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Revealing phylogenetic relationships of Cyprinidae based on DNA barcoding in Merangin Jambi Geopark, Indonesia

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Abstract. *Sukmono T, Kaswari T, Utomo PEP, Wulandari T, Wibowo SE, Rolin F, Nurjirana. 2026. Revealing phylogenetic relationships of Cyprinidae based on DNA barcoding in Merangin Jambi Geopark, Indonesia. Biodiversitas 27 (3): d270317. https://doi.org/10.13057/biodiv/d270317.* Cyprinidae, a dominant freshwater fish family, plays a crucial role in biodiversity and ecosystem functioning. The Merangin Jambi Geopark, under evaluation for the UNESCO Global Geopark Network, hosts a rich freshwater fish fauna, but morphological identification is challenging due to overlapping characters. This study employed DNA barcoding of the mitochondrial COI gene to identify species and investigate phylogenetic relationships of Cyprinidae. A total of 26 individuals representing 14 species across 10 genera were analyzed. The Cytochrome C Oxidase subunit I (COI) gene (~650 bp) was amplified and sequenced. Sequence analysis was performed using Basic Local Alignment Search Tool (BLAST), and a phylogenetic tree was constructed in MEGA 12. Sequence similarity ranged from 88.11% to 99.56%, with most species exceeding 96% identity, indicating strong intraspecific homogeneity and clear intergeneric divergence. Genetic distances ranged from 0.000 to 0.179, reflecting population stability in species such as *Barbodes lateristriga* and *Rasbora spilotaenia*, and high divergence in species like *Luciosoma spilopleura* and *Epalzeorhynchos kalopterus*. Phylogenetic reconstruction revealed two major clades, with samples clustering consistently with GenBank reference sequences, confirming accurate species identification and taxonomic placement. Based on IUCN status, most species were categorized as Least Concern, though several were Data Deficient or Not Evaluated, highlighting the need for local conservation attention. These findings demonstrate that DNA barcoding effectively complements morphological taxonomy and provides a robust framework for biodiversity monitoring. Furthermore, the study contributes to local conservation by informing habitat protection, species management, and sustainable freshwater resource utilization in the Merangin Jambi Geopark.

Keywords: Biodiversity conservation, COI gene, freshwater fish, genetic diversity, species identification

INTRODUCTION

Merangin Geopark is one of the most valuable natural assets of Jambi Province, situated in Merangin District along the Batang Merangin River. The area was officially recognized as a member of the Global Geopark Network (GGN) under UNESCO during the 216th Executive Board Session in Paris, France, on May 24, 2023. The geopark is managed under three main pillars: geodiversity, cultural diversity, and biodiversity. Research on geological and paleontological aspects of Merangin Geopark has long attracted national and international scholars, while its biodiversity highlights ecological interconnectedness and shared responsibility for conservation (Prasetio et al. 2017; Utama et al. 2023). Despite its ecological importance, the ichthyofaunal diversity of Merangin Geopark has not been comprehensively explored. Investigating fish diversity and habitats is crucial because the geopark is located along the Batang Merangin River, particularly from the middle to downstream sections. However, fish communities in the area face severe threats from illegal gold mining activities. The use of dredgers, excavators, and needle-hole mining methods has led to water quality degradation, reduced habitat carrying capacity, and loss of local fish species (Romiyanto et al. 2015; Yulianti et al. 2017; Farisi et al. 2022; Mustafa 2024).

Among the ichthyofauna recorded in the geopark, Cyprinidae represent the most species-rich and ecologically important family. Despite their dominance, accurate species identification remains problematic because morphological characters often overlap among taxa. This creates uncertainty in taxonomic resolution and obscures our understanding of their evolutionary relationships within the Geopark. Thus, there is a pressing need to apply molecular approaches to clarify Cyprinidae diversity and their genetic connectivity in this unique ecosystem.

A study by Sukmono et al. (2022) documented 28 fish species in the geopark, representing 25 genera and 11 families. The most dominant were Cyprinidae, Sisoridae, and Botiidae, with Cyprinidae being the richest, comprising 15 species such as *Barbodes binotatus* (Valenciennes, 1842), *Crossocheilus oblongus* (Kuhl & Van Hasselt, 1823), *Labiobarbus leptocheilus* (Valenciennes, 1842), *Osteochilus microcephalus* (Valenciennes, 1842), *Tor tambroides* (Bleeker, 1854), and *Tor tambra* (Valenciennes, 1842). Most Cyprinids are adapted to fast-flowing, rocky river habitats, with special traits enabling them to cling to substrates or resist strong currents (Kottelat et al. 1993). However, morphological identification of Cyprinidae is challenging due to high similarity in body form among species. Such resemblance often reflects genetic homology inherited from common ancestors (Marzouk 2016). Phylogenetic relationships may be clarified using morphology- or molecular-based approaches. Previous works (McLennan 1994; Jonsson and Jonsson 2011) highlight that species in similar habitats tend to evolve comparable morphologies and behaviors, complicating taxonomy but offering insights into evolutionary processes.

These morphological similarities may conceal cryptic species, resulting in taxonomic ambiguities that cannot be resolved by morphology alone. Advances in molecular techniques, particularly DNA barcoding, have addressed these limitations. DNA barcoding has been widely applied in fish identification, proving effective in overcoming taxonomic difficulties (Ankola et al. 2021; Nair et al. 2024). DNA barcoding has shown success in fish species identification (Sukmono et al. 2015). The Cytochrome C Oxidase I (COI) gene has become the most commonly used marker for distinguishing fish and invertebrate species (Andújar et al. 2018; Fiteha et al. 2020; Malkani et al. 2022). DNA barcoding has successfully revealed genetic and phylogenetic structures in diverse taxa, including cephalopods (Wen et al. 2017), flying fishes (Exocoetidae) (Gordeeva and Shakhovskoi 2017), bagrid catfishes in China (Zou et al. 2020), seabreams from the eastern Atlantic (Nuryanto et al. 2023), the blue swimming crab (*Portunus pelagicus* (Linnaeus, 1758)) (Joesidawati et al. 2023), and serranid fishes in Raja Ampat (Ayu et al. 2024). Integrating DNA barcoding with other molecular approaches has advanced fisheries management and biodiversity conservation strategies (Pavan-Kumar et al. 2020; Elías-Gutiérrez et al. 2021; Shetty and Shingadia 2023). Building on the morphological survey by Sukmono et al. (2022), this study specifically aims to: (i) identify Cyprinidae species molecularly using COI barcoding; (ii) analyze intra and interspecific genetic distances; and (iii) reconstruct phylogenetic relationships. The resulting data are expected to complement morphological identification and provide a robust foundation for biodiversity monitoring and freshwater fish conservation in Merangin Geopark.

MATERIALS AND METHODS

Study area

This study conducted the fish sampling along the Batang Merangin River, a part of the Merangin Geopark area in Merangin District, Jambi Province, Indonesia. The sampling stations were determined using a purposive method, taking into account the conditions of the Geopark sites, the presence of rapids, local fishing locations, and river estuaries. Samples were collected from four stations: Station 1 (Air Batu Village), Station 2 (Fossil Wood area), Station 3 (Pulau Batu area), and Station 4 (Muara Karing Waterfall area). Station 1 (Air Batu Village), characterized by relatively calm river flow with riverbanks dominated by settlements and plantations that potentially contribute organic input from human activities; the margins are lined with granite rocks and riparian vegetation such as bamboo, *Shorea* spp., palms, and sugar palms. Station 2 (Fossil Wood area) features rocky channels with moderate to strong currents and a substrate dominated by fossilized wood and gravel, reflecting relatively well preserved natural conditions. Station 3 (Pulau Batu area) consists of shallow riffles with mixed sand and gravel substrates and open river stretches. Station 4 (Muara Karing Waterfall area) represents the confluence of a tributary with the Batang Merangin River, characterized by fluctuating currents, mixed sand mud substrates, and higher turbidity due to sedimentation processes (Figure 1).

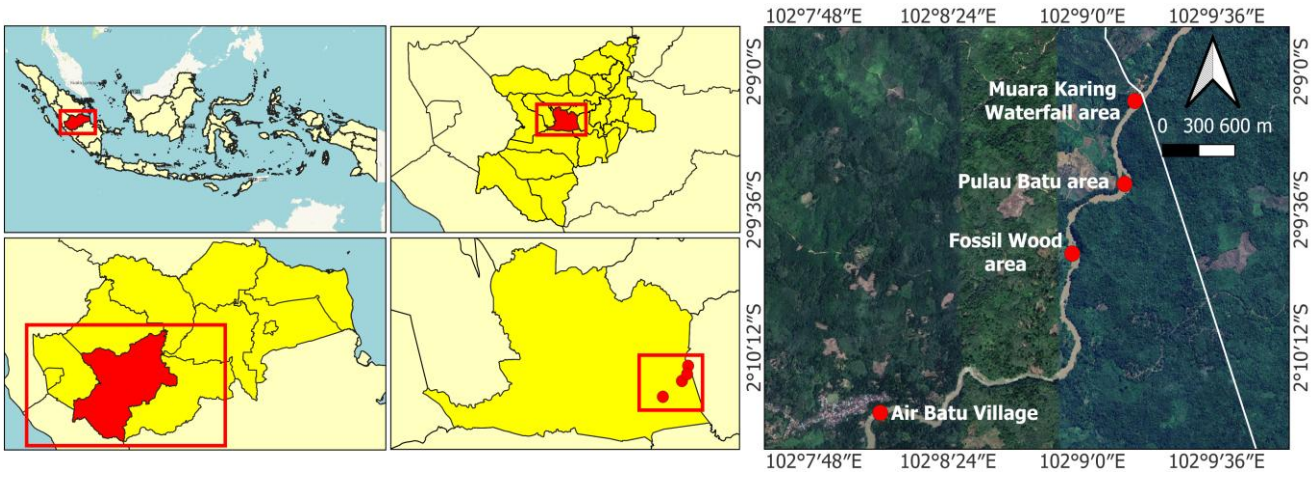

Figure 1. Locations of Cyprinidae family samples collected from the Batang Merangin River, Jambi, Indonesia

The fishing gear used included gill nets with mesh sizes of 0.5, 0.75, and 1 inch, cast nets, and scoop nets. This was due to the strong currents and murky water at the sampling location, which affected the catch. Sampling was conducted in the morning, afternoon, and evening. Scoop nets were used to catch small fish around the rocks in the Geopark. Species that were still ambiguous or cryptic were further tested in the laboratory based on morphometric and molecular characteristics. In total, we obtained 26 individual fish, representing 14 species of the Cyprinidae family, from these stations. Rapid imaging and morphological identification were conducted on the fish directly at each station, using a comprehensive range of sources for morphological identification. The identification results will be compared with several fish identification books (Kottelat et al. 1993; Hui and Kottelat 2009; Kottelat and Whitten 2009; Sukmono and Margaretha 2017), and the online database (Froese and Pauly 2016) at www.fishbase.org. Fish caught using gill nets usually die, and tissue from the right pectoral fin is removed and preserved in 96% ethanol. Specimens are fixed in 10% formalin and then transferred to a 70% alcohol solution after one week. Samples measuring more than 15 cm will be injected with 70% alcohol through the cloaca and toward the abdomen to expedite fixation.

Procedures

Each specimen obtained is given a specimen voucher with the code GIF (Indonesian Fish Geopark). The voucher is created by photographing the specimens live and dead, and then preserving them in 10% formalin and 70% alcohol. For DNA analysis, they are preserved in absolute ethanol. DNA barcoding analysis was conducted in several stages, including DNA extraction, PCR amplification, electrophoresis, and sequencing. DNA was extracted from the right pectoral fin of fish specimens preserved in absolute ethanol using the Qiagen DNeasy Blood and Tissue Kit, following the manufacturer's protocol. The mitochondrial Cytochrome C Oxidase subunit I (COI) gene fragment (~650 bp) was amplified using the forward primer Fish F1 (5′-TCA ACC AAC CAC AAA GAC ATT GGC AC-3′) and the reverse primer Fish R1 (5′-TAG ACT TCT GGG TGG CCA AAG AAT CA-3′) (Ward et al. 2005). These primers were applied to 26 fish samples collected from Merangin Geopark. The PCR reaction had a total volume of 25 µL, consisting of: 5 µL DNA sample, 12.5 µL GoTaq Master Mix, 1 µL forward primer, 1 µL reverse primer, and 5.5 µL nuclease-free water. PCR amplification was conducted in 30 cycles using a GeneAmp PCR System 9700 (PE), with thermal conditions as follows: Denaturation at 94°C for 5 seconds, annealing at 52°C, and extension at 72°C for 30 seconds. The PCR products were then analyzed through electrophoresis using a horizontal electrophoresis system at 100 volts for 45 minutes to visualize the DNA bands on an agarose gel. Finally, verified PCR products were sent to 1st BASE Malaysia for DNA sequencing using.

Data analysis

The DNA sequencing results were first examined using BioEdit software to ensure that the length of the DNA sequences matched the target, which was approximately ±650 bp. Primer regions were then corrected by aligning the sequences using Molecular Evolutionary Genetics Analysis (MEGA) 12 software. Based on this correction, a consensus DNA sequence was obtained for each tested species. The consensus sequences were then compared with DNA sequences available in GenBank using the BLAST (Basic Local Alignment Search Tool) system via the website www.genbank.ncbi.nlm.nih.gov. A BLAST result showing ≥97% similarity was considered indicative of the same species. After species identification was confirmed, further analyses were conducted using MEGA 12, which included the construction of a phylogenetic tree with the Neighbor-Joining (NJ) method based on the Kimura 2-Parameter (K2P) model, along with analyses of nucleotide composition and statistics such as conserved and variable sites.

RESULTS AND DISCUSSION

Species composition

A total of 26 individuals representing 14 species across 10 genera of the Cyprinidae family were identified using morphological characters and confirmed by molecular analysis of the mitochondrial COI gene (Table 1). The genus *Barbodes* dominated the composition (27%), consisting of *Barbodes lateristriga* (Valenciennes, 1842) and *Barbodes binotatus* (Valenciennes, 1842), with *Barbodes lateristriga* being the most frequently encountered species. Other genera included *Osteochilus* (*Osteochilus waandersii* (Bleeker, 1853), *Osteochilus* sp.), *Tor* (*Tor tambra*, *Tor tambroides*), and *Labiobarbus* (*Labiobarbus leptocheilus*, *Labiobarbus festivus* (Heckel, 1843)). Several species were represented by a single genus, including *Rasbora spilotaenia* (Hubbs & Brittan, 1954), *Epalzeorhynchos kalopterus* (Bleeker, 1850), *Crossocheilus oblongus*, *Luciosoma* sp., and *Lobocheilos bo* (Popta, 1904) (Figure 2).

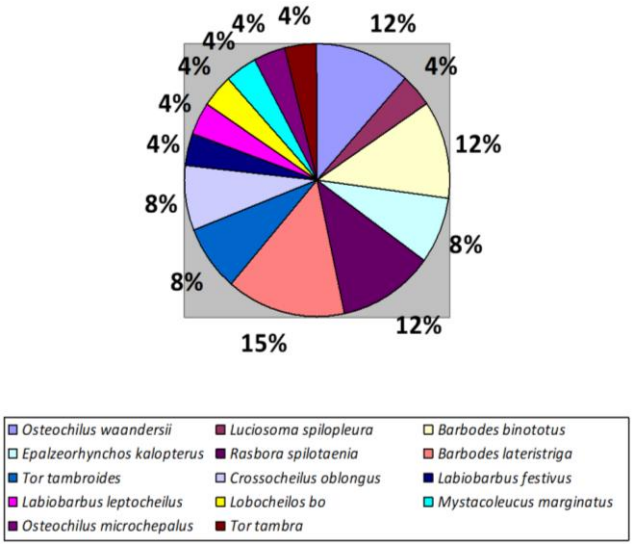

Figure 2. Composition of Cyprinidae fishes from the Merangin Geopark based on DNA barcoding (COI)

Table 1. Composition of Cyprinidae fishes from the Merangin Geopark based on DNA barcoding (COI)

Spesies	Stations				Individu total	Percentage (%)
	Air Batu Village	Fossil Wood area	Pulau Batu area	Muara Karing Waterfall area		
Osteochilus waandersii (Bleeker, 1853)	2	-	-	1	3	12
Luciosoma sp.	1	-	-	-	1	4
Barbodes binotatus (Valenciennes, 1842)	-	1	-	2	3	12
Epalzeorhynchos kalopterus (Bleeker, 1850)	-	-	-	2	2	8
Rasbora spilotaenia (Hubbs & Brittan, 1954)	-	-	2	1	3	12
Barbodes lateristriga (Valenciennes, 1842)	-	2	-	2	4	15
Tor tambroides (Bleeker, 1854)	-	-	-	2	2	8
Crossocheilus oblongus (Kuhl & Van Hasselt, 1823)	2	-	-	-	2	8
Labiobarbus festivus (Heckel, 1843)	-	1	-	-	1	4
Labiobarbus leptocheilus (Valenciennes, 1842)	-	1	-	-	1	4
Lobocheilos bo (Popta, 1904)	-	-	-	1	1	4
Mystacoleucus marginatus (Valenciennes, 1842)	1	-	-	-	1	4
Osteochilus sp.	-	-	-	1	1	4
Tor tambra (Valenciennes, 1842)	-	-	-	1	1	4

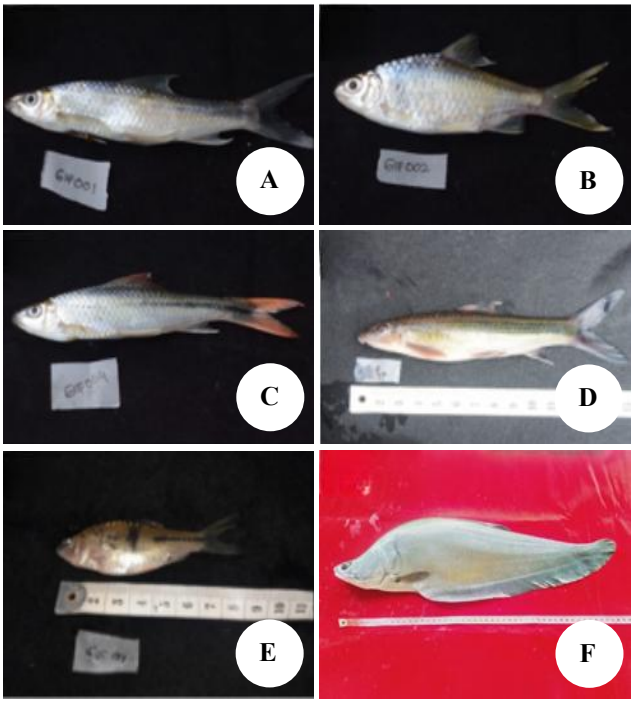

Figure 2. Selected morphologically identified species from Merangin Geopark and outgroup: A. *Labocheilos bo*, B. *Mystacoleucus marginatus*, C. *Osteochilus waandersii*, D. *Epalzeorhynchos kalopterus*, E. *Barbodes lateristriga*, F. *Chitala lopis* (outgroup)

BLAST analysis and identification

BLAST analysis revealed COI sequence similarity with National Center for Biotechnology Information (NCBI) references ranging from 88.11% to 99.56% (Table 2). Most sequences exhibited high identity (96.24-99.56%), whereas four sequences showed <95% similarity (*O. waandersii* GIF 018 and GIF 029, *O. microchepalus* GIF 006, and *L. spilopleura* GIF 021). Species with BLAST identity >98% indicate high genetic homogeneity (Ward et al. 2005; Hubert et al. 2015). All sequences had an E-value of 0 and an average query coverage of 98.46%±1.70% (range 94-100%), supporting robust species-level identification. Notably, multiple individuals of *B. lateristriga* (GIF 011, 012, 013, 033) consistently showed 96.24% similarity, suggesting a stable population with minimal intraspecific divergence, suggesting that individuals of this species share a common recent ancestry and likely experience ongoing gene flow within the Merangin watershed (Hebert et al. 2003; Ward et al. 2005; Hubert et al. 2015; Shen et al. 2016). Based on the International Union for Conservation of Nature (IUCN) Red List, 65.4% of samples (8 species) were categorized as Least Concern (LC), 15.4% (3 species: *L. festivus*, *T. tambra*, *T. tambroides*) as Data Deficient (DD), and 19.2% (3 species: *Lobocheilos bo*, *B. binotatus*) as Not Evaluated (NE). These results highlight the need for further conservation assessments for DD and NE species.

Genetic distance

The genetic distance analysis revealed a clear pattern of mitochondrial divergence among the cyprinid fishes examined, providing strong support for species delimitation and phylogenetic structure inferred in this study. Pairwise genetic distances ranged from 0.0000 to 0.1791 (Table 3), a range that is widely reported in mitochondrial DNA studies of freshwater fishes and is considered appropriate for evaluating both intra and interspecific variation within Cyprinidae (Ward et al. 2005; April et al. 2011). Intraspecific genetic distances were consistently low, often reaching zero, indicating strong genetic cohesion within species. For example, *B. lateristriga, B. binotatus, R. spilotaenia*, and *E. kalopterus* showed intraspecific divergence values between 0.0000 and 0.0014. Such low levels of mitochondrial divergence are characteristic of conspecific individuals and are typically interpreted as evidence of either recent common ancestry or ongoing gene flow within populations (Hebert et al. 2003; Ward et al. 2005).

Table 2. BLAST results and IUCN status of Cyprinidae from Merangin Geopark

Species	Query cover (%)	E. value	BLAST (%)	Status IUCN
Lobocheilos bo GIF 001	100	0	99.43	NE
Mystacoleucus marginatus GIF 002	99	0	98.41	LC
Labiobarbus leptocheilus GIF 003	100	0	99.14	LC
Osteochilus waandersii GIF 004	94	0	99.54	LC
Labiobarbus festivus GIF 005	100	0	99.14	DD
Osteochilus sp. GIF 006	100	0	91.24	NE
Crossocheilus oblongus GIF 007	95	0	99.40	LC
Rasbora spilotaenia GIF 010	99	0	97.98	LC
Barbodes lateristriga GIF 011	99	0	96.24	LC
Barbodes lateristriga GIF 012	99	0	96.24	LC
Barbodes lateristriga GIF 013	99	0	96.24	LC
Tor tambra GIF 014	100	0	99.28	DD
Tor tambroides GIF 015	99	0	98.70	DD
Crossocheilus oblongus GIF 016	95	0	99.24	LC
Osteochilus sp. GIF 018	100	0	91.24	LC
Luciosoma sp. GIF 021	100	0	88.11	LC
Tor tambroides GIF 023	99	0	98.70	DD
Barbodes binotatus GIF 024	97	0	99.26	NE
Barbodes binotatus GIF 025	97	0	99.26	NE
Barbodes binotatus GIF 026	97	0	99.12	NE
Epalzeorhynchos kalopterus GIF 027	99	0	99.56	LC
Epalzeorhynchos kalopterus GIF 028	99	0	99.56	LC
Osteochilus sp. GIF 029	97	0	93.81	LC
Rasbora spilotaenia GIF 031	99	0	98.11	LC
Rasbora spilotaenia GIF 032	99	0	97.98	LC
Barbodes lateristriga GIF 033	99	0	96.24	LC

This pattern is congruent with previous barcoding and phylogenetic studies of Southeast Asian cyprinids, which have demonstrated that intraspecific COI divergence rarely exceeds 2% (0.02) in well-defined species (Hubert et al. 2015). The observed genetic homogeneity also supports the monophyletic clustering of these taxa in the phylogenetic tree and confirms the reliability of the molecular identification. In contrast, genetic distances between species belonging to the same genus were markedly higher, reflecting evolutionary divergence following speciation. The genetic distance between *T. tambra* and *T. tambroides* was approximately 0.0229, exceeding typical intraspecific thresholds and supporting their recognition as distinct species. Comparable levels of divergence have been reported in other mahseer lineages, where recent diversification and historical river connectivity have shaped genetic structure (Nguyen et al. 2008; Walton et al. 2024).

Within *Osteochilus*, interspecific distances ranged from 0.0931 to 0.1060, values that fall well within the range expected for distinct cyprinid species (April et al. 2011). These results reinforce the taxonomic validity of *O. waandersii* and the sampled *Osteochilus* spp., as also supported by morphological diagnoses in regional taxonomic revisions (Kottelat 2013). Notably, *L. leptocheilus* and *L. festivus* exhibited zero genetic distance, suggesting identical mitochondrial haplotypes. Similar cases have been reported in cyprinid fishes and may result from recent speciation, mitochondrial introgression, or insufficient resolution of single-locus markers (Song et al. 2008; Hubert et al. 2015). This finding highlights the limitation of relying solely on mitochondrial DNA and underscores the need for integrative taxonomic approaches incorporating nuclear genes and morphology.

Genetic distances between genera were substantially higher, generally ranging from 0.10 to 0.17, reflecting deep evolutionary separation among cyprinid lineages. The highest divergence values were observed in comparisons involving *Luciosoma* and *Rasbora*, which are known to occupy distinct phylogenetic positions within Cyprinidae (Chen and Mayden 2009). Such intergeneric distances are consistent with thresholds commonly reported in molecular systematic studies and provide strong support for generic-level separation (April et al. 2011). The concordance between genetic distance patterns and the topology of the phylogenetic tree indicates a strong phylogenetic signal in the dataset. This agreement between distance-based and tree-based approaches strengthens confidence in the inferred evolutionary relationships.

Phylogenetic structure and regional species richness

The clear monophyly of genera such as *Osteochilus*, *Tor*, *Barbodes*, and *Epalzeorhynchos* shows that mitochondrial DNA markers can robustly resolve species boundaries (Figure 3). This aligns with reported high fish species richness in the Merangin Geopark area, where 28 species from 25 genera and 11 families were recorded during field surveys (Sukmono et al. 2025). The presence of these taxa within phylogenetic clades suggests genetic integrity consistent with regional ichthyofaunal inventories (Sukmono et al. 2025). The diverse riverine environments of Batang Merangin, characterized by fast currents and rocky substrates, create microhabitats that can drive lineage diversification in cyprinid fishes. This environmental heterogeneity is documented as shaping ecomorphological variation among fish assemblages in the geopark (Sukmono et al. 2025).

The genetic distinctiveness we observe in lineages like *Tor tambra* versus *T. tambroides* likely reflects divergent evolutionary responses to such environmental niches. Phylogenetic resolution within *B. binotatus* and *C. oblongus* also points to potential cryptic diversity that may be overlooked by morphology alone. This has direct implications for biodiversity assessments, since cryptic species inflate regional species richness and could affect IUCN Red List status evaluations if formally recognized through integrative taxonomic studies.

Table 3. Genetic distance among Cyprinidae fish in Merangin Geopark

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Lobocheilos bo GIF 001																									
Mystacoleucus marginatus GIF 002	0,1132																								
Labiobarbus leptocheilus GIF 003	0.1074	0.1160																							
Osteochilus waandersii GIF 004	0.1117	0.1146	0.1089																						
Labiobarbus festivus GIF 005	0.1074	0.1160	0.0000	0.1089																					
Osteochilus sp. GIF 006	0.1146	0.1060	0.0931	0.1060	0.0931																				
Crossocheilus oblongus GIF 007	0.1046	0.1232	0.1189	0.1304	0.1189	0.1146																			
Rasbora spilotaenia GIF 010	0.1490	0.1533	0.1519	0.1605	0.1519	0.1619	0.1533																		
Barbodes lateristriga GIF 011	0.1132	0.1203	0.1232	0.1246	0.1232	0.1246	0.1160	0.1433																	
Barbodes lateristriga GIF 012	0.1132	0.1203	0.1232	0.1246	0.1232	0.1246	0.1160	0.1433	0.0000																
Barbodes lateristriga GIF 013	0.1132	0.1203	0.1232	0.1246	0.1232	0.1246	0.1160	0.1433	0.0000	0.0000															
Tor tambra GIF 014	0.1203	0.1146	0.1275	0.1203	0.1275	0.1175	0.1060	0.1533	0.1175	0.1175	0.1175														
Tor tambroides GIF 015	0.1160	0.1089	0.1261	0.1203	0.1261	0.1218	0.1046	0.1504	0.1189	0.1189	0.1189	0.0229													
Crossocheilus oblongus GIF 016	0.1046	0.1218	0.1175	0.1318	0.1175	0.1132	0.0014	0.1533	0.1146	0.1146	0.1146	0.1060	0.1046												
Osteochilus sp. GIF 018	0.1146	0.1060	0.0931	0.1060	0.0931	0.0000	0.1146	0.1619	0.1246	0.1246	0.1246	0.1175	0.1218	0.1132											
Luciosoma sp. GIF 021	0.1633	0.1662	0.1648	0.1748	0.1648	0.1691	0.1676	0.1619	0.1662	0.1662	0.1662	0.1590	0.1547	0.1676	0.1691										
Tor tambroides GIF 023	0.1160	0.1089	0.1261	0.1203	0.1261	0.1218	0.1046	0.1504	0.1189	0.1189	0.1189	0.0229	0.0000	0.1046	0.1218	0.1547									
Barbodes binotatus GIF 024	0.1289	0.1218	0.1232	0.1203	0.1232	0.1304	0.1261	0.1547	0.1189	0.1189	0.1189	0.1318	0.1261	0.1246	0.1304	0.1576	0.1261								
Barbodes binotatus GIF 025	0.1289	0.1218	0.1232	0.1203	0.1232	0.1304	0.1261	0.1547	0.1189	0.1189	0.1189	0.1318	0.1261	0.1246	0.1304	0.1576	0.1261	0.0000							
Barbodes binotatus GIF 026	0.1275	0.1203	0.1218	0.1189	0.1218	0.1289	0.1246	0.1533	0.1175	0.1175	0.1175	0.1304	0.1246	0.1232	0.1289	0.1590	0.1246	0.0014	0.0014						
Epalzeorhynchos kalopterus GIF 027	0.1318	0.1332	0.1447	0.1375	0.1447	0.1375	0.1304	0.1705	0.1361	0.1361	0.1361	0.1390	0.1390	0.1318	0.1375	0.1791	0.1390	0.1533	0.1533	0.1519					
Epalzeorhynchos kalopterus GIF 028	0.1318	0.1332	0.1447	0.1375	0.1447	0.1375	0.1304	0.1705	0.1361	0.1361	0.1361	0.1390	0.1390	0.1318	0.1375	0.1791	0.1390	0.1533	0.1533	0.1519	0.0000				
Osteochilus sp. GIF 029	0.1275	0.1189	0.1146	0.1275	0.1146	0.1032	0.1203	0.1734	0.1318	0.1318	0.1318	0.1332	0.1289	0.1189	0.1032	0.1777	0.1289	0.1318	0.1318	0.1304	0.1519	0.1519			
Rasbora spilotaenia GIF 031	0.1476	0.1519	0.1504	0.1590	0.1504	0.1605	0.1519	0.0014	0.1418	0.1418	0.1418	0.1519	0.1490	0.1519	0.1605	0.1605	0.1490	0.1533	0.1533	0.1519	0.1691	0.1691	0.1719		
Rasbora spilotaenia GIF 032	0.1476	0.1519	0.1504	0.1590	0.1504	0.1605	0.1519	0.0014	0.1418	0.1418	0.1418	0.1519	0.1490	0.1519	0.1605	0.1605	0.1490	0.1533	0.1533	0.1519	0.1691	0.1691	0.1719	0.0000	
Barbodes cf. lateristriga GIF 033	0.1132	0.1203	0.1232	0.1246	0.1232	0.1246	0.1160	0.1433	0.0000	0.0000	0.0000	0.1175	0.1189	0.1146	0.1246	0.1662	0.1189	0.1189	0.1189	0.1175	0.1361	0.1361	0.1318	0.1418	0.1418

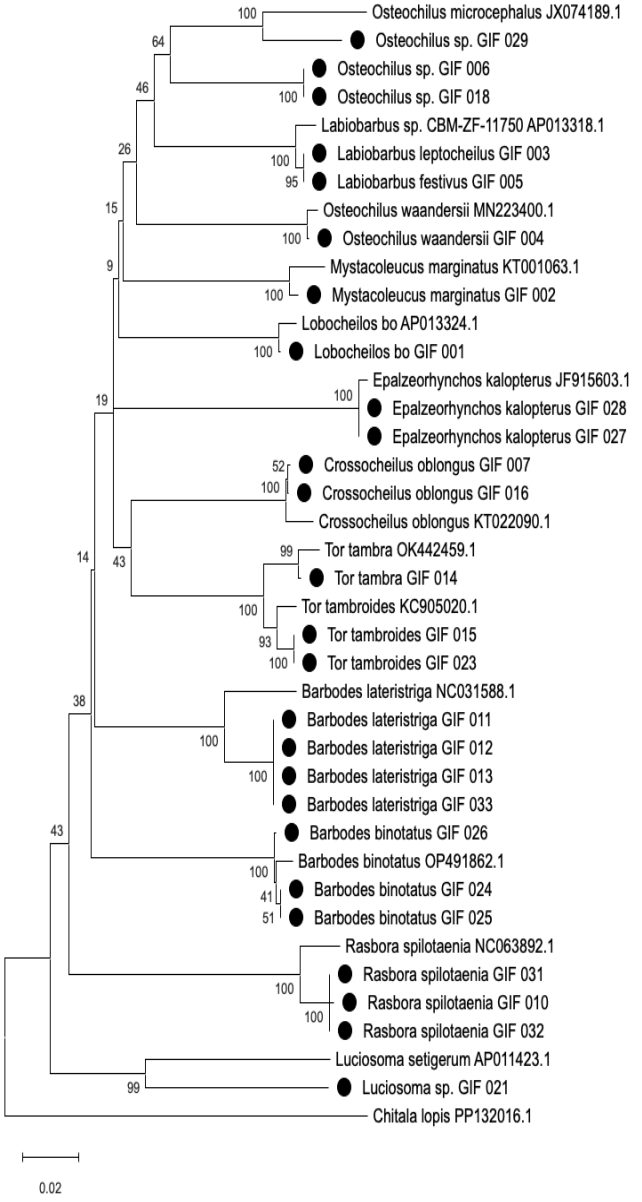

Figure 3. Neighbor Joining (NJ) tree of 26 samples (filled circles indicate specimens collected in this study) from 14 species of Cyprinidae (1000 bootstrap replicates)

Evolutionary and biodiversity implications

The Merangin Jambi Geopark encompasses an area with high biodiversity values that extends beyond geology, including over 372 faunal species and rare or endangered taxa (Merangin Jambi UNESCO Global Geopark 2025). The molecular evidence for genetically distinct fish lineages reinforces the need to consider ichthyofaunal conservation as a component of geopark management strategies.

The combination of low intraspecific and high interspecific genetic distances suggests that the freshwater fish assemblage analyzed here comprises both genetically stable lineages and taxa with complex evolutionary histories. In the context of Merangin Jambi Geopark, these findings underscore the region's importance as a reservoir of freshwater biodiversity shaped by historical river dynamics and habitat heterogeneity.

From a conservation perspective, the detection of minimal genetic divergence among some nominal species highlights the risk of overlooking cryptic diversity or misinterpreting species boundaries. Integrative taxonomic frameworks that combine molecular, morphological, and ecological data are therefore essential to accurately document biodiversity and inform conservation planning in geopark-managed river systems (Dayrat 2005; Kottelat 2013).

The integration of molecular phylogenetic results with biodiversity inventories enhances our capacity to identify priority taxa and habitats within the geopark. Given the documented diversity of fish species and unique environmental conditions, future research should focus on expanding genetic sampling (including nuclear markers) and exploring population structure across watersheds to inform conservation planning.

Discussion

The molecular identification and phylogenetic reconstruction of freshwater fishes in the Merangin Geopark provide new insights into the diversity of Cyprinidae within one of the key tropical river systems in Sumatra. DNA barcoding using the mitochondrial COI gene successfully identified 26 specimens representing 14 species and 10 genera. High BLAST identity values, averaging 97.35% similarity, indicate a high reliability of species delineation and confirm the robustness of COI as a barcoding marker for freshwater fishes, particularly within Cyprinidae. The effectiveness of COI as a barcoding marker has been consistently demonstrated in large-scale studies across Asia and Africa, where it reliably resolves species-level identifications in morphologically similar taxa (Shen et al. 2016; Andújar et al. 2018; Adeoba et al. 2019; Sherzada et al. 2019; Khan et al. 2024; Ashour et al. 2025). Moreover, the high sequence coverage and E-values observed in this study support the validity of taxonomic placement and minimize the potential amplification of pseudogenes, Nuclear Mitochondrial DNA insertions (NUMTs), or contamination artifacts.

The high genetic similarity observed among individuals of *B. lateristriga*, *B. binotatus*, and *R. spilotaenia* indicates the presence of relatively stable population structures within the Merangin watershed. Such patterns are consistent with river systems exhibiting stable hydrological connectivity, which allows gene flow between upstream and downstream reaches and prevents population fragmentation. Similar patterns of low intraspecific divergence have been reported in Cyprinidae assemblages of the Yangtze River (Shen et al. 2016) and the Nile Basin (Ashour et al. 2025), where continuous ecological corridors maintain genetic homogeneity among populations. The geomorphology of the Merangin River, characterized by moderate current velocity, sandy to gravel substrates, and well-oxygenated water, likely facilitates dispersal among cyprinid populations. These conditions have been recognized as key ecological factors supporting the success and distribution of *Barbodes* and *Osteochilus* species in Southeast Asian tropical river systems (Sukmono

and Margaretha 2017; Chakraborty 2021; Hasan et al. 2022; Jana 2024).

In contrast, higher genetic divergence observed in *L. spilopleura*, *O. microcephalus*, and *O. waandersii* suggests localized adaptation, restricted movement, and ecological specialization to specific microhabitats. Historical drainage shifts, ecological gradients, or environmental heterogeneity in the Merangin watershed may explain these divergences. *Luciosoma* species are known to inhabit fast-flowing upper river reaches and exhibit strong rheophilic tendencies, resulting in limited dispersal and increased population structuring (Chua 2020; Wantania et al. 2025). Higher divergence in these taxa may indicate ongoing or incipient speciation, similar to adaptive radiation patterns observed in African Cyprinidae in complex watersheds (Iyabo 2018; Adeoba et al. 2019; Barbosa et al. 2021; Ericson et al. 2021). The genetic distance values observed in this study, ranging from 0.000 to 0.179, fall within the ranges associated with species-level differentiation and interspecific divergence in Cyprinidae (Zafar et al. 2024; Anjum et al. 2025; Li et al. 2025). These findings reinforce the utility of COI divergence thresholds in delineating species boundaries, particularly in taxa with overlapping morphological traits. The highest genetic distance, reaching approximately 0.179, indicates clear genetic boundaries that can be effectively used for molecular species delineation with genetic markers such as COI or Cyt b. For instance, the divergence between *L. spilopleura* and other species, as well as *E. kalopterus*, confirms that they are evolutionarily distinct species with substantial genetic diversity (Tadmor-Levi et al. 2022; Khan et al. 2024).

Phylogenetic reconstruction revealed two well-supported major clades consistent with previously published mitochondrial phylogenies (Zheng et al. 2016; Wang et al. 2023). The first clade comprised *Barbodes*, *Crossocheilus*, *Osteochilus*, *Labiobarbus*, *Rasbora*, and *Tor*, indicating shared evolutionary histories and ecological affinities. The second clade was dominated by *Epalzeorhynchos* and *Luciosoma*, reflecting distinct lineage diversification likely shaped by habitat preferences and hydrological compartmentalization. The close phylogenetic grouping of *L. leptocheilus* and *L. festivus* may indicate recent divergence events or incomplete lineage sorting, consistent with molecular studies reporting subtle genetic structure among *Labiobarbus* species in Asia (Li et al. 2025). Additionally, the clustering of *C. oblongus* with substrate-dependent grazers supports the hypothesis that ecological functional traits can provide phylogenetically informative signals, especially among benthic-feeding cyprinids (Baran and Guerin 2012; Budiantoro et al. 2024).

From a conservation perspective, this study provides critical insights into the status of *T. tambra* and *T. tambroides*, both classified as Data Deficient by the IUCN. These species hold considerable economic and cultural value but face increasing threats from overfishing, sedimentation, and hydropower development. The complexity of *Tor* taxonomy emphasizes the need for integrated molecular and morphological approaches to define species boundaries and population structures accurately (Asiah et al. 2020; Jaafar et al. 2021; Muchlisin et al. 2022). Identifying *Tor* species in Merangin provides essential baseline data for guiding conservation prioritization and sustainable fisheries management, particularly in community-based riverine resource systems.

Ecologically, the phylogenetic and genetic patterns observed underscore the importance of habitat structure, connectivity, and geomorphological processes in shaping genetic diversity. Tropical river ecosystems are highly dynamic, with factors such as sediment load, seasonal flood pulses, watershed land use, and channel morphology influencing fish distribution and dispersal (Chakraborty 2021; Jana 2024). Studies in Sulawesi have shown that stream fish assemblages are highly dependent on habitat connectivity and complexity, with fragmentation leading to rapid genetic differentiation and localized extinction (Möhring et al. 2025; Wantania et al. 2025). In the context of the Merangin Geopark, ongoing anthropogenic pressures including sand mining, agricultural runoff, and riparian forest loss pose emerging threats to genetic connectivity and long-term biodiversity persistence (Romiyanto et al. 2015; Yulianti et al. 2017; Farisi et al. 2022; Mustafa 2024).

The predominance of species currently listed as Least Concern by the IUCN indicates relatively stable ecological conditions. However, the presence of Data Deficient and Not Evaluated taxa highlights gaps in monitoring and population assessment. Molecular datasets, such as those generated in this study, can contribute to updating species distribution maps, informing future refining threat assessments, and guiding habitat protection priorities. Importantly, DNA barcoding enables early detection of population changes through efficient biomonitoring, particularly when integrated with environmental DNA (eDNA) and high-throughput sequencing approaches (Andújar et al. 2018; Ankola et al. 2021; Elías-Gutiérrez et al. 2021).

In conclusion, this study provides an initial molecular baseline for Cyprinidae diversity in the Merangin Geopark and contributes to a broader understanding of tropical freshwater biodiversity, species coexistence mechanisms, and evolutionary processes in riverine ecosystems. By revealing both genetic homogeneity in widespread taxa and divergence in ecologically specialized lineages, these findings underscore the interplay between hydrological connectivity, habitat diversity, and evolutionary history. Integrating molecular evidence with ecological and conservation considerations strengthens the foundation for long-term biodiversity monitoring, habitat management, and sustainable fisheries governance in the Merangin region.

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