Zoological Studies **61**:58 (2022)
doi:10.6620/ZS.2022.61-58

Zoological Studies

Open Access

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)

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Received 19 January 2022 / Accepted 25 July 2022 / Published 25 November 2022
Communicated by Hin-Kiu Mok

The Bengal Spined Anchovy, *Stolephorus taurus* sp. nov. is described from 21 specimens from the northern Bay of Bengal. The new species closely resembles *Stolephorus dubiosus* Wongratana, 1983, which is redescribed. Both species have a predorsal scute, spine on the pelvic scute, long maxilla posteriorly slightly short of or just reaching the posterior margin of the opercle, 25 or more gill rakers on the lower limb of the first gill arch, and double black lines on the dorsum posterior to the dorsal fin. However, the new species differs from *S. dubiosus* in having a longer pelvic fin with the posterior tip of the depressed fin beyond vertical through the dorsal-fin origin (vs. usually not reaching to vertical through dorsal-fin origin), longer pectoral fin, second dorsal- and third dorsal-fin rays, second anal- and third anal-fin rays, and greater interorbital width. *Stolephorus taurus* sp. nov. is closely related to *Stolephorus baganensis* Delsman, 1931 and *S. dubiosus*, although at least 2% mean *p*-distance divergence in the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene separates each of the three species. A phylogenetic reconstruction of the evolution of the number of prepelvic scutes within *Stolephorus* indicated that having six scutes was the most likely ancestral condition in the genus, and was later reduced in the evolution of *Stolephorus* to five or four scutes. One such reduction occurred recently in the lineage of *Stolephorus taurus* sp. nov.

Key words: Clupeomorpha, Taxonomy, Bay of Bengal, *Stolephorus baganensis*, *Stolephorus tri*.

BACKGROUND

Stolephorus Lacepède, 1803, comprising 41 valid marine and/or brackish water Indo-Pacific species, is included in the subfamily Engraulinae (family Engraulidae) (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–e 2021a–c 2022; Hata et al. 2019 2020a b 2021 2022; Gangan et al. 2020). Among them, *Stolephorus dubiosus* Wongratana, 1983, distributed in the Indo-West Pacific from the Bay of Bengal to Borneo (Wongratana 1983; Whitehead et al. 1988; Wongratana et al. 1999), is

Citation: Hata H, Lavoué S, Motomura H. 2022. 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). Zool Stud **61**:58. doi:10.6620/ZS.2022.61-58.

diagnosed by the presence of spines on the pelvic and predorsal scutes (the latter just anterior to the dorsal-fin origin), 25 or more gill rakers on the lower limb of the first gill arch, and a long maxilla with the posterior tip just reaching the posterior margin of the opercle. During a revisionary study of this genus, a species previously identified as *S. dubiosus* from the Indian and Pacific oceans was found to comprise two distinct species, clearly separated morphologically and genetically. The Indian Ocean species, described herein as new, had longer fins than true *S. dubiosus* (endemic to the western Pacific Ocean and redescribed herein). In addition, two mitochondrial nucleotide markers, the complete cytochrome *b* gene and partial cytochrome *c* oxidase subunit I (*COI*) gene, were used to evaluate the genetic distinctiveness of the new species compared with 21 other species of *Stolephorus* (including two morphologically similar species, *S. dubiosus* and *Stolephorus baganensis* Delsman, 1931). The phylogenetic tree of *Stolephorus* was used to reconstruct the evolution of prepelvic scute numbers within the genus.

MATERIALS AND METHODS

Counts and proportional measurements followed Hata and Motomura (2017). All measurements were made with digital calipers to the nearest 0.01 mm. Standard and head lengths are abbreviated as SL and HL, respectively. Osteological characters, including vertebral counts, were observed on radiographs of 8 specimens of *S. baganensis*, 13 *S. dubiosus* and 14 *Stolephorus taurus* sp. nov. "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. Institutional codes generally followed Sabaj (2020). USMFC indicates Universiti Sains Malaysia Fish Collection, School of Biological Sciences, Penang, Malaysia. The ethical guidelines for experimental use of animals, is not applicable for this study.

A phylogenetic tree of the genus *Stolephorus* based on two molecular markers (the complete [1140 base pairs (bp)] cytochrome *b* gene and partial [about 650 bp] *COI* gene) both being newly sequenced for two specimens each of *S. baganensis* and *Stolephorus teguhi* Kimura, Hori and Shibukawa 2009, and one specimen of *S. dubiosus* (Table 1), following Hata et al. (2019). The cytochrome *b* gene was amplified using the following primers: forward L14740 (5'-CCG TTG TAT TCA ACT ACA GAA-3') and reverse H15913 (5'-TCG ATC TCC GGA TTA CAA GAC CG-3') (all primer references in Hata et al. 2019). The partial *COI* gene was amplified using the following primers: forward COI_FishF1 (5'-TCA ACC AAC CAC AAA GAC ATT GGC AC-3') and reverse COI_FishR2 (5'-ACT TCA GGG TGA CCG AAG AAT CAG AA-3'). The sequences subsequently generated were deposited into the GenBank database (accession numbers given in Table 1).

Data from the five newly-sequenced specimens were combined with the data set of 27 specimens of *Stolephorus* previously examined by Hata et al. (2019 2020a b 2021), plus data from six specimens available in GenBank and examined by Lavoué et al. (2010), Egan et al. (2018), and Gangan et al. (2020). Cytochrome *b* and *COI* sequences were separately aligned by eye, with no indels required. The final alignment combining the two genes comprised 1788 nucleotide positions (38 specimens of *Stolephorus*) (Table 1). Two specimens of the genus *Encrasicholina* Fowler, 1938 were collectively used to root the phylogenetic tree. Uncorrected pairwise genetic distances (*i.e.*, *p*-distances) were calculated for each gene using Mega v10.1.7 (Stecher et al. 2020).

An ultrametric phylogenetic tree was inferred using a Bayesian method under a relaxed molecular clock in BEAST v.2.6.5 (Bouckaert et al. 2019). The BEAST input file was built in BEAUti v.2.6.5, and the GTR + G model of sequence evolution selected. The respective monophyly of the ingroup and outgroup (*i.e.*, the two species of *Encrasicholina*) was *a priori* enforced to root the tree. The relative age of the tree root was calibrated to "1". Two independent runs of 10 million generations each were performed using BEAST v.2.6.5. Estimations of trees and divergence times were sampled once every 1000 generations and the parameters of each run checked for convergence with Tracer v.1.7.2 software (available at https://github.com/beast-dev/tracer/releases). After removing the burn-in portion of each run (25%), the remaining tree samples from the two runs were pooled into a combined file using LogCombiner v.2.6.5, and the maximum clade credibility tree with posterior probabilities at nodes, calculated from the file using TreeAnnotator v.2.6.5.

The evolutionary history of the number of prepelvic scutes was reconstructed onto the ultrametric phylogenetic tree assuming a model of character evolution in which transitions between each state occur at the same rate (model "Mk1"). Character state reconstructions were performed using Mesquite v3.61 (Maddison and Maddison 2019). A discrete category (corresponding to the number of prepelvic scutes 4, 5 or 6) was assigned to each species, with the exception of *Stolephorus tamilensis* Gangan, Pavan-

Kumar, Jahageerdar, and Jaiswar, 2020 (prepelvic scute numbers variable, 5 or 6). Although the latter species was successively categorized, its categorization did not modify the reconstruction hypothesis regarding the ancestral state in *Stolephorus* (see DISCUSSION).

RESULTS

Stolephorus dubiosus Wongratana, 1983

(English name: Thai Anchovy)
(Figs. 1–6; Tables 2, 3)

Table 1. Information on the genetic markers used in the present study. "/" indicates corresponding sequence undetermined; bold accession numbers indicate sequences determined in present study; Cytb cytochrome *b*, *COI* cytochrome *c* oxidase subunit I

	Museum registration #		Accession numbers	
Species	[DNA tissue code]	Origin	Cytb	*COI*
Stolephorus acinaces	No voucher [SI17]	Fish market, Sibu, Malaysia	MH380743[3]	MH380655[3]
	No voucher [SI18]	Fish market, Sibu, Malaysia	MH380397[3]	MH380518[3]
Stolephorus andhraensis	NTUM 12328 [Bg14]	Fish market, Bangkok, Thailand	MH380656[1]	MH380744[1]
	NTUM 12328 [Bg18]	Fish market, Bangkok, Thailand	MH380657[1]	MH380745[1]
Stolephorus babarani	KAUM–I. 62918	off Iloilo, Panay Island, Philippines	MH380365[2]	MH380486[2]
	KAUM–I. 62920	off Iloilo, Panay Island, Philippines	MH380366[2]	MH380487[2]
Stolephorus baganensis	USMFC (82) 00032 [IK100]	Sungai Batu, Penang Isl., Malaysia	**MT080913**	**MT080441**
	USMFC (82) 00035 [IK104]	Sungai Batu, Penang Isl., Malaysia	**MT080916**	**MT080444**
Stolephorus balinensis	KAUM–I. 106302	Ho Chí Minh, Vietnam	MH380435[1]	MH380556[1]
	KAUM–I. 106303	Ho Chí Minh, Vietnam	MH380436[1]	MH380557[1]
Stolephorus bataviensis	KAUM–I. 110294	off Dong-gang, Pingtung, Taiwan	MH380335[1]	MH380456[1]
	KAUM–I. 110295	off Dong-gang, Pingtung, Taiwan	MH380336[1]	MH380457[1]
Stolephorus baweanensis	KAUM–I. 94725	Ha Long Bay, northern Vietnam	MH380355[1]	MH380476[1]
	KAUM–I. 94779	Ha Long Bay, northern Vietnam	MH380356[1]	MH380477[1]
Stolephorus belaerius	ADC10_55.3 #4	Mhlathuze estuary, South Africa	/	HQ945937[7]
Stolephorus eldorado	KAUM–I. 113149	Donggang, Taiwan	MH380330[1]	/
	KAUM–I. 94509	Ha Long Bay, northern Vietnam	MH380318[1]	/
Stolephorus brachycephalus	JFBM 48023	Australia	MG958178[5]	/
Stolephorus continentalis	KAUM–I. 94540	Ha Long Bay, northern Vietnam	MH380306[1]	MH380450[1]
	KAUM–I. 94541	Ha Long Bay, northern Vietnam	MH380307[1]	MH380451[1]
Stolephorus dubiosus	NTUM 12329	Ganh Rai Bay, southern Vietnam	**MH380393**	**MH380514**
	No voucher [KU06]	Kuching, Malaysia	MH380633[1]	MH380723[1]
Stolephorus holodon	ADC55.2-3	Mlalazi Estuary, South Africa	/	JF4945987
Stolephorus indicus	KAUM–I. 59676	off Phuket, Thailand	MH380398[4]	MH380519[4]
	KAUM–I. 59677	off Phuket, Thailand	MH380399[4]	MH380520[4]
Stolephorus mercurius	KAUM–I. 60731	off Nha Trang, Khánh Hòa, Vietnam	MH380374[1]	MH380495[1]
	KAUM–I. 60732	off Nha Trang, Khánh Hòa, Vietnam	MH380375[1]	MH380496[1]
Stolephorus nelsoni	JFBM 48063	Australia	MG958177[5]	/
Stolephorus oceanicus	KAUM–I. 106329	Ho Chí Minh, Vietnam	MH380659[1]	/
	KAUM–I. 106330	Ho Chí Minh, Vietnam	MH380315[1]	/
Stolephorus rex	KAUM–I. 80769	off Oton, Panay Island, the Philippines	MH380384[4]	MH380505[4]
Stolephorus tamilensis	No voucher [CIFEFGB-SNS-0086]	Thoothukudi, Tamil Nadu, India	/	KX768892[6]
	No voucher [CIFEFGB-SNS-0087]	Thoothukudi, Tamil Nadu, India	/	KX768893[6]
Stolephorus taurus sp. nov.	No voucher [CL14]	Fish market, Calcutta, India	AP011567[8]	AP011567[8]
Stolephorus teguhi	FRLM 34849	Pintukota, Lembeh Island, Bitung, North Sulawesi, Indonesia	/	**ON79125[4]**
	FRLM 34852	Pintukota, Lembeh Island, Bitung, North Sulawesi, Indonesia	/	**ON79125[5]**
Stolephorus tri	NTUM 12578 [SI56]	Fish market, Sibu, Malaysia	MH380390[1]	MH380511[1]
	NTUM 12578 [SI57]	Fish market, Sibu, Malaysia	MH380391[1]	MH380512[1]
Encrasicholina heteroloba	No voucher [Ra81]	Fish market, Ranong, Thailand	MT080923[3]	MT080451[3]
Encrasicholina punctifer	No voucher [Ra79]	Fish market, Ranong, Thailand	MT080919[3]	MT080447[3]

Sequence sources: [1]Hata et al. (2019), [2]Hata et al. (2020a), [3]Hata et al. (2020b), [4]Hata et al. (2021), [5]Egan et al. (2018), [6]Gangan et al. (2020); [7]D. Steinke and collaborators (unpublished), [8]Lavoué et al. (2010).

Stolephorus baganensis baganensis (not of Delsman): Hardenberg 1934: 333 [in part: Susang, Labuan, Batavia (currently Jakarta), Cheribon (Cirebon), Kendal, Semarang, Tuban, Surabaja (Surabaya), and Kumai, Indonesia].

Stolephorus dubiosus Wongratana, 1983: 400, fig. 18 (in part: original description; type locality: Songkhla Lake, Thailand; other localities: Paknam, Bangkok, Samutsakorn, Nakornsrithammaraj, and Surajthani, Thailand; Aluhaluh on Barito River, Kalimantan, Indonesia); Wongratana 1987a: 107 (in part: Thailand, Malay Peninsula, and Indonesia); Wongratana 1987b: 8 (in part: Gulf of Thailand and Java Sea); Whitehead et al. 1988: 411, unnumbered fig. (in part: Gulf of Thailand to Java Sea); Kottelat et al. 1993: 31, fig. 94 (in part: Sundaland and Thailand); Wongratana et al. 1999: 1734, unnumbered fig. (in part: Gulf of Thailand, Java Sea to Kalimantan); Nakashima 2005: 72 (Samut Prakan Province, Thailand); Jutagate et al. 2009: 123 (Pak Panang Bay and estuary of Pak Panang River, Thailand); Matsunuma 2013: 33, unnumbered fig. (Bang Pakong, Gulf of Thailand, Thailand); Tran et al. 2013: 43, unnumbered fig. (Mekong Delta, southern Vietnam); Kottelat 2013: 55 (Songkhla Lake, Thailand); Rupawan 2017: 132 (Panjan Strait, Riau Province, Sumatra, Indonesia); Hata et al. 2019: 30, fig. 14 (in part: Kuching, Sarawak, Malaysia; Songkhla Lake and Gulf of Thailand, Thailand); Syafei et al. 2020: 4, fig. 2 (Pabean Bay, Indramayu, West Java, Indonesia); Hata et al. 2020b: table 1 (in part: Bangkok, Thailand); Nagao Natural Environment Foundation 2021: 55, unnumbered fig. (Mekong Basin in Vietnam).

Holotype: BMNH 1969.4.22.1826, 70.0 mm SL, Songkhla Lake, Thailand, 2 May 1966, I. A. Ronquillo.

Non-type specimens: 22 specimens, 49.9–78.1 mm SL. THAILAND: BMNH 1977.11.30.63, 63.2 mm SL, Nakornsrithammaraj; THNHM-F021231, 68.1 mm SL, THNHM-F021232, 72.1 mm SL, THNHM-F021233, 65.6 mm SL, THNHM-F021234, 60.7 mm SL, THNHM-F021235, 64.4 mm SL, Bang Pakong River estuary, Chachoengsao Province; THNHM-F021236, 58.2 mm SL, Gulf of Thailand; THNHM-F021237, 66.0 mm SL, THNHM-F021238, 64.5 mm SL, THNHM-F021239 (cleared and stained), 63.6 mm SL, Thachin River estuary, Muang, Samut Sakhon Province; NSMT-P. 55363, 3 specimens, 55.1–59.1 mm SL, Songkhla Lake, 1.5 m depth, shrimp trap; NSMT-P 127425, 3 specimens, 49.9–59.4 mm SL, Songkhla Lake; URM-P 12176, 65.1 mm SL, Songkhla; URM-P 27308, 59.4 mm SL, URM-P 27309, 63.4 mm SL, Pak Nam, Samut Prakan Province; USNM 119676, 2 specimens, 58.4–62.3 mm SL, Bangpakong River. VIETNAM: NTUM 12329, 78.1 mm SL, Ganh Rai Bay.

Diagnosis: A species of *Stolephorus* with the following combination of characters: predorsal scute and spine on pelvic scute present; gill rakers on first gill arch 20–24 (modally 21) (upper series), 26–29 (28) (lower series), 46–53 (49) in total; gill rakers on second gill arch 16–19 (16) (upper series), 25–29 (27) (lower series), 41–48 (43) in total; gill rakers on third gill arch 12–14 (13) (upper series), 14–17 (15) (lower series), 27–31 (28) in total; gill rakers on fourth gill arch 8–11 (10) (upper series), 11–14 (12) (lower series), 20–25 (22) in total; prepelvic scutes 5–7 (6); maxilla long, posterior tip just reaching or slightly short of posterior margin of opercle; small teeth on dorsal surface of hyoid bone; posterior border of preopercle convexly rounded; distinct paired dark patches on parietal and occipital regions; no dark lines on dorsum anterior to dorsal-fin origin; double pigmented lines on dorsum from dorsal-fin base end to caudal-fin base; no melanophores below eye or on mandibular tip; posterior tip of pelvic fin usually not reaching vertical through dorsal-fin origin (sometimes reaching to vertical through first or second dorsal-fin ray origin) when depressed; body scales not deciduous, with numerous separations of grooves; pectoral fin short, 15.6–17.4% SL; pelvic fin short, 9.5–10.8% SL; second dorsal-fin ray short, 4.9–8.5% SL; third dorsal-fin ray short, 16.8–19.0% SL; second anal-fin ray short, 4.3–5.9% SL; third anal-fin ray short, 13.4–15.1% SL; interorbit narrow, 21.5–24.8% HL.

Description: Data for holotype presented first, followed by other specimen data in parentheses (if different). Counts and measurements, expressed as percentages of SL or HL, given in tables 2 and 3.

Body laterally compressed, elongate, deepest at dorsal-fin origin. Dorsal profile of head and body gradually elevated from snout tip to dorsal-fin origin, thereafter, nearly linear, gently lowering to uppermost point of caudal-fin base. Ventral profile of head and body gently lowering from snout tip to just below pectoral-fin insertion, thereafter parallel to body axis to anal-fin origin. Ventral contour from anal-fin origin to lowermost point of caudal-fin base gently elevated. Single spine-like scute just anterior to dorsal-fin origin (Fig. 2). Abdomen rounded, covered with five (four to seven) spine-like scutes anterior to pelvic-fin insertion. Pelvic scute attached to pelvic girdle, with a hard backwardly projecting spine (Fig. 3). No spine-like scutes on ventral surface posterior to pelvic fin. 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, posterior tip pointed, reaching to (or just short of) posterior margin of opercle. Premaxilla and first supramaxilla elongate. Second supramaxilla asymmetrical, lower

part larger than upper part. Lower jaw slender. Conical teeth in single rows on each jaw and palatines. Several teeth on vomer. Several rows of teeth on inner surface of pterygoids. Small conical teeth on dorsal surface of hyoid bone. 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 margins of preopercle and opercle rounded, smooth. Subopercle with rounded posterior margin. Gill 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 distally, most of isthmus muscle exposed (not covered by gill membrane). Head scales absent. Lateral line absent. Fins scaleless, except for broad triangular sheath of scales on caudal fin. Scales on lateral surface cycloid, thin, not deciduous. Numerous separations of grooves on body scales (Fig. 4). 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. First dorsal- and anal-fin rays minute. Anteriormost three rays of both dorsal and anal fins closely spaced. Anal-fin origin just below bases of tenth (eighth to eleventh) 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 pointed,

Table 2. Meristics of specimens of *Stolephorus taurus* sp. nov., *S. baganensis*, and *S. dubiosus*

	Stolephorus taurus sp. nov.			*Stolephorus baganensis*			*Stolephorus dubiosus*		
	Holotype	Paratypes		Neotype of *Stolephorus baganensis*	Non-types		Holotype	Non-types	
	OCF-P 10434	*n* = 19		BMNH 1967.11.13.526	*n* = 30		BMNH 1969.4.22.1826	*n* = 22	
Standard length (mm)	52.2	39.8–56.4	Modes	67.6	27.3–70.9	Modes	70.0	49.9–78.1	Modes
Dorsal-fin rays (unbranched)	3	3	3	3	3	3	3	3	3
Dorsal-fin rays (branched)	11	11–13	12	12	11–12	12	11	11–13	11
Anal-fin rays (unbranched)	3	3	3	3	3	3	3	3	3
Anal-fin rays (branched)	18	17–19	18	18	17–20	18	18	17–19	18
Pectoral-fin rays (unbranched)	1	1	1	1	1	1	1	1	1
Pectoral-fin rays (branched)	12	11–13	12	12	10–12	11	11	10–12	11
Pelvic-fin rays (unbranched)	1	1	1	1	1	1	1	1	1
Pelvic-fin rays (branched)	6	6	6	6	6	6	6	6	6
Gill rakers on 1st gill arch (upper)	21	19–22	21	17	15–19	17	21	20–24	21
Gill rakers on 1st gill arch (lower)	27	25–29	26	22	20–25	22	28	26–29	28
Gill rakers on 1st gill arch (total)	48	45–49	48	39	35–43	40	49	46–53	49
Gill rakers on 2nd gill arch (upper)	15	14–16	15	13	11–14	12	16	16–19	16
Gill rakers on 2nd gill arch (lower)	25	24–26	25	21	19–23	21	27	25–29	27
Gill rakers on 2nd gill arch (total)	40	39–42	40	34	31–37	35	43	41–48	43
Gill rakers on 3rd gill arch (upper)	12	11–12	12	10	9–11	10	13	12–14	13
Gill rakers on 3rd gill arch (lower)	15	13–16	14	12	11–13	12	14	14–17	15
Gill rakers on 3rd gill arch (total)	27	24–28	26	22	20–24	22	27	27–31	28
Gill rakers on 4th gill arch (upper)	9	8–10	9	9	7–9	8	9	8–11	10
Gill rakers on 4th gill arch (lower)	11	11–12	11	10	9–13	10	12	11–14	12
Gill rakers on 4th gill arch (total)	20	19–22	20	19	16–21	18	21	20–25	22
Gill rakers on posterior face of 3rd gill arch	6	4–7	5	6	3–6	5	6	5–7	6
Prepelvic scutes	5	4–6	5	5	4–7	6	5	5–7	6
Scale rows in longitudinal series	34	33–35	34	35	34–37	35	35	34–36	35
Transverse scales	8	8–9	8	8	8	8	8	8–9	8
Pseudobranchial filaments	18	15–19	16	17	16–20	12	17	16–20	19
Abdominal vertebrae	19	18–19	19	-	19	19		18–19	19
Caudal vertebrae	20	20–21	20	-	20	20		19–21	20
Total vertebrae	39	38–39	39	-	39	39		38–40	39

not reaching vertical through pelvic-fin insertion. Upper, posterior, and lower contours of pectoral fin nearly straight. Pelvic fin shorter than pectoral fin. Posterior tip of depressed pelvic fin not reaching to vertical through dorsal-fin origin (rarely reaching to base of first or second dorsal-fin ray). Caudal fin forked, upper and lower margins of both lobes nearly straight. Posterior tips of both lobes pointed.

Skeleton of hyoid arch (Fig. 5): All branchiostegal rays paddle-shaped (posteriorly broad). No branchiostegal rays connected to hypohyal, two rays on epihyal.

Caudal skeleton (Fig. 6): Each hypural free, except for second and third conjoined. Dorsal margin of first hypural smooth, without distinct projection. Posterior margins of second and third hypurals broadly concave. Dorsal margins of fourth and fifth hypurals projected anteriorly. Sixth hypural elongate.

Coloration when fresh (based on color photographs of THNHM-F021231–021235, 021237):

Table 3. Morphometrics of specimens of *Stolephorus taurus* sp. nov., *S. baganensis*, and *S. dubiosus*

	Stolephorus taurus sp. nov.			*Stolephorus baganensis*			*Stolephorus dubiosus*		
	Holotype	Paratypes		Neotype of *Stolephorus baganensis*	Non-types		Holotype	Non-types	
	OCF-P 10434	*n* = 19		BMNH 1967.11.13.526	*n* = 30		BMNH 1969.4.22.1826	*n* = 22	
Standard length (mm; SL)	52.2	39.8–56.4	Means	67.6	27.3–70.9	Means	70.0	49.9–78.1	Means
As % SL									
Head length (HL)	24.4	23.5–26.5	25.0	25.3	23.5–26.6	24.8	24.1	23.2–26.4	24.7
Body depth	24.1	21.3–24.3	22.9	24.6	20.2–26.1	23.6	23.7	20.4–27.3	22.5
Pre-dorsal-fin length	54.1	50.3–56.2	52.9	53.9	50.6–56.5	53.6	55.5	51.8–55.9	53.9
Snout tip to pectoral-fin insertion	27.1	24.4–27.3	26.1	27.3	24.9–28.6	26.7	26.6	25.2–28.1	26.9
Snout tip to pelvic-fin insertion	44.8	42.2–47.9	44.9	44.5	42.9–47.7	44.9	44.4	43.0–47.8	44.8
Snout tip to anal-fin origin	64.6	62.8–66.3	64.2	64.2	61.3–67.7	64.3	63.2	61.9–66.9	63.9
Dorsal-fin base length	12.4	12.1–14.5	13.3	14.6	12.0–14.6	13.6	14.4	11.9–14.8	13.4
Anal-fin base length	19.2	18.7–20.9	19.6	21.8	18.8–23.2	21.3	22.4	18.5–22.0	20.6
Caudal-peduncle length	19.1	16.1–20.0	17.9	17.6	15.1–19.7	17.3	16.1	15.8–19.5	17.8
Caudal-peduncle depth	11.6	10.2–12.4	11.5	11.1	7.9–12.1	10.6	9.6	9.5–11.6	10.5
D–P1	35.2	34.7–38.5	36.7	36.4	30.9–38.6	35.8	37.2	34.4–38.4	36.3
D–P2	27.2	22.3–26.4	25.2	25.9	21.4–29.0	25.5	26.3	23.1–28.0	24.9
D–A	24.7	23.2–25.6	24.3	25.9	21.6–27.9	25.3	25.5	21.8–27.9	23.7
P1–P2	18.9	17.4–23.3	19.8	18.1	16.1–21.8	19.0	17.9	17.4–23.2	19.3
P2–A	21.3	16.9–22.8	19.6	16.9	16.9–22.9	19.4	20.0	17.1–21.6	19.5
Pectoral-fin length	17.9	17.8–18.7	18.1	broken	16.5–20.0	18.0	16.5	15.6–17.4	16.7
Pelvic-fin length	12.0	11.6–12.7	12.1	broken	8.7–11.6	10.7	9.5	9.5–10.8	10.2
Maxilla length	21.2	20.7–21.9	21.1	broken	19.2–22.2	20.9	20.8	19.2–22.2	20.5
Mandible length	16.7	16.8–18.4	17.5	16.4	15.6–18.0	16.8	17.3	15.4–17.6	16.6
Supramaxilla end to maxilla end	5.2	3.9–5.3	4.8	broken	3.4–6.2	5.1	5.2	4.1–5.7	4.7
1st unbranched dorsal-fin ray length	2.1	1.2–2.5	1.8	1.6	1.4–3.9	1.9	2.3	1.1–2.1	1.4
2nd unbranched dorsal-fin ray length	10.0	8.7–10.0	9.2	7.0	6.8–10.8	8.1	7.2	4.9–8.5	7.3
3rd dorsal-fin ray length	broken	19.5–20.2	19.8	broken	17.8–19.9	18.9	broken	16.8–19.0	18.0
1st unbranched anal-fin ray length	2.3	1.3–2.9	2.1	1.7	1.2–3.5	2.0	1.5	0.7–2.4	1.6
2nd unbranched anal-fin ray length	6.6	6.0–7.3	6.4	broken	3.6–6.9	5.3	4.6	4.3–5.9	5.2
3rd anal-fin ray length	15.8	15.8–17.5	16.4	broken	13.4–17.3	15.7	broken	13.4–15.1	14.4
As % HL									
Orbit diameter	34.0	30.3–34.5	32.2	29.5	30.1–37.2	32.7	30.4	28.8–33.5	31.3
Eye diameter	27.9	24.2–30.9	27.3	24.4	21.7–29.3	25.9	26.3	23.2–28.8	26.4
Snout length	13.1	11.9–14.8	13.2	13.1	11.6–14.7	13.0	16.0	13.6–16.7	15.1
Interorbital width	25.6	25.2–28.3	26.2	23.0	20.6–26.0	24.0	24.3	21.5–24.8	23.3
Postorbital length	54.8	51.1–56.2	53.9	58.1	51.7–59.0	55.1	57.7	52.4–58.0	55.4

Abbreviations: D–P1 (distance between dorsal-fin origin and pectoral-fin insertion); D–P2 (distance between dorsal-fin origin and 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).

Fig. 1. *Stolephorus dubiosus*: (a) Lateral view of holotype (BMNH 1969.4.22.1826, 70.0 mm SL, Thailand); (b) lateral view in fresh condition; (c) dorsal and (d) ventral views in preserved condition of non-type specimen (THMHM-F021237, 66.0 mm SL, Samut Sakhon Province, Thailand).

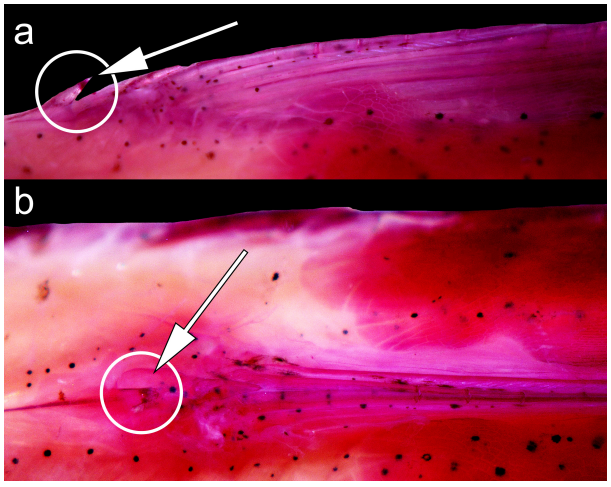

Fig. 2. (a) Lateral and (b) dorsal views of dorsal-fin origin of *Stolephorus dubiosus*, NSMT-P 127425, 55.7 mm SL, Songkhla Lake, Thailand (stained with Alizarine Red). Arrows indicate predorsal scute.

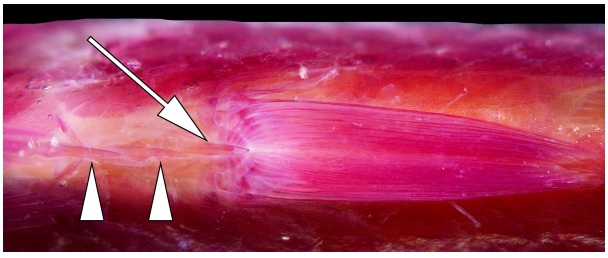

Fig. 3. Ventral view of pelvic fin of *Stolephorus dubiosus*. NSMT-P 127425, 49.9 mm SL, Songkhla Lake, Thailand (stained with Alizarine Red). Triangles and arrow indicate prepelvic scutes and hard spine on pelvic scute, respectively.

Body milky-white, a silver longitudinal band of width subequal to pupil diameter extending from just behind upper opercular margin to caudal-fin base. Lateral surface of head uniformly silver. Snout yellowish-white, semi-translucent. Melanophores scattered on snout tip. Scale pockets on upper part of body yellowish-black. Dorsal fin whitish, semi-translucent, melanophores scattered along fin rays. Pectoral, pelvic, and anal fins uniformly whitish, transparent, without melanophores.

Fig. 4. Stained scale removed from right side of midbody (just below dorsal fin) of *Stolephorus dubiosus*. NSMT-P 127425, 49.9 mm SL, Songkhla Lake, Thailand (left-right inverted). Grooves on posterior part forming numerous separations.

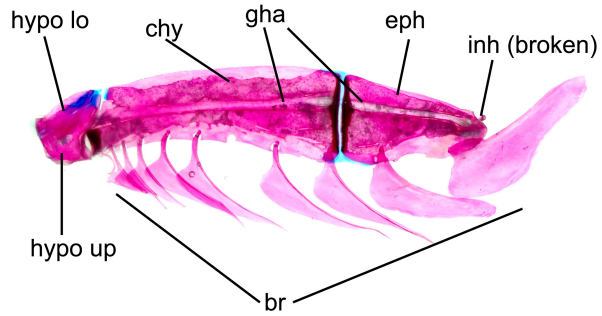

Fig. 5. Left side of left hyoid arch of *Stolephorus dubiosus* (THNHM-F021239, 63.6 mm SL, cleared and stained). hypo lo, lower hypohyal; hypo up, upper hypohyal; chy, ceratohyal; gha, groove for hyoidean artery; eph, epihyal; inh, interhyal (broken); br, branchiostegal rays (seventh branchiostegal ray detached).

Caudal fin yellow, melanophores scattered along fin rays. Posterior margin of caudal fin black. Iris and pupil silver and black, respectively.

Coloration of preserved specimens: Body uniformly pale; silver longitudinal band usually lost. Pairs of distinct dark patches on parietal and occipital regions. Scale pockets on dorsum to upper lateral surface of body margined black. Double pigmented lines dorsally posterior to dorsal fin (Fig. 1c). A few melanophores scattered anteriorly on snout. All fins whitish. Melanophores scattered along fin rays of dorsal and caudal fins. Pectoral, pelvic, and anal fins semi-transparent, without melanophores. Caudal fin margined black.

Distribution: *Stolephorus dubiosus* is distributed in the western Pacific Ocean from southern Vietnam (Mekong Delta) to Songkhla, Thailand (based on specimens examined in this study), although molecular evidence and some literature records indicate that it is also distributed in Sumatra, Java, and Borneo (Wongratana 1983; Rupawan 2017; Syafei et al. 2020; Fig. 7). The species mainly inhabits estuarine or brackish waters of large-scale rivers (Whitehead et al. 1988; Wongratana et al. 1999; this study).

Morphological comparisons: *Stolephorus dubiosus* is easily distinguished from all other congeners, except for *S. baganensis*, *Stolephorus tri* Bleeker, 1852, and *S. taurus* sp. nov., in having a spine-like scute located just anterior to the dorsal-fin origin and a small spine on the pelvic scute. *Stolephorus bengalensis* Dutt and Babu Rao, 1959, *Stolephorus diabolus* Hata, Lavoué and Motomura, 2022, *Stolephorus eclipsis* Hata, Lavoué and Motomura, 2022, and *Stolephorus eldorado* Hata, Lavoué and Motomura, 2022 also have a spine-like scute just anterior to the dorsal-fin origin, but lack a spine on the pelvic scute (Whitehead et al. 1988;

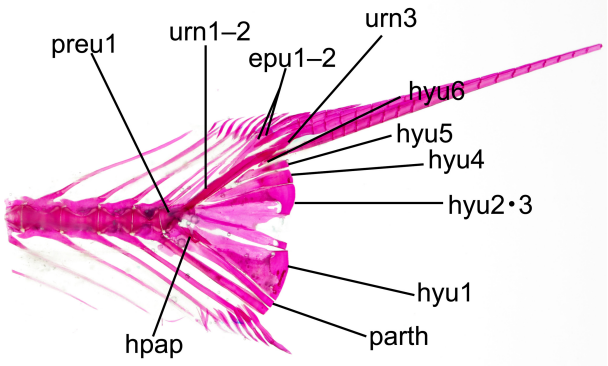

Fig. 6. Left side of caudal-fin complex of *Stolephorus dubiosus* (THNHM-F021239, 63.6 mm SL, cleared and stained. Caudal-fin rays removed). preu, preural centrum; hpap, hypurapophysis; urn, uroneural bone; epu, epural; hyu, hypural; parth, parhypural bone.

Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–e 2020 2021a b; Hata et al. 2019 2020a b 2021 2022; Gangan et al. 2020; this study). *Stolephorus dubiosus* differs from *S. baganensis* and *S. tri* in having higher counts of lower gill rakers on the first gill arch [26–29 in *S. dubiosus* vs. 21–24 (rarely 20 or 25) in *S. baganensis* and 18–22 in *S. tri*]. *Stolephorus dubiosus* is also distinguished from *S. baganensis* in having the pelvic fin posteriorly short of the dorsal-fin origin (rarely reaching to vertical through first or second dorsal-fin ray origin in *S. dubiosus* vs. reaching to vertical through third to fifth dorsal-fin ray origin in *S. baganensis*). Dorsal pigmentation from the occipital area to the dorsal-fin origin also separates *S. dubiosus* (no dark lines) and *S. tri* (usually paired dark lines; fig. 19 in Hata et al. 2019). Comparisons of *S. dubiosus* with *S. taurus* are given under Remarks for the latter.

Remarks: *Stolephorus dubiosus* was originally described by Wongratana (1983) from specimens collected from the Pacific coast of Thailand, Kalimantan, and northeastern India. Subsequently, the species has been considered distributed in both the eastern Indian and western Pacific oceans (Whitehead et al. 1988; Wongratana et al. 1999). However, specimens from the Indian Ocean previously identified as *S. dubiosus* are newly recognised herein as a new species (described below), the distributional range of true *S. dubiosus* therefore being restricted to the western Pacific Ocean (Fig. 7). Before *S. dubiosus* was described by Wongratana (1983), the species had been frequently confused with *S. baganensis*. However, because specimens collected from Indonesia, reported by Hardenberg (1934) as *S. b. baganensis*, had 25–29 lower gill rakers on the first gill arch, they probably included *S. dubiosus*.

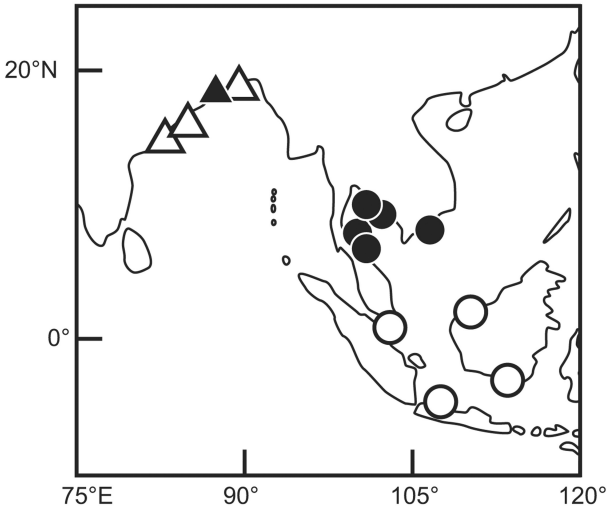

Fig. 7. Distributional records of *Stolephorus dubiosus* (circles) and *S. taurus* sp. nov. (triangles). Closed symbols, based on specimens examined in this study; open symbols, based on literature records or molecular evidence.

***Stolephorus taurus* sp. nov.**

(English name: Bengal Spined Anchovy)
(Fig. 8; Tables 2, 3)
urn:lsid:zoobank.org:act:457E9BDD-B565-4CCD-80C8-83F92055D3B7

Anchoviella baganensis baganensis (not of Delsman): Dutt and Babu Rao, 1959: 160 (Kakinada, Andhra Pradesh, India).

Stolephorus dubiosus (not of Wongratana): Wongratana 1983: 400 (in part: Orissa, India); Wongratana 1987a: 107 (in part: Bay of Bengal); Wongratana 1987b: 8 (in part: Bay of Bengal); Whitehead et al. 1988: 411 (in part: northern part of Bay of Bengal); Kottelat et al. 1993: 31 (in part: India); Wongratana et al. 1999: 1734 (in part: northern part of Bay of Bengal); Hata et al. 2019: 30 (in part: India); Gangan et al. 2020: 566, fig. 5 (Digha, Kolkata, India); Hata et al. 2020b: table 1 (in part: India).

Holotype: OCF-P 10434, 52.2 mm SL, estuary of Hooghly River, West Bengal, India (purchased in a fish market in Kolkata, West Bengal, India), 9 June 1985.

Paratypes: 19 specimens, 39.8–57.7 mm SL (all purchased with the holotype): KAUM–I. 157580, 46.5 mm SL, KAUM–I. 157581, 53.2 mm SL, NSMT-P 141123, 49.0 mm SL, NSMT-P 141124, 48.6 mm SL, URM-P 10942, 5 specimens, 44.9–53.2 mm SL, URM-P 10943, 10 specimens, 39.8–46.7 mm SL.

Diagnosis: A species of *Stolephorus* with the following combination of characters: predorsal scute and spine on pelvic scute present; gill rakers on first gill arch 19–22 (modally 21) (upper series), 25–29 (26) (lower series), 45–49 (48) in total; gill rakers on second gill arch 14–16 (15) (upper series), 24–26 (25) (lower series), 39–42 (40) in total; gill rakers on third gill arch 11 or 12 (12) (upper series), 13–16 (14) (lower series), 24–28 (26) in total; gill rakers on fourth gill arch 8–10 (9) (upper series), 11 or 12 (11) (lower series), 19–22 (20) in total; prepelvic scutes 4–6 (5); maxilla long, posteriorly just reaching or slightly short of posterior margin of opercle; small teeth on dorsal surface of hyoid bone; posterior border of preopercle convexly rounded; distinct paired dark patches on parietal and occipital regions; no dark lines on dorsum anterior to dorsal-fin origin; double pigmented lines on dorsum from end of dorsal-fin base to caudal-fin base; no melanophores below eye or on tips of snout and mandible (sometimes a few on snout); posterior tip of pelvic fin reaching to third to sixth dorsal-fin ray base when depressed; body scales not deciduous, with relatively a few separations

of grooves; pectoral fin long, 17.8–18.7% SL; pelvic fin long, 11.6–12.7% SL; second dorsal-fin ray long, 8.7–10.0% SL; third dorsal-fin ray long, 19.5–20.2% SL; second anal-fin ray long, 6.0–7.3% SL; third anal-fin ray long, 15.8–17.5% SL; interorbit wide, 25.2–28.3% HL.

Description: Data for holotype presented first, followed by paratype data in parentheses (if different). Counts and measurements, expressed as percentages of SL or HL, are given in tables 2 and 3.

Body laterally compressed, elongate, deepest at dorsal-fin origin. Dorsal profile of head and body gradually elevated from snout tip to dorsal-fin origin, thereafter gently lowering to uppermost point of caudal-fin base. Ventral contour of head and body lowering from snout tip to just below pectoral-fin insertion, subsequently parallel to body axis to anal-fin origin. Ventral profile from anal-fin base to lowermost point of caudal-fin base gradually elevated. Abdomen rounded, covered with five (four to six) spine-like scutes anterior to pelvic-fin insertion. Pelvic scute joined to pelvic girdle, former with hard backwardly projecting spine. No spine like scutes on ventral surface posterior to pelvic fin. Single spine-like scute just anterior to dorsal-fin origin. 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, posterior tip pointed, just short of or just reaching posterior margin of opercle. Lower jaw slender. Conical teeth in single rows on each jaw and palatines. Several teeth on vomer. Several rows of teeth on inner surface of pterygoids. Small teeth on dorsal surface of hyoid bone. 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 margins of preopercle and opercle smoothly rounded. Subopercle with rounded posterior margin. Gill 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 distally, most of isthmus muscle exposed, not covered by gill membrane. Head scales absent. Fins scaleless, except for broad triangular sheath of scales on caudal fin. Scales on lateral surface cycloid, thin, not deciduous. Relatively a few separations of grooves on body scales (Fig. 9). 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. First dorsal- and anal-fin rays minute. Anteriormost three rays of both dorsal and anal fins closely spaced. Anal-fin origin just below bases of tenth (ninth to twelfth) 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 pointed, not reaching vertical through pelvic-fin insertion. Upper, posterior, and lower contours of pectoral fin nearly straight. Pelvic fin shorter than pectoral fin. Posterior tip of depressed pelvic fin reaching to vertical through fourth (third to sixth) dorsal-fin ray base. Caudal fin

Fig. 8. Lateral (a), dorsal (b), and ventral (c) views of the holotype of *Stolephorus taurus* sp. nov., OCF-P 10434, 52.2 mm SL, estuary of Hooghly River, West Bengal, India.

forked, upper and lower margins of both lobes nearly straight. Posterior tips of both lobes pointed.

Coloration of preserved specimens: Body uniformly pale ivory with whitish longitudinal band, width slightly less than pupil diameter, from just behind upper opercular margin to caudal-fin base. Pairs of dark patches on parietal and occipital regions. No dark lines on dorsum anterior to dorsal fin. Double broken lines of melanophores on dorsum from end of dorsal-fin base to caudal-fin base. Melanophores scattered along posterior margin of dorsal scale pockets. No melanophores on snout, suborbital area and tips of both jaws. Melanophores densely scattered in gill opening. All fins whitish, semi-transparent. Melanophores scattered along caudal-fin rays.

Distribution: Currently known from northern Bay of Bengal. According to Dutt and Babu Rao (1959; as *S. baganensis baganensis*) and Wongratana (1983; as *S. dubiosus*), *S. taurus* occurs westward to at least the Godavari River estuary, Andhra Pradesh, India. Moreover, molecular evidence indicated that the new species also occurs in the western part of Bangladesh (Fig. 7). *Stolephorus taurus* mainly inhabits estuaries or brackish waters. In the coastal area of West Bengal State, India, it is abundantly fished and marketed fresh or dried.

Etymology: The specific name *taurus* is derived from Greek meaning "bull", in reference to the hard spine on the dorsum of the species.

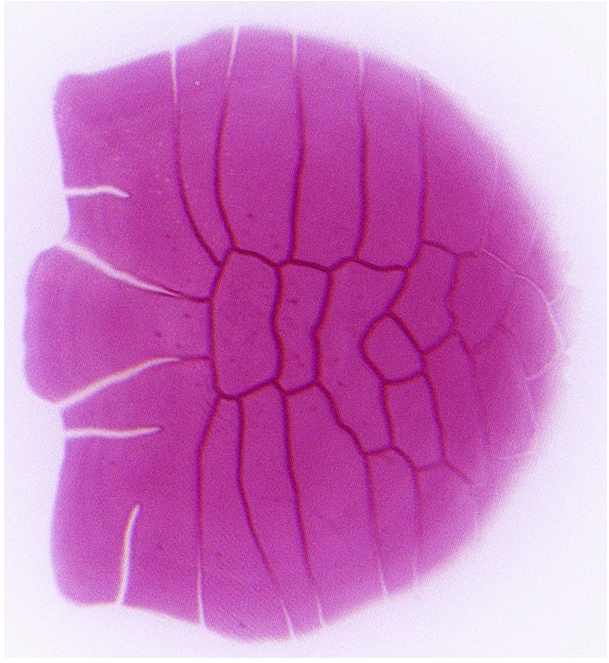

Fig. 9. Stained scale removed from right side of midbody (just below dorsal fin) of paratype of *Stolephorus taurus*. KAUM–I. 157581, 53.2 mm SL, estuary of Hooghly River, West Bengal, India (left-right inverted). Grooves on scales forming a few separations.

Morphological comparisons: The new species is assignable to the genus *Stolephorus*, as defined by Whitehead et al. (1988) and Wongratana et al. (1999), due to having a long isthmus muscle reaching anteriorly to the posterior margin of the gill membrane, prepelvic scutes, and hidden urohyal, and the absence of postpelvic scutes.

Stolephorus taurus most closely resembles *S. dubiosus*, both sharing a predorsal scute, spine on the pelvic scute, long maxilla, posteriorly just reaching or slightly beyond the posterior opercular margin, double pigmented lines on the dorsum from the end of the dorsal-fin base to the caudal-fin base (not before the dorsal-fin origin), non-deciduous scales, and 25 or more lower gill rakers on the first gill arch (Wongratana 1983 1987a b; Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–e; Hata et al. 2019 2020a b 2021 2022; Gangan et al. 2020; this study). However, the new species can be distinguished from *S. dubiosus* by the longer pectoral (17.8–18.7% SL in *S. taurus* vs. 15.6–17.4% in *S. dubiosus*) and pelvic fins (11.6–12.7% SL vs. 9.5–10.8%), the latter posteriorly reaching to vertical through the base of the third to sixth dorsal-fin rays when depressed [vs. usually not reaching to vertical through dorsal-fin origin (sometimes reaching to vertical through base of first or second dorsal-fin rays)], longer second dorsal-fin (8.7–10.0% SL vs. 4.9–8.5%), third dorsal-fin (19.5–20.2% SL vs. 16.8–19.0%), second anal-fin (6.0–7.3% SL vs. 4.3–5.9%) and third anal-fin rays (15.8–17.5% SL vs. 13.4–15.1%), a wider interorbit (25.2–28.3% of HL vs. 21.5–24.8%) (Table 3; Fig. 10), and body scales with relatively few separations formed by grooves (vs. numerous separations; Figs. 4, 9). The new species has been frequently recorded from the Indian coast as *S. dubiosus* (*e.g.*, Wongratana 1983; Gangan et al. 2020), although prior to the description of the latter, it was occasionally confused with *S. baganensis*. However, *S. taurus* can be distinguished from *S. baganensis* by the higher counts of gill rakers (gill rakers on first, second, third and fourth gill arches 19–22 + 25–29 = 45–49, 14–16 + 24–26 = 39–42, 11 or 12 + 13–16 = 24–28, and 8–10 + 11 or 12 = 19–22, respectively, in *S. taurus* vs. 15–19 + 21–24 (rarely 20 or 25) = 35–43, 11–14 + 19–23 = 31–37, 9–11 + 11–13 = 20–24, 7–9 + 9–13 = 16–21, respectively, in *S. baganensis*) and longer pelvic fin (11.6–12.7% SL in *S. taurus* vs. 8.7–11.6% in *S. baganensis*) (Hata et al. 2019; this study). Because the mean number of lower gill rakers on the first gill arch of specimens collected from the Bay of Bengal and reported by Dutt and Babu Rao (1959) as *Anchoviella baganensis baganensis* was 26.21, those specimens probably included *S. taurus*.

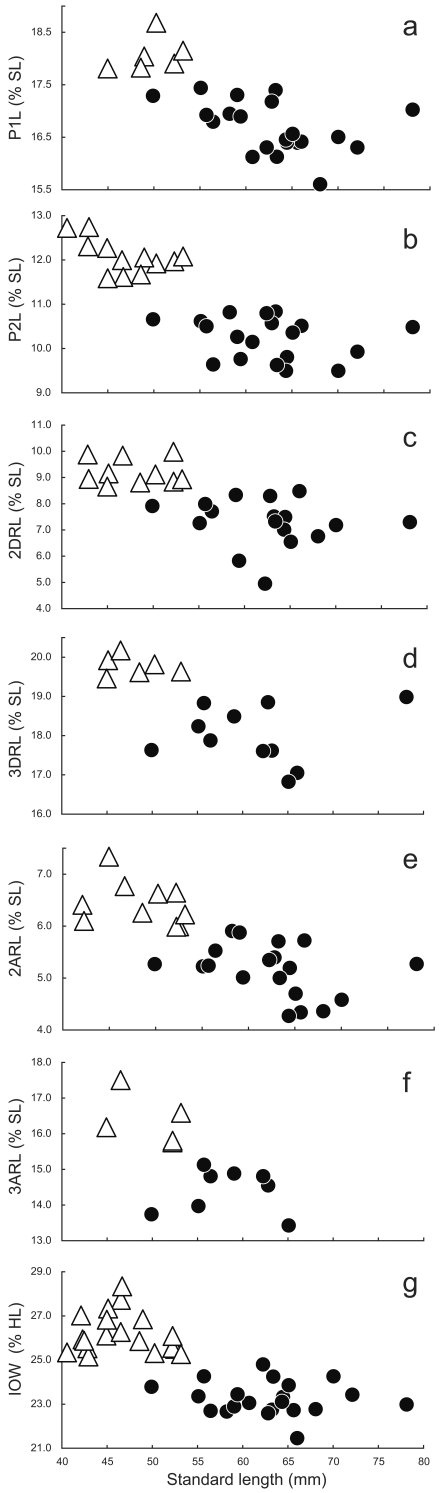

Fig. 10. Morphometric comparisons between *Stolephorus dubiosus* (*open triangles*) and *S. taurus* sp. nov. (*closed circles*). (a) for pectoral-fin length (P1L; as % of standard length; SL); (b) for pelvic-fin length (P2L; as % of SL); (c) for second dorsal-fin ray length (2DRL; as % of SL); (d) for third dorsal-fin ray length (3DRL; as % of SL); (e) for second anal-fin ray length (2ARL; as % of SL); (f) for third anal-fin ray length (as % of SL); (g) for interorbital width (as % of head length; HL) to SL.

Key to species of *Stolephorus* with a predorsal scute and spine on the pelvic scute

1a. Gill rakers few, upper, lower, and total gill rakers on first gill arch usually fewer than 20, 25, and 44, respectively 2
1b. Gill rakers numerous, upper, lower and total gill rakers on first gill arch more than 18, 24, and 43, respectively 3
2a. Paired dark lines on dorsum from occiput to dorsal-fin origin (rarely absent); depressed pelvic fin posteriorly not reaching to vertical through dorsal-fin origin; gill rakers few, lower gill rakers on first gill arch 18–22 .... *S. tri* (Singapore, Malaysia, and Indonesia)
2b. No dark lines on dorsum anterior to dorsal fin; posterior tip of depressed pelvic fin reaching to vertical through third to fifth dorsal-fin ray base; lower gill rakers on first gill arch 21–24 .... *S. baganensis* (Andaman coast of Thailand to Borneo)
3a. Pelvic fin short, 9.5–10.8 % SL, its posterior tip not reaching to vertical through dorsal-fin origin (rarely reaching to vertical through first or second dorsal-fin ray base); pectoral fin short, 15.6–17.4 % SL ..... *S. dubiosus* (southern Vietnam to Borneo)
3b. Pelvic fin long, 11.6–12.7 % SL, its posterior tip reaching to vertical through third to fifth dorsal-fin ray base; pectoral fin long, 17.8–18.7 % SL ..... *S. taurus* (Bay of Bengal)

DISCUSSION

Based on the phylogenetic analysis (Fig. 11), the "spined *Stolephorus*" (*S. baganensis*, *S. dubiosus*, *S. taurus*, and *S. tri*, characterised by a predorsal scute and spine on the pelvic scute) form a monophyletic group, which is closely related to the clade formed by *Stolephorus acinaces* Hata, Lavoué and Motomura, 2020, *Stolephorus andhraensis* Babu Rao,1966, *S. eldorado*, and *Stolephorus tamilensis* Gangan, Pavan-Kumar, Jahageerdar, and Jaiswar, 2020, along with *Stolephorus holodon* (Boulenger, 1900) (Fig. 11). Notably, *S. eldorado*, included in the clade, lacks a spine on the pelvic scute, but has a predorsal scute (Hata et al. 2022). A co-occurring presence of a predorsal scute and spine on the pelvic scute is common to all species within the subfamily Coiliinae, but only in some species of *Stolephorus* (subfamily Engraulinae) (Whitehead et al. 1988; Wongratana et al. 1999). Therefore, the combination of the two characters likely represents the primitive condition in the genus *Stolephorus* which was already present in the most recent common ancestor of the Engraulinae.

An intriguing morphological characteristic of *Stolephorus* is the variation in number of prepelvic scutes, from four to six. In this respect, the mode of prepelvic scutes of all "spined *Stolephorus*" is six, except in *S. taurus*, which has only five scutes. *Stolephorus acinaces*, *S. andhraensis*, *S. eldorado* and *S. holodon* also have a mode of six scutes (Hata et al. 2020b 2022), although the mode of scutes of *S. tamilensis* was not given in the original description of

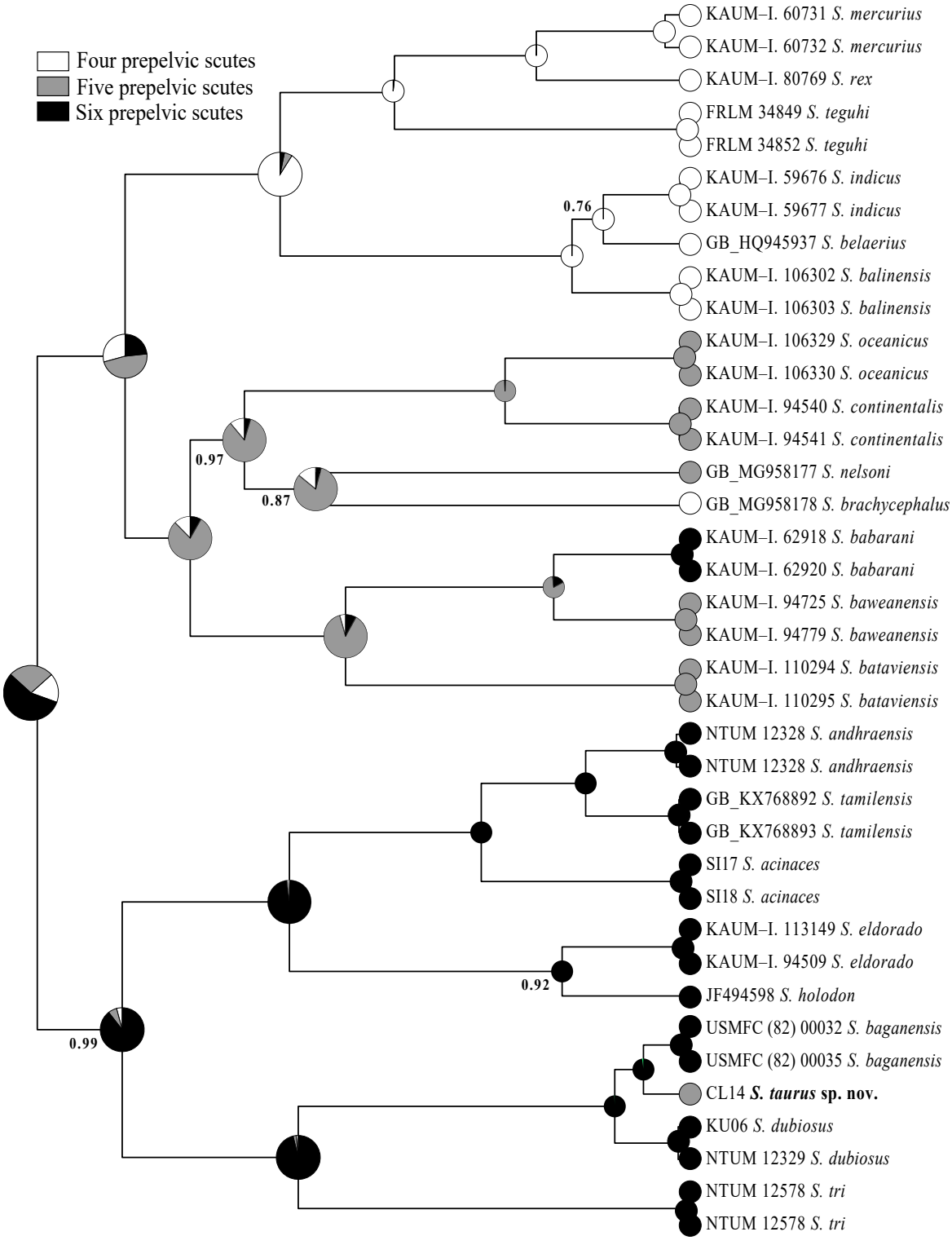

Fig. 11. Ultrametric Bayesian phylogenetic tree of 22 species of the genus *Stolephorus* with evolution of the (modal) number of prepelvic scutes. Modal number of prepelvic scutes classified into three categories: six prepelvic scutes (black), five prepelvic scutes (grey), four prepelvic scutes (white)**.** Character states at nodes estimated using likelihood optimization and a symmetric one-rate (“Mk1”) model of evolution. At each node, relative probabilities of each diet category drawn using pie charts, with corresponding coding-colour. Pie charts at deepest nodes enlarged for clarity. *Stolephorus* specimens identified by museum registration number, specimen code or GenBank (GB) sequence accession number (see Table 1 for details). Outgroups *Encrasicholina* not shown. Branch lengths proportional to relative time (tree height scaled to 1). Posterior Probabilities shown at nodes when < 1.

this species (see Gangan et al. 2020, where the number of scutes was shown as five or six).

The most-likely reconstruction of the evolution of the number of prepelvic scutes within *Stolephorus*, as seen on the present phylogenetic tree (Fig. 11), indicates that the most recent common ancestor of *Stolephorus* possessed six prepelvic scutes (the ancestral condition). A reduction in the number of prepelvic scutes occurred subsequently within *Stolephorus* at least four times. The first important reduction event (from six to five) occurred in the clade including *Stolephorus oceanicus* (Hardenberg, 1933), *Stolephorus continentalis* Hata and Motomura, 2018, *Stolephorus brachycephalus* Wongratana, 1983, *Stolephorus nelsoni* Wongratana, 1987, *Stolephorus bataviensis* Hardenberg, 1933, *Stolephorus baweanensis* Hardenberg, 1933 and *Stolephorus babarani* Hata, Lavoué and Motomura, 2020. All these species modally have five prepelvic scutes, except *S. brachycephalus* which has only four scutes (the mode of which was based on only nine specimens, as shown in Hata and Motomura 2018d) and *S. babarani* which has six scutes (the mode of which was based on only eight of 25 type specimens of *S. babarani*, due to the poor condition of the other 17 specimens, as shown in Hata et al. 2020b). Examining a greater number of specimens from these last two species may result in changed modes for prepelvic scutes. A second important reduction event from five to four occurred in the clade comprising *Stolephorus balinensis* (Bleeker, 1849), *Stolephorus belaerius* Hata, Lavoué and Motomura, 2021, *Stolephorus indicus* (van Hasselt, 1823), *Stolephorus mercurius* Hata, Lavoué and Motomura, 2021, *Stolephorus rex* Jordan and Seale, 1926, and *Stolephorus teguhi* Kimura, Hori and Shibukawa, 2009. All six of these species modally have four prepelvic scutes. The last two reductions occurred later and independently in *S. taurus* (from six to five) and *S. brachycephalus* (from five to four).

It is therefore hypothesised that the ancestral condition in *Stolephorus* is a greater number of scutes, including more prepelvic scutes and a spine on the pelvic scute, and that the derived condition is fewer scutes, combined with the loss of the predorsal scute and spine on the pelvic scute.

In the subfamily Engraulinae, the genus *Stolephorus* is considered to be the sister group of all other genera (Lavoué et al. 2017), which (with the exception of *Encrasicholina*) lack spine-like scutes on the body (Whitehead et al. 1988). *Encrasicholina*, which diverged just after *Stolephorus* (Lavoué et al. 2017), includes *Encrasicholina purpurea* (Fowler, 1900), a species lacking a prepelvic scute (Whitehead et al. 1988; Wongratana et al. 1999). Therefore, the reduction in number of spine-like scutes occurred independently several times within the subfamily Engraulinae.

CONCLUSIONS

A new species, *Stolephorus taurus*, was described, and a closely related congener, *S. dubiosus*, was redescribed. A predorsal scute and spine on pelvic scute, commonly observed in these two species as well as two additional species considered to be related, *S. baganensis* and *S. tri*, most likely represent the primitive condition in the genus *Stolephorus*. These characters appeared in the most recent common ancestor of the subfamily Engraulinae. Moreover, the number of prepelvic scutes is likely to decrease on several independent occasions during the evolution of these fishes, as a tendency for the entire subfamily Engraulinae, including *Stolephorus*.

Comparative material examined

Stolephorus baganensis (31 specimens, 27.3–70.9 mm SL): listed in Hata et al. (2019) and 14 additional specimen: URM-P 46196, 52.3 mm SL, Kuala Tungkal, Jambi, Sumatra, Indonesia; USMFC (82) 00032, 55.8 mm SL, Sungai Batu, George Town, Malaysia; USMFC (82) 00035, 2 specimens, 59.6–64.0 mm SL, Sungai Batu, George Town, Malaysia; USMFC (82) 00050, 3 specimens, 60.7–68.6 mm SL, estuary of Merbok River, Jeti Semeling, Malaysia; ZRC 3569, 7 specimens, 54.9–66.5 mm SL, Bagan-siapiapi, Riau, Sumatra, Indonesia. *Stolephorus tri* (27 specimens, 45.5–95.1 mm SL): listed in Hata et al. (2019) and 3 additional specimens: URM-P 44379, 74.7 mm SL, Tanjung Sepat, Selangor, Malaysia; USMFC (82) 00008, 2 specimens, 77.9–78.6 mm SL, Teluk Bahang, Pulau Pinang, Penang, Malaysia.

Acknowledgments: This paper and the new species name were registered with ZooBank under urn: lsid:zoobank.org:pub:74D3FCA0-2666-4C5C-AB26-544D61E513E6. We thank O. Crimmen, J. Maclaine and D. Nicholson (BMNH), S. Kimura (FRLM), G. Shinohara and M. Nakae (NSMT), W.-J. Chen and M. Lin (NTUM), K. Miyamoto (OCF), and K. P. Lim and Z. Jaafar (ZRC) for opportunities to examine specimens of *Stolephorus*. We also thank Y. Haraguchi and other volunteers, and students of KAUM for curatorial assistance, and G. Hardy (Ngunguru, New Zealand), for reading the manuscript and providing help with English. This study was supported in part by JSPS KAKENHI Grant Number 19K23691, JSPS Fellows (DC2: 29-6652) and the Sasakawa Scientific Research Grant

from the Japan Science Society (28-745) to HH; JSPS KAKENHI Grant Numbers 20H03311 and 21H03651; the JSPS Core-to-core CREPSUM JPJSCCB2020009; 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 to HM; and short term research grant 304/PBIOLOGI/6315400 from Universiti Sains Malaysia to SL.

Authors' contributions: All authors collected specimens, worked up data, and wrote the manuscript. All authors read and approved the manuscript.

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

Availability of data and materials: The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Consent for publication: All authors consent to the publication of this manuscript.

Ethics approval consent to participate: Not applicable.

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