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# *Stolephorus lotus*, a New Anchovy (Teleostei: Clupeiformes: Engraulidae) from the Northern Territory, Australia

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A new anchovy *Stolephorus lotus* sp. nov., is described based on 30 specimens collected from Van Diemen Gulf, Northern Territory, Australia. The species closely resembles *Stolephorus acinaces* Hata, Lavoué and Motomura, 2020 and *Stolephorus andhraensis* Babu Rao, 1966, in having a long maxilla (posterior tip just reaching or extending slightly beyond the posterior margin of the opercle), indented posterior preopercular margin, anal fin with 16–18 branched fin rays, and 21–23 lower gill rakers, and lacking a predorsal scute and pelvic scute spine. However, the new species differs from the other two species in having higher counts of longitudinal series of scale rows and predorsal scales (37–39 and 20 or 21, respectively vs. 35–38 and 17–19 in the other two) and a more anteriorly located anal-fin origin (below bases of sixth to eighth dorsal-fin rays vs. eighth to tenth dorsal-fin rays).

**Key words:** Actinopterygii, *Stolephorus acinaces*, *Stolephorus andhraensis*, Taxonomy.

## BACKGROUND

*Stolephorus* Lacepède 1803, an Indo-Pacific genus of marine and brackish water anchovies (Clupeiformes: Engraulidae), comprises 42 valid species (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–d 2021a–c 2022; Hata et al. 2019 2020a b 2021 2022a b; Gangan et al. 2020). The genus is defined by the presence of a long isthmus muscle reaching anteriorly to the posterior margin of the gill membrane, the urohyal covered by the isthmus muscle, and the presence of prepelvic scutes, in addition to the absence of postpelvic scutes (Whitehead et al. 1988; Wongratana et al. 1999).

Six species of *Stolephorus*, *Stolephorus advenus* Wongratana 1987, *Stolephorus brachycephalus* Wongratana 1983, *Stolephorus carpentariae* (De Vis 1882), *Stolephorus grandis* Hata and Motomura 2021, *Stolephorus nelsoni* Wongratana 1987, and *Stolephorus waitei* Jordan and Seale 1926 are recognized as endemic to the Australian Continent (Whitehead et al. 1988; Wongratana et al. 1999; Hata and Motomura 2018c; Hata et al. 2019).

During a revisionary study of *Stolephorus*, 30 specimens from Van Diemen Gulf, Northern Territory, Australia were found to be characterized by a unique combination of characters among congeners. This new species is described here.

## MATERIALS AND METHODS

Counts and measurements follow Hata and Motomura (2017). All measurements were made to the nearest 0.01 mm using digital calipers. “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

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scute, posterior to the pelvic scute, and anterior to the dorsal-fin origin, respectively. Abbreviations are as follows: SL, standard length (snout tip to posterior extremity of the hypurals); HL, head length (snout tip to posteriormost point of opercle); UGR, LGR and TGR, rakers on upper limb, lower limb and total gill rakers, respectively, with numbers associated indicating the specific gill arch. Institutional abbreviations follow Sabaj (2020). ANCOVA (analysis of covariance) and PCA (principal component analysis) were performed with EZR (Kanda 2012).

## RESULTS

### *Stolephorus lotus* sp. nov.

(New English name: Lotus Anchovy)
(Figs. 1, 2; Tables 1–4)
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*Holotype*: NTM S. 15265-006, 40.0 mm SL, west of Pocock's Beach, Finke Bay, southern part of Van Diemen Gulf, Northern Territory, Australia (12°13'33"S, 132°09'32"E) 3m depth, 6 July 1999, coll. by A. Pickworth et al.

*Paratypes*: 29 specimens (31.6–40.6 mm SL), all collected with the holotype: KAUM–I. 157133, 1 (39.8 mm SL); KAUM–I. 157134, 1 (38.6 mm SL); NSMT-P 141107, 1 (39.4 mm SL); NSMT-P 141108, 1 (37.7 mm SL); NTM S. 15265-009, 25 (31.6–40.6 mm SL).

*Diagnosis*: A species of *Stolephorus* with the following unique combination of characters: maxilla long, 86.7–92.6% HL (mean 89.4%), its posterior tip just reaching to or slightly beyond posterior margin of opercle; posterior margin of preopercle concave, indented; predorsal scutes absent; prepelvic scutes 6–8 (modally 6); pelvic scute without spine; dorsal fin with three unbranched and 11–13 (modally 13) branched rays; anal fin with three unbranched and 16–18 (modally 17) branched rays, its origin located just below origin of sixth to eighth dorsal-fin ray; 1UGR 15–17 (modally 15), 1LGR 21–23 (modally 22), 1TGR 36–39 (modally 37); 2UGR 10 or 11 (modally 11), 2LGR 19 or 20 (modally 20), 2TGR 29–31 (modally 31); 3UGR 8 or 9 (modally 9), 3LGR 11–12 (modally 12), 3TGR 19–21 (modally 20); 4UGR 6 or 7 (modally 6), 4LGT 8–10 (modally 9), 4TGR 14–17 (modally 15); gill rakers 3 or 4 (modally 4) on hind face of third gill arch; transverse scales 8 or 9 (modally 9); pseudobranchial filaments 16–18 (modally 18); paired dark patches on parietal region; no dark lines on dorsum; no black spots on suborbital area and tip of lower jaw; depressed pelvic fin not reaching posteriorly to vertical through dorsal-fin origin; pre-dorsal fin length short, 48.6–52.9% SL (mean 51.2%); body rather elongate, its depth 15.9–17.7% SL (mean 17.1%); anal-fin base short, 17.2–20.2% SL (mean 18.8%); caudal peduncle long, 20.1–22.8% SL (mean 21.0%).

*Description*: Data for holotype presented in parentheses. Counts and measurements, expressed as percentages of SL or HL (Tables 1 and 2). Body laterally compressed, elongate, deepest at dorsal-fin origin; dorsal profile of head and body slightly convex from snout tip to dorsal-fin origin, gently lowering to uppermost point of caudal-fin base; ventral profile of head and body slightly convex from lower jaw tip to pelvic-fin insertion, thereafter slowly rising to lowermost point of caudal-fin base; abdomen somewhat rounded, covered with six to eight (seven) spine-like scutes; 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 beyond posterior margin of eye; maxilla long, its posterior tip pointed, just reaching to or slightly beyond (just reaching to) posterior margin of opercle (Fig. 2); lower jaw slender; single row of conical teeth on both jaws, palatine, and inner side of pterygoid; several distinct conical teeth on vomer; no teeth on upper edges of anterior and posterior ceratohyals; several rows of small fine conical teeth on basihyal and basibranchial; eye large, round, covered with adipose eyelid, laterally on head and 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 concave, 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, visible from side of head when mouth opened; single row of small spines on both of anterior and posterior 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 membrane on each side joined distally, most of isthmus muscle exposed, not covered by gill membrane; sensory canal on preopercle having many branches, one of them extending on opercle; branch on opercle finely branched; body scales deciduous, all scales on body and fin bases completely lacking on all specimens examined in this study; 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; three anteriormost rays of dorsal and anal fins unbranched; anteriormost three rays of both dorsal and anal fins closely spaced; first dorsal- and anal-fin rays reduced; anal-fin origin just below base of sixth to eighth (seventh) dorsal-fin ray; posterior tip of depressed anal fin not reaching caudal-fin base; uppermost pectoral-fin ray unbranched, inserted below body axis; 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; posterior tip of depressed pelvic fin not reaching vertical through dorsal-fin origin; caudal fin forked, posterior tips pointed.

*Coloration of preserved specimens*: Body uniformly pale, light ivory longitudinal band narrower than eye running just behind upper opercular margin to caudal-fin base. No melanophores scattered on head and dorsum except for paired dark patches on parietal region. Ground color of fin rays transparent, colorless. Melanophores scattered along fin rays of caudal fin and anal-fin base. Melanophores dense, forming a dark spot centrally at base of lower lobe of caudal fin. Melanophores scattered on gill rakers. Peritoneum darkly pigmented. Fresh coloration unknown.

*Distribution*: Currently known only from Van Diemen Gulf, Northern Territory, Australia.

*Biological notes*: Ovarian eggs (oval shape, *ca.* 0.5 and 0.2 mm major and minor diameters, respectively) were found in three paratypes (NTM S. 15265-009), indicating that the species is mature at < 40 mm SL.

*Etymology*: The specific name "lotus", to be treated as a noun in apposition, refers to waterlilies, characterized by notched leaves, reminiscent of the indented preopercle of the new species.

*Comparisons*: *Stolephorus lotus* sp. nov. is

**Table 1.** Counts of specimens of *Stolephorus lotus* sp. nov.

| | Holotype | Paratypes | | *t*-test | |
|---|---|---|---|---|---|
| | NTM S. 15265-006 | *n* = 29 | | vs. *S. acinaces* | vs. *S. andhraensis* |
| Standard length (mm) | 40.0 | 31.6–41.6 | Modes | *p* value | |
| Dorsal-fin rays (unbranched) | 3 | 3 | 3 | 1 | 1 |
| Dorsal-fin rays (branched) | 11 | 11–13 | 13 | 0.0004** | 0.0564 |
| Anal-fin rays (unbranched) | 3 | 3 | 3 | 1 | 1 |
| Anal-fin rays (branched) | 17 | 16–18 | 17 | 0.2687 | 0.0558 |
| Pectoral-fin rays (unbranched) | 1 | 1 | 1 | 1 | 1 |
| Pectoral-fin rays (branched) | 11 | 10–12 | 11 | 0.0767 | 0.5798 |
| Pelvic-fin rays (unbranched) | 1 | 1 | 1 | 1 | 1 |
| Pelvic-fin rays (branched) | 6 | 6 | 6 | 1 | 1 |
| Gill rakers on 1st gill arch (upper) | 16 | 15–17 | 15 | 0.2513 | 0.0000** |
| Gill rakers on 1st gill arch (lower) | 22 | 21–23 | 22 | 0.3717 | 0.0000** |
| Gill rakers on 1st gill arch (total) | 38 | 36–39 | 37 | 0.7346 | 0.0000** |
| Gill rakers on 2nd gill arch (upper) | 10 | 10–11 | 11 | 0.0000** | 0.0000** |
| Gill rakers on 2nd gill arch (lower) | 19 | 19–20 | 20 | 0.0571 | 0.0000** |
| Gill rakers on 2nd gill arch (total) | 29 | 29–1 | 31 | 0.0011* | 0.0000** |
| Gill rakers on 3rd gill arch (upper) | 8 | 8–9 | 9 | 0.0006** | 0.0000** |
| Gill rakers on 3rd gill arch (lower) | 11 | 11–12 | 12 | 0.0003** | 0.0000** |
| Gill rakers on 3rd gill arch (total) | 19 | 19–21 | 20 | 0.0001** | 0.0000** |
| Gill rakers on 4th gill arch (upper) | 6 | 6–7 | 6 | 0.1877 | 0.7571 |
| Gill rakers on 4th gill arch (lower) | 9 | 8–10 | 9 | 0.1328 | 0.0013* |
| Gill rakers on 4th gill arch (total) | 15 | 14–17 | 15 | 0.9071 | 0.0142* |
| Gill rakers on posterior face of 3rd gill arch | 4 | 3–4 | 4 | 0.0485* | 0.1154 |
| Prepelvic scutes | 7 | 6–8 | 6 | 0.0197* | 0.0010** |
| Scale rows in longitudinal series | 37 | 37–39 | 38 | 0.0000** | 0.0000** |
| Predorsal scales | 20 | 20–21 | 20 | 0.0000** | 0.0000** |
| Transverse scales | 8 | 8–9 | 9 | 0.2555 | 0.0016* |
| Pseudobranchial filaments | 18 | 16–18 | 18 | 0.0205* | 0.0767 |
| Vertebrae | | 38–39 | 39 | 0.4324 | 0.6559 |
| Number of dorsal-fin rays before anal-fin origin | 7 | 6–8 | 7 | 0.0000** | 0.0000** |

*: significant at 5% level. **: significant at 0.1% level.

easily distinguished from all congeners, except *Stolephorus acinaces* Hata, Lavoué and Motomura 2020, *Stolephorus andhraensis* Babu Rao 1966, *S. carpentariae*, *Stolephorus hindustanensis* Hata and Motomura 2022, *Stolephorus holodon* (Boulenger 1900), *Stolephorus ronquilloi* Wongratana 1983, and *Stolephorus tamilensis* Gangan, Pavan-Kumar, Jahageerdar and Jaiswar 2020 in having a long maxilla with the posterior tip just reaching or extending slightly beyond the posterior margin of the opercle, the posterior margin of preopercle indented, no spots on the suborbital area or snout and mandible tips, the pelvic scute without a spine, and predorsal scutes absent (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a–d 2021a–c, 2022; Hata et al. 2019 2020a b 2021 2022a b; Gangan

**Table 2.** Morphometrics of specimens of *Stolephorus lotus* sp. nov.

| | Holotype | Paratypes | | ANCOVA | |
|---|---|---|---|---|---|
| | NTM S. 15265-006 | *n* = 29 | | vs. *S. acinaces* | vs. *S. andhraensis* |
| Standard length (mm; SL) | 40.0 | 31.6–41.6 | Means | *p* value | |
| As % of SL | | | | | |
| Head length (HL) | 22.7 | 22.2–25.1 | 23.3 | 0.0000** | 0.0016* |
| Body depth | 17.7 | 15.9–17.7 | 17.1 | 0.0000** | 0.0000** |
| Pre-dorsal fin length | 51.5 | 48.6–52.9 | 51.2 | 0.0000** | 0.0000** |
| Snout tip to pectoral-fin insertion | 25.7 | 24.8–26.7 | 25.6 | 0.0000** | 0.2192 |
| Snout tip to pelvic-fin insertion | 42.1 | 42.0–45.7 | 43.9 | 0.0037* | 0.9106 |
| Snout tip to anal-fin origin | 60.2 | 59.1–62.7 | 61.0 | 0.0011* | 0.0043* |
| Dorsal-fin base length | 14.3 | 13.4–15.8 | 14.7 | 0.0009** | 0.0260* |
| Anal-fin base length | 20.2 | 17.2–19.8 | 18.8 | 0.9367 | 0.0000** |
| Caudal-peduncle length | 20.1 | 20.1–22.8 | 21.0 | 0.1961 | 0.0000** |
| Caudal-peduncle depth | 8.9 | 8.2–9.8 | 9.2 | 0.2615 | 0.5160 |
| Orbit diameter | 8.0 | 7.1–8.7 | 8.2 | 0.0000** | 0.1985 |
| Eye diameter | 5.9 | 6.4–7.7 | 6.9 | 0.5253 | 0.7497 |
| Snout length | 3.8 | 3.5–4.0 | 3.8 | 0.0000** | 0.0002** |
| D–P1 | 33.5 | 32.7–36.1 | 34.3 | 0.9749 | 0.7939 |
| D–P2 | 22.0 | 20.5–23.0 | 21.9 | 0.3454 | 0.6464 |
| D–A | 18.1 | 18.1–19.9 | 19.0 | 0.0000** | 0.0000** |
| P1–P2 | 17.6 | 16.5–20.4 | 18.9 | 0.0062* | 0.0143 |
| P2–A | 17.6 | 17.5–20.3 | 18.9 | 0.4599 | 0.0106* |
| Pectoral-fin length | 14.8 | 13.1–15.1 | 14.3 | 0.2356 | 0.0934 |
| Pelvic-fin length | 7.6 | 6.7–8.0 | 7.4 | 0.0235* | 0.5218 |
| Maxilla length | 20.3 | 20.2–22.1 | 20.8 | 0.0018* | 0.0000** |
| Mandibular length | 15.8 | 15.0–16.6 | 15.9 | 0.0000** | 0.0096* |
| Supramaxilla end to maxilla end | 6.3 | 5.2–6.6 | 6.0 | 0.6678 | 0.0000** |
| 1st unbranched dorsal-fin ray length | 1.8 | 1.1–2.3 | 1.6 | 0.0000** | 0.0155* |
| 2nd unbranched dorsal-fin ray length | 7.4 | 7.2–8.6 | 7.9 | none | 0.0122* |
| 3rd dorsal-fin ray length | 16.4 | 15.2–17.7 | 16.5 | 0.2846 | 0.0003** |
| 1st unbranched anal-fin ray length | 2.2 | 1.0–2.2 | 1.6 | 0.0016* | 0.0003** |
| 2nd unbranched anal-fin ray length | 5.8 | 4.7–6.4 | 5.5 | 0.1678 | 0.4144 |
| 3rd anal-fin ray length | 13.6 | 11.7–14.0 | 13.1 | 0.7076 | 0.5894 |
| As % of HL | | | | | |
| Orbit diameter | 35.2 | 30.9–37.1 | 35.1 | 0.2252 | 0.3198 |
| Eye diameter | 25.9 | 26.9–33.0 | 29.8 | 0.0001** | 0.0198 |
| Snout length | 16.9 | 15.0–17.4 | 16.3 | 0.8833 | 0.0432 |
| Maxilla length | 89.3 | 86.7–92.6 | 89.4 | 0.0000** | 0.0000** |
| Interorbital width | 21.3 | 19.6–22.7 | 21.2 | 0.1082 | 0.0007** |
| Postorbital length | 49.7 | 48.6–53.0 | 49.9 | 0.0946 | 0.0327* |

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). *: significant at 5% level. **: significant at 0.1% level.

et al. 2020). The numbers of lower and total gill rakers on first gill arch separate *S. lotus* (1LGR: 21–23; 1TGR 36–39) from *S. hindustanensis* (1LGR 24–27; 1TGR 42–46), *S. holodon* (1LGR 25–30; 1TGR 44–51, based on specimens examined in this study), *S. ronquilloi* (1LGR 28 or 29; 1TGR 47–49), and *S. tamilensis* (1LGR 25–28; 1TGR 40–47). Moreover, the new species differs from *S. hindustanensis* and *S. ronquilloi* in lacking double dark lines on the dorsum posterior to the dorsal fin (vs. distinct double pigmented lines exist in the other two) and in having an elongate body (body depth 15.9–17.7% of SL in *S. lotus* vs. more than 21.1%). *Stolephours lotus* is further distinguished from *S. tamilensis* by its slender body (body depth 15.9–17.7% of SL in *S. lotus* vs. 19.9–23.4% of SL in *S. tamilensis*), greater distance between the snout tip to the pectoral-fin insertion (24.8–26.7% of SL vs. 21.6–24.0%), and the longer maxilla (86.7–92.6% of HL vs. 64.4–76.7%). In addition, the new species differs from *S. carpentariae* in having the anal fin with 16–18 branched fin rays (vs. 19 or 20 in *S. carpentariae*), its origin below the sixth to eighth dorsal-fin ray bases (vs. second to sixth dorsal-fin rays) and 16–18 pseudobranchial filaments (vs. 11–14) (Wongratana 1987a b; Whitehead et al. 1988; Wongratana et al. 1999; Gangan et al. 2020; Hata and Motomura 2022; this study).

Counts of longitudinal series of scale rows and predorsal scales of *S. lotus* sp. nov. [37–39 (modally 38) and 20 or 21 (20), respectively] are higher than those in *S. acinaces* [35–38 (36) and 18 or 19 (19), respectively] and *S. andhraensis* [35–38 (36) and 17–19 (19), respectively; Table 3]. In addition, the anal-fin

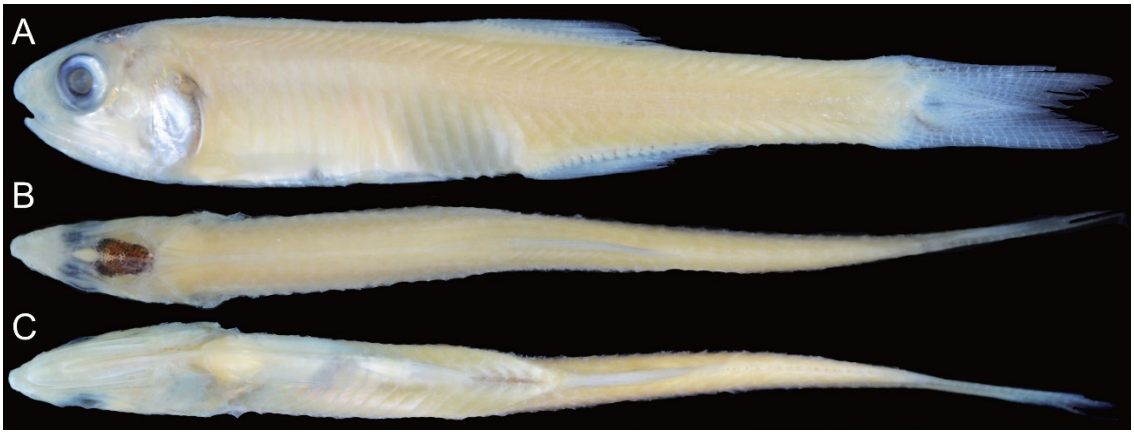


**Fig. 1.** (A) Lateral, (B) dorsal, and (C) ventral views of holotype of *Stolephorus lotus* sp. nov. (NTM S. 15265-006, 40.0 mm SL, Van Diemen Gulf, Northern Territory, Australia).

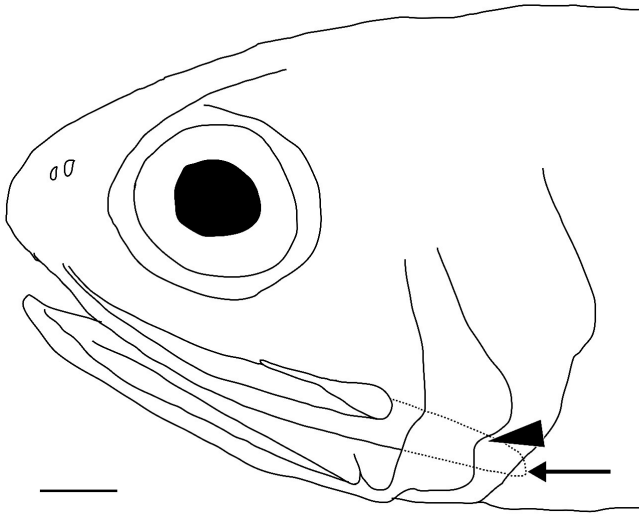

**Fig. 2.** Head of paratype of *Stolephorus lotus* sp. nov., NTM S. 15265-009, 36.2 mm SL, Van Diemen Gulf, Northern Territory, Australia. Dots indicate posterior part of maxilla. Triangle and arrow indicate cavity of preopercle and posterior tip of maxilla, respectively. Scale bar indicates 1 mm.

origin in *S. lotus* sp. nov. is located more anteriorly than in *S. acinaces* and *S. andhraensis* (anal fin originating below bases of sixth to eighth dorsal-fin rays in *S. lotus* sp. nov. vs. eighth to tenth dorsal-fin rays). Also, the number of branched dorsal-fin rays in the new species is usually lower than in *S. acinaces* and *S. andhraensis* (11–13 vs. 12–14, respectively; Table 4). The new species is also distinguished from *S. acinaces* by its shorter head [22.2–25.1% SL (22.2–24.0% in specimens 35–41 mm SL) vs. 23.0–25.5% (24.0–25.5% in specimens 35–41 mm SL)] and predorsal-fin length (48.6–52.9% SL vs. 51.8–55.8%), a narrower body (15.9–17.7% SL vs. 17.0–21.9%), and longer maxilla (86.7–92.6% HL vs. 75.5–87.4%) (Fig. 3, Table 2; Hata et al. 2020b: table 3). It differs from *S. andhraensis* in having slightly higher counts of TGR on each gill arch (36–39, 29–31, 19–21 TGR on 1st, 2nd, and 3rd gill arches, respectively vs. 33–37, 26–29, 17–19, respectively in *S. andhraensis*) and a longer caudal peduncle (20.1–22.8% SL vs. 16.9–19.9%) (Figs. 4, 5, Tables 1, 2; Hata et al. 2020b: tables 2, 3).

Welch's *t*-test for comparison of meristic characters between *S. lotus* and *S. acinaces* showed that *p* values of 8 and 4 characters in the pair were $< 0.01$ and $0.1 < p < 5$, respectively, with no significant differences in other meristic characters (Table 1). In addition, ANCOVA analysis of 35 morphometric characters showed significant differences ($p < 5$) in 18 (head length, body depth, pre-dorsal-fin length, snout tip to pectoral-fin insertion, snout tip to pelvic-

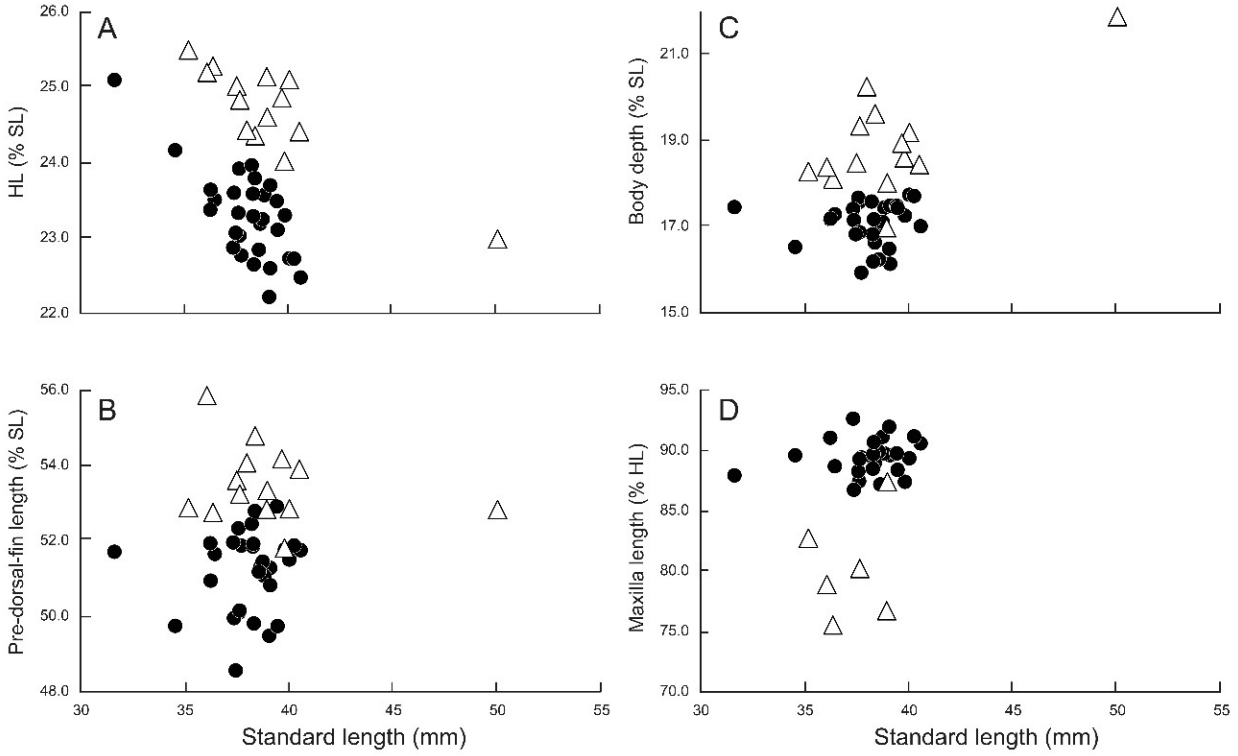


**Fig. 3.** Relationships of selected measurements relative to standard length (SL) or head length (HL) versus SL in *Stolephorus lotus* sp. nov. (circles) and *S. acinaces* (triangles). A, head length (as % of SL); B, predorsal fin length as % SL; C, body depth as % SL; D, maxilla length as % HL.

**Table 3.** Frequency distribution of longitudinal series of scale rows in *Stolephorus lotus* sp. nov., *S. acinaces*, and *S. andhraensis*

| | | Longitudinal series scale rows | | | | |
|---|---|---|---|---|---|---|
| | | 35 | 36 | 37 | 38 | 39 |
| *Stolephorus lotus* sp. nov. | *n* = 30 | | | 9 | 16 | 5 |
| *Stolephorus acinaces* | *n* = 14 | 5 | 6 | 2 | 1 | |
| *Stolephorus andhraensis* | *n* = 22 | 2 | 10 | 8 | 2 | |

fin insertion, pre-anal-fin length, dorsal-fin base length, orbit diameter, snout length, distance between dorsal-fin origin to anal-fin origin, distance between insertions of pectoral and pelvic fins, pelvic-fin length, maxilla length, mandibular length, first dorsal-fin ray length, first anal-fin ray length in % SL and eye diameter and maxilla length in % HL) between *S. lotus* and *S. acinaces* (Table 2).

Comparing *S. lotus* with *S. andhraensis*, Welch's *t*-test for comparison of meristic characters between *S. lotus* and *S. andhraensis* showed that *p* values of 13 and 3 characters in the pair were < 0.01 and 0.1 < *p* < 5, respectively, with no significant differences in other meristic characters (Table 1). Additionally, ANCOVA analysis of 35 morphometric characters showed significant differences ($p < 5$) in 20 (head length, body depth, pre-dorsal-fin length, pre-anal-fin length, dorsal-fin base length, anal-fin base length, caudal-peduncle length, snout length, distance between dorsal-fin origin to anal-fin origin, distance between pelvic-fin insertion to anal-fin origin, maxilla length, mandibular length, distance between posterior ends of supramaxilla and maxilla, lengths of first dorsal, second, and third dorsal-fin rays and first anal-fin ray length in % SL and maxilla length, interorbital width and postorbital length in % HL) between *S. lotus* and *S. andhraensis* (Table 2).

A PCA plotting graph of the three species of *Stolephorus* based on 29 morphological characters is shown in figure 6. PCA yielded six PCs (with eigenvalue > 1), responsible for 79.38% variation in the morphological data (Table 5). PC1, PC2 and PC3

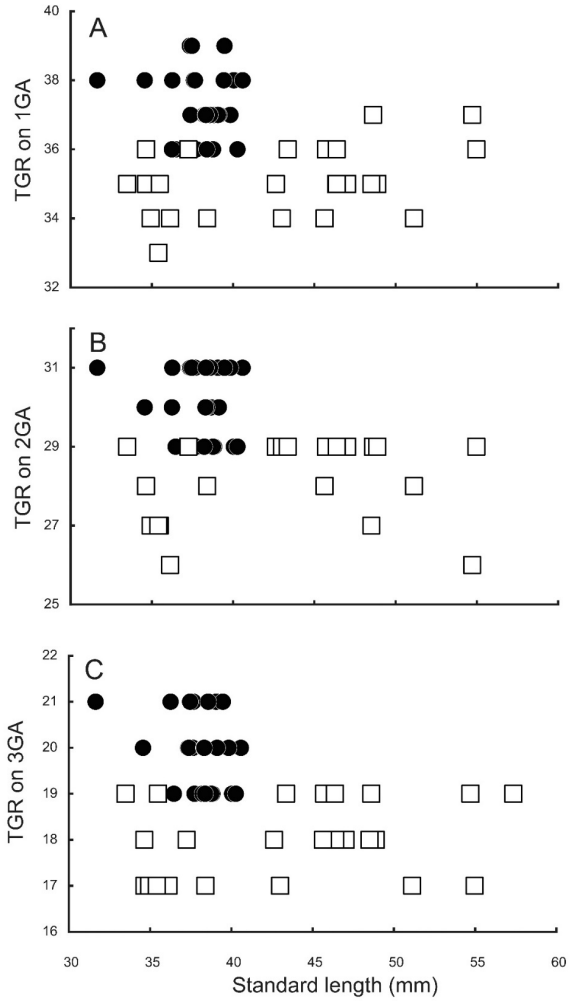


**Fig. 4.** Relationships of total gill raker numbers (TGR) on (A) first gill arch (1GA), (B) second gill arch (2GA) and (C) third gill arch (3GA) to SL in *Stolephorus lotus* sp. nov. (circles) and *S. andhraensis* (squares).

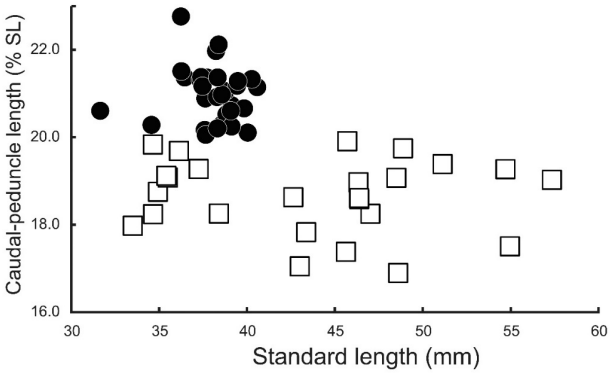


**Fig. 5.** Relationships of caudal-peduncle length to SL in *Stolephorus lotus* sp. nov. (circles) and *S. andhraensis* (squares).

**Table 4.** Frequency distribution of branched dorsal-fin rays in *Stolephorus lotus* sp. nov., *S. acinaces*, and *S. andhraensis*

| | | Branched dorsal-fin rays | | | |
|---|---|---|---|---|---|
| | | 11 | 12 | 13 | 14 |
| *Stolephorus lotus* sp. nov. | *n* = 30 | 5 | 10 | 15 | |
| *Stolephorus acinaces* | *n* = 14 | | 1 | 12 | 1 |
| *Stolephorus andhraensis* | *n* = 25 | | 9 | 15 | 1 |

accounted for 24.89%, 15.27%, and 11.85% variation, respectively. The loading matrix on PC1, PC2, and PC3 identified 9 characters with high loading (> 0.3). These are head length, lower-jaw length, distance between origins of dorsal fin and anal fin, 1LGR, 1TGR, 2UGR, 3UGR, 3LGR, and 3TGR (Table 6). The PC1 vs. PC1 plot unambiguously separated *S. lotus* from *S. acinaces* and *S. andhraensis* (Fig. 6).

## DISCUSSION

Although Wongratana et al. (1999), Paxton et al. (2006), and Larson et al. (2013) included the north and northeastern coasts of Australia in the distributional range of *S. andhraensis*, no specimens of that species collected from Australian waters were found in this study. Therefore, the aforementioned Australian records were probably based on *S. lotus* sp. nov., which the number of Australian endemic species of *Stolephorus* to six. Regarding a number of species of the genus *Stolephorus* that have long been considered distributed in both Southeast Asia (Sunda Shelf) and the Australian Continent (Australia and New Guinea): recent studies have shown that species distributed in these two regions are also geographically separated, as in the case of *S. andhraensis* and *S. lotus* sp. nov. *Stolephorus waitei*, which until recently had been regarded as widely distributed in the Indo-West Pacific (*e.g.*, Whitehead et al. 1988; Wongratana et al. 1999), was shown by Hata et al. (2019) to comprise three species, *Stolephorus bataviensis* Hardenberg 1933 (Taiwan to Indonesia), *Stolephorus baweanensis* Hardenberg 1933 (India to Vietnam and Indonesia), and the "true" *S. waitei* (possibly endemic to the northeastern coast of Australia). *Stolephorus commersonnii* Lacepède 1803, which was regarded by Wongratana et al. (1999) to be distributed in the Indo-West Pacific from the eastern coast of Africa to the northern coast of Australia, is now known to include four species, *Stolephorus rex* Jordan and Seale 1926 (India to the Philippines and Indonesia), *Stolephorus mercurius* Hata, Lavoué and Motomura 2021 (India to Japan), *Stolephorus zephyrus* Hata, Lavoué and Motomura 2021 (eastern coast of Africa), and *Stolephorus grandis* Hata and Motomura 2021 (Hata et al. 2021; Hata and Motomura 2021b). Moreover, *Stolephorus indicus* (van Hasselt 1823), which was regarded by Whitehead et al. (1988) and Wongratana et al. (1999) to be widely distributed in the Indo-West Pacific (from the eastern coast of Africa to China, off the northern coast of Australia, and in French Polynesia) has been recently divided into five species, *Stolephorus balinensis* (Bleeker 1849) (Southeast Asia), *Stolephorus belaerius* Hata, Lavoué and Motomura 2021 (eastern coast of Africa), *S. commersonnii* (Mauritius endemic), "true" *S. indicus* (northern Indian Ocean), and *Stolephorus scitulus* (Fowler 1911) (Fiji to French Polynesia) (Hata et al. 2021). However, the identity of Australian specimens previously identified as *S. indicus* is not yet clear (Hata et al. 2021).

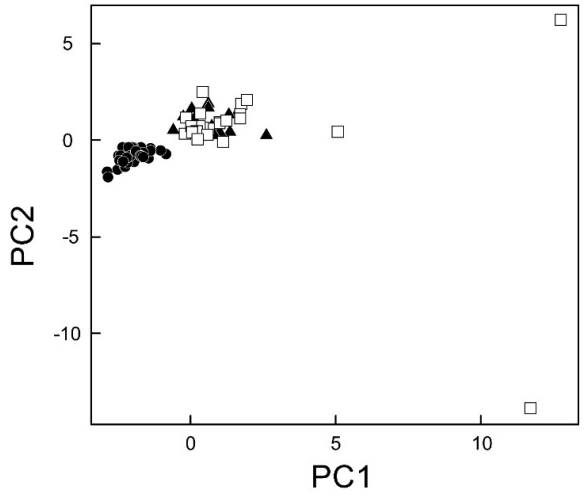


**Fig. 6.** A principal components analysis (PCA) graph plotting the first two components for *Stolephorus lotus* sp. nov. (circles), *S. acinaces* (triangles), and *S. andhraensis* (squares) based on 29 morphological characters.

Species of the genus *Stolephorus* are epipelagic

**Table 5.** Principal component analysis (PCA) of morphometric characters of *Stolephorus lotus* sp. nov., *S. acinaces*, and *S. andhraensis*

| Component | Eigenvalues | % of variance | Cumulative variance |
|---|---|---|---|
| 1 | 7.22 | 24.89 | 24.89 |
| 2 | 4.43 | 15.27 | 40.16 |
| 3 | 3.44 | 11.85 | 52.00 |
| 4 | 2.24 | 7.73 | 59.74 |
| 5 | 1.99 | 6.85 | 66.60 |
| 6 | 1.41 | 4.88 | 71.48 |

(Whitehead et al. 1988; Wongratana et al. 1999). Accordingly, it is likely that the region of deep sea between the Sahul Continent and Sundaland, which existed as an extensive landmass in the last Pleistocene glacial period (Voris 2000), restricted the gene flow between populations in the two areas, thereby promoting the divergence between species. Two nemipterid fishes, *Scolopsis taenioptera* (Cuvier in Cuvier and Valenciennes 1830) and *Scolopsis meridiana* Nakamura, Russell, Moore, and Motomura 2018 are a similar example of allopatrically distributed sister species in the same areas (Hung et al. 2017; Nakamura et al. 2018). However, few surveys of taxonomic and ichthyofaunal studies of Australian species of Engraulidae have been done, therefore further research is needed to determine the patterns of diversification of the Engraulidae in the Australian Continent.

*Comparative material examined*: *Stolephorus acinaces* (14 specimens, 35.2–50.0 mm SL): listed in Hata et al. (2020b); *Stolephorus andhraensis* (25 specimens, 33.5–57.4 mm SL): listed in Hata et al. (2020b) and five additional specimens: HDB-E5-146, 5 specimens, 37.3–43.4 mm SL, eastern Johor Strait, Singapore; *Stolephorus holodon* (15 specimens, 31.5–82.3 mm SL): BMNH 1898.12.17.7–8, syntypes of *Engraulis holodon*, 39.5–41.7 mm SL, Zwartkops River, Algoa Bay, South Africa; BMNH 1970.10.22.25–28, 3 of 4 specimens, 31.5–39.0 mm SL, Maputo Bay, Maputo, Mozambique; RUSI 5320, 71.5 mm SL, Durban, South Africa; RUSI 17380, 67.0 mm SL, estuary of Kwelera, South Africa; RUSI 36158, 82.3 mm SL, Port St. Jones, Transkei District, South Africa; SAM 12747, syntype of *Engraulis holodon*, 39.2 mm SL, Zwartkops River, Algoa Bay, South Africa; SAM 14860, 58.3 mm SL, Durban, South Africa; SAM 24382, 2 specimens, 77.1–80.4 mm SL, ca. 20 km southeast of estuary of Tugela River; SU 31337, 2 specimens, 49.1–77.8 mm SL, Durban, Kwazulu-Natal, South Africa; USNM 437518, 69.2 mm, Delagoa Bay at south end of island near Costa Da Sol some 5 miles northeast of Lourenco Marques on west side of bay, Maputo Province, Mozambique.

**Table 6.** The contribution (loading) of morphometric characters over six principal components (PC 1–6) in *Stolephorus lotus* sp. nov., *S. acinaces*, and *S. andhraensis*

| Character | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| Branched dorsal-fin ray counts | 0.09 | 0.14 | 0.10 | -0.13 | 0.14 | -0.29 |
| Counts of gill rakers on 1st gill arch (upper) | -0.15 | 0.01 | -0.02 | -0.16 | 0.012 | -0.34 |
| Counts of gill rakers on 1st gill arch (lower) | -0.19 | 0.39 | -0.09 | -0.07 | -0.06 | 0.08 |
| Counts of gill rakers on 1st gill arch (total) | -0.19 | 0.39 | -0.09 | -0.06 | 0.06 | 0.03 |
| Counts of gill rakers on 2nd gill arch (upper) | -0.24 | -0.10 | 0.31 | -0.02 | -0.14 | 0.15 |
| Counts of gill rakers on 2nd gill arch (lower) | -0.29 | 0.16 | 0.22 | -0.03 | -0.07 | 0.16 |
| Counts of gill rakers on 2nd gill arch (total) | -0.29 | 0.16 | 0.22 | -0.03 | -0.07 | 0.16 |
| Counts of gill rakers on 3rd gill arch (upper) | -0.26 | -0.15 | 0.30 | -0.02 | -0.04 | -0.10 |
| Counts of gill rakers on 3rd gill arch (lower) | -0.25 | -0.15 | 0.32 | -0.01 | -0.06 | -0.10 |
| Counts of gill rakers on 3rd gill arch (total) | -0.25 | -0.14 | 0.33 | -0.01 | -0.04 | -0.10 |
| Number of scale rows in longitudinal series | -0.04 | -0.08 | -0.16 | -0.22 | -0.22 | -0.11 |
| Predorsal-scale counts | -0.05 | -0.10 | -0.16 | 0.02 | -0.24 | 0.40 |
| Prepelvic-scute counts | -0.15 | -0.12 | -0.003 | 0.26 | -0.08 | -0.25 |
| Number of dorsal-fin rays before anal-fin origin | 0.20 | 0.12 | 0.29 | -0.08 | -0.07 | 0.10 |
| Head length | -0.16 | 0.41 | -0.07 | -0.03 | 0.03 | 0.04 |
| Body depth | 0.20 | 0.13 | 0.29 | 0.12 | 0.16 | 0.16 |
| Pre-dorsal-fin length | 0.20 | 0.17 | 0.16 | 0.12 | -0.15 | -0.02 |
| Snout tip to pectoral-fin insertion | 0.08 | 0.09 | 0.02 | 0.23 | -0.56 | -0.02 |
| Dorsal-fin base length | 0.09 | 0.16 | 0.14 | -0.08 | 0.10 | -0.52 |
| Anal-fin base length | -0.007 | 0.10 | 0.03 | 0.51 | 0.003 | -0.19 |
| Caudal-peduncle length | -0.18 | -0.07 | -0.15 | -0.32 | -0.15 | -0.16 |
| Length of orbit | 0.08 | 0.18 | -0.04 | 0.04 | -0.48 | -0.24 |
| Snout length | 0.22 | 0.13 | 0.03 | 0.17 | -0.18 | -0.06 |
| Distance between origins of dorsal and anal fins | 0.20 | 0.12 | 0.33 | 0.11 | 0.09 | 0.11 |
| Lower-jaw length | -0.18 | 0.41 | -0.08 | -0.03 | 0.02 | 0.03 |
| Supramaxilla end to maxilla end | -0.17 | 0.001 | -0.06 | 0.38 | 0.19 | -0.09 |
| 1st unbranched anal-fin ray length | -0.20 | -0.001 | -0.15 | 0.21 | -0.05 | 0.08 |
| 1st unbranched dorsal-fin ray length | -0.20 | -0.07 | -0.14 | 0.23 | -0.16 | -0.03 |
| 3rd unbranched dorsal-fin ray length | -0.17 | -0.06 | -0.13 | 0.30 | 0.31 | -0.02 |

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

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

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

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

**Ethics approval consent to participate:** Not applicable.

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