



***Scomber indicus*, a new species of mackerel (Scombridae: Scombrini) from Eastern Arabian Sea**

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ABSTRACT

Scomber indicus, a new species of mackerel is described based on the specimens collected from the eastern Arabian Sea. The species is differentiated from its nearest congener *Scomber australasicus*, in having 29-32 gill rakers on lower limb of first gill arch, posteriormost part of hypohyal blunt, with presence of a pit between the hypohyal and the ceratohyal and also in having a posteriorly directed haemal spine which is deeply curved in the basal region. Genetic differentiation and divergence between the newly described species and the 4 valid species of the genus *Scomber* viz., *S. scombrus*, *S. japonicus*, *S. australasicus* and *S. colias* were compared using cytochrome c oxidase 1 and cytochrome b gene sequences. The new species was found closest to *S. colias* followed by *S. japonicus* with Kimura 2 parameter (K2P) values of 1.4 and 1.8% respectively. In the phylogenetic tree, sequences of *Scomber indicus* sp. nov. formed a distinct well separated clade with significant bootstrap values as compared to the sequences of *S. scombrus*, *S. japonicus*, *S. australasicus* and *S. colias* indicating their distinctiveness and separate species status.

Keywords: Arabian Sea, Indian chub mackerel, New species, *Scomber indicus*

Introduction

Scombridae (Perciformes) is one of the largest and most economically important fish family comprising the most advanced scombroid fishes viz., mackerels, tunas and bonitos with at least 54 species in 15 genera (Collette *et al.*, 2001; Eschmeyer and Fong, 2015). Taxonomy of the genus *Scomber* Linnaeus, 1758 is complicated with inconsistent genetic and morphological characters as well as poor species descriptions. Though 28 species were described, presently this genus contains only four recognised species viz., Atlantic mackerel *Scomber scombrus* Linnaeus, 1758 from the north Atlantic, Mediterranean and Black sea, chub mackerel *Scomber japonicus* Houttuyn, 1782 from Indian Ocean, Pacific Ocean and adjacent seas, Pacific mackerel *Scomber australasicus* Cuvier, 1832 from western Pacific and Indian Ocean and Atlantic chub mackerel *Scomber colias* Gmelin, 1789 from east and west coasts of Atlantic Ocean, overlapping with *S. australasicus* in the north-western Pacific (Collette and Nauen, 1983; Collette, 1999; Collette, 2003; Catanese *et al.*, 2010; Eschmeyer and Fong, 2015).

The genus *Scomber* in general has a monophyletic origin with *S. scombrus* being the earliest diverged extant species differing from the other three species in the loss of

swim bladder (Cheng *et al.*, 2011). The origin of *Scomber* species is proposed to be in the Atlantic with subsequent radiation into the Pacific and Indo-Pacific regions (Cheng *et al.*, 2011). However, the divergence between *S. scombrus* and the other three species happened much earlier than the divergence between the latter. Many studies have pointed out high morphological and genetic similarities between these three species indicating the possibility of gene flow and introgressive hybridisation after speciation (Scoles *et al.*, 1998; Catanese *et al.*, 2010; Cheng *et al.*, 2011).

S. australasicus and *S. japonicus* are only the known members of the genus in the Indian Ocean (Collette and Nauen, 1983; Baker and Collette, 1998). Baker and Collette (1998) clarified that the species known as *S. japonicus* from northern Indian Ocean is actually *S. australasicus*. Species under *Scomber* never formed a major constituent in the Indian fishery, which is comparatively large in terms of the number of vessels operated and area covered under fishing. Whilst, *Scomber* sp. had been reported as stray landings at Vizhinjam (as *S. australasicus*, Gopakumar *et al.*, 1993) and Karwar (as *S. japonicus*, Ganga and Gowda, 1999). Recently, in the year 2015, specimens of *Scomber* sp. identical to *S. australasicus* were recorded all along the coast of Arabian Sea from Veraval in Gujarat to Cape Comorin in Tamil Nadu

in substantial quantities in the commercial landings mainly from trawlers and gillnetters. On closer examination, several disparities in morphological traits were noticed. Subsequent investigations by comparing cytochrome c oxidase subunit 1 and cytochrome b gene sequences confirmed the distinctiveness of the new species.

Materials and methods

Specimens were collected from Kochi, Kerala during May to June 2015 (during pre and early south-west monsoon) from trawl and gillnets. Fortyseven specimens were used for morphological and meristic analyses. The collected specimens were all adults and comprised mainly of spent males and females. Morphometric measurements were taken using digital vernier calipers (Mitutoyo) to the nearest 0.1 mm as in Collette and Aadland (1996). Number of dorsal and anal fin spines, pattern of palatine teeth, gill rakers on the lower limb of first gill arch and anatomy of the hyoid arch were examined under a dissection microscope. Position of the first haemal spine, interneural bones under the first and second dorsal fins and vertebral counts were examined from X-ray radiographs.

DNA extraction and amplification of the cytochrome c oxidase 1 (CO1) and cytochrome b gene sequences

The standard phenol/chloroform extraction protocol as per Sambrook and Russel (2001) was followed for DNA extraction from tissue samples. A 650 bp region of the cytochrome c oxidase subunit 1 (CO1) and cytochrome b genes were amplified using the universal primers (Folmer *et al.*, 1994; Samonte *et al.*, 2000) in six and eight individuals respectively. PCR reaction mixture comprised 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 mM MgCl₂, 200 μM of each dNTPs, 0.2 μM of each oligonucleotide, 1 unit of Taq DNA polymerase and 50 ng of template DNA. The amplifications were carried out in Biorad T100 thermocycler (Biorad, USA) with the following PCR conditions: initial

denaturation at 94°C for 4 min followed by 33 cycles of : denaturation at 94°C for 30 sec, annealing at 42°C for 30 sec, extension at 72°C for 40 sec and a final extension at 72°C for 7 min for amplification of CO1 gene and initial denaturation at 94°C for 4 min followed by 33 cycles of : denaturation at 94°C for 30 sec, annealing at 46°C for 30 sec, extension at 72°C for 40 sec and a final extension at 72°C for 7 min for amplification of cytochrome b gene.

The PCR products were purified using PCR purification kit (Qiagen) and subsequent sequencing was carried out with LCO1490 and HC02198 (Folmer *et al.*, 1994) primers using the BigDye Terminator Sequencing Ready Reaction v3.0 kit (Applied Biosystems). A 565 bp region of the CO1 gene and a 586 bp region of the cytochrome b gene were amplified in all the sampled individuals for phylogenetic analysis.

Sequence alignment and analysis

The CO1 and cytochrome b sequences obtained were aligned with sequences (retrieved from GenBank) of other valid species under the genus *Scomber*; viz., *S. scombrus*, *S. japonicus*, *S. australasicus* and *S. colias* using Clustal W in MEGA 6. A phylogenetic tree was constructed using UPGMA method with 1000 bootstraps. Tree topology was also tested using maximum likelihood, maximum parsimony and neighbour-joining methods. The tree was then rooted with CO1 and cytochrome b sequences of *Katsuwonus pelamis* retrieved from GenBank. Genetic divergence between all the species was analysed using Kimura 2 parameter (K2P) distance values in MEGA 6.

Results

Scomber indicus sp. nov. Abdussamad, Sandhya & Arun

Common name: Indian chub mackerel

Holotype: CMFRI GB.31.135.12.7, 257 mm FL (Fig. 1-5 and Table 1a,b), caught off Kochi, south-eastern Arabian



Fig. 1. *Scomber indicus* sp. nov. CMFRI GB.31.135.12.7, 257 mm FL

Sea, India, 28 May 2015 (Fig.1). GenBank Accession no: KT461735.

Paratypes: CMFRI GB.31.135.12.7.1, 245 mm FL, caught off Kochi, south-eastern Arabian Sea, India, 28 May 2015, GenBank Accession no: KT461738; CMFRI GB.31.135.12.7.2, 256 mm FL, caught off Kochi, south-eastern Arabian Sea, India, 6 June 2015, GenBank Accession no: KT461740; NBFGR CH 1146, 267 mm FL, caught off Kochi, south-eastern Arabian Sea, India, 6 June 2015; NBFGR CH 1147, 256 mm FL, caught off Kochi, south-eastern Arabian Sea, India, 29 July 2015.

Diagnosis: First dorsal spines X-XIII; second dorsal rays ii, 10; dorsal finlets 5; anal finlets 5; pectoral fin rays 19-21; pelvic fin rays i, 5; anal fin rays I, ii, 10; branchiostegal rays 7. Gill rakers on first gill arch 14-15+29-32 = 43-47. Posteriormost part of hypohyal blunt with a small pit between the hypohyal and the ceratohyal (Fig. 2a,b). Total interneural bones

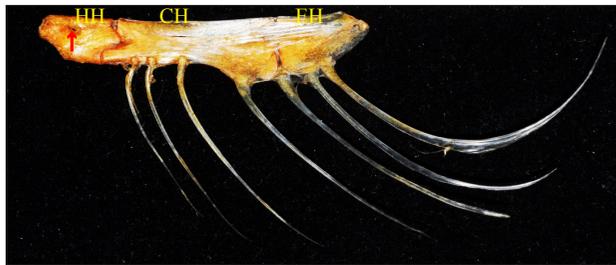


Fig. 2a. Hyoid arch of *S. indicus*. HH - Hypohyal, CH - ceratohyal, EH - Epihyal. Arrow shows pit in the dorsal hypohyal

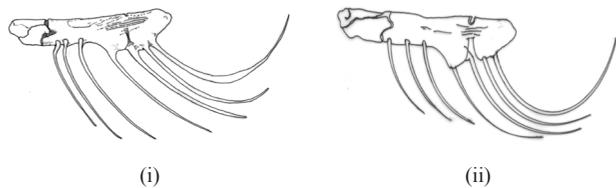


Fig. 2b. Hyoid arch morphology of (i): *S. indicus*, (ii): *S. japonicus* (redrawn from Matsui, 1967)

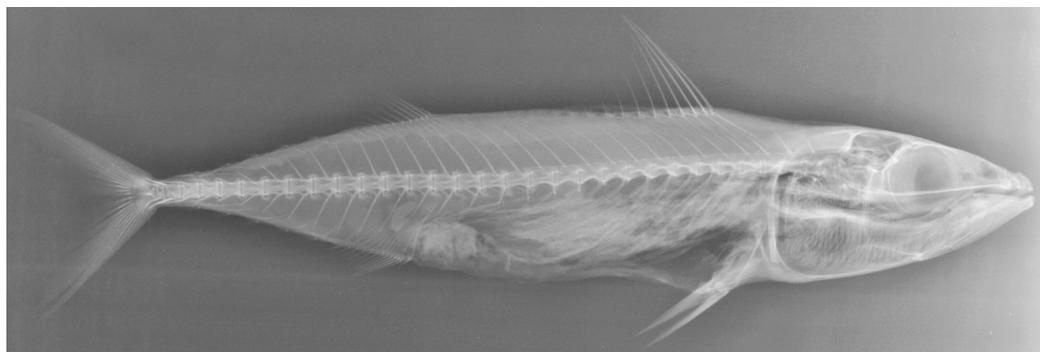


Fig. 4. X-ray radiograph of *S. indicus* showing position of the first haemal spine, interneural bones under the first and second dorsal fins and the vertebrae

35-38 with 17-20 below the first dorsal, 12 below the second and 6 below dorsal finlets. Last proximal interneural supporting the first dorsal fin in between 13th and 14th neural spine. First haemal spine posterior to first interhaemal process. Anterior portion of the first haemal spine following haemapophysis broader with a sharp curve than that in *S. australasicus*, with the posterior spinous process projecting almost horizontally (Fig. 3a,b). Interhaemal bones 13 above anal fin and 6 above anal finlets. Total vertebrae 31 including urohyal (abdominal 14+caudal 17). Swimbladder present. Longest gillraker shorter than the longest gill filaments. First haemal spine on the anterior portion of the 15th vertebrae (Fig. 4). Sagittal otolith rectangular in shape with pointed rostrum and oblique posterior (Fig. 5a).

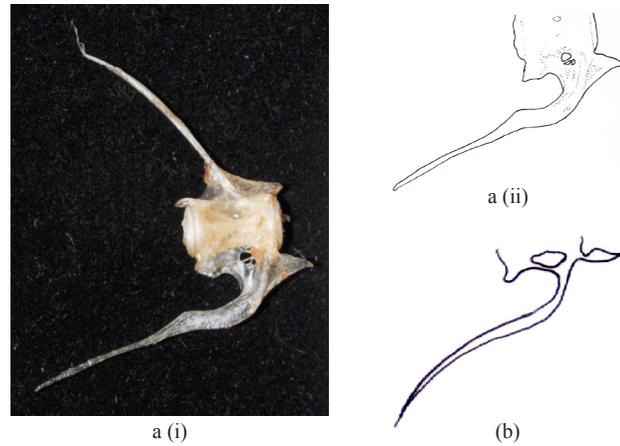


Fig. 3. First haemal spine of (a) *S. indicus*, (b) *S. australasicus* (redrawn from Matsui, 1967)

Otolith is almost rectangular with pointed rostrum in all species of *Scomber* except in *S. scombrus*, where it is almost oval with pointed rostrum. The new species differ from the other four species in the presence of medially positioned pointed rostrum and a blunt antirostrum. In others the rostrum is positioned below the median line with pointed antirostrum above (Fig. 5b).



Fig. 5a. Lateral view of sagittal otolith of *S. indicus*, 245 mm FL

Description: Detailed morphometry and meristic counts of holotype and paratypes of *S. indicus* sp. nov. are given in Table 1. Body fusiform, elongate and rounded. Snout pointed. Well developed adipose eyelid covering nearly half of head ($53.93 \pm 2.25\%$ FL) and with a central slit at pupil. Body covered with small cycloid scales. Scales around pectoral region and origin of lateral line larger compared to others but no well defined corselet. Mouth oblique; vomer and palatines toothed, palatine teeth in close double rows and running in

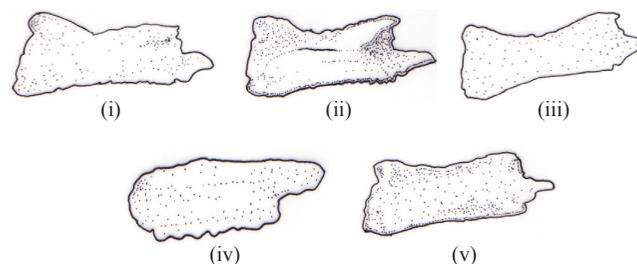


Fig. 5b. Otolith morphology of (i) *S. japonicus* (redrawn from Shiraishi *et al.*, 2008); (ii) *S. australasicus* (redrawn from <http://oto.biodiv.tw>); (iii) *S. colias* (redrawn from Vasconcelos *et al.*, 2011); (iv) *S. scombrus* (redrawn from <http://www.sefsc.noaa.gov>); (v) *S. indicus* sp. nov. (specimens between 250-300 mm FL)

to each other. Body depth shorter than head length, body depth at first dorsal origin $19.04 \pm 0.73\%$ FL. Head length $26.66 \pm 0.82\%$ FL; first dorsal fin base length $15.71 \pm 1.17\%$ FL; snout length $26.37 \pm 1.23\%$ HL and greater than interorbital length. Interorbital flat, more than eye diameter; eye diameter $23.71 \pm 1.08\%$ HL; Pectoral fin length $12.99 \pm 0.57\%$ FL, reaching to 6 - 7th first dorsal spines. Pelvic origin anterior

Table 1a. Morphometric data for *Scomber indicus* sp. nov. (n=47) including that of holotype and paratype specimens

Morphometric parameters (cm)	Holotype	Paratype 1	Paratype 2	Mean \pm SD (n=47)	Min.	Max.
Total length (TL)	27.43	26.28	27.52	28.34 ± 0.75	26.43	30.11
Fork length (FL)	25.72	24.54	25.63	26.55 ± 0.71	24.64	28.01
	Expressed as % FL					
Standard length	94.73	91.53	92.99	92.92 ± 0.34	92.28	94.09
Pre-pectoral length	29.13	26.25	30.59	28.57 ± 0.98	26.47	30.95
Pre-pelvic length	36.03	33.53	36.45	35.34 ± 0.67	33.81	36.88
Pre-1 st dorsal length	36.73	34.31	37.4	36.03 ± 0.66	34.59	37.84
Pre-2 nd dorsal length	65.62	62.62	65.42	64.37 ± 0.61	63.14	66.2
Pre-anal length	69.72	66.17	68.73	68.39 ± 0.68	66.71	69.55
Pectoral length	13.24	11.83	14.24	12.99 ± 0.57	11.93	14.41
Pelvic length	10.44	8.03	11.74	10.24 ± 0.73	8.1	11.88
1 st dorsal height	11.66	9.44	12.77	11.44 ± 0.77	9.52	12.92
1 st dorsal base length	16.02	11.79	17.67	15.71 ± 1.17	11.89	17.88
2 nd dorsal base length	9.52	8.14	10.27	9.34 ± 0.43	8.21	10.39
Inter-dorsal distance	13.41	11.04	15.95	13.15 ± 1.1	11.13	16.14
Anal base length	8.04	6.43	8.88	7.89 ± 0.51	6.48	8.99
Body depth at 1 st dorsal origin	19.41	17.06	20.07	19.04 ± 0.73	17.2	20.31
Body depth at 1 st dorsal insertion	19.17	16.75	21.56	18.8 ± 0.98	16.89	21.82
Caudal depth	2.92	2.63	3.11	2.86 ± 0.11	2.65	3.15
Distance between 1 st to 10 th spine on 1 st dorsal	12.95	11.14	13.66	12.7 ± 0.55	11.23	13.82
Distance between 10 th spine on 1 st dorsal to 2 nd dorsal	16.48	14.86	18.21	16.17 ± 0.68	14.98	18.43
Head length (HL)	27.18	24.84	28.16	26.66 ± 0.82	25.04	28.49
	Expressed as % HL					
Snout length	25.58	24.22	29.63	26.37 ± 1.23	24.06	29.78
Eye diameter	23	21.39	26.74	23.71 ± 1.08	21.25	26.87
Post-orbital length	48.55	46.54	52.99	50.04 ± 1.64	46.23	53.25
Adipose covering	52.32	48.22	57.95	53.93 ± 2.25	47.9	58.24

Table 1b. Major meristic counts of holotype and paratype specimens of *Scomber indicus* sp. nov.

Meristic characters	Holotype	Paratype 1	Paratype 2
First dorsal spines	XI	X	XII
Second dorsal spines and rays	2+10	2+10	2+10
Dorsal finlets	5	5	5
Anal finlets	5	5	5
Anal fin spine and rays	1,2+10	1,2+10	1,2+10
Pelvic fin spine and rays	1+5	1+5	1+5
Pectoral fin rays	21	20	21

to dorsal fins with pelvic slightly smaller than or equal to pectorals; interpelvic process small and single. Distance from 10th spine on first dorsal to origin of second dorsal fin greater than distance between the 1st and 10th spine on first dorsal. Dorsal fin membranes not smooth, curtain like. Second dorsal fin base length $9.34 \pm 0.43\%$ FL; pre-first dorsal fin length $36.03 \pm 0.66\%$ FL; pre-second dorsal fin length $64.37 \pm 0.61\%$ FL; prepectoral length $28.57 \pm 0.98\%$ FL; prepelvic length $35.34 \pm 0.67\%$ SL; preanal length $68.39 \pm 0.68\%$ FL.

Anal fin origin posterior to that of second dorsal fin (below 5-6 fin rays on second dorsal fin) origin; anal fin spine small and separate. Anal fin base length $7.89 \pm 0.51\%$ FL; caudal peduncle slender. Two small keels on the sides of caudal peduncle, central keel absent. Caudal depth $2.86 \pm 0.11\%$ FL.

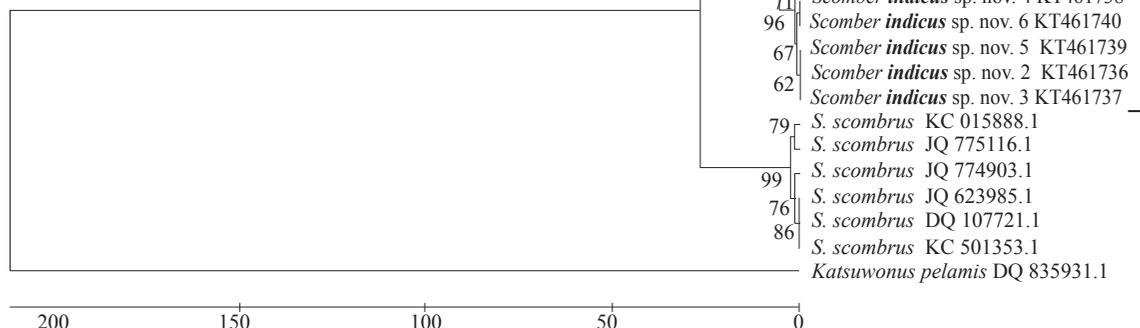
Colour: Dark bluish on the dorsal side with greenish wavy/undulate bands, which extends a little below lateral line; belly pale with broken lines/spots. Pectorals black, pelvics pale. Small black spots on pectorals. Dorsal fins and inner opercular region dusky.

Distribution: Presently known only from Arabian Sea, possibly have wider distribution in the northern Indian Ocean

Etymology: The name *S. indicus* is based on the collection locality i.e., northern Indian Ocean.

Genetic analyses

All partial sequences of COI and cytochrome b region obtained from a total of 14 specimens of *S. indicus* sp. nov. were deposited in GenBank with the accession numbers from

Fig. 6. UPGMA tree based on COI sequences of different species of *Scomber*

KT461727 - KT461740. The phylogenetic tree constructed using 31 sequences of COI (Fig. 6.) and 35 sequences of cytochrome b (Fig. 7.) of the five *Scomber* species including *S. indicus* sp. nov. showed distinct clustering among species with significant bootstrap values. Similar tree topology was also obtained when phylogenetic analyses were conducted using maximum likelihood, maximum parsimony and neighbour joining methods. Within species, Kimura 2 parameter (K2P) distance values for COI varied between 0.2-0.8% among the four valid species of *Scomber*. K2P distance percentage values (Table 2) between species for COI showed 2.2, 1.8, 1.4 and 10% divergence between *S. indicus* sp. nov. and *S. australasicus*, *S. japonicus*, *S. colias* and *S. scombrus* respectively. Significant divergence was also observed in cytochrome b gene sequences between *S. indicus* sp. nov. and other valid species of *Scomber*. The K2P values for cytochrome b showed 4.4, 3.8, 3.4 and 18.2% divergence between *S. indicus* sp. nov. and *S. australasicus*, *S. japonicus*, *S. colias* and *S. scombrus* respectively. Genetically, the new species is closest to *S. colias* followed by *S. japonicus*. The polymorphic sites in 565 bp region of COI and 586 bp region of cytochrome b genes in the species cluster of *S. japonicus*/*S. australasicus*/*S. colias*/*S. indicus* sp. nov. are shown in Fig. 8 and 9.

Comparison with congeners

S. indicus sp. nov. is morphologically most similar to the spotted mackerel *S. australasicus* from Western Australia and genetically closer to *S. colias*. The original descriptions of all *Scomber* species are poor, even though they formed commercial fisheries in the respective regions warranting a revision of genus with molecular and morphological support, examining materials from wide geographical localities. Comparison of the morphological and meristic characteristics of *S. indicus* with other valid species of *Scomber* is given in Table 3.

S. indicus sp. nov. can be separated from *S. scombrus* in having swim bladder, first haemal spine located posterior to the first interhaemal process, 14+17 vertebrae and also based on sagittal otolith morphology which is rectangular in shape, with pointed anterior region and oblique posterior (Fig. 5a,b;

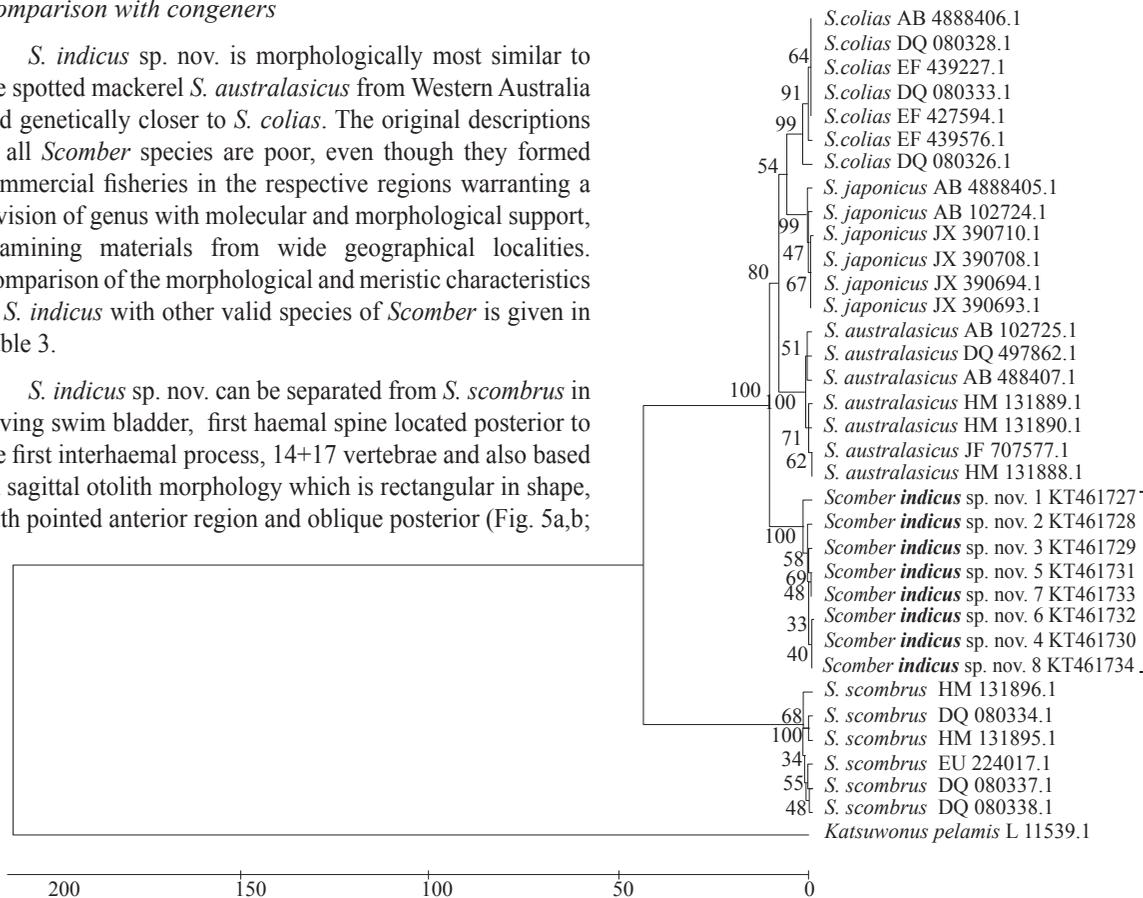


Fig. 7. UPGMA tree based on cytochrome b sequences of different species of *Scomber*

<http://www.sefsc.noaa.gov>) vs no swim bladder, first haemal spine anterior to the first interhaemal process and 13+18 vertebrae in *S. scombrus* (Matsui, 1967; Collette, 1999).

S. japonicus is differentiated from *S. indicus* sp. nov. on the basis of first dorsal fin spine counts (IX-X vs X-XIII); number of gillrakers [(12-15)+(27-34) = 39-46 vs (14-15) + (29-31) = 33-47]; number of interneural bones under first dorsal (12-15 vs 15-20); distance from tenth dorsal fin spine to origin of second dorsal fin (less than vs greater than distance between first and last spine); shape of lateral posteriormost part of hypohyal (blunt vs pointed) which has a small pit between the hypohyal and the ceratohyal (Fig. 2b; Matsui, 1967; Collette and Nauen, 1983) and also based on

the morphology of otolith (Shiraishi *et al.*, 2008) (Fig. 5a,b), *S. colias* differ from *S. indicus* sp. nov. in having IX- X first dorsal fin spines and 29-51 gill rakers and having different otolith morphology (Fig. 5a,b) which is kidney shaped (Baradad *et al.*, 2010; Vasconcelos *et al.*, 2011; Villamore *et al.*, 2014). Other distinguishing features are: body depth 5 in total length vs >5.8, head 4.20 in TL vs 3.8, first dorsal height 2 in head length vs 2.2-2.6 in *S. colias* and *S. indicus* sp. nov. respectively (Leim and Scott, 1966).

S. australasicus can be distinguished from *S. indicus* sp. nov. in having XIII spines in the first dorsal fin, 24-28 gill rakers (vs 29-32 in *S. indicus*) on lower limb of first gill arch and in having pointed posteriormost margin of hypohyal

Table 2. Kimura 2 parameter (K2P) distance values based on COI sequences and standard error values between different species of *Scomber* (K2P values on the left side and standard error on the right side of the diagonal)

Species	<i>S. indicus</i>	<i>S. japonicus</i>	<i>S. australasicus</i>	<i>S. colias</i>	<i>S. scombrus</i>
<i>S. indicus</i>	-	0.005	0.006	0.004	0.013
<i>S. japonicus</i>	0.018	-	0.004	0.003	0.013
<i>S. australasicus</i>	0.022	0.016	-	0.004	0.013
<i>S. colias</i>	0.014	0.010	0.014	-	0.013
<i>S. scombrus</i>	0.101	0.098	0.099	0.100	-

<i>S. japonicus</i>	GCACGGCCCTTAAGCTTGCTTATCCGAGCTGAACCTAAGTCAACCAGGGTCCCTTCTCGGCGACGACCAAACTACACGTAATTGTTACGGCCACGCTT
<i>S. australasicus</i>
<i>S. colias</i>T..T..
<i>S. indicus</i> sp.nov.
<i>S. japonicus</i>	CGTTATAATCTTCTTTTAGTAAATGCCAGTTATGATTGGAGGGTTCGGAAACTGACTGATCCCCCTAATGATCGGAGCCCCGACATGGCATTCCCCG
<i>S. australasicus</i>G.....
<i>S. colias</i>G.....
<i>S. indicus</i> sp.nov.
<i>S. japonicus</i>	ATAAATAACATAAGCTTCTGACTTCTGCCCCCTCTCTCTGCTGCTCTGTCTTCTTCGGCAGTTGAAGCCGGTSCCGAACTGGCTGAACAGTTTAT
<i>S. australasicus</i>A.....A.....C.....T.....
<i>S. colias</i>A.....T.....
<i>S. indicus</i> sp.nov.T.....A.....T.....
<i>S. japonicus</i>	CTCCCTCGCTGGGAACTAGCACACGCGGGGCATCAGTTGATTAAACCACTTCTCACTCCACCTAGCAGGTGTTTCTCAATCCTTGGGGCCATTA
<i>S. australasicus</i>G.....
<i>S. colias</i>G.....
<i>S. indicus</i> sp.nov.G.....A.....
<i>S. japonicus</i>	CTTCATCACACAATCATTAACATAAAACCTGCAGGTGTATCCCAATACCAAAACCCCTCTGTCTGAGCAGTCTTAATTACAGCTGTCTTCTCTCT
<i>S. australasicus</i>G.....
<i>S. colias</i>
<i>S. indicus</i> sp.nov.T.....T.....
<i>S. japonicus</i>	CTATCCCTACCAGTTCCTTGTCTGCGGCAATACAATGCTCCTAACAGACCGAAATCTAAATACTAC
<i>S. australasicus</i>
<i>S. colias</i>T.....T.....
<i>S. indicus</i> sp.nov.T.....G.....

Fig. 8. Polymorphic sites in 565 bp region of CO1 gene in *S. japonicus*/*S. australasicus*/*S. colias*/*S. indicus* sp. nov. group

<i>S. japonicus</i>	TTCCGAGTCCCATACGTCGGTACTACCCCTCGTTGAGTGAATCTGAGGCGGCTTCTCAGTAGCAATGCCACCCTCACCCGGTCTTTGCTTCCACTT
<i>S. australasicus</i>A.....G.....A.....C.....
<i>S. colias</i>	C.....A.....A.....A.....
<i>S. indicus</i> sp.nov.A.....A.....G.....A.....
<i>S. japonicus</i>	CTATCCCAATCGTATCCTGGCAGCAAACTTCTCACCTGCTATTCCTACATGAGACCGGGTCAAAACAACCAATGGCTAACTCCACGCGAGC
<i>S. australasicus</i>A.....A.....G.....T.....G.....
<i>S. colias</i>C.....A.....T.....T.....
<i>S. indicus</i> sp.nov.A.....T.....
<i>S. japonicus</i>	AAATCTCCTTCCACCATACTTCACTACAAGACCTCCTTGGCTTTGCCGCTCCTCGTGGCCCTCCTCTCTCGCACTTCTCTCCCAACCTCT
<i>S. australasicus</i>T.....T.....
<i>S. colias</i>T.....T.....
<i>S. indicus</i> sp.nov.T.....G.....T.....T.....
<i>S. japonicus</i>	GGGAGACCCCGACAATTTACACCCAGCTAACCCCAATAGTAAACCCCTCCTCATATTAGCCCTGAATGATACTTCTATTTCATACGCAATTTCTCGCTC
<i>S. australasicus</i>T.....T.....
<i>S. colias</i>	A.....T.....G.....
<i>S. indicus</i> sp.nov.T.....
<i>S. japonicus</i>	ATTCCAACAAGCTAGGAGGAGTCTTGCACCTAGCCCTCCATTTTAACTTTATGTTAGTCCCCTTCTACACACATCTAAACACGAGCACTAACA
<i>S. australasicus</i>	..C.....C.....
<i>S. colias</i>G.....
<i>S. indicus</i> sp.nov.C.....G.....
<i>S. japonicus</i>	TCCGCCAGCATCACAGTTCCTATTTTGAACCCCTTGTGCGCAGAGTGTGCTCCTAACCTGAATGGAGGCATGCCAGCAGAACAG
<i>S. australasicus</i>A.....A.....
<i>S. colias</i>A.....A.....
<i>S. indicus</i> sp.nov.A.....C.....ACAA.....T.....CAT.....

Fig. 9. Polymorphic sites in 586 bp region of cytochrome b gene in *S. japonicus*/*S. australasicus*/*S. colias*/*S. indicus* sp. nov. group

without a pit between the hypohyal and the ceratohyal. Further, the anterior portion of first haemal spine following haemapophysis in *S. indicus* is broader with a sharp curve than that in *S. australasicus* (Fig. 3b; Matsui, 1967). Otolith of *S. indicus* (Fig. 5a,b) is entirely different from that of *S. australasicus* (<http://oto.biodiv.tw>; Furlani *et al.* (2007); Whitley, 1964).

Day (1888) reported *Scomber janesaba* with distribution range from Persian Gulf to Japan (possibly including Indian seas), which was later synonymised with *S. japonicus*

Houttuyn, 1782 (Collette and Nauen, 1983). However *S. japonicus* in Indian Ocean was identified as *S. australasicus* by Collette and Nauen (1983). Beaufort and Chapman (1951) reported *S. australasicus* from Philippines and Taiwan, which was subsequently described as a new species *Rastrelliger faughni* Matsui, 1967. Carpenter *et al.* (1997) reported *S. japonicus* and *S. australasicus* from western Arabian region.

S. indicus sp. nov. described in the present study, is closest to *S. colias* genetically whereas it is closest to *S. australasicus*

Table 3. Comparison of the meristic and morphological characteristics of *S. indicus* sp. nov. with other valid species of *Scomber*

Species/ Features	<i>S. scombrus</i>	<i>S. japonicus</i>	<i>S. australasicus</i>	<i>S. colias</i>	<i>S. indicus</i> sp. nov.
Reference	Collette and Nauen (1983); Matsui (1967)	Collette and Nauen (1983), Matsui (1967)	Collette and Nauen, 1983 Matsui (1967)	Gmelin (1789)	Present study
Swimbladder	Absent	Present	Present	Present	Present
Vertebral count	13+18	14+17	14+17	14+17	14+17 (n=11)
First haemal spine	Anterior to first interneural process.	Posterior to first interneural process	Posterior to first interneural process. Anterior portion of first haemal spine following haemapophysis without a sharp curve and narrower than in <i>S. indicus</i>	-----	Posterior to first interneural process. Anterior portion of first haemal spine following haemapophysis broader and with a sharp curve than that in <i>S. australasicus</i> (n=11)
Interneural bones under first dorsal fin	21-28	12-15 + 8 + 6 = 26-29	15-20 + 7-9 + 6 = 30-33	-----	17-20 + 12 + 6 = 35-38 (n=11)
Dorsal fin spines	XI-XIII	IX-X	X-XIII	IX-X	X-XIII (n=47)
Interdorsal distance	Distance from last dorsal fin spine to origin of second dorsal fin greater than (1.5 times) the distance between first and last spine	Distance from last dorsal fin spine to origin of second dorsal fin less than the distance between first and last spine	Distance from tenth dorsal fin spine to origin of second dorsal fin greater than the distance between first and tenth spine	Distance from last dorsal fin spine to origin of second dorsal fin equal to or slightly greater than the distance between first and last spine	Distance from tenth dorsal fin spine to origin of second dorsal fin greater than the distance between first and tenth spine (n=47)
Space between first dorsal fin groove and second dorsal fin	Clearly greater (approximately 1.5 times) than length of groove	Less than length of groove	Approximately equal to length of groove	Less than length of groove	Slightly greater than length of groove (n=47)
Palatine	Wide. Teeth in two widely spaced rows	Narrow. Teeth in single or double rows; when double, rows are close running into each other	Narrow. Teeth in single or double rows; when double, rows close running into each other	Narrow. Teeth in single or double rows; when double, rows close running into each other	Narrow. Teeth in single or double rows; when double, rows close running into each other (n=47)
Anal fin origin	Opposite that of second dorsal fin or nearly so	Opposite that of second dorsal fin or somewhat posterior	Clearly more posterior than that of second dorsal fin, approximately opposite 4 th ray of second dorsal	Opposite that of second dorsal fin or somewhat posterior	Clearly more posterior than that of second dorsal fin, approximately opposite 5 th - 6 th ray of second dorsal (n=47)
Anal fin spine	Conspicuous, joined to the fin by a membrane but clearly independent of it.	Conspicuous clearly separated from anal rays but joined to them by a membrane.	Independent from anal fin	-----	Independent from anal fin (n=47)
Colour/ markings on the body	Markings on back oblique to near vertical, with relatively less undulating; belly unmarked.	Back with oblique lines (zigzag and undulating); belly unmarked (Pacific populations) or marked by spotting or wavy broken lines (Atlantic populations)	Back with oblique lines (zigzag and undulating); belly pearly-white marked with thin, wavy, broken lines which in places appear as speckling	Back with oblique zigzagging lines while the belly is paler and spotted or marked with broken wavy lines	Back with oblique lines (zigzag and undulating); belly marked by spotting or wavy broken lines which in places appear as speckling
Gill rakers on first gill arch	-----	12-15 + 27-34 = 39-46	Lower arm 24-28	29-51	14-15 + 29-32 = 43-47
Hyoid arch	-----	Larger than that of <i>S. australasicus</i> ; lateral posteriormost part of hypohyal nearly pointed; with a pit between the pointed part and the ceratohyal	Smaller than of <i>S. japonicus</i> ; lateral posteriormost part of hypohyal pointed; without a pit between the pointed part and the ceratohyal	-----	Lateral posteriormost part of hypohyal blunt with a small pit between the hypohyal and the ceratohyal
Otolith	Oval shaped, with a blunt rostrum dorsally	Rectangular shaped with a blunt rostrum ventrally with a downward curve and a pointed antirostrum	Rectangular shaped with a long rostrum ventrally, with a prominent pointed antirostrum	Rectangular in shape with a ventral stout rostrum and pointed antirostrum	Rectangular with pointed rostrum positioned medially without a prominent antirostrum

morphologically. The intra-generic distances between the new species and *S. colias*/*S. japonicus*/*S. australasicus* were low (1.4, 1.8 and 2.2% respectively) which shows that the new species is very closely related to all the three species. Low intra-generic distances have also been reported between *S. colias*/*S. japonicus*/*S. australasicus* when analysed using complete mitogenome sequences and these values are even lower than that reported within *Thunnus* species or *Auxis* species (Catanese *et al.*, 2010). This has been explained as due to introgressive hybridisation after speciation which has also been documented in other *Scomber* and *Thunnus* species (Stepien and Rosenblatt, 1996; Alvarado Bremer *et al.*, 2005). *S. indicus* sp. nov. might have diverged from any one of its close relatives by expanding its habitat range into the Arabian Sea.

Presence of different populations of *Scomber* spp. with observable morphological features has been reported by Collette and Nauen (1983), Scoles *et al.* (1998) and Tzeng (2007). However, recent studies have given distinct species status to some of these populations especially to Atlantic populations as *S. colias* (Collette, 1999; Catanese *et al.*, 2010) based on significant morphological, meristic and genetic differentiation. In the present study also, we observed substantial morphological, meristic and genetic divergence between the new species from Indian waters and other valid species of *Scomber*. Subsequent to this study, we have observed shoals of *S. indicus* sp. nov. juveniles along the coastal waters of central and northern Kerala (since July 2016). This indicates that a viable population of this species is getting established in this region and the probable reasons behind this are being investigated.

Acknowledgments

Authors are grateful to Subal Kumar Roul, Prakasan, D., Ratheesh, T. B. and Wilson Sebastian for the help and support in this work. Stefan Merker, Dagmar Beermann and Markus Weinhardt, R. Fricke of the State Museum of Natural History, Stuttgart, Germany are also acknowledged for images and information of *S. colias* from their collections. Special thanks are also due to Mark McGrouther from Australian Museum, Sydney for supporting with information on *S. australasicus*. We also thank the two reviewers for their valuable comments to improve the quality of this manuscript.

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