* 64 mm SL; (bottom) *C. crassispinosa,* 41 mm SL.

rows on body at level of anal fin origin 10 to 15, vertical rows from upper corner of gill opening to caudal fin base 34 to 44; gill rakers on lower limb of first gill arch usually 13 or 14; vertebrae usually 37 or 38; sexual dimorphism characterised mainly by deeper body of males, but in some species males have the second dorsal and anal fin outline more pointed posteriorly and the posteriormost rays of the second dorsal fin are more elongate.

Remarks—*Chilatherina* and *Centratherina* have previously been recognised as distinct genera (Regan 1914; Weber & de Beaufort 1922; and Munro 1967). The traditional character used to separate these groups is the constitution of the slender rays of the first dorsal fin; in *Chilatherina* they are supposedly segmented, and unsegmented in *Centratherina*. I have examined a large series of both forms and find no difference in the composition of these spines. They are invariably unsegmented (**Fig. 22**). Therefore, I have placed *Centratherina* in the synonymy of *Chilatherina*. Munro (1964), after examining the spination of several *Centratherina* commented "possibly *Centratherina* cannot be retained as a separate genus."

This genus is separable from the closely related *Melanotaenia* on the basis of the shape of the premaxillary bone. It generally lacks the abrupt bend between

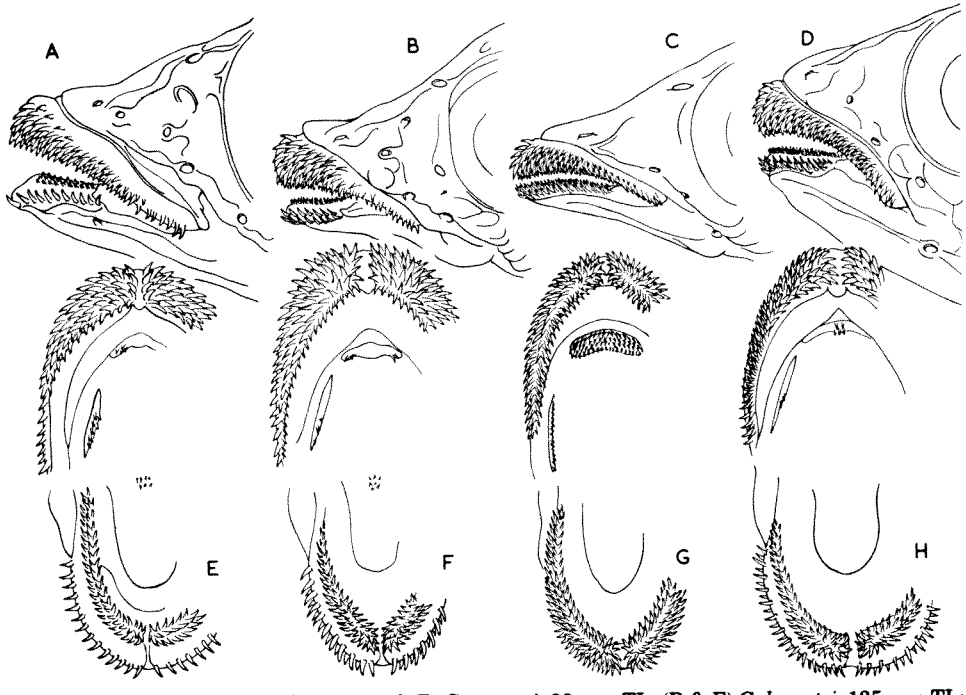

Fig. 23—Dentition of *Chilatherina:* (A & E) *C. campsi,* 88 mm TL; (B & F) *C. lorentzi,* 135 mm TL; (C & G) *C. sentaniensis,* 95 mm TL; (D & H) *C. crassispinosa,* 100 mm TL (drawings from Munro, 1964).

the anterior horizontal portion and the lateral part (**Figs. 23, A-D**). However, the lip swelling at the tip of the snout frequently conveys the impression of a bent premaxillary (**Figs. 7A & B**). The difference in this feature with relation to the various genera is not readily apparent in **Fig. 6**, because of the two-dimensional restrictions of the drawings.

The genus contains four known species which are confined to northern New Guinea.

DISCUSSION

Rosen (1974) discussed the taxonomic position of the atherinoid fishes and their relatives. He introduced a new ordinal name, Atheriniformes, which encompasses three suborders, Exocoetoidei, Cyprinodontoidei, and Atherinoidei. The latter group contains two superfamilies including Atherinoidea which is comprised of Melanotaeniidae, Atherinidae, and Isonidae, the latter a small group of specialised marine fishes mainly adapted to shallow coastal areas of heavy surge. These families are separable from the superfamily Phallostethidae on the basis of the following characters: pelvic fins abdominal, subabdominal, or thoracic in position, not modified into clasping organ; first pleural rib on third vertebra; adductor arcus paltini muscle restricted to posterior part of orbit. On the basis of these characters and other anatomical features mentioned by Rosen the melanotaeniids and atherinids are considered to be monophyletic sister groups. It is probable that the melanotaeniids evolved from a marine or estuarine atherinid-like ancestor.

A phylogenetic analysis of the genera of Melanotaeniidae is presented in **Fig. 24.** *Pseudomugil* and *Popondetta* are considered to be sister groups on the basis of several similarities. Both genera have the pectoral fins inserted in a peculiar fashion which results in these fins extending well above the dorsal profile of the body during the "up-stroke" movement while swimming. Although reduction characters are not necessarily indicative of a common phylogeny, these genera are unique among the melanotaeniids in having lost the inter-dorsal pterygiophores (sometimes represented by a single, small rudiment), and in possessing a rounded dorsal head on the cleithrum without a posterior projection (**Figs. 11D & E**). Several other features are shared by these genera, which are found in only a few other members of the family including: (1) lateral 'wing' of pelvic girdle attached to fourth pleural rib (present only in *Cairnsichthys*); (2) eight or less horizontal scale rows (only *Rhadinocentrus* has so few); (3) 27 to 32 vertebrae (only *Iriatherina* has a similar count); and (4) all fin spines weakly developed (this feature shared also by *Cairnsichthys* and *Rhadinocentrus*). In addition, the shape of the premaxillary is very similar (**Figs. 6, F & G**).

Although some of these characters or character states represent apparent

specialisations, the majority appear to be plesiomorphic. Thus, these genera are considered to be the most primitive members of the family. It is noteworthy that some *Pseudomugil* populations are estuarine dwellers which parallels the mode of life which is hypothesized for the ancestral melanotaeniid stock.

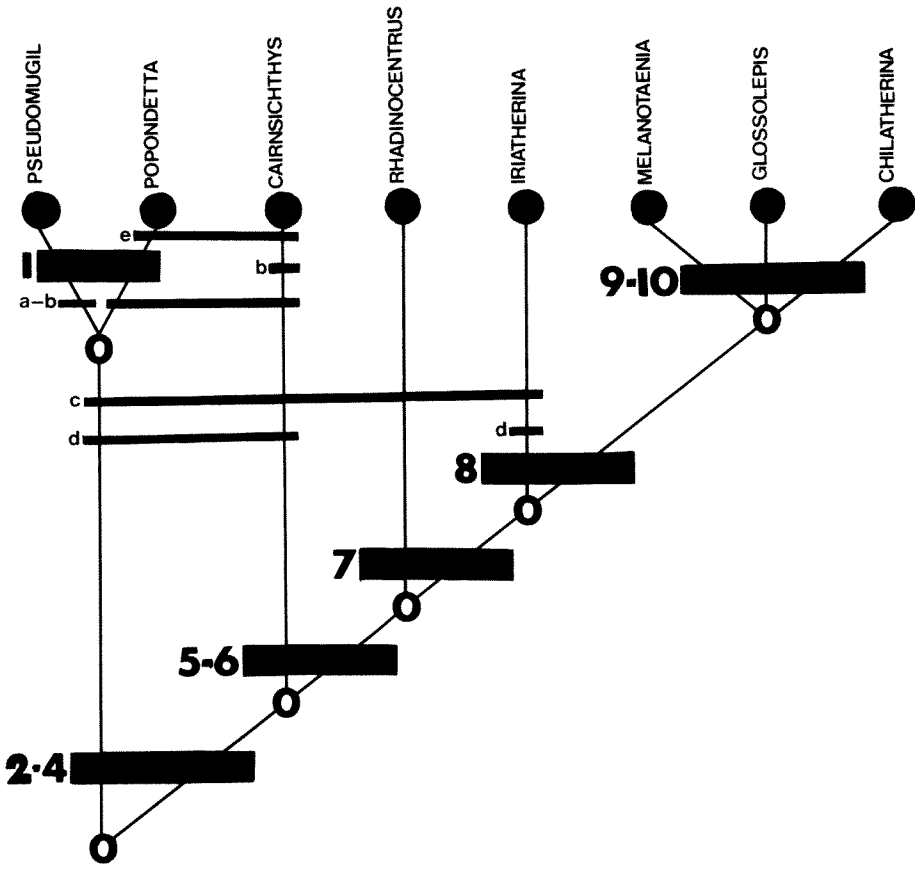

Fig. 24—Phylogenetic analysis of the genera of melanotaeniidae. Shaded squares represent the following apomorphic character expressions: (1) pectoral fins extend well above the dorsal profile while swimming; (2) modified inter-pelvic area (Fig. 2B); (3) distinctive premaxillary shape with a few to many teeth on outside of lips; (4) characteristic sexual dimorphism usually featuring elongated fin rays in males and colour intensity differences; (5) 2 or 3 (rarely 4) inter-dorsal pterygiophores; (6) horizontal scale rows usually in excess of 9 (i.e., greater overall scale density); (7) lateral "wing" of pelvic girdle anchored to 3rd pleural rib; (8) strong spine at beginning of second dorsal fin; (9) strong spines at beginning of first dorsal, anal, and pelvic fins; (10) teeth on vomer and palatines. Hypothesized convergent characters are indicated by thin horizontal lines: (a) anal fin originates on posterior half of body; (b) lower hypural plate autogenous; (c) loss or some reduction of posterior process of cleithrum; (d) reduced vertebral counts, usually less than 35 total elements; (e) lack or weakness of scale radii.

However, *Pseudomugil* retains the atherinid-like position of the anal fin (i.e., on posterior half of body).

The remaining five genera are hypothesized to be a monophyletic assemblage based on the common possession of 2 or 3 (rarely 4) inter-dorsal pterygiophores, a condition considered to be apomorphic for melanotaeniids. In addition, all except *Cairnsichthys* are synyapomorphic with regards to the lateral muscular attachment of the pelvic girdle to the third pleural rib. *Cairnsichthys, Rhadinocentrus,* and *Iriatherina* represent a complex of phyletic lines considered to represent an intermediate stage of specialisation. They retain certain primitive features such as the lack of stout, well-developed fin spines and relatively low gill raker counts. In addition, the posterior process on the cleithral head (**Figs. 11, B & C**) is intermediate in shape between *Popondetta* and *Pseudomugil,* which lack the process, and *Melanotaenia, Glossolepis* and *Chilatherina* which have a well-developed process.

Melanotaenia, Glossolepis, and *Chilatherina* share many morphological features and are hypothesized to be monophyletic sister groups. The most prominent synapomorphy in these genera is the presence of an enlarged, stout spine at the beginning of the pelvic, anal, and two dorsal fins, and also the presence of conical teeth on the vomer and palatines (**Fig. 9**). They also have the highest gill raker, branched caudal ray, and vertebral counts for the family. In addition, the development of external jaw teeth (**Figs. 7, A-C; 9, A-C; and 24, A-D**) is most strongly manifested in this trio. On the basis of these features they are considered to be the most advanced members of the family.

Quirichthys stramineus (Whitley) is a small atherinoid fish which has been collected from the Ord, Katherine, and Gregory River systems of northern Australia. It has been variously shuffled between the Atherinidae and Telmatherinidae (considered by the author as a subfamily of Atherinidae confined to fresh waters of the Celebes). Some workers whom I have recently communicated with suggested it may, in fact, belong to the Melanotaeniidae, primarily on the basis of the similar premaxillary dentition (**Fig. 6l**). The present study indicates that it is an atherinid, possessing features typical of the Australian members of the family, including a relatively long median ascending process on the premaxillary (**Fig. 6l**), an autogenous parahypural (**Fig. 5,** lower), lateral muscular attachment of pelvic girdle to the fourth rib, and lack of the inter-pelvic modification (**Figs. 1-2**).

Convergent characters—Several character states appear to be incongruous with the proposed phylogeny and therefore represent probable examples of convergence within the family. These include the rearward position of the anal fin in *Pseudomugil,* an autogenous lower hypural plate in *Pseudomugil* and *Cairnsichthys,* the lack or weakness of scale radii in *Popondetta* and *Cairnsichthys,* the loss or reduction of the posterior process of the cleithrum in all genera except *Pseudomugil* and *Popondetta,* and a trend towards reduced

vertebral counts in the groups which are here considered to be most primitive. These convergent character states are summarised in **Fig. 24** (horizontal lines **a-e**).

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LIST OF NOMINAL SPECIES OF MELANOTAENIIDAE

The nominal species of melanotaeniids are listed alphabetically (by species) below. Each species name is followed by the author(s) name, year of publication, page number, and locality (Aru = Aru Islands; Aus. = Australia; N.N.G. = northern New Guinea; S.N.G. = southern New Guinea; Wag. = Waigeo). The right column contains the present allocation. Complete references are given at the end of the paper.

Species	Present allocation
Pseudomugil signatus affinis Whitley, 1935b: 228 (Aus.)	*Pseudomugil signifer*
Rhombatractus affinis Weber, 1908: 234 (N.N.G.)	*Melanotaenia affinis*
Melanotaenia ajamaruensis Allen & Cross, in press (S.N.G.)	*Melanotaenia ajamaruensis*
Rhombatractus archboldi Nichols & Raven, 1934: 1 (S.N.G.)	*Melanotaenia goldiei*
Neoatherina australis Castelnau, 1875: 32 (Aus.)	*Melanotaenia splendida australis*
Chilatherina axelrodi Allen, 1980: 48 (N.N.G.)	*Chilatherina axelrodi*
Melanotaenis boesemani Allen & Cross, in press (S.N.G.)	*Melanotaenia boesemani*
Centratherina bulolo Whitley, 1938: 227 (N.N.G.)	*Chilatherina crassispinosa*
Anisocentrus campsi Whitley, 1956: 26 (N.N.G.)	*Chilatherina campsi*
Aidapora carteri Whitley, 1935b: 224 (Aus.)	*Melanotaenia splendida inornata*
Rhombatractus catherinae de Beaufort, 1910: 250 (Wag.)	*Melanotaenia catherinae*
Aristeus cavifrons Macleay, 1882: 69 (Aus.)	*Melanotaenia splendida inornata*
Rhombatractus crassispinosa Weber, 1913: 567 (N.N.G.)	*Chilatherina crassispinosa*
Atherinichthys duboulayi Castelnau, 1878: 143 (Aus.)	*Melanotaenia fluviatilis*
Melanotaenia dumasi Weber, 1908: 240 (S.N.G.)	*Melanotaenia goldiei*
Melanotaenia exquisita Allen, 1978: 97 (Aus.)	*Melanotaenia exquisita*

Chilatherina fasciata Regan, 1914: 282 (N.N.G.)	*Chilatherina lorentzi*
Aristeus fitzroyensis Castelnau, 1878: 141 (Aus.)	*Melanotaenia splendida splendida*
Aristeus fluviatilis Castelnau, 1878, 141 (Aus.)	*Melanotaenia fluviatilis*
Charisella fredericki Fowler, 1939: 90 (S.N.G.)	*Melanotaenia goldiei*
Pseudomugil furcatus Nichols, 1955: 2 (N.N.G.)	*Popondetta furcatus*
Pseudomugil gertrudae Weber, 1911: 23 (Aru)	*Pseudomugil gertrudae*
Aristeus goldiei Macleay, 1883: 269 (S.N.G.)	*Melanotaenia goldiei*
Melanotaenia gracilis Allen, 1978: 98 (Aus.)	*Melanotaenia gracilis*
Glossolepis incisus Weber, 1908: 241 (N.N.G.)	*Glossolepis incisus*
Pseudomugil inconspicuus Roberts, 1978: 53 (S.N.G.)	*Pseudomugil inconspicuus*
Aida inornata Castelnau, 1875: 10 (Aus.)	*Melanotaenia splendida inornata*
Melanotaenia japenensis Allen & Cross, in press (N.N.G.)	*Melanotaenia japenensis*
Melanotaenia kabia Herre, 1935: 397 (N.N.G.)	*Glossolepis multisquamatus*
Rhombatractus kochii Weber, 1908: 237 (S.N.G.)	*Melanotaenia goldiei*
Melanotaenia lacustris Munro, 1964: 159 (S.N.G.)	*Melanotaenia lacustris*
Aristeus lineatus Macleay, 1881: 626 (Aus.)	*Melanotaenia fluviatilis*
Rhombatractus lorentzii Weber, 1908: 236 (N.N.G.)	*Chilatherina lorentzi*
Aristeus loriae Perugia, 1894: 549 (S.N.G.)	*Melanotaenia splendida rubrostriata*
Melanotaenia maculata Wber, 1908: 239 (S.N.G.)	*Melanotaenia splendida rubrostriata*
Melanotaenia maccullochi Ogilby, 1915: 118 (Aus.)	*Melanotaenia maccullochi*
Melanotaenia monticola Allen, in press (S.N.G.)	*Melanotaenia monticola*
Melanotaenia multisquamata Weber & de Beaufort, 1922: 290 (S.N.G.)	*Glossolepis multisquamatus*

Melanotaenia neglecta Rendahl, 1922: 179 (Aus.)	*Melanotaenia fluviatilis*
Atherina nigrans Richardson, 1843: 180 (Aus.)	*Melanotaenia nigrans*
Strabo nigrofasciatus Kner & Steindachner, 1867: 373 (Aus.)	*Melanotaenia splendida splendida*
Nematocentrus novaeguineae Ramsay & Ogilby, 1886: 13 (S.N.G.)	*Melanotaenia goldiei*
Pseudomugil novaeguineae Weber, 1908: 233 (S.N.G.)	*Pseudomugil novaeguineae*
Melanotaenia ogilbyi Weber, 1910: 230 (S.N.G.)	*Melanotaenia ogilbyi*
Melanotaenia oktediensis Allen & Cross, in press (S.N.G.)	*Melanotaenia oktediensis*
Rhadinocentrus ornatus Regan, 1914: 280 (Aus.)	*Rhadinocentrus ornatus*
Pseudomugil paludicola Allen & Moore, in press (S.N.G.)	*Pseudomugil paludicola*
Melanotaenia papuae Allen, in press (S.N.G.)	*Melanotaenia papuae*
Melanotaenia parkinsoni Allen, in press (S.N.G.)	*Melanotaenia parkinsoni*
Rhombatractus patoti Weber, 1907, 403 (Aru)	*Melanotaenia splendida rubrostriata*
Aristeus perporosus De Vis, 1884: 694 (Aus.)	*Melanotaenia fluviatilis*
Rhombatractus praecox Weber & de Beaufort, 1922: 298 (N.N.G.)	*Melanotaenia praecox*
Glossolepis pseudoincisus Allen & Cross, in press (N.N.G.)	*Glossolepis pseudoincisus*
Zantecla pusilla Castelnau, 1873: 88 (Aus.)	*Melanotaenia nigrans*
Melanotaenia pygmaea Allen, 1978: 99 (Aus.)	*Melanotaenia pygmaea*
Melanotaenia rosacea Herre, 1935: 398 (N.N.G.)	*Glossolepis multisquamatus*
Nematocentris rubrostriatus Ramsay & Ogilby, 1886: 14 (S.N.G.)	*Melanotaenia splendida rubrostriata*
Aristeus rufescens Macleay, 1881: 625 (Aus.)	*melanotaenia splendida splendida*
Rhadinocentrus rhombosomoides Nichols & Raven, 1928: 1 (Aus.)	*Cairnsichthys rhombosomoides*
Rhombatractus senckenbergianus Weber, 1911: 25 (Aru)	*Melanotaenia goldiei*

Rhombatractus sentaniensis Weber, 1908: 235 (N.N.G.)	*Chilatherina sentaniensis*
Rhombosoma sepikensis Herre, 1935: 400 (N.N.G.)	*Melanotaenia affinis*
Nematocentris sexlineatus Munro, 1964: 162 (S.N.G.)	*Melanotaenia sexlineata*
Atherina signata Gıunther, 1867: 64 (Aus.)	*Pseudomugil signifer*
Pseudomugil signifer Kner, 1865: 275 (Aus.)	*Pseudomugil signifer*
Melanotaenia solata Taylor, 1964: 129 (Aus.)	*Melanotaenia splendida australis*
Nematocentris splendida Peters, 1866: 516 (Aus.)	*melanotaenia splendida splendida*
Nematocentris tatei Zietz, 1896: 178 (Aus.)	*Melanotaenia splendida tatei*
Pseudomugil tenellus Taylor, 1964: 132 (Aus.)	*Psuedomugil tenellus*
Centratherina tenuis Nichols, 1956: 1 (N.N.G.)	*Chilatherina campsi*
Rhombosoma trifasciata Rendahl, 1922: 182 (Aus.)	*Melanotaenia trifasciata*
Rhombatractus vanheurni Weber & de Beaufort, 1922: 299 (N.N.G.)	*Melanotaenia vanheurni*
Glossolepis wanamensis Allen & Kailola, 1979: 40 (N.N.G.)	*Glossolepis wanamensis*
Rhombatractus weberi Regan, 1908: 155 (S.N.G.)	*Melanotaenia goldiei*
Iriatherina werneri Meinken, 1974: (S.N.G.)	*Iriatherina werneri*
Nematocentris winneckei Zietz, 1896: 179 (Aus.)	*Melanotaenia splendida tatei*

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