

Resurrection of nominal species previously regarded as junior synonyms of *Thrissina baelama* (Fabricius, 1775) and their re-descriptions (Teleostei: Clupeiformes: Engraulidae)

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Abstract. Examination of available type specimens, original descriptions, as well as many non-type specimens collected over extensive geographic ranges, of seven nominal species previously regarded as junior synonyms of *Thrissina baelama* (Fabricius, 1775) confirmed the validities of five taxa. These are *Thrissina evermanni* (Jordan & Seale, 1906), *Thrissina polynemoides* (Günther, 1868), *Thrissina samam* (Montrouzier, 1857), and *Thrissina tuberculosa* (Lacepède, 1803). These four resurrected taxa are re-diagnosed with detailed colour descriptions. Additionally, *Engraulis nesogallicus* Bennett, 1832 and *Engraulis macrops* Kishinouye, 1911 are regarded herein as a junior synonym of *T. tuberculosa* and *T. samam*, respectively. Neotypes are designated for *T. baelama*, *E. nesogallicus*, *T. samam*, and *T. tuberculosa*, with clarification of their taxonomic histories.

Key words. *Thryssa baelama*, *Thrissina encrasicholoides*, taxonomy, neotype, Actinopterygii, Clupeomorpha

INTRODUCTION

The genus *Thrissina* Jordan & Seale, 1925 (Teleostei: Clupeiformes: Engraulidae) is diagnosed by the following suite of characters: presence of both prepelvic and postpelvic scutes, a pectoral fin without a filamentous extension, small conical teeth on both jaws, and a dorsal fin with 12 or more fin rays. There are currently 29 accepted species in this genus, which preferentially inhabit marine and/or estuarine waters in the Indo-Pacific region (Roberts, 1978; Wongratana, 1983, 1987; Whitehead et al., 1988; Wongratana et al., 1999; Gill et al., 2018; Hata & Motomura, 2019; Hata & Nakae, 2019; Hata & Koeda, 2020; Hata, 2020; Hata et al., 2020, 2021b, 2022a).

Traditionally, specimens with a short maxilla, posteriorly not reaching to the preopercle posterior margin; and ventral scutes totalling fewer than 18, have been regarded as a single species widely distributed in the Indo-Pacific, *Thrissina baelama* (Fabricius, 1775) (generic name and authorship frequently treated as *Thryssa* and Forsskål, respectively; Fricke, 2008;

Kottelat, 2013), while seven nominal species, *Clupea tuberculosa* Lacepède, 1803, *Engraulis nesogallicus* Bennet, 1832, *Engraulis encrasicholoides* Bleeker, 1851, *Engraulis samam* Montrouzier, 1857, *Engraulis polynemoides* Günther, 1868, *Anchovia evermanni* Jordan & Seale, 1906, and *Engraulis macrops* Kishinouye, 1911, have been regarded as junior synonyms of *T. baelama* (Weber & de Beaufort, 1913; Fowler, 1941; Whitehead et al., 1966; Whitehead, 1967b, 1972). After the publication of Whitehead's (1972) work, Nelson (1982) proceeded to demonstrate the validity of *E. encrasicholoides* due to the presence of scutes anterior to the pectoral fin and placed the nominal species in the genus *Thrissina*. Whitehead et al.'s (1988) review of the genus followed Nelson's (1982) opinion and defined *T. baelama* as an Indo-Pacific species characterised by a short maxilla with elongated first and second supramaxillae, 18–26 lower gill rakers on the first gill arch, 12–18 abdominal scutes, and no scutes anterior to the pectoral fin (Fig. 1), considering the remaining six nominal species to be junior synonyms of *T. baelama* (Table 1).

Re-examination of specimens previously identified as *T. baelama* revealed consistent differences. Consequently, we re-assessed all seven nominal species treated as junior synonyms of *T. baelama* by Whitehead et al. (1988). We found evidence for the validity of four of these species based on differing gill raker counts, dorsal fin pigmentation, and proportional characters. These five species are allopatric within the Indo-Pacific [the true *Thrissina baelama* (Red Sea endemic), *T. evermanni* (Fiji, Tonga, and Samoa), *T. polynemoides* (eastern coast of Africa and Madagascar), *T. samam* (Japan to New Britain), and *T. tuberculosa* (Mauritius)].

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Table 1. Historical taxonomic statuses of nominal species of *Thrissina* considered in this study.

Nominal species	Whitehead et al. (1988) and Wongratana et al. (1999)	This study
<i>Clupea baelama</i> Fabricius (1775)	valid as <i>Thryssa baelama</i>	valid as <i>Thrissina baelama</i>
<i>Clupea tuberculosa</i> Lacepède 1803	junior synonym of <i>Thryssa baelama</i>	valid as <i>Thrissina tuberculosa</i>
<i>Engraulis nesogallicus</i> Bennett, 1832	junior synonym of <i>Thryssa baelama</i>	junior synonym of <i>Thrissina tuberculosa</i>
<i>Engraulis samam</i> Montrouzier, 1857	junior synonym of <i>Thryssa baelama</i>	valid as <i>Thrissina samam</i>
<i>Engraulis polynemoides</i> Günther, 1868	junior synonym of <i>Thryssa baelama</i>	valid as <i>Thrissina polynemoides</i>
<i>Anchovia evermanni</i> Jordan and Seale, 1906	junior synonym of <i>Thryssa baelama</i>	valid as <i>Thrissina evermanni</i>
<i>Engraulis macrops</i> Kishinouye, 1911	junior synonym of <i>Thryssa baelama</i>	junior synonym of <i>Thrissina samam</i>

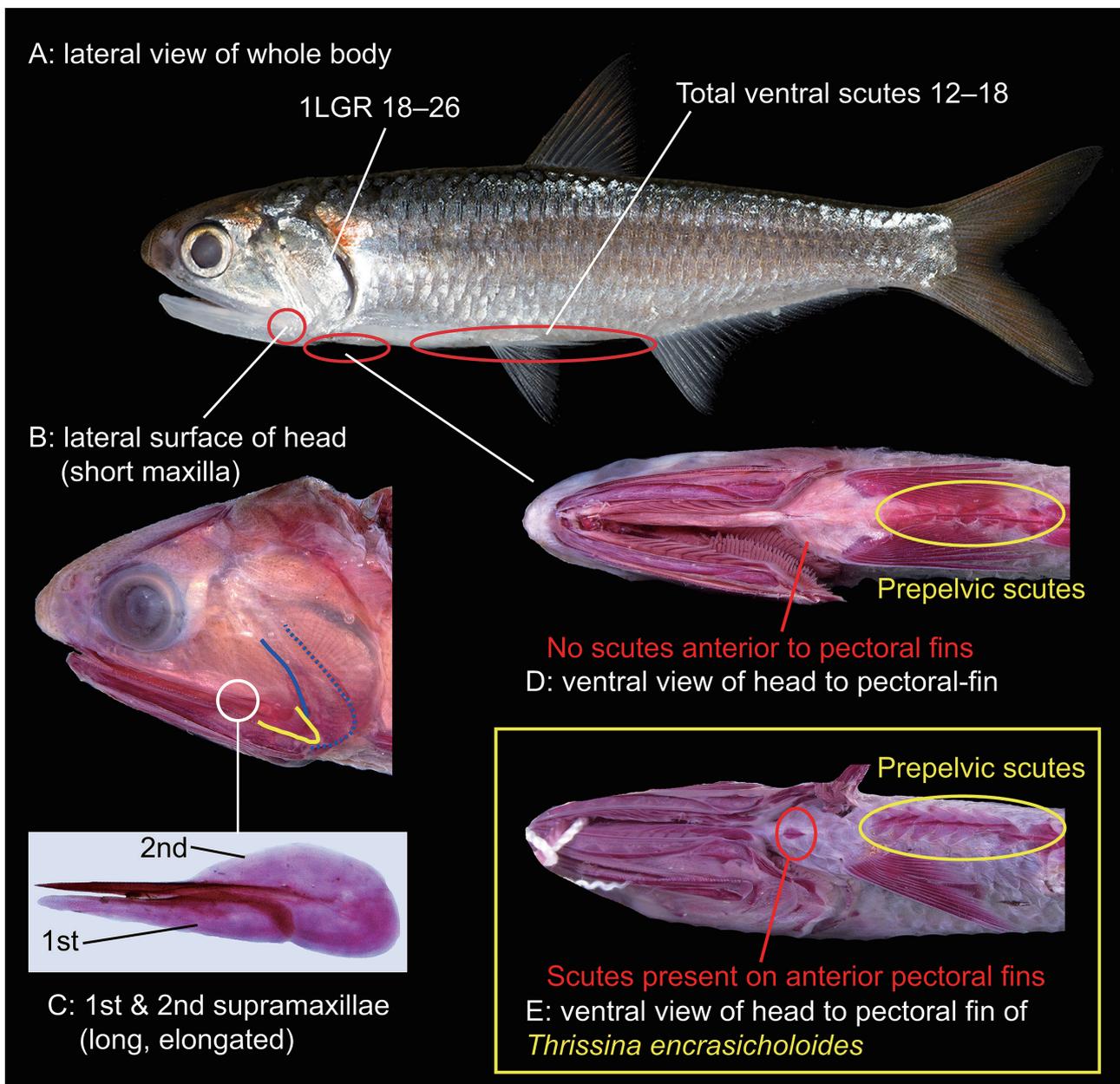


Fig. 1. A–D, Diagnostic characters of species previously identified as *Thrissina baelama* [A, lateral view of whole body, B, head (yellow line indicates posterior part of maxilla; blue line and broken lines indicate anterior and posterior margins of preopercle, respectively), C, first and second supramaxillae (left-right inverted), D, ventral view of isthmus (no scutes located anterior to pectoral fins)] and E, ventral view of isthmus of *Thrissina encrasicholoides* (scutes located anterior to pectoral fins) (A: fresh condition, 72.9 mm SL, Sulawesi, Indonesia; B–D: *T. samam*, NSMT-P 144842, 58.4 mm SL, Ryukyu Archipelago, Japan; E: *T. encrasicholoides*, NSMT-P 50306, 69.8 mm SL, Philippines) (B–E, alizarin stain).

MATERIAL AND METHODS

Counts and proportional measurements follow Hata & Motomura (2019). All measurements were made with digital callipers to the nearest 0.01 mm. Standard and head lengths are abbreviated as SL and HL, respectively. Osteological characters, including vertebral counts, were observed based on radiographs of 25 *T. baelama*, 7 *T. evermanni*, 39 *T. samam*, 9 *T. polynemoides*, and 6 *T. tuberculosa*. Institutional codes follow Sabaj (2020). Analysis of covariance (ANCOVA) was performed with EZR (Kanda, 2012).

RESULTS

The investigation clearly demonstrated morphological differences among the five species previously identified as *Thrissina baelama*. A principle components analysis (PCA), based on 26 measurements shown in Table 2 and total gill rakers (TGR) on the first to fourth gill arches resulted in the separation of the five species, with generally marginal overlaps (Fig. 2). Welch's T-test for comparison of meristic characters among the five species showed significant differences ($p < 5$) in at least four characters between each species (Tables 3–7). In addition, an ANCOVA of 26 morphometric characters of the five species, also shown in Tables 2, 8–11 showed significant differences ($p < 5$) in at least 4 characters between each species.

An identification key to the five species is provided. Four nominal species previously regarded as junior synonyms of *T. baelama* by Whitehead et al. (1988), *T. evermanni*, *T. polynemoides*, *T. samam*, and *T. tuberculosa*, are resurrected. Two other nominal species previously regarded as junior synonyms of *T. baelama*, viz. *Engraulis macrops* Kishinoye, 1911 and *Engraulis nesogallicus* Bennett, 1832, are newly recognised as junior synonyms of *T. samam* and *T. polynemoides* respectively. A summary of the historical changes in the taxonomic status of the different species is given in Table 1.

TAXONOMY

Common features of *Thrissina baelama*, *T. evermanni*, *T. polynemoides*, *T. samam*, and *T. tuberculosa*

Body oblong, laterally compressed, rather elongate, deepest at dorsal-fin origin. Dorsal profile of head and body nearly straight, but gradually elevated from snout tip to dorsal-fin origin, thereafter 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, nearly straight from pelvic-fin insertion to end of anal-fin base, slightly concave at caudal peduncle. A series of hard, well-developed scutes with a sharp posteriorly projecting edge on rounded abdomen, originating posterior to end of pectoral-fin base, ending just before anus. Anus just anterior to anal-fin origin. Caudal peduncle rather compressed.

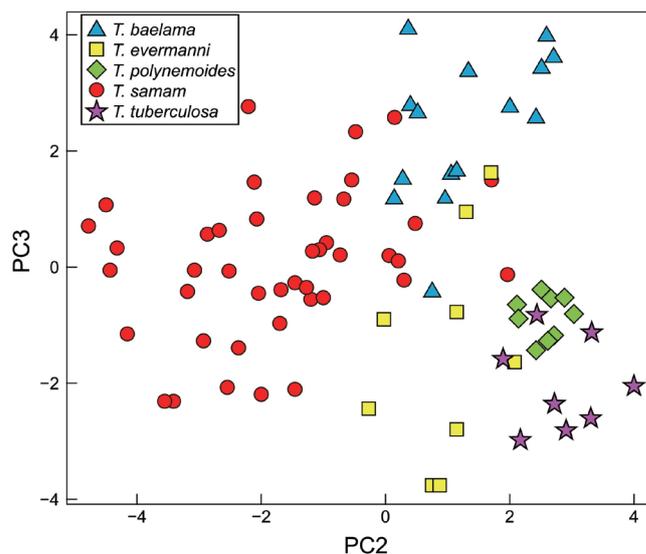


Fig. 2. Scatter plots of principal component 2 and 3 scores on 26 measurements and counts of total gill rakers on first to fourth gill arches for specimens of *Thrissina baelama* (triangles), *T. evermanni* (squares), *T. polynemoides* (diamonds), *T. samam* (circles), and *T. tuberculosa* (stars).

Snout rounded, its length less than eye diameter. Mouth large, inferior, ventral to body axis, extending backward beyond posterior margin of eye. Maxilla short, its posterior tip slightly beyond anterior margin of preopercle, but not reaching to posterior margin. First and second supramaxillae elongate, long. Lower jaw slender, shorter than upper jaw. Single row of small conical teeth on both jaws. Several small conical teeth on vomer. Several rows of conical teeth on palatine. Teeth patches on endopterygoids. No teeth on dorsal surfaces of basihyal and basibranchial. Eye large, round, covered with thin adipose eyelid, positioned laterally on head dorsal to horizontal through pectoral-fin insertion, visible in dorsal view. Pupil round. Orbit elliptical. Nostrils close to each other, anterior to orbit. Posterior margins of preopercle and opercle smooth. Subopercle with rounded posterior margin. Opercular membrane without serrations. Interorbital space flat, its width less than eye diameter. Pseudobranchial filaments present, exposed, length of longest filament shorter than eye diameter. Gill rakers long, slender, rough, visible from side of head when mouth opened. Asperities on gill rakers evenly sized. 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, isthmus muscle mostly exposed (not covered by gill membrane).

Scales cycloid, thin, deciduous except for ventral scutes, absent on head and fins. Scales on lateral surface of body with numerous vertical grooves. Lateral line absent. Dorsal-fin origin posterior to vertical through base of last pelvic-fin ray. Dorsal and anal fins each with minute first ray. Spine-like scute on dorsal-fin origin. Anal-fin origin posterior to posterior end of dorsal-fin base; posterior tip of depressed fin not reaching caudal-fin base. Uppermost pectoral-fin ray unbranched, not extended as filament. Pectoral fin inserted below lateral midline of body; posterior tip of fin pointed; dorsal, ventral, and posterior margins of fin nearly straight.



Fig. 3. A, Neotype of *Clupea baelama*, BMNH 1963.12.9.27, 69.5 mm SL, Red Sea near Port Sudan, Sudan, and B, non-type specimen of *Thrissina baelama* (fresh condition) (BPBM 27411, 83.4 mm SL, Port Sudan, Sudan; courtesy of Bishop Museum).

Pelvic fin shorter than pectoral fin, insertion anterior to dorsal-fin origin; posterior tip of depressed fin pointed, reaching to vertical through middle of dorsal-fin base, not reaching to anus. Caudal fin forked, posterior tips of both lobes pointed, dorsal and ventral margins of both lobes nearly straight.

Key to species previously identified as *Thrissina baelama* by Whitehead et al. (1988)

Note: *Thrissina baelama* sensu Whitehead et al. (1988) was diagnosed by a short maxilla posteriorly not reaching the preopercle posterior margin, and total ventral scutes fewer than 18 and ending anteriorly below the pectoral fin (Fig. 1).

1. 1TGR \leq 36 *T. samam* (Japan to New Guinea)
- 1TGR \geq 38 (36–40 in *T. baelama*) 2
2. Several distinct black blotches on anterior part of dorsal fin ..
..... *T. tuberculosa* (Mauritius)
- Distinct blotches on dorsal fin absent..... 3
3. 1TGR 41 or more
..... *T. polynemoides* (eastern coast of Africa and Madagascar)
- 1TGR 40 or less 4
4. Pre-dorsal-fin length greater than 50.6% of SL; snout longer than 4.9% of SL *T. evermanni* (Fiji to Tonga)
- Pre-dorsal-fin length shorter than 50.4% of SL; snout shorter than 4.8% of SL *T. baelama* (Red Sea)

***Thrissina baelama* (Fabricius, 1775)**

[English name: Baelama Anchovy]

(Fig. 3; Tables 2, 3)

Clupea baelama, *encrasicholus*? (see Remarks): Fabricius, 1775: 72 [original locality: Djiddae (currently Jeddah), Saudi Arabia; type locality, Port Sudan, Sudan, based on newly designated neotype].

Clupea encrasicholus (not of Linnaeus): Niebuhr, 1775: XIII (index of species names)

Clupea baelama: Bloch & Schneider, 1801: 429 (Jeddah, Saudi Arabia).

Thrissina baelama: Whitehead, 1965: 271 (Red Sea and Gulf of Aden).

Thryssa baelama: Whitehead et al., 1988 (in part): 425 (Red Sea); Wongratana et al., 1999 (in part): 1743 (Red Sea).

Neotype. BMNH 1963.12.9.27, 69.5 mm SL, Red Sea near Port Sudan, Sudan.

Other material examined. 25 specimens, 57.5–103.2 mm SL: HUI 20178, 2 specimens, 86.1–92.9 mm SL, Eilat, Israel; BPBM 27411, 10 specimens, 75.0–85.0 mm SL, Port Sudan, Sudan; BMNH 1963.12.9.28–30, 3 specimens, 57.5–61.7 mm SL, Red Sea near Port Sudan, Sudan; BMNH 1963.12.9.1–19, 10 of 19 specimens, 83.3–103.2 mm SL, Gulf of Aden, Djibouti City, Djibouti or Mukalla, Yemen.

Diagnosis. A species of *Thrissina* with the following combination of characters: short maxilla, its posterior tip not

Table 2. Morphometrics of specimens of *Thrissina baelama*.

	<i>Thrissina baelama</i>				
	Neotype	Non-type specimens		ANCOVA	
	BMNH 1963.12.9.27–30A	n = 25	Means ± SD	p values	
Standard length (mm; SL)	69.5	57.5–103.2		5 > p > 0.1	0.1 > p
As % of SL					
Head length (HL)	28.7	25.8–30.8	27.2 ± 1.15	TP, TT	
Body depth	23.0	21.2–26.9	24.5 ± 1.32		TS, TT
Pre-dorsal fin length	48.2	48.0–50.4	49.3 ± 0.83		TE, TP, TS, TT
Snout tip to pectoral-fin insertion	29.8	27.2–31.2	28.8 ± 0.90	TE, TT	
Snout tip to pelvic-fin insertion	46.5	42.9–47.0	44.9 ± 1.29		
Snout tip to anal-fin origin	66.7	64.8–69.6	66.5 ± 1.17		TT
Dorsal-fin base length	10.3	10.0–11.8	11.0 ± 0.53	TS, TT	
Anal-fin base length	26.9	25.0–27.5	26.4 ± 0.68		
Caudal-peduncle length	9.7	8.7–10.4	9.3 ± 0.39		TE, TP, TS, TT
Caudal-peduncle depth	10.2	10.1–11.5	10.5 ± 0.37		TE, TS, TT
D–P1	30.9	29.2–32.0	30.6 ± 0.99		
D–P2	22.7	21.6–26.7	24.5 ± 1.25	TE	TS, TT
D–A	25.8	25.3–30.4	27.9 ± 1.46		
P1–P2	17.7	15.1–18.9	17.0 ± 1.15		
P2–A	20.8	20.1–23.5	22.0 ± 1.00		TT
Orbit diameter	7.7	6.8–8.7	7.5 ± 0.45	TP	TT
Snout length	4.6	3.9–4.8	4.4 ± 0.22		TE, TP, TS, TT
Pectoral-fin length	19.2	16.4–20.1	18.2 ± 1.00	TS, TT	
Pelvic-fin length	14.2	12.6–14.9	13.6 ± 0.60	TP, TS	TT
Maxilla length	22.7	20.6–23.3	21.7 ± 0.70		TP, TT
Lower-jaw length	21.2	18.8–22.4	20.0 ± 0.84	TS	TP, TT
Supramaxilla end to maxilla end	2.6	2.3–3.0	2.6 ± 0.15	TE	
As % of HL					
Orbit diameter	26.8	25.9–28.8	27.5 ± 0.81		TT
Snout length	16.1	15.0–17.7	16.1 ± 0.63		TE, TP, TS, TT
Interorbital width	24.3	22.4–25.8	24.1 ± 0.77		
Postorbital length	58.2	55.1–60.6	58.1 ± 1.63	TP	TT

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); TE (*Thrissina evermanni*); TP (*Thrissina polynemoides*); TS (*Thrissina samam*); TT (*Thrissina tuberculosa*).

reaching to posterior margin of opercle; first supramaxilla elongated, longer than half length of second; abdomen covered with 5–8 + 9–10 = 14–17 keeled scutes; no scutes anterior to pectoral fin; 1UGR 15–18, 1LGR 20–23, 1TGR 36–40; 2UGR 12–15, 2LGR 20–23, 2TGR 33–38; 3UGR 10–13, 3LGR 12–14, 3TGR 23–27; 4UGR 9–11, 4LGR 9–12, 4TGR 18–22; no distinct black blotches on dorsal fin; caudal peduncle rather deep [10.1–11.5% (mean 10.5%) of SL] and short [8.7–10.4% (usually shorter than 10%; mean 9.3%) of SL]; pre-dorsal-fin short, 48.0–50.4% of SL; snout

short, 3.9–4.8% of SL; body rather elongate, 23.0–26.9% (rarely 21.2%; mean 24.5%) of SL.

Colour of fresh specimens. Body uniformly silver. Dorsum bluish-black, upper lateral surface of body greenish-blue. Lateral surface of mid-part of snout transparent. Narrow non-pigmented ring-like band surrounding anterior part of snout. Branches of cephalic lateralis sensory canal on upper part of gill opening orange, forming an orange blotch. Fin rays of dorsal and caudal fins greenish-grey. Dorsal and caudal

Table 3. Meristics of specimens of *Thrissina baelama*.Abbreviations: TE (*Thrissina evermanni*); TP (*Thrissina polynemoides*); TS (*Thrissina samam*); TT (*Thrissina tuberculosa*).

	<i>Thrissina baelama</i>				
	Neotype	Non-type specimens	ANCOVA		
	BMNH 1963.12.9.27–30A	n = 25	Means ± SD	p values	
Standard length (mm; SL)	69.5	57.5–103.2		5 > p > 0.1	0.1 > p
Dorsal-fin rays (unbranched)	3	3	3 ± 0		
Dorsal-fin rays (branched)	12	10–13	12 ± 0.69		
Anal-fin rays (unbranched)	4	3–4	4 ± 0.27	TT	
Anal-fin rays (branched)	28	22–31	28 ± 1.51		
Pectoral-fin rays (unbranched)	1	1	1 ± 0		
Pectoral-fin rays (branched)	12	11–14	12 ± 0.64	TT	
Pelvic-fin rays (unbranched)	1	1	1 ± 0		
Pelvic-fin rays (branched)	6	6	6 ± 0		
Gill rakers on 1st gill arch (upper)	17	15–18	17 ± 0.63		TP, TS, TT
Gill rakers on 1st gill arch (lower)	22	20–23	21 ± 0.74	TE	TP, TS, TT
Gill rakers on 1st gill arch (total)	39	36–40	38 ± 1.17	TE	TP, TS, TT
Gill rakers on 2nd gill arch (upper)	13	12–15	13 ± 0.78		TP, TS, TT
Gill rakers on 2nd gill arch (lower)	21	20–23	21 ± 0.68		TE, TS, TP, TT
Gill rakers on 2nd gill arch (total)	34	33–38	34 ± 1.16		TE, TS, TP, TT
Gill rakers on 3rd gill arch (upper)	11	10–13	11 ± 0.64	TE	TS, TP, TT
Gill rakers on 3rd gill arch (lower)	14	12–14	14 ± 0.70	TE, TT	TP, TS
Gill rakers on 3rd gill arch (total)	25	23–27	26 ± 1.08	TE	TP, TS
Gill rakers on 4th gill arch (upper)	9	9–11	10 ± 0.67	TT	TP, TS
Gill rakers on 4th gill arch (lower)	12	9–12	12 ± 0.89	TS	TP, TT
Gill rakers on 4th gill arch (total)	21	18–22	22 ± 1.05		TP, TS, TT
Gill rakers on posterior face of 3rd gill arch	7	5–8	7 ± 0.80	TS	
Prepelvic scutes	6	5–8	6 ± 0.72		
Postpelvic scutes	9	9–10	9 ± 0.49		TS
Total scutes on abdomen	15	14–17	15 ± 0.75		
Scale rows in longitudinal series	34	33–36	34 ± 0.63		
Transverse scales	8	8–9	9 ± 0.46		
Pseudobranchial filaments	19	17–24	20 ± 1.99	TS	
Total vertebrae	40	39–40	40 ± 0.37	TE	

fins, posteriorly margined black. Pectoral, pelvic, and anal fins whitish, semi-transparent. Iris and pupil bluish-black and silver, respectively.

Colour of preserved specimens. Body uniformly silver, sometimes pale whitish; dorsum dark; upper lateral surface light brown. Melanophores densely scattered over entire body and head. Narrow non-pigmented ring-like band surrounding anterior part of snout. Melanophores scattered along fin rays of dorsal and caudal fins. Pectoral, pelvic, and anal fins without melanophores. No distinct black blotches on dorsal fin.

Distribution. *Thrissina baelama* is distributed in the Red Sea and Gulf of Aden (Fig. 4).

Comparisons. *Thrissina baelama* has been considered conspecific with the four species re-described herein, all five being easily separable from all other congeners [except for *Thrissina encrasicholoides* (Bleeker, 1852)] in having a short maxilla, posteriorly not reaching to the opercle posterior margin, and ventral scutes totaling fewer than 18. Moreover, the former five species differ from *T. encrasicholoides* in having the prepelvic scutes ending anteriorly below the pectoral fin (vs. one or two prepelvic scutes immediately

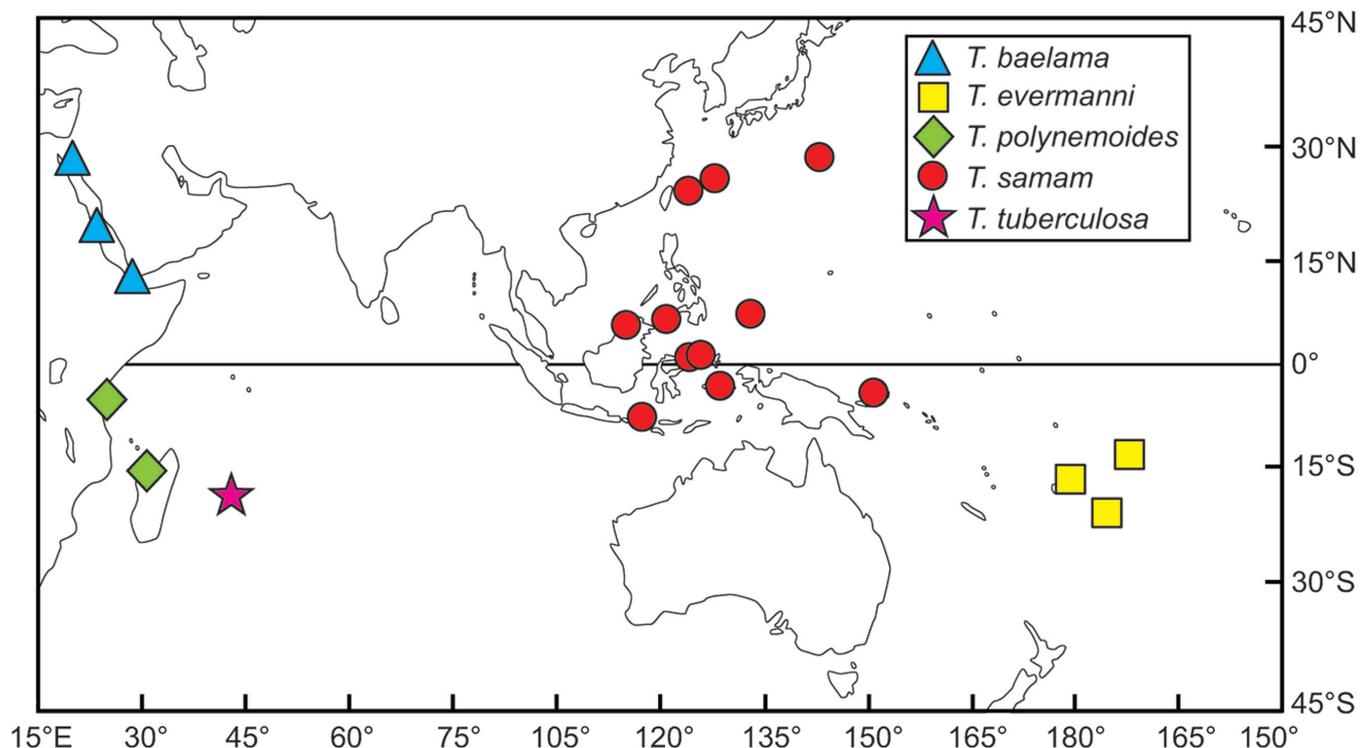


Fig. 4. Distributional records of *Thrissina baelama* (triangles), *T. evermanni* (squares), *T. polynemoides* (diamonds), *T. samam* (circles), and *T. tuberculosa* (star), based on specimens examined in this study.

behind the isthmus in *T. encrasicholoides*; Nelson, 1982; Whitehead et al., 1988; Wongratana et al., 1999; Hata & Koeda, 2020; Fig. 1).

Remarks. *Thrissina baelama* (Fabricius, 1775) [for a long time attributed incorrectly to P. S. Forsskål (e.g., Whitehead et al., 1988; Wongratana et al., 1999), but corrected by Fricke (2008)], was based on a clupeiform fish (specimen not retained) from Djiddae (currently Jeddah), Saudi Arabia (Fricke, 2008). To date, six engraulid species [viz., *Encrasicholina gloria* Hata & Motomura, 2016, *Encrasicholina heteroloba* (Rüppell, 1837), *Encrasicholina macrocephala* Hata & Motomura, 2015, *Encrasicholina pseudoheteroloba* (Hardenberg, 1933), *Stolephorus meteorum* Hata, Lavoué, Bogorodsky, Alpermann & Motomura, 2023, and *T. baelama*] have been recorded from the Red Sea (Whitehead, 1965; Whitehead et al., 1988; Hata & Motomura, 2016a, b; Hata et al., 2023; this study). However, Fabricius (1775) described *Clupea baelama* as having keeled scutes on the abdomen (from the pelvic fin to the anal-fin origin), the nominal species here identified as *T. baelama* being the only engraulid species from the Red Sea with postpelvic scutes [species of *Encrasicholina* and *Stolephorus* all lack postpelvic scutes (Whitehead et al., 1988; Wongratana et al., 1999)]. Although the Djiddae specimen was originally described under the name “*Clupea baelama, encraisicholus?*” [*Clupea encraisicholus* being a Linnaean species (Linnaeus, 1758), currently treated as *Engraulis encraisicholus* (e.g., Whitehead et al., 1988; Nizinski & Munroe, 2016)], Fricke (2008) considered *Clupea baelama* Fabricius, 1775 to be a nomen nudum, on the basis of Fabricius’ (1775) description

simply regarding “baelama” as an Arabic name for the species, rather than a new species description. However, Kottelat (2013) regarded *C. baelama* as an available name under Article 15.1 (ICZN, 1999), due to the name having been proposed conditionally before 1961. In the original description (Fabricius, 1775: p. 72), the name “*Clupea baelama, encraisicholus?*” was capitalised, but not italicised. Because the names of other species described as new in the same book (e.g., *Clupea dorab*, the description following that of *C. baelama*), Fabricius (1775) can be regarded as having described *C. baelama* as a new species, although foreseeing the possibility that his *C. baelama* was conspecific with *C. encraisicholus*. Moreover, on page 72, Fabricius (1775) provided the local (Arabic) names “Lâaf”, “Baelama”, and “Sardin”, all italicised and written in lowercase except for the first letter, a style repeated for similar notes following the other species described as new. On the basis of these facts, *C. baelama* is considered to be an available name using the Arabic name “baelama” as the specific name. Although Fricke (2008), who regarded *C. baelama* Fabricius, 1775 as an unavailable name, suggested “*Clupea baelama* Bloch and Schneider (1801)” as an applicable name for Fabricius’s (1775) species, Bloch & Schneider (1801) simply referred to the name, rather than describing a new species.

Because no type specimens of the nominal species are known, BMNH 1963.12.9.27 (Fig. 3), collected from the Red Sea, near Port Sudan, is herein designated as the neotype of *C. baelama*, fixing that collection locality as the type locality of *C. baelama* under Article 76.3 (ICZN, 1999).



Fig. 5. A, Holotype of *Anchovia evermanni*, USNM 51719, 105.0 mm, and B, paratype of *Anchovia evermanni*, USNM 451580, 98.3 mm SL, Apia, Samoa.

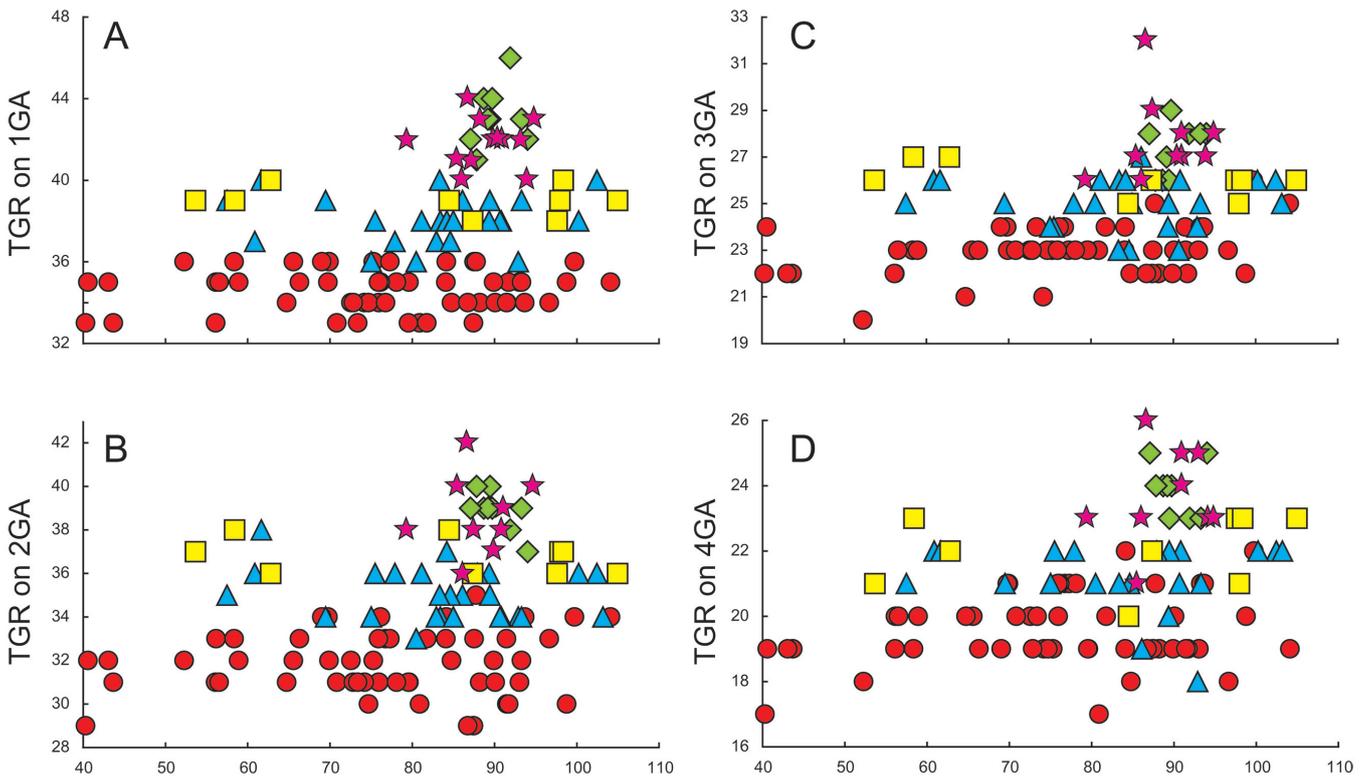


Fig. 6. Relationships of total gill-raker numbers (TGR) on A, first gill arch (1GA), B, second gill arch (2GA), C, third gill arch (3GA), and D, fourth gill arch (4GA) to standard length in *Thrissina baelama* (blue triangles ▲), *T. evermanni* (yellow squares ■), *T. polynemoides* (green diamonds ◆), *T. samam* (red circles ●), and *T. tuberculosa* (pink stars ★).

***Thrissina evermanni* (Jordan & Seale, 1906)**
 [English name: Evermann's Baelama Anchovy]
 (Fig. 5; Tables 4, 8)

Anchovia evermanni Jordan & Seale, 1906: 188, fig. 4 (type locality Apia, Upolu Island, Samoa).

Thryssa baelama (not of Fabricius): Whitehead et al., 1988 (in part): 425 (Fiji to Tonga); Wongratana et al., 1999 (in part): 1743 (Fiji to Tonga).

Holotype. USNM 51719, 105.0 mm SL, Apia, Samoa, 1902, D. S. Jordan and V. L. Kellogg.

Paratypes. 4 specimens, 84.5–98.3 mm SL: CAS-SU 8730, 3 specimens 84.5–98.0 mm SL, Apia, Samoa; USNM 451580, 98.3 mm SL, collected with the holotype.

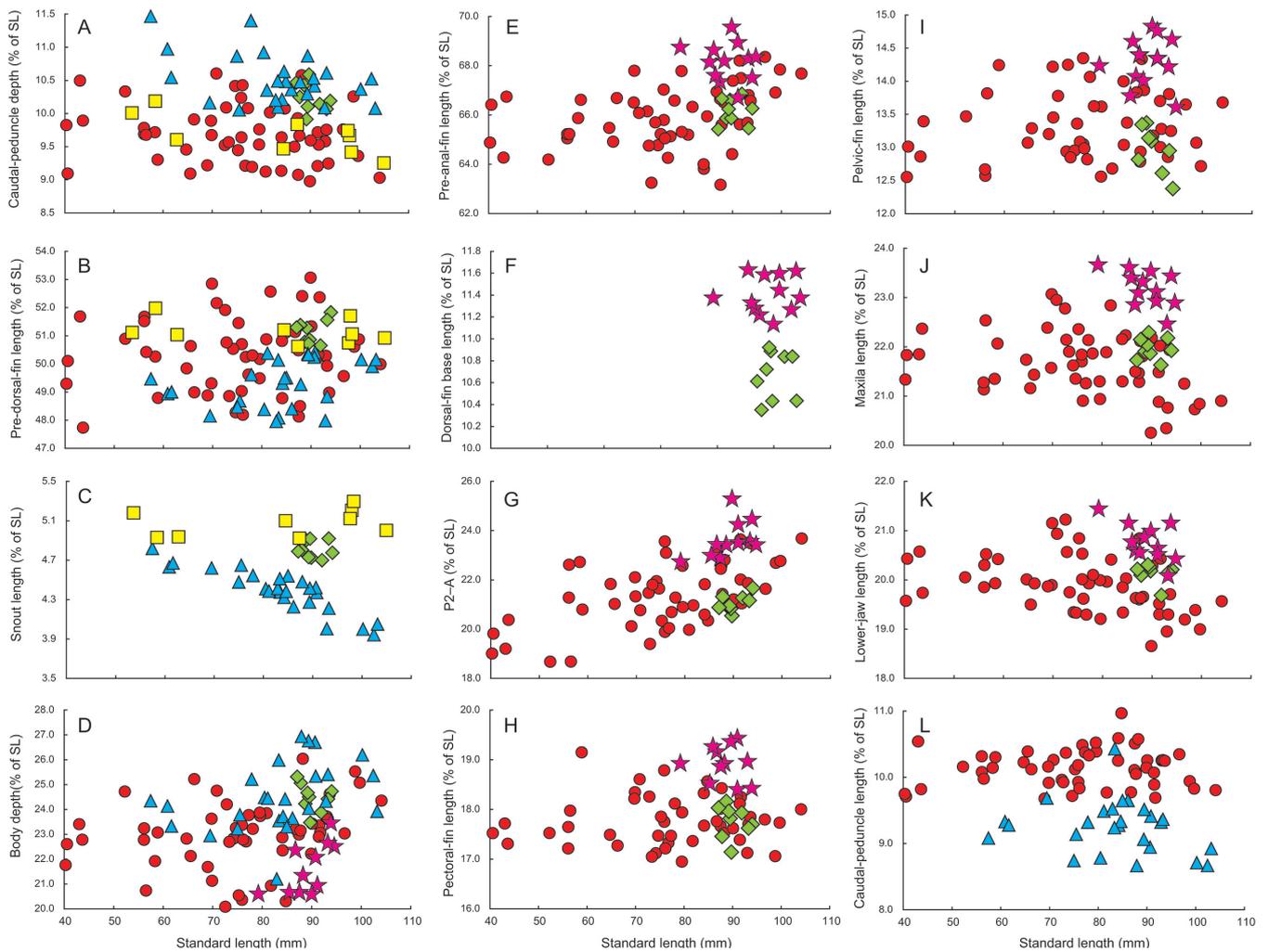


Fig. 7. Morphometrics of *Thrissina baelama* (blue triangles ▲), *T. evermanni* (yellow squares ■), *T. polynemoides* (green diamonds ◆), *T. samam* (red circles ●), and *T. tuberculosa* (pink stars ★) (all vs. standard length; SL). A, Ratio of caudal-peduncle depth to SL; B, pre-dorsal-fin length to SL; C, snout length to SL; D, body depth to SL; E, pre-anal-fin length to SL; F, dorsal-fin base length to SL; G, distance from pelvic-fin insertion to anal-fin origin to SL; H, pectoral-fin length to SL; I, pelvic-fin length to SL; J, maxilla length to SL; K, lower-jaw length to SL; L, caudal-peduncle length to SL.

Other material examined. 4 specimens, 53.7–87.3 mm SL: BMNH 1971.8.25.112–114, 3 specimens, 53.7–62.8 mm SL, Fiji; BPBM 41796, 87.3 mm SL, Tonga.

Diagnosis. A species of *Thrissina* with the following combination of characters: short maxilla, its posterior tip not reaching to posterior margin of opercle; first supramaxilla elongated, longer than half length of second; abdomen covered with 4–6 + 8–10 = 12–16 keeled scutes; no scutes anterior to pectoral fin; 1UGR 16–18, 1LGR 21–23, 1TGR 38–40; 2UGR 13–15, 2LGR 22–24, 2TGR 36–38; 3UGR 11–12, 3LGR 13–15, 3TGR 25–27; 4UGR 10–11, 4LGR 10–12, 4TGR 20–23; no distinct black blotches on dorsal fin; caudal peduncle narrow [9.3–10.2% (mean 9.7%) of SL] and long (9.7–10.5% of SL); pre-dorsal-fin long, 50.6–52.0% of SL; snout long, 4.9–5.3% of SL.

Colour of preserved specimens. Body uniformly silver, sometimes pale. Dorsum dark brown. Upper lateral surface of body light brown. Melanophores densely scattered over entire body and head. Narrow non-pigmented ring-like band surrounding anterior part of snout. Melanophores scattered

along dorsal- and caudal-fin rays. Pectoral, pelvic, and anal fins without melanophores. No distinct black blotches on dorsal fin.

Distribution. Currently known from Fiji, Tonga, and Samoa (Fig. 4).

Comparisons. *Thrissina evermanni* (1TGR 38–40) is diagnosed by a gill raker range intermediate between those of *T. samam* (1TGR < 37) and *T. polynemoides* (1TGR > 39), and *T. tuberculosa* (1TGR > 40) (Fig. 6). *Thrissina evermanni* can be distinguished from *T. baelama* (1TGR 36–40), with which it shares very similar gill raker numbers, by the narrower caudal peduncle (9.3–10.2% of SL vs. 10.1–11.5%), and longer pre-dorsal-fin (50.6–52.0% of SL vs. 48.0–50.4%) and snout (4.9–5.3% of SL vs. 3.9–4.8%). The long snout of *T. evermanni* also differentiates that species from *T. polynemoides* (snout length: 4.7–4.9% of SL) and *T. tuberculosa* (4.7–5.0%) (Fig. 7). Moreover, *T. evermanni* has a narrower caudal peduncle than *T. polynemoides* (9.3–10.2% of SL in *T. evermanni* vs. 9.9–10.6% in *T. polynemoides*). Additionally, *T. evermanni* differs from *T. tuberculosa* by

Table 4. Meristics of specimens of *Thrissina evermanni*.

Abbreviations: TB (*Thrissina baelama*); TP (*Thrissina polynemoides*); TS (*Thrissina samam*); TT (*Thrissina tuberculosa*).

	<i>Thrissina evermanni</i>					
	Holotype	Paratypes	Non-type specimens	T-test		
	USNM 51719	n = 4	n = 3	Modes ± SD	p values	
Standard length (mm)	105.0	84.5–98.3	53.7–87.3		5 > p > 0.1	0.1 > p
Dorsal-fin rays (unbranched)	3	3	3	3 ± 0		
Dorsal-fin rays (branched)	11	11	12	12 ± 0.42		
Anal-fin rays (unbranched)	3	3–4	4	3 ± 0.42		
Anal-fin rays (branched)	30	27–28	26–29	27 ± 1.13	TT	
Pectoral-fin rays (unbranched)	1	1	1	1 ± 0		
Pectoral-fin rays (branched)	13	11–12	11–13	12 ± 0.67		
Pelvic-fin rays (unbranched)	1	1	1	1 ± 0		
Pelvic-fin rays (branched)	6	6	6	6 ± 0		
Gill rakers on 1st gill arch (upper)	16	17–18	16–17	17 ± 0.57		TP, TS
Gill rakers on 1st gill arch (lower)	23	21–22	22–23	22 ± 0.57	TB	TP, TS, TT
Gill rakers on 1st gill arch (total)	39	38–40	38–40	39 ± 0.67	TB	TP, TS, TT
Gill rakers on 2nd gill arch (upper)	14	13–15	14–15	14 ± 0.63	TP	TS, TT
Gill rakers on 2nd gill arch (lower)	22	22–24	22–23	22 ± 0.68	TP, TT	TS, TB
Gill rakers on 2nd gill arch (total)	36	36–38	36–38	36 ± 0.79	TP, TT	TS, TB
Gill rakers on 3rd gill arch (upper)	12	11–12	12	12 ± 0.31	TB, TP, TT	TS
Gill rakers on 3rd gill arch (lower)	14	13–14	14–15	14 ± 0.57	TB, TT	TS
Gill rakers on 3rd gill arch (total)	26	25–26	26–27	26 ± 0.67	TB, TP	TS
Gill rakers on 4th gill arch (upper)	11	10–11	10–11	11 ± 0.50	TP, TT	TS
Gill rakers on 4th gill arch (lower)	12	10–12	11–12	12 ± 0.68	TP, TS	
Gill rakers on 4th gill arch (total)	23	20–23	21–23	23 ± 1.05		TP, TS, TT
Gill rakers on posterior face of 3rd gill arch	7	7–8	6–9	7 ± 0.82	TS	TT
Prepelvic scutes	5	4–6	5–6	6 ± 0.82	TS	
Postpelvic scutes	9	8–10	9	9 ± 0.57		
Total scutes on abdomen	14	12–16	14–15	15 ± 1.07		
Scale rows in longitudinal series	35	35–37	33–36	36 ± 1.33		
Transverse scales	9	8–9	9	9 ± 0.47		
Pseudobranchial filaments	23	19–23	21–25	23 ± 1.81	TP	
Total vertebrae		40	40	40 ± 0	TB, TS	

lacking black blotches anteriorly on the dorsal fin (vs. several distinct black blotches present in *T. tuberculosa*).

Remarks. *Thrissina evermanni* was originally described as *Anchovia evermanni* by Jordan and Seale (1906), based on five specimens collected from Apia, Upolu Island, Samoa. Although the original description designated a single specimen (USNM 51719) as the holotype, that lot included two specimens (Fricke et al., 2022), one (105.0 mm SL, 127.7 mm TL; 1LGR 23) being untagged and the other (98.3 mm SL; 1LGR 22) with two metal tags. The former matched the original description in both specimen size [five inches in total length (ca. 12.7 cm)] and gill raker number

(23 gill rakers on lower gill limb of first gill arch), and is here considered to be the holotype of the nominal species. The smaller specimen is now reregistered as USNM 451580.

***Thrissina polynemoides* (Günther, 1868)**

[English name: African Baelama Anchovy]

(Fig. 8; Tables 5, 9)

Engraulis polynemoides Günther, 1868 (type locality: Madagascar).
Thrissina baelama (not of Fabricius): Losse, 1966: 177 (Dar-es-Salaam and Zanzibar, Tanzania; Mombasa and Malindi, Kenya); Losse, 1968: 110, pl. 4a (Dar-es-Salaam and Zanzibar, Tanzania; Mombasa and Malindi, Kenya).



Fig. 8. A, Holotype of *Engraulis polynemoides* (BMNH 1979.7.5.26, 93.3 mm SL, Madagascar), and B, non-type specimen of *T. polynemoides* (BMNH 1966.11.16.985–992, 94.0 mm SL, Mombasa, Kenya).

Thryssa baelama (not of Fabricius): Whitehead et al., 1988 (in part): 425 (east Africa to Madagascar); Wongratana et al., 1999 (in part): 1743 (east Africa to Madagascar); Fricke et al., 2018: 52 (Madagascar).

Holotype. BMNH 1979.7.5.26, 93.3 mm SL, Madagascar.

Other material examined. 8 specimens, 87.1–94.0 mm SL: BMNH 1966.11.16.985–992, 8 specimens, 87.1–94.0 mm SL, Mombasa, Kenya.

Diagnosis. A species of *Thrissina* with the following combination of characters: short maxilla, 21.6–22.3% of SL; its posterior tip not reaching to posterior margin of opercle; first supramaxilla elongated, longer than half length of second; lower jaw rather long, 19.7–20.3% of SL; abdomen covered with 5–7 + 9–10 = 14–17 keeled scutes; no scutes anterior to pectoral fin; 1UGR 18–20, 1LGR 23–26, 1TGR 41–46; 2UGR 14–16, 2LGR 22–25, 2TGR 37–40; 3UGR 12–13, 3LGR 14–16, 3TGR 26–29; 4UGR 11–12, 4LGR 12–13, 4TGR 23–25; no distinct black blotches on dorsal fin; caudal peduncle rather narrow [9.9–10.6% (mean 10.2%) of SL] and long (9.1–10.1% of SL); pre-dorsal-fin long, 50.7–51.8% of SL; pre-anal-fin length short, 65.6–66.9% of SL; dorsal-fin base short, 10.4–10.9% of SL; distance between pelvic-fin insertion and anal-fin origin short, 20.5–21.7% of SL; pectoral fin short, 17.1–18.2% of SL; pelvic fin short, 12.4–13.4% of SL; snout short, 4.7–4.9% of SL; body rather elongated, 23.5–25.3% (mean 24.5%) of SL.

Colour of preserved specimens. Body uniformly silver, sometimes pale ivory. Dorsum dark brown. Melanophores densely scattered over entire body and head. Narrow non-pigmented ring-like band surrounding anterior part of snout.

Melanophores scattered along dorsal- and caudal-fin rays. Pectoral, pelvic, and anal fins without melanophores. No distinct black blotches on dorsal fin.

Distribution. The species is currently known from Madagascar and Kenya (Fig. 4).

Comparisons. *Thrissina polynemoides* has the highest gill raker counts among the five species redescribed in this study [41–46 (modally 43) in *T. polynemoides* vs. 40 or fewer in *T. baelama*, *T. evermanni*, and *T. samam*, 40–44 (modally 42) in *T. tuberculosa*; Fig. 6]. *Thrissina polynemoides* further differs from *T. baelama* in having greater pre-dorsal-fin (50.7–51.8% of SL in *T. polynemoides* vs. 48.0–50.4% in *T. baelama*) and snout lengths [4.7–4.9% in SL vs. 3.9–4.8% (shorter than 4.6% in specimens > 80 mm SL)] (Fig. 7). Moreover, *T. polynemoides* differs from *T. tuberculosa* by lacking a black spot anteriorly on the dorsal fin (vs. black spots present in *T. tuberculosa*), and having a deeper body (23.5–25.3% of SL in *T. polynemoides* vs. 20.6–23.4% in *T. tuberculosa*), and shorter head and body proportions, including preanal length (65.4–66.9% of SL vs. 66.7–69.6%), dorsal-fin base (10.4–10.9% of SL vs. 11.2–11.6%), pelvic-fin insertion to anal-fin origin (20.5–21.7% of SL vs. 22.7–25.3%), pectoral fin (17.1–18.2% of SL vs. 18.4–19.4%), pelvic fin (12.4–13.4% of SL vs. 13.6–14.8%), maxilla (21.6–22.3% of SL vs. 22.5–23.7%), and lower jaw [19.7–20.3% (mean 20.1%) of SL vs. 20.1–21.4% (20.8%)].

Remarks. Although this nominal species has long been regarded as a junior synonym of *T. baelama* (e.g., Whitehead et al., 1988; Kottelat, 2013), the present study found both species to be valid.

Table 5. Meristics of specimens of *Thrissina polynemoides*.

Abbreviations: TB (*Thrissina baelama*); TE (*Thrissina evermanni*); TS (*Thrissina samam*); TT (*Thrissina tuberculosa*).

	<i>Thrissina polynemoides</i>				
	Holotype	Non-type specimens		T-test	
	BMNH 1979.7.5.26	n = 8	Modes ± SD	p values	
Standard length (mm)	93.3	87.1–94.0		5 > p > 0.1	0.1 > p
Dorsal-fin rays (unbranched)	3	3	3 ± 0		
Dorsal-fin rays (branched)	12	10–12	12 ± 0.68		
Anal-fin rays (unbranched)	4	4	4 ± 0	TS	
Anal-fin rays (branched)	31	27–31	27 ± 1.55		
Pectoral-fin rays (unbranched)	1	1	1 ± 0		
Pectoral-fin rays (branched)	11	12	12 ± 0.31	TT	
Pelvic-fin rays (unbranched)	1	1	1 ± 0		
Pelvic-fin rays (branched)	6	6	6 ± 0		
Gill rakers on 1st gill arch (upper)	19	18–20	19 ± 0.63		TB, TE, TS
Gill rakers on 1st gill arch (lower)	24	23–26	24 ± 0.82	TT	TB, TE, TS
Gill rakers on 1st gill arch (total)	43	41–46	43 ± 1.37	TT	TB, TE, TS
Gill rakers on 2nd gill arch (upper)	15	14–16	15 ± 0.47		TB, TS
Gill rakers on 2nd gill arch (lower)	24	22–25	24 ± 0.87	TE	TB, TS
Gill rakers on 2nd gill arch (total)	39	37–40	39 ± 0.87		TB, TS
Gill rakers on 3rd gill arch (upper)	13	12–13	13 ± 0.47	TE	TB, TS
Gill rakers on 3rd gill arch (lower)	15	14–16	14 ± 0.67		TB, TS
Gill rakers on 3rd gill arch (total)	28	26–29	28 ± 1.05	TE	TB, TS
Gill rakers on 4th gill arch (upper)	11	11–12	11 ± 0.47	TE	TB, TS
Gill rakers on 4th gill arch (lower)	12	12–13	13 ± 0.50	TE	TB, TS
Gill rakers on 4th gill arch (total)	23	23–25	24 ± 0.74		TB, TE, TS
Gill rakers on posterior face of 3rd gill arch	6	7–9	7 ± 0.83	TS	
Prepelvic scutes	5	5–7	6 ± 0.74		
Postpelvic scutes	9	9–10	9 ± 0.47		
Total scutes on abdomen	14	14–17	14 ± 1.13		
Scale rows in longitudinal series	35	34–35	34	TT	
Transverse scales	9	8–9	9		
Pseudobranchial filaments	24	18–22	18 ± 2.12	TE, TS	
Total vertebrae	40	40–41	40 ± 0.47		

***Thrissina samam* (Montrouzier, 1857)**

[English name: Samam Baelama Anchovy]

(Figs. 1A–D, 9; Tables 6, 10)

Engraulis samam Montrouzier, 1857: 487 (original type locality: Woodlark Island, Louisiade Archipelago, Papua New Guinea; type locality: Garrer Bay, New Britain, Papua New Guinea based on neotype designated herein).

Engraulis macrops Kishinouye, 1911: 385, pl. XXX, fig. 3 (type locality: Haha Island, Ogasawara Islands, Japan).

Engraulis baelama (not of Fabricius): Weber & de Beaufort, 1913 (in part): 33 (Lombok and Aru Islands, Indonesia).

Thrissocles baelama (not of Fabricius): Fowler, 1941 (in part): 683 [Tawitawi Island; Mareveles (currently Mariveles), Pagapas

Bay, and Batangas, Luzon; Mindanao; Cebu; Gomomo Island; Iloilo, Panay; Jolo Island; Palawan; Cagayancillo; Mindoro; Leyte, Philippines; Danawan Island, Malaysia; Buru Island, Indonesia].

Thryssa baelama (not of Fabricius): Whitehead et al., 1988 (in part): 425 (Ogasawara Islands and Philippines to Papua New Guinea); Wongratana et al., 1999 (in part): 1743 (Ogasawara Islands and Philippines to Papua New Guinea); Aonuma & Yagishita, 2013 (in part): 304, unnumbered fig. (Ogasawara Islands and Ryukyu Archipelago, Japan).

Thrissina baelama (not of Fabricius): Hata & Koeda, 2021: 11, fig. 1 (Okinawa Island, Ryukyu Archipelago, Japan); Hata et al., 2022b: 35 (Okinawa Island, Philippines, and Palau).



Fig. 9. A, Neotype of *Engraulis samam* (BMNH 1971.2.8.49, 79.6 mm SL, New Britain, Papua New Guinea), and B, non-type specimen of *Thrissina samam* (fresh condition) (NSMT-P 145681, 87.4 mm SL, Sulawesi, Indonesia).

Neotype. BMNH 1971.2.8.49, 79.6 mm SL, Garrer Bay, New Britain, Papua New Guinea (mouth of cove surrounded by coral reef and mangrove); 6 September 1970.

Other materials examined. 52 specimens, 40.3–104.1 mm SL: **JAPAN:** NSMT-P 2058, 89.9 mm SL, Ogasawara Islands; NSMT-P 19049, 2 specimens, 56.1–58.4 mm SL, NSMT-P 19050, 2 specimens, 64.7–65.6 mm SL, Nagura River, Ishigaki Island, Yaeyama Islands, Ryukyu Archipelago; ZUMT 11282, 84.1 mm SL, ZUMT 11283, 91.5 mm SL, Ryukyu Archipelago; ZUMT 39727, 40.3 mm SL, Okinawa Island, Okinawa Islands, Ryukyu Archipelago. **PHILIPPINES:** ZUMT 41003, 69.8 mm SL, ZUMT 41004, 58.9 mm SL, ZUMT 40900, 2 of 8 specimens, 75.9–76.2 mm SL, Jolo Island. **PALAU:** NSMT-P 136575, 52.3 mm SL, Urukthapel Island, 1 m depth; ZUMT ABE 3039, 69.0 mm SL, ZUMT ABE 3040, 2 specimens, 56.5–73.4 mm SL, ZUMT 62054, 7 specimens, 84.1–104.1 mm SL, Palau. **MALAYSIA:** KAUM-I. 12499, 87.5 mm SL, off Tanjung Lipat, Kota Kinabalu, Sabah. **INDONESIA:** BPBM 19427, 80.9 mm SL; Poka, northwest of Ambon Bay, Ambon. BPBM 36472, 2 specimens, 81.8–84.8 mm SL, Laha, Ambon; NSMT-P 52718, 79.5 mm SL, NSMT-P 56892, 2 specimens, 91.5–98.8 mm SL, NSMT-P 136629, 74.2 mm SL, SNMT-P 136644, 3 of 5 specimens, 40.6–43.7 mm SL, NSMT-P 136649, 1 of 7 specimens, 74.7 mm SL, NSMT-P 138469, 93.0 mm SL, Kuta, Lombok; NSMT-P 61318, 56.2 mm SL, Mawali, Lembah Island; NSMT-P 63691, 66.1 mm SL, NSMT-P 136645, 88.2 mm, Ambon; NSMT-P 145681, 87.4 mm SL, NSMT-P 145682, 76.8 mm

SL, NSMT-P 145683, 70.8 mm SL, NSMT-P 145684, 72.9 mm SL, NSMT-P 145685, 77.3 mm SL, NSMT-P 145686, 91.7 mm SL, NSMT-P 145687, 90.1 mm SL, NSMT-P 145688, 86.8 mm SL, MZB 26553, 78.1 mm, Tanahwangko, Sulawesi. **PAPUA NEW GUINEA:** BMNH 1971.2.8.50–58, 4 specimens, 69.9–75.9 mm SL, Garrer Bay, New Britain, Papua New Guinea (mouth of cove surrounded by coral reefs and mangroves)

Diagnosis. A species of *Thrissina* with the following combination of characters: short maxilla, 20.3–23.1% of SL; its posterior tip not reaching to posterior margin of opercle; first supramaxilla elongated, longer than half length of second; lower jaw rather long, 18.7–21.2% of SL; abdomen covered with 4–8 + 8–10 = 13–16 keeled scutes; no scutes anterior to pectoral fin; 1UGR 14–16, 1LGR 18–21, 1TGR 33–36; 2UGR 10–14, 2LGR 18–21, 2TGR 29–35; 3UGR 9–12, 3LGR 11–14, 3TGR 20–26; 4UGR 6–10, 4LGR 9–12, 4TGR 17–22; no distinct black blotches on dorsal fin; caudal peduncle rather narrow [9.0–10.6% (mean 9.7%) of SL] and long (9.7–11.0% of SL); pre-dorsal-fin length 47.7–53.1% of SL; pre-anal-fin rather short, 63.2–68.3% of SL; distance between pelvic-fin insertion and anal-fin origin rather short, 18.7–23.7% of SL; pectoral fin rather short, 16.9–19.1% of SL; pelvic fin rather short, 12.6–14.3% of SL; body rather elongated, 20.1–26.0% (mean 23.0%) of SL.

Colour of fresh specimens. Body uniformly silver. Dorsum black, upper lateral surface of body bluish-grey, with small densely scattered orange spots (also on upper lateral surface

Table 6. Meristics of specimens of *Thrissina samam*.Abbreviations: TB (*Thrissina baelama*), TE (*Thrissina evermanni*); TP (*Thrissina polynemoides*); TT (*Thrissina tuberculosa*).

	<i>Thrissina samam</i>				
	Neotype	Non-type specimens	T-test		
	BMNH 1971.2.8.49	n = 52	Modes ± SD	p values	
Standard length (mm)	79.6	40.3–104.1		5 > p > 0.1	0.1 > p
Dorsal-fin rays (unbranched)	3	3	3 ± 0		
Dorsal-fin rays (branched)	11	10–13	12 ± 0.58		
Anal-fin rays (unbranched)	4	3–4	4 ± 0.34	TP, TT	
Anal-fin rays (branched)	29	26–30	28 ± 1.19		
Pectoral-fin rays (unbranched)	1	1	1 ± 0		
Pectoral-fin rays (branched)	12	10–13	12 ± 0.75		
Pelvic-fin rays (unbranched)	1	1	1 ± 0		
Pelvic-fin rays (branched)	6	6	6 ± 0		
Gill rakers on 1st gill arch (upper)	15	14–16	15 ± 0.63		TB, TE, TP, TT
Gill rakers on 1st gill arch (lower)	20	18–21	20 ± 0.70		TB, TE, TP, TT
Gill rakers on 1st gill arch (total)	35	33–36	35 ± 1.00		TB, TE, TP, TT
Gill rakers on 2nd gill arch (upper)	11	10–14	12 ± 0.77		TB, TE, TP, TT
Gill rakers on 2nd gill arch (lower)	20	18–21	19 ± 0.86		TB, TE, TP, TT
Gill rakers on 2nd gill arch (total)	31	29–35	31 ± 1.44		TB, TE, TP, TT
Gill rakers on 3rd gill arch (upper)	10	9–12	10 ± 0.69		TB, TE, TP, TT
Gill rakers on 3rd gill arch (lower)	13	11–14	13 ± 0.61		TB, TE, TP, TT
Gill rakers on 3rd gill arch (total)	23	20–26	23 ± 1.04		TB, TE, TP, TT
Gill rakers on 4th gill arch (upper)	9	6–10	9 ± 0.76		TB, TE, TP, TT
Gill rakers on 4th gill arch (lower)	10	9–12	10 ± 0.63	TB, TE	TP, TT
Gill rakers on 4th gill arch (total)	19	17–22	19 ± 1.09		TB, TE, TP, TT
Gill rakers on posterior face of 3rd gill arch	6	5–8	6 ± 0.79	TB, TE, TP, TT	
Prepelvic scutes	4	5–8	6 ± 0.78	TE, TT	
Postpelvic scutes	9	8–10	9 ± 0.41	TT	
Total scutes on abdomen	13	13–16	15 ± 0.76		
Scale rows in longitudinal series	34	34–36	34 ± 0.60		
Transverse scales	9	8–9	9 ± 0.50		
Pseudobranchial filaments	23	17–27	20 ± 2.04	TB, TP, TT	
Total vertebrae	39	39–40	40 ± 0.30	TE	

of head). Lateral surface of mid-part of snout transparent. Narrow non-pigmented ring-like band surrounding anterior part of snout. Branches of cephalic lateralis sensory canal on upper part of gill opening distinctly orange, forming an orange blotch above a faded black blotch. Fin rays of dorsal and caudal fins black. Dorsal and caudal fins, centrally reddish-orange, posteriorly margined black. Pectoral, pelvic, and anal fins whitish, semi-transparent. Iris and pupil bluish-black and silver, respectively.

Colour of preserved specimens. Body uniformly pale ivory. Dorsum dark brown. Melanophores densely scattered over

entire body and head. Narrow non-pigmented ring-like band surrounding anterior part of snout. Melanophores scattered along fin rays of dorsal and caudal fins. Pectoral, pelvic, and anal fins without melanophores. No distinct black blotches on dorsal fin.

Distribution. *Thrissina samam* is distributed in the western Pacific from the Ogasawara Islands and Ryukyu Archipelago, Japan, to Palau and New Britain, Papua New Guinea (Fig. 4).

Comparisons. *Thrissina samam* is characterised by the lowest gill raker numbers among the five species described

herein [1TGR, 33–36 in *T. samam* (vs. 38 or more in *T. evermanni*, *T. polynemoides*, and *T. tuberculosa*; 36–40 in *T. baelama*); 2TGR, 29–35 in *T. samam* (vs. 36 or more in *T. evermanni*, *T. polynemoides*, and *T. tuberculosa*; 33–38 in *T. baelama*); 3TGR, 20–26 in *T. samam* (vs. 25 or more in *T. evermanni*, *T. polynemoides*, and *T. tuberculosa*; 23–27 in *T. baelama*); 4TGR, 17–22 in *T. samam* (vs. 20 or more in *T. evermanni*, *T. polynemoides*, and *T. tuberculosa*; 18–22 in *T. baelama*) (Fig. 6)]. The former further differs from *T. baelama* in having a narrower body [20.1–26.0% (mean 23.0%) of SL in *T. samam* vs. 23.0–26.9% (mean 24.5%; one of 26 specimens 21.2%) in *T. baelama*], and caudal peduncle [9.0–10.6% (mean 9.7%) of SL vs. 10.1–11.5% (10.5%)], greater pre-dorsal-fin length [47.7–53.1% (mean 50.3%) of SL vs. 48.0–50.4% (mean 49.3%; never greater than 51%)], and longer caudal peduncle [9.7–11.0% (mean 10.1%) of SL vs. 8.7–9.7%, usually less than 10% (one specimen only 10.4%; mean 9.3%)] (Fig. 7). Furthermore, *T. samam* is also distinguished from *T. tuberculosa* by lacking black blotches anteriorly on the dorsal fin (vs. several distinct black blotches present in *T. tuberculosa*), and shorter pre-anal-fin length [63.2–68.3% (mean 65.9%) of SL in *T. samam* vs. 66.7–69.6% (68.2%) in *T. tuberculosa*], pelvic-fin insertion to anal-fin origin distance [18.7–23.7% (mean 21.4%) of SL vs. 22.7–25.3% (23.6%)], pectoral-fin length [16.9–19.1% (mean 17.8%) of SL vs. 18.4–19.4% (18.9%)], pelvic-fin length [12.6–14.4% (mean 13.3%) of SL vs. 13.6–14.8% (14.3%)], maxilla length [20.3–23.1% of SL (mean 21.7%) vs. 22.5–23.7% (23.2%)], and lower-jaw length [18.7–21.2% (mean 19.9%) of SL vs. 20.1–21.4% (mean 20.7%)] (Fig. 7).

Remarks. *Engraulis samam* was described by Montrouzier (1857) based on specimens collected from Woodlark Island, who reported that he had made a drawing of the specimen. However, both the type specimens and drawing have been lost (Wongratana, 1980; Kottelat, 2013; Fricke et al., 2022; this study). The original description noted *E. samam* as having a triangular dorsal fin, the anal and caudal fins well separated, a serrated abdomen (a probable reference to the abdomen being entirely covered with ventral scutes), the dorsal body contour nearly straight, and the body elongate (depth approx. 18% of total length). These characters place the species in the genus *Thrissina*, as defined by Whitehead et al. (1988) and Wongratana et al. (1999) (as *Thryssa*). To date, six species of *Thrissina* [viz., *Thrissina brevicauda* (Roberts, 1978), *Thrissina hamiltonii* (Gray, 1835), *Thrissina rastrorsa* (Roberts, 1978), *T. samam*, *Thrissina scrachleyi* (Ramsay & Ogilby, 1886), *Thrissina setirostris* (Broussonet, 1782)] have been recorded from New Guinea (Whitehead et al., 1988; Wongratana et al., 1999). The original description of *E. samam* also noted “La direction du préopercule et de l’opercule est très-oblique. Pas de prolongement aux maxillaires [margins of preopercle and opercle oblique. Not extended to the maxilla]”, the latter character probably referring to the short maxilla, its posterior tip not reaching to the preopercle posterior margin. Because *T. hamiltonii* and *T. setirostris* both have a long maxilla, posteriorly well beyond the opercle posterior margin (Whitehead et al., 1988; Wongratana et al., 1999; Hata et al., 2022a), they are considered specifically distinct from *E. samam*. Because

Montrouzier (1857) also described *E. samam* as inhabiting coastal waters, *T. rastrorsa* and *T. scrachleyi*, recorded only from middle and upper stretches of the Fly River (Roberts, 1978), are also thought to be different species. Moreover, the length of Montrouzier’s (1857) *E. samam* (4 inches, approx. 10.2 cm total length) also differentiates that species from *T. brevicauda*, which attains only 56.5 mm SL (Roberts, 1978). Finally, Montrouzier’s (1857) *E. samam* had a red spot above the gill slit, a colour feature found in *T. samam* specimens recognised herein.

Engraulis macrops was described by Kishinouye (1911) from specimens approx. 12 cm total length, collected from Haha Island, Ogasawara Islands, Japan in April 1907. Although the name was spelled as “*Engraulis macrops*” in the main account and the plate legend on p. 386, it was given as “*Engraulis macropus*” on pl. XXX, the latter simply being a spelling error (Kottelat, 2013). This was upheld by Whitehead et al. (1988) and Fricke et al. (2022), although erroneously stated as “*micropus*”. Although the type specimens of *E. macrops* are apparently lost (Kottelat, 2013; Fricke et al., 2022; this study), the meristic characters given in the original description generally matched those of *T. samam* specimens examined in the present study. Moreover, an NSMT specimen collected from the Ogasawara Islands was found to be conspecific with *T. samam*. *E. macrops* is therefore considered to be a junior synonym of *T. samam*. A specimen collected from New Britain (BMNH 1971.2.8.49, 79.6 mm SL; Fig. 9) is herein designated as the neotype of *Engraulis samam* Montrouzier, 1857, the collection locality becoming the type locality of the nominal species under Article 76.3 (ICZN, 1999).

***Thrissina tuberculosa* (Lacepède, 1803)**

[English name: Mauritian Baelama Anchovy]

(Fig. 10; Tables 7, 11)

Clupea tuberculosa Lacepède, 1803: 425 (original type locality: Mauritius, Mascarenes; type locality: Black River District, Mauritius, based on neotype designated herein).

Engraulis nesogallicus Bennet, 1832: 168 (original type locality: Mauritius, Mascarenes; type locality: Black River District, Mauritius, based on neotype designated herein).

Thrissocles baelama (not of Fabricius): Fowler, 1941 (in part): 683 (Mauritius).

Thryssa baelama (not of Fabricius): Whitehead et al., 1988 (in part): 425 (Mauritius); Wongratana et al., 1999 (in part): 1743 (Mauritius).

Neotype. BPBM 41797, also neotype of *Engraulis nesogallicus*, 90.9 mm SL, Black River District, Mauritius, 0–1.5 m depth.

Other materials examined. 11 specimens, 79.3–94.6 mm SL: BPBM 20277, 11 specimens, 79.3–94.6 mm SL, collected with the neotype.

Diagnosis. A species of *Thrissina* with the following combination of characters: short maxilla, 22.5–23.7% of SL; its posterior tip not reaching to posterior margin of opercle; first supramaxilla elongated, longer than half length of



Fig. 10. Neotype of *Clupea tuberculosa*, BPBM 41797, 90.9 mm SL, Black River District, Mauritius (also neotype of *Engraulis nesogallicus*): A, fresh condition (courtesy of Bishop Museum); B, preserved condition.

second; lower jaw rather long, 20.1–21.4% of SL; abdomen covered with 5–7 + 9–11 = 14–16 keeled scutes; no scutes anterior to pectoral fin; 1UGR 17–20, 1LGR 23–24, 1TGR 40–44; 2UGR 14–17, 2LGR 22–25, 2TGR 36–42; 3UGR 12–15, 3LGR 13–17, 3TGR 26–32; 4UGR 9–12, 4LGR 12–14, 4TGR 21–26; distinct black blotches on dorsal fin; pre-anal fin rather long, 66.7–69.6% of SL; dorsal-fin base long, 11.1–11.6% of SL; distance between pelvic-fin insertion and anal-fin origin rather long, 22.7–25.3% of SL; pectoral fin rather long, 18.4–19.4% of SL; pelvic fin rather long, 13.6–14.8% of SL; body elongate, 20.6–23.4% (mean 21.6%) of SL.

Colour of fresh specimens. Body uniformly silver. Dorsum and upper lateral surface of body green, with small densely scattered orange spots (also on upper lateral surface of head). Lateral surface of mid-part of snout transparent. Narrow non-pigmented ring-like band surrounding anterior part of snout. Branches of cephalic lateralis sensory canal on upper part of gill opening distinctly orange, forming an orange blotch. Fin rays of dorsal and caudal fins greenish-brown. Dorsal and caudal fins, centrally reddish-orange, posteriorly margined black. Pectoral, pelvic, and anal fins whitish, semi-transparent. Iris and pupil bluish-black and silver, respectively.

Colour of preserved specimens. Body uniformly light brown. Dorsum dark brown. Melanophores densely scattered over entire body and head. Narrow non-pigmented ring-like band surrounding anterior part of snout. Melanophores scattered along dorsal- and caudal-fin rays. Pectoral, pelvic, and anal fins without melanophores. Distinct black blotches anteriorly on dorsal fin.

Distribution. *Thrissina tuberculosa* is distributed only in waters off Mauritius (Fig. 4), so far as is known, and is considered a Mauritian endemic.

Comparisons. Among the five species redescribed in this study, *T. tuberculosa* is uniquely characterised by black spots anteriorly on the dorsal fin (Fig. 11).

Remarks. The original description of *Clupea tuberculosa* was based on a specimen collected from Mauritius by Lacepède (1803). Although Fricke (1999) suggested that the nominal species was a synonym of *Stolephorus commersonnii* Lacepède, 1803, supposing both names to have been based on the same manuscript description of *S. commersonnii*, Hata et al. (2021a) indicated that the two nominal species were clearly based on different descriptions (descriptions of *S. commersonnii* and *C. tuberculosa* having been given on pp. 381 and 382–383, and pp. 425 and 460, respectively).

Table 7. Meristics of specimens of *Thrissina tuberculosa*.Abbreviations: TB (*Thrissina baelama*), TE (*Thrissina evermanni*); TP (*Thrissina polynemoides*); TS (*Thrissina samam*).

	<i>Thrissina tuberculosa</i>				
	Neotype	Non-type specimens	T-test		
	BPBM 41797	n = 11	Modes ± SD	p values	
Standard length (mm)	90.9	79.3–94.6		5 > p > 0.1	0.1 > p
Dorsal-fin rays (unbranched)	3	3	3 ± 0		
Dorsal-fin rays (branched)	13	11–12	11 ± 0.64		
Anal-fin rays (unbranched)	4	4	4 ± 0.28	TB, TE, TS	
Anal-fin rays (branched)	30	27–30	29 ± 0.90		
Pectoral-fin rays (unbranched)	1	1	1 ± 0		
Pectoral-fin rays (branched)	11	10–12	12 ± 0.64	TB, TP	
Pelvic-fin rays (unbranched)	1	1	1 ± 0		
Pelvic-fin rays (branched)	6	6	6 ± 0		
Gill rakers on 1st gill arch (upper)	19	17–20	19 ± 0.86		TB, TE, TS
Gill rakers on 1st gill arch (lower)	23	23–24	23 ± 0.43	TP	TB, TE, TS
Gill rakers on 1st gill arch (total)	42	40–44	42 ± 1.14	TP	TB, TE, TS
Gill rakers on 2nd gill arch (upper)	16	14–17	15 ± 0.90	TE	TB, TS
Gill rakers on 2nd gill arch (lower)	23	22–25	23 ± 0.76	TE	TB, TS
Gill rakers on 2nd gill arch (total)	39	36–42	39 ± 1.55	TE	TB, TS
Gill rakers on 3rd gill arch (upper)	12	12–15	12 ± 0.90	TE	TB, TS
Gill rakers on 3rd gill arch (lower)	15	13–17	15 ± 0.92	TB	TS
Gill rakers on 3rd gill arch (total)	27	26–32	27 ± 1.61	TE	TS
Gill rakers on 4th gill arch (upper)	10	9–12	12 ± 0.95	TB	TS
Gill rakers on 4th gill arch (lower)	14	12–14	12 ± 0.80		TB, TE, TS
Gill rakers on 4th gill arch (total)	24	21–26	23 ± 1.30		TB, TE, TS
Gill rakers on posterior face of 3rd gill arch	8	6–10	8 ± 1.04	TS	
Prepelvic scutes	6	5–7	5 ± 0.66	TS	
Postpelvic scutes	9	9–11	9 ± 0.64	TS	
Total scutes on abdomen	15	14–16	14 ± 0.79		
Scale rows in longitudinal series	35	34–36	35 ± 0.50	TP	
Transverse scales	8	8–9	8 ± 0.50		
Pseudobranchial filaments	17	17–22	21 ± 1.68	TS	
Total vertebrae	40	40–41	40 ± 0.35		

Therefore, the two names are not objective synonyms. Although the original description of *C. tuberculosa* was brief, fin-ray counts of the dorsal (14), anal (30), pelvic (7), and pectoral (14) fins generally matched those of specimens of *T. tuberculosa* examined in this study (except slightly higher numbers of pectoral-fin rays (11–13 in this study) and anal-fin rays (31–34 in this study)). Nine species of Engraulidae occur off the African east coast to Mauritius, [viz. *Encrasicholina intermedia* Hata & Motomura, 2016, *Encrasicholina pseudoheteroloba* (Hardenberg, 1933), *Engraulis capensis* Gilchrist, 1913, *Stolephorus belaeus* Hata, Lavoué & Motomura, 2021, *Stolephorus holodon* (Boulenger, 1900), *Stolephorus commersonii* Lacepède, 1803, *T. polynemoides*, *T. tuberculosa*, and *Thrissina*

vitrirostris (Gilchrist & Thompson, 1908)]. Anal-fin ray counts shown by Lacepède (1803) approximated those of *T. polynemoides* or *T. tuberculosa* determined in the present study [31–35 in *T. polynemoides* and 31–34 in *T. tuberculosa* vs. fewer than 23 in species of *Encrasicholina*, *Engraulis*, and *Stolephorus*; 39–42 in *T. vitrirostris* (Whitehead et al., 1988; Hata & Motomura, 2016a, b, 2019; Hata et al., 2021a; this study)]. Finally, Lacepède's (1803) *C. tuberculosa* had a red spot above pectoral fin, a colour feature found in *T. tuberculosa* specimens recognised herein. However, since no specimens of *T. polynemoides* have been confirmed from Mauritius to date, *T. tuberculosa* is considered to be a valid Mauritian species, and not conspecific with the other eight engraulid species (above).

Table 8. Morphometrics of specimens of *Thrissina evermanni*.

	<i>Thrissina evermanni</i>					
	Holotype	Paratypes	Non-type specimens	ANCOVA		
	USNM 51719	n = 4	n = 3	Means ± SD	p values	
Standard length (mm; SL)	105.0	84.5–98.3	53.7–87.3		5 > p > 0.1	0.1 > p
As % of SL						
Head length (HL)	26.2	26.4–26.9	26.6–28.3	27.2 ± 0.81		TP, TT
Body depth	22.3	21.9–23.5	23.5–27.3	23.7 ± 1.75		TP, TT
Pre-dorsal fin length	50.9	50.8–51.7	50.6–52.0	51.2 ± 0.41		TB
Snout tip to pectoral-fin insertion	28.0	27.3–28.6	28.1–28.8	28.2 ± 0.49	TB, TP	TT
Snout tip to pelvic-fin insertion	44.7	44.0–45.8	44.0–45.2	44.7 ± 0.65	TP	
Snout tip to anal-fin origin	66.6	64.1–68.3	64.3–66.3	65.7 ± 1.29		TT
Dorsal-fin base length	10.6	10.8–11.7	11.5–12.1	11.4 ± 0.49		TP
Anal-fin base length	25.5	26.1–26.5	25.8–27.3	26.3 ± 0.59	TP	
Caudal-peduncle length	10.2	9.7–10.5	9.8–10.4	10.1 ± 0.25	TP, TT	TB
Caudal-peduncle depth	9.3	9.4–9.7	9.6–10.2	9.7 ± 0.28		TB, TP
D–P1	31.6	30.2–31.4	30.3–31.2	30.9 ± 0.4		
D–P2	22.4	22.4–24.1	23.1–25.3	23.5 ± 0.96	TB	
D–A	27.0	27.7–29.1	27.7–29.1	28.1 ± 0.65		
P1–P2	17.5	15.3–18.6	15.1–16.3	16.4 ± 1.03	TS	
P2–A	22.3	21.6–22.9	21.0–22.9	22.1 ± 0.70		TP, TT
Orbit diameter	6.5	7.2–7.7	7.6–8.1	7.4 ± 0.43		TT
Snout length	5.0	5.1–5.3	4.9–5.2	5.1 ± 0.13	TS, TT	TB, TP
Pectoral-fin length	16.4	16.3–18.0	18.0–20.4	18.1 ± 1.28	TT	
Pelvic-fin length	13.1	13.0–13.7	13.6–14.4	13.6 ± 0.48	TP	TT
Maxilla length	20.4	20.9–21.6	21.9–22.8	21.6 ± 0.71		TP, TT
Lower-jaw length	19.3	19.4–20.2	20.0–20.7	20.0 ± 0.46	TP	TT
Supramaxilla end to maxilla end	2.32	2.0–3.0	2.2–2.6	2.4 ± 0.25	TB, TS	
As % of HL						
Orbit diameter	24.7	26.6–28.7	27.0–28.6	27.3 ± 1.20		TT
Snout length	19.1	19.0	17.4–18.5	18.7 ± 0.80	TB, TS	TP, TT
Interorbital width	23.3	19.9	24.2–25.7	24.4 ± 0.91		
Postorbital length	58.9	57.3–60.4	55.3–59.6	58.2 ± 1.53	TP, TT	

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); TB (*Thrissina baelama*); TP (*Thrissina polynemoides*); TS (*Thrissina samam*); TT (*Thrissina tuberculosa*).

Table 9. Morphometrics of specimens of *Thrissina polynemoides*.

	<i>Thrissina polynemoides</i>				
	Holotype	Non-type specimens		ANCOVA	
	BMNH 1979.7.5.26	n = 8	Means ± SD	p values	
Standard length (mm; SL)	93.3	87.1–94.0	Means ± SD	5 > p > 0.1	0.1 > p
As % of SL					
Head length (HL)	27.3	27.3–28.0	27.6 ± 0.53	TB, TS	TE
Body depth	24.4	23.5–25.3	24.5 ± 0.54	TS	TE, TT
Pre-dorsal fin length	51.6	50.7–51.8	51.2 ± 0.39		TB
Snout tip to pectoral-fin insertion	28.2	28.1–29.7	28.8 ± 0.54	TE, TS	
Snout tip to pelvic-fin insertion	44.5	44.9–46.2	45.4 ± 0.54	TE, TS	
Snout tip to anal-fin origin	65.5	65.4–66.9	66.1 ± 0.49		TT
Dorsal-fin base length	10.8	10.4–10.9	10.7 ± 0.21	TS	TE, TT
Anal-fin base length	25.8	26.5–27.2	26.8 ± 0.42	TE, TS, TT	
Caudal-peduncle length	9.1	9.1–10.1	9.6 ± 0.35	TE	TB, TS
Caudal-peduncle depth	10.1	9.9–10.6	10.2 ± 0.20		TE, TS, TT
D–P1	30.9	30.0–32.9	31.4 ± 0.90		
D–P2	24.1	22.7–24.5	23.8 ± 0.58		
D–A	28.1	26.5–28.1	27.5 ± 0.57		
P1–P2	17.1	16.8–18.7	17.5 ± 0.57		
P2–A	21.2	20.5–21.7	21.1 ± 0.31	TS	TE, TT
Orbit diameter	7.2	7.0–8.1	7.5 ± 0.30		TB, TT
Snout length	4.9	4.7–4.9	4.8 ± 0.08		TB
Pectoral-fin length	17.6	17.1–18.2	17.8 ± 0.30		TT
Pelvic-fin length	13.0	12.4–13.4	13.0 ± 0.31	TB, TE, TS	TT
Maxilla length	22.2	21.6–22.3	22.0 ± 0.20	TB, TS	TE, TT
Lower-jaw length	20.1	19.7–20.3	20.1 ± 0.17	TB, TE, TS	TT
Supramaxilla end to maxilla end	2.6	2.3–2.8	2.6 ± 0.16		
As % of HL					
Orbit diameter	26.5	25.5–29.7	27.2 ± 1.10	TS	TT
Snout length	18.0	16.9–17.8	17.4 ± 0.34		TB, TE
Interorbital width	25.2	23.5–24.7	24.1 ± 0.51		
Postorbital length	56.2	54.4–58.1	57.1 ± 1.11	TB, TE, TS	

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); TB (*Thrissina baelama*); TE (*Thrissina evermanni*); TS (*Thrissina samam*); TT (*Thrissina tuberculosa*).

Table 10. Morphometrics of specimens of *Thrissina samam*.

	<i>Thrissina samam</i>				
	Neotype	Non-type specimens	Means \pm SD	ANCOVA	
	BMNH 1971.2.8.49	n = 52		p values	
Standard length (mm; SL)	79.6	40.3–104.1		5 > p > 0.1	0.1 > p
As % of SL					
Head length (HL)	27.7	25.2–30.0	27.6 \pm 1.11	TP, TT	
Body depth	23.7	20.1–26.0	23.0 \pm 1.30	TP	TB, TT
Pre-dorsal fin length	50.2	47.7–53.1	50.3 \pm 1.27	TT	TB
Snout tip to pectoral-fin insertion	28.4	26.4–30.8	28.9 \pm 1.00	TP	
Snout tip to pelvic-fin insertion	43.7	42.5–47.2	44.7 \pm 0.89	TP	
Snout tip to anal-fin origin	65.3	63.2–68.3	65.9 \pm 1.25		TT
Dorsal-fin base length	10.8	10.4–12.5	11.4 \pm 0.55	TB, TP	
Anal-fin base length	25.9	25.1–27.0	26.3 \pm 0.48	TP, TT	
Caudal-peduncle length	10.4	9.7–11.0	10.1 \pm 0.28		TB, TP, TT
Caudal-peduncle depth	9.8	9.0–10.6	9.7 \pm 0.43		TB, TP
D–P1	31.2	28.4–32.9	30.8 \pm 1.16	TT	
D–P2	23.8	20.5–25.0	23.1 \pm 1.12		TB
D–A	26.2	24.2–28.9	27.1 \pm 1.00		
P1–P2	16.5	15.1–19.0	17.0 \pm 1.02	TE	
P2–A	20.9	18.7–23.7	21.4 \pm 1.33	TP	TT
Orbit diameter	7.8	7.1–8.3	7.6 \pm 0.33		TT
Snout length	4.3	4.1–5.4	4.7 \pm 0.40	TE, TT	TB
Pectoral-fin length	17.9	16.9–19.1	17.8 \pm 0.49	TB	TT
Pelvic-fin length	13.6	12.6–14.3	13.3 \pm 0.51	TB, TP	TT
Maxilla length	20.9	20.3–23.1	21.7 \pm 0.63	TP	TT
Lower-jaw length	19.2	18.7–21.2	19.9 \pm 0.56	TB TP	TT
Supramaxilla end to maxilla end	2.8		2.7 \pm 0.26	TE	
As % of HL					
Orbit diameter	28.1	25.9–29.7	27.7 \pm 0.86	TP	TT
Snout length	15.4	14.5–19.5	17.1 \pm 1.23	TE	TB
Interorbital width	23.1	21.2–28.2	23.9 \pm 1.47	TT	
Postorbital length	58.7	52.6–59.9	57.5 \pm 1.53	TP	TT

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); TB (*Thrissina baelama*), TE (*Thrissina evermanni*), TP (*Thrissina polynemoides*); TT (*Thrissina tuberculosa*).

Table 11. Morphometrics of specimens of *Thrissina tuberculosa*.

	<i>Thrissina tuberculosa</i>				
	Neotype	Non-type specimens	Means ± SD	ANCOVA	
	BPBM 41797	n = 11		p values	
			5 > p > 0.1	0.1 > p	
Standard length (mm; SL)	90.9	79.3–94.6			
As % of SL					
Head length (HL)	27.3	26.9–28.9	27.5 ± 0.49	TB, TS	TE
Body depth	22.1	20.6–23.4	21.6 ± 0.98		TB, TE, TP, TS
Pre-dorsal fin length	51.4	50.4–52.2	51.3 ± 0.55	TS	TB
Snout tip to pectoral-fin insertion	29.1	27.8–30.1	29.2 ± 0.65	TB	TE
Snout tip to pelvic-fin insertion	45.5	43.8–46.5	45.0 ± 0.75		
Snout tip to anal-fin origin	66.7	67.3–69.6	68.2 ± 0.75		TB, TE, TS, TP
Dorsal-fin base length	11.4	11.1–11.6	11.4 ± 0.16	TB	TP
Anal-fin base length	25.3	25.3–27.3	25.9 ± 0.57	TP, TS	
Caudal-peduncle length	9.9	8.8–10.5	9.5 ± 0.53	TE	TB, TS
Caudal-peduncle depth	9.4	9.1–9.9	9.6 ± 0.25		TB, TP
D–P1	31.1	28.0–31.8	30.4 ± 1.15	TS	
D–P2	22.8	21.6–24.6	22.9 ± 0.88		TB
D–A	27.6	25.4–28.7	27.4 ± 0.93		
P1–P2	17.1	15.9–19.8	17.1 ± 1.05		
P2–A	23.5	22.7–25.3	23.6 ± 0.71		TB, TE, TP, TS
Orbit diameter	7.7	7.9–8.6	8.0 ± 0.23		TB, TE, TP, TS
Snout length	4.9	4.7–5.0	4.9 ± 0.08	TE, TS	TB
Pectoral-fin length	18.4	18.4–19.4	18.9 ± 0.34	TB, TE	TB, TP, TS
Pelvic-fin length	14.3	13.6–14.8	14.3 ± 0.37		TE, TP, TS
Maxilla length	22.9	22.5–23.7	23.2 ± 0.35		TB, TE, TP, TS
Lower-jaw length	20.5	20.1–21.4	20.8 ± 0.36		TB, TE, TP, TS
Supramaxilla end to maxilla end	2.8	2.2–3.7	2.7 ± 0.38		
As % of HL					
Orbit diameter	28.2	28.4–31.6	29.2 ± 0.82		TB, TE, TP, TS
Snout length	17.8	16.6–18.4	17.6 ± 0.47		TB, TE
Interorbital width	23.5	23.4–25.3	24.4 ± 0.55	TS	
Postorbital length	57.9	54.3–59.3	56.6 ± 1.36	TE	TB, TS

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); TB (*Thrissina baelama*), TE (*Thrissina evermanni*); TP (*Thrissina polynemoides*); TS (*Thrissina samam*).

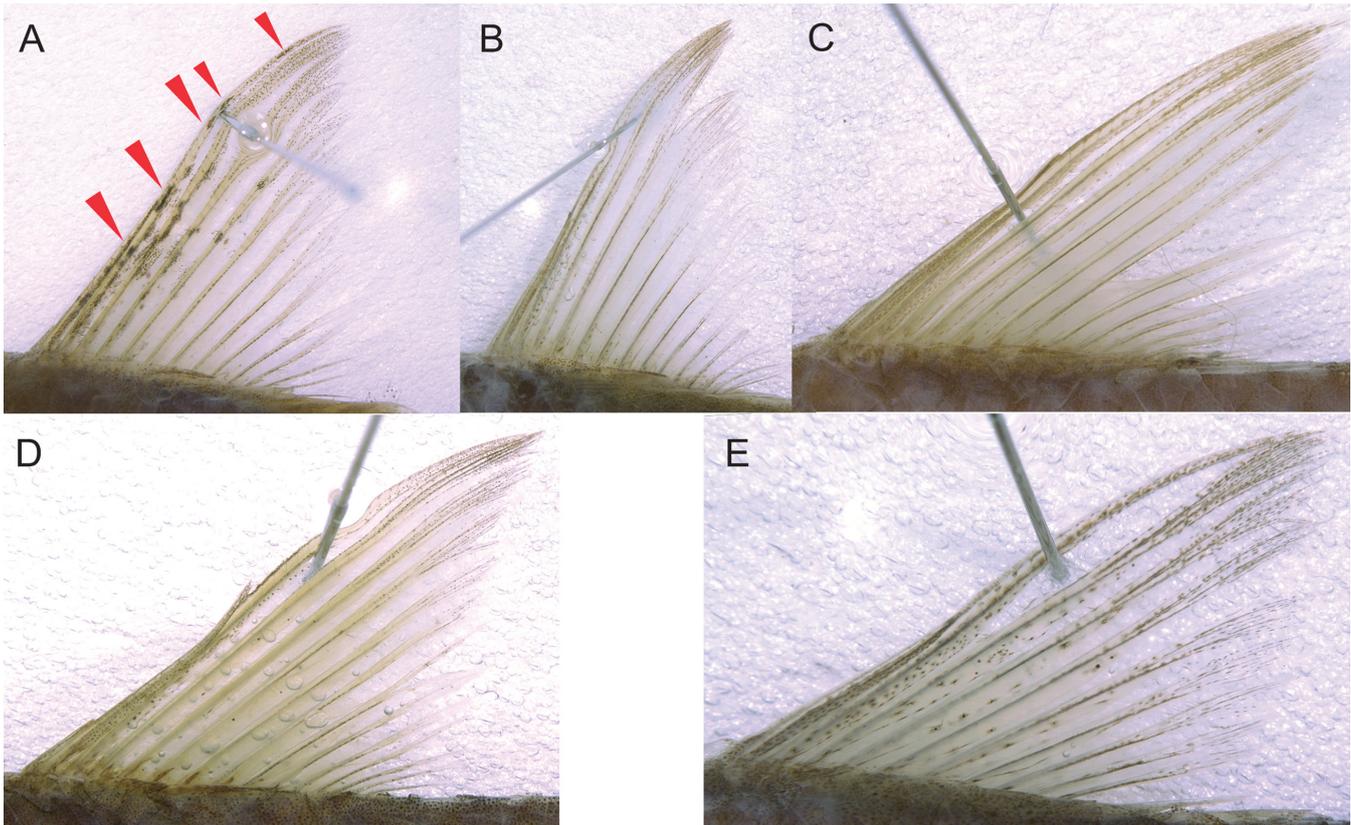


Fig. 11. Dorsal fins of A, *Thrissina tuberculosa* (BPBM 20277, 86.6 mm SL, Mauritius; triangles indicate several distinct dark spots scattered on anterior part), B, *T. baelama* (BMNH 1963.12.9.1–19, 102.4 mm SL, Djibouti), C, *T. evermanni* [BPBM 41796, 87.3 mm SL, Tonga (left-right inverted)], D, *T. polynemoides* (BMNH 1966.11.16.985–992, 89.5 mm SL, Mombasa, Kenya), and E, *T. samam* (BMNH 1971.2.8.50–58, 75.3 mm SL, New Britain, Papua New Guinea).

Although no type specimens exist for *Engraulis nesogallicus* (originally *E. Neso-Gallicus*) (Kottelat, 2013; Fricke et al., 2022; this study), the original description by Bennett (1832) noted dorsal-, anal-, pelvic-, and pectoral-fin ray numbers as 14, 32, 7, and 14, respectively, which generally matched those of specimens of *T. tuberculosa* examined here, and supported the former being considered conspecific with *T. tuberculosa* (in addition to their coincident type localities). In the absence of type specimens of either species (Whitehead, 1967a; Kottelat, 2013; Fricke et al., 2022; this study), BPBM 41797, 90.9 mm SL (Fig. 10), collected from Black River District, Mauritius is herein designated as the neotype of *Clupea tuberculosa* Lacepède, 1803 and *Engraulis nesogallicus* Bennett, 1832, the collection locality becoming the type locality for both nominal species under Article 76.3 (ICZN, 1999). Therefore, *E. nesogallicus* becomes a junior objective synonym.

Comparative material: *Encrasicholina macrocephala*, RUSI 11270, 2 specimens, 46.7–53.8 mm SL, Red Sea. *Thrissina encrasicholoides*, NSMT-P 50306, 69.8 mm SL, Philippines.

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