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Integrative taxonomic evidence confirms the presence of *Mola alexandrini* (Ranzani, 1839) in Indian waters

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Taxonomic study of ocean sunfishes is marked by a protracted and complex history due to their morphological similarity. Presently, the genus *Mola* includes three valid species: *M. tecta*, *M. alexandrini*, and *M. mola*, following the recent synonymization of *M. ramsayi* with *M. alexandrini* based on a comprehensive revision of the genus, which confirmed the latter's widespread distribution across the world's oceans. However, in Indian waters, ocean sunfishes (*Mola* spp.) have been reported under the names *M. ramsayi*, *M. mola*, and *M. alexandrini*. In the absence of a detailed taxonomic study and limited reference sequences of the Indian *Mola* in the public databases, current study aimed to assess the taxonomy of the genus *Mola* using an integrative approach, based on joint examination of morphological, anatomical, and genetic methods. Based on a thorough review of the literature, detailed morphological comparisons of fresh specimens collected from the east and west coasts of India during 2017–2023 with congeners, and molecular characterization using two mitochondrial regions (D-loop and COI), the present study confirms that specimens from the Indian EEZ belong to *M. alexandrini* and had previously been misidentified as *M. mola* or *M. ramsayi*. Maximum likelihood phylogenetic analysis revealed well-supported clades (bootstrap values ~70% and above), with the specimens clustering consistently with *M. alexandrini*. This study suggests that *M. mola* is either absent from Indian waters or its occurrence remains doubtful. Our findings further highlight the importance of an integrative taxonomic approach for a better understanding of the zoogeographies of enigmatic genera such as *Mola*.

Introduction

Ocean sunfishes, also known as molids (family Molidae, Order Tetradontiformes), are among the most distinctive marine teleost, characterized by their unique body shape, including the complete absence of a true caudal fin, and their huge size, reaching over 3 m in total length and more than 2,000 kg in body mass (Sawai et al., 2018). Although research on molid morphology and taxonomy dates back to the 16th century, their systematics remain as a long-standing legacy of taxonomic confusion that continues to the present day (Fraser-Brunner, 1951; Sawai et al., 2018). This taxonomic confusion arises because all molid species undergo significant morphological transformation during early life stages, which are poorly documented, and continue to exhibit such morphological changes as they grow larger (Fraser-Brunner, 1951; Martin and Drewry, 1978; Hellenbrecht et al., 2019). Additionally, information on key life history traits, particularly size at maturity of most molids is either lacking or poorly understood. Establishing a key diagnostic characteristic for each species at different life stages is therefore vital for accurate species identification and effective fisheries and molid resource management (Sawai et al., 2020). Several morphological characteristics in *Mola* spp. develop with size and should be observed with utmost caution, including head bump, chin bump, wavy clavus, ossicles and body scale structure (see Nyegaard et al., 2018; Sawai et al., 2018).

Historically, Fraser-Brunner (1951) conducted the first comprehensive review of Molidae based on morphology, reexamining all nominal species documented in the literature. He accepted only three genera and five valid species (including two subspecies) within the family: *Ranzania laevis laevis*, *R. laevis makua*, *Masturus lanceolatus*, *M. oxyuropterus*, *Mola mola*, and *M. ramsayi*. Subsequently, Parenti (2003) provided the first checklist of Molidae, listing 19 nominal genera and 57 nominal species, though recognizing only 4 valid species across 2 or 3 genera (*Masturus lanceolatus, Mola mola, M. ramsayi* and *Ranzania laevis*) depending on the author. However, Fraser-Brunner's classification remained widely accepted and endorsed by major taxonomic authorities until recent studies. More recently, Nyegaard et al. (2018) confirmed the presence of three distinct species within the genus *Mola*: *M. tecta* (a new species from New Zealand and Australia), *M. ramsayi* and *M. mola*, using an integrative taxonomic approach and provided a provisional key to distinguishing the adult forms of *Mola* species. This represented the first discovery of a new *Mola* species in 125 years. Subsequently, Sawai et al. (2018) found that *M. ramsayi* is no longer a valid species and resurrected *M. alexandrini* (Ranzani 1839) from synonymy with *M. mola* (Fraser-Brunner, 1951), treating it as the senior synonym of *M. ramsayi*. They redescribed *M. alexandrini* as a valid species based on the rediscovered dried holotype (MZUB, 190 cm total length) that was unnumbered, along with 21 additional fresh and preserved specimens. Due to the absence of a type specimen, a neotype was designated for *M. mola* to facilitate comparison with *M. alexandrini*, given the historical confusion between these species. However, Britz (2022) questioned the validity of *M. alexandrini* (Ranzani, 1839) following a meticulous analysis of morphometric data and images from Sawai et al. (2018), the

purported holotype and Ranzani's (1839) illustration of *O. alexandrini*. Britz identified discrepancies suggesting that Sawai et al. (2018) may have been misled, and the putative holotype of *M. alexandrini* cannot be a type specimen because of the mismatches between the reported length and the image/illustration. In light of this confusion and following an additional literature review, Sawai and Nyegaard (2023) again confirmed the valid species status of *M. alexandrini* (Ranzani, 1839) by addressing the issues raised by Britz (2022). At present, the genus *Mola* is therefore considered to include only three valid species: *M. alexandrini* (Ranzani 1839), *M. mola* (Linnaeus 1758), and *M. tecta* Nyegaard et al., 2017 (Nyegaard et al., 2018; Sawai et al., 2018; Sawai and Nyegaard, 2023).

The first molecular investigation of Molidae was undertaken by Streelman et al. (2003), who developed five nuclear DNA microsatellite markers specific to *M. mola*. Yamanoue et al. (2004) subsequently determined the first complete mitochondrial genomes and phylogeny of three molids: *R. laevis*, *M. lanceolatus*, and *M. alexandrini* (as *M. mola*). Sagara et al. (2005) identified two distinct clades of *M. mola* in Japanese waters through phylogenetic analysis of full nucleotide sequences of the mitochondrial D-loop region. In the same year, Bass et al. (2005) identified four genetically distinct clades based on analysis of D-loop and cytochrome b mitochondrial regions. Yoshita et al. (2009) validated the global classification of *Mola* species into three distinct groups (designated as *Mola* sp. A, *Mola* sp. B, and *Mola* sp. C) through a molecular phylogenetic analysis of the D-loop region based on the specimens collected from both inside and outside Japanese waters. Yamanoue et al. (2010) developed a multiplex PCR method for genotyping the mitochondrial DNA of *Mola* sp. A and *Mola* sp. B in Japan. Nyegaard et al. (2018) confirmed the presence of three distinct species within the genus *Mola* (*Mola* sp. A, *Mola* sp. B and *Mola* sp. C as *M. ramsayi, M. mola, M. tecta*, respectively), as first suggested by Yoshita et al. (2009), using morphological characteristics and mitochondrial DNA analysis (D-loop and COI). Recently, Sawai et al. (2018) clarified the nomenclatural status of the two remaining genetically identified species (*Mola* sp. A as *M. alexandrini* and *Mola* sp. B as *M. mola*) through an extensive morphological and molecular studies.

On the Indian coast, ocean sunfishes of the genus *Mola* have usually been reported as *M. mola*, and in certain instances as *M. ramsayi* and *M. alexandrini* (see Table 1). The first record dates back to 1975 in the name of *M. mola* from Satpati, Bombay coast (present name Mumbai) in the Arabian Sea (Khan, 1975). Afterwards, the species was reported from various parts of the country: Visakhapatnam (Ram Bhaskar et al., 1988), northwestern Indian EEZ (Somvanshi, 1996), Veraval (Monoj Kumar et al., 1998), Tuticorin (Chellappa et al., 2002), Kayalpatnam (Chellappa et al., 2006), Chennai (Mohan et al., 2006), Malpe (Thomas et al., 2006), Parangipettai (Murugan et al., 2007), Calicut (Monoj Kumar and Pavithran, 2007), Karwar (Praveen Dube et al., 2013), Munambam (Kishore et al., 2013), Digha (Ray et al., 2019), Panchupada (Fullonton et al., 2020), Kakinada (Chatla and Padmavathi, 2021), Vasai (Thakurdas et al., 2022) and recently from southwest coast of India (Devi et al., 2023). Most of these publications are distribution records based on surface morphology and photographic evidence

TABLE 1 Records of *Mola* spp. from Indian EEZ during the period from 1973 to 2023.

Sl.No.	Date	Location	Gear caught	Depth of fishing (m)	Length range (cm) (TL)	Weight range (kg)	n	Species reported	Source
1	25 February 1973	Off Satpati, Mumbai, Maharastra	Gillnet		124.0	ND	1	*M. mola*	Khan, 1975
2	06 May 1986	Off Visakhapatnam, Andhra Pradesh	Hook & line	200	91.2	ND	1	*M. mola*	Ram Bhaskar et al., 1988
3	May, October and November 1992	Northwestern Indian EEZ	Longline	1152-1937	ND	ND	8	*M. mola*	Somvanshi, 1996
4	March 1997	Bhidia Fish Landing Centre, Veraval, Gujarat	trawl net	25-50	87.0-103.0	40-49	4	*M. mola*	Monoj Kumar et al., 1998
5	12 June 2001 & 08 July 2001	Off Keela Vaipaar, Tuticorin, Tamil Nadu	drift gill net	60-80	63.0-65.0	11.5-12	2	*M. mola*	Chellappa et al., 2002
6	2005	Thiruvaikulam, Kayalpatnam, Tamil Nadu	drift gill net	60-100	ND	ND	4	*M. mola*	Chellappa et al., 2006
7	17 August 2006	Chennai Fisheries Harbour, Tamil Nadu	trawl net	ND	83.5	10.5	1	*M. ramsayi*	Mohan et al., 2006
8	07 January 2006	Malpe Fisheries Harbour, Karnataka	trawl net	ND	ND	ND	1	*M. mola*	Thomas et al., 2006
9	25 March 2007	Parangipettai, Tamil Nadu	drift gill net	400 - 500	118.0	50	1	*M. mola*	Murugan et al., 2007
10	14 December 2006	Beypore Fishing Harbour, Calicut, Kerala	trawl net	70	70.0	19	1	*M. mola*	Monoj Kumar and Pavithran, 2007
11	27 August 2013	Karwar Fisheries Harbour, Karnataka	purse seine	40	95.0	50	1	*M. mola*	Praveen Dube et al., 2013
12	06 September 2013	Munambam Fisheries Harbour, Cochin, Kerala	trawl net	ND	111.0	50	1	*M. ramsayi*	Kishore et al., 2013
13	ND	Digha Mohona, West Bengal	trawl net	ND	68.5-78.0	ND	2	*M. mola*	Ray et al., 2019
14	March to May, 2018	Panchupada Estuary, Odisha	ND	ND	ND	ND	2	*M. mola*	Fullonton et al., 2020
15	2010-2019	Indian EEZ	longline	ND	ND	ND	1	*M. mola*	Kar et al., 2020
16	11 December 2018	Kakinada Fishing Harbor, Andhra Pradesh	trawl net	20-100	93.5	62	1	*M. alexandrini*	Chatla and Padmavathi, 2021
17	12 November 2021	Naigav night market, Palghar, Maharashtra	gillnet	ND	81.0	28	1	*M. mola*	Thakurdas et al., 2022
18	2019 to 2020	Sunghumugham, Kerala	ND	ND	ND	ND	2	*M. mola & M. alexandrini*	Devi et al., 2023
19	03 January 2017	Digha Mohana, West Bengal	trawl net	30–45	61.3	16.8	1	*M. alexandrini*	Present study
20	08 March 2018	Balaramgadi Fish Landing Center, Odisha	trawl net	30–45	ND	ND	2	*M. alexandrini*	Present study
21	14 December 2018	Chandinipal Fish Landing Centre, Odisha	trawl net	30–45	73.1	23.7	1	*M. alexandrini*	Present study
22	24 February 2019	Paradeep Fishing Harbour, Odisha	trawl net	40–70	60.0	15.8	1	*M. alexandrini*	Present study
23	15 December 2022	Digha Mohona, West Bengal	trawl net	30-45	58.9	8.0	1	*M. alexandrini*	Present study
24	20 December 2022	Balaramgadi Fish Landing Center, Odisha	trawl net	30-45	66.4	17.7	1	*M. alexandrini*	Present study
25	04 January 2023	Digha Mohona, West Bengal	trawl net	30-45	68.0	12.7	1	*M. alexandrini*	Present study

(Continued)

TABLE 1   Continued

Sl.No.	Date	Location	Gear caught	Depth of fishing (m)	Length range (cm) (TL)	Weight range (kg)	n	Species reported	Source
26	03 February 2023	Digha Mohona, West Bengal	trawl net	30-45	76.5	21.5	1	*M. alexandrini*	Present study
27	01 February 2023	Paradeep Fishing Harbour, Odisha	trawl net	40-70	ND	ND	1	*M. alexandrini*	Present study
28	14 February 2023	Vasai, Maharashtra	bagnet	30–40	80	27	1	*M. alexandrini*	Present study
29	15 February 2023	Paradeep Fishing Harbour, Odisha	trawl net	40-70	ND	ND	1	*M. alexandrini*	Present study
30	24 February 2023	Digha Mohona, West Bengal	trawl net	30-45	ND	ND	2	*M. alexandrini*	Present study
31	27 February 2023	Digha Mohona, West Bengal	trawl net	30-45	82.1-87.1	26.2-33.0	2	*M. alexandrini*	Present study
32	04 March 2023	Paradeep Fishing Harbour, Odisha	trawl net	40-70	60	ND	1	*M. alexandrini*	Present study

ND, no data; TL, total length.

and lack detailed meristic counts and supporting molecular data. *Mola* spp. are difficult to distinguish from each other, especially during the early life stages and smaller sizes, due to strong morphological similarities, resulting in frequent misidentifications and erroneous GenBank submissions (Nyegaard et al., 2018; Sawai et al., 2018; present study). Therefore, traditional taxonomic tools stand alone are not sufficient for reliable identifications of these contentious species.

Given the lack of detailed taxonomic studies and the limited availability of reference sequences for Indian *Mola* in public databases, this study tests whether Indian *Mola* records attributed to *M. mola* represent misidentifications of *M. alexandrini* using an integrative taxonomy approach that combines classical taxonomic tools (such as morphology and anatomical traits) with molecular data generated from two mitochondrial regions, D-loop and COI. The COI region serves as the standard DNA barcode for fishes, which enables reliable species discrimination, while the rapidly evolving mitochondrial control region (D-loop) provides additional resolution among closely related species. Together, these two mitochondrial regions are effective for taxonomic clarification within the genus *Mola* (Nyegaard et al., 2018).

Materials and methods

Specimen collection

Morphological data were gathered from seven fresh specimens of *Mola* spp. obtained from the east coast (West Bengal and Odisha) and west coast (Maharashtra) of India (Figure 1). The specimens were directly collected from the fish landing sites, brought to the laboratory on crushed ice for detailed taxonomic analysis, and promptly photographed to maintain their original shape and color. Additionally, photographs of landed specimens were obtained with assistance from local fishermen whenever feasible.

External morphology

The specimens were provisionally identified based on recent literature (Nyegaard et al., 2018; Sawai et al., 2018). Meristic counts were recorded following the methods outlined by Yoshita et al. (2009), with dorsal, anal, and clavus fin rays counted through dissection or X-rays. Clavus ossicles were enumerated by both tactile examination along the clavus's rear margin and via X-rays. The total fin rays of the dorsal, clavus, and anal complex (D + C + A fin rays) were counted following the method described by Gudger (1937). Morphometric measurements adhered to protocols outlined by Yoshita et al. (2009); Nyegaard et al. (2018); Sawai et al. (2018), using measuring tape, scales, and calipers with a precision of 0.1 cm. Morphological observations, including the clavus margin shape, the presence or absence of a smooth band at the clavus base, smooth band back-fold, a head and chin bump, and scale shape in the middle region of the body, are generally based on the methods of Fraser-Brunner (1951); Yoshita et al. (2009); Nyegaard et al. (2018); Sawai et al. (2018).

Review of Indian records

A total of 18 publications documenting 35 specimens record of *Mola* spp. from Indian waters were reviewed to update the species distribution range (see Table 1). The report and record underwent meticulous scrutiny, including a detailed examination of photographs and descriptions provided in the papers.

Molecular sequencing and phylogenetic analysis

Tissue samples from the *Mola* specimens were collected and preserved in 95% ethanol to carry out molecular characterization. We extracted total DNA using the NucleoSpin®Tissue kit (Macherey-Nagel, Germany) following the instructions of the manufacturer. The quality and quantity of the extracted DNA
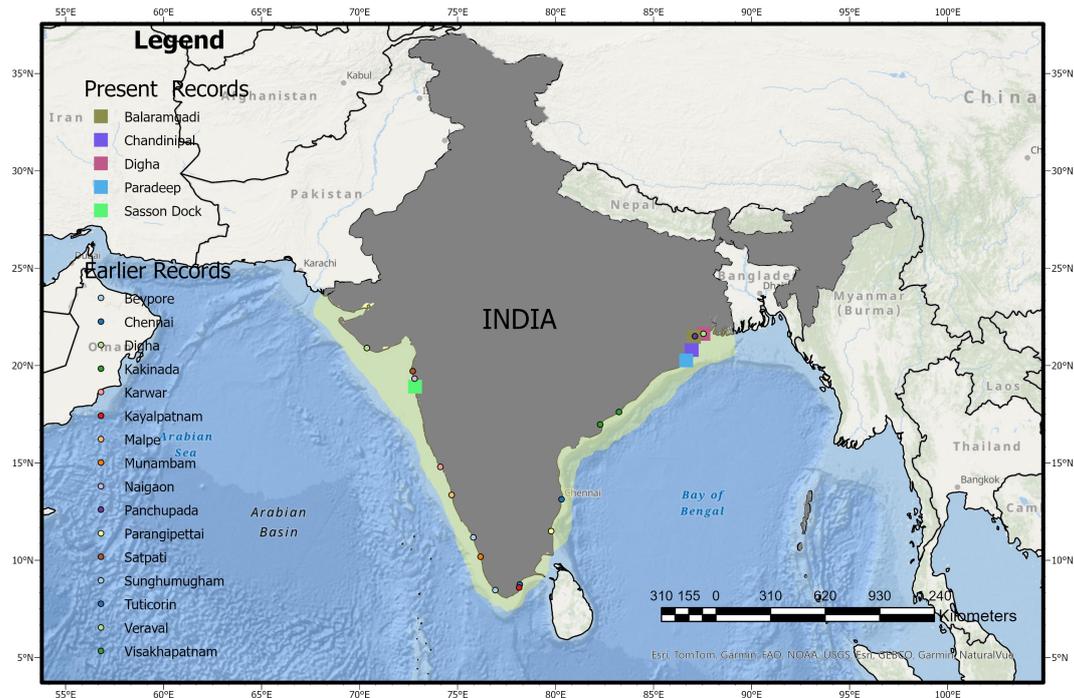
FIGURE 1
Map showing the records of *Mola alexandrini* (circles indicates earlier records and squares indicates present records) and distribution of *M. alexandrini* (shaded area) in the Indian waters.

were assessed using a NanoDrop One Microvolume UV-Vis Spectrophotometer (Thermo Fisher Scientific). The molecular phylogenetic studies were performed using COI and D-loop regions of mitochondria that provide robust resolution in closely related *Mola* species. As our objective was taxonomic identification and correction of earlier misidentifications, nuclear markers were not selected. They were amplified respectively using universal fish primers F1 and R1 (Ward et al., 2005) and specific *Mola*A and *Mola*B primers (Yoshita et al., 2009).

PCR amplification was performed in 25 µl reactions containing 2X PCR Master mix (Takara Bio INC), 10 µM of primers, and 20 ng template DNA. COI amplification began with an initial denaturation at 94°C for 5 min, followed by 25 cycles of denaturation 94°C for 30 s, annealing at 50°C for 30 s, and extension at 72°C for 35 s, and a final extension at 72°C for 5 min. To amplify the D-loop region, the reaction mixture was preheated to 98°C for 10 minutes, followed by 25 cycles of denaturation at 98°C for 30 s, annealing at 58°C for 40 s, and extension at 72°C for 1 min, with a final extension at 72°C for 5 min. PCR products were visualized on a 1.5% agarose gel alongside a NEX-GEN 100 bp DNA ladder (Genetix Biotech, India) and then sent to M/s. Eurofins Genomics India Pvt Ltd, Bengaluru, India for sequencing. Forward and reverse DNA sequences were aligned and assembled using the BioEdit sequence alignment editor, version 7.0.5.2 (Hall, 1999). Phylogenetic analyses included sequences retrieved from NCBI, including those of *M. tecta, M. mola*, and *M. alexandrini* (see Supplementary Table S1). These analyses were performed using MEGA version 10.2.1 (Kumar et al., 2018), with the best-fitting model selected using the Akaike Information Criterion (AIC) in MEGA. Both maximum likelihood and

neighbor-joining trees were constructed with 1,000 bootstrap replicates. *Masturus lanceolatus* was used as an outgroup in these analyses, and evolutionary distances were calculated using the Kimura 2-parameter model in MEGA 10. Haplotype network analysis with the D-loop sequences was carried out to explore the relationships among mitochondrial haplotypes of *Mola* species, using PopART v1.7 (Leigh and Bryant, 2015) based on the TCS algorithm.

Additional investigations

The stomach contents of five specimens were analyzed by transferring them into a container and sorting the prey items into different taxa manually. Sex was determined through macroscopic examination.

Results

Mola alexandrini (Ranzani, 1839)

(Bumphead sunfish, Figures 2–9; Tables 2, 3).

Materials examined (*n* = 7)

CMFRI/DRS/MA1, 01 male, 58.9 cm TL, Digha Mohana, West Bengal (21°36′ 58.3272′′N 87°29′ 56.8644′′E), sandy silt, trawl, 30–45 m, 15 December 2022 collected by Subal Kumar Roul; ZSI/EBRC/F153701, 01 unsexed, 66.4 cm TL, Balaramgadi Fish Landing Center, Odisha (21°28'24.46555"N 87°3'14.95855"E), sandy silt,
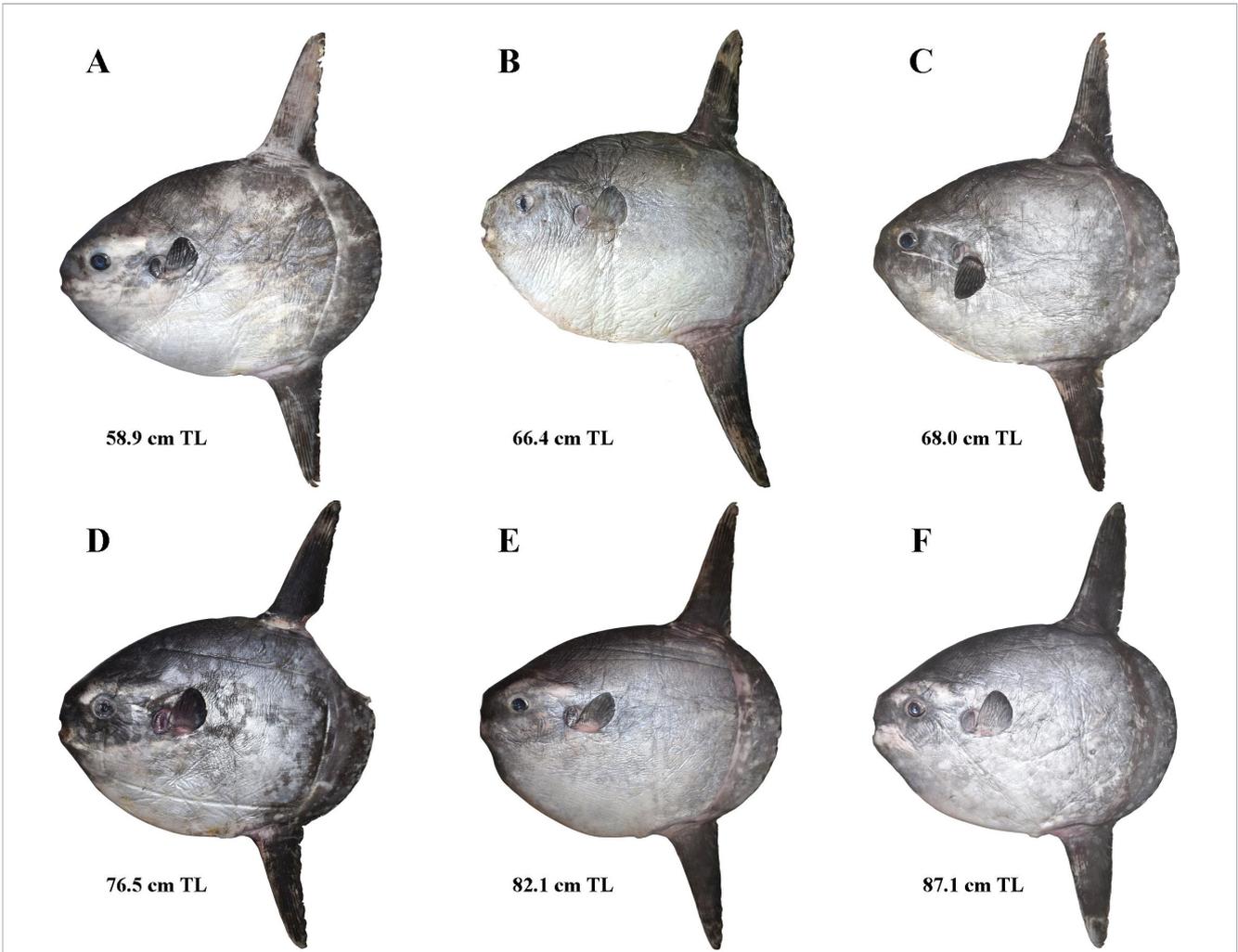
FIGURE 2
Fresh specimens of *Mola alexandrini*: **(A)** 58.9 cm TL, Digha Mohana, West Bengal; **(B)** 66.4 cm TL, Balaramgadi Fish Landing Center, Odisha; **(C)** 68 cm TL, Digha Mohana, West Bengal; **(D)** 76.5 cm TL, Digha Mohana, West Bengal; **(E)** 82.1 cm TL, Digha Mohana, West Bengal; **(F)** 87.1 cm TL, Digha Mohana, West Bengal.

FIGURE 3
Photographic identification of specimens of *Mola alexandrini*: **(A)** 61.3 cm TL, Digha Mohana, West Bengal; **(B)** length unknown, Balaramgadi Fish Landing Center, Odisha; **(C)** length unknown, Paradeep Fishing Harbour, Odisha; **(D)** length unknown, Paradeep Fishing Harbour, Odisha; **(E)** length unknown, Digha Mohana, West Bengal; **(F)** 60.0 cm TL, Paradeep Fishing Harbour, Odisha.
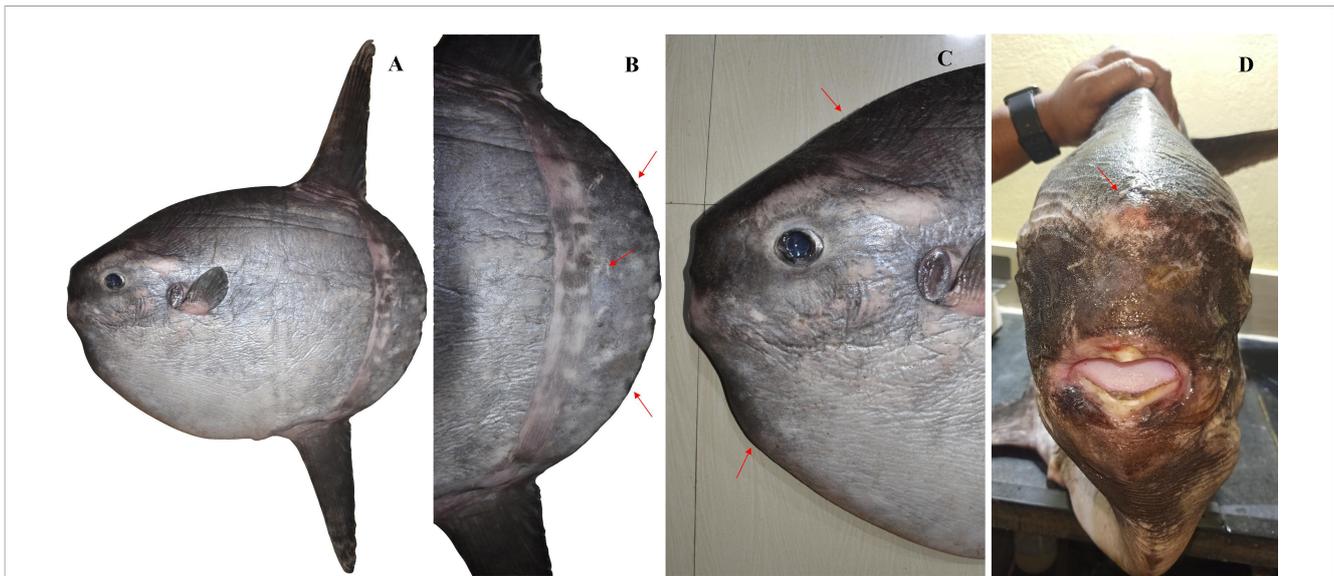
FIGURE 4
Mola alexandrini specimen (82.1 cm TL). **(A)** Body profile (lateral view); **(B)** rounded clavus, not wavy and without indents (arrow indicates), with a smooth band on the clavus and no back-fold (arrow indicates); **(C)** head and chin without a protuberance (bump) (arrow indicates); **(D)** snout with an ossicle (arrow indicates).

trawl, 30–45 m, 20 December 2022, collected by Biswajit Panda; CMFRI/DRS/MA2, 01 male, 68 cm TL, Digha Mohana, West Bengal (21°36′58.3272″N 87°29′56.8644″E), sandy silt, trawl, 30–45 m, 04 January 2023 collected by Subal Kumar Roul; CMFRI/DRS/MA3, 01 male, 76.5 cm TL, Digha Mohana, West Bengal (21°36′58.3272″N 87°29′56.8644″E), sandy silt, trawl, 30–45 m, 03 February 2023 collected by Subal Kumar Roul; CMFRI/MRS/MA1, 01 unsexed, 80 cm TL, Sasson Dock, Maharashtra (18°54′38.05″N; 72°49′34.27″E), sandy silt, dolnet, 30–40 m, 14 February 2023 collected by Ajay Nakhawa; CMFRI/DRS/MA4, 01 female, 82.1 cm TL, Digha Mohana, West Bengal (21°36′58.3272″N 87°29′56.8644″E), sandy silt, trawl, 30–45 m, 27 February 2023 collected by Subal Kumar Roul; CMFRI/DRS/MA5, 01 male, 87.1 cm TL, Digha Mohana, West Bengal (21°36′58.3272″N 87°29′56.8644″E), sandy silt, trawl, 30–45 m, 27 February 2023 collected by Subal Kumar Roul.

Photographic records (*n* = 8)

01, 61.3 cm TL, Digha Mohana, West Bengal (21°36′58.3272″N 87°29′56.8644″E), sandy silt, trawl, 30–45 m, 03 January 2017, collected by Anil Mohapatra; 02, length unknown, Balaramgadi Fish Landing Center, Odisha (21°28′24.46555″N 87°3′14.95855″E), sandy silt, trawl, 30–45 m, 08 March 2018, collected by Ganesh Chandra Tarai; 01 unsexed, length unknown, Paradeep Fishing Harbour, Odisha (20°17.345′N, 086°42.422′E), sandy silt, trawl, 40–70 m, 01 February 2023, collected by Smrutirekha Acharya; 01, length unknown, Paradeep Fishing Harbour, Odisha (20°17.345′N, 086°42.422′E), sandy silt, trawl, 40–70 m, 15 February 2023, collected by Jagannath Swain; 02, length unknown, Digha Mohana, West Bengal (21°36′58.3272″N 87°29′56.8644″E), sandy silt, trawl, 30–45 m, 24 February 2023, collected by Subal Kumar Roul; 01, 60.0 cm TL, Paradeep Fishing Harbour, Odisha

(20°17.345′N, 086°42.422′E), sandy silt, trawl, 40–70 m, 04 March 2023, collected by Jagannath Swain.

Description of pre-adult/juvenile specimens

The morphometric measurements, meristic counts, and observations of *M. alexandrini* from both current and previous studies are detailed in Tables 2, 3. The body shape is orbicular, deep, and laterally compressed, with a broad and rounded clavus replacing the true caudal fin, which is not wavy and lacks indents (Figures 2-4). The clavus features a smooth band lacking a back-fold (Figure 4B). The anal and dorsal fins are spineless, triangular, and positioned opposite each other in specimens measuring 58.9 to 87.1 cm in total length. There are no pelvic fins, while the small, rounded pectoral fins are situated mid-laterally and fit into shallow grooves along the sides of the body. The mouth is small and terminal, with fused teeth forming a beak-like shape (Figure 4D). A pair of tiny nostrils is positioned in front of the eyes, while an oval-shaped gill opening, covered by a soft gill membrane, is found in front of the pectoral fins. The gill rakers are hidden beneath a gelatinous layer. The surface of the body is adorned with small conical scales that have branching tips, creating a dotted appearance when seeing from above (specimens 58.9-87.1 cm TL) (see Figure 5). Scales present in the smooth band area are smaller compared to those in adjacent areas. The head and chin lack bumps (specimens 58.9-87.1 cm TL), lacking lateral ridges above or below the eyes. Pectoral fin rays 11-12, dorsal fin rays 17-19, anal fin rays 16-17, clavus fin rays 16-20, and clavus ossicles 11-16 (specimens 58.9-87.1 cm TL). A snout ossicle is present, while a chin ossicle is absent (specimens 58.9-87.1 cm TL). Two smaller fin rays are situated between two paraxial fin rays at the center of the clavus (Figure 6A). External dimorphism between sexes is not apparent, but gonad shapes differ: females have a single, spherical ovary, while males possess paired, elongated, rod-like testes (see Figure 7).
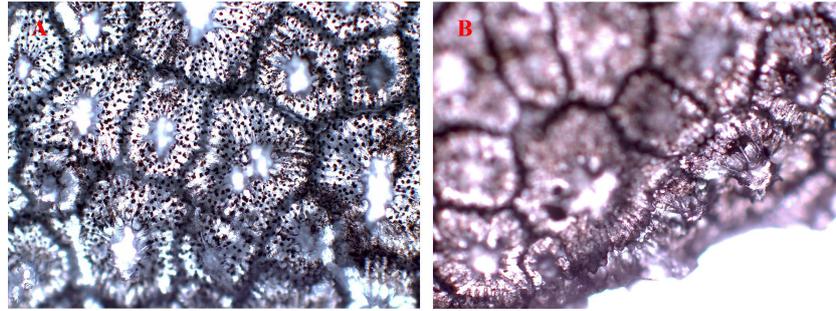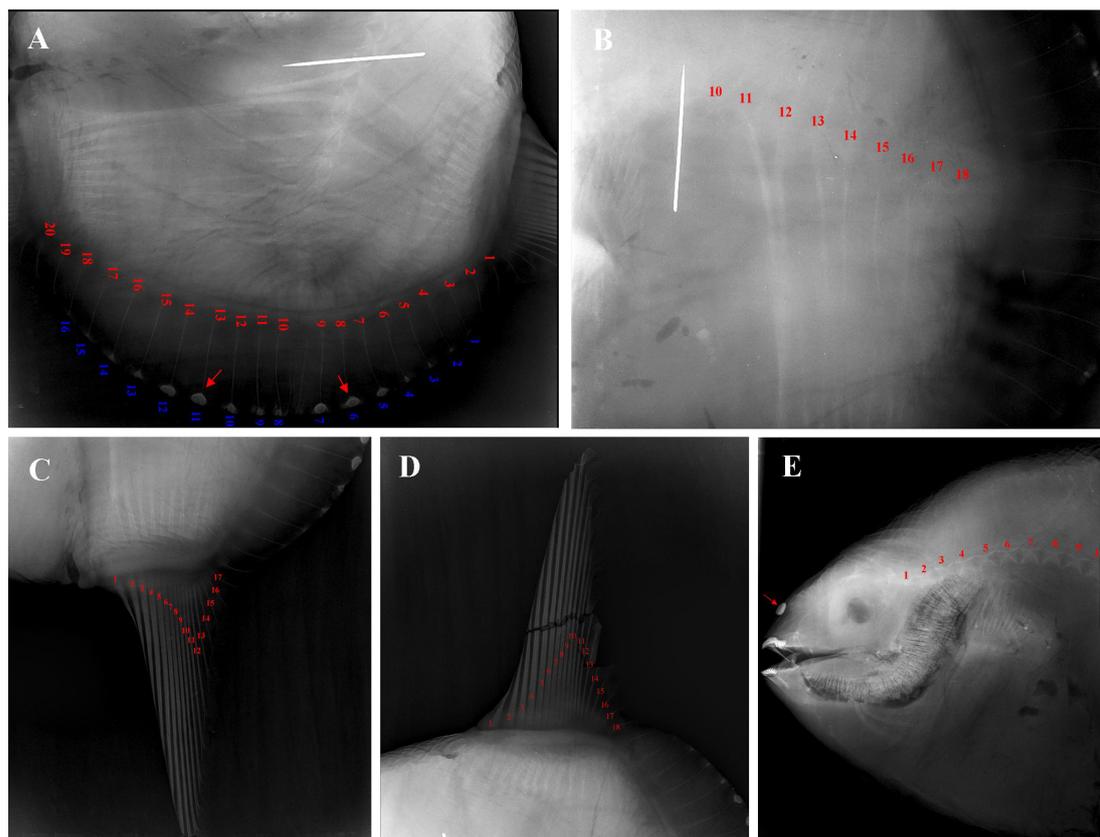
FIGURE 5
Scale morphology of Mola alexandrini on the body behind the pectoral fin. **(A)** and **(B)** Small conical scales with branching tips that create a dotted appearance.

Color of fresh specimens

The freshly collected specimens in this study exhibit a darker gray coloration dorsally and a dusky white coloration ventrally. All fins, including the posterior clavus area, also appear gray like the dorsal region, with numerous large or small paler spots observed towards the posterior clavus area (See Figures 2-4).

Habitat and geographic distribution

It inhabits both coastal and offshore waters along the coastline, caught in various gears operating at water depths ranging from 20 to 1937 meters (see Table 1). Previous reports and this study have revealed that *M. alexandrini* is widely distributed throughout the Indian coastline (see Figure 1; Table 1).

FIGURE 6
Meristic counts of *Mola alexandrini* from the X-radiograph. **(A)** Clavus (arrow indicates the ossicle on the clavus; number indicates clavus fin rays); **(B)** Vertebral bones (number indicates vertebral count); **(C)** Anal fin rays (number indicates count); **(D)** Dorsal fin rays (number indicates count); **(E)** Vertebral bones (arrow indicates the ossicle on the snout; number indicates vertebral count).

FIGURE 7
Gonad morphology of *Mola alexandrini*. **(A)** Round-shaped of ovary; **(B)** Paired, elongated, rod-like testes.
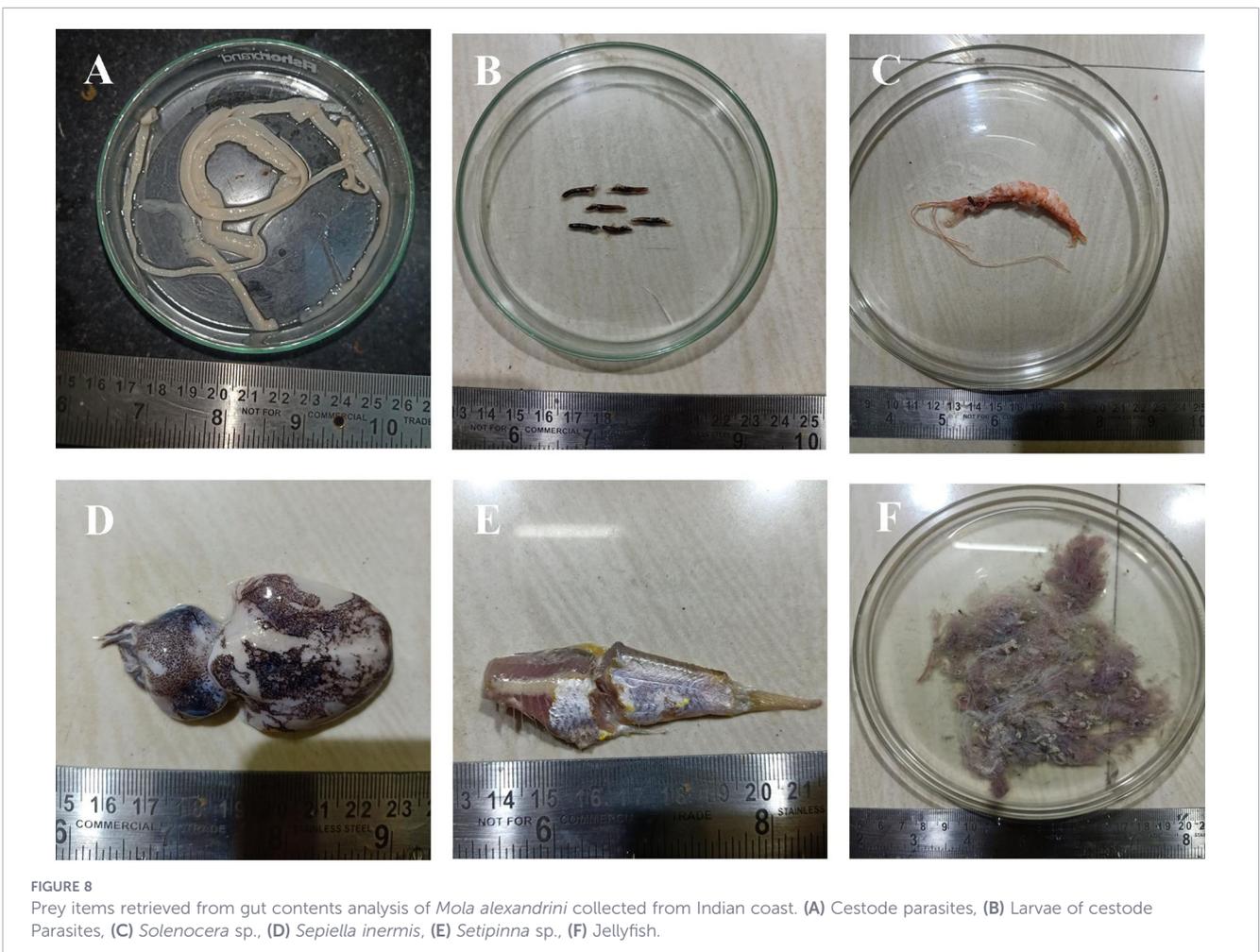

FIGURE 8
Prey items retrieved from gut contents analysis of *Mola alexandrini* collected from Indian coast. **(A)** Cestode parasites, **(B)** Larvae of cestode Parasites, **(C)** *Solenocera* sp., **(D)** *Sepiella inermis*, **(E)** *Setipinna* sp., **(F)** Jellyfish.
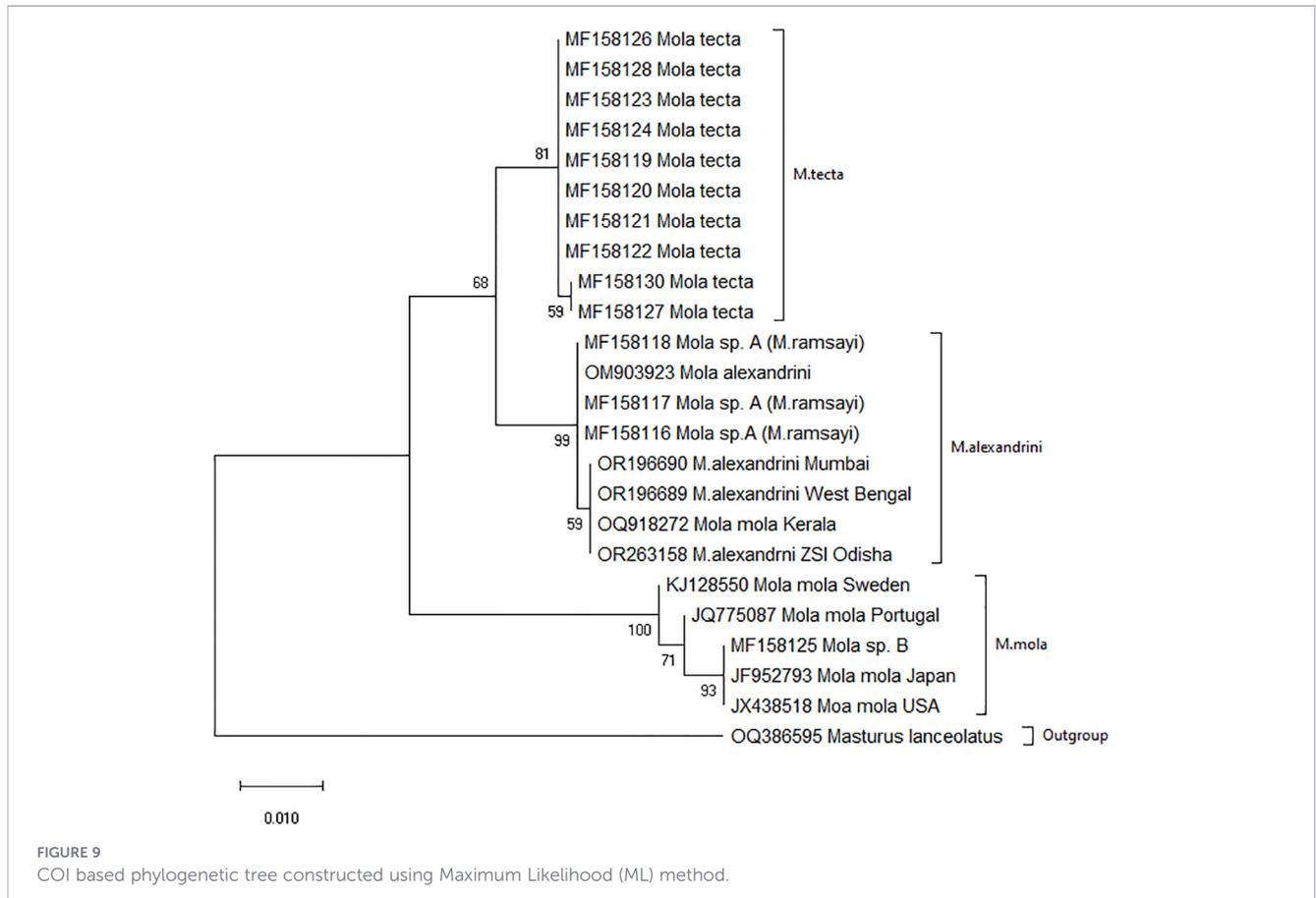
FIGURE 9
COI based phylogenetic tree constructed using Maximum Likelihood (ML) method.

TABLE 2 Morphological comparison of *Mola alexandrini*, *M. tecta*, and *M. mola*.

Species	*Mola alexandrini*				*Mola tecta*	*Mola mola*
	Holotype MZUB (unnumbered)	BMNH 1883.11.29.22	Other specimens (Sawai et al., 2018)	Present specimens	Other specimens (Nyegaard et al., 2018)	Other specimens (Sawai et al., 2018)
Total length (cm)	190.0 TL	229.1 TL	29.3–325.0 TL, *n* = 20	58.9-87.1 TL, *n* = 15	49.9–242.0 TL, *n* = 25	28.2–277.0 TL, *n* = 34
Meristic characters (means)						
Pectoral fin rays	12	12	11–12 (11.7), *n* = 14	11-12 (11.8), *n* = 7	11–12 (11.9)	10–13 (11.8)
Dorsal fin rays	18	18	16–19 (17.6), *n* = 10	17-19 (18.3), *n* = 7	17–19 (18.1)	18–19 (18.4)
Anal fin rays	17	17	15–17 (16.5), *n* = 10	16-17 (16.7), *n* = 7	16–18 (17.1)	17–18 (17.4)
Clavus fin rays	ND	ND	14–24 (17.3), *n* = 12	16-20 (18.7), *n* = 7	15–17 (15.9)	11–14 (12.3)
Dorsal +Clavus +Anal fin rays	ND	ND	48–57 (52.0), *n* = 10	51-55 (54.2), *n* = 7	50–52 (51.3)	47–50 (48.5)
Ossicles on clavus	11–13	12	8-15 (11.8), *n* = 10, >60 cm TL	11-16 (12.8), *n* = 7, >59 cm TL	5–7 (5.8)	8–9 (8.6)
Total vertebrae	ND	ND	ND	18, *n* = 7	ND	ND

(Continued)

TABLE 2 Continued

Species	*Mola alexandrini*				*Mola tecta*	*Mola mola*
	Holotype MZUB (unnumbered)	BMNH 1883.11.29.22	Other specimens (Sawai et al., 2018)	Present specimens	Other specimens (Nyegaard et al., 2018)	Other specimens (Sawai et al., 2018)
Morphological observations						
Shape of clavus edge	Round	Round	Round	Round, $n = 15$	Rounded with an indent, $n = 24$	Wavy (>126.4 cm TL), $n = 14$
Smooth band	Present	Present	Present	Present, $n = 15$	Present, $n = 25$	Present, $n = 34$
Smooth band backfold	Absent	Absent	Absent, $n = 19$; present, $n = 1$	Absent, $n = 15$	Present, $n = 24$	Absent, $n = 34$
Head bump	Present	Present	Present (>162.5 cm TL), $n = 12$	Absent, $n = 15$	Absent, $n = 25$	Absent, $n = 34$
Shape of body scale	Rectangular	Rectangular	Rectangular (>162.5 cm TL), $n = 11$	Conical with branching of tip (<90 cm TL), $n = 7$	Conical with branching of tip, $n = 17$	Conical with branching of tip (>109.9 cm TL), $n = 14$
Chin bump	Present	Present	Present (>135.0 cm TL), $n = 13$	Absent (<90 cm TL), $n = 15$	Absent, $n = 25$	Absent, $n = 34$

ND, no data; TL, total length.

TABLE 3 Measurements of *Mola alexandrini* from this study and previous literature.

Species	*Mola alexandrini*				
	Holotype MZUB (unnumbered)	BMNH 1883.11.29.22	Other small specimens (means) (Sawai et al., 2018)	Other large specimens (means) (Sawai et al., 2018)	Present specimens (means)
Total length (cm)	190.0 TL	229.1 TL	29.3–51.5, $n = 6$	181.3–269.0, $n = 5$	58.9-87.1 TL, $n = 7$
% of TL					
Pre-clavus band length	76.3	81.2	82.9–87.5 (84.9), $n = 6$	80.3–83.1 (81.9), $n = 5$	82.2-85.2 (83.1)
Pre-anal fin length	ND	ND	ND	ND	56.0-62.5 (59.1)
Pre-dorsal fin length	ND	ND	ND	ND	51.6-64.5 (60.9)
Pre-pectoral fin length	ND	ND	ND	ND	313-34.2(32.4)
Clavus length	ND	ND	ND	ND	15.1-18.5 (16.7)
Clavus width	ND	ND	ND	ND	53.0-67.1 (61.3)
Dorsal fin height	ND	ND	ND	ND	45.0-53.0 (49.1)
Dorsal fin base length	ND	ND	ND	ND	21.4-28.7 (25.0)
Anal fin height	ND	ND	ND	ND	42.8-50.9 (47.5)
Anal fin base length	ND	ND	ND	ND	22.3-27.4 (23.7)
Pectoral fin length	ND	ND	ND	ND	11.6-14.8 (13.5)
Pectoral fin base length	ND	ND	ND	ND	6.0-8.1 (7.0)
Head length	ND	ND	ND	ND	27.3-28.2 (27.6)
Head depth	ND	ND	ND	ND	37.4-49.0 (44.1)

(Continued)

TABLE 3 Continued

Species	Mola alexandrini				
	Holotype MZUB (unnumbered)	BMNH 1883.11.29.22	Other small specimens (means) (Sawai et al., 2018)	Other large specimens (means) (Sawai et al., 2018)	Present specimens (means)
% of TL					
Head bump length	18.6	11.0	9.9–14.2 (11.4), n = 5	7.7–16.0 (10.6), n = 5	8.6-13.6 (11.4)
Snout length	ND	ND	ND	ND	12.7-15.3 (13.8)
Orbit diameter (Horizontal)	ND	ND	ND	ND	5.0-6.1 (5.6)
Orbit diameter (vertical)	ND	ND	ND	ND	4.2-5.1 (4.7)
Post-orbital length	ND	ND	ND	ND	10.7-15.8 (11.7)
Inter-orbital width	ND	ND	ND	ND	13.1-17.1 (15.7)
Upper jaw length	ND	ND	ND	ND	3.7-5.6- (4.6)
Lower jaw length	ND	ND	ND	ND	3.4-5.3 (3.9)
Pre-pectoral fin depth	ND	ND	ND	ND	56.0-65.8 (61.5)
Maximum body depth	65.3	57.4	67.8–72.7 (69.6), n = 6	56.3–62.8 (59.6), n = 5	64.7-71.1 (67.9)
Total body depth	ND	ND	150.5–160.0 (154.6), n = 4	112.9–155.8 (129.0), n = 5	147.5-157.6 (152.6)

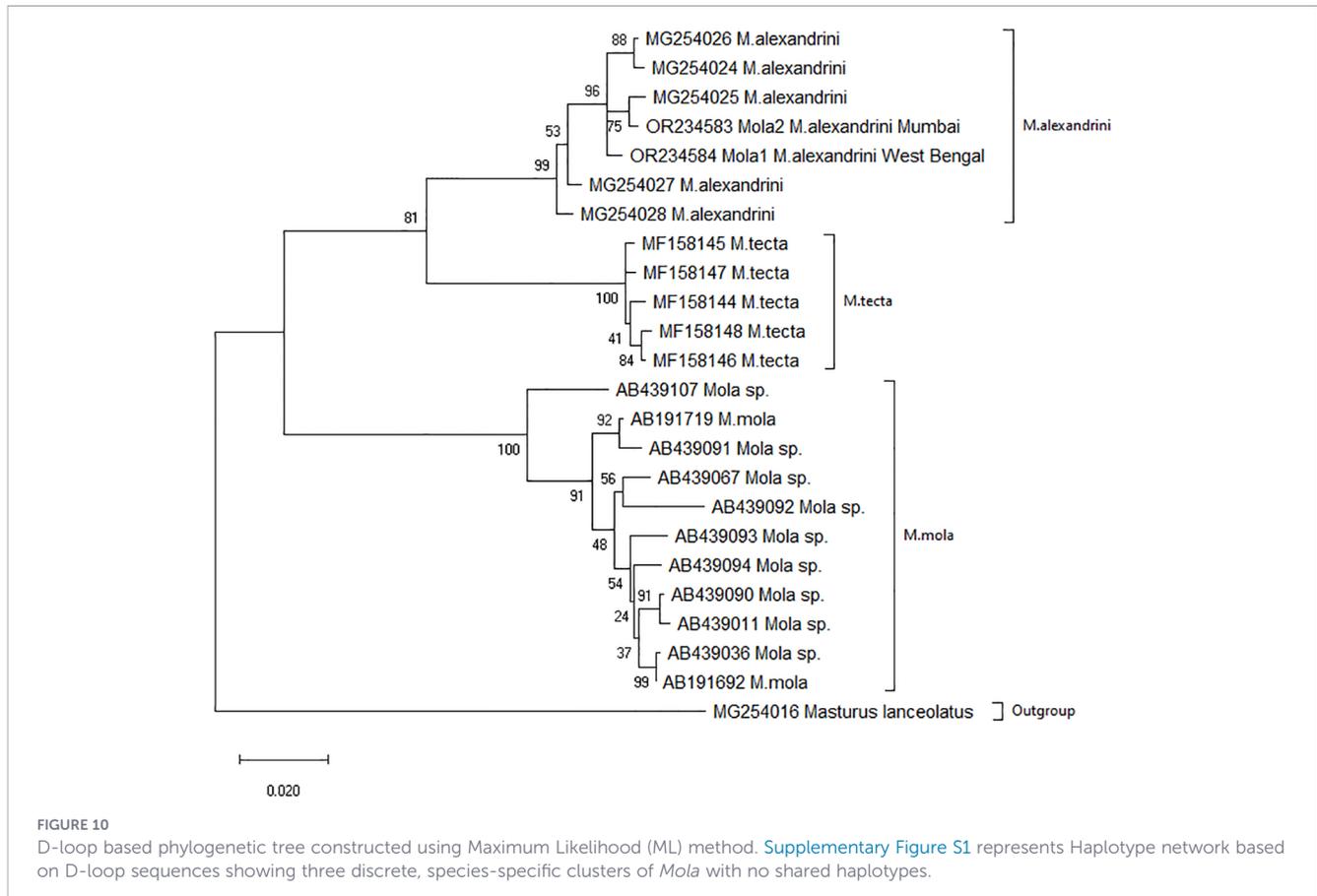ND, no data; TL, total length.

Biology

Analysis of gut contents from five specimens (58.9-87.1 cm TL) revealed that major prey items of *M. alexandrini* include octopus (*Cistopus* sp.), cuttlefish (*Sepiella inermis*), clupeids (*Setipinna* sp.), shrimps (*Solenocera* sp.), unidentified jellyfish and cestode parasites (Figure 8). All specimens exhibited heavy infestations of parasites in the liver and gills (identification in progress). Gonad morphology differed between sexes, with females possessing a single-lobed, ball-shaped ovary, while males had bilobed, elongated, rod-like testes (see Figure 7).

Fishery and utilization

In India, these fishes are seldom caught as by-catch in various gears such as trawls, gillnets, ring seines, and hook and line (see Table 1). Despite the ocean sunfish meat being considered a delicacy in countries like Taiwan and Japan, there are no reports of consumption in India, possibly due to their unique shape and lack of nutritional information. Often, these fish are not auctioned as traders struggle to find buyers due to the lack of consumer demand and low market value for these species domestically (personal observation).

Phylogenetic analysis

The final alignment of the COI sequences of Molidae comprised 642 characters, of which 38 were parsimony-informative. The Maximum Likelihood (ML) phylogenetic tree constructed using the Kimura 2-parameter model with a discrete Gamma distribution (K2P+G) recovered three major clades (Figure 9). All major clades were supported by bootstrap values greater than 70%. The sequences generated in this study clustered within the clade corresponding to *Mola alexandrini*. The trimmed alignment of D-loop sequences, including newly generated sequences and those retrieved from databases, consisted of 845 characters, with 148 parsimony-informative sites. The ML tree inferred using the Tamura 3-parameter model with Gamma distribution (T92+G) also recovered three distinct clades corresponding to the three species included in the analysis (Figure 10). Each *Mola* clade was monophyletic and supported by ML bootstrap values exceeding 70%. Pairwise genetic divergence among species groups, estimated after complete deletion of missing data, is presented in Table 4. Within *Mola mola*, samples from the Atlantic and Pacific Oceans showed a net nucleotide sequence divergence of 3.8% in the D-loop region. The D-loop TCS haplotype network also showed three discrete clusters with no shared haplotypes among species

FIGURE 10
D-loop based phylogenetic tree constructed using Maximum Likelihood (ML) method. Supplementary Figure S1 represents Haplotype network based on D-loop sequences showing three discrete, species-specific clusters of *Mola* with no shared haplotypes.

(Supplementary Figure S1); well separated by multiple mutational steps, indicating clear genetic divergence and supporting species-level differentiation.

Discussion

In the present study, *Mola alexandrini* is documented based on seven fresh specimens and eight photographic records collected from both the east and west coasts of India. An integrative assessment combining literature review, morphological examination, and molecular characterization using two mitochondrial markers (COI and D-loop) indicates that *M. alexandrini* is widely distributed along the Indian coastline. In contrast, the occurrence of *M. mola* in Indian waters appears to be absent or remains doubtful. Sawai et al. (2018) confirmed that *M. ramsayi* is not a valid species, whereas *M. alexandrini* is a distinct species with a widespread distribution across the world's oceans,

including the Indian coast. Their findings based on morphological and genetic evidence, further pointed out that the distribution of *M. mola* is biased towards the Northern Hemisphere, with no verified records from the Indian Ocean. In contrast, *M. tecta* appear to be distributed predominantly in the temperate waters of the Southern Hemisphere (Nyegaard et al., 2018). Nevertheless, the distributional ranges of all *Mola* species warranted re-evaluation in future studies due to widespread species confusion and persistent taxonomic uncertainties, particularly concerning *M. mola* (Sawai et al., 2018).

Despite recent advances in species-level taxonomic resolution and improved clarity regarding the geographic distributions of *Mola* species, several recent studies continued to misidentify and report ocean sunfishes from Indian waters as *M. mola* (Ray et al., 2019; Fullonton et al., 2020; Kar et al., 2020; Thakurdas et al., 2022; Devi et al., 2023). Such misidentifications likely arise because many of these records involve large individuals, for which the collection of detailed morpho-meristic data in the field is particularly challenging. Counts of dorsal, anal, and clavus fin rays and associated ossicles are difficult to obtain accurately and are often

TABLE 4 K2P genetic distances (D-loop above diagonal, COI below diagonal) over sequence pairs between groups of *Mola* species.

Species	M. alexandrini	M. tecta	M. mola	M. lanceolatus
M. alexandrini	—–	8.72	12.70	17.39
M. tecta	1.85	—–	13.88	15.87
M. mola	5.08	4.94	—–	18.43
*Masturus lanceolatus_* Outgroup	9.87	9.86	11.53	—–

under- or overestimated when assessed by tactile examination, as these structures are hidden by the thick subcutaneous gelatinous layer. Moreover, some clavus fin rays may be erroneously counted as dorsal or anal fin rays. Accurate enumeration of fin rays, ossicles, and vertebrae therefore requires dissections of medium to large specimens or X-radiography of smaller individuals; however, such approaches are often impractical for very large specimens due to difficulties associated with transport, preservation, and storage. Consequently, much of the published morpho-meristic information from Indian waters is likely biased toward the historically well-known species *M. mola*, even after recent taxonomic revisions (Nyegaard et al., 2018; Sawai et al., 2018). These limitations highlight that reliance on morphology alone is insufficient for reliable species identification in ocean sunfishes, and that an integrative approach combining morphological, anatomical and molecular evidence provides a more accurate and robust framework for resolving the taxonomy of enigmatic taxa (Roul et al., 2021; Jeena et al., 2022).

The fin ray and clavus ossicle counts observed in the present study are consistent with those reported for *M. alexandrini* by Sawai et al. (2018), including 11–12 pectoral fin rays, 16–19 dorsal fin rays, 15–17 anal fin rays, 14–25 clavus fin rays, 51–55 D+C+A fin rays, and 0–15 clavus ossicles (Table 2). In addition, diagnostic characters such as rounded clavus margin, and clavus with a smooth band lacking a back-fold were observed, in agreement with Sawai et al. (2018). However, head and chin bumps as well as lateral ridges above or below the eyes, were absent in the present specimens, likely because all individuals examined were juveniles (58.9–87.1 cm TL), as these features are known to develop with age (Sawai et al., 2018). Previous studies have shown that rectangular scale shape is a reliable diagnostic character for *M. alexandrini* in specimens exceeding 162.5 cm TL, whereas scale morphology remains uncertain in individuals smaller than 70.0 cm TL (Sawai et al., 2018). In contrast, the present study identified a conical scale shape with branching tips in specimens ranging from 58.9 to 87.1 cm TL, while scale morphology in individuals below this size range remains unresolved.

Public sequence databases such as GenBank may contain misidentified entries, particularly for morphologically conserved and taxonomically complex groups like *Mola*, with some sequences deposited prior to recent taxonomic revisions (Sawai et al., 2018). Therefore, molecular inferences based solely on public databases should be interpreted with caution, a limitation addressed here by integrating genetic data with detailed morphological and anatomical evidence. Comparative phylogenetic analyses of COI and D-loop sequences from this study and publicly available data confirm that the Indian specimens are *M. alexandrini*. While COI is effective for species-level identification in *Mola* (Nyegaard et al., 2018), the major mitochondrial noncoding region (D-loop) allows better intraspecific differentiation in closely related groups due to its relatively rapid rate of evolution (Stepien and Kocher, 1997). Phylograms of these two regions showed consistent results, supporting the taxonomic conclusions of Sawai et al. (2018). The D-loop phylogeny further revealed geographic structuring between eastern and western Pacific populations of *Mola mola*, a pattern not evident in the COI analysis and consistent with previous findings (Yoshita et al., 2009). Historically, *M. alexandrini* has been regarded as a Southern Hemisphere species by various authors (Fraser-Brunner, 1951; Heemstra, 1986; Bass et al., 2005) and has not been documented in any ocean other than the Indian Ocean. Overall, from the combined morphological and molecular evidence from this study, as well as prior research, it is clear that *M. alexandrini* is commonly distributed throughout the world's oceans including Indian water (see Figure 1).

Conclusion

This study resolves the taxonomic ambiguity surrounding ocean sunfishes in Indian waters by applying an integrative approach that combines morphological, anatomical, and molecular data. The present findings support the identification of Indian *Mola* specimens as *Mola alexandrini*, thereby refining species-level understanding within the Indian Exclusive Economic Zone. This clarification contributes to a more accurate interpretation of regional *Mola* diversity and distribution. The findings highlight the limitations of morphology-based identifications in morphologically conserved taxa that undergo substantial ontogenetic change. Difficulties associated with large body size, incomplete meristic data, and inconsistent reference sequences in public databases can perpetuate misidentifications if not carefully addressed. By integrating classical taxonomy with molecular data, this study demonstrates a robust framework for resolving such challenges and improving taxonomic reliability. Beyond systematics, accurate species identification is essential for understanding ecological patterns, fisheries interactions, and life-history traits of ocean sunfishes. The reference material and genetic data generated here provide a foundation for re-evaluating historical records and for guiding future research across all life stages (pre-juvenile, juvenile, and adult) along the Indian coast. Improved taxonomic resolution will be critical for informing species-specific conservation assessments and management strategies for ocean sunfishes in Indian waters, particularly in the context of increasing fishing pressure and limited biological data.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because this article does not contain any experimental studies with animals performed by any of the authors. Dead specimens were collected from the fish landing centers; therefore no ethical approval was required.

Author contributions

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2026.1772707/full#supplementary-material

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