# Adrianichthys roseni and Oryzias nebulosus, two new ricefishes (Atherinomorpha: Beloniformes: Adrianichthyidae) from Lake Poso, Sulawesi, Indonesia

Lynne R. Parenti<sup>1⊠</sup> and Bambang Soeroto<sup>2</sup>

<sup>1</sup> Division of Fishes, Section of Vertebrate Zoology, Department of Systematic Biology, National Museum of Natural History, MRC 159, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA (e-mail: parenti.lynne@nmnh.si.edu)

<sup>2</sup> Department of Biology, Universitas Sam Ratulangi, Manado, Sulawesi, Indonesia (e-mail: bam@manado.wasantara.net.id)

Received: October 18, 2002 / Revised: July 18, 2003 / Accepted: August 11, 2003

# Ichthyological Research

©The Ichthyological Society of Japan 2004

Ichthyol Res (2004) 51: 10–19 DOI 10.1007/s10228-003-0187-1 **Abstract** Two new species of ricefishes or buntingi, Adrianichthys roseni and Oryzias nebulosus, are described from Lake Poso, Sulawesi Tengah, Indonesia, bringing to 12 the number of endemic ricefishes known from Sulawesi. Adrianichthys roseni and its sole congener, A. kruyti, are distinguished from other relatively large-bodied ricefishes, Xenopoecilus, in having orbits that project beyond the dorsal profile of the head; paired preethmoid cartilages (versus single or absent in Xenopoecilus); and 13-16 (versus 8-13) dorsal fin rays. Also, as in A. kruyti, the lower jaw of A. roseni is enclosed in the upper jaw when the mouth is closed; however, the upper jaw is not as large and broadly expanded as in A. kruyti. Adrianichthys roseni differs further from A. kruyti in having fewer scales in a lateral series (approximately 63-65 versus 70-75), attaining a smaller maximum recorded standard length (90mm versus 109 mm), and having the lateral process of the pelvic bone in line with the fifth, rather than the eighth, pleural rib. Oryzias nebulosus shares with O. nigrimas, also from Lake Poso, a unique sexual dichromatism in preserved specimens: adult males are dark gray to black, whereas females are a lighter grayishyellow to brown. Relative to O. nigrimas, O. nebulosus is a small species (maximum recorded SL 33 mm versus 51 mm), with pelvic fins relatively anterior (lateral process of pelvic bone is in line with the third, fourth, or fifth, modally fourth, rather than the fourth or fifth, modally fifth, pleural rib), dorsal fin relatively anterior (origin above the 12-14th anal fin ray as opposed to the 15-17th anal fin ray), precaudal vertebrae 11-13, modally 12 (versus 13-14, modally 13), and relatively straight, narrow and slender (as opposed to curved, broad, and robust) ossified and cartilaginous portions of the gill arches. Endemic buntingi are threatened by introduction of exotic species, overfishing, and pollution. A conservation plan includes rearing native fishes for local use as ornamental fishes and possible reintroduction.

**Key words** Ricefishes · Sulawesi · Buntingi · Adrianichthys roseni sp. nov. · Oryzias nebulosus sp. nov.

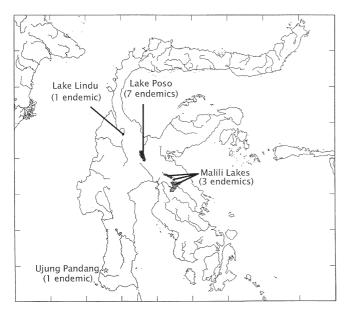
icefishes, comprising the family Adrianichthyidae in the atherinomorph order Beloniformes, are known best by the medaka Oryzias latipes (Temminck and Schlegel, 1846), a species used extensively in experimental biology for over a century (Yamamoto, 1975). Today the medaka is considered one of the three most important model fish organisms, along with the zebrafish Danio rerio, and the pufferfish Takifugu rubripes (see Clark and Elgar, 2000; Ishikawa, 2000). Ricefishes range broadly throughout fresh and brackish waters of central Eurasia, Central and Southeast Asia, the Indian subcontinent, and throughout the Indo-Australian archipelago as far east as Timor, Indonesia. Of the approximately 25 ricefish species currently recognized, including the 2 new species described herein, 12 are endemic to Sulawesi, one of the large, geologically complex islands of the Indo-Australian archipelago (Naruse et al., 1993) (Table 1).

Scientific knowledge of the endemic ricefish fauna of Sulawesi dates from description of *Haplochilus celebensis* 

Weber, 1894, from the southwestern arm of Sulawesi. This report was followed more than a decade later by description of Xenopoecilus sarasinorum Popta, 1905, from Lake Lindu, Adrianichthys kruyti Weber, 1913, and Xenopoecilus poptae Weber and de Beaufort, 1922, from Lake Poso, and Aplocheilus marmoratus Aurich, 1935 and Aplocheilus matanensis Aurich, 1935 from the Malili Lakes. A monograph diagnosing atherinomorph fishes (then classified as the order Atheriniformes) by Rosen (1964) brought attention to comparative anatomy of large Sulawesi ricefishes. There was no further description of ricefishes from Sulawesi until Kottelat's (1989a,b, 1990a) explorations resulted in discovery and description of new species (Xenopoecilus oophorus Kottelat, 1990b, Oryzias nigrimas Kottelat, 1990b, and Oryzias orthognathus Kottelat, 1990b from Lake Poso, and Oryzias profundicola Kottelat, 1990c from the Malili Lakes) and redescription and designation of neotypes for Aurich's (1935) two Malili Lakes species. Current classification of the 12 endemic Sulawesi ricefishes is given in Table 1

**Table 1.** Ricefishes or buntingi, family Adrianichthyidae, known from Sulawesi

Sulawesi Tengah (Lake Poso) Adrianichthys kruyti Weber, 1913 Adrianichthys roseni sp. nov. Oryzias nebulosus sp. nov. Oryzias nigrimas Kottelat, 1990b Oryzias orthognathus Kottelat, 1990b Xenopoecilus oophorus Kottelat, 1990b Xenopoecilus poptae Weber and de Beaufort, 1922 Sulawesi Tengah (Lake Lindu) Xenopoecilus sarasinorum Popta, 1905 Sulawesi Selatan (Malili Lakes) Oryzias marmoratus (Aurich, 1935) Oryzias matanensis (Aurich, 1935) Oryzias profundicola Kottelat, 1990c Sulawesi Selatan (Ujung Pandang and vicinity) Oryzias celebensis (Weber, 1894)



**Fig. 1.** Map of Sulawesi, Indonesia, indicating type localities of the 12 endemic adrianichthyid species. Lake Poso, 7 endemics: *Adrianichthys kruyti, Xenopoecilus oophorus, X. poptae, A. roseni* sp. nov., *O. nigrimas, O. nebulosus* sp. nov., *O. orthognathus*; SW Sulawesi (Ujung Pandang), 1 endemic: *Oryzias celebensis*; Malili Lakes, 3 endemics: *O. marmoratus, O. matanensis, O. profundicola*; and Lake Lindu, 1 endemic: *Xenopoecilus sarasinorum* 

and type localities in Fig. 1. Malili Lakes are used here in the sense of Kottelat (1990c: Fig. 1) to refer collectively to the five lakes of the Malili River drainage: Towuti, Matano, Mahalona, Wawontoa, and Masapi (Fig. 1).

Here, we describe two new species of ricefishes, ikan padi (in Indonesian), or buntingi (in Sulawesi vernacular), Adrianichthys roseni and Oryzias nebulosus, from Lake Poso, a tectonic lake in Sulawesi Tengah, Indonesia. Sulawesi is a particularly rich area of endemism for atherinomorph fishes. In addition to the ricefishes, there are 10 endemic species of beloniform hemiramphids in the sis-

ter genera *Dermogenys* and *Nomorhamphus* (Meisner, 2001), and an estimated 17 species of atheriniform telmatherinins (Kottelat, 2002). The only other known native freshwater fishes in Sulawesi are in the perciform family Gobiidae (Whitten et al., 1987a). We comment on current threats to this unique freshwater ichthyofauna and consider conservation prospects.

## Methods

Methods of measurements and counts follow Uwa and Parenti (1988) and Kottelat (1990b). Meristic characters recorded are dorsal-fin rays; anal-fin rays; pelvic-fin rays; pectoral-fin rays; principal caudal-fin rays; procurrent fin-rays (dorsal/ventral); vertebrae (total = precaudal + caudal); branchiostegal rays; and scales in a lateral series. Scale counts are approximate because many scales are missing, especially from specimens of relatively small species; scale pockets were counted to estimate number of scales in a lateral series when scales were missing. Counts were made from cleared and stained preparations (following Dingerkus and Uhler, 1977), radiographs, and alcohol specimens. Morphometric characters recorded 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; depth of the body at the anal-fin origin; predorsal length, tip of the snout to the dorsal-fin origin; preanal length, tip of the snout to the analfin origin; length of the dorsal-fin base; length of the anal-fin base; and depth of the caudal peduncle. Measurements are of straight-line distances recorded with metric dial calipers to the nearest tenth of a millimeter. In descriptive accounts, measurements are reported as a range of percentage of standard length (SL), with the value for the holotype in square brackets following the range.

Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al., 1985), except as follows: CMK (collection of Maurice Kottelat), UNSRAT (Universitas Sam Ratulangi, Manado, Indonesia), and ZSM/LIPI (collections held in trust by ZSM for Lembaga Ilmu Pengetahuan Indonesia, Indonesian Institute of Sciences).

# Adrianichthys roseni sp. nov.

(New English name: Rosen's buntingi) (Figs. 1, 2, 3A, 4A)

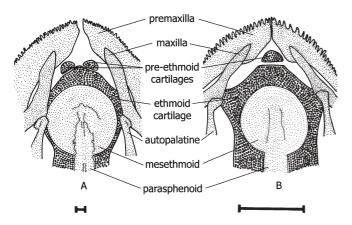
Adrianichthys kruyti (not of Weber); Rosen and Parenti, 1981: 16, Fig. 15b (Lake Poso, dorsal gill arch osteology); Parenti, 1989:80, Fig. 1 (Lake Poso, photo).

**Holotype.** MZB 6732 (ex. USNM 322424), gravid female, 90 mm SL, Lake Poso, Sulawesi Tengah, Indonesia, 4–5 September 1978, collected by N.J. Wilimovsky.

**Paratype.** USNM 322425, cleared and counterstained female, 73 mm SL, collected with the holotype.



Fig. 2. Adrianichthys roseni sp. nov., Lake Poso, Sulawesi Tengah, Indonesia, MZB 6732 (ex. USNM 322424), holotype, female, 90 mm SL



**Fig. 3.** Diagrammatic representation of the ethmoid region of the skull and anterior portion of the jaws and jaw suspensorium, dorsal view, in *Adrianichthys roseni* sp. nov., USNM 322425 (**A**); and *Xenopoecilus oophorus*, CMK 6360 (**B**). Cartilage is represented by *open circles* and bone by *stippling*; anterior is up. *Bars* 0.5 mm

**Non-type specimen.** USNM 326628, cleared and counterstained for bone, cartilage, and nerves, female, 69 mm SL, collected with the holotype.

**Differential diagnosis.** Adrianichthys roseni is like its sole congener, A. kruyti, and differs from other large Sulawesi ricefishes, Xenopoecilus spp., in having orbits that project beyond dorsal profile of head; paired, rather than single, preethmoid cartilages (absent in X. sarasinorum; Fig. 3, see Comparisons, below); and 13–16 dorsal-fin rays (versus 8–13 dorsal-fin rays in Xenopoecilus spp.). Also like A. kruyti, the lower jaw of A. roseni is enclosed in the upper jaw, however, the upper jaw is not as large and broadly expanded (Fig. 4). In addition, A. roseni differs from A. kruyti in having fewer scales in a lateral series (approximately 63–65 versus 70–75), and having the lateral process of pelvic bone in line with the fifth, rather than the eighth, pleural rib.

**Description.** Counts and proportional measurements are summarized in Table 2. Body slender, laterally com-

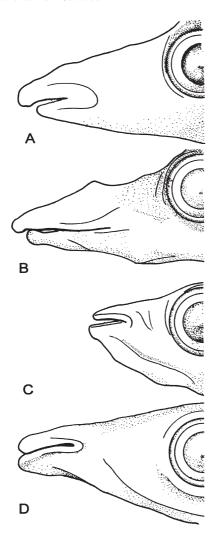
**Table 2.** Meristic and morphometric data for the holotype (MZB 6732) and paratype (USNM 322425) and nontype (USNM 326628) of *Adrianichthys roseni* sp. nov

Character	Holotype MZB 6732	Paratype {Non-type}	
Dorsal-fin rays	13	15 {16}	
Anal-fin rays	25	25	
Pelvic-fin rays	6	6	
Pectoral-fin rays	13	14 {15}	
Principal caudal-fin rays	I,5/6,I	I,5/6,I	
Procurrent fin rays	3/3	3/3	
Vertebrae	36(14+12)	36(14+12)	
Branchiostegal rays	5	5	
Scales in lateral series	65	63	
Head length	32	31	
Snout length	14	14	
Eye diameter	8	7	
Body depth	17	14	
Predorsal length	76	72	
Preanal length	61	62	
Dorsal-fin base	13	12	
Anal-fin base	28	21	
Caudal peduncle depth	8	8	

Morphometric data are given as %SL

Meristic data only are recorded on the non-type

pressed; body depth 14–17 [17]. 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. Eye relatively large, 7–8 [8], orbits project beyond dorsal profile of head; dorsal surface of head concave, articulation point of autopalatine and maxilla project slightly beyond dorsal profile. Fleshy, incompletely scaly, basal portion of dorsal and anal fins project slightly beyond primary body profile. Scales small, cycloid, and relatively deciduous; 63–65 [65] in a lateral series. Anal-fin rays without contact organs. Large, rounded genital papilla in female holotype. Medialmost pelvic-fin ray not connected to body via a mem-



**Fig. 4.** Diagrammatic representation of the head of (**A**) *Adrianichthys roseni* sp. nov., holotype, MZB 6732, eye diameter 7.2 mm, (**B**) *Adrianichthys kruyti*, CMK 5776, eye diameter 6.7 mm, (**C**) *Xenopoecilus oophorus*, USNM 340431, eye diameter 5 mm, and (**D**) *Xenopoecilus poptae*, USNM 340430, eye diameter 5 mm, to show the relative size of the upper and lower jaw

brane. 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; ethmoid cartilage without anterior indentation. Ossified and cartilaginous portions of the gill arches elongate. First pleural rib on parapophysis of third vertebra; lateral process of pelvic bone in line with fifth pleural rib. Caudal skeleton with two epural bones, one relatively large, straight, ventral accessory bone.

Color in life.—Unknown.

Color in alcohol.—Overall ground coloration pale yellow, belly pale whitish-yellow. Faint transverse irregular bar

slightly darker than ground coloration posterior to pectoralfin. Fins hyaline.

**Distribution and habitat.** Endemic to Lake Poso, Sulawesi Tengah (see Fig. 1). No habitat data are available for this single collection, but this species is likely to be pelagic as are other large bunting in Lake Poso.

**Etymology.** The specific name, *roseni*, honors the late Donn E. Rosen, in recognition of his enthusiasm, generosity, and enduring contributions to atherinomorph systematics.

**Comparisons.** Large ricefishes currently classified in the genera *Adrianichthys* and some species of *Xenopoecilus* are characterized by the presence of a single or paired cartilage that together we call preethmoid cartilages. The cartilage is paired in *A. roseni* (Fig. 3A) and *A. kruyti* and single in *X. poptae* (Fig. 3B) and *X. oophorus*. The preethmoid cartilage is absent in *X. sarasinorum* and *Oryzias* (viz. Yabumoto and Uyeno, 1984: Fig. 2).

Ricefishes lack a rostral cartilage (Rosen and Parenti, 1981; Yabumoto and Uyeno, 1984; Parenti, 1993). We do not interpret the preethmoid and rostral cartilage as homologues for several reasons. The preethmoid cartilage is anterior to and in close association with the median ethmoid cartilage, not the premaxillae, as is the rostral cartilage. Further, the preethmoid and ethmoid cartilages are united by a continuous perichondrium. Also, these cartilages do not move independently, relative to each other, as does the rostral cartilage relative to the ethmoid cartilage during jaw opening and closing in those atherinomorphs that have a rostral cartilage (see Alexander, 1967).

Ricefish preethmoid cartilages may be homologous with the trabecular cornu, paired remnants of the embryonic trabecular cartilages. The trabecular cornu are fused into a single trabecular communis in most teleost fishes, whereas persistence of paired trabeculae is more typical of primitive actinopterygians (see Goodrich, 1930) in which the skull is characteristically dorso-ventrally flattened (Smith, 1960). Presence of these cartilages in large ricefishes may be correlated developmentally with their dorsoventrally flattened skulls.

The four species described from Lake Poso in the genera *Adrianichthys* and *Xenopoecilus* may be distinguished by the relative differences in the size and shape of the upper and lower laws (Fig. 4). In *Adrianichthys*, the lower jaw is enclosed in the upper jaw, however, the upper jaw of *A. roseni* (Fig. 4A) is not as large and broadly expanded as it is in *A. kruyti* (Fig. 4B). In contrast, in *X. oophorus* and *X. poptae*, the lower jaw is longer than the upper jaw (Fig. 4C,D).

Position of the pelvic fins varies among adrianichthyids. Pelvic fins are more posterior in larger species, those species that reach a greater SL, although this relationship does not hold in all species. Position of the pelvic fin is recorded by the pleural rib to which the lateral process of the pelvic bone is in line with and to which it may be attached via a ligament. Pelvic fins are relatively posterior in *Adrianichthys*; the lateral process of the pelvic bone is in line with the fifth or eighth pleural rib in *A. roseni* and *A. kruyti*, respectively. The first pleural rib is on the third vertebra in all Sulawesi ricefishes, so this is equivalent to saying

that the pelvic fin origin is opposite the 8th or 11th vertebra, respectively, in these two species.

**Remarks.** Measurements and counts were recorded from the holotype and paratype. The triple-stained non-type is highly distorted and, therefore, was not measured. The paratype has become somewhat disarticulated following clearing and staining and may no longer reflect accurate median fin ray counts and other characters.

# *Oryzias nebulosus* sp. nov.

(New English name: nebulous ricefish) (Figs. 1, 5, 7B, 8B)

**Holotype.** MZB 11649, adult male, 32.5 mm SL. Lake Poso at Peura, eastern shore of lake approx. 10 km S of Tentena, Sulawesi Tengah, Indonesia, collected by L.R. Parenti, K.D. Louie, P. Beta, et al., 13 August 1995.

**Paratypes.** MZB 11650, 21 (22.3–32.9 mm SL, 6 of which have been cleared and counterstained), collected with the holotype. USNM 367129, 5 (27.5–33 mm SL, 1 of which has been cleared and counterstained), eastern shore of Lake Poso approximately 17 km S of Tentena, Sulawesi Tengah, Indonesia, collected by L.R. Parenti, K.D. Louie, P. Beta, et al., 12 August 1995. USNM 354692, 9 (24.5–31.7 mm SL), west bank of Poso R. just where it empties into lake at Pamona Caves, Lake Poso, Indonesia, collected by L.R. Parenti, K.D. Louie, P. Beta, et al., 13 August 1995.

**Differential diagnosis.** Oryzias nebulosus shares with O. nigrimas (Fig. 6), also from Lake Poso, a unique sexual dichromatism in preserved specimens: adult males are dark gray to black, whereas females are a lighter grayish-yellow to brown. Some adult males of both species have external conical teeth on the jaws (viz. Kottelat, 1990b: Fig. 2, bottom). Relative to O. nigrimas, O. nebulosus is a small species (maximum recorded SL 33 mm versus 51 mm), with pelvic fins relatively anterior (lateral process of pelvic bone is in line with the third or fourth rather than the fourth or fifth pleural rib; see frequency distribution in Table 3), precaudal vertebrae 11–13, modally 12 (versus 13 or 14, modally 13; Table 4), and dorsal fin relatively anterior (origin above 12–

14th anal-fin ray as opposed to the 15–17th anal-fin ray; Table 5), and straight, narrow and slender (as opposed to curved, broad and robust) ossified and cartilaginous portions of the gill arches (Figs. 7, 8; see Comparisons, below). The dorsal body profile of *O. nebulosus* arches gently from head to dorsal-fin origin, whereas in *O. nigrimas* it is relatively straight in smaller specimens to convex in larger specimens (Kottelat, 1990b: 52).

**Description.** Counts and proportional measurements are summarized in Table 6. Body short, relatively deep; body depth 20-25 [25]. Mouth terminal, jaws subequal, lower jaw projects slightly beyond upper jaw. Dorsal body profile arches gently 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. Eye relatively large, 7–9 [7], orbits meet dorsal profile of head. Basal portion of dorsal and anal fins 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. Medialmost pelvic-fin ray connected to body via a membrane along its proximal half. Caudal fin emarginate, dorsal and ventral segmented caudal-fin rays just slightly longer than middle rays. Males with short, slightly conical, tubular genital papilla; females with small, bilobed genital 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

**Table 3.** Frequency distribution of the position of the pelvic fins in *Oryzias nigrimas* and *O. nebulosus* sp. nov., recorded as the pleural rib with which the lateral process of the pelvic bone is in line

Pleural rib	3	4	5
O. nigrimas	_	1	17
O. nebulosus	5	14	8

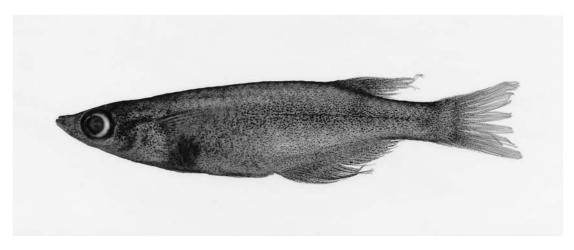


Fig. 5. Oryzias nebulosus sp. nov., Lake Poso, Sulawesi Tengah, Indonesia, MZB 11649, holotype, male, 32.5 mm SL

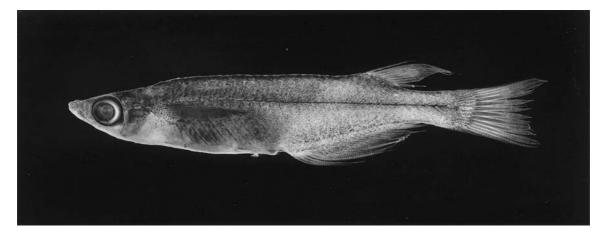


Fig. 6. Oryzias nigrimas, Lake Poso, Sulawesi Tengah, Indonesia, CMK 6358, paratype, male, 45.5 mm SL

**Table 4.** Frequency distribution of the number of precaudal vertebrae in *Oryzias nigrimas* and *O. nebulosus* sp. nov

Precaudal vertebrae	11	12	13	14
O. nigrimas	_	_	11	7
O. nebulosus	3	14	10	_

**Table 5.** Frequency distribution of dorsal-fin position recorded as the anal-fin ray opposite the dorsal fin origin in *Oryzias nigrimas* and *O. nebulosus* sp. nov

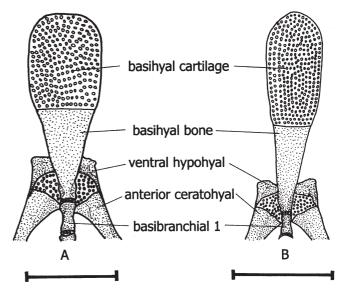
Anal-fin ray	12	13	14	15	16	17
O. nigrimas <sup>a</sup> O. nebulosus			8	5	4	X 

Values for holotypes in bold

premaxilla. No preethmoid cartilage; ossified portions of mesethmoid disc shaped; anterior border of ethmoid cartilage irregular. Ossified and cartilaginous portions of the gill arches slender and narrow. First pleural rib on parapophysis of third vertebra; first epineural bone attaches to parapophysis of first vertebra dorsal to, and not in horizontal line with, posterior epineural bones; lateral process of pelvic bone in line with third or fourth pleural rib. Caudal skeleton with two epural bones, one relatively straight ventral accessory bone. Procurrent caudal-fin rays hooked slightly at their base

Color in life.—Live color of *Oryzias nebulosus* was not recorded at capture. As this species has been combined in collections with *O. nigrimas*, with which it shares a similar preserved color pattern, both species likely share general characteristics of color in life (see Kottelat, 1990b: 52–54).

Color in alcohol.—Ground color yellowish-gray, belly pale yellow. Pigmentation variable in preserved specimens



**Fig. 7.** Anterior section of the ventral portion of the gill arches in *Oryzias nigrimas*, paratype, CMK 6361 (**A**); and *Oryzias nebulosus* sp. nov., paratype, USNM 367129 (**B**). Cartilage is represented by *open circles* and bone by *stippling*; anterior is up. *Bars* 1 mm

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-colored 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. Genital papilla densely pigmented in gravid females, pale gray in other specimens. Fins dusky to dark brown or black, more densely pigmented in males.

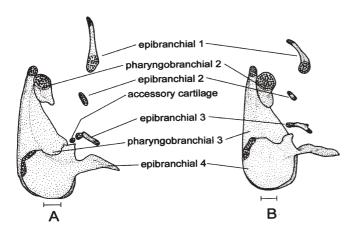
**Distribution and habitat.** Eastern shore of Lake Poso and its tributary stream, the Poso R., at Tentena, Sulawesi

<sup>&</sup>lt;sup>a</sup> Kottelat (1990b: 52) recorded the range of this character in *O. nebulosus* as from the 15th to the 17th anal fin ray

Table 6. Morphometric and meristic data for holotype and paratypes of Oryzias nebulosus sp. nov.

Character	Holotype MZB 11649	Paratypes	Mean
Dorsal-fin rays	10	9–11	9.4
Anal-fin rays	22	21–22	21.7
Pelvic-fin rays	6	6	6
Pectoral-fin rays	11	9–11	10.4
Principal caudal-fin rays	I,4/5,I	I,4/5-6,I	4/5.1
Procurrent fin rays	5/6	4-5/5-6	4.7/5.7
Vertebrae	30(12+18)	31-32 (11-13 + 18-20)	31.3
Branchiostegal rays	5	5	5
Scales in lateral series	34	32–36	33.9
Head length	23	23–26	23.9
Snout length	6	6–8	6.6
Eye diameter	7	7–9	8
Body depth	25	20–23	21.7
Predorsal length	73	76–79	76.8
Preanal length	59	56–62	59.6
Dorsal-fin base	9	7–10	8.3
Anal-fin base	27	25–29	26.2
Caudal peduncle depth	10	8–9	8.6

See Remarks for details on which paratype specimens were used for data recording



**Fig. 8.** Dorsal portion of the gill arches in *Oryzias nigrimas*, USNM 348723 (**A**); and *Oryzias nebulosus* sp. nov., paratype, MZB 11650 (**B**). Cartilage is represented by *open circles* and bone by *stippling*; interarcual cartilage is absent; anterior is up. *Bars* 0.33 mm

Tengah, Indonesia (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 traveled along the lake shore, including the mouth of the tributary stream. Many of the specimens are infested with parasitic copepods, Lernaea sp., as reported by Kottelat (1990b: fig. 2) for Oryzias nigrimas. Specimens were taken along with those of O. nigrimas, with which this species may be confused.

**Etymology.** The specific name *nebulosus*, misty or foggy, to connote a species previously unrecognized among the melanistic *Oryzias* in Lake Poso.

**Comparisons.** Oryzias nigrimas and O. nebulosus may be distinguished by the relative size and shape of the ossified and cartilaginous portions of the gill arches (Figs. 7, 8). The gill arches of *O. nigrimas* are relatively broad and robust. The ossified portion of the basihyal is subtriangular and the cartilaginous portion broad and rectangular (Fig. 7A). The dorsolateral ramus of the fifth ceratobranchial is relatively straight. The fourth epibranchial bone and toothplates of the third pharyngobranchial bone are broad and robust, and the anterior ramus of the third pharynobranchial curves away from the midline (Fig. 8A). In contrast, in O. nebulosus, the gill arches are relatively narrow and slender (Figs. 7B, 8B). The ossified portion of the basihyal is subrectangular and the cartilaginous portion narrow and rectangular (Fig. 7B). The dorsolateral ramus of the fifth ceratobranchial curves gently toward the slender lateral ramus of the fourth epibranchial bone. The anterior ramus of the third pharynobranchial is relatively straight (Fig. 8B). The slender and narrow gill arches of *O. nebulosus* are correlated with its overall small size, relative to O. nigrimas. Degree of ossification is not correlated with overall size, however. The second epibranchial is largely cartilaginous in O. nigrimas whereas it is more fully ossified in O. nebulosus. There is an accessory cartilage between the fourth epibranchial and fourth pharyngobranchial in O. nebulosus (Fig. 8A), which is absent in O. nigrimas (Fig. 8B). Degree of ossification is not considered here to be diagnostic.

Among ricefishes, pelvic fins are most anterior in several subgroups of *Oryzias* in which the lateral process of the pelvic bone is in line with the third or fourth pleural rib: *Oryzias marmoratus* (Aurich, 1935), *Oryzias matanensis* (Aurich, 1935), and *O. profundicola*, relatively deep-bodied

species from the Malili Lakes, and some *Oryzias* species outside of Sulawesi (e.g., O. latipes as illustrated by Yabumoto and Uyeno, 1984: fig. 17). Pelvic fins are relatively anterior in O. nebulosus in which the lateral process of the pelvic bone is in line with the third, fourth, or fifth pleural rib, modally the fourth. Pelvic fins are relatively posterior in O. nigrimas, in which the lateral process of the pelvic bone is in line with the fourth or fifth pleural rib, modally the fifth rib. Although the ranges overlap in O. nigrimas and O. nebulosus, the modal value for each species is distinct (Table 3). Anterior position of pelvic fins in O. nebulosus is correlated with a relatively low number of precaudal vertebrae, ranging from 11 to 13, modally 12, versus 13 or 14, modally 13, in O. nigrimas (Table 4), and a relatively anterior dorsal fin (origin above 12–14th anal-fin ray as opposed to the 15– 17th anal fin ray; Table 5; see also Kottelat, 1990b: 52).

**Remarks.** We do not necessarily imply that *Oryzias* nigrimas and O. nebulosus are sister species and defer further analysis of relationships among adrianichthyid species to a phylogenetic analysis underway by the first author. The sexual dichromatism of O. nebulosus and O. nigrimas, in which males are dark brown to black and females are pale yellow to gray, is characteristic also of the Lake Poso halfbeak Nomorhamphus celebensis (see Kottelat et al., 1993; Schaller, 1994). Data were augmented by those in Kottelat (1990b). Meristic data, exclusive of scale counts, for the paratypes reported in Table 6 were recorded from six cleared and stained specimens (MZB 11650); morphometric data, plus scale counts, were recorded from eight alcohol specimens in that lot, and from the nine specimens in USNM 354692. Renny Hadiaty (MZB) kindly examined the holotype of O. nigrimas (MZB 5859, originally ZSM/LIPI 1) for us.

### **Conservation Status**

Threats to endemic fishes of Sulawesi lakes include exotic fish introduction, eutrophication, intensive fishing, and to a lesser extent, sawdust and pesticide pollution. Exotic fish introduction is a primary cause of extinction or decline of native species in a lake. Unfortunately, most if not all lakes in Indonesia have already suffered from exotic fish introduction, intentional or accidental. Government agencies in Sulawesi intentionally introduced common carp or ikan mas (Cyprinus carpio), Mozambique tilapia (Oreochromis mossambicus), Nile tilapia (Oreochromis niloticus), walking catfish (Clarias batrachus), (Barbonymus tawes gonionotus), and nilem carp (Osteochilus hasselti) (Soeroto et al., 1990). Fish farmers, aquarists, or hobbyists accidentally introduced the ornamental swordtails and platyfishes (Xiphophorus helleri and Xiphophorus maculatus), bichirs (Polypterus sp.), and, recently, tambaqui (Colossoma macropomum). The tambaqui was caught by an angler in Lake Matano in 2000.

Negative effects of exotic fish introduction include predation, competition, disease, pest contamination, and parasite infestation of native species. These effects are not realized sufficiently, however. Floating nets and fish pens are used currently in Lake Poso by the Regional Fisheries Agency with carp, tilapia, and eels (*Anguilla* spp.) as their main objects. A university in Ujung Pandang proposes to introduce carp and tilapia into Lakes Matano and Towuti (Renny Hadiaty, personal communication).

Eutrophication is another threat to lakes. Poso, Matano, and Towuti are clear, oligotrophic lakes with fishes that are sensitive to turbidity. Sources of eutrophication are domestic wastes from settlements, fertilizers from ricefields, and clove and cocoa plantations surrounding the lake. Eutrophication from fertilizers is particularly acute in Lake Poso. Timampu village in Lake Towuti and Soroako in Lake Matano are prime examples of areas made turbid by domestic wastes. Rapid development of villages surrounding the lakes, together with logging activities, is expected to cause future, severe eutrophication.

Intensive fishing, primarily light fishing at night, is also responsible for the decline of fish population in the lakes, especially in Lake Towuti. Sulawesi biologists, including the second author, have proposed that local governments stop light fishing in Lake Towuti. Discussion on this matter is ongoing, as alternative livelihoods need to be offered to the fishermen.

Sawdust pollution persists in Lake Towuti, in Timampu village and its nearest neighbor, Pekaloa. Prominent hills of sawdust are close to the shores of the two villages. Pollution from organic acid, phenolic substances, tannin, and creosote materials has had adverse impacts on the aquatic biota. Reduction in pH and poisoning by these materials in an alkaline lake such as Towuti need to be addressed (Soeroto, 2000).

Despite these threats to the native fishes in Sulawesi lakes, there is some reason for optimism. The large buntingi of Lake Poso, currently classified in the genera Adrianichthys and Xenopoecilus, were considered nearly extinct or endangered by Whitten et al. (1987b) and Soeroto and Tungka (1996). Adrianichthys kruyti, for example, has not been collected since 1983. Recent field observations by Kottelat (1990b: 64-65), Soeroto and Tungka (1991, 1996), and Parenti and colleagues (reported herein) indicate that some Lake Poso buntingi, once the basis of an important local fishery, are now rare, but not extinct. Xenopoecilus oophorus, in particular, was abundant and all three Malili lakes endemic ricefishes were collected in reasonably large numbers in a 1995 expedition (see Comparative Materials, below). Further, X. poptae has been collected recently. Five specimens of X. poptae (UNSRAT uncatalogued) were collected from Poso in 1999 by Iwan Bauda, and an additional specimen (UNSRAT uncatalogued) was collected in March 2003 by Lusiana Sigilipu at Pendolo, the southern town of Lake Poso.

Oryzias species are relatively easy to breed and maintain under laboratory conditions (viz. Yamamoto, 1975). Scientists from UNSRAT are currently breeding the endemic buntingi as part of a conservation plan. In Manado, O. nigrimas has been bred since 1992, O. matanensis since 2000, and O. marmoratus and O. profundicola since 2002. Xenopoecilus oophorus, which dies soon after being caught, rendering it difficult to keep, has been bred successfully

from fertilized eggs taken from the female. This information may help conserve these fishes by encouraging their use in local ornamental fish culture or in the reintroduction of endemics. As part of a conservation plan, we also support a ban on further exotic fish introduction, particularly in the lakes with endemic fish species, such as Poso, Matano, Towuti, and Lindu. Recent collecting and detailed study of existing collections has resulted in the discovery and description of buntingi as it has for other understudied Sulawesi taxa, such as the atherinomorph phallostethids (viz. Parenti and Louie, 1998) and halfbeaks (e.g., Meisner and Louie, 2000). Additional endemics likely await discovery and description.

Comparative material examined. Adrianichthys kruyti: Holotype, ZMA 100.643, 109 mm SL, Lake Poso, Sulawesi Tengah, collected by A.C. Kruyt, November 1909-January 1910; ZMH 22572, 1 (86.7 mm SL), CMK 5776, 1 (76.7 mm SL), Lake Poso, at its outlet, immediately north of Tentena, collected by S. Gütebier, P. Sander, J. Weber, and S. Zabansky, September 1983. Xenopoecilus poptae: Syntypes, ZMA 100.644, 6 (85–192 mm SL), Lake Poso, collected by A.C. Kruyt, November 1909-January 1910; USNM 322423, 2 (155-168 mm SL, the larger specimen cleared and counterstained), Lake Poso (no specified locality), collected by N.J. Wilimovsky, 4-5 September 1978; ZMH 22573, 1 (113.4mm SL), ZMH 22575, 2 (eviscerated males?, 154-171 mm SL), ZMH 22576, 3 (106-138 mm SL), ZMH 22577, 1 (116.5 mm SL, cleared and stained for bone), CMK 5775 (formerly ZSM 27820), 1 (142 mm SL), Lake Poso, at its outlet, immediately north of Tentena, collected by S. Gütebier, P. Sander, J. Weber, and S. Zabansky, September 1983; UNSRAT uncatalogued, female, 146 mm SL, collected by Adrian Sigilipu, April 1991; USNM 340430 (subadult male, 76.0 mm SL), Lake Poso, west bank of Poso R. just where it empties into lake at Pamona Caves, collected by L.R. Parenti, K.D. Louie, P. Beta, and Young, 11 August 1995; UNSRAT uncatalogued, 5, Lake Poso, collected by Iwan Bauda, 1999. Xenopoecilus oophorus: Paratypes, ZSM/ LIPI-6, 5 (21.1-35.8 mm SL), CMK 6360, 1 (27.5 mm SL, cleared and counterstained), Lake Poso, east shore between Tentena and Peura, collected by M. Kottelat, 23-25 September 1988; USNM 340431, 633 (9.2-69.3 mm SL), Lake Poso, west bank of Poso R. just where it empties into lake at Pamona Caves, collected by L.R. Parenti, K.D. Louie, P. Beta, and Young, 11 August 1995; USNM 350469, 336 (9-66.3 mm SL), same locality, collected by L.R. Parenti, K.D. Louie, P. Beta, and boatmen, 13 August 1995; USNM 348386, 93 (8.6-66.8 mm SL, 2 cleared and counterstained), USNM 348724, 268 (8.0-59.1 mm SL), Lake Poso, eastern shore approx. 17 km S of Tentena, collected by L.R. Parenti, K.D. Louie, P. Beta, et al., 12 August 1995. Oryzias marmoratus: ZSM/LIPI-7, 8 (13.0-35.5 mm SL), CMK 6381 (adult female, 36.5 mm SL, counterstained), small rivulets flowing into the lake on a sandy beach at Lingkoburanga, about 6km S of Timampu, Lake Towuti, Sulawesi Selatan (type locality), collected by M. Kottelat, 22 June 1988; USNM 348528, 24 (13.4–40.2 mm SL), Sg. Lingkoburanga where it enters Lake Towuti, approx. 8km S of Timampu, collected by L.R. Parenti, K.D. Louie, and P. Haji, 9 August 1995; USNM 348574, 8 (20.6–26.5 mm SL), first stream just S of Sg. Lingkoburanga, where stream enters Lake Towuti, collected by L.R. Parenti, K.D. Louie, and P. Haji, 9 August 1995; USNM 348529, 505 (10.2-35.1 mm SL, 10 cleared and counterstained), Lake Mahalona, Sg. Tombalala where it enters on SW shore of Lake Mahalona, collected by L.R. Parenti, K.D. Louie, P. Haji, and T. Amos, 8 August 1995. Oryzias matanensis: CMK 6195, 10 (40.2-44.5 mm SL, 1 male, 42.5 mm SL, and 1 female, 44.5 mm SL, cleared and counterstained), Lake Matano, Sulawesi Selatan, E of Soroako (type locality), collected by M. Kottelat, 19 June 1988; USNM 340422, 12 (15.2-30.7 mm SL), western shore of Lake Matano at Soroako, collected by local fisherman, 7 August 1995; USNM 340428, 73 (14.9-47.3 mm SL), collected by L.R. Parenti, K.D. Louie, T. Amos, and Dahlan, 6 August 1995; USNM 340429, 249 (7.6-46.1 mm SL), western shore of Lake Matano, stream entering small inlet approx. 6-7km N of Soroako, collected by L.R. Parenti, K.D. Louie, T. Amos, and boatmen, 7 August 1995. Oryzias nigrimas: Paratypes, CMK 6358, 10 (20.6–46.0 mm SL), CMK 6361, 3 (38.5-40.0 mm SL, cleared and counterstained), ZMA 120.335, 10 (5 males, 5 females, 23.2–43.5 mm SL), Lake Poso, east shore between Tentena and Peura, Sulawesi Tengah, collected by M. Kottelat, 24-25 June 1988; USNM 348722, 202 (6.3-27.5 mm SL) Lake Poso, east and west shore of lake from where it empties at Tentena, S about 1.5 km, collected by L.R. Parenti, K.D. Louie, and boatman, 11 August 1995; USNM 350559, 104 (10-46.9 mm SL), Lake Poso at Peura, eastern shore about 10 km S of Tentena, collected by L.R. Parenti, K.D. Louie, P. Beta, and boatmen, 13 August 1995; USNM 348723, 33 (17.4–47.3 mm SL, 6 cleared and counterstained), Lake Poso, eastern shore about 17km S of Tentena, collected by L.R. Parenti, K.D. Louie, P. Beta, and Young, 12 August 1995; USNM 350558, 92 (13.9-50.8mm SL), Lake Poso, west bank of Poso R. just where it empties into lake at Pamona Caves, collected by L.R. Parenti, K.D. Louie, P. Beta, and boatmen, 13 August 1995, USNM 350560, 68 (12.9-51 mm SL), same locality, collected by L.R. Parenti, K.D. Louie, P. Beta, and Young, 11 August 1995. Oryzias profundicola: Paratypes, CMK 6485, 3 (female 40.5 mm SL, male 45.5 mm SL, and male 46.0 mm SL cleared and counterstained), Watidi, 4–7 km E of Timampu, Lake Towuti, Sulawesi Selatan, collected by M. Kottelat and A. Werner, 15 March 1989; USNM 348530, 6 (17.9-42.1 mm SL), Sg. Lingkoburanga where it enters lake, approximately 8 km S of Timampu, Lake Towuti, collected by L.R. Parenti, K.D. Louie, and P. Haji, 9 August 1995; USNM 348575, 12 (18.4–29.2 mm SL), first stream just S of Sg. Lingkoburanga where it enters Lake Towuti, collected by L.R. Parenti, K.D. Louie, and P. Haji, 9 August 1995.

Acknowledgments Permission to collect freshwater fishes in Sulawesi was granted by the Lembaga Ilmu Pengetahuan Indonesia (LIPI) to Kristina Louie, University of California, Los Angeles, and logistical support and other assistance was gratefully received from the Department of Fisheries, Universitas Sam Ratulangi, Manado, Dr. Massud and T. Amos, Department of Fisheries, Universitas Hassannudin, Ujung Pandang, Soetikno Wirjoatmodjo (LIPI), and Mohd. Amir and Renny Hadiaty (MZB). Maurice Kottelat (CMK, formerly ZSM) kindly provided loans of material from Sulawesi and discussed ricefish systematics with the first author. Bruce B. Collette (National Marine Fisheries Service) kindly commented on an earlier draft. Access to specimens in their care was graciously provided by M.N. Feinberg, S. Schaefer, and M.L.J. Stiassny (AMNH), W.N. Eschmeyer, T. Iwamoto, and D. Catania (CAS), R. Carveth, J.D. McPhail, and the late N. Wilimovsky (UBC), I. Isbrücker and H. Nijssen (ZMA), and H. Wilkens (ZMH). Jeff Clayton (USNM) provided expert technical assistance. Specimens of A. roseni, O. nebulosus, and O. nigrimas were photographed by T. Britt Griswold (Figs. 2, 5, and 6). Figure 4 was drawn by Mary Ellen Didion Carsley, who assisted with other figure preparation. Partial support for this research was received from the U.S. National Science Foundation through grant BSR 87-00351 to the first author. Two anonymous reviewers provided extensive, critical comments for which we are most grateful.

# Literature Cited

Alexander RM (1967) Mechanisms of the jaws of some atheriniform fish. J Zool Lond 151:233–255

- Aurich H (1935) Mitteilungen der Wallacea-Expedition Woltereck. Mitteilung XIII. Fische I. Zool Anz 112:97–107
- Clark MS, Elgar G (2000) *Fugu rubripes*: a fish model genome. In: Clark MS (ed) Comparative genomics. Kluwer, Boston, pp 71–96
- Dingerkus G, Uhler LD (1977) Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol 52:229–232
- Goodrich ES (1930) Studies on the structure and development of vertebrates. Macmillan, London
- Ishikawa Y (2000) Medakafish as a model system for vertebrate developmental genetics. BioEssays 22:487–495
- Kottelat M (1989a) Der Matano-See. Aquar Terr Z 42:616-618
- Kottelat M (1989b) Der Towuti-See. Aquar Terr Z 42:681-684
- Kottelat M (1990a) Sulawesi: Flussfische. Aquar Terr Z 43:735–738
- Kottelat M (1990b) Synopsis of the endangered Buntingi (Osteichthyes: Adrianichthyidae and Oryziidae) of Lake Poso, Central Sulawesi, Indonesia, with a new reproductive guild and descriptions of three new species. Ichthyol Explor Freshw 1:49–67
- Kottelat M (1990c) The ricefishes (Oryziidae) of the Malili Lakes, Sulawesi, Indonesia, with description of a new species. Ichthyol Explor Freshw 1:151–166
- Kottelat M (2002) Aquatic ecosystems: neglected biodiversity. In: Wikramanayake E, Dinerstein E, Loucks CJ, Olson DM, Morrison J, Lamoreux J, McKnight M, Hedao P (eds) Terrestrial ecoregions of the Indo-Pacific. A conservation assessment. Island Press, Washington, DC, pp 30–35
- Kottelat M, Whitten AJ, Kartikasari SN, Wirjoatmodjo S (1993) Freshwater fishes of Western Indonesia and Sulawesi. Periplus Editions (HK) Ltd., Hong Kong, in collaboration with the Environmental Management Development in Indonesia (EMDI) Project, Ministry of State for Population and Environment, Republic of Indonesia, Jakarta
- Leviton AE, Gibbs RH Jr, Heal E, Dawson CE (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resources collections in herpetology and ichthyology. Copeia 1985:802–832
- Meisner AD (2001) Phylogenetic systematics of the viviparous halfbeak genera *Dermogenys* and *Nomorhamphus* (Teleostei: Hemiramphidae: Zenarchopterinae). Zool J Linn Soc 133:199–283
- Meisner AD, Louie KD (2000) Nomorhamphus kolonodalensis, a new species of viviparous halfbeak from Sulawesi (Teleostei: Hemiramphidae). Ichthyol Explor Freshw 11: 361–368
- Naruse K, Shima A, Matsuda M, Sakaizumi M, Iwamatsu T, Soeroto B, Uwa H (1993) Distribution and phylogeny of rice fish and their relatives belonging to the suborder Adrianichthyoidei in Sulawesi, Indonesia. Fish Biol J Medaka 5:11–15
- Parenti LR (1989) Why ricefish are not killifish. J Am Killifish Assoc 22:79–84
- Parenti LR (1993) Relationships of atherinomorph fishes (Teleostei: Atherinomorpha). Bull Mar Sci 52:170–196
- Parenti LR, Louie KD (1998) Neostethus djajaorum, new species from Sulawesi, Indonesia, the first phallostethid fish (Teleostei, Atherinomorpha) known from east of Wallace's Line. Raffles Bull Zool 46:139–150

- Popta CML (1905) Note XXII. *Haplochilus sarasinorum*, n. sp. Notes Leyden Mus 25:239–247
- Rosen DE (1964) The relationships and taxonomic position of the halfbeaks, killifishes, silversides and their relatives. Bull Am Mus Nat Hist 127:217–268
- Rosen DE, Parenti LR (1981) Relationships of *Oryzias*, and the groups of atherinomorph fishes. Am Mus Novitat 2719:1–25
- Schaller D (1994) Schwarzmännchen, *Oryzias nigrimas*. Teil 1: Einführung und Systematik. Aquarium 305:18–20
- Smith HM (1960) Evolution of chordate structure. An introduction to comparative anatomy. Holt, Rinehart and Winston, New York
- Soeroto B (2000) The biodiversity and management strategy of endemic fish species in Lake Towuti, South Sulawesi, Indonesia. Proposal submitted to the ASEAN Regional Centre For Biodiversity Conservation (ARCBC), University of the Philippines, Los Baños Laguna, Sam Ratulangi University, Manado
- Soeroto B, Tungka F (1991) Fish fauna, fisheries and Adrianichthyoidei in Lake Poso. In: Phylogeny and species differentiation of Adrianichthyoidei in Indonesia. Study report. Monbusho International Scientific Research Program, pp 12–14 (place of publication unknown)
- Soeroto B, Tungka F (1996) The inland fishes and the distribution of Adrianichthyoidea of Sulawesi Island, with special comments on the endangered species in Lake Poso. In: Kichener DJ, Suyanto A (eds) Proceedings of the first international conference on eastern Indonesian-Australian vertebrate fauna, Manado, Indonesia, November 22–26, 1994. Western Australian Museum for Lembaga Ilmu Pengetahuan Indonesia, Perth, pp 1–5
- Soeroto B, Tungka F, Darwisito S (1990) Introduksi liar di Perairan Umum Daerah Minahasa (unintentional introduction in the open water of Minahasa Regency). J Fak Perikanan UNSRAT 1:177–186
- Temminck CJ, Schlegel H (1846) Pisces. In: Fauna Japonica, sive descriptio animalium quae initinere per Japoniam suscepto annis 1823–30 collegit, notis observationibus et adumbrationibus illustravit. P.F. de Siebold, Leiden, parts 10–14:173–269
- Uwa H, Parenti LR (1988) Morphometric and meristic variation in ricefishes, genus *Oryzias*: a comparison with cytogenetic data. Jpn J Ichthyol 35:159–166
- Weber M (1894) Die Süsswasser-Fische des Indischen Archipels, nebst Bemerkungen über den Ursprung der Fauna von Celebes. Zool Ergeb Reise Niederl Ostind 3:405–476
- Weber M (1913) Neue Beiträge zur Kenntnis der Süsswasserfische von Celebes. Ergebnisse einer Reise von E.C. Abendanon in Celebes. Bijdr Dierk 19:197–213
- Weber M, de Beaufort LF (1922) The fishes of the Indo-Australian Archipelago, vol 4. Heteromi, Solenichthyes, Synentognathi, Percesoces, Labyrinthici, Microcyprini. Brill, Leiden
- Whitten AJ, Mustafa M, Henderson GS (1987a) The ecology of Sulawesi. Gadjah Mada University Press, Yogyakarta
- Whitten AJ, Nash SV, Bishop KD, Clayton L (1987b) One or more extinctions from Sulawesi, Indonesia? Conserv Biol 1:42–48
- Yabumoto Y, Uyeno T (1984) Osteology of the ricefish, *Oryzias latipes*. Bull Kitakyushu Mus Nat Hist 5:143–161
- Yamamoto T (1975) Medaka (killifish) biology and strains. Series of stock culture in biological field. Keigaku, Tokyo