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## A Review of Respiratory Adaptations in Aquatic and Terrestrial Chordates

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### **Abstract**

Respiration is a fundamental physiological process that enables organisms to meet their metabolic energy demands through efficient gas exchange with the environment. In chordates, respiratory adaptations have evolved in close association with habitat transitions from aquatic to terrestrial ecosystems, resulting in diverse structural and functional mechanisms for oxygen uptake. This review synthesizes current knowledge on respiratory adaptations across major chordate groups, highlighting the evolutionary modifications in respiratory organs, including gills, lungs, skin, and accessory air-breathing structures. Aquatic chordates primarily utilize gill-based respiration, characterized by extensive vascularized lamellae and countercurrent exchange systems that maximize oxygen extraction from water. Transitional forms such as amphibians exhibit dual respiratory modes, combining cutaneous, buccopharyngeal, and pulmonary respiration, reflecting their amphibious lifestyle. In contrast, terrestrial chordates, including reptiles, birds, and mammals, possess increasingly complex lung architectures and ventilation strategies adapted to aerial respiration and higher metabolic demands. Birds demonstrate highly efficient unidirectional airflow supported by air sacs, whereas mammals rely on alveolar lungs and diaphragmatic breathing. Comparative analysis reveals that respiratory evolution is closely linked to environmental oxygen availability, metabolic rate, and ecological specialization. Respiratory adaptations in chordates illustrate a progressive evolutionary trend that has facilitated successful colonization of diverse habitats, emphasizing the integral role of respiratory physiology in vertebrate adaptation, survival, and diversification.

**Keywords:** Respiration, Chordates, Gill Adaptations, Lung Evolution, Terrestrialization.

### **Introduction**

Respiration is a fundamental physiological process that ensures the acquisition of oxygen and the elimination of carbon dioxide, thereby sustaining cellular metabolism and energy production in living organisms. Within the phylum Chordata, respiratory mechanisms have undergone remarkable diversification to accommodate the contrasting demands of aquatic and terrestrial environments. Aquatic chordates, such as fishes and larval amphibians, primarily rely on gill-based respiration, where specialized vascularized filaments facilitate efficient diffusion of



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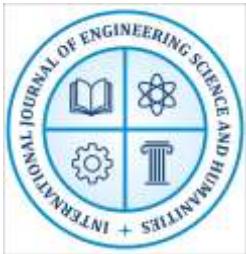
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dissolved oxygen from water. In contrast, terrestrial chordates—including reptiles, birds, and mammals—have evolved lung-based systems that optimize gaseous exchange in an aerial medium, characterized by higher oxygen availability but also increased risks of desiccation and evaporative water loss. These structural and functional modifications reflect adaptive responses to variations in oxygen concentration, buoyancy constraints, ventilation mechanics, and metabolic requirements. The transition from water to land during vertebrate evolution marked a pivotal milestone, necessitating the reorganization of respiratory surfaces, ventilation strategies, and circulatory integration to maintain efficient oxygen transport under gravity-dependent conditions.

A comparative review of respiratory adaptations in aquatic and terrestrial chordates reveals a continuum of evolutionary innovations shaped by ecological pressures and phylogenetic constraints. In fishes, countercurrent exchange mechanisms in gills maximize oxygen uptake even in hypoxic aquatic environments, while amphibians exhibit dual respiratory modes—cutaneous, buccopharyngeal, and pulmonary—reflecting their amphibious lifestyle. Reptiles demonstrate more compartmentalized lungs with costal ventilation, whereas birds possess a highly specialized unidirectional airflow system involving parabronchi and air sacs, enabling exceptionally high aerobic efficiency required for sustained flight. Mammalian lungs, with their alveolar architecture and diaphragm-driven ventilation, provide a large surface area and precise regulation of gas exchange to support endothermy and high metabolic activity. These varied respiratory strategies illustrate how structural complexity, surface area optimization, and ventilation-perfusion coupling have co-evolved to meet distinct environmental and physiological demands. Understanding these comparative adaptations not only elucidates the evolutionary trajectory of chordates but also provides insights into functional morphology, ecological specialization, and the physiological constraints that govern life across aquatic and terrestrial habitats.

## Concept of Respiration in Living Organisms

Respiration in living organisms refers to the complex physiological and biochemical processes through which cells obtain energy by the oxidation of organic substrates, primarily glucose, to produce adenosine triphosphate (ATP). It is a fundamental life process that ensures the continuous supply of energy required for cellular activities such as growth, movement, reproduction, and homeostasis. At the cellular level, respiration involves a series of enzyme-mediated reactions including glycolysis, the Krebs cycle, and oxidative phosphorylation, occurring mainly within the mitochondria. These processes utilize oxygen as the terminal electron acceptor in aerobic organisms, leading to the release of carbon dioxide, water, and energy. In contrast, some organisms can perform anaerobic respiration in the absence of oxygen, yielding comparatively less energy but still sustaining essential metabolic functions.



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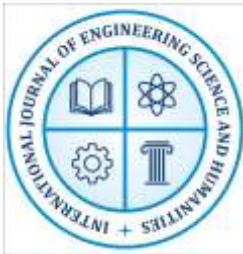
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Respiration must be distinguished from breathing; while breathing is the mechanical process of inhalation and exhalation, respiration encompasses the entire metabolic sequence of gas exchange, transport, and cellular oxidation. In multicellular organisms, specialized respiratory structures such as gills, lungs, skin, or tracheal systems facilitate efficient gas exchange with the external environment. The effectiveness of respiration depends on the maintenance of diffusion gradients, large respiratory surface areas, and efficient transport mechanisms like circulatory systems containing respiratory pigments such as hemoglobin. From an evolutionary perspective, the concept of respiration is closely linked to environmental adaptations, as organisms inhabiting aquatic and terrestrial ecosystems have developed diverse respiratory strategies to meet their metabolic demands. Thus, respiration is not merely a biochemical reaction but an integrated physiological system essential for sustaining life and enabling adaptive success across different habitats.

## **Evolutionary Significance of Respiratory Adaptations in Animals**

Respiratory adaptations in animals represent a crucial evolutionary response to varying environmental conditions and metabolic demands, enabling efficient acquisition and utilization of oxygen for cellular respiration. Throughout evolutionary history, the transition from simple diffusion-based gas exchange in primitive organisms to the development of specialized respiratory organs such as gills, lungs, and tracheal systems reflects increasing organismal complexity and activity levels. Early aquatic organisms relied on body surface diffusion due to their small size and low metabolic rates; however, as body size, tissue specialization, and locomotory activity increased, the need for more efficient oxygen uptake mechanisms became essential. This selective pressure led to the evolution of gills in aquatic animals, which provide a large surface area and thin epithelial barriers to maximize oxygen diffusion from water.

The shift from aquatic to terrestrial life marked a major evolutionary milestone, necessitating profound respiratory modifications. Terrestrial environments offered higher oxygen availability but posed challenges such as desiccation and the need for internalized respiratory surfaces. Consequently, lungs evolved as invaginated, vascularized structures that minimized water loss while enhancing gas exchange efficiency. In amphibians, the coexistence of cutaneous and pulmonary respiration illustrates an intermediate evolutionary stage, whereas reptiles, birds, and mammals exhibit increasingly complex lung architectures suited for higher metabolic rates. The avian respiratory system, with its unidirectional airflow and air sac system, represents a highly efficient adaptation supporting the energetic demands of flight, while mammalian alveolar lungs provide an extensive surface area for rapid gas exchange required for endothermy. Respiratory adaptations have played a pivotal role in the adaptive radiation of animals by enabling exploitation of diverse ecological niches. They are closely associated with metabolic evolution,



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thermoregulation, and activity levels, thereby influencing survival, distribution, and ecological dominance of different animal groups across aquatic and terrestrial habitats.

## Literature Review

Respiratory adaptations in chordates reflect a complex evolutionary continuum shaped by environmental oxygen availability, metabolic demands, and structural constraints of the gas-exchange interface. Foundational comparative work has emphasized that vertebrate respiratory organs, whether gills, lungs, or cutaneous surfaces, are unified by the need to maximize diffusive conductance while maintaining structural integrity. Maina (2017) provided a comprehensive synthesis of vertebrate gas exchangers, highlighting that the functional architecture of respiratory surfaces is governed by surface area expansion, barrier thinness, and perfusion efficiency. This design principle is further elaborated by Maina and West (2018), who examined the blood–gas barrier as a bioengineering compromise between mechanical strength and minimal diffusion distance. Their analysis demonstrates that the delicate alveolar and parabronchial membranes represent optimized evolutionary solutions that balance the risk of rupture under ventilatory pressures with the need for rapid oxygen flux. Kardong's (2019) comparative anatomy framework reinforces this integrative perspective by tracing the phylogenetic progression from aquatic gill systems to complex pulmonary structures in tetrapods, emphasizing how respiratory morphology co-evolved with circulatory modifications. Collectively, these works establish that respiratory adaptations in chordates are not isolated innovations but coordinated anatomical and physiological transformations enabling efficient oxygen uptake across diverse habitats.

Aquatic chordates exhibit specialized respiratory mechanisms adapted to the physicochemical limitations of water, particularly its lower oxygen content and higher density compared with air. Heim et al. (2020) demonstrated that respiratory medium imposes strong constraints on body size evolution, revealing that marine macrofauna are limited by diffusion capacities and circulatory delivery systems. Their findings suggest that the interplay between gill surface area and circulatory efficiency determines metabolic ceilings in aquatic organisms. Complementing this macroevolutionary view, Nelson and Benfey (2019) reviewed air-breathing fishes, illustrating transitional respiratory strategies in species that exploit both aquatic and aerial oxygen sources. These fishes possess modified swim bladders, buccopharyngeal cavities, or labyrinth organs that function as auxiliary lungs, enabling survival in hypoxic waters and representing evolutionary precursors to terrestrial respiration. Such dual systems underscore the plasticity of respiratory design in chordates and highlight the role of environmental oxygen fluctuations as a key selective pressure. Maina's comparative morphological analysis further supports that gill lamellae exhibit extensive surface folding and countercurrent exchange mechanisms to enhance diffusion efficiency in water. Therefore, aquatic respiratory adaptations exemplify structural specialization for maximizing gas exchange within the constraints imposed by an aqueous



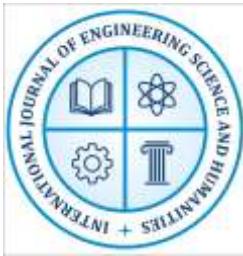
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medium, while transitional forms reveal evolutionary experimentation preceding the emergence of fully terrestrial lungs.

The transition from aquatic to terrestrial respiration represents one of the most profound evolutionary shifts in chordate history, involving coordinated morphological, physiological, and behavioral innovations. Perry and Sander (2019) reconstructed the evolution of the tetrapod respiratory apparatus, demonstrating that early lung structures likely evolved in aquatic ancestors as buoyancy or accessory breathing organs before becoming the primary respiratory surfaces on land. This evolutionary trajectory is echoed in the work of Sander and Claessens (2018), who detailed how reptiles and birds exhibit intermediate and advanced pulmonary designs, respectively, reflecting progressive refinements in ventilation and gas exchange efficiency. Reptilian lungs show septate internal partitioning that increases surface area, whereas avian parabronchial lungs achieve unidirectional airflow and continuous oxygen extraction, representing one of the most efficient respiratory systems among vertebrates. These structural transitions were accompanied by skeletal and muscular modifications, such as the development of rib ventilation and air sacs, which facilitated effective pulmonary ventilation in a gravitational environment. Kamenz et al. (2017), although focused on early terrestrial arthropods, provide broader evolutionary context by illustrating how respiratory structures adapt microanatomically during terrestrialization, emphasizing the selective pressure for internalized gas-exchange surfaces to minimize desiccation. Together, these studies demonstrate that terrestrial respiratory adaptations were driven by the need to prevent water loss, increase oxygen extraction efficiency, and support higher metabolic rates associated with active locomotion on land.

Beyond organ-level adaptations, respiratory evolution in chordates also involves physiological and molecular innovations that enhance oxygen transport and utilization. Locascio et al. (2023) investigated the evolution of nitric oxide synthase pathways in chordates, revealing their role in regulating vascular tone and respiratory physiology. Nitric oxide-mediated modulation of blood flow allows dynamic matching of perfusion to ventilation, optimizing oxygen uptake under varying metabolic demands. This molecular perspective complements structural analyses by showing that efficient respiration depends not only on anatomical surfaces but also on regulatory mechanisms that control gas exchange and circulatory integration. Sobac et al. (2019) explored allometric scaling of heat and water exchanges in mammalian lungs, demonstrating that lung architecture scales predictably with body size to maintain efficient thermoregulation and respiratory water balance. Their theoretical modeling indicates that larger mammals possess disproportionately complex pulmonary branching systems to maintain adequate surface area for diffusion, highlighting the role of scaling laws in shaping respiratory design. Zwicker et al. (2017) further examined the geometric constraints of nasal cavities, showing that labyrinth-like nasal structures enhance heat and moisture exchange while also contributing to respiratory



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airflow conditioning. These findings collectively illustrate that respiratory adaptations operate across multiple biological levels—from molecular signaling and vascular regulation to organ geometry and whole-body scaling—ensuring that oxygen acquisition remains efficient across a wide range of chordate sizes and ecological niches.

Cutaneous respiration represents an additional adaptive strategy in certain chordates, particularly in early developmental stages and amphibious taxa. Ferner (2018) demonstrated that newborn marsupials possess highly vascularized and thin skin that permits significant cutaneous gas exchange before the full maturation of pulmonary systems. This temporary reliance on skin respiration exemplifies ontogenetic plasticity, whereby respiratory modes shift during development to accommodate changing physiological requirements. Cutaneous exchange is also prominent in amphibians, reflecting a retained ancestral mechanism that complements pulmonary and buccopharyngeal respiration. The persistence of such strategies underscores the evolutionary flexibility of chordate respiratory systems, enabling organisms to exploit multiple gas-exchange pathways depending on environmental and developmental conditions. Integrating these diverse perspectives, it becomes evident that respiratory adaptations in aquatic and terrestrial chordates represent a continuum rather than a dichotomy. Aquatic gill-based respiration, transitional air-breathing strategies, fully terrestrial lungs, molecular regulatory systems, and cutaneous exchange all contribute to a multifaceted evolutionary narrative. Overall, the reviewed literature demonstrates that the evolution of respiratory adaptations in chordates is driven by the interaction of environmental oxygen availability, structural constraints on diffusion surfaces, circulatory integration, and developmental plasticity. These coordinated innovations collectively enabled chordates to colonize diverse ecological habitats, from oxygen-poor aquatic environments to highly aerobic terrestrial ecosystems, thereby illustrating the central role of respiratory evolution in vertebrate diversification and ecological success.

## Literature Summary Table

S. No.	Author(s) & Year	Study Focus	Key Findings	Relevance to Respiratory Adaptations
1	Ferner (2018)	Skin structure in newborn marsupials	Demonstrated that thin, highly vascularized skin in neonatal marsupials facilitates significant cutaneous gas exchange during early development.	Highlights the evolutionary role of integumentary respiration as an auxiliary mechanism in early life stages of mammals.
2	Heim et al. (2020)	Respiratory medium and	Found that oxygen availability in water and	Shows how respiratory medium directly



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		circulatory anatomy in marine macrofauna	circulatory design constrain body size evolution in marine organisms.	influences anatomical and evolutionary scaling in aquatic animals.
3	Kamenz et al. (2017)	Microanatomy of Devonian book lungs	Revealed structural complexity of early book lungs, suggesting early adaptations for aerial respiration during terrestrialization.	Provides fossil evidence for evolutionary transition from aquatic to terrestrial respiration.
4	Kardong (2019)	Comparative vertebrate anatomy and evolution	Comprehensive synthesis of respiratory structures across vertebrates, detailing gills, lungs, and accessory organs.	Serves as a foundational reference for understanding comparative respiratory adaptations in chordates.
5	Locascio et al. (2023)	Evolution of nitric oxide synthase in chordates	Identified conserved roles of nitric oxide signaling in regulating respiratory physiology across chordate lineages.	Demonstrates molecular-level evolutionary conservation influencing respiratory control mechanisms.
6	Maina (2017)	Comparative respiratory morphology in vertebrates	Explained functional design principles of gas exchangers emphasizing surface area, diffusion distance, and vascularization.	Clarifies structural-functional optimization in respiratory organs during vertebrate evolution.
7	Maina & West (2018)	Blood-gas barrier design	Discussed the trade-off between thinness for diffusion efficiency and strength to prevent structural failure in lungs.	Explains biomechanical constraints shaping lung evolution and efficiency in higher vertebrates.
8	Nelson & Benfey (2019)	Diversity of air-breathing fishes	Documented multiple independent origins of air-breathing mechanisms in fishes using modified gills	Illustrates convergent evolution of respiratory adaptations in hypoxic aquatic environments.



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			or accessory organs.	
9	Perry & Sander (2019)	Evolution of respiratory apparatus in tetrapods	Reconstructed evolutionary modifications from gill-based respiration to lung-based systems in early tetrapods.	Key to understanding major evolutionary transition from aquatic to terrestrial respiration.
10	Sander & Claessens (2018)	Respiratory evolution in reptiles and birds	Identified transitional lung ventilation mechanisms leading to efficient avian air-sac systems.	Highlights progressive refinement of pulmonary respiration supporting high metabolic demands.
11	Sobac et al. (2019)	Allometric scaling in mammalian lungs	Demonstrated scaling relationships between lung structure, heat exchange, and body size.	Shows how

## Respiratory Adaptations in Aquatic Chordates

Aquatic chordates exhibit a wide range of respiratory adaptations that enable efficient extraction of dissolved oxygen from water, a medium that contains significantly less oxygen than air and presents higher resistance to diffusion. The primary respiratory organ in most aquatic chordates, especially fishes, is the gill, which is structurally specialized to maximize surface area and minimize diffusion distance. Gill filaments and secondary lamellae provide an extensive vascularized surface through which gas exchange occurs by diffusion. A key adaptation is the countercurrent exchange mechanism, where blood flows in the opposite direction to water passing over the gills, maintaining a continuous diffusion gradient and allowing maximal oxygen uptake efficiency. In cartilaginous fishes, gill slits and spiracles facilitate continuous water flow, while bony fishes utilize opercular pumping to ventilate gills effectively. Some aquatic chordates inhabiting oxygen-poor or stagnant waters have evolved accessory respiratory organs, such as modified swim bladders, labyrinth organs, or buccopharyngeal cavities, enabling facultative air breathing. This dual respiratory strategy is particularly evident in lungfishes and certain teleosts, allowing survival in hypoxic environments and reflecting evolutionary flexibility in respiratory design. Additionally, many aquatic chordates exhibit physiological adaptations such as high-affinity hemoglobin, increased gill surface area, and enhanced ventilatory movements to optimize oxygen extraction. In early chordates and larval forms, cutaneous respiration also contributes significantly due to thin and permeable integument. These structural and physiological features collectively illustrate how aquatic chordates have evolved highly efficient mechanisms to cope with the physical constraints of water, ensuring adequate oxygen supply to



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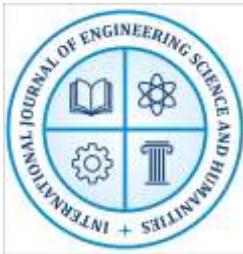
sustain metabolic activities and supporting their ecological diversification across diverse aquatic habitats.

## Transitional Respiratory Adaptations: Amphibians

Amphibians represent an evolutionary transitional group that exhibits both aquatic and terrestrial respiratory adaptations, reflecting their dual life cycle and semi-aquatic mode of existence. During the larval stage, amphibians such as tadpoles rely primarily on gills for aquatic respiration, which are later replaced or supplemented by lungs during metamorphosis as they shift toward a terrestrial lifestyle. This ontogenetic transformation illustrates a significant evolutionary step in the transition from water to land. Adult amphibians possess relatively simple sac-like lungs with limited internal partitioning compared to those of reptiles, birds, and mammals, making pulmonary respiration less efficient; therefore, they compensate through cutaneous respiration, wherein gas exchange occurs across the moist, highly vascularized skin. The skin's permeability is maintained by mucous secretions and dense capillary networks, allowing oxygen diffusion directly into the bloodstream and carbon dioxide elimination, especially during periods of low activity or submersion in water. Buccopharyngeal respiration also contributes, involving rhythmic movements of the buccal cavity to ventilate air and enhance gas exchange. Amphibians typically employ a positive-pressure ventilation mechanism, forcing air into the lungs by raising the floor of the buccal cavity, unlike the negative-pressure breathing observed in higher vertebrates. These multiple respiratory pathways provide remarkable physiological flexibility, enabling amphibians to survive in fluctuating environments with varying oxygen availability. Consequently, amphibian respiratory adaptations represent a crucial evolutionary intermediary stage, demonstrating how vertebrates gradually modified their respiratory systems to accommodate the challenges associated with terrestrialization while retaining ancestral aquatic features for survival in amphibious habitats.

## Conclusion

Respiratory adaptations in aquatic and terrestrial chordates illustrate a remarkable evolutionary continuum shaped by environmental constraints, metabolic demands, and structural innovations. The transition from simple diffusion-based respiration in early aquatic organisms to highly specialized respiratory organs such as gills and lungs represents a fundamental step in vertebrate evolution. Aquatic chordates developed efficient gill systems with extensive surface areas, thin diffusion barriers, and countercurrent exchange mechanisms to optimize oxygen extraction from water, a medium with relatively low oxygen availability. These adaptations enabled sustained metabolic activity and ecological diversification in diverse aquatic habitats. Conversely, the colonization of terrestrial environments imposed new physiological challenges, including the need to prevent desiccation and efficiently utilize atmospheric oxygen. This led to the evolution



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of internalized lungs with increased compartmentalization, enhanced vascularization, and advanced ventilation mechanisms that improved gas exchange efficiency.

Amphibians serve as a crucial transitional group, displaying a combination of gill-based, cutaneous, and pulmonary respiration, thereby demonstrating the gradual evolutionary shift from aquatic to terrestrial life. The progression observed in reptiles, birds, and mammals shows further refinement of respiratory structures, with reptiles exhibiting more developed lungs, birds evolving highly efficient unidirectional airflow systems supported by air sacs, and mammals possessing alveolar lungs capable of sustaining high metabolic rates associated with endothermy. These successive modifications highlight the close relationship between respiratory design, energy requirements, and ecological specialization.

Overall, respiratory adaptations have played a pivotal role in shaping vertebrate survival, distribution, and evolutionary success across diverse ecosystems. They not only reflect structural and functional optimization in response to environmental pressures but also underscore the dynamic interplay between physiology and habitat. Understanding these adaptations provides valuable insights into evolutionary biology, comparative physiology, and the resilience of chordates to changing environmental conditions, thereby emphasizing the central importance of respiratory evolution in the broader context of animal adaptation and diversification.

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