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A New Cryptic Species of Splitfin Fish from Taiwan with Revision of the Genus Synagrops (Acropomatiformes: Synagropidae

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A new species of splitfin fish, *Synagrops atrumoris* sp. nov., from Dongsha Island, Taiwan, South China Sea, is described based on its morphological characteristics, including osteology and otolith morphology, and DNA sequence. *Synagrops atrumoris* sp. nov. is closely similar to *Synagrops japonicus* and can be distinguished by its black mouth cavity covering the lower portion of the tongue, posteriorly enlarged and complex basioccipital fossae, and a triangular otolith with a strong postero-dorsal angle, as well as a strong genetic difference. In addition, the taxonomy of the genus *Synagrops* was revised. Available published data, together with our results, suggest that *S. bellus* is a synonym of *S. japonicus*.

Key words: Taxonomy, Ichthyology, Biodiversity, Otolith, Phylogenetic analyses

BACKGROUND

The fish order Acropomatiformes, commonly known as lanternbellies, have oblong and moderately compressed bodies covered by ctenoid or cycloid scales with notable ventral light-emitting organs in some members (Okamoto 2014). They are primarily found in the deeper-shelf, upper slope, and seamounts of tropical and subtropical areas of the world (Smith-Vaniz et al. 1999; Okamoto and Gon 2018; Santos et al. 2019). There are 20 families and over 300 species under the order Acropomatiformes *sensu* Smith et al. (2022). One of the families is Synagropidae Smith, 1961, previously classified within the family Acropomatidae, which previously included seven genera: Acropoma, Apogonops, Doederleinia, Malakichthys, Neoscombrops, Synagrops, and Verilus. In more recent reports by Ghedotti et al. (2018) and Smith et al. (2022), the genus Synagrops was classified under the family Synagropidae. The genus Synagrops can be distinguished from other genera based on its non-serrated pelvic-fin spines, separated two dorsal fins with IX + I, 9 elements, anal fin with II spines, no vacant interneural gap under D1, naked head with a robust cranial crest forming a W shape, pre-dorsal formula 0/0/0+2, basioccipital fossae extending to the ventral part of the exoccipital, posteriorly opening the myodome, no denticles at the preopercle but with 1–3 strong ridges, small rows of

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teeth on the ectopterygoid, subrectangular shaped otolith, and 25 total vertebrae (Schwarzhans and Prokofiev 2017).

To date, there are only two species recognized under the genus Synagrops: Synagrops japonicus (Döderlein, 1883) and Synagrops bellus (Goode and Bean, 1896) (Schwarzhans and Prokofiev 2017). Synagrops japonicus and S. bellus are geographically isolated and are currently considered two separate species. However, it is necessary to mention that Heemstra et al. (2022) synonymized S. bellus with S. japonicus without providing any rational evidence. Synagrops japonicus is only found in the Indo-West Pacific, while S. bellus is distributed in the Atlantic (Heemstra 2016; Schwarzhans and Prokofiev 2017). However, studies have reported potential range expansion through the transport of juveniles from ballast waters (Orsi-relini 2009; Serena et al. 2022), wherein S. japonicus was also reported in the Mediterranean Sea (Hannachi et al. 2015; Serena et al. 2022) and S. bellus in New Caledonia, Western Pacific (Fricke et al. 2011).

Until now, the Japanese splitfin *S. japonicus* has been reported around Taiwan (Wang and Lee 2019; Xu et al. 2019; Shao 2023). However, a putative new cryptic species under *Synagrops* has been identified based on its morphological characters (including osteological characters and otoliths) and *COI* sequences. The purpose of the present work is to describe the new species and revise the genus *Synagrops*.

MATERIALS AND METHODS

Sampling and specimen preparation

Fresh specimens were collected from commercial trawl fishing around Dongsha (Pratas) Island, Taiwan (coordinates 18°56' to 20°40'N and 112°57 to 116°49'E) from 2022 to 2023 (Fig. 1). Researchers were not present during the actual fishing but instead acquired the samples from the landing sites. Thirty specimens of *S. atrumoris* sp. nov. (> 100 mm SL) were analyzed and compared with 30 specimens of *S. japonicus* (Table 1; Tables S1–S2). Museum specimens of *S. japonicus* from the Biodiversity Research Museum, Academia Sinica, Taipei, Taiwan (ASIZP; n = 20) and the National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (NMMB-P; n = 121), and *S. bellus* collected



Fig. 1. Sampling sites of S. atrumoris sp. nov. and the distribution of S. japonicus in Taiwan based on actual data and published reports (Shao 2023).

from the Atlantic Ocean and deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States (MCZ; n = 49), were also examined (Tables S1–S2). Length (mm) was measured using a digital caliper and weighed (g) using a digital scale. All specimens were then photographed and preserved in 75% ethyl alcohol. Muscle tissue from the right side of the caudal region was collected and preserved in 95% ethyl alcohol and stored at -20°C for DNA extraction. Sagittal otoliths (n = 63) and dry skeletons (n = 9) were prepared for otolith and osteological analyses. The holotype and paratypes of *S. atrumoris* sp. nov. are deposited at ASIZP under the

registration code ASIZP0081726–ASIZP0081733, and NMMBP under the registration code NMMBP39198, NMMBP39199, and NMMBP39120 (Table S3).

Morphological and meristic analyses

Methods for taking morphometric and meristic data followed Hubbs and Lagler (1958), with modifications on the measurements of body depth and the 1st dorsal fin height. The following morphometric characters for *S. atrumoris* sp. nov. were measured: Standard length (SL), measured from tip of snout to posterior end of hypural plate; head length (HL),

Table 1. Morphometric and meristic data of *Synagrops atrumoris* sp. nov., *Synagrops japonicus* (Döderlein, 1883), and

 Synagrops bellus (Goode and Bean, 1896)

	Synag	grops atrumoris sp. nov.		Synagrops japonicus			
	Holotype	Paratypes	This study (fresh collections)	Museum collections	Museum collections of S. bellus		
No. of specimens		29 ASIZP0081726–0081733	30 (Table S2)	5 from NMMBA and 5 from ASIZP (Table S2)	15 from MCZA (Table S2)		
SL (mm)	173.6	112.7–206.9	64.3-202.5	73.4–220.0	99.7–191.7		
%SL		Range (mean)	Range (mean)	Range (mean)	Range (mean)		
HL	35.1	33.0-37.7 (35.4)	33.4-39.4 (36.2)	25.7-40.2 (35.2)	32.9–38.5 (35.3)		
PDL	36.9	34.0-40.7 (37.7)	34.3-42.6 (39.0)	36.4-43.3 (40.2)	35.8-40.1 (37.8)		
PAL	67.2	64.2–74.9 (68.6)	65.6-79.2 (68.3)	62.8-71.9 (68.8)	66.0-72.6 (69.5)		
PPL	35.9	33.3-37.2 (35.5)	29.4-38.6 (35.6)	32.5-40.3 (36.0)	32.9–38.0 (35.3)		
PVL	37.4	33.8-40.5 (36.8)	31.9-43.0 (34.2)	30.9-40.6 (35.3)	34.2-40.6 (36.7)		
BD	25.2	22.4-28.1 (24.5)	22.5-28.3 (24.7)	22.6-26.2 (24.5)	23.5-26.0 (25.3)		
ED	10.3	9.2–11.5 (10.4)	9.1–12.0 (10.6)	8.3–11.3 (10.6)	9.4–11.8 (10.7)		
SN	10.1	8.0-12.8 (9.6)	7.7-11.5 (9.7)	8.0-10.7 (9.5)	7.9–9.9 (8.9)		
IW	9.1	8.2-10.2 (9.3)	4.1-10.5 (8.9)	8.1-9.9 (8.9)	8.6-9.9 (9.3)		
UJL	14.4	13.0–15.8 (14.4)	12.6-15.7 (14.5)	13.3–16.1 (14.5)	13.7–14.9 (15.5)		
LJL	14.5	13.9–17.1 (15.3)	14.0-16.9 (15.6)	14.6-17.1 (15.6)	15.5-17.6 (16.4)		
SOH	4.1	2.7-6.5 (3.8)	2.4-8.0 (3.9)	1.3–3.5 (3.9)	1.5-2.7 (2.3)		
POL	16.2	15.3-20.1 (16.5)	9.8-19.6 (17.0)	9.2-33.5 (19.9)	12.8–17.4 (15.6)		
DS1	20.3	15.0-22.1 (19.3)	16.6-23.7 (19.7)	14.9-21.3 (19.7)	12.7-21.0 (18.3)		
DS2	14.8	11.9–17.3 (15.0)	12.0-18.4 (15.4)	12.6–17.5 (15.4)	10.4–19.4 (16.6)		
PFL	22.1	16.8-26.3 (22.4)	18.0-26.9 (23.1)	15.3–25.1 (23.1)	20.5-23.2 (25.6)		
VSL	13.6	10.6-14.6 (12.8)	10.9-15.7 (13.0)	9.3-14.0 (13.0)	8.7-15.9 (12.2)		
VFL	18.4	15.7-22.8 (19.4)	13.6-22.6 (19.4)	16.2–23.0 (19.4)	19.1–24.3 (21.9)		
AS1	2.2	1.6-3.8 (2.3)	1.5-3.4 (2.2)	1.8-2.8 (2.2)	1.4-2.6 (2.0)		
AS2	6.8	5.7-8.5 (6.7)	5.5-7.9 (6.7)	5.7-7.6 (6.6)	6.1–7.7 (7.1)		
AFL	15.2	11.0-17.1 (15.2)	12.2–17.9 (14.7)	10.5–17.2 (14.5)	12.0–17.6 (15.2)		
CFL	21.7	22.0-29.3 (26.3)	24.7-30.9 (27.0)	23.0-27.6 (24.9)	22.5-29.1 (25.1)		
FL	12.4	10.2-20.0 (12.7)	10.1–16.2 (13.4)	12.4–18.1 (14.4)	10.7–14.8 (18.1)		
CPL	24.2	22.6-28.9 (25.2)	22.4–29.5 (25.0)	19.5–30.3 (24.2)	18.6–24.8 (22.1)		
CPD	9.8	9.2-11.1 (10.2)	9.7-11.5 (10.6)	9.5–11.9 (10.3)	8.9-10.1 (10.7)		
Dorsal fin elements	IX, I, 9	IX, I, 9	IX, I, 9	IX, I, 9	IX, I, 9		
Anal fin elements	II, 7	II, 7	II, 7	II, 7	II, 7		
Pectoral fin elements	15	15-16	15-16	15–16	14–16		
Pelvic fin spines	I, 5	I, 5	I, 5	I, 5	I, 5		
Caudal fin elements	9 + 8	8 - 9 + 8 - 10	8 - 9 + 8 - 10	8-9 + 8-10	8 - 10 + 8 - 10		
Gill rakers	2 + 10	2-3+9-10	2 - 3 + 9 - 10	3 + 9 - 10	2-4+10-13		
Lateral Scale	31	29–32	29–33	29–32	28-31		

measured from tip of snout to posterior margin of the gill cover; predorsal length (PDL), measured from tip of snout to origin of dorsal fin; preanal length (PAL), measured from tip of snout to origin of anal fin; prepectoral length (PPL), measured from tip of snout to upper base of pectoral fin; pre-ventral fin length (PVL), measured from tip of snout to origin of pelvic fin; body depth (BD), measured from the pelvic fin base to the adjacent dorsal point; eye diameter (ED), measured from the anterior to posterior portion of the eye; snout length (SN), measured from tip of snout to anterior margin of the eye; interorbital width (IW) measured as the narrowest distance of eye; upper jaw length (UJL), measured from tip of snout to posterior end of maxilla; lower jaw length (LJL), measured from tip of the lower jaw to articulate; suborbital height/depth (SOH), measured from the lower margin of eye to gill cover; postorbital length (POL), measured from the posterior margin of the eye to gill cover; 1st dorsal fin height (DS1), length of 3rd dorsal spine; 2nd dorsal fin height (DS3), length of the longest dorsal fin ray; pectoral fin length (PFL), length of the longest pectoral fin ray; pelvic spine length (VSL), length of the pelvic spine; pelvic fin length (VFL), length of the longest pelvic fin ray; 1st anal spine length (AS1), length of the 1st anal spine; 2nd anal spine length (AS2), length of the 2nd anal spine; anal fin length (AFL), length of the longest anal ray; caudal fin length (CFL), measured from middle of hypural to end of the upper lobe; fork length (FL), length of the shortest ray of the caudal fin; caudal peduncle length (CPL), measured from the posterior end of the anal fin base to middle of the hypural; caudal peduncle depth (CPD), narrowest area of the caudal peduncle. Meristic data such as dorsal fin elements, dorsal spine and fin ray; anal fin elements, anal spine and fin ray; pelvic fin elements, pelvic spine and fin ray; pectoral fin elements, pectoral rays; caudal fin elements, unsegmented unbranched soft ray, segmented unbranched soft ray, segmented branch soft rays and spines of the upper lobe and lower lobe; gill rakers, developed rakers on the outer surface of the 1st gill arch on the upper and lower limbs; and lateral line scales, scales at the lateral line of the left side including the small scales on caudal-fin base, were examined on the left side of the specimens unless damaged. Radiographic images were taken at the National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (NMMBA) to count the vertebrae (the ural centrum with attached hypural complex was counted as one vertebra).

Phylogenetic analyses

Thirty samples of *S. atrumoris* sp. nov. and 10 *S. japonicus* were used for the phylogenetic analyses.

DNA extraction was done using DNA extraction Kit S (Cat No./ID: GS100, Geneaid). PCR amplification of partial mitochondrial COI gene (650 bp) was then performed by adding 5 ng template DNA, 12.5 µL of 2x Taq PCR MasterMix (GN-PCR201-01, Genomix), and 12.5 µmol each of the forward and reverse primers; FishF1+2 (5'-TCR ACY AAY CAY AAA GAY ATY GGC AC-3'); reverse: FishR1 (5'-TAG ACT TCT GGG TGG CCA AAG AAT CA-3') or FishR2 (5'-ACT TCA GGG TGA CCG AAG AAT CAG AA-3') into the mixture until it reaches 25 µL final volume using distilled water (Chang et al. 2016). The thermal cycling procedure was done in one cycle at 95°C for 4 min, then 35 cycles of denaturation at 95°C for 30 s, at 45–55°C for 30 s, followed by 72°C for 30 s and, finally, at 72°C for 7 min. A DNA Fragment Extraction Kit (Geneaid, Taipei, Taiwan) was used to purify the PCR products, which were submitted to Mission Biotech Inc., Taipei, Taiwan, together with the forward primer for sequencing. Quality score-based training of sequence ends to Q20 was manually performed using FinchTV. COI sequences were submitted to GenBank. Additional sequences from GenBank were downloaded to develop the tree (Table 2). Parascombrops spinosus (Acropomatiformes: Synagropidae), Parascombrops philippinensis (Acropomatiformes: Synagropidae), and Bathyclupea hoskynii (Acropomatiformes: Bathyclupeidae) were used as outgroups in the analysis (Smith et al. 2022). COI sequences were then aligned in MACSE v2 software based on the corresponding amino acid translation of protein-coding nucleotide sequences (Ranwez et al. 2018). A Neighbor-Joining (NJ) analysis based on Kimura 2-parameter (K2P) distance metric was done to build a distance tree with 10,000 bootstrap replicates in MEGA 11.0.10 (Tamura et al. 2021).

RESULTS

SYSTEMATICS

Order Acropomatiformes Gill, 1893 Family Synagropidae Smith, 1961 Genus Synagrops Günther, 1887

Synagrops atrumoris sp. nov. Mediodia & Lin (Figs. 2–9) urn:lsid:zoobank.org:act:EB93B24D-AC2A-48EB-ACDC-568526CA7218

English name: Dongsha Blackmouth splitfin; Chinese name: 東沙黑口尖牙鱸.

Holotype: ASIZP0081729 (173.6 mm SL) collected in Dongsha Island, Taiwan, South China Sea

Source	Scientific name	Sampling Locality	NBCI accession number	Specimen accession number	Haplotype code
This study	S. atrumoris sp. nov.	Dongsha Island, Taiwan, South China Sea	OR918329	M44	AH_1
			OR918330	M43	
			OR918337	M35	
			OR918338	M34	
			OR918343	M25	
			OR918347	M21	
			OR918350	M18	
			OR918351	M17	
		Dongsha Island, Taiwan, South China Sea	OR918331	M42	AH_2
			OR918348	M20	
		Dongsha Island, Taiwan, South China Sea	OR918332	M40	AH_3
		Dongsha Island, Taiwan, South China Sea	OR918333	M39	AJH_4
			OR918344	M24	
			OR918354	M12	
		Dongsha Island, Taiwan, South China Sea	OR918334	M38	AH_5
		Dongsha Island, Taiwan, South China Sea	OR918335	M37	AH_6
		Dongsha Island, Taiwan, South China Sea	OR918336	M36	AH_7
		Dongsha Island, Taiwan, South China Sea	OR918339	M33	AH_8
		Dongsha Island, Taiwan, South China Sea	OR918341	M27	AH_9
		Dongsha Island, Taiwan, South China Sea	OR918342	M26	AH_10
		Dongsha Island, Taiwan, South China Sea	OR918345	M23	AH_11
		Dongsha Island, Taiwan, South China Sea	OR918346	M22	AH_12
		Dongsha Island, Taiwan, South China Sea	OR918349	M19	AH_13
		Dongsha Island, Taiwan, South China Sea	OR918352	M16	AH 14
		Dongsha Island, Taiwan, South China Sea	OR918353	M15	AJH 15
		Dongsha Island, Taiwan, South China Sea	OR918355	M11	AH 16
		Dongsha Island, Taiwan, South China Sea	OR918356	M7	AH 17
		Dongsha Island, Taiwan, South China Sea	OR918357	M4	AH 18
		Dongsha Island, Taiwan, South China Sea	OR918358	M3	AH 19
GenBank	S. japonicus	Western Australia	JN313205		АЈН 15
	J.J.	Western Australia	JN313203		AJH 4
		Western Australia	IN313204		IH 27
This study	S japonicus	Dongsha Island Taiwan South China Sea	OR922331	\$1020	IH 20
	5. jupomeus	Boligsha Island, Tarwall, Bouar China Bea	OR922334	SJ020	511_20
		Dongsha Island Taiwan, South China Sea	OR922325	SJ026	IH 21
		Dongsha Island, Taiwan, South China Sea	OR922326	\$1025	IH 22
		Boligsha Island, Tarwall, Bouar China Bea	OR922329	SI022	511_22
		Dongsha Island Taiwan South China Sea	OR922327	\$1024	ш 23
		Dongsha Island, Taiwan, South China Sea	OR922328	SI023	IH 24
		Doligsha Island, Tarwan, bouth China Sea	OR922323	SI018	511_24
		Dongsha Island Taiwan South China Sea	OR022335	\$1021	TH 25
		Dongsha Island, Taiwan, South China Sea	OR922330	SJ010	JII_25
ConDonlo	C in an in a	Dongsha Island, Talwan, South China Sea	UR922552	53019	JH_20
GenBank	S. Japonicus	South China Sea	KP200/04		JH_20
		Taiwan	KU945455		JH _28
		Taiwan	KU943432		JH _29
		laiwan	KU943431		JH _30
		laiwan	KU892833		JH _31
		Japan	JF952871		JH _32
		Japan	JF952870		JH_33
		Japan	JF494629		JH_34
		Japan	JF494625		JH_35
GenBank	S. bellus	Mexico	MF041138		BH_36
		Mexico	MF041302		BH_37
		Mexico	MF041378		BH_38
		Mexico	MF041464		BH_39
		United States of America	MG856877		BH_40
		Mexico	KR086919		BH_41
		United States of America	KT883640		BH_42
		Mexico	HM389721		BH 43
		United States of America	MG856390		_
	Parascombrops spinosus	United States of America	MH378633		OH 44
	Parascombrops philippinensis	Philippines	ON398606		OH 45
	Bathyclupea hoskynii	India	KP244494		OH 46

Table 2. The haplotypes of the *COI* gene of the genus *Synagrops* from freshly collected samples and NCBI sequences and three species used as outgroups in the study

(coordinates 18°56'N, 112°57'E).

Paratypes: Twenty-nine specimens with 124.6–179.6 mm SL collected from near the holotype locality: ASIZP0081726 (5 specimens, 155.7–178.7), ASIZP0081726 (6 specimens, 154.2–171.1), ASIZP0081728 (10 specimens, 136.3–179.6), ASIZP0081730 (8 specimens, 124.6–170.4), and ASIZP0081731 (1 specimen, 137.8).

Diagnosis: A species of *Synagrops* differs from its congeners with the following combinations of characters: black mouth cavity covering the lower portion of the tongue in larger individuals (> 100 mm SL), basioccipital fossae are posteriorly enlarged and complex, triangular otolith with a pointed anterior rim and vertical posterior rim.

Description: Morphometric and meristic values are provided in table 1. Data presented are for the holotype and range of paratypes in parenthesis. Body elongated, less compressed laterally. Head massive and naked with a prominent W-shaped cranial crest. Mouth terminal and large. Eyes large with small black pigments circulating the margin. Snout short. Anus near the pelvic fin base. Dorsal, pelvic, and anal fins with prominent dark spots at the tip. The 1st and 2nd dorsal fins are separated. First dorsal spine in the 1st dorsal fin shortest, 3rd fin longest. The third fin ray in the 2nd dorsal fin longest. First dorsal-fin rays IX; 2nd dorsal fin rays I, 9 (I, 8-9). Anal fin near the posterior part of the body. First anal spine shorter than 2nd anal spine. Third anal fin ray longest. The pterygiophore of the proximal-middle radial 1st anal fin broad and bent towards the 1st haemal spine. Anal-fin rays II, 7. Pectoral fin not reaching anus. Pectoral-fin rays i15-15i (i15-16i). Non-serrated pelvic spine. Pelvic-fin rays I, 5. Caudal fin forked. Principal caudal-fin rays 9 + 8 (8-9 + 8-9), complete caudal fin formula including procurrent rays is 8, i, 9+8, i, 8. Small rows (2-5) of denticles on the ectopterygoid. The lateral side of the lower jaw with 2 (2–3, n = 8) strong canines and 4 (4–5, n = 8) small canines protruding in the upper jaw. Small serrations in preopercle with 2-3 rounded small ridges at the lower rear margin. Swimbladder reaching cranium. Gills with 2 (2-3) short rakers at the upper arch and 10 (8–10) long at the lower arch; rakers dark brown to black; gill filaments reddish pink. Predorsal formula 0/0/0+2/. Vertebrae count 25 (10 abdominal and 15 caudal). Scales cycloid and easily shed. Lateral scales 30 (29–32).

Coloration: Body color black-to-gray with a metallic sheen in the entire body, pale-cream color without scales. Metallic color in the ventral part of the body.

Osteological notes: Skeletal characters of the new species were studied in all skeleton parts. It generally resembles that of *S. japonicus*. The only significant

differences were identified in the otic region of the skull and the immediately adjacent portion of the vertebral column. Due to that reason, only the neurocranium (especially its otic portion) and the anterior-most part of the vertebral column are emphasized in the study. The neurocranium in the dorsal view is almost squarish in shape, somehow broader posteriorly. The skull roof is ornamented by a system of anteriorly diverging ridges and large openings, creating a prominent W-shaped cranial crest. The dorsal part of the otic section is extensively covered by epaxial musculature. The dorsal margin of the neurocranium in lateral view is convex, while the ventral margin is more or less straight (the only exception is the ventrally prominent vomerine section). The neurocranium in the lateral view is significantly lower and shorter in the ethmoid region than in the otic region. The orbit is large, approximately 40% of the length of the neurocranium. The supraoccipital crest is short but relatively deep. The openings of the myodome are enlarged dorsally, and the prootic participate in the construction of the myodome margins just by small and short sections in the anterolateral corners. The basioccipital fossae are emarginated by the exoccipital laterally (the ventral margin of this skeletal element is swollen), the prootic anterolaterally, and the basioccipital anteriorly and medially. The medial section of the basioccipital protrudes at the caudal part to the lateral spurs and is in contact with the medial side of the exoccipital. The posterior part of the basioccipital fossae is shifted posteriorly, and its margin is defined by ventro-laterally bony outgrowths of the 1st vertebra. The whole complex of the basioccipital fossae in S. atrumoris sp. nov. is antero-posteriorly segmented, and the complete construction extends to the 1st vertebra.

Otolith: The otolith is triangular with a pointed anterior rim and a vertical posterior rim. The dorsal and ventral rims are oblique anteriorly, interrupted by distinctive angles forming the highest part of the otolith. Beyond these angles, both rims exhibit a relatively horizontal and flat profile towards the pronounced angle. Notably, there is a pronounced angle situated at both the postero-dorsal and postero-ventral corners. However, the postero-ventral angle appears more prominent and may extend further towards the posterior. The otoliths are thin. The outer face is concave, and the inner face is convex. The dorsal margin is irregular with small crenulations, specifically on the anterodorsal margin. The horizontal part of the ventral margin and the posterior margin are crenate. The sulcus is deep and well-differentiated into the ostium and cauda. A funnel-like ostium is widely open antero-dorsally. There is a large oblong ostial colliculum situated below the longitudinal midline of the ostium. The cauda is deepened slightly, directing upward before curving strongly (about 90°) at the most posterior region, with its tip directing antero-ventrally. It is narrowing towards the neck. Cristae are well-developed. A notch is present and the antirostrum is small.

Etymology: The specific name is a combination of the Latin "*atrum*", meaning black, and "*oris*", meaning mouth, in relation to its diagnostic black mouth floor.

Distribution: Currently known from the Dongsha Islands, Taiwan, and the South China Sea. Possibly from the south of Scott Reefs, Western Australia (see below).

Size: The largest sample examined in this study is 206.88 mm SL.

Phylogenetic analyses: Out of 68 COI sequences used in this study from 3 taxa, we have detected 46 haplotypes and 506 aligned base pairs, which contained 169 variable sites and 102 parsimony informative sites. The NJ tree revealed there are two groups (Group 1 and Group 2) with high supports (bootstrapping value > 90) (Fig. 9), and the average pairwise genetic distance (K2P) between these two groups is 0.06. Group 1 includes S. bellus and nearly all S. japonicus specimens, but the two species nest each other within the group. The average K2P distance within the group is 0.01. Group 2 contains all specimens belong to S. atrumoris sp. nov. and three sequences of S. japonicus (74-128 mm SL) from south of Scott Reefs, Western Australia (JN313203-JN313205), and the average K2P distance within the group is 0.01.

DISCUSSION

Cryptic nature of the new species

The poorly studied species of the genus *Synagrops*, *S. atrumoris*, has been recognized within the large collection of *S. japonicus* specimens from the landings of the trawling fishery. The new species can be unquestionably placed within the genus *Synagrops* based on the non-serrated pelvic fin spine, 2 anal fin spines, naked top of the head, and small rows of teeth on the ectopterygoid (Schwarzhans and Prokofiev 2017).

Although most of the morphological characters are similar in both species (Tables 1–2; Fig. 3), *S. atrumoris* can be differentiated from *S. japonicus* by a number of characters, of which the most easily recognizable is the coloration of the mouth cavity (Fig. 4). Based on the 121 specimens of *S. japonicus* in the NMMBA-P, we found five specimens with black mouths, in addition to the two specimens out of 20 examined from ASIZP. However, it is necessary to validate this classification

by checking the basioccipital fossa and the otolith, which can further verify the distinction between the two species. Synagrops atrumoris has an entirely black mouth covering the lower portion of the tongue in larger individuals (> 100 mm SL), while in S. *japonicus* the roof of the mouth is black, especially in large specimens, but the lower portion of the tongue is light-colored (Fig. 4). However, there are S. *japonicus* that individuals have black mouths but with grayish coloration on the tongue with patches of white spots. The mouth coloration is difficult to distinguish in smaller-sized specimens. In both species, the otic part of the skull shows differences in the morphology and construction of posterior openings for myodome and basioccipital fossa (Fig. 5). The posterior openings for the myodome are symmetrically located at the anteroventral surface of the otic section. In S. atrumoris, the openings are enlarged dorsally, and the prootic participate in the construction of their margins just by small and short sections in the antero-lateral corners (Fig. 5). The same structure in S. japonicus is shifted to a more ventral position (and thus seems larger in the ventral view), and the prootic emarginated significantly larger portion of its anterior, lateral, and posterior edges (Fig. 5). There is also similarity in the construction of the myodome and basioccipital fossae between S. japonicus and S. bellus which are visible in radiographs (Fig. 6).

Another distinguishable difference between these two species is in the construction of the basioccipital fossae (Figs. 6-7). These openings are bilaterally symmetrical, located just in front of the basioccipital and 1st vertebra articulation and housing anteriorly enlarged and bifurcated swim bladder horns (Schwarzhans and Prokofiev 2017). In S. atrumoris, the basioccipital fossa is emarginated by the exoccipital laterally (the ventral margin of this skeletal element is swollen), the prootic antero-laterally, and the basioccipital anteriorly and medially (Fig. 7). The medial section of the basioccipital gives distal rise to lateral spurs in contact with the medial side of the exoccipital. The posterior part of the basioccipital fossa is shifted posteriorly, and its margin is defined by ventro-lateral bone, which outgrows on the 1st vertebra. The whole complex of the basioccipital fossae in S. atrumoris is antero-posteriorly segmented and construction is completed by the 1st vertebra. Contrary to this state, the basiccipital fossae of S. japonicus are simple, large, and widely opened posteroventrally, their posterior part is not enlarged, and the 1st vertebra is not incorporated into the construction of this structure. Furthermore, the basioccipital lacks the lateral spurs (Fig. 7). The individual bony elements supporting this structure show significant differences in proportions.

Moreover, the otolith shape of S. atrumoris is triangular with a pointed anterior rim and a vertical posterior rim (Fig. 8), while S. japonicus has a pentagonal shape with a tapered anterior end (Rivaton and Bourret 1999; Smale et al. 1995; Lin and Chang 2012; Nolf 2013). Both otoliths have a concave outer face and convex inner face, but that of S. atrumoris is moderately thicker than that of S. japonicus, particularly in the anterior portion (Fig. 8E1-2 vs G1-2). Serena et al. (2022) documented a right otolith of S. japonicus, which they mistakenly identified as a left otolith in their publication. This particular otolith exhibits similarities to that of S. atrumoris, but the specimen was broken on the anterior portion, and the figure provided in the publication was not properly oriented, resulting in a distortion of the specimen's appearance.

The two monophyletic groups with high support in NJ phylogenetic tree and a notable genetic distance between them demonstrate that *S. atrumoris* (Group 2) is a distinct species from *S. japonicus* and *S. bellus*

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(Group 1) (Fig. 9). *S. japonicus* and *S. bellus* form a monophyletic group with a low average within-group K2P genetic distance, suggesting that *S. japonicus* and *S. bellus* are actually a single species. Given that the



Synagrops atrumoris sp. nov.

Fig. 2. *Synagrops atrumoris* sp. nov. A, ASIZP0081729, holotype, 173.60 mm SL, fresh and B, radiograph. Scale bar = 10 mm.



Fig. 3. *Synagrops atrumoris* sp. nov., A–D, paratypes, fresh, A, ASIZP0081728, 159.0 mm SL; B, ASIZP0081728, 130.3 mm SL; C, ASIZP0081728, 176.8 mm SL; D, ASIZP0081728, 137.6 mm SL. *Synagrops japonicus* (Döderlein, 1883), E–F, non-types, fresh, E, ASIZP0081733, 168.6 mm SL; F, ASIZP0081733, 156.5 mm SL. *Synagrops bellus* (Goode and Bean, 1896) G–H, non-types, preserved, G, MCZ49930 172 mm SL; H, MCZ49930 213 mm SL. Scale bar = 10 mm.



Fig. 4. Mouth color of *Synagrops atrumoris* sp. nov., paratype, ASIZP0081731, 165.5 mm SL, *Synagrops japonicus* (Döderlein, 1883), non-type, ASIZP0081731, 152.8 mm SL, and *Synagrops bellus* (Goode and Bean, 1896), non-type, MCZ49930, 172.98 mm SL. A, fresh and B, preserved in alcohol. Not to scale.



Fig. 5. Neurocrania of A–B, *Synagrops atrumoris* sp. nov., non-type, CHLP2000314, 178.9 mm SL, and C–D, *Synagrops japonicus* (Döderlein, 1883), non-type, CHLP2000309, 184.1 mm SL showing ventral (A and C), and lateral views (B and D) emphasizing the prootic, exoccipital, basioccipital, 1st vertebra, and 2nd vertebra. The actual images are presented in figure S1. Scale bar = 10 mm.

external morphology of *S. atrumoris* and *S. japonicus* are extremely similar for smaller individuals (< 100 mm SL) the three small-sized specimens of *S. japonicus* from the south of Scott Reefs, Western Australia (JN313203–JN313205, ~74 mm SL, Table 2, Fig. 9) which clustered in Group 2 are very likely *S. atrumoris*. The detection of these Australian *S. atrumoris* specimens in the NJ analysis indicates a potential broader geographical range of the new species.

Ecological and geographical significance of the new species

The specimens used in this study were bycatch of trawl fishing along the South China Sea with depths ranging from 300-600 meters. Based on available specimens in our collection, we have observed that the abundance of the new species is considerably low compared to the common *S. japonicus*. Out of 1145



Fig. 6. Radiographs showing the ventral view of the neurocrania of A, *Synagrops atrumoris* sp. nov., paratype, ASIZP0081728, 152.54 mm SL, B, *Synagrops japonicus* (Döderlein, 1883), non-type, ASIZP0081733, 147.51 mm SL, and C, *Synagrops bellus* (Goode and Bean, 1896), non-type, MCZ49930, 172.98 mm SL. Not to scale.

samples, 2.7% were juvenile (not differentiated in this study), 12.8% were *S. atrumoris* and 84.9% were *S. japonicus*. The highest number of *S. atrumoris* was collected from February to May 2022–2023 (82.8%), and much fewer were collected in June and July 2022–2023 (18.2%). These temporal differences may suggest the possibility of seasonal occurrence of *S. atrumoris* compared to *S. japonicus*. We suggest conducting a temporal assessment of the stocks to validate this assumption. Moreover, we recorded the highest number of smaller-sized *S. japonicus* (< 100 mm SL) in March and July 2022–2023.

The highest prevalence of *S. japonicus* juveniles might be influenced by the spawning season and the meandering of the Kuroshio Current in Taiwan which was also observed by Wang and Lee (2019). We observed variability in the sizes of *S. atrumoris*

(112.7-202.5 mm SL) and S. japonicus (64.3-206.9 mm SL) from the samples collected. Specimens of S. japonicus have a wider range of sizes compared to that of S. atrumoris. The smallest-sized S. japonicus is 64.3 mm while the smallest S. atrumoris is 112.7 mm. This is likely attributed to the prevalence of smallsized S. *japonicus* with white mouths, a characteristic confirmed through molecular analysis. In addition, the comparative higher abundance of S. japonicus over S. atrumoris may further contribute to this phenomenon. The largest S. japonicus sample from our collection only measured 202.0 mm SL, which is relatively smaller than the report of Masuda et al. (1984) of about 300 mm SL (350 mm SL, the largest record). No specimens measuring less than 112 mm displayed black mouths. Notably, all individuals with a size below 100 mm exhibit white mouths. This intensifies the difficulty in



Fig. 7. Prootic (A–D), exoccipital (E–H), and basioccipital (I–L) of *Synagrops atrumoris* sp. nov., non-type, CHLP2000314, 178.9 mm SL, and *Synagrops japonicus* (Döderlein, 1883), non-type, CHLP2000310, 174.2 mm SL. The actual images are presented in figure S2. Scale bars = 5 mm.

differentiating the juveniles of *S. atrumoris* based on mouth coloration only.

Our study described the differences in the otic region of the skull and the shape of the otoliths between S. atrumoris and S. japonicus. This result is vital as it suggests the differentiated functioning of their hearing ability. An increased otolith-to-sulcus area ratio is expected to improve hearing ability (Schulz-Mirbach et al. 2019). As observed in S. atrumoris, a higher otolithto-sulcus area ratio than S. japonicus (Fig. 7) might facilitate more effective hearing abilities and make it more adaptive to ecological changes and/or avoiding predators (Hawkins and Popper 2014). Moreover, the complex structure of the basioccipital fossae housing the horns of the swim bladder and the addition of lateral spurs may be an ancillary hearing structure that could improve the hearing capabilities of S. atrumoris. Various adaptations on the anterior portion of the swim bladder have also been observed in various groups of teleosts, like Moridae (Paulin 1988), Clupeidae (Mann et al. 2001), and catfishes (Ladich 2023), which is expected to increase hearing capacity. Further, Popper

et al. (2022) also discussed that enlarged otoliths and the connection of the swim bladder to the ear correlate with advancements in sound source localization and heightened sound discrimination abilities. Therefore, these differences might be an evolutionary adaptation of *Synagrops* species to improve hearing, but such issues require further investigation.

Synonymy of Synagrops japonicus and Synagrops bellus

The genus *Synagrops* Günther, 1887 under the family Acropomatidae proposed by Johnson (1984) previously contained 12 species. Schwarzhans and Prokofiev (2017) revised the species assignment of *Synagrops* which now only includes *S. japonicus* and *S. bellus* based on distinguishable characters, such as the smooth pelvic and dorsal fin, two anal spines, numerous denticles on the ectopterygoid, presence of basioccipital fossa, posterior openings of the myodome, and subrectangular otolith. Most authors agreed that these two recognized species represent the genus *Synagrops*.



Fig. 8. Otoliths (right sagitta) of *Synagrops* from Taiwan. A–E, *Synagrops atrumoris* sp. nov., paratypes; A, CHLOL24862, 178.76 mm SL; B, CHLOL24863, 136.34.11 mm SL, C, CHLOL24864, 186.12 mm SL, D, CHLOL24865, 119.29 mm SL, E, holotype, CHLOL24861, 173.60 mm SL, F–G, *Synagrops japonicus* (Döderlein, 1883), non-types, F, CHLOL24866, 152.54 mm SL, G, CHLOL24867, 114.35 mm SL, 1, ventral views, 2, dorsal views. Scale bar = 1 mm.



Fig. 9. Neighbor-joining tree based on the cytochrome oxidase subunit I (*COI*) gene showing the relationships of *Synagrops atrumoris* sp. nov., *Synagrops japonicus* (Döderlein, 1883), and *Synagrops bellus* (Goode and Bean, 1896). Haplotype names (AH, *S. atrumoris* sp. nov., JH, *S. japonicus*, BH, *S. bellus*, and AJH, haplotype of *S. atrumoris* sp. nov. and *S. japonicus*) are presented in table 2. Support values > 70 are presented.

However, recent studies considered *Synagrops* under the family Synagropidae Smith, 1961 (Ghedotti et al. 2018; Serena et al. 2022; Smith et al. 2022), which includes three other genera, namely *Parascombrops, Caraibops*, and *Kaperangus* (Van der Laan et al. 2023).

Hypoclydonia bella Goode and Bean, 1896 is the senior synonym of *S. bellus* Goode and Bean, 1892, while *Melanostoma japonicum* Döderlein, 1883 is the senior synonym and *S. natalensis* Gilchrist, 1922 is the junior synonym of *S. japonicus* (Döderlein, 1883) (Van der Laan et al. 2023). The two species recognized under the genus *Synagrops*, *S. japonicus* and *S. bellus*, are synonymized in this study, agreeing with the report of Heemstra et al. (2022). Based on the original description of *S. bellus* (Goode and Bean, 1896) and specimens from the MCZ museum collection, it does not differ in its morphological characteristics from *S. japonicus* and *S. bellus* (Table 1), and other works also highlighted the close morphological relationship between *S. japonicus* and *S. bellus* (Mochizuki 1989; Mejía et al. 2001).

Our results showed no differences in the morphological and meristic characters of S. japonicus and S. bellus. Osteological description, as presented through radiographs, showed the identical characteristics of the posterior openings of the myodome and basioccipital fossa of both species (Fig. 7). It is also worth mentioning that the otoliths of S. japonicus and S. bellus appear very similar (Rivaton and Bourret 1999; Brenha-Nunes et al. 2016). Moreover, the molecular analyses showed the cluster of S. japonicus and S. bellus, suggesting the synonymy of both species. Hannachi et al. (2015) and Serena et al. (2022) also emphasized the need to conduct further studies to determine the geographic distribution of S. japonicus after it was reported in the Mediterranean Sea, believed to be introduced by ballast waters. In such a case, S. japonicus would have a much wider species distribution, including the East Atlantic. In conclusion, the genus Synagrops only includes S. japonicus (syn. S. bellus) and S. atrumoris.

CONCLUSIONS

Synagrops atrumoris sp. nov. can be distinguished from its congeners based on the black mouth cavity covering the lower portion of the tongue, a triangular otolith with a strong postero-dorsal angle, and the basioccipital fossae, which are posteriorly enlarged and more complex as compared to *S. japonicus*. Phylogenetic analyses (*COI*) supported the delineation of *S. atrumoris* as a new species. Moreover, *S. bellus* is synonym of *S. japonicus*. The genus *Synagrops* only includes *S. japonicus* (syn. *S. bellus*) and *S. atrumoris*. Acknowledgments: This work and the new species name were registered with ZooBank under urn:lsid:zoobank.org:pub:98DE6CDB-52C4-4337-A74C-6F2CA0523C83. We thank Dr. Shih-Pin Huang (Biodiversity Research Museum, Academia Sinica) and Andrew D. Williston and Meaghan Sorce (Museum of Comparative Zoology) for the comparative materials. We are grateful to Hsin-Wei Liu, Shing-Lai Ng, Yen-Ting Lin, Tai-Yen Lin, Ning Labbish Chao, and Ming-Hua Chiang for their assistance during sample collection and preparation. Funding: Mobility Plus Project between Academia Sinica, Taipei, Taiwan and Czech Academy of Sciences, Czech Republic: Cenozoic fossil fishes from Taiwan and the Czech Republic - the once thrived ichthyofaunas to C-HL and TP. The National Science and Technology Council, Taiwan (Grant No. 110-2116-M-001-009, 111-2116-M-001-033, 112-2116-M-001-017-MY3) and Academia Sinica, Taipei, Taiwan to C-HL. TP is supported by the Institute of Geology of the Czech Academy of Sciences (RVO67985831).

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Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: All data are available in the paper. The type specimens are deposited at the Biodiversity Research Museum, Academia Sinica, Taiwan, and the National Museum of Marine Biology and Aquarium, Pingtung. Other materials are deposited at C-H Lin Marine Paleontology Laboratory, Greenhouse Building R246, Biodiversity Research Center, Academia Sinica, 128 Academia Road, Sec. 2, Nankang, Taipei 11529, Taiwan. Detailed measurements are available from the corresponding author and can be accessed by proper request. CO1 sequences are available in GenBank.

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Supplementary materials

Fig. S1. Neurocrania of A–B, *Synagrops atrumoris* sp. nov., non-type, CHLP2000314, 178.9 mm SL, and C–D, *Synagrops japonicus* (Döderlein, 1883), non-type, CHLP2000309, 184.1 mm SL showing ventral (A and C), and lateral (B and D) views emphasizing the prootic, exoccipital, basioccipital, 1st vertebra, and 2nd vertebra. Scale bar = 10 mm. (download)

Fig. S2. Actual images of prootic (A–D), exoccipital (E–H), and basioccipital (I–L) of *Synagrops atrumoris* sp. nov., non-type, CHLP2000314, 178.9 mm SL, and *Synagrops japonicus* (Döderlein, 1883), non-type, CHLP2000310, 174.2 mm SL showing the dorsal and ventral views. Scale bars = 5 mm. (download)

Table S1. List of comparative materials of *Synagrops japonicus* (Döderlein, 1883) and *Synagrops bellus* (Goode and Bean, 1896) used in this study. (download)

Table S2. Specimens of *Synagrops japonicus* (Döderlein, 1883) and *Synagrops bellus* (Goode and Bean, 1896) for morphological and meristic analysis in this study. (download)

Table S3. The accession numbers of type specimens of *Synagrops atrumoris* sp. nov. collected in Dongsha Island, Taiwan, from trawl fishing and deposited at the Biodiversity Research Museum, Academia Sinica, and National Museum of Marine Biology and Aquarium, Pingtung. (download)