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A New “Beakless” Halfbeak of the Genus *Nomorhamphus* from Sulawesi (Teleostei: Zenarchopteridae)

Hirozumi Kobayashi^{1,2}, Kawilarang W. A. Masengi³, and Kazunori Yamahira²

A new viviparous halfbeak, *Nomorhamphus aenigma*, new species, from the upper stream of the Cerekang River in central Sulawesi, Indonesia is described. The new species is distinguished from all other zenarchopterids by the complete absence of elongate lower jaws. Although secondary loss of elongate jaws is also known from several hemiramphids, *N. aenigma*, new species, is clearly different from them by having no elongate jaws throughout ontogeny.

UNDERSTANDING the evolution of novel traits and their functions are major objectives of biology (e.g., Gails, 1996; Futuyma, 1998). The possibility that a new adaptive trait can be caused by heterochronic developmental shift has been debated for more than 100 years in the context of evolutionary development, since Haeckel’s (1866) recapitulation theory (e.g., de Beer, 1940; Gould, 1977; Smith, 2003).

Beloniformes is known to have a variety of heterochronic stages of jaw elongation (e.g., Sewertzoff, 1927; Lovejoy et al., 2000, 2004). Among the five families of this order (Lovejoy et al., 2004; Nelson et al., 2016; Betancur-R et al., 2017; Collette and Bemis, 2019a), Belonidae (needlefishes) has both elongate upper and lower jaws, most Hemiramphidae (halfbeaks) and Zenarchopteridae (viviparous halfbeaks) only have elongate lower jaws, and Exocoetidae (flyingfishes) and Adrianichthyidae (ricefishes) have non-elongate upper and lower jaws (Nelson et al., 2016). Species with elongate jaws are known to go through non-elongate jaw stages during the initial stage of their development (e.g., Lovejoy et al., 2004; Gunter et al., 2014). For example, in needlefishes there is a “halfbeak-like” stage in which only the lower jaw elongates, and in halfbeaks (Hemiramphidae and Zenarchopteridae) there is a “ricefish-like” stage in which the upper and lower jaws are not elongate (e.g., Sewertzoff, 1927; Uchida et al., 1958; Hardy and Johnson, 1974; Collette et al., 1984; Collette, 2005; Chen, 2014). These inter-family heterochronic variations in jaw development patterns have been well discussed in the context of phylogeny (e.g., Levit et al., 2004; Lovejoy et al., 2004) and evolutionary development (e.g., Gunter et al., 2014).

Heterochronic variation in beloniform jaw morphology is thought to have provided potential materials for adaptations to evolve in this order (Gunter et al., 2014), which is distributed worldwide and in a variety of habitats, from freshwater to marine environments (Nelson et al., 2016). For example, Boughton et al. (1991) compared stomach contents among individuals in different ontogenetic stages and suggested that maxillary elongation in needlefishes might be related to the ontogenetic change from planktivory to carnivory. In contrast, to our knowledge, lower jaw functions

in halfbeaks have not been examined by such comparative approaches.

Nomorhamphus is a genus in the Zenarchopteridae that is endemic to Sulawesi Island, which is an island of the Indo-Australian Archipelago, and the Philippines (Meisner, 2001; Kottelat, 2013; Kraemer et al., 2019a). Although 20 species have been described in this genus to date, all described species had elongate lower jaws (Meisner, 2001; Huylebrouck et al., 2012, 2014; Kraemer et al., 2019a). Interestingly, although the degree of jaw elongation varies among species, no species in the genus, and even in Zenarchopteridae, that completely lacked elongate jaws were reported. Such a species without elongate lower jaws would provide a good model system for examining the process of jaw development and testing the adaptive significance of lower jaws in this group.

Here, we describe a new species of *Nomorhamphus* that completely lacks elongate mandibles from a river in central Sulawesi. This species is the first discovered zenarchopterid with no elongate lower jaw. We discuss the phylogenetic position of this species within the genus, forms of heterochrony, and evolutionary reasons for the lack of lower jaw elongation.

MATERIALS AND METHODS

Individuals of the new species of *Nomorhamphus* were collected using a beach seine from two sites in the upper part of Cerekang River, one approximately 1 km downstream from Laroeha Village and the other near Landangi Village, Southern Sulawesi Province (Fig. 1). Cerekang River is a river that shares an estuarine region with Larona River, which is the only drainage from the Malili lake system. In total, 18 individuals (five males, ten females, and three juveniles) were collected during field collections on 21 and 25 November 2018.

The collected individuals were euthanized with MS-222, fixed in 10% neutralized formalin, and then transferred to 70% ethanol for storage. Fish specimens were deposited in the Museum Zoologicum Bogoriense, Cibinon (MZB), Wallacean Collection of Natural History, Manado City Museum, Sulawesi Utara (WMSU), and National Museum of Nature and Science, Tokyo (NSMT). Identifications of fish species

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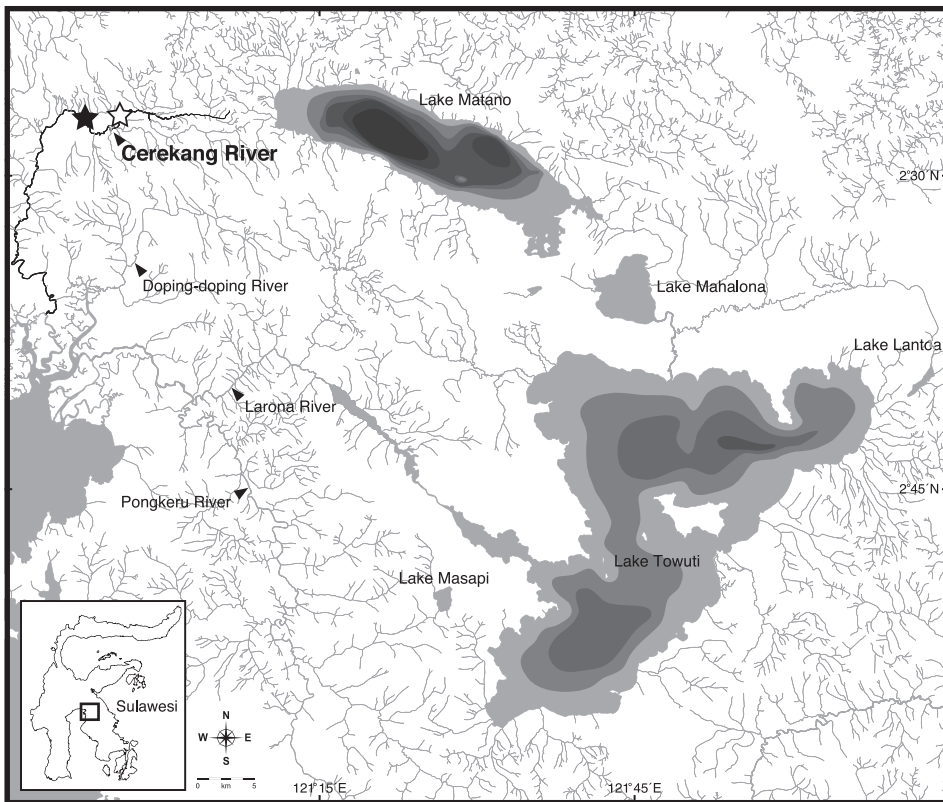


Fig. 1. Map showing the type locality of *Nomorhamphus aenigma*, new species. Map by T. von Rintelen, modified. The black and white stars indicate the type locality (holotype and seven paratypes) and locality of ten paratypes, respectively.

collected along with the new *Nomorhamphus* followed Kottelat et al. (1993), Larson (2001), Mandagi et al. (2018), and Kraemer et al. (2019b).

Measurements were taken from point to point using a digital caliper to the nearest 0.1 mm. They were reported as a range of percentages of the standard length (SL) with the values for the holotype in brackets. Points of measurements and abbreviations followed Huylebrouck et al. (2012). Counts of the unpaired fin rays and vertebrae (total = precaudal + caudal) were obtained from radiographs (Softex, E-3). The hypural centrum was treated as a caudal vertebra. Numbers of the paired fin rays were counted directly under a stereo microscope (Leica, MZ6). Meristics were also reported as a range, with the holotype values in brackets. In undissected male specimens, the first segment of each anal-fin ray was not clearly visible because of muscle that covers the anal-fin base. Similarly, the entire fourth through seventh anal-fin rays were not visible because the membrane covered the anterior part of anal fin. For this reason, a male specimen, NSMT-P 136105 (33.1 mm SL), was cleared and stained, and the drawing of the andropodium was made using a camera lucida. The species description template followed Kraemer et al. (2019a). Terms for modified anal-fin rays of males followed Brembach (1976, 1991), Meisner and Burns (1997), and Meisner (2001).

***Nomorhamphus aenigma*, new species**

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Figures 1–6, Table 1

Holotype.—MZB 25100 (Figs. 2, 3), male, 34.7 mm SL, upper reaches of Cerekang River near by Laroeha Village, Malili River basin, Sulawesi Selatan, Indonesia, 2°27'39.7"S,

121°04'03.0"E, K. W. A. Masengi, I. F. Mandagi, and S. A. Lawelle, 25 November 2018.

Paratypes.—MZB 25101–25104, 4 females, 27.9–37.8 mm SL, NSMT-P 136106–136107, 1 male, 1 female, 26.8–43.0 mm SL, WMSU 00001, male, 28.1 mm SL, collected with the holotype; MZB 25098–25099, 2 females, 41.6–60.9 mm SL, NSMT-P 136102–136105, 2 males, 2 females, 31.3–52.2 mm SL, WMSU 00002, female, 30.1 mm SL, WMSU 00012–00014, 3 juveniles, 10.2–23.3 mm SL, Cerekang River near by Landangi Village, Malili River basin, Sulawesi Selatan, Indonesia, 2°26'57.7"S, 121°05'47.8"E, H. Kobayashi, K. W. A. Masengi, I. F. Mandagi, S. A. Lawelle, R. Kakioka, S. Ansai, and K. Yamahira, 21 November 2018.

Diagnosis.—*Nomorhamphus aenigma* is distinguished from all other congeners by the absence of any elongation of the lower jaw throughout ontogeny. *Nomorhamphus aenigma* is also distinguished from all other congeners by a combination of the short and expanded teeth on gill rakers, 22–23 precaudal and 16–17 caudal vertebrae, 13–14 anal-fin rays, 12 segments in the male first anal-fin ray, and distal tips of the male second and third anal-fin rays having no contact with each other.

Description.—Morphometric and meristic characters are provided in Table 1. Mouth subterminal; lower jaw had no elongation or appendage, distance between distal tip of upper to lower jaw (LJLB) 0.7–1.9 [0.9]. Upper jaw longer than wide, upper jaw length/upper jaw width (UJL/UJW) 1.2–1.7 [1.4]. One row of conical teeth at the front of the upper and lower jaws, followed by irregular rows of conical teeth up to the end of the jaws. Gill rakers short, base expanded with six to nine conical teeth on the dorsal surface

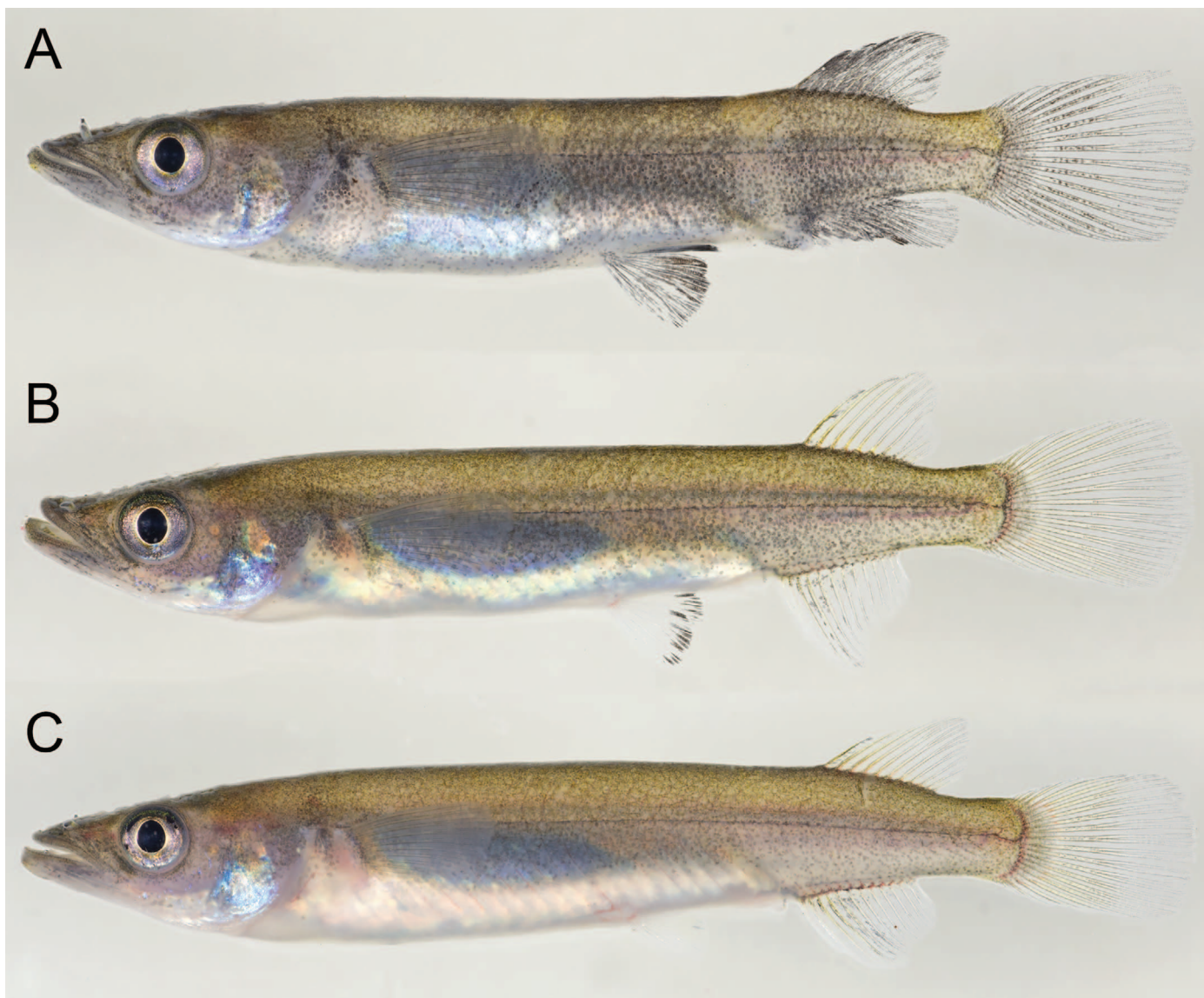


Fig. 2. Photographs of *Nomorhamphus aenigma*, new species, immediately after fixation. (A) MZB 25100, holotype (male, 34.7 mm SL), (B) MZB 25103, paratype (female, 37.8 mm SL), (C) NSMT-P 136106, paratype (female, 43.0 mm SL).



Fig. 3. Preserved specimens of *Nomorhamphus aenigma*. Upper: MZB 25100, holotype (male, 34.7 mm SL), lower: MZB 25099, paratype (female, 41.6 mm SL).



Fig. 4. Type locality of *Nomorhamphus aenigma*, Cerekang River, approximately 600 m downstream from Laroeha Village, Luwu Timur District, Regency of Wasuponda, Sulawesi Selatan. Photo taken 3 September 2019.

of the gill rakers. Eye relatively large, bony orbital diameter (ORBL) 5.9–8.2 [7.8]. Body deep, body depth on pectoral-fin base (BDP1) 15.7–19.5 [18.2] and body depth on pelvic-fin base (BDP2) 14.9–19.2 [17.0]. Caudal peduncle depth 7.6–8.6 [8.1].

Predorsal scales deeply embedded. Vertebrae number 38–39 [38] (precaudal 22–23 [22] + caudal 16–17 [17]). Fifth hypural fused to dorsal hypural plate. Anal-fin rays 13–14 [14]; dorsal-fin rays 10–12 [12]; pectoral-fin rays 11–12 [12]; pelvic-fin rays 6. Caudal fin truncate, principal caudal-fin rays $i,5-6/6,i$ [$i,5/6,i$] (mode $i,6/6,i$), procurrent caudal-fin rays $6-7/6-7$ [$7/7$] (mode $6/6$).

Males have modified anal-fin fleshy covering. For a stained specimen (NSMT-P 136105), the first anal-fin ray has 12 segments. The second anal-fin ray has also 12 segments with a narrow spiculus outwards. The second anal-fin ray is shorter than the third. The second and third anal-fin rays do not contact each other. The third, fourth, and fifth anal-fin rays have 18, 8, and 10 segments.

Color in life.—Body translucent beige in base color (Fig. 2); striped black in males and uniform pale black in females.

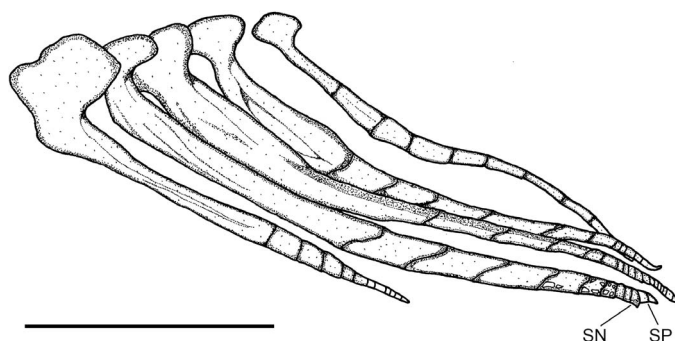


Fig. 5. Diagrammatic representation of the modified anal-fin rays (andropodium) of *Nomorhamphus aenigma*, NSMT-P 136105, 33.1 mm SL. Scale bar = 1 mm, SN: spinae, SP: spiculus.

Interoperculum brilliant. Belly brilliant sky blue in holotype, others white. Throat white. Iris upper and lower parts black, middle part yellow with a yellow edge. Diffuse black pigmentation on pectoral fin and oval spot on the base of pectoral fin. Base of pectoral-fin rays dark hyaline. Pelvic fins black in males; in females translucent or black pigmentation on distal tip. Base of dorsal- and anal-fin rays black. Dorsal and anal fin black in males; pale beige with irregular black pigmentation in females. Base of caudal fin dark hyaline. Other part of caudal fin black in males; pale beige in females.

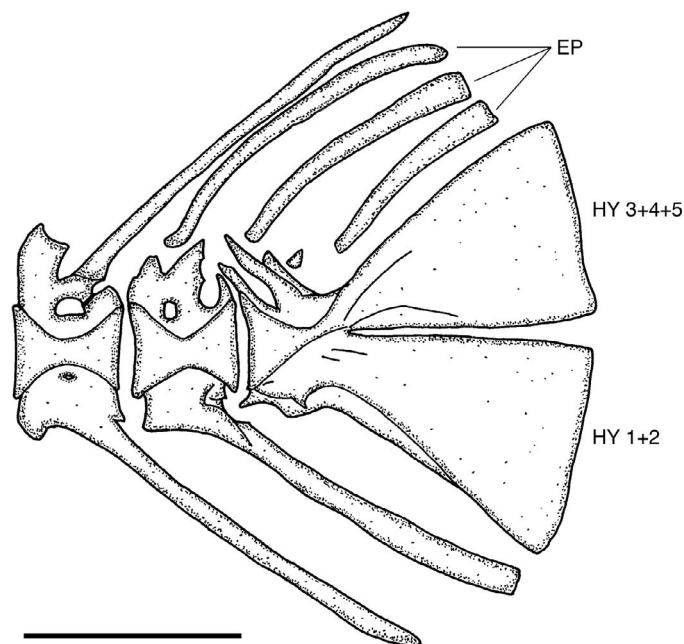


Fig. 6. Diagrammatic representation of the caudal skeleton of *Nomorhamphus aenigma*, NSMT-P 136105, 33.1 mm SL, male. Scale bar = 1 mm. EP, epural; HY, hypural.

Table 1. Meristic and morphometric characters of *Nomorhamphus aenigma* (holotype and 13 paratypes).

	Holotype MZB 25100	Paratypes (males, <i>n</i> = 3)			Paratypes (females, <i>n</i> = 10)		
		Range	Mode		Range	Mode	
Standard length (SL)	34.7	25.8–31.3			30.3–60.9		
Meristics							
Anal-fin rays	13	14	14		13–15	14	
Dorsal-fin rays	11	11–12	12		10–12	11	
Pectoral-fin rays	11	11–12	12		12	12	
Pelvic-fin rays	6	6	6		6	6	
Precaudal vertebrae	22	22–23	22		22–23	22	
Caudal vertebrae	16	16–17	16		16–17	16	
Total vertebrae	38	38–39	39		38–39	38	
Principal caudal-fin rays	5/6	6/6	6/6		6/6	6/6	
Procurent caudal-fin rays	7/7	6/6–7/6	6/6		6/6–7/6	6/6	
In percent of standard length		Range	Mean	±SD	Range	Mean	±SD
Total length including beak (TL)	121.6	121.0–121.3	121.1	0.1	117.2–122.2	119.2	1.4
Head length (HDL)	31.4	30.6–31.3	31.0	0.3	28.4–32.6	30.3	1.3
Lower jaw length Brembach (LJLB)	0.9	0.7–1.1	0.9	0.2	0.9–1.9	1.2	0.3
Lower jaw length (LJL)	13.3	13.5–14.4	13.9	0.4	11.8–14.2	13.1	0.8
Upper jaw length (UJL)	12.7	11.9–12.8	12.4	0.3	11.0–13.7	12.1	0.7
Upper jaw width (UJW)	9.2	8.9–9.0	8.9	0	8.3–11.1	9.2	0.8
Bony orbital diameter (ORBL)	7.8	7.8–8.2	8.0	0.2	5.9–8.2	7.2	0.7
Interorbital distance	8.9	8.9–9.9	9.4	0.4	8.5–9.8	9.1	0.4
Snout length	10.4	10.0–10.4	10.2	0.2	9.0–11.1	10.0	0.7
Postorbital length of head	13.3	13.2–14.2	13.6	0.4	12.6–14.6	13.4	0.7
Snout to pectoral fin distance (SN-P1)	33.7	33.1–34.5	33.6	0.6	31.2–34.1	32.8	0.9
Snout to pelvic fin distance (SN-P2)	59.1	59.7–61.3	60.3	0.8	58.0–62.3	60.1	1.4
Body width at pectoral fin base	11.0	9.7–11.4	10.8	0.8	9.6–12.7	11.1	1.0
Body depth at pectoral fin base (BDP1)	18.2	15.7–19.2	17.5	1.4	16.6–19.5	17.6	1.0
Body depth at pelvic-fin base (BDP2)	17.0	14.9–19.2	16.8	1.8	15.2–18.6	17.0	1.0
Depth of caudal peduncle	8.1	8.2–8.6	8.4	0.2	7.6–8.5	8.1	0.3
Length of caudal peduncle	11.5	10.1–11.7	10.8	0.7	10.1–12.2	11.1	0.6
Pelvic fin to caudal fin distance (P2-C)	44.1	43.1–43.3	43.2	0.1	40.1–43.4	41.9	1.0
Length of pectoral fin	19.9	16.0–17.9	17.0	0.8	16.0–19.0	17.0	0.9
Length of pectoral-fin base	7.2	5.2–6.7	6.0	0.6	4.4–6.9	5.6	0.7
Length of dorsal fin	18.2	18.5–19.2	18.9	0.3	16.1–18.2	17.3	0.7
Length of dorsal-fin base	11.5	12.5–13.7	13.0	0.6	10.8–12.8	11.8	0.6
Length of anal fin	16.4	16.7–17.5	17.1	0.3	14.3–18.2	15.9	1.3
Length of anal-fin base	9.8	10.9–11.9	11.5	0.5	12.0–13.8	13.0	0.6
Length of pelvic fin	12.4	10.0–12.5	11.0	1.1	9.3–10.2	9.7	0.3
Length of pelvic-fin base	2.6	2.2–2.9	2.5	0.3	1.7–3.2	2.3	0.4
Length of caudal fin	20.7	19.0–20.6	20.0	0.7	17.1–20.4	18.8	1.2
Proportions							
Lower jaw length Brembach in SL	115.7	89.3–140.5	111.4	21.5	53.8–114.3	86.3	18.8
Lower jaw length in SL	7.5	7.0–7.4	7.2	0.2	7.0–8.5	7.7	0.5
Upper jaw length/upper jaw width (UJL/UJW)	1.4	1.5–1.6	1.6	0	1.2–1.7	1.4	0.2

Color in alcohol.—Background color beige (Fig. 3) with a thin mid-lateral stripe from pectoral to caudal fin, more prominent posteriorly. Black pigment on lower anterior edge of the bony orbital. Distinct oval spot on pectoral-fin base. Uniform distribution of melanophores on the head and the dorsal and flank of the trunk; high concentration of melanophores anterior and dorsal to the distinct oval spot on pectoral-fin base. Black pigment all over dorsal-fin rays and irregularly on anal-fin rays in males. Irregular black pigment on dorsal- and anal-fin rays in females.

Sexual dimorphism.—Females grow larger than males (maximum SL recorded: 34.7 mm in males, 60.9 mm in females).

The bodies of each sex have dark coloration, but only males exhibit a striped pattern when they are in breeding condition. Males have an andropodium.

Distribution and habitat.—*Nomorhamphus aenigma* is known from the main stream of Cerekang River in Sulawesi Selatan, Indonesia (Fig. 1). The river belongs to the Malili River basin. The holotype was collected from a locality near Laroeha Village. The type locality (2°27'39.7"S, 121°04'03.0"E) is approximately 10 m in width and 1.5 m in depth, partially shaded by forest canopy, and has mud and gravel as substrates (Fig. 4). *Nomorhamphus rex* (Fig. 7), *Oreochromis*

niloticus, *Oryzias dopingdopingensis*, *Osteochilus vittatus*, *Redigobius penango*, and *Telmatherina* sp. co-occurred.

Etymology.—The specific name “aenigma,” from ancient Greek noun for “riddle,” refers to the riddle raised by this species: “why are the mandibles of most halfbeaks long?”

Comparisons.—This new species is classified into the genus *Nomorhamphus* because males possess a modified anal-fin fleshy covering, it lacks notably elongate lower jaws, and it has uniserial teeth not extending medially in a concave row from the outer row of teeth (Meisner, 2001). *Nomorhamphus aenigma* is distinguished from all other congeners by the complete absence of elongate lower jaws.

This new species is further distinguished from other Sulawesi-endemic congeners as follows. The new species differs from *N. brembachi*, *N. ebrardtii*, *N. hageni*, *N. lanceolatus*, *N. liemi*, *N. megarrhamphus*, and *N. weberi* by having fewer anal-fin rays (13–14 [14] in *N. aenigma* vs. more than 15 in the others; Meisner, 2001; Huylebrouck et al., 2014). It further differs from *N. megarrhamphus* and *N. weberi* by having a first anal-fin pterygiophore that is thickened and not angled anteriorly (see Meisner, 2001) and fewer precaudal vertebrae (22–23 [22] in *N. aenigma* vs. 24–27 in *N. megarrhamphus* and *N. weberi*; Meisner, 2001). The new species is distinguished from *N. brembachi* and *N. liemi* by having a second anal-fin ray without further longitudinal segmentation (Kraemer et al., 2019b). It is distinguished from *N. hageni* by fewer caudal vertebrae (16–17 [16] in *N. aenigma* vs. 18–19 in *N. hageni*; Meisner, 2001). The new species also differs from *N. ebrardtii*, *N. lanceolatus*, and *N. sagittarius* by its characteristic straight spiculus (Fig. 5); it is not lanceolate and does not contact the distal tip of the third anal-fin ray. In addition, *N. aenigma* is also distinguished from *N. lanceolatus* by more precaudal vertebrae (22–23 [22] in *N. aenigma* vs. 21 in *N. lanceolatus*; data from 11 topotype comparative specimens in this study). It is further distinguished from *N. kolonodalensis* by the many conical teeth on the dorsal surface of gill rakers (vs. 1–3 teeth on the dorsal surface of some gill rakers on the second and third arches in *N. kolonodalensis*; Meisner, 2001). In addition, *N. aenigma* is also distinguished from *N. kolonodalensis* by the fifth hypural plate being completely fused to dorsal hypural plate (Fig. 6; vs. the fifth hypural partially separated from the dorsal hypural plate along most of its length in *N. kolonodalensis*; Meisner and Louie, 2000). The new species is distinguished from *N. rex* by the absence of an elongate third or fourth segment in the second anal-fin ray (see Huylebrouck et al., 2012; Kraemer et al., 2019b). It differs from *N. versicolor* by having more segments in the first anal-fin ray (12 in *N. aenigma* vs. 3 in *N. versicolor*; Kraemer et al., 2019a). The new species cannot be distinguished from *N. celebensis* and *N. towoetii* by most morphometric and meristic characters, except for lower jaw length: *N. aenigma* has clearly shorter jaws than the other two species (LJLB 0.7–1.9 [0.9] in *N. aenigma*, vs. 2.9–6.2 and 3.9–7.7 in *N. celebensis* and *N. towoetii*, respectively; Material Examined in this study).

The new species is also distinguished from all Philippine-endemic *Nomorhamphus*. It differs from *N. bakeri*, *N. manifestus*, *N. pectoralis*, *N. philippinus*, *N. pinnimaculatus*, and *N. viviparus* by the second anal-fin ray being shorter than the third (vs. the second anal-fin ray being longer than the third; see Meisner, 2001). The new species is distinguished

from *N. bakeri* and *N. rossi* by lacking an elongate segment in the second anal-fin ray (see Meisner, 2001). The new species is also distinguished from *N. pectoralis* and *N. robertsi* by fewer anal-fin rays (13–14 [14] in *N. aenigma* vs. more than 15 in *N. pectoralis* and *N. robertsi*; Meisner, 2001; Huylebrouck et al., 2014). In addition, it differs from *N. pinnimaculatus* by having more precaudal vertebrae (21–22 [22] in *N. aenigma* vs. 20–21 in *N. pinnimaculatus*; Meisner, 2001).

DISCUSSION

Nomorhamphus aenigma is clearly distinguishable from all other species of *Nomorhamphus* by the complete absence of an elongate lower jaw. However, *N. aenigma* shares several traits with some congeners, which indicates that they are phylogenetically closely related. In particular, genital morphologies of *N. aenigma* were shared with those of *N. celebensis*, *N. kolonodalensis*, and *N. towoetii*, which are distributed in central Sulawesi around the ancient Malili-Poso lake systems (Meisner, 2001). Additionally, male *N. aenigma* and *N. celebensis* also share breeding colors; both males become jet black, and similar stripes appear on the bodies. In addition, body colorations of female *N. aenigma* are very similar to those of female *N. towoetii*; both females have uniform black bodies. These findings indicate that *N. aenigma* is particularly closely related to these central Sulawesi species. Phylogeographic analyses of ricefishes (Adrianichthyidae) on Sulawesi Island also revealed that the species of *Oryzias* distributed in the Malili-Poso lake systems formed a monophyletic group (Mokodongan and Yamahira, 2015), which supported our morphological assessment.

However, *N. aenigma* also shares several common characteristics with *N. rex* and *N. versicolor*, which are distributed in western Sulawesi (Lake Lindu, Tana Toraja, and surrounding areas; Huylebrouck et al., 2012; Kraemer et al., 2019a); *N. aenigma* and *N. versicolor* share irregular pigmentation of female dorsal and anal fins, and *N. aenigma* and *N. rex* share small numbers of caudal vertebrae. We also found that *N. aenigma* co-occurs with *O. dopingdopingensis*, which is phylogenetically close to *Oryzias* in western Sulawesi (Mandagi et al., 2018). These facts support an alternative view that *N. aenigma* is closely related to the western Sulawesi *Nomorhamphus*. Overall, *N. aenigma* characters overlap with those of a variety of species; therefore, it is difficult to determine the phylogenetic position of *N. aenigma* within *Nomorhamphus* based on this study alone. Molecular phylogenetic analyses may clarify this issue in the future.

Because the genus *Nomorhamphus* branched off more recently in the phylogeny of Zenarchopteridae (Collette, 1995; Meisner, 2001; Lovejoy et al., 2004; De Bruyn et al., 2013), and all other genera in the family (*Dermogenys*, *Hemirhamphodon*, *Tondanichthys*, and *Zenarchopterus*) have elongate lower jaws, it is probable that *N. aenigma* secondarily lost elongate jaws. Jawless halfbeaks have been reported from four genera of the family Hemiramphidae, i.e., *Arrhamphus*, *Chriodorus*, *Melapedalion*, and *Oxyporhamphus* (Seale, 1910; Lovejoy et al., 2004; Collette, 2005; Collette and Bemis, 2019b). Discovery of the jawless species of Zenarchopteridae in the present study suggests that the secondary loss of elongate jaws is far more common among beloniforms than previously known.

However, our preliminary observations revealed that juveniles of *N. aenigma*, including newly hatched ones



Fig. 7. Photographs of *Nomorhamphus rex* immediately after fixation. Upper: NSMT-P 136117 (male, 35.5 mm SL), lower: NSMT-P 136116 (female, 47.6 mm SL).

(10.2–23.3 mm SL), have no elongate jaw, indicating that this species has no elongate jaw throughout ontogeny, unlike the jawless hemiramphids in which juveniles have elongate jaws but their size is reduced through ontogeny (Collette et al., 1984; Collette, 2005; Chen, 2014; Collette and Bemis, 2019b). Because other species of *Nomorhamphus* and zenarchopterids pass through a “ricefish-like” stage in which the upper and lower jaws do not elongate (e.g., Mohr, 1936; Collette et al., 1984; Gunter et al., 2014), the short jaws of *N. aenigma* may represent pedomorphosis (Gould, 1977; McNamara, 1997). Pedomorphosis can result from neoteny and/or post-displacement; the former refers to deceleration of growth rates of a character, whereas the latter indicates delay in the timing at which growth of a character begins (Alberch et al., 1979; Futuyma, 1998). Detailed investigations of jaw development are needed to clarify which forms of heterochrony result in the short jaw of *N. aenigma*.

This heterochronic change in jaw length may have induced a shift in ecological niche in the wild. Hirota et al. (2015) reported that superficial neuromasts are well developed on the lower jaw of *Zenarchopterus dunckeri*, which indicates that the lower jaw may have functions to detect water flow. Considering that members of this group are surface-dwellers, it is likely that their elongate lower jaws play roles in detecting food on the surface, such as falling insects. If so, loss of jaw elongation in *N. aenigma* may indicate loss of this function. Interestingly, *N. rex* (Fig. 7), which is sympatric with *N. aenigma*, also has well-developed superficial neuromasts on the elongate part of the lower jaw (Kobayashi, unpubl.), which indicates that *N. aenigma* may have evolved short jaws as ecological character displacement. Indeed, this is supported by our observation that, in the wild, *N. rex* swim in the surface layer of the river, whereas *N. aenigma* swim in the middle and lower layers (Kobayashi et al., pers. obs.). To test this hypothesis, detailed comparisons

of feeding habits between these two sympatric species are necessary in the future.

MATERIAL EXAMINED

Dermogenys orientalis: MZB 25151–25152, 2 females, 50.5–52.8 mm SL, NSMT-P 136167–136169, 1 male, 2 females, 30.1–58.3 mm SL, WMSU 00011, 1 female, 50.2 mm SL, Baring, Pangkajene Dan Kepulauan Regency, Sulawesi Selatan, Indonesia, D. F. Mokodongan and H. Kobayashi, June 2017.

Dermogenys siamensis: NSMT-P 66094, 1 female, 32.0 mm SL, Trang Province east coast of Libong Island, Malay Peninsula, Andaman Sea, Thailand, K. Shibukawa, March 2003.

Nomorhamphus brembachi: MZB 6392, 1 male, 1 female, 42.7–50.3 mm SL, Bossolo, Sulawesi Selatan, Indonesia, K. D. Louis, January 1995; MZB 14391, 3 males, 2 females, 41.6–64.3 mm SL, Sungai Kasikebo, Bantimurung, Maros, Sulawesi Selatan, Indonesia, R. K. Hadiaty and Harun, June 2006.

Nomorhamphus celebensis: ZMA 104.377, lectotype, female, 66.6 mm SL, River at Lappa Kanrü, Sulawesi Island, Indonesia, Sarasin; MZB 5776, 5 males, 5 females, 39.0–75.3 mm SL, Tindole, Pamona Selatan, Poso, Sulawesi Tengah, Indonesia, Latifah, February 1986.

Nomorhamphus ebrardtii: RMNH 10535–10536, 2 paralectotypes, 2 females, 52.5–54.1 mm SL, Kabaena and Rumbia, Sulawesi Tenggara, Indonesia, J. Elbert, October 1909.

Nomorhamphus hageni: SMF 6521, lectotype, female, 91.4 mm SL, RMNH 10537, paralectotype, female, 87.8 mm SL, Penango, Sulawesi Tenggara, Indonesia, J. Elbert, October 1909; RMNH 10538, paralectotype, male, 49.9 mm SL,

Rumbia, Sulawesi Tenggara, Indonesia, J. Elbert, October 1909.

Nomorhamphus kolonodalensis: MZB 25122–25126, 1 male, 6 females, 34.7–48.1 mm SL, NSMT-P 136123–136126, 136129–136131, 3 males, 4 females, 37.0–60.8 mm SL, Mondowe, Morowali Utara, Sulawesi Tengah, Indonesia, J. Montenegro, April 2018.

Nomorhamphus lanceolatus: MZB 25127–25131, 3 males, 2 females, 25.8–34.3 mm SL, NSMT-P 136137–136138, 136141–136145, 2 males, 5 females, 36.4–52.7 mm SL, WMSU 00003–00004, 1 male, 1 female, 35.7–37 mm SL, Wawolambo River, Sulawesi Tenggara, Indonesia, H. Kobayashi, S. A. Lawelle, and I. F. Mandagi, November 2018.

Nomorhamphus liemi: MZB 25132–25134, 1 male, 2 females, 38.8–65.3 mm SL, NSMT-P 136127–136128, 136132–136136, 1 male, 3 females, 47.5–58.0 mm SL, WMSU 00005–00006, 1 male, 1 female, 44.2–59.8 mm SL, Padangloang River, Mallawa, Sulawesi Selatan, Indonesia, local villagers, September 2019.

Nomorhamphus megarrhamphus: NSMT-P 136148, 1 female, 58.9 mm SL, Lake Towuti, Sulawesi Selatan, Indonesia, K. Yamahira and B. Soeroto, December 2005.

Nomorhamphus pinnimaculatus: ZRC 46175 (former part of CMK 9980), 10 paratypes, 7 males, 3 females, 18.9–38.0 mm SL, creek at eastern end of Tunga, raffles, Leyte Island, Philippines, M. Kottelat, July 1993.

Nomorhamphus rex: MZB 20724, holotype, male, 44.4 mm SL, MZB 20725, 20727–20730, 5 paratypes, 2 males, 3 females, 28.7–45.2 mm SL, Wewu River near by Laroeha Village, South Sulawesi, Indonesia, F. Harder and R. K. Hadiaty, May 2004; NSMT-P 136108–136117, 4 males, 6 females, 25.1–59.4 mm SL, upper reaches of Cerekang River, Landangi Village, Sulawesi Selatan, Indonesia, H. Kobayashi, K. W. A. Masengi, I. F. Mandagi, S. A. Lawelle, R. Kakioka, S. Ansai, and K. Yamahira, November 2018.

Nomorhamphus sagittarius: MZB 25135–25144, 8 males, 2 females, 27.8–39.9 mm SL, NSMT-P 136149–136158, 5 males, 5 females, 40.3–70.3 mm SL, WMSU 00007–00008, 1 male, 1 female, 36.7–39.5 mm SL, Mangolo River, Sulawesi Tenggara, Indonesia, H. Kobayashi, S. A. Lawelle, I. F. Mandagi, K. W. A. Masengi, and K. Yamahira, December 2018.

Nomorhamphus towoetii: ZMH 4532, holotype, female, 68.1 mm SL, ZMH 25922–25923, 2 paratypes, females, 47.9–63.2 mm SL, Lake Towuti, Roth-Woltereck, December 1958; MZB 5973, 2 males, 2 females, 38.9–49.6 mm SL, Balambano River, Sulawesi Selatan, Indonesia, M. Kottelat, June 1998; MZB 25145–25150, 4 males, 2 females, 28.9–37.6 mm SL, NSMT-P 136159–136166, 5 males, 3 females, 37.4–56.3 mm SL, WMSU 00009–00010, 1 male, 1 female, 45.1–46.1 mm SL, Wasuponda River, Sulawesi Selatan, Indonesia, H. Kobayashi, R. Kakioka, S. Ansai, and K. Yamahira, December 2018.

Nomorhamphus versicolor: MZB 25105–25110, 4 males, 2 females, 36.4–61.0 mm SL, Kumo River in northwestern

Lake Lindo, Sulawesi Tengah, Indonesia, D. F. Mokodongan, H. Kobayashi, Ape, and F. Y. Tantu, June 2017.

Nomorhamphus viviparus: ZMB 6267, syntype, female, 49.0 mm SL, Bassey River, Samar Island, Philippines, F. Jagor.

Nomorhamphus weberi: MZB 5976, 15 females of 39 ex., 58.2–64.3 mm SL, Lake Matano, Sulawesi Selatan, Indonesia, M. Kottelat and A. Kottelat-Kloetzli, June 1988; NSMT-P 136147, 1 female, 31.9 mm SL, Lake Matano, Sulawesi Selatan, Indonesia, K. Yamahira, R. Kakioka, and S. Ansai, December 2018.

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