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A New and Unique Species of Ricefish (Teleostei: Adrianichthyidae: *Oryzias*) from the Lariang River Basin, Sulawesi, Indonesia, and the First Known Sympatric Ricefish Species Pair from Sulawesi Rivers

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A majority of ichthyological research on Sulawesi is focused on the island's ancient lakes, whereas many, even large, river systems remain unstudied. This is particularly true for the Lariang River in the central highlands of Sulawesi, the island's longest river with the largest drainage basin. Recent collection efforts there revealed a previously unknown species of ricefish (Teleostei: Adrianichthyidae: *Oryzias*), which is described herein. It is distinguished from its congeners by its high, non-overlapping scale count in lateral series. Interestingly, it occurs in sympatry with another recently described ricefish species. A phylogenetic analysis based on mitochondrial ND2 gene sequences recovered both species as sister lineages, making them the first known case of a riverine species pair in this family. The new species is further separated from its close relatives because it is a transfer-brooding species within a clade of pelvic-brooding species, suggesting a secondary reversal of reproductive modes. Possibly related to this, it also has the most pronounced rheophilic ecology of all known ricefish species. This discovery highlights the diversity of evolutionarily derived lineages found on Sulawesi and stresses the importance of additional explorative surveying to record it.

THE ricefish family (Adrianichthyidae) is among the few lineages of freshwater fishes that radiated on the isolated Indonesian island Sulawesi (Miesen et al., 2016; Hilgers and Schwarzer, 2019). Located in the zoogeographic transition zone Wallacea, dispersal from Oriental and Australasian regions shaped the island's biodiversity (Stelbrink et al., 2012). Given that seawater constitutes an effective barrier to the dispersal of most freshwater organisms, the island's inland ichthyofauna is dominated by species which evolved from marine ancestors or require access to marine waters at some stage in their life cycle (Kottelat, 2013; Miesen et al., 2016). Apart from the ricefishes, only halfbeaks (Zenarchopteridae), sailfin silversides (Telmatherinidae), and a few lineages of gobies (e.g., *Glossogobius*, Gobiidae; *Mugilogobius*, Oxudercidae) have radiated within Sulawesi freshwaters.

Ricefishes are the most species rich of the Sulawesi freshwater fish radiations. Currently, 24 species are recognized as endemic to the island, classified into two genera: *Oryzias* (20 species) and *Adrianichthys* (4 species; Fricke et al., 2024; see Parenti, 2008 for a systematic review). Together, they comprise more than half of all known ricefish species, despite Sulawesi constituting only a small fraction of the total distribution area of the family, ranging from Japan to the Indian subcontinent (Parenti, 2008; Hilgers and Schwarzer, 2019). Evolutionary drivers of ricefish diversification on Sulawesi remain only partially understood, but geological complexity and ecological opportunities, i.e., available ecological niches due to the presence of diverse habitats and reduced competition as a consequence of the island's depauperate freshwater ichthyofauna, appear highly plausible. A notable evolutionary development among some of the Sulawesi ricefishes can be seen in pelvic brooding, a derived reproductive mode where females carry clusters of fertilized eggs until the fry hatch (e.g., Spanke et al., 2021; Flury et al., 2023).

Ichthyological research in Sulawesi has focused to a substantial degree on the island's ancient lakes with their spectacular endemism and radiations (Whitten et al., 2001; Vaillant et al., 2011; von Rintelen et al., 2012; Miesen et al., 2016), while many river drainages remained scientifically unexplored. However, new species of ricefishes were increasingly reported from lotic waters, with six such species described since 2010 (Parenti and Hadiaty, 2010; Herder et al., 2012; Parenti et al., 2013; Mandagi et al., 2018; Utama et al., 2022).

The Lariang River is the largest river of Sulawesi in terms of both its total length (~300 km) and its catchment size (>7,000 km^2). Discharging into the Strait of Makassar, it drains a substantial area west of Lake Poso in Central Sulawesi (Sulawesi Tengah and Sulawesi Barat Provinces). As most of the basin is located in remote and very sparsely populated mountain regions (Overseas Technical Cooperation Agency, Government of Japan [JICA], 1971), the aquatic fauna of the Lariang River system remained largely unexplored. Still, from a faunistic perspective, it may represent a

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hotspot for locally endemic species, as exemplified by the description of an unusual species of *Caridina* restricted to the portion of the drainage located in the Napu Valley (Klotz et al., 2023). Additional new aquatic species are likely to be discovered, as only a low number of sampling locations have been visited so far in the drainage.

During recent expeditions to the remote valleys of Bada and Napu, two alluvial or lacustrine highland plains drained by the Lariang River (JICA, 1971; Klotz et al., 2023), we recorded the recently described pelvic-brooding *Oryzias kalimpaaensis* and a sympatric transfer-brooding species of *Oryzias* that is described herein. These species were retrieved in a phylogenetic sister relationship and thus constitute the first known case of a sympatric riverine species pair among Sulawesi ricefishes. The phylogenetic relationships and ecology of these fishes are discussed, complemented by brief notes on the possible relationship to a fossil species.

MATERIALS AND METHODS

Specimens were collected between August and September 2023 using a beach seine, frame net, or DC electrofishing unit (EFGI 650, Bretschneider Spezialelektronik, Germany), and euthanized in a clove oil solution at a concentration of ~0.1 ml clove oil per of liter water. They were subsequently fixed in 6–10% formalin, and afterward transferred to 70% ethanol for storage, or directly stored in 96% ethanol if specimens died before euthanization. A clip of the right pectoral fin was taken prior to fixation as a tissue sample for DNA extraction and stored in 96% ethanol. Meristic counts and morphometric measurements followed Kottelat (1990a) and Parenti and Soeroto (2004). Point-to-point measurements of all formalin-fixed specimens were taken with a digital caliper to the nearest 0.1 mm. For each specimen, morphometric measurements were converted to percentage of standard length (SL), except for measurements of head characters (snout length, eye diameter, interorbital width), which were converted to percentage of head length (HL). Following the value range obtained from the specimens, mean values are specified in brackets. For meristic characters, median values are specified in brackets following their range. Specimens were compared to all known Sulawesi species of *Oryzias*, with emphasis on those from Central and South Sulawesi. Osteological characteristics were examined using μ-CT scans (Skyscan 1173, Bruker, USA; Source Voltage 68 kV, Source Current 117 μA, Exposure 500 ms, Rotation Steps 0.3°) of selected specimens. Reconstructions of μ-CT scans were visualized in the FIJI extension for ImageJ (Schindelin et al., 2012).

A molecular phylogeny was reconstructed using sequences of the mitochondrial ND2 gene coding for the NADH dehydrogenase 2 protein. DNA was extracted using MagAttract HMW DNA kits (QIAGEN, Germany), and target amplification followed Mokodongan and Yamahira (2015). Sanger sequencing was performed at BGI Genomics, China. Base-calling checks of chromatograms and sequence alignment were performed in MEGA X version 10.2.2 (Kumar et al., 2018). Alignments were augmented with published MT-ND2 sequences of related species from Mokodongan and Yamahira (2015), Horoiwa et al. (2021), Gani et al. (2022), and Utama et al. (2022), as well as selected mitochondrial genomes. Using a maximum likelihood analysis approach, we reconstructed a phylogenetic topology including all available species of *Oryzias* from Sulawesi and several non-Sulawesi species of *Oryzias* as outgroups, as well as a more reduced phylogeny including only species belonging to the Western Central Sulawesi clade (Mokodongan and Yamahira, 2015). Maximum likelihood phylogenetic reconstruction as well as substitution model testing were performed in IQ-Tree version 2.2.2.7 (Minh et al., 2020), which identified GTR+F+I+G4 as the best-fitting model according to BIC using ModelFinder integrated into IQ-Tree 2. For the phylogeny reconstruction, 1,000 bootstrap replicates were calculated. The sequence data generated herein are deposited in NCBI GenBank under accession numbers PQ219720–PQ219761.

Limited and often imprecise baseline data were available on the watersheds within the geographic regions in question. Due to this constraint, hydrology was analyzed and interpreted with QGIS Desktop 3.28.12 using DEM data (SRTM 1 Arc-Second Global) obtained from USGS EarthExplorer (downloaded from https://earthexplorer.usgs.gov).

Specimens are deposited in zoological collections, institutional abbreviations follow Sabaj (2020). Holotype and a paratype series are deposited at MZB, BRIN in Bogor, Indonesia, and paratype series deposited at ichthyological collections of Museum Koenig Bonn, LIB, Germany. Some living specimens of the new species, as well as *O. kalimpaaensis*, from the Bada Valley were acquired through aquarium trade imports to Germany, allowing for aquarium observations on reproductive ecology and documentation of live coloration.

***Oryzias polylepis*, Möhring, Mokodongan, and Herder, new species**

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Figures 1–4, Table 1

Holotype.—MZB 28041, 46.7 mm SL (male), Lariang River near Lengkeka Village, Bada Valley, District Lore Barat, Poso Regency, Sulawesi Tengah, 01°52′38.05″S, 120°12′8.83″E, 752 m MSL, J. Möhring, F. K. Lakiu, and M. Mejía Estrada, 15 August 2023 (Figs. 1A, 2).

Paratypes.—MZB 28042–28048, 32.7–46.2 mm SL (4 males, 3 females), same metadata as holotype, except collected 14–15 August 2023; MZB 28049–28052, 34.8–39.5 mm SL (4 females), Malei River at Gintu Village, Bada Valley, District Lore Selatan, Poso Regency, Sulawesi Tengah, 01°53′13.95″S, 120°14′6.25″E, 760 m MSL, F. Herder and D. F. Mokodongan, 21 September 2023; ZFMK ICH-136000–136007, 35.3–52.5 mm SL (5 males, 3 females), same metadata as holotype, except collected 14–15 August 2023.

Non-type material.—MZB 28053–28054, 38.7–44.4 mm SL (2 males), Lariang River, Watutau Village, Napu Valley, District Lore Peore, Poso Regency, Sulawesi Tengah, 01°33′34.53″S, 120°20′16.96″E, 1,084 m MSL, J. Möhring, A. Gani, Z. Jusman, and D. F. Mokodongan, 30 September 2023; MZB 28055–28069, 35.8–45.3 mm SL (4 males, 11 females), Pembangu River, Watutau Village, Napu Valley, District Lore Peore, Poso Regency, Sulawesi Tengah, 01°33′51.41″S, 120°20′33.00″E, 1,085 m MSL, J. Möhring, A. Gani, Z. Jusman, and D. F. Mokodongan, 30 September 2023; ZFMK ICH-136008–136022,

Fig. 1. Preserved specimens of *Oryzias polylepis*. (A) MZB 28041, holotype, male (46.7 mm SL) and (B) MZB 28047, female (40.8 mm SL), both from Lariang River, Bada Valley, Poso Regency, Central Sulawesi; (C) MZB 28059, male (41.9 mm SL) and (D) ZFMK ICH-136027, female (42.7 mm SL) specimens from Pembangu River, Napu Valley, Poso Regency, Central Sulawesi.

37.7–49.3 mm SL (8 males, 7 females), same metadata as holotype, except collected 14 August 2023, pres. 96% ethanol; ZFMK ICH-136023, 39.3 mm SL, male, Lariang River, Watutau Village, Napu Valley, District Lore Peore, Poso Regency, Sulawesi Tengah, 01°33′34.53″S, 120°20′16.96″E, 1,084 m MSL, J. Möhring, A. Gani, Z. Jusman, and D. F. Mokodongan, 30 September 2023; ZFMK ICH-136024–136039, 32.2–47.1 mm SL (4 males, 12 females), Pembangu River, Watutau Village, Napu Valley, District Lore Peore, Poso Regency, Sulawesi Tengah, 01°33′51.41″S, 120°20′33.00″E, 1,085 m MSL, J. Möhring, A. Gani, Z. Jusman, and D. F. Mokodongan, 30 September 2023.

Table 1. Meristic and morphometric data for examined specimens. Except for the holotype, data are reported as range. In parentheses, median values for meristic characters and averages for morphometric traits are given. Morphometric values are given as percentage range of standard length (SL), except for measurements of head characters, which are given as percentage of head length (HL). The holotype is included in the columns 'Males Bada Valley' and 'Combined.'

Character	Holotype	Males Bada Valley (*n* = 10)	Females Bada Valley (*n* = 10)	Males Napu Valley (*n* = 11)	Females Napu Valley (*n* = 23)	Combined (*n* = 44)
Anal-fin rays	21	20–22 (21)	19–22 (20–21)	20–23 (21)	20–23 (21)	19–23 (21)
Dorsal-fin rays	12	11–13 (12)	11–13 (12)	11–13 (11)	11–13 (12)	11–13 (12)
Pelvic-fin rays	6	6–7 (6)	6–7 (6–7)	6–7 (7)	6–7 (7)	6–7 (7)
Pectoral-fin rays	13	12–13 (13)	12–13 (13)	11–13 (12)	11–14 (13)	11–14 (13)
Principal caudal-fin rays	i,4/5,i	i,4/5,i	i,4/5,i	i,4/5,i	i,4/5,i	i,4/5,i
Procurrent caudal-fin rays	6/9	6–9/8–11 (7–8/9)	7–10/7–11 (8/9–10)	7–9/8–9 (8/8)	5–9/7–10 (7/8)	5–10/7–11 (7/9)
Scales in lateral series	88	83–90 (88)	80–86 (83–84)	81–94 (86)	79–92 (85)	79–94 (85)
Standard length (mm)	46.7	38.7–52.5 (44.3)	32.7–40.8 (37.0)	35.8–45.3 (39.8)	32.2–47.1 (39.4)	32.2–52.5 (40.2)
Percentage of SL						
Head length	25.1	24.5–25.9 (25.2)	23.1–26.0 (24.8)	24.8–27.3 (25.5)	23.4–26.7 (24.9)	23.1–27.3 (25.1)
Predorsal length	68.7	66.5–69.9 (68.2)	68.1–70.4 (69.1)	67.3–70.9 (68.6)	67.2–72.8 (69.3)	67.2–72.8 (68.9)
Preanal length	57.2	54.5–57.3 (55.9)	55.5–58.5 (57.1)	54.4–58.7 (56.6)	55.7–60.2 (57.9)	54.4–60.2 (57.1)
Body depth	19.3	18.3–21.4 (20.1)	15.2–18.3 (16.8)	18.6–21.2 (19.6)	16.0–18.4 (17.4)	15.2–21.4 (18.3)
Dorsal-fin base	15.2	14.2–19.3 (15.6)	12.7–15.2 (13.7)	13.4–15.7 (14.6)	12.3–14.6 (13.4)	12.3–19.3 (14.1)
Anal-fin base	27.4	26.5–28.0 (27.3)	23.9–28.4 (26.5)	25.0–28.9 (27.1)*	23.2–27.3 (25.5)	23.2–28.9 (26.3)
Pectoral fin length	21.2	19.2–21.9 (20.4)	17.3–20.0 (18.4)**	16.9–21.0 (19.2)**	16.3–20.2 (17.9)**	16.3–21.9 (18.7)
Pelvic fin length	10.1	10.0–11.7 (10.7)	10.4–13.1 (11.9)	9.2–11.7 (10.4)	10.8–13.8 (12.3)	9.2–13.8 (11.6)
Caudal peduncle length	17.8	17.6–20.2 (18.5)	17.5–19.7 (18.5)	18.3–19.9 (19.2)*	17.1–21.1 (18.8)	17.1–21.1 (18.8)
Caudal peduncle depth	9.0	8.5–9.7 (9.1)	7.5–8.9 (8.3)	8.5–9.8 (9.1)	8.0–9.3 (8.6)	7.5–9.8 (8.7)
Percentage of HL						
Snout length	36.8	28.7–36.8 (31.9)	26.3–32.5 (30.7)	26.2–41.6 (32.3)	27.4–37.6 (33.5)	26.2–41.6 (32.4)
Interorbital width	60.7	55.1–60.7 (58.7)	55.8–67.4 (61.5)	51.4–59.4 (56.3)	50.9–63.7 (58.0)	50.9–67.4 (58.4)
Eye diameter	33.3	33.3–37.4 (35.1)	32.6–40.7 (36.1)	33.9–37.9 (35.9)	33.0–39.4 (36.3)	32.6–40.7 (35.9)

* One specimen excluded from measurements due to damage.

** Two specimens excluded from measurements due to damage.

Fig. 2. (A) Holotype (MZB 28041) immediately after euthanization (image flipped horizontally to match comparison standards) and (B) maximum intensity projection of μ-CT reconstruction of holotype.

Diagnosis.—*Oryzias polylepis* is distinguished from all other known species of *Oryzias*, as well as all species of *Adrianichthys* except *A. poptae*, by its high number of scales in the lateral series (79–93 vs. <75; Parenti, 2008). It differs from *A. poptae* by its substantially smaller adult standard length (52 mm vs. 190 mm SL) and in having a substantially shorter snout (6.8–9.3 vs. 13.0–17.0) with superior and small mouth, vs. elongated snout with large terminal mouth in *A. poptae*.

Among the Sulawesi-endemic ricefish species, *O. polylepis* is further distinguished from *O. asinua*, *O. celebensis*, *O. dopingdopingensis*, *O. hadiatyae*, *O. landangiensis*, *O. matanensis*, *O. soerotoi*, *O. wolasi*, and *O. woworae* by the number of dorsal-fin rays (11–13 vs. <11; Parenti, 2008; Herder and Chapuis, 2010; Parenti and Hadiaty, 2010; Parenti et al., 2013; Mokodongan et al., 2014; Mandagi et al., 2018; Utama et al., 2022). From *O. eversi*, it differs in the number of anal-fin rays (19–23 vs. 17–18; Herder et al., 2012) and pectoral-fin rays (11–14 vs. 10). It is distinguished from geographically close endemic pelvic-brooding species of Lake Lindu, *O. bonneorum* and *O. sarasinorum*, by having fewer principal caudal-fin rays (i,4/5,i vs. i,5/6,i; Parenti, 2008) and a shorter head (23.1–26.4 vs. 29.0–32.0). It differs from sympatric *O. kalimpaaensis* by having a shorter head (23.1–26.4 vs. 30.6–33.2; Gani et al., 2022) and larger eyes relative to head length (32.6–40.7 vs. 26.3–29.6). Lacustrine species occurring in Lakes Mahalona, Lantoa, and Towuti, *O. loxolepis*, *O. marmoratus*, and *O. profundicola*, possess deeper bodies (15.2–21.4 vs. 24.8–35.2; Parenti, 2008; Kobayashi et al., 2023) and a truncate or round instead of lunate caudal-fin edge (Figs. 1–4). The *Oryzias* endemic to Lake Poso, *O. nebulosus*, *O. nigrimas*, and *O. orthognathus*, all differ from *O. polylepis* by their greater predorsal length (67.2–70.6 vs. 73.0–79.8; Parenti, 2008).

Oryzias polylepis differs in life coloration from all other *Oryzias*, except *O. sarasinorum*, by the presence of a broad reflective silver lateral band extending from the pectoral fin to the end of the caudal peduncle. The presence of a series of dark blotches along the lateral line in males distinguishes *O. polylepis* from all other Sulawesi species except *O. bonneorum*, *O. dopingdopingensis*, *O. landangiensis*, and *O. matanensis* (Parenti, 2008; Mandagi et al., 2018; Utama et al., 2022).

Description.—A medium to large *Oryzias*, maximum length recorded 52.5 mm SL. Body cigar-shaped and elongated, anterior body section cylindrical, posteriorly more laterally compressed (Figs. 1–4). Mouth superior, lower jaw enlarged and protruding far beyond upper jaw. Mouth gape oblique and conspicuously deep (Fig. 2B). Jaws with villiform teeth which are largest in anterior two-thirds of dentary; males with large external conical teeth on upper and lower lips, especially near joints; frequently also with enlarged caniniform teeth on upper and lower jaw tips. Snout length short to medium (26.3–37.6 [32.4]), eyes relatively large (32.6–40.7 [35.9]), especially in relation to short head (23.1–27.3 [25.1]). Dorsal profile straight without arch, ventral profile moderately convex, no defined ventral concavity as in pelvic-brooding species. Caudal peduncle long (17.1 21.1 [18.8]). Pelvic-fin insertion between fourth and fifth pleural rib (Fig. 2B).

Scales are remarkably small and numerous; scale shape varies from cycloid to ellipsoid, with shape changing allometrically, i.e., largest specimens had most vertically stretched ellipsoid scales; not as deciduous as in other congeners. Males with elongated dorsal- and anal-fin rays, relatively small gaps between fin-ray tips and fin-membrane edges (Fig. 4). Long caudal peduncle creating a large gap between end of dorsal- and anal-fin tips and caudal base. Anal-fin shape in females obtuse trapezoid with rounded tips (Figs. 1B, D, 3B, C); males with disproportionally longer anterior anal-fin rays, giving fin edge a concave appearance (Figs. 1A, C, 2–4). Anal and dorsal-fin rays in females comparatively short. Median pelvic-fin rays connected to ventral body by a membrane along about one-fourth to one-third of its length. Caudal-fin edge lunate; procurrent caudal-fin rays long and numerous (5–10/7–11 [7/9]), extending relatively far back onto caudal peduncle, dorsally ending between spinae tips of second- and third-last and ventrally between third- and fourth-last vertebrae (Fig. 2B).

Dorsal-fin rays 11–13 [12]. Anal-fin rays 20–23 [21]. Pelvic-fin rays 6–7 [7]. Pectoral-fin rays 11–14 [13]. Principal caudal-fin rays i,4,5,i. Procurrent caudal-fin rays dorsally 5–10 [7], ventrally 7–11 [9]. Scales in lateral series 79–93 [85]. Vertebrae 30. Branchiostegal rays 5.

Color in life.—General body coloration grayish brown with slight olive-green hue (Figs. 2–4). Ventral body white–translucent. Eyes light blue. Three to nine grayish blotches along lateral line in males, also present in females, but generally fainter or absent (Fig. 3B, C). Dorsal-fin base yellowish-brown. Anal-fin base grayish to yellowish hyaline. Caudal-fin base and caudal-fin margins yellowish to orange. Pectoral fins translucent white in females, with grayish-black pigmentation in males. No vertical stripes along back (cf. *O. kalimpaaensis*). Prominent luminous band with blue-purplish reflections along the lateral line from pectoral-fin insertion until caudal peduncle. Similar reflective blue shine on operculum.

During courtship, males present a continuous blackish stripe on head and back that becomes progressively narrower posteriorly, similar to related species of *Oryzias*. The area of the reflective lateral band on lateral body also becomes darker during courtship. Between this band and dorsal stripe, base color brightens up yellowish to greenish golden. Further, dorsal and anal fins become dark gray to blackish, yellow to orange color of caudal-fin margins becomes more brilliant, and blotches along the lateral line

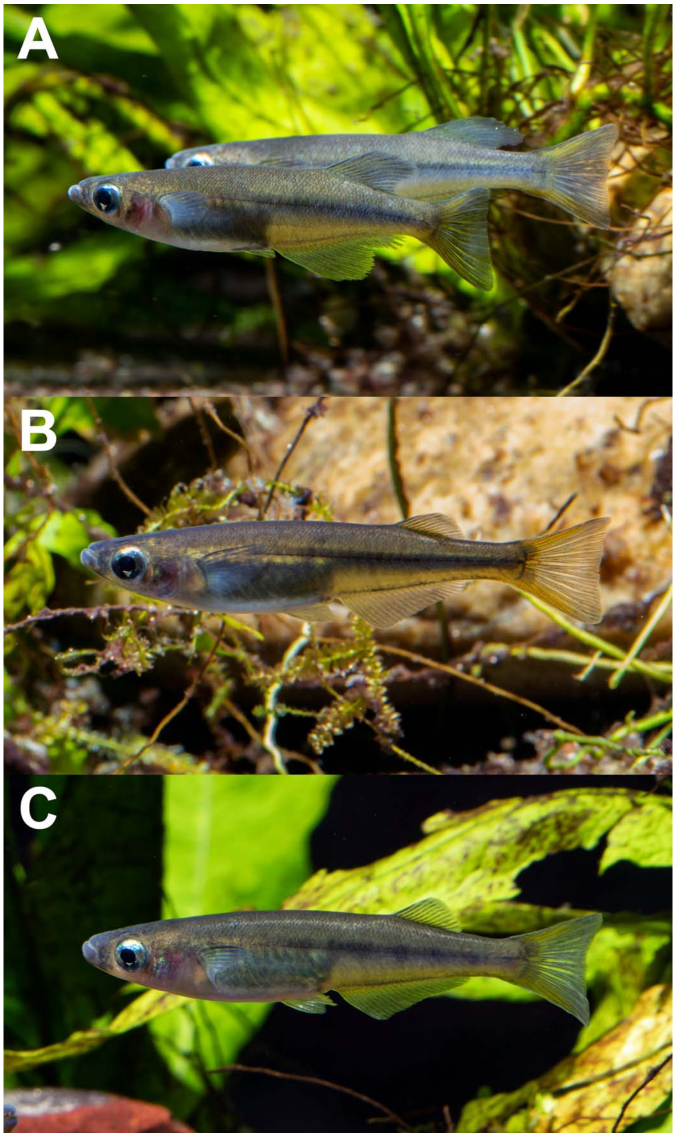

Fig. 3. Life coloration of fish from the type locality under aquarium conditions (uncatalogued specimens). (A) Two males in normal coloration. (B) Female in normal coloration. (C) Female faintly showing the distinctive blotches along the lateral line.

become darker and more visible. Blotches are especially prominent in sparring males.

Color in alcohol.—Base color pale brown (Fig. 1). Scales on dorsal flanks and back with blackish pigmentation in posterior half, giving the back a darker brown appearance. A dark gray-brown dorsal stripe progressively narrowing down in width from upper lip until anterior dorsal-fin insertion in males, but also less prominently visible in some females. Narrow blackish mid-lateral stripe from pectoral-fin base to hypural plate. Three to nine round to oval dark brown to blackish lateral blotches in males. Despite being visible in living specimens, blotches are mostly absent in females; only one to two visible in some of the specimens. Ventral body cream to light brown, slightly brighter than base color. Male with very sparse light brown pigmentation along anal-fin base. Dorsal head and snout blackish brown. Throat and ventral snout cream to light brown. Fins translucent; dorsal, anal, and caudal fins with light grayish-brown pigmentation in males, much more vanished in females. Caudal-fin margins and caudal-fin-ray insertion light brown.

Fig. 4. Two sparring males from type locality (uncatalogued specimens). Note the dark spots on the side and the concave anal fin.

Sexual dimorphism.—Similar to other ricefishes, males have elongated, filamentous dorsal- and anal-fin rays (Figs. 1–4). Larger males have a fleshy extension of the dorsal-fin base with a row of larger cycloid scales. Males with more prominent dark blotches along the lateral line and more pronounced pigmentation on the dorsal, anal, and pelvic fins; translucent in females. Both sexes with yellow to orange caudal-fin margins in life, but more prominently in males (Figs. 2A, 3). Adult males with prominent external teeth on the lips; tooth expression most prominent in largest specimens. Body depth is greater in males (16.0–18.4 vs. 18.4–21.4), while females possess longer pelvic fins (10.4–13.8 vs. 9.2–11.7).

Distribution.—*Oryzias polylepis* is so far known only from the Lariang River drainage, Central Sulawesi, Indonesia that drains westward into the Strait of Makassar. The majority of the watershed is located in remote upland regions, with the upstream half of the Lariang River's main channel situated at altitudes between 1,200 and 400 m MSL (Fig. 5).

At present, this species is known from five sites in two remote highland valleys: three sites in Bada Valley, with two at the Lariang River main channel near Lengkeka Village and Bomba Village (latter uncatalogued specimens; 01°51′10.37″S, 120°16′46.44″E) and one at lower Malei River near the Gintu Village; two sites in Napu Valley at Watutau Village, namely Lariang River and lower Pembangu River, a main tributary of the former in the southern part of the valley (Fig. 5). The species was not recorded in Wuasa River at Wuasa Village (01°25′32.12″S, 120°19′2.23″E), northern Napu Valley, or the Malei River near Runde Village (01°54′12.74″S, 120°14′26.93″E) in southern parts of Bada Valley. We assume that the species is more widespread in the Lariang River drainage, but additional sampling is required for confirmation.

Habitat and ecological notes.—Lariang River near Lengkeka Village, Bada Valley (Fig. 6A, B): This is a large river (width up to 80 m) with moderate to fast flow; ∼200 km upstream

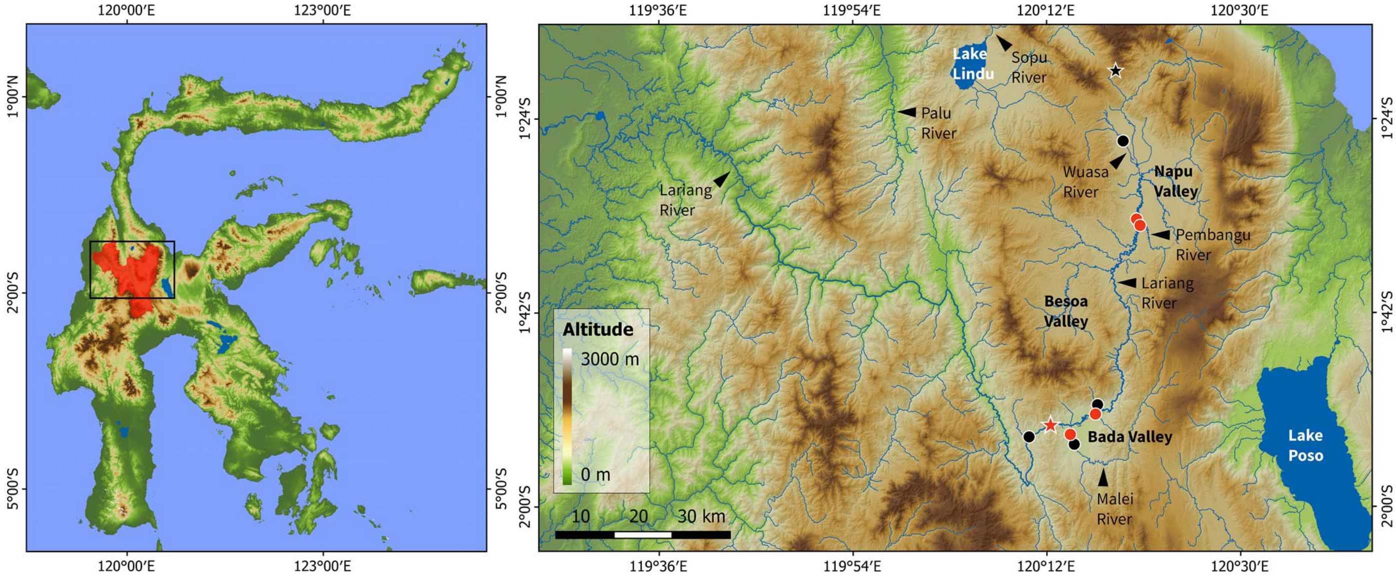

Fig. 5. Map of collection localities. Left: topological overview of Sulawesi. The upslope area (= drainage basin) of the Lariang River is depicted as a red shape. The window section is shown in more detail on the right, including hydrological features. Red star indicates type locality of *O. polylepis*. Black star indicates Lake Kalimpa'a (also known as Lake Tambing), type locality of *O. kalimpaaensis*. Black circles represent locations at which only the latter was collected, red circles where both species were collected (includes type locality). *Oryzias polylepis* always occurred together with *O. kalimpaaensis*.

of river mouth. The type locality is a narrow pass of the Lariang River (15–25 m wide, >2 m deep) west of the main Bada Valley plain through a short ravine with stronger water current, between two stretches of rapids (Fig. 6A); substrate heterogenous, consisting of light-colored sand, stones, and boulders (Fig. 6B). Abundant driftwood, partial canopy cover, only minor human use in form of small cocoa tree plantations. Underwater visibility <20 cm. Water temperature 27.1°C, pH 8.2, conductivity ~600 µS. Sympatric native fish species collected are *Oryzias kalimpaaensis* (Fig. 7) and *Lentipes mindanaoensis*. Not collected but reported by locals are *Anguilla* spp., *Belobranchus belobranchus* ("Bou Ebe"), and two larger fish, known locally as "Patoga" and "Bangkoko," identified preliminarily herein as *Lates calcarifer* and *Mesopristes cancellatus*, respectively. Introduced species include *Barbodes binotatus*, *Osteochilus vittatus*, *Oreochromis* sp., *Aplocheilus armatus*, *Gambusia* sp., *Poecilia reticulata*, and *Trichopodus trichopterus*.

Lower Malei River at Gintu Village, Bada Valley: Water clear, tea-like stain, underwater visibility >2 m. 25–45 m wide. Substrate diverse, including sand, gravel, and mudstone boulders. Water temperature 24°C, pH 8.1, conductivity ~200 µS. Sympatric native fish species recorded are *O. kalimpaaensis*, *L. mindanaoensis*, *Sicyopterus* sp. aff. *erythropterus* (likely the same species identified as *S. erythropterus* in Jamonneau et al., 2024), and *Anguilla* sp. Introduced species were abundant and include *Barbodes binotatus*, *Osteochilus vittatus*, *Oreochromis* sp., *Aplocheilus armatus*, *Gambusia* sp., and *Poecilia reticulata*.

Lariang River at Watutau Village, Southern Napu Valley: 15–30 m wide, up to 2 m deep, ~270 km upstream of the river mouth. Water visibility <0.5 m. Moderate water flow. Substrate mostly sand, partly muddy in shallower water, riverbank with gravel, rocks, or mudrocks. Abundant crustaceans, including *Caridina* spp. (especially *C. clandestina*), *Macrobrachium* spp., and several species of freshwater crabs. Plenty of overhanging riparian vegetation (e.g., *Phragmites karka*). The only other native fish species observed was *O. kalimpaaensis*. Introduced fish species present were *Barbodes binotatus*, *Osteochilus vittatus*, *Oreochromis* sp., *Aplocheilus armatus*, *Gambusia* sp., *Poecilia reticulata*, *Channa striata*, and *Trichopodus trichopterus*.

Pembangu River at Watutau Village, Southern Napu Valley (Fig. 6C, D): Major tributary of Lariang River in southern Napu Valley, 5–15 m wide, up to 1 m deep, strongly meandering in its lower course. Moderate to fast waterflow. Substrate heterogeneous, consisting mostly of sand and gravel on mudrock bed. Plentiful overhanging riparian vegetation (e.g., *P. karka*). *Oryzias polylepis* was mostly collected close to steeper banks and underneath overhanging reeds (Fig. 6D), often in stronger current. Underwater visibility ~0.5 m. Cooccurring fish and crustacean species as described for Lariang River in Napu Valley.

Rather atypical for ricefishes, *O. polylepis* is a strong active swimmer and was always collected in microhabitats with moderate to strong current, usually in deeper waters (water depth >0.5 m). Moreover, it was primarily collected in waters with reduced underwater visibility and, unlike the sympatric *O. kalimpaaensis*, was consistently absent from smaller tributary streams with clear and cool water. Due to this, fish could not be observed underwater *in situ*. Aquarium observations revealed a fast and often restless swimming behavior, regularly favoring high current velocity spots. Feces of freshly collected specimens contained remains of phytoplankton. However, under aquarium conditions, they are not selective and were fed on aquatic invertebrates and fish larvae.

Reproductive biology.—Unlike all other endemic *Oryzias* known from western Central Sulawesi, *O. polylepis* is a transfer brooder (i.e., it does not carry its eggs connected to the body until hatching of larvae as in pelvic-brooding ricefishes). Traits typically associated with pelvic brooding in

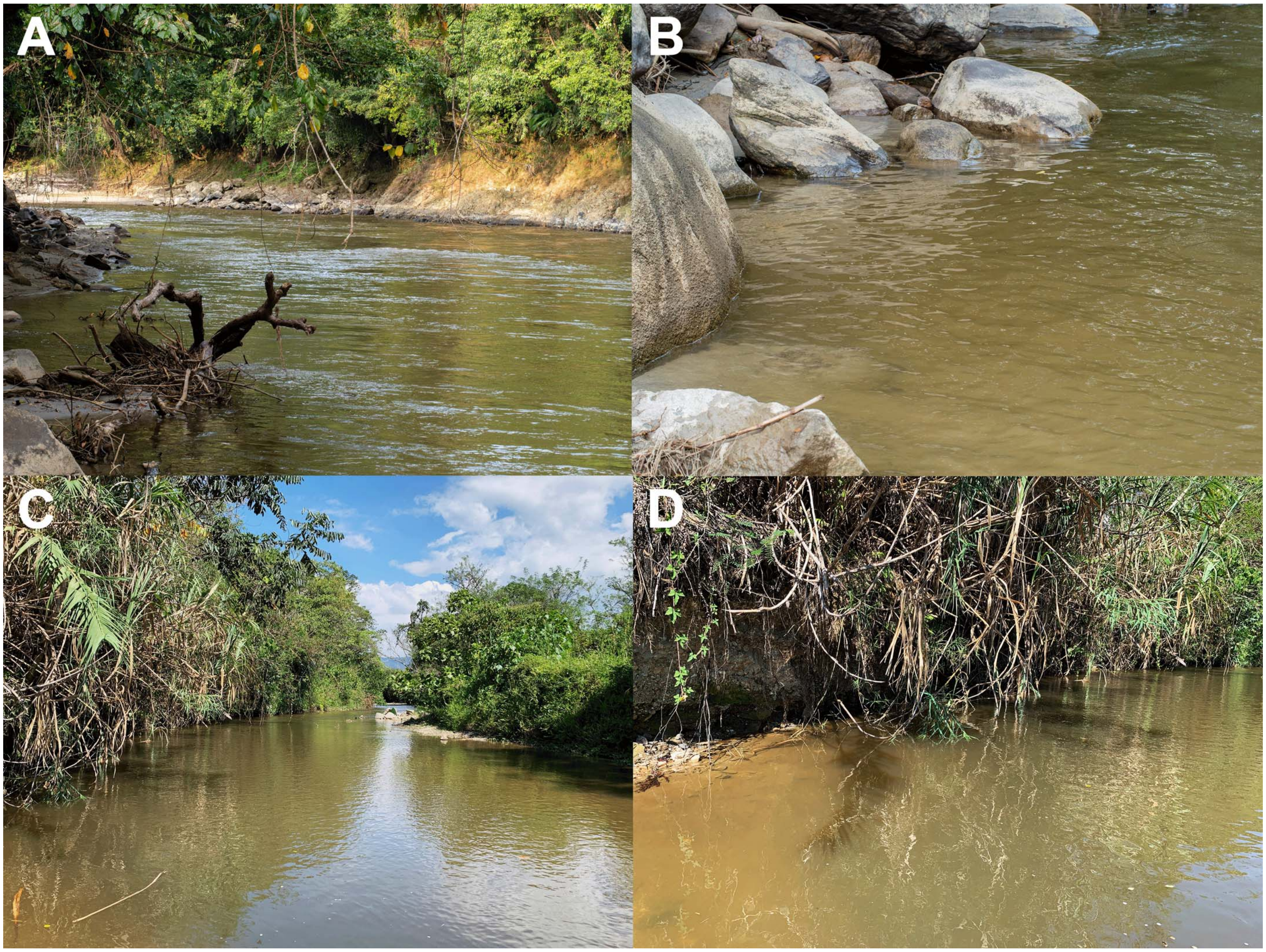

Fig. 6. Habitat at collection localities. (A, B) Type locality at Lariang River near Lengkeka Village, Bada Valley, Poso Regency, Central Sulawesi; (C, D) Pembangu River near Watutau Village in Napu Valley, Poso Regency, Central Sulawesi. (B) and (C) depict microhabitats in which *O. polylepis* was collected. (Photographs A and B by M. Mejía Estrada.)

females of related species are partially present but less pronounced in *O. polylepis*. Most prominently, the pelvic fins of female *O. polylepis* are only slightly enlarged (Figs. 1, 3). The ventral body does not form the distinct concavity seen in pelvic-brooding species. Extended egg-carrying was not observed in females collected in nature or under aquarium conditions. In the aquarium, females carry a cluster of up to ~15 eggs on the genital pore post-mating and deposit them inside spawning mops (submersed synthetic yarn bundles) after a few hours at most. Eggs are rather large, with diameters of approximately 1.6–1.8 mm. Spawning substrate in nature is unknown. In a typical mating event, males approach females by swimming beside or underneath them; males then briefly tilt their body to the side, which causes the reflective lateral band to flash, possibly signaling conspecifity to the female, before attempting the typical mating clasp also seen in other ricefishes.

Conservation status.—At the time of collection, *O. polylepis* was abundant at all sites where it was recorded. However, despite its remoteness, the Lariang River watershed is impacted by numerous potentially harmful human activities. These include the release of toxic tailings from gold mining, as reported by locals for several areas in the Lariang River watershed (e.g., by locals from the Bada Valley for areas downstream of the Bada Valley) and by locals in the southern Napu Valley. There are also plans for hydroelectric dam construction along the river (PT Nusantara Infrastructure Tbk, 2015; PT Indonesia Hydro Consult, 2020; Power Technology, 2021) with unknown impacts for *O. polylepis*, but certain detrimental impacts on diadromous species. The latter are target species for local fishers, and some, like the eleotrid goby *Belobranchus belobranchus*, also have local cultural importance (Yuniati et al., 2020).

Around one-tenth of the specimens of *O. polylepis* collected were infested with *Lernaea* sp., a widespread parasite also seen on other wild Sulawesi ricefishes species (Kottelat, 1990b; Parenti and Soeroto, 2004; Möhring et al., pers. obs., 2019, 2023; Schwarzer et al., pers. obs., 2019; Gani et al., 2022; Herder et al., 2022). Although supporting data are lacking, it appears likely that this parasite was introduced to Sulawesi by stocking of non-native fish species (Kottelat, 1990b; Whitten et al., 2001). The abundance of parasitized specimens in many species all over Sulawesi suggests that ricefishes are particularly susceptible to infestation from *Lernaea*.

Fig. 7. *Oryzias kalimpaaensis*, the sympatric pelvic-brooding sister species. (A) Sparring male and (B) female, both from the type locality of *O. polylepis* (uncatalogued specimens). Note the elongated pelvic fins and abdominal cavity of the female, both typical characteristics of pelvic-brooding species which are less pronounced in *O. polylepis*.

Despite the remoteness of the area, introduced fish species are numerous and widespread in the Lariang basin. *Anabas testudineus* ("Kosa/Koha") and *Channa striata* ("Gabus") were already reported by Kruyt (1938) from the Besoa Valley, also located within the drainage basin southwest of Napu Valley (Fig. 5), and appear to represent ancient introductions (Whitten et al., 2001). The cyprinid *Barbodes binotatus*, which was perhaps introduced accidentally with stocking of the larger, co-occurring cyprinid *Osteochilus vittatus*, or potentially on purpose for mosquito control, is extremely abundant and at many sites (such as the Malei River at Runde Village, and all smaller streams less than 5 m wide visited in Bada Valley) comprised most of the fish biomass. *Oreochromis* sp. is also widespread, as are *Gambusia* sp., *Poecilia reticulata*, and *Aplocheilus armatus*. *Trichopodus trichopterus* and *Clarias* sp. were recorded multiple times. The presence of nationally banned *Pterygoplichthys* sp. in the Lariang River at Tuare Village, Bada Valley is also worrisome, as this popular ornamental catfish species is known to cause ecological and economic damage when introduced (Page and Robins, 2006; Orfinger and Goodding, 2018; Patoka et al., 2020).

Etymology.—*Polylepis*—from ancient Greek "polus" (= many), an adjective, and "lepis" (= scale), a noun, in reference to its small and plentiful scales, reflected in high scale counts in lateral series. Compound noun, indeclinable.

Local names: Napu Valley (Bahasa Napu)—"Antowo." Mainly for *Oryzias kalimpaaensis*, but no distinction made between species; our information from local villagers in Watutau Village indicate that Antowo is not *Aplocheilus armatus* ("Kepala Timah"), as was reported in Mondolu et al. (2011). Bada Valley (Bahasa Bada)—"Rono." Identical to Lindu and Lake Poso (Pamona) areas for *Oryzias* spp. and smaller *Adrianichthys* spp.

Phylogenetic relationships.—*Oryzias polylepis* belongs to a clade of *Oryzias* restricted to western Central and Southern Sulawesi (Fig. 8A). It is closely related to the sympatric second ricefish species recorded from the Lariang drainage, *O. kalimpaaensis*, and both species were retrieved in a sister species relationship in the molecular phylogeny based on mitochondrial MT-ND2 sequences. Both species formed monophyletic groups, respectively, and no haplotype sharing was observed, suggesting complete reproductive isolation (Fig. 8B). Within *O. polylepis* and *O. kalimpaaensis*, haplotypes did not cluster according to geographic location, and numerous individual haplotypes were shared between specimens from collection sites in Napu and Bada Valleys.

DISCUSSION

Riverine sympatry.—At all locations where *O. polylepis* was collected, it occurred in sympatry with the closely related pelvic-fin brooder *O. kalimpaaensis* (Fig. 7). *Oryzias kalimpaaensis* itself was described only recently from small Lake Kalimpa'a, located in the highlands northwest of the Napu Valley (Gani et al., 2022). Here, we extend this record to the Lariang River and several of its tributaries. In the species description, Lake Kalimpa'a was assumed to be part of the Palu River watershed via the Sopu River. However, GIS analyses, local informants, and a visit to the lake confirmed that it is in fact part of the Lariang River basin. Our collections indicate that *O. kalimpaaensis*, while originally assumed to be restricted to only a single lake, is actually widespread in the Lariang River basin.

The present discoveries constitute the first known case of a sympatric riverine sister species pair among Sulawesi ricefishes. In Sulawesi, sympatry of ricefish species was previously known from three large lakes, namely Lake Poso (*O. nebulosus*, *O. nigrimas*, *O. orthognathus*, *Adrianichthys* spp.), Lake Towuti (*O. loxolepis*, *O. marmoratus*, *O. profundicola*), and Lake Lindu (*O. bonneorum*, *O. sarasinorum*; Parenti, 2008; Kobayashi et al., 2023). The degree of reproductive isolation among the lake species varies from clearly defined entities in Lake Poso (Sutra et al., 2019; Kakioka et al., 2021) to abundant intermediates in Lake Towuti (Herder and Chapuis, 2010; Mandagi et al., 2021).

In the case of the sympatric Lariang *Oryzias*, no indications of hybridization are present. Both species are clearly differentiated by non-overlapping characteristics and distinct haplotypes; intermediate individuals were not recorded. Both species are reciprocally monophyletic and together form the sister to a clade of known pelvic-brooding species of *Oryzias*: *O. eversi*, *O. sarasinorum*, and *O. bonneorum*. The phylogenetic position of the new, transfer-brooding species within this clade, as well as relatively short distances to its sister species, suggest that its reproductive mode evolved from pelvic brooding back to transfer brooding. Longer pelvic fins and slightly shortened pelvic ribs, both traits commonly seen in pelvic-brooding species (Spanke et al., 2021), support this assumption. As an alternative, though presumably less likely, it remains possible

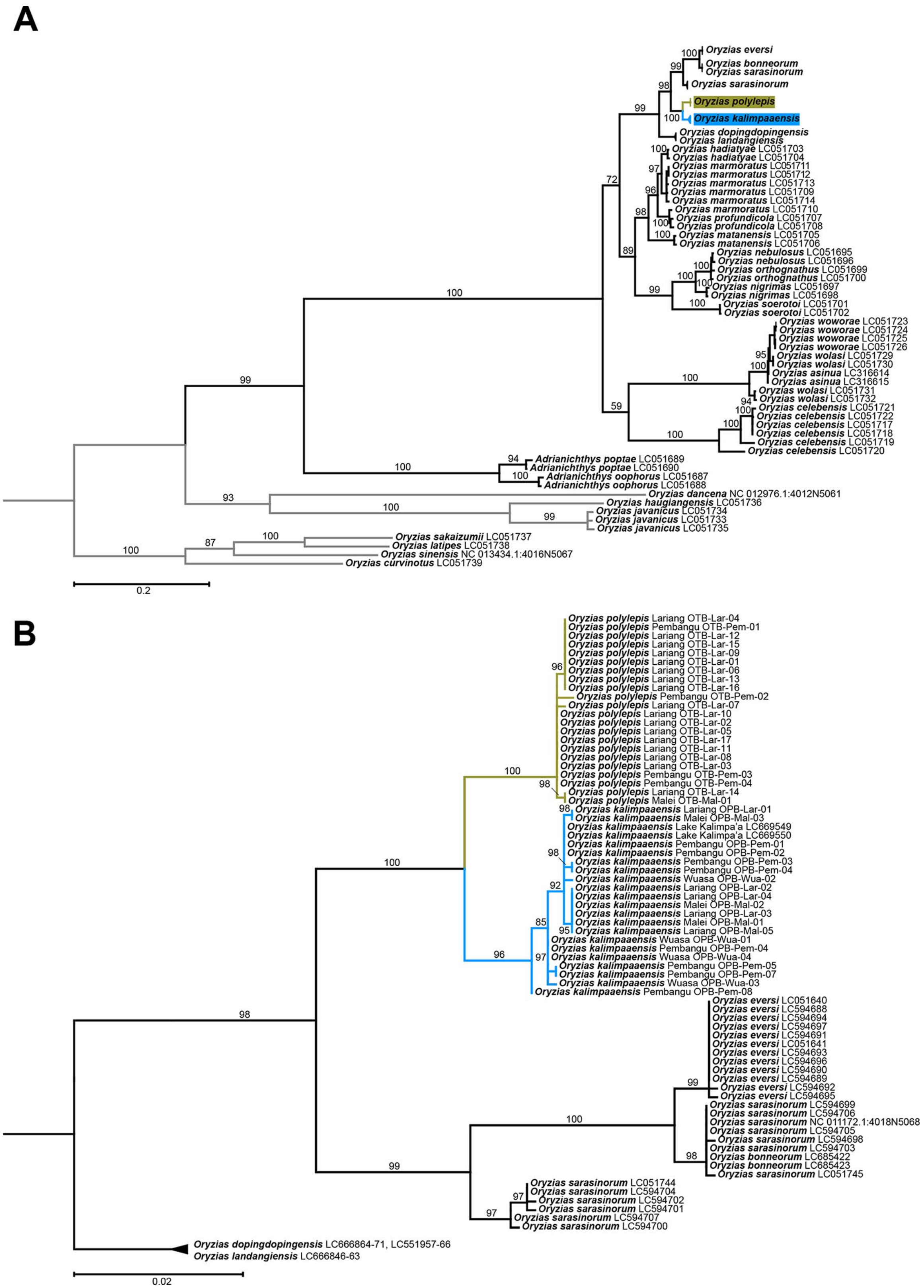

Fig. 8. Molecular phylogeny based on mitochondrial ND2 sequences, augmented using published sequence data for selected species from Mokodongan and Yamahira (2015; refer here for locality abbreviations), Horoiwa et al. (2021), Gani et al. (2022), and Utama et al. (2022). *Oryzias kalimpaaensis* and *O. polylepis* were retrieved as sister species, both forming monophyletic groups. (A) General topology of the phylogeny and (B) partial topology focusing on the clade in which the new species was recovered. Triangular tips are collapsed. Branches of non-Sulawesi lineages are colored gray. Bootstrap values based on 1,000 replicates are given for all non-intraspecies splits branches in (A), and for all splits with support >75% in (B). Blue and kaki color indicate *O. kalimpaaensis* and *O. polylepis*, respectively. See Data Accessibility for tree file.

that pelvic brooding evolved independently in *O. kalimpaaensis* compared to the lineage comprising *O. bonneorum*, *O. eversi*, and *O. sarasinorum*, although no morphological evidence for this is apparent at present. Either way, these phylogenetic insights indicate that pelvic brooding is a dynamically evolving reproductive mode in *Oryzias*.

Pronounced differences in male courtship coloration between *O. polylepis* and *O. kalimpaaensis*, namely presence of dark dorsal and lateral stripes and dark lateral blotches in *O. polylepis* vs. uniformly dark ash-gray with slate blue dorsal and anal fins in *O. kalimpaaensis* (Fig. 7A), might play a role in reinforcing species integrity under sympatric conditions. However, the evolutionary drivers of speciation are difficult to reconstruct due to incomplete knowledge of the basin's geological history. A role of potential former large lakes (Napu, Besoa, and Bada Valleys) located within the watershed, as well as numerous river capture events among Palu, Poso, Kalaena (Bone), and Lariang River catchments (Nugraha et al., 2024), provide tempting hypotheses, but remain difficult to test.

Oryzias polylepis and *O. kalimpaaensis* are regularly found in the same habitats in Bada and Napu Valleys, and they are frequently collected together in the same spot. However, *O. polylepis* is a faster, more active swimmer and prefers more open waters than *O. kalimpaaensis*, which tends to stay close to the substrate or sheltering structures like overhanging vegetation, driftwood, or rocks. In the field, *O. polylepis* was collected mostly in deeper waters and stronger current (>0.5 m depth) than its pelvic-brooding sister species. In agreement with these observations, *O. polylepis* shares features commonly seen in other free-swimming rheophilic fishes inhabiting medium to strong current, for example the elongated, slender body shape, long caudal peduncle, and deep oblique mouth gape present in selected Danionidae (e.g., Asian *Barilius*, *Danio* or African *Chelaethiops*, *Engraulicypris*). The possible secondary loss of pelvic brooding in *O. polylepis* might be another adaptation to its rheophilic ecology, as constant swimming in the current would likely result in intense drag and eventually premature loss of egg clusters. Ricefishes in general are not considered typical of fish inhabiting swift-flowing waters and are mostly restricted to lentic ecosystems or rivers with slow to moderate current. Only a few other ricefish species are known from similar habitats, namely the sympatric *O. kalimpaaensis* and *O. celebensis* from South-West Sulawesi. Both *Oryzias polylepis* and *O. kalimpaaensis* were abundant at the collection sites, suggesting high population densities. They may constitute a main prey species for several predatory fish species like *Belobranchus belobranchus*, *Lates calcarifer*, and other piscivorous animals.

Apart from differences in habitat use, differences in mouth shape between *O. polylepis* and *O. kalimpaaensis* also suggest disparity in trophic ecology. *Oryzias polylepis* is at least partly planktivorous, evident from feces of freshly collected specimens, which contained remains of phytoplankton. Aquarium observations showed that *O. kalimpaaensis*, while also eating small planktonic prey, tends to be more predatory and actively hunts larger prey such as small freshwater shrimps (*Caridina* spp.) and juvenile fish, catching them through suction feeding, which appears to be facilitated by its comparatively long snout and consequentially larger buccal cavity (cf. Fig. 7).

Relationship to fossil species.—There is the possibility that *O. polylepis* is closely related to the fossil *Lithopoecilus brouweri* de Beaufort 1934, described from Gimpu, Sulawesi Tengah. The fossil's type locality is geographically proximate and also situated within the modern Lariang River basin, only ~60 km downstream from Lengkeka Village, the type locality of *O. polylepis*. While its assignment to the family Adrianichthyidae was unquestionable, the phylogenetic position of the fossil has been the subject of speculation and was considered either intermediate between *Adrianichthys* and *Oryzias* (de Beaufort, 1934) or the common ancestor of *O. eversi* and *O. sarasinorum* (Horoiwa et al., 2021; Yamahira et al., 2021). Due to its rather poor state of preservation (an illustration of the fossil can be found in Frickhinger, 1991), morphological comparisons of the specimen to modern species are only possible to a limited extent. However, it does match some important osteological features of *O. polylepis* (Fig. 2B): apart from the elongated body shape, both appear to share a short snout and a deep oblique mouth gape, which distinguishes them from all known pelvic-brooding ricefishes. Short and non-filamentous dorsal- and anal-fin rays of the fossil specimen may indicate a female fish, while short pelvic-fin rays may indicate a transfer-brooding species. Since no reliable age estimates are available at present, it is not possible to discuss the role of the fossil species in the evolution of the extant Lariang *Oryzias*, but the hypotheses that it is ancestral or an extinct close relative to *O. polylepis*, or possibly belonging to the ancestral lineage of *O. kalimpaaensis* and *O. polylepis*, remain to be considered.

MATERIAL EXAMINED

Adrianichthys kruyti: ZMA 100.643, holotype.

Adrianichthys oophorus: ZFMK-ICH 121920–121926, Indonesia, Sulawesi Tengah, Lake Poso.

Adrianichthys poptae: NMB 3090, syntype, ZMH 22573, 1, ZMH 22575, 2, ZMH 22576, 3.

Oryzias asinua: MZB 21464, 2, Indonesia, Sulawesi Tenggara, District Asinua.

Oryzias bonneorum: MZB 15499, holotype, Indonesia, Sulawesi Tengah, Lake Lindu.

Oryzias celebensis: MZB 2688, 4, MZB 5862, 3, Indonesia, Sulawesi Selatan, Regency of Maros Indonesia.

Oryzias dopingdopingensis: MZB 23873, holotype, Indonesia, Sulawesi Selatan; MZB 23874–23882, 9 paratypes.

Oryzias eversi: MZB 20780, holotype, MZB 20781, 1 paratype, Indonesia, Sulawesi Selatan, District Rantepao.

Oryzias hadiatyae: MZB 18491, holotype, MZB 18503, 1 paratype, MZB 18504, 1 paratype, MZB 18505, 1 paratype, MZB 18506, 1 paratype, Indonesia, Sulawesi Selatan, Lake Masapi.

Oryzias kalimpaaensis: MZB 26462, holotype, MZB 26463–26466, 4 paratypes, ZFMK ICH-128486–128492, 7 paratypes, ZRC 62531, 4 paratypes, Indonesia, Sulawesi Tengah, Lake Kalimpa'a; MZB 28070–28080, 34.5–47.4 mm SL (7 males, 4 females), Lariang River, near Lengkeka Village, Bada Valley, District Lore Barat, Poso Regency, Sulawesi Tengah, 01°52′38.05″S, 120°12′8.83″E, 752 m MSL, J. Möhring, F. K. Lakiu, and M. Mejía Estrada, 14–15 August 2023; MZB 28081–28091, 37.0–46.7 mm SL (6 males, 5 females), Malei River, near Runde Village, Bada Valley, District Lore Barat, Sulawesi Tengah, 01°54′12.74″S, 120°14′26.93″E, 765 m MSL, J. Möhring, F. K. Lakiu, Aro, and M. Mejía Estrada, 14 August 2023; MZB 28092–28093, 38.4–41.4 mm SL (2 females), Malei River at Gintu Village, Bada Valley, District Lore Selatan, Poso Regency, Sulawesi Tengah, 01°53′13.95″S, 120°14′6.25″E, 760 m MSL, F. Herder and D. F. Mokodongan, 21 September 2023; MZB 28094–28101, 32.9–50.2 mm SL (3 males, 5 females), Wuasa River, near Wuasa Village, Napu Valley, District Lore Utara, Poso Regency, Sulawesi Tengah, 01°25′32.12″S, 120°19′2.23″E, 1,103 m MSL, J. Möhring, F. K. Lakiu, M. Mejía Estrada, and J. K. Poba, 22 July 2023; MZB 28102–28120, 34.6–52.8 mm SL (5 males, 14 females), Pembangu River, Watutau Village, Napu Valley, District Lore Peore, Poso Regency, Sulawesi Tengah, 01°33′51.41″S, 120°20′33.00″E, 1,085 m MSL, J. Möhring, A. Gani, Z. Jusman, and D. F. Mokodongan, 30 September 2023.

Oryzias landangiensis: MZB 26270, holotype, MZB 26271–26275, 5 paratypes.

Oryzias loxolepis: ZFMK ICH-136040–136044, Indonesia, Sulawesi Selatan, Lake Towuti.

Oryzias marmoratus: MZB 2686, 7, MZB 2690, 1, Indonesia, Sulawesi Selatan, Lake Wawontoa; MZB 2695, 5, MZB 2697, 5, Indonesia, Sulawesi Selatan, Lake Towuti.

Oryzias matanensis: MZB 21379, 1, Indonesia, Sulawesi Selatan, Lake Matano.

Oryzias nebulosus: MZB 21381, 2, Indonesia, Sulawesi Tengah, Lake Poso.

Oryzias nigrimas: MZB 5859, holotype, MZB 5872, 5 paratypes, Indonesia, Sulawesi Tengah, Lake Poso.

Oryzias orthognathus: MZB 5870, holotype, Indonesia, Sulawesi Tengah, Lake Poso.

Oryzias profundicola: MZB 5868, holotype, MZB 5861, 1 paratype, MZB 5866, 1 paratype, MZB 5867, 2 paratypes, Indonesia, Sulawesi Selatan, Lake Towuti.

Oryzias sarasinorum: RMNH 7664, 3 syntypes, MZB 25209–25213, 5, ZFMK-ICH-121927–121931, 5.

Oryzias soerotoi: MZB 21377, holotype, MZB 21378, 9 paratypes, ZFMK 49943–49947, 5 paratypes.

Oryzias wolasi: MZB 21465, 2, Indonesia, Sulawesi Tenggara, District Wolasi.

Oryzias woworae: MZB 21380, 1, Indonesia, Sulawesi Tenggara, Muna Island, District Parigi.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/i2024051. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License. ZooBank publication urn:lsid:zoobank.org:pub:9AAE45B7-BB76-4FF9-AF84-5BCC252A6F18.

AI STATEMENT

The authors used DxO Pure Raw 3, a tool that utilizes AI machine learning, for denoising the RAW files of the photographs shown in the figures.

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LITERATURE CITED

de Beaufort, L. F. 1934. On a fossil fish from Gimpoe (Central-Celebes). Verhandlungen Geologie en Mijnbouw Genoot. Nederland en Koloniën, Geology Series 10:180.

Flury, J. M., K. Meusemann, S. Martin, L. Hilgers, T. Spanke, A. Böhne, F. Herder, D. F. Mokodongan, J. Altmüller, D. Wowor, B. Misof, A. W. Nolte, and J. Schwarzer. 2023. Potential contribution of ancient introgression to the evolution of a derived reproductive strategy in ricefishes. Genome Biology and Evolution 15:evad138.

Fricke, R., W. N. Eschmeyer, and R. van der Laan (Eds.). 2024. Eschmeyer's Catalog of Fishes: General, Species, References. https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 22 April 2024).

Frickhinger, K. A. 1991. Fossilien Atlas Fische. First edition. Mergus-Verlag für Natur- und Heimtierkunde Baensch, Melle.

Gani, A., N. Suhendra, F. Herder, J. Schwarzer, J. Möhring, J. Montenegro, M. Herjayanto, and D. Mokodongan. 2022. A new endemic species of pelvic-brooding ricefish (Beloniformes: Adrianichthyidae: *Oryzias*) from Lake Kalimpa'a, Sulawesi, Indonesia. Bonn Zoological Bulletin 71:77–85.

Herder, F., and S. Chapuis. 2010. *Oryzias hadiatyae*, a new species of ricefish (Atherinomorpha: Beloniformes: Adrianichthyidae) endemic to Lake Masapi, Central Sulawesi, Indonesia. The Raffles Bulletin of Zoology 58:269–280.

Herder, F., R. K. Hadiaty, and A. W. Nolte. 2012. Pelvic-fin brooding in a new species of riverine ricefish (Atherinomorpha: Beloniformes: Adrianichthyidae) from Tana Toraja, Central Sulawesi, Indonesia. The Raffles Bulletin of Zoology 60:467–476.

Herder, F., J. Möhring, J. M. Flury, L. V. Utama, L. Wantania, D. Wowor, F. B. Boneka, B. Stelbrink, L. Hilgers, J. Schwarzer, and J. Pfaender. 2022. More non-native fish species than natives, and an invasion of Malawi cichlids, in ancient Lake Poso, Sulawesi, Indonesia. Aquatic Invasions 17:72–91.

Hilgers, L., and J. Schwarzer. 2019. The untapped potential of medaka and its wild relatives. eLife 8:e46994.

Horoiwa, M., I. F. Mandagi, N. Sutra, J. Montenegro, F. Y. Tantu, K. W. A. Masengi, A. J. Nagano, J. Kusumi, N. Yasuda, and K. Yamahira. 2021. Mitochondrial introgression by ancient admixture between two distant lacustrine fishes in Sulawesi Island. PLoS ONE 16:e0245316.

Jamonneau, T., H. Dahruddin, G. Limmon, T. Sukmono, F. Busson, Nurjirana, A. Gani, J. Patikawa, E. Wuniarto, S. Sauri, U. Nurhaman, D. Wowor, D. Steinke, P. Keith, and N. Hubert. 2024. Jump dispersal drives the relationship between micro- and macroevolutionary dynamics in the Sicydiinae (Gobiiformes: Oxudercidae) of Sundaland and Wallacea. Journal of Evolutionary Biology 37:1458–1473.

Kakioka, R., N. Sutra, H. Kobayashi, S. Ansai, K. W. A. Masengi, A. J. Nagano, N. Okuda, R. Tanaka, M. Sato, and K. Yamahira. 2021. Resource partitioning is not coupled with assortative mating in sympatrically divergent ricefish in a Wallacean ancient lake. Journal of Evolutionary Biology 34:1133–1143.

Klotz, W., T. Rintelen, A. Annawaty, D. Wowor, and K. von Rintelen. 2023. *Caridina clandestina*, new species, an unusual new freshwater shrimp (Crustacea: Decapoda: Atyidae) from the remote high elevation Napu Valley of Sulawesi, Indonesia. The Raffles Bulletin of Zoology 71:12–25.

Kobayashi, H., D. F. Mokodongan, M. Horoiwa, S. Fujimoto, R. Tanaka, K. W. A. Masengi, and K. Yamahira. 2023. A new lacustrine ricefish from central Sulawesi, with a redescription of *Oryzias marmoratus* (Teleostei: Adrianichthyidae). Ichthyological Research 70:490–514.

Kottelat, M. 1990a. Synopsis of the endangered Buntingi (Osteichthyes: Adrianichthyidae and Oryziidae) of Lake Poso, Central Sulawesi, Indonesia, with a new reproductive guild and description of three new species. Ichthyological Exploration of Freshwaters 1:49–67.

Kottelat, M. 1990b. The ricefishes (Oryziidae) of the Malili Lakes, Sulawesi, Indonesia, with description of a new species. Ichthyological Exploration of Freshwaters 1:151–166.

Kottelat, M. 2013. The fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. The Raffles Bulletin of Zoology Suppl. 27:1–663.

Kruyt, A. C. 1938. De West-Toradjas op Midden-Celebes. Noord-Hollandsche Uitgevers-Maatschappij, Amsterdam.

Kumar, S., G. Stecher, M. Li, C. Knyaz, and K. Tamura. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35:1547–1549.

Mandagi, I. F., R. Kakioka, J. Montenegro, H. Kobayashi, K. W. A. Masengi, N. Inomata, A. J. Nagano, A. Toyoda, S. Ansai, M. Matsunami, R. Kimura, J. Kitano, J. Kusumi, and K. Yamahira. 2021. Species divergence and repeated ancient hybridization in a Sulawesian lake system. Journal of Evolutionary Biology 34:1767–1780.

Mandagi, I. F., D. F. Mokodongan, R. Tanaka, and K. Yamahira. 2018. A new riverine ricefish of the genus *Oryzias* (Beloniformes, Adrianichthyidae) from Malili, Central Sulawesi, Indonesia. Copeia 106:297–304.

Miesen, F. W., F. Droppelmann, S. Hüllen, R. Hadiaty, and F. Herder. 2016. An annotated checklist of the inland fishes of Sulawesi. Bonn Zoological Bulletin 64:77–106.

Minh, B. Q., H. A. Schmidt, O. Chernomor, D. Schrempf, M. D. Woodhams, A. von Haeseler, and R. Lanfear. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37:1530–1534.

Mokodongan, D. F., R. Tanaka, and K. Yamahira. 2014. A new ricefish of the genus *Oryzias* (Beloniformes, Adrianichthyidae) from Lake Tiu, Central Sulawesi, Indonesia. Copeia 2014:561–567.

Mokodongan, D. F., and K. Yamahira. 2015. Origin and intra-island diversification of Sulawesi endemic Adrianichthyidae. Molecular Phylogenetics and Evolution 93:150–160.

Mondolu, T., K. Nelloh, N. P. Tokari, H. Tebo, S. Limba, and M. Gae. 2011. Kamus Napu–Indonesia–Inggris. *In*: Sulang Language Data and Working Papers. R. Hanna (ed.). Sulawesi Language Alliance, Online. http://sulang.org/sites/default/files/sulangdict002-v1.pdf (accessed 10 February 2024).

Nugraha, A. M. S., J. Hennig-Breitfeld, R. Puspita, A. D. Switzer, and R. Hall. 2024. Detrital zircons and heavy minerals from the Palu Formation, Sulawesi, Indonesia: constraints on exhumation of the Palu Metamorphic Complex and drainage evolution. Journal of the Geological Society 181:jgs2023-118.

Orfinger, A. B., and D. D. Goodding. 2018. The global invasion of the suckermouth armored catfish genus *Pterygoplichthys* (Siluriformes: Loricariidae): annotated list of species, distributional summary, and assessment of impacts. Zoological Studies 57:e7.

Overseas Technical Cooperation Agency, Government of Japan (JICA). 1971. Report on Geological Survey of Central Sulawesi, Indonesia. Vol. 1–General. https://openjicareport.jica.go.jp/pdf/10796506.pdf (accessed 10 January 2024).

Page, L. M., and R. H. Robins. 2006. Identification of sailfin catfishes (Teleostei: Loricariidae) in Southeastern Asia. The Raffles Bulletin of Zoology 54:455–457.

Parenti, L. R. 2008. A phylogenetic analysis and taxonomic revision of ricefishes, *Oryzias* and relatives (Beloniformes, Adrianichthyidae). Zoological Journal of the Linnean Society 154:494–610.

Parenti, L. R., and R. K. Hadiaty. 2010. A new, remarkably colorful, small ricefish of the genus *Oryzias* (Beloniformes, Adrianichthyidae) from Sulawesi, Indonesia. Copeia 2010:268–273.

Parenti, L. R., R. K. Hadiaty, D. Lumbantobing, and F. Herder. 2013. Two new ricefishes of the genus *Oryzias* (Atherinomorpha: Beloniformes: Adrianichthyidae) augment the endemic freshwater fish fauna of Southeastern Sulawesi, Indonesia. Copeia 2013:403–414.

Parenti, L., and B. Soeroto. 2004. *Adrianichthys roseni* and *Oryzias nebulosus*, two new ricefishes (Atherinomorpha: Beloniformes: Adrianichthyidae) from Lake Poso, Sulawesi, Indonesia. Ichthyological Research 51:10–19.

Patoka, J., M. Takdir, Yonvitner, H. Aryadi, R. Jerikho, J. Nilawati, F. Y. Tantu, L. Bohatá, A. Aulia, M. M. Kamal, Y. Wardiatno, and M. Petrtýl. 2020. Two species of illegal South American sailfin catfish of the genus *Pterygoplichthys* well-established in Indonesia. Knowledge & Management of Aquatic Ecosystems 421:28.

Power Technology. 2021. Lariang, Indonesia. https://www.power-technology.com/marketdata/lariang-indonesia/ (accessed 23 April 2024).

PT Indonesia Hydro Consult. 2020. Projects undertaken. https://indonesia-hydro.com/projects_undertaken (accessed 23 April 2024).

PT Nusantara Infrastructure Tbk. 2015. Indonesian Hydro Power Development. https://www.nusantarainfrastructure.com/other-detail/indonesian-hydro-power-development (accessed 23 April 2024).

von Rintelen, T., K. von Rintelen, M. Glaubrecht, C. D. Schubart, and F. Herder. 2012. Aquatic biodiversity hotspots in Wallacea: the species flocks in the ancient lakes of Sulawesi, Indonesia, p. 290–315. *In*: Biotic Evolution and Environmental Change in Southeast Asia. D. Gower, K. Johnson, J. Richardson, B. Rosen, L. Rüber, and S. Williams (eds.). Cambridge University Press, Cambridge.

Sabaj, M. H. 2020. Codes for natural history collections in ichthyology and herpetology. Copeia 108:593–669.

Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longair, T. Pietzsch, S. Preibisch, C. Rueden, S. Saalfeld, B. Schmid, J.-Y. Tinevez, D. J. White, V. Hartenstein, K. Eliceiri … **A. Cardona.** 2012. Fiji: an open-source platform for biological-image analysis. Nature Methods 9:676–682.

Spanke, T., L. Hilgers, B. Wipfler, J. M. Flury, A. W. Nolte, I. V. Utama, B. Misof, F. Herder, and J. Schwarzer. 2021. Complex sexually dimorphic traits shape the parallel evolution of a novel reproductive strategy in Sulawesi ricefishes (Adrianichthyidae). BMC Ecology and Evolution 21:57.

Stelbrink, B., C. Albrecht, R. Hall, and T. von Rintelen. 2012. The biogeography of Sulawesi revisited: is there evidence for a vicariant origin of taxa on Wallace's "anomalous island"? Evolution 66:2252–2271.

Sutra, N., J. Kusumi, J. Montenegro, H. Kobayashi, S. Fujimoto, K. W. A. Masengi, A. J. Nagano, A. Toyoda, M. Matsunami, R. Kimura, and K. Yamahira. 2019. Evidence for sympatric speciation in a Wallacean ancient lake. Evolution 73:1898–1915.

Utama, I. V., I. F. Mandagi, S. A. Lawelle, K. W. A. Masengi, K. Watanabe, N. Sawada, A. J. Nagano, J. Kusumi, and K. Yamahira. 2022. Deeply divergent freshwater fish species within a single river system in central Sulawesi. Molecular Phylogenetics and Evolution 173:107519.

Vaillant, J. J., G. D. Haffner, and M. E. Cristescu. 2011. The ancient lakes of Indonesia: towards integrated research on speciation. Integrative and Comparative Biology 51:634–643.

Whitten, T., M. Mustafa, and G. S. Henderson. 2001. The Ecology of Sulawesi. Fourth edition. Periplus Editions.

Yamahira, K., S. Ansai, R. Kakioka, H. Yaguchi, T. Kon, J. Montenegro, H. Kobayashi, S. Fujimoto, R. Kimura, Y. Takehana, D. H. E. Setiamarga, Y. Takami, R. Tanaka, K. Maeda … **J. Kitano.** 2021. Mesozoic origin and 'out-of-India' radiation of ricefishes (Adrianichthyidae). Biology Letters 17:20210212.

Yuniati, E., S. Indriyani, J. Batoro, and Y. Purwanto. 2020. Ethnozoology of the ritual and magic of the To Bada Ethnic Group in the Lore Lindu Biosphere Reserve, Central Sulawesi, Indonesia. Biodiversitas Journal of Biological Diversity 21:2645–2653.