

REDESCRIPTION AND DISTRIBUTIONAL RANGE EXTENSION OF THE POORLY KNOWN ANCHOVY *STOLEPHORUS* *BRACHYCEPHALUS* (TELEOSTEI: CLUPEIFORMES: ENGRAULIDAE)

Harutaka Hata^{1*} and Hiroyuki Motomura²

ABSTRACT

The poorly known anchovy *Stolephorus brachycephalus* Wongratana, 1983 (Clupeiformes: Engraulidae) is redescribed on the basis of 14 type and 14 non-type specimens from Papua Tengah (Indonesia), Gulf of Papua (Papua New Guinea), and Queensland (Australia). Previously, only small specimens (< 4.2 cm standard length) of the species had been recorded, the morphology of larger individuals therefore being unknown. In addition, validity of the diagnostic characters of *S. brachycephalus*, previously used to distinguish the species from *Stolephorus nelsoni* Wongratana, 1987, a morphologically most similar species, is reassessed.

Keywords: Actinopterygii, Clupeomorpha, distribution, Australian waters, *Stolephorus nelsoni*, taxonomy

INTRODUCTION

The Indo-Pacific anchovy genus *Stolephorus* includes at least 47 valid species (WHITEHEAD *ET AL.*, 1988; WONGRATANA *ET AL.*, 1999; KIMURA *ET AL.*, 2009; HATA & MOTOMURA, 2018a–e, 2021a–c, 2022a, b, 2023a, b, 2024a, b; HATA *ET AL.*, 2019, 2020a, b, 2021, 2022a, b, 2023; GANGAN *ET AL.*, 2020), many being abundantly caught, mainly in tropical waters, and utilized as food fish or for bait (NISHISHIMAMOTO, 1963; BALDWIN, 1977; DALZELL, 1994; ISSF & IPNLF, 2019). However, the taxonomy of the genus remains unsettled, numerous new species having been described in recent years (e.g., GANGAN *ET AL.*, 2020; HATA & MOTOMURA, 2023a, b, 2024a, b; HATA *ET AL.*, 2023). Furthermore, some established species have been recorded from only a small number of specimens, and are poorly known morphologically as a consequence. One of these, *Stolephorus brachycephalus* Wongratana, 1983, has been infrequently reported since its original description, with little known about its distribution limits, biology, and adult fish morphology (including diagnostic characters). During revisionary research of *Stolephorus*, numerous specimens of *S. brachycephalus* (26.5–51.1 mm standard length), collected from Indonesia, Papua New Guinea, and Australia, were located in museum fish collections, thereby enabling the present account of detailed morphological and biological information on the species.

¹ Okinawa Institute of Science and Technology, 1919-1 Tancha, Onna-son, Kunigami-gun Okinawa 904-0495, Japan.

² The Kagoshima University Museum, 1-21-30 Korimoto, Kagoshima 890-0065, Japan.

* Corresponding author. E-mail: k2795502@kada.kagoshima-u.ac.jp

Received 13 January 2024; accepted 31 March 2024.

MATERIALS AND METHODS

Methods for counts and proportional measurements followed HATA & MOTOMURA (2017). All measurements were made with digital calipers to the nearest 0.01 mm. “Pelvic scute” refers to a scute associated with the pelvic girdle, and “prepelvic scute”, “postpelvic scute” and “predorsal scute” to hard spine-like scutes anterior to the pelvic scute, posterior to the pelvic scute, and anterior to the dorsal-fin origin, respectively. Abbreviations are as follows—SL, standard length; UGR, LGR and TGR, upper limb, lower limb and total gill rakers, respectively, with associated numbers indicating the specific gill arch; 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 dorsal- and anal-fin origins; P1-P2, distance between pectoral- and pelvic-fin insertions; P2-A, distance from pelvic-fin insertion to anal-fin origin. Counts and measurements (expressed as percentages of SL) are given in Tables 1 and 2. Osteological characters were observed on radiographs. Institutional codes follow SABAJ (2020).

RESULTS

Stolephorus brachycephalus Wongratana, 1983

(Fig. 1; Tables 1, 2)

Stolephorus brachycephalus Wongratana, 1983: 401, fig. 19 (type locality: east side of Daru Wharf, Gulf of Papua, south coast of Papua New Guinea); BALDWIN, 1984: 155 (Papua New Guinea); WONGRATANA, 1987a: 107 (Gulf of Papua and north coast of Australia); WONGRATANA, 1987b: 7 (Gulf of Papua, Papua New Guinea; Northern Territory and Queensland, Australia); WHITEHEAD *ET AL.*, 1988: 406, unnumbered fig. (Gulf of Papua, south coast of Papua New Guinea); WONGRATANA *ET AL.*, 1999: 1730, unnumbered fig. (Gulf of Papua and off northern Australia in Gulf of Carpentaria); LARSON, 1999: 27 (Kakadu National Park, Northern Territory, Australia); PAXTON *ET AL.*, 2006: 314 (east side of Daru Wharf, Gulf of Papua, Papua New Guinea); LARSON *ET AL.*, 2013: 31 (Northern Territory, Australia); HATA & MOTOMURA, 2018d: table 1, fig. 3 (Gulf of Papua, south coast of Papua New Guinea).

Materials examined: 28 specimens, 26.5–51.1 mm SL. AMS I.22790-008, 9 specimens, 34.9–41.2 mm SL, south bank of Norman River, Queensland, Australia; BMNH 1979.3.21.447, holotype of *S. brachycephalus*, 41.8 mm SL, east side of Daru Wharf, Gulf of Papua, Papua New Guinea, coll. T. R. Roberts; BMNH 1979.3.21.448–452, 5 paratypes of *Stolephorus brachycephalus*, 26.6–35.0 mm SL, east side of Daru Wharf, Gulf of Papua, Papua New Guinea; BMNH 1979.8.16.828, dissected, east side of Daru Wharf, Gulf of Papua, Papua New Guinea; CSIRO H 5510-01, 51.1 mm SL, Mawati River Estuary, Papua Tengah, Indonesia (04°58'S, 137°07'E), 6–9 m depth; TU 178908, 3 specimens, 45.3–50.8 mm SL, Ajikwa Estuary, Papua Tengah, Indonesia; USNM 270294, 8 paratypes of *S. brachycephalus*, 25.6–28.1 mm SL, east side of Daru Wharf, Gulf of Papua, Papua New Guinea.

Diagnosis.—A species of *Stolephorus* with the following combination of characters: 1UGR 15–17 (modally 15), 1LGR 20–22 (21), 1TGR 35–38 (35); 2UGR 11–13 (12), 2LGR 18–21 (19), 2TGR 29–34 (32); 3UGR 9–11 (9), 3LGR 10–12 (11), 3TGR 19–23 (20); 4UGR 6–9 (7), 4LGR 8–11 (10), 4TGR 14–19 (17); prepelvic scutes 2–5 (4); scale rows in longitudinal series 32–34 (34); transverse scales 8; vertebrae 37–39 (38); anal fin with 19–22 (20) branched rays; pectoral fin with 10–12 (11) branched rays; 10–11 (11) branchiostegal rays;

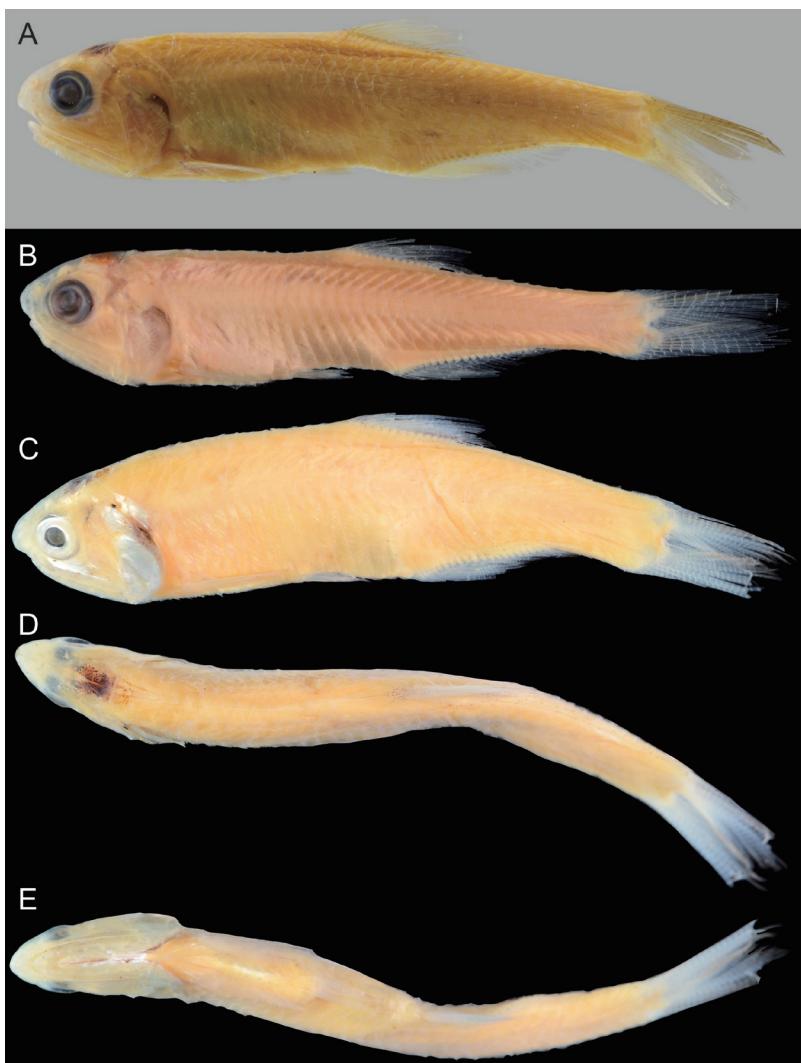


Figure 1. Preserved specimens of *Stolephorus brachycephalus* (A: holotype, BMNH 1979.3.21.447, 41.8 mm SL, from Gulf of Papua, Papua New Guinea; B: paratype, USNM 270294, 26.5 mm SL, from Gulf of Papua, Papua New Guinea; [C] lateral, [D] dorsal, and [E] ventral views of non-type specimen, TU 178908, 50.8 mm SL, Papua Tengah, Indonesia). Photographs by Harataka Hata.

pseudobranchial filaments 13–18 (15); long maxilla, posterior tip slightly short of or extending slightly beyond posterior border of opercle; no predorsal scutes; pelvic scute without spine-like projection; a pair of distinct dark patches on parietal region; no dark lines on dorsum; no black spots on snout and lower jaw tips, or below eye; anal-fin base long, 21.6–26.2% (mean 24.1%) of SL; anal-fin origin just below base of seventh to eleventh dorsal-fin rays; caudal peduncle short, 12.6–15.2% (14.2%) of SL; snout short, 3.6–4.3% (4.1%) of SL.

Description.—Counts and measurements, expressed as percentages of SL, given in Tables 1 and 2. Body laterally compressed, deepest at dorsal-fin origin. Dorsal profile of body gently rising from snout tip to dorsal-fin origin, thereafter gradually lowering to caudal-fin base. Ventral profile of body lowering from snout tip to point just below posterior tip of opercle, subsequently nearly straight and parallel with body axis to anal-fin origin. Ventral profile thereafter elevated to caudal-fin base. Abdomen somewhat rounded, covered with two to five spine-like posteriorly projecting scutes. Pelvic scute without spine. Postpelvic and predorsal scutes absent. Anus just anterior to anal-fin origin. Snout tip rounded, projecting; snout length less than eye diameter. Mouth large, inferior, ventral to body axis, extending backward beyond posterior margin of eye. Maxilla long, its posterior tip pointed, slightly short of or extending slightly beyond posterior border of opercle. Lower jaw slender. Uniserial conical teeth on both jaws. One or two rows of conical teeth on palatines and anterior part of pterygoid. Small sparse conical teeth on inner surface of central part of pterygoid. Several rows of small dense conical teeth on dorsal surfaces of basihyal and basibranchial. No teeth on upper edge of hyoid arch in individuals < 35 mm SL (single row of conical teeth on upper edge of ceratohyal in individuals > 35 mm SL). Several distinct conical teeth on vomer. Eye large, round, covered with thin adipose eyelid, positioned laterally on head dorsal to horizontal through pectoral-fin insertion, visible in dorsal view. Pupil round. Orbit elliptical. Nostrils close to each other, anterior to orbit. Posterior margin of preopercle rounded in most specimens, otherwise indented. Subopercle and opercle with smoothly rounded posterior margins. Gill membrane without serrations. Interorbital space flat, width less than eye diameter. Pseudobranchial filaments present, length of longest filament shorter than eye diameter. Gill rakers long, slender, rough, visible from side of head when mouth opened. Small asperities on both surfaces of gill rakers. Isthmus muscle long, reaching anteriorly to posterior margin of gill membranes. Urohyal hidden by isthmus muscle (not visible without dissection). Gill membranes on each side joined distally, most of isthmus muscle exposed (not covered by gill membrane). Body scales deciduous, completely lacking on all specimens examined, except for prepelvic scutes. Head scales absent. Fins scaleless, except for broad triangular sheath of scales on caudal fin. Dorsal-fin origin posterior to vertical through base of last pelvic-fin ray, slightly posterior to middle of body. Dorsal and anal fins with three anteriormost rays unbranched, closely spaced. First dorsal- and anal-fin rays minute. Anal-fin origin just below base of seventh to eleventh (eleventh in holotype) dorsal-fin ray. Posterior tip of depressed anal fin not reaching caudal-fin base. Uppermost pectoral-fin ray unbranched, inserted below midline of body. Posterior tip of pectoral fin not reaching to pelvic-fin insertion. Dorsal, ventral, and posterior margins of pectoral fin nearly linear. Pelvic fin shorter than pectoral fin. Posterior tip of depressed pelvic fin short of vertical through dorsal-fin origin or reaching to vertical through base of fifth (fourth in holotype) dorsal-fin ray. Caudal fin forked, posterior tips pointed.

Color of preserved specimens.—Body uniformly pale. A few melanophores scattered on dorsal surface of snout. No melanophores on jaws or suborbital area. A pair of dark patches on parietal region; a few pigment spots on occipital area. Melanophores scattered on posterior margins of dorsal scale pockets on body. Small uniserial black spots on ventral surface from anal-fin origin to caudal-fin base (more distinct in smaller specimens). All fins transparent. Melanophores scattered anteriorly on lower part of dorsal fin. Melanophores scattered on entire caudal fin, except centrally and on lower margin.

Table 1. Meristics of specimens of *Stolephorus brachycephalus* and *S. nelsoni*.

<i>Stolephorus brachycephalus</i>							<i>Stolephorus nelsoni</i>					
Standard length (SL; mm)	holotype			paratypes			non-types		holotype		paratypes	
	BMNH 1979.3.21.447	n = 13	n = 14	BMNH 57157	n = 3	n = 24	AMNH	n = 3	AMNH	n = 3	AMNH	n = 24
Dorsal-fin rays (unbranched)	3	3	3	3	3	3	3	3	3	3	3	3
Dorsal-fin rays (branched)	13	12-14	12-13	13	13	13	13	13	12-13	13	13	13
Anal-fin rays (unbranched)	3	3	3	3	3	3	3	3	3	3	3	3
Anal-fin rays (branched)	20	19-22	19-22	20	16	17-18	15-18	15-18	15-18	17	17	17
Pectoral-fin rays (unbranched)	1	1	1	1	1	1	1	1	1	1	1	1
Pectoral-fin rays (branched)	11	10-12	10-12	11	12	12-13	11-14	11-14	11-14	12	12	12
Pelvic-fin rays (unbranched)	1	1	1	1	1	1	1	1	1	1	1	1
Pelvic-fin rays (branched)	6	6	6	6	6	6	6	6	6	6	6	6
Caudal-fin rays	19	19	19	19	19	19	19	19	19	19	19	19
Gill rakers on 1 st gill arch (upper)	15	15-16	15-17	15	19	18-19	16-19	16-19	16-19	18	18	18
Gill rakers on 1 st gill arch (lower)	21	20-22	20-22	21	23	23-24	20-24	20-24	20-24	23	23	23
Gill rakers on 1 st gill arch (total)	36	35-38	35-38	35	42	42-43	37-43	37-43	37-43	40	40	40
Gill rakers on 2 nd gill arch (upper)	11	11-13	12-13	12	14	13-14	12-14	12-14	12-14	13	13	13
Gill rakers on 2 nd gill arch (lower)	18	18-21	19-21	19	22	21-23	18-23	18-23	18-23	22	22	22
Gill rakers on 2 nd gill arch (total)	29	30-33	31-34	32	36	34-36	30-37	30-37	30-37	35	35	35
Gill rakers on 3 rd gill arch (upper)	9	9-10	9-11	9	12	11	9-12	9-12	9-12	11	11	11
Gill rakers on 3 rd gill arch (lower)	11	10-12	11-12	11	13	13	12-14	12-14	12-14	13	13	13
Gill rakers on 3 rd gill arch (total)	20	19-22	20-23	20	25	24	21-26	21-26	21-26	23	23	23

Table 1 (continued).

	<i>Stolephorus brachycephalus</i>				<i>Stolephorus nelsoni</i>			
	holotype	paratypes		non-types	holotype	paratypes		non-types
		BMNH	n = 13	n = 14		AMNH	n = 3	n = 24
Standard length (SL; mm)	41.8	26.5–35.0	34.9–51.1	modes	571.57	71.6	64.8–71.6	41.2–88.6 modes
Gill rakers on 4 th gill arch (upper)	6	6–9	7–8	7	9	9	8–10	9
Gill rakers on 4 th gill arch (lower)	9	8–10	9–11	10	11	11	9–12	11
Gill rakers on 4 th gill arch (total)	15	14–19	16–19	17	20	20	18–22	20
Gill rakers on posterior face of 3 rd gill arch	5	3–6	3–6	5	7	5–6	3–7	6
Prepelvic scutes	4	2–5	3–5	4	4	5	4–7	5
Branchiostegal rays	10	10–11	10–11	11	13	12	12–14	13
Longitudinal scales of scale rows	33	33–34	32–34	34	35	36	34–36	35
Transverse scales	8	8	8	8	8	8	8	8
Pseudobranch filaments	18	13–17	14–18	15	18	20–21	16–22	18
Number of dorsal-fin rays before anal-fin origin	11	8–10	7–11	9	10	11–12	10–13	11
Pectoral-fin rays with melanophores	0	0	0	0	0	0	0	0
Vertebrae	37–38	37–39	38	38	39	39	39–40	39

Table 2. Morphometrics of specimens of *Stolephorus brachycephalus* and *S. nelsoni*.

As % SL	<i>Stolephorus brachycephalus</i>			<i>Stolephorus nelsoni</i>		
	holotype		paratypes	non-types	holotype	paratypes
	BMNH 1979.3.21.447	n = 13	n = 14	AMNH 57157	n = 3	n = 24
Standard length (SL; mm)	41.8	26.5–35.0	34.9–51.1	means	71.6	64.8–71.6
						41.2–88.6
						means
Head length	26.4	26.6–26.9	25.6–27.0	26.5	28.4	27.0–27.2
Body depth	20.2	18.2–20.9	20.8–26.5	21.0	23.7	22.8–23.9
Pre-dorsal fin length	52.4	52.6–57.3	52.4–55.1	54.3	55.2	52.6–54.1
Snout tip to pectoral-fin insertion	27.1	27.5–29.1	27.6–29.7	28.6	30.1	29.5–30.9
Snout tip to pelvic-fin insertion	44.4	42.7–46.4	43.8–46.4	44.9	49.1	47.5–48.3
Snout tip to anal-fin origin	60.6	56.7–64.9	61.3–65.2	62.5	66.7	64.9–67.0
Dorsal-fin base length	15.1	14.9–16.4	14.8–16.6	15.6	16.7	15.4–16.8
Anal-fin base length	22.3	21.6–25.2	21.7–26.2	24.1	17.2	17.3–18.6
Caudal-peduncle length	14.3	12.6–15.2	13.1–15.1	14.2	18.1	16.5–18.2
Caudal-peduncle depth	8.9	6.9–10.0	9.9–11.0	9.6	10.0	9.8–10.3
D-P1	33.6	32.6–36.0	33.5–37.2	34.3	34.8	34.6–35.2
D-P2	22.8	21.1–23.6	23.0–28.1	23.6	25.6	23.9–25.5
D-A	23.8	20.6–23.1	22.5–26.6	23.2	25.6	25.1–25.8
P1–P2	17.7	14.6–17.6	16.4–20.2	17.1	19.5	18.6–20.5
P2–A	17.7	16.7–18.4	16.5–20.4	17.8	17.7	18.7–19.8
Pectoral fin length	17.4	13.5–17.5	17.1–19.1	17.4	broken	16.9–17.1
Pelvic fin length	9.4	9.3–10.8	9.3–10.9	10.0	9.3	8.9–9.0

Table 2 (continued).

	<i>Stolephorus brachycephalus</i>				<i>Stolephorus nelsoni</i>			
	holotype	paratypes		non-types	holotype	paratypes		non-types
		BMMNH	n = 13	n = 14		AMNH	n = 3	n = 24
Standard length (SL; mm)	41.8	26.5–35.0	34.9–51.1	means	71.6	64.8–71.6	41.2–88.6	means
1979.3.21.447	19.9	21.0–23.1	22.0–22.9	21.9	22.9	22.5	21.1–22.9	22.1
Maxilla length	17.8	17.5–19.3	17.6–18.9	18.4	18.8	17.6–18.1	17.1–18.6	17.9
Mandibular length	5.2	4.2–5.8	5.0–5.7	5.0	4.8	4.8	4.2–5.4	4.9
Supramaxilla end to maxilla end	1.9	1.0–2.4	1.1–2.8	2.0	2.1	1.5–1.8	1.1–2.3	1.8
1 st unbranched dorsal-fin ray length	9.3	9.2–9.3	8.6–9.6	9.2	broken	7.4–7.8	6.8–8.5	7.7
2 nd unbranched dorsal-fin ray length	broken	broken	19.9–20.5	20.2	broken	broken	15.4–17.9	16.6
3 rd dorsal-fin ray length	1.9	1.3–2.6	1.3–2.8	2.0	1.8	1.4–1.8	0.9–2.5	1.6
1 st unbranched anal-fin ray length	5.5	4.4–6.3	5.2–6.3	5.7	5.1	4.7–4.9	4.4–6.7	5.2
2 nd unbranched anal-fin ray length	broken	15.1	16.4	15.8	broken	broken	11.9–14.1	13.3
3 rd anal-fin ray length	7.0	7.5–8.8	7.8–8.7	8.2	9.2	8.6–8.9	8.2–9.8	8.9
Orbit diameter	5.9	5.6–7.0	6.3–7.2	6.7	6.7	6.3–7.5	6.3–8.3	7.0
Eye diameter	4.3	3.6–4.3	3.8–4.3	4.1	5.4	4.8–5.0	4.5–5.5	5.0
Snout length	6.8	6.2–7.1	6.2–6.9	6.7	6.7	6.2–7.2	6.0–7.8	6.7
Interorbital width	14.6	13.4–14.8	13.2–14.4	13.9	14.5	13.3–14.0	12.4–14.7	13.6
Postorbital length								

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 and anal-fin origin)

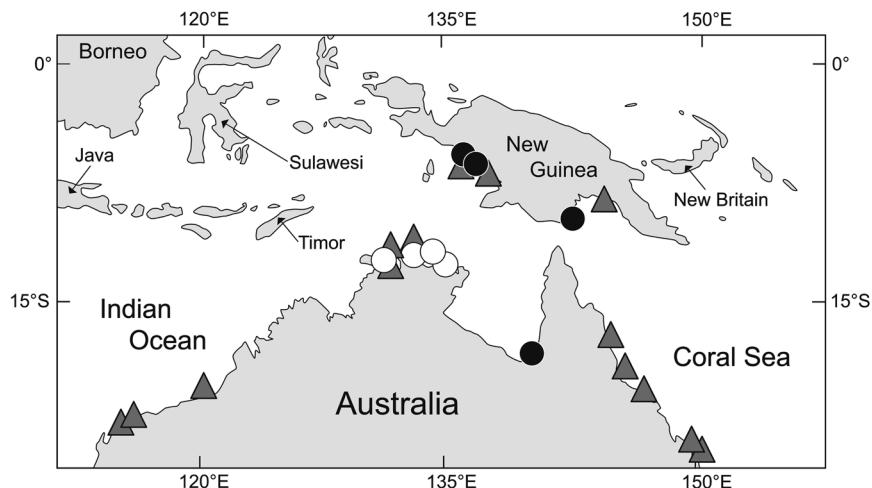


Figure 2. Distributional records of *Stolephorus brachycephalus* (solid black circles: specimens examined in this study; white circles: literature records) and *S. nelsoni* (solid gray triangles: examined specimens).

Distribution.—*Stolephorus brachycephalus* is distributed off the south coast of New Guinea from Ajikwa River estuary (Papua Tengah, Indonesia) to Daru (West Province, Papua New Guinea), and the north coast of Australia from the Northern Territory to the Gulf of Carpentaria (WONGRATANA *ET AL.*, 1999; LARSON *ET AL.*, 2013; this study; Fig. 2).

DISCUSSION

Stolephorus brachycephalus was described by WONGRATANA (1983) from 15 specimens collected from the Gulf of Papua, Papua New Guinea. Although the species has been recorded from Australian waters (e.g., LARSON, 1999; WONGRATANA *ET AL.*, 1999), voucher specimen records, photographs or illustrations have not been published. Because *S. brachycephalus* has at no time been reported from areas other than Papua New Guinea and Australia, the present specimens represent the first records of the species from Indonesian waters, in addition to including the first specimen-based records from Australia. It is now apparent that the species is distributed around the entire coast of New Guinea, in addition to coastal waters off the Northern Territory and Gulf of Carpentaria, Australia (Fig. 2).

As noted by WONGRATANA *ET AL.* (1999), the biology of the species is unknown. However, some of the present specimens had been collected from river estuaries, suggesting that *S. brachycephalus* may sometimes occur in brackish waters.

WONGRATANA *ET AL.* (1999) compared *S. brachycephalus* with *Stolephorus nelsoni* Wongratana, 1987, the latter being a morphologically closely related and sympatric with *S. brachycephalus* off the south coast of New Guinea and north coast of Australia (Fig. 2), showing that the former had fewer ILGR (20–22 in *S. brachycephalus* vs. 24 in *S. nelsoni*)

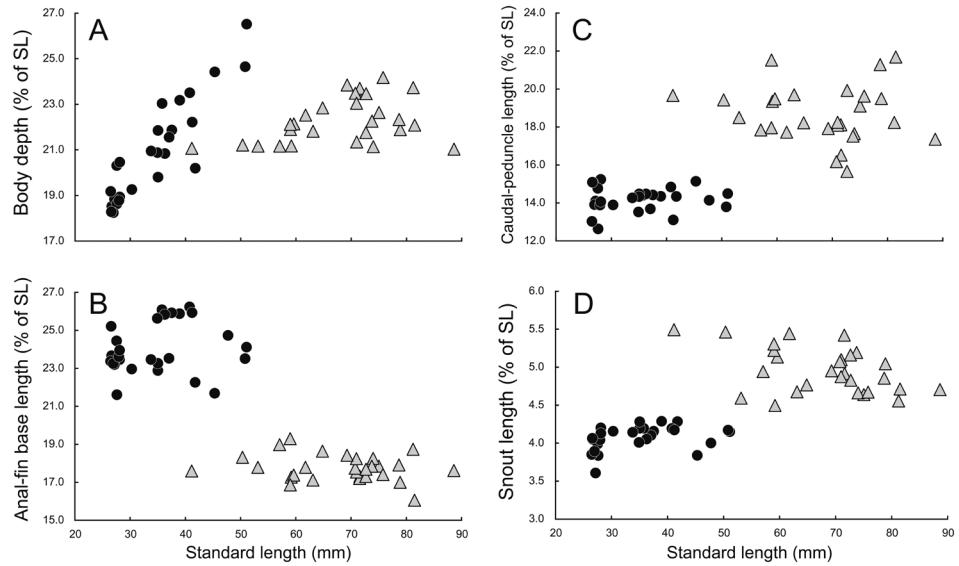


Figure 3. Relationships of (A) body depth, (B) anal-fin base, (C) caudal-peduncle length, and (D) snout length to standard length in *Stolephorus brachycephalus* (black circles) and *S. nelsoni* (gray triangles).

and branchiostegal rays (10 or 11 vs. 12 or 13), and lacked teeth on the dorsal surface of the hyoid arch (vs. small teeth present). HATA & MOTOMURA (2018d) compared nine type specimens of *S. brachycephalus* with 17 specimens (including the holotype and 1 paratype) of *S. nelsoni* and showed that in addition to the characters listed by WONGRATANA *ET AL.* (1999), *S. brachycephalus* could also be distinguished from *S. nelsoni* by more branched anal-fin rays (20–22 vs. 15–17), fewer branched pectoral-fin rays (10–12 vs. 12–14), a narrower body (18.2–20.3% of SL vs. 21.1–23.7%), longer anal-fin base (21.6–24.4% vs. 16.1–19.3%), and shorter caudal peduncle (12.6–15.2% of SL vs. 15.7–21.7%) and snout (3.6–4.3% of SL vs. 4.5–5.5%). However, as they pointed out, the standard length ranges of the specimens of *S. brachycephalus* (26.5–41.8 mm) and *S. nelsoni* (41.2–81.5 mm) examined by them barely overlapped, with the above morphometric data therefore being unsuitable for differentiation between the two species. Since no records of *S. brachycephalus* to date, following the original description of the species, have included specimens > 41.8 mm SL (SL of the holotype), ontogenetic morphological changes and the morphology of large individuals have remained unknown.

During the present study, several specimens of *S. brachycephalus* > 40 mm SL were found, enabling a detailed assessment of the morphology of larger individuals. Because the body depth/SL proportion of the species increases with growth (reaching 26.5% SL), that feature cannot be used to separate *S. brachycephalus* from *S. nelsoni* (Fig. 3A). Moreover, specimens of *S. brachycephalus* > 40 mm SL had teeth on the dorsal surface of ceratohyal, not apparent in smaller specimens, and rendering the condition of hyoid arch invalid for distinguishing between the two species. However, counts of branched anal-fin rays, branched pectoral-fin

Table 3. Frequency distribution of branched anal-fin rays, branched pectoral-fin rays, branchiostegal rays, scale rows in longitudinal series and vertebrae in *Stolephorus brachycephalus* and *S. nelsoni*, based on specimens examined in this study.

		Branched anal-fin rays							
		15	16	17	18	19	20	21	22
<i>Stolephorus brachycephalus</i>	<i>n</i> = 27					3	12	8	4
<i>Stolephorus nelsoni</i>	<i>n</i> = 27	3	8	14	2				
		Branched pectoral-fin rays							
<i>Stolephorus brachycephalus</i>	<i>n</i> = 27	10		11	12	13		14	
<i>Stolephorus nelsoni</i>	<i>n</i> = 28		10	11	12	13		14	
		Branchiostegal rays							
<i>Stolephorus brachycephalus</i>	<i>n</i> = 26	10		11	12	13		14	
<i>Stolephorus nelsoni</i>	<i>n</i> = 27		7	19		10	14	3	
		Scale rows in longitudinal series							
<i>Stolephorus brachycephalus</i>	<i>n</i> = 26	32		33	34	35		36	
<i>Stolephorus nelsoni</i>	<i>n</i> = 28		1	10	15				
				4	20		4		
		Vertebrae							
<i>Stolephorus brachycephalus</i>	<i>n</i> = 12	37		38	39	40			
<i>Stolephorus nelsoni</i>	<i>n</i> = 3		3	8	1				
				2	1				

Table 4. Frequency distribution of total gill rakers on first, second, third, and fourth gill arches in *Stolephorus brachycephalus* and *S. nelsoni*, based on specimens examined in this study.

		Total gill rakers on first gill arch								
		35	36	37	38	39	40	41	42	43
<i>Stolephorus brachycephalus</i>	<i>n</i> = 27	10	5	8	4					
<i>Stolephorus nelsoni</i>	<i>n</i> = 28			1	1	6	7	6	3	4
		Total gill rakers on second gill arch								
		29	30	31	32	33	34	35	36	37
<i>Stolephorus brachycephalus</i>	<i>n</i> = 27	1	3	8	9	3	3			
<i>Stolephorus nelsoni</i>	<i>n</i> = 27		1	2	7	5	7	3	2	
		Total gill rakers on third gill arch								
		19	20	21	22	23	24	25	26	
<i>Stolephorus brachycephalus</i>	<i>n</i> = 27	1	10	7	7	2				
<i>Stolephorus nelsoni</i>	<i>n</i> = 27			1	5	9	8	3	1	
		Total gill rakers on fourth gill arch								
		14	15	16	17	18	19	20	21	22
<i>Stolephorus brachycephalus</i>	<i>n</i> = 27	1	5	6	8	5	2			
<i>Stolephorus nelsoni</i>	<i>n</i> = 27					8	6	11	1	1

rays, branchiostegal rays (Table 3), and GR (Table 4), in addition to longer anal-fin base, and shorter caudal peduncle and snout, remained diagnostic (Fig. 3B–D). Furthermore, numbers of scale rows in the longitudinal series and vertebrae in *S. brachycephalus* are fewer than in *S. nelsoni* (32–34 [modally 34] and 37–39 [38], respectively, in *S. brachycephalus* vs. 34–36 [35] vs. 39–40 [39], respectively, in *S. nelsoni*; Table 3).

Stolephorus brachycephalus can be distinguished from all congeners, except for *Stolephorus bavarani* Hata, Lavoué & Motomura, 2020, *Stolephorus bataviensis* Hardenberg, 1933, *Stolephorus baweanensis* Hardenberg, 1933, *Stolephorus celsior* Hata & Motomura, 2021, and *Stolephorus concursus* Hata & Motomura, 2021, the former being diagnosed by the anal-fin with 20–22 (rarely 19) branched rays, the fin origin being located posterior to the seventh dorsal-fin ray origin, a long maxilla with the posterior tip slightly short of or extending slightly beyond the opercle posterior border, and the absence of the predorsal scute (HATA ET AL., 2019, 2020a; HATA & MOTOMURA, 2021a). Moreover, *S. brachycephalus* differs from the above five species in lacking melanophores on the lower-jaw tip and suborbital area (vs. present on tips of snout and lower jaw, and suborbital area [in larger individuals] in the other five species) (WHITEHEAD ET AL., 1988; WONGRATANA ET AL., 1999; KIMURA ET AL., 2009; HATA & MOTOMURA, 2018a–e, 2021a–c, 2022a, b, 2023a, b, 2024a, b; HATA ET AL., 2019, 2020a, b, 2021, 2022a, b, 2023; GANGAN ET AL., 2020).

Comparative material examined: *Stolephorus nelsoni* (28 specimens: 41.2–88.6 mm SL): AMNH 57157, holotype of *Stolephorus nelsoni*, 71.6 mm SL, Eighty Mile Beach, Western Australia, Australia, 15 May 1969, coll. G. J. Nelson, W. H. Butler and D. E. Rosen; AMS IB. 3173, 59.2 mm SL, off Darwin, Northern Territory, Australia, 1954, F. R. Wells; AMS I. 26599-006, 61.7 mm SL, Cairns, Queensland, Australia; AMS I. 28535-001, 41.2 mm SL, Mackenzie Island, Queensland, Australia; CSIRO H 6548-11, 72.7 mm SL, approx. 6 km east of Deepwater, Queensland, Australia (24°26'S, 152°04'E), 14 m depth; CSIRO H 7497-02, 63.1 mm SL, approx. 6 km northwest of Goold Island, Queensland, Australia (18°08'S, 146°06'E), 7 m depth; CSIRO H 8838-02, 75.8 mm SL, Gulf of Papua, Purari, Papua New Guinea, 13–14 m depth; NTM S. 11733-001, 50.4 mm SL, northwest of Table Head, Port Essington, Northern Territory, Australia (11°13'01.2"S, 132°07'58.8"E); NTM S.12898-003, 2 specimens, 59.0 mm SL, north of Bowra Shoals, Fog Bay, Northern Territory, Australia (12°42'S, 130°11'E), 20–21 m depth; NTM S.13281-017, 7 specimens, 59.6–81.5 mm SL, northeast of Point Charles, Beagle Gulf, Northern Territory, Australia (12°19'9"S, 130°40'75"E); NTM S. 14844-001, 2 specimens, 72.7–73.8 mm SL, estuary of Otokwa River, Irian Jaya, Indonesia (04°56'2"S, 137°15'7"E); ROM 39271, 2 paratypes of *Stolephorus nelsoni*, 64.8–69.3 mm SL, Cleveland Bay, 3–8 km southeast of Townsville, Queensland, Australia; TU 170905, 2 specimens, 70.8–71.0 mm SL, approx. 3 km off Kawora Estuary, Irian Jaya, New Guinea, Indonesia; TU 204545, 2 specimens, 53.1–57.1 mm SL, Minajerwi estuary, Irian Jaya, New Guinea, Indonesia; USNM 280176, paratype of *Stolephorus nelsoni*, 71.6 mm SL, Eighty Mile Beach, Western Australia, Australia; WAM P. 13382.001, 88.6 mm SL, Onslow, Ashburton, Western Australia, Australia (21°38'S, 115°07'E); WAM P. 32645.002, 1 of 4 specimens, 81.2 mm SL, approx. 3.75 km east of Locker Island, Western Australia, Australia (21°44'16.5"S, 114°47'41.4"E–21°44'08.8"S, 114°48'16.0"E), 7.7 m depth.

ACKNOWLEDGEMENTS

We thank R. Arrindell (AMNH), M. McGrouther, A. Hay, S. Reader, K. Parkinson, and I. Riley (AMS), O. Crimmen and J. Maclaine (BMNH), A. Graham, J. Pogonoski, W. White, W. Zhang, S. Appleyard, and H. O'Neill (CSIRO), B. Russell, M. Hammer, and G. Dally (NTM), N. Lujan and M. Burridge (ROM), J. G. Mann and H. L. Bart Jr. (TU), T. Munroe, K. Murphy, D. Pitassy, L. Willis, and A. Reft (USNM), and G. Moore and J. Ritchie (WAM) for opportunities to examine specimens of *Stolephorus*. We also thank G. Hardy (Ngunguru, New Zealand), for checking an early version of the manuscript. This study was supported in part by the Sasakawa Scientific Research Grant from the Japan Science Society (28-745); a Grant-in-Aid from the Japan Society for the Promotion of Science for JSPS Fellows (DC2: 29-6652); JSPS KAKENHI Grant Numbers 19K23691, 20H03311 and 21H03651; JSPS Overseas Research Fellowships (202160519); the JSPS Core-to-Core CREPSUM JPJSCCB20200009; and the “Establishment of Glocal Research and Education Network in the Amami Islands” project of Kagoshima University adopted by the Ministry of Education, Culture, Sports, Science and Technology, Japan.

REFERENCES

- BALDWIN, W. J. 1977. A review on the use of live baitfishes to capture skipjack tuna, *Katsuwonus pelamis*, in the tropical Pacific Ocean with emphasis on their behavior, survival and availability. *NOAA Tech. Rep., NMFS Circ* 408: 8–35.
- BALDWIN, W. J. 1984. *Stolephorus pacificus*, a new species of tropical anchovy (Engraulidae) from the western Pacific Ocean. *Micronesica* 19(1–2): 151–156.
- DALZELL, P. 1994. Whitebait of stolephorid anchovies. *South Pacific Commission Fisheries Newsletter* 68: 20–23.
- GANGAN, S. S., A. PAVAN-KUMAR, S. JAHAGEERDAR, AND A. K. JAISWAR. 2020. A new species of *Stolephorus* (Clupeiformes: Engraulidae) from the Bay of Bengal. *Zootaxa* 4743: 561–574. <https://doi.org/10.11646/zootaxa.4743.4.6>
- HATA, H., S. LAVOUÉ, S. V. BOGORODSKY, T. J. ALPERMANN, AND H. MOTOMURA. 2023. A new *Stolephorus* (Teleostei: Clupeiformes: Engraulidae: Engraulinae) from the Red Sea. *Ichthyol. & Herpet.* 111: 191–203. <https://doi:10.1643/i2022064>
- HATA, H., S. LAVOUÉ, AND H. MOTOMURA. 2019. Taxonomic status of seven nominal species of the anchovy genus *Stolephorus* described by Delsman (1931), Hardenberg (1933), and Dutt and Babu Rao (1959), with redescription of *Stolephorus tri* (Bleeker 1852) and *Stolephorus waitei* Jordan and Seale 1926 (Clupeiformes: Engraulidae). *Ichthyol. Res.* 67(1): 7–38. <https://doi:10.1007/s10228-019-00697-7>
- HATA, H., S. LAVOUÉ, AND H. MOTOMURA. 2020a. *Stolephorus babarani*, a new species of anchovy (Teleostei: Clupeiformes: Engraulidae) from Panay Island, central Philippines. *Zootaxa* 4178(4): 509–520. <https://doi:10.11646/zootaxa.4718.4.5>
- HATA, H., S. LAVOUÉ, AND H. MOTOMURA. 2020b. *Stolephorus acinaces*, a new anchovy from northern Borneo, and redescription of *Stolephorus andhraensis* (Babu Rao, 1966) (Clupeiformes: Engraulidae). *Mar. Biodivers.* 50(6): 1–11. <https://doi:10.1007/s12526-020-01115-2>
- HATA, H., S. LAVOUÉ, AND H. MOTOMURA. 2021. Taxonomic status of nominal species of the anchovy genus *Stolephorus* previously regarded as synonyms of *Stolephorus commersonii* Lacepède 1803 and *Stolephorus indicus* (van Hasselt 1823), and descriptions of three new species (Clupeiformes: Engraulidae). *Ichthyol. Res.* 68(3): 327–372. <https://doi:10.1007/s10228-020-00792-0>
- HATA, H., S. LAVOUÉ, AND H. MOTOMURA. 2022a. Description of three new species previously identified as *Stolephorus bengalensis* (Dutt and Babu Rao, 1959) or *Stolephorus insularis* Hardenberg, 1933, and a redescription of *S. bengalensis* (Chordata, Osteichthyes, Clupeiformes, Engraulidae). *ZooKeys* 1121: 145–173. <https://doi:10.3897/zookeys.1121.84171>

- HATA, H., S. LAVOUÉ, AND H. MOTOMURA. 2022b. A new species of *Stolephorus* from the eastern Indian Ocean and redescription of *Stolephorus dubiosus* Wongratana, 1983, with comments on the evolution of prepelvic scute numbers within *Stolephorus* (Clupeiformes: Engraulidae). *Zool. Stud.* 61: e58. <https://doi:10.6620/ZS.2022.61-58>
- HATA, H., AND H. MOTOMURA. 2017. A new species of anchovy, *Encrasicholina austera* (Clupeiformes: Engraulidae), from Fiji, southwestern Pacific. *N. Z. J. Zool.* 44: 122–128. <http://dx.doi.org/10.1080/03014223.2016.1268177>
- HATA, H., AND H. MOTOMURA. 2018a. *Stolephorus continentalis*, a new anchovy from the northwestern South China Sea and redescription of *Stolephorus chinensis* (Günther 1880) (Clupeiformes: Engraulidae). *Ichthyol. Res.* 65 (3): 374–382. <https://doi.org/10.1007/s10228-018-0621-z>
- HATA, H., AND H. MOTOMURA. 2018b. First record of the anchovy, *Stolephorus teguhi* (Engraulidae) from the Philippines. *Philip. J. Syst. Biol.* 11(2): 20–24.
- HATA, H., AND H. MOTOMURA. 2018c. Additional specimens of the poorly known anchovy *Stolephorus multibranchus* (Clupeiformes: Engraulidae) from Kosrae, Caroline Islands. *Biogeography*. 20: 78–84. <https://doi:10.11358/biogeo.20.78>
- HATA, H., AND H. MOTOMURA. 2018d. Redescription and distributional range extension of the poorly known anchovy *Stolephorus nelsoni* (Clupeiformes: Engraulidae). *Acta Ichthyol. Piscat.* 48: 381–386. <https://doi:10.3750/AIEP/02501>
- HATA, H., AND H. MOTOMURA. 2018e. *Stolephorus insignitus*, a new anchovy from the western Pacific, and redescription of *Stolephorus apiensis* (Jordan and Seale 1906) (Clupeiformes: Engraulidae). *Ichthyol. Res.* 66(2): 280–288. <https://doi:10.1007/s10228-018-00675-5>
- HATA, H., AND H. MOTOMURA. 2021a. Two new species of *Stolephorus* (Teleostei: Clupeiformes: Engraulidae) from the western Pacific. *Raff. Bull. Zool.* 69: 109–117. <https://doi.org/10.26107/RBZ-2021-0009>
- HATA, H., AND H. MOTOMURA. 2021b. *Stolephorus grandis*, a new anchovy (Teleostei: Clupeiformes: Engraulidae) from New Guinea and Australia. *Zootaxa* 5004: 481–489. <https://doi:10.11646/zootaxa.5004.3.5>
- HATA, H., AND H. MOTOMURA. 2021c. 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). *Zool. Stud.* 60: 65. <https://doi:10.6620/ZS.2021.60-65>
- HATA, H., AND H. MOTOMURA. 2022a. Redescription of *Stolephorus ronquilloi* Wongratana, 1983 and description of *Stolephorus hindustanensis*, a new anchovy from the Western Coast of India (Teleostei: Clupeiformes: Engraulidae). *Taxonomy* 2: 124–135. <https://doi:10.3390/taxonomy2010010>
- HATA, H., AND H. MOTOMURA. 2022b. *Stolephorus lotus*, a new anchovy (Teleostei: Clupeiformes: Engraulidae) from the Northern Territory, Australia. *Zool. Stud.* 61: 87. <https://doi:10.6620/ZS.2022.61-87>
- HATA, H., AND H. MOTOMURA. 2023a. Description of *Stolephorus horizon* n. sp. from Fiji and Tonga, and redescription of *Stolephorus scitulus* (Fowler, 1911) (Teleostei: Clupeiformes: Engraulidae). *Taxonomy* 3: 356–380. <https://doi:10.3390/taxonomy3030021>
- HATA, H., AND H. MOTOMURA. 2023b. Redescription and extended distribution of the poorly known Australian anchovy *Stolephorus advenus* (Actinopterygii: Clupeiformes: Engraulidae). *Acta Ichthyol. Piscat.* 53: 209–216. <https://doi.org/10.3897/ajep.53.109943>
- HATA, H., AND H. MOTOMURA. 2024a. A new species of the anchovy genus *Stolephorus* Lacepède 1803, and redescriptions of *Stolephorus carpentariae* (De Vis 1882) and *Stolephorus holodon* (Boulenger 1900) (Clupeiformes: Engraulidae). *Ichthyol. Res.* <https://doi.org/10.1007/s10228-024-00971-3>
- HATA, H., AND H. MOTOMURA. 2024b. A new species of anchovy, *Stolephorus astrum* (Teleostei: Clupeiformes: Engraulidae), from Palau, Micronesia. *Raffles Bull. Zool.* 72; 150–161. <https://doi.org/10.26107/RBZ-2024-0013>
- ISSF (INTERNATIONAL SEAFOOD SUSTAINABILITY FOUNDATION) AND IPNLF (INTERNATIONAL POLE & LINE FOUNDATION). 2019. *Skippers Guidebook to Pole-and-line Fishing Best Practices*. ISSF, Washington, DC and IPNLF, London, 53 pp.
- KIMURA, S., K. HORI, AND K. SHIBUKAWA. 2009. A new anchovy, *Stolephorus teguhi* (Clupeiformes: Engraulidae) from north Sulawesi, Indonesia. *Ichthyol. Res.* 56 (3): 292–295.
- LARSON, H. K. 1999. *Report to Parks Australia North, on the Estuarine Fish Inventory of Kakadu National Park, Northern Territory Australia. MAGNT Research Report, No. 5*. Museums and Art Galleries of the Northern Territory, Darwin. 50 pp.
- LARSON, H. K., R. S. WILLIAMS, AND M. P. HAMMER. 2013. An annotated checklist of the fishes of the Northern Territory, Australia. *Zootaxa* 3696(1): 1–293. <http://dx.doi.org/10.11646/zootaxa.3696.1.1>

- NISHISHIMAMOTO, S. 1963. Anchovies from the Ryukyu Islands. *Bull. Arts Sci. Div., Univ. Ryukyus. Math. Nat. Sci.* 6: 54–63.
- PAXTON, J. R., J. E. GATES, D. J. BRAY, AND D. F. HOESE. 2006. Engraulidae. Anchovies. Pages 310–317 in D. F. Hoese, D. J. Bray, J. R. Paxton, and G. R. Allen (eds.), *Zoological Catalogue of Australia. Volume 35. Fishes. Parts 1–3*. CSIRO Publishing, Collingwood.
- SABAJ, M. H. 2020. Codes for natural history collections in ichthyology and herpetology. *Copeia* 108: 593–669.
- WHITEHEAD, P. J. P., G. J. NELSON, AND T. WONGRATANA. 1988. FAO species catalogue, Vol 7. Clupeoid fishes of the world (suborder Clupoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 2 – Engraulidae. *FAO Fisher. Synop.*, no. 125 7(2): i–viii + 305–579.
- WONGRATANA, T. 1983. Diagnoses of 24 new species and proposal of a new name for a species of Indo-Pacific clupeoid fishes. *Japan. J. Ichthyol.* 29 (4): 385–407.
- WONGRATANA, T. 1987a. Four new species of clupeoid fishes (Clupeidae and Engraulidae) from Australian waters. *Proc. Biol. Soc. Wash.* 100(1): 104–111.
- WONGRATANA, T. 1987b. Two new species of anchovies of the genus *Stolephorus* (Engraulidae), with a key to species of *Engraulis*, *Encrasicholina*, and *Stolephorus*. *Am. Mus. Novitat.* 2876: 1–8.
- WONGRATANA, T., T. A. MUNROE, AND M. S. NIZINSKI. 1999. Order Clupeiformes. Engraulidae. Anchovies. Pages 1698–1753 in K. E. Carpenter, and V. H. Niem (eds.), *FAO species identification guide for fishery purposes. The living marine resources of the western central Pacific, Vol. 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae)*. FAO, Rome.