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Taxonomic review of the genus *Johnius* (Perciformes: Sciaenidae) from East Malaysian waters, with comments on newly recorded *Johnius* species

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Abstract

In terms of sheer abundance, taxonomic diversity, and species richness, Malaysia has one of the most diverse Sciaenidae in the Indo-West Pacific. Up to ten valid species of the sciaenid fish genus *Johnius* (e.g., *J. amblycephalus* (Bleeker, 1855), *J. belangerii* (Cuvier, 1830), *J. borneensis* (Bleeker, 1850), *J. carouna* (Cuvier, 1830), *J. coitor* (Hamilton, 1822), *J. heterolepis* Bleeker, 1873, *J. macrorhynus* (Lal Mohan, 1976), *J. plagiostoma* (Bleeker, 1849), *J. sasakii* Hanafi *et al.*, 2022 and *J. weberi* Hardenberg, 1936), and with additional newly recorded species as *J. trewavasae* Sasaki, 1992, have been recorded to occur in East Malaysia (Borneo Island) coastal waters. The newly recorded species is a close congener to *J. heterolepis* Sasaki, 1992 and can be well distinguished by several characters and molecular evidence. The goal of this study is to review the taxonomic status of *Johnius* species in East Malaysia, Borneo Island, by using a literature review, morphological inference and molecular characters. Principal Component Analysis (PCA) successfully discriminates based on second anal spine length and gill raker length within sampled specimens. A phylogenetic tree based on cytochrome oxidase subunit I (COI) showed intraspecific levels of genetic differentiation within *Johnius* of East Malaysia, which forms a monophyletic group. Moreover, the new record of *Johnius trewavasae* in East Malaysia represented that the distribution of the subtropical genus *Johnius* extended to the southernmost part of the tropical region.

Key words: coastal fishes, DNA barcoding, neighbor-joining, new record, *Johnius trewavasae*

Introduction

The genus *Johnius* Bloch (1793) is the most diverse among the Sciaenidae family in the Old World. This family consists of small to medium-sized sciaenid fish native to the region. There are now 33 identified species within this genus (Fricke *et al.*, 2023; Sasaki, 2001; Parenti, 2020). The genus *Johnius*, established by Bloch in 1793 with the type species *Johnius carutta*, as defined by Gill in 1862, has often been used to classify many sciaenid fishes found in the Indo-West Pacific region. In 1977, Trewavas conducted a comprehensive analysis of the naming and alternative terms for the genus *Johnius*. In 1989, Sasaki refined the definition of the genus and the tribe Johniini based on numerous distinct characteristics, one of which is a gas bladder shaped like a hammer with 13–17 tree-like lateral appendages. The first lateral branch extends towards the posterior corner of the gill aperture and becomes

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visible on the supracleithrum bone under the skin. This trait is crucial for identifying taxa within the genus *Johnius* (Iwatsuki *et al.*, 2012; Henriques *et al.*, 2016; Chao *et al.*, 2019). Furthermore, it possesses a distinctive sagittal otolith that is triangular in form and a huge lapilli otolith. *Johnius* species are widely distributed throughout the Indo-West Pacific seas, inhabiting all salinity levels and occupying the continental shelf, particularly on sandy or muddy substrates. Their spawning sites are often found in estuary waters (Mok *et al.*, 2009). Although these coastal fish are often seen and frequently gathered in significant quantities, there is little knowledge of their life history and biology (Chao *et al.*, 2015), especially in the seas of East Malaysia (Borneo Island), where the group's distribution is poorly understood.

Previous work has suggested multiple genera for this particular genus (Fricke *et al.*, 2023), causing significant doubt surrounding the taxonomic classification of similar taxa such as *Johnius* (e.g., *Wak*, *Bola*) (Chu *et al.*, 1963; Mohan, 1972; Trewavas, 1977; Talwar, 1995). The genus *Johnius* comprises ten valid species that are currently recognised in Malaysian waters: *J. amblycephalus* (Bleeker, 1855), *J. belangerii* (Cuvier, 1830), *J. borneensis* (Bleeker, 1850), *J. carouna* (Cuvier, 1830), *J. coitor* (Hamilton, 1822), *J. heterolepis* Bleeker, 1873, *J. macrorhynus* (Mohan, 1976), *J. plagiostoma* (Bleeker, 1850), *J. sasakii* Hanafi *et al.*, 2022, and *J. weberi* Hardenberg, 1936. These species are primarily found in the estuaries and coastal waters of the South China Sea region and are predominantly restricted to Malaysian waters (Trewavas, 1977; Sasaki, 2001; Hanafi *et al.*, 2022). The species *J. amblycephalus*, *J. belangerii*, and *J. carouna* have a wide distribution, ranging from southern Taiwan to Malaysia and extending to the western Persian Gulf. Their distribution appears to align with the warm water of the South China Current. On the other hand, *J. carouna*, *J. coitor*, *J. heterolepis*, *J. macrorhynus*, *J. plagiostoma*, *J. sasakii*, and *J. weberi* are found in the Western Pacific, specifically in the South China Sea, the Strait of Malacca, and the Bay of Bengal (Chu *et al.*, 1963; Trewavas, 1977; Sasaki, 1996; Sasaki, 2001; Fricke *et al.*, 2023). These species seem limited to the warmest waters of the tropical current surrounding the equator region.

The purpose of this research is to address the taxonomic issues that affect this economically significant group of organisms in East Malaysia and the surrounding area of the South China Sea region. This objective will be achieved by providing updated descriptions and voucher specimen references. The economic desirability of these taxa poses a potential threat to their survival since some species are captured in large numbers on a daily basis (Wong & Yong 2020). Therefore, accurate identification is essential. This study provides the first analysis to ascertain the biodiversity of *Johnius* species in the East Malaysian area, with a particular emphasis on Borneo Island.

Hanafi *et al.* (2023) conducted a thorough taxonomic analysis of the genus *Johnius*, specifically focusing on Taiwanese waters. The study was centred on the newly identified *J. taiwanensis* found in that area. Therefore, the comprehensive investigation and analysis of the seas in East Malaysia are of utmost importance. *Johnius sasakii* Hanafi *et al.* 2022, was discovered and characterised in the waters of East Malaysia with the following characteristics to classify it as a new species: (i) a lower count of gill rakers on the lower limb (with a mode of 9); (ii) a shorter length of the second anal fin spine (8–10% of the standard length); and (iii) a slightly greater depth of the body (26–28% of the standard length). This species has often been misidentified as *J. heterolepis*, *J. carouna*, and *J. macrorhynus* for many years (Sasaki, 2001; Hanafi *et al.*, 2022). The discovery of this new species has emphasised the intricate nature of the morphology and nomenclature within the *Johnius* genus, as well as the need for a taxonomic evaluation in the specific location of Borneo Island.

The aim of this study is to reassess and redefine the taxonomic classification of the *Johnius* species. It also seeks to provide a comprehensive description and analysis of each *Johnius* species, as well as revise a classification key for the species found in the waters of East Malaysia and Borneo. This will be achieved through morphological analysis, literature review, and the examination of COI barcoding sequences. In addition, this research presents the geographic distribution of *Johnius* species in the waters of East Malaysia, including the recent documented expansion of *J. trewavasae* in the waters of Sarawak. This extension of distribution will be further examined and addressed in the study.

Methods and Materials

Meristic and morphometric characters were examined. Specimens were collected during February and March 2017 from several fish landing ports in East Malaysia, Borneo, as illustrated in Fig. 1. The samples were identified using genetic markers and by comparing morphological characteristics to voucher specimens stored at Taiwan's

National Museum of Marine Biology and Aquarium (NMMBA). We analysed *Johnius* species specimens from the field and fish collections (Hanafi *et al.*, 2022; 2023). Descriptions and identification keys have also been utilised to cross-reference with all species (Trewavas, 1977; Lal Mohan, 1984; Sasaki, 1992, 1999, 2001; Fricke *et al.*, 2023) .

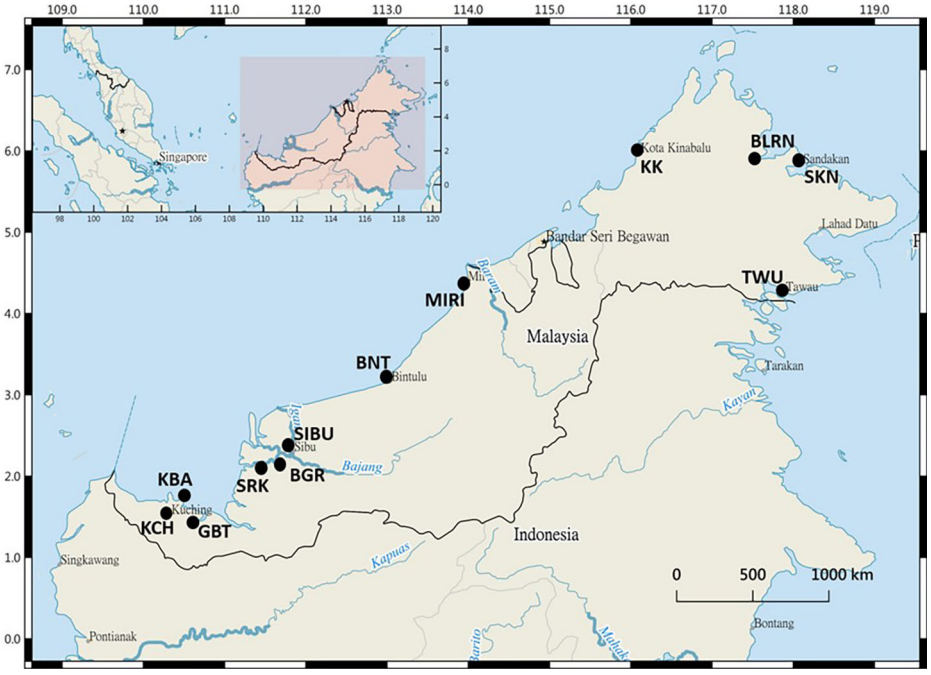

FIGURE 1. Sites of collection samples of *Johnius* species in East Malaysia (Acronym sites: Tawau (TWU); Sandakan (SKN), Beluran (BLRN), Kota Kinabalu (KK), Miri (MIRI), Bintulu (BNT), SIBU (SIBU), Betangor (BGR), Sarikei (SRK), Bako (KBA), Goebilt (GBT) and Kuching (KCH).

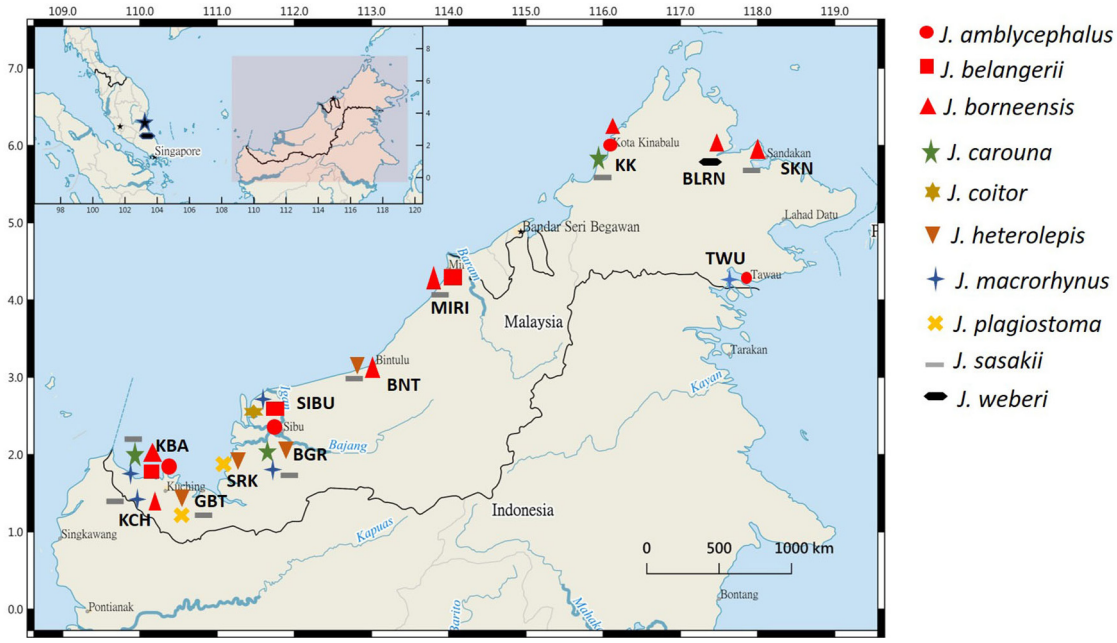

FIGURE 2. Spatial distribution and species composition in sites of collection samples of *Johnius* species in East Malaysia (Acronym sites: Tawau (TWU); Sandakan (SKN), Beluran (BLRN), Kota Kinabalu (KK), Miri (MIRI), Bintulu (BNT), SIBU (SIBU), Betangor (BGR), Sarikei (SRK), Bako (KBA), Goebilt (GBT) and Kuching (KCH).

Morphological data. Following Hanafi *et al.*, 2023, measurements were done using digital calipers and recorded to the closest 0.1 mm. The National Museum of Marine Biology and Aquarium (NMMBA) in Taiwan received 212 voucher specimens (Table 1). Counting and measuring methods were usually based on Hubbs and Lagler (2004), while morphological structure and descriptions for *Johnius* were based on Trewavas (1977), Chao (1978), Chao *et al.* (2019), Sasaki (1989), and Hanafi *et al.* (2022; 2023). The specimen is preserved and photographed according to the procedures outlined by Seah *et al.* (2015). Gill raker counts include primitive rakers on the first right gill arch (Hanafi *et al.*, 2022; 2023).

TABLE 1. Taxa, vouchers, locality and catalogue specimens of the *Johnius* sample collection and museum examination in this study.

No	TAXON	MUSEUM ID	SPECIMEN	LOCALITY	COUNTRY	INDIVIDUAL
1	*Johnius amblycephalus*	34752	SIBU05	Sibu	East Malaysia	1
2	*Johnius amblycephalus*	34754	MIRI08	Miri	East Malaysia	4
3	*Johnius amblycephalus*	34753	KBA06	Bako	East Malaysia	1
4	*Johnius belangerii*	37079	SIBU015	Sibu	East Malaysia	2
5	*Johnius belangerii*	37077	MIRI04	Miri	East Malaysia	5
6	*Johnius belangerii*		KBA02	Bako	East Malaysia	3
7	*Johnius belangerii*	37078		Kota Kinabalu	East Malaysia	4
8	*Johnius borneensis*	37080	SKN06	Sandakan	East Malaysia	2
9	*Johnius borneensis*		BLRN03	Beluran	East Malaysia	1
10	*Johnius borneensis*	37086, 26522	KK05	Kota Kinabalu	East Malaysia	8
11	*Johnius borneensis*	37083		Tawau	East Malaysia	1
12	*Johnius borneensis*	37085	MIRI05	Miri	East Malaysia	8
13	*Johnius borneensis*	37081	BNT20	Bintulu	East Malaysia	1
14	*Johnius borneensis*	37082	KBA03	Bako	East Malaysia	1
15	*Johnius borneensis*	37084	KCH08	Kuching	East Malaysia	2
16	*Johnius carouna*	34742	KK07c,d	Kota Kinabalu	East Malaysia	5
17	*Johnius carouna*	34741	BGR06	Betangor	East Malaysia	7
18	*Johnius carouna*	27643	BKB02	Bako	East Malaysia	10
19	*Johnius carouna*	37088		Tawau	East Malaysia	2
20	*Johnius carouna*	37089		Sandakan	East Malaysia	10
21	*Johnius carouna*	34740		Beluran	East Malaysia	10
22	*Johnius carouna*	34743		Goebilt	East Malaysia	10
23	*Johnius coitor*	37096	SIBU02	Sibu	East Malaysia	3
24	*Johnius coitor*	33374		Sri Aman	East Malaysia	1
25	*Johnius heterolepis*	34748	BNT08	Bintulu	East Malaysia	10
26	*Johnius heterolepis*	34749, 34751	KBA01	Bako	East Malaysia	25
27	*Johnius heterolepis*	37090	SRK05d	Sarikei	East Malaysia	4
28	*Johnius heterolepis*	35556	BGR07,	Betangor,	East Malaysia	6
29	*Johnius heterolepis*	34750	GBT02	Goebilt	East Malaysia	10
30	*Johnius heterolepis*	21541, 21711, 23665, 23656		Pantai Remis	West Malaysia	14
31	*Johnius macrorhynus*	34745	TWU05	Tawau	East Malaysia	7
32	*Johnius macrorhynus*	37091	SIBU06, SIBU013	Sibu	East Malaysia	6
33	*Johnius macrorhynus*	34744	KBA04b	Bako	East Malaysia	1
34	*Johnius macrorhynus*	34747	KCH11	Kuching	East Malaysia	1

.....Continued on the next page

TABLE 1. (Continued)

No	TAXON	MUSEUM ID	SPECIMEN	LOCALITY	COUNTRY	INDIVIDUAL
35	*Johnius macrorhynus*	34746	BGR05	Betangor	East Malaysia	9
36	*Johnius plagiostoma*	37101	GBT01	Goebilt	East Malaysia	10
37	*Johnius plagiostoma*	37100	SRK02	Sarikei	East Malaysia	3
38	*Johnius sasakii*	37092	MIRI03	Miri	East Malaysia	2
39	*Johnius sasakii*	37093		Tawau	East Malaysia	6
40	*Johnius sasakii*	34736, 34737	BNT05	Bintulu	East Malaysia	6
41	*Johnius sasakii*	37095	SKN08	Sandakan	East Malaysia	3
42	*Johnius sasakii*	34734	BGR06	Betangor	East Malaysia	1
43	*Johnius sasakii*	34743	GBT03	Goebilt	East Malaysia	3
44	*Johnius sasakii*	37094	KK07a,f,g	Kota Kinabalu	East Malaysia	10
45	*Johnius sasakii*	34733	KBA05	Bako	East Malaysia	1
46	*Johnius sasakii*		KCH12	Kuching	East Malaysia	1
47	*Johnius trewavasae*	37087		Sarikei	East Malaysia	4
48	*Johnius weberi*		GBT0220	Goebilt	East Malaysia	1
49	*Johnius weberi*	37097	BLRN09	Beluran	East Malaysia	3
50	*Johnius weberi*	37099		Tawau	East Malaysia	2

In the computer system PAST 3.19, a principal component analysis (PCA) was used to examine the log-transformed data in a covariance matrix. Prior to the analysis, the dataset was standardized. The PCA was terminated using the broken-stick model, and the variables were interpreted based on the highest and lowest loading values for the specified axes. The constant values were omitted from the PCA. Bivariate scatterplots were utilized to demonstrate the diagnostic morphological difference of the morphometric data based on the PCA analysis, while ranges were employed in the study of the meristic data. Unless otherwise specified, all measures in the text are provided as percentages of the standard length (SL) (Hanafi *et al.*, 2023).

Molecular analyses. The cytochrome c oxidase I (COI) gene was utilized to build phylogeny relationships for 21 individuals of *Johnius* using available data. The voucher specimens' pectoral-fin clips were kept in 95% ethanol for DNA extraction. Before being placed at the National Marine Museum and Biology (NMMBA), the voucher specimens were fixed in 10% formalin, conserved in 70% ethanol, and given catalogue numbers. Table 2 displays information on voucher specimens.

A DNA extraction kit (G-spinTMTotal from iNtRON Biotechnology, Inc., Seongnam, South Korea) was used to extract genomic DNA. The COI gene region was amplified and sequenced using the primers Johni 76F: 5' CCTCTGTYTRTGGGTTTACAATC 3' and Johni 916R: 5' TTRCCAGAATAATAYGCAACGA 3' (Lo *et al.*, 2017). Each polymerase chain reaction (PCR) sample was a 50 µl reaction comprising 20 µl of sterile water, 2 µl of genomic DNA, 25 µl of Master Mix (NEXproTM, Korea), and 1.5 µl of each primer at 10 mM. The PCR cycle conditions were as described by Lo *et al.* (2017). An Applied Biosystems Veriti 96-Well Thermal Cycler (Applied Biosystems, Inc., Foster City, CA, USA) was used to run PCR reactions. Sanger sequencing was carried out by MyTACG Bioscience Enterprise in Malaysia. MEGA v7.0 was used to modify and align all sequences (Kumar *et al.* 2018).

MEGA7 v7.0 generated a Neighbor-Joining (NJ) phylogenetic tree (Kumar *et al.* 2018). Kimura's two-parameter model of substitution (K2P distance) was used to estimate the NJ bootstrap values across 1000 repetitions (Kimura 1980). The Akaike information criterion (AIC) was used to automate model selection (Lefort *et al.* 2017). The best-fit models were the HKY85 +G model with a constant invariable site and the program's estimated gamma shape parameter of 0.099. The outgroup *Dendrophysa russelii* was employed to root the tree. Table 2 displays the GenBank accession numbers for all sequences.

TABLE 2. Taxa, vouchers, locality and GenBank accession numbers of specimens of *Johnius* used in the phylogeny analysis.

No	Taxon	(NMMBA)	Specimen Number	Locality	Country	GenBank No.
1	*Dendrophysa russelli*	-	-	-	-	NC017606
2	*Dendrophysa russelli*	-	-	-	-	JQ728562
3	*Johnius amblycephalus*	37076	KK04	Kota Kinabalu	East Malaysia	-
4	*Johnius amblycephalus*	26503	KK04	Kota Kinabalu	East Malaysia	-
5	*Johnius amblycephalus*	NTUM11503	May689	Kuala Perlis	West Malaysia	KX777913
6	*Johnius amblycephalus*	-	WJC426	Chiayi	Taiwan	KX777914
7	*Johnius belangerii*	37077	MIRI04a	Miri	East Malaysia	OK254148
8	*Johnius belangerii*	37079	SIBU15b	Sibu	East Malaysia	OK254143
9	*Johnius borneensis*	37080	SKN06-2	Sandakan	East Malaysia	OK254157
10	*Johnius borneensis*	37084	KCH08b	Kuching	East Malaysia	OK254158
11	*Johnius carouna*	34740	BLRN	Beluran	East Malaysia	
12	*Johnius carouna*	34741	BGR06g	Betangor	East Malaysia	OK255536
13	*Johnius carouna*	34742	KK07c	Kota Kinabalu	East Malaysia	OK255537
14	*Johnius coitor*	37096	SIBU02d	Sibu	East Malaysia	OK255664
15	*Johnius coitor*	37096	SIBU02b	Sibu	East Malaysia	OK255665
16	*Johnius heterolepis*	37090	SRK05d	Sarikei	East Malaysia	OK255548
17	*Johnius heterolepis*	34748	BNT08d	Bintulu	East Malaysia	OK255556
18	*Johnius macrorhynus*	37091	SIBU06	Sibu	East Malaysia	-
19	*Johnius macrorhynus*	34745	TWU05	Tawau	East Malaysia	-
20	*Johnius plagiostoma*	37100	SRK02b	Sarikei	East Malaysia	OK255569
21	*Johnius plagiostoma*	37101	GBT0126	Goebilt	East Malaysia	OK255570
22	*Johnius sasakii*	37095	SKN08-4	Sandakan	East Malaysia	OK257864
23	*Johnius sasakii*	34736	BNT018	Bintulu	East Malaysia	OK257863
24	*Johnius trewavasae*	37087	SRK06d	Sarikei	East Malaysia	OK271429
25	*Johnius weberi*	37097	BLRN08-1	Beluran	East Malaysia	OK392095
26	*Johnius weberi*	37097	BLRN09-2	Beluran	East Malaysia	OK392099

Results

Genus *Bola* Hamilton, 1822 and *Wak* Lin, 1938 as a junior synonym of *Johnius* Bloch, 1793

According to Hanafi *et al.*, (2023) comprehensive review, both *Wak* Lin (1938) and *Bola* Hamilton (1822) are junior synonyms, sharing the same type species, *Bola coitor* Hamilton. These findings were obtained after a thorough analysis of Hamilton's (1822) monograph and a survey of pertinent literature. *Bola coitor* exhibits characteristics similar to the type species of the genus *Johnius*, *Johnius carutta* Bloch, 1793, including an inferior mouth with undifferentiated teeth in the lower jaw and a hammer-shaped gasbladder, as suggested by Trewavas (1964) and confirmed by Talwar (1969).

Synonyms and invalid names of nominal species of *Johnius* Bloch, 1793

Several taxonomic names of Malaysian species often used in the literature have been identified as questionable identifications. Table 3 lists all *Johnius* species found in Malaysian sources, along with their current status. Sasaki (1999) acknowledged *J. glaucus* and *J. goldmanni* as nomen dubium. Mohsin *et al.* (1996) and Chin *et al.* (1998)

TABLE 3. *Johnius* species listed in several references from East Malaysia waters and their status.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Remarks
J. amblycephalus	+			V	V	V		V	V			V	V	V	Valid
J. belangerii	+	V	V	V	V	V	V	V			V	V	V	V	Valid
J. borneensis	+			V	V	V		V				V		V	Valid
J. carouna	+			V	V	V					X (*J. borneensis*)	V		V	Valid
J. coitor	+			V	V	V		X (*J. carouna*)				X (*J. carouna*)			Valid
J. glaucus						n						n			Syn. *J. carouna*
J. goldmanni						n						n			Syn. *J. borneensis*
J. heterolepis	+			V	V	V						V			Valid
J. latifrons				V	V										Gulf of Thailand
J. macropterus				V	V	V						V			Indian Ocean
J. macrorhynus	+			V	V	V			V	V		V			Valid
J. plagiostoma	+			V	V							V			Valid
J. sasakii	+														Valid
J. trachycephalus				V	V							V			Valid
J. trewavasae	+			V	V										Valid
J. weberi	+			V	V							V			Valid

Reference name: (1) This study; (2) Mohsin *et al.*, 1996; (3) Chin *et al.* 1998; (4) Sasaki (2000); (5) Sasaki, 2001; (6) DOFM, 2009; (7) Lim, 2009; (8) Ambak *et al.* 2010; (9) Matsunuma *et al.* 2011; (10) Kimura *et al.* 2015; (11) Ng *et al.* 2015; (12) Atan *et al.* 2010; (13) Lim *et al.* 2018; (14) Seah *et al.* 2021.

v Correct record; x Incorrect record; s Synonym name; n Nomen dubium; + This study

misidentified and photographed *J. dussumieri* as *J. amblycephalus*, whereas *J. glaucus* and *J. goldmanni* are junior synonyms of *J. carouna* and J. *borneensis* (Sasaki, 1999). However, since *J. elongatus* is exclusively found in Indian coastal waters, the species described and photographed by Atan *et al.* (2010) was misdiagnosed as *J. macrorhynus*. *Johnius carutta* Bloch, 1793; *J. dussumieri* (Cuvier, 1830); *J. elongatus* Lal Mohan, 1976; and *J. macropterus* (Bleeker, 1853) are all valid names that are exclusively found in the Indian Ocean. Meanwhile, *J. latifrons* (Sasaki, 1992) and *J. trachycephalus* (Bleeker, 1850) are also valid species endemically dispersed in the Gulf of Thailand. One additional species, *Johnius trewavasae* Sasaki, 1992 was discovered for the first time in Malaysia, increasing its known range to south-eastern Malaysia (Borneo shoreline).

Several references in Table 3 have been revised and corrected from the East Malaysia literature review (Mohsin *et al.*, 1996; Chin *et al.*, 1998; Sasaki, 2000; Mohamad Faisal, 2009; Lim, 2009; Ambak *et al.*, 2010; Matsunuma *et al.*, 2011; Kimura *et al.*, 2015; Ng *et al.*, 2015; Atan *et al.*, 2010; Shah, 2017; Lim *et al.*, 2018; Seah *et al.*, 2021) with Fig. 2 were provided to show the spatial distribution of *Johnius* species in the East Malaysian waters. Descriptions and identification keys were also utilised to cross-check against all species, as described by Trewavas (1977), Lal Mohan (1984), Sasaki (1992, 1999, 2001), and Fricke *et al.* (2023).

Integrated identification of East Malaysian *Johnius* species

Morphological measurements. The sheared PCA analysis (Fig. 3) of the factor loadings data (Table 4) revealed that size contributed to 26.4% of the observed variance. Sheared PC2 and PC3 accounted for 19.61% and 6.79%, respectively, of the observed variance. The loadings of both components were similar on sheared PC2. The highest loadings were observed at gill raker length (GRL/ED) (0.74) in eye diameter (ED) and maxillary length (MxL/HL) (0.37) in head length (HL). For PC3, the loadings were highest at the second spine anal ray length (2ndAL/HL) (0.0.87) in head length (HL).

The scatterplot clusters with 95% confidence interval polygons for *Johnius* species from East Malaysia were compared to assess morphological divergence (Fig. 3). The PCA of the morphometric data indicated substantial overlap among the studied characteristics. Upon plotting PC1 versus PC2, several clusters were apparent, indicating a well-structured variance in morphometric traits across the studied species. This differentiation allowed for a clear distinction between interspecific species and individuals that were previously classified as the same species. The principal component analysis (PCA) results reveal the presence of 11 *Johnius* species with distinct physical characteristics in the seas of East Malaysia.

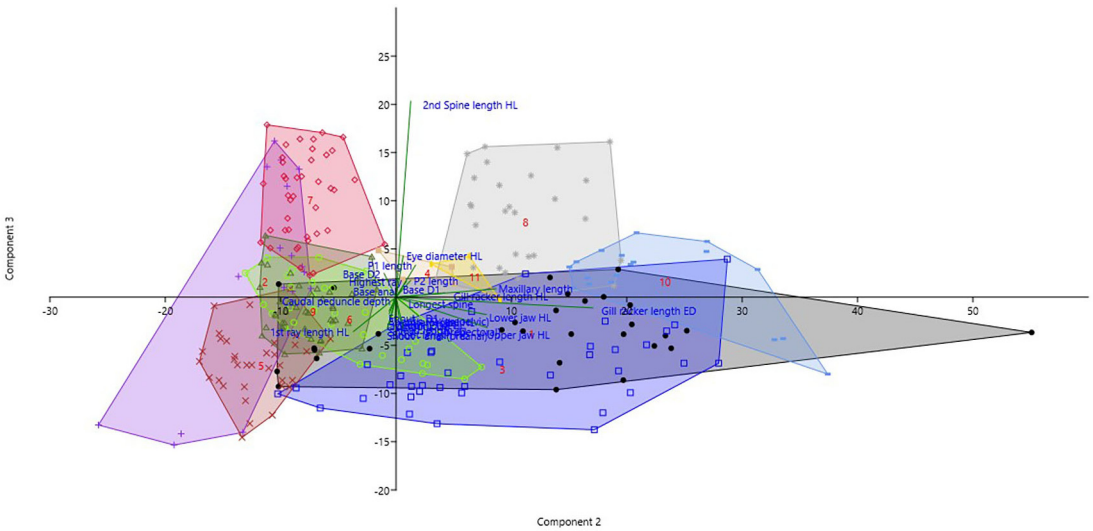

FIGURE 3. Scatterplots with 95% confidence interval ellipses of the sheared second principal component (PC2) and sheared third principal component (PC3) of morphometric data on *Johnius* from East Malaysia waters. *Johnius amblycephalus* (1, black dots), *J. belangerii* (2, blue plus), *J. borneensis* (3, violet square), *J. coitor* (4, brown fill square), *J. macrorhynus* (5, gold cross), *J. heterolepis* (6, coral circle), *J. carouna* (7, aqua diamond), *J. carouna* (8, gray star), *J. sasakii* (9, green triangle), *J. plagiostoma* (10, maroon dash), and *J. weberi* (11, orange bar).

TABLE 4. Morphological character factor loadings (correlations between variables and PC axes) for PC2 and PC3 within the genus *Johnius*. Character acronyms and definitions are explained in Hanafi *et al.* (2023).

	PC 2	PC 3
Head length	0.00	-0.11
P1 length	0.07	0.14
P2 length	0.05	0.07
Depth (D1–P2)	0.00	-0.09
Width (P1–P1)	0.00	-0.09
Base D1	0.05	0.00
Longest spine	0.08	0.00
Base D2	-0.05	0.11
Highest ray	0.04	0.07
Base anal	0.02	0.03
Snout—anal (preanal)	-0.03	-0.14
Snout—D1	-0.03	-0.06
Snout—D2	0.01	-0.10
Snout—P1 (prepectoral)	-0.02	-0.12
Snout—P2 (prepelvic)	-0.02	-0.08
Caudal peduncle depth	-0.01	-0.02
Snout length HL	0.03	-0.14
Maxillary length	0.37	0.04
Upper jaw HL	0.34	-0.13
Lower jaw HL	0.34	-0.07
Eye diameter HL	0.03	0.18
Interorbital HL	0.08	-0.08
2nd spine length HL	0.05	**0.87**
1st ray length HL	-0.16	-0.15
Gill raker length HL	0.18	0.02
Gill raker length ED	**0.74**	-0.05

Molecular phylogeny. The COI sequences that were aligned included a total of 613 base pair sequence characters. Among them, 51 characters provided useful information for parsimony analysis, 52 characters were varied but did not contribute to parsimony analysis, and 472 characters remained constant throughout. The NJ analyses generated phylogenetic trees with consistent structures but varying bootstrap support (BS) values (Fig. 4). The COI sequence-based phylogenetic tree identified six main lineages consisting of 11 species, excluding *J. macrorhynus* (Fig. 4). The first lineage included taxa of *Dendrophysa russelli* as an outgroup, followed by the subsequent lineage, *J. amblycephalus*, which served as a basal species with a significant bootstrap support (BS:100%) value. Whereas the third and fourth lineages comprised of taxa of *J. plagiostoma* (BS: 100%), followed by *J. borneensis* with modest bootstrap support (BS: 35%). Furthermore, the fifth clade, which includes *J. coitor* (BS: 23%), is separated into two distinct groups (BS: 15%). This clade independently diverges from *J. carouna* and *J. heterolepis* as a sister clade (BS: 30%). Additionally, there are derived clades consisting of *J. sasakii* (BS: 13%) and *J. weberi* (BS: 13%), both of which independently diverged from their respective sister clades, *J. trewavasae* and *J. belangerii* (BS: 21%) (Table 5). Nevertheless, the genetic differences within this lineage make it possible to identify all species of *Johnius* from East Malaysia, which forms a highly monophyletic clade. The validity of this finding is reinforced by the inclusion of further morphological statistical analysis and genetic evidence data provided in this study (Fig. 4 and Table 5).

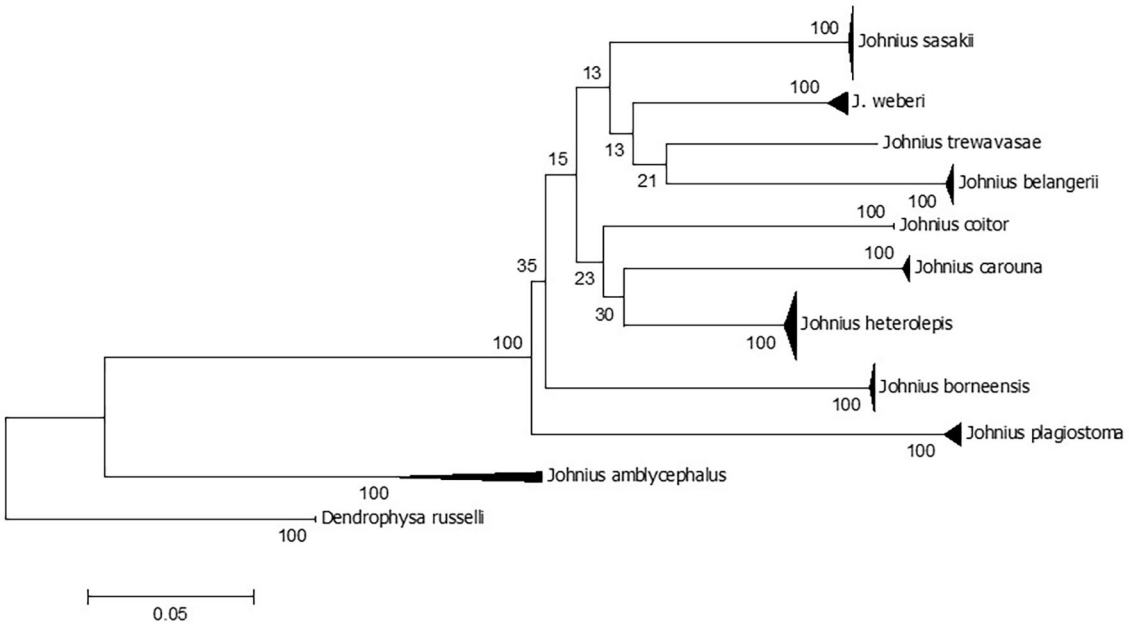

FIGURE 4. Neighbor-joining phylogenetic tree of *Johnius* based on COI sequences. Bootstrap values (neighbor-joining [NJ]/ maximum likelihood [ML]) are shown on the nodes.

TABLE 5. Genetic distances for the COI gene among eleven *Johnius* species from East Malaysia and *Dendrophysa russelii* as an outgroup.

	1	2	3	4	5	6	7	8	9	10	11
1. Johnius_sasakii											
2. Johnius_weberi	**0.14**										
3. Johnius_trewavasae	0.15	0.16									
4. Johnius_belangerii	0.18	0.15	0.15								
5. Johnius_coitor	0.18	0.22	0.23	0.20							
6. Johnius_carouna	0.19	0.19	0.17	0.17	0.17						
7. Johnius_heterolepis	0.15	0.15	0.15	0.15	0.15	0.14					
8. Johnius_borneensis	0.19	0.17	0.18	0.18	0.21	0.21	0.16				
9. Johnius_plagiostoma	0.22	0.25	0.20	0.23	0.25	0.23	0.23	0.25			
10. Johnius_amblycephalus	0.38	0.36	0.38	0.38	0.36	0.35	0.33	0.35	**0.40**		
11. Dendrophysa_russellii	0.34	**0.40**	0.36	0.39	0.36	0.37	0.34	0.34	0.37	0.25	

Systematics

Genus *Johnius* Bloch, 1793

Johnius Bloch, 1793, Naturg. Ausland. Fische (pt. 7), p. 132—type *Johnius carutta* Bloch, designated by Gill, 1861, Proc. Acad. Nat. Sci, Philadelphia, p. 85.

Bola Hamilton, 1822, Fish. Ganges, p. 173—type *Bola coitor* Hamilton, designated by Jordan, 1917, Genera of Fishes, p. 114. Syn. nov.

Wak Lin, 1938, Lingnan. Sci. J., 17 (2) p. 378—substitute name for *Bola* Hamilton allegedly preoccupied by *Bola* Gunther; type by original designation *Bola coitor* Hamilton.

Diagnosis. This genus *Johnius* is distinguished from other Sciaenidae genera by the following combination of feature states: (2) Barbel presents or missing, median with the median mental pore at the front of its base; (3) Hammer head in the form of a swimbladder right behind the transverse septum. A lateral branch extends to the

anterolateral face of the pectoral arch at the intersection of the cleithrum and supracleithrum, where its palmate twiglets sit between the bone and the skin; (4) swimbladder appendages without dorsal limbs; (5) Sagitta, with the tadpole pattern's long axis obliquely or nearly at right angles to the otolith's long axis The otolith's anterior section is thick. (6) Vertebrae 25 (10–12 abdominal, 13–15 caudal), exceptionally 24 (10+14); (7) The inferior apophyses of the fourth vertebra join below the haemal canal to form an arch to which the swimbladder is linked; (8) Predorsal bone two or three; (9) Scaly soft dorsal and anal fins; and (10) the presence of a large foramen in the prootic bone (Hanafi *et al.*, 2023).

Key to the species of *Johnius* in the East Malaysian waters

1a. Chin with barbel . . . . . *J. amblycephalus* (Bleeker, 1855)
1b. Chin without barbel 2
2a. Upper jaw and inner row of lower jaw teeth enlarged, conical 3
2b. Upper jaw and inner row of lower jaw teeth uniform, molariform 4
3a. Snout rounded . . . . . *J. plagiostoma* (Bleeker, 1850)
3b. Snout pointed . . . . . *J. borneensis* (Bleeker, 1851)
4a. Body dark pigmented; lower fins black . . . . . *J. belangerii* (Cuvier, 1830)
4b. Body silvery to light yellow; lower fins pale 5
5a. Scales moderately small, upper scale rows 7–11, lower scale rows 11–17 6
5b. Scales large, upper scale rows 4–7, lower scale rows 6–14 7
6a. Gill rakers on the 1st arch slender and long, 9–12 gill rakers on the lower limb of 1st arch with length longer than half of gill filaments length. . . . . *J. coitor* (Hamilton, 1822)
6b. Gill rakers on the 1st arch stiff and short, 7–9 gill rakers on lower limb of 1st arch with length shorter than half of gill filaments length . . . . . *J. weberi* (Hardenberg, 1936)
7a. Lower jaw with inner row of molariform teeth posteriorly . . . . . *J. macrorhynus* (Mohan, 1976)
7b. Lower jaw teeth all conical, uniform in size 8
8a. Total outer gill rakers of 1st arch 16–18. . . . . *J. carouna* (Cuvier, 1830)
8b. Total outer gill rakers of 1st arch 13–15. 9
9a. Total outer gill rakers of 1st arch (mode 12) with lower limb of 8–10 (mode 8), total scale rows 8–11 (mode 8) respectively . . . . . *J. trewavasae* Sasaki, 1992
9b. Total outer gill rakers of 1st arch (mode 14) with lower limb 8–11 (mode 9–10), total scale rows 9–20 (mode 15) respectively 10
10a. Gill rakers of outer gill rakers of 1st arch at the upper limb, 4–5 (mode 4) and lower limb 9–11 (mode 10) respectively. . . . . *J. heterolepis* Bleeker, 1873
10b. Gill rakers of outer gill rakers of 1st arch at the upper limb, 4–6 (mode 5) and lower limb 8–10 (mode 9) respectively. . . . . *J. sasakii* Hanafi *et al.* 2022

Johnius amblycephalus (Bleeker, 1855)

(Common name: Bearded croaker)
(Fig. 5, Table 6)

Umbrina amblycephalus Bleeker 1855: 412 (type locality: Ambon Island, Molucca Islands, Indonesia. Syntypes: RMNH 8289).
Johnius amblycephalus (Bleeker, 1855): Sasaki, 2000: 621; Sasaki, 2001: 3139; Mohamad Faisal, 2009: 97; Ambak *et al.* 2010: 174; Matsunuma *et al.* 2011:139; Atan *et al.* 2010: 194; Lim *et al.* 2018: 138; Seah *et al.* 2021: 99.
Johnius coitor (non of Hamilton, 1822): Ng *et al.*, 2015: 327.
Johnius dussumieri (non of Cuvier, 1830): Mohsin & Ambak, 364; Chin, 1998: 186.

Material examined. Non-types: NMMB-P37076 (10, 106.49 to 153.76 mm SL), Kota Kinabalu, Sabah, Malaysia, 4 March 2017; NMMB-P26538 (3, 145.85 to 173.38 mm SL), Pulau kambing, Terengganu, Malaysia, 30 December 2014; NMMB-P34752 (163.89 mm SL), Sibu, Sarawak, Malaysia, 3 March 2017; NMMB-P34753 (108.1 mm SL), Bako, Sarawak, Malaysia, 17 March 2017; Endau, Johor, Malaysia, 10–11 June 2014; NMMB-P21557 (123.38 mm SL), Endau, Johor, Malaysia, 10–11 June 2014; NMMB-P32820 (129.9 mm SL), Pangkor Island, Perak, Malaysia, 11 September 2009; NMMB-P34754 (4, 85.66 to 148.65 mm SL), Miri, Sarawak, Malaysia, 7 March 2017; NMMB-P26503 (129.06 mm SL), Kota Kinabalu, Sabah, Malaysia, 4 April 2017; NMMB-P21532 (143.7 mm SL), NMMB-P26498 (2, 138.08 to 141.6 mm SL), Pantai Remis, Perak, Malaysia, 4 June 2014; NMMB-P21530 (153.77 mm

SL), Kuala Kurau, Perak, Malaysia, 1–2 June 2014; NMMB-P26501 (3, 120.21 to 146.75 mm SL), Kuala Kedah, Kedah, Malaysia, 19 May 2014; NMMB-P25512 (3, 105.03 to 134.51 mm SL), Tanjung Gemok, Pahang, Malaysia, 10 June 2014.

FIGURE 5. Photographs of the comparative materials. *Johnius amblycephalus,* NMMB-P 37076, 106 mm SL, Kota Kinabalu, Sabah, Malaysia, 4 March 2017.

Diagnosis. A species of *Johnius* with the following combination of characters: Snout steep, bluntly rounded, projecting in front of upper jaw; mouth inferior; a stiff, blunt barbel on chin; lower jaw with a band of villiform teeth; gill rakers stiff, less than 1/2 length of gill filaments at angle of arch, 6 to 9 on lower limb of first gill arch; second spine moderately short, 20 to 36% of head length; caudal fin slightly rhomboidal, S-shaped or truncate; scales small, 7 to 12 scale rows above lateral line to origin of dorsal fin, 13 to 18 scale rows below lateral line to origin of anal fin (Hanafi *et al.* 2023).

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

Remarks. *Johnius amblycephalus* can be easily differentiated from the rest of other *Johnius* species in the East Malaysian waters by the presence of a single mental barbel at the lower jaw. *Johnius amblycephalus* is abundant and was available collected from stretching the Sabah and Sarawak states, Malaysia until Taiwan waters (Hanafi *et al.* 2023).

Johnius belangerii **(Cuvier, 1830)**

(Common name: Belanger croaker)
(Fig. 6, Table 6)

Corvina belengerii Cuvier 1830: 120 (type locality: Malabar, India. Syntypes: MNHN 0000-761).
Johnius belangerii (Cuvier, 1830): Mohsin & Ambak, 1996: 366; Chin, 1998: 138; Sasaki, 2000: 621; Sasaki, 2001: 3141; Lim, 2009: 200; Mohamad Faisal, 2009: 97; Ambak *et al.* 2010: 174; Lim *et al.* 2018: 138; Seah *et al.* 2021: 100.
Johnius dussumieri (non of Cuvier, 1830): Atan *et al.* 2010: 195.

Material examined. Non-types: NMMB-P37077 (5, 129.9 to 156.92 mm SL), Miri, Sarawak, Malaysia, 7 March 2017; NMMB-P37078 (4, 131.24 to 152 mm SL), Kota Kinabalu, Sabah, Malaysia, 4 March 2017; NMMB-P37079 (2, 130.33 to 154 mm SL), Sibu, Sarawak, Malaysia, 12 March 2017; NMMB-P21552 (4, 97.25 to 182.5 mm SL),

NMMB-P26493 (2, 115.59 to 133 mm SL), Tanjung Piandang, Perak, Malaysia, 2 June 2014; NMMB-P31394 (8, 147.37 to 164.73 mm SL), Muar, Johor, Malaysia, 19 March 2019; NMMB-P26511 (3, 107.65 to 133.41 mm SL), NMMB-P26499 (3, 89.68 to 101.31 mm SL), Kuala Kurau, Perak, Malaysia, 4 June 2014; NMMB-P21522 (8, 82.1 to 117.08 mm SL), Kuala Kurau, Perak, Malaysia, 8 June 2014; NMMB-P28323 (110.9 mm SL), Kuala Kurau, Perak, Malaysia, 2 June 2014; NMMB-P26496 (3, 106.46 to 113.27 mm SL), Kuala Kurau, Perak, Malaysia, 23 November 2014; NMMB-P26510 (3, 98.35 to 155.89 mm SL), NMMB-P21533 (5, 80.41 to 129.42 mm SL), NMMB-P26523 (4, 71.4 to 78.01 mm SL), Pantai Remis, Perak, Malaysia, 4–6 June 2014; NMMB-P26513 (3, 119.45 to 141.37 mm SL), NMMB-P27638 (127.8 mm SL), Sungai Udang, Perak, Malaysia, 19 January 2015; NMMB-P21713 (144.72 mm SL), NMMB-P21714 (30, 92.18 to 145.95 mm SL), Matang, Perak, Malaysia, 21 April 2011; NMMB-P21536 (141.34 mm SL), Bagan Panchor, Perak, Malaysia, 5 June 2014.

Diagnosis. A species of *Johnius* with the following combination of characters: snout steep, obtusely rounded, slightly projecting in front of upper jaw; mouth small, inferior; 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, 8 to 10 on lower limb of first gill arch; second spine long, stiff, 31 to 45% of head length; and scales moderately small, 7 to 11 scale rows above lateral line to origin of dorsal fin, 12 to 17 scale rows below lateral line to origin of anal fin (Hanafi *et al.*, 2023).

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

Remarks. *Johnius belangerii* is a common species distribute in the East Malaysian waters, also in the Taiwanese waters (Hanafi *et al.* 2023). It was abundantly collected from several sites off the Sarawak states, but few in Sabah states. This might due to ecological sandy and muddy area distribution available for this species to distribute. The variation in the shape band pattern observed in this species throughout collection sites implies it is a morphologically complex species (Hanafi *et al.*, 2023).

FIGURE 6. Photographs of the comparative materials. *Johnius belangerii* NMMB-P 37077, 130 mm SL, Miri, Sarawak, Malaysia, 7 March 2017.

Johnius borneensis **(Bleeker, 1851)**

(Common name: Sharptooth hammer croaker)

(Fig. 7, Table 6)

Otolithus borneensis Bleeker, 1851: 268 (type locality: Bandjarmasin, Borneo, Indonesia. Holotype (unique): RMNH 5980).

Johnius borneensis (Bleeker, 1851): Sasaki, 2000: 621; Sasaki, 2001: 3154; Ambak *et al.* 2010: 174; Lim *et al.* 2018: 138; Seah *et al.* 2021: 100.

Johnius carouna (non of Cuvier, 1830): Ng *et al.* 2015: 327.

Johnius glaucus (syn. of Day, 876): Mohamad Faisal, 2009: 98; Atan *et al.*, 2010: 195.
Johnius goldmanni (syn. of Bleeker, 1851): DOF Malaysia, 2009.

Material examined. Non-types: NMMB-P37080 (4, 81.22 to 171.61 mm SL), Sandakan, Sabah, Malaysia, 26–27 February 2017; NMMB-P37081 (123.82 mm SL), Bintulu, Sarawak, Malaysia, 11 March 2017; NMMB-P37082 (88.44 mm SL), Bako, Sarawak, Malaysia, 17 March 2017; NMMB-P37083 (173.28 mm SL), Tawau, Sabah, Malaysia, 23 February 2017; NMMB-P37084 (2, 125.13 to 189.47 mm SL), Kuching, Sarawak, Malaysia, 17 March 2017; NMMB-P37085 (8, 112.48 to 146.3 mm SL), Miri, Sarawak, Malaysia, 7 March 2017; NMMB-P37086 (7, 118.57 to 153.76 mm SL), NMMB-P26522 (130.4 mm SL), Kota Kinabalu, Sabah, Malaysia, 4 March 2017; NMMB-P31385 (151.69 mm SL), Muar, Johor, Malaysia, 19 March 2019; NMMB-P21543 (3, 108.06 to 170.76 mm SL), NMMB-P26492 (3, 120.62 to 153.71 mm SL), Pantai Remis, Perak, Malaysia, 14 June 2014; NMMB-P26514 (3, 141.99 to 181.76 mm SL), NMMB-P21545 (3, 131.06 to 180.39 mm SL), Kuala Kurau, Perak, Malaysia, 1–2 June 2014; NMMB-P23651 (11, 142.71 to 182.21 mm SL), NMMB-P23652 (3, 153.76 to 202.71 mm SL), Kuala Kedah, Kedah, Malaysia, 19 May 2014; NMMB-P21520 (2, 26.13 to 130.07 mm SL), NMMB-P21554 (2, 136.5 to 139.46 mm SL), Endau, Johor, Malaysia, 10–11 June 2014; NMMB-P21549 (2, 131.56 to 199.24 mm SL), Bagan Panchor, Perak, Malaysia, 5 June 2014; NMMB-P26515 (3, 129.82 to 148.61 mm SL), Tanjung Gemok, Pahang, Malaysia, 10 June 2014.

Diagnosis. A species of *Johnius* with the following combination of characters: snout pointed, but not swollen or projecting; mouth large, oblique; teeth well differentiated into large and small in both jaws, but none canine-like; gill rakers slender, about 1/2 length of gill filaments at angle of arch, 9 to 15 on lower limb of first gill arch; second anal spine moderately long, 18 to 42% of head length; and scales moderately large, 5–6 scale rows above lateral line to origin of dorsal fin, 10 to 12 scale rows below lateral line to origin of anal fin (Hanafi *et al.*, 2023).

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

Remarks. *Johnius borneensis* is also a common species widely distributed in the East Malaysia waters, and Taiwanese waters (Hanafi *et al.* 2023). However, it was intensely collected at abundant sites at the Sarawak states, comparing with Sabah states due to ecological factor such as sandy and muddy habitat.

FIGURE 7. Photographs of the comparative materials. *Johnius borneensis* NMMB-P 37080, 82 mm SL, Sandakan, Sabah, Malaysia, 26–27 February 2017.

***Johnius carouna* (Cuvier, 1830)**
(Common name: Caroun croaker)
(Fig. 8, Table 6)

Corvina carouna Cuvier, 1830: 125 (type locality: Malabar, India. Syntype: MNHN 0000-7529
Johnius carouna (Cuvier, 1830): Sasaki, 2000: 621; Sasaki, 2001: 3142; Mohamad Faisal, 2009: 97; Atan *et al.* 2010: 194; Seah *et al.* 2021: 101.
Johnius belangerii (non of Cuvier, 1830): Atan *et al.*, 2010: 194.
Johnius carutta non of Bloch, 1793: Mohsin & Ambak, 1996: 174.
Johnius coitor (non of Hamilton, 1822): Ambak, 2010: 174; Atan *et al.*, 2010: 194.
Johnius goldmani (syn. of Bleeker, 1854): Mohamad Faisal, 2009: 98; Atan *et al.*, 2010: 195.

Material examined. Non-types: NMMB-P37088 (2, 98.16 to 106.76 mm SL), Tawau, Sabah, Malaysia, 23 February 2017; NMMB-P37089 (10, 102.9 to 116.37 mm SL), Sandakan, Sabah, Malaysia, 26–27 February 2017; NMMB-P21551 (4, 89.17 to 136.9 mm SL), Pantai Remis, Perak, Malaysia, 4–6 June 2014; NMMB-P27642 (7, 92.85 to 124.33 mm SL), Pantai Remis, Perak, Malaysia, 10 August 2016; NMMB-P34742 (5, 97.98 to 98.26 mm SL), Kota Kinabalu, Sabah, Malaysia, 4 March 2017; NMMB-P34741 (7, 89.35 to 97.13 mm SL), Betangor, Sarawak, Malaysia, 14 March 2017; NMMB-P21550 (6, 92.86 to 97.58 mm SL), NMMB-P26525 (3, 90.45 to 107.46 mm SL), NMMB-P26504 (4, 104.88 to 141.26 mm SL), Kuala Kurau, Perak, Malaysia, 4 June 2014; NMMB-P21535 (104.11 mm SL), Bagan Panchor, Perak, Malaysia, 5 June 2014; NMMB-P21716 (B) (18, 62.7 to 107.09 mm SL), Matang, Perak, Malaysia, 21 April 2011; NMMB-P34740 (10, 113.45 to 122.58 mm SL), Beluran, Sabah, Malaysia, 28 February 2017; NMMB-P26533 (4, 92.54 to 121.9 mm SL), Kuala Kedah, Kedah, Malaysia, 19 May 2014; NMMB-P34743 (10, 106.09 to 141.28 mm SL), Goebilt, Sarawak, Malaysia, 17 March 2017; NMMB-P27643 (10, 92.79 to 130.83 mm SL), Bako, Sarawak, Malaysia, 17 March 2014; NMMB-P31392 (7, 117.27 to 160 mm SL), Muar, Johor, Malaysia, 19 March 2019.

Diagnosis. A species of *Johnius* with the following combination of characters: snout bluntly rounded, slightly projecting in front of upper jaw; mouth small, inferior; lower jaw with a band of villiform teeth; gill rakers long, stiff, about 1/2 length of gill filaments at angle of arch, 10 to 12 on lower limb of first gill arch; second spine long, stiff, 32 to 50% of head length; and scales moderately large, 5 to 7 scale rows above lateral line to origin of dorsal fin, 8 to 11 scale rows below lateral line to origin of anal fin (Hanafi *et al.*, 2022).

FIGURE 8. Photographs of the comparative materials. *Johnius carouna* NMMB-P 27643, 113 mm SL, Bako, Sarawak, Malaysia, 17 March 2017.

Distribution. Indo-West Pacific, India and Myanmar east to Borneo, north to northern Vietnam and southern China.

Remarks. *Johnius carouna* can be distinguished from sympatric congener species, *J. sasakii*, by the second anal spine length longer and stiffer and the gill raker count more higher (10 to 12 in *carouna* vs 8 to 10 in *sasakii*). *Johnius carouna* also is a common species and abundant especially concentrated in Sarawak states. It was collected at several sites of the Bako, Betangor, and Kota Kinabalu.

Johnius coitor (Hamilton, 1822)

(Common name: Coitor croaker)
(Fig. 9, Table 6)

Bola coitor Hamilton, 1822: 75 (type locality: Ganges River as far as Kanpur and Jumna River at Angra and at Visakhapatum, India. No types known.
Johnius coitor (Hamilton, 1822): Sasaki, 2000: 621; Sasaki, 2001: 3144; Mohamad Faisal, 2009: 98.

Material examined. Non-types: NMMB-P37096 (3, 109.25 to 136.62 mm SL), Sibu, Sarawak, Malaysia, 12 March 2017; NMMB-P33374 (121.72 mm SL), Pasar Tamu Sri Aman, Sarawak, Malaysia, 19 November 2019.

Diagnosis. A species of *Johnius* with the following combination of characters: snout steep, obtusely pointed; mouth small, inferior; small eye, 12 to 16% of HL; gill rakers moderately long, slender, about 1/2 to 2/3 length of gill filaments at angle of arch, 9 to 11 on lower limb of first gill arch; second anal spine length long, stiff, about 35 to 40% of HL; and scales moderately small, 7 to 9 scale rows above lateral line.

Distribution. Eastern Indian Ocean, western Pacific; Bay of Bengal (India and Bangladesh) and to eastern Australia.

Remarks. *Johnius coitor* is rare, endemic species and only distributed in the East Malaysia waters, concisely at the Sibu site collection. In previous, Sasaki (2001) has mentioned the species distribution recorded in the Borneo and Malay Peninsula, but no types are known. Thus, this study gives the first clear baseline information based on voucher specimen, genetic information and morphological measurement in detailed. In addition, it also available collected at one site at the Sarawak states, which based on our observation collected at freshwater river which caught in the ~120 km upstream at Rajang River. This is might due to this species much prefer riverine ecological factor such as sandy and muddy habitat with the highly freshwater intrusion for their life preference. However, this study needs to provide in detail with the environmental and biological evidence as supporting data.

FIGURE 9. Photographs of the comparative materials. *Johnius coitor*: NMMB-P 37096, non-type, 136 mm SL, Sibu fish landing port, Sarawak, Malaysia, 12 March 2017.

TABLE 6. Morphometric measurement of *J. amblycephalus, J. belangerii, J. borneensis, J. carouna* and *J. coitor*.

SPECIES	*J. amblycephalus*	*J. belangerii*	*J. borneensis*	*J. carouna*	*J. coitor*
	(n=31)	(n=17)	(n=30)	(n=30)	(n=4)
Morphometric measurements					
Standard length(mm)	106–156	82–157	86–185	88–148	108–136
As percentage of SL					
Head length	28.4–32.1(30.4±1.0)	28.6–32.5(30.4±1.3)	29.5–34.3(32.0±1.1)	25.5–32.3(29.83±1.4)	28.9–30.2(2935±0.6)
Pectoral fin length	9.2–34.9(21.8±3.7)	17.3–19.6(18.6±0.6)	12.8–24.1(19.0±2.2)	13.12–26.2(21.5±2.6)	20.7–22.7(21.5±0.8)
Pelvic fin length	14.7–32.2(17.4±2.9)	16.6–21.0(18.8±1.3)	12.2–19.0(16.5±1.8)	13.5–19.9(16.8±1.5)	18.9–21.8(20.1±1.3)
Body depth	22.6–28.1(25.9±1.4)	27.3–32.2(29.2±1.5)	25.8–32.3(29.2±1.5)	20.0–31.6(26.5±2.1)	26.3–27.6(27.1±0.6)
Body width	13.9–19.2(16.1±1.3)	13.0–16.0(14.7±0.8)	11.3–19.1(15.5±1.5)	10.4–19.4(14.1±1.6)	14.4–17.1(15.5±1.2)
1st dorsal fin base length	18.5–25.6(22.0±1.9)	18.2–23.5(20.6±1.5)	15.2–25.1(20.7±1.8)	15.9–26.9(20.3±2.0)	19.5–22.6(20.4±1.5)
4th spine of 1st dorsal fin length	16.2–27.9(21.3±2.7)	11.3–17.7(15.6±1.5)	10.5–17.9(14.8±1.6)	11.3–18.8(15.2±1.7)	14.3–17.5(15.9±1.4)
2nd dorsal fin base length	31.1–40.4(34.7±2.7)	37.5–46.5(41.2±2.2)	32.1–42.4(38.2±2.4)	35.1–43.7(40.1±2.1)	38.3–41.9(40.5±1.8)
5th ray of 2nd dorsal fin length	6.2–11.8(9.2±1.4)	7.8–12.2(10.1±1.2)	6.8–14.7(10.1±1.7)	7.9–17.3(10.4±1.5)	9.1–11.2(10.3±1.0)
Anal fin base length	8.4–11.0(9.4±0.7)	8.7–12.0(10.2±1.0)	7.0–10.4(8.8±0.7)	7.4–10.8(8.8±0.7)	9.2–10.6(9.9±0.6)
2nd spine of anal fin length	6.3–10.8(8.5±1.1)	8.9–13.4(11.3±1.2)	5.6–13.6(8.4±1.6)	9.6–14.7(11.9±1.3)	10.3–11.6(11.1±0.6)
1st ray of anal fin length	7.9–14.0(12.4±1.3)	13.0–16.0(14.4±0.7)	8.0–16.6(12.4±1.8)	9.7–16.5(13.2±1.3)	15.2–15.4(15.3±0.1)
Preanal length	61.8–69.8(66.9±1.7)	65.8–69.3(67.8±1.2)	64.2–78.6(71.6±2.3)	62.5–72.7(68.3±2.0)	63.3–67.0(65.8±1.7)
Predorsal length	32.3–37.0(34.7±1.2)	33.3–37.1(34.7±1.2)	32.8–36.7(35.2±1.0)	27.0–38.0(34.0±2.1)	34.5–36.5(35.8±0.9)
Snout to origin of 2nd dorsal fin length	52.2–59.0(54.6±1.7)	50.3–57.3(53.1±1.8)	51.7–57.9(54.4±1.5)	43.6–57.5(52.3±2.5)	52.0–56.7(54.5±2.1)
Prepectoral length	28.1–38.1(31.4±1.8)	28.0–31.4(29.6±0.9)	29.2–34.6(32.0±1.3)	22.7–34.3(30.1±2.2)	30.9–32.0(31.3±0.5)
Prepelvic length	27.8–36.3(33.5±1.7)	32.7–35.1(33.9±0.6)	33.2–38.1(36.0±1.3)	27.0–34.3(30.1±2.2)	33.5–35.5(34.4±0.8)
Caudal peduncle depth	7.6–10.1(9.0±0.7)	7.6–10.1(9.7±0.6)	7.8–10.9(9.8±0.8)	2.2–10.5(9.2±1.1)	7.6–7.9(7.8±0.2)
As percentage of HL					
Snout length	25.9–34.0(30.3±2.1)	24.5–29.2(27.1±1.4)	22.3–33.4(29.6±2.1)	23.8–30.2(27.1±1.5)	32.1–33.6(32.6±0.7)
Upper jaw length	35.2–56.1(48.7±5.4)	35.2–50.5(42.1±4.3)	36.9–56.0(46.7±5.5)	34.7–52.6(43.6±5.7)	42.3–45.6(43.8±1.4)
Tip upper jaw to hinge length	26.1–38.0(32.9±3.5)	24.8–37.1(29.6±4.0)	28.2–46.9(37.5±4.8)	22.6–39.8(30.4±5.0)	27.1–29.9(28.9±1.3)
Tip lower jaw to hinge length	19.5–33.6(28.1±3.5)	22.0–33.3(26.5±3.5)	19.8–42.7(33.8±5.1)	21.0–46.4(27.2±5.2)	24.8–27.5(26.0±1.1)
Eye diameter	19.2–27.1(22.8±1.9)	20.8–32.6(25.3±3.4)	19.3–27.3(22.6±1.6)	20.3–35.2(24.8±2.5)	12.3–16.5(14.1±1.8)
Interorbital width	26.7–36.1(29.1±1.6)	18.5–24.4(20.8±2.1)	24.9–31.8(27.3±1.6)	20.9–29.2(25.1±1.8)	26.2–28.0(27.0±0.9)

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TABLE 6. (Continued)

SPECIES	*J. amblycephalus*	*J. belangerii*	*J. borneensis*	*J. carouna*	*J. coitor*
	(n=31)	(n=17)	(n=30)	(n=30)	(n=4)
2nd spine of anal fin length	20.0–36.1(28.2±3.8)	31.0–45.9(37.3±4.8)	17.9–42.5(26.2±5.1)	31.7–49.3(40.8±4.5)	35.6–40.1(37.7±2.0)
1st ray of anal fin length	26.0–47.2(40.8±4.6)	43.8–54.0(47.6±3.0)	25.3–52.1(38.7±5.7)	33.6–52.9(45.2±4.0)	50.2–53.1(51.8±1.3)
Gill raker length	2.2–10.1(6.1±2.4)	2.2–6.6(3.7±1.3)	1.7–8.9.1(5.2±1.9)	2.7–9.1(4.5±1.4)	2.8–3.8(3.4±0.5)
Gill filament length	10.8–19.4(14.4±2.7)	8.6–13.8(11.1±1.4)	7.8–16.9(11.5±2.0)	7.8–21.0(12.3±2.8)	8.9–9.5(9.2±0.3)
As percentage of ED					
Gill raker length	10.7–81.2(28.4±13.9)	9.6–14.8(12.1±1.6)	7.8–39.8(22.8±7.6)	9.8–36.6(18.5±6.5)	21.2–28.1(24.7±3.1)
Gill filament length	41.7–93.8(63.4±11.9)	26.3–60.3(43.8±10.1)	31.2–71.3(50.9±7.5)	29.7–84.7(50.3±12.1)	56.98–74.2(66.5±7.1)

TABLE 7. Morphometric measurement of *J. heterolepis, J. macrorhynus, J. plagiostoma, J. sasakii* and *J. weberi*.

SPECIES	*J. heterolepis*	*J. macrorhynus*	*J. plagiostoma*	*J. sasakii*	*J. weberi*
	(n=30)	(n=30)	(n=19)	(n=18)	(n=3)
Morphometric measurements					
Standard length(mm)	86–133	82–200	71–103	100–147	116–128
As percentage of SL					
Head length	28.7–32.6(31.1±0.9)	27.4–33.3(30.7±1.1)	28.0–31.3(29.8±0.9)	27.7–32.3(30.2±1.2)	29.9–30.9(30.3±0.5)
Pectoral fin length	16.4–22.7(19.3±1.7)	14.3–21.1(17.2±1.8)	15.7–22.3(19.4±1.6)	16.6–24.9(19.7±2.3)	17.2–19.5(18.7±1.3)
Pelvic fin length	12.8–16.7(15.2±0.9)	10.5–17.5(14.3±1.6)	14.6–18.5(16.8±1.0)	12.7–20.0(16.1±2.0)	15.3–16.7(16.0±0.7)
Body depth	22.8–32.0(26.9±1.7)	24.5–30.4(27.5±1.4)	26.0–30.1(28.3±1.0)	25.2–29.0(27.1±1.2)	20.9–24.6(23.1±2.0)
Body width	12.9–17.3(14.7±1.0)	12.7–19.8(15.7±1.7)	14.0–16.0(15.1±0.5)	13.4–18.5(15.5±1.8)	9.4–14.5(11.9±2.5)
1st dorsal fin base length	15.4–20.9(18.0±1.5)	16.3–21.3(18.8±1.2)	16.6–21.4(18.9±1.2)	15.9–23.1(19.3±2.0)	19.0–21.4(20.0±1.3)
4th spine of 1st dorsal fin length	9.5–16.4(13.0±1.5)	10.7–16.9(14.2±1.5)	10.1–16.6(14.1±1.6)	11.9–16.7(13.8±1.3)	14.0–15.4(14.8±0.8)
2nd dorsal fin base length	36.3–42.7(39.7±1.8)	34.3–43.2(38.7±1.9)	39.9–44.4(42.1±1.2)	35.8–44.8(39.7±2.5)	38.2–42.0(40.6±2.0)
5th ray of 2nd dorsal fin length	7.9–13.0(10.1±1.1)	6.6–11.0(8.5±0.9)	8.3–13.1(11.1±1.4)	7.0–14.4(9.8±1.7)	11.4–12.8(12.0±0.8)
Anal fin base length	8.6–10.7(9.5±0.6)	7.3–11.7(8.7±0.7)	9.1–11.8(10.5±0.7)	6.8–10.2(8.8±0.9)	8.1–10.3(9.5±1.2)
2nd spine of anal fin length	7.6–11.0(8.9±0.8)	4.8–9.3(6.9±0.9)	7.2–12.2(10.0±1.2)	7.4–10.2(8.5±0.8)	9.4–11.0(10.3±0.8)
1st ray of anal fin length	10.7–14.4(12.8±1.0)	8.9–13.1(10.8±1.0)	10.7–15.9(14.0±1.2)	9.0–13.3(10.9±1.0)	13.5–15.1(14.1±0.8)
Preanal length	65.7–74.2(70.2±1.7)	65.7–74.0(70.2±2.0)	67.5–72.0(69.1±1.4)	67.1–73.3(70.6±1.5)	68.5–69.4(69.1±0.5)

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TABLE 7. (Continued)

SPECIES	*J. heterolepis*	*J. macrorhynus*	*J. plagiostoma*	*J. sasakii*	*J. weberi*
	(n=30)	(n=30)	(n=19)	(n=18)	(n=3)
Predorsal length	32.9–37.1(35.5±1.1)	32.5–38.1(34.8±1.1)	29.2–33.9(31.8±1.2)	31.8–36.2(33.7±1.3)	32.6–34.2(33.4±0.8)
Snout to origin of 2nd dorsal fin length	49.2–55.8(52.4±1.9)	50.1–56.0(52.3±1.3)	46.6–51.1(48.8±1.3)	49.3–55.0(51.7±1.7)	50.0–54.9(52.3±2.5)
Prepectoral length	28.9–35.1(32.3±1.5)	29.4–39.4(32.0±2.3)	27.6–31.2(29.6±0.9)	27.4–32.8(30.3±1.5)	30.1–30.4(30.3±0.2)
Prepelvic length	33.1–38.7(36.1±1.3)	32.1–40.1(35.8±1.4)	31.9–36.0(34.0±1.1)	31.0–36.5(34.0±1.5)	32.4–34.8(33.5±1.2)
Caudal peduncle depth	8.7–11.1(10.1±0.6)	8.5–10.4(9.2±0.4)	7.6–9.6(9.0±0.5)	8.7–10.7(9.5±0.4)	8.8–9.5(9.0±0.3)
As percentage of HL					
Snout length	21.1–29.6(25.8±2.0)	22.6–32.6(29.0±2.3)	17.9–32.0(22.2±3.7)	23.0–29.5(26.3±2.0)	26.6–32.1(29.4±1.6)
Upper jaw length	34.8–43.6(39.4±2.8)	33.1–45.3(39.0±3.7)	47.0–53.7(51.2±1.9)	34.0–42.6(38.2±2.8)	51.1–56.4(53.8±1.5)
Tip upper jaw to hinge length	25.5–34.9(30.3±2.7)	23.8–32.3(27.2±2.3)	34.5–40.7(38.7±1.8)	26.4–35.4(29.1±2.7)	39.4–44.9(42.3±1.7)
Tip lower jaw to hinge length	20.6–31.9(27.3±2.8)	18.2–29.7(22.9±2.5)	34.1–38.1(36.2±1.2)	21.2–29.0(24.9±2.5)	28.5–42.0(36.3±4.6)
Eye diameter	20.1–29.4(23.9±2.4)	19.0–25.9(22.1±1.5)	22.0–32.5(28.6±3.1)	18.0–24.4(21.6±2.0)	20.3–25.7(22.4±1.5)
Interorbital width	19.5–29.7(24.6±2.7)	21.5–29.2(24.6±1.9)	24.7–29.5(26.4±1.3)	23.8–27.9(26.0±1.3)	24.0–28.0(25.6±1.1)
2nd spine of anal fin length	24.7–34.1(28.8±2.4)	15.5–28.9(24.6±3.0)	24.3–39.6(33.6±3.9)	24.9–35.6(29.2±2.6)	22.5–31.6(27.8±2.4)
1st ray of anal fin length	35.1–46.1(41.1±2.8)	27.8–41.6(35.3±3.1)	35.2–53.2(47.1±5.0)	30.7–46.7(36.3±3.5)	41.8–48.1(44.5±2.0)
Gill raker length	1.7–6.7(3.7±1.2)	1.1–3.1(2.0±0.5)	8.3–13.2(10.6±1.7)	2.4–4.9(3.2±0.7)	1.6–3.5(2.3±0.5)
Gill filament length	7.4–11.3(9.4±0.9)	7.4–13.7(9.7±1.4)	6.3–10.9(8.3±1.0)	8.8–14.0(11.2±1.5)	7.5–12.2(10.1±1.4)
As percentage of ED					
Gill raker length	8.8–29.9(16.4±6.1)	4.8–12.6(9.2±2.2)	28.4–57.4(37.7±9.2)	11.3–19.9(14.6±2.4)	7.9–13.8(10.3±1.6)
Gill filament length	27.8–54.0(39.6±6.5)	33.3–63.5(45.8±6.0)	22.2–33.7(29.0±2.5)	37.7–59.9(51.9±3.4)	33.3–52.7(45.0±5.3)

***Johnius heterolepis* Bleeker, 1873**
(Common name: Heterolepis croaker)
(Fig. 10, Table 7)

Johnius heterolepis Bleeker, 1873: 456 (type locality: Sarawak and Sabah, Borneo.) Syntype: RMNH 6042 (2)
Johnius heterolepis Bleeker, 1873: Sasaki, 1992: 193; Sasaki, 2000: 621; Sasaki, 2001: 3145; Mohamad Faisal, 2009: 98; Atan *et al.* 2010: 195.

Material examined. Non-types: NMMB-P37090 (4, 77.95 to 117.86 mm SL), Sarikei, Sarawak, Malaysia, 14 March 2017; NMMB-P23664 (119.81 mm SL), NMMB-P21541 (2, 104.94 to 128.85 mm SL), NMMB-P21711 (125.93 mm SL), NMMB-P23665 (3, 103.17 to 138.95 mm SL), NMMB-P23656 (8, 102.43 to 123.8 mm SL), Pantai Remis, Perak, Malaysia, 4–6 June 2014; NMMB-P34749 (10, 90.32 to 119.07 mm SL), NMMB-P34751 (15, 105 to 113.9 mm SL), Bako, Sarawak, Malaysia, 17 March 2017; NMMB-P34750 (10, 81.24 to 101.56 mm SL), Goebilt, Sarawak, Malaysia, 17 March 2017; NMMB-P35556 (6, 90.3 to 112.64 mm SL), Betangor, Sarawak, Malaysia, 14 March 2017; NMMB-P23657 (2, 103.81 to 127.65 mm SL), Tanjung Gemok, Pahang, Malaysia, 10 June 2014; NMMB-P21527 (2, 103.14 to 127.33 mm SL), Tanjung Piandang, Perak, Malaysia, 3 June 2014; NMMB-P34748 (10, 91.9 to 112.84 mm SL), Bintulu, Sarawak, Malaysia, 9 March 2017; NMMB-P23658 (7, 91.34 to 112.68 mm SL), Kuala Kedah, Kedah, Malaysia, 3 June 2014; NMMB-P21537 (120.15 mm SL), Bagan Panchor, Perak, Malaysia, 5 June 2014.

FIGURE 10. Photographs of the comparative materials. *Johnius heterolepis* NMMB-P 37090, 78 mm SL, Sarikei, Sarawak, Malaysia, 14 March 2017.

Diagnosis. A species of *Johnius* with the following combination of characters: snout steep, obtusely pointed; mouth small, inferior; moderate eye, 20 to 29% of HL; gill rakers moderately slender, about 1/2 length of gill filaments at angle of arch, 9 to 11 on lower limb of first gill arch; second anal spine length short, slender, about 25 to 34% of HL; and scales larges, 5 to 6 scale rows above lateral line (Hanafi *et al.*, 2022).

Distribution. Western Pacific; Gulf of Thailand, Malaysia and Indonesia.

Remarks. *Johnius heterolepis* can be distinguished from most similar sympatric congener species, *J. sasakii*, by the snout pointed (snout blunt in *sasakii*) and the gill raker slender and count more higher (9 to 11 in *heterolepis* vs short, stiff, 8 to 10 in *sasakii*). *Johnius heterolepis* also is a common species, dominant and abundant especially concentrated in Sarawak states. It was collected at several sites of the Goebilt, Sarikei, and Bintulu.

***Johnius macrorhynus* (Lal Mohan, 1976)**
(Common name: Big-nose croaker)
(Fig. 11, Table 7)

Johnieops macrorhynus Lal Mohan, 1976: 20 (type locality: Mumbai, India) Holotype: FMRI 189; Paratypes: FMRI 190/1-19 (19).
Johnius macrorhynus (Mohan, 1976): Sasaki, 2000: 621; Sasaki, 2001: 3150; Mohamad Faisal, 2009: 98; Atan *et al.* 2010: 195; Matsunuma *et al.*, 2011: 139; Kimura *et al.*, 2015: 63.
Johnius elongatus non of Mohan, 1976: Atan *et al.*, 2010: 195

Material examined. Non-types: NMMB-P37091 (6, 147.41 to 172.69 mm SL), Sibu, Sarawak, Malaysia, 13 March 2017; NMMB-P26507 (3, 127.64 to 157.48 mm SL), Kuala Kedah, Kedah, Malaysia, 19 May 2014; NMMB-P34745 (7, 147.48 to 164.82 mm SL), Tawau, Sabah, Malaysia, 23 February 2017; NMMB-P21544 (212.17 mm SL), Tanjung Piandang, Perak, Malaysia, 3 June 2014; NMMB-P34746 (9, 133.95 to 188.67 mm SL), Betangor, Sarawak, Malaysia, 14 March 2017; NMMB-P21548 (5, 126.96 to 170.6 mm SL), NMMB-P26520 (3, 138.5 to 160.28 mm SL), Pantai Remis, Perak, Malaysia, 4 June 2014; NMMB-P31393 (11, 96 to 177 mm SL), Muar, Johor, Malaysia, 19 March 2019; NMMB-P21518 (4, 142.76 to 163.88 mm SL), Tanjung Gemok, Pahang, Malaysia, 10 July 2014; NMMB-P34747 (137.25 mm SL), Kuching, Sarawak, Malaysia, 17 March 2017; NMMB-P26502 (3, 144.9 to 175.51 mm SL), NMMB-P21558 (155.76 mm SL), Endau, Johor, Malaysia, 11 June 2014; NMMB-P34744 (115.97 mm SL), Bako, Sarawak, Malaysia, 17 March 2017.

Diagnosis. A species of *Johnius* with the following combination of characters: snout bluntly rounded, slightly projecting in front of upper jaw; mouth small, inferior; lower jaw with a band of villiform teeth and an inner, short row of molariform teeth posteriorly; gill rakers very short, stumpy, about 1/4 length of gill filaments at angle of arch, 7 to 8 on lower limb of first gill arch; second spine rather short, slender, 15 to 28% of head length; and scales moderately large, 4 to 5 scale rows above lateral line to origin of dorsal fin, 7 to 9 scale rows below lateral line to origin of anal fin (Hanafi *et al.*, 2022).

Distribution. Indo-West Pacific; Pakistan and India east to South China Sea.

Remarks. *Johnius macrorhynus* can be distinguished from sympatric congener species, *J. carouna* and *J. sasakii*, by the second anal spine rather short and slender (vs long, stiff, in *carouna* and short, stiff in *sasakii*) and the gill raker very short, stumpy and lower count, 7 to 8 (vs short, stiff 10 to 12 in *carouna* and short, stiff, 8 to 10 in *sasakii*). *Johnius macrorhynus* also is a common species, and abundant especially concentrated in Sarawak states. It was collected at several sites of the Goebilt, Sarikei, and Sibu**.**

FIGURE 11. Photographs of the comparative materials. *Johnius macrorhynus* NMMB-P 37091, 148 mm SL, Sibu, Sarawak, Malaysia, 13 March 2017.

***Johnius plagiostoma* (Bleeker, 1849)**
(Common name: Big-eye croaker)
(Fig. 12, Table 7)

Corvina plagiostoma Bleeker, 1849: 10 (type locality: Madura Straits near Surabaya and Kammal, Java, Indonesia.) Syntypes: RMNH 5984 (2)
Johnius plagiostoma (Bleeker, 1850): Sasaki, 1999: 276; Sasaki, 2000: 621; Sasaki, 2001: 3157; Mohamad Faisal, 2009: 98; Atan *et al.*, 2010: 195

Material examined. Non-types: NMMB-P37100 (3, 90.97 to 95.43 mm SL), Sarikei, Sarawak, Malaysia, 14 March 2017; NMMB-P37101 (10, 80.93 to 103.56 mm SL), Goebilt, Sarawak, Malaysia, 17 March 2017; NMMB-P31389 (2, 87.72 to 103.64 mm SL), Muar, Johor, Malaysia, 19 March 2019: NMMB-P21525 (3, 81.16 to 94.65 mm SL), Tanjung Piandang, Perak, Malaysia, 6 June 2014; NMMB-P26489 (3, 91.15 to 110.23 mm SL), Kuala Kurau, Perak, Malaysia, 1 June 2014; NMMB-P26500 (3, 87.39 to 105.49 mm SL), Kuala Kurau, Perak, Malaysia, 23 November 2019.

Diagnosis. A species of *Johnius* with the following combination of characters: snout rounded, never pointed; mouth large, strongly oblique; large eye, 22 to 32% of head length; gill rakers long, slender, equal or slightly shorter than length of gill filaments at angle of arch, 15 on lower limb of first gill arch; second anal spine length long, stiff, about 24 to 40% of HL; and scales moderately small, 8 scale rows above lateral line.

Distribution. Eastern Indian Ocean, western Pacific: Bangladesh and Myanmar east to Java, Borneo and Vietnam.

Remarks. *Johnius plagiostoma* can be easily differentiated from the rest of other *Johnius* species in the East Malaysian waters by the oblique mouth and obviously large eye. *Johnius plagiostoma* is abundant and was available collected only from Sarawak states, specifically in Goebilt and Sarikei collection sites, which mainly segregated in the large mouth and delta riverine system. This might be due to the ecological factor of freshwater and marine waters mainly mixed up, suitable for the species habitat and availability of food resources.

FIGURE 12. Photographs of the comparative materials. *Johnius plagiostoma*: NMMB-P 37101, non-type, 95.43 mm SL, Goebilt fish landing port, Sarawak, Malaysia, 17 March 2017.

***Johnius sasakii* Hanafi, Chao, Seah, Chen, Chang and Liu, 2021**
(Common name: Sasaki croaker)
(Fig. 13, Table 7)

Johnius sasakii Hanafi *et al.* 2022: 397 (type locality: Fish landing port at Bako, Sarawak.)

FIGURE 13. Photographs of the comparative materials. *Johnius sasakii* NMMB-P 37092, 123 mm SL, Miri, Sarawak, Malaysia, 23 February 2017.

Material examined. Type specimens: Holotype. NMMB-P 34733, 1 [111 mm SL], fish landing port at Bako, Sarawak collected by Norhafiz Hanafi on 17 March 2017. Paratypes. NMMB-P 34734, 1 (110 mm SL), fish landing port at Betangor, Sarawak, Malaysia, collected by Norhafiz Hanafi, 14 March 2017. NMMB-P 34735, 3 (103–108 mm SL), fish landing port at Sandakan, Sabah, Malaysia, collected by Norhafiz Hanafi, 27 February 2017. NMMB-P 34736, 1 (134 mm SL), fish landing port at Bintulu, Sarawak, Malaysia, collected by Norhafiz Hanafi, 9 March 2017. NMMB-P 34737, 5 (122–147 mm SL),) fish landing port at Bintulu, Sarawak, Malaysia, collected by Norhafiz Hanafi, 11 March 2017. NMMB-P 34738, 4 (105–118 mm SL), fish landing port at Miri, Sarawak, Malaysia, collected by Norhafiz Hanafi, 7 March 2017. NMMB-P 34739, 3 (100– 146 mm SL), fish landing port at Kota Kinabalu, Sabah, Malaysia, collected by Norhafiz Hanafi, 4 March 2017.
Non-types: NMMB-P37092 (2, 123.32 to 125.46 mm SL), Miri, Sarawak, Malaysia, 7 March 2017; NMMB-P37093 (6, 113.39 to 130.95 mm SL), Tawau, Sabah, Malaysia, 23 February 2017; NMMB-P37094 (10, 103.67 to 138.71 mm SL), Kota Kinabalu, Sabah, Malaysia, 4 March 2017; NMMB-P37095 (3, 100.03 to 130.27 mm SL), Sandakan, Sabah, Malaysia, 26–27 February 2017.

Diagnosis. A species of *Johnius* with the following combination of characters: number of total outer gill rakers of 1st arch, 8 to 10 (mode 9); second anal spine short and stiff, 25 to 35% SL; body depth moderately deep, 25 to 29% SL; the number of scale rows above lateral line, 4–6 (mode 5); body scales moderately large and ctenoid; and snout bluntly rounded.

Distribution. Western Pacific: Sarawak and Sabah, Borneo, Malaysia.

Remarks. *Johnius sasakii* can be distinguished from sympatric congener species, *J. carouna* and *J. heterolepis*, by the second anal spine rather short and stiff (vs long, stiff, in *carouna* and short, slender in *heterolepis*) and the gill raker short, stiff, and lower count, 8 to 10 (vs short, stiff, 10 to 12 in *carouna* and 9 to 11 in *heterolepis*). *Johnius sasakii* also is a common species, and abundant stretching from Sabah and Sarawak states. It can be was collected at several sites of the Sandakan until Kuching (Hanafi *et al.* 2022).

Johnius weberi Hardenberg, 1936

(Common name: Weber croaker)
(Fig. 14, Table 7)

Johnius weberi Hardenberg, 1936: 251 (type locality: Telok Pekadai, Kapaus River, Borneo; mouth of Pekadai; mouth of Peniti River; Pedang Tukar Bay). Syntypes: (6) ZMA 113119 (2), 113120 (2).
Johnius weberi Hardenberg, 1936: Sasaki, 2000: 621; Sasaki, 2001: 3153; Mohamad Faisal, 2009: 98; Atan *et al.*, 2010: 196.

FIGURE 14. Photographs of the comparative materials. *Johnius weberi*: NMMB-P 37098, non-type, 117.55 mm SL, Kuala Pahang fish landing port, Pahang, Malaysia, 2 April 2017.

Material examined. Non-types: NMMB-P37097 (3, 115.97 to 126.43 mm SL), Beluran, Sabah, Malaysia, 28 February 2017; NMMB-P37098 (5, 117.55 to 122.51 mm SL), Kuala Pahang, Pahang, Malaysia, 2 April 2017; NMMB-P37099 (2, 134.33 to 129.36 mm SL), Tawau, Sabah, Malaysia, 23 May 2017; NMMB-P23652 (2, 104.33 to 118.12 mm SL), Kuala Kedah, Kedah, Malaysia, 3 June 2014; NMMB-P21716 (A) (30, 62.25 to 112.97 mm SL), Matang, Perak, Malaysia, 21 April 2011.

Diagnosis. A species of *Johnius* with the following combination of characters: medium species with elongate body, body depth 21 to 24% of standard length; snout swollen, projecting well in front of upper jaw; mouth small, inferior; moderately small eye, 20 to 25% of HL; gill rakers short, stiff, about 1/3 to 1/2 length of gill filaments at angle of arch, 7 to 9 on lower limb of first gill arch; second anal spine length moderately long, slender, about 22 to 31% of HL; and scales moderately small, 7 to 10 scale rows above lateral line.

Distribution. Eastern Indian Ocean, western Pacific: Indonesia east to Papua New Guinea, north to Vietnam and Hong Kong (China).

Remarks. *Johnius weberi* can be differentiated from the rest of other *Johnius* species in the East Malaysian waters by the obvious swollen snout, yellowish to silvery body color, with long elongate body and also with the long and slender second anal spine length. *Johnius weberi* is rare and was endemic species mainly can be collected at mangrove mouth river with highly freshwater recharge stretching from the Sabah states. It was only collected at the Beluran collection sites in our sampling survey.

Johnius trewavasae Sasaki, 1992

(Common name: Trewavas croaker)
(Fig. 15–16, Table 8–9)

Johnius trewavasae Sasaki, 1992: 191 (type locality: Taiwan Strait. Holotype: HUMZ 109504. Paratypes: ANSP 52863 (1), 53478 (2); CAS-SU 60859 (1), 60870 (1), 60918 (1), 61045 (3, 2 c&s), 61080 (2), 61484 (2); HUMZ 109501 (1).
Johnius trewavasae Sasaki, 1992: Sasaki, 2000: 621; Sasaki, 2001: 3152; Ng *et al.*, 2015: 327.

Material examined. Non-types: NMMB-P15218 (5, 117.11 to 141.73 mm SL), Guangdong, China, 1 June 2010; NMMB-P37087 (4, 110.49 to 136.29 mm SL), Sarikei, Sarawak, Malaysia, 14 March 2017; NMMB-P23653 (3, 129.67 to 133.81 mm SL), Tanjung Gemok, Pahang, Malaysia, 10 June 2014.

FIGURE 15. Photographs of the comparative materials. *Johnius trewavasae*, NMMB-P33709, non-type, 170.9 mm SL, Sarikei fish landing port, Sarawak, Malaysia, 14 March 2017.

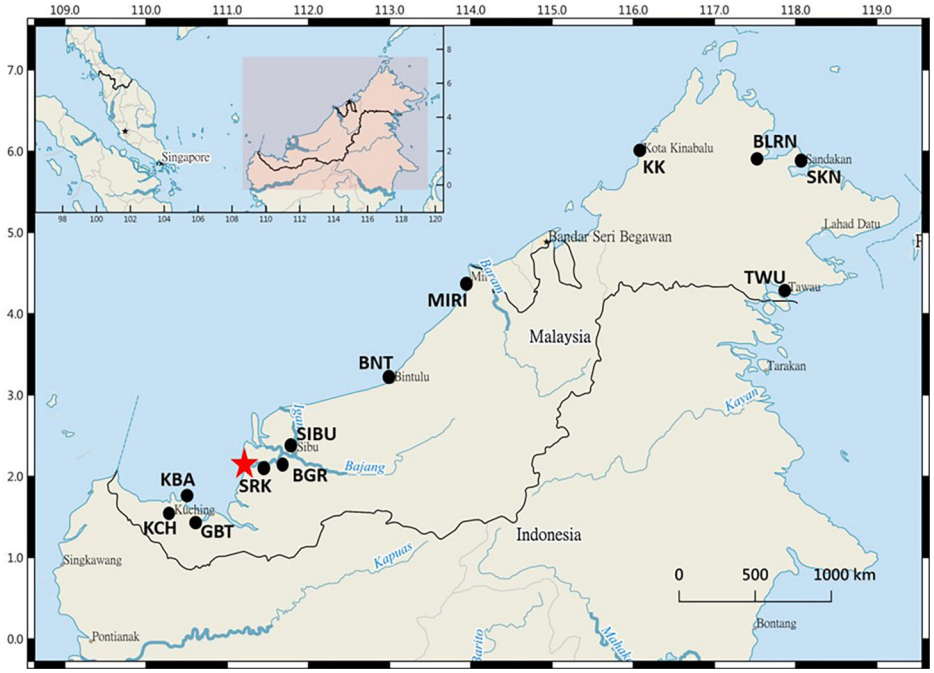

FIGURE 16. New record of site of collection samples of *Johnius trewavasae* in Sarikei (SRK), Sarawak, East Malaysia.

Diagnosis. A species of *Johnius* with the following combination of characters: snout steep, obtusely rounded; chin lacking barbel; scales above lateral line 4 to 6, below lateral line 7 to 10; gill rakers very short, obtuse, gill rakers at lower limb 8 to 10; second anal spine length 25 to 37% HL; scales ctenoid on body, large, and easily fallout.

Description. Counts and measurements of the type specimens are shown in Table 8. The following data is provided for the Sasaki (1992) measurement first as comparison, followed by the size range and mean for the 4 voucher specimens.

Small species with a moderately elongated body; body depth 25 to 29% of standard length. Eye moderately

large, 18 to 24% of head length. Interorbital width 23 to 27% 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 26 to 31 soft rays; anal fin with II spines and 7 or 8 (most frequently 7) soft rays, second spine rather short, slender, 25 to 35% of head length; caudal fin rhomboidal. Scales large, those on flanks much larger than those on the lateral line, 4 or 6 scale rows above lateral line to origin of dorsal fin, 6 to 14 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.

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

Remarks. Among the *Johnius* (*Johnius*) species with pointed snout and large ctenoid scales (4–6 scales above lateral line), *J. trewavasae* can be mainly differentiated from *J. macrorhynus* and *J. heterolepis* by the lower number of gills raker count on the lower limb (obtuse, short, 8–10 in *trewavasae* vs. stumpy, short, 7–8 in *macrorhynus* vs. slender, short, 9–11 in *heterolepis*) and a shorter lower jaw (33.8–38.4% HL in *trewavasae* vs. 33.8–38.4% HL in *macrorhynus* vs. 40.3–44.2% HL in *heterolepis*). Meanwhile, main criteria of *J. macrorhynus* can be distinguished by *J. trewavasae* by the presence of an inner, short row of molariform teeth at posteriorly. In addition, *J. trewavasae* can be easily differs from *J. carouna* and *J. sasakii* in having the slender and rather short second anal spine fin length (24–37% of HL in *trewavasae* vs. stiff, long, 32–49% of HL in *carouna* vs. stiff, short, 25–35% of HL in *sasakii*) respectively.

TABLE 8. Morphometric and meristic measurements (expressed as %HL, %SL and %ED) of *Johnius trewavasae.*

	Sasaki (1992)	Voucher specimen, NMMB-P 37087 (N=4)			
		Min	Max	Mean	SD
Standard Length (mm)	110.9	100.0	146.9	117.7	
Head Length (mm)	34.4	29.2	44.2	35.6	
Eye Diameter (mm)	7.4	6.6	8.8	7.6	
Counts					
1st dorsal-fin spine	10	10	10	10	0.0
2nd dorsal-fin spine	1	1	1	1	0.0
2nd dorsal-fin soft rays	27	26	31	28	0.0
Anal-fin spine	2	2	2	2	0.0
Anal-fin soft rays	7	7	7	7	0.0
Pectoral-fin rays	17	11	18	16	0.0
Outer gill rakers of 1st arch	15	13	15	14	0.0
upper limb	6	4	6	5	0.0
lower limb	9	8	10	9	0.0
Inner gill rakers of 1st arch	11	10	13	11	0.0
upper limb	3	3	4	3	0.0
lower limb	8	6	9	8	0.0
Pored lateral line scales	51	37	49	47	0.0
Scales above lateral line	6	4	6	5	0.0
Scales below lateral line	9	6	14	10	0.0
Circumpeduncular scales	14	11	17	14	0.0

.....Continued on the next page

TABLE 8. (Continued)

	Sasaki (1992)	Voucher specimen, NMMB-P 37087 (N=4)			
		Min	Max	Mean	SD
Measurements as %HL					
Snout length	23.2	23.0	29.5	26.3	2.0
Maxillary length	41.3	34.0	42.6	38.2	2.8
Eye diameter	21.5	18.0	24.4	21.6	2.0
Interorbital width	23.4	23.8	27.9	26.0	1.3
2nd spine length	31.6	24.9	35.6	29.2	2.6
1st ray length	39.6	30.7	46.7	36.3	3.5
Measurements as %SL					
Snout to anal-fin origin	69.3	67.1	73.3	70.6	1.5
Snout to 2nd dorsal-fin origin	53.2	49.3	55.0	51.7	1.7
Snout to 1st dorsal-fin origin	33.3	31.8	36.2	33.7	1.3
Snout to pectoral-fin insertion	31.2	27.4	32.8	30.3	1.5
Snout to pelvic-fin insertion	35.4	31.0	36.5	34.0	1.5
Pectoral-fin length	21.3	16.6	24.9	19.7	2.3
Head length	31.0	27.7	32.3	30.2	1.2
Pelvic-fin length	15.3	12.7	20.0	16.1	2.0
Body depth (D1-P2)	27.0	25.2	29.0	27.1	1.2
Body width (P1-P1)	15.6	13.4	18.5	15.5	1.8
1st dorsal-fin base length	20.1	15.9	23.1	19.3	2.0
longest spine length	14.9	11.9	16.7	13.8	1.3
2nd dorsal-fin base length	40.1	35.8	44.8	39.7	2.5
longest ray length	8.9	7.0	14.4	9.8	1.7
Anal-fin base length	9.5	6.8	10.2	8.8	0.9
2nd spine length	9.8	7.4	10.2	8.5	0.8
1st ray length	12.3	9.0	13.3	10.9	1.0
Caudal-peduncle depth	10.6	8.7	10.7	9.5	0.4
Pelvic-fin tip to vent	12.7	13.8	22.8	18.4	2.7
Vent to anal-fin origin	4.4	3.2	7.9	5.7	1.2
Measurements as %ED					
Longest gill raker on 1st arch	14.9	11.3	19.9	14.6	2.4
Longest gill filament on 1st arch	55.7	37.7	59.9	51.9	3.4

TABLE 9. Genetic distances for the COI gene among congener species with *Johnius trewavasae* species and *Dendrophysa russelii* as an outgroup.

Species	**1**	**2**	**3**	**4**	**5**	**6**
1. Johnius_heterolepis						
2. Johnius_carouna	0.13					
3. Johnius_trewavasae	0.15	0.16				
4. Johnius_sasakii	0.15	0.17	0.16			
5. Johnius_amblycephalus	0.33	0.34	0.36	0.37		
6. Dendrophysa_russelii	0.34	0.37	0.36	0.34	0.24	

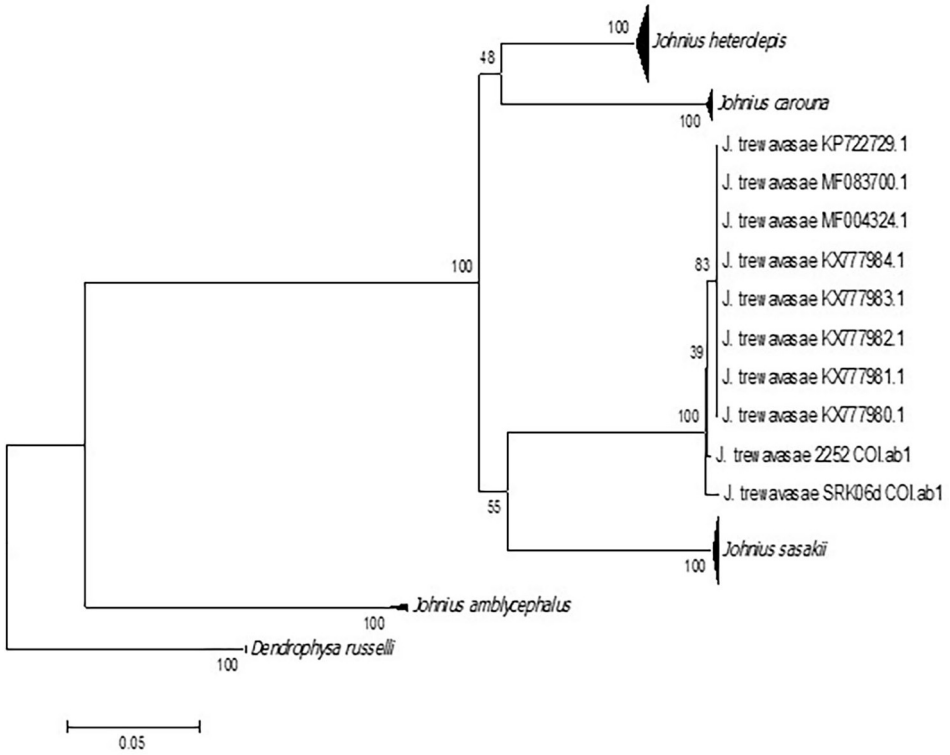

FIGURE 17. Neighbor joining tree of COI gene was reconstructed with sequences of *Johnius amblycephalus*, *J. sasakii, J. carouna, J. heterolepis* and *J. trewavasae*. Bootstrap support values were showed at nodes. Name with asterisk represents the sample from the present study.

According to Ng *et al.*, (2015) and Sasaki (2000), both references mentioned *J. trewavasae* has been recorded occurring in Malaysia waters. Moreover, this species was synonym and frequently misapplied name as *J. heterolepis* and *J. macrorhynus* in Malaysian waters. Indicates from the Fig. 16 shown the new extension of record sites in the East Malaysia waters, concisely at the Sarikei, Sarawak states. According to Ng *et al.*, (2015) and Sasaki (2001) previous collection discovered *J. trewavasae* (LSUMZ 16645) occurring in the Eastern Johor Strait, Malaysia or Singapore waters. Thus, the extension distribution evidence discovered from this study shown several population of *J. trewavasae* might be has been established in the Malaysian waters.

Molecular verification. This work produced phylogenetic tree sequences utilising COI genetic markers with congener *Johnius* species in East Malaysian seas and demarcated them with GenBank sequences to clarify the taxonomic status of *J. trewavasae* with congener species (Lo *et al.*, 2017), as shown in Fig. 17. *Johnius trewavasae* was a sister clade to *J. sasakii* and a sister group to *J. heterolepis* and *J. carouna*, according to the phylogenetic tree connection (Fig. 17). Meanwhile, *Dendrophysa russelii* is the outgroup clade, with a strong bootstrap value confirming the connection and validation species, while *J. amblycephalus* is the basal clade. According to pairwise K2P genetic distances (Table 9), *J. trewavasae* is 16% distinct from *J. sasakii*, 16% different from *J. carouna*, 15% different from *J. heterolepis*, 36% different from *J. amblycephalus*, and 36% different from the outgroup *D. russelii*. In conclusions, the *Johnius* species in this section formed a monophyletic clade, which integrated with complementary approach supported by morphological and genetic evidence confirming the *J. trewavasae* status.

Discussion

Questionable record and taxonomy assessment in the East Malaysian waters

Several references (Sasaki, 2000, 2001; Mohamad Faisal, 2009; Atan *et al.*, 2010) have misidentified *Johnius* specimens from East Malaysian (EM) waters. This might be owing to a paucity of taxonomic works accessible at

the time, which prompted the writers to misidentify specimens due to their similar looks. Sasaki (1992) reinstated the *J. glaucus* and *J. goldmanni* naming complex in the EM waters due to their general similarities. Hanafi *et al.* (2022) recently revised doubtful specimens of *'J. heterolepis*', *'J. carouna*', and *'J. macrorhynus*' taxa from East Malaysia, and it was discovered that this species could be distinguished from other *Johnius* species based on several characteristics, thus describing it as a valid species*, J. sasakii*. Moreover, Hanafi *et al.* (2022) mentioned *J. sasakii* distributional pattern is much restricted and confined to Borneo Island and the southern South China Sea adjacent region.

This research combined the findings of morphological and genetic techniques, confirming eleven genuine species of *Johnius* in the seas of East Malaysia. Furthermore, all *Johnius* taxa are morphologically and genetically similar, and they form a single phylogenetic cluster, supporting the conclusion that all species analysed belong to a single monophyletic group. Our results are comparable with those of Lo *et al.* (2015; 2017) in the basal group clade (*D. russelii* (as an outgroup), *J. amblycephalus*, *J. plagiostoma*, and *J. borneensis*), except that the phylogenetic position of *J. plagiostoma*, *J. belangerii*, *J. coitor*, and *J. weberi* varies in clade position. These differences might be ascribed to different sampling locations and species encountered; nonetheless, Lo *et al.* (2017) conclusions on the *Johnius* relationship remain ambiguous in several taxa. This might be owing to the species encountered in the East Malaysian waters, which has resulted in a distinct phylogenetic relationship in this particular zoogeographical zone.

Evolutionary stages shaping the biodiversity pattern of *Johnius* in East Malaysia

In habitats susceptible to harm, where biodiversity estimates may have been exaggerated, it is crucial to accurately evaluate biodiversity in order to understand evolutionary processes and implement effective conservation strategies. Moreover, without a conclusive determination of the species arrangement, it is unfeasible to engage in a dependable discourse about the historical events and factors that have contributed to the existing biogeographic patterns of the genus *Johnius*. To identify the possible factors contributing to the diversity of the genus in the seas of East Malaysia, it is necessary to redefine the components of the *Johnius* species complexes. Recent taxonomic reviews have been conducted on the following genera: *Haemulon* (Carvalho *et al.*, 2020), *Bairdiella* (Marceniuk *et al.*, 2019a), *Orthopristis* (Marceniuk *et al.*, 2019b), *Pogonias* (Azpelicueta *et al.*, 2019), and *Peprilus* (Marceniuk *et al.*, 2016). These evaluations provided us with valuable insights into the variety of these coastal species. These studies provide important additions to the descriptive biogeography of coastal fish in the western Pacific.

The revalidation of *J. sasakii* confirms the existence of a distinctive fauna of animal species in East Malaysia, namely on Borneo Island, which is considered to be part of the southern South China Sea area (Hanafi *et al.*, 2022). The existence of separate marine-estuarine fish faunas in the northern and southern regions of the South China Sea (SCS) is indicated by the presence of *J. sasakii* in East Malaysia (Hanafi *et al.*, 2022), *J. taiwanensis* in the Taiwanese (Chao *et al.*, 2019), and the newly discovered occurrence of *J. trewavasae* on the Sarawak coast. Several studies have shown variations in the fish species found in reefs in these two regions (Pyle *et al.*, 2008; Williams *et al.*, 2015; Hubert *et al.*, 2017). However, there is a lack of biogeographic analyses focusing on the coastal and estuarine fish populations in these regions (Marceniuk *et al.*, 2016). Prior to recent times, data on the marine and estuarine fish species in the western Pacific indicated that the majority of the species present in the northern South China Sea (SCS) were also present in the southern SCS (Wei *et al.*, 2016). This was probably due to the absence of significant physical obstacles separating the two regions. In conjunction with the outcomes of prior investigations (Hanafi *et al.*, 2022, southern SCS; Hanafi *et al.*, 2023, northern SCS), the results of the current research suggest that this notion needs reevaluation and experimentation with other taxonomic categories.

Biogeographical pattern of *Johnius* species distribution in the present day

The current study findings confirm the presence of a distinct fauna of *Johnius* fishes in the waters of East Malaysia (EM) (Hanafi *et al.*, 2022) and Taiwan (TW) (Hanafi *et al.*, 2023). These findings support the conclusions made by Sasaki (1999; 2000), who identified the South China Sea region as a province of the domain. The presence of distinct faunas along Brazil's North-Northeast and Southeast-South coasts suggests that the Vitória-Trindade

seamount chain may have created a separate area for species interaction on the eastern coast of Brazil during periods of marine regression in the Quaternary and Tertiary epochs (Marceniuk *et al.*, 2019b). The identification of *M. cuiaranensis* and *M. gracilis*, along with the recent findings on *Macrodon ancylodon* and *M. atricauda* (Carvalho-Filho *et al.* 2010) and *Orthopristis scapularis* and *O. ruber* (Marceniuk *et al.* 2019), constitute important progress in our comprehension of the variety of fish species in coastal areas.

The geographical extent of the *Johnius* species in the South China Sea seems to be primarily influenced by three prominent oceanic current systems, including the South China, North China Coastal, and Kuroshio Currents (Shen *et al.*, 2011). The South China Current, originating from the South China Sea and heading northward towards the Taiwan Strait, merges with the North China Coastal Current. This results in mixing warm water from the South China Current with cold water from the North China Coastal Current, which flows southward from the Yellow Sea and East China Sea. *Johnius amblycephalus*, *J. belangerii*, and *J. borneensis* have a wide distribution range as a result of their high tolerance for varying temperatures and salinity. The distribution range of the southern species (*J. carouna*, *J. coitor*, *J. heterolepis*, *J. macrorhynus*, *J. plagiostoma*, *J. sasakii*, and *J. weberi*) appears to be influenced by the warm water of the South China Current. On the other hand, the northern species (*J. distinctus*, *J. grypotus*, *J. taiwanensis*, and *J. trewavasae*) seem to be confined to the cold waters of the North China Coastal Current, which flows southward during the winter due to the northeastern monsoon (Hanafi *et al.*, 2023; Zhang *et al.*, 2019). The strong correlation between oceanographic current systems and the distribution of *Johnius* species is likely due to their temperature preferences. The temperature variations between the South China Sea current and the China Coastal Current may vary from 6 to 11°C (Chu & Guihua, 2003; Shen *et al.*, 2011). *Johnius* may serve as an excellent indicator species for global change in this specific environment. This is corroborated by the discovery of two recently identified species, *J. sasakii,* and *J. taiwanensis*, which further emphasises the need for more extensive biogeographic investigations on the marine and estuarine fish fauna in the coastal areas of the South China Sea.

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References

Ambak, M.A., Isa, M.M., Zakaria, M.Z. & Mazlan, M.A. (2010) *Fishes of Malaysia. 2nd Edition*. Penerbit UMT, Terengganu, 301 pp.

Atan, Y., Jaafar, H. & Majid, A.R.A. (2010) *Ikan laut Malaysia: glosari nama sahih species ikan*. Dewan Bahasa dan Pustaka, Kuala Lumpur, 290 pp.

Azpelicueta, M.D.L.M., Delpiani, S.M., Cione, A.L., Oliveira, C., Marceniuk, A.P. & Díaz de Astarloa, J.M. (2019) Morphology and molecular evidence support the validity of *Pogonias courbina* (Lacepède, 1803)(Teleostei: Sciaenidae), with a redescription and neotype designation. *PLoS One*, 14 (6), e0216280. https://doi.org/10.1371/journal.pone.0216280

Carvalho, C.O., Marceniuk, A.P., Oliveira, C. & Wosiacki, W.B. (2020) Integrative taxonomy of the species complex *Haemulon steindachneri* (Eupercaria; Haemulidae) with a description of a new species from the western Atlantic. *Zoology*, 141, 125782. https://doi.org/10.1016/j.zool.2020.125782

Carvalho-Filho, A., Santos, S. & Sampaio, I. (2010) *Macrodon atricauda* (Günther, 1880)(Perciformes: Sciaenidae), a valid species from the southwestern Atlantic, with comments on its conservation. *Zootaxa*, 2519 (1), 48–58. https://doi.org/10.11646/zootaxa.2519.1.3

Chao, L.N. (1978) A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). *NOAA Technical Report NMFS*

Circular, 415, 1–64.
Chao, N.L., Chang, C.W., Chen, M.H., Guo, C.C., Lin, B.A., Liou, Y.Y., Shen, K.N. & Liu, M. (2019) *Johnius taiwanensis*, a new species of Sciaenidae from the Taiwan Strait, with a key to *Johnius* species from Chinese waters. *Zootaxa*, 4651 (2), 259–270.
https://doi.org/10.11646/zootaxa.4651.2.3
Chao, N.L., Frédou, F.L., Haimovici, M., Peres, M.B., Polidoro, B., Raseira, M., Subirá, R. & Carpenter, K. (2015) A popular and potentially sustainable fishery resource under pressure extinction risk and conservation of Brazilian Sciaenidae (Teleostei: Perciformes). *Global Ecology and Conservation*, 4, 117–126.
https://doi.org/10.1016/j.gecco.2015.06.002
Chin, P.K. (1998) *Marine food fishes and fisheries of Sabah/Chin Phui Kong; foreword by Dr. Mahathir bin Mohamad; photographs by Tomoyoshi Kajiwara*. Natural History Publications (Borneo) in association with Science and Technology Unit, Kota Kinabalu, Sabah. [unknown pagination]
Chu, P.C. & Guihua, W. (2003). Seasonal variability of thermohaline front in the central South China Sea. *Journal of oceanography*, 59, 65–78.
https://doi.org/10.1023/A:1022868407012
Chu, Y.T., Lo, Y.L. & Wu, H.L. (1963) *A study on the classification of the Sciaenoid fishes of China, with description of new genera and species*. Shanghai Science and Technology Press, Shanghai, 140 pp.
Cuvier, G. & Valenciennes, A. (1830) *Histoire naturelle des poissons. Tome cinquième. Livre cinquième. Des Sciénoïdes. Vol. 5*. F. G. Levrault, Paris, 499 pp., pls. 100–140. [Cuvier authored volume. xx + 374 pp. in Strasbourg edition]
Fricke, R., Eschmeyer, W.N. & Van der Laan, R. (2023) *Catalogue of fishes: genera, species, references*. *Electronic Version.* California Academy of Sciences, San Francisco, California. Available from: http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp (accessed 31 January 2023)
Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology*, 59 (3), 307–321.
https://doi.org/10.1093/sysbio/syq010
Hanafi, N., Chen, M.H., Seah, Y.G., Chang, C.W., Liu, S.Y.V., Lai, C.C. & Chao, N.L. (2023) Taxonomic Revision of the Genus Croaker *Johnius* (Perciformes: Sciaenidae) in Taiwanese Waters. *Journal of Marine Science and Engineering*, 11 (3), 471.
https://doi.org/10.3390/jmse11030471
Hanafi, N., Chen, M.H., Seah, Y.G., Chang, C.W., Liu, S.Y.V. & Chao, N.L. (2022) *Johnius sasakii*, a new species of croaker (Perciformes: Sciaenidae) with a key to *Johnius* from East Malaysia, Borneo. *Zootaxa*, 5116 (3), 393–409.
https://doi.org/10.11646/zootaxa.5116.3.5
Henriques, R., Potts, W.M., Sauer, W.H., Santos, C.V., Kruger, J., Thomas, J.A. & Shaw, P.W. (2016) Molecular genetic, life-history and morphological variation in a coastal warm-temperate sciaenid fish: evidence for an upwelling-driven speciation event. *Journal of Biogeography*, 43 (9), 1820–1831.
https://doi.org/10.1111/jbi.12829
Hubbs, C.L. & Lagler, K.F. (2004) *Fishes of the Great Lakes region*. *Rev. Edition by G.R. Smith*. University of Michigan Press, Ann Arbor, Michigan, 332 pp.
https://doi.org/10.3998/mpub.17658
Hubert, N., Dettai, A., Pruvost, P., Cruaud, C., Kulbicki, M., Myers, R.F. & Borsa, P. (2017). Geography and life history traits account for the accumulation of cryptic diversity among Indo-West Pacific coral reef fishes. *Marine Ecology Progress Series*, 583, 179–193.
https://doi.org/10.3354/meps12316
Iwatsuki, Y., Jawad, L.A. & Al-Mamry, J.M. (2012) *Johnius (Johnius) majan* sp. nov., a sciaenid fish (Pisces: Sciaenidae) from Oman, Indian Ocean. *Ichthyological Research*, 59, 151–155.
https://doi.org/10.1007/s10228-011-0265-8
Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16 (2), 111–120.
https://doi.org/10.1007/BF01731581
Kimura, S., Arshad, A., Imamura, H. & Ghaffar, M.A. (2015) *Fishes of the northwestern Johor Strait, peninsular Malaysia*. University Putra Malaysia Press, Serdang, 108 pp.
Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35 (6), 1547.
https://doi.org/10.1093/molbev/msy096
Lal Mohan, R.S. (1972) A synopsis of the Indian genera of the fishes of the family Sciaenidae. *Indian Journal of Fisheries*, 16, 82–98.
Lal Mohan, R.S. (1976) Two new species of sciaenid fishes *Johnius elongatus* and *Johnieops macrorhynus* from India. *Matsya*, 1, 19–25.
Lal Mohan, R.S., Trewavas, E. & Whitehead, P.J.P. (1984) Sciaenidae. *In*: Fishers, W. & Bianchi, G. (Eds.), *FAO species identification sheets for fishery purposes. Vol. 4. Western Indian Ocean. Fishing Area 51*. FAO, Rome, pp. SCIAEN-SCIAEN Umbr 6.

Lefort, V., Longueville, J.E. & Gascuel, O. (2017) SMS: smart model selection in PhyML. *Molecular Biology and Evolution*, 34 (9), 2422–2424.
https://doi.org/10.1093/molbev/msx149

Lim, A.P.K. & Gambang, A.C. (2009) *Field Guide to Marine & Estuarine Fishes of Sarawak*. Fisheries Research Institute, Bintawa, 316 pp.

Lim, A.P.K., Ahmad, A., Nor Azman, Z. & Mohd Saki, N. (2018) *Field Guide to Fishes and Crustaceans of the Southeast Asian Region*. *SEAFDEC/MFRDMD/39*. Jabatan Perikanan Malaysia, Putrajaya, 246 pp.

Lo, P.C., Liu, S.H., Chao, N.L., Nunoo, F.K., Mok, H.K. & Chen, W.J. (2015) A multi-gene dataset reveals a tropical New World origin and Early Miocene diversification of croakers (Perciformes: Sciaenidae). *Molecular Phylogenetics and Evolution*, 88, 132–143.
https://doi.org/10.1016/j.ympev.2015.03.025

Lo, P.C., Liu, S.H., Nor, S.A.M. & Chen, W.J. (2017) Molecular exploration of hidden diversity in the Indo-West Pacific sciaenid clade. *PLoS ONE*, 12 (4), e0176623.
https://doi.org/10.1371/journal.pone.0176623

Marceniuk, A.P., Caires, R., Siccha-Ramirez, R. & Oliveira, C. (2016) Review of the harvestfishes, genus *Peprilus* (Perciformes: Stromateidae), of the Atlantic coast of South America. *Zootaxa*, 4098 (2), 311–332.
https://doi.org/10.11646/zootaxa.4098.2.6

Marceniuk, A.P., Molina, E.G., Caires, R.A., Rotundo, M.M., Wosiacki, W.B. & Oliveira, C. (2019a) Revision of *Bairdiella* (Sciaenidae: Perciformes) from the western South Atlantic, with insights into its diversity and biogeography. *Neotropical Ichthyology*, 17 (1). [published online]
https://doi.org/10.1590/1982-0224-20180024

Marceniuk, A.P., Caires, R.A., Machado, L., Cerqueira, N.N.C.D., Serra, R.R.M.D.S. & Oliveira, C. (2019b) Redescription of *Orthopristis ruber* and *Orthopristis scapularis* (Haemulidae: Perciformes), with a hybridization zone off the Atlantic coast of South America. *Zootaxa*, 4576 (1), 109–126.
https://doi.org/10.11646/zootaxa.4576.1.5

Matsunuma, M., Motomura, H., Matsuura, K., Shazili, N.A.M. & Ambak, M.A. (Eds.) (2011) *Fishes of Terengganu – east coast of Malay Peninsula, Malaysia*. National Museum of Nature and Science, Universiti Malaysia Terengganu and Kagoshima University Museum, Kagoshima, ix + 251 pp.

Mok, H.K., Yu, H.Y., Ueng, J.P. & Wei, R.C. (2009) Characterization of sounds of the blackspotted croaker *Protonibea diacanthus* (Sciaenidae) and localization of its spawning sites in estuarine coastal waters of Taiwan. *Zoological Studies*, 48 (3), 325–333.

Mohamad Faisal, M.S., Yusri, A., Abdul Rahman, A.M., Lim, A.P.K., Irman, I. & Nurul Syuhada, H.A.K. (2009) *Valid Local Name of Malaysian Marine Fishes*. Department of Fisheries Malaysia, Putrajaya. [unknown pagination]

Mohsin, A.K.M. & Ambak, M.A. (1996) *Marine fishes and fisheries of Malaysia and neighbouring countries*. Universiti Pertanian Malaysia Press, Serdang, Selangor Darul Ehsan, 744 pp.

Ng, H.H., Tan, H.H., Lim, K.K., Ludt, W.B. & Chakrabarty, P. (2015) Fishes of the eastern Johor Strait. *Raffles Bulletin of Zoology*, 31, 303–337.

Parenti, P. (2020) An annotated checklist of fishes of the family Sciaenidae. *Journal of Animal Diversity*, 2 (1), 1–92.
https://doi.org/10.29252/JAD.2020.2.1.1

Pyle, R.L., Earle, J.L. & Greene, B.D. (2008) Five new species of the damselfish genus *Chromis* (Perciformes: Labroidei: Pomacentridae) from deep coral reefs in the tropical western Pacific. *Zootaxa*, 1671 (1), 3–31.
https://doi.org/10.11646/zootaxa.1671.1.2

Sabaj, M.H. (2019) *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 7.1. Updated 21 March 2019*. American Society of Ichthyologists and Herpetologists, Washington, D.C. [unknown pagination]

Sasaki, K. (1989) Phylogeny of the Family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Memoirs of the Faculty of Fisheries Hokkaido University*, 36 (1–2), 1–137.
https://doi.org/10.1007/BF02905681

Sasaki, K. (1992) Two new and two resurrected species of the sciaenid genus *Johnius* (*Johnius*) from the West Pacific. *Japanese Journal of Ichthyology*, 39 (3), 191–199.
https://doi.org/10.1007/BF02905476

Sasaki, K. (1996) Sciaenid fishes of the Indian Ocean (Teleostei, perciformes). *Memoirs of the Faculty of Science Kochi University*, Series D: Biology, 16, 83–96.

Sasaki, K. (1999) *Johnius* (*Johnieops*) *philippinus,* a new species sciaenid from the Philippines, with a synopsis of species included in the subgenus a *Johnieops*. *Ichthyological Research*, 46 (3), 271–279.
https://doi.org/10.1007/BF02678513

Sasaki, K. (2000) A checklist of the fishes of the South China Sea. *In*: Randall, J.E. & Lim, K.K.P. (Eds.), *Raffles Bulletin of Zoology Supplement*, 8, pp. 621.

Sasaki, K. (2001) Sciaenidae. *In*: Carpenter, K.E. & Niem, V.H. *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Vol. 5. Bony Fishes. Part 3. Menidae to Pomacentridae*. FAO, Rome, pp. 3117–3174.

Seah, Y.G., Hanafi, N., Mazlan, A.G. & Chao, N.L. (2015) A new species of *Larimichthys* from Terengganu, east coast of Peninsular Malaysia (Perciformes: Sciaenidae). *Zootaxa*, 3956 (2), 271–280.
https://doi.org/10.11646/zootaxa.3956.2.7

Seah, Y.G., Mohd Sharol, A., Mazlan, A.G. & Mat Jaafar, T.N.A. (2021) *Marine Fishes of Kuantan: Malaysia Biodiversity Information System (MyBIS)*. Penerbit UMT, Terengganu, Kuala Nerus, 172 pp.

Shah, N.H.A. (2017) *Revision of croakers (perciformes: sciaenidae) identification by using integrative approaches*. Master Dissertation, Universiti Malaysia, Terengganu. Terengganu. [unknown pagination]

Shen, K.N., Jamandre, B.W., Hsu, C.C., Tzeng, W.N. & Durand, J.D. (2011) Plio-Pleistocene sea level and temperature fluctuations in the northwestern Pacific promoted speciation in the globally-distributed flathead mullet *Mugil cephalus*. *BMC evolutionary biology*, 11 (1), 1–17.
https://doi.org/10.1186/1471-2148-11-83

Talwar, P.K. (1995) *Fauna of India and the adjacent countries. Pisces Perciformes: Sciaenidae*. Zoological Survey of India, Calcutta, vii (unnumbered) + 144 pp.

Talwar, P.K. (1969) *On the generic relationship of Bola coitor Hamilton (Pisces: Sciaenidae) with a redescription of the species*. Master's Dissertation, Indian Academy of Sciences, Bengaluru. [unknown pagination]

Trewavas, E. (1964) The sciaenid fishes with a single mental barbel, *Copeia*, 1964 (1), 107–117.
https://doi.org/10.2307/1440838

Trewavas, E. (1977) The sciaenid fishes (croakers or drums) of the Indo-West-Pacific. *Transactions of the Zoological Society of London*, 33, 253–541.
https://doi.org/10.1111/j.1096-3642.1977.tb00052.x

Wei, Z., Fang, G., Xu, T., Wang, Y. & Lian, Z. (2016) Seasonal variability of the isopycnic surface circulation in the South China Sea derived from a variable-grid global ocean circulation model. *Acta Oceanologica Sinica*, 35, 11–20.
https://doi.org/10.1007/s13131-016-0791-3

Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O. & Brainard, R.E. (2015) Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS ONE*, 10 (4), e0120516.
https://doi.org/10.1371/journal.pone.0120516

Wong, H.S. & Yong, C.C. (2020) Fisheries regulation: A review of the literature on input controls, the ecosystem, and enforcement in the Straits of Malacca of Malaysia. *Fisheries Research*, 230, 105682.
https://doi.org/10.1016/j.fishres.2020.105682

Zhang, L.L., Liu, M., Fang, L.P., Xu, Q. & Lin, J.J. (2019) Reproductive Biology of *Johnius taiwanensis* (Perciformes: Sciaenidae) in Fujian Waters, Southern China. *Zoological studies*, 58, 38.