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New records of the Saber Anchovy *Stolephorus acinaces* (Teleostei: Clupeiformes: Engraulidae) from Vietnam

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ABSTRACT

Four specimens of *Stolephorus acinaces* Hata, Lavoué and Motomura, 2020 (previously known only from the type specimens collected from the northern coast of Borneo) were collected from southern Vietnam, and their identification confirmed by analysis of the cytochrome oxidase subunit I (COI) gene. The specimens represent the northernmost records of the species, which is redescribed, including a fresh color description for the first time, and are suggestive of a wide distribution in the southern Bien Dong Sea.

Keywords: Actinopteri, Clupeomorpha, distribution, Bien Dong Sea, *Stolephorus andhraensis*, taxonomy.

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INTRODUCTION

The anchovy genus *Stolephorus* includes 47 valid species [1–23], some of which are abundantly caught and constitute an important fisheries resource in Vietnam [24–26]. Because the genus is taxonomically confused, misidentifications still frequently occur in many publications, despite many new species having been described in recent years (e.g., Kimura et al., (2009) [3]; Gangan et al., (2020) [23]; Hata and Motomura (2024) [13, 14]). In addition, because the distribution limits of many species are still unknown, distributional records of species of *Stolephorus* have also been reported frequently (e.g., Kimura et al., (1999) [27]; Hata and Motomura (2018, 2020, 2024) [28–32]; Gouda et al., (2023) [33]; Hata et al., (2024) [34]).

Recently, three specimens of a species of *Stolephorus* not previously recorded from Vietnam were collected from Nha Trang, southern Vietnam. Conspecific with an additional specimen recently found in the fish collection of the University of Michigan Museum of Zoology, the specimens were identified as *Stolephorus acinaces* Hata, Lavoué and Motomura, 2020, a species previously known only from the northern coast of Borneo, Malaysia [18]. Accordingly, the newly-reported specimens represent the first Vietnamese and northernmost records of the species. A detailed description of the specimens—including nucleotide sequences of the mitochondrial cytochrome oxidase subunit I (COI) gene of two specimens—and an identification key to all species of *Stolephorus* recorded from Vietnam are given.

MATERIALS AND METHODS

Methods for counts and proportional measurements, shown in Tables 1 and 2, followed Hata and Motomura (2017) [35]. 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. Osteological characters were observed on soft X-ray photographs. Institutional codes follow Sabaj (2020) [36].

The “barcode” fragment (648 base-pairs) of the COI gene was sequenced in two specimens of *Stolephorus acinaces* collected in the Vietnamese marine region (KAUM–I. 117474 and KAUM–I. 117375). DNA was extracted from ethanol-preserved tissue fin clips. Polymerase chain reaction (PCR) amplification and sequencing of the COI gene followed standard protocols [37], with annealing at 55°C. Amplification of the partial COI gene used the following primers: forward COI_FishF1 (5′-TCAACCAACCACAAAGA CATTGGCAC-3′) and reverse COI_FishR2 (5′-ACTTCAGGGTGACCGAAGAATCAGAA-3′) [37]. PCR products were sent to Apical Scientific Sdn. Bhd. (Selangor, Malaysia) for purification and bi-directional sequencing by Sanger Sequencing technology, using the same PCR primers. Raw forward and reverse sequences were de novo assembled in Mega v.11.0.13 [38]. Consensus sequences generated in this study have been deposited in the GenBank database under accession numbers PQ470027 and PQ470028.

The COI data from the two newly sequenced specimens of *Stolephorus acinaces* were compared with the COI data from six specimens from Malaysia examined by Hata et al., (2020) [18], including one paratype (GenBank accession numbers: MH380515-8, MH380654-5). COI-based uncorrected pairwise genetic distances were calculated using Mega v.11.0.13.

RESULTS

Stolephorus acinaces Hata, Lavoué and Motomura, 2020 (Figs. 1, 2; Tables 1, 2)

Stolephorus andhraensis (not of Babu Rao): Rainboth et al., (2012) [39]: 60 (Mekong plume, Vietnam).

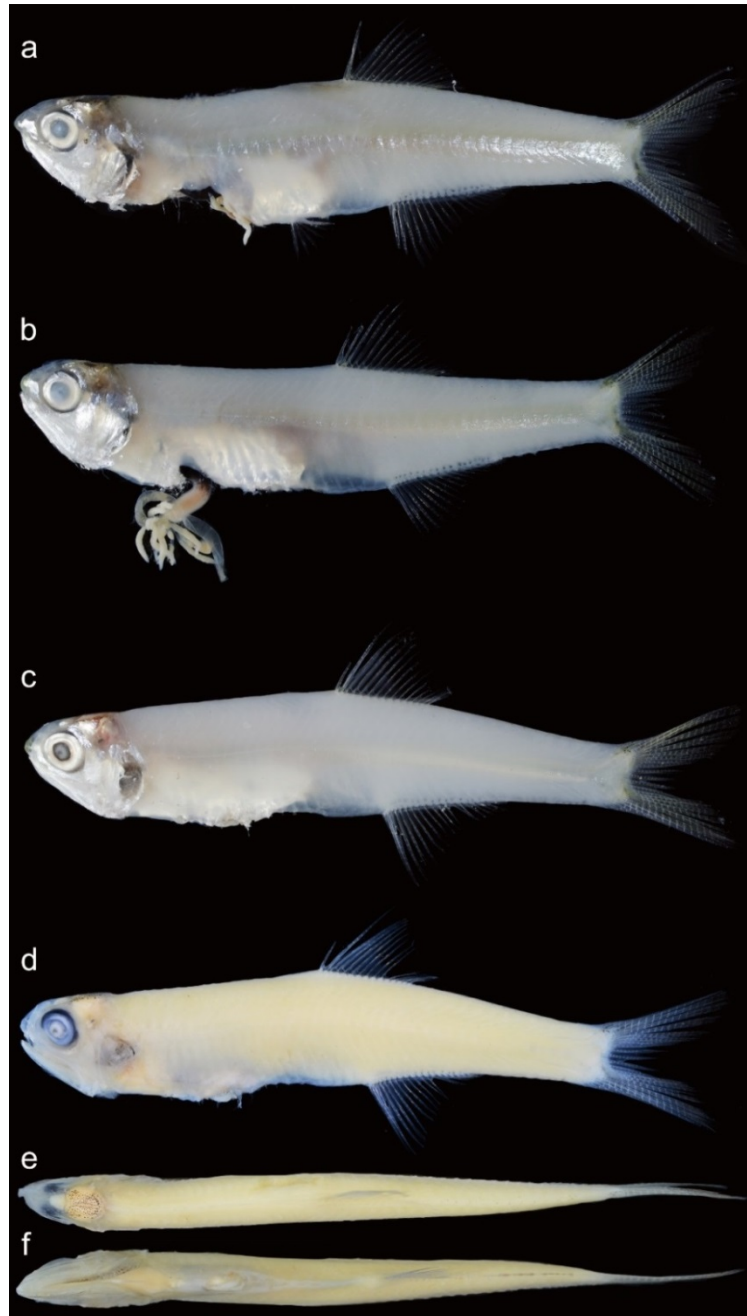


Figure 1. *Stolephorus acinaces* from Nha Trang, Southern Vietnam: Lateral views in fresh condition. **a:** KAUM-I. 117465, 53.9 mm standard length (SL), **b:** KAUM-I. 117474, 47.1 mm SL, **c:** KAUM-I. 117375, 40.5 mm SL; **d:** lateral, **e:** dorsal, and **f:** ventral views in preserved condition of KAUM-I. 117465

Table 1. Meristics of specimens of *Stolephorus acinaces*

	This study				Hata et al. (2020)		Modes
	Non-types (from Vietnam)				Holotype	Paratypes	
	UMMZ 240205	KAUM–I. 117375	KAUM–I. 117474	KAUM–I. 117465	CAS-SU 66945	n = 13	
Standard length (mm)	40.4	40.5	47.1	53.9	39.0	35.2–50.0	
Dorsal-fin rays (unbranched)	3	3	3	3	3	3	3
Dorsal-fin rays (branched)	13	13	14	14	13	12–14	13
Anal-fin rays (unbranched)	3	3	3	3	3	3	3
Anal-fin rays (branched)	17	17	18	17	16	16–18	16
Pectoral-fin rays (unbranched)	1	1	1	1	1	1	1
Pectoral-fin rays (branched)	10	11	11	11	11	10–11	11
Pelvic-fin rays (unbranched)	1	broken	broken	1	1	1	1
Pelvic-fin rays (branched)	6	broken	broken	6	6	6	6
Caudal-fin rays	19	19	19	19	19	19	19
Gill rakers on 1st gill arch (upper)	16	16	15	16	15	14–16	15
Gill rakers on 1st gill arch (lower)	22	23	22	24	22	21–23	22
Gill rakers on 1st gill arch (total)	38	39	37	40	37	36–38	37
Gill rakers on 2nd gill arch (upper)	10	10	10	12	10	9–11	10
Gill rakers on 2nd gill arch (lower)	20	22	21	21	19	18–20	19
Gill rakers on 2nd gill arch (total)	30	32	31	33	29	27–31	29
Gill rakers on 3rd gill arch (upper)	8	8	9	9	8	7–9	8
Gill rakers on 3rd gill arch (lower)	11	12	11	13	11	10–12	11
Gill rakers on 3rd gill arch (total)	19	20	20	22	19	17–20	19
Gill rakers on 4th gill arch (upper)	6	6	6	6	7	5–7	6
Gill rakers on 4th gill arch (lower)	10	9	9	10	8	8–10	9
Gill rakers on 4th gill arch (total)	16	15	15	16	15	14–17	15
Gill rakers on posterior face of 3rd gill arch	4	4	4	4	4	3–4	4

	This study				Hata et al. (2020)		
	Non-types (from Vietnam)				Holotype	Paratypes	
	UMMZ 240205	KAUM-I. 117375	KAUM-I. 117474	KAUM-I. 117465	CAS-SU 66945	n = 13	
Prepelvic scutes	5	broken	4	broken	3	3–7	6
Longitudinal scales of scale rows	36	37	36	36	36	35–38	36
Predorsal scales	19	18	19	18	19	18–19	19
Transverse scales	8	8	8	8	9	8–9	9
Pseudobranch filaments	17	17	15	17	17	14–18	17

Table 2. Morphometrics of specimens of *Stolephorus acinaces*

	This study				Hata et al. (2020)		
	Non-types (from Vietnam)				Holotype	Paratypes	
	UMMZ 240205	KAUM-I. 117375	KAUM-I. 117474	KAUM-I. 117465	CAS-SU 66945	n = 13	
Standard length (SL; mm)	40.4	40.5	47.1	53.9	39.0	35.2–50.0	Means
As % SL							
Head length (HL)	24.4	23.6	22.4	22.7	25.1	23.0–25.5	24.4
Body depth	broken	20.7	20.9	21.5	17.0	18.0–21.9	19.3
Pre-dorsal-fin length	53.4	54.9	52.3	53.5	52.8	51.8–55.8	53.5
Snout tip to pectoral-fin insertion	26.1	24.9	23.4	24.0	26.6	23.7–27.8	25.9
Snout tip to pelvic-fin insertion	44.2	broken	broken	45.4	43.2	41.2–45.3	43.1
Snout to anal-fin origin	61.8	63.5	63.9	62.1	63.0	58.8–64.1	62.3
Dorsal-fin base length	14.7	16.7	16.7	16.3	15.0	14.0–16.8	15.6
Anal-fin base length	19.2	19.1	18.6	19.5	18.6	16.9–20.0	18.8
Caudal-peduncle length	21.4	21.4	20.6	20.5	19.7	19.8–21.9	20.5
Caudal-peduncle depth	8.9	9.9	9.7	10.3	9.2	9.0–10.7	9.6
D–P1	36.8	37.3	37.7	38.2	32.3	32.0–37.7	35.1
D–P2	22.9	broken	broken	23.7	20.5	20.3–23.3	21.9

	This study				Hata et al. (2020)		
	Non-types (from Vietnam)				Holotype	Paratypes	
	UMMZ 240205	KAUM-I. 117375	KAUM-I. 117474	KAUM-I. 117465	CAS-SU 66945	n = 13	
D–A	19.7	22.2	22.0	21.6	19.1	19.4–22.8	20.7
P1–P2	19.9	broken	broken	22.3	18.2	15.7–22.6	18.6
P2–A	18.8	broken	broken	16.1	19.6	15.7–21.5	18.4
Pectoral-fin length	14.2	broken	broken	broken	14.4	14.3–15.2	14.5
Pelvic-fin length	7.5	broken	broken	7.0	7.2	6.7–7.6	7.1
Maxilla length	20.6	20.1	19.4	broken	19.3	19.1–21.5	20.1
Lower-jaw length	15.5	16.1	16.1	15.3	15.9	15.2–17.2	16.2
Supramaxilla end to maxilla end	6.1	5.2	5.6	broken	6.0	5.3–7.0	5.8
1st dorsal-fin ray length	1.5	1.6	1.6	1.2	1.2	0.7–1.6	1.2
2nd dorsal-fin ray length	7.1	broken	broken	5.8	broken	broken	6.5
3rd dorsal-fin ray length	16.0	17.0	broken	broken	broken	15.7–16.7	16.4
1st anal-fin ray length	1.4	1.7	1.2	1.3	1.5	0.9–1.9	1.3
2nd anal-fin ray length	3.1	5.8	broken	4.7	Broken	4.9–5.4	4.8
3rd anal-fin ray length	13.2	14.8	broken	broken	13.0	13.1–14.0	13.5
As % HL							
Orbit diameter	32.8	36.9	33.4	33.6	35.2	32.5–38.1	35.2
Eye diameter	26.4	30.7	29.4	27.7	27.8	24.9–29.8	27.6
Snout length	17.1	17.3	18.3	18.4	15.0	14.7–19.0	16.7
Maxilla length	84.3	85.3	86.6	broken	76.5	75.5–87.4	82.1
Interorbital width	21.6	23.5	22.6	21.9	19.6	20.6–24.2	21.9
Postorbital length of the head	50.3	48.4	50.6	51.7	49.8	46.8–51.5	49.4

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).

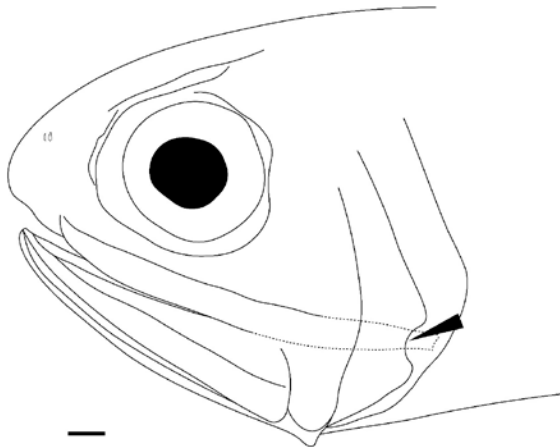


Figure 2. Head of *Stolephorus acinaces*, KAUM–I. 117465, 53.9 mm SL, Nha Trang, Vietnam.

Dots indicate posterior part of maxilla (posterior tip broken). Arrow indicates cavity of preopercle. Scale bar indicates 1 mm

Stolephorus acinaces Hata et al., (2020) [18]: 7, figs. 5, 6 (type locality: Sandakan, Sabah, Malaysia; paratype locality: Kuching, Sarawak, Malaysia); Hata and Motomura, 2022b: 9 (Sandakan, Sabah, Malaysia and Kuching, Sarawak, Malaysia); Hata and Motomura, 2024a; 16 (Sandakan, Sabah, Malaysia and Kuching, Sarawak, Malaysia).

Material examined. KAUM–I. 117375, 40.5 mm SL, off Nha Trang, Khánh Hòa Province, Vietnam (purchased at Dam Market); KAUM–I. 117465, 53.9 mm SL, KAUM–I. 117474, 47.1 mm SL, Nha Trang, Vietnam (purchased at Vĩnh Lương Fish Landing Port), coll. N. V. Quan et al.; UMMZ 240205, 40.4 mm SL, Cai Lon River (Mekong distributary), 3–4 km from river mouth in Rach Gia Bay, Kien Giang Province, Vietnam (9°51'N, 105°07'E), < 7 m depth.

Diagnosis (modified from Hata, Lavoué and Motomura, 2020). A species of *Stolephorus* with the following combination of characters: 1UGR 14–16 (modally 15), 1LGR 21–24 (22), 1TGR 36–40 (37); 2UGR 9–12 (10), 2LGR 18–22 (19), 2TGR 27–33 (29); 3UGR 7–9 (8), 3LGR 10–13 (11), 3TGR 17–22; 4UGR 5–7 (6), 4LGR 8–10 (9), 4TGR 14–17 (15); prepelvic scutes 3–7 (6); long maxilla, posterior tip slightly short of or just reaching posterior border of opercle; no predorsal scutes; pelvic scute without spine-like projection; posterior border of preopercle

indented; posterior tip of pelvic fin not reaching to vertical through dorsal-fin origin; distinct paired dark patches on parietal region; no dark lines on dorsum; no black spots below eye or on lower-jaw tip; caudal peduncle relatively long, its length 19.7–21.9% (mean 20.5%) of SL; pectoral fin rather long, its length 14.3–15.2% (14.5%) of SL; pelvic fin rather short, its length 6.7–7.6% (7.1%) of SL.

Description of Vietnamese specimens.

Counts and measurements, expressed as percentages of SL or HL, given in Tables 1 and 2. Body laterally compressed, elongate, 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 to body axis until anal-fin origin. Ventral profile thereafter elevated to caudal-fin base. Abdomen somewhat rounded, covered with several spine-like scutes (most scutes lost in all specimens). Pelvic scute without spine. Postpelvic and predorsal scutes absent. Anus just anterior to anal-fin origin. Snout tip rounded; 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, just reaching to posterior margin of opercle. Lower jaw slender. Single row of conical teeth on each jaw and palatines. Several distinct conical teeth on vomer. Teeth patch on pterygoid. No teeth on upper edge of hyoid. Single row of conical teeth on upper edges of basihyal and basibranchial. Eye large, round, covered with 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 indented (Fig. 2). 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 less than eye diameter. Gill rakers long, slender, rough, visible from side of head when mouth opened. Single row of asperities on anterior surface of gill

rakers. 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 distally, most of isthmus muscle exposed (not covered by gill membrane). Body scales deciduous, completely lost on specimens, 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 and closely spaced. First dorsal- and anal-fin rays minute. Anal-fin origin just below base of ninth or tenth 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, insertion anterior to vertical through dorsal-fin origin (pelvic fin lost in KAUM-I. 117375 and 117474). Posterior tip of depressed pelvic fin not reaching to vertical through dorsal-fin origin. Caudal fin forked, posterior tips pointed.

Coloration of fresh specimens. Body milky-white, a silver longitudinal band (width slightly narrower than pupil diameter) running along middle of body. Cheek and opercle silver. Maxilla transparent. Snout tip yellow. No black spot on lateral surface of head. Black blotch on nape. Scale pockets on dorsum margined with black. Melanophores scattered along anal-fin base and lower margin of caudal peduncle. Pectoral and pelvic fins translucent, whitish. Fin rays of dorsal and anal fins orangish-white. Melanophores scattered on anterior lower part of dorsal fin. Caudal fin orangish, posterior margin of both lobes and fin base black. Peritoneum silver. Iris silver, pupil black (this is the first report of fresh coloration of *S. acinaces*).

Coloration of preserved specimens. Body uniformly pale. No black spot on lateral surface of head. A pair of dark patches on parietal region and a few pigment spots on occipital area. Melanophores scattered on dorsum posterior to dorsal fin. Small uniserial black spots on ventral

surface from anal-fin origin to caudal-fin base. All fins transparent. Melanophores scattered on anterior lower part of dorsal fin. Melanophores scattered on entire caudal fin, except centrally and along lower margin, forming a dense dark spot centrally on base of lower lobe.

Distribution. *Stolephorus acinaces*, formerly known only from the northern coast of Borneo, Malaysia (Hata et al., 2020b; this study), is newly recorded from southern Vietnam (Fig. 3).

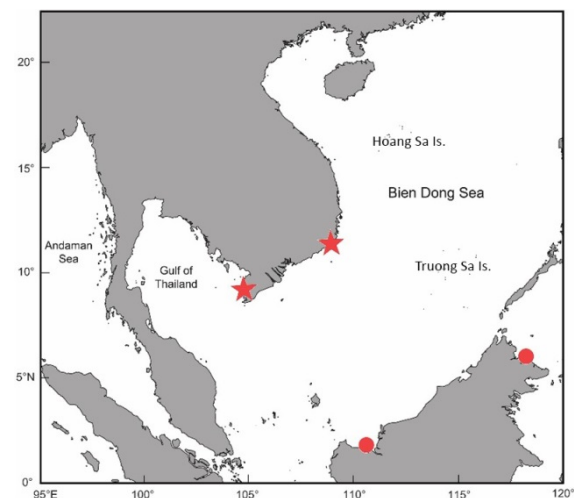


Figure 3. Distributional records of *Stolephorus acinaces*. Stars and circles represent localities of specimens examined in this study, and previous records, respectively

IDENTIFICATION

The Vietnamese specimens were assigned to the genus *Stolephorus*, defined by Whitehead et al., (1988) [1] and Wongratana et al., (1999) [2] as having a long isthmus muscle reaching anteriorly to the posterior margin of the gill membrane, hidden urohyal and prepelvic scutes, and the postpelvic scutes absent. Moreover, the specimens closely matched the diagnostic features of *S. acinaces* given by Hata et al., (2020) [17] and Hata and Motomura (2022, 2024) [9, 13]: long maxilla with posterior tip slightly short of or just reaching posterior border of opercle; indented preopercular margin; no predorsal scute; pelvic scute without spine; dorsum without dark lines; no melanophores

scattered on suborbital area or lower-jaw tip; depressed pelvic fin not reaching to vertical through dorsal-fin origin; no teeth on dorsal surface of hyoid arch. Other meristic and morphometric characters, including counts of predorsal scales and longitudinal series of scale rows, of the Vietnamese specimens generally matched those of *S. acinaces* given by Hata et al., (2020) [18], except for slight differences in gill raker numbers on the first to third gill arch, and distance from the snout tip to pelvic-fin insertion, D–P1, D–P2, postorbital length, and pectoral fin (Tables 1, 2). Hata et al., (2020) [18] and Hata and Motomura (2022, 2024) [10, 13] indicated the morphological differences between *S. acinaces* and *Stolephorus andhraensis* Babu Rao, 1966 [higher gill raker numbers, longer caudal peduncle and pectoral fin, and shorter pelvic fin] and *Stolephorus lotus* Hata and Motomura, 2022 [lower numbers of longitudinal series scale rows and predorsal scales; higher number of dorsal-fin rays; longer head to predorsal-fin length and maxilla, and deeper body]. The present study confirmed these characters as diagnostic for *S. acinaces* from the other two species.

Sequencing of the COI gene subsequently confirmed the identification of the two specimens of *S. acinaces* from Vietnam, their sequences differing from those of *S. acinaces* from Malaysia [18] by only one to five nucleotides, corresponding to uncorrected pairwise genetic distances between 0.15% and 0.77%. Such values were well below the threshold of 2% marking the limit between intra- and inter-specific differentiation [37]. The two COI sequences of *S. acinaces* from Vietnam differed to each other by a single nucleotide (0.15%).

REMARKS

Distributional records of *S. acinaces*

Stolephorus acinaces was originally described by Hata et al. (2020) [18] from 14 specimens collected from Sandakan (Sabah State) and Kuching (Sarawak State), northern coast of Borneo. To these was added a further

(non-type) specimen from Sandakan, in a comparison of the species with *Stolephorus brevis* Hata and Motomura, 2024 [13]. Because no additional specimens of *S. acinaces* have been reported, the present specimens represent the first records of *S. acinaces* from Vietnam, the Nha Trang specimens being the northernmost records, and suggestive of a wide distribution in the southern Bien Dong Sea (Fig. 3).

Species of the genus *Stolephorus* in Vietnamese waters

Based on recent taxonomic studies, at least 10 species [e.g., *S. acinaces*, *Stolephorus baganensis* Delsman, 1931, *Stolephorus balinensis* (Bleeker, 1849), *Stolephorus baweanensis* Hardenberg, 1933, *Stolephorus continentalis* Hata and Motomura, 2018, *Stolephorus dubiosus* Wongratana, 1983, *Stolephorus eldorado* Hata, Lavoué and Motomura, 2022, *Stolephorus mercurius* Hata, Lavoué and Motomura, 2021, *Stolephorus oceanicus* Hardenberg, 1933, and *Stolephorus tri* (Bleeker, 1852)] have been recorded from Vietnamese waters and confirmed by voucher specimens [4, 16, 19–21, 39–41, this study]. Although *Stolephorus indicus* (van Hasselt, 1823) has also been recorded from Vietnam by many authors (e.g., Orsi (1974) [42]; Rainboth et al., (2012) [39]; Nagao Natural Environment Foundation (2021) [41]), specimens referred to “*S. indicus*” in the Northwestern Pacific including Vietnam, are currently included in a separate species, *S. balinensis* [19]. Similarly, specimens previously treated as *Stolephorus commersonnii* Lacepède, 1803, *Stolephorus insularis* Hardenberg, 1933, and *Stolephorus waitei* Jordan and Seale, 1926 in Vietnam (e.g., Orsi (1974) [42]; Rainboth et al., (2012) [39]; Hata (2018) [26, 43]) are now included in *S. mercurius*, *S. eldorado*, and *S. baweanensis*, respectively [16, 19, 20]. Moreover, specimens previously treated as *Stolephorus chinensis* (Günther, 1880) have been shown to include at least three species, true *S. chinensis*, *Stolephorus continentalis* Hata and Motomura, 2018, and *Stolephorus oceanicus* Hardenberg, 1933. Among them, *S. continentalis* and *S. oceanicus* have been recorded from northern and southern parts of Vietnam,

respectively [4, 16]. Although Rainboth et al., (2012) [39] reported *S. andhraensis* from the Mekong estuary based on a specimen deposited in the University Michigan, no specimen identified as *S. andhraensis* was observed in the

collection during this study. Furthermore, that species has at no time been recorded from Vietnamese waters, Rainboth et al., (2012)'s [39] records of *S. andhraensis* are thought to be a misidentification of *S. acinaces*.

Key to species of *Stolephorus* recorded from Vietnam

- 1a. Predorsal scute present.....2
- 1b. Predorsal scute absent.....5
- 2a. Pelvic scute without spine; body scales deciduous.....*S. eldorado*^a
- 2b. Pelvic scute with backwardly-directed spine; body scales not deciduous.....3
- 3a. Gill rakers numerous, 1TGR \geq 46; 2TGR \geq 41; 3TGR \geq 27; 4TGR \geq 20.....*S. dubiosus*^b
- 3b. Gill rakers less numerous, 1TGR < 44; 2TGR < 38; 3TGR < 25; 4TGR < 22.....4
- 4a. Pelvic fin short, not reaching to vertical through dorsal-fin origin when depressed; paired dark lines usually present on dorsum both before and after dorsal fin; 1LGR 18–22; few separations of grooves on body scales.....*S. tri*^c
- 4b. Pelvic fin long, posteriorly beyond vertical through dorsal-fin origin when depressed; paired dark lines only present on dorsum posterior to dorsal fin; 1LGR 20–25; numerous separations of grooves on body scales.....*S. baganensis*^b
- 5a. Paired dark lines on dorsum present; depressed pelvic fin posteriorly reaching to vertical through dorsal-fin origin.....*S. mercurius*^d
- 5b. No dark lines on dorsum; depressed pelvic fin not reaching to vertical through dorsal-fin origin.....6
- 6a. Maxilla short, posteriorly just reaching or extending slightly beyond anterior margin of preopercle.....*S. balinensis*^d
- 6b. Maxilla rather long, posteriorly just reaching or extending beyond posterior margin of preopercle.....7
- 7a. Melanophores scattered at least on tips of snout and lower jaw (also on suborbital in adults); 1LGR 19–22; maximum SL reaching 9 cm.....*S. baweanensis*^c
- 7b. No melanophores scattered on lateral surface of head; 1LGR > 24 (21–24 in *S. acinaces*; 19–21 in *S. andhraensis*); max. SL < 7 cm (8.2 cm in *S. continentalis*).....8
- 8a. Posterior margin of preopercle indented; 1TGR \leq 40.....*S. acinaces*^e
- 8b. Posterior margin of preopercle rounded, not indented; 1TGR > 41.....9
- 9a. Transverse scales 8; vertebrae 38–40 (modally 39).....*S. oceanicus* (distributed south of Da Nang)^c
- 9b. Transverse scales 10; vertebrae 40–42 (modally 41).....*S. continentalis* (distributed north of Ha Long Bay)^c

Data based on: a: [20]; b: [21]; c: [16]; d: [19]; e: this study.

Comparative material examined

Stolephorus baganensis: USNM 316674, 2 specimens, 62.2–66.9 mm SL, Vung Tau, Ba Ria - Vung Tau Province, Vietnam (obtained at fish market in Vung Tau). *Stolephorus tri*: UMMZ 225767, 73.9 mm SL, approx. 27 km southeast of estuary of Hau River (Mekong Basin), Vietnam (9°14'42.0"N, 106°17'36.0"E).

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REFERENCES

- [1] P. J. Whitehead, G. J. Nelson, and T. Wongratana, *FAO species catalogue. Vol. 7. Clupeoid fishes of the world (Suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies, and wolf-herrings. Part 2. Engraulidae*, 1988.
- [2] T. Wongratana, "Engraulidae," in *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific*, vol. 3, pp. 1697–1743, 1999.
- [3] S. Kimura, K. Hori, and K. Shibukawa, "A new anchovy, *Stolephorus teguhi* (Clupeiformes: Engraulidae), from North Sulawesi, Indonesia," *Ichthyological Research*, vol. 56, no. 3, pp. 292–295, 2009. DOI: 10.1007/s10228-009-0103-4.
- [4] H. Hata and H. Motomura, "*Stolephorus continentalis*, a new anchovy from the northwestern South China Sea, and redescription of *Stolephorus chinensis* (Günther 1880) (Clupeiformes: Engraulidae)," *Ichthyological Research*, vol. 65, no. 3, pp. 374–382, 2018. DOI: 10.1007/s10228-018-0621-z.
- [5] H. Hata and H. Motomura, "*Stolephorus insignis*, a new anchovy from the western Pacific, and redescription of *Stolephorus apiensis* (Jordan and Seale 1906) (Clupeiformes: Engraulidae)," *Ichthyological Research*, vol. 66, no. 2, pp. 280–288, 2019. DOI: 10.1007/s10228-018-00675-5.
- [6] Hata, H., & Motomura, H. (2021). Two new species of *Stolephorus* (Teleostei: Clupeiformes: Engraulidae) from the western Pacific. *Raffles Bulletin of Zoology*, 69, 109–117. DOI: 10.26107/RBZ-2021-0009
- [7] H. Hata and H. Motomura, "*Stolephorus grandis*, a new anchovy (Teleostei: Clupeiformes: Engraulidae) from New Guinea and Australia," *Zootaxa*, vol. 5004, no. 3, pp. 481–489, 2021. DOI: 10.11646/zootaxa.5004.3.5.
- [8] H. Hata and H. Motomura, "A new species of the anchovy genus *Stolephorus* Lacepède 1803 from North Sumatra, Indonesia, and redescription of *Stolephorus pacificus* Baldwin 1984 and *Stolephorus teguhi* Kimura, Hori and Shibukawa 2009 (Teleostei: Clupeiformes: Engraulidae)," *Zoological Studies*, vol. 60, e65, 2021. DOI: 10.6620/ZS.2021.60-65.
- [9] H. Hata and H. Motomura, "Redescription of *Stolephorus ronquilloi* Wongratana, 1983 and description of *Stolephorus hindustanensis*, a new anchovy from the Western Coast of India (Teleostei: Clupeiformes: Engraulidae)," *Taxonomy*, vol. 2, no. 1, pp. 124–135, 2022. DOI: 10.3390/taxonomy2010010.
- [10] H. Hata and H. Motomura, "*Stolephorus lotus*, a new anchovy (Teleostei: Clupeiformes: Engraulidae) from the Northern Territory, Australia," *Zoological Studies*, vol. 61, e87, 2022. DOI: 10.6620/ZS.2022.61-87.
- [11] H. Hata and H. Motomura, "Description of *Stolephorus horizon* n. sp. from Fiji and Tonga, and redescription of *Stolephorus scitulus* (Fowler, 1911) (Teleostei: Clupeiformes: Engraulidae)," *Taxonomy*, vol. 3, no. 3, pp. 356–380, 2023. DOI: 10.3390/taxonomy3030021.
- [12] H. Hata and H. Motomura, "Redescription and extended distribution of a poorly known Australian anchovy, *Stolephorus advenus* (Actinopterygii: Clupeiformes: Engraulidae)," *Acta Ichthyologica et Piscatoria*, vol. 53, pp. 209–216, 2023. DOI: 10.3897/aiep.53.109943.
- [13] H. Hata and H. Motomura, "A new species of the anchovy genus *Stolephorus* Lacepède

- 1803, and redescrptions of *Stolephorus carpentariae* (De Vis 1882) and *Stolephorus holodon* (Boulenger 1900) (Clupeiformes: Engraulidae),” *Ichthyological Research*, vol. 72, no. 1, pp. 98–116, 2025. DOI: 10.1007/s10228-024-00971-3.
- [14] H. Hata and H. Motomura, “A new species of anchovy, *Stolephorus astrum* (Teleostei: Clupeiformes: Engraulidae), from Palau, Micronesia,” *Raffles Bulletin of Zoology*, vol. 72, pp. 150–161, 2024. DOI: 10.26107/RBZ-2024-0013.
- [15] H. Hata and H. Motomura, “Redescription and distributional range extension of the poorly known anchovy *Stolephorus brachycephalus* (Teleostei: Clupeiformes: Engraulidae),” *Natural History Bulletin of the Siam Society*, vol. 66, no. 1, pp. 3–17, 2024.
- [16] H. Hata, S. Lavoué, and H. Motomura, “Taxonomic status of seven nominal species of the anchovy genus *Stolephorus* described by Delsman (1931), Hardenberg (1933), and Dutt and Babu Rao (1959), with redescrptions of *Stolephorus tri* (Bleeker 1852) and *Stolephorus waitei* Jordan and Seale 1926 (Clupeiformes: Engraulidae),” *Ichthyological Research*, vol. 67, no. 1, pp. 7–38, 2020. DOI: 10.1007/s10228-019-00697-7.
- [17] H. Hata, S. Lavoué, and H. Motomura, “*Stolephorus babarani*, a new species of anchovy (Teleostei: Clupeiformes: Engraulidae) from Panay Island, central Philippines,” *Zootaxa*, vol. 4718, no. 4, p. zootaxa-4718, 2020. DOI: 10.11646/zootaxa.4718.4.5.
- [18] H. Hata, S. Lavoué, and H. Motomura, “*Stolephorus acinaces*, a new anchovy from northern Borneo, and redescription of *Stolephorus andhraensis* Babu Rao, 1966 (Clupeiformes: Engraulidae),” *Marine Biodiversity*, vol. 50, no. 6, 102, 2020. DOI: 10.1007/s12526-020-01115-2.
- [19] H. Hata, S. Lavoué, and H. Motomura, “Taxonomic status of nominal species of the anchovy genus *Stolephorus* previously regarded as synonyms of *Stolephorus commersonnii* Lacepède 1803 and *Stolephorus indicus* (van Hasselt 1823), and descriptions of three new species (Clupeiformes: Engraulidae),” *Ichthyological Research*, vol. 68, no. 3, pp. 327–372, 2021. DOI: 10.1007/s10228-020-00792-0.
- [20] H. Hata, S. Lavoué, and H. Motomura, “Description of three new species previously identified as *Stolephorus bengalensis* (Dutt & Babu Rao, 1959) or *Stolephorus insularis* Hardenberg, 1933 and a re-description of *S. bengalensis* (Chordata, Osteichthyes, Clupeiformes, Engraulidae),” *ZooKeys*, vol. 1121, 145, 2022. DOI: 10.3897/zookeys.1121.84171.
- [21] H. Hata, S. Lavoué, and H. Motomura, “A new species of the Bengal Spined Anchovy *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),” *Zoological Studies*, vol. 61, e58, 2022. DOI: 10.6620/ZS.2022.61-58.
- [22] H. Hata, S. Lavoué, S. V. Bogorodsky, T. J. Alpermann, and H. Motomura, “A new *Stolephorus* (Teleostei: Clupeiformes: Engraulidae: Engraulinae) from the Red Sea,” *Ichthyology & Herpetology*, vol. 111, no. 2, pp. 191–203, 2023. DOI: 10.1643/i2022064.
- [23] S. S. Gangan, A. Pavan-Kumar, S. Jahageerdar, and A. K. Jaiswar, “A new species of *Stolephorus* (Clupeiformes: Engraulidae) from the Bay of Bengal, India,” *Zootaxa*, vol. 4743, no. 4, zootaxa-4743, 2020. DOI: 10.11646/zootaxa.4743.4.6.
- [24] SEAFDEC, *The Southeast Asian State of Fisheries and Aquaculture 2012*, Bangkok: Southeast Asian Fisheries Development Center, 2012, 130 pp.
- [25] N. T. T. Anh, N. T. K. Anh, and P. T. T. Thuy, “Enhancing stakeholders’ role in the value chain for sustainable fisheries development: A case of anchovy fisheries in Vietnam,” *Fish for the People*, vol. 10, no. 2, pp. 33–41, 2012.
- [26] H. Hata, “*Stolephorus insularis* Hardenberg, 1933,” in S. Kimura, H. Imamura, V. Q. Nguyen, and T. D. Pham, Eds., *Fishes of Ha Long Bay, the natural world heritage site in northern Vietnam*, Mie University, Fisheries Research Laboratory, 2018, pp. 41.

- [27] S. Kimura, T. Sado, Y. Iwatsuki, and T. Yoshino, "Record of an engraulid fish, *Stolephorus commersonnii* from Ishigaki I., southern Japan," *Japanese Journal of Ichthyology*, vol. 46, no. 1, pp. 45–50, 1999. DOI: 10.11369/jji1950.46.45.
- [28] H. Hata and H. Motomura, "First record of the anchovy, *Stolephorus teguhi* (Engraulidae) from the Philippines," *Philippine Journal of Systematic Biology*, vol. 11, pp. 20–24, 2018.
- [29] H. Hata and H. Motomura, "Additional specimens of the poorly known anchovy *Stolephorus multibranchus* (Clupeiformes: Engraulidae) from Kosrae, Caroline Islands," *Biogeography*, vol. 20, pp. 78–84, 2018. DOI: 10.11358/bioge0.20.78.
- [30] H. Hata and H. Motomura, "Redescription and distributional range extension of a poorly known anchovy *Stolephorus nelsoni* (Actinopterygii: Clupeiformes: Engraulidae)," *Acta Ichthyologica et Piscatoria*, vol. 48, pp. 381–386, 2018.
- [31] H. Hata and H. Motomura, "First Northern Hemisphere records of the Samoan Anchovy, *Stolephorus apiensis* (Actinopterygii: Clupeiformes: Engraulidae)," *Acta Ichthyologica et Piscatoria*, vol. 50, pp. 367–372, 2020. DOI: 10.3750/AIEP/03015.
- [32] H. Hata and H. Motomura, "Material evidence of *Stolephorus mercurius* (Teleostei: Clupeiformes: Engraulidae) from Sri Lanka, with a key to Sri Lankan species of *Stolephorus*," *Biogeography*, vol. 26, pp. 25–28, 2024.
- [33] R. Gouda, S. Patra, S. Patro, S. S. Mishra, and A. Mohapatra, "First record of *Stolephorus mercurius* Hata et al. 2021 (Clupeiformes: Engraulidae) from Indian Ocean with a note and key to identification of Indian Ocean species of the genus *Stolephorus* Lacepède 1803," *Thalassas: An International Journal of Marine Sciences*, vol. 39, no. 1, pp. 443–448, 2023. DOI: 10.1007/s41208-023-00519-8.
- [34] H. Hata, K. Wibowo, S. Lavoué, J. J. Pogonoski, S. A. Appleyard, and H. Motomura, "Enhanced data on *Stolephorus grandis* and *Stolephorus waitei* (Teleostei: Clupeiformes: Engraulidae), two species endemic to the Sahul Shelf, western Pacific Ocean," *Zootaxa*, vol. 5538, no. 1, pp. 1–22, 2024. DOI: 10.11646/zootaxa.5538.1.1.
- [35] H. Hata and H. Motomura, "A new species of anchovy, *Encrasicholina auster* (Clupeiformes: Engraulidae) from Fiji, southwestern Pacific Ocean," *New Zealand Journal of Zoology*, vol. 44, no. 2, pp. 122–128, 2017. DOI: 10.1080/03014223.2016.1268177.
- [36] M. H. Sabaj, "Codes for natural history collections in ichthyology and herpetology," *Ichthyology & Herpetology*, vol. 108, no. 3, pp. 593–669, 2020. DOI: 10.1643/ASIHCONDONS2020.
- [37] R. D. Ward, T. S. Zemlak, B. H. Innes, P. R. Last, and P. D. Hebert, "DNA barcoding Australia's fish species," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 360, no. 1462, pp. 1847–1857, 2005. DOI: 10.1098/rstb.2005.1716.
- [38] K. Tamura, G. Stecher, and S. Kumar, "MEGA11: molecular evolutionary genetics analysis version 11," *Molecular Biology and Evolution*, vol. 38, no. 7, pp. 3022–3027, 2021. DOI: 10.1093/molbev/msab120.
- [39] W. J. Rainboth, C. Vidthayanon, and M. D. Yen, *Fishes of the Greater Mekong Ecosystem with Species List and Photographic Atlas*, Miscellaneous Publications Museum of Zoology, University of Michigan, no. 201, 2012, pp. i–xvi, 1–173, pls. 1–121.
- [40] D. D. Tran, K. Shibukawa, P. T. Nguyen, H. P. Ha, L. X. Tran, H. V. Mai, and K. Utsugi, *Fishes of Mekong Delta, Vietnam*, Can Tho University Publishing House, 2013.
- [41] Nagao Natural Environment Foundation, *Fishes of the Indochinese Mekong*, Nagao Natural Environment Foundation, 2021.
- [42] J. J. Orsi, "A check list of the marine and freshwater fishes of Vietnam," *Publications of the Seto Marine Biological Laboratory*, vol. 21, no. 3–4, pp. 153–177, 1974. DOI: 10.5134/175867.
- [43] H. Hata, "Stolephorus waitei Jordan and Seale, 1926," in S. Kimura, H. Imamura, V. Q. Nguyen, and T. D. Pham, Eds., *Fishes of Ha Long Bay, the natural world heritage site in northern Vietnam*, Mie University, Fisheries Research Laboratory, 2018, pp. 42.