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A New Species of *Thrissina* from Philippines (Teleostei: Clupeiformes: Engraulidae) with Comments on the Biogeography and Speciation of this Genus in Southeast Asia

Harutaka Hata[1,*], Sébastien Lavoué[2], Mudjekeewis D. Santos[3], and Lauren Sallan[1]

[1]*Macroevolution Unit, Okinawa Institute of Science and Technology, 1919-1 Tancha, Onna-son, Kunigami-gun, Okinawa 904-0495, Japan.*
**Correspondence: E-mail: k2795502@kadai.jp (Hata).*
E-mail: Lauren.Sallan@oist.jp (Sallan)
[2]*School of Biological Sciences, Universiti Sains Malaysia, 11800, Penang, Malaysia. E-mail: microceb@hotmail.com (Lavoué)*
[3]*Genetic Fingerprinting Laboratory, National Fisheries Research and Development Institute, Fisheries Building Complex, BPI Compound Visayas Avenue, Vasra, Quezon City 1128 Philippines. E-mail: mudjiesantos@gmail.com (Santos)*

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Thrissina invicta sp. nov. is described based on 46 specimens collected from Philippine Islands. The new species is morphologically most similar to *Thrissina katana* Hata, Lavoué and Motomura 2022, *Thrissina malabarica* (Bloch 1795), and *Thrissina mystica* Hata, Lavoué and Motomura 2025, three species previously included in "*Thryssa hamiltonii*." However, *Thrissina invicta* sp. nov. differs from these species by several morphological metrics including higher counts of gill rakers and lower counts of vertebrae, as well as both a longer head and a deeper body. The new species is most likely to be the sister taxon to *T. katana* due to their close morphological similarity based on preserved specimens in museums, but this is yet to be confirmed by genetic analysis. If they are sister taxa, their divergence may have resulted from allopatric speciation during the long isolation of shelf areas around the Philippine Islands from those around Sundaland (now the islands of Southeast Asia, Indonesia, Brunei and Malaysia) during Pleistocene era intervals of low sea levels associated with glacial maxima. The current overlapping distribution of *Thrissina invicta* sp. nov. and *T. katana* off Palawan Island is interpreted as a secondary contact zone, highlighting the influence of both Philippine Islands and Sundaland in the assembling of the marine ichthyofauna of this island.

Keywords: Actinopterygii, Clupeomorpha, Taxonomy, *Thrissina katana*, *Thryssa hamiltonii*

BACKGROUND

The genus *Thrissina* Jordan and Seale 1925, an Indo-West Pacific engraulid genus, currently includes at least 38 valid species (Roberts 1978; Wongratana 1983 1987; Whitehead et al. 1988; Wongratana et al. 1999; Gill et al. 2018; Hata and Motomura 2019; Hata et al. 2020 2021 2022a 2023a b 2025; Hata 2022; Hata and Lavoué 2024). This number of valid species is likely an underestimate, given inadequate sampling of *Thrissina* populations and dependence on older, inadequate diagnoses that did not capture significant morphological differences. *Thrissina hamiltonii* (Gray 1835) (previously treated as a member of the genus *Thryssa*; see Whitehead et al. 1988) was thought to contain all individuals with a maxilla extending posteriorly beyond opercular margin but not reaching pectoral-fin insertion, paired dark lines on dorsum, a black blotch on the

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cleithrum, small conical teeth on both jaws. However, recent studies of new and old material indicated that at least three species were hidden under this name, viz., *Thrissina katana* Hata, Lavoué and Motomura 2022, *Thrissina malabarica* (Bloch 1795) (senior synonym of *T. hamiltonii*), and *Thrissina mystica* Hata, Lavoué and Motomura 2025 (Hata et al. 2022a 2023b 2025). Based on the geographic distribution of these taxa, it was hypothesized that the origin and differentiation of these species of the genus *Thrissina* was likely driven by geographic isolation due to Pleistocene eustatic sea level changes.

Based on this evidence for geographically-restricted species within *Thrissina*, we have continued to investigate the taxonomy of populations of "*T. hamiltonii*" in Southeast Asia and the West Pacific using museum specimens, fisheries surveys and published data. We found that *Thrissina* specimens from Philippines differ significantly from the other three species in several characters, including a lower count of vertebrae, higher counts of gill rakers, a larger head and a deeper body. In the present study, Philippine specimens are described as a new species of *Thrissina*, bringing the number of species represented by specimens previous recognized as *T. hamiltonii* by Whitehead et al. (1988) to four. Although there is no genetic data available for the new species at present, we also provide the first mitochondrial cytochrome oxidase subunit I (*COI*) sequence of a specimen of *T. katana* from Philippines.

MATERIALS AND METHODS

Counts and proportional measurements followed Hata and Motomura (2019). All measurements were made with digital calipers to the nearest 0.01 mm. Osteological characters, including vertebral counts, were observed from radiographs. "Pelvic scute" refers to the scute associated with the pelvic-fin insertion, whereas "prepelvic" and "postpelvic scutes" refer to the scutes anterior and posterior to the pelvic scute, respectively. Abbreviations: SL, standard length; and UGR, LGR and TGR, gill rakers on upper limb, lower limb and total gill rakers, respectively, the associated numbers indicating the specific gill arch. Institutional abbreviations follow Fricke and Eschmeyer (2025). Nomenclature and authorship of the genus *Thrissina* Jordan and Seale 1925 follow Kottelat (2013). Kruskal-Wallis test, analysis of variance (ANOVA), and PCA (principal component analysis) were performed with EZR (Kanda 2013).

Because our description is based on preserved specimens and photographic records, we could not obtain genetic data for *Thrissina invicta* sp. nov. However, the "barcode" fragment of the mitochondrial cytochrome oxidase subunit I (*COI*) was determined for a specimen of *T. katana* (USNM 431601) from Palawan Island, representing the first genetic data for this species from Philippines.

Total genomic DNA was extracted from a 95% ethanol-preserved tissue sample using a modified CTAB (Cetyl Trimethyl Ammonium Bromide) method (Grewe et al. 1993). The partial *COI* gene was amplified by PCR amplification carried out with a T100TM Thermal Cycler (BIO-RAD, Hercules, California, USA) using the primers FISH-BCL (5'-TCAACYAATCAYAAAG ATATYGGCAC-3') and FISH-BCH (5'-TAAACTTCA GGGTGACCAAAAAATCA-3') (Baldwin et al. 2009). The PCR mixture was carried out in a total volume of 25 μL, which contained 15.75 μL of ddH2O, 5.5 μL 5X MyTaq™ Red Buffer (Bioline; www.bioline.com), 0.5 μL of each 10 μM primer, 0.25 μL of i-Taq™ DNA polymerase (iNtRON Biotechnology) and 2.5 μL of genomic DNA. The thermal cycle profile consisted of an initial 94°C denaturation step for 10 min, 35 cycles of 94°C for 1 min, annealing for 1 min at 48.0°C, extension at 72°C for 1.5 min, followed by a final extension at 72°C for 10 min. The PCR sample was sent to Apical Scientific Sdn. Bhd. (Selangor, Malaysia) for purification and bidirectional sequencing using Sanger technology and the same PCR primers as indicated above.

The new sequence, deposited in GenBank under the accession number PX412912, was combined with the *COI* sequences examined in Hata et al. (2025) comprising 18 specimens of *T. katana*, 16 specimens of *T. malabarica* and six specimens of *T. mystica* (GenBank numbers provided in Hata et al. (2025) and in Fig. 1). The phylogenetic relationships among sequences were inferred by maximum likelihood (ML) using the general time-reversible model of nucleotide substitution with rate heterogeneity following a discrete gamma distribution (GTR + Γ), using the software RAxML-NG (Kozlov et al. 2019). The tree was rooted with a specimen of *Thrissina valenciennesi* which is the sister group of the "*Thrissina malabarica*" species complex (see Hata and Lavoué 2024). The robustness of each node was determined by bootstrap support (500 replicates).

Uncorrected mean pairwise genetic distances (*p*-distances) were calculated between the new sequence PX412912 and the *COI* sequences of *T. katana*, *T. malabarica* and *T. mystica* using MEGA 12.1 (Stecher et al. 2026).

RESULTS

Thrissina invicta sp. nov.

(New English name: Philippine Thryssa)
(Figs. 2, 3; Tables 1–2)
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Thrissocles hamiltonii (not of Gray): Fowler 1941: 675 (in part: Philippines); Legasto 1975: 220 (San Miguel Bay, Luzon, Philippines).

Thrissa hamiltoni [sic] (not of Gray): Matsubara 1955: 196 (in part: Philippines).

Thryssa hamiltonii (not of Gray): Rau and Rau 1980: 227 (Philippines); Pauly 1982: 26, appendix 1 (San Miguel Bay, Luzon, Philippines); Whitehead et al. 1988: 432 (in part: Philippines); Wongratana et al. 1999: 1748 (in part: Philippines); Gonzales 2013: 31, fig. 44 (Palawan, Philippines).

Holotype: USNM 138490, 154.1 mm SL, female, off Iloilo City, Panay, Philippines.

Paratypes: 45 specimens (62.3–190.1 mm SL),

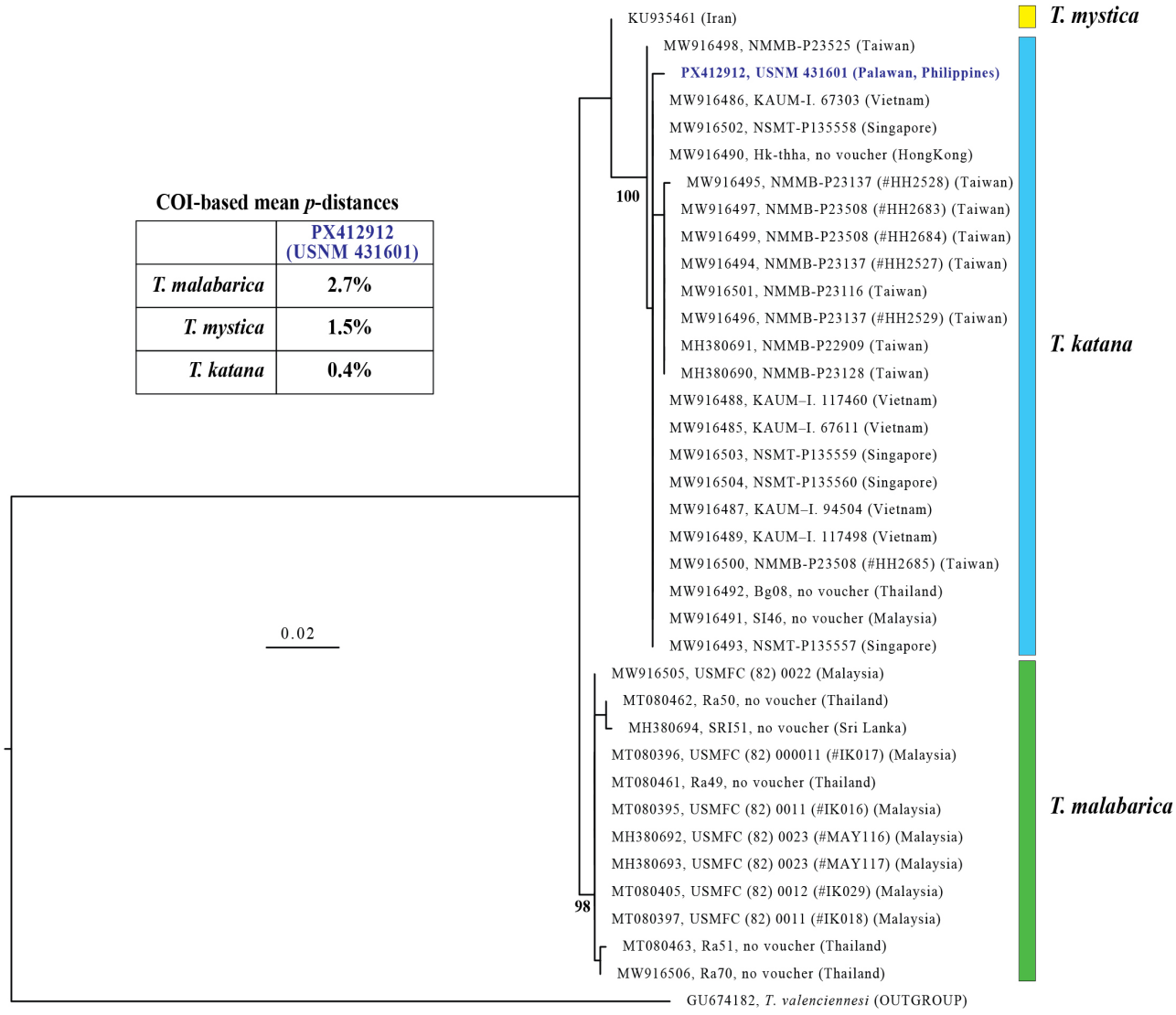

Fig. 1. Maximum-likelihood phylogenetic tree of three species of the "*Thrissina malabarica*" species complex, *T. malabarica*, *T. mystica* and *T. katana* (Clupeiformes: Engraulidae), based on cytochrome oxidase I gene (total: 648 characters). The haplotype KU935461 represents six specimens collected from the same locality (see Afrand et al. 2020). The newly determined haplotype (PX412912) from a specimen of *T. katana* collected in the Philippines is highlighted in blue. The inserted table shows *COI*-based mean genetic *p*-distances between this haplotype and other haplotypes of *T. malabarica*, *T. mystica*, and *T. katana*. *Thrissina* specimens are each identified by the GenBank sequence accession number, followed by specimen code (if no voucher is available) or museum registration number (with a specimen code when this number is not unique), and country of origin. The tree is rooted with a specimen of *T. valenciennesi*; branch lengths are proportional to the number of substitutions (scale = 0.02 substitution/position); numbers at interspecific nodes indicate bootstrap proportions. Abbreviation: *T.*, *Thrissina*. Species-code color corresponds to that of figures 5–6.

all specimens were collected from Philippines. ANSP 49227, 2 specimens, 142.7–168.9 mm SL, Philippine Islands; ANSP 77864, 146.0 mm SL, Philippine Islands; CAS 9660, 159.2 mm SL, Cavite, Luzon; CAS 20328, 155.8 mm SL, Manila, Luzon; CAS 49534, 2 specimens, 146.3 mm and approx. 148.8 mm SL (snout broken), Guinlo, Malampaya Sound, Palawan; CAS 49542, 3 specimens, 127.3–147.3 mm SL, Manila Bay, Luzon; CAS 248770, 2 specimens, 117.9–172.3 mm SL, Manila Bay, Manila, Luzon (obtained at Novatas Fish Landing Port); CAS-SU 38404, 190.1 mm SL, Rizal, Luzon; CAS-SU 38405, 162.7 mm SL, Ragay Gulf, Luzon; KAUM–I. 180822, 137.4 mm SL, KAUM–I. 180823, 131.0 mm SL, USNM 466404, 7 specimens, 121.5–154.1 mm SL, off Daet, Camarines Norte, Luzon; USNM 138491, 15 specimens, 62.3–91.1 mm SL, mouth of Malampaya River, Malampaya Sound, Taytay, Palawan, 1–2 m depth; USNM 138493, 2 specimens, 98.1–153.7 mm SL, off Catbalogan, Western Samar, Samar; USNM 138494, 5 specimens, 127.4–158.1 mm SL, Tacloban, Leyte.

Diagnosis: A species of *Thrissina* that can be distinguished from other congeners by the following combination of characters: maxilla moderate, its posterior tip slightly beyond posterior margin of opercle, but not reaching pectoral-fin insertion; teeth on both jaws small, not caniniform; first supramaxilla small, oval (sometimes absent); tip of snout above level of eye center; paired dark lines along dorsum from occipital area to caudal-fin base at least in preserved specimens; distinct black blotch behind upper part of gill opening; no saddle-like blotch on nape; anal fin with 4 unbranched and 32–38 (modally 35; rarely 41) branched rays; transverse scales 12; scale rows

Fig. 2. (A) lateral, (B), dorsal, and (C) ventral views of holotype (USNM 138490, 154.1 mm SL, Panay, Philippines) and (D) lateral view of paratype (USNM 138491, 67.2 mm SL, Palawan, Philippines) of *Thrissina invicta* sp. nov.

in longitudinal series usually 40–43 (modally 41); 1UGR 10–12 (modally 11), 1LGR 13–17 (modally 15), 1TGR 25–28 (modally 26; rarely 23 or 24); 2UGR 9–11 (modally 10), 2LGR 14–17 (modally 16), 2TGR 24–28 (modally 26; rarely 23); 3UGR 6–8 (modally 8), 3LGR 9–10 (modally 9), 3TGR 15–18 (modally 17); 4UGR 4–8 (modally 7), 4LGR 8–10 (modally 9), 4TGR 13–18 (modally 16); gill rakers 3–7 (modally 5) on posterior face of third gill arch; abdomen covered with 16–20 (modally 17) + 9–11 (modally 10) = 26–31 (modally 27) keeled scutes; vertebrae 44 or 45 (modally 45); melanophores scattered on pectoral-fin rays of most individuals > 110 mm SL; head long, 23.6–26.8% (mean 25.2%) of SL; body deep, depth 27.8–32.7% (mean 29.8%) of SL; snout length long, 4.0–4.8% (mean 4.3%) of SL; postorbital region long, 14.2–15.9% (mean 14.9%) of SL; maxilla long, 22.5–26.8% of SL (mean 24.7%); lower jaw long, 17.9–19.9% (mean 18.9%) of SL; distance from snout tip to pectoral-fin insertion long, 26.2–29.7% (mean 27.8%) of SL; dorsal-fin base long, 8.4–10.5% (mean 9.5%) of SL; pelvic fin long, 8.0–10.1% (mean 8.9%) of SL; anal-fin base long, 32.5–35.8% (mean 34.1%) of SL; first supramaxilla oval, minute, sometimes absent; second supramaxilla long, 4.9–6.2% (mean 5.5%) of SL.

Description: Counts and measurements, expressed as percentages of SL, given in tables 1 and 2. Data for holotype presented in parentheses. Body strongly compressed laterally, greatest depth at dorsal-fin origin. Dorsal profile of head and body gently elevated from snout tip to dorsal-fin origin, gradually lowering to uppermost point of caudal-fin base. Ventral profile of body dropping from mandibular tip to pelvic-fin insertion, thereafter parallel with body axis to anus,

Table 1. Meristics of specimens of *Thrissina invicta* sp. nov.

Thrissina invicta sp. nov.						
	Holotype	Paratypes		Krustal-Wallis test		
	USNM 138490	*n* = 45		vs. *T. katana*	vs. *T. malabarica*	vs. *T. mystica*
Standard length (mm)	154.1	62.3–190.1	Modes ± SD	*P* value		
Dorsal-fin rays (unbranched)	3	3	3 ± 0	0.3204	1	1
Dorsal-fin rays (branched)	11	10–11	11 ± 0.3	0.2399	0.4240	0.5146
Anal-fin rays (unbranched)	4	4	4 ± 0	0.1814	0.0575	0.1590
Anal-fin rays (branched)	36	32–41	35 ± 1.5	0.4955	0.8516	0.0000**
Pectoral-fin rays (unbranched)	1	1	1 ± 0	1	1	1
Pectoral-fin rays (branched)	11	10–12	11 ± 0.4	0.0003**	0.0996	0.0000**
Pelvic-fin rays (unbranched)	1	1	1 ± 0	1	1	1
Pelvic-fin rays (branched)	6	6	6 ± 0	1	1	1
Gill rakers on 1st gill arch (upper)	12	10–12	11 ± 0.6	0.0000**	0.0000**	0.0000**
Gill rakers on 1st gill arch (lower)	16	13–17	15 ± 0.7	0.0000**	0.0000**	0.0000**
Gill rakers on 1st gill arch (total)	28	23–28	26 ± 1.1	0.0000**	0.0000**	0.0000**
Gill rakers on 2nd gill arch (upper)	10	9–11	10 ± 0.6	0.0000**	0.0000**	0.0000**
Gill rakers on 2nd gill arch (lower)	16	14–17	16 ± 0.7	0.0000**	0.0000**	0.0000**
Gill rakers on 2nd gill arch (total)	26	23–28	26 ± 1.2	0.0000**	0.0000**	0.0418*
Gill rakers on 3rd gill arch (upper)	8	6–8	8 ± 0.5	0.0000**	0.0000**	0.0000**
Gill rakers on 3rd gill arch (lower)	10	9–10	9 ± 0.5	0.0000**	0.0000**	0.0125*
Gill rakers on 3rd gill arch (total)	18	15–18	17 ± 0.8	0.0000**	0.0000**	0.0000**
Gill rakers on 4th gill arch (upper)	7	4–8	7 ± 0.8	0.0000**	0.0000**	0.0120*
Gill rakers on 4th gill arch (lower)	10	8–10	9 ± 0.6	0.0000**	0.0000**	0.0000**
Gill rakers on 4th gill arch (total)	17	13–18	16 ± 1.1	0.0000**	0.0000**	0.0000**
Gill rakers on posterior face of 3rd gill arch	4	3–7	5 ± 0.8	0.0002**	0.0000**	0.0213*
Prepelvic scutes	19	16–20	17 ± 0.8	0.2672	0.0053*	0.5538
Postpelvic scutes	10	9–11	9 ± 0.6	0.0000**	0.1654	0.2560
Total scutes on abdomen	29	26–31	16 ± 1.1	0.0014*	0.1303	0.9241
Scale rows in longitudinal series	43	40–43	41 ± 0.9	0.0000**	0.0000**	0.0000**
Transverse scales	12	12	12 ± 0	0.0000**	0.0000**	0.0000**
Total vertebrae	45	44–45	45 ± 0.5	0.0000**	0.0022*	0.0001**
Pectoral-fin rays with melanophores	1	0–11	0 ± 3.1	0.3061	0.0092*	0.1270

*Significant at 5% level. **Significant at 0.1% level.

gently rising to end of anal-fin base, thereafter parallel with body axis to lowermost point of caudal-fin base. Abdomen covered by 16 to 20 (19) and 9 to 11 (10) sharp, needle-like scutes from isthmus to pelvic scute, and from pelvic scute to anus, respectively. Anus just anterior to anal-fin origin. Caudal peduncle compressed, depth greater than orbit diameter. Pectoral-fin insertion slightly anterior to posterior tip of opercle, above level of maxilla tip. Uppermost ray of pectoral fin not extended as filament; first pectoral-fin ray unbranched, other rays branched. Posterior tip of pectoral fin pointed, slightly beyond pelvic-fin insertion. Upper, lower, and posterior margins of pectoral fin nearly straight. Pelvic-fin insertion anterior to dorsal-fin origin. Posterior tip of depressed pelvic fin not reaching vertical through dorsal-fin origin. Anteriormost pelvic-fin ray unbranched, other rays branched. Dorsal-fin origin anterior to anus. Anterior three rays unbranched, other rays branched. Outer margin of dorsal fin rising from fin origin to third fin ray tip, subsequently lowering to last fin-ray tip. Single spine-like scute located just anterior to dorsal-fin origin. Anal-fin origin posterior to vertical through 8th dorsal-fin ray origin (just below 11th dorsal-fin ray origin). Outer margin of anal fin lowering from fin origin to fourth or fifth (fourth) fin ray tip, almost parallel with ventral profile of body. Caudal fin forked, posterior tips of both lobes pointed, upper and lower margins of caudal fin nearly straight. Head compressed. Snout length much shorter than orbit diameter. Snout tip rounded, approximately at level of upper margin of eye. Eye round, covered with adipose eyelid; positioned laterally on head, dorsal to horizontal through pectoral-fin insertion. Pupil round. Orbit elliptical. Nostrils close to each other, anterior to anterior margin of orbit and above body axis. Posterior margin of preopercle convex, smooth. Subopercle with rounded posterior margin. Opercular membrane without serrations. Pseudobranchial filaments present, covered with fleshy membrane. Interorbital space flat. Mouth large, inferior, below body axis, extending backward beyond posterior

Table 2. Morphometrics of specimens of *Thrissina invicta* sp. nov.

	Thrissina invicta sp. nov.					
	Holotype	Paratypes		ANOVA		
	USNM 138490	*n* = 45		vs. *T. katana*	vs. *T. malabarica*	vs. *T. mystica*
Standard length (mm; SL)	154.1	62.3–190.1	Means ± SD	*P* value		
As % of SL						
Head length	24.3	23.6–26.8	25.2 ± 0.8	0.0000**	0.0000**	0.0000**
Body depth	30.0	27.8–32.7	29.8 ± 1.2	0.0000**	0.9088	0.0000**
Pre-dorsal-fin length	52.1	51.1–54.7	52.7 ± 0.8	0.3262	0.0000**	0.2805
Snout tip to pectoral-fin insertion	26.6	26.2–29.7	27.8 ± 1.0	0.0000**	0.0000**	0.0000**
Snout tip to pelvic-fin insertion	42.1	40.8–44.8	42.7 ± 0.8	0.0000**	0.0006**	0.1226
Pre-anal-fin length	63.5	59.8–66.4	62.9 ± 1.7	0.9918	0.5824	0.9797
Dorsal-fin base length	9.4	8.4–10.5	9.5 ± 0.6	0.0118*	0.0011*	0.0000**
Anal-fin base length	34.8	32.5–35.8	34.1 ± 1.0	0.0000**	0.0000**	0.9848
Caudal-peduncle length	8.9	7.2–9.7	8.5 ± 0.6	0.8484	0.7954	0.1836
Caudal-peduncle depth	10.3	9.5–11.5	10.5 ± 0.5	0.0000**	0.1175	0.0000**
D–P1	37.5	35.0–40.0	37.5 ± 1.5	0.5088	0.2995	0.0149*
D–P2	31.1	28.3–34.8	31.3 ± 1.7	0.0014*	0.2050	0.0000**
D–A	29.9	27.9–32.0	29.8 ± 1.2	0.0000**	0.1678	0.0000**
P1–P2	17.1	15.0–18.8	16.6 ± 0.9	0.9995	0.6440	0.9259
P2–A	23.1	17.9–25.0	21.8 ± 2.0	0.0382*	0.0203*	0.9223
Pectoral-fin length	20.5	19.0–21.0	20.2 ± 0.5	0.0000**	0.6962	1.0000
Pelvic-fin length	8.2	8.0–10.1	8.9 ± 0.6	0.0051*	0.0000**	0.0000**
Maxilla length	23.6	22.5–26.8	24.7 ± 0.9	0.0000**	0.0000**	0.0000**
Lower-jaw length	18.8	17.6–19/9	18.9 ± 0.5	0.0000**	0.0001**	0.0000**
Supramaxilla end to maxilla end	6.9	6.1–8.7	7.4 ± 0.6	0.0000**	0.0000**	0.0238*
Postorbital length	14.8	14.2–15.9	14.9 ± 0.4	0.0000**	0.0227*	0.0000**
Second supramaxilla length	5.6	4.9–6.2	5.5 ± 0.3	0.0104*	0.4582	0.0000**

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 from pelvic-fin insertion to anal-fin origin. *Significant at 5% level. **Significant at 0.1% level.

margin of eye. Mandible slender, much shorter than maxilla. Maxilla rather long, posterior tip pointed, beyond posterior margin of opercle, but not reaching pectoral-fin base. First supramaxilla small, oval (present in holotype; absent in 7 of 45 paratypes). Small conical teeth in single row on both jaws. Several rows of small conical teeth on palatine. Several conical teeth on vomer. Patch of small, conical teeth on ectopterygoid. Several rows of conical teeth on upper edges of basihyal and basibranchials. No teeth on dorsal surface of hyoid. Gill rakers long, slender, bearing similarly-sized serrae. Gill membranes on each side joined distally, most isthmus muscle exposed, not covered by gill membrane. Scales absent on head and fins. Scales on lateral surface of body cycloid, thin, deciduous, those on lateral body surface with several centrally continuous vertical grooves and numerous longitudinal striae posteriorly. Lateral line absent.

Coloration of preserved specimens: Body uniformly silvery. Dorsum to upper part of lateral surface of body right brown to purplish-brown. Remaining body scales yellowish. Snout to dorsum of occipital area and around eye yellowish semi-transparent. Branches of cephalic lateralis sensory canal on upper part of gill opening black, forming a distinct black blotch. Melanophores scattered along posterior margin of dorsal scale pockets. Paired dark lines on dorsum (indistinct in some paratypes and holotype). Most specimens > 95 mm SL with numerous melanophores scattered on both jaws, infraorbital area, and preopercle (Fig. 3). Melanophores scattered on dorsum of snout, along fin rays of dorsal fin. Pelvic and anal fins without melanophores. Pectoral-fin with scattered melanophores on first to tenth fin rays (from uppermost) in most specimens larger than 120 mm SL (Fig. 3). Melanophores scattered along caudal-fin rays. Caudal-fin posteriorly margined black. In addition, a color photograph of a fresh individual collected from Palawan shown by Gonzales (2013: 31, fig. 44, as *Thryssa hamiltonii*), having deep body, is thought to be the new species.

Distribution: *Thrissina invicta* sp. nov. is currently observed only from Luzon Islands and Visayan Islands, Philippines (Fig. 4).

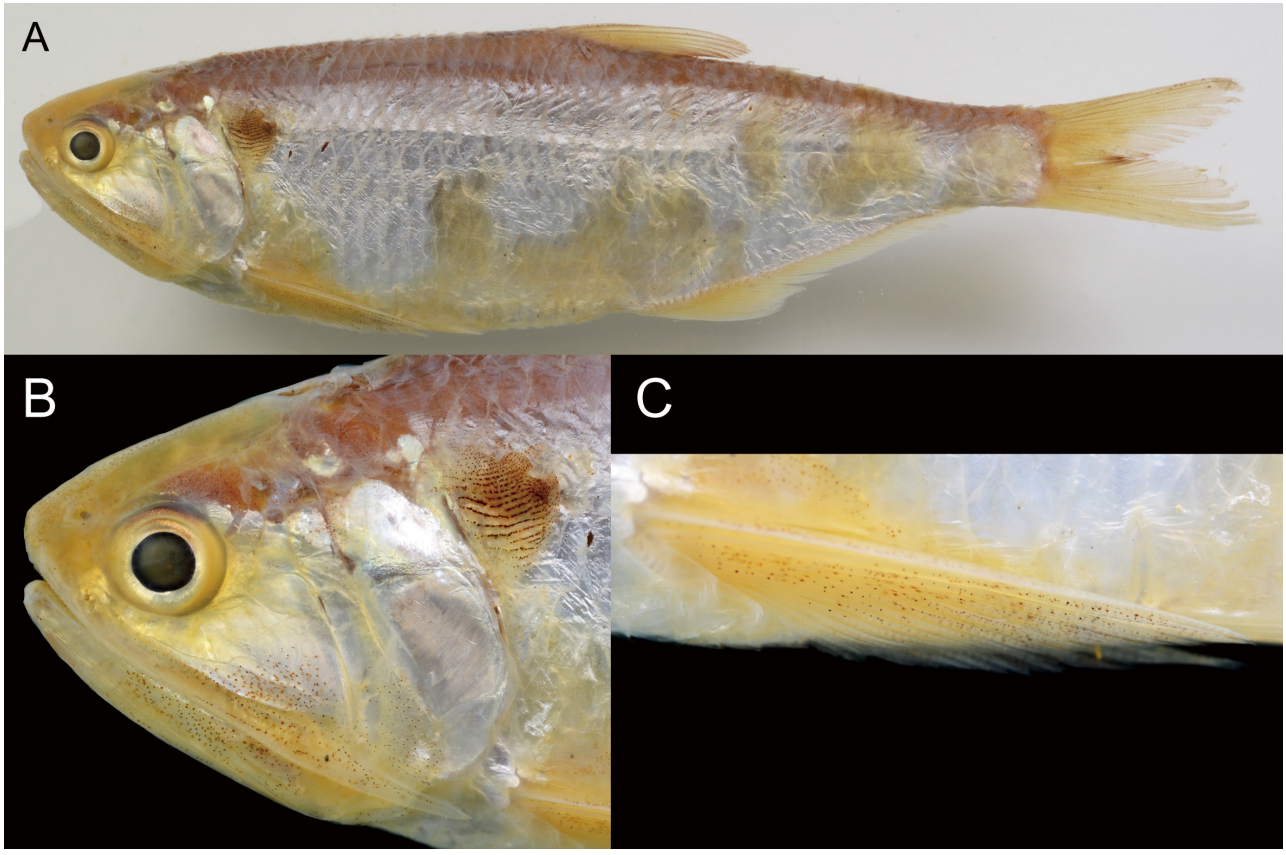

Fig. 3. Specimen of *Thrissina invicta* sp. nov. having pectoral fin and maxilla with scattered melanophores (USNM 138493, paratype, 153.7 mm SL, Samar, Philippines). (A) Lateral view of whole body, (B) lateral view of head (melanophores scattered on both jaws, infraorbital area, and preopercle), and (C) pectoral fin (melanophores scattered on 11 uppermost fin rays).

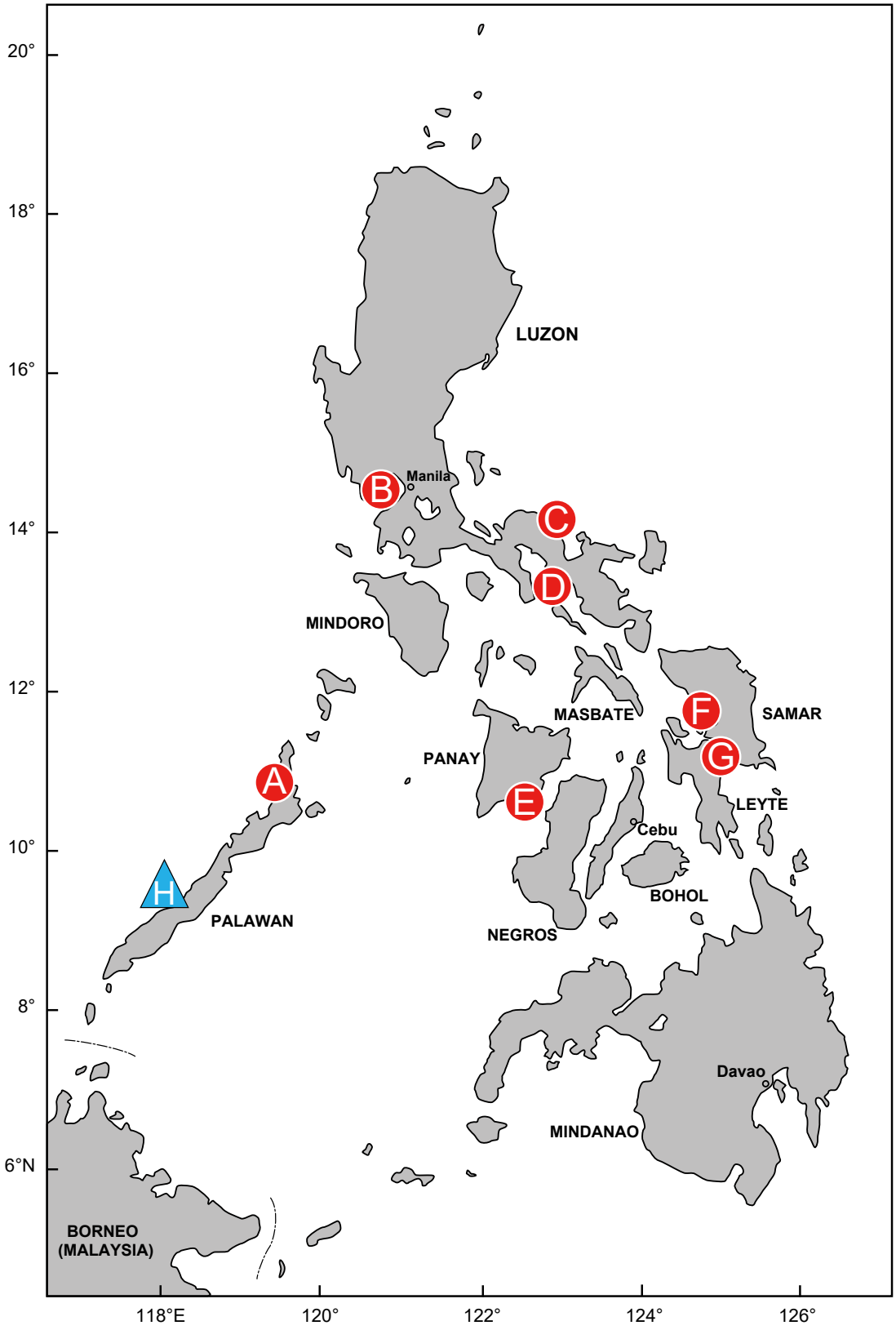

Fig. 4. Distributional records of *Thrissina invicta* sp. nov. (red circles) and *T. katana* (blue triangle) around Philippine waters based on specimens examined in this study. (A) mouth of Malampaya River, Palawan; (B) Manila Bay, Luzon; (C) Daet, Luzon; (D) Ragay Gulf, Luzon; (E) Iloilo City, Panay; (F) Catbalogan, Samar; (G) Tacloban, Leyte; and (H) Malanut Bay, Palawan.

Etymology: The specific name *invicta*, a Latin adjective meaning invincible, refers to the highest gill raker counts among the related species.

Morphological comparisons: *Thrissina invicta* sp. nov. is assigned to the genus *Thrissina*, conforming to the definitions of Whitehead et al. (1988) and Wongratana et al. (1999) (as *Thryssa*) in having strongly keeled prepelvic and postpelvic scutes on the ventral edge, a spine-like scute on the dorsal-fin origin, dorsal and anal fins with 13 or 14 and 36–42 (rarely 45) rays, respectively, the uppermost pectoral-fin ray not extended as a filament, and conical teeth on both jaws. The new species is identified as *Thryssa hamiltonii* following the identification key in Whitehead et al. (1988) because it has almost the same numbers of ventral scutes, gill rakers, and anal-fin rays, a long maxilla extended posteriorly beyond the opercle, distinct black blotch behind upper part of gill opening and small teeth on both jaws. As stated in the introduction, Whitehead et al.'s (1988) *Thryssa hamiltonii* was recently found to contain three species based on morphological and genetic differences among populations: *Thrissina katana* Hata, Lavoué and Motomura 2022, *Thrissina malabarica* (Bloch 1795) (senior synonym of *T. hamiltonii*), and *Thrissina mystica* Hata, Lavoué and Motomura 2025 (Hata et al. 2022a 2023b 2025). *Thrissina invicta* sp. nov. can likewise be distinguished from all three; from *T. katana* by having more gill rakers (1TGR 23–28 in *T. invicta* sp. nov. vs. 20–25 in *T. katana*; 2TGR 23–28 vs. 20–24; Fig. 5A, B), transverse scales [12 vs. 11 or 12 (modally 11); Fig. 5C], fewer scale rows in longitudinal series [40–43 (modally 41) vs. 41–45 (43); Fig. 5D] and total vertebrae [44 or 45 (45) vs. 45–47 (46); Fig. 5E], longer head [23.6–26.8% (mean 25.2%) of SL in *T. invicta* sp. nov. vs. 22.6–25.8% (23.9%) in *T. katana*; Fig. 6A], deeper body [27.8–32.7% (mean 29.8%) of SL vs. 23.9–30.7% (27.7%); Fig. 6B], longer snout [4.0–4.8% of SL (mean 4.3%) vs. 3.5–4.4% (4.0%); Fig. 6C], postorbital length [14.2–15.9% (mean 14.9%) of SL vs. 13.5–15.7% (14.3%); Fig. 6D], maxilla [22.5–26.8% (mean 24.7%) of SL vs. 21.0–25.0% (22.7%); Fig. 6E], lower jaw [17.6–19.9% (mean 18.9%) of SL vs. 16.6–19.5% (17.9%); Fig. 6F], and distance from snout tip to pectoral-fin insertion [26.2–29.7% (mean 27.8%) of SL vs. 24.0–28.0% (26.3%); Fig. 6G]. *Thrissina invicta* sp. nov. is easily distinguished from *T. malabarica* by having higher counts of gill rakers on each gill arch (1TGR and 2TGR ≥ 23 in *T. invicta* sp. nov. vs. 22 ≤ in *T. malabarica*; Fig. 5A, B) and transverse scales [12 vs. 11 or 12 (modally 11); Fig. 5C], larger head [23.6–26.8% (mean 25.2%) of SL vs. 23.2–25.4% (24.3%); Fig. 6A], longer anal-fin base [32.5–35.8% (mean 34.1%) of SL vs. 30.7–33.9% (mean 32.9%; rarely > 35%); Fig. 6H], pelvic fin [8.0–10.1% (mean 8.9%) vs. 6.6–8.4% (7.6%); Fig. 6I], and maxilla [22.5–26.8 (mean 24.7%) vs. 21.2–24.4% (23.1%); Fig. 6E]. The new species differs from *T. mystica* in having more gill rakers (1TGR 23–28 in *T. invicta* sp. nov. vs. 22–26 in *T. mystica*; 2TGR 23–28 vs. 22–26; Fig. 5A, B), scale rows in longitudinal series [40–43 (modally 41) vs. 38–42 (40); Fig. 5D], and transverse scales [12 vs. 11 or 12 (modally 11); Fig. 5C], fewer branched anal-fin rays [32–38 (modally 35; rarely 41) vs. 35–40 (modally 37; rarely 34); Fig. 5F], larger head [23.6–26.8% (mean 25.2%) of SL in *T. invicta* sp. nov. vs. 22.9–25.4% (24.0%) in *T. mystica*; Fig. 6A], deeper body [27.8–32.7% (mean 29.8%) of SL vs. 26.1–29.6% (27.7%); Fig. 6B], longer dorsal-fin base [8.4–10.5% (mean 9.5%) of SL vs. 8.0–9.4% (8.7%); Fig. 6J], pelvic fin [8.0–10.1% (mean 8.9%) of SL vs. 7.4–8.7% (8.0%); Fig. 6I], postorbital length [14.2–15.9% (mean 14.9%) of SL vs. 13.2–14.8% (14.0%); Fig. 6D], maxilla [22.5–26.8 (mean 24.7%) vs. 22.0–25.6% (mean 23.5%); Fig. 6E], lower jaw [17.6–19.9% (mean 18.9%) of SL vs. 17.3–19.3% (18.2%); Fig. 6F], and second supramaxilla [4.9–6.2% (mean 5.5%) vs. 4.6–5.6% (5.1%); Fig. 6K].

Kruskal-Wallis test combined with the Steel-Dwass test for comparison of meristic characters between *T. invicta* sp. nov. and each of the following species, *T. katana*, *T. malabarica*, and *T. mystica*, revealed statistically significant differences ($p < 0.01$) in 18, 15, and 14 characters, respectively. *P* values were $0.1 < p < 5$ for one character between *T. invicta* sp. nov. and *T. katana*, three characters between *T. invicta* sp. nov. and *T. malabarica*, and four characters between *T. invicta* sp. nov. and *T. mystica*, and no significant differences in other meristic characters (Table 1). In addition, ANOVA combined with Tukey Honestly Significant Difference test of 22 morphometric characters revealed significant differences ($p < 0.05$) in 17, 12, and 14 characters between *T. invicta* sp. nov. and *T. katana*, between *T. invicta* sp. nov. and *T. malabarica*, and between *T. invicta* sp. nov. and *T. mystica*, respectively (Table 2).

DISCUSSION

Based on museum specimens and previous records, we found that *T. invicta* sp. nov. is widely distributed in the Luzon Islands and Visayan Islands, Philippines (Fig. 4). As stated in the Background and Morphological comparison sections, previously identified *Thryssa hamiltonii* (of Whitehead et al. 1988) now includes four species, *Thrissina invicta* sp. nov., *Thrissina katana*, *Thrissina malabarica*, and *Thrissina mystica*. Based on the *COI* gene, the last three species are closely related

and form a monophyletic group (Hata et al. 2025: fig. 9). Although there is no available genetic data of *Thrissina invicta* sp. nov., we hypothesized that the new species belongs to the same monophyletic group, likely as the sister species of *T. katana* because both species are morphologically most similar to each other and they share adjacent distribution area (the western Pacific from Taiwan, South China Sea coast of China to Singapore, Java, Borneo, Ogasawara Islands, and Palau; Hata et al. 2022a, fig. 4; this study). As mentioned in the introduction, several recent speciation events of engraulid fishes, including the genus *Thrissina*, may have been mediated by changes in oceanic topography and currents due to sea level fall during Pleistocene glacial periods, leading to long-term geographical isolation. For example, Hata and Motomura (2022) suggested that Pleistocene era exposure of the Sunda Shelf (South China Sea) and the Sahul Shelf (Australian region), which were separated by a deep ocean trench, led to allopatric speciation by preventing gene flow between various populations in these two regions. Similar to the Australian region, Philippine Islands were never connected by shallow waters to the Eurasian continent, including the Sundaland, during the Pleistocene (Heaney 1985 1986; Voris 2000). Therefore, the gene flow between the ancestral population of the

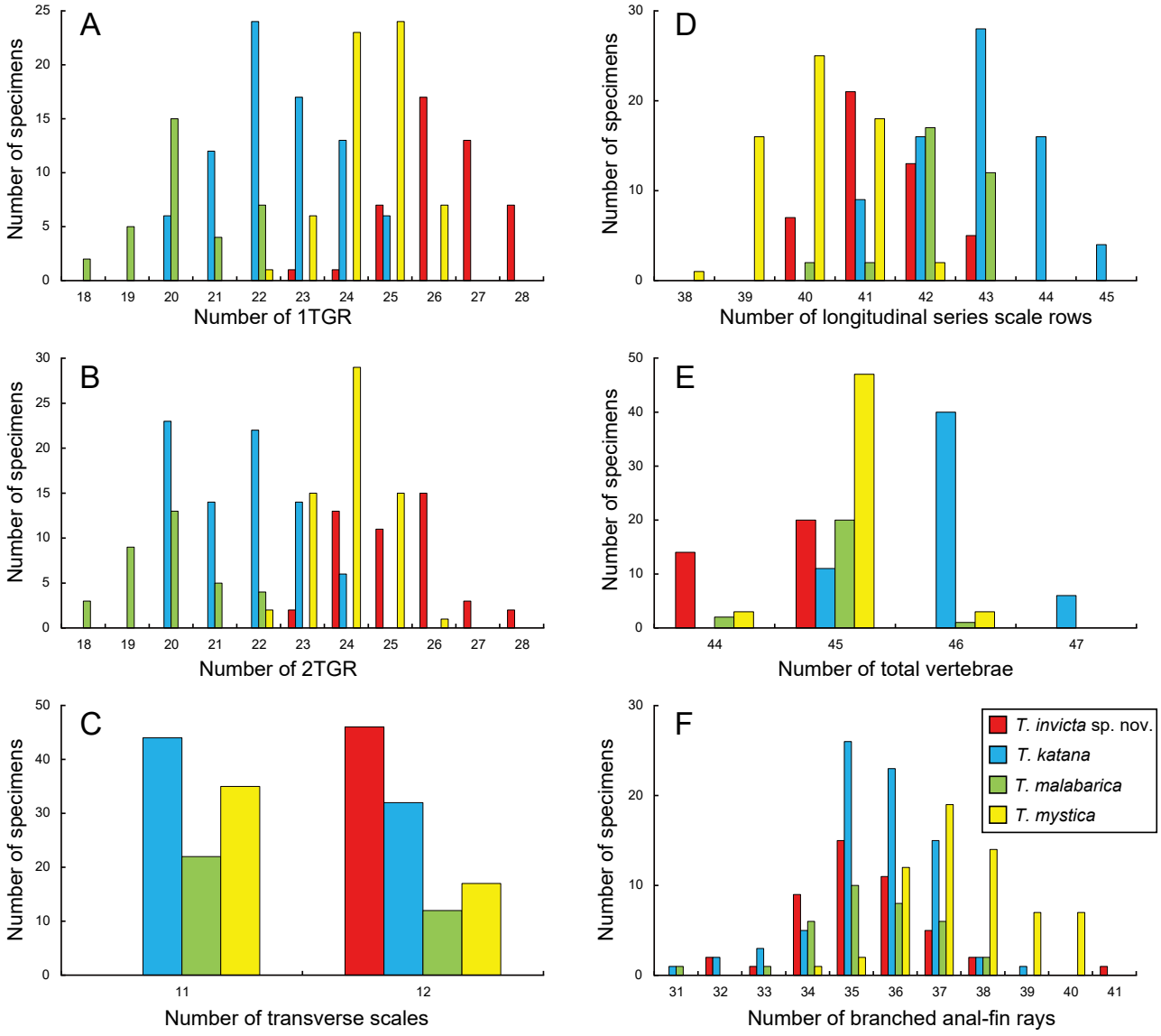

Fig. 5. Frequency distributions of selected meristics of *Thrissina invicta* sp. nov. (red bars), *T. katana* (blue bars), *T. malabarica* (green bars), and *T. mystica* (yellow bars): A, number of total gill rakers on first gill arch (1TGR); B, total gill rakers on second gill arch (2TGR); C, transverse scales; D, longitudinal series scale rows; E total vertebrae; F, branched anal-fin rays.

new species in Philippines Islands and that of *T. katana* in other regions is likely to have been limited, which would have led to genetic isolation and speciation.

The morphological and molecular (*COI* sequence PX412912) identification of a specimen of *T. katana* (USNM 431601; Fig. 7) from Malanut Bay in the western part of Palawan extends the distribution of this species to Philippines. The *COI* sequence of USNM 431601 represents a unique haplotype within *T. katana* (Fig. 1), differing by only 0.4% mean *p*-distance from the other *COI* haplotypes of *T. katana* (*i.e.*, corresponding to less than 3 nucleotide differences), and by 2.7% and 1.5% from the *COI* haplotypes of *T. malabarica* and *T. mystica*, respectively (Hata et al. 2022a 2025) (Fig. 1). *Thrissina invicta* sp. nov., for which we do not yet have genetic data, has also been observed from Palawan Island (*i.e.*, from Malampaya Sound in eastern Palawan, located in western Luzon Islands). Palawan Island is close to Borneo Island, located on the eastern edge of the Sundaland. The current width of the Balabac Strait separating Palawan Island and Borneo Island is 50 km (Wang and Li 2009). We hypothesize that during the Pleistocene glacial periods, when the strait was narrower than currently observed (Tougard 2001), *T. katana* expanded northward its distribution from Borneo Island. Other Sundaic species, such as the tiger *Panthera tigris* (Linnaeus 1758), have been confirmed to have migrated

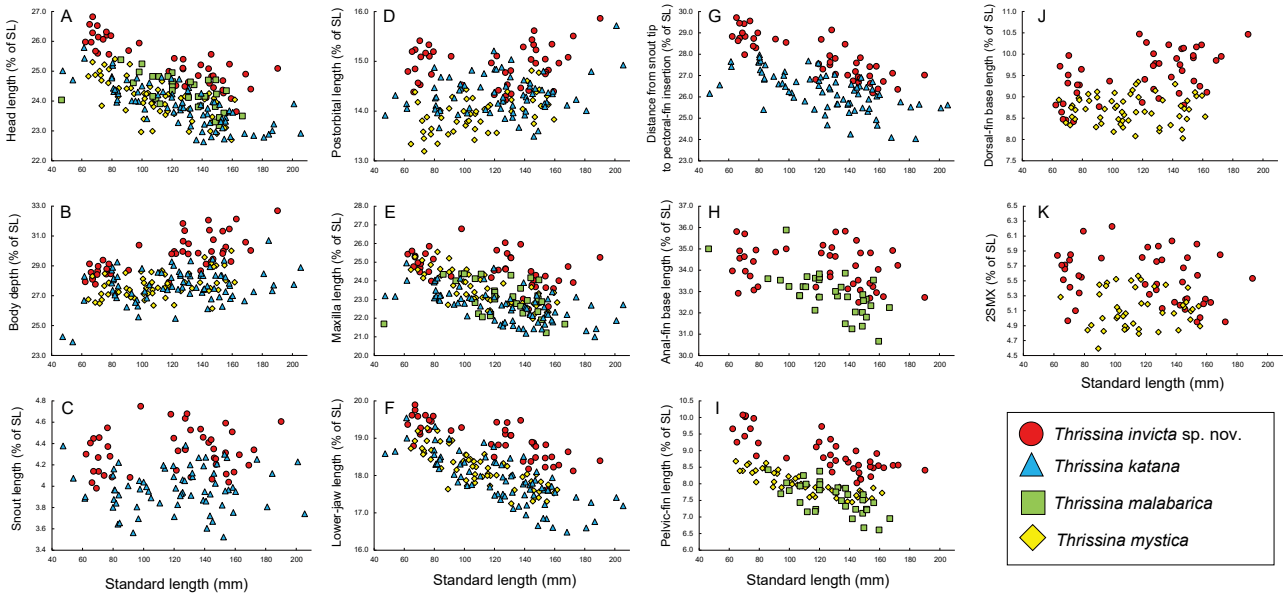

Fig. 6. Relationships of A, head length; B, body depth; C, snout length; D, postorbital length; E, maxilla length; F, lower-jaw length; G, distance from snout tip to pectoral-fin insertion; H, anal-fin base length; I, pelvic-fin length; J, dorsal-fin base length; K, second supramaxilla length (2SMX) [all as % of standard length (SL) to SL in *Thrissina invicta* sp. nov. (red circles), *T. katana* (blue triangles), *T. malabarica* (green squares), and *T. mystica* (yellow diamonds).

Fig. 7. Fresh specimen of *Thrissina katana* from Malanut Bay, western coast of Palawan, Philippines (USNM 431601, 139.4 mm standard length). Photo courtesy of the National Museum of Natural History, Smithsonian Institution.

from northern Borneo Island to Palawan Island, approx. 11,000 years ago or before (Piper et al. 2007 2008; Sherani 2019; Esselstyn et al. 2004). The co-occurrence of *T. invicta* sp. nov. and *T. katana* in Palawan Island represents, therefore, a secondary contact zone. This suggests that the rich and complex marine fish fauna of Palawan has been influenced by Pleistocene sea level variations and it is a mixture of species with origins in The Philippine and Sundaland shelf waters. To test this speciation scenario hypothesis, more research are needed, including haplotype analysis.

Species of the genus *Thrissina* in Philippines: Whitehead et al. (1988) and Wongratana et al. (1999), in their taxonomic revisions of the genus *Thrissina* (as *Thryssa*), included the Philippine Islands in the distributional ranges of *Thrissina baelama* (Fabricius 1775), *Thrissina encrasicholoides* (Bleeker 1852), and *Thrissina setirostris* (Broussonet 1782). These three species were also reported from Philippines by Fowler (1941) and Hata et al. (2022b 2023a) based on voucher specimens. Subsequently, Hata et al. (2023a) showed that the Philippine species previously regarded as *T. baelama* should, in fact, be treated as *T. samam* (Montrouzier 1857). Moreover, Whitehead et al. (1988) and Wongratana et al. (1999) showed that *Thrissina dussumieri* (Valenciennes 1848) and *Thrissina hamiltonii* (Gray 1835) are presumably distributed in the Philippines. Thereafter, Hata et al. (2022b) reported two specimens of *T. dussumieri* collected from Philippines (ZUMT 39508, 82.4 mm SL, ZUMT 39509, 79.3 mm SL; precise collection localities unknown). The distributional ranges of "*Thrissina hamiltonii*" in Philippines is as described above, and, in total, six species of *Thrissina* are confirmed to be distributed in Philippines.

Key to species of *Thrissina* recorded from Philippines

1a. Maxilla short, posteriorly not beyond posterior margin of preopercle; 1LGR ≥ 18; first supramaxilla long, elongated [fig. 1C in Hata et al. (2023a)] 2
1b. Maxilla long, posteriorly beyond opercular margin 1LGR ≤ 19; first supramaxilla minute, oval (sometimes absent) 3
2a. Scute present anterior to pectoral fins [fig. 1E in Hata et al. (2023a)] ..... *T. encrasicholoides* [a]
2b. No scutes on anterior to pectoral fins [fig. 1D in Hata et al. (2023a)] ..... *T. samam* [b]
3a. Maxilla very long, its posterior tip beyond pectoral-fin tip 4
3b. Maxilla moderately long, its posterior tip not reaching to pectoral-fin insertion 5
4a. 1LGR 17–19; ventral scutes 21–24; maxilla just reaching or not to pelvic fin insertion ..... *T. dussumieri* [a]
4b. 1LGR 10–12; ventral scutes 25–28; maxilla posteriorly well beyond pelvic-fin insertion in adults. ..... *T. setirostris* [a]
5a. Total vertebrae mostly 46; 1TGR mostly 25 or more .... *T. invicta* sp. nov. [c]
5b. Total vertebrae 44 or 45; 1TGR 25 or less ..... *T. katana* [c]

[a] Data based on Whitehead et al. (1988); [b] Hata et al. (2023a); [c] this study.

CONCLUSIONS

A new species, *Thrissina invicta* sp. nov., is described based on 46 specimens collected from various localities in Philippine Islands. Although *T. invicta* sp. nov. resembles *Thrissina katana* Hata, Lavoué and Motomura 2022, *Thrissina malabarica* (Bloch 1795), and *Thrissina mystica* Hata, Lavoué and Motomura 2025, the new species is distinguished from the other three by unique combination of morphological characters including large head, deep body, more gill rakers, and fewer vertebrae. The speciation between the new species and the related species is thought to be promoted by long isolation of the Philippine of shelf areas around the Philippine Islands from those around Sundaland. With this new species, a total of six species of *Thrissina* have been confirmed to be distributed in the Philippines.

Comparative material examined: *Thrissina katana* (84 specimens, 47.3–205.5 mm SL): listed in Hata et al. (2025) and 15 additional specimens: ASIZP 70841, 168.2 mm SL, Matsu Islands, Taiwan; CAS 47087, 2 specimens, 148.0–160.3 mm SL, 1.25 nautical miles southwest of Ngaremediu Pt., Urukthapel Island, on the extreme west side of the southward extending reef, Palau (7°13'47.0"N, 134°26'26.0"E); KAUM–I. 189910, 130.5 mm SL, off Kuantan, Pahang, Malaysia (purchased at Pasar Nelayan Pantai Sepat); NMMB-P5010, 1 of 3 specimens, 186.6 mm SL, Penghu, Taiwan; NMMB-P23116, 82.0 mm SL, Taijiang, Tainan, Taiwan; NMMB-P23128, 181.0 mm SL, OISTICH 628, 132.4 mm SL, OISTICH 630, 116.9 mm SL, OISTICH 703, 149.0 mm SL, Ko-tzai-liao, Kaohsiung, Taiwan; PMBC 39073, 2 specimens, 80.5–100.0 mm SL, Songkhla Lake, Thailand; USNM 72521, 2 specimens, 113.0–121.1 mm SL, Jakarta, Java, Indonesia; USNM 138497, 61.8 mm SL, Sebatik Island, Borneo, Malaysia / Indonesia; USNM 431601, 139.4 mm SL, Malanut Bay, western coast of Palawan (purchased at Puerto Princesa City Market). *Thrissina malabarica* (34 specimens, 46.5–166.7 mm SL): listed in Hata et al. (2025) and 2 additional specimens: KAUM–I. 210262, eastern part of Johor Strait, Johor; MZB 29222, 117.2 mm SL, off Rawa Saban, Tangerang, Java (obtained at Cituis Fish Market, Pakuhaji, Tangerang, Banten). *Thrissina mystica*: 62 specimens, listed in Hata et al. (2025).

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Authors' contributions: H.H., S.L. and M.D.S. collected the specimen data, all authors wrote 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. Specimen's measurements are available from the corresponding author upon reasonable request. All specimens examined in this study have been recently deposited in museum collections (see Materials and Methods). All nucleotide sequences are deposited and available in GenBank.

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