



# Phylogeny, genetic diversity and divergence dating of *Monodactylus argenteus* (Linnaeus, 1758) (Actinopterygii: Monodactylidae) from marine waters of Odisha Coast, Bay of Bengal, India

Bijayalaxmi Sahu<sup>1,2</sup> • Tapan Kumar Barik<sup>2</sup> • Amiya Kumar Patel<sup>1</sup>

<sup>1</sup> Department of Biotechnology and Bioinformatics, Sambalpur University, Jyoti Vihar-768019, Burla, Odisha, India

<sup>2</sup> P.G. Department of Zoology, Berhampur University, Bhanja Bihar-760007, Berhampur, Odisha, India

## Correspondence

Amiya Kumar Patel; Department of Biotechnology and Bioinformatics, Sambalpur University, Jyoti Vihar-768019, Burla, Odisha, India

✉ [amiya\\_gene@yahoo.com](mailto:amiya_gene@yahoo.com)

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## Abstract

Among the many different types of aquatic life found in marine ecosystems, fish are the most diverse and commercially important organisms. To support their conservation and management, accurate species identification, genetic, and phylogenetic association studies are crucial. *Monodactylus argenteus*, the silvery Moony fishes were collected from Gopalpur-on-sea, Odisha Coast of the Bay of Bengal, India and identified as using traditional morpho-taxonomy methods followed by DNA barcoding using cytochrome c oxidase subunit I (COI) gene. Following identification, the phylogeny, genetic diversity, and divergence time of *M. argenteus* were investigated. The current study looked at the number of variable sites, parsimony informative sites, nucleotide diversity, and haplotype diversity. The 16 sequenced individuals of *M. argenteus* produced a total of 13 haplotypes, with 11 unique haplotypes and two shared haplotypes. There were 67 polymorphic sites, including 56 parsimony informative sites and 11 singleton variable sites with 72 mutations. Phylogenetic tree was drawn and all the sequences clustered in agreement with their species level taxonomic classification were observed. The divergence time of the *M. argenteus* species was estimated to be in the late oligocene sub-epoch, about 25.98 mya, using the RelTime maximum likelihood method. The findings of this study serve as noteworthy confirmation of the utility of DNA barcode sequences for tracking diversity of species and also contribute information on the phylogeny, genetic diversity, and divergence dating of *M. argenteus*.

**Keywords:** cytochrome c oxidase subunit I; divergence dating; DNA barcoding; silvery moony fish

## 1 | INTRODUCTION

Fish are essential aquatic creatures with over 35,000 species found worldwide and make a substantial contribution to the current vertebrate population (Zhang and Hanner 2012; Bingpeng *et al.* 2018). These species are important contributors to biodiversity, revenue generation, and the source of protein and mineral dietary supplements for humans (Ward *et al.* 2005; Rasmussen *et al.* 2009; Ug-

wumba and Ugwumba 2003). Investigating fisheries and evaluating natural reserves need the characterisation, identification, and evaluation of biodiversity (Ardura *et al.* 2013; Vartak *et al.* 2015).

Conventional classification reliant on morphology may be deceptive owing to convergent evolution. With the advent of new technical terms like DNA barcoding, identification, and systematics have changed over time

(Manktelow 2010). DNA barcoding is a new method that has been in use since 2004 for the identification of living organisms (Lange *et al.* 2004). Phylogenetics offers a more precise classification, particularly when employing molecular methods (such as DNA barcodes). In contrast to morphological traits, which are more susceptible to environmental influences, molecular characters offer more accurate representations of evolutionary relationships (Hillis *et al.* 1994). Molecular characters such as DNA or amino acid sequences are less subjective (Suárez-Díaz and Anaya-Muñoz 2008), consistent across different environments and life stages, have a high degree of resolution when it comes to differentiating closely related species (Romano and Cairns 2000), and can differentiate species that appears to be similar to the naked eye (Erwin 1989). It aids in updating or validating current taxonomy, often leading to reclassification of species or genera. Comprehending genetic divergence and gene flow facilitates research on adaptation and speciation. Phylogenetic analysis helps scientists construct a "tree of life" by shedding light on the origins of life and supporting the study of biodiversity and evolution. It identifies common ancestors, divergence points, as well as cryptic and evolutionarily distinct species. Morphological characteristics are still significant, though, as they reveal details about an organism's ecology, behaviour, and other characteristics (Anjum *et al.* 2025). For these reasons, scientists use morphological and molecular characteristics in combination to gain a thorough understanding of the taxonomic relationships across various groups of species (Pisani *et al.* 2007).

Phylogenetic analysis is crucial for understanding the origins, relationships, classification, conservation, and ecological roles of fish. It helps to locate cryptic species, tracks the dispersal and evolution of fish species across geographical regions, and supports habitat protection by revealing ecosystem-specific lineages. In fisheries management, genetic analysis offers numerous benefits, particularly through the facilitation of tools that allow for unambiguous specimen identification and stock structure evaluation (Ward 2000; Barik *et al.* 2018). Genetic data has become increasingly important for evaluating genetic variety in populations, which is critical for a species' survival in its environment. Establishing conservation priorities will be facilitated by the interpretation of genetic data (Bernatchez 1991). Several genes are targeted for identification and characterisation purposes.

Monodactylidae, often known as monos, moony-fishes, or fingerfishes, is a family of the series Eupercaria (Betancur-R *et al.* 2017). They primarily inhabit marine or brackish environments but sporadically invade freshwater areas. Particularly, *Monodactylus* species are frequently found in estuaries. There are four living species in the genus *Monodactylus*, which make up the family Monodactylidae (Fricke *et al.* 2025). Most species are popular

aquarium fish because of their silvery colour with yellow and black patterns, especially the juveniles are attractive (Nelson 1994; Froese and Pauly 2025). Beautiful silvery moonfish *Monodactylus argenteus* are popular in aquariums. The front is decorated with two vertical black lines, one passing through the eye and the other across the gill. They are more attractive when they are young because they also have a dorsal fin that is a bright yellow colour. A variety of descriptive common names, including silver moony, silver moonfish, silver batfish, diamondfish, diamond moonfish, kitefish, fingerfish, and even Malayan angel, have been given to this fish due to its disc-like shape and glossy silver hue (Froese and Pauly 2025). As no previous study using any source of data has attempted a phylogenetic analysis of the species *M. argenteus*, the current study was aimed to explore the genetic diversity, phylogeny, and divergence dating of this species were examined using the COI gene in the Bay of Bengal, Odisha Coast, India.

## 2 | METHODOLOGY

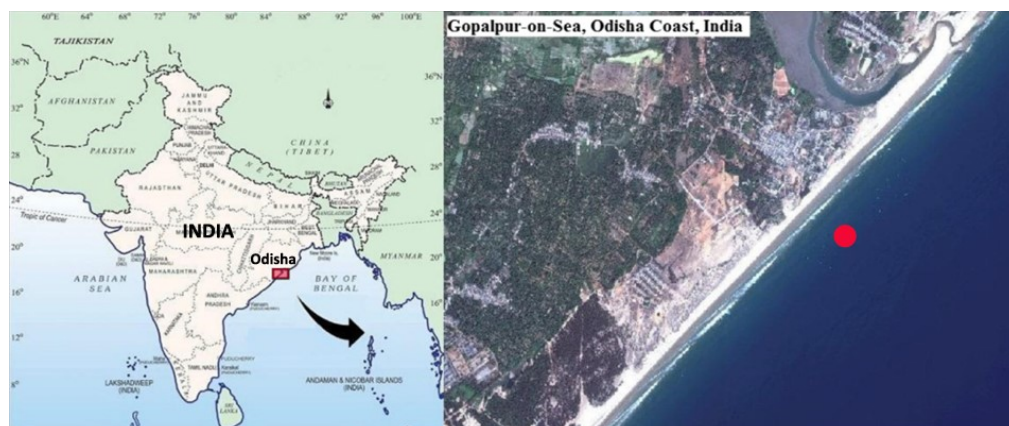
During the daily fishing activity by the local fishermen at Gopalpur-on-sea, Odisha Coast, Bay of Bengal (19.26°N 84.86°E; Figure 1); four *M. argenteus* fish were collected on 2 June 2020 and brought to the laboratory under freezing condition. According to the taxonomic characteristics listed in the leading taxonomic guides, such as Commercial Sea Fishes of India (Talwar and Kacker 1984), the specimen was carefully categorised. However, the samples were assigned to the appropriate species in accordance with the authoritative taxonomic keys, and species nomenclature follows Eschmeyer's Catalog of Fishes (Fricke *et al.* 2022). Two specimens were processed for molecular study. Right-side fin clips and lateral muscle tissue were taken out and kept in 95% ethanol under deep freezing conditions for isolation of DNA.

Total genomic DNA was isolated from the frozen muscle tissue of collected fish using the salting-out procedure (Sambrook and Russell 2001) with some minor modifications. Using a NanoDrop Lite spectrophotometer (Thermo Scientific, USA), the concentration and purity of the extracted DNA were estimated and also visualized in 1% agarose gel electrophoresis. Extracted DNA was stored at -20°C until further use.

Isolated DNA was used as a template for PCR amplification with M13-tailed oligonucleotide primers earlier reported by Ivanova *et al.* (2007), targeting the 5' region of mitochondrial COI gene (Table 1). The amplification was performed in 25 µL reaction mixture of 100 ng template DNA, 10 µmol L<sup>-1</sup> of each specific primer, 10 mmol L<sup>-1</sup> of dNTPs mix, 2 units of Taq DNA polymerase (Himedia Laboratories), and 1X PCR assay buffer containing 20 mmol L<sup>-1</sup> MgCl<sub>2</sub>. The PCR conditions were initial denaturation at 95°C for 2 min, followed by 35 cycles of 30 s at

94°C, 30 s at 54°C, 1 min at 72°C, and a final extension at 72°C for 10 min. The PCR products were visualised by 1.5% agarose gel electrophoresis. Before sequencing, PCR

products were purified, and the most intense purified products were sequenced commercially.



**FIGURE 1** Gopalpur-on-sea, Bay of Bengal, Odisha Coast, India.

**TABLE 1** PCR primers used for the DNA barcoding.

Primer	Primer sequence (5' to 3')
VF2_t1	TGTAACGACGGCCAGTCAACCAACCACAAAGACATTGGCAC
FR1d_t1	CAGGAAACAGCTATGACACCTCAGGGTGTCCGAARAAYCARAA
FishF2_t1	TGTAACGACGGCCAGTCGACTAATCATAAAGATATCGGCAC
FishR2_t1	CAGGAAACAGCTATGACACTTCAGGGTGACCGAAGAATCAGAA

\*Note: COI amplification in our study was done by the use of Fish cocktail primers (1:1:1:1).

Using the software Bioedit, both the forward and reverse sequences were reviewed manually. The noisy sequences were trimmed at both ends, and the quality values of the sequences were considered. The accurate barcode sequences were created, aligned and further consensus sequences were constructed (Hall 1999). Using ExPASy, the protein-coding sequences were converted to amino acids and checked for the presence of stop codons. In order to determine whether the sequence belonged to the locus targeted, the NCBI (National Center for Biotechnology Information, [www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov)) web server's BLASTN programme was used (Altschul *et al.* 1990). The fragment that showed 100% alignment with no gap or insertions/deletions was chosen. The sequences were then submitted to NCBI database, and accession numbers were obtained (Ref. MZ405085 and ON384430).

Overall diversity comparison and pairwise comparison between different places were done in order to derive haplotype diversity. To ascertain the genealogical relationships of haplotypes, a median-joining network (Bandelt *et al.* 1999) was built in PopART v1.7 (<http://popart.otago.ac.nz>). Even if they exist, mobile species exposed to genetic statistical differentiation tests frequently don't show any population subdivision (Palumbi and Warner 2003). Using DnaSp v6.12.03, intra-population polymorphism of the gene sequences was analysed. Additionally, analyses were done on the number of variable sites, nucleotide diversity (Jukes and Cantor 1969), haplotype diversity (Nei and Tajima 1983), and

parsimony informative sites. The Tajima's D test (Tajima 1989), Fu and Li's D and F tests (Fu and Li 1993) were conducted to test the neutrality using the dataset.

Phylogenetic tree was built with the method of maximum likelihood (ML) using MEGA X software (Kumar *et al.* 2018). For this study, 42 COI sequences were used, 16 of which were from the same species *M. argenteus*, 2 from *Monodactylus falciformis*, and the rest from various families of the series Eupercaria, with the exception of *Karalla dussumieri* from the family Leognathidae, which was used as an outgroup. Excluding one sequence generated in this study, all sequences were obtained from NCBI database. As only the sequences of *M. argenteus* and *M. falciformis* of the family Monodactylidae were available in the NCBI database, and there was no more sequence information from Monodactylidae family in the public databases, the sequences of sister families were included in this analysis. For ML analysis, the model test was done. Using the best-fitting model, ML phylogenetic tree was constructed with a total of 1000 bootstrap replicates. The phylogenetic positions of the sampled species in cognation to the same species, other species of the family Monodactylidae, and species of the sister families respectively were investigated using comprehensive mitochondrial COI sequence datasets.

The RelTime with ML technique in MEGA X was used to estimate the divergence time of the species *M. argenteus* (Kumar *et al.* 2018). The divergence time was calculated using the sequences of the mtCOI genes of *M. ar-*

*genteus*, as well as a few other sequences obtained from GenBank. Since the RelTime method only needs the minimum and/or maximum calibration boundaries, we selected the following fossil evidence time boundaries from the original studies: (1) fossil evidence of the genera *Scolopsis* and *Gerres* (25.2 – 46 Mya), for the entirety of the group Monodactylidae (Rabosky et al. 2013, 2018). The outgroup clade was automatically eliminated from the analysis under the presumption that the equivalent rates of evolution between the in-group and out-group sequences could not be tested.

### 3 | RESULTS

*Monodactylus argenteus* (Figure 2) were identified based on morpho-taxonomy (Table 2), which was then reconfirmed by molecular taxonomy using DNA barcoding. Two COI amplicons of size 615 bp and 633 bp of *M. argenteus* were generated. No insertions/deletions, heterozygous sites, or stop codons were observed, supporting that the amplified sequences constitute the functional mitochondrial COI sequences. BLAST outcomes of the nucleotide sequence succeeded to identify sequence similarity with species identity of >99%.



**FIGURE 2** *Monodactylus argenteus*, collected from Gopalpur-on-sea, Odisha Coast, Bay of Bengal, India.

Genetic diversity is the differences in genes and genotypes within a species that play an important role in the existence of a species. The nucleotide composition of our sequence was 30.24% (T), 27.32% (C), 24.72% (A) and 17.72% (G) respectively whereas the average nucleotide composition of all the 16 sequences was 30.16% (T), 26.47% (C), 24.89% (A) and 18.48% (G) respectively. The GC content (45.04%) in our generated sequence was slightly higher than the average GC content (44.95%) of all 16 sequences. The nucleotide frequencies were 24.84% (A), 30.12% (T/U), 26.64% (C), and 18.40% (G). The transition/transversion rate ratios were  $k_1 = 11.654$  (purines) and  $k_2 = 8.068$  (pyrimidines). The overall transi-

tion/transversion bias was found to be  $R = 4.808$ . The Consortium for the Barcode of Life (CBOL) has advised to use the Kimura-2-parameter model (K2P) to determine genetic distance (Kimura, 1980; Shen et al., 2016). In the current study, the intraspecific and intragenus genetic distances between the organisms were determined using the K2P model. The average K2P distances of the COI sequences of the *M. argenteus* at intraspecies level was 0.047.

**TABLE 2** Morphometric and meristic data of *Monodactylus argenteus*.

Characters	Measurements
Total length (TL)	13.4 cm
Standard length (SL)	10.8 cm
<b>% of total length</b>	
Fork length	93
Anal fin length	33.9
Dorsal fin with soft ray length	76.7
Caudal fin length	24.7
Caudal height	30.1
Head length	23.8
Pre-dorsal length	36.2
Pre-anal length	34.1
Pre-pectoral length	24.4
Pre-pelvic length	24.5
Body depth	66.4
<b>% of head length</b>	
Eye diameter	41.2
Snout length	18.5
Pre-orbital length	15.2
<b>Meristic counts</b>	
Dorsal fin (spine + soft rays)	VIII+30
Pectoral fin (soft rays)	18
Anal fin (spine + soft rays)	III+31
Pelvic fin (spine + soft rays)	I+3

The general topology of the median-joining network (Figure 3) corresponded with the phylogenetic tree (Figure 4). There was one high frequency, widespread haplotype at the centre of the network, radiated by some small low frequency derived haplotypes. There were 67 polymorphic sites, of which 56 (83.58%) were parsimony informative sites and 11 (16.42%) were singleton variable sites. Within the dataset, a total of 72 mutations were discovered. The 16 sequenced individuals produced a total of 13 haplotypes, with 11 of them being unique haplotypes (84.62%) and two being shared haplotypes (15.38%). The dominant haplotype was Hap6 (sequences of Saudi Arabia, Madagascar, Mozambique) while the other shared haplotype was Hap3 (sequences of Kerala, India, and Sri Lanka). The COI sequence of the collected specimen represented a unique haplotype, which was only distributed over Odisha Coast of the Bay of Bengal. The nucleotide diversity ( $\pi$ ) and haplotype diversity ( $H_d$ )

of *M. argenteus* populations in this study were 0.05 and 0.967 respectively.

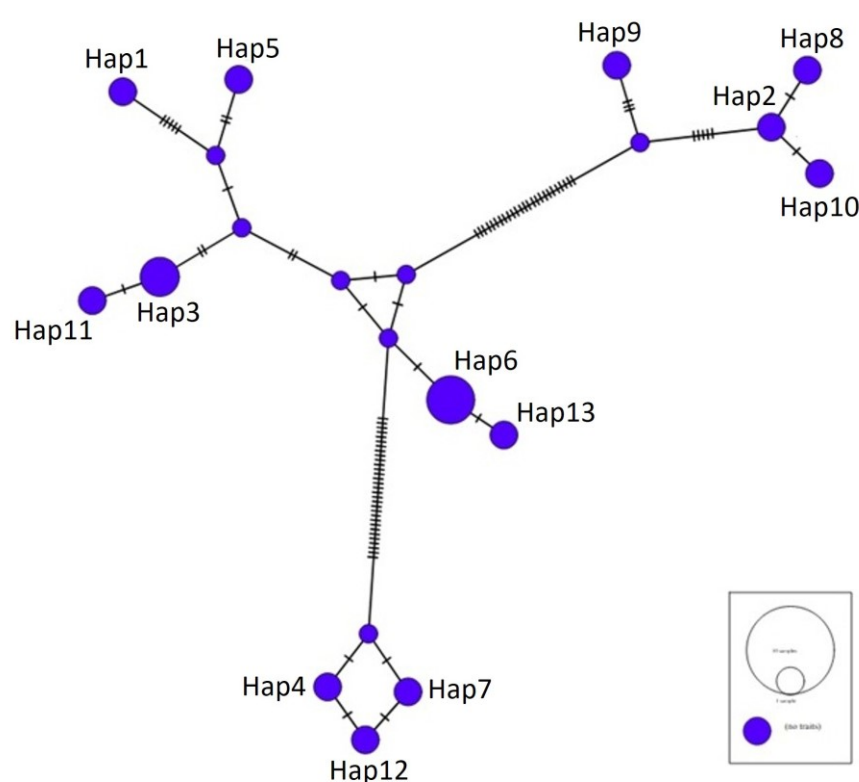
HKY+G+I was found as the best-fitting model with BIC value of 16434.053 for ML analysis. In ML tree, sequences from the same species were clustered together, displaying homology and more or less conspecific distances between them (newly obtained in this work and retrieved from NCBI). Additionally, sequences from the same family that were retrieved from NCBI were grouped together in a single cluster. The maximum likelihood phylogenetic tree (Figure 4) showed the genetic divergence between the families of the series Eupercaria. The generated sequence of *M. argenteus* showed close similarity with the sequence of the same species reported from Tamil Nadu, India. The mtDNA sequences of *M. argenteus* were separated into four major clades. Clade I consisted of five sequences, which were from Kerala, India; Sri Lanka; Kansas, USA; Tamil Nadu, India and Gopalpur-on-sea, Odisha, India, and Clade II consisted of four sequences from Saudi Arabia; Mozambique; United Arab Emirates, and Madagascar. Clade III consisted of sequences from Australia; Philippines; Micronesia; Taiwan while Clade IV consisted of the sequences from China and Vietnam. Clade I was the most geographically inclusive with sequences from 5 localities. The average K2P distance of the COI sequences of the family Monodactylidae was 0.118 at interspecies level. The family Monodactylidae

was evolutionary closer to the family Emmelichthyidae and then to the family Lutjanidae (Figure 4).

The *Monodactylus* genus was estimated to have diverged at the beginning of the Eocene epoch. According to estimates, the divergence of the *Monodactylus* clade from its common ancestor took place in the early Eocene sub-epoch around 52.92 Mya, and that of the *M. argenteus* species during the early Oligocene sub-epoch about 30.13 Mya (Figure 5).

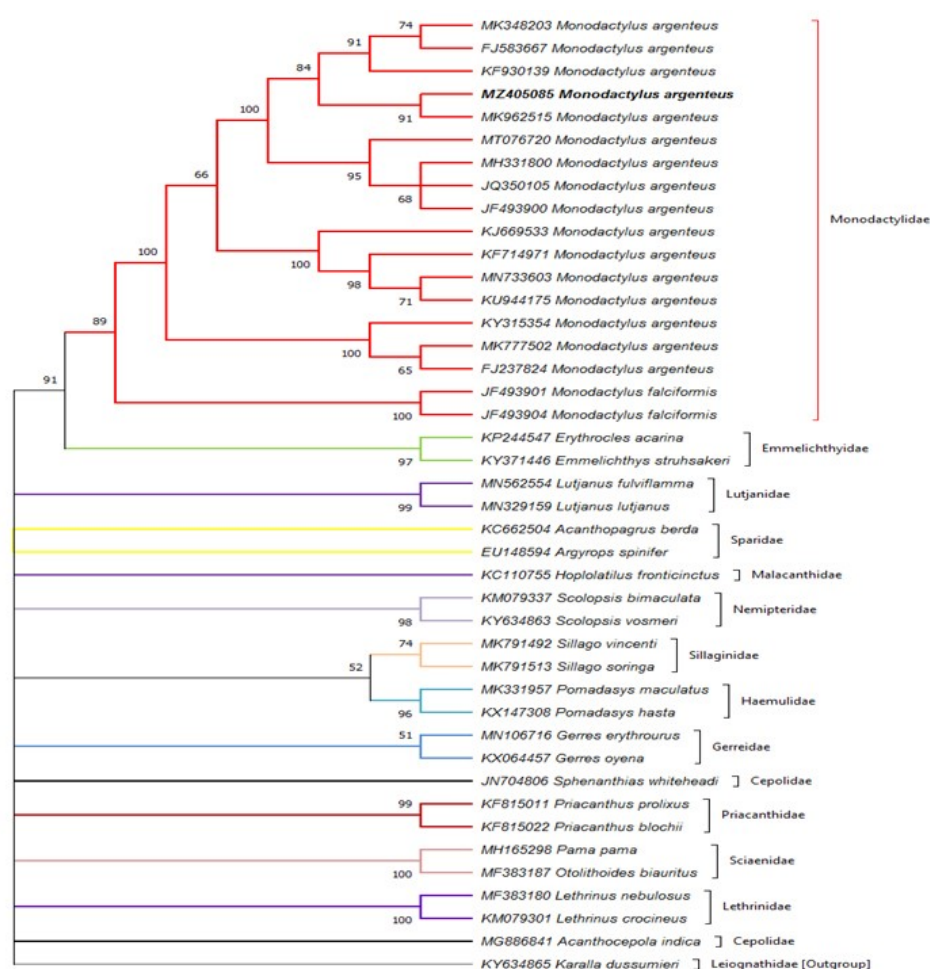
#### 4 | DISCUSSION

In a marine ecosystem, factors that affect dispersals, including as ocean currents, historical variation, and geographic distance, along with differences in dispersion ability and habitat discontinuities, have a significant impact on the evolution of population structure (Saarman *et al.* 2010). Dispersal is a very important, dynamic process, and mounting data suggests that it may contribute significantly to the marine invasion on a number of levels. While the creation and maintenance of biodiversity (Levene 1953; Gavrillets 2003) and the contraction and extension of species' geographic ranges (Kirkpatrick and Barton 1997), as well as the evolutionary dynamics of species interactions, all depend heavily on migration to the local environment (Kaltz and Shykoff 1998). We can gain critical insights into these processes using genetic studies (Barik *et al.* 2020).

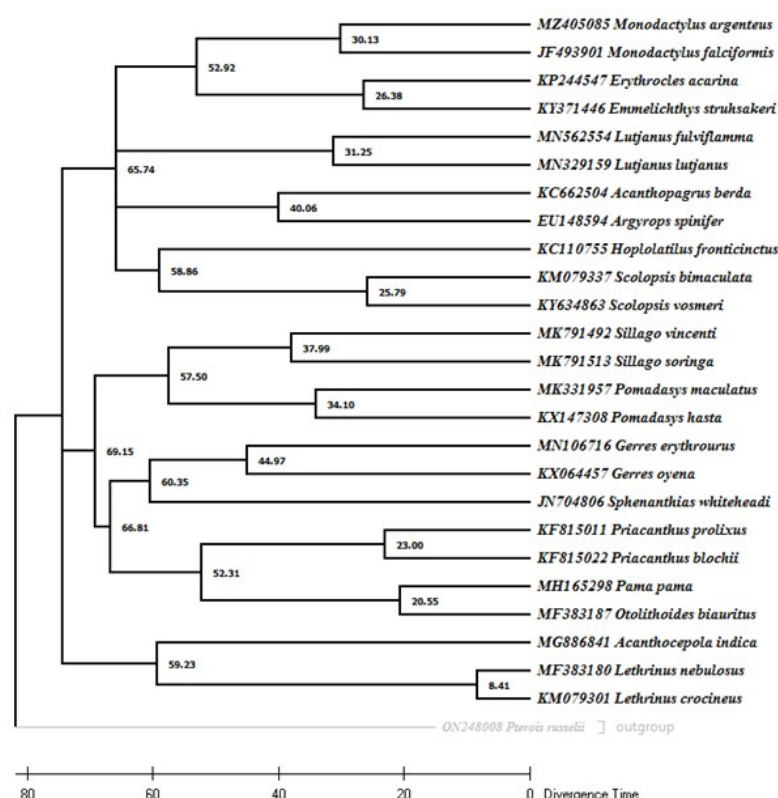


**FIGURE 3** Median-joining haplotype networks of COI gene of *Monodactylus argenteus*. Size of the circles designates the frequencies of individual appear in sample. Mutations are represented by lines, and the rate of mutation is shown by dashes along the lines.





**FIGURE 4** Maximum likelihood phylogenetic tree for *Monodactylus argenteus* based on Hasegawa-Kishino-Yano model (Hasegawa *et al.* 1985). Tree with highest log likelihood (-7777.49) was shown. The percentage of trees in which the associated taxa clustered together was shown next to the branches. Branches resulting in partitions with less than 50% bootstrap replicates were collapsed. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.7772)). The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 28.92% sites). The sequence in bold was generated in the study. Accession No.: MZ405085 was generated in the present study.



**FIGURE 5** Time-calibrated phylogenetic tree of family Monodactylidae. Time tree was inferred using Tamura-Nei substitution model (Tamura and Nei 1993) and RelTime method to the user-supplied phylogenetic tree (Tamura *et al.* 2012, 2018). Branch lengths of phylogenetic tree were calculated using Maximum likelihood (ML) method and the General Time Reversible (GTR) substitution model (Nei and Kumar 2000). Estimated log likelihood value of the tree is -7320.35. Discrete Gamma distribution was used to model evolutionary rate differences among sites [5 categories (+G, parameter = 0.5649)]. The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 28.58% sites). The analysis involved 26 nucleotide sequences. Numbers on the branches represent the time (in Mya) of different nodes. Accession No.: MZ405085 was generated in the present study.

*Monodactylus argenteus* was reported earlier in Chilika Lagoon, Odisha (Mohapatra *et al.* 2007); however, it was recorded for the first time in the Gopalpur-on-sea of the Odisha Coast, Bay of Bengal. The nucleotide composition of the COI gene sequences of *M. argenteus* showed that AT content (55%) is higher than GC content (45%). Rate of transition/transversion ratio ( $k_1$  &  $k_2$ ) and overall transition/transversion bias ( $R$ ) showed that the transitions were more recurrent compared to the transversions, because of higher  $k_1$ ,  $k_2$ , and  $R$  value (i.e., more than 1). At the first codon position in *M. argenteus* species, the utilization of T (16.7%) was the lowest as compared to other bases C (26.8%), A (25.5%), and G (31%). However, T (41.9%) was used the highest in the second codon position, and the other bases were A (15.1%), C (28.3%), and G (14.7%). At the third codon position, the usage of G (9.8%) was the least frequent, whereas the use of other bases was A (34%), T (31.9%), and C (24.3%). Surprisingly, the third codon position in COI gene sequences of *M. argenteus* clearly favours the anti-G bias, having the least usage of G (9.8%). The second codon position favours the T bias, which is in contrast with the first codon position, clearly showing anti-T bias, which was supported by earlier studies (Wang *et al.* 2014; Bingpeng *et al.* 2018; Barik *et al.* 2021). The codon positions of mitochondrial genes underwent varied degrees of base-mutation selection pressure during the evolution of species, resulting in base use bias in codon sites. The combinational impact of both neutral and selection pressure on a genome is assessed by the codon use analysis. Higher haplotype diversity and lower nucleotide diversity in *M. argenteus* indicated the modest level of genetic variability in the populations under study. Tajima's  $D$  values of *M. argenteus*, considering mutations and also the segregating sites were positive, which indicated balancing selection or decrease in population size (Tajima 1989; Stajich and Hahn 2005). These inferences were also supported by Fu and Li's  $D$  and  $F$  test values. However, all these values did not reach the level of significance. The *Monodactylus* genus was estimated to have diverged at the beginning of the Eocene epoch. Based on molecular dating phylogeny, the *Monodactylus* genus had radiated from the common ancestor in the early Eocene sub-epoch, around 52.92 Mya, and that of *M. argenteus* was in the early Oligocene sub-epoch at about 30.13 Mya. This kind of circumstance demonstrated that the various morphological defining traits are likely the result of the selected environmental pressure. The species clustered with their respective group despite having diverged at distinct times. The family Monodactylidae was evolutionary closer to the family Emmelichthyidae and then to the family Lutjanidae, which was inferred in the maximum likelihood analysis of the current study.

The species must have genetic variation in order to

live and adapt to changing ecological conditions (Patil *et al.* 2016). The present study is based on the genetic and phylogenetic analysis of the fish species *M. argenteus* (Linnaeus 1758) from Gopalpur-on-sea, Odisha Coast, Bay of Bengal, using DNA barcoding. In order to identify an individual as belonging to a specific recognised species, DNA barcoding uses a genetic marker. Even among species belonging to the same genus, the single gene locus sequence of the same species generated high bootstrap-supported clusters with no interspecific overlap. One can deduce that there is no geographical structure from the haplotype network. The groups under study have a moderate level of genetic diversity, as evidenced by the high haplotype diversity and low nucleotide diversity.

# CONFLICT OF INTEREST

The author declares no conflict of interest.

# AUTHORS' CONTRIBUTION

Conceptualization: BS, TKB & AKP, Methodology: BS & TKB, Validation: BS, TKB & AKP, Formal analysis: BS, Investigation: BS & TKB, Resources: BS, TKB & AKP, Writing – Original Draft Preparation: BS, Writing – Review & Editing: BS, TKB & AKP, Visualization: BS, TKB & AKP, Supervision: TKB & AKP.

# DATA AVAILABILITY STATEMENT

The datasets have been deposited in the NCBI database (accession numbers MZ405085 and ON384430).

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**B Sahu**  <https://orcid.org/0009-0000-0240-7048>

**TK Barik**  <https://orcid.org/0000-0003-3814-4061>

**AK Patel**  <https://orcid.org/0000-0002-1619-3607>