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Assessment of the diversity of the family Sillaginidae in the Indian Ocean with emphasis on the taxonomic identity of *Sillago sihama*

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Abstract

The present study contributes to the taxonomy of the family Sillaginidae, with comments on the distribution of its species in the Indian Ocean and an emphasis on the taxonomy and distribution of *Sillago sihama*. Thirty described and putative species with Indian Ocean distribution are listed, and a distribution range for each species is provided based on published data and results from the present study. A comprehensive phylogenetic analysis of the barcoding portion of the mitochondrial COI gene is provided together with three approaches for molecular species delimitation, which includes 44 to 47 genetic lineages (depending on the species delimitation approach used) in the family Sillaginidae, 33 of them applying to described species and also 8 putative species, formerly misidentified as *S. sihama*. Inclusion of specimens from South Africa, Iran, Pakistan, India, Bangladesh and the southern Red Sea (type locality) reveals one genetic lineage representing the true *Sillago sihama*. Distribution of the species is confined to the Red Sea and the Indian Ocean, and other records under the name *S. sihama* are based on misidentifications. Several undescribed species identified as *S. sihama* are distributed in the Indo-West Pacific region and closely resemble *S. sihama*, but are not identical with this species and can be identified as members of different evolutionary lineages. Two species, *S. sihama* and *S. soringa*, reported from Bangladesh, represent the easternmost record of both species. These two species are described in detail, including swimbladder morphology. The study also shows that specimens from India identified as *Sillago ingenuua* McKay, 1985 are nested within a lineage previously referred to as *S. ingenuua* A, but are different from the lineage *S. ingenuua* B, representing a confirmed record of the clade *S. ingenuua* in the northern Indian Ocean. Comments on misidentifications of *S. sihama* from the Indian Ocean and western Pacific are provided. Furthermore, we propose that *Sillago erythraea* should be resurrected from its synonymy with *S. sihama*. As *Sillago suezensis* is identical with the former species, it becomes a junior synonym of *S. erythraea*.

Key words: DNA barcoding, Red Sea, phylogeny, sillaginids, *Sillago*, swimbladder, integrative taxonomy

Introduction

Fishes of the family Sillaginidae Richardson, 1846 are commonly known as sand whitings or sand borers. They generally inhabit inshore coastal waters or estuarine areas of rivers with open sandflats or muddy substrates. Many

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species are commercially exploited across the Indo-West Pacific and are the target of sport fishing along the coastline in some countries. Species of this family are widely distributed in the Indo-West Pacific region (McKay 1985, 1992; Johnson 1993; Nelson *et al*. 2016). Sillaginids are easily identified to family level due to their uniform shape and similar coloration. Uniformity in morphological characters such as an elongate body, long conical snout, long-based soft dorsal and anal fins, and the horizontal lower edge of the preopercle, has resulted in confusion of the species. It is common to find e.g. mixed consignments of two or more species in fish markets, although experienced fishermen are less likely to be confused (McKay 1992).

Presently, the family includes 39 species and 5 genera, with *Sillago* divided into three subgenera (*Parasillago*, *Sillaginopodys* and *Sillago*) based on swimbladder morphology (McKay 1992). In an extensive phylogeny of the family, Kaga (2013) raised *Sillaginopodys* to genus level but did not recognize a division of *Sillago* into subgenera. The genus *Sillago* contains 35 valid species and can be divided into two groups: the first characterised by the presence of a less-developed swimbladder with a single posterior extension, whereas species of the other group have a well-developed swimbladder with two posterior extensions (Cheng *et al*. 2020). Saha *et al*. (2022) provided a key to 15 described species and one unnamed species (from Chinese waters) with two posterior extensions. Previously it was assumed that *S. sihama* (Fabricius, 1775), a species with two posterior extensions of the swimbladder, was widely distributed in the Indo-West Pacific region (McKay 1992). Recent research found that there are at least eight divergent molecular lineages that are currently subsumed under the name *S. sihama* in the Indo-West Pacific region (Cheng *et al*. 2020, Fig. 2). These so-called *S. sihama* are externally similar to *S. sihama* (type locality, southern Red Sea), but are neither identical with this species nor to each other, as these cryptic species belong to well divergent mitochondrial DNA lineages. The most important taxonomic characteristics for the proper diagnosis of these cryptic *Sillago* species can be in general structural differences in their swimbladder (McKay 1985; 1992) but this is beyond the scope of the present study.

Three different approaches for species delimitation (Automatic Barcode Gap Discovery (ABGD), Assemble Species by Automatic Partitioning (ASAP) and Poisson Tree Processes (PTP) model) indicate as to what degree the divergent evolutionary lineages represent separate species. A phylogenetic analysis of the barcoding portion of the mitochondrial COI gene carried out in this study shows at least 44 genetic lineages (according PTP method) in the family Sillaginidae, 33 of them applying to described species, and also includes eight putative species named *S.* cf. *sihama*, that were previously confused with *S. sihama*. The geographic distribution of 30 described and undescribed Sillaginidae species in the Indian Ocean was compiled from records, combining data from published studies, the present study, and data from GenBank and BOLD systems (BOLD, www.boldsystems.org; Ratnasingham & Hebert 2007). In this study, an emphasis is laid on the clarification of published misidentifications of *S. sihama*, made by comparing compiled literature mainly containing molecular data. The phylogenetic analysis showed that *S. sihama* is a Red Sea and Indian Ocean species with a confirmed easternmost record from Bangladesh. This finding is corroborated by examination of specimens for external morphological characters and also swimbladder structure and vertebral features. Moreover, in the present study, *S. soringa* Dutt & Sujatha, 1982 is reported from Bangladesh as another easternmost record, with detailed description of specimens. Also, we explored evolutionary divergence in *Sillago ingenuua* McKay, 1985, thereby confirming previous result, i.e. presence of two lineages distributed in the western Pacific, *S. ingenuua* A and *S. ingenuua* B sensu Gao *et al*. (2023), and extending the range of the former lineage to India, representing the first confirmed record of the species in the Indian Ocean.

The findings of the present study give evidence of the species richness of Sillaginidae in the geographic areas specified above. For some species extended distribution ranges are confirmed, whereas corrections of previous distributions due to species misidentification lead to more confined distribution ranges. Accurate information on the distribution of species of the family Sillaginidae as presented in this study is an essential prerequisite for the exploration of their biogeographical and evolutionary history.

Materials and methods

Sampling

Fish specimens were collected from the Bay of Bengal, Bangladesh, and Chennai, India. From Bangladesh, fresh fish specimens were collected from local fishermen when they caught these fishes by dragnet on the sandy bottom

inshore. From Chennai, India, fresh fish specimens were collected from a fish shop. First, epaxial white muscle tissue was collected from nine fresh specimens of four Sillaginidae species and preserved in 95% ethanol at -20°C until DNA extraction (see below). Voucher specimens were then preserved in 95 % ethanol in Fishery Ecology Laboratory, Fisheries College, Ocean University of China, Qingdao, China (FEL_OUC) and Fisheries Laboratory, Department of Zoology, Jagannath University, Dhaka, Bangladesh (FL_JNU).

Other specimens of silliganid fishes examined herein were collected by trawling with a commercial bottom trawl in 2012 and 2014 in the southern Red Sea off Jizan, Saudi Arabia (Bogorodsky *et al*. 2014). After tissue sampling and photographic documentation, vouchers were formalin fixed and subsequently subjected to long term storage in 75 % ethanol. Voucher specimens were deposited in collections of the Senckenberg Research Institute and Natural History Museum Frankfurt (SMF, Germany) and the King Abdulaziz University Marine Museum, Jeddah (KAUMM, Saudi Arabia).

Species of the family Sillaginidae from India, Japan, Korea, China and Vietnam were listed based on literature records and those from Bangladesh based on freshly collected specimens. References, and genus and species classification, follow Fricke (2024) and Fricke *et al*. (2024).

Morphological study

All measurements were taken to the nearest 0.1 mm with a MITUTOYO digital caliper, and body mass was recorded to the nearest 0.1 g using a digital weight scale. For morphological identification, 19 morphometrics, 9 meristics, body and fin color, and swimbladder characteristics were compared. The number of vertebrae was counted by dissection of non-type specimens and x-rays of voucher specimens. The structure of the swimbladder was studied by dissection of non-type specimens following Shao *et al*. (1986) and Kaga & Ho (2012). Counts and measurements were taken according to McKay (1985).

Molecular study

Genomic DNA was extracted from some of the tissue samples by proteinase K digestion and a standard phenol-chloroform method (Sambrook *et al*. 1989). Cytochrome oxidase subunit I (COI) fragment was amplified using FishF1 and FishR1 primer (Ward *et al*. 2005) to analyze genetic differences among sillaginids following Gao *et al*. (2011). Sanger sequencing of purified PCR reaction products was carried out using the PCR primers. Other sequences obtained in this study were generated by combinations of methods used in routine DNA barcoding and (partly modified) protocols of BOLD datasystems (see Winterbottom *et al.* (2023) for details). The cited sequences and six COI sequences obtained in this study were deposited in GenBank (accessions OM184306–OM184311, see Table 1).

Publically available barcoding sequences of sillaginid species were obtained from GenBank and BOLD and—together with sequences generated in this study—were aligned in order to estimate a maximum likelihood gene tree. For phylogenetic reconstructions, the optimal partitioning scheme and the respective model of sequence evolution was estimated in PartitionFinder2 version 2.1.1 (Lanfear *et al.* 2016) for each codon position (using options 'rcluster' (Lanfear *et al.* 2014) and 'kmeans' (Frandsen *et al.* 2015)). The COI gene tree was estimated with RAxML v8.2.X (Stamatakis 2006, 2014) via its web server version at https://www.trex.uqam.ca (Boc *et al*. 2012). The support of resulting branches was evaluated in 1,000 bootstrapped replicates.

Automatic Barcode Gap Discovery (ABGD), Assemble Species by Automatic Partitioning (ASAP) and a Poisson Tree Processes (PTP) model were used to delimit the number of species (Puillandre *et al.* 2012; Zhang *et al*. 2013; Puillandre *et al.* 2021). The ABGD approach was carried out online (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) with default settings of model variables except a relative gap width (X) of 1.1 that had no impact on the result by either using Jukes-Cantor (JC69) and or Kimura (K80) TS/TV distances. The ASAP method was also performed using a web server (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html). We used various settings to assess the impact of the different substitution models to compute the distances and found no impact, hence we report the results obtained with default settings. The PTP model was estimated using the web server at https://species.h-its.org/ptp/ with the RAxML tree as input data with outgroups as the root. During the MCMC process 500.000 generations were sampled (thinning: 100) with a burn-in of 0.1.

TABLE 1. Details of specimens used in genetic analysis of COI with individual ID, sampling location, GenBank accession numbers and references.

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillaginopsis domina	FEL_OUC142276	n/a	Bangladesh, Cox's Bazar	MT890670	n/a	Saha *et al*. 2022
Sillaginopsis domina	FEL_OUC142284	n/a	Bangladesh, Cox's Bazar	MT890671	n/a	Saha *et al*. 2022
Sillaginopsis domina	FEL_OUC142293	n/a	Bangladesh, Cox's Bazar	MT890672	n/a	Saha *et al*. 2022
Sillaginodes punctatus	BW-A1515	CSIRO H 3962-05	Southeastern Australia	EF609465	FOAC516-05	Ward & Holmes 2007
Sillaginodes punctatus	AU-pun1	n/a	Australia, Queensland Museum	KU051719	ANGBF44291-19	Cheng *et al*. 2020
Sillaginodes punctatus	AU-pun4	n/a	Australia, Queensland Museum	KU051720	ANGBF44292-19	Cheng *et al*. 2020
Sillaginopodys chondropus	PK-cho384	n/a	Pakistan, Karachi	MF571939	GBMNB4170-20	Cheng *et al*. 2020
Sillaginopodys chondropus	PK-cho385	n/a	Pakistan, Karachi	MF571940	GBMNB4171-20	Cheng *et al*. 2020
Sillaginopodys chondropus	ADC09_198.1#2	n/a	Mozambique	JF494511	DSFSF060-09	Steinke *et al*. 2016
Sillaginopodys chondropus	ADC09_198.1#3	n/a	Mozambique	JF494512	DSFSF022-09	Steinke *et al*. 2016
Sillaginopodys chondropus	ADC198.1#4	n/a	South Africa	JF494514	TZMSA204-04	Steinke *et al*. 2016
Sillaginopodys chondropus (Orig ID *S. sihama*)	ADC10-878	n/a	South Africa	n/a	DSLAG579-10	BOLD
Sillaginopodys chondropus	BIF0269	MZB-BIF00269	Indonesia, Java	KU692894	BIFB244-13	Dahruddin *et al*. 2016
Sillaginopodys chondropus	n/a	NBFGR.TS SC2	India	MK814151	GBMNC17096-20	BOLD
Sillaginopodys chondropus	n/a	NBFGR.TS SC3	India	MK814152	GBMNC17095-20	BOLD
Sillaginops macrolepis	FELOUCcx1	n/a	Japan, Iriomote Island	MZ677462	n/a	Saha *et al*. 2022
Sillago aeolus	BS-aeo1	n/a	China, Basuo	KU051731	ANGBF44297-19	Cheng *et al*. 2020
Sillago aeolus	XM-aeo18	n/a	China, Xiamen	KU051736	ANGBF44302-19	Cheng *et al*. 2020
Sillago aeolus	WZ-aeo1	n/a	China, Wenzhou	KU051746	ANGBF44311-19	Cheng *et al*. 2020
Sillago aeolus	FCG-aeo1	n/a	China, Fangchenggang	MF571923	GBMNB4154-20	Cheng *et al*. 2020
Sillago aeolus	ZJ-aeo1	n/a	China, Zhanjiang	KU051751	ANGBF44315-19	Cheng *et al*. 2020
Sillago aeolus	ST-aeo1	n/a	China, Shantou	KU051741	ANGBF44306-19	Cheng *et al*. 2020
Sillago aeolus	TW-aeo1	n/a	Taiwan, China	MF571927	GBMNB4158-20	Cheng *et al*. 2020
Sillago aeolus	HA-011216-3A	n/a	Vietnam	MZ422225	CDAO186-18	BOLD
Sillago aeolus	n/a	n/a	Singapore	MN690437	GBMNC13054-20	BOLD

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago analis	n/a	HI09-SA25	Australia	JX875485	GBGCA3358-13	Krück *et al*. 2013
Sillago analis	n/a	HI09-SA26	Australia	JX875486	GBGCA3357-13	Krück *et al*. 2013
Sillago analis	n/a	HI09-SA27	Australia	JX875487	GBGCA3356-13	Krück *et al*. 2013
Sillago asiatica	SY-asi1	n/a	China, Sanya	KU051912	GBMIN124613-17	Cheng *et al*. 2020
Sillago asiatica	SY-asi2	n/a	China, Sanya	KU051913	ANGBF44326-19	Cheng *et al*. 2020
Sillago asiatica	ST-asi1	n/a	China, Shantou	KU051917	GBMIN129872-17	Cheng *et al*. 2020
Sillago asiatica	HD-01116-3A	n/a	Vietnam	MZ422272	CDAO184-18	Zhang & Hanner 2012
Sillago asiatica	R2A-290317-2A	n/a	Vietnam	MZ422200	CDAO185-18	Zhang & Hanner 2012
Sillago attenuata	QG17-108	n/a	Arabian Gulf, Qatar	n/a	LIDMA3726-22	Present study
Sillago attenuata	PK-att478	n/a	Pakistan, Karachi	MF571920	GBMNB4151-20	Cheng *et al*. 2020
Sillago attenuata	PK-att489	n/a	Pakistan, Karachi	MF571921	GBMNB4152-20	Cheng *et al*. 2020
Sillago attenuata	PK-att492	n/a	Pakistan, Karachi	MF571922	GBMNB4153-20	Cheng *et al*. 2020
Sillago bassensis	n/a	B2	Australia	HM131482	ANGBF789-12	Xue *et al*. 2010
Sillago bassensis	n/a	B3	Australia	HM131483 HM131484	ANGBF790-12	Xue *et al*. 2010
Sillago bassensis (Orig ID *S. vittata*)	n/a	JD278	Australia	KR493054	GBMIN119160-17	Dias *et al*. 2015
Sillago burrus (Orig ID *S.* cf. *burrus* 1)	n/a	JD279	Western Australia	KR493055	GBMIN124080-17	Dias *et al*. 2015
Sillago burrus (Orig ID *S.* cf. *burrus* 2)	BW-A9189		Australia	HQ956529	FOAL892-10	BOLD
Sillaginodes punctatus (Orig ID *S.* cf. *burrus* 2)	n/a	JD280	Western Australia	KR493056	GBMIN119161-17	Dias *et al*. 2015
Sillago caudicula	ADC10-688	n/a	South Africa	n/a	DSLAG389-10	Steinke *et al*. 2016
Sillago ciliata	UG0520	n/a	Australia, Queensland	JX887794	LIFS705-08	Krück *et al*. 2013
Sillago ciliata	BW-A1511	CSIRO uncat	Australia, Queensland	JX887795	FOAC512-05	Krück *et al*. 2013
Sillago erythraea	KAU12-790	SMF 35017	Red Sea, Saudi Arabia, Jizan	n/a	RSSIL001-24	Present study

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago erythraea	KAU12-791	SMF 35017	Red Sea, Saudi Arabia, Jizan	n/a	RSSIL002-24	Present study
Sillago erythraea	Jaffa 1	HUJ19696	Mediterranean, Israel	FJ155362	GBGC7680-09	Tikochinski *et al*. 2013
Sillago erythraea	Herzelia 1	HUJ19720	Mediterranean, Israel	FJ155363	GBGC7679-09	Tikochinski *et al*. 2013
Sillago erythraea	Michmoret 1	HUJ19752	Mediterranean, Israel	FJ155364	GBGC7678-09	Tikochinski *et al*. 2013
Sillago erythraea	Ssue	n/a	Red Sea, Egypt	LC572149	GBMNB74095-20	BOLD
Sillago erythraea	BIM E68	TAU.P.14736	Mediterranean, Israel	n/a	BIM181-13	BOLD
Sillago erythraea	n/a	n/a	Mediterranean, Turkey	KY176637	ANGBF44620-19	BOLD
Sillago flindersi	AU-fli1	n/a	Australia	KU051726	ANGBF44335-19	Cheng *et al*. 2020
Sillago flindersi	AU-fli2	n/a	Australia	KU051727	ANGBF44336-19	Cheng *et al*. 2020
Sillago flindersi	AU-fli3	n/a	Australia	KU051728	ANGBF44337-19	Cheng *et al*. 2020
Sillago indica	PK-ind1	n/a	Pakistan, Karachi	KM350229	GBMIN128119-17	Cheng *et al*. 2020
Sillago indica	PK-ind2	n/a	Pakistan, Karachi	KM350230	GBMIN128120-17	Cheng *et al*. 2020
Sillago indica	MU59	NBFGR:MU SI 59	India	MK814158	GBMNC17089-20	Divya *et al*. 2021
Sillago indica (Orig ID *S. sihama*)	n/a	NBFGR:CHNSi si	India	KC774669	ANGBF44439-19	BOLD
Sillago ingenuua	DS-ing1	n/a	China, Dongshan	KU051978	ANGBF44340-19	Cheng *et al*. 2020
Sillago ingenuua	TH-ing4	n/a	Thailand, Songkhla	KU051984	ANGBF44345-19	Cheng *et al*. 2020
Sillago ingenuua	ID-ing1	n/a	Indonesia, Java	KU051999	ANGBF44360-19	Cheng *et al*. 2020
Sillago ingenuua	G2A-04716-1	n/a	Vietnam	MZ421521	CDAO226-18	BOLD
Sillago ingenuua	FEL_JNUCH121911	n/a	India, Chennai	OM184306	n/a	Present study
Sillago ingenuua	FEL_JNUCH121918	n/a	India, Chennai	OM184307	n/a	Present study
Sillago ingenuua (Orig ID *S.* sp. 2 SL-2013)	Sisp2H1	NBFGR:CHNSisp2	India	KC858289	ANGBF44618-19	BOLD
Sillago cf. *ingenuua* 1	TW-ing1	n/a	China, Taiwan	KU051989	ANGBF44350-19	Cheng *et al*., 2020
Sillago cf. *ingenuua* 1	TW-ing2	n/a	China, Taiwan	KU051990	ANGBF44351-19	Cheng *et al*., 2020
Sillago cf. *ingenuua* 1	BW-A1540	CSIRO H 4027-03	Western Australia	EF609469	FOAC541-05	Ward & Holmes 2007

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago japonica	QD-jap1	n/a	China, Qingdao	KU051932	GBMIN119734-17	Cheng *et al*. 2020
Sillago japonica	LZ-jap1	n/a	China, Laizhou	KU051937	ANGBF44379-19	Cheng *et al*. 2020
Sillago japonica	XM-jap1	n/a	China, Xiamen	KU051970	ANGBF44412-19	Cheng *et al*. 2020
Sillago japonica	ZS-jap1	n/a	China, Zhoushan	MF571935	GBMNB4166-20	Cheng *et al*. 2020
Sillago japonica	BG-jap1	n/a	China, Beibu Gulf	KU051924	ANGBF44369-19	Cheng *et al*. 2020
Sillago japonica	ASIZP0800441	ASIZP0064820	Taiwan	n/a	FTW569-09	BOLD
Sillago japonica	n/a	n/a	Japan	LC201788	ANGBF44426-19	Kawai *et al*. 2017
Sillago japonica	KP-jap1	n/a	Korea, Busan	MF571925	GBMNB4156-20	Cheng *et al*. 2020
Sillago lutea	BW-A17000	CSIRO H 8836-07	Papua New Guinea	n/a	FOAQ836-22	BOLD
Sillago maculata	AU-mac1	n/a	Australia	KU051721	ANGBF44431-19	Cheng *et al*. 2020
Sillago maculata	AU-mac2	n/a	Australia	KU051722	ANGBF44432-19	Cheng *et al*. 2020
Sillago maculata	AU-mac3	n/a	Australia	KU051723	ANGBF44433-19	Cheng *et al*. 2020
Sillago malabarica	MN11	NBFGR:MN ScfS 11	India, Kochi	MK814121	GBMNC17126-20	Divya *et al*. 2021
Sillago malabarica	MN15	NBFGR:MN ScfS 15	India, Kochi	MK814122	GBMNC17125-20	Divya *et al*. 2021
Sillago malabarica	MN20	NBFGR:MN ScfS 20	India, Kochi	MK814123	GBMNC17124-20	Divya *et al*. 2021
Sillago mengjialensis	FEL_OUCCO21986	n/a	Bangladesh, Cox's Bazar	MT890678	n/a	Saha *et al*. 2022
Sillago mengjialensis	FEL_OUCCO21987	n/a	Bangladesh, Cox's Bazar	MT890679	n/a	Saha *et al*. 2022
Sillago mengjialensis (Orig ID *S. sihama*)	n/a	F1711SM-17	Bangladesh	MT375171	GBMNC17422-20	BOLD
Sillago mengjialensis (Orig ID *S. sihama*)	n/a	F1712SM-21	Bangladesh	MK340719	ANGBF56258-19	BOLD
Sillago mengjialensis (Orig ID *S.* sp.1 SL-2013)	Sisp1H2	NBFGR:CHNSisp1	India	KC858288	ANGBF44617-19	BOLD
Sillago mengjialensis (Orig ID *S. asiatica*)	KL215	n/a	Malaysia	MH674072	GBMNB4873-20	BOLD

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago mengjialensis (Orig ID *S. sihama*)	BW-A10294	CSIRO uncat	Indonesia, Java	JN312946	FOAM331-10	BOLD
Sillago muktijoddhai	FEL_OUC142267	n/a	Bangladesh, Cox's Bazar	MT890674	n/a	Saha *et al*. 2022
Sillago muktijoddhai	FEL_OUC142270	n/a	Bangladesh, Cox's Bazar	MT890675	n/a	Saha *et al*. 2022
Sillago muktijoddhai	FEL_OUC142377	n/a	Bangladesh, Sunderban	MT890676	n/a	Saha *et al*. 2022
Sillago muktijoddhai (Orig ID *S. sihama*)	n/a	DUZM_MF_186	Bangladesh	MH429345	ANGBF44589-19	Ahmed *et al*. 2021
Sillago muktijoddhai (Orig ID *S. sihama*)	n/a	F1602sb-34-3	Bangladesh, Khulna	MF629720	SUN122-18	Habib *et al*. 2017
Sillago nierstraszi (Orig ID *S.* sp.)	BW-A1544	CSIRO uncat	Australia, Gulf of Carpentaria	n/a	FOAC545-05	BOLD
Sillago nigrofasciata	FD1	n/a	China, Fuding	KU051808	ANGBF44493-19	Xiao *et al*. 2021
Sillago nigrofasciata	XMH1	n/a	China, Xiamen	MF571928	GBMNB4159-20	Cheng *et al*. 2020
Sillago nigrofasciata	ZHH1	n/a	China, Zhuhai	MF571934	GBMNB4165-20	Cheng *et al*. 2020
Sillago nigrofasciata	CGH1	n/a	China, Fangchenggang	MF571924	GBMNB4155-20	Cheng *et al*. 2020
Sillago nigrofasciata	TWSP11	n/a	Taiwan, China	KU051878	ANGBF44557-19	Cheng *et al*. 2020
Sillago panhwari	PK-pan198	n/a	Pakistan, Karachi	MF571945	GBMNB4176-20	Cheng *et al*. 2020
Sillago panhwari	PK-pan219	n/a	Pakistan, Karachi	MF571947	GBMNB4178-20	Cheng *et al*. 2020
Sillago panhwari	PK-pan285	n/a	Pakistan, Karachi	MF571914	GBMNB4145-20	Cheng *et al*. 2020
Sillago panhwari	BL1	n/a	Arabian Gulf, Bahrain	KU051787	ANGBF44472-19	Cheng *et al*. 2020
Sillago panhwari (Orig ID *S.* sp. LR-2016)	n/a	CEW0573	Arabian Gulf, Saudi Arabia	KU499792	ANGBF44619-19	Rabaoui *et al*. 2019
Sillago parasihama	ZJ-1	n/a	China, Zhanjiang	MF571929	GBMNB4160-20	Cheng *et al*. 2020
Sillago parasihama	ZJ-2	n/a	China, Zhanjiang	MF571930	GBMNB4161-20	Cheng *et al*. 2020
Sillago parasihama	ZJ-3	n/a	China, Zhanjiang	MF571931	GBMNB4162-20	Cheng *et al*. 2020
Sillago parvisquamis	n/a	JP-par1	Japan	HQ389247	NGBF6877-12	Gao *et al*. 2011
Sillago parvisquamis	n/a	JP-par2	Japan	HQ389248	NGBF6886-12	Gao *et al*. 2011
Sillago parvisquamis	n/a	JP-par3	Japan	HQ389249	NGBF6876-12	Gao *et al*. 2011

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago robusta	BW-A1551	CSIRO H 3989-01	Australia, New South Wales	EF609470	FOAC552-05	Ward & Holmes 2007
Sillago schomburgkii	BW-A1535	CSIRO H 4388-04	Australia	n/a	FOAC536-05	BOLD
Sillago schomburgkii	BW-A1536	CSIRO H 4388-05	Australia	n/a	FOAC537-05	BOLD
Sillago schomburgkii	BW-A1537	CSIRO H 4388-06	Australia	n/a	FOAC538-05	BOLD
Sillago shaoi	XM-sha5	n/a	China, Xiamen	KU051872	GBMIN124612-17	Xiao *et al*. 2016
Sillago shaoi	XM-sha6	n/a	China, Xiamen	KU051873	ANGBF44554-19	Xiao *et al*. 2016
Sillago shaoi	DS-sha1	n/a	China, Dongshan	KU051886	ANGBF44563-19	Xiao *et al*. 2016
Sillago shaoi	TWSP12	n/a	China, Taiwan	KU051879	GBMIN129867-17	Xiao *et al*. 2016
Sillago sihama	FEL_OUCM8192	n/a	Bangladesh, Maheshkhali	MT890680	n/a	Present study
Sillago sihama	FEL_OUCM8193	n/a	Bangladesh, Maheshkhali	n/a	n/a	Present study
Sillago sihama	n/a	FCC2002SB-01	Bangladesh	OK175819	GBMNE44091-21	BOLD
Sillago sihama	KAU14-301	SMF 35900	Red Sea, Saudi Arabia, Jizan	n/a	RSSIL003-24	Present study
Sillago sihama	PK-sih358	n/a	Pakistan, Karachi	MF571917	GBMNB4148-20	Cheng *et al*. 2020
Sillago sihama	n/a	HUJ19716-1	Red Sea, Eritrea	FJ155365	GBGC7677-09	Tikochinski *et al*. 2013
Sillago sihama	WL-M188	n/a	India, Maharashtra	EF609615	WLIND188-07	Lakra *et al*. 2011
Sillago sihama	ADC198.3-10	n/a	South Africa	JF494527	TZMSC158-05	Steinke *et al*. 2016
Sillago sihama	n/a	ZMSBUK24	Iran	MK887283	n/a	GenBank
Sillago cf. *sihama* 1	TH-sih1	n/a	Thailand, Ranong	KU051822	ANGBF44505-19	Cheng *et al*. 2020
Sillago cf. *sihama* 1	LLD2	n/a	Thailand, Ranong	KU051823	ANGBF44506-19	Cheng *et al*. 2020
Sillago cf. *sihama* 1	LLD3	n/a	Thailand, Ranong	KU051824	ANGBF44507-19	Cheng *et al*. 2020
Sillago cf. *sihama* 1	n/a	USNM 444114	Myanmar, Tanintharyi	MH235720	n/a	GenBank
Sillago cf. *sihama* 1	SP-65-2	USMFC (53) 00003	Malaysia, Kedah	MW498797	DBMR171-19	Zainal Abidin *et al*. 2021
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	PI-0179	USNM 403179	Philippines, Luzon Island	n/a	PHILA179-13	Present study
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	RP-106	USNM 408906	Philippines, Luzon Island	n/a	PHILA580-13	Present study

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	PHIL-034	USNM 437644	Philippines, Panay Island	n/a	PHILA1671-16	Present study
Sillago cf. *sihama* 2 (Orig ID *S. asiatica*)	n/a	ASIZP0801172	China, Taiwan	KU892862	ZOSKT1631-16	Chang *et al*. 2017
Sillago cf. *sihama* 2 (Orig ID *S. japonica*)	n/a	ASIZP0801174	China, Taiwan	KU892863	ZOSKT1632-16	Chang *et al*. 2017
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	BW-A1541	CSIRO H 3921-01	Australia, Queensland	EF609471	FOAC542-05	Ward & Holmes 2007
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	BW-A1542	CSIRO uncat	Australia, Queensland	n/a	FOAC543-05	Ward & Holmes 2007
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	BW-A17001	CSIRO H 8841-14	Papua New Guinea	n/a	FOAQ837-22	BOLD
Sillago cf. *sihama* 2	ZJJHD1	n/a	China	KU051813	GBMIN129865-17	Cheng *et al*. 2020
Sillago cf. *sihama* 2	BS-sih3	n/a	China, Basuo	KU051819	GBMIN119731-17	Cheng *et al*. 2020
Sillago cf. *sihama* 2	ZJ-sih1	n/a	China, Zhanjiang	KU051881	GBMIN129868-17	Cheng *et al*. 2020
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	BW-A5890	CSIRO uncat	Indonesia, Lombok	n/a	FOAH979-08	BOLD
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	BW-A8857	CSIRO LM415	Indonesia, Lombok	HQ955952	FOAK874-10	BOLD
Sillago cf. *sihama* 2 (Orig ID *S. sihama*)	BW-A5891	CSIRO uncat	Indonesia, Lombok	n/a	FOAH980-08	BOLD
Sillago cf. *sihama* 3	ASIZP0807085	n/a	China, Taiwan	MF571941	GBMNB4172-20	Cheng *et al*. 2020
Sillago cf. *sihama* 3	BW-A8761	CSIRO uncat	Indonesia, Bali	n/a	FOAK968-10	BOLD
Sillago cf. *sihama* 3	BW-A8858	CSIRO LM416	Indonesia, Lombok	n/a	FOAK875-10	BOLD
Sillago cf. *sihama* 3 (Orig ID *S. soringa*)	PB21	n/a	India, Port Blair	MK791513	GBMNC16827-20	Divya *et al*. 2021
Sillago cf. *sihama* 3 (Orig ID *S. soringa*)	PB58	n/a	India, Port Blair	MK791514	GBMNC16826-20	Divya *et al*. 2021
Sillago cf. *sihama* 3 (Orig ID *S. sihama*)	ADC198.3-3	n/a	South Africa	JF494522	TZMSA480-04	Steinke *et al*. 2016

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago cf. *sihama* 3 (Orig ID *S. sihama*)	ADC10_198.3 #20	n/a	Mozambique	HQ561464	DSFSG117-10	Steinke *et al*. 2016
Sillago cf. *sihama* 3 (Orig ID *S. sihama*)	SAIAB 80731-1	SAIAB 80731	Tanzania	n/a	SAIAB865-08	BOLD
Sillago cf. *sihama* 3 (Orig ID *S. sihama*)	SAIAB 77085-T26	SAIAB 77085	Seychelles	n/a	SAIAB371-06	BOLD
Sillago cf. *sihama* 3 (Orig ID *S. sihama*)	F1707SM-28	n/a	Bangladesh	MK340718	ANGBF56257-19	Habib *et al*. 2021
Sillago cf. *sihama* 3 (Orig ID *S. lutea*)	n/a	DOS05508	Vietnam	MK777540	GBMNB7550-20	Thu *et al*. 2019
Sillago cf. *sihama* 4 (Orig ID *S. sihama*)	PHIL-459	USNM 438069	Philippines, Luzon Island	n/a	PHILA2096-16	Present study
Sillago cf. *sihama* 5 (Orig ID *S. asiatica*)	RP-186	USNM 408986	Philippines, Luzon Island	n/a	PHILA660-13	Present study
Sillago cf. *sihama* 5 (Orig ID *S. asiatica*)	RP-187	USNM 408987	Philippines, Luzon Island	n/a	PHILA661-13	Present study
Sillago cf. *sihama* 5 (Orig ID *S. sihama*)	PHIL-462	USNM 438072	Philippines, Luzon Island	n/a	PHILA2099-16	Present study
Sillago cf. *sihama* 5 (Orig ID *S. asiatica*)	BIF1157	MZB- BIF01157	Indonesia, Jawa Tengah	KU692891	BIFD718-13	Dahruddin *et al*. 2016
Sillago cf. *sihama* 5 (Orig ID *S. asiatica*)	BIF1156	MZB- BIF01156	Indonesia, Jawa Tengah	KU692893	BIFD717-13	Dahruddin *et al*. 2016
Sillago cf. *sihama* 6	PK-sih228	n/a	Pakistan, Karachi	MF571949	GBMNB4180-20	Cheng *et al*. 2020
Sillago cf. *sihama* 6	PK-sih2	n/a	Pakistan, Karachi	MF571942	GBMNB4173-20	Cheng *et al*. 2020
Sillago cf. *sihama* 6	PK-sih3	n/a	Pakistan, Karachi	MF571943	GBMNB4174-20	Cheng *et al*. 2020
Sillago cf. *sihama* 6 (Orig ID *S. sihama*)	LQDWL-MP1415-FISH-314	n/a	India, Gujarat	n/a	ANGEN282-15	BOLD
Sillago cf. *sihama* 6 (Orig ID *S. sihama*)	n/a	CEW0186	Arabian Gulf, Saudi Arabia	KU499575	n/a	Rabaoui *et al*. 2019
Sillago cf. *sihama* 7 (Orig ID *S. sihama*)	ADC12_198.3 #27	n/a	South Africa	KF489761	DSFSG834-12	Steinke *et al*. 2016

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TABLE 1. (Continued)

Species*	Sample ID	Voucher number	Sampling location	GenBank accession no.	BOLD ID	Reference
Sillago cf. *sihama* 7 (Orig ID *S. sihama*)	ADC12_198.3 #25	n/a	South Africa	KF489762	DSFSG802-12	Steinke *et al*. 2016
Sillago cf. *sihama* 7 (Orig ID *S. sihama*)	ADC12_198.3 #26	n/a	South Africa	KF489763	DSFSG809-12	Steinke *et al*. 2016
Sillago cf. *sihama* 8	PK-sih260	n/a	Pakistan, Karachi	MF571912	GBMNB4143-20	Cheng *et al*. 2020
Sillago cf. *sihama* 8	PK-sih263	n/a	Pakistan, Karachi	MF571913	GBMNB4144-20	Cheng *et al*. 2020
Sillago cf. *sihama* 8	PK-sih309	n/a	Pakistan, Karachi	MF571915	GBMNB4146-20	Cheng *et al*. 2020
Sillago cf. *sihama* 8 (Orig ID *S. sihama*)	n/a	CHFB1195	Iran	n/a	CHFB118-12	BOLD
Sillago sinica	DY-sin1	n/a	China, Dongying	KU052008	ANGBF44590-19	Cheng *et al*. 2020
Sillago sinica	PT-sin1	n/a	China, Pingtan	KU052025	ANGBF44604-19	Cheng *et al*. 2020
Sillago sinica	RS-sin1	n/a	China, Rushan	KU052029	ANGBF44608-19	Cheng *et al*. 2020
Sillago sinica	ZG1	n/a	China, Zhoushan	MF571936	GBMNB4167-20	Cheng *et al*. 2020
Sillago sinica	n/a	PKU 2043	Korea	KC708229	GBGCA2694-13	Bae *et al*. 2013
Sillago soringa	FEL_JNUSS22025	n/a	Bangladesh, St. Martin's Island	OM184308	n/a	Present study
Sillago soringa	FEL_JNUSS22030	n/a	Bangladesh, St. Martin's Island	OM184309	n/a	Present study
Sillago soringa (Orig ID *S. arabica*)	PK-ara188	n/a	Pakistan, Karachi	MF571937	GBMNB4168-20	Cheng *et al*. 2020
Sillago sp. BOLD-2019	BW-A10295	CSIRO uncat	Indonesia, Java	JN312947	FOAM332-10	BOLD
Sillago vincenti	FEL_JNUCH12192	n/a	India, Chennai	OM184310	n/a	Present study
Sillago vincenti	FEL_JNUCH12199	n/a	India, Chennai	OM184311	n/a	Present study
Sillago vincenti	n/a	NBFGR-MN-SV-40	India	MK791510	GBMNC16830-20	Divya *et al*. 2021
Sillago vincenti	n/a	NBFGR-MS-SV-6	India	MK791511	GBMNC16829-20	Divya *et al*. 2021
Sillago vincenti	n/a	NBFGR-SV-3949	India	MK791512	GBMNC16828-20	Divya *et al*. 2021

*Orig ID: Original identification, given in brackets, was changed on basis of COI sequence analysis.
n/a: not available.

Results

Morphological identification

Sillago sihama (Fabricius, 1775)

Figures 1A–C, 2A & B, 3, 8B, Table 2

Atherina sihama Fabricius in Niebuhr (ex Forsskål), 1775: 70 (Red Sea, Yemen, Al-Luhayya).
Northern whiting; Sand smelt; Silver sillago

Materials examined. Bangladesh: FEL_OUC uncat. [tissue sample M8191–M8193], 3 specimens, 88.7–140.8 mm standard length (SL), Maheshkhali, 21.77°N, 91.89°E, August 2019; FL_JNU uncat. [MA12038–MA12051], 14 specimens, 77.0–100.2 mm SL, Maheshkhali, January 2020; FL_JNU uncat. [SM112101–SM112107], 7 specimens, 112.4–159.0 mm SL, St. Martin's Island, 20.61°N, 92.32°E, November 2021; additional 40 specimens, 76.6–110.3 mm SL, Maheshkhali, January 2020; 7 specimens, 63.3–143.5 mm SL, Cox's Bazar (21.45°N, 91.96°E), November 2019. **southern Red Sea:** HUJF 19716, 184.0 mm SL, Eritrea, photograph; KAUMM 462 [KAU12-006], 182.0 mm SL, Saudi Arabia, off Jizan, 15 February 2012; KAUMM 67 [KAU12-789], 124.0 mm SL, Saudi Arabia, off Jizan, 29 February 2012; KAUMM 67 [KAU12-789], 112.0 mm SL, Saudi Arabia, off Jizan, 01 March 2012; SMF 35900 [KAU14-301], 195.0 mm SL, Saudi Arabia, off Jizan, 01 November 2014; SMF 35911 [KAU14-351], 135.0 mm SL, Saudi Arabia, off Jizan, 04 November 2014.

Comparative material: ***Sillago erythraea*:** SMF 35017 [KAU12-790 & 791], 2, 128.0–134.0 mm SL, southern Red Sea, Saudi Arabia, off Jizan, 29 February 2012; KAUMM 468, 120 mm SL, southern Red Sea, Saudi Arabia, off Jizan, 31 October 2014. ***Sillago mengjialensis*:** FEL_OUC142378, holotype, 98 mm SL, Bangladesh, Cox's Bazar. ***Sillago muktijoddhai*:** FEL_OUC142377, holotype, 92 mm SL, Bangladesh, Cox's Bazar. ***Sillago* cf. *sihama* 2:** ZJOU_FEBL 021131, 131.0 mm SL, China, Fujian, Zhangzhou, photograph.

Diagnosis: *Sillago sihama* is distinguished by dorsal-fin rays XI + I,20–23; anal-fin rays II,21–23; 66–74 scales in the lateral line; 4–5 scales above the lateral line; 3–4 + 8–9 gill rakers on the first arch; 12–15 (mostly 14) abdominal, 5–10 (mostly 8) modified, 11–16 (mostly 13) caudal and 32–35 (mostly 35) total vertebrae. The body is brownish dorsally, silver ventrally; area between posterior nostril and dorsoanterior edge of orbit unpigmented; first dorsal fin with black pigment on first two membranes at spine tips; anal fin lacking black dots. The swimbladder is long with two anterior extensions, two posterior extensions without a lacuna at the base; the anterolateral extension of the swimbladder extends into the anterior short blind tubule and posterior one kinked, long and complex, and 10–11 lateral processes. The general body shape is shown in Figure 1A–C. Counts and measurements are given in Table 2. Frequency distribution for meristic counts is given in Table 3.

Color of fresh specimens (Fig. 1A & B)**:** The body is unmarked, brownish, silvery gray or silvery tan dorsally, silver on sides and ventrally. Area between posterior nostril and dorsoanterior edge of orbit unpigmented. First dorsal fin with some dusky pigment on the membranes, first two membranes much darker at spine tips; membranes of the second dorsal fin with dusky pigment adjacent anteriorly to each ray. The anal fin is light yellowish to whitish without black dots, with a white margin along anterior one-third of the fin. The caudal fin is light yellowish, usually blackish along dorsal and ventral edges of each lobe. Pectoral and pelvic fins are light yellowish.

Swimbladder (Fig. 2A & B)**:** The swimbladder is long. Two anterior extensions are divided and end on each side of the basioccipital over the auditory capsule. An anterolateral extension originates anteriorly on both sides of the swimbladder and then bifurcates into anterior and posterior subextensions. The anterior subextensions are short, simple blind tubules, but the posterior one is kinky, long and complex, extending along the abdominal wall and terminating near the bases of two posterior extensions. The entire lateral surface of the main body of the swimbladder has 10–11 robust and horn-like lateral processes (anterior 4–5 stout and horn-like, posterior 6–7 small and triangular) and penetrate the musculature. Posterior sub-extensions of the swimbladder are ventrally adjacent to the lateral processes but not interconnected with each other. Two posterior tapering extensions of the swimbladder extend into the caudal region. Bases of the two posterior extensions are adherent and two posterior extensions are well-knit, without a lacuna in between. A single duct-like process arises from the ventral surface of the swimbladder, and extends to the urogenital opening. The duct-like process originates anteriorly at the termination of the swimbladder and anterior to the base of two posterior extensions. A sub-extension is attached to the sanguineous vesicle near the vertebrae.

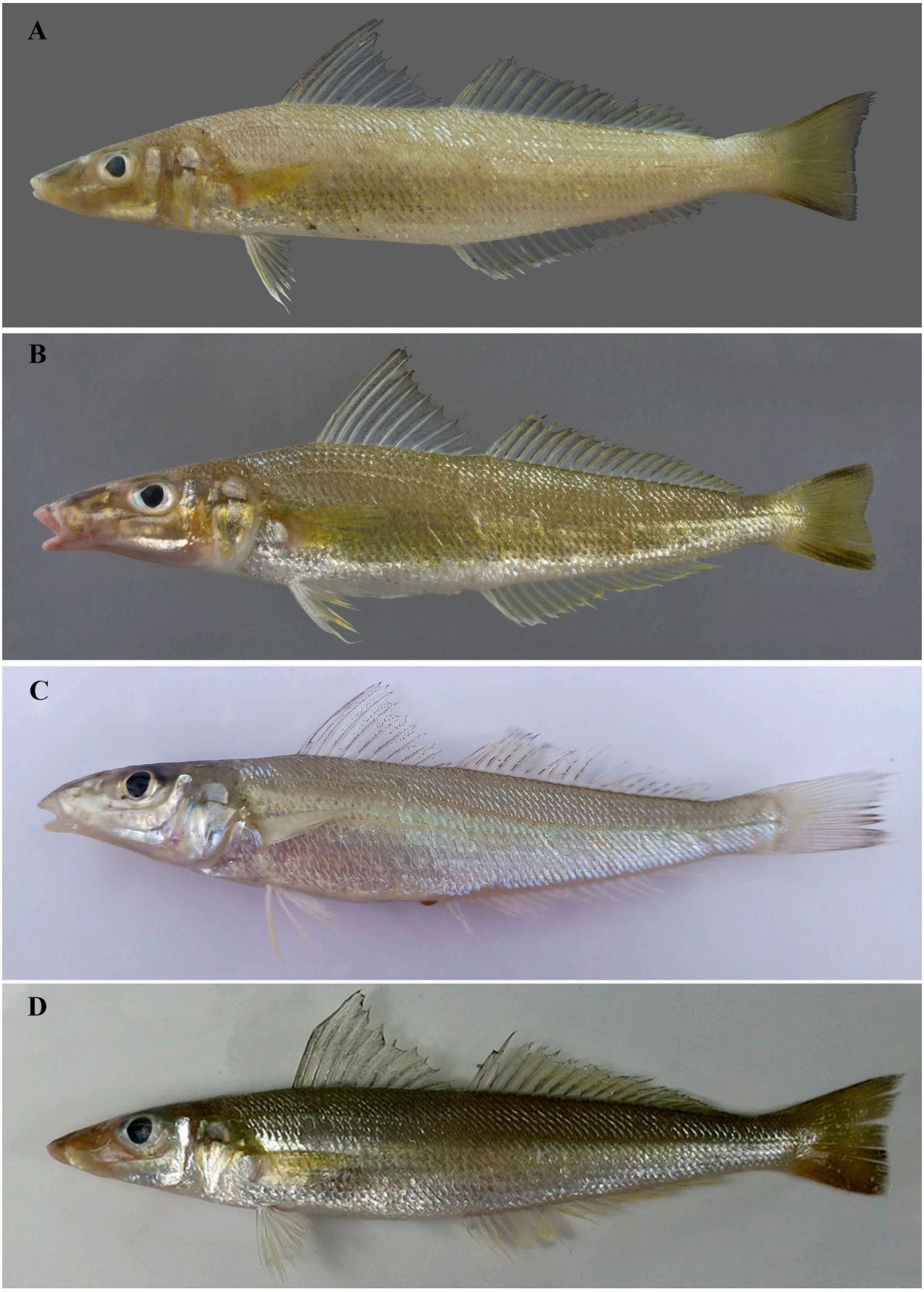

FIGURE 1. A: *Sillago sihama*, KAUMM 462 [KAU12-006], 182.0 mm SL, Jizan, Saudi Arabia, southern Red Sea; **B**: *S. sihama*, SMF 35900 [KAU14-301], 195.0 mm SL, Jizan, Saudi Arabia, southern Red Sea; **C**: *S. sihama*, 98.9 mm SL, Maheshkhali, Bangladesh; **D**: *S.* cf. *sihama* 2, ZJOU_FEBL021131, 131.0 mm SL, Fujian, Zhangzhou, China (Xiao 2018).

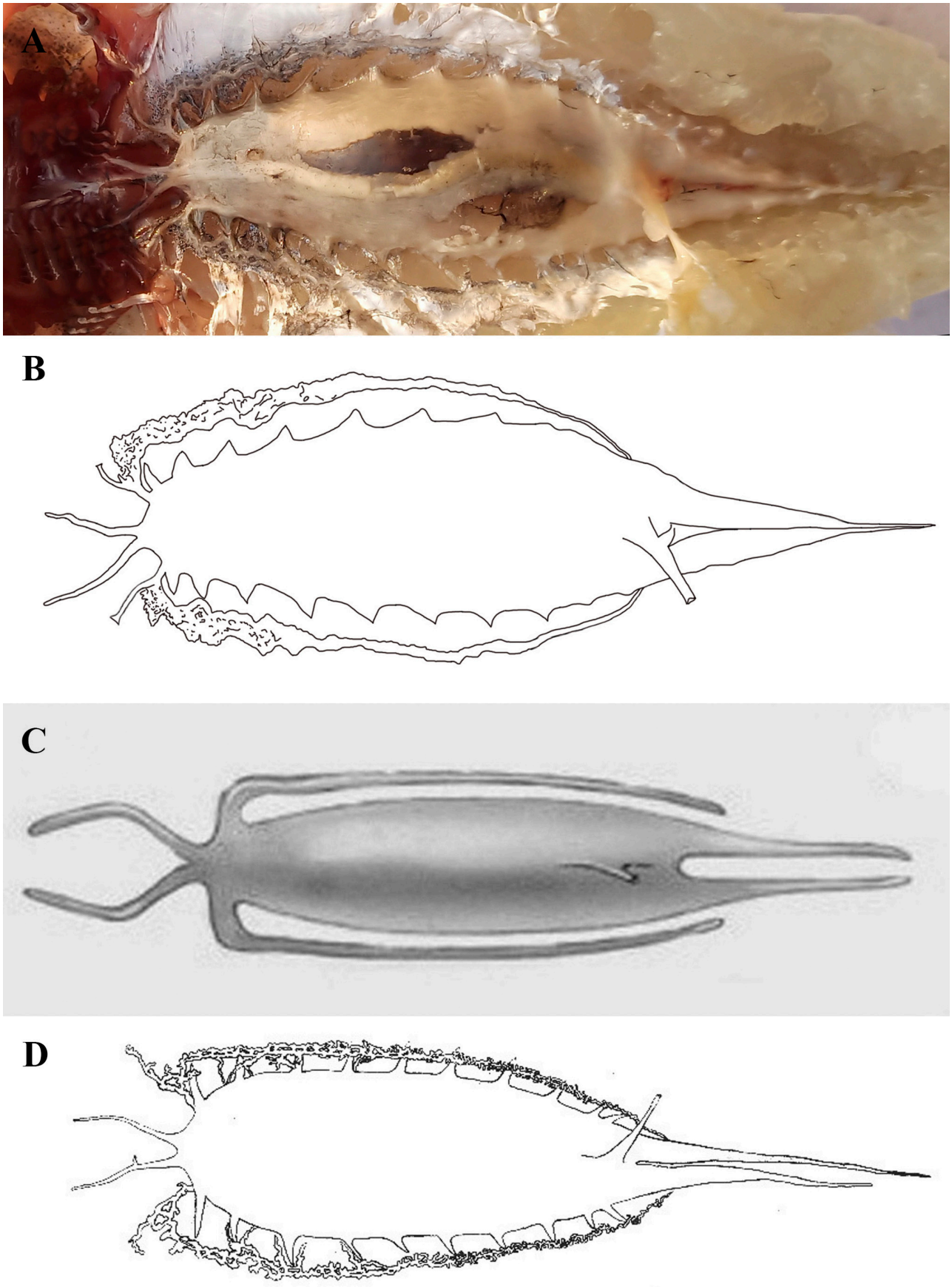

FIGURE 2. A & B: Swimbladder of *Sillago sihama*, Bangladesh; **C**: Swimbladder of *Sillago sihama*, Eritrea, southern Red Sea (Golani *et al*. 2013); **D**: Swimbladder of *Sillago* cf. *sihama* 2, China (Xiao 2018).

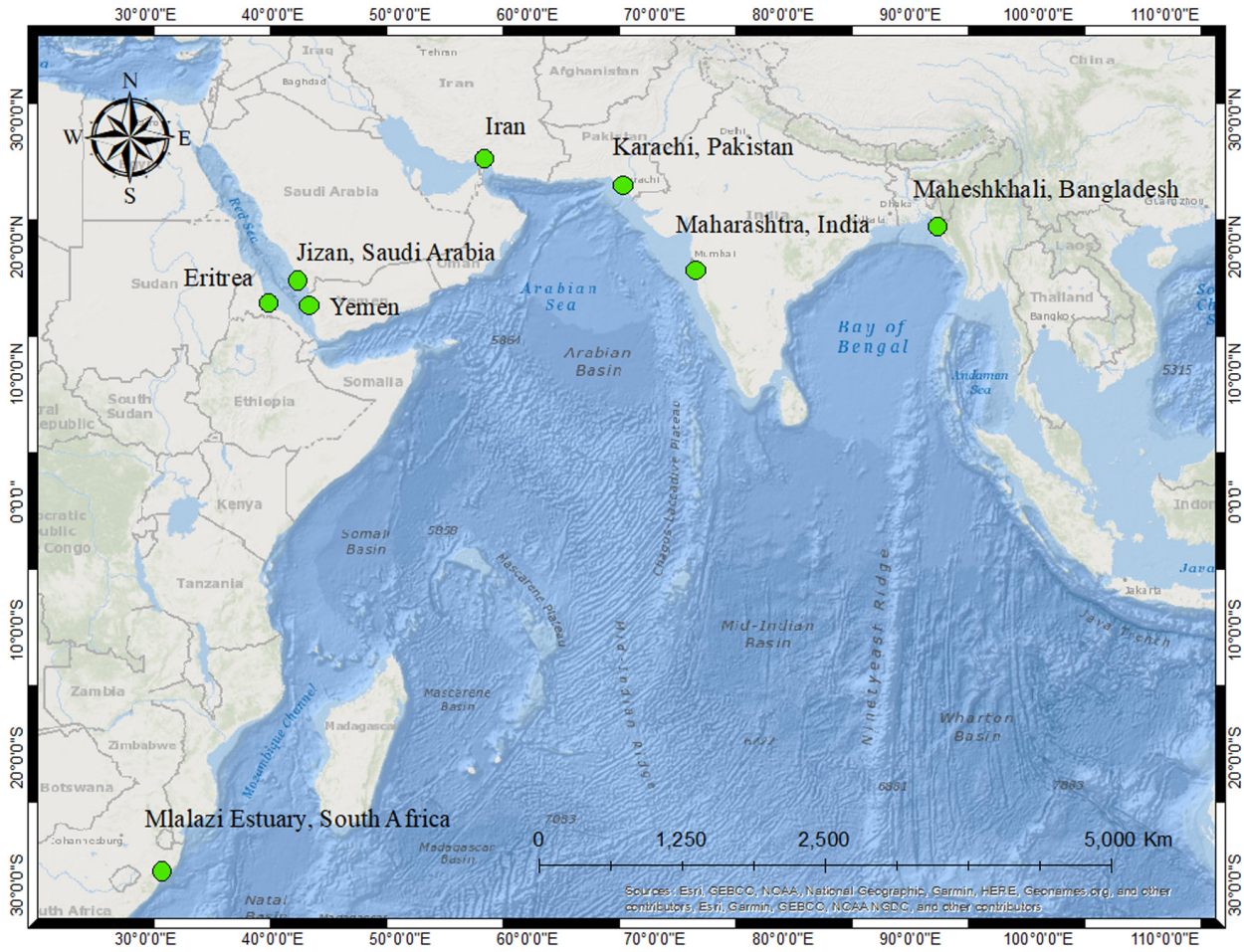

FIGURE 3. Distribution of *Sillago sihama* in the Indian Ocean.

TABLE 2. Meristic counts and morphometric measurements of *S. sihama* and *S. soringa* from Bangladesh.

Meristic and morphometric measurements	*S. sihama* [a] n=72 (Bangladesh)	*S. soringa* [a] n=30 (St. Martin's Island, Bangladesh)	*S. soringa* [a] n=4 (Chennai, India)	*S. soringa* [b] n=5 (Visakhapatnam, India)
Dorsal fins	XI + I,20–23	X–XI + I,20–22	XI + I,21	XI + I,21
Anal fin	II,21–23	II,20–22	II,22–23	II,22
Pectoral-fin rays	15–17	15–16	14–16	15–16
Pelvic-fin rays	I,5	I,5	I,5	I,5
Caudal-fin rays	17	17	16–17	-
Scales in lateral line	66–74	68–72	68–70	64–68
Scales above/below lateral line	4–5/10–12	4–5/10	4–5/8–9	4–5/9–10
Gill rakers on first arch	3–4+8–9=11–13	4+8–9=12–13	4+8=12	3–4+1+8–9
Vertebrae (AV+HV+CV)	12–15+5–10+11–16=32–35	12–14+6–7+11–14=32–34	13–14+6+14=33–34	AV+5–7+CV=34
Total weight (TW, g)	3.2–40.2	5.1–12.9	18.6–26.2	-
Total length (TL), in mm	76–165.5	80.8–119.6	133.3–140.5	123–153

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TABLE 2. (Continued)

Meristic and morphometric measurements	*S. sihama* [a] n=72 (Bangladesh)	*S. soringa* [a] n=30 (St. Martin's Island, Bangladesh)	*S. soringa* [a] n=4 (Chennai, India)	*S. soringa* [b] n=5 (Visakhapatnam, India)
Standard length (SL), in mm	63.3–159	69.6–104.5	116.6–123.9	-
As % of SL				
Head length (HL)	24.5–29.1	26.5–31.8	27.0–28.0	27.6–29.2
Upper jaw length (UJL)	4.5–7.1	3.9–6.9	4.0–5.9	-
Lower jaw length (LJL)	4.2–7.3	3.4–6.0	3.6–5.9	-
Postorbital length (PL)	8.1–10.7	9.19–11.9	9.7–10.1	-
Snout length (slw)	3.5–9.7	6.41–9.9	8.0–8.9	-
Eye diameter (ED)	5.5–9.6	5.37–8.1	5.5–7.1	-
Interorbital width (IW)	4.0–6.0	4.28–6.1	4. 5–5.2	-
Caudal peduncle depth (CPD)	5.9–7.8	5.3–8.3	6.6–7.5	-
Caudal peduncle length (CPL)	5.6–13.0	6.6–11.4	8.6–9.8	-
First dorsal-fin base (D1L)	13.4–22.9	16.2–25.1	19.9–22.4	-
Second dorsal-fin base (D2L)	33.3–38.1	31.0–39.0	33.8–36.9	-
Anal-fin base (AL)	33.8–42.3	35.1–46.1	37.9–39.3	-
Pectoral-fin length (ptl)	11.6–16.8	11.9–17.9	13.3–17.2	-
Pelvic-fin length (pvl)	11.9–20.1	12.1–16.2	10.1–15.2	-
Body width (BW)	11.1–15.5	9.9–16.7	11.7–13.1	-
Body depth (BD)	12.3–19.6	10.6–17.5	16.2–18.2	17.1–19.2
As % of HL				
Eye diameter (ED)	21.1–34.1	18.9–28.8	19.7–25.8	23.5–28.6
Interorbital width (IW)	13.5–22.3	13.5–21.9	16.6–19.1	19.1–21.1
Snout length (SLw)	17.3–35.9	22.6–34.7	28.8–33.0	38.2–40.0
Postorbital length (PL)	26.9–39.8	30.3–42.0	35.2–37.3	36.8–40.0
CPD/CPL	50.9–96.5	54.0–87.0	68.2–81.6	-

a: present study; b: Dutt & Sujatha 1982

Distribution: *Sillago sihama*, originally described from the southern Red Sea (Yemen), is widely distributed in the Indian Ocean, sampled from the southern Red Sea (Eritrea and Saudi Arabia), Arabian Sea (western India, Pakistan), northeastern Arabian Gulf (Hormozgan, Iran), South Africa (Mlalazi Estuary, Tugela Bank and Mhlathuze Estuary), and Bay of Bengal, Bangladesh (Maheshkhali, Cox's Bazar and St. Martin's Island) (Lakra *et al*. 2011; Golani *et al*. 2013; Bogorodsky *et al*. 2014; Steinke *et al*. 2016; Cheng *et al*. 2020; Divya *et al*. 2021 (as *S. intermedius*); Amir *et al*. 2022; Afrand *et al*. 2023; present study) (Fig. 3).

Remarks: Habib & Islam (2020) listed *S. sihama* from Bangladesh based on six sources, but all these publications lack descriptions of collected material. Later, Ahmed *et al*. (2021) included specimens under the name *S. sihama* in their phylogenetic analysis, but further study revealed that this material represents another species, namely *Sillago muktijoddhai* Gao & Saha, 2022. Accordingly, *S. sihama* is reported as the first confirmed, easternmost record from Bangladesh in the present study.

Unfortunately, there is no published literature on the structure of the swimbladder for *S. sihama* samples from India, Pakistan, Iran and South Africa. However, there were marked differences in the swimbladder between specimens from Bangladesh (Fig. 2A & B) and Eritrea based on available published literature (Golani *et al*. 2013;

Fig. 2C in present study). According to Golani *et al*. (2013), the swimbladder of *Sillago sihama* (Eritrea) lacks an anterior subextension of the anterolateral extension, and the two posterior tapering extensions are separated from each other. The posterior sub-extensions of the anterolateral extension are smooth but differ from those in *S. sihama* (Bangladesh). These differences include the presence of an anterior subextension of the anterolateral extension, two posterior extensions joined to each other, and each posterior subextension of the anterolateral extension is a complex. Previously Kaga (2013) raised this question with detailed comments and stated that Golani *et al*. (2013) must have overlooked anterior sub-extensions of the anterolateral extension. Moreover, these authors did not provide any swimbladder photographs (just schematic drawings) and did not indicate which specimens were examined for swimbladder morphology. Therefore, swimbladder morphology described in the present study is applicable to the true *S. sihama* and can be useful for comparison with undescribed species in future.

TABLE 3. Frequency distribution for meristic counts of *S. sihama* and *S. soringa*.

Meristic characters	*S. sihama* [a] n=72 (Bangladesh)	*S. soringa* n=30 (St. Martin's Island, Bangladesh)	*S. soringa* [a] n=4 (Chennai, India)
D2 rays			
I,20	25	6	-
I,21	39	23	4
I,22	7	1	-
A rays			
II,20	-	1	-
II,21	24	10	-
II,22	46	19	3
II,23	2	-	1
GR1			
3+8	22	-	-
3+9	5	-	-
4+8	34	13	4
4+9	10	17	-
Vertebrae			
32	-	-	1
33	1	4	1
34	2	13	-
35	14	11	-
	28	-	-

Sillago soringa **Dutt & Sujatha, 1982**

Figures 4 & 5, Table 2

Sillago soringa Dutt & Sujatha, 1982: 611–614, fig. 1 (India, Visakhapatnam).
Soringa sillago

Materials examined. Bangladesh: FL_JNU uncat. [SS22015, SS22035, SS22042, SS22043 and SS22044], 5 specimens, 81.8–101.2 mm SL, St. Martin's Island, 20.62°N, 92.32°E, February 2020; additional 25 specimens, 69.6–102.2 mm SL, St. Martin's Island, February 2020. **India:** 4 specimens, 116.6–123.9 mm SL, Chennai, 13.29°N, 80.32°E, December 2019; F7734/2, holotype; F7735/2, 4 paratypes, 123.0–153.0 mm TL, Visakhapatnam, photograph.

Comparative material: ***Sillago vincenti*****:** FL_JNU uncat. [CH12191–CH121910], 10 specimens, 141.8–220.3 mm SL, December 2019, India, Chennai. ***Sillaginopsis domina*****:** FEL_OUC uncat. [tissue sample 142276, 142284, and 142293], 3 specimens, Bangladesh, Cox's Bazar, October 2018; FL_JNU uncat. [PP121910, PP121915 and PP121916], 3 specimens, 180–195 mm SL, December 2019, Bangladesh, Patharghata.

Diagnosis: *Sillago soringa* is differentiated by dorsal-fin rays X–XI + I,20–22; anal-fin rays II,20–22; 68–72 lateral line scales; 4–5 scales above the lateral line; 4 + 8–9=12–13 gill rakers on the first arch; 12–14 (mostly 13) abdominal, 6–7 (mostly 7) modified, 11–14 (mostly 13) caudal, and 32–34 (mostly 33) total vertebrae; swimbladder

long with a single anterior extension and a single posterior extension, short anterolateral extension and ten lateral processes. The general body shape is shown in Figure 4A. Counts and measurements are given in Table 2.

Color of fresh specimens (Fig. 4A)**:** Body brown dorsally, whitish ventrally. Dorsal fins hyaline dusted with black dots, with dots on second dorsal fin arranged in two longitudinal rows. Anal fin light yellowish to whitish dusted with black dots. Caudal fin mainly hyaline, with dusky pigment posteriorly. Pectoral and pelvic fins hyaline.

Swimbladder (Fig. 4B & C)**:** The swimbladder with one anterior extension projecting forward, anterolateral extension curved backward along each side for a short distance, only one posterior extension, and ten lateral processes. The duct-like process is visible.

Distribution: *Sillago soringa* is distributed in the northern Indian Ocean, including the southeast coast of India (Jayasankar 1991), the east coast of India (McKay 1992) and presently, the southernmost part of Bangladesh (St. Martin's Island) (Fig. 5).

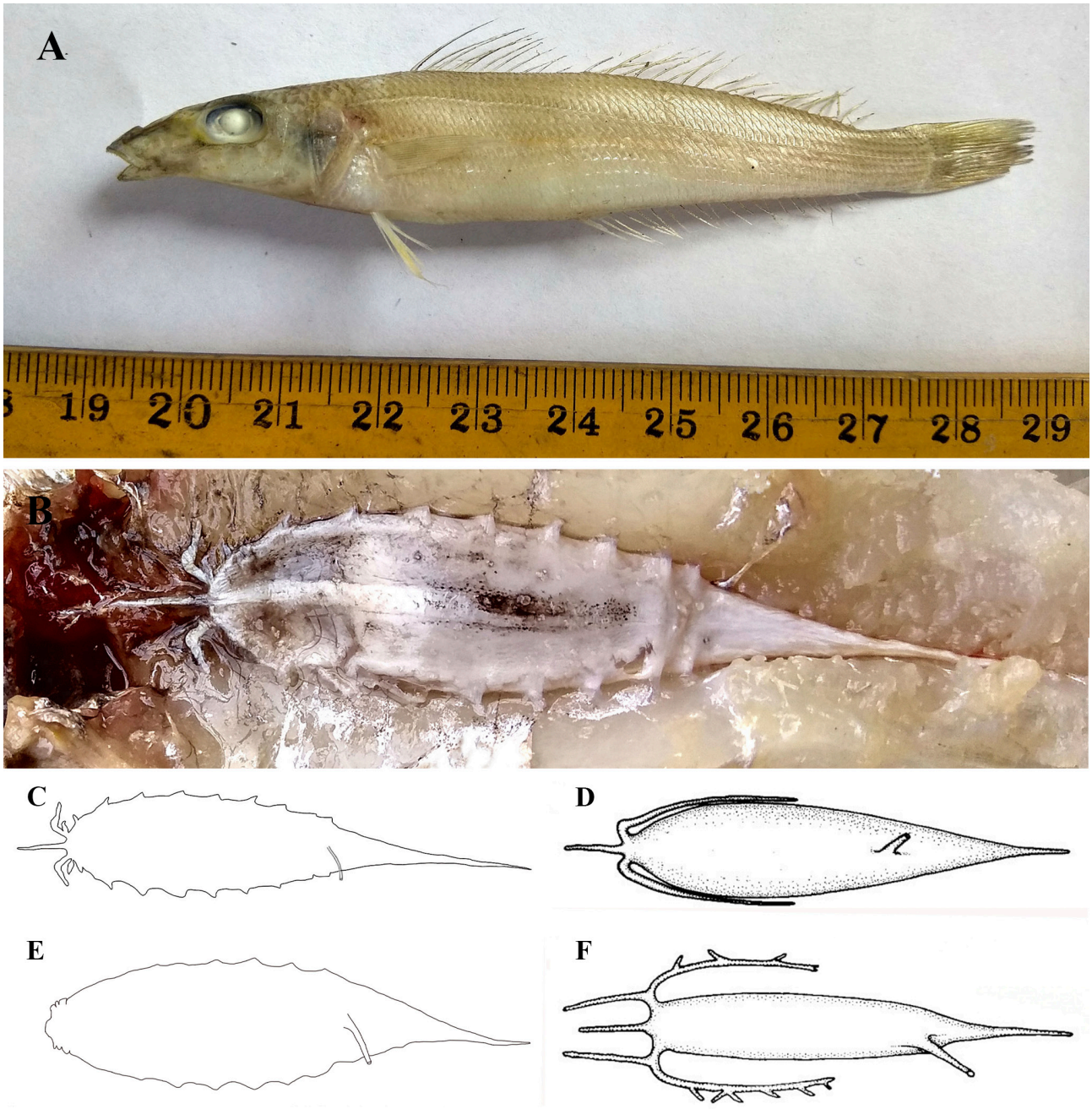

FIGURE 4. A: *Sillago soringa*, FL_JNUSS22035, 82.7 mm SL, St. Martin's Island, Bangladesh; **B & C**: Swimbladder of *S. soringa*, Bangladesh; **D**: Swimbladder of *S. asiatica* (McKay 1992); **E**: Swimbladder of *S. vincenti*, Chennai, India; **F**: Swimbladder of *S. boutani* (McKay 1992).

Comparison: Meristics, morphometric measurements and structure of the swimbladder of *S. soringa* from Bangladesh match the previous description of *S. soringa* from India by Dutt & Sujatha (1982) (Table 2). Frequency distribution for meristic counts is given in Table 3.

Often *Sillago mengjialensis* Gao, Baki & Saha, 2022, *S. muktijoddhai*, and *S. soringa* were found as a mixed group, so identification should be made based on body color and swimbladder morphology. As *S. soringa* resembles *S. sihama* but is difficult to differentiate without observation of the swimbladder (Dutt & Sujatha 1982; McKay 1992), it was most probably misidentified as *S. sihama* in Bangladesh. The species can be distinguished from *S. sihama* by having 33 vertebrae (versus 35), black dots on the anal fin and its swimbladder structure (a single posterior extension in *S. soringa* versus two posterior extensions in *S. sihama*). *Sillaginopsis domina* (Cuvier, 1816) can be differentiated easily from *S. soringa* by a very elongated second dorsal-fin spine, small eyes and absence of a swimbladder.

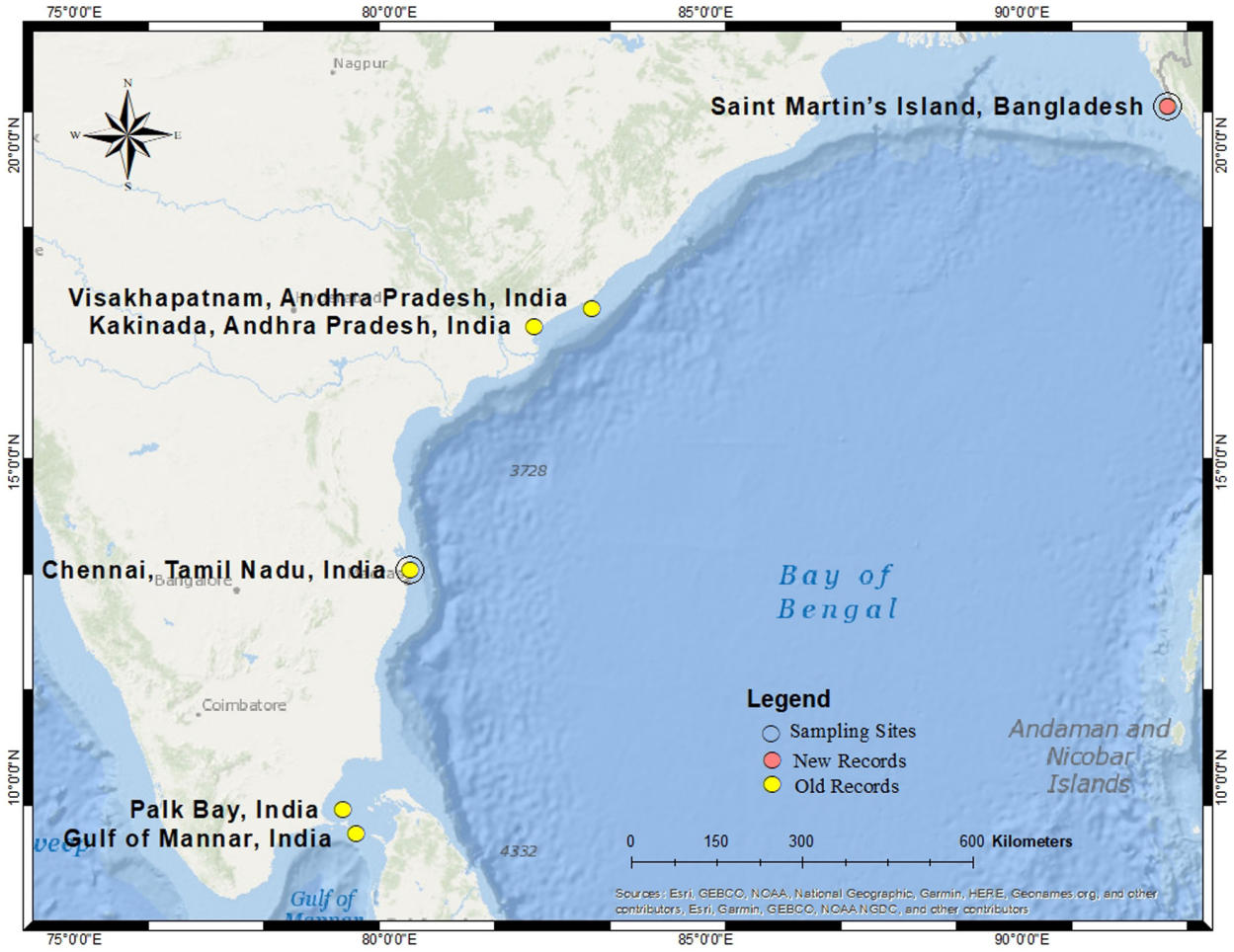

FIGURE 5. Sampling sites in the present study and distribution of *Sillago soringa*.

Sillago soringa is also similar to and can be confused with *S. vincenti* McKay, 1980, *S. boutani* Pellegrin, 1905 and *S. asiatica* McKay, 1982 but these three species have not yet been recorded from Bangladesh. However, *S. soringa* can be distinguished from these three species by combination of several characters, e.g., absence of black dots on body below lateral line, presence of black dots on the anal fin, number of vertebrae (usually 33 versus 34–38 in other three species) and swimbladder structure (Table 4). Among these four species, *S. soringa* is more similar to *S. asiatica*, but the anterolateral extension of the swimbladder is much shorter in *S. soringa* than in *S. asiatica*. Differences in the structure of the swimbladder among *S. soringa*, *S. asiatica*, *S. vincenti* and *S. boutani* are shown in Figure 4C–F.

TABLE 4. Comparison of *S. soringa* with closely related species.

	S. soringa [a, b, c]	*S. vincenti* [a, d]	*S. boutani* [e]	*S. asiatica* [e]
1. Black dots on flank below lateral line	Absent	Minute discrete black dots present	Absent	Absent
2. Black dots on anal fin	Present	Absent	Absent	Present
3. Swimbladder:				
a. Anterior extension	One, finger-like	One, short and bulbous	One, finger-like	One, finger-like
b. Anterolateral extension	Recurved backward for a short distance along the sides	Three lobate projections	Branch into anterior and posterior sub-extensions: anterior one simple blind tubule, longer than anterior extension and posterior one with some stunted blind tubule, unilateral and outward, about one-third of the body of swim bladder in length	Recurved extension longer than *S. soringa*
c. Posterior extension	One	One	One	One
4. Vertebrae	12–14+5–7+11–14=32–34	13–16+4–6+13–15=32–35	13–14+3–4+21=38	13–14+5–7+13–16=34
5. Distribution	Southeast and East coast of India and St. Martin's island, Bangladesh	East and west coast of India	Gulf of Tonkin and South-Eastern China	Gulf of Thailand to Taiwan

a: present study; b: Dutt & Sujatha 1982; c: Sujatha 1987; d: McKay 1980; e: McKay 1992.

Sillago ingenuua **McKay, 1985**

Figure 6 A & B

Sillago ingenuua McKay, 1985: 44 (Chantaburi, Gulf of Thailand).
Bay sillago

Materials examined. India: FL_JNU uncat. [CH121911, CH121915–CH121918, CH121920, CH121922 and CH121923], 9 specimens, 122.9–141.4 mm SL, Chennai, December 2019.

Comparative material: *Sillago ingenuua*: FEL_OUC 176002, 122.5 mm SL, China, Fujian, Dongshan.

Brief description: Dorsal-fin rays XI+I,17; anal-fin rays II,16–17; scales in lateral line 66–71; scale rows above lateral line 4–5; vertebrae: 13–14+9–10+9–12=32–34. Swimbladder with a short median anterior extension, a single posterior extension and about 5 small, pointed anterolateral projections. Body color is pale yellowish brown. The general body shape and swimbladder are shown in Figure 6A–C.

Geographical distribution: According to the phylogenetic analysis and species delimitation approaches *Sillago ingenuua* is divided into two (ASAP and PTP) or three (ABGD) genetic lineages (Fig. 7): *Sillago ingenuua* A from the Gulf of Thailand (type locality), Indonesia, Vietnam, China, and Malaysia (BOLD number MUHD029-15, private sequences as *S. sihama*); *S. ingenuua* B from Western Australia, eastern Australia (BOLD number FOAL889-10) and Taiwan (both lineages were recognized by Gao *et al*. 2023); and *S. ingenuua* from Chennai, India. *Sillago ingenuua* was also reported from Sri Lanka (De Bruin *et al*. 1994) but no genetic material was available from that area.

Remarks: Two separate lineages with 4.9 % and 6.9 % genetic divergence were previously detected in *S. ingenuua*, based on COI sequences and 13 concatenated protein coding gene sequences in the absence of significant morphological differences (Tikochinski *et al*. 2013; Cheng *et al*. 2020; Gao *et al*. 2023). One is *Sillago ingenuua* A from China, Vietnam, Thailand and Indonesia, and Malaysia, another is *Sillago ingenuua* B from Australia and Taiwan. Because there is insufficient distance (1.6 %) between *S. ingenuua* from India and *S. ingenuua* A, the former was included as the member of that lineage. In this study, we first report *S. ingenuua* A from the Indian Ocean, specimens of which form a monophyletic group within *S. ingenuua* A and are recognized as a potential separate species by the ABGD approach for species delimitation only, whereas PTP and ASAP do not suggest a separation from their western Pacific Ocean conspecifics. In this species, an integrative taxonomic study is needed to resolve the actual species boundaries.

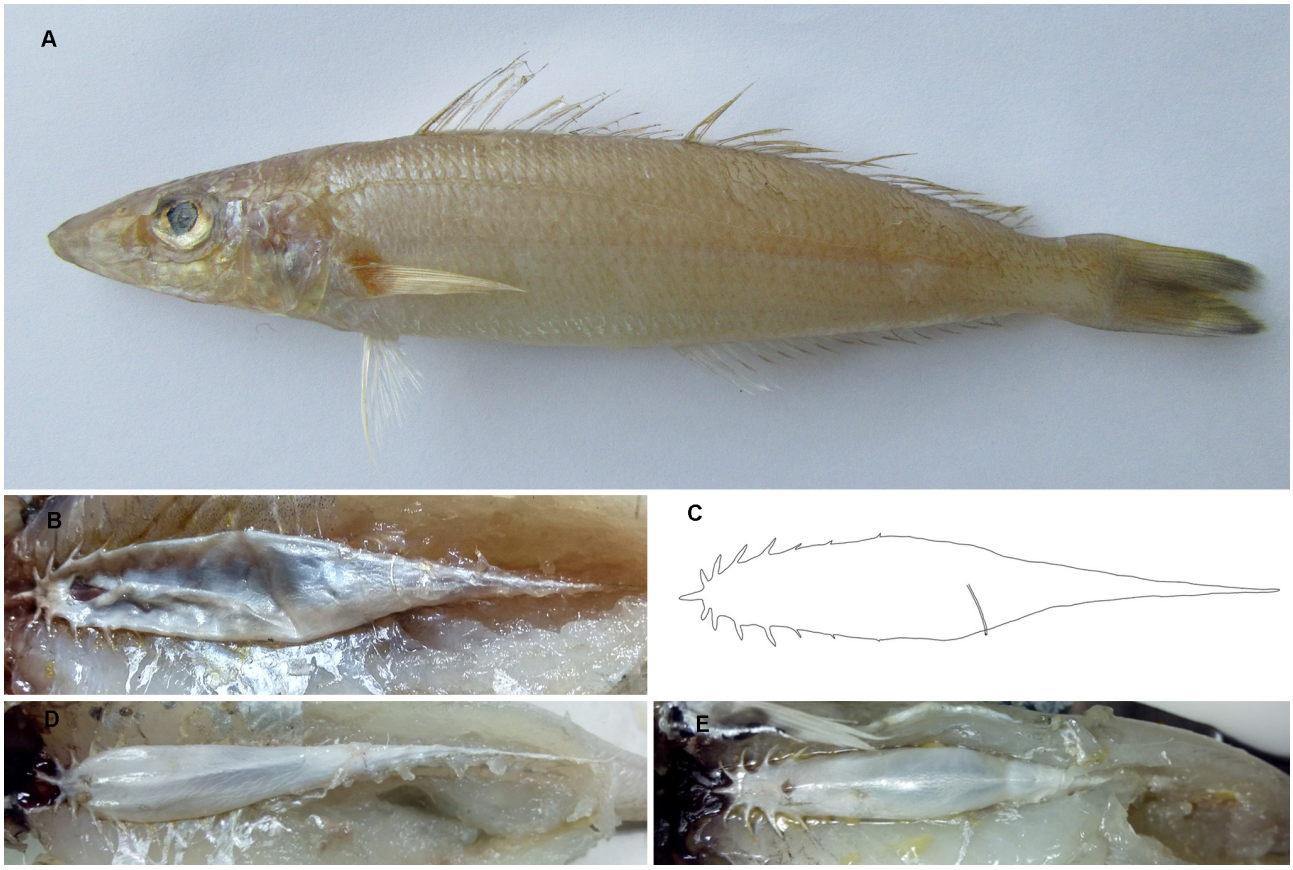

FIGURE 6. A: *Sillago ingenuua* A, FL_JNUCH121922, 130.1 mm SL, Chennai, India; **B** & **C**: Swimbladder of *Sillago ingenuua* A, Chennai, India; D: Swimbladder of *Sillago ingenuua*, Dongshan, China (Xiao 2018); E: Swimbladder of *Sillago ingenuua* B, Taiwan (Xiao 2018).

Phylogenetic analysis of the COI gene and species delimitation

The species delimitation approaches used in this study resulted 47 putative species in the ABGD analysis (partition with prior maximal distance P=1.29e-02), 45 putative species according to ASAP (threshold distance 0.019327) and 44 putative species as of PTP (Fig. 7). Therefore, we propose that there are a minimum 44 species in the family Sillaginidae. *Sillago sihama* from Bangladesh, western India, Pakistan, Iran, South Africa, and Red Sea (Saudi Arabia and Eritrea) form a lineage in the phylogenetic tree with a mean intraspecific genetic distance of 0.2 % (Fig. 7). The *S. sihama* lineage shows 3.3–25.9 % genetic distance to other 43 sillaginids. The swimbladder of *S. sihama* (Bangladesh) is most similar to *S.* cf. *sihama* 2 from China (Fig. 2D) but both form monophyletic lineages in the COI based analysis and possess a significant interspecific genetic distance (4.3 %). According to ABGD, *S.* cf. *sihama* 2 is a lump of three lineages (which were not distinguished by PTP and ASAP) and according to ASAP *S.* cf. *sihama* 3 consists of two divergent lineages (which were not distinguished by PTP and ABGD) (Fig. 7). The divergent molecular lineages were not labeled as different species here because interclade genetic distance with less than 2% usually is below the interspecific level and results from species delimitation approaches were ambiguous.

The mean intraspecific genetic distance is 0.7 % within *S. soringa* from Bangladesh and 5.7–25.5 % between *S. soringa* and other 43 sillaginids. The lowest interspecific genetic distance is 5.7 % between *S. soringa* and *S. asiatica*, and morphologically they are also closely related species (McKay 1992). However, the COI sequences of the *S. soringa* from Bangladesh were not similar to *S. soringa* sequences (MK791513, MK791514) previously submitted to GenBank (Divya *et al*. 2021), and this may be due to the misidentification of fishes without studying their swimbladders. In the phylogenetic tree (Fig. 7), *S. soringa* from Bangladesh clustered with a specimen from Pakistan (MF571937), which was originally identified as *S. arabica* McKay & McCarthy, 1989 (Cheng *et al.* 2020). Given the results from our morphological examination of specimens from Bangladesh and the high sequence similarity of specimens of *S. soringa* from Bangladesh and the specimen from Pakistan, we reassign the latter to

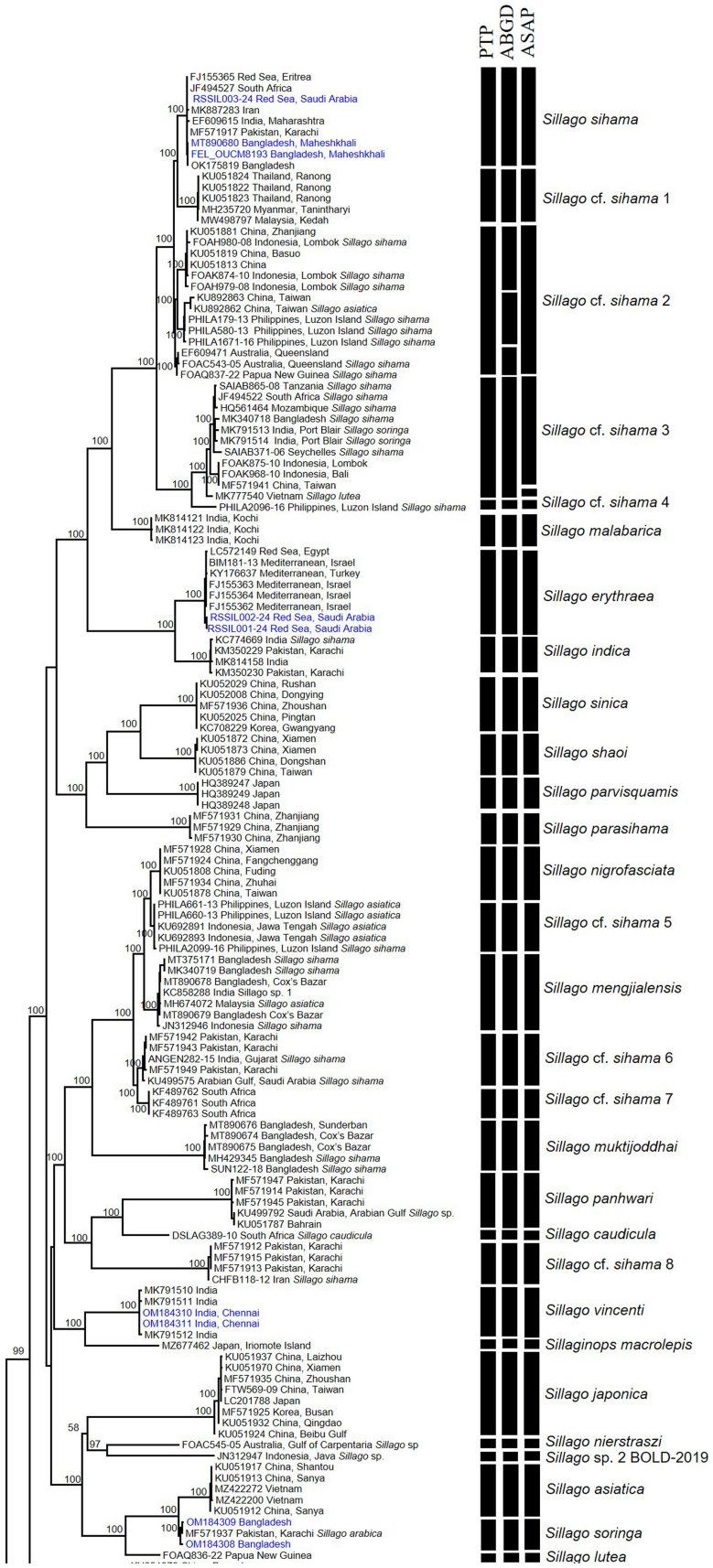

FIGURE 7. Phylogenetic tree using COI gene sequences of 45 species of Sillaginidae based on maximum likelihood method. Three species of the suborder Percoidei, *Callanthias japonicus*, *Dicentrarchus labrax* and *Pempheris schwenkii*, were selected as outgroup species. Findings from species delimitation approaches on the basis of COI gene sequences using the PTP, ABGD and ASAP methods are presented as vertical bars that link extreme taxa in the tree if allocated to the same hypothetical species.

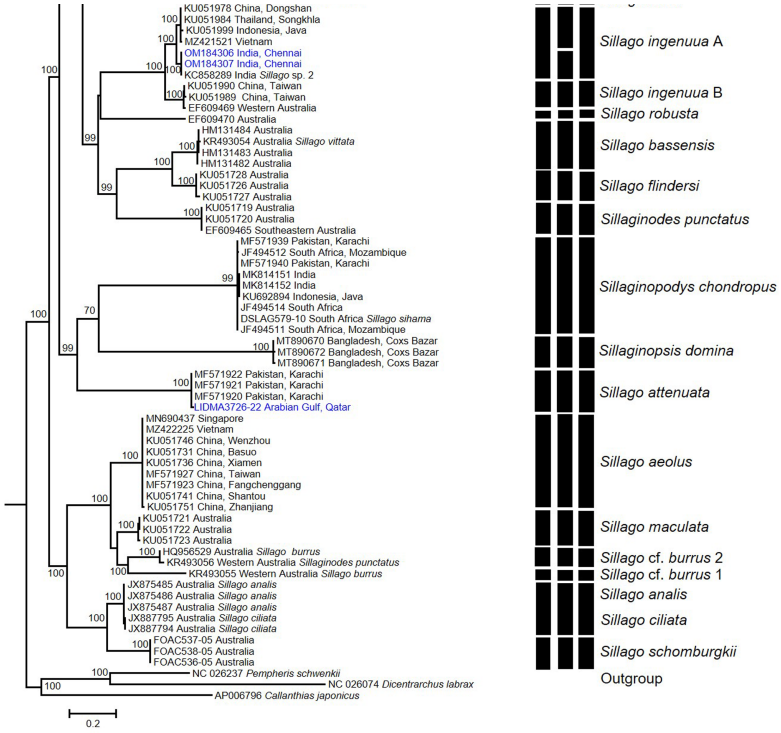

FIGURE 7. Continued.

S. soringa. The voucher of this specimen was unfortunately not preserved and therefore not available for morphological examination.

The mean intraspecific genetic divergence is 0.2 % within *S. ingenuua* from India, and 1.6 % and 5.4 % from *S. ingenuua* A and *S. ingenuua* B, respectively. This result implies that *S. ingenuua* from India is similar to *S. ingenuua* A sensu Gao *et al*. (2023) (Fig. 7), as well as being morphologically similar (Fig. 6). According to ABGD, *S. ingenuua* A from India and *S. ingenuua* A from the western Pacific Ocean are recognized as potentially different species, but they are recognized as one species according to the outcome of the ASAP and PTP analyses. According to both, ABGD and ASAP, *S. ingenuua* A and *S. ingenuua* B are different species as was recently suggested by Gao *et al*. (2023). However, these two (or three) hypothetical species have no apparent distinctive morphology. This might indicate that these species are still in the process of speciation, where they at first acquire molecular divergence, whereas clear morphological and/or behavioral diversification is still evolving.

The present phylogenetic tree shows a presence of eight genetic lineages from the Indo-West Pacific which were formerly misidentified as *S. sihama*, four of them are probably close related to *S. sihama* (Fig. 7). No specimens but one *S.* cf. *sihama* 2 (Fig. 1D) of these eight lineages were examined, but this is a matter of further comprehensive integrate studies. However, it needs to be noted that the COI gene tree does not resolve higher relationships among Sillaginidae species and it does not support a division into two groups as inferred by Cheng *et al*. (2020) from their multigene phylogenetic tree. So, the phylogenetic relationships of the species in Sillaginidae will need to be reassessed using a more complete taxon sampling also at a deeper generic level by multigene phylogenetic analyses.

Erroneous records of *S. sihama* from the western Pacific Ocean

Sillago sihama was reported from Japanese waters by Sano & Mochizuki (1984) as one of four species of the genus, the other three being *S. japonica* Temminck & Schlegel, 1843, *S. maculata* Quoy & Gaimard, 1824 and *S. parvisquamis* Gill, 1861. They mentioned *S. sihama* is a rare species in Japan, and included a description of the species' swimbladder based on specimens from Taiwan. In the same year, Masuda *et al*. (1984) also recorded *S. sihama* for Japanese waters as a result of a misidentification of *S. parvisquamis*. Hayashi (2002) reported five

species of *Sillago* from Japan including misidentified *S. sihama* and a previously unreported species, *Sillaginops macrolepis* (Bleeker, 1858). More recently Motomura (2020) listed the same five species, also including *S. sihama*. Here, we show that *S. sihama* is only found in the Indian Ocean, and the so-called *S. sihama* from Japan is the misidentification of *S.* cf. *sihama* 2 (present study).

Sillago sihama was first recorded from Korea by Jordan & Starks (1905) and was again listed by Kim *et al*. (2005) as one of four species of *Sillago* in Korean waters together with *S. aeolus* Jordan & Evermann, 1902, *S. japonica* and *S. parvisquamis* The same four species were again reported and the presence of *S. sihama* was suspected by Kwun & Kim (2010). According to the biogeographic distribution of *Sillago* lineages shown herein, the previous records of *S. sihama* are misidentifications of an undescribed species, i.e. *S.* cf. *sihama* 2.

Sillago sihama was also reported from China as one of thirteen sillaginids (Xiao *et al*. 2018, 2021; Yu *et al*. 2022), and Shao *et al*. (1986) reported the species from Taiwan (see also the Fish Database of Taiwan). Xiao (2018) revised Sillaginidae in China, including 7 valid species, *Sillaginopodys chondropus* (Bleeker, 1849), *Sillago aeolus*, *S. asiatica*, *S. ingenuua*, *S. japonica*, *S. sinica* Gao & Xue, 2011, *S. shaoi* Gao & Xiao, 2016, and four putative species *S.* cf. *sihama* 2, *Sillago* sp., *Sillago* sp. ZJ and *Sillago* sp. TW; three possibly invalid scientific names *S. megacephalus* Lin, 1933, *S. boutani* and *S. microps* McKay, 1985; and two doubtful records: *S. ciliata* Cuvier, 1829 and *S. parvisquamis*. It is impossible to say whether *S. boutani* and *S. microps* are invalid species or not because holotypes of both species exist and should be re-examined. Recently, two species were described as new from the southern coast of China: *Sillago* sp. (sensu Xiao 2018) and *S.* cf. *sihama* 8 (sensu Cheng *et al.* 2020) as *S. nigrofasciata* (Xiao *et al*. 2021), and *Sillago* sp. ZJ (sensu Xiao 2018) and *S.* sp. (sensu Cheng *et al.* 2020) as *S. parasihama* (Yu *et al*. 2022), respectively. Yu *et al*. (2022) included specimens from China in their phylogenetic analysis under the name *S. sihama*, but in fact these specimens belong to *S.* cf. *sihama* 2 (present study).

Sillago sihama was also reported as one of seven sillaginids from Vietnam, the others being *Sillago aeolus*, *S. asiatica*, *S. boutani*, *S. ingenuua*, *S. japonica*, and *S. nigrofasciata* (as *S. indica*) (McKay 1992; Kimura *et al*. 2018; Thu *et al*. 2019). Zworykin (2014) listed *S. maculata* and *S. sihama*. However, *S. maculata* is a misidentification of *S. aeolus*, as its COI sequence (MZ422225) is available from Vietnam and *S. maculata* is an endemic species of the eastern coast of Australia (Kuiter 1993). In this study, the so-called *S. sihama* is also a misidentification of *S.* cf. *sihama* 2, because a COI sequence of *S. sihama* from Vietnam (BOLD access number MEKON165-20, unpublished sequence) is nesting to *S.* cf. *sihama* 2. Most likely the misidentification of *S. sihama* and other sillaginid species from the South China Sea occurred as a consequence of the lack of detailed morphological studies (including swimbladder morphology) pointing to the necessity of additional study for positive identification of species of *Sillago*.

Sillago sihama was also reported from neighboring areas, from the Gulf of Thailand by Yoshida *et al*. (2013) and from the Philippines (Panay Island) by Motomura *et al*. (2017). Specimens identified as *S. sihama* from these areas are needed for an integrated study to assign them either to other described or undescribed species.

Sillaginidae fishes from the northern Indian Ocean with emphasis on misidentified records of *S. sihama*

The following nine species of the family were reported from the northern part of the Arabian Sea, and their distributions summarized in this study: *Sillaginopodys chondropus*, *Sillago arabica*, *S. attenuata* McKay, 1985, *S. caudicula* Kaga, Imamura & Nakaya, 2010, *S. indica* McKay, Dutt & Sujatha, 1985, *S. panhwari* Panhwar, Farooq, Qamar, Shaikh & Mairaj, 2017, *S. sihama*, *S.* cf. *sihama* 6, and *S.* cf. *sihama* 8. Randall (1995) reproduced photographs of three species taken from the Arabian Gulf (*S. arabica*, *S. attenuata*, and *S. sihama*), Eagderi *et al*. (2019) listed the same three species in their checklist. However, there is only a single record of *S. sihama* in the northeastern part of the Arabian Gulf (Afrand *et al*. 2023). Zajonz *et al*. (2019) listed one species of Silliganidae from Socotra as *S.* cf. *sihama*, but without available material it is impossible to provide a positive identification.

In the northern part of the Indian Ocean eight sillaginids are known in coastal waters of Pakistan, such as *Sillaginopodys chondropus*, *Sillago arabica*, *S. attenuata*, *S. indica*, *S. panhwari*, *S. sihama* (Cheng *et al*. 2020 as *Sillago* cf. *sihama* 1; Amir *et al*. 2022; present study), *S.* cf. *sihama* 6 and *S.* cf. *sihama* 8. Panhwar *et al*. (2017) described *Sillago panhwari* from the northern Arabian Sea coast of Pakistan and examined specimens named *S. sihama*. However, in addition to *S. sihama* there are two cryptic species under that name in Pakistan waters. *Sillago* cf. *sihama* 6 was recognised by Cheng *et al*. (2020) as *S.* sp. 2 and *Sillago* cf. *sihama* 8 by Amir *et al*. (2022) as *S.*

sp. 1, respectively.

Thirteen species of sillaginids are distributed in the coastal waters of India, e.g., *Sillaginopodys chondropus* and *Sillaginopsis domina* (both recorded by Dutt & Sujatha 1980); *Sillago indica*, *S. ingenuua*, and *S. lutea* (reported by McKay 1985); *S. intermedia* Wongratana, 1977 (by Dutt & Sujatha 1984); *S. malabarica* (Bloch & Schneider, 1801) (by Divya *et al*. 2021); *S. mengjialensis*, *S. muktijoddhai*, and *S. sihama* (present study), *S. soringa* (by Dutt & Sujatha 1982), *S. vincenti* (by McKay 1980; Krishnan & Mishra 2001; Mahesh *et al*. 2018), *S.* cf. *sihama* 3, and *S.* cf. *sihama* 6. For the first time three species belonging to the family Sillaginidae viz., *Sillaginopsis domina* (previously as *Sillaginopsis panijus* (Hamilton, 1822)), *S. sihama* and *S. maculata* were reported from Indian waters (Day 1876). McKay (1980) described a new species, *S. vincenti*, based on specimens collected from Kerala State, India. Taxonomic status of 7 species of Sillaginidae belonging to 3 genera (*Sillago argentifasciata*, *S. macrolepis*, *S. maculata*, *S. parvisquamis*, *S. sihama*, *Sillaginopodys chondropus*, and *Sillaginopis panijus*) were given by Dutt & Sujatha (1980) from the western Bay of Bengal. In this report, specimens of *Sillago macrolepis* were incorrectly assigned to that species and later were described as *Sillago lutea* by McKay (1985), *S. maculata* was later identified as *S. intermedia* (Dutt & Sujatha 1984), and *S. argentifasciata* and *S. parvisquamis* were misidentifications of *Sillago ingenuua* and *S. indica*, respectively (McKay 1985). Dutt & Sujatha (1982) described a new species, *S. soringa* from Visakhapatnam, India. *Sillago aeolus* was listed without detailed morphological characters from the Mallipattinam coast, southeast coast of India by Varadharajan *et al*. (2012), and may be a misidentification. Divya *et al*. (2021) resurrected *S. malabarica* from the synonymy with *S. sihama* and redescribed it. Sequences of *S. mengjialensis*, *S. muktijoddhai*, *S.* cf. *sihama* 3 are available in BOLD as *S. sihama* and *Sillago* sp., the latter was misidentified as *S. soringa* (Divya *et al*. 2021).

Three species of the family, namely *Sillaginopsis domina* (as *S. panijus*), *Sillago maculata* and *Sillago sihama*, were recorded from the Bay of Bengal, Bangladesh (Rahman 1989; Rahman *et al*. 2009). Descriptions of *S. maculata* and *S. sihama* lack data of the morphology of the swimbladder (Rahman *et al*. 2009), therefore they cannot be positively identified, and in the absence of voucher specimens, further examination is not possible. *Sillago maculata* is a species endemic to Australia (Kuiter 1993), therefore the record from Bangladesh is misidentification, furthermore, *S. sihama* is considered a cryptic species complex (Cheng *et al*. 2020). Two new species, *Sillago mengjialensis* and *Sillago muktijoddhai* were recently described and added to fauna of Bangladesh (Saha *et al*. 2022). Previously four species namely *S. mengjialensis*, *S. muktijoddhai*, *S. sihama* and *S. soringa* were misidentified as so-called *S. sihama* (Habib *et al*. 2017; Ahmed *et al*. 2021; Saha *et al*. 2022). Presently a COI sequence of undescribed species *Sillago* cf. *sihama* 3 (MK340718) was submitted in GenBank as *S. sihama* (Habib *et al*. 2021). However, the presence of *S. sihama* was confirmed only in the present study. In summary, six sillaginids occur in the coastal waters of Bangladesh, including *Sillaginopsis domina* and five species of *Sillago*, e.g., *S. mengjialensis*, *S. muktijoddhai*, *S. sihama*, *S.* cf. *sihama* 3 and *S. soringa*. The sixth species of the family, *Sillago* cf. *sihama* 3, from Bangladesh, was discovered through molecular study. This putative species is widely distributed in the Indo-West Pacific and further study is needed for its description.

Updated data of the geographical distributions of the Sillaginidae fishes from the Indian Ocean

***Sillaginodes punctatus* (Cuvier in Cuvier & Valenciennes, 1829):** Western Australia (type locality) and southern Australia (McKay 1992).

***Sillaginopsis domina* (Cuvier, 1816):** Northern Indian Ocean, including India (type locality), Bangladesh and Myanmar (Bay of Bengal), southward to Malaysia, and east possibly to the Indonesian Archipelago (Andaman Sea) (McKay 1992; Psomadakis *et al*. 2020; Ahmed *et al*. 2021; present study). Psomadakis *et al*. (2015) included the species in their FAO Species Identification Guide but Panhwar *et al*. (2017) demonstrated that the species does not occur in Pakistan waters. *Sillaginopsis panijus* is a junior synonym of *S. domina* according to Kottelat (2013).

***Sillago arabica* McKay & McCarthy, 1989:** Northwestern Indian Ocean: Arabian Gulf (type locality: Saudi Arabia, Tanajib Bay) and Pakistan (McKay 1992; Panhwar *et al*., 2017). Heemstra (2022) reported the species from Mozambique but the photographed specimen has 20 rays in second dorsal fin instead 22–24 rays known for the species. Samples of tissue from Mozambique are necessary for comparison with samples from northwestern Indian Ocean. One sample from Iran was included in the genetic analysis (Afrand *et al*. 2023) but they noted that a single specimen differs from *S. arabica* in some details of morphology.

***Sillago attenuata* McKay, 1985:** Northwestern Indian Ocean: Arabian Gulf (type locality: Saudi Arabia, Tarut

Bay), also recorded in the Arabian Sea from the Gulf of Oman and Pakistan (McKay 1992; Panhwar *et al*. 2017; Cheng *et al*. 2020; Heemstra 2022; present study).

***Sillago bassensis* Cuvier in Cuvier & Valenciennes, 1829:** Western and southern Australia. One specimen from the Western Australia (KR493054) under the name *S. vittata* McKay, 1985 is nested in a lineage with *S. bassensis*. Additional study is needed.

***Sillago burrus* 2 Richardson, 1842:** Western Australia (present study).

***Sillago caudicula* Kaga, Imamura & Nakaya, 2010:** Western Indian Ocean: Oman (type locality), Madagascar, and South Africa (Kaga *et al*. 2010; Kaga & Heemstra 2013; present study).

***Sillago erythraea* Cuvier in Cuvier & Valenciennes, 1829:** Red Sea (type locality: Eritrea, Massawa), also has invaded the eastern Mediterranean Sea via the Suez Canal. A doubtful record from Karnataka, India, (BOLD: AAA7605, private sequence as *Sillago* sp.), the source and quality of the sample need to be checked. *Sillago suezensis* Golani, Fricke & Tikochinski, 2013 is a junior synonym (authors, in preparation).

***Sillago indica* McKay, Dutt & Sujatha in McKay, 1985:** Northern Indian Ocean: west and east coasts of India (type locality: Visakhapatnam) and Pakistan (McKay 1992; Panhwar *et al*. 2017; Cheng *et al*. 2020; Divya *et al*. 2021). Records from Vietnam by Kaga & Ho (2012) and Kimura *et al*. (2018) are probably based on misidentification of similar *S. nigrofasciata* Gao & Xiao, 2018, because specimens differ in body and fin coloration. Genetic comparison is unavailable although both are nearly identical in meristics, morphometric measurements and swimbladder structure.

***Sillago malabarica* (Bloch & Schneider, 1801):** Northern Indian Ocean: recorded from the western coast of India (Kerala, Karnataka, Goa and Maharashtra) to eastern coast of India (type locality: Tranquebar [Tharangambadi]) (Divya *et al*. 2021). Previously it was considered a synonym of *S. sihama* until Divya *et al*. (2021) redescribed the species. *Sillago acuta* Cuvier, 1816 is an unnecessary substitute for *S. malabarica* (Fricke *et al*. 2024).

***Sillago mengjialensis* Gao, Baki & Saha in Saha, Song, Yu, Baki, McKay, Qin & Gao, 2022:** Northeastern Indian Ocean: west and east coasts of India (BOLD: BIN AAE1180), Bangladesh (type locality), Malaysia and western Indonesia (Saha *et al*. 2022; present study). Previously reported as *S. sihama* from Bangladesh (Saha *et al*. 2022).

***Sillago muktijoddhai* Gao & Saha in Saha, Song, Yu, Baki, McKay, Qin & Gao, 2022:** Northern Indian Ocean: coastal areas of Bangladesh (type locality) and eastern coast of India (as *Sillago sihama* private sequence in BOLD: ADL7988 from Tamil Nadu, India). Previously reported as *S. sihama* from Bangladesh by Habib *et al*. (2017) and Ahmed *et al*. (2021).

***Sillago panhwari* Panhwar, Farooq, Qamar, Shaikh & Mairaj, 2017:** Northern Indian Ocean: Pakistan (type locality) and Arabian Gulf (Bahrain, Saudi Arabia, and United Arab Emirates) (Rabaoui *et al*. 2019 [as *Sillago* sp.]; Ludt *et al*. 2020 [as *S. sihama*]; Cheng *et al*. 2020; Amir *et al*. 2022).

***Sillago schomburgkii* Peters, 1864:** Eastern Indian Ocean: Western Australia to southeastern Australia (type locality: Adelaide) (McKay 1992).

***Sillago sihama* (Fabricius in Niebuhr, 1775):** Indian Ocean from the southern Red Sea (type locality: Yemen), northeastern Arabian Gulf (Iran), and eastern part of the Arabian Sea, south to South Africa, east to Bangladesh (present study, see above).

***Sillago* cf. *sihama* 1:** Andaman Sea: Myanmar, Thailand and Malaysia (present study).

***Sillago* cf. *sihama* 6:** Northern Indian Ocean: Pakistan and western India (Cheng *et al*. 2020; Amir *et al*. 2022 [as *Sillago* sp. 1]; present study). Also reported in the Arabian Gulf (Saudi Arabia) under the name *S. sihama* by Rabaoui *et al*. (2019).

***Sillago* cf. *sihama* 7:** South Africa (Steinke *et al*. 2016).

***Sillago* cf. *sihama* 8:** Northern Indian Ocean: Pakistan and Iran (Cheng *et al*. 2020; Amir *et al*. 2022 (as *Sillago* sp. 2); present study).

***Sillago soringa* Dutt & Sujatha, 1982:** Northern Indian Ocean: India (type locality) and Bangladesh (McKay 1992; present study).

***Sillago* sp. BOLD-2019:** Indonesia (western Java) (present study).

***Sillago vincenti* McKay, 1980:** West and east coasts of India (type locality: Kerala) (McKay 1992; Krishnan & Mishra 2001; Mahesh *et al*. 2018; Divya *et al*. 2021).

Geographical distribution of the Sillaginidae fishes reported from both Indian and western Pacific Oceans

***Sillaginopodys chondropus* (Bleeker, 1849):** Indo-West Pacific: South Africa, Mozambique, northward to Pakistan and India, eastward to Myanmar, Indonesia (type locality: Java, Jakarta), northern Papua New Guinea, Thailand, Philippines and Taiwan (McKay 1992; Satapoomin 2011; Panhwar *et al*. 2017; Psomadakis *et al*. 2020). The species has been reported from the western Pacific (e.g., McKay 1985; Shao *et al*. 1986) but at present no specimens are available for genetic analysis and an additional study is needed whether the species is a single widespread or represented by a sister species in the Western Pacific.

***Sillago analis* Whitley, 1943:** Reported from Western Australia (type locality: Shark Bay) to eastern Australia (Queensland) and Papua New Guinea (McKay 1992).

***Sillago burrus* 1 Richardson, 1842:** Known from Western Australia (type locality: Dampier Archipelago) to eastern Australia and Indonesia (McKay 1992).

***Sillago ingenuua* A McKay, 1985:** Provisionally Indo-West Pacific, with records from India (Chennai), Malaysia, Gulf of Thailand (type locality), Indonesia, Vietnam, and China (McKay 1992; present study). As described above there are two genetic lineages under the name *S. ingenuua* and additional study is needed.

***Sillago intermedia* Wongratana, 1977:** In the Indian Ocean it is reported from Sri Lanka, India and western Thailand, originally described from the western Pacific from the Gulf of Thailand (McKay 1992; De Bruin *et al*. 1994; Kimura *et al*. 2009). Divya *et al*. (2021) included in their phylogenetic tree six specimens under the name *S. intermedius* but listed these specimens in Table 1 with the name *S. sihama*, and all specimens are nested to genetic lineage of the true *S. sihama* (Divya, pers. comm.). At present, no specimens of the species are available for phylogenetic analysis.

***Sillago lutea* McKay, 1985:** Western Australia (type locality: Exmouth Gulf), northward and eastward to Gulf of Carpentaria, also reported from Seychelles, India, Sri Lanka and Andaman Sea at Phuket (McKay 1992; De Bruin *et al*. 1994; Satapoomin 2011; Heemstra 2022). Records from Seychelles, India and Sri Lanka should be confirmed. A single specimen from Vietnam identified as *S. lutea* nesting within *S.* cf. *sihama* 3.

***Sillago robusta* Stead, 1908:** Western Australia from Fremantle northward to Shark Bay and eastern Australia from southern Queensland to New South Wales (type locality) (McKay 1992).

***Sillago* cf. *sihama* 3:** Recorded from South Africa, Mozambique, Tanzania, Seychelles, Bangladesh, India (Port Blair), Indonesia, Vietnam and China (present study). Also available from Kenya, Mayotte and western Thailand but sequences are private (BOLD: BIN AAA7599) as *Sillago* sp. from Kenya and Mayotte, and as *Sillago sihama* from Thailand. Reported from India as *S. soringa* by Divya *et al*. (2021).

Discussion

Previously, in the most comprehensive phylogenetic analysis, Cheng *et al*. (2020) recognized eight genetic lineages under the name *S. sihama*. Their lineage *S. sihama* 1 is recognized as the true *S. sihama* in the present study; the lineage *S. sihama* 2 as *S.* cf. *sihama* 1; the lineages *S. sihama* 3 and 4 are combined as *S.* cf. *sihama* 2; the lineage *S. sihama* 5 as *S.* cf. *sihama* 8; the lineages *S. sihama* 6 and 7 are retained as *S.* cf. *sihama* 6 and 7, respectively; the lineage *S. sihama* 8 was described as a new species *S. nigrofasciata* by Xiao *et al.* (2021). The present study increased the number of undescribed species of *Sillago* based on a comprehensive phylogenetic analysis and confirmed prevailing misidentification of the so-called *Sillago sihama* in many areas of the Indo-West Pacific region. We show here that *Sillago sihama* is a species of Sillaginidae with a long history of misidentifications. It was known as a widely distributed Indo-West Pacific species until the present study showed that the species is restricted to the Indian Ocean. Although recorded as *S. sihama* from Japan, Korea, Philippines, Gulf of Thailand, and Vietnam, all these records are based on counting characters without using swimbladder descriptions or molecular data. Gao *et al*. (2011), Xiao *et al*. (2016; 2021) and Yu *et al*. (2022) named their specimens from China as *S. sihama*, however, all specimens belong to *S.* cf. *sihama* 2 (Saha *et al*. 2022; present study). *Sillago megacephalus* is an available name for *S.* cf. *sihama* 2 but this is beyond of the aim of the present study.

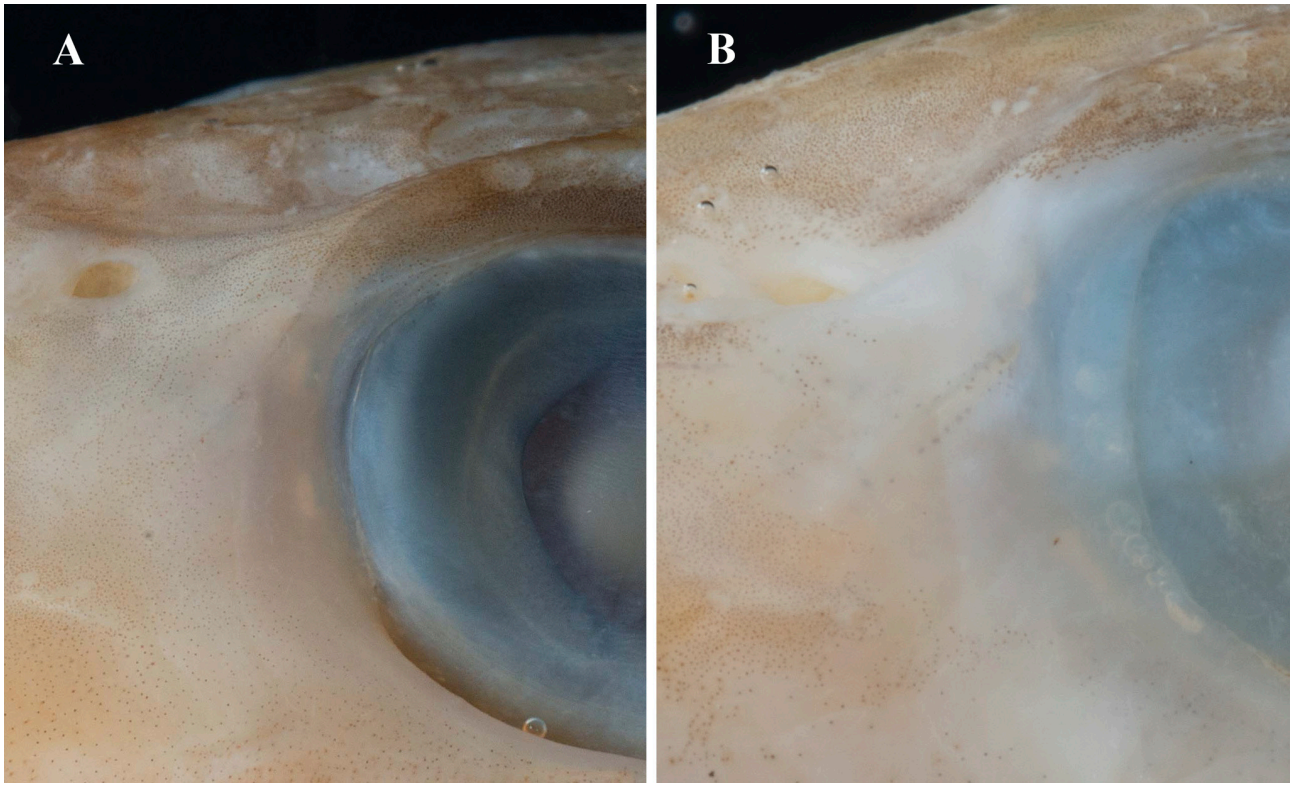

FIGURE 8. Head close-up showing area between posterior nostril and dorsoanterior edge of orbit. **A:** *Sillago erythraea*. SMF 35017; **B:** *Sillago sihama*, KAUMM 67. Photos by Sven Traenkner (SMF).

Since its original description in 1775 based on material from the southern Red Sea, *Sillago sihama* was the sole species known from the Red Sea (Golani & Bogorodsky 2010), until Golani *et al*. (2011) redescribed another species, *Sillago erythraea*. However, Golani *et al*. (2013) later stated synonymy of *S. erythraea* with *S. sihama* and described a new species *S. suezensis* restricted to the northern part of the Red Sea. Golani *et al*. (2013) used a paralectotype of *Sillago erythraea* (MNHN A-3127) from the Gulf of Suez as paratype of *Sillago suezensis* and identified the lectotype of *S. erythraea* (MNHN A-3137) from Eritrea as *S. sihama*, and provisionally stated that *S. sihama* is restricted to the southern Red Sea. They distinguished *S. suezensis* from *S. sihama* in lacking scales on the preopercle and on most of the opercle (versus completely scaled in *S. sihama*), "in the shape of the swimbladder with the lateral extensions each spreading a blind tubule anterolaterally (tubule missing in *S. sihama*)", and the position of the nostril tending to be lower than in *S. sihama*. Kaga (2013) commented that operculum scales are deciduous and easily shed, the absence of tubules (i.e., anterior subextension of anterolateral extension) is an error of examination, and position of nostrils is a doubtful character. Paratype specimens of *S. suezensis* (SMF 34724) from Israel and three specimens (SMF 35017 and KAUMM 468) trawled in southern Saudi Arabia were examined herein. Scale pockets on preopercle and dorsally on opercle are present in all specimens. The main character distinguishing the two species is the presence of lateral pale stripe on the side of body in fresh specimens as well as a stripe remaining in preserved specimens of *S. suezensis* whereas no stripe is visible in fresh or preserved specimens of *S. sihama*. A pale stripe is clearly visible in the lectotype of *S. erythraea* (MNHN A-3137). Furthermore, the area between posterior nostril and dorsoanterior edge of orbit is covered with melanophores in all examined specimens of *S. erythraea* whereas the area is unpigmented in all examined specimens of *S. sihama* (Fig. 8). Hence *S. erythraea* is proposed as a valid species with *S. suezensis* in its synonymy and is being redescribed in a separate publication. Consequently, *S. erythraea* is distributed throughout the entire Red Sea and is also known as a Lessepsian migrant.

Of the 44 genetic lineages of sillaginids identified in this study, 22 lineages, including lineages associated with 16 described and 6 undescribed putative species, are distributed exclusively in the Indian Ocean. Further sampling and extensive morphological study together with an integrated molecular approach will improve the taxonomy of *Sillago* species, especially those that were previously identified as *S. sihama* from the Indo-West Pacific.

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Conflict of interest

No conflict of interest.

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Data accessibility statement

Sequences generated in this study were submitted in GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/) with accession no OM184306–OM184311 and in BOLD (www.boldsystems.org) with accession number LIDMA3726-22, RSSIL001-24, RSSIL002-24, RSSIL003-24, PHILA179-13, PHILA580-13, PHILA1671-16, PHILA2096-16, PHILA660-13, PHILA661-13, PHILA2099-16.