

# A phylogenetic analysis and taxonomic revision of ricefishes, *Oryzias* and relatives (Belontiiformes, Adrianichthyidae)

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Ricefishes, known best by the model organism, the medaka, *Oryzias latipes* Temminck & Schlegel, 1846, comprise the family Adrianichthyidae, which ranges broadly throughout fresh and brackish waters of Central, South and Southeast Asia and the Indo-Malay-Philippines Archipelago as far east as Timor. Twenty-eight Recent species are recognized here in two monophyletic genera, *Adrianichthys* and *Oryzias*. *Xenopoecilus* and *Horaichthys* are placed in synonymy of *Oryzias* for the first time. *Adrianichthys* comprises four species from Lake Poso, Sulawesi, Indonesia. *Oryzias* comprises 24 species that live throughout the range of the family. A fossil genus and species, †*Lithopoecilus brouweri* from the Miocene of central Sulawesi, is included tentatively in the Adrianichthyidae. Evidence for the sister group relationship of adrianichthyids and exocoetoids is reviewed briefly and that relationship corroborated. Monophyly of adrianichthyids is likewise strongly supported here. Species groups within *Oryzias* are diagnosed as monophyletic largely based on osteology, colour pattern and meristic variation. They correspond only in part to species groups previously recognized based on chromosome constitution. Miniature species do not comprise a monophyletic group; disjunct absolute size in close relatives has evolved repeatedly. *Oryzias latipes* is a member of a species complex that includes *O. luzonensis*, *O. curvinotus* and the miniatures *O. sinensis* and *O. mekongensis*. A new species, ***Oryzias bonneorum* sp. nov.**, is described from Lake Lindu, Sulawesi, Indonesia. Lectotypes are designated for *Haplochilus celebensis* Weber, 1894 and *Haplochilus timorensis* Weber & de Beaufort, 1922. No claim to original US Government works. Journal compilation © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 154, 494–610.

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## INTRODUCTION

*Oryzias latipes* has been known broadly by its Japanese name, medaka, and is identified with rice paddies, suggesting the English common name, ricefish, since Temminck & Schlegel (1846: 225) concluded their species description: ‘On désigne ce poisson au Japon sous le nom de Medaka. Il y est très-commun dans les eaux stagnantes, telles que les champs de riz inondés, notamment en été’ [This fish is known in Japan by the name medaka. It is very

common there in stagnant waters, such as flooded rice paddies, particularly in the summer.] When placing *Poecilia latipes* Temminck & Schlegel, 1846, in a new genus, *Oryzias*, 60 years later, Jordan & Snyder (1906) coined a name based on the Latin word for rice, *Oryza*, also a genus of rice plants.

The medaka has been one of the most widely used species in experimental vertebrate biology for over a century. Attributes of the medaka that encouraged its laboratory use include small size, external sexual dimorphism, relatively large and clear eggs, long development time, ease of maintenance in freshwater aquaria, wide availability and reasonable cost. The medaka is the first fish in which Mendelian laws of

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inheritance were demonstrated (Toyama, 1916) and partially Y-linked inheritance was established (Aida, 1921). It is the first animal in which complete reversal of sex differentiation was induced by hormone administration (Yamamoto, 1952; see also Yamamoto, 1967, 1975). In 1959, Briggs & Egami compiled a bibliography of over 350 citations covering the use of the medaka in fields such as embryology, genetics, toxicology, comparative anatomy, endocrinology, systematics and taxonomy. Nearly one thousand scientific papers were compiled in a subsequent medaka bibliography by Egami & Yamamoto (1975). A complete, up-to-date bibliography of the medaka, well beyond the scope and purpose of the present study, would include several thousand scientific and popular articles (see Iwamatsu, 1997, 2006).

Today, the medaka is one of the three most important model organisms among bony fishes along with the zebrafish, *Danio rerio* (Hamilton, 1822) and the Japanese pufferfish, *Takifugu rubripes* (Temminck & Schlegel, 1850) (see Clark & Elgar, 2000; Ishikawa, 2000; Wittbrodt, Shima & Scharl, 2002). It is among the first teleost species to have its genome sequenced (Kasahara *et al.*, 2007). Inducing and characterizing mutations (Shimada *et al.*, 2002), detecting mutations in transgenic individuals (Ozato, Wakamatsu & Inoue, 1992; Winn *et al.*, 2000), generating transgenic individuals (Tanaka & Kinoshita, 2001), identifying the role of the neural crest during development (Langille & Hall, 1988), and documenting spontaneous tumour development (Masahito *et al.*, 1989) are just several, varied examples among many of biological investigation and experimentation using the medaka during the past two decades.

The popularity of the medaka as a laboratory animal remains strong and interest in its natural history is seemingly unlimited. Four medaka, two males and two females, were aboard the US space shuttle COLUMBIA for 15 days in 1994 and performed the first successful vertebrate mating in space, captured on videotape (Ijiri, 1995). The development and swimming behaviour of medaka fry under microgravity was observed on a subsequent COLUMBIA mission in early 2003 (Niihori *et al.*, 2004). Living stocks of *Oryzias* species have long been maintained in Japanese universities (Iwamatsu *et al.*, 1993). A World Medaka Aquarium at the Nagoya Higashiyama Zoo, Nagoya, Japan, has maintained *Oryzias* species and *Oryzias latipes* mutants (Matsuyama, 1994). A journal devoted to the biology of the medaka, *The Fish Biology Journal MEDAKA*, was published by the Laboratory of Freshwater Fish Stocks, Nagoya University, Japan. The medaka has a homepage, <http://biol1.bio.nagoya-u.ac.jp:8000/> (Hori & Watanabe, 1995), with links to other popular medaka web-sites.



**Figure 1.** *Oryzias dancena* (Hamilton, 1822), the first described ricefish species, USNM 313908, adult female, 23.8 mm SL, above; adult male, 25.0 mm SL, below. Sri Lanka. Female is carrying a cluster of embryos.

Despite, or perhaps because of, the popularity of the medaka, knowledge of *Oryzias* biology has been limited until relatively recently to *O. latipes* and just several congeners, such as *O. dancena* (Fig. 1), the first described ricefish species (Roberts, 1998), *O. javanicus* (viz. Iwamatsu *et al.*, 2003) or *O. sarsinorum* (viz. Sovrano *et al.*, 1999; Sovrano, Bisazza & Vallortigara, 2001; Sovrano, 2004), classified formerly in the genus *Xenopoecilus* (see below). *Oryzias* comprised just ten species according to Yamamoto (1975; Table 1): *Oryzias latipes*, *O. melastigma* (now recognized as *O. dancena* or *O. carnaticus*, following Roberts, 1998), *O. celebensis*, *O. timorensis*, *O. javanicus*, *O. curvinotus*, *O. minutillus*, *O. luzonensis*, *O. matanensis* and *O. marmoratus*. A note on electrophoretic comparison of proteins among *Oryzias* species was introduced by Sakaizumi (1985: 521) as follows: 'Recently several Japanese zoologists have begun comparative studies of the phylogeny of *Oryzias*. The aim of this joint effort is to reexamine each nominal species morphologically, karyologically, biochemically and genetically.'

The late Hiroshi Uwa (1986, 1991a, b, 1993), Shinshu University, Matsumoto, Japan, and colleagues (e.g. Uwa & Ojima, 1981; Uwa & Jeon, 1987; Uwa & Parenti, 1988; Magtoon *et al.*, 1992; Takata *et al.*, 1993) described some of the remarkable variation in cytogenetic characters among *Oryzias* species, including chromosome number and constitution and cellular DNA content. Investigations by Uwa and colleagues also included description of a new species, *Oryzias mekongensis* Uwa & Magtoon, 1986, and a new subspecies, *Oryzias latipes sinensis* Chen, Uwa & Chu, 1989, recognized herein at the species level, as in Kottelat (2001a, b).

**Table 1.** Classification of ricefishes, family Adrianichthyidae, as recognized in the present study

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Family Adrianichthyidae Weber, 1913  
 Genus *Adrianichthys* Weber, 1913  
*A. kruyti* Weber, 1913  
*A. oophorus* (Kottelat, 1990a) **comb. nov.**  
*A. poptae* (Weber & de Beaufort, 1922) **comb. nov.**  
*A. roseni* Parenti & Soeroto, 2004  
 Genus *Oryzias* Jordan & Snyder, 1906  
*O. latipes* (Temminck & Schlegel, 1846)  
***O. bonneorum* sp. nov.**  
*O. carnaticus* (Jerdon, 1849)  
*O. celebensis* (Weber, 1894)  
*O. curvinotus* (Nichols & Pope, 1927)  
*O. dancena* (Hamilton, 1822)  
*O. haugiangensis* Roberts, 1998  
*O. hubbsi* Roberts, 1998  
*O. javanicus* (Bleeker, 1854)  
*O. luzonensis* (Herre & Ablan, 1934)  
*O. marmoratus* (Aurich, 1935)  
*O. matanensis* (Aurich, 1935)  
*O. mekongensis* Uwa & Magtoon, 1986  
*O. minutillus* Smith, 1945  
*O. nebulosus* Parenti & Soeroto, 2004  
*O. nigrimas* Kottelat, 1990a  
*O. orthognathus* Kottelat, 1990a  
*O. pectoralis* Roberts, 1998  
*O. profundicola* Kottelat, 1990b  
***O. sarasinorum* (Popta, 1905) comb. nov.**  
***O. setnai* (Kulkarni, 1940) comb. nov.**  
*O. sinensis* Chen *et al.*, 1989  
*O. timorensis* (Weber & de Beaufort, 1922)  
*O. uwai* Roberts, 1998  
 Genus †*Lithopoecilus* (de Beaufort, 1934)  
 †*L. brouweri* de Beaufort (1934) (Miocene of central Sulawesi).

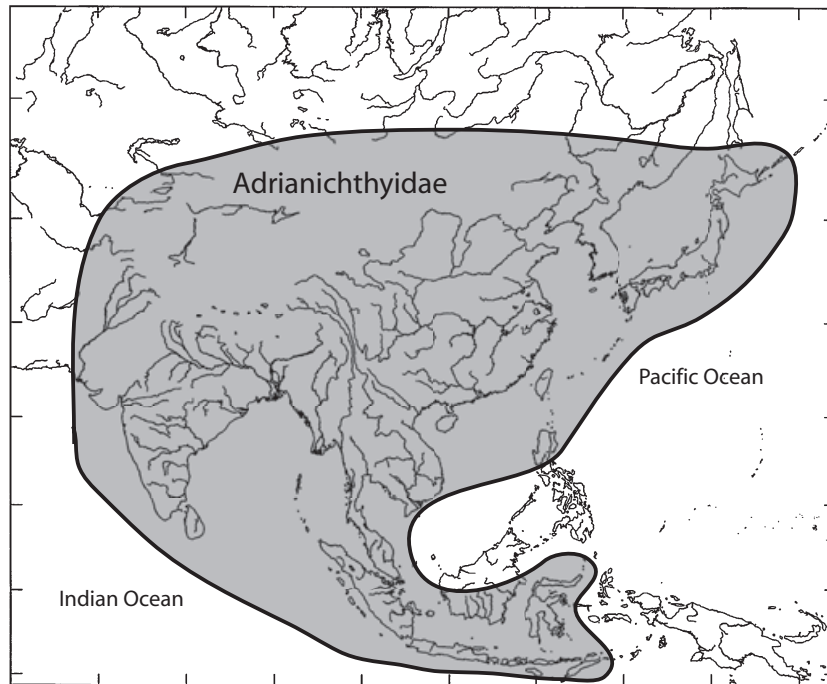
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Recent advances in ricefish systematics at the species level have also been made by Maurice Kottelat (1989a, b, 1990a, b, c), who rediscovered and redescribed two Sulawesi species, *Oryzias matanensis* and *O. marmoratus*, originally described in 1935 by H. Aurich from specimens believed to have been destroyed subsequently during the Second World War. Four new species, recognized herein as *Oryzias orthognathus*, *O. nigrimas*, *O. profundicola* and *Adrianichthys oophorus*, were described by Kottelat (1990a, b). Four more new species, *Oryzias haugiangensis*, *O. hubbsi*, *O. pectoralis* and *O. uwai*, were described by Tyson R. Roberts (1998). With Bambang Soeroto, I described two new species, *Adrianichthys roseni* and *Oryzias nebulosus*, from Lake Poso, Sulawesi (Parenti & Soeroto, 2004), and add a third here, *Oryzias bonneorum*, from material collected in

Lake Lindu, Sulawesi, in 1939. Ricefishes as a group are 'under-described' (Roberts, 1998: 213), and it is likely that more, detailed studies of population variation within some of the wide-ranging taxa recognized here, such as *O. sinensis*, *O. latipes*, *O. dancena* (Fig. 1) and *O. carnaticus* (see Roberts, 1998), will result in description of additional species. As I was completing this monograph, Tyson R. Roberts informed me of his discovery of additional new species from south Asia, and Renny Hadiaty (MZB) informed me of collections of new species from Sulawesi. It is essential that collecting of ricefish specimens throughout their range continues so as to discover, catalogue and appreciate their diversity. Ricefish populations are threatened with extinction throughout much of their range, especially in regions with relatively high human population density, such as Japan (K. Matsuura, pers. comm., 1999; The Environment Agency, 1999; Hosoya, 2000; Matsuura *et al.*, 2000) and Taiwan (Lin *et al.*, 1999; Tzeng *et al.*, 2006), or where exotics have been introduced, such as Sulawesi (Whitten *et al.*, 1987b; Parenti & Soeroto, 2004).

In stark contrast to these active population- or species-level studies, broad, comparative anatomical studies or analyses of ricefish phylogenetic relationships have received scant attention. Few studies had as a goal a comparative study among *Oryzias* species throughout its range or, rarer still, between *Oryzias* and species classified in the genera *Adrianichthys* Weber, 1913, *Xenopoecilus* Regan, 1911a and *Horaichthys* Kulkarni, 1940. Phylogenetic relationships of *Oryzias* to other fishes were clarified only relatively recently. The suborder Cyprinodontoidei of Rosen (1964) included two superfamilies: Cyprinodontoidea, the killifishes, recognized as the order Cyprinodontiformes by Parenti (1981), and Adrianichthyoidea, including three families, Adrianichthyidae, Oryziidae and Horaichthyidae, collectively called ricefishes here. The monograph by Rosen (1964), most often cited for removing *Oryzias* from the family Cyprinodontidae *s.l.* (e.g. Turner, 1965; Yamamoto, 1975) and for diagnosis of atherinomorph fishes (see Parenti, 1993, 2005), is significant also for calling attention to the then little-known endemic ricefishes of Sulawesi, the genera *Adrianichthys* and *Xenopoecilus*.

In 1981, Rosen & Parenti reclassified ricefishes in the neoteleost atherinomorph order Beloniformes, removing them from the Cyprinodontiformes with which they had been associated since their description. In the revised classification, ricefishes comprised the family Adrianichthyidae, equivalent to the superfamily Adrianichthyoidea, sister group of the superfamily Exocoetoidea (halfbeaks, needlefishes, flying fishes and sauries) in the Beloniformes (Rosen &



**Figure 2.** Approximate distributional limits of ricefishes, the family Adrianichthyidae, outlined and shaded. In the Philippines ricefishes are native only to the island of Luzon. Distribution throughout mainland China is estimated.

Parenti, 1981; Collette *et al.*, 1984; Parenti, 1993). The family-groups Oryziidae (= Oryziatidae Myers, 1938) and Horaichthyidae Kulkarni, 1940 were considered by Rosen & Parenti (1981) to be synonyms of Adrianichthyidae Weber, 1913, the oldest family-group name for ricefishes, a classification followed here (Table 1). This taxonomy was not accepted universally in part because Rosen & Parenti (1981) did not elaborate reasons for family-group synonymy beyond presenting brief evidence for the hypothesis that the three families comprised a monophyletic group (see Eschmeyer, 1990; Kottelat, 1990a). Philosophical justification for the Rosen & Parenti synonymy includes the requirements that family-groups be diagnosed as monophyletic, and that they include more than one genus to avoid redundancy of genus-group and family-group names. Ricefish monophyly, supported by Rosen (1964), Rosen & Parenti (1981), Collette *et al.* (1984) and Parenti (1987), among others, is well corroborated below.

Here, I classify ricefishes within two Recent genera, *Adrianichthys* with four species and *Oryzias* with 24 species, together ranging broadly throughout central Eurasia, Central and Southeast Asia and the Indo-Malay-Philippines Archipelago east to Timor (Fig. 2; Rosen, 1964; Yamamoto, 1975; Roberts, 1998). The family Adrianichthyidae *s.s.* (see Eschmeyer, 1990), comprising just *Adrianichthys* and *Xenopoecilus*, is

paraphyletic (Table 1, and Phylogenetic analysis). The family Oryziidae *s.s.* is equivalent to the genus *Oryzias* and, following the conclusions of the present study, is paraphyletic without *Oryzias sarasinorum* (Table 1), described in *Xenopoecilus*, and without *Horaichthys setnai*. The family Horaichthyidae equals the genus *Horaichthys* and its one included species, here recognized as *Oryzias setnai*, a new combination. Thus, *Xenopoecilus* and *Horaichthys* are placed in synonymy of *Oryzias* for the first time. The Miocene †*Lithopoecilus brouweri* de Beaufort, 1934 is the sole fossil taxon referred to the Adrianichthyidae; its closest relatives within the family are unknown.

Kiyoshi Naruse, University of Tokyo, and colleagues (Naruse *et al.*, 1993; Naruse, Sakaizumi & Shima, 1994; Naruse, 1996; Takehana, Naruse & Sakaizumi, 2005) have carried out some of the few molecular analyses of ricefish phylogeny, and prepared genetic linkage maps (Naruse *et al.*, 2000, 2004) and sequenced the genome (Kasahara *et al.*, 2007) of the medaka. 12S rRNA genes were sequenced in 12 species of ricefishes and used to hypothesize relationships based on genetic distance (Naruse, 1996). Preliminary species groups based on a neighbour-joining tree contradicted a monophyletic *Xenopoecilus s.l.* (Fig. 3A) in a report that concluded (Naruse, 1996: 8): 'Combined analyses of nuclear markers like allozymes and nuclear DNA sequence

data, as well as morphology, will be necessary to determine the actual [phylogenetic; my interpretation] position of fishes of *Xenopoecilus*.’ Paraphyly of *Xenopoecilus* was suggested by Rosen (1964) who nevertheless treated his *X. sarasinorum* and *X. poptae* as congeners. Sequences of nuclear tyrosinase and mitochondrial 12S and 16S rRNA genes formed the database for a recent phylogenetic analysis of 15 species of ricefishes (Takehana *et al.*, 2005). One most-parsimonious cladogram was generated from a combined nuclear and mitochondrial dataset (Fig. 3B). The results of the molecular phylogenetic analyses are compared with the new morphological phylogenetic analysis in the Discussion. To avoid confusion, I use the new classification (Table 1) supported by the phylogenetic analysis (Fig. 4) in the following discussions.

Atherinomorph fishes have a unique reproductive morphology, including testis and egg types (Parenti & Grier, 2004; Parenti, 2005). Although ricefishes, as far as is known, are oviparous or ovoviviparous, the broad variation in modes of reproduction within the group makes them ideal candidates for studying the evolution of teleost reproductive systems (viz. Breder & Rosen, 1966). The miniature Indian ricefish, *Oryzias latipes*, forms encapsulated, barbed sperm bundles or spermatophores that are passed from male to female (Kulkarni, 1940). Fertilized eggs are laid following internal fertilization. Ricefishes are known to facultatively retain embryos (Amemiya & Murayama, 1931), probably correlated with the female behaviour of carrying clusters of eggs from fertilization to hatching (Fig. 1). Females of some of the large ricefishes of Sulawesi carry embryos in a pronounced abdominal concavity behind the pelvic fins, a phenomenon that led Kottelat (1990a) to name a new reproductive guild: pelvic brooders. Hermaphroditism and/or livebearing have long been suspected in several species (e.g. Rosen, 1964; Wourms, 1994).

Understanding how these various reproductive modes evolved requires a robust phylogenetic framework at the species level built on morphology and molecular data. In evaluating the compilation of a draft genome for the medaka, Kasahara *et al.* (2007) identified gene categories that evolve rapidly in mammals, such as reproduction and host defence, and that are thought to be critical to the speciation

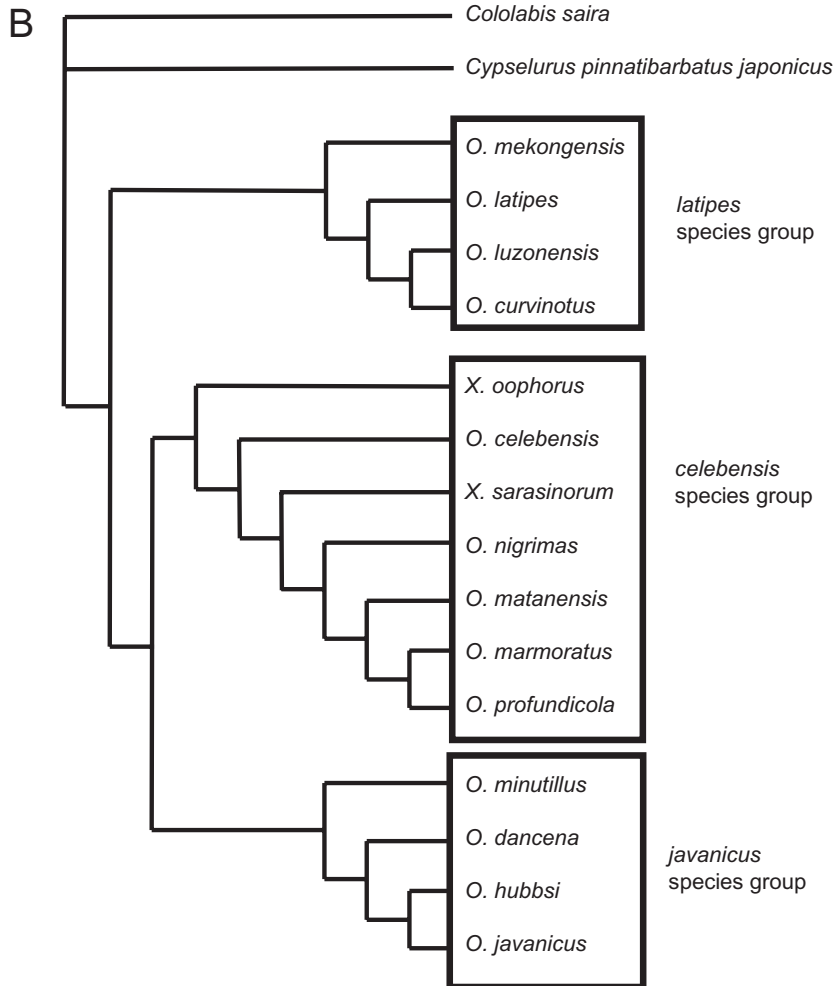
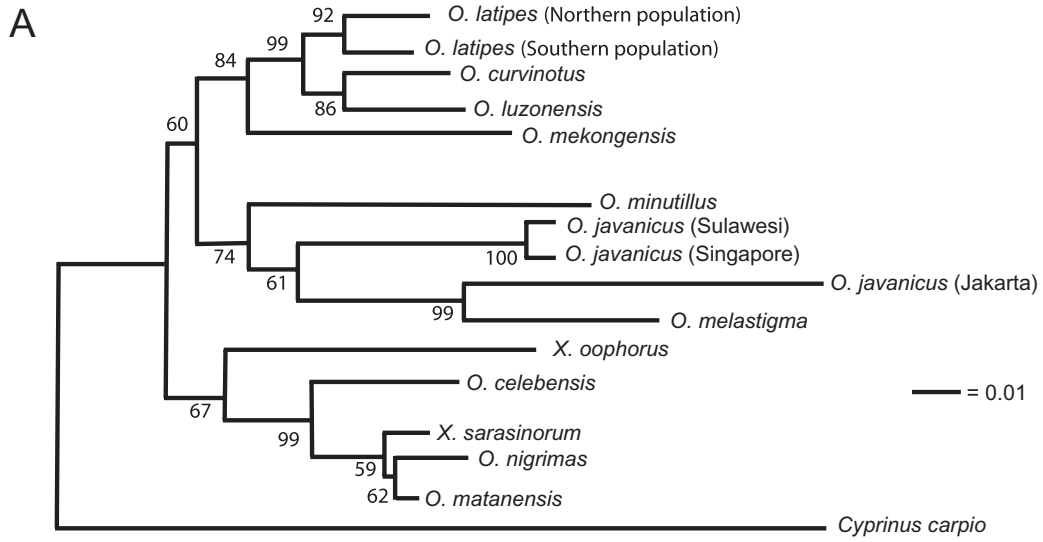
process. These gene categories were slowly evolving in geographically disjunct, yet interbreeding medaka strains, leading to the speculation that (Kasahara *et al.*, 2007: 716–717): ‘the reduced rate in the reproduction- and sex-related [gene] categories might explain why the two medaka strains can mate and produce fertile offspring after a long period of geographical and genetic separation.’

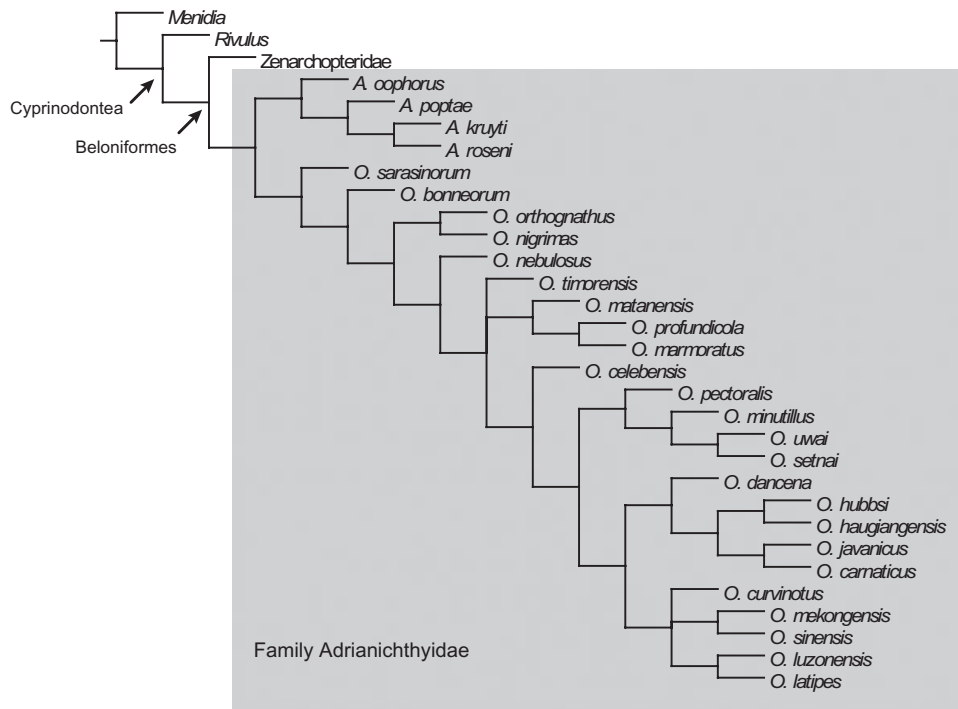
The current study complements these and others by providing a phylogenetic framework based principally on comparative morphology of all of the 28 known ricefish species. The phylogenetic hypothesis can be used to interpret the kind and extent of morphological variation among taxa with, for example, different reproductive modes or distributions, and to test molecular hypotheses.

### SPECIES LIMITS OF THE MEDAKA

The medaka, *Oryzias latipes*, as understood herein, is broadly distributed throughout eastern China, including Hainan Island, Laos, Taiwan, east Korea, and throughout the Japanese archipelago (Uwa & Parenti, 1988; Chen *et al.*, 1989; Uwa, 1991a; Roberts, 1998). At least four populations referred to *O. latipes* have been recognized based on allozyme and karyological differentiation: northern Japan, southern Japan, east Korea and China-west Korea (Table 2; Takehana *et al.*, 2003). Northern and southern Japanese medaka populations have long been known to be differentiated genetically as well as isolated geographically (e.g. Sakaizumi, Egami & Moriwaki, 1980; Sakaizumi, Moriwaki & Egami, 1983; Sakaizumi, 1984). For example, four of 21 protein loci are nearly fixed between the northern and southern Japanese populations (Sakaizumi, 1984). Analysis of DNA sequence data has revealed further differentiation among the Japanese populations of the medaka (Takehana *et al.*, 2003). Sixty-three mtDNA haplotypes formed three clusters that correspond to the northern and southern Japanese populations, and a third population limited to the Kanto region, Honshu Island. Differentiation of the geographically distinct populations of medaka from east Korea, northern Japan and southern Japan has not been recognized taxonomically. All are referred herein to *Oryzias latipes*.

**Figure 3.** Molecular hypotheses of ricefish relationships. A, hypothesis of relationships among 12 species of ricefishes based on a neighbour-joining analysis of 12S ribosomal RNA gene sequence data (modified from Naruse, 1996: fig. 4). The outgroup is *Cyprinus carpio*, the common carp. Values at each node represent bootstrap percentages. Scale bar equals 0.01 unit of tree length. B, hypothesis of relationships among 15 species of ricefishes based on a maximum parsimony analysis of nuclear and mitochondrial sequence data (modified from Takehana *et al.*, 2005: fig. 3). The outgroup taxa are two exocoetoid beloniforms: *Cololabis saira*, the Pacific saury, and *Cypselurus pinnatibarbus japonicus*, a flyingfish. Branch lengths are arbitrary. Terminal taxa may represent more than one population.





**Figure 4.** Strict consensus of two cladograms of relationships among 28 species of ricefishes, family Adrianichthyidae (shaded) as produced by the phylogenetic analysis based on the characters coded as listed (Appendix 1) and as presented in a data matrix (Appendix 2). Unsupported nodes were collapsed. Support at each node is discussed in the text. Coded outgroup taxa representing the major atherinomorph lineages are *Menidia* (Atheriniformes), *Rivulus* (Cyprinodontiformes) and Zenarchopteridae (Beloniformes, suborder Exocoetoidei). Cyprinodontea = Cyprinodontiformes plus Beloniformes (following Dyer & Chernoff, 1996). See Phylogenetic analysis for discussion and details.

East Korean and China–West Korean populations were also recognized based on allozymic and karyological differentiation (e.g. Sakaizumi & Jeon, 1987; Takehana, Jeon & Sakaizumi, 2004a). The distinctness of these two populations was corroborated recently using cytochrome *b* data (Takehana *et al.*, 2004b). *Oryzias sinensis*, described as the subspecies *Oryzias latipes sinensis* Chen *et al.*, 1989, represents the China–West Korean population, although the name, at either the species or the subspecies level, is not used broadly or consistently (see also Roberts, 1998). The Chinese–West Korean population, for example, was referred to as *O. latipes* by Takehana *et al.* (2004b) and as *O. latipes sinensis* by Uwa (1991a). A comprehensive study of allozyme, karyological, sequence and morphological variation among populations of *Oryzias* throughout continental Asia is needed to propose species limits and recognize distribution patterns. *Oryzias sinensis* is a miniature species, following the arbitrary definition that specimens reach no larger than 26 mm standard length (SL) (e.g. Weitzman & Vari, 1988). *Oryzias latipes* is not a miniature by this definition. Here, description of *O. latipes* is based on specimens from both southern

and northern Japan, with variation noted. Similarly, description of *O. sinensis* is based on specimens from south-western China, including the type locality, Kunming. Variation and distribution of these and other Chinese *Oryzias* species (namely *O. minutillus* and *O. curvinotus*) and intermediate populations, is described, and recommendations for future studies on *Oryzias* are proposed. Those who use the medaka as a model organism should be aware of the provenance of their specimens and deposit vouchers of their material in recognized archival collections.

## MATERIAL AND METHODS

The principal aim of this study is to propose a hypothesis of phylogenetic relationships among ricefish species based largely on morphology that can be used to support a revised classification. Phylogenetic systematics or cladistics is the most rigorous method of phylogeny reconstruction (Hennig, 1966; Nelson & Platnick, 1981) and is the method used here, as in other studies on ricefish relationships (e.g. Rosen & Parenti, 1981; Collette *et al.*, 1984; Takehana *et al.*, 2005; see Li, 2001, and discussion below, for a

**Table 2.** Chromosome constitution and genome size in representative populations of 14 species of *Oryzias*, following Hinegardner & Rosen (1972), Uwa (1986, 1991a, b, 1993), Uwa & Iwata (1981), Chen *et al.* (1989), Magtoon *et al.* (1992), Takata *et al.* (1993), Naruse *et al.* (1994), Naruse (1996), Lin *et al.* (1999) and Lamatsch *et al.* (2000)

Informal group	Species	Locality	2n	NF	Constitution (pairs)	Large chromosomes	DNA (pg per nucleus)	
Monoarmed	<i>O. dancena</i>	Chindambaram	48	48	24A	0	1.8	
	<i>O. hubbsi</i>	Jakarta	48	48	23A + 1ST	0	1.8	
	<i>O. javanicus</i>	Singapore	48	48	1ST + 23A	0	1.7	
Monoarmed/	<i>O. minutillus</i>	Phuket	48	48	1ST + 23A	0	—	
		Phuket	42	42	21A	0	1.5	
		Menghai	42	42	21A	0	—	
Fused	Rayong	40	44	1M + SM + 18A	1	1.5		
	Bangkok	34	44	4M + 1SM + 12A	4	1.5		
	Chiang Rai	32	44	5M + 1SM + 10A	5	1.5		
	Chiang Mai	30	44	6M + 1SM + 8A	6	1.5		
	Ratchaburi	28	44	7M + 1SM + 6A	7	1.5		
	Yang Talat	48	58	1M + 4SM + 12ST + 7A	0	1.5		
Biarmed	<i>O. mekongensis</i>	Hong Kong	48	82	4M + 13SM + 5ST + 2A	0	1.5	
	<i>O. curvinotus</i>	Hainan	48	64	1M + 7SM + 16ST + A	0	—	
Fused	<i>O. latipes</i>	Matsuyama (S. Japan)	48	68	2M + 8SM + 1ST + 13A	0	1.7	
		Aomori (N. Japan)	48	70	2M + 9SM + 2ST + 11A	0	—	
		E. Korea	48	68	2M + 8SM + 1ST + 13A	0	—	
		—	48	68	2M + 8SM + 1ST + 13A	0	2.2	
Fused	<i>O. luzonensis</i>	Solsona	48	96	24M + SM	0	1.9	
		Kunming	46	68	3M + 8SM + 2ST + 10A	1	—	
	<i>O. sinensis</i>	Shanghai	46	70	3M + 9SM + 2ST + 9A	1M (+ST)	1.7	
		W. Korea	46	68	3M + 8SM + 1ST + 13A	1	—	
	Fused	<i>O. celebensis</i>	Taiwan	46	—	—	—	—
			Ujung Pandang	36	48	4M + 2SM + 12A	4	1.7
Lake Poso			38	48	3M + 2SM + 14A	3	1.7–1.8	
Malili lakes			42	—	1M + 2SM + 1ST + 17A	1	—	
Fused	<i>O. marmoratus</i>	Lake Matano	42	—	1M + 2SM + 18A	1	—	
	<i>O. sarasinorum</i>	Lake Lindu	42	—	2M + ?	2	—	

A, acrocentric; M, metacentric; SM, submetacentric; ST, subtelocentric; n, haploid chromosome number; NF, chromosome arm number.



phenetic analysis of ricefish relationships). Outgroup comparisons were made to character states in the zenarchopterids and other exocoetoid fishes, sister group of the ricefishes (Rosen & Parenti, 1981; Collette *et al.*, 1984), and in other atherinomorph fishes – cyprinodontiforms (Parenti, 1981) and atheriniforms (Parenti, 1989; Saeed *et al.*, 1989; Dyer & Chernoff, 1996). Zenarchopterids are internally fertilizing, fresh and brackish water halfbeaks that live throughout Southeast Asia (Aschliman, Tibbetts & Collette, 2005). They are not the sister group of ricefishes, but are of similar size and habitat and are used here to describe and interpret character variation in ricefishes. Other acanthomorph fishes were used to describe further character variation. Material used in the outgroup comparisons is listed below; ricefish material examined is listed in the species accounts or is referred to directly in the text.

Taxa are diagnosed as monophyletic by homologous, shared derived characters, or synapomorphies. I endorse a phylogenetic species concept (*sensu* Rosen, 1978, 1979): species are the smallest recognizable, morphologically or genetically distinct groups of males and females that may share homologous, derived characters, termed autapomorphies. Some species recognized herein have no identifiable autapomorphies and the monophyly of their included populations has not been corroborated. Thus, the practical definition of a species used here is closer to the phylogenetic species concept of Wheeler & Platnick (2000: 58): ‘... the smallest aggregation of ... populations or ... lineages diagnosable by a unique combination of characters.’

Ricefish species have been recognized traditionally by variation in external meristic and morphometric data, but these data are widely understood as being inadequate to describe completely specific variation and to infer phylogenetic relationships (e.g. Uwa & Parenti, 1988). My differential diagnoses of species differ somewhat from those of Kottelat (1990a, b) for Sulawesi ricefishes in part because of differences in systematic philosophy, but also because I classify ricefish species in two genera rather than four.

Characters were chosen that reflect disjunct differences among taxa, such as presence or absence of structures, as well as those that exhibit continuous variation among taxa, such as position of the pelvic fins, which varies from relatively posterior to anterior, or number of dorsal-fin rays, which is higher in larger species and lower in smaller species. Characters that vary within species are coded to minimize polymorphisms (Farris, 1966; Wiens, 1995, 1998, 2000; Poe & Wiens, 2000). Coding is described for each character and the consequences of coding are discussed further under Phylogenetic analysis. Methods such as step-matrix gap-weighting (Wiens, 2001) are not used here

for continuous variables because meristic data on beloniforms were compiled from a variety of sources in which character variation was reported usually as a range, rarely with a mean or mode, and presented without frequency data (e.g. Collette *et al.*, 1984; Roberts, 1998). Also, although most ricefish species are abundant in collections, four species are known to science from fewer than ten specimens each: *A. roseni*, *A. kruyti*, *O. bonneorum* and *O. timorensis*.

Select meristic data, summarized for the 28 recognized ricefish species (Table 3), complement the summaries of meristic data for a subset of ricefish species by Collette *et al.* (1984: table 92), Iwamatsu & Hirata (1980), Iwamatsu (1986, 1997, 2006), Uwa & Parenti (1988), Kottelat (1990a, b), Roberts (1998) and Parenti & Soeroto (2004). Methods of measurements and counts follow Uwa & Parenti (1988) and Kottelat (1990a), except as noted. My counts and measurements differ from those reported by Kottelat (1990a, b) and (Roberts, 1998) for some characters. For the most part, this can be attributed to the condition of specimens and shrinkage following long-term storage in alcohol. Scale counts are approximate as many scales are missing, particularly from specimens of relatively small species; scale pockets were counted in some specimens to estimate number of scales in a lateral series. Measurements are of straight-line distances recorded with metric dial calipers to the nearest tenth of a millimetre; they are more accurate for adults and larger species. Measurements are reported as a range of percentage of standard length, with the value for the holotype, lectotype or neotype, when known, after the range in parentheses. Morphometric characters are standard length, tip of the snout to caudal flexure; head length, tip of the snout to posterior extent of the operculum; snout length, tip of the snout to the orbit; eye diameter; and depth of the body at the anal-fin origin. Additional measurements recorded on material of the new species, *O. bonneorum*, are: predorsal length, tip of the snout to the dorsal-fin origin; preanal length, tip of the snout to the anal-fin origin; length of the dorsal-fin base; length of the anal-fin base; and depth of the caudal peduncle. Some characters that vary among ricefishes, such as position of the pelvic fins, may be described either through morphometrics (e.g. distance from pelvic-fin origin to tip of the snout; see also Uwa & Parenti, 1988) or by a landmark (the pleural rib with which the lateral process of the pelvic bone is in line). I describe these characters using landmarks, rather than measurements, because landmarks are more reliably observed in distorted or dehydrated specimens and in cleared and stained or radiographed material. Additional observed character variation within groups of ricefish species is tabulated (Tables 4 and 5).

**Table 3.** Ranges of select meristic data in ricefish species

Character	Pc	Ca	TV	DF	AF	PF	BR	PT	SLS	DFO
Species										
<i>A. kruyti</i>	14–15	21–22	36	14–17	24–25	6	5	14–16	70–75	23
<i>A. roseni</i>	14	22	36	13–16	25	6	5	13–15	63–65	23
<i>A. poptae</i>	15–17	20–22	36–37	11–13	24–27	7	5–7	13–14	75–85	23
<i>A. oophorus</i>	15	21	36	8–10	20–22	6	5–6	12	58–65	22–23
<i>O. sarasinorum</i>	15	19	34	11–12	21–22	7	5–6	10–11	70–75	20–21
<i>O. orthognathus</i>	13	20	33	8–11	21–25	7	5	11–12	45–57	22–23
<i>O. timorensis</i>	12–13	17–19	30–31	9–10	17–19	6	5	10–11	31–34	21
<i>O. celebensis</i>	11–12	18–20	30–31	8–10	17–23	6	5–6	10–11	29–33	22–23
<i>O. nigrimas</i>	13–14	19	32–33	8–11	21–25	6	5	11–12	34–37	22–24
<i>O. nebulosus</i>	11–13	18–20	30–32	9–11	21–22	6	5	9–11	32–36	20–21
<i>O. profundicola</i>	11	18	29	10–14	26–29	6	5	10–11	32–34	18–19
<i>O. marmoratus</i>	12	18	30	8–12	20–26	6	5	10	31–32	20
<i>O. matanensis</i>	12	18	30	8–9	20–25	6	5	11–12	41–47	21–22
<i>O. latipes</i>	11–13	17–20	27–32	5–7	17–22	5–7	5–6	9–11	28–32	22–23
<i>O. sinensis</i>	10–11	18–19	28–30	6–7	16–20	6	5	8–10	29–30	21–22
<i>O. carnaticus</i>	10–11	18–20	28–30	6–7	21–24	6	5	11–13	26–30	22
<i>O. curvinotus</i>	11–12	17–18	28–30	5–6	17–20	6	4–5	10–11	27–28	22
<i>O. bonneorum</i>	12–13	19	31–32	12–13	19–20	6	5–6	11–12	36–39	20
<i>O. javanicus</i>	10–13	17–18	27–31	6–8	18–25	5–6	5	10–13	27–30	22–23
<i>O. luzonensis</i>	11–12	18–19	29–31	5–7	15–19	6	5–6	11	30–35	20–21
<i>O. dancena</i>	10–11	17–18	28–29	6–8	19–24	6	4–5	10–11	25–28	22–23
<i>O. mekongensis</i>	10–11	17–20	27–31	5–7	13–18	5–6	4–5	6–8	29–32	19–20
<i>O. minutillus</i>	8–11	16–18	24–29	5–7	17–21	5	4–5	7–8	26–29	19–20
<i>O. setnai</i>	8–10	21–25	31–34	6–7	27–32	5	4	10	32–34	27
<i>O. pectoralis</i>	10–11	19–21	30–32	6–7	19–20	6	5	9–10	32–34	23
<i>O. uwai</i>	9–10	16–18	25–28	6–7	18–21	6	4	7–8	26–27	20
<i>O. hubbsi</i>	9–10	17–19	27–28	5–6	16–19	6	4–5	8–9	28–29	20
<i>O. haugiagensis</i>	10–11	17–19	27–29	6–7	19–22	6	5–6	10–11	24–28	20–21

Pc, precaudal or abdominal vertebrae; Ca, caudal vertebrae; TV, total vertebrae; DF, dorsal-fin rays; AF, anal-fin rays; PF, pelvic-fin rays; BR, branchiostegal rays; PT, pectoral-fin rays; SLS, scales in a lateral series; DFO, dorsal-fin origin, recorded as the vertebra(e) above which dorsal fin originates.

Description of osteological characters follows Rosen (1964) with modifications or corrections by Parenti (1981, 1987, 1993), Rosen & Parenti (1981), Stiassny (1990, 1993) and Dyer & Chernoff (1996) and as described herein for newly discovered characters. At least one specimen of each species, except *Adrianichthys kruyti* for which material was insufficient, was counterstained with alcian blue and alizarin red, according to the protocol of Dingerkus & Uhler (1977). When available, at least one male and one female, but for most species, more than two specimens, were counterstained. Atherinomorph osteology was surveyed using dissection, radiography or staining for bone by Kulkarni (1940, 1948), Ramaswami (1946) and Rosen (1964), all of whom illustrated or discussed little variation in cartilage. Cartilage characters are critical to the present study, and hence use of some skeletal descriptions and illustrations in these earlier studies is limited. Examination of cartilage is facili-

tated by counterstaining, but such preparations are not always necessary; the preethmoid cartilages (described in Parenti & Soeroto, 2004, and below) of *Adrianichthys kruyti* were examined using light transmitted through dissected, alcohol-preserved specimens. Bone and cartilage of the adult *Oryzias latipes* was illustrated by Yabumoto & Uyeno (1984). Bone and cartilage development of the skull, jaws and jaw suspensorium and gill arches of the medaka was described and illustrated by Langille & Hall (1987). Triple stained material is stained for bone, cartilage and nerves (Song & Parenti, 1995).

One right ventral fifth ceratobranchial bone was removed from counterstained preparations of six species, cleaned manually, and two-step dehydrated in 95% ethanol and air. Specimens were observed using a Zeiss SV8 stereomicroscope and a Hitachi S520 scanning electron microscope (SEM). Counts were made from cleared and stained preparations,

**Table 4.** Distribution of enlarged teeth on the premaxilla and dentary of male and female ricefish. Numbers of specimens recorded for each character state are in parentheses. Dashes = unknown

	Males		Females		Catalog number(s)
	Premaxilla	Dentary	Premaxilla	Dentary	
<i>A. kruyti</i>	–	–	Absent (1)	Absent (1)	ZMH 22571
<i>A. oophorus</i>	Absent (2)	Absent (2)	Absent (2)	Absent (2)	USNM 348386, 350469
<i>A. poptae</i>	Absent (3)	Absent (3)	Absent (1)	Absent (1)	USNM 322423, 340430, ZMH 22575
<i>A. roseni</i>	–	–	Absent (3)	Absent (3)	USNM 322425, 326628, MZB 6732
<i>O. latipes</i>	Present (1)	Present (1)	Present(1)	Absent (1)	CAS-SU 20125 [Nagasaki]
	Present (3)	Present (3)	Absent (3)	Absent (3)	AMNH 26760 [Nagoya]
<i>O. carnaticus</i>	Present (5)	Present (5)	Present (2)	Absent (2)	AMNH 20560
<i>O. celebensis</i>	Present (3)	Present (3)	Absent (3)	Absent (3)	CAS 58034, USNM 340424
<i>O. curvinotus</i>	Present (6)	Present (6)	Absent (2)	Absent (2)	AMNH 10493
<i>O. dancena</i>	Present (3)	Present (3)	Absent (3)	Absent (3)	CAS-SU 35653, USNM 342156
<i>O. bonneorum</i>	Present (1)	Present (1)	Absent (1)	Absent (1)	ZMA 123.863
<i>O. haugiangensis</i>	Present (1)	Present (1)	Absent (1)	Absent (1)	CAS 93898
<i>O. hubbsi</i>	Present (1)	Present (1)	Absent (1)	Absent (1)	CAS 58029
<i>O. javanicus</i>	Present (2)	Present (2)	Present (2)	Absent (2)	CAS 58026
<i>O. luzonensis</i>	Present (3)	Present (3)	Absent (1)	Absent (1)	CAS 58032, CAS-SU 29564
<i>O. marmoratus</i>	Present (2)	Present (2)	Absent (4)	Absent (4)	USNM 348529
<i>O. matanensis</i>	Present (1)	Present (1)	Absent (1)	Present (1)	CMK 6195
<i>O. mekongensis</i>	Present (4)	Present (4)	Absent (2)	Absent (2)	CAS 58027,58030
<i>O. minutillus</i>	Absent (1)	Absent (1)	Absent (2)	Absent (2)	CAS 58022
<i>O. nebulosus</i>	Present (2)	Present (2)	Absent (7)	Absent (7)	USNM 367129, MZB 11650
<i>O. nigrimas</i>	Present (1)	Present (1)	Absent (1)	Absent (1)	CMK 6361; CMK 6358
<i>O. orthognathus</i>	Absent (1)	Absent (1)	Absent (1)	Absent (1)	CMK 6362
<i>O. pectoralis</i>	Present (1)	Absent (1)	Absent (1)	Absent (1)	CAS 92321
<i>O. profundicola</i>	Present (2)	Present (2)	Absent (1)	Absent (1)	CMK 6485
<i>O. sarasinorum</i>	Present (3)	Absent (3)	Absent (1)	Absent (1)	CMK 6556, CMK 6557
<i>O. setnai</i>	Present (5)	Absent (5)	Present (3)	Absent (3)	AMNH 36576
<i>O. sinensis</i>	Present (2)	Present (2)	Absent (2)	Absent (2)	AMNH 38404, USNM 356076
<i>O. timorensis</i>	Present (1)	Present (1)	Absent (1)	Absent (1)	ZMA 100.571, ZMA 120.761
<i>O. uwai</i>	Absent (1)	Absent (1)	Absent (2)	Absent (2)	CAS 92310

radiographs, scanning electron micrographs and alcohol specimens. Published photographs of ricefishes in aquaria (e.g. Uwa, 1985a; Iwamatsu *et al.*, 1993; Seegers, 1997) and field notes were used as a record of live coloration.

Cytogenetic characters (Table 2) are coded and used to infer phylogenetic relationships among ricefishes; they are complete for fewer than half of the recognized ricefish species. Experimental data on relative success of interspecific hybridization among ricefish species (e.g. Sakaizumi, Shimizu & Hamaguchi, 1992; Iwamatsu, Mori & Hori, 1994) are likewise incomplete. Such data are not reported here because they are not considered to be a reliable indicator of species phylogenetic relationships (see Rosen, 1979: 275–278; Kasahara *et al.*, 2007: 717, and Introduction).

Character codes are listed (Appendix 1) and the distribution of these characters among taxa is presented in a matrix or data table (Appendix 2). Species

autapomorphies are not included in the matrix, but discussed in the differential diagnoses of species. The phylogenetic systematic analysis computer program NONA ver. 2 (Goloboff, 1999) was used with *Win-Clada* (Nixon, 1999–2002) to analyse the matrix under the principle of parsimony. Selected characters are also expressed as trees to specify taxon relationships (see Nelson, 1996; Williams & Ebach, 2005, 2006). Differences between these two approaches and their consequences for understanding relationships among ricefish species is discussed further in the Phylogenetic analysis.

Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton *et al.*, 1985), except as follows: ASIZB (Institute of Zoology, Academia Sinica, Beijing, China), CMK (Collection of Maurice Kottelat, Cornol, Switzerland), CTNRC (Center of Thai National Reference Collection,

**Table 5.** Position of pelvic fins, P, and articulation of first pleural rib, R, in ricefishes

Vertebra	1	2	3	4	5	6	7	8	9	10
Species										
<i>A. kruyti</i>	–	–	R	–	–	–	–	–	–	P
<i>A. oophorus</i>	–	–	R	–	–	–	–	P	–	–
<i>A. poptae</i>	–	–	R	–	–	–	–	P	–	–
<i>A. roseni</i>	–	–	R	–	–	–	P	–	–	–
<i>O. nigrimas</i>	–	–	R	–	–	–	P	–	–	–
<i>O. orthognathus</i>	–	–	R	–	–	P	P	–	–	–
<i>O. sarasinorum</i>	–	–	R	–	–	–	P	–	–	–
<i>O. bonneorum</i>	–	–	R	–	–	–	P	–	–	–
<i>O. celebensis</i>	–	R	R	–	P	P	–	–	–	–
<i>O. timorensis</i>	–	R	R	–	–	P	–	–	–	–
<i>O. latipes</i>	–	R	R	–	–	P	–	–	–	–
<i>O. luzonensis</i>	–	–	R	–	–	P	–	–	–	–
<i>O. pectoralis</i>	–	–	R	–	P	–	–	–	–	–
<i>O. nebulosus</i>	–	–	R	–	P	P	P	–	–	–
<i>O. marmoratus</i>	–	–	R	–	P	–	–	–	–	–
<i>O. matanensis</i>	–	–	R	–	P	–	–	–	–	–
<i>O. profundicola</i>	–	–	R	–	P	–	–	–	–	–
<i>O. carnaticus</i>	–	–	R	–	P	–	–	–	–	–
<i>O. javanicus</i>	–	–	R	–	P	–	–	–	–	–
<i>O. curvinotus</i>	–	–	R	–	P	–	–	–	–	–
<i>O. dancena</i>	–	–	R	–	P	–	–	–	–	–
<i>O. haugiangensis</i>	–	–	R	–	P	–	–	–	–	–
<i>O. hubbsi</i>	–	–	R	–	P	–	–	–	–	–
<i>O. mekongensis</i>	–	R	–	–	P	–	–	–	–	–
<i>O. minutillus</i>	–	R	–	P	P	–	–	–	–	–
<i>O. setnai</i>	–	R	–	P	P	–	–	–	–	–
<i>O. sinensis</i>	–	R	–	–	P	–	–	–	–	–
<i>O. uwai</i>	–	R	–	P	P	–	–	–	–	–

Thailand), UNSRAT (Universitas Sam Ratulangi, Manado, Sulawesi, Indonesia), ZSM/LIPI (collections held in trust by ZSM for Lembaga Ilmu Pengetahuan Indonesia, Indonesian Institute of Sciences). Species synonymies include original descriptions, character variation, distribution records, conservation status and other pertinent systematic reports. They are not intended to be exhaustive compilations of citations of ricefish species. Most aquarium and other popular, educational (e.g. Iwamatsu, 1974), genetic and experimental biological literature, especially that on the medaka, *Oryzias latipes*, is excluded. Much of this literature has been summarized by Iwamatsu (1997, 2006) in the two editions of his authoritative book on ricefish biology. Characters of the medaka are based on natural populations, not aquarium strains that may show variation in colour pattern, vertebral column formation and other systems (Yamamoto, 1975). The Catalog of Fishes on-line database, by W. N. Eschmeyer, accessed in 2006 at <http://www.calacademy.org/research/ichthyology/catalog>, and the FishBase database, accessed in 2006 at <http://www.fishbase.org>,

may be consulted for additional information on ricefishes and other taxa.

A common name is provided for each extant species, in part following the conventions established by Kottelat (1990a, b), Seegers (1997) and FishBase. Alternative common names are given in the Remarks section for each species, as known. In the illustrations, bone is represented by stippling, and cartilage by open circles, unless noted.

#### COMPARATIVE MATERIAL EXAMINED

##### Percopsiformes

*Percopsis omiscomaycus*: USNM 308216 (10 cleared and counterstained); USNM 308217 (5 cleared and counterstained)

##### Gadiformes

*Microgadus tomcod*: USNM 352582 (6 cleared and triple stained)

##### Mugilomorpha

*Mugil cephalus*: USNM 156159 (4 cleared and counterstained)

## Atherinomorpha

## Order Atheriniformes

*Melanotaenia* sp.: USNM 320967 (4 cleared and counterstained)

*Melanotaenia splendida*: USNM 308410 (7 cleared and counterstained)

*Odontesthes nigricans*: USNM 214436 (1 cleared and tripled stained)

*Pseudomugil novaeguineae*: USNM 217157 (4 cleared and stained for bone only)

## Order Cyprinodontiformes

## Suborder Aplocheiloidei

*Epiplatys bifasciatus*: USNM 247082 (2 cleared and counterstained)

*Rivulus breviceps*: USNM 93443 (2 cleared and counterstained)

## Suborder Cyprinodontoidei

*Belonesox belizanus*: USNM 134595 (1 cleared and counterstained)

*Brachyrhaphis cascajalensis*: USNM 293458 (2 cleared and counterstained)

*Fundulus heteroclitus*: USNM 278883 (1 cleared and counterstained)

## Order Beloniformes

## Suborder Exocoetoidei

## Family Belontiidae

*Belonion apodion*: USNM 199540 (5 cleared and stained for bone only)

*Belonion dibranchodon*: USNM 199463 (1 cleared and stained for bone only)

*Potamorhaphis guianensis*: USNM 234949 (17 alcohol specimens)

Family Zenarchopteridae (see Aschliman *et al.*, 2005)

*Dermogenys palawanensis*: USNM 138673 (3 cleared and counterstained)

*Dermogenys robertsi*: CAS 137635 (2 cleared and counterstained)

*Dermogenys siamensis*: USNM 109702 (2 cleared and counterstained)

*Hemirhamphodon kuekenthali*: USNM 330828 (1 cleared and counterstained)

*Nomorhamphus rossi*: USNM 363187 (2 cleared and counterstained)

#### RELATIONSHIPS OF ADRIANICHTHYIDAE TO OTHER ATHERINOMORPH FISHES

Ricefishes had been placed traditionally in the order Cyprinodontiformes until they were reclassified as a sister group of the exocoetoids in the order Beloniformes, the cyprinodontiform sister group, by Rosen & Parenti (1981). This hypothesis of ricefish relationships has been well corroborated by morphologists (Parenti, 2005; Fig. 4) and molecular systematists (M. Miya, pers. comm., 2003), and challenged recently

only by Li (2001) who contended that morphological evidence supports the close relationship of ricefishes to cyprinodontiforms. Twenty-eight characters and their states in cyprinodontiforms, ricefishes and exocoetoids were tabulated by Li (2001: table 1) who calculated an undefined 'specialized degree' of each taxon. According to Li, the 'specialized degree' of Cyprinodontiformes is 66.5, that of ricefishes 65.7 and that of exocoetoids 54.3 (Li, 2001: 585). This metric was offered as evidence that ricefishes are more closely related to cyprinodontiforms than to exocoetoids.

Li and I disagree not only in the description of characters, but also in how they should be used to interpret phylogenetic relationships. Some characters tabulated by Li and used to calculate the 'specialized degree' are irrelevant to the question of ricefish relationships. For example, the number of basibranchials was coded by Li (2001) as plesiomorphic (three basibranchials) in ricefishes, exocoetoids and aplocheiloid cyprinodontiforms, and apomorphic (two basibranchials) in cyprinodontoid cyprinodontiforms. This coding is correct, but the character is silent on relationships of ricefishes to either exocoetoids or cyprinodontiforms. Other characters were dismissed by Li (2001) using particular arguments. For example, absence of an interhyal bone is a cogent beloniform synapomorphy, following Rosen & Parenti (1981) and below; Li (2001: 26) argues that although the interhyal is present in all cyprinodontiforms, it is cartilaginous in some, and therefore shows a 'degenerate tendency'.

Beloniform synapomorphies enumerated by Rosen & Parenti (1981) and Parenti (2005) include: (1) interhyal bone absent; (2) interarcual cartilage absent; (3) presence of only a single, ventral hypohyal bone; (4) relatively small second and third epibranchials; (5) vertical reorientation of the second pharyngobranchial bone; and (6) caudal skeleton characterized by the lower caudal lobe with more principal rays than in the upper caudal lobe. An additional beloniform synapomorphy proposed by Rosen & Parenti (1981), i.e. large, ventral flanges on the fifth certibranchials, was interpreted by Stiassny (1990) as an atheriniform synapomorphy, and I concur (see also Parenti, 2005).

To the above six beloniform synapomorphies, I add a seventh: parietals extremely small or absent. Parietal bones are absent from ricefishes at all stages of development (Kulkarni, 1948; Yabumoto & Uyeno, 1984; Langille & Hall, 1987). In exocoetoid beloniforms '... the parietals, when present, are very small, separated by the supraoccipital' (Regan, 1911b: 328). This is in contrast to the cyprinodontiforms *Aplocheilus*, *Xiphophorus* and *Gambusia*, for example, in which parietals are present (Ramaswami,

1946). Parietals may be present or absent in cyprinodontoid cyprinodontiforms, such as poeciliids (e.g. Rosen & Bailey, 1963). Likewise, parietals are present in atherinopsid and notocheirid atheriniforms, yet are absent in atherines (Dyer & Chernoff, 1996). Li (2001: 585) argues that the absence of parietals among a variety of cyprinodontiform taxa and beloniforms is evidence of their close relationship. I disagree with this interpretation because well-formed parietals are present in most and basal cyprinodontiforms.

Another putative beloniform synapomorphy, ventral position of the lateral line neuromasts, is considered here and discussed further under monophyly of the family Adrianichthyidae (see character 17, below). Exocoetoids have long been known to have a well-developed ventral lateral line, but the polarity of this character in phylogeny reconstruction has been questioned (e.g. Rosen & Parenti, 1981: 16–17) largely because other atherinomorphs – atheriniforms, cyprinodontiforms and ricefishes – have been described incorrectly as having no lateral line because the scales may be pitted, but are rarely pored. The posterior lateral line nerve is well developed in these atherinomorphs (e.g. Ishikawa, 1994; material here of *O. carnaticus*, AMNH 20650), as in exocoetoids, and the body has numerous superficial neuromasts, but there are no pored lateral line scales. Differences in neuromast patterns noted by Yamamoto (1975: fig. 10-2a) include the absence of neuromasts from the mid-lateral trunk region in the medaka and their presence in the cyprinodontiform *Fundulus*, following Denny (1937). Recent study of lateral line development at the cellular level confirms the unique pattern of the medaka, compared with other model organisms such as the zebrafish, and offers an ontogenetic mechanism – ventral neuromast migration – to shift the lateral component in adults (Sapède *et al.*, 2002: 613): ‘At the time the hair cells differentiate . . . the L-PLL [lateral branch of the posterior lateral line] neuromasts have already migrated all the way to the ventral midline, towing their innervating axons along the way.’ Homology of the ventral position of the lateral line in exocoetoids and ricefishes may be tested with additional developmental studies; I consider it additional evidence of their sister group relationship.

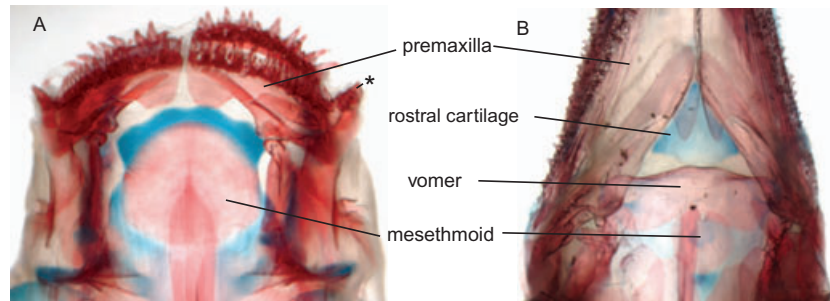
The explicitly phenetic, rather than phylogenetic, arguments raised by Li (2001) do not reject the hypothesis of Rosen & Parenti (1981) that ricefishes are beloniform fishes. Furthermore, Li (2001) unfortunately did not have access to more recent literature (e.g. Parenti, 1993) in which some of the characters he dismisses, such as ‘prolonged embryonic development’, were re-evaluated as atherinomorph, rather than cyprinodontiform, synapomorphies (see Parenti, 2005).

Monophyly of the exocoetoids (*sensu* Rosen & Parenti, 1981; Collette *et al.*, 1984) is well corroborated and need not be reviewed here. Ricefishes are hypothesized to be the sister group of exocoetoids and therefore polarity of the characters used to infer phylogenetic relationships among ricefish species will be hypothesized using comparison with exocoetoid, cyprinodontiform and atheriniform outgroup taxa. The relationships among the atherinomorph orders, reviewed extensively elsewhere (Rosen & Parenti, 1981; Parenti, 1993, 2005; Dyer & Chernoff, 1996), will not be tested further here.

#### MONOPHYLY OF THE ADRIANICHTHYIDAE

Monophyly of ricefishes, the family Adrianichthyidae (including Oryziidae and Horaichthyidae), has been well supported (Rosen & Parenti, 1981; Collette *et al.*, 1984; Parenti, 1987). Yet, none of these studies presented a comprehensive, detailed list and explanation of family-level synapomorphies. Monophyly of the Adrianichthyidae *s.l.* has thus been questioned by Kottelat (1990a) and others. In describing new ricefishes, Roberts (1998: 213) considered that the genus *Oryzias* was in the ‘. . . family Oryziidae or Adrianichthyidae . . .’. Classification is arbitrary. But, as explained in the Introduction and following the conclusions of this study, the families Oryziidae and Adrianichthyidae as recognized traditionally are both paraphyletic, and Horaichthyidae is monotypic. It is essential to begin this phylogenetic study of ricefishes with a justification of their monophyly, equivalent to a phylogenetic diagnosis of the family Adrianichthyidae (Fig. 4).

A detailed, well-illustrated osteology of the medaka, *Oryzias latipes*, by Yabumoto & Uyeno (1984) serves as an osteological description of a representative ricefish species. This is not meant to be interpreted as the ricefish *bauplan* (*sensu* Wake, 1991: 545). Some characters figured and discussed in Yabumoto & Uyeno (1984) and elsewhere (e.g. Rosen, 1964; Rosen & Parenti, 1981; Parenti, 1987) are described but not illustrated here. Characters of the medaka noted or illustrated by Yabumoto & Uyeno (1984) that are not treated below are either not considered diagnostic of ricefishes or do not vary within ricefishes. The interhyal bone is absent in all ricefishes; as in the above discussion, this is a beloniform synapomorphy (Rosen & Parenti, 1981). Uninformative characters, discussed elsewhere (e.g. Parenti, 1981; Rosen & Parenti, 1981), such as absence of the ectopterygoid (absent in ricefishes, cyprinodontiforms and most exocoetoids) and absence of the dorsal hypohyal (absent in all beloniforms), are not considered here. For example, atheriniforms and aplocheiloid cyprinodontiforms have both a dorsal and a ventral hypohyal,



**Figure 5.** A, *Oryzias bonneorum*, ZMA 123.863, adult male, 41 mm SL; B, *Nomorhamphus rossi*, USNM 363187, adult female, 67 mm SL. Anterior portion of skull and outer jaws. Rostral cartilage and vomer are absent in all adrianichthyids, present in other beloniforms. Large teeth on the posterior ramus of the premaxilla are indicated by a star in A.

whereas the dorsal hypohyal is absent in derived cyprinodontiforms, the suborder Cyprinodontoidei (*sensu* Parenti, 1981). Presence or absence of the dorsal hypohyal is uninformative at the level of ricefish relationships.

The 17 unambiguous, unreversed synapomorphies that I propose to diagnose ricefishes are explained below. Coding of character states is given in Appendix 1 and the data matrix in Appendix 2. Additional ricefish synapomorphies are recovered in the parsimony analysis, discussed below under Phylogenetic analysis.

## OSTEOLOGY

### SKULL

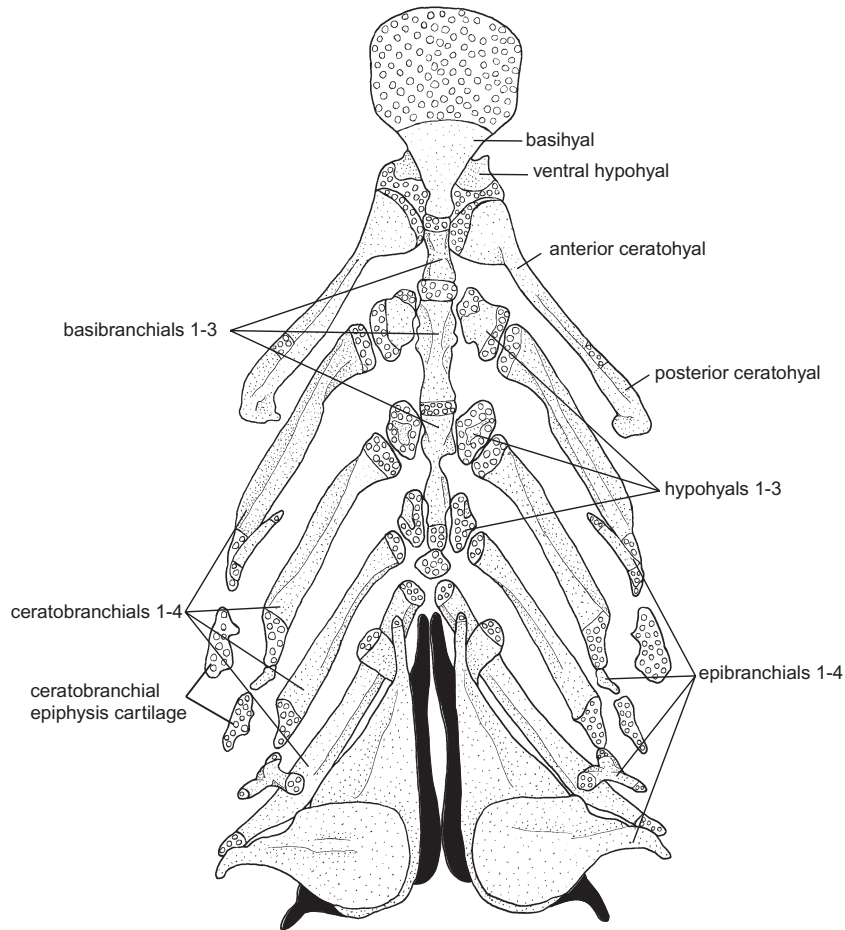
(1) *Vomer*: Present [0]; absent [1]. The vomer (pre-vomer of Rosen, 1964) is absent in ricefishes at all stages of development (Fig. 5A). This is in contrast to outgroup exocoetoids (e.g. *Dermogenys siamensis*, *Hemirhamphodon kuekenthali* and *Nomorhamphus rossi*; Fig. 5B), most cyprinodontiforms (e.g. *Fundulus heteroclitus* and *Rivulus breviceps*), atheriniforms (e.g. *Melanotaenia splendida*), and the acanthomorphs *Percopsis*, *Microgadus* and *Mugil*, in which the vomer is present. The vomer is absent in some cyprinodontiforms [e.g. the East African/Madagascan *Pantanodon*, see Rosen (1965), and the Andean *Orestias*, see Parenti (1984)], interpreted here as independent losses because of support for both cyprinodontiform and beloniform monophyly (Parenti, 1981, 1993, 2005; Rosen & Parenti, 1981). *Orestias* is also a relatively derived cyprinodontoid, according to the analyses of Parenti (1981, 1984) and Parker & Kornfield (1995). *Pantanodon* comprises two species, the type, *P. podoxys* Myers, 1955, and *P. madagascariensis* (Arnoult, 1963), which was described in *Oryzias* and reclassified by Rosen (1965). *Pantanodon* shares numerous cyprinodontiform and cyprinodontoid synapomorphies such as a symmetrical caudal fin with a single epural that mirrors an autogenous parhypural

and two basibranchial bones, respectively, that reject its classification as a ricefish (see Parenti, 1981).

### GILL ARCHES

The ventral portion of the gill arches includes a triangular or subtriangular, ossified basihyal that has a relatively large, anterior cartilaginous portion (Fig. 6). Posterior to the basihyal, there are three ossified basibranchials followed posteriorly by a cartilaginous fourth. The posterior cartilage of the third ossified basibranchial extends ventrally beyond the cartilaginous fourth basibranchial. There are three ossified hypobranchials on either side of the midline. There are five ossified ceratobranchials on either side, the fifth with a toothplate. This condition is comparable with that of outgroup halfbeaks, such as *Hemirhamphodon*, and aplocheiloid cyprinodontiforms, such as *Rivulus*, and atheriniforms (see Parenti, 1981). Two gill arch characters are described here as synapomorphic for ricefishes.

(2) *Articular surface of fourth epibranchial bone*: Slightly expanded [0]; greatly expanded [1]. Osteology of the dorsal portion of the gill arches of ricefishes and other beloniforms was illustrated by Rosen & Parenti (1981: figs 11–17). The dorsal portion of the ricefish gill arch skeleton consists of two pharyngobranchial bones, pharyngobranchial 2 and 3, and their associated toothplates, and four epibranchial bones, epibranchials 1–4 (Fig. 6). Epibranchial 1 is extremely small and cartilaginous in some *Oryzias* (see character 50, below). The second and third epibranchial bones were described as small relative to the first and fourth in cyprinodontiforms and beloniforms by Rosen & Parenti (1981: 21), and this was one of five characters used to support the sister group relationship of these two orders by Parenti (2005). Variation in the ossification or relative size of epibranchial bones 1 and 2 in ricefishes is described here (characters 50 and 51). The interarcual cartilage (*sensu* Travers, 1981) is absent (see character 3, below; Springer & Johnson, 2004: 189).



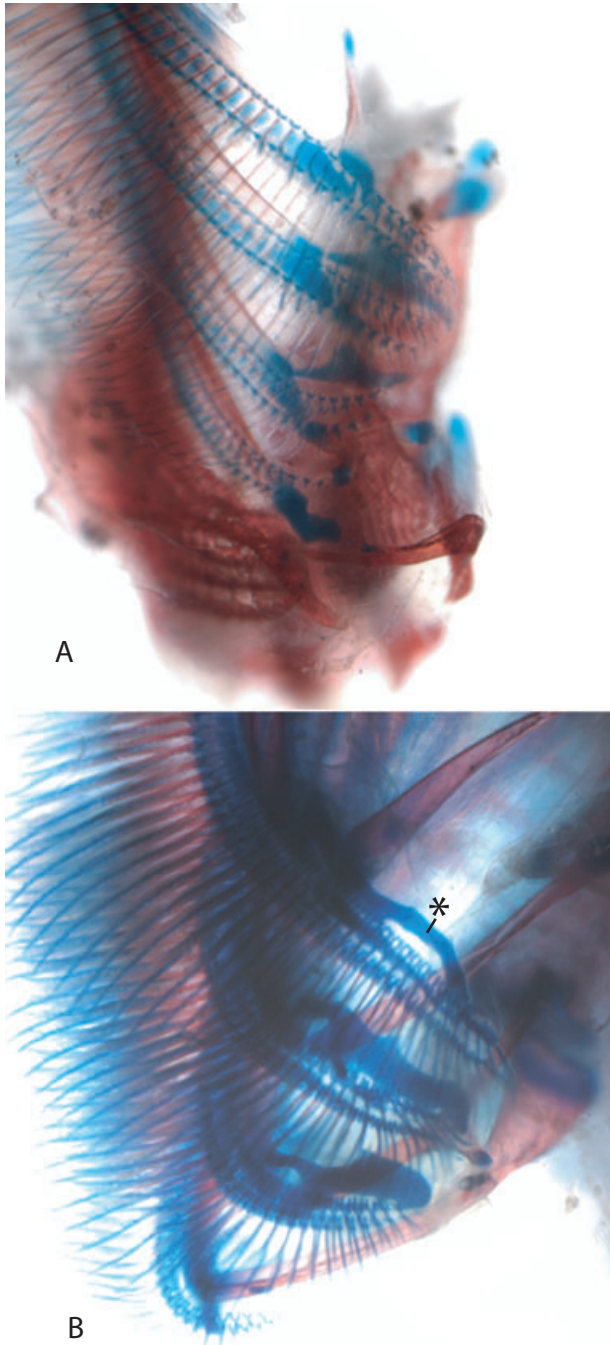
**Figure 6.** *Oryzias mekongensis*, CAS 58027, adult female, 16.5 mm SL. Diagrammatic representation of osteology of gill arch and hyoid apparatus. Fifth ceratobranchials are blackened. Anterior is up.

The fourth epibranchial as the prominent supporting bone and no fourth pharyngobranchial element were considered diagnostic of atherinomorphs by Rosen & Parenti (1981). Percopsiform fishes also have a large fourth epibranchial bone, which was noted by Parenti (1993) as possibly indicating a close relationship with atherinomorphs. A derived character of the dorsal portion of the gill arches in ricefishes is a greatly expanded articular surface of the fourth epibranchial bone (Fig. 6; Rosen & Parenti, 1981: figs 11, 14, 15; Yabumoto & Uyeno, 1984: fig. 8b). This is in contrast to the rod-like fourth epibranchial bone with a slightly expanded articular surface in exocoetoids (Rosen & Parenti, 1981: figs 16, 17). The prominent dorsal pharyngeal bone of *Oryzias latipes* was misidentified as the fourth pharyngeal rather than third pharyngeal bone by Langille & Hall (1987: 149; see Parenti, 1993).

(3) *Ceratobranchial epiphysis*: Simple cartilaginous connection [0]; complex cartilaginous connection [1]. In ricefishes, a ceratobranchial epiphysis is repre-

sented by relatively large cartilages which may be branched (Fig. 7A; Rosen & Parenti, 1981: fig. 14; Yabumoto & Uyeno, 1984: fig. 8a; Springer & Johnson, 2004: pl. 98). Large, branched, cartilages are associated with the posterior extent of the ceratobranchials and may form a complex connection between the epibranchials of the dorsal portion and ceratobranchials of the ventral portion of the gill arches (see especially Rosen & Parenti, 1981: fig. 14a). In some taxa, they are separate from the ceratobranchials, and have been called interarcual cartilages (e.g. Rosen & Parenti, 1981: fig. 11a; Fig. 6) or accessory cartilages (e.g. *Oryzias profundicola*, Parenti, 1993: fig. 4). The large cartilages are attached to ceratobranchials 2, 3 and 4 and may be in contact with the epibranchial of the preceding arch (e.g. Rosen & Parenti, 1981: fig. 14a). Similar cartilages are in cyprinodontiform poeciliid taxa in the tribe Gambusiini, such as *Brachyrhaphis cascajalensis* and *Belonesox belizanus*, although these taxa differ from ricefishes in having an elongate cartilage associated with cera-





**Figure 7.** A, *Oryzias bonneorum*, ZMA 123.863, adult male, 41 mm SL. B, *Belonesox belizanus*, USNM 134595, adult male, 80 mm SL. Lateral view of gill arches to demonstrate complex, branched, cartilaginous ceratobranchial epiphysis. Elongate cartilage associated with ceratobranchial one is starred in B. Anterior is up.

tobranchial 1 (starred in Fig. 7B). None of these cartilages is present in other cyprinodontoids examined (e.g. *Fundulus*), and therefore they are not considered to be diagnostic of cyprinodontoid cyprinodontiforms

*sensu* Parenti (1981). There is no comprehensive survey of such cartilages, and hence the distribution of this character is unknown.

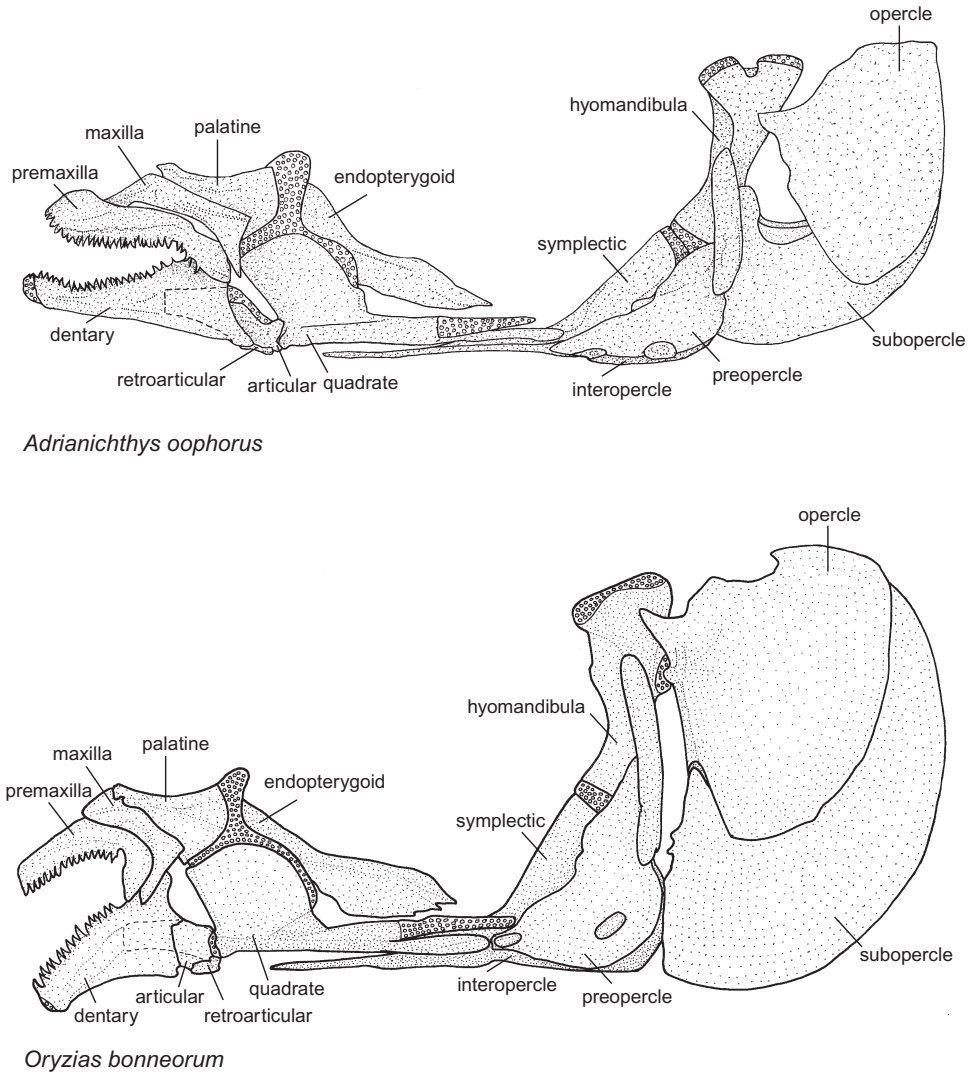
(4) *Toothplate on the fourth ceratobranchial bone*: Present [0]; absent [1]. A prominent tooth-patch on the fourth ceratobranchial characterizes outgroup zenarchopterids, aplocheiloid cyprinodontiforms (including *Rivulus*) and atheriniforms. The fourth ceratobranchial of ricefishes is edentulous.

#### JAW AND JAW SUSPENSORIUM

(5) *Palatine shape and articulation with upper jaw*: Palatine head relatively narrow and without strong connection to maxilla [0]; palatine head expanded and articulating with the maxilla (or premaxilla) via a dense ligament [1]. The head of the palatine (= autopalatine) bone of ricefishes is expanded into a cup-like structure that articulates with the maxilla (or premaxilla) via a dense ligament. There is no cartilage at the head of the palatine (Fig. 8; Yabumoto & Uyeno, 1984: fig. 7), as described and illustrated by Rosen (1964: fig. 1) who probably misinterpreted the dense ligament as cartilage. In large ricefish species, such as *Adrianichthys poptae* (Fig. 9), the dorsal portion of the head of the palatine has a bony cap, what Rosen (1964: fig. 2) termed a sesamoid ossification. The palatine articulates with the maxilla in all ricefish species except the highly autapomorphic, miniature *Oryzias setnai*, in which the maxilla is absent and the palatine articulates directly with the premaxilla.

(6) *Rostral cartilage*: Present [0]; absent [1]. The rostral cartilage is absent in ricefishes at all stages of development (Fig. 5A), in contrast to the condition in outgroup zenarchopterids (e.g. *Dermogenys siamensis*, *Hemirhamphodon kuekenthali*, *Nomorhamphus rossi*; Fig. 5B) in which the rostral cartilage is robust. What I identify as the rostral cartilage in halfbeaks was called the 'preethmoid cartilage' of Clemen, Wanninger & Greven (1997). The heart-shaped cartilage that Clemen *et al.* (1997) called the 'preethmoid' is in close association with the premaxillary ascending processes in halfbeaks, and moves with the premaxillae as the mouth is opened and closed; it is therefore identified as the rostral cartilage. A preethmoid cartilage that may be single or paired in the genus *Adrianichthys* was described and illustrated by Parenti & Soeroto (2004); its states are discussed below under character 33.

(7) *Meckel's cartilage and articular bone*: Meckel's cartilage runs the length of the dentary and the articular bone is orientated anteriorly relative to the body axis [0]; Meckel's cartilage about one-half length of the dentary and articular bone is orientated dorsally relative to the body axis [1]. Meckel's cartilage is approximately one-half the length of the dentary



**Figure 8.** A, *Adrianichthys oophorus*, USNM 350469, subadult, 41 mm SL; B, *Oryzias bonneorum*, ZMA 123.863, adult female, 40 mm SL. Diagrammatic representation of jaws and jaw suspensorium drawn to same scale. Dashed line approximates outline of Meckel's cartilage. Anterior is to the left.

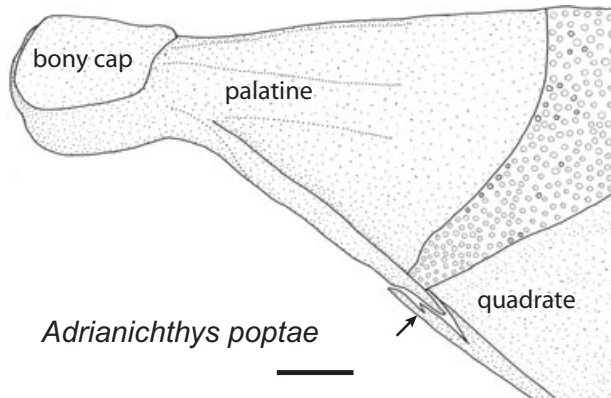
(Fig. 8; Parenti, 1981: fig. 31a; Parenti, 1987: 563) in ricefishes, as opposed to running nearly the entire length of the dentary in other atherinomorph fishes (Parenti, 1981: fig. 31b, c), excluding the elongate, anterior portion of the lower jaw in exocoetoids. The articular bone is correspondingly small and, with Meckel's cartilage, orientated dorsally relative to the body axis, rather than anteriorly as in other atherinomorphs (Parenti, 1981: fig. 31).

(8) *Symphysis between left and right dentary*: Ligamentous [0]; cartilaginous [1]. A cartilaginous symphysis unites the left and right dentary in all ricefishes. Using developmental series, Langille & Hall (1987: fig. 15a, b) identified the cartilage at the anterior tip of the dentary (see Parenti, 1987: figs 1, 2) as a remnant of Meckel's cartilage. Hence, this

character and 7 above, small Meckel's cartilage and reorientation of the articular, may be correlated developmentally. In outgroup taxa, the dentaries are joined medially via a ligament.

(9) *Metapterygoid*: Present [0]; absent [1]. Ricefishes lack a metapterygoid bone in the jaw suspensorium (Fig. 8; Yabumoto & Uyeno, 1984: fig. 7a, b). The metapterygoid is present in atheriniforms, exocoetoids (Meisner, 2001: fig. 9) and aplocheiloid cyprinodontiforms (Parenti, 1981: fig. 29); it is absent in cyprinodontoid cyprinodontiforms (Parenti, 1981: fig. 30).

(10) *Pterygoquadrate cartilage*: Confluent with dorsal margin of palatine and quadrate [0]; enlarged dorsally [1]. The pterygoquadrate cartilage is greatly enlarged dorsally and extends beyond the articulation



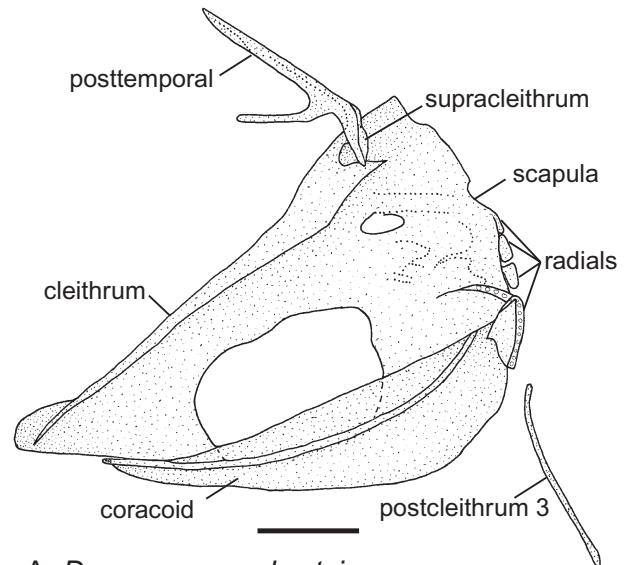
**Figure 9.** *Adrianichthys poptae*, USNM 322423, adult female, 168 mm SL. Diagrammatic representation of the anterior ramus of the palatine. Arrow indicates point of articulation of the palatine and quadrate bones. Anterior is to the left. Scale bar = 1 mm.

of the palatine and the quadrate in all ricefishes (Fig. 8). The pterygoquadrate cartilage meets the cartilage on the ventromedial margin of the lateral ethmoid. This is in contrast to the condition in other atherinomorphs in which the cartilage is confluent with the dorsal margin of the bones of the jaw suspensorium (e.g. Parenti, 1981: figs 29, 30).

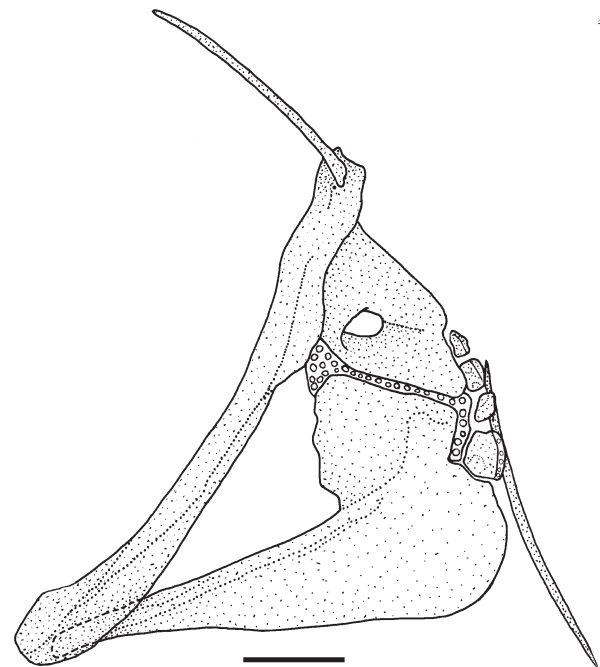
(11) *Mandibulo-lacrima* ligament: Present [0]; absent [1]. Exocoetoids were characterized by Dyer & Chernoff (1996: 58) as having a strong ligament that connects the ventromedial end of the lacrimal to the anguloarticular (or 'mandible'). This ligament is absent in *Oryzias* (including *Horaichthys*), as noted by Dyer & Chernoff (1996), and in *Adrianichthys*. A tendon between the lacrimal and anterior portion of the A1 section of the adductor mandibulae was proposed as an atherinomorph synapomorphy by Stiassny (1990). Homology of the A1 lacrimal tendon of atheriniforms and some cyprinodontiforms, and the lacrimal ligament of exocoetoids, remains to be tested.

#### INFRAORBITAL BONES

(12) *Dermosphenotic* position relative to *sphenotic*: Anterior [0]; lateral or posterior [1]. The ricefish infraorbital series comprises two bones, the lacrimal and the dermosphenotic (Yabumoto & Uyeno, 1984: fig. 1), as in other beloniforms and cyprinodontiforms (Rosen, 1964; Rosen & Parenti, 1981). The dermosphenotic of the cyprinodontiform *Fundulus* and the halfbeak *Nomorhamphus* lie anterior to the lateral ramus of the sphenotic. In contrast, the dermosphenotic of ricefishes is relatively posterior and lies lateral or posterior to the lateral arm of the sphenotic (Yabumoto & Uyeno, 1984: fig. 1); the dermosphenotic is excluded from the orbit.



**A. *Dermogenys robertsi***



**B. *Adrianichthys oophorus***

**Figure 10.** A, *Dermogenys robertsi*, CAS 137635, 39 mm SL; B, *Adrianichthys oophorus*, USNM 350469, 41 mm SL. Diagrammatic representation of the left shoulder girdle. Anterior is to the left. Scale bar = 1 mm.

#### PECTORAL GIRDLE

(13) *Supracleithrum*: Present [0]; absent [1]. The supracleithrum is variously present or absent in atherinomorphs, and is present in outgroup taxa, such as the exocoetoid *Dermogenys* (Fig. 10A; see Parenti, 1993) and the aplocheiloid *Rivulus*, and, for

example, the cyprinodontoid *Pantodon* (e.g. Rosen, 1965: fig. 8), as well as *Melanotaenia*. The supracleithrum is absent from the pectoral girdle of all ricefishes (Fig. 10B). I interpret absence of the supracleithrum as a synapomorphy of ricefishes because the bone is present in local outgroup exocoetoids, in cyprinodontiforms with few exceptions (e.g. the poeciliid *Tomeurus*, Parenti, 1981: fig. 8d) and in atheriniforms. All ricefishes have a single, ventral postcleithrum (= postcleithrum 3), as in outgroup exocoetoids, e.g. *Dermogenys* (Fig. 10A).

(14) *Posttemporal bone*: Forked [0]; simple [1]. The posttemporal bone is simple, rather than forked or with a ventral arm, in all ricefishes (Fig. 10B). The posttemporal bone has a ventral arm in exocoetoids (Fig. 10A; Meisner, 2001), most cyprinodontiforms and atheriniforms. The ventral arm is relatively short in some cyprinodontiform taxa (Parenti, 1981: figs 7, 8).

(15) *Anterior ramus of coracoid*: Narrow, with cartilaginous tip [0]; broad, particularly at point of articulation with the cleithrum, without cartilage [1]. A broad anterior ramus of the coracoid was coded by Dyer & Chernoff (1996: 37) as a synapomorphy of the atheriniform atherines and the genus *Iso*, and was considered convergent with *Oryzias* (including *Horaichthys*). It also characterizes *Adrianichthys* (Fig. 10B) and hence is proposed here as a ricefish synapomorphy.

#### CAUDAL SKELETON

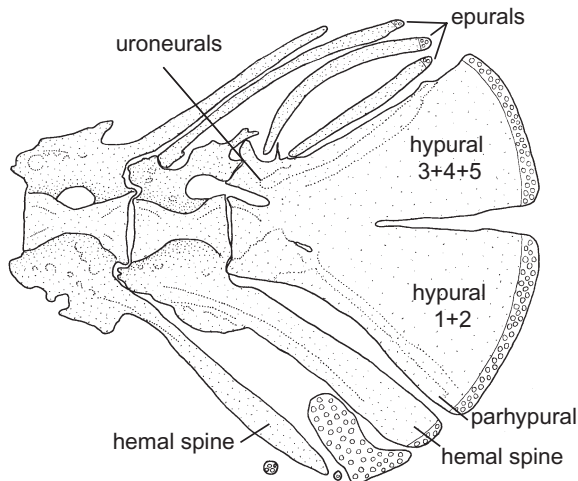
(16) *Ventral accessory bone in caudal skeleton*: Absent [0]; present [1]. In the exocoetoid caudal skeleton, represented by *Hemirhamphodon kuekenthali*, there are three ossified epurals between the uroneurals and neural spine of preural centrum 2 (Fig. 11A). One or two relatively large blocks of cartilage, and smaller cartilages, lie between the haemal spines of preural centra 2 and 3; none is ossified. A ricefish caudal skeleton is represented by *Oryzias bonneorum* (Fig. 11B): there are two ossified epurals opposed to two autogenous elements, one cartilage and one bone that lie between the haemal spines of preural centra 2 and 3. Ossification of one of the autogenous ventral elements (Fig. 11B–F), what has been termed variously a ventral accessory caudal bone (Parenti, 1993) or an extra caudal ossicle (Fujita, 1990, 1992), is a ricefish synapomorphy. In larger ricefishes, such as *Adrianichthys roseni*, there is just one large, relatively straight ventral accessory bone and no block of cartilage between the haemal spines. In contrast, in the miniature *Oryzias setnai* (see Parenti, 1993: fig. 10), there is one ventral accessory cartilage and remnant of a second. The caudal skeleton of an adult *O. minutillus* (Fig. 11D) is like that of an adult *O.*

*latipes*: there are two ossified epurals, and ventrally, one accessory caudal bone and one accessory cartilage. It differs in that the ossified accessory element is the posterior, rather than the anterior, element between the haemal spines of preural centra 2 and 3. In some specimens, as in adult male *O. sinensis* (AMNH 10344), *O. mekongensis* (Fig. 11E; CAS 58027), *O. luzonensis* (CAS 58032), *O. javanicus* (CAS 58026), *O. timorensis* and some *O. celebensis*, both ventral accessory elements may be ossified, indicating that ossification of one particular accessory cartilage is not fixed in development, nor is ossification correlated with adult size.

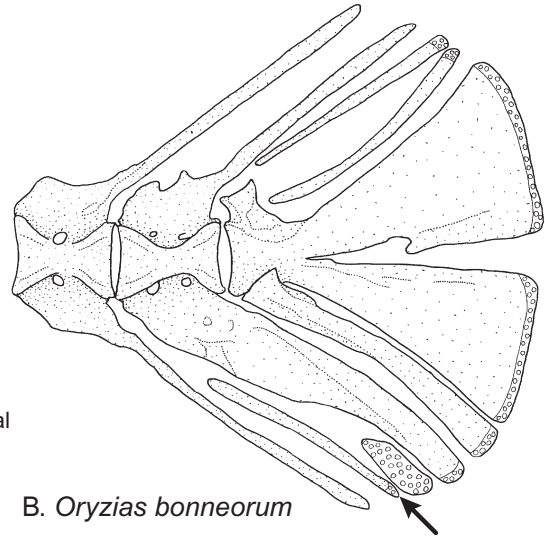
This ventral accessory bone in *O. latipes* was called an extra caudal ossicle by Yabumoto & Uyeno (1984) who pointed out its similarity, in both size and position, to the so-called Y-bone (Monod, 1968; Patterson & Rosen, 1989: fig. 6) or ventral accessory bone (Rosen & Patterson, 1969) of gadiform fishes. Gadiform fishes have both dorsal (X) and ventral (Y) accessory bones that are variously present or absent among taxa and individuals (see Patterson & Rosen, 1989: 13, for discussion). Accessory cartilages or bones characterize the caudal skeleton of many other actinopterygian fishes (e.g. Rosen, 1973; Stiassny, 1990). A cartilage between the distal ends of the haemal spines of PU2 and PU3 was reported in a variety of atheriniforms (Dyer & Chernoff, 1996). The ricefish ventral accessory bone may be homologous with the ventral interhaemal cartilage of atheriniforms, and possibly also with the Y-bone of gadiforms and of the zeid *Zeniopsis nebulosa* (see Fujita, 1990, 1992; Parenti, 1993). The element from which the extra caudal ossicle developed could not be determined by Fujita (1992), who studied the developmental osteology of the caudal skeleton of *Oryzias latipes*. The X and Y bones of gadiforms may be free neural and haemal spines, respectively, that remain following vertebral fusion or loss (Rosen & Patterson, 1969; Markle, 1989). Alternatively, the Y-bone may be a remnant of an anal-fin radial (Markle, 1989: fig. 17a). Further investigation is necessary to test the hypothesis of homology of the Y-bone in ricefishes, gadiforms and other taxa.

#### LATERAL LINE SYSTEM

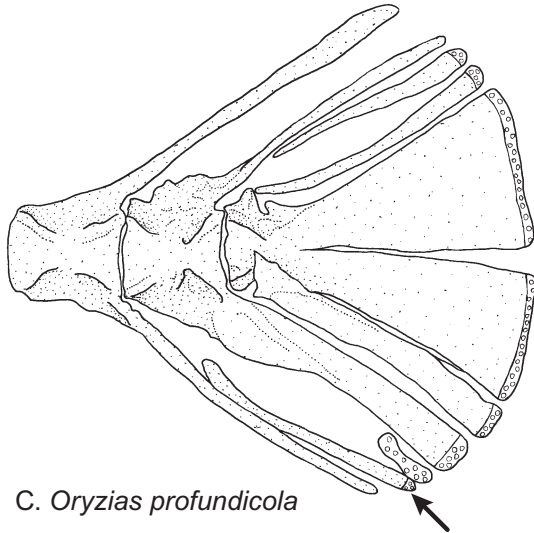
(17) *Position of the lateral branch of the posterior lateral line nerve in adults and type of scales*: Mid-lateral, with few or only weakly developed pored lateral line scales [0]; ventral, with pored lateral line scales [1]; ventral, without pored lateral line scales [2]. The ricefish lateralis system is characterized by large neuromasts on the head and superficial neuromasts distributed over the body surface. There are no canal organs and no perforated lateral line scales



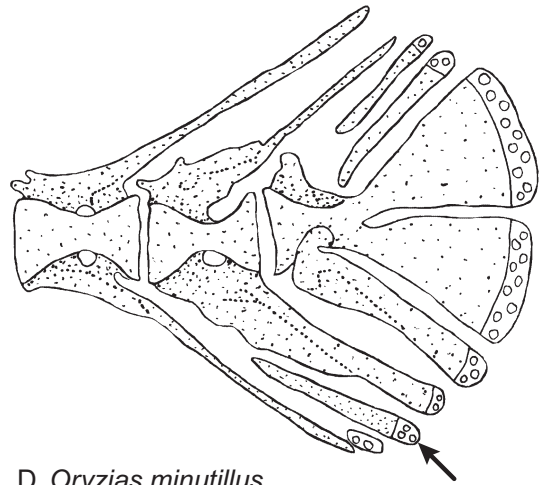
A. *Hemirhamphodon kuekenthali*



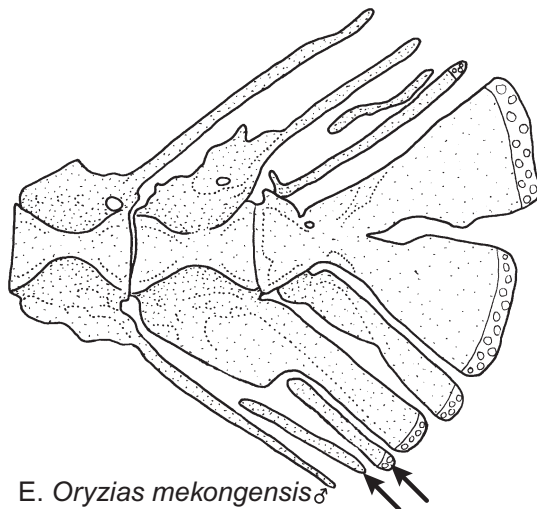
B. *Oryzias bonneorum*



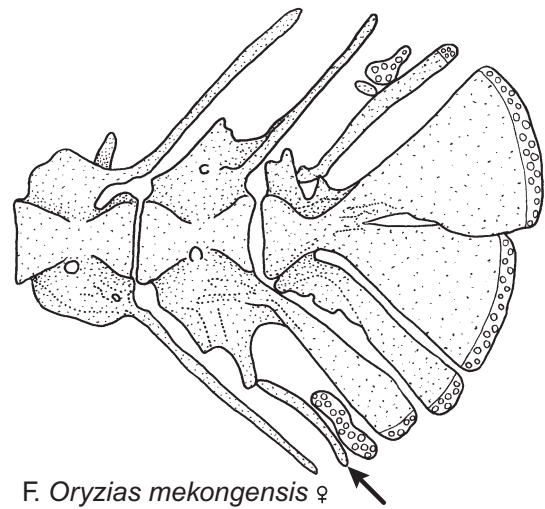
C. *Oryzias profundicola*



D. *Oryzias minutillus*



E. *Oryzias mekongensis* ♂



F. *Oryzias mekongensis* ♀

**Figure 11.** A, *Hemirhamphodon kuekenthali*, USNM 330828, adult male, 50 mm SL; B, *Oryzias bonneorum*, ZMA 123.863, adult male, 41 mm SL; C, *Oryzias profundicola*, CMK 6485, adult male, 46 mm SL; D, *Oryzias minutillus*, CAS 58022, adult female, 13.5 mm SL; E, *Oryzias mekongensis*, CAS 58027, adult male, 15.0 mm SL; F, *Oryzias mekongensis*, CAS 58027, adult female, 16.5 mm SL. Diagrammatic representation of caudal skeleton. Arrows point to extra caudal ossicle(s); the element is cartilaginous in *Hemirhamphodon*. All drawn to same scale.

(Yamamoto, 1975; Ishikawa, 1994). This is in contrast to other beloniform fishes, except some zenarchopterids, which have well-developed canal neuromasts in the posterior lateral line and a well-developed, ventral posterior lateral line. See also discussion above under Relationships of Adrianichthyidae to other Atherinomorph fishes.

#### PHYLOGENETIC RELATIONSHIPS AMONG RICEFISH SPECIES

Here, I describe and discuss the states of 67 characters (18–85) that provide the bulk of the data used to interpret phylogenetic relationships among ricefish species. Distribution of states of all characters (1–85) is discussed in the Phylogenetic analysis following the character description. Species autapomorphies are largely not discussed here, but included in the Key to Adrianichthyid genera and species and systematic accounts, which follow the Discussion.

##### BODY AND SQUAMATION

(18) *Size at hatching*: Large, greater than 4.5 mm [0]; small, 4.5 mm or less [1]. Atherinomorphs have a relatively long developmental period; fertilized eggs may hatch 1–2 weeks, vs. 1 or 2 days, post-fertilization, or even enter diapause in which fertilized eggs may not hatch for periods of 6 months or more (see Parenti, 1993, 2005). Size at hatching in beloniforms in part mirrors egg size: belonids hatch at 6.8–14.4 mm, hemiramphids *s.l.* at 4.8–11 mm, scomberesocids at as small as 6.0–8.5 mm, exocoetids at 3.5–6.1 mm, and two adrianichthyids at 3.5–4.5 mm (Collette *et al.*, 1984: 339). Length at hatching was reported by Collette *et al.* (1984) for two adrianichthyid species, placed here in the genus *Oryzias*, *O. setnai* and *O. melastigma* (either *O. dancena* or *O. carnaticus*). The total length of a newly hatched larva of *O. setnai* was reported as 3.5–4 mm (Kulkarni, 1940). The average total length of a medaka fry was reported as 4.6 mm (Yamamoto, 1975). Size at hatching has not been documented previously for species in the genus *Adrianichthys*, and the only species in which it is likely to be assessed is *A. oophorus*, a pelagic species that was relatively abundant in Lake Poso in 1995 (see Parenti & Soeroto, 2004). A yolk-sac embryo (pre-hatching) of *A. oophorus* (USNM 348724)

measured approximately 5 mm SL; the smallest hatched embryo in that catalogued lot measured approximately 6.5 mm SL. Therefore, minimum size at hatching for *Adrianichthys* is estimated at between 5.0 and 6.5 mm SL.

(19) *Maximum adult body size*: 60 mm SL or larger [0]; greater than 50 mm SL and less than 60 mm SL [1]; greater than 40 mm SL and less than 50 mm SL [2]; greater than 26 mm SL and less than 40 mm SL [3]; 26 mm SL or less [4]. The maximum observed SL for ricefish species ranges from a low of 16.1 mm for *O. uwai* to a high of 192 mm for *A. poptae*. All *Adrianichthys* species reach over 60 mm SL, and exocoetoids can be much larger, exceeding 1 m in *Tylosurus acus*, for example (see Collette, 2003). All *Oryzias* species mature at less than 60 mm SL and no species exceeds that size. I divide *Oryzias* species arbitrarily into four groups based on range of SL, which correspond to states of this character: (1) elongate, adults reaching a maximum size of more than 50 mm but less than 60 mm SL (*O. sarasinorum*, *O. bonneorum*, *O. orthognathus* and *O. nigrimas*); (2) intermediate, adults reaching a maximum size of more than 40 mm but less than 50 mm SL (*O. matanensis*, *O. marmoratus* and *O. profundicola*); (3) small, adults reaching a maximum size of more than 26 mm but less than 40 mm SL (*O. curvinotus*, *O. latipes*, *O. luzonensis*, *O. javanicus*, *O. dancena*, *O. carnaticus*, *O. celebensis*, *O. timorensis* and *O. nebulosus*); and (4) miniature, adults no larger than 26 mm SL (*O. haugiangensis*, *O. hubbsi*, *O. setnai*, *O. uwai*, *O. mekongensis*, *O. pectoralis*, *O. minutillus* and *O. sinensis*).

Miniature South American freshwater fish species were defined arbitrarily by Weitzman & Vari (1988) as those that are sexually mature at about 20 mm SL and reach no greater than 25 or 26 mm SL. This definition of miniature was adopted by Kottelat & Vidthayanon (1993: table 4) who compiled a list of 47 miniature species-level taxa then known from South and Southeast Asia. I also adopt this definition here, and recognize eight miniature ricefish species, as above, although *Oryzias curvinotus* reaches just 27.2 mm SL and would be classified as a miniature ricefish were the definition of miniature modified slightly. Evolution of body size is discussed following the Phylogenetic analysis below.

(20) *Body depth*: Slender bodied, reaching no more than 26% SL in adults [0]; somewhat deep bodied,

reaching more than 26% and less than 33% SL [1]; extremely deep bodied, reaching more than 33% SL in adults [2]. Two ricefishes are extremely deep bodied: *O. dancena* (Fig. 1) reaches a body depth of 34% SL, and *O. profundicola* reaches 35%. Five species are somewhat deep bodied: *O. carnaticus*, *O. haugianguensis*, *O. javanicus*, *O. marmoratus* and *O. matanensis*. All other ricefishes are relatively slender bodied, as defined here, as are outgroup exocoetoids and aplocheiloid cyprinodontiforms. Atheriniforms may be somewhat deep-bodied, as is the outgroup genus *Melanotaenia*, or slender-bodied.

(21) *Scales in a lateral series*: Fewer than 40 [0]; 40–57 [1]; 58–65 [2]; 70 or more [3]. Scales in a lateral series among ricefishes range from a low of 24 in the miniature *O. haugianguensis* to a high of 85 in *A. poptae* (Table 3). The coding scheme adopted here recognizes four discrete states of scale number. Three ricefish species have 70 or more scales in a lateral series: *A. kruyti*, *A. poptae* and *O. sarasinorum*. The two other *Adrianichthys* species, *A. roseni* and *A. oophorus*, have 63–65 and 58–65 scales, respectively, whereas all other *Oryzias* have 57 scales or fewer. *Oryzias orthognathus* and *O. matanensis* have scales in a lateral series that range from 40 to 57. The remaining ricefishes are coded for the phylogenetic analysis as having fewer than 40 scales in a lateral series. Although some species are further diagnosed and differentiated by scale number, that variation is not coded here for the purposes of a phylogenetic analysis because of extensive overlap among the range of scale numbers.

Number of predorsal scales, rather than total number of scales in a lateral series, is recorded traditionally for halfbeaks. *Dermogenys bispina*, for example, was described as having 25–34 predorsal scales (Meisner & Collette, 1998). Zenarchopterids are coded as polymorphic for this character as the number of total scales may be 40 or somewhat higher. *Rivulus* is likewise polymorphic for scale counts under this coding scheme, having a reported 34–51 (Parenti, 1981). Number of scales in a lateral series is quite variable throughout cyprinodontiforms, ranging from none in scaleless *Orestias* species to a reported high of 96 in the genus *Anableps* (Parenti, 1981). Atheriniforms of the genus *Melanotaenia* have relatively large scales and a reported 31–37 vertical scale rows in all subspecies of *M. splendida* (see Allen & Cross, 1982).

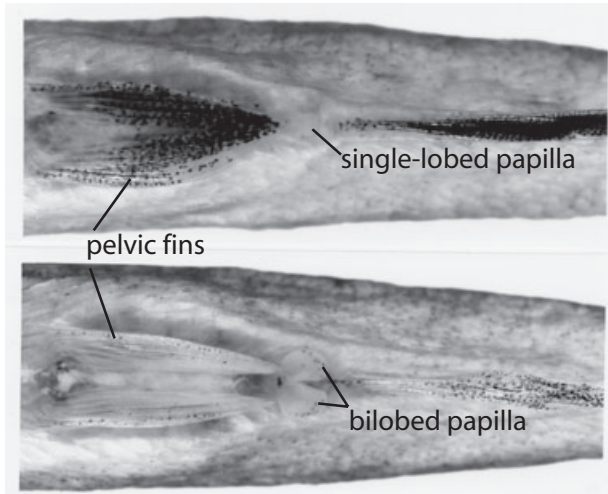
(22) *Head length*: Small to moderate, less than 30% SL [0]; large, 31% or more SL [1]. Head length ranges from 14 to 19% SL in the miniature *O. setnai*, which has the smallest head relative to body length of all ricefishes. Head length ranges from 20 to 30% SL in the majority of ricefishes. Head length is greatest in the large *Adrianichthys* (*A. kruyti* and

*A. poptae*) in which it reaches 35% SL, and *A. roseni* in which it reaches 32% SL. The fourth species of *Adrianichthys*, *A. oophorus*, has a head of moderate length, like most *Oryzias* species, ranging from 25 to 27% SL. Two of the miniatures have relatively large heads: *O. haugianguensis* (range 28–33% SL) and *O. hubbsi* (range 25–32% SL), a character state not correlated with an elongate oral jaw. Variation in this character is coded as discrete, i.e. using the greatest head length reached rather than a range of head lengths, because it is a character of absolute size, as is SL.

(23) *Snout length*: Less than 12% SL [0]; 12% SL or greater [1]. The snout of the largest *Adrianichthys* species (*A. kruyti*, *A. poptae* and *A. roseni*) is relatively long, ranging from 13 to 17% SL. This is in contrast to *A. oophorus* and all *Oryzias* species in which the snout is 11% SL or shorter. The elongate snouts of *Adrianichthys* species were considered homologous with the 'beaks' of exocoetoid beloniform fishes by Parenti (1987).

(24) *Eye size*: Small to moderate diameter, reaching no greater than 9% SL [0]; large diameter, reaching 10% or more of SL [1]. Eye size is the diameter of the eye recorded as a percentage of the standard length. As for some other characters, variation here is coded as discrete, i.e. as the greatest eye diameter reached rather than a range of eye diameters. Even though eye diameter is expressed as a percentage of standard length, the largest ricefishes have among the smallest eyes (e.g. *A. poptae* at 6–7% SL) as well as relatively large eyes (e.g. *A. kruyti*, 8–10% SL). *Oryzias profundicola* has the largest eyes of all ricefishes, ranging from 9 to 13% SL. By the coding used for this character, nine of the 27 ricefish species have relatively large eyes, and *O. bonneorum* is polymorphic. Eye size varies greatly among atherinomorph fishes and I code all outgroups here as polymorphic (see, e.g., Allen & Cross, 1982).

(25) *Urogenital papillae of female*: Single lobed [0]; bilobed [1]; bilobed and greatly enlarged [2]. The urogenital papilla of *Adrianichthys* males and females is relatively small and single lobed. *Oryzias bonneorum* adult males have what appears to be an intromittent organ that can be everted, here considered an autapomorphy of that species; females of *O. bonneorum* and *O. sarasinorum* have a single-lobed papilla. Males of other *Oryzias* species have a single-lobed urogenital papilla, whereas breeding females have a relatively large and distinctly bilobed papilla (Fig. 12). The papillae are distinctly enlarged in *O. hubbsi*, *O. haugianguensis* (Fig. 13A), *O. javanicus* and *O. carnaticus*. They reach their largest relative size in adult female *O. hubbsi* (Fig. 13B), an autapomorphy of that species.

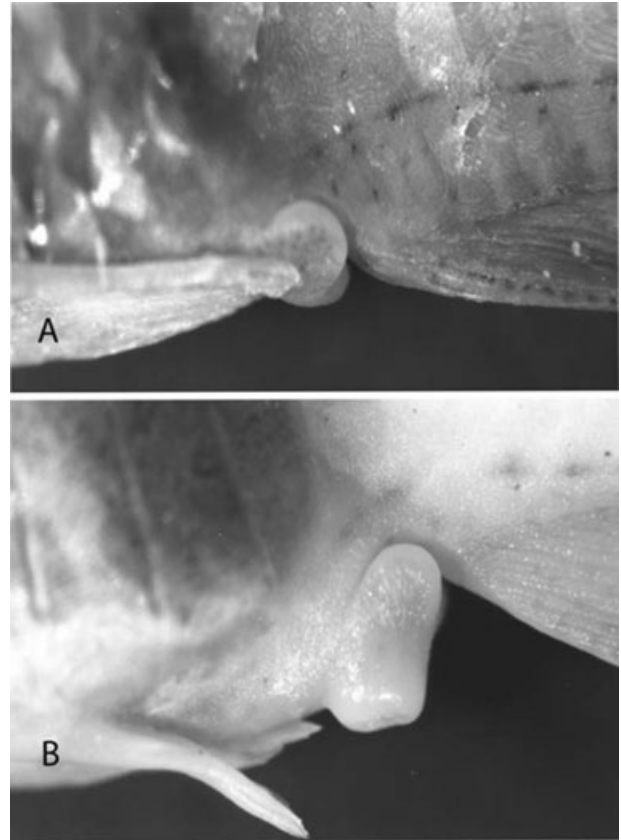


**Figure 12.** *Oryzias matanensis*, CMK 6195, male, 44.5 mm SL (above), female, 40.2 mm SL (below), ventral view of midbody. Note small, single-lobed urogenital papilla in male, bilobed papilla in female.

#### PIGMENTATION

(26) *Dark brown to black nuptial coloration of males:* Absent [0]; present [1]. Two *Oryzias* species from Lake Poso (*O. nebulosus* and *O. nigrimas*) are distinguished from all other ricefishes by a unique sexual dichromatism: in alcohol, males are dark brown to black and females are grey (see Kottelat *et al.*, 1993: pl. 43). The nuptial coloration of live, male *O. nigrimas* has been described as dark bluish grey to black (see Kottelat, 1990a). This sexual dichromatism also characterizes some Sulawesi halfbeaks, such as *Nomorhamphus towoetii* (see Kottelat *et al.*, 1993: pl. 42). Live, nuptial colour pattern of *O. nebulosus* has not been reported; it is predicted to be similar to that of *O. nigrimas*.

(27) *Dark brown blotches on body of males:* Absent [0]; present at midbody [1]; present as a series of regular midlateral brown blotches and irregular dark brown blotches on entire lateral surface of body [2]. Ricefish species from the Malili Lakes (*O. marmoratus*, *O. matanensis* and *O. profundicola*), Lake Lindu (*O. bonneorum*), south-western Sulawesi and Timor (*O. celebensis*, *O. timorensis*) have a colour pattern characterized by irregular brown blotches that may form faint to dark brown vertical bars at midbody in males and some females (Fig. 14). The Malili Lakes species are further characterized by a pattern of dark brown blotches or bars on the entire lateral surface (see also Iwamatsu *et al.*, 1993). *Oryzias sarasinorum* is characterized by a silvery lateral band, a species autapomorphy. In all other natural populations of ricefishes, the ventral surface of the body is yellowish, whereas the dorsal and lateral surfaces of the body may have



**Figure 13.** A, *Oryzias haugiangensis*, CAS 93898, female, 16 mm SL. B, *O. hubbsi*, CAS 92322, female, 16 mm SL. Lateral view of body to show large bilobed urogenital papilla just posterior to pelvic fins of adult females. Extremely large urogenital papilla is an autapomorphy of the miniature *O. hubbsi*.

sparse to dense, dark brown to black chromatophores, and appear spotted (e.g. Seegers, 1997), but no distinct blotches or bars. Groups of melanophores form distinct spots (e.g. Fig. 15) or rows (Fig. 16) in some species (see below).

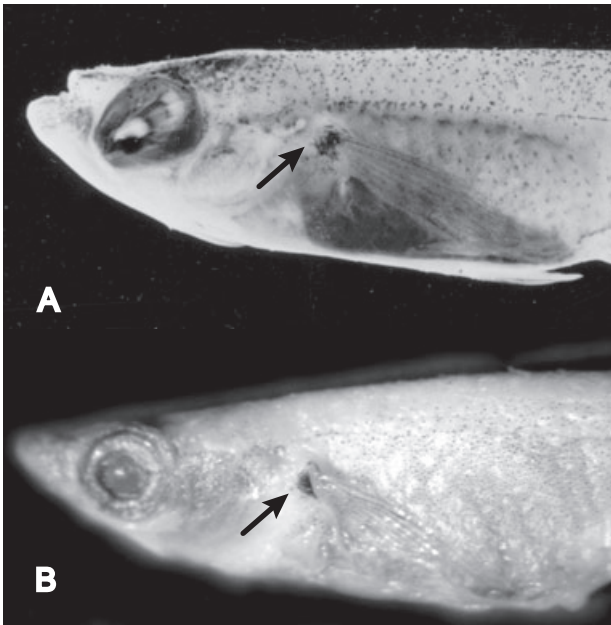
(28) *Interrupted, horizontal dark brown bar from the eye to the lower jaw:* Absent [0]; present [1]. A distinct row of melanophores runs from the eye to the lower jaw in the miniatures *O. uwai* and *O. setnai* (Fig. 16). There is no such horizontal pigmentation pattern in other ricefishes.

(29) *Brown to black spot at base of pectoral fin:* Absent [0]; present [1]. A discrete brown to black spot on the dorsal portion of the pectoral-fin base is present in two miniatures: *O. mekongensis* and *O. pectoralis* (Fig. 15). A discrete pectoral-fin base spot was considered diagnostic of *O. pectoralis* by Roberts (1998: 221). In the description of *O. mekongensis*, Uwa & Magtoon (1986: 475) noted '... a cluster of black specks at the base of pectoral fins.' The pectoral-



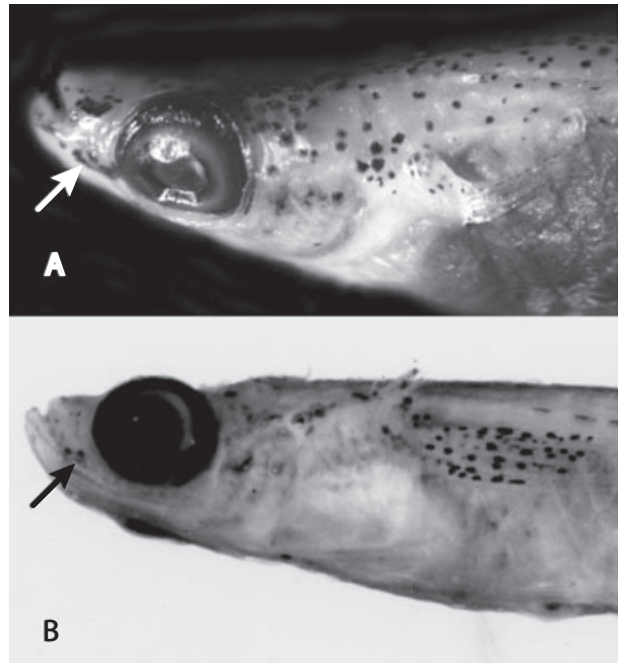


**Figure 14.** *Oryzias celebensis* (Weber, 1894), Sulawesi Selatan, Indonesia, ZSM/LIPI 19, male, 31.4 mm SL, above, female, 29.1 mm SL, below.

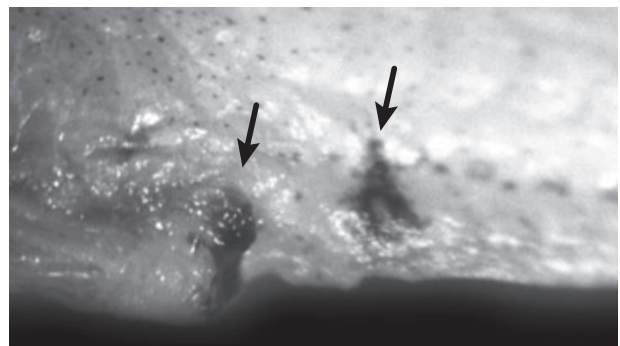


**Figure 15.** A, *Oryzias mekongensis*, USNM 268540, holotype, male, 13.0 mm SL. B, *Oryzias pectoralis*, CAS 92321, paratype, male, 20.1 mm SL. Arrows point to blackish spot at pectoral-fin base in each species.

fin base of *O. setnai* also has scattered melanophores, considered homologous with the pectoral spot here. (30) *Pigmented anal or urogenital region*: Absent [0]; present [1]. The miniatures *O. minutillus* and *O. pectoralis* (Fig. 17), have melanic pigment around the anus or urogenital region, a state described by Roberts (1998: 219) as melanoproctism. Melanophores accompanied by a discrete black blotch are also present on the base of the first several anal-fin rays in

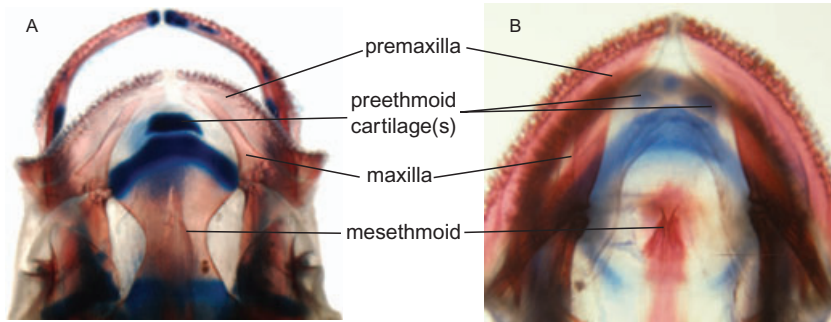


**Figure 16.** A, *Oryzias uwai*, CAS 92309, paratype, female, 13.0 mm SL; B, *Oryzias setnai*, USNM 277482, female, 17.5 mm SL. Arrows point to interrupted, horizontal dark brown bar from the eye to the tip of the lower jaw in *O. uwai*, and to the posterior extent of the lower jaw in *O. setnai*.

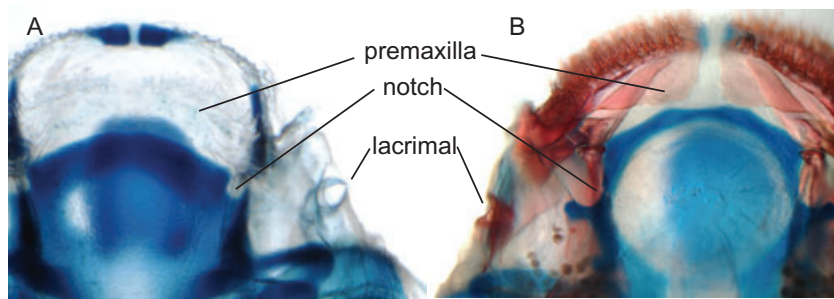


**Figure 17.** *Oryzias pectoralis*, CAS 92321, paratype, male, 19.0 mm SL. Lateral view of midbody. Note perianal melanophores (left arrow) and black blotch on anterior base of anal fin (right arrow). Anterior is to the left.

some specimens of *O. setnai* (see also Kulkarni, 1940) or just anterior to the anal-fin rays in *O. uwai*. These states are all considered homologous here. (31) *Colour on caudal fin in life*: Hyaline to dusky [0]; yellow to orange dorsal and ventral caudal-fin margins [1]. *Oryzias celebensis*, *O. luzonensis*, *O. curvinotus* and some populations of *O. latipes*, *O. javanicus* and *O. sinensis* (see Iwamatsu *et al.*, 1993; Kottelat, 2001b: fig. 408; Seegers, 1997) have



**Figure 18.** A. *Adrianichthys oophorus*, USNM 348386, female, 60 mm SL; B. *A. roseni*, USNM 322425, female, 73 mm SL. Anterior portion of skull, jaws and jaw suspensorium. The cartilage that may be seen between the two preethmoid cartilages in B is the cartilaginous symphysis of the dentaries. Anterior is up.



**Figure 19.** A, *O. javanicus*, juvenile, USNM 348513, 18.5 mm SL; B, *O. matanensis*, CMK 6195, female, 44.5 mm SL. Detail of ethmoid region of skull and oral jaws. Note closed lacrimal canal in *O. javanicus*, open canal in *O. matanensis*.

yellowish dorsal and ventral margins of the caudal-fin rays. *Oryzias mekongensis*, *O. profundicola* and *O. marmoratus* (see Seegers, 1997) have bright orange to orangish-red subdistal margins of the caudal fin. The caudal fin is hyaline to dusky in other ricefishes in which it has been recorded, as well as outgroup beloniforms and cyprinodontiforms.

(32) *Pigmentation pattern on caudal-fin rays in alcohol-preserved material*: Hyaline or dusky [0]; distinct dark brown to black lines on middle rays [1]. *Adrianichthys*, *O. orthognathus*, *O. bonneorum*, *O. nigrimas*, *O. nebulosus*, *O. matanensis* and *O. timorensis* have hyaline to dusky caudal-fin rays as do outgroup beloniform and cyprinodontiform taxa. Distinct dark brown to black lines outline the middle rays in all other *Oryzias* species (e.g. Fig. 14), except for the miniature *O. minutillus*.

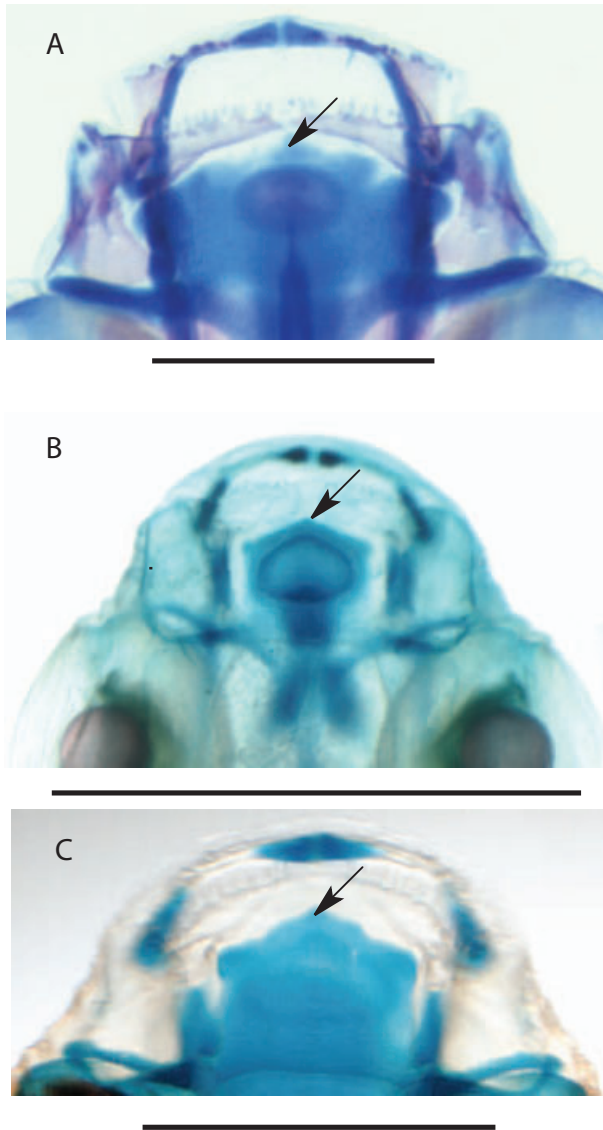
SKULL

(33) *Preethmoid cartilage(s)*: Absent [0]; paired cartilages [1]; single, median cartilage [2]. *Adrianichthys* species have either a single or a paired cartilage that Parenti & Soeroto (2004: fig. 2) called preethmoid cartilage(s). The cartilage is single in *A. poptae* and *A. oophorus* (Fig. 18A), and paired in *A. kruyti* and

*A. roseni* (Fig. 18B). Although ricefishes have been described as lacking the rostral cartilage, Parenti & Soeroto (2004) did not interpret the preethmoid and rostral cartilage as homologous (see character 6, above). Presence of the cartilages in large ricefishes may be correlated ontogenetically with formation of their dorso-ventrally flattened skulls (see character 36, below). These cartilages are not found in any other atherinomorph fishes, as far as known, and no ontogenetic transformation of the cartilages has been described in ricefishes.

(34) *Ethmoid cartilage anterior margin*: Straight and entire [0]; irregular and indented anteromedially [1]; distinct anteromedial projection [2]. The anterior margin of the ethmoid cartilage of *O. latipes* was illustrated as uninterrupted or entire by Yabumoto & Uyeno (1984: fig. 2c), illustrated here for *O. javanicus* (Fig. 19A). In *O. bonneorum* (Fig. 5A) and other Sulawesi *Oryzias*, as well as *O. timorensis*, *O. dancena*, *O. carnaticus* and *O. luzonensis*, the anterior margin of the ethmoid cartilage is irregular and may be indented medially (Fig. 19B), with a distinct gap between the left and right side in some specimens.

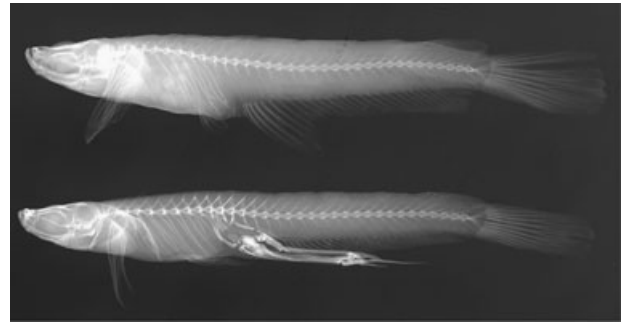
An anteromedial projection of ethmoid cartilage characterizes the miniatures *O. setnai*, *O. uwai*,



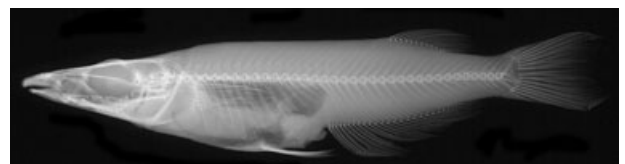
**Figure 20.** A, *Oryzias setnai*, USNM 277482, 14.5 mm SL; B, *O. uwai*, CAS 92310, 12 mm SL; C, *O. minutillus*, CAS 58022, 11 mm SL. Anterior portion of skull and jaw and jaw suspensorium. Arrow points to the medial anterior extension of the ethmoid cartilage. Scale bar = 0.5 mm.

*O. minutillus* (Fig. 20) and *O. mekongensis* (see Iwamatsu, 1986: fig. 2). This projection of the ethmoid cartilage is not present in other miniatures, nor is it present in juvenile stages of species that are not considered miniatures, e.g. *O. javanicus* (Fig. 19A). The anteromedial projection of the ethmoid cartilage posterior to and nearly meeting the preethmoid cartilage in *Adrianichthys* (Fig. 18A) is less pronounced and not proposed here as homologous with the anterior projection in the miniature species.

(35) *Ethmoid cartilage lateral margin*: Entire [0]; distinct notch bordered posteriorly by anterior margin



**Figure 21.** *Oryzias setnai* (Kulkarni, 1940), USNM 197764, Bombay, India, female, 18 mm SL, above; male, 18.5 mm SL, below. Radiograph.



**Figure 22.** *Adrianichthys roseni*, holotype, MZB 6732, adult female, 90 mm SL. Radiograph.

of lateral ethmoid [1]. The ethmoid cartilage caps the anterior margin of the mesethmoid, the lateral ethmoid lies lateral to the posterior margin of the mesethmoid and the palatine lies dorsal or lateral to the ethmoid cartilage and mesethmoid in outgroup halfbeaks, *Adrianichthys* (Fig. 18), *O. sarasinorum*, *O. bonneorum* (Fig. 5A), *O. orthognathus*, *O. nigrimas*, *O. nebulosus* and *O. timorensis*. In all other *Oryzias*, there is a distinct notch in the ethmoid cartilage through which the palatine passes (Fig. 19). The posterior border of the notch is formed by the anterior margin of the lateral ethmoid cartilage. It is distinct in miniatures *O. hubbsi* and *O. pectoralis*; in some other miniature species, the ethmoid region is not as well developed, and the ethmoid cartilage is rectangular and slightly indented (Fig. 20). This may represent an early ontogenetic stage of development of the notch.

(36) *Ethmoid region of skull in lateral and dorsal view*: Convex and narrow [0]; flat and broad [1]. The ethmoid region of the skull is slightly convex in lateral view, and relatively narrow dorsally, in *Oryzias* species (Fig. 21; Yabumoto & Uyeno, 1984: fig. 2b). In contrast, the ethmoid region of the skull is flat and broad in *Adrianichthys* (Fig. 22).

(37) *Mesethmoid ossification*: Round or oval [0]; subrectangular [1]; semicircle anteriorly with subrectangle posteriorly [2]; indented anteriorly [3]. The mesethmoid ossification is round or oval in most ricefish species (Figs 5A, 19B) as it is in many other atherinomorphs (Rosen, 1964: fig. 5a, b; Parenti,

1981). The mesethmoid ossification is subrectangular in the miniatures *O. setnai* and *O. uwai* (Fig. 20A, B). The mesethmoid ossification of adult *A. poptae* and *A. oophorus* uniquely forms a semicircle followed by a subrectangular portion posteriorly (Fig. 18A; Rosen, 1964: figs 6, 7). *Oryzias latipes* and *O. luzonensis* have an ossified mesethmoid that is round or suboval and with a medial, anterior indentation in some specimens (Iwamatsu, 1986: fig. 2).

(38) *Orbits*: Confluent with dorsal surface of head [0]; project somewhat beyond dorsal profile of head [1]; project markedly beyond dorsal profile of head [2]. Bony orbits projecting beyond the dorsal surface of the head was proposed by Parenti & Soeroto (2004) as a synapomorphy of *A. roseni* (Fig. 22) and *A. kruyti*. Although the condition is not as marked, the orbits project somewhat beyond the dorsal profile of the head in the other *Adrianichthys* species, *A. kruyti* and *A. oophorus* (e.g. Kottelat *et al.*, 1993: pl. 44). The dorsal margin of the orbits is coded as confluent with the dorsal surface of the head in other ricefishes (e.g. Fig. 1) and outgroup taxa.

(39) *Lacrimal sensory canals*: Open [0]; closed [1]. The dermosphenotic and preopercular canals of atherinomorphs are carried in open, bony grooves (e.g. Fig. 5A). The lacrimal sensory canal is either carried in open, bony grooves or is largely bone-enclosed and covered by epidermis. The lacrimal canal is open (Fig. 19B) in outgroup halfbeaks, *Adrianichthys*, *O. sarasinorum*, *O. bonneorum*, *O. orthognathus*, *O. nigrimas*, *O. nebulosus*, *O. profundicola*, *O. matanensis*, *O. marmoratus*, *O. timorensis*, *O. celebensis*, *O. latipes*, *O. luzonensis*, *O. curvinotus*, *O. sinensis*, *O. pectoralis*, *O. uwai*, *O. setnai*, *O. mekongensis* and *O. minutillus*. The lacrimal canal is closed (Fig. 19A) in five species: *O. javanicus*, *O. carnaticus*, *O. dancena*, *O. hubbsi* and *O. haugiangensis*.

Variation in the structure and form of cephalic pit organs in four *Oryzias* species was described by Iwamatsu, Ohta & Saxena (1984a). *Oryzias latipes* and *O. celebensis* were noted as having 'naked', or open, pit organs, whereas *O. melastigma* (probably = *O. dancena*), and *O. javanicus* with 'sunken', or closed, pit organs (Iwamatsu *et al.*, 1984a: fig. 1). Furthermore, Iwamatsu *et al.* (1984a: fig. 4) observed, using developmental series of their *O. melastigma*, that the 'naked type' is an immature stage of the 'sunken type'. The open and closed pit organs correspond to the open and closed lacrimal sensory canal as described above. More detailed examination of pit lines, including the underlying innervation patterns, may lead to the description of additional characters in ricefishes. I treat these characters as homologues.

(40) *Preopercular sensory canal and dermosphenotic (posterior infraorbital) canal*: Separate [0]; continuous

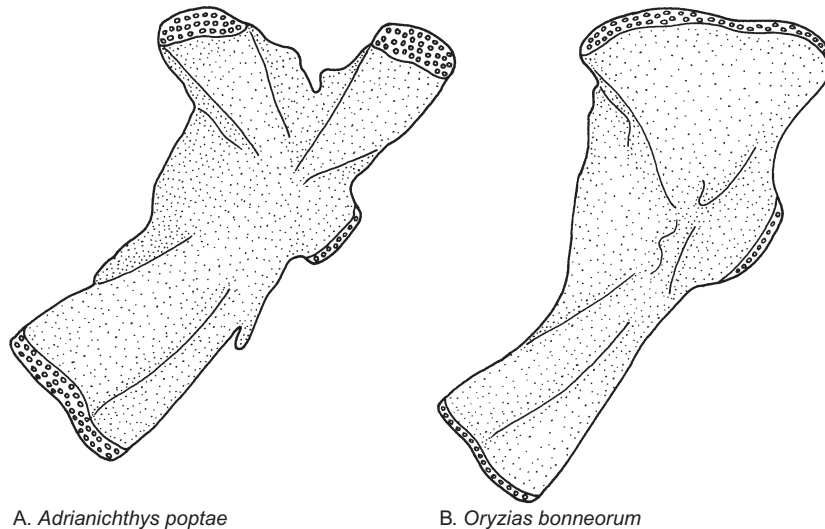
[1]. The preopercular sensory canal is continuous with that of the pterotic in mugilids, atheriniform atherinopsids and *Iso* (see Dyer & Chernoff, 1996: 25). An inferred derived state in atheriniforms is separation of the dorsal extent of the preopercular and pterotic canals (Dyer & Chernoff, 1996). The preopercular and dermosphenotic canals were reported by Dyer & Chernoff (1996) to be continuous in *Oryzias* and the atheriniform *Dentatherina*. These canals are continuous in *Oryzias* species except for *O. bonneorum* and *O. sarasinorum*. They are also separate in *Adrianichthys* as well as outgroup zenarchopterids (e.g. *Nomorhamphus rossi*) and cyprinodontiforms (e.g. *Fundulus heteroclitus*).

#### JAW AND JAW SUSPENSORIUM

(41) *Upper and lower jaw length*: Subequal [0]; upper jaw extends beyond lower jaw [1]. The upper jaw extends beyond the lower jaw in two ricefishes: *Adrianichthys kruyti*, which has an enlarged, 'duck-bill' upper jaw, and *A. roseni* (Fig. 22), in which the upper jaw is not as prominent. The upper and lower jaws of other ricefishes are roughly equal in length. The lower jaw is at roughly a 90° angle to the body axis in *O. orthognathus*, a species autapomorphy.

(42) *Premaxilla*: Distinct articular and ascending processes [0]; flat and broad without distinct articular and ascending processes [1]. *Adrianichthys* (Fig. 22) has a broad upper jaw that attains its largest relative size in *A. kruyti*, the so-called 'duck-bill' ricefish. The premaxilla is flat and broad and lacks distinct articular and ascending processes; it is nearly confluent with the maxilla (Fig. 18), as in zenarchopterids. This is in contrast to the upper jaw of *Oryzias* (Fig. 5A) in which the premaxilla has distinct articular and ascending processes and is distinctly curved as in other outgroup taxa, such as cyprinodontiforms (Parenti, 1981: fig. 3). The broad upper jaw of *Adrianichthys* is like that of exocoetoid fishes, and may be considered beaked (Parenti, 1987; see also character 23, above). Among atherinomorphs, the atheriniforms and cyprinodontiforms have a protrusible upper jaw, whereas the upper jaw is non-protrusible in beloniforms (Alexander, 1967). Exocoetoids have small ascending processes of the premaxillae associated with a rostral cartilage (see Alexander, 1967: fig. 8), absent in ricefishes (see character 6).

(43) *Maxilla*: With small to broad dorsal process that overlaps the premaxilla [0]; relatively straight and without dorsal process [1]. A relatively broad, dorsal process of the maxilla overlies the posteromedial section of the premaxilla in all *Oryzias* species except for *O. setnai* in which the maxilla is absent, one of the many autapomorphies of that species. The dorsal process of the maxilla in outgroup taxa, such



**Figure 23.** A, *Adrianichthys poptae*, USNM 322423, adult female, 168 mm SL; B, *Oryzias bonneorum*, ZMA 123.863, adult female, 40 mm SL. Diagrammatic representation of the hyomandibula. Both drawn to same scale.

as cyprinodontiforms (Parenti, 1981: fig. 5d), is similarly broad and overlaps the premaxilla. The maxilla lacks a dorsal process and lies, relatively straight, posterior to the premaxilla in *Adrianichthys*. This character is coded as inapplicable in *O. setnai* which lacks a maxilla (see also character 5).

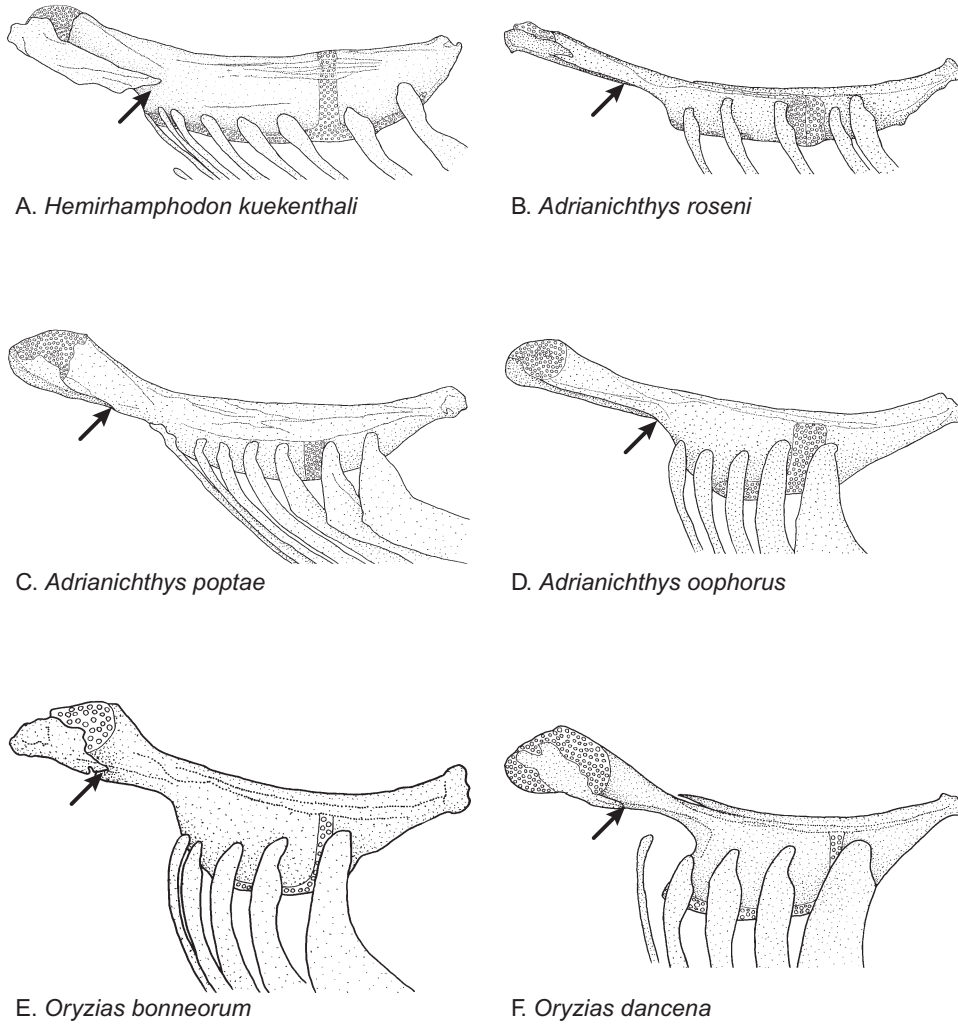
(44) *Oral jaw teeth size and arrangement*: One to three irregular rows of conical teeth on the premaxilla and dentary [0]; up to five irregular rows of small, villiform teeth that form a pavement dentition and no large teeth posteriorly [1]. Upper and lower jaws of *Adrianichthys* have up to five irregular rows of small villiform teeth and no large teeth posteriorly. The teeth form a uniform, flat pavement on the dentigerous surface of the premaxillae and dentaries (Fig. 18). The oral jaw teeth of *Oryzias* are relatively large and conical and distributed in a few irregular rows along the premaxilla and dentary (Yabumoto & Uyeno, 1984: figs 5, 6); they do not form a pavement dentition.

(45) *Enlarged teeth posteriorly on premaxilla*: Absent in both males and females [0]; present in males only [1]; present in males and females [2]. Large, posterior teeth on the premaxillae of males (Parenti, 1987: fig. 1) characterize many *Oryzias* species, including *O. bonneorum* (Fig. 5A) and *O. javanicus* (Fig. 19A). Such teeth are not characteristic of the majority of atherinomorph species, yet they are present in close outgroup taxa, such as the zenarchopterid *Dermogenys siamensis*, and are also variably present in atheriniform fishes, including species in the genera *Melanotaenia*, *Pseudomugil*, *Telmatherina* and *Iso* (see Dyer & Chernoff, 1996: 28–29). Large teeth on the posterior ramus of the premaxilla and perpen-

dicular to the principal tooth rows on the dentary have been described in male medaka, whereas these teeth have been described as absent in female medaka (see Yabumoto & Uyeno, 1984: figs 5, 6). Variation in this character among select atherinomorphs was described by Dyer & Chernoff (1996: 28–29) as two characters: enlarged distal premaxillary teeth, and external premaxillary teeth. Because the enlarged distal teeth of ricefishes may be on the premaxilla and on the external surface of the bone or not depending on the size and number of teeth, I code this variation in one, multistate character. Observed variation of this character among ricefishes is tabulated (Table 4).

(46) *Enlarged teeth posteriorly on dentary*: Absent in both males and females [0]; present in males, rarely in females [1]. In some *Oryzias* species, such as *O. carnaticus* and *O. javanicus*, males have enlarged teeth posteriorly on the premaxilla and the dentary, whereas females have enlarged teeth only on the premaxilla, as coded in character 45, above. In specimens identified herein as *O. dancena*, males have enlarged teeth posteriorly on the premaxilla and the dentary, whereas females have no enlarged teeth on either the premaxilla or the dentary. Observed variation of this character among ricefishes is tabulated (Table 4). *Oryzias matanensis* females have enlarged teeth on the dentary and this is expected to occur in other taxa.

(47) *Hyomandibula articulation with otic region of skull*: Bifid head [0]; single head [1]. The dorsal ramus of the hyomandibula is bifid and has separate cartilages that articulate with the sphenotic and pterotic bones of the skull in *Adrianichthys* (Fig. 23A). In



**Figure 24.** A, *Hemirhamphodon kuekenthali*, USNM 330828, adult male, 50 mm SL; B, *Adrianichthys roseni*, USNM 322425, adult female, 73 mm SL; C, *Adrianichthys poptae*, USNM 322423, adult female, 168 mm SL; D, *Adrianichthys oophorus*, USNM 348386, female, 60 mm SL; E, *Oryzias bonneorum*, ZMA 123.863, adult female, 40 mm SL; F, *Oryzias dancena*, USNM 342156, adult male, 24.5 mm SL. Diagrammatic representation of the hyoid bar. Arrows indicate posterior extent of the ramus of the ventral hypohyal. Beloniform fishes lack an interhyal. All drawn to same scale.

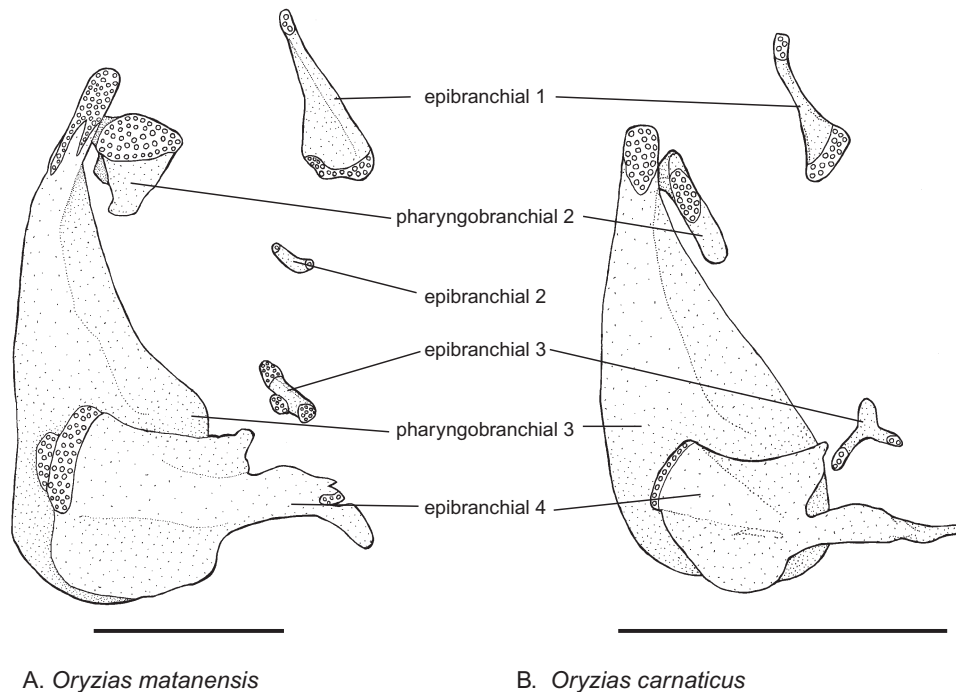
*Oryzias*, the dorsal ramus of the hyomandibula is single and articulates with the skull via a cartilage relatively broad anteriorly and posteriorly, and thinner in the middle (Fig. 23B; Iwamatsu & Hirata, 1980: fig. 5). The head of the hyomandibula is bifid in exocoetoids, cyprinodontiforms (see Parenti, 1981: figs 29, 30) and atheriniforms.

(48) *Articulation of palatine and quadrate bones:* Palatine and quadrate articulate via elongate flanges that overlap anteriorly [0]; no flanges on the ventral surface of the palatine and the quadrate [1]. The palatine has a ventral ramus that overlaps and interdigitates with the dorsal ramus of the quadrate in *Adrianichthys* (Fig. 9) and *O. sarasinorum*. These rami are absent in all other *Oryzias*; the palatine and

quadrate do not meet along the anterior border of the jaw suspensorium (Fig. 8B; Iwamatsu & Hirata, 1980: fig. 5).

GILL ARCHES

(49) *Ventral hypohyal:* Broad posterior ramus [0]; elongate blade-like ramus along the ventral face of the anterior ceratohyal [1]; blunt posterior ramus [2]. Exocoetoid fishes have a posterior ramus on the ventral hypohyal that is relatively broad and robust, as in *Hemirhamphodon* (Fig. 24A). In *Adrianichthys* (Fig. 24B–D), the posterior ramus is extremely long and blade-like, reaching its greatest length relative to the hyoid bar in *A. oophorus* (Fig. 24D). In *Oryzias*



**Figure 25.** A, *Oryzias matanensis*, CMK 6195, male, 42.5 mm SL; B, *Oryzias carnaticus*, CAS 37089, female, 26.5 mm SL. Diagrammatic representation of the dorsal portion of the gill arches. Scale bar = 1 mm.

(24E, F), the ventral hypohyal has a short, blunt posterior ramus that just overlaps the anterior portion of the anterior ceratohyal bone.

(50) *Epibranchial one*: Ossified [0]; cartilaginous [1]. The first epibranchial element was illustrated as a small block of cartilage in *O. setnai* (see Rosen & Parenti, 1981: fig. 15a). It is similarly cartilaginous in the miniature *O. uwai*. This is in contrast to the state in all other ricefishes, including the other miniatures, and outgroup taxa, in which the element is fully ossified, albeit reduced in some.

(51) *Epibranchial two*: Fully ossified, with a broad point of articulation with the ceratobranchial cartilage [0]; notably smaller than the other epibranchial bones and without a broad point of articulation with the ceratobranchial cartilage, may be cartilaginous or absent in some specimens [1]. The second epibranchial bone is fully ossified, about equal in length to the third epibranchial bone, and has a broad point of articulation with the ceratobranchial cartilage in *Adrianichthys* (Rosen & Parenti, 1981: figs 11B, 15B). In contrast, the second epibranchial bone is notably smaller than the third epibranchial bone, and lacks a broad point of articulation with the ceratobranchial cartilage in *Oryzias* (Rosen & Parenti, 1981: figs 11A, 14, 15A; Parenti & Soeroto, 2004: fig. 8). Furthermore, epibranchial 2 may be ossified (Fig. 25A) or cartilaginous or absent (Fig. 25B) in *Oryzias*.

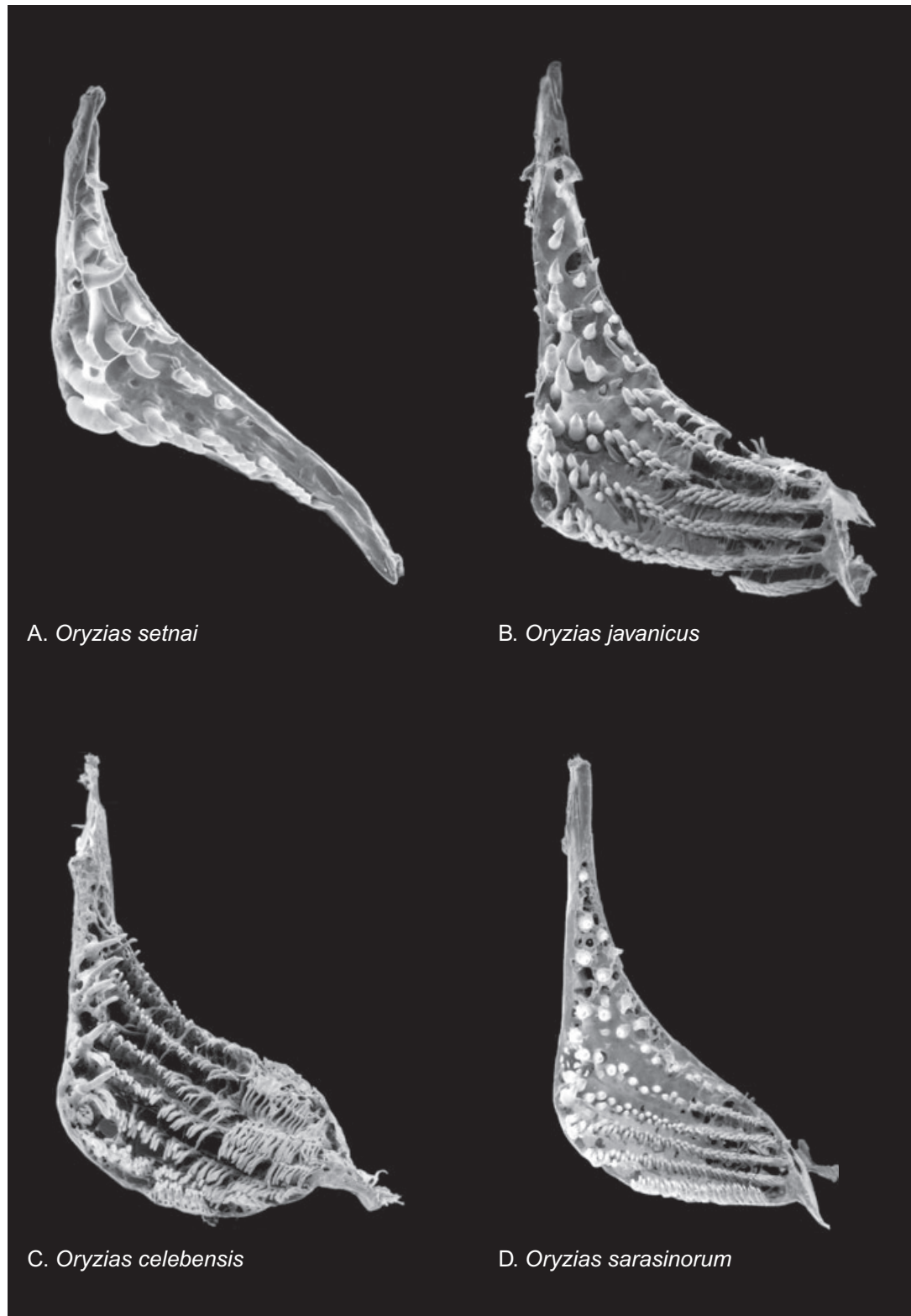
(52) *Ceratobranchial bone five toothplate*: Triangular [0]; rectangular or suboval [1]. All outgroup taxa and

*Adrianichthys* species have a triangular fifth ceratobranchial bone toothplate. The toothplate is distinctly rectangular or suboval in *Oryzias* species, except for the miniature *O. setnai* in which it is triangular (Fig. 26A), a possible modification from the rectangular form, yet coded here as triangular. The fifth ceratobranchial bone toothplate is rectangular in other miniature ricefishes, including *O. uwai*.

(53) *Fifth ceratobranchial tooth arrangement*: Diagonal rows [0]; horizontal rows [1]. Teeth on the fifth ceratobranchial toothplates are arranged in diagonal rows in *Adrianichthys* as in nearly all outgroups. These teeth are arranged in discrete horizontal rows in *Oryzias*, including the miniature *O. setnai* (Fig. 26).

Exocoetoids are not an appropriate outgroup to assess polarity of this character. One exocoetoid synapomorphy is fusion of the left and right fifth ceratobranchial bones to form a median, lower pharyngeal tooth plate (Rosen, 1964: 237). Teeth are distributed irregularly throughout the fused toothplate, typically with an enlarged posterior row; their arrangement cannot be described as either diagonal or horizontal.

Row number (i.e. size of the ceratobranchial toothplate) appears to be directly correlated with body size (character 19), and hence is not coded as a separate character here. In two of the largest ricefishes, *A. poptae* and *A. roseni*, tooth rows on each fifth ceratobranchial number ten or more and 12 or more,



**Figure 26.** A, *Oryzias setnai*, CAS 56255, male, 18 mm SL, SEMX134. B, *Oryzias javanicus*, CAS 58026, adult male, 26 mm SL, SEMX53. C, *Oryzias celebensis*, CAS 58034, adult female, 29 mm SL, SEMX40, teeth on right half of toothplate dislodged during specimen preparation. D, *Oryzias sarasinorum*, ZMA 123.863, female, 40 mm SL, SEMX23. SEM of a right fifth ceratobranchial bone and toothplate. Anterior is up.



respectively. Tooth row counts may be imprecise because teeth are not necessarily arranged in discrete rows, particularly in larger specimens. The miniatures *O. uwai* and *O. setnai* have just two or three rows (Fig. 26A).

The fifth ceratobranchial toothplate of some species has a small, incomplete, posteriormost row of teeth, as in *O. javanicus* (Fig. 26B) and *O. celebensis* (Fig. 26C). Some species are sexually dimorphic such that adult males have an incomplete posteriormost row, but adult females do not (Fig. 26D). The distribution of this character could not be determined with accuracy with the material at hand. An immature male *O. latipes* (CAS 57464), 11.5 mm SL, has three complete rows and no incomplete, posterior row. Rows are apparently added in series from anterior to posterior during growth, with appearance of the incomplete, posteriormost row correlated with sexual maturity (see also Parenti, 1987). Fewer rows, therefore, including absence of the incomplete, posteriormost row, appears to be a juvenile or an adult female character. Ontogenetic series of each species could provide data to confirm or reject this hypothesis.

(54) *Branchiostegal-ray number*: Six or more [0]; five [1]; four [2]. Branchiostegal-ray number varies from four to seven in ricefishes. Branchiostegal rays number six or seven in the miniature needlefish genus *Belonion* and eight to 15 in other exocoetoids (Collette, 1966). More than three anterior branchiostegal rays was considered diagnostic of exocoetoids by Rosen (1964: 239–240). A short, anteriormost, sixth branchiostegal ray characterizes some, but not all, specimens of *O. bonneorum*, *O. sarasinorum* and *O. celebensis*.

Branchiostegal-ray number is not necessarily correlated with size, although five of the eight miniatures, *O. hubbsi*, *O. setnai*, *O. uwai*, *O. mekongensis* and *O. minutillus*, as well as *O. curvinotus* and *O. dancena*, have as few as four branchiostegal rays. Most specimens of *O. haugiensis* have five rays; there is a small anterior sixth ray in some specimens. The largest ricefish species, *Adrianichthys poptae*, has from five to seven branchiostegal rays (Fig. 24C; Table 3).

(55) *Branchiostegal ray arrangement*: Posterior branchiostegal rays articulate with a relatively large posterior ceratohyal [0]; posteriormost branchiostegal ray articulates with a truncated posterior ceratohyal [1]. Arrangement of branchiostegal rays in beloniform fishes differs from the typical atherinomorph arrangement in that the anterior rays barely contact the hyoid bar (Fig. 24A; Kulkarni, 1940; Rosen, 1964). In *Adrianichthys poptae*, *A. kruyti* and *A. roseni*, the posterior ceratohyal is relatively large and the two posteriormost branchiostegal rays are associated with the posterior ceratohyal (Fig. 24B, C). In contrast, in

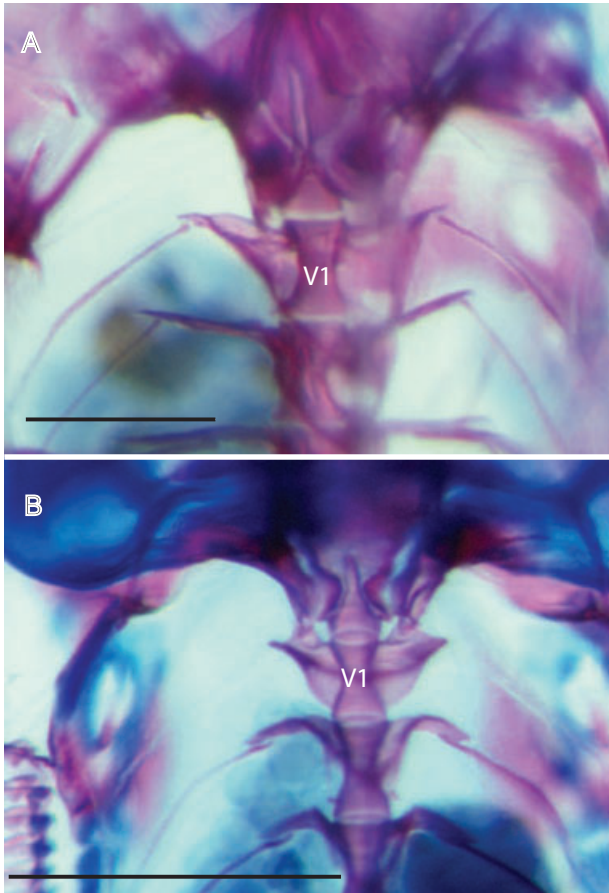
*A. oophorus* and *Oryzias* (Fig. 24D–F), the posterior ceratohyal is somewhat truncate and carries only the posteriormost branchiostegal ray.

#### AXIAL SKELETON

(56) *Total number of vertebrae*: 36 or more [0]; 34 or fewer [1]. Number of precaudal, caudal and total vertebrae in ricefishes is tabulated (Table 3). *Oryzias* has a low total number of vertebrae for beloniforms, 24–34. *Adrianichthys* has 36–37 total vertebrae. Other beloniforms have 36–97 vertebrae (Collette *et al.*, 1984: table 92; B. B. Collette, pers. comm., 2007). Within *Oryzias*, there is no consistent correlation between size, measured as maximum SL, and total number of vertebrae: maximum for the miniature *O. setnai* is 34 and the number in *O. minutillus* ranges from 24 to 29 (Table 3), for example.

(57) *Number of precaudal vertebrae*: 14 or more [0]; 12 or 13 [1]; 11 or fewer [2]. Total number of vertebrae is roughly correlated with number of precaudal vertebrae, which range from 14 to 17 in *Adrianichthys* and from eight to 15 in *Oryzias* (Table 3). Variation in the number of precaudal vertebrae among *Oryzias* species that is not correlated with total number of vertebrae is notable. In the miniature *O. setnai*, for example, precaudal vertebrae number from eight to ten, among the lowest numbers for *Oryzias*, whereas total vertebrae range from 31 to 34, the maximum for *Oryzias*. The high number of caudal vertebrae in *O. setnai* is correlated with a long anal fin (character 69) and posterior dorsal fin (character 68).

(58) *First pleural rib*: Attaches to third vertebra [0]; attaches to second vertebra [1]. The first pleural rib is on the parapophysis of the third vertebra in nearly all ricefishes and in the outgroup exocoetoids examined with the exception of the genera *Belonion* and *Hemirhamphodon* (see Collette, 1966). The first pleural rib is on the parapophysis of the second vertebra in five miniature species: *O. sinensis*, *O. uwai*, *O. setnai*, *O. mekongensis* and *O. minutillus*. In the sole cleared and stained specimen of *O. timorensis* examined, the first complete pleural rib on each side of the body attaches to the third vertebra. There is a small, incomplete pleural rib on the left side of the body associated with the second vertebra. Similarly, in some collections of *O. latipes* (e.g. AMNH 26760SW), *O. nebulosus* and *O. celebensis*, there is a small, isolated bone near the transverse process of the second vertebra which may represent a rudimentary pleural rib. I score *O. timorensis*, *O. latipes*, *O. nebulosus* and *O. celebensis* as polymorphic for this character, but acknowledge that additional surveys and material, especially of *O. timorensis*, may allow a more accurate description of variation in these species.



**Figure 27.** A, *Melanotaenia splendida*, USNM 308410, 24 mm SL; scale bar = 1 mm. B, *Oryzias setnai*, USNM 277482, 17 mm SL; scale bar = 0.5 mm. Dorsal portion of skull and anterior vertebrae. V1 = first vertebra. Anterior is up.

(59) *Transverse processes of first vertebra*: Elongate [0]; short or absent [1]. Transverse processes on the first vertebra of all *Adrianichthys* species, *O. sarasinorum*, *O. bonneorum*, and outgroup taxa such as *Dermogenys palawanensis*, *Hemirhamphodon kuekenthali* and *Melanotaenia splendida* are elongate and perpendicular to the body axis (Fig. 27A). In all other *Oryzias*, transverse processes of the first vertebra are short or absent and are associated with a relatively thin epineural bone or ligament (Fig. 27B). Furthermore, the first two epineural bones are orientated posterolaterally and not in line with the posterior epineural bones (Yabumoto & Uyeno, 1984: fig. 11).

#### PAIRED FINS

##### *Pectoral fins*

(60) *Pectoral-fin ray number*: 13 or more [0]; 9–12 [1]; eight or fewer [2]. Pectoral-fin ray number varies from a high of 16 in *A. kruyti* to a low of six to eight in the

miniature *O. mekongensis* (Table 3). Pectoral-fin ray number overlaps among species. For example, two other miniatures, *O. hubbsi* and *O. sinensis*, have 8–9 or 8–10 rays, respectively, whereas *O. carnaticus* has 11–13 and *O. javanicus* has 10–13. Under the coding scheme adopted for this character, these four species are polymorphic. Pectoral-fin ray number is not necessarily correlated with absolute size as the miniature *O. setnai* has ten rays.

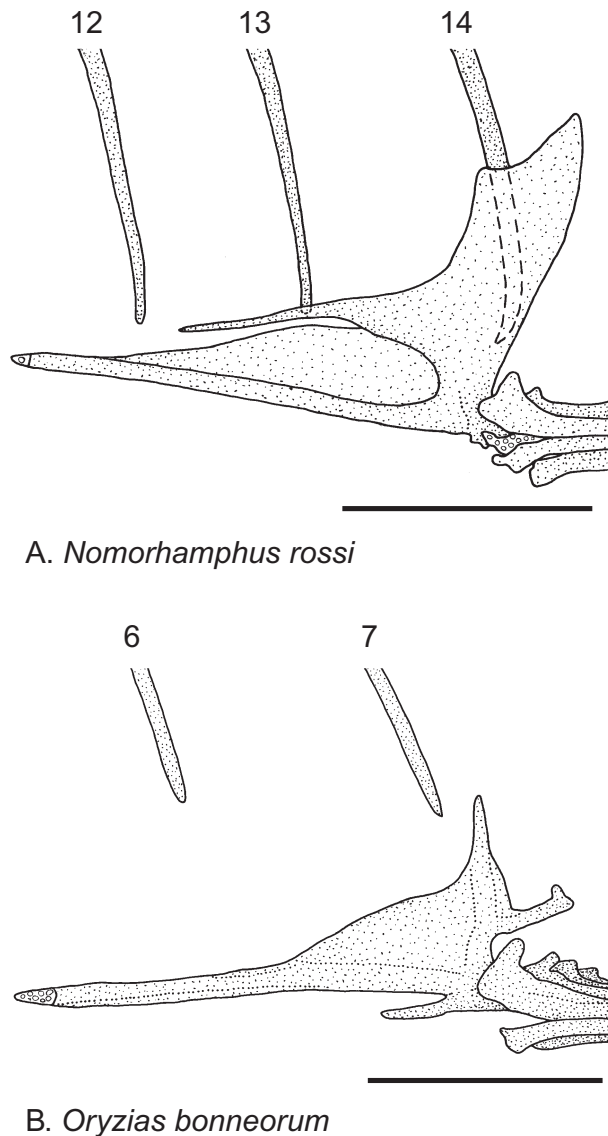
(61) *Pectoral-fin ray bony processes*: Absent [0]; present [1]. Bony processes (sometimes called contact organs; Wiley & Collette, 1970: 190) on the posterior anal-fin rays are well documented in male *O. latipes* and other ricefishes (see character 70, below). Similar, yet relatively fewer in number, bony processes are also present on the medial pectoral-fin rays of male *O. latipes* (see Yamamoto, 1975: fig. 8-5), *O. luzonensis*, *O. sinensis* and *O. mekongensis*.

##### *Pelvic fins*

(62) *Pelvic bone*: No lateral strut or process [0]; lateral strut expanded dorsally, with or without flared, wing-like processes [1]; lateral strut needle-like and elongate [2]. The pelvic bone of all beloniforms has a lateral process or strut that extends dorsally along the lateral surface of the body wall. In halfbeaks (e.g. *Nomorhamphus*, Fig. 28A), *Adrianichthys* and most *Oryzias* (Fig. 28B), the lateral strut is expanded dorsally and has flared, wing-like processes in some individuals (Yabumoto & Uyeno, 1984: fig. 16). In *O. javanicus*, *O. dancena*, *O. carnaticus* and *O. haugiangensis*, the lateral strut is narrow, needle-like and elongate. A lateral strut, or spur (Rosen, 1964), also characterizes some atheriniforms, but not cyprinodontiforms.

(63) *Pelvic-fin rays*: End anterior to anal fin [0]; extend posterior to anal-fin origin in males [1]. Ricefish species typically have paired pelvic fins that extend to a point anterior to the anal-fin origin in males and extend posterior to the anal-fin origin in females (see Yamamoto, 1975: fig. 1-1). Pelvic fins of adult female *O. sarasinorum* may extend well beyond the anal-fin origin, especially in females carrying embryo clusters (e.g. Fig. 54; Böhm, 1997: fig. 5; Parenti, 2005: fig. 10). Male *O. setnai* have two pelvic fins, whereas adult females have only one pelvic bone, with fin rays, on the left side of the body, another species autapomorphy. The pelvic fins of male *O. setnai* and male and female *O. sinensis* may be elongate and extend posterior to the anal-fin origin.

(64) *Pelvic-fin position*: Pelvic fins anterior, in line with pleural rib of vertebra five or less [0]; pelvic fins in line with pleural rib of vertebra six or seven [1]; pelvic fins posterior, in line with pleural rib of vertebra eight or higher [2]. Position of the pelvic fins varies greatly among adrianichthyids, as it does



**Figure 28.** A, *Nomorhamphus rossi*, USNM 363187, adult male, 45 mm SL; B, *Oryzias bonneorum*, ZMA 123.863, adult male, 41 mm SL. Diagrammatic representation of pelvic bones and their position relative to the pleural ribs. Numbers above pleural ribs denote the vertebra to which the rib is attached. Scale bar = 1 mm.

among atherinomorphs (see Dyer & Chernoff, 1996: 39). Adult pelvic-fin position in beloniforms is recorded here by noting the pleural rib with which the lateral process of the pelvic bone is aligned. Pelvic fins tend to be more posterior in larger species, those species that reach a greater SL, although this relationship does not hold in all species (Table 5). Pelvic fins are extremely posterior in some beloniforms, such as the belonid *Belone belone*, in which the pelvic fins are associated with vertebra 36 (B. B. Collette, pers. comm., 2005). The lateral process of the pelvic bone is

in line with the pleural rib of the fourteenth vertebra in the halfbeak *Nomorhamphus rossi* (Fig. 28A). Among other outgroups, *Melanotaenia* has relatively anterior pelvic fins, with pelvic bones in line with vertebra 5, whereas the *Rivulus* has relatively posterior pelvic fins, with pelvic bones in line with vertebra 9.

The lateral pelvic process is in line with the fifth, sixth or eighth pleural rib in *Adrianichthys*, attaching to the seventh, eighth or tenth vertebra, respectively (Table 5). Among *Oryzias* species, the lateral pelvic process is in line with a rib that attaches to the fourth, fifth, sixth or seventh vertebra (Fig. 28B; Table 5). Pelvic fins are the most anterior in species in which the lateral pelvic process is in line with the third pleural rib. In *O. nebulosus* the pelvic fins may be in line with the third, fourth or fifth rib, modally the fourth (Parenti & Soeroto, 2004). In three miniatures, *O. minutillus*, *O. setnai* and *O. uwai*, the first pleural rib is on the second vertebra and the pelvic fins are the most anterior, in line with the third pleural rib, but on the fourth vertebra.

(65) *Pelvic-fin ray number*: Six or seven [0]; five [1]. Number of pelvic-fin rays ranges from five to seven in ricefishes. Six is the plesiomorphic number, based on outgroup comparison (e.g. Parenti, 1981), and is also the most common number. Seven pelvic-fin rays characterize some of the larger ricefish, *A. poptae*, *O. orthognathus* and some specimens of *O. latipes*. Five pelvic-fin rays characterize two of the miniature species, *O. minutillus* and *O. setnai*. Three species are polymorphic for pelvic-fin ray number under this coding scheme (*O. latipes*, *O. javanicus* and *O. mekongensis*). Of outgroup taxa coded in the data matrix, only the atheriniform *Melanotaenia* has an I, five pelvic-fin ray formula, with one spine followed by five segmented rays.

(66) *Pelvic-fin connection to body*: Medialmost pelvic-fin ray separate from body [0]; medialmost pelvic-fin ray connected along one-half its length to body via a membrane [1]. This character was described by Kottelat (1990a: 52) in an artificial key to ricefishes to distinguish between the then known *Adrianichthys* species (*A. ophorus*, *A. kruyti* and *A. poptae* following the classification herein) from the *Oryzias* species (*O. nigrimas* and *O. orthognathus*) in Lake Poso, Sulawesi. The medialmost pelvic-fin ray is also not connected to the body in *O. sarasinorum*, *O. bonneorum*, *A. roseni* and outgroup taxa (see also Dyer & Chernoff, 1996: 39).

#### MEDIAN FINS

##### *Dorsal fin*

(67) *Dorsal-fin ray number*: 14 or more [0]; 11–13 [1]; 8–10 [2]; never more than eight [3]. Total number of

dorsal-fin rays in ricefishes is highest in *Adrianichthys kruyti* and *A. roseni* which have 14–17 and 13–16 dorsal-fin rays, respectively. Exocoetoids also have a relatively high number of dorsal-fin rays (Collette *et al.*, 1984: table 92) *Adrianichthys poptae* and *A. oophorus* have ranges of 11–13 and 8–10, respectively. Among *Oryzias* endemic to Sulawesi (*O. sarasinorum*, *O. bonneorum*, *O. orthognathus*, *O. nigrimas*, *O. nebulosus*, *O. celebensis*, *O. matanensis*, *O. profundicola* and *O. marmoratus*) and Timor (*O. timorensis*), the dorsal-fin ray number ranges from eight to 14, with overlap among species (Table 3). Within the coding system adopted for this character, six Sulawesi endemics (*A. roseni*, *O. orthognathus*, *O. nigrimas*, *O. nebulosus*, *O. profundicola* and *O. marmoratus*) are polymorphic. Total number of dorsal-fin rays is never more than eight in all other *Oryzias*.

Outgroup coding for this character is somewhat problematic. Cyprinodontiforms and beloniforms have a single, soft-rayed dorsal fin. Atheriniforms, in contrast, have two dorsal fins, a first spinous dorsal and a second dorsal fin with at least one anterior spine followed by soft rays, as in mugilids and perciform fishes. It has been inferred that the first dorsal fin of atheriniforms was lost in cyprinodontiforms and beloniforms and select atheriniforms, such as the phallostethids (Parenti, 1993). This hypothesis is open to further test and is not the subject of the current study. Therefore, I code character 67 as inapplicable to the outgroup *Melanotaenia*.

(68) *Dorsal-fin position*: Posterior, origin at or posterior to vertebra 22 [0]; anterior, origin anterior to vertebra 22 [1]. Adult dorsal-fin position was described by Uwa & Parenti (1988) using pre-dorsal length, the straight-line distance from the tip of the snout to the dorsal-fin origin. *Oryzias latipes* (including *O. sinensis*) and *O. curvinotus* were distinguished from putative close relatives by having a relatively posterior dorsal fin (Uwa & Parenti, 1988). Here, I describe position of the adult dorsal-fin by recording the vertebra(e) above which the dorsal fin originates. The dorsal-fin origin is above vertebra 22 in *O. curvinotus* and vertebrae 22 or 23 in *O. latipes* as opposed to vertebrae 20 or 21 in *O. luzonensis* (Table 3). The dorsal-fin is the most posterior in the miniature *O. setnai*, another autapomorphy of that species, in which the dorsal-fin origin is above vertebra 27 (Table 3; Fig. 21). In other ricefishes with a high number of vertebrae, the dorsal-fin origin is not as posterior; for example, in *A. roseni*, the dorsal fin originates above vertebra 23 (Table 3; Fig. 22). The most deep-bodied ricefish, *O. profundicola*, also has the most anterior dorsal-fin which is opposite vertebrae 18–19. As for character 67, this character is coded as inapplicable to the outgroup *Melanotaenia*.

#### *Anal fin*

(69) *Anal-fin ray number*: 23 or fewer [0]; 24 or more [1]. Anal-fin ray number in ricefishes varies from a low of 13–18 in *O. mekongensis* to a high of 27–32 in *O. setnai*, with a great degree of overlap among species (Table 3). Five ricefish species have 24 or more total anal-fin rays: *A. kruyti*, *A. roseni*, *A. poptae*, *O. profundicola* and *O. setnai* (Table 3). Sixteen species have 23 or fewer anal-fin rays: *A. oophorus*, *O. sarasinorum*, *O. bonneorum*, *O. timorensis*, *O. celebensis*, *O. nebulosus*, *O. latipes*, *O. sinensis*, *O. curvinotus*, *O. luzonensis*, *O. minutillus*, *O. pectoralis*, *O. uwai*, *O. hubbsi*, *O. mekongensis* and *O. haugiagensis*. Within the coding system adopted for this character, seven species (*O. nigrimas*, *O. marmoratus*, *O. matanensis*, *O. orthognathus*, *O. carnaticus*, *O. dancena* and *O. javanicus*) are polymorphic. *Rivulus* has a reported 11–14 anal-fin rays (Parenti, 1981), whereas zenarchopterids have from eight to 17 anal-fin rays (Collette *et al.*, 1984: table 92). *Melanotaenia* is coded as polymorphic for this character following Allen & Cross (1982).

(70) *Anal-fin ray bony processes*: Absent [0]; present [1]. Distinct bony processes (also called contact organs because of their inferred role in mating; see Yamamoto & Egami, 1974) on the posterior anal-fin rays of males are a well-known characteristic of *O. latipes* and also reported previously in *O. luzonensis*, *O. dancena*, *O. carnaticus*, *O. javanicus*, *O. haugiagensis*, *O. pectoralis*, *O. sinensis* and *O. curvinotus*. The processes are largest and most well developed in large, male *O. latipes* and *O. luzonensis*. They are also present, yet minute, in mature males of the miniatures *O. hubbsi* and *O. mekongensis* (see Iwamatsu, 1986: fig. 3). The processes are absent in *Adrianichthys* and all other *Oryzias* species as well as outgroup taxa.

(71) *Anal-fin shape and relative length of fin rays*: Anteriormost fin ray short followed by elongate rays with rays decreasing in length posteriorly [0]; anal-fin rays approximately the same length [1]; anterior portion of fin with elongate rays set off from rest of fin [2]. The anal fin of *Adrianichthys* species and most *Oryzias* species, such as *O. celebensis* and *O. javanicus* (Iwamatsu, 1986: fig. 3), is subtriangular in shape, with the anteriormost fin ray short, followed by several elongate rays decreasing in length posteriorly. The anal fin of male *O. latipes* (including *O. sinensis*), *O. curvinotus*, *O. luzonensis* and *O. mekongensis* was described as 'parallelogram-shaped' by Uwa & Parenti (1988: 164) to indicate that, relative to other ricefishes, the posterior anal-fin rays are elongate and relatively the same length as the anterior rays. This is especially marked in *O. luzonensis* (see Iwamatsu, 1986: fig. 3).

The anal fin of male and female *O. uwai*, *O. minutillus* and *O. setnai* is characterized by the anterior portion of the fin elongate and set off from the rest of the fin (Fig. 21). Anterior rays of the anal fin of *O. setnai* females are thickened; those of males are modified into an intromittent organ, autapomorphies of that species (Fig. 21).

#### Caudal fin

(72) *Caudal-fin shape*: Lunate or emarginate [0]; truncate [1]; rounded and with somewhat elongate middle rays [2]. *Adrianichthys*, *O. sarasinorum*, *O. bonneorum*, *O. orthognathus*, *O. nigrimas* and *O. nebulosus* have lunate or emarginate caudal fins, with the dorsal and ventral caudal-fin rays longer than middle rays. Miniatures, except for *O. haugiagensis*, have a rounded caudal-fin. All other ricefishes have a distinctive, truncate caudal fin (Fig. 1). Outgroup atheriniforms and beloniforms have lunate or emarginate caudal fins, whereas one of the diagnostic characters of cyprinodontiforms is a symmetrical caudal fin which may be rounded, truncate or lunate (Parenti, 1981). *Rivulus* has a rounded, symmetrical caudal fin.

(73) *Principal caudal-fin rays*: More principal rays in dorsal lobe or a number equal to that in the ventral lobe [0]; more principal rays in the ventral than in the dorsal lobe, numbering  $i,5/6,i$  or greater [1];  $i,4/5,i$  [2];  $i,3/4,i$  [3]. The caudal fin of beloniform fishes is asymmetrical, with the lower, or ventral, lobe with more principal rays than the upper, or dorsal, lobe following the interpretation of Rosen & Parenti (1981: 17). There are never more principal rays in the dorsal lobe, as Rosen & Parenti (1981) considered diagnostic for euteleosts. Principal caudal-fin ray numbers were reported by them as, for example,  $i,6-7,i$ , meaning one unbranched ray and six branched rays in the dorsal lobe and seven branched rays and one unbranched ray in the ventral lobe. Principal caudal-fin ray numbers in ricefishes were defined by Roberts (1998: 214) as ‘... all branched caudal fin rays plus one upper and one lower unbranched ray’ who reported caudal-fin rays as in *Oryzias dancena*, for example, as 6/6 in his table 1, but as 3–4,5/6,4–5 for *O. dancena* specimens from Chindambaram (Roberts, 1998: 215–216). The count for these Chindambaram specimens is of all caudal-fin rays: three to four dorsal procurrent, five dorsal principal (one unbranched and four branched), six ventral principal (five branched and one unbranched), and four to five ventral procurrent rays. Here, I report principal caudal-fin rays as, for example,  $i,5/6,i$  in *Adrianichthys kruyti* or  $i,4/5,i$  in *O. latipes* to demonstrate that the caudal fin is asymmetrical and that the ventral lobe has more principal rays than does the dorsal lobe. The lowest number of

$i,3/4,i$  is recorded in three miniature species: *O. minutillus*, *O. setnai* and *O. uwai*.

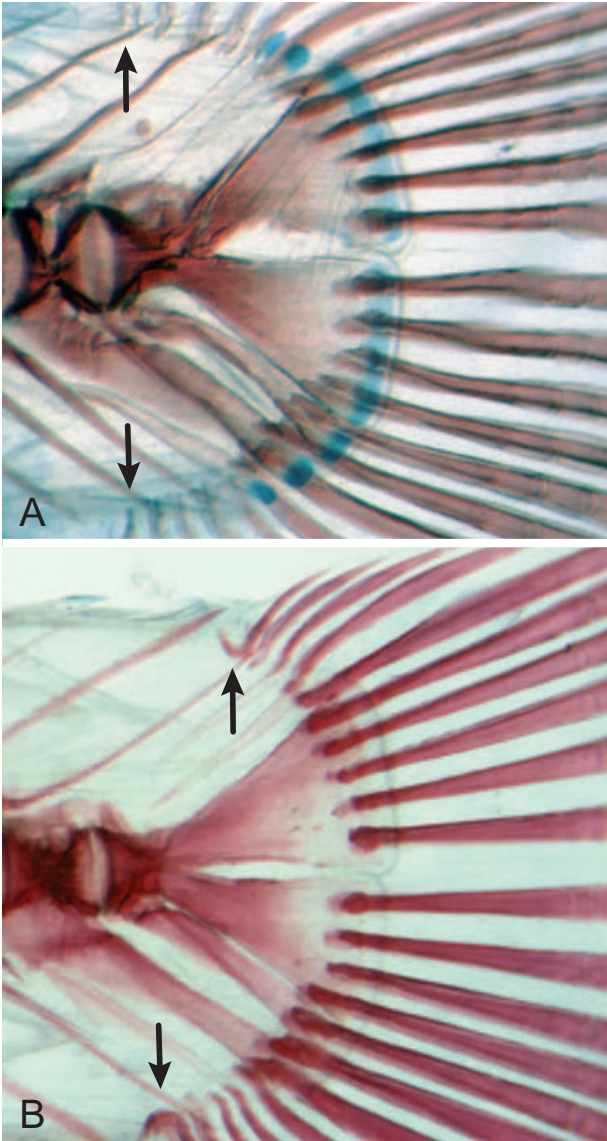
(74) *Procurrent caudal-fin ray number*: High, four or more dorsal and five or more ventral rays [0]; low, three or fewer dorsal and four or fewer ventral rays [1]. Caudal-fin ray numbers have been reported inconsistently in ricefishes possibly because there are a high number of procurrent caudal fin-rays in some species. The dorsal and ventral lobes of the caudal fin of *A. oophorus*, for example, are nearly symmetrical in that they have 13 total rays in the dorsal lobe and 14 in the ventral lobe (Fig. 29A). In the dorsal lobe, there are seven procurrent rays, one unbranched principal ray and five branched principal rays; in the ventral lobe, there are six branched principal rays, one unbranched principal ray and seven procurrent rays. The procurrent caudal-fin ray number is low in three of the miniatures: *O. mekongensis*, *O. pectoralis* and *O. setnai*.

(75) *Procurrent caudal-fin ray shape*: Simple [0]; hooked [1]. Procurrent caudal-fin rays may be simple or distinctly hooked at their proximal portion as in *A. poptae*, *A. oophorus*, *O. sarasinorum*, *O. bonneorum*, *O. orthognathus* (Fig. 29B), *O. nebulosus*, *O. profundicola* and *O. nigrimas*. The procurrent rays are just slightly hooked in *O. matanensis*, *O. marmoratus* and *O. timorensis*. The procurrent caudal-fin rays are straight in all other ricefishes and outgroup taxa.

(76) *Epural number*: One ossified epural [0]; two or three ossified epurals [1]; two epurals, one ossified, one cartilaginous [2]. Ossified epurals number three in halfbeaks, e.g. *Hemirhamphodon* (Fig. 11A), one or two in *Melanotaenia*, and one in *Rivulus* as well as other cyprinodontiforms (Rosen, 1964; Parenti, 1981). Ossified epurals number two in ricefishes, with the exception of *O. setnai* and *O. mekongensis*, in which the anterior epural is present as a small cartilage or bone in both adult females (Fig. 11F) and males (Fig. 11E). There may be additional blocks of cartilage between the ossified epurals, but in no specimen are there more than two accessory elements. Three epurals characterize an array of acanthomorph taxa (viz. Nelson, 2006).

## REPRODUCTIVE MORPHOLOGY AND BIOLOGY

(77) *Reproductive mode*: Oviparous, external fertilization, embryos develop outside of female [0]; oviparous, external or facultatively internal fertilization, embryos develop for at least some time while attached to female [1]; ovoviviparous or viviparous, internal fertilization [2]. Ricefishes are oviparous or ovoviviparous (see Yamamoto, 1975). Eggs have a thick chorion or zona pellucida and are filamentous (Kulkarni,



**Figure 29.** A, *Adrianichthys oophorus*, USNM 348386, 60 mm SL. B, *Oryzias orthognathus*, USNM 350562, 43.5 mm SL. Caudal fin osteology. Arrows point to anterior-most dorsal and ventral procurent rays. Note hooked proximal portion of the procurent rays in B.

1940: fig. 15), as is typical for oviparous atherinomorphic fishes (Rosen, 1964; Parenti & Grier, 2004). Females may carry bundles of fertilized eggs (Fig. 1) for 1–2 weeks or more prior to hatching. The developing embryos are held together in a clump, and presumably to the body of the adult female, via long attachment filaments on the zona pellucida, a diagnostic character of atherinomorphic fishes (Parenti, 1993, 2005). Facultative internal fertilization and retention of fertilized eggs in the typically oviparous ricefishes was reported by Amemiya & Murayama

(1931) who discovered developing embryos in the gonoduct of a female *O. latipes*. A cluster of fertilized eggs or embryos held between the body and the pelvic fins has been reported in at least nine ricefish species: *A. oophorus*, *O. sarasinorum*, *O. nigrimas*, *O. matanensis*, *O. marmoratus*, *O. dancena* (Fig. 1), *O. javanicus*, *O. luzonensis* as well as *O. latipes* (see Parenti, 2005). Embryos in the clusters are relatively well developed, with large, well-formed eyes and pigmented bodies, and appear near hatching.

Fertilization is internal in *O. setnai*, the males of which pass spermatophores, encapsulated sperm bundles, via a modified anal fin to the female (Kulkarni, 1940; Grier, 1984). Fertilized eggs are extruded one-by-one or in a larger mass, over a relatively broad area, rather than one location (Kulkarni, 1940: 413). Spermatophores are also formed in some species of the halfbeak genus *Zenarchopterus* (see Grier & Collette, 1987). Homology of spermatophores is open to test: they were identified as primary spermatophores (formed in testicular lobule cysts) in *O. setnai*, vs. secondary spermatophores (formed within the posterior part of the testis) in *Zenarchopterus* (Grier & Collette, 1987: 310–311).

Mode of reproduction is inferred as oviparous for the remaining ricefishes, except for *O. bonneorum* in which the two largest males have what appears to be an intromittent organ that can be everted. This species may have internal fertilization. Some ricefishes may be hermaphroditic (see character 79), but this has not been confirmed.

(78) *Abdominal concavity*: Absent [0]; present [1]. The egg-carrying buntingi, *A. oophorus* (Kottelat, 1990a: fig. 6), carries an embryo cluster in a pronounced abdominal concavity between the body and the pelvic fins until hatching. A new reproductive guild, ‘pelvic brooders’, was named by Kottelat (1990a: 62) for species that exhibit this type of brooding. Similarly elongate pelvic fins and an abdominal concavity characterizes other large ricefishes, e.g. *A. roseni* (Fig. 22) and *A. poptae*, although material is insufficient to determine mode of reproduction in *Adrianichthys* species (see character 79; Kottelat, 1990a). The abdominal concavity is most pronounced in *A. oophorus*, an autapomorphy of that species. Other ricefish females carry a bundle of embryos until hatching (e.g. Fig. 1) and these may lie between the pelvic fins and the body (e.g. Fig. 54; see character 77 above). ‘Pelvic brooding’ is probably exhibited by a larger number of ricefish species, such as *O. sarasinorum* (e.g. Kottelat *et al.*, 1993); distribution of that reproductive mode could not be determined here. Furthermore, material was insufficient to determine if female *O. sarasinorum* carried embryos in a similar concavity or if, instead, the embryos were carried on

either side of the body (e.g. Kottelat *et al.*, 1993: pl. 44); that species is coded as 'unknown' for this character.

(79) *Testis morphology*: Paired, symmetric [0]; single lobed [1]; paired, bilaterally asymmetric [2]. Teleost testes are typically paired, symmetrical organs (Grier, 1984). Paired testes run laterally, inside the body wall on either side of the gut, as in the viviparous halfbeaks *Dermogenys*, *Hemirhamphodon* and *Nomorhamphus* (Downing & Burns, 1995). Testes are similarly paired in some cyprinodontiforms, as reported in the oviparous Cyprinodontidae *s.l.* and viviparous goodeids and *Anableps*, and beloniforms such as the viviparous Hemiramphidae (= Zenarchopteridae) and oviparous Belonidae (see Grier, 1984). The testis is a single, median organ, inferred to be fused from paired testes, in the viviparous members of the cyprinodontiform family Poeciliidae (*sensu* Parenti, 1981; see also Grier, 1984). The testis may also be single in some species of the exocoetoids *Strongylura* and *Tylosurus* (Collette, 2003). All atheriniforms, as far as known, have a unique testis type, identifiable via histology, in which spermatogonia are restricted to the distal end of testis lobules (see comparison and table in Parenti & Grier, 2004). Ricefish testes exhibit marked gross morphological variation. The testis of the internally fertilizing ricefish *O. setnai* is a single, bulbous organ, with no evidence of fusion (Grier, 1984). This is in contrast to the testes of oviparous *Oryzias*, as reported in a survey of testis morphology among nine species by Hamaguchi (1996). Paired testes form from bilateral gonadal rudiments in *O. latipes*, although they are notably larger on the right side of the body. The medaka, in turn, is distinct from the other *Oryzias* species surveyed by Hamaguchi (1996). In *O. celebensis*, *O. javanicus*, *O. marmoratus*, *O. mekongensis*, *O. melastigma* (either *O. dancena* or *O. carnaticus*) and *O. minutillus*, a single gonadal rudiment on the right side of the body develops into a single-lobed testis. In *O. curvinotus* and *O. luzonensis*, gonadal rudiments form only on the right side of the body, yet testicular tissue also develops on the left side of the body to form paired testes in adults (Hamaguchi, 1996). Here, I code *O. latipes*, *O. curvinotus* and *O. luzonensis* as having paired, bilaterally asymmetric testes. *Oryzias setnai* is coded 'unknown' for this character because it is not known whether the single, bulbous testis results from the fusion of paired testes or the development of just one of the testes.

Gonad morphology within the genus *Adrianichthys* is less well known. Kottelat (1990a: 57) reported that Klie (1988), in her dissertation on the morphology and histology of *Adrianichthys kruyti*, concluded that one specimen, ZMH 22571, is a ripe female and that a second, ZMH 22570, is hermaphroditic, having a

testis on one side of the body cavity and an ovary on the other. The small number and relatively poor condition of specimens examined precludes recognition and description of any further possible sexual dimorphism within *A. kruyti* or *A. roseni* as part of the present study. *Adrianichthys oophorus* is known from abundant material, although males are rarer than females. Testes are paired in two adult males of *A. oophorus* (USNM 340431) as they are in an adult male *A. poptae* (USNM 322423).

(80) *Egg size*: Small, less than 1.5 mm in diameter [0]; large, 1.5 mm in diameter or greater [1]. Atheriniform fishes produce relatively large, spherical eggs with long attachment filaments (Rosen & Parenti, 1981; Parenti, 2005) and fluid, not granular, yolk (Parenti & Grier, 2004). *Oryzias* eggs, at less than 1.0 to nearly 1.5 mm in diameter, are the smallest among beloniforms (Kulkarni, 1940; Collette *et al.*, 1984; Iwamatsu, 1986; Kottelat, 1990a). Size has been reported in the above references for eight *Oryzias* species, as coded in the data matrix: *O. luzonensis*, *O. celebensis*, *O. latipes*, *O. mekongensis*, *O. melastigma* (either *O. dancena* or *O. carnaticus*), *O. minutillus*, *O. javanicus* and *O. setnai*. Eggs are reported to be 2.0–2.1 mm in diameter in *A. oophorus* (Kottelat, 1990a), and range from 1.5 to 2.5 mm in exocoetids, hemiramphids *s.l.*, and scomberesocids, and from 3 to 4 mm in belonids (Collette *et al.*, 1984). A female *O. sarasinorum* (CMK 6557) carries a cluster of embryos that measure about 1.5 mm; size of embryos cannot be measured accurately as they may be somewhat dehydrated in alcohol. Developing embryos are larger than unfertilized eggs; therefore I code *O. sarasinorum* as having a small egg.

Polarity of egg size is somewhat ambiguous as egg diameter in cyprinodontiforms, the beloniform sister group, varies from a reported 0.9 to 3.0 mm (Able, 1984: table 97) and in atheriniforms from 0.55 to 2.5 mm (White, Lavenberg & McGowen, 1984: table 93). Basal members of cyprinodontiform lineages (following Parenti, 1981) have relatively large eggs: *Aplocheilus lineatus*, Aplocheilidae (2.0 mm), *Plancterus kansae*, Fundulidae (2.3–2.4 mm), and *Valencia hispanica*, Valenciidae (2.5–2.6 mm). The atheriniform *Melanotaenia* is reported to have an egg just 1 mm in diameter (White *et al.*, 1984).

## CYTOGENETIC DATA

### GENOME SIZE

(81) *Genome size*: 1.9 pg per nucleus or greater [0]; less than 1.9 pg per nucleus [1]. Genome size is listed here for 11 species of *Oryzias* (Table 2), compiled from Uwa (1986, 1993) and other sources, as noted. Genome size varies from 1.5 pg per nucleus in the

miniatures *O. mekongensis* (see Uwa & Magtoon, 1986) and *O. minutillus* (see Magtoon & Uwa, 1985), to 1.9 pg per nucleus in *O. luzonensis* (see Formacion & Uwa, 1985), and 2.2 pg per nucleus in *O. latipes* (see Lamatsch *et al.*, 2000). The relatively high value of 1.9 pg per nucleus was considered by Formacion & Uwa (1985) to be an autapomorphy of *O. luzonensis* before a higher number was reported in *O. latipes*.

Reduction in genome size has been interpreted as a hallmark of teleost evolution (Hinegardner, 1968; Hinegardner & Rosen, 1972). Different methods of estimating genome size make outgroup comparison difficult and determination of the plesiomorphic genome size ambiguous (Cavalier-Smith, 1985). The haploid genome of the medaka has been reported to be 680–850 Mb (Tanaka, 1995; Naruse *et al.*, 2000), roughly twice that of *Takifugu rubripes*, 400 Mb (Clark & Elgar, 2000), and roughly one half that of *Danio rerio*, 1700 Mb (Hinegardner & Rosen, 1972; Postlethwait *et al.*, 1994). The most recent report of the medaka genome size is 700.4 Mb (Kasahara *et al.*, 2007). Genome size, measured as picograms of DNA per nucleus (diploid genome), has likewise been estimated in *D. rerio* (4.6 pg), *O. latipes* (2.2 pg) and the freshwater pufferfish *Tetraodon fluviatilis* (0.70 pg) (Lamatsch *et al.*, 2000). *Rivulus urophthalmus* was reported to have a diploid genome of 3.0 pg per nucleus and the halfbeak *Dermogenys pusillus* a diploid genome of 1.48 pg per nucleus by Hinegardner & Rosen (1972). They also noted that, within a taxon, viviparous species had less DNA than did oviparous species.

#### CHROMOSOME NUMBER AND CONSTITUTION

Chromosome number and limited data on chromosome constitution have been reported for 14 species of *Oryzias* (Table 2), compiled from Uwa (1993: 869, 1991a, b), Uwa & Iwata (1981), Uwa, Wang & Chen (1988), Chen *et al.* (1989), Magtoon *et al.* (1992), Takata *et al.* (1993), Naruse *et al.* (1994), Naruse (1996), Lin *et al.* (1999) and Lamatsch *et al.* (2000). Diploid chromosome number ranges from 28 to 48. Diploid chromosome number is 48 in *O. javanicus*, *O. dancena*, *O. hubbsi*, *O. latipes*, *O. mekongensis*, *O. luzonensis* and *O. curvinotus*. *Oryzias javanicus* and *O. dancena* have nearly all acrocentric chromosomes, whereas the other five species have at least one submetacentric. *Oryzias celebensis*, *O. minutillus*, *O. marmoratus*, *O. matanensis* and *O. nigrimas* have a diploid chromosome number of 42 or fewer, including several extremely large metacentric and at least one submetacentric chromosome, as far as known (Table 2). *Oryzias sinensis*, as recognized herein, has 46 diploid chromosomes (Chen *et al.*, 1989).

Forty-eight diploid, acrocentric chromosomes has been interpreted as the plesiomorphic chromosome

constitution at the level of the Clupeocephala (Brum & Galetti, 1997; see also Naruse *et al.*, 2004 and Kasahara *et al.*, 2007). The number and composition of chromosomes is highly variable among atherinomorph fishes (Ebeling & Chen, 1970), ranging from eight to 24 haploid chromosomes in a large array of taxa (Gyldenholm & Scheel, 1971). Furthermore, chromosome arm number has been tabulated for only a limited number of taxa (Table 2). *Melanotaenia maccullochi*, *Dermogenys pusillus* and several *Rivulus* species are reported to have a haploid chromosome number of 24 (Gyldenholm & Scheel, 1971). Alternatively, Hinegardner & Rosen (1972) report a haploid chromosome number of 22 for *Rivulus urophthalmus*. A reduction in the number of diploid chromosomes has been correlated in some populations with the presence of large metacentric chromosomes, inferred to have been formed by centric fusion (Uwa, 1986). The correlation is not precise: *O. minutillus* specimens from Phuket have 42 diploid chromosomes and no large chromosomes, whereas *O. sinensis* specimens from Shanghai have 46 diploid chromosomes and one large metacentric. The data of Table 2 are coded in the data matrix in the following four characters:

(82) *Diploid chromosome number*: 46–48 diploid chromosomes [0]; 44 or fewer diploid chromosomes [1]. Outgroups *Melanotaenia* and zenarchopterids are coded 0; *Rivulus* is coded as polymorphic for diploid chromosome number.

(83) *Chromosome arm number*: 48 or fewer [0]; 58 or more [1]. This character is unreported in outgroup taxa.

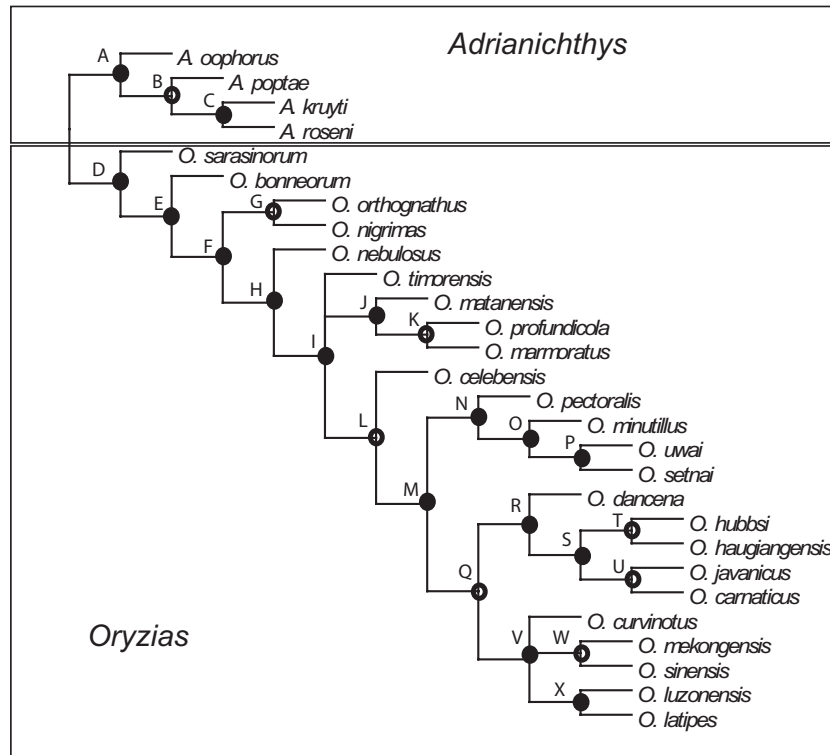
(84) *Chromosome constitution*: Acrocentric chromosomes (monoarmed) [0]; metacentric chromosomes (biarmed or fused) [1]. Following the classification of Uwa (1986), species are coded as monoarmed if they have nearly all acrocentric chromosomes; those species with metacentric chromosomes may be fused or biarmed.

(85) *Extremely large metacentric chromosomes*: Absent [0]; present [1].

#### PHYLOGENETIC ANALYSIS

The characters discussed above and coded in the 31 taxa by 85 character data matrix, Appendix 2, form the data used in a parsimony analysis of ricefishes. Multistate characters were treated as unordered (non-additive; Fitch, 1971) and no weighting scheme was applied. Two most parsimonious trees, each with a length of 195 steps, consistency index (CI; Kluge & Farris, 1969) of 0.58 and retention index (RI; Farris, 1989) of 0.81 were recovered using the parsimony ratchet (Nixon, 1999), set at 200 replications, in NONA ver. 2. Nodes for which there was no support were collapsed. The strict consensus of these two





**Figure 30.** Cladogram of relationships among ricefish species, classified herein in two monophyletic genera, *Adrianichthys* and *Oryzias*. Character states at each lettered node are described and discussed in the text. Nodes marked by solid circles are supported by at least one synapomorphy; those marked by an open circle are supported only by homoplasies under a fast character state optimization. Character support at each node is discussed in the Phylogenetic analysis.

trees has a length of 196, CI of 0.58 and RI of 0.80 (Figs 4, 30).

Characters and character states, given as character number [character state number], for ricefishes (family Adrianichthyidae; Fig. 4) and for species groups at each lettered node (Fig. 30) are explained below. Support is reported for the fast optimization of character states, an optimization procedure that favours reversal over parallelism (Farris, 1970; De Pinna, 1991; Fig. 31). Most, but not all, nodes are supported by uncontradicted synapomorphies. Rather than collapse the nodes supported only by homoplasies (marked by open circles in Fig. 30) or evaluate nodes by indices such as Bremer support (Bremer, 1994), ambiguous optimizations and homoplasies are discussed and, in several cases, re-stated as explicit proposals of homology.

#### *Ricefish monophyly*

Characters 1–17, discussed above, provide unambiguous support for ricefish monophyly. Character state 17 [1], ventral branch of the posterior lateral line nerve in adults with pored lateral line scales, is optimized on the cladogram as a synapomorphy of zenarchopterids plus adrianichthyids, and 17 [2], ventral

branch of the posterior lateral line nerve in adults without pored lateral line scales, a ricefish synapomorphy. An additional nine synapomorphies are recovered in the parsimony analysis, each of which is represented by an alternative state at one or more of the internal nodes (Figs 30, 31). The nine synapomorphies are: 21 [3], scales in a lateral series number 70 or more; 49 [1], ventral hypohyal with an elongate, blade-like ramus along the ventral face of the anterior ceratohyal; 54 [1], five branchiostegal rays; 55 [1], posteriormost branchiostegal ray articulates with a truncated posterior ceratohyal; 67 [1], dorsal-fin rays number 11–13; 75 [1], procurrent caudal-fin rays are hooked; 82 [1], 44 or fewer diploid chromosomes; 84 [1], metacentric chromosomes (biarmed); and 85 [1], extremely large metacentric chromosomes. The single homoplasy at this node is: 60 [1], 9–12 pectoral fin-rays. This character is reversed in Node B to state 60 [0] and, thus, is not considered as strong additional support for ricefish monophyly.

#### *Ricefish phylogeny*

Node A: *Adrianichthys*. Monophyly of the genus *Adrianichthys* is supported by seven synapomorphies in the parsimony analysis: 33 [2], preethmoid

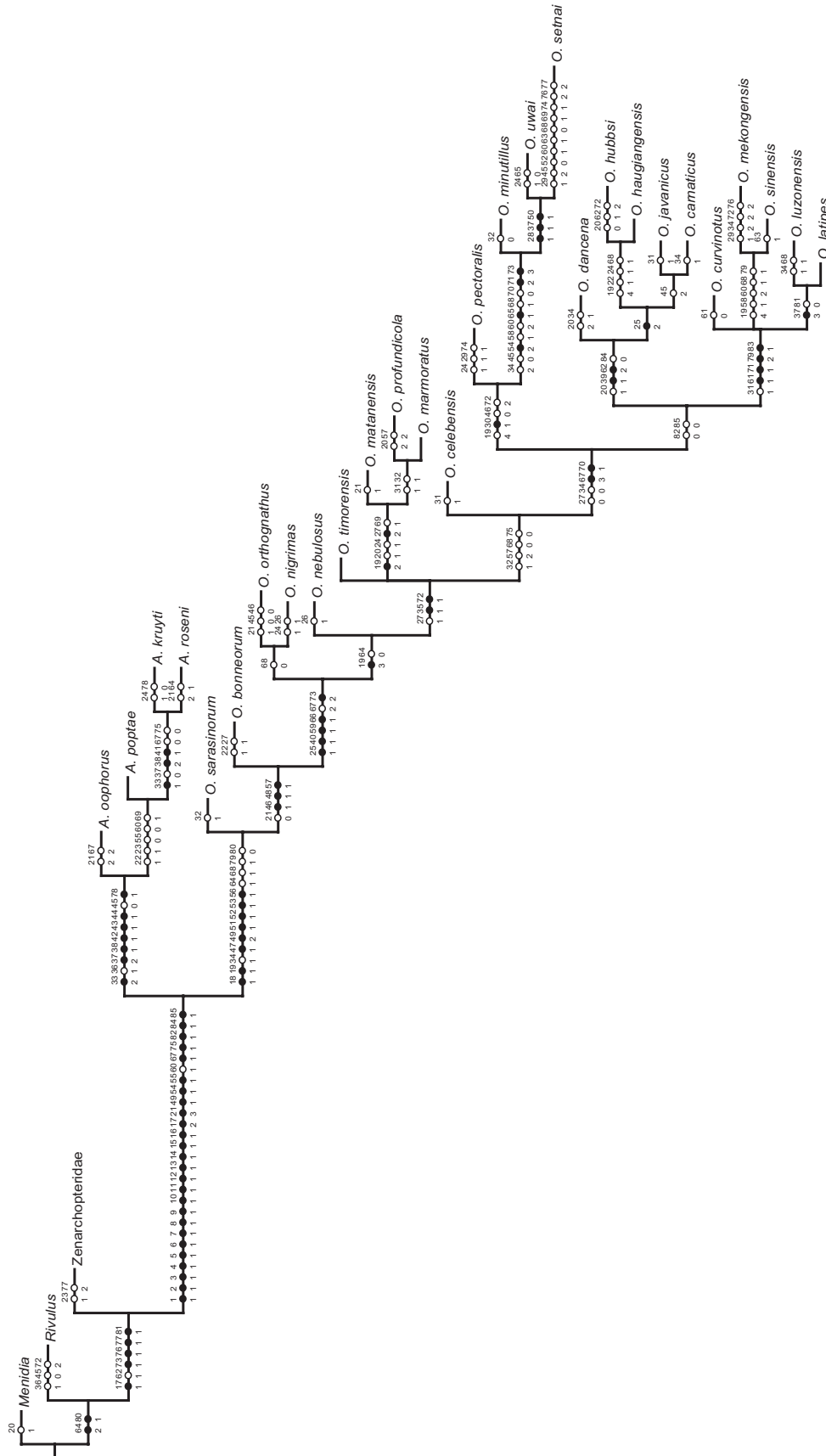


Figure 31. Cladogram of relationships among ricefish species and outgroup taxa with character states recovered at each node under a fast character state optimization as inferred using *WinClada* and *NONA*. See text for discussion.

cartilages present; 37 [2], mesethmoid ossification forms a semicircle anteriorly with subrectangle posteriorly; 38 [1], orbits project somewhat beyond dorsal profile of head; 42 [1], the premaxilla is flat and broad and lacks distinct articular and ascending processes; 43 [1], the maxilla relatively is straight and lacks a dorsal process; 44 [1], oral jaw teeth are small and villiform and arranged in up to five irregular rows that form a pavement dentition; and 78 [1], abdominal concavity. The analysis also recovered two homoplastic character states at this node: 36 [1], the ethmoid region of skull in lateral and dorsal view is flat and broad; and 45 [0], there are no enlarged teeth posteriorly on premaxilla. These two characters states are homoplastic with the genus *Rivulus*. Relative to zenarchopterids and *Menidia*, they are synapomorphies of *Adrianichthys* and I interpret them as additional diagnostic generic characters. Character 37 [2] is not considered a synapomorphy of *Adrianichthys* as this character is unique to *A. oophorus* and *A. kruyti* (see discussion below under Node C). Similarly, 78 [1] is reversed in *A. kruyti*.

Node B: *Adrianichthys poptae*, *A. kruyti* and *A. roseni*. These three species share five homoplastic characters: 22 [1], a large head, reaching 31% or more of SL; 23 [1], a long snout, reaching 12% or more of SL; 55 [0], posterior branchiostegal rays articulate with a relatively large posterior ceratohyal; 60 [0], 13 or more pectoral-fin rays; and 69 [1], a long anal fin, with 24 or more rays. A large head is also characteristic of *O. bonneorum*, *O. hubbsi* and *O. haugiangensis*, a large snout of zenarchopterids, a long anal fin of *O. setnai*, and a large pectoral fin of outgroup taxa. Character 55 [0] is characteristic of outgroup taxa. Of these characters, 69 [1], a long anal fin, is considered support for monophyly of the three species included in Node B.

Node C: *Adrianichthys kruyti* and *A. roseni*. This sister group relationship is supported by three synapomorphies: 33 [1], preethmoid cartilages are paired; 38 [2], orbits project markedly beyond the dorsal profile of the head; and 41 [1], the upper jaw extends beyond lower jaw. Three homoplasies recovered at this node are: 37 [0], mesethmoid ossification round or oval; 67 [0], 14 or more dorsal-fin rays; and 75 [0], simple, rather than hooked, procurrent rays. Simple procurrent rays represent a reversal from the synapomorphy, 75 [1], hooked procurrent rays, that is optimized in this analysis as diagnostic of ricefishes. Simple procurrent rays are also a character state at Node L, below.

There is character support for a sister-group relationship between *Adrianichthys oophorus* and *A. poptae*, but that clade is not recovered in the parsimony analysis because of the unambiguous support for Node C. Character 33, presence of preethmoid cartilages, a synapomorphy of the four species of

*Adrianichthys* in the parsimony analysis, is optimized on the cladogram as (0(1(1(2,2))))), state 1 for *A. kruyti* and *A. roseni*, state 2 for *A. poptae* and *A. oophorus*, and state 0 for all other taxa. There is no evidence of a transformation, e.g. from ontogeny, among the states from 0 to 1 to 2. The relationship (0(1(1(2,2)))) results from application of the parsimony algorithm (Williams & Ebach, 2006), whereas the relationship (0(1,2)) is the homologue that is specified by the distribution of the preethmoid character states. Furthermore, a mesethmoid ossification in the form of a semicircle anteriorly and subrectangle posteriorly, 37 [2], is unique to *A. oophorus* and *A. poptae*, yet optimized on the cladogram as a synapomorphy of *Adrianichthys*. Character 37 [0], mesethmoid ossification round or oval, is optimized as a character reversal at Node C, but it does not provide strong, additional support for the sister group relationship of *A. kruyti* and *A. roseni*.

Prior to this revision, three species comprised the genus *Xenopoecilus*, two of which are placed in *Adrianichthys*, *A. oophorus* and *A. poptae*, and the other in *Oryzias*, *O. sarasinorum*. No explicit synapomorphies have ever been proposed for the genus *Xenopoecilus* and it is considered paraphyletic here, as suggested by Rosen (1964) and as in both molecular analyses (Naruse, 1996; Takehana *et al.*, 2005).

Node D: *Oryzias*. Monophyly of the genus *Oryzias* is supported by eight synapomorphies: 18 [1], small size at hatching, 4.5 mm or less; 19 [1], maximum adult body size is less than 60 mm SL; 47 [1], hyomandibula has a single head articulating with the otic region of the skull; 49 [2], the ventral hypohyal has a blunt posterior ramus; 51 [1], epibranchial two is notably smaller than the other epibranchial bones, lacks a broad point of articulation with the ceratobranchial cartilage, and may be cartilaginous or absent in some specimens; 52 [1], the ceratobranchial bone 5 toothplate is rectangular or suboval; 53 [1], fifth ceratobranchial teeth are arranged in horizontal rows; and 56 [1], total vertebrae number 34 or fewer. Five homoplasies are also recovered at this node: 34 [1], ethmoid cartilage anterior margin is irregular and indented anteromedially; 64 [1], pelvic fins are in line with pleural rib of vertebrae 6 or 7; 68 [1], the dorsal fin is anterior, its origin anterior to vertebra 22; 79 [1], testis is a single lobed organ; and 80 [0], small egg. The numerous reversals of characters 34, 64 and 68 offer weak support of *Oryzias* monophyly. Character state 79 [2], bilaterally asymmetric paired testes, is a putative synapomorphy of Node V. The last character, small egg, is interpreted here as a putative *Oryzias* synapomorphy, although data are available on a minority of ricefish taxa.

Node E: *Oryzias*, minus *O. sarasinorum*. Three osteological synapomorphies support this clade com-

prising 23 species of *Oryzias*: 46 [1], enlarged teeth posteriorly on dentary are present in males, rarely in females; 48 [1], palatine and quadrate bones articulate without anterior, elongate flanges; and 57 [1], 12–13 precaudal vertebrae. There is one homoplasy at this node: 21 [0], fewer than 40 scales in a lateral series. There are two states of character 21 among taxa within Node E: 21 [0], fewer than 40, and 21 [1], 40–57 scales in a lateral series. Given the distribution of this character among ricefishes, and the strong support for ricefish monophyly and Node D, an additional synapomorphic character of Node E may be stated as: 57 or fewer scales in a lateral series.

Node F: Node E minus *O. bonneorum*. Five synapomorphies diagnose the 22 included species: 25 [1], bilobed urogenital papilla in females; 40 [1], preopercular sensory canal and dermosphenotic (posterior infraorbital) canal continuous rather than separate; 59 [1], transverse processes of the first vertebra short or absent; 66 [1], medialmost pelvic-fin ray connected along one-half its length to the body via a membrane; and 73 [2], principal caudal-fin rays number no more than i,4/5,i. There is one homoplasy at this node: 67 [2], 8–10 dorsal-fin rays. There are numerous reversals and polymorphic conditions of character 67 among *Adrianichthys* and species included in nodes D, E, F and G; 67 [2] offers little additional support for monophyly of the taxa included in Node F.

Node G: *Oryzias orthognathus* and *O. nigrimas*. These two endemic species of Lake Poso, Sulawesi, share one homoplasy: 68 [0], the dorsal fin is relatively posterior, its origin is at or posterior to vertebra 22. This character state represents a reversal of the state at Node D, a relatively anterior dorsal fin and is also characteristic of the miniature *O. setnai*. It is not interpreted as strong support for a sister group relationship of the two species.

Node H: *Oryzias* minus the large pelagic species of the Sulawesi lakes Poso and Lindu. One synapomorphy and one homoplasy differentiate the included taxa. The synapomorphy is: 19 [3], maximum adult body size greater than 26 mm SL and less than 40 mm SL. The 20 species included in Node H are all relatively small, reaching less than 40 mm SL, or are miniature, reaching less than 26 mm SL. The homoplasy is: 64 [0], pelvic fins are anterior, in line with the pleural rib of vertebra 5 or less. The anterior position of the pelvic fins is interpreted as an additional putative synapomorphy at Node H. It is an unambiguous characteristic of all included species, save for *O. nebulosus* and *O. celebensis*, which are both polymorphic for this character.

Node I: Node H minus *O. nebulosus*. Two synapomorphies support monophyly of the 19 included species: 35 [1], lateral margin of the ethmoid cartilage forms a distinct notch bordered posteriorly by the anterior

margin of lateral ethmoid, and 72 [1], the caudal fin is truncate, rather than distinctly lunate. A further derived state of the caudal fin, 72 [2], diagnoses taxa included in Node N. A lunate caudal fin is characteristic of the larger, pelagic, lake-dwelling ricefish species. There is one homoplasy at this node: 27 [1], dark brown blotches at mid body of males. This character is not interpreted as support for Node I monophyly as it represents the absence of a distinctive pigmentation pattern found in species exclusive to this node.

Node J: Malili Lakes Buntingi, *O. matanensis*, *O. profundicola* and *O. marmoratus*, are supported as monophyletic by two synapomorphies and three homoplasies. The synapomorphies are: 19 [2], maximum adult body size is greater than 40 and less than 50 mm SL; and 27 [2], males have a pigmentation pattern characterized by a series of regular mid-lateral blotches and irregular dark brown blotches on the entire lateral surface of the body. The homoplasies are: 20 [1], somewhat deep bodied, reaching more than 26% and less than 33% SL; 24 [1], eye diameter relatively large, reaching 10% or more of SL; and 69 [1], 24 or more anal-fin rays. These homoplastic characters are interpreted as additional support for monophyly of the Malili Lakes ricefishes. Anal-fin ray number was coded as polymorphic in *O. marmoratus* and *O. matanensis*; both have relatively long anal fins that range over 24 anal-fin rays. Character state 19 [2], optimized as a synapomorphy, may be interpreted as a reversal from a relatively small, but not miniature, size at Node H.

Node K: *Oryzias profundicola* and *O. marmoratus*. Two homoplasies of pigmentation pattern are recovered at this node: 31 [1], yellow dorsal and ventral caudal-fin margins; and 32 [1], pigmentation pattern on caudal-fin rays in alcohol-preserved material consists of distinct dark brown to black lines on middle rays, a character state distributed broadly among taxa included within Node I. Yellow dorsal and ventral caudal-fin margins are also characteristic of taxa included in Node V; these are interpreted as independent acquisitions and treated here as support for monophyly of Node K, the sister group relationship of *O. profundicola* and *O. marmoratus* and Node V.

Node L: The parsimony analysis recovered four homoplasies at this node: 32 [1], pigmentation pattern in alcohol-preserved material marked by distinct dark brown to black lines on the middle caudal-fin rays; 57 [2], 11 or fewer precaudal vertebrae; 68 [0], dorsal fin is relatively posterior, its origin at or posterior to vertebra 22; and 75 [0], procurvent caudal-fin rays are simple, rather than hooked, at their proximal portion. This is a weakly supported node and monophyly of included taxa is not proposed.

With better material, character state 32 [1] would likely be recovered as an additional synapomorphy of Node I. Alcohol-preserved material of *O. timorensis* is poor and faded and no longer demonstrates natural pigmentation patterns accurately. The absence of this pigmentation pattern may be an additional autapomorphy of *O. matanensis* (see Systematic accounts). Node M: This node includes all of the non-Sulawesi ricefishes, except for the easternmost *O. timorensis*. It includes Uwa's (1986, 1991a, b) monoarmed and biarmed chromosome groups as well as all of the miniature species which themselves do not form a monophyletic group. Two synapomorphies diagnose this node: 67 [3], dorsal fin is small and never has more than eight rays; and 70 [1], bony processes are present on anal-fin rays of mature males (interpreted here as reversed in the miniatures *O. minutillus*, *O. uwai* and *O. setnai*). Two homoplasies are also recovered at this node: 27 [0], no dark brown blotches on body of males; and 34 [0], ethmoid cartilage anterior margin straight and entire. The homoplasies are not interpreted as additional support for Node M monophyly.

Node N: *Oryzias pectoralis*, *O. minutillus*, *O. uwai* and *O. setnai*. This group of four miniature species is characterized by one synapomorphy and three homoplasies. The synapomorphy is: 30 [1], pigmented anal or urogenital region. The three homoplasies are: 19 [4], maximum adult body size is 26 mm SL or less, the character of miniaturization; 46 [0], no enlarged teeth posteriorly on the dentary; and 72 [2], caudal fin rounded and with somewhat elongate middle rays. The rounded and elongate caudal fin is considered additional support of Node N monophyly. A rounded caudal fin characterizes two other miniatures, *O. hubbsi*, in Node T, and *O. mekongensis*, in Node W, both of which are sister to miniature species with truncate caudal fins.

Node O: *Oryzias minutillus*, *O. uwai* and *O. setnai*. These three miniatures share four synapomorphies: 54 [2], four branchiostegal rays; 65 [1], five pelvic-fin rays (reversed in *O. uwai*); 71 [2], anterior portion of the anal fin with elongate rays set off from rest of fin; and 73 [3], principal caudal-fin rays number  $i, 3/4, i$ , the lowest number for ricefishes. Six homoplasies also characterize this node: 34 [2], the ethmoid cartilage has a distinct anteromedial projection (also found in miniature *O. mekongensis*); 45 [0], no enlarged teeth posteriorly on the premaxilla (this character is reversed in *O. setnai*); 58 [1], first pleural rib is on the second, rather than the third, vertebra (this is also a character of the miniatures *O. sinensis* and *O. mekongensis*); 60 [2], eight or fewer pectoral-fin rays (also a character of the miniature *O. mekongensis*, reversed in *O. setnai*); 68 [1], dorsal fin is anterior, its origin anterior to vertebra 22 (this character is reversed in

*O. setnai*), and 70 [0], there are no bony processes on the anal-fin rays of males.

Node P: *Oryzias uwai* and *O. setnai*. Recognition of this node represents the first explicit statement of the phylogenetic relationships of *O. setnai* to other ricefishes. This sister group relationship is supported by three synapomorphies: 28 [1], there is an interrupted, horizontal dark brown bar that runs from the eye to the lower jaw; 37 [1], mesethmoid is uniquely subrectangular, rather than being round or oval; and 50 [1], the first epibranchial is cartilaginous, not ossified. Node Q: Two homoplasies of chromosome constitution characterize this node: 82 [0], diploid chromosome number of 46 or 48; and 85 [0] no extremely large metacentric chromosomes. Interpretation of monophyly of this node is problematic in large part because there are no chromosome data for most of the species included in Node M which, itself, is hypothesized to be monophyletic, as above. Absence of extremely large, metacentric chromosomes and 46–48 diploid, acrocentric chromosomes would, outside of this phylogenetic analysis, be considered symplesiomorphies and not evidence for monophyly of Node Q taxa, as discussed above under Chromosome constitution. The phylogenetic analysis rejects monophyly of the fused chromosome group; the character states at Node Q may be reinterpreted as synapomorphies (see Discussion).

Node R: *Oryzias dancena*, *O. hubbsi*, *O. haugiagensis*, *O. javanicus* and *O. carnaticus*. This species group is diagnosed by two synapomorphies: 39 [1], the lacrimal sensory canals are closed, rather than open; and 62 [2], the pelvic bone lateral strut is needle-like and elongate. Two homoplasies also characterize these five species: 20 [1], somewhat deep bodied, reaching more than 26% and less than 33% SL (*O. dancena* is one of the most-deep bodied ricefish and is coded 20 [2] for this character); and 84 [0], acrocentric chromosomes (monoarmed). The last character is unknown in *O. haugiagensis*. The species included in Node R correspond in part to the species of Uwa's (1986) monoarmed chromosome group (see Discussion).

Node S: *Oryzias hubbsi*, *O. haugiagensis*, *O. javanicus* and *O. carnaticus* are diagnosed as monophyletic by a single synapomorphy: 25 [2], the bilobed urogenital papilla of females is enlarged.

Node T: *Oryzias hubbsi* and *O. haugiagensis*. These two species share four homoplasies: 19 [4], maximum adult body size is 26 mm SL or less, the character of miniaturization; 22 [1], head is large, 31% or more of SL; 24 [1], eye diameter is relatively large, reaching 10% or more of SL; and 68 [1], dorsal fin is anterior, its origin anterior to vertebra 22.

Node U: *Oryzias javanicus* and *O. carnaticus*. A single homoplastic character unites these two species:

45 [2], teeth are enlarged posteriorly on the premaxilla in males and females. This character state is also interpreted as an autapomorphy of *O. setnai*.

Node V: *Oryzias curvinotus*, *O. mekongensis*, *O. sinensis*, *O. luzonensis* and *O. latipes*, species comprising the biarmed chromosome group of Uwa (1986), form a monophyletic group in this analysis supported by four synapomorphies: 61 [1], bony processes on the pectoral-fin rays (reversed in *O. curvinotus*); 71 [1], anal-fin rays are approximately the same length, forming what has been described as a 'parallelogram-shaped' fin; 79 [2], testes are paired, bilaterally asymmetric organs; and 83 [1], chromosome arms number 58 or more. One homoplasy is also recovered at this node: 31 [1], yellow to orange dorsal and ventral caudal-fin margins, which does not strengthen the hypothesis of monophyly of included species.

Node W: *Oryzias mekongensis* and *O. sinensis*. Five homoplasies are shared by these two species: 19 [4], maximum adult body size is 26 mm SL or less, the character of miniaturization; 58 [1], the first pleural rib is on the second, rather than the third, vertebra; 60 [2], eight or fewer pectoral-fin rays (*O. sinensis* is polymorphic with 8–10 pectoral-fin rays); 68 [1], the dorsal fin is anterior, its origin anterior to vertebra 22; and 79 [1], testis is single lobed.

Node X: *Oryzias luzonensis* and *O. latipes*. These two species are diagnosed as sister taxa by one synapomorphy: 37 [3], mesethmoid ossification is indented anteriorly; and one homoplasy: 81 [0], genome size is 1.9 pg per nucleus or greater. In this analysis, character 81 [1] is recovered as a synapomorphy of zenarchopterids plus adrianichthyids, with reversal to 81 [0] in *O. latipes* and *O. luzonensis*. I interpret an increase in genome size as a putative synapomorphy of these two species, yet acknowledge that a more precise statement of evolution of genome size in ricefishes requires data on those species for which this character is unknown.

## DISCUSSION

The phylogenetic analysis described above has resulted in a hypothesis of relationships of ricefishes (Figs 4, 30, 31) based on phenotypic characters (morphology and chromosome constitution) and limited data on reproductive biology. Monophyly of ricefishes and the two recognized genera, *Adrianichthys* and *Oryzias*, is well supported. Likewise, monophyly of *Xenopoeilus s.l.* is rejected as its included three species are placed here in *Adrianichthys* (*A. kruyti* and *A. oophorus*) or *Oryzias* (*O. sarasinorum*). The close relationships of the highly autapomorphic *Horaichthys setnai* Kulkarni, 1940, lie with a group of miniature ricefishes described in *Oryzias* and its

reclassification as *Oryzias setnai* (Kulkarni, 1940) is well justified under the philosophy of cladistic classification.

The phylogenetic analysis (Figs 30, 31) may be used to interpret the evolution of size in ricefishes as well as other beloniforms with respect to phenotypic (morphology and chromosome constitution) variation. Miniatures do not comprise a monophyletic group, yet they are all restricted to Node M. One could argue whether miniaturization here should be described as parallel evolution of morphology among closely related species (Hanken, 1984; Hanken & Wake, 1993). Miniaturization of ricefishes has been achieved in different ways and miniatures may be placed in clades that are diagnosed by characters that are not necessarily related to small size. *Oryzias hubbsi* and *O. haugiensis* are morphologically like miniaturized adult *O. javanicus*, *O. carnaticus* and *O. dancena*, their close relatives: all five species have closed, rather than open, lacrimal sensory canals, for example. Likewise, the miniatures *O. mekongensis* and *O. sinensis* are members of a species group that includes *O. curvinotus*, *O. latipes* and *O. luzonensis* characterized by an anal fin with rays that are approximately the same length, forming a 'parallelogram-shaped' anal fin. The four remaining miniatures, *O. pectoralis*, *O. minutillus*, *O. uwai* and *O. setnai*, share a pigmented anal or urogenital region and an elongate, rounded caudal fin. The rounded caudal fin could be interpreted as a character of miniaturization, especially as the last three species have an extremely reduced caudal skeleton with just  $i,3/4,i$  principal caudal-fin rays. Yet, the miniature *O. haugiensis* has a truncate caudal fin. *Oryzias setnai* shares inferred homoplastic characters with large ricefish species: *O. setnai*, *A. kruyti* and *A. poptae*, for example. All have relatively long anal fins, and *O. setnai* has up to 34 vertebrae, the highest number in *Oryzias* and closer to the range of 36–37 in *Adrianichthys*.

Disjunct size differentiates groups of ricefishes at all levels in the hierarchy, not just within the node that includes the miniatures. The sister genera *Adrianichthys* and *Oryzias* comprise groups of relatively large and small ricefish species, respectively. Absolute size, measured as SL, TL or BL (body length), also varies across beloniform lineages. There are numerous, additional examples in beloniform classification of close relatives with notably disjunct body size, such as the marine scomberesocids, the sauries. The four recognized saury species are classified in two genera each with two sister species: *Scomberesox saurus* (Walbaum, 1792), reaching 450 mm SL, and *S. simulans* (Hubbs & Wisner, 1980), reaching 130 mm TL; and *Cololabis saira* (Brevoort, 1856), reaching 400 mm TL, and *C. adocoetus* Böhlke,

1951, reaching just 51 mm TL (Hubbs & Wisner, 1980; Nelson, 2006). The two small saury species, *S. simulans* and *C. adocoetus*, were referred to as dwarfs by Hubbs & Wisner (1980), implying that they evolved through reduction in size. Each of the dwarfs has one, rather than two ovaries, no swimbladder, and fewer gill rakers, branchiostegal rays, pectoral-fin rays and vertebrae than their larger sister species (Collette *et al.*, 1984: 350).

The phylogenetic hypothesis presented here stands in contrast to two previously published hypotheses of ricefishes by Naruse (1996) and Takehana *et al.* (2005). A detailed, node-by-node, comparison or consensus between the results of the two molecular hypotheses (Fig. 3) and the current study (Figs 4, 30, 31) is impractical because these approaches differ in two critical areas: taxon sampling and outgroup comparison. Both molecular studies omit the two largest ricefishes, *A. kruyti* and *A. poptae*, four of the eight miniature species, *O. pectoralis*, *O. uwai*, *O. setnai* and *O. haugiangensis*, as well as other taxa known only from a few, historical specimens. Some of these species may never be available for molecular study, but tissues from some, such as *O. setnai*, are probably obtainable. Omitting the large ricefishes means not being able to recover the relationship of *A. oophorus* to its congeners, as recognized here. No non-beloniform taxon was included in the analysis of Takehana *et al.* (2005) and just two exocoetoid species, a flyingfish and a saury, served as an outgroup to the ingroup ricefishes. The exocoetoids are highly derived relative to ricefishes in a number of morphological characters, including form of the pharyngeal jaws (Rosen & Parenti, 1981; Collette *et al.*, 1984); relying solely on exocoetoids for outgroup comparison does not constitute a test of ricefish monophyly and may not provide an appropriate outgroup for polarity decisions in a parsimony analysis.

One major conflict among the analyses which is probably due to differences in choice of outgroups is monophyly vs. paraphyly of the fused chromosome or *celebensis* group (Fig. 3B). Variation of chromosome constitution among and within ricefish species has led to proposals of potential cytogenetic character transformation series, such as from monoarmed (acrocentric) to biarmed (metacentric) to fused (large metacentric) chromosomes (Uwa, 1986, 1991b) and subsequent classification of ricefish species in these groups. Classification of ricefish species by chromosome group, although appealing, is not straightforward. *Oryzias minutillus* was classified first in Uwa's fused chromosome group because populations from Bangkok and Chiang Mai have large metacentric (= fused) chromosomes (Uwa, 1986; Table 2). Examination of additional specimens from throughout Thailand led to the subsequent reclassification of *O.*

*minutillus* in Uwa's monoarmed group because of the predominance of acrocentric chromosomes in populations from Phuket and Menghai (Uwa, 1991b); *O. minutillus* populations may be classified as monoarmed or fused.

Classification of *O. minutillus* in the monoarmed group agrees with the clustering in the neighbour-joining tree (Naruse, 1996; Fig. 3A) and with the molecular phylogenetic analysis (Takehana *et al.*, 2005; Fig. 3B), lending support to the notion that Uwa's (1986) three chromosome groups form the framework for a natural classification. The current study (Figs 4, 30, 31), in contrast, unambiguously supports monophyly only of Uwa's biarmed chromosome group, the *latipes* species group of Figure 3B. The monoarmed group, the *javanicus* species group of Figure 3B, is recovered, in part, except for the position of *O. minutillus*. The fused chromosome group, the *celebensis* species group of Figure 3B, paraphyletic in the current study, includes species with some of the most divergent morphologies. *Adrianichthys oophorus* and *O. celebensis*, for example, differ markedly in an array of morphological characters, including lunate vs. truncate caudal fin, preethmoid cartilages present vs. absent, bifid vs. single head of the hyomandibula, 36 vs. 30–31 vertebrae, and 58–65 vs. 29–33 scales in a lateral series, respectively, to name just a few. Monophyly of the fused chromosome group is rejected here on the basis of morphology interpreted with respect to characters in a thorough sampling of ricefish species and a range of atherinomorphic outgroup taxa.

Maps have been used to support classification of ricefishes in chromosome groups by Uwa (1993), Iwamatsu (2006) and others who argue that distribution mirrors classification: roughly, the monoarmed group lives in south Asia, the biarmed group in north and east Asia, and the fused group east in Sulawesi, east of Wallace's Line, a classic biogeographical boundary. This ignores overlap of species groups; for example, the monoarmed *O. javanicus* was described from Java, but also lives in south-western Sulawesi. More importantly, even if the three groups were allopatric and there was no confusion over the classification by chromosome group, relationships among the groups – not their allopatry – would dictate the amount and kind of biogeographical information they convey. Distribution neither confirms nor rejects phylogeny (Nelson & Platnick, 1981; Humphries & Parenti, 1999). Furthermore, ricefishes present just one set of relationships among the areas they occupy. The biogeographical question that should be asked is: how are the area relationships of ricefishes, as specified by their phylogeny, similar to or different from those of other taxa in the biota? This requires com-

pilation of area cladograms from a broad array of taxa, which is beyond the scope of the present study.

Despite the utility of morphology as advocated here, it has not been able to resolve relationships of ricefish species at lower levels with unambiguous synapomorphies. Additional data, both molecular and morphological, are needed to provide a robust hypothesis of relationships among all 28 ricefish down to the species level. Reproductive biology and morphology, just touched upon here, is one area expected to shed light on, for example, the relationship of the internally fertilizing *O. setnai* to other ricefishes, or the existence and type of hermaphroditism in ricefishes. Developmental studies are also needed to provide more data to test some of the statements of morphological homology proposed here. These studies must be carried out on a range of taxa, the medaka and close relatives as well as more distantly related species, such as the large buntingi of Lake Poso, Sulawesi. Outgroup comparison must be made to non-beloniform, as well as beloniform, taxa to describe and interpret the hierarchy of character distributions. Such a broad, comparative approach can only enhance the role of the medaka as a model organism.

## SYSTEMATIC ACCOUNTS

### ORDER BELONIFORMES

#### FAMILY ADRIANICHTHYIDAE WEBER, 1913

##### TYPE GENUS *ADRIANICHTHYS* WEBER, 1913

Adrianichthyidae Weber, 1913 (type genus *Adrianichthys* Weber, 1913).

Oryziatini Myers, 1938 (type genus *Oryzias* Jordan & Snyder, 1906, as tribe in the subfamily Fundulinae, family Cyprinodontidae).

Horaichthyidae Kulkarni, 1940 (type genus *Horaichthys* Kulkarni, 1940).

Oryziatinae Myers, 1955 (type genus *Oryzias* Jordan & Snyder, 1906, as subfamily of Cyprinodontidae).

Oryziatidae Rosen, 1964 (type genus *Oryzias* Jordan & Snyder, 1906; objective synonym of Oryziatini Myers).

Oryziidae.- Steyskal, 1980 (modified spelling of family-group name based on *Oryzias*).

*Diagnosis:* The family Adrianichthyidae is diagnosed as monophyletic by 17 unambiguous synapomorphic characters: vomer absent, articular surface of the fourth epibranchial bone greatly expanded; ceratobranchial epiphysis represented by complex, branched cartilages; ceratobranchial 4 edentulous; palatine bone articulates with the maxilla (or premaxilla) via a dense ligament; rostral cartilage absent; Meckel's cartilage one-half length of the

dentary and articular bone orientated dorsally relative to the body axis; cartilaginous symphysis between the left and right dentary; metapterygoid absent; pterygoquadrate cartilage enlarged dorsally; no mandibulo-lacrima ligament; dermosphenotic lateral or posterior to sphenotic; supracleithrum absent; posttemporal bone simple, with no ventral arm; anterior ramus of coracoid relatively broad, particularly at point of articulation with the cleithrum, and without cartilage; ventral accessory bone in the caudal skeleton; and ventral branch of the posterior lateral line nerve in adults without pored lateral line scales. An additional nine synapomorphies are reversed at internal nodes on the consensus cladogram (Figs 30, 31 and Discussion): scales in a lateral series number 70 or more; ventral hypohyal has an elongate blade-like ramus along ventral face of anterior ceratohyal; five branchiostegal rays; posteriormost branchiostegal ray articulates with truncated posterior ceratohyal; dorsal fin rays number 11–13; hooked procurrent caudal-fin rays; 44 or fewer diploid chromosomes; metacentric chromosomes (biarmed); and extremely large metacentric (fused) chromosomes present.

*Composition:* Two Recent genera, *Adrianichthys* Weber, 1913, with four species *A. kruyti* Weber, 1913, *A. poptae* (Weber & de Beaufort, 1922) **comb. nov.**, *A. oophorus* (Kottelat, 1990a) **comb. nov.**, and *A. roseni* Parenti & Soeroto, 2004, and *Oryzias* Jordan & Snyder, 1906, with 24 species, *O. carnaticus* (Jerdon, 1849), *O. celebensis* (Weber, 1894), *O. curvinotus* (Nichols & Pope, 1927), *O. dancena* (Hamilton, 1822), *O. bonneorum* **sp. nov.**, *O. haugiangensis* Roberts, 1998, *O. hubbsi* Roberts, 1998, *O. javanicus* (Bleeker, 1854), *O. latipes* (Temminck & Schlegel, 1846), *O. sinensis* Chen *et al.*, 1989, *O. luzonensis* (Herre & Ablan, 1934), *O. marmoratus* (Aurich, 1935), *O. matanensis* (Aurich, 1935), *O. mekongensis* Uwa & Magtoon, 1986, *O. minutillus* Smith, 1945, *O. nebulosus* Parenti & Soeroto, 2004, *O. nigrimas* Kottelat, 1990a, *O. orthognathus* Kottelat, 1990a, *O. pectoralis* Roberts, 1998, *O. profundicola* Kottelat, 1990b, *O. sarasinorum* (Popta, 1905) **comb. nov.**, *O. setnai* (Kulkarni, 1940) **comb. nov.**, *O. timorensis* (Weber & de Beaufort, 1922), and *O. uwai* Roberts, 1998. A fossil genus and species, †*Lithopoecilus brouweri* de Beaufort, 1934, from the Miocene of Sulawesi, is included tentatively here.

*Remarks:* Authorship of the family-group name based on the genus *Oryzias* has been attributed to Rosen (1964: 225) who used the phrase 'Oryziatidae, new family' apparently unaware that Myers (1938: 137) authored the tribe Oryziatini. Spelling of the



## KEY TO ADRIANICHTHYID GENERA AND SPECIES

This artificial key is based on the above phylogenetic analysis, but does not mirror it precisely. Included is information from published ricefish keys from three geographical regions: Lake Poso, Sulawesi (Kottelat, 1990a), Malili lakes, Sulawesi (Kottelat, 1990b), and south Asia (Roberts, 1998).

- 1a. Maximum adult size nearly 200 mm SL; several rows of villiform teeth on upper and lower oral jaws; total vertebrae 36–37; preethmoid cartilage(s) present; flat, broad ethmoid region of skull; premaxilla flat and broad with no distinct articular and ascending processes; dorsal ramus of hyomandibula bifid, with separate cartilages for articulation with sphenotic and pterotic bones; second epibranchial bone fully ossified, roughly equal in length to third epibranchial bone.....*Adrianichthys* 2.
- 1b. Maximum adult size about 60 mm SL; one to three rows of small conical teeth on upper and lower oral jaws; total vertebrae 24–34; no preethmoid cartilages; ethmoid region of skull slightly convex dorsally; premaxilla short with distinct ascending processes; dorsal ramus of hyomandibula with single large cartilage that articulates with sphenotic and pterotic bones; second epibranchial bone, ossified or not, notably smaller than other epibranchial elements, or absent.....*Oryzias* 5.
- 2a. Anal-fin rays 20–22; dorsal-fin rays 8–10; scales in a lateral series 58–65.....*Adrianichthys oophorus*.  
(Lake Poso, Sulawesi Tengah)
- 2b. Anal-fin rays 24–27; dorsal-fin rays 11–17; scales in a lateral series 63–85.....3.
- 3a. Upper jaw protrudes, lower jaw completely included in upper jaw; dorsal-fin rays 14–17; preethmoid cartilages paired.....4.
- 3b. Jaws subequal or lower jaw slightly longer than upper jaw, lower jaw not included in upper jaw; dorsal-fin rays 11–13; preethmoid cartilage single.....*Adrianichthys poptae*.  
(Lake Poso, Sulawesi Tengah)
- 4a. Upper jaw broadly expanded into ‘duck-bill’; pelvic fins posterior, in line with vertebra 10; scales in a lateral series approximately 70–75.....*Adrianichthys kruyti*.  
(Lake Poso, Sulawesi Tengah)
- 4b. Upper jaw extends slightly over lower jaw; pelvic fins anterior, in line with vertebra 7; scales in a lateral series approximately 63–65.....*Adrianichthys roseni*.  
(Lake Poso, Sulawesi Tengah)
- 5a. Caudal fin lunate or emarginate.....6.
- 5b. Caudal fin truncate or rounded.....10.
- 6a. Approximately 70–75 scales in a lateral series; elongate body with silvery midlateral band.....*Oryzias sarasinorum*.  
(Lake Lindu, Sulawesi Tengah)
- 6b. Fewer than 60 scales in a lateral series; no silvery midlateral band on body.....7.
- 7a. Simple urogenital papilla in females; preopercular sensory canal and dermosphenotic (posterior infraorbital) canal separate; transverse processes of first vertebra elongate; medialmost pelvic-fin ray not connected to body via a membrane; principal caudal-fin rays number  $i,5/6,i$ .....*Oryzias bonneorum*.  
(Lake Lindu, Sulawesi Tengah)
- 7b. Bilobed urogenital papilla in females; preopercular sensory canal and dermosphenotic (posterior infraorbital) canal continuous; transverse processes of first vertebra short or absent; medialmost pelvic-fin ray connected along one-half its length to the body via a membrane; principal caudal-fin rays number no more than  $i,4/5,i$ .....8.
- 8a. Lower jaw protrudes at nearly 90° to body axis, mouth gape directed dorsally; 45–54 scales in a lateral series; preserved males and females uniformly covered with dark brown to black chromatophores.....*Oryzias orthognathus*.  
(Lake Poso, Sulawesi Tengah)
- 8b. Jaws subequal, mouth gape nearly horizontal; fewer than 40 scales in a lateral series; sexually dichromatic, preserved males dark grey to black, females pale grey.....9
- 9a. Dorsal-fin origin relatively posterior, opposite vertebrae 22–24.....*Oryzias nigrimas*.  
(Lake Poso, Sulawesi Tengah)
- 9b. Dorsal-fin origin relatively posterior, opposite vertebrae 20–21.....*Oryzias nebulosus*.  
(Lake Poso, Sulawesi Tengah)
- 10a. Dark brown to black blotches of males form irregular vertical bar on the body.....11.
- 10b. Males with no distinct dark brown to black vertical bars or blotches on the body.....15.
- 11a. Anal-fin rays 26–29; body depth 30–35% SL.....*Oryzias profundicola*.  
(Lake Towuti, Sulawesi Selatan)
- 11b. Anal-fin rays 20–26; body depth 25–31% SL.....12.

- 12a. Scales in a lateral series 41–47.....*Oryzias matanensis*.  
(Lake Matano, Sulawesi Selatan)
- 12b. Scales in a lateral series fewer than 36.....13.
- 13a. Dark brown blotches distributed irregularly on the body, and a row of five to nine larger blotches irregularly distributed dorsal to a midaxial stripe; relatively large-bodied, reaching 40 mm SL; eye relatively large, 10–12% SL.....*Oryzias marmoratus*.  
(Lakes Mahalona, Towuti and Wawantoa, Sulawesi Selatan)
- 13b. Dark brown blotches of males present, only at midbody and forming irregular vertical bars, no blotches over lateral surface of body; relatively small-bodied, reaching no more than 35 mm SL; eye relatively small, 7–8% SL.....14.
- 14a. Dorsal-fin origin relatively anterior, opposite vertebra 21.....*Oryzias timorensis*.  
(Timor)
- 14b. Dorsal-fin origin relatively posterior, opposite vertebrae 22–23.....*Oryzias celebensis*.  
(Sulawesi Selatan and Timor)
- 15a. First complete pair of pleural ribs on second vertebra.....16.
- 15b. First complete pair of pleural ribs on third vertebra.....20.
- 16a. First six anal-fin rays of males elongate and highly modified into an intromittent organ; adult females usually with only one (the left) pelvic fin; maxilla absent; caudal vertebrae 21 or more; dorsal fin posterior, opposite vertebra 27.....*Oryzias setnai*.  
(western India)
- 16b. Anal-fin rays of males not modified into an intromittent organ; females with two pelvic fins; maxilla present; caudal vertebrae 20 or fewer dorsal fin anterior, opposite vertebra 24 or less.....17.
- 17a. Complete branchiostegal rays 4, some specimens with a minute 5th ray; principal caudal-fin rays i,3/4,i.....18.
- 17b. Complete branchiostegal rays 5; principal caudal-fin rays i,4/5,i.....*Oryzias sinensis*.  
(Kazakhstan, Laos, Thailand, China, west Korea, Taiwan)
- 18a. Pelvic fins elongate in females, may extend posteriorly beyond anal-fin origin; interrupted, horizontal dark brown bar from the eye to the tip of the lower jaw.....*Oryzias uwai*.  
(Myanmar)
- 18b. Pelvic fins small, do not meet anal-fin origin; no horizontal dark brown bar from the eye to the tip of the lower jaw.....19.
- 19a. Pelvic-fin rays five; anal-fin rays 17–21; dorsal- and anal-fin rays elongate in males; no enlarged teeth posteriorly on jaw; caudal fin of male without orangish-red margins.....*Oryzias minutillus*.  
(Thailand, Yunnan Province, China)
- 19b. Pelvic-fin rays six; anal-fin rays 13–18; dorsal- and anal-fin rays not elongate in males; enlarged teeth posteriorly on premaxilla and dentary in males; bright orangish-red subdistal marginal stripes in caudal fin of male.....*Oryzias mekongensis*.  
(Thailand, Laos and Kampuchea)
- 20a. Anal fin subtriangular, anteriormost fin ray short, followed by several elongate rays decreasing in length posteriorly.....23.
- 20b. Anal fin ‘parallelogram-shaped’, posterior anal-fin rays elongate and relatively same length as anterior rays...  
.....21.
- 21a. Bony processes on medial pectoral-fin rays of males.....22.
- 21b. No bony processes on medial pectoral-fin rays of males.....*Oryzias curvinotus*.  
(southern China, Vietnam)
- 22a. Dorsal-fin origin relatively posterior, opposite vertebrae 22–23.....*Oryzias latipes*.  
(Japan, east Korea, China, Laos)
- 22b. Dorsal-fin origin relatively anterior, opposite vertebrae 20–21.....*Oryzias luzonensis*.  
(Luzon, Philippines)
- 23a. Discrete black blotch on dorsal half of the pectoral-fin base in both sexes.....*Oryzias pectoralis*.  
(Laos, Vietnam)
- 23b. No discrete black blotch on dorsal half of pectoral-fin base.....24.
- 25a. Moderately deep-bodied, greatest depth no more than 30% SL.....27.
- 25b. Extremely deep-bodied, greatest depth nearly 34% SL.....*Oryzias dancena*.  
(India, Sri Lanka, Bangladesh, Myanmar)

- 27a. Pectoral-fin rays eight to nine; caudal fin rounded and elongate; pelvic bone lateral strut blunt.....*Oryzias hubbsi*.  
(western Java)
- 27b. Pectoral-fin rays ten or more; caudal fin truncate; pelvic bone lateral strut needle-like and elongate.....28.
- 28a. Dorsal-fin origin anterior, opposite vertebrae 20–21; miniature, reaching no more than 26 mm SL.....*Oryzias haugiagensis*.  
(Vietnam)
- 28b. Dorsal-fin origin posterior, opposite vertebra 22 or 23; reaching over 32 mm SL.....29.
- 29a. Anterior margin of ethmoid cartilage irregular, indented medially, with distinct gap between the left and right side.....*Oryzias carnaticus*.  
(India, Sri Lanka, Bangladesh)
- 29b. Anterior margin of ethmoid cartilage uninterrupted or entire.....*Oryzias javanicus*.  
(Thailand, Peninsular Malaysia, Singapore, and Indonesia)

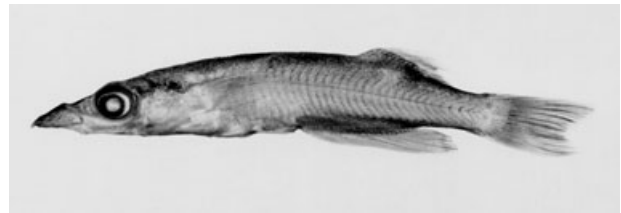
family-group name was modified subsequently to Oryziidae by Steyskal (1980).

#### GENUS *ADRIANICHTHYS* WEBER, 1913

*Adrianichthys* Weber, 1913: 204–205 [type species: *Adrianichthys kruyti* Weber, 1913, by monotypy. Gender masculine].

**Diagnosis:** *Adrianichthys* is diagnosed as monophyletic by five unambiguous synapomorphies: paired or single preethmoid cartilage(s); orbits project somewhat beyond dorsal profile of head; premaxilla flat and broad with no distinct articular and ascending processes; maxilla relatively straight without dorsal process; and upper and lower jaw with two to four irregular rows of small, villiform teeth that form a pavement dentition. In addition, the ethmoid region of the skull is flat and broad, in lateral view, and there are no enlarged teeth posteriorly on the premaxilla, two characters also found in cyprinodontiforms, but not in ricefishes of the genus *Oryzias*.

**Distribution and conservation status:** The four species of *Adrianichthys* are endemic to Lake Poso, a tectonic, freshwater lake in Sulawesi Tengah with an area of 323 km<sup>2</sup> and a maximum depth of 450 m (Whitten, Mustafa & Henderson, 1987a: 255). The large ricefishes, or buntingi in the local vernacular, of Lake Poso and Lake Lindu are considered by Whitten *et al.* (1987a) to be endangered and some species possibly extinct, due in part to the introduction, at unknown dates, of exotic fish species such as tilapia, *Oreochromis mossambicus*, and common carp, *Cyprinus carpio* (see Whitten *et al.*, 1987a; Groombridge, 1994; and the IUCN website, <http://www.iucnredlist.org>). *Adrianichthys kruyti* and *A. poptae* were considered nearly extinct or endangered by Soeroto & Tungka (1996). Field observations and collections by Kottelat (1990a: 64–65), Soeroto & Tungka (1996), Parenti & Soeroto (2004) and Parenti and colleagues in 1995



**Figure 32.** *Adrianichthys kruyti* Weber, 1913, Lake Poso, Sulawesi Tengah, Indonesia, ZMH 22572, male, 86.7 mm SL.

(reported in material examined below) support the contention that some Lake Poso ricefishes, once the basis of an important local fishery, are now rare, but not extinct. *Adrianichthys oophorus*, in particular, was abundant in 1995.

#### *ADRIANICHTHYS KRUYTI* WEBER, 1913

TEBINGKOLO

FIGURE 32

*Adrianichthys kruyti* Weber, 1913: 198–206, figs 1–4 [type locality: Indonesia: Sulawesi Tengah, Lake Poso].- Weber & de Beaufort, 1922: 379–381 [comparisons, distribution].- Rosen, 1964: 222–263 [systematics, characters, comparisons].- Nijssen, van Tuijl & Isbrücker, 1982: 69 [ZMA type specimen].- Parenti, 1987: 569 [characters, comparisons].- Whitten *et al.*, 1987a: 295, table 4.10 [distribution].- Whitten *et al.*, 1987b: 43–48, table 1, fig. 2 [conservation].- Kottelat, 1990a: 57–58, table 2 [characters, photographs].- Soeroto & Tungka, 1996: 22–26 [distribution, conservation status].- Seegers, 1997: 15, 18 [listed, photograph].- Parenti & Soeroto, 2004: 10–19 [comparisons, conservation status].  
*Adrianichthys kruytii*.- Soeroto & Tungka, 1991: 12–14 [listed, habitat].

**Differential diagnosis:** *Adrianichthys kruyti* is distinguished from all other ricefishes by the autapomorphy of an enlarged, overhanging, ‘duck-bill’-shaped upper

jaw that completely encloses the lower jaw in adults. In addition, *A. kruyti* differs from its sister species, *A. roseni*, by having more scales in a lateral series (approximately 70–75 vs. 63–65), relatively posterior pelvic fins (opposite vertebra 10 as opposed to vertebra 7) and attaining a greater recorded maximum standard length (109 vs. 90 mm). *Adrianichthys kruyti* is like *A. roseni*, and differs from its other congeners, *A. oophorus* and *A. poptae*, by having large orbits that project markedly beyond the dorsal profile of the head; paired (rather than single) preethmoid cartilages; and 13–17 dorsal-fin rays (vs. 8–13 dorsal-fin rays).

*Description:* Large-bodied, maximum size of specimens examined 109 mm SL. Body slender, elongate and laterally compressed; body depth 14–20 [18]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth subterminal, elongate upper and lower jaws; enlarged, overhanging, duck-bill-shaped, upper jaw completely encloses lower jaw. Dorsal and ventral body profile relatively straight from head to dorsal- and anal-fin origins. Head length 34–35 [35]; snout length 16; eye moderate to large, 8–10 [10], orbits project beyond dorsal surface of head; dorsal surface of head concave, articulation point of palatine and maxilla projects beyond dorsal profile. Fleishy, incompletely scaly, basal portion of dorsal and anal fins project beyond primary body profile. Scales small, cycloid and relatively deciduous, 70–75 in a lateral series. Anal-fin rays without contact organs. Short, slightly bilobed, urogenital papilla in some specimens. Medialmost pelvic-fin ray not connected to body via a membrane. Caudal fin slightly lunate, dorsal and ventral caudal-fin rays longer than middle rays.

Premaxilla flat and broad with no distinct articular or ascending processes, nearly confluent with maxilla; premaxilla and dentary with pavement dentition comprising four to five irregular rows of small, villiform teeth; no enlarged, caniniform teeth on posterolateral ramus of premaxilla or dentary. Paired preethmoid cartilages; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage straight. Palatine and quadrate articulate via elongate flanges that overlap anteriorly. Dorsal ramus of hyomandibula bifid, separate cartilages articulate with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; lateral process of pelvic bone attaches to eighth pleural rib. Caudal skeleton with two epural bones; one long, relatively straight, ventral accessory bone. Fifth ceratobranchial toothplates subtriangular with pavement dentition anteriorly followed posteriorly by eight to nine discrete tooth rows; no small, incomplete posterior row. Basihyal bone elongate and

triangular; basihyal cartilage rectangular. Epibranchial elements fully ossified; epibranchial 2 with a broad point of articulation with ceratobranchial cartilage.

Dorsal-fin rays 14–17 [16]. Anal-fin rays 24–25 [24]. Pelvic-fin rays 6. Pectoral-fin rays 14–16 [15]. Principal caudal-fin rays i,5/6,i. Procurent fin-rays, dorsal 5, ventral 6–7. Vertebrae 36 (14–15 + 21–22). Branchiostegal rays 5.

*Cytogenetic data:* Unknown.

*Colour in life:* Unknown.

*Colour in alcohol:* Ground colour pale yellow, belly pale whitish yellow. Dorsal surface of head and dorsal and lateral surface of body with minute, sparse to dense, dark brown to black chromatophores that outline myomeres in some specimens. Fins with scattered light brown chromatophores or hyaline. Holotype completely bleached.

*Distribution and habitat:* A pelagic species endemic to Lake Poso, Sulawesi Tengah (Parenti & Soeroto, 2004: fig. 1).

*Remarks:* Data were augmented by those in Kottelat (1990a: table 3). Other common names for this species are duckbilled buntingi or duck-bill poso minnow (Seegers, 1997: 18).

*Material examined:* Four specimens (76.7–109 mm SL).

Holotype. INDONESIA. Sulawesi Tengah: Lake Poso, A. C. Kruyt, i.1913, ZMA 100.643, 1 (109 mm).

Non-type specimens. INDONESIA. Sulawesi Tengah: Lake Poso, at its outlet, immediately north of Tentena, ZMH 22571, 1 (single female specimen in two pieces: head and pectoral girdle, and body from anal-fin origin to posterior extent of caudal fin), ZMH 22572, 1 (86.7 mm), CMK 5776, 1 (formerly ZSM 27821) (76.7 mm, eviscerated), S. Gütebier, P. Sander, J. Weber & S. Zabansky, ix.1983.

#### *ADRIANICHTHYS OOPHORUS* (KOTTELAT, 1990A)

##### COMB. NOV.

##### EGGCARRYING BUNTINGI

##### FIGURES 8A, 10B, 18A, 24D, 29A, 33

*Xenopoecilus oophorus* Kottelat, 1990a: 59, figs 5, 6 [type locality: Indonesia: Sulawesi, Lake Poso].- Soeroto & Tungka, 1991: 12–14 [listed, biology reproductive behaviour]- Uwa, 1991b: 15–18 [chromosomes, morphometrics].- Soeroto & Tungka, 1996: 22–26 [distribution, conservation status].- Seegers,



**Figure 33.** *Adrianichthys oophorus* (Kottelat, 1990a), Lake Poso, Sulawesi Tengah, Indonesia, USNM 340431, female, 58 mm SL, carrying cluster of embryos.

1997: 15, 18 [listed, photographs].- Parenti & Soeroto, 2004: 10–19 [comparisons, conservation status].- Springer & Johnson, 2004: 128–129, pl. 98 [gill arch morphology].

**Differential diagnosis:** *Adrianichthys oophorus* is distinguished from congeners by having fewer dorsal-fin rays (8–10 vs. 11–13 in *A. poptae* and 13–17 in *A. kruyti* and *A. roseni*), fewer anal-fin rays (20–22 vs. 24–27), fewer pectoral-fin rays (12 vs. 13–16), a relatively small head (reaching 27% SL as opposed to reaching 32% or more) and short snout (reaching 9% SL, as opposed to 14% or more). *Adrianichthys oophorus* shares with *A. poptae* a single, rather than paired, subtriangular preethmoid cartilage, and ossified portions of mesethmoid semicircular anteriorly and subrectangular posteriorly (vs. disc-shaped). *Adrianichthys oophorus* shares with *A. poptae* and *A. roseni* an abdominal concavity between the pelvic fins and anal fin to carry developing embryos, and is most pronounced in *A. oophorus*.

**Description:** Large-bodied, maximum size of specimens examined 69.3 mm SL. Body elongate, slender, laterally compressed; body depth 16–18. Extremely pronounced abdominal concavity between pelvic fins and anal fin to carry developing embryos. Mouth terminal, upper and lower jaws subequal or lower jaw extending somewhat beyond upper jaw. Dorsal and ventral body profile relatively straight from head to dorsal and anal fin origin, dorsal body profile slightly convex posterior to head. Head length 25–27; snout length 8–9; eye moderate, 8–9, orbits project slightly beyond dorsal surface of head; articulation point of palatine and maxilla does not project beyond dorsal profile. Fleshy, incompletely scaly, basal portion of anal fin projects slightly beyond primary body profile. Scales small, cycloid and relatively deciduous; 58–65 in a lateral series. Anal-fin rays without contact organs. Relatively long, tubular urogenital papilla in some specimens. Medialmost pelvic-fin ray not connected to body via a membrane. Caudal fin lunate, dorsal and ventral segmented caudal-fin rays longer than middle rays.

Premaxilla flat and broad with no distinct articular or ascending processes; premaxilla and dentary with two irregular rows of small, villiform teeth; no enlarged, caniniform teeth on posterolateral ramus of premaxilla or dentary. Subtriangular preethmoid cartilage single; ossified portions of mesethmoid semicircular anteriorly and subrectangular posteriorly; anterior border of ethmoid cartilage straight. Palatine and quadrate articulate via elongate flanges that overlap anteriorly. Dorsal ramus of hyomandibula bifid, with separate cartilages that articulate with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; lateral process of pelvic bone attaches to sixth pleural rib. Caudal skeleton with two epural bones; one relatively straight, ventral accessory bone. Fifth ceratobranchial toothplates subtriangular, with pavement dentition anteriorly followed posteriorly by four or five tooth rows; no small, incomplete posterior row. Basihyal bone elongate and triangular; basihyal cartilage rectangular. Epibranchial elements fully ossified; epibranchial 2 with a broad point of articulation with ceratobranchial cartilage.

Dorsal-fin rays 8–10. Anal-fin rays 20–22. Pelvic-fin rays 6. Pectoral-fin rays 12. Principal caudal-fin rays i,5/6,i. Procurrent fin-rays, dorsal 7, ventral 7. Vertebrae 36 (15 + 21). Branchiostegal rays 5–6.

**Cytogenetic data:** A metaphase chromosome figure of *A. oophorus* published by Uwa (1991b: fig. 3) demonstrates what appears to be 40 pairs of chromosomes. The preparation was considered inadequate for an accurate characterization of karyotype.

**Colour in life:** Body translucent and fins hyaline; melanophore pattern as described below in alcohol.

**Colour in alcohol:** Ground colour greyish brown dorsally with ventral surface of body and caudal peduncle white. Dark brown to black chromatophores concentrated on dorsal surface of head and along middorsal surface of body to caudal fin. A thin, black midlateral stripe, with scattered melanophores above and below, from the head to the caudal peduncle. Fins hyaline.

**Distribution and habitat:** A pelagic species endemic to Lake Poso, Sulawesi Tengah (Parenti & Soeroto, 2004: fig. 1). Hundreds of specimens, both large adults and juveniles, were collected at night in open waters of Lake Poso during a 1995 expedition. Individuals were attracted to a boat using kerosene lamps and then collected using dip nets. Many individuals, in addition to those listed below, were seen but not taken.



**Figure 34.** *Adrianichthys poptae* (Weber & de Beaufort, 1922), Lake Poso, Sulawesi Tengah, Indonesia, ZMA 100.644, syntype of *Xenopocilus poptae*, male, 180 mm SL.

*Remarks:* The largest specimen of *A. oophorus* examined by Kottelat (1990a: fig. 6, ZSM/CMK 6240, 65.1 mm, paratype) has an embryo cluster held in an abdominal concavity between the body and the pelvic fins. The observations of spawning in December to January (Soeroto & Tungka, 1991), June (Kottelat, 1990a) and August (specimens reported below) suggest that *A. oophorus* spawns year-round. Data were augmented by those in Kottelat (1990a). The holotype (ZSM/LIPI 5, 37.2 mm SL) was not examined by me. Another common name for this species is egg carrying poso minnow (Seegers, 1997: 18).

*Material examined:* 1335 specimens (8.0–69.3 mm SL).

Paratypes. INDONESIA. Sulawesi Tengah: Lake Poso, east shore between Tentena and Peura, ZSM/LIPI 6, 5 (21.1–35.8 mm), ZSM/CMK 6360 (formerly CMK 6236), 1 (27.5 mm, cleared and counterstained), M. Kottelat, 23–25.ix.1988.

Non-type specimens. INDONESIA. Sulawesi Tengah: Lake Poso, west bank of Poso R. where it empties into lake at Pamona Caves, USNM 340431, 633 (9.2–69.3 mm), L. R. Parenti, K. D. Louie, P. Beta & Young, 11 Aug 1995, USNM 350469, 335 (9–66.3 mm, 5 of which have been cleared and counterstained), L. R. Parenti, K. D. Louie, P. Beta & boatmen, 13.viii.1995. Lake Poso, eastern shore approx. 17 km S of Tentena, USNM 348386, 93 (8.6–66.8 mm, 6 of which have been cleared and counterstained), USNM 348724, 268 (8–59.1 mm), L. R. Parenti, K. D. Louie, P. Beta *et al.*, 12.viii.1995.

**ADRIANICHTHYS POPTAE** (WEBER & DE BEAUFORT, 1922) *COMB. NOV.*

POPTA'S BUNTINGI

FIGURES 9, 23A, 24C, 34, 35

*Xenopocilus poptae* Weber & de Beaufort, 1922: 379, fig. 100 [type locality: Indonesia: Sulawesi, Lake Poso].- Rosen, 1964: 222–263 [comparative anatomy, relationships, classification].- Parenti, 1987: 569



**Figure 35.** *Adrianichthys poptae* (Weber & de Beaufort, 1922), Lake Poso, Sulawesi Tengah, Indonesia, CMK 5775, male, 142 mm SL.

[characters, comparisons].- Whitten *et al.*, 1987a: 295, table 4.10 [distribution].- Whitten *et al.*, 1987b: 43–48, table 1 [Sulawesi, conservation].- Kottelat & Sutter, 1988: 55 [note on type material].- Soeroto & Tungka, 1991: 12 [listed].- Uwa, 1991b: 15–18 [chromosomes, morphometrics].- Wourms, 1994: 566 [comment on possible viviparity].- Soeroto & Tungka, 1996: 1–5 [distribution, conservation status].- Seegers, 1997: 15, 18 [listed, photograph X97235-4 mislabelled *Xenopocilus sarasinorum*].- Parenti & Soeroto, 2004: 10–19 [comparisons, conservation status].

*Differential diagnosis:* *Adrianichthys poptae* is distinguished from congeners by having seven pelvic-fin rays (vs. six or fewer pelvic-fin rays), and eye relatively small (6–7% SL vs. 9% or more), and from all other ricefishes by attaining the largest recorded maximum standard length of 192 mm (vs. a maximum of 109 mm SL in the next largest ricefish species, *A. kruyti*). It shares with *A. oophorus* a uniquely shaped ethmoid region of the skull in which ossified portions of the mesethmoid are semicircular anteriorly and subrectangular posteriorly (vs. disc-shaped), and a single, rather than paired, preethmoid cartilage.

*Description:* Large-bodied, maximum size of specimens examined 192 mm SL. Body laterally compressed, slender; body depth 12–20. Abdominal concavity between pelvic fins and anal fin. Mouth terminal, upper and lower jaws subequal or lower jaw extending somewhat beyond upper jaw. Dorsal and ventral body profile relatively straight from head to dorsal- and anal-fin origins. Head length 28–35; snout length 13–17; eye small, 6–7, orbits project slightly beyond dorsal surface of head, especially in larger specimens; articulation point of palatine and maxilla projects slightly beyond dorsal profile. Fleshy, incompletely scaly, basal portion of dorsal and anal fin projects beyond primary body profile. Scales small to minute, cycloid and relatively deciduous; 75–85 in a lateral series. Anal-fin rays without contact organs.

Short urogenital papilla in some specimens. Medial-most pelvic-fin ray not connected to body via a membrane. Caudal fin lunate, dorsal and ventral segmented caudal-fin rays longer than middle rays.

Premaxilla flat and broad with no distinct articular or ascending processes; premaxilla and dentary with four to five irregular rows of small, villiform teeth; no enlarged, caniniform teeth on posterolateral ramus of premaxilla or dentary. Subtriangular preethmoid cartilage single; ossified portions of mesethmoid semicircular anteriorly and subrectangular posteriorly; anterior border of ethmoid cartilage straight. Palatine and quadrate articulate via elongate flanges that overlap anteriorly. Dorsal ramus of hyomandibula bifid, with separate cartilages that articulate with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; lateral process of pelvic bone attaches to sixth pleural rib. Caudal skeleton with two epural bones; one large, relatively straight, ventral accessory bone. Fifth ceratobranchial toothplates subtriangular with pavement dentition anteriorly followed posteriorly by eight to ten tooth rows; no small, incomplete posterior row in males and females. Basihyal bone elongate and triangular; basihyal cartilage rectangular. Epibranchial elements fully ossified; epibranchial 2 with a broad point of articulation with ceratobranchial cartilage.

Dorsal-fin rays 11–13. Anal-fin rays 24–27. Pelvic-fin rays 7. Pectoral-fin rays 13–14. Principal caudal-fin rays i,5/6,i. Procurrent fin-rays, dorsal 6, ventral 6. Vertebrae 36–37 (15–17 + 20–22). Branchiostegal rays 5–7.

*Cytogenetic data:* Unknown.

*Colour in life:* Body somewhat translucent, and with melanophore pattern as described below in alcohol.

*Colour in alcohol:* Ground colour pale yellow, belly pale whitish yellow. Dorsal surface of head and dorsal and lateral surface of body with dense dark brown to black chromatophores. Fins hyaline, or somewhat dusky in larger specimens.

*Distribution and habitat:* A pelagic species endemic to Lake Poso, Sulawesi Tengah (Parenti & Soeroto, 2004: fig. 1).

*Remarks:* Weber & de Beaufort (1922: 379) completed their description with the statement 'Length of 11 specimens examined 97.5–204 mm.' Eleven specimens, presumably syntypes, all now or originally part of ZMA 100.644, have been located. These are the ten examined syntypes, below, and the single specimen in NMB 3090 (formerly ZMA 100.644) (171 mm) listed

by Kottelat & Sutter (1988: 55) and Kottelat (1990a), but not examined by me. A twelfth specimen, BMNH 1913.12.15.6 (female, 165 mm), was received by the BMNH on exchange from ZMA, possibly from M. Weber, and registered in 1913, 3 years after the syntypes were collected and 9 years before publication of the original description. This specimen is also possibly part of the syntype series. Like all specimens originally from ZMA 100.644, the body of the BMNH specimen is now soft and bleached, many scales are lost, and fin-rays are broken. I do not designate a lectotype from among the syntypes because I am unable to determine which specimens comprise Weber & de Beaufort's type series. Data were augmented by those in Kottelat (1990a). Another common name for this species is elongate poso minnow (Seegers, 1997: 18).

*Adrianichthys poptae* has been considered endangered (Kottelat, 1990a; Soeroto & Tungka, 1996). At least eight specimens have been collected since 1991; the most recent known to me were collected in March 2003 (Parenti & Soeroto, 2004).

*Material examined:* 22 specimens (76–192 mm SL). Syntypes. INDONESIA. Sulawesi Tengah: Lake Poso, A. C. Kruiy, xi.1909–i.1910 ZMA 100.644, 6 (85–192 mm); CAS-SU 33909 (formerly ZMA 100.644), 2 (180 mm), AMNH 20480 (formerly ZMA 100.644), 2 (one specimen 175 mm, one specimen heavily dissected and not measured).

Non-type specimens. INDONESIA. Sulawesi Tengah: Lake Poso (no specified locality), N. J. Wilimovsky, 4–5.ix.1978, USNM 322423, 2 males (155–168 mm, the larger specimen cleared and counterstained); Lake Poso, at its outlet, immediately north of Tentena, S. Gütebier, P. Sander, J. Weber & S. Zabansky, ix.1983, ZMH 22573, 1 (113.4 mm), ZMH 22575, 2 (eviscerated males?, 154–171 mm), ZMH 22576, 3 (106–138 mm), ZMH 22577, 1 (116.5 mm, cleared and stained for bone), CMK 5775 (formerly ZSM 27820), 1 (142 mm); Lake Poso, west bank of Poso R. where it empties into lake at Pamona Caves, USNM 340430, 1 (immature, 76 mm), L. R. Parenti, K. D. Louie, P. Beta & Young, 11.viii.1995; Lake Poso, no specified locality, BMNH 1913.12.15.6, 1 (adult female, 165 mm), possible syntype, received by the BMNH on exchange from ZMA, possibly through M. Weber.

*ADRIANICHTHYS ROSENI* PARENTI & SOEROTO, 2004

ROSEN'S BUNTINGI

FIGURES 18B, 22, 24B, 36

*Adrianichthys kruiyti*.- Rosen & Parenti, 1981: 16, fig. 15b [dorsal gill arch osteology].- Parenti, 1989: 80, fig. 1 [photo].



**Figure 36.** *Adrianichthys roseni* Parenti & Soeroto, 2004, Lake Poso, Sulawesi Tengah, Indonesia, MZB 6732, holotype, gravid female, 90 mm SL.

*Adrianichthys roseni* Parenti & Soeroto, 2004: 10–19, figs 1, 2a, 5 [type locality: Indonesia: Sulawesi, Lake Poso].

**Differential diagnosis:** *Adrianichthys roseni* is like its sister species, *A. kruyti*, and differs from congeners, *A. oophorus* and *A. poptae*, in having large orbits that project markedly beyond the dorsal profile of the head; paired, rather than single, preethmoid cartilages; and a large dorsal fin (with 13–16 vs. 8–13 dorsal-fin rays). The lower jaw of *A. roseni* is enclosed in the expanded upper jaw, but the upper jaw is not as large and broadly expanded as in *A. kruyti*. In addition, *A. roseni* differs from *A. kruyti* in having fewer scales in a lateral series (approximately 63–65 vs. 70–75) having more anterior pelvic fins (opposite vertebra 7 as opposed to vertebra 10) and attaining a smaller maximum standard length (90 vs. 109).

**Description:** Large-bodied, maximum size of specimens examined 90 mm SL. Body slender, laterally compressed; body depth 14–17 [17]. Abdominal concavity between pelvic fins and anal fin. Mouth subterminal, elongate upper and lower jaws, upper jaw slightly longer than, and enclosing, lower jaw. Dorsal and ventral body profile relatively straight from head to dorsal- and anal-fin origins. Head length 31–32 [32]; snout length 14; eye moderate, 7–8, orbits project beyond dorsal surface of head; dorsal surface of head concave, articulation point of palatine and maxilla project slightly beyond dorsal profile. Fleshy, incompletely scaly, basal portion of dorsal and anal fin project slightly beyond primary body profile. Scales small, cycloid and relatively deciduous; 63–65 in a lateral series. Anal-fin rays without contact organs. Large, rounded, urogenital papilla in gravid female holotype. Medialmost pelvic-fin ray not connected to body via a membrane. Caudal fin slightly lunate, dorsal and ventral segmented caudal-fin rays longer than middle rays.

Premaxilla flat and broad with no distinct articular or ascending processes; premaxilla and dentary with pavement dentition comprising four to five irregular

rows of small, villiform teeth; no enlarged, caniniform teeth on posterolateral ramus of premaxilla or dentary. Paired preethmoid cartilages; ossified portions of mesethmoid round; anterior border of ethmoid cartilage straight. Palatine and quadrate articulate via elongate flanges that overlap anteriorly. Dorsal ramus of hyomandibula bifid, separate cartilages articulate with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; lateral process of pelvic bone attaches to fifth pleural rib. Caudal skeleton with two epural bones, one relatively large, straight, ventral accessory bone. Fifth ceratobranchial toothplates subtriangular with pavement dentition anteriorly followed posteriorly by eight to nine tooth rows; no small, incomplete posterior row. Basihyal bone elongate and triangular; basihyal cartilage rectangular. Epibranchial elements fully ossified; epibranchial 2 with a broad point of articulation with ceratobranchial cartilage.

Dorsal-fin rays 13–16 [13]. Anal-fin rays 25. Pelvic-fin rays 6. Pectoral-fin rays 13–15 [15]. Principal caudal-fin rays i,5/6,i. Procurent fin-rays, dorsal 6, ventral 7. Vertebrae 36 (14 + 22). Branchiostegal rays 5.

**Cytogenetic data:** Unknown.

**Colour in life:** Unknown.

**Colour in alcohol:** Overall ground colouration pale yellow, belly pale whitish yellow. Faint transverse irregular bar just slightly darker than ground coloration posterior to pectoral fin. Fins hyaline.

**Distribution and habitat:** Endemic to Lake Poso, Sulawesi Tengah (Parenti & Soeroto, 2004: fig. 1). No habitat data are available for the single collection of this species. It is presumed to be a pelagic species like its congeners.

**Remarks:** Measurements were taken on the holotype and paratype. The triple stained nontype is highly distorted and therefore was not measured. Counts were verified on a radiograph of the holotype because the paratype has become disarticulated in glycerin. The three known specimens are all female.

**Material examined:** Three specimens (69–90 mm SL). Holotype. INDONESIA. Sulawesi Tengah: Lake Poso, N. J. Wilimovsky, 4–5.ix.1978, MZB 6732 (ex. USNM 322424), 1 (gravid female, 90 mm).

Paratype. INDONESIA. Sulawesi Tengah: Lake Poso, USNM 322425, 1 (cleared and counterstained, female, 73 mm), collected with the holotype.

Non-type specimen. INDONESIA. Sulawesi Tengah: Lake Poso, USNM 326628, 1 (cleared and counter-



stained for bone, cartilage, and nerves, female, 69 mm), collected with the holotype.

GENUS *ORYZIAS* JORDAN & SNYDER, 1906

*Oryzias* Jordan & Snyder, 1906: 289 [type species: *Poecilia latipes* Temminck & Schlegel, 1846, by original designation and monotypy. Gender masculine].

*Xenopoeilus* Regan, 1911a: 374 [type species: *Haplochilus sarasinorum* Popta, 1905, by monotypy. Gender masculine].

*Horaichthys* Kulkarni, 1940: 385 [type species: *Horaichthys setnai* Kulkarni, 1940, by original designation and monotypy. Gender masculine].

**Diagnosis:** *Oryzias* is diagnosed as monophyletic by eight synapomorphies: small size at hatching, 4.5 mm or less; maximum adult body size less than 60 mm SL; hyomandibula with a single head articulating with otic region of skull; ventral hypohyal with a blunt posterior ramus; epibranchial 2 notably smaller than other epibranchial bones, lacking a broad point of articulation with the ceratobranchial cartilage, and cartilaginous or absent in some specimens; ceratobranchial bone 5 toothplate rectangular or suboval; fifth ceratobranchial teeth are arranged in horizontal rows; and total vertebrae number 34 or fewer. An additional character, small egg, is included tentatively as a ninth synapomorphy, although data for most ricefish species are lacking.

**Distribution and conservation status:** Naturally broadly distributed in fresh and brackish waters from the Indian subcontinent through continental and insular Asia, including Hainan Island, China, the Japanese Archipelago, Taiwan, and Luzon, the Philippines, the Malay Peninsula across the Indo-Malay-Philippines Archipelago as far east as Timor (Fig. 2). Yamamoto (1975) indicated on a map that *O. melastigma* (probably *O. dancena*) lives in Pakistan. I have examined no ricefish specimens from Pakistan. Furthermore, Jayaram (1981) does not give Pakistan as a locality for *O. melastigma*, and Mirza (1975, 1990) does not include ricefishes in his reports on freshwater fishes of Pakistan. Therefore, I am unable to confirm the natural occurrence of ricefishes in Pakistan. *Oryzias latipes* has apparently been introduced into Iran (Coad, 1995) and New York, USA (Hensley & Courtenay, 1980; see also Fuller, Nico & Williams, 1999). *Oryzias* populations are threatened or endangered throughout much of their natural range, especially in regions with relatively high human population density, such as Japan (K. Matsuura, pers. comm., 1999; Matsuura *et al.*, 2000) and Taiwan (Lin *et al.*, 1999; Tzeng *et al.*, 2006).



**Figure 37.** *Oryzias latipes* (Temminck & Schlegel, 1846), Kagoshima Prefecture, Japan, USNM 70779, male, 28.2 mm SL.

**Remarks:** *Oryzias* was considered a synonym of the cyprinodontiform killifish genus *Aplocheilus* by George S. Myers (1931) and collaborators (e.g. Herre & Myers, 1937), although the name *Panchax* was still used then for ricefishes (e.g. Fowler, 1938). Use of the names *Aplocheilus*, *Panchax* and *Oryzias* for groups of Asian killifish and ricefish species was reviewed by Smith (1938) who demonstrated that *Panchax* is an objective synonym of *Aplocheilus*, a cyprinodontiform (see also Myers, 1938: 137; Parenti, 1981: 351–352; Eschmeyer, 1990: 290). By 1955, Myers recognized (p. 7) the then cyprinodont ‘Subfamily Oryziatinae. The medakas. One genus: *Oryzias*, found from Japan to India.’

*ORYZIAS LATIPES* (TEMMINCK & SCHLEGEL, 1846)

MEDAKA

FIGURE 37

*Poecilia latipes* Temminck & Schlegel, 1846: 224, pl. 102, fig. 5 [type locality: Japan, Nagasaki].- Boeseman, 1947: 167–168 [characters, lectotype designation].

*Haplochilus latipes*.- Günther, 1866: 311 [Nagasaki].

*Aplocheilus latipes*.- Jordan & Snyder, 1901: 57 [checklist, Yokohama, Japan].

*Oryzias latipes*.- Jordan & Snyder, 1906: 289–290 [*Poecilia latipes* Temminck & Schlegel as type species of new genus, *Oryzias*].- Oshima, 1919: 256–257 [report from Taiwan, characters].- Oshima, 1926: 1–25 [comparison with *Oryzias* from Hainan Is.].- Jordan & Tanaka, 1927: 264 [report from Amami-Oshima and Okinawa, Japan].- Smith, 1938: 166 [classification, characters].- Briggs & Egami, 1959: 363–380 [annotated bibliography].- Magnuson, 1962: 313 [reproductive biology; behaviour].- Rosen & Bailey, 1963: fig. 3c [skull].- Iwai, 1964: 31 [neuro-mast structure].- Rosen, 1964: 227 [classification in family Oryziatidae].- Wiley & Collette, 1970: 190 [contact organs].- Arai, 1973: 173 [chromosomes].- Satoh & Egami, 1972: 385–394 [sex differentiation of germ cells].- Ali & Lindsey, 1974: 959–976 [heritable and temperature-induced meristic variation].- Egami

No claim to original US Government works.

- & Yamamoto, 1975: 276–365 [bibliography].- Yamamoto, 1975 [biology, comparisons].- Grier, 1976: 419–431 [testis structure].- Schrey, 1978: 335 [taxonomy of *Oryzias*].- Hensley & Courtenay, 1980: 490 [status of introduced population in New York].- Sakaizumi *et al.*, 1980 [genetic differentiation of populations in Japan].- Sakaizumi *et al.*, 1983 [genetic differentiation of populations in Japan].- Liu, 1984: 418–419 [characters; report from Fujian Prov.].- Sakaizumi, 1984: 795–800 [genetic differentiation of northern and southern Japanese populations].- Iwamatsu *et al.*, 1984b: 653–663 [hybridization with *O. celebensis*; characters].- Sakaizumi, 1985: 521–522 [electrophoretic comparisons].- Uwa, 1985a: 3 [photograph of live specimens; distribution].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Langille & Hall, 1987 [developmental osteology].- Parenti, 1987: 561 [characters; comparisons].- Sakaizumi & Jeon, 1987: 13–20 [allozyme divergence among Korean populations].- Uwa & Jeon, 1987: 139–147 [karyotypes of Korean populations].- Langille & Hall, 1988 [development of neural crest].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Zhang, 1989: 295–296 [report from Pearl R., China].- Chen *et al.*, 1990: 171–172 [distribution in Qiantang R., China].- Zhang, 1990: 219–220 [distribution in Shanghai region].- Fujita, 1990: 343 [caudal skeleton].- Fujita, 1992: 107–109 [caudal skeleton ontogeny].- Iwamatsu, 1993 [biology, comparisons].- Ishikawa, 1994: 17–24 [lateral line innervation].- Iwamatsu, 1994: 825–839 [stages of normal development].- Zhou, 1994: 494–496 [distribution in Sichuan Prov.].- Coad, 1995: 25 [listed from Iran as an introduction].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Seegers, 1997: 19, 20 [photographs].- Roberts, 1998: 221 [characters; relationships].- Yuma, Hosoya & Nagata, 1998: 111, 122 [distribution in Japan].- Anken & Bourrat, 1998: 1–92 [brain atlas].- Albert *et al.*, 1999: 650 [brain weight].- Fuller *et al.*, 1999: 285–286 [status of introduced populations in the United States].- Hosoya, 2000: 135–139 [conservation status in Japan].- Ishikawa, 2000: 487–495 [model system for vertebrate developmental genetics].- Matsuura, Doi & Shinohara, 2000: 189–192 [distribution in Japan].- Matsuura *et al.*, 2000: 64 [reported as an endangered species living in a moat of the Imperial Palace, Tokyo].- Winn *et al.*, 2000 [detection of mutations in transgenic individuals].- Naruse *et al.*, 2000 [genome size].- Parenti, 2000b: 600 [listed].- Teather, Boswell & Gray, 2000: 813–818 [early life-history parameters].- Tatsuzawa, Sakaizumi & Kano, 2001: 89 [report from Mage-Shima Island, Japan, as a possible introduction; conservation status].- Kim & Park, 2002: 300 [Korea].- Youn, 2002: 219 [Korea].- Jang, Lucas & Joo, 2003: 119 [distribution in South Korean national parks].- Matsuda *et al.*, 2003: 159–161 [genetics of sex determination and comparison with *O. curvinotus*].- Parenti & Grier, 2004: 336 [atherinomorph testis type, listed].- Takehana *et al.*, 2005: 417–428 [phylogenetic relationships inferred from molecules].- Kasahara *et al.*, 2007: 714–718 [draft genome].
- Oryzias latipes latipes*.- Chen *et al.*, 1989: 239–246 [comparisons with *O. latipes sinensis*].- Uwa, 1991a: 361–367 [karyology, relationships].- Seegers, 1997: 15 [listed].- Sakai, Sato & Nakamura, 2001: 89–90 [conservation status; listed from Ryukyus, Japan].- Wittbrodt *et al.*, 2002: 53–64 [status as model organism].
- Differential diagnosis:* *Oryzias latipes* is a member of the biarmed chromosome group of Uwa (1986), along with *O. luzonensis*, *O. curvinotus* and the miniatures *O. sinensis* and *O. mekongensis*, that have anal-fin rays of approximately the same length, forming a ‘parallelogram-shaped’ fin (as opposed to a subtriangular-shaped fin that tapers posteriorly) and chromosome arms numbering 58 or more (as opposed to 48 or fewer). *Oryzias latipes* and *O. luzonensis* are the largest species of this group that also share a mesethmoid ossification that is indented anteriorly in some specimens, and a genome size of 1.9 pg per nucleus or greater. They are like *O. curvinotus* and differ from the two miniatures by having the first pleural rib on the third, rather than the second, vertebra in most specimens, and paired, bilaterally asymmetric, as opposed to single lobed, testes. They are like the miniatures, and differ from *Oryzias curvinotus* by having bony processes on the pectoral-fin rays. *Oryzias latipes* has a dorsal fin that is posterior (opposite vertebrae 22–23 as opposed to vertebrae 20–21) and an ethmoid margin that is straight, rather than irregular, relative to *O. luzonensis*. Chromosome arm number is reported as 68 in *O. latipes* from southern Japan and 70 from northern Japan, and 96 in *O. luzonensis* (Table 2).
- Description:* Small, maximum size of specimens examined 35.6 mm SL. Body compressed laterally, body depth 19–24. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 25–27 [25]; snout length 5–7; eye moderate, 8–9, orbits do not project beyond dorsal surface of head. Basal portion of dorsal and anal fin does not project significantly beyond primary body profile. Scales relatively large, cycloid; 28–32 [31] in a lateral series. Elongate, filamentous dorsal- and anal-fin rays

in males; medial pectoral-fin rays and posterior anal-fin rays with large, bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Pelvic-fin rays of some female specimens elongate, nearly meeting anal-fin origin. Caudal fin truncate. Males with a short, tubular urogenital papilla; females with enlarged, slightly bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two or three enlarged posterior teeth on the premaxilla and dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage straight. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra, rarely second; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fourth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and one accessory cartilage. Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by six discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial two notably smaller than the other epibranchial elements.

Dorsal-fin rays 5–7 [6]. Anal-fin rays 17–22. Pelvic-fin rays 5–7 [6]. Pectoral-fin rays 9–11. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 5, ventral 6. Vertebrae 27–32 (11–13 + 17–20). Branchiostegal rays 5–6.

*Cytogenetic data:* *Oryzias latipes* is a highly variable species with a biarmed chromosome constitution (Table 2). Populations from southern Japan are reported to have 48 diploid chromosomes, including two metacentric, eight submetacentric, one subtelo-centric and 13 acrocentric pairs. There are no populations with large metacentrics. Chromosome arm number (NF) totals 68 in populations from southern Japan and Korea and 70 from northern Japan.

*Colour in life:* Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum. Caudal fin with yellowish dorsal and ventral submarginal band in some populations.

*Colour in alcohol:* A diffuse to discrete row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Females with a subrectangular, males with a smaller, subtriangular black peritoneum. A faint to discrete black line along the anal-fin base. Dorsal and anal fin interradiation membranes with scattered melanophores. Specimens examined from Korea are dark brown above the midline; each dorsal scale is nearly filled with brown pigment.

*Distribution and habitat:* Widely distributed throughout eastern China, Hong Kong and Hainan Is., east Korea, the Japanese Archipelago from Honshu Island to the Ryukyu Islands in fresh to brackish water habitats (see Uwa & Parenti, 1988; Matsuura *et al.*, 2000: 189) and Laos (Roberts, 1998). The type locality of *Poecilia latipes* Temminck & Schlegel, 1846 is Nagasaki, Kyushu Is., southern Japan. Identification of Chinese and Laotian populations requires further study. Some of the material referred to here as *O. latipes* may be re-identified as *O. sinensis*. The Chinese specimens referred here to *O. sinensis* are miniature by the definition adopted here, not reaching more than 26 mm SL. The Laotian specimens are not miniature, reaching a reported 31.3 mm SL. Furthermore, the Laotian specimens have the first pleural rib on the third, not the second, vertebra, agreeing with *O. latipes*, not *O. sinensis*. Reports of *O. latipes* from localities throughout China (e.g. Zhang, 1990, Shanghai) may be of specimens referable to *O. sinensis*.

*Remarks:* Morphometric and meristic data are supplemented by those in Boeseman (1947), Iwamatsu *et al.* (1982), Iwamatsu (1986) and Uwa & Parenti (1988).

Jordan & Snyder's (1906: 289) diagnosis of the genus *Oryzias* includes an illustration of a specimen of *Oryzias latipes* that is approximately 41 mm TL, or 33 mm SL. They also state that many specimens were collected at Wakanoura and Kawatana in 1900. One large collection of *O. latipes*, CAS-SU 9866, from Wakanoura, includes a 32.5-mm SL specimen in a vial with a label that reads 'drawn'. I conclude that this is the specimen illustrated by Jordan & Snyder (1906).

Some local common names for *O. latipes* in Japan are tayu (in Amami-Oshima) and takami or takamigua (in Okinawa; Jordan & Tanaka, 1927: 264). Another common name for *O. latipes* in English is the Japanese ricefish, and, in Chinese, qing jiang yu (J. Song, pers. comm., 2004).

*Material examined*: 1321 specimens (7.5–35.6 mm SL).

Lectotype of *Poecilia latipes*. JAPAN. RMNH 2713a, 1 (35 mm), designated by Boeseman (1947: 168).

Paralectotypes of *Poecilia latipes*. JAPAN: RMNH 2713b, 1 (33 mm), RMNH 2713c, 1 (31 mm), RMNH 2714a–c, 3, (24–31 mm).

Non-type specimens. JAPAN. HONSHU IS.: Aomori Pref., Aomori, CAS 58021, 4 (28.2–30.0 mm), M. Sakaizumi, viii.1979.

Aichi Pref., Nagoya, Kichi R., AMNH 26760, 44 (16.5–26.7 mm, 6 of which have been cleared and counterstained, 10 of which have been cleared and stained solely with alizarin), USNM 152491, 38 (18.5–29.1 mm), D. S. Jordan, 1922.

Iwate Pref., Ichinoseki, CAS-SU 20123, 1 (26.5 mm), D. S. Jordan & J. O. Snyder.

Fukui Pref: Lake Ichinoseki, Mikato-cho, Mikatagun, CAS 56259, 2 (21.7–30.0 mm), 20.iv.1978.

Nagano Pref., Suwa, CAS 58024, 77 (16.5–22.6 mm), W. Magtoon & H. Uwa, 9.viii.1985.

Ibaraki Pref., Lake Kasumigaura, USNM 152514, 7 (19.5–27 mm), K. Hattori, 1922.

Shiga Pref., Lake Biwa Aquarium, Ohtsu City, CAS 57464, 7 (juveniles, 5 of which have been cleared and counterstained, 1 of which was removed for histological preparation), pres. 1.x.1985, CAS 57465, 8 (2.5–8.5 mm).

Kyoto Pref., Isazu R., Maizuru City, CAS 56258, 1 (28.5 mm), 15.vii.1974.

Miyagi Pref., Shiuhara (= Shiogama?) CAS-SU 23865, 2 (19.0–28.0 mm, both specimens dehydrated), FMNH 55559, 6 (21–27 mm), D. S. Jordan; Shiogama Rikuzen, USNM 71305, 36 (16.7–30.6 mm), J. O. Snyder & M. Smith, 1938.

Ishikawa Pref., Nanao, ricefields, USNM 71188, 20 (11.5–34.2 mm), D. S. Jordan, J. O. Snyder & M. Sindo, 20.vii.1906.

Wakayama Pref., Kii Suido, Wakanoura, CAS-SU 9866, 101 (18.8–32.5 mm; one specimen, 32.5 mm, in vial with label that reads 'drawn'), BMNH (1923.2.26: 160–169, 97 (18–34 mm), USNM 62334, 31 (19.4–29.5 mm), D.S. Jordan & J. O. Snyder, possibly 1900.

Shimane Pref., Oki Is., Saigo, USNM 71195, 48 (16.5–35.0 mm), D. S. Jordan, J. O. Snyder & M. Sindo, vii.1906.

KYUSHU IS.: Kagoshima Pref.; Kagoshimawan, CAS-SU 24663, 1 (18.5 mm), Akune, Satsuma, USNM 70779, 254 (13.5–33.5 mm, 2 of which have been cleared and counterstained), J. O. Snyder & M. Smith, 1938.

Nagasaki Pref., Iki Is., Tasou R., Ashibe-cho, CAS 56257, 4 (16.6–24.9 mm), 2.viii.1976, Kawatana, CAS-SU 20125, 77 (12.2–35.6 mm, 3 of which have been cleared and counterstained), D. S. Jordan & J. O. Snyder.

RYUKYU ISLANDS, OKINAWA IS.: Okinawa Pref., southern half of island, CAS 54866, 4 (18.3–26.1 mm), T. D. White, vii.1947, CAS-SU 23664, 5 (13.5–18.0 mm), H. Kuroiwa, Tingan, USNM 164237, 6 (13–30 mm), Hanashito, 25.ii.1954.

CHINA. Shandong (Shantung) Prov.: Jinan (Tsinan), Da Ming Hu, ANSP 51944, 6 (16.0–18.0 mm), A. P. Jacot, 1.x.1926, ANSP 51950, 1 (7.5 mm), A. P. Jacot, 21.xi.1924; North Gardens in rice and lotus fields, ANSP 51951, 2 (19.0–21.0 mm), A. P. Jacot, autumn 1927–1928 (field no. APJ27-NG-F). Jinan (Tsinan), BMNH 1928.1.16: 4–6, 5 (17–20 mm), E. Hindle.

Beijing Prov., Xinan, USNM 337323, 20 (17–25 mm), ex. ASIZB 44193; Huairou, Huairou Reservoir, boat launch at observatory, USNM 337325, 1 (24.2 mm), L. R. Parenti & C.-G. Zhang, 24.iii.1995.

Gansu Prov., upper Huang He (Yellow R.), ASIZB 52348, 6.

Hebei Prov., outside Beijing: Yenching University, USNM 89214, 5 (12.3–15 mm, distorted), Y. Ching, 1.vii.1928, AMNH 14469, 3 (23.3–26.5 mm), Reinke, viii.1927.

Shanxi Prov., lower Huang He (Yellow R.), ASIZB 42666, 7.

Guangxi (Kwangsi) Autonomous Region, Wo Chow, CAS-SU 30247, 56 (12.5–25.0 mm), A. W. Herre, 14.ii.1934.

Zhejiang (Chekieng) Prov., Zhoushan (Choushan) Is., CAS-SU 32587, 84 (13.5–23.7 mm), CAS-SU 68377, 1 (15.9 mm), A. W. Herre, 2.x.1936.

Fujian (Fukien) Prov., Gangken, CAS-SU 39569, 1 (25 mm), J. L. Gressitt, 25.vii.1936. Among (Gi-Mei), USNM 336717, 2 (25.5–27 mm), 9.ix.1963. SFU uncat, 5 (20–27 mm), 9.vii.1963.

SOUTH KOREA. Busan (Fusan), USNM 45266, 37 (24–33 mm), P. Jouy, 28 May 1886, Masan, small rocky creek 1.25 mi S of Masan, USNM 163873, 3 (29–31 mm), R. MacEwan, 4.vii.1951, near Chayo (35°17'08"N, 128°42'54"W), USNM 162685, 6 (18–26 mm), V. G. Springer, 11.iv.1952; Kyongsangnam-do: Ulsan-shi, Song'am-dong, Ch'ongniang R., eastern Korean drainage emptying into Sea of Japan, CAS 60708, 15 (25.9–28.9 mm), S.-R. Jeon, 29.xi.1986, laboratory specimens fixed 7.vii.1987.

TAIWAN. Kizanto: ANSP 76433, 28 (20–30.5 mm), M. Oshima, 9.iv.1917 (field no. MO17-K-4-9), CAS-SU 23166, 9 (24.4–31.5 mm), M. Oshima; Taiko, CAS-SU 23115, 5 (12.2–21 mm), M. Oshima.

LAOS. Nam Theun watershed: ricepaddy near Tha Bac, CAS 92323, 125 (14.6–29.6 mm, 9 of which, 16.0–24.3 mm, have been cleared and stained solely with alizarin), T. R. Roberts & P. Vongsay, 20.xi.1995; roadside ditches and paddy on road from Laksao to Tha Bac, CAS 92324, 2 (27.7–31.3 mm), T. R. Roberts, 8–17 Jun 1995.



**Figure 38.** *Oryzias bonneorum* sp. nov., holotype, Lake Lindu, Sulawesi Tengah, Indonesia, male, MZB 15499, male, 52 mm SL.

### **ORYZIAS BONNEORUM SP. NOV.**

#### BONNES' BUNTINGI

FIGURES 5A, 7A, 8B, 11B, 23B, 24E, 26D, 28B, 38  
*Xenopocilus sarasinorum*.- Rosen, 1964: 222–263 [in part, comparative anatomy, relationships, classification].- Rosen & Parenti, 1981: 10 [in part, characters].- Parenti, 1987: 561 [in part, characters, comparisons].- ?Kottelat *et al.*, 1993: pl. 44 [photo of adult male].

*Differential diagnosis:* *Oryzias bonneorum* is readily distinguished from *O. sarasinorum*, the other Lake Lindu endemic, by its relatively deeper body (17–20% SL as opposed to a relatively slender 13–5% SL), male pigment pattern with up to nine brownish vertical bars on the side of the body (as opposed to a silvery lateral band), 36–39 scales in a lateral series (as opposed to 70–75), and 31–32 vertebrae (as opposed to 34).

*Description:* Data for the holotype and three paratypes are summarized in Table 6. Elongate, maximum size of specimens examined 52 mm SL (male holotype). Body laterally compressed; body depth 17–20 [19]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, upper and lower jaws slightly elongate; lower jaw extends beyond upper jaw. Dorsal and ventral body profile somewhat convex from head to dorsal- and anal-fin origins. Head length 31–32 [31]; snout length 7–9 [9]; eye moderate 9–10 [10] orbits do not project beyond dorsal surface of head. Fleshy, incompletely scaly, basal portion of dorsal and anal fin project slightly beyond primary body profile. Scales large, cycloid and relatively deciduous; 36–39 [38] in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray not connected to body via a membrane. Caudal fin slightly lunate, dorsal and ventral segmented caudal-fin rays longer than middle rays. Urogenital papilla single-lobed in

females. Males with subconical tubular urogenital papilla, everted in some preserved specimens.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two to three irregular rows of caniniform teeth; enlarged, caniniform teeth posteriorly on the premaxilla and dentary of males. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; lateral process of pelvic bone attaches to fifth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. Fifth ceratobranchial toothplates subtriangular, with pavement dentition anteriorly, followed by five to six discrete rows of unicuspid teeth; small, incomplete posterior row in males. Basihyal bone triangular, basihyal cartilage elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 12–13 [13]. Anal-fin rays 19–20 [20]. Pelvic-fin rays 6. Pectoral-fin rays 11–12 [11]. Principal caudal-fin rays i,5/6,i. Procurrent fin-rays, dorsal 4–5 [5], ventral 5–6 [6]. Vertebrae 31–32 [32] (12–13 + 19). Branchiostegal rays 5–6 [5].

*Cytogenetic data:* Unknown.

*Colour in life:* Unknown.

*Colour in alcohol:* Ground colour brownish overall. Up to nine faded vertical brownish bands in the three adult males. Fins hyaline to dusky.

*Distribution and habitat:* Endemic to Lake Lindu, Sulawesi Tengah (Parenti & Soeroto, 2004: fig. 1), and probably a pelagic species like its congener, *O. sarasinorum*.

*Remarks:* Characters of this species have probably been described in the literature as those of *Xenopocilus sarasinorum* Popta, 1905, classified herein as *Oryzias sarasinorum*, the only other ricefish known from Lake Lindu. This species may have internal fertilization and therefore is also possibly live-bearing. Additional specimens, including fresh material, are required to understand better the reproductive biology of *O. bonneorum*. Scale pockets were counted to estimate number of scales in a lateral series in all specimens counted; numbers are relatively accurate, but not precise. Nonetheless, they are

**Table 6.** Morphometric and meristic data for holotype (MZB 15499) and three paratypes (ZMA 123.863) of *Oryzias bonneorum* sp. nov.

Character	Holotype	Paratypes (N = 3)	Mean
Dorsal-fin rays	13	12–13	12.5
Anal-fin rays	20	19–20	19.5
Pelvic-fin rays	6	6	6
Pectoral-fin rays	11	11–12	11.25
Principal caudal-fin rays	i,5/6,i (est.)	i,5/6,i	i,5/6,i
Procurrent fin rays	5/6	4–5/5–6	4.75/5.75
Vertebrae	32 (13 + 19)	32(13 + 19)	32(13 + 19)
Branchiostegal rays	5	5–6	5.5
Scales in lateral series	38	36–39	37.5
Head length	31	31–32	31.25
Snout length	9	7–8	8
Eye diameter	10	9–10	9.5
Body depth	19	17–20	19
Predorsal length	72	76–78	75.75
Preanal length	65	64–65	65
Dorsal-fin base	14	11–13	12.5
Anal-fin base	20	21–23	21
Caudal peduncle depth	10	9–10	9.75
Standard length (mm)	52	38.5–45	44

sufficient to separate this species from *O. sarasinorum*, the other Lake Lindu endemic.

**Etymology:** The trivial name *bonneorum* to honour C. Bonne and J. Bonne-Wepster, systematic entomologists who worked throughout Indonesia in the early 20<sup>th</sup> century and collected fish to determine if they were eating mosquito larvae.

**Material examined:** Six specimens (38.5–52 mm SL). Holotype. INDONESIA. Sulawesi Tengah: Lake Lindu, C. Bonne, iv.1939, MZB 15499, male, 52 mm SL. Paratypes. INDONESIA. Sulawesi Tengah: Lake Lindu, ZMA 123.863, 5, (38.5–45 mm, of which a male, 41 mm and a female, 40 mm, have been cleared and counterstained), collected with the holotype.

*ORYZIAS CARNATICUS* (JERDON, 1849)

SPOTTED RICEFISH

FIGURES 25B, 39

*Aplocheilus carnaticus* Jerdon, 1849: 331 [type locality: India: Carnatic: river that passes by Waniambaddy (= Vaniyambadi); no drawings or type specimens].

?*Panchax cyanophthalma* Blyth, 1858: 288 [type locality: India: Calcutta fish bazars; no figures or type specimens].



**Figure 39.** *Oryzias carnaticus* (Jerdon, 1849), Trincomalee, Sri Lanka, AMNH 20650, male, 26.5 mm SL.

?*Panchax argenteus* Day, 1868: 706 [type locality: India: Madras].- Whitehead & Talwar, 1976: species 174 in unnumbered table [list, notice of possible type specimens in Calcutta and London].- Ferraris, McGrouther & Parkinson, 2000: 294 [report of syntype catalogued as AMS B.7492, but not found]. ?*Haplochilus argenteus*.- Day, 1873: cclxxvi [characters; Madras].

*Oryzias melastigma*.- Smith, 1938: 165–166 [classification].- Herre, 1939: 328, 331 [listed, distribution in Andaman Is., material].- Herre, 1941: 342 [listed as an accidentally introduced species in Andaman Is.].- Hubbs, 1941: 446 [comparison with *Horaichthys setnai* Kulkarni, 1940].- Ramaswami, 1946: 181–192 [osteological comparisons of skull with cyprinodontiform].- Kulkarni, 1948: 65–119 [comparative anatomy, osteology].- Rosen, 1964: 227 [classification in family Oryziatidae].- Schrey, 1978: 335–338 [photograph, taxonomy of *Oryzias*].- Uwa, Iwamatsu

& Saxena, 1983: 43–47 [karyotype and cellular DNA content].- Sakaizumi, 1985: 521–522 [electrophoretic comparisons].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Rahman, 1989: 63 [listed from Bangladesh].- Pethiyagoda, 1991: 177–179 [distribution throughout Sri Lanka; photographs].- Talwar & Jhingran, 1991: 745–746 [characters and distribution, India, accidental introduction in Andaman Is.].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Seegers, 1997: 15, 20, 21 [listed, photographs].- Menon, 1999: 266 [listed from India].  
*Oryzias carnaticus*.- Labhart, 1978: 53–54 [characters].- Schrey, 1978: 335 [taxonomy of *Oryzias*].- Roberts, 1998: 217–218 [synonymy, characters, distribution].

*Differential diagnosis:* *Oryzias carnaticus* is a small *Oryzias*, in a group including *O. dancena*, *O. haugiangensis* and *O. javanicus* that share closed rather than open lacrimal sensory canals (as does *O. hubbsi*) and a pelvic bone with a lateral strut that is needle-like and elongate, rather than blunt. *Oryzias carnaticus*, *O. hubbsi*, *O. haugiangensis* and *O. javanicus* have an enlarged, bilobed urogenital papilla in females. *Oryzias carnaticus* is like *O. javanicus* in having enlarged teeth posteriorly on the premaxilla of both sexes and a relatively posterior dorsal fin, and is distinct from *O. javanicus* in having an ethmoid cartilage anterior margin irregular and indented anteromedially, as opposed to straight, and lacking yellowish caudal fin margins in life.

*Description:* Small, maximum size of specimens examined 32.5 mm SL. Body compressed laterally, body depth 21–28. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 24–28; snout length 6–8; eye moderate, 8–9, orbits meet dorsal surface of head. Basal portion of dorsal and anal fin project slightly beyond primary body profile. Scales relatively large, cycloid; 26–30 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays with bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin truncate. Male with short, tubular urogenital papilla; female with large, bilobed urogenital papilla.

Premaxilla short and broad with blunt ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males and females with two

to four enlarged posterior teeth on the premaxilla, males with two to four enlarged teeth on dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped, suboval; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal largely bone-enclosed and covered by epidermis. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; elongate lateral process of pelvic bone attaches to or in line with third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and one accessory cartilage. Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by four discrete rows of unicuspid teeth, no small, incomplete posterior row. Basihyal bone triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 absent.

Dorsal-fin rays 6–7. Anal-fin rays 21–24. Pelvic-fin rays 6. Pectoral-fin rays 11–13. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 4, ventral 4–6. Vertebrae 28–30 (10–11 + 18–20). Branchiostegal rays 5.

*Cytogenetic data:* Probably reported in the literature as *O. melastigma* (see cytogenetic data for *O. dancena*, below).

*Colour in life:* Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum. Tips of elongate anal and dorsal fin rays of males whitish.

*Colour in alcohol:* A diffuse, faint row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Females with a subrectangular, males with a smaller, subtriangular black peritoneum. A discrete black line along the anal-fin base. Dorsal and anal fin interradiation membranes with scattered melanophores. Specimens from Orissa State, India, with relatively dense, small, dark brown chromatophores on dorsal surface of head and body. These may form small, discrete blotches, hence the common name spotted ricefish (Seegers, 1997).

*Distribution and habitat:* Eastern India, Andaman Islands, Sri Lanka and Bangladesh in coastal brackish and freshwater habitats (herein and Roberts, 1998: 217–218).

*Remarks:* The original description of *Aplocheilus carnaticus* concludes (Jerdon, 1849: 331): 'I procured specimens of this minute fish in the river that passes by Waniambaddy in the Carnatic. It is very nearly allied in form, number of rays, etc. to *A. Melastigma* McL., but that is said not to exceed an inch in length, and, being from Calcutta, is probably distinct.' Jerdon's species was considered a synonym of *O. melastigma*, here *O. dancena*, following (Roberts, 1998), by most authors until Labhart (1978) briefly differentiated the two species, primarily on colour pattern. I treat *Aplocheilus carnaticus* Jerdon, 1849 as a distinct species following Labhart (1978) and Roberts (1998). As for *Oryzias dancena*, below, it is nearly impossible, without voucher specimens or illustrations, to determine whether citations for *O. melastigma* refer to material that would now be identified as *O. carnaticus* or *O. dancena*.

Identification and origin of the ricefish species on the Andaman Islands has been uncertain. No ricefishes were listed by Day (1871) in an early account of fishes from the Andamans. Over 70 years later in his list of fishes from the Andaman Islands, Herre (1941: 342) referred to a lot of seven specimens, now CAS-SU 37089, as *Oryzias melastigma*, and concluded that they represented 'no doubt an accidentally introduced species'. One specimen was subsequently separated from the rest of those in CAS-SU 37089 and placed in a vial along with a hand-written note that reads 'HOLOTYPE OF *Oryzias herrei* Myers (n. sp.)', a name that was never published. The handwriting matches that of the late George S. Myers, Stanford University. Localities reported by Herre (1939: 331) for the specimens he examined in part match those of the CAS-SU material, below, although Herre did not report collector or date of collection other than that the specimens were sent to him by the Zoological Survey of India. Talwar & Jhingran (1991: 746) reported that *O. melastigma* was introduced accidentally into the Andamans along with Rohu (*Labeo* spp.) fry. I examined material from the Andaman Islands, below, and conclude that it agrees well with *O. carnaticus* in having, for example, 12 pectoral-fin rays rather than 10 or 11 as in *O. dancena* and *O. javanicus*.

Meristic data and information in the species synonymy are supplemented by those in Roberts (1998). Another common name for this species is spotted medaka (Seegers, 1997: 20).

*Material examined:* 513 specimens (5–32.5 mm SL). INDIA. Port Okha: N. side of Okha Pt., USNM 246914, 10 (5–16.5 mm), ANTON BRUUN, 9.iii.1963; Orissa: freshwater streams 1–2 km inland along coast between Konark and Puri, CAS 60738, 28 (6.4–27.7 mm), T. R. Roberts, 28.ii.1985. Madras: CAS-SU 41531, 5 (12.4–26.6 mm), A. W. Herre, 4.i.1941.

Andaman Islands, South Andaman, Port Blair, creek N of South Corbyn's Cove, CAS-SU 37089, 7 (20.0–32.5 mm, one female, 26.5 mm, of which has been cleared and counterstained), H. S. Rao, 15.ii.1935. South Andaman, no specified locality, CAS-SU 37088, 19 (9.5–28.5 mm), H. S. Rao, 1 Dec 1934. North Andaman, from a shallow stream near base camp, CAS-SU 35658, 2 (18.8–20 mm).

SRI LANKA. Trincomalee, estuaries 1.5 mi. NW of Mahaweli R., western mouth, western side of road, USNM 313915, 120 (7.2–26.4 mm), C. C. Koenig, 9.iv.1970; Akurala, SW coast, flooded pits under tidal influence, AMNH 20650, 59 (11.8–26.5 mm, 5 of which have been cleared and stained solely with alizarin, 6 of which have been cleared and counterstained, and 1 male of which has been triple stained), R. Jonklaas, 21.iv.1965.

BANGLADESH. Ganges Basin: Sundarbans: Karamjol Creek, large, strongly tidal creek about 5.5 km down Passur R. from Mongla, CAS 92307, 234 (11.6–25.0 mm, 12 of which have been cleared and stained, 4 of which have been cleared and counterstained), T. R. Roberts, 21.v.1996; large, strongly tidal creek on right side of Passur R. about 15–20 km downstream from Mongla, CAS 92308, 25 (18.7–26.7 mm), T. R. Roberts, 22.v.1996; first large tidal stream on road from Cox Bazar to Tek Naf, CAS 92616, 4 (9.2–12.5 mm), T. R. Roberts & M. N. Sarker, 5 Jun 1996.

#### ORYZIAS CELEBENSIS (WEBER, 1894)

##### CELEBES RICEFISH

##### FIGURES 14, 26C

*Haplochilus celebensis* Weber, 1894: 426 [type locality: Indonesia: Sulawesi, Makassar [Ujung Pandang] and Maros R. near Maros].- Boulenger, 1897: 429 [listed from Macassar (= Ujung Pandang), southern Celebes (Sulawesi)].- Nijssen *et al.*, 1982: 70 [ZMA type specimens].

*Aplocheilus celebensis*.- Weber & de Beaufort, 1912: XX [recorded from Timor].- Weber & de Beaufort, 1922: 373 [synonymy; characters].- Aurich, 1935: 102–104 [comparisons; report from Lake Sidenreng; key].

*Oryzias celebensis*.- Rosen, 1964: 227 [classification in family Oryziatidae].- Schrey, 1978: 335 [taxonomy of *Oryzias*].- Uwa, Iwamatsu & Ojima, 1981: 95–99



[karyotype and banding analyses].- Hamaguchi, 1983: 553–561 [asymmetrical development of gonads].- Iwamatsu *et al.*, 1984b: 653–663 [hybridization with *O. latipes*, characters].- Sakaizumi, 1985: 521–522 [electrophoretic comparisons].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Whitten *et al.*, 1987a: 295, table 4.10 [Sulawesi, distribution].- Whitten *et al.*, 1987b: 43–48, table 1 [Sulawesi, conservation].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Kottelat, 1990c: 735–736, fig. 9 [report from south-western arm of Sulawesi].- Kottelat *et al.*, 1993: 89 [listed; characters].- Soeroto & Tungka, 1996: 1–5 [distribution, habitat].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Seegers, 1997: 15, 19 [listed, photograph].- Albert *et al.*, 1999: 650 [brain weight]. Parenti, 2000a: 2150 [listed].- Larson & Pidgeon, 2004: 196, 198 [listed from East Timor].

*Differential diagnosis:* *Oryzias celebensis* and *Oryzias timorensis* are both relatively small ricefishes, reaching not more than 35 mm SL, with truncate caudal fins and a colour pattern characterized by dark brown to black vertical bars on the sides of the body, as in the larger-bodied Malili lakes buntingi. *Oryzias celebensis* differs from *O. timorensis* in having a relatively posterior dorsal-fin origin, opposite vertebra 22–23 (vs. 21), a deeper body (body depth 22–26 vs. 21–24% SL), and a dorsal body profile that is relatively straight from head to dorsal-fin origin (as opposed to arching gently).

*Description:* Small, maximum size of specimens examined 35 mm SL. Body compressed laterally, body depth 22–26 [26]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 24–26 [25]; snout length 5–9 [7]; eye moderate, 7–8 [7], orbits do not project beyond dorsal surface of head. Single-lobed testis on right side of body of males. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales relatively large, cycloid; 29–33 [30] in a lateral series. Elongate, slightly filamentous dorsal- and anal-fin rays in males, the fourth dorsal-fin ray the longest; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half in males, along its entire length in females. Caudal fin truncate. Male with a short, slightly conical, tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with caniniform teeth in irregular rows; males with two or three enlarged posterior teeth on the premaxilla and dentary and fleshy lips through which the tooth tips project. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fourth pleural rib or lies between third and fourth pleural rib. Caudal skeleton with two epural bones; one or two ventral accessory bones (in specimens with only one, the element appears to be composed of two accessory bones united). Fifth ceratobranchial toothplate suboval, with teeth in irregular rows anteriorly, followed by eight discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone triangular, basihyal cartilage extremely long, broad and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 8–10 [8]. Anal-fin rays 17–23 [20]. Pelvic-fin rays 6. Pectoral-fin rays 10–11 [11]. Principal caudal-fin rays i,4–5/5,i [i,4/5,i]. Procurent fin-rays, dorsal 4, ventral 5–7 [5]. Vertebrae 30–31 (11–12 + 18–20)[30 (11 + 19)]. Branchiostegal rays 5–6 [5].

*Cytogenetic data:* *Oryzias celebensis* is a species with a fused chromosome constitution (*sensu* Uwa, 1986, 1991a, b; Table 2). *Oryzias celebensis* has 36 diploid chromosomes, including eight metacentrics, four submetacentrics and 24 or 26 acrocentrics. The four metacentric pairs are extremely large and hypothesized to have been formed by centric fusion. Chromosome arm number totals 48.

*Colour in life:* Body nearly transparent dorsal to midline and posterior to silvery peritoneum, subrectangular in females, subtriangular in males, and both sexes with a silvery opercular region. Caudal fin with yellow–orange dorsal and ventral submarginal band.

*Colour in alcohol:* Type specimens nearly all faded to a uniform light straw colour, except for silver peritoneum. Ground colour pale straw. Females with a subrectangular, males with a smaller, subtriangular black peritoneum. A discrete row of melanophores from the dorsal surface of the head to the dorsal-fin

origin, a diffuse, faint midlateral black line on the body from the posterior extent of the head to the caudal fin, distinctly darker from midbody to base of the caudal fin and onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Diffuse light to dark brown bars extend dorsal and ventral to the midline, especially in mature males. In some specimens (e.g. CAS 58034), medial dorsal-fin rays are jet black and there is a jet black blotch on the base of the caudal peduncle. A faint black line along the anal-fin base. Interradial membranes of all fins with scattered melanophores.

*Distribution and habitat:* Lives in the south-western arm of Sulawesi (Parenti & Soeroto, 2004: fig. 1) in Lake Tempe and inland and coastal rivers and streams (see Soeroto & Tungka, 1996), and River Mota Talau area, East Timor (Weber & de Beaufort, 1912; Larson & Pidgeon, 2004).

*Remarks:* The original description concludes (p. 426): 'Grösste Länge 3.8 cm (mit gerechnet)' [Greatest length 3.8 cm (caudal fin included)]. The largest specimen in ZMA 112.585, a female approximately 38 mm TL, 29.5 mm SL, is herein designated the lectotype of *Haplochilus celebensis*. Remaining specimens in that lot, now ZMA 123.748 and ZMA 100.567, the other syntype lot (Nijssen *et al.*, 1982: 70), are now paralectotypes. Morphometric and meristic data are supplemented by those in Aurich (1935) and Uwa & Parenti (1988). Data for the lectotype are given in brackets, above. Another common name for this species is the Celebes medaka (Seegers, 1997: 19).

*Material examined:* 344 specimens (8.2–35 mm SL). Lectotype of *Haplochilus celebensis*. INDONESIA. Sulawesi: Makassar [Ujung Pandang], Maros R. near Maros, ZMA 112.585, 1, (female, 28.5 mm), designated herein.

Paralectotypes of *Haplochilus celebensis*. Sulawesi: Makassar [Ujung Pandang], Maros R. near Maros, ZMA 123.748 (formerly ZMA 112.585), 18 (15–28 mm); Sawah, ZMA 100.567, 26 (16.0–28.2 mm), M. Weber, 1888.

Non-type specimens. INDONESIA. Sulawesi Selatan: road from Ujung Pandang to Malino, Sungai Jeneberang at Desa Lanna, Kecamatan Parangloe, Kab. Gowa, ZSM/LIPI 19, 11 (22.4–31.5 mm), M. Kottelat, 9.vi.1988; Ujung Pandang, BMNH 1912.12.30: 8–9, 2(28.5–32 mm), CAS 58034, 40 (26.0–29.0 mm, 4 of which have been cleared and counterstained), K. Hirota & T. Iwamatsu, ii.1979, maintained as a laboratory stock and preserved 29.xi.1985 by H. Uwa; Pangkep, Minasatene, Panaekang (Area Longron): USNM 340423, 2 (19.2–



**Figure 40.** *Oryzias curvinotus* (Nichols & Pope, 1927), Hainan Island, China, AMNH 14766, paratype, male, 19.5 mm SL.

21.8 mm) K. Louie & T. Amos, 24.vii.1995; Gowa, Limbung, approx. 5 km SE of road from Ujung Pandang to Patalasang, USNM 340424, 20 (15.5–25.8 mm, 2 of which have been cleared and counterstained), L. R. Parenti, K. D. Louie & T. Amos, 3.viii.1995. Maros, Tanralili, approx. 12 km SE of turnoff at Batanahse on road from Ujung Pandang to Maros; Carangki village, USNM 340421, 217 (9.4–24.5 mm), L.R. Parenti, K. D. Louie & T. Amos, 5.viii.1995; Maros, Tanralili, approx. 15 km SE of turnoff at Batanahse on road from Ujung Pandang to Maros; at Maros dam, USNM 340427, 12 (8.2–28.1 mm), L. R. Parenti, K. D. Louie & T. Amos, 5.viii.1995. Aquarium specimens: USNM 316513, 5 (30–35 mm, cleared and counterstained).

*ORYZIAS CURVINOTUS* (NICHOLS & POPE, 1927)

HAINAN MEDAKA

FIGURE 40

*Oryzias latipes*.- Oshima, 1926: 19 [Hainan Is., China].- Harada, 1943 [Hainan Is., China].  
*Aplocheilus curvinotus* Nichols & Pope, 1927: 380, fig. 43 [type locality: China: Nodda, Hainan Is.; tentative classification in *Oryzias* as subgenus *Aplocheilus*].- Nichols, 1943: 234–235 [in subgenus *Oryzias*; synonymy; China].  
*Oryzias curvinotus*.- Rosen, 1964: 227 [classification in family Oryziatidae].- Uwa, Tanaka & Formacion, 1982: 15–17 [karyotype and banding analyses of species probably not *O. curvinotus*; see Uwa, 1991a].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons, distribution].- Uwa, 1991a: 361–367 [characters and comparisons].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Parenti, 2000b: 600 [listed].- Matsuda *et al.*, 2003: 159–161 [genetics of sex determination and comparison with *O. latipes*].  
*Oryzias cf. curvinotus*.- Kottelat, 2001a: 10, 56, fig. 118 [report from Quang Ninh Prov., Vietnam; characters].

*Differential diagnosis:* *Oryzias curvinotus* is a member of the biarmed chromosome group of Uwa (1986), along with *O. luzonensis*, *O. latipes* and

the miniatures *O. sinensis* and *O. mekongensis*, distinguished from other ricefishes by having anal-fin rays of approximately the same length, forming a 'parallelogram-shaped' fin (as opposed to a subtriangular-shaped fin that tapers posteriorly), and chromosome arms numbering 58 or more (as opposed to 48 or fewer). *Oryzias curvinotus* is distinguished from these species by lacking bony processes on the pectoral-fin rays. It is like most specimens of *O. latipes* and *O. luzonensis* in having the first pleural rib on the third, rather than the second vertebra and paired, bilaterally asymmetric, as opposed to single lobed, testes, and like *O. sinensis* in having the pelvic fins in line with the third, rather than the fourth pleural rib.

*Description:* Small, maximum size of specimens examined 27.2 mm SL. Body compressed laterally, body depth 18–23 (specimens dehydrated). No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 21–26; snout length 5–8; eye moderate, 8–9, orbits meet dorsal surface of head. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales relatively large, cycloid; 27–28 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; posterior anal-fin rays with bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin truncate. Male with a short, tubular urogenital papilla; female with small, bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two or three enlarged posterior teeth on the premaxilla and dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage straight. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone, one accessory cartilage. Fifth ceratobranchial toothplates subtriangular, with teeth

in irregular rows anteriorly, followed by six discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 5–6. Anal-fin rays 17–20. Pelvic-fin rays 6. Pectoral-fin rays 10–11. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 4, ventral 4–5. Vertebrae 28–30 (11–12 + 17–18). Branchiostegal rays 4–5.

*Cytogenetic data:* *Oryzias curvinotus* has a biarmed chromosome constitution (See Uwa, 1991a; Table 2). Populations show marked variation in karyology and it is likely that further, detailed analysis will result in the recognition of additional taxa. *Oryzias curvinotus* specimens from Hong Kong were reported to have  $2n = 48$  chromosomes, with four metacentric, 13 submetacentric, five subtelocentric and two acrocentric pairs, and arm number (NF) of 82. Cellular DNA content was estimated at 1.5 pg per nucleus. Specimens from Hainan Island also have  $2n = 48$  chromosomes, but differ by having one metacentric, seven submetacentric, 16 subtelocentric and one acrocentric pairs, with an arm number of 64. Karyotype data and banding analyses of specimens identified as *O. curvinotus* were published by Uwa *et al.* (1982: 15–17). According to Uwa (1991a: 366), those specimens represent an undescribed species intermediate between *O. mekongensis* and *O. latipes* based on inferred chromosomal rearrangements.

*Colour in life:* Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum. Caudal fin with yellowish dorsal and ventral submarginal band.

*Colour in alcohol:* A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Females with a subrectangular, males with a smaller, subtriangular black peritoneum. A faint black line along the anal-fin base. Dorsal-, anal- and pelvic-fin interradiation membranes with scattered melanophores.

*Distribution and habitat:* Widely distributed throughout southern China, including Hainan, Guangdong and Hong Kong, and Vietnam in coastal brackish to freshwater habitats (Uwa & Parenti, 1988; Kottelat, 2001a).

*Remarks:* Morphometric and meristic data are supplemented by those in Uwa & Parenti (1988). Another common name for this species is Hainan ricefish.

*Material examined:* 69 specimens (13.1–27.2 mm SL). Holotype. CHINA. Hainan Is.: Nodda: AMNH 8398 (male, 23 mm), Third Asiatic Expedition, C. H. Pope, xi.1922–viii.1923.

Paratypes. CHINA. Hainan Is.: Nodda: AMNH 14766, 6 (17.5–19.5), Third Asiatic Expedition, C. H. Pope, xi.1922–viii.1923.

Non-type specimens. CHINA. Hainan Is.: Nodda: AMNH 10493, 34 (13.1–20 mm, 2 of which have been cleared and counterstained, 5 of which have been cleared and stained solely with alizarin), Third Asiatic Expedition, C. H. Pope, xi.1922–viii.1923. Hong Kong: Fan Ling, CAS-SU 61181, 8 (20–24.5 mm), R. L. Bolin, 1954, CAS 40759, 4 (21–24 mm), Hong Kong Survey, 19.iii.1954. Guangdong Prov., Guangzhou (Canton), Lingnan Univ., CAS-SU 30248, 3 (19.1–25.1 mm), A. W. Herre, 14.ii.1934; Taiping, CAS-SU 28185, 10 (14.6–23.5 mm), A. W. Herre, 25.ix.1931, CAS-SU 39658, 3 (21.2–27.2 mm), J. L. Gressitt, 14.vii.1936.

*ORYZIAS DANCENA* (HAMILTON, 1822)

DEEP-BODIED RICEFISH

FIGURES 1, 24F

*Cyprinus dancena* Hamilton, 1822: 342, 393 [type locality ‘estuary below Calcutta;’ no type specimens, description based on unpublished drawing].

nec *Aplocheilus melastigmus* McClelland, 1839: 301, 427, pl. 42, fig. 3a, b [type locality: India: ‘tanks in Calcutta’].

*Aplocheilus maclellandi* Bleeker, 1854: 323 [based on McClelland, 1839, pl. 55, fig. 4, as Hamilton’s lost figures of *Cyprinus dancena*, following Roberts, 1998].

?*Panchax cynaophthalma* Blyth, 1858: 288 [type locality: India: Calcutta fish bazars; no figures or type specimens].

*Aplocheilus MacClellandi* Bleeker, 1860: 491.

?*Panchax argenteus* Day, 1868: 706 [type locality: India: Madras].- Whitehead & Talwar, 1976: species 174 in unnumbered table [list, notice of possible type specimens in Calcutta and London].- Ferraris *et al.*, 2000: 294 [report of syntype catalogued as AMS B.7492, but not found].

?*Haplocheilus argenteus*.- Day, 1873: cclxxvi [characters; Madras].

*Haplocheilus melastigmus*.- Day, 1873: cclxxvi [characters; Calcutta and Myanmar (formerly Burma)].

*Haplocheilus melastigma*.- Duncker, 1912: 249, 257–258 [report from Sri Lanka].

*Oryzias melastigma*.- Smith, 1938: 165–166 [classification].- Hubbs, 1941: 446 [comparison with *Horaichthys setnai* Kulkarni, 1940].- Ramaswami, 1946: 181–192 [osteological comparisons of skull with cyprinodontiforms].- Kulkarni, 1948: 65–119 [comparative anatomy, osteology].- Rosen, 1964: 227 [classification in family Oryziatidae].- Schrey, 1978: 335–338 [photograph, taxonomy of *Oryzias*].- Uwa *et al.*, 1983: 43–47 [karyotype and cellular DNA content].- Sakaizumi, 1985: 521–522 [electrophoretic comparisons].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Rahman, 1989: 63 [listed from Bangladesh].- Pethiyagoda, 1991: 177–179 [distribution throughout Sri Lanka; photographs].- Talwar & Jhingran, 1991: 745–746 [characters and distribution, India].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Seegers, 1997: 15, 20, 21 [listed, photographs].- Menon, 1999: 266 [listed from India]. *Panchax melastigma*.- Munro, 1955: 85 [Sri Lanka, characters].

*Oryzias melanostigma*.- Jayaram, 1981: 296 [India, Bangladesh].

*Oryzias dancena*.- Roberts, 1998: 214–217, fig. 1 [new combination, synonymy, characters, distribution].- Albert *et al.*, 1999: 650 [brain weight].- Parenti, 2000a: 2150 [listed].- Parenti, 2005: 24 [photograph]. *Panchax cyanophthalmus*.- Menon, 1999: 266 [as a synonym of *Oryzias melastigma* (McClelland, 1839)].

*Differential diagnosis:* *Oryzias dancena* is a small *Oryzias*, in a group including *O. carnaticus*, *O. haugiensis* and *O. javanicus* that share closed, rather than open lacrimal sensory canals (as does *O. hubbsi*) and a pelvic bone with a lateral strut that is needle-like and elongate, rather than blunt. *Oryzias dancena* is one of the most deep-bodied ricefishes, with body depth reaching 34% SL, vs. no more than 28% SL in other species in this group. In addition, *O. dancena* females have relatively moderate-sized, not greatly enlarged, bilobed urogenital papilla.

*Description:* Small, maximum size of specimens examined 30.7 mm SL. Body compressed laterally, deep bodied, body depth 24–34. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile convex from head to anal-fin origin, particularly in larger specimens. Dorsal surface of head slightly convex just anterior to orbits. Head length 23–27; snout length 5–7; eye moderate, 7–8, orbits meet dorsal surface of head. Single-lobed testis on right side of body of males. Basal portion of dorsal

and anal fin do not project significantly beyond primary body profile. Scales relatively large, cycloid; 25–28 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays with bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin truncate to slightly rounded. Male with a short, tubular urogenital papilla; female with moderate, slightly bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two or three enlarged posterior teeth on the premaxilla and dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal largely bone-enclosed and covered by epidermis. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and one accessory cartilage. Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by six discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 6–8. Anal-fin rays 19–24. Pelvic-fin rays 6. Pectoral-fin rays 10–11. Principal caudal-fin rays i, 4–5/5, i. Procurrent fin-rays, dorsal 4, ventral 5. Vertebrae 28–29 (10–11 + 17–18). Branchiostegal rays 4–5.

*Cytogenetic data:* *Oryzias dancena* has a monoarmed chromosome constitution (Uwa, 1986, 1991b) and is characterized by having a diploid chromosome number of 48, comprising 24 acrocentric pairs, and a chromosome arm number of 48 (Table 2). Genome size is recorded as 1.8 pg DNA per nucleus.

*Colour in life:* Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum.

*Colour in alcohol:* A discrete row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Females with a subrectangular, males with a smaller, subtriangular black peritoneum. A faint black line along the anal-fin base. Dorsal and anal fin interradiation membranes with scattered melanophores.

*Distribution and habitat:* India, Sri Lanka, Bangladesh and Myanmar in coastal brackish and freshwater habitats. *Oryzias melastigma* (probably *O. dancena*) was reported from Pakistan by Yamamoto (1975) who did not cite any material. I know of no *Oryzias* specimens from Pakistan; Mirza (1975, 1990) did not include that genus in his lists of freshwater fishes of Pakistan.

*Remarks:* The first scientific description of a ricefish, identified as a minnow, family Cyprinidae, was not recognized until Roberts's (1998: 214–217) investigation. McClelland's (1839) type specimens of *Aplocheilichthys melastigmus* are apparently lost (Uwa & Parenti, 1988). As for *Oryzias carnaticus*, above, it is nearly impossible, without voucher specimens or illustrations, to determine whether citations for *O. melastigma* refer to material that would now be identified as *O. dancena* or *O. carnaticus*. Meristic data and information in the synonymy are supplemented by that in Roberts (1998).

*Material examined:* 457 specimens (8.7–30.7 mm SL). INDIA. Chindambaram: CAS 60740, 4 (21.6–23.0 mm), laboratory stock, O. P. Saxena, x.1981; CAS 58028, 71 (19.2–26.0 mm, 5 of which have been cleared and counterstained), O. P. Saxena & T. Iwamatsu, x.1981; Madras, CAS-SU 30562, 11 (19.5–25.7 mm), Madras Fisheries Dept., 4.iv.1934; Ganges Delta, ZMA 100.549, 20 (11.4–22.9 mm), L. F. de Beaufort, 6.i.1938; Ganges Delta at Uttarbhag: CAS-SU 35653, 63 (15.5–28.7 mm, 4 of which have been cleared and counterstained), A. W. Herre, iv.1937; Pulta, Bengal, CAS-SU 35654, 1 (24.5 mm), A. W. Herre, 10.iv.1937; Orissa: Gopalpur, Ganjam Dist., CAS-SU 41530, 8 (18.5–30.7 mm), H. A. Hafiz, 26.i.1941; Pondicherry: USNM 86539, 2 (26.5–26.9 mm), E. Deschamps, xi.1901; Vishakhapatnam Harbor: USNM 246915, 5 (23.9–26.3 mm), ANTON BRUUN, 13.iv.1963, USNM 246916, 78 (14.9–27.4 mm), ANTON BRUUN, 12–14.iv.1963.

SRI LANKA. Trincomalee: estuaries about 3 mi. N of Mahaweli River's mouth, W side of road, USNM 247510, 32 (13.2–29.6 mm), C. Koenig, 9.iv.1970, N end of harbor, USNM 313916, 11 (21.0–27.9 mm),



**Figure 41.** *Oryzias haugiagensis* Roberts, 1998, Bassac River, Vietnam, CAS 93898, paratype, female, 16.0 mm SL.

C. Koenig, 5.iv.1970; Jaffna area: Pasaioor village, USNM 313906, 1 (19.7 mm), T. R. Roberts, 17.iii.1970; Colombo: Kelani R. about 1/4 mile from its mouth at village at Mattakuliya near Colombo, USNM 313908, 47 (12.5–27.7 mm), T. R. Roberts, 12.iii.1970; north of Colombo, USNM 313913, 1 (20 mm), T. R. Roberts, 14.iii.1970. Vaddukkodai: Kakaithivu fish landing, about 3 mi S of Vaddukkodai, USNM 313910, 37 (13.8–24.5 mm), T. R. Roberts, 17.iii.1970; Eastern Prov: Batticaloa Dist. Just S of Kallu at S end of causeway, USNM 313912, 1 (13.9 mm), T. Iwamoto, 11.vi.1970; Nagombo Pt.: lagoon next to Pitipana fishery station, 2 mi S of Negombo Pt., USNM 313914, 3 (20.7–22.0 mm), T. Iwamoto, 6.v.1970. Munyal Lagoon: about 20 mi. S of Puttalam, USNM 313917, 17 (8.7–18.8 mm), T. R. Roberts, 14.iii.1970.

MYANMAR. Rangoon (= Yangon) Div., Rangoon (= Yangon): BMNH 1911.8.14: 18, 1 (28 mm, female), J. P. Arnold, CAS-SU 69099 (ex. SU 40208), 2 (16.5–22.8 mm), A. W. Herre, xi.1940, Insein township at fisheries lab off BPI road, USNM 342156, 39 (10–24.5 mm, of which one male 24.5 mm, and one female 23.0 mm have been cleared and counterstained), C. J. Ferraris & D. Catania, 10.iv.1996; small tidal creek off Pazundung Cr., CAS 60737, 2 (12.0–13.8 mm), T. R. Roberts, 10.iii.1985.

*ORYZIAS HAUGIANGENSIS* ROBERTS, 1998

HAU GIANG MEDAKA

FIGURES 13A, 41

?*Oryzias* sp. 'Vietnam'.- Stallknecht, 1989: 128 [report of a possibly new ricefish species from Vietnam].

*Oryzias javanicus*.- Rainboth, 1996: 171, figure (Mekong).

*Oryzias haugiagensis* Roberts, 1998: 222, fig. 2f [type locality: Vietnam: Bassac R. [Hau Giang] at Can Tho and north bank of Mekong R. below Vinh Long].- Parenti, 2000a: 2150 [listed].- Parenti, 2000b: 600 [listed].

*Differential diagnosis:* *Oryzias haugiagensis* is a miniature species (largest specimen known 20.8 mm) in a group that includes *O. carnaticus*, *O. dancena*

and *O. javanicus* that share closed, rather than open, lacrimal sensory canals (as does *O. hubbsi*) and a pelvic bone with a lateral strut that is needle-like and elongate, as opposed to blunt. *Oryzias haugiagensis* shares with *O. carnaticus*, *O. javanicus* and another miniature, *O. hubbsi*, enlarged urogenital papilla in females. The miniatures *Oryzias haugiagensis* and *O. hubbsi* both have a large head (31% or more of SL), large eye diameter (reaching 10% or more of SL), and an anterior dorsal fin (its origin anterior to vertebra 22). They differ in that the lateral strut of the pelvic bone is blunt in *O. hubbsi*. *Oryzias haugiagensis* further differs from *O. hubbsi* in having a truncate, rather than rounded, caudal fin; urogenital papillae of females not as greatly enlarged; and 10–11 (as opposed to eight to nine) pectoral-fin rays.

*Description:* Miniature, maximum size of specimens examined 20.8 mm SL. Body compressed laterally, body relatively deep, depth 27–31 [30]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile convex to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 28–33 [28]; snout length 8–10 [9]; eye large, 10–12 [11], orbits meet dorsal surface of head. Basal portion of dorsal fin projects beyond primary body profile. Scales relatively large, cycloid; 24–28 [24] in a lateral series (scale count approximate). Dorsal-fin rays elongate, anal-fin slightly rounded; anal-fin rays of some males with small, bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half. Caudal fin truncate. Male with short tubular urogenital papilla; female with relatively large, bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with a single irregular row of caniniform; males with up to four large canine teeth on lateral ramus of the premaxilla and an opposing large tooth on the dentary in some male specimens. No preethmoid cartilage; ossified portions of mesethmoid large, disc-shaped; anterior border of ethmoid cartilage straight. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in closed, bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; elongate lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one ventral accessory

bone and one accessory cartilage. Fifth ceratobranchial toothplate triangular, with teeth in irregular rows anteriorly, followed by four discrete rows of unicuspid teeth, and an incomplete posterior row. Basihyal bone elongate, triangular, basihyal cartilage elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 6–7. Anal-fin rays 19–22. Pelvic-fin rays 6. Pectoral-fin rays 10–11. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 4–5, ventral 5. Vertebrae 27–29 (10–11 + 17–19). Branchiostegal rays 5–6.

*Cytogenetic data:* Unknown.

*Colour in life:* Unknown.

*Colour in alcohol:* Ground colour pale to medium brown. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. A faint black line along the anal-fin base. Dorsal and anal fin interradial membranes with scattered melanophores. Body covered with minute melanophores.

*Distribution and habitat:* Endemic to the Mekong delta, Vietnam, in tidal habitats.

*Material examined:* 269 specimens (10.4–20.8 mm SL).

Holotype. VIETNAM. UMMZ 233088, male, 17.1 mm, Bassac R. [Hau Giang] at Can Tho, R. E. Arden & O. K. Minn, 3.xi.1974.

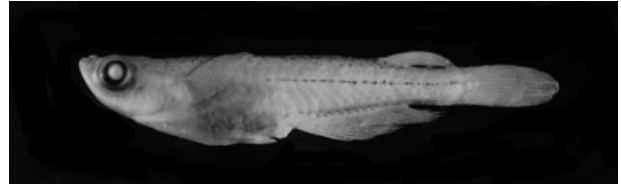
Paratypes. VIETNAM. UMMZ 218674, 223 (13–18.9 mm, 14 of which, 15.6–18.9 mm, have been cleared and stained solely for bone), CAS 93898 (ex. UMMZ 218674) 25, (2 of which have been cleared and counterstained), Bassac R. [Hau Giang] at Can Tho, R. E. Arden & O. K. Minn, 3.xi.1974; UMMZ 224693, 18 (10.4–20.8 mm), flooded sedge patch at E end of Can Tho Is. In Bassac R., 3.5 km SE of Can Tho, 19.vii.1974, M. L. Smith & R. P. Weidenbach; UMMZ 227299, 2 (14.7–18.1 mm), N bank of Mekong R. At mouth of canal 2 km below Vinh Long, 22.vi.1974, M. L. Smith, R. P. Weidenbach & Chanh.

*ORYZIAS HUBBSI* ROBERTS, 1998

HUBBS'S MEDAKA

FIGURES 13B, 42

*Oryzias javanicus.*- Uwa & Iwata, 1981: 24–26 [karyotype and cellular DNA content of wild-caught speci-



**Figure 42.** *Oryzias hubbsi* Roberts, 1998, laboratory stock of fish collected in Jakarta, Java, Indonesia, CAS 92322, paratype, male, 14.5 mm SL.

mens subsequently used as type series of *O. hubbsi* Roberts, 1998].- Uwa, 1986: 867–875 [cytogenetic comparisons].

*Oryzias hubbsi* Roberts, 1998: 222, fig. 2g [type locality: Indonesia: Java: Jakarta and near Bandung].- Parenti, 2000a: 2150 [listed].

*Differential diagnosis:* *Oryzias hubbsi* is a miniature (largest specimen known 21.3 mm) ricefish species in a group including *O. carnaticus*, *O. dancena*, *O. haugiensis* and *O. javanicus* that share closed rather than open lacrimal sensory canals. *Oryzias hubbsi* shares with another miniature, *Oryzias haugiensis*, a large head (31% or more of SL), large eye diameter (reaching 10% or more of SL), and an anterior dorsal fin (its origin anterior to vertebra 22). They differ in that the lateral strut of the pelvic bone is blunt (rather than elongate and needle-like) in *O. hubbsi*. *Oryzias hubbsi* further differs from *O. haugiensis* in having a rounded, rather than truncate, caudal fin; extremely enlarged urogenital papilla in females (the largest in ricefishes); and eight to nine (as opposed to 10–11) pectoral-fin rays.

*Description:* Miniature, maximum size of specimens examined 21.3 mm SL. Body compressed laterally, slender, body depth 19–24 [19]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile slightly convex or rounded from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 25–32 [29]; snout length 8–9 [9]; eye large, 9–10 [9], orbits meet dorsal surface of head. Basal portion of dorsal fin projects slightly beyond primary body profile. Scales relatively large, cycloid; 28–29 in a lateral series (scale count approximate). Dorsal and anal fin slightly rounded, no elongate fin rays; anal-fin rays with extremely small bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half. Caudal fin rounded, elongate. Male with short tubular

urogenital papilla; female with extremely large, bilobed urogenital papilla.

Premaxilla short and broad with no distinct ascending process; premaxilla and dentary with a single irregular row of caniniform teeth; enlarged unicuspid premaxillary and dentary tooth in males. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage straight. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal largely bone-enclosed and covered by epidermis. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone in line with third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and one accessory cartilage. Fifth ceratobranchial toothplate triangular, with teeth in four discrete rows of unicuspid teeth, the most anterior row with just two teeth, and no incomplete posterior row. Basihyal bone triangular, basihyal cartilage elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

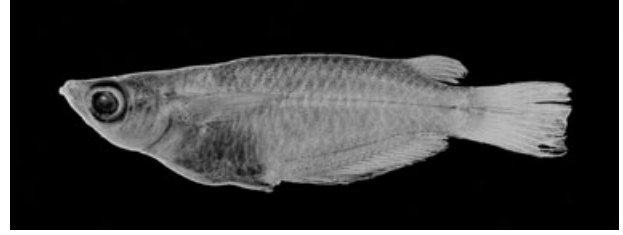
Dorsal-fin rays 5–6. Anal-fin rays 16–19. Pelvic-fin rays 6. Pectoral-fin rays 8–9. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 5, ventral 5. Vertebrae 27–28 (9–10 + 17–19). Branchiostegal rays 4–5.

*Cytogenetic data:* Laboratory stocks of *O. hubbsi*, then identified as *O. javanicus*, were reported to have  $2n = 48$ , with 23 pairs of acrocentric chromosomes, one pair of subtelocentric chromosomes and an arm number (NF) of 48 (Uwa & Iwata, 1981; Table 2).

*Colour in life:* Unknown.

*Colour in alcohol:* Ground colour pale straw. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. A faint black line along the anal-fin base. Dorsal- and anal-fin interradiation membranes with scattered melanophores. Body covered with minute melanophores in some specimens.

*Distribution and habitat:* Endemic to western Java, Indonesia, from streams in Jakarta and the low, hilly areas at elevations from about 700 to 1000 m in the vicinity of Bandung.



**Figure 43.** *Oryzias javanicus* (Bleeker, 1854), Java, Indonesia, CAS 35626, male, 28.5 mm SL.

*Material examined:* 123 specimens (10.6–21.3 mm SL). Holotype. INDONESIA. Java: Jakarta, CAS 58029, female, 17.5 mm, laboratory stock from wild-caught fish, K. Hirata & T. Iwamatsu, 1.v.1983.

Paratypes. INDONESIA. Java: CAS 92322, 6 (14.4–16.6 mm, 1 of which, 15.5 mm, has been cleared and counterstained) taken with the holotype; UMMZ 146573, 58 (10.6–21.3 mm, 8 of which, 14.3–19.6 mm, have been cleared and stained for bone), Situ Tjiburuj, near Padalarang, 20 km W of Bandung, elev. c. 700 m, C. L. Hubbs, 22.v.1929; UMMZ 146571,30 (10.9–17.9 mm), Lake Bagendit, near Garut, elev. c. 700 m, C. L. Hubbs & V. Arragon, 26.v.1929; UMMZ 198991, 12 (13.5–18.9 mm), environs of Jakarta, i.1940, Director of Batavia (= Jakarta) Museum; UMMZ 146572, 4 (13.9–18.1 mm), Tjiti = is (creek) just below road near mouth in Tjimanoeck, 3 km N of Gatur, elev. nearly 700 m, C. L. Hubbs, V. Arragon, *et al.*, 26.v.1929; UMMZ 146557, 2 (15.1–15.5), pond in Botanical Gardens, Buitenzorg (= Bogor), A. Thienemann, 29.ix.1928; UMMZ 146574, 4 (13.6–18.2 mm), trib. and ricefields to Tjikunir, Tjiwaelen system (or E fork), 2 km N of Kampong Tjikunir, 7 km W of Tasikmalaja, C. L. Hubbs, 28.v.1929; UMMZ 146567, 2 (12.7–17.0 mm), Outer Harbor Canal and connected waters about aquarium, Pase Ikan district, Batavia (= Jakarta), coll. C. L. Hubbs, 8.v.1929.

Non-type specimens. INDONESIA. Java: CAS 92327 (ex. CAS 58029), 2 specimens cleared and counterstained; Buitenzorg (= Bogor), USNM 72563, 2 (15.5–17.2 mm), Bryant & Palmer, 3.iv.1909.

#### ORYZIAS JAVANICUS (BLEEKER, 1854)

##### JAVANESE MEDAKA

##### FIGURES 19A, 26B, 43

*Aplocheilus javanicus* Bleeker, 1854: 323–324 [type locality: Indonesia: Panimbang R., Perdana, Java].-Weber & de Beaufort, 1922: 372–373 [comparisons, distribution].-Aurich, 1935: 104 [listed, key].-Smith, 1945: 425 [comparison with *Oryzias minutillus*].

*Aplocheilus maclellandi* Bleeker, 1854: 323–324 [comparisons with figure of *Aplocheilus javanicus* in McClelland, 1839].



*Haplochilus javanicus*.- Günther, 1866: 311 [classification in *Haplochilus*].

*Haplochilus javanicus* var. *trilineata* Popta, 1911: 13–14 [description of new variety from Lombok].

*Panchax javanicus*.- Fowler, 1938: 71, 254 [listed].

*Oryzias javanicus*.- Alfred, 1961: 13 [Seletar and Serangoon rivers, Singapore].- Rosen, 1964: 227 [classification in family Oryziatidae].- Alfred, 1966: 43–45 [characters, synonymy, report from Singapore].- Schrey, 1978: 335 [taxonomy of *Oryzias*].- Iwamatsu *et al.*, 1982: 190 [report from Pontianak, West Kalimantan, Indonesian Borneo].- Sakaizumi, 1985: 521–522 [electrophoretic comparisons].- Magtoon, 1986: 859–865 [distribution in Thailand, relationships, karyotype].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Hori, Phang & Lam, 1988: 1770–1772 [salinity tolerance].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Roberts, 1989: 1 [conclusion that presence in Pontianak is an introduction].- Lim & Ng, 1990: 82 [photo, characters, Singapore].- Mok & Munro, 1991: 235 [ecological observations in Singapore].- Kottelat *et al.*, 1993: 89 [listed; characters; distribution in Sundaland, Sulawesi, Lombok].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Soeroto & Tungka, 1996: 1–5 [distribution].- Seegers, 1997: 15, 19 [listed, photographs].- Roberts, 1998: 223 [characters, relationships, distribution].- Parenti, 2000a: 2150 [listed].- Parenti, 2000b: 600 [listed].- Kakuno, Fujii & Koyama, 2001: 35–37 [gonad development].- Tan & Lim, 2004: 110 [report from Natuna archipelago, Indonesia].

*Oryzias javan*.- incorrect spelling; Travers, 1981: 857 [absence of interarcual cartilage].

*Oryzias melastigmus*.- Labhart, 1978: 53 [listed in synonymy].

*Differential diagnosis:* *Oryzias javanicus* is a small *Oryzias*, in a group including *O. dancena*, *O. haugiangensis* and *O. carnaticus* that share closed rather than open lacrimal sensory canals (as does *O. hubbsi*) and a pelvic bone with a lateral strut that is needle-like and elongate, rather than blunt. *Oryzias carnaticus*, *O. hubbsi*, *O. haugiangensis* and *O. javanicus* have enlarged, bilobed urogenital papillae in females. *Oryzias javanicus* is like *O. carnaticus* in having enlarged teeth posteriorly on the premaxilla of both sexes, and is distinct in having an ethmoid cartilage anterior margin that is straight, rather than irregular and indented anteromedially, and having yellowish caudal fin margins.

*Description:* Small, maximum size of specimens examined 33.6 mm SL. Body compressed laterally, body depth 24–30. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal,

jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 23–27; snout length 6–7; eye moderate, 8–9, orbits meet dorsal surface of head. Single-lobed testis on right side of body of males. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales relatively large, cycloid; 27–30 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays with bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin truncate. Male with a short, tubular urogenital papilla; female with relatively large, bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two to five enlarged posterior teeth on the premaxilla and dentary; females with two or three enlarged posterior teeth on the premaxilla only; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage straight. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal largely bone-enclosed and covered by epidermis. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and a second accessory cartilage or bone. Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by six discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage elongate and rectangular. Epibranchial elements fully ossified; epibranchial two notably smaller than the other epibranchial elements.

Dorsal-fin rays 6–8. Anal-fin rays 18–25. Pelvic-fin rays 5–6. Pectoral-fin rays 10–13. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 4, ventral 5. Vertebrae 27–31 (10–13 + 17–18). Branchiostegal rays 5.

*Cytogenetic data:* *Oryzias javanicus* has a monoarmed chromosome constitution (Uwa, 1986, 1991b) and is characterized by having a diploid chromosome number of 48, comprising 23 acrocentric and one

subtelocentric pair, and a chromosome arm number of 48 (Table 2). Genome size is recorded as 1.7 pg DNA per nucleus.

*Colour in life:* Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum. Caudal fin with yellowish dorsal and ventral submarginal band.

*Colour in alcohol:* A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a discrete midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular black peritoneum. A discrete black line along the anal-fin base. Dorsal and anal fin interradiation membranes with scattered melanophores. Specimens from Lombok (e.g. ZMA 100.570) are uniformly faded to a pale yellow, with silvery abdomen and faint melanophores.

*Distribution and habitat:* Broadly distributed in brackish waters throughout Thailand, Peninsular Malaysia, Singapore, and Indonesia (Sumatra, Java, Borneo, Bali, Lombok, Sulawesi).

*Remarks:* Bleeker (1854: 323–324) compared his new species, *Aplocheilus javanicus*, with a species referred to as *Aplocheilus mccllellandi* Bleeker, known from a figure in McClelland (1839). Bleeker stated that *A. javanicus* was nearly identical to *A. mccllellandi*, but differed by having fewer anal-fin rays and a narrower body depth. I do not designate a lectotype from among the syntypes because I have been unable to locate the entire type series and am uncertain of the type status of some of the specimens catalogued as types. The RMNH catalogue, for example, lists RMNH 6979 as a paratype lot, whereas Eschmeyer's online database lists BMNH 1866.5.2.101 as syntypes. Morphometric and meristic data are supplemented by those in Iwamatsu *et al.* (1982) and Uwa & Parenti (1988). Another common name for this species is Javanese ricefish (Seegers, 1997: 21).

A report of *O. javanicus* from Pontianak, Kalimantan, Indonesian Borneo by Iwamatsu *et al.* (1982) was considered an introduction by Roberts (1989). This species is abundant in recent collections from south-eastern Kalimantan (D. Lumbantobing, pers. comm., 2007; material, below); I conclude that it is native to Borneo.

*Material examined:* 997 specimens (6.2–33.6 mm SL). Syntypes. INDONESIA. Panimbang R., Perdana, RMNH 6979 (7 males, 6 females), BMNH 1866.5.2.101 (male).

Non-type specimens. INDONESIA. Java: about 20 mi. SE of Surabaya, CAS-SU 68380, 11 (8.0–18.5 mm), J. P. Heath, ix.1961; Pulau Edam, 13 km N of Jakarta, semi-stagnant pool, CAS 73123, 1 (25.8 mm), CAS 35626, 8 (24.5–28.5 mm), F. B. Steiner, 8.xi.1975, CAS 35689, 4 (25.9–27.2 mm), F. B. Steiner, 20.xii.1975. Lombok: river near Labuan Tring, west coast of Lombok (8°44.5'S, 116°2.5'E), ZMA 100.570, 10 (20.5–28.0 mm), M. Weber, 19–21.iii.1899; Praya, RMNH 10518, 1 (female?, 22.5 mm), Sunda Expedition 1909–1910 (Dr. J. Elbert), 27.vi.1909. Borneo: Kalimantan Selatan: Desa Pulau Salak, Kecamatan Kintap Hilir, road to Pagatan, (03°37.114'S; 115°52.664'E), 29 m alt., USNM 391946, 53 (13–25 mm), D. Lumbantobing, D. Rudaya & A. Daely, 17.viii.2007; River on Magalau-Sungaikupang road, between Kalamian R. and Cantung R. (02°51.696'S, 116°03.959'E), 36 m alt., USNM 391947, 1 (22.5 mm), D. Lumbantobing, D. Rudaya & A. Daely, 20.viii.2007. Bali: NSMT-P 67703, 5 (9.2–23.2 mm), K. Shibukana, 3.xi.2003.

THAILAND. Phuket Is.: Nai-Han, CAS 58033, 10 (13.0–21.5 mm), N. Tawimsunnuk, H. Uwa & W. Magtoon, 2.ii.1985; Patong Bay, USNM 246908, 530 (6.2–33.6 mm), USNM 246912, 1 (28.7 mm), USNM 246913, 5 (6.1–26.5 mm), ANTON BRUUN, 22.iii.1963.

MALAYSIA. Penang, Pulau Penang, CAS-SU 32783, 2 (15.8–23.5 mm), A. W. Herre, 24.iii.1937.

SINGAPORE. CAS-SU 35670,45 (18–26 mm), A. W. Herre, 11.iii.1937, CAS-SU 31134, 18 (13.2–24.3 mm, 2 of which have been cleared and counterstained), A. W. Herre, 1934, CAS 7476, 1 (18 mm, dehydrated and faded), E. Wigham, 1934; Sg. Mandai, FMNH 47156, 3 (males, 21.5–22.5 mm), A. W. Herre, 14.iii.1934, CAS 58026, 50 (17.6–26.1 mm, 4 of which have been cleared and counterstained), G. Loy, R. Hori & H. Uwa, 12.ii.1985; Poyan R., BMNH 1970.7.22: 38–39, 68 (17–27 mm, adult female 21.8 mm carrying embryo cluster), 28.vi.1966; Sg. Buloh, just outside of nature reserve, small stream entering Straits of Johore, USNM 348513, 224 (9.4–23.9 mm, 14 of which have been cleared and counterstained), L. R. Parenti, H. K. Larson, K. Lim & N. Sivasothi, 5.ix.1997.

*ORYZIAS LUZONENSIS* (HERRE & ABLAN, 1934)

PHILIPPINE MEDAKA

FIGURE 44

*Aplocheilus luzonensis* Herre & Ablan, 1934: 275–277, pl. 1 [type locality: Philippines: Solsona, Ilocos Norte, Luzon Is.]- Blanco, 1947: 89–93 [breeding and embryology].



**Figure 44.** *Oryzias luzonensis* (Herre & Ablan, 1934), Luzon Island, Philippines, CAS-SU 29079, male, 28.5 mm SL.

*Oryzias luzonensis*.- Yamamoto, 1975: 24 [listed].- Formacion & Uwa, 1985: 285–291 [cytogenetic characters and species differentiation].- Sakaizumi, 1985: 521–522 [electrophoretic comparisons].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Ibarra & Stewart, 1987: 10 [FMNH type specimens].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].

**Differential diagnosis:** *Oryzias luzonensis* is a small ricefish species (largest specimens examined 32.7 mm SL) and member of the biarmed chromosome group of Uwa (1986), along with *O. latipes*, *O. curvinotus* and the miniatures *O. sinensis* and *O. mekongensis*. These species have anal-fin rays of approximately the same length, forming a ‘parallelogram-shaped’ fin, and chromosome arms numbering 58 or more, reaching the highest recorded number of 96 in *O. luzonensis*. *Oryzias luzonensis* and *O. latipes* are the largest species of this group that also share a mesethmoid ossification that is indented anteriorly in some specimens, and a genome size of 1.9 pg per nucleus or greater. They are like *O. curvinotus* and differ from the two miniatures by having the first pleural rib on the third rather than the second vertebra in most specimens and paired, bilaterally asymmetric, as opposed to single lobed, testes. They are like the miniatures, and differ from *Oryzias curvinotus* by having bony processes on the pectoral-fin rays. *Oryzias luzonensis* has a dorsal fin that is anterior (opposite vertebrae 20–21 as opposed to vertebrae 22–23) and an ethmoid margin that is irregular relative to those of *O. latipes*.

**Description:** Small, maximum size of specimens examined 32.7 mm SL. Body compressed laterally, body depth 20–24. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting just slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin.

Dorsal surface of head slightly convex just anterior to orbits. Head length 20–24; snout length 5–6; eye moderate, 7–9, orbits meet dorsal surface of head. Basal portion of dorsal and anal fin project somewhat beyond primary body profile. Scales relatively large, cycloid; 30–35 in a lateral series. Somewhat filamentous dorsal- and anal-fin rays in males; medial pectoral fin-rays and posterior anal-fin rays with large, bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin truncate. Male with a short, tubular urogenital papilla; female with small, bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two or three enlarged posterior teeth on the premaxilla and dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular, interrupted anteriorly. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fourth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and a second accessory cartilage or bone. Fifth ceratobranchial toothplates suboval, with teeth in irregular rows anteriorly, followed by six discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 5–7. Anal-fin rays 15–19. Pelvic-fin rays 6. Pectoral-fin rays 11. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 5, ventral 6. Vertebrae 29–31 (11–12 + 18–19). Branchiostegal rays 5–6.

**Cytogenetic data:** *Oryzias luzonensis* has a biarmed chromosome constitution, with  $2n = 48$  chromosomes, comprising a combination of 24 metacentric and submetacentric pairs; chromosome arm number (NF) totals 96 (Formacion & Uwa, 1985; Table 2). *Oryzias luzonensis* has the second largest recorded genome size of any *Oryzias* species, 1.9 pg per nucleus (Table 2).

**Colour in life:** Grey, with yellow sheen dorsally and silvery along sides; dorsal-, anal-, pelvic-fins and dorsal and ventral caudal-fin rays yellowish or

hyaline; pectorals hyaline (Herre & Ablan, 1934: 275). Body nearly translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum. Caudal fin with yellowish dorsal and ventral submarginal band.

*Colour in alcohol:* Ground colour pale yellow to grey, belly pale whitish yellow. A discrete row of melanophores from the dorsal surface of the head to the dorsal-fin origin; dorsal surface of head and lateral surface of body with minute, sparse to dense, dark brown to black chromatophores, larger and more prominent on posterior portion of body of males, and forming scattered spots in some specimens. Females with a subrectangular, males with a smaller, subtriangular dark brown to black peritoneum. Caudal-fin rays of males dusky, dark brown line along proximal half of membranes between median caudal-fin rays; dorsal and anal margins of caudal fin hyaline. Submarginal dark brown band in anal fin of adult males.

*Distribution and habitat:* Endemic to Luzon Is., the Philippines, from creeks and rice fields (Herre & Ablan, 1934). *Oryzias luzonensis* is the only ricefish endemic to the Philippine archipelago.

*Remarks:* Herre & Ablan (1934: 276) designated a 'Type: No. 41062, Fish and Game Administration collection, 30 mm in length, and 29 cotypes [= paratypes] from 24–30 mm in length, collected by the junior author from a creek and from rice fields at Solsona, Ilocos Norte, Luzon, Dec 1933. Over 500 living specimens collected at the same time were placed in the Manila Aquarium, Fish and Game Administration, and are under our observation at the time of writing, December 20, 1933. More than 500 alcoholic specimens, 9–30 mm in length, from the same locality, are also in the collection. A few cotypes and other specimens are also in the collection of Stanford University, California.' The holotype has not been identified in any collection, has probably been destroyed, and is considered lost. No lot of 29 specimens can be identified either. One paratype lot, SU 29079, containing 111 specimens collected by Guillermo L. Ablan from the type locality on 4.xi.1933 was listed by Böhlke (1953: 52). The 112 specimens in this lot at CAS range from 11.8 to 30 mm SL. There are an additional four specimens, FMNH 47042, from this locality, listed by Ibarra & Stewart (1987: 10) as paratypes. Morphometric and meristic data are supplemented by those in Herre & Ablan (1934) and Uwa & Parenti (1988). The local common name for this species in Ilocos is *coscosleng* (Blanco, 1947).



**Figure 45.** *Oryzias marmoratus* (Aurich, 1935), Lake Towuti, Sulawesi Selatan, Indonesia, ZSM/LIPI 7, male, 34.7 mm SL, above, female, 33 mm SL, below.

*Material examined:* 689 specimens (11–32.7 mm).

Paratypes. PHILIPPINES. Luzon Is.: creek and rice-fields at Solsona, Ilocos Norte Prov., CAS-SU 29079, 112 (11.8–30 mm), G. L. Ablan, Oct, 3–4.xi.1933; FMNH 47042, 4.

Non-type specimens. PHILIPPINES. Luzon Is.: Solsona, Ilocos Norte Prov., CAS-SU 29564, 556 (11–32.7 mm, 2 of which have been cleared and counterstained, and 12 of which, 21.7–32.0 mm, have been cleared and stained for bone only), A. W. Herre, 12.iv.1934; FMNH 47387, 10 (12.5–29 mm), G. A. Lopez, 12.iv.1934; CAS 58032, 7 (25.1–28.0 mm, 2 of which have been cleared and counterstained), M. J. Formacion & H. Uwa, 16.xii.1982.

#### ORYZIAS MARMORATUS (AURICH, 1935)

##### MARMORATED RICEFISH

##### FIGURE 45

*Aplocheilus marmoratus* Aurich, 1935: 102–104, fig. 1b [type locality: Indonesia: Sulawesi, small rivulets flowing into lake at Lingkoburanga, Lake Towoeti [Towuti]].

*Oryzias marmoratus*.- Yamamoto, 1975: 24 [listed].- Schrey, 1978: 334–338 [photograph, taxonomy of *Oryzias*].- Whitten *et al.*, 1987a: 295, table 4.10 [Sulawesi, distribution].- Whitten *et al.*, 1987b: 43–48, table 1 [Sulawesi, conservation].- Kottelat, 1989b: 682, fig. 11 [report from Lake Towuti].- Kottelat, 1990b: 155–159, figs 2–5, tables 3–5 [redescription, comparisons].- Kottelat *et al.*, 1993: 90 [listed; characters].- Naruse *et al.*, 1994: 49 [cytogenetic data].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Seegers, 1997: 15, 20 [listed, photograph].- Albert *et al.*, 1999: 650 [brain weight].

*Differential diagnosis:* The Malili Lakes buntingi of Sulawesi, *O. marmoratus*, *O. profundicola* and *O. matanensis*, are readily distinguished from all other ricefishes by their distinctive pigmentation pattern: males have a series of regular midlateral brown to black blotches and irregular dark brown blotches over the entire lateral surface of the body. They are all somewhat deep bodied, reaching more than 26% SL; have a relatively large eye, diameter reaching 10% or more of SL; and have relatively long anal fins that range to over 24 anal-fin rays. *Oryzias marmoratus* is further distinguished by the live colour pattern of adult males: head and body greyish-brown with diffuse, dark brown blotches distributed irregularly on the body, and a row of five to nine larger blotches irregularly distributed dorsal to the midaxial stripe; there is a proximal row of dark purple to black spots on the membranes between anal-fin rays, and the posterior half of anal-fin margin is black. *Oryzias marmoratus* and *O. matanensis* have 8–12 and 8–9 dorsal-fin rays, respectively, whereas *O. profundicola* has 10–14. *Oryzias marmoratus* and *O. profundicola* have 31–32 or 32–34 scales in a lateral series, respectively, whereas *O. matanensis* has 41–47.

*Description:* Intermediate, maximum size of specimens examined 40.2 mm SL. Body compressed laterally, moderately deep, body depth 25–30. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile arching gently from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 24–27; snout length 7–9; eye large, 10–12, orbits do not project beyond dorsal surface of head. Single-lobed testis on right side of body of males. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales of moderate size, cycloid, and somewhat deciduous; 31–32 in a lateral series. Elongate, slightly filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half in males, along its entire length in females. Caudal fin truncate. Male with a short, slightly conical, tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth in irregular rows up to seven teeth deep, although the closely packed teeth of males makes these counts imprecise; males with two to three rows of external conical teeth on the upper and lower oral jaws, and thick and fleshy lips through

which just the tooth tips project. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. Fifth ceratobranchial tooth-plates subtriangular, with teeth in irregular rows anteriorly, followed by eight discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 8–12. Anal-fin rays 20–26. Pelvic-fin rays 6. Pectoral-fin rays 10. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 5, ventral 6. Vertebrae 30 (12 + 18). Branchiostegal rays 5.

*Cytogenetic data:* *Oryzias marmoratus* has a fused chromosome constitution with  $2n = 42$  chromosomes (Table 2; Naruse *et al.*, 1994).

*Colour in life:* (From Kottelat, 1990b: 156): Males greyish-brown on head and body. Diffuse dark brown blotches dispersed on body, including a row of five to nine larger blotches dorsal to midaxial stripe. Eyes blue. Filamentous dorsal-fin rays yellow or hyaline, distal margin of dorsal-fin black. Dorsal and ventral margin of caudal fin bright yellow; two to four longitudinal dark purple stripes on proximal half of membranes between median caudal-fin rays. A proximal row of dark purple to black spots on the membranes between anal-fin rays; posterior half of anal fin with a black margin. Pelvic fin bright yellow; pectoral fin hyaline.

*Colour in alcohol:* Ground colour yellowish-grey. Dorsal surface of head and dorsal and lateral surface of body with dense dark brown to black chromatophores. A discrete row of melanophores from dorsal surface of head to dorsal-fin origin, an interrupted midlateral black line from head to base of caudal fin. Females with diffuse line of dark chromatophores from a point just posterior to anal-fin origin, along body just dorsal to anal-fin base to middle of caudal peduncle. Fins of females and pectoral and pelvic fins of males hyaline to dusky. Urogenital papilla of females and of males immaculate or with several

melanophores. Dorsal- and anal-fin rays of males dusky except at their margins which are hyaline. A proximal row of black spots on membranes between anal-fin rays; posterior half of anal fin with a black margin. Caudal fin-rays of males dusky, a dark line along proximal half of membrane between median caudal-fin rays.

*Distribution and habitat:* Endemic to lakes of the Malili River basin, Sulawesi Selatan, Indonesia: lakes Towuti, Wawontoa and Mahalona (Parenti & Soeroto, 2004: fig. 1). Found in creeks, streams and rice paddies along the lakeshore (Kottelat, 1990a).

*Remarks:* A neotype for *Oryzias marmoratus* (ZSM 27172, now ZRC 38449) was designated by Kottelat (1990b: 155) from material he collected in 1988 from Lake Towuti, after concluding that the 22 syntypes from lakes Towuti and Mahalona were lost or destroyed. A neotype was designated because Kottelat (1990b) recognized variation among populations from lakes Towuti, Wawontoa and Mahalona and acknowledged that material he identified as *O. marmoratus* (Aurich) may include more than one species and possible hybrids with *O. profundicola* Kottelat (1990b). I base my diagnosis and description of *Oryzias marmoratus* on data on the neotype (from Kottelat, 1990b), which I did not examine, and other specimens from the restricted type locality. Data were augmented by those in Kottelat (1990b). Another common name for this species is marmorated medaka (Seegers, 1997: 20).

*Material examined:* 546 specimens (10.2–40.2 mm SL).

INDONESIA. Sulawesi Selatan: Lake Towuti, small rivulets flowing into the lake on a sandy beach at Lingkoburanga, about 6 km S of Timampu, type locality, ZSM/LIPI 7, 8 (13.0–35.5 mm), and CMK 6381 (ex. CMK 6222), 1 (adult female, 36.5 mm, counterstained), M. Kottelat, 22.vi.1988; Sg. Lingkoburanga where it enters Lake Towuti, approx. 8 km S of Timampu, USNM 348528, 24 (13.4–40.2 mm), L. R. Parenti, K. D. Louie & P. Haji, 9.viii.1995. First stream just S of Sg. Lingkoburanga, where stream enters Lake Towuti, USNM 348574, 8 (20.6–26.5 mm), L. R. Parenti, K. D. Louie & P. Haji, 9.viii.1995. Lake Mahalona, Sg. Tombalala where it enters on SW shore of Lake Mahalona, USNM 348529, 505 (10.2–35.1 mm, 10 of which have been cleared and counterstained), L. R. Parenti, K. D. Louie, P. Haji & T. Amos, 8.viii.1995.



**Figure 46.** *Oryzias matanensis* (Aurich, 1935), Lake Matano, Sulawesi Selatan, Indonesia, CMK 6195, male, 43.3 mm SL, above, female, 43.4 mm SL, below.

#### ORYZIAS MATANENSIS (AURICH, 1935)

##### MATANO RICEFISH

##### FIGURES 12, 19B, 25A, 46

*Aplocheilus matanensis* Aurich, 1935: 103–104, fig. 1a [type locality: Indonesia: Sulawesi, East of Soroako, Lake Matano].

*Oryzias matenensis*.- Incorrect spelling.- Yamamoto, 1975: 24 [listed].

*Oryzias matanensis*.- Whitten *et al.*, 1987a: 295, table 4.10 [Sulawesi, distribution].- Whitten *et al.*, 1987b: 43–48, table 1 [Sulawesi, conservation].- Kottelat, 1989a: 616, plate [report from Lake Matano].- Kottelat, 1990b: 159–161, figs 6, 7, tables 5 and 6 [redescription, comparisons].- Kottelat *et al.*, 1993: 90 [listed; characters].- Naruse *et al.*, 1994: 49 [cytogenetic data].- Seegers, 1997: 15, 18 [listed, photograph].- Albert *et al.*, 1999: 650 [brain weight].- Parenti & Grier, 2004: 336 [atherinomorph testis type, listed].

*Differential diagnosis:* The Malili Lakes buntingi of Sulawesi, *O. marmoratus*, *O. profundicola* and *O. matanensis*, are readily distinguished from all other ricefishes by their distinctive pigmentation pattern: males have a series of regular midlateral blotches and irregular dark brown blotches on the entire lateral surface of the body. They are all somewhat deep bodied, reaching more than 26% SL; have a relatively large eye, diameter reaching 10% or more of SL; and have relatively long anal fins that range to over 24 anal-fin rays. *Oryzias matanensis* is distinguished by having 41–47 scales in a lateral series, whereas *Oryzias marmoratus* and *O. profundicola* have 31–32 and 32–34, respectively. *Oryzias matanensis* is

further distinguished by the distinctive colour pattern of adult males: vertically elongate black blotches in a more-or-less regular midaxial row, and several smaller black blotches distributed irregularly on body, denser in posterior half. *Oryzias marmoratus* and *O. matanensis* have 8–12 or 8–9 dorsal-fin rays, respectively, whereas *O. profundicola* has 10–14.

*Description:* Intermediate, maximum size of specimens examined 47.3 mm SL. Body compressed laterally, moderately deep, body depth 26–31. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projects slightly beyond upper jaw. Dorsal body profile arching gently from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 25–29; snout length 7–9; eye large, 10–11; orbits do not project beyond dorsal surface of head. Basal portion of dorsal and anal fin does not project significantly beyond primary body profile. Scales of moderate size, cycloid, and somewhat deciduous; 41–47 in a lateral series. Elongate, slightly filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half in males, along its entire length in females. Caudal fin truncate to slightly lunate. Male with a short, slender, slightly conical or blunt, tubular urogenital papilla; female with bilobed urogenital papilla (Fig. 12).

Premaxilla short and broad with indistinct ascending process; premaxilla and dentary with two irregular rows of small, caniniform teeth, males with two to three rows of external conical teeth on the upper and lower oral jaws, and thick and fleshy lips through which tooth tips project; females with one or two large, conical teeth on lateral portion of the dentary. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one slightly convex, ventral accessory bone. Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by eight discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone triangular, basihyal car-

tilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 8–9. Anal-fin rays 20–25. Pelvic-fin rays 6. Pectoral-fin rays 11–12. Principal caudal-fin rays i,4–5/5,i. Procurrent fin-rays, dorsal 4–5, ventral 5–6. Vertebrae 30 (12 + 18). Branchiostegal rays 5.

*Cytogenetic data:* *Oryzias matanensis* has a fused chromosome constitution with  $2n = 42$  chromosomes (Table 2; Naruse *et al.*, 1994).

*Colour in life:* (From Kottelat, 1990b: 160): Males greyish-brown on head and body. Vertically elongate black blotches in a more-or-less regular midaxial row; several smaller black blotches distributed irregularly on body, denser in posterior half. Eyes blue. Dorsal, anal, caudal and pelvic fins blackish; pectoral fin hyaline. Females with light brown head; body with smaller, indistinct black blotches or immaculate.

*Colour in alcohol:* Ground colour yellowish-grey. Dorsal surface of head and dorsal and lateral surface of body with dense dark brown to black chromatophores. A dense row of melanophores from dorsal surface of head to dorsal-fin origin, a thin, midlateral black line from head to just anterior to base of caudal fin. Females with diffuse line of dark chromatophores dorsal from a point just posterior to anal-fin origin, along body just dorsal to anal-fin base to middle of caudal peduncle. Fins of females hyaline or slightly dusky. Pectoral and pelvic fins of males dusky to dense melanophores. Urogenital papilla of females and of males immaculate or with a few, minute melanophores along posterior margin. Dorsal- and anal-fin rays of males dusky except at their margins which are hyaline. Caudal fin-rays of males dusky, dark line along proximal half of membranes between median caudal-fin rays; dorsal and anal margins of caudal fin hyaline.

*Distribution and habitat:* Endemic to Lake Matano of the Malili River basin, Sulawesi, Indonesia (Parenti & Soeroto, 2004: fig. 1). Found around the lake in quiet backwaters and along steep shores (Kottelat, 1990b).

*Remarks:* Kottelat (1990b: 159–160) designated a neotype for *Oryzias matanensis* (ZSM 27368) from material that he collected in 1988 from Lake Matano, after concluding that the ten syntypes from the lake were lost or destroyed. I did not examine the neotype. Data were augmented by those in Kottelat (1990b). Another common name for this species is Matano medaka (Seegers, 1997: 20).



**Figure 47.** *Oryzias mekongensis* Uwa & Magtoon, 1986, Yang Talat, Thailand, USNM 268540, holotype, male, 13.0 mm SL.

*Material examined:* 344 specimens (7.6–47.3 mm SL). INDONESIA. Sulawesi Selatan: Luwu: Muha: Lake Matano, E of Soroako, (field number 88–19), type locality, CMK 6195, 10 (40.2–44.5 mm, of which one male, 42.5 mm, and one female, 44.5 mm, have been cleared and counterstained), M. Kottelat, 19.vi.1988; western shore of Lake Matano at Soroako, USNM 340422, 12 (15.2–30.7 mm), local fisherman, 7.viii.1995, USNM 340428, 73 (14.9–47.3 mm), L. R. Parenti, K. D. Louie, T. Amos & Dahlan, 6.viii.1995; western shore of Lake Matano, stream entering small inlet approx. 6–7 km N of Soroako, USNM 340429, 249 (7.6–46.1 mm), L. R. Parenti, K. D. Louie, T. Amos & boatmen, 7.viii.1995.

*ORYZIAS MEKONGENSIS* UWA & MAGTOON, 1986  
MEKONG MEDAKA

FIGURES 6, 11E, F, 15A, 47

*Oryzias* sp.- Kottelat, 1985: 272 [report of an apparently new species from Tonlé Sap, Phnom Penh, Kampuchea].- Magtoon, 1986: 859–865 [report of undescribed species from Thailand].- Uwa, 1985a: 3 [photograph of live specimens; distribution].- Uwa, 1985b: 7 [distribution, cytogenetic comparisons].- Uwa, 1986: 867–875 [cytogenetic comparisons; Yang Talat, Thailand].

*Oryzias mekongensis* Uwa & Magtoon, 1986: 474–475, figs 1–3 [type locality: Thailand: Mekong basin, Kalasin Prov., Yang Talat].- Iwamatsu, 1986: 99–109 [comparative anatomy].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Collette, Parin & Nizinski, 1992: 3 [USNM type specimens].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Rainboth, 1996: 172, figure [Mekong].- Roberts, 1998: 220–221 [characters, relationships, distribution].- Kottelat, 2001b: 143, fig. 405 [characters, distribution].

*Differential diagnosis:* *Oryzias mekongensis* is a miniature species (largest specimen examined 16.7 mm) of the biarmed chromosome group of Uwa (1986),

along with *O. luzonensis*, *O. latipes*, *O. curvinotus* and the miniature *O. sinensis*, that have anal-fin rays of approximately the same length, forming a ‘parallelogram-shaped’ fin, and chromosome arms numbering 58 or more. *Oryzias mekongensis* is distinguished from all other ricefishes by a low number of anal-fin rays, ranging from 13 to 18, and bright orangish-red, rather than yellow, submarginal bands on the dorsal and ventral portions of the caudal fin in life. *Oryzias mekongensis* and *O. sinensis* both have the first pleural rib on the second, rather than the third, vertebra. They are like *O. latipes* and *O. luzonensis*, and differ from *Oryzias curvinotus*, by having bony processes on the pectoral-fin rays.

*Description:* Miniature, maximum size of specimens examined 16.7 mm SL. Body compressed laterally, slender, body depth 17–18 [17]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile straight from head to dorsal-fin origin; ventral body profile straight from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 24–25 [24]; snout length 4–5 [4]; eye moderate, 7–9 [8], orbits meet dorsal surface of head. Single-lobed testis on right side of body of males. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales relatively large, cycloid; 29–32 in a lateral series. Somewhat filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs or with a few, small contact organs on posterior anal-fin rays. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin elongate and rounded. Male with a short, tubular urogenital papilla; female with small, slightly bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two or three enlarged posterior teeth on the premaxilla and dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid suboval; ethmoid cartilage rectangular with anterior projection. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of second vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fourth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and a second accessory



cartilage or bone. Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by six discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 5–7 [6]. Anal-fin rays 13–18 [15]. Pelvic-fin rays 5–6. Pectoral-fin rays 6–8. Principal caudal-fin rays  $i, 4/5, i$ . Procurrent fin-rays, dorsal 3–4, ventral 4–5. Vertebrae 27–31 (10–11 + 17–20). Branchiostegal rays 4–5.

*Cytogenetic data:* *Oryzias mekongensis* has a biarmed chromosome constitution. Diploid chromosomes number 48, with one metacentric, four submetacentric, 12 subtelocentric and seven acrocentric pairs. Chromosome arms number 58; genome size is 1.5 picograms of DNA per nucleus. (Table 2).

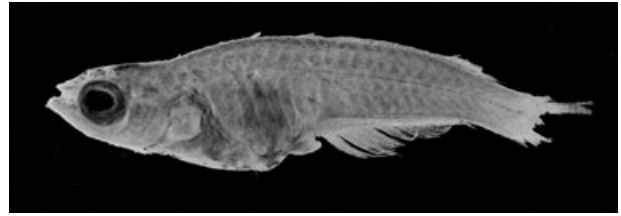
*Colour in life:* Body translucent, with brownish yellow mottling overall and bright orange submarginal bands on the dorsal and ventral portions of the caudal fin. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum.

*Colour in alcohol:* Ground colour pale yellow, a black line from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin, a black line along the anal-fin base, a black submarginal line on dorsal and on ventral portion of the caudal fin, body covered with scattered melanophores concentrated at the pectoral-fin base. Interrupted brown horizontal bar from eye to tip of lower jaw. Females with a subrectangular, males with a smaller, subtriangular blackish peritoneum.

*Distribution and habitat:* Widely distributed throughout the Mekong basin in north-east Thailand, Laos and Kampuchea, in clear water swamps (Kottelat, 2001b). This species may be associated with acidic waters (Roberts, 1998: 220).

*Remarks:* Additional paratypes listed in the original description, but not examined by me, include CTNRC 42.2612–2620 (9), 42.2621 (1), 42.2622 (1) and NSMT-P 23233–38 (6), 23239–44 (6). Morphometric and meristic data are supplemented by those in Uwa & Parenti (1988).

*Material examined:* 99 specimens (9–16.7 mm SL). Holotype. THAILAND. Kalasin Prov.: Yang Talat, USNM 268540, male, 13.0 mm, W. Magtoon & H. Uwa, 19.iv.1984.



**Figure 48.** *Oryzias minutillus* Smith, 1945, Bangkok, Thailand, USNM 107958, holotype, female, 14.0 mm SL.

Paratypes. THAILAND. Kalasin Prov.: Yang Talat, USNM 268541, 3 (1 male and 2 females, 11.4–13.1 mm), W. Magtoon & H. Uwa, 19.iv.1984.

Non-type specimens. THAILAND. Kalasin Prov.: Yang Talat: CAS 58030, 40 (10.0–14.0 mm, 4 of which have been cleared and counterstained), W. Magtoon & H. Uwa, 19.iv.1984; Srisaket, CAS 58027, 4 (14.0–15.5 mm, 2 of which have been cleared and counterstained), W. Magtoon, 16.ix.1984, pres. 6.xii.1985. Sakon Nakhon Prov.: Nong han just NE of Nakhon, USNM 246920, 5 (10–15 mm), 7.i.1971.

LAOS. Vientiane: AMNH 56084, 43 (9–12 mm), C. W. Heckman, 6.i.1970, rice paddy at kilometre 10, highway 13, NW of Vientiane, AMNH 56082, 2 (9.5–12 mm), C. W. Heckman, 7.v.1972, vicinity of Vientiane, aquarium specimen, AMNH 56083, 1 (16.7 mm), C. W. Heckman, vii.1971.

#### ORYZIAS MINUTILLUS SMITH, 1945

##### DWARF MEDAKA

##### FIGURES 11D, 20C, 48

*Oryzias minutillus* Smith, 1945: 424–425, fig. 95. [type locality: Thailand: Bangkok].- Rosen, 1964: 227 [systematics].- Scheel, 1969: 5–7, fig. 1 [behaviour, reproduction, characters].- Schrey, 1978: 338 [taxonomy of *Oryzias*].- Magtoon & Uwa, 1985: 157–160 [karyotype, relationships].- Magtoon, 1986: 859–865 [distribution in Thailand, relationships, karyotype].- Uwa, 1986: 867–875 [cytogenetic comparisons].- Uwa & Magtoon, 1986: 475–477 [comparison with *O. mekongensis*].- Ashida & Uwa, 1987: 1003 [karyotype polymorphism].- Uwa *et al.*, 1988: 332–340 [karyotype, distribution, China].- Uwa & Parenti, 1988: 159 [morphometric and cytogenetic comparisons].- Chen *et al.*, 1989: 239–246 [comparison with *O. latipes sinensis*, and report from Yunnan Province, China].- Chen, 1990: 227–228 [distribution in Yunnan].- Collette *et al.*, 1992: 3 [USNM type specimens].- Magtoon *et al.*, 1992: 489–497 [karyotype and geographical variation].- Takata *et al.*, 1993: 319–326 [genetic differentiation].- Hamaguchi, 1996: 757–763 [description and comparison of testis structure].- Seegers, 1997: 15, 21 [listed, photographs].- Roberts, 1998:

No claim to original US Government works.

219–220 [characters, relationships, distribution].- Kotelat, 2001b: 143, fig. 406 [characters, distribution].

*Oryzias* sp. undet.- Roberts, 1998: 220 [specimens from Menghai, southern Yunnan].

**Differential diagnosis:** *Oryzias minutillus* is a miniature species (maximum size of specimens examined 17 mm, but with most adults known less than 14 mm) hypothesized to be most closely related to two other miniatures, *Oryzias uwai* and *O. setnai*, with which it shares the anterior portion of the anal fin with elongate rays set off from the rest of the fin; a medial extension of the ethmoid cartilage; and principal caudal-fin rays number i,3/4,i, the lowest for all ricefishes. It shares with *O. setnai* five, rather than six pelvic fin-rays, but lacks the many autapomorphies of that species. Four miniatures, *O. minutillus*, *O. pectoralis*, *O. setnai* and *O. uwai*, share the characters of a pigmented anal or urogenital region and an elongate, rounded caudal fin.

**Description:** Miniature, maximum size of specimens examined 17 mm SL. Body compressed laterally, slender, body depth 18–19 [18]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile slightly convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 21–25 [21]; snout length 4–5 [4]; eye moderate, 7–8 [7] orbits do not project beyond dorsal surface of head. Single-lobed testis on right side of body of males. Basal portion of dorsal fin projects slightly beyond primary body profile. Scales relatively large, cycloid; 26–29 in a lateral series. Dorsal and pectoral fins elongate, anal fin slightly rounded; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half; pelvic fins relatively small, do not extend to anal-fin origin. Caudal fin rounded. Male with a short, tubular urogenital papilla; female with small, slightly bilobed urogenital papilla.

Premaxilla short and broad with barely distinct ascending process; premaxilla and dentary with a single irregular row of caniniform teeth; no large canine teeth on lateral ramus of the premaxilla or dentary. No preethmoid cartilage; mesethmoid cartilaginous or weakly ossified, when ossified, mesethmoid small and suboval; ethmoid cartilage rectangular with anterior projection. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of second

vertebra; first epipleural bone attaches to first vertebra; lateral process of pelvic bone in close association with third or fourth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and one accessory cartilage. Anteriormost dorsal and ventral procurent rays hooked at base. Fifth ceratobranchial toothplate triangular, with teeth in irregular rows anteriorly, followed by two discrete rows of unicuspid teeth, and no incomplete posterior row. Basihyal bone triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 5–7 [6]. Anal-fin rays 17–21 [19]. Pelvic-fin rays 5. Pectoral-fin rays 7–8. Principal caudal-fin rays i,3/4,i. Procurent fin-rays, dorsal 4, ventral 6. Vertebrae 24–29 (8–11 + 16–18). Branchiostegal rays 4–5.

**Cytogenetic data:** *Oryzias minutillus* is a highly variable species cytogenetically as demonstrated by Magtoon *et al.* (1992: table I) who reported variation among 18 populations from throughout Thailand (see Table 2). Diploid chromosome number and constitution varies from 28, comprising seven large metacentric, one submetacentric and six acrocentric pairs, to 42, comprising 21 acrocentric pairs. Genome size is 1.5 pg of DNA per nucleus in all reported populations (Magtoon & Uwa, 1985; Uwa, 1986; Table 2). Chromosome arm number (NF) varies from 42 to 44. *Oryzias minutillus* was grouped first with other species that have a fused chromosome constitution because populations from Bangkok and Chiang Mai have large metacentric (= fused) chromosomes (Uwa, 1986; Table 2). Examination of populations from throughout Thailand led to the recharacterization of *O. minutillus* as having a monoarmed chromosome constitution because of the predominance of acrocentric chromosomes in populations from Phuket and Menghai (Uwa, 1991b). In the phylogenetic analysis, it is coded as polymorphic for chromosome constitution.

**Colour in life:** Body translucent, and with melanophore pattern as described below in alcohol. Dorsal surface of eye green in males, golden in females (Scheel, 1969). Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum.

**Colour in alcohol:** A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Females

with a subrectangular, males with a smaller, subtriangular blackish peritoneum. A faint black line along the anal-fin base. Perianal melanophores in both sexes. Dorsal and anal fin interradiial membranes with scattered melanophores. Abdomen black or silvery.

*Distribution and habitat:* Chao Phrya basin and Salween basins, Thailand, Mekong basin in northern Thailand and Kampuchea, and Yunnan Province, China, in clear water swamps (Kottelat, 2001b).

*Remarks:* Roberts (1998: 220) considered the specimens from Menghai, Yunnan, to represent an undescribed species because they are larger than most other *O. minutillus*, and differ in cytogenetic and some morphological characters. I continue to refer these specimens to *O. minutillus* because their proportions and counts, as reported by Uwa *et al.* (1988: 335), are consistent with *O. minutillus* populations from Thailand. Furthermore, their diploid chromosome number (42) as reported by Uwa *et al.* (1988) is consistent with the chromosome numbers of all *O. minutillus* populations (Table 2). A karyotype of 42 acrocentric chromosomes was considered 'basic' for this species, with reductions resulting from pericentric inversions and centric fusions (Uwa *et al.*, 1988; Takata *et al.*, 1993). Morphometric and meristic data are supplemented by those in Uwa & Parenti (1988). Another common name for this species is Thai-medaka (Magtoon *et al.*, 1992).

*Material examined:* 86 specimens (6.5–17 mm SL). Holotype. THAILAND. Central Thailand: small canal in Bangkok, USNM 107958, 1 (female, 14.0 mm), H.M. Smith, 10.v.1934. Paratypes. THAILAND. Central Thailand: small canal in Bangkok, USNM 109789, 4 (1 male and 3 females, 12.2–13.3 mm), collected with the holotype. Non-type specimens. CHINA. Yunnan Prov.: Menghai, Xishiangbanna, CAS 60237, 4 (13.2–17 mm), H. Uwa, R.-F. Wang & Y.-R. Chen, 24.viii.1986. THAILAND. GVF reg. 1540, sta. 82, CAS 40758, 1 (16 mm), R. R. Rofen, 24.xi.1957; Chiang Mai, CAS 58023, 5 (8.0–11.0 mm, 2 of which have been cleared and counterstained), W. Magtoon & H. Uwa, 25.iv.1984; Bangkok, CAS 58022, 19 (6.5–12.1 mm, 4 of which have been cleared and counterstained), W. Magtoon, 16.i.1983; Nakhon Sithammarat Prov. at Thungsong, CAS 60741, 9 (11.5–13.0 mm), W. Magtoon & H. Uwa, 10.xii.1984; W of Bangkok, Klong Ta Pa at Ban pong, USNM 229287, 2 (10–12.5 mm), T. R. Roberts & P. Wongrat, 15.iv.1973. Phuket Is., Teacher's College, CAS 58025, 11 (10.0–13.5 mm, 2 of which have been cleared and counterstained), N.



**Figure 49.** *Oryzias nebulosus* Parenti & Soeroto, 2004, Lake Poso, Sulawesi Tengah, Indonesia, MZB 11649, holotype, male, 32.5 mm SL.

Tawimsunnuk, H. Uwa & W. Magtoon, 2.ii.1985; Trat Prov., Ban Pret Nok, about 17 Km SSW of Trat, ZRC 35689–35718, 30.

#### ORYZIAS NEBULOSUS PARENTI & SOEROTO, 2004

##### NEBULOUS RICEFISH

##### FIGURE 49

*Oryzias nebulosus* Parenti & Soeroto, 2004: 10, 14–17, figs 5, 7, 8 [type locality: Indonesia: Sulawesi, Lake Poso].

*Differential diagnosis:* *Oryzias nebulosus* shares with *O. nigrimas*, also from Lake Poso, a unique sexual dichromatism in preserved specimens: adult males are dark grey to black, whereas females are a lighter greyish yellow to brown. Relative to *O. nigrimas*, *O. nebulosus* is a small (maximum size 33 mm as opposed to 51 mm SL), relatively deep-bodied species (body depth 20–25, as opposed to 18–22% SL), with fewer precaudal vertebrae (11–13 vs. 13–14). These last three characters are shared with the Malili Lakes buntingi, *O. marmoratus*, *O. matanensis* and *O. profundicola*, from which *O. nigrimas* is readily distinguished by colour pattern and by having a lunate, rather than truncate, caudal fin.

*Description:* Small, maximum size of specimens examined 33 mm SL. Body short, relatively deep; body depth 20–25 [25]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal, lower jaw projects slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile convex from snout to anal-fin origin. Dorsal surface of head slightly concave just anterior to orbits. Head length 22–25 [23]; snout length 6–8 [6]; eye moderate, 7–9 [7], orbits meet dorsal surface of head. Basal portion of dorsal and anal fin project slightly beyond primary body profile. Scales of moderate size, cycloid and somewhat deciduous; 32–36 [34] in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs.

No claim to original US Government works.

Medialmost pelvic-fin ray connected to body via a membrane along its proximal half. Caudal fin lunate, dorsal and ventral segmented caudal-fin rays just slightly longer than middle rays. Male with short, slightly conical, tubular urogenital papilla; female with small, bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with irregular row of external conical teeth on the upper and lower oral jaws, and one large and two small conical teeth on posterior ramus of the premaxilla. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra (rudimentary rib on second vertebra in some specimens); first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. Procurrent caudal-fin rays hooked slightly at their base. Fifth ceratobranchial toothplates subtriangular, with pavement dentition anteriorly, followed by four to five discrete rows of unicuspid teeth; small, incomplete posterior row. Basihyal bone elongate, triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 9–11 [10]. Anal-fin rays 21–22 [22]. Pelvic-fin rays 6 [6]. Pectoral-fin rays 9–11 [11]. Principal caudal-fin rays i,4/5–6,i. Procurrent fin-rays, dorsal 5, ventral 6. Vertebrae 30–32 (11–13 + 18–20). Branchiostegal rays 5.

*Cytogenetic data:* Unknown.

*Colour in life:* Live colour of *O. nebulosus* was not recorded at capture. As this species has been confused in collections with *O. nigrimas*, with which it shares a similar, unique preserved colour pattern, both species probably share general characteristics of colour in life (see Kottelat, 1990a: 53–54, and description of *O. nigrimas*, below).

*Colour in alcohol:* Ground colour yellowish-grey, belly pale yellow. Pigmentation variable in preserved specimens from pale yellowish overall in smaller specimens to dark brown to black in large males. Dorsal surface of head and dorsal and lateral surface of body with dense dark brown to black chromatophores. A

diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin. Females and lighter-coloured males with diffuse line of dark brown to black chromatophores dorsal from just posterior to anal-fin origin, along body just dorsal to anal-fin base to middle of caudal peduncle. Urogenital papilla heavily pigmented in gravid female, pale grey in other specimens. Fins dusky to dark brown or black, more heavily pigmented in males.

*Distribution and habitat:* Eastern shore of Lake Poso and its tributary stream, the Poso River, at Tentena, Sulawesi Tengah, Indonesia (Parenti & Soeroto, 2004: fig. 1). Specimens were collected in the morning by seine and dip nets in clear water over a bottom of sand, pebbles and fallen branches, and at night using kerosene lamps and dip nets from a boat that travelled along the lake shore, including the mouth of the tributary stream. Many of the specimens are infested with parasitic copepods.

*Remarks:* The sexual dichromatism of *O. nebulosus* and *O. nigrimas*, in which males are dark brown to black and females are pale yellow to grey, is characteristic also of *Nomorhamphus celebensis*, from Lake Poso (see Kottelat *et al.*, 1993), and *N. towotii*, from lakes Poso and Towuti (see Meisner, 2001: 261). Data were augmented by those in Kottelat (1990a).

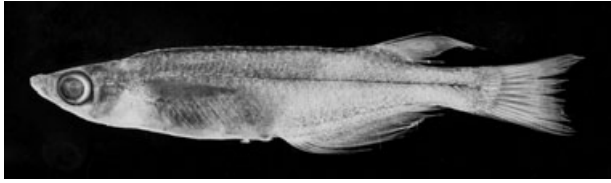
*Material examined:* 37 specimens (22.3–33 mm SL). Holotype. INDONESIA. Sulawesi Tengah: Lake Poso at Peura, eastern shore of lake approx. 10 km S of Tentena, L. R. Parenti, K. D. Louie, P. Beta, *et al.*, 13.viii.1995, MZB 11649 (adult male, 32.5 mm). Paratypes. INDONESIA. Sulawesi Tengah: MZB 11650 22 (22.3–32.9 mm, 6 of which have been cleared and counterstained), collected with the holotype; Lake Poso, eastern shore approx. 17 km S of Tentena, USNM 367129 5 (27.5–33.0 mm, 1 of which has been cleared and counterstained), L. R. Parenti, K. D. Louie, P. Beta *et al.*, 12.viii.1995; Lake Poso, west bank of Poso R. where it empties into lake at Pamona Caves, USNM 354692, 9 (24.5–31.7 mm), L. R. Parenti, K. D. Louie, P. Beta, *et al.*, 13.viii.1995.

#### ORYZIAS NIGRIMAS KOTTELAT, 1990A

##### BLACK BUNTINGI

##### FIGURE 50

*Oryzias nigrimas* Kottelat, 1990a: 52–54, fig. 2, tables 1 and 2 [type locality: Indonesia: Sulawesi Tengah, Lake Poso, eastern shore between Tentena and Peura].- Uwa, 1991b: 15–18 [karyotype, morphometrics].- Kottelat *et al.*, 1993: 90 [listed;



**Figure 50.** *Oryzias nigrimas* Kottelat, 1990a, Lake Poso, Sulawesi Tengah, Indonesia, CMK 6358, male, 45.5 mm SL.

characters].- Naruse *et al.*, 1994: 49 [cytogenetic data].- Schaller, 1994: 18–20 [photos, habitat description, taxonomy].- Seegers, 1997: 15, 21, 22 [listed, photographs, possibly *O. nebulosus*].

*Differential diagnosis:* *Oryzias nigrimas* is distinguished from all other ricefishes by a unique sexual dichromatism in life: adult males are dark bluish grey to black, especially when breeding, whereas females are a lighter greyish brown. *Oryzias nigrimas* shares with *O. nebulosus* a unique sexual dichromatism in preserved material: adult males are dark grey to black, whereas females are a lighter greyish yellow to brown. Relative to *O. nebulosus*, *O. nigrimas* is large (maximum size 51 mm) and slender-bodied, with pre-caudal vertebrae 13–14 (vs. 11–13). *Oryzias nigrimas* differs from *O. orthognathus*, the other large (both reach over 50 mm SL) *Oryzias* in Lake Poso, by having 34–37, as opposed to 45–57, scales in a lateral series, and six, as opposed to seven, pelvic-fin rays.

*Description:* Elongate, maximum size of specimens examined 51 mm. Body slender, elongate, laterally compressed; body depth 18–22. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal. Dorsal and ventral body profile gently arching from head to dorsal- and anal-fin origins. Dorsal surface of head slightly convex just anterior to orbits. Head length 22–25; snout length 6–8; eye moderate to large, 8–10, orbits do not project beyond dorsal surface of head. Basal portions of dorsal and anal fin do not project significantly beyond primary body profile. Scales of moderate size, cycloid and somewhat deciduous; 34–37 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half. Caudal fin lunate, dorsal and ventral segmented caudal-fin rays just slightly longer than middle rays. Male with a short, slightly conical, tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two to three rows of external conical teeth on the upper and lower oral jaws. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fifth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. There are two ventral accessory bones in one of the cleared and stained specimens (CMK 6361). Procurrent caudal-fin rays hooked at their base. Fifth ceratobranchial tooth-plates subtriangular, with pavement dentition anteriorly, followed by four to five discrete rows of unicuspid teeth; small, incomplete posterior row. Basihyal bone triangular, basihyal cartilage elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 8–11. Anal-fin rays 21–25. Pelvic-fin rays 6. Pectoral-fin rays 11–12. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 5, ventral 6. Vertebrae 32–33 (13–14 + 19). Branchiostegal rays 5.

*Cytogenetic data:* *Oryzias nigrimas* has a fused chromosome constitution (*sensu* Uwa, 1986, 1991a, b; Naruse *et al.*, 1994; Table 2) and has 38 diploid chromosomes, including six metacentrics, four submetacentrics and 28 acrocentrics. The metacentrics are extremely large and have been hypothesized to have been formed by centric fusion. Chromosome arm number (NF) totals 48 and nuclear organizing regions (NORs) are on the short arms of a submetacentric pair of chromosomes (Uwa, 1991b).

*Colour in life:* (From Kottelat, 1990a: 53–54): Females greyish brown on dorsal and lateral surfaces, lighter grey belly; fins hyaline. Males dark bluish-grey to black on dorsal and lateral surfaces; fins dark bluish-grey to black, except for greyish caudal fin; filamentous dorsal- and anal-fin rays bluish-white at their tips. Eyes blue, and with a shiny blue patch on ‘throat’.

*Colour in alcohol:* Ground colour yellowish-grey, belly pale yellow. Pigmentation quite variable in preserved specimens from pale overall in smaller specimens to

darkly pigmented in large males. Dorsal surface of head and dorsal and lateral surface of body with dense dark brown to black chromatophores. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin. Females and lighter-coloured males with diffuse line of dark chromatophores dorsal from just posterior to anal-fin origin, along body just dorsal to anal-fin base to middle of caudal peduncle. Urogenital papilla heavily pigmented in gravid female, paler brown to cream in other specimens. Fins of females, and pectoral and pelvic fins of males, hyaline. Dorsal, anal and caudal fins of males dusky to darkly pigmented.

*Distribution and habitat:* A pelagic species endemic to Lake Poso, Sulawesi Tengah, Indonesia.

*Remarks:* The holotype, ZSM/LIPI 1 (42.6 mm), collected with the paratypes, below, was not examined by me. Data were augmented by those in Kottelat (1990a). Other common names for this species are black medaka or black ricefish (Seegers, 1997: 21).

*Material examined:* 521 specimens (6.3–51 mm SL). Paratypes. INDONESIA. Sulawesi Tengah: Lake Poso, east shore between Tentena and Peura (field number 88–26), CMK 6358 (formerly CMK 6236), 10 (20.6–46.0 mm), CMK 6361 (formerly CMK 6236), 3 (38.5–40.0 mm, cleared and counterstained), ZMA 120.335, 10 (5 males, 5 females, 23.2–43.5 mm), M. Kottelat, 24–25.vi.1988.

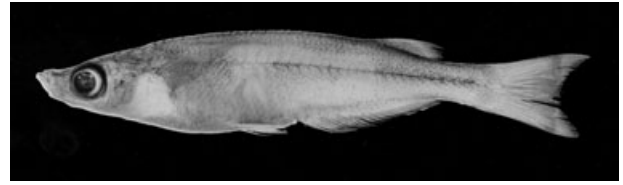
Non-type specimens. INDONESIA. Sulawesi Tengah: Lake Poso, east and west shore of lake from where it empties at Tentena, S about 1.5 km, USNM 348722, 202 (6.3–27.5 mm), L. R. Parenti, K. D. Louie & boatmen, 11.viii.1995; Lake Poso at Peura, eastern shore about 10 km S of Tentena, USNM 350559, 103 (10.1–46.9 mm), L. R. Parenti, K. D. Louie, P. Beta & boatmen, 13.viii.1995; Lake Poso, eastern shore about 17 km S of Tentena, USNM 348723, 33 (17.4–47.3 mm, 6 of which have been cleared and counterstained), L. R. Parenti, K. D. Louie, P. Beta & Young, 12.viii.1995; Lake Poso, west bank of Poso R. where it empties into lake at Pamona Caves, USNM 350558, 92 (13.9–50.8 mm), L. R. Parenti, K. D. Louie, P. Beta & boatmen, 13.viii.1995, USNM 350560, 68 (12.9–51 mm), L. R. Parenti, K. D. Louie, P. Beta & Young, 11.viii.1995.

*ORYZIAS ORTHOGNATHUS* KOTTELAT, 1990A

SHARPJAWED BUNTINGI

FIGURES 29B, 51

*Oryzias orthognathus* Kottelat, 1990a: 54–56, fig. 3, tables 1 and 2 [type locality: Indonesia: Sulawesi



**Figure 51.** *Oryzias orthognathus* Kottelat, 1990a, Lake Poso, Sulawesi Tengah, Indonesia, ZSM/LIPI 4, female, 49.9 mm SL.

Tengah, Lake Poso, eastern shore between Tentena and Peura].- Kottelat *et al.*, 1993: 90 [listed; characters].- Seegers, 1997: 15, 22 [listed, photograph].

*Differential diagnosis:* *Oryzias orthognathus* is unique among ricefishes in having a lower jaw at an abrupt angle (nearly 90°) to the body axis; premaxilla correspondingly flat and extremely broad, with caniniform teeth in two irregular rows, outer teeth large and inner teeth fine, and no teeth on the medial portion of the premaxilla. *Oryzias orthognathus* differs from *O. nigrimas*, the other large (both reach over 50 mm SL), pelagic *Oryzias* in Lake Poso, by having 45–57, as opposed to 34–37, scales in a lateral series, seven, as opposed to six, pelvic-fin rays, and by lacking the distinctive sexual dichromatism of *O. nigrimas*.

*Description:* Elongate, maximum size of specimens examined 50.1 mm. Body slender, elongate, laterally compressed; body depth 17–22. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, lower jaw at an abrupt angle (nearly 90°) to the body axis, and longer than upper jaw. Dorsal and ventral body profile nearly straight from head to dorsal- and anal-fin origins. Dorsal surface of head slightly convex between orbits. Head length 22–26; snout length 7–8; eye moderate, 8–9, orbits do not project beyond dorsal surface of head. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales relatively small, cycloid and somewhat deciduous; 45–57 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane. Caudal fin slightly lunate, dorsal and ventral segmented caudal-fin rays longer than middle rays. Male with a short, slightly conical, tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla flat and extremely broad with distinct ascending process; caniniform teeth in two irregular rows, those in the outer row large and those in the inner row fine; no teeth on the medial portion of the

premaxilla. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular and may be indented anteriorly. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fourth or fifth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. Procurrent caudal-fin rays hooked at their base. Fifth ceratobranchial toothplates subtriangular, with pavement dentition anteriorly, followed by eight to nine discrete rows of unicuspid teeth, including a small, incomplete posterior row in the counterstained specimen of a female. Basihyal bone triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 8–11. Anal-fin rays 21–25. Pelvic-fin rays 7. Pectoral-fin rays 11–12. Principal caudal-fin rays  $i,4/5,i$ . Procurrent fin-rays, dorsal 5, ventral 6. Vertebrae 33 (13 + 20). Branchiostegal rays 5.

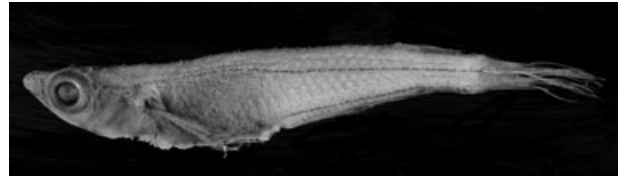
*Cytogenetic data:* Unknown.

*Colour in life:* Females golden brown on dorsal and lateral surfaces, whitish on belly. Males silvery grey on dorsal and lateral surfaces. Fins hyaline, except for caudal fin which has a yellow-orange dorsal and ventral margin, and one or two longitudinal purple lines on median rays (following Kottelat, 1990a: 56).

*Colour in alcohol:* Ground straw-coloured, belly pale whitish yellow. Dorsal surface of head and dorsal and lateral surface of body with dense dark brown to black chromatophores. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, an irregular, midlateral black line from the head to base of the caudal fin. Females with diffuse line of dark chromatophores dorsal from just posterior to anal-fin origin, along body just dorsal to anal-fin base to middle of caudal peduncle. Fins hyaline.

*Distribution and habitat:* A pelagic species endemic to Lake Poso, Sulawesi Tengah, Indonesia.

*Remarks:* The holotype, ZSM/LIPI 3 (50.0 mm), collected with the paratypes, below, was not examined by me. Data were augmented by those in Kottelat (1990a) and Uwa (1991b). Other common names for



**Figure 52.** *Oryzias pectoralis* Roberts, 1998, Nam Theun basin, Laos, CAS 92321, paratype, female, 17.5 mm SL.

this species are pointed head medaka or pointed head ricefish (Seegers, 1997: 22).

*Material examined:* Thirty specimens (16.8–50.1 mm SL).

Paratypes. INDONESIA. Sulawesi Tengah: Lake Poso, east shore between Tentena and Peura (field no. 88–26), M. Kottelat, 24–25.vi.1988, CMK 6362 (ex. CMK 6236) (female, 43.0 mm), counterstained, ZSM/LIPI 4, 8 (17.2–50.1 mm).

Non-type specimens. INDONESIA. Sulawesi Tengah: Lake Poso at Peura, eastern shore approx. 10 km S of Tentena, USNM 350562, 16 (16.8–46.5 mm, a male, 43.5 mm, and a female, 46.5 mm, of which have been cleared and counterstained), L. R. Parenti, K. D. Louie, P. Beta & boatmen, 13.viii.1995; Lake Poso, west bank of Poso R. where it empties into lake at Pamona Caves, USNM 350561, 5 (29.0–43.6 mm), L. R. Parenti, K. D. Louie, P. Beta & boatmen, 13.viii.1995.

#### ORYZIAS PECTORALIS ROBERTS, 1998

##### PECTORAL-FIN SPOT MEDAKA

##### FIGURES 15B, 17, 52

?*Oryzias* sp. 'Vietnam' Stallknecht, 1989: 128 [report of a possibly new ricefish species from Vietnam].

*Oryzias pectoralis* Roberts, 1998: 221, fig. 2e [type locality: Laos: Nam Theun Basin, rice paddy near Laksao, Nakai plateau].- Kottelat, 2001a: 10, 56, fig. 119 [report from Quang Ninh Prov., Vietnam; characters].- Kottelat, 2001b: 144, fig. 407 [characters, distribution].

*Differential diagnosis:* *Oryzias pectoralis* is a miniature ricefish (largest specimen known is 22.3 mm) that along with *O. minutillus*, *O. uwai* and *O. setnai* comprises a group of four miniatures characterized by a pigmented anal or urogenital region and an elongate caudal fin. *Oryzias pectoralis* differs from these other miniatures by having bony processes on the anal-fin rays and a larger caudal fin, with  $i,4/5,i$ , as opposed to  $i,3/4,i$ , principal rays. *Oryzias pectoralis* and *O. mekongensis* share a black spot on the dorsal portion of the pectoral-fin base. *Oryzias pectoralis* is

No claim to original US Government works.

readily distinguished from all other ricefishes by having dense melanophores on the abdominal part of the body, and extremely elongate, somewhat filamentous, caudal-fin rays.

*Description:* Miniature, maximum size of specimens examined 22.3 mm SL. Body compressed laterally, slender, depth 24. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile slightly convex or rounded from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 24–26 [24]; snout length 9–11 [10]; eye moderate to large, 8–10 [10], orbits meet dorsal surface of head. Basal portion of dorsal fin projects slightly beyond primary body profile. Scales relatively large, cycloid; 32–34 [32] in a lateral series. Dorsal and anal fin slightly rounded, no elongate fin rays; anal-fin rays with bony contact organs in males. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half. Caudal fin extremely elongate and filamentous. Male with short tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with a single irregular row of caniniform teeth; males with up to three large canine teeth on lateral ramus of the premaxilla and an opposing large tooth on the dentary. No preethmoid cartilage; ossified portions of mesethmoid suboval; anterior border of ethmoid cartilage straight. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone in line with third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and one accessory cartilage. Fifth ceratobranchial toothplate triangular, with anterior teeth in irregular rows anteriorly, followed by four discrete rows of unicuspid teeth, and no incomplete posterior row. Basihyal bone triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 absent.

Dorsal-fin rays 6–7. Anal-fin rays 19–20. Pelvic-fin rays 6. Pectoral-fin rays 9–10. Principal caudal-fin rays i,4/5,i. Procurent fin-rays, dorsal 3, ventral 3. Vertebrae 30–32 (10–11 + 19–21). Branchiostegal rays 5.

*Cytogenetic data:* Unknown.

*Colour in life:* Unknown.

*Colour in alcohol:* Ground colour pale straw. A diffuse row of melanophores from dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. A faint black line along the anal-fin base. Dorsal and anal fin interradiation membranes with scattered melanophores. Body covered with minute melanophores, most dense on abdomen. Discrete black blotch on dorsal half of pectoral-fin in both sexes. Perianal melanophores and discrete black blotch on base of first several anal-fin rays in some specimens.

*Distribution and habitat:* Nam Theun watershed (Mekong basin), Laos, and Quang Ninh Province, Vietnam, in rice paddies, swamps and sheltered areas of slow flowing rivers (Roberts, 1998; Kottelat, 2001a, b).

*Remarks:* Roberts (1998) noted that although this species was described from a single collection from the Nam Theun basin, it is likely to be more widely distributed in Laos, and possibly also Vietnam. Kottelat (2001a) reported *O. pectoralis* from Quang Ninh Province, Vietnam, but did not provide museum catalogue numbers.

*Material examined:* Nineteen specimens (16.1–22.3 mm SL).

Holotype. LAOS. Nam Theun basin: rice paddy near Laksao, Nakai plateau, CAS 92320 (male, 21.1 mm), T. R. Roberts, 19.xi.1995.

Paratypes. LAOS. Nam Theun basin: CAS 92321, 18 (16.1–22.3 mm, 4 of which have been cleared and stained solely with alizarin, 4 of which have been cleared and stained solely with alcian blue; 1 of which has been cleared and counterstained), collected with the holotype.

#### *ORYZIAS PROFUNDICOLA* KOTTELAT, 1990B

##### YELLOW-FINNED BUNTINGI

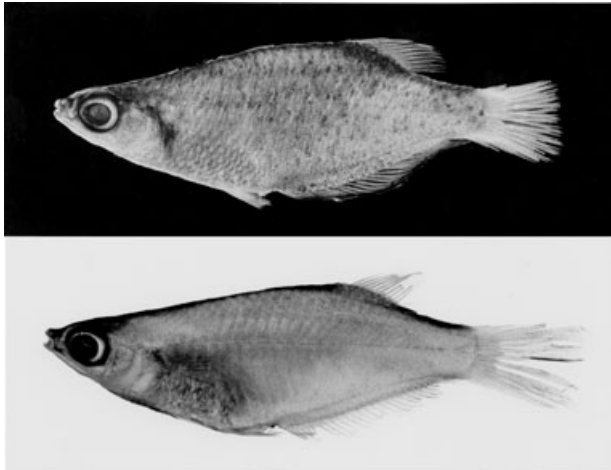
##### FIGURES 11C, 53

*Oryzias matanensis*.- Schrey, 1978: 334–338 [photograph, report from lakes Matano and Towoeti [Towuti], Sulawesi].

*Oryzias* sp. n., Kottelat, 1989b: 682, fig. 6 [report of an undescribed species from Sulawesi, Lake Towuti].

*Oryzias profundicola* Kottelat, 1990b: 161–164, figs 8–11, tables 5 and 6 [type locality: Indonesia:





**Figure 53.** *Oryzias profundicola* Kottelat, 1990b, Lake Towuti, Sulawesi Selatan, Indonesia, CMK 6485, male, 45.3 mm SL, above, female, 41.0 mm SL, below.

Sulawesi, Lake Towuti, Tandjung Posombuwang, about 3 km south of Timampu].- Kottelat *et al.*, 1993: 90 [listed; characters].- Parenti, 1993: 190, fig. 4 [dorsal and part of ventral portion of gill arches illustrated].- Seegers, 1997: 15, 22 [listed, photograph].- Albert *et al.*, 1999: 650 [brain weight].

*Differential diagnosis:* The Malili Lakes buntingi of Sulawesi, *O. marmoratus*, *O. profundicola* and *O. matanensis*, are readily distinguished from all other ricefishes by their distinctive pigmentation pattern: males have a series of regular midlateral blotches and irregular dark brown blotches on the entire lateral surface of the body. They are all somewhat deep bodied, reaching more than 26% SL; have a relatively large eye, diameter reaching 10% or more of SL; and have relatively long anal fins that range to over 24 anal-fin rays. *Oryzias profundicola* is the most deep-bodied ricefish, distinguished by the autapomorphy of a body depth that reaches 35% SL (vs. 34% or less in all other ricefishes), has the largest eyes (ranging from 9 to 13% SL), and the most anterior dorsal-fin (opposite vertebrae 18–19). *Oryzias profundicola* has 10–14 dorsal-fin rays, whereas *O. marmoratus* and *O. matanensis* have 8–12 and 8–9, respectively. Furthermore, *Oryzias marmoratus* and *O. profundicola* have 31–32 and 32–34 scales in a lateral series, respectively, whereas *O. matanensis* has 41–47.

*Description:* Intermediate, maximum size of specimens examined 46 mm SL. Body deep, 30–35, and compressed laterally. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or upper jaw slightly longer than lower jaw. Dorsal and ventral body profile arching

abruptly from head to dorsal- and anal-fin origins. Dorsal surface of head slightly convex just anterior to orbits. Head length 22–25; snout length 7–8; eye moderate to large, 9–13, orbits do not project beyond dorsal surface of head. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales of moderate size, cycloid and somewhat deciduous; 32–34 in a lateral series. Elongate, slightly filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half. Caudal fin truncate. Male with a short, slightly conical, tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two to three rows of external conical teeth on the upper and lower oral jaws, and thick and fleshy lips through which the tooth tips project. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to third pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by six to seven discrete rows of unicuspid teeth; small, incomplete posterior row. Basihyal bone triangular, basihyal cartilage elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 10–14. Anal-fin rays 26–29. Pelvic-fin rays 6. Pectoral-fin rays 10–11. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 5, ventral 6. Vertebrae 29 (11 + 18). Branchiostegal rays 5.

*Cytogenetic data:* Unknown.

*Colour in life:* (From Kottelat, 1990b: 162): Females light brown on head and body; fins hyaline, except for anal fin which has a grey margin. Males greenish brown on head and body. Diffuse dark brown blotches dispersed on body, including a row of five to eight larger blotches dorsal to midaxial stripe. Eyes blue. Filamentous dorsal-fin rays yellow along margin, and sometimes with a subproximal dark purple blotch between median dorsal-fin rays. Dorsal and ventral

margin of caudal fin bright yellow; one to two dark purple stripes on proximal half of membranes between median caudal-fin rays. A proximal row of dark purple to black spots on the membranes between anal-fin rays. Pelvic fin yellow; pectoral fin hyaline.

*Colour in alcohol:* Ground colour yellowish-grey. Dorsal surface of head and dorsal and lateral surface of body with dense dark brown to black chromatophores. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a diffuse midlateral black line from the head to base of the caudal fin. Females with diffuse line of dark chromatophores dorsal from a point just posterior to anal-fin origin, along body just dorsal to anal-fin base to middle of caudal peduncle. Fins of females and pectoral and pelvic fins of males hyaline. Bilobed urogenital papilla of females with dense small, dark grey chromatophores; urogenital papilla of males with larger and fewer scattered dark brown chromatophores. Dorsal- and anal-fin rays of males dusky except at their margins, which are hyaline. Caudal fin-rays of males dusky, dark line along proximal half of membranes between median caudal-fin rays; dorsal and anal margins of caudal fin hyaline.

*Distribution and habitat:* Endemic to Lake Towuti of the Malili River basin, Sulawesi Selatan, Indonesia (Parenti & Soeroto, 2004: fig. 1), along gently sloping shores with large boulders on a sand and pebble substrate (Kottelat, 1990b: 164).

*Remarks:* The holotype, ZSM/LIPI 12 (37.2 mm), from Lake Towuti, Tandjung Posombuwang, about 3 km S of Timampu by M. Kottelat, 29.vi.1988, was not examined by me. Data were augmented by those in Kottelat (1990b). Other common names for this species are yellow finned medaka or yellow finned ricefish (Seegers, 1997: 22).

*Material examined:* Twenty-one specimens (17.9–46 mm SL).

Paratypes. INDONESIA. Sulawesi Selatan: Lake Towuti, Watidi, 4–7 km E of Timampu (field number 89–15), M. Kottelat & A. Werner, 15.iii.1989, CMK 6485, 3 (female 40.5 mm, male 45.5 mm, and male 46 mm cleared and counterstained).

Non-type specimens. INDONESIA. Sulawesi Selatan: Lake Towuti, Sungei Lingkoburanga where it enters lake, approx. 8 km S of Timampu, USNM 348530, 6 (17.9–42.1 mm), L. R. Parenti, K. D. Louie & P. Haji, 9.viii.1995; Lake Towuti, first stream just S of Sungei



**Figure 54.** *Oryzias sarasinorum* (Popta, 1905), Lake Lindu, Sulawesi Tengah, Indonesia, female, CMK 6557, 53.4 mm SL, carrying a cluster of embryos between pelvic fins and body.

Lingkoburanga where it enters lake, USNM 348575, 12 (18.4–29.2 mm), L. R. Parenti, K. D. Louie & P. Haji, 9.viii.1995.

**ORYZIAS SARASINORUM (POPTA, 1905) COMB. NOV.**

SARASINS' BUNTINGI

FIGURE 54

*Haplochilus sarasinorum* Popta, 1905: 239 [type locality: Indonesia: Sulawesi Tengah, Lake Lindu].- Nijssen *et al.*, 1982: 70 [ZMA type specimens].

*Xenopoecilus sarasinorum*.- Regan, 1911a: 373 [as type by monotypy of new genus, *Xenopoecilus*].- Weber & de Beaufort, 1922: 378 [comparisons, distribution].- Rosen, 1964: 222–263 [in part, comparative anatomy, relationships, classification].- Parenti, 1987: 561 [in part, characters, comparisons].- Whitten *et al.*, 1987a: 295, table 4.10 [Sulawesi, distribution].- Kottelat & Sutter, 1988: 55 [note on type material].- Bleher, 1989: 30–32 [photograph, report of collection from Lake Lindu, Sulawesi Tengah].- Kottelat *et al.*, 1993: pl. 44 [photograph of female carrying cluster of embryos].- Seegers, 1997: 15, 18 [listed, photograph].- Sovrano *et al.*, 1999: 175–180; Sovrano *et al.*, 2001: 237–244; Sovrano, 2004: 385–391 [left-eye preference, brain specialization].- Parenti, 2005: 24 [photograph].

*Xenopoecilus saracinorum*. Incorrect spelling.- Naruse *et al.*, 1994: 47–52 [biology, comparisons].- Naruse, 1996: 3–7, figs 2–4 [relationships, karyology].

*Xenopoecilus sanarisorum*. Incorrect spelling.- Böhm, 1997: 642 [report from Lake Lindu; photographs].

*Differential diagnosis:* *Oryzias sarasinorum* is unique among ricefish in having a broad, silvery, lateral band that extends from the posterior margin of the head to the caudal peduncle in life and in some preserved specimens. The species is distinguished from other *Oryzias*, and is more similar to *Adrianichthys* species, by having a high number of scales in a lateral series (70–75 vs. 24–54). It is further distinguished from congeners by palatine and quadrate bones articulat-

ing via elongate flanges anteriorly, and by having 15, rather than 14 or fewer, precaudal vertebrae. Like *A. oophorus*, it is a pelvic brooder.

*Description:* Elongate, maximum size of specimens examined 58 mm SL. Body slender, elongate, laterally compressed; body depth 13–15. Size and extent of abdominal concavity between pelvic fins and anal fin could not be determined. Mouth terminal, upper and lower jaws slightly elongate; lower jaw extends beyond upper jaw. Dorsal and ventral body profile nearly straight from head to dorsal- and anal-fin origins. Head length 29; snout length 11; eye moderate, 9, orbits do not project beyond dorsal surface of head. Fleshy, incompletely scaly, basal portion of dorsal and anal fin project slightly beyond primary body profile. Scales small, cycloid and relatively deciduous; 70–75 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray not connected to body via a membrane. Caudal fin slightly lunate, dorsal and ventral segmented caudal-fin rays longer than middle rays. Urogenital papilla single-lobed in females. Males with subconical tubular urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two to three irregular rows of caniniform teeth; enlarged, caniniform teeth posteriorly on the premaxilla and dentary of males. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. Palatine and quadrate articulate via elongate flanges that overlap anteriorly. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra; lateral process of pelvic bone attaches to fifth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. Fifth ceratobranchial toothplates subtriangular, with pavement dentition anteriorly, followed by five to six discrete rows of unicuspid teeth; small, incomplete posterior row in males. Basihyal bone triangular, basihyal cartilage elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 11–12. Anal-fin rays 21–22. Pelvic-fin rays 7. Pectoral-fin rays 10–11. Principal caudal-fin rays i,5/6,i. Procurrent fin-rays, dorsal 6, ventral 6–8. Vertebrae 34(15 + 19). Branchiostegal rays 5–6.

*Cytogenetic data:* A fused chromosome constitution (Naruse, 1996: 6, fig. 3) with two pairs of large meta-centric chromosomes. Chromosome constitution of *O. sarasinorum* is otherwise considered to be poorly known.

*Colour in life:* Ground colour beige-yellowish with a 'central "luminous" stripe' that reflects light strongly (Bleher, 1989: 32).

*Colour in alcohol:* Ground colour pale yellow, belly pale whitish yellow. A broad, silvery, lateral band extends from posterior margin of the head to caudal peduncle in some specimens, other specimens bleached. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, an irregular, midlateral black line from the posterior border of the head to base of the caudal fin. Fins hyaline to dusky.

*Distribution and habitat:* Endemic to Lake Lindu, Sulawesi Tengah (Parenti & Soeroto, 2004: fig. 1). *Oryzias sarasinorum* is a pelagic species; adults live in the open waters of Lake Lindu (Bleher, 1989; Böhm, 1997); females carry clusters of embryos between the pelvic fins and abdomen.

*Remarks:* The description of *Haplochilus sarasinorum* was based on '25 Exemplare von 57–69 mm. [total Länge]' (Popta, 1905: 239). Part of the syntypic series, collected from Lake Lindu by Fritz and Paul Sarasin, vii.1902, has been examined, below. Additional syntypes in the Naturhistorisches Museum Basel, Switzerland (see Kottelat & Sutter, 1988: 55), not examined by me, are: NMBA 1014–1020 (7), NMBA 1032–1037 (6) and NMBA 1040 (1). I do not designate a lectotype from among the syntypes because I have been unable to locate the entire type series. Also, the poor condition of examined syntypes precludes the advantage of designating any one specimen as the primary type. The bodies of many specimens are dehydrated and distorted (see illustration in original description), making some measurements imprecise, in particular depth of the body and of the caudal peduncle. The two ricefish species now known from Lake Lindu, *Oryzias sarasinorum* (Popta, 1905) and *Oryzias bonneorum*, described above, cannot be confused given the material at hand. Popta (1905) clearly indicated that her new species had 75 scales in a lateral series and remarked on the silvery body, characters of *O. sarasinorum*, not *O. bonneorum*. One of Popta's (1905) syntypes, AMNH 20481, a specimen cleared and stained some decades ago, agrees better with *O. bonneorum* than *O. sarasinorum* in having, for example, 13 + 18 = 31 vertebrae. Another common name for this species is Sarasins' minnow (Seegers, 1997: 18). The second specimen in AMNH 20481 was probably the one illustrated in Rosen (1964). If so, some of his illustrations are probably of *O. bonneorum*, not *O. sarasinorum*. The outline drawings of *O. sarasinorum* on Rosen's (1964) figure 3D,E are probably of that species.



**Figure 55.** *Oryzias setnai* (Kulkarni, 1940), Bombay, India, USNM 197764, male, 18.5 mm SL, above; female, 16.5 mm SL, below. Left pectoral fin in female specimen is folded anteriorly.

*Material examined:* Fourteen specimens (35–58 mm SL).

*Syntypes.* INDONESIA. Sulawesi Tengah: Lake Lindu: RMNH 7664, 3 (54–58 mm), ZMA 100.648, 1 (54 mm), BMNH 1914.2.13: 26–27, 2 (55–57 mm), formerly in NMBA, and AMNH 20481 (ex. ZMA 100.648), 2 [possibly = *O. bonneorum*] (35 mm and a second heavily dissected specimen of unrecorded SL, both cleared and stained for bone), F. & P. Sarasin, vii.1902.

*Non-type specimens.* INDONESIA. Sulawesi Tengah: Lake Lindu, C. Bonne, iv.1939, ZMA 100.649, 2, dehydrated, (39–58 mm), 2.5 km N of Tomato, H. Bleher, 24.vi.1989, CMK 6556, 3, males, (42.6–49.7 mm, the largest cleared and counterstained for bone and cartilage), CMK 6557, female, (53.4 mm).

**ORYZIAS SETNAI** (KULKARNI, 1940) COMB. NOV.

ANU

FIGURES 16B, 20A, 21, 26A, 27B, 55

*Horaichthys setnai* Kulkarni, 1940: 385–421, figs 2–20 [type locality: Navlaki, Kathiawar coast, north and south of Bombay, India].- Hubbs, 1941: 446–447 [characters, relationships].- Hubbs & Hubbs, 1945: 289–295, table XIX [bilateral asymmetry].- Kulkarni, 1948: 65–119 [comparative anatomy, osteology].- Silas, 1959: 256 [distribution].- Rosen & Bailey, 1963: fig. 3d, 28 [skull, comparison with poeciliid *Tomeurus*].- Rosen, 1964 [comparative anatomy, classification].- Menon & Yazdani, 1968: 141 [syntypes listed].- Rosen & Parenti, 1981: 6–16, fig. 15a [dorsal gill arch osteology].- Grier, 1984: 833–839 [testis structure, spermatophore formation].- Parenti, 1987: 561 [characters, comparisons].- Grier & Collette, 1987: 309–311 [comparison of spermatophore formation with that of *Zenarchopterus*].- Talwar & Jhingran, 1991: 746–747 [characters, distribution].- Parenti, 1993: 190, fig. 10 [caudal skeleton].- Menon, 1999: 267 [listed from India, citations].- Parenti & Grier, 2004: 336 [atherinomorph testis type, listed].

*Differential diagnosis:* *Oryzias setnai* is a highly autapomorphic species, distinguished from all other ricefishes by males with first six rays of the anal fin elaborate and elongate, separated from rest of the fin as an intromittent organ, used to transfer spermatophores (barbed, encapsulated sperm bundles) to females, who lay fertilized eggs; second to sixth anal-fin rays of females elongate and thickened; females bilaterally asymmetric with only the left pelvic bone and pelvic-fin rays and urogenital opening left of the ventral midline in most specimens; testes single (as opposed to paired), bulbous; maxilla absent. Head length the smallest of all ricefishes, ranging from 14 to 19% SL, as opposed to 20% or more in all other ricefishes. Dorsal-fin origin the most posterior among ricefishes; the dorsal-fin lies above vertebra 27 as opposed to above or anterior to vertebra 24. Teeth are enlarged posteriorly on the premaxilla in both sexes, as in *O. javanicus* and *O. carnaticus*, not considered as close relatives. *Oryzias setnai* shares with three other miniatures, *O. pectoralis*, *O. uwai* and *O. minutillus*, a pigmented anal or urogenital region and an elongate, rounded caudal fin. *Oryzias setnai* is hypothesized to be most closely related to *O. uwai* and *O. minutillus* with which it shares  $i,3/4,i$  rather than  $i,4/5,i$  principal caudal-fin rays, a medial extension of the ethmoid cartilage, and anterior anal-fin rays elongate and set off from the rest of the fin. *Oryzias setnai* and *O. uwai* share an interrupted, horizontal dark brown bar that runs from the eye to the lower jaw; a mesethmoid that is uniquely subrectangular, rather than round or oval; and a first epibranchial that is cartilaginous, not ossified.

*Description:* Miniature, maximum size of specimens examined 22.5 mm SL. Body elongate, slender, compressed laterally, body depth 14–20. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth subterminal, lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile relatively straight from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 14–19; snout length 3–4; eye moderate, 7–8, orbits meet dorsal surface of head. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales relatively large, cycloid; 32–34 in a lateral series. Anal-fin rays of males without bony contact organs; first six anal-fin rays elaborate and elongate, separated from rest of the fin as an intromittent organ used to transfer spermatophores (encapsulated sperm bundles) to females (Kulkarni, 1940). Females bilaterally asymmetric in having only left pelvic bone and pelvic-fin rays, and urogenital opening left of ventral midline in

most specimens. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin with elongate middle rays.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with a single, irregular row of caniniform teeth; males and females with two or three enlarged posterior teeth on the premaxilla, no enlarged teeth on the dentary; tooth tips project through lips. Maxilla absent. No preethmoid cartilage; ossified portions of mesethmoid subrectangular; ethmoid cartilage rectangular with anterior projection. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of second vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone in line with third pleural rib in females, fourth pleural rib in males. Caudal skeleton with two epural bones; two ventral accessory cartilages. Fifth ceratobranchial toothplates triangular, with teeth in irregular rows anteriorly, followed by 2–3 rows of unicuspid teeth. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial 1 cartilaginous; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 6–7. Anal-fin rays 27–32. Pelvic-fin rays 5. Pectoral-fin rays 10. Principal caudal-fin rays i,3–4/4,i. Procurrent fin-rays, dorsal 2–3, ventral 3–4. Vertebrae 31–34 (8–10 + 21–25). Branchiostegal rays 4.

*Cytogenetic data:* Unknown.

*Colour in life:* Nearly transparent, hence one common name, Indian glaskilli; discrete blackish spot just posterior to orbit; scattered minute melanophores on dorsal and anal fin interradiial membranes, body, and upper jaw.

*Colour in alcohol:* A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. An interrupted, horizontal dark brown bar from the eye to the tip of the lower jaw in some specimens. A faint black line along the anal-fin base. Urogenital region with dense brown to black spot(s). Dorsal and anal fin interradiial membranes, body and upper jaw, with scattered, minute melanophores.

*Distribution and habitat:* Fresh and brackish water habitats along the west coast of India from near the Gulf of Kutch to Trivandrum (Kerala) near the southern extent of the Indian subcontinent (Silas, 1959; Talwar & Jhingran, 1991).

*Remarks:* A detailed osteological and soft anatomical study was included as part of Kulkarni's (1940) original description of *Horaichthys setnai*. Data were augmented by those in Kulkarni (1940).

Böhlke (1953: 54) refers to the CAS-SU type material by stating: "These specimens are called syntypes because of Kulkarni's statement in the original description: "Type-specimens.- No. F13203/1, Zoological Survey of India (Indian Museum), Calcutta." The lot, CAS-SU 35960, was collected from brackish water near Bombay, India, by C. V. Kulkarni in 1938. Here, I also recognize USNM 118687 (4) and UMMZ 131839 (4) as part of the syntype series. These eight specimens were collected from Bombay by Kulkarni in 1938. Half of these specimens were sent later that year by S. L. Hora of the Zoological Survey of India to George S. Myers, then of Stanford University, and half to Carl L. Hubbs, then of the University of Michigan. Myers subsequently donated his four specimens to the USNM where they were accessioned on 1.iv.1941. A hand-written note, part of the accession records, dated 22.iv.1941, from Myers to Leonard P. Schultz, then of the USNM, states: 'As to the *Horaichthys*, I sent you all 4 of the first specimens Hora sent to me (as detailed in Kulkarni's paper) since Hora later sent me more material. The four you have are the ones on which I based my opinion of the fish, as sent to Hora and Kulkarni.' Specimens of the new fish were sent to Myers and to C. L. Hubbs, then at the University of Michigan, prior to its description, '... to obtain views of other ichthyologists interested in this group of fishes' (Kulkarni, 1940: 380). I likewise view the specimens in USNM 118687 and UMMZ 131839 as syntypes because they were on hand as Kulkarni prepared the description of his new species. An additional 87 syntypes are catalogued as ZSI F13202/1-13204/1 (Menon & Yazdani, 1968). An additional lot, USNM 197764, also collected by Kulkarni, no date recorded, is not considered part of the syntype series because it has a much later date of accession (12.ii.1964) and cannot be confirmed as part of the material Kulkarni had at hand when he was preparing his description. I do not designate a lectotype from among the syntypes because I am uncertain if the above syntypes comprise the entire type series.

Other common names for this species include thready killifish or thready top-minnow (Talwar & Jhingran, 1991: 746), Malabar ricefish (Robins *et al.*, 1991) and Indian Glaskilli (Seegers, 1997: 18).



**Figure 56.** *Oryzias sinensis* Chen *et al.*, 1989, Hua-gong Yuan, Yunnan Province, China, USNM 309183, male, 22.9 mm SL.

*Material examined:* 335 specimens (7.5–22.5 mm SL). Syntypes. INDIA. Brackish water near Bombay: CAS-SU 35960, 17 (10 males, 17.9–19 mm, 8 females, 19–21.3 mm), USNM 118687, 4 (2 males, 2 females, 17.5–20 mm), UMMZ 131839, 4 (18–20 mm), C.V. Kulkarni, 1938.

Non-type specimens. INDIA. Karnataka State: Shambavi R., 30 km N of Mangalore, about 1–2 km inland, CAS 56255, 53 (19 males, 29 females, 5 juv. or sex undet., 11.0–18 mm, 4 of which, 2 males and 2 females, have been cleared and counterstained), USNM 277482, 106 (7.5–22.5 mm, 4 of which have been cleared and stained with alcian blue, 2 of which have been counterstained, 2 of which have been cleared and stained with alizarin), BMNH 1985.9.11: 1–45, 27 (10.5–17.5 mm), ANSP 157315, 34 (10.0–17.0 mm, 4 of which have been cleared and stained solely with alizarin), T. R. Roberts, i.1985; Bombay Prov., Uttan in Thana dist., USNM 197764, 6 (2 males, 4 females, 16.5–18.3 mm); AMNH 36576, 84 (10–18.1 mm, 10 of which have been cleared and counterstained), C. V. Kulkarni, no date recorded.

ORYZIAS SINENSIS CHEN *ET AL.*, 1989

CHINESE MEDAKA

FIGURE 56

*Oryzias latipes*.- Nichols, 1943: 234 [in subgenus *Oryzias*, synonymy; characters in specimens from Shandong (Shantung), China].- Uwa & Parenti, 1988: 159–164 [population from Kazakhstan].- Uwa *et al.*, 1988: 332–340 [karyotype; distribution in south-western China].- Roberts, 1998: 221 [as synonym of *O. latipes*, comparisons].- Lin *et al.*, 1999 [Taiwan population compared with ricefish from Japan and mainland China].- Tzeng *et al.*, 2006: 285, 291–293 [population demographics and distribution].  
*Aplocheilus* sp.- Abdil'dayev & Dubitskiy, 1974: 287–289 [report of a population from the Ili River basin, Kazakhstan].

*Oryzias latipes sinensis* Chen *et al.*, 1989: 239 [type locality: China: Kunming, Yunnan Province; as subspecies of *O. latipes* (Temminck & Schlegel, 1846)].- Chen, 1990: 227–228 [distribution in Yunnan].- Yu,

1996: 30 [listed in checklist of vertebrates from Taiwan].- Uwa, 1991a: 361–367 [karyology, relationships].- Seegers, 1997: 15 [listed].- Tzeng *et al.*, 2006: 288, table 1, fig. 2 [population demographics and distribution].

*Oryzias sinensis*.- Kottelat, 2001a: 10, 56, fig. 120 [expected to be in Vietnam; characters].- Kottelat, 2001b: 144–145, fig. 408 [characters, distribution].- Kim & Park, 2002: 302 [Korea].- Youn, 2002: 219, 545 [Korea].- Jang *et al.*, 2003: 119 [distribution in South Korean national parks].

*Oryzias* spec. 'China', possibly = *sinensis* Chen *et al.*, 1989.- Seegers, 1997: 22 [photographs of male and female from southern China].

*Differential diagnosis:* *Oryzias sinensis* is a miniature species of *Oryzias* (maximum size recorded by Chen *et al.*, 1989 is 26 mm) and member of the biarmed chromosome group of Uwa (1986), along with *O. luzonensis*, *O. latipes*, *O. curvinotus* and the miniature *O. mekongensis* that have anal-fin rays of approximately the same length, forming a 'parallelogram-shaped' fin, and chromosome arms numbering 58 or more. *Oryzias sinensis* and *O. mekongensis* both have the first pleural rib on the second, rather than the third, vertebra. They are like *O. latipes* and *O. luzonensis*, and differ from *Oryzias curvinotus* by having bony processes on the pectoral-fin rays. *Oryzias sinensis* is distinguished from all other ricefish species with a biarmed chromosome constitution by having a diploid chromosome number of 46, as opposed to 48 (Table 2).

*Description:* Miniature, maximum size of specimens examined 26 mm SL. Body compressed laterally, body depth 18–21. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile slightly convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 24–29; snout length 6–9; eye moderate, 7–9, orbits meet dorsal surface of head. Basal portion of dorsal and anal fin project somewhat beyond primary body profile. Scales relatively large, cycloid; 29–30 in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal- and pectoral-fin rays with bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion; pelvic fins meet or extend beyond anal-fin origin in some specimens. Caudal fin rounded to truncate. Male with a short, tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular

rows of caniniform teeth; males with two or three enlarged posterior teeth on the premaxilla and dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage straight. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of second vertebra; first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fourth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone and a second accessory cartilage or bone. Fifth ceratobranchial toothplates subtriangular, with teeth in three irregular rows anteriorly, followed by three discrete rows of unicuspid teeth and no incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 6–7. Anal-fin rays 16–20. Pelvic-fin rays 6. Pectoral-fin rays 8–10. Principal caudal-fin rays i,4/5,i. Procurrent fin-rays, dorsal 5–6, ventral 6. Vertebrae 28–30 (10–11 + 18–19). Branchiostegal rays 5.

*Cytogenetic data:* *Oryzias sinensis* has a biarmed chromosome constitution, with  $2n = 46$  chromosomes, comprising three metacentric, eight or nine submetacentric, one or two subtelocentric and nine, ten or 13 acrocentric pairs. One large chromosome pair has been reported in populations from Kunming, Shanghai and west Korea. Chromosome arm number (NF) ranges from 68 to 70. Cell size was recorded as 1.7 pg DNA per nucleus (Chen *et al.*, 1989; Uwa, 1991a; Table 2).

*Colour in life:* Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum.

*Colour in alcohol:* A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin that continues onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. Females with a subrectangular, males with a smaller, subtriangular black peritoneum. A faint black line along the anal-fin base. Dorsal and anal fin interradiation mem-

branes with scattered melanophores. I have examined five lots of *Oryzias* from Taiwan, ANSP 76433, CAS-SU 23166, CAS-SU 23115 and FMNH 59113, all now dehydrated and distorted, and USNM 356076, collected in 1999. One specimen in the ANSP lot, an adult male, 26 mm, has a unique colour pattern: the midlateral black line prominent in many ricefish species is interrupted, i.e. formed by individual blotches along the midlateral portion of the body from approximately the second scale posterior to the pectoral-fin base to the caudal peduncle where the blotches are small and indistinct. There is an irregular row of indistinct blotches dorsal to, and two irregular rows of blotches ventral to, the midlateral row.

*Distribution and habitat:* Widely distributed throughout continental Eurasia from as far west as Kazakhstan, Mekong basin in Laos, Thailand and Yunnan, Irawaddy, Salween, Yuan Jiang and Nanpang Jiang basins, south-western China, Taiwan and west Korea in clear water swamps (Kottelat, 2001b: 144; my personal observation in Taiwan).

*Remarks:* *Oryzias latipes sinensis* was included by Yu (1996: 30) in a checklist of the vertebrates of Taiwan. Ricefish had long been thought to be extinct in Taiwan, but were rediscovered there in 1993 (Lin *et al.*, 1999; Tzeng *et al.*, 2006). Meristic data are supplemented by those in Chen *et al.* (1989). Another common name for this species is Chinese ricefish (Seegers, 1997: 22). I have not examined the type specimens which are maintained at the Kunming Institute of Zoology (holotype no. 8610002).

The material listed below includes the collections of ricefishes made in China in the 1920s and 1930s and sent to the Smithsonian Institution by David Crockett Graham and now housed in the USNM. Graham was a missionary and naturalist who made or oversaw extensive, historically valuable natural history collections in mountainous south-west China. Many of his collections are from the vicinity of 'Suifu', now Yibin, at the confluence of the Mi and Jinsha (a tributary of the Yangtze or Chang Jiang) rivers, in Sichuan Province near the border with Yunnan.

*Material examined:* 800 specimens (7.8–26 mm SL). CHINA (no specified locality or province unknown). USNM 112459, 1 (21 mm), Y. T. Chu, USNM 86529, 21 (12.8–19.2 mm), D. C. Graham, 14.ii.1924; West China. USNM 87388, 3 (21.9–24 mm), D. C. Graham, 1925.

CHINA. Yunnan Prov.: Hua-gong Yuan, type locality near Kunming Institute of Zoology, USNM 309183, 10 (17.2–23.4 mm, 2 of which, 17.2–18.5 mm, have been cleared and counterstained); Huahongdong,

Kunming, CAS 60238, 12 (18–21 mm), H. Uwa, R.-F. Wang, and Y.-R. Chen, 27.x.1986; Baoshan Prefecture, Tengchong market, C. J. Ferraris & X.-Y. Chen, 24.x.1998, CAS 207735, 39 (12–21.8 mm); Baoshan Prefecture, Longchuanjiang trib. at Longkou, Qushi township, 25°26'4"N, 98°35'30"E, C. J. Ferraris & X.-Y. Chen, 25.x.1998, CAS 207736,80 (13.7–22.6 mm); Lang Yun Yuan, USNM 89212, 3 (22.5–25.7 mm), Y. Ching, 23.vi.1928.

Chongqing (Chungking) Prov., USNM 130054, 1 (13.5 mm), D. C. Graham, ix.1930, USNM 91706, 1 (female, 22.7 mm), D. C. Graham, 6–27.v.1930. USNM 91702, 4 (16.7–20.7 mm), D. C. Graham, 6–27.v.1930. Yenchingku, near Wanxian (Wanshien), AMNH 10483, 1 (17 mm), Third Asiatic Expedition, W. Granger, xi.1921–i.1922.

Sichuan (Szechuan) Prov.: Chengdu (Chengtu), USNM 102373, 1 (14.5 mm), USNM 102985, 9 (all dried), D. C. Graham, 1–6.i.1936, USNM 91662, 1 (18 mm), D. C. Graham, 1.iv.1930–14.vi.1930. Qianwei (Chien Way), USNM 89207, 11 (14–21 mm), D. C. Graham, 4.i.1928. Yibin (Suifu), USNM 130191, 9 (16–21 mm), D. C. Graham, 1922, USNM 86523, 7 (14–22 mm), D. C. Graham, 17.i.1924, USNM 87453, 98 (11–18 mm), D. C. Graham, x.1924, USNM 89152, 32 (11–20 mm), D. C. Graham, 1.iii.1928, USNM 89153, 1 (22 mm), D. C. Graham, iv.1928, USNM 89154, 1 (22 mm), D. C. Graham, v.1928, USNM 89205, 39 (13–20 mm), D. C. Graham, 31.i.1928, USNM 89206, 6 (13–20 mm), D. C. Graham, 30.xii.1927, USNM 89208, 20 (12–21 mm), D. C. Graham, 18–24.i.1928, USNM 89311, 3 (17–22 mm), D. C. Graham, 21.vi.1928, USNM 89337, 1 (15 mm), D. C. Graham, 24.x.1928, USNM 91630, 163 (14–22 mm, 4 of which have been cleared and counterstained), D. C. Graham, 15.iii–15.iv.1929, USNM 91597, 1 (15 mm), D. C. Graham, 20.iv.1929, USNM 91605, 2 (19–26 mm), D. C. Graham, 1.vi.1929, USNM 130147, 1 (18 mm), D. C. Graham, 1.vi.1929, USNM 91644, 2 (18–20 mm), D. C. Graham, 25–26.xi.1929, USNM 130055, 2 (19–21 mm), D. C. Graham, 16.xii.1929, USNM 91693, 3 (18–21 mm), D. C. Graham, 1930, USNM 130056, 6 (distorted), D. C. Graham, 25–29.iii.1930, USNM 130057, 3 (16–21 mm), D.C. Graham, 1.iv.1930. Changlin-Chien, USNM 89312, 1 (19 mm), D. C. Graham, 17.vi.1928. Yashan, USNM 86673, 2 (16–18 mm), D. C. Graham, iii.1924. Ya'an (Yachow), USNM 89328, 12 (7–18 mm), D. C. Graham, 8–11.vii.1928.

Shandong (Shantung) Prov., Hwang He (Yellow R.), Jinan (Tsinan), AMNH 10344, 72 (18.7–26 mm, 6 of which have been cleared and counterstained), Third Asiatic Expedition, W. Granger, Summer, 1924.

Shanghai Prov., Shanghai, CAS 58031, 24 (20.5–25.5 mm), Univ. Tokyo laboratory stock.



**Figure 57.** *Oryzias timorensis* (Weber & de Beaufort, 1922), Timor, Indonesia, ZMA 100.571, lectotype, female, 29.5 mm SL.

TAIWAN. Shori: FMNH 59113, 6 (14–17 mm), M. Oshima, no date; I-Lan Co.; USNM 356076, 15 (7.8–20.8 mm, 2 of which, a female, 20.8 mm, and a male, 16.5 mm, have been cleared and counterstained), L. R. Parenti, S.-M. Lin & G. Shang, 18.iii.1999.

KAZAKHSTAN. Alma Alta: Iri R., AMNH 38404, 16 (10–25 mm, 2 of which, 21.9–23.7, have been cleared and counterstained), N. V. Parin, 21.vi.1974.

*ORYZIAS TIMORENSIS* (WEBER &  
DE BEAUFORT, 1922)

TIMOR RICEFISH

FIGURE 57

*Aplocheilus celebensis*.- Weber & de Beaufort, 1912: 135 [listed].- Nijssen *et al.*, 1982: 70 [ZMA type specimens].

*Haplochilus timorensis* Weber & de Beaufort, 1922: 373 [type locality: Indonesia: Timor, Mota Talau].- Nijssen *et al.*, 1982: 70 [ZMA type specimens].

*Aplocheilus timorensis*.- Weber & de Beaufort, 1922: 373 [synonymy; characters].- Aurich, 1935: 104 [listed, key].

*Oryzias timorensis*.- Hoedeman, 1958: 27–28, fig. 6g [frontal squamation pattern].- Rosen, 1964: 227 [classification in family Oryziatidae].- Nolf, 1985: 68, fig. 52D [illustration of right saccular otolith].- Uwa & Parenti, 1988: 159 [morphometric comparisons].- Parenti, 1993: 187–188, fig. 9 [dorsal-fin osteology].- Larson & Pidgeon, 2004: 196 [listed from East Timor].

*Differential diagnosis:* *Oryzias timorensis* and *O. celebensis* are both relatively small ricefishes, reaching not more than 35 mm SL, with truncate caudal fins and a colour pattern characterized by dark brown to black vertical bars on the sides of the body, as in the larger-bodied Malili lakes buntingi. *Oryzias timorensis* differs from *O. celebensis* in having a relatively anterior dorsal-fin origin, opposite vertebra 21 (as opposed to 22–23), a more slender body (body depth 21–24 as opposed to 22–26), and a dorsal body profile



arching gently from head to dorsal-fin origin (as opposed to having a relatively straight dorsal body profile).

*Description:* Small, maximum size of specimens examined 30 mm SL. Body compressed laterally, body depth 21–24 [24]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, jaws subequal or lower jaw projecting slightly beyond upper jaw. Dorsal body profile arching gently from head to dorsal-fin origin; ventral body profile somewhat convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 27–30 [28]; snout length 7–8 [7]; eye small to moderate 6–8 [8], orbits meet dorsal surface of head. Basal portion of dorsal and anal fin do not project significantly beyond primary body profile. Scales relatively large, cycloid; 31–34 [34] in a lateral series. Elongate, filamentous dorsal- and anal-fin rays in males; anal-fin rays without bony contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal portion. Caudal fin truncate. Male with a short, tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with distinct ascending process; premaxilla and dentary with two irregular rows of caniniform teeth; males with two or three enlarged posterior teeth on the premaxilla and dentary; tooth tips project through lips. No preethmoid cartilage; ossified portions of mesethmoid disc-shaped; anterior border of ethmoid cartilage irregular. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of third vertebra (rudimentary pleural rib on second vertebra on left side of the cleared and stained female); first epipleural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epipleural bones; lateral process of pelvic bone attaches to fourth (complete) pleural rib. Caudal skeleton with two epural bones; one or two ventral accessory bones (in one specimen, the single element appears to be composed of two accessory bones fused together at their proximal portions). Fifth ceratobranchial toothplates subtriangular, with teeth in irregular rows anteriorly, followed by six discrete rows of unicuspid teeth, including a small, incomplete posterior row. Basihyal bone relatively short and triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial elements fully ossified; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 9–10 [9]. Anal-fin rays 17–19 [19]. Pelvic-fin rays 6. Pectoral-fin rays 10–11 [11]. Princi-

pal caudal-fin rays  $i, 4/5, i$ . Procurrent fin-rays, dorsal 4–5 [5], ventral 5–6 [6]. Vertebrae 30–31 (12–13 + 17–19) [30 (13 + 17)]. Branchiostegal rays 5.

*Cytogenetic data:* Uwa & Parenti (1988: 164) predicted that *O. timorensis* has large or fused metacentric chromosomes and a correspondingly low number of chromosomes as in *O. celebensis*.

*Colour in life:* Body translucent, and with melanophore pattern as described below in alcohol. Females with a subrectangular, males with a smaller, subtriangular silvery peritoneum and both sexes with a silvery operculum.

*Colour in alcohol:* Specimens faded in preservative; ground colour a uniform pale yellowish brown. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin where it ends in an indistinct blotch, and a faint black line along the anal-fin base. The colour pattern was described by Weber & de Beaufort (1922: 374) as 'Brownish, belly darkish (peritoneum shining through). A fine dark line ending in a more-or-less conspicuous black blotch at end of caudal. A similar line runs above base of anal and unites with that of the other side behind anal. A median dorsal line present in young specimens. A row of darkish blotches on middle of sides of trunk generally present.'

*Distribution and habitat:* Endemic to Timor, Indonesia, the easternmost limit of the range of ricefishes (Fig. 2).

*Remarks:* Morphometric and meristic data are supplemented by those in Uwa & Parenti (1988). The only specimens examined by me are the eight syntypes originally catalogued as ZMA 100.571. I designate an adult male, 29.5 mm, ZMA 100.571, herein as lectotype of *Haplochilus timorensis* Weber & de Beaufort, 1922. The remaining seven syntypes, now paralectotypes, comprise ZMA 120.761. Data for the lectotype are given in brackets, above.

*Material examined:* Eight specimens (17–30 mm SL). Lectotype of *Haplochilus timorensis*. INDONESIA. Timor: Mota Talau, M. Oyens, 1911, ZMA 100.571 (male, 29.5 mm), designated herein. Paralectotypes of *Haplochilus timorensis*. INDONESIA. Timor: Mota Talau, ZMA 120.761 (ex. ZMA 100.571), (2 males, 5 females, 17.0–30.0 mm, including 1 female, 25.7 mm cleared and counterstained).



**Figure 58.** *Oryzias uwai* Roberts, 1998, Sittang basin, Myanmar, CAS 92310, paratype, male, 10.6 mm SL.

*ORYZIAS UWAI* ROBERTS, 1998

UWA'S MEDAKA

FIGURES 16A, 20B, 58

*Oryzias minutillus*.- Uwa *et al.*, 1988: 332–339 [in part, Rangoon; distribution, comparison with *O. minutillus* and specimens of *O. latipes* referred here to *O. sinensis*].

*Oryzias uwai* Roberts, 1998: 218–219, fig. 2c [type locality: Myanmar: Rangoon, Irrawaddy and Sittang basins].

**Differential diagnosis:** *Oryzias uwai* is a miniature ricefish (largest specimen known is just 16.1 mm SL), hypothesized to be closely related to *Oryzias minutillus* and *O. setnai* with which it shares  $i,3/4,i$  rather than  $i,4/5,i$  principal caudal-fin rays, a medial extension of the ethmoid cartilage, and anterior anal-fin rays elongate, set off from the rest of the fin, and from which it differs by having larger pelvic fins, with six rather than five rays in most specimens. *Oryzias uwai* and *O. setnai* share an interrupted, horizontal dark brown bar that runs from the eye to the lower jaw; a mesethmoid that is uniquely subrectangular, rather than round or oval; and a first epibranchial that is cartilaginous, not ossified. Four miniatures, *O. uwai*, *O. pectoralis*, *O. setnai* and *O. minutillus*, have a pigmented anal or urogenital region and an elongate, rounded caudal fin, a character also of *O. hubbsi* and *O. mekongensis*.

**Description:** Miniature, maximum size of specimens examined 16.1 mm SL. Body compressed laterally, slender, body depth 21–24 [24]. No pronounced abdominal concavity between pelvic fins and anal fin. Mouth terminal, lower jaw projecting slightly beyond upper jaw. Dorsal body profile relatively straight from head to dorsal-fin origin; ventral body profile slightly convex from head to anal-fin origin. Dorsal surface of head slightly convex just anterior to orbits. Head length 29–30 [30]; snout length 9–10 [10]; eye moderate to large, 8–10 [10], orbits meet dorsal surface of head. Basal portion of dorsal fin projects slightly beyond primary body profile. Scales relatively large, cycloid; 26–27 [27] in a lateral series (scale count approximate). Dorsal and pectoral fins elongate, anal fin slightly rounded; anal-fin rays without bony

contact organs. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half; pelvic fins large, extend to or beyond anal fin origin in females. Caudal fin with elongate middle rays. Male with short tubular urogenital papilla; female with bilobed urogenital papilla.

Premaxilla short and broad with barely distinct ascending process; premaxilla and dentary with a single irregular row of caniniform teeth; no large canine teeth on lateral ramus of the premaxilla or dentary of males. No preethmoid cartilage; mesethmoid cartilaginous or weakly ossified, when ossified, mesethmoid small and suboval; ethmoid cartilage rectangular with anterior projection. No flanges on the ventral surface of the palatine and the quadrate. Dorsal ramus of hyomandibula not distinctly bifid, single cartilage articulates with sphenotic and pterotic. Lacrimal sensory canal carried in open bony groove. First pleural rib on parapophysis of second vertebra; first epipleural bone attaches to second vertebra; lateral process of pelvic bone in close association with third or fourth pleural rib. Caudal skeleton with two epural bones; one ventral accessory bone. Anteriormost dorsal and ventral procurrent rays hooked at base. Fifth ceratobranchial toothplate triangular, with teeth in irregular rows anteriorly, followed by two discrete rows of unicuspid teeth, and no incomplete posterior row. Basihyal bone triangular, basihyal cartilage extremely elongate and rectangular. Epibranchial 1 cartilaginous; epibranchial 2 notably smaller than the other epibranchial elements.

Dorsal-fin rays 6–7. Anal-fin rays 18–21. Pelvic-fin rays 6. Pectoral-fin rays 7–8. Principal caudal-fin rays  $i,3/4,i$ . Procurrent fin-rays, dorsal 4, ventral 5. Vertebrae 25–28 (9–10 + 16–18). Branchiostegal rays 4.

**Cytogenetic data:** Karyotype data for *O. minutillus* from Thailand were reported by Uwa *et al.* (1988). Although they referred the now type specimens of *O. uwai* (then all CAS-SU 40208) to *O. minutillus*, they had no fresh Myanmar specimens from which karyotype data could be obtained.

**Colour in life:** Unknown.

**Colour in alcohol:** Ground colour pale straw. A diffuse row of melanophores from the dorsal surface of the head to the dorsal-fin origin, a midlateral black line from the head to base of the caudal fin, continues faintly onto the caudal fin on the membrane just dorsal and ventral to the first ray above and below the midline, respectively. An interrupted, horizontal dark brown stripe from the eye to the tip of the lower jaw, faded or indistinct in larger specimens. A faint black line along the anal-fin base. Dorsal and anal fin interradiation membranes with faint scattered melano-

phores or hyaline. Perianal region with dense brown to black spot. Pectoral and pelvic fins hyaline. Body with small melanophores.

*Distribution and habitat:* Irrawaddy, Rangoon and Sittang basins, Myanmar.

*Material examined:* 118 specimens (8.6–16.1 mm SL). Holotype. MYANMAR. Rangoon: CAS-SU 40208, holotype (male, 16.1 mm), A. W. Herre, xi.1940. Paratypes. MYANMAR. Rangoon: CAS-SU 69787 19 (12.2–15.9 mm), collected with the holotype; Sittang R. drainage, Dayame Chaung, 1.5 km. N of Daik-U., T. R. Roberts, 9.iii.1985; Pegu Div., CAS 60739, 6 (12.4–13.8 mm); Mandalay rice paddies, T. R. Roberts, 20–24.iv.1993, CAS 92309, 20 (8.6–13.5 mm, 7 of which, 9.3–11.6 mm, have been cleared and stained solely with alizarin); Sittang basin, backwater of Bai Nar Chaung near Dabeinzu, K. E. Witte, 4.iv.1996, CAS 92310, 72 (8.8–15.9 mm, 10 of which, 10.2–14.8 mm, have been cleared and stained solely with alizarin, 4 of which, 12–13.5 mm, have been cleared and counterstained).

#### GENUS †*LITHOPOECILUS* DE BEAUFORT, 1934

†*Lithopoecilus* de Beaufort, 1934: 180–181 [type species: †*Lithopoecilus brouweri* de Beaufort, 1934, by monotypy].

†*Lithofundulus* Frickhinger, 1991: 707, 1995: 707 [unjustified emendation of †*Lithopoecilus*].

#### †*LITHOPOECILUS BROUWERI* DE BEAUFORT, 1934

†*Lithopoecilus brouweri* de Beaufort, 1934: 180–181 [type locality: Gimpoe Basin, central Sulawesi].- Rosen, 1964: 225 [relationships].- Patterson, 1993: 638 [listed, relationships].

†*Lithofundulus brouweri* Frickhinger, 1991: 707, 1995: 707 [listed as †*Lithofundulus brouweri* de Beaufort, an apparent lapsus for †*Lithopoecilus brouweri* de Beaufort, 1934; age given as Miocene; characters, photograph].

*Remarks:* The following description is from the English translation of Frickhinger's (1991) atlas of fossil fishes (Frickhinger, 1995: 707): 'Small fishes of slender shape. Head elongate. Eyes large. Snout somewhat pointed. Dorsal fin small, in the posterior half of the body, opposite the considerably larger anal fin.' The caption to a photograph of the fossil indicates its length as approximately 6 cm, and its age as Miocene. †*Lithopoecilus* was considered by de Beaufort (1934) to be intermediate between *Oryzias* and the larger adrianichthyids, *Adrianichthys* species herein. The size and characters of the specimen as

given by Frickhinger do not contradict that assessment, although I have not examined the fossil and cannot place it unambiguously in either *Oryzias* or *Adrianichthys*.

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## APPENDIX 1

## CHARACTER CODING

- (1) *Vomer*: Present [0]; absent [1].
- (2) *Articular surface of fourth epibranchial bone*: Slightly expanded [0]; greatly expanded [1].
- (3) *Ceratobranchial epiphysis*: Simple cartilaginous connection [0]; complex cartilaginous connection [1].
- (4) *Toothplate on the fourth ceratobranchial bone*: Present [0]; absent [1].
- (5) *Palatine shape and articulation with upper jaw*: Palatine head relatively narrow and without strong connection to maxilla [0]; palatine head expanded and articulating with the maxilla (or premaxilla) via a dense ligament [1].
- (6) *Rostral cartilage*: Present [0]; absent [1].
- (7) *Meckel's cartilage and articular bone*: Meckel's cartilage runs the length of the dentary and the articular bone is orientated anteriorly relative to the body axis [0]; Meckel's cartilage about one-half length of the dentary and articular bone is orientated dorsally relative to the body axis [1].
- (8) *Symphysis between left and right dentary*: Ligamentous [0]; cartilaginous [1].
- (9) *Metapterygoid*: Present [0]; absent [1].
- (10) *Pterygoquadrate cartilage*: Confluent with dorsal margin of palatine and quadrate [0]; enlarged dorsally [1].
- (11) *Mandibulo-lacrimonal ligament*: Present [0]; absent [1].
- (12) *Dermosphenotic position relative to sphenotic*: Anterior [0]; lateral or posterior [1].
- (13) *Supracleithrum*: Present [0]; Absent [1].

- (14) *Posttemporal bone*: Forked [0]; simple [1].
- (15) *Anterior ramus of coracoid*: Narrow, with cartilaginous tip [0]; broad, particularly at point of articulation with the cleithrum, without cartilage [1].
- (16) *Ventral accessory bone in caudal skeleton*: Absent [0]; present [1].
- (17) *Position of the lateral branch of the posterior lateral line nerve in adults and type of scales*: Mid-lateral, with few or only weakly developed pored lateral line scales [0]; ventral, with pored lateral line scales [1]; ventral, without pored lateral line scales [2].
- (18) *Size at hatching*: Large, greater than 4.5 mm [0]; small, 4.5 mm or less [1].
- (19) *Maximum adult body size*: 60 mm SL or larger [0]; greater than 50 mm SL and less than 60 mm SL [1]; greater than 40 mm SL and less than 50 mm SL [2]; greater than 26 mm SL and less than 40 mm SL [3]; 26 mm SL or less [4].
- (20) *Body depth*: Slender bodied, reaching no more than 26% SL in adults [0]; somewhat deep bodied, reaching more than 26% and less than 33% SL [1]; extremely deep bodied, reaching more than 33% SL in adults [2].
- (21) *Scales in a lateral series*: Fewer than 40 [0]; 40–57 [1]; 58–65 [2]; 70 or more [3].
- (22) *Head length*: Small to moderate, less than 30% SL [0]; large, 31% or more SL [1].
- (23) *Snout length*: Less than 12% SL [0]; 12% SL or greater [1].
- (24) *Eye size*: Small to moderate diameter, reaching no greater than 9% SL [0]; large diameter, reaching 10% or more of SL [1].
- (25) *Urogenital papillae of female*: Single lobed [0]; bilobed [1]; bilobed and greatly enlarged [2]. (26) *Dark brown to black nuptial coloration of males*: Absent [0]; present [1].
- (27) *Dark brown blotches on body of males*: Absent [0]; Present at midbody [1]; present as a series of regular midlateral brown blotches and irregular dark brown blotches on entire lateral surface of body [2].
- (28) *Interrupted, horizontal dark brown bar from the eye to the lower jaw*: Absent [0]; present [1].
- (29) *Brown to black spot at base of pectoral fin*: Absent [0]; present [1].
- (30) *Pigmented urogenital region*: Absent [0]; present [1].
- (31) *Colour on caudal fin in life*: Hyaline to dusky [0]; yellow to orange dorsal and ventral caudal-fin margins [1].
- (32) *Pigmentation pattern on caudal-fin rays in alcohol-preserved material*: Hyaline or dusky [0]; distinct dark brown to black lines on middle rays [1].
- (33) *Preethmoid cartilage(s)*: Absent [0]; paired cartilages [1]; single, median cartilage [2].
- (34) *Ethmoid cartilage anterior margin*: Straight and entire [0]; irregular and indented anteromedially [1]; distinct anteromedial projection [2].
- (35) *Ethmoid cartilage lateral margin*: Entire [0]; distinct notch bordered posteriorly by anterior margin of lateral ethmoid [1].
- (36) *Ethmoid region of skull in lateral and dorsal view*: Convex and narrow [0]; flat and broad [1].
- (37) *Mesethmoid ossification*: Round or oval [0]; rectangular [1]; semicircle anteriorly with subrectangle posteriorly [2]; indented anteriorly [3].
- (38) *Orbits*: Confluent with dorsal surface of head [0]; project somewhat beyond dorsal profile of head [1]; project markedly beyond dorsal profile of head [2].
- (39) *Lacrimal sensory canals*: Open [0]; closed [1].
- (40) *Preopercular sensory canal and dermosphenotic (posterior infraorbital) canal*: Separate [0]; continuous [1].
- (41) *Upper and lower jaw length*: Subequal [0]; upper jaw extends beyond lower jaw [1].
- (42) *Premaxilla*: Distinct articular and ascending processes [0]; flat and broad without distinct articular and ascending processes [1].
- (43) *Maxilla*: With small to broad dorsal process that overlaps the premaxilla [0]; relatively straight and without dorsal process [1].
- (44) *Oral jaw teeth size and arrangement*: One to three irregular rows of conical teeth on the premaxilla and dentary [0]; up to five irregular rows of small, villiform teeth that form a pavement dentition and no large teeth posteriorly [1].
- (45) *Enlarged teeth posteriorly on premaxilla*: Absent in both males and females [0]; present in males only [1]; present in males and females [2].
- (46) *Enlarged teeth posteriorly on dentary*: Absent in both males and females [0]; present in males, rarely in females [1].
- (47) *Hyomandibula articulation with otic region of skull*: Bifid head [0]; single head [1].
- (48) *Articulation of palatine and quadrate bones*: Palatine and quadrate articulate via elongate flanges that overlap anteriorly [0]; no flanges on the ventral surface of the palatine and the quadrate [1].
- (49) *Ventral hypohyal*: Broad posterior ramus [0]; elongate blade-like ramus along the ventral face of the anterior ceratohyal [1]; blunt posterior ramus [2].
- (50) *Epibranchial one*: Ossified [0]; cartilaginous [1].
- (51) *Epibranchial two*: Fully ossified, with a broad point of articulation with the ceratobranchial cartilage [0]; notably smaller than the other epi-

- branchial bones and without a broad point of articulation with the ceratobranchial cartilage, may be cartilaginous or absent in some specimens [1].
- (52) *Ceratobranchial bone five toothplate*: Triangular [0]; rectangular or suboval [1].
- (53) *Fifth ceratobranchial tooth arrangement*: Diagonal rows [0]; horizontal rows [1].
- (54) *Branchiostegal-ray number*: Six or more [0]; five [1]; four [2].
- (55) *Branchiostegal ray arrangement*: Posterior two branchiostegal rays articulate with a relatively large posterior ceratohyal [0]; posteriormost branchiostegal ray articulates with a truncated posterior ceratohyal [1].
- (56) *Total number of vertebrae*: 36 or more [0]; 34 or fewer [1].
- (57) *Number of precaudal vertebrae*: 14 or more [0]; 12–13 [1]; 11 or fewer [2].
- (58) *First pleural rib*: Attaches to third vertebra [0]; attaches to second vertebra [1].
- (59) *Transverse processes of first vertebra*: Elongate [0]; short or absent [1].
- (60) *Pectoral-fin ray number*: 13 or more [0]; 9–12 [1]; eight or fewer [2].
- (61) *Pectoral-fin ray bony processes*: Absent [0]; present [1].
- (62) *Pelvic bone*: No lateral strut or process [0]; lateral strut expanded dorsally, with or without flared, wing-like processes [1]; lateral strut needle-like and elongate [2].
- (63) *Pelvic-fin rays*: End anterior to anal fin [0]; extend posterior to anal-fin origin in males [1].
- (64) *Pelvic-fin position*: Pelvic fins anterior, in line with pleural rib of vertebra five or less [0]. Pelvic fins in line with pleural rib of vertebra six or seven [1]; pelvic fins posterior, in line with pleural rib of vertebra eight or higher [2].
- (65) *Pelvic-fin ray number*: Six or seven [0]; five [1].
- (66) *Pelvic-fin connection to body*: Medialmost pelvic-fin ray separate from body [0]; medialmost pelvic-fin ray connected along one-half its length to body via a membrane [1].
- (67) *Dorsal-fin ray number*: 14 or more [0]; 11–13 [1]; 8–10 [2]; fewer than eight [3].
- (68) *Dorsal-fin position*: Posterior, origin at or posterior to vertebra 22 [0]; anterior, origin anterior to vertebra 22 [1].
- (69) *Anal-fin ray number*: 23 or fewer [0]; 24 or more [1].
- (70) *Anal-fin ray bony processes*: Absent [0]; present [1].
- (71) *Anal-fin shape and relative length of fin rays*: Anteriormost fin ray short followed by elongate rays with rays decreasing in length posteriorly [0]; anal-fin rays approximately the same length [1]; anterior portion of fin with elongate rays set off from rest of fin [2].
- (72) *Caudal-fin shape*: Lunate [0]; truncate [1]; rounded and with somewhat elongate middle rays [2].
- (73) *Principal caudal-fin rays*: More principal rays in dorsal lobe or a number equal to that in the ventral lobe [0]; more principal rays in the ventral than in the dorsal lobe, numbering i,5/6,i or greater [1]; i,4/5,i [2]; i,3/4,i [3].
- (74) *Procurrent caudal-fin ray number*: High, more than four dorsal and five ventral rays [0]; low, four or fewer dorsal and five or fewer ventral rays [1].
- (75) *Procurrent caudal-fin ray shape*: Simple [0]; hooked [1].
- (76) *Epural number*: One ossified epural [0]; two or three ossified epurals [1]; two epurals, one ossified, one cartilaginous [2].
- (77) *Reproductive mode*: Oviparous, external fertilization, embryos develop outside of female [0]; oviparous, external or facultatively internal fertilization, embryos develop for at least some time while attached to female [1]; ovoviviparous or viviparous, internal fertilization [2].
- (78) *Abdominal concavity*: Absent [0]; present [1].
- (79) *Testis morphology*: Paired, symmetric [0]; single lobed [1]; paired, bilaterally asymmetric [2].
- (80) *Egg size*: Small, less than 1.5 mm in diameter [0]; large, 1.5 mm in diameter or greater [1].
- (81) *Genome size*: 1.9 pg per nucleus or greater [0]; less than 1.9 pg per nucleus [1].
- (82) *Diploid chromosome number*: 46–48 diploid chromosomes [0]; 44 or fewer diploid chromosomes [1].
- (83) *Chromosome arm number*: 48 or fewer [0]; 58 or more [1].
- (84) *Chromosome constitution*: Acrocentric chromosomes (monoarmed) [0]; Metacentric chromosomes (biarmed or fused) [1].
- (85) *Extremely large metacentric chromosomes*: Absent [0]; present [1].

## APPENDIX 2

DATA MATRIX. NA = NOT APPLICABLE; ? = UNKNOWN

Character	1	2	3	4	5	6	7	8	9	10
Taxon										
<i>Melanotaenia</i>	0	0	0	0	0	0	0	0	0	0
<i>Rivulus</i>	0	0	0	0	0	0	0	0	0	0
Zenarchopteridae	0	0	0	0	0	0	0	0	0	0
<i>A. kruyti</i>	1	1	1	1	1	1	1	1	1	1
<i>A. roseni</i>	1	1	1	1	1	1	1	1	1	1
<i>A. poptae</i>	1	1	1	1	1	1	1	1	1	1
<i>A. oophorus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. sarasinorum</i>	1	1	1	1	1	1	1	1	1	1
<i>O. bonneorum</i>	1	1	1	1	1	1	1	1	1	1
<i>O. orthognathus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. nigrimas</i>	1	1	1	1	1	1	1	1	1	1
<i>O. nebulosus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. profundicola</i>	1	1	1	1	1	1	1	1	1	1
<i>O. matanensis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. marmoratus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. celebensis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. timorensis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. luzonensis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. latipes</i>	1	1	1	1	1	1	1	1	1	1
<i>O. curvinotus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. mekongensis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. javanicus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. carnaticus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. dancena</i>	1	1	1	1	1	1	1	1	1	1
<i>O. hubbsi</i>	1	1	1	1	1	1	1	1	1	1
<i>O. haugiensis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. pectoralis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. minutillus</i>	1	1	1	1	1	1	1	1	1	1
<i>O. sinensis</i>	1	1	1	1	1	1	1	1	1	1
<i>O. uwai</i>	1	1	1	1	1	1	1	1	1	1
<i>O. setnai</i>	1	1	1	1	1	1	1	1	1	1
Character	11	12	13	14	15	16	17	18	19	20
Taxon										
<i>Melanotaenia</i>	0	0	0	0	0	0	0	0	0	1
<i>Rivulus</i>	0	0	0	0	0	0	0	0	0	0
Zenarchopteridae	0	0	0	0	0	0	1	0	0	0
<i>A. kruyti</i>	1	1	1	1	1	1	2	?	0	0
<i>A. roseni</i>	1	1	1	1	1	1	2	?	0	0
<i>A. poptae</i>	1	1	1	1	1	1	2	?	0	0
<i>A. oophorus</i>	1	1	1	1	1	1	2	0	0	0
<i>O. sarasinorum</i>	1	1	1	1	1	1	2	?	1	0
<i>O. bonneorum</i>	1	1	1	1	1	1	2	?	1	0
<i>O. orthognathus</i>	1	1	1	1	1	1	2	?	1	0
<i>O. nigrimas</i>	1	1	1	1	1	1	2	?	1	0
<i>O. nebulosus</i>	1	1	1	1	1	1	2	?	3	0
<i>O. profundicola</i>	1	1	1	1	1	1	2	?	2	2
<i>O. matanensis</i>	1	1	1	1	1	1	2	?	2	1
<i>O. marmoratus</i>	1	1	1	1	1	1	2	?	2	1

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APPENDIX 2 *Continued*

Character	11	12	13	14	15	16	17	18	19	20
<i>O. celebensis</i>	1	1	1	1	1	1	2	?	3	0
<i>O. timorensis</i>	1	1	1	1	1	1	2	?	3	0
<i>O. luzonensis</i>	1	1	1	1	1	1	2	?	3	0
<i>O. latipes</i>	1	1	1	1	1	1	2	1	3	0
<i>O. curvinotus</i>	1	1	1	1	1	1	2	?	3	0
<i>O. mekongensis</i>	1	1	1	1	1	1	2	?	4	0
<i>O. javanicus</i>	1	1	1	1	1	1	2	?	3	1
<i>O. carnaticus</i>	1	1	1	1	1	1	2	1	3	1
<i>O. dancena</i>	1	1	1	1	1	1	2	1	3	2
<i>O. hubbsi</i>	1	1	1	1	1	1	2	?	4	0
<i>O. haugiagensis</i>	1	1	1	1	1	1	2	?	4	1
<i>O. pectoralis</i>	1	1	1	1	1	1	2	?	4	0
<i>O. minutillus</i>	1	1	1	1	1	1	2	?	4	0
<i>O. sinensis</i>	1	1	1	1	1	1	2	?	4	0
<i>O. uwai</i>	1	1	1	1	1	1	2	?	4	0
<i>O. setnai</i>	1	1	1	1	1	1	2	1	4	0
Character	21	22	23	24	25	26	27	28	29	30
Taxon										
<i>Melanotaenia</i>	0	0	0	0/1	0	0	0	0	0	0
<i>Rivulus</i>	0/1	0	0	0/1	0	0	0	0	0	0
Zenarchopteridae	0/1	0	1	0/1	0	0/1	0	0	0	0
<i>A. kruyti</i>	3	1	1	1	0	0	0	0	0	0
<i>A. roseni</i>	2	1	1	0	0	0	0	0	0	0
<i>A. poptae</i>	3	1	1	0	0	0	0	0	0	0
<i>A. oophorus</i>	2	0	0	0	0	0	0	0	0	0
<i>O. sarasinorum</i>	3	0	0	0	0	0	0	0	0	0
<i>O. bonneorum</i>	0	1	0	0/1	0	0	1	0	0	0
<i>O. orthognathus</i>	1	0	0	0	1	0	0	0	0	0
<i>O. nigrimas</i>	0	0	0	1	1	1	0	0	0	0
<i>O. nebulosus</i>	0	0	0	0	1	1	0	0	0	0
<i>O. profundicola</i>	0	0	0	1	1	0	2	0	0	0
<i>O. matanensis</i>	1	0	0	1	1	0	2	0	0	0
<i>O. marmoratus</i>	0	0	0	1	1	0	2	0	0	0
<i>O. celebensis</i>	0	0	0	0	1	0	1	0	0	0
<i>O. timorensis</i>	0	0	0	0	1	0	1	0	0	0
<i>O. luzonensis</i>	0	0	0	0	1	0	0	0	0	0
<i>O. latipes</i>	0	0	0	0	1	0	0	0	0	0
<i>O. curvinotus</i>	0	0	0	0	1	0	0	0	0	0
<i>O. mekongensis</i>	0	0	0	0	1	0	0	0	1	0
<i>O. javanicus</i>	0	0	0	0	2	0	0	0	0	0
<i>O. carnaticus</i>	0	0	0	0	2	0	0	0	0	0
<i>O. dancena</i>	0	0	0	0	1	0	0	0	0	0
<i>O. hubbsi</i>	0	1	0	1	2	0	0	0	0	0
<i>O. haugiagensis</i>	0	1	0	1	2	0	0	0	0	0
<i>O. pectoralis</i>	0	0	0	1	1	0	0	0	1	1
<i>O. minutillus</i>	0	0	0	0	1	0	0	0	0	1
<i>O. sinensis</i>	0	0	0	0	1	0	0	0	0	0
<i>O. uwai</i>	0	0	0	1	1	0	0	1	0	1
<i>O. setnai</i>	0	0	0	0	1	0	0	1	1	1

APPENDIX 2 *Continued*

Character	31	32	33	34	35	36	37	38	39	40
Taxon										
<i>Melanotaenia</i>	0	0	0	0	0	0	0	0	0	0
<i>Rivulus</i>	0	0	0	0	0	1	0	0	0	0
Zenarchopteridae	0	0	0	0	0	0	0	0	0	0
<i>A. kruyti</i>	?	0	1	0	0	1	0	2	0	0
<i>A. roseni</i>	?	0	1	0	0	1	0	2	0	0
<i>A. poptae</i>	0	0	2	0	0	1	2	1	0	0
<i>A. oophorus</i>	0	0	2	0	0	1	2	1	0	0
<i>O. sarasinorum</i>	0	1	0	1	0	0	0	0	0	0
<i>O. bonneorum</i>	0	0	0	1	0	0	0	0	0	0
<i>O. orthognathus</i>	0	0	0	1	0	0	0	0	0	1
<i>O. nigrimas</i>	0	0	0	1	0	0	0	0	0	1
<i>O. nebulosus</i>	?	0	0	1	0	0	0	0	0	1
<i>O. profundicola</i>	1	1	0	1	1	0	0	0	0	1
<i>O. matanensis</i>	0	0	0	1	1	0	0	0	0	1
<i>O. marmoratus</i>	1	1	0	1	1	0	0	0	0	1
<i>O. celebensis</i>	1	1	0	1	1	0	0	0	0	1
<i>O. timorensis</i>	?	0	0	1	1	0	0	0	0	1
<i>O. luzonensis</i>	1	1	0	1	1	0	3	0	0	1
<i>O. latipes</i>	1	1	0	0	1	0	3	0	0	1
<i>O. curvinotus</i>	1	1	0	0	1	0	0	0	0	1
<i>O. mekongensis</i>	1	1	0	2	1	0	0	0	0	1
<i>O. javanicus</i>	1	1	0	0	1	0	0	0	1	1
<i>O. carnaticus</i>	0	1	0	1	1	0	0	0	1	1
<i>O. dancena</i>	0	1	0	1	1	0	0	0	1	1
<i>O. hubbsi</i>	0	1	0	0	1	0	0	0	1	1
<i>O. haugiangensis</i>	?	1	0	0	1	0	0	0	1	1
<i>O. pectoralis</i>	?	1	0	0	1	0	0	0	0	1
<i>O. minutillus</i>	0	0	0	2	1	0	0	0	0	1
<i>O. sinensis</i>	1	1	0	0	1	0	0	0	0	1
<i>O. uwai</i>	?	1	0	2	1	0	1	0	0	1
<i>O. setnai</i>	0	1	0	2	1	0	1	0	0	1
Character	41	42	43	44	45	46	47	48	49	50
Taxon										
<i>Melanotaenia</i>	0	0	0	0	1	0	0	0	0	0
<i>Rivulus</i>	0	0	0	0	0	0	0	0	0	0
Zenarchopteridae	0	0	0	0	1	0	0	0	0	0
<i>A. kruyti</i>	1	1	1	1	0	0	0	0	1	0
<i>A. roseni</i>	1	1	1	1	0	0	0	0	1	0
<i>A. poptae</i>	0	1	1	1	0	0	0	0	1	0
<i>A. oophorus</i>	0	1	1	1	0	0	0	0	1	0
<i>O. sarasinorum</i>	0	0	0	0	1	0	1	0	2	0
<i>O. bonneorum</i>	0	0	0	0	1	1	1	1	2	0
<i>O. orthognathus</i>	0	0	0	0	0	0	1	1	2	0
<i>O. nigrimas</i>	0	0	0	0	1	1	1	1	2	0
<i>O. nebulosus</i>	0	0	0	0	1	1	1	1	2	0
<i>O. profundicola</i>	0	0	0	0	1	1	1	1	2	0
<i>O. matanensis</i>	0	0	0	0	1	1	1	1	2	0
<i>O. marmoratus</i>	0	0	0	0	1	1	1	1	2	0
<i>O. celebensis</i>	0	0	0	0	1	1	1	1	2	0
<i>O. timorensis</i>	0	0	0	0	1	1	1	1	2	0

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APPENDIX 2 *Continued*

Character	41	42	43	44	45	46	47	48	49	50
<i>O. luzonensis</i>	0	0	0	0	1	1	1	1	2	0
<i>O. latipes</i>	0	0	0	0	1/2	1	1	1	2	0
<i>O. curvinotus</i>	0	0	0	0	1	1	1	1	2	0
<i>O. mekongensis</i>	0	0	0	0	1	1	1	1	2	0
<i>O. javanicus</i>	0	0	0	0	2	1	1	1	2	0
<i>O. carnaticus</i>	0	0	0	0	2	1	1	1	2	0
<i>O. dancena</i>	0	0	0	0	1	1	1	1	2	0
<i>O. hubbsi</i>	0	0	0	0	1	1	1	1	2	0
<i>O. haugiangensis</i>	0	0	0	0	1	1	1	1	2	0
<i>O. pectoralis</i>	0	0	0	0	1	0	1	1	2	0
<i>O. minutillus</i>	0	0	0	0	0	0	1	1	2	0
<i>O. sinensis</i>	0	0	0	0	1	1	1	1	2	0
<i>O. uwai</i>	0	0	0	0	0	0	1	1	2	1
<i>O. setnai</i>	0	0	NA	0	2	0	1	1	2	1
Character	51	52	53	54	55	56	57	58	59	60
Taxon										
<i>Melanotaenia</i>	0	0	0	0	0	0	0	0	0	0
<i>Rivulus</i>	0	0	0	0	0	0	0	0	0	0
Zenarchopteridae	0	0	NA	0	0	0	0	0	0	0
<i>A. kruyti</i>	0	0	0	1	0	0	0	0	0	0
<i>A. roseni</i>	0	0	0	1	0	0	0	0	0	0
<i>A. poptae</i>	0	0	0	0/1	0	0	0	0	0	0
<i>A. oophorus</i>	0	0	0	0/1	1	0	0	0	0	1
<i>O. sarasinorum</i>	1	1	1	0/1	1	1	0	0	0	1
<i>O. bonneorum</i>	1	1	1	0/1	1	1	1	0	0	1
<i>O. orthognathus</i>	1	1	1	1	1	1	1	0	1	1
<i>O. nigrimas</i>	1	1	1	1	1	1	0/1	0	1	1
<i>O. nebulosus</i>	1	1	1	1	1	1	1/2	0/1	1	1
<i>O. profundicola</i>	1	1	1	1	1	1	2	0	1	1
<i>O. matanensis</i>	1	1	1	1	1	1	1	0	1	1
<i>O. marmoratus</i>	1	1	1	1	1	1	1	0	1	1
<i>O. celebensis</i>	1	1	1	0/1	1	1	1/2	0/1	1	1
<i>O. timorensis</i>	1	1	1	1	1	1	1	0/1	1	1
<i>O. luzonensis</i>	1	1	1	0/1	1	1	1/2	0	1	1
<i>O. latipes</i>	1	1	1	0/1	1	1	1/2	0/1	1	1
<i>O. curvinotus</i>	1	1	1	1/2	1	1	1/2	0	1	1
<i>O. mekongensis</i>	1	1	1	1/2	1	1	2	1	1	2
<i>O. javanicus</i>	1	1	1	1	1	1	1/2	0	1	0/1
<i>O. carnaticus</i>	1	1	1	1	1	1	2	0	1	0/1
<i>O. dancena</i>	1	1	1	1/2	1	1	2	0	1	1
<i>O. hubbsi</i>	1	1	1	1/2	1	1	2	0	1	1/2
<i>O. haugiangensis</i>	1	1	1	0/1	1	1	2	0	1	1
<i>O. pectoralis</i>	1	1	1	1	1	1	2	0	1	1
<i>O. minutillus</i>	1	1	1	1/2	1	1	2	1	1	2
<i>O. sinensis</i>	1	1	1	1	1	1	2	1	1	1/2
<i>O. uwai</i>	1	1	1	2	1	1	2	1	1	2
<i>O. setnai</i>	1	0	1	2	1	1	2	1	1	1

APPENDIX 2 *Continued*

Character	61	62	63	64	65	66	67	68	69	70
Taxon										
<i>Melanotaenia</i>	0	0	0	0	0	0	NA	NA	0/1	0
<i>Rivulus</i>	0	0	0	2	0	0	0	0	0	0
Zenarchopteridae	0	1	0	2	0	0	0	0	0	0
<i>A. kruyti</i>	0	1	0	2	0	0	0	0	1	0
<i>A. roseni</i>	0	1	0	1	0	0	0/1	0	1	0
<i>A. poptae</i>	0	1	0	2	0	0	1	0	1	0
<i>A. oophorus</i>	0	1	0	2	0	0	2	0	0	0
<i>O. sarasinorum</i>	0	1	0	1	0	0	1	1	0	0
<i>O. bonneorum</i>	0	1	0	1	0	0	1	1	0	0
<i>O. orthognathus</i>	0	1	0	1	0	1	1/2	0	0/1	0
<i>O. nigrimas</i>	0	1	0	1	0	1	1/2	0	0/1	0
<i>O. nebulosus</i>	0	1	0	0/1	0	1	2	1	0	0
<i>O. profundicola</i>	0	1	0	0	0	1	0/1/2	1	1	0
<i>O. matanensis</i>	0	1	0	0	0	1	2	0/1	0/1	0
<i>O. marmoratus</i>	0	1	0	0	0	1	1/2	1	0/1	0
<i>O. celebensis</i>	0	1	0	0/1	0	1	2	0	0	0
<i>O. timorensis</i>	0	1	0	0	0	1	2	1	0	0
<i>O. luzonensis</i>	1	1	0	0	0	1	3	1	0	1
<i>O. latipes</i>	1	1	0	0	0/1	1	3	0	0	1
<i>O. curvinotus</i>	0	1	0	0	0	1	3	0	0	1
<i>O. mekongensis</i>	1	1	0	0	0/1	1	3	1	0	1
<i>O. javanicus</i>	0	2	0	0	0/1	1	3	0	0/1	1
<i>O. carnaticus</i>	0	2	0	0	0	1	3	0	0/1	1
<i>O. dancena</i>	0	2	0	0	0	1	3	0	0/1	1
<i>O. hubbsi</i>	0	1	0	0	0	1	3	1	0	1
<i>O. haugiangensis</i>	0	2	0	0	0	1	3	1	0	1
<i>O. pectoralis</i>	0	1	0	0	0	1	3	0	0	1
<i>O. minutillus</i>	0	1	0	0	1	1	3	1	0	0
<i>O. sinensis</i>	1	1	1	0	0	1	3	0/1	0	1
<i>O. uwai</i>	0	1	0	0	0	1	3	1	0	0
<i>O. setnai</i>	0	1	1	0	1	1	3	0	1	0
Character	71	72	73	74	75	76	77	78	79	80
Taxon										
<i>Melanotaenia</i>	0	0	0	0	0	0	0	0	0	0
<i>Rivulus</i>	0	2	0	0	0	0	0	0	0	1
Zenarchopteridae	0	0	1	0	0	1	2	0	0	1
<i>A. kruyti</i>	0	0	1	0	0	1	1	0	?	?
<i>A. roseni</i>	0	0	1	0	0	1	1	1	?	?
<i>A. poptae</i>	0	0	1	0	1	1	1	1	0	?
<i>A. oophorus</i>	0	0	1	0	1	1	1	1	0	1
<i>O. sarasinorum</i>	0	0	1	0	1	1	1	?	?	0
<i>O. bonneorum</i>	0	0	1	0	1	1	1	0	?	?
<i>O. orthognathus</i>	0	0	2	0	1	1	1	0	?	?
<i>O. nigrimas</i>	0	0	2	0	1	1	1	0	?	?
<i>O. nebulosus</i>	0	0	2	0	1	1	1	0	?	?
<i>O. profundicola</i>	0	1	2	0	1	1	1	0	?	?
<i>O. matanensis</i>	0	1	2	0	1	1	1	0	?	?
<i>O. marmoratus</i>	0	1	2	0	1	1	1	0	1	?
<i>O. celebensis</i>	0	1	2	0	0	1	1	0	1	0

APPENDIX 2 *Continued*

Character	71	72	73	74	75	76	77	78	79	80
<i>O. timorensis</i>	0	1	2	0	1	1	1	0	?	?
<i>O. luzonensis</i>	1	1	2	0	0	1	1	0	2	0
<i>O. latipes</i>	1	1	2	0	0	1	1	0	2	0
<i>O. curvinotus</i>	1	1	2	0	0	1	1	0	2	?
<i>O. mekongensis</i>	1	2	2	0/1	0	2	1	0	1	0
<i>O. javanicus</i>	0	1	2	0	0	1	1	0	1	0
<i>O. carnaticus</i>	0	1	2	0	0	1	1	0	1	0
<i>O. dancena</i>	0	1	2	0	0	1	1	0	1	0
<i>O. hubbsi</i>	0	2	2	0	0	1	1	0	?	?
<i>O. haugiangensis</i>	0	1	2	0	0	1	1	0	?	?
<i>O. pectoralis</i>	0	2	2	1	0	1	1	0	?	?
<i>O. minutillus</i>	2	2	3	0	0	1	1	0	1	0
<i>O. sinensis</i>	1	1	2	0	0	1	1	0	?	?
<i>O. uwai</i>	2	2	3	0	0	1	1	0	?	?
<i>O. setnai</i>	2	2	3	1	0	2	2	0	?	0
Character	81	82	83	84	85					
Taxon										
<i>Melanotaenia</i>	0	0	?	0	0					
<i>Rivulus</i>	0	0/1	?	?	?					
Zenarchopteridae	1	0	?	0	0					
<i>A. kruyti</i>	?	?	?	?	?					
<i>A. roseni</i>	?	?	?	?	?					
<i>A. poptae</i>	?	?	?	?	?					
<i>A. oophorus</i>	?	?	?	?	?					
<i>O. sarasinorum</i>	?	?	?	1	1					
<i>O. bonneorum</i>	?	?	?	?	?					
<i>O. orthognathus</i>	?	?	?	?	?					
<i>O. nigrimas</i>	1	1	0	1	1					
<i>O. nebulosus</i>	?	?	?	?	?					
<i>O. profundicola</i>	?	?	?	?	?					
<i>O. matanensis</i>	?	1	?	1	1					
<i>O. marmoratus</i>	?	1	?	1	1					
<i>O. celebensis</i>	1	1	0	1	1					
<i>O. timorensis</i>	?	?	?	?	?					
<i>O. luzonensis</i>	0	0	1	1	0					
<i>O. latipes</i>	0	0	1	1	0					
<i>O. curvinotus</i>	1	0	1	1	0					
<i>O. mekongensis</i>	1	0	1	1	0					
<i>O. javanicus</i>	1	0	0	0	0					
<i>O. carnaticus</i>	?	?	?	?	?					
<i>O. dancena</i>	1	0	0	0	0					
<i>O. hubbsi</i>	1	0	0	0	0					
<i>O. haugiangensis</i>	?	?	?	?	?					
<i>O. pectoralis</i>	?	?	?	?	?					
<i>O. minutillus</i>	1	1	0	0/1	1					
<i>O. sinensis</i>	1	0	1	1	0					
<i>O. uwai</i>	?	?	?	?	?					
<i>O. setnai</i>	?	?	?	?	?					