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Redescription and extended distribution of a poorly known Australian anchovy, *Stolephorus advenus* (Actinopterygii: Clupeiformes: Engraulidae)

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Abstract

The false Indian anchovy, *Stolephorus advenus* Wongratana, 1987 (Engraulidae), previously known only from the type specimen from the Northern Territory, Australia, is redescribed herewith and its validity confirmed, on the basis of the holotype and nine additional specimens from the northern coast of Australia. Although the significance of differences between *S. advenus* and some congeners with a similarly short maxilla has been unclear, the diagnostic reliability of some characters, including melanophores absent on the dorsal- and anal-fin bases, pectoral fin and occipital region, fewer pseudobranchial filaments, and greater number of prepelvic scutes, is confirmed. An extended distribution of the species around the northern coast of Australia is also reported.

Keywords

Clupeomorpha, ichthyofauna, *Stolephorus balinensis*, *Stolephorus indicus*, taxonomy

Introduction

Stolephorus Lacepède, 1803, an Indo–Pacific genus of marine and/or brackish water anchovies (Engraulidae), comprises 45 valid species (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a, 2018b, 2018c, 2018d, 2021a, 2021b, 2021c, 2022a, 2022b, 2023; Hata et al. 2019, 2020a, 2020b, 2021, 2022a, 2022b, 2023; Gangan et al. 2020). Although the genus was previously considered congeneric with the morphologically similar genus *Encrasicholina* Fowler, 1938 (e.g., Whitehead 1967, 1972; Wongratana 1983), the two genera were separated by Nelson (1983) and Whitehead et al. (1988), with Lavoué et al. (2017) later proposing that *Stolephorus* represented the earliest generic offshoot within Engraulinae. *Stolephorus advenus* Wongratana, 1987 (false Indian anchovy) has been known to date only from the holotype, collected from Cobourg Peninsula, Australia, and was, in all respects, very poorly known.

During an examination of Australian species of *Stolephorus*, nine additional specimens of *S. advenus*, collected from several localities along the northern coast of Australia, were identified. The specimens, with additional morphological and biological information confirming the validity of the species, are described in detail herein.

Methods

Counts and measurements follow Hata and Motomura (2017), and are presented as percentage of standard length or head length. All measurements were made with digital

calipers to the nearest 0.1 mm. "Pelvic scute" refers to the scute associated with the pelvic-fin insertion, whereas "prepelvic", "postpelvic", and "predorsal scutes" refer to the scutes anterior to the pelvic scute, posterior to the pelvic scute, and just anterior to the dorsal-fin origin, respectively. Abbreviations are as follows—SL is the standard length; UGR, LGR, and TGR are the rakers on upper limb, lower limb, and total gill rakers, respectively, with associated numbers indicating the specific gill arch; and SMX-MX is the distance between posterior margins of supramaxilla and maxilla. Institutional abbreviations follow Sabaj (2020).

Comparative material examined. *Stolephorus balinensis* (Bleeker, 1849), 119 specimens, 43.4–148.4 mm SL: listed in Hata and Motomura (2023) and 15 additional specimens: BBM-ICH 1963-1348-38, 3 specimens, 84.1–99.3 mm SL, Muar, Johor Strait, Malaysia; BPBM 19216, 2 of 5 specimens, 98.4–102.0 mm SL, Ambon, Indonesia; BPBM 26469, 2 specimens, 86.0–94.2 mm SL, Cebu Island, Philippines; BPBM 29883, 2 specimens, 124.8–125.3 mm SL, Montong, west coast of Lombok, Indonesia; CAS 230421, 1 of 4 specimens, 91.7 mm SL, southwest of Babelthuap Island, Palau (07°23′17″N, 134°30′40″E), 2–6 feet (approx. 0.6–1.8 m) depth; CAS 235774, 99.9 mm SL, 1 of 3 specimens, mouth of Mae Nam Prasae River, Rayong (12°41′45″N, 101°42′11″E); CAS-SU 29219, 4 specimens, 84.1–89.9 mm SL, Palau.

Stolephorus belaerius Hata, Lavoué et Motomura, 2021, 27 specimens, 63.4–127.1 mm SL: listed in Hata et al. (2021) and 2 additional specimens: CAS 58503, 97.3 mm SL, Mombasa, Kenya; LACM 31618-18, 76.3 mm SL, 1 of 5 specimens, Hasini Creek, Manda Island, Kenya.

Stolephorus commersonnii Lacepède, 1803, 16 specimens, 62.1–112.3 mm SL: listed in Hata et al. (2021).

Stolephorus horizon Hata et Motomura, 2023, 34 specimens, 62.3–108.1 mm SL; *Stolephorus indicus* (van Hasselt, 1823), 41 specimens, 53.3–133.6 mm SL; *Stolephorus meteorum* Hata, Lavoué, Bogorodsky, Alpermann, et Motomura 2023, 20 specimens, 49.2–115.0 mm SL; *Stolephorus scitulus* (Fowler, 1911), 46 specimens, 47.6–102.7 mm SL: listed in Hata and Motomura (2023).

Results

Family Engraulidae
Stolephorus Lacepède, 1803

Stolephorus advenus Wongratana, 1987

English name: false Indian anchovy

(Fig. 1; Tables 1, 2)

Stolephorus advenus Wongratana, 1987—Wongratana (1987a): 106, fig. 2 (type locality: north of Saulte Point, Cobourg Peninsula, Northern Territory, Australia).—Wongratana (1987b: 7 (Cobourg Peninsula, Northern Territory, Australia).—Whitehead et al. (1988): 403, unnumbered figs. (north of Saulte Point, Cobourg Peninsula, Northern Territory, Australia).—Wongratana et al. (1999): 1726, unnumbered figs. (north of Saulte Point, Cobourg Peninsula, Northern Territory, Australia).—Paxton et al. (2006): 314 (north of Saulte Point, Cobourg Peninsula, Northern Territory, Australia).—Hata et al. (2021): 332 (north of Saulte Point, Cobourg Peninsula, Northern Territory, Australia).

Material examined. 10 specimens, 49.1–79.6 mm SL, all specimens collected from Australia.

Holotype. NTM S. 10031-153, 72.2 mm SL, holotype of *Stolephorus advenus*, north of Saulte Point, Cobourg Peninsula, Northern Territory, 18 Oct. 1981, H. Larson leg.

Non-type specimens. CSIRO A 2911, 53.3 mm SL, Gulf of Carpentaria, approx. 13 km east of Sydney Island,

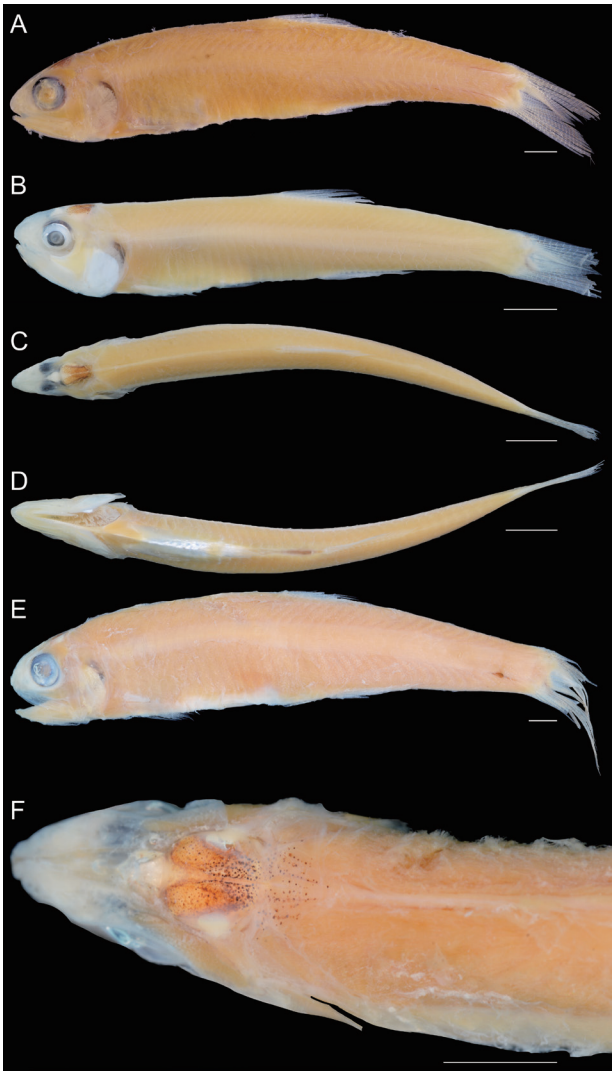

Figure 1. Specimens of *Stolephorus advenus* [**A**: holotype, NTM S. 10031-153, 72.2 mm SL, Cobourg Peinsula, Northern Territory, Australia (photograph taken by S. Tashiro); **B**: lateral, **C**: dorsal, and **D**: ventral views of non-type specimen, NTM S. 13803-003, 49.1 mm SL, Clarence Strait, Northern Territory, Australia (melanophores absent on occipital region); **E**: lateral view of whole body and **F**: dorsal view of head of non-type specimen, CSIRO CA 2688, 79.6 mm SL, Gulf of Carpentaria, Northern Territory (melanophores scattered on occipital region); scale bars indicate 0.5 mm].

Queensland (16°42′36″S, 139°34′48″E), 16.5 m depth; CSIRO A 2916, 56.3 mm SL, CSIRO A 2917, 52.3 mm SL, Gulf of Carpentaria, approx. 14 km east of Sydney Island, Queensland (16°40′12″S, 139°36′30″E), 14.6 m depth; CSIRO B 288, 3 specimens, 53.8–56.3 mm SL, Gulf of Carpentaria, approx. 9 km east of Sydney Island, Queensland (16°43′00″S, 139°33′00″E), 16.5 m depth; CSIRO CA 2555, 74.2 mm SL, approx. 20 km east of Tasman Point, Groote Eylandt, Northern Territory (14°20′S, 136°10′E), 18 m depth; CSIRO CA 2688, 79.6mm SL, north of Groote Eylandt, Gulf of Carpentaria, Northern Territory; NTM S. 13803-003, 49.1 mm SL, Howard Channel, Clarence Strait, Northern Territory (12°05′S, 131°02′E).

Diagnosis. A species of *Stolephorus* with the following combination of characters: maxilla short, 13.7%–14.5% of SL, its posterior tip not reaching anterior margin of preopercle; posterior margin of preopercle convex, rounded; no predorsal scutes; prepelvic scutes 6 or 7 (modally 7); pelvic scute without spine; dorsal fin with three unbranched and 12–15 (14) branched rays; anal fin with three unbranched and 15–17 (16) branched rays, its origin just below base of ninth to eleventh dorsal-fin ray; 1UGR 17–19 (18), 1LGR 24–27 (25), 1TGR 42–45 (42), 2UGR 10–13 (11), 2LGR 20–23 (22), 2TGR 30–35 (33), 3UGR 8–11 (9), 3LGR 11–13 (12), 3TGR 20–22 (21), 4UGR 6–9 (7), 4LGT 9–10 (9), 4TGR 15–18 (17); gill rakers 3 or 4 (4) on posterior face of third gill arch; transverse scales 8; pseudobranchial filaments 15–18 (16); total vertebrae 41 or 42 (42); pelvic fin short, 7.6%–8.0% of SL, tip of depressed pelvic fin not reaching posteriorly to vertical through dorsal-fin origin; head short, 21.6%–22.9% of SL; body rather deep, 17.4%–20.9% of SL; pectoral fin rather long, 13.5%–14.2% of SL; pairs of dark patches on parietal area (sometimes also on occipital area); no dark lines on dorsum; no black spots on suborbital area and tip of lower jaw; no melanophores on bases of dorsal and anal fins, and pectoral fin.

Description. Counts and measurements, expressed as percentages of SL, given in Tables 1 and 2. Body laterally compressed, elongate, deepest at dorsal fin origin. Dorsal profile of head and body gently elevated from snout tip to dorsal-fin origin, thereafter gradually lowering to uppermost point of caudal-fin base. Ventral profile of head and body gently lowering from lower-jaw tip to below pectoral fin, thereafter nearly straight (parallel to body axis) to anal-fin origin, gradually elevated along anal-fin base, thereafter nearly straight (parallel to body axis) to lowermost point of caudal-fin base. Abdomen rounded, covered with six or seven spine-like prepelvic scutes anterior to pelvic fin insertion. Pelvic scute without spine. Postpelvic and predorsal scutes absent. Anus just anterior to anal-fin origin. Snout round, projecting, length less than eye diameter. 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 or-

Table 1. Meristics of examined specimens of *Stolephorus advenus*.

Count	Holotype	Non-types	Modal value
	NTM S. 10031-153	*n* = 9	
Dorsal-fin rays (unbranched)	3	3	3
Dorsal-fin rays (branched)	15	15–17	14
Anal-fin rays (unbranched)	3	3	3
Anal-fin rays (branched)	16	15–17	16
Pectoral-fin rays (unbranched)	1	1	1
Pectoral-fin rays (branched)	16	11–15	12
Pelvic-fin rays (unbranched)	Broken	1	1
Pelvic-fin rays (branched)	Broken	6	6
Caudal-fin rays	19	19	19
Gill rakers on 1st gill arch (upper)	19	17–18	18
Gill rakers on 1st gill arch (lower)	25	24–27	25
Gill rakers on 1st gill arch (total)	44	42–45	42
Gill rakers on 2nd gill arch (upper)	13	10–12	11
Gill rakers on 2nd gill arch (lower)	20	20–23	22
Gill rakers on 2nd gill arch (total)	33	30–35	33
Gill rakers on 3rd gill arch (upper)	11	8–9	9
Gill rakers on 3rd gill arch (lower)	11	11–13	12
Gill rakers on 3rd gill arch (total)	22	20–22	21
Gill rakers on 4th gill arch (upper)	9	6–7	7
Gill rakers on 4th gill arch (lower)	9	9–10	9
Gill rakers on 4th gill arch (total)	18	15–17	17
Gill rakers on posterior face of 3rd gill arch	4	3–4	4
Prepelvic scutes	7	6–7	7
Scale rows in longitudinal series	38	36–38	38
Transverse scales	8	8	8
Pseudobranchial filaments	Broken	15–18	16
Total vertebrae	42	41–42	42
Pectoral-fin rays with melanophores	0	0	0

Table 2. Morphometrics of examined specimens of *Stolephorus advenus*.

Character	Holotype	Non-types	Mean values
	NTM S. 10031-153	*n* = 9	
Absolute values [mm]			
Standard length (SL)	72.2	49.1–79.6	
Relative values (% SL)			
Head length	22.6	21.6–22.9	22.2
Body depth	19.7	17.4–20.9	19.4
Pre-dorsal fin length	53.7	52.1–53.8	53.2
Snout tip to pectoral fin insertion	23.5	21.9–26.0	23.5
Snout tip to pelvic fin insertion	43.0	40.4–43.9	42.4
Snout tip to anal fin origin	62.5	61.0–64.7	62.6
Dorsal fin base length	14.8	13.3–14.3	13.9
Anal fin base length	15.1	14.7–16.3	15.4
Caudal peduncle length	24.8	21.2–23.4	22.7
Caudal peduncle depth	9.1	8.0–8.9	8.6
D–P1	—	34.2–38.9	36.4
D–P2	Broken	21.1–24.4	22.8
D–A	—	18.6–21.1	20.1
P1–P2	Broken	18.0–21.5	19.8
P2–A	Broken	19.8–21.1	20.3
Pectoral fin length	14.1	13.5–14.2	13.8
Pelvic fin length	Broken	7.6–8.0	7.7
Maxilla length	14.3	13.7–14.5	14.2
Mandibular length	14.9	13.5–4.9	14.3
Supramaxilla end to maxilla end	—	1.3–1.9	1.7
1st unbranched dorsal-fin ray length	1.3	1.0–1.7	1.4
2nd unbranched dorsal-fin ray length	6.8	5.7–7.1	6.5
3rd dorsal-fin ray length	Broken	13.4–13.5	13.4
1st unbranched anal-fin ray length	Broken	0.7–1.3	1.0
2nd unbranched anal-fin ray length	4.9	4.0	4.5
3rd anal-fin ray length	Broken	Broken	
Orbit diameter	11.4	7.1–8.4	8.3
Eye diameter	6.9	5.5–6.8	6.4
Snout length	3.3	3.6–4.4	3.8
Interorbital width	—	4.6–5.0	4.9
Postorbital length	9.9	10.5–13.3	11.0

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).

bit. Mouth large, inferior, ventral to body axis, extending backward beyond posterior margin of eye. Maxilla short, its posterior tip slightly short of anterior margin of preopercle. Lower jaw slender. Single row of conical teeth on each jaw and palatines. Several conical teeth on vomer. Small fine teeth patch on pterygoids. No teeth on upper edge of hyoid. Several rows of conical teeth on upper edges of basihyal. Posterior margins of preopercle, subopercle and opercle rounded, smooth. 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 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. 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 closely spaced and unbranched. First dorsal- and anal-fin rays minute. Dorsal profile of dorsal fin elevated from dorsal-fin origin to third fin ray tip, thereafter lowering to last dorsal-fin ray tip. Anal-fin origin just below base of ninth 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 not reaching vertical through pelvic-fin insertion. Dorsal, ventral, and posterior contours of pectoral fin nearly straight. Pelvic fin shorter than pectoral fin; pelvic-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, tips of both lobes pointed.

Coloration of preserved specimens. Body uniformly pale ivory or pale brown. Indistinct light brown longitudinal band narrower than eye running from opercle to caudal-fin base. Paired dark patches on parietal regions, but no melanophores on occipital area (a few melanophores in some specimens). No dark lines on dorsum.

No melanophores on dorsal, pectoral, pelvic, and anal fins, and lateral surface of head. Melanophores scattered along caudal-fin rays. Fins pale, semi-transparent. Melanophores scattered on gill rakers, gill arch, gill filaments, inner side of hyoid, and pseudobranchial.

Distribution. *Stolephorus advenus* has been recorded along the northern coast of Australia from Clarence Strait, Northern Territory to southern Gulf of Carpentaria (around Sydney Island, Queensland) (Wongratana 1987a; Whitehead et al. 1988; Wongratana et al. 1999, this study; Fig. 2).

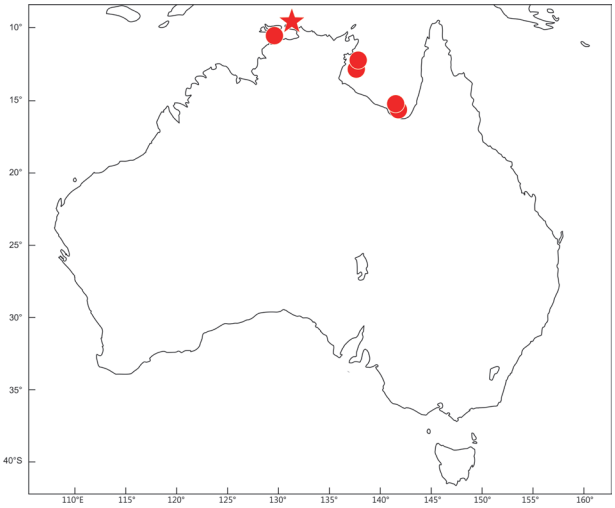

Figure 2. Distributional records of *Stolephorus advenus* based on specimens examined in this study (red star: type locality; red dot: non-type specimens).

Discussion

Stolephorus advenus was described by Wongratana (1987a) based on a single specimen (holotype), collected from Cobourg Peninsula, Australia (Fig. 1A). Although the original description stated that the holotype had five prepelvic scutes and 24 1LGR, re-examination of the specimen confirmed the presence of seven prepelvic scutes and 25 1LGR. The pelvic fin was also missing from the holotype, but Wongratana (1987a) speculated that when depressed, the pelvic fin of *S. advenus* would not have reached the vertical through the dorsal-fin origin. The additional specimens examined in the presently reported study confirm the validity of that speculation. Although Wongratana (1987a) and Wongratana et al. (1999) stated that *S. advenus* lacked melanophores on the occipital region, some of the additional specimens actually have melanophores scattered on that region (Fig. 1F). Furthermore, following their revisional studies of *Stolephorus*, Whitehead et al. (1988) and Wongratana et al. (1999) indicated that *S. advenus* could be distinguished from all congeners, except *Stolephorus indicus*, by the short maxilla (posteriorly not reaching the preopercle posterior margin) and 1LGR fewer than 30. However, since those studies, numerous new or cryptic species of *Stolephorus* have been described, with Whitehead's et al. (1988) "*Stolephorus indicus*" actually representing at least seven species, *Stolephorus balinensis*, *Stolephorus belaerius*, *Stolephorus commersonnii*, *Stolephorus horizon*, *Stolephorus indicus*, *Stolephorus meteorum*, and *Stolephorus scitulus*. Accordingly, *S. advenus* can be presently distinguished from all other congeners, except the latter seven species previously regarded as "*S. indicus*", by having a shorter maxilla (see above), 1LGR fewer than 30, the pelvic fin not reaching posteriorly the vertical through the dorsal-fin origin, and no dark lines on the dorsum. In addition, *S. advenus* differs from all seven species previously included in "*S. indicus*" as follows: maxilla not reaching posteriorly anterior margin of preopercle, 13.7%–14.5% of SL [vs. just reaching or slightly beyond anterior margin; longer than 15% of SL (14.3%–17.5% in *S. balinensis*)]; no melanophores scattered along bases of dorsal and anal fins, or on entire pectoral fin [vs. melanophores present along bases of dorsal and anal fins, and on upper part of pectoral fin (no melanophores on pectoral fin of *S. horizon*)]; ventral scutes 6 or 7 [vs. 5 or fewer (rarely 6 in *S. balinensis* and *S. meteorum*)], and pseudobranchial filaments 15–18 (vs. 19 or more). Furthermore, the shorter head of *S. advenus* (21.6%–22.9% of SL) separates it from *S. horizon* (22.6%–25.2%), *S. indicus* (23.0%–26.7%), and *S. meteorum* (23.7%–26.0%). The body depth of *S. advenus* (17.4%–20.9% of SL) is greater than that of *S. commersonnii* (14.2%–17.8%) and *S. scitulus* (14.6%–16.9%), the pectoral fin is longer (13.5%–14.2% of SL in *S. advenus*) than in *S. balinensis* (11.3%–13.9%), and the pelvic fin is shorter (7.6%–8.0% of SL in *S. advenus*) than in *S. belaerius* (7.9%–10.3%) (Whitehead et al. 1988; Wongratana et al. 1999; Kimura et al. 2009; Hata and Motomura 2018a, 2018b, 2018c, 2018d, 2021a, 2021b, 2021c, 2022a, 2022b, 2023; Hata et al. 2019, 2020a, 2020b, 2021, 2022a, 2022b, 2023; Gangan et al. 2020; this study; Fig. 3).

Although the known distribution of the species was limited to the type locality (Cobourg Peninsula, Northern Territory, Australia), both Whitehead et al. (1988) and Wongratana et al. (1999) suggested that *S. advenus* may be distributed (hence question marks on their distribution maps) along the northern coast of Western Australia and the Gulf of Carpentaria. Such a distribution is partially confirmed in the presently reported study (Fig. 2), since there are still no specimens recorded in Western Australia. The biology or habitat of *S. advenus* is also still totally unknown. Whitehead et al. (1988) and Wongratana et al. (1999) presumed that the species is coastal pelagic, and schooling. The collection of some of the specimens described here in coastal waters 14.6–18 m depth is indeed suggestive that the species is coastal. Based on the standard length of the holotype, Whitehead et al. (1988) and Wongratana et al. (1999) also suggested a maximum standard length of 7.2 cm, which is slightly shorter than the largest specimen (CSIRO CA 2688, 79.6 mm SL) measured in the present study.

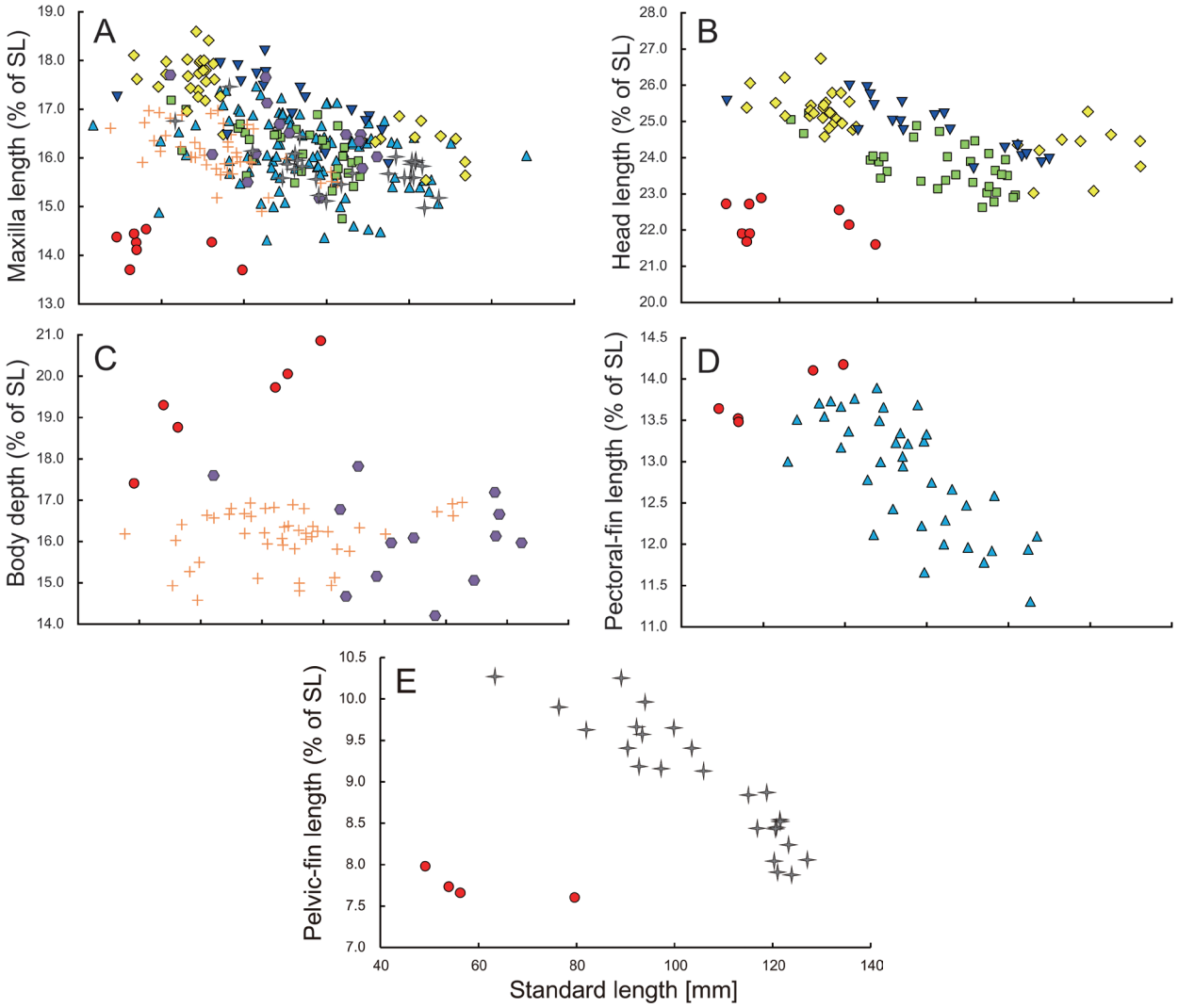

Figure 3. Maxilla length (**A**), head length (**B**), body depth (**C**), pectoral-fin length (**D**), and pelvic-fin length (**E**) (all as % of standard length; SL) relative to SL in *Stolephorus advenus* (red circles), *S. balinensis* (blue triangles), *S. belaerius* (gray stars), *S. commersonnii* (purple hexagons), *S. horizon* (green squares), *S. indicus* (yellow diamonds), *S. meteorum* (dark blue inverted triangles), and *S. scitulus* (orange crosses).

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