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A New Species of the Anchovy Genus *Stolephorus* Lacepède 1803 from North Sumatra, Indonesia, and Redescriptions of *Stolephorus pacificus* Baldwin 1984 and *Stolephorus teguhi* Kimura, Hori and Shibukawa 2009 (Teleostei: Clupeiformes: Engraulidae)

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Stolephorus leopardus sp. nov. is described here, and *Stolephorus pacificus* and *Stolephorus teguhi* are redescribed. Those three species are distinguished among congeners by the presence of more than 30 gill rakers on the lower limb of the first gill arch and a short maxilla, posteriorly just reaching the anterior border of the preopercle. *Stolephorus pacificus* and *S. teguhi* have rarely been reported since they were originally described, and therefore detailed morphological data and further diagnostic characters are provided. *Stolephorus leopardus*, in turn, is described based on four specimens collected on Nias Island, North Sumatra Province, Indonesia. The new species can be distinguished from *S. pacificus* and *S. teguhi* by a shorter pectoral fin (15.6–16.3% of standard length vs. longer than 16.5%), a longer snout (4.7–4.8% of standard length vs. < 4.5%), and an intermediate number of total gill rakers on the first gill arch (63–68 in *S. leopardus* vs. 57–63 in *S. pacificus* and 72–82 in *S. teguhi*). In addition, the new species differs from *S. pacificus* in having a dark line on the dorsum (vs. line absent), numerous melanophores laterally on the head (vs. a few melanophores on the snout and mandible tips), and higher counts of branched anal-fin rays [19–21(modally 19) vs. 17–19 (18)]. *Stolephorus leopardus* is further distinguished from *S. teguhi* by a shorter anal-fin base (22.4–22.5% of standard length vs. 22.7–25.3%).

Key words: Clupeomorpha, Indian Ocean, Morphology, Southeast Asia, Taxonomy.

BACKGROUND

The anchovy genus *Stolephorus* Lacepède 1803 (Clupeiformes: Engraulidae) currently includes 36 valid species that usually inhabit marine and/or estuarine waters in the Indo-Pacific region (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–e 2021a b; Hata et al. 2019 2020a b 2021; Gangan et al. 2020). *Stolephorus pacificus* Baldwin 1984 and *Stolephorus teguhi* Kimura, Hori and Shibukawa 2009 are distinguished from congeners by having more than 30 gill rakers on the lower limb of the first gill arch and a short maxilla, posteriorly just reaching the anterior margin of the preopercle (Baldwin

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1984; Whitehead et al. 1988; Wongratana et al. 1999, Kimura et al. 2009).

During a revisionary study of the genus, four engraulid specimens from Nias Island, North Sumatra Province, Indonesia, also with numerous gill rakers and a short maxilla, were identified as a hitherto unknown species of *Stolephorus*, which is described herein. In addition, *S. pacificus* and *S. teguhi* are redescribed.

MATERIALS AND METHODS

Counts and measurements follow Hata and Motomura (2017), and are presented as percentage of standard length or head length. All measurements were made with digital calipers to the nearest 0.1 mm. "Pelvic scute" refers to the scute associated with the pelvic-fin insertion, whereas "prepelvic", "postpelvic", and "predorsal scutes" refer to the scutes anterior to the pelvic scute, posterior to the pelvic scute, and just anterior to the dorsal-fin origin, respectively. All specimens were examined in this study, except for the holotype of *S. teguhi*, from which anatomical data were obtained from Kimura et al. (2009). Abbreviations are as follows—SL: standard length; HL: head length; UGR, LGR and TGR: rakers on upper limb, lower limb and total gill rakers, respectively, with numbers associated indicating the specific gill arch; and SMX-MX: distance between posterior margins of supramaxilla and maxilla. Institutional abbreviations follow Sabaj (2020).

RESULTS

Stolephorus pacificus Baldwin 1984

(English name: Pacific Anchovy)
(Fig. 1; Tables 1–3)

Stolephorus pacificus Baldwin 1984: 152, fig. 1 (type locality: Acfayan Bay, Guam; paratype localities: Talofofo Bay, Guam and Coquille Harbor, Kosrae); Wongratana 1987: 7 (Guam and Kosrae); Whitehead et al. 1988: 417, unnumbered fig. (Guam and Kosrae); Myers 1999: 62, fig. 1h (Guam and Kosrae); Wongratana et al. 1999: 1739, unnumbered fig. (Guam and Kosrae); Myers and Donaldson 2003: 609 (Guam); Kimura et al. 2009: 295, fig. 1c (Acfayan Bay, Guam); Hata et al. 2021: 368 (Acfayan Bay, Guam).

Holotype: BPBM 28190, 54.6 mm SL, Acfayan Bay, Guam, 14 Jan. 1970.

Paratypes: 26 specimens, 28.4–64.9 mm SL. BMNH 1983.2.3.1–4, 4 specimens, 49.2–54.1 mm SL, Acfayan Bay, Guam, 12 Nov. 1971; BPBM 25405, 64.9 mm SL, Talofofo Bay, Guam, 14 Mar. 1948; BPBM 28191, 10 specimens, 28.4–55.3 mm SL, Acfayan Bay, Guam, 14 Jan. 1970; BPBM 28782, body broken, Coquille Harbor, Kosrae, 1.5 m depth, 25 June 1971; USNM 263476, 10 specimens, 48.4–59.9 mm SL, Talofofo Bay, Guam, 13 Mar. 1948.

Diagnosis: A species of *Stolephorus* with the following combination of characters: 1UGR 21–26, 1LGR 32–38, 1TGR 57–62; 2UGR 18–20, 2LGR 29–35, 2TGR 47–53; 3UGR 13–15, 3LGR 17–20, 3TGR 30–35; 4UGR 10–12, 4LGR 13–15, 4TGR 23–27; prepelvic scutes 1–4; short maxilla, its posterior tip just reaching or slightly short of preopercle anterior margin, 13.8–18.1% of SL; no predorsal scutes; pelvic scute without spine; posterior border of preopercle convex, rounded; distinct paired dark patches on parietal area; obvious dark patch on occipital region; no lines of pigment on dorsum; melanophores absent on lateral head surface, a few scattered on tips of snout and lower jaw; posterior tip of pelvic fin reaching to vertical through second to fifth dorsal-fin ray base; SMX-MX 10.2–16.8% of maxilla length (13.6–16.8% in specimens > 48.4 mm SL); postorbital length 48.5–53.3% of HL; snout long, 4.4–4.8% of SL; pectoral fin long, 16.5–18.3% of SL.

Description: Data for holotype presented first, followed by paratype data in parentheses (if different). Measurements and counts are presented in tables 1 and 2. Body compressed laterally, elongated, deepest at dorsal-fin origin. Dorsal profile gently elevated from snout tip to dorsal-fin origin, thereafter lowering to caudal-fin base. Ventral profile lowering from snout tip to pelvic-fin insertion, thereafter elevating to caudal-fin base. Abdomen rounded, with four (one to four) needle-like prepelvic scutes. Predorsal and postpelvic scutes absent. Pelvic scute without spine. Anus situated just anterior to anal-fin origin. Caudal peduncle compressed. Snout tip rounded; snout length less than eye diameter. Mouth large, inferior, ventral to body axis, extending backward beyond posterior margin of eye. Lower jaw slender. Maxilla short, its posterior tip pointed, just reaching to anterior border of preopercle (just short of anterior border of preopercle in some paratypes). Single row of conical teeth on each jaw and palatines. Small conical teeth in patch on vomer. Eye large, round, positioned laterally on head, and dorsal to horizontal through upper margin of pectoral-fin insertion, visible in dorsal view. Pupil round. Orbit elliptical. Nostrils close to each other, anterior to orbit. Posterior margins of preopercle and opercle smooth. Subopercle with rounded posterior margin. Opercular membrane without serrations. Interorbital space flat. Interorbital width less than eye diameter. Pseudobranchial filaments present, length of longest filament less than eye diameter. Gill rakers long, slender, rough, visible from side of head when mouth opened. Isthmus muscle long, reaching anteriorly to

posterior margin of gill membranes. Urohyal hidden by isthmus muscle, not visible without dissection. Gill membrane on each side joined anteriorly, isthmus muscle mostly exposed, not covered by gill membrane. Scales cycloid, thin, deciduous, absent on head. Scales on fins completely lacking on specimens except for alar scales on caudal fin. Lateral line absent. Anteriormost point of pelvic-fin insertion anterior to middle of body. Posterior tip of depressed pelvic fin reaching to vertical through fifth (second to fifth) dorsal-fin ray base. Dorsal and anal fins each with minute first ray, three anteriormost rays unbranched. Anal-fin origin just below origin of eighth (eighth to eleventh) dorsal-fin ray. Uppermost pectoral-fin ray unbranched, inserted below midline of body; posterior tip of fin not reaching to vertical through pelvic-fin insertion.

Coloration of preserved specimens: Body uniformly pale brown, a pale ivory longitudinal band, its width slightly less than pupil diameter, extending from just upper opercular margin to caudal-fin base. A pair of dark patches behind occiput without a following pair of dark lines. Melanophores scattered on bases of dorsal and anal fins, and posterior margins of scales on dorsum, caudal-fin rays, and anterior dorsal-fin rays; absent on lateral surface of head; present on ventral surface of body from end of anal-fin base to caudal-fin base. Live and fresh coloration unknown.

Distribution: Currently known only from Guam, Mariana Islands and Kosrae, Caroline Islands (Baldwin 1984; Whitehead et al. 1988; this study; Fig. 2).

Fig. 1. (A) Lateral and (B) dorsal views of the holotype of *Stolephorus pacificus*. BPBM 28190, 54.6 mm SL, Acfayan Bay, Guam.

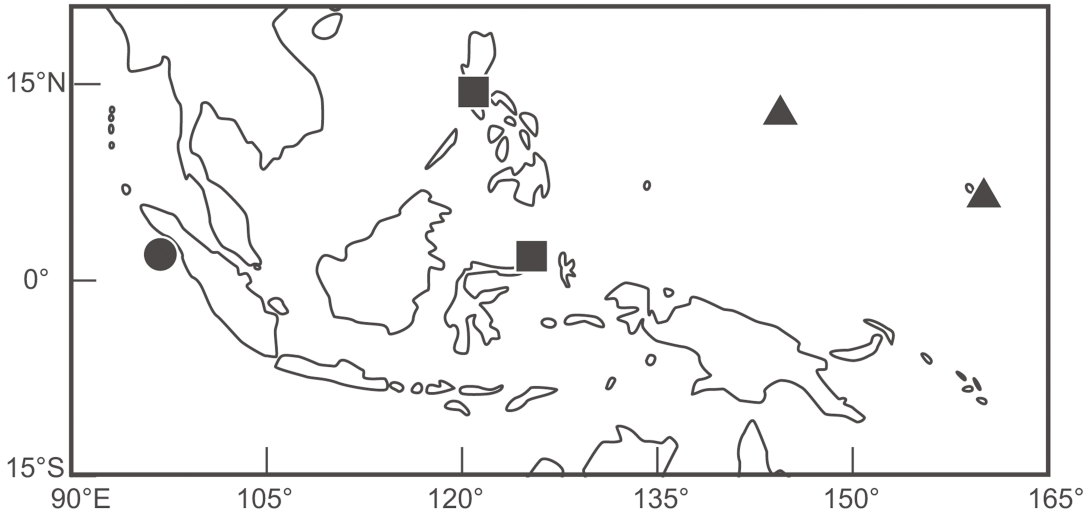

Fig. 2. Records of *Stolephorus pacificus* (triangles), *S. teguhi* (squares), and *S. leopardus* sp. nov. (circles), based on specimens examined in this study.

Comparisons: *Stolephorus pacificus* is easily distinguished from congeners, except *Stolephorus advenus* Wongratana 1987, *Stolephorus balinensis* (Bleeker 1849), *Stolephorus belaerius* Hata, Lavoué and Motomura 2021, *Stolephorus commersonnii* Lacepède 1803, *Stolephorus indicus* (van Hasselt 1823), *Stolephorus scitulus* (Fowler 1911), *S. teguhi* and *S. leopardus* by having a short maxilla, posteriorly just reaching to the preopercle anterior margin. It also differs from those species, except *S. teguhi* and *S. leopardus*, in having more than 31 gill rakers on the first gill arch (vs. less than 29 in *S. teguhi* and *S. leopardus*) and the pelvic fin extending posteriorly beyond the vertical through the dorsal-fin origin (vs. anterior to dorsal-fin origin) (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–e 2021a b; Hata et al. 2019 2020a b 2021; Gangan et al. 2020).

In the original description of *S. teguhi*, Kimura et al. (2009) compared *S. pacificus* with their new species, stating that the ratio of SMX-MX (13.4–16.2% of maxilla length in *S. pacificus* vs. 6.6–12.7% in *S. teguhi*) and postorbital length (51.1–54.9% of HL vs. 55.4–59.1%) separated the two species [based on the type specimens of *S. teguhi* (49–77 mm SL) and *S. pacificus* (> 45 mm)]. However, our examination of small specimens of *S. teguhi* (40.3 mm) and *S. pacificus* (28.4–41.1 mm SL) revealed that such ratios failed to clearly separate the two species, the smaller specimens being characterized by overlapping ratios (SMX-MX: 11.2–11.7% of maxilla length in *S. pacificus*; postorbital length: 50.7% of HL in *S. teguhi*; Table 1; Fig. 3). However, specimens > 45 mm SL of the two species can be separated by the ratios proposed by Kimura et al. (2009) (SMX-MX: 13.6–16.8% of maxilla length in *S. pacificus* vs. 6.3–12.2% in *S. teguhi*; postorbital length: 48.5–53.3% of HL vs. 53.8–58.2%; Fig. 3). Furthermore, *S. pacificus* is easily distinguished from *S. teguhi* by having lower counts of gill rakers on the first, second, third, and fourth gill arches (Table 2; Fig. 4), branched anal-fin rays [17–19 (modally 18) vs. 19–21 (19); Table 3], and the dorsum without dark lines (vs. a dark line present; Figs. 1B, 5C) (Kimura et al. 2009; Hata and Motomura 2018b; this study). A detailed comparison of *S. pacificus* and *S. leopardus* sp. nov. is given under the description of the latter.

Remarks: *Stolephorus pacificus* was described by Baldwin (1984) on the basis of 44 specimens collected from Guam, Micronesia and Kosrae Island, Caroline Islands. Subsequently, Kimura et al. (2009) examined the holotype and 24 paratypes of *S. pacificus* for comparison with their new species, *S. teguhi*. Since its description, no additional specimens of *S. pacificus* have been found, and the species is still known only from the type specimens.

***Stolephorus teguhi* Kimura, Hori and Shibukawa 2009**

(English name: Sulawesi Anchovy)
(Fig. 5; Tables 1–3)

Stolephorus teguhi Kimura et al. 2009: 292, fig. 1a, b, 3 (type locality: Pintu Kota, Lembeh I., North Sulawesi, Indonesia; paratype localities: Tanjung Merah, Bitung, North Sulawesi, Indonesia); Hata and Motomura 2018b: 21, fig. 1 (Pagapas Bay, Luzon, Philippines).

Holotype: MZB 17.282, 69 mm SL [counts and measurements cited from the original description, Kimura et al. (2009)], Pintu Kota, Lembeh Island, North Sulawesi, Indonesia, 20 Jan. 2000, beach seine, coll. by K. Matsuura, S. Kimura and T. Peristiwady.

Paratypes: 14 specimens, 50.1–77.8 mm SL. AMS-I. 44677-001, 55.9 mm SL, BMNH 2008.9.22.2, 65.2 mm SL, BPBM 40921, 65.1 mm SL, FRLM 25583, 61.9 mm SL, FRLM 25802, 51.6 mm SL, FRLM 25803, 50.1 mm SL, FRLM 26462, 63.4 mm SL, NSMT-P 91708, 75.3 mm SL, NSMT-P 91709, 73.8 mm SL, NSMT-P 91710, 70.0 mm SL, Pintu Kota, Lembeh Island, North Sulawesi, Indonesia, collected with beach seine; FRLM 24609, 71.0 mm SL, FRLM 24777, 77.8 mm SL, MNHN 2008-1932, 74.9 mm SL, RMNH. PISC 84067, 69.4 mm SL, Tanjung Merah, Bitung, North Sulawesi, Indonesia, collected with beach seine.

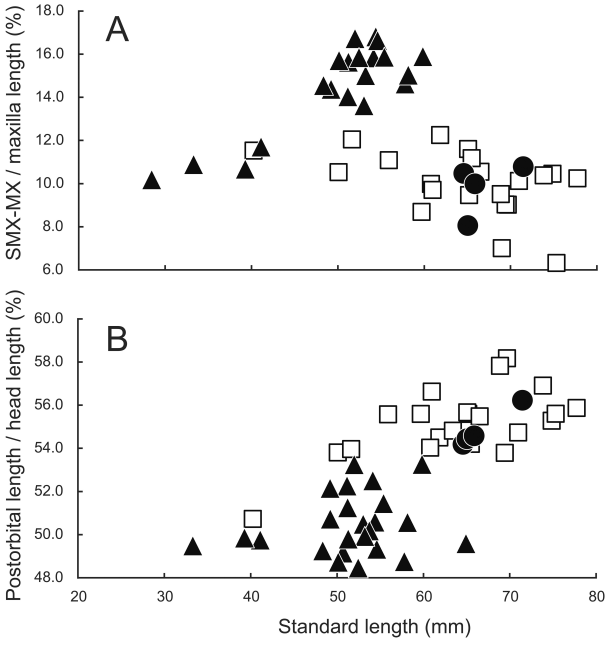

Fig. 3. Relationships of (A) distance between posterior ends of supramaxilla and maxilla (SMX-MX) (as % of maxilla length; MX) and (B) postorbital length (as % of head length) to standard length in *Stolephorus pacificus* (triangles), *S. teguhi* (squares), and *S. leopardus* sp. nov. (circles).

Non-type specimens: 7 specimens, 40.2–68.9 mm SL. FRLM 34849, 68.9 mm SL, FRLM 34850, 60.8 mm SL, FRLM 34851, 65.5 mm SL, FRLM 34852, 61.0 mm SL, FRLM 34853, 66.5 mm SL, Pintu Kota, Lembeh Island, North Sulawesi, Indonesia, collected with beach seine; KAUM–I. 43983, 40.2 mm SL, Labuhan Kompeni, Lembeh Island, North Sulawesi, Indonesia, collected with beach seine; USNM 138538, 59.7 mm SL, Pagapas Bay, Batangas Province, Luzon, Philippines, 1 m depth, seine net.

Diagnosis: A species of *Stolephorus* with the following combination of characters: 1UGR 31–36, 1LGR 41–46, 1TGR 72–82; 2UGR 22–26, 2LGR 37–41, 2TGR 60–67; 3UGR 16–19, 3LGR 20–25, 3TGR 36–43; 4UGR 12–13, 4LGR 14–17, 4TGR 26–30; prepelvic scutes 2–5; short maxilla, its posterior tip just reaching or slightly short of preopercle anterior margin, 15.4–17.6% of SL; no predorsal scutes; pelvic scute

Table 1. Morphometrics of specimens of *Stolephorus pacificus*, *S. teguhi*, and *S. leopardus* sp. nov.

	Stolephorus pacificus			*Stolephorus teguhi*				*Stolephorus leopardus* sp. nov.		
	Holotype	Paratypes		Holotype*	Paratypes	Non-types		Holotype	Paratypes	
	BPBM 28190	*n* = 25		MZB 17.282	*n* = 14	*n* = 7		RMNH.PISC. 84312	*n* = 3	
Standard length (mm; SL)	54.6	28.4–64.9	Means	69	50.1–77.8	40.2–68.9	Means	64.6	65.0–71.5	Means
As % of SL										
Head length (HL)	24.7	24.1–26.4	25.2	25.1	23.6–26.7	25.5–27.2	25.7	26.4	25.5–25.9	25.9
Body depth	21.3	17.5–22.2	19.6	21.4	20.2–22.7	19.7–21.3	21.2	21.4	19.5–21.0	20.7
Pre-dorsal fin length	52.9	49.0–56.9	54.3	53.5	50.6–55.4	54.0–57.4	54.5	55.7	56.4–57.4	56.6
Snout tip to pectoral-fin insertion	28.1	24.5–29.1	26.8	26.8	26.1–28.7	26.8–28.2	27.4	27.6	26.5–27.7	27.3
Snout tip to pelvic-fin insertion	46.2	44.0–47.4	45.4	44.8	44.7–47.9	44.8–48.4	46.3	44.7	44.6–44.9	44.7
Snout tip to anal-fin origin	64.5	54.4–65.6	63.0	63.4	62.3–66.3	62.8–65.5	64.4	62.2	62.4–63.8	62.8
Dorsal-fin base length	15.4	14.1–16.7	15.3	15.0	13.2–15.8	13.1–15.5	14.6	13.2	14.1–14.8	14.2
Anal-fin base length	21.8	18.9–22.8	20.8	23.5	22.7–25.3	22.8–24.3	23.4	22.4	22.5	22.5
Caudal- peduncle length	13.8	14.0–17.4	15.6	16.2	14.0–16.3	14.2–15.6	15.3	16.5	13.9–15.7	15.4
Caudal-peduncle depth	10.3	8.4–11.3	9.7		9.5–10.9	9.3–10.5	10.1	11.1	9.3–10.2	10.1
D–P1	33.8	32.8–36.0	34.6		33.7–38.2	34.4–37.6	35.9	34.6	35.2–35.6	35.2
D–P2	22.7	20.1–23.4	21.9		22.9–25.4	22.1–25.0	23.8	24.4	22.4–24.5	23.8
D–A	22.8	19.8–23.0	21.6		21.9–23.5	21.1–23.6	22.5	22.4	21.2–22.2	21.8
P1–P2	19.7	17.5–23.4	19.8		19.7–22.8	17.7–22.2	20.7	18.1	18.1–19.7	18.7
P2–A	17.7	15.4–19.1	17.6		16.3–21.4	17.0–20.2	18.6	18.1	17.5–18.1	17.9
Pectoral-fin length	broken	16.5–18.3	17.3	17.5	16.5–18.8	17.0–18.5	17.5	16.3	15.6–16.3	16.1
Pelvic-fin length	11.6	10.2–13.0	11.4	11.4	10.6–12.6	9.8–11.8	11.2	11.0	10.1	10.3
Snout length	4.4	3.5–4.3	4.0	5.5**	3.7–4.4	3.8–4.5	4.0	4.8	4.7–4.8	4.7
Maxilla length	17.7	13.8–18.1	16.6	16.6	15.4–17.5	16.4–17.6	16.8	17.6	17.3–17.5	17.5
Lower-jaw length	16.4	15.5–17.4	16.3		16.0–17.9	16.2–17.9	16.7	17.3	16.5–17.3	17.1
Supramaxilla end to maxilla end	2.9	1.4–2.9	2.4		1.0–2.3	1.4–2.0	1.7	2.2	1.4–2.0	1.9
1st unbranched dorsal-fin ray length	1.3	0.9–3.2	1.7		2.0–2.6	1.4–3.1	2.4	2.4	0.8–2.3	1.9
2nd unbranched dorsal-fin ray length	broken	7.1–9.6	8.3		7.7–9.5	8.9–9.4	8.8	broken	7.4–7.7	7.6
3rd dorsal-fin ray length	broken	18.4–20.4	19.4							
1st unbranched anal-fin ray length	1.4	0.9–2.0	1.5		2.0–2.6	1.4–3.1	2.4	2.4	0.8–2.3	1.9
2nd unbranched anal-fin ray length	broken	4.2–6.7	5.7		7.7–9.5	8.9–9.4	8.8	broken	7.4–7.7	7.6
3rd anal-fin ray length	broken	12.1–15.3	14.0		12.0–15.3	14.4–15.1	14.3	broken	13.1–13.3	13.2
As % of HL										
Orbit diameter	36.3	31.6–37.6	34.4		29.4–35.2	31.5–33.5	32.3	29.2	31.1–32.0	31.0
Eye diameter	26.2	21.5–29.5	25.7	25.6	22.7–28.6	27.4–29.9	27.1	24.4	24.5–27.4	25.7
Snout length	17.8	14.6–17.0	16.0	22.1**	14.6–18.3	14.5–17.2	15.7	18.1	18.1–18.4	18.2
Interorbital width	23.4	19.8–25.7	23.5		22.8–26.4	22.7–25.1	24.0	23.7	21.9–23.5	23.0
Postorbital length	49.3	48.5–53.3	50.5	57.0	53.8–58.2	50.7–57.8	55.2	54.2	54.4–56.2	54.9
As % of maxilla length										
Supramaxilla end to maxilla end	16.6	10.2–16.8	14.5	7.0	6.3–12.2	8.7–11.5	10.0	10.5	8.1–10.8	9.8

Abbreviations: D–P1 (distance from dorsal-fin origin to pectoral-fin insertion); D–P2 (distance from dorsal-fin origin to pelvic-fin insertion); D–A (distance between origins of dorsal- and anal fins); P1–P2 (distance between insertions of pectoral- and pelvic fins); P2–A (distance between pelvic-fin insertion to anal-fin origin). *Data from Kimura et al. (2009). **Probably based on measurement error (see Remarks of *S. teguhi*).

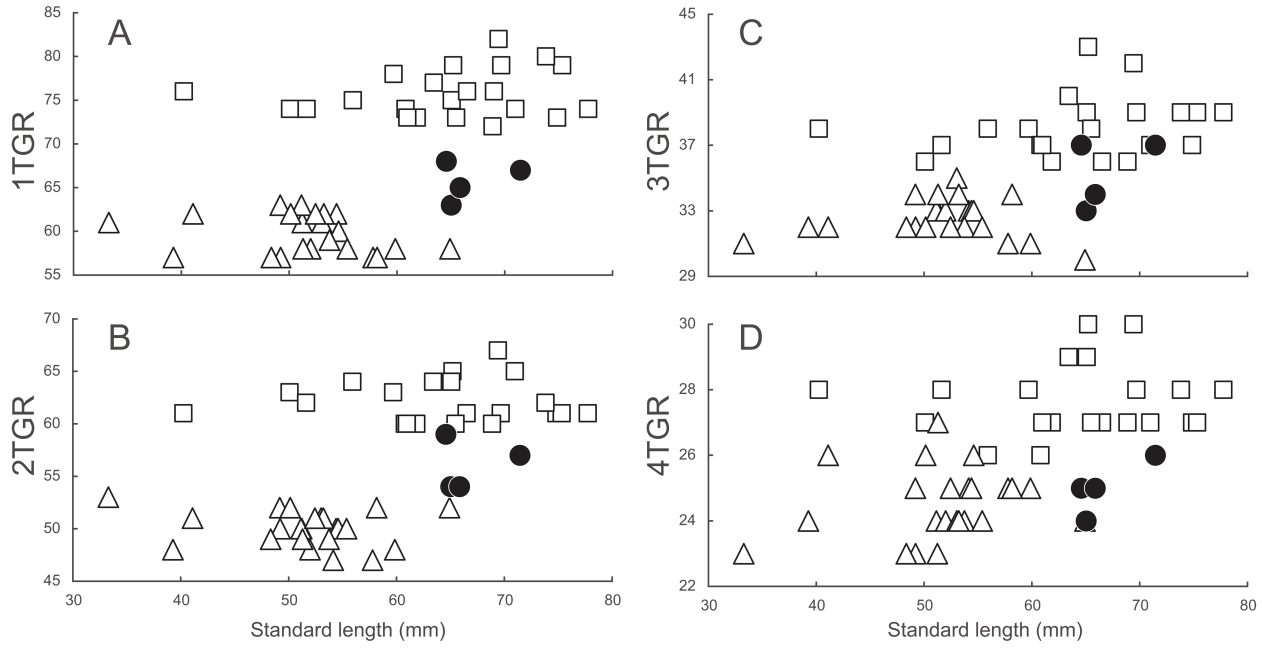

Fig. 4. Relationships of total gill raker numbers (TGR) on (A) first gill arch (1GA), (B) second gill arch (2GA), (C) third gill arch (3GA), and (D) fourth gill arch (4GA) to standard length in *Stolephorus pacificus* (triangles), *S. teguhi* (squares), and *S. leopardus* sp. nov. (circles).

Fig. 5. (A) Lateral view of a non-type specimen of *Stolephorus teguhi* (fresh condition), KAUM–I. 43983, 40.2 mm SL, Lembeh Island, North Sulawesi, Indonesia; lateral (B) and dorsal (C) views of the paratype of *Stolephorus teguhi*, NSMT-P 91709, 73.8 mm SL, Lembeh Island, North Sulawesi, Indonesia.

without spine; posterior border of preopercle convex, rounded; distinct paired dark patches on parietal and occipital regions; single dark line on dorsum from occipital region to upper margin of caudal-fin base; numerous black spots on snout and both upper and lower jaws; scales on dorsum with black margin; posterior tip of pelvic fin reaching to vertical through second to seventh dorsal-fin ray base; SMX-MX 6.3–12.2% of maxilla length; postorbital length 50.7–58.2% of HL(53.8–58.2% in specimens > 50 mm SL); snout short, 3.7–4.5% of SL; pectoral fin long, 16.5–18.8% of SL.

Description: Measurements and counts are presented in tables 1 and 2. Body compressed laterally, elongated, deepest at dorsal-fin origin. Dorsal profile gently elevated from snout tip to dorsal-fin origin, thereafter lowering to caudal-fin base. Ventral profile decreasing from snout tip to pelvic-fin insertion, thereafter elevating to caudal-fin base. Abdomen rounded, with two to five needle-like prepelvic scutes. Predorsal and postpelvic scutes absent. Pelvic scute without spine. Anus located just anterior to anal-fin origin. Caudal peduncle compressed. Snout tip rounded, snout length less than eye diameter. Mouth large, inferior, ventral to body axis, extending backward beyond posterior margin of eye. Lower jaw slender. Maxilla short, its posterior tip pointed, just reaching to anterior border of preopercle. Single row of conical teeth on each jaw and palatines. Small conical teeth in patch on vomer. Eye large, round, positioned laterally on head and dorsal to horizontal through upper point of pectoral-fin insertion, visible in dorsal view. Pupil round. Orbit elliptical. Nostrils close to each other, anterior to orbit. Posterior margins of preopercle and opercle smooth. Subopercle with rounded posterior margin. Opercular membrane without serrations. Interorbital space flat. Interorbital width less than eye diameter. Pseudobranchial filaments present, length of

Table 2. Meristics of specimens of *Stolephorus pacificus*, *S. teguhi*, and *S. leopardus* sp. nov.

	Stolephorus pacificus			*Stolephorus teguhi*				*Stolephorus leopardus* sp. nov.		
	Holotype	Paratypes		Holotype*	Paratypes	Non-types		Holotype	Paratypes	
	BPBM 28190	*n* = 25		MZB 17.282	*n* = 14	*n* = 7		RMNH.PISC. 84312	*n* = 3	
Standard length (mm)	54.6	28.4–64.9	Modes	69	50.1–77.8	40.2–68.9	Modes	64.6	65.0–71.5	Modes
Dorsal-fin rays (unbranched)	3	3	3	3	3	3	3	3	3	3
Dorsal-fin rays (branched)	13	12–14	13	12	12	11–12	12	11	12	12
Anal-fin rays (unbranched)	3	3	3	3	3	3	3	3	3	3
Anal-fin rays (branched)	19	17–19	18	20	19–21	19–21	19	19	19–21	19
Pectoral-fin rays (unbranched)	1	1	1	1	1	1	1	1	1	1
Pectoral-fin rays (branched)	12	11–14	12	12	12–13	12–13	13	13	12–13	13
Pelvic-fin rays (unbranched)	1	1	1	1	1	1	1	1	1	1
Pelvic-fin rays (branched)	6	6	6	6	6	6	6	6	6	6
Caudal-fin rays	19	19	19	19	19	19	19	19	19	19
Gill rakers on 1st gill arch (upper)	25	21–26	25	32	31–36	31–35	31	29	26–28	28
Gill rakers on 1st gill arch (lower)	35	32–38	36	44	41–46	41–43	42	39	37–39	39
Gill rakers on 1st gill arch (total)	60	57–63	58	76	73–82	72–78	74	68	63–67	-
Gill rakers on 2nd gill arch (upper)	20	17–20	18		22–26	22–23	23	22	19–21	-
Gill rakers on 2nd gill arch (lower)	30	29–35	31		37–41	37–40	38	37	34–36	-
Gill rakers on 2nd gill arch (total)	50	47–53	50		60–67	60–63	61	59	54–57	54
Gill rakers on 3rd gill arch (upper)	15	13–16	14		16–19	16–8	17	16	14–16	16
Gill rakers on 3rd gill arch (lower)	18	17–20	18		20–25	20–21	20	21	19–21	21
Gill rakers on 3rd gill arch (total)	33	30–35	32		36–43	36–38	39	37	33–37	37
Gill rakers on 4th gill arch (upper)	11	10–12	11		12–13	12–13	12	10	10–11	10
Gill rakers on 4th gill arch (lower)	15	13–15	14		14–17	14–16	15	15	14–15	15
Gill rakers on 4th gill arch (total)	26	23–27	25		26–30	26–28	27	25	24–26	25
Gill rakers on posterior face of 3rd gill arch	8	5–8	6		4–9	5–7	6	5	4–5	5
Prepelvic scutes	4	1–3	3	3	2–5	3–4	4	3	3–4	3
Scale rows in longitudinal series	35	34–37	35	36	34–37	34–37	34	33	33–34	33
Transverse scales	8	8	8		8	8–9	8	8	8	8
Pseudobranchial filaments	17	15–21	17		16–20	17–19	17	18	18	18

*Data from Kimura et al. (2009).

longest filament less than eye diameter. Gill rakers long, slender, rough, visible from side of head when mouth opened. Isthmus muscle long, reaching anteriorly to posterior margin of gill membranes. Urohyal hidden by isthmus muscle, not visible without dissection. Gill membrane on each side joined anteriorly, isthmus muscle mostly exposed, not covered by gill membrane. Scales cycloid, thin, deciduous, absent on head and fins, except for alar scales. Lateral line absent. Anteriormost point of pelvic-fin insertion anterior to middle of body. Posterior tip of depressed pelvic fin reaching to vertical through second to seventh dorsal-fin ray origin. Dorsal and anal fins each with minute first ray, three anteriormost rays unbranched. Anal-fin origin just below origin of seventh to tenth dorsal-fin ray. Uppermost pectoral-fin ray unbranched, inserted below midline of body; posterior tip of fin not reaching to vertical through pelvic-fin insertion.

Coloration of fresh specimens: [Based on color photographs of two specimens (FRLM 26462 and KAUM–I. 43983)]. Body silvery-white, a longitudinal silver band narrower than pupil diameter extending from just behind upper opercular margin to caudal-fin base. Lateral surface of head almost uniformly silver, snout semi-translucent. Melanophores densely scattered on dorsum of head. Fin rays translucent, pectoral and caudal fins slightly yellowish. Melanophores present on fin rays of dorsal, pectoral, and caudal fins, and bases of dorsal and anal fins. Scale pockets on dorsum darkly margined.

Coloration of preserved specimens: Body uniformly pale, a longitudinal band of melanophores narrower than pupil diameter, from just behind upper opercular margin to caudal-fin base. Pairs of distinct dark patches on parietal and occipital regions. A narrow dark line running from occipital region to upper margin of caudal-fin base. Melanophores densely distributed on dorsal surface of head, snout tip, both of upper and lower jaws, and upper parts of anterior margin of preopercle and posterior margin of gill opening. Scale pockets on dorsum darkly margined. All fins semi-translucent. Melanophores present on fin rays of dorsal, pectoral, and caudal fins, and on anterior parts of pelvic and anal fins, bases of dorsal and anal fins, and ventral surface of body from end of anal-fin base to caudal-fin base.

Distribution: Currently known only from Lembe Island and Bitung, North Sulawesi, Indonesia and Pagapas Bay, Batangas Province, Luzon, Philippines (Kimura et al. 2009; Hata and Motomura 2018b; this study; Fig. 2).

Comparisons: The gill raker numbers on first, second, third, and fourth gill arches in this species are the highest recorded in the genus, with no congeneric species having more than 40 gill rakers on the lower limb of the first gill arch (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–e 2021a b; Hata et al. 2019 2020a b 2021; Gangan et al. 2020; this study). Detailed comparisons of *S. teguhi* with *S. pacificus* and *S. leopardus* sp. nov. (described below) are given under "Comparisons" for each species. Although *S. teguhi* is similar to *Stolephorus babarani* Hata, Lavoué and Motomura 2020, *Stolephorus bataviensis* Hardenberg 1933, *Stolephorus baweanensis* Hardenberg 1933, and *Stolephorus waitei* Jordan and Seale 1926 in sharing scattered melanophores on the snout and both upper and lower jaws, the former is easily distinguished from the others by having a short maxilla, its posterior tip just reaching the preopercle anterior margin, 15.4–17.6% of SL (vs. beyond or slightly short of posterior margin and > 17.9% of SL in in the others), and higher gill raker count on 1LGR (vs. fewer than 26) (Hata et al. 2019 2020a; this study).

Remarks: *Stolephorus teguhi* was originally described by Kimura et al. (2009) based on 15 specimens collected from Lembe Island and Bitung, North Sulawesi, Indonesia. The snout length proportion for the holotype of *S. teguhi* given by Kimura et al. (2009) (5.6% of SL) is likely based on a measurement error, because specimens examined in this study have a range between 3.7–4.4% for that character. Subsequently, Hata and Motomura (2018c) reported the species from Pagapas Bay, Batangas Province, Luzon, Philippines. Hata and Motomura (2018c) also suggested that the species is widely distributed from the Celebes Sea to the eastern part of the South China Sea, but no specimens supporting that suggestion have been recorded so far.

***Stolephorus leopardus* sp. nov.**

(New English name: Leopard Anchovy)
(Fig. 6; Tables 1–3)
urn:lsid:zoobank.org:act:16BEE9A0-A409-4718-8222-1A70010BDF47

Holotype: RMNH.PISC.84312, 64.6 mm SL, Lahewa, Nias Island, Indonesia.

Paratypes: 3 specimens, 65.0–71.5 mm SL. RMNH.PISC.84313, 71.5 mm SL, RMNH.PISC.84314, 65.0 mm SL, RMNH.PISC.84315, 65.9 mm SL, collected with the holotype.

Diagnosis: A species of *Stolephorus* with the following combination of characters: 1UGR 26–29, 1LGR 37–39, 1TGR 63–68; 2UGR 19–22, 2LGR 34–37, 2TGR 54–59; 3UGR 14–16, 3LGR 19–21, 3TGR 33–37; 4UGR 10–11, 4LGR 14–15, 4TGR 24–26; gill rakers on posterior face on third gill arch 4–5; prepelvic

scutes 3–4; short maxilla, posterior tip just reaching or slightly short of anterior margin of preopercle, 17.3–17.6% of SL; no predorsal scutes; pelvic scute without spine; posterior border of preopercle convex, rounded; distinct paired dark patches on parietal and occipital regions; single dark line on dorsum from occipital area to upper portion of caudal-fin base; numerous black spots on snout and both upper and lower jaws; scales on dorsum with black margin; posterior tip of pelvic fin reaching to vertical through third to fifth dorsal-fin ray base; anal-fin base short, 22.4–22.5% of SL; pectoral fin short, 15.6–16.3%; SMX-MX 8.1–10.8% of maxilla length; postorbital length 54.2–56.2% of HL; snout long, 4.7–4.8% of SL.

Description: Data for holotype presented first, followed by paratype data in parentheses (if different). Measurements and counts are presented in tables 1 and 2. Body compressed laterally, elongated, deepest at dorsal-fin origin. Dorsal profile gently elevated from snout tip to dorsal-fin origin, thereafter lowering to caudal-fin base. Ventral profile decreasing from snout tip to pelvic-fin insertion, thereafter elevating to caudal-fin base. Abdomen rounded, with three (three or four) needle-like prepelvic scutes. Predorsal and postpelvic scutes absent. Pelvic scute without spine. Anus situated just anterior to anal-fin origin. Caudal peduncle compressed. Snout tip rounded; snout length less than eye diameter. Mouth large, inferior, ventral to body axis, extending backwards beyond posterior margin of eye. Lower jaw slender. Maxilla short, its posterior tip pointed, just reaching to anterior border of preopercle. Single row of conical teeth on jaws and palatines. Small conical teeth in patch on vomer. Eye large, round, positioned laterally on head dorsal to horizontal through upper point of pectoral-fin insertion, visible in dorsal view. Pupil round. Orbit elliptical. Nostrils close to each other, anterior to orbit. Posterior margins of preopercle and opercle smooth. Subopercle with rounded posterior margin. Opercular membrane without serrations. Interorbital space flat. Interorbital width less than eye diameter. Pseudobranchial filaments present, length of longest filament less than eye diameter. Gill rakers long, slender, rough, visible from side of head when mouth opened. Isthmus muscle long, reaching anteriorly to posterior margin of gill membranes. Urohyal hidden by isthmus muscle, not visible without dissection. Gill membrane on each side joined anteriorly, isthmus muscle mostly exposed, not covered by gill membrane. Lateral line absent. Anteriormost point of pelvic-fin insertion anterior to middle of body. Posterior tip of depressed pelvic fin reaching to vertical through third (third or fourth) dorsal-fin ray base. Dorsal and anal fins each with minute first ray, three anteriormost rays unbranched. Anal-fin origin just below base of seventh (eighth to ninth) dorsal-fin ray. Uppermost pectoral-fin ray unbranched, inserted below midline of body; posterior tip of fin not reaching to vertical through pelvic-fin insertion.

Coloration of preserved specimens: Body uniformly pale brown; a light pale longitudinal band, slightly narrower than pupil diameter, from just behind upper opercular margin to caudal-fin base. Pairs of distinct dark patches on parietal and occipital regions. A dark line running from occipital region to upper portion of caudal-fin base. Melanophores densely distributed on dorsal surface of head, snout tip, both jaws, upper part of anterior margin of preopercle, and posterior margin of gill opening. All fins semi-translucent. Melanophores present on fin rays of dorsal, pectoral, and caudal fins, and on anterior parts of pelvic and anal fins, and ventral

Fig. 6. (A) Lateral and (B) dorsal views of the holotype of *Stolephorus leopardus* sp. nov. RMNH.PISC.84312, 64.6 mm SL, Nias Island, west of Sumatra, Indonesia.

surface of body from end of anal-fin base to caudal-fin base. Scale pockets on dorsum darkly margined. Fresh coloration unknown.

Distribution: *Stolephorus leopardus* sp. nov. is currently known only from Lahewa, Nias Island, North Sumatra Province, Indonesia (Fig. 2).

Etymology: The specific name *leopardus* is derived from Latin meaning "leopard", in reference to the numerous black spots on the head.

Comparisons: The new species is assignable to the genus *Stolephorus*, as defined by Whitehead et al. (1988) and Wongratana et al. (1999), having a long isthmus muscle reaching anteriorly to the posterior margin of the gill membrane, prepelvic scutes, and a hidden urohyal, and lacking postpelvic scutes. *Stolephorus leopardus* most closely resembles *S. pacificus* and *S. teguhi*, all three species sharing a short maxilla, posteriorly just reaching the anterior margin of preopercle, lacking predorsal scutes, with numerous gill rakers (1LGR > 31), and the pelvic fin reaching posteriorly beyond the vertical through the dorsal-fin origin (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–e 2021a b; Hata et al. 2019 2020a b 2021; Gangan et al. 2020). However, the new species is easily distinguishable from *S. pacificus* by the presence of numerous melanophores on the snout, on both upper and lower jaws, on upper part of the gill opening, and on the dorsum of the head anterior to the interorbital area (vs. a few melanophores only on snout and mandible tips in *S. pacificus*), pairs of distinct dark patches on both the parietal and occipital regions (vs. an obvious dark patch on the occipital area), a dark line on the dorsum from the occipital area to the caudal-fin base (vs. no dark lines on dorsum; Figs. 1B, 6B), a shorter pectoral fin (15.6–16.3% of SL vs. 16.5–18.3%; Fig. 7A) and SMX-MX (8.1–10.8% of maxilla length vs. 10.2–16.8%), a longer snout (4.7–4.8% of SL vs. 3.5–4.4%; Fig. 7B) and postorbital area (54.2–56.2% of HL vs. 48.5–53.3%), and higher numbers of branched anal-fin rays [19–21 (modally 19) vs. 17–19 (18); Table 3]. Gill raker numbers on first, second, third, and fourth arches tend to be higher in *S. leopardus* than in *S. pacificus* (Table 2; Fig. 4). Furthermore, *S. leopardus* differs from *S. teguhi* in having lower numbers of gill rakers on first, second, third, and fourth gill arches (Table 2; Figs. 3, 4), a shorter pectoral fin (15.6–16.3% of SL vs. 16.5–18.8% in *S. teguhi*; Fig. 7A) and anal-fin base (22.4–22.5% of SL vs. 22.7–25.3%; Fig. 7C), and a longer snout (4.7–4.8% of SL vs. 3.7–4.5%; Fig. 7B). The range of 1TGR of *Stolephorus multibranchus* Wongratana 1987 slightly overlaps that of *S. leopardus* (24–28 + 32–36 =

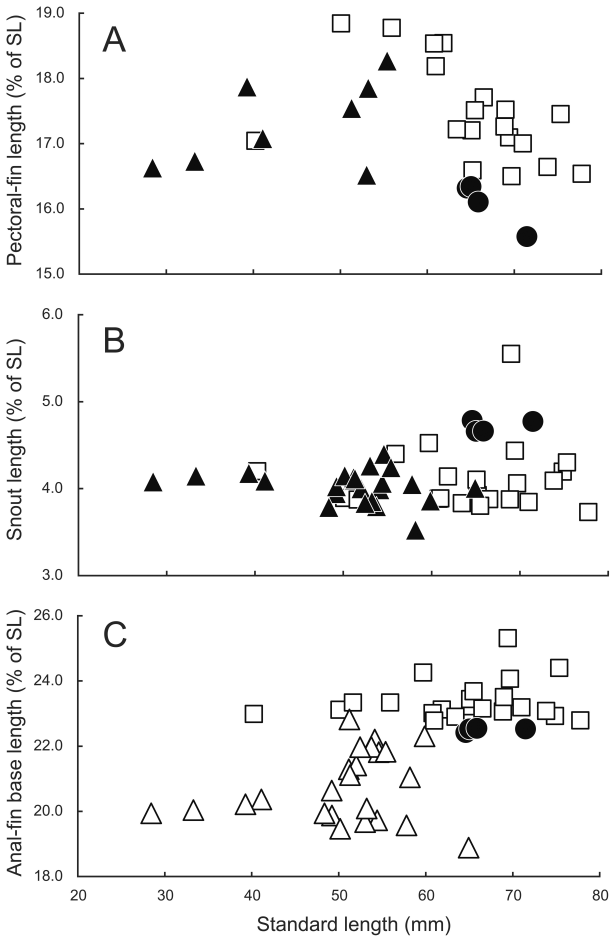

Fig. 7. Relationships of (A) pectoral-fin length (as % of standard length; SL), (B) snout length (as % of SL), and (C) anal-fin base length (as % of SL) to SL in *Stolephorus pacificus* (triangles), *S. teguhi* (squares), and *S. leopardus* sp. nov. (circles).

Table 3. Frequency distribution of branched anal-fin ray counts of *Stolephorus pacificus*, *S. teguhi*, and *S. leopardus* sp. nov.

		Branched anal-fin rays				
		17	18	19	20	21
Stolephorus pacificus	*n* = 25	9	13	3		
Stolephorus teguhi	*n* = 22			10	9	3
Stolephorus leopardus sp. nov.	*n* = 4			3		1

57–64 in *S. multibranchus* vs. 26–29 + 37–39 = 63–68 in *S. leopardus*). However, *S. multibranchus* has double dark lines on the dorsum extending to the dorsal-fin origin. *Stolephorus multibranchus* also clearly differs from *S. leopardus* in having a long maxilla, posteriorly just reaching or just short of the preopercle posterior border, 18.0–21.1% of SL (vs. posterior tip of maxilla just reaching anterior margin of preopercle, 17.3–17.6% in *S. leopardus*; Hata and Motomura 2018b; this study).

Key to species of *Stolephorus* with a short maxilla (just reaching the anterior margin of preopercle), numerous gill rakers (1LGR > 31), and the depressed pelvic fin extending posteriorly beyond vertical through the dorsal-fin origin

1a. 1LGR more than 40 ..... *S. teguhi* (Luzon, Philippines and North Sulawesi, Indonesia)
1b. 1LGR less than 40 2
2a. Gill rakers on first gill arch 21–26 + 32–38 = 57–63; no dark line on dorsum; a few melanophores only, scattered on snout and mandible tips ..... *S. pacificus* (Guam and Kosrae)
2b. Gill rakers on first gill arch 26–29 + 36–39 = 62–68; dark line on dorsum from occipital area to caudal-fin base; numerous melanophores on snout, both jaws, and upper part of gill opening ..... *S. leopardus* sp. nov. (Nias Island, North Sumatra Province, Indonesia)

DISCUSSION

The three species considered in the present study have an insular distribution and share a relatively large number of gill rakers when compared with congeners. Within *Stolephorus*, only three other species with up to 30 1LGRs are known: *Stolephorus apiensis* (Jordan and Seale 1906): 1LGR 28–30, recorded from Japan, New Ireland, Fiji, and Samoa; *S. multibranchus*: 1LGR 32–36, endemic to Micronesia; and *Stolephorus ronquilloi* Wongratana 1983: 1LGR 28–30, endemic to Philippines (Wongratana 1983 1987; Whitehead et al. 1988; Wongratana et al. 1999; Hata and Motomura 2018c e 2020). Like *S. pacificus*, *S. teguhi*, and *S. leopardus*, these three species are distributed only in insular areas, rather than being associated with continental land masses. Another insular species, *S. babarani* (1LGR 21–23, endemic to Panay, Philippines) has a higher 1LGR number than its sister species, *S. baweanensis* (1LGR 19–22), distributed from India to the southern coast of China, and including Indonesia) (Hata et al. 2020a). Two other species endemic to insular areas, *S. commersonnii* (1LGR 25–27, Mauritius endemic) and *S. scitulus* (1LGR 25–28, Fiji to French Polynesia), long regarded as *S. indicus* with *S. balinensis* (1LGR 20–25, Gulf of Thailand to southern Japan and Papua New Guinea), *S. belaerius* (1LGR 22–24, along the eastern coast of Africa from Kenya to Mozambique and Madagascar), and true *S. indicus* (1LGR 21–25, along the Eurasian Continent from the Red Sea to Ranong, Thailand), have a larger number of gill rakers than *S. balinensis*, *S. belaerius*, and *S. indicus*, which are associated with continental landmasses (Hata et al. 2021).

Engraulid fishes are typically microphagous, filtering plankton, and species with more gill rakers are able to take in smaller plankton (Uotani 1985). Large-sized plankton are dominant in eutrophic ecosystems, such as estuarine and coastal waters, whereas small-sized plankton are dominant in oligotrophic waters (Stockner 1988; Maita and Odate 1988; Tada et al. 1994). Therefore, it is possible that the larger number of gill rakers in certain species represents an adaptation to less abundant planktonic prey due to less abundant nutrient sources (Dugdale and Goering 1967; Shiozaki et al. 2009).

CONCLUSIONS

A new species, *Stolephorus leopardus* sp. nov., is described, and two known congeners, *Stolephorus pacificus* Baldwin 1984 and *Stolephorus teguhi* Kimura, Hori, and Shibukawa 2009, are redescribed. The numerous gill rakers characteristic of insular species of *Stolephorus* are suggested to have resulted from adaptation to oligotrophic waters.

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Authors' contributions: HH collected the specimen data and wrote the manuscript. HH and HM designed the research, and read and approved the manuscript.

Competing interests: The authors declare that they have no conflict of interest.

Availability of data and materials: Morphometric and meristic data of the species described in this study are all shown in tables 1 and 2. Specimen's measurements are available from the corresponding author upon reasonable request. All specimens examined in this study have been recently deposited in museum collections (see MATERIALS AND METHODS).

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Ethics approval consent to participate: Not applicable.

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