Ichthyol. Explor. Freshwaters, Vol. 8, No. 2, pp. 107-150, 30 figs., 1 tab., October 1997
© 1997 by Verlag Dr. Friedrich Pfeil, München, FRG – ISSN 0936-9902

Descriptive anatomy of *Cairnsichthys rhombosomoides* and *Iriatherina werneri* (Teleostei: Atheriniformes), and a phylogenetic analysis of Melanotaeniidae

Aarn* and Walter Ivantsoff*

The comparative osteology of *Cairnsichthys rhombosomoides* and *Iriatherina werneri* is described in detail. Phylogenetic analysis of Melanotaeniidae was conducted with a computer program examining the distribution of 46 characters over 22 taxa. Melanotaeniidae is monophyletic and comprises 8 genera, *Bedotia* and *Rheocles* endemic to Madagascar, and 6 genera from Australia and New Guinea. Atheriniformes is considered to be monophyletic and comprise 8 families, including Telmatherinidae, of Sulawesi, and Pseudomugilidae, of Australia and New Guinea. Within Melanotaeniidae, the hierarchy of relationships is: (*Iriatherina*, (((*Bedotia*, *Rheocles*), (*Cairnsichthys*, *Rhadinocentrus*)), (*Chilatherina*/*Glossolepis*/*Melanotaenia*))). The analysis did not resolve the latter trichotomy. It is hypothesised that the disparate distribution of the family reflects recent evolution from cosmopolitan marine Atheriniformes.

Historical introduction

Richardson (1843) described *Atherina nigrans* from Port Essington (Darwin, Northern Territory 12°27'S 130°50'E) with a 'peculiar angular form of the mouth'. Gill (1862) established *Melanotaenia* for this fish, signalling the possible ocurrence of a large assemblage of fish, unknown to European naturalists, in the infant British colonies of present-day Australia.

Kner (1866; cited in Derijst, 1989) described *Pseudomugil signifer*, presumably from Sydney, New South Wales (33°53'S 151°13'E) and subsequently established Pseudomugilidae (Kner, 1867; cited in Derijst, 1989).

Gill (1894) established Melanotaeniinae, comprising *Melanotaenia* and *Rhombatractus* (=*Melanotaenia*; Regan, 1914). The subfamily was defined with a 'strong spine in the dorsal fin', in contradistinction to other atherinoids; forward placement of the ventral fins, anus and anal fin origin; and presence in the freshwaters of the 'Australasian realm'.

Ogilby (1896) considered that 20 species in 5 nominal genera, gathered from present-day Australia and New Guinea, were sufficiently different from atherinids to warrant the establishment of a new family. Melanotaeniidae was diagnosed on the basis of examination of external and oral morphology of *Rhombatractus*, and published descriptions of the other 4 genera.

Boulenger (1897) described *Telmatherina celebensis*, from Sulawesi, with bilateral compression and decreased vertebral count, lacking the lateral

---

* School of Biological Sciences, Macquarie University 2109, Australia.

band characteristic of atherinids. Munro (1958) established (without diagnosis) Telmatherinidae, including *Quiris stramineus* Whitley (=*Craterocephalus stramineus*; Crowley & Ivantsoff, 1992) of northern Australia. Subsequently, Munro (1967) defined Telmatherinidae, based on an examination of *Charisella fredericki* Fowler (=*Melanotaenia goldei* Macleay; Allen, 1980).

Weber (1908) considered Melanotaeniinae to be an atherinid subfamily. Weber drew attention to the (morphologic and geographic) proximity of *Telmatherina*, while noting differences in dorsal fin elements and position. Weber provided revised definitions of *Pseudomugil*, *Rhombatractus* and *Melanotaenia*, and established *Glossolepis* on the basis of differences in jaw structure, scale shape and organisation, and gill raker density.

Regan (1914) revised Melanotaeniinae, synonymising 14 species (in 7 genera) with *M. nigrans* while excluding *Pseudomugil* (suggesting a greater affinity with *Telmatherina*) to 'form a natural group'. Regan noted allometric growth and referred to dentition, fins, squamation and jaw symmetry in establishing 5 new genera: *Chilatherina* (2 species) and *Centratherina* (=*Chilatherina*; Allen, 1980) with the 'lower jaw inferior', *Anisocentrus* and *Rhombosoma* (both =*Melanotaenia*; Allen, 1980) and describing *Rhadinocentrus ornatus* with 'jaws equal anteriorly' and 'all the rays slender and flexible' in the first dorsal fin. Regan considered melanotaeniids were not sufficiently distinct (from atherinids) to warrant subfamilial status.

Previously, Regan (1903) described *Bedotia madagascariensis* from Madagascar with a less-protractile mouth, notched premaxillaries, forward-placed pelvic fins and a truncate caudal fin (compared to other atherinds). *Rheocles* Jordan and Hubbs was subsequently established (Jordan & Hubbs, 1919) for *Eleotris sikorae* Sauvage, described as a 'robust' fish bearing few, compact gill rakers.

Jordan & Hubbs (1919) remarked on the resemblances between the Madagascan genera *Bedotia* and *Rheocles*, and the Australonesian melanotaeniines (the 3 groups being treated as subfamilies). Jordan & Hubbs maintained *Pseudomugil* and *Telmatherina* in Melanotaeniinae.

De Beaufort (1922) detailed melanotaeniine anatomy, suggesting that bilateral compression of the body necessitated repositioning of the second dorsal and anal fins craniad, and the pelvics ventrad, to maintain equilibrium. The absence of a distinct premaxillary dorsal process ('proximal peduncle') was suggested to restrict jaw motion to pivotting about the attachment at (the bend of) the premaxilla. While de Beaufort noted similarities (body-form and fins) with *Telmatherina* and *Bedotia*, the 'most essential feature' of Melanotaeniinae was considered to be oral anatomy, and it was speculated that feeding usually entailed scraping the upper jaw along fixed objects.

Gosline (1962) attempted to identify interrelationships amongst 'percesocine' fishes but expected that *Pranesus* (=*Atherinomorus*), used in that study, would differ from *Melanotaenia*. Rosen (1964) attempted a novel alignment in creating the order Atheriniformes. The definition of the limits of Atheriniformes has provided the impetus for substantial research during the past 30 years. Rosen listed 23 anatomical characters, and remarked on reproductive similarities (sexual dimorphism and egg morphology), of the group. Subfamilies were not listed in Rosen's manuscript. Rosen referred to Jordan & Hubbs (1919) on the geographic distribution of genera, apparently including *Bedotia*, *Rheocles* and *Pseudomugil* in Atherinidae, distinct from Melanotaeniidae (*Telmatherina* not examined).

Greenwood et al. (1966) listed 21 'characteristic trends' of Series Atherinomorpha (i.e. a revision and elevation of Rosen's Atheriniformes), establishing equivalent ranking to the 7 other extant teleost superorders. Suborder Atherinoidei comprised 5 families: Melanotaeniidae, 'Atherinidae (including Bedotiidae, Pseudomugilidae)' and 3 others (telmatherinids not listed).

Munro (1967) defined Melanotaeniidae, Pseudomugilidae and Telmatherinidae on the basis of external morphology, considering the 3 families to have descended from marine atherinids. Meinken (1974) described *Iriatherina werneri* from Irian Jaya (West Irian) on the basis of oral anatomy and fin morphology. Meinken considered this fish an atherinid (Ährenfische) and noted a superficial resemblance to *Telmatherina*. However, the head and extravagant sexual dimorphism evident in the first dorsal fin of *Iriatherina* separated it from *Telmatherina* and *Pseudomugil*.

Patten (1978) considered Atherinidae (Atherinoidei of Greenwood et al., 1966) to comprise 6 subfamilies (phallostethids and Madagascan fish not examined). The musculoskeletal anatomy of many atherinid species, plus some atherinopsids, *Iso*, *Atherion*, *Telmatherina ladigesi*, *Pseudomugil signifer* and 4 *Melanotaenia* spp., was detailed. Melanotaeniinae, including the 'less advanced' *Telmatherina* with *Pseudomugil* and *Melanotaenia*, was considered the sister group to Atherininae

Zeiske et al. (1979) examined the structure of the nasal organ of 5 melanotaeniid species (*Glossolepis* sp., *Chilatherina* sp. and 3 *Nematocentrus* (=*Melanotaenia*; Allen, 1980) spp.) and suggested that epithelial organisation was 'relatively primitive' (compared to cyprinodontids). Melinkat & Zeiske (1979) examined the anatomy and mechanics of this organ in *Bedotia geayi*, concluding that the mechanism of ventilation in this species was different to that of other Atheriniformes, except notocheirids.

Allen (1980) revised Melanotaeniidae, considering it to comprise 8 genera (6 'rainbowfish' and 2 'blue-eye' genera). Three rainbowfish genera were monotypic: *Iriatherina*, *Rhadinocentrus* and *Cairnsichthys* (established for *R. rhombosomoides* Nichols & Raven). Allen identified the interpelvic modification (the pelvic fins connected to the ventral body wall by a fine membrane, enclosing an asquamate area cranial to the anus), the reduced premaxillary dorsal process ('short median ascending process'), presence of teeth outside the mouth, and sexual dimorphism as definitive characteristics of Melanotaeniidae. Allen noted that a complete pelvic-body membrane occurred in various non-atheriniform groups, but only a partial membrane was (putatively) present in some atherinids and *Bedotia* (although not reported in the literature; Stiassny & Reinthal (1992) described the 'region from rounded interpelvic scale to anus naked' in 3 species of *Rheocles*), but conceived Melanotaeniidae as geographically restricted to present-day Australia and New Guinea, a probable sister-group of Atherinidae. Interestingly, Allen's analysis placed blue-eyes (with high-set pectoral fins, reduced/lacking interdorsal pterygiophores, reduced cleithrum caudodorsal enclosure, pelvic fin attached to fourth pleural rib) plesiomorphic to other genera, while fin spine and additional dentigerous surfaces in *Melanotaenia*, *Glossolepis* and *Chilatherina* were considered apomorphic characters. Subsequently, Derijst (1989) ascertained priority for the family name Pseudomugilidae over Melanotaeniidae, for Allen's definition of the family.

Grier et al. (1980) investigated teleost spermatogonia and found the telogonic testis (spermatogonia restricted to the distal portion of the testis) to be an atherinomorph autapomorphy. Jamieson (1991) published micrographs of spermatocytes of some Australian melanotaeniids, remarking that 'sperm structure in atheriniforms suggests that familial classification of the atherinid-melanotaeiniid section of the order may require revision'.

Rosen & Parenti (1981) considered Rosen's (1964) proposed relationships to be based on somewhat 'unworkable' characters. They listed 13 apomorphies (including 2 novel gill-arch characters) for Atherinomorpha, and a further 4 apomorphies, which could be used to demarcate the paraphyletic 'Division 1'. Melanotaeniidae (including Pseudomugilidae), Bedotiidae, and Telmatherinidae were 3 of the 6 families comprising this division. Rosen & Parenti suggested that Bedotiidae most closely resembled a hypothetical 'atherinoid' precursor (on the basis of fin placement, fin elements and vertebral count), that melanotaeniids were slightly more derived (in dorsal fin architecture) and that pseudomugilids, phallostethids and freshwater/marine atherinids approached the advanced state of cyprinodontids and exocoetids. Further, 'Atherinidae might only be definable by exclusion of both bedotiids and melanotaeniids'. Parenti (1984) gave 2 further characters (premaxilla articular process reduced, enhanced 'decoupling' of rostral cartilage to premaxilla) to support a basal niche for (Bedotiidae + Melanotaeniidae), and expanded the hypothesis by suggesting that pseudomugilid affinities were with telmatherinids and phallostethids (sharing a large meniscus or bone interposed between maxilla and vomer, and an enlarged first anal pterygiophore).

White et al. (1984) reported 2 developmental characteristics, in part gleaned from the literature (short preanal length at the time of flexure and the dorsal pigmentation pattern), as atheriniform apomorphies. However, Parenti (1984, 1989, 1993) disputed the universality of these putative characters. Dyer & Chernoff (1996) also expressed reservation on including these characters in their analysis.

Parenti (1993) listed 14 atherinomorph apomorphies, substantially revising Rosen & Parenti (1981), but maintained the paraphyly of Divison 1. She argued that ichthyologists needed to define characters and homologies precisely, and examine proposed outgroups thoroughly, to establish the sister-group to atherinomorphs, identify unequivocal division 1 synapomorphies and determine atherinoid interrelationships. An analysis of the structure of the first dorsal fin of atherinomorphs, mugilids and outgroups echoed the widely-accepted contention that Bedotiidae was the most basal atherinomorph clade.

Saeed et al. (1989) accepted Pseudomugilidae, a clade distinct from the 6 genera comprising Melanotaeniidae. Pseudomugilidae was diagnosed on the basis of the absence of the mesethmoid, a single rostral infraorbital and the articular coronoid process as high as the dentary. Pseudomugilidae was separated into Pseudomugilinae, with an elongate first epibranchial uncinate process, absence of the articularmaxillary ligament and 2 other characters, and Kiunginae (type species *Kiunga ballochi* Allen) with a 'keel-like' abdominal outgrowth, derived maxilla-lateral ethmoid articulation and 5 further characters. Ivantsoff et al. (1991) subsequently described *Scaturiginichthys vermeilipinnis* and established Scaturiginichthyinae.

Stiassny (1990) argued for monophyly of both *Bedotia* and *Rheocles*, within a monophyletic Bedotiidae. The family was characterised with median exostoses on the caudal 6-7 vertebrae, lachrymal plus one elongate rostral infraorbital, and asymmetric pelvic medial processes. *Bedotia* was characterised with reduced/absent pelvic cranial spinous processes, paired median basibranchial toothplates and a premaxillary notch. *Rheocles* was characterised with fusion of the parhypural to the lower hypural plate. She noted that an indistinct subdivision of m. pharyngocleithralis (= m. pharyngoclavicularis; Winterbottom, 1974) was common to *Bedotia*, *Rheocles* and the basal mugilid *Agonostomus* but not melanotaeniids. She suggested 4 apomorphies supporting a sister-group alignment between Atherinomorpha and the proposed Mugilomorpha. Expanding this hypothesis, Stiassny (1993) presented a revised set of 7 apomorphies supporting the above relationship, also noting that *Bedotia*, *Rheocles* and melanotaeniids shared an underived (large) supracleithrum while *Bedotia*, *Rheocles* and *Agonostomus* shared a plesiomorphic configuration of m. levator operculi. Stiassny & Raminosa (1994) suggested that there was need for a further revision of *Bedotia* and *Rheocles*.

Kottelat (1990, 1991) investigated the ichthyofauna of Sulawesi, recognising 3 genera and 16 species of telmatherinids. Saeed & Ivantsoff (1991) established the telmatherinid genus *Kalyptatherina* for *Pseudomugil helodes* Allen and Ivantsoff, from islands off the west coast of New Guinea. Telmatherinidae was diagnosed with a short rostrum, reduced first vertebral neural spine and reduced fourth pharyngobranchial toothplate, while other 'distinguishing' osteological characters were given pending the publication of a detailed analysis of Telmatherinidae.

Saeed et al. (1994) pursued their analysis of atheriniform interrelationships, partitioning division 1 between new world Atherinopsoidea (with one apomorphic character) and old world Atherinoidea (with 4 apomorphies), considering the latter to comprise 7 families (including Bedotiidae, Melanotaeniidae, Telmatherinidae and Pseudomugilidae). The distribution of 9 characters across Atherinoidea placed Bedotiidae and Melanotaeniidae as plesiomorphic, while pseudomugilids were placed closest to phallostethids, the latter 2 families sharing apomorphic disc-like supracleithra and reduction/loss of interdorsal pterygiophores.

Zhu et al. (1994) examined 2 DNA sequences from representatives of 26 populations of *Melanotaenia* spp. and one *Glossolepis* sp. They concluded that parsimony analysis of nucleotide sequence evolution data accorded reasonably with postulated relationships (based on morphological analysis) within *Melanotaenia*.

Nelson's (1994) synopsis was compiled from characteristics published elsewhere in the literature. Nelson recognised 3 suborders in Atheriniformes: Bedotioidei, Melanotaenioidei (including Pseudomugilidae) and Atherinoidei (including Telmatherinidae), with 'interrelationships of the five families ... uncertain' in the third suborder.

Dyer & Chernoff (1996) proposed a phylogenetic analysis of Atheriniformes, and provided a detailed assessment of melanotaeniid relationships. Atheriniformes was diagnosed with 10 characters, including 3 autapomorphies. Melanotaeniidae was diagnosed with a restricted caudal myodome, 3 or more pleural ribs caudal to the origin of the anal fin, and 4 other characters. The family comprised Bedotiinae, Melanotaeniinae and Pseudomugilinae (= Pseudomugilini + Telmatherinini). Bedotiinae was diagnosed with a pterotic shelf (not canal), caudal extension of the parasphenoid, enclosed mandibular sensory canal and no spine in the anal fin. Melanotaeniinae was diagnosed with 2 characters, the pelvic-body membrane providing 'additional support'. However, Dyer & Chernoff suggested their analysis of this clade was somewhat sketchy. Seven characters listed as diagnostic of Pseudomugilinae included ligamentous attachment of nasal to palatine, enlarged submaxillary meniscus with hyaline cartilage core, maxillary shaft expanded proximally, tendon of m. adductor mandibulae to distal half of maxilla and 'plate'-like first anal pterygiophore. Dyer & Chernoff disputed pseudomugilid characters listed by Saeed et al. (1989) and Saeed & Ivantsoff (1991), providing instead a set of 'novel' characters derived from examination of *Pseudomugil signifer* and *P. tenellus*. In fact, most of these characters (and others) were given as diagnotic traits by Saeed et al. (1989). Two specimens of *Telmatherina ladigesi* were examined and a single apomorphy proposed.

Dyer & Chernoff (1996) disputed the notion that bedotiines and melanotaeniines were 'primitive atherinoids', suggesting rather that the (percomorph-like) enlarged dorsal mesethmoid, deep body and pungent fin spines (in *Melanotaenia*) were (within Atheriniformes) derived characteristics.

Aarn & Ivantsoff (1996) detailed the anatomy of the melanotaeniid *R. ornatus*, listing this fish's apomorphies. It was reiterated that detailed anatomical analyses of *C. rhombosomoides* and *I. werneri* were prerequisite for clarification of melanotaeniid systematics. Aarn et al. (in press) identify atherinid (lachrymal caudal notch, pelvic ventrolateral spinous process) and melanotaeniid (angular premaxilla, pelvic-body membrane) characteristics which are variably-distributed in Telmatherinidae, and describe a fifth telmatherinid genus.

In summary, more than a century of research culminated in the synthesis formalised by Rosen (1964) (in part suggested earlier; see Parenti, 1993), just prior to the rise of phylogenetic systematics. This invigorated research into atheriniform interrelationships, culminating in the comprehensive phylogenetic analysis of Dyer & Chernoff (1996) in which important novel atheriniform apomorphies were identified. This manuscript presents new anatomical data, proposing a new definition and phylogenetic analysis of Melanotaeniidae.

Descriptive anatomy

Methods. Procedures for clearing and staining, disarticulation and illustration of specimens follow Aarn & Ivantsoff (1996). Details of these procedures, for prepared specimens from museums other than MQU, were not available. Terminology follows Aarn & Ivantsoff (1996) and the recommendations of Anon. (1983). Sulawesi is the name of the territory formerly known as Celebes. New Guinea is the name of the island comprising Irian Jaya and Niugini.

Fin elements were counted on a maximum of 12 fish from each collection: some collections had less than 12 specimens, and some fins were damaged. Vertebrae, pleural ribs, epineurals and pterygiophores, and gill rakers of the lower left gill-arch, were counted in cleared and stained fish.

Melanotaeniidae Gill, 1896

Type genus. *Melanotaenia* Gill,1862

Diagnosis. An atheriniform family of brackish- and fresh-waters of Australia and New Guinea, and Madagascar, differing from other Atheriniformes in the following combination of characteristics: dorsal mesethmoid large; rostral cartilage piriform; narrow meniscus between vomerine and maxillary condyles; upper jaw fixed; premaxilla ventral margin angular; premaxilla postmaxillary process reduced or absent; coronoid process of dentary low; palatine robust; dentary incisure extensive; toothed surfaces reduced, teeth rarely present on ectopterygoid; mesopterygoid edentulous; premaxillary teeth displaying moderate to marked anisometry; interopercle caudodorsal margin notched; hypobranchial III deltoid, without marked rostroventral tapering; epibranchial I uncinate process moderately or markedly elongate; ceratobranchial V broad in most species; epibranchial IV large, with large medial condyle; 32-41 vertebrae; first neural spine enlarged; 1-3 interdorsal pterygiophores; parhypural generally reduced, fused to lower hypural plate; anal fin originates cranial to 3+ pleural ribs; 2 postcleithra: small, scale-like dorsal, and trabecular (coursing on craniolateral face of first rib) ventral, elements; pelvic cranial spinous process truncate; pelvic fin attached ligamentously to pleural rib 2-4; pelvic ventrolateral spinous process absent; anus situated between pelvic fins; membrane between ventral body wall and inner pelvic fin ray; body deep to discoidal.

Subfamily Melanotaeniinae Gill, 1894

Diagnosis. External ramus of maxilla moderate to elongate, premaxilla large and elongate; first anal pterygiophore reduced.

Cairnsichthys Allen, 1980

Diagnosis. A monotypic melanotaeniid genus with the vomer rostral margin markedly convex, vomerine condyles directed caudolaterally. Nasal forming rostral roof of orbit. Maxillary external ramus elongate, narrow-hemispatulate, maxilla resting in deep sulcus of premaxilla. Mandibular sensory canal enclosed. Rostral infraorbital series of 2 elements. Flexible spine at start of anal fin, most specimens with flexible spine at start of second dorsal fin. Supracleithrum broad. Pelvic fin lacking cranial spinous process, attached ligamentously to fourth pleural rib.

Cairnsichthys rhombosomoides (Nichols & Raven)

(Fig. 1a-b)

External morphology. Body slender, rhombofusiform with slight sigmoid flexure, caudal body laterally-compressed. Mouth terminal, jaws equal rostrally, oblique caudally. Angle of mouth extending caudal to transverse plane through rostral margin of orbit, with upper jaw enclosing lower jaw. Several rows of small, conical teeth extending along premaxilla outside gape. Deep indentation ('notch') at junction of rostrotransverse and caudolateral rami of upper jaw. Labial prominence of lower jaw filling notch. Rostral nares papilla adjacent to notch. Rostrum slightly depressed in preserved fish.

First dorsal fin small, rhomboidal, originating on cranial half of body well behind pectoral tips, of V-VI flexible spines. Second dorsal fin of 14-15 rays, caudal 10-11 branching subterminally. Anal originating caudal to pelvic tips and origin of first dorsal, terminating just cranial to termination of second dorsal, with small spine and 19-21 rays, caudal 16-20 branching subterminally. Second dorsal and anal fins extended from body as moderate sectors. Caudal fin symmetric, emarginate, of 9+8 (dorsal + ventral) principal branched and unbranched rays. Pectoral fin broad-fusiform, with dorsal 'spur' (minute spine) and 10-12 rays (dorsal ray unbranched). Pelvic fin originating before pectoral tip, deltoid, with small lateral spine and 5 branched rays, medial ray attached to ventral body wall by fine membrane. Anus caudal to origin of last pelvic ray. Urogenital papilla between anus and anal fin. Urogenital orifices in asquamate area bounded by pelvic-body membranes.

Body, except jaws and vent, covered in faintly-crenulate cycloid scales. Scales in lateral series from pectoral axilla to origin of caudal fin 36-38, in transverse rows betwen origins of dorsal and anal fins 10.

Live colouration relatively drab, prominent black midlateral line with blue and gold iridescent spots unevenly distributed over yellow/olive dorsum, silver ventrum and transparent median fins. Caudal fin yellow. Sexual dimorphism inapparent, but second dorsal and anal fins reportedly edged with yellow in males (Merrick & Schmida, 1984). Colour most intense on largest fish.

Specimens stored in 70 % ethanol with prominent black band traversing midlateral row of largest scales, from pectoral axilla to tip of caudal peduncle. Scales above band with centrifugal pigmentation, forming reticulated pattern, scales below lacking reticulation. Black line coursing along dorsal body contour, from interorbital plane through base of dorsal fins to tip of caudal peduncle. Lachrymal, opercular and belly regions grey. Some specimens with faint black submarginal crescent in second dorsal and anal fins. Caudal rays heavily pigmented proximally, becoming faint peripherally.

Largest documented specimen 66 mm SL (Allen, 1980); largest examined osteologically 64 mm SL.

Musculoskeletal anatomy

Cranium. Cranium broad, snout depressed below roof of orbit (Figs. 2a-c). Vomer edentulous, broad-deltoid, rostral margin convex, condyles for articulation with maxillae triangular, directed caudolaterally. Vomer dorsal surface bearing small lateral processes contacting ethmoid cartilage; vomer parasphenoid process reduced (Fig. 3). Strong vomeropalatine ligament directed bilaterally from angle of vomerine condyle to rostroventral process of palatine.

Parasphenoid rostral process spatulate

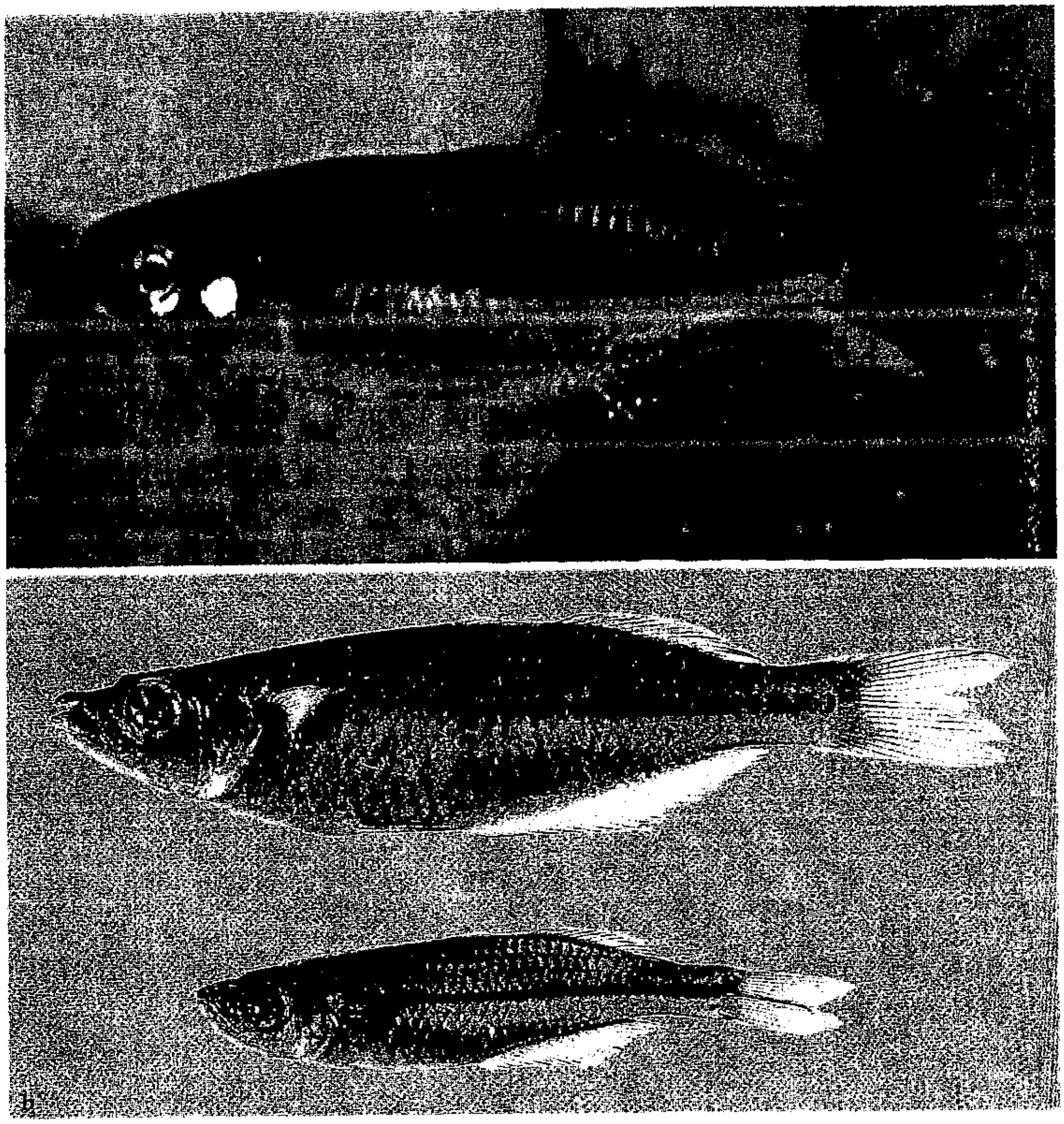


Fig. 1. *Cairnsichthys rhombosomoides*: a, aquarium specimen (photograph by Neil Armstrong); b, MQU I.470, 62 mm SL (upper fish) and 34 mm SL (lower fish).

(Fig. 2b), extending from rostral angle (above vomer, beneath ethmoid) caudally to form ventromedian interorbital septum, coursing beneath prootic median synthesis, terminating in circular caudal fossa, caudal to transverse plane through basioccipital rostral angle. Alar process, contacting prootic, truncated. Ventral fenestration (Dyer & Chernoff, 1996) in some immature specimens, between alar processes and caudal fossa. Secondary lateral expansion caudal to ala. Basisphenoid belophragm base broad, contacting dorsal surface of parasphenoid between alae; meningosts directed laterally to contact free rostral margin of prootics close to median prootic synthesis.

Ethmoid cartilage widest rostrally, narrowing caudoventrally to form rostral interorbital septum. Ethmoid rostrodorsally contacting piri-

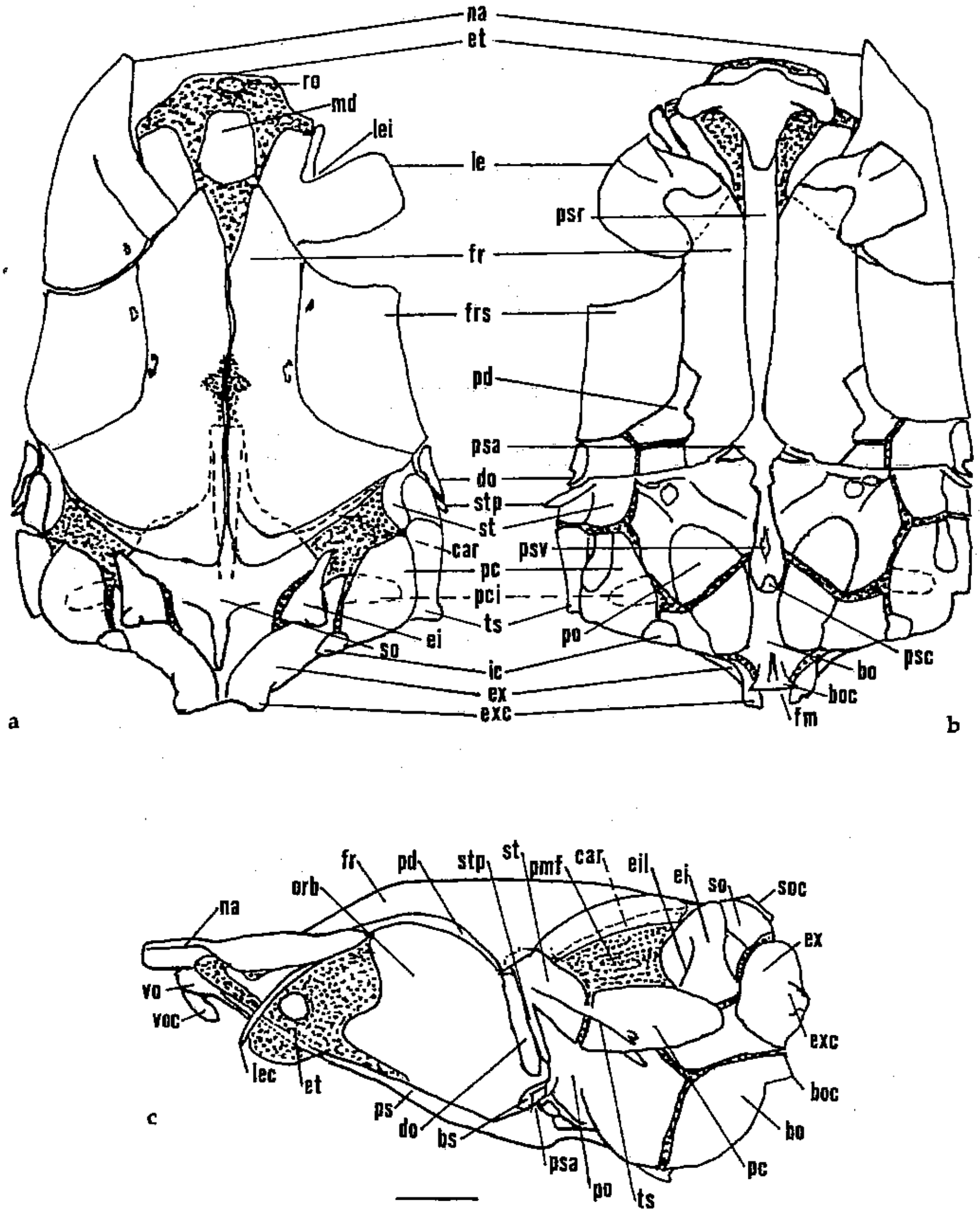
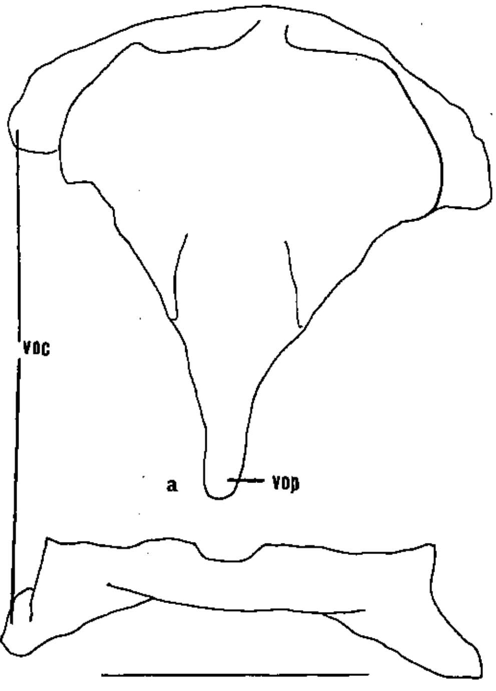


Fig. 2. *Cairnsichthys rhombosomoides*, MQU I.471, 47 mm SL. Cranium in: **a**, dorsal aspect; **b**, ventral aspect; **c**, lateral aspect. Abbreviations: **bo**, basioccipital; **boc**, basioccipital condyle; **bs**, basisphenoid; **car**, parietal cartilage; **do**, dermosphenoid; **ei**, epiotic; **eil**, epiotic lateral ridge; **et**, ethmoid cartilage; **ex**, exoccipital; **exc**, exoccipital condyle; **fm**, foramen magnum; **fr**, frontal; **frs**, frontal supraoccipital lamina; **ic**, intercalar; **le**, lateral ethmoid; **lec**, lateral ethmoid condyle; **lei**, lateral ethmoid incisure; **md**, dorsal mesethmoid; **na**, nasal; **orb**, orbit; **pc**, pterotic; **pci**, pterotic incisure; **pd**, pterosphenoid; **pmf**, posttemporal fossa; **po**, prootic; **ps**, parasphenoid; **psa**, parasphenoid ala; **psc**, parasphenoid caudal foramen; **psr**, parasphenoid rostral ramus; **psv**, parasphenoid ventral fenestration; **ro**, rostral cartilage; **so**, supraoccipital; **soc**, supraoccipital crest; **st**, sphenotic; **stp**, sphenotic postorbital process; **ts**, temporal shelf; **vo**, vomer; **voc**, vomerine condyle. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

form rostral cartilage, middorsally contacting dorsal mesethmoid, caudodorsally contacting frontals, laterally fused to lateral ethmoids and ventrally contacting vomer and parasphenoid. Ethmoid dorsal face slightly depressed. Lateral ethmoids widely-separated, at rostral margin of orbits, dorsally attached to nasal ventromedial crest. Lateral ethmoid rostral angle at level of transverse plane through vomerine condyles, caudal to ethmoid cartilage rostral margin. Lateral ethmoid deeply excavated rostrolaterally, forming palatine facet. Caudoventral margin almost transverse, bearing shallow palatine sulcus. Caudolateral vertical border convex, ventral angle forming small lachrymal condyle. Dorsal mesethmoid forming large rhomboidal lamina, contacting lateral ethmoids, nasals and rostral angle of frontals (Fig 4).



▷

Fig. 3. *Cairnsichthys rhombosomoides*, MQU I.469, 41 mm SL. Vomer in: **a**, dorsal aspect; **b**, rostral aspect. Abbreviations: **voc**, vomerine condyle; **vop**, vomer parasphenoid process. Scale bar: 1 mm.

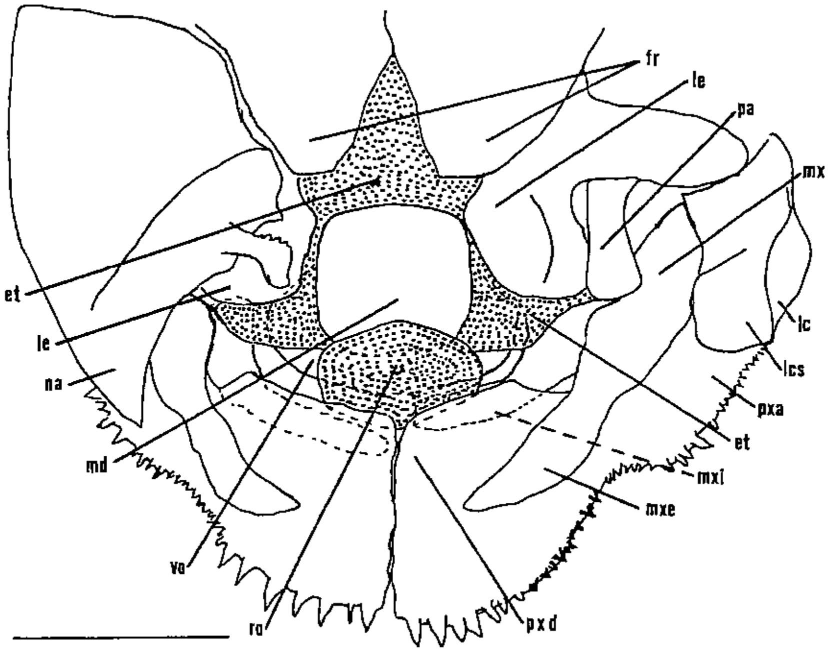


Fig. 4. *Cairnsichthys rhombosomoides*, MQU I.472, 36 mm SL. Facies in rostrodorsal aspect. Abbreviations: **et**, ethmoid cartilage; **fr**, frontal; **lc**, lachrymal; **lcs**, lachrymal subnasal shelf; **le**, lateral ethmoid; **md**, dorsal mesethmoid; **mx**, maxilla; **mxi**, maxilla internal ramus; **na**, nasal; **pa**, palatine; **pxa**, premaxilla alveolar ramus; **pxd**, premaxilla dorsal process; **ro**, rostral cartilage; **vo**, vomer. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

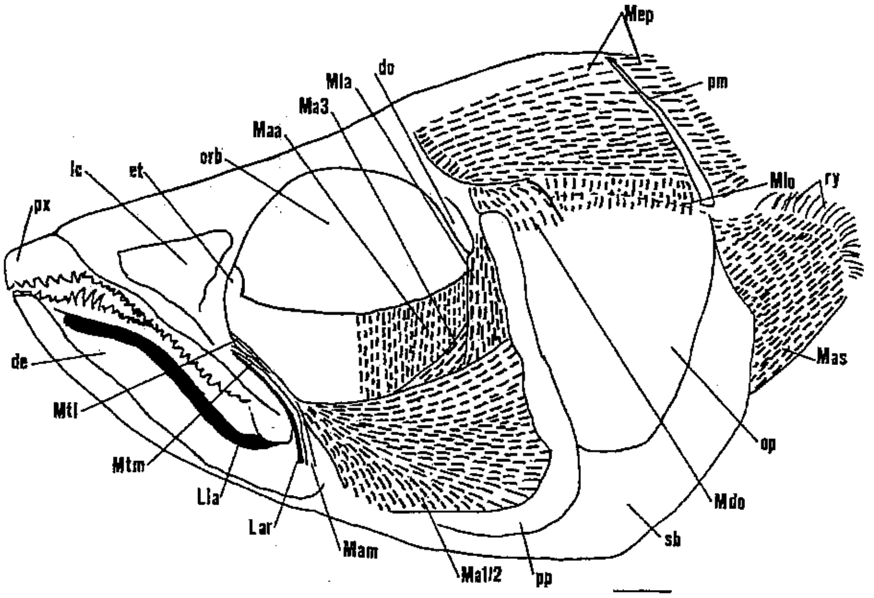


Fig. 5. *Cairnsichthys rhombosomoides*, MQU I.472, 41 mm SL. Superficial musculature and ligaments of head and pectoral region. Abbreviations: **de**, dentary; **do**, dermosphenoid; **et**, ethmoid cartilage; **Lar**, articularmaxillary ligament; **lc**, lachrymal; **Lla**, labial ligament; **Ma1/2**, m. adductor mandibulae, A1 and A2 sections; **Ma3**, m. adductor mandibulae, A3 section; **Maa**, m. adductor arcus palatini; **Mam**, m. adductor mandibulae, mandibular branch; **Mas**, m. abductor superficialis; **Mdo**, m. dilator operculi; **Mep**, epaxial musculature; **Mla**, m. levator arcus palatini; **Mlo**, m. levator operculi; **Mtl**, tendon of m. adductor mandibulae to lachrymal; **Mtm**, tendon of m. adductor mandibulae to maxilla; **op**, opercle; **orb**, orbit; **pm**, posttemporal; **pp**, preopercle; **px**, premaxilla; **ry**, fin ray; **sb**, subopercle. Scale bar: 1 mm. Dashed lines: muscles.

Nasal elongate and broad, falcate rostromedial margin forming perimeter of rostral fossa. Broader caudal portion of nasal dorsal and lateral to lateral ethmoid, extending caudal to lateral ethmoid to contact frontal, forming substantial part of roof of orbit. Prominent dorsal sensory crest directed rostrolaterally on rostral portion (Fig. 2a), small sensory trabecula midcaudally. Median ventral ridge extending from rostral angle to transverse plane at level of lateral ethmoid excavation, giving origin (rostrally) to nasolachrymal, and (caudally) to ethmonasal, ligaments.

Frontal irregular, narrow rostromedially adjacent to caudal extension of nasal, above ethmoid. Frontal caudal portion broad, forming most of roof of cranial vault, and roof of orbit. Frontals joined along asymmetric caudomedian suture, rostrally persistent fontanel causing discontinuity, above ethmoid. Shallow sulcus demarcating (median) calvarial lamina of frontal from supraorbital lamina, 2-3 small sensory trabeculae about sulcus.

Supraoccipital forming caudal roof of cranial vault, with deltoid rostral process lying ventral to caudomedian angle of frontals. Supraoccipital crest moderately developed.

Sphenotic at caudal margin of orbit in contact with caudolateral angle of frontal (Fig. 2c). Sphenotic postorbital process directed ventrolaterally, somewhat caudally, giving origin to m. levator arcus palatini.

Pterotic contacting caudal margin of sphenotic, coursing around caudolateral margin of skull to contact epiotic. Deep, narrow indentation extending centrifugally. Small process on ventral face, adjacent to apex of indentation, delimiting caudal extent of hyomandibula facet. Temporal shelf extending horizontally, rostral angle derived from sphenotic, caudal (larger) portion from pterotic.

Epiotic somewhat triangular, dorsal apex lying ventral to supraoccipital, oblique caudal border contacting exoccipital, ventral base contacting pterotic. Epiotic bearing prominent lateral ridge for articulation with posttemporal and insertion of epaxial musculature (Fig. 5).

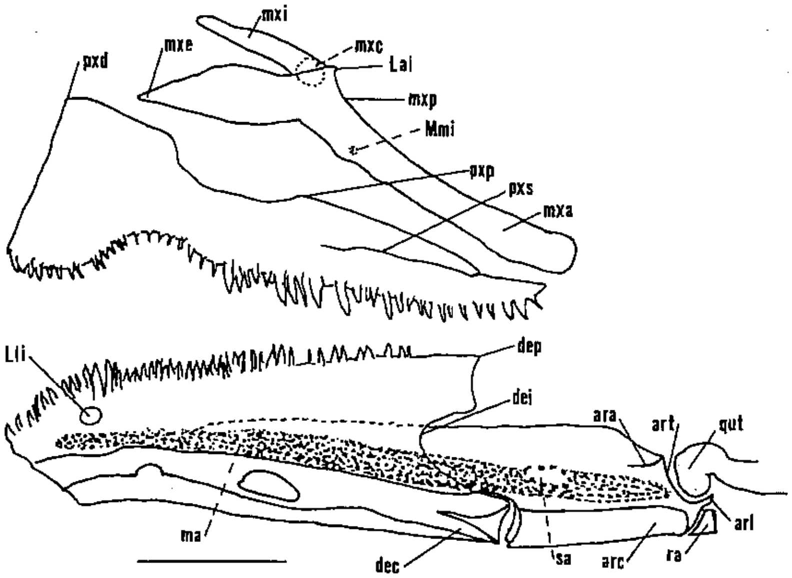


Fig. 6. *Cairnsichthys rhombosomoides*, MQU I.469, 37 mm SL. Jaws. Abbreviations: **ara**, articular process of origin of articularmaxillary ligament and mandibular branch of m. adductor mandibulae; **arc**, articular neural canal; **arl**, articular lateral muscular process; **art**, articular trochlear groove; **dec**, dentary neural canal; **dei**, dentary caudal incisure; **dep**, dentary coronoid process; **Lai**, insertion of articularmaxillary ligament; **Lli**, insertion of labial ligament; **ma**, mandibular cartilage; **mmi**, insertion of adductor tendon to maxilla; **mxa**, maxilla alveolar ramus; **mxc**, maxillary condyle; **mxe**, maxilla external ramus; **mxi**, maxilla internal ramus; **mxp**, maxilla palatine sulcus; **pxd**, premaxilla dorsal process; **pxp**, premaxilla postmaxillary process; **pxs**, premaxilla lateral sulcus; **qut**, quadrate tubercle; **ra**, retroarticular; **sa**, supraangular. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

Exoccipital forming dorsal portion of base of skull, dorsally contacting supraoccipital and epiotic, laterally contacting pterotic, ventrally contacting basioccipital. Exoccipitals joined above foramen magnum, paired exoccipital (minor occipital) condyles projecting caudally to articulation with first vertebra.

Basioccipital forming caudoventral angle of skull, extending rostrad dorsal to parasphenoid caudal foramen, rostrolaterally contacting prootics, dorsolaterally contacting exoccipitals, caudally forming major occipital condyle. Axialpectoral (Baudelot's) ligament originating (bilaterally) from prominence on caudal angle of otic bulla, caudolateral to centre of basioccipital, directed laterally. Prootic expansive, laminar, forming rostral floor of skull, rostrodorsally contacting pterosphenoid and sphenotic, caudodorsally contacting pterotic, caudally contacting basioccipital. Prootics meeting in median plane, dorsal to alae and caudal extension of parasphenoid. Otic bulla ellipsoid, bilaterally extending from basioccipital to prootic rostrolateral region, enclosing otoliths.

Pterosphenoid forming partial septum between orbit and cranial vault, dorsally contacting frontal, laterally contacting sphenotic, ventromedially contacting prootic, indented medial margin free.

Jaws. Upper jaw not protrusible. Maxilla bifurcating rostrally to give elongate tubiform internal, and hemispatulate external, rami, about premaxilla dorsal process (Fig. 6). Maxilla internal ramus bound in dense connective tissue beneath rostral cartilage. Condyle for articulation with vomer at base of internal face of internal ramus, biconcave discoidal meniscus interposed between maxilla and vomer. Shallow dorsal sulcus for palatine just caudal to bifurcation. Articularmaxillary ligament inserting on dorsal spine of maxilla somewhat caudal to bifurcation. Maxillary tendon of m. adductor mandibulae inserting on ventromedian face of maxilla caudal to ligament. Maxilla alveolar (lateral) ramus elongate, resting in sulcus on external face of premaxilla, extending caudad beyond caudal angle of premaxilla.

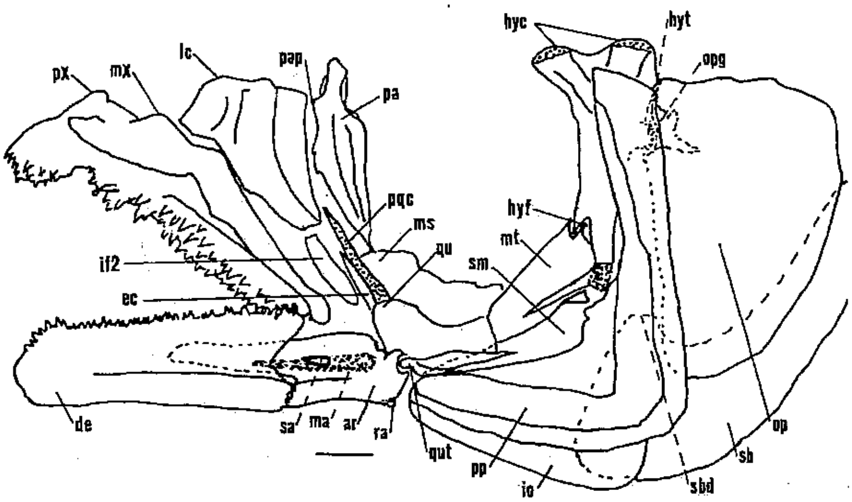


Fig. 7. *Cairnsichthys rhombosomoides*, MQU I.470, 64 mm SL. Suspensorium and jaws. Abbreviations: **ar**, articular; **de**, dentary; **ec**, ectopterygoid; **hyc**, hyomandibula condyle; **hyf**, hyomandibula foramen; **hyt**, hyomandibula tubercle; **if2**, infraorbital 2; **io**, interopercle; **lc**, lachrymal; **ma**, mandibular cartilage; **ms**, mesopterygoid; **mt**, metapterygoid; **mx**, maxilla; **opg**, opercle glenoid cavity; **op**, opercle; **pa**, palatine; **pap**, palatine rostroventral process; **pp**, preopercle; **pqc**, palatoquadrate cartilage; **px**, premaxilla; **qu**, quadrate; **qut**, quadrate tubercle; **ra**, retroarticular; **sa**, supraangular; **sb**, subopercle; **sbd**, subopercle dorsal process; **sm**, symplectic. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

Premaxilla irregular, rostromedian symphyseal part with low dorsal process and deep ventral extension, separated from alveolar ramus by prominent dorsal and ventral notches. Postmaxillary process very low, edentulous dorsal lamina of premaxilla alveolar ramus terminating rostral to caudad extension of dentigerous lamina. Premaxilla bearing several rows of caniniform teeth; largest teeth on rostromedian alveolar surface, teeth very small about ventral notch, larger teeth along alveolar ramus extending caudad beyond caudal angle of premaxilla.

Dentaries joined in median symphysis. Dentary coronoid process low, caudal incisure shallow, caudodorsal angle caudad to caudoventral angle. Several rows of small caniniform teeth from symphysis along alveolar ramus, largest teeth adjacent to premaxillary notch, directed somewhat laterally; caudodorsal angle edentulous. Labial ligament rising from internal face of caudal angle of maxilla and premaxilla, and lateral face of articular coronoid process, coursing rostrally on lateral face of dentary alveolar ramus to insertion at labial prominence (Fig. 5).

Articular elongate, low, lacking coronoid process. Articular caudal processs giving origin to articularmaxillary ligament just rostal to insertion of small mandibular branch of m. adductor mandibulae. Trochlear groove at caudolateral angle of articular forming ginglymus (hinge joint) with quadrate tubercle (Fig. 6). Mandibular (Meckel's) cartilage extending from origin close to dentary symphysis along internal face of dentary, to caudal angle of articular, always lower than articular. Elongate supraangular (coronomeckelian) bone attached to dorsal surface of mandibular cartilage at level of rostroventral angle of articular. Retroarticular small, at caudoventral angle of lower jaw. Mandibular sensory canal on ventrolateral face of dentary and articular, enclosed by perforate osseous sheaf.

Suspensorium. Comprising palatoquadrate assemblage, ectopterygoid, mesopterygoid, metapterygoid, symplectic, preopercle and hyomandibula (all edentulous) (Fig. 7).

Palatine with robust rostral process lacking ventral deviation (Fig. 8), resting in maxillary sulcus. Palatine ethmoid process attached to lateral ethmoid. Rostroventral process small, contacting lateral ethmoid. Palatine caudodorsally contacting mesopterygoid, extending caudoventrally as narrow trabecula to contact quadrate. Quadrate with compact vertical lamina, ventral

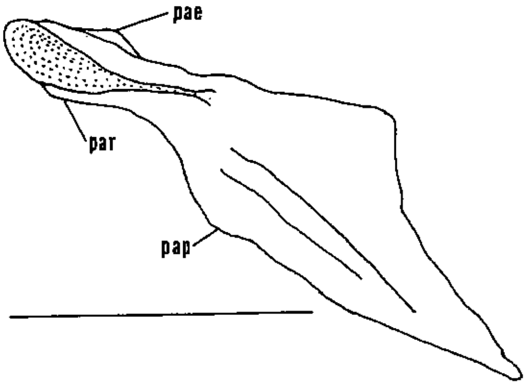


Fig. 8. *Cairnsichthys rhombosomoides*, MQU I.469, 41 mm SL. Palatine in lateral aspect. Abbreviations: **pae**, palatine ethmoid process; **pap**, palatine rostroventral process; **par**, palatine rostral process. Scale bar: 1 mm. Stippling: cartilage.

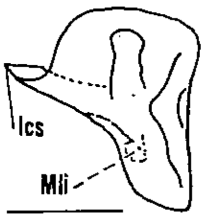


Fig. 9. *Cairnsichthys rhombosomoides*, MQU I.469, 37 mm SL. Lachrymal in lateral aspect. Abbreviations: **lcs**, lachrymal subnasal shelf; **Mli**, insertion of adductor tendon on lachrymal. Scale bar: 1 mm. Dotted lines: obscured structures.

to mesopterygoid, and elongate preopercle (lateral) ramus bearing large rostral tubercle and trabecular caudal extension.

Ectopterygoid narrow, arcuate, on medial face of palatine ventral trabecula (Fig. 7). Mesopterygoid thin, narrow, encapsulating orbit ventrolaterally. Metapterygoid almost straight, rostrally contacting quadrate caudal cartilage, dorsal to symplectic, caudodorsally contacting ventral and rostral processes of hyomandibula. Symplectic narrow-piriform, extending from incisure in quadrate to form conical cartilage, articulating with hyomandibula ventral cuneiform cartilage.

Hyomandibula irregular, long axis vertical, 2 dorsal condyles capped with cartilage articulating with facets of sphenotic and pterotic. Small rostroventral ramus and rostral border of hyomandibula ventral angle contacting metapterygoid. Ventral cuneiform cartilage forming expansive synarthrosis with symplectic, medial face giving origin to interhyal ligament. Hyomandibula lateral face bearing vertical ridge contacting preopercle. Large caudal tubercle, with cartilaginous articular surface, forming enarthrosis (ball and socket joint) with opercle glenoid cavity.

Preopercle forming rightangular canal, open ventrally and caudally, ventral ramus shorter and slightly curved.

Opercular series. Consisting of interopercle, opercle and subopercle. Interopercle deep, with shallow caudodorsal indentation, dorsal border deep to preopercle horizontal ramus. Opercle rectangular except convex caudoventral margin. Dorsal margin almost linear, below level of horizontal plane through hyomandibula dorsal condyles. Medial surface rostral border bearing tubercle with glenoid fossa for articulation with hyomandibula; small osseous ridge extending briefly caudad from tubercle. Subopercle distorted-fusiform, curled about caudoventral margin of opercle, bearing large rostrodorsal process.

Circumorbital series. Consisting of lachrymal and second infraorbital (rostrally), and dermosphenoid. Lachrymal with rhomboidal dorsal portion and deltoid ventral portion, apex directed caudoventrally (Fig. 9). Lachrymal dorsal border entire, subnasal shelf on medial face projecting rostrally beyond lachrymal rostral border. Horizontal sensory canal at caudal margin of lateral face; caudal transverse face concave, accomodating condyle of lateral ethmoid. Tendon from m. adductor mandibulae inserting on medial face close to caudal angle of subnasal shelf. Second infraorbital forming elongate osseous canal coursing caudoventrally.

Dermosphenoid forming elongate cuneiform canal, apex lying deep, superficial face open. Dermosphenoid extending from caudomedian angle of frontal supraorbital lamina, on rostral face of sphenotic postorbital processs, to level of horizontal plane through middle of orbit.

Hyobranchial apparatus. Comprising median unpaired glossohyal cartilage, basishyal, (3) basibranchials and urohyal, bilaterally paired dorsal and ventral hypohyals, ceratohyal, epihyal, (6) branchiostegals, interhyal, (3) hypobranchials, (5) ceratobranchials, (4) epibranchials and (3) pharyngobranchials, and associated toothplate/patches (Fig. 10a-b).

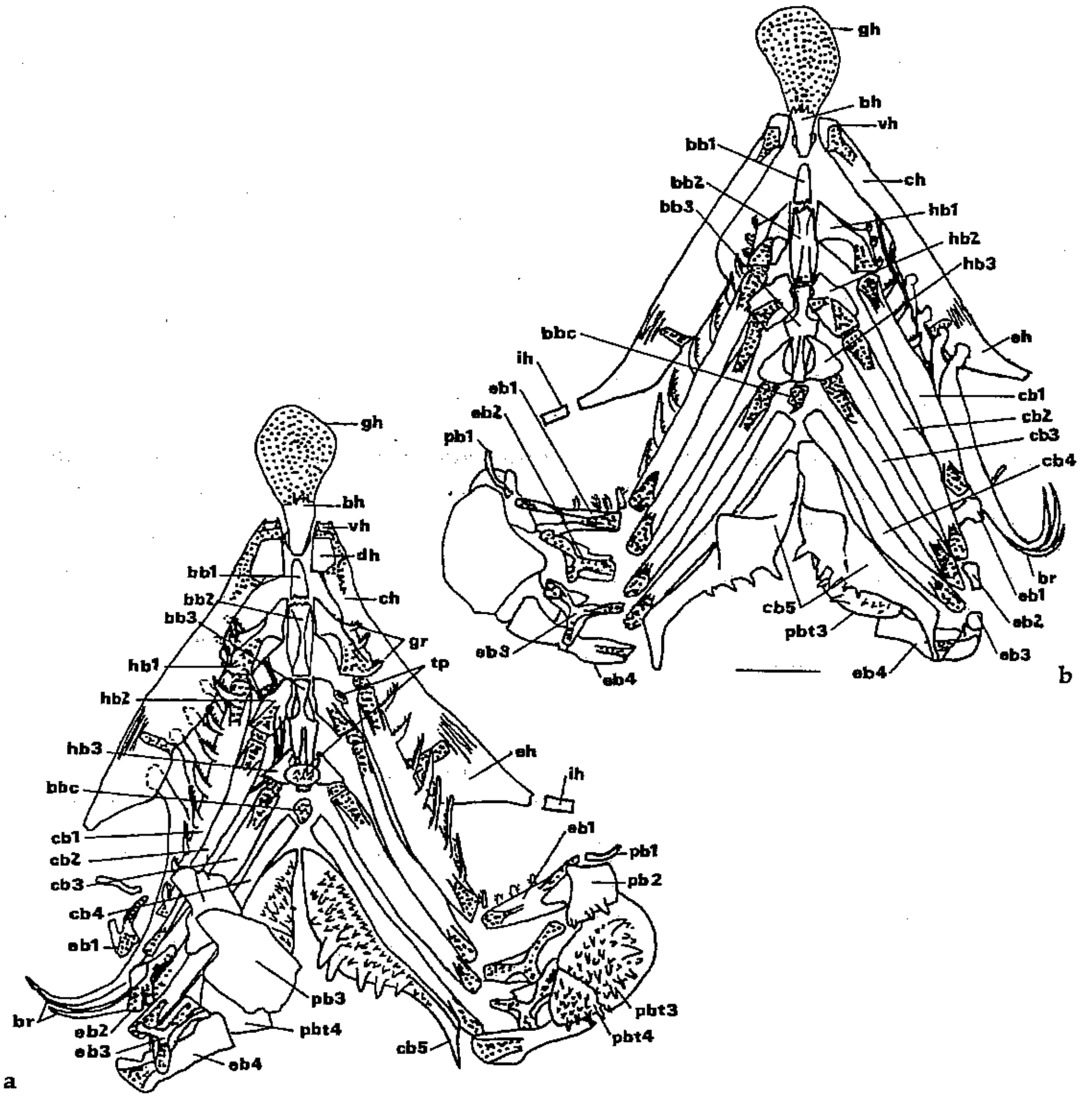


Fig. 10. *Cairnsichthys rhombosomoides*, MQU I.470, 38 mm SL. Hyobranchial apparatus, right pharyngobranchials teased open, in **a**, dorsal aspect; **b**, ventral aspect (urohyal removed). Abbreviations: **bb**, basibranchial; **bbc**, basibranchial cartilaginous pedicle; **bh**, basihyal; **br**, branchiostegal; **cb**, ceratobranchial; **ch**, ceratohyal; **dh**, dorsal ypohyal; **eb**, epibranchial; **eh**, epihyal; **gh**, glossohyal; **gr**, gill raker; **hb**, hypobranchial; **ih**, interhyal; **pb**, pharyngobranchial; **pbt**, pharyngobranchial toothplate; **tp**, toothpatch; **vh**, ventral hypohyal. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

Glossohyal ovate, caudally fused to deltoid basihyal, both edentulous. Basihyal bilaterally contacing medial face of dorsal hypohyals, caudal apex contacting rostral apex of first basibranchial. First basibranchial small, laterally contacing dorsal hypohyals, caudally contacting second basibranchial. Second basibranchial elongate, rostrolaterally contacting first hypobranchials, rostroventrally contacting urohyal, caudally contacting third basibranchial. Third basibranchial largest element of basibranchial series, rostrolaterally contacting second hypobranchials, caudal portion encircled by third hypobranchials and dorsal median toothpatch, terminating caudov-

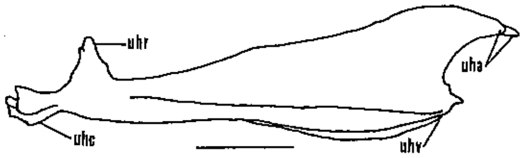


Fig. 11. *Cairnsichthys rhombosomoides*, MQU I.470, 64 mm SL. Urohyal in lateral aspect. Abbreviations: **uha**, urohyal ala; **uhc**, urohyal condyle; **uhr**, urohyal rostrodorsal process; **uhv**, urohyal ventral canal. Scale bar: 1 mm.

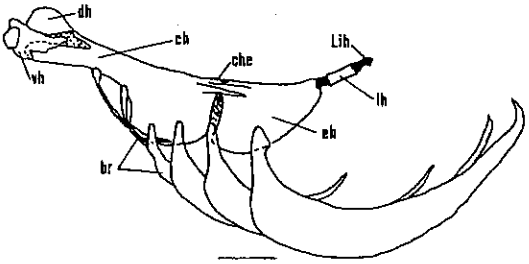


Fig. 12. *Cairnsichthys rhombosomoides*, MQU I.470, 64 mm SL. Hyoid bar in lateral aspect. Abbreviations: **br**, branchiostegal; **ch**, ceratohyal; **che**, ceratohyal-epihyal osseous lamella; **dh**, dorsal hypohyal; **eh**, epihyal; **ih**, interhyal; **Lih**, interhyal ligament; **vh**, ventral hypohyal. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

entrally as cartilaginous pedicle. Cartilaginous nodule in horizontal basibranchial plane, above pedicle.

Urohyal elongate (Fig. 11), rostral condyles attached ligamentously to ventromedian face of ventral hypohyals, rostrodorsal articular process approaching second basibranchial, ventromedian margin an open canal, caudal border emarginate, with small dorsal alae.

Dorsal hypohyal irregular-hemispherical (Fig.12). Ventral hypohyal irregular, joined to fellow ligamentously at large rostromedian condyle. Ceratohyal rostrally fused to hypohyals, caudally extending as narrow collar to vertical caudal lamina. Cartilaginous fusion between ceratohyal and (smaller) epihyal reinforced dorsally with osseous lamellae. Epihyal caudal margin directed caudodorsally, caudodorsal angle giving origin to interhyal ligament containing elongate interhyal sesamoid. Rostral 2 (small) branchiostegals rising from ventral border of collus of ceratohyal. Intermediate 2 branchiostegals articulating with facets on ceratohyal lateral face. Caudal 2 branchiostegals on lateral face of epihyal, occasionally penultimate branchiostegal on ceratohyal-epihyal synchondrosis.

First hypobranchial angular, directed caudally, bearing 2-3 small gill rakers. Second hypobranchial smaller than first, directed caudolaterally. Third hypobranchial oriented vertically, dorsal angle contacting median basibranchial toothpatch, curling around third basibranchial, ventral angle almost contacting fellow towards median plane.

Rostral 4 ceratobranchials elongate, narrow, dorsal surfaces bearing occasional small toothplates. Rostral 3 ceratobranchials rostrally contacting respective hypobranchials, fourth hypobranchial contacting median cartilaginous nodule. First ceratobranchial bearing 7-8 fusiform gill rakers. Longest gill raker less than first hypobranchial; gill rakers bearing few denticles. Fifth ceratobranchial deltoid, rostral angle contacting rostromedian face of fourth ceratobranchial, broadest midlength, caudal angle bearing large tubiform process. Dorsal surface supporting lower pharyngeal toothplate, with largest caniniform teeth towards midlateral region. Ventral surface bearing broad muscular process.

First epibranchial stout, bifurcating distally, rostral process contacting first epibranchial, uncinate process contacting small spherical interarcual cartilage resting on second pharyngobranchial. Second epibranchial angular, with proximal ramus larger than distal ramus, contacting second and third pharyngobranchials. Third epibranchial stellate, contacting third pharyngobranchial, small process contacting fourth pharyngobranchial dorsal process. Fourth epibranchial largest element of series, angular, large distal ramus articulating with median caudodorsal condyle of third pharyngobranchial.

First pharyngobranchial small, near-linear edentulous rod. Second pharyngobranchial almost rhomboidal, attached to rostral border of third pharyngobranchial, dorsal border narrow, ventral margin bearing 2-3 rows of teeth. Third pharyngobranchial irregular, bearing enlarged third, and caudally contacting reduced fourth, pharyngeal toothplates, largest caniniform teeth towards centre of third toothplate.

Vertebrae and ribs. Total vertebrae 36-38, precaudal 16-17, caudal 19-21, epineurals on all pre-

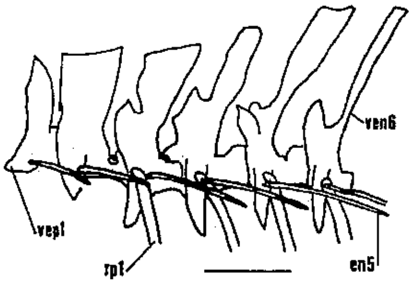


Fig. 13. *Cairnsichthys rhombosomoides*, MQU I.471, 47 mm SL. First 6 vertebrae. Abbreviations: **en**, epineural; **rp**, pleural rib; **ven**, vertebral neural process; **vep**, vertebral parapophysis. Scale bar: 1 mm.

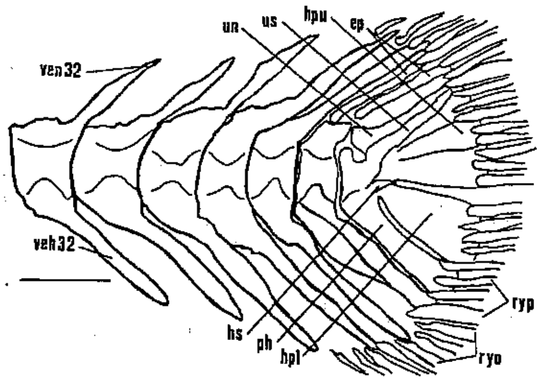


Fig. 14. *Cairnsichthys rhombosomoides*, MQU I.471, 47 mm SL. Caudal fin and last few vertebrae. Abbreviations: **ep**, epural; **hpl**, lower hypural plate; **hpu**, upper hypural plate; **hs**, hypurapophysis; **ph**, parhypural; **ryo**, procurrent ray; **ryp**, principal ray; **un**, uroneural; **us**, urostyle; **veh**, vertebral haemal spine; **ven**, vertebral neural spine. Scale bar: 1 mm.

caudal and first 5-6 caudal vertebrae. Precaudal vertebrae with large laterally-directed parapophyses, caudal facet contacting proximal angle of pleural rib from third to final precaudal vertebrae, parapophyses directed ventrally in first 3-4 caudal vertebrae, developed as haemal arches then spines in subsequent vertebrae, largest haemal spine on penultimate vertebra.

First vertebra articulating with occipital condyles, bearing moderate neural plate. Second to fourth vertebrae with broad neural plates (Fig 13). Subsequent 8-9 vertebrae with tall vertical neural spines and slender cranial dorsal zygapophyses, neural spines becoming inclined caudad in cau-

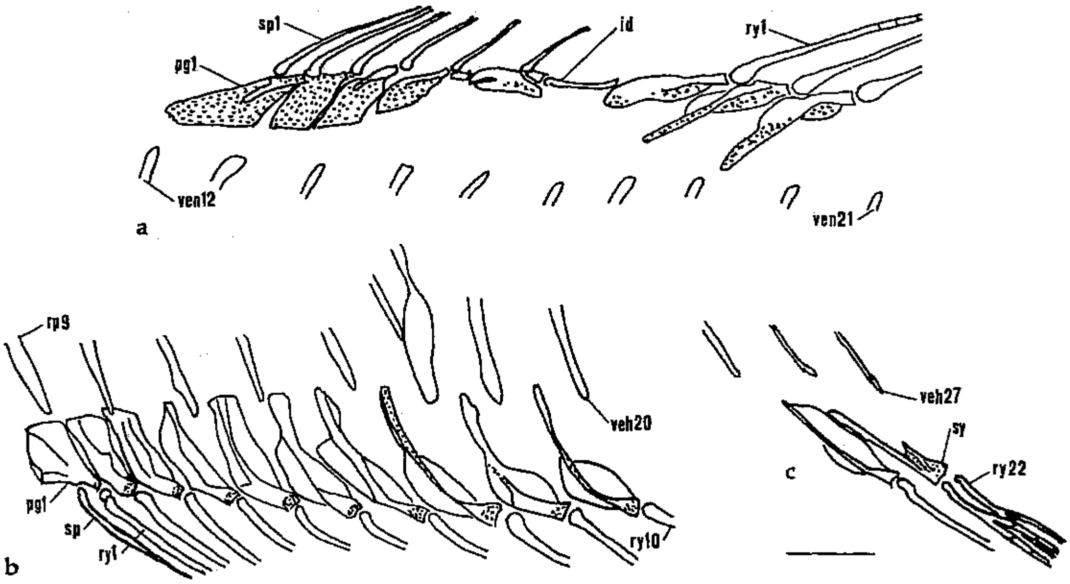


Fig. 15. *Cairnsichthys rhombosomoides*, MQU I.471, 47 mm SL. Fins and supports: **a**, dorsal fins and supports; **b**, anal fin spine and first few rays, and supports; **c**, anal fin caudal rays and supports. Abbreviations: **id**, interdorsal pterygiophore; **pg**, pterygiophore; **rp**, pleural rib; **ry**, fin ray; **sp**, fin spine; **sy**, fin stay; **veh**, vertebral haemal spine; **ven**, vertebral neural process. Scale bar: 1 mm. Stippling: cartilage.

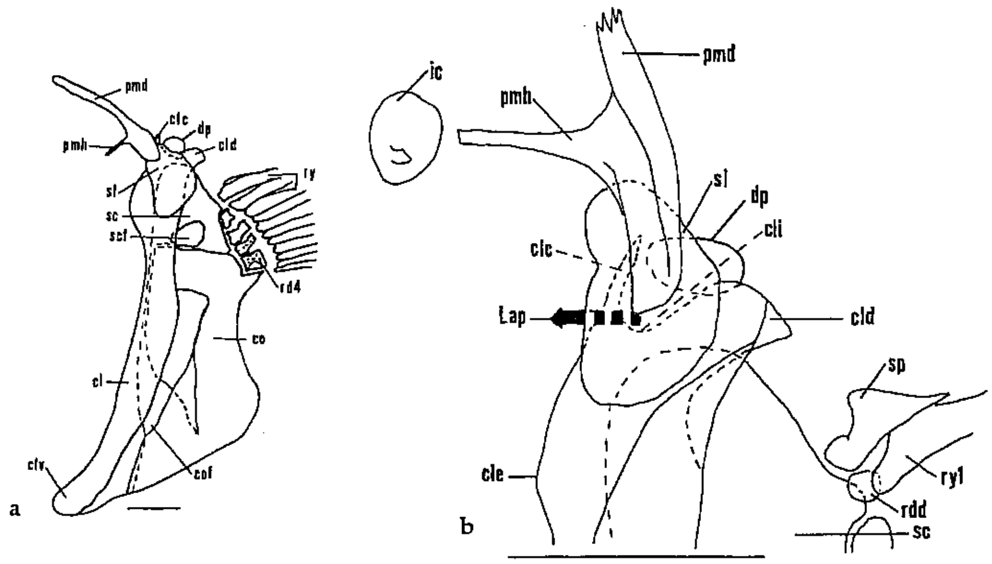


Fig. 16. *Cairnsichthys rhombosomoides*, MQU I.471, 47 mm SL. Pectoral fin: **a**, whole; **b**, detail. Abbreviations: **cl**, cleithrum; **clc**, cleithrum craniodorsal spine; **cld**, cleithrum caudodorsal process; **cle**, cleithrum medial cranial process; **cli**, cleithrum dorsal incisure; **clv**, cleithrum ventral process; **co**, coracoid; **cof**, coracoid foramen; **dp**, dorsal postcleithrum; **ic**, intercalar; **Lap**, axialpectoral ligament; **pmd**, posttemporal dorsal ramus; **pmh**, posttemporal horizontal ramus; **rd**, proximal radial; **rdd**, distal radial; **ry**, fin ray; **sc**, scapula; **scf**, scapula foramen; **sl**, supracleithrum; **sp**, fin spine. Scale bar: 1 mm. Dotted lines: obscured structures.

dal vertebrae, much reduced in penultimate vertebra, cranial dorsal zygapophyses disappearing until distal 10 caudal vertebrae. Ventral zygapophyses developed on distal 10 caudal vertebrae.

Marked median exostosis about spines and zygapophyses of distal 5 caudal vertebrae.

Two elongate epurals above penultimate centrum, radiating caudodorsally (Fig. 14). Terminal hemivertebra fused to caudodorsally-directed urostyle, well-developed uroneural on urostyle cranial margin. Upper hypural plate ventral to urostyle, comprising (unfused) hypurals 3-5. Lower hypural plate of fused hypurals 1-2. Large autogenous parhypural at cranial border of first hypural, bearing caudolaterally-directed parhypurapophysis. Tubiform radial cartilage between distal angles of penultimate and adjacent cranial vertebra haemal spines.

Fins and girdles. First dorsal fin originating at level of transverse plane through vertebral centra 13-15 (Fig. 15a). Large, shallow pterygiophore supporting cranial 2 spines, subsequent spines supported individually by single pterygiophore. Two shallow interdorsal pterygiophores. Second dorsal fin commencing at level of centra 19-21 (caudal to visceral cavity), each ray supported by individual pterygiophore except caudal 2 rays, on single pterygiophore, at level of centra 28-30.

Anal fin originating slightly caudal to (within one centra of) origin of first dorsal. Spine and first ray supported by small curved pterygiophore (Fig. 15b), subsequent rays supported individually, except terminal 2 rays on single pterygiophore (Fig. 15c). Some specimens with single bifid anal pterygiophore.

Caudal fin commencing at level of penultimate vertebra, with 7-8 dorsal and 7-8 ventral procurrent rays, principle ray hemitrichia originating on hypurals and parhypural (Fig. 14).

Pectoral girdle somewhat quadrilateral (Fig. 16a), below horizontal plane through vertebral centra, extending cranioventrally from first intercostal space to contact fellow about median intercleithral cartilage at level of transverse plane through caudal angle of orbit. Cleithrum medial cranial process, craniodorsal spine and caudodorsal process. Incisure betweeen spine and caudodorsal process. Cleithrum cranial border everted, giving origin to pectoral abductor musculature.

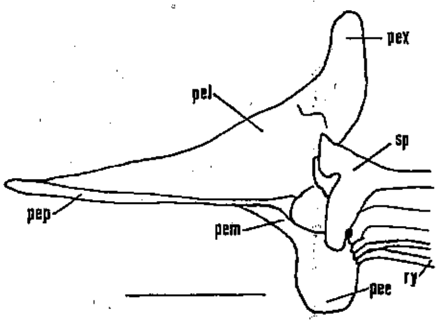


Fig. 17. *Cairnsichthys rhombosomoides*, MQU I.471, 47 mm SL. Pelvic fin in ventral aspect. Abbreviations: **pee**, pelvic medial process; **pel**, pelvic lateral plate; **pem**, pelvic medial plate; **pep**, pelvic central part; **pex**, pelvic caudodorsal process; **sp**, fin spine; **ry**, fin ray. Scale bar: 1 mm.

Scapula irregular-triangular, large foramen towards cranial margin. Dorsal 2 proximal radials at caudal margin of scapula, third proximal radial largely supported at caudodorsal angle of coracoid, large fourth proximal radial on coracoid. Coracoid caudal border concave, ventral angle lying superficial to cleithrum rostroventral process. Spine ('spur') and one or 2 dorsal rays on scapula, ventral rays supported on proximal radials, ossified spherical distal radials associated with base of dorsal 9 rays.

Supracleithrum broad (Fig. 16b), superficial to cleithral incisure, axialpectoral ligament attached to medial face. Posttemporal reduced, bearing stout dorsal ramus and short ventral ramus, poorly-developed sensory canal coursing vertically on lateral face. Dorsal postcleithrum ovate, deep to cleithrum caudodorsal process. Ventral postcleithrum dorsal angle at proximal third of first rib cranial face, lying deep to coracoid caudal border, extending ventral to horizontal plane through distal angle of second rib.

Pelvic fin with elongate central part (Fig. 17), reduced medial plate, opposite first to third intercostal space. Caudolateral process elongate, margin smooth, extending dorsally on lateral aspect of fourth rib distal angle. Pelvic medial process round, overlapping contralateral process. Pelvic cranial spinous process absent. Caudomedial spinous process well-developed, directed caudodorsally.

Subfamily Iriatherininae new subfamily

Diagnosis. External ramus of maxilla reduced, premaxilla compact; first anal pterygiophore plate-like; accessory axialpectoral ligament; odontodes around jaws.

Iriatherina Meinken

Diagnosis. A monotypic melanotaeniid genus displaying marked sexual dimorphism through extravagant fin development in males. Cranium narrow, gape reduced. Vomerine condyles directed rostroventrally. Ectopterygoid fused to palatoquadrate assemblage. Metapterygoid, and hyomandibula rostral process, absent. Rostral infraorbital series of 2 elements. Pungent spine at start of second dorsal and anal fins.

Iriatherina werneri Meinken
(Fig. 18a-b)

External morphology. Body slender, rhomboid, laterally-compressed. Mouth small, subterminal, oral fissure oblique. Upper jaw ventral profile convex, bearing row of large canine teeth extending outside mouth. Lower jaw extending rostrad to upper jaw, lower lip bulbous, denticulate in aged fish. Angle of mouth rostral to transverse plane through rostral margin of orbit. Orbit large, eye prominent. Rostrum depressed in preserved fish.

In adult males, first dorsal fin of VII-VIII filamentous soft spines, originating on cranial half of body, extending to caudal peduncle. Second dorsal fin of elongate spine and 7-8 rays, first 3 rays thick, unbranched and markedly elongate, remainder branching subterminally. Anal fin originating caudal to transverse plane through origin of first dorsal fin, of stout spine and 11-13 rays, first 4-5 rays thick, unbranched and elongate, next 7-9 rays branching subterminally. Second dorsal and anal fins arcuate-elongate, extending beyond incisure of caudal fin. Caudal fin symmetric, lyre-shaped, of 9+8 (dorsal + ventral) principal (branched and unbranched) rays, extending caudally approximately half-body length. Pectoral fin falcate, with elongate dorsal spur and 9-11 rays, dorsal ray unbranched. Pelvic fin narrow, of elongate lateral spine and 5 rays branching subterminally, medial ray attaching to

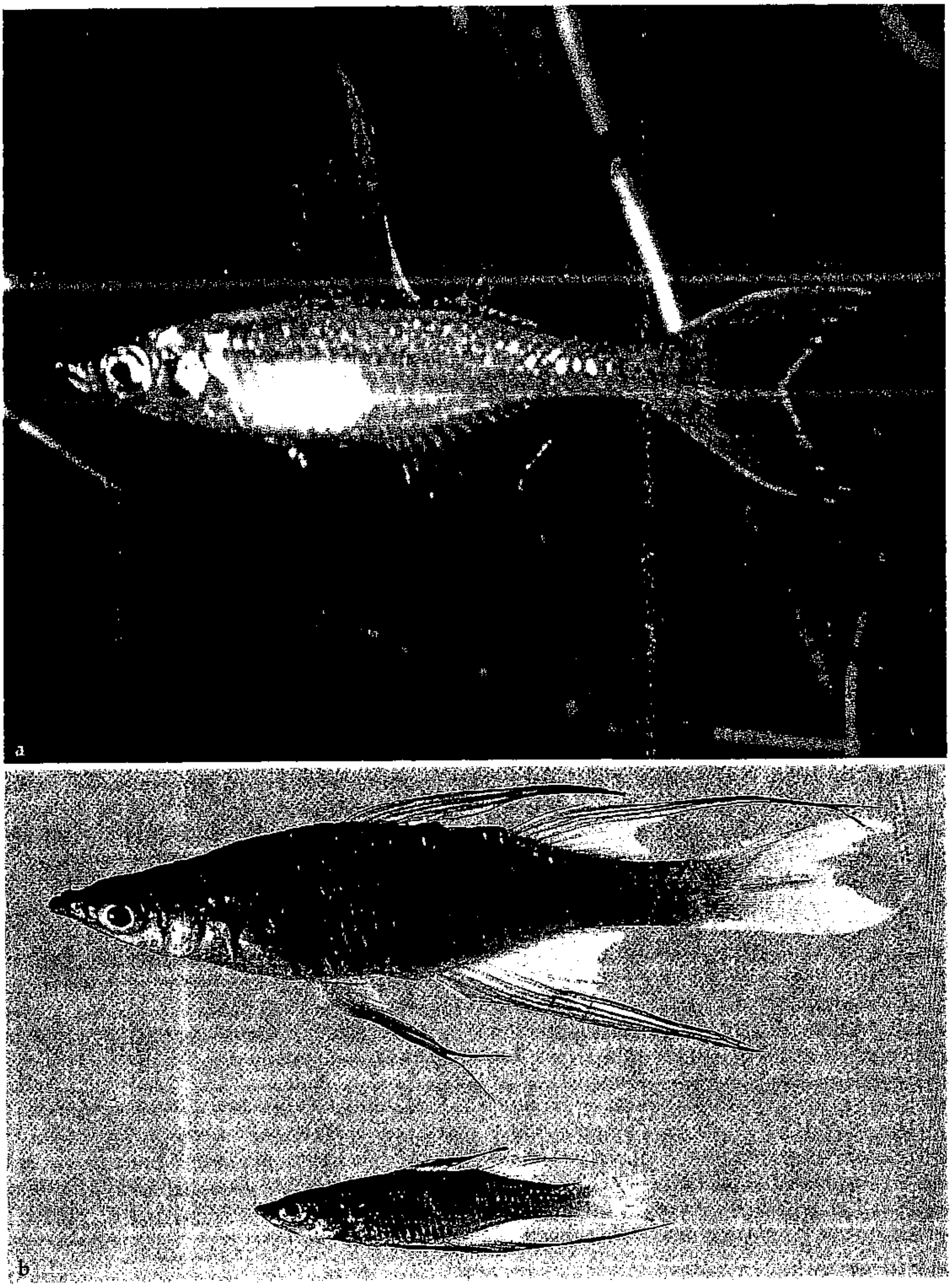


Fig. 18. *Iriatherina werneri*: **a**, aquarium specimen (photograph by Gerry Allen); **b**, MQU I.133, 39 mm SL (upper fish) and MQU I.463, 19 mm SL (lower fish).

ventral body wall via fine membrane. Pectoral tip almost attaining transverse plane through origin of caudal peduncle. Females and subadult males without elongation of fins.

Anus midway between base of last pelvic ray and origin of anal fin, urogenital papilla behind anus, both orifices in asquamate area bounded by pelvic-body membranes.

Body, except jaws and perigenital area, covered in deeply-crenulated cycloid scales. Scales in lateral series from axilla to origin of caudal fin 31-32, in transverse rows between origins of dorsal and anal fins 10-11.

Live colouration pale olive dorsally, belly and thoracic regions silver: in males, iridescent pale blue hue predominant, most intense in dorsal cervical region. Narrow midlateral band present. Elongate elements of second dorsal (in males) and first dorsal, anal and pelvic fins (both sexes) darkly pigmented. Specimens stored in 70% ethanol overall pale yellow, dorsum olive, midlateral band and elongate fin elements dark.

Largest uncleared specimen examined 39 mm SL (MQU I-133), largest specimen examined osteologically 34 mm SL.

Musculoskeletal anatomy

Cranium. Cranium narrow, snout level with roof of orbit (Fig. 19a-c). Vomer edentulous, elongate, narrow. Rostrodorsal margin elevated, contacting ethmoid cartilage. Condyles projecting rostroventrally beyond ethmoid.

Parasphenoid rostral process narrow, coursing from rostral angle (superior to vomer) to form ventral interorbital septum. Parasphenoid alae contacting rostroventral margin of prootics and terminating with caudal fossa ventral to basioccipital. Basisphenoid consisting of narrow median belophragm and short meningosts.

Ethmoid cartilage elongate-trapezoid, between transverse planes through base of vomerine condyle and rostral third of orbit. Ethmoid caudoventral median expansion forming (perforate) rostral interorbital septum. Lateral ethmoid forming transverse rostral limit of orbit, rostroventral angle produced as prominent lachrymal condyle, ventral margin directed caudomedially, bearing palatine sulcus. Lateral ethmoids making direct contact between interorbital septum (dorsally) and parasphenoid (ventrally). Dorsal mesethmoid forming large rhomboidal ossification on ethmoid dorsal surface. Rostral cartilage developing from bilateral spherical primordia (Fig. 20), forming rectangular block in adults (transverse axis greater than median axis), firmly attached to rostral margin of ethmoid.

Nasal elongate, with sensory canal open dorsally, nasal caudal angle not contributing to orbit. Frontal narrow, coursing from rostral contact with nasal, above ethmoid, to caudal angle above supraoccipital. Median interfrontal synthesis symmetric, interrupted rostrally by fontanel. Frontal medial lamina with sensory canal encircling sulcus demarcating supraorbital lamina. Frontal supraorbital lamina narrow, eye protruding beyond margin of orbit.

Supraoccipital forming caudal roof of cranial vault, large deltoid rostral process extending to intraorbital symphyseal cartilage, paired parietal processes extending bilaterally to sphenotics. Supraoccipital crest low.

Sphenotic contacting dorsocaudal rim of orbit, bearing ventrally directed postorbital process. Pterotic caudal to sphenotic, coursing caudomedially to contact epiotic ventral angle and exoccipital. Centrifugal indentation in superior lamina of pterotic, ventral surface bearing condyle articulating with hyomandibula. Temporal canal coursing obliquely from rostral angle, lateral to sphenotic, along pterotic to caudal termination in irregular exostoses. Intercalar small, lying in sulcus at caudal angle of pterotic-exoccipital synchondrosis.

Epiotic rounded, lateral ridge receiving posttemporal dorsal ramus and epaxial musculature. Exoccipital irregular, between supraoccipital dorsally and basioccipital ventrally. Caudal facet developed as ridge, from lateral angle deep to intercalar, coursing medially and forming tubercle of origin of accessory axialpectoral ligament. Exoccipitals fused in median plane on caudal surface of cranium, each exoccipital forming condyle articulating with parapophysis of first vertebra.

Basioccipital forming caudoventral braincase, with paired otic bullae. Axialpectoral ligaments rising bilaterally from caudal angle of basiocipital. Occipital condyle produced from caudal surface of basioccipital, articulating with first vertebral centrum. Prootic large, irregular, forming floor of cranial vault and rostral portion of otic bulla. Pterosphenoid elongate, medial margin slightly concave, forming rudimentary partition between orbit and braincase.

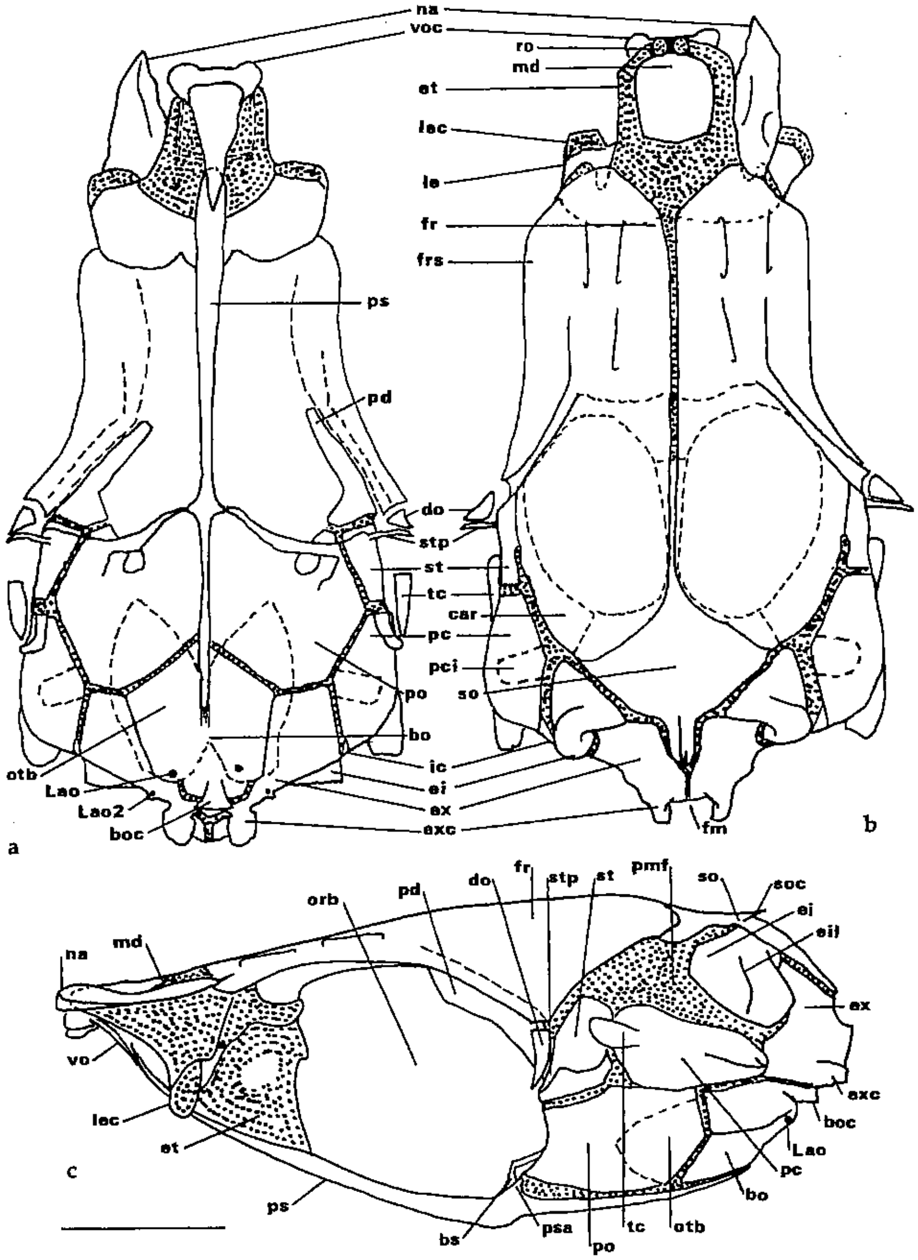


Fig. 19. *Iriatherina werneri*, MQU I.463, 20 mm SL. Cranium in: a, ventral aspect; b, dorsal aspect; c, lateral aspect. Abbreviations: **bo**, basioccipital; **boc**, basioccipital condyle; **bs**, basisphenoid; **car**, parietal cartilage; **do**, dermosphenoid; **ei**, epiotic; **eil**, epiotic lateral ridge; **et**, ethmoid cartilage; **ex**, exoccipital; **exc**, exoccipital condyle; **fm**, foramen magnum; **fr**, frontal; **frs**, frontal supraoccipital lamina; **ic**, intercalar; **Lao**, origin of axialpectoral ligament on basioccipital; **Lao2**, origin of accesory axialpectoral ligament on exoccipital; **le**, lateral ethmoid; **lec**, lateral ethmoid condyle; **md**, dorsal mesethmoid; **na**, nasal; **orb**, orbit; **otb**, otic bulla; **pc**, pterotic; **pci**, pterotic incisure; **pd**, pterosphenoid; **pmf**, posttemporal fossa; **po**, prootic; **ps**, parasphenoid; **psa**, parasphenoid ala; **ro**, rostral cartilage; **so**, supraoccipital; **soc**, supraoccipital crest; **st**, sphenotic; **stp**, sphenotic postorbital process; **tc**, temporal canal; **vo**, vomer; **voc**, vomerine condyle. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

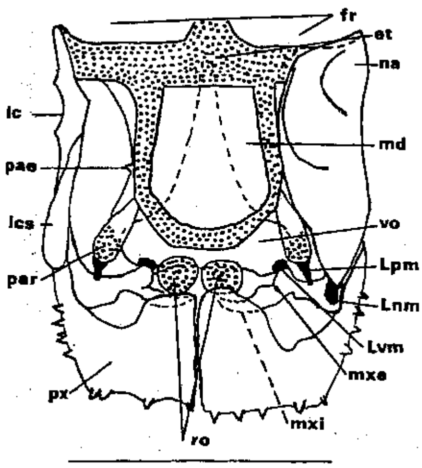


Fig. 20. *Iriatherina werneri*, MQU I.463, 24 mm SL. Facies in rostrodorsal aspect. Abbreviations: **et**, ethmoid cartilage; **fr**, frontal; **lc**, lachrymal; **lcs**, lachrymal subnasal shelf; **Lnm**, nasomaxillary ligament; **Lpm**, palatomaxillary ligament; **Lvm**, vomeromaxillary ligament; **md**, dorsal mesethmoid; **mxe**, maxilla external ramus; **mxi**, maxilla internal ramus; **na**, nasal; **pa**, palatine; **pae**, palatine ethmoid process; **par**, palatine rostral process; **px**, premaxilla; **ro**, rostral cartilage; **vo**, vomer. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

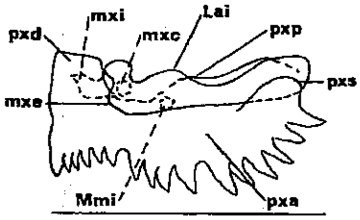
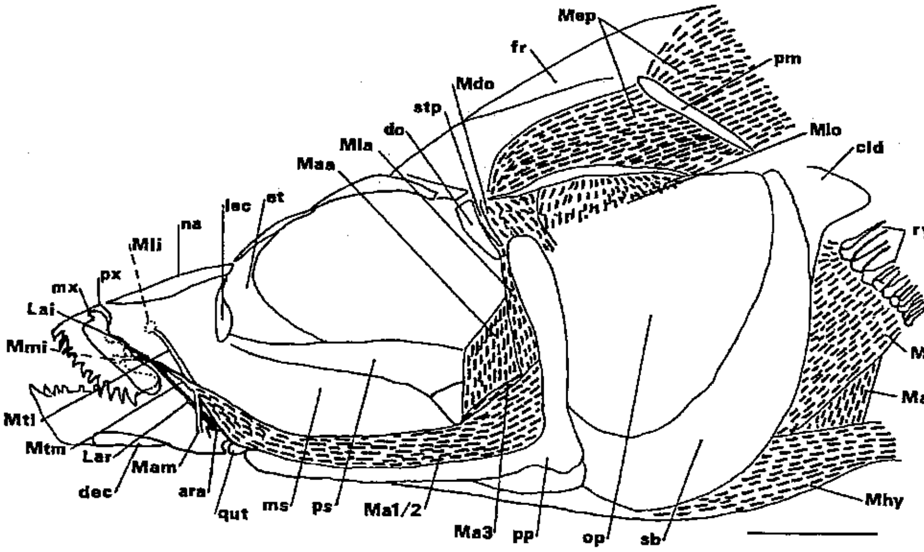


Fig. 22. *Iriatherina werneri*, MQU I.463, 20 mm SL. Maxilla and premaxilla in lateral aspect. Abbreviations: **Lai**, insertion of articularmaxillary ligament; **mmi**, insertion of adductor tendon to maxilla; **mxc**, maxillary condyle; **mxe**, maxilla external ramus; **mxi**, maxilla internal ramus; **pxa**, premaxilla alveolar ramus; **pxd**, premaxilla dorsal process; **pxp**, premaxilla postmaxillary process; **pxs**, premaxilla lateral sulcus. Scale bar: 1 mm. Dotted lines: obscured structures.

Jaws. Upper jaw not protrusible. Maxilla stout, external ramus reduced. Internal ramus tubiform, angular. Condyle for articulation with vomer at base of internal ramus, narrow meniscus between maxilla and vomer. Small sulcus for palatine caudal to condyle, rostral to prominent spinous process for insertion of articularmaxillary ligament. Maxillary branch of m. adductor mandibulae inserting on internal face of maxilla (Fig. 21), caudal to level of spinous process.

Premaxilla compact and continuous (lacking ventral notch) from rostral symphyseal margin to caudal angle. Broad, moderately elevated dorsal, and low postmaxillary, processes present. Premaxilla lateral face, caudal angle, with small sulcus for maxilla (Fig. 22). Premaxilla ventral margin bearing up to 3 rows of large caniniform teeth in aged fish.



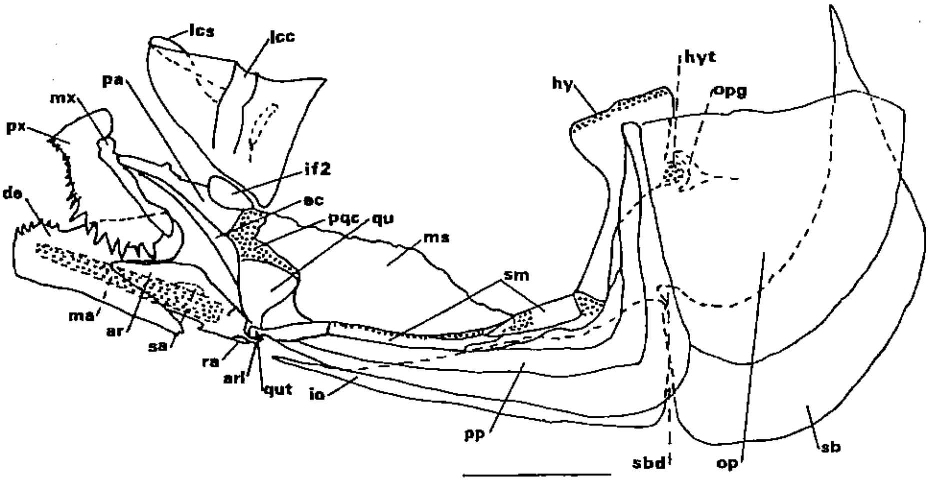


Fig. 23. *Iriatherina werneri*, MQU I.463, 22 mm SL. Suspensorium and jaws, infraorbitals displaced dorsally. Abbreviations: **ar**, articular; **arl**, articular lateral process; **de**, dentary; **ec**, ectopterygoid; **hy**, hyomandibula; **hyt**, hyomandibula tubercle; **if2**, infraorbital 2; **io**, interopercle; **lcc**, lachrymal neural canal; **lcs**, lachrymal subnasal shelf; **ma**, mandibular cartilage; **ms**, mesopterygoid; **mx**, maxilla; **op**, opercle; **opg**, opercle glenoid cavity; **pa**, palatine; **pp**, preopercle; **pqc**, palatoquadrate cartilage; **px**, premaxilla; **qu**, quadrate; **qut**, quadrate tubercle; **ra**, retroarticular; **sa**, supraangular; **sb**, subopercle; **sbd**, subopercle dorsal process; **sm**, symplectic. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

Dentary short, broad (Fig. 23). Fibrocartilaginous lower labial prominence over dentary symphyseal margin in adults, bearing odontodes. Teeth in 1-3 rows on dorsal margin of dentary, toward symphysis. Dentary coronoid process high.

Articular rhomboidal, lower than dentary coronoid process. Lateral surface of caudal angle giving origin to broad, short articularmaxillary ligament and small mandibular branch of m. adductor mandibulae. Mandibular cartilage coursing along internal face of dentary and articular. Supraangular bone elongate, on dosal surface of cartilage just rostral to caudal angle of dentary. Open mandibular sensory canal coursing along ventrolateral aspect of dentary and articular. Retroarticular small, elongate, at ventrocaudal angle of articular.

Suspensorium. Palatine rostral process resting in maxillary sulcus. Palatine attached ligamentously to caudal face of vomerine condyle. Rostroventral prominence well-developed, contacting ethmoid. Caudodorsal border contacting mesopterygoid, ventral ramus contacting quadrate and ectopterygoid (Fig. 23).

◁ Fig. 21. *Iriatherina werneri*, MQU I.463, 24 mm SL. Superficial musculature and ligaments of head and pectoral region, rostral infraorbitals removed. Abbreviations: **ara**, process of origin of articularmaxillary ligament; **cld**, cleithrum caudodorsal process; **dec**, dentary neural canal; **do**, dermosphenoid; **et**, ethmoid cartilage; **fr**, frontal; **Lai**, insertion of articularmaxillary ligament; **Lar**, articularmaxillary ligament; **lec**, lateral ethmoid condyle; **Ma1/2**, m. adductor mandibulae, A1and A2 sections; **Ma3**, m. adductor mandibulae, A3 section; **Maa**, m. adductor arcus palatini; **Mam**, m. adductor mandibulae, mandibular branch; **Map**, m. abductor profundus; **Mas**, m. abductor superficialis; **Mdo**, m. dilator operculi; **Mep**, epaxial musculature; **Mhy**, hypaxial musculature; **Mla**, m. levator arcus palatini; **Mli**, insertion of adductor tendon to lachrymal; **Mlo**, m. levator operculi; **mmi**, insertion of adductor tendon to maxilla; **ms**, mesopterygoid; **Mtl**, tendon of m. adductor mandibulae to lachrymal; **Mtm**, tendon of m. adductor mandibulae to maxilla; **mx**, maxilla; **na**, nasal; **op**, opercle; **pm**, posttemporal; **pp**, preopercle; **ps**, parasphenoid; **px**, premaxilla; **qut**, quadrate tubercle; **ry**, fin ray; **sb**, subopercle; **stp**, sphenotic postorbital process. Scale bar: 1 mm. Dotted lines: obscured structures; dashed lines: muscles.

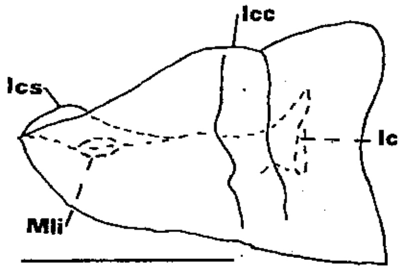


Fig. 24. *Iriatherina werneri*, MQU I.133, 34 mm SL. Lachrymal in lateral aspect. Abbreviations: lcc, lachrymal neural canal; lcd, lachrymal condyle; lcs, lachrymal subnasal shelf; Mli, insertion of adductor tendon on lachrymal; Scale bar: 1 mm. Dotted lines: obscured structures.

Quadrate somewhat square, rostroventral angle developed as tubercle to form ginglymus with caudal glenoid cavity of articular. Quadrate caudal ramus narrow, in close contact with symplectic. Ectopterygoid laminar, fused to rostromedial margin of palatoquadrate. Mesopterygoid elongate, narrow, forming rudimentary ventrolateral support for orbit. Symplectic forming elongate trabeculum, from quadratic incisure to synchondrosis with ventral angle of hyomandibula. Metapterygoid absent.

Preopercle with very elongate horizontal, and short vertical, rami, forming rightangular sensory canal open ventrally and caudally. Hyomandibula short, becoming narrow ventrally, lacking rostral process. Hyomandibula caudal margin forming large tubercle for articulation with opercle.

Opercular series. Interopercle narrow-deltoid, with shallow dorsal sulcus about origin of interhyal ligament. Opercle somewhat rectangular, caudoventral angle curved. Superior margin coursing caudodorsally. Medial face bearing large tubercle, with glenoid cavity. Subopercle arcuate, small process formed at rostrodorsal angle, subopercle coursing around caudoventral angle of opercle to termination as narrow caudodorsal filament.

Circumorbital series. Comprising 2 rostral, and one caudal, elements (cf. *Cairnsichthys*). Lachrymal deltoid, horizontal axis elongate (Fig. 24). Lateral face bearing vertical sensory canal. Medial face bearing subnasal shelf, and large tubercle caudally contacting lateral ethmoid condyle. Lachrymal tendon of m. aductor mandibulae inserting on small process immediately beneath rostral angle of subnasal shelf. Second infraorbital small, round, oriented obliquely, ventral to lachrymal sensory canal.

Dermosphenoid short, contacting rostral face of sphenotic postorbital process, continuous with caudal angle of frontal sensory canal.

Hyobranchial apparatus. Principle elements similar to, but narrower than, *Cairnsichthys*. Ceratobranchial toothpatches absent.

Glossohyal narrow, elongate, fused to small conical basihyal. Basibranchial series narrow, consisting of 3 osseous trabeculae and (caudal) cartilaginous nodule. Basibranchial bones articulating bilaterally with rostral angles of hypobranchials, cartilage nodule articulating bilaterally with fourth and fifth ceratobranchials.

Urohyal narrow, elongate, bearing fused small rostral condyles, low rostrodorsal process, and caudodorsal alae.

Dorsal hypohyal small, ventral hypohyal large, ligamentous attachment between ventral hypohyals. Ceratohyal collus fused to hypohyals, contacting 2 small rostral branchiostegals. Ceratohyal caudal region laminar, contacting 2 large intermediate branchiostegals. Ceratohyal caudal border forming synchondrosis with epihyal, reinforced dorsally with horizontal osseous trabeculae. Epihyal almost square, contacting caudal 2 branchiostegals, caudodorsal angle giving rise to interhyal ligament. Interhyal ligament with short interhyal sesamoid.

First hypobranchial almost straight, directed caudally, bearing 3 lamellar gill rakers. Second hypobranchial small, rectangular element. Third hypobranchial coursing around caudal angle of third basibranchial. First 4 ceratobranchials virtually straight. First ceratobranchial bearing 10-11gill rakers, longest element approximately equal to first hypobranchial. Fifth ceratobranchial expanded horizontally, bearing lower pharyngeal toothplate with 5-6 rows of caniniform teeth.

First epibranchial small, distal rami widely-spaced, uncinate process contacting tubiform interarcual cartilage. Second epibranchial small, angular. Third epibranchial slightly larger, more angular, than second. Fourth epibranchial large, rightangular, with prominent caudal muscular process.

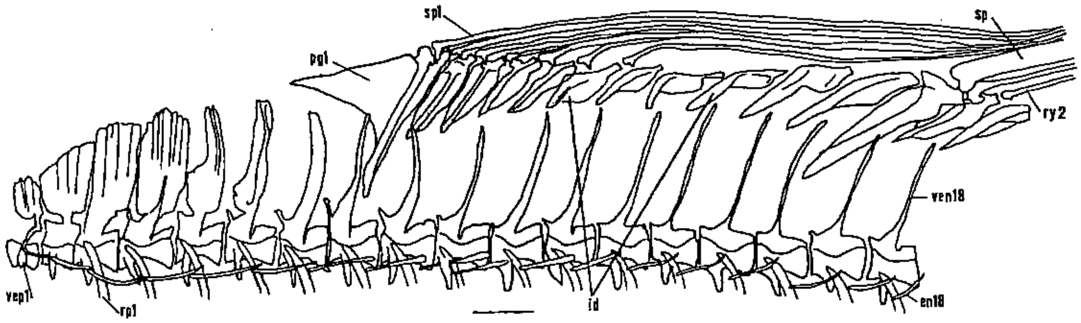


Fig. 25. *Iriatherina werneri*, MQU I.133, 34 mm SL. Vertebrae and dorsal fins, and supports. Abbreviations: **en**, epineural; **id**, interdorsal pterygiophores; **pg**, pterygiophore; **rp**, pleural rib; **ry**, fin ray; **sp**, spine; **ven**, vertebral neural process; **vep**, vertebral parapophysis. Scale bar: 1 mm.

First pharyngobranchial short, deltoid, edentulous. Second pharyngobranchial club-shaped, expanded ventral margin dentigerous. Third pharyngobranchial bearing large ovate third, and smaller square fourth, upper pharyngeal toothplates.

Vertebrae and ribs. Total vertebrae 32-34, precaudal 18-20, caudal 13-14, epineurals restricted to precaudal vertebrae. First vertebra small (Fig. 25), with reduced neural plate and small parapophyses articulating with exoccipital condyles. Second vertebra with large neural plate and moderate, laterally-directed parapophyses. Second vertebral parapophysis of some specimens contacting small (rib-like) trabeculum. Third to fifth vertebrae with large, broad neural plates. Neural plates of subsequent few vertebrae becoming narrow, reduced to neural spines from vertebra 8-10, penultimate vertebra lacking neural spine.

Pleural ribs rising from caudal facet of parapophyses of third to final precaudal vertebrae. Parapophyses of first few caudal vertebrae produced as ventrally-directed haemal arches, each subsequent vertebra producing haemal spine, haemal spine massively developed in penultimate vertebra.

Cranial dorsal zygapophyses present from second vertebra, maximally-developed from fourth to sixth verterbrae, diminishing caudally and absent in last 4-5 vertebrae. Caudal dorsal zygapophyses present but never well-developed, fused to neural spine in last 4 vertebrae. Cranial and caudal ventral zygapophyses small, cranial series slightly developed from vertebra 25/26 to 29/30, caudal series from vertebra 20/21 to 30/31.

Slight median exostosis associated with final 3 or 4 vertebrae (Fig. 26). Two epurals (in most specimens) above final 2 vertebral centrae. Terminal hemivertebra fused to urostyle, urostyle cranial aspect bearing small, irregular uroneural. Upper hypural plate consisting of fused hypurals 4-5 and unfused hypural 3, lower hypural plate of fused hypurals 1-2. Parhypural large and autogenous, or small and fused to cranial aspect of lower hypural plate. Small parhypurapophysis present, directed caudally. Preural ventral radial cartilage at cranial border of penultimate vertebral haemal spine, dorsal radial cartilage(s) variable.

Fins and girdles. First dorsal fin originating at level of transverse plane through vertebra 9-11 (Fig. 25). Large, deep cranially-expanded ptery-

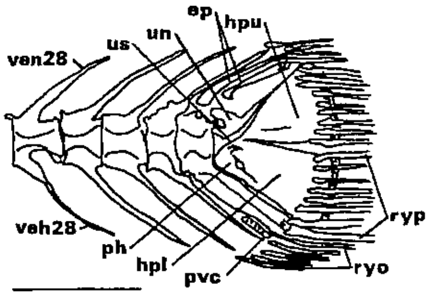


Fig. 26. *Iriatherina werneri*, MQU I.463, 20 mm SL. Caudal fin and last few vertebrae. Abbreviations: **ep**, epural; **hpl**, lower hypural plate; **hpu**, upper hypural plate; **ph**, parhypural; **pvc**, preural ventral cartilage; **ryo**, procurrent ray; **ryp**, principal ray; **un**, uroneural; **us**, urostyle; **veh**, vertebral haemal spine; **ven**, vertebral neural spine. Scale bar: 1 mm. Stippling: cartilage.

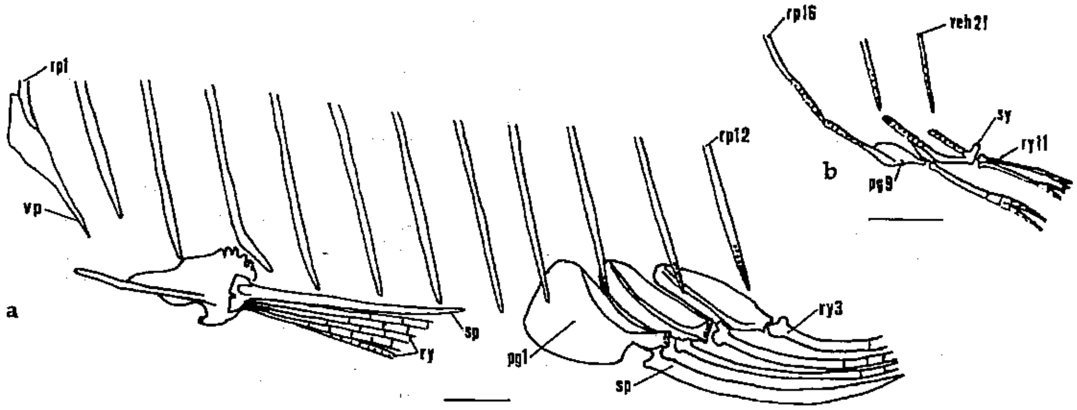
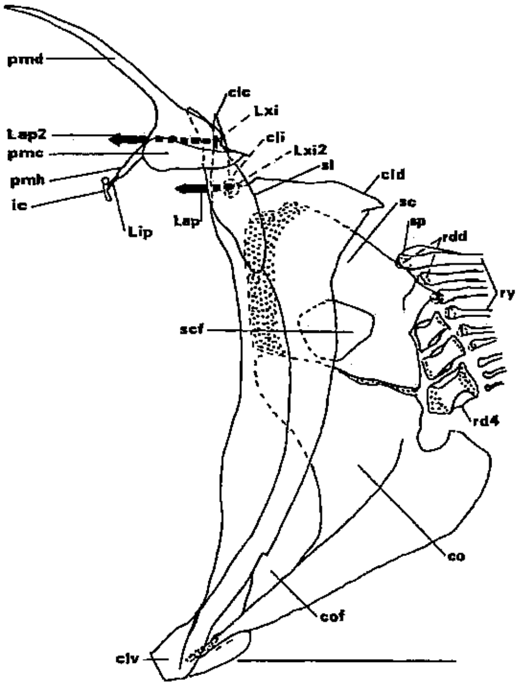


Fig. 27. *Iriatherina werneri*, MQU I.133, 34 mm SL. Ventral fins and supports: a, pelvic fin and first few anal fin elements; b, terminal anal fin elements. Abbreviations: pg, pterygiophore; rp, pleural rib; ry, fin ray; sp, fin spine; sy, fin stay; veh, vertebral haemal spine; vp, ventral postcleithrum. Scale bar: 1 mm. Stippling: cartilage.

giophore supporting cranial 2 spines, subsequent spines supported individually by single pterygiophore. Four to five obtusely-angled interdorsal pterygiophores. Second dorsal fin commencing at level of transverse plane through vertebra 18-21 (ie. level with caudal limit of visceral cavity). Massive deep pterygiophore supporting spine and first ray, subsequent rays supported individually by single pterygiophore, final 2 rays on common pterygiophore. Second dorsal fin caudal pterygiophore at level of transverse plane through vertebra 24-26.

Anal fin originating at level of transverse plane through vertebra 15-17. Eight pleural ribs caudal to origin of anal fin. Spine and first ray supported by large, laminar pterygiophore (Fig. 27), subsequent rays supported individually by single pterygiophore, final 2 rays on common pterygiophore. Anal fin caudal pterygiophore approximately one vertebral centra cranial to level of second dorsal fin caudal pterygiophore.

Caudal fin commencing at level of final vertebra, with 5 dorsal and 5 ventral procurrent rays.



◁

Fig. 28. *Iriatherina werneri*, MQU I.463, 22 mm SL. Pectoral fin. Abbreviations: clc, cleithrum craniodorsal spine; cld, cleithrum caudodorsal process; cli, cleithrum dorsal incisure; clv, cleithrum ventral process; co, coracoid; cof, coracoid foramen; ic, intercalar; Lap, axialpectoral ligament; Lap2, accessory axialpectoral ligament; Lip, ligament from intercalar to posttemporal horizontal ramus; Lxi, insertion of axialpectoral ligament; Lxi2, insertion of accessory axialpectoral ligament; pmc, posttemporal neural canal; pmd, posttemporal dorsal ramus; pmh, posttemporal horizontal ramus; rd, proximal radial; rdd, distal radial; ry, fin ray; sc, scapula; scf, scapula foramen; sl, supracleithrum; sp, spine. Scale bar: 1 mm. Stippling: cartilage; dotted lines: obscured structures.

Pectoral girdle rounded (Fig. 28), below horizontal plane through vertebral centrae, extending cranioventrally to intercleithral cartilage at level of transverse plane midway between rear of orbit and occiput. Cleithrum bearing craniodorsal spine and caudodorsal process, separated by dorsal incisure. Axialpectoral ligament coursing centripetally through base of incisure, accessory axialpectoral ligament inserting on spine. Cleithrum ventral process expanded.

Scapula rhomboidal, longer axis horizontal, large foramen toward ventral border. Dorsal 3 proximal radials supported at caudal margin of scapula in subadult fish, third radial tending to migrate ventrad in aged fish, fourth proximal radial supported at caudodorsal margin of coracoid. Coracoid of broad dorsal, and narrow arcuate caudal, portions, coursing cranioventrally to contact ventral expansion of cleithrum. Dorsocaudal angle of coracoid not extended as shelf below fourth radial. Expansive foramen between cleithrum and coracoid.

Pectoral spur and 3 rays supported on scapula, ventral rays on proximal radials. Distal radials spherical, associated with base of largest 7-8 rays, ossifying in aged fish.

Supracleithrum narrow, axialpectoral ligament attaching to medial face. Posttemporal small, dorsal and ventral rami widely separated, well-developed sensory canal oriented horizontally. Ligament between intercalar and posttemporal ventral ramus partially ossified in aged fish. Dorsal postcleithrum ovate. Ventral postcleithrum short, on cranioventral aspect of reduced first pleural rib, extending ventrally toward tip of second rib.

Pelvic girdles joined at medial processess via strong interpelvic ligament, in ventral midline. Pelvic caudolateral processes attached ligamentously to fourth pleural rib, in most specimens (Fig. 29). Pelvic median lamina opposite first 3 (or 2) intercostal spaces. Small cranial, and large oblique caudal, spinous processes present. Pelvic fin spine robust.

Cairnsichthys rhombosomoides and *Iriatherina werneri* possess autapomophies confirming the monotypic status of each species. This advancement in knowledge of melanotaeniid anatomy provides the basis for the following reappraisal of melanotaeniid systematics

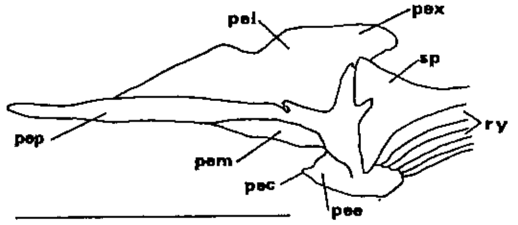


Fig. 29. *Iriatherina werneri*, MQU I.463, 20 mm SL. Pelvic fin in ventral aspect. Abbreviations: **pec**, pelvic cranial spinous process; **pee**, pelvic medial process; **pel**, pelvic lateral plate; **pem**, pelvic medial plate; **pep**, pelvic central part; **pex**, pelvic caudodorsal process; **sp**, fin spine; **ry**, fin ray. Scale bar: 1 mm.

Phylogenetic analysis of Melanotaeniidae

Introduction

The expansion of museum collections, improved preparation techniques and refinement of optical instrumentation has lead to increased precision in the recognition, and definition, of phenetic characters. In principle, the method of outgroup comparison eliminates subjectivity in the interpretation of character-state polarity. The transcription of character states into programmable data can then be used to generate phylogenetic analyses, based on parsimony or conforming to other selective constraints.

The analyst may identify a single apomorphic state with more than one 'character' – and conversely identify a group of 'characters' derived from a single apomorphic state (Funk, 1983).

Methods. The following classification is adopted: Atherinomorpha is considered to be the sister group of (Percomorpha + Mugilomorpha) (Stiassny, 1990). Atheriniformes is considered to be the sister group of (Cyprinodontiformes + Beloniformes) (Parenti, 1984). Atherinopsidae and Notocheiridae (= Isonidae) are considered plesiomorphic atheriniform families (Dyer & Chenoff, 1996). The derived atheriniform families (Infraorder Atherines; Dyer & Chenoff, 1996) are considered to be Atherionidae (*Atherion*), Phallostethidae (including *Dentatherina*; Dyer & Chernoff, 1996), Atherinidae, Telmatherinidae, Pseudomugilidae and Melanotaeniidae.

Characters are listed in the sequence followed previously for anatomical descriptions. Characters used in the analysis define atherine families and/or demonstrate variation within Melanotaeniidae. Some characters reported in other analyses of Atheriniformes were found to be inconsistent or incorrect; others are not considered here. Where appropriate, acknowledgement is made for initial definition of a character.

Forty-six characters distributed across 22 taxa were encoded. Character states were designated plesiomorphic (0), derived (1, 2...) or not applicable (n/a) by the method of outgroup comparison. Taxa displaying more than one character state were interpreted as polymorphic, all characters were considered unordered, and all characters were assigned equal weight. Outgroups were selected from representative percomorph, mugilid, cyprinodontiform, beloniform, atherinopsid (Menidiinae) and notocheirid (*Iso*) taxa.

Phylogenetic analysis was conducted with PAUP version 3.1.1. The search for most-parsimonious trees was conducted using 'bootstrap' (100 replicates) and simple heuristic methods, and consensus of resultant trees was obtained by majority-rule (Swofford, 1993).

Characters

In the present analysis, characters 25, 28 and 33 describe fin spination, body shape, and post-cleithral morphology, respectively. Each of these is considered a single anatomical trait. To dissociate, for example, character 25 into four (presence/absence of spine in first dorsal, second dorsal, pectoral, and anal, fins) or more (presence of more than one spine in a fin) characters may overemphasise (in computer-generated phylogenies) an evolutionary tendency.

1. Ethmoid. The ethmoid is ossified in mugilomorphs and percomorphs. Rosen (1964) reported a uni- or bi-laminar discoidal mesethmoid in atherinomorphs. Cyprinodontiformes have a bilaminar discoidal ossification of the ethmoid. After Tigano & Parenti (1988), a dorsal ossification of the ethmoid is herein termed the dorsal mesethmoid.

Saeed et al. (1994) reported a nasal septum in *Myxus*, *Iso* and atherinopsids. The ethmoid is ossified in the median plane, from the dorsal mesethmoid to the dorsal margin of the vomer and/or parasphenoid, in mugilomorphs, percomorphs, *Iso*, *Bedotia* and *Rheocles*. In menidiines, the dorsal mesethmoid interdigitates with one (or two) flange(s) extending caudodorsally from the rostrodorsal border of the vomer. In other Atheriniformes there is cartilage above the vomer and parasphenoid, the cartilage intervening between the latter 2 bones and dorsal mesethmoid.

A dorsal mesethmoid is present in *Atherion*, *Dentatherina*, phallostethines, atherinids, telmatherinids and melanotaeniids. However, the dorsal mesethmoid was reported to be absent in *Notocheirus*, the atherinid genus *Craterocephalus* (Patten, 1978) except *C. mugiloides* (Crowley, 1990) and pseudomugilids (Saeed et al., 1989). Absence of the dorsal mesethmoid in pseudomugilids is associated with truncation of the rostrum, and close approximation of contralateral lateral ethmoids (Saeed et al., 1989). In telmatherinids also, the lateral ethmoids are close to the median plane.

Saeed & Ivantsoff (1991) described the dorsal mesethmoid as small in telmatherinids and large in melanotaeniids.

(0 = ethmoidal ossified in vertical and horizontal planes; 1 = dorsal and ventral mesethmoids; 2 = single dorsal mesethmoid, rostral margin contacting vomer dorsal flange; 3 = dorsal mesethmoid, no flange from vomer; 4 = ethmoid unossified).

2. Oral anatomy, upper jaw morphology and protrusibility. Plasticity of the prehensile apparatus probably facilitated adaptability to novel dietary regimes, in new habitats, during the evolution of Galapagos finches (Darwin, 1859), acanthopterygians (Greenwood et al., 1966) and other vertebrate groups. Mugilids have a non-protrusible upper jaw, while percomorphs may have highly-protrusible jaws.

Plesiomorphically, the atheriniform premaxilla is loosely fixed to the rostral cartilage, which is in turn loosely attached to the ethmoid, affording the upper jaw a substantial degree of protrusibility (Alexander, 1967). *Agonostomus*, menidiines, atherinids, telmatherinids, pseudomugilids and phallostethines generally have: a small gape; a narrow vomer with rostroventrally-projecting condyles; a maxilla with a small external, and larger tubiform internal, ramus; the maxillary tendon of m. adductor mandibulae inserting on the (medial face of the) caudal maxilla ('lower maxillary shaft'; Greenwood et al., 1966); an elongate premaxilla dorsal process; a premaxilla postmaxillary process; an elevated dentary coronoid process; a cylindrical submaxillary meniscus; and an elongate rostral cartilage. Variations include a relatively low premaxilla dorsal process (*Atherinomorus, Alepidomus* and *Teramulus*) and extravagant premaxilla postmaxillary process (*Atherina* spp. and telmatherinids).

Saeed et al. (1989) diagnosed pseudomugilids with a tall articular (although this is not the case in *Pseudomugil novaeguineae*, which has a distinctive large gape and low dentary and articular) and described *Kiunga* with the maxilla articulating directly with the lateral ethmoid. Both fish have a non-protrusible upper jaw.

Richardson (1843) noted the angular mouth of *Melanotaenia nigrans*. Regan (1903) described *Bedotia* with a notch in the alveolar margin of the premaxilla. Smith (1965) described *Teramulus* with a premaxilla notch. Stiassny (1990) noted that the notch was prominent in *Bedotia*, and less-developed in *Rheocles*. Allen (1980: fig. 6) described an 'abrupt bend' between rostral and alveolar rami of the premaxilla in some melanotaeniid genera, and coincidentally illustrated the notch. Opposite the notch is the dentary labial prominence, bearing large caniniform teeth in melanotaeniids except *Iriatherina*, which has a peculiar reduced mouth.

Saeed et al. (1994) referred to the portion of the cranium, rostral to the lateral ethmoid incisure, as the rostrum, and characterised melanotaeniids with a long rostrum. The lateral ethmoid is extended rostrally ('well-developed anterior arm of the lateral ethmoid'; Patten, 1978), on the lateral facet of the ethmoid (bilaterally). *Cairnsichthys* and *Rhadinocentrus* have a somewhat truncated rostrum.

In melanotaeniids the upper jaw is non-protrusible. De Beaufort (1922) suggested that firmly fixing the upper jaw, as in *Chilatherina*, facilitated scraping algae from submersed objects. Associated with a fixed upper jaw are: a wide gape; a broad vomer with rostrolaterally-projecting condyles; an elongate maxillary external ramus; maxillary tendon of m. adductor mandibulae inserting on the (medial face of the) rostral maxilla; a low premaxillary dorsal process; a low dentary coronoid process; a discoidal submaxillary meniscus; and a fixed, piriform rostral cartilage. *Iriatherina* has a small head, reduced gape, small maxilla external ramus, and somewhat raised dentary coronoid process.

(0 = upper jaw protrusible; 1 = upper jaw not protrusible, otherwise pseudomugilid-like oral anatomy; 2 = upper jaw not protrusible).

3. Ethmomaxillary ligament. In mugilomorphs, percomorphs and most Atheriniformes (including most atherinids, telmatherinids and pseudomugilids), this ligament is elongate, originating bilaterally on the lateral ethmoid or caudal region of the dorsal mesethmoid, and inserting on the maxilla external ramus. Dyer & Chernoff (1996) noted that the ligament is attached mid-length to the palatine in atherinopsids.

In *Chilatherina, Glossolepis, Melanotaenia* and most Madagascan melanotaeniids, the ethmomaxillary ligament originates on the rostral region of the dorsal mesethmoid. At this juncture, ossified processes develop in aged fish. The ligament inserts at the caudal margin of the bifurcation of the maxilla.

The ligament is absent in *Craterocephalus* (Patten, 1978), which has an autapomorphic arrangement of rostral ligaments, and absent (replaced by connective tissue, between the rostral angle of the lateral ethmoid and the caudal margin of the bifurcation of the maxilla) in *Cairnsichthys, Rhadinocentrus, Iriatherina, Rheocles sikorae* and *R. wrightae* (Stiassny, 1990).

(0 = ethmomaxillary ligament elongate, from lateral ethmoid or caudal dorsal mesethmoid; 1 = ligament attached mid-length to palatine; 2 = ligament from rostral dorsal mesethmoid; 3 = ligament absent).

4. Vomerine condyles. Dyer & Chernoff (1996) identified curvature of the ventral face of the vomer as autapomorphic for Atheriniformes. In atheriniform outgroups and most Atheriniformes, the vomerine condyles project rostroventrally. Melanotaeniids (except *Iriatherina*) have a broad head, and the condyles project rostrolaterally. In *Cairnsichthys*, the condyles are caudally-placed.

(0 = vomerine condyles directed rostrally; 1 = condyles directed rostrolaterally; 2 = condyles directed caudolaterally)

5. Vomer-mesopterygoid ligament. A short ligament connects the vomer to the mesopterygoid rostral angle in pseudomugilids (Ivantsoff et al., in press). Stiassny (1986) proposed that the basal acanthomorph condition was 2 palatovomerine ligaments (bilaterally) binding structures in this region.

(0 = vomer-mesopterygoid ligament absent; 1 = ligament present).

6. Nasal forming part of orbit. In atherinids, the lateral margin of the lateral ethmoid is vertical or slightly arcuate. In those atherinids in which the margin is arcuate, the caudolateral angle of the nasal is incorporated into the orbit, and is joined ligamentously to the lateral ethmoid.

In *Atherion* (Patten, 1978), *Cairnsichthys* and phallostethines (Roberts, 1971) the lateral margin of the lateral ethmoid is arcuate, and the nasal contributes substantially to the rim of the orbit. In *Atherion* the frontal supraorbital lamina is narrow, the dorsolateral margin of the eye is not covered, and the arcuate nasal is denticulate.

In *Cairnsichthys* and phallostethines, the frontal and nasal are broad, the lateral ethmoid lateral ramus is relatively truncated and dorsomedially tapers to make a reduced contact with the nasal. The nasal extends caudally, dorsal to the lateral ethmoid, and forms a broad contact with the frontal. In *Bedotia*, the nasal and frontal are broad, the lateral ethmoid has an arcuate lateral margin, but only the caudolateral angle of the nasal is in the orbit. Other melanotaeniids have a narrower nasal and frontal, the lateral margin of the lateral ethmoid is vertical, and the caudolateral angle of the nasal is virtually excluded from the orbit.

(0 = nasal not in orbit; 1 = nasal partially in orbit; 2 = nasal substantially in orbit).

7. Temporal sensory shelf/canal. Extrascapular bones, enclosing the laterosensory canal in the temporal region, are present in mugilids, *Iso* and some atherinopsids (Saeed et al., 1994). Atherinids, *Atherion*, telmatherinids, *Iriatherina*, *Melanotaenia*, *Chilatherina* and *Glossolepis* have a temporal sensory canal, coursing along the lateral aspect of the sphenotic and pterotic. In *Dentatherina*, the canal is composed of distinct sphenotic and pterotic portions (Patten & Ivantsoff, 1983). *Bedotia*, *Rheocles*, *Cairnsichthys* and *Rhadinocentrus* have a temporal shelf, discontinous at the junction of sphenotic and pterotic portions. Pseudomugilids have an undivided temporal shelf.

(0 = extrascapulars present; 1 = temporal sensory canal; 2 = entire temporal shelf; 3 = discontinuous temporal shelf).

8. Basisphenoid. The basisphenoid is absent in *Rhadinocentrus* (Aarn & Ivantsoff, 1996) and phallostethines. In some *Pseudomugil* spp., the basisphenoid belophragm consists of 2 parallel trabeculae.

(0 = basisphenoid present; 1 = basisphenoid absent).

9. Articularmaxillary ligament. Patten (1978) described this ligament as 'diffuse' in *Craterocephalus*. It is absent in pseudomugilids except *Kiunga* (Saeed et al., 1989).

(0 = articularmaxillary ligament present; 1 = ligament diffuse; 2 = ligament absent).

10. Premaxillary sulcus. The premaxilla alveolar ramus bears a deep sulcus, in which the maxilla rests, in *Cairnsichthys*. In *Bedotia* and *Iriatherina*, a sulcus forms at the premaxilla caudal angle. In *Atherina*, *Pseudomugil novaeguineae*, *Rheocles*, *Rhadinocentrus* and *Melanotaenia* there is a shallow shelf ('maxillary shelf') on the lateral facet of the premaxilla.

(0 = premaxilla sulcus absent; 1 = small sulcus present; 2 = large sulcus present).

11. Dentary and premaxillary teeth. *Agonostomus* has small teeth associated with the oral cavity, on the jaws, vomer, palatine, ectopterygoid, mesopterygoid and hyobranchial apparatus. Reduction of toothed surfaces, and anisometry of teeth, has occurred during the evolution of Atheriniformes. The dentary and premaxillary teeth of menidiines, *Iso*, atherinids, *Atherion*, *Dentatherina* and most telmatherinids are uniformly small and conical. *Kalyptatherina*, *Kiunga*, *Pseudomugil novaeguineae*, *Bedotia*, *Rheocles*, *Cairnsichthys*, *Rhadinocentrus*, some *Melanotaenia* spp., *Chilatherina* and phallostethines display moderate anisometry of dentary and premaxillary teeth, and have some caniniform teeth. Other melanotaeniids and pseudomugilids have a reduced gape, with fewer teeth on the premaxilla, and there is pronounced anisometry of the premaxillary teeth.

(0 = dentary and premaxillary teeth isometric; 1 = teeth moderately anisometric; 2 = premaxillary teeth markedly anisometric).

12. Labial ligament hyaline cartilage. Dyer & Chernoff (1996) identified hyaline cartilage in the labial ligament as a phallostethid autapomorphy

(0 = labial ligament without hyaline cartilage; 1 = hyaline cartilage present).

13. Lachrymal tendon of m. adductor mandibulae. Melinkat & Zeiske (1979: fig. 5) described the insertion of the lachrymal tendon in *Bedotia geayi* as being toward the rostral angle of the lachrymal subnasal shelf. Stiassny (1990) identified the tendon as a synapomorphy of (Atheriniformes + Beloniformes); homology is discussed by Dyer & Chernoff (1996).

In most *Craterocephalus* spp. and *Rhadinocentrus* the tendon inserts on a small process ventral to the subnasal shelf. Some *Rhadinocentrus* specimens (QM I.14520) from the type locality have a bifid ligament, with branches to both insertions (Aarn & Ivantsoff, 1996). In *Cairnsichthys*, the tendon inserts towards the caudal angle of the subnasal shelf. In some *Craterocephalus* spp. and pseudomugilids, the tendon inserts on the rostromedial margin of the lachrymal, ventral to the rostral angle of the subnasal shelf. In other melanotaeniids, the tendon inserts on the lachrymal shelf.

(0 = lachrymal tendon absent; **1** = tendon inserting on subnasal shelf; **2** = tendon ventral to subnasal shelf; **3** = tendon to margin of lachrymal).

14. Palatine rostral attachments. In some atherinids (Patten, 1978), telmatherinids, *Atherion, Dentatherina*, melanotaeniids and phallostethines (Dyer & Chernoff, 1996), the palatine rostral process rests in, or against, a sulcus on the maxilla, forming a ginglymus. The articulation may be fixed with connective tissue, or a palatomaxillary ligament (in larger fish). The palatine is also attached with connective tissue toward the rostral angle of the nasal ventromedian crest, and to the ethmoid at the palatine ethmoid process.

In atherinids, telmatherinids, and pseudomugilids (Saeed et al., 1989), the palatine is directed dorsally, attaching to the nasal ventromedian crest by a variously-developed nasopalatine ligament. In *Craterocephalus* (Patten, 1978) the palatine is reduced rostrally, directed dorsally, and attached to the prominent (but occasionally reduced; Crowley & Ivantsoff, 1992) nasal ventral process, located midlength along the nasal medial border.

Caudoventral to the palatine rostral process is a rostroventral process ('ventral anterior process of palatine'; Patten, 1978) attaching to the lateral ethmoid. The process is robust in those groups with a well-developed ginglymus, but reduced in some atherinids (including *Craterocephalus*; Dyer & Chernoff, 1996), phallostethids and pseudomugilids (Saeed et al., 1989). In menidiines the palatine also supports the ethmomaxillary ligament (character 3).

(0 = palatine robust, forming ginglymus with maxilla; **1** = palatine directed dorsally; **2** = palatine reduced, attached to nasal ventral process).

15. Metapterygoid. In pseudomugilids (Saeed et al., 1989), except *Scaturiginichthys*, and some phallostethines the metapterygoid is fused to the symplectic. In *Iriatherina, Kiunga* and other phallostethines it is absent.

(0 = metapterygoid autogenous; **1** = metapterygoid fused to symplectic; **2** = metapterygoid absent).

16. Number of rostral infraorbitals. Rosen (1964) cited reduction of the circumorbital bone series as an atherinomorph characteristic. *Atherion, Dentatherina*, atherinids, telmatherinids, *Chilatherina, Glossolepis* and *Melanotaenia* have 3 rostral infraorbitals – the lachrymal and 2 accessory rostral infraorbitals. The 2 accessory bones displaying varying degrees of fusion in some *Craterocephalus* spp. (Crowley & Ivantsoff, 1992), *Glossolepis multisquamata* (Dyer & Chernoff, 1996) and some *Melanotaenia* spp. The rostral series is reduced to 2 elements in phallostethines, *Iriatherina, Bedotia, Rheocles* and *Cairnsichthys*. Further reduction to a solitary, tall lachrymal occurs in Beloniformes (Dyer & Chernoff, 1996), Cyprinodontiformes, *Rhadinocentrus* and pseudomugilids.

(0 = 3+ rostral infraorbitals, accessory infraorbitals occasionally fused; **1** = 2 rostral infraorbitals; **2** = lachrymal only).

17. Lachrymal caudal notch. The lachrymal of atheriniform outgroups has a different morphology to that of Atheriniformes. In atherinomorphs, the lateral ethmoid forms a cartilaginous condyle, which contacts the caudal face of a tuberosity on the medial surface of the lachrymal. In fish with a narrow head, the condyle may project laterally beyond the tuberosity forming a notch in the caudal margin of the lachrymal. Dyer & Chernoff (1996) cited this as an atherinid autapomorphy, although not well-developed in some *Craterocephalus* spp. The notch is well-developed in telmatherinids except *Kalyptatherina* (Aarn et al., in press).

(0 = non-atherinomorph lachrymal; **1** = lachrymal notch absent; **2** = lachrymal notch present).

18. Branchiostegals. Most Atheriniformes have 6 branchiostegals bilaterally. The number is reduced in *Iso, Dentatherina* (Patten & Ivantsoff, 1983), phallostethines, *Kiunga* (Saeed et al., 1989) and *Scaturiginichthys* (Ivantsoff et al., 1991).

(0 = 6 branchiostegals; 1 = fewer than 6 branchiostegals).

19. Epibranchials. In mugilids, the epibranchials are of approximately equivalent size but different geometry. The first epibranchial has a very small uncinate process, contacting a trabecular interarcual cartilage. Dyer & Chernoff (1996) identified absence of the uncinate process as a phallostethid apomorphy.

Epibranchial IV is much larger than epibranchials I-III in most Atheriniformes and outgroups. In atherinids and telmatherinids, epibranchials III-IV are of similiar size, somewhat larger than epibranchials I-II. The uncinate process is short. In melanotaeniids the uncinate process is longer. In *Rhadinocentrus* the interarcual cartilage is absent (absent also in some Cyprinodontiformes; Parenti, 1981), the uncinate process is long (Aarn & Ivantsoff, 1996). In pseudomugilids except *Kiunga* (Saeed et al., 1989) the processes are elongate and equal, the interarcual cartilage is small and near-spherical.

(0 = epibranchials approximately equal and/or uncinate process absent or short; 1 = epibranchial IV massive, uncinate process short; 2 = epibranchials III and IV approximately equal, uncinate process short; 3 = epibranchial IV massive, uncinate process somewhat elongate; 4 = epibranchial IV massive, uncinate process somewhat elongate, interarcual cartilage absent; 5 = epibranchial IV massive, uncinate processes elongate).

20. Number of vertebrae. Greenwood et al. (1966) cited 'vertebrae commonly numbering 24' in acanthopterygians, and 'vertebral number high' in atherinomorphs. Mugilomorphs have 24-26 vertebrae (Gosline, 1962), whereas Beloniformes (less Adrianichthyoidei) have 60+. Lindsey (1988) summarised environmental factors known to cause meristic variation, including vertebral number.

The number of vertebrae is variable in Atheriniformes. *Iso*, menidiines, *Atherion*, *Dentatherina* and most atherinids generally have 40+ vertebrae. Crowley & Ivantsoff (1992) stated 29-39 vertebrae as the range in *Craterocephalus*. Telmatherinids have 32-38 vertebrae (except *Kalyptatherina*, 29-31). Melanotaeniids have 32-41 vertebrae. Pseudomugilids have 28-31 vertebrae (except *Pseudomugil novaeguineae* 34-36, and *Scaturiginichthys vermeilipinnis* 27-28). Phallostethines have 31-40 vertebrae (Parenti, 1989).

Allen (1980) postulated that 40+ vertebrae was a plesiomorphic state (relative to melanotaeniids). Reduction of total vertebrae may be associated with attaining maturity at a small size (in *Rhadinocentrus*, *Iriatherina* and pseudomugilids), and/or development of a lacustrine deep-body form.

(0 = modally 24-26 vertebrae; 1 = modally 27-31 vertebrae; 2 = modally 32+ vertebrae).

21. Cranial vertebral neural processes. Elongation of either (dorsally) vertebral neural processes or (ventrally) pleural ribs may result in a deep body-form. Slender Atheriniformes, atherinids, telmatherinids and pseudomugilids have a small, narrow first vertebral neural process. Chedhomme & Gaudant (1984: fig. 17) illustrated *Paleoatherina formosa* with tall cranial vertebral neural processes, but the first vertebra was not figured.

Saeed et al. (1994) proposed an elongate, broad first neural process, providing attachment for some epaxial musculature, to be plesiomorphic. The first vertebral neural process is moderately developed in *Telmatherina ladigesi*, *Bedotia*, *Rheocles* and *Iriatherina*. Other melanotaeniids have a large first neural process.

The subsequent 3-6 vertebrae of telmatherinids and melanotaeniids have tall, enlarged 'neural plates'; these processes are particularly high in *Chilatherina*, *Glossolepis* and most *Melanotaenia* spp.

(0 = small first vertebral neural process; 1 = moderate to broad first process; 2 = broad and tall process).

22. Caudal vertebral exostoses. Stiassny (1990) identified exostosis (exuberant bone formation) of the last 6 or 7 vertebrae as synapomorphic for *Bedotia* and *Rhecles*.

(0 = caudal vertebrae not thickened; 1 = exostoses present).

23. Reduction of urostyle, upper hypural plate fusion. In most melanotaeniid larvae the upper hypural plate forms from 3 elements, although only 2 are present in *Rhadinocentrus*. *Pseudomugil signifer* hatch after flexion of the notochord, with a truncate urostyle, and the upper and lower hypural plates are each of a single element (Aarn et al., 1997) The urostyle is absent in phallostethines and most adult pseudomugilids, and reduced in *Dentatherina* and other pseudomugilids. Hypurals of the upper hypural plate are fully fused in adult phallostethines, pseudomugilids, *Iriatherina* and *Rhadinocentrus*.

(0 = urostyle elongate, 3 autogenous upper hypurals; 1 = urostyle reduced and/or upper hypurals fused; 2 = urostyle absent, upper hypurals fused).

24. Parhypural. The parhypural is large and autogenous in mugilids, *Iso*, menidiines, *Atherion*, *Dentatherina*, phallostethines, atherinids (Patten, 1978), telmatherinids, *Bedotia* (Stiassny, 1990), *Cairnsichthys* (Allen, 1980) and some populations of *Pseudomugil signifer* (Saeed et al., 1989). In other melanotaeniids it is reduced and fused to the ower hypural plate, although approximately 50% of the *Iriatherina* and *Rhadinocentrus* specimens examined have a reduced, unfused parhypural.

(0 = parhypural large, autogenous; 1 = parhypural reduced, fused to lower hypural plate).

25. Median fin spines. Acanthopterygians display variable fin spine development, with spines present in 'most species' (Greenwood et al., 1966) including mugilids and percomorphs examined, but absent in Cyprinodontiformes and Beloniformes

Menidiines, atherinids and *Rheocles* (Stiassny, 1990) have a small flexible spine at the start of the second dorsal and anal fins. The second dorsal spine is solely supported by the corresponding pterygiophore. The anal spine and first anal ray are supported on a common, enlarged pterygiophore. *Atherion*, phallostethines and telmatherinids have an anal spine but no second dorsal spine. Most pseudomugilid (Saeed et al., 1989) d *Bedotia* spp. specimens have a flexible anal spine, but no second dorsal spine: other species of these genera lack the anal spine. *Dentatherina* has a spine in the second dorsal, but lacks an anal spine.

Cairnsichthys and *Rhadinocentrus* have an anal spine – most specimens have a flexible second dorsal spine. In *Iriatherina*, there is a large pungent spine in both the second dorsal and anal fins, and large flexible spines in the first dorsal fin. The pungent spines are supported by enlarged pterygiophores. The other melanotaeniids additionally have pungent spines in the first dorsal fin (Allen, 1980).

(0 = more than one pungent spine in anal and each dorsal fin; or no fin spines; 1 = flexible spine in second dorsal and anal; 2 = anal spine only; 3 = second dorsal spine only; 4 = pungent spine in second dorsal and anal; 5 = pungent spine in both dorsals and anal).

26. First dorsal fin vestigial, persistent ventral fin fold. Parenti (1989) suggested that these 2 phallostethine characteristics were paedomorphic – both are also present in *Kiunga* (Saeed et al., 1989). A ventral body keel is also present in *Iso*. Arthur (1984) hypothesised that a small adult body size was advantageous when food sources are limited.

(0 = adults with 2 well-developed dorsal fins, no ventral keel; 1 = adults with reduced first dorsal fin, presence of ventral keel).

27. Interdorsal pterygiophores. In percomorphs, the dorsal fins are united. In mugilomorphs, there are 0-4 narrow, obtusely-angled interdorsal pterygiophores. Cyprinodontiformes and Beloniformes have a single dorsal fin. *Atherion* and atherinids have 4-7 interdorsal pterygiophores (absent in some *Craterocephalus* spp.; Crowley & Ivantsoff, 1992), *Dentatherina* 8-10, telmatherinids 4-5 except *Kalyptatherina* with 3 (or 2; Saeed & Ivantsoff, 1991). Melanotaeniids modally have 3 pterygiophores (range 2-4), except *Cairnsichthys* and *Rhadinocentrus*, which have 1-2. Interdorsal pterygiophores are rudimentary/absent in *Iso*, menidiines, phallostethines and pseudomugilids (Allen, 1980) except *Pseudomugil reticulatus* (Ivantsoff et al., in press).

(0 = single dorsal fin, or mugilomorph-type interdorsal pterygiophores; 1 = 4+ pterygiophores; 2 = modally 3 pterygiophores; 3 = modally 2 ptergiophores; 4 = 1-2 pterygiophores; 5 = pterygiophores rudimentary/absent).

28. Second dorsal and anal fin origins, body depth and compression. As discussed above, de Beaufort (1922) suggested that changes in fin placement were necessarily concomitant with the transition from a fusiform ('open water form'; Robinson & Wilson, 1995) to a compressed, deep-bodied ('benthic') form. Alexander (1974) suggested that a deep body was suited to life in aquatic vegetation. Cranial relocation of the anal fin and first anal pterygiophore was restricted by the urogenital ducts. In Atheriniformes the level of origin of the second dorsal and anal fins, and body form, may be considered to form a transformation series, and are thus considered to be components of a single character.

Patten (1978) tabulated the number of anal

fin radials cranial to the first haemal spine. Here, the number of pleural rib distal angles ('rib tips'), located caudal to the level of the origin of the spine of the anal fin, is considered .

In mugilids, *Iso*, menidiines, *Atherion*, *Dentatherina*, phallostethines, atherinids, *Paratherina*, pseudomugilids, *Bedotia* and *Rheocles* the second dorsal fin originates caudal to the last pleural rib. In other telmatherinids and the remaining melanotaeniids, the second dorsal fin originates cranial to the last rib. In *Iso*, *Atherion*, *Dentatherina*, phallostethines, atherinids and *Paratherina*, the anal originates caudal to the last rib. In *Craterocephalus* and other telmatherinids, the anal originates cranial to the level of the last 1-3 ribs (in *Tominanga*, last 3-4 ribs). In most pseudomugilids, the position of the pterygiophore is as in telmatherinids. In *Pseudomugil novaeguineae* and *P. reticulatus*, the anal originates cranial to the last 4-5 ribs. In *Bedotia* and *Rheocles* the anal originates cranial to the last 3-6 ribs. In *Cairnsichthys* and *Rhadinocentrus*, the anal originates cranial to the last 6-8 ribs: the proximal radial of one or more anal pterygiophores is bifid in most *Rhadinocentrus* and some *Cairnsichthys* specimens. In *Rhadinocentrus* the anal fin is placed far cranially and the caudal fin has an enlarged ventral lobe. In *Iriatherina*, the anal originates cranial to the last 7-8 ribs. In *Chilatherina*, *Glossolepis* and *Melanotaenia* the anal originates cranial to the last 10-12 ribs.

'Deep-bodied' has been defined quantitatively as body depth >25 % of standard length (Dyer & Chernoff, 1996). In general, menidiines and atherinids are slender-fusiform or -tubiform. *Atherion* and *Dentatherina* are particularly tubiform, while some *Craterocephalus* spp. (including *C. stramineus*) are deep-bodied.

Iso has a distinctive 'hatchet' shape due to marked bilateral compression, and elongation of the pleural ribs.

In general, Atheriniformes (except atherinopsids and *Tominanga*) which penetrate freshwaters develop a deep body: ventral elongation of the ribs and dorsal elongation of the vertebral neural processes. *Paratherina*, *Kalyptatherina*, pseudomugilids, *Bedotia*, *Rheocles*, *Cairnsichthys* and *Rhadinocentrus* are relatively deep-bodied. *Telmatherina* is deep-bodied and compressed: *Chilatherina*, *Glossolepis* and some *Melanotaenia* spp. become near-discoidal (Weber, 1908: pl. 11; Regan, 1914: pl. 31).

(**0** = second dorsal and anal fins originate caudal to pleural ribs, body slender or 'hatchet' shape; **1** = second dorsal caudal to last rib, anal cranial to last rib, body slender; **2** = second dorsal caudal to last rib, anal cranial to 1-5 ribs, body relatively deep; **3** = second dorsal at or caudal to last rib, anal cranial to 3-6 ribs, body relatively deep; **4** = second dorsal cranial to last rib, anal cranial to 1-5 ribs, body relatively deep; **5** = second dorsal cranial to last rib, anal cranial to 6-8 ribs, some bifid pterygiophores, body relatively deep; **6** = second dorsal cranial to last rib, anal cranial to 10+ ribs, body discoidal; **n/a** = not applicable, single dorsal fin).

29. Shape of first anal pterygiophore. In atheriniform outgroups the first anal pterygiophore is elongate, narrow, craniodorsally-oriented, and generally caudal to the visceral cavity (character 28). This is the plesiomorphic condition in *Iso*, menidiines, *Atherion*. In *Bedotia* and *Rheocles* the pterygiophore is craniodorsally-oriented but very reduced (and positioned cranial to the last 3-6 pleural ribs).

Patten (1978) characterised atherinids with the first anal pterygiophore (fused first 2 proximal radials supporting a spine and an unbranched ray) forming a large triangular 'anal plate'. In telmatherinids and pseudomugilids, the pterygiophore is tall, with a concave profile abutting the caudoventral angle of the visceral cavity. In *Pseudomugil novaeguineae*, *P. reticulatus* and *Iriatherina* the pterygiophore is slightly truncated.

In *Cairnsichthys*, *Rhadinocentrus*, *Chilatherina*, *Glossolepis* and *Melanotaenia* the pterygiophore is short and narrow.

In phallostethines, the pterygiophore is an elongate rightangular bone at the caudal termination of the visceral cavity. *Dentatherina* has a very elongate horizontal pterygiophore, with a caudodorsal process (Ivantsoff et al., 1987: fig. 4).

(**0** = first anal ptergiophore narrow, directed craniodorsally; **1** = pterygiophore plate-like; **2** = pterygiophore elongate/right-angular; **3** = pterygiophore short and narrow; **4** = pterygiophore craniodorsally oriented, very reduced)

30. Caudal principal rays. Greenwood et al. (1966) noted 17 caudal branched rays in 'more primitive' acanthopterygians. There are 9+8 (dorsal + ventral) principal branched and unbranched caudal rays in *Iso*, menidiines, *Atherion*, *Dentatherina* atherinids, telmatherinids and melanotaeniids (except *Rhadinocentrus*: 8+8 rays). Pseudomugilids have 8+8-7 rays while phallostethines have 7-6+7-6 rays.

(0 = caudal rays 9+8; 1 = rays 8+8; 2 = rays 8+7; 3 = rays<8+7).

31. Pectoral fin shape. The pectoral fin is moderately tall, with a straight-to-slightly-concave caudal margin in mugilids, many percomorphs, menidiines, *Atherion*, *Dentatherina* and atherinids (Patten, 1978), *Bedotia*, *Rheocles* and *Cairnsichthys*. The fin is set lower, with an arcuate caudal border, the ventral interpectoral contact located further rostrally, in telmatherinids, pseudomugilids and other melanotaeniids. In *Iriatherina* the pectoral is very low-set, the scapula and coracoid foramina are relatively large (Fig. 28).

(0=pectoral fin tall; 1=pectoral fin low-rounded).

32. Supracleithrum/axialpectoral ligament. In mugilids and some atherinopsids (Dyer & Chernoff, 1996) the axialpectoral ligament originates on the first vertebra and inserts on the medial face of the elongate supracleithrum. In other mugilids, atherinopsids, atherinids, telmatherinids and melanotaeniids the ligament originates on the basioccipital. Variations to this arrangement are present in some atherinids (Patten, 1978), *Atherion* and *Dentatherina* (Patten & Ivantsoff, 1983). In *Craterocephalus*, the ligament originates very close to the foramen magnum. In *Rhadinocentrus* (Aarn & Ivantsoff, 1996) the ligament inserts on the cleithrum. The supracleithrum is broad in *Cairnsichthys*: it is reduced in pseudomugilids, in which it is round-reniform, and in phallostethines, in which it is ovate: in the latter 2 groups the axialpectoral ligament is absent.

In *Iriatherina* an accessory axialpectoral ligament is present, attached to the cleithrum craniodorsal spine.

(0 = axialpectoral ligament to elongate supracleithrum; 1 = accessory axialpectoral ligament present; 2 = axialpectoral ligament to cleithrum only; 3 = axialpectoral ligament absent, supracleithrum reduced).

33. Postcleithrum/cleithrum caudodorsal process. In mugilids, percomorphs, *Iso* and menidiines the postcleithrum comprises 2-3 elements, coursing from the level of the horizontal plane towards the ventral midline, deep to the caudal border of the pectoral fin. Parenti (1981) discussed postcleithral variation in Cyprinodontiformes. Gosline (1962) postulated that the postcleithrum functioned to support the pelvic fin in certain fish, including mugilids: in percomorphs it may support pectoral and pelvic fins, while in Atheriniformes it supports the pectoral fin.

In atherinids, the postcleithrum consists of 2 large laminar plates, occasionally in contact, the dorsal postcleithrum deep to the cleithrum caudodorsal process, the ventral postcleithrum on the lateral aspect of the first rib. In some *Craterocephalus* spp., the ventral postcleithrum is somewhat narrower. In telmatherinids and melanotaeniids, the dorsal postcleithrum is reduced and 'scale-like', the ventral postcleithrum is somewhat broad proximally but narrow distally. In *Dentatherina*, the cleithrum caudodorsal process is not developed, the dorsal postcleithrum is absent, the ventral postcleithrum is a broad flange cranial to the first rib. In *Atherion*, some atherinids lacking the cleithrum caudodorsal process, and pseudomugilids, the dorsal postcleithrum is absent, and the ventral postcleithrum is a narrow trabeculum on the cranial facet of the first pleural rib. In phallostethines, the postcleithra are absent (Parenti, 1986), presumably incorporated into the pelvic modification

(0 = large laminar postcleithra, of 2-3 elements; 1 = dorsal postcleithrum reduced, ventral postcleithrum trabecular; 2 = dorsal postcleithrum absent, ventral postcleithrum laminar; 3 = dorsal postcleithrum absent, ventral postcleithrum trabecular; n/a = not applicable, phallostethine condition).

34. Posttemporal canal. An osseous sensory canal is fused to the posttemporal in some atherinids (including *Craterocephalus*), *Iriatherina*, *Chilatherina*, *Glossolepis* and *Melanotaenia*. A small canal, bearing odontodes, is present in *Atherion*. Telmatherinids, pseudomugilids, *Bedotia*, *Rheocles*, *Cairnsichthys* and *Rhadinocentrus* lack a posttemporal canal.

(0 = posttemporal canal present; 1 = posttemporal canal absent).

35. Pectoral spur. The pectoral dorsal spur (rudimentary pectoral spine) is absent in phallostethines and pseudomugilids.

(0 = pectoral spur present; 1 = pectoral spur absent).

36. Pelvic cranial spinous process. Stiassny (1990) characterised percomorphs with the pelvic cranial spinous process directed ventrally. Atheriniformes (except phallostethines) have a pelvic fin medial process that overlaps the process of the contralateral fin. A cranial spinous process usually arises from the medial process, giving origin to m. abductor pelvicus superficialis. The spinous process is absent in *Pseudomugil novaeguineae*, some specimens of *P. signifer* (Saeed et al., 1989), some *Bedotia* spp. (Stiassny, 1990) and *Cairnsichthys* (Allen, 1980), in which fishes the muscle arises on the ventromedian fibrous raphe.

(**0** = pelvic cranial spinous process directed ventrally; **1** = process not directed ventrally; **2** = process absent; **n/a** = not applicable).

37. Pelvic girdle caudodorsal process site of attachment. In atherinomorph outgroups, the pelvic girdle caudomedially contacts the ventral postcleithrum. In Atheriniformes, the pelvic caudodorsal angle is attached ligamentously to a pleural rib. In *Iso*, menidiines, *Dentatherina* (Patten & Ivantsoff, 1983) and *Cairnsichthys* the process is elongate.

In *Iso* the caudolateral process is markedly elongate and contacts rib 3. In atherinids, the angle is attached to rib 4-7 (Patten, 1978). In telmatherinids, pseudomugilids, *Bedotia* and *Rheocles* attachment is to rib 4-5 (rib 3 in some *P. reticulatus* – Ivantsoff et al., in press). In *Atherion*, attachment is to rib 3 (Patten, 1978); in *Dentatherina*, to rib 5 (Patten & Ivantsoff, 1983) or 6.

In *Cairnsichthys*, attachment is to rib 4. In *Rhadinocentrus* the anal fin originates far-cranially, the pelvic girdle is truncate and attached to rib 2 (occasionally rib 3 – Allen, 1980), and the caudal fin has an expanded dorsal lobe. In *Iriatherina*, attachment is to rib 3-4. In the remaining melanotaeniids attachment is to rib 3.

(**0** = pelvic caudolateral process attached to pleural rib 5+; **1** = process to rib 4; **2** = process to rib 3; **3** = process to rib 2; **n/a** = not applicable).

38. Pelvic ventrolateral spinous process/pelvic fin spine position. Dyer & Chernoff (1996) identified the pelvic ventrolateral spinous process ('pelvic ventral spine'), arising from the pelvic lateral plate, between the insertions of the dorsal and ventral pelvic arrector muscles on either side of the basal indentation of the pelvic fin spine. There is a small process in this position in *Agonostomus*. In some atherinids (e.g. *Atherinomorus*) the process is well-developed and spatulate, in others (eg. some *Craterocephalus* spp.) it is linear, in others (including *Alepidomus* and some *Craterocephalus* spp.) it is absent. This process is present in telmatherinids except *Telmatherina ladigesi* (Dyer & Chernoff, 1996) and *Kalyptatherina*.

In pseudomugilids, *Bedotia*, *Rheocles*, *Cairnsichthys* and *Rhadinocentrus* the spinous process is absent, the spine is placed close to the medial plate. In the remaining melanotaeniids, the spine is strongly developed, lying over the pelvic central part: the indentation at the base of the spine is obliterated.

(**0** = pelvic spinous process absent; **1** = spinous process present; **n/a** = not applicable).

39. Pelvic medial process asymmetry. Stiassny (1990: fig 14) reported asymmetry of the medial processes of the pelvic fin as synapomorphic for *Bedotia* and *Rheocles*.

(**0** = pelvic medial processes symmetric; **1** = processes asymmetric).

40. Pelvic fin elements. The pseudomugilid *Scaturiginichthys vermeilipinnis* has fewer pelvic fin elements than the general atheriniform I-5 configuration (Ivantsoff et al., 1991), probably an adaptation to shallow pools.

(**0** = pelvic fin configuration I-5; **1** = less than I-5; **n/a** = not applicable).

41. Pelvic-body membrane. Allen (1980: fig. 2b) noted the presence of a partial pelvic-body membrane in some atherinoids, including *Bedotia*, and well-developed membranes in melanotaeniids and various percomorphs.

In some mugilids, cranially the inner pelvic ray is attached to the ventral midline, very similar to the state in *Bedotia*. This is the general situation in Atheriniformes. In other mugilids, some atherinopsines, pseudomugilids and melanotaeniids there is a pelvic-body membrane: some uncleared *Telmatherina ladigesi* (CMK 6101, ZMA 119.412) and *Kalyptatherina* (AMS I.22838) have the membrane (or debris resulting from damage to it). In melanotaeniids the membrane extends the entire length of the pelvic girdle.

(**0** = pelvic-body membrane absent; **1** = membrane present; **2** = membrane elongate **n/a** = not applicable).

42. Position of the anus. The anus is situated cranial and adjacent to the genital papilla, in the ventral midline. In mugilids, menidiines, atherinopsines, *Iso* and *Rheocles* the anus is caudal to the pelvic tips, almost at the origin of the anal fin. In atherinids, the anus is between the pelvics. In pseudomugilids and other melanotaeniids, the anus is within the interpelvic membrane-bound asquamate area. In telmatherinids the anus is placed very close to the overlapping pelvic medial processes, the pelvic caudal spinous processes are truncated and directed laterally (except in *Telmatherina ladigesi* and *Kalyptatherina*, in which the position of the anus is somewhat caudal).

(0 = anus caudal to pelvic tips; 1 = anus between pelvics; 2 = anus adjacent to pelvic medial processes).

43. Peri-anal squamation. Most Atheriniformes and outgroups have small peri-anal scales. Two species of *Rheocles* lack peri-anal squamation (Stiassny & Reinthal, 1992). In atherinids and telmatherinids there is an elongate peri-anal scale. Pseudomugilids have an elongate peri-anal scale, to the medial border of which attaches the pelvic-body membrane. In other melanotaeniids the peri-anal scales (lateral to the membrane) are small.

(0 = small peri-anal scales; 1 = peri-anal region asquamate; 2 = elongate peri-anal scale).

44. External genitalia. The external genitalia of *Melanotaenia duboulayi* (Aarn et al., 1997), *Rhadinocentrus* and *Iriatherina* is produced as a fleshy rosette.

(0 = genitalia unornamented; 1 = genitalia ornamented).

45. Scale morphology. Atherinomorph outgroups have ctenoid or heavily-armoured scales. Scales lack prominent rostral crenulations in *Atherion*, *Dentatherina*, atherinids and *Cairnsichthys*. Other Atheriniformes have crenulations on the larger lateral scales; some *Glossolepis* spp. have scales with a crenulated caudal margin, not arranged in regular rows along the body (Weber, 1908).

(0 = ctenoid or armoured scales; 1 = scales lacking crenulations; 2 = scales crenulated rostrally; 3 = scales crenulated rostrally and caudally).

46. Odontodes. Teeth occur on the external surface of the premaxilla in some atherinids, telmatherinids, pseudomugilids and melanotaeniids. External 'teeth', not associated with the bite, are also present in *Teramulus*, *Tominanga*, *Paratherina*, *Telmatherina* (Munro, 1967) and *Iriatherina*. *Atherion* and *Notocheirus* additionally have odontodes on the head, as far caudal as the post-temporal canal.

(0 = odontodes absent; 1 = odontodes restricted to external jaws; 2 = odontodes distributed on head).

Results

Phylogenetic analysis using the simple heuristic search option yielded 12 most-parsimonious trees (length 184), in which ordering of (*Dentatherina* + Phallostethinae) (as monophyletic or paraphyletic), (Atherinidae+Telmatherinidae) (as monophyletic or paraphyletic) and (*Chilatherina*+*Glossolepis*+*Melanotaenia*) (3 possible hierarchies) differed. A 'bootstrap' analysis (100 replicates) generated a consensus tree with an unresolved polytomy of 6 in-group taxa (Atherionidae, Phallostethidae, Atherinidae, Telmatherinidae, Pseudomugilidae and Melanotaeniidae). The hierarchy of relationships in Melanotaeniidae (Fig. 30) was: (*Iriatherina*, (((*Bedotia*, *Rheocles*), (*Cairnsichthys*, *Rhadinocentrus*)), (*Chilatherina*/*Glossolepis*/*Melanotaenia*))).

Discussion

This further analysis of Melanotaeniidae has benefitted from anatomical data unavailable to Allen (1980) and Dyer & Chernoff (1996). It is not the present purpose to re-analyse Atheriniformes, although examination of the ethmoid and pelvic/peri-anal regions identified novel character states of Atheriniformes. Here, *Dentatherina* is in Phallostethidae (*sensu* Dyer & Chernoff, 1996). However, Pseudomugilidae (see also Ivantsoff et al., in press) and Telmatherinidae (see also Aarn et al., in press) are considered to be valid families. The authors accept Dyer & Chernoff's (1996) placement of *Bedotia* and *Rheocles* with the melanotaeniids of Australia and New Guinea, but concede that support for this group on biogeographic grounds (below) is speculative. After extensive examination of *Chilatherina*, *Glossolepis* and *Melanotaenia*, no consistent characters facilitating resolution of the trichotomy were found. These genera may require redefinition on a basis other than osteology and meristics.

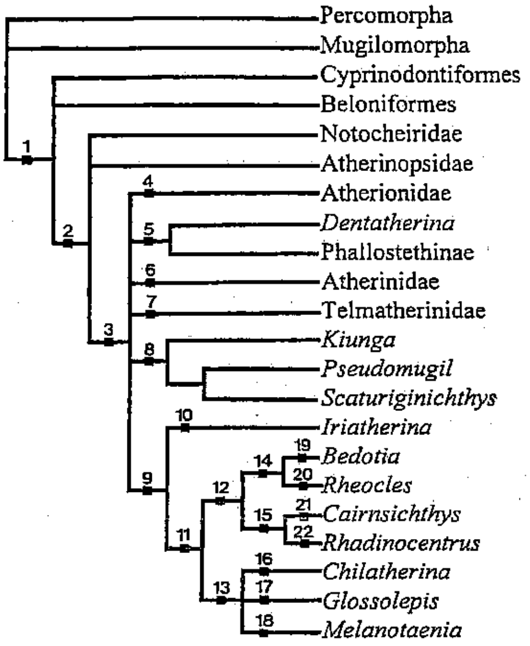


Fig. 30. Cladogram of systematic relationships of Melanotaeniidae. Diagnostic characters at each node listed; postulated character reversals (within Melanotaeniidae) indicated by R.

Node 1. Atheriniformes. Characters discussed by Parenti (1993), Dyer & Chernoff (1996).

Node 2. Notocheiridae. Characters discussed by Dyer & Chernoff (1996).

Node 3. Atherinopsidae. Characters discussed by Dyer (in press).

Node 4. Atherionidae. Characters discussed by Dyer & Chernoff (1996).

Node 5. Phallostethidae. Characters discussed by Dyer & Chernoff (1996).

Node 6. Atherinidae. Characters discussed by Parenti (1989); Dyer & Chernoff (1996).

Node 7. Telmatherinidae. Characters discussed by Saeed & Ivantsoff (1991), Aarn et al. (in press)

Node 8. Pseudomugilidae. Characters discussed by Saeed et al. (1989), Ivantsoff et al. (in press).

Node 9. Melanotaeniidae. Upper jaw non-protrusible (character 2); ethmomaxillary ligament from rostrodorsal mesethmoid, or absent (character 3); first neural process moderate to tall (character 21); one to 3 interdorsal pterygiophores (character 27); anal fin origin cranial to last 3 pleural ribs (character 28); dorsal postcleithrum reduced, ventral postcleithrum trabecular (character 33); elongate pelvic-body membrane (character 41).

Node 10. Iriatherininae. Reduced external ramus of maxilla, premaxilla compact (character 2); metapterygoid absent (character 15); fusion of upper hypurals (character 23); pungent spine in second dorsal and anal fins (character 25); first anal pterygiophore plate-like (character 29); accessory axialpectoral ligament (character 32); genital rosette (character 44); odontodes on jaws (character 46).

Node 11. Melanotaeniinae. Maxilla external ramus moderate to elongate, premaxilla large and elongate (character 2); first anal fin pterygiophore reduced (character 29).

Node 12. Bedotiini. Temporal shelf (character 7); posttemporal canal absent (character 34).

Node 13. Melanotaeniini. Characters discussed by Allen (1980). Three rostral infraorbitals (character 16); pungent spine in anal and both dorsal fins (character 25); anal fin cranial to 10+ ribs, body discoidal (character 28); pelvic fin attached ligamentously to rib 3 (character 37).

Node 14. (*Bedotia* + *Rheocles*). Characters discussed by Stiassny (1990). Median ossification of mesethmoid (character 1 R); caudal vertebral exostoses (character 22); second dorsal fin origin caudal to last pleural rib (character 28); first anal pterygiophore reduced, but different morphology to other melanotaeniines (character 29); pelvic fin attached to pleural rib 4-5 (character 37); pelvic medial process asymmetry (character 39).

Node 15. (*Cairnsichthys* + *Rhadinocentrus*). Lachrymal tendon inserting ventral to subnasal shelf (character 13); one or 2 interdorsal pterygiophores (character 27).

Node 16. *Chilatherina*. Moderate anisometry of premaxillary teeth (character 11).

Node 17. *Glossolepis*. Marked anisometry of premaxillary teeth (character 11); some species with crenulate caudal margin of scales (character 45).

Node 18. *Melanotaenia*. Some species with marked anisometry of premaxillary teeth (character 11).

Node 19. *Bedotia*. Nasal forming part of orbit (character 6); parhypural autogenous (character 24 R); no spine in second dorsal (character 25).

Node 20. *Rheocles*. Ethmomaxillary ligament absent in 2 species (character 3); anus caudal to pelvic tips (character 42 R); peri-anal region asquamate in 2 species (character 43).

Node 21. *Cairnsichthys*. Vomerine condyles directed caudolaterally (character 4); nasal substantially in orbit (character 6); extensive premaxillary sulcus (character 10); parhypural autogenous (character 24 R); pelvic cranial spinous process absent (character 36); pelvic fin attached to rib 4 (character 37).

Node 22. *Rhadinocentrus*. Characters discussed by Aarn & Ivantsoff (1996). Basisphenoid absent (character 8); rostral infraorbital series reduced to lachrymal only (character 16); interarcual cartilage absent (character 19); upper hypurals fused (character 23); caudal principal rays 8+8 (character 30); axialpectoral ligament to cleithrum (character 32); pelvic fin to rib 2 (character 37); genital rosette (character 44).

Bamber & Henderson (1988) hypothesised that phenotypic plasticity enabled marine atherinids to colonise estuaries. Evidence of plasticity was obtained from morphological studies. In the absence of competitors, estuarine atherinids invaded and speciated in some freshwaters of the New World, Madagascar and Australia. Atherinidae, as presently conceived (Nelson, 1994) consists largely of cosmopolitan old world estuarine and marine forms, with some purely freshwater representatives (including populations of *Atherina boyeri* and *Atherinosoma microstoma*, and various *Craterocephalus* spp.). Some species may have re-entered the oceans: Crowley (1990) considered the distribution of *Craterocephalus* to be consistent with such an evolutionary progression. Telmatherinids, pseudomugilids and melanotaeniids are fresh- or brackish-water forms.

Madagascar has been isolated from the African mainland for at least 65 Ma (Archer, 1984), predating the earliest fossil evidence of Atheriniformes (Chedhomme & Gaudant, 1984). Austral-

Table 1. Character data matrix for 16 atherine taxa and 6 outgroups.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Percomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Mugilomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyprinodontiformes	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	1	0	0
Beloniformes	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	2	0	0	0
Iso	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	2	0	0	0
Menidiinae	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	2	0	0	0
Atherion	3	0	0	0	0	2	1	0	0	0	0	0	1	0	0	0	1	0	1	2	0	0	0
Dentatherina	3	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0	2	0	1	1
Phallostethinae	3	0	0	0	0	2	2	1	0	0	1	1	1	0	1/2	1	1	1	0	2	0	0	2
Atherinidae	3/4	0	0/3	0	0	0	1	0	0/1	0	0	0	1/2	0-2	0	0/1	1/2	0	2	2	0	0	0
Telmatherinidae	3	0	0	0	0	0	1	0	0	0	0/1	0	1	1	0	0	1/2	0	2	2	0	0	0
Kiunga	4	1	0	0	1	0	2	0	0	0	1	0	3	1	2	2	1	1	3	1	0	0	2
Pseudomugil	4	0	0	0	1	0	2	0	2	0	2	0	3	1	1	2	1	0	5	1	0	0	2
Scaturiginichthys	4	0	0	0	1	0	2	0	2	0	2	0	3	1	0	2	1	1	5	1	0	0	2
Iriatherina	3	1	3	0	0	0	1	0	0	1	2	0	1	0	2	1	1	0	3	2	1	0	1
Bedotia	0	2	2	0	0	1	3	0	0	1	1	0	1	0	0	1	1	0	3	2	1	1	0
Rheocles	0	2	2/3	1	0	0	3	0	0	0	1	0	1	0	0	1	1	0	3	2	1	1	0
Cairnsichthys	3	2	3	2	0	2	3	0	0	2	1	0	2	0	0	1	1	0	3	2	2	0	0
Rhadinocentrus	3	2	3	1	0	0	3	1	0	0	1	0	2	0	0	2	1	0	4	2	2	0	1
Chilatherina	3	2	2	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	3	2	2	0	0
Glossolepis	3	2	2	1	0	0	1	0	0	0	2	0	1	0	0	0	1	0	3	2	2	0	0
Melanotaenia	3	2	2	1	0	0	1	0	0	0	1/2	0	1	0	0	0	1	0	3	2	2	0	0

Character	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Percomorpha	0	0	0	0	n/a	0	3	0	0	0	0	0	0	n/a	0	0	0	0/1	0	0	0	0	0
Mugilomorpha	0	0	0	0	0	0	3	0	0	0	0	0	1	n/a	0	0	0	0/1	0	0	0	0	0
Cyprinodontiformes	0	0	0	0	0/2	0	0	0	0	?	0	0	1	n/a	0	0	0	0	0	0	0	2	0
Beloniformes	0	0	0	0	0	0	0	0	0	0	0	0	1	n/a	0	0	0	0	0	0	0	2	0
Iso	0	0	0	5	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	2	0/2
Menidiinae	0	1	0	5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0
Atherion	0	2	0	1	0	0	0	0	0	3	0	0	1	2	0	0	0	0	0	0	0	1	2
Dentatherina	0	3	0	1	0	2	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	1	0
Phallostethinae	0	2	1	5	0	2	3	0	3	n/a	0	1	n/a	n/a	n/a	n/a	n/a	n/a	0	0	0	1	0
Atherinidae	0	1	0	1	0/2	1	0	0	0	0	0/1	0	1	0/1	1	0	0	0	0/1	2	0	1	0
Telmatherinidae	0	2	0	1/3	0124	1	0	1	0	1	1	0	1	0/1	1	0	0	0/1	1/2	2	0	2	0/1
Kiunga	1	2	1	5	2	1	2	1	3	3	1	1	1	0	0	0	0	1	1	2	0	2	0
Pseudomugil	1	2	0	5	2	1	1/2	1	3	3	1	1	1	0/1	0	0	0	1	1	2	0	2	0
Scaturiginichthys	1	2	0	5	2	1	2	1	3	3	1	1	1	0	0	0	1	1	1	2	0	2	0
Iriatherina	1	4	0	2	5	1	0	1	1	1	0	0	1	1/2	0	0	0	2	1	0	1	2	1
Bedotia	0	2	0	2	3	4	0	0	0	1	1	0	1	0/1	0	1	0	0	1	0	0	2	0
Rheocles	1	1	0	2	3	4	0	0	0	1	1	0	1	0/1	0	1	0	0	0	0/1	0	2	0
Cairnsichthys	0	1/2	0	4	5	3	0	0	0	1	1	0	2	1	0	0	0	2	1	0	0	2	0
Rhadinocentrus	1	1/2	0	4	5	3	1	1	2	1	1	0	1	3	0	0	0	2	1	0	1	2	0
Chilatherina	1	5	0	2	6	3	0	1	0	1	0	0	1	2	0	0	0	2	1	0	0	2	0
Glossolepis	1	5	0	2	6	3	0	1	0	1	0	0	1	2	0	0	0	2	1	0	0	2/3	0
Melanotaenia	1	5	0	2	6	3	0	1	0	1	0	0	1	2	0	0	0	2	1	0	0	2	0

ia and New Guinea were linked as recently as 6 000 years BP (Powell et al., 1984).

Iriatherina (and some *Melanotaenia* spp.) has a distribution spanning the Torres Straight. *Iriatherina* inhabits the upper level of densely-vegetated, slow-flowing brackish- and fresh-waters. It may be the least-derived descendant of a melanotaeniid precursor species. Extravagant fin development, reduction of the mouth, and small body-size may be adaptations for the particular habitat of *Iriatherina*.

Bedotia and *Rheocles* occur on the eastern seaboard of Madagascar and may be exclusively freshwater forms (Stiassny & Raminosa, 1994). They occupy a similar habitat (oligotrophic highland streams) to *Cairnsichthys* of the eastern seaboard of Australia. *Rhadinocentrus* has a purely freshwater distribution in subtropical eastern Australia, from highland streams to coastal lakes. Morphological analysis supports a close relationship between these geographically-disparate lineages.

Melanotaenia is a wide-ranging, environmentally-tolerant, speciose genus in Australia and New Guinea. *Chilatherina* and *Glossolepis* occur predominantly north of the central dividing range of New Guinea. Meristic variation, and the inconsistency of (osteological and other reported) characters, indicate that re-evaluation of the status of these 3 genera is warranted.

The authors caution that the application of parsimony, in computer-based analyses of phylogenetic relationships, may equate character states resulting from convergent evolution. This would result in false monophyletic groupings. Comparative osteology, without a consideration of ecological and functional anatomical adaptation, may erroneously associate homoplasious traits (such as those associated with small adult body-size/paedomorphism) rather than identify common evolutionary descent. Further progress in the understanding of melanotaeniid systematics should consider evidence from comparative developmental and molecular genetic studies.

Material examined

Institutional abbreviations follow Leviton et al. (1985). CMK is material in the collection of Maurice Kottelat. For each collection, institutional identification (number and size of cleared and stained fish examined); and location, if recorded, is given.

Acanthopterygii: Percomorpha: Beryciformes: Anomalopidae: *Anomalops katoptron*. AMS I.19291 (2, 44-64 mm SL). Diretmidae: *Diretmus argentea*. MQU F/607 (2, 34-39 mm SL). Monocentridae. *Cleidopus gloriamaris*. AMS I.16174 (1, 42 mm SL); Queensland, Moreton Bay, Stradbroke Island.

Zeiformes: Zeidae: *Cyttomimus affinis*. AMS I.20651-002 (1, 74 mm SL); Queensland, Danger Point.

Gasterosteiformes: Gasterosteidae: *Pungitius pungitius*. MQU uncat. (7, 28-41 mm SL); Maine, Damariscotta River, Love's Cove.

Mugilomorpha: Mugilidae: *Agonostomus monticola*. CAL-SU 18622 (3, 37-54 mm SL); Panama. – USNM 314423 (3, 41-70 mm SL); Dominican Republic, Santo Domingo, Paraiso. *Liza argentea*. MQU unreg. (2, 115-130 mm SL); New South Wales, Smith's Lake. *Mugil cephalus*. MQU unreg. (4, 52-92 mm SL); New South Wales, Sydney. *Myxus elongatus*. MQU unreg. (3, 78-105 mm SL); New South Wales, Sydney.

Atherinomorpha: Cyprinodontiformes: Cyprinodontidae: *Aplocheilus* sp. AMS uncat. (2, 30-35 mm SL); Thailand, 10 km north of Bangsapan. *Fundulus* sp. MQU uncat. (3, 46-52 mm SL); Maine, Damariscotta River, Love's Cove. Poeciliidae: *Gambusia holbrooki*. MQU unreg. (3, 18-28 mm SL); New South Wales, Smith's Lake. *Poecilia reticulata*. MQU unreg. (2, 16-22 mm SL); Queensland, Gordonvale.

Beloniformes: Hemiramphidae: *Hemirhamphodon* sp. AMS uncat. (2, 28-46 mm SL); Thailand, Petchabury. *Hyporhampus australis*. MQU unreg. (3, 96-108 mm SL); New South Wales, Smith's Lake.

Atheriniformes: Notocheiridae: *Iso rhothophilus*. MQU I.122 (5, 42-48 mm SL); New South Wales, Seal Rocks.

Atherinopsidae: Menidiinae: *Atherinella crystallina*. CAS 44714 (2, 36-45 mm SL). *Eurystole eriarcha*. MQU I.124 (8, 35-48 mm SL); California, Baha, Los Freiles. *Membras martinica*. MQU I.246 (2, 44-64 mm SL); Georgia, McIntosh County, Dobby River. *Menidia menidia*. MQU I.494 (5, 45-62 mm SL); Maine, Damariscotta River.

Atherines: Atherionidae: *Atherion elymus*. MQU uncat. (6, 32-48 mm SL); Hong Kong. *A. maccullochi*. MQU uncat. (1, 50 mm SL).

Phallostethidae: Dentatherininae: *Dentatherina merceri*. AMS I.22652 (7, 22-29 mm SL); Indonesia, Moluccas, Ceram. – USNM 210180 (3, 18-

24 mm SL); Indonesia, Moluccas, Ceram. Phallostethinae: *Gulaphallus bikolanus*. AMNH 50592 (1, 19 mm SL); Philippines, Luzon, Guinobatan River. *Neostethus borneensis*. USNM 321316 (2, 14-16 mm SL); Brunei, Dolhakim River. *N. lankesteri*. AMS I.19355 (2, 27-31 mm SL); Borneo, East Kalimantan, Balikapan. *Phenacostethus smithi*. USNM 088668 (1, 14 mm SL); Thailand, Bangkok.

Atherinidae: *Alepidomus evermanni*. MQU WI.78-6 (2, 25-33 mm SL); Cuba, Arroyo Bano de Guadalupe Camaguey. *Atherina breviceps*. MQU I.343 (2, 43-52 mm SL); South Africa. *A. hepsetus*. MQU WI.74-11 (1, 78 mm SL); France, Port Banyuls. *A. presbyter*. MQU WI.74-10 (2, 62-63 mm SL); France, Brittany, Roscoff. *Atherinomorus cylindricus*. MQU I.152 (1, 43 mm SL); Santa Cruz, Utupua Island. *A. lacunosa*. AMS I.28110 (3, 39-50 mm SL); Madagascar, Nosy Be. *A. ogilbyi*. MQU unreg. (3, 42-51 mm SL); New South Wales, Narooma. *A. stipes*. MQU I.475 (2, 30-34 mm SL); Cuba, Guantanama Bay. *Atherinosoma elongata*. MQU WI.73-15 (6, 56-64 mm SL); South Australia, Edithburg. *A. endrachtensis*. MQU I.375 (5, 36-39 mm SL); Solomon Islands. *A. microstoma*. MQU unreg. (3, 41-46 mm SL); New South Wales, Narrabeen Lake. *Craterocephalus marjoriae*. MQU I.394 (2, 30-32 mm SL); Queensland, Mary River. *C. mugiloides*. MQU WI.75-46 (7, 34-44 mm SL); Western Australia, Swan River. *C. stercusmuscarum stercusmuscarum*. MQU JMP.75-74 (5, 29-42 mm SL); Queensland, Loftus Creek. *C. stramineus*. AMS I.20863 (4, 18-31 mm SL); Northern Territory, south of Wickham Gorge. – MQU I.303 (2, 32-41 mm SL); Northern Territory, Wickham River. – MQU uncat. (3, 37-42 mm SL); Northern Territory, Katherine River. *Hypoatherina barnesi*. AMS I.28110 (1, 39 mm SL); Madagascar, Nosy Be. *H. ovalaua*. MQU I.022 (1, 58 mm SL); New Guinea, New Ireland, Kalili. *Stenatherina panatella*. MQU I.176 (1, 68 mm SL); Fiji, Rotuma Island.

Telmatherinidae: *Kalyptatherina helodes*. AMS I.22838 (3, 17-20 mm SL); Irian Jaya, Misool Island. *Paratherina wolterecki*. CMK 6481 (1, 39 mm SL); Sulawesi, Lake Towuti. *Telmatherina antoniae*. CMK 6588 (5, 59-84 mm SL); Sulawesi, Lake Matano. – ZMA 110.181 (1, 46 mm SL); Sulawesi, Lake Matano. – CMK 7577 (2, 59-67 mm SL); Sulawesi, Lake Matano. – NT S.12706 (2, 18-25 mm SL); Sulawesi, Lake Towuti. *T. bonti*. CMK 6232 (2, 26-38 mm SL); Sulawesi, Lake Towuti. *T. elongata*. CMK 6589 (1, 65 mm SL); Sulawesi: Lake Matano. *T. ladigesi*. CMK 6101 (5, 14-24 mm SL); Sulawesi: Bantimurung. – CMK 6108 (1, 44 mm SL); Sulawesi, Bantimurung. – MQU uncat. (1, 43 mm SL); aquarium specimen. – ZMA 119.412 (uncleared specimen, 46 mm SL); Sulawesi. *T. opudi*. CMK 6593 (2, 45-47 mm SL); Sulawesi, Lake Matano. *T. sarasinorum*. CMK 6591(2, 41-47 mm SL); Sulawesi, Lake Matano. *T. wahjui*. CMK 6594 (2, 36-43 mm SL); Sulawesi, Lake Matano. *Tominanga aurea*. CMK 6595 (2, 40-55 mm SL); Sulawesi, Lake Mahalona. *T. sanguicauda*. CMK 7578 (1, 49 mm SL); Sulawesi, Lake Towuti.

Pseudomugilidae: *Kiunga ballochi*. AMS I.23842 (2, 21-26 mm SL); New Guinea, Upper Fly River. *Pseudomugil furcata*. MQU I.374 (2, 34-39 mm SL); New Guinea, Safia Creek. *P. gertrudae*. MQU uncat. (3, 17-24 mm SL); Queensland, Jardine River. *P. novaeguineae*. MQU I.369 (1, 37 mm SL); New Guinea, 5 km north of Kiunga. *P. reticulatus*. WAM uncat. (8, 22-31 mm SL); Irian Jaya. *P. signifer*. MQU I.83-9 (2, 28-38 mm SL); Queensland, Cairns. – MQU uncat. (3, 20-28 mm SL); New South Wales, Smith's Lake. *Scaturiginichthys vermeilipinnis*. MQU I.461 (3, 12-14 mm SL); Queensland, Edgbaston, northwest of Aramac.

Melanotaeniidae: Iriatherininae: *Iriatherina werneri*. MQU I.133 (1, 34 mm SL); Queensland, Jardine River. – MQU I.463 (7, 16-20 mm SL); New Guinea, Bensbach River. – MQU I.468 (10, 14-24 mm SL); Queensland, Jardine River. Melanotaeniinae: *Bedotia geayi*. MQU I.200 (5, 43-78 mm SL); aquarium specimens. – USNM 199271 (2, 52-55 mm SL); Madagascar, Fianarantsoa Province, Ifanadiana. *Bedotia* sp. AMNH 88008 (1, 34 mm SL); Madagascar, Namorona River. *Bedotia* sp. AMS I.25045001 (1, 54 mm SL); Madagascar, Sakafiana River (tributary of Faravory River). *Cairnsichthys rhombosomoides*. MQU I.469 (11, 29-58 mm SL); Queensland, Babinda. – MQU I.470 (6, 31-64 mm SL); Queensland, Babinda. – MQU I.471 (6, 25-49 mm SL); Queensland, Mulgrave River. *Chilatherina axelrodi*. MQU uncat. (3, 38-46 mm SL); aquarium specimens. *C. crassispinosa*. WAM P.30197 (3, 44-64 mm SL); New Guinea, Erap River. *C. lorentzi*. WAM P.26741 (3, 34-57 mm SL); New Guinea, Puive Creek. *C. sentaniensis*. WAM P.27782 (6, 51-77 mm SL); Irian Jaya, Lake Sentani. *Glossolepis incisus*. MQU I.364 (4, 33-58 mm SL); Irian Jaya, Lake Sentani. – MQU uncat. (2, 42-49 mm SL); aquarium specimens. *G. maculosus*. WAM P.29839 (3, 49-57 mm SL); New Guinea, Omsis River. *G. ramuensis*. WAM P.29602 (3, 48-63 mm SL); New Guinea, Gogol River. *G. wanamensis*. WAM P.26975 (2, 47-58 mm

SL); New Guinea, Lake Wanam. *Melanotaenia affinis*. MQU I.502 (12, 19-89 mm SL); New Guinea, Passam. *M. arfakensis*. WAM P.29950 (3, 23-19 mm SL); Irian Jaya, Prafi River. *M. boesmani* WAM P.27866 (3, 30-43 mm SL); Irian Jaya, Lake Ajamaru. *M. duboulayi*. MQU I.256 (6, 18-38 mm SL); Queensland, Fraser Island. *M. gracillis*. WAM P.25427 (3, 36-50 mm SL); Western Australia, Drysdale River. *M. lacustris*. WAM P.28158 (3, 58-71 mm SL); New Guinea, Lake Kutubu. *M. nigrans*. MQU uncat. (3, 38-48 mm SL); Northern Territory, Twin Falls. *M. monticola*. WAM P.28157 (4, 34-58 mm SL); New Guinea, Omei Creek. *M. oktedensis*. WAM P.27802 (3, 44-46 mm SL); New Guinea, upper Fly River. *M. pygmae*. WAM P.25034 (3, 28-35 mm SL);. Western Australia, Cascade Creek. *Rhadinocentrus ornatus*. MQU I.257 (11, 19-34 mm SL); Queensland, Fraser Island, Lake Coomboo. – MQU I.472 (11, 25-48 mm SL); Queensland, Seary's Creek. – QM I.14520 (6, 21-29 mm SL); Queensland, Moreton Island, Eager's Creek. *Rheocles aloatrensis*. MQU I.449 (4, 44-58 mm SL); Madagascar, Lac Vert.

Acknowledgments

The authors wish to thank Brian Dyer and Barry Chernoff for access to their manuscript prior to publication. Two anonymous reviewers provided poignant criticism, and a framework to reassess the intent, of this manuscript. The authors are indebted to the following individual and staff for generously lending valuable specimens: American Museum of Natural History; Australian Museum; California Academy of Sciences; Maurice Kottelat; Northern Territory Museum; Queensland Museum; Smithsonian Institution; Western Australian Museum; and the Zoological Museum, Amsterdam.

Literature cited

Aarn & W. Ivantsoff. 1996. Descriptive anatomy of *Rhadinocentrus ornatus* (Osteichthyes: Melanotaeniidae). Ichthyol. Explor. Freshwaters, 7: 41-58.

Aarn, W. Ivantsoff & B. Hansen. 1997. Differential developmental characteristics of two rainbowfish and a blue-eye (Teleostei: Atheriniformes: Melanotaeniidae and Pseudomugilidae) of eastern Australia, with a discussion of adult habitat preferences. Fishes of Sahul, 11: 507-519.

Aarn, W. Ivantsoff & M. Kottelat. In press. A new telmatherinid genus from Sulawesi, and a phylogenetic analysis of Telmatherinidae (Teleostei: Atheriniformes). Ichthyol. Explor. Freshwaters.

Alexander, R. M. 1967. Mechanisms of the jaws of some atheriniform fish. J. Zool., London, 151: 233-255.

— 1974. Functional design in fishes. Huthchinson, London, 160 pp.

Allen, G. R. 1980. A generic classification of the rainbowfishes (Family Melanotaeniidae). Rec. West. Austr. Mus., 8: 449-490.

Anon. 1983. Nomina anatomica veterinaria. World Association of Veterinary Anatomists, Ithaca, 209 pp.

Archer, M. 1984. Earth-shattering concepts for historical zoogeography. Pp. 45-59 in M. Archer & G. Clayton (eds.), Vertebrate zoogeography and evolution in Australasia. Hesperian Press, Carlisle, Western Australia, 1203 pp.

Arthur, W. 1984. Mechanisms of morphological evolution. Wiley-Interscience, New York, 275 pp.

Bamber, R. N. & P. A. Henderson. 1988. Pre-adaptive plasticity in atherinids and the estuarine seat of teleost evolution. J. Fish Biol., 33 (Suppl. A): 17-23.

Beaufort, L. F. de. 1922. Some remarks on the anatomy of the Melanotaeniinae. Bijdr. Dierk., 22: 259 – 263.

Boulenger, G. A. 1897. An account of the freshwater fishes collected in Celebes by Drs. P. & F. Sarasin. Proc. Zool. Soc. London, 1897: 426-429.

Chedhomme, J. & J. Gaudant. 1984. Sur une nouvelle espèce du genre *Paleoatherina* Gaudant (poissons téleostéens, Atherinomorpha) découverte dans l'Eocène supérieur continental des environs d'Orgnac-L'Aven (Ardèche). Géologie Méditerranéenne, 11: 303-309.

Crowley, L. E. L. M. 1990. Biogeography and the systematics of the endemic freshwater fish genus *Craterocephalus* (Family: Atherinidae). Unpubl. Ph. D. thesis, Macquarie University, Australia, 333 pp.

Crowley, L. E. L. M. & W. Ivantsoff. 1992. Redefinition of the freshwater fish genus *Craterocephalus* (Teleostei: Atherinidae) of Australia and New Guinea with an analysis of three species. Ichthyol. Explor. Freshwaters, 3: 273-287.

Darwin, C. 1859. The origin of species. Penguin, Harmondsworth, 477 pp.

Derijst, E. 1989. Annotations to the original descriptions and bibliographical references of the genera *Melanotaenia* and *Pseudomugil*, with comment to the validity of the family-group names Pseudomugilidae, Zanteclidae, Neoatherinidae and Melanotaeniidae. Rainbowfish, 4: 66-70.

Dyer, B. S. In press. Phylogenetic revision of Atherinopsinae (Teleostei, Atheriniformes, Atherinopsidae), with comments on the systematics of the South American freshwater fish genus *Basilichthys* Girard. Misc. Publ. Mus. Zool. Univ. Michigan.

Dyer, B. S. & B. Chernoff. 1996. Phylogenetic relationships among the atheriniform fishes (Teleostei, Atherinomorpha). Zool. J. Linn. Soc., 117: 1-69.

Funk, V. A. 1983. The value of natural classification. Pp. 18-21 in J. Felsenstein (ed.), Numerical taxonomy. Springer, New York, 644 pp.

Gill, T. N. 1862. Notice of a collection of the fishes of California presented to the Smithsonian Institution by Mr. Samuel Hubbart. Proc. Acad. Nat. Sci. Philad., 14: 274-284.

— 1894. An Australasian subfamily of freshwater atherinoid fishes. Amer. Nat., 28: 708.

Gosline, W. A. 1962. Systematic position and relationships of the percesocine fishes. Pacific Sci., 16: 207-217.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman & G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist., 131: 339-455.

Grier, H. J., J. R. Linton, J. F. Leatherland & V. L. de Vlaming. 1980. Structural evidence for two different testicular types in teleost fishes. Amer. J. Anat., 159: 331-345.

Ivantsoff, W., Aarn, M. A. Shepherd & G. R. Allen. In press. *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. Aqua.

Ivantsoff, W. & G. R. Allen. 1984. Two new species of *Pseudomugil* (Pisces: Melanotaeniidae) from Irian Jaya and New Guinea. Austr. Zool., 21: 479-489.

Ivantsoff, W., B. Said & A. Williams. 1987. Systematic position of the family Dentatherinidae in relationship to Phallostethidae and Atherinidae. Copeia, 1987: 649-658.

Ivantsoff, W., P. Unmack, B. Saeed & L. E. L. M. Crowley. 1991. A redfinned blue-eye, a new species and genus of the family Pseudomugilidae from central western Queensland. Fishes of Sahul, 6: 277-282.

Jamieson, B. G. M. 1991. Fish evolution and systematics: evidence from spermatozoa. Cambridge Universtiy Press, Cambridge, 319 pp.

Jordan, D. S. & C. L. Hubbs. 1919. Studies in ichthyology. A monographic review of the family of Atherinidae or silversides. Leland Stanford Jr. Univ. Publ., Univ. Ser., 1919: 1-87, pls. 1-12.

Kner, R. 1866. Specielles Verzeichnis der während der Reise der kaiserl. Fregatte 'Novara' gesammelten Fische. SitzBer. Akad. Wiss. Wien, 53: 542-550.

— 1865-67. Fische. In: Reise der Österreichischen Fregatte 'Novarra' um die Erde in den Jahren 1857-59, unter den Befehlen des Commodore B. von Wullerstorf-Urbain. Zoologischer Theil, 433 pp.,16 pls.

Kottelat, M. 1990. Sailfin silversides (Pisces: Telmatherinidae) of Lakes Towuti, Mahalona and Wawontoa (Sulawesi, Indonesia) with descriptions of two new genera and two new species. Ichthyol. Explor. Freshwaters, 1: 35-54.

— 1991. Sailfin silversides (Pisces: Telmatherinidae) of Lake Matano, Sulawesi, Indonesia, with descriptions of six new species. Ichthyol. Explor. Freshwaters, 1: 321-344.

Leviton, A. E., R. H. Gibbs, E. Heal & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia, 1985: 802-832.

Lindsey, C. C. 1988. Factors controlling meristic variation. Pp. 197-274 in W. S. Hoar & D. J. Randall (eds.), Fish physiology, Vol XIB. Academic Press, Sydney, 436 pp.

Meinken, H. 1974. Aus Neu-Guinea kommt eine neue Gattung und Art der Ährenfische (Pisces, Atherinidae). Das Aquarium, 8 (55): 9-11.

Melinkat, R. & E. Zeiske. 1979. Functional morphology of ventilation of the olfactory organ in *Bedotia geayi* Pellegrin 1909 (Teleostei, Atherinidae). Zool. Anz., 203: 354-368.

Merrick, J. R. & G. E. Schmida. 1984. Australian freshwater fishes. Biology and management. Griffin Press, Netley, Australia, 409 pp.

Munro, I. S. R. 1958. Handbook of Australian fishes, number 24. Austr. Fish. Newsl., 17: 97-100.

— 1967. The fishes of New Guinea. Department of Agriculture, Stock and Fisheries, Port Moresby, 650 pp.

Nelson, J. S. 1994. Fishes of the world. Third edition. Wiley, New York, 600 pp.

Nichols, J. T. & H. C. Raven. 1928. A new melanotaeniid fish from Queensland. Amer. Mus. Novit., 296: 1-2.

Ogilby, J. D. 1896. A new family of Australian fishes. Proc. Linn. Soc. New South Wales, 21: 118-135.

Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fish (Teleostei, Atherinomorpha). Bull. Amer. Mus. Nat. Hist., 168: 335-557.

— 1984. On the relationships of phallostethid fishes (Atherinomorpha), with notes on the anatomy of *Phallostethus dunckeri* Regan, 1913. Amer. Mus. Novit., 2779: 1-12.

— 1986. Homology of pelvic fin structures in female phallostethid fishes (Atherinomorpha, Phallostethidae). Copeia, 1986: 305-310.

— 1989. A phylogenetic revision of the phallostethid fishes (Atherinomorpha, Phallostethidae). Proc. Cal. Acad. Sci., 46: 243-277.

— 1993. Relationships of atherinomorph fishes (Teleostei). Bull. Mar. Sci., 52: 170-196.

Patten, J. M. 1978. Osteology, relationships and classification of hardyheads of the subfamily Atherininae (Pisces: Atherinidae). Unpubl. M. Sc. thesis, Macquarie University, Australia, 170 pp.

Patten, J. M. & W. Ivantsoff. 1983. A new genus and species of atherinid fish, *Dentatherina merceri*, from the Western Pacific. Japan. J. Ichthyol., 29: 329-339.

Powell, C. M., B. D. Johnson & J. J. Veevers. 1984. Interaction of Australia and South-east Asia. Pp. 38-42 in J. J. Veevers (ed.), Phanerozoic earth history of Australia. Clarendon Press, Oxford, 418 pp.

Regan, C. T. 1903. Descriptions de poissons nouveaux. Rev. Suisse Zool., 1903: 416-417.

— 1914. Report on the freshwater fishes collected by the British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea. Trans. Zool. Soc. Lond., 20: 275-285.

Richardson, J. 1843. Contributions to the ichthyology of Australia. Ann. Mag. Nat. Hist., 2: 169-182.

Roberts, T. R. 1971. Osteology of the Malaysian phallostethid fish *Ceratostethus bicornis*, with a discussion of the evolution of remarkable structural novelties in its jaws and external genitalia. Bull. Mus. Comp. Zool., 12: 393-418.

Robinson, B. W. & D. S. Wilson. 1995. Experimentally induced morphological diversity in Trinidadian guppies (*Poecilia reticulata*). Copeia, 1995: 294-305.

Rosen, D. E. 1964. The relationships and the taxonomic position of the halfbeaks, killifishes, silversides and their relatives. Bull. Amer. Mus. Nat. Hist., 127: 217-268.

Rosen, D. E. & L. R. Parenti. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes. Amer. Mus. Novit., 2719: 1-25.

Saeed, B. & W. Ivantsoff. 1991. *Kalyptatherina*, the first telmatherinid genus known outside of Sulawesi. Ichthyol. Explor. Freshwaters, 2: 227-238.

Saeed, B., W. Ivantsoff & G. R. Allen. 1989. Taxonomic revision of the family Pseudomugilidae (Order Atheriniformes). Austr. J. Mar. Freshw. Res., 40: 719-787.

Saeed, B., W. Ivantsoff & L. E. L. M. Crowley. 1994. Systematic relationships of atheriniform families within division 1 of the series Atherinomorpha (Acanthopterygii) with relevant historical perspectives. Vopr. Ikhtiol., 34: 1-32.

Smith, J. L. B. 1965. Fishes of the family Atherinidae of the Red Sea and Western Indian Ocean with a new freshwater genus and species from Madagascar. Ichthyol. Bull. Rhodes Univ., 31: 601-632.

Stiassny, M. L. J. 1986. The limits and relationships of the acanthomorph teleosts. J. Zool., London, Ser. B, 1: 411-460.

— 1990. Notes on the anatomy and relationships of the bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). Amer. Mus. Novit., 2979: 1-33.

— 1993. What are grey mullets? Bull. Mar. Sci., 52: 197-219.

Stiassny, M. L. J. & N. Raminosa. 1994. The fishes of the inland waters of Madagascar. Ann. Mus. R. Afr. Centr., Zool., 275: 133-149.

Stiassny, M. L. J. & P. N. Reinthal. 1992. Description of a new species of *Rheocles* (Atherinomorpha, Bedotiidae) from the Nosivolo Tributary, Mangoro River, Eastern Malagasy Republic. Amer. Mus. Novit., 3031: 1-8.

Swofford, D. L. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.1.1. Smithsonian Institution, Washington.

Tigano, C. & L. R. Parenti. 1988. Homology of the median ethmoid ossifications of *Aphanius fasciatus* and other atherinomorph fishes. Copeia, 1988: 866-870.

Weber, M. 1908. Nova Guinea. Vol. 5. Zoologie. Brill, Leiden, 600 pp.

White, B. N., R. J. Lavenberg & G. E. McGowen. 1984. Atheriniformes: development and relationships. Pp. 355-362 in H. G. Moser (ed.), Ontogeny and systematics of fishes. Spec. Publ. Amer. Soc. Ichthyol. Herpetol., 1: 1-760.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Philad., 125: 225-317.

Zeiske, E., Breuker, H. & R. Melinkat. 1979. Gross morphology and fine structure of the olfactory organ of rainbow fish (Atheriniformes, Melanotaeniidae). Acta. Zool., 60: 173-186.

Zhu, D., B. G. M. Jamieson, A. Hugall & C. Moritz. 1994. Sequence evolution and phylogenetic signal in control-region and cytochrome b sequences of rainbow fishes (Melanotaeniidae). Mol. Biol. Evol., 11: 672-683.

Received 31 May 1996
Revised 19 February 1997
Accepted 4 July 1997