frontiers | Frontiers in Marine Science

ORIGINAL RESEARCH
published: 09 June 2022
doi: 10.3389/fmars.2022.888463

Resolved and Redeemed: A New Fleck to the Evolutionary Divergence in the Genus *Scomberomorus* Lacepède, 1801 (Scombridae) With Cryptic Speciation

N. S. Jeena[1]*, Summaya Rahuman[1], Subal Kumar Roul[1], P. Abdul Azeez[1], R. Vinothkumar[1], H. M. Manas[1], E. A. Nesnas[2], A. Margaret Muthu Rathinam[1], S. Surya[1], Prathibha Rohit[1], E. M. Abdussamad[1] and A. Gopalakrishnan[1]

[1] ICAR-Central Marine Fisheries Research Institute, Cochin, India, [2] Department of Fisheries, Port Blair, India

Edited by:
Christian Marcelo Ibáñez,
Andres Bello University, Chile

Reviewed by:
Claudio F. Cornejo,
University of Concepcion, Chile
Mathias Hüne,
Centro de Investigación para la Conservación de los Ecosistemas Australes (ICEA), Chile

***Correspondence:**
N. S. Jeena
jeenans@rediffmail.com

Specialty section:
This article was submitted to Marine Evolutionary Biology, Biogeography and Species Diversity, a section of the journal Frontiers in Marine Science

Received: 02 March 2022
Accepted: 21 April 2022
Published: 09 June 2022

Citation:
Jeena NS, Rahuman S, Roul SK, Azeez PA, Vinothkumar R, Manas HM, Nesnas EA, Rathinam AMM, Surya S, Rohit P, Abdussamad EM and Gopalakrishnan A (2022) Resolved and Redeemed: A New Fleck to the Evolutionary Divergence in the Genus Scomberomorus Lacepède, 1801 (Scombridae) With Cryptic Speciation. Front. Mar. Sci. 9:888463. doi: 10.3389/fmars.2022.888463

The genus *Scomberomorus*, with 18 nominal species, sustains a significant heterogeneous fishery throughout its range. The sole molecular systematic study of this genus concerned the species group *S. regalis*, which contains the new world taxa. The species diversity of *Scomberomorus* in the northern Indian Ocean has not been studied at the molecular level, often leading to misidentifications. Here, novel genetic data are provided that reconfigure species boundaries from the region. We used single and multilocus data (eight mitochondrial and three nuclear genes) to infer phylogenetic relationships, species delimitation, and the resurrection of a time-calibrated phylogenetic tree. Our aim was also to verify the hypothesis of geographical races in *S. guttatus* predicated on variable vertebral counts. Interestingly, all species delimitation analyses have recovered another highly cryptic species in the nominal *S. guttatus* previously believed to have an Indo-Pacific distribution. *Scomberomorus guttatus* (Bloch and Schneider, 1801) in the *sensu stricto*, is redeemed from its type locality based on genetic data and preliminary morphomeristic investigations and has a restricted distribution in the Bay of Bengal. The cryptic species *Scomberomorus* aff. *guttatus* which exhibits >10% genetic divergence from *S. guttatus* is resurrected here from the synonymy of the latter as *Scomberomorus leopardus* (Shaw, 1803). Widespread in the Indo-Pacific, this species contains two major molecular operational taxonomic units (MOTUs) with a divergence threshold of over 2% between them. Our analysis suggests that vertebral counts must be coupled with other features to identify the species/lineages in the nominal S. guttatus. The heterogeneity in the *S. guttatus* species group is discussed in relation to the ecological diversity of the region which facilitates larval recruitment and niche specialization. The results also revealed two allopatric putative species in *S. commerson*, found primarily in the Pacific and Indian Oceans. This study added genetic data from *S. lineolatus* and *S. koreanus*, not previously represented in the sequence repositories. Estimation of divergence time indicated that the Indo-West Pacific species group undergoes multiple diversification events besides the recent splits detected within *S. leopardus*.

Keywords: *Scomberomorus*, phylogeny, species delimitation, divergence, resurrection, northern Indian Ocean, ecology

INTRODUCTION

Scombridae represents one of the most important elements of the Pelagiaria clade (Betancur-R et al., 2017) and forms the largest and state-of-art family in Scombroidei (Collette and Russo, 1984; Fricke et al., 2021). The family includes epipelagic, commercially important, edible and recreational fishes and currently has 51 valid species in two subfamilies. Its subfamily Scombrinae is divided into four tribes, and the genus *Scomberomorus*, first proposed by Lacepède (1801) from Martinique Island, falls within the tribe Scomberomorini. Heretofore, the genus comprises 18 nominal species, better known as Spanish mackerels and seerfishes, with a wide distribution from tropical to temperate neritic waters within 20°C isotherms (Collette and Nauen, 1983; Collette and Russo, 1984; Collette, 2003). Although pelagic, they exhibit restricted species ranges, with the exception of *Scomberomorus commerson* (Lewis, 1981), indicating their limited open ocean migrations. Members of this genus are also recognized around the world as valued table fish that support diverse fisheries in their ranges (Collette and Nauen, 1983). In their magnum opus on Spanish mackerels, Collette and Russo (1984) evaluated the species relationships and systematic position of *Scomberomorus* within the Scombridae through a comprehensive cladistic analysis and proposed six monophyletic species groups in the genus based on synapomorphies. In 2003, Collette listed all valid species of *Scomberomorus* in his "Annotated checklists of fishes of family Scombridae Rafinesque 1815" which is followed globally. Their type localities, ranges, and IUCN status are shown in **Table 1**.

Scomberomorus spp. have long been a regular subject of stock structure studies for the purpose of establishing appropriate management and monitoring plans (Welch et al., 2015), while the exclusive molecular systematics has been restricted to the *Scomberomorus regalis* species group, identified as the most derived clade in the genus (Banford et al., 1999). Genetic studies have primarily aimed at genetic stock identifications or phylogeography of species from major fishing areas. The species in focus were *Scomberomorus semifasciatus* (Australia: Broderick et al., 2011), *Scomberomorus brasiliensis* (Western South Atlantic: da Cunha et al., 2020), *Scomberomorus sierra* (Eastern Pacific: López et al., 2010), *Scomberomorus concolor* (Gulf of California: Magallón-Gayón et al., 2016), *Scomberomorus guttatus* (Persian Gulf: Abedi et al., 2011), *Scomberomorus cavalla* (Brazil: Santa Brígida et al., 2007), etc. Of all the species, the most extensive investigation was performed on *S. commerson* using a wide range of mitochondrial and nuclear molecular markers in the Pacific (e.g., Sulaiman and Ovenden, 2010; Fauvelot and Borsa, 2011; Habib and Sulaiman, 2016) and in the rim countries of the Indian Ocean (e.g., Hoolihan et al., 2006; Abedi et al., 2012; Divya et al., 2018; Vineesh et al., 2018; Johnson et al., 2021).

Biodiversity loss is one of the most serious issues with direct consequences, and species form the meter of biodiversity and conservation (Halasan et al., 2021). Spanish mackerels are harvested and exploited indiscriminately, compounded by their biological attributes (Zacharia et al., 2016; Hashemi and Doustdar, 2022). It is recommended that genetics needs to be well-integrated into the global biodiversity index while assessing conservation and risk priorities (Garner et al., 2020). *Scomberomorus* accounts for nearly 35% of reported Scombrids, but data-rich status regarding their genetic and life history research is limited to a few such as *S. cavalla*, *S. commerson*, and *Scomberomorus maculatus* (Juan-Jordá et al., 2013). The IUCN Red List (IUCN 2022. Version 2021-3, https://www.iucnredlist.org) assigns "near threatened" status to *S. commerson* and *Scomberomorus munroi*, "vulnerable" to *S. concolor*, and "data deficient" to *S. guttatus*, *Scomberomorus niphonius*, *Scomberomorus plurilineatus*, and *Scomberomorus sinensis*, while the remaining 11 species are of least concern. Despite shaping a cardinal transoceanic fishery, the molecular taxonomy of this group remained confined to the sole phylogenetic assessment study by Banford et al. (1999), who evaluated the effect of the Eastern Pacific/Eastern Atlantic biogeographic track (Rosen, 1975) on the diversification of new world taxa of the species group *S. regalis*. It may be added that certain species of Spanish mackerels are not yet represented in the GenBank (e.g., *Scomberomorus lineolatus*, *Scomberomorus koreanus*, and *Scomberomorus multiradiatus*). The void in the accurate identification and systematics of the Spanish mackerels necessitates detailed investigations from the respective oceanic provinces, including the Indian Ocean, which is an integral part of the speciose Central Indo-Pacific (Miller et al., 2018), for more comprehensive data coverage.

The Northern Indian Ocean, an element of the Indian Ocean covering 29% of the global ocean area (Wafar et al., 2011), is bifurcated by landmasses to the north into two intracontinental seas, viz., the Arabian Sea to the west and the Bay of Bengal to the east (Monolisha et al., 2018). In the review of "Scombrids of the world", Collette and Nauen (1983) listed four species in *Scomberomorus* from India, viz., *S. commerson* (Lacepède, 1800), *S. guttatus* (Bloch and Schneider, 1801), *S. lineolatus* (Cuvier, 1829), and *S. koreanus* (Kishinouye, 1915). Silas (1964), who redescribed *S. guttatus*, proposed a wide distribution of the species in the Indo-Pacific while simultaneously predicting the likelihood of geographic races therein based on variations in vertebral counts cited in the earlier literature. Later, Devaraj (1976) who discovered *S. koreanus* in the Palk Bay (Indian Ocean) supported this observation and added some significant morphological measurements to distinguish the races. Differences in morphometry have been reported in *S. guttatus* distributed along the Indian coastline (Rao, 1975). Collette and Russo (1984) found no significant differences in morphometric data between

TABLE 1 | Distribution, type locality, type specimen, and IUCN status of the nominal species in the genus *Scomberomorus* (Collette and Nauen, 1983; Collette and Russo, 1984; Collette, 2003; Froese and Pauly, 2022; https://www.iucnredlist.org).

Sl. no.	Scientific name	Common name	Type locality	Type specimen (museum ID)	Distribution	IUCN status
1.	*S. commerson* (Lacepède, 1800)	Narrow-barred Spanish mackerel or Narrow-Barred King Mackerel	No locality	No types known	Widespread throughout tropical and subtropical waters of the Indo-Western Pacific and has traversed the Suez Canal into the eastern Mediterranean	Near threatened
2.	*S. brasiliensis* Collette, Russo, and Zavalla-Camin, 1978	Serra Spanish mackerel	Belém market, Brazil	Holotype: USNM 217550	Caribbean and Gulf of Mexico coasts of Central and South America from Belize at least as far south as Rio Grande do Sul, Brazil	Least concern
3.	*S. cavalla* (Cuvier, 1829)	King mackerel	Brazil	No types known	Western Atlantic from Massachusetts through the West Indies to Rio de Janeiro, Brazil	Least concern
4.	*S. concolor* (Lockington, 1879)	Monterey Spanish mackerel	San Francisco market; probably from Monterey, California, USA	Holotype (unique): CAS (lost in 1906)	Eastern tropical Pacific, apparently now confined to the Gulf of California	Vulnerable
5.	**S. guttatus* (Bloch and Schneider, 1801)	Indo-Pacific king mackerel	Tranquebar, India	Lectotype: ZMB 8759 (dry)	Indo-Western Pacific coasts from the Persian Gulf east through the East Indies and north to the Sea of Japan	Data deficient
6.	*S. koreanus* (Kishinouye, 1915)	Korean seerfish	West coast of Korea	Holotype (unique): whereabouts unknown	Continental Indo-Western Pacific from Bombay, India, east to Singapore and north to the Sea of Japan	Least concern
7.	**S. lineolatus* (Cuvier, 1829)	Streaked seerfish	Vishakhapatnam (Vizagapatam), India	No types known	Continental Indo-Western Pacific from Bombay, India, east to the Gulf of Thailand and Java	Least concern
8.	*S. maculatus* (Mitchill, 1815)	Spanish mackerel or Atlantic Spanish mackerel	New York, USA	Holotype (unique): whereabouts unknown	Western Atlantic from Cape Cod, Massachusetts, to Miami, Florida, and the Gulf of Mexico from Florida to Yucatan, Mexico	Least concern
9.	*S. multiradiatus* Munro, 1964	Papuan seerfish	Off n. mouth of Fly R., Gulf of Papua, Papua New Guinea	Holotype: CSIRO C3172	Restricted to the Gulf of Papua off the mouth of the Fly River	Least concern
10.	*S. munroi* Collette and Russo, 1980	Australian spotted mackerel	Deception Bay, north of Brisbane, Queensland, Australia	Holotype: AMS I.21029-001	Coasts of the northern three quarters of Australia and the southern coast of Papua New Guinea	Near threatened
11.	*S. niphonius* (Cuvier, 1832)	Japanese Spanish mackerel	Japan	No types known	Subtropical and temperate waters of China, the Yellow Sea, and the Sea of Japan north to Vladivostok	Data deficient
12.	*S. plurilineatus* Fourmanoir, 1966	Queen Mackerel or Kanadi kingfish	Near Nosy Be (Nossi-Bé), Madagascar	Holotype: apparently discarded	Western Indian Ocean from Kenya and Zanzibar, the west coast of Madagascar, and the Seychelle Islands south to Natal, South Africa	Data deficient
13.	*S. queenslandicus* Munro, 1943	Queensland school mackerel	Cape Cleveland, n. Queensland, Australia	Holotype: QM I.6588	Inshore coastal waters of southern Papua New Guinea and the northern three-quarters of Australia	Least concern
14.	*S. regalis* (Bloch, 1793)	Cero	Martinique, West Indies	No types known	Tropical and subtropical waters of the western Atlantic from Massachusetts to Rio de Janeiro, Brazil	Least concern
15.	*S. semifasciatus* (Macleay, 1883)	Broad-barred king mackerel or Broad-barred Spanish mackerel	Lower Burdekin R., Queensland, Australia	Holotype (unique): AMS I.18288	Estuarine and coastal waters of southern Papua New Guinea and the northern three-quarters of Australia	Least concern
16.	*S. sierra* Jordan and Starks, 1895	Pacific sierra or Sierra	Mazatlán, Sinaloa, w. Mexico	Lectotype: SU 1720	Eastern tropical Pacific from southern California to northern Chile and the Galápagos Islands	Least concern
17.	*S. sinensis* (Lacepède, 1800)	Chinese mackerel or Chinese seerfish	China	No types known	Western Pacific from Japan and China south to Vietnam and Cambodia where it enters the Mekong River	Data deficient
18.	*S. tritor* (Cuvier, 1832)	West African Spanish mackerel	Gorée, Senegal	Lectotype: MNHN A-6871	Eastern Atlantic, concentrated in the Gulf of Guinea from the Canary Islands south to southern Angola; rare in the Mediterranean Sea	Least concern

**Denotes that its distribution and IUCN status need to be reassessed based on the present study.*

populations of *S. guttatus* in the Arabian Sea and the Bay of Bengal, while it was evident in the races from the Pacific. They also observed a difference in the number of vertebrae between these two population clusters. Rao and Lakshmi (1993) suggested that *S. lineolatus*, distributed in the south-east coast of India, is a natural interspecific hybrid and not a valid species, which was refuted by Collette (1994) with a recommendation to include molecular methods to define and characterize the species in *Scomberomorus*. In the Indian context, taxonomic assessment supported by vanguard molecular tools remained a veritable blank, except for the classic works of the predecessors mentioned above.

Understanding evolutionary processes in marine realms where cryptic speciation is common can reveal barriers to gene flow, and species–level molecular phylogenies have been used to describe biogeographical regions (Crandall et al., 2019). Alongside this, molecular species delineation has been widely used either as a standalone technique or in combination with an integrative taxonomic approach to species identification (Luo et al., 2018). Therefore, the objectives of this study are as follows: i) generation of multilocus molecular impressions of all available species of the genus along the Indian coast and island ecosystems; ii) phylogenetic reconstruction of the genus based on globally available data for the individual loci such as the universal barcode region, i.e., the mitochondrial *cytochrome c oxidase subunit 1* (*COI*), *cytochrome b* (*Cyt b*) fragment, along with multilocus methods using concatenated sequences of mitochondrial and nuclear markers comparable to previous studies; iii) recognition of the molecular operational taxonomic units (MOTUs) within *Scomberomorus* using the single-locus and multilocus species delimitation approach to assess the species diversity; and iv) resurrection of a dated phylogeny using multispecies coalescent analysis. This study also aimed to validate the hypothesis regarding the occurrence of geographic races in the Indian Ocean congeners and the results are expected to complement the universal database on this genus with glimpses into the diversity of the northern Indian Ocean.

MATERIALS AND METHODS

Sampling and Overview of Materials

A total of 210 specimens of the genus *Scomberomorus* were collected in different seasons from 2019 to 2021 from different predesignated sampling sites along the coast of India, covering samples by type locality (topotypes) (**Figure 1**, **Table 2**). *Pampus candidus*, *Brama* sp., *Lepidocybium flavobrunneum*, and *Kajikia audax* were selected as outgroups for phylogenetic analysis based on the available literature (Miya et al., 2013) and digitally documented after collection (**Supplementary Figure 1**). All specimens were tentatively identified by morphological taxonomy (Collette and Nauen, 1983) and their fin or muscle tissues were preserved in absolute ethanol for future molecular studies. In addition, data mining of mitochondrial *COI*, *Cyt b*, *NADH dehydrogenase subunit 2* (*NADH2*), *ATPase subunits* (*ATPase 6* and *ATPase 8*), and nuclear [*aldolase exon 5/intron 5* (*ALD*), *rhodopsin* (*RHO*), *titin-like protein* (*Tmo-4c4*)] genes were extracted from previous literature and nucleotide databases to represent the maximum species in *Scomberomorus*. The identity of the species underrepresented in GenBank (e.g., *S. sinensis*, *Scomberomorus tritor*, and *S. multiradiatus*) was deciphered by comparison, wherever possible, with either the morphological characters or the limited genetic data. Total genomic DNA (gDNA) was extracted from all tissue samples by the standard phenol–chloroform method (Sambrook et al., 1989). Isolated gDNA was visualized in 0.8% agarose gel, while NanoDrop One (Thermo Fisher Scientific, USA) determined the

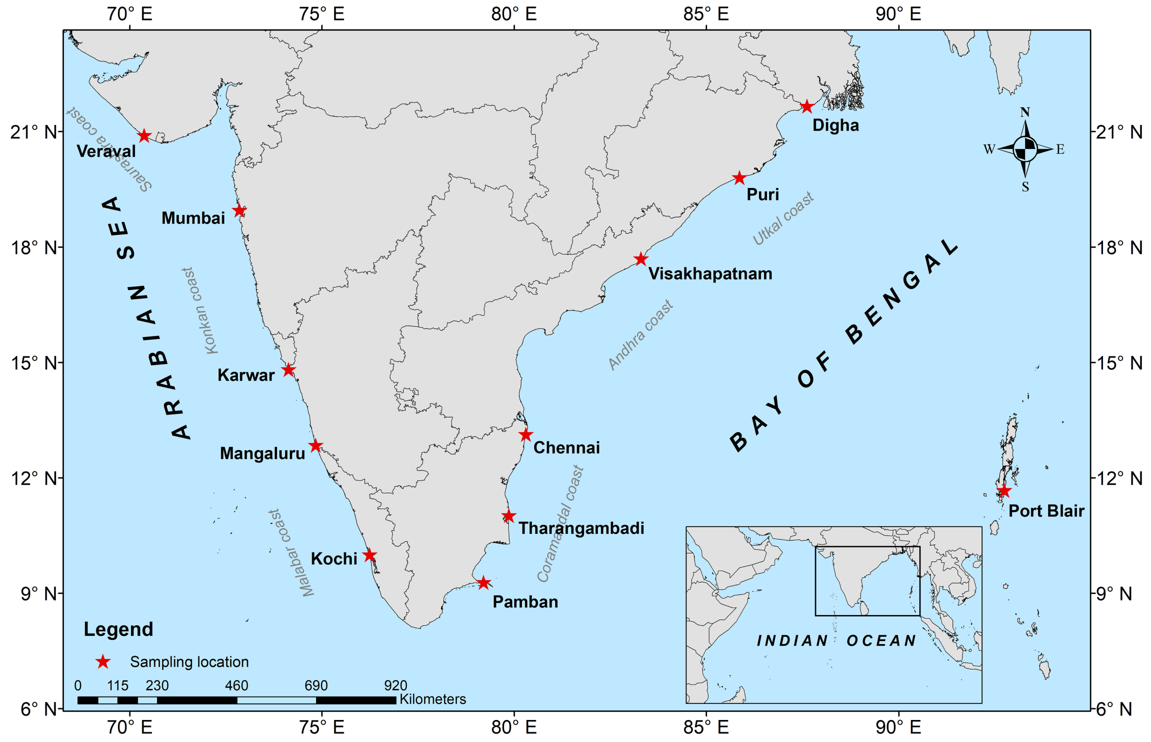

FIGURE 1 | Map showing the sampling locations of *Scomberomorus* spp. along the Indian coast.

TABLE 2 | Locations of sampling (fishing harbors) and fishery information of *Scomberomorus* spp. along the Indian coastline including the Andaman Islands.

Nominal species examined	Location	Code (lat. and long.)	Sample size (n)	Gear used, depth of operation, and nature of the bottom	Period of collection
Scomberomorus guttatus	Gujarat	Veraval (20°54′19.23″N, 070°22′52.03″E)	30	Gillnet, 15–50 m, muddy	October 2019
	Maharashtra	New ferry Wharf, Mumbai (18°57′29″N, 72° 51′01″E)	10	Trawl, 40–50 m, muddy	October 2019, October 2021
	Karnataka	Karwar (14°48′6.4224″N, 74°7′2.0892″E)	10	Gillnet, 40–50 m, muddy	January 2022
		Mangalore (12°51′28.728″N, 74°49′ 57.2736″E)	8	Trawl, 20–25 m, sandy mixed with clay	February 2020
		Malpe (13°20′50.19″N, 74°42′4.842″E)	8	Trawl, 20–25 m depth, sandy mixed with clay	February 2021
	Kerala	Calicut (9°58′6.1572″N, 76°14′35.6856″E)	2	Trawl, 40–80 m, muddy to rocky	July 2019
	Tamil Nadu	Pamban (9°16′46.9416″N, 79°12′20.448″E)	1	Trawl, 40–80 m, sandy	February 2021
		Nagapattinam (10°44′49.2108″N, 79°50′ 9.8412″E)	7	Trawl and gillnet, 50–100 m, clayey	December 2020
		†Tharangambadi (Tranquebar) (11°2′ 9.8052″N, 79°52′22.6452″E)	6	Hook and line and gillnet, 15–50 m, clayey	January 2021
		Cuddalore (11°42′52″N, 79°46′3″E)	4	Trawl and gillnet, 20–60 m, clayey	November 2020
		Kovalam (12.7925°N, 80.2530°E)	10	Hook and line, 30–40 m, muddy	May 2021
		Kasimedu, Chennai (13°7′41.6964″N, 80° 17′49.3764″E)	10	Trawl, 40–50 m, sandy	November 2020
	Andhra Pradesh	Visakhapatnam (17.696°N, 83.301°E)	10	Gillnet, 30–40 m, rocky	August 2019, February 2021
	Odisha	Paradeep (20°17.345′N, 086°42.422′E)	20	Trawl, 40–70 m, sandy silt	August 2019
		Puri (20°17.345′N, 086°42.422′E)	4	Gillnet, 5–10 m, sandy silt	October 2019
	West Bengal	Digha Mohana (21°36′58.3272″N, 87°29′ 56.8644″E)	10	Trawl, 30–45 m, sandy silt	September 2021
	Andaman and Nicobar Island	Junglighat, Port Blair (11°39′33.00″N, 92° 43′41.64″E)	8	Trawl and gillnet, 10–30 m, sandy to muddy	January 2021
Scomberomorus commerson	Gujarat	Veraval (20°54′19.23″N, 070°22′52.03″E)	2	Gillnet, 15–50 m, muddy	October 2019
	Kerala	Cochin (9°56′21.1164″N, 76°15′46.152″E)	5	Trawl, 40–80 m, muddy to rocky	November 2020
	Tamil Nadu	Mandapam (10°45′03.8″N, 79°50′24.0″E)	1	Trawl, 30–60 m, sandy	September 2019, October 2019
		Nagapattinam (10°44′49.2108″N, 79°50′ 9.8412″E)	3	Trawl and gillnet, 50–100 m, clayey	December 2019, September 2020
		Pamban (9°16′46.9416″N, 79°12′20.448″E)	3	Trawl, 40–80 m, sandy	September 2019
	Andhra Pradesh	Visakhapatnam (17.696°N, 83.301°E)	3	Gillnet, 40 m, rocky	July 2019
	Odisha	Puri (20°17.345′N, 086°42.422′E)	4	Gillnet, 5–10 m, sandy silt	September 2019
	West Bengal	Digha Mohana (21°36′58.3272″N, 87°29′ 56.8644″E)	4	Trawl, 30–45 m, sandy silt	September 2021
	Andaman and Nicobar Island	Junglighat, Port Blair (11°39′33.00″N, 92° 43′41.64″E)	4	Gillnet, 10–30 m, sandy to muddy	January 2021
Scomberomorus koreanus	Gujarat	Veraval (20°54′19.23″N, 070°22′52.03″E)	1	Gillnet, 15–50 m, muddy	October 2019
	Maharashtra	Naigaon, Thane (19°19′32″N, 72°48′54″E)	4	Gillnet, 30–40 m, muddy	October 2019
	Tamil Nadu	Kasimedu, Chennai (13°7′41.6964″N, 80° 17′49.3764″E)	2	Trawl, 40–50 m, sandy	January 2021
	Andhra Pradesh	Visakhapatnam (17.696°N, 83.301°E)	2	Gillnet, 30–40 m depth, rocky	February 2021
	Orissa	Paradeep (20°17.345′N, 086°42.422′E)	2	Trawl, 40–70 m, sandy silt	October 2019, December 2019
	West Bengal	Digha Mohana (21°36′58.3272″N, 87°29′ 56.8644″E)	5	Trawl, 30–45 m, sandy silt	September 2021
Scomberomorus lineolatus	Tamil Nadu	Pamban (9°16′46.9416″N, 79°12′20.448″E)	7	Trawl, 40–80 m, sandy	August 2020
		Dhanushkodi (9°10′16.7088″N, 79°25′ 26.346″E)	–	Shore seine, 5–10 m, sandy	November 2020
		Thoothukudi (8°47′36.96″N, 78°9′37.7676″E)	–	Trawl, 60–100 m, sandy	September 2020

†*Indicates the type locality of S. guttatus.*

quality and quantity. High-quality gDNA was stored in duplicate at −80°C for further downstream processes.

Polymerase Chain Reaction Amplification, Purification, and Sequencing

The identified specimens and the outgroups were barcoded to confirm their genetic identity. After this, no fewer than five individuals were selected for multigene amplification, taking into account collection sites and topotypes. We targeted 11 regions of DNA, eight genes from the mitochondrial (mt) genome [coding: *COI*, Cyt *b*, *ATPase subunits 6* and *8*, *NADH2*; non-coding: *D-loop*/Control Region (CR), *12S rRNA* (*12S ribosomal RNA*), and *16S rRNA* (*16S ribosomal RNA*)] and three nuclear loci (*ALD*, *RHO*, and *Tmo-4C4*) which, depending on their availability in GenBank, were assigned to different analyses. Amplification was carried out in a 50-µl reaction using basic polymerase chain reaction (PCR) conditions and cycling parameters following the primers and annealing temperatures (**Table 3**). Our analysis included multiple mt genes to increase the phylogenetic signal and to inspect the presence of accidental pseudogene amplification, while nuclear genes in particular provide regions with slower substitution rates (Banford et al., 1999). Amplified DNA fragments were visualized in 1.2%–2% agarose gel depending on the size of the product, purified, and bidirectionally sequenced.

Sequence Analysis and BLAST Annotation

Amplified sequences were aligned using the ClustalW algorithm (Thompson et al., 1994), which was manually edited using BioEdit v7.1.9 (Hall, 1999) to remove gaps and severe base pair mismatches. Curated coding regions were translated into amino acids to check for the presence of pseudogenes. All generated sequences were compared to the sequences downloaded from nucleotide databases using the search tool BLAST (Altschul et al., 1990). All amplified sequences were deposited in GenBank and the accession numbers with details were given along with the sequences retrieved from GenBank and BOLD (**Supplementary Tables 1, 2** and **Table 4**).

Phylogenetic Analyses

Initially, phylogenetic analysis using a single locus (*COI* and *Cyt b* with a truncated length of 632 and 763 bp, respectively) was implemented to incorporate maximal sequences representing the nominal species in *Scomberomorus*, while multigene analysis focused on increasing the phylogenetic signals, thereby verifying the validity of the primary investigation results. Three hundred and seventy-eight sequences belonging to 15 nominal species (**Supplementary Table 1**) and 122 sequences from available species (**Supplementary Table 2**) of the genus were included in the *COI* and *Cyt b*-based analyses, respectively. *COI* contained sequences from all species (except *S. sinensis*, *S. multiradiatus*, and *S. tritor*) along with those generated in this study (n = 148). We also evaluated the possible genealogical relationships between haplotypes in the putative species complex containing cryptics through a haplotype network with a maximal connectivity limit of 95%, mapped with their COI barcodes using the TCS algorithm implemented in POPART version 1.7 (Leigh et al., 2015). For the multilocus dataset, five sequences per species were selected from our samples. It included alignments of *COI*, *Cyt b*, *ATP8*, *ATP6*, *NADH2*, *RHO*, *ALD*, and *TMO* resulting in 632, 1,032, 168, 684, 1,047, 762, 410, and 499 base pairs, respectively. These gene fragments were selected to contain the maximum number of congeneric species, and only those with better data coverage/mitogenomes were included in the analysis. The saturation in each codon of each gene was tested using DAMBE v.7 (Xia, 2018) with no evidence of saturation detected at any of the codon positions. The concatenation resulted in a final length of 5,235 bp (**Table 4**).

TABLE 3 | Details of the PCR primers used in this study.

Sl. no.	Target gene	Primer pair and sequence (5′–3′)	Reference	Annealing temperature
1.	*Cytochrome oxidase subunit 1* (*COI*)	Fish F2: TCGACTAATCATAAAGA TATCGGCAC Fish R2: ACTTCAGGGTGACCGAAGAATCAGAA	Ward et al. (2005).	53°C
2.	*Cytochrome b* (*Cyt b*)	CyBF-GluDG: TGACTTGAARAACCAYCGTTG	Palumbi (1996)	45°C–58°C
		CyBR-H16460: CGAYCTTCGGATTAACAAGACCG	Perdices et al. (2002)	
		CyB-F14734-Glu: AACCACCGTTGTTATTCAACT	Kawaguchi et al. (2001)	
		CyBR-CB3: GGCAAATAGGAARTATCATTC	Palumbi (1996)	
		L14724: GACTTGAAAAACCACCGTTG H15915: CTCCGATCTCCGGATTACAAGAC	Xiao et al. (2001)	
		Cytb A: CCATGAGGACAAATATCATTYTGRGG Cytb C: CTACTGGTTGTCCTCCGATTCATGT	Bossuyt and Milinkovitch (2000)	
3.	*ATP6/8 gene*	ATP8.2L8331: AAAGCRTYRGCCTTTTAAGC COIII.2H9236: GTTAGTGGTCAKGGGCTTGGRTC	Sivasundar et al. (2001)	55°C
4.	*NADH dehydrogenase subunit 2* (*NADH2*)	ND2-WGln-ScF: ACTCTTTGTGCTTCCACTACAC ND2-WAla-ScR: AGGAGATGTGGGGTAATGTCC	This study	50°C–55°C
5.	*12S ribosomal subunit* (*12S rRNA*)	12S-WPhe-ScF: AGATGRGCCCTAGAAAGCTCC 12S-WVal-ScR: CAGGGTAATCCGATTTGCAC	This study	50°C
6.	*16S ribosomal RNA* (*16S rRNA*)	16Sar: CGCCTGTTTATCAAAAACAT 16Sbr: CCGGTYTGAACTCAGATCAYGT	Palumbi et al. (1991)	52°C
7.	*D-loop* (*CR*)	Dloop-Thr-F: AGCACCGGTCTTGTAAACCG Dloop-Phe-R: GGGCTCATCTTAACATCTTCA	Cheng et al. (2012)	50°C
8.	*Rhodopsin gene fragments 1* (*RHO*)	RH-193F: CNTATGAATAYCCTCAGTACTACC RH-1039R: TGCTTGTTCATGCAGATGTAGA	Chen et al. (2003)	48°C–53°C
9.	*Aldolase-1* (*ALD*)	Ald-W1N: TGYGCNCAGTAYAARAARSAYGG Ald-W2N: CDGGVAGRATYTCDGGCTCNACRAT	This study	45°C–60°C
		Ald-1: TGTGCCCAGTATAAGAAGGATGG Ald-2: CCCATCAGGGAGAATTTCAGGCTCCACAA	Lessa and Applebaum (1993)	
10.	*Titin-like protein* (*Tmo-4C4*)	Tmo4C4-W-NF: CCTCCNGCYTTYCTHAARCCWCT Tmo4C4-W-NR: TCATCVYGYTCCTGVGTDAYAWARTC	This study	50°C–57°C
		Tmo-4C4F: CCTCCGGCCTTCCTAAAACCTCTC Tmo-4C4R: CATCGTGCTCCTGGGTGACAAAGT	Streelman and Karl (1997)	

Sequences of the primer pair, its reference, and annealing temperature are displayed.

TABLE 4 | Code to *Scomberomorus* spp. individuals sequenced and accession numbers from GenBank generated in this study used for multilocus phylogenetic analysis are exhibited.

Correct species	*COI*		*Cyt b*		*ATPase*		*NADH2*		*RHO*		*ALD*		*Tmo-4C4*	
	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.
*S. guttatus**	SgutCh3	MZ854044	SgutCh3	MZ955296	SgutCh3	MZ955361	SgutCh3	MZ955314	SgutCh3	OM363556	SgutCh3	OM363601	SgutCh3	OM363579
	SgutNgpt5	MZ854039	SgutNgpt5	MZ955298	SgutNgpt5	OM363530	SgutNgpt5	MZ955313	SgutNgpt5	OM363557	SgutNgpt5	OM363602	SgutNgpt5	OM363580
	SgutTnq2	MZ854050	SgutTnq2	MZ955299	SgutTnq2	MZ955360	SgutTnq2	MZ955315	SgutTnq2	MZ955334	SgutTnq2	OK041511	SgutTnq2	OM363581
	SgutAPS1	MZ914459	SgutAPS1	MZ955297	SgutAPS1	OM363531	SgutAPS1	OM363542	SgutAPS1	OM363558	SgutAPS1	OM363603	SgutAPS1	OM363582
	SgutWB1	OM343183	SgutWB1	OM363524	SgutWB1	OM363529	SgutWB1	OM363543	SgutWB1	OM363559	SgutWB1	OM363604	SgutWB1	OM363583
S. aff. *guttatus* 1*	Saff. gutVzg2	MZ872475	S aff. gutVzg2	MZ955283	S aff. gutVzg2	MZ955352	S aff. gutVzg2	MZ955300	S aff. gutVzg2	OM363560	S aff. gutVzg2	MZ962388	S aff. gutVzg2	MZ955337
	Saff. gutMg2	MZ872472	S aff. gutMg2	MZ955281	S aff. gutMg2	OM363532	S aff. gutMg2	OM363544	S aff. gutMg2	OM363561	S aff. gutMg2	OM363612	S aff. gutMg2	OM363584
	Saff. gutCh4	MZ872476	S aff. gutCh4	MZ955282	S aff. gutCh4	OM363533	S aff. gutCh4	OM363545	S aff. gutCh4	MZ955328	S aff. gutCh4	OM363614	S aff. gutCh4	OM363585
	Saff. gutOR2	MZ872467	S aff. gutOR2	MZ955284	S aff. gutOR2	MZ955353	S aff. gutOR2	MZ955301	S aff. gutOR2	OM363562	S aff. gutOR2	MZ962389	S aff. gutOR2	OM363586
	Saff. gutWB7	MZ872464	S aff. gutWB7	MZ955280	S aff. gutWB7	OM363534	S aff. gutWB7	MZ955302	S aff. gutWB7	OM363563	S aff. gutWB7	OM363613	S aff. gutWB7	OM363587
S. aff. *guttatus* 2*	SaffgutVrl-17	MZ955343	SaffgutVrl-17	MZ955288	SaffgutVrl-17	MZ955343	SaffgutVrl-17	MZ955304	SaffgutVrl-17	OM363564	SaffgutVrl-17	MZ962384	SaffgutVrl-17	OM363588
	SaffgutM3	MZ955349	SaffgutM3	MZ955279	SaffgutM3	MZ955349	SaffgutM3	OM363546	SaffgutM3	OM363565	SaffgutM3	OM363615	SaffgutM3	OM363589
	SaffgutK1	MZ927103	SaffgutK1	MZ955285	SaffgutK1	MZ955345	SaffgutK1	OM363547	SaffgutK1	OM363566	SaffgutK1	OM363617	SaffgutK1	MZ955335
	SaffgutMg7	MZ872493	SaffgutMg7	MZ955287	SaffgutMg7	MZ955344	SaffgutMg7	MZ955303	SaffgutMg7	OM363567	SaffgutMg7	MZ962387	SaffgutMg7	OM363590
	SaffgutCh1	MZ872495	SaffgutCh1	MZ955286	SaffgutCh1	MZ955347	SaffgutCh1	OM363548	SaffgutCh1	MZ955327	SaffgutCh1	OM363616	SaffgutCh1	OM363591
	SaffgutM4	MZ872497	SaffgutM4	MZ955278	SaffgutM4	MZ955350	SaffgutM4	MZ955306	SaffgutM4	OM363568	SaffgutM4	MZ962386	SaffgutM4	OM363592
	SaffgutMg3	MZ872501	SaffgutMg3	OM363525	SaffgutMg3	MZ955351	SaffgutMg3	MZ955307	SaffgutMg3	MZ955329	SaffgutMg3	MZ962383	SaffgutMg3	MZ955336
	SaffgutK4	MZ927109	SaffgutK4	OM363526	SaffgutK4	OM363535	SaffgutK4	MZ955305	SaffgutK4	OM363569	SaffgutK4	MZ962385	SaffgutK4	OM363593
*S. koreanus**	SkorM2	MZ854035	SkorM2	MZ955293	SkorM2	MZ955357	SkorM2	MZ955311	SkorM2	MZ955331	SkorM2	OK041509	SkorM2	MZ955341
	SSKOR0	MZ854037	SSKOR0	MZ955294	SSKOR0	MZ955356	SSKOR0	MZ955310	SSKOR0	MZ955332	SSKOR0	OK041508	SSKOR0	MZ955340
	SKWB7	OM416533	SKWB7	OM363527	SKWB7	OM363536	SKWB7	OM363549	SKWB7	OM363570	SKWB7	OM363605	SKWB7	OM363594
	SKCh2	OM416535	SKCh2	OM363528	SKCh2	OM363537	SKCh2	OM363550	SKCh2	OM363571	SKCh2	OM363606	SKCh2	OM363595
*S. lineolatus**	SlinPbn1	MZ871761	SlinPbn1	OM417808	SlinPbn1	MZ955358	SlinPbn1	MZ955312	SlinPbn1	OM363572	SlinPbn1	OM363607	SlinPbn1	OM363596
	SlinPbn2	MZ871762	SlinPbn2	OM417809	SlinPbn2	OM363538	SlinPbn2	OM363551	SlinPbn2	OM363573	SlinPbn2	OM363608	SlinPbn2	OM363597
	SlinPbn3	MZ871764	SlinPbn3	OM417810	SlinPbn3	MZ955359	SlinPbn3	OM363552	SlinPbn3	MZ955333	SlinPbn3	OK041510	SlinPbn3	MZ955342
	SlinPbn4	MZ871763	SlinPbn4	MZ955295	SlinPbn4	OM363539	SlinPbn4	OM363553	SlinPbn4	OM363574	SlinPbn4	OM363609	SlinPbn4	OM363598
	SlinPbn5	MZ871765	SlinPbn5	OM417811	SlinPbn5	OM363540	SlinPbn5	OM363554	SlinPbn5	OM363575	SlinPbn5	OM363610	SlinPbn5	OM363599
S. cf. *commerson* 2	Scomncoc1	MZ854025	Scomncoc1	MZ955289	Scomncoc1	OM363541	Scomcoc1	MZ955309	Scomncoc1	OM363576	Scomncoc1	OK041506	Scomncoc1	MZ955339
	ScomnOR2	MZ854034	ScomnOR2	MZ955291	ScomnOR2	MZ955355	ScomnOR2	MZ955308	ScomnOR2	OM363577	ScomnOR2	OK041507	ScomnOR2	MZ955338
	ScomnPbn1	MZ854024	ScomnPbn1	MZ955290	ScomnPbn1	MZ955354	ScomnPbn1	OM363555	ScomnPbn1	OM363578	ScomnPbn1	OM363611	ScomnPbn1	OM363600
S. maculatus	JJ7:10	DQ874752	Smacl1	EU349359	HB261	AF076098	HB261	AF076127	JJ7:10	DQ874798	HB261	AF076140	JJ7:10	DQ874830
	SPMK8	DQ835938	Smacl3	EU349361	HB266	AF076099	HB265	AF076122	JJ7:10	DQ874798	HB265	AF076142	JJ7:10	DQ874830
S. regalis	JJ13:2	DQ874759	Sregll1	EU349370	HB872	AF076103	HB872	AF076126	JJ13:2	DQ874805	HB872	AF076147	–	–
	BAHA8007	JQ839886	Sergll2	EU349369	STRI3836	AF076100	STRI3836	AF076124	JJ13:2	DQ874805	STRI3836	AF076143	–	–
S. brasiliensis	SCBR4	DQ835919	ScbBra016	DQ080322	HB704	AF076108	HB704	AF076130	ScbBra016	DQ080411	HB704	AF076145	–	–
	HRCB:51436	JQ365542	ScbBra014	DQ080323	STRI4277	AF076109	STRI4277	AF076129	ScbBra014	DQ080412	STRI4277	AF076144	–	–
S. sierra	–	NC033887	–	NC033887	HB857	AF076112	HB857	AF076132	–	–	HB857	AF076146	–	DQ080411
	SEMAR-146	HQ974552	–	KX462521	HB1191	AF076113	HB1191	AF076133	–	–	HB1191	AF076139	–	DQ080411
S. concolor	–	NC033531	–	NC033531	HB966	AF076115	HB966	AF076131	–	–	HB966	AF076148	–	–

(Continued)

TABLE 4 | Continued

Correct species	COI		Cyt b		ATPase		NADH2		RHO		ALD		Tmo-4C4	
	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.	Code	Accession no.
	–	KX925518	–	KX925518	–	KX925518	HB966	AF076131	–	–	HB966	AF076148	–	–
S. cavalla	–	NC008109	–	NC008109	–	NC008109	–	NC008109	JJ7:11	DQ874799	HB803	AF076138	JJ7:11	DQ874831
	JJ7:11	DQ874753	Scavll3	EU349353	HB803	AF076119	HB803	AF076137	JJ7:11	DQ874799	HB803	AF076138	JJ7:11	DQ874831
Pampus candidus	PcanVer1	OM436013	PcanVer1	MW337238	PcanVer	ON193432	PcanVer	ON166824	PcanVer1	OK137201	PcanVer1	OM417804	PcanVer1	OK137207
Brama sp.	–	KT908039	–	KT908039	–	KT908039	–	KT908039	Bmye	OK137205	Bmye	OM417807	–	–
Lepidocybium flavobrunneum	–	AP012519	–	AP012519	–	AP012519	–	AP012519	Lflav	OK137200	Lflav	OM417805	Lflav	OK137206
Kajikia audax	–	NC_012678	–	NC_012678	–	NC_012678	–	NC_012678	VizhKAud3	OK137203	VizKAud3	OM417806	–	–

**Indicates species used for BP&P analysis, along with adjacent sequences.*

Mitochondrial data were retrieved from the complete mitogenomes of the outgroups (except for *P. candidus*) after the species were confirmed with barcodes (accession nos. OM436012–OM436014). The individual and concatenated matrices were analyzed under the Bayesian inference (BI) and maximum likelihood (ML) method. The best-fit model (GTR) and partition for the datasets were identified using PartitionFinder v1.1.1 (Lanfear et al., 2017) under the parameters greedy algorithm, unlinked branch length, and Bayesian information criterion (BIC). BI analysis was performed through Markov chain Monte Carlo (MCMC) sampling implemented in MrBayes v3.2 (Ronquist et al., 2012) with 5 million iterations in two independent runs, sampling every 1,000 generations and 10% burn-in. Tracer v1.7 (Rambaut et al., 2018) evaluated the convergence of analyses and ensured that the effective sample size (ESS) values were above 200. Finally, the ML analysis was performed in IQ-TREE by 1,000 standard bootstrap with a given best-fit model and partition. The BI and ML phylogram topologies and their respective statistical supports—posterior probability (PP) and bootstrap support (BS) scores—were visualized in FigTree v.1.4.3.

Species Delineation Analyses

The delineation analysis was performed at two levels with previously used data from *COI* and *Cyt b* fragments, followed by a final validation using a multiple gene data matrix, considered here as one locus. Three species delineation analyses [two tree-based methods: the Generalized Mixed Yule Coalescent model (GMYC; Pons et al., 2006; Fujisawa and Barraclough, 2013) and multirate Poisson tree processes (mPTP; Kapli et al., 2017); and a distance-based method: Automatic Barcode Gap Discovery (ABGD; Puillandre et al., 2012)] were used to delineate and discover diversity among genera. The ultrametric trees generated separately for single and multiple genes by MCMC sampling in BEAST v2.6.4 (Bouckaert et al., 2019) were used as input files for single (sGMYC) and multiple-threshold (mGMYC) models, respectively. In BEAST analyses, independent runs were performed on single and multilocus data incorporating a relaxed clock log-normal and a partition and best-fit model akin to phylogenetic analysis for 10 million generation sampling every 1,000 generations. After assessing convergence between runs and ESS scores, both sGMYC and mGMYC analyses were performed using SPLIT packages implemented in R 4.0.2 (R Core Team, 2020). ML phylogram for mPTP analysis executed in Python v.3 (Van Rossum and Drake, 2009) with PTP package (Zhang et al., 2013) was generated in IQ-TREE v1.6.12 (Nguyen et al., 2015), with provided partition and 1,000 standard bootstrap. A distance-based ABGD analysis was performed following the arguments Pmin = 0.001, Pmax = 0, steps = 20, relative gap width = 1, Nb bins (for distance distribution = 20), and genetic distance as simple distance.

An additional confirmatory species delineation for the cryptic species complex using concatenated gene data was performed using the Bayesian Phylogenetics and Phylogeography program (BP&P; Yang and Rannala, 2010). This is a robust method that models the evolution of multilocus data and is widely used for explicit taxon identification and in the analyses of taxon evolution and divergence (Luo et al., 2018). The analysis was carried out with a user-specified guide tree which estimates the probability that each node represents a speciation event (i.e., a split between two distinct species) in bpp v4.4.1 (Yang, 2015). A total of 27 sequences with the concatenated dataset (**Table 4**) were used for the construction of the guide tree [L, ((T,K),(E,(V, W)))], where L = *S. lineolatus*, T = *S. guttatus*, K = *S. koreanus*, and E, V, and W = *S.* aff. *guttatus*, in BEASTv 2.4. rjMCMC algorithm 1 with fine-tuning parameter epsilon = 2 and species model prior m = 1, mutation rate across locus = 1, and an independent rates clock model were chosen to run the analysis. An inverse gamma prior IG (alpha, beta) for ancestral population size (theta) and root age (tau) were estimated using assigned prior values. The assigned alpha and beta values for theta prior were 6 and 0.002, whereas the tau prior values were 4 and 0.06, respectively.

Genetic Distance

Intra- and interspecific sequence divergence (uncorrected p-distance) of nominal species and MOTUs were calculated after species delineation analysis using the above *COI*, *Cyt b*, and concatenated gene sequences under uniform rates in MEGA 11 (Tamura et al., 2021). In MEGA 11, the criterion for the complete deletion of missing data was adopted, resulting in 3,316 nucleotides (all mitochondrial and nuclear *ALD* fragments used for multilocus phylogenies) being required to calculate genetic distance.

Divergence Time Estimation

The estimation of divergence time of 10 nominal species was performed using the sequences of eight mitochondrial genes (*COI*, *Cyt b*, *ATP6* and *8*, *NADH2*, *12S rRNA*, *16S rRNA*, and *D-loop*) with a total length of 5,554 bp. Of these, the sequences of six species were retrieved from GenBank (https://www.ncbi.nlm.nih.gov/genbank/), while the remaining four were gathered from this study. To include maximum molecular data and to ensure full coverage of sequences without any data loss from all the species, only mitochondrial genes were used for this analysis. The concluding data matrix for the analysis contained only one individual per species (**Table 5**). The estimation of evolutionary rates and approximate time to most recent common ancestors (TMRCA) of each species included in the analysis were assessed by BEAST v2.6.4 (Bouckaert et al., 2019). The analysis was conducted with an uncorrelated relaxed clock model using the GTR/GTR+I+G nucleotide substitution model recovered from PartitionFinder v1.1.1. Speciation for the tree prior was selected as the Yule model and alternative calibration points were incorporated with three fossils under the normal distribution. Firstly, the root age of the basal node of the phylogram was calibrated with a lower and upper boundary of 79.66–98 million years ago (mya) (Santini et al., 2013). The second calibration point was fixed to the *Acanthocybium solandri–Gymnosarda unicolor* clade with a minimum age of 52 mya and an upper boundary of 79.66 mya to calibrate its stem age (Purdy et al., 2001; Santini et al., 2013). Also, we constrain the crown node of the *Scomberomorus* genus with a Paleocene fossil between 56 and 59.2 mya (Sepkoski, 2002). Input file prepared by BEAUti in the BEAST package. The MCMC run for 100 million generations was executed twice, thinning every 1,000 trees to recover time-stamped phylogenies, and 25% of the initial samples were discarded as burn-in by TreeAnnotator v2.6.4. Tracer v1.7 evaluated the convergence of analysis and ensured that the ESS scores for all parameters were above 200. The chronogram after analysis was viewed in FigTree.

Estimation of Vertebral Counts

Since some of the aforementioned literature discussed the variation in the number of vertebrae in *S. guttatus*, this meristic trait was checked for 25 specimens each of *S. guttatus*, collected from the type locality, east coast (Odisha and West Bengal) and west coast (Gujarat) of India, along with five specimens from other *Scomberomorus* species. Vertebral counts were determined both from X-radiographs taken at the respective sites and by manual counting after preparing a dry vertebral column following James (2008). Specimens were boiled to 110°C to separate the meat from the bone and the bones were brushed under running water after boiling.

TABLE 5 | Accession numbers retrieved from GenBank and generated in this study for molecular divergence estimation.

Sl. no.	Species	*COI*	*Cyt b*	*ATPase*	*NADH2*	*12S rRNA*	*16S rRNA*	*D-loop*
1.	*S.* aff. *guttatus* 1	MZ872475	MZ955283	MZ955352	MZ955300	MZ927331	MZ927328	OL362237
2.	*S.* aff. *guttatus* 2a	MZ955343	MZ955288	MZ955343	MZ955304	MZ927337	MZ927323	OL362236
3.	*S.* aff. *guttatus* 2b	MZ872497	MZ955278	MZ955350	MZ955306	MZ927335	MZ927330	OL362235
4.	*S. guttatus*	MZ854050	MZ955298	MZ955360	MZ955315	MZ923804	MZ922477	OM417812
5.	*S. koreanus*	MZ854035	MZ955293	MZ955357	MZ955311	MZ923800	OM348536	OL362240
6.	*S. lineolatus*	MZ871763	MZ955295	OM363539	OM363553	MZ923799	MZ922478	OL362241
7.	*S.* cf. *commerson* 2	MZ854025	MZ955289	OM363541	MZ955309	MZ923803	MZ922475	OL362239
8.	*S. cavalla*	NC008109	NC008109	NC008109	NC008109	NC008109	NC008109	NC008109
9.	*S. concolor*	NC033531	NC033531	NC033531	NC033531	NC033531	NC033531	NC033531
10.	*S. sierra*	NC033887	NC033887	NC033887	NC033887	NC033887	NC033887	NC033887
11.	*S. semifasciatus*	NC021391	NC021391	NC021391	NC021391	NC021391	NC021391	NC021391
12.	*S. munroi*	NC021390	NC021390	NC021390	NC021390	NC021390	NC021390	NC021390
13.	*S. niphonius*	NC016420	NC016420	NC016420	NC016420	NC016420	NC016420	NC016420
14.	*S. colias*	NC013724	NC013724	NC013724	NC013724	NC013724	NC013724	NC013724
15.	*A. solandri*	AP012945	AP012945	AP012945	AP012945	AP012945	AP012945	AP012945
16.	*G. unicolor*	NC022496	NC022496	NC022496	NC022496	NC022496	NC022496	NC022496

RESULTS

BLAST Results and Identity of the Species

Identity of COI barcodes for *Scomberomorus* spp. generated in this study were verified with all available species (n = 13) in nucleotide databases. The reliable barcodes for *S. lineolatus* and *S. koreanus* were also generated here and their incorrectly labeled sequences in various nucleotide databases were thus recognized. The identity of *S. koreanus* could be confirmed using the published *Tmo-4C4* sequence (DQ388095; Orrell et al., 2006). Some species like *S. tritor* and *S. sinensis* were exclusively represented by the *Cyt b* gene in NCBI. Search results employing *Cyt b* were correct identifications in most cases, apart from some errors (see **Supplementary Tables 1, 2**). Although there is no genetic information for *S. multiradiatus*, morphological evidence and a geographic distribution restricted to the Gulf of Papua (Collette and Russo, 1984) isolated it from the others.

Phylogenetic Analyses Using COI Sequences and the Multilocus Data

The COI-based Bayesian phylogeny and IQ tree contained two major clades (**Figure 2**). Major clade I branched into two subclades with a Bayesian posterior probability (BPP) of 0.75. Subclade I was further bifurcated into two groups with high BPP (0.97). Species morphologically identified as *S. guttatus* have been resolved into distinct barcode clusters representing diverged species in phylogenetic analysis. In this study, sequences identical to those of *S. guttatus* collected and identified from the type locality (Tranquebar, India) and adjacent areas are considered to represent *S. guttatus* (Bloch and Schneider, 1801) in *sensu stricto* (see *Discussion*). The cryptic species with indistinguishable morphological resemblance to *S. guttatus* is referred to as *S.* aff. *guttatus* in the phylograms and in the manuscript. Thus, group I included *S. guttatus*, *S.* aff. *guttatus*, *S. koreanus*, and *S. plurilineatus.* Also, *S.* aff. *guttatus* contained two reciprocally monophyletic lineages tentatively designated as *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2. The latter had two haplogroups, hereinafter referred to as *S.* aff. *guttatus* 2a and *S.* aff. *guttatus* 2b in the manuscript. *Scomberomorus* aff. *guttatus* 2a was represented by a larger number of sequences, while the other had only a limited number. Sequence analysis indicated a restricted distribution of *S. guttatus* in the Bay of Bengal, Bangladesh, and Myanmar. *Scomberomorus* aff. *guttatus* 1 included individuals from the Bay of Bengal and the western Pacific Ocean (South China Sea) and some from the Arabian Sea, while *S.* aff. *guttatus* 2 comes exclusively from the Arabian Sea. *Scomberomorus plurilineatus* clusters with this cryptic species, while *S. koreanus* and *S. guttatus*, clustering around *S. plurilineatus*, occupy an interchangeable position with respect to BI and IQ-based phylograms. In addition, *S. munroi* and *S. niphonius* form sister clade to the cryptic species + *S.*

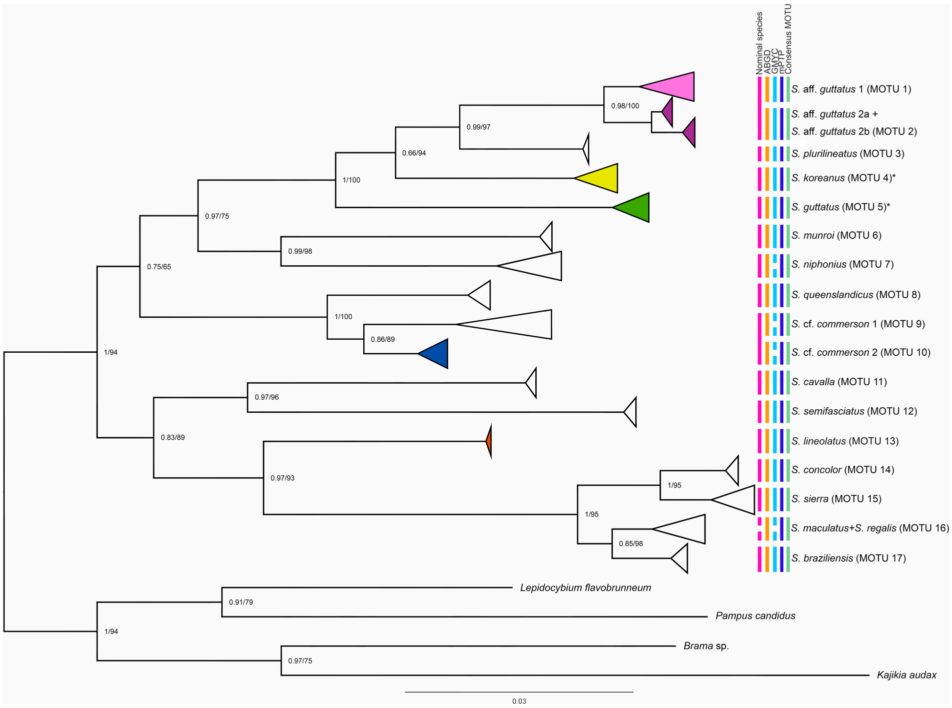

FIGURE 2 | Phylogenetic tree depicting the relationships between *Scomberomorus* spp. based on Bayesian inference (BI) superimposed on maximum likelihood (ML) analysis of partial COI sequences (**Supplementary Table 1**). The node numbers specify the posterior probability and bootstrap support values, respectively. Leaves are collapsed to indicate the well-supported clades and species from India are highlighted in colors. The nominal species, results of delineation methods, and consensus MOTUs are indicated by different colors to the right of the phylogram.

plurilineatus + *S. koreanus* + *S. guttatus*. Subclade II included *Scomberomorus queenslandicus* and *S. commerson*, the latter of which was further subdivided into two groups tentatively designated as *S.* cf. *commerson* 1 and *S.* cf. *commerson* 2 residing mostly in the Pacific and Indian Oceans, respectively.

Major clade II also had two subclades: one subclade included *S. cavalla* and *S. semifasciatus*, while the other included *S. lineolatus* and the rest of the species. *Scomberomorus concolor* and *S. sierra* formed a strongly supported group in this, while *S. maculatus* + *S. regalis* and *S. brasiliensis* formed another. The *Cyt b* gene generated a tree topology (**Supplementary Figure 2**) that was incongruent with the COI-based phylogram.

The TCS haplotype network based on mutational steps revealed a clear grouping pattern with three major haplogroups in the cryptic complex of *S. guttatus* (**Supplementary Figure 3A**) and two haplogroups in *S. commerson* (**Supplementary Figure 4A**). The geographical distribution of these haplogroups was also depicted (**Supplementary Figures 3B–D**, **4B**). The analysis showed a clear genetic differentiation between the haplotypes of *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2 from *S. guttatus*. The first two mentioned were 10 mutational steps apart, and when taken together, they were 61 mutational steps away from the third. Similarly, the two groups in *S. commerson* were 18 mutational steps away from each other.

The concatenated multilocus phylogeny depicted the relationships between the 10 nominal species (**Figure 3**). The Bayesian and IQ phylogenetic trees showed the same topology. There were two major clades (BPP-1) and the first one had two strongly supported subclades: one with (*S.* aff. *guttatus* 1 + *S.* aff. *guttatus* 2) + (*S. guttatus* + *S. koreanus*), while the second subclade contained *S. lineolatus* and *S.* cf. *commerson* 2. Major clade II clustered *S. cavalla* outside the group of *S. concolor* and *S. sierra* and another group of *S. brasiliensis*, *S. maculatus*, and *S. regalis*.

Species Delimitation and Evolutionary Divergence Based on COI Sequences

The ABGD analysis detected a barcode gap at 1.7% identifying 17 hypothetical species (MOTUs) in the initial partition. The GMYC and mPTP analyses detected 21 and 17 MOTUs, respectively. The results of the species delineation analyses are given in **Figure 2**. Of the consensus MOTUs (n = 17), 12 nominal species, viz., *S. cavalla* (Cuvier, 1829); *S. commerson* (Lacepède, 1800); *S. concolor* (Lockington, 1879); *S. koreanus* (Kishinouye, 1915); *S. lineolatus* (Cuvier, 1829); *S. munroi* Collette and Russo, 1980; *S. plurilineatus* Fourmanoir, 1966; *S. queenslandicus* Munro, 1943; *S. brasiliensis* Collette, Russo and Zavala-Camin, 1978; *S. niphonius* (Cuvier, 1832); *S. semifasciatus* (Macleay, 1883); and *S. sierra* Jordan and Starks, 1895 were recovered by all the analyses. The two nominal species *S. regalis* (Bloch, 1793) and *S. maculatus* (Mitchill, 1815) were identified as

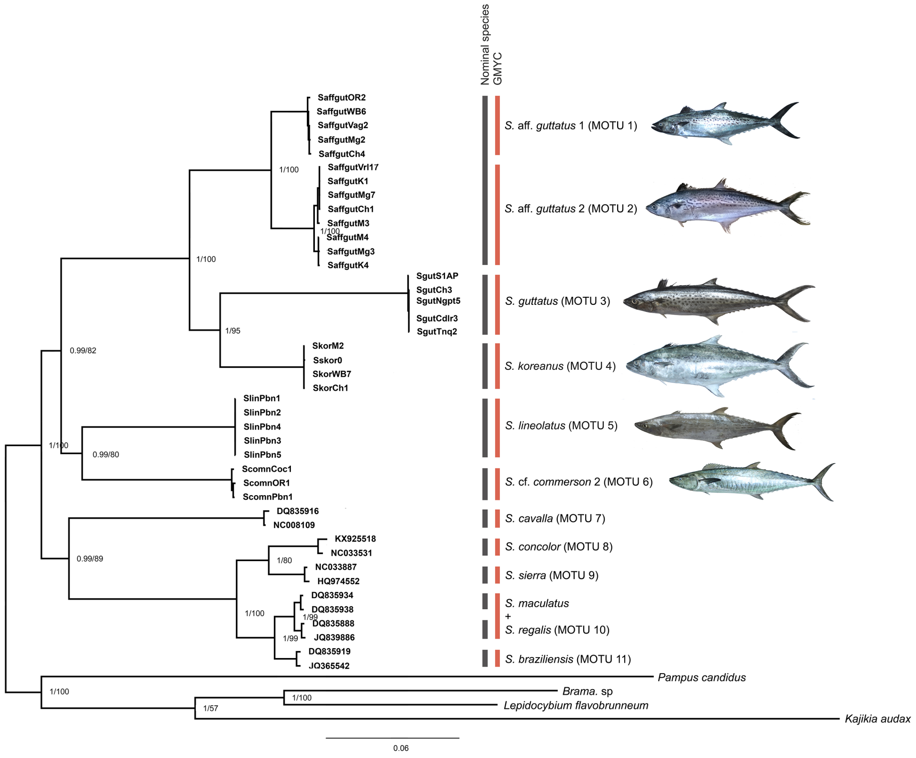

FIGURE 3 | Bayesian inference (BI) phylogram superimposed on maximum likelihood (ML) based on concatenated multilocus data is represented (**Table 4**). The node numbers specify the posterior probability and bootstrap support values, respectively. The nominal species and the GMYC entities from the GMYC delineation method are indicated by different colors to the right.

a single MOTU in all analyses except GMYC. Interestingly, three consensus MOTUs or hypothetical species could be identified in nominal *S. guttatus* with all delimitation methods. Apart from *S. guttatus* from the type locality, two MOTUs, i.e., *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2, have been identified on the Indian coast including the island ecosystems (Andaman and Nicobar Islands). *Scomberomorus* aff. *guttatus* 2a had a smaller intercladal divergence (0.59%) with *S.* aff. *guttatus* 2b. However, the maximum genetic divergence was found between *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2b. Sequence identity searches based on the BLAST results of various genes and species delimitation analyses indicated that certain COI barcodes of *S. guttatus* are classified as *S. plurilineatus*. Some others actually represented *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2, a misidentification primarily due to the deceptive spotting pattern in the *S. guttatus* complex.

Scomberomorus commerson also branched into two allopatric putative species in all analyses, though GMYC analysis delimited two more entities (**Figure 2**). *Scomberomorus niphonius* (Cuvier, 1832) formed a single MOTU except in GMYC. *Scomberomorus lineolatus* and *S. koreanus*, previously not represented in nucleotide databases, represented two different MOTUs.

The COI-based genetic distance values between the recognized nominal species and consensus MOTUs containing novel hypothetical species are shown in **Tables 6A, B**, respectively. The nominal species on analysis showed a maximum intraspecific divergence of 10.60% (*S. guttatus*), followed by *S. commerson* (4.43%), while the minimum intraspecific distance was 0.00% in *S. plurilineatus* and *S. lineolatus*. The maximum inter-MOTU distance was 12.35% (between *S. semifasciatus* and *S. cavalla*), while the minimum distance was 0.44% between *S. maculatus* and *S. regalis*. The p-distance values between *S. guttatus* and *S.* aff. *guttatus was* 10.26%–10.41%, while it was 2.28% between *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2. Between *S.* cf. *commerson* 1 and *S.* cf. *commerson* 2, it was 3.74%.

Species Delimitation Using *Cyt b* Sequences

GMYC analysis of the *Cyt b* gene amid the limited number of proxies from each geographic region revealed 18 MOTUs

TABLE 6 | COI-based genetic distance (uncorrected p-distance) values between the **(A)** nominal species and **(B)** consensus MOTUs containing novel hypothetical species are presented.

(A)

Sl. no.	Nominal species	Maximum intragroup distance	Nearest neighbor (NN)	Distance to NN
1.	*S. guttatus*	0.1060	*S. plurilineatus*	0.0729
2.	*S. plurilineatus*	0.0000	*S. koreanus*	0.0663
3.	*S. koreanus*	0.0095	*S. plurilineatus*	0.0663
4.	*S. munroi*	0.0015	*S. niphonius*	0.0934
5.	*S. niphonius*	0.0128	*S. munroi*	0.0934
6.	*S. queenslandicus*	0.0031	*S. commerson*	0.0536
7.	*S. commerson*	0.0443	*S. niphonius*	0.1010
8.	*S. cavalla*	0.0015	*S. lineolatus*	0.1122
9.	*S. semifasciatus*	0.0015	*S. cavalla*	0.1235
10.	*S. lineolatus*	0.0000	*S. commerson*	0.1054
11.	*S. concolor*	0.0032	*S. sierra*	0.0283
12.	*S. sierra*	0.0143	*S. concolor*	0.0283
13.	*S. maculatus*	0.0079	*S. regalis*	0.0045
14.	*S. regalis*	0.0095	*S. maculatus*	0.0045
15.	*S. brasiliensis*	0.0063	*S. maculatus*	0.0245

(B)

Sl. no.	Consensus MOTUs	Nearest neighbor (NN)	Distance to NN
1.	*S.* aff. *guttatus* 1	*S.* aff. *guttatus* 2	0.0228
2.	*S.* aff. *guttatus* 2	*S.* aff. *guttatus* 1	0.0228
3.	*S. plurilineatus*	*S.* aff. *guttatus* 2	0.0621
4.	*S. koreanus*	*S. plurilineatus*	0.0662
5.	*S. guttatus*	*S. koreanus*	0.0904
6.	*S. munroi*	*S. niphonius*	0.0934
7.	*S. niphonius*	*S. munroi*	0.0934
8.	*S. queenslandicus*	*S.* cf. *commerson* 1	0.0592
9.	*S.* cf. *commerson* 1	*S.* cf. *commerson* 2	0.0374
10.	*S.* cf. *commerson* 2	*S.* cf. *commerson* 1	0.0374
11.	*S. cavalla*	*S. lineolatus*	0.1120
12.	*S. semifasciatus*	*S. cavalla*	0.1235
13.	*S. lineolatus*	*S.* cf. *commerson* 2	0.1025
14.	*S. concolor*	*S. sierra*	0.0277
15.	*S. sierra*	*S. concolor*	0.0277
16.	*S. maculatus*	*S. regalis*	0.0044
17.	*S. regalis*	*S. maculatus*	0.0044
18.	*S. brasiliensis*	*S. maculatus*	0.0240

representing the species records in GenBank and identified here (**Supplementary Table 2**; **Supplementary Figure 2**). Despite the absence of *S. plurilineatus*, *S. queenslandicus*, and *S. regalis* that were present in the COI-based analysis, the *Cyt b* data revealed two additional GMYC entities representing two other nominal species, viz., *S. tritor* and *S. sinensis*. Interestingly, another GMYC species of uncertain taxonomic status represented as *S. guttatus* in GenBank from Taiwan and as *Scomberomorus* sp. here was evident in *Cyt b*-based analyses, while their COI barcodes were not available. The observed p-distance between *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2 was 1.82%, while *Scomberomorus* sp. showed a divergence of 10.42%–10.55% from above. These three showed a divergence of 10.38% to 12.57% from *S. guttatus*. The p-distance was 4.31% between *S.* cf. *commerson* 1 and *S.* cf. *commerson* 2. These values are comparable to the COI-based distances between the above MOTUs. A divergence of 6.61% was observed between *Scomberomorus* sp. and its nearest neighbor *S. koreanus* (**Supplementary Table 3**). *Cyt b* sequences from *S. sierra* of the eastern Pacific (JQ434072–JQ434074) were seen to represent *S. concolor*. Similarly, sequences such as DQ497884 (Taiwan) identified as *S. koreanus* and AY986968 identified as *S. commerson* (China) represented *S.* aff. *guttatus* 1.

Validation of Species Boundaries Using Multilocus Data

GMYC analysis of the multilocus data revealed 10 nominal species or 11 MOTUs (**Figure 3**). The genetic distance values between the nominal species and consensus MOTUs are given in **Tables 7A, B**. Concordant results with the previous two single-locus analyses indicating three MOTUs in nominal *S. guttatus* were demonstrated here. The maximum intraspecific divergence (12.2%) was observed in the nominal species *S. guttatus*. The p-distance values between *S. guttatus* and *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2 were 11.69% and 11.99%, respectively. The p-distance was 2.14% between *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2. The maximum inter-MOTU distance was 13.11% (between *S. cavalla* and *S.* cf. *commerson* 2), while the minimum was 0.60% between *S. maculatus* + *S. regalis* and *S. brasiliensis*. Similar to the COI-based analysis, *S. maculatus* and *S. regalis* formed a single GMYC entity here.

According to rjMCMC algorithms 1 and 0, the BP&P analysis considered *S. lineolatus*, *S. guttatus*, *S. koreanus*, and three lineages in *S.* aff. *guttatus* as distinct species, with all nodes resolved with a posterior probability of 1.0, that corroborated with the multilocus tree topologies from phylogenetic analyses. The sister relationship of *S. guttatus* with *S. koreanus* was recovered here. The status of the species in *S.* aff. *guttatus* is restored similarly to all the tree topologies. In contrast to the phylogenetic and other species delineation analyses, BP&P recognized *S.* aff. *guttatus* 2a and *S.* aff. *guttatus* 2b into two separate species (**Supplementary Figure 5**).

Divergence Dating

The topology of the chronogram (**Figure 4**) mostly corroborated with both single and multilocus phylograms. The crown age of the *Scomberomorus* genus has been estimated at 57.3 mya in the late Paleocene [highest posterior density (HPD): 56.3–58.4 mya] and diversification in the Eocene. The regalis group species, *S. concolor* and *S. sierra*, split from *S. cavalla* by 46 mya (HPD: 41–

TABLE 7 | Concatenated genetic distance (uncorrected p-distance) values between the **(A)** nominal species and **(B)** consensus MOTUs containing novel hypothetical species as well are shown.

(A)

Sl. no.	Nominal species	Nearest neighbor (NN)	Distance to NN
1.	*S. guttatus*	*S. koreanus*	0.0914
2.	*S. koreanus*	*S. guttatus*	0.0914
3.	*S. lineolatus*	*S.* cf. *commerson* 2	0.1090
4.	*S. commerson*	*S. lineolatus*	0.1090
5.	*S. cavalla*	*S.* cf. *commerson* 2	0.1311
6.	*S. concolor*	*S. sierra*	0.0369
7.	*S. sierra*	*S. concolor*	0.0369
8.	*S. maculatus*	*S. regalis*	0.0060
9.	*S. regalis*	*S. regalis*	0.0060
10.	*S. brasiliensis*	*S. maculatus*	0.0222

(B)

Sl. no.	GMYC entities	Nearest neighbor (NN)	Distance to NN
1.	*S.* aff. *guttatus* 1	*S.* aff. *guttatus* 2	0.0214
2.	*S.* aff. *guttatus* 2	*S.* aff. *guttatus* 1	0.0214
3.	*S. guttatus*	*S. koreanus*	0.1075
4.	*S. koreanus*	*S.* aff. *guttatus* 1	0.0839
5.	*S. lineolatus*	*S.* cf. *commerson* 2	0.1090
6.	*S.* cf. *commerson* 2	*S. lineolatus*	0.1090
7.	*S. cavalla*	*S.* cf. *commerson* 2	0.1311
8.	*S. concolor*	*S. sierra*	0.0369
9.	*S. sierra*	*S. concolor*	0.0369
10.	*S. maculatus* + *S. regalis*	*S. brasiliensis*	0.0060
11.	*S. brasiliensis*	*S. maculatus* + *S. regalis*	0.0222

49.5 mya), whereas *S. concolor* and *S. sierra* recently separated by 8.5 mya (HPD: 7.2–9.9 mya). The probability of diversification of Indo-West Pacific species was predicted in the early Eocene, i.e., 54.4 mya (HPD: 51.9–56.5 mya). The predicted recent common ancestral ages between *S. commerson–S. lineolatus* and *S. munroi* and *S. niphonius* have been estimated to be 45 mya (HPD: 37–45.5 mya) and 41.9 mya (HPD: 38.5–45.6 mya), respectively. The crown age of *S. guttatus–S. koreanus* species has been estimated at 24.9 mya (HPD: 22.5–27.5 mya), while *S. koreanus* split from *S.* aff. *guttatus* group by 20.2 mya (HPD: 17.8–22.8 mya). Split in *S.* aff. *guttatus* into three lineages was observed at 3.7 mya (HPD: 3–4.5 mya) and 0.91 mya (HPD: 0.6–1.2 mya).

Vertebral Count

Vertebral counts and X-radiographs of all available species from Indian waters are provided for comparison (**Supplementary Table 4**; **Figure 5**). *Scomberomorus koreanus*, *S. commerson*, and *S. lineolatus* showed a total vertebral count of 46, 44, and 46, respectively. The vertebral count of *S. guttatus was* 47–49 (usually 48), while it was 49–51 (usually 50) for *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2 (**Supplementary Figure 6**).

DISCUSSION

Phylogenetic Analyses

COI and *Cyt b* fragments generated incongruent gene trees in this study, which is not unexpected in Scombridae, where the phylogenetic signal varies with genes (Miya et al., 2013). The low BPP support for the subclade containing *S. queenslandicus* and *S. commerson* to the major clade I in the COI-based phylogram indicates their rather fragile affiliation within this major clade. Similarly, different levels of resolution for the species–level relationships could be observed in numerous groups of fish in individual gene trees (Clements et al., 2003; Wright et al., 2012). The incongruence in gene trees arises due to differences in their evolutionary history and various other events like incomplete lineage sorting, gene duplications, extinctions, introgression or hybridization, etc. (Som, 2015). MtDNA introgression occurs between species in *Scomberomorus* (e.g., Morgan et al., 2013), and the possibility of incomplete lineage sorting in the youngest lineages in Scombridae has been suggested (Ollé et al., 2022).

Collette and Russo (1984), based on a cladistic analysis of 58 characters, identified six species groups in *Scomberomorus*, viz., the "*sinensis* group," which contains only *S. sinensis*; the "*commerson* species group" with *S. commerson*, *S. niphonius*, *S. queenslandicus*, and *S. cavalla*; the monotypic "*munroi* species group"; the "*semifasciatus* species group" with *S. semifasciatus*, *S. plurilineatus*, and *S. lineolatus*; the "*guttatus* species group" with *S. guttatus*, *S. multiradiatus*, and *S. koreanus*; and the "*regalis* species group" with *S. regalis*, *S. tritor*, *S. maculatus*, *S. concolor*, *S. sierra*, and *S. brasiliensis*. They considered *S. tritor* to be the basal primitive species in the *regalis* species group and considered *S. sierra*, *S. brasiliensis*, and *S. regalis* to be the three most advanced species.

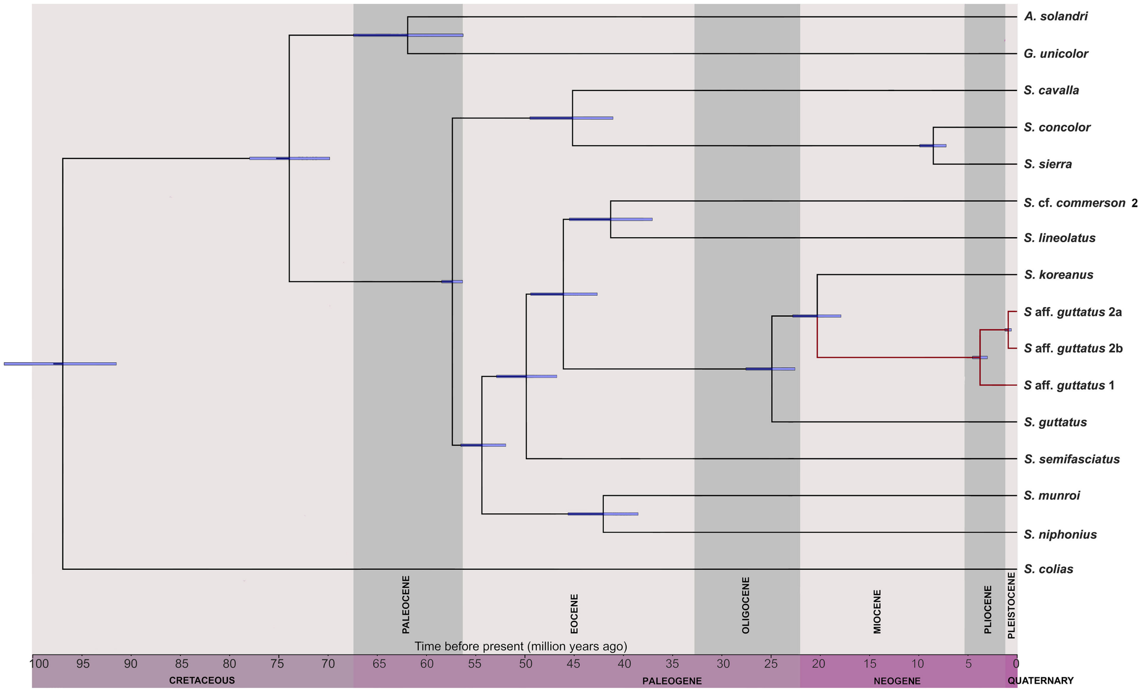

FIGURE 4 | An ultrametric tree of *Scomberomorus* species (with maximum molecular data) scaled to geographical time is illustrated. Blue bars at the nodes indicate 95% confidence interval of internal nodes, and the clade highlighted in red color indicates *S. guttatus* and its cryptics.

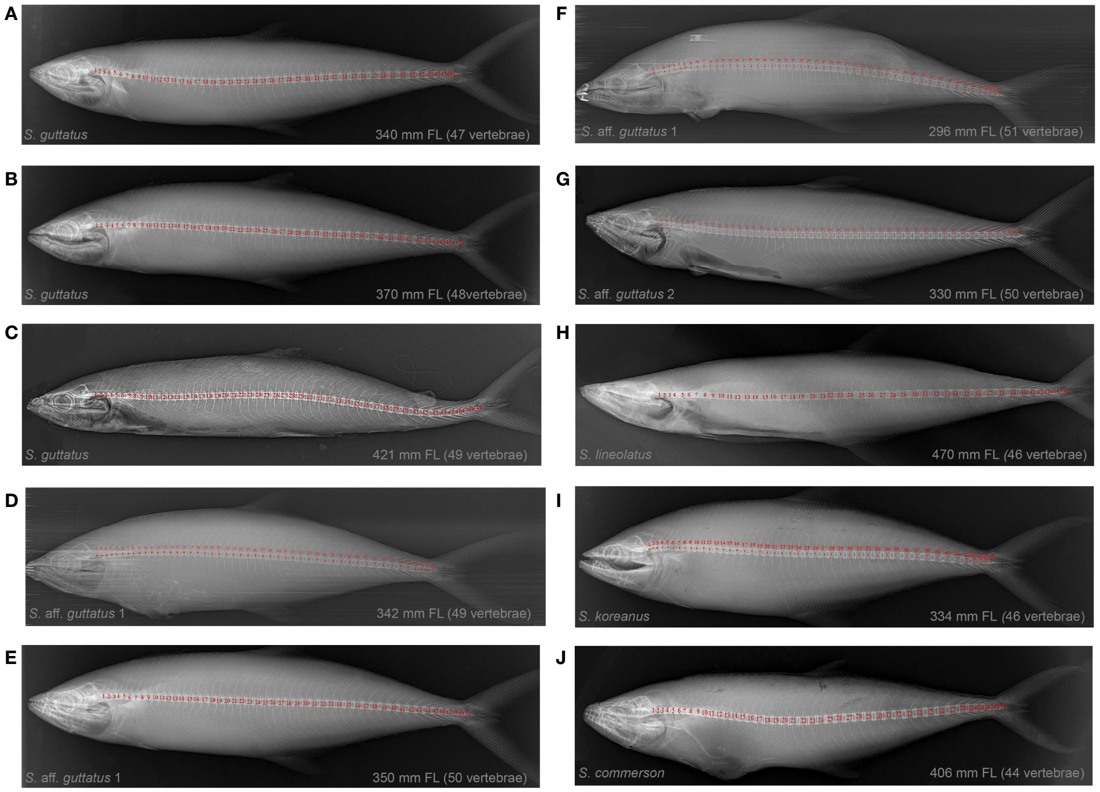

FIGURE 5 | Digital X-ray images of *Scomberomorus* species **(A–J)** from the Northern Indian Ocean revealing the diversity, fork length (FL), and number of vertebrae.

The "*guttatus* species complex" in the COI-based phylogenetic tree contained *S.* aff. *guttatus* 1, *S.* aff. *guttatus* 2 (2a and 2b), *S. koreanus*, *S. guttatus*, and *S. plurilineatus*, and the grouping of the last one to this complex deviated from the "*guttatus* species group" proposed by Collette and Russo (1984). The TCS network showed consistent genealogical relationships. A similar genetic structure consistent with the phylogenies has been observed in the TCS network topology of the cryptic *S. guttatus* complex and *S. commerson*. Overall, *S.* aff. *guttatus* has two distinct haplogroups with a star-like topology with the predominance of a single haplotype, suggesting recolonization events through founder effects or population expansions after a bottleneck event (Allcock and Strugnell, 2012). A similar situation was observed in *S. commerson*. A star pattern with radial distribution was also shared in *S. guttatus*. The formation of haplogroups in *S.* aff. *guttatus* 2 can be an outcome of incomplete lineage sorting due to recent divergence (Van Velzen et al., 2012).

In the coalescent species tree, the clustering of *S. munroi* with *S. niphonius* and the placement of the new world taxa (Banford et al., 1999) in a highly supported clade with *S. cavalla* outgroup agree with Santini et al. (2013). Species–level relationships deduced from molecular data were generally inconsistent with the previously published morphological groupings by Collette and Russo (1984).

Phylogenies illustrate the historical relationships within a group of species and help study the processes of cladogenesis, and the shape of a phylogenetic tree provides clues to patterns of speciation and extinction within the clade. Taxon sampling has a strong impact on the accuracy of phylogenetic reconstruction methods, and reduced taxon sampling leads to an increase in phylogenetic tree imbalance (Heath et al., 2008; Nabhan and Sarkar, 2012). Increased sampling of taxa allows more accuracy, as exemplified in Salmonidae (Crête-Lafrenière et al., 2012). It is expected that the strength of the phylogenetic signal inferred from the concatenated gene sequences will be useful as the number of taxa increases, and therefore, we recommend global sampling and inclusion of all available species to elucidate the systematic relationships in the genus *Scomberomorus*.

Species Diversity Using Delimitation Analyses

Through delimitation analyses of *COI* and *Cyt b* gene fragments, we confirmed the identity of all valid species except *S. maculatus* and *S. regalis*. The latter two formed a single MOTU, an observation which is not surprising in light of the previous reports pointing to mitochondrial introgression in *Scomberomorus* (Banford et al., 1999; Paine et al., 2007; Morgan et al., 2013) and other scombrids (Puncher et al., 2015). Banford et al. (1999) observed that these two readily distinguishable inhabitants of the Western Atlantic are seasonally sympatric, and hypothesized the probability of ephemeral hybridization and subsequent mitochondrial introgression and recommended a comprehensive geographic and molecular assessment. Although the single-locus species delimitation approach can sometimes lead to an over- and/or underestimation of species diversity (Hofmann et al., 2019), its authenticity was confirmed here with the concordant result of the GMYC analysis of multilocus data.

The incongruence in the number of MOTUs from various molecular species delimitation methods can be due to their difference in a number of aspects. ABGD, GMYC, and PTP were developed for the analysis of single-locus data, although the latter two are often applied to concatenations of multilocus data. ABGD is sensitive to singleton sequences, while GMYC showed tendencies for oversplitting the number of species when there are violations of the model (Pentinsaari et al., 2017). Moreover, PTP and GMYC are sensitive to gene flow (Luo et al., 2018). Here, we used simple rules to find consensus between discordant MOTU delimitations using the best fit between species and MOTUs.

The Indo-Pacific king mackerel, *S. guttatus*, is dominant next to *S. commerson* in FAO Fishing Area 51 (Siddeek, 1995; Devaraj and Mohamad Kasim, 1998; Secretariat, IOTC, 2015). It is noteworthy that the nominal *S. guttatus* showed high intraspecific divergence, an indication of cryptic speciation events (Ge et al., 2021), and contained three consensus MOTUs with morphological similitude in all analyses except in BP&P, which produced four Bayesian species. BP&P is believed to be more accurate than other multilocus coalescent methods, showing lower rates of species overestimation and underestimation, and is generally robust to various potential confounders (Luo et al., 2018). Nevertheless, this method tends to delimit only the population structure and not the number of species, and hence, validation of genome-based results with multiple data types such as phenotypic and ecological information is required (Sukumaran and Knowles, 2017).

The species distribution along the Indian coast derived from our extensive sampling is depicted in **Figure 6**. Analysis of specimens from the type locality of *S. guttatus* and regions up to Chennai (Cuddalore, Kovalam, Nagapattinam, Kovalam) indicated the occurrence of only one haplogroup from these areas on the Coromandel Coast. The same formed a fraction of samples from other sites of fishery (Chennai, Visakhapatnam, Odisha, and West Bengal) located in the Bay of Bengal. The species having a genetic identity with the above deserves the status to be adorned as the original *S. guttatus* identified by Bloch and Schneider in (1801), as it is the only available species in type locality. It differed from the other two MOTUs in the nominal

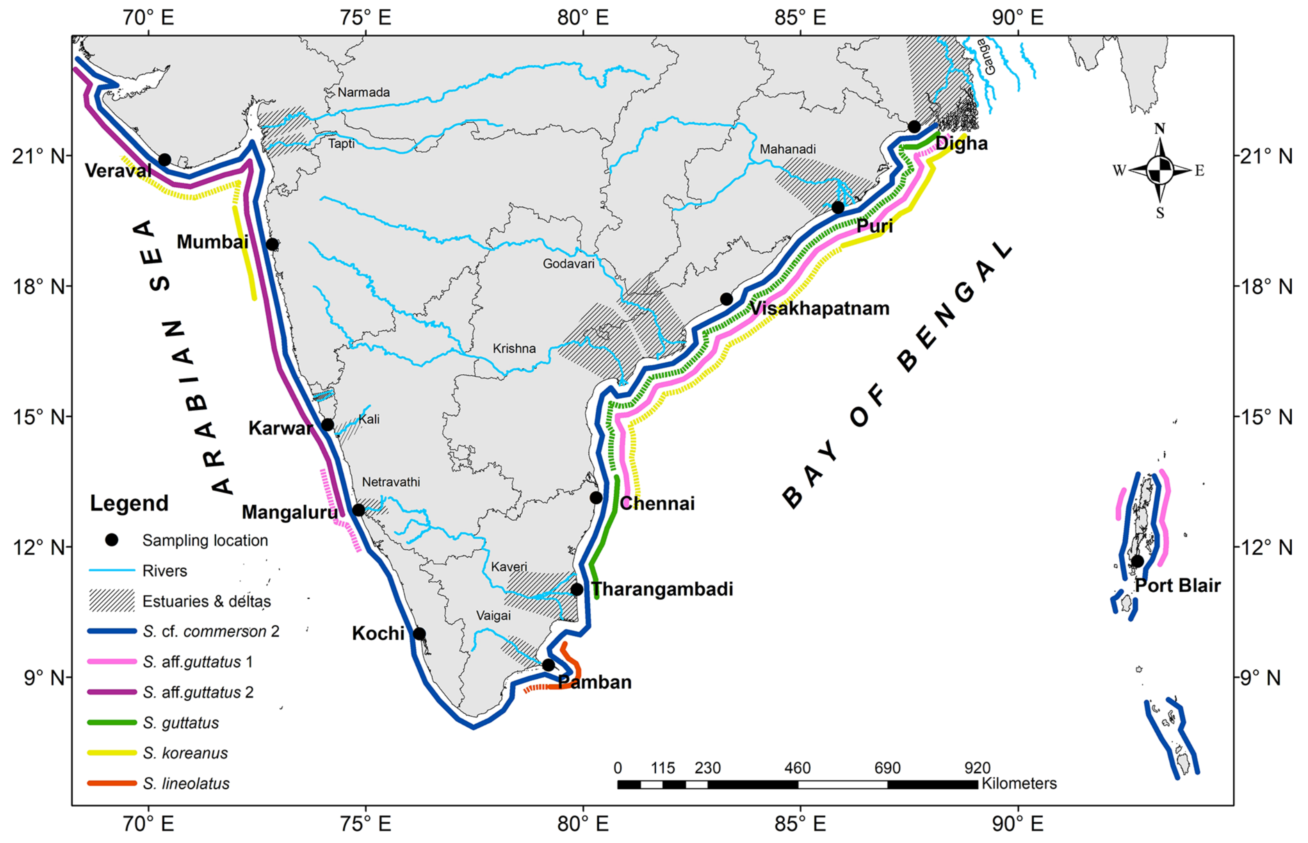

FIGURE 6 | Geographical distribution of *Scomberomorus* spp. in the northern Indian Ocean based on the present study. The intense and sparse distribution of each MOTU is indicated by thick and dotted lines, respectively.

species by high genetic divergence. The lean and slightly cylindrical body shape of this species resembles the only existing type specimen collected from Tranquebar, India (**Figure 7A**: ZMB 8759: lectotype, stuffed, 361 mm SL) although its meristic trait such as vertebrae is not visible (**Figure 7B**). The cryptic MOTUs, viz., *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2, hitherto hidden among the nominal species, were widespread in the collections. The *Scomberomorus* sp. from Taiwan recovered in *Cyt b*-based analysis and clades with *S. koreanus* represent a species with an uncertain taxonomic status that cannot be verified with the current level of information.

The allopatric putative species in *S. commerson*, i.e., *S.* cf. *commerson* 1 and *S.* cf. *commerson* 2, were consistent with some previous studies using mtDNA CR (Fauvelot and Borsa, 2011) with extensive geographic coverage across oceans. *Scomberomorus commerson* has a typically pelagic lifestyle at all developmental stages (Thangaraja and Al-Aisry, 2001) and is considered to be more migratory than all other congeners (Collette, 2001). Incidental occurrence of eggs/larvae of the Pacific Ocean lineage in the Indian Ocean (**Supplementary Table 1**) supports this observation. Significant differences in morphometry and spawning season between the Indo-Pacific populations were observed by Collette and Russo (1984) and Kaymaram (2010), respectively. Fauvelot and Borsa (2011) stated that the samples from the northwestern Indian Ocean, consisting of the Persian Gulf and the Oman Sea (identical to *S.* cf. *commerson* 2) and those from the Western Pacific, i.e., Southeast Asia and Oceania (*S.* cf. *commerson* 1), represent two cryptic species with a deep phylogeographic split. The additional GMYC entities observed in this study also support previous observations of geographic differentiation in this species (e.g., Sulaiman and Ovenden, 2010; Vineesh et al., 2018).

However, *S. lineolatus*, another valid species which is least abundant in the seerfishes in India (CMFRI FRAD, 2020), showed a limited distribution in Pamban up to Tuticorin (personal observation of the authors), although the literature describes its occurrence from Mumbai, Malabar to Palk Bay and Chennai (Collette and Russo, 1984). The shift in the fishery for *S. guttatus* and *S. lineolatus* from their former areas of frequent occurrence (Southern Gulf of Mannar and Visakhapatnam, respectively) is reminiscent of a similar trend observed for *S. concolor* (Fitch and Flesching, 1949). It is interesting to note the restricted distribution pattern of the nominal *S. guttatus* and *S. koreanus* along the Indian coast with an apparent break in the marine regions adjacent to peninsular India, the reasons for which will be discussed in the upcoming session.

Divergence Time

Although the phylogenetic investigation in the *regalis* species group has been performed, a comprehensive investigation on divergence time estimation for the *Scomberomorus* genus is yet to be undertaken. To procure the most reliable information from

FIGURE 7 | Lectotype of *Scomberomorus guttatus* (ZMB 8759) collected from Tranquebar, India. **(A)** Dry, stuffed specimen (373 mm FL and 361 mm SL), and **(B)** Computed Tomography (CT) Scan.

fossil-calibrated molecular data, molecular dating was carried out with species having at least 70% of the genes selected for the analysis. The results derived from our study differ from all previous investigations (Banford et al., 1999; Santini et al., 2013). The first split from the most recent common ancestor of *Scomberomorus* divided the Western Atlantic (*S. cavalla*)–Eastern Pacific species (*S. concolor* and *S. sierra*) with the Indo-West Pacific species group (*S. munroi*, *S. niphonius*, *S. semifasciatus*, *S. commerson*, *S. lineolatus*, *S. guttatus*, *S. koreanus*, and *S.* aff. *guttatus*). The recent split of the *regalis* species group suggested by previous nuclear sequence data (Banford et al., 1999) was also supported in this study, though the divergence time varies, which can be rectified if more species from the *regalis* group are added for divergence dating. The Indo-West Pacific species group has undergone multiple diversification events; of these events, the most interesting divergence was perceived in the crown group, comprising *S. guttatus*–*S. koreanus* and encircling cryptic species. *Scomberomorus koreanus* and *S.* aff. *guttatus* diverged from the common ancestor (*S. guttatus*) during the Miocene followed by population expansion of *S.* aff. *guttatus* during the Pliocene. Both divergence and expansion of the latter were probably materialized due to climatic or oceanographic changes that occurred during the Miocene–Pliocene periods that might have changed the population connectivity leading to range expansions (Renema et al., 2008). The early Miocene period is characterized by the redistribution of salt and heat resulting in significant changes in flow and climate patterns in the Indian Ocean (Bialik et al, 2019). Furthermore, the diversification of *S.* aff. *guttatus* into three lineages in the Pliocene could be accelerated by the increase in productivity associated with the biogenic bloom, and shifts in monsoon activity occurred in the Miocene period in the Indian Ocean (Karatsolis et al., 2022). The superimposed climatic changes with local adaptations followed by reproductive aggregation possibly led to sympatric speciation in this genus (Qvarnström et al., 2016; Beal et al., 2020).

Validation of Geographical Races Based on Vertebral Counts

The variations in vertebral counts, both in the precaudal and caudal regions, are observed in a number of species in *Scomberomorus*. The vertebral count observed for *S. commerson*, *S. lineolatus*, and *S. koreanus* agrees with previous observations on these species (Collette and Russo, 1984). The wide range (47–51) in nominal *S. guttatus* is discussed here. Jones and Silas (1961) observed 48 or 49 vertebrae in *S. guttatus* examined from the peninsular (Vizhinjam) and south-east coast (Tuticorin) of India. They indicated that Kishinouye (1923) observed the vertebral count of 51 for *Cybium guttatum* from Formosan waters and observed an insightful range of variation of this meristic character in *S. guttatus*. Subsequently, in 1964, Silas redescribed the species from specimens collected in the southern part of the Gulf of Mannar (Tuticorin, India). Later, Devaraj (1976) observed vertebral counts of 49–50 (mostly 50) in samples collected from the northern part of the Gulf of Mannar, which he considered to be the typical *S. guttatus*. He suggested that the *S. guttatus* from the southern Gulf of Mannar reported by Silas (1964), as well as the specimens of the contiguous Arabian Sea, characterized by shortening of the precaudal region and elongation of the caudal region, may belong to a different race suspected to be *S. guttatus*. It should be noted that the occurrence of *S. guttatus* in the southern Gulf of Mannar and Pamban is currently very rare and the authors were only able to collect very few specimens during the period of this study (2019–2021), contrary to previous observations (Jones and Silas, 1961; Devaraj, 1976; Devaraj, 1998). However, the species shares the fishery with *S. commerson* in the northern part of the Gulf (from Tranquebar to Nagapattinam), from where the authors were able to collect only one species with 47–49 (usually 48) vertebrae.

The cryptic species *S.* aff. *guttatus* in the Indian Ocean has 49–51 vertebrae (usually 50), while its vertebral count in the Western Pacific is usually 51 (Lee and Yang, 1983). Collette and Russo (1984) reported that the Indian Ocean population has a mode of 50 vertebrae, while populations in the East Indies, Gulf of Thailand, and China have 51 as mode. We examined the X-rays of lectotype (MNHN A.5771, Java, 1,075 mm FL, vertebrae 51) and paralectotype (MNHN A. 5715, Mumbai, 1,145 mm FL, vertebrae 50) of *Cybium kuhlii* (http://n2t.net/ark:/65665/3b5aba155-8948-4776-b613-ff753884c14d and http://n2t.net/ark:/65665/3cf8430ff-c20c-4d82-9424-cf17063a007b), currently synonymized with *S. guttatus*, to confirm our observations. The lectotype of *C. kuhlii* from Java and the paralectotype from Mumbai represent the Pacific and Indian Ocean lineages, respectively.

The number of vertebrae is often cited as a meristic character of diagnostic importance in fish taxonomy. The count sometimes differs between populations of a species along with its geographical range, or across the ranges of related species (e.g., Roul et al., 2021), similar to the observations here. Parallel differences in vertebral counts can also occur within the species (Hubbs, 1922). The vertebral number is influenced by a number of factors like ambient temperatures during the ontogeny of individual fish (Jordan, 1892), inheritance, etc., and the separation of environmental and genetic influences is a complex process (McDowall, 2008). Therefore, this character can be considered only in combination with other features for diagnostic purposes.

History of Seerfishes in the Northern Indian Ocean

The historical provenance of Spanish mackerels from the Indian subcontinent begins with *S. guttatus*, originally described as *Scomber guttatus* by Bloch and Schneider (1801) from Tranquebar (Tharangambadi), Tamil Nadu, India. Two years later, Russell (1803) described the seerfishes vernacularly known as “Wingeram” and “Konam” from Vizagapatam (present-day Visakhapatnam) on the Coromandel coast of India as Scomber Wingeram and Scomber Konam. They added that the latter was rarer and of inferior quality compared with the English seerfish (Wingeram) of the same size. Later that year, Shaw (1803) from the same locality, based on Russell’s description and figures of Wingeram and Konam, described them as *Scomber leopardus* and *Scomber maculosus*, respectively. Cuvier then described in Cuvier and Valenciennes, 1831, *Cybium lineolatum* from Malabar, *Cybium interruptum* from Pondicherry (Puducherry), *C. kuhlii* from Bombay, and *C. commerson* from Pondicherry and Malabar in India. Day (1878) also reported five species of seerfishes from the Indian Seas under the genus *Cybium*, viz., *C. kuhlii*, *C. interruptum*, *C. guttatum*, *C. commersonii*, and *C. lineolatum*. Jones and Silas (1961), in examining their taxonomy from India, refined all to three valid species, *S. guttatus*, *S. lineolatus*, and *S. commerson*. They synonymized Day's *C. kuhlii* and *C. guttatum* with *S. guttatus*, *C. interruptum* and *C. lineolatum* with *S. lineolatus*, and *C. commersonii* with *S. commerson*. Because the original description of *Scomber guttatus* in Bloch and Schneider (1801) is sparse, Silas (1964) redescribed *S. guttatus*. He considered "Wingeram" defined by Russell (1803), later described as *Scomber leopardus* by Shaw (1803), identical to *S. guttatus*. Considering the main characters, he also considered *Cybium koreanum* Kishinouye, 1915 as a subspecies of *S. guttatus* and divided the latter into two subspecies, viz., *S. guttatus guttatus* (Bloch and Schneider, 1801) and *S. guttatus koreanus* (Kishinouye, 1915). However, Devaraj (1976) proved that *S. koreanus* is distinct from *S. guttatus* and not a subspecies of the latter, unlike Silas (1964).

Resurrection of Cryptic Species Based on Genetic Evidence

Scomberomorus aff. *guttatus* in the cryptic complex with two MOTUs showed a p-distance of 10.26%–10.4% with *S. guttatus*. There exists a divergence of more than 2% between the two MOTUs, which is widely accepted as the heuristic limit for species delineation using COI barcodes (Pereira et al., 2013). Although geographical populations of conspecifics can exhibit genetic distances in excess of 2% (Ward et al., 2005), the likelihood that these MOTUs represent two potentially cryptic species of recent origin cannot be ignored. Albeit, their divergence is not reflected in the *aldolase exon 5/intron 5* regions, although the distance estimates of this nuclear gene are high among closely related taxa in the *S. regalis* complex that have been dated to a recent origin (Banford et al., 1999). This is due to insufficient time for the accumulation of mutations in nuclear markers (Allio et al., 2017). Microsatellite-based analysis of *S. guttatus* revealed a unit stock from the Persian Gulf (Abedi et al., 2011), and mtDNA sequences in GenBank from this region were identical to *S.* aff. *guttatus* 2.

Scomberomorus guttatus is characterized by the fine auxiliary branches radiating on either side of the anterior third of the lateral line, intestine with 2 folds and 3 limbs, and 47–52 vertebrae (Collette and Nauen, 1983). The first two features are common to *S. guttatus* and the cryptic species identified in this study, while differing in their morphometry and modes of vertebral counts. The occurrence of doppelganger in the *S. guttatus* species complex which is too cryptic to be identified by external morphology and its geographic populations also add to the difference in vertebral numbers noted by previous researchers. However, it can be observed that typical S. guttatus has a lesser body depth compared to the above. Their cryptic nature can be attributed to their morphological convergence in response to analogous selective regimes (Ingram and Mahler, 2013) which are discussed subsequently.

FIGURE 8 | Images of **(A)** *Scomberomorus guttatus*, collected from Tranquebar, India; **(B, C)** *Scomberomorus leopardus* (= *S.* aff. *guttatus* 1 and *S.* aff. *guttatus* 2, respectively) resurrected in this study. FL indicates fork length of the specimen.

Hence, based on the genetic results of specimens from type locality, vertebral counts of 47–49 (usually 48), and examination of lectotype (ZMB 8759; **Figure 7**), the identity of *S. guttatus* (Bloch and Schneider, 1801) is confirmed (**Figure 8A**) and its morphological redescription is strongly recommended.

It may be added that Shaw (1803) described *Scomber leopardus*, which was later synonymized with *S. guttatus* (Bloch and Schneider, 1801), based on the image and the original description of "Scomber Wingeram" provided by Russell (1803) from Visakhapatnam on the coast of Coromandel. Our study showed the occurrence of both species on the Coromandel coast, but since the type locality contains only *S. guttatus* which is less abundant in Visakhapatnam, the available senior synonym *Scomber leopardus* Shaw, 1803 (= *Scomberomorus leopardus*) merits the distinction to be accepted for the cryptic species. Based on the barcode criterion of mtDNA clustering and critical examination of Russell's drawing (33.2 cm long), we here resurrect *Scomberomorus leopardus* (Shaw, 1803) (**Figures 8B, C**; **Supplementary Figure 7**) from the synonymy of *S. guttatus* as a valid species, which needs to be redescribed. The vertebral counts of this species have a mode of 50 for the Indian Ocean lineage, while it is reported to be 51 for the Western Pacific lineage.

It can be added that some junior synonyms, viz., *Cybium interruptum* and *C. kuhlii*, are also available in the literature (synonymized with *S. guttatus*) originally described by Cuvier and Valenciennes (1831) from Pondicherry and Bombay, respectively. Although *C. interruptum* was successively included in the same manuscript by Cuvier and Valenciennes (1831), we believe that *C. interruptum* cannot be applied to *S.* aff. *guttatus* 1 due to the availability of a senior synonym, *Scomber leopardus* Shaw, 1803 from the same geographic region. If the Arabian Sea counterpart of *S. leopardus* (i.e., *S.* aff. *guttatus* 2; **Figure 8C**) and the counterpart from the Bay of Bengal and Western Pacific (*S.* aff. *guttatus* 1; **Figure 8B**) turn out to be distinct on further analysis, the senior name *Cybium kuhlii* [= *Scomberomorus kuhlii* (Cuvier in Cuvier and Valenciennes, 1831)] will be applicable to the former. *S. leopardus* can be retained for the latter since its genesis lies in the Bay of Bengal region. In general, naming/reviving a species generally requires multiple lines of evidence along with the "Generalized Lineage Species Concept" (Coates et al., 2018), and therefore, a detailed study on the apparent phenotypic differentiation in the cryptic species and the redescription of *S. guttatus* are in progress.

Similarly, for the Indian Ocean complement of *S. commerson* (i.e., *S.* cf. *commerson* 2) which has been shown to be distinct on the basis of detailed molecular analysis, the name *Scomber maculosus* Shaw, 1803 (= *Scomberomorus maculosus*) described by Shaw (1803), based on the Konam of Russell (1803), will probably be applicable. However, in the absence of a type specimen of *S. commerson*, originally described as *Scomber commerson* after a figure from Commerson's manuscripts, and the absence of any indication of type locality in the original description, the identity of the species can only be established by designation of a type based on the Rules of the International Code of Zoological Nomenclature.

Ecological Adaptations in the *Scomberomorus guttatus* Species Group

The *S. guttatus* species group contains *S. guttatus*, *S. koreanus*, and *S. multiradiatus* (Collette and Russo, 1984). The first two are available in the northern Indian Ocean. *Scomberomorus guttatus*, a neritic species thought to be less migratory than *S. commerson*, inhabits the coastal waters at depths between 15 and 200 m and is generally encountered in turbid waters with lower salinity (Fischer and Whitehead, 1974; Collette, 2001) which corroborate with the collection data from this study (**Table 2**). The habitat of *S. guttatus* is captured from river mouths and estuaries in Indonesia (Hardenberg, 1936), West Bengal in India (Hora, 1953; Dutta et al., 2021), etc., indicating their tendency to ascend estuaries of large rivers. Similarly, *S. koreanus* exhibited a remarkable ability to ascend brackish parts of rivers (Kishinouye, 1923). Species range boundaries indicate a species' ecological niche in space (Sexton et al., 2009), and species morphology is partially related to its ecological niche (Schluter, 2000).

Habitat use, diet, and environmental tolerance are usually measured niche subsets (Slatyer et al., 2013). Selection on habitat preferences can be a strong reproductive barrier that promotes divergence with gene flow (Berner and Thibert-Plante, 2015). The niche breadth and size of the geographical range of *S. guttatus* is of lesser magnitude in India limited to the east coast, with more aggregations in Tamil Nadu and West Bengal and also in Bangladesh, while the niche expanse is wider for *S. leopardus*. The range of all *Scomberomorus* spp. in India is shown in **Figure 6**. The west coast of India is a coast of submergence (except for the Malabar Coast; **Figure 1**) with a steep slope and narrow width with only a few west-flowing rivers, forming estuaries while draining into the Arabian Sea. In contrast, the east coast is an emergent coast (Swathi Lekshmi, 2020) with the Bay of Bengal receiving discharge from many east-flowing rivers, fostering larger estuaries and major deltas. The estuaries on the west coast lie mainly between Gujarat and Karnataka, while the extensive east coast estuarine system is in the stretch from West Bengal to Tamil Nadu (Faruque and Ramachandran, 2014a; Faruque et al., 2014b) (**Figure 6**). The intensity of the seasonal monsoons and the precipitation patterns show a great difference in the Indian subcontinent, and the latter along with other factors creates fluctuations in salinity by freshwater runoff and determines the hydrography of the aforementioned monsoonal estuaries. Tamil Nadu receives more annual precipitation during the winter monsoon (October to November) than most other parts of the country which get it during the southwest monsoon (June–September) (Venkataramana et al., 2021). The Ganges/Brahmaputra and Irrawaddy/Salween River systems transport huge amounts of water and sediment to the northeastern Indian Ocean during and after the rainy season (June to August), resulting in the formation of freshwater pools and seasonal salinity differences (Jöhnck et al., 2020). Deltas and estuarine systems formed by the river Ganges in the northern part of the Bay of Bengal (Gangetic delta in Bangladesh) and the Southern Bay of Bengal (Hoogly-Matlah estuary forming the Sunderbans delta in India) form a highly productive marine ecosystem (Mukhopadhyay et al., 2006) that maintains a salinity gradient due to seasonal freshwater discharge and regular tidal influxes. *Scomberomorus guttatus*, *S. leopardus*, and *S. koreanus* have a preference for coastal and estuarine habitats which results in their adherence to these areas.

As Jordan (1922) pointed out in one of his ecogeographical rules, the nearest relative of any given form often occurs in adjacent areas usually across some barrier to distribution. This holds true for the *S. guttatus* complex. This occurrence represents an early declaration of the concept of allopatric speciation or perhaps vicariance (McDowall, 2008). The peninsular region of India can act as an apparent geographical barrier due to its steep slope and non-availability of suitable habitats for larval settlement. Besides, *Scomberomorus* spp. have pelagic eggs and larvae (Vijayaraghavan, 1955; Jones, 1961; Collette, 1986; da Cunha et al., 2020). Although information on larval dispersal with monsoon currents is sparse for the *S. guttatus* complex, the range overlap between the MOTUs of the lineages in *S.* aff. *guttatus* (= *S. leopardus*) near Mangaluru (southern Karnataka) indicates that the larvae entering the currents and circulations in the southern peninsula of the Indian subcontinent (Rao and Sreenivas, 2020) settle only in their most appropriate niches.

Recruitment and population dynamics of fish are mainly driven by their feeding ecology and dietary plasticity (Sui et al., 2021). Vijayaraghavan (1955) suggested that the dietary component of *S. guttatus* changes with habitat and season. The gut content analysis of *S. guttatus* from the north-eastern Arabian Sea showed that their major food is *Acetes* sp. followed by clupeids (Chellappan et al., 2018). This area is rich in extremely euryhaline *Acetes* spp., which provide food for many predators (Deshmukh, 2007; Metillo et al., 2015). This contradicts the feeding pattern observed on the south and south-east coasts of India, where the prey is S*ardinella* spp. and whitebaits (Devaraj, 1998). Piscine prey abundance is expected to affect larval survival and recruitment of *Scomberomorus*, as illustrated by the larval survival strategy with an early switching of diet from planktivory to piscivory, which reduces the duration of the larval stage (Shoji et al., 2005). Chale-Matsau (1996) posited that the abundance of *S. plurilineatus* on the KwaZulu-Natal coastline was related to the appearance of the inshore marine prey species *Sardinops sagax* along the coast rather than to spawning. It can be observed that the highly productive areas along the Indian coast where *S. guttatus* spp. inhabit provide crustacean and piscine preys that can aid in their larval recruitment.

The spawning season observed for *S. guttatus* on the south-east coast of India is April to July with a spawning peak in July (Krishnamoorthi, 1958), while Devaraj et al. (1987) suggested an extended spawning season from January to August with a peak from April to May. Collette and Nauen (1983) indicated it from April to July around Rameswaram Island between India and Sri Lanka. On the east coast of India (Andhra Pradesh), the peak spawning period is between November and April (Uma Mahesh et al., 2017), while on the west coast along the northern Arabian Sea, it is May (Chellappan et al., 2018). Season is longer with a peak in January to August in Indonesian waters (Noegroho et al., 2018), but the peak recruitment is from May to July in Bangladesh (Rashid et al., 2010). The difference in spawning times in *S. guttatus* can be due to differences in biotic and abiotic parameters in the area (Roa-Ureta et al., 2019) coupled with life-history traits of the nominal *S. guttatus* which is now revealed to contain cryptic species.

Fidelity to spawning sites (probably upwelling areas) rather than adaptations to oceanographic regimes has been postulated as one of the reasons for the incidence of genetically discrete groups in *S. sierra* (López et al., 2010). In the current context of limited information on spawning grounds along the coastline, except for the reports by Devaraj (1987) and Jones (1961), which were limited to the south-east and south-west coasts of India respectively, the above postulate cannot be verified. Recent studies evidence that marine species with pelagic larval stages are subjected to high levels of local recruitment, which can lead to reduced gene flow, niche specialization through local adaptation, and sexual selection, leading to divergence and speciation (Milá et al., 2017). Fišer et al. (2018) pointed out that cryptic species show differences in their requirements along their Grinnellian niche. Speciation is a protracted process and a continuum of reproductive isolation (Stankowski and Ravinet, 2021), which are effects from the chance fixation of diverse, epistatic incompatibilities in discrete populations subjected to identical selective pressures (Rosser et al., 2019). Though many factors point to the probability that the distribution pattern of *S. guttatus* species complex in India is more connected with ecological niche and feeding regime, further studies are recommended to establish the relevant eco–evo interactions (Lowe et al., 2017).

CONCLUSION

The congeneric species in *Scomberomorus* from the northern Indian Ocean have not yet been subjected to molecular taxonomic studies. Our study aimed to generate multilocus data comparable to previous studies for phylogenetic reconstruction, species delimitation, resurrection of a dated phylogeny, and validation of the hypothesis of geographic races in *S. guttatus*. We have collected all the nominal species available along the Indian coast, and our analysis showed that the nominal *S. guttatus* contains a highly cryptic species. The latter contains two geographically separated lineages distributed mainly on the east and west coasts. Based on genetic detection of specimens from the type locality and subsequent confirmatory analyses, *S. guttatus* (Bloch and Schneider, 1801) is redeemed and the cryptic species *S. leopardus* (Shaw, 1803) is resurrected. The two geographical races of *S. leopardus* that cross the cutoff of species delimitation may also represent two cryptic species for which further morphomeristic studies are recommended. The Indo-Pacific king mackerel, *S. guttatus*, thought to have a panoceanic distribution between the Persian Gulf and the Sea of Japan, is now restricted to the Bay of Bengal, while the cryptic species enjoys a wider distribution. This information on species composition is highly significant for management as its fishery is "collapsed" in certain regions (Ju et al., 2020). Reliable molecular data were generated here and included in the global database for the underrepresented species such as *S. lineolatus* and *S. koreanus*. The phylogenetic position of

Indian counterparts has been ascertained and their divergence time was estimated. The geographical distribution of available species and doppelgangers was discussed in terms of their habitat preference, diet, and biological information. Our study demonstrated the necessity for global data from all species in order to arrive at a thorough conclusion about the systematics of this genus to verify its concordance with morphological groupings in the previous literature. Recognition of species in catch is essential to avoid overexploitation and to assess the potential impact of fisheries on fish populations, particularly for species with a restricted geographical range (akin to many members of *Scomberomorus*) that are more vulnerable to climate change (Dineshbabu et al., 2020). It is extremely important to conduct niche breadth and range size studies with a wide sampling to predict their vulnerability to altering climatic conditions.

DATA AVAILABILITY STATEMENT

All gene sequences generated in this study are deposited with the NCBI under accession numbers MZ955278-MZ955299, MZ955300-MZ955315, MZ955327-MZ955334, MZ955335-MZ955342, MZ955343-MZ955361, MZ962383-MZ962389, OL362234-OL362241, OM363524-OM363528, OM363529-OM363541, OM363542-OM363555, OM363556-OM363578, OM363579-OM363600, OM363601-OM363617, OM417804- OM417807, OM417808-OM417811, OM436012-OM436014, OK086368, ON193432, ON166824, OK137200-OK137203, OK137205, OK137206-OK137207, OK041506-OK041511, MZ927323-MZ927330, OM348536, MZ922475, MZ922477-MZ922478, MZ923800-MZ923804, MZ923799, MZ927331-MZ927338, MZ854022-MZ854034, MZ914677-MZ914678, ON150870, MZ854035- MZ854038, ON128513, MZ854039- MZ854053, MZ914449-MZ914459, MZ914681, ON127539-ON127549, ON129805-ON129822, ON204167-ON204170, MZ871761-MZ871765, MZ872464-MZ872504, ON207807-ON207814, OM343183, MZ927112, OM416532-OM416538, and are accessible at https://www.ncbi.nlm.nih.gov/nuccore.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this work does not contain any experimental studies with live animals. Fish samples caught in various gears were collected from the fishing harbors/landing centers and used for the genetic and morphological/anatomical investigations.

AUTHOR CONTRIBUTIONS

NJ conceptualized the work, analyzed the data, and wrote the manuscript. SR carried out the lab work, submitted and analyzed the molecular data, and assisted in draft preparation. SKR incorporated the taxonomic information, reviewed the manuscript, and provided all samples from the north-east coast of India. PA provided samples from the north-west coast and prepared the GIS-based maps. Specimens were given by RV and AM from the south-east coast, HM from Visakhapatnam, SS and EA from Kerala, and EN from Andaman. PR provided samples from Mangalore and gave extensive support to this work. AG coordinated the work. All authors contributed to the article and approved the submitted version.

ACKNOWLEDGMENTS

We would like to thank the Director of ICAR-CMFRI, Kerala, India, for providing facilities. We thank A. Anuraj, Joe Kizhakudan, Ajay D. Nakhawa, C. Anulekshmi, K. M. Rajesh and Y. Gladston for their participation in sampling additional materials. Pradeep from Cuddalore is thanked for assisting with the collections in the area. We also thank V. Mahesh for the sample and image provided. Our thanks go to Edda Aßel, Collection Manager, Ichthyology, and Dr. Peter Bartsch, Sc. Head of Ichthyology Collection, Museum für Naturkunde, Berlin who provided photographs, CT-image and information on the lectotype. Special thanks to Geethu Gopinath for the help in molecular lab work. The authors acknowledge the partial funding they received from the in-house project of the Marine Biotechnology Division, CMFRI (MBT/GNM/25) to carry out part of the molecular work.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.888463/full#supplementary-material

REFERENCES

Abedi, E., Mohammadi, M., and Qasemi, A. (2011). Genetic Stock Structure of *Scomberomorus Guttatus* Using Microsatellite Markers in the Persian Gulf. *J. Oceanogr.* 2 (6), 15–21. doi; 10.5829/idosi.aejaes.2012.12.10.656

Abedi, E., Zolgharnein, H., Salari, M. A., and Qasemi, A. (2012). Genetic Differentiation of Narrow-Barred Spanish Mackerel (*Scomberomorus Commerson*) Stocks Using Microsatellite Markers in the Persian Gulf. *Am. Eurasian J. Agric. Environ. Sci.* 12 (10), 1305–1310. doi; 10.5829/idosi.aejaes.2012.12.10.656

Allcock, A. L., and Strugnell, J. M. (2012). Southern Ocean Diversity: New Paradigms From Molecular Ecology. *Trends Ecol. Evol.* 27, 520–528. doi: 10.1016/j.tree.2012.05.009

Allio, R., Donega, S., Galtier, N., and Nabholz, B. (2017). Large Variation in the Ratio of Mitochondrial to Nuclear Mutation Rate Across Animals: Implications for Genetic Diversity and the Use of Mitochondrial DNA as a Molecular Marker. *Mol. Boil. Evol.* 34 (11), 2762–2772. doi: 10.1093/molbev/msx197

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., and Lipman, D. J. (1990). Basic Local Alignment Search Tool. *J. Mol. Biol.* 215 (3), 403–410. doi: 10.1016/S0022-2836(05)80360-2

Banford, H. M., Bermingham, E., Collette, B. B., McCafferty, S. S., Stackebrandt, E., and Goodfellow, M. (1999). Phylogenetic Systematics of the *Scomberomorus Regalis* (Teleostei: Scombridae) Species Group: Molecules, Morphology and Biogeography of Spanish Mackerels. *Copeia*, (3), 596–613. doi: 10.2307/1447593

Beal, L. M., Vialard, J., Roxy, M. K., Li, J., Andres, M., Annamalai, H., et al. (2020). A Road Map to IndOOS-2: Better Observations of the Rapidly Warming Indian Ocean. *Bull. Am. Meteorol. Soc* 101 (11), E1891–E1913. doi: 10.1175/BAMS-D-19-0209.1

Berner, D., and Thibert-Plante, X. (2015). How Mechanisms of Habitat Preference Evolve and Promote Divergence With Gene Flow. *J. Evol. Biol.* 28 (9), 1641–1655. doi: 10.1111/jeb.12683

Betancur-R, R., Wiley, E. O., Arratia, G., Acero, A., Bailly, N., Miya, M., et al. (2017). Phylogenetic Classification of Bony Fishes. *BMC Evol. Biol.* 17, 162. doi: 10.1186/s12862-017-0958-3

Bialik, O. M., Frank, M., Betzler, C., Zammit, R., and Waldmann, N. D. (2019). Two-Step Closure of the Miocene Indian Ocean Gateway to the Mediterranean. *Sci. Rep.* 9, (1–10). doi: 10.1038/s41598-019-45308-7

Bloch, M. E., and Schneider, J. G. (1801). "M.E. Blochii, Systema Ichthyologiae Iconibus Cx Ilustratum," in *Post Obitum Auctoris Opus Inchoatum Absolvit, Correxit, Interpolavit*. Ed. J. G. Schneider (Berolini, Berlin: Saxo Berolini).

Bossuyt, F., and Milinkovitch, M. C. (2000). Convergent Adaptive Radiations in Madagascan and Asian Ranid Frogs Reveal Covariation Between Larval and Adult Traits. *Proc. Natl. Acad. Sci.* 97, 6585–6590. doi: 10.1073/pnas.97.12.6585

Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., et al. (2019). Beast 2.5: An Advanced Software Platform for Bayesian Evolutionary Analysis. *PloS Comput. Biol.* 15, e1006650. doi: 10.1371/journal.pcbi.1006650

Broderick, D., Ovenden, J. R., Buckworth, R. C., Newman, S. J., Lester, R. J. G., and Welch, D. J. (2011). Genetic Population Structure of Grey Mackerel *Scomberomorus Semifasciatus* in Northern Australia. *J. Fish Biol.* 79 (3), 633–661. doi: 10.1111/j.1095-8649.2011.03055.x

Chale-Matsau, J. R. (1996). *Age and Growth of the Queen Mackerel (Scomberomorus Plurilineatus) and Seventy-four (Polysteganus Undulosus) of KwaZulu Natal, South Africa. Dissertation* (University of Natal, Durban, South Africa).

Chellappan, A., Sarang, J. D., Kamble, S. D., Akhilesh, K. V., Deshmukh, V. D., and Singh, V. V. (2018). Biological Aspects of Spotted Seerfish *Scomberomorus Guttatus* (Bloch and Schneide) (Scombridae) From North-Eastern Arabian Sea. *Indian J. Fish.* 65 (2), 42–49.

Chen, W. J., Bonillo, C., and Lecointre, G. (2003). Repeatability of Clades as a Criterion of Reliability: A Case Study for Molecular Phylogeny of Acanthomorpha (Teleostei) With Larger Number of Taxa. *Mol. Phylogenet. Evol.* 26 (2), 262–288. doi: 10.1016/S1055-7903(02)00371-8

Cheng, Y. Z., Xu, T. J., Jin, X. X., Tang, D., Wei, T., Sun, Y. Y., et al. (2012). Universal Primers for Amplification of the Complete Mitochondrial Control Region in Marine Fish Species. *Mol. Biol.* 46 (5), 727–730. doi: 10.1134/S0026893312040024

Clements, K. D., Gray, R. D., and Choat, J. H. (2003). Rapid Evolutionary Divergences in Reef Fishes of the Family Acanthuridae (Perciformes: Teleostei). *Mol. Phylogenet. Evol.* 26 (2), 190–201. doi: 10.1016/S1055-7903(02)00325-1

CMFRI, FRAD (2020). *Marine Fish Landings in India 2019* (Kochi: Technical Report. ICAR-Central Marine Fisheries Research Institute).

Coates, D. J., Byrne, M., and Moritz, C. (2018). Genetic Diversity and Conservation Units: Dealing With the Species-Population Continuum in the Age of Genomics. *Front. Ecol. Evol.* 6. doi: 10.3389/fevo.2018.00165

Collette, B. B. (1986). "Scombridae (Including Thunnidae, Scomberomoridae, Gasterochismatidae and Sardidae)," in *Fishes of the North-Eastern Atlantic and the Mediterranean, Volume 2*. Eds. P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielsen and E. Tortonese (Paris: UNESCO), 981– 997.

Collette, B. B. (1994). *Scomberomorus Lineolatus* is a Valid Species of Spanish Mackerel, Not an Interspecific Hybrid: A Reply. *J. Nat. Hist.* 28 (5), 1205–1208. doi: 10.1080/00222939400770601

Collette, B. B. (2001). "Scombridae. Tunas (Also, Albacore, Bonitos, Mackerels, Seerfishes, and Wahoo)," in *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Vol. 6. Bony Fishes Part 4 (Labridae to Latimeriidae), Estuarine Crocodiles*. Eds. K. E. Carpenter and V. Niem (Rome: FAO), 3721–3756.

Collette, B. B. (2003). *Family Scombridae Rafinesque 1815-Mackerels, Tunas, and Bonitos, Annotated Checklists of Fishes, 19* (San Francisco, California: California Academy Sciences), 28.

Collette, B. B., and Nauen, C. E. (1983). Scombrids of the World: An Annotated and Illustrated Catalogue of Tunas, Mackerels, Bonitos, and Related Species Known to Date. V. 2. *FAO Fish. Synop.* 125, vii137.

Collette, B. B., and Russo, J. L. (1984). Morphology, Systematics, and Biology of the Spanish Mackerels (*Scomberomorus*, Scombridae). *Fish. Bull.* 82 (4), 545–692.

Crandall, E. D., Riginos, C., Bird, C. E., Liggins, L., Treml, E., Beger, M., et al. (2019). The Molecular Biogeography of the Indo-Pacific: Testing Hypotheses With Multispecies Genetic Patterns. *Glob. Eco. Biogeogr.* 28 (7), 943–960. doi: 10.1111/geb.12905

Crête-Lafrenière, A., Weir, L. K., and Bernatchez, L. (2012). Framing the Salmonidae Family Phylogenetic Portrait: A More Complete Picture From Increased Taxon Sampling. *PloS One* 7 (10), e46662. doi: 10.1371/journal.pone.0046662

Cuvier, G. (1829). *Le Règne Animal, Distribué D'après Son Organisation, Pour Servir De Base À L'histoire Naturelle Des Animaux Et D'introduction À L'anatomie Comparée*, Vol. 2. v .2. Chez Déterville, Paris, i–xv 1–406 .

Cuvier, G., and Valenciennes, A. (1831). *HistoireNaturelle Des Poissons. Tome Huitième. Livre Neuvième. Des Scombéroïdes*, Vol. v. 8. Levrault, Paris i–xix 5 pp. 1–509Pls. 209–245.

da Cunha, D. B., Rodrigues-Filho, L. F. S., de Luna Sales, J. B., Rêgo, P., Queiroz, C., Sampaio, I., et al. (2020). Molecular Inferences on *Scomberomorus Brasiliensis*, From the Western South Atlantic, Based on Two Mitochondrial Genes. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.558902

Day, F. (1878). *The Fishes of India; Being a Natural History of the Fishes Known to Inhabit the Seas and Fresh Waters of India, Burma, and Ceylon*. Bernard Quaritch, London i–xx553–779 139–195.

Deshmukh, V. D. (2007). Predators of Non-Penaeid Prawns of Mumbai Coast. *J. Bombay Nat. Hist. Soc* 104 (3), 266–274.

Devaraj, M. (1976). Discovery of the Scombrid *Scomberomorus Koreanus* (Kishinouye) in India, With Taxonomic Discussion on the Species. *Jpn. J. Ichthyol.* 23 (2), 79–87.

Devaraj, M. (1987). Maturity, Spawning and Fecundity of the Spotted Seer, *Scomberomorus Guttatus*, in the Gulf of Mannar and Palk Bay. *Indian J. Fish.* 34, 48–77.

Devaraj, M. (1998). Food and Feeding Habits of the Spotted Seer, *Scomberomorus Guttatus* (Bloch and Schneider), in the Gulf of Mannar and Palk Bay. *Mar. Biol. Assoc. India.* 40, 105–124.

Devaraj, M., and Mohamad Kasim, H. (1998). Seerfish Fishery of the World. *Mar. Biol. Assoc. India.* 40, 51–68.

Dineshbabu, A. P., Zacharia, P. U., Sujitha, T., Shoba, J. K., Rajesh, K. M., Vivekanandan, E., et al. (2020). Assessment of Stock Vulnerability of Indian Marine Fishes to Past Changes in Climate and Options for Adaptation. *Clim. Res.* 79 (3), 175–192. doi: 10.3354/cr01586

Divya, P. R., Vineesh, N., Kathirvelpandian, A., Basheer, V. S., and Gopalakrishnan, A. (2018). Population Structure of Spanish Mackerel *Scomberomorus Commerson* (Lacepede 1800) in the Northern Indian Ocean Determined Using Microatellite Markers. *Aquat. Living Resour.* 31 (22), 1–10. doi: 10.1051/alr/2018011

Dutta, S., Orlov, A., and Hazra, S. (2021). Population Biology and Exploitation Status of Four Commercially Important Marine Fishes of the Northern Bay of Bengal, India. *Iran J. Fish. Sci.* 20 (1), 62–83.

Faruque, B. M., and Ramachandran, K. V. (2014a). "The Continental Shelf of Western India," in *Continental Shelves of the World: Their Evolution During the Last Glacio-Eustatic Cycle*, vol. 41 . Eds. F. L. Chiocci and A. R. Chivas (London, Memoirs: Geological Society), 213–220.

Faruque, B. M., Vaz, G. G., and Mohapatra, G. P. (2014b). "The Continental Shelf of Eastern India," in *Continental Shelves of the World: Their Evolution During the Last Glacio-Eustatic Cycle*, vol. 41 . Eds. F. L. Chiocci and A. R. Chivas (London, Memoirs: Geological Society), 221–229.

Fauvelot, C., and Borsa, P. (2011). Patterns of Genetic Isolation in a Widely Distributed Pelagic Fish, the Narrow-Barred Spanish Mackerel (*Scomberomorus Commerson*). *Biol. J. Linn. Soc* 104 (4), 886–902. doi: 10.1111/j.1095-8312.2011.01754.x

Fischer, W., and Whitehead, P. J. P. (1974). "Eastern Indian Ocean Fishing Area 57 and Western Central Pacific Fishing Area 71," in *FAO Species Identification Sheets for Fishery Purposes*, vol. IV, (Rome: Food and Agriculture Organization of the United Nations). pp 196.

Fišer, C., Robinson, C. T., and Malard, F. (2018). Cryptic Species as a Window Into the Paradigm Shift of the Species Concept. *Mol. Ecol.* 27 (3), 613–635. doi: 10.1111/mec.14486

Fitch, E. J., and Flesching, A. O. (1949). A Brief Account of the Monterey Spanish Mackerel (*Scomberomorus Concolor*). *California Fish Game.* 35, 275–280.

Froese, R., and Pauly, D. (Eds.) (2022). Fish Base World Wide Web Electronic Publication. Available at: http://www.fishbase.org

Fricke, R., Eschmeyer, W. N., and van der Laan, R. (2021) *Eschmeyer's Catalog of Fishes: Genera, Species, References*. Available at: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (Accessed 28 April 2021).

Fujisawa, T., and Barraclough, T. G. (2013). Delimiting Species Using Single-Locus Data and the Generalized Mixed Yule Coalescent Approach: A Revised Method and Evaluation on Simulated Data Sets. *Syst. Biol.* 62, 707–724. doi: 10.1093/sysbio/syt033

Garner, B. A., Hoban, S., and Luikart, G. (2020). Iucn Red List and the Value of Integrating Genetics. *Conserv. Genet.* 21 (5), 795–801. doi: 10.1007/s10592-020-01301-6

Ge, Y., Xia, C., Wang, J., Zhang, X., Ma, X., and Zhou, Q. (2021). The Efficacy of DNA Barcoding in the Classification, Genetic Differentiation, and Biodiversity Assessment of Benthic Macroinvertebrates. *Ecol. Evol.* 11 (10), 5669–5681. doi: 10.1002/ece3.7470

Habib, A., and Sulaiman, Z. (2016). High Genetic Connectivity of Narrow-Barred Spanish Mackerel (*Scomberomorus Commerson*) From the South China, Bali and Java Seas. *Zool. Ecol.* 26 (2), 93–99. doi: 10.1080/21658005.2016.1161121

Halasan, L. C., Geraldino, P. J. L., and Lin, H. C. (2021). First Evidence of Cryptic Species Diversity and Population Structuring of *Selaroides Leptolepis* in the Tropical Western Pacific. *Front. Mar. Sci* 8, 756163. doi: 10.3389/fmars.2021.756163

Hall, T. A. (1999). BioEdit: A User-Friendly Biological Sequence Alignment Editor and Analysis Program for Windows 95/98/Nt. *Nucleic Acids Symposium Ser.* 41, 95–98.

Hardenberg, J. D. F. (1936). On a Collection of Fishes From the Estuary and the Lower and Middle Course of the River Kapuas (W. Borneo). *Treubia Buitzenzorg* 15, 225–254.

Hashemi, S. A. R., and Doustdar, M. (2022). Fishery Status of Narrow-Barred Spanish Mackerel (*Scomberomorus Commerson*, Lacepede 1800) in the Northern Waters of the Oman Sea, Iran. *Iran. J. Ichthyol.* 8 (4), 311–321. doi: 10.22034/iji.v8i4.669

Heath, T. A., Hedtke, S. M., and Hillis, D. M. (2008). Taxon Sampling and the Accuracy of Phylogenetic Analyses. *J. System. Evol.* 46 (3), 239–257. doi: 10.3724/SP.J.1002.2008.08016

Hofmann, E. P., Nicholson, K. E., Luque-Montes, I. R., Köhler, G., Cerrato-Mendoza, C. A., Medina-Flores, M., et al. (2019). Cryptic Diversity, But to What Extent? Discordance Between Single-Locus Species Delimitation Methods Within Mainland Anoles (Squamata: Dactyloidae) of Northern Central America. *Front. Genet.*, 10, 11. doi: 10.3389/fgene.2019.00011

Hoolihan, J. P., Anandh, P., and van Herwerden, L. (2006). Mitochondrial DNA Analyses of Narrow-Barred Spanish Mackerel (*Scomberomorus Commerson*) Suggest a Single Genetic Stock in the ROPME Sea Area (Arabian Gulf, Gulf of Oman, and Arabian Sea). *ICES J. Mar. Sci.* 63, 1066–1074. doi: 10.1016/j.icesjms.2006.03.012

Hora, S. L. (1953). Rising Salinity of the Hooghly River-Fishes Provide Evidences. *Indian J. Pwr. Riv. Vall. Dev.* 3 (6), 12–15.

Hubbs, C. L. (1922). Variations in the Number of Vertebrae and Other Meristic Characters of Fishes Correlated With the Temperature of Water During Development. *Am. Nat.* 56, 360–372. doi: 10.1086/279875

Ingram, T., and Mahler, D. L. (2013). SURFACE: Detecting Convergent Evolution From Comparative Data by Fitting Ornstein-Uhlenbeck Models With Stepwise Akaike Information Criterion. *Methods Ecol. Evol.* 4 (5), 416–425. doi: 10.1111/2041-210X.12034

James, P. S. B. R. (2008). Osteo-Taxonomic Distinction of Fishes of the Family Leiognathidae. *Indian J. Fish.* 55 (4), 305–310.

Jöhnck, J., Kuhnt, W., Holbourn, A., and Andersen, N. (2020). Variability of the Indian Monsoon in the Andaman Sea Across the Miocene-Pliocene Transition. *Paleoceanogr. Paleoclimatol.* 35 (9), e2020PA003923. doi: 10.1029/2020PA003923

Johnson, M. G., Mgaya, Y. D., and Shaghude, Y. W. (2021). Analysis of the Genetic Stock Structure and Phylogenetic Relationship of Narrow-Barred Spanish Mackerel *Scomberomorus Commerson* (Lacépède 1800) Along the Northern Tanzanian Coastal Waters Using Mitochondrial DNA. *Reg. Stud. Mar. Sci.* 101862. doi: 10.1016/j.rsma.2021.101862

Jones, S. (1961). Notes on Eggs, Larvae and Juveniles of Fishes From Indian Waters VIII. *Scomberomorus Guttatus* (Bloch and Schneider), Ix. *Scomberomorus Commerson* (Lacepede) and X. *Scomberomorus Lineolatus* (Cuvier). *Indian J. Fish.* 8 (1), 107–120.

Jones, S., and Silas, E. G. (1961). On Fishes of the Subfamily Scomberomorinae (Family Scombridae) From Indian Waters. *Indian J. Fish.* 8 (1), 189–206.

Jordan, D. S. (1892). Relations of Temperature to Vertebrae Among Fishes. *Proc. U. S. Natl. Mus.* 1891, 107–120.

Jordan, D. S. (1922). *The Days of a Man: Being Memories of a Naturalist, Teacher and Minor Prophet of Democracy. Two Volumes* (Yonkers on Hudson, NY: World Book Company).

Juan-Jordá, M. J., Mosqueira, I., Freire, J., and Dulvy, N. K. (2013). The Conservation and Management of Tunas and Their Relatives: Setting Life History Research Priorities. *PloS One* 8 (8), e70405. doi: 10.1371/journal.pone.0070405

Ju, P., Tian, Y., Chen, M., Yang, S., Liu, Y., Xing, Q., et al. (2020). Evaluating Stock Status of 16 Commercial Fish Species in the Coastal and Offshore Waters of Taiwan Using the CMSY and BSM Methods. *Front. Mar. Sci.* 7, 618. doi: 10.3389/fmars.2020.00618

Kapli, P., Lutteropp, S., Zhang, J., Kobert, K., Pavlidis, P., Stamatakis, A., et al. (2017). Multi-Rate Poisson Tree Processes for Single-Locus Species Delimitation Under Maximum Likelihood and Markov Chain Monte Carlo. *Bioinf.* 33 (11), 1630–1638. doi: 10.1093/bioinformatics/btx025

Karatsolis, B.-T., Lougheed, B. C., De Vleeschouwer, D., and Henderiks, J. (2022). Abrupt Conclusion of the Late Miocene-early Pliocene Biogenic Bloom at 4.6-4.4 Ma. *Nat. Commun.* 13, 353. doi: 10.1038/s41467-021-27784-6

Kawaguchi, A., Miya, M., and Nishida, M. (2001). Complete Mitochondrial DNA Sequence of *Aulopus Japonicus* (Teleostei: Aulopiformes), a Basal Eurypterygii: Longer DNA Sequences and Higher-Level Relationships. *Ichthyol. Res.* 48, 213–223. doi: 10.1007/s10228-001-8139-0

Kaymaram, F., Hossainy, S. A., Darvishi, M., Talebzadeh, S. A., and Sadeghi, M. S. (2010). Reproduction and Spawning Patterns of the *Scomberomorus Commerson* in the Iranian Coastal Waters of the Persian Gulf and Oman Sea. *Iran. J. Fish. Sci.* 9 (2), 233–244.

Kishinouye, K. (1915). Contributions to the Study of Mackerels, Seerfishes, and Tunnies. *Proc. Sci. Fish. Assoc. (Suisan Gakkai Ho)* 1, 1–24.

Kishinouye, K. (1923). Contributions to the Comparative Study of the So-Called Scombroid Fishes. *J. Coll. Agricult Imperial Univ. Tokyo.* 8 (3), 293–476.

Krishnamoorthi, B. (1958). Observations on the Spawning Season and the Fisheries of the Spotted Seer, *Scomberomorus Guttatus* (Bloch and Schneider). *Indian J. Fish.* 5, 270–281.

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., and Calcott, B. (2017). PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Mol. Biol. Evol.* 34, 772–773. doi: 10.1093/molbev/msw260

Lee, S. C., and Yang, H. C. (1983). Fishes of the Suborder Scombroidei of Taiwan. *Bull. Inst. Zool. Acad. Sin.* 22 (2), 217–242.

Leigh, J. W., Bryant, D., and Nakagawa, S. (2015). Popart: Full-Feature Software for Haplotype Network Construction. *Methods Ecol. Evol.* 6, 1110–1116. doi: 10.1111/2041-210X.12410

Lessa, E., and Applebaum, G. (1993). Screening Techniques for Detecting Variation in DNA Sequences. *Mol. Ecol.* 2, 121–129. doi: 10.1111/j.1365-294X.1993.tb00006.x

Lewis, A. (1981). *Population Genetics, Ecology and Systematic of Indo-Australian Scombrid Fishes, With Particular Reference to Skipjack Tuna (Katsuwonus Pelamis). Ph.D. Thesis* (Canberra: Australian National University), 314.

López, M. D., Alcocer, M. U., and Jaimes, P. D. (2010). Phylogeography and Historical Demography of the Pacific Sierra Mackerel (*Scomberomorus Sierra*) in the Eastern Pacific. *BMC Genet.* 11 (1), 1–12. doi: 10.1186/1471-2156-11-34

Lowe, W. H., Kovach, R. P., and Allendorf, F. W. (2017). Population Genetics and Demography Unite Ecology and Evolution. *Trends Ecol. Evol.* 32 (2), 141–152. doi: 10.1016/j.tree.2016.12.002

Luo, A., Ling, C., Ho, S. Y., and Zhu, C. D. (2018). Comparison of Methods for Molecular Species Delimitation Across a Range of Speciation Scenarios. *Syst. Biol.* 67 (5), 830–846. doi: 10.1093/sysbio/syy011

Magallón-Gayón, E., Diaz-Jaimes, P., and Uribe-Alcocer, M. (2016). Spatial and Temporal Genetic Homogeneity of the Monterey Spanish Mackerel, *Scomberomorus Concolor*, in the Gulf of California. *PeerJ* 4, e2583. doi: 10.7717/peerj.2583

McDowall, R. M. (2008). Jordan's and Other Ecogeographical Rules, and the Vertebral Number in Fishes. *J. Biogeogr.* 35 (3), 501–508. doi: 10.1111/j.1365-2699.2007.01823.x

Metillo, E. B., Cadelinia, E. E., Hayashizaki, K. I., Tsunoda, T., and Nishida, S. (2015). Feeding Ecology of Two Sympatric Species of *Acetes* (Decapoda: Sergestidae) in Panguil Bay, the Philippines. *Mar. Freshwater Res.* 67 (10), 1420–1433. doi: 10.1071/MF15001

Milá, B., Van Tassell, J. L., Calderón, J. A., Rüber, L., and Zardoya, R. (2017). Cryptic Lineage Divergence in Marine Environments: Genetic Differentiation at Multiple Spatial and Temporal Scales in the Widespread Intertidal Goby *Gobiosoma Bosc*. *Ecol. Evol.* 7 (14), 5514–5523. doi: 10.1002/ece3.3161

Miller, E. C., Hayashi, K. T., Song, D., and Wiens, J. J. (2018). Explaining the Ocean's Richest Biodiversity Hotspot and Global Patterns of Fish Diversity. *Proc. R. Soc* 285 (1888), 20181314. doi: 10.1098/rspb.2018.1314

Miya, M., Friedman, M., Satoh, T. P., Takeshima, H., Sado, T., Iwasaki, W., et al. (2013). Evolutionary Origin of the Scombridae (Tunas and Mackerels): Members of a Paleogene Adaptive Radiation With 14 Other Pelagic Fish Families. *PloS One* 8 (9), e73535. doi: 10.1371/journal.pone.0073535

Monolisha, S., Platt, T., Sathyendranath, S., Jayasankar, J., George, G., and Jackson, T. (2018). Optical Classification of the Coastal Waters of the Northern Indian Ocean. *Front. Mar. Sci.* 5. doi: 10.3389/fmars.2018.00087

Morgan, J. A., Macbeth, M., Broderick, D., Whatmore, P., Street, R., Welch, D. J., et al. (2013). Hybridisation, Paternal Leakage and Mitochondrial DNA Linearization in Three Anomalous Fish (Scombridae). *Mitochondrion.* 13 (6), 852–861. doi: 10.1016/j.mito.2013.06.002

Mukhopadhyay, S. K., Biswas, H. D. T. K., De, T. K., and Jana, T. K. (2006). Fluxes of Nutrients From the Tropical River Hooghly at the Land–Ocean Boundary of Sundarbans, Ne Coast of Bay of Bengal, India. *J. Mar. Syst.* 62 (1-2), 9–21. doi: 10.1016/j.jmarsys.2006.03.004

Nabhan, A. R., and Sarkar, I. N. (2012). The Impact of Taxon Sampling on Phylogenetic Inference: A Review of Two Decades of Controversy. *Brief. Bioinform.* 13 (1), 122–134. doi: 10.1093/bib/bbr014

Nguyen, L. T., Schmidt, H. A., Von Haeseler, A., and Minh, B. Q. (2015). Iq-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. *Mol. Biol. Evol.* 32 (1), 268–274. doi: 10.1093/molbev/msu300

Noegroho, T., Boer, M., and Adrianto, L. (2018). Size Structure and Population Dynamics of Indo-Pacific King Mackerel (*Scomberomorus Guttatus*) in Kepulauan Riau's Water, Indonesia. *Aquacult Aquarium Conserv. Legislation.* 11 (4), 1081–1088.

Ollé, J., Vilà-Valls, L., Alvarado-Bremer, J., Cerdenares, G., Duong, T. Y., Hajjej, G., et al. (2022). Population Genetics Meets Phylogenetics: New Insights Into the Relationships Among Members of the Genus *Euthynnus* (Family Scombridae). *Hydrobiologia* 849 (1), 47–62. doi: 10.1007/s10750-021-04707-6

Orrell, T. M., Collette, B. B., and Johnson, G. D. (2006). Molecular Data Support Separate Scombroid and Xiphioid Clades. *Bull. Mar. Sci.* 79 (3), 505–519.

Paine, M. A., McDowell, J. R., and Graves, J. E. (2007). Specific Identification of Western Atlantic Ocean Scombrids Using Mitochondrial DNA Cytochrome C Oxidase Subunit I (COI) Gene Region Sequences. *Bull. Mar. Sci.* 80 (2), 353–367.

Palumbi, S. R. (1996). "Nucleic Acids II: The Polymerase Chain Reaction," in *Molecular Systematics*. Eds. D. M. Hillis, C. Mortiz and B. K. Mable (Sunderland, MA: Sinauer), 205–248.

Palumbi, S. R., Martin, A. P., Romano, S., Mcmilan, W. O., Stice, L., and Grabowski, G. (1991). *A Simple Fool's Guide to PCR* (Honolulu, HI: University of Hawaii Press).

Pentinsaari, M., Vos, R., and Mutanen, M. (2017). Algorithmic Single-Locus Species Delimitation: Effects of Sampling Effort, Variation and Nonmonophyly in Four Methods and 1870 Species of Beetles. *Mol. Ecol. Resour.* 17 (3), 393–404. doi: 10.1111/1755-0998.12557

Perdices, A., Bermingham, E., Montilla, A., and Doadrio, I. (2002). Evolutionary History of the Genus *Rhamdia* (Teleostei: Pimelodidae) in Central America. *Mol. Phylogenet. Evol.* 25, 172–189. doi: 10.1016/S1055-7903(02)00224-5

Pereira, L. H., Hanner, R., Foresti, F., and Oliveira, C. (2013). Can DNA Barcoding Accurately Discriminate Megadiverse Neotropical Freshwater Fish Fauna? *BMC Genet.* 14 (1), 1–14. doi: 10.1186/1471-2156-14-20

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., et al. (2006). Sequence-Based Species Delimitation for the DNA Taxonomy of Undescribed Insects. *Syst. Biol.* 55, 595–609. doi: 10.1080/10635150600852011

Puillandre, N., Lambert, A., Brouillet, S., and Achaz, G. J. M. E. (2012). ABGD, Automatic Barcode Gap Discovery for Primary Species Delimitation. *Mol. Ecol.* 21 (8), 1864–1877. doi: 10.1111/j.1365-294X.2011.05239.x

Puncher, G. N., Arrizabalaga, H., Alemany, F., Cariani, A., Oray, I. K., Karakulak, F. S., et al. (2015). Molecular Identification of Atlantic Bluefin Tuna (*Thunnus Thynnus*, Scombridae) Larvae and Development of a DNA Character-Based Identification Key for Mediterranean Scombrids. *PloS One* 10 (7), e0130407. doi: 10.1371/journal.pone.0130407

Purdy, R. W., Schneider, V. P., Applegate, S. P., McLellan, J. H., Meyer, R. L., and Slaughter, B. H. (2001). The Neogene Sharks, Rays, and Bony Fishes From Lee Creek Mine, Aurora, North Carolina. *Smithson. Contrib.* 90, 71–202.

Qvarnström, A., Ålund, M., McFarlane, S. E., and Sirkiä, P. M. (2016). Climate Adaptation and Speciation: Particular Focus on Reproductive Barriers in Ficedula Flycatchers. *Evol. Appl.* 9 (1), 119–134. doi: 10.1111/eva.12276

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., and Suchard, M. A. (2018). Posterior Summarisation in Bayesian Phylogenetics Using Tracer 1.7. *Syst. Biol.* 67 (5), 901–904. doi: 10.1093/sysbio/syy032

Rao, K. S. (1975). Biometric Comparison of the Spotted Seer, *Scomberomorus Guttatus* (Bloch and Schneider) From Five Localities Along the Indian Coast. *Matsya* 1, 63–78.

Rao, K. S., and Lakshmi, K. (1993). *Scomberomorus Lineolatus* (Cuvier), an Interspecific Natural Hybrid (*s. Commerson* (Lacépède)× *S. Guttatus* (Bloch and Schneider)) Off Visakhapatnam, India. *J. Nat. Hist.* 27 (2), 471–491. doi: 10.1080/00222939300770231

Rao, G. N., and Sreenivas, P. (2020). Anomalous Circulation Around the Southern Indian Peninsula Observed During Winter 2009; and the Generation Mechanisms. *Ind. J. Geo Mar. Sci.* 49 (03), 343–351.

Rashid, H., Mustafa, M. G., and Dewan, S. (2010). Population Dynamics and the Management of the Indo-Pacific King Mackerel *Scomberomorus Guttatus* From the Upper Bay of Bengal Off Bangladesh Coast. *Bangladesh Veterinarian.* 27 (2), 82–90. doi: 10.3329/bvet.v27i2.7558

R Core Team (2020). *R: A Language and Environment for Statistical Computing* R Foundation for Statistical Computing, (Vienna: R Foundation for Statistical Computing URL). Available at: https://www.R-project.org/.

Renema, W., Bellwood, D. R., Braga, J. C., Bromfield, K., Hall, R., Johnson, K. G., et al. (2008). Hopping Hotspots: Global Shifts in Marine Biodiversity. *Science* 321, 654–657. doi: 10.1126/science.1155674

Roa-Ureta, R. H., Lin, Y. J., Rabaoui, L., Al-Abdulkader, K., and Qurban, M. A. (2019). Life History Traits of the Narrow-Barred Spanish Mackerel (*Scomberemorus Commerson*) Across Jurisdictions of the Southeast Arabian Peninsula: Implications for Regional Management Policies. *Reg. Stud. Mar. Sci.* 31, 100797. doi: 10.1016/j.rsma.2019.100797

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., and Höhna, S. (2012). MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Syst. Biol.* 61, 539–542. doi: 10.1093/sysbio/sys029

Rosen, D. E. (1975). A Vicariance Model of Caribbean Biogeography. *Syst. Zool.* 24, 431–464. doi: 10.2307/2412905

Rosser, N., Freitas, A. V., Huertas, B., Joron, M., Lamas, G., Mérot, C., et al. (2019). Cryptic Speciation Associated With Geographic and Ecological Divergence in Two Amazonian Heliconius Butterflies. *Zool. J. Linn. Soc* 186 (1), 233–249. doi: 10.1093/zoolinnean/zly046

Roul, S. K., Jeena, N. S., Kumar, R., Vinothkumar, R., Rahangdale, S., Rahuman, S., et al. (2021). Postulating the Modality of Integrative Taxonomy in Describing the Cryptic Congener *Pampus Griseus* (Cuvier) and Systematics of the Genus Pampus (Perciformes: Stromateidae). *Front.Mar. Sci.* 8. doi: 10.3389/fmars.2021.778422

Russell, P. (1803). *Descriptions and Figures of Two Hundred Fishes; Collected at Vizagapatam on the Coast of Coromandel* (London: W. Bulmer and Co). 2 vols. v. 1–2:i–vii 78 pp. 85 pp., 197pls.

Sambrook, J., Fritish, E. F., and Maniatis, T. (1989). *Molecular Cloning: A Laboratory Manual* (Cold Spring Harbor: Cold Spring Harbor Laboratory Press).

Santa Brígida, E. L., Cunha, D. B. D., Rego, P. S. D., Sampaio, I., Schneider, H., and Vallinoto, M. (2007). Population Analysis of *Scomberomorus Cavalla* (Cuvie) (Perciformes, Scombridae) From the Northern and Northeastern Coast of Brazil. *Braz. J. Biol.* 67 (4), 919–924. doi: 10.1590/S1519-69842007000500016

Santini, F., Carnevale, G., and Sorenson, L. (2013). First Molecular Scombrid Timetree (Percomorpha: Scombridae) Shows Recent Radiation of Tunas Following Invasion of Pelagic Habitat. *Ital. J. Zool.* 80 (2), 210–221. doi: 10.1080/11250003.2013.775366

Schluter, D. (2000). Ecological Character Displacement in Adaptive Radiation. *Am. Nat.* 156, S4–S16. doi: 10.1086/303412

Secretariat, IOTC (2015) *Assessment of Indian Ocean Indo-Pacific King Mackerel (Scomberomorus Guttatus) Using Data Poor Catch-Based Methods.* Available at: http://www.iotc.org.

Sepkoski, J. J.Jr (2002). A Compendium of Fossil Marine Animal Genera. *Bull. Am. Paleontol.* 363, 1–560.

Sexton, J. P., McIntyre, P. J., Angert, A. L., and Rice, K. J. (2009). Evolution and Ecology of Species Range Limits. *Annu. Rev. Ecol. Evol. Syst.* 40, 415–436. doi: 10.1146/annurev.ecolsys.110308.120317

Shaw, G. (1803). *General Zoology or Systematic Natural History Pisces* (London: G. Kearsley), 1800–1826. Pisces in vol. 4(1803) and vol. 5 (1804);(pt. 2), i–xi 187–632, Pls. 26–92.

Shoji, J., Masuda, R., Yamashita, Y., and Tanaka, M. (2005). Effect of Low Dissolved Oxygen Concentrations on Behavior and Predation Rates on Red Sea Bream *Pagrus Major* Larvae by the Jellyfish *Aurelia Aurita* and by Juvenile Spanish Mackerel *Scomberomorus Niphonius*. *Mar. Biol.* 147 (4), 863–868. doi: 10.1007/s00227-005-1579-8

Siddeek, M. S. M. (1995). Review of Fisheries Biology of Scomberomorus and Acanthocybium Species in the Western Indian Ocean (FAO Area 51). in *Proceedings. IPTP collective* volume no. 9, Colombo (Sri Lanka)

Silas, E. G. (1964). "Cybium Crockewitti Bleeker, (1850) and Cybium Koreanum Kishinouye, (1915) Considered Synonyms of Scomberomorus Guttatus (Bloch and Schneider) With a Rediscription and Annotated Bibliography of S. Guttatus," in *Proceedings of Symposium on Scombroid Fishes, Marine Biological Association of India, Mandapam Camp, Symposium Series 1*, 309–342.

Sivasundar, A., Bermingham, E., and Ortí, G. (2001). Population Structure and Biogeography of Migratory Freshwater Fishes (*Prochilodus*: Characiformes) in Major South American Rivers. *Mol. Ecol.* 10, 407–417. doi: 10.1046/j.1365-294x.2001.01194.x

Slatyer, R. A., Hirst, M., and Sexton, J. P. (2013). Niche Breadth Predicts Geographical Range Size: A General Ecological Pattern. *Ecol. Lett.* 16 (8), 1104–1114. doi: 10.1111/ele.12140

Som, A. (2015). Causes, Consequences and Solutions of Phylogenetic Incongruence. *Brief. Bioinform.* 16 (3), 536–548. doi: 10.1093/bib/bbu015

Stankowski, S., and Ravinet, M. (2021). Defining the Speciation Continuum. *Evol.* 75 (6), 1256–1273. doi: 10.1111/evo.14215

Streelman, J. T., and Karl, S. A. (1997). Reconstructing Labroid Evolution With Single-Copy Nuclear DNA. *Proc. R. Soc London B* 264, 1011–1020. doi: 10.1098/rspb.1997.0140

Sui, H., Xue, Y., Li, Y., Xu, B., Zhang, C., and Ren, Y. (2021). Feeding Ecology of Japanese Spanish Mackerel (*Scomberomorus Niphonius*) Along the Eastern Coastal Waters of China. *Acta Oceanol. Sin.* 40 (8), 98–107. doi: 10.1007/s13131-021-1796-0

Sukumaran, J., and Knowles, L. L. (2017). Multispecies Coalescent Delimits Structure, Not Species. *Proc. Natl. Acad. Sci.* 114 (7), 1607–1612. doi: 10.1073/pnas.1607921114

Sulaiman, Z. H., and Ovenden, J. R. (2010). Population Genetic Evidence for the East–West Division of the Narrow-Barred Spanish Mackerel (*Scomberomorus Commerson*, Perciformes: Teleostei) Along Wallace's Line. *Biodivers. Conserv.* 19, 563–574. doi: 10.1007/s10531-009-9699-y

Swathi Lekshmi, P. S. (2020). "Features of Indian Coastal Area in the Backdrop of Coastal Security," in *India's National Security: A Maritime Security Perspective*. Ed. R. Suresh, Vij Books India Private Limited, New Delhi,142–149.

Tamura, K., Stecher, G., and Kumar, S. (2021). Mega 11: Molecular Evolutionary Genetics Analysis Version 11. *Mol. Biol. Evol.* 38, (7), 3022–7 doi: 10.1093/molbev/msab120

Thangaraja, M., and Al-Aisry, A. (2001). "Studies on the Occurrence and Abundance of Fish Eggs and Larvae in the Waters of Sultanate of Oman," in *Proceedings of 1st International Conference on Fisheries, Aquaculture and Environment in NW Indian Ocean* (Muscat, Sultanate of Oman: Sultan Qaboos University), 13–36.

Thompson, J. D., Higgins, D. G., and Gibson, T. J. (1994). Clustal W: Improving the Sensitivity of Progressive Multiple Sequence Alignment Through Sequence Weighting, Position-Specific Gap Penalties and Weight Matrix Choice. *Nucleic Acids Res.* 22, 4673–4680. doi: 10.1093/nar/22.22.4673

Uma Mahesh, V., Ghosh, S., Sreeramulu, K., Rao, M. V., and Satish Kumar, M. (2017). Fishery, Biology and Stock Assessment of Spotted Seer, *Scomberomorus Guttatus* (Bloch and Schneider) Off Andhra Pradesh. *Mar. Biol. Assoc. India.* 59 (1), 67–72. doi: 10.6024/jmbai.2017.59.1.1934-10

Van Rossum, G., and Drake, F. L. (2009). Python 3 Reference Manual. *Scotts Valley*, CA: CreateSpace.

Van Velzen, R., Weitschek, E., Felici, G., and Bakker, F. T. (2012). DNA Barcoding of Recently Diverged Species: Relative Performance of Matching Methods. *PloS One* 7 (1), e30490. doi: 10.1371/journal.pone.0030490

Venkataramana, V., Sarma, V. V. S. S., Gawade, L., and Reddy, A. M. (2021). Magnitude of River Discharge Determines the Food Habit and Community Composition of Zooplankton in the Indian Estuaries During Monsoon. *Estuar. Coast. Shelf. Sci.* 262, 107601. doi: 10.1016/j.ecss.2021.107601

Vijayaraghavan, P. (1955). Life-History and Feeding Habits of the Spotted Seer *Scomberomorus Guttatus* (Block and Schneider). *Indian J. Fish.* 2 (2), 360–372.

Vineesh, N., Divya, P. R., Kathirvelpandian, A., Mohitha, C., Shanis, C. P. R., Basheer, V. S., et al. (2018). Four Evolutionarily Significant Units Among Narrow-Barred Spanish Mackerel (*Scomberomorus Commerson*) in the Indo-West Pacific Region. *Mar. Biodivers.* 48 (4), 2025–2032. doi: 10.1007/s12526-017-0714-3

Wafar, M., Venkataraman, K., Ingole, B., Ajmal Khan, S., and LokaBharathi, P. (2011). State of Knowledge of Coastal and Marine Biodiversity of Indian Ocean Countries. *PloS One* 6 (1), e14613. doi: 10.1371/journal.pone.0014613

Ward, R. D., Zemlak, T. S., Innes, B. H., Last, P. R., and Hebert, P. D. N. (2005). DNA Barcoding Australia's Fish Species. *Philos. Trans. R. Soc. B: Biol. Sci.* 360, 1847–1857. doi: 10.1046/10.1098%2Frstb.2005.1716

Welch, D. J., Newman, S. J., Buckworth, R. C., Ovenden, J. R., Broderick, D., Lester, R. J., et al. (2015). Integrating Different Approaches in the Definition of Biological Stocks: A Northern Australian Multi-Jurisdictional Fisheries Example Using Grey Mackerel, *Scomberomorus Semifasciatus*. *Mar. Policy* 55, 73–80. doi: 10.1016/j.marpol.2015.01.010

Wright, J. J., David, S. R., and Near, T. J. (2012). Gene Trees, Species Trees, and Morphology Converge on a Similar Phylogeny of Living Gars (Actinopterygii: Holostei: Lepisosteidae), an Ancient Clade of Ray-Finned Fishes. *Mol. Phylogenet. Evol.* 63 (3), 848–856. doi: 10.1016/j.ympev.2012.02.033

Xia, X. (2018). Dambe7: New and Improved Tools for Data Analysis in Molecular Biology and Evolution. *Mol. Biol. Evol.* 35 (6), 1550–1552. doi: 10.1093/molbev/msy073

Xiao, W. H., Zhang, Y. P., and Liu, H. Z. (2001). Molecular Systematics of Xenocyprinae (Teleostei: Cyprinidae): Taxonomy, Biogeography, and Coevolution of a Special Group Restricted in East Asia. *Mol. Phylogenet. Evol.* 18, 163–173. doi: 10.1006/mpev.2000.0879

Yang, Z. (2015). The BPP Program for Species Tree Estimation and Species Delimitation. *Curr. Zool.* 61 (5), 854–865. doi: 10.1093/czoolo/61.5.854

Yang, Z., and Rannala, B. (2010). Bayesian Species Delimitation Using Multilocus Sequence Data. *Proc. Natl. Acad. Sci. U. S. A.* 107 (20), 9264–9269. doi: 10.1073/pnas.0913022107

Zacharia, P. U., Dineshbabu, A. P., Thomas, S., Kizhakudan, S. J., Vivekanandan, E., Pillai, S. L., et al. (2016). *Relative Vulnerability Assessment of Indian Marine Fishes to Climate Change Using Impact and Adaptation Attributes* (Kochi, India: CMFRI Special Publication No.125, (CMFRI-NICRA Publication No. 5), Central Marine Fisheries Research Institute), pp. 192.

Zhang, J., Kapli, P., Pavlidis, P., and Stamatakis, A. (2013). A General Species Delimitation Method With Applications to Phylogenetic Placements. *Bioinformatics* 29 (22), 2869–2876. doi: 10.1093/bioinformatics/btt499

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.