

Research Insight

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Mitochondrial DNA Analysis for Resolving the Phylogenetic Relationships of Tilapia Species

Xian Li ¹, Xiaoli Chen ¹, Rudi Mai ² ✉

¹ Tropical Animal Resources Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China

² Tropical Marine Fisheries Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China

✉ Corresponding author: rudi.mai@hitar.org

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Abstract *Oreochromis* spp. (Tilapias) are commercially important fishes with extensive distribution in Africa and other tropical and subtropical regions. Due to morphological similarity, high incidence of hybridization, and complex domestication history, the phylogenetic relationships and taxonomic limits of tilapia species are disputed. In this study, mitochondrial DNA (mtDNA) sequences-COI, CYTB, and D-loop gene fragments-were resolved for some representative *Oreochromis* species and geographical populations. Phylogenetic trees were reconstructed using Neighbor-Joining (NJ), Maximum Likelihood (ML), and Bayesian Inference (BI) methods to infer evolutionary relationships. The analyses revealed clear genetic differentiation among tilapia species, while some local strains and hybrid populations contained admixed lineages or overlapping taxonomic signals. Genetic distances among populations generally corresponded to geographic separation, suggesting the combined effects of natural selection and human activity on genetic structure. Functional analysis of the variants of mitochondrial genes identified key loci with a putative association with energy metabolism and reproductive adaptation, suggesting their roles in ecological adaptation and phenotypic evolution. The study explains phylogenetic structure among *Oreochromis* species, verifies the feasibility of mtDNA in species identification, germplasm conservation, and molecular breeding, and provides basic data and theoretical basis for further study on tilapia molecular evolution and environmental adaptation.

Keywords *Oreochromis*; Mitochondrial DNA; Phylogeny; Genetic diversity; Molecular marker

1 Introduction

The genus *Oreochromis* of the family Cichlidae is a complex and ecologically variable group of African and Middle Eastern freshwater fish. The genus comprises more than 30 validly described species, as well as a variety of locally distinct populations or subspecies. The tilapias occupy a very wide range of aquatic habitats, from rivers and lakes to reservoirs and brackish water. Their adaptability to different ecological conditions has fostered their widespread introduction throughout the world, particularly for aquaculture and aquatic vegetation control. As a result, *Oreochromis* species are now established in Asia, Latin America, and certain Pacific Islands. However, rampant hybridization, phenotypic similarity, and rapid evolutionary radiation within the genus have imposed great difficulty on taxonomy and species classification, leading to long-standing disputes in their systematic classification (Kinaro et al., 2016; Geletu and Zhao, 2022).

Tilapias, especially *Oreochromis niloticus*, *O. mossambicus*, and *O. aureus*, are the most important aquaculture species globally due to their high growth rate, high fertility, tolerance to low water quality, and diversification to different types of farming systems. They play a crucial role in food security and rural livelihood in developing countries, particularly low- and middle-income countries. Tilapia aquaculture contributes significantly to global freshwater aquaculture production, as per FAO reports. Over the past few years, advancements have been made in aquaculture technology like Recirculating Aquaculture Systems (RAS), Biofloc Technology (BFT), and Integrated Multi-Trophic Aquaculture (IMTA) further optimizing production efficiency and profitability. Tilapia is also being produced on commercial scale, as in smallholder systems for the development of local economies as well as food security. However, large breeding and translocation have increased the risk of genetic homogenization and introgression, raising alarm for conservation of indigenous germplasm (Ford et al., 2019; Fatsi et al., 2020).

Mitochondrial DNA (mtDNA) has been a useful marker in phylogenetic and evolutionary studies due to its maternal inheritance, relatively high mutation rate, and absence of recombination. In tilapias, mtDNA markers including cytochrome oxidase I (COI), cytochrome b (CYTB), and the D-loop region have been extensively used for elucidating species relationships, genetic divergences, and detecting hybridization events. Recent studies have demonstrated that mtDNA data can easily resolve problematic phylogenetic relationships, particularly in cryptic or closely related species, founded on morphology characters alone. Additionally, mtDNA has been important in revealing the origin and evolutionary history of domestic strains. The objectives of this study are to compare mitochondrial DNA sequences of representative *Oreochromis* species for resolving their phylogenetic relationships, estimating intra- and interspecific genetic diversity, and providing molecular evidence for guiding taxonomy, conservation, and breeding programs. In doing this, the current study expects to improve our understanding of tilapia evolutionary biology and aid in sustainable management of their genetic resources.

2 Genetic Basis and Phylogenetic Differentiation of Tilapias

2.1 Species composition and phylogenetic relationships within the genus *Oreochromis*

The genus *Oreochromis* comprises morphologically disparate group of tilapia species with a complex evolutionary history that is the product of ancient and contemporary hybridization events, as revealed by recent genome-scale phylogenies. These broader-level systematics are complemented by molecular phylogenies at fine taxonomic scales using mitochondrial and nuclear markers, which have revealed repeated adaptation to environmental extremes (e.g., temperature and salinity) within the genus. Of specific interest is the *subgenus Alcolapia*, now embedded in *Oreochromis*, as taxonomic updates unfold. Mitochondrial and nuclear DNA trees generally fall in disagreement, perhaps due to incomplete lineage sorting and introgression, with the consequence of obscuring species limits and evolutionary history (Ford et al., 2019; Mojekwu et al., 2020; Ciezarek et al., 2024).

2.2 Genetic diversity and geographic differentiation among tilapia populations

Tilapia are characterized by great genetic diversity and geographically related differentiation due to natural biogeographic and man-imposed factors such as translocations and aquaculture introductions (Popoola, 2024; Tibihika et al., 2024; Kwikiriza et al., 2025). Mitochondrial and nuclear markers have described certain genetic clusters within and across regions with some of the populations (e.g., Ethiopian and Ugandan) being highly differentiated and with surfacing genetic resources (Tibihika et al., 2024; Kwikiriza et al., 2025). Genetic diversity is usually lost in farmed or stocked populations, however, by bottlenecks, founder effects, and inbreeding. Introduction of foreign strains and hybridization incidents have also reshaped the genetic landscape, sometimes leading to admixture and loss of local genetic purity (Tibihika et al., 2019; Tesfaye et al., 2021; Nyaku, et al., 2023) (Figure 1).

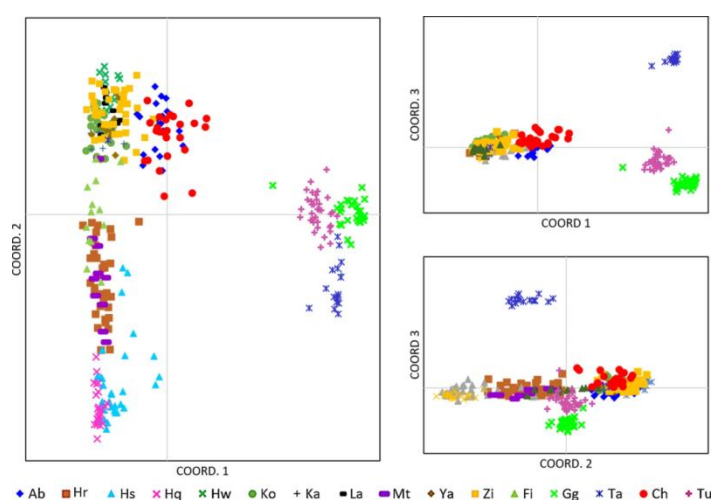


Figure 1 Principal Coordinate Analysis (PCoA) plots illustrating genetic similarity of Nile tilapia populations in Ethiopia considering all populations. The first axis explains 26.2%, second axis 10% and third axis 7.2% of the variation, accumulating to 43.3% (Adopted from Tesfaye et al., 2021)

2.3 Impact of hybridization and introgression on phylogenetic resolution

Introgression and hybridization occur frequently in both wild and captive tilapia populations as a result of deliberate introduction for aquaculture and accidental escapes. Ancient gene flow contributed to diversification of the genus, whereas modern hybridization, especially between introduced and native species, poses a threat to the genetic integrity of wild populations. Introgression obscures phylogenetic relationships, creating mito-nuclear discordance and impeding species identification. In some, hybridization has resulted in new species or strains with new adaptive traits, but hybridization may also homogenize unique genetic lineages and undermine conservation plans (Ford et al., 2019; Mojekwu et al., 2020; Etherington et al., 2022; Yu et al., 2022; Ciezarek et al., 2023).

3 Mitochondrial Data Construction and Phylogenetic Analysis Methods

3.1 Sampling of tilapia specimens and strategies for mtDNA extraction and sequencing

Tilapia samples are usually collected from heterogeneous populations and tissue or blood samples are preserved for DNA extraction. Methods applied to the extraction rely on commercial kits such as Quik-gDNATM miniPrep or Aqualex extraction kits to recover high-quality mitochondrial DNA (mtDNA) for downstream use. Both Sanger and next-generation sequencing (NGS) technology are used for the purpose of sequencing, with NGS (i.e., Illumina platforms) enabling the assembly of complete mitogenomes and production of large genetic data ready for application in phylogenetic studies (Ekerette et al., 2018; Nyaku, et al., 2023).

3.2 Alignment and quality control of mitochondrial genes

After sequencing, chromatograms are examined and edited using software such as BioEdit for sequence quality. Multiple sequence alignment is done using software such as MEGA, which allows polymorphic, monomorphic, and parsimony-informative sites to be identified. Quality control includes removal of low-quality reads and use of specialized pipelines (e.g., Mitopore, mtGrasp) to enhance data reliability and standardization to enable strong downstream phylogenetic analysis (Ekerette et al., 2018).

3.3 Phylogenetic tree construction and model selection

Phylogenetic distances are estimated using numerous varied methods such as Neighbor-Joining (NJ), Maximum Likelihood (ML), and Maximum Parsimony (MP). Software such as MEGA is utilized for these analyses in which model selection is chosen based on data best representing. BI and machine learning-based approaches can be used with more advanced datasets in order to increase trees accuracy and support values. Method choice is determined by sequence diversity, data set size, and study objective (Ekerette et al., 2018; Gamage et al., 2020).

3.4 Genetic distance calculation and topological analysis of phylogenetic relationships

Genetic distances between populations or species are quantified with models such as Kimura 2-parameter, providing quantitative divergence estimates. Molecular variance analysis (AMOVA) is used to decompose genetic variation within and between populations. Phylogenetic networks and trees are interpreted to assess clustering, monophyly, and the presence of differentiated lineages, to support conclusions about evolutionary relationships and population structure (Ikpeme et al., 2019; Nyaku, et al., 2023; Kwikiriza et al., 2025) (Figure2).

4 Phylogenetic Relationships and Divergence Signals in Tilapias

4.1 Sequence variation and inter-specific differentiation based on mtDNA

Mitochondrial DNA (mtDNA) sequence polymorphism is a potent tool for assessing evolutionary history and inter-species differentiation. It has been found that while ancient mitochondrial markers (e.g., COI, CYTB, D-loop) continue to be favorites, analyses based on full mtDNA sequences make more robust and secure phylogenetic inferences than the ones based on short gene fragment sequences. This further confirms the importance of marker choice for successful differentiation of species and evolutionary information.

4.2 Phylogenetic relationships and lineage divergence among geographic populations

Phylogenetic analyses using mtDNA often reveal deep intraspecific divergence and clearly defined lineages that are geographic locality-specific. Such patterns are suggestive of complex evolutionary histories, with genetic divergence among populations shaped by historical biogeography and limited gene flow. In some taxa,

monophyletic clades correspond to geographic origin, which is in accordance with the role of geographic isolation in lineage divergence.

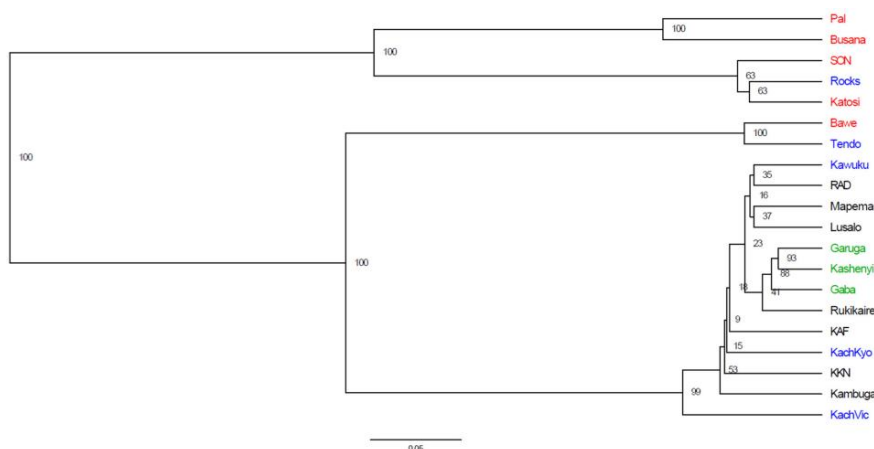


Figure 2 UPGMA dendrogram of the different populations of tilapia species constructed using Nei's genetic distance (Adopted from Kwikiriza et al., 2025)

Image caption: support is given by bootstrap values. Red: Cages, Blue: Hatcheries, Green: Wild and Black: Ponds (Adopted from Kwikiriza et al., 2025)

4.3 Identification of hybrids and cryptic species and their evolutionary implications

Mitochondrial analyses will frequently disclose cryptic lineages and supposed hybridization events. However, mito-nuclear discordance where mtDNA and nuclear DNA suggest different evolutionary histories is widespread. Discordance is caused by ancient introgression, incomplete lineage sorting, or recent hybridization and complicates recovery of true cryptic species. Integrative approaches that use both mtDNA and nuclear markers are recommended for accurate delimitation of species and inference of evolutionary processes (Abreu et al., 2020).

4.4 Monophyletic/paraphyletic status of key populations and taxonomic interpretations

Phylogenetic analyses reveal the general trend of finding that not all populations or species are monophyletic for mtDNA and some are paraphyletic due to hybridization or incomplete lineage sorting. While mtDNA can resolve much of the relationships, nuclear markers can reveal more in the way of complexity, such as admixture or no well-defined species boundaries. These findings suggest the prudence with which taxonomic inference based on mtDNA alone should be conducted and their support for the use of integrative taxonomic methods (Abreu et al., 2020).

5 Mitochondrial Genetic Mechanisms of Adaptive Evolution in Tilapias

5.1 Selective pressures from ecological factors on mitochondrial evolution rates

Environmental and climatic factors can impose selective pressures on mitochondrial genomes, possibly regulating their evolution rates. Accounts in other groups indicate mitochondrial genes are subjected to strong purifying selection with varied intensity between species and genes depending on the metabolic requirements and environmental stress. For example, energy production genes like *ND1*, *ND2*, *ND6*, *COIII*, and *ATP8* may be under higher purifying selection in harsher environments of some species, and such mechanisms may dominate in tilapias taking on varied aquatic environments (Ghosh et al., 2024).

5.2 Functional evolution of mitochondrial genes related to energy metabolism and reproductive adaptation

Mitochondrial genes play a central role in energy metabolism, particularly through oxidative phosphorylation (OXPHOS). Adaptive evolution in such genes can affect ATP and reactive oxygen species (ROS) production, which can impact organismal performance, life-history characteristics, and adaptation to new thermal or ecological environments. Furthermore, mitochondrial genetic variation can influence reproductive traits, with evidence that mtDNA variants have a role in sperm performance and can be the target of sex-specific selection, which may find applicability for tilapia reproductive adaptation (Koch et al., 2021).

5.3 Functional correlation between phenotypic variation and mtDNA polymorphism

mtDNA variation is now widely believed to be functionally significant, permitting variation in metabolic rate, behavior, and other phenotypic traits within and among populations. Environmental heterogeneity and negative frequency-dependent selection can potentially preserve mtDNA polymorphism, mediating genetic diversity with ecological and phenotypic diversity. This suggests tilapia mtDNA variation can be accountable for adaptive phenotypic variation relevant to ecological success (Dowling and Wolff, 2023).

5.4 An integrated model of “mitochondrial variation-function-ecology” in tilapia adaptation

One integration framework proposes that ecological stresses drive mitochondrial genetic variation, which affects mitochondrial function and organismal phenotype. This interactive dynamic process-selection pressure acting across biological scales (organism, tissue, cell, mitochondrion)-evokes adaptation to environment stresses. Mitochondrial-nuclear environments mediate such influences, rendering an integrated mitochondrial genetics-based model of tilapia adaptation applicable (Koch et al., 2021; Dowling and Wolff, 2023; Li et al., 2024).

6 Theoretical and Practical Significance of Mitochondrial Research in Tilapias

6.1 Advancing molecular evolution and phylogenetic theory in fishes

Mitochondrial DNA (mtDNA) research has contributed considerably to enhancing the understanding of molecular evolution and phylogenetic relationships in fishes. By examining the D-loop and cytochrome b regions, researchers have been capable of resolving molecular divergence patterns, population structure, and evolutionary history among tilapia species. They provide baseline information for phylogeny reconstruction, tracing maternal lineages, and the processes of genetic adaptation and differentiation in fish populations (Aminisarteshnizi et al., 2024).

6.2 Providing molecular evidence for germplasm conservation and breeding of tilapias

Mitochondrial markers are excellent markers employed in assessing genetic diversity, population structure, and integrity of lineage, all of which are critical to germplasm conservation and selective breeding programs. mtDNA can be applied for identification of private haplotypes, detection of introgression, and tracing of genetic variation at and among populations. This molecular evidence supports the development of improved breeding schemes, conservation of unique genetic resources, and management of hybridization risks in farmed and wild tilapia populations (Ekerette et al., 2018; Bian et al., 2019; Chu et al., 2021; Wu et al., 2021).

6.3 Application potential of mtDNA in species identification, market regulation, and resource management

Technical uses of mtDNA analysis are also evident in the identification of species, especially in processed items where morphological features are difficult to determine. DNA barcoding using mtDNA markers such as COI is an effective method to identify species in the marketplace, guarantee food safety, and prevent mislabeling. Second, mtDNA data are accessible to resource management and possess the capacity to track stock origin, ensuring genetic diversity, as well as guiding regulatory decision-making towards sustainable fishery and aquaculture management (Wu et al., 2021; Chu et al., 2021; Nascimento et al., 2022).

7 Limitations and Future Research Directions

7.1 Limitations of mtDNA data and the need for nuclear genome integration

Mitochondrial DNA (mtDNA) is widely used in phylogenetic and population genetic studies owing to its high mutation rate and maternal inheritance. Nevertheless, its uniparental inheritance, lack of recombination, and low effective population size could limit it to completely distinct evolutionary relationships and population structure. In addition, the presence of nuclear mitochondrial DNA segments (NUMTs) might make the analysis difficult with resulting misplacement of phylogenetic signals. The integration of nuclear DNA markers with mtDNA enhances the resolution and precision of phylogenetic and phylogeographic hypotheses and allows for improved understanding of evolutionary processes and reduces the prospect of drawing false conclusions based on mtDNA alone (Dong et al., 2021).

7.2 Challenges in sample coverage and data representativeness

Representative and broad sampling coverage are still an issue in mtDNA studies. Limited geographic or taxonomic sampling may give rise to skewed results and mask actual genetic diversity and population structure patterns. Partial or skewed sampling may further hinder the detection of rare haplotypes or cryptic lineages, reducing the power of phylogenetic analysis and conservation assessment. Improved sampling designs and use of high-quality, large reference alignments can enable the resolution of such issues as well as enhance the solidity of mtDNA-informed studies.

7.3 Lack of experimental validation and ecological correlation for functional mtDNA variants

While mtDNA variation is often associated with phenotypic and ecological character, experimental evidence for functional effect is rare. The majority of reports are based on correlative data, and the ecological relevance of specific mtDNA variants has been inadequately examined. The requirement exists for integrative systems synthesizing genetic, functional, and ecological data to prove the adaptive worth of mtDNA variants and determine their functions in organismal fitness and adaptation (Kopinski et al., 2021; Wang and Wang, 2024).

7.4 Establishing a multi-marker and multi-scale framework for phylogenetic and adaptive studies of tilapias

Subsequent work should involve the development of multi-marker and multi-scale models integrating mtDNA, nuclear DNA, and additional genomic data. Throughputs in high-throughput sequencing and improvements in bioinformatics now make it possible to simultaneously analyze thousands of nuclear and mitochondrial loci simultaneously, increasing phylogenetic resolution and the detection of mito-nuclear discordance. All such integrative approaches are critical for robust species delimitation, understanding adaptive evolution, and informing conservation and management in tilapias and other groups (Lareau et al., 2023).

8 Concluding Remarks

Phylogenies of large molecular datasets, integrating both mitochondrial and nuclear markers, have clarified the evolutionary relationships among *Oreochromis* species. Multi-marker phylogenies have pervasive mito-nuclear discordance, which is often due to incomplete lineage sorting or introgression, but nuclear phylogenies reproduce major clades regularly and confirm the nesting of *Alcolapia* in *Oreochromis*. The findings have instigated taxonomic revision and improved understanding of the adaptation and diversification of *Oreochromis*, especially in stressful environments such as soda lakes.

Ancient and recent hybridization has played a role in the evolutionary history of *Oreochromis*, producing genetic variation and, in certain cases, hybrid speciation. However, ongoing hybridization-typically by aquaculture introductions-is compromising the genetic integrity of native populations. Geographical isolation and ecological adaptation, including to stressful environments, have independently resulted in lineage divergence and repeated evolution of major adaptive traits within the genus.

Molecular markers, particularly mtDNA and nuclear markers, are excellent tools for correct species identification, taxonomic delimitation, and hybrid detection. These methods are the foundation for conservation efforts through the facilitation of the revelation of genetic structure, establishing distinctive lineages, and tracking introgression. Molecular data are used to guide breeding programs, for genetic diversity assurance, and market regulation through accurate species identification even in processed products, aquaculture, and resource management.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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