

Research Report

Open Access

Evolutionary Pathways of Fishes: Insights from Fossil Records and Molecular Phylogenetics

Xianming Li¹, Lingfei Jin² ✉

¹ Aquatic Biology Research Center, Cuiqi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China

² Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China

✉ Corresponding author: lingfei.jin@jicacat.org

International Journal of Aquaculture, 2025, Vol.15, No.5 doi: [10.5376/ija.2025.15.0025](https://doi.org/10.5376/ija.2025.15.0025)

Received: 20 Aug., 2025

Accepted: 10 Oct., 2025

Published: 25 Oct., 2025

Copyright © 2025 Li and Jin, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Li X.M., and Jin L.F., 2025, Evolutionary pathways of fishes: insights from fossil records and molecular phylogenetics, International Journal of Aquaculture, 15(5): 255-265 (doi: [10.5376/ija.2025.15.0025](https://doi.org/10.5376/ija.2025.15.0025))

Abstract Fish, as the oldest and diverse group of vertebrates, play an important role in the history of biological evolution. This study summarizes the main stages and characteristics of fish evolution pathways, focusing on combining fossil record with molecular phylogenetic research to reveal the evolution of fish from early jawless fish to modern diversified taxa. We reviewed the important discoveries of early jawless fish fossils and the outbreak of fish diversity during the Silurian and Devonian periods; explored the profound impact of the origin of the jaw on predation strategies, as well as the early differentiation of boneless and cartilage fish in the Paleozoic era. Analysis of morphological characteristics and molecular phylogenetic evidence of radial fin fish. Based on the latest molecular phylogenetic research, we reconstructed the evolutionary relationships of important fish populations and conducted case analysis in combination with key evolutionary events. Finally, we emphasize the importance of combining fossil evidence with molecular clock calibration, and combining fossil and molecular insights can help deepen our understanding of the origins and adaptive evolution mechanisms of fish biodiversity.

Keywords Fish evolution; Fossil record; Molecular phylogenetic; Origin of jaw; Adaptive radiation

1 Introduction

Fish are the earliest vertebrates and the most abundant vertebrate group. In the history of animal evolution, the emergence of fish marks an important stage in the evolution of vertebrates, and its evolutionary path is of foundational significance for understanding the subsequent emergence of amphibians, reptiles, birds and mammals. As early as the late Cambrian period, the earliest vertebrates similar to fish had appeared in the ocean, such as the Haikou fish and Kunming fish found in Chengjiang, China, and are considered to be the oldest known vertebrate fossils (Cartwright and Collins, 2007). After Ordovician-Silurian radiation, fish gradually differentiated into multiple branches, including jawless and jawless, laying the foundation for the further evolution of vertebrates.

Fossil record provides direct morphological evidence and chronological frameworks that allow us to reconstruct key nodes in fish evolution. Fossils can determine when a certain group first appeared, what anatomical characteristics it had, and how these characteristics change over time. But fossil evidence alone is often not sufficient to fully reveal the evolutionary relationship: fossil records have problems with incomplete and biasedness, and some soft body features are difficult to preserve (Carroll, 2012). At the same time, the fossil abundance of strata in different periods varies due to geological processes. Therefore, the introduction of molecular phylogenetic methods can compensate for the shortcomings of fossil record by comparing the genome and molecular characteristics of fresh fish (Chen et al., 2014).

This study will sort out the important fossil discoveries about the early evolution of fish in the field of paleontology, including the emergence, diversity and extinction events of jawless and jawless fish; summarize the new understanding of the relationship between major fish taxa by molecular phylogenetics, such as redefining the internal phylogenetic structure of bone fish through high-throughput sequencing data; analyze several key evolutionary events and adaptive radiation cases, explore the integration of fossils and molecular evidence, and

finally propose a prospect and summary of future research. Through this framework, we hope to fully present the complex course of fish evolutionary paths and how fossils and molecular biology can proof-develop the understanding in this field.

2 Evidence of Early Origin of Fish and Paleozoic Fossils

2.1 The discovery of the earliest jawless fish fossils (such as armored fish)

The origin of fish can be traced back to the Early Cambrian period 500 million years ago. Primitive vertebrates that appeared at that time usually had no jaws and no paired fins, and were collectively called jawless. Typical early jawless fish include some ancient fishes that are covered with armor, such as members of the subclass of the Armor. Armors are also called "armor fish" because their heads and front of the torso are covered with bone decks. The earliest fossils of armor discovered so far are mainly unearthed from the late Ordovician to the early Silurian strata, indicating that jawless species were quite prosperous about 460 to 440 million years ago (Romano et al., 2018; Randle et al., 2022). For example, rich fossils of armor fish were found in the formations of the Silurian Lando Verestrachi period (about 438 million years ago) in the Tarim Basin of China, including the Zhang family's Western Regions, Jiangxia fish and the recently reported new species of Nianzhong Changxing fish. These discoveries pushed the jaw fossil record forward by about 11 million years. Jawless fish have original morphological characteristics: their bodies are slender or flat, and they have no upper and lower jaw structures. They mostly make a living by filtering or sucking microorganisms. Although the "Haikou fish" and "Kunming fish" found in the Chengjiang fossil reservoir in the Early Cambrian period in Yunnan, China are not typical armored fish, they are regarded as the most primitive vertebrates.

2.2 Fish diversity in silurian and devonian

The Silurian was a critical period in the history of fish evolution and was called "the dawn of fish". In the mid-Silurian period, the earliest records of jawed fish appeared. A variety of jawed fish that have been fully preserved in the early Silurian fossil repository in Chongqing, China, including representatives of primitive squid and cartilage fish. These findings suggest that in the early Silurian period, jaw species had begun to diversify and fill niches. By the end of the Silurian period and the subsequent Devonian period, fish experienced unprecedented radiation evolution, and the Devonian period was therefore often called the "Age of Fish". A large number of different types of jawed fish appeared in the early Devonian period: including the extinct sharks and rays of the charcoalis, and the two major branches of the radial fin and fermented fin (Lu et al., 2017). Fossil records show that fish have become the main vertebrate group in the Devonian marine and river ecosystems, occupying various ecological niches ranging from filter feeding, small claspers to top predators. In the marine strata of the mid-Devonian period, both jaw fossils of large predatory shield skinfish were found, and small intact skeletons of early radial finfish were found, representing two levels of predator and prey (Choo et al., 2017). With the rise of jaws, jawless fish gradually declined and became extinct during the Devonian period.

2.3 Correlation between fossil evidence and paleoecological environment

Paleozoic fish fossils not only record the evolution of anatomical structures, but also reflect the changes in the paleoecological environment at that time. By analyzing the rock sedimentary characteristics and companion biota of fish-containing fossil formations, the environment and ecological habits of early fish can be inferred. The Silurian "lower red layer" strata in southern China is characterized by red sandstone and is interpreted as the sedimentation of the shallow sea or delta environment in the nearshore. The large number of armor fish fossils found in these lower red layers showed that the shallow sea area of the South China plate at that time was a prosperous area of armor fish. Fish fossils from similar eras also appeared in the red layer of the Tata Eltag Formation in the Tarim Basin in Xinjiang, including armored fish and spinyfish (Figure 1). This similar cross-regional biological combination means that in the early Silurian period, there may be biological exchanges between the South China plate and the Tarim plate, which are not geographically far apart (Liu et al., 2023; Li et al., 2024). Fossil evidence supports the "Tarim-South China Joint Plate" hypothesis that the two continents may be connected or adjacent during the Silurian period, thus sharing similar fish communities. In addition to geographical comparison, fish fossils can also reflect the paleoenvironmental conditions. For example, in the

Silurian strata of the Nianzhong Changxing fish found in the Tarim Basin, a large area of wave mark structure was also preserved at the same strata, indicating that the area was at the shallow sea tide zone at that time.

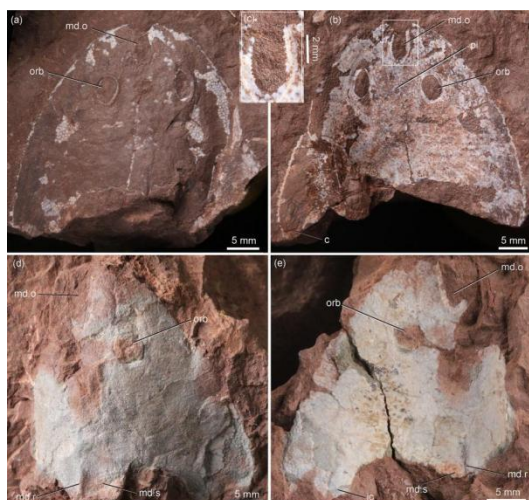


Figure 1 Photographs of *Jiangxialepis rongi* sp. nov. (Adopted from Liu et al., 2023)

Image caption: (a, b) the internal (a) and external (b) moulds of a nearly complete headshield, holotype, IVPP V30966.1. (c) close-up of the median dorsal opening, box region of Figure 2(b), showing the sawtooth margin. (d, e) the internal (d) and external (e) moulds of an incomplete headshield, IVPP V30966.2. Abbreviations: c, cornual process; ic, inner cornual process; md.o, median dorsal opening; md.r, median dorsal ridge; md.s, median dorsal spine; orb, orbital opening; pi, pineal opening (Adopted from Liu et al., 2023)

3 The Origin of Jaws and the Differentiation of Bone Fish and Cartilage Fish

3.1 The effect of jaw evolution on predation strategies

The emergence of jaw is a revolutionary innovation in the history of vertebrate evolution. The jawed species (Gnathostomata) is named after it, including all vertebrates with upper and lower jaw bones. For jawless fish, food acquisition is mainly through filter feeding or adsorption, and the recipe and body size are greatly limited. And the evolution of the jaw makes active predation possible. Judging from the fossil records, the earliest jaws appeared around the end of the Ordovician and the beginning of the Silurian period. At that time, the jaws may have a simple structure but were sufficient to perform the predation function. A series of evolutionary steps are believed to lead to the formation of the jaw: including the evolutionary transformation of the first two gill arches, namely, the original gill arch evolved into a jaw arch structure that supports and moves the upper and lower jaws. This anatomical innovation significantly enhanced the ecological competitiveness of early fish. Jaws can actively hunt invertebrates and even other fish, allowing them to rise rapidly in ecosystems (Deakin et al., 2022).

Changes in predation strategies in turn promote diversification of fish morphology: predation of large prey requires strong bite force and corresponding head muscle attachment, and predation of live prey requires more flexible jaw movement, which puts selective pressure on skull and muscle structure (Jobbins et al., 2024). There is evidence that after the rise of jaw species, jawless fish were threatened by new predators and their populations dropped sharply, and may eventually become extinct at the end of the Devonian. The bite marks on the jawless fish deck in the fossils are a direct record of this predation interaction.

3.2 Early differences between cartilage and bone fish

Shortly after the appearance of Silurian, the jaws differentiated into two main branches: the cartilage and the bones. These two major groups were clearly separated from the end of the Silurian to the early Devonian period, and each evolved in different directions. Cartilage fish include the living sharks, rays and squids, and their bones are mainly composed of cartilage and lack real hard bones. Bonefish include most of the fish we are familiar with (such as carp, bass and other radial fin fish) and meat-fin fish (such as lung fish and quadruped ancestors), which have mineralized bone bones. Paleozoic fossils show that both jawed fish experienced significant radiation during the Devonian period (Schnetz et al., 2024).

The causes of differentiation between cartilage fish and bone fish may be related to niche differentiation and genetic development. Bonefish evolves the stubborn and true teeth of the endoskeleton, which gives them stronger support and bite ability; while cartilage fish retain cartilage bones, making the body lighter and more flexible, and develop shield scales and continuous growth and replacement teeth on the surface of the skin, which is conducive to swimming and predation. Most of the radial-finned fishes in early bone fish have smaller sizes, thin scales and light bones, and are active in nearshore or freshwater environments, and may feed on small invertebrates and plankton.

Some special fish fossils discovered in the early days of the Silurian period in China provide an interesting perspective on this disagreement. For example, there is a fish called "Shenacanthus" in the newly reported Silurian Chongqing biota. It has the anatomy of a cartilage fish, but the front of the body is covered with a large bone deck - a feature that was previously only seen in squidfish (Zhu et al., 2022).

3.3 Multidisciplinary research methods for jaw structure and function evolution

To gain an in-depth understanding of the origin and evolution of jaws, paleontologists and evolutionary biologists have adopted a multidisciplinary cross-cutting approach. In terms of morphology, the internal structure of ancient fish skulls and jaw bones can be studied in detail through three-dimensional reconstruction techniques such as high-precision CT scans. By scanning the fossil of the Silurian Chongqing biota fish with synchronous radiation CT, researchers have seen for the first time the details of the teeth, skulls and even fins of the earliest jawed fish (DeLaurier, 2018).

In the field of biomechanics, by establishing a digital model of the jaw and using finite element analysis, the bite force and stress distribution of ancient fish can be simulated, thereby inferring their bite function. For example, for shield-skinned fish like Duns, simulation studies have shown that the jaw muscles and leverage systems can produce a great bite force enough to break shelled prey, which is consistent with the bitten invertebrate shells found in fossils.

Developmental biology and molecular genetics also provide clues to the origin of the jaw. Embryological studies of present animals show that the neural crest cells responsible for the formation of the gill arch in fish embryos partially evolve into upper and lower jaw structures in jawed species. Therefore, comparing the development of gill arches of jawless species (such as lampreys) with those of jawless species, we can find the differential genes.

4 Ray Fin Fish Diversification and Dominant Position

4.1 Characteristics of bones and fin structures of radial fin fish

The radial fin fish (Actinopterygii) is the most numerous and widely distributed branch in the Bonefish. Their name "radial fins" are derived from their unique fin support structure: each fin is supported by multiple slender bone fin strips, which are arranged radially and are deployed or folded by muscles. This fin structure gives the radial-finned fish a highly flexible motility and fine control of water flow, which is in sharp contrast to the thick fleshy finned fish's. The skeletal system of radial-finned fish is mainly composed of rigid bones, including axial bones centered on the spine, appendage bones and skulls. Early radial-finned fish body spindle-shaped, covered with rhombic hard scales. These rhombic scales are composed of hard scales and are gradually replaced by thin and flexible round scales or comb scales during the evolution process, making the body lighter and more flexible. A major feature of the skull of a radial-finned fish is that the maxilla is not completely fixed to the skull, but is connected by joints and ligaments, which allows the anterior part of the jaw to protrude to a certain extent, which is conducive to prey consumption (Datovo and Rizzato, 2018). This "retractable" jaw is very obvious in many modern radiant fin fish. For example, bass can instantly extend its mouth forward when preying to cause negative pressure to suck prey. The caudal fins of radial fin fish are generally symmetrical and crooked tails, which are different from the heterotails that are significantly up-broken by cartilage fish, providing effective propulsion. It is the characteristics of these skeletons and fins that enable radial fin fish to show excellent maneuverability in the water and can adapt to the changing water environment. From high-speed swimming predators to maneuvering and flexible coral reef fish, all lifestyles have corresponding morphological adaptations.

4.2 Molecular evidence revealing the evolutionary relationships of ray-finned fishes

Although ray-finned fishes are highly diverse and morphologically varied, molecular phylogenetics has helped clarify their evolutionary relationships. Since the late 20th century, comparisons of mitochondrial DNA and nuclear gene sequences have continually refined the phylogenetic tree of ray-finned fishes. In particular, over the past five years, large-scale genome sequencing and transcriptome sequencing projects of fishes have greatly advanced this field. Molecular evidence has revealed that some traditional taxonomic units require adjustment. For example, groups that were previously classified together based on morphology, such as *Cypriniformes* and *Acipenseriformes*, are in fact distantly related on molecular trees. Similarly, some morphologically highly specialized deep-sea fishes (e.g., spiny-rayed scales fishes) have been found to belong to the evolutionary lineage of Osteoglossiformes rather than being independent orders as traditionally assumed (Near and Thacker, 2024). These findings suggest that morphological similarities among different groups may be the result of convergent evolution, and that molecular data are essential for clarifying true phylogenetic relationships.

The establishment of molecular phylogenies has also reshaped our understanding of the evolutionary sequence of ray-finned fishes. For a long time, bichirs, sturgeons, and gars were regarded as primitive ray-finned fish groups, but genomic studies in the late 2010s showed that these ancient fishes are not each other's closest relatives; rather, they diverged from the main ray-finned fish lineage at very early stages (Sallan, 2014). Beyond evolutionary relationships, molecular evidence has also provided estimates of divergence times among ray-finned fish lineages. Molecular clock analyses, calibrated with fossils, have been used to infer the origin periods of major clades. Results indicate that most modern order-level groups of ray-finned fishes had already emerged during the Mesozoic, with groups such as *Salmoniformes* beginning to diversify in the Jurassic. Moreover, during the mass extinction at the end of the Cretaceous, many teleost lineages survived and subsequently radiated further in the Cenozoic. This resilience is closely tied to the strong adaptive capacity and broad ecological diversity of teleost fishes.

4.3 The impact of diversification of radial fin fish on the pattern of modern aquatic ecosystems

In marine ecosystems, from shallow sea coral reefs to deep sea dark areas, there are radiant fin fish. Colorful damselfish, clownfish, and thornail fish on the coral reefs form a complex food web, which together with invertebrates and algae maintain the ecological balance of the coral reef. In the oceanic seas, clustered middle and upper-level fish such as mackerel and herring are important food chain mediators. They filter out plankton and are preyed by large predators. Specialized radiated fin fishes in the deep-sea environment, such as squid fish with luminescent organs, lion fish that can withstand high pressure and low temperatures, etc., filling the ecological niche that other vertebrates cannot access. This distribution breadth from the surface to the deep sea can be achieved in vertebrates only by radial fin fish (Bak et al., 2023).

In freshwater ecosystems, radiated fin fish are the absolute rulers. The fish in the world's big rivers and lakes are all radiant fin fish. They conquered various inland water bodies with amazing adaptability; crucian carp and carp in the still water of lakes can survive under hypoxia (Alfaro, 2018) and gain energy through omnivorousness. These various fish work together to maintain the material flow and energy circulation of freshwater ecology.

5 Reconstruction of Fish Evolution Pathways by Molecular Phylogenetics

5.1 Application of nuclear genes and mitochondrial genes in phylogenetic development

Molecular phylogenetics uses genetic information from different sources to reconstruct relationships between species. Among them, nuclear genes and mitochondrial genes are the two main sources of data, each with its characteristics and complement each other. Mitochondrial DNA (mtDNA) is widely used in species or genus-level phylogenetic analysis because it is present in cellular mitochondria, with relatively simple structure, has a faster evolution rate in animals and is mostly maternal. For example, mitochondrial sequences such as cytochrome b (*cyt b*) gene and 16S *rRNA* gene have a long history of application in fish taxonomy research (Parhi et al., 2019). The advantages of mtDNA are haplotype structure, no recombination, and easy to analyze, but the disadvantages are that they represent a single genetic lineage, are susceptible to maternal history, and different genes may have the problem of evolutionary rate saturation.

In fish phylogenetic studies, mitochondrial and nuclear gene data are often used in combination to learn from each other's strengths and weaknesses. For example, in the molecular phylogenetic research of carp, researchers not only analyze mitochondrial genome sequences to reveal the relationship between low-order taxonomies, but also combine nuclear genes (such as *RAG1*) to determine higher-order evolutionary branches, thus building a more comprehensive phylogenetic tree structure (Near and Keck, 2013).

5.2 Correction of traditional classification by genomic data

Many past classifications based on morphology have been reassessed under genomic evidence, some have been supported and others have been overturned. Some hidden evolutionary relationships have been discovered, which has brought important changes to our understanding of fish phylogenetics. Genome data clarifies the attribution of many taxa (Wang and Chen, 2025). Former taxonomists regarded eels and cypress (Pacific eels) as members of the eels due to their similar appearance, but genomic evidence shows that cypress is actually closer to the cypress and is very different from the real eels, so they should establish a different family.

Genome data found some conjunctive or multi-line problems in traditional classifications. The previous "Caraceae" covers many subfamilies such as carp, carp, whitefish, etc. in the classic classification, but the molecular phylogenetic tree shows that the old "Caraceae" is not a single family. Some subfamilies (such as the subfamily of the cleft fish) are actually far from relatives with other members of the Caraceae, and should be split out and promoted to independent families (Yang et al., 2015).

Genome studies reveal new evolutionary locations in some taxa. For example, many teaching materials used the view that bone fish can be divided into two categories: radial fin fish and meat fin fish, among which radial fin fish are divided into primitive soft fin fish (such as sturgeon, multi-fin fish) and true radial fin fish. But 21st century systematic genomics confirm that sturgeons and multifin fish do not form one.

5.3 Case analysis: molecular phylogenetic reconstruction of *Cyprinus* fish

The *Cycadaceae* is the most widely distributed and most species among freshwater fish. The phylogenetic relationship of the *Cycadaceae* has long been a hot topic and difficult issue in fish taxonomy, because the subfamilies within the *Cycadaceae* are highly morphologically diverse, and traditional morphological characteristics are sometimes difficult to clarify the evolution order. The introduction of molecular phylogenetics provides new ideas for clarifying the internal relationships of the *Cycadaceae* family. Yang et al. used a data set of 53 nuclear genes and 14 mitochondrial genes to phylogenetic reconstruction of the main group of *Cycadaceae* endemic to East Asia. The research results propose a new model of phylogenetic development of the *Cyprinus* family. First, confirm that the entire *Cyprinus* family originates from a single line, and no matter how different the morphology is, they share a common ancestor; second, the *Cyprinus* family is divided into several main branches, among which *Cyprinus* and the *Cyprinus* family form sister groups with the *Cyprinus* family, including the grass carp subfamily. The subordinate family, the Loach family, etc., which were originally regarded as independent families, may be nested in or adjacent to the *Cyprinus* family evolution trees (Yang et al., 2015).

Molecular phylogenesis also combines with fossil records, providing clues for the geographical evolution of cycadaceae. Through molecular clock calibration, it is assumed that the origin of the *Cycadaceae* was approximately in the Early Cretaceous period (about 193 million years ago). Fossil evidence and biogeographic analysis show that Asia is likely to be the center of origin of the *Cycadaceae* family, and then the *Cycadaceae* family spread to Europe, Africa and other places through events such as plate drift and land bridge diffusion.

6 Key Evolutionary Events and Adaptive Radiation

6.1 Transformation and adaptation of ocean-freshwater environment

During the long history of fish evolution, there have been many events that migrate from the ocean to freshwater or return to the ocean from freshwater. These environmental transformations are accompanied by physiological and morphological adaptation and evolution, and are one of the important driving forces for fish radiation and diversification. Originally vertebrates were thought to have originated from the ocean, but about 40% of today's

bony fish live in freshwater environments, indicating that many lineages have successfully completed the ocean-to-freshwater leap. Taking bone fish as an example, in the late Paleozoic and early Mesozoic period, some primitive bone fish such as the ancient cod and the radial fin fish began to enter the estuary and rivers to adapt to the salinity environment with a large change. By the Cretaceous and Cenozoic, different groups independently invaded freshwater many times, resulting in a rich freshwater fish phase.

The transition of fish from ocean to freshwater environment requires overcoming a range of physiological challenges. The ion concentration in freshwater is much lower than that in seawater, and fish must evolve effective gill and kidney regulation mechanisms to prevent excessive salt loss in the body and avoid excessive water entry (Corush, 2019). Ocean-freshwater transitions are often accompanied by species radiation, as geographical barriers in different water systems can lead to rapid species formation. A large lake cichlids in Africa and a river catfish in South America are typical examples: after the ancestors entered the inland from the ocean, they faced the new environment and new ecological niche, and experienced amazing adaptive radiation, resulting in a large number of endemic species. The freshwater environment is relatively closed and the isolation between each basin is high, which makes the fish lineages in different water bodies evolve and diversify independently. At the same time, freshwater environments are more susceptible to geological and climate change (such as drying lakes and diverting rivers), which will drive the isolation and differentiation of local populations and ultimately form new species (Brito et al., 2022).

6.2 Diversification of body shape, breeding methods and foraging strategies

Adaptive radiation of fish is reflected in multiple morphological and life history characteristics, among which the evolution of body shape, innovation in reproductive methods and differentiation of foraging strategies are the three most significant aspects. Diversified body size: The body length of fish spans six orders of magnitude, from damselfly less than 1 cm to whale sharks over 10 meters, with a weight difference of more than one million times. In early vertebrate evolution, small fish survived and gained dominance after extinction events in the late Devonian period, a phenomenon known as the "Lilliput effect". Although most fish are oviparous by in vitro fertilization, many special reproductive patterns have evolved, including oviparous and viviparous. There are more than 50 types of ovoviparous species recorded in bony fish. Ovoviparous refers to the hatching of fertilized eggs in the mother's body, but the embryos mainly rely on yolk to provide nutrition. This is a transitional model between oviparous and viviparous. Evolution of ovoviparous can increase the survival rate of offspring, especially when predation pressure is high or the environment is unstable, protecting embryos in the mother is an effective strategy.

Foraging strategy differentiation: The food properties of fish cover almost all possible types, including filter feeding of plankton, feeding of bottom mud microorganisms, herbivorous, insectivorous, etc. The study found that the fish morphology is highly matched with its food properties. For example, carnivorous fish usually have large forward-protruding mouths, sharp teeth, and short digestive tracts; while filter-feeding fish have wide mouths, fine gill rakes, and long digestive tracts (Corn et al., 2022). Even within the same lake or coral reef, different fishes avoid competition through "trait differentiation" due to food resources separation (McCord et al., 2021).

6.3 Case analysis: rapid radiation of Cichlids in great lakes in Africa

The Great Rift Valley Lake in eastern Africa has nurtured one of the fastest and most eye-catching adaptive radiations in the history of biological evolution, the explosive diversity of cichlid fish. Take Lake Malawi as an example. The lake covers an area of about 30 000 square kilometers and was formed about 2 million years ago. However, in such a "short" geological time, about 700 species of cichlids have appeared in Lake Malawi. They evolved from a common ancestor, but differentiated into completely different ecological types: some feed on algae and evolved into algae-scraped lips and teeth; some prey on small fish, large in size and high-speed swimming ability; some specialize in molluscs, whose teeth are blunt and thick, can crush screw shells. Such extensive niche differentiation is largely attributed to the unique jaw structure of the cichlid. Cichlids have a highly malleable pharyngeal jaw that can adapt quickly to different foods. This "dual jaw system" allows cichlids to evolve multiple feeding functions in a short period of time, providing a morphological basis for radiation (Svardal et al., 2019).

In addition to morphological adaptation, the behavioral and reproductive isolation mechanisms of cichlids also promote rapid species formation. Many cichlids are oral hatched fish, and females hatch fertilized eggs in their mouths. During courtship, the female fish will select the body color and pattern of the specific male fish for mating. Svardal et al. (2019) genome research found that the gene communication of Lake Malawi cichlids is complex, and multiple lineage radiation is connected to each other through hybridization networks, rather than simply tree-like bifurcations (Figure 2). This means that during the radiation process, different new species do not evolve completely independently, but occasionally infiltration, which accelerates the spread of adaptive genes among populations and promotes diversity.

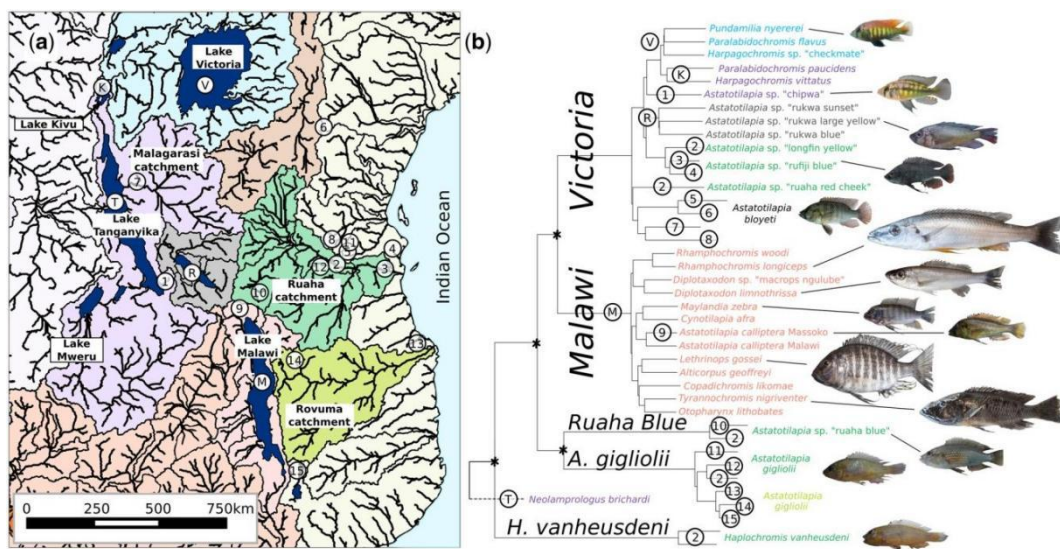


Figure 2 Sampling and genetic relationships. (a) Map of East African river catchments and sampling locations. (b) NJ tree of pairwise genetic distances between all samples (Adopted from Svardal et al., 2019)

7 Integration of Fossil Record and Molecular Evidence

7.1 The role of fossil calibration in molecular clock estimation

The molecular clock method can calculate the time when species divergence occurs by comparing the differences in DNA or protein sequences in different species, combined with a relatively constant rate assumption. However, the molecular clock must be calibrated to obtain absolute time, which requires the help of fossil recording. The origin time of many major taxa is directly anchored by key fossils (Nguyen and Ho, 2020). The differences between radial-finned fish and meat-finned fish can be calibrated by the earliest bone fish fossils at the end of the Silurian (about 420 million years ago); the differences between shark-shaped and ray-shaped can be referred to as the appearance time of the teeth fossils of cartilage fish in the early Devonian period; the differentiation of the large branches of true bone fish can be based on the presumption of the primitive bone tongue fish and the whole bone fish fossils from the Late Triassic-early Jurassic. Wu et al. (2019) used the molecular biogeographic study of climbing perch (a freshwater fish), and calibrated the origin time of the family Climbing perch. Combined with other fossil constraints, their molecular clock analysis infers that the Climbing Peridae diffuses into Africa through the Indian plate during the Eocene.

7.2 Application of interdisciplinary methods in evolutionary path analysis

Research on fish evolution paths is showing a trend of highly interdisciplinary integration. In addition to paleontology and molecular biology, the integration of the following disciplines and methods is promoting new developments in fish evolution research:

Geological and paleogeographic analysis links the location of fish fossil discovery with plate movements and paleoenvironmental changes in geological history, which can explain the geographical background of biological evolution. By constructing paleogeographic models, researchers found that the Tarim plate was adjacent to the South China plate during the Silurian period, providing the possibility for the cross-regional distribution of

armored fishes (Gardner et al., 2019). Developmental biology and Evo-Devo compare the similarities and differences in embryonic development of existing biological species, especially gene expression, to give a glimpse into the mechanisms of ancient evolutionary events (Diogo, 2018).

In addition to traditional molecular clocks, statistical methods can now integrate fossil and molecular data to build "synthetic evolutionary models". Total fossil incidence, species diversity curve, etc. can be placed in the Bayesian framework together with the molecular phylogenetic tree to infer the diversity rate of each branch. Such macroevolutionary models have been used in fish groups such as the Orozoite, identifying the rate of differentiation and possible drivers of their specific time in geological history (Sun and Mai, 2025). Although it is extremely difficult to extract DNA from fish fossils, there have been cases of successful extraction of ancient DNA for fish remains tens of thousands of years ago in the Holocene or Ice Age. Paleo DNA can directly reveal the genetic diversity and evolutionary dynamics of past fish populations.

8 Prospects and Conclusions

Although fish evolution research has made great progress, there are still some limitations and unsolved mysteries in our understanding of its long history. The incompleteness of fossil record remains a major challenge. There is a relatively scarcity of fish fossils found in many critical periods or key areas, resulting in a "blank" in the evolutionary sequence. In terms of molecular phylogenetics, the contradiction between different data and methods still exists. Systematic trees constructed by different genes occasionally produce topological conflicts, or have insufficient resolution for some fast radiation nodes. This is particularly evident in higher-order phylogenetics (such as the ancient trunk relationship) and low-order fast-differentiated taxa (such as the internal relationship of cichlid radiation).

Multidisciplinary data fusion itself also has bottlenecks. Data scales and properties vary in different fields, and combining them requires careful methodological design. For example, how to quantify and compare the relationship between developmental gene expression and fossil morphology, how to extrapolate modern ecological observations to geological time scales, etc., these need to be further explored. Fish evolution research also faces some new challenges. Global climate change and human activities are profoundly affecting contemporary fish diversity, and species distribution and evolutionary trajectories may be artificially altered. How to distinguish current changes from natural changes in geological periods and explore the potential impact of the Anthropocene on the future evolution of fish is an emerging topic.

Some emerging technologies and methods are expected to break through the current bottleneck and inject new impetus into fish evolution research. Among them, what is worth looking forward to is the advancement of ancient DNA technology. At present, ancient DNA is mostly used in fish specimens since the ice age, but with the improvement of sequencing and extraction methods, it is not ruled out that DNA fragments can be obtained from older fossils. Another revolutionary field is comparative genomics and functional genomics. As thousands of fish genomes are sequenced, we will fully enter the era of big data, and we can compare the differences in the structure, number of genes, regulatory sequences and other differences in different fish genomes. At the same time, artificial intelligence and computing simulation will also play a greater role in this field. Machine learning can assist in analyzing a large number of fossil morphological pictures or three-dimensional models, extract classification characteristics from objective data, and judge environmental adaptation patterns.

Studying the evolutionary path of fish is not only about tracing the history of a group itself, but also is of great significance to understanding the origin and adaptation mechanism of diversity in the entire vertebrate. Fish cover the first occurrence of many key evolutionary events in vertebrates: jaw, teeth, paired appendages, lung and swimmer bladder, inner nostrils, ovoviparity, etc. They all evolved first in fish and then improved and expanded in other vertebrates later. Therefore, the story of fish is actually the first half of our vertebrate evolution.

Acknowledgements

Thank you to all reviewers for their meticulous review, and also thank the members of the research team and technicians for their support in experimental design and data analysis.

Conflict of Interest Disclosure

The authors confirm that the study was conducted without any commercial or financial relationships and could be interpreted as a potential conflict of interest.

References

- Alfaro M., 2018, Resolving the ray-finned fish tree of life, *Proceedings of the National Academy of Sciences*, 115: 6107-6109.
<https://doi.org/10.1073/pnas.1807018115>
- Bak T.M., Camp R.J., Heim N.A., McCauley D.J., Payne J., and Knope M., 2023, A global ecological signal of extinction risk in marine ray-finned fishes (class Actinopterygii), *Cambridge Prisms*, 1: e25.
<https://doi.org/10.1017/ext.2023.23>
- Carroll R.L., 2012, The importance of recognizing our limited knowledge of the fossil record in the analysis of phylogenetic relationships among early tetrapods, *Fieldiana Life and Earth Sciences*, 2012(5): 5-16.
<https://doi.org/10.3158/2158-5520-5.1.5>
- Cartwright P., and Collins A., 2007, Fossils and phylogenies: integrating multiple lines of evidence to investigate the origin of early major metazoan lineages, *Integrative and Comparative Biology*, 47(5): 744-751.
<https://doi.org/10.1093/icb/icm071>
- Chen W., Santini F., Carnevale G., Chen J., Liu S., Lavoué S., and Mayden R., 2014, New insights on early evolution of spiny-rayed fishes (Teleostei: Acanthomorpha), *Frontiers in Marine Science*, 1: 1-17.
<https://doi.org/10.3389/fmars.2014.00053>
- Choo B., Zhu M., Qu Q., Yu X., Jia L., and Zhao W., 2017, A new osteichthyan from the late Silurian of Yunnan China, *PLoS ONE*, 12(3): e0170929.
<https://doi.org/10.1371/journal.pone.0170929>
- Corn K.A., Friedman S.D., Burress E.D., Martinez C.M., Larouche O., Price S.A., and Wainwright P.C., 2022, The rise of biting during the Cenozoic fueled reef fish body shape diversification, *Proceedings of the National Academy of Sciences of the United States of America*, 119(31): e2119828119.
<https://doi.org/10.1073/pnas.2119828119>
- Corush J.B., 2019, Evolutionary patterns of diadromy in fishes: more than a transitional state between marine and freshwater, *BMC Evolutionary Biology*, 19(1): 168.
<https://doi.org/10.1186/s12862-019-1492-2>
- Datovo A., and Rizzato P.P., 2018, Evolution of the facial musculature in basal ray-finned fishes, *Frontiers in Zoology*, 15(1): 40.
<https://doi.org/10.1186/s12983-018-0285-6>
- De Brito V., Betancur-R R., Burns M.D., Buser T.J., Conway K.W., Fontenelle J.P., Kolmann M.A., McCraney W., Thacker C., and Bloom D., 2022, Patterns of phenotypic evolution associated with marine/freshwater transitions in fishes, *Integrative and Comparative Biology*, 62(2): 406-423.
<https://doi.org/10.1093/icb/icac085>
- Deakin W.J., Anderson P.S.L., Boer W., Smith T.J., Hill J.J., Rücklin M., Donoghue P.C.J., and Rayfield E., 2022, Increasing morphological disparity and decreasing optimality for jaw speed and strength during the radiation of jawed vertebrates, *Science Advances*, 8(11): eabl3644.
<https://doi.org/10.1126/sciadv.abl3644>
- DeLaurier A., 2018, Evolution and development of the fish jaw skeleton, *Wiley Interdisciplinary Reviews: Developmental Biology*, 8(2): e337.
<https://doi.org/10.1002/wdev.337>
- Diogo R., 2018, Evolutionary developmental biology (Evo-Devo-Path) or macroevolutionary medicine: linking anatomy evolution development and human pathologies, *The FASEB Journal*, 32: 775-1.
https://doi.org/10.1096/fasebj.2018.32.1_supplement.775.1
- Gardner J.D., Surya K., and Organ C.L., 2019, Early tetrapodomorph biogeography: controlling for fossil record bias in macroevolutionary analyses, *bioRxiv*, 18(7): 699-709.
<https://doi.org/10.1101/726786>
- Jobbins M., Rücklin M., Villagra M., Lelièvre H., Grogan E., Szrek P., and Klug C., 2024, Extreme lower jaw elongation in a placoderm reflects high disparity and modularity in early vertebrate evolution, *Royal Society Open Science*, 11(1): 231747.
<https://doi.org/10.1098/rsos.231747>
- Li X., Zhang Y., Lin X., Zhu M., Zhao W., Tang L., Shan X., and Gai Z., 2024, New findings of *Changxingaspis* (*Xiushuiaspidae galeaspida*) from the silurian of tarim basin and Zhejiang Province China, *Acta Geologica Sinica-English Edition*, 98(3): 531-540.
<https://doi.org/10.1111/1755-6724.15168>
- Liu W., Shan X., Lin X., Shen Y., Liu Y., Zhang Z., and Gai Z., 2023, The first *Eugaleaspiforme* fish from the Silurian of the Tarim Basin reveals a close relationship between the Tarim and South China blocks at 438 mya, *Palaeogeography Palaeoclimatology Palaeoecology*, 628: 111774.
<https://doi.org/10.1016/j.palaeo.2023.111774>
- Lu J., Giles S., Friedman M., and Zhu M., 2017, A new stem sarcopterygian illuminates patterns of character evolution in early bony fishes, *Nature Communications*, 8(1): 1932.
<https://doi.org/10.1038/s41467-017-01801-z>

- McCord C.L., Nash C.M., Cooper W.J., and Westneat M.W., 2021, Phylogeny of the damselfishes (*Pomacentridae*) and patterns of asymmetrical diversification in body size and feeding ecology, PLoS ONE, 16(10): e0258889.
<https://doi.org/10.1371/journal.pone.0258889>
- Near T.J., and Keck B.P., 2013, Free from mitochondrial DNA: nuclear genes and the inference of species trees among closely related darter lineages (Teleostei: Percidae: Etheostomatinae), Molecular Phylogenetics and Evolution, 66(3): 868-876.
<https://doi.org/10.1016/j.ympev.2012.11.009>
- Near T.J., and Thacker C.E., 2024, Phylogenetic classification of living and fossil ray-finned fishes (*Actinopterygii*), Bulletin of the Peabody Museum of Natural History, 65(1): 3-302.
<https://doi.org/10.3374/014.065.0101>
- Nguyen J., and Ho S., 2020, Calibrations from the fossil record, Cham: Springer International Publishing, 2021: 117-133.
https://doi.org/10.1007/978-3-030-60181-2_8
- Parhi J., Tripathy P.S., Priyadarshi H., Mandal S.C., and Pandey P., 2019, Diagnosis of mitogenome for robust phylogeny: a case of *Cypriniformes* fish group, Gene, 713: 143967.
<https://doi.org/10.1016/j.gene.2019.143967>
- Randle E., Keating J.N., and Sansom R.S., 2022, A phylogeny for Heterostraci (stem-gnathostomes), bioRxiv, 11(5): e70030.
<https://doi.org/10.1101/2022.08.11.503478>
- Romano M., Sansom R., and Randle E., 2018, Morphospace saturation in the stem-gnathostomes pteraspidiiformes heterostracans: an early radiation of a 'bottom' heavy clade, PeerJ, 6: e5249.
<https://doi.org/10.7717/peerj.5249>
- Sallan L.C., 2014, Major issues in the origins of ray-finned fish (*Actinopterygii*) biodiversity, Biological Reviews, 89(4): 950-971.
<https://doi.org/10.1111/brv.12086>
- Sun C.M., and Mai R.D., 2025, Origin and evolutionary history of oysters based on comparative phylogenomics and fossil evidence, Bioscience Methods, 16(4): 183-191.
<https://doi.org/10.5376/bm.2025.16.0017>
- Svardal H., Quah F., Malinsky M., Ngatunga B., Miska E., Salzburger W., Genner M., Turner G., and Durbin R., 2019, Ancestral hybridization facilitated species diversification in the lake Malawi cichlid fish adaptive radiation, Molecular Biology and Evolution, 37: 1100-1113.
<https://doi.org/10.1093/molbev/msz294>
- Wang L.T., and Chen L., 2025, Reconstructing the phylogenetic relationships of *Scomberomorus* spp.: evolutionary history from whole-genome data, International Journal of Marine Science, 15(3): 130-143.
<https://doi.org/10.5376/ijms.2025.15.0012>
- Yang L., Sado T., Hirt M., Pasco-Viel E., Arunachalam M., Li J., Wang X., Freyhof J., Saitoh K., Simons A., Miya M., He S., and Mayden R., 2015, Phylogeny and polyploidy: resolving the classification of cyprinine fishes (Teleostei: *Cypriniformes*), Molecular Phylogenetics and Evolution, 85: 97-116.
<https://doi.org/10.1016/j.ympev.2015.01.014>
- Zhu Y.A., Li Q., Lu J., Chen Y., Wang J., Gai Z., Zhao W., Wei G.B., Yu Y., Ahlberg P., and Zhu M., 2022, The oldest complete jawed vertebrates from the early Silurian of China, Nature, 609: 954-958.
<https://doi.org/10.1038/s41586-022-05136-8>



Disclaimer/Publisher's Image caption

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.