



Johnius sasakii, a new species of croaker (Perciformes: Sciaenidae) with a key to *Johnius* from East Malaysia, Borneo

NORHAFIZ HANAFI^{1*}, MENG-HSIEN CHEN^{1,2,3}, YING GIAT SEAH^{4,5}, CHIH-WEI CHANG^{1,2,6}, SHANG YIN VANSON LIU⁷ & NING LABBISH CHAO^{6,8}

¹Department of Oceanography (Marine Biology group), National Sun Yat-sen University, Kaohsiung, Taiwan

²Marine Ecology and Conservation Research Center, National Academy of Marine Research, Kaohsiung, Taiwan

³Institute of Marine Ecology and Conservation, National Sun Yat-sen University, Kaohsiung, Taiwan

✉ mhchenvc@gmail.com; <https://orcid.org/0000-0002-1868-7061>

⁴Faculty of Fisheries and Food Science, University Malaysia Terengganu (UMT), Kuala Nerus, Malaysia

✉ ygseah@umt.edu.my; <https://orcid.org/0000-0002-2976-4448>

⁵Fish Division, South China Sea Repository and Reference Centre, Institute of Oceanography and Environment, University Malaysia Terengganu (UMT), Kuala Nerus, Malaysia

⁶National Museum of Marine Biology and Aquarium, and Graduate Institute of Marine Biology, National Dong Hwa University, Pingtung, Taiwan

✉ changcw1831@gmail.com; <https://orcid.org/0000-0002-0659-9582>

⁷Department of Marine Biotechnology and Resources, National Sun Yat-Sen University, Kaohsiung, Taiwan

✉ oceandiver6426@gmail.com; <https://orcid.org/0000-0002-9472-3941>

⁸Bio-Amazonia Conservation International, Boston, Massachusetts, USA.

✉ croackerchao@gmail.com; <https://orcid.org/0000-0002-0474-8740>

*Corresponding author. ✉ hafizhanafi90@gmail.com; <https://orcid.org/0000-0003-3662-3843>

Abstract

A new sciaenid fish, *Johnius sasakii* **sp. nov.** from the East Malaysian coastal waters of Sabah and Sarawak, Borneo is described herein. *Johnius sasakii* **sp. nov.** can be separated from the close congeners, *Johnius heterolepis* and *Johnius carouna* by having less gill rakers on the lower limb of the first gill arch (mode number 9 vs. 10 for *J. heterolepis*; 11 for *J. carouna*). It can be distinguished from *J. heterolepis* with the higher modal number of gill rakers on the upper limb of first gill arch (5 vs. 4), shorter anal-fin base length (9% vs. 10% of SL) and first anal-fin ray length (10–12% vs. 12–13% of SL) respectively. Furthermore, *J. sasakii* **sp. nov.** can be further differentiated from *J. carouna* by its shorter second anal-fin spine length 7–10% SL (usually 8–10%) vs. 11–14% SL (usually 11–12%) and slightly deeper body depth 25–29% SL (usually 26–28%) vs. 23–28% SL (usually 24–26%). Meanwhile, *J. sasakii* **sp. nov.** can be easily differentiated from *J. macrorhynchus* by a present of molariform teeth on inner rows of jaws and stumpy gill rakers. *Johnius (Johnius) sasakii* **sp. nov.** can be clearly distinguished from species of the subgenus *J. (Johnieops)* by the lack of enlarged outer row teeth on upper jaw. A Kimura 2-parameter genetic distance comparison of 450 bp sequences of mitochondrial 16S rRNA and 488 bp nuclear gene S7 showed that *J. sasakii* **sp. nov.** are highly differentiated from *J. heterolepis* (16S: 10.4%, S7: 5.8%), *J. carouna* (16S: 19.3%, S7: 8.4%); and *J. macrorhynchus* (16S: 16.7%, S7: 8.1%) respectively. The study highlights that the genetic approach from mtDNA and nDNA can contribute to the confirmation of taxonomic status of sympatric species in genus *Johnius*.

Key words: taxonomy, sympatric, genetic, South China Sea

Introduction

There are nearly 100 species of sciaenid fishes in the Indo-West Pacific (IWP) region (Trewavas 1977; Lal Mohan 1984; Sasaki 1989; Chao *et al.* 2019). The genus *Johnius* Bloch, 1793 is a small to medium-sized group endemic to the region with 32 recognized species (Fricke *et al.* 2020). The genus *Johnius*, type species, *Johnius carutta* Bloch, 1793, designated by Gill (1862), has been widely applied to several sciaenid fishes of the Indo-West Pacific. Trewavas (1977) reviewed the nomenclature and synonyms of genus *Johnius*; Sasaki (1989) defined the genus and the tribe Johniini by several synapomorphic characters: i) a hammer-shaped gas bladder with 13–17 arborescent lateral

appendages; ii) the first lateral branch extends to the dorsal corner of the gill opening, appearing externally on the supracleithrum bone under the skin, which is the main diagnostic character for the genus *Johnius* (see Chao *et al.* 2019); iii) unique in its triangular shaped sagittal and iv) a large lapilli otolith.

All 32 species of *Johnius* have small mouths, sub-terminal to inferior in position. Lal Mohan (1975) separated *Johnius* into two subgenera: *J. (Johnius)* defined by slightly enlarged teeth on the upper jaw, and lower jaw teeth uniform in size or the inner rows of lower jaw teeth molariform (e.g., *J. belangerii* (Cuvier, 1830), *J. carouna* (Cuvier, 1830), *J. coitor* (Hamilton, 1822), *J. heterolepis* Bleeker, 1873, *J. macrorhynchus* (Lal Mohan, 1976) and *J. weberi* Hardenberg, 1936) (Fig. 1); and *J. (Johnieops)* defined by distinctly enlarged teeth on upper and lower jaws, and inner row of lower jaw teeth enlarged (e.g., *J. borneensis* (Bleeker, 1851), *J. distinctus* (Tanaka, 1916), *J. plagiosoma* (Bleeker, 1849) and *J. philippinus* Sasaki, 1999 (Fig. 1); and the following four *J. (Johnius)* species have present a short barbel on the chin (*J. amblycephalus* (Bleeker, 1855), *J. fuscolineatus* (von Bonde, 1923), *J. macropterus* (Bleeker, 1853) and *J. mannarensis* Lal Mohan, 1971).

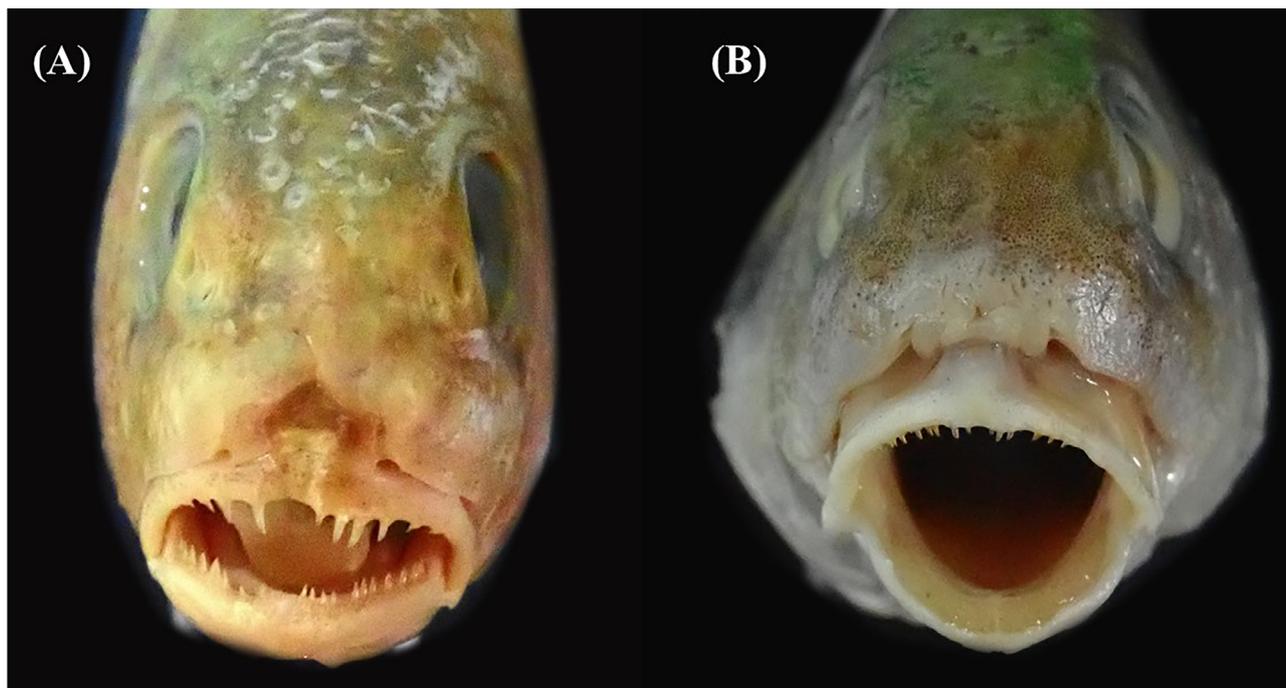


FIGURE 1. (A) The distinctly enlarged teeth on upper and lower jaws from *Johnius (Johnieops) borneensis*, NMMB-P 15389 (147 mm SL) (front view). (B) The slightly enlarged teeth on upper jaw; small and uniform teeth on lower jaw from paratype of *Johnius (Johnius) sasakii* sp. nov., NMMB-P 34743 (143 mm SL) (front view).

Most species of the genus *Johnius* have a restricted or limited distributions in the Indian and Pacific Oceans (e.g., Trewavas 1977; Lal Mohan 1975; Sasaki 1992, 1999). However, several species of *Johnius* are widely distributed in the Indo-West Pacific (e.g., *J. amblycephalus*, *J. belangerii*, and *J. borneensis*). According to Sasaki (2000; 2001), there are 15 *Johnius* species in the South China Sea region and 10 species of *Johnius (Johnius)* in Malaysian waters (Sasaki 2001). Of those with a Malaysian distribution, in particular, species such as *J. plagiosoma*, *J. carouna*, *J. heterolepis*, *J. weberi*, *J. coitor* and *J. macrorhynchus* are commonly distributed on the coast of Borneo, East Malaysia. Morphological shape, meristic counts and pigmentation are very similar in *J. (Johnius)* species, leading to uncertainty and misidentifications in many publications (Trewavas 1977; Randall & Lim 2000; Sasaki 2001). Moreover, identifications become more complex when species in adjacent region are taken into account (*J. trewavasae* Sasaki, 1992; *J. taiwanensis* Chao *et al.*, 2019); synonymized are names frequently applied (*J. sina* (Cuvier, 1830); *J. tingi* (Tang, 1937)); and similar diagnostic characters (*J. carouna*, *J. heterolepis*, and *J. macrorhynchus*) are considered when defining the species. Furthermore, recently resurrected (*J. grypotus* (Richardson, 1846), *J. heterolepis* Bleeker, 1873; *J. cantori* Bleeker, 1874) and new described species (*J. majan* Iwatsuki *et al.*, 2012 and *J. taiwanensis* Chao *et al.* 2019) are not being recognized or included.

Recently, we found that a series of *Johnius* specimens obtained through field collection in March 2017 at East Malaysia, Borneo exhibited a wide range of second anal-fin spine length which confused identification but were

similar to *Johnius heterolepis* or *Johnius carouna*. We validated the identification with a genetic approach with *J. heterolepis* and *J. carouna* specimens and determined these represented an undescribed species.

Herein we describe a new species, *Johnius sasakii* **sp. nov.** which is commonly found in Sarawak and Sabah, East Malaysia, (Borneo). Morphologically, this species was the most similar to *J. heterolepis*. In addition, morphological characteristics of *J. sasakii* **sp. nov.** such as short second anal-fin spine length, were shared with sympatric congener *J. macrorhynchus*; and a blunt snout and short gill rakers with sympatric *J. carouna*.

This study also carried out a phylogenetic analysis of four commonly encountered similar *Johnius* species (*J. amblycephalus* as basal ingroup, *J. heterolepis*, *J. carouna*, and *J. macrorhynchus*) from East Malaysia waters with *Dendrophysa russelli* (Cuvier, 1830) as an outgroup, using partial 16S rRNA and S7 gene sequences to validate the taxonomic status of *J. sasakii* **sp. nov.** with the other species. The results of these analyses provide additional evidence that *J. sasakii* **sp. nov.** is a new species from Borneo and clarify the status of taxa within this complex species. A key to species of *Johnius* in East Malaysian (Borneo) waters is included.

Materials and methods

Morphological data. Specimens were collected from Lembaga Kemajuan Ikan Malaysia (LKIM) fish landing ports in Sabah and Sarawak waters, Malaysia between February and March 2017. A total of 18 specimens had been mutually agreed to be deposited at the National Museum of Marine Biology and Aquarium, Taiwan (NMMBA). Institution codes for specimens examined follow Sabaj (2019). Specimens examined are deposited NMMBA. Methods of counting and measuring generally followed Hubbs & Lagler (2004), and terms of morphological structure and descriptions for sciaenids followed Trewavas (1977), Chao (1978), Sasaki (1989) and Chao *et al.* (2019). Standard length, head length and eye diameter are abbreviated as SL, HL and ED, respectively. The procedures for preservation and photography of specimens follow Seah *et al.* (2015). Gill raker counts are the total number of rakers at upper and lower limbs including rudimentary rakers on the first right gill arch. The lateral line scale counts are the number of pored scales excluding those distal to the posterior end of the hypural plates. A long incision was made over the isthmus of the cleithrum to examine the delicate appendages on the anterior part of gas bladder. Gas bladders were extracted from the body cavity when possible and photographed both ventrally and dorsally. Drumming muscles were also observed. The right-side sagittal otoliths were extracted, its medial surface was photographed along with *in situ* dorsal views with the inner surface to the left, as is standard. Total vertebrae counts were made from radiographs and registered as pre-caudal and caudal vertebrae.

Molecular data. Genomic DNA was extracted from muscle tissues using 10% Chelex 100 resin (Bio-Rad; www.biorad.com). The polymerase chain reaction (PCR) was conducted using an MJ Mini Thermal Cycler PTC-1148 (Bio-Rad; Hercules, CA) using PCR solutions containing 1 ml of genomic DNA, 3 ml of 10× PCR buffer, 2.4 ml of 2.5mM dNTPs, 1 ml of each primer, 0.1 ml of TaKaRa EX-Taq polymerase (TaKaRa Bio Inc.; www.takarabio.com) and distilled water to bring the final volume to 30 ml. In the PCR reagents, we used 16S ribosomal rDNA 16S-L1987 (5' GCCTCGCCTGTTTACCAAAAAC 3') and 16S mitochondria gene H2609 (5' CCGGTCT-GAACTCAGATCACGT 3') (Santos *et al.* 2013) with S7 nuclear gene S7 Fga (5' CGCTTTAAAGTCGTTTA-ATCGGCGC 3') and S7 Rga (5' GGCCTTTGTCTCTGTGGGAGAAAC 3') (Henriques *et al.* 2016). The PCR conditions consisted of initial denaturation at 95°C for 5 min, 35 cycles of denaturation at 95°C for 1 min, annealing at 55°C (16S rDNA) and 62°C (S7) for 1 min, extension at 72°C for 1 min and a final extension at 72°C for 5 min. The PCR products were purified using a Davinch™ PCR Purification Kit (Davinch-K Co.; www.davinch-k.com). The DNA was sequenced (Applied Biosystems ABI 3730XL sequencer; www.appliedbiosystems.com) using an ABI PRISM BigDye™ Terminator Cycle Sequencing Ready Reaction Kit v3.1 (Applied Biosystems Inc.; Foster City, CA). Sequences were aligned using ClustalW (Thompson *et al.* 1994) in BioEdit version 7 (Hall 1999). The dataset of the mitochondrial 16S and nuclear gene S7 used in this study was derived from a total of 50 individuals of various *Johnius* species and outgroup species (*Dendrophysa russelli*), and were submitted to the National Centre for Biotechnology Information (NCBI) database (Table 1). The genetic divergences among species were estimated under the Kimura 2-parameter (K2P) model as well as a neighbour-joining (NJ) and Maximum-Likelihood (ML) tree with 5000 bootstrap replications was generated by using Mega version 5 (Tamura *et al.* 2007).

TABLE 1. Genbank and accession number for *Johnius* (*Johnius*) sequences used by the present study. All localities are in Sarawak and Sabah of East Malaysia, Borneo.

Initial identification	Final identification	Locality (n)	Catalogue number	Genbank accession number	
				16S	S7
<i>Johnius carouna</i>	<i>Johnius sasakii</i> sp. nov.	Bako (1),	NMMB-P34733 (holotype)	MW507169	MT966836
		Bintulu (6),	NMMB-P34736–34737	MW507161–507168	MT966837–MT966838
		Sandakan (3),	NMMB-P34735	MW507173–507175	MT966831–MT966834
		Kota Kinabalu (3),	NMMB-P34739	MW507170–507172	MT966835
		Miri (4),	NMMB-P34738	MW507176–507181	MT966842–MT966845
		Betangor (1)	NMMB-P34734	MW507182	MT966839
<i>J. carouna</i>	<i>J. carouna</i>	Beluran (9),	NMMB-P34740	MT947093–MT947095	MT951365–MT951366
		Goebilt (3),	NMMB-P34743	MT947097–MT947101	MT951370, MT951373
<i>J. macrorhynchus</i>	<i>J. macrorhynchus</i>	Bako (1),	NMMB-P34744	MT947127	MT951377
		Betangor (7),	NMMB-P34746	MT947118–MT947126	MT951375–MT951376, MT951380–MT951382
		Tawau (2)	NMMB-P34745	MT947130–MT947133	MT951378, MT951382
<i>J. heterolepis</i>	<i>J. heterolepis</i>	Bako (5),	NMMB-P34749	MT953941–MT953946	MT966825–MT966828
		Bintulu (1),	NMMB-P34748	MT953933	MT966822
		Betangor (5),	NMMBP-35556	MT953928–MT953932	MT966820, MT966824
<i>J. amblycephalus</i>	<i>J. amblycephalus</i>	Sibu (1),	NMMB-P34752	MT947062	MT951360
		Bako (1),	NMMB-P34753	MT947063	MT951361
<i>D. russelli</i>	<i>D. russelli</i>	Miri (4)	NMMB-P34754	MT947064	MT951362–MT951364
		Beluran (1)		MW548694	MW556744

Taxonomy

Johnius sasakii sp. nov.

(Fig. 2, Table 2–4)

Holotype. NMMB-P 34733, 1 [111 mm SL], fish landing port at Bako, Sarawak collected by Norhafiz Hanafi on 17 March 2017.

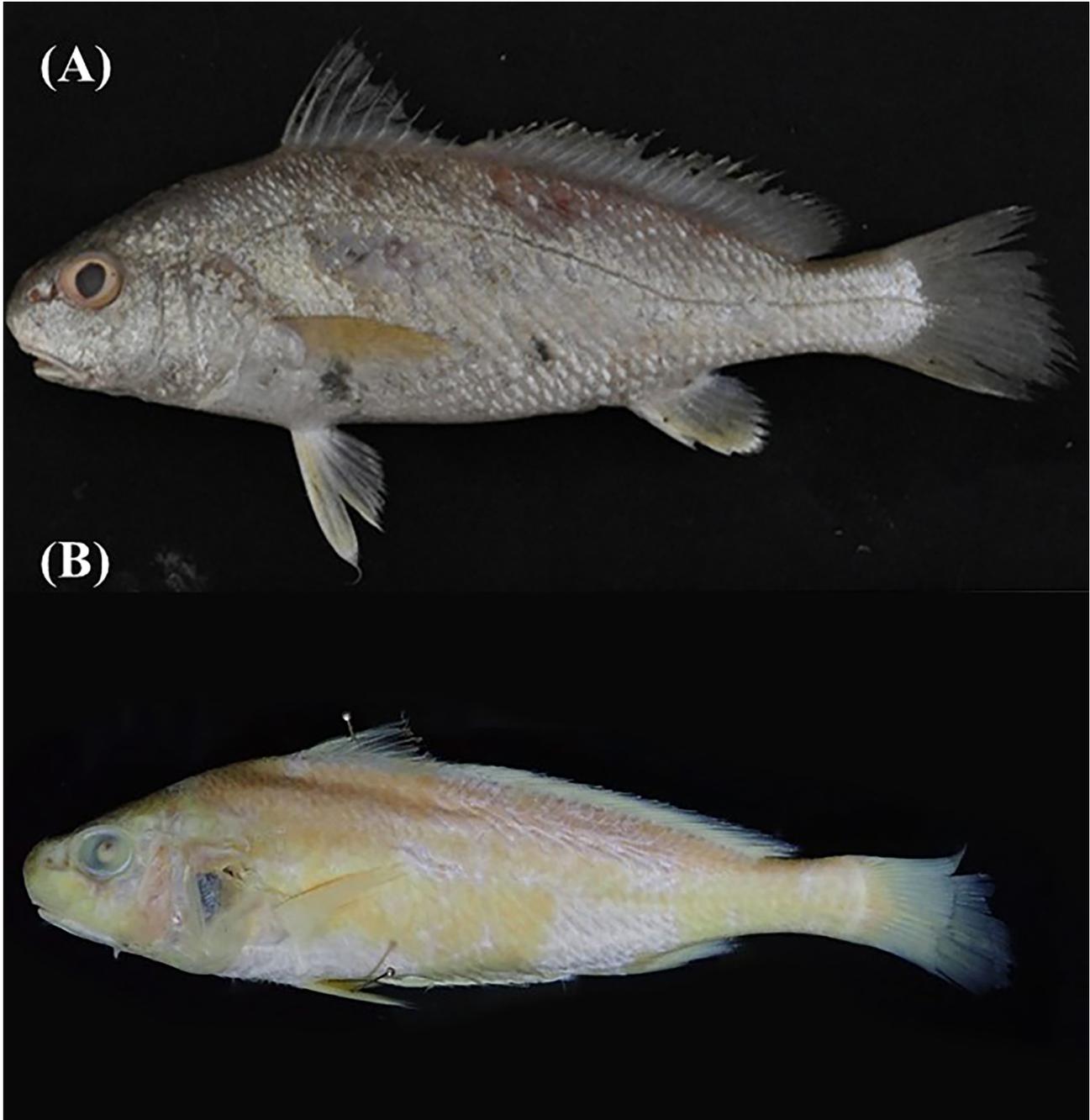


FIGURE 2. Holotype of *Johnius sasakii* sp. nov., (A) Fresh specimen, (B) preserved specimen, NMMB-P 34733, 111 mm SL, Bako, Sarawak, Malaysia, 17 March 2017, collected by Norhafiz Hanafi, fish market.

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.

Diagnosis. A species of *Johnius* distinguished by the following combination of characters: number of total outer gill rakers on first arch, 4–6 (mode 5) + 8–10 (mode 9) = 13–15; second anal-fin spine short and stiff, 7–10% of SL (usually 8–10%); body moderately deep, 25–29% of SL (usually 26–28%); first anal-fin ray length, 9–13% of SL (usually 10–12%); anal-fin base length short, 7–10% of SL (mode 9%); pre-anal length, 67–74% of SL (usually 70–71%); scale rows above lateral line, 4–6 (mode 5); body scales moderately large and ctenoid; snout bluntly rounded.

Description. Counts and measurements of the type specimens are shown in Table 2 and 3. The following data is provided for the holotype first, followed by the size range and mean for the 17 paratypes.

TABLE 2. Morphometric and meristic data of type specimen of *Johnius sasakii* sp. nov. in present study. SD = standard deviation.

	Holotype	Paratypes (17 individuals)			
	NMMB-P 34733	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					
1 st dorsal-fin spine	10	10	10	10	0.0
2 nd dorsal-fin spine	1	1	1	1	0.0
2 nd 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 1 st 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 1 st 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
Vertebrae	23	23	23	23	0.0
precaudal	10	10	10	10	0.0
caudal	13	13	13	13	0.0
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
2 nd spine length	31.6	24.9	35.6	29.2	2.6
1 st ray length	39.6	30.7	46.7	36.3	3.5

.....continued on the next page

TABLE 2. (Continued)

	Holotype	Paratypes (17 individuals)			
	NMMB-P 34733	Min	Max	Mean	SD
Measurements as %SL					
Snout to anal-fin origin	69.3	67.1	73.3	70.6	1.5
Snout to 2 nd dorsal-fin origin	53.2	49.3	55.0	51.7	1.7
Snout to 1 st 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
1 st 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
2 nd 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
2 nd spine length	9.8	7.4	10.2	8.5	0.8
1 st 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 1 st arch	14.9	11.3	19.9	14.6	2.4
Longest gill filament on 1 st arch	55.7	37.7	59.9	51.9	3.4

*Abbreviation: D1 means to first dorsal-fin spine length; P2 means to pelvic-fin length; and P1 means to pectoral-fin length.

Body moderately deep, 27% of SL, dorsal and ventral profiles evenly arched. Snout bluntly rounded, about 23% of HL, slightly projecting in front of upper jaw. Three upper and three marginal snout pores. Three pairs of mental pores, anterior pair with two small openings, very closely positioned. No mental barbel. Upper jaw (premaxilla) with, a single, outer row of closely spaced villiform teeth, and an inner band of small, conical teeth, comprising seven anterior and six posterior rows. Lower jaw (dentary) with broad band of uniformly small, conical teeth, comprising five or six anterior and three or four posterior rows. Eye moderately large, 21% of HL, circular. Anterior and posterior nostrils circular and somewhat ovate, respectively, just before eye, the latter twice the size of former. Gill rakers short and slender, 15% of ED; gill filaments approximately 3.75 times longer than gill rakers at angle of gill arch (Fig. 3). Scales rather large, cycloid on head (except occiput), throat, membrane of soft dorsal, anal, and caudal fins; body scales ctenoid, ctenii well developed, having only radiated marginal grooves (smooth to touch). Third dorsal-fin spine longest. First soft ray of pelvic-fin with a short filament, with a dim black spot on upper pectoral-fin base. Second anal-fin spine short, stiff, 10% of SL, or 32% of HL, about $\frac{2}{3}$ of first anal-fin soft ray. Caudal fin rhomboid. Swim bladder hammer-shaped, with 15 arborescent appendages along entire lateral surface (Fig. 4). Sagitta in medial view is typical Johninae pattern (Fig. 5) (see Trewavas, 1977).

Color when fresh. Based on color photographs of the type material of *Johnius sasakii* sp. nov. with head and upper body iridescent mauve or bronze, creamy white on lower lateral and ventral surfaces (Figs. 2, 6A). Roof mouth lining whitish. Upper operculum appearing darkish owing to a densely pigmented branchial cavity. Peritoneum of anterior abdominal cavity punctuated with black pigmentation. Spinous and soft dorsal-fins dusky brownish hyaline, a basal quarter of both pale; upper part of pectoral-fin dusky brownish hyaline, pelvic-fin slightly mottled

anteriorly, a few rays creamy-white distally; anal-fin slightly mottled dusky brownish; caudal fin brownish hyaline, dark distally.



FIGURE 3. First gill arch on left side of *Johnius sasakii* sp. nov. (paratype: NMMB-P 34739, 146 mm SL).



FIGURE 4. Swimbladder of *Johnius sasakii* sp. nov. (paratype, NMMB-P 34739, 146 mm SL), with 14 pairs of lateral appendages followed by a hammer-shape, with a number of arborescent appendages along the entire lateral surface (ventral view).

Color in preservative. Head and upper body brownish tan, the lower part of body and operculum whitish-yellow; fins brownish tan, dorsal and caudal fins with black margins.

Geographic distribution. All known specimens of the species were collected from the coast of Sabah and Sarawak, East Malaysia.

Etymology. Named in honor of the ichthyologist, Dr Kunio Sasaki, Professor at Kochi University, Japan, who has made significant contributions to the taxonomy of Sciaenidae and *Johnius*.

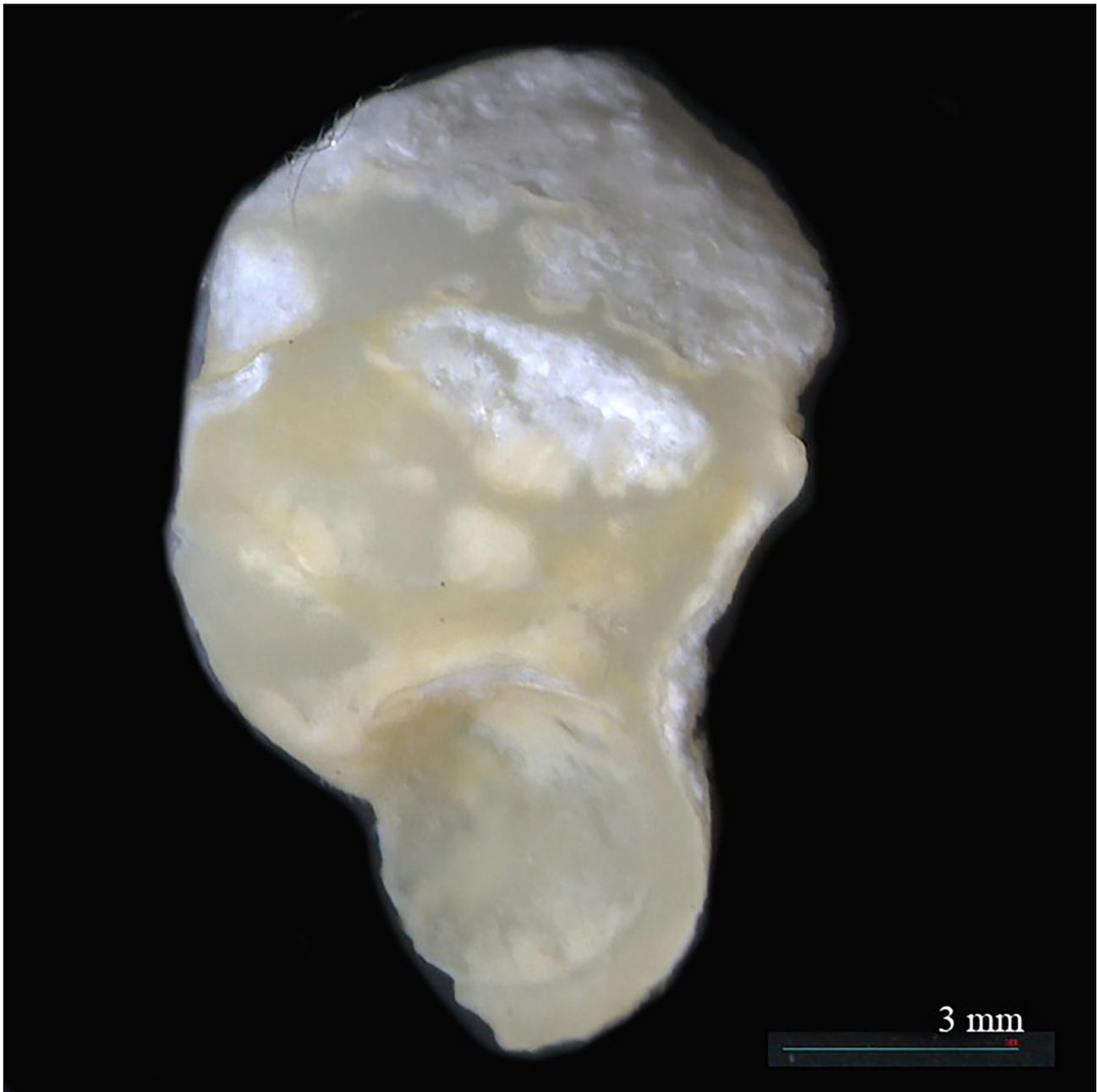


FIGURE 5. Inner surface of sagitta of *Johnius sasaki* **sp. nov.**, paratype, NMMB-P 34739, 146 mm SL.

Comparisons. *Johnius sasaki* **sp. nov.** resembles *J. belangerii*, *J. weberi* and *J. coitor* in possessing slightly enlarged teeth on upper jaw and villiform teeth at the inner row on lower jaw (including molariform teeth on inner rows lower jaw for *J. macrorhynchus*), in having no mental barbel, and dorsal-fin spines IX–XI; meanwhile *J. sasaki* **sp. nov.** is most similar to *J. heterolepis*, *J. carouna*, and *J. macrorhynchus* in possessing scale rows above lateral line from dorsal-fin origin 4–8 (usually 5–6); scale rows below lateral line from anal-fin origin 6–14 (usually 6–10); and scales moderately large.

Johnius sasaki **sp. nov.** can be separated from the most similar species, *J. heterolepis*, by the following combination of characters: snout profile more blunted (*vs.* more pointed); gill raker length more shorter, stiff (*vs.* moderately long, slender); fewer outer gill rakers on the lower limb of the first arch (mode 9 *vs.* mode 10); more outer gill rakers on the upper limb of the first arch (mode 5 *vs.* mode 4); shorter anal-fin base length (mode 9% *vs.* 10% of SL); shorter first anal-fin ray length (10–12% *vs.* 12–13% of SL); and higher number of scale rows above and below the lateral line (mode 5 and 10 *vs.* mode 4 and 7), respectively (Fig. 6, Table 3).

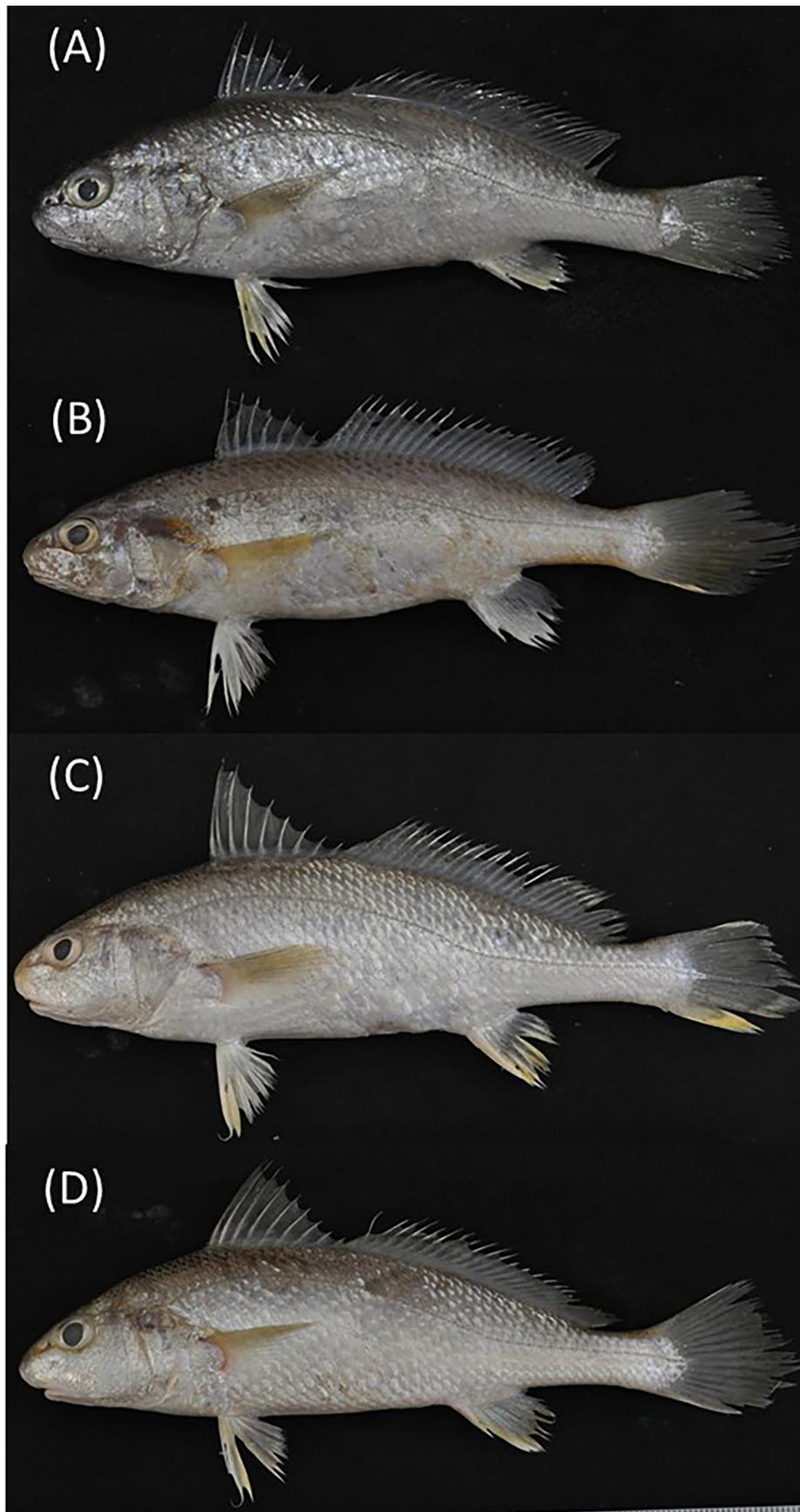


FIGURE 6. Photographs of the comparative materials. (A) *Johnius sasakii* **sp. nov.**; NMMB-P 34738, paratype, 114 mm SL, (B) *Johnius heterolepis* NMMB-P 35556, 105 mm SL, (C) *Johnius carouna*, NMMB-P 34743 141 mm SL and (D) *Johnius macrorhynchus*; NMMB-P 34744, 116 mm SL.

TABLE 3. Frequency distribution of selected meristics and morphometrics of *Johnius sasakii* **sp. nov.**, *J. carouna* and *J. heterolepis* from the South China Sea region.

Counts	n	Upper limb of outer gill rakers				Lower limb of outer gill rakers						Total outer gill rakers of 1 st arch						
		4	5	6	Mean	8	9	10	11	12	Mean	13	14	15	16	17	18	Mean
<i>Johnius sasakii</i>	18	3	11	4	5.1	2	14	2			9.0	5	7	6				14.1
sp. nov.																		
<i>Johnius carouna</i>	11		5	6	5.5			1	6	4	11.3				3	7	1	16.8
<i>Johnius heterolepis</i>	11	10	1		4.1		1	9	1		10.0		10	1				14.1

Counts	n	Second anal-fin spine length (%SL)											Mean		
		7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Johnius sasakii</i>	18	1	5	7	5										8.9
<i>Johnius carouna</i>	11						3	6	1	1					12.3
<i>Johnius heterolepis</i>	11			4	6	1									9.6

Counts	n	Body depth (%SL)										Mean	
		23	24	25	26	27	28	29	30	31	32	33	
<i>Johnius sasakii</i>	18			1	5	5	5	2					27.1
<i>Johnius carouna</i>	11	1	4	2	2	1	1						25.0
<i>Johnius heterolepis</i>	11		1	3	2	3	2						26.1

Counts	n	First anal-fin ray length (%SL)									Mean	
		9	10	11	12	13	14	15	16	17	18	
<i>Johnius sasakii</i>	18	1	5	6	5	1						11.0
<i>Johnius carouna</i>	11			1	1	3	4	2				13.4
<i>Johnius heterolepis</i>	11			1	3	6	1					12.5

Counts	n	Anal-fin base length (%SL)							Mean
		7	8	9	10	11	12	13	
<i>Johnius sasakii</i>	18	1	5	10	2				8.8
<i>Johnius carouna</i>	11			2	7	2			9.8
<i>Johnius heterolepis</i>	11				9	2			10.1

Counts	n	Pre-anal length (%SL)												Mean
		66	67	68	69	70	71	72	73	74	75	76	77	78
<i>Johnius sasakii</i>	18		1	1	1	5	7	1	1	1				70.6
<i>Johnius carouna</i>	11	1	3	3	2	2								68.0
<i>Johnius heterolepis</i>	11		1	1	4	2	1			1	1			70.1

Counts	n	Scale rows above lateral line						Scale rows below lateral line								
		4	5	6	7	8	9	5	6	7	8	9	10	11	13	14
<i>Johnius sasakii</i>	18	1	10	7		5.4		1	1	5	1	4	1	3	2	10
<i>Johnius carouna</i>	11		8	2	1	5.4		8	2	1						6.6
<i>Johnius heterolepis</i>	11	7	4			4.4	4	1	1	1	4					7.5

Counts	n	Total scale rows													Mean
		9	10	11	12	13	14	15	16	17	18	19	20	21	
<i>Johnius sasakii</i>	18			1	2	2	2		3	2	3	2	2	15.9	
<i>Johnius carouna</i>	11			8		1	1	1						11.8	
<i>Johnius heterolepis</i>	11	4		1	1		1	4						12.1	

TABLE 4. Comparison of select meristic and morphometric characters among congeneric species of *Johnius* (*Johnius*) from East Malaysia

	<i>J. sasakii</i> sp. nov. (n=18)	<i>J. carouna</i> (n=11)	<i>J. heterolepis</i> (n=11)	<i>J. macrorhynchus</i> (n=10)
Voucher number	NMMB-P34733-34739	NMMB-P34740-34743	NMMB-P34748-34751	NMMB-P34744-34747
Type status	Paratype	Voucher specimens	Voucher specimens	Voucher specimens
Type locality	East Malaysia	East Malaysia	East Malaysia	East Malaysia
Standard length (mm)	100.0–146.9	87.8–141.4	88.1–112.2	116.5–188.3
Counts				
Dorsal-fins rays	26–31	28–34	25–28	27–28
Scales above lateral line	4–6	5–7	4–5	4–5
Scales below lateral line	6–14	8–11	8–10	7–9
Number of lower limb of outer gill rakers	8–10	10–12	9–11	7–8
Total outer gill rakers of 1 st arch	13–15	16–18	14–15	11–13
Measurement (%SL)				
Head length	27.7–32.3(30.2±1.2)	25.9–30.7(27.7±1.2)	30.4–32.7(31.4±0.8)	28.8–31.4(30.4±0.7)
Body depth	25.2–29.0(27.1±1.2)	23.2–28.0(25.0±1.4)	23.8–27.9(26.1±1.3)	26.0–32.2(27.7±1.7)
2 nd spine of anal-fin length	7.4–10.2(8.8±0.8)	11.3–13.8(12.3±0.8)	8.7–11.0(9.6±0.6)	6.3–8.5(7.5±0.7)
1 st ray of anal-fin length	9.0–13.3(10.9±1.0)	10.9–14.7(13.4±1.1)	10.9–13.9(12.5±0.8)	9.8–12.0(10.9±0.7)
Anal-fin base length	6.8–10.2(8.8±0.9)	9.0–10.6(9.8±0.5)	9.7–10.8(10.1±0.4)	8.2–11.0(9.5±0.9)
Pre-anal length	67.1–73.6(70.6±1.5)	65.9–70.3(68.0±1.4)	67.2–74.7(70.1±2.4)	66.9–72.2(70.1±1.8)
Measurement (%HL)				
Snout length	23.0–29.5(26.3±2.0)	23.8–28.6(26.3±1.4)	21.1–29.4(25.6±2.5)	27.5–32.3(29.9±1.2)
Upper jaw length	34.0–42.6(38.3±2.8)	38.0–43.8(41.0±1.8)	35.0–42.8(40.4±2.6)	35.5–43.5(40.7±2.3)
Tip upper jaw to hinge length	26.4–35.4(29.1±2.7)	24.4–29.7(26.5±1.5)	27.6–33.0(29.9±1.7)	24.2–29.8(26.8±1.6)
Tip lower jaw to hinge length	21.2–29.0(24.9±2.5)	21.8–26.3(24.0±1.4)	24.7–29.8(26.8±1.4)	19.7–24.8(22.3±1.5)
Eye diameter	18.0–24.4(21.6±2.0)	20.9–26.6(23.3±1.6)	19.3–24.7(21.2±1.5)	19.0–24.4(21.9±1.5)
Interorbital width	23.8–27.9(26.0±1.3)	22.0–29.3(26.6±2.3)	20.3–28.2(24.9±2.6)	21.6–25.7(23.8±1.4)
2 nd spine of anal-fin length	24.9–35.6(29.2±2.6)	38.8–49.4(44.5±2.7)	27.4–34.1(30.7±1.8)	16.8–27.8(22.8±2.8)
1 st ray of anal-fin length	30.7–46.7(36.3±2.8)	43.2–54.3(48.6±2.5)	35.2–44.6(39.9±2.5)	30.2–37.3(33.8±2.5)
Measurement (%ED)				
Gill raker length	11.8–19.9(14.6±2.4)	13.6–26.9(15.8±2.8)	11.7–19.0(16.6±2.4)	4.8–11.1(9.7±0.7)

*Parentheses indicate as mean and standard deviation.

Johnius sasakii **sp. nov.** can also be differentiated from *J. carouna* by total outer gill rakers of first arch 13–15 vs. 16–18; number of lower limb outer gill rakers, 8–10 (mode 9) vs. 10–12 (mode 11); second anal-fin spine length rather shorter, 7–10% of SL (usually 8–10%) vs. 11–14% of SL (usually 11–12%); body depth slightly deeper, 25–29% of SL (usually 26–28%) vs. 23–28% of SL (usually 24–26%); first anal-fin ray length shorter, 9–13% of SL (usually 10–12%) vs. 11–15% of SL (usually 13–14%); anal-fin base length shorter, 7–10% of SL (mode 9%) vs. 9–11% of SL (mode 10); and pre-anal length slightly longer, 67–74% of SL (usually 70–71%) vs. 66–70% of SL (usually 67–68%) (Table 3 and 4), respectively. *Johnius sasakii* **sp. nov.** can be further be differentiated from *J. macrorhynchus*: by dentition of lower jaw villiform (vs. molariform teeth on inner rows); higher number and structure of lower gill rakers on the first arch (8–10, short and slender vs. 7–8, short and stumpy); second anal-fin spine length short and stiff (24.9–35.6% of HL vs. 16.8–27.8% of HL rather short and slender) (Fig. 6, Table 4).

Molecular comparison. To clarify the taxonomic status of *J. sasakii* **sp. nov.**, we compared sequences of two genetic markers (16S mtDNA and S7 nDNA) with similar morphological *Johnius* species. Based on pairwise K2P genetic distances (Table 5 and 6), *J. sasakii* **sp. nov.** is clearly differentiated from *J. carouna* by 16S:19.3%, S7: 8.4%; *J. macrorhynchus* by 16S: 16.7%, S7: 8.1%; *J. heterolepis* by 16S:10.4%, S7: 5.8%; *J. amblycephalus* by 16S:21.2%, S7: 10.9%; and the outgroup *D. russelli* by 16S:24.8%, S7: 12.6% respectively.

TABLE 5. Genetic distances for 16S gene among five *Johnius* (*Johnius*) species and outgroups.

	1	2	3	4	5
<i>J. sasakii</i> sp. nov. (1)					
<i>J. amblycephalus</i> (2)	0.212				
<i>J. carouna</i> (3)	0.193	0.264			
<i>J. macrorhynchus</i> (4)	0.167	0.215	0.168		
<i>J. heterolepis</i> (5)	0.104	0.155	0.146	0.122	
<i>D. russelli</i> (6)	0.248	0.171	0.253	0.254	0.194

TABLE 6. Genetic distances for S7 gene among five *Johnius* (*Johnius*) species and outgroups.

	1	2	3	4	5
<i>J. sasakii</i> sp. nov. (1)					
<i>J. amblycephalus</i> (2)	0.109				
<i>J. carouna</i> (3)	0.084	0.1			
<i>J. macrorhynchus</i> (4)	0.081	0.098	0.062		
<i>J. heterolepis</i> (5)	0.058	0.089	0.068	0.073	
<i>D. russelli</i> (6)	0.126	0.145	0.121	0.126	0.116

The NJ and ML trees obtained high support of bootstrap value (BS>90%) based on mtDNA and nDNA markers shared identical topologies where the specimens of *J. sasakii* **sp. nov.** grouped together in a monophyletic clade, which can be separated from the other *Johnius* species (Figs. 7 and 8a). The concordant phylogenetic topology derived from both mtDNA and nDNA markers indicate that the sister species of *J. sasakii* **sp. nov.** is the *J. heterolepis* (Figs. 7 and 8a), meanwhile *J. carouna* and *J. macrorhynchus* form a sister group to *J. sasakii* **sp. nov.** and *J. heterolepis*. In addition, haplotypes of partial nDNA S7 intron can be separated from *J. carouna* by three fixed nucleotide differences (Fig. 8b), indicating a significant level of genetic variation can be inferred from nuclear gene between *J. sasakii* **sp. nov.** and *J. carouna*.

Remarks. We did not record *J. latifrons* Sasaki 1992 and *J. trachycephalus* (Bleeker 1851) from Malaysian waters during our survey, however, these species were included by Sasaki (2000) based on Sasaki (1992) concerning on *J. latifrons*, and Trewavas (1977) on *J. trachycephalus* from Thailand and Vietnam. Because we have no confirmed records of *J. latifrons* and *J. trachycephalus* in Malaysian waters, we included it in the key to the species. Only eight species of *Johnius* (*Johnius*) have been reliably documented from Malaysian waters (Sasaki 2000; 2001).

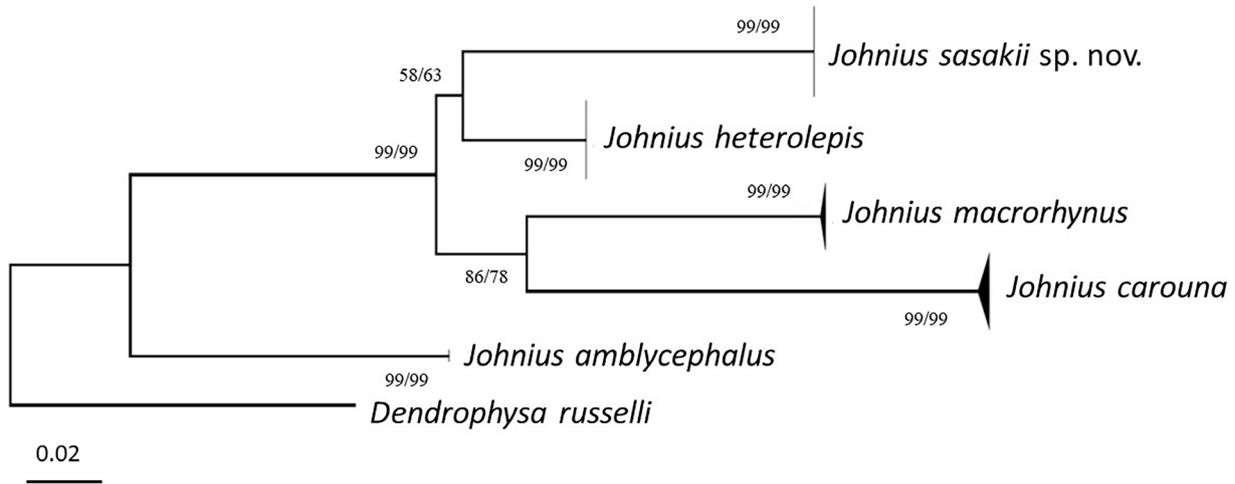


FIGURE 7. Phylogenetic trees reconstructed using the mtDNA 16S genes of five *Johnius* (*Johnius*) species. Values above the branches are respective bootstrap values from 5000 replications for the Neighbour-Joining (NJ) and Maximum-Likelihood (ML) analyses. Bar indicates genetic distances of 0.02.

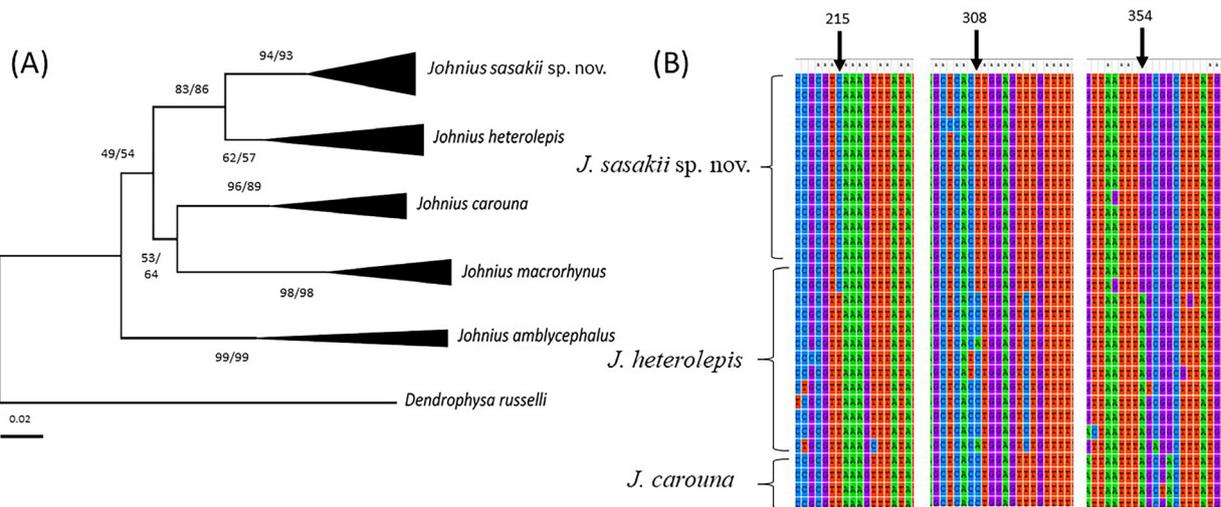


FIGURE 8. (A) Phylogenetic trees reconstructed using the nDNA S7 genes of 5 *Johnius* (*Johnius*) species. Values above the branches are respective bootstrap values from 5000 replications for the Neighbour-Joining (NJ) and Maximum-Likelihood (ML) analyses. Bar indicates genetic distances of 0.02. (B) Three nucleotide differences (black arrow) at the sites 215, 308, and 354 nucleotides in the homozygote nuclear gene S7 of *J. sasakii* sp. nov.

Key to the species of *Johnius* in the East Malaysia (Northern Borneo)

- 1a. Distinctly enlarged teeth on upper jaw and inner row of lower jaw teeth enlarged, conical *J. (Johnieops)* (Fig. 1 (A)) 2
- 1b. Slightly enlarged teeth on upper jaw and inner row of lower jaw teeth uniform in size or molariform *J. (Johnius)* (Fig. 1 (B)). 3
- 2a. First pair of mental pores separated by symphysis, snout rounded; second anal-fin spine length 40–50% of head length *J. plagiostoma* (Bleeker, 1850)
- 2b. First pair of mental pores by a crescent-shaped groove, snout pointed; second anal-fin spine length 24–42% of head length *J. borneensis* (Bleeker, 1850)
- 3a. Chin with barbel *J. amblycephalus* (Bleeker, 1855)
- 3b. Chin without barbel 4
- 4a. Dorsal-fin spines VIII or IX (usually IX); scale rows above lateral line from dorsal-fin origin 10–15, scale rows below lateral

	line from anal-fin origin 17–21	<i>J. trachycephalus</i> (Bleeker, 1850)	
4b.	Dorsal-fin spines IX to XI (usually X); scale rows above lateral line from dorsal-fin origin 4–11, scale rows below lateral line from anal-fin origin 6–17		5
5a.	Scales moderately small, scale rows above lateral line from dorsal-fin origin 7–11; scale rows below lateral line from anal-fin origin 11–17		6
5b.	Scales moderately large, scale rows above lateral line from dorsal-fin origin 4–8 (usually 5–6), scale rows below lateral line from anal-fin origin 6–14 (usually 6–10)		9
6a.	Body dark pigmented; lower fins black	<i>J. belangerii</i> (Cuvier, 1830)	
6b.	Body silvery to light yellow; lower fins pale		7
7a.	Gill rakers slender, 9–12 on lower limb gill arch and moderately long $\frac{1}{2}$ – $\frac{2}{3}$ length of gill filaments at angle of arch	<i>J. coitor</i> (Hamilton, 1822)	
7b.	Gill rakers stiff, 7–9 on lower limb of gill arch and short $\frac{1}{3}$ – $\frac{1}{2}$ length of gill filaments at angle of arch		8
8a.	Body depth 25–30% of standard length; second anal-fin spine length short, stiff, 26–32% of head length	<i>J. latifrons</i> Sasaki, 1992	
8b.	Body depth 20–25% of standard length; second anal-fin spine length long, stiff, 33–41% of head length	<i>J. weberi</i> (Hardenberg, 1936)	
9a.	Lower jaw with inner row of molariform teeth posteriorly	<i>J. macrorhynchus</i> (Mohan, 1976)	
9b.	Lower jaw teeth all conical, uniform in size		10
10a.	Total outer gill rakers of 1 st arch 16–18	<i>J. carouna</i> (Cuvier, 1830)	
10b.	Total outer gill rakers of 1 st arch 13–15		11
11a.	Gill rakers of outer gill rakers of 1 st arch at the upper limb, 4–5 (mode 4) and lower limb 9–11 (mode 10) respectively	<i>J. heterolepis</i> Bleeker, 1873	
11b.	Gill rakers of outer gill rakers of 1 st arch at the upper limb, 4–6 (mode 5) and lower limb 8–10 (mode 9) respectively	<i>J. sasakii</i> sp. nov. this study	

Additional material examined

Johnius carouna: NMMB-P 34740, 9 (88–104 mm SL), fish landing port at Beluran, Sabah, Malaysia, collected by Norhafiz Hanafi, 28 February 2017. NMMB-P 34743, 3 (113–141 mm SL), fish landing port at Goebilt, Sarawak, Malaysia, collected by Norhafiz Hanafi, 17 March 2017.

Johnius macrorhynchus: NMMB-P 34744, 1 (116 mm SL), fish landing port at Bako, Sarawak, Malaysia, collected by Norhafiz Hanafi, 17 March 2017. NMMB-P 34745, 2 (162–176 mm SL), fish landing port at Tawau, Sabah, Malaysia, collected by Norhafiz Hanafi, 23 February 2017. NMMB-P 34746, 7 (134–188 mm SL), fish landing port at Betangor, Sarawak, Malaysia, collected by Norhafiz Hanafi, 14 March 2017.

Johnius heterolepis: NMMB-P 34748, 1 (105 mm SL), fish landing port at Bintulu, Sarawak, Malaysia, collected by Norhafiz Hanafi, 9 March 2017. NMMB-P 34749, 5 (90–112 mm SL), fish landing port at Bako, Sarawak, Malaysia, collected by Norhafiz Hanafi, 17 March 2017. NMMB-P 35556, 5 (88–112 mm SL), fish landing port at Betangor, Sarawak, Malaysia, collected by Norhafiz Hanafi, 14 March 2017.

Johnius amblycephalus: NMMB-P 34752, 1 (163 mm SL), fish landing port at Sibul, Sarawak, Malaysia, collected by Norhafiz Hanafi, 13 March 2017. NMMB-P 34753, 1 (108 mm SL), fish landing port at Bako, Sarawak, Malaysia, collected by Norhafiz Hanafi, 17 March 2017. NMMB-P 34754, 4 (85–150 mm SL), fish landing port at Miri, Sarawak, Malaysia, collected by Norhafiz Hanafi, 7 March 2017.

Johnius borneensis: NMMB-P 15389 (147 mm SL), fish landing port of Donggang, Pingtung, Taiwan, collected by Ning Labbish Chao, 4 September 2010.

Acknowledgements

This study was supported by the Department of Oceanography, National Sun Yat-sen University (NSYSU) and Bio-Amaonia Conservation International which supported field collection. The collection was done under permit number JKM/MBS.1000-2/2JLD.12(54) and LKIM:KQ406/538/3. The authors would like to thank the Global Sciaenidae Conservation Network, NMMBA and IUCN Sciaenidae Red List Authority for establishing this research collaboration of the multinational collaborators to study Malaysian sciaenids. We would like to thank the Fisheries Development Authority of Malaysia (LKIM) for their assistance. We would also like to thank fish collection managers and Dr Hsuan-Ching Ho of the National Museum of Marine Biology and Aquarium (NMMBA) for curatorial and radiography support.

References

- Chao, L.N. (1978) A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). *NOAA Technical Report NMFS Circular*, 415.
- 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>
- Fricke, R., Eschmeyer, W.N. & Van der Laan, R. (2021) Catalog of fishes: genera, species, references. Electronically accessible: an online version 8 June 2021. California Academy of Sciences, San Francisco, CA, USA. Available from: <http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp> (accessed 10 July 2021)
- Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. In *Nucleic Acids symposium series*. (Vol. 41, No. 41, pp. 95-98). [London]: Information Retrieval Ltd: c1979–c2000.
- 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>
- 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 (2), 151–155.
<https://doi.org/10.1007/s10228-011-0265-8>
- Lal Mohan, R.S. (1975) Two new species of Sciaenid fishes *Johnius elongatus* and *Johnieops macrorhynchus* from India. *Mat-sya*, 1, 19–25.
- Lal Mohan, R.S. (1984) Systematic position of the sciaenid *Corvina carouna* Cuvier 1830. *Indian Journal of Fisheries*, 31 (3), 374–377.
- 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>
- Randall, J.E. & Lim, K.K.P. (2000) A checklist of the fishes of the South China Sea. *Raffles Bulletin Zoological Supplementary*, 8, 569–667.
- Sabaj, M.H. (2019) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 7.1. 21 March 2019. American Society of Ichthyologists and Herpetologists, Washington, D.C. Electronically accessible. Available from: <http://www.asih.org/> (accessed 1 January 2022)
- Santos, S., de Fátima Gomes, M., dos Santos Ferreira, A.R., Sampaio, I. & Schneider, H. (2013) Molecular phylogeny of the western South Atlantic Sciaenidae based on mitochondrial and nuclear data. *Molecular phylogenetics and evolution*, 66 (1), 423–428.
<https://doi.org/10.1016/j.ympev.2012.09.020>
- 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. (1990) *Johnius grypotus* (Richardson, 1846), resurrection of a Chinese sciaenid species. *Japanese Journal of Ichthyology*, 37 (3), 224–229.
- 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. (1999) *Johnius (Johnieops) philippinus*, a new sciaenid from the Philippines, with a synopsis of species included in the subgenus 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, 621 p. In: Randall, J.E. & Lim, K.K.P. (Eds.), *Raffles Bulletin Zoology Supplementary*, (8), 569–667
- Sasaki, K. (2001) Sciaenidae. In: Carpenter, K.E. & Niem, V.H. (Eds.), *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 5: Bony Fishes Part 3 (Menidae to Pomacentridae)*. Rome, FAO, 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>
- Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007) MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, 24 (8), 1596–1599.
<https://doi.org/10.1093/molbev/msm092>
- Thompson, J.D., Desmond, G.H. & Toby, J.G. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence

alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22 (22), 4673–4680.

<https://doi.org/10.1093/nar/22.22.4673>

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>