Journal of *Marine Science and Engineering*

MDPI

Article

Taxonomic Revision of the Genus Croaker *Johnius* (Perciformes: Sciaenidae) in Taiwanese Waters

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Abstract: Given the identification of the new species *Johnius taiwanesis*, the *Johnius* genus in Taiwanese water is here reviewed through a collection of field samples, museum specimens, and a review of the Taiwanese scientific literature. Seven valid *Johnius* species were successfully identified and distinguished based on gill raker length, tip of upper jaw to mouth hinge length, tip of lower jaw to mouth hinge length, and length of second spine of anal fin. Our phylogenetic tree based on cytochrome oxidase subunit I (COI) showed the existence of high interspecific genetic diversity within the genus *Johnius* forming a monophyletic group. The *Johnius* species in Taiwan are mainly distributed in a latitude ranging from Xingda (22.4° N) to Hsinchu (24.8° N) with *J. taiwanensis*, *J. distinctus*, and *J. belangerii* representing the most abundant species caught throughout the year. *Johnius amblycephalus* and *J. borneensis* were only caught in the summer, while *J. trewavasae* was rarely caught. In conclusion, we provide a dichotomous key for the genus *Johnius* in Taiwan waters.

Keywords: systematics; DNA barcoding; dubious taxa; Changyun Rise; dominant species

Citation: Hanafi, N.; Chen, M.-H.; Seah, Y.G.; Chang, C.-W.; Liu, S.Y.V.; Lai, C.-C.; Chao, N.L. Taxonomic Revision of the Genus Croaker *Johnius* (Perciformes: Sciaenidae) in Taiwanese Waters. *J. Mar. Sci. Eng.* **2023**, *11*, 471. https://doi.org/10.3390/jmse11030471

Academic Editor: Dariusz Kucharczyk

Received: 11 January 2023
Revised: 19 February 2023
Accepted: 20 February 2023
Published: 22 February 2023

1. Introduction

Members of the fish genus *Johnius* can be found in a broad range of salinities and depths (down to 200 m) on the continental shelf over sandy or muddy bottoms in the Western Indo-Pacific Ocean. Their breeding habitats are in estuarine waters [1,2]. While these coastal fish are widespread and often collected in huge numbers as bycatch, little is known about their biology and life history [3,4]. This is especially true in Taiwanese waters, where even the distribution of the group is poorly known [2,5].

Several writers have struggled to accurately identify species using morphological or genetic methodologies owing to a paucity of information in the genus *Johnius*. Lo et al. [6] recently employed a DNA-based approach to reconstruct 14 *Johnius* species in the Western Indo-Pacific area. However, because of a lack of established baseline data, using molecular and delimitation studies to tackle nomenclature concerns restricted their applicability.

Various genera and subgenera of *Johnius* have been recognized in Taiwanese waters in the current literature [7], although there has been much confusion concerning the taxonomic

level of taxa linked to *Johnius* (e.g., *Wak*, *Bola*) [8–11]. As a result, there is a need to reassess the taxonomy of this genus using both genetic and morphological approaches on fresh samples and museum specimens.

Johnius taiwanensis Chao et al., 2019 was identified in Taiwanese waters initially and was based on the following criteria for a new species: (i) a distinct body color pattern with a grayish dorsal region; (ii) upper two-thirds of the body clearly separated from a whitish-to-yellowish belly by a distinct line; (iii) a cavernous head with scales securely adhered; and (iv) a black dot on the topmost axilla of the pectoral fin [5]. For decades, this species has been misdiagnosed as *J. belangerii*, *J. macrorhynus*, *J. sina*, or *Wak sina* [8,12–14]. This new species finding highlighted the complexities of the genus *Johnius* taxonomy and the necessity for a taxonomic review.

The current study aimed to (i) revise and redescribe the taxonomic status of Taiwanese *Johnius* species, (ii) provide a detailed description of each species, (iii) create a key to these species, (iv) review the phylogenetic relationships within the genus using morphological and molecular data, and (v) report the geographical distribution of the genus in Taiwanese waters.

2. Materials and Methods

2.1. Sampling and Examination of Specimens

Fish sampling. Throughout our investigation, a total of 2508 *Johnius* specimens were sampled in the field using different kinds of gear, such as gill nets and trawling, and on land by subsampling and monitoring fish markets. Between March 2019 and March 2020, monthly samples were collected from Miaoli fish landing ports in northwestern Taiwan (Figure 1). The Miaoli coast is a vital landing point for marine fishing in Taiwan's far north. We also learned about the sample locations. The *Johnius* collection data were integrated from February 2000 to November 2003. We also utilized data from Shao et al. [15], who performed a comprehensive survey in Taiwan's coastal waters, and Liou's [16] survey collection in Yunlin.

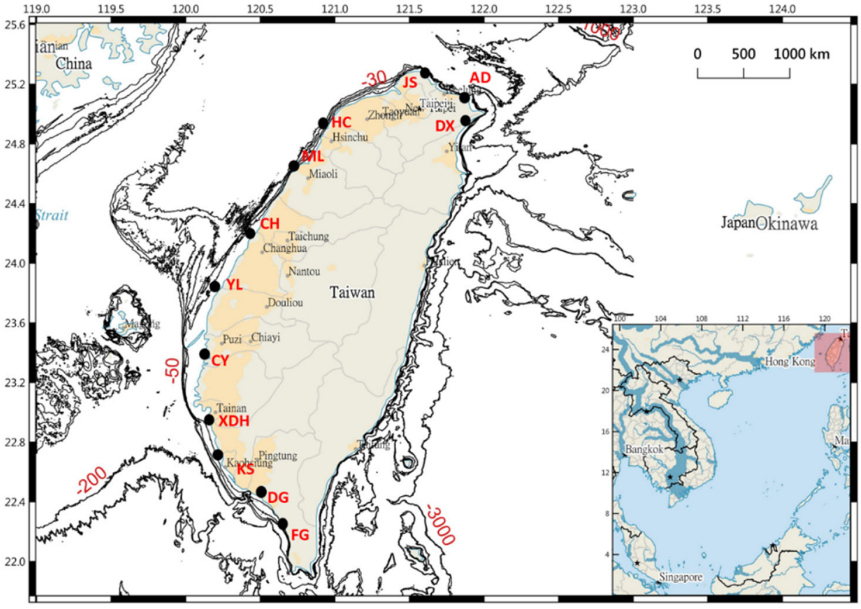

Figure 1. Sampling sites of *Johnius* species in Taiwan (Acronyms for sites: Daxi (DX); AoDi (AD), Jinshan (JS), Hsinchu (HC), Miaoli (ML), Changhwa (CH), Yunlin (YL), Chiayi (CY), Xingdaohe (XDH), Kaohsiung (KS), Donggang (DG), and Fenggang (FG). The red outlier numbers around Taiwan indicates the bathymetry.

Museum collections. We evaluated all 674 known type and non-type specimens of *Johnius* species in the fish collections of Taiwan's National Museum of Marine Biology and

Aquarium (NMMBA) and Academia Sinica's Biodiversity Research Center (BRCAS). Other museum abbreviations used for voucher numbers include Chinese Academy of Sciences (CAS), Institute of Zoology Fish Collection (IZFC), and Rijksmuseum van Natuurlijke Historie (RMNH).

2.2. Integrated Approach to Verifying Johnius Species

In addition to the fresh fish individuals utilized for morphological identification, 34 tissue samples were taken for genetic analyses. Morphological comparisons were carried out using 46 exemplar fresh fish to classify all fresh fish.

Morphological data. The protocols utilized in this investigation for specimen preservation and photography were the same as those reported by Seah et al. [17]. Genomic DNA were isolated from tissue samples for molecular analysis. Pectoral fin clips were acquired from 34 field-collected specimens. For DNA extraction, the clips were kept in 95% ethanol. Field specimens for morphological analyses were then fixed in 10% formalin and later transferred into 70% alcohol prior to further investigations. Morphometric measurements of 46 specimens were taken with digital calipers and recorded to the nearest 0.1 mm (Figure 2 and Table 1). Methods of counting and measuring generally followed Hubbs and Lagler [18], while morphological structure and descriptions for *Johnius* were based on Hanafi et al. [19]. The total number of rakers on the upper and lower limbs, including rudimentary rakers on the first right gill arch, was used to calculate gill raker counts. The number of porous scales from the opercle tips to the end hypural plates was used to calculate the lateral line scales. The voucher specimens were stored at the NMMBA.

In the computer application PAST 3.19 [20], a principal component analysis (PCA) was used to analyze the log-transformed data in a covariance matrix. The data were changed using log transformation to attain normal distribution. Prior to the analysis, the dataset was standardized as a percentage value. The broken-stick model was employed as the stopping criterion for the PCA, and the variables were interpreted based on the greatest and lowest loading values for the chosen axes. The PCA did not include the constant value. Bivariate scatterplots were utilized to highlight the diagnostic morphological difference in the morphometric data based on the PCA analysis, and ranges were employed to analyze the meristic data. Unless otherwise noted, measures in the text below are provided as percentages of the standard length (SL).

Phylogenetic analyses. Phylogenetic connections were rebuilt for 34 individuals from seven *Johnius* species using the cytochrome c oxidase I (COI) gene, with additional sequences retrieved from the NCBI database. Table 2 displays the voucher specimen and GenBank sequencing information.

The Tissue Genomic DNA Mini Kit GT100 was used to extract genomic DNA from animal tissue (Geneaid, New Taipei City, Taiwan). To amplify and sequence the COI gene region, Johni 76F: 5′ CCTCTGTYTRTGGGTTTACAATC 3′ and Johni 916R: 5′ TTRCCAGAATAATAYGCAACGA 3′ [6] were employed. Each sample for the polymerase chain reaction (PCR) consisted of a 50 µL reaction containing 20 µL of sterile water, 2 µL of 50 µL genomic DNA, 25 µL of Master Mix (NEXproTM, Seoul, Korea), and 1.5 µL of 10 mM of each primer. The PCR cycling conditions were modified from Lo et al. [6]. The PCR conditions consisted of initial denaturation at 95 °C for 3 min, 35 cycles at 95 °C for 1min, annealing at 52 °C for 1 min, extension at 72 °C for 1 min, and a final extension at 72 °C for 5 min. PCR reactions were performed using an Applied Biosystems Veriti 96-Well Thermal Cycler (Applied Biosystems, Inc., Foster City, CA, USA). Sanger sequencing was accomplished via genomic sequencing in New Taipei City, Taiwan. MEGA v7.0 [21] was used to edit and align all sequences.

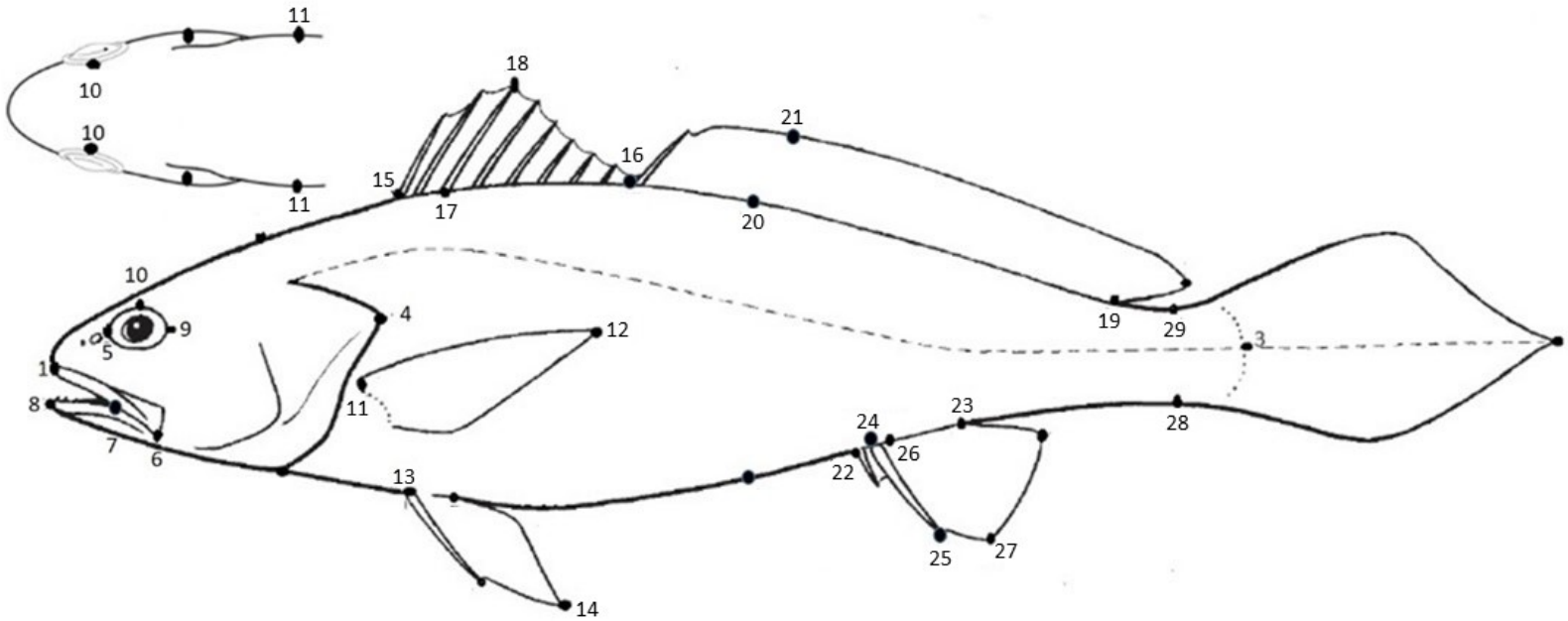

Figure 2. Schematic drawing of a sciaenid fish showing "landmarks" used for morphological measurements based on a truss network protocol, anchored at 29 homologous anatomical landmarks with the exception of gill raker length (see Table 1 for the specific definition of each measurement).

Table 1. Definition of morphometric measurements and meristic counts for the genus *Johnius*.

	Character	Description	Acronym	Landmark
28	Morphometric measurements			
	Total length	Tip of snout to tip of caudal	TL	1–2
	Standard length	Tip of snout to end of hypural	SL	1–3
	Head length	Tip of snout to posterior edge of operculum	HL	1–4
	Snout length	Tip of snout to anterior edge of orbit	SnL	1–5
	Upper jaw length	Tip of snout to the posterior edge of maxilla	UJL	1–6
	Tip of upper jaw to mouth hinge length	Tip of snout to hinge of mouth	UJHL	1–7
	Tip of lower jaw to mouth hinge length	Tip of mandible to hinge of mouth	LJHL	8–7
	Eye diameter	The greatest bony diameter of orbit	ED	5–9
	Interorbital width	The smallest width between both orbits	IOW	10–10
	Pectoral fin length	Insertion of pectoral fin to distal of pectoral fin	P1L	11–12
	Pelvic fin length	Insertion of pelvic fin to the distal of pelvic fin	P2L	13–14
	Body depth	Origin of first dorsal fin spine to insertion of pelvic fin	BD	13–15

Table 1. *Cont.*

	Character	Description	Acronym	Landmark
	Body width	The greatest width between pectoral fin insertion	BW	11–11
	1st dorsal fin base length	Origin to end of first dorsal fin	D1BL	15–16
	Length of 4th spine of 1st dorsal fin	Proximal to distal of fourth spine at first dorsal fin	4D1L	17–18
	2nd dorsal fin base length	Origin to end of second dorsal fin	D2BL	16–19
	Length of 5th ray of 2nd dorsal fin length	Proximal to distal of fifth ray at second dorsal fin	5RD2L	20–21
	Anal fin base length	Origin to end of anal fin	ABL	22–23
	Length of 2nd anal fin spine	Proximal to distal of second anal spine	2AL	24–25
	Length of 1st anal fin ray	Proximal to distal of first anal ray	1RAL	26–27
	Predorsal length	Tip of snout to origin of first dorsal fin	PD1L	1–15
	Distance between snout to origin of 2nd dorsal fin	Tip of snout to origin of second dorsal fin	PD2L	1–16
	Prepectoral length	Tip of snout to insertion of pectoral fin	PP1L	1–11
	Prepelvic length	Tip of snout to insertion of pelvic fin	PP2L	1–13
	Preanal length	Tip of snout to origin of the anal fin	PAL	1–22
	Caudal peduncle depth	The smallest depth of the tail base	CPD	28–29
	Gill raker length	Proximal to distal of gill raker at the first gill arch junction	GRL	-
	Gill filament length	Proximal to distal of gill filament at the first gill arch junction	GFL	-
15	Meristic counts			
	Dorsal fin spine	Number of spines in dorsal fin	DFS	-
	Dorsal fin ray	Number of soft dorsal fin rays in dorsal fin	DFR	-
	Anal fin spine	Number of spines in anal fin	AFS	-
	Anal fin ray	Number of soft dorsal fin rays in anal fin	AFR	-
	Pectoral fin ray	Number of soft dorsal fin rays in pectoral fin	PFR	-
	Outer gill raker of 1st arch	Number of total gill rakers at outer arch	OGR	-
	Upper limb at outer gill raker	Number of upper limbs in gill raker at outer arch	UOGR	-
	Lower limb at outer gill raker	Number of lower limbs in gill raker at outer arch	LOGR	-
	Inner gill raker of 1st arch	Number of total gill rakers at inner arch	IGR	-
	Upper limb at inner gill raker	Number of upper limbs in gill raker at inner arch	UIGR	-
	Lower limb at inner gill raker	Number of lower limbs in gill raker at inner arch	LIGR	-
	Lateral line pored scale	Number of scales along lateral line	LLS	-
	Circumpeduncular scales	Number of scales at the circumference caudal peduncle	CPS	-
	Scales above lateral line	Number of scales from origin of dorsal fin to the lateral line scales	SALL	-
	Scales below lateral line	Number of scales from origin of anal fin to the lateral line scales	SBLL	-

Table 2. Taxa, vouchers, locality, and GenBank accession numbers of specimens of locally known *Johnius* species and *Dendrophysa russelii* used in the DNA COI barcoding analysis.

Taxon	Voucher Specimen (NMMB-P)	GSCN Specimen	Localition Sites	Country	Number of Individuals	GenBank No.
Dendrophysa russelii	-	-	-	Taiwan	2	NC017606, JQ728562
J. amblycephalus	37066	-	-	-	3	KX777910, KX777912, KX777913
J. belangerii	-	869, 868 870, 871	-	Taiwan	4	-
J. belangerii	37067	2137, 2105, 2214, 2216	Miaoli	Taiwan	1	OK253026
J. belangerii	-	-	-	Taiwan	1	MG917695
J. borneensis	-	-	-	Taiwan	1	MG917696
J. borneensis	-	-	-	-	1	NC041308
J. borneensis	37068	-	-	-	2	KX777940-KX777941
J. distinctus	37069	TSI02	Miaoli	Taiwan	4	OK326790-OK326800
J. taiwanensis	37073	YLN0202	Yunlin	Taiwan	1	OK355352
J. taiwanensis	37074	2175, 2021	Miaoli	Taiwan	1	OK355356
J. taiwanensis	-	-	-	Taiwan	3	MG917694, NC022464, KF211426
J. trewavasae	37071	2252	Miaoli	Taiwan	1	OK253997
J. trewavasae	-	2251	Miaoli	Taiwan	1	-
J. trewavasae	-	-	-	Taiwan	5	KX777980-KX777984
J. trewavasae	-	-	-	-	3	KP722729, MF083700, MF004324
J. grypotus	23015	-	Shangdong	China	8	NC021130, KC491206

Abbreviation: GSCN—Global Sciaenidae Conservation Network.

MEGA7 v7.0 was also used to create a Neighbor-Joining (NJ) phylogenetic tree [21]. The NJ bootstrap values were calculated with 1000 repetitions using Kimura's two-parameter substitution model (K2P distance) [22]. In PhyML, a maximum likelihood (ML) analysis was carried out using the web server Smart Model Selection [23]. Based on the Akaike information criterion (AIC), an automated model selection method was developed [24]. The software predicted a gamma shape value of 0.099 for the HKY85 + G model with a fixed, invariable site. The outgroup *Dendrophysa russelii* was employed to root the tree.

Bayesian analyses (BAs) were carried out using MrBayes GPU [25]. MCMCMC sampling was carried out using four chains that were run for 200,000 generations, with GTR + gamma, HKY85 + gamma, and K80 + gamma model parameters specified in jModeltest 0.1.1 [26] for COI. After deleting trees acquired before the chains were stable, Bayesian posterior probabilities were chosen from the 50% majority rule consensus of trees sampled every 20 generations (determined via empirical checking of likelihood values). Drummond and Rambaut [27] evaluated the convergence of all parameters using Tracer V. 1.5 to investigate the trail of the parameters over generations.

3. Results

3.1. Genus Wak Lin, 1938, Accepted as a Junior Synonym of Johnius Bloch, 1793

Based on Fowler's [28] comment, Lin [29] recommended the new generic name *Wak* as a replacement for *Bola* Hamilton, 1822, with *Bola coitor* as the type species. *Wak* Lin [29] was recognized as a legitimate genus by Chu, Lo, and Wu [8], and it contained all Indo-Pacific sciaenids having a terminal mouth with distinct teeth in both jaws and a hammer-shaped gas bladder.

A comprehensive examination of Hamilton's [30] monograph and a review of the relevant literature clearly show that (i) Hamilton [30] used the term *Bola* in the generic sense, and (ii) *Wak* Lin [29] is a junior objective synonym of *Bola* Hamilton, with the same type species, *Bola coitor* Hamilton. *Bola coitor*, as previously suggested by Trewavas [31] and later verified by Talwar [32], has an inferior mouth with undifferentiated teeth in the lower jaw and a hammer-shaped gas bladder, and so is congeneric with *Johnius carutta* Bloch, 1793, the type species of the genus *Johnius*. This discovery renders the genus names *Wak* and *Bola* obsolete, and all species previously identified under these two genera names are now classified as *Johnius*.

3.2. Synonyms and Invalid Names of Nominal Species of Johnius Bloch, 1793

Several references from the Taiwanese literature have been edited and rectified [4,12,13,33–39]. Following Trewavas [10], Lal Mohan [40], Sasaki [4,41,42], and Fricke et al. [7], descriptions and identification keys have been utilized to cross-check against all species.

Several taxonomic names of Taiwanese *Johnius* species that are often used in the literature have been identified as questionable identifications. Table 3 lists the *Johnius* species recorded from Taiwan waters, along with their present taxonomic position. The species *J. carutta* and *J. dussumieri* were valid names; however, they are exclusively found in the Indian Ocean and were incorrectly reported from Taiwan. Furthermore, *J. macrorhynus* is valid, but only from the Indian Ocean to Vietnam and Borneo. *Johnius fasciatus* Chu et al., 1963 is a junior synonym of *J. belangerii* (Cuvier, 1830) (see [10]), while *J. sina* (Cuvier, 1830) is a junior synonym of *J. dussumieri* (Cuvier, 1830) (see [43]). Furthermore, the species *Wak tingi* (Tang, 1937) and *J. tingi* (Tang, 1937) is a junior synonym of *J. distinctus* (Tanaka, 1916) (see Sasaki and Amaoka [44]). Meanwhile, Chao et al. [5] recently reported a new species from Taiwan waters as *J. taiwanensis*, which is usually misdiagnosed as *J. macrorhynus* or *J. belangerii* based on morphology and molecular comparison.

Table 3. *Johnius* species as listed in several book references from Taiwan, and their taxonomic status. Correct names listed in the body of the table.

Species	This Study	[33]	[12]	[13]	[4]	[34]	[35]	[36]	[37]	[38]	[39]	Remarks
J. amblycephalus	+	v	v	v	v	v	v	v	v	v	v	
J. belangerii	+	x *Atrobucca nibe*	v	v	v	v	v		v	v	v	
J. borneensis	+				v					v		
J. carutta		x *J. distinctus*			v							Indian Ocean
J. distinctus	+					v	v	v	v	v	v	
J. dussumieri							x *J. belangerii*	x *J. borneensis*			x *J.borneensis*	Indian Ocean
J. fasciatus		n *J. belangerii*										
J. grypotus	+						x *J. taiwanensis*	x *J. taiwanensis*			x *J. belangerii*	
J. macrorhynus			x *J. grypotus*	x *J. trewavasae*	v	x *J. trewavasae*	x *J. trewavasae*	x *J. taiwanensis*			x *J. trewavasae*	Indian Ocean to South China Sea
J. sina				x *J. borneensis*			x *J. borneensis*					Indian Ocean
J. taiwanensis	+								v	x *J. trewavasae*	v	
J. tingi				n *J. distinctus*								
J. trewavasae	+				v							
Wak tingi		s *J. distinctus*										

v correct record; x incorrect record; s synonym name; n nomen dubium; + this study.

3.3.Integrated Identification of Taiwan Johnius species

Morphology. Size accounted for 60.63% of the observed variation, according to the sheared PCA (Figure 3) of the factor loadings data (Table 4). Sheared PC1 and PC2 accounted for 43.36% and 15.27%, respectively, of the observed variation. The loadings on sheared PC1 were greatest at gill raker length (GRL) (0.74). In contrast, the stress on sheared PC2 was greatest at the tip of the upper jaw to mouth hinge length (UJHL), tip of the lower jaw to mouth hinge length (ULHL), and second anal spine length (2AL).

Table 4. Morphological character factor loadings (correlations between variables and PC axes) for PC1 and PC2 within the genus *Johnius*. Character acronyms and definitions are explained in Table 1.

Characters Acronym	PC 1	PC 2
HL	−0.06	0.11
P1L	−0.04	0.12
P2L	−0.01	0.05
BD	0.00	−0.08
BW	−0.12	−0.01
D1BL	−0.03	−0.07
4D1L	−0.17	−0.03
D2BL	0.14	−0.24
5RD2L	0.05	−0.08
ABL	0.05	−0.14
PAL	−0.09	0.20
PD1L	−0.10	0.08
PD2L	−0.14	0.07
PP1L	−0.07	0.13
PP2L	−0.06	0.03
CPD	−0.06	−0.03
SnL/HL	−0.13	0.17
UJL	0.13	0.13
UJHL	0.27	0.45
LJHL	0.26	0.64
ED/HL	0.10	−0.09
IOW/HL	0.12	0.01
2AL/HL	0.24	−0.34
1RAL/HL	0.16	−0.11
GRL/HL	0.19	−0.04
GFL/HL	0.06	−0.07
GRL/ED	0.74	−0.09

The scatterplot clusters with 95% confidence interval polygons for *Johnius* species from Taiwan's western coast were compared to test for sympatric morphological divergence (Figure 3). The PCA of the morphometric data revealed significant non-overlap in the investigated features. When PC1 was plotted against PC2, several clusters emerged, showing highly organized variation in morphometric characteristics across the species investigated. This distinguished interspecific species from previously thought-to-be-conspecific individuals. The PCA findings indicate the occurrence of seven morphologically diverse *Johnius* species in Taiwanese waters.

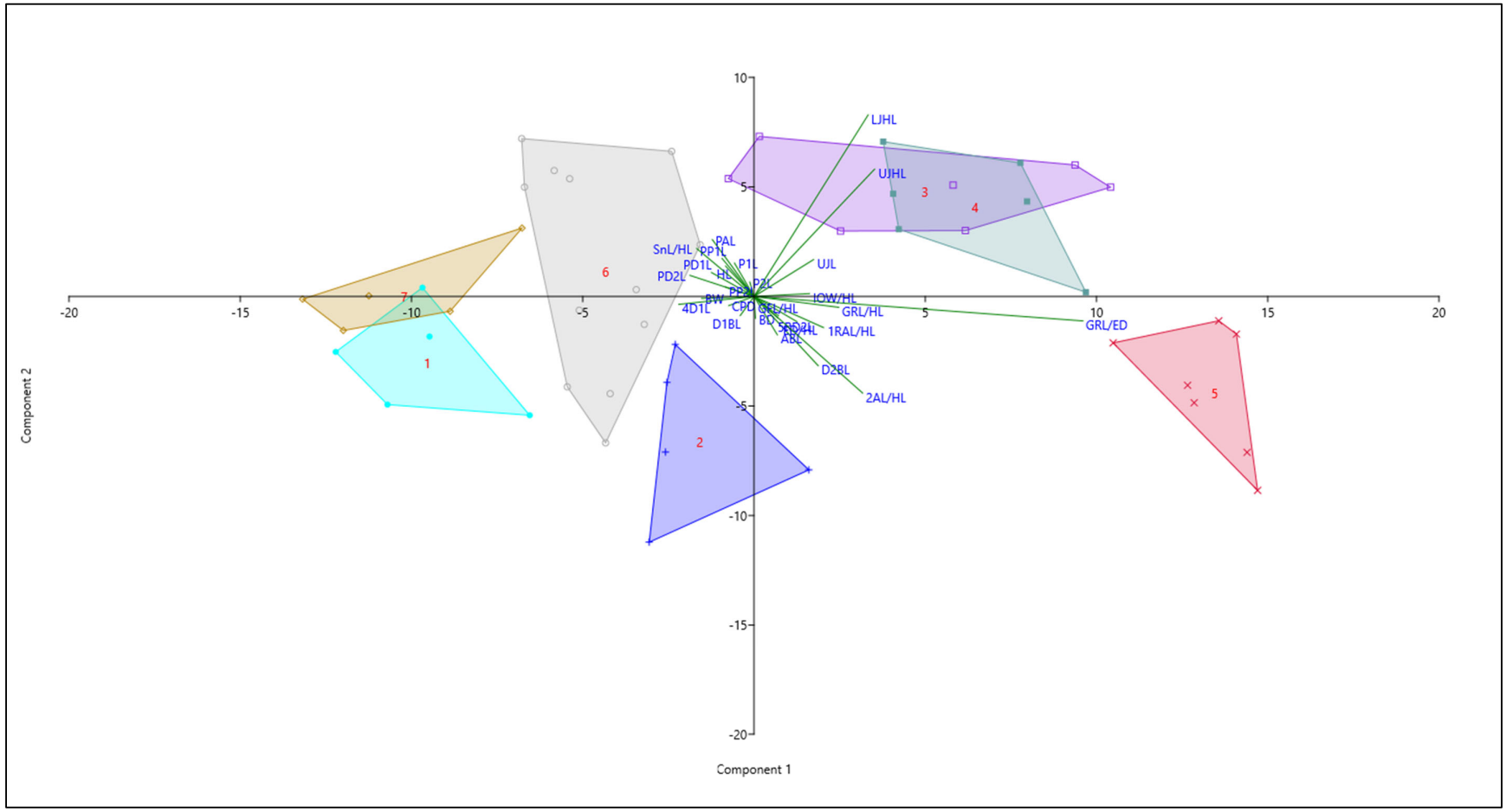

Figure 3. Scatterplots with 95% confidence interval polygons of the sheared first principal component (PC1) and sheared second principal component (PC2) of morphometric data for *Johnius* species from Taiwan. *J. amblycephalus* (1, dot), *J. belangerii* (2, plus), *J. borneensis* (3, hollow square), *J. distinctus* (4, filled square), *J. grypotus* (5, cross), *J. taiwanensis* (6, circle), *J. trewavasae* (7, diamond).

Molecular analyses. The aligned COI sequences had 613 base pairs, 51 of which were parsimony informative, 52 of which were variable but parsimony uninformative, and 472 of which were constant. Phylogenetic trees with the same topology but differing bootstrap (BS) and posterior probability (PP) support values were constructed using NJ, ML, and BA analysis (Figure 4). The COI-sequence-based phylogenetic tree indicated two major lineages (Figure 4). With a high support value (BS:100%; PP: 1), the initial lineage comprised *D. russelii* as an outgroup and *J. amblycephalus* as the basal species from Taiwan. The second lineage had high support values as well (BS:100%; PP: 1), and contained species of *J. borneensis* and *J. distinctus* (BS:89/57%; PP: 0.72). *Johnius grypotus* was positioned at the base of the most derived lineage (BS:88/78%; PP: 1) as a sister group to *J. taiwanensis* (BS:81/78%; PP: 0.9), followed by *J. belangerii* and *J. trewavasae* (BS:54/57%). The Taiwanese *Johnius* species formed a monophyletic group, which was supported by both morphological and genetic evidence (Figure 4 and Table 5).

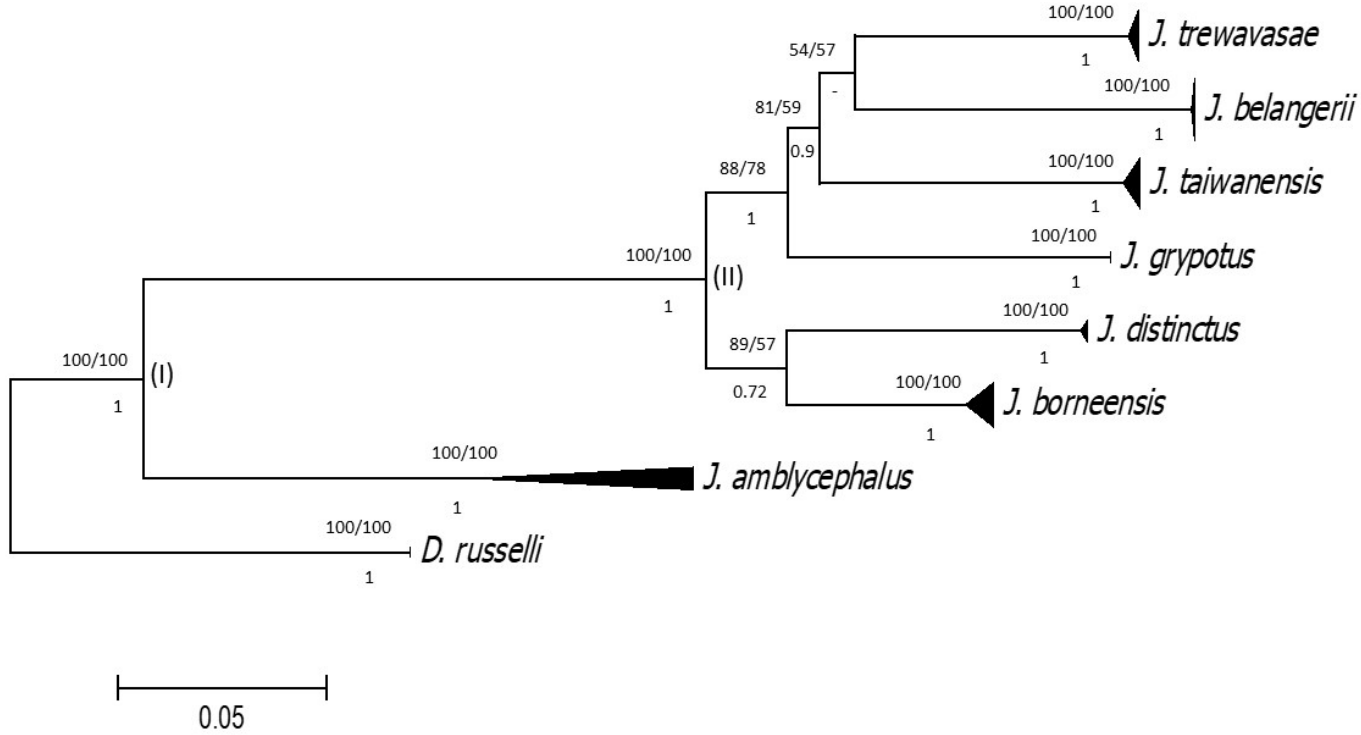

Figure 4. Phylogenetic tree of the *Johnius* species obtained from the COI gene. The numbers below each branch refer to Bayesian analysis (BA) posterior probability values, and the numbers below each branch and at nodes refer to neighbor-joining (NJ) and maximum likelihood (ML) bootstrap value significances, respectively. Only values above 50% are given. *Dendrophysa russelii* were used as an outgroup.

Table 5. Genetic distances for the COI gene among seven *Johnius* species from Taiwan and *Dendrophysa russelii* as an outgroup.

	1	2	3	4	5	6	7
J. amblycephalus (1)							
J. belangerii (2)	0.38						
J. borneensis (3)	0.35	0.18					
J. distinctus (4)	0.34	0.21	0.12				
J. grypotus (5)	0.36	0.17	0.17	0.19			
J. taiwanensis (6)	0.37	0.17	0.19	0.21	0.16		
J. trewavasae (7)	0.37	0.15	0.19	0.21	0.17	0.21	
D. russelli (8)	0.26	0.4	0.33	0.35	0.36	0.33	0.37

4. Systematics

List of genus synonyms:

Johnius Bloch, 1793. *Naturgesch. auslaänd. Fische*, Part 7. J. Morino & Comp., Berlin: 132 (type species: *Johnius carutta* Bloch).
Bola Hamilton-Buchanan, 1822. *Fishes of Ganges:* 73 (type species: *Bola coitor* Hamilton-Buchanan; junior synonym); Talwar, 1970, *Proc. Indian Acad. Sci.*, 72B: 266.
Apeches Gistel, 1848. *Naturges. Thierr.*: ix (type species: *Johnius carutta* Bloch; substitute name for *Johnius* Bloch).
Pseudomycterus Ogibly, 1908. Proc. Roy. Soc. Qld.,21: 94 (type species: *Pseudomycterus maccullochii* Ogilby).
Wak Lin, 1938. *Lingnan Sci. J.*, 17(2): 35, 378 (type species: *Bola coitor* Hamilton-Buchanan; substitute name for *Bola* Hamilton-Buchanan, 1822, unnecessary substitute name preoccupied by *Bola* Gunther).
Blythia Talwar, 1971. (non-*Blythia* Theobald, 1868), J. Inland Fish. Soc. India, 3: 23 (type species: *Umbrina dussumieri* Valenciennes; junior synonym).

Blythsciaena Talwar, 1975. *Newsl. Zool. Surv. India* 1 (2): 17 (type species: *Umbrina dussumieri* Valenciennes); substitute name for *Blythia* Talwar, the name being preoccupied by the snake genus *Blythia* Theobald, 1868.

Diagnosis. The genus *Johnius* can be distinguished from other genera of Sciaenidae by the following character states: (i) the anterior portion of the gas bladder against the septum transversum is expanded laterally into a hammer shape, and the end of the lateral arborescent branch extends to the anterolateral face of the pectoral arch at the intersection of the cleithrum and supracleithrum, which is visible externally; (ii) sagitta, with a tadpole-shaped sulcus obliquely or nearly at right angles to the otolith's long axis, and the "tail" extended and deepened as a hollow cone; (iii) soft dorsal and scaly anal fins; (iv) presence of a large foramen in the prootic bone [45].

Johnius amblycephalus (Bleeker, 1855)
(Figure 5A; Table 6)

Figure 5. Photographs of *Johnius* species here described, with specimens deposited in the Taiwan National Museum of Marine Biology and Aquarium (NMMBA). (**A**) *Johnius amblycephalus*; NMMB-P37066, 137.09 mm SL; (**B**) *Johnius belangerii* NMMB-P37067, 139.37 mm SL; (**C**) *Johnius borneensis* NMMB-P37068, 101.86 mm SL; (**D**) *Johnius distinctus* NMMB-P37069, 87.27 mm SL.

Table 6. Morphometric measurements and meristic counts of *J. amblycephalus*, *J. belangerii*, *J. borneensis*, *J. distinctus*, *J. taiwanensis*, *J. trewavasae*, and *J. grypotus*.

Species	*J. amblycephalus* (n = 5)	*J. belangerii* (n = 5)	*J. borneensis* (n = 7)	*J. distinctus* (n = 6)	*J. grypotus* (n = 6)	*J. taiwanensis* (n = 12)	*J. trewavasae* (n = 5)
Standard length (mm)	121–163	139–175	100–147	87–172	79–130	120–142	140–147
Meristic counts							
1st dorsal fin spine	10	10	10	10	10	10	10
2nd dorsal fin spine	1	1	1	1	1	1	1
2nd dorsal fin soft rays	23–25	27–29	27–29	28–29	24–26	23–26	24–26
Anal fin spine	2	2	2	2	2	2	2
Anal fin soft rays	7	7	7	7	7–8	7	7
Pectoral rays	16–18	16–17	16–18	16–18	16–17	14–17	16–17
Outer gill rakers of 1st arch	13–14	13–15	15–18	17–18	15–18	14–15	12–13
Upper limb	4	4	5–6	6–7	4–6	4–5	4–5
Lower limb	8–9	9–11	10–12	11–13	11–12	8–10	7–8
Inner gill rakers of 1st arch	9–10	10–12	11–14	12–13	11–12	10–11	11–12
Upper limb	3	3	3–4	3–4	3–4	3	4
Lower limb	6–7	7–9	8–10	8–9	7–9	7–8	7–8
Lateral line pored scales	46–50	47–49	47–50	47–48	44–48	46–49	44–47
Circumpeduncular scales	14–17	14–16	14–17	13–15	12–14	14–15	12–13
Scales above lateral line	7–8	7	5–6	5–6	5–6	5–6	4–5
Scales below lateral line	12–13	11–12	10–12	10–11	9–12	10–11	8–10
Scales on body	Cycloid	Ctenoid	Ctenoid	Ctenoid	Ctenoid	Ctenoid	Ctenoid
Scales on head	Cycloid	Ctenoid	Cycloid	Cycloid	Cycloid	Ctenoid and Cycloid	Cycloid
Morphometric measurements							
As a percentage of SL							
Head length	29.9–31.8 (31 ± 0.8)	28.2–31.6 (30 ± 1.3)	320.5–31.8 (31 ± 0.5)	30.1–32.0 (31 ± 0.9)	27.8–29.7 (29 ± 0.7)	29.1–32.0 (30 ± 0.9)	30.1–31.6 (31 ± 0.7)
Pectoral fin length	20.3–21.8 (21 ± 0.6)	18.0–19.6 (19 ± 0.7)	16.7–22.2 (20 ± 2.3)	19.2–22.7 (20 ± 1.5)	17.4–20.0 (19 ± 0.9)	16.3–23.3 (21 ± 1.8)	15.2–21.6 (18 ± 2.4)
Pelvic fin length	16.2–17.9 (17 ± 0.7)	16.3–17.8 (17 ± 0.6)	14.6–17.6 (17 ± 1.0)	15.0–18.0 (17 ± 1.3)	14.5–17.3 (16 ± 1.2)	14.9–19.3 (17 ± 1.2)	15.1–16.2 (16 ± 0.5)
Body depth	25.0–28.5 (27 ± 1.4)	28.6–31.2 (30 ± 1.1)	27.0–29.3 (29 ± 0.9)	23.2–28.5 (27 ± 2.3)	26.8–29.4 (28 ± 0.9)	26.5–30.1 (28 ± 1.1)	25.6–27.9 (27 ± 0.9)
Body width	16.3–19.1 (18 ± 1.2)	14.9–16.2 (15 ± 0.5)	14.3–16.7 (15 ± 0.8)	13.7–15.6 (15 ± 0.8)	13.4–15.5 (14 ± 0.7)	15.2–16.8 (16 ± 0.6)	15.6–18.3 (17 ± 1.1)
1st dorsal fin base length	20.6–22.0 (21 ± 0.5)	20.0–23.0 (21 ± 1.1)	19.5–22.0 (21 ± 0.9)	16.6–19.9 (18 ± 1.5)	16.3–21.2 (19 ± 1.6)	17.3–21.5 (20 ± 1.4)	18.3–20.4 (19 ± 0.8)
Length of 4th spine of 1st dorsal fin	18.3–22.9 (21 ± 2.2)	13.4–16.1 (15 ± 1.1)	12.7–15.7 (15 ± 1.1)	12.3–13.0 (13 ± 0.3)	9.7–15.8 (13 ± 2.2)	11.9–16.3 (14 ± 1.4)	12.5–16.3 (15 ± 1.5)
2nd dorsal fin base length	34.3–38.7 (37 ± 1.7)	39.6–43.6 (42 ± 1.5)	36.8–40.7 (39 ± 1.4)	37.7–41.4 (39 ± 1.7)	39.3–43.1 (41 ± 1.2)	34.5–42.4 (38 ± 2.5)	35.1–38.7 (37 ± 1.5)
Length of 5th ray of 2nd dorsal fin	6.2–10.9 (8 ± 1.8)	8.1–9.0 (8 ± 0.4)	7.2–8.5 (7 ± 0.5)	6.0–7.7 (7 ± 0.7)	9.9–13.2 (11 ± 1.1)	6.8–12.0 (10 ± 1.8)	7.0–7.9 (8 ± 0.4)
Anal fin base length	9.7–11.0 (10 ± 0.5)	10.7–11.7 (11 ± 0.4)	8.7–10.2 (9 ± 0.55)	10.5–11.4 (11 ± 0.4)	10.4–12.3 (12 ± 0.7)	7.9–10.4 (9 ± 1.0)	9.1–11.4 (10 ± 0.9)
Length of 2nd anal fin spine	7.2–9.5 (8 ± 1.0)	9.4–10.4 (10 ± 0.4)	7.7–10.2 (9 ± 0.8)	7.3–12.2 (9 ± 2.1)	8.6–10.8 (9 ± 0.9)	7.6–9.5 (9 ± 0.6)	8.4–8.7 (9 ± 0.1)
Length of 1st anal fin ray	10.6–12.8 (12 ± 0.9)	12.7–13.3 (13 ± 0.3)	11.6–13.6 (12 ± 0.7)	10.9–15.2 (13 ± 1.8)	11.0–13.7 (12 ± 1.1)	10.4–13.9 (13 ± 1.1)	11.6–12.5 (12 ± 0.4)
Preanal length	66.9–70.4 (69 ± 1.3)	66.0–70.1 (68 ± 1.5)	68.2–72.6 (70 ± 1.5)	68.6–72.0 (71 ± 1.6)	65.4–68.4 (67 ± 1.0)	66.7–71.3 (69 ± 1.5)	70.8–74.8 (72 ± 1.6)
Predorsal length	32.9–36.0 (35 ± 1.2)	33.9–35.4 (35 ± 0.7)	33.2–34.5 (33 ± 1.2)	33.5–35.3 (35 ± 0.8)	31.4–33.6 (33 ± 0.8)	32.3–37.1 (35 ± 1.5)	34.5–37.5 (35 ± 1.3)
Distance from snout to origin of 2nd dorsal fin	54.0–55.7 (55 ± 0.7)	51.2–55.3 (53 ± 1.5)	52.1–54.1 (53 ± 0.6)	49.3–51.8 (51 ± 1.2)	47.1–51.9 (49 ± 1.7)	50.7–55.2 (53 ± 1.4)	51.8–53.2 (52 ± 0.5)

Table 6. *Cont.*

Species	*J. amblycephalus* (n = 5)	*J. belangerii* (n = 5)	*J. borneensis* (n = 7)	*J. distinctus* (n = 6)	*J. grypotus* (n = 6)	*J. taiwanensis* (n = 12)	*J. trewavasae* (n = 5)
Prepectoral length	30.9–32.6 (32 ± 0.7)	29.8–30.9 (30 ± 0.5)	30.5–34.5 (33 ± 1.2)	31.1–34.2 (32 ± 1.4)	27.6–30.2 (29 ± 0.9)	30.2–32.8 (31 ± 0.8)	30.5–33.2 (32 ± 1.1)
Prepelvic length	33.5–35.2 (34 ± 0.7)	33.5–35.2 (34 ± 0.8)	32.0–36.9 (35 ± 1.6)	33.7–35.9 (35 ± 1.0)	32.5–34.0 (33 ± 0.5)	33.5–36.6 (35 ± 1.0)	36.2–38.0 (37 ± 0.7)
Caudal peduncle depth	9.1–10.0 (10 ± 0.4)	8.9–10.2 (10 ± 0.5)	8.5–10.5 (10 ± 0.6)	8.2–9.7 (9 ± 0.7)	8.0–9.5 (9 ± 0.5)	8.8–14.3 (10 ± 1.7)	9.6–10.2 (10 ± 0.3)
As a percentage of HL							
Snout length	27.0–29.2 (28 ± 0.8)	24.6–30.0 (28 ± 2.0)	26.3–30.9 (28 ± 1.8)	25.8–30.9 (28 ± 2.1)	26.0–27.4 (27 ± 0.6)	25.5–32.1 (29 ± 2.5)	28.9–35.1 (32 ± 2.7)
Upper jaw length	41.0–45.7 (43 ± 1.8)	39.1–43.5 (42 ± 1.7)	43.5–47.4 (45 ± 1.5)	42.4–46.8 (45 ± 1.9)	39.4–48.5 (45 ± 3.1)	41.1–45.9 (43 ± 1.5)	41.1–43.4 (42 ± 1.1)
Tip upper jaw to hinge length	25.0–28.0 (26 ± 1.3)	25.9–30.9 (29 ± 1.8)	34.3–38.0 (36 ± 1.3)	32.1–34.9 (34 ± 1.2)	30.4–34.1 (32 ± 1.4)	25.9–31.4 (29 ± 2.1)	27.0–33.6 (29 ± 2.6)
Tip lower jaw to hinge length	18.8–23.2 (21 ± 2.0)	18.8–25.8 (23 ± 2.5)	27.4–32.0 (29 ± 1.9)	27.2–30.7 (29 ± 1.5)	23.5–30.0 (26 ± 2.5)	19.9–32.3 (26 ± 4.3)	20.1–27.6 (22.5 ± 3.0)
Eye diameter	19.0–23.4 (21 ± 1.6)	21.9–25.4 (23 ± 1.4)	21.4–25.2 (24 ± 1.4)	21.1–25.8 (22 ± 2.3)	21.9–26.4 (25 ± 1.5)	20.3–24.1 (22 ± 1.1)	22.9–25.2 (24 ± 0.9)
Interorbital width	27.5–29.3 (28 ± 0.7)	21.8–24.3 (23 ± 1.1)	24.3–26.3 (25 ± 0.8)	25.2–28.6 (27 ± 1.4)	27.3–30.1 (29 ± 1.1)	24.0–27.5 (26 ± 0.9)	22.4–23.8 (23 ± 0.6)
2nd spine of anal fin length	22.6–31.9 (27 ± 4.0)	32.2–36.5 (34 ± 2.2)	25.0–33.5 (30 ± 2.6)	26.4–31.1 (28 ± 2.1)	29.8–37.4 (33 ± 3.1)	25.4–31.6 (28 ± 1.8)	27.0–28.9 (28 ± 0.7)
1st ray of anal fin length	34.5–40.4 (38 ± 2.4)	41.7–46.9 (44 ± 2.5)	36.7–43.7 (40 ± 2.4)	36.9–41.8 (40 ± 2.3)	37.5–47.4 (44 ± 3.9)	35.7–45.4 (41 ± 3.0)	37.3–41.3 (39 ± 1.8)
Gill raker length	1.8–2.6 (2 ± 0.3)	2.4–3.5 (3 ± 0.5)	3.5–5.5 (5 ± 0.8)	4.0–5.3 (5 ± 0.5)	5.8–7.6 (6 ± 0.6)	1.6–3.0 (3 ± 0.2)	1.4–2.0 (2 ± 0.2)
Gill filament length	9.5–11.6 (11 ± 1.0)	8.6–10.2 (9 ± 0.6)	7.7–11.1 (9 ± 1.2)	8.3–10.9 (9 ± 1.1)	9.6–14.9 (12 ± 1.8)	8.4–11.4 (10 ± 0.9)	8.5–10.8 (10 ± 0.9)
As a percentage of ED							
Gill raker length	9.5–12.4 (11 ± 1.2)	9.6–14.9 (13 ± 2.2)	15.4–22.8 (19 ± 3.1)	18.4–22.8 (21 ± 1.6)	23.2–28.7 (26 ± 1.7)	7.9–13.0 (11 ± 1.7)	6.3–7.9 (7 ± 0.6)
Gill filament length	44.1–60.9 (51 ± 6.8)	34.3–43.7 (40 ± 3.9)	11–12 (42 ± 0.4)	36.3–50.8 (42 ± 5.9)	39.4–62.6 (49 ± 8.8)	39.7–52.7 (45 ± 4.2)	36.0–44.8 (40 ± 3.4)

Percentages are displayed as ranges. Figures in parentheses indicate mean values and standard deviation; SL: standard length; HL: head length; ED: eye diameter.

Synonyms:

Umbrina amblycephalus Bleeker 1855: 412 (type locality: Ambon Island, Molucca Islands, Indonesia. Syntypes: RMNH 8289).

Johnius amblycephalus (Bleeker, 1855): Shen [33]: 70, Figure 331-1; Yu and Shen [12]: 93, Figure 20; Shen [13]: 377, pl. 110-2; Sasaki [4]: 3139; Shao and Chen [34]: 245; Shen and Wu [35]: 487; Shao [36]: 148; Chen et al. [37]: 216; Koeda and Ho [38]: 895; Shao [39].

Material examined. *Non-types*: ASIZP0059867 (123.7 mm SL), Bali, Taipei, Taiwan, 27 August, 1998; ASIZP0063559 (148.72 mm SL), Miaoli, Taiwan, 3 December 2002; ASIZP0062285 (129.48 mm SL), Xingda Harbor, Kaohsiung, Taiwan, 25 May 2001; ASIZP0066441 (M), ASIZP0066426 (112.85 mm SL), Donggang, Pingtung, Taiwan, 7 October 2005; ASIZP0064289 (113.19 mm SL), Miaoli, Taiwan, 1 September 2004; ASIZP0066429 (113.72 mm SL), Donggang, Pingtung, Taiwan, 7 October 2005; ASIZP0065217 (132.55 mm SL), ASIZP0065216 (139.30 mm SL), Donggang, Pingtung, Taiwan, 28 April 2005; ASIZP0058600 (140.41 mm SL), Tongsiao, Miaoli, Taiwan, 10 April 1990; NMMB-P37065 (5, 120.81 to 153.76 mm SL), Miaoli, Taiwan, 12 August 2019; NMMB-P37066 (137.09 mm SL), Yunlin, Taiwan, 7 March 2019; NMMB-P32933 (4, 126.1 to 135.43 mm SL), Changhua, Taiwan, 16 February 2019; NMMB-P27214 (2, 132.9 to 135.43 mm SL), Donggang, Pingtung, Taiwan, 5 October 2013; NMMB-P27241 (4, 83.56 to 102.69 mm SL), Donggang, Pingtung, Taiwan, 5 October 2010; NMMB-P28406 (141.72 mm SL), Budai, Chiayi, Taiwan, 18 September 2017; NMMB-P23040 (2, 96.73 to 109.07 mm SL), Xinhuwei River, Taiwan, 15 December 2012; NMMB-P24325 (3, 116.08 to 139.17 mm SL), Kezailiao, Kaohsiung, Taiwan, 13 July 2016; NMMB-P14271 (94.59 mm SL), Dongshi, Chiayi Taiwan, 11 September 2011; NMMB-P27275 (52.25 mm SL), Donggang, Donggang, Pingtung, Taiwan, 7 September 2017; NMMB-P11012 (4, 126.6 to 137.15 mm SL), Hengchun, Pingtung, Taiwan, 4 September 2010; NMMB-P27199 (114.16 mm SL), Longfeng, Miaoli, Taiwan, 15 December 2019; NMMB-P12936 (4, 51.36 to 87.23 mm SL), Donggang, Pingtung, Taiwan, 21 July 1979; NMMB-P8916 (113.92 mm SL), Donggang, Pingtung, Taiwan, 9 December 2004; NMMB-P32214 (148.66 mm SL), NMMB-P32215 (153.77 mm SL), NMMB-P32216 (160.04 mm SL), NMMB-P32217 (M), NMMB-P32218 (142.9 mm SL), Donggang, Pingtung, Taiwan, 14 March 2010; NMMB-P27200 (139.13 mm SL), Zhunan, Miaoli, Taiwan, 15 December 2014; NMMB-P23041 (138.60 mm SL), Jiangjun, Tainan, Taiwan, 19 June 2014; NMMB-P27205 (137.15 mm SL), Dongshi, Chiayi, Taiwan, 16 September 2014; NMMB-P23042 (137.14 mm SL), Jiangjun, Tainan, Taiwan, 13 May 2014; NMMB-P19336 (144.15 mm SL), Yunlin, Taiwan, 13 March 2014.

Diagnosis. Snout steep, bluntly rounded; mouth inferior; a stiff, blunt barbel on chin; gill rakers stiff, less than 1/2 length of gill filaments at angle of arch, eight to nine on lower limb of first gill arch; caudal fin slightly rhomboidal, S-shaped, or truncated; scales small, seven to eight scale rows above the lateral line.

Description. A small- to medium-sized species with a moderately deep body. Snout steep, bluntly rounded, projecting in front of upper jaw; mouth inferior; a stiff, blunt barbel on chin; teeth differentiated into large and small in upper jaw only, the large one close-set, not canine-like, and forming an outer series; lower jaw with a band of villiform teeth. Gill rakers stiff, less than 1/2 length of gill filaments at angle of arch, eight to nine on lower limb of first gill arch. Dorsal fin with X spines, followed by a notch, second part of fin with I spine and 23 to 25 soft rays, second to fifth spines prolonged; anal fin with II spines and seven soft rays, second spine moderately short, 22.6 to 31.9% of head length; caudal fin slightly rhomboidal, S-shaped, or truncated. Scales small, 7 to 8 scale rows above lateral line to origin of dorsal fin, 12 to 13 scale rows below lateral line to origin of anal fin; scales on head and body cycloid (smooth to the touch); small scales present on soft parts of dorsal and anal fins; lateral line scales reaching hind margin of caudal fin. Swimbladder hammer-shaped, with 14 pairs of arborescent appendages along its sides, the first pair entering head beyond transverse septum and sending a palmate branch to the front of the pectoral arch. Sagitta with a tadpole-shaped impression, the head of which has its long axis lying obliquely to that of the sagitta and the tail expanded and deepened as a hollow cone, connected with the head by a narrow groove.

Color. Back and flanks black or dark brown, belly whitish or cream yellow; upper part of the rather high spinous part of dorsal fin black.

Distribution. Indo-West Pacific, west to Pakistan, east to southern China and northeastern Australia.

Remarks. *Johnius amblycephalus* can be differentiated from other *Johnius* species in Taiwan waters by the presence of a single mental barbel at the lower jaw. *Johnius amblycephalus* is abundant and was collected from the Miaoli and Yunlin counties, Taiwan.

***Johnius belangerii* (Cuvier, 1830)**

(Figure 5B; Table 6)

Synonyms:

Johnius belangerii (Cuvier, 1830): Yu and Shen [12]: 95, Figure 22; Shen [13]: 377, pl. 110–3; Shao and Chen [34]: 245; Chen et al. [37]: 217; Sasaki [4]: 3141; Shao [39].

Johnius belangerii (not sensu Cuvier, 1830): Shen [33]: 70, Figure 331-4,

Johnius dussumieri (not sensu Cuvier, 1830): Shen and Wu [35]: 487,

Johnius fasciatus (not sensu Cuvier, 1830): Shen [33]: 70, Figure 331-2,

Johnius grypotus (not sensu Sasaki, 1990): Shao [39].

Material examined. *Non-types*: ASIZP0080295 (115.01 mm SL), Luzhuguo, Tainan, Taiwan, 3 March 2016; ASIZP0059874 (140.28 mm SL), Bali, Taipei, Taiwan, 27 August 1998; ASIZP0061721 (83.97 mm SL), Miaoli, Taiwan, 20 March 2002; ASIZP0059042 (157.48 mm SL), Tongsiao, Miaoli, Taiwan, 8 August 1989; ASIZP0062913 (72.21 mm SL), Mauli, Taiwan, 8 August 1989; ASIZP0066421 (135.68 mm SL), ASIZP0066556 (133.09 mm SL), ASIZP0066402 (1148.43 mm SL), Wuchi, Taichung, Taiwan, 8 October 2005; ASIZP0071040 (146.78 mm SL), Matsu, Taiwan, 29 February 2008; ASIZP0080495 (2, 160.25–163.71 mm SL), Kinmen, Taiwan, 24 January 2012; ASIZP0074811 (149.87 mm SL), Beigan, Matzu, Taiwan, 30 September 2009; NMMB-P37067 (6, 139.37 to 184.64 mm SL), NMMB-P22482 (153.76 mm SL), Zhunan, Miaoli, Taiwan, 12 August 2019; NMMB-P18787 (146.22 mm SL), NMMB-P18788 (153.76 mm SL), NMMB-P18789 (166.93 mm SL), Kinmen, Taiwan, 24 October 2012; NMMB-P27184 (135.66 mm SL), NMMB-P27639 (127.61 mm SL), NMMB-P23057 (2, 115.39 to 130.87 mm SL), Boziliao, Yunlin, Taiwan, 31 July 2014; NMMB-P23050 (6, 132.6 to 152.57 mm SL), NMMB-P23043 (11, 98.8 to 132.31 mm SL), NMMB-P23044 (11, 81.18 to 125.07 mm SL), NMMB-P23045 (8, 78.58 to 125.28 mm SL), NMMB-P23048 (5, 84.2 to 129.56 mm SL), NMMB-P28315 (41.62 mm SL), Mailiao, Yunlin, Taiwan, 15 December 2012; NMMB-P27963 (15, 133.49 to 141.55 mm SL), NMMB-P27960 (7, 128.65 to 145.04 mm SL), Budai, Chiayi, Taiwan, 18 November 2017; NMMB-P32011 (3, 141.39 to 173.97 mm SL), Zhunan, Miaoli, Taiwan, 22 March 2019; NMMB-P14028 (6, 146.84 to 194.97 mm SL), Wuqi, Taichung, Taiwan, 11 September 2011; NMMB-P25883 (145.34 mm SL), Boziliao, Yunlin, Taiwan, 31 July 2011; NMMB-P28298 (3, 137.5 to 153.76 mm SL), Kinmen, Taiwan, 18 October 2012; NMMB-P23046 (2, 113.48 to 138.42 mm SL), Mailiao, Yunlin, Taiwan, 22 May 2011; NMMB-P34114 (2, 155.76 to 162.22 mm SL), Changhua, Taiwan, 11 September 2011; NMMB-P27225 (4, 151.29 to 153.76 mm SL), Budai, Chiayi, Taiwan, 12 August 2017; NMMB-P27223 (4, 142.27 to 148.13 mm SL), NMMB-P27204 (129.14 mm SL), Budai, Chiayi, Taiwan, 26 August 2017; NMMB-P30112 (10, 110.58 to 163.79 mm SL), Lukang, Changhua, Taiwan, 11 June 2013; NMMB-P32430 (12, 126.02 to 140.61 mm SL), Xingda, Kaohsiung, Taiwan, 3 April 2011; NMMB-P28306 (127.08 mm SL), Yunlin, Taiwan, 11 June 2013; NMMB-P19372 (153.76 mm SL), Changhua, Taiwan, 14 March 2013; NMMB-P8472 (123.55 mm SL), NMMB-P8489 (93.33 mm SL), NMMB-P8449 (127.42 mm SL), NMMB-P8465 (85.85 mm SL), NMMB-P8447 (2, 135.35–144.13 mm SL), Wuqi, Taichung, Taiwan, 6 May 2005; NMMB-P28303 (2, 101.89 to 124.43 mm SL), Changhua, Taiwan, 26 May 2013; NMMB-P8472 (123.55 mm SL), Taichung, Taiwan, 6 May 2005; NMMB-P23049 (61.4 mm SL), Yunlin, Taiwan, 16 July 2014; NMMB-P23087 (65.17 mm SL), Yunlin, Taiwan, 4 September 2014; NMMB-P23086 (48.14 mm SL), NMMB-P23051 (39.85 mm SL), Mailiao, Yunlin, Taiwan, 16 July 2014; NMMB-P23581 (138.23 mm SL), Matsu, Taiwan, 8 August 2016; NMMB-P19369 (108.71 mm SL), Boziliao, Yunlin, Taiwan, 13 March 2013; NMMB-P32427 (4, 118.52 to

198.72 mm SL), Chiayi, Taiwan, 3 April 2011; NMMB-P35949 (6, 116.07 to 150.19 mm SL), Cianjhen, Kaohsiung, Taiwan, 1 September 2021.

Diagnosis. Snout steep, obtusely rounded; mouth small, inferior; gill rakers very short, club-shaped, less than 1/2 length of gill filaments at angle of arch, 9 to 11 on lower limb of first gill arch; scales moderately small, seven scale rows above lateral line.

Description. A small- to medium-sized species with a moderately deep body; body depth 28.6 to 31.2% of standard length. Eye large, 21.9 to 25.4% of head length. Interorbital width 21.8 to 24.3% of head length. Snout steep, obtusely rounded, slightly projecting in front of upper jaw; mouth small, inferior; upper jaw extending backward below middle of eye; no barbel on chin; teeth differentiated into large and small in upper jaw only, the large ones close-set, not canine-like, forming outer series; lower jaw with a band of villiform teeth. Gill rakers very short, club-shaped, less than 1/2 length of gill filaments at angle of arch, 9 to 11 on lower limb of first gill arch. Dorsal fin with X spines, followed by a notch, second part of fin with I spine and 27 to 29 soft rays; anal fin with II spines and seven soft rays, second spine long, stiff, 32.2 to 36.5% of head length; caudal fin rhomboidal. Scales moderately small, 7 scale rows above lateral line to origin of dorsal fin, 11 to 12 scale rows below lateral line to origin of anal fin; scales cycloid (smooth to the touch) on snout, strongly ctenoid (very rough to the touch) on other parts of head and body; small scales present on soft parts of dorsal and anal fins; lateral line scales reaching tip of caudal fin. Swimbladder hammer-shaped, with 15 pairs of arborescent appendages along its sides, the first pair entering head beyond transverse septum and sending a palmate branch to the front of the pectoral arch. Sagitta with a tadpole-shaped impression, the head of which has its long axis lying obliquely to that of the sagitta and the tail expanded and deepened as a hollow cone, connected with the head by a narrow groove. Twenty-five vertebrae.

Color. Dark-pigmented, but pigments sometimes irregular and irregularly concentrated into short, dark bars along back or on dorsal fin; spinous part of dorsal fin black, lower fins also black in many cases; dark blotch shows through gill cover.

Distribution. Indo-West Pacific, west to the Persian Gulf, east to southern China and Indonesia.

Remarks. Johnius belangerii is a common species. It was collected from several sites off the Miaoli, Changhua, and Yunlin counties, Taiwan. The variation in the shape band pattern observed in this species implies it is a morphologically complex species.

***Johnius borneensis* (Bleeker, 1850)**

(Figure 5C; Table 6)

Synonyms:

Johnius borneensis (Bleeker, 1851): Koeda and Ho [38]: 895; Sasaki [4]: 3139.

Johnius dussumieri (not sensu Cuvier, 1830): Shao [36]: 148; Shao, [39].

Johnius sina (not sensu Cuvier, 1830): Yu and Shen [12]: 96, Figure 23; Shen [13]: 378, pl. 110–5; Shen and Wu [35]: 488.

Material examined. *Non-types*: ASIZP0066432 (101.50 mm SL), ASIZP0066166 (98.87 mm SL), ASIZP0066444 (123.12 mm SL), ASIZP0066457 (123.94 mm SL), Donggang, Pingtung, Taiwan, 7 October 2005; ASIZP0073599 (119.65 mm SL), Wanggong, Changhua, Taiwan, 9 July 2013; ASIZP0062286 (151.30 mm SL), Xingda Harbor, Kaohsiung, Taiwan, 1 March 2001; ASIZP0064726 (133.92 mm SL), Donggang, Pingtung, Taiwan, 16 August 2004; ASIZP0063560 (185.63 mm SL), Mauli, Taiwan, 3 December 2002; NMMB-P37068 (8, 101.86 to 147.13 mm SL), Chiayi, Taiwan, 30 March 2019; NMMB-P37075 (132.05 mm SL), Yunlin, Taiwan, 7 March 2019; NMMB-P32219 (147.61 mm SL), NMMB-P32208 (195.76 mm SL), NMMB-P32209 (204.79 mm SL), NMMB-P32206 (198.35 mm SL), Donggang, Pingtung, Taiwan, 14 March 2010; NMMB-P11416 (2, 153.76 to 159.97 mm SL), Nanfangao, Yilan, Taiwan, 18 November 2009; NMMB-P15389 (6, 135.84 to 154.76 mm SL), Donggang, Pingtung, Taiwan, 4 September 2010; NMMB-P4631 (161.47 mm SL), Donggang, Pingtung, Taiwan, 21 July 1979; NMMB-P7906 (164.99 mm SL), Donggang, Pingtung, Taiwan, 11 June 2014; NMMB-P27232 (7, 151.32 to 154.76 mm SL), Boziliao, Kaohsiung, Taiwan, 19 August 2017; NMMB-P11017 (3, 153.76 to 182.68 mm SL), Donggang, Pingtung, Taiwan,

4 September 2014; NMMB-P23053 (35, 43.67 to 107.7 mm SL), NMMB-P23055 (11, 51.18 to 73.21 mm SL),Yunlin, Taiwan, 21 August 2012; NMMB-P27242 (8, 81.7 to 91.39 mm SL), Donggang, Pingtung, Taiwan, 5 October 2010; NMMB-P30123 (141.78 mm SL), Tashi, Yilan, Taiwan, 5 June 2010; NMMB-P23054 (20, 41.89 to 48.4 mm SL), Zhoushui River, Yunlin, Taiwan, 4 December 2013; NMMB-P1731 (3, 62.75 to 93.5 mm SL), Da'an, Taipei, Taiwan, 30 November 2005; NMMB-P19258 (82.4 to 114 mm SL), Donggang, Pingtung, Taiwan, 10 November 2011; NMMB-P23056 (107.03 mm SL), Zhoushui River, Yunlin, Taiwan, 16 July 2014; NMMB-P4137 (3, 59.63 to 77.72 mm SL), Xingda, Kaohsiung, Taiwan, 3 October 1984; NMMB-P5318 (110.84 mm SL), Taichung, Taiwan, 2 June 1991; NMMB-P4092 (2, 102.5 to 109.3 mm SL), Chijin, Kaohsiung, Taiwan, 15 December 1983; NMMB-P30118 (120.54 mm SL), Budai, Chiayi, Taiwan, 26 August 2017; NMMB-P8294 (67.18 mm SL), Kaohsiung, Taiwan, 11 September 1989; NMMB-P30126 (103.14 mm SL), Donggang, Pingtung, Taiwan, 14 June 2010; NMMB-P23057 (3, 49.94 to 71.32 mm SL), NMMB-P23058 (5, 46.36 to 61.36 mm SL), Mailiao, Yunlin, Taiwan, 4 December 2013; NMMB-P2678 (63.09 mm SL), Kaoping River, Kaohsiung, Taiwan, 20 August 1995; NMMB-P23059 (67.18 mm SL), Xinhuwei River, Yunlin, Taiwan, 6 August 2013; NMMB-P32204 (384.67 mm SL), NMMB-P32205 (190.14 mm SL), NMMB-P32207 (183.76 mm SL), Fangliao, Pingtung, Taiwan, 14 March 2014; NMMB-P12941 (174.98 mm SL), Tongkang, Pingtung, Taiwan, 1 April 2002; NMMB-P35086 (158.76 mm SL), Taichung, Taiwan, 7 November 2019; NMMB-P34446 (98.03 mm SL), Anping, Tainan, Taiwan, 14 December 1987.

Diagnosis. Snout pointed, but not swollen or projecting; mouth large, oblique; gill rakers slender, about 1/2 length of gill filaments at angle of arch, 10 to 12 on lower limb of first gill arch; scales moderately large, five to six scale rows above lateral line.

Description. A medium-sized species with a deep body. Eye moderately large, 21.4 to 25.2% of head length. Snout pointed, but not swollen or projecting; mouth large, oblique; upper jaw extending backward below posterior half of eye; no barbel on chin; teeth in narrow bands, well differentiated into large and small in both jaws, but not canine-like; the large ones widely spaced, forming outer series in upper jaw, inner series in lower jaw. Gill rakers slender, about 1/2 length of gill filaments at angle of arch, 10 to 12 on lower limb of first gill arch. Dorsal fin with X spines, followed by a notch, second part of fin with I spine and 27 to 29 soft rays; anal fin with II spines and 7 soft rays, second anal spine moderately long, 25 to 33.5% of head length; caudal fin rhomboidal. Scales on head cycloid (smooth), those on body ctenoid (rough to the touch); small scales present on soft parts of dorsal and anal fins; lateral line scales reaching tip of caudal fin. Swimbladder hammer-shaped, with 15 pairs of arborescent appendages along its sides, the first pair entering head beyond transverse septum and sending a palmate branch to the front of the pectoral arch. Sagitta with a tadpole-shaped impression, the head of which has its long axis lying obliquely to that of the sagitta and the tail expanded and deepened as a hollow cone connected with the head by a narrow groove.

Color. Head and body dusky mauve above, silver-white below; two dusky streaks usually present along the mid-sides; fins pale yellow or cream, outer two-thirds of spinous dorsal fin black, sometimes a dusky streak along the soft dorsal fin.

Distribution. Indo-West Pacific, west to the Persian Gulf, east to southern China, Taiwan, northern and northeastern Australia, and New Guinea.

Remarks. *Johnius borneensis* can be distinguished from similar sympatric congener, *J. (Johnieops), J. distinctus*, by the absence of a white lateral line streak and the lack of a black lateral line streak at the dorsal spine area. *Johnius borneensis* is a common species. It was collected at several sites off the Miaoli and Yunlin counties, Taiwan.

***Johnius distinctus* (Tanaka, 1916)**

(Figure 5D; Table 6)

Synonyms:

Johnius distinctus (Tanaka, 1916): Sasaki and Amaoka [44]; 466–468; Shao and Chen [34]: 246; Shen and Wu [35]: 487; Shao [36]: 148; Chen et al. [37]: 218; Koeda and Ho [38]: 897; Shao [39].

Johnius carutta (not of Bloch, 1793): Shen [33]: 70, Figure 331-3.
Johnius tingi: Yu and Shen [12]: 98, Figure 24; Shen [13]:378, pl. 110–6.
Wak tingi: Shen [33]: 70, Figure 331–8.

Material examined. *Non-types*: ASIZP0055023 (3, 180.35–241.38 mm SL), Wanli, Taipei, Taiwan, 13 January 1978; ASIZP0063557 (2, 170.48–171.81 mm SL), Mauli, Taiwan, 12 February 2002; ASIZP0058871 (150.74 mm SL), Wanggong, Changhua, Taiwan, 26 March 1990; ASIZP0065793 (166.82 mm SL), ASIZP0065801 (158.95 mm SL), ASIZP0065819 (150.63 mm SL), ASIZP0066151 (163.32 mm SL), Wuchi, Taichung, Taiwan, 29 April 2005; ASIZP0058706 (135.08 mm SL), Wuchi, Taichung, Taiwan, 1 May 1990; ASIZP0078345 (2, 157.7–176.55 mm SL), Taipei market, Taiwan, 29 April 2005; ASIZP0060957 (3, 173.89–178.3 mm SL), Jinshan, Taipei, Taiwan, 23 October 2000; NMMB-P37069 (10, 87.27 to 176.5 mm SL), Budai, Chiayi, Taiwan, 17 March 2019; NMMB-P24848 (4, 97.02 to 111.7 mm SL), Donggang, Pingtung, Taiwan, 9 August 2016; NMMB-P11022 (3, 140.3 to 153.28 mm SL), Daxi, Yilan, Taiwan, 6 September 2010; NMMB-P4628 (2, 161.86 to 178.7 mm SL), Taichung, Taiwan, 18 January 1962; NMMB-P19035 (46.33 mm SL), NMMB-P17664 (211.97 mm SL), Hengchun, Pingtung, Taiwan, 13 September 2010; NMMB-P24923 (12, 147.1 to 174.88 mm SL), Miaoli, Taiwan, 24 March 2016; NMMB-P11018 (2, 176.52 to 186.1 mm SL), Hengchun, Pingtung, Taiwan, 5 September 2010; NMMB-P30122 (181.28 mm SL), Donggang, Pingtung, Taiwan, 5 May 2010; NMMB-P23061 (162.82 mm SL), Mailiao, Yunlin, Taiwan, 15 December 2012; NMMB-P31315 (172.45 mm SL), Jiangjun, Tainan, Taiwan, 13 March 2013; NMMB-P30108 (173.8 mm SL), NMMB-P28432 (9, 169.58 to 197.52 mm SL), NMMB-P27220 (9, 84.62 to 184.61 mm SL), Zhunan, Miaoli, Taiwan, 12 January 2015; NMMB-P4627 (202.37 mm SL), Penghu, Taiwan, 28 January 1961; NMMB-P24924 (4, 138.42 to 181.28 mm SL), Miaoli, Taiwan, 14 May 2016; NMMB-P27213 (5, 141.65 to 161 mm SL), NMMB-P24922 (14, 112.31 to 174.85 mm SL), Miaoli, Taiwan, 30 January 2016; NMMB-P15206 (6, 1148.72 to 164.7 mm SL), Penghu, Taiwan, 9 March 2010; NMMB-P24922 (14, 112.31 to 174.85 mm SL), Miaoli, Taiwan, 30 January 2016; NMMB-P27218 (6, 124.83 to 189.86 mm SL), Howan, Pingtung, Taiwan, 15 December 2014; NMMB-P28294 (7, 153.76 to 164.92 mm SL), Tongkang, Pingtung, Taiwan, 16 March 2010; NMMB-P27243 (17, 113.18 to 115.32 mm SL), Kezailiao, Kaohsiung, Taiwan, 5 November 2017; NMMB-P27230 (4, 168.7 to 190.91 mm SL), Chingshan, Tainan, Taiwan, 16 September 2017; NMMB-P27182 (139.63 mm SL), NMMB-P27183 (155.76 mm SL), NMMB-P23060 (147.13 mm SL), Jiangjun, Tainan, Taiwan, 28 August 2014; NMMB-P25869 (2, 128.01 to 142.662 mm SL), Hengchun, Pingtung, Taiwan, 9 April 2017; NMMB-P32008 (2, 163.76 to 158.9 mm SL), Zhunan, Miaoli, Taiwan, 22 March 2019; NMMB-P22480 (2, 153.50 to 153.73 mm SL), Miaoli, Taiwan, 12 November 2016; NMMB-P11022 (3, 140.3 to 150.71 mm SL), Daxi, Yilan, Taiwan, 6 September 2010; NMMB-P24848 (107.07 mm SL), Donggang, Pingtung, Taiwan, 9 August 2016; NMMB-P21559 (4, 99.79 to 120.9 mm SL), Matsu, Taiwan, 10–11 November 2013; NMMB-P30115 (130.55 mm SL), Budai, Chiayi, Taiwan, 26 August 2017; NMMB-P30125 (126.37 mm SL), Taiwan, 7 November 2015.

Diagnosis. Snout steep, obtusely rounded, not projecting in front of upper jaw; mouth large, oblique; gill rakers short, spinulose, somewhat club-shaped, less than 1/2 length of gill filaments at angle of arch, 11 to 13 on lower limb of first gill arch; scales moderately large, five to six scale rows above lateral line.

Description. A medium-sized species with a deep body. Eye moderately large, 21.1 to 25.8% of head length. Snout pointed, but not swollen or projecting; mouth large, oblique; upper jaw extending backward below posterior half of eye; no barbel on chin; teeth in narrow bands, well differentiated into large and small in both jaws, but not canine-like; the large ones widely spaced, forming outer series in upper jaw, inner series in lower jaw. Gill rakers slender, less than 1/2 length of gill filaments at angle of arch, 11 to 13 on lower limb of first gill arch. Dorsal fin with X spines, followed by a notch, second part of fin with I spine and 28 to 29 soft rays; anal fin with II spines and 7 soft rays, second anal spine moderately long, 26.4 to 31.1% of head length; caudal fin rhomboidal. Scales on head cycloid (smooth), those on body ctenoid (rough to the touch); small scales present on soft parts of dorsal and anal fins; lateral line scales reaching tip of caudal fin. Anterior part of

swimbladder hammer-shaped, with 15 pairs of arborescent appendages along its sides, the first pair entering the head beyond the transverse septum and sending a palmate branch to the front of the pectoral arch. Sagitta with a tadpole-shaped impression, the head of which has its long axis lying obliquely to that of the sagitta and the tail expanded and deepened as a hollow cone connected with the head by a narrow groove.

Color in preservative (holotype greatly faded). Body dark gray on back and flank, creamy white below; lateral line pale along its length except on the caudal fin, conspicuous in dark gray flank. Mouth lining pale except for gray-speckled palate; operculum black owing to blackish branchial cavity; peritoneum black. Upper 1/3 and base of spinous dorsal black, upper margin and base of soft dorsal black; pectoral fin gray; pelvic fin pale; anal fin sprinkled with a few melanophores; caudal fin gray.

Distribution. Distributed in the Northwest Pacific region, including the coast of China, Taiwan, South Korea, and Japan. In Taiwan, it is distributed along the western and northern coasts.

Remarks. *Johnius distinctus* can be distinguished from a similar congener, *J.* (*Johnieops*), *J. borneensis*, by the presence of a white lateral line streak and a black lateral line streak at the dorsal spine area. *Johnius distinctus* is an abundant species. It was collected at several sites in off the Miaoli, Hsinchu, Yunlin, and Chiayi counties, Taiwan.

***Johnius grypotus* (Richardson, 1846)**

(Figure 6A; Table 6)

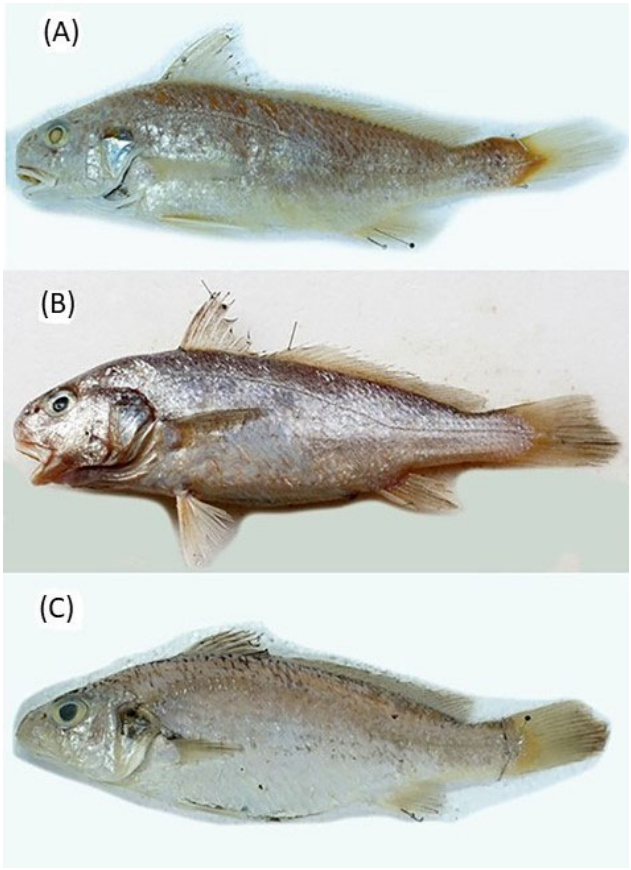

Figure 6. Photographs of Johnius species here described, with specimens deposited in the Taiwan National Museum Marine Biology and Aquarium (NMMBA). (**A**) *Johnius grypotus* NMMB-P23015, 140.22 mm SL; (**B**) *Johnius taiwanensis* NMMB-P37073, 122.62 mm SL; and (**C**) *Johnius trewavasae* NMMB-P37071, 117.42 mm SL. *Diagnosis*. Steep snout, obtusely rounded; mouth inferior; gill rakers slender, long, more than 1/2 length of gill filaments at angle of arch, 11 to 12 on lower limb of first gill arch; caudal fin pointed; scales very deciduous, scales small, 5 to 6 scale rows above lateral line.

Synonyms:

Johnius grypotus: Sasaki [46]: 224, CAS 30322, 101.9, Taiwan, northwest to northeast of Keelung, 8–9 May 1972.

Johnius macrorhynus (not sensu Mohan, 1976): Yu and Shen, [12]: 93, Figure 21.

Material examined. *Non-types*: NMMB-P23015, (8, 93.22 to 132.71 mm SL), Shangdong Coast, Yellow Sea, China, 22 October 2015.

Description. Small-sized species with moderately deep body; body depth 26.8 to 29.4% of standard length. Eye large, 21.9 to 26.4% of head length. Interorbital width 27.3 to 30.1% of head length. Snout steep, obtusely rounded, slightly projecting in front of upper jaw; mouth small, inferior; upper jaw extending backward below middle of eye; no barbel on chin; teeth differentiated into large and small in upper jaw only, lower jaw with a band of villiform teeth. Gill rakers long, more than 1/2 length of gill filaments at angle of arch, 11 to 12 on lower limb of first gill arch. Dorsal fin with X spines, followed by a notch, second part of fin with I spine and 24 to 26 soft rays; anal fin with II spines and 7 to 8 soft rays, second spine long, stiff, 29.8 to 37.4% of head length; caudal fin pointed. Scales moderately large, 5 to 6 scale rows above lateral line to origin of dorsal fin, 9 to 12 scale rows below lateral line to origin of anal fin; scales cycloid on snout, ctenoid on other parts of head and body; small scales present on soft parts of dorsal and anal fins; lateral line scales reaching tip of caudal fin. Swimbladder hammer-shaped, with 15 pairs of arborescent appendages along its sides, first pair entering head beyond transverse septum and sending a palmate branch to front of the pectoral arch. Sagitta with tadpole-shaped impression, with long axis of head lying obliquely to that of the sagitta and tail expanded and deepened as hollow cone, connected with head by narrow groove.

Color when fresh. Head and body silvery, slightly grayish dorsally, whitish ventrally, with brilliant iridescent shine. Pectoral, pelvic, and anal fins tinged yellow.

Color in preservatives. Grayish-brown above, whitish below. Mouth lining pale except for gray-speckled palate. Branchial cavity and peritoneum varying from lightly mottled to black. Pectoral axil lightly mottled. Spinous dorsal blackish distally, soft dorsal mottled gray; pectoral and pelvic fins pale; anal fin spotted with few melanophores; caudal fin gray.

Distribution. *Johnius grypotus* is distributed along the coast of China and Taiwan, from the Gulf of Pohai to Hainan, and it is a common species of *J.* (*Johnius*) in Chinese waters.

Remarks. Johnius grypotus is morphologically similar to *J. coitor* (Hamilton, 1822) and *J. carouna* (Cuvier, 1830) in having ctenoid scales, more than 10 lower gill rakers, and lacking chin barbel. However, it differs from the above in having usually eight anal soft rays (vs. seven; Trewavas [10]; Lal Mohan et al. [37]; Sasaki [45]). Moreover, *J. grypotus* differs from *J. coitor* in its less pointed snout, larger eye (vs. 5.6–6.9% SL, 18.9–23.5% SL; Sasaki [45]), and wider interorbital space (vs. 6.4–7.6% SL, 22.1–26.1% HL); from *J. carouna* in its greater number of transverse scales (vs. 5/1/9–12; Lal Mohan et al. [37]). Based on Yu and Shen [12] and Sasaki [45], the type location of *J. grypotus* is Keelung, in the northern part of Taiwan, and it has not been reported further south. This fish apparently prefers colder water.

***Johnius taiwanensis* Chao, Chang, Chen, Guo, Lin, Liou, Shen and Liu, 2019**

(Figure 6B; Table 6)

Synonyms:

Johnius taiwanensis Chao et al. [5]; Chen et al. [37]: 219; Koeda and Ho, [38]: 898, NMMBP-24335; Shao [36].

Johnius borneensis (not sensu Bleeker, 1850): Koeda and Ho [38]: 896, KAUM-I, 125005–125006.

Johnius grypotus (not sensu Sasaki, 1990): Shen and Wu [35]: 487; Shao [36]: 150.

Johnius macrorhynus (not sensu Mohan, 1976): Shao [33]: 150.

Material examined. Types: Holotype: NMMBP 23063 (126 mm SL), Jiangjun Port, Tainan, Taiwan, 19 June 2014. Paratypes: NMMBP 8464 (118 mm SL), Wuqi Harbor, Taichung, 6 May 2005; NMMBP 19365 (3, 133 to 160 mm SL), Wenzai Port, Zhanghua, 14 March 2013; NMMBP 19373 (9, 115 to 162 mm SL), Taizi, Yunlin, 13 March 2013; NMMBP 23065 (2,

128 to 134 mm SL), Mailiao, Zhoushui River, Yunlin, 12 September 2014; NMMBP 23067 (135 mm SL), Jiangjun Port, Tainan, 19 June 2014; NMMBP 23070 (88 mm SL), Mailiao, Zhoushui River, Yunlin, 27 May 2014; NMMBP 23580 (170 mm SL), Matzu, 8 August 2016; NMMBP 24335 (99 mm SL), Kezai Liao Port, Kaohsiung, 13 July 2016; NMMBP 24925 (2, 116 to 133 mmm SL), Mailiao, Zhoushui River, Yunlin, 24 March 2016; NMMBP 25882 (3, 110 to 130 mm SL), Jiangjun Port, Tainan, 19 June 2014; NMMBP 27962, (2, 117 to 126 mm SL), Budai Port, Chiayi, 18 September 2017; NMMBP 31330 (3, 153 to 164 mm SL), Zhubei Harbor, Miaoli, 22 March 2019; NMMBP 31331 (111 mm SL), Zhuwei Port, Taoyuan, 15 March 2019.

Non-types: ASIZP0058728 (126.15 mm SL), Fangyuan, Changhua, Taiwan, 26 July 1989; ASIZP0065780 (163.22 mm SL), Wuchi, Taichung, Taiwan, 29 April 2005; ASIZP0071045 (143.56 mm SL), ASIZP0071070 (169.34 mm SL), Matsu, Taiwan, 29 February 2008; ASIZP0060520 (6, 132.42–166.26 mm SL), Nangan Island, Matsu, Taiwan, 16 March 2003;NMMB-P37073 (6, 122.62 to 132.23 mm SL), Yunlin, Taiwan, 7 March 2019; NMMB-P37074 (6, 119.18 to 131.37 mm SL), Miaoli, Taiwan, 18 June 2019; NMMB-P25881 (3, 120.81 to 134.88 mm SL), Bozihliao, Yunlin, Taiwan, 31 July 2014; NMMB-P19368 (2, 125.55 to 144.36 mm SL), Changhua, Taiwan, 14 March 2013; NMMB-P23066 (4, 68.35 to 129.71 mm SL), Yunlin, Taiwan, 21 August 2012; NMMB-P30110 (8, 112.36 to 154.42 mm SL), NMMB-P27228 (2, 139 to 144.29 mm SL), Budai, Chiayi, Taiwan, 26 August 2017; NMMB-P27222 (26, 131.29 to 141.97 mm SL), NMMB-P27202 (163.76 mm SL), Budai, Chiayi, Taiwan, 23 September 2017; NMMB-P27227 (4, 137.77 to 153.76 mm SL), NMMB-P27202 (163.76 mm SL), NMMB-P27961 (2, 145.06–138.77 mm SL), Dongshi, Chiayi, Taiwan, 16 September 2017; NMMB-P23064 (4, 115.54 to 135.63 mm SL), NMMB-P23068 (7, 86.95 to 137.77 mm SL), NMMB-P23069 (121.3 mm SL), Xinhuwei River, Yunlin, Taiwan, 15 December 2017; NMMB-P19374 (3, 125.53 to 144.8 mm SL), Jiangjun, Tainan, Taiwan, 13 March 2013; NMMB-P23016 (4, 131.3 to 138.8 mm SL), Bozihliao, Yunlin, Taiwan, 14 March 2013; NMMB-P35085 (160.11 mm SL), Taichung, Taiwan, 11 August 2019; NMMB-P30106 (153.76 mm SL), Zhunan, Miaoli, Taiwan, 30 January 2016; NMMB-P33380 (156.77 mm SL), Donggang, Pingtung, Taiwan, 19 November 2018; NMMB-P4377 (2, 127.47 to 137.94 mm SL), Taichung, Taiwan, 22 June 1991; NMMB-P23071 (130.76 mm SL), Yunlin, Taiwan, 21 August 2012; NMMB-P27203 (140.31 mm SL), Anping, Tainan, Taiwan, 19 November 2018; NMMB-P27185 (36.61 mm SL), NMMB-P28310 (5, 71.34 to 90.57 mm SL), Zhuoshui River, Yunlin, Taiwan, 4 December 2013; NMMB-P25866 (99.2 mm SL), Changhua, Taiwan, 16 February 2017.

Diagnosis. Snout pointed, bluntly rounded; scales firmly attached, coarsely ctenoid on body (including throat), scales above lateral line 5–6, below lateral line 9–10; gill rakers long, slender, gill rakers 5–7 +1 + 10–12; caudal fin pointed; body mostly grayish-silver, upper two-thirds of body darker and separated from whitish to yellowish belly; pelvic fin pale.

Description. A medium-sized species with a moderately elongated body. Eye moderately large, 20 to 23% of head length. Snout steep, obtusely rounded, slightly projecting in front of upper jaw; mouth small, inferior; upper jaw extending backward below middle of eye; no barbel on chin; teeth differentiated into large and small in upper jaw only, the large ones close-set, not canine-like, forming outer series; lower jaw with a band of villiform teeth. Gill rakers short, slender, less than 1/2 length of gill filaments at angle of arch, 10 to 12 on lower limb of first gill arch. Dorsal fin with IX or X (most frequently X) spines, followed by a notch, second part of fin with I spine and 24 to 28 soft rays; anal fin with II spines and 7 soft rays, second spine long, stiff, about 31% of head length; caudal fin rhomboidal. Scales moderately large, 5 to 6 scale rows above lateral line to origin of dorsal fin, 9 to 10 scale rows below lateral line to origin of anal fin; scales cycloid (smooth to the touch) on snout, strongly ctenoid (very rough to the touch) on other parts of head and body; small scales present on soft parts of dorsal and anal fins; lateral line scales reaching tip of caudal fin. Swimbladder hammer-shaped, with 14 to 15 pairs of arborescent appendages along its sides, the first pair entering head beyond transverse septum and sending a palmate branch to the front of the pectoral arch. Sagitta with a tadpole-shaped

impression, the head of which has its long axis lying obliquely to that of the sagitta and the tail expanded and deepened as a hollow cone, connected with the head by a narrow groove. Twenty-five vertebrae.

Color. Mostly grayish-silver, upper two-thirds of body darker and separated from whitish to yellowish belly by a distinct line; spinous part of dorsal fin black, lower fins in many cases also black; triangular dark patch showing through gill cover.

Distribution. *Johnius taiwanensis* is a shallow coastal species commonly found along both sides of the Taiwan Strait, the west coast of Taiwan from Taoyuan to Kaohsiung, and the southeast coast of mainland China from Zhoushan Islands of Zhejiang, to Fujian, Guangdong, and Hong Kong.

Remarks. *Johnius taiwanensis* differs from other species of the subgenus *J.* (*Johnius*), with *J. belangerii* having smaller scales, with seven to eight scale rows above the lateral line. *J. trewavasae* has larger scales in five to six rows. *Johnius grypotus* has a longer second anal fin spine, being longer than 30% of the head length (less than 30% in *J. taiwanensis*). *Johnius trewavasae* also has a silvery-gray back and whitish belly, but the head is strongly cavernous and soft, and the scales on the body fall off easily. In contrast, *J. taiwanensis* has a cavernous but firm head and firmly attached scales. *Johnius trewavasae* also has very short, tubercle-like gill rakers that differ from those in *J. taiwanensis*.

***Johnius trewavasae* Sasaki, 1992**

(Figure 6C; Table 6)

Johnius macrorhynus (not sensu Mohan, 1976): Shen [13]: 378, pl. 110–4; Shao and Chen [34]: 246; Shen and Wu [35]: 488; Shao [39].

Johnius taiwanensis (not sensu Chao et al., 2019): Koeda and Ho, [38]: 898, NMMBP-30661.

Material examined. *Non-types*: ASIZP0073600 (142.93 mm SL), Wanggong, Changhua, Taiwan, 9 July 2013; ASIZP0065818 (157.90 mm SL), Wuchi, Taichung, Taiwan, 29 April 2005; NMMB-P37070 (13, 103.56 to 142.04 mm SL), Miaoli, Taiwan, 18 June 2019; NMMB-P37071 (14, 117.42 to 142.03 mm SL), Miaoli, Taiwan, 21 August 2019; NMMB-P37072 (5, 137.46–142.92 mm SL), Miaoli, Taiwan, 30 June 2019; NMMB-P24256 (124.40 mm SL), Dajia River, Taipei, Taiwan, 10 June 1986; NMMB-P30661 (105.79 mm SL), Kezailiao, Kaohsiung, Taiwan, 25 October 2018; NMMB-P23062 (87.06 mm SL), Yunlin, Taiwan, 21 August 2012; NMMB-P28295 (4, 135.95 to 146.37 mm SL), Tongkang, Pingtung, Taiwan, 17 March 2010; NMMB-P25865 (5, 141.61 to 145.12 mm SL), Hengchun, Pingtung, Taiwan, 9 April 2017; NMMB-P11014 (4, 129.93 to 153.76 mm SL), Hengchun, Pingtung, Taiwan, 4 September 2010; NMMB-P11021 (2, 137.9 to 153.76 mm SL), Hengchun, Pingtung, Taiwan, 5 September 2010; NMMB-P8485 (3, 96.5 to 126.23 mm SL), NMMB-P8476 (2, 102.81 to 139.70 mm SL), Wuqi, Taichung, Taiwan, 5 May 2005; NMMB-P19367 (143.76 mm SL), Yunlin, Taiwan, 14 March 2013; NMMB-P19371 (2, 131.04 to 151.01 mm SL), Nanliao, Kaohsiung, Taiwan, 14 March 2013; NMMB-P22570 (111.83 mm SL), Anping, Tainan, Taiwan, 1 April 2019; NMMB-P19370 (127.99 mm SL), Changhua, Taiwan, 14 March 2013; NMMB-P19693 (96.07 mm SL), Daxi, Yilan, Taiwan, 25 February 2013; NMMB-P1017 (118.48 mm SL), Tainan, Taiwan, 31 July 1997; NMMB-P32431 (4, 124.36 to 133.89 mm SL), Xingda, Kaohsiung, Taiwan, 3 April 2011.

Diagnosis. Snout steep, obtusely rounded; chin lacking barbel; scales above lateral line 5–6, below lateral line 7–10; gill rakers very short, obtuse, gill rakers 4–5 + 1 + 6–8; second anal spine length 7.6–11.3% SL (25.0–37.0% HL); scales on body large, easily fallout, ctenoid.

Description. Small species with a moderately elongated body; body depth 24 to 30% of standard length. Eye moderately large, 22 to 27% of head length. Interorbital width 22 to 24% of head length. Snout steep, obtusely rounded, projecting slightly in front of upper jaw; mouth small, inferior; upper jaw extending backward below front margin of pupil; no barbel on chin; teeth differentiated into large and small in upper jaw only, the large ones close-set, not canine like, forming outer series; lower jaw with a band of villiform teeth. Gill rakers short, obtuse, about 1/5 length of gill filaments at angle of arch, 6 to 8 on lower limb of first gill arch. Dorsal fin with X to XI (most frequently X) spines, followed by a notch, second part of fin with I spine and 24 to 27 soft rays; anal fin with II spines

and 7 or 8 (most frequently 7) soft rays, second spine rather short, slender, 25 to 37% of head length; caudal fin rhomboidal. Scales large, those on flanks much larger than those on the lateral line, 5 or 6 scale rows above lateral line to origin of dorsal fin, 7 to 10 scale rows below lateral line to origin of anal fin; scales cycloid (smooth) on head and throat, ctenoid (rough to the touch) on other parts of head and body; small scales present on soft parts of dorsal and anal fins; lateral line scales reaching tip of caudal fin. Swimbladder hammer-shaped, with about 14 pairs of arborescent appendages along its sides, the first pair entering head beyond transverse septum and sending a palmate branch to front of the pectoral arch. Sagitta with a tadpole-shaped impression, with long axis of its head lying obliquely to that of the sagitta and tail expanded and deepened as hollow cone connected with the head by a narrow groove. Twenty-five vertebrae.

Color. Dark mottled pattern dorsally, creamy white ventrally; scale pockets on dorsal side of head and body with broad, dark margins; spinous dorsal fin black, pectoral fins gray, pelvic fins pale.

Distribution. Singapore, north of Taiwan, Hong Kong, and Shanghai.

Remarks. Johnius trewavasae and *J. heterolepis* are both characterized by large scales, resulting in low counts for scales above and below the lateral line (5–6 and 7–10 in *J. trewavasae*, 5 and 9–10 in *J. heterolepis*). Among the 10 *J.* (*Johnius*) species with ctenoid scales (5–6 scales above lateral line, 9–12 below), *J. trewavasae* is differentiated from *J. hypostoma* and *J. laevis* by the low number of dorsal soft rays in the latter two (24–27 in *J. trewavasae* vs. 31–33 in *J. hypostoma*, 29–34 in *J. laevis*). Although the soft dorsal soft ray number in *J. carouna* (27–29) overlaps that of *J. trewavasae*, the former differs in having a strong second anal spine (11.7–14.2% SL vs. 9.6–11.3% SL in *J. trewavasae*). *Johnius carouna* differs from *J. trewavasae* in having the last pleural rib on the 10th vertebra (vs. 11th in *J. trewavasae*) and a greater number of lower gills rakers (10–14 vs. 6–8, respectively). *Johnius trewavasae* is itself distinguishable from *J. heterolepis* in having 6–8 obtuse lower gill rakers (vs. 9–11 slender ones in *J. heterolepis*) and a shorter lower jaw (33.8–38.4% HL vs. 40.3–44.2, respectively).

Key to the Species of Johnius Occurring in Taiwan Waters

1a. Chin with barbel..... *J. amblycephalus*
1b. Chin without barbel..... 2
2a. Inner row of lower jaw teeth enlarged..... 3
2b. Inner row of lower jaw teeth uniform in size..... 4
3a. Lateral line with distinct white streak; spinous dorsal fin with distinct black blotch on upper 1/3..... *J. distinctus*
3b. Lateral line without white streak; spinous dorsal fins are often dark-tipped or grayish ..... *J. borneensis*
4a. Scales small, seven to eight scale rows above lateral line from dorsal fin origin; lower fins often dark gray to black..... *J. belangerii*
4b. Scales large, five to six scale rows above lateral line from origin dorsal fin..... 5
5a. Caudal fin pointed; gill rakers slender, comprising more than 40% of gill filaments; prepelvic to the isthmus region ctenoid scaled, rarely cycloid scales..... ..... *J. grypotus*
5b. Caudal fin rhomboidal; gill rakers short, comprising less than 40% of gill filaments; prepelvic to the isthmus region ctenoid scaled, gradually turning cycloid scales..... 6
6a. Gill rakers very short, 6.3−7.9% of eye diameter; outer gill rakers of first arch 12−13 ..... *J. trewavasae*
6b. Gill rakers short, 7.9−13.0% of eye diameter; outer gill rakers of first arch 14−15..... ..... *J. taiwanensis*

5. Discussion

This study integrated the results of both morphological and molecular approaches, confirming seven valid species of *Johnius* in Taiwan waters. Furthermore, all *Johnius* specimens are morphologically and genetically identical and constitute a single phylogenetic cluster, supporting the conclusion that all specimens studied are monophyletic. In the basal group clade (*J. amblycephalus*, *J. borneensis*, and *J. distinctus*), our findings are consistent with those of Lo et al. [6], except in that the phylogenetic position of *J. grypotus*, *J. taiwanensis*, *J. belangerii*, and *J. trewavasae* differs. These variations might be attributed to various sample locations and species encountered; with more *Johnius* sequences available from the NCBI database, Lo et al. [6]'s results on the *Johnius* relationship remain equivocal in numerous taxa. Lin et al. [47] recently produced the full genome and phylogenetic position of *J. taiwanensis*, which in Chinese waters is a sister clade to *J. trewavasae*; the two are then sister clades to *J. belangerii*. This might be owing to the absence of *J. carouna* in Taiwanese waters, which has resulted in a distinct phylogenetic tree in this zoogeography zone.

The morphological traits of *Johnius* differ across species, for example, in the gill rakers and mouth structure. This might be due to ecophenotypic variables that alter gill rakers, jaw length, and anal spine length in sympatric species to compete for coastal habitat. Comparable research on the genus *Cynoscion* by Aguirre and Shervette [48] supports our hypothesis that function-related morphological divergences might be correlated with ecological niches. A similar concept was also demonstrated with other fishes [49,50]. A similar hypothesis was tested for populations of the Asian cyprinid *Lobocheilos rhabdoura*. In this species, specimens inhabiting fast-flowing sections of streams had more slender bodies compared to specimens inhabiting slow-moving habitats [51]. Therefore, ecophenotypic forces may have a significant effect on shaping competing organisms to adjust to each respective ecosystem.

J. macrorhynus does not occur in Taiwanese waters, although it has been recorded there (Table 3). *J. grypotus* and *J. trewavasae* are sometimes mistaken for *J. macrorhynus*. They are found across Taiwan; however, since they are morphologically similar, they are often misconstrued or treated as a complex species. This prompted Sasaki [46] and Sasaki [41] to describe *J. grypotus* and *J. trewavasae* as new species. Later, Chao et al. [5] updated dubious records of "*J. macrorhynus*" [14] from Taiwan, compared this material to other *Johnius* species, and determined *J. taiwanensis* to be a valid species. More than half of the Taiwanese references referring to "*J. macrorhynus*" were corrected, demonstrating that over 70% were misdiagnosed as *J. taiwanensis* [15], with the remaining misidentified as *J. grypotus* [12] and *J. trewavasae* [13,34,35,39]. Parenti [52] also discussed the taxonomic status of *J. sina* (Cuvier, 1830), which is often referenced in the Taiwanese literature, either as *J. sina* or as a synonym of *J. dussumieri*. Another detailed revision by Sasaki [43] on both holotype specimens revealed that *J. sina* is a junior synonym of *J. dussumieri* (see Sasaki [42]: 274; [43]: 92). Thus, neither the record of *J. macrorhynus* nor *J. dussumieri* in Taiwanese references is valid.

Johnius species are mostly found in Taiwan's central and western waterways. The Changyun Rise (CYR) (Figure 1) separates *Johnius* assemblages geographically by creating a shallow euphotic environment (approximately 60 m) with high levels of primary production [53]. Most *Johnius* species need shallow tropical and subtropical coastal waters (200 m) and are often represented by small- to medium-sized fishes with a tiny mouth that is sub-terminal to inferiorly positioned [2]. *J. taiwanensis*, for example, lives in southeast China's shallow coastal waters, on both sides of the Taiwan Strait, on the east sides of Zhejiang, Fujian, Guangdong, and Hong Kong, and on the western side of Taiwan [2,5]. Chen [54] supports this conclusion by revealing that the species composition in Miaoli separates fishing areas using the set net technique, naming *J. distinctus* as a sandplain resident and seasonal species with peak abundance between October and February. Liou [16] discovered that *J. amblycephalus* is primarily taken in the summer after analyzing trawl catches and surveying markets near the Yunlin coast. This study further reported this species to be associated with estuaries along the western coast of Taiwan. While these data

do not demonstrate a substantial difference in seasonal migratory patterns across locations, they did provide early insight into seasonal distribution patterns among *Johnius* species in Taiwan waters.

6. Conclusions

Morphology, molecular biology, and a literature assessment verified that seven valid *Johnius* species occur in Taiwanese waters. We considerably improved the identification of these species by redescribing them in detail and providing a dichotomous key. COI gene sequence data from the NCBI database, as well as museum vouchers, offer a strong foundation for future research. This information will be useful for ecological surveys and fishery management. Our extensive sample strategy provided us with further information on the distribution of local *Johnius* species. *Johnius* assemblages were mainly present in the central-western part of Taiwan waters. Sympatric occurrence may have resulted in speciation via competition, which may be represented in observable morphological variety, such as mouth shape and dentition. According to our phylogenetic analysis, *J. amblycephalus* is the most basal local species, while *J. belangerii*/*J. trewavasae* is the most derived.

Author Contributions: N.H., M.-H.C., Y.G.S., C.-W.C., S.Y.V.L., C.-C.L. and N.L.C. collected the specimens and N.H. performed the molecular analysis and morphometrics examinations. N.H. further produced and analyzed the data and wrote the initial drafts of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work was funded by the MOST 110-2621-M-110-001, MOST 111-2611-M-110-006, and MOST 111-2621-M-110-002 to M.-H.C.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: This article was written in part to fulfill the Ph.D. degree requirements of the first author at the National Sun Yat-sen University (NSYSU), which provided the funding for this study. We would like to thank the Global Sciaenidae Conservation Network, NMMBA, and IUCN SSC Croaker and Drum Fishes Red List Authority, which made this collaborative study possible. We gratefully acknowledge the assistance of Kwang-Tsao Shao and Shih-Pin Huang from the Biodiversity Research Center, Academia Sinica, who provided us with the distributional data and specimens from Taiwan coastal waters. We further thank fish collection manager and curator Hsuan-Ching Ho of the National Museum of Marine Biology and Aquarium for curatorial and facility support.

Conflicts of Interest: The authors declare that they have no competing interest.

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