International Journal of Molecular Evolution and Biodiversity 2024, Vol.14, No.4, 147-161
http://ecoevopublisher.com/index.php/ijmeb

Review Article Open Access

Systematic Evolution and Radiation of Vertebrates: Reconstructing Phylogenetic Relationships and Unveiling Speciation Mechanisms

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International Journal of Molecular Evolution and Biodiversity, 2024, Vol.14, No.4 doi: 10.5376/ijmeb.2024.14.0017
Received: 04 Jun., 2024
Accepted: 11 Jul., 2024
Published: 18 Jul., 2024

Preferred citation for this article:
Liu Z., and Wang W.F., 2024, Systematic evolution and radiation of vertebrates: reconstructing phylogenetic relationships and unveiling speciation mechanisms, International Journal of Molecular Evolution and Biodiversity, 14(4): 147-161 (doi: 10.5376/ijmeb.2024.14.0017)

Abstract This study explores the evolutionary history and radiation of vertebrates, focusing on reconstructing phylogenetic relationships and unveiling the mechanisms of speciation. By integrating molecular and morphological data, the review elucidates the complexity of vertebrate lineages and the dynamic processes driving speciation, including allopatric, sympatric, peripatric, and parapatric mechanisms. Key findings highlight the significance of adaptive radiation and genetic studies in understanding how species diversify through ecological opportunities and evolutionary innovations. Case studies provide unique insights into the patterns and processes of vertebrate evolution. These studies emphasize the importance of phylogenetic knowledge in biodiversity conservation and the preservation of evolutionary potential. Emerging technologies and interdisciplinary approaches are identified as crucial for advancing future research in vertebrate evolution. This study contributes to the broader understanding of biodiversity and evolutionary processes, providing a foundation for future research and conservation efforts.
Keywords Vertebrates; Phylogenetics; Speciation; Adaptive radiation; Biodiversity conservation

1 Introduction

The study of vertebrate evolution is crucial for understanding the complex history of life on Earth. Vertebrates, a diverse group of animals with backbones, have undergone significant evolutionary changes over millions of years, leading to the vast array of species we see today. The importance of studying vertebrate evolution lies in its ability to shed light on the mechanisms that drive biodiversity and adaptation. By examining the evolutionary trajectories of vertebrates, researchers can gain insights into the processes that generate and maintain biological diversity (Streelman and Danley, 2003; Donoghue and Keating, 2014).

Vertebrates are divided into several major lineages, including fish, amphibians, reptiles, birds, and mammals. Each of these groups has experienced unique evolutionary paths, resulting in a wide range of morphological, ecological, and behavioral adaptations. For instance, the transition from jawless to jawed vertebrates marked a significant evolutionary milestone, characterized by genomic, embryologic, and phenotypic changes (Donoghue and Keating, 2014). Additionally, the study of vertebrate systematics has revealed the intricate relationships among different species, highlighting the role of both natural and sexual selection in shaping vertebrate diversity (Streelman and Danley, 2003; Cooney and Thomas, 2020).

This study aim to reconstruct the phylogenetic relationships among vertebrates. Understanding these relationships is essential for elucidating the evolutionary history and connections between different vertebrate species. Recent advances in molecular phylogenetics and phylogenomics have provided powerful tools for resolving these relationships, even among groups with complex evolutionary histories. Meanwhile, the study seek to unveil the mechanisms of speciation and radiation that have contributed to the diversification of vertebrates. Speciation, the process by which new species arise, is often linked to morphological and ecological changes. By examining the rates of speciation and morphological evolution across different vertebrate clades, we can identify patterns and drivers of diversification. Additionally, understanding the role of genetic factors, such as gene regulation and genome duplication, can provide insights into the molecular mechanisms underlying adaptive evolution.

2 Phylogenetic Relationships Among Vertebrates

2.1 Major vertebrate lineages

Vertebrates are broadly classified into five major groups: fishes, amphibians, reptiles, birds, and mammals. Each group represents a significant evolutionary lineage with unique characteristics and adaptations.

Fishes, the most diverse group, including jawless fishes (Agnatha), cartilaginous fishes (Chondrichthyes), and bony fishes (Osteichthyes). Amphibians, including frogs, salamanders, and caecilians, amphibians are characterized by their dual life stages, aquatic larvae, and terrestrial adults. Reptiles, encompassing turtles, lizards, snakes, and crocodiles, are primarily terrestrial and exhibit a wide range of adaptations. Birds, descendants of theropod dinosaurs, are characterized by feathers, beaks, and high metabolic rates. Mammals, distinguished by the presence of mammary glands, hair, and three middle ear bones, include monotremes, marsupials, and placental mammals.

The evolutionary relationships among these major vertebrate groups have been extensively studied. Molecular and morphological data have helped clarify the divergences and common ancestors of these lineages. For example, the transition from fish to tetrapods marks a significant evolutionary event, with amphibians representing the earliest tetrapods. Reptiles and birds share a common ancestor, with birds evolving from theropod dinosaurs. Mammals diverged from a common ancestor with reptiles, with monotremes representing the most basal lineage (Irisarri et al., 2017).

2.2 Recent advances in phylogenetic studies

Recent advances in genomic technologies and bioinformatics have significantly enhanced phylogenetic studies. Next-generation sequencing (NGS) technologies, such as RAD sequencing and ultraconserved element (UCE) sequence capture, have enabled the generation of large-scale genomic datasets, providing high-resolution phylogenies (Suchan et al., 2017). Bioinformatics tools and coalescent-based methods have improved the accuracy of species tree reconstruction, even in the presence of gene tree incongruence and gene flow.

Several case studies highlight the impact of these advances. For instance, RAD sequencing has resolved the phylogeny of the fly genus Chiastocheta, which was previously unresolved using mitochondrial markers alone. Similarly, UCE data have been used to resolve the rapid radiation of gallopheasants, demonstrating the effectiveness of these methods in addressing difficult phylogenetic questions (Meiklejohn et al., 2016). Whole-genome sequencing has also been employed to resolve the phylogenetic relationships of closely related flycatcher species, revealing patterns of gene flow and introgression (Nater et al., 2015).

3 Speciation Mechanisms in Vertebrates

3.1 Allopatric speciation

Geographic isolation can result from physical barriers such as mountains, rivers, or oceans, which prevent gene flow between populations. Over time, these isolated populations undergo genetic changes due to mutation, natural selection, and genetic drift, eventually leading to speciation. This mechanism is well-documented in various vertebrate groups, particularly in island and continental populations.

Island populations: The Lesser Antillean anoles provide a classic example of allopatric speciation. Geological and molecular phylogenetic evidence shows that Martinique anoles, which were isolated on precursor islands, exhibit significant genetic divergence. However, secondary contact after island coalescence revealed less reproductive isolation than expected, suggesting incomplete allopatric speciation (Thorpe et al., 2010).

Continental populations: In freshwater zooplankton of the genus Daphnia, allopatric speciation accounts for a significant portion of cladogenetic events. Intercontinental splits, particularly in the circumarctic region, align with bird migration routes, indicating recent dispersal and vicariance scenarios linked to continental fragmentation (Adamowicz et al., 2009).

3.2 Sympatric speciation

Sympatric speciation occurs without geographic isolation, often driven by ecological niche differentiation or sexual selection. This mechanism is more controversial but has been supported by several case studies. In the Hydrobatinae subfamily of storm-petrels, sympatric speciation by allochrony (seasonal breeding differences) has been suggested. For instance, *Hydrobates castro* and *H. monteiroi* breed in different seasons on the Azores, indicating reproductive isolation without geographic separation (Figure 1) (Wallace et al., 2017).

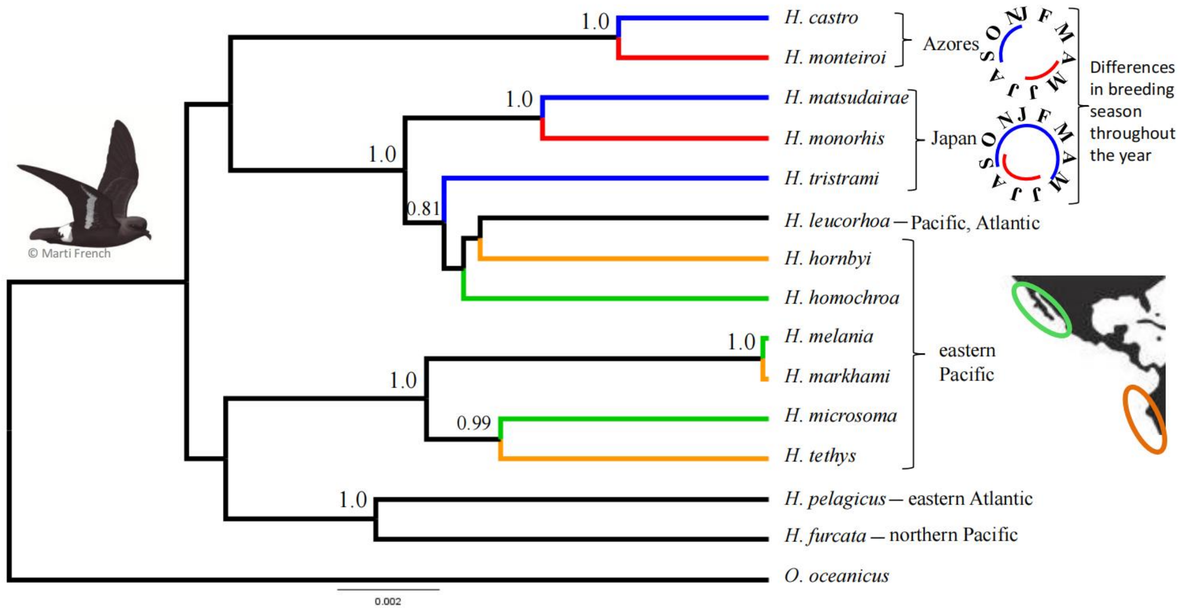

Figure 1 The evolutionary relationships and breeding season differences among various species of the Hydrobatinae subfamily (storm-petrels) (Adapted from Wallace et al., 2017)

Image caption: The branch lengths represent genetic differences between species, with the values (such as 1.0 and 0.81) indicating node support values. The higher the support value, the higher the credibility of the branch. The upper right corner of the figure shows the significant differences in breeding seasons between *H. castro* and *H. monteiroi* in the Azores. The scale bar (0.002) at the bottom of the figure represents the branch lengths in the phylogenetic tree (Adapted from Wallace et al., 2017)

3.3 Peripatric and parapatric speciation

In peripatric speciation, small peripheral populations experience strong genetic drift and selection pressures, leading to rapid divergence. Parapatric speciation involves populations that are adjacent but experience different selective pressures across an environmental gradient.

Peripheral isolates: The land snail genus *Theba* on the Canary Islands demonstrates peripatric speciation. Cryptic diversification driven by non-adaptive allopatric differentiation and secondary gene flow has been observed, with some sympatric forms showing complete reproductive isolation (Greve et al., 2012).

Hybrid zones: In the Cuban green anoles, partial island submergence during the Miocene led to allopatric speciation. Subsequent unification of Cuba allowed for secondary contact, with distinct species maintaining their identity despite occasional hybridization, indicating a role for hybrid zones in speciation (Glor et al., 2004).

4 Adaptive Radiation in Vertebrates

4.1 Concept and significance of adaptive radiation

Adaptive radiation is a fundamental concept in evolutionary biology, referring to the rapid diversification of a single ancestral species into multiple species, each adapted to exploit different ecological niches. This process is significant because it explains how a single lineage can give rise to a wide variety of forms and functions, contributing to the biodiversity we observe today. Conditions that favor adaptive radiation include the availability of unoccupied niches, ecological opportunities, and key innovations that allow organisms to exploit new resources or environments (Pincheira-Donoso et al., 2015). The 2018 American Genetic Association meeting held in

Waimea, Hawaii, our knowledge of ecologically, geographically, and taxonomically diverse radiations (Figure 2), providing a more comprehensive display of the diversity of processes encompassed under the umbrella of adaptive radiation (Gillespie et al., 2020).

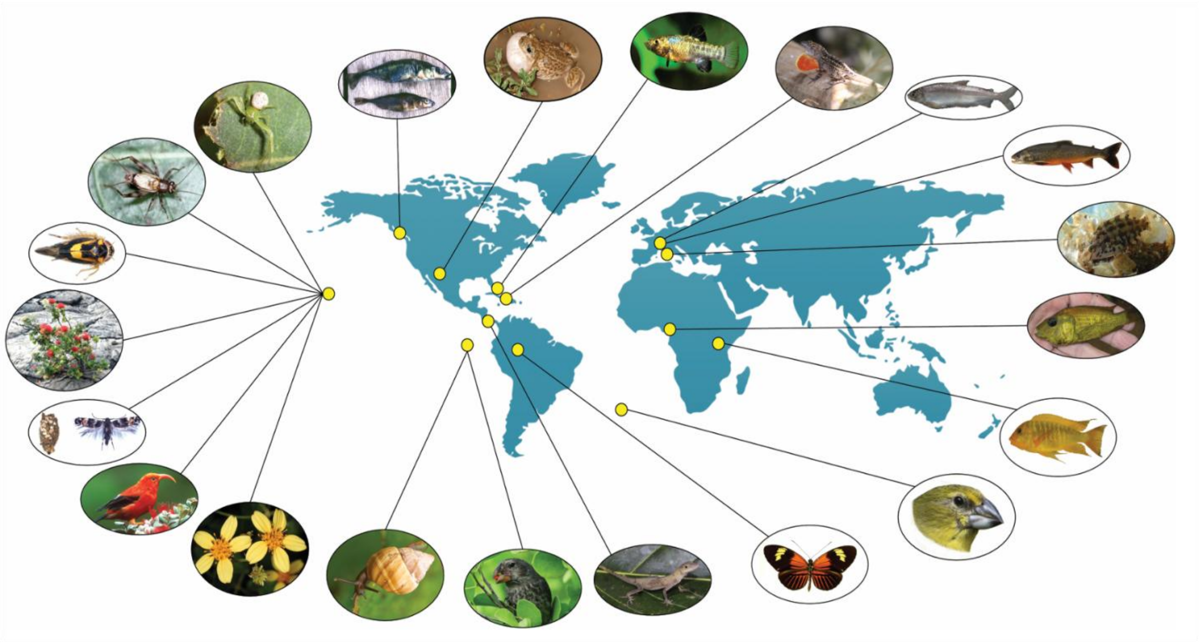

Figure 2 Model systems studied by contributors of the AGA 2018 President's Symposium: Origins of Adaptive Radiation (Adopted from Gillespie et al., 2020)

Image caption: Yellow dots represent areas where field studies have been conducted and do not accurately represent the full geographic distribution of each group. Anti-clockwise from top-right: Mediterranean labrine wrasses, Alpine charr (*Salvelinus umbla* complex), European Alpine whitefish (*Coregonus* spp.), Caribbean Anolis lizards, San Salvador pupfish (*Cyprinodon* sp.), spadefoot toads (*Spea* sp.), stickleback fish (*Gasterosteus aculeatus*), Hawaiian spiders, Laupala crickets, Nesophrosyne leafhoppers, Hawaiian Metrosideros plants, Hyposmocoma moths, Hawaiian honeycreepers, Hawaiian Bidens, Galapagos land snails (*Bulimulus* sp.), Darwin's finches (*Geospiza* sp.), mainland Anolis lizards, Heliconius butterflies, Nesospiza finches of the Tristan da Cunha archipelago, African Great Lake cichlids, and Cameroon crater lake cichlids. Photography credits anti-clockwise from top right: O. Seehausen, O. Seehausen, O. Seehausen, J. Stroud, C. Martin, D. Pfennig, A. Hendry, R. Gillespie, K. Shaw, G. Bennett, E. Stacy, D. Rubinoff, J. Jeffreys, M. Knope, C. Parent, A. Hendry, J. Stroud, J. Mallet, P. Ryan, C. Wagner, C. Martin (Adopted from Gillespie et al., 2020)

4.2 Classic examples of adaptive radiation

Darwin's finches are a classic example of adaptive radiation, where a single ancestral species of finch diversified into multiple species with different beak shapes and sizes, each adapted to different food sources on the Galápagos Islands. This diversification was driven by ecological opportunities and the absence of competing species (Gillespie et al., 2020).

Cichlid fishes in the African Great Lakes represent another well-documented case of adaptive radiation. These fishes have diversified into hundreds of species with varying feeding strategies, body shapes, and behaviors. Mechanisms driving this rapid diversification include ecological opportunities, hybridization, and genetic covariation, which have facilitated the evolution of novel traits and species (Bell and Travis, 2005; Keller et al., 2012; Ford et al., 2015).

Anolis lizards in the Caribbean have also undergone adaptive radiation, resulting in a wide variety of species adapted to different microhabitats, such as tree trunks, branches, and grass. This diversification is driven by ecological opportunities and morphological innovations that allow the lizards to exploit different niches (Gillespie et al., 2020).

4.3 Evolutionary innovations and key adaptations

Evolutionary innovations play a crucial role in adaptive radiation by providing the means for organisms to exploit new ecological opportunities. These innovations can lead to the development of key adaptations that facilitate diversification (Sosa and Pilot, 2023).

The evolution of flight in birds is a prime example of an evolutionary innovation that led to adaptive radiation. The ability to fly allowed birds to access new habitats and resources, leading to the diversification of numerous bird species with varying forms and functions (Parsons, 2016).

The evolution of viviparity (live birth) in mammals is another key adaptation that has facilitated adaptive radiation. This reproductive strategy allowed mammals to occupy a wide range of ecological niches, leading to the diversification of species with different feeding strategies, behaviors, and morphologies (Rintelen and Glaubrecht, 2005; Givnish, 2015).

5 Genetic Basis of Speciation and Adaptation

5.1 Genomic studies of speciation

Genomic studies have significantly advanced our understanding of the genetic basis of speciation. One key area of focus is the identification of speciation genes and the patterns of genetic divergence that accompany the speciation process. For instance, research on *Ficedula flycatchers* has shown that heterogeneous differentiation landscapes, characterized by regions of elevated differentiation known as "differentiation islands", emerge among populations within species. These differentiation islands evolve recurrently in the same genomic regions among independent lineages, primarily driven by background selection and selective sweeps in regions of low recombination rather than gene flow (Burri et al., 2015). Similarly, studies have highlighted the complexity of interpreting genomic islands of differentiation, suggesting that these regions may arise due to reduced diversity rather than reduced gene flow (Cruickshank and Hahn, 2014).

The concept of genomic islands of speciation has been explored in various species. For example, in the rapid radiation of Lake Victoria cichlid fishes, genomic studies have identified signals of divergent selection and hybrid speciation, revealing the role of hybridization in generating novel genetic combinations and new species. Additionally, research on the evolution of genomic islands has shown that linkage between selected alleles can increase the establishment probability of new mutations, although this mechanism alone may not fully explain the evolution of genomic islands (Yeaman et al., 2016).

5.2 Role of natural selection and genetic drift

Natural selection plays a crucial role in driving adaptive traits that contribute to speciation. For instance, studies on amphibians have demonstrated how genomic data can shed light on the molecular adaptations and phenotypic evolution in complex landscapes, highlighting the importance of natural selection in shaping adaptive traits (Sun et al., 2020). Similarly, research on cichlid fishes has shown how genomic techniques can identify genes underlying phenotypic differences among species, providing insights into the genetic basis of adaptive evolution.

Environmental adaptations and sexual selection are key drivers of speciation. In the case of Lake Victoria cichlid fishes, species pairs exhibit differences in male nuptial coloration, feeding ecology, and depth distribution, which are driven by natural selection and sexual selection (Keller et al., 2012). Additionally, studies on birds have shown that pre-mating barriers to gene exchange, caused by natural selection and sexual selection, often arise before post-mating genetic incompatibilities, emphasizing the role of behavioral and ecological factors in speciation.

5.3 Hybridization and introgression

Hybridization and introgression play significant roles in gene flow and adaptive evolution. Hybridization events can introduce novel genetic combinations that fuel speciation, as seen in the rapid radiation of Lake Victoria cichlid fishes, where intergeneric hybridization events have led to the evolution of new species with novel trait combinations. Additionally, genomic studies on flycatchers have revealed patterns of gene flow among species, with distinct patterns of reduced introgression on certain chromosomes, highlighting the complex interplay between hybridization and speciation (Nater et al., 2015).

Hybrid speciation and adaptive introgression are important mechanisms in the evolution of new species. For example, in the case of terrestrial annelids, local adaptation and regulatory divergence have been identified as key evolutionary forces driving cryptic speciation, with hybridization playing a role in shaping genome evolution (Marchán et al., 2020). Similarly, research on cichlid fishes has shown how hybridization can lead to the formation of new species with adaptive traits, contributing to the high speciation rates observed in these radiations.

6 Fossil Record and Evolutionary History

6.1 Importance of fossil evidence

Fossils provide the only direct evidence of extinct life forms, offering a unique window into the evolutionary history of vertebrates. They allow scientists to trace the lineage of vertebrates back to the Ordovician period, where the first fragmentary fish bones appear in the record. Fossils are crucial for understanding the diversification of life on Earth, as they capture the morphological characteristics of species that no longer exist, thus providing a more complete picture of evolutionary transitions (Koch and Parry, 2020). The integration of fossil data into phylogenetic analyses has been shown to significantly alter our understanding of evolutionary relationships, often providing unique insights that cannot be obtained from extant taxa alone.

Major fossil discoveries have had profound impacts on our understanding of vertebrate evolution. For instance, the discovery of transitional fossils such as *Tiktaalik roseae*, which bridges the gap between fish and tetrapods, and *Archaeopteryx*, which links reptiles and birds, have provided critical evidence for evolutionary transitions. These fossils not only fill gaps in the fossil record but also help to confirm hypotheses about the evolutionary pathways that led to the diversity of life we see today. The fossil record of early vertebrates, including groups like anaspids, thelodonts, and galeaspids, has been instrumental in elucidating the gradual assembly of key vertebrate characteristics.

6.2 Transitional fossils and evolutionary transitions

Transitional fossils are pivotal in understanding the evolutionary transitions between major groups of vertebrates. *Tiktaalik roseae*, discovered in the Devonian strata, is a prime example of a transitional fossil that exhibits both fish and tetrapod characteristics, providing insight into the fish-to-tetrapod transition (Donoghue and Keating, 2014). Similarly, *Archaeopteryx*, from the Late Jurassic period, showcases a blend of avian and reptilian features, highlighting the evolutionary transition from reptiles to birds. These fossils are not only significant for their intermediate forms but also for their ability to validate evolutionary theories and timelines.

6.3 Dating techniques and evolutionary timelines

Dating techniques such as radiometric dating and molecular clock methods are essential for constructing accurate evolutionary timelines. Radiometric dating allows scientists to determine the age of fossils by measuring the decay of radioactive isotopes, providing a chronological framework for evolutionary events. Molecular clock methods, on the other hand, estimate divergence times based on the rate of genetic mutations, offering a complementary approach to fossil-based dating (Etienne et al., 2012).

The construction of evolutionary timelines involves integrating fossil data with molecular and morphological data from extant species. Bayesian total-evidence dating, which combines these data sources, has been particularly effective in accommodating the uncertainties associated with fossil placement and dating the phylogenetic tree (Zhang et al., 2015). This approach has been used to refine the timelines of major evolutionary events, such as the radiation of Hymenoptera, by incorporating information about fossilization and sampling processes. The resulting timelines provide a more nuanced understanding of the tempo and mode of vertebrate evolution, allowing for rigorous tests of evolutionary hypotheses (Donoghue and Keating, 2014).

7 Case Analysis: Evolutionary Radiation of Mammals

7.1 Phylogenetic relationships and divergence

The phylogenetic relationships within mammals have been extensively studied using both molecular and fossil data. Recent advancements in phylogenetic methods, particularly those that do not rely solely on fossils, have significantly enhanced our understanding of mammalian evolution. For instance, a comprehensive phylogeny of rodents, the most diversified mammalian clade, was constructed using a molecular supermatrix of 11 mitochondrial and nuclear genes covering 1 265 species. This study revealed distinct diversification patterns among different rodent clades, such as Myomorpha and Sciuroidea, highlighting the complexity of mammalian phylogenetic relationships (Fabre et al., 2012).

Additionally, the use of large comparative sequence data sets has provided robust phylogenetic trees for mammals. For example, Upham et al. (2019) developed a robust evolutionary timescale for all approximately 6,000 extant mammal species by creating a set of reliable trees that capture root-to-tip uncertainties in both topology and divergence times. Their “backbone-and-patch” tree-building approach applied a newly assembled supermatrix of 31 genes to two levels of Bayesian inference (Figure 3).

Fossil evidence, combined with molecular data, has been crucial in estimating divergence times within mammals. Molecular phylogenetic analyses calibrated with fossils have provided a time frame for the mammalian radiation, supporting the long-fuse model of diversification. This model suggests that the Cretaceous Terrestrial Revolution and the Cretaceous-Paleogene (KPg) mass extinction played significant roles in opening up ecological niches, thereby promoting mammalian diversification (Meredith et al., 2011).

Moreover, the use of relaxed molecular clocks has allowed for more accurate estimates of divergence times. For instance, a study on rodent diversification employed a relaxed molecular clock dating approach, which provided a time framework for speciation events and identified shifts in diversification rates within major rodent clades. These molecular time trees, when compared with the fossil record, suggest that extinction events have led to the loss of diversification signals for many Paleogene nodes, highlighting the interplay between fossil preservation and molecular data in understanding mammalian evolution.

7.2 Adaptive radiations in mammals

Adaptive radiations have been a key driver of mammalian diversification. The diversification of placental mammals, for example, has been linked to the end-Cretaceous mass extinction, which created new ecological opportunities. This event is thought to have catalyzed the rapid radiation of various mammalian subclades, including placentals, which diversified from small insectivorous ancestors into a wide range of ecological niches (Grossnickle et al., 2019).

Similarly, the radiation of marsupials is another example of adaptive radiation in mammals. Marsupials have undergone significant diversification, particularly in Australia, where they have evolved to occupy a variety of ecological niches. Phylogenetic studies have shown that marsupials and placentals have distinct evolutionary histories, with marsupials experiencing their own unique adaptive radiations (Upham et al., 2019).

7.3 Speciation mechanisms in mammals

Speciation in mammals can occur through both allopatric and sympatric mechanisms. Allopatric speciation, where populations are geographically isolated, has been a common mode of speciation in mammals. For instance, the fragmentation of continents during the Cretaceous period likely contributed to the allopatric speciation of placental mammals, as different populations became isolated and evolved independently (Hallström and Janke, 2010).

Sympatric speciation, where new species arise within the same geographic area, has also been observed in mammals, although it is less common. Ecological niche differentiation and adaptive traits play crucial roles in sympatric speciation. For example, the diversification of New World monkeys (Platyrrhini) has been linked to ecological niche differentiation, with early phenotypic diversification in body size followed by stasis, suggesting that ecological factors have driven their speciation (Aristide et al., 2015).

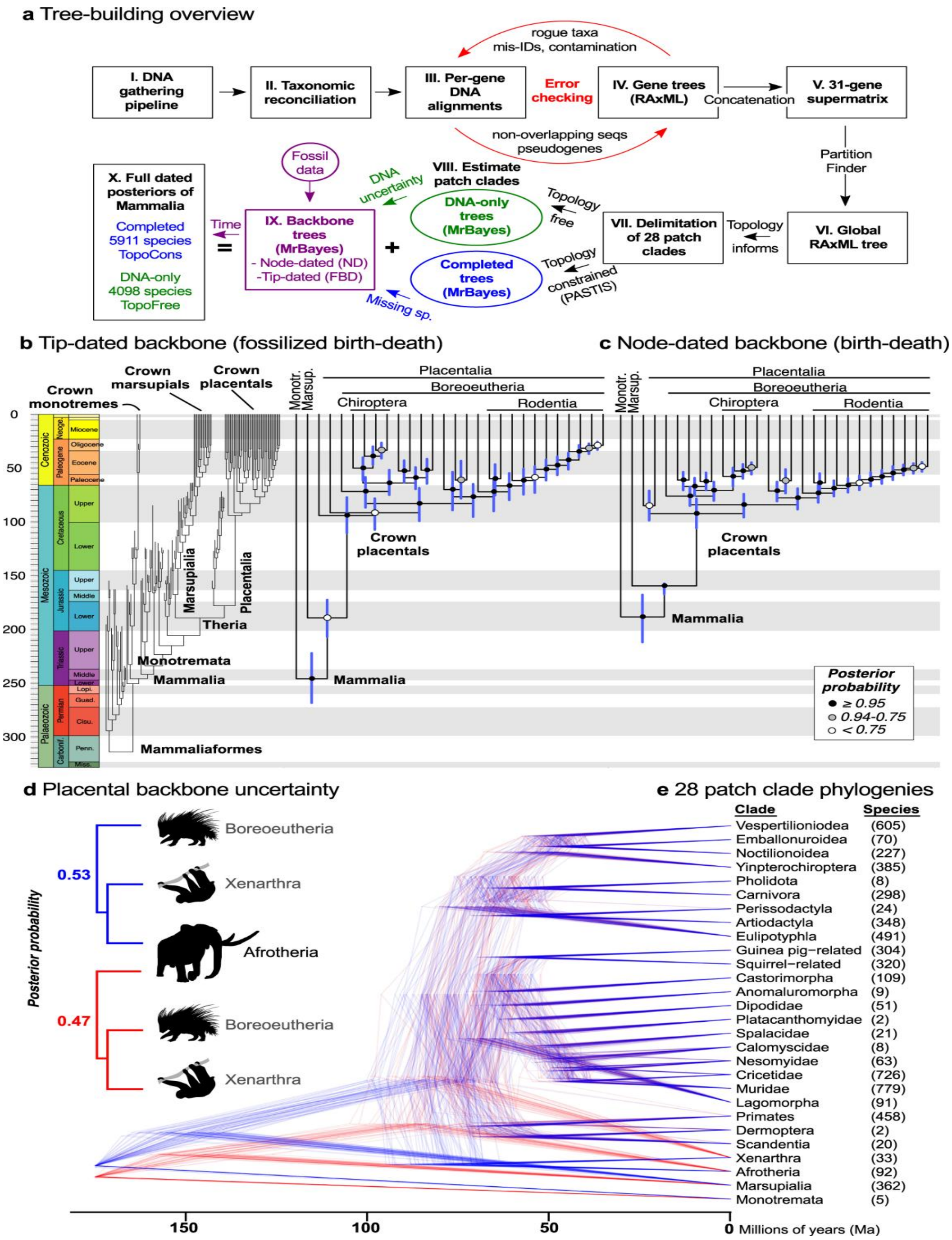

Figure 3 Building the backbone-and-patch mammalia phylogenies (Adopted from Upham et al., 2019)

Image caption: (a) Schematic overview of DNA sequence gathering from NCBI, taxonomic matchup, iterative error checking, and estimating a global ML tree from the resulting supermatrix (31 genes by 4 098 species). Patch phylogenies were then delimited, estimated using Bayesian inference, and joined to fossil-calibrated backbone trees (node- or tip-dated). The resulting posterior samples of 10 000 fully dated phylogenies either had the global ML tree topology constrained (completed trees of 5 911 species, "TopoCons") or no topology constraints (DNA-only trees, "TopoFree"). (b, c) Comparison of results from the time-calibrated backbones as pruned to the 28 patch clade representatives. The tip-dated analysis uses fossil taxa as extinct tips in the tree (left side) and then pruned (right side), whereas the node-dated approach uses exponential priors from minimum to soft-max ages. Trees are maximum clade credibility summaries of 10 000 trees. Circles at nodes indicate PP values according to the legend. (d) Topological and age uncertainty in the backbones included the unresolved base of Placentalia, which slightly favors the Atlantogenata hypothesis (blue) versus Exafroplacentalia (red; shown for the node-dated backbone). (e) Bayesian phylogenies of 28 patch clades were separately estimated in relative-time units for rescaling to representative divergence times on the backbone. Combining sets of backbones and patch clades yielded four posterior distributions for analysis; Carbonif., Carboniferous; Cisu., Cisuralian; FBD, fossilized birth - death; Guad., Guadalupian; Lopi., Lopingian; Marsup., Marsupialia; mis-ID, misidentification; Miss., Mississippian; ML, maximum-likelihood; Monotr., Monotremata; NCBI, National Center for Biotechnology Information; Nioge., Neogene; PASTIS, Phylogenetic Assembly with Soft Taxonomic Inferences; Penn., Pennsylvanian; PP, posterior probability; RAxML, Randomized Axelerated Maximum Likelihood (Adopted from Upham et al., 2019)

Ecological niches and adaptive traits are fundamental to the speciation mechanisms in mammals. The ability of mammals to exploit diverse ecological niches has been a driving force behind their adaptive radiations. For example, the ecological diversification of early mammals during the Cretaceous Terrestrial Revolution involved the exploitation of new niches, leading to the radiation of various mammalian groups.

Adaptive traits, such as body size, dietary specialization, and locomotor adaptations, have also played significant roles in mammalian speciation. Studies on the diversification of rodents and other mammalian groups have shown that shifts in diversification rates are often associated with the evolution of new adaptive traits, which enable species to exploit different ecological niches and reduce competition (Venditti et al., 2011).

8 Conservation Implications of Evolutionary Studies

8.1 Importance of phylogenetic knowledge in conservation

Phylogenetic knowledge plays a crucial role in conservation prioritization by helping identify species and populations that are evolutionarily distinct and therefore irreplaceable. Traditional conservation approaches often focus on species richness or endemism, but these do not necessarily capture the evolutionary history and genetic diversity of species. By incorporating phylogenetic information, conservation efforts can be more effectively directed towards preserving the evolutionary potential of biodiversity.

For instance, the use of phylogenetic networks to prioritize populations for conservation has been demonstrated in species like the spotted owl and the mountain pygmy-possum. These networks better represent population differentiation and allow for the ranking of populations based on their genetic distinctiveness, which is critical for maintaining the evolutionary potential of species as their ranges become fragmented (Volkmann et al., 2014). Similarly, a novel framework integrating phylogenetic and intraspecific diversity has been applied to amphibians and reptiles in the Iberian Peninsula, highlighting the importance of accounting for the evolutionary continuum in conservation planning (Carvalho et al., 2017).

The conservation of phylogenetically distinct species is essential as these species often represent unique evolutionary lineages with no close relatives. For example, the evolutionary distinctness of chondrichthyan fishes (sharks, rays, and chimaeras) has been used to identify priority areas for conservation. These species embody significant evolutionary history, and their conservation is crucial to avoid the loss of unique genetic information (Stein et al., 2018). Additionally, the preservation of phylogenetic diversity in urban waterbodies has been shown to be important for maintaining the evolutionary heritage of cladoceran communities, despite the challenges posed by phylogenetic uncertainty (Mimouni et al., 2016).

8.2 Genetic diversity and conservation strategies

Genetic studies are vital for managing endangered species as they provide insights into the genetic health and diversity of populations. This information is crucial for developing strategies to enhance genetic diversity and reduce the risk of inbreeding and genetic drift. For example, whole-genome sequencing has been used to resolve evolutionary relationships and understand gene flow among closely related species, which is essential for making informed conservation decisions.

Genetic rescue, which involves introducing individuals from genetically diverse populations to increase genetic variation, is a practical application of genetic studies in conservation. Maintaining genetic diversity is also critical for the long-term survival of species, as it enhances their ability to adapt to changing environments. The use of phylogenetic diversity as a metric for conservation planning has been shown to be effective in preserving the evolutionary potential of floras in biodiversity hotspots, such as the Cape of South Africa.

8.3 Addressing threats to evolutionary lineages

Habitat loss, climate change, and human activities pose significant threats to evolutionary lineages by reducing population sizes, fragmenting habitats, and altering ecosystems. These threats can lead to the loss of unique evolutionary lineages and reduce the overall genetic diversity of species (Forest et al., 2007). For example, the prioritization of conservation areas using phylogenetic information has been shown to be effective in mitigating the impacts of these threats by focusing efforts on areas with high evolutionary distinctiveness.

To preserve evolutionary potential, conservation strategies must incorporate phylogenetic information to identify and protect areas and species that represent significant evolutionary history. This includes using phylogenetic diversity as a core metric in conservation planning and prioritizing areas that maximize the preservation of evolutionary pathways. The integration of phylogenetic diversity into systematic conservation planning has been demonstrated to enhance the persistence and evolutionary potential of biodiversity (Pellens et al., 2016). Additionally, the use of advanced genetic techniques and modeling approaches can help resolve species relationships and inform conservation strategies that account for gene flow and genetic diversity (Waters et al., 2010).

9 Future Directions and Research Needs

9.1 Emerging technologies in evolutionary biology

The field of evolutionary biology is rapidly evolving with the advent of new technologies that hold the potential to revolutionize our understanding of phylogenetic relationships and speciation mechanisms. One such technology is CRISPR, which allows for precise genetic modifications and can be used to study gene function and evolutionary processes in unprecedented detail. Additionally, environmental DNA (eDNA) is emerging as a powerful tool for biodiversity monitoring and ecosystem assessment. eDNA enables the detection of species presence and biodiversity assessment from environmental samples such as water, sediment, or air, without the need for direct observation or capture of organisms (Ruppert et al., 2019). This method is particularly useful for studying cryptic or elusive species and can provide insights into ancient ecosystems when combined with dating techniques (Hassan et al., 2022).

Machine learning is another promising tool that can be integrated into evolutionary studies. By analyzing large datasets generated from genomic studies, machine learning algorithms can identify patterns and make predictions about evolutionary relationships and speciation events. The integration of omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, into evolutionary biology can provide a comprehensive understanding of the molecular mechanisms underlying evolution. These technologies can be used to study gene expression, protein function, and metabolic pathways, offering a holistic view of the evolutionary processes (Wang et al., 2020).

9.2 Interdisciplinary approaches

The complexity of evolutionary processes necessitates an interdisciplinary approach that combines paleontology, genomics, ecology, and behavior. Paleontology provides crucial insights into the fossil record and the historical context of evolutionary events, while genomics offers detailed information on genetic variation and evolutionary relationships. Ecology and behavior studies help to understand the interactions between organisms and their environments, which are key drivers of evolution.

Collaborative and interdisciplinary research is essential for advancing our understanding of vertebrate evolution. By bringing together experts from different fields, we can develop more comprehensive models of evolutionary processes and address complex questions that cannot be answered by a single discipline alone. For example, combining eDNA with traditional ecological methods can enhance biodiversity monitoring and conservation efforts. Similarly, integrating genomic data with paleontological findings can provide a more complete picture of the evolutionary history of vertebrates (Hassan et al., 2022).

9.3 Addressing knowledge gaps

Despite significant advancements in evolutionary biology, there are still many under-studied lineages and regions that require further investigation. Identifying these gaps is crucial for developing a more complete understanding of vertebrate evolution. For instance, many studies using eDNA have focused on aquatic ecosystems, with less attention given to terrestrial environments and certain taxonomic groups such as invertebrates, plants, and reptiles

(Hassan et al., 2022). Expanding research efforts to include these under-represented areas can provide new insights into the diversity and evolutionary history of vertebrates.

Long-term monitoring and large-scale phylogenetic projects are also essential for addressing knowledge gaps. Continuous monitoring of ecosystems using eDNA and other methods can track changes in biodiversity and detect early signs of environmental stress or species decline (Thomsen and Willerslev, 2015). Large-scale phylogenetic projects that integrate data from multiple sources, including genomics, paleontology, and ecology, can help to reconstruct the evolutionary relationships of vertebrates and identify key speciation events (Wang et al., 2020). By addressing these knowledge gaps, we can develop more effective conservation strategies and improve our understanding of the mechanisms driving vertebrate evolution.

10 Concluding Remarks

This study reviewed the phylogenetic relationships and speciation mechanisms in vertebrates, highlighting their crucial roles in biodiversity and evolution. By integrating molecular and morphological data, we gained deeper insights into the complexity of vertebrate lineages and the dynamic processes of various speciation mechanisms, including allopatric, sympatric, peripatric, and parapatric speciation. Additionally, the findings on adaptive radiation and genetic studies demonstrated how species rapidly diversify through ecological opportunities and evolutionary innovations. Genetic research provided profound insights into gene flow, introgression, and adaptive evolution, offering critical evidence for understanding speciation and adaptive radiation.

This study significantly contributes to understanding biodiversity and evolution. By combining fossil records, molecular data, and ecological behavior studies, we can construct more comprehensive models of evolutionary processes, revealing key events and processes in vertebrate evolution. These findings not only expand our knowledge of vertebrate evolutionary history but also provide a scientific basis for biodiversity conservation. Particularly, the application of phylogenetic information in conservation prioritization helps identify and protect evolutionarily distinct and irreplaceable species and populations, thereby preserving the evolutionary potential of Earth.

We encourage continued research in evolutionary biology and the integration of emerging technologies. New technologies such as CRISPR, environmental DNA (eDNA), and machine learning will further enhance our understanding of evolutionary processes and offer new research avenues. Evolutionary studies are not only crucial for scientific advancement but also play a vital role in ecological conservation. By deeply studying evolutionary mechanisms and speciation processes, we can develop more effective conservation strategies to maintain biodiversity and ecosystem health.

We hope future research will continue to address current knowledge gaps, especially in under-studied lineages and regions. Long-term monitoring and large-scale phylogenetic projects will help address these gaps and advance scientific and conservation efforts. In-depth and widespread application of evolutionary research will preserve the biodiversity and evolutionary heritage of Earth for future generations.

Acknowledgments

The authors extend sincere thanks to two anonymous peer reviewers for their feedback on the manuscript.

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.

References

Adamowicz S., Petrusek A., Colbourne J., Hebert P., and Witt J., 2009, The scale of divergence: a phylogenetic appraisal of intercontinental allopatric speciation in a passively dispersed freshwater zooplankton genus, Molecular Phylogenetics and Evolution, 50(3): 423-436.
https://doi.org/10.1016/j.ympev.2008.11.026
PMid:19124080

Aristide L., Rosenberger A., Tejedor M., and Perez S., 2015, Modeling lineage and phenotypic diversification in the New World monkey (Platyrrhini, Primates) radiation, Molecular Phylogenetics and Evolution, 82 Pt B: 375-385.
https://doi.org/10.1016/j.ympev.2013.11.008
PMid:24287474

Bell M., and Travis M., 2005, Hybridization, transgressive segregation, genetic covariation, and adaptive radiation, Trends in Ecology & Evolution, 20(7): 358-361.
https://doi.org/10.1016/j.tree.2005.04.021
PMid:16701394

Burri R., Nater A., Kawakami T., Mugal C., Olason P., Smeds L., Suh A., Dutoit L., Bureš S., Garamszegi L., Hogner S., Moreno J., Qvarnström A., Ruzic M., Sæther S., Sætre G., Török J., and Ellegren H., 2015, Linked selection and recombination rate variation drive the evolution of the genomic landscape of differentiation across the speciation continuum of Ficedula flycatchers, Genome Research, 25: 1656-1665.
https://doi.org/10.1101/gr.196485.115
PMid:26355005 PMCid:PMC4617962

Carvalho S., Velo-Antón G., Tarroso P., Portela A., Barata M., Carranza S., Moritz C., and Possingham H., 2017, Spatial conservation prioritization of biodiversity spanning the evolutionary continuum, Nature Ecology &Evolution, 1.
https://doi.org/10.1038/s41559-017-0151
PMid:28812637

Cooney C., and Thomas G., 2020, Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades, Nature Ecology & Evolution, 5: 101-110.
https://doi.org/10.1038/s41559-020-01321-y
PMid:33106601

Cruickshank T., and Hahn M., 2014, Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow, Molecular Ecology, 23.
https://doi.org/10.1111/mec.12796
PMid:24845075

Donoghue P., and Keating J., 2014, Early vertebrate evolution, Palaeontology, 57.
https://doi.org/10.1111/pala.12125

Etienne R., Haegeman B., Stadler T., Aze T., Pearson P., Purvis A., and Phillimore A., 2012, Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record, Proceedings of the Royal Society B: Biological Sciences, 279: 1300-1309.
https://doi.org/10.1098/rspb.2011.1439
PMid:21993508 PMCid:PMC3282358

Fabre P., Hautier L., Dimitrov D., and Douzery E., 2012, A glimpse on the pattern of rodent diversification: a phylogenetic approach, BMC Evolutionary Biology, 12: 88.
https://doi.org/10.1186/1471-2148-12-88
PMid:22697210 PMCid:PMC3532383

Ford A., Dasmahapatra K., Rüber L., Gharbi K., Cezard T., and Day J., 2015, High levels of interspecific gene flow in an endemic cichlid fish adaptive radiation from an extreme lake environment, Molecular Ecology, 24: 3421-3440.
https://doi.org/10.1111/mec.13247
PMid:25997156 PMCid:PMC4973668

Forest F., Forest F., Richard G., Mathieu R., Davies T., Davies T., Cowling R., Faith D., Balmford A., Manning J., Proches S., Bank M., Reeves G., Hedderson T., and Savolainen V., 2007, Preserving the evolutionary potential of floras in biodiversity hotspots, Nature, 445: 757-760.
https://doi.org/10.1038/nature05587
PMid:17301791

Gillespie R., Bennett G., Meester L., Feder J., Fleischer R., Harmon L., Hendry A., Knope M., Mallet J., Martin C., Parent C., Patton A., Pfennig K., Rubinoff D., Schluter D., Seehausen O., Shaw K., Stacy E., Stervander M., Stroud J., Wagner C., and Wogan G., 2020, Comparing adaptive radiations across space, time, and taxa, The Journal of Heredity, 111(1), 1-20.
https://doi.org/10.1093/jhered/esz064
PMid:31958131 PMCid:PMC7931853

Givnish T., 2015, Adaptive radiation versus 'radiation' and 'explosive diversification': why conceptual distinctions are fundamental to understanding evolution, The New Phytologist, 207(2): 297-303.
https://doi.org/10.1111/nph.13482
PMid:26032979

Glor R., Gifford M., Larson A., Losos J., Schettino L., Lara A., and Jackman T., 2004, Partial island submergence and speciation in an adaptive radiation: a multilocus analysis of the Cuban green anoles, Proceedings of the Royal Society of London. Series B: Biological Sciences, 271: 2257-2265.
https://doi.org/10.1098/rspb.2004.2819
PMid:15539351 PMCid:PMC1691862

Greve C., Gimnich F., Hutterer R., Misof B., and Haase M., 2012, Radiating on oceanic islands: patterns and processes of speciation in the land snail genus *Theba* (Risso 1826), PLoS ONE, 7.
https://doi.org/10.1371/annotation/5cfe7c14-9385-427b-ac34-7e893af0cb8c

Grossnickle D., Smith S., and Wilson G., 2019, Untangling the multiple ecological radiations of early mammals, Trends in Ecology & Evolution, 34(10), 936-949.
https://doi.org/10.1016/j.tree.2019.05.008
PMid:31229335

Hallström B., and Janke A., 2010, Mammalian evolution may not be strictly bifurcating, Molecular Biology and Evolution, 27: 2804-2816.
https://doi.org/10.1093/molbev/msq166
PMid:20591845 PMCid:PMC2981514

Hassan S., Khurshid Z., Sabreena, Bali B., Ganai B., Sayyed R., Poczai P., and Zaman M., 2022, A critical assessment of the congruency between environmental DNA and palaeoecology for the biodiversity monitoring and palaeoenvironmental reconstruction, International Journal of Environmental Research and Public Health, 19.
https://doi.org/10.3390/ijerph19159445
PMid:35954801 PMCid:PMC9368151

Irisarri I., Baurain D., Brinkmann H., Delsuc F., Sire J., Kupfer A., Petersen J., Jarek M., Meyer A., Vences M., and Philippe H., 2017, Phylotranscriptomic consolidation of the jawed vertebrate timetree, Nature Ecology & Evolution, 1: 1370-1378.
https://doi.org/10.1038/s41559-017-0240-5
PMid:28890940 PMCid:PMC5584656

Keller I., Wagner C., Greuter L., Mwaiko S., Selz O., Sivasundar A., Wittwer S., and Seehausen O., 2012, Population genomic signatures of divergent adaptation, gene flow and hybrid speciation in the rapid radiation of Lake Victoria cichlid fishes, Molecular Ecology, 22.
https://doi.org/10.1111/mec.12083
PMid:23121191

Koch N., and Parry L., 2020, Death is on our side: Paleontological data drastically modify phylogenetic hypotheses, Systematic Biology, 69(6), 1052-1067.
https://doi.org/10.1093/sysbio/syaa023
PMid:32208492

Marchán D., Novo M., Sánchez N., Domínguez J., Cosín D., and Fernández R., 2020, Local adaptation fuels cryptic speciation in terrestrial annelids, Molecular Phylogenetics and Evolution, 146, 106767.
https://doi.org/10.1016/j.ympev.2020.106767
PMid:32081763

Meiklejohn K., Faircloth B., Glenn T., Kimball R., and Braun E., 2016, Analysis of a rapid evolutionary radiation using ultraconserved elements: evidence for a bias in some multispecies coalescent methods, Systematic Biology, 65(4): 612-627.
https://doi.org/10.1093/sysbio/syw014
PMid:26865273

Meredith R., Janecka J., Gatesy J., Ryder O., Fisher C., Teeling E., Goodbla A., Eizirik E., Simão T., Stadler T., Rabosky D., Honeycutt R., Flynn J., Ingram C., Steiner C., Williams T., Robinson T., Burk-Herrick A., Westerman M., Ayoub N., Springer M., and Murphy W., 2011, Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification, Science, 334: 521-524.
https://doi.org/10.1126/science.1211028
PMid:21940861

Mimouni E., Beisner B., and Pinel-Alloul B., 2016, Phylogenetic diversity and its conservation in the presence of phylogenetic uncertainty: a case study of cladoceran communities in urban waterbodies, Biodiversity and Conservation, 25: 2113-2136.
https://doi.org/10.1007/s10531-016-1181-z

Nater A., Burri R., Kawakami T., Smeds L., and Ellegren H., 2015, Resolving evolutionary relationships in closely related species with whole-genome sequencing data, Systematic Biology, 64: 1000-1017.
https://doi.org/10.1093/sysbio/syv045
PMid:26187295 PMCid:PMC4604831

Parsons K., 2016, Adaptive radiations: insights from Evo-Devo, 37-45.
https://doi.org/10.1016/B978-0-12-800049-6.00141-4

Pellens R., Faith D., and Grandcolas P., 2016, The future of phylogenetic systematics in conservation biology: linking biodiversity and society, 375-383.
https://doi.org/10.1007/978-3-319-22461-9_19

Pincheira-Donoso D., Harvey L., and Ruta M., 2015, What defines an adaptive radiation? macroevolutionary diversification dynamics of an exceptionally species-rich continental lizard radiation, BMC Evolutionary Biology, 15.
https://doi.org/10.1186/s12862-015-0435-9
PMid:26245280 PMCid:PMC4527223

Prasad A., Allard M., and Green E., 2008, Confirming the phylogeny of mammals by use of large comparative sequence data sets, Molecular Biology and Evolution, 25: 1795-1808.
https://doi.org/10.1093/molbev/msn104
PMid:18453548 PMCid:PMC2515873

Rintelen T., and Glaubrecht M., 2005, Anatomy of an adaptive radiation: a unique reproductive strategy in the endemic freshwater gastropod *Tylomelania* (Cerithioidea: Pachychilidae) on Sulawesi, Indonesia and its biogeographical implications, Biological Journal of The Linnean Society, 85: 513-542.
https://doi.org/10.1111/j.1095-8312.2005.00515.x

Ruppert K., Kline R., and Rahman M., 2019, Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: a systematic review in methods, monitoring, and applications of global eDNA, Global Ecology and Conservation, 17, e00547.
https://doi.org/10.1016/j.gecco.2019.e00547

Savolainen V., Anstett M., Lexer C., Hutton I., Clarkson J., Norup M., Powell M., Springate D., Salamin N., and Baker W., 2006, Sympatric speciation in palms on an oceanic island, Nature, 441: 210-213.
https://doi.org/10.1038/nature04566
PMid:16467788

Sosa F., and Pilot M., 2023, Molecular mechanisms underlying vertebrate adaptive evolution: a systematic review, Genes, 14.
https://doi.org/10.3390/genes14020416
PMid:36833343 PMCid:PMC9957108

Stein R., Mull C., Kuhn T., Aschliman N., Davidson L., Joy J., Smith G., Dulvy N., and Mooers A., 2018, Global priorities for conserving the evolutionary history of sharks, rays and chimaeras, Nature Ecology & Evolution, 2: 288-298.
https://doi.org/10.1038/s41559-017-0448-4
PMid:29348644

Streelman J., and Danley P., 2003, The stages of vertebrate evolutionary radiation, Trends in Ecology and Evolution, 18: 126-131.
https://doi.org/10.1016/S0169-5347(02)00036-8

Suchan T., Espíndola A., Rutschmann S., Emerson B., Gori K., Dessimoz C., Arrigo N., Ronikier M., and Alvarez N., 2017, Assessing the potential of RAD-sequencing to resolve phylogenetic relationships within species radiations: the fly genus *Chiastocheta* (Diptera: Anthomyiidae) as a case study, Molecular Phylogenetics and Evolution, 114: 189-198.
https://doi.org/10.1016/j.ympev.2017.06.012
PMid:28645767

Sun Y., Zhang Y., and Wang K., 2020, Perspectives on studying molecular adaptations of amphibians in the genomic era, Zoological Research, 41: 351-364.
https://doi.org/10.24272/j.issn.2095-8137.2020.046
PMid:32390371 PMCid:PMC7340517

Thomsen P., and Willerslev E., 2015, Environmental DNA - an emerging tool in conservation for monitoring past and present biodiversity, Biological Conservation, 183: 4-18.
https://doi.org/10.1016/j.biocon.2014.11.019

Thorpe R., Surget-Groba Y., and Johansson H., 2010, Genetic tests for ecological and allopatric speciation in anoles on an island archipelago, PLoS Genetics, 6.
https://doi.org/10.1371/journal.pgen.1000929
PMid:20442860 PMCid:PMC2861690

Upham N., Esselstyn J., and Jetz W., 2019, Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation, PLoS Biology, 17.
https://doi.org/10.1371/journal.pbio.3000494
PMid:31800571 PMCid:PMC6892540

Venditti C., Meade A., and Pagel M., 2011, Multiple routes to mammalian diversity, Nature, 479: 393-396.
https://doi.org/10.1038/nature10516
PMid:22012260

Volkmann L., Martyn I., Moulton V., Spillner A., and Mooers A., 2014, Prioritizing populations for conservation using phylogenetic networks, PLoS ONE, 9.
https://doi.org/10.1371/journal.pone.0088945
PMid:24586451 PMCid:PMC3938429

Wallace S., Morris-Pocock J., González-Solís J., Quillfeldt P., and Friesen V., 2017, A phylogenetic test of sympatric speciation in the Hydrobatinae (Aves: Procellariiformes), Molecular Phylogenetics and Evolution, 107: 39-47.
https://doi.org/10.1016/j.ympev.2016.09.025
PMid:27693526

Wang S., Yan Z., Hänfling B., Zheng X., Wang P., Fan J., and Li J., 2020, Methodology of fish eDNA and its applications in ecology and environment, The Science of the Total Environment, 755 Pt 2: 142622.
https://doi.org/10.1016/j.scitotenv.2020.142622
PMid:33059148

Waters J., Rowe D., Burridge C., and Wallis G., 2010, Gene trees versus species trees: reassessing life-history evolution in a freshwater fish radiation, Systematic biology, 59(5): 504-517.
https://doi.org/10.1093/sysbio/syq031
PMid:20603441

Yeaman S., Aeschbacher S., and Bürger R., 2016, The evolution of genomic islands by increased establishment probability of linked alleles, Molecular Ecology, 25.
https://doi.org/10.1111/mec.13611
PMid:27206531

Zhang C., Stadler T., Klopfstein S., Heath T., and Ronquist F., 2015, Total-evidence dating under the fossilized birth-death process, Systematic Biology, 65: 228-249.
https://doi.org/10.1093/sysbio/syv080
PMid:26493827 PMCid:PMC4748749