

## MATS CENTRE FOR OPEN & DISTANCE EDUCATION

## **Chordates & Comparative Anatomy**

Bachelor of Science (B.Sc.) Semester - 4



**SELF LEARNING MATERIAL** 



## **DSCC402**

## ZOOLOGY IV B: CHORDATE AND COMPARATIVE ANATOMY

MATS University

## CHORDATE AND COMPARATIVE ANATOMY CODE: ODL/MSS/BSCB/402

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#### March, 2025

FIRST EDITION: 2025 ISBN: 978-93-49916-46-3

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Printed & Published on behalf of MATS University, Village-Gullu, Aarang, Raipur by Mr. Meghanadhudu Katabathuni, Facilities & Operations, MATS University, Raipur (C.G.)

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#### MODULE INTRODUCTION

Course has five MODULEs. Under this theme we have covered the following topics:

MODULE 1 INTRODUCTION TO CHORDATE

MODULE 2 CHORDATE II

MODULE 3 COMAPARATIVE ANATOMY I

MODULE 4 COMPARATIVE ANATOMY II

MODULE 5 COMPARATIVE ANATOMY III

The book will explore the anatomical and physiological adaptations of chordates, comparing their structures across different taxa to highlight evolutionary relationships, functional morphology, and ecological significance. This book is designed to help you think about the topic of the particular MODULE.

We suggest you do all the activities in the MODULEs, even those which you find relatively easy. This will reinforce your earlier learning.

#### **MODULE 1**

#### **INTRODUCTION TO CHORDATES**

#### 1.0 Objective

- To understand the origin and evolution of chordates.
- To study the classification and general characteristics of fishes, amphibians, reptiles, birds, and mammals.
- To analyze the fossil evidence supporting chordate evolution.
- To compare chordates with non-chordates.

#### **UNIT 01**

#### Origin of Chordates: Fishes, Amphibia, Reptiles, Aves & Mammals

#### **Definition and Characteristics**

Chordates: Animals Within the phylum Chordata being to a large and diverse group of animals characterized by a number of unique features which distinguish them from other animal phyla. Chordates are characterized by the presence of four structures —in some stage of development—: a notochord, a dorsal hollow nerve cord, pharyngeal slits and a post-anal tail. It provides structural support and is a precursor to the vertebral column in vertebrates. The tube, which is positioned above the notochord, develops into the central nervous system. The pharyngeal slits, found in the pharyngeal region, serve the function of filter feeding in primitive chordates and develop towards structures such as gill slits in aquatic vertebrates and diverse gland and skeletal components in terrestrial lineages. The post-anal tail is an extension of the primary body beyond the anus, forming a propulsive organ in various chordate lineages. Chordates display bilateral symmetry and have a true coelom or body cavity with a complex set of organs. Their body plan is segmented in nature, particularly with respect to the arrangement of muscles, nerves, and skeletal elements. Unlike many invertebrates, chordates have a closed circulatory system, which includes a ventral heart that pumps blood through vessels. Now the digestive system is complete, with the mouth at one end and anus at the other, the organs





able to process the food more efficiently. Respiratory structures differ across groups of chordates, from pharyngeal gills in aquatic forms to lungs in terrestrial species. Excretory system Excretory system in animals The excretory system filter, secrete and reabsorb waste products The excretory system in the human body consist of two pairs of kidney kidneys filter waste products of blood. They have an elaborated endocrine system to control different physiological phenomena by hormones. Traditionally, the phylum Chordata has been divided into three subphyla: the Urochordata (or tunicates), Cephalochordata (or lancelets), and Vertebrata (or vertebrates). Urochordates (sea squirts) show the chordate features only in their larval days, then they metamorphose into a sessile adult that has little in common with your average chordate. Examples include lancelets, which are classified as cephalochordates, and where all four chordate traits are preserved throughout the animals' lifetimes, making lancelets the closest modern relatives of vertebrates. Vertebrates, which comprise the most diverse and widely recognized group of chordates, are characterized by the presence of a vertebral column that replaces or encases the notochord in adults, a well-evolved brain encased in a cranium, and paired appendages, along with other complex adaptations.

#### **Theories of Chordate Origin**

Ampioxus, the ancestral chordate, has also attracted considerable interest; evolutionary biologists have long debated where it fits in the shape of the animal tree of life, with many proposed hypotheses explaining how this body plan emerged. These theories aim to connect chordates with whatever it is that they descended from (invertebrates) based on different aspects of anatomy, embryology, and molecular biology. Cordate evolution was traditionally thought to proceed from a non-chordate ancestor, as was suggested by the Echinoderm theory first proposed by William Bateson in the late nineteenth century and elaborated by Walter Garstang. This theory is based on the early developmental states between echinoderms and chordates and similarities in coelom formation and traits of the larval stages. Garstang in particular argued that the chordates had larval forms of the neotene type, so that sexual maturity was reached whilst the larval form of the organisms was retained, from a group of echinoderms alive at the time. Although echinoderms and chordates are both deuterostomes (animals whose embryonic blastopore becomes the anus), the distinct morphological differences between adult forms has caused numerous scientists to doubt this direct relationship. In the 19th century Anton Dohrn promoted the so-called Annelid Theory to explain the evolution of chordates from ancestors resembling annelids, which involved inversion of the dorsoventral axis. The ventral nerve cord of annelids is homologous with the dorsal nerve cord of chordates, the dorsal blood vessel of annelids is homologous with the ventral heart of chordates and so on. Although this notion accounts for some anatomical characteristics in a beautiful way, it has been an issue for embryological proof and the reality that annelids originated from the protostome lineage (creatures whose blastopore creates the mouth) that isn't the equivalent deuterostome lineage that incorporates chordates.

Hubrecht championed the Nemertean Theory, suggesting that nemertean worms (a.k.a ribbon worms) were the progenitors of chordates. The theory states that this is due to similarities between the notochord of the nemerteans and the notochord of the chordates, as well as both groups having a closed circulatory system. However, differences in embryology, and more recently in molecules, have belied a close relationship between nemerteans and chordates. According to Jefferies's calcichordate theory, chordates evolved from calcichordates, calcichordates were primitive echinoderms that had features of both echinoderms and chordates. So far, the fossil evidence for these organisms exhibits subdivison of transitional features, but the current interpretation remains disputed and the theory has Yet to be widely accepted. The Deuterostome Theory is the most favored modern explanation for the origins of chordates, suggesting that chordates have a common ancestor with other deuterostome phyla, especially echinoderms and hemichordates. Molecular phylogenetic analyses provide strong support for this hypothesis, consistently grouping these phyla together. In this perspective, the purported deuterostome ancestor had properties such as pharyngeal slits and a filter-feeding mode of life. Hemichordates, which have pharyngeal slits and a not hollow dorsal nerve cord, are especially important in chordate origins. In hemichordates the pharyngeal slits are used for filter feeding '! so it appears that as in the chordate lineage these structures ultimately became adapted for respiration

## Notes



in vertebrates. Recent molecular and developmental studies have offered new perspectives on the origins of chordates. However, it is not only the morphological studies that may have overestimated the differences between animal phyla: the discovery of conserved developmental genes, e.g. Hox genes, crossing very diverse animal phyla has disclosed deep homologies not apparent by purely morphological [genetical] studies of bilaterian animals. Perspective on the evolution of chordates from invertebrate ancestors is continuously being sharpened by comparative embryology and paleontology, coupled with molecular data such as those discussed.

#### The Fossil Record and Early Chordates

Due to the soft-bodied structure of primitive chordates, the fossil record of early representatives of this phylum is scant, but it furnishes critical information for reconstructing their evolution. However, a number of key fossil discoveries have shed light on the early evolution of chordates and vertebrates. One of the oldest examples of this mystery chordate were fossils identified in the Chengjiang fauna, from the early Cambrian (about 525 million years ago), in China. Similarly, the fossil fish known as Myllokunmingia and Haikouichthys, which were both found in these deposits, are some of the oldest-known vertebrates or vertebrate-like creatures. These primitive fishes had a notochord, myomeres and pharyngeal arches and were therefore early vertebrates or close relatives of the vertebrates. Another important Cambrian fossil is Pikaia gracilens from the Burgess Shale of Canada (505 Ma), which is often interpreted as a primitive chordate - possibly a relative of the cephalochordates. Pikaia has a notochord and segmented muscles, with a putative pharyngeal region, but its precise phylogenetic positioning is debated. Another candidate group of early chordates would be the Yunnanozoans from the Chengjiang faunule. These fossils have gastuls with structures that are interpreted to be pharyngeal slits and possibly also a notochord, but these interpretations have been challenged by some researchers. Vetulicolians, strange Cambrian creatures with a bipartite body plan, have also been suggested to be primitive chordates or deuterostomes, but their precise relationships are debated. The Cambrian is also when conodonts emerged: strange creatures best known from their tooth-like elements constructed from calcium phosphate. For decades, these represented our only understanding of conodonts, and various theories arose about what they actually were. But rare



soft-tissue fossils found toward the end of the 20th century indicated that conodonts may have had eyes, possible pharyngeal arches and V-type muscles that made them seem like vertebrates or close relatives of vertebrates. These tooth-like elements, now thought to function as feeding apparatus, are among the oldest mineralized structures in the chordate lineage.

Also during this time, vertebrates underwent a gradual transformation into a group named ostracoderms, a large class of early jawless fish-like vertebrates with bony armor that existed between the Ordovician and Devonian periods (485 to 359 million years ago). They included heterostracans, osteostracans, galeaspids, and anaspids, which possessed a bony armor or scales covering the head and anterior regions of the body. Ostracoderms possessed paired eyes and olfactory organs, had well-developed sensory systems and most possessed a distinctive head shield. These are jawless filter feeders or mouth brooders for substrate feeding. Another major evolutionary transition occurred in the form of jaws, originating from the anterior pharyngeal arches in the Silurian with the emergence of placoderms (armored jawed fishes) and acanthodians ("spiny sharks"), around 444–419 million years ago. Placoderms — which littered the watery ecosystems of the Devonian era, too - were known for their armored plates and early jaws, which gave the time period the moniker "Age of Fishes." And the placoderm fossil called Entelognathus, found in China, is highly preserving and closely resembles the jaws of modern vertebrates. After that, jawed vertebrates diversified into two major groups by late Silurian and early Devonian: cartilaginous fishes (chondrichthyans) and bony fishes (osteichthyans). Chondrichthyans (sharks, rays, and chimaeras) have skeletons largely of cartilage; osteichthyans (ray-finned fishes, actinopterygians, and the lobe-finned fishes, sarcopterygians) have skeletons largely of bone. Charles Darwin, during the onset of his theory of evolution, recognized that among the chordates the lobe-finned fishes are of great importance because they are understood as the ancestors of tetrapods (four-limbed vertebrates).



This transition from aquatic to terrestrial environments, one of the most momentous events during vertebrate evolution, is evidenced by spectacular fossils like Tiktaalik roseae from the late Devonian (Fig. 1A) (1). Discovered in Arctic Canada, Tiktaalik had characteristics that were between lobe-finned fishes and early tetrapods, including a flattened head, eyes atop the skull, ribs able to prop up its body on land and limb-like fins with wrist-like joints. Some other transitional forms are Acanthostega and Ichthyostega, early tetrapods that retained fish-like features including lateral line systems and tail fins while gaining adaptations for life on land, e.g. digits (fingers/toes) and more beefy limbs. These fossils together depict the gradual evolution of chordate characteristics and the transition away from primitive soft-bodied forms to the diverse vertebrate lineages that would later lead to amphibians, reptiles, birds and mammals. Although the fossil record is far from complete, it shows the evolutionary development of chordates and there's no reason to doubt that complex structures formed incrementally with transitional adaptations to different ecological environments.

#### **Relationship with Non-Chordate**

Comparative anatomy, embryology, paleontology, and, more recently, molecular phylogenetics, have illuminated the relationship of chordates to non-chordate animals. These methods have uncovered both deep evolutionary relationships and significant divergences and led to a foundation for understanding how chordates fit into the selective picture of metazoan evolution. From a phylogenetic standpoint, chordates are securely located within the deuterostome lineage, one of the two major branches of bilaterian animals. Deuterostomes have a few traits that distinguishes them from other types of organisms, including radial cleavage of the embryo, enterocoely formation of the coelom - outpocketing from the archenteron, and development of the blastopore into the anus and not the mouth. The three main phyla within deuterostomia are Chordata (vertebrates and related animals), Echinodermata (sea stars, sea urchins, and a few other animals), and Hemichordata (acorn worms and pterobranchs). Xenoturbellida and Xenacoelomorpha are other small deuterostome phyla, and their precise inter-relationships are still debated. Hemichordates have a few striking features in common with chordates making

them of particular relevance to understanding vertebrate origins. Notably, hemichordates have pharyngeal slits, which are structures that define chordates and are absent in echinoderms. The other distinguishing features of the hemichordate body plan consist of a dorsal nerve cord (not as hollow as the one in cordata) and the stomochord (previously believed to be homologous to the chordate notochord; now commonly thought to be a convergent trait). Both hemichordates and chordates have pharyngeal slits, implying that these structures were possessed by the common ancestor of all deuterostomes and that echinoderms lost these structures. Pharyngeal slits are thought to have served the function of filter feeding in hemichordates and this was likely also the original function of the slits in early chordate ancestors before they were modified for respiration in veretebrates. However, they are developmentally and genetically analogous to chordates (note that this abiogenesis-giving common ancestor has a radial symmetry as an adult, which is derived). After fertilization, the echinoderm embryo becomes a bilaterally symmetric larva with deuterostome development. The metamorphosis from bilateral larvae to radial adults represents one of the most radical transformations in the animal kingdom. 3.5 Molecular studies consistently show a close relationship between echinoderms and hemichordates, a clade called Ambulacraria that includes both groups as sister groups to chordates. This suggests that the last common ancestor of all deuterostomes was a pharyngealslitted, filter-feeding, bilaterally symmetric marine creature.

Outside of the deuterostome lineage, chordates are also related to the protostomes (the other major lineage of bilaterian animals), which include arthropods (insects, crustaceans, etc.), mollusks (clams, snails, octopi), annelids (earthworms, leeches, etc.), and a number of other phyla. The Protostomes, on the other hand, are characterized by spiral cleavage, schizocoely (splitting of mesodermal bands), and development of the blastopore into the mouth. This split of the deuterostome lineage from the protostome collective is among the earliest and most fundamental of all splits that have occurred in bilaterian evolution, with the split being dated to more than 600 million years ago. Molecular and developmental studies have uncovered surprising similarities between chordates and some protostome groups,

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despite the deep evolutionary divergences of these taxa. One example, conserved developmental genes like theHox genes which guide the body plan for various animal phyla, have shown this common playbook originated before the deuterostome-protostome divergence. In a similar fashion, the discovery of homologous neural patterning genes in both chordate and protostome phyla supports the idea that the centralized nervous system originated before these lineages diverged from each other, albeit the NS has been differentially modified between groups.

Understanding of the relationships among chordates and their more distantly related non-bilaterian relatives, specifically the cnidarians (jellyfish, corals) and sponges, can shed light on the early history of animal evolution. These groups separated prior to the evolution of bilateral symmetry, a coelom, and many of the other bilaterian traits. Molecular studies, however, have discovered evolutionary-conserved genetic ingredients that regulate fundamental developmental processes, indicating a shared ancestry of all animals (Metazoa). Some genes that are induced in the developing chordate nervous system are found in cnidarians, signaling that some of the genetic encoding for nervous system development predated the divergence of the two phyla, even if cnidarians lack a centralized nervous system and instead have a rudimentary nerve net. Hence continuity and innovation are the hallmarks of the evolutionary history linking the chordates and the non-chordate animals. Many of the defining traits of chordates can be traced to evolutionary ancestral states shared with other groups of animals, while other traits are distinct innovations that arose within the vertebrate ancestry. But, understanding these should provide a basis to pursue the genetic, developmental, and \$ecological\$ factors that have formed chordate evolution and the incredible diversity of fishes, amphibians, reptiles and mammals we see today.

#### **Evolution of Fishes**

Fish evolution is the oldest story in vertebrate history — over 500 million years — and it has led to some astounding diversity. Fishes, defined as gilled vertebrates that primarily live in water and that have fins, arose from several independent lineages that had developed various adaptations for the aquatic world and that laid down the template for the vertebrate bodyplan on which all subsequent vertebrates are built. The first vertebrate-like animals emerged in the Cambrian (525-520 million years ago) These organisms, alongside Chengjiang biota members such as Myllokunmingia and Haikouichthys are considered a part of the oldest known vertebrate or vertebrate like organisms from the fossil record. These fishlike animals exhibited fundamental vertebrate features, including a notochord, myomeres, and structures interpreted as these pharyngeal arches. They were devoid of jaws and paired fins, possessing instead a row of V-shaped blocks of muscle and a primitive tail fin with which to swim. These simple forms probably processed small organic particles they filtered out of the surrounding water, as do modern lancelets. Jawless fishes underwent a major early radiation during the Ordovician and Silurian periods (485-419 million years ago) with the emergence of a diverse assemblage of armored jawless vertebrates known as ostracoderms. Ostracoderms were a diverse group of jawless fishes with external armor composed of bone or similar mineralized tissue, and included several distinct lineages such as heterostracans, osteostracans, galeaspids and anaspids. The weapon was known to be used in combat and was an effective weapon against intruders, as it helped the horse grow armor plates across the head and anterior body region to protect from attack by predators. These animals fed using specialized features and many forms had circular, jawless mouths that were surrounded with plates for suction feeding on small prey or organic material in sediment. For instance, osteostracans had paired fins, signifying a crucial evolutionary transition toward the paired appendages that are typical of subsequent vertebrates.

The development of jaws is a major evolutionary transition in vertebrate evolution, most notably occurring during the late silurian (c. 425 million years ago). Jaws are derived from the anterior pharyngeal arches, skeletal elements that initially supported the gills of jawless ancestors. This transition freed the group to switch from a more passive predatory lifestyle and diversified feeding habits. Among the first representatives of jawed vertebrates are placoderms (armored jawed fishes)

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and acanthodians (so-called "spiny sharks"), which were abundant in the Devonian (419–359 million years ago), often called the "Age of Fishes" due to the enormous diversity of fish groups that evolved at that time. Placoderm descents, with their heavy armor plates and rudimentary jaw articulation, prevailed as the dominant vertebrates within a number of Devonian ecosystems. They varied from small forms to massive predators such as Dunkleosteus, which could measure 10 meters and boasted enormous plates used to shred its prey instead of teeth. New findings, especially of highly preserved specimens from China, have shown that some placoderms bore features previously believed to be only found in living jawed vertebrates and may be more closely related to them than previously thought. The acanthodians (from the Greek 'acanth', meaning 'spine', and 'odon', meaning 'tooth') were another group of important early jawed vertebrates, characterized by having many spines to support their fins. Once thought to be a separate lineage, these fish may actually represent a paraphyletic lineage, with some acanthodians more closely related to sharks and others to bony fishes. Little wonder that confusion still remains about some of these groups. This new classification sheds light on the intricate evolutionary links between early vertebrates.

By the late Devonian, two main lineages of jawed fishes had appeared that would become ancestral to all subsequent jawed vertebrates: the Chondrichthyes (cartilaginous fishes) and the Osteichthyes (bony fishes). Chondrichthyans: Primitive Skeleton '! Specialized Skeleton (Early) – The common ancestors of modern sharks, rays, and chimaeras evolved skeletons that were composed principally of cartilage (as opposed to bone), a feature once thought primitive and now considered a specialized adaptation. They evolved unique features including multiple rows of replaceable teeth, an unusual electrosensory system (ampullae of Lorenzini) and internal fertilization. Early chondrichthyans, such as Cladoselache from the late Devonian already show the streamlined bodyforms characteristic of modern sharks. Bony fishes (also called osteichthyans) split into Actinopterygii (ray-finned fishes) and a second lineage called Sarcopterygii (lobe-finned fishes). Ray-finned fishes (about 30,000 species), which include most of today's fishes, are distinguished by fins with bony rays. Their evolutionary path has consistently shown major radiations,

including early representatives like Cheirolepis in the Devonian, and then palaeoniscoids and holosteans are groups that preceded teleosts, who dominate contemporary aquatic communities. The teleosts, possessing the most sophisticated jaw apparatus and fin morphologies to date became explosively diversified beginning in the Cretaceous adapting to almost every aquatic habitat imaginable and leading to a variety of specialized feeding strategies, locomotor modes and reproductive strategies. Lobed fishes (coelacanths, lungfishes, and the descendants of tetrapods) have muscular fins supported by a central skeletal axis. Although today they are less diverse (only eight living species) this group was very important in vertebrate evolution, as the lineage from which tetrapods originated. Several features that would play a role in the landward transition — including internal nostrils (for breathing air) and muscular fins, able to bear weight — evolved in lobe-finned fishes. Today, the lungfishes can breathe air, thanks to specialized lungs, a wellness program that allows them to survive in low-oxygen waters, or even when the puddles they live in dry up in the temporary drought.

Different sensory systems evolved during fish evolution to sense and deploy information from the external environment. The lateral line system, which senses water movements and pressure changes, is a unique trait among vertebrates that live in aquatic environments. In a similar vein, these organisms exhibited specialized chemosensory organs and well-developed eyes that were already adapted for the aquatic environment. The arrival of brains and central nervous systems with specialized regions to handle different types of sensory information and complex behaviors. The evolutionary history of fishes is thus not only the dawn of vertebrate history, but a vast radiation event of multiple body plans that established the vertebrate body plan and explored many adaptations to life in the water. From this foundation would arise the tetrapods, vertebrates adapted for life on land, starting with the amphibians.

#### **Emergence of Amphibians**

One of the important transitions in vertebrate evolution the emergence of amphibians from fish ancestors is the transition from water to land. The transition

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from an aquatic lifestyle to a land-dwelling form was not stylistically trivial and was accompanied by extensive modularity, functional robustness, and various evolutionary traits transforming the whole organism, allowing subsequent vertebrates to diversify into the land. The land vertebrate lineage that led to the ancestors of amphibians are sarcopterygian (lobe-finned) fishes, particularly the transfishing clade Tetrapodomorpha. Some of these fishes had pre-adaptations that them evolutionarily prepare for the transition to land, e.g. muscular fins supported by internal skeletal structures, primitive lungs (or lung-like structures in them) that could8 be used to respire air, choanae (internal nostrils) that allowed them to breathe air without having to open their mouths. Some of these adaptations arose initially for life in low-oxygen aquatic habitats, such as shallow, plant-choked swamps or periodically dry puddles, not immediately for living on land. Several amazing transitional fossils have been discovered to support the fish-tetrapod transition. A late Devonian lobe-finned fish called Eusthenopteron had limb bones homologous to those in tetrapods, but was a fully aquatic animal. A more derived transitional form, Tiktaalik roseae, was identified in Arctic Canada in 2004. This creature, from roughly 375 million years ago, displayed features intermediate between those of fish and those of tetrapods: a flattened crocodile-shaped head with eyes on the top (rather than the sides) in a typical fish, a neck so the head could move independently of the body, ribs that could support its weight in shallow water or on land, and fins with wrist-like joints. But Tiktaalik had retained features that were fish-like, like scales and fin rays.

The first true tetrapods, like Acanthostega and Ichthyostega from the late Devonian of Greenland, had four limbs with digits instead of fins but still possessed many adaptations to aquatic life. Each hand and foot of Acanthostega had eight digits, making it clear that the pentadactyl (five-fingered) limb characteristic of later ectoderms had not yet evolved. Like fishes, these early tetrapods bore lateral line systems (sensory organs that respond to water displacement) and tail fins, suggesting they spent a lot of time below the water's surface. Its limbs and shoulder/hip girdles, while slightly more robust than those of its fish ancestors, were relatively weak, again suggesting movement by "swimming" through shallow water or across muddy substrates but not walking on land as we would understand it. These early

generations of tetrapods would evolve into true amphibians during the Carboniferous period (359-299 million years ago). By the early Carboniferous a wide variety of tetrapods had evolved, such as the temnospondyls, which were the ancestors of modern amphibians, and the anthracosaurs, from which the amniotes (reptiles, birds and mammals) descended. The Carboniferous was defined by giant coal swamps—warm, humid forest ecosystems that were perfectly conducive to the early diversification of tetrapod animals. These environments had plenty of food resources, less predation pressure from aquatic predators than in fully marine environments, and wet conditions that helped stave off desiccation, a major problem for animals adapted to water. Some early amphibians developed adaptations for a semi-terrestrial existence. Their skeletons were thicker, with sturdier limbs and girdles that could bear the weight of their body and resist gravity. Such changes in the skull included alterations in jaw structure and sensory systems better suited for picking up airborne and ground movement signals than those in water. The lungs evolved as the primary respiratory organ amongst these terrestrial creatures, although many still have cutaneous respiration (the ability to breathe through their skin) still functional. But, despite these adaptations for living on land, the earliest amphibians were still very dependent on water for reproduction: They laid eggs in water, and their larvae (the equivalent of modern-day tadpoles) developed into more land-adapted adult forms after metamorphosing.

There was a spectacular diversification of amphibian body forms during the Carboniferous and early Permian (359-270 million years ago). Temnospondyls, which proved the most diverse group among early amphibians, included small, salamander-like forms, as well as the large, crocodile-like, 5-meter-long predators such as Prionosuchus of Brazil from the Permian. Another major group, the lepopsondyls, also included small, often eel- or snake-like animals that occupied different aquatic and semi-aquatic niches. Some early amphibians had reptilian adaptations while still retaining amphibian-like features in reproduction and development, such as seymouriamorphs. The end of the Paleozoic, with the catastrophic Permian-Triassic mass extinction (about 252 million years ago),

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slashed amphibian diversity. More modern amphibian groups arose during the recovery from the extinction. Modern amphibians (Lissamphibia) probably originated from temnospondyl stock in the Triassic (252-201 Myr ago), but precise relationships and timing are debated. Modern amphibians are divided into three orders: Anura (frogs and toads), Caudata (salamanders and newts), and Gymnophiona (caecilians). These groups developed specific adaptations to fit their respective ecological roles while still possessing key amphibian traits. Frogs have an unusual morphology for the purpose of jumping locomotion, and they are definitively present in the fossil record from the Early Jurassic onwards; for example, Prosalirus from the Kayenta Formation of Arizona is one of the earliest-known anurans with adaptations for jumping (saltatorial) locomotion. Salamanders, which kept a more elongate, generalized tetrapod body plan, are known from Middle Jurassic deposits in England and Central Asia. Caecilians, a clade of limbless amphibians adapted to burrowing modes of life, have a sparse fossil record, the most ancient definite fossils being from the Early Jurassic of Arizona.

Modern amphibians — there are approximately 8,000 species — have many unique traits in common: moist, often glandular skin that plays roles in respiration and fluid regulation; an aquatic larval stage for most if not all species; external fertilization (although there are exceptions); and ectothermic (cold-blooded) physiology. Most amphibians, in contrast to the more terrestrial amniotes, are still confined to moist habitats to avoid desiccation and generally require bodies of water in which to reproduce, but a wide diversity of specialized reproductive strategies has evolved in an attempt to accommodate to a variety of environmental conditions. Thus, the evolution of amphibians accounts not only for an intermediate stage in vertebrate evolution, but also for the rise of a successful and unique and vertebrate lineage that continues to be expansive in its range today. The evolutionary history of these fishes, which spans the last 300 million years, exemplifies the vicissitudes and possibilities afforded by a transition to land and serves as a prologue to the subsequent success of fully terrestrial vertebrates, the amniotes.

#### **Rise of Reptiles**

This evolutionary story begins with the evolutionary emergence of the amniotic egg, a key innovation that allowed these vertebrates to reproduce away from water. This innovation first emerged—385-360 million years ago in the late Carboniferous period—about the time amniotes (reptiles, birds, and mammals) split from their amphibian ancestors. The amniotic egg has specialized membranes (the amnion, chorion, and allantois), and it allows the developing embryo to exist in a fluid-filled cavity and effectively creates a "little private pond" that facilitates reproduction on land. Amphibian adaptations that preceded this reproductive novelty included waterproof skin with scales to inhibit desiccation; lungs that were more effective at extracting oxygen from the air; and kidneys that could sequester water by excreting uric acid rather than urea or ammonia. Reducing the group five, the oldest amniotes were small lizard-like animals (e.g. Hylonomus & Paleothyris from the carboniferous) These animals, about 20-30 cm long, had a primitive reptilian body plan, but lacked later derived features of some reptile groups. They probably filled insectivore niches in the coal swamp forests of the Carboniferous, taking advantage of a terrestrial resource that was less available to their amphibious contemporaries. These early forms may seem superficially like small modern reptiles, but they are the common ancestors to all subsequent amniote lineages, including mammals and birds. Some of the most notable early reptiles had their origins during the Permian period (299-252 million years ago), as dozens of reptile lineages diversified and adapted to numerous ecological niches as they migrated across the supercontinent Pangaea. That radiation included the emergence of several major groups: the anapsids (reptiles lacking temporal openings in the skull, including the ancestors of turtles), the synapsids (characterized by a single temporal opening, leading to the lineage that produced mammals) and the diapsids (with two temporal openings, leading to most modern reptiles and birds). So the evolution of those different skull configurations, related in part to the evolution of the openings behind the eyes that allowed for bigger and more powerful jaw muscles to attach, were key adaptations for diverse feeding strategies.

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During the late Carboniferous and Permian periods, synapsids completely dominated terrestrial ecosystems. Among the earliest examples, pelycosaurs, were well known sail-backed predators such as Dimetrodon, as well as herbivorous pelycosaurs like Edaphosaurus. By the Mid to Late Permian, more advanced synapsids called therapsids appeared, some of which developed increasingly mammal-like features, including differentiated teeth, a more erect posture and possibly the first inklings of endothermy (warm-bloodedness). In traditional systems, synapsids are technically classified as "reptiles" but represent a separate evolutionary lineage from the other "reptiles" and are now re-discovered as the group that would become mammals. Diapsids, the line that would eventually lead to the vast majority of modern reptiles and birds, were also increasingly diversified in the late Permian, and especially after the Permian-Triassic mass extinction event (252 million years ago), which sent synapsid dominance into retreat. Early diapsids spread out into multiple lineages, including the lepidosauromorphs (which gave rise to the modern tuataras, lizards and snakes) and the archosauromorphs (which gave rise to crocodilians, pterosaurs, dinosaurs and birds). The evolutionary placement of turtles is somewhat enigmatic with various molecular and morphological studies placing turtles in different locations in the reptile tree and turtles have a unique shell formed from modified ribs and dermal bone. During the Triassic (252-201 million years ago), there was a spectacular radiation of reptile shapes, taking up the ecological positions left open by victims of the Permian-Triassic extinction. Archosaurs ("ruling reptiles") were especially diverse and dominant at this time. This group encompasses a unique arrangement of the ankles along with diverse modifications of the skull, and includes the line leading to the crocodilians (Pseudosuchia) and the line that led to the dinosaurs and birds (Avemetatarsalia). Primitive archosaurs were highly diverse, with niche occupying forms such as phytosaurs (crocodile-like animals with nostrils located near the eyes), aetosaurs (armored herbivores), rauisuchians (large terrestrial predators), and early crocodylomorphs. The Triassic also featured the emergence of the first dinosaurs: initially small, bipedal forms that subsequently diversifed into the dominant terrestrial vertebrates of the Mesozoic.

The Mesozoic was also a time when marine reptiles underwent diversification, adapting to a life in the oceans by convergently evolving streamlined bodies, paddle-like limbs, and other aquatic specializations. These included ichthyosaurs (dolphinlike reptiles that developed live birth rather than laying eggs), plesiosaurs (notable for long necks and four flipperlike limbs), mosasaurs (huge marine lizards related to today's monitor lizards) and multiple lineages of turtles. Pterosaurs took to the sky like the first vertebrate animals Bone Wing (with wings) as they evolved into the hollow bone structure, enlarged brains, wing membranes supported by a long fourth finger. Dinosaurs first appeared in the fossil record in the late Triassic and they remained the dominant terrestrial vertebrates throughout the Jurassic (201–145 million years ago) and Cretaceous (145–66 million years ago) periods.

#### **UNIT 02**

## General characters and classification- Fishes, Amphibia, Reptiles, Aves & Mammals

#### Vertebrates and Their Classification

Vertebrates are one of the most heterogeneous and successful groups of animals in the animal kingdom. Vertebrates belong to the phylum Chordata and are defined by a notochord, a dorsal hollow nerve cord, pharyngeal slits and a post-anal tail, all of which must be present during some stage of development. Vertebrates are characterized by their vertebral column or backbone, both of which support the body structure and protect the spinal cord. This innovation has enabled vertebrates to become one of the most successful groups in evolution, able to thrive in virtually every habitat on the planet. Vertebrates first evolved more than 500 million years ago and, in the early stages of that journey, primitive fish-like organisms emerged from the ancient oceans. With a series of remarkable adaptations, vertebrates gradually expanded to new habitats and evolved myriad forms. This evolutionary tale is embodied in the five major classes of vertebrates: Pisces (the fishes), Amphibia, Reptilia, Aves (the birds), and Mammalia (the mammals). For every class, a major evolutionary advance that facilitates the exploitation of new

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ecological roles and resources. The five vertebrate classes show enormous diversity in forms, functions and ecological adaptations. From the fishes' sleek bodies as adaptations for aquatic life to the feathered wings as adaptations for flight in birds, and from scaleless, moist skin in amphibians to fur-covered bodies in mammals, in regard to body plans vertebrates have some astonishing evolutionary innovations. The lab works on several projects designed to understand the features of these groups, how they are classified, and what we can learn about evolution, ecology and speciation.

#### **Pisces (Fishes)**

#### **General Features of Fishes**

Fishes were the first group of vertebrates to evolve and are highly adapted to an aquatic mode of life. The first vertebrates to evolve, they set many of the basic vertebrate features even as they developed highly specialized adaptations to living in a watery environment. Fishes are the most diverse vertebrate group: More than 34,000 species have been described, and they occupy nearly every aquatic environment on the planet, from deep ocean trenches to mountain streams. The body of the fish is usually itself streamlined, which is an adaptation to minimize drag while swimming. This hydrodynamic form enables them to efficiently navigate through water, a critical characteristic for evading predators and capturing prey. Most fishes have two pairs of fins and other unpaired fins which function to propel, steer, stabilize, and brake. The caudal (tail) fin supplies the majority of propulsive force, while dorsal and anal fins provide stabilization. The paired pectoral and pelvic fins support maneuvering, stopping, and holding position. The scales of the fish integumentary system serve as a protective covering for the body and minimize drag. The most extravagant scales vary from the placoid scales of sharks, to the cycloid and ctenoid scales of bony fishes. The skin of fishes has many mucous glands that secrete a slimy coating that decreases friction with water and provides some protection against parasites and pathogens. The majority of fishes perform respiration using gills, which are specialized structures that extract dissolved oxygen out of water. Water

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flows in through the mouth, across the gills and out through the gill slits. The numerous blood vessels in the gills are arranged to allow maximum uptake of oxygen by countercurrent exchange, where blood flows in the opposite direction to water, increasing efficacy.

In fishes, the circulatory system includes a two-chamber heart that sends deoxygenated blood to the gills for oxygenation and then pumps it to the rest of the body. This is in contrast to the dual circulation seen with terrestrial vertebrates. Most fishes achieve neutral buoyancy thanks to a swim bladder, a gas-filled sac that can be expanded or contracted to allow the fish to move through the water column without expending energy. Fish have great vision, chemoreceptors to taste and smell their food and a specialized lateral line system that is sensitive to pressure differences and vibrations in the water. Other fishes have specialized electroreceptors that are able to detect the electrical fields created by other organisms or the environmental surroundings. While reproduction strategies vary, most species are oviparous (egg-laying), laying their eggs in water through external fertilization. But some species also have internal fertilization, and a range of parental care strategies have evolved from basic guarding of the nest to mouthbrooding and viviparity.

#### **Classification of Fishes**

The traditional classification divides fishes into three major classes, though modern systematic approaches have revised this significantly based on evolutionary relationships:

**Class Agnatha (Jawless Fishes):** These are the most primitive extant vertebrates, characterized by:

- · Absence of jaws and paired fins
- · Cartilaginous skeleton
- · Notochord persists throughout life



- · Circular, sucker-like mouth with keratinized teeth
- · No scales
- · Seven or more pairs of gill pouches

This class includes two living groups:

- 1. Order Petromyzontiformes (Lampreys): Freshwater and marine species with parasitic and non-parasitic life histories. Parasitic lampreys attach to other fish using their sucker-like oral disc and rasp away tissue with their keratinized teeth.
- 2. Order Myxiniformes (Hagfishes): Marine scavengers with slime glands that produce copious mucus when threatened. Unlike lampreys, hagfishes lack true vertebrae and possess tentacles around their mouths.

**Class Chondrichthyes (Cartilaginous Fishes)** This class includes sharks, rays, skates, and chimaeras, characterized by:

- · Cartilaginous skeleton (calcified in some parts)
- · Placoid scales (dermal denticles)
- · Multiple gill slits without operculum
- · Powerful jaws with multiple rows of replaceable teeth
- · Claspers in males for internal fertilization
- No swim bladder (use large, oil-filled liver for buoyancy)
- Well-developed sense organs, including electroreceptors (ampullae of Lorenzini)

Major orders include:

1. Order Selachii (Sharks): Streamlined predators with powerful tails and numerous teeth.



- 2. Order Batoidea (Rays and Skates): Flattened bodies with enlarged pectoral fins, often bottom-dwelling.
- **3.** Order Holocephali (Chimaeras): Deep-sea fishes with large heads and single gill opening covered by an operculum.

**Class Osteichthyes (Bony Fishes)** The largest and most diverse class of vertebrates, characterized by:

- · Ossified skeleton
- · Cycloid, ctenoid, or ganoid scales
- · Gill chamber covered by operculum
- · Swim bladder for buoyancy control
- · Usually oviparous with external fertilization

This class is traditionally divided into two major subclasses:

- 1. Subclass Actinopterygii (Ray-finned Fishes) Comprising over 30,000 species, these fishes have:
  - Fins supported by dermal rays
  - · Symmetrical (homocercal) tail fin
  - · Includes familiar fishes like salmon, trout, cod, perch, and many others

#### Major orders include:

- Order Clupeiformes: Herrings, sardines, anchovies
- · Order Cypriniformes: Carps, minnows, barbs
- · Order Siluriformes: Catfishes
- · Order Salmoniformes: Salmon, trout, pike
- Order Perciformes: The largest order, including perch, tuna, mackerel, and many coral reef fishes



- 2. Subclass Sarcopterygii (Lobe-finned Fishes) A smaller group with muscular fins supported by a central axis of bones:
  - Order Coelacanthiformes: Coelacanths, once thought extinct until discovered alive in 1938
  - Order Dipnoi (Lungfishes): Air-breathing fishes with modified swim bladders functioning as lungs

The Sarcopterygii are of particular evolutionary interest as they are closely related to the ancestors of tetrapods (four-limbed vertebrates), representing the transition from aquatic to terrestrial life.

Modern phylogenetic classification recognizes additional complexity in fish relationships, particularly among the jawless and primitive jawed fishes. The traditional three classes described above do not reflect all evolutionary relationships, and newer systems place greater emphasis on monophyletic groupings, where all members share a common ancestor.

#### Amphibia

#### **General Characteristics of Amphibians**

Amphibians provide key insight into an evolutionary transition in vertebrates, occupying a position between living in the water and on land. The name "Amphibia" (from the Greek for "both lives") is quite representative of their life history, with most species going through an aquatic larval stage as well as a more terrestrial adult. This class comprises about 8,000 known species found around the world, but they're especially diverse in tropical areas. The body of an amphibian is usually tetrapod (having four limbs), and this is one of the most significant evolutionary innovations in the history of vertebrates. It possesses two pairs of pentadactyl (five-digited) limbs which have been secondarily reduced or lost in some species. Most amiphibians have a rather flat body with a wide head and no significant neck, so they move with greater efficiency on land but can still swim if need be. The integumentary system of amphibians is unique;

their skin is relatively smooth, moist, glandular, and lacks scales. This skin has several functionalities, including the fact that it is extremely vascular and acts as a secondary respiratory organ, allowing gas exchange through the skin surface directly. The skin has several mucous glands, which keep the skin moist for cutaneous respiration, and poison glands, which secrete toxins to defend against predators. These toxins range from mildly irritating to deadly; poison dart frogs make some of the most powerful natural toxins on record. They have highly complicated and often metamorphic respiration. Most larvae respire through external gills, whereas adults use a combination of lungs, skin (cutaneous respiration), and sometimes the lining of the mouth (buccopharyngeal respiration). This respiratory adaptability enabled proto-amphibians to invade both aquatic and terrestrial niches, but it also constrains modern amphibians to damp environments.

In amphibians, circulatory system is much more developed than in fishes. They have a three-chambered heart - having two atria and one ventricle that is partially separated into two with flow to the arterial pulmonary system and systemic flow. This is an intermediate level between the single-circuit system of the fishes and the entire double circuit of birds and mammals. Amphibians, like other ectothermic ("cold-blooded") animals, rely on external sources of heat to regulate their body temperature. This restricts their activity in cold environments, but enables them to live with lower energy demand than endothermic animals. This is one of the reasons for many species' hibernation or aestivation in adverse seasons. Sensory systems of amphibians are adapted to elements of both aquatic and terrestrial habitats. They have well-developed eyes with eyelids, a middle ear with a single ossicle (the columella) used to detect aerial sounds, and different chemoreceptors. Many amphibians have a specialized sense organ known as the lateral line system, common to fishes, in their larval stage that detects water movements and shifts in pressure. Amphibians are unique class of vertebrates characterised by life-cycle with metamorphosis. Most species lay eggs without shells in water, which develop into aquatic larvae (tadpoles in frogs and toads) with gills and a tail. These larvae metamorphose explosively into the adult form, complete with lungs, limbs and other adaptations for life on land. But there is considerable variation in reproductive

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strategies; for example, some species display direct development (i.e., skipping the larval stage), viviparity (live birth), or neoteny (retention of larval traits in sexually mature adults, as seen in axolotls).

#### **Classification of Amphibians**

Modern classification recognizes three living orders of amphibians:

**Order Anura (Frogs and Toads)** The largest amphibian order with approximately 7,000 species, characterized by:

- · Tailless body as adults
- · Elongated hind limbs adapted for jumping or swimming
- Fusion of skull bones creating a rigid cranium
- · Short, broad body with no distinct neck
- · Well-developed vocal structures and complex mating calls
- · Dramatic metamorphosis from tadpole to adult

Anura includes several families:

- **Ranidae (True Frogs)**: Includes the common frog (Rana temporaria) and bullfrog (Rana catesbeiana)
- **Bufonidae (True Toads)**: Includes the common toad (Bufo bufo)
- Hylidae (Tree Frogs): Arboreal species with adhesive toe pads
- Dendrobatidae (Poison Dart Frogs): Small, colorful frogs with potent skin toxins
- Pipidae (Clawed Frogs): Fully aquatic frogs including the model organism Xenopus laevis

**Order Urodela/Caudata (Salamanders and Newts)** Approximately 700 species characterized by:

- · Elongated body with distinct tail in both larvae and adults
- Two pairs of equal-sized limbs placed laterally
- · Less dramatic metamorphosis than anurans
- · Generally secretive lifestyle

Major families include:

- Salamandridae (True Salamanders and Newts): Including fire salamanders and common newts
- Ambystomatidae (Mole Salamanders): Including the axolotl (Ambystoma mexicanum)
- Plethodontidae (Lungless Salamanders): Respire entirely through skin and mouth lining
- Cryptobranchidae (Giant Salamanders): Including the largest living amphibians, reaching up to 1.8 meters

**Order Gymnophiona/Apoda (Caecilians)** Approximately 200 species of limbless, burrowing amphibians characterized by:

- Elongated, snake-like body without limbs
- · Reduced eyes, sometimes covered by skin or bone
- · Specialized tentacle between eye and nostril as sensory organ
- · Segmented appearance due to ring-like folds in the skin
- Strong skull adapted for burrowing
- · Mostly tropical distribution

Caecilians are the most poorly elucidated group of the amphibians, with many species left uninvestigated owing to their secretive, burrowing way of life. Recent studies have demonstrated incredible reproductive adaptations, such as in some species, where offspring feast on the mothers' modified skin. The fossil record also includes several extinct amphibian groups, such as the Labyrinthodontia

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and Lepospondyli, that were major components of Paleozoic and early Mesozoic ecosystems, in addition to these three extant orders. These ancient amphibians ranged from small, salamander-like forms to massive, crocodile-like predators with squat skulls and powerful jaws. Amphibians have a complex evolutionary history. Modern amphibians (Lissamphibia) probably descended from early tetrapods in the Permian Period, and the first tetrapods came from lobe-finned fishes (Sarcopterygii) of the Devonian Period, around 370 million years ago. Early tetrapods such as Ichthyostega and Acanthostega still had many adaptations inherited from their fish ancestors but also underwent changes that helped them adapt to life on land.

#### Reptilia

#### **General Characteristics of Reptiles**

The reptiles can be considered a critical evolutionary step in the history of vertebrates and the first group of vertebrates that completely transitioned to the dry land. Their land-based adaptations allowed them to occupy habitats that were unavailable to amphibians, and they diversified dramatically through the Mesozoic Era, colloquially referred to as the "Age of Reptiles." Reptiles now live in a wide range of climates, with some 11,000 species found on every continent from the tundra to the tropics, inhabiting everything from deserts to tropical forests to oceans. All reptiles are equipped with the unique amniotic egg, specialized with extra membranes (amnion, chorion, and allantois) and a dermal shell, which prevents desiccation. This adaptation liberated reptiles from moisture dependence for breeding, enabling them to become the first fully terrestrial vertebrates. Neither of these solutions were perfect, which is why it is believed the amniotic egg was able to develop, which allows a self-contained aquatic environment for the embryo and food via the yolk sac. The reptilian integumentary system has keratinized scales that originate from the epidermis, serving as a waterproofing barrier that prevents dehydration in terrestrial environments. These scales offer protection compositionally and allow for flexibility; in some taxa (most notably snakes) they provide a mode of locomotion. Reptiles shed skin on a regular basis (ecdysis) to allow for growth and to replace worn scales. Reptiles, like birds and mammals,



only use lungs to breath, they do not also respire through skin like the amphibians. Reptile lungs are more elaborate than those of amphibians, with a larger internal surface area for gas exchange. Unlike other groups, birds possess true lungs, but they employ specialized air sacs for ventilation via costal breathing of intercostal muscles or, in several groups, of specialized structures, such as the hepatic piston mechanism, present in crocodilians.

Most reptiles have a heart with three chambers which is astonishingly a leap from the two-chambered system seen in fish, alongside the basic pattern of the circulatory system. However, there is some separation of the ventricle in many species, and complete separation (four-chamber heart) in crocodilians. This design helps to allow some separation between oxygen-rich and oxygen-poor blood, making oxygen delivery to tissues more effective. Being ectotherms, reptiles use behavior (moving between sun and shade) to regulate body temperature. This thermoregulatory response is complex — in fact, many species can maintain fairly stable body temperatures during their active phases. Some large reptiles can also retain heat, due to their mass, in a phenomenon called gigantothermy. Reptiles' excretory system indicates adaptation because they have to retain water, so they excrete uric acid instead of urea (as a primary nitrogen waste). Uric acid is considerably less poisonous than ammonia, and excreting it requires far less water, which allows it to be disposed of as a semi-solid paste, with precious water galore. The reptilian nervous system is more advanced than that of amphibians, with a larger brain and more complex sensory systems. Hearing, typically as elaborate as vision; and in many species [including the heat-sensing pits of the pit vipers, to the Jacobson's organ (vomeronasal organ) used for chemical detection. Reptiles can be oviparous (egg-laying) or viviparous (giving live birth), with viviparity evolving independently in several lineages (like many snakes and lizards). A few viviparous reptiles form a rudimentary placenta, linking maternal-end and embryonic tissues. Parental care runs the gamut, from no parental care in most species to extensive nest guarding in crocodilians and some pythons.

#### **Classification of Reptiles**

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Reptiles were traditionally grouped into four orders, but modern phylogenetic methods have revealed a more complex picture of reptiles' relationships, particularly with birds (Class Aves), which are now understood to be a lineage of specialized reptiles descended from theropod dinosaurs..

**Order Testudines/Chelonia (Turtles and Tortoises)** Approximately 350 species characterized by:

- · Bony shell consisting of carapace (dorsal) and plastron (ventral)
- · Toothless jaws with keratinized beaks
- · Inability to protrude the tongue
- · No temporal fenestrae in the skull
- · Unique position of limb girdles inside the ribcage
- · Long lifespan and slow growth rate

Major subgroups include:

- Cryptodira (Hidden-necked Turtles): Pull head straight back into shell
- Pleurodira (Side-necked Turtles): Fold neck sideways under shell
- Terrestrial Forms (Tortoises): Specialized for land locomotion with elephant-like feet
- Aquatic Forms (Terrapins, Sea Turtles): Specialized for swimming with paddle-like limbs

**Order Squamata (Lizards, Snakes, and Amphisbaenians)** The largest reptilian order with over 10,000 species, characterized by:

- · Overlapping scales
- · Movable quadrate bone allowing jaw kinesis
- · Regular shedding of skin (ecdysis)

- · Males with hemipenes (paired copulatory organs)
- · Diverse adaptations for varied lifestyles

This order includes three major suborders:

- 1. Suborder Lacertilia/Sauria (Lizards) Extremely diverse group including:
  - Iguanidae (Iguanas): Large herbivorous lizards of the Americas
  - Agamidae (Agamids): Old World counterparts to iguanas
  - Chamaeleonidae (Chameleons): Specialized arboreal lizards with prehensile tails and projectile tongues
  - Gekkonidae (Geckos): Often nocturnal with specialized toe pads for climbing
  - Varanidae (Monitor Lizards): Large predatory lizards including the Komodo dragon
- 2. Suborder Serpentes (Snakes) Limbless reptiles characterized by:
  - · Extremely flexible jaws with multiple points of kinesis
  - · No external ears or movable eyelids
  - · Elongated body with numerous vertebrae
  - · Sensory adaptations including heat-sensing pits in some families

Major families include:

- Colubridae: Largest snake family, mostly non-venomous
- Elapidae: Venomous snakes with fixed front fangs, including cobras and coral snakes
- Viperidae: Venomous snakes with hinged fangs, including rattlesnakes and vipers

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- Boidae: Constrictors like boas and pythons
- 3. Suborder Amphisbaenia (Worm Lizards) Specialized burrowing reptiles with:
  - · Ringed appearance similar to earthworms
  - · Reduced or absent limbs
  - · Compact skull adapted for digging
  - · Small or absent eyes

Order Crocodilia (Crocodiles, Alligators, Caimans, and Gharials) Twenty-

five species of large, semi-aquatic predators characterized by:

- · Four-chambered heart (unique among non-avian reptiles)
- · Secondary palate allowing breathing while mouth is open underwater
- · Powerful jaws with conical teeth set in sockets
- · Armor of bony plates (osteoderms) beneath scales
- · Complex parental care
- · Vocal communication

Major families include:

- **Crocodylidae (True Crocodiles)**: Found in Africa, Asia, Australia, and the Americas
- Alligatoridae (Alligators and Caimans): Found in the Americas and China
- Gavialidae (Gharials): Fish-eating specialists with narrow snouts, found in India and Nepal

**Order Rhynchocephalia** This order contains only one living genus, Sphenodon (tuataras), found exclusively in New Zealand, characterized by:


- · Primitive features including a diapsid skull with complete arcades
- · Third eye (parietal eye) with lens, retina, and nerve connections
- Teeth fused to jaw bone (acrodont dentition)
- · Unique chewing motion with forward-backward jaw movement
- Extremely slow growth and metabolism
- · Long lifespan (potentially exceeding 100 years)

Tuataras are often called "living fossils" as they retain many features of their Mesozoic ancestors with little change.

In modern phylogenetic classification, Class Reptilia is considered paraphyletic if birds are excluded, as birds share a more recent common ancestor with crocodilians than crocodilians do with other reptiles. The clade Archosauria includes both crocodilians and birds, while the broader clade Sauropsida includes all reptiles and birds.

The fossil record of reptiles is extensive, including numerous extinct groups such as:

- Dinosaurs: Dominated terrestrial ecosystems for over 160 million years
- **Pterosaurs**: The first flying vertebrates
- Ichthyosaurs and Plesiosaurs: Marine reptiles that returned to aquatic life
- Therapsids: Mammal-like reptiles, some of which gave rise to true mammals
- Many others: Including mosasaurs, pelycosaurs, and pareiasaurs

Aves (Birds)

### **General Characteristics of Birds**



Birds are one of the most successful vertebrate lineages, with nearly 10,500 extant species filling nearly every terrestrial habitat and many aquatic ones. Although birds are highly derived reptiles, their adaptations for flight have also allowed them to take advantage of aerial niches that are unavailable to most other vertebrates. They are widespread, play various roles in ecosystems, and exhibit behaviors that are nothing short of elaborate, suggesting their success at adapting and evolving. Feathers, complex integumentary structures of reptilian origin, are the major distinguishing feature of birds. Feathers provide insulation, waterproofing, aerodynamic surfaces for flight and, often, elaborate visual displays for communication and courtship. Feathers come in different types, with various specialized functions, including contour feathers that smooth the external body covering, down feathers that provide insulation, and flight feathers on wings and tail. Single or multi-molt can occur once or multiple times annually depending on the species and feathers are replaced by a continual process of molting. The avian skeleton has undergone extreme adaptations for flight. Notably, bones are pneumatized (air space-containing) and related to the respiratory system, reducing weight with retained strength. Other specializations include modification of the forelimbs into wings (with digits either fused or reduced in number), and enlargement of the sternum into a keel-shaped structure to which powerful flight muscles are attached in the majority of flying forms. The skull is light with a kinetic structure to permit movement in the upper jaw, and vertebrae are fused in multiple regions to give rigidity.

Birds have the most efficient respiratory system of any vertebrate, with a flowthrough system that includes air sacs that expand into hollow bones. This enables one-way ventilation of the lungs, allowing for complete oxygen extraction, even at high altitudes with limited oxygen availability. This enables a high metabolic demand for flight with significant respiratory efficiency. Birds are endothermic ("warm-blooded"): the high body temperature they maintain is relatively constant regardless of ambient temperature. Their metabolic rate ranks among the highest in the animal kingdom, required to power flight muscles and fuel their active lifestyle. The insulation that feathers provide helps retain body heat so birds can survive in chilled environments. A fully four-chambered heart in the circulatory system allows for total separation of oxygen-rich and oxygen-poor blood. This efficient circulation, combined with a rapid heart rate, accommodates the high oxygen demands of these muscles during flight. Bird blood has nucleated red blood cells (unlike mammals), and has a higher oxygen-carrying capacity than other vertebrates. Its digestive system is adapted for high-throughput food processing, featuring a crop for storage, a gizzard for mechanical degradation of food (with the help of ingested stones or grit), and a relatively short intestine. Most birds do not possess a urinary bladder; they excrete nitrogenous wastes with minimum water loss in uric acid, an adaptation that decreases body weight. Nervous systemA well-developed brain that has an enlarged cerebellum and cerebrum, accommodating complex spatial navigation, learning, memory, and sophisticated behavior. Sensory systems are extremely specialized, and vision even more so. Birds tend to have acute color vision (often with UV sensitivity), fast visual processing, and high visual acuity. Most species you have good hearing, but smell is more variable in importance over the various groups.

Birds replicate: internal fertilisation; in males no external genital assembly (only in primitive groups such as ratites). All birds lay amniotic eggs with hard, calcified shells, though the size, shape, color and number of eggs vary widely across species. In most species, this care ranges from simple incubation to complex feeding and protection of young. Most species are monogamous for at least one breeding season, and elaborate courtship displays are common. Birds exhibit complex behaviors and have developed advanced modes of communication through songs, displays, and social behaviors. Migration is among the most impressive behaviors of birds, with some species flying thousands of kilometers between breeding and wintering areas while orienting themselves with the help of the stars, Earth's magnetic field and features of the landscape, among other mechanisms.

#### **Classification of Birds**

Modern bird classification recognizes two main superorders within Class Aves:

**Superorder Palaeognathae (Ancient Jaws)** A small group of flightless or weak-flying birds characterized by:

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- · Primitive palate structure
- Simple feathers lacking barbicels (hooks that connect feather barbs)
- · Large eggs relative to body size
- Presence of a penis in males (unlike neognaths)

### This group includes:

- Order Struthioniformes: Ostriches
- Order Rheiformes: Rheas
- · Order Casuariiformes: Cassowaries and emus
- · Order Apterygiformes: Kiwis
- Order Tinamiformes: Tinamous (the only palaeognaths capable of flight)

**Superorder Neognathae (New Jaws)** The vast majority of living birds (approximately 10,300 species) characterized by:

- · Modified palate structure
- · Complex feathers with interlocking barbicels
- Generally smaller eggs relative to body size
- Lack of male penis (with exceptions)

This diverse superorder includes many orders, the major ones being:

### 1. Order Anseriformes (Waterfowl)

- Ducks, geese, swans
- · Broad bills with filtering lamellae
- Webbed feet, waterproof feathers
- Precocial young (hatch in advanced state)

#### 2. Order Galliformes (Landfowl)

- · Chickens, turkeys, pheasants, quail
- · Ground-dwelling with strong legs
- · Short, rounded wings for burst flight
- · Specialized for scratching soil for food

#### 3. Order Columbiformes

- · Pigeons, doves
- · Produce "crop milk" for young
- · Strong flight capabilities

#### 4. Order Sphenisciformes

- · Penguins
- · Flightless with wing-like flippers for swimming
- · Dense, waterproof feathers
- Primarily Antarctic and Southern Hemisphere distribution

#### 5. Order Procellariiformes (Tubenoses)

- · Albatrosses, petrels, shearwaters
- · Tube-like nasal passages for salt excretion
- · Oceanic lifestyle, some covering vast distances

### 6. Order Pelecaniformes

- · Pelicans, cormorants, frigatebirds
- · Fish-eating with various specialized bill types
- Many have throat pouches or gular sacs

**Notes** 



## 7. Order Ciconiiformes

- Storks, herons, ibises
- · Long legs and bills for wading
- · Specialized for wetland feeding

## 8. Order Falconiformes

- · Hawks, eagles, falcons
- · Hooked bills and sharp talons
- · Keen vision for hunting
- · Sexual dimorphism with females larger than males

## 9. Order Gruiformes

- Cranes, rails, coots
- · Diverse group often associated with wetlands
- · Many have specialized territorial calls

## 10. Order Charadriiformes

- Shorebirds, gulls, auks
- · Diverse adaptations for coastal and marine environments
- · Many undertake long migrations

## 11. Order Strigiformes

- Owls
- · Nocturnal with specialized vision and hearing
- · Silent flight adaptations
- · Forward-facing eyes with binocular vision

## 12. Order Caprimulgiformes

- · Nightjars, nighthawks
- · Nocturnal insect hunters
- · Cryptic coloration for daytime camouflage

### 13. Order Apodiformes

- · Swifts and hummingbirds
- · Specialized for aerial lifestyle
- · Rapid wing beat and high metabolic rate

### 14. Order Coraciiformes

- · Kingfishers, bee-eaters, rollers
- · Often colorful with specialized feeding behaviors
- Many nest in tunnels or cavities

### **15. Order Piciformes**

- · Woodpeckers, toucans
- · Specialized bills for drilling or fruit eating
- · Zygodactyl feet (two toes forward, two backward)

### 16. Order Psittaciformes

- · Parrots, cockatoos, macaws
- · Intelligence and vocal learning
- · Strong, curved bills for processing seeds and nuts
- · Zygodactyl feet for manipulating food

## 17. Order Passeriformes (Perching Birds)

• The largest and most diverse order, containing over 60% of all bird species

Notes



- · Songbirds, crows, sparrows, finches, warblers, and many others
- · Specialized vocal organ (syrinx) for complex vocalizations
- · Anisodactyl feet with three toes forward, one backward for perching
- · Diverse ecological adaptations for virtually all terrestrial habitats
- · Complex social behaviors and learning abilities

One major reason for the continued and quite dramatic revisions in most bird classification is that new analysis our relationships led to splits or merges of orders. Molecular and other data have played a particularly important role in resolving phylogenetic relationships of bird taxa that evolved rapidly during their initial radiation. Birds are descended from theropod dinosaurs, and probably the earliest true bird with mixed dinosaurian and avian characteristics was Archaeopteryx (150 million years ago), an early transitional form. The survival of birds through the so-called Cretaceous-Paleogene extinction event that wiped out non-avian dinosaurs opened the door for the evolution of the countless different forms found today.

### Mammalia (Mammals)

### **UNIT 03**

### **General Characteristics of Mammals**

Mammals are the youngest class of vertebrates and have evolved a number of unique features that have allowed for their iconic diversification and ecological success. With around 6,400 species, mammals are found in almost every environment on Earth, from deep oceans to high mountains, dense forests to bare deserts. All mammals, despite this diversity, have certain common features that characterise the class. One key characteristic that sets mammals apart is the existence of mammary glands among females, which produce milk as a form of sustenance for their babies. This enabled extended infant care within a safety envelope that the mother provided during the next few days of neonatal life, thus driving the evolutionary success of mammals. Lactation allows for



more nutritional freedom and reduces the risk of infant mortality, promoting more sophisticated behavioral development. Hair or fur, which consists of keratin, are characteristic of the mammalian integumentary system. Hair has various functions: insulation for thermoregulation, protective coloration, sensory reception (vibrissae or whiskers) and, in some cases, defense or display.

The vertebrate subphylum is one of the most diverse and successful animal groups on Earth known for a backbone or spinal column. From the deep oceans to the highest mountains, vertebrates have managed to evolve to virtually every habitat on our planet over millions of years. This article takes an in-depth look at the five clasess of vertebrates, namely: fishes, amphibians, reptiles, aves (birds), and mammals, including their unique features, evolutionary significance, diversity, and ecological roles, as well as their intricate relationship with humans and the natural environment.

#### **Fishes: The First Vertebrates**

Fishes evolved as the earliest of all the vertebrates some 530 million years ago during the Cambrian period, where the first vertebrate animals can be found in the fossil record. Today, fishes are the largest and most diverse group of vertebrates, with >34,000 described species occupying virtually every aquatic realm on the planet. However, fishes have been incredibly successful organisms due to combinations of their versatility and sets of traits that make them so effective at living in water. Water takes up over 70 percent of Earth's surface, offering a wide and diverse habitat for fishes to diversify and specialize. Everything from the intense demands of the deepest ocean trenches to high mountain streams, from hyper saline environments to freshwater systems, fishes have made some of the most amazing adaptations to survive in these extreme conditions. Because jawless fishes (Agnatha), cartilaginous fishes (Chondrichthyes) and bony fishes (Osteichthyes) each became different evolutionary lines, they were characterized by unique sets of traits contributing to their success. Jawless fishes - represented today by lampreys and hagfishes — are the most primitive living vertebrates. They do not have paired fins, jaws, or scales instead they have a circular sucking



mouth, smooth skin and a cartilaginous skeleton. While these animals have an ancient pedigree and primitive characteristics, they have persisted for hundreds of millions of years thanks to specialized adaptations. They've also evolved a parasitic lifestyle; lampreys latch onto other fish with their rasping tongues and feast on their blood and tissues. Hagfishes, on the other hand, secrete huge volumes of slime when threatened, successfully deterring predators and earning them the moniker "slime eels" — not that they are true eels. The next step nearly 100 million years later were the cartilaginous fishes, including sharks, rays and chimaeras. Jaws, paired fins and increasingly complex sensory systems enabled these predators to rule the ancient seas. Their skeletons are entirely made of cartilage, which, while not as dense as bone, supports and lends incredible flexibility to the body. And sharks, arguably the most recognizable members of the group, have undergone little change in basic design over the past 400 million years — a testament to the successof their evolutionary tweaks. Their sleek bodies, strong tails and multiple rows of teeth that are continually replaced all contribute to their prowess as predators. Sharks have an amazing ability to sense their surroundings that goes beyond their infamous iterations; they also have electroreception that enables them to tap into the minute electrical fields generated by the contraction of an animal's muscles through ampullae of Lorenzini, the organs responsible for this ability that can "feel" the heartbeats of prey buried in sand or otherwise obscured in sensory obfuscation like murked water.

The bony fishes are the largest and most diverse group, making up about 96 percent of all living fish species. The development of a hard skeleton, swim bladder for controlling buoyancy, and operculum covering the gills allowed them to maneuver well, breathe efficiently, and conserve energy. Among the familiar forms in this group are salmon, tuna and cod, but also more exotic fauna like the bioluminescent lure of the deep-sea anglerfish, the prehensile tail and male pregnancy of the seahorse, and the precise jets of water that allow the archer fish to shoot insects down. Gills are among the most important adaptations of fishes to life in an aquatic environment (Bäuerle et al. 2014). Most species pull oxygen from water with the help of gills — specialized organs with large surface areas

and abundant supplies of blood. Water passes over the gills, and oxygen diffuses through filament membranes into the blood stream, where carbon dioxide moves the other way. This counter-current exchange system is remarkably efficient, removing as much as 80 percent of available oxygen from the water. Lungfishes and some catfishes have developed supplemental breathing systems, such as primitive lungs that can extract oxygen from air, so they can endure in oxygenimpoverished waters or even make brief forays onto land. Fish reproduction shows astounding diversity. Most species are oviparous, and they lay eggs that are fertilised outside the body. Others, such as salmon, make epic migrations thousands of kilometers long to arrive at exact spawning grounds. Some, including most sharks and some bony fishes, are viviparous, providing live young after internal fertilization and development. In between these extremes are ovoviviparous species, in which eggs develop in the mother but in the absence of a direct food supply. Parental care ranges from none to much more elaborate nest-building, mouth-brooding or the male seahorse's specialized brood pouch, where embryos develop until they are born. Fishes occupy a multitude of ecological roles, in keeping with their diversity of form. They are primary consumers, secondary consumers, and apex predators, occupying almost every trophic level in aquatic food webs. Algal grazers like herbivorous fishes maintain algal populations on coral reefs, the planktivorous species regulate populations of zooplankton and predatory fishes maintain the balance of aquatic ecosystems through predation (Friedlander et al. Migratory species such as salmon link marine and freshwater ecosystems, bringing nutrients upstream when they return to spawn. Their carcasses enrich stream and forest ecosystems after they die postspawn, and they provide essential nutrients for plants and animals well beyond the ocean. Fishes are a significant part of human-nature interactions in every epoch throughout history: from prehistoric subsistence fishing to contemporary commercial fisheries, aquaculture, and recreational angling, through to keeping ornamental species in aquaria. Global consumption of fish accounts for about 17 percent of animal protein consumed by people, and the fish industry supports the livelihoods of hundreds of millions. But overfishing, habitat destruction,





pollution and climate change now threaten many fish populations and the ecosystems they live in. Sustainable fisheries management and aquatic habitat conservation are pressing needs to sustain healthy and diverse fish populations worldwide.

#### **Early Terrestrial Life: Amphibians**

Amphibians hold an important factor in vertebrate evolution as the first successful land-dwelling vertebrates, reliant on both aquatic and terrestrial habitats for their life cycle. These early vertebrates transitioned to life on land, around 370 million years ago during Devonian period but not without retaining strong links to their watery roots. Indeed, the term amphibian itself literally meaning "both lives" (in reference to their alternate lifestyles of living as juvenile organisms in water and as adults primarily on land), aptly describes their bipedal nature that appears to be an evolutionary development that correlates with the ability to metamorphose their own bodies. Those amphibians we see today fall into one of almost 8,000 species in three distinct orders: Anura (frogs and toads), Caudata (salamanders and newts), and Gymnophiona (caecilians). Although their actual diversity is much lower than that of vertebrates such as mammals, herpetofauna exhibit a wealth of diversity in anatomy, physiology and life history strategies. Among amphibians, frogs and toads are the most numerous and familiar, with specialized jumping legs and wide, flat heads. The lizards shape has remained more or less the same across species, and salamanders and newts still have four equal limbs along their elongated, lizard-like body, and caecilians have shaped up in a slime-like, limbless worm-like way suited for life in the tropical soil, adapted to burrowing. It took deep physiological and anatomical change to make the leap from water to land. And here, we see a transition that leads to the first terrestrial vertebrates (or at least the first vertebrates that can be confidently described as terrestrial) — stronger limbs more capable of supporting their weight against gravity, lungs to supplement or replace gill respiration, and more complex circulatory systems to distribute oxygen throughout the body. These transitional features can still be seen among modern amphibians, most of which

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exhibit a combination of respiratory pathways. Most adult amphibians primarily breathe with lungs, although some water-dwelling salamanders keep their gills through their lifespan, and all adult amphibians also absorb some gasses through their skin, which is kept moist for cutaneous respiration (skin respiration). This secondary respiratory route also lets some salamanders live without lungs altogether and allows many other amphibians to hibernate underwater, absorbing oxygen straight from the surrounding water through their skin.

This pervious dermis, though serving respiratory benefits, also poses considerable challenges to life on land. Reptiles, birds, and mammals have either scales, feathers, or fur along with cornified layers of their skin that minimize the loss of water from their bodies, while amphibians do not have efficient barriers to evaporative water loss. Their smooth, glandular skin remains extremely susceptible to desiccation, restricting most species to moist habitats and nocturnal activity patterns. As a defense against this potential to dry out, amphibian skin has many specialized glands that measure mucus slickness levels and secrete mucus to keep everything wet, as well as various compounds for protection. These secretions vary from mild irritants to potent toxins, such as the infamous batrachotoxins of poison dart frogs that indigenous Amazonian peoples have used to poison blowgun darts when hunting. Amphibians generally reproduce in a manner that mirrors the evolutionary link between aquatic and terrestrial existence. The majority of species reproduce via external fertilization - females deposit gelatinous eggs into water where males fertilize them - harkening back to their fish ancestor. These eggs did not have the amniotic membranes and shells fully developed in reptiles, birds and mammals, leaving them susceptible to desiccation and necessitating aquatic or hypermoist conditions for development. The resulting aquatic larvae, or tadpoles in the case of frogs and toads, undergo dramatic metamorphosis, essentially retooling every body system as they become terrestrial adults. It also entails reorganizing their circulatory system, substantial remodeling of the skull and sense organs, and reconfiguration of the digestive tract (most tadpoles go from herbivory to carnivory during their metamorphosis). But amphibians have also developed a wide range of alternative



reproductive strategies that minimize or eliminate their need for standing water. Some lay eggs in humid terrestrial habitats like leaf litter or bromeliads, and others evolved forms of parental care. Male Surinam toads, say, push fertilized eggs into pockets on the female's back, where they develop directly into tiny adults. Some salamanders and caecilians keep fertilized eggs in the female's body until fully school kids are delivered. The South American marsupial frogs even hold their eggs in specialized brood pouches, almost like the marsupial mammals, lowering risk of predation or environmental stresses.

Ecologically, amphibians are important for both aquatic and terrestrial ecosystems. As larvae, they moderate algal populations and serve as prey to aquatic predators, and as adults control invertebrate communities and are food for many vertebrate predators. Because of their places in food webs, they play key roles as conduits for energy transfer across aquatic and terrestrial systems. Amphibians are also particularly sensitive to shifts in their environment because of their permeable skin and dual-habitat lifestyle, and are widely recognized as important bioindicators - living indicators of ecosystem health. This same sensitivity, though, has played a role in today's amphibian extinction crisis. Since the 1980s, researchers have reported worrying drops in amphibian populations around the globe, and about 41 percent of species are currently at risk of extinction — the largest percentage of any vertebrate group. There are many factors contributing to this crisis, including habitat destruction, pollution, climate change, over-collection for the pet and food trades, and emerging infectious diseases. Chytridiomycosis, caused by the fungal pathogen Batrachochytrium dendrobatidis, has been especially deleterious, resulting in the extinction of species and mass die-offs on a number of continents. This global decline is not just a loss of biodiversity; it's a warning of wider environmental degradation, as the same forces threatening amphibians affect whole ecosystems. For amphibians, conservation has now expanded to include habitat protection, captive breeding programs, disease management strategies, and international policy initiatives. Acknowledging that amphibian diversity must be preserved if we are to adapt at the same time to both the threats we face now and those posed by environmental change, these initiatives focus on providing hope and potential



solutions. As living manifestations of a pivotal evolution transition, amphibians provide unparalleled insights into vertebrate development, physiology and adaptation, while their ecological roles render them non-replaceable members of healthy ecosystems worldwide.

#### **Reptiles: The Kings of Life on Land**

From this basic body plan, reptiles evolved over 320 million years ago in the late Carboniferous period, allowing vertebrates to spread across land in a new and revolutionary way. In contrast to their amphibian forbears, reptiles evolved the amniotic egg - a more elaborate bundle of egg with a protective shell, and specialized membranes and nutritive yolk that made it possible for embryos to develop completely on land without an aquatic phase. This pivotal innovation, together with a water-conserving scaly skin, more efficient lungs, and fully terrestrial reproductive modes, freed reptiles from the shackles of aquatic dependency and allowed them to invade a wide array of terrestrial habitats that were previously closed to vertebrates. The age of reptiles, known as the Mesozoic Era, encompassed the time when these living beings flourished in a wide range of forms and ruled Earth's ecosystems for more than 160 million years. Regardless of being long extinct-though birds, derived from theropod dinosaurs, are technically a kind of dinosaur-they have left a huge history that chronicles their reign of 66 million years alongside the prosperous and at present over 11,000 species of modern reptiles from 4 orders; Crocodilia (crocodiles and alligators), Sphenodontia (tuatara), Squamata (lizards and snakes) and Testudines (turtles and tortoises). The evolution of reptilian skin is a key adaptation to life on land. In contrast to the wet and highly permeable skin of amphibians, reptile skin is composed of three to five layers of keratinized cells organized into the suits, scutes, or plates that provide a very effective barrier to water loss. This waterproof coating gave reptiles the ability to explore into areas of less moisture and be active during the day; times when amphibians would run the risk of desiccation. Periodic shedding of this skin, called ecdysis, allows for growth and removes parasites. In snakes, this phenomenon is especially dramatic: the snake



often sheds the entire skin in one continuous piece as the animal literally slithers out of its old skin. As ectothermic ("cold-blooded") organisms, heat during scale is primarily derived from environmental heat sources to maintain optimum body temperatures, making thermoregulation a challenge for reptiles. One could see this as a drawback, but rather, it is a power-saving adaptation. In contrast with endothermic (warm-blooded) birds and mammals, which require considerable energy to produce internal heat within their body, reptiles are ectothermic and rely on behavioral thermoregulation to take advantage of temperature gradients in their environment, such as basking in the sunlight to warm up, searching for shade to cool down, and adjusting their position and posture to maximize heat absorption or dissipation. That strategy uses about one-tenth the energy of endothermy, enabling reptiles to survive on drastically less food and thrive in low-resource environments where endotherms would starve. Compared to amphibians, the reptilian circulatory system shows multiple refinements that were favoured during evolution, and groups can show quite a range of structures. Unlike mammals which have a four-chambered heart, most reptiles have a threechambered heart-two atria and partially separated ventricle - which helps separate oxygenated and deoxygenated blood to some extent. However, crocodilians have evolved no less than a true four-chambered heart like birds and mammals, convergently evolving in response to the challenges of their semiaquatic predatory lifestyle. Many reptiles can too dramatically alter their metabolic rate based on their environment, entering brumation (winter dormancy) or aestivation (summer dormancy) to endure seasonal extremes.

The reproductive strategies in reptiles highlight their independence from the water. Internal fertilization is inherent to all reptiles, and while the majority of species are oviparous (egg-laying), many species have developed viviparity— or retention of fertilized embryos within the body of the female until live birth. Certain viviparous species, like some skinks and boas, evolve specialized placenta-like organs that facilitate nutrient and gaseous transfer with the mother, resembling mammalian reproduction. Even within egg-laying species, parental care ranges significantly— from giving up after laying eggs to elaborate nest building and

defense, as with crocodilians, which might guard a nest for months and assist hatchlings into the water with care. Reptiles also have special adaptations to the various lifestyles that they lead when sensing the world around them. Most species have excellent vision, and some diurnal lizards have among the best color vision of all vertebrates. Snakes have evolved specialized chemosensory adaptations via their bifurcated tongues and vomeronasal organs (Jacobson's organs) that enable them to "taste" particles in the air, tracking prey with breathtaking accuracy. The pit vipers and some of the boas have specialized heat-sensing organs that can detect temperature differentials as small as 0.001°C, which gives them effectively "infrared vision" so they can hunt in pitch darkness. Some reptiles can even sense Earth's magnetic field for navigation for long-distance movements. Reptilian ecological roles encompass a range of trophic levels and habitat types. Crocodilians and monitor lizards are large predators that regulate prey populations and structure communities. Herbivorous tortoises and iguanas influence plant community composition through selective grazing and seed dispersal. Insect-eating lizards keep invertebrate populations in check, and snakes help regulate rodent populations. Marine turtles move nutrients between oceanic and coastal ecosystems via nesting, and burrow-dwelling species such as gopher tortoises create habitat for many other animals. These many ecological functions make reptiles important members of functioning ecosystems worldwide. Humanreptile relations have been complicated since time immemorial — tinged with fear, reverence, exploitation and fascination. Cultural perspectives on reptiles span the gamut, from serpent gods in ancient cultures to the vilification of snakes in some religions. Historically, reptiles have been hunted for meat, eggs, skins, and traditional medicines for thousands of years. Today, they also sustain large industries, including such ones as pet trade, ecotourism and clinical research. Now, unsustainable exploitation, habitat destruction, pollution, invasive species and climate change threaten around 21 percent of reptile species with extinction, the study found.

Conservation efforts for reptiles need to be multifaceted, including habitat preservation and protection, sustainable harvest regulations, captive breeding initiatives, and reducing negative public perceptions through education. With

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narrow thermal optima, many reptiles are especially sensitive to climate change as it threatens to exceed their adaptive capacity in some areas, which combined with their ectothermic mode of life renders them particularly vulnerable. Increasing temperatures are of special concern for species with temperature-dependent sex determination, including many turtles, as warmer incubation temperatures produce predominantly female hatchlings, possibly resulting in skewed sex ratios and population declines. Nevertheless, and unlike other terrestrial vertebrates, reptiles — which have lived on Earth for the last 320 million years — resisted extinction and adapted to major environmental transitions, such as the last mass extinction event. Their survival in a range of environments speaks to successful evolutionary adaptations and their crucial role in the biological fabric of the planet.

#### Aves: Masters of the Sky

The origin of birds is one of the greatest transformational events within vertebrate history. Evolving from small, feathered theropod dinosaurs some 150 million years ago, birds have radiated into more than 10,500 species that inhabit nearly every terrestrial ecosystem and many aquatic ones on Earth. The evolutionary hallmark of modern birds — feathers — was originally developed by their dinosaurian forebears, perhaps for insulation or display, before being commandeered for flight. This evolutionary recycling, among many other adaptations, has enabled birds to dominate the aerial habitat while conserving and specializing more for the benefits of their lineage as reptiles. Feathers rank high on the list of avian adaptations, unique structures that play many essential roles. In addition to flight, feathers serve functions in insulation, waterproofing, display, camouflage, and, in some cases, tactile sensation and sound production. Their astonishing diversity of form and function ranges from the stiff, flight feathers of eagles to the waterproof contour feathers of ducks to the showy display plumes of birds-of-paradise to the modified bristles around the mouths of insect-catching nightjars. The microstructure of feathers — a central shaft that supports interlocking barbs and barbules — produce a lightweight but strong surface able to create lift while being flexible and replaceable through periodic molting. The avian skeleton is an instance of evolutionary refinement in the direction of flight efficiency. Birds also inherited the hollow, pneumatic bones of their dinosaurian forebears, replacing mass with strength by adding internal struts and fusing certain elements. A keeled sternum (breastbone) provides attachment surfaces where powerful flight muscles can attach, while the furcula ("wishbone") acts as a spring that stores energy during wingbeats. Air sacs, unique to this clade, extended from the lungs, where they accommodated air and penetrated the length of the body, including bone, vastly improving respiratory efficiency. In contrast, birds employ a unidirectional airflow mechanism, allowing for a constant flow of fresh oxygen to the avian lungs even during exhalation, thereby facilitating a highly efficient oxygen extraction process that meets the increased metabolic requirements associated with flight. A unique respiratory system helps sustain birds' endothermic metabolism, keeping body temperatures high and stable, at a mean of 38–42°C (100–108°F), several degrees warmer than most mammals. Even though this adaptive process is energetically expensive, this elevated metabolism allows such sustained high-energy high-energy phenomena such as powered-flight and precise thermoregulation environmental independence. All this, plus good insulation from feathers, means birds can remain active in environments from Antarctic winter to desert summer, paving the way to their global distribution.

These high metabolic demands are supported by an avian heart and circulatory system. Birds have fully four-chambered hearts as do mammals, but usually at larger relative sizes and higher pressures. A hummingbird's heart, for example, can account for as much as 2.5 percent of its body weight (0.5 percent in humans) and beat more than 1,200 times per minute while flying. This dynamic cardio-ventilatory system ensures oxygen and nutrient delivery to muscle tissues functioning at rates that would lead to mammalian muscle failure from oxygen debt. Avian sensory systems are heavily biased toward superb vision. Birds have the largest eyes relative to head size than any other vertebrate group, while visual acuity in some species can outstrip human vision eightfold. Many species are capable of seeing into the ultraviolet spectrum, perceiving patterns invisible to human eyes, such as plumage markings that demonstrate mate quality, or fruiting structures that indicate ripeness. This ability to see even more colors is due to the presence

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of two additional cone types in the retina, and the presence of specialized oil droplets that filter the light that comes into their eyes. Apart from vision, most birds have evolved highly specialized behavioral adaptations to their given ecological niche, such as the remarkable magnetoreception of migratory birds — birds that can detect Earth's magnetic field and use it to orient and navigate in a similar way to how we we use a map — the finely tuned sense of hearing of owls that can locate prey with pinpoint precision in total darkness, or the hyper-sensitivity of tube-nosed seabirds that can scent food sources thousands of kilometers away across otherwise featureless oceans. As setting their general structural differences to practical purposes, the avian brain shows exceptional human capabilities per gram compared to the mammalian brain. The organization is distinct from the layered cortex of mammals, with birds instead evolving enlarged clusters of neurons in regions known as the pallium that perform similar functions to the mammalian cerebral cortex. Recent studies have shown that birds pack a higher density of neurons than mammals per unit volume, with corvids and parrots having actually equivalent neuron densities to primates. Its neural architecture enables many species a suite of higher cognitive functions - tool use, problem-solving, self-recognition, episodic memory, complex vocal learning and more. Corvids (crows, ravens and jays) and psittacines (parrots) show cognitive flexibility in numerous tasks to the same extent as great apes, showcasing convergent evolution of intelligence even with 300 million years of separate evolutionary history.

Birds still lay amniotic eggs, taken from their reptilian ancestors, but those eggs have undergone some radical changes. The calcareous eggshell offers structural support and protection while permitting gas exchange, and most lineages of oviparous species actively warm their eggs while brooding to achieve optimal developmental temperatures. In monogamous species, parental investment begins during incubation and encompasses the extensive care of altricial (helpless) offspring until fledged independence, with both parents contributing resources. This reproductive strategy, though energetically costly, substantially enhances the survival of the offspring relative to the low parental investment more typical of most reptiles. Birds serve ecological functions in nearly every terrestrial ecosystem and many aquatic environments. Birds perform important ecological functions as pollinators, seed dispersers, predators, prey, scavengers, and ecosystem engineers that sustain ecosystem health and services. Hummingbirds pollinate tens of thousands of plant species throughout the Americas, fruit-eating birds scatter seeds in fragmented habitats, predatory birds keep rodents and insects in check, scavengers like vultures remove carcasses from environments that might otherwise spread disease. The decline (or loss) of such avian ecological services can ignite cascading impacts throughout ecosystems, emphasising the importance of birds beyond their intrinsic, beautiful and interesting nature. Historically, human-bird relationships have been complex. They have provided food, represented gods, aided hunting, passed messages, been the subjects of art and literature, served as indicators of the planet's health and become objects of recreation and observation. New economic relationships encompass the poultry industry, ecotourism, bird watching and the pet trade. Unfortunately, human activity has caused the extinction of around 1,200 bird species since 1500, while around 12 percent of birds alive today are threatened. The principal threats are habitat destruction, invasive species, pollution, direct exploitation — and, more and more, climate change, which disrupts seasonal timing, changes habitat suitability and alters food availability.

He holds a bachelor's degree in courses on conservation biology, ecology, evolutionary biology, behavior, veterinary science and wildlife management as well as research degrees in nature conservation. The predictably high density of birds and their well-documented ecology make bird flagships valuable to broader conservation efforts; protecting bird habitats tends to protect many other sympatric species. The successful adaptation of birds over a 150 million year time span across changing environmental conditions is evidenced by their diversity, abundance and global distribution. The only surviving descendants of the dinosaurs, birds are at once ancient lineages and high-tech evolutionary trials, repackaging the demands of flight into a medium for immense diversification across ecological niches, geographic realms and life history strategies.

#### Mammals: The Age of Parental Investment



The Late Triassic emergence of mammals some 200 million years ago added a vertebrate class characterized by a niche suite of remarkable adaptations, comprising hair insulation, mammary glands to nurioush offspring, heterodont dentition specialization, increased thermoregulation via endothermy, and an enormously increased brain to provide behavioral capacity. Despite being competitive only at the very small end of the food chain in the Mesozoic Era, when they were outnumbered by a vast array of reptilian fauna, mammals underwent a spectacular diversification after the mass extinction event that wiped out non-avian dinosaurs 66 million years ago, giving rise to some 6,400 extant species as small as the Etruscan shrew, weighing just 2 grams, all the way up to the blue whale, which can exceed 150,000 kilograms in weight-the largest animal ever to have inhabited our planet. The defining feature from which all mammals derive their name — mammary glands — is an evolutionary innovation that is of exceptional importance. These specialized exocrine glands produce milk, a complex substance comprising proteins, lipids, carbohydrates, minerals, vitamins, and bioactive compounds precisely adapted to the nutritional needs of the developing infant. Milk composition differs dramatically between species in line with varied developmental strategies. Marine mammals have milk with as much as 50 percent fat, promoting fast growth and insulation in aquatic media, while primates secrete relatively dilute milk over long periods, facilitating slower growth and longer learning. Aside from nutrition, milk has antibodies that provide passive immunity for young, as well as compounds that impact gut microbiome development. With lactation providing this nutritional head start, mammals have been able to pursue a diversity of reproductive strategies and a notable investment in parental care of offspring survival.

As an insulator, hair captures air near the body and forms a thermal barrier between skin and surroundings. The composition of hair differs greatly among species, ranging from the fine, dense underfur of arctic mammals to quills in porcupines to the sensitive whiskers (vibrissae) found in many predators to the modified scales on pangolins. Certain species (e.g., cetaceans or whales and dolphins) secondarily lost a majority of their body hairs for adaptation to the aquatic environment, mammals, hair, too, plays important roles in camouflage, species recognition, sexual display, and physical protection. Therefore, mammalian skin, with its pool of sweat glands, is an adjunct to hair thermoregulation. These specialized structures are especially numerous in primates and are highly developed in humans, secreting water and electrolytes that evaporate from the surface of the skin, efficiently dissipating excess heat. This process of evaporative cooling enables mammals to remain active under temperature extremes that would drive other vertebrates to seek shelter. Additional specialized skin glands produce oils that waterproof hair and skin, pheromones to promote chemical communication, and defensive compounds to deter predators.

The mammalian skeleton, though preserving the anatomy of the vertebrate bauplan, shows adaptations to multiple locomotor strategies. Appendicular skeletons are highly plastic and evolutionary modification can reshape skeletal elements into structures that range from the running limbs of horses where lateral digits have been reduced, to digging forelimbs in moles, to bat wings and seal and whale flippers. The vertebral column exhibits regional specialization with separate cervical, thoracic, lumbar, sacral, and caudal regions. The mammalian skull has evolved to house a larger brain and sites to attach powerful jaw muscles, and it fits specialized heterodont dentition - teeth that are differentiated into incisors, canines, premolars and molars and allow for precise processing of food before swallowing. This dental specialization is a reflection of mammals' high metabolic needs. Mammals are endotherms, whose high and relatively constant body temperatures are sustained through internal heat generation, and as a result, they demand much more energy per unit body mass than ectothermic vertebrates. Specialized dentition coupled with compartmentalized digestion allows for efficient food processing that meets the energetic demands. Herbivorous mammals have developed especially sophisticated digestive strategies, such as the multi-chambered stomachs of ruminants, and specialized cecums in many rodents and lagomorphs, often containing symbiotic microorganisms that break down cellulose from plant materials into metabolites, demonstrating another instance in which mutualistic relationships have allowed

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further expansion of available ecological niches. Mammalian respiratory system promotes higher metabolic rates via increased efficiency. The diaphragm — a muscular structure unique to mammals that separates thoracic and abdominal cavities and enables deeper, more controlled breathing — is another reason our lung capacity is much greater relative to our sizes. Within the lungs are millions of alveoli — microscopically small air sacs encircled by capillaries that create a vast surface area for gas exchange. This improved respiratory efficiency combines with a fully developed four-chambered heart and double circulatory system that separates oxygenated from deoxygenated blood, allowing for maximal delivery of oxygen to tissues.

The hallmark of mammals is arguably the expanded cerebral cortex, a brain region that enables sophisticated cognitive behaviours, learning, and flexible behaviour. Mammals tend to have greater brain-to-body mass ratios than other vertebrates, with primates, elephants, and cetaceans showing especially high encephalization. This neural faculty underpins complex sensory processing, motor control, social cognition, problem solving, and in some, self-awareness, tool use, culture, and language ability. The mammalian brain further controls sophisticated endocrine systems mediating growth, metabolism, reproduction, and stress responses, enabling graduated physiological changes in response to environmental challenges. Thus, mammalian sensory adaptations reflect both specialization and integration. Mammals developed and refined certain senses to spectacular degrees depending on their ecological niche, but all tetrapods share the basic sensory modalities—vision, hearing, smell, taste, and touch. Nocturnal animals, for instance, have heightened senses of smell, hearing, and touch to make up for their scarce vision in the dark. Echolocation: Bats and toothed whales independently evolved elaborate echolocation systems that form detailed acoustic images of surroundings. The eyes of prey species are usually located on the sides of their faces, giving them a panoramic field of view for detecting predators, whereas the eyes of predators are faced forward, which gives them very good depth perception for hunting purposes. All these different types of sensory inputs, processed through the expanded, larger mammalian

brain, enable mammals to form complex mental representations of their surroundings. Parental investment shows a gradient across mammalian reproductive strategies. Monotremes (platypuses and echidnas) have retained the ancestral egg-laying condition, but they incubate their young and nurse them after they hatch. Marsupials give birth to very immature offspring that continue their development attached to mammary glands, sometimes within a protective pouch. Placental mammals, which make up about 94 percent of all extant mammalian species, nurture embryonic development via a complex placenta that allows the exchange of nutrients, gases and wastes between maternal and fetal bloodstreams. This prolonged internal maturation allows placentals to give birth to relatively advanced young capable of more elaborate behaviors soon after birth. Extended lactation is a signature of mammalian reproduction, and social learning—helping teach generations how to survive—is another important form of maternal investment common across all three groups.

Mammals are ecologically important in almost all terrestrial and many aquatic ecosystems. Mammals impact community structure and ecosystem function at multiple levels as primary consumers, predators, seed dispersers, soil engineers, and habitat modifiers. Even in savanna ecosystems, for example, herbivores such as elephants help prevent woodland encroachment. These apex predators such as wolves suppress prey populations and trigger trophic cascades that cascade through many other species. Through dam-building, beavers create wetland habitat, converting the hydrology and biodiversity of landscapes. Fruiteating bats and primates are seed dispersers that provide resistance and resilience to plant community regeneration, helping to paint the landscape. Mammals serve diverse ecological functions and are considered key species in many ecosystems, where their presence or loss can have far-reaching consequences for biodiversity and ecosystem services. Human-mammal relationships encompass utilitarian, ecological, and emotional domains. As our closest evolutionary relatives, mammals have historically and up to the present continue to provide humans with food, clothing, transportation, labor, companionship and research models. Mammal domestication, which started around 15,000 years ago, had an enormous impact on human civilization, with dogs, cattle, horses and sheep MATS Center For Distance & Online Education, MATS University

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becoming critical to the agricultural development and the evolution of culture. Mammals, today, have their most prominent role in conservation-tigers, gorillas and whales, among others, use their charismas as the figureheads of habitat protection and biodiversity preservation. Sadly, a human causing including habitat destruction, overhunting, pollution, and climate change threaten about 25 percent of mammalian species to extinction, with larger species particularly vulnerable because of their habitat and key population pressure, lower reproductive rates, and historical hunting pressure. These approaches have resulted in conservation strategies that increasingly recognize the importance of protecting habitat connectivity and ecological processes over large spatial extents, and that consider human needs by utilizing sustainable practices for areas hosting the greatest diversity of native mammals. Conservation success often hinges on understanding the complex socioecological and physiological needs of mammals, along with the social, economic, and political drivers of human impacts on wildlife populations. And as our scientific knowledge of mammalian biology continues to grow, so too does our understanding of their ecological importance, evolutionary significance, and value in their own right as sentient beings with whom we share a distant common ancestor, and a potential common fate here on earth.

### SELFASSESSMENT QUESTIONS

## Multiple Choice Questions (MCQs):

- 1. Which of the following is NOT a characteristic of chordates?
- a) Presence of a notochord
- b) Dorsal hollow nerve cord
- c) Ventral solid nerve cord
- d) Pharyngeal gill slits
- 2. The **theory of chordate origin** that suggests chordates evolved from echinoderms is called:

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- a) Hemichordate theory
- b) Neotenic theory
- c) Echinoderm theory
- d) Protochordate theory
- 3. Which of the following chordates is considered **jawless**?
- a) Sharks
- b) Lampreys
- c) Frogs
- d) Snakes
- 4. Amphibians are adapted for:
- a) Only aquatic life
- b) Only terrestrial life
- c) Both aquatic and terrestrial life
- d)Aerial life
- 5. Which vertebrate group is characterized by **amniotic eggs**?
- a)Amphibians
- b) Fishes
- c) Reptiles
- d) Jawless vertebrates
- 6. Birds belong to which class?
- a) Reptilia
- b) Aves



c)Amphibia

d) Mammalia

7. Mammals are characterized by:

a) Cold-blooded nature

b) Presence of mammary glands

c) External fertilization

d) Oviparous reproduction only

8. The main difference between reptiles and amphibians is:

a) Reptiles lay eggs, while amphibians do not

b) Amphibians live only on land

c) Reptiles have dry, scaly skin, while amphibians have moist skin

d) Amphibians have a four-chambered heart

9. The main function of a notochord is:

a) Digestion

b) Support and movement

c) Reproduction

d) Excretion

10. Which class of vertebrates first evolved the ability to fly?

a)Amphibians

b) Reptiles

c) Birds

d) Mammals

#### **Short Questions:**

- 1. Define chordates and mention their key characteristics.
- 2. What are the three fundamental features of all chordates?
- 3. Explain the significance of the notochord in chordates.
- 4. How do chordates differ from non-chordates?
- 5. What is the protochordate theory of chordate origin?
- 6. Name the five main vertebrate classes and give one example of each.
- 7. Differentiate between jawless fish and cartilaginous fish.
- 8. What is the importance of fossil evidence in understanding the origin of chordates?
- 9. What are amniotes and how do they differ from amphibians?
- 10. Give an example of a living fossil among chordates and explain its significance.

#### Long Questions:

- 1. Explain the origin of chordates with reference to major theories.
- 2. Describe the general classification of vertebrates with key features.
- 3. Compare the skeletal structures of fishes, amphibians, reptiles, birds, and mammals.
- 4. Discuss the adaptations of chordates for different modes of life (aquatic, terrestrial, aerial).
- 5. What is the relationship between chordates and non-chordates? Provide examples.

## INTRODUCTION TO CHORDATES

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- 6. Explain the evolutionary significance of amphibians in the transition from water to land.
- 7. Discuss the major adaptations in reptiles that enabled them to become fully terrestrial.
- 8. Describe the adaptive radiation of mammals and explain why they dominate modern ecosystems.
- 9. How do birds differ structurally from reptiles despite their evolutionary connection?
- 10. What are the key anatomical differences between mammals and other vertebrates?



#### MODULE 2

#### **CHORDATE II**

#### 2.0 Objective

- To understand specialized respiratory adaptations in fishes.
- To analyze parental care strategies in fishes and amphibians.
- To differentiate between poisonous and non-poisonous snakes.
- To study migration and flight adaptations in birds.

#### **UNIT 04**

#### Fishes: Accessory Respiratory Organs and Parental Care

Fish have evolved diverse respiratory adaptations and parental care strategies that allow them to thrive in a range of aquatic environments. Although gills are the main respiratory organ in many fish, many fish also have evolved secondary mechanisms to extract oxygen from their environment, especially in low-O2 environments. These modifications to their respiratory systems and their extensive parental care strategies are two of the most ingenious evolutionary adaptations fish have to make it through adversity as individuals and to pass on their genetic material to future generations.

#### **Divergent Evolution of Respiratory Physiology in Fish**

#### Primary Respiratory Structures — Gills

Gills are the primary respiratory organ in fishes, which are comprised of filaments that have tons of lamellae that provide them with an extremely high surface area for gas exchange. Within the opercular cavity, these fragile structures are arranged on gill arches. In teleost fish, there are four pairs of gill arches, containing many filaments. The gill filaments include networks of

#### **CHORDATE II**



capillaries through which dissolved oxygen in water diffuses into the blood and carbon dioxide diffuses out. Gill respiration efficiency is affected by different factors like temperature, oxygen content, proprioceptive characteristic, and ventilation rate. Fish take an active molats retreat helping flow across their gills, coordinated movements of the buccal and opercular cavities create directional water flow and a pressure differential that support continuous ventilation. This buccal-opercular pump mechanism is illustrated by the expansion of the buccal cavity that draws water in through the mouth, followed by its contraction with opercular expansion to push water across the gills and out of the opercular openings. The gill epithelium contains specialized cells, chloride cells (also known as ionocytes), that play a role in ion exchange and maintain osmotic balance, thus permitting adaptation to different aquatic environments. These cells actively absorb ions in freshwater fish to compensate for the constant diffusion of water into their bodies, and release ions in marine species to make up for osmotic loss of water to the environment. In this vein, gills serve both a respiratory and an osmoregulatory function, enabling them to function as very efficient multifunctional organs that allowed fish to thrive in many different aquatic environments over their long evolutionary history.

#### **Cutaneous Respiration**

Oxygen absorption through skin, known as cutaneous respiration, Though not a typical means of respiration for most fish, this is an important auxiliary source of oxygen, especially among species that reside in low-oxygen habitats. The amount of gas exchanged through cutaneous respiration is therefore largely dependent on skin thickness, vascularization and the surface area-to-volume ratio of the fish. Small fish with high surface area-to-volume ratios, like many species of minnows, are able to get a large part of their oxygen needs through their skin. The process is especially essential for juvenile fish, which typically have thinner skin and a much higher metabolic need per unit size. In certain species, cutaneous respiration enables them to survive brief excursions in the air or in stagnant, hypoxic waters. Overevolution of specialized structures for



cutaneous respiration has occurred in part of fish families. Scaleless catfish (family Clariidae) have highly vascularised skin that greatly increases O2 absorption. Likewise, many eel species have thin and highly permeable skin, allowing for significant cutaneous gas exchange that supplements their gill respiration. These modifications are especially beneficial when these fishes migrate over land or live in mud burrows, making contact gill respiration difficult.

#### **Buccopharyngeal Respiration**

In buccopharyngeal respiration, gas exchange occurs across the richly vascularized epithelium lining the mouth and pharyngeal cavity. This form of respiration acts as an alternative oxygen uptake mechanism for some fish taxa, especially those that occasionally come out of water or inhabit hypoxic habitats. The process usually consists of a fish coming to the water surface, borrowing some air, that is retained in the buccopharyngeal cavity where oxygen diffuses through a highly perfused epithelium into the blood. The opercular openings or mouth expel this air. In these species, the buccopharyngeal cavity shows adaptations such as increased vasculature, folds of epithelium to maximize surface area, and a muscle array that permits prolonged residence of air. A classic example of fish form buccopharyngeal respiration is mudskippers (family Oxudercidae). These amphibious fish spend long stretches on exposed mudflats in low tide, from which they draw oxygen from air trapped in their massively developed buccopharyngeal chambers. Other examples are some loaches (family Cobitidae and weatherfishes family Botiidae) that sometimes gulp air from the water surface, particularly when dissolved-oxygen level drops. Suprabranchial chambers lined by respiratory epithelium in the snakehead fishes (family Channidae) enable them to rise to the surface and breathe air for extended periods in stagnant, low-oxygen water.

Air-Breathing Organs in Fish: The adaptation of some fish to breathing air is well established; over 300 species, including well-known examples such as lungfish (Dipnoi) and Clarias catfish (Clariidae), have evolved specialized air-breathing organs for extracting oxygen directly from atmospheric air, allowing these fish to

#### **CHORDATE II**



survive periodic anoxia in shallow waters. Also, these structures are some of the most well-known examples of convergent evolution, for they've evolved in multiple lineages of fish independently.

Lungs and Lung-like Organs: True lungs arose in ancient fish lineages as well and remain today in primitive groups such as the lungfishes (Dipnoi). These structures are paired, sac-like, and open into the pharynx through a pneumatic duct and have highly vascularized inner surfaces allowing for gas exchange. (African lungfish (Protopterus sp. has paired lungs with lots of internal subdivisions that maximize respiratory surface area. During drought, these fish may burrow into mud, forming a mucus-lined cocoon and depending exclusively on aerial respiration until waters return. The South American lungfish (Lepidosiren paradoxa) and the Australian lungfish (Neoceratodus forsteri) also use their lungs to supplement their breathing but the Australian type does not depend on breathing air as much. Bichirs (Polypterus sp.) have paired ventral lungs opening into the pharynx enabling them to inhabit poorly oxygenated waters. Their capacity to exploit aerial-derived O2 was probably fundamental to the archaic origins of vertebrate air-breathing. Some fish, such as the primitive bowfin (Amia calva), possess a gas bladder that serves as a respiratory organ; they have a pneumatic duct leading from the gas bladder to the pharynx for this purpose.

**Modified Swim Bladders:** Numerous teleost fish species have adapted their swim bladders to serve as additional respiratory structures. In contrast to hydrostatic swim bladders, these respiratory gas bladders are richly vascularized and can communicate with the digestive tract via a pneumatic duct that enables gas intake. They are generally arranged with internal compartmentalization that maximizes the surface area available for gas exchange. The fish known as arapaima (Arapaima gigas) from the Amazon basin have a rich vascularized swim bladder that acts almost like a lung. It's a giant fish that needs to break the surface frequently to take in air, its gills alone can't sufficiently extract enough oxygen from the oxygen-poor water it calls home. The tarpon (Megalops

atlanticus) has also evolved a modified gas bladder for aerial respiration, which is again useful for living in oxygen-poor estuarine conditions.

**Suprabranchial Chambers:** Suprabranchial chambers, to which a number of fish families have convergently evolved, are specialized compartments above the gill cavity, lined with respiratory epithelium. These chambers allow fish to contain air near blood vessels, allowing oxygen to diffuse into the blood. The climbing perch (Anabas testudineus) bears labyrinthine organs, maze-like formations derived from modified gill plates, located within suprabranchial chambers. These extremely vascularized structures allow the fish to extract oxygen from swallowed air, permitting them to survive in stagnant waters and even sporadic overland migrations. The kissing gourami (Helostoma temminkii) has a similar modification with a suprabranchial organ formed from modified gill arches that allows it to breathe out of the water.

#### **Specialized Adaptations of the Digestive System**

Some fish use parts of their digestive tract for breathing. The best known is the electric eel (Electrophorus electricus), obtaining around 80% of their oxygen via a highly vascularised posterior part of the oral cavity. This fish comes to the surface routinely to gulp air into this specialized respiratory epithelium. Some species of catfish, such as members of the family Loricariidae, use intestinal respiration in which the posterior portion of the digestive tract has been modified to become vascularized. These fish gulp air, which travels through the digestive tract where oxygen is assimilated, after which the deoxygenated air is expelled through the vent.

**Dendritic Organs:** Some catfish species (Clarias batrachus and relatives) have branched dendritic organs formed by extensions of gill arches into specialized suprabranchial chambers. These highly vascularized branching structures greatly enhance the surface area for aerial respiration. This adaptation enables these fish to survive in waters with critically low oxygen levels and, during the rainy season, to walk short distances across land, bridging the gap between body of water.

#### **CHORDATE II**



**Parental Care in Fishes:** For fish, parental care behaviors are a major investment in offspring survival, frequently at significant energetic costs to the parents. These behaviours have evolved independently in multiple fish lineages and differ widely in the intensity and duration, from simple nest guarding to elaborate mouthbrooding.

#### The Types of parental care in fishes

Substrates Spawning and Nest Building: During this extensive time frame, there is evidence that several species engage in substrate spawning behaviors, depositing their eggs on specific or even prepped surfaces. This is a simple kind of parental investment that makes offspring more likely to survive. Nest-building behavior can vary from minimal clearing of substrate areas to complex structures constructed from variable materials. The male three-spined stickleback (Gasterosteus aculeatus) constructs a tunnel-like nest of plant material held together by kidney secretions and patrols the nest, fanning water over the eggs with his fins to circulate it. This ensures sufficient oxygenation and averts fungal infections. Male largemouth bass (Micropterus salmoides) excavate shallow depressions on lake or river bottoms in which the females lay eggs, and then guard these nests from predators until eggs develop into free-swimming fry. Some of the most extreme nest builders are the Tanganyikan cichlids of the genus Lamprologus, which build and maintain complex rock structures as breeding sites. These structures not only serve to deter potential predators from eating the eggs but can also establish territories that can be maintained across several breeding seasons. And many wrasse species build bubble nests, mixing mucus secretions with air at the water surface to create floating egg storage containers that male fish carefully guard.

**Egg Guarding:** Active egg guarding is a widespread strategy of parental care in several lineages of fish. Typical guarding behaviours include chasing away would-be predators and stirring the water around the eggs, a process known as aeration, to avoid hyphae being suspended and infecting the eggs. Individuals of a species of fish called bluegill sunfish (Lepomis macrochirus), for example, are
known to aggressively defend nest territories against predators of their eggs, using both displays to frighten potential egg predators and direct attacks against them. They also flutter their fins over the nest to draw fresh, oxygen-rich water over the embryos as they develop. Male damselfish also aggressively defend territories that contain egg masses, attacking potential predators that are much larger than they are when they are detected near the nest. A common reproductive strategy among cichlids is biparental guarding of eggs deposited on flat substrates. The fish take turns protecting the nest closely, so while one parent stays on guard, the other takes the opportunity to feed. They regularly "mouth" the eggs, physically removing dead eggs and debris, and will fan water across the clutch through fin oscillations. Many fish exhibit this behavior, including the convict cichlid (Amatitlania nigrofasciata), for example, which successfully protect their eggs and free-swimming fry from would-be predator fish.

**Brood Pouch Incubation:** The offspring of some fish groups develop inside specialized structures where they become protected and receive physiological support. The seahorses, pipefishes and seadragons (family Syngnathidae) have the most elaborate brood pouch structures (of all fish). In seahorses (genus Hippocampus), the male has a specialized ventral brood pouch into which females deposit eggs following a complex courtship ritual. Once sealed within the pouch, the developing embryos become embedded in specialized tissues that supply them with oxygen and nutrients and remove waste products, operating much like a mammalian placenta. During this time, the male's body experiences a lot of physiological changes that regulate osmotic conditions and immunological protection. Following a gestational period of 10 days to 6 weeks (depending on the species and the water temperature), the male goes through labor-like contractions, releasing fully formed, independent juvenile seahorses. Pipefishes (subfamily Syngnathinae) brood pouch complexity varies considerably, from a simple ventral site of attachment to a fully enclosed brood pouch. In the weedy seadragon (Phyllopteryx taeniolatus), males carry their eggs on specialised areas of the tail, rather than in an enclosed pouch. All of these varying structures for carrying offspring involve some combination of

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protection and physiological support while they are developing and presumably enhance offspring survivability.

Mouthbrooding: Mouthbrooding is arguably one of the most specialized fish parental care strategies; it refers both to the incubation of eggs and (occasionally) fry in the buccal cavity of a parent fish. This behavior has independently evolved in multiple fish families, such as cichlids, catfishes and cardinalfishes. Maternal mouthbrooding is practiced by some African cichlids (tribe Haplochromini), including the showroom eye-catching fish from Lakes Malawi and Victoria. Females gather eggs in their mouths during or shortly after fertilisation, and incubate them for periods usually around 2-3 weeks long. While incubating, the female normally does not eat, which is a serious metabolic sacrifice. Benefits inside the buccal cavity include protection from predators and a steady flow of oxygen-rich water. Even after it hatches, fry continue to retreat to their mother's mouth as a safe haven, entering their mother's mouth for protection when threatened. A type of mouthbrooding where eggs are carried in the mouth of the father is common in some fish groups (e.g. cardinalfishes [family Apogonidae]). Male cardinalfish carry clutches of fertilized eggs into their mouths, brooding and providing shelter for developing embryos, while the females are free to feed and energetically recuperate. The male jawfish (family Opistognathidae) also broods eggs in his mouth, and on occasion "turns" them by expelling and swallowing them to optimize breathing. Biparental mouthbrooding is much less common but does happen in some species of cichlid including Sarotherodon galilaeus, in which both parents rear the eggs by taking turnsbrooding. In this way, each parent can intermittently feed while the chicks remain continuously protected.

**Skin Mucus Feeding:** An extreme example of the provision of specialized skin mucus as fry food has been documented, although the carer was found to be dead when they were killed and eaten by the fry. Certain species of cichlids, specifically sympatric ones of either the genus Symphysodon, commonly known as discus fish, and Geophagus, best showcase this behavior. The mucus produced by adult discus fish on their body surface is the primary food source for their fry

during the first weeks of life. This mucus contains key nutrients, growth factors, and antibodies to support both development of the offspring and immune system function. Once hatched, the fry actively feed on this mucus by grazing, or nibbled, the sides of their parents. The parents can pivot their body position to allow for this feeding and show incredible tolerance to the habitual nibbling. Mucus analysis shows it includes both proteins and lipids that feed the fry, as well as leukocytes that help shield the fry from infections. The behavior has been documented in other genera of cichlids and some marine reef fishes and is a fascinating intermediate of egg guarding and more complex provisioning behaviors. Not only does this strategy ensure nutritional provision, but it also provides the beneficial microbiota and immune factors crucial to offspring at these key developmental stages.

### **Strategies for Parental Care**

Mouthbrooding in Cichlids: The cichlid family (Cichlidae) has some of the most sophisticated mouthbrooding behaviours of any fishes, with elaborate adaptations that facilitate offspring survival. Thus, there are notable examples of this strategy in cichlids, particularly among the Lake Malawi and Lake Tanganyika haplochromines. The mouthbreeding Tropheus moorii native to Lake Tanganyika has developed specialized courtship and spawning strategies to maximize fertilization while minimizing egg loss to predation. The female drops few, relatively large eggs into the water, scoops them up in her mouth, approaches the male, who then displays his anal fin covered with many small specialized egg-shaped spots. These egg-dummies encourage the female to try to gather them up, which prompts the male to release sperm that fertilizes eggs she has already captured in her mouth. This clever design allows for high fertilization rates while maintaining egg protection. Since the embryos will be sheltered in the female's buccal cavity during the incubation period, which lasts about 3 weeks, its buccal cavity shows physiological alterations, nodular skin cysts develop in the buccal mucosa (which becomes highly vascularized) and/or epithelial modulations that favor passive gas exchange to the developing embryos. [Her feeding is severely diminished or halted completely, which is a significant energy trade-off.] The buccal cavity is a highly oxygenated environment, MATS Center For Distance & Online Education, MATS University

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allowing the embryos to develop rapidly, while being sheltered from predators improves survivorship. Following hatching in the mouth, she continues to provide protection by allowing fry to swim into her mouth when the threat of danger arises. They develop inside the parents' mouth, but only for a very short time; eventually, as fry, they spend increasingly longer periods outside of the parents mouth until they \$Q\rightarrow \infty\$. Root-sucking fishes, e.g. Cyphotilapia frontosa, even display repeated retrievals of free-wandering fry, prolonging protection for weeks post-hatching.

### Nest Building in Sticklebacks

The three-spined stickleback (Gasterosteus aculeatus) has served as a model organism to study the evolution and genetics underlying parental care behavior, including nest building and egg guarding. When the breeding season arrives, male sticklebacks transform morphologically, sporting bright red throats and blue eyes that aid in territorial displays and attracting mates. In preparation for the breeding season, when testosterone and 11-ketotestosterone levels peak, males stake out territories and build nests made of plant material, algae, and debris from the surrounding area. The process of nest building is a stereotyped sequence, starting with the excavation of a shallow depression in the substrate through vigorous swimming movements. The male then carries plant materials in his mouth to the nest site and arranges them using careful head movements and secretes a glycoprotein called spiggin that is produced in his kidneys that works as an adhesive to hold materials together. This produces a tubelike structure with clear entrance and exit holes. Once the nest is completed, the male courts females with a distinctive zigzag dance, attracting receptive females to the nest. As soon as a female enters and lays eggs, the male rushes in to fertilize them, subsequently drives the female away, and takes on all parental duties. He keeps the nest clean, repairs any damage and constantly pumps oxygen into the developing embryos by briefly fanning faint pectoral fins over the surface of the brood, a behavior that takes up to 30% of his time during incubation. Studies have demonstrated increased fanning rate based on oxygen needs, suggesting this is a plastic change based on what the embryo requires. Males also guard



the nest from egg eaters and remove dead or sick eggs to help limit the spread of pathogens. Paternal care continues for a few days, as the male fishes out any stray fry and returns them to the vicinity of the nest until they are developmentally advanced enough to disperse independently.

Among these fishes, the anabantoids, or labyrinth fishes, have developed a complex paternal investment strategy that features the building of floating bubble nests. This is a group of species that includes popular aquarium fish like siamese fighting fish (Betta splendens) and paradise fish (Macropodus opercularis), and which build bubble nests at the water surface and use them to store eggs and developing embryos. Male Betta splendens build nests by gulping in air and expelling it at the water surface as bubbles get stabilized by oral mucus. These bubbles are arranged according to species-specific patterns that can range from simple clusters to complex floating platforms, which are reinforced with plant materials. Courtship, the most intense part of the construction process, serves as a period where males will spend a lot of time caring for and developing their nests. Spawning then takes place under the bubble nest after courtship displays such as finnage spreading and color manefestation. Eggs and sperm are released simultaneously during the embrace and fertilised eggs drift slowly downwards. The male promptly gathers these eggs into his mouth and pastes them inside the bubble matrix, where they stick because they have a slightly sticky coat. This placement gives the growing embryos access to the oxygen-rich surface layer of water and provides protection from aquatic predators. After casting their eggs, the female is usually chased away, and the male takes over completely taking care of the nest and guarding the offspring. He constantly repairs the nest, keeping any fallen eggs and putting them back into the bubble structure. The male protects the territory from intruders and ensures circulation of oxygen around the eggs by creating gentle currents with his fins. The fry remaining associated with the bubble nest and the male will retrieve any strays until they are developed enough to disperse.

#### Parental Care in the Mouth-brooding Ariid Catfishes



Remarkable paternal mouthbrooding behaviours in marine catfishes of the family Ariidae exemplify the extreme energetic investments that some fishes make in the care of offspring. In some species like Galeichthys feliceps, males brood relatively few but extremely large eggs (ovum) in buccal cavities for an extended duration. The breeding cycle starts with the female releasing a small number of noticeably large eggs (usually 20-50) which can grow to a diameter of up to 15 to 25 mm and are considered to be amongst the largest of all known fish eggs. After external fertilization, the male scoops the eggs up with his mouth and keeps them there for the duration of their development. This oral incubation period is exceptionally long, anywhere between 8-11 weeks depending on the species and water temperature, one of the longest reported incubation periods in teleost fishes. While the male broods the female, which can take two weeks or up to (the record) 30 days, he feeds very little, and eventually not at all. Extensive weight loss and muscle catabolism have been demonstrated in brooding males with concomitant liver glycogen depletion, revealing the high metabolic expense associated with this form of parental investment (Hahn et al., 2003, Huber et al., 1997). However, prior to brood rearing, there are also changes from the calyx morphology, where the epithelium structure of the roof of buccal cavity undergoes drastic and morphogenetic changes and incorporates more blood vessels, promoting oxygen diffusion to the embryos being brooded. The maximum per egg YS levels are enough to sustain not just embryonic development but also subsequent growth until release, and thus the release of well-developed juveniles—not weak larvae. After curing for this long period, when they are ultimately released, the young catfish can be up to almost half grown, and are ready to swim actively and avoid predators. This strategy substantially enhances the offspring's chances of survival but at a significant energetic expense of the paternal caregiver.

## Adaptations for Respiration and the Evolution of Brood Care

The development of accessory respiratory organs in fish and the evolution of various forms of parental care can be seen as two most interesting examples of how adaptations to environmental constraints and speciesspecific reproductive

strategies have contributed to improving the chances for a successful brood. Such traits have repeatedly evolved independently among fish lineages, suggesting they are adaptive. Air-breathing in fish is associated with colonization of tropical freshwater habitats that exhibit seasonal hypoxia. In these habitats, warmer temperatures decrease the amount of oxygen carried by the water while simultaneously increasing fishes' metabolic demands for oxygen. Moreover, seasonal drying of the water column and the widely fluctuating water level create strong selection for individuals capable of harvesting molecular oxygen from the atmosphere. Here, comparative studies across air-breathing fish lineages show general convergences in function but also diverse structural implementations. The lacy organs of the anabantoids, the modified swim bladders of the osteoglossids and the dendritic organs of the clariid catfishes are other examples, each conducting similar gas exchange functions, yet all contrasting greatly with one another in the anatomical origins and structures of their components. These patterns indicate that selection for air-breathing capacity repeatedly targeted the evolution of alternative ancestral architectures across clades confronting analogous ecological obstacles. According to the study, evolution of air-breathing adaptations occurred in freshwater rather than marine environments, because of more stable oxygen availability in oceans. The transition to air-breathing is fundamentally a key evolutionary innovation that may have eventually enabled vertebrate colonization of the land, and groups of fishes, such as the lungfishes and lobe-finned fishes, were a key evolutionary bridge in this transition.

#### **Evolution of Parent Care Behaviors**

The evolution of parental care senescence in fish has adapted to ecological pressures acting on progeny fitness, acting as a buffer to mitigate the negative reproductive effects due to parental senescence. The occurrence and degree of parental care are typically correlated to egg size, developmental susceptibility and environmental stability. High fecundity of small eggs is usually associated with low investment per offspring, with high reproductive output compensated for probabilistically via quantity rather than quality. On the other hand, species that produce few, large eggs tend to show more advanced behaviors in the realm

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of parental care. This is a key evolutionary strategy trade-off that has long been known to exist. Environmental predictability also shapes parental care evolution. Pelagic species living in less predictable habitats, however, are less likely than species living in stable environments such as reef-associated fishes to exhibit elaborate parental care. Moreover, predation pressure is one of the main selective forces promoting protective parental behaviors. Phylogenetic analyses suggest that parental investment has independently evolved multiple times across fish taxa with subsequent elaboration and specialization of care within lineages after the initiation of building basic care patterns. Comparative studies of cichlid fishes, for example, indicate that substrate spawning with biparental guarding probably is the primitive state, and that mouthbrooding evolved several times separately from this behavioral background. Importantly, the sex of the caregiver varies among fish taxa, ranging from paternal care dominant in families such as Gasterosteidae (sticklebacks) and Syngnathidae (seahorses) to maternal care in many cichlids, to biparental care in others. These differences probably reflect variation in certainty of parentage, energetic costs and potential for repeated matings, for each sex.

Thus, many different species of fish have evolved to have a diverse range of respiratory adaptations as well as parental care strategies that demonstrate the myriad of ingenuity that natural selection has developed to solve such ecological challenges. The evolution of accessory respiratory items allowing fish to invade otherwise inhospitable environments, restricted by oxygen availability, and diverse offspring-feeding practices, permitting high juvenile survival with low ressources engagement in alternate environments. Fish have adapted to land by developing accessory respiratory adaptation from buccopharyngeal breathing to complex lungs and labyrinthine organs to survive in environments where oxygen may be limited. These adaptations may have set the stage for the evolution of respiratory systems that would later allow vertebrates to both successfully colonize terrestrial habitats and evolve into the myriad of forms we see today, meaning that their significance extends well beyond the scope of fish biology into the realm of vertebrate evolution as a whole. In a related manner, fish taxa

display a range of parental care behaviors demonstrating base tenets of reproductive investment strategies. This diverse spectrum of care patterns among the various fish groups is mediated by trade-offs between offspring quantity and quality, between current and future reproductive potential, and between the sexes in terms of parental investment. Collectively, these adaptations towards respiration and reproduction highlight the impressive evolutionary plasticity of fish which have occupied nearly all of the aquatic environments on Earth through countless adaptive radiations. Researching these adaptations has inspired numerous practical studies that have contributed to the understanding of ecological principles, evolutionary processes, and the biological basis of vertebrate diversity.

#### **UNIT 05**

#### **Amphibia: Parental Care**

Amphibians are an intriguing class of vertebrates that have managed to invade many different types of habitats worldwide, including tropical rainforests, temperate forests, and desert. Despite their long-standing evolutionary success, these organisms are constantly exposed to a multitude of environmental insults, particularly during their susceptible life stages. These challenges have shaped the evolution of an extraordinary adaptive strategy for nocturnal amphibians: parental care as a strategy to increase offspring survival. Though previously believed more uncommon in amphibians (only about 10% of all amphibians are thought to participate in some form of parental investment), newer studies upon investigation show parental care systems to be much more diverse and abundant than previously appreciated. This reproductive strategy is the most energetically and resource intensive among animals, the most extensive means utilized by parents to maximize the chances of their offspring's survival (often to their own detriment). Parental care in amphibians is especially interesting because amphibians share unique life history traits, the most important being their biphasic lifestyle with aquatic larvae, and terrestrial adults. This dual existence exerting divergent selective pressures at different life stages, requiring diverse adaptations

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to ensure reproductive success. The convergent evolution of parental care behaviors in various amphibian lineages indicates their potential adaptive function under similar ecological conditions. Predation pressure, habitat instability, resource limitation, and physiological limitations throughout development are the main drivers of the evolution of these behaviors.

Huddled together, just off the ground, the gelatiny eggs have an astounding range of amphibian parental care behaviors, from basic egg attendance to complex forms of viviparity that involve specialized nutritional provisioning. Such behavioral acts can be performed by either of the parents, although there is an overwhelming bias towards female care in some/female care in some communities representing interesting evolutionary patterns shaped by sexual selection and ecological factors. Care varies widely in type and duration of care, from short-term egg guarding to extended parental investment continuing long after metamorphosis. These behaviours are also important because they provide insight into the evolution of reproductive strategies among vertebrates more generally. It provides insights into the ways that environmental pressures drive behavioral adaptations and the way these adaptations feedback into ecological relationships, population dynamics and speciation processes. Knowledge of reproductive behaviors and their environmental dependencies are critical for management and conservation of these increasingly threatened organisms, especially in the backdrop of global amphibian decline.

## **Types of Parental Care in Amphibians**

Amphibians' diverse strategies of parental care embody their extraordinary adaptive radiations to diverse ecological opportunities. These strategies fit into general categories based on: (1) type of care; (2) parent type; and (3) developmental stage. All of these strategies are different solutions to the core problem of ensuring offspring survival in environments that are often rife with danger for developing embryos and larvae.

**Egg Attendance and Defense:** The most common, and presumably ancestral, type of parental care in amphibians is for parents to stay with their eggs, guarding

them against predators, pathogens, and harsh environmental conditions. This behavior is common among anurans (frogs and toads) and salamanders. For example, some dendrobatid frogs (poison dart frogs) demonstrate egg attendance, with males periodically moistening eggs with water stored in their bladders to prevent drying. Glass frog (Centrolenidae) females stay near to their egg clutches found on leaves above running water, defending themselves against predatory wasps and flies. African bullfrog (Pyxicephalus adspersus) males aggressively guard their eggs and tadpoles in shallow pools, and when conditions worsen, they will sometimes dig channels to connect drying pools to larger bodies of water. Many plethodontid salamanders, including members of the genus Desmognathus, coil around their egg clutches, and this posture serves as protection from both a predator and dehydration, as skin secretions provide moisture to the eggs and may also contain antimicrobial compounds that inhibit the growth of fungi.

**Egg Transport:** Some amphibian species developed a mechanism to transport eggs or larvae away from oviposition sites and to more advantageous developmental environments. This particularly reflects the behaviour of members of the dendrobatid frogs group, where males carry freshly-hatched tadpoles on their backs from the terrestrial nests to a proper aquatic environment, such as small streams, water-filled holes in trees or the leaf axils of bromeliad plants. The Surinam toad (Pipa pipa) has a fascinating adaptation in which fertilized eggs penetrate and become embedded in the porous, spongy skin of the mother's back where they'll develop until they pop out fully formed, ready to hop away! One of the most famous cases is the Australian gastric-brooding frog (Rheobatrachus spp., extinct), which would swallow its fertilized eggs, stop secreting acid, and turn its stomach into a brood chamber for fully developed froglets, which it would later regurgitate.

**Nutrients/feeding:** Some amphibians offer their developing embryos more nutrients than they receive from their egg yolk. This nutritional input comes in multiple formats, depending on the species. In poison dart frogs of the genus Oophaga, females visit their tadpoles regularly, depositing unfertilized trophic

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eggs that the developing larvae can eat. The marsupial frog (Gastrotheca spp.) The females hold eggs below a specialized dorsal pore, where the eggs develop; in some species potential tadpoles are then popped into water and in others retained until they kiteventually or starfish-like emerge fully formed as froglets. Caecilians, an understudied order of limbless amphibians, show striking maternal care in certain species, in which females develop a specialized, nutrient- and energy-rich outer layer of skin that the young scrape off with specialized teeth to sustain them as they develop, a type of maternal dermatophagy.

**Nest Building and Maintenance:** Many amphibians spend a lot of energy building and maintaining specialized nests that provide beneficial microclimates for developing young. Throughout amplexus, foam-nesting frogs (Leptodactylidae and Rhacophoridae) form foam masses by beating secretions along with their hind limbs. These nests are often built above water, where they keep eggs safe from aquatic predators and desiccation while still allowing good oxygen exchange. The males of the Darwin's frog (Rhinoderma darwinii) maintain small territories for the deposition of female eggs, and, once embryonic development begins, the males absorb the embryos into their vocal sacs, where they continue to develop until they emerge as little frogs. Many neotropical species build "leaf nests," folding leaves over egg clutches, and creating moist microhabitats. The redeyed treefrog (Agalychnis callidryas) lays eggs in clutches on leaves in water and even parents will reposition eggs, adjusting the clutch height for humidity or positioning for predator avoidance.

**Tadpole Guarding and Defense:** In many species of amphibians, parental care covers free-swimming larvae as well as the eggs. The male giant African bullfrog (Pyxicephalus adspersus) stays with schools of tadpoles, defending them aggressively from predators and, when temporary pools begin to dry, sometimes excavating channels to deeper water. The Brazilian treefrog (Hypsiboas faber) builds unique clay nests in shallow water in which males protect the tadpoles against predators and regulate the water quality. In certain species of poison dart frogs, tadpoles grow in small, isolated water bodies with scarce resources, and parents not only carry tadpoles to such sites, but continue to nurture and

eggs or siblings before producing completely terrestrial juveniles. This adaptation negates the need for the aquatic larval stage, enabling this species to occupy

protect them throughout their development. The midwife toad (Alytes

obstetricans) also shows exceptional paternal care, with the males wrapping

egg strings around their hind legs and clutching them for several weeks, dipping

Viviparous, Ovoviviparous: The most extreme form of parental investment

in amphibians is retention of developing offspring in the maternal body. The

alpine salamander (Salamandra atra) holds eggs that are still in development in

its oviducts, where embryos feed on egg yolk initially and then on unfertilized

high alpine environments where suitable larval development is rare due to lack

and carrying them in water to keep them moist until they hatch.

of bodies of water. The caecilian Typhlonectes compressicauda keeps developing young in the oviducts, feeding them though the specialized fetal teeth with which they scrape nutrient-rich secretions from the oviduct lining. Certain South American marsupial frogs (Gastrotheca spp.) hold eggs in a unique dorsal pouch that develops directly into froglets, completely avoiding the tadpole phase, facilitating reproduction in ephemeral habitats without permanent water bodies.

Biparental Care; Most Amphibians provide care by a single parent, but a few species exhibit care by both parents, which is a type of higher parental investment. Ranitomeya imitator 92 exhibits an obligatory form of biparental care, where collaborative efforts between males and females include identifying sites for oviposition in plant axils filled with water, in which females oviposit eggs that males eventually fertilize, and biparental transport of tadpoles followed by feeding of trophic eggs by both parents. In the Andean marsupial frog (Gastrotheca riobambae), the male fertilizes the eggs, which are then transferred to the female's dorsal pouch for brooding, but males may not stray far from the female, potentially offering protec-tion or other benefits. In contrast, the mimic poison frog (Ranitomeya imitator) has more extensive biparental care, and both parents defend territories, transport tadpoles, and females produce nutritive eggs, while males protect against predators and cannibalistic conspecilies. The impressive





diversity of parental care systems in amphibians exemplifies the diversity of evolutionary solutions to the problem of maximizing offspring survival. Each strategy is the result of a complex interaction of ecological pressures, physiological limitations, and evolutionary history. This fissured diversity equally reflects the significance of behavioral adaptations in permitting amphibians to occupy a plethora of habitats and ecological roles, making them evolutionarily successful despite their environmental sensibility.

## **Advantages of Parental Care**

Despite these benefits, evolutionarily parental care in amphibians is suggested to support offspring viable and reproductive success, thus benefiting evolutionary fitness of parent(s). These benefits need to surpass the considerable costs of delivering care (such as greater metabolic costs, breeding time lost, and predator pressure on the caring sex). Specific benefits of parental care can vary depending on the ecological context and the specific strategy used, but many general categories of benefits can be recognized across amphibians.

**Improved Protection from Predators:** One of the most-important features of parental care is protection, because predation is the major source of mortality for amphibian eggs and larvae. Protection of clutches by parents prevents potential predators by means of direct actions such as aggression or alarm calls, or because the presence of aggressive parents makes nests cryptic and harder to detect. With respect to the glass frog (Hyalinobatrachium valerioi), female attendance at egg clutches can decrease predation by wasps and flies by more than 80% as compared with unattended clutches. The big, aggressive male African bullfrog (Pyxicephalus adspersus) can do serious damage to any predators that approach its tadpole school, essentially creating a predator-free zone around its youngsters. The presence of parents may also promote earlier hatching or elicit embryo escape responses following a predator approach, as shown in red-eyed treefrogs (Agalychnis callidryas) whose embryos can hatch prematurely when exposed to snake predators, and embryo escape is promoted when parents are present.

**Defense against pathogens and parasites:** Amphibians' eggs and larvae are susceptible to a number of pathogens and parasites, particularly fungus infections, which can wipe out whole clutches. Many different mechanisms of the protective effects of parental care against these threats can be evaluated. Many parents that brood eggs periodically rotate, clean, or ventilate egg clutches, removing dead or infected eggs and limiting transmission of pathogens. The skin exudates of attending parents may have antimicrobial compounds that inhibit the growth of fungi and bacteria. For example, in the plethodontid salamander Desmognathus fuscus, females that remain with their egg clutches secrete antimicrobial peptides that greatly reduce rates of fungal infection. Likewise, túngara frog (Engystomops pustulosus) foam nests include proteins that have antimicrobial functions that protect developing embryos. Certain escorting parents purge dead eggs from clutches, controlling the spread of saprophytic fungi, which might otherwise infect healthy eggs, a behavior seen across several species of dendrobatid frogs.

Water and Osmotic Balance: Amphibian development is highly dependent on water availability, and the eggs of many species are particularly susceptible to desiccation when laid on land. Certain behaviours are performed by parents to maintain adequate hydration levels. Some attending male frogs, such as members of the family Dendrobatidae, periodically urinate over egg clutches or bring water to nests, preventing desiccation during dry periods. The skin of the attending parents can also retain moisture, which helps maintain humidity around the egg clutches. This is not significant for amphibian salamanders like Zwadins, as these species lack lungs, and their skin contains many permeable molecules that allow water to pass from their skin to the eggs. In contrast, in hypoxic aquatic environments, parents may facilitate embryo aeration through movements that promote water circulation around the egg masses, increasing the availability of oxygen to the developing embryos. Building specialised nests, like the foam nests of rhacophorid frogs, creates a microhabitat that maintains a balance between desiccation resistance and gas exchange, ensuring that eggs are safe from desiccation and flooding.

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**Thermoregulation:** Temperature regulation is an important aspect of parental care for some amphibians, especially for species that reproduce in environments with thermal variation. If parents attend eggs, they can mitigate variations in temperature through behavioral thermoregulation by shifting the egg clutch or positioning themselves in a way that maximizes developmental temperature. In several high-elevation species of salamander, females coil around egg masses, transferring metabolic heat that keeps egg temperatures elevated relative to ambient temperature during cold periods. In contrast, in warmer environments, parents may shade eggs during peak temperatures or move clutches to cooler microhabitats as appropriate. Such thermal buffering is crucial given the temperature-dependence of amphibian development, and that extreme temperatures can lead to developmental abnormalities or mortality. Making specialized nests: Colonies that excavate burrows (e.g. Some leptodactylid frogs, figs 12–13), create thermally stable environments, protecting developing offspring against temperature extremes.

If an egg contains large amounts of yolk, it can provide enough nutrients for early development, however some species of amphibians provide nutrition after egg-laying, thus increasing the growth rate and chance of survival for the offspring. Maternal dietary provisioning most directly occurs in trophic egg depositions, as in species such as strawberry poison dart frogs (Oophaga pumilio) in which females lay unfertilized, trophic eggs for tadpoles (p272). These nutritional subsidies permit tadpoles to develop in small, nutrient-poor aquatic bodies, such as in axils of bromeliads, broadening the latitudes of potential breeding sites. Maternal dermatophagy during gestation affords developing caecilian offspring nutrient-rich skin secretions that nourish embryos and facilitate rapid growth at a vulnerable life stage, as the mother nourishes her progeny via lipidrich secretions from her skin. Some give birth to live young, such as certain viviparous salamanders of the genus Salamandra. These salamanders provide nutrition through special structures, analogous to the mammalian placenta, which transfer nutrients directly to the developing embryos. These alternative provisioning mechanisms lead to larger sizes at metamorphosis which, in turn, are associated with increased post-metamorphic survival and accelerated reproductive maturity.

**Parental Care, Habitat Selection and Modification:** In many cases, parental care requires parents to select and modify a developmental habitat in a way that enhances the chances for offspring survival. The evolutionary longevity of such axial behavior has led to many dendrobatid frogs to transport tadpoles to specific microhabitats with appropriate predator and competitor profiles, indicating that some species make sophisticated assessments of habitat quality. The gladiator frog (Hypsiboas faber) builds clay nests that keep tadpoles safe from most aquatic predators but filter out debris to allow quality water. Foam-nesting frogs deposit their nests in sites where such long-term timing of hatching coincidences with seasonal floods, littering tadpoles into their aquatic habitat when conditions for development are most appropriate. Darwin's frogs (Rhinoderma darwinii), male, modify their habitat to an extreme extent, turning their vocal sacs into a brooding chamber, thus completely sheltering developing young from environmental threats. Such behaviours serve to extend the parents' phenotype, generating new developmental niches that bolster offspring survival.

**Extended Social Learning and Development:** In species with prolonged parental care, not only do parents protect offspring from physical harm, but they might also help them learn how to behave more confidently and social with their peers. Some species of tadpoles exhibit social learning, allowing them to gain information about food, predators, or habitat characteristics from their parents or siblings. In species with more elaborate breeding habitats, like poison dart frogs using discrete bodies of water in the forest, parent-guided dispersal helps offspring find suitable microhabitats that they might not independently find otherwise. The long-term association of parents with their offspring in some species may allow traching of bacteria that host microbes that protect against pathogens like the deadly chytrid fungus. Social learning is less documented in amphibians compared to other vertebrate classes, but



emerging evidence indicates that social learning plays a more prominent role than previously considered, particularly in species with extended care.

**Increased Parental Care in response to Environmental Change:** As an adaptive response, parental care allows parents to respond quickly to different environmental conditions, enabling them to provide more or less care depending on the current challenges they face. In droughts, attending parents including the African bullfrog can dig out channels from the drying pools to more permanent water bodies, rescuing tadpoles from desiccation-such behavioral plasticity cannot be achieved by fixed developmental pathways. Likewise, poison dart frog parents can speed up their tadpole feeding timetable in periods of low resource availability, prioritizing offspring nutrition in bad environmental conditions. For example, in those species where parents carry tadpoles to water bodies, they can select destinations according to current predator abundance or water quality or competitor density, making complex decisions that maximize the probability of offspring survival in the face of spatial variability. This behavioral plasticity can render parental care buffering in the face of environmental unpredictability, potentially accounting for the repeated evolution of such behaviors in temporally or spatially heterogeneous environments.

Decreased Sibling Competition and Cannibalism: In many amphibian species, intraspecific competition and cannibalism are major sources of mortality, especially when resources are scarce. Parental care can reduce threats in multiple ways. When resources are plentiful, parents pass on nutrition directly to their offspring, providing external sources of food, which mitigates the incentive for siblings to cannibalize each other (emphases added). In dendrobatid frogs that lay single tadpoles in different water bodies, parental care prevents competition by spatially redistributing siblings. In some regulations, attending parents actively separate siblings being aggressive towards each other. The choice to remove dead or immunocompromised young, seen in numerous species of frogs, could help limit the spread of disease while also preventing cannibalism from occurring. Collectively, these mechanisms promote brood survival by mitigating potentially deleterious competitive interactions.

Parental care is strikingly beneficial across a wide range of ecological circumstances, with its often-drastic benefits in amphibians providing the clearest example of its adaptive importance. Although the modalities differ among species and environments, parental care consistently increases offspring survival through a number of complementary pathways, from physical protection, to physiological mediation and behavioral facilitation. These benefits need to be significant enough to counterbalance the high energetic and opportunity costs of providing care, which is why these behaviors have evolved independently multiple times across the amphibian class. Understanding these advanced stages and their rich, diverse complexity and occurrence helps us recognize the important role of bi-polar traits as sexual selection pressures in early stages (polyandry), and this study clarifies how complex functional morphology explains the cost-benefit trade-offs in parental fitness. This is crucial for understanding the reproductive strategic pressures and choices in amphibians.

#### Patterns of Evolution in their Ecological Context

Examining the evolution of parental care in amphibians reveals remarkably similar relationships between ecology, phylogeny, and sexual selection. This reproductive strategy has evolved multiple times independently through the amphibian tree of life, indicating the adaptive value of this reproductive strategy to certain environmental conditions. Amphibians exhibit diverse reproductive behaviours; however, the evolutionary trends of parental behaviours remain unclear. Phylogenetic analyses show that parental care has arisen in an independent manner at least 40 times in amphibians, and has arisen at especially high frequency in some lineages, including Dendrobatidae (poison dart frogs), Hemiphractidae (marsupial frogs), and Plethodontidae (lungless salamanders). The repeated evolution of parental care reveals that it may be a convergent solution to a similar reproductive challenge in such a genetically diverse array of amphibian groups. And it also Turned out that the evolutionary pathways seem to be mainly one-



way—the once-caregiving parents evolving into non-caring parents is exceptionally rare (probably because what helped them evolve to take care of their tadpoles, created new challenges for both sexes that made reverting to ancestral condition less favourable in future). Populations across amphibians tend to show significant differences in which parent provides care and reproductive mode, and many lineages conform to one of three common mating systems that evolve alongside different fertilization modes. In frog species with external fertilization in which males can monopolize females and have high paternity certainty by guarding eggs they fertilize, male care prevails over female care. Internal fertilization Sperm transfer Sperm storage Within-species variation: Sperm transfer Outside species variation: Sperm transfer In contrast, the examples of female care are more common in the species with internal fertilization, e.g. salamanders and caecilians, where the females retained control over offspring post-fertilization. This pattern is consistent with theoretical predictions from sexual selection theory, indicating that parental investment is related to certainty of parentage. That said, there are also many exceptions, suggesting that even when assured of paternity, we enact more than one selection mechanism.

The presence and type of parental care in amphibians is strongly influenced by ecological factors. Predation pressure is a major driver, with increased levels of parental care in habitats with high density of egg and larval predators. Breeding in ephemeral water bodies is generally associated with higher investments in parental care, especially those that involve nest construction, egg attendance and tadpole transport, that reduce the risks provided by habitat unpredictability. Species that swap their eggs for larvae to on-beat zooplankton also found in their phytotelmata (water-in-plants such as bromeliad axils) are known for extremely high rates of parental care likely driven by resource-limited environments and high competition. The threat of desiccation posed by terrestrial gate deposition also strongly predicts the evolution of egg attendance behaviors that prevent eggs from drying out. Climate influences the evolution of parental care as well, with tropical amphibians displaying far greater diversity and

complexity of care behaviors than temperate species. This pattern may mirror longer breeding seasons, enhanced predation pressure, and greater competition in tropical environments, which together make the benefits of parental investment all the greater. Certain parental care strategies, such as viviparity and direct development are more prevalent in high-elevation habitats or unpredictable rainfall regions, enabling reproduction without reliance on benign standing-water bodies. Coevolution of parental care with other life history traits shows patterns of cooccurrence between care and juvenile life history, reproduction and adult life history. Whereas animals without parental care can afford to lay many more, smaller eggs, species with parental care tend to lay fewer, larger eggs, suggesting a reproductive strategy more focused on investing in quality rather than quantity. Parental care is often associated with prolonged developmental periods, indicating that care behaviours may have evolved alongside slower developmental life histories that increase offspring quality. Direct development (loss of the free-swimming tadpole phase) often coevolves with egg attendance, providing a protected environment for the evolution of this specialized developmental modality.

The potential for females to choose mates based on the expression of care behaviors has been an important selective factor influencing the evolution of parental care. In some poison dart frogs, females prefer to mate with males exhibiting higher levels of parental efficacy, thereby elaborating care behaviors through sexual selection. In native dendrobatids, the quality of male-constructed nests is an honest signal of male quality, and females base their mating decisions on nest attributes that are not directly influenced by male phenotypic quality. These dynamics establish feedback loops where sexual selection reinforces and possibly elaborates parental care behaviors beyond their direct survival utility. Parental care is shaped largely by social and mating systems, with monogamous species being more likely to display biparental care than polygamous ones. In territorial frogs, we expect resource defense polygyny, where males defend territory in part as a form of care (Salmon, 1987); in polyandrous systems, we might expect the opposite, as males seek opportunities to mate with multiple females while the females invest more heavily toward offspring actively while the males pursue more females. Causality in such

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relationships can be bidirectional-mating systems may influence care patterns, but the demands of parental care can also limit the evolution of mating systems. Parental care not only affects individual fitness but also shapes community structure and ecosystem functioning. Paternal investment has evolved then, at least in part, because species with some form of parental care can often exploit ecological niches that are unavailable to species that provide no care, such as temporary water bodies, terrestrial nesting locations, or predator-rich environments. This habitat specialization can contribute to higher species diversity of amphibian communities and new ecological interactions. Parental care behaviors such as tadpole transport and feeding structure complex spatial distribution patterns of resources, which can affect nutrient cycling in forest ecosystems. Parental care patterns have conservation implications because species with complex care behaviors may be especially vulnerable to habitat fragmentation, climate change and other anthropogenic disturbances. Many species dependent on care, for example, require specialized microhabitats for successful reproduction, such as certain phytotelmata or streamside oviposition sites, which may be disproportionately impacted by forest degradation. On the other hand, certain types of parental care, such as those that buffer environmental variability, may confer resilience to certain elements of climate change, although this potential advantages remains poorly considered.

Frontiers for present and future research in amphibian parental care involve the investigation of the neurobiological and hormonal bases of parental care behavior, the potential for transgenerational mediation of effects through parental behavior and the effects of parental care on adaptive responses to new threats like emerging pathogens and climate change. Because the care strategies observed in amphibians are extremely diverse, amphibians serve as an excellent system for answering fundamental questions about behavioral evolution, parent-offspring conflict, and the interaction between ecological and sexual selection. Here, we show that the evolution of amphibian parental care is mediated by a complex mixture of phylogenetic, ecological and reproductive forces that provide a rich adaptive landscape in which multiple selective pressures converge. This range of strategies

not only adds to our knowledge of amphibian biology, but can also reveal general evolutionary theories surrounding parental investment in the animal kingdom. There is no doubt that with modern advances in research approaches, especially in the fields of molecular phylogenetics, behavioral ecology, and neurophysiology, our knowledge of these incredible behaviors will only increase to illuminate new levels of complexity hidden in the already remarkable worlds of amphibian parental care.

#### **Physiological and Molecular Mechanisms**

Understanding the physiological and molecular basis of parental care behavior has the potential to be an exciting frontier in amphibian science, linking topics in behavioral ecology with neuroendocrinology and molecular mechanisms. Although mechanisms responsible for parental care in amphibians are less understood than similar processes in birds or mammals, recent studies are starting to uncover the physiological underpinnings of parental care in these systems from various amphibian lineages. Hormonal control underlies parental care behaviors, and multiple pivotal hormones have been implicated in caretaking initiation and maintenance across amphibians. The hormone prolactin, sometimes known as the "parenting hormone," mediates many of these behaviors in careproviding species, with elevated prolactin levels correlating with egg attendance, brood transport behaviors, and nutritional provisioning. Experimental elevation of prolactin in poison dart frogs increases tadpole transport and feeding behaviors, while prolactin antagonists reduce both behaviors, suggesting a causal relationship. In several amphibian species, parent-offspring bonding and recognition has been shown to be influenced by the neuropeptides oxytocin and its non-mammalian homolog mesotocin, which may facilitate the sustained attention needed for the extended care behaviors required from parents. These neuropeptides seem to be especially important in species where parents must distinguish their own offspring from others, such as dendrobatid frogs that preferentially feed their tadpoles. Sex steroid hormones have complex interactions with certain parental behaviors, and these interactions often have patterns that are different from those found in mammals. In a number of species





of male frogs that exhibit paternal care, higher testosterone levels correlate with displaying care behaviours, a pattern opposite that observed in mammals where paternal care is commonly associated with suppressed testosterone. This reversed pattern may represent the beneficial dual effects of testosterone on both territoriality and offspring defense in these species, marking how ecological context is needed to understand the relationship between hormones and behavior. Estradiol is a major regulator of maternal care in many amphibians, but egg attendance and nutritional provisioning behaviours specifically, and pharmacological and experimental manipulations strongly support a causal pathway whereby estradiol enhances the expression of maternal care behaviours.

Stress hormones, and corticosterone especially, show complex, species- and ecologically-context-dependent relationships with care behaviors. For example, in some amphibians, successful parental care is accompanied by reduced stress responses, suggesting that parents will persist alongside their offspring even in the face of predation risk or resource scarcity. Importantly, moderate elevations in this hormone actually promote aspects of the care given to the offspring, and these behaviors are particularly directed to protect against predation, leading some to propose an adaptive function for controlled stress responses during parental care. The interplay between stress hormones and other neuroendocrine systems may be crucial, and evidence for a role of prolactin in buffering against care suppression induced by stress is seen across several species. The similarity or difference of the brain regions underpinning normal parental care between amphibians and additional vertebrates is still uncertain. This finding suggests a more nuanced relationship between preoptic activity and care behavior, as numerous amphibians exhibit preoptic recruitment during care, a behavior controlled by the preoptic area across vertebrate lineages. Interestingly, neuroimaging in poison dart frogs has demonstrated activation of the medial pallium (the structure homologous to the mammalian hippocampus) during tadpole transport, which may reflect spatial memory-related functions in their use for finding a suitable deposition site. The medial amygdala, a region that has been consistently linked to social recognition across vertebrates, displays increased activity when parent frogs are exposed to chemical cues from offspring and likely contributes to recognition mechanisms that promote selective care. There are major alterations in neurotransmitter systems supporting caregiving that occur across the transition to parenthood, as this state produces rapid and large changes in the neurochemistry of the brain. Dopaminergic systems are a conserved feature of motivation and reward across vertebrates and have been shown to be upregulated within the regions of the brain associated with parental behavior in several species of amphibians. Such increased dopaminergic signaling might establish rewarding experiences with offspring proximity, allowing care behaviors to be reinforced via positive feedback mechanisms. Moreover, serotonergic systems that modulate anxiety and aggressive behaviour are also altered during parental phases, potentially allowing for the reduced offensive aggression towards young and the increased defence of territorial resources observed in many species that provide care.

In addition to oxytocin/mesotocin, peptide hormones have specific roles in amphibian parental care. Arginine vasotocin controls key water balance behaviors underlying egg hydration in terrestrial breeding species, with exogenous application enhancing egg-moistening behaviors in dart frogs. In some amphibians, prolactin-releasing peptide seems to mediate stress-induced reductions in parental behavior, and so may serve as a nexus between environmental challenges and care decisions. These peptide systems establish dynamic neuroendocrine interconnected networks that integrate numerous facets of parental care as a function of external conditions and offspring demand. In species in which parent-offspring recognition and response to offspring signals are critical to their success, sensory mechanisms comprising parent-offspring communication constitute a major component of the factors promoting successful care. In many amphibian systems, chemical communication is predominant, whereby parents can recognize chemical cues produced by their offspring via the vomeronasal organ or external main olfactory epithelium. The use of specialized chemical signals by tadpoles of certain dendrobatid frogs is a key aspect of a more complex chemical communication system involving maternal feeding behaviors. Acoustic communication is less widespread, but where it exists, it can

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become exceedingly precise, such as with Darwin's frog, in which the calls made from developing embryos are only responded to by males, leading to ingestion into the vocal sac when embryos have reached the right age. Many amphibians are ovoviviparous or viviparous, in which the maternal–offspring interface provides rich physiological adaptations for internal development. Vampire bats are one of several mammals that regurgitate blood to supplement their diet, and some viviparous salamanders form placental analogs that facilitate respiratory gas and nutrient exchange supported by specialized vascular techniques from the mother. Maternal dermatophagy in caecilians involves cyclical skin changes, resulting in a specialized, nutrient-rich layer that offspring feed on, showing a remarkable convergence with mammalian lactation. These specialized tissues require fascinating molecular responses, such as the unique expression profiles of nutrient transporters and signaling molecules that control mother-offspring physiological coordination.

Molecular architecture of parental care behaviors has started to unravel through genetic and genomic studies. Additionally, comparative transcriptomics between care-providing and non-care species have highlighted differences in gene expression related to reward circuitry, social recognition, and emotional regulation. They hypothesized that parental care evolves through convergence on the same molecular pathways, despite disparate evolutionary origins, leading to similar patterns of gene expression in the preoptic area across distant amphibian lineages that evolved parental care independently. Differences in epigenetic modifications, especially in DNA methylation patterns in specific brain regions involved in regulating social behavior, have been observed between parental and non-parental individuals, indicating possible changes in gene expression profiles that may mediate the transformation to parental status. Such metabolic adaptations are consistent with the energetic investment associated with parental care, which can be high in species with prolonged periods of care. Attending moms have lower feeding rates but remain energy balanced by metabolically ratcheting up responses like fat mobilization and glucose dynamics.

Some parents during those periods enter a hypometabolic state akin to halting torpor, conserving energy while remaining vigilant to threats. The recent metabolic adaptations that allow for this sustained energy allocation are essential for successful completion of care in the face of reduced foraging opportunities. Parental allocation of resources appears still in parental investment, for instance, wherein the skin physiology of attending mothers and fathers is characterized with specialized adaptations advantageous for offspring development. Many species increase antimicrobial peptide production during parental phases, augmenting the immune protection afforded by parental attendance. Attending species have different mucus composition, in which wetter molecules that help transfer moisture from the environment to the eggs are produced more. For species that engage in maternal dermatophagy, the nutrient composition of the skin secretions undergoes a marked change in the parental phase, where it becomes replete in proteins, lipids and essential micronutrients that can promote offspring growth.

Immune adaptations in the parent phase balance the competing need to protect the offspring while ensuring self-maintenance. Many attending parents exhibit redistributed immune investment, whereby innate immunity is upregulated to defend against pathogens that may pose a threat to offspring, sometimes at a cost to adaptive immune responses. The microbiome of participating parents is often compositionally altered to promote the production of antifungal metabolites that may protect eggs from pathogens, particularly fungi, which present a significant mortality risk. These immunological shifts are ornate compromises between short-term investment in progeny and long-term maintenance of individual fitness for future offspring. Environmental sensing mechanisms help parents to modulate care behaviors according to local conditions, providing adaptive behavioral flexibility. Sensory specializations capable of detecting water quality, predator presence, or resource availability help inform reproductive parents' decisions related to nest maintenance, offspring relocation, or nutritional provisioning. These external environmental inputs converge with internal physiological states via poorly characterized but likely complex neural circuits centered around the preoptic area and extended social behavior network. This



integration enables the contextual modulation of care behaviors, enhancing offspring survival across fluctuating environments. Chronobiological adaptations align the timing of parental behaviors with the delivery of caregiving. Attending parents exhibit biased temporal activity patterns that promote their offspring against time-varying threats like diurnal or nocturnal predators. For temperate species that breed during short seasons, changes in day length with the seasons initiate hormonal cascades that prepare physiology for parental care even before breeding occurs. Such temporal regulation mechanisms ensure that physiological and behavioral parental adaptations are matched with offspring developmental needs and environmental conditions.

#### **UNIT 06**

#### **Reptilia: Poisonous and Non-poisonous Snakes**

Snakes (suborder Serpentes) are long, limbless reptiles of the order Reptilia. They are one of the most successful and diverse lineages of vertebrates, originating from lizard ancestors more than 100 million years ago. Today around 3,900 species of snakes can be found in almost every continent apart from Antarctica, filling a range of ecological niches from deserts and tropical rainforests to oceans and temperate zones. Such impressive plasticity is due to their specialized anatomy and physiology that allowed them to become efficient predators. The snake body plan — long, limbless, and highly kinetic skull — has been fabulously successful for snakes, allowing them to capture and consume prey items that can be many times larger than the diameter of their own head. These bodies with scales, offering protection, preventing loss of water in them, and helping locomotion have led to their evolution to keep up in various environments. In spite of their differences, all snakes have some common characteristics: they are carnivorous, they shed their skin on a cyclical basis in a process known as ecdysis, and they are ectothermic, meaning that they control their body temperature behaviorally rather than physiologically. Unlike other reptiles, snakes have several unique anatomical adaptations that make them special. Its skeleton

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is modified, with 200 to 400 individual vertebrae (humans have only 33), with ribs attached to almost every vertebra, providing mobility and structure for its extremely long body. The snake skull is an evolutionary engineering marvel made up of many loosely fitted bones that afford impressive jaw mobility. This kinetic skull, along with very elastic skin and connective tissues, allows snakes to feed on prey far wider than the diameter of their head — a feeding mode that is not possible for most other vertebrates. The most common kind, which all but a small handful of snakes possess, are specialized teeth that are the same shape in nonvenomous species and evolved into fangs in venomous species, that curve backward to keep prey from escaping after it has been bitten. Their sensory systems have developed specialized adaptations, including infrared-detecting pit organs in some families (like vipers and pythons), chemosensory vomeronasal organs that they access with their forked tongues, and ground-sensing adaptations that allow them to pick up vibrations through their jawbones. Internally, snakes display additional adaptations: their paired organs are asymmetrical (one is usually reduced or moved) to fit their narrow body shape and their hollow hearts are able to accommodate for massive pressure changes that would otherwise be fatal during the consumption of huge prey.

Snakes have an intriguing evolutionary story to tell as vertebrates. The fossil record and molecular data indicate that snakes originated from lizard-like ancestors around the middle of the cretaceous period, about 100-120 million years ago. Fossils of the earliest snakes already have many of the distinguishing features seen in snakes today, suggesting that the evolutionary transition from lizard-like ancestors to more familiar forms happened quickly in the fossil record. Most researchers agree that snakes came from burrowing lizard ancestors, a fact that can be surmised through vestigial characteristics like diminished eyes, lack of external ears, and long, flexible bodies — all adaptations that serve an underground life. Several primitive lineages of extant snakes also have such features, and so the authors propose a "burrowing hypothesis" in which they suggest the evolutionary tree would have originally been both "slinking and digging" with the anatomy providing advantages for burrowing. After this first adaptation towards burrowing, snakes went through an incredible

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adaptive radiation, filling many ecological roles and evolving specialized adaptations for different ways of hunting. This divergence has led to the astonishing diversity in snake species we see today, from minuscule thread snakes only few inches long (10 cm) to enormous pythons or anacondas measuring more than 19 feet (6 meters)! One of the most remarkable modifications that have occurred across the process of evolution has been the evolution of venom delivery systems by multiple snake lineages. For this article, we summarized different types of locomotion, where snakes adapt their movement styles to their habitats and hunting methods, making them the most specialized movers in the vertebrate world (Table 1). The most prevalent style of snake movement, called serpentine locomotion (or lateral undulation), involves the snake pushing off surface irregularities while forming S-shaped curves that move down the body. Most of the species employ this efficient gait over the complex terrain. Vehicle equipment style as set as Vehicle post-set — 010% of the world population have poor antivenom availability (11), high-cost antivenom production and distribution processes, weak cold-chain infrastructure for antivenom storage (12), inadequate training of healthcare workers (12), as well as new shortages of antivenom due to market failure and production challenges (13). These challenges are being addressed with multidimensional efforts such as better antivenom production, innovative therapy (eg, small-molecule inhibitors and recombinant antivenoms), improved distribution systems, and better healthcare infrastructure in the most affected regions.

Understanding snake venom has provided extraordinary insights and applications in various fields of biology: from evolutionary biology to pharmacology and medicine. From an evolutionary standpoint, venoms represent a model system for investigating accelerated evolution, gene duplication events, and neofunctionalization (the gradual acquisition of novel toxic functions by ancestral physiological proteins). From a medical standpoint, snake venom components have contributed to the discovery of multiple pharmaceuticals: bradykininpotentiating peptides derived from the venom of Bothrops jararaca were the basis for captopril, the first angiotensin-converting enzyme (ACE) inhibitor for hypertension and heart failure; the disintegrins in viper venoms gave rise to the important antiplatelets eptifibatide and tirofiban, used in coronary syndromes; and ziconotide, a potent non-opioid pain therapy, derived from cone snail venom (albeit shares mechanism with some components of snake venoms). Other than the abovementioned approved drugs, venom-based compounds are being evaluated against cancer (by means of the cell-targeting properties of some toxins), neurodegenerative diseases (based on neuroprotective peptides), and autoimmune diseases (using immunomodulatory elements of venom). Snake venom proteins, such as thrombinlike enzymes, are used as diagnostic tools in coagulation assays and other laboratory tests. Venomics-the comprehensive characterisation of venom composition using proteomics, genomics and transcriptomics has changed our perception of venom complexity and evolution and pave the way for better antivenom development. Future research will lead to development of universal antivenom using synthetic antibody technologies, illegal venom-based products as agricultural pesticides, and use of venom peptides as research tools to study ion channels, receptors, and other targets in cells, exemplifying how these ancestral poisons have still ameliorated humanity and scientific knowledge.

#### **Non-Poisonous Snakes**

The vast majority of snakes worldwide are nonvenomous, approximately 80% of the nearly 3,900 described snake species. These different kinds of reptiles have also developed a host of adaptations for capturing prey and defending against predators that don't depend on the production of venom. If we wait until we get bitten by a non-venomous snake, we never will, because they are spread over dozens of families, particularly the largest (Colubridae, which contains around 66% of all living species of snakes, although members of this family contain harmless, rear-fanged informational systems) and other families (the Pythons, Boas and Lamprophiidae's house snakes and more, hundreds of specialized niches). In contrast to the widely recognized morphological adaptations associated with venom delivery in venomous members of the group (i.e., specialized dentition, venom glands), many non-venomous species have relatively generalized skull morphology. Nevertheless, this generalization has facilitated massive evolutionary radiation, allowing non-

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venomous snakes to fill nearly all terrestrial and a few aquatic niches worldwide. Compensating for their lack of venom as a primary option for predation or defense are specialized adaptations for hunting, defense, reproduction, and using resources, which have resulted in their ecological success. The incredible diversity among non-venomous snakes - from tiny, barely earthworm-sized blind snakes, to hulking, 6-meter-long constrictors — is a testament to the evolutionary success of their alternative survival tactics. Since non-venomous snakes lack the ability to hunt using a venom-based mechanism, they have therefore evolved a range of alternative predatory strategies. Constriction is among the most evolutionarily successful and widespread forms of hunting, used by several families of snakes such as Boidae, Pythonidae and many colubrids. Coil around the prey and prevent lung expansion and blood flows, which can cause death within approximately 10 minutes through circulatory arrest, rather than suffocation or crushing as commonly believed. Studies have shown that constricting snakes finely adjust the force exerted in accordance with the size of the prey and the resistance offered, and can even detect heartbeats and know when the prey has died. In addition to constriction, many nonvenomous species also use specialized hunting strategies, such as ambush predation (when snakes remain still until prey comes within striking distance), active foraging (searching systematically for prey by moving constantly), or intermediate strategies that blend aspects of both hunting styles. The adaptations for feeding can be highly specialized in some species: egg-eating snakes have modified vertebral processes that can crack an egg after ingestion and an expandable esophagus retains contents while regurgitating the shell; fish specialists have unique head shapes and behaviors to present foragers for aquatic prey; and some fossorial species can locate and excavate prey via adaptations of specialized senses to find prey situated underground in burrows.

### UNIT 07 AVES:

### **Migration and Flight Adaptation in Birds**

Migration is among the most spectacular and complex of all animal behaviors, and there's no more spectacular manifestation of that than in birds. Every year billions of birds migrate thousands of kilometers across land masses and oceans, responding to seasonal variations in resource supply and opportunities for reproduction. This remarkable behaviour has evolved independently several times throughout avian lineages and demonstrates the astounding flexibility of birds and their tailored interaction with the aerial realm. Powered flight evolved as recently as ~150 million years ago and granted birds the unique ability to exploit resources across divergently distributed geographic ranges and inhabit seasonal environments that would otherwise be uninhabitable during non-optimal periods. Migration in birds is a varied phenomenon, including the extraordinary non-stop flights of Bar-tailed Godwits, which fly over 11,000 kilometers without stopping in a single go across the Pacific Ocean, and the intricate multi-point journeys made by many of songbirds that engulf multiple stopover sites for refueling. The Arctic Tern is the pinnacle of extreme avian migration, migrating from its Arctic breeding ground to its wintering site in the Antarctic each year in a round-trip distance of 70,000 kilometers, allowing also for more daylight exposure than any other animal on the planet. Migration is not only a very common behavior, but also exists along a continuum from obligate complete migration, where entire populations migrate between separate breeding and nonbreeding ranges, to obligate partial migration where only some individuals of the population migrate, to facultative migration which occurs when individuals migrate if the environmental conditions degrade beyond some threshold. Nomadic species such as crossbills follow unpredictable food resources instead of fixed migratory routes, and altitudinal migrants like certain mountain-dwelling species just move up and down elevation gradients in line with seasonal change. Migration timing is orchestrated by an elaborate interplay of endogenous circannual rhythms and environmental cues perceived by the animals, like photoperiod, temperature, food availability, and weather. In many species, different age classes or sexes migrate at different times or to different destinations

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(differential migration). In some species, males arrive earlier than females at their breeding grounds to establish territories, a phenomenon called protandry.

The navigation and orientation mechanisms allowing birds to navigate while migrating are among the most sophisticated sensory systems in the animal kingdom. They have a multi-modal navigational toolbox—including the detection of Earth's magnetic field via specialized photoreceptors containing magnetically sensitive proteins known as cryptochromes, which are especially concentrated in the right eye and brain. This magnetoreception is supplemented by celestial navigation based on star patterns and the position of the sun as well as the ability to sense patterns of polarized light in the sky. Seabirds use olfactory navigation to create an odor map of their surroundings, while familiar landmark recognition is critical as birds approach a destination. In a lot of species, first migration young birds depend on genetically hardwired vector navigation-flying in one direction for a certain amount of time-but a more sophisticated map system comes with experience. The brain underpinnings explaining these impressive talents involve specialized regions, such as the hippocampus, which is larger in migratory than in non-migratory species, as allomorphisms that can be linked to the cognitive demands of long-distance navigation. Recent studies using tracking technologies have shown that some birds are able to correct for the effects of wind drift and adjust their flight trajectories in response to unexpected displacement, indicating a degree of navigational flexibility that goes beyond basic compass orientation. The timing of the migration and the physiological preparations needed for successful migration are directed by complex interactions between environmental cues like temperature and food availability, the endocrine system, and changes in gene expression. Migratory birds undergo a myriad of changes weeks or months prior to migration that result in what has been referred to as migratory syndrome, including increased feeding (hyperphagia), the accumulation of fat reserves, changes in circadian rhythms, and modifications in muscle composition to improve endurance. These preparations exemplify the degree

to which migration pervades both the physiology and life history of migratory birds—namely, migratory behavior is not just that, a behavior, but an essential component of their biology.

Migration has deep ecological consequences, linking distinct ecosystems and allowing nutrients, energy, parasites, and pathogens to be transferred across great expanses of geography. Wintering fecal migrants saltang each other in through dispersals with mutualisms between continents by pollination and predator-prey interactions. Migratory birds are seasonally abundant and affect the timing of many important ecological processes, and may influence the evolution of resident species that interact with migratory species. Conservation of migratory birds in general is a unique challenge, requiring protection of habitat networks that cross multiple countries and political jurisdictions. Climate change is especially threatening of migratory birds as it can cause phenological mismatches where the timing of energy-derived migration fails to align with critical resources such as food availability. Habitat degradation at stopover sites, which serve as essential refueling stations, can create bottlenecks that impact entire populations, while light pollution can disrupt navigational cues and kill individuals directly through collisions with buildings. In spite of these challenges, migration remains a successful evolutionary strategy for hundreds of bird species, enabling them to exploit spatiotemporally patchy resources and thereby maximizing reproductive success in a temporally fluctuating environment. These adaptations, which support bird migration through things like navigation systems, flight muscles, and metabolism, serve as potential examples of the evolutionary innovations that define the class Aves as why birds have been so successful in evolution, enabling them to inhabit virtually every terrestrial and coastal ecological niche on Earth. Through cutting edge tracking technologies, genomic analysis, and interdisciplinary approaches, we continue to unpick the aspects of bird migration so as to understand this phenomenon even better, revealing ever more complex and nuanced facets around these epic voyages that have fascinated humans since antiquity.

#### **Anatomical Adaptations**



Birds are the ultimate aerial conquerors, but this is made possible by a collection of unique anatomical adaptations that together convert a vertebrate body plan into an efficient flying machine. The avian skeleton is one of the most extreme examples of evolutionary adaptation for flying, achieving a compromise between the apparently opposite requirements of strength and lightness through unusual structural innovations. Birds have pneumatic bones — hollow structures reinforced with internal struts known as trabeculae — that greatly decrease weight while also maintaining mechanical strength. This pneumatization is most pronounced in the skull, vertebrae, and the proximal limb bones that articulate directly with the respiratory system via small apertures known as pneumatic foramina that enable air sacs to penetrate into the interior of the bones. The extent of skeletal pneumatization usually reflects flapping potential, peaking in passing birds that exploit soaring (e.g. frigates, vultures) and is to a lesser extent reduced in diving birds, where greater bone density helps combat buoyancy in the water. In addition to pneumaticity, the avian skeleton has many other adaptations for flight. In the flying bird, a significant ventral projection, the keel (carina) of the sternum or breastbone, has developed to provide an extended surface area for the insertion of the large flight muscles responsible for wing motion. This keel can be relatively large in those birds whose style of flight was characterized by powerful sustained flight, and this structure is especially prominent in hummingbirds and related flies. The furcula (wishbone), created by the fusion of the clavicles, acts as a spring that allows birds to store and release energy during their wingbeats, and that helps maintain offers them proper spacing between the shoulders while in the air, all the while doubling as a crucial point of attachment for flight muscles.

Birds possess many fused thoracic vertebrae which give rise to a rigid thoracic spine and contribute stability during flight and synsacrum (a fusion of lumbar, sacral, and anterior caudal vertebrae) which generates a rigid pelvic region to distribute the forces generated during powerful wing downstrokes. A graviportal posture such as this preserves the ability of the tail to serve crucial aerodynamic functions such as stability, steering, and braking by anchoring the tail feather
within the pygostyle and assisted by core muscles in the fused group of terminal caudal vertebrae. In the avian forelimb, there have been dramatic modifications into a wing, including elongation of the manus (hand) bones, reduction of digits to three, and fusion of the carpometacarpus, resulting in a stout yet lightweight structure that can support primary flight feathers. The forelimb bones, including the radius and ulna, are adapted to each for hindering rotation and keeping the wings aligned during flight, but provide enough flexibility for folding at rest. The humerus also has a large deltopectoral crest to which the strong pectoralis muscles attach; the size and shape of this crest differs with flight style between taxa. Wings in wingless birds (like ostriches and penguins), however, are reduced and/or adapted through use for new roles, for instance balance in running and for propulsion underwater. Whole animals biology: natural selection exerts pressure on metazoan creatures to develop specialized adaptations for the extreme metabolic demands of flight, especially for the ascent of heat, across both the respiratory and circulatory systems. Among vertebrates, the avian respiratory system is the most efficient, consisting of a flow-through system with unidirectional airflow through comparatively rigid lungs linked with a series of nine air sacs that occupy the body cavity and extend into pneumatic bones. It allows for much more efficient exchange, crucial for the high metabolic rates needed for flight, unlike the bidirectional tidal breathing of mammals, because it permits continuous gas exchange during both inspiration and expiration.

This respiratory system is further complemented by crosscurrent gas exchange in the parabronchi (which are analogous to the mammalian alveoli or air sacs), allowing birds to extract far more oxygen from each breath than the mammalian counter part. Their respiratory efficiency is matched by their cardiovascular system, which is adapted to their high metabolic requirement through a completely separated, four-chambered heart that prevents the mixing of oxygenated and deoxygenated blood, higher blood pressure than similar mammal species, larger heart-to-body mass ratios and a higher density of more numerous mitochondria in their cardiac tissue. Long-distance migratory birds—bar-tailed godwits and

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ruby-throated hummingbirds those most extreme-exhibit outstanding cardiovascular adaptations that enable sustained high heart rates for hours or even days of continuous flight across thousands of kilometers. Their central nervous system has also been adapted to the challenges of the air, with reorganization needed for the three-dimensionality of flight. Birds have large cerebellums for motor coordination, an organ that is crucial for high coordination in species that engage in acrobatics during flight. Due to the necessity of having access to accurate vectors of position and acceleration for maintaining static equilibrium, specialized vestibular systems in birds are tuned for high-frequency responses, while visual-processing centromeres occupy a larger overall fraction of the avian brain relative to other vertebrates, a reflection of the central dogma of high-speed locomotion (in this case, aerial) in birds being vision. Even the avian visual modality has adapted to their aerial lifestyle, with new ocular specializations for flight, including larger eyes compared to their head size, a much greater density of photoreceptors for potent resolution, a higher frequency of flicker fusion for keeping up to date with fastpaced visual changes during flight, and specific oil droplets in their cone cells for increased color discrimination and diminished chromatic aberration. Birds are typically tetrachromatic, and many species have sensitivity into the ultraviolet range, allowing them to perceive plumage patterns that are invisible to human eyes and possibly assisting them in navigating using polarized light patterns in the sky.

Although most anatomical modifications in birds are focused on weight reduction, the digestive system is a trade-off between weight minimization and the high energy cost of flight. Many birds have developed a crop—an expandable pouch in the esophagus—that permits them to traverse midday deserts of energy-dense foods, eating in bulk and stashing some of their meal for later digesting, which conveniently reduces the burden of carrying heavy foods on long migrations. An organ known as the gizzard (a muscular compartment of the stomach that can contain foreign starches, grit, or gastroliths) can supplement the loss of teeth by pounding food during the digestive process, giving birds the ability to take in tough cellulose from plants or exoskeletons from insects without incurring the cost of maintaining heavy jaw muscles and teeth. The digestive organs are highly plastic in many species, particularly long-distance migrants, atrophying quickly in migration, when not in use, to minimize flight weight and regenerating along stopover sites or wintering grounds. You should give the visual system of birds particular note because it is adapted specifically for flying. In addition to sharing the above-referenced general traits of tetrachromatic vision and high visual acuity, many birds have specialized retinal structures with extremely high density of photoreceptors, like the fovea in raptors, which offers us several times the resolution capacity of human visioncrucial for spotting prey during flight from altitude. Predatory birds such as falcons can detect the ultraviolet reflections of urine trails left by rodent prey, and are able to visualize a fluoresecent pathway highlighting the past movements of potential prey along a senory landscape. In fact, lots of species have evolutionary developed specific oil droplets in their cone cells which work as a filter, increasing their perception of colors while also reducing chromatic aberration in high-speed flight. Depending on ecological niche and style of flying, the placement of the eyes varies greatly; for instance, predatory birds have forward-facing eyes, giving enhanced binocular vision and depth perception, while most prey species have laterally facing eyes enabling almost 360 degree vision and sight of predators before they get to the prey. In all, these varied anatomical and physiological adaptations turn birds into aerial exemplars, exploiting the three-dimensional freedom of the air with an efficiency unrivaled by any other vertebrate group and indeed by planes and drones of human design. The elaborate combination of light skeletal structures with powerful musculature, advanced respiratory and circulatory systems, and specialized sensory capabilities, makes up a flying machine with extraordinary performance and versatility, allowing birds to do everything from long-distance, transcontinental migrations, hovering accurately to suck nectar from flowers, diving at speeds of over 200 miles per hour, or threading forest canopies without collision.

#### **Muscular Adaptations**

Bird muscles are a marvel of an evolutionary design, evolutionarily brought into existence with an eye towards satisfying the unique power and endurance requirements associated with flight, without overloading (increasing) the weight of the bird as a whole. In contrast to the terrestrial animals that recruit many muscle

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groups to produce locomotion, birds have evolved to devote amazing amounts of their muscle mass to flight, with the flight muscles of many species around 25-35% of total body weight—an astounding functional specialization that illustrates how flight is integrated into bird physiology. Most of the power for downstroke, the most energetically-demanding stage in the cycle, comes from the huge pectoralis major muscle, which can contribute 15-20% of the entire body mass of some species, e.g., pigeons. This muscle originates on the keel of the sternum and inserts on the ventral surface of the humerus by way of a tendon that passes through the triosseal canal, establishing a mechanical arrangement that transforms contraction of the muscle into the powerful downstroke that provides most of the lift and thrust of flapping flight. Avian flight style dictates pectoralis architecture, resulting in the shorter, highly pennate fibres of swift-flying birds such as falcons compared to those of the long, low pennation of albatross SOARing species, in which muscle design facilitates endurance eating over rapid muscle recruitment. One of the greatest mechanical accommodations in vertebrate anatomy is the supracoracoideus muscle, which is responsible for the critical upstroke phase of the wingbeat cycle. In contrast to the linear action of the pectoralis, the supracoracoideus works in a pulley-like system: it originates on the sternum deep to the pectoralis, and its tendon travels through the triosseal canal (formed by the union of the coracoid, scapulae, and furcula) to insert the humerus on the dorsal surface of the humerus. This setup truly turns a downward muscle pull into an upward wing stroke, allowing birds to position this ancient upstroke muscle on the ventral side of the body, the location most conducive to maintaining the center of gravity for flight, rather than the dorsal site, where it would contribute to a top-heaviness that would interrupt flying stability.

The relative size of these two main flight muscles varies widely by manner of flight: in hummingbird species that, unlike other birds, produce lift equally on the down and upstroke of hover, a supracoracoideus can reach half the mass of the pectoralis, whereas in soaring birds whose flight relies more on passive gliding this muscle may represent 10-15% of the pectoralis. In addition to these two major flight muscles, birds have a complex network of smaller muscles that allow fine control of wing shape and orientation. The tensor propatagialis complex regulates the leading edge of the wing by moving the propatagium — the stretchy skin fold between shoulder and wrist that forms the leading edge of the inner wing. The wing has complex feather muscles that facilitate controlled adjustments to feather position, adjusting wing camber and area to changing aerodynamic demands throughout the flight cycle. Unlike human-made flying machines, birds are capable of modifying their wings dynamically depending on their current flight conditions through a process known as wing morphing. They also possess both structural and biochemical adaptations in the muscle fibers responsible for flight. Access the muscle characteristics and adaptations of avian species is common and often enable the characterization of the pectoralis muscle in many birds as a heterogeneous mixture of fiber types (e.g., fast-glycolytic fibers for power, fast oxidative-glycolytic fibers for sustained power output, slow oxidative fibers for endurance adaptation). The relative proportions of these fiber types vary according to migratory type and flight style: long-distance migrants such as sandpipers and arctic terns have a high proportion of oxidative fibers with high mitochondrial density and myoglobin content, conferring fatigue resistance during multi-day non-stop flights, whereas birds specialized for rapid acceleration and maneuverability, such as sparrowhawks and flycatchers, have a higher proportion of fast-glycolytic fibers that develop greater power but fatigue more quickly. Hummingbirds are an extreme example of specialization: their flight muscles consist almost entirely of fast oxidative-glycolytic fibers that blend together the speed essential for their extremely high wingbeat frequencies (up to 80 beats s"1 in some species) and the oxidative capacity needed to maintain performance over prolonged hovering durations.

The fiber architecture of these flight muscles can also exhibit adaptive variation, as both fiber length and pennation angle (angle of muscle fibre insertion to the muscle's central tendon) and sarcomere length are tuned to maximize performance in specific flight modes. The cellular machinery in these muscle fibers is highly adapted for the aerobic demands of flight. Almost a third of the volume of avian

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flight muscles is occupied by the cell organelles which generate aerobic energy (mitochondria), with flight muscles of hummingbirds and other species capable of extreme power output having the highest mitochondrial density recorded for any vertebrate tissue. These mitochondria are positioned to minimize the diffusion distance for oxygen and adenosine triphosphate (ATP) and are arranged in dense aggregates around lipid droplets to allow rapid access to skeletal muscle fatty acid fuel during prolonged flight. The sarcoplasmic reticulum, which mediates calcium cycling during contraction and relaxation, is especially elaborate in avian flight muscles, facilitating the rapid calcium release and reuptake needed for the rapid contraction frequencies typical of flapping flight. Mammalian muscle enzymes reflect the metabolic power of avian flight musculature, the activities of enzyme classes used in carbohydrate and fat metabolism are extraordinarily high. Fatty acid oxidation enzymes show especially high activity in long-distance migratory birds, enabling them to extract energy efficiently from fat reserves in prolonged flight. The adaptive diversity of flight muscle myoglobin content is well documented, with the highest concentrations found in those species that regularly undergo oxygen limitation during flight, such as high-altitude migrants like barheaded geese, that traverse the Himalayas at altitudes above 9000m where atmospheric O 2 levels are <50% those at sea level. Found largely in migrating species is one of the most dramatic muscular adaptations: plasticity. For longdistance flights, birds, such as the garden warbler and thrushes, experience dramatic modifications in muscle composition and size, e.g., flight muscle hypertrophy, upregulation of oxidative enzyme activities and fatty acid binding proteins, and intramuscular fat stores that provide fuel that is readily accessible. On the other hand, many birds selectively atrophy muscles not important for flight in order to lose weight for migration, including the legs and digestive tract musculature that may be rebuilt when they reach stopover sites or wintering grounds.

The actual muscular control of bird wings doesn't stop at the big flight muscles, but instead juts out into a finely-achieved system of small muscles that allow multidimensional control. The avian wing includes a number of joints (including shoulder, elbow, wrist and finger) and these are moved by distinct muscles, permitting finely controlled variations in wing shape during flight. Being able to quickly change the shape of their wings in flight — their angle of sweep, their aspect ratio, their camber and their area — allows birds to perform better than planes at a range of flight conditions. Scapulohumeralis muscles rotate and abduct the humerus as well as bend and extend the elbow joints; muscles attached to the forearm, such as the biceps brachii, the triceps, and the brachialis control this critical angle between upper and lower wingsman. The complex muscle groups that make up the wrist and hand, such as the extensor metacarpi radialis and flexor carpi ulnaris, allow for advanced manipulation of the distal wing, to which the primary flight feathers that generate thrust are attached. Apart from the wings, another flight-critical system of birds is tail musculature, and the complex of levator, depressor and lateral movement muscles allow precise control of this critical aerodynamic surface, which contributes to stability, and early on in flight history also function as the first control surfaces. Birds use the muscles of the tail to make this structure an airbrake when landing, a stabilizer when flying slowly, and a rudder for steering and balance. The neuromuscular control systems ence controlling these muscles exhibit specialized adaptations for flight, such as unusually high motor neuron to muscle fiber ratios in muscles requiring fine control, specialized proprioceptors that report on wing position and loading, and unique stretchactivated sensory structures that sense small changes in feather position. These sensory-motor adaptations allow for the incredible precision behind avian flight, enabling birds to make microsecond adjustments to wing configuration in reaction to altering aerodynamic conditions, a capacity still out of the reach of even the most advanced human-crafted flying machines. The intricacy of the flight musculature underlying avian flight constitutes one of the most remarkable biomechanical designs in nature—a dynamically integrated system that combines outstanding power economy with fine-scale control, unparalleled endurability across its seconds-long production for escape flight to the multi-days-ten-hours sustained exertion of migrant transoceanic flight, and unparalleled plasticity to

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enable the swift response to varying physiological demands and environmental conditions. First, this muscular machinery, evolved over millions of years, makes birds the undisputed champions of powered vertebrate flight and allows the remarkable aerial maneuvers, that have captivated people for millennia, from the 200-plus-mph stooping dives of peregrine falcons to the hovering precision of hummingbirds and the transoceanic treks of Arctic terns.

#### **Feather Adaptations**

Feathers, the unique feature of class Aves, were a tremendously radical adaptation that paved the way for powered flight, insulation, waterproofing and visual signaling all through a single, highly adaptable structure in the vertebrate body. No other biological material is quite like feathers, which combine extraordinary mechanical properties — lightweight yet strong, supple yet durable, water-repellent yet breathable — to make them one of evolution's most successful developments. Feathers are made from a protein called beta-keratin, the primary structural component of all feathers, similar to but distinct from alpha-keratin, the protein that makes up mammalian hair, and â-Keratin itself exists in a complex hierarchical arrangement from molecular through many levels of organization to give rise to a whole feather. Feathers are believed to have emerged long before flight, given that exquisitely detailed fossils from theropod dinosaurs demonstrate that these rudimentary feather-like structures were originally selected for thermal insulation and visualization, only to be commandeered for aerodynamic purposes as birds took to the air. Modern birds have now evolved different feather types, each responsible for different functions and working as integrated systems critical to bird flight, thermoregulation and many more aspects of avian biology. The flight feathers (remiges and rectrices) include the most aerodynamically important feathers and shape the primary airfoil surfaces of the wings and tail. These pennaceous feathers exhibit a strongly asymmetric vane structure, with a narrower, stiffer leadingedge vane than trailing-edge vane—an adaptation to resist twisting of the feathers about their shafts during aerodynamic loading in the course of the wingbeat cycle. Feathers consist of a shaft called a rachis, with side branches called barbs and outer branches called barbules; the good mechanical properties of flight-feather marts Center For Distance & Online Education, MATS University rachides, in particular, has long been recognized, especifically its high stiffness-tomass ratio, due to a sandwich structure of dense cortex surrounding a lowdensity, foam-like medulla. This arrangement results in a high bending stiffnessto-weight ratio, analogous to purpose-built I-beams, enabling the flight feathers to resist deformation from the huge aerodynamic loads they encounter during flight without a significant weight penalty.

The specific configuration of flight feathers varies adaptively between species based on flight style and ecology. Birds that fish or hunt by precision-dive (e.g. swifts, falcons), however, have very narrow, sharply pointed wings with little overlap between adjacent primary feathers, minimizing drag at very high speeds, but decreasing low-speed maneuverability. To the contrary species from the forest that trade speed for maneuverability with broad wings and distinct slots, between the distal geometrically parallel primary feathers that act as multiple airfoils allowing nature to by pass the crossover between the progression of stall that occurs for any given flight speed hindering stall recovery through the slowing of the flight through choked environment. High-flying specialists such as albatrosses and vultures have wings with very high aspect ratios (the ratio of wingspan to chord width blurs up) and unique -primaries (the three outermost quills) work patterns that minimize induced drag at high for an attached gliding flight. Flight feathers at the microscopic scale have complex structural adaptations to improve function. The barbs that branch out to the side from the rachis are joined with their neighboring barbs by smaller secondary barbs called barbules, which carry tiny hooks (hamuli) that form a zipper, letting the feather vane work as a continuous aerodynamic surface but also, when needed, separate and reconnect. This complex microstructure allows birds to keep their feathers intact while flying but still deform adequately to absorb gusts, acting like a fail-safe against destructive levels of feather deflection. Excessive force removes the divine barbule connections not tearing apart, but locally separating, and can be realignedvia preening. S(ë) of flight feathers is adaptable across and within species, with the rigidity and resilience of keratin calibrated with regard to usage. In multiple species, leading-edge primary flight feathers are less flexible (i.e., contain relatively more rigid beta-keratin) than trailing-edge feathers, increasing resistance to aerodynamic

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twisting, while the keratin composition of diving birds' feathers reveals specialized adaptations to resist both aerodynamic and hydrodynamic forces.

In addition to feathers associated with flight, birds have several other types of feathers important for successful flight and migration. Contouring feathers on the body and wing draft produce a shape that has less drag aerially while still serving as insulation material to maintain temperature between body sections from air currents. These contour feathers usually undergo special timing of molting in migratory species to assure good insulation in order to minimize heat loss and aerodynamic efficiency during migration. Contour feathers microstructure presents unevenness across the body surface, where regions affected by higher airflow velocities in flight (e.g., head, leading edges) contain closely arranged barbules that detach less easily under aerodynamic stress. Beneath the outer contour feathers are down feathers, which have no or almost no rachis, and long, floppy barbs with no hook barbules. These form an insulating layer, effectively keeps air trapped close to the body, generating superb thermal efficiency which is essential for keeping the body temperature stable during high-altitude migration, when temperatures can plunge below "30 °C. True long-distance migrants commonly exhibit substantially more down feather density, in the period preceding migration, which improves their thermoregulatory ability during inherently high-temperature expansive migration, potentially crossing several climate zones. Semiplume feathers, which have structural elements of both contour and down feathers, are located at the interface between these two types of feathers and compose an intermediate category having combined functions in insulation and aerodynamic profiling. Some species have powder down, which are specialized feathers that never stop disintegrating into a fine powder that helps them withstand rain and water in inclement weather on their migratory paths. Bristle feathers have stiff rachis and few or no barbs and play specialized sensory functions near the mouth, eyes, and nostrils of many species possibly providing aerodynamic feedback similar to the vibrissae of mammals during flight. Filoplume feathers are composed of a long, bare rachis with a tuft of barbs at the tip, and are highly innervated, providing proprioceptive feedback about feather position and motion, enabling birds to make small adjustments to feather positioning in flight as needed to accommodate

These various feather types are efficiently shaped and positioned across the surface of the body to fulfill both aerodynamic and thermoregulatory roles. The wing feathers are laid out in very hierarchical groupings that form a working airfoil as the wing is extended. Several primary flight feathers (usually from 9–12 in number) are attached to the hand (manus) and are used to provide both thrust and to influence airflow at the wingtip - each primary can be independently twisted and rotated at its base to allow a range of precise control for each individual feather that can lead to complex manipulation of wingtip vortices. Next up are the secondary flight feathers, which attach to the ulna of the forearm (the bird's other 'wing'), forming the back edge of the inner wing and playing an important role in lift creation, while tertial feathers fill in the gap between the secondaries and the bird's body so as to maintain the airfoil. Specialized covert feathers (feathers that cover and lie above larger feathers, aka coverts) cover discrete attachment points of flight feathers, smoothing both upper and lower wing surfaces, and therefore reducing drag and stabilizing airflow. Alula, or bastard wing, are small feathers along the first digit (thumb) that acts as a leading-edge slot, which increases slow-flight performance by postponing stall, especially important during landing and takeoff. The arrangement of wing feathers is unique in that it provides a structure that can be finely (and actively) altered in flight to change wing camber, area, and twist, enabling birds to tailor wing aerodynamic shape to the various performance requirements of different flight modes-from high-lift requirements at takeoff to drag reduction priorities of cruising flight. The tail feathers (rectrices) together provide an important control surface which aids in stability, steering, and braking. Rectrices can spread and narrow, as well as raise and lower, enabling adjustments in flight path and stability, and their shape and stiffness properties vary adaptively across species according to requirements for maneuverability and habitat. Migratory birds have specially adapted feathers for long-distance flight, with reduced weight due to keratin distribution optimization, greater durability from reinforced barbule attachments, and specialized molt strategies for optimal feather condition during migration. whereas many migratory species perform a complete prebasic molt after breeding but prior to migration, leaving them with fresh, unworn

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plumage for their long migrations, and others have developed complex sequenced molting strategies that result in plumage replacement during the migratory period without compromising the dispersal ability of the feathered structures. The molecular and cellular bases of feather development are among the best studied aspects of avian biology, highlighting complex genetic regulatory pathways that govern feather morphogenesis, pigmentation, and structural characteristics. Recent advances in the fields of developmental biology and genomics have started to uncover how subtle differences in expression of a handful of key regulatory genes produces the stunning diversity of feather shapes across species, from the aerodynamic flight feathers of albatrosses adapted for over-water soaring, to thermogenic contour feathers of high-flying migrants like bar-headed geese as they cross the Himalayas to the water-repellent plumage of migratory waterfowl which must retain insulation and flight ability in spite of persistent submersion. The remarkable functional versatility of feathers, along with their ability for rapid evolutionary change, has been crucial to birds' success as the most speciose group of terrestrial vertebrates and has driven the evolution of widely-diistributed and successful ecological migratory strategies in birds.

#### **Beak and Feeding Adaptations**

The avian beak is one of the most multifunctional structures in nature, an organ that has experienced astonishing diversification to enable specialized feeding on wildly disparate ecological resources, but also to serve essential roles in preening, nest building, defensive use, courtship, and thermoregulation. While other vertebrates use heavy jaws and teeth, a lightweight but strong beak—composed mainly of a thin keratin layer over a bony core—typifies the weight-saving adaptations necessary for flight. Beak morphology in migratory birds represents a trade-off between adaptation to a specific mode of feeding versus constraints imposed by long-distance travel, requiring functional compromises that allow successful foraging across often geographically distinct breeding and wintering habitats, with potentially divergent food sources in use. The remarkable diversity in size and form of beaks among the ~10,000 bird species is one of the most well-known examples of vertebrate adaptive radiation, with morphological

specializations ranging from the massive, crushing bills of seed-eating grosbeaks to the delicate, nectar-probing bills of hummingbirds, the filter-feeding lamellae of ducks, the chisel-like structures of woodpeckers, and the hooked weapons of raptorial taxa. This diversity of morphology is achieved by variation in a number of critical parameters: length, depth, width, curvature, tomia structure (cutting edge structure), tip shape, and internal reinforcement schemes. Recent advances in evolutionary developmental biology have increasingly illuminated the developmental origin of this variation, highlighting how relatively subtle changes in the timing, location and amplitude of expression of key regulatory genes can produce radically divergent beak morphologies. Studies of Darwin's finches on the Galápagos Islands have revealed many genes, including BMP4 and CaM, whose levels of expression correlate with the aspects of beak shape, illustrating the mechanistic insight of how evolution has generated such astonishing diversity from a common ancestor. Beaks in most birds serve primarily a feeding function, its morphology closely matched with dietary specialization. Granivorous (seedeating) birds usually have short, conical beaks with high bite forces, sometimes including a special palatine formation that allows seeds to be manipulated and stripped of their husks effectively by means of a muscular tongue. Specifically, among migratory granivores, beak morphology may adapt according to the type of seeds available when the birds are present at different times of their annual cycle, with evidence for plasticity in beak dimensions during the annual cycle, reflecting differential wear and growth of beak structure to maximise feeding efficiency as diet composition varies between breeding and wintering grounds.

Birds feeding on insects exhibit a great variety of adaptations of the beak form depending on their hunting style and prey type. Swallows and swifts, two groups of aerial insectivores, have developed wide, flat beaks that increase the area of capture during flight, and many also possess rictal bristles that assist with both prey detection and capture success. Gleaning insectivores that pluck insects off of vegetation, like warblers, tend to have comparatively slender, pointed beaks adapted for maneuvering around small prey items among leaves and twigs. Bark-

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foraging specialists (e.g. nuthatches) have straight, chisel-like beaks adapted specifically for probing crevices whereas ground-foraging insectivores tend to display intermediate morphologies that balance versatility with efficiency (Feraud et al. 2015). The migratory insectivores encountered a challenge of seasonal variation in prey type and foraging substrate at their breeding and wintering grounds, resulting in beak morphologies which need to perform under a range of conditions and not be maximally specialized for one prey type or microhabitat. Nectarivorous birds, such as hummingbirds and sunbirds, have evolved long, tubular bills that enable them to reach nectar deep inside a flower; this morphological adaptation has co-evolved with the morphology of the flowers of plants they pollinate, ensuring both the bird's foraging efficiency and subsequent pollination. The correlation between beak length and corolla tube depth is a classic example of ecological specialization, with some indigenous nectarivores demonstrating remarkable adaptations to particular plant partners across their range. ESM The Most common Regularity of Nectarivorous Beaks: Tongue Morphological Specializations. Some migratory nectarivores, including rubythroated hummingbirds, have to preserve these highly specialized feeding adaptations while making remarkable long-distance itineraries, including nonstop flights over the Gulf of Mexico. There are several beak specializations of piscivorous (fish-eating) birds that depend on how they hunt. Pelicans, plungediving specialists, have pouch-like pouches that work like nets, and, as with herons and egrets, who have vicious spear-like beaks designed for impaling prey, mergansers whole tomia (the leading edges of their jaws) are serrated, to keep slippery fish from escaping. These species not only demonstrate commensurate adaptations within the skull and jaw musculature, such as specialized reinforcement patterns that decrease impact loads during predation and other behavioral regimes, but also display adapted musculature geometry for accelerating strikes or persistent grip. Adaptations throughout the kinetic skull in many piscivorous birds allow for controlled flexion about specific intercepts in the skull, augmenting speed and force of prey capture kinematics.

#### SELFASSESSMENT QUESTIONS

## b) Buccal cavity c) Lungs d) Skin

1. Which of the following is NOT an accessory respiratory

## 2. Which of the following fish exhibits mouthbrooding as a parental care strategy?

a) Catfish

a) Gills

organ in fishes?

- b) Tilapia
- c) Shark
- d) Goldfish
- 3. What is the primary function of cutaneous respiration in amphibians?
- a) Reproduction
- b) Respiration through the skin
- c) Protection from predators
- d) Digestion of food

## 4. Which of the following is a neurotoxic snake venom component?

- a) Cobra venom
- b) Rattlesnake venom

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c) Viper venom

d) None of the above

#### 5. Which structure helps birds maintain altitude during flight?

a) Large intestine

#### b) Hollow bones

c) Thick skin

d) Heavy muscles

6. Bird migration is mainly influenced by:

- a) Wind direction
- b) Seasonal food availability
- c) Predators
- d) Reptilian ancestors
- 7. Which of the following birds exhibit long-distance migration?
- a) Penguins
- b) Swallows
- c) Chickens
- d) Owls

## 8. Which adaptation allows birds to have lightweight but strong bodies?

- a) Presence of scales
- b) Hollow bones
- c) Thick skin

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d) Large intestines

#### 9. Which part of a snake's body is responsible for venom secretion?

- a) Tongue
- b) Liver
- c) Fangs
- d) Lungs

#### 10. Which is NOT a characteristic of non-poisonous snakes?

- a) Round pupils
- b) Small fangs
- c) Presence of venom glands
- d) Slower reflexes compared to venomous snakes

#### **Short Questions:**

- 1. What are accessory respiratory organs in fishes?
- 2. Define parental care and give one example from amphibians.
- 3. Differentiate between neurotoxic and hemotoxic venom.
- 4. What is cutaneous respiration? In which animals is it found?
- 5. How do fish perform air-breathing in low-oxygen environments?
- 6. What are the different types of parental care in fishes?
- 7. How can you distinguish between a poisonous and non-poisonous snake?
- 8. What is the role of hollow bones in birds?
- 9. Give two examples of migratory birds and their migration routes.



10. How do snakes detect their prey without external ears?

#### Long Questions:

- 1. Describe the accessory respiratory organs in fishes and their role in survival.
- 2. Explain different types of parental care in fishes and amphibians with examples.
- 3. Discuss the structure and function of venom in snakes. How does it affect prey?
- 4. Compare the flight adaptations of birds with terrestrial reptiles.
- 5. Explain the importance of bird migration and the factors that influence it.
- 6. Differentiate between the circulatory system of amphibians, reptiles, and birds.
- 7. How do poisonous snakes inject venom? What are their adaptations for hunting?
- 8. Discuss the importance of parental care in amphibians. How does it benefit offspring?
- 9. What skeletal adaptations help birds in flight? Provide structural comparisons.



10. Describe the evolutionary significance of amphibians as a transition group between fish and reptiles.



#### MODULE 3

#### **COMPARATIVE ANATOMY I**

#### 3.0 Objective

- To study the vertebrate integument and its evolutionary adaptations.
- To analyze the circulatory system's variations across different vertebrate groups.
- To understand the evolution of the heart, aortic arches, and the portal system.

#### **UNIT 08**

#### Vertebrate integument and its derivatives

The integument, from the Latin for covering (integumentum), is one of the most spectacular evolutionary adaptations documented among vertebrate lineages. The integument, the body's largest organ system, is an important interface between the organism and its environment. This delicate boundary system has developed to serve many indispensable purposes: protection from physical injury, pathogens, and radiation; regulation of body temperature and water balance; and sensory perception, social communication and, in some taxa, even gas exchange. The structural and functional versatility of the vertebrate integument is mirrored in its evolutionary history across a range of ecological niches, from aquatic to terrestrial, from polar to tropic. Vertebrates have a skin structure that comprises two major components: the epidermis and the dermis. The epidermis is the outermost layer and comes from embryonic ectoderm, made of stratified epithelial cells known as keratinocytes. Keratin, present in the skin as the predominant structural protein synthesized by these cells, a fibrous protein that gives the epidermis high tensile strength and is impervious to water. The dermis is the layer of skin deep to the epidermis and

arises from embryonic mesoderm (the mesenchyme). The dermis is mainly made up of dense, irregular connective tissue with large amounts of collagen fibers, giving both strength and elasticity. Between these two main layers is often the basement membrane, a thin, specialized extracellular matrix that attaches the epidermis to the dermis.

The transition from aquatic to terrestrial environment represented a major step in vertebrate evolution and represented a strong selective pressure on the vertebrate integument. The early aquatic vertebrate integument was relatively simple and primarily functioned in protection and osmoregulation. But the demands of life on land — such as desiccation, temperature extremes and increased mechanical stresses - shaped the evolution of more elaborate integumentary features. This underpinned the amazing diversity of epidermal and dermal derivatives seen in modern vertebrate taxa, from fish scales to bird feathers to mammal hair. Recent studies have shown that the integument is not just a passive protective barrier but a signalling organ system with endocrine, immune, and neurosensory functions. The integument produces vitamin D, secretes antimicrobial peptides, and contains specialized receptors that sense temperature, pressure, and pain. Additionally, integument has deeper evolutionary implications, as it plays a critical role in mate choice, species recognition, and adaptation to different ecological niches, all of which drive diversification and speciation. Comparative studies of integumentary structures have been aided by advances in developmental biology that have highlighted the molecular mechanisms that underlie morphogenesis of these structures, exposing conserved genetic pathways that have been tweaked during vertebrate evolution to yield the remarkable diversity of skin structures we see today.

#### **Comparative Integumentary Structures of Vertebrates**

The fabulous diversity of integumentary structures within vertebrate taxa exemplifies one of the most spectacular examples of adaptive radiation in the evolution of animals. In all cases, comparative studies illustrate both conserved traits common to all vertebrates, as well as lineage-specific structures that arise

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in concert with distinct functional demands and evolutionary histories. The integument is relatively simple among agnathans, the most basal vertebrates, such as lampreys and hagfish. The epidermis is mucus-secreting and not extensively keratinized (as in more derived vertebrates). Instead, their skin is covered with innumerable unicellular glands that form a protective, smooth slime. The dermis of these organisms is thin with low cell type differentiation, particularly when compared with higher vertebrates. This ancestral trait offers a window into the earliest phases of vertebrate integmentary evolution. Chondrichthyans (sharks, rays, and chimaeras) possess a more durable integument, the primary feature of which are placoid scales, often referred to as dermal denticles. These structures, homologous to vertebrate teeth, have a pulp cavity that is surrounded by dentine and covered by vitrodentine, an enamel-like material. Placoid scales, which are arranged in a regular fashion upon the body surface to promote hydrodynamic efficiency and minimize drag during swimming. Chondrichthyans have a relatively thin epidermis, and well-developed dermis with abundant collagen fibers in a crossed-helical arrangement for strength and flexibility. Osteichthyans (bony fishes) exhibit a more diverse array of scale types. The actinopterygians (ray-finned fishes) normally have a low scale density with overlapping cycloid or ctenoid scales arising from bony tissue developed within the dermis. These scales grow throughout life by adding concentric rings analogous to tree rings, allowing the determination of age in many species. Sarcopterygians, such as the coelacanth and lungfishes, possess cosmoid scales, comprising layers of bone, dentine, and enamel-like cosmine. The bony fish epidermis is rich with mucous cells and has some species that have alarm substance-filled cells which release pheromones on nerve damage on the skin, signaling conspeciess of danger.

Such adaptation to land required major changes in the vertebrate integument, most vividly evidenced in amphibians. Extant amphibians feature a thin skin that is highly permeable, and assist in respiratory gas exchange, a characteristic that is unique among tetrapods. Their skin is also rich in multicellular glands, including mucous glands that keep the skin moist, and granular (poison) glands that secrete chemicals to deter predators. Molting maintains the epidermal homeostasis in amphibians, which is controlled by thyroid hormones. Amphibians have different variation, where skins of some amphibians still possess dermal scales, but for many, dermal scales have been lost to a certain degree, this might be related to the significance of cutaneous respiration in this group. Reptiles are the key transitional clade in developing a fully land adapted integument. The epidermis is heavily keratinized, creating a specialized body covering impermeable to water to prevent desiccation. Human skin consists of multiple layers, of which the outermost layer is the epidermis that undergoes ecdysis (shedding)(5) to provide room for growth and renewal. In contrast to the fish, reptilian scales are primarily epidermal structures made from â-keratin, often overlying dermal osteoderms. From small, granular scales of lizards to large, keeled scales of crocodilians and the specialized scutes of chelonians, the pattern, shape, and texture of these scales vary dramatically throughout reptilian taxa. As modified archosaurs, birdshave evolved the most complex epidermal appendages of vertebrates: feathers. These complex structures, made of primarily â-keratin, first evolved in the context of thermoregulation and were subsequently co-opted for flight in multiple lineages. The avian integument is also notable for leg and foot scales, clawed digits, and an evolved keratinous beak that replaces teeth. Birds have a thin layer of dermis, and subcutaneous fat is arranged in disjoint deposits rather than as a continuous layer, an adaptation reducing mass for flight.

Mammals likely possess the greatest diversity of integumentary specializations. Hair, composed of á-keratin, and growing from complex follicular units containing sebaceous and sweat glands, is the defining feature of mammalian integument. Mammalian dermis is thick, highly vascularized and its structure varies regionally to meet functional demands. Nails, claws, hooves, horns, antlers, quills and baleens are some of the unique mammalian integumentary derivatives; they all are variations of keratinized epidermal structures. Such a thick layer of subcutaneous adipose tissue facilitates insulation and becomes advantageous as an energy store in mammals—both of which are remarkable thermoregulatory

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advantages. In vertebrate taxa, integumentary coloration is used for camouflage, social signaling and thermoregulation. Coloration results from different mechanisms: usually pigment cells (chromatophores), structural colors from refraction of light, or a mixture of both. The developmental and genetic basis for these distinct integumentary structures is gradually being uncovered, highlighting striking conservation in some molecular pathways, along with lineage-specific innovations that have fostered morphological diversification.

## Glandular, dermal derivatives (glands, scales, horns, claws, feathers & hairs)

Vast evolutionary diversification of the vertebrate epidermis has resulted in an astounding diversity of specialized structures with diverse functions in various taxonomic groups. While these epidermal derivatives have different morphologies, they share a common ectodermal origin and similar molecular pathways, which is a classic example of descent with modification, a principle of evolution.

Integumentary Glands: Integumentary glands are among the most primitive of epidermal specializations, and they are found in a variety of forms in each of the vertebrate classes. These secretory structures usually arise as invaginations of the epidermis and their unique morphology and secretory products are indeed adaptations to specific ecological demands. Mucous glands, common in a number of aquatic and semi-aquatic vertebrates, excrete glycoproteins that create a protective and lubricating mucus layer. In fishes, this secretion is produced by unicellular goblet cells dispersed across the epidermis, and it serves to reduce friction during swimming and to act as a first line of defense against pathogens. Amphibians have developed more complex, multicellular mucous glands in order to keep their skin moist, which is important for cutaneous respiration and minimizes water loss during relatively rare sojourns on land. Defensive substances include those derived from poison or granular glands, especially evolved particularly in amphibians

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that secrete toxic or noxious compounds. These vary between the mild skin irritants of some frogs to the potent neurotoxins of dendrobatid "poison dart" frogs, where the toxins are frequently sequestered from dietary sources. Similar glands are also present in some fish (e.g., the venomous spines of scorpaenids) and some reptiles (e.g., the nuchal glands of some natricine snakes).

The most diverse integumentary glands by far belong to mammals, reflecting their adaptation to a wide range of ecological niches. Sebaceous glands which usually occur with hair follicles, release an oily liquid called sebum, which waterproofs the skin and hair and prevents microbial growth. Eccrine sweat glands, which are widely distributed across body surface in humans and some other mammals, produce a hypotonic secretion that is important for thermoregulation via evaporative cooling. The larger apocrine sweat glands, found only in certain skin areas, secrete a thicker fluid with proteins and lipids that can be decomposed by skin comensal bacteria and therefore are responsible for the body odor, and it can act in chemical signalling. Besides the distinctive mammary glands which provide milk to nurse their young, mammalian glands may also include scent glands (for territorial marking or communication, such as elephants' temporal glands or the anal glands of carnivores), and even more exotic examples such as the infraorbital glands of male platypuses that secrete venom for defensive use.

Scales: Another important group of epidermal derivatives are scales, which have a complicated evolutionary history, with different kinds of scales evolving independently in different lineages of vertebrates. Fish scales are extremely diverse in structure and composition. They are dentine-based structures covered by vitrodentine (akin to enamel), and possess a pulp cavity with blood vessels and nerves, in accordance with their homology with teeth, as can be recognized for placoid scales or dermal denticles of chondrichthyans. Ganoid scales, which are found in bichirs and gars, are composed of an inner layer of bone and an outer layer made up of ganoine, a specialized enamel-like substance. Unlike other types of scales, elasmoid scales — including the cycloid and ctenoid scales that are

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found on most teleost fishes - are made of acellular bone and collagen and grow continuously throughout an animal's life via the accretion of growth rings. Reptile scales are fundamentally different from fish scales in that they are essentially epidermal appendages constructed of â-keratin. They are created during development by controlled patterns of epidermal thickening and folding, where the underlying dermis conforms to this pattern. This is also manifested in the tocotoums (which appears to bridge between skin and feather) and imbricate scales of birds, which are in comparison to the highly complex ornamental structures that evolved in many types of reptiles. Rather it is a reflection of the vast diversity of reptiles and their adaptations to different niches regarding the presence of reptilian scales, ranging from the small, granular scales of many lizards, and the large scutes of crocodilians, to the unique shell of turtles (which combines epidermal scutes with dermal bone) of reptilian scale morphology.FlioretycarnispecingtusRummamentratus Paramount meridiancrilab's appear out of the tropics and bear a pair of scabs, or large scutes in common parent behavior. Ecdysis (the shedding and replacement of the keratinized layer - growth and regeneration) is periodic.

Birds maintain scales on their feet and legs, which are homologous to those of reptiles, but feathers cover most of their bodies. This pairing illustrates the evolutionary link between scales and feathers, lending support to developmental studies indicating they form from similar initial conditions. Some mammals, most significantly, pangolins with their unique overlapping scales, and armadillos with their hardened lens-like plates of skin, convergently evolved scale-like barriers, although they are distinct in embryogenesis and composition from true reptilian scales.

Horns, Claws, and Hooves: Horns, claws and hooves are keratinized epidermal structures specialized for defense, offense or locomotion, respectively, and all represent specific structural adaptations associated with their niche. Claws, shared by numerous tetrapods, is a curved, pointed keratinized sheath covering a digit's terminal phalanx. The claw develops from a germinative layer at its base, as new keratin forces the older stuff toward the front. The amount of MATS Center For Distance & Online Education, MATS University curvature, acute versus blunt tip, and retractability vary widely in nature, representative of their function ranging from climbing and grasping to burrowing and predation. Hooves are specialised claws adapted for bearing weight in ungulate mammals. They touch on a hard, keratinized wall (which is equivalent to the human nail plate) that wraps around the tip of the digit, and a softer sole that makes contact with the ground. Internally, however, are interlocking keratin tubules arranged in such a way as to provide both tensile strength and flexural rigidity, with growth occurring constantly from the coronary band, which balances wear and maintains the hoof capsule for a lifetime. True horns, which are found in groups including cattle and antelopes (bovids), are permanent, unbranched structures that have a bony core derived from the frontal bone of the head and are covered by a sheath (called a horn) of keratin that grows continuously from the base. In comparison, the antlers of cervids (deer) are purely bony, flesh-covered structures (covered in velvet (a specialized skin)) that are both shed and regrown annually and are most often branched. Rhinoceros "horns" are be weirder still, because they consist of tightly compacted bundles of keratin fibers and lack bone altogether. Other horn-like structures are the branched sheath of keratin over a bone for a pronghorn (shed every year), the gabled ossicores of giraffoids (which are never shed) and the keratinized casques of hornbills and cassowaries.

**Feathers:** Feathers, the synapomorphy of all avialan theropods (birds), are the most complex epidermal derivatives found in Vertebrates. Feathers, predominantly composed of â-keratin proteins, grow from follicular structures characteristic of those from which reptilian scales arise, bolstering their evolutionary origin from scales in dinosaurian progenitors. A Feather develops from an epidermal placode that forms a tubelike feather germ. This structure is elongated and further differentiates into the mature feather via a complex process involving cell proliferation, differentiation and programmed cell death which generate the branching structure characteristic of the mature feather. Once grown, feathers are dead structures, renewed through molting cycles regulated

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by hormones and photoperiod. Pennaceous feathers are structured around a central shaft or rachis from which extend barbs, which in turn bear barbules with microscopic hooklets (hamuli) that zip the barbs up into a continuous vane. This hierarchical organization provides fantastic structural properties: strength, flexibility, and lightweight construction necessary for flight. Plumulaceous (down) feathers do not have hooks on their barbules, forming a fluffy structure in which air is trapped and provides thermal insulation. In addition to their primary functions of flight and insulation, feathers are used in display (often via structural coloration or pigment-based coloration), waterproofing, sensory perception (filoplumes), and sound production (some species). The genetic and developmental processes guiding feather formation have been well documented, and many of the involved signaling pathways (e.g., Sonic hedgehog, BMP, and Wnt) are widely conserved during vertebrate skin appendage formation.

Hair: Hair, the defining structure of the integumentary system in mammals, derived independently from feathers, yet performs analogous insulation, sensation and display functions. Made mostly of á-keratin (as opposed to the â-keratin of reptilian scales and well-feathered birds), hair grows from complex follicular units buried in the dermis. The hair follicle arises from an epidermal placode which invaginates into the underlying dermis and is a complex structure, comprising a number of different cell populations. The structure of hair itself has three layers: an outer cuticle of overlapping scales, a cortex of keratin-filled cells that provides strength, and sometimes an inner medulla of loosely arranged cells and air spaces. At the follicle base is the hair bulb with a germinative matrix of rapidly dividing cells that forms the growing hair. The follicle is associated with sebaceous glands, arrector pili muscles that can erect the hair, and a rich sensory and vascular supply. In general, hair grows in cycles with three different phases: an active growth phase (anagen), a transitional phase (catagen), and a resting phase (telogen). These phases last longer or shorter in different body regions and species, resembling the final length and thickness of the hair. Unlike feathers, which are replaced wholesale during a molting phase, mammalian hair is usually replaced in a mosaic fashion, preserving a continuous coverage. The astounding variety of mammalian hair species comprises the fine underfur and stiffer guard hairs found in most mammals, the modified vibrissae (whiskers) that are crucial for tactile sensation, and more extreme specializations like quills in porcupines and echidnas, pangolin scales (also modified hair), and whale baleen plates (mysticetes). Just like feathers, the color of hair can be due to pigmentation (mainly melanins), or rarely, structural color effects.

#### **Dermal Derivatives**

The structural and functional diversity of the vertebrate integument is largely attributed to the specialized derivatives of embryonic mesoderm, the source of the dermis. Dermal derivatives, while far less conspicuous than epidermal structures, are critical for protection, support, and physiology in vertebrate lineages.

**Dermal Ossifications:** Dermal ossifications, or osteoderms, are among the oldest and most common dermal derivatives, being present in various forms of different vertebrate lineages. They form within the dermis and do not replace cartilaginous precursors, making them different from the endochondral bones of the axial and appendicular skeleton. Dermal bones constituted a full armor in the bodies of numerous primitive vertebrates, such as the ostracoderms and the placoderms. This condition holds true, as this elaborate dermal skeleton was gradually lost during vertebrate evolution and survives only in some genera as skull bones, clavicles, and gastralia. The postcranial dermal skeleton of fish is most commonly represented by the scales — in many taxa comprising a considerable bony component that is formed within the dermis and overlaid by epidermal-derived enamel-like substances. In modern tetrapods, osteoderms are most highly developed in crocodilians, where they encompass a wide armor of interlocking bony plates that tautly cover the dermis, overlaid with epidermal scales. These osteoderms have channels through which blood vessels run and, in some species, such osteoderms play a role in heat exchange. Similar, though usually less, dermal ossifications are found in many lizards, especially in the anguids



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(alligator lizards, glass lizards) and the helodermatids (like the Gila monsters). Dermal ossification has led to the most extreme developments of dermal bone of any living reptile in turtles, whose carapace and plastron contain elongated ribs and gastralia as well as extensive dermal bone to form a protective shell.

Amphibians do not have substantial dermal ossifications, but a few members within the order Caudata develop scales within dermal pockets that convergently evolved on the basis of a fibrous tissue layer rather than on the basis of dermal bone, as seen from fish scales. Extensive dermal armor is present in the Xenarthra among mammals, particularly in armadillos, which have a carapace of overlapping bony scutes. Dermal ossifications are more restricted in some other mammals, which include the ossified dermal shields of certain rhinos and bone antlers in cervids, both of which are modified osteoderms that are covered by skin (velvet) during their growth, which is temporary in nature. Histologically, osteoderms typically are composed of a thick layer of compact bone surrounding a cancellous core and broadly mimic the structure of the membrane bones surrounding the brain. The development of scalae is a product of dermal fibroblasts differentiating into osteoblasts in the presence of inductive signals, indicating the diverse developmental plasticity of dermal connective tissue.

**Chromatophores:** In vertebrates, specialized pigment cells called chromatophores are present in the dermis, and as they produce, store and even redistribute pigment granules, they have a substantial impact on skin color. Although the epidermis can also include pigment—specifically melanin in mammals—the dermal chromatophores are chiefly accountable for the dynamic and diverse coloration patterns found in numerous vertebrates. Chromatophores of vertebrates are traditionally classified in several different chromatophore types according to their spectral properties and pigment content. Melanophores hold dark granules of melanin (which are called melanosomes). Yellow to red pigments, which mainly include pteridines and carotenoids, are present in xanthophores and erythrophores. Iridophores and leucophores typically contain crystalline platelets of guanine or other purines which reflect and scatter light, producing

structural colors through thin-film interference. One of only a few types of blue pigmented organelles, cyanophores have been described in several fish species. The distribution and density of chromatophore types follows diverse patterns across vertebrate taxa. All major chromatophore types are typically found in fishes, amphibians, and reptiles, which is responsible for the remarkable diversity and often variable colour patterns observed in these groups. In contrast, and as described in the paper pioneered by d'Orgeix et al., birds rely more markedly on carotenoid pigments (derived from dietary) and feather microstructure for color, although dermal chromatophores also play a role in exposed skin coloration. Chromatophore diversity is reduced in mammals, with the primary pigment cell type being a melanocyte (melanin is synthesized and passed to epidermal keratinocytes).

In many lower vertebrates, such as teleost fishes, amphibians, and some reptiles, chromatophores can physically change their shape by redistribution of pigment granules in the cell. Such dynamic changes in coloration, regulated by neuronal and endocrine mechanisms, allows quick modifications of background coloration, temperature regimes or social situations. In contrast, morphological colour change is a longer-term change in chromatophore number, size, or pigment content, generally linked to developmental stages, seasonal changes, or pathological conditions. Chromatophores are derived from the neural crest, a vertebrate-specific, multipotent cell population that can migrate widely during embryogenesis. The specification, migration and ultimate patterning of chromatophores is controlled by complex genetic networks, comprising transcription factors such as MITF and Sox10, signalling molecules such as Wnt, and guidance cues that secrets orderly pattern of their atwhich to patern.

**Dermal Vascular Networks:** The dermis is rich in vascular networks not only used for basic nourishment, but also for thermoregulation, in- flammation and, in many species, functions related to specific pigmentation or even respiration. Dermal vascular supply includes a deep plexus at the dermal-hypodermal junction, a superficial plexus at the dermal-epidermal boundary, and connecting vessels between these layers. This pattern has regional specialization throughout the body,

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with tissue areas that have high metabolic demands or specialized functions having particularly dense capillary networks. Dermal vasculature is essential for thermoregulation in endothermic vertebrates (birds and mammals). During heat, vasodilation increases blood perfusion in the skin to promote heat loss via radiation, conduction, and convection. In cold conditions, vasoconstriction decreases cutaneous blood flow, helping to maintain core body heat. Arteriovenous anastomoses are specialized vascular structures that shunt blood directly from arteries to veins, allowing for rapid control of blood flow through the capillary beds and, thereby, the rate of heat exchange. Highly specialized vascular heat exchange systems can be found in cetacean rete mirabile in the flukes and dorsal fins, vascular networks in the bills and legs of birds, and specialized regions in larger mammals devoted to thermal windows. In many ectothermic vertebrates, dermal vascular control plays a role in behavioral thermoregulation, with vasodilation enabling enhanced uptake of external heat and darker color. Thermoregulation-related dramatic coloration changes can be seen in some reptiles and are partly mediated by changes in blood flow that modify the visibility of underlying chromatophores

In amphibians, where skin is highly vascularized and can serve as a co-opted respiratory organ, dermal vasculature becomes especially specialized 19. The capillaries are very close to the skin surface, and the diffusion barrier is very small, making gas exchange efficient. This cutaneous respiration is essential in terrestrial amphibians, especially when metabolic demands are low and in obligate aquatic species such as the Titicaca water frog, which entirely lacks lungs. The vascular structure of the dermal region also contributes significantly to immune and wound healing function. These inflammatory features contribute to the normal responsefollowing inflammation, blood vessels weaken and expand, which allowsmore immune cells and mediators to migrate into the inflamed tissues. After injury, angiogenesis (the growth of new blood vessels) is critical for granulation tissue formation and healing of the wounded integument.

Sensory Receptors: The dermis contains a variety of sensory receptors that convey information about the external environment and the state of the integument itself to vertebrates. These receptors, while differing in complexity and specificity among taxa, make it possible for the organism to sense touch, pressure, vibration, temperature, pain and, in some taxa, specialized modalities such as electroreception. Mechanoreceptors include several different types sensitive to mechanical deformation of the skin. Overview of Meissner's corpuscles Meissner's corpuscles are rapidly adapting receptors located in the dermal papillae of mammals and respond to light touch and low-frequency vibration. A second type of mechanoreceptor are the Pacinian corpuscles, found slightly deeper in the dermis or hypodermis that are also rapidly adapting but respond to high frequency vibration and changes in pressure. Merkel cell-neurite complexes, stationary at the epidermal-dermal junction, are slowly adapting receptors that relay information on sustained pressure and texture discrimination. Ruffini endings, located in the deeper dermis, are sensitive to stretch and slow, ongoing pressure. Thermoreceptors encompass separate populations for the detection of warmth (mediated by TRP channels that depolarize with increasing temperature) and cold (mediated by another set of TRP channels activated upon cooling). These receptors allow for discrimination of small temperature differences and are also involved in thermoregulatory behaviors in vertebrate taxa.

These are called nociceptors (pain receptors) and they are sensitive to potentially damaging stimuli. They include mechanonociceptors that are activated by extreme pressure, thermonociceptors that respond to extreme temperatures, and chemoreceptors that are sensitive to inflammatory mediators and irritants. The dermis also contains pruriceptors — specialized receptors that produce the sensation of itch when activated by certain chemical stimuli. Apart from these broad sensory endowments, many vertebrates bear specialized dermal receptors for niche habitats. Ampullae of Lorenzini are clusters of electroreceptors found in chondrichthyans, which can sense very small electrical fields generated by prey, or used in navigational behavior. In hot, dry environments, sensory pits in

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crotaline and boid snakes can detect infrared radiation, forming a thermographic image of prey or parts of the environment. Mechanosensory lateral line system of fishes and aquatic amphibians containing neuromast organs are sensitive to water motion and pressure gradients, which allow schooling behavior, prey detection and obstacle avoidance. For example, many specialized integumentary sense organs have both a dermal and epidermal contribution that work in concert. Mammalian vibrissae (whiskers) are exquisitely sensitive tactile structures comprised of specialized hair follicles highly innervated by sensory structures. This is akin to bill-tip organs of many birds and push rods in monotremes that associate epidermal and dermal sensory structures for tactile foraging. The neural circuitry involved in processing integumentary sensory information is built upon a diverse layer of organization, ranging from simple to complex reflex arcs to elaborate cortical representations. In mammals, especially higher primates, large areas of the somatosensory cortex are used to process tactile information from highly sensitive regions such as fingertips and lips. This neural investment speaks to the evolutionary importance of integumentary sensation for survival across a variety of ecological contexts.

The evolution of the vertebrate integument is arguably one of the most dynamic adaptive responses in biological systems that transitioned from as a basic protective envelope in primitive aquatic lineages to a highly sophisticated, multifunctional organ system across extant taxa. The integument has enabled occupation of effectively every habitat on Earth — from the deepest oceans to highest mountains, and from poles to deserts — through diversification of both epidermal and dermal derivatives. The origin and evolution of the integument are emblematic of the major transitions in vertebrate evolution. The transition to terrestrial ecosystems led to the evolution of water-impermeable epidermal barrier and specialized gas exchange surfaces. The evolution of endothermy in birds and mammals was enabled by insulating structures—that is, feathers and hair—that transformed thermal physiology. During these transitions, the fundamental structural plan for epidermis and dermis has been retained, but the particular derivatives have diversified to fulfill the demands of each ecological setting.

Contemporary comparative studies yielded unexpected homologies between predictive structures. The close developmental and molecular relationships of scales, feathers, and hair indicate common ancestral mechanisms modified during evolution. Likewise, the common neural crest ancestry of diverse pigment cells in vertebrate lineages suggests ancient commonalities in coloration mechanism.

The integument remains a frontier of biological research, with new findings continually emerging regarding its physiological roles, developmental processes, and evolutionary origins. Here, we summarize how technological advances in genomics, developmental biology, and biomechanics are yielding unprecedented insights into the molecular basis of skin appendage formation, the mechanobiology of protective structures and the genetic basis of adaptation to distinct environments. In addition to its scientific significance, understanding vertebrate integument has practical relevance for diverse disciplines. Biomimetic approaches take lessons from natural integumentary designs to create new material qualities such as lotus effect self-cleaning surfaces, water-repellency, structural coloration. Comparative studies across vertebrates also can inform medical research about skin development and regeneration, which has the potential to lead to treatments for wounds, burns and congenital disorders. Conservationists are placing greater emphasis on the specialized integumentary adaptations of endangered species when designing management strategies. Our exploration, if limited to the vertebrate integument, reminds us how far we have come since the days of trying to make sense of the fossil record but also how far we have to go before we can say we understand how organisms are able to adapt to their environments. At the interface of the organism and the environment, the skin and its derivatives is still an excellent example of the form follows function axiom in living systems, each specialized structure contributing to the narrative of vertebrate evolution.

#### **UNIT 09**

#### **General Plan of Circulation in Various Groups**

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The circulatory system is one of the most rudimentary physiological systems in animals, developing from diffusion mechanisms in primitive organisms to complex, systematized solutions in vertebrates. This tour de force covers topics such as blood structure and function, the evolutionary journey of the heart, the formation of aortic arches, and the specialized portal systems that have evolved through the different taxonomic groups.

#### The structure and function of blood

Blood is the main transport medium in closed circulatory systems, using throughout the body to transport and exchange essential substances between blood and tissues and skeletal muscles, maintaining homeostasis. Its composition and functions have developed in parallel with greater organismal complexity, mirroring environmental demands and metabolic needs where evolution has taken place.

Blood Composition: The two major components in vertebrate blood are the plasma and the formed elements. Plasma is a clear straw-colored fluid that makes up about 55% of blood volume, and is made primarily of water (90-92%); proteins; electrolytes; nutrients; hormones; waste of respiratory gases, etc. The other 45% is composed of the formed elements: erythrocytes (red blood cells), leukocytes (white blood cells) and the thrombocytes of mammals (platelets) or thromocytes (nucleated blood cells) of non-mammalian vertebrates. The most numerous cellular component of blood, erythrocytes are mainly responsible for the transportation of oxygen. All mammals lack mature erythrocytes, which is unique in vertebrate evolution because now there is no need for a nucleus and most organelles, allowing for more hemoglobin to build up and increase the amount of oxygen that can be carried. In comparison, most non-mammalian vertebrates have nucleated erythrocytes that are generally larger and more sparse. They are much less numerous than erythrocytes, but are involved in the immune defence against pathogens and foreign substances. The different types of cells can be grouped into granulocytes (neutrophils, eosinophils, and basophils) and agranulocytes (lymphocytes and
monocytes), and each has a specialized role when it comes to immune response and inflammation. Different species show wide variations in the relative proportions of leukocyte types, which reflects differences in immune strategies and environmental challenges. They are necessary for hemostasis; initiate coagulation cascade prevents excessive loss of blood upon injury of blood vessel. Platelets are small, anucleate baubles derived from megakaryocytes in mammals, and thrombocytes are present as whole, nucleated organelles in non-mammalian vertebrates.

Blood Function: Various functions of blood include transport functions and regulatory and protective functions that ensure survival of the whole organism. Transport functions include moving oxygen from respiratory surfaces to tissues that utilize oxygen, as well as moving carbon dioxide and other metabolic wastes to places where they can be excreted. The blood also plays a part in distributing nutrients which we have absorbed through the digestive system to the cells all over the body, meeting the metabolic demands where ever it be in relation to the digestive tract. These regulatory functions encompass heat distribution by maintaining body temperatures, pH balance by buffering systems, and regulating fluid volume homeostasis by osmotic pressure. Blood is also a key medium of endocrine signaling, enabling hormones to travel to distant target tissues in a timely and efficient manner. Protective functions include defense against pathogens via leukocytes and immunoglobulins and hemostasis via platelets and coagulation factors. These systems provide protection against pathogens and help to stem life-threatening hemorrhaging, respectively, and are major contributors to the fitness of more complex animals.

**Comparative Hematology:** Blood has a tremendous variation in its composition and properties in the various animal taxa, showing evolutionary adaptations to particular ecological niches and physiological requirements. In many invertebrates with open circulatory systems, hemolymph is functionally similar to blood but differs significantly in the variety of properties and types of cells found within. Phyla with hemocyanin, such as many arthropods and mollusks, have blue hemolymph when oxygenated as opposed to red-blooded in vertebrates and

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cephalopods with hemoglobin. Variation in erythrocyte morphology, hemoglobin composition, and oxygen-binding properties are common to vertebrates. Fish blood cells are generally larger and fewer than those of mammals but possess specialized structures for oxygen transport that respond to different aquatic environments. Their erythrocytes are even larger than those of amphibians, which occupy an intermediate aquatic-terrestrial position. The avian erythrocytes are nucleated like the reptilian ones but have additional adaptations to high-altitude, including greater hemoglobin affinity to oxygen with functional intricacies in the respiratory mechanisms. Mammals have evolved the most derived erythrocyte features, as their cells are small, biconcave, anucleate disc-shaped units that are optimized for effective oxygen transport in high metabolic rate organisms. These adaptations underscore the selective pressures underlying blood evolution across vertebrate lineages, and the close relationship between circulatory system structure and functional requirements.

**Evolution of the Heart:** However, the evolution of the vertebrate heart has allowed for an impressive diversification from a relatively open and simple contractile vessel in the earliest members of the phylum to its more complicated and multi-chambered manifestation in avian and mammalian species. This evolutionary pathway represents higher requirements for efficient circulation and facilitated movement from aquatic to terrestrial environments

**Primitive Contractile Vessels:** The simplest circulatory systems, seen in hemichordates and cephalochordates such as amphioxus (Branchiostoma), do not have a true heart but instead have contractile blood vessels that push hemolymph through the body. Note that in amphioxus, circulation occurs through the rhythmic contraction of the ventral aorta and other large vessels, with many small contractile bulbs at the bases of the afferent branchial arteries. These areas of the structure rhythmically expand and contract creating a primitive form of peristalsis systematic flow establishing the basis foundation of pressure and flow in the circulatory system later to be elaborated upon in more complex vertebrates.

#### Heart of Fish: The Two Chamber System

The first true vertebrate hearts appeared in cyclostomes (lampreys and hagfish) as a simple sequential four-chambered structure composed of a sinus venosus, atrium, ventricle and conus arteriosus. Although it is commonly referred to as a "two-chambered heart" because it has only one atrium and one ventricle, this system is a significant evolutionary leap in that blood does flow in one direction through separate chambers. In these primitive vertebrates, deoxygenated blood from the body flows into the sinus venosus, through the atrium and ventricle, where it is propelled out of the heart through the conus arteriosus into the gills for oxygenation before it is distributed to the body. Among cartilaginous and bony fishes this basic pattern is retained with some modifications. In addition, the chondrichthyan heart has a well-developed sinus venosus and a muscular conus arteriosus with multiple rows of valves preventing backflow. In the teleost fishes, the conus arteriosus is greatly reduced and replaced by an elastic bulbus arteriosus that acts as a pressure reservoir to smooth the flow of blood through the gills. This system, efficient for aquatic respiration but restrictive to metabolic rate and levels of activity because of blood mixing within systemic circulation, operates under the same principles.

#### Hearts of Amphibians: Separated Partially

Inclusion of terrestrial systems raised new circulatory constraints, leading to the evolution of partially divided circulatory systems in amphibians. The amphibian heart usually has three chambers, two atria (right and left) and one ventricle, making it a transitional form between the two-chamber fish heart and the fully divided hearts seen in the amniotes. The right atrium collects 'dirty' blood from the body, whilst oxygenated blood from the lungs (and skin in the case of cutaneous respiration) flows to the left atrium. While the single ventricle may imply that oxygenated and deoxygenated blood completely mix, amphibians have structural adaptations that mitigate mixing, most notably the spiral valve (a crescent-shaped ridge in the ventricle) and the trabeculated wall of the ventricle. The unique morphology of the bypassing circuits establishes preferential flow, sending deoxygenated blood directly to the

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pulmonary circuit and oxygenated blood to the systemic circuit. The partial separation of pulmonary and systemic circulation this indicates is an important evolutionary milestone since it allows for more efficient delivery of oxygen to tissues, while still retaining the capacity to do both aquatic and terrestrial respiration.

#### More Than a Feeling: The Reptilian Hearts of Separation

Reptilian heart anatomy is impressively diverse, from the three-chambered heart of most squamates (lizards and snakes) to the functionally four-chambered heart of crocodilians. For most reptiles, heart includes two completely divided atria and incomplete ventricle (septum ventricular), which separates when constricted. This structure minimizes mixing of blood more than in amphibians while still permitting shunting between pulmonary and systemic circulation under specific circumstances (e.g., diving, during digestion). The crocodilian heart is the most advanced of the reptilian condition, with a full ventricular septum developing during ventricular contraction and the foramen of Panizza between the two systemic aortic arches. This structure is found in the lungs of diving mammals, and enables controlled blood shunting, where blood flow is restricted to the lungs while allowing blood to flow to the brain. The similarities and differences in reptilian heart morphology across lineages illustrate evolutionary adaptations to varying ecological, metabolic, and physiological pressures setting the stage for the fully divided (four-chambered) circulation observed in modern birds and mammals.

#### Hearts of Birds and Mammals: Total Separation

In birds and mammals, four-chambered hearts evolved to be completely divided, providing a classic example of convergent evolution due to similarities in energetic and metabolic demands and endotherms. These hearts have two atria and two fully divided ventricles, resulting in completely separate pulmonary and systemic circuits without admixture of arterial with venous blood. By completely separating the two circuits, the pressure demands can be much higher in the systemic circuit without imposing excessive pressure on the delicate pulmonary capillaries, which facilitates the high metabolic rates characteristic of endothermy. Although their structure resembles each other in general, the avian and mammalian hearts have distinct adaptations that mirror their placed evolutionary origins and physiology in demand. Avian hearts are also larger relative to body size than those of mammals, with a thicker right ventricular wall, adaptations for the high-pressure needs of flight. Mammals, on the other hand, have a more elaborate conduction system, including the atrioventricular node and bundle of His, which allows more exact regulation of cardiac contraction across larger body sizes. The evolution of the vertebrate heart shows a progressive separation of chambers and specialization of circuits leading to the fully separated circulation of endothermic vertebrates. This evolution reveals the close association between cardiovascular structure and metabolic needs, as well as the way selective pressures have shaped one of vertebrate body's most crucial organ systems.

**Evolution of Aortic Arches:** The aortic arch system is one of the most plastic and evolutionarily important aspects of the vertebrate circulatory system, showing dramatic remodeling during vertebrate evolution. This mirrors the evolution from fish to tetrapods, where these structures were originally derived from the branchial arch arteries of ancient fishes before undergoing significant innovation to meet the varying circulatory needs of animals that ultimately adapted to land.

#### **Ontogenetic Pattern and Evolutionary Implications**

Thus, the embryonic development of aortic arches is a well-conserved phenomenon throughout vertebrate evolution. In early vertebrate embryos, six pairs of aortic arches form in cranial to caudal sequence to link the ventral aorta to the paired dorsal aortae, traversing the pharyngeal (branchial) arches. This basic framework, laid down early in vertebrate history, offers a developmental foundation onto which divergent adult-patterns of circulation have been built with the retention, remodeling or loss of particular arches. The astonishing degree of conservation of this embryonic scheme among vertebrates, spanning fishes

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to mammals, is a paradigmatic instance of developmental constraint in evolution. But the fate of these embryonic vessels differs sharply between lineages, illustrating how shared developmental precursors can be remodeled to perform new functions during evolution. Understanding evolution through the lens of aortic arch transformation, therefore, offers valuable thoughts about not only the mechanisms of change, but also the compromises between conservation and innovation during vertebrate development.

Aortic Arches in Fishes: In fishes these embryonic aortic arches develop into the afferent and efferent branchial arteries that supply the gills. Typically this will leave four to six pairs of these vessels intact in adult fishes, correlating to aortic arches 3-6 of the embryonic plan (some variation occurs among species). Each arch then bifurcates again to create a broad system of capillaries in the gill lamellae, where gas exchange occurs, then recombined into efferent vessels that joins collectively to the dorsal aorta. In Agnathan jawless fishes such as lampreys and hagfishes, the aortic arch system is a relatively simple affair with multiple arches providing respiratory function. As new ways of processing food developed later, jaws began to evolve through modifications to the first few anterior arches to supply the jaw musculature; the first arch was often reduced or adapted to create a jaw structure. Following this, diversification in cartilaginous and bony fishes produced a variety of specialized systems including the pseudobranch (derived from the first gill); modifications in arch number and arrangement. These adaptations are observed in fish aortic arches and respond to the variety of aquatic elements and such resources and are set by these structural patterns for the three major types of fish, which set the stage for some of the requirements when terrestrial vertebrate circulation evolved. Transitioning to life on land called for a dramatic makeover of this system, repurposing vessels that had originally grounded their use in gill circulation for new functions in air-breathing vertebrates.

**Transformation in Tetrapods:** As vertebrates were moving on land, they began to respire by lungs instead of by gills, which required a major consolidation

of the aortic arch system. The embryonic aortic arches of tetrapods are retained and modified in a selective process resulting in some aortic arches developing into major arteries(like subclavian and pulmonary arteries) while others completely regress. In 2013, researchers were able to show that the genes involved during the embryonic aortic arches formation were in fact ancestral features. Creating the first incorporation of terrestrial life, amphibians have three surviving aortic arches in adulthood: the carotid arch (lesser aortic arch arch 3), the systemic arch (aortic arch 4), and the pulmonary arch (lesser aortic arch 6). The carotid arch feeds the head and brain, the systemic arch is the main pathway of blood to the body, and the pulmonary arch sends blood to lungs and skin to pick up oxygen (gas exchange). This trend is consistent with the bimodal respiration of amphibians, which tend to utilize both pulmonary and cutaneous respiration. The basic pattern is further modified in reptiles, the arrangements differ between lineages. In contrast, most reptiles possess paired systemic arches (right and left fourth arches) so that shunting can occur between pulmonary and systemic circulation. Such a dual systemic arch arrangement, which is common to the reptilian lineage, reflects an autosomal condition for amniotes, with separate adaptations subsequently developing for both birds and mammals.

#### **Continuum of Avian and Mammalian Specializations**

Interestingly, birds and mammals independently transitioned to single systemic arch systems, each selecting for different sets of arch retention, resulting in a paradigmatic example of convergent evolution. In birds, the right fourth aortic arch remains to form the definitive systemic arch (the aortic arch), and in mammals, the aortic arch is formed from the left fourth arch. This major evolutionary difference in which birds retain a functional connection between the arches while the analogous route in mammals closes completely and the vessel stems are independent is of great evolutionary interest originating from common reptilian ancestors through the evolutionary development of arches leading into the great vessels.

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The following are the persistent vessels from the embryonic aortic arches in mammals:

- The third arches that form the common carotid arteries and proximal parts of the internal carotid arteries
- · Left fourth arch with resulting definitive aortic arch
- $\cdot$  The remains of right fourth arch leading to proximal right subclavian artery
- The sixth arches, the proximal portions persisting as the proximal pulmonary arteries, and the left distal portion as the ductus arteriosus (which closes after birth)

The mammalian condition is actually a derived pattern that has been optimized for the fully-separated (and therefore hydraulic) pulmonary and systemic circulation of endothermic metabolism. These adult transitions are dynamic and shaped by asymmetric development, selective apoptosis and hemodynamic effects on blood vessel geometry. The aortic arches across vertebrates display an extraordinary plasticity of developmental systems to accommodate significant shifts in lifestyle and physiology. The aortic arch system has continually been remodeled throughout vertebrate evolution, evolving to meet functional demands from [i]the multiple parallel arches of gill respiration in fishes[/i] to the highly specialized configurations of birds and mammals while remaining fundamentally constrained by its developmental origins.

## **Portal Systems**

One well known example of this specialized circulatory arrangement are portal systems, with blood traveling through two capillary beds in series before returning to the heart, rather than the direct route heart'!arteries'!capillaries'!veins'!heart. These systems support specialized functions, such as nutrient processing, hormone regulation, and waste clearance, and have adapted through distinctive modulations across vertebrate lineages.

**Basic Rules of Portal Circulation:** What makes a portal system unique is that blood from one capillary network is collected in a portal vein to be transferred to a second capillary bed, and direct return to the heart does not occur. The candelabrum configuration, therefore, creates specific hemodynamic environments and functional specializations whereby distinct organs metabolize blood-borne regulatory factors. Blood flow in the portal system is driven by the pressure differential created by the heart, but, after traversing the first capillary bed, the pressure is lower than that in the main systemic circulation. Most vertebrates have two major portal systems: the hepatic portal system that delivers nutrientrich blood from the digestive organs to the liver where they need to be processed, and the hypothalamo-hypophyseal portal system that is responsible for neuroendocrine control between the hypothalamus and anterior pituitary. Some other systems that can be termed portal exist in some vertebrate groups: a renal portal system in some non-mammalian vertebrates, and specialized portal arrangements in some tissues.

**Hepatic Portal System:** The hepatic portal system is the evolutionarily most extensive and functionally most important portal circulation in vertebrates and has essential roles in metabolism of nutrients, detoxification and homeostasis. In this system, blood from the digestive tract that is loaded with absorbed nutrients is collected via tributaries of the hepatic portal vein and then delivered directly to the liver for processing before entering the general circulation. This setup provides a number of advantages: it permits the liver to collect and store nutrients when they are abundant, to process detoxification of potentially harmful agents absorbed from the intestine before they reach general circulation, and also accommodates first-pass metabolism for drugs and various compounds. Key liver checkpoint regulating blood composition entering the systemic circulation according to metabolic needs and environmental challenges

The hepatic portal system is remarkably conserved throughout the evolution of vertebrates, maintaining similar morphology from fishes to mammals while major differences in digestive physiology exist. The system harvests blood primarily

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from the stomach, intestines, and spleen in elasmobranchs and teleost fishes, whereas in tetrapods, pancreatic blood enters the hepatic portal circulation as well. The variation in the relative size and branching pattern of the hepatic portal vein within animals is known to reflect differences in digestive anatomy and metabolic demand. The concentration is why the hepatic portal system is highly developed in mammals, whose portal vein receives blood from the superior mesenteric and inferior mesenteric veins (which drain the small and large intestines), the splenic vein (which drains the spleen and part of the stomach), as well as from various gastric veins (which drain the stomach). On entering the liver, the portal vein divides repeatedly, generating progressively smaller vessels that ultimately deliver blood to the hepatic sinusoids where exchange occurs with hepatocytes. The processed blood exits the liver through the hepatic veins, which drain into the inferior vena cava for return to the heart.

Renal Portal System: Renal portal system: a system of veins in the bodies of many non-mammalian vertebrates that carries blood from the hind body to the kidneys before returning to the heart. This system gathers venous blood from the tail and hindlimbs through the caudal and iliac veins, respectively, and injects it at the renal capillaries via afferent renal veins (renal portal veins). Blood leaving the kidneys through efferent renal veins drains into the posterior cardinal veins (or their derivatives) after being processed and filtered by the kidneys. The functional role of the renal portal system is different among the vertebrate places. In fishes and amphibians, this system may help in the decantation of nitrogenous waste, owing to increased renal blood flow and urea/ammonia extraction. Most reptiles and birds possess well-developed renal portal systems containing renal portal valves (or valves of Hampton), which permit blood to be shunted around the kidney under some physiological conditions (e.g., diving or dehydration) to conserve water and redirect blood to other vital organs. In mammals there is no true renal portal system with blood from the posterior part of the body returning directly to the right atrium through the inferior vena cava, bypassing the kidneys. This evolutionary loss probably reflects adaptations in renal physiology and water sparing mechanisms in various mammalian lineages and the higher metabolic demands that select for closer circulatory circuits with lower resistance in mammals.

#### Hypothalamo Hypophyseal Portal System

Specific neuroendocrine portal circulation — the hypothalamo-hypophyseal portal system — connects the hypothalamus and anterior pituitary (adenohypophysis), allowing fine-control of diverse physiological functions via hormones. This arrangement differs from other portal systems that carry nutrients or waste products, as the one connecting the hypothalamus to the anterior pituitary (by way of blood carriers) transports regulatory neuropeptides (releasing and inhibiting hormones) from hypothalamic nuclei to act at the anterior pituitary site, where these compounds modulate the synthesis and secretion of other hormones. The blood vessels in this system arise as capillaries in a structure called the median eminence of the hypothalamus, where neurosecretory cells secrete factors regulating its function. These capillaries merge, forming the hypophyseal portal veins that follow the pituitary stalk and branch again into capillaries in the anterior pituitary. A circuit in which hypothalamic signals arrive at pituitary endocrine cells with minimal dilution ensures maximal regulatory precision and efficiency. The hypothalamo-hypophyseal portal system therefore is highly conserved throughout vertebrate evolution, with similar vessel anatomy from teleost fishes to mammals which differ vastly in their brain organization and endocrine system. This conservation highlights the central role of hypothalamic control of pituitary function across vertebrates, integrating processes as diverse as growth, metabolism, reproduction, and stress response.

**Specialized Portal Systems:** Outside of the major portal systems discussed above, vertebrates have numerous specialized portal configurations that support various physiological roles. The posterior lobe of the pituitary, or neurohypophysis, uses the hypophyseal portal system to transport neurohormones (oxytocin and vasopressin/antidiuretic hormone) that were synthesized in the hypothalamus to the posterior pituitary for release. These have all been suggested as distinct entities from the hypothalamo-hypophyseal

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portal system, but together these systems exemplify strong neurovascular interactions between the hypothalamus and the pituitary gland. And some vertebrates also have specialized portal arrangements in certain tissues. For example, ie the choroidal rete mirabile which is a counter-current exchanger that helps deliver oxygen to the retina in teleost fishes. Birds exhibit a specific portal system in their thermoregulatory salt glands is associated with an increased efficiency of ion extraction. Soul et al.926 have built on previous research explaining the great interstitial perfusion of sporadic mitochondria microclimates that feature local, portal-like vascularization within tissues of some vertebrates (for example, mammals host a counter-current multiplier system which accentuates diffusion and serves to concentrate salts in the renal medulla and fishes of the physoclist variety host rete mirabile in their swim bladders). The presence of different types ans locations of portal systems across vertebrate taxa demonstrates the ability of the circulatory system to adapt to specific physiological needs. Such configurations minimize resource waste, augment regulatory specificity, and enhance functional efficiency to a degree that could not be achieved through simple serial perfusion, a fact that highlights the highengineering principles of vertebrate circulatory systems.

The vertebrate circulatory system is a triumph of evolutionary engineering, evolving from simple contractile vessels in primitive chordates to the sophisticated, multi-chambered hearts and specialized vascular circuits characteristic of mammals and birds. This evolutionary trajectory is a product of a series of modifications in response to environmental pressures, increased metabolic demands, and shifts from aquatic to terrestrial habitats. The blood, the main mode of transport, has evolved with these structural changes, acquiring specific cellular components and biochemical properties for particular physiological needs. The heart has transitioned from a simple propulsive chamber to a complex four-chambered pump, illustrating that evolutionary change is incremental, with each subsequent improvement building upon its predecessors, including new adaptations. Alongside lungs, aortic arches evolved from structures primarily for respiration of gills in an aquatic state; this represent a major alteration showing the repeated pattern of co-option in evolutionary innovation of your own terrestrial vertebrates. Internal structures such as portal systems demonstrate how circulation can become modified to facilitate specialized hemodynamics conducive to functional fitness in organs and tissues. These elements work in unison as an integrated system to regulate homeostasis, metabolism, and promote the various lifestyles seen among vertebrate lineages. Not only does number and arrangement of hearts provide information about the history of vertebrate design, the study of circulatory evolution helps shed light on the basic principles of integration of vertebrate bodies and organ systems and the continuing evolution of animal life on Earth.

#### SELFASSESSMENT QUESTIONS

#### Multiple Choice Questions (MCQs):

- 1. Which of the following is an epidermal derivative in vertebrates?
- a) Scales in reptiles
- b) Feathers in birds
- c) Hair in mammals
- d) All of the above

#### 2. Which vertebrate group has a two-chambered heart?

- a)Amphibians
- b) Fishes
- c) Reptiles

d) Mammals

## 3. Which structure in vertebrates is responsible for gas

exchange?

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b) Kidneys

c) Liver

d) Lungs

8. The hepatic portal system carries blood from the:

- a) Heart to lungs
- b) Digestive organs to liver
- c) Brain to spinal cord
- d) Kidneys to the bladder

# 9. Which of the following is NOT an evolutionary adaptation of the integument?

- a) Scales in reptiles
- b) Feathers in birds
- c) Hollow bones in birds
- d) Fur in mammals

## 10. The role of blood in vertebrates includes:

- a) Oxygen transport
- b) Nutrient distribution
- c) Immunity
- d) All of the above

#### **Short Questions:**

- 1. What is the function of the integumentary system?
- 2. Define epidermal and dermal derivatives in vertebrates.

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- 3. What are the three major components of blood?
- 4. How does the vertebrate heart evolve from fishes to mammals?
- 5. What is the function of aortic arches in vertebrates?
- 6. Differentiate between open and closed circulatory systems.
- 7. What is the significance of the hepatic portal system?
- 8. How does the integumentary system help in thermoregulation?
- 9. What are scales, feathers, and fur derived from?
- 10. How does blood contribute to immune defense in vertebrates?

## Long Questions:

- 1. Discuss the evolution of vertebrate integument and its derivatives.
- 2. Explain the differences in the circulatory system of fish, amphibians, reptiles, birds, and mammals.
- 3. Describe the formation and function of the aortic arches in vertebrates.
- 4. Compare and contrast the structure of the heart in different vertebrate groups.
- 5. Explain how integumentary modifications help vertebrates adapt to different environments.
- 6. Describe the hepatic portal system and its importance in vertebrate circulation.
- 7. Discuss the role of skin, hair, and feathers in vertebrate adaptation.
- 8. Compare the blood composition and its function in vertebrates.
- 9. Explain how the portal system differs from general circulation.



10. Discuss the evolutionary significance of integumentary glands in different vertebrate classes.

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## MODULE 4

## **COMPARATIVE ANATOMY II**

#### 4.0 Objective

- To compare and contrast the digestive systems of different vertebrate groups.
- To analyze the evolutionary modifications in respiratory organs.
- To study skeletal adaptations in vertebrates.
- To understand the variations in the urinogenital system across vertebrates.

#### **UNTI 10**

#### Comparative account of digestive system in vertebrates

#### **Overview of the Digestive System in Vertebrates**

The digestive system is one of the most physiologically pivotal systems in vertebrates, and has evolved over millions of years to extract nutrients from a wide variety of food sources found in disparate ecological niches. This remarkable system reflects the principles of evolutionary tuning: incredible variance across the vertebrate radiation in design with a preserved functional architecture. In its simplest form, the vertebrate digestive tract is a tubular alimentary canal that runs from mouth to anus and various accessory glands that secrete necessary digestive enzymes and other substances. This malleable conduit, known alternatively as the gastrointestinal tract, developed from a tubular form among primitive chordates to a multi-chambered, partitioned system amongst higher vertebrates, reflecting adaptations driven by diet and ecological needs. The basic arrangement is similar for all vertebrates: Food enters through the anterior end, where it is mechanically and chemically broken down, digested

and absorbed before waste products are eliminated at the posterior end. As species adapted to different environments and food sources, however, their digestive systems have evolved to suit the demands of their diets, resulting in similarly specialized digestive adaptations that vary in form and function between vertebrate groups. One of the most notable aspects of this high-level overview is also the transition: it highlights how the vertebrate digestive system ultimately adapted to two different food sources - aquatic and terrestrial - as well as extreme morphological and ecological differences in feeding and digestive systems. In early aquatic vertebrates (e.g. jawless fish), the digestive system is largely a simple, straight tube with little specialization. With the evolution of jaws, vertebrates moved into new ecological niches, which required compartmentalization and specialization of the digestive tract. New environments required new adaptations including drastic changes to the digestive tract to accommodate new food sources and feeding rates and to maximize water retention in a terrestrial setting. The emergence of complex shaped teeth in terrestrial vertebrates promoted the mechanical digestion of food, as did the evolution of specialized chambers in the stomach and intestine which improve chemical digestion and nutrient uptake. Comparative analysis of vertebrate digestive systems reveals both functional adaptation to particular diets and the evolutionary relationships between vertebrate lineages. The spiral valve in intestine of certain fish and the ceca in birds are examples of evolutionarily optimized structures demonstrating digestion in certain ecological niches. Through studying these differences in digestive structure and function, researchers are uncovering insights regarding the ways in which vertebrates evolved to occupy a wide array of ecological niches and exploit varied food sources throughout evolutionary time.

Digestive systems are an important example of evolutionary modifications of body plans, and comparative analysis of digestive system anatomy across vertebrate taxa reveals how important physiological processes have been reshaped and refined in response to novel ecological and nutritional challenges.

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The transition from a relatively simple alimentary canal evident in cyclostomes to the highly compartmentalized digestive tract encountered in the ruminant mammals serves as a classic example of adaptive radiation behind the evolution of the vertebrate digestive system. Such comparative analyses help illuminate evolutionary relationships, as well as functional convergence, in which similar digestive traits evolved independently in distantly related groups that have faced similar ecological challenges. (For instance, both birds and mammals evolved specialized chambers for microbial fermentation of plant material independently, though in separate regions of the digestive tract.) This convergence highlights how important digestive efficiency is for the survival and adaptation of vertebrate animals. The analysis of digestive systems across species provides valuable insights into the evolutionary trade-offs that have shaped the development of these structures, showcasing how physiology has been fine-tuned over generations to meet dietary needs. Structural adaptations in terms of length, diameter, surface area and specialized regions of the digestive tract reflect adaptations to specific diets and feeding strategies. Herbivores and carnivores have different intestinal systems; carnivores have shorter intestines because animal protein is easier to digest than plant material. The differences in digestive anatomy are strong evidence that natural selection shapes physiological systems to meet the demands of particular ecological niches.

#### The Functions of the Digestive System

The true vertebrate digestive system carries out a sophisticated set of functions that are all interconnected and critical for the organism to survive, grow and breed. The main function is food processing; the conversion of food into absorbable nutrients that can be used by the cells in the body. This process starts with ingestion, which involves transferring food to the oral cavity of the animal, where it undergoes physical breakdown (in many vertebrates occurs through mastication). This mechanical digestion increases food particle surface area to make chemical digestion easier. After ingestion, chemical digestion is the crucial process performed by the digestive system where the macromolecules present from the food—carbohydrates, proteins, lipids, and nucleic acids—are hydrolyzed into their basic building blocks through different digestive enzymes. These

hydrolytic reactions are catalyzed by enzymes produced by serous and mucous cells that line the digestive tract. These enzymes hydrolize polysaccharides to monosaccharides, proteins to amino acids, lipids to fatty acids and glycerol, and nucleic acids to nucleotides. This chemical degradation is a prerequisite for converting food into molecular constituents that are sufficiently small for uptake through the intestinal epithelium. Digestion involves complex neural and hormonal controls that coordinate the secretion of digestive enzymes and the movement of food down the alimentary canal, enabling the effective processing of intake materials across physiological states.

Another important function of the digestive system is that of absorption, the transfer of digested nutrients from the lumen of the alimentary canal to the circulatory and lymphatic systems for distribution to body cells. In the small intestine, this process takes place mainly where many unique anatomical structures like villi and microvilli enhance surface area for absorption. Nutrients are absorbed by various mechanisms - monosaccharides and amino acids commonly fed by the active transport method (mostly in the small intestine), fatty acids are diffused to enter via intestinal epithelium, before repacked in chylomicrons, whereas water and electrolytes are taken in osmotically and facilitated diffusion. The efficiency of absorption differs between vertebrate groups and reflects adaptations to different diets and environments. For example, meat eaters consuming protein-dense diets have shorter small intestines than do herbivores, which need long intestines to optimize nutrient absorption from plant matter. The digestive system has critical roles beyond digestion and absorption, especially in the context of water balance in terrestrial vertebrates, which are challenged by the need to conserve water. An extensive colon in many higher vertebrates is the means for regulating hydration by reabsorbing water. Further, the digestive diet operates in detox, with the liver processing ablative substances taking in doses through the intestinal tract prior to being passed into the overall circulation. This detoxifying function is especially significant for vertebrates that may ingest toxic plant compounds or animal venoms as part of their natural diets.

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The digestive system is more than your body's food processing tool: It plays critical roles in immune defense and endocrine regulation. Gastrointestinal tract contains the largest aggregate of lymphoid tissue in the body termed as gutassociated lymphoid tissue (GALT) and serves as a crucial first line of defence against the pathogens enter with food. Given the near-constant exposure of the digestive epithelium to environmental antigens and pathogens, this immune function is especially critical. The digestive system also functions as an endocrine organ, with specialized cells distributed along the alimentary canal that release hormones which control digestion, appetite, and metabolism. For instance, cells within the stomach and small intestine release hormones, including ghrelin, cholecystokinin and peptide YY that affect hunger, satiety and the secretion of digestive enzymes. Additionally, another significant function of the digestive system is the elimination of waste, wherein undigested food leftovers, metabolic waste products, and harmful substances are excreted from the body in the form of feces. This evolutionary strategy of elimination in the context of whatever high order organism we are discussing involves co-ordinated contractions of muscle, pushing waste material through the large intestine and out of the body, a process which varies in different vertebrate groups according to diet and metabolic rate. When taken together, these diverse functions reveal the digestive system's central role in vertebrate physiology, and highlight the fact that the digestive system is involved in processes that reach well beyond the acquisition of nutrients and into the realms of homeostasis, defense, and regulation.

Beyond its primary role in digestion, the vertebrate digestive system is home to communities of symbiotic microorganisms that play important contributions to host nutrition and physiology. These microbial communities, collectively known as the gut microbiota, differ substantially by vertebrate taxon in composition and metabolic potential, mirroring variation in diet, digestive morphology, and evolutionary history. Although in some cases this interaction can become pathogenic, in many instances we instead see a mutualistic symbiosis, where both partner organisms benefit from being in association with one another. Gut microbes help degrade certain complex food ingredients that can not be digested by the digestive enzymes of the host, such as cellulose and other polysaccharides of plant structure in herbivorous species. These microbes ferment these otherwise indigestible materials, producing short-chain fatty acids that the host can absorb and use as an energy source. Furthermore, gut microbiota can provide essential vitamins and amino acids which may be low in the host's diet leading to an essential dietary sufficiency. The significance of microbial contributions to digestion varies by group of vertebrates and is particularly critical in the digestion of plants in herbivores with specialized fermentation chambers, so ruminant mammals have a rumen or cecum in many birds and reptiles. In addition to their nutritional contributions, gut microbiota have crucial roles in immune system development, resistance to pathogens and even in interaction with the CNS via the gut-brain axis reiterating how fundamental these symbiotic interactions are to vertebrate health and function.

#### Variation in the Alimentary Canal among Vertebrate Classes

The widest range of structural and functional diversity in the alimentary canal among vertebrate groups is related to the various feeding types and the consequent differences in nutrition. In the simplest vertebrates, the cyclostomes (lampreys and hagfish), the alimentary canal is a simple, relatively straight tube without much regional specialization. In contrast, the alimentary canal shows more complexity with different regions of it becoming specialized for particular digestive roles throughout the vertebrate tree of life. In the case of fish, the digestive tract usually includes a mouth, pharynx, short esophagus, stomach (some species lack one), intestine and anus or cloaca. A spiral valve, a corkscrewshaped twist of the body of the intestine, works to increase the surface area for absorption while at the same time, slowed the progress of food through the intestine, thus increasing digestion and requiring a shorter intestine than other types of fish possess. This is an early evolutionary solution to maximizing nutrient extraction while exploiting the limitations of body architecture. In amphibians, the alimentary canal is generally the same as in fish, but adapted to their partiallyterrestrial existence. Amphibian larvae generally have an elongated intestine designed to process plant food, and metamorphosis remodels the digestive tract dramatically to process the more caraivorous dies of adults. This outogeneticity

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metamorphosis strongly parallels the evolution from aquatic to terrestrial life and changes in digestive physiology that came with it. In reptiles, which also exhibit further specialization of the alimentary canal with regional differentiation, they are adapted to feeding and drinking less often, holding water better, and with greater digestive efficiency. Anatomy The reptilian digestive tract is generally defined by the presence of an esophagus, a stomach, a small intestine, a large intestine, and a cloaca. Many reptiles, and especially carnivorous ones such as snakes, have developed extraordinary adaptations to consume large prey items infrequently over time, including highly distensible esophagi and stomachs, potent digestive enzymes, and the ability to greatly enhance digestive function immediately after a meal. Certain herbivorous reptiles, including most lizards and tortoises, have also evolved expanded hindguts or ceca in which symbiotic microorganisms ferment the plant matter, an organization parallel to what it found in herbivorous birds and mammals. Because they evolved under constraints imposed by flight and a high metabolic workload, the avian digestive system represents a divergence in evolutionary history with the specializations of the system unique. Birds don't have teeth and instead use their muscular gizzard packed with grit or stones to mechanically grind food, serving basically the same purpose as mastication in many mammals. The crop, an expanded portion of the esophagus below the throat, acts as a temporary holding tank, enabling birds to swallow food quickly that can be digested more slowly. This adaptation is especially useful in species that feed in exposed areas where extended feeding could elicit a higher predation risk. Small birds that sequester the protein needed to develop wings and flight muscles—such as those that lessons such as protein and fat increase beaks and rely on seeds—have shorter intestines than those made of relatively difficult-to-digest leaves, while the two-part stomach makes processing food chemical and mechanical if compared to rodents or pigsUãá in the singlechambered stomach, and for more advanced birds who migrate longer distanceslighter and cleaner in the form of guts is good on gliding in the air.

The range of morphologies and modifications of the mammalian alimentary canal is distinctly greater than in the vertebrates, corresponding to the other extensive adaptive radiation of mammals into practically all types of the environment. A mouth with a

variety of dentition from herbivore to carnivore, muscle pharynx, esophagus, stomach, small intestine, large intestine, and rectum ending in an anus, each with specific regional function, not to mention the associated organs, is normally found in mammals. The stomach is particularly diverse among mammals, ranging from a simple, one-chambered stomach found in carnivores and many omnivores to a complex, multi-chambered stomach seen in ruminants and some other herbivores. The function of the ruminant stomach, which us a four chambered stomach consisting of the rumen, reticulun, omasum, and abomasum, This is possibly the most extreme level of specialization of any vertebrate digestive tract, and thus allowing these animals to exploit fibrous plant substrates through symbioses on microbial fermentation and specialized digestion. Mammalian intestine length and complexity differ greatly as well. Carnivores have short and simple intestinal tracts while herbivores have long and complex intestines. Such diversity tells us most about the contrasting processing needs of an animal and the high fiber, sometimes more nutrient depleted plant diets, as well as the requirement to access the nutrients in plant tissues often making their digestion an order of magnitude more divergent than carnivorous digestion. The mammalian colon is adapted for reabsorption of water and, in some species, for fermentation of undigested plant material. Bacteria digest cellulose in the cecum, a blind sac located at the junction of the small and large intestines, an end organ especially well-developed in herbivorous species that serves as a fermentation chamber of symbiotic microorganisms. From these diverse specializations of the mammalian alimentary canal we can see how the pressures of evolution have molded digestive anatomy to the specific needs of each group.

In vertebrates, these general differences in the morphology of the alimentary canal extend to the microscopic specializations of the digestive epithelium, allowing for variations in functional capacity. Across vertebrate lineages, the mucosal surface of the alimentary canal displays remarkable adaptations that increase in complexity with higher surface area, from fish to mammals. Fish intestines typically possess simple intestinal mucosa with primary folds; in amphibians and reptiles the degree of folding is more complex. With many finger-like projections termed villi and

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microscopic microvilli on individual epithelial cells that collectively create a structure called the "brush border" that can dramatically increase the amount of surface area available for nutrient absorption, birds and mammals show the most extreme intestinal surface specializations. These micro-scale adaptations correlate with their metabolic needs, and high-maintenance species tend to have more complex faculty amplification at the surface. A third major difference between vertebrate groups is in the distribution and density of specialized secretory cells in the alimentary canal. These consist of mucus-secreting goblet cells that protect the digestive epithelium, enteroendocrine cells that secrete regulatory hormones, etc. The relative and regional densities of these cell types differ with diet and digestive strategy. For example, carnivores generally have greater densities of cells that produce protein-digesting enzymes and herbivores have more developed regions for carbohydrate processing. In addition, invertebrates differ in how smooth muscle is arranged within the alimentary canal, with invertebrate groups having differing amounts of motility patterns and food transit times. While gross anatomical features get most of the attention, these microscopic specializations, though invisible to the naked eye and less obviously contributing to the different digestive potentials and efficiencies of vertebrate species, further illustrate how adaptations manifest not just as gross anatomical features, but also at other biological scales, allowing various vertebrates to obtain nutrients under a range of ecological conditions.

## Comparative Structure of the Digestive Tracts of Major Vertebrate Groups

#### Fish

In bony fishes, the general architecture of the digestive system is ancestral among living vertebrates, and there are primitive traits and specializations of aquatic existence. Many fish have a mouth with different types of teeth all used for varied feeding strategies — from the spiny, pointed teeth of carnivorous fish to flat, crushing teeth of those with hard-shelled prey, to the total absence of teeth in filter feeders. Tetrapods have a clear neck (the area between their head and body) region, but many fish have the mouth leading directly into a pharynx

that's slitted and pierced with gills. The pharynx of fishes has a dual roles in respiration and food processing mechanism, in particular, in filter feeding fishes when the specialized gill rakers are involved in trapping food particles from the splashing water that is passing by the gill slits. Now the esophagus of fish is usually short, muscular, and distensible; its main function is to carry food relatively rapidly to the stomach or intestine. The majority of fish have a separate stomach, but some groups of seamless, such as particular cyprinids (carp and minnows parrots), labyrinth fish and some other fish do not have a stomach and the esophagus is directly contiguous to the intestine. When it is present, the fish stomach is highly variable in size, shape and complexity, ranging from a simple sac to an elongated, tubular form, and usually correlates with diet and feeding intensity. Carnivorous fish and many species of fishes that are omnivorous have expandable stomachs, permitting the consumption of relatively large prey items at long intervals, while herbivorous fishes generally have smaller, less distensible stomachs adapted to more continuous feeding on plant material or small invertebrates. As in other vertebrates, stomach acid production and pepsin secretion in fish occur in a manner designed to initiate the digestion of protein that will continue in the intestine.

The Fish Intestine According to its Diets The length, diameter, and complexity of the intestine of fish vary widely from species to species. Carnivorous fish generally have short straight intestines since their protein-rich diet is highly digestible, and the length of intestines is often less than that of body length, generally with an intestinal to body length ratio < 1:1. While herbivorous fish have a intestine which range from ranging over 15 times their body length, herbivorous fish need this extended residence time to digest and absorb their plant material. Most fish have pyloric caeca, finger-like projections of the anterior intestine that help increase the surface area for both digestion and absorption without needing a larger length of intestine. The number of these caeca varies wildly between species, from none at all, to more than 200 in some salmon, and is usually related to feeding behavior, and what is needed to effectively digest food consumed. A conspicuous specialization that is found in

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elasmobranchs (sharks and rays) and some primitive bony fish is the spiral valve or spiral intestine, which is an internal corkscrew-shaped ridge that increases surface area, while slowing the passage of food through a relatively short intestine. It is an evolutionary response to the need for greater digestive efficiency incorporated within the space restrictions of an elongated body plan suited for swimming. Posterior intestine usually expands slightly into a brief rectum before ending at the vent, or (in elasmobranchs and many primitive bony fish types) at a cloaca, the common opening of digestive, urinary, and reproductive systems. This configuration is different to the separate openings found in most teleost fish and tetrapods, representing a more ancestral condition of vertebrates.

Fish have various accessory glands that secrete enzymes and other constituents necessary in the digestion process. The liver is an organ that is highly developed in fish, as it takes up a large portion of the body cavity and performs important functions, including roles in digestion, detoxification, storage of glycogen and vitamin A and some other vitamins, and production of blood proteins. Lipid is accumulated highly and is an important energy reserve in fishes liver, most notably, carnivorous fishes. Generally, fish have a gallbladder to store and concentrate bile that the liver produces, allowing it to be released into the intestine to emulsify fats. The pancreas of fish can take several forms; in some species it is a compact discrete organ, as seen in higher vertebrates, while in others it consists of diffuse post-ganglionic tissue dispersed along blood vessels or embedded within the liver (collectively a hepatopancreas). Despite its anatomical arrangement, the fish pancreas carries out similar fundamental functions as other vertebrates, secreting digestive enzymes to the anterior intestine and producing hormones that regulate metabolism. One unique characteristic of the digestive system of most fish is the large gut microbiota present with a relatively short and uncomplicated intestinal tract. These microbial communities vary based on diet, environmental conditions, and host species, and they play an essential role in digestion, especially in herbivorous and detritivorous fish eating plant material or organic detritus. The digestive physiology of fish is additionally adapted to life in the aquatic environment in other ways, including mechanisms to maintain the appropriate salt and water balance across the digestive epithelium in response to osmoregulatory challenges of freshwater or marine environments. Thus, these are different specializations of the fish digestive system based on their ecologies and how evolution has altered this basic physiological system.

#### Amphibians

Fish-like amphibians that have retained many of these characteristics also lack specialized digestive systems adapted to wood, but other advanced amphibian species possess these adaptations. Extensive chewing is rendered impossible by the weak dentition of most adult amphibians, which typically have a broad mouth and small, conical teeth for grasping prey rather than rending it. The exception is caecilians (limbless amphibians), which have larger teeth suited to their burrowing, carnivorous way of life. Most amphibians have very specialized tongues, and in anurans (frogs and toads) the tongue is usually attached at the front of the mouth and can be thrown out very quickly to predate, which is an adaptation to landbased feeding. Amphibian esophagus is short and muscular and opens into a simple sac-like stomach secreting hydrochloric acid and pepsin for initial protein digestion Most adult amphibians have a small intestine that is only moderately coiled and relatively short, which is a reflection of their predominantly carnivorous diet, high in easily-digestible animal protein. The intestine (colon) is usually short, and opens into a cloaca (a common chamber for the digestive, urinary, and reproductive systems). This cloacal arrangement is a primitive vertebrate condition shared with most fish, reptiles, and birds but not most mammals. Amphibians have a large, well-developed liver that secretes bile, which is stored in the gallbladder and released into the small intestine to assist in the digestion of fat. The pancreas of amphibians produces digestive enzymes that operate similarly to those of other vertebrates, aiding in the digestion of proteins, carbohydrates, and lipids in the small intestine. Together, these digestive organs allow adult amphibians to process the insects, worms and other small prey that make up most of their diet.

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If amphibian digestive versatility isn't interesting enough, perhaps the most incredible example occurs during metamorphosis in species that have aquatic forms in their larval stage, especially in the Anura. Tadpoles are mostly herbivorous omnivorous, their very long widely coursed intestines specialized to digest algae and other parts of plants rich in cellulose. This lengthened intestine undergoes extensive programmed cell death and remodeling during metamorphosis, being shortened considerably to create the digestive system of the adult carnivoreadapted frog or toad. This intestinal remodeling is one of the most extreme in any vertebrate group, involving changes in intestinal length, mucosal epithelium reorganization, digestive enzyme secretion patterns and motility. This process of transformation is largely orchestrated by thyroid hormones and involves intricate interactions between cell death, proliferation, and differentiation events. This metamorphosis remodeling provides a compelling parallel with the evolutionary transition of herbivorous fish-like ancestors to more carnivorous tetrapods, essentially recapitulating an evolutionary major transition in vertebrate feeding ecology during ontogeny. It also is a remarkable example of physiological flexibility: One species is able to efficiently exploit two food resources at different life stages, reducing competition between juvenile and adult forms. Such dramatic digestive remodeling, however, does not happen with all amphibians. Salamanders, whose larvae are like carnivorous mini-adults, undergo less extensive remodeling of digestive anatomy during development, whereas directdeveloping amphibians that lack a free-living larval stage entirely avoid this remodeling process.

Amphibians display adapta-tions in their digestive physiology to accommodate their semi aquatic life style in conjunction with their ectothermic metabolism. Similar to other ectotherms, the digestive function in amphibians will vary considerably with shifts in the environmental temperature, which overall tended to speed up digestive processes due to higher activity of digestive enzymes, as well as enhanced gut motility. Because of this temperature dependence, behavioral thermoregulation is required, and many amphibians choose postfeeding microhabitats that promote body temperatures now optimal for digestion. Transitions between aquatic and terrestrial environments present additional challenges for amphibians dealing with water balance across the digestive epithelium. Whereas submersion in freshwater poses the problem of osmotic water influx, extended residence out of water necessitates conservation of water that could be lost in the feces. In terrestrial phases, the amphibian colon plays a crucial role in water reabsorption and has a high degree of regulatory capacity, the availability of environmental conditions catering to this capacity. Considerable plasticity in digestive physiology in response to season and food availability is also seen in amphibians. During hibernation or estivation, many species substantially downregulate digestive function, with reduced secretion of digestive enzymes and decreased intestinal motility. On the other hand, feeding post-dormancy is correlated with an upregulation of digestive processes in rapid succession, including increased enzyme production and absorption capacity. This flexibility in resource use allows amphibians to adjust to the fluctuations in food availability common in many of their habitats. Amphibian digestive adaptations thus tell a tale not only of their evolutionary history and ecological niche, but their very physiology, and the pressures of maintaining a successful lifestyle, transitioning from water to air, and what those evolutionary and selection forces continue to look like for vertebrates as a whole.

#### Reptiles

The digestive tract of reptiles is an important evolutionary advancement to fully terrestrial living and includes adaptations for infrequent feeding, water conservation, and processing a wide variety of food from hypercarnivorous to herbivorous. Reptiles have a highly developed oral cavity with different types of teeth adapting to its feeding behavior. Carnivorous reptiles usually display sharp, conical teeth that are adapted to seize and grasp the prey; herbivorous reptiles have specialized teeth for cropping the vegetation or have no teeth at all, having instead a pair of horny beaks, like the turtle and tortoise. Many reptiles process food orally to some extent (though true mastication is less developed than in mammals), unlike amphibians. The reptile tongue is extraordinarily diverse, used in everything from the projectile tongue MATS Center For Distance & Online Education, MATS University

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of mandibular symphysis in some species, especially snakes. The stomach of reptiles is usually simple and sac-like, with strong acid secretions and pepsin to digest protein. The stomach can physically expand far beyond its resting state in some carnivorous reptiles, especially snakes, which need to accommodate large prey items, along with corresponding increase in acid and enzyme secretion, ultimately allowing them to break down that huge meal. In contrast, herbivorous reptiles such as tortoises generally possess muscular guts specialized for grinding up tough plant material, and often have distinct regions for different tasks in the digestive process.

Reptilian intestines display wide variation with respect to diet. Carnivorous reptiles have short intestines that are simple due to the high digestibility of animal products, whereas herbivorous reptiles have much longer intestines that are often much more complex, allowing plant material time for fermentation and absorption. This pattern follows the carnivore-herbivore dichotomy of other vertebrate groups and is a classic case of convergent evolution among digestive adaptations. There is especially pronounced specialization in herbivorous reptiles including iguanas and herbivorous tortoises, which often have greatly expanded hind guts or ceca that are used for fermentation of the plant material through symbiotic microorganisms to yield shortchain fatty acids that can in turn be absorbed and used as energy sources. This arrangement is functionally similar to the fermentation chambers of herbivorous birds and mammals, although their exact anatomical implementations differ. The reptilian large bowel has significant roles in water resorption and waste consolidation, but such activities are particularly important for terrestrial animals, such as reptiles, which cannot afford to lose much water in feces. The efficacy of these water-saving mechanisms differ among the reptilian clades, and are most effective in those species adapted to desert habitats. Like amphibians and birds, the reptilian digestive tract ends in a cloaca that receives the products of digestive, urinary, and reproductive systems. In many reptiles, especially species that inhabit deserts, the cloaca is also a place for final reabsorption of water before waste leaves the body, which further improves water retention.

There are several notable differences in the physiology of reptiles in regards to digestion, many of these contributing to their ectothermic metabolism and irregular feeding habits. In contrast to endothermic birds and mammals, which maintain relatively stable body temperatures, reptiles show marked temperature dependence in digestion. In fact, generally, as body temperatures rise digestion is sped up as the activity of digestive enzymes increases and gastrointestinal motility (movement) increases; for this reason many reptiles will thermoregulate behaviorally following a meal, seeking out hotter microhabitats to improve the efficiency of digestion. At extremely high or low temperatures, though, digestion can stop altogether, with food sitting packed in the stomach, unprocessed, until conditions become more favorable again. Many reptiles, especially carnivorous varieties like large snakes, exhibit notable physiological plasticity to adapt to irregular, massive feeds, a phenomenon termed sit-and-wait or ambush feeding. After the consumption of prey which can make up to almost 100 % of the predator's body mass in some snake species, reptiles like these show massive acute upregulation of digestive function, a physiological occurrence called the: "specific dynamic action" or postprandial metabolic response. This includes the rapid proliferation of intestinal epithelial cells, increased production of digestive enzymes, increased blood flow to digestive organs, and upregulation of nutrient transport systems, all in an effort to efficiently clear and process the large meal before putrefaction can take place. During the intervals between these rare feeding events, digestive function is likely greatly downregulated, including atrophy of the intestinal mucosa and diminished secretion of digestive enzymes to conserve energy during this and frequently prolonged fasting state. This extreme plasticity in digestive function represents a specialized adaptation to feast-or-famine feeding ecology, distinctly different from the relatively stable digestive states maintained with greater frequency in most mammals and birds.

Reptiles digestive glands are similar to other vertebrate groups but also have specializations. The reptilian liver is large and performs similar functions as in other vertebrates, including bile production, detoxification, and metabolic regulation.

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However, in many classes, especially those that undergo seasonal deprivation of food, the liver is used as an energy reserve and a vital site for glycogen and lipid storage that can be used during periods of fasting. The gallbladder is usually intact and waiting to squirt some bile out during a meal. As in other vertebrates, the pancreas secretes a complementary set of digestive enzymes, including proteases, amylase, and lipase; it also secretes hormones for blood glucose homeostasis. One common aspect of many reptiles is the marked downregulation of these digestive glands during fasting, with decreased or absent secretion until after feeding when stimulation resumes. Differences in gut microbiota composition are notably associated with diet, as specific microbes present in the gut microbiota of herbivorous reptiles contribute to their ability to ferment plant-derived materials, and particularly the complex polysaccharides that are resistant to degradation by the host's endogenous digestive enzymes. These microbial communities are particularly critical for hindgut-fermenting reptiles such as tortoises and iguanas. On the other hand, even strictly carnivorous reptiles harbor abundant and diverse gut microbiome that can assist digestion, immunity, and other physiological processes. The critical nature of these microbial assisting roles in reptilian digestion shall not be underestimated, as the negative effects of antimicrobial medications on digestive function in captive reptiles, especially with herbivorous representatives, have been widely reported. All of these systems have been adapted to meet the challenges associated with the transition to land, ectothermic metabolism, and different feeding modes, demonstrating the diversity in digestive anatomy and physiology found in this vertebrate class.

#### Birds

As flight imposes particular challenges, and the demands of endothermy are energetically costly, the avian digestive system displays many unique adaptations that are based both on original reptilian "body plan" features and highly derived specializations. Probably the most obvious difference with the avian digestive system is the utter lack of teeth, which were lost sometime in evolution and replaced by a relatively lightweight beak of keratin that allows for a high diversity of feeding mechanisms but a what would seem to be processing abilities that leave much to be desired; This loss of teeth is an adaptation, allowing a lighter head for flight, while the mechanical functions of teeth were transferred to other sites within the digestive tract. Birds have a unique muscular tongue which varies substantially in morphology between species, from the hard, pointy tongues of insectivorous birds to the soft tongues of frugivores to the specialised tongues found in nectarivorous species such as hummingbirds and honeyeaters. The tongue assists in the manipulation of food during chewing and in swallowing, but generally has little function in chemical digestion. The avian esophagus is muscular and distensable and may contain a specialized outpocketing known as the crop. This expandable sac acts as a temporary storage chamber through which birds can rapidly ingest food for a long-term unique digestive process elsewhere. The crop is especially developed in granivorous (seed-eating) species and in some other groups, such as pigeons and doves that secrete crop "milk" to feed nestlings. The cropping function of food storage has multiple adaptive benefits, such as decreased time spent foraging in potentially risky exposure, transport of food to nestlings, and initial softening through hydration. Apart from specialized features of the anterior digestive tract, birds also have distinctly a avian two-chambered stomach which mainly consist of proventriculus and gizzard which are the site of chemical and mechanical digestion respectively.

The avian stomach is one of the most specialized segments within vertebrate digestive systems as it consists of two functionally and anatomically distinct chambers. Many glands in the proventriculus or glandular stomach (anterior chamber) secrete hydrochloric acid and pepsinogen for the initiation of protein digestion by means of chemicals. This region is functionally equivalent to the glandular stomach of other vertebrates. The posterior chamber, the ventriculus or gizzard, is highly muscularized with a abrasive, koilin lining (a protein akin to keratin) that in many species operates in concert with consumed grit or stones (gastroliths) to mechanically pulverize food. That grinding action replaces the physical processing that would otherwise happen with mastication, providing

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an elegant solution to the evolutionary problem of toothlessness. The development and shape of the gizzard can vary dramatically according to diet, being more highly developed in granivorous birds that eat hard seeds and nuts, and less developed in carnivores and frugivores, whose diets are less reliant on mechanical processing. This two-chambered arrangement of the stomach demonstrates that selection pressure acts to allocate digestive processes to different regions of the alimentary canal when ancestral forms are evolutionarily constrained (here, by the weight limitations imposed by flight).

#### UNIT 11

#### **Comparative Account of Respiratory Organs in Vertebrates**

#### **Definition and Importance of Respiration**

Respiration is one of the basic physiological processes by which organisms interact with their environment to absorb oxygen and excrete carbon dioxide. Oxygen is a necessary ingredient of the process used for cellular metabolism, as it utilized as the terminal acceptor in the electron transport chain, allowing for the production of ATP via oxidative phosphorylation. Although a cell cannot use an abundance of energy, without proper respiratory mechanisms, cells would be unable to produce enough energy to perform its essential functions, resulting in cell dysfunction and finally organismal death. Respiration, in its most basic sense, can be divided into two processes; external respiration is the gas exchange between the organism and its environment through respiratory organs and internal respiration gets the use of oxygen and the production of carbon dioxide on a cellular basis. The efficiency of these processes is critical for homeostasis and meets the differing metabolic needs of vertebrate organisms adapted to diverse ecological niches and activity patterns. Respiration, however, is a lot more than just exchanging gases. It is essential for maintaining acid-base homeostasis by modulating carbon dioxide levels, regulates temperature in endothermic vertebrates through loss of heat with evaporation, and in some aquatic vertebrates, the respiratory surfaces participate in osmoregulation and nitrogen excretion. Furthermore, the adaptive radiation of respiratory mechanisms has
been an important factor that has facilitated habitat exploration by vertebrates, enabling vertebrates to inhabit a wide range of ecosystems, including aquatic and terrestrial environments, as well as different levels of metabolism which are associated with varying lifestyles and ecological niches.

#### The role of vertebrate respiratory organs

Respiratory organs are specialized anatomical structures in vertebrates that mediate chemical exchange with the internal environment of the organism and external environment. These structures have adapted over evolutionary time to optimize gas exchange in environmental media and metabolic requirements. The primary jobs of respiratory organs are to maximize diffusion surface area, keep the distance for diffusion very small between the environment and blood (the thin the distance slow the exchange via gradient) and ventilation (which is required to maintain the difference in concentration). However, extracting oxygen from water, a medium that contains only one-twentieth of the oxygen of the same volume of air and that is more dense and viscous, requires highly specialized respiratory organs in aquatics vertebrates. Such adaptations usually consist of gill structures that are richly perfused with blood and extract dissolved oxygen from water flowing over their surfaces. Terrestrial vertebrates, in contrast, have to contend with the risk of desiccation and need structural support to avoid collapse of the respiratory surfaces. They have modified lungs that are used internally and have multiple branching with a high level of internal surface area that keep the lung sacs from drying out. Respiratory systems in vertebrates are also well integrated with the circulatory system to allow gases to be transported efficiently throughout the body. For example, the development of specialized respiratory pigments, such as hemoglobin, has increased the blood's oxygen-carrying capacity, and various cardiovascular adaptations, including the gradual separation of pulmonary and systemic circulations, have increased the efficiency with which gases are transported to match the metabolic needs of more complex vertebrate body plans and lifestyles.

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**ANATOMY II** 

#### Fishes: Multitude of Gill Structures



The most diverse vertebrate class, fishes have invaded nearly all aquatic habitats ranging from freshwater to marine environments and their corresponding respiratory structures highlight this ecological diversity. Gills are the main respiratory organs of fish and they are highly vascularised structures adapted to extracting dissolved oxygen from water. This is highly encouraged by the fact that the gill filaments are stacked in rows along bony or cartilaginous arches known as gill arches, which gives rise to the basic structure of these organs, not to forget the many secondary lamellae attached to the filaments, offering an enormous surface area for gas diffusion. In most teleost (bony) fishes, the respiratory system consists of four to five pairs of gill arches with primary gill filaments, and the gills are covered within an opercular cavity on both lateral sides of the head. Water enters through the mouth, flows over the gills then out through opercular openings in a unidirectional flow that maximizes the efficiency of gas exchange. Coordinated expansions and contractions of the buccal and opercular cavities established a pressure differential that assists in the movement of water over the surfaces of the gills. Cartilaginous fishes (sharks, rays, and chimaeras) have a different gill architecture, characterized by five to seven gill slits located on either side of the pharynx and are not covered by a protective operculum. Like other fishes, they have pairs of gill pouches which open separately to the outside; water flow is ensured through swimming with the mouth open (ram ventilation), or using active pumping mechanisms. This enables effective gas exchange while minimizing resistance to prograde thrust in these relatively active predators.

Some groups of fish adapted to environmental extremes show specialized respiratory adaptations. They have both gills and primitive lungs, which evolved from the swim bladder, and they can breathe air during droughts or when living in oxygen-poor waters. The even more diverse "labyrinth" organs of anabantoid fishes (e.g., bettas and gouramis) and the specialized pharyngeal chambers of walking catfish are also considered supplemental air-breathing structures, demonstrating convergent evolution of respiratory adaptations in response to the same ecological pressures, as well. The opposite-direction arrangement of blood and water flows in fish gills was one very efficient design to help accomplish this

gas exchange. The blood moves counter to water flow as it flows over the surfaces of the gills, this maintains a favorable concentration gradient for oxygen to diffuse throughout the length of the exchange surface. This leads to a high-efficiency process of oxygen extraction, enabling fish, despite the considerably lower oxygen concentration in water than in air, to extract 80-90% of the oxygen present in water.

#### **Amphibians: Breathing From the Inside Out**

Amphibians represent the first group of tetrapods to originate from a semiterrestrial ancestral condition, placing them at a critical juncture in vertebrate evolution, and their respiratory systems have evolved in such a way to display a considerable array of structures and strategies used for gas exchange. Most adult amphibians employ several respiratory surfaces, such as simple saccular lungs, the richly vascularised skin (cutaneous respiration), and in some species; the buccopharyngeal cavity. While this may seem less than efficient as a gas exchange method, this unique combination of aquatic and terrestrial respiration is more of an evolutionary trade-off to better adapt the organism to the challenges of life in the water and on land. Compared to amniotes, lungs of amphibians are relatively simple and usually consist of paired sacs with little internal compartmentalization. Lungs in frogs and toads have a few internal ridges that increase surface area, salamander lungs are more like simple sacs and have less compartmentalization. Limbless amphibians called caecilians possess asymmetrical lungs, with the right lung usually longer than the left, an adaptation tied to their long body shape. Although their lungs are relatively simple in structure, amphibians do have lungs, providing a supplementary source of oxygen, particularly during times of increased metabolic activity. In amphibians, cutaneous respiration is of critical importance, as they have highly vascularized skin that acts as a principal site of gas exchange. For example, in members of the family Plethodontidae, lungs have been completely lost, and the functions of these organs are instead performed directly across the skin and buccopharyngeal cavity. Being small, having a low metabolic rate, and occupying moist habitats prevent drying Notes



out of the respiratory surfaces, allowing this adaptation. The fact that they rely on cutaneous respiration also limits the body size and ecology of this group of amphibians, emphasizing the trade-offs associated with different respiratory strategies.

Amphibian breathing is very different from that of other land vertebrates. Unlike mammals, which rely on a diaphragm and inspiration to fill lungs, amphibians have little rib movement and contact a positive pressure system of buccal pumping. In the process, the floor of the mouth drops to bring air in via the nostrils, which are then closed, while the floor of the mouth rises, pushing air to the lungs. Exhalation is passive, propelled by the elastic recoil of the lungs and the pressure of abdominal organs. In order to transition to terrestrial respiration, however, it is clear that something further was needed — and indeed this mechanism, while less efficient than the negative-pressure breathing of amniotes, represented a significant step in evolutionary history. Larval amphibians have a third respiratory trick up their sleeve, commonly using external gills throughout their life in water. These small, feathery structures are located along the gill arches and provide a large surface area for gas exchange in water. As metamorphosis continues, these external gills are usually lost or incorporated into the body, and the switch to pulmonary and cutaneous breathing happens. We discuss how this ontogeny tracks the evolution of habitation from an aquatic environment to a terrestrial one, and how it emphasizes the developmental plasticity of the amphibian breathers.

#### The Classification of Class Reptilia: Adaptations for Life on Land

Of all the vertebrate groups, reptiles show the greatest advance in adapting to life on land, and their respiratory systems fully reflect this commitment. Unlike amphibians that tend to depend on cutaneous respiration systems, almost all of the reptiles' skin is relatively impermeable, keratinized skin which minimizes water loss but additionally carries a higher demand for efficient pulmonary gas exchange. In the evolution of the lung, one can see significant improvements in metameric compartmentalization and access to increased surface area for gas exchange between the amphibian and reptilian lung. The fundamental architecture of the reptilian lung differs quite a bit between groups. In squamates (lizards and snakes), there is usually some form of compartmentalization, where the anterior portion of the lungs is more subdivided and vascularized than the posterior region. This heterogeneity results in a functional gradient in the lung, with gas exchange occurring predominantly in the more anterior, more subdivided regions. In snakes, elongated body shape has caused asymmetrical development of the lungs, which are normally well-developed on the right side but reduced and/or vestigial on the left side. Some snakes also have tracheal lungs that branch off from the trachea, providing extra surface area for gas exchange. Chelonians (turtles and tortoises) have a multichambered lung with numerous internal subdivisions to increase surface area. The rigidity of their shell restricts the thoracic breathing functions found in other amniotes, necessitating unique ventilation modes. The lungs of crocodilians are the most complex of the reptiles, having extensive branching and compartmentalization so that they approach the complexity of those in birds. They also have a complete secondary palate and a muscular diaphragmaticus that aids in more efficient ventilation, adaptations that are likely due to their active predatory lifestyle and semi-aquatic environment.

In most reptiles, pulmonary ventilation occurs by costal (rib) movements and visceral movement. Okay, so when the ribs move out and up, the thoracic cavity expands, generating negative pressure that well, sucks air into the lungs. Opposite contraction of the intercostal muscles and movement of the visceral mass then compresses the lungs, forcing air out. The genesis for this is an interesting evolutionary development, because the ability to pull rather than push air is far to the evolution of reptilian lung structure outstrips amphibian buccal pumping. The unique aspect of reptilian respiration is how they utilize a single, undivided ventricle (in contrast to the completely divided ventricle of crocodilians). Despite this potential disadvantage, reptiles achieve functional separation of oxygenated and deoxygenated blood through anatomical features — such as muscular ridges within the ventricle — as well as temporal separation of pulmonary and systemic blood flow. Such a configuration also enables cardiac shunting, or the capacity to redistribute blood flow between the pulmonary and systemic circulations based on physiological demands, such as during diving or basking.

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#### The Avian Respiratory System and Air Sacs

Because birds are very specialized in all functions of their bodies, their breathing system is one of the most efficient gas exchange systems among vertebrates, through a special structure of the lungs (parabronchi) and air sacs that allows a unidirectional flow of fresh air. These adjustments in physiology accompany the increased metabolic demands of powered flight and endothermy, enabling birds to actively maintain activity at high altitudes, where atmospheric oxygen partial pressure is dramatically lowered. The remarkable efficiency of avian respiratory system is illustrated by fact that it can extract oxygen from incoming air with almost double the efficiency as the mammalian system. The avian respiratory system is built on the foundation of AP- structures like comparatively fixed and inextensible lungs, paired with an extensive series of nine air sacs that serve as bellows for air movement through the respiratory system. These numerous air sacs extend into the bones (the pneumatisation) and throughout the body cavity, serving to lighten the bird for flight and utilizing the volume changes required for ventilation. These air sacs consist of pair of cervical, anterior thoracic, posterior thoracic, and abdominal, plus an unpaired interclavicular air sac. The lungs of birds are parabronchial, consisting of many small, parallel-running, continuously ventilated tubules (parabronchi). From these parabronchi, smaller air capillaries branch out and mingle with blood capillaries, creating a huge surface for gas exchange. This orientation allows for crosscurrent exchange, as blood traversing through the air capillary network runs nearly perpendicular to the air flow through the parabronchi, improving the efficiency of oxygen extraction beyond that of simple countercurrent or concurrent exchange systems.

Avian respiration is characterized by this unique airflow through the lungs, which happens during both the inhalation and exhalation phases of the breathing cycle; in fact air flows in a single direction. This is accomplished by a process of how air flows through the respiratory system over two full cycles of breathing: new air flows into the posterior air sacs on inhalation, flows through the lungs on the first exhalation, flows into the anterior air sacs on the second inhalation, and finally exits the system on the second exhalation. This unidirectional flow of fresh air through their gas exchange tissues is unidirectional and continuous, avoiding the dead space ventilation of the tidal breathing used by mammals that limits ventilation efficiency. Bird lungs operate via a system of air sacs in the bird's body, coordinated by the action of the sternum, ribs, and abdominal muscles to alter the volume of the air sacs. During inspiration, the sternum shifts ventrally and the ribs shift cranially, enlarging the thoracoabdominal cavity and pulling air into the posterior air sacs. The sternum moves dorsally (backward) and the ribs caudally (downward), compressing the air sacs and pushing air through the system during exhalation. With this mechanism and the unidirectional pattern of airflow, birds are able to carry out efficient gas exchange during powered flight and also at high altitudes where the oxygen levels are low.

#### Mammals: The Respiratory System of Mammals

The mammalian breathing system comprises an enhanced arrangement for the land, including a highly divided lung with millions of years of intense internal division, giving the gas exchange region crazy surface region. These adaptations promote a complex pulmonary vasculature and negative-pressure ventilation depended on diaphragm muscles to accommodate high metabolic rates linked with endothermy and wide-ranging ecological niches of mammals in terrestrial, aquatic and aerial systems. Mammalian lungs are composed of a hierarchical branching structure where the trachea first bifurcates into primary bronchi, followed by multiple generations of bifurcations giving rise to smaller armed airways (secondary bronchi, tertiary bronchi, bronchioles, terminal bronchioles). This large degree of branching terminates in respiratory bronchioles and alveolar ducts that open into clusters of alveoli, the main sites where gases are exchanged. The surface area of the human lung epitomizes this incredible efficiency; with about 300 million alveoli, the total area for gas exchange would be 50-100 square meters, all rolled up and house alongside thoracic wall. The alveoli are specialized structures for large amounts of gas exchange making up their walls of alveolar type I pneumocyte (flat serous epithelium) to minimize the difference between air and blood for the purpose of diffusion. Interspersed with these cells are type II pneumocytes, which secrete surfactant, a mixture of phospholipids and proteins

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that lower surface tension and prevents the collapse of the alveoli during expiration. The alveolar walls are richly invested with pulmonary capillaries to form a large air-blood interface that allows the diffusion of gas along their concentration gradients -O2 from the alveolar air into capillary blood and CO2 in the opposite direction.

Mammalian ventilation takes place via a negative-pressure mechanism that relies critically on the diaphragm itself, a muscular sheet in the shape of an inverted dome that delineates the thoracic and abdominal cavities. The diaphragm flattens when it contracts, and the external intercostal muscles lift (expand) the ribs during inhalation, creating negative pressure to draw air into the lung. Exhalation at rest is passive and occurs due to the passive elastic recoil of the lungs and relaxation of respiratory muscles, though during exercise or in conditions of respiratory distress, contractions of the internal intercostal and abdominal muscles may cause active exhalation. Although the basic mammalian respiratory pattern is conserved across species, significant modifications do occur in some groups. Diving mammals - which include whales and seals - also have reinforced airways to prevent collapse under pressure, as well as a greater storage capacity for oxygen in their blood and muscles from having higher concentrations of hemoglobin and myoglobin, plus the ability to restrict blood flow to nonessential tissues during dives, which enables them to conserve oxygen for the brain and heart. Bats, the only true flying mammals, have proportionately larger lungs and more efficient gas exchange surfaces than terrestrial mammals of comparable body size, which can be viewed as adaptations similar to some avian respiratory system features related to the heightened energy demands of powered flight.

#### **Evolution and Development of Respiration and Breathing**

Over hundreds of millions of years, vertebrate respiratory organs have evolved in response to changing environmental conditions and metabolic demands. This trend has driven evolution towards:

· a greater surface area for gas exchange

- shorter diffusion distances between the environment (the respiratory medium) and blood
- more elaborate ventilation mechanisms to maintain higher metabolic rates and levels of activity.

The earliest vertebrates, jawless fishes including extinct taxa like the ostracoderms and living taxa like lampreys and hagfishes, had relatively simple gill structures used for aquatic respiration. This led to the evolution of more organized, countercurrent-arranged gill filament systems and lamellae in jawed fishes which were hydrodynamically efficient at removing atmospheric gases from water. On the other hand, in some fishes lineages, especially in the lobe-finned fishes (Sarcopterygii), primitive lung-like structures—like those found in tetrapods evolved from outpockting of the pharynxs as and supplementary respiratory organs in poorly oxygenated aquatic environaments. These structures would eventually become the evolutionary basis for the lungs of tetrapods. Early tetrapods also had to make radical changes to their respiratory system to adapt to life on land. The lungs of the ancestors wearing down their number became the main breathing organs, and the adult gills lost. Early amphibians still relied heavily upon cutaneous respiration, which persists in modern amphibians. The multicameral, saccular lungs of amphibians, which were ventilated by buccal pumping, were a simpler form of lungs and represented an intermediate evolutionary step toward the terrestrial respiratory systems. As amniotes (reptiles, birds, and mammals) evolved, the area of gas exchange became even more internalized and compartmentalized, and this limited reliance on cutaneous respiration while protecting against drying out in the terrestrial environment.

A later branch of amniote lineages resulted in divergent responses to the water loss breathing problem on land. In mammal lineages, however, the lungs evolved a branching system of alveoli, and the movement of a muscular diaphragm allowed for efficient negative-pressure ventilation. In the lineage that evolved into birds, an astonishingly disparate system evolved comprising rigid, parabronchial lungs ventilated via air sacs and in unidirectional flow pattern. Reptiles still had a more

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primitive lung architecture than birds and mammals but were very diverse in form with some lizards having simple saccular lungs and crocodilians possessing a complex (compartmentalized) lung structure. Such evolutionary trends represent not just adaptations to disparate environmental media (water vs. air), but also responses to rising metabolic demands. The transition from ectothermy characteristic of many fish, amphibians, and reptiles to endothermy in birds and mammals required increasingly effective respiratory systems that would deliver higher rates of oxygen consumption. The independent origins of highly efficient respiratory structures in birds and mammals reflect the selective pressure imposed by endothermy and active lifestyles, leading to convergent evolution even in the context of different anatomical arrangements.

#### Physiological Mechanisms and Functional Adaptations

The variety of respiratory structures found in each group of vertebrates is accompanied by an array of physiological modifications, which increase the efficiency of gas exchange and meet the metabolic demands of different lifestyles and habitats. These adaptations include alterations to the very organ systems responsible for respiration, but they also encompass tunings of circulatory networks, respiratory pigments, and even the pathological mechanisms that integrate the function of respiration with metabolic demands. The evolution of vertebrate physiology has progressed with regard to the integration of respiratory and circulatory systems. In fish, the oxygen-poor blood is delivered directly to the gills for oxygenation, then the newly oxygenated blood is then transported around the body in a single-circuit circulation. During the evolution of air-breathing in tetrapods, a double circulation with separate pulmonary and systemic circuits gradually developed. This system is taken most to its extreme in birds and mammals, in which the oxygenated and deoxygenated blood is completely separated within a four-chambered heart, allowing for maximal efficiency in oxygen delivery to tissues. To compensate for this, oxygen in the animal body is transported via blood, which is further supplemented by breathing organs such as lungs or gills under the control of respiratory pigments like hemoglobin. Despite the conservation of the basic protein architecture of hemoglobin across vertebrates,

there is extensive diversity in the properties of heme–oxygen interactions that signify adaptation to varied oxygen niches and differing metabolic needs. For example, diving mammals exhibit higher hemoglobin oxygen affinity than terrestrial mammals, promoting oxygen loading in the lungs for a short time on the surface. The hemoglobin of hypoxia-tolerant species is also often modified to facilitate oxygen binding at low oxygen partial pressures.

Complex neural and chemical pathways are involved in the control of respiration, as ventilation rate and depth are adjusted to various changing metabolic demands and environmental conditions. In most vertebrates, central chemoreceptors that respond to shifts in blood CO2 levels (indicated by changes in blood pH) provide the most robust stimulus for respiratory change, with peripheral chemoreceptors that assess blood O2 levels providing additional input. Several regulatory systems are showing increasing complexity from fish to mammals, including the mammalian medulla oblongata respiratory control center, which integrates various inputs to optimize performance. At the far end of the evolutionary tree, specializations can be seen among vertebrates living under extreme respiratory stress. Deepdiving marine mammals, for instance, have a suite of specialized adaptations such as increased oxygen storage, selective vasoconstriction and metabolic suppression — that prolong their underwater tolerance. The adaptation of mammalian and avian high-altitude professionals includes the enlargement of the lung volume, increased pulmonary diffusion capacity and hemoglobin changes which improve oxygen uptake in the rarefied air milieu. Species dwelling in arid landscapes typically evolve adaptations in how they respire to minimize water loss, one of which is the use of nasal countercurrent heat exchangers that recover breath moisture from exhaled air to reduce respiratory water loss.

#### **Environmental Challenges and Adaptive Responses**

The various respiratory structures and strategies found among different vertebrate groups are in response to the broad array of environmental challenges. These adaptations have allowed vertebrates to diversify in and colonise nearly every niche on the planet, from deep-sea trenches, mountain peaks, arid deserts to humid forests. Despite the overall unity in the process of physiologic gas exchange, MATS Center For Distance & Online Education, MATS University

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it is driven by the unique challenges of each environment that has shaped the evolution of specialized respiratory systems that efficiently mediate gas exchange while overcoming the added challenges of water loss, buoyancy control, and other environmental toxins. Aquatic environments pose the primary challenge of extracting oxygen from water, which has 30 times less oxygen per unit volume than air and is denser and more viscous. Fish gills are an answer to this problem, as they tradeoff increased surface area and thin epithelium with a countercurrent arrangement of blood and water flow to maximize breathing efficiency. Certain fish species that live in oxygen-poor waters have evolved further adaptations, such as the increased gill surface area observed in the active species tuna and mackerel, or a type of supplementary respiratory organ such as the labyrinth organs present in anabantoid fishes that allow aerial respiration. Amphibious vertebrates face specific challenges during movement transition between aquatic and terrestrial environments. Amphibians have developed multi-modal respiratory paradigms of respiration with cutaneous, buccopharyngeal and pulmonary respiration utilized at different extension (i.e. amphibians demonstrate an evolutionary trade-off supporting dual habitat occupation). Likewise, semiaquatic reptiles such as turtles and crocodilians possess well-adapted internal functionality such as the ability to resorb oxygen through cloacal respiration in select turtle species, as well as their ability to direct blood flow during diving; these adaptations allow for prolonged periods spent in water, all while allowing for an efficient respiration ability in the air when on land.

The terrestrial environment brings the threat of desiccation through the respiratory surfaces, favoring the evolution of amniotes' internalized, compartmentalized lungs. Many of the species have evolved additional specialized adaptations to extreme aridity in desert environments, including nasal countercurrent heat and moisture exchangers in desert rodents, and the ability of desert reptiles to tolerate large body temperature changes, which diminishes the need for evaporative cooling as through panting or sweating that would increase evaporative loss of water. Aerial environments, especially in terms of high-altitudes, are associated with lower partial pressure of inhaled oxygen and decreased air density. As the

vertebrate group most adapted to living in the air, birds have a remarkably well-adapted respiratory system for meeting these challenges. Airflow through avian lungs occurs in one direction, preventing stale air from mixing with fresh air, while respiratory capillaries are placed in a cross current arrangement with the parabronchi they surround, enabling greatly boosted efficiency of oxygen extraction. These adaptations also allow some bird species — which include bar-headed geese — to fly at altitudes of more than 9,000 meters where the partial pressure of oxygen is less than a third of what it is at sea level.

The performance of respiratory organ systems is first, being its results of the comparative method among the groups of vertebrates following the path of evolution with through a story of adaptation and innovation that shows us the close relationship between form and function and the environment of a biological system. At the same time, vertebrate gas exchange systems also showcase evolutionary constraints and historical contingencies, as when the ancestral gills of vertebrate fish were adapter to become the lungs of species-mammals; this connects with the additional amazing process of lungs of mammals to satisfy the large air sac system in birds that allows varying adaptations toward various ecological niches and rates of metabolism. During this evolution, numerous improvements and adaptations occurred, escalating in complexity and compartmentalization from the basic transfer of gases through diffusion over the surface of primitive chordates, to the complex, active ventilation and highly compartmentalized lungs present in mammals, and the unique and efficient unidirectional respiratory system of birds. The evolution of these adaptations has not been isolated, however, but intimately tied to corresponding changes in circulatory systems, metabolic regulation, and behavioral tactics to maximize respiratory function across a wide spectrum of environmental conditions and work rates. Ongoing studies further advance our knowledge of vertebrate respiratory systems, using modern imaging, molecular techniques, and computational models to explore the intricate structural arrangements, developmental pathways, and functional properties of these respiratory regulators. Genomic comparisons are identifying underlying evolutionary

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changes behind respiratory adaptation in different vertebrate groups while controlled environmental physiological approaches are uncovering the physiological limits and plasticity of respiratory function in response to systemslevel challenges, including climate change, pollution, and disease. Such knowledge has implications for our understanding both of basic science and our developed practices in many applied fields. At a basic science level, the developmental and evolutionary origins of respiratory structures provide broad insights into morphogenesis and adaptation. In applied contexts, comparative insights into respiratory physiology inform human respiratory health, artificial respiratory support systems, and conservation strategies for vulnerable taxa facing respiratory limitations due to environmental change. Vertebrate respiratory adaptations are nothing short of extraordinary and continue to serve as a fountain of inspiration and discovery in our understanding of organismal biology, ecology, and evolution.

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#### **Skeletal system- Comparative account**

The origin of skeletal system is one of the central and oldest anatomical novelties in the animal kingdom because it is the basic structure of body shape and a physical organization that supports movement by its complex mechanic interactions with muscles and connective tissues. This extraordinary biological machine has been honed through hundreds of millions of years of evolution, branching into tens of thousands of different versions in various animal lineages, while still retaining its basic functions. At its core, the skeletal system has many essential biological functions; it provides structural support against gravity, it protects essential organs, it enables the motion of muscles, it acts as a storage facility for calcium and phosphate minerals, and it houses hematopoietic tissue, which produces blood. Developments of skeletal systems represent key steps in the transition to increasingly complex animals, facilitating increasing body size, mobility and complex predator-prey interactions. From the hydrostatic skeletons of simple invertebrates to the complex endoskeletons of mammals, the evolution and development of skeletal structures are tightly linked to an organism's ecological niche, locomotory needs and evolutionary history. The plethora of skeletal configurations we see around us today presents an extraordinary case study of how natural selection has tailored skeletal anatomical systems to tackle the unique challenges that organisms encounter in their surroundings. As such, the comparative analysis of skeletal systems provides important information on evolutionary relationships, developmental constraints, and adaptations among various lineages in the animal kingdom. Studying homologous structures among various vertebrate lineages enables scientists to piece together evolutionary trajectories and understand the genetic and developmental pathway underlying skeletal diversity. With comparative approaches, the remarkable conservation of basic skeletal patterns among vertebrates, as well as the evolutionary innovations that have arisen in response to particular environmental pressures, are clear. The evolutionary history of the skeletal system exemplifies a balance between rigidity and flexibility, between conserved development and evolutionarily mediated change. It indicates how biological systems could preserve basic structural functions whilst also embracing incredible functional diversity. The evolution of the skeletal system, from the primitive notochords found in early vertebrates to the intricate endoskeletons seen in contemporary mammals, sheds light on more general laws of evolutionary biology and functional anatomy.

#### **Types of Skeletons**

**Hydrostatic Skeletons:** Before we turn to the primary skeletal types, it is important to note that many invertebrates make use of hydrostatic skeletons — fluid-filled cavities surrounded by muscles that provide structural support through the incompressibility of liquids under pressure. No skeletons, however, no bones — just ocean softies like the bacteria-sized creatures that will eventually grace the ancient sea floors, or the jelly-things or the worms, which we'll hear more about later, an early evolutionary solution to the problems of support and movement. Hydrostatic skeletons function with Pascal's law: when pressure is

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applied in a pressurized body of fluid, the pressure is distributed uniformly in all directions (that is the definition of a fluid) and that creates controlled deformations in the shape of the organism (if the organism can push muscles against a hydraulic-filled cavity). It is this system that powers an earthworm's peristaltic movement and a jellyfish's jet propulsion, showing that even though it looks deceptively simple, powerful things can come in small packages. Hydrostatic skeletons, though lacking the rigid components of more complicated skeletons, also have many advantages such as flexibility, self-repair capabilities, and functioning without the metabolic expense of mineralised tissues. Such systems show that evolutionary solutions to the same basic mechanical problems can (and do) arise through completely different structural arrangements from those found in vertebrates.

**Exoskeletons:** Exoskeletons are an evolutionary innovation that first appeared in arthropods-insects, crustaceans, arachnids, and their relatives-who together make up Earth's most diverse animal phylum. This external skeleton is a tough cuticle made up of mostly chitin (a polysaccharide) and protein, which is sometimes strengthened with calcium carbonate in crustaceans. The exoskeleton multiple functions at once: it provides structural support, it protects against predators and environmental hazards, it prevents desiccation in terrestrial environments, and it creates points of attachment for muscles. The arthropod ectoskeleton is remarkably advanced in its architecture, generally composed of several layers with distinct mechanical properties. The epicuticle is the outermost layer that provides waterproofing and chemical resistance, while the procuticle beneath provides mechanical strength through its chitin-protein matrix. Many crustaceans calcify their exoskeleton too, making a tough protective shell. The process was so complicated that more than one sea creature has to undergo molting (ecdysis), in which they shed the skeleton and secrete a new, larger one, because one of the major limitations of the exoskeletal system is that they cannot grow in unison with the rest of the organism, posing several challenges to its survival. This process corresponds to a critical period in the arthropod life cycle where great energy is expended, and the organism is temporarily devoid of its most prominent protective feature. Even with this limitation, the exoskeleton has been remarkably successful inside the phylogenetic tree, allowing arthropods to invade practically every habitat on Earth and to diversify into millions of different species.

The evolutionary success of the exomusculature comes down to a few key points: it offers great protection for the investment, hinders water loss in land-living conditions, and creates a mechanical loop system that enables precise movement with joint flexing. For instance, the insect exoskeleton is lightweight and has aided the evolution of flight, while the crustacean calcified exoskeleton provides strong protection against predation in aquatic environments. The exoskeleton of arthropods has been adapted to many uses and it can be seen how the mouthparts of insects or the defensive spines of crustaceans, as examples, exemplify this diversity. Exoskeletal elements extend down the animal kingdom beyond arthropods. Mollusks generate shells made of calcite (primarily calcium carbonate), and echinoderms secrete calcium carbonate crystals into dermal tissues that dress and give rise to test plates and spines. These type of exoskeletons show the many different evolutionary paths that support and protection systems have taken in various animal lines, independent from each other.

**Endoskeletons:** Representing the upmost distinguishing feature of the chordate group, notably the vertebrates, the endoskeleton is an internal skeletal system embedded within the body tissues. While the exoskeleton forms a single continuous barrier external barrier, the endoskeleton is composed of discrete elements (bones and cartilage) contained in soft tissues and serves as an internal framework that grows continuously with the organism. This arrangement of an internal skeleton that is actually a characteristic of larger organisms that actively provide structural support while maintaining their flexibility and eliminate the need to shed their arthropods on a regular basis. The vertebrate endoskeleton evolved from a complex of structures dating back to the notochord — a flexible, rod-like structure made of vacuolated cells and surrounded by fibers — that provided support along the axis of the body in primitive chordates. In many vertebrates, the notochord like structures persist in the form of intervertebral discs in mammals.

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This evolutionary composite of a notochord and a vertebral column is had also been one of the major innovations in vertebrate evolution, forming a segmented axial support system, necessary for flexible movement and to protect the spinal cord. The endoskeleton of vertebrates consists mainly of two specialized forms of connective tissue — cartilage and bone. Cartilage, which is made up of chondrocytes surrounded by a flexible matrix of collagen fibers and proteoglycans, serves as an embryonic precursor for many bones, and also serves as a structural material in some places throughout life. Bone, in contrast, has a mineralized matrix of crystal calcium phosphate (hydroxyapatite) deposited within an organic scaffold of collagen fibers to form a material with extraordinary mechanical properties—high tensile strength and considerable compressive resistance.

This endoskeletal system has some major advantages for the process of evolution: In contrast to exoskeletons, endoskeletons can grow gradually with the organism, meaning that arthropods avoid the vulnerable molting phases. Because the skeleton is located internally, vertebrates can achieve larger sizes than would be possible with an external skeleton, an exoskeleton. Furthermore, the segmented arrangement of endoskeletal elements enables the evolution of maximal joint specialization, furthering the potential for diverse movement and mammalian locomotor innovation. Most important, perhaps, is the fact that the endoskeleton has muscles attached to lever-like bones by way of tendons, which forms a mechanically efficient system for movement. Because the vertebrate limb incorporates many degrees of freedom, this arrangement facilitates fine control over applying force and inducing movement to the structure, which likely contributes to the impressive variations of locomotion seen among vertebrate lineages. The endoskeletal system has shown outstanding adaptability to diverse locomotor requirements from the swimming of fish to the flight of birds and the bipedal gait of humans. Endoskeletal elements are found mainly in vertebrates, but also occur in some invertebrate groups. Examples include the calcite skeletons (ossicles) of the echinoderms and the internalized shells or cartilaginous structures of cephalopod mollusks such as squid and cuttlefish. They illustrate an important principle of evolutionary biology, as this is a case of convergent evolution toward internalized skeletal components, which despite variation remain remarkably similar and indicate the advantages of such endoskeletal systems for different animal lineages.

#### **Comparative Anatomy Skeletal System**

**Axial Skeleton:** It is composed of the skull, vertebral column, ribs, and sternum The axial skeleton forms the vertebrate body's central axis through which vital organs and neural structures are housed. This part of the skeletal system is an example of te remarkable inherent conservatism of evolutionary patterns in vertebrates, but also evolutionary plasticity, adapting to numerous ecological niches and locomotor demands.

The Skull: The vertebrate skull is among the most complex skeletal framework made up of many bones forming around the brain and sensory organs, and behind feeding and respiration. Most importantly, the development of the skull gives insight into the intermediate modifications that took place from the original state of early vertebrates to the specialized configuration observed in most mammals, birds, and reptiles today. In basal vertebrates, the skull mainly comprised a cartilage (chondrocranium)-based braincase that protected the brain and sensory capsules that contained organs of the special sense. As vertebrates evolved, dermal bones — which develop in the skin and not in the cartilaginous tissue of the embryo - covered this primitive braincase, forming a heavier covering. In modern vertebrate skulls, this compositional construction remains apparent in the fusion of chondrocranium and dermal elements, albeit the relative contribution of each is widely heterogeneous between groups. However, comparative analysis shows a trend of skull consolidation through vertebrate evolution. Fish also have many independent cranial elements that are often only loosely joined to allow special jaw function and gill ventilation. Compared to fish, amphibians also demonstrate a loss of cranial elements, most notably the gill-associated opercular bones. There is even more fusion of bones in reptiles, as adjacent bones show strong sutures and developing ossifications which create a stronger cranial matrix. While mammals evolved a

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widely varied array of cranial forms, birds are highly cranially specialized, with many elements fused to form a light-weight, strong skull optimized for flight. Mammals have the most aggressively consolidated skulls, with fewer but larger cranial elements tightly sutured together.

The mammalian skull is an exemplary case of how developmentally derived constraints co-act with physical constraints to shape cranial anatomy. In the course of evolution of the mammals, some bones that constituted the jaw articulation, in the descendants of reptiles were incorporated in the middle ear and developed the specific tympanic ossicles of mammals (the malleus, incus and stapes). This stunning repurposing reminds us that those new structures can be dramatically altered to fill different roles, yet retain their embryological heritage. The vertebrate skull shows spectacular specializations with respect to feeding ecology as well. Carnivorous mammals tend to have pronounced sagittal crests for the attachment of powerful temporal muscles, whereas herbivores have expanded areas for attachment of masticatory muscles adapted for grinding vegetation. A wide variety of cranial modifications exist in birds: teeth have disappeared and been replaced with lightweight, keratinized beaks that have adapted to a variety of feeding strategies ranging from the beaks of raptors (procured for ripping flesh) to the specialization of filter-feeding flamingos.

The Vertebral Column: Vertebrates are defined by a unique bodyplan feature the vertebral column, which developed as a series of segmented vertebrae surrounded the notochord and later replaced it, forming the primary axial support structure and its main component the spinal cord. This fascinating feature has evolved extensively among vertebrates whilst preserving its primary function of providing axial support, safeguarding the spinal cord and enabling locomotion. Vertebrae typically consist of a weight-bearing vertebral body (centrum), vertebral arch, and several vertebral processes. This basic pattern exhibits amazing diversification among vertebrate lineages, taking into account different locomotor strategies and environmental constraints. Fish tend to have many (and relatively simple) vertebrae, with little or no regional diversity. Lateral undulation, the primary swimming motion, is primarily facilitated by the vertebral columns, while the caudal region is specialized to support the tail fin. In comparison, fewer regional adaptations are observed among amphibians, but those that are, are more distinctive, particularly in the evolution of a specialized sacral region to articulate the vertebral column with the pelvic girdle, a major adaptation to locomotion on land.

In reptiles, there is a higher degree of specialization of the vertebrae, differentiating the regional segments of the spine into distinct cervical, thoracic, sacral, and caudal sections. This is because multicondylar joints, i.e. joints at which multiple axes meet, were able to provide more stability without removing flexibility in the animal and this phenomenon is not rare to see among reptiles which have additional articulations between successive vertebrea (zygapophyses and accessory articulations). Birds show the most remarkable aspect of vertebral evolution among vertebrates an extreme fusion of many elements leads to numerous stiff portions, which are critical for meeting the mechanical needs of flight. The bird neck is highly flexible to compensate for reduced mobility in other segments of the vertebral column. Although there is some variation in the number of these vertebrae across species, mammals exhibit the most apparent regionalization of the vertebral column: the naming of the regions is generally based on vertebrae present in those regions, including cervical, thoracic, lumbar, sacral, and caudal. Furthermore, the cervical column is composed of seven vertebrae in almost all mammal species (178), from the short-necked (e.g., whales) to the long-necked (e.g., giraffes), and constitutes one of the most abrupt cases of developmental constraint in vertebrate macroevolution (339). Locomotor adaptability in the thoracolumbar region is notably very different in different types of walking mammals.

**Ribs and Sternum:** In centuries past, the ribs and the sternum became paramount members of the axial skeleton (collective member of the ribs, spine, and skull), straddle the thoracic cavity, guarding essential organs from damage whilst also

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serving the purpose of allowing for expansion of the lungs upon movement of the ribcage around these fusion points. Differences in body form, mobility, and respiration between the two are revealed in comparative anatomy of the structures. Within each segment between vertebrae are series of serially repeated ribs that run into their myoseptum (connective-tissue wall that separates the muscle), giving structural support to segments of the body wall, but not forming a thoracic cage. As amphibians have a more aquatic lifecycle and will use a combination of respiration including buccal ventilation, they tend to have shorter ribs that are not formed into a complete ribcage. In reptiles ribs well developed and articulated with most vertebrae, forming in conjunction with a sternum a complete thoracic cage. Literal translation of an elongated body and skeletal structure translates to snakes expanding their rib length along most of their body length, which helps the snake squirm on the ground and protects the organs along the long body. In turtles, ribs are heavily modified, fused with dermal elements to make the characteristic carapace, a stunning example of skeletal evolution.

Particularly telling in birds are the highly specialized ribs and their unique uncinate processes—posterior projections that overlap adjacent ribs, reinforcing the thoracic cage against the strains incurred during flight. The sternum becomes modified in birds so that a large keel (carina) projects from it, providing points of attachment for the massive pectoral muscles that power the downstroke of flight. Because flightless birds rely less on these muscles, they often have reduced keels. Mammals have a cage structure in the thorax due to ribs that connects with the thoracic vertebrae behind and sternum in front, allowing for ribs to move during costal respiration using distinct intercostals and diaphragm. In most mammals, the sternum develops from multiple sternebrae that fuse to form a singe mid-line structure that protects thoracic organs and serves as an attachment point for ribs and pectoral muscles.

#### **Appendicular Skeleton**

The appendicular skeleton, which includes the pectoral and pelvic girdles and their supporting limbs, is one of evolutionary conservation greatest successes and adaptive radiations of vertebrate anatomy. Yet, if there is a mind boggling diversity of vertebrate limbs from fish fins to bird wings, and primate forelimbs, comparative analysis shows that a basic scheme, preserved for more than 400 million years, has been sustained but through extraordinary functional specialization.

**Pectoral Girdle and Forelimbs:** The pectoral girdle connects the forelimbs to the axial skeleton and stabilizes the forelimbs in a flexible way for many functions seen throughout vertebrate evolution. By contrast, the comparative anatomy of this structure reflects a history of evolutionary loss of parts, yet also functional specialization. In basal fish, the pectoral girdle is comprised of multiple dermal bones derived from the skull, forming a stiff framework providing structural support to pectoral fins. As the vertebrate lineage made the transition to land, this arrangement was modified significantly, giving even more importance to the endochondral elements (scapula and coracoid) that offered increased attachment sites for the muscles that propel limb motion. The typical amphibian pectoral girdle exhibits a loss of many of the dermal elements along with a prominent scapula and coracoid bones which are indicative of the evolutionary transition from the aquatic to the terrestrial phase. Reptiles exhibit more variation, including differences in the relative size and arrangement of the scapula, coracoid and clavicle dependent on locomotor strategies. Birds show extreme pectoral girdle specialization related to flight. The scapulae are long and blade-like, and the coracoids are stout struts designed to withstand the compression forces imparted by the powerful downstroke of flight. The clavicles articulate to create the furcula (wishbone), which functions as a spring, storing and releasing energy throughout the flapping cycle.

Pectoral girdle is highly modified in mammals with coracoid reduced or absent as a separate element (as coracoid process of scapula) and clavicle either retained or lost depending on function of forelimb. Cursorial mammals (horses, deer) have completely lost the clavicle, accomplishing a more stable attachment of the forelimb onto the axial skeleton entirely through muscular connections.

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Arboreal/ and brachiatating mammals(e.g. primates)maintain well developed clavicles, about which considerable distance of forelimb from thorax is maintained, providing more mobility. Of course, the tetrapod forelimb is one of the best-known examples of homology in vertebrate anatomy, in which the same basic components — humerus, radius, ulna, carpals, metacarpals and phalanges — are adapted in function for very different purposes. This archetype, which was present in early tetrapods such as Ichthyostega, has been conserved for more than 350 million years of evolution and yet allows for some astounding specialization. In amphibians, the forelimb is still relatively generalized, configuration suitable for both aquatic paddling and terrestrial locomotion. From lizards with sprawling limbs to snakes with vestigial limbs and marine reptiles with flippers, forelimb modifications are diverse among reptiles.

In birds, extreme forelimb specialization for flight is exemplified by elongation of the manus elements, reduction in the number of digits and fusion of skeletal elements distal to the wrist to create a bony support structure for the tissue of the flight feathers, which is both compliant and light. These adaptations illustrate that the pentadactyl limb pattern can be radically altered yet retain its core developmental architecture. Forelimb adaptations are arguably the most diverse among vertebrates and reflect the occupation of several ecological niches by mammals. The long radius and ulna support the wing membrane in bats, while a big humerus supports strong muscles for digging in moles. The limb is specialized for rapid and efficient locomotion with reduction and fusion of carpal elements and loss of lateral digits in ungulates. Opposable thumbs and precise control of individual digits have given primates greater manipulative ability, while whales and dolphins have adapted the pentadactyl limb for swimming through proportional modification, rather than radical structural alteration.

**Pelvic Girdle and Hindlimbs:** The pelvic girdle connects the hindlimbs to the vertebral column, usually via sacral articulation that transmits forces between the appendicular and axial skeletons. Specialized structures show evolutionary alterations associated with locomotor specialisation, especially during the shift to

terrestrial environments and further towards a variety of locomotor behaviours. In fish the pelvic girdle is usually a rudimentary cartilaginous or bony structure embedded in the body wall without a direct link to the vertebral column and this reflects the minor role pelvic fins have in propulsion for most species. Transition to land would necessitate a much stouter pelvis to support the weight of the body and provide propulsive forces, necessitating the evolution of the classic tetrapod pelvic girdle of ilium, ischium, and pubis bones that articulate with the sacrum. The simple pelvic girdle of amphibians has long ilia that articulate with a single sacral vertebra, yielding limited mechanical support for life on land. Reptiles exhibit improved pelvic architecture, where ilium articulus with more sacral vertebrae for a higher trochanteric extension for a stronger hindlimb to axial skeleton connection. In birds and other dinosaurs, the pelvic girdle was especially modified in relation to differing postural and locomotor strategies, exhibiting markedly different configurations known as "bird-hipped" (ornithischian) and "lizard-hipped" (saurischian)

Mammals show considerable pelvic specialization with respect to locomotor mode and in some cases, reproductive functional demands. Cursorial mammals generally possess a narrow, elongated pelvis that allows for the hindlimbs to be placed directly under the body to efficiently support weight. Primates have wider, shorter pelves that allow for a wide range of hindlimb movements, whereas cetaceans (whales and dolphins) retain only vestigial pelvic elements indicative of their swimming lifestyle and loss of functional hindlimbs. The tetrapod hindlimb, as for the forelimb, exhibits stunning conservation of the underlying pentadactyl template despite extreme functional lability among groups. The tetrapod bauplan (femur, tibia, fibula, tarsals, metatarsals, phalanges), underlying skeletal elements that could be identified, appeared in congruent developmental mosaics, while accommodating diverse specializations. Amphibians have relatively unspecialized hindlimbs, although many frogs exhibit extreme elongation of the hindlimb elements associated with jumping locomotion. Reptile hindlimb configuration is

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diverse, ranging from the sprawling limbs of lizards to absence of external limbs in snakes and some lizards. At least in birds, hindlimb specialization for bipedal locomotion is extreme (reduction of the fibula, fusion of distal tarsal and metatarsal elements into the tarsometatarsus, and other foot modifications related to perching, swimming, or terrestrial locomotion). Hindlimb specializations are diverse among mammals, much like those of forelimbs. Warranted elongation of the hindlimb elements and reduced lateral digits are present in jumping mammals such as kangaroos, while more extreme digit loss leads to the single-toed condition of cursorial forms such as horses (Hildebrand et al. 2009). Digging (fossorial) mammals have long, powerful hindlimbs with digging claws, and paddled mammals have an assortment of modified feet (e.g. webbed otters) through to completely modified hindlimbs changed into flukes in the case of whales and dolphins.

#### **Comparison across Major Vertebrate Groups**

Skeletal system comparative anatomy vertebrate form evolution biodiversity. Through the skeletal characteristics of each of the four major groups, we can see both similar features that indicate a common evolutionary ancestor and specific adaptations that arose in various lineages.

**Fish:** Fish are the most ancestral group of vertebrates and exhibit the basic skeletal elements from which all vertebrate skeletons evolved. The skeleton usually includes a skull, vertebral column, ribs, and fin supports, with a wide range in ossification between groups. Thus, fish skull gave room for the specialized feeding mechanism, and complex arrangements of bones are there supporting the jaws and opercular apparatus which are responsible for gill ventilation. The skulls of most teleosts (contemporary bony fish) exhibit extensive kinesis across cranial joints that permit protrusion of the jaws and suck feeding, while elasmobranchs (sharks and rays) have comparatively simpler, more rigid cranial configurations. In fish, the vertebral column acts as a scaffolding for lateral undulation during swimming, with vertebral adaptations found between groups associated with swimming style. Fast-swimming species of pelagic fish, such as tuna, often exhibit reinforced articulations of their vertebrae that restrict lateral flexibility, transferring

greater force to the powerful caudal fin. In contrast, anguilliform swimmers such as eels have many highly flexible vertebral articulations that enable their sinuous swimming motion. The appendicular skeleton of bony fish consists chiefly of the supports for paired (pectoral and pelvic) and median (dorsal, anal, and caudal) fins. The pectoral and pelvic fins, the homologues of tetrapod limbs, have adapted in numerous ways associated with swimming, contact with the substrate or, in certain taxa, with unique functions such as the modified pectoral fins of flying fish or a suction disc formed by the pelvic fins of remoras.

Amphibians: Amphibians were the first vertebrates to take hold of the terrestrial environments, and their skeletons contain intermediate features between crude aquatic and advanced terrestrial vertebrates. Their skeleton is modified for somewhat terrestrial movement, but still retains characters suggestive of their earlier aquatic mode of life and their modern amphibious lifestyle. A notable adaptation in all amphibians is the modified skull and jaw; the amphibian skull has lost many of the bones found in fish skulls and has gained specialized air conducting structures in many orders of amphibians. The amphibian skull is derived from its fish ancestor, with a great modification from the fish condition in the paired fins, pharyngeal arches, and craniofacial skeletons reducing bones and walls of the skull and jaw and developing new structures to capture prey on land. Modern amphibians lose most of the dermal bones characteristic of early tetrapods, resulting in a lighter, more kinetic skull structure. The amphibian vertebral column tends to be less numerous than that of fish, with more robust centra able to support body weight for the terrestrial environment. The formation of a differentiated sacral region articulating with the pelvic girdle is a key change facilitating the move onto land, but the strength of this articulation is weak compared to fully terrestrial vertebrates. The amphibian appendicular skeleton exhibits the basic tetrapod design, with pectoral and pelvic girdles supporting paired limbs composed of the defining elements found in the extremities of all tetrapods. Wings and limbs in general have evolved from fin-like structures, thus retaining a sprawling posture and low ability to support body mass out of water for a prolonged period of time. The hindlimbs are also highly specialized for

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jumping in many of the modern amphibians, especially frogs, with highly elongate elements and muscular adaptations to provide the propulsive power over these very long levers.

Reptiles: Reptiles were the first vertebrates to reach a fully terrestrial way of life, and this was accomplished by a range of adaptations such as a more powerful skeleton that could support the body weight constantly on land. Their skeletal system varied greatly in relation to different locomotor strategies and body plans, from the limbed condition of lizards and crocodilians to the limbless modification of snakes. In contrast, a lizard has a more solid skull (relative to amphibians), since bones in the skull have a more developed shape and fit together in such a way as to provide more support and strength. In many lizards and snakes, kinetic skulls (in which the various cranial elements can move with respect to one another) allow for the consumption of large prey items. Temporal fenestration consists of two openings in the skull roof separated by bars of bone, providing sites for jaw muscles to attach and lightening the skull weight, with a distinct pattern being characteristic for major reptilian lineages. The vertebral column of reptiles is more regionally differentiated than that of amphibians, the cervical, thoracic, sacral and caudal regions being distinct in most reptiles. These articulations of more vertebrae provide greater stability while retaining as much flexibility, enabling better terrestrial locomotion. First, snakes exhibit extreme vertebral specialization, with many repeated vertebrae (200-400 on average, and often even more) possessing specialized articulations that allow for the great muscular flexibility typical to serpentine locomotion. The appendicular skeleton of reptiles also shows considerable variation, as seen in the fully-developed limbs of lizards and crocodilians, as opposed to the vestigial pelvic and pectoral elements still present in many snakes. The limbed condition generally retains the sprawling posture ancestral for tetrapods, though some reptiles (notably certain dinosaur lineages) acquired a more erect limb posture. The limbs in sea turtles and other aquatic reptiles are modified into flippers by elongation of the elements rather than by genuine alterations of structure.

**Birds:** As specialized archosaur reptiles, birds possess a skeletal system dramatically adapted to flight with extensive pneumatisation (air spaces within bones), fusion of skeletal elements, and overall reduction in skeletal mass. However extreme these specializations may be, the generalizes avian skeleton shows its undeniable reptilian origin and retains many adaptations for aerial locomotion. The avian cranial structure details the extensive element fusion that provides a lightweight but stiff framework, large braincase and small jaw system. Teeth have been replaced by a lightweight keratinous beak (an important weight-saving adaptation), and a kinetic skull provides small movements that enhance both feeding efficiency and the manipulation of objects with the beak. Avian vertebral column is highly flexible in certain regions but also bolstered to rigidity. The cervical region, which has 13-25 vertebrae, enables much movement of the head, which compensates the limited movement of the trunk. In contrast, the thoracic vertebrae frequently fuse among themselves and also with elements of the pelvis, creating a rigid notarium and synsacrum providing stable points of anchorage for the musculature used in the aileron and resisting dynamic stresses elicited by such muscular effort during flight. The pectoral girdle of birds is highly specialized for flight, with a large keel on the sternum for the attachment of powerful pectoral muscles, long coracoids resistant to compressive forces during downstroke, and a flexible furcula (fused clavicles) that acts as a spring, storing and releasing energy during successive wing beats. Forelimbs are modified into wings by way of elongation of the manus elements, reduction in digit number, and fusion of distal structures to form a stiff yet light support structure for flight feathers.superf[[\*Here you mention "elements", it is ". The skeletal aerodynamics, of the avian hindlimbs, used for bipedal movement are advanced by means of the fusion of distal tarsal and metatarsal components into the tarsometatarsus, shortening of the digits, and adaptations of the foot for perching, swimming or ambulation. The parallelism of the femur to the long axis of the body not only allows for an efficient bipedal upright posture, it also ensures the body maintains its center of gravity; aligned over the feet.

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Mammals: A hallmark of mammal skeletons is regionalization, limb differentiation for various locomotor modes, and new adaptations to match their endotherm and activity levels. Their skeleton displays a combination of conservative characters retained through the clade and extraordinary specializations within distinct lineages. Compared to their reptilian ancestors, mammalian skulls are much more consolidated, possessing fewer yet larger bones that are firmly sutured together. The dentary (lower jaw) directly articulates with the squamosal bone of the cranium — a hallmark of mammals, due to the evolution of the bones of the reptilian jaw joint into the ossicles of the middle ear. Another mammal character evident in skull morphology is heterodont dentition, with a variety of tooth types serving different purposes. Vertebrae along the mammalian vertebral column are distinctly regionalized, and a sequence of cervical, thoracic, lumbar, sacral, and caudal vertebrae display unique morphologies. The stable number of cervical vertebrae (typically seven regardless of neck length) is an extreme case of developmental constraint, whereas thoracolumbar vertebral number and morphology vary depending on individual locomotor specializations. The mammalian appendicular skeleton displays some of the most dramatic adaptations among vertebrates, indicative of the diversity of ecological niches occupied by the group. The pectoral girdle in this group is characterized by reduced coracoid (retaining the form of the coracoid process of the scapula) and varying degrees of clavicular development associated with forelimb use. The pelvic girdle forms a strong ring with articulation at the sacrum and strong hindlimb muscle attachment. While adhering to a pentadactyl ground plan, mammalian limbs undergo dramatic diversification; from elongate digits suspending wing membranes in bats to the single-toed arrangement of the horse to the flipper-like adaptations in whales and seals. For all of this diversity, the underlying homology for limb elements persists, though evolutionary modifications occurred, yet development lags behind the modifiable capacity.

#### Examining the Evolution of the Vertebrate Skeleton

Such diversity might be thought to reflect varying ecological niches or locomotor demands, but the underlying structural arrangement (essentially what vertebrates look like, internally) maintains remarkable fidelity to the basic archetype derived from early evolutionary history. Moreover, these arrangements are where the evolutionary history, development, and functional demands of life converge, producing the groups of vertebrates we can recognize today with skeletal variations.

Aquatic Adaptations: Correlatively, aquatic vertebrates experience unique biomechanical constraints on locomotion and buoyancy in water, which is reflected in convergent skeletal adaptations in disparate evolutionary lineages. The skeletal specializations of fish (the predominantly aquatic vertebrate group) are extensive, including streamlined skulls to diminish the resistive effects of water, vertebrae modified for various swimming styles, and fin adaptations for turbulence control. Secondary aquatic vertebrates (those derived from terrestrial ancestors) demonstrate striking convergent evolution of skeletal features despite their disparate evolutionary origins. Cetaceans (whales and dolphins), sirenians (manatees and dugongs), pinnipeds (seals and sea lions), marine reptiles (sea turtles, mosasaurs), and aquatic birds (penguins, loons) are different groups return to aquatic life, and they all show similar adaptations. Convergent features mostly include: (1) limb transformation into paddle-like structures (a change in the relative proportion of element-lengths rather than structure itself)(2) streamlining of the skull and its waffles and lightweightness (3) a greater (cetaceans) or lesser (sea turtles) fluidity of vertebrae and bones which created rigidity (4) reduction in the pelvic girdle and non-functional hindlimbs in completely waterbound species and (5) alteration of bone density either greater density to serve as a quarry in shallow divers or decreased density in deep divers. The adaptations seen in the vertebral column of aquatic mammals related to mode of swimming are particularly striking. Cetaceans have extremely flexible vertebral columns that enable them to perform dorsoventral undulation; specialized articulations allow for the vigorous vertical motion of the tail flukes. Their cervical vertebrae are usually compressed or fused, so they cannot swivel their heads as much, but this results in a more MATS Center For Distance & Online Education, MATS University

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hydrodynamic shape. In contrast, pinnipeds exhibit less flexibility in the cervical region but have developed specializations in the lumbar region to facilitate their unique swimming patterns.

Terrestrial Adaptations: One of the key challenges of vertebrate evolution was the transition to land, which entailed a plethora of skeletal changes to accommodate supportive and locomotary functions against gravity, as well as changes in respiration. Additionally, more robust limb girdles attaching to the vertebral column, more robust limb elements capable of bearing body weight, and more rigid vertebral articulations assisted in effective terrestrial locomotion. The lineages of terrestrial vertebrates have different solutions to the problems of terrestrial locomotion. (The skeleton of this amphibian is block-like, having partial capacity for weight-associated functions and outward limb skeleton orientation; intermediate forms.) Reptilians are better adapted for terrestrial living, possessing more robust limb girdles and vertebral joints, but the vast majority retain a sprawling position that reduces locomotor efficiency. Mammals show the greatest diversity of terrestrial locomotor adaptations, with several distinct patterns among groups. Cursorial (running) mammals such as horses, deer and cheetahs exhibit limb modifications such as: (1) elongation of distal limb elements leading to longer stride length; (2) reduction or loss of lateral digits decreasing limb mass and aiding in more energy-efficient foot placement; (3) restriction of limb movement to the parasagittal plane, lessening energy expenditures in limb contraction; and (4) fusion of elements such as the radius with the ulna or the tibia with the fibula leading to more stable limb supports. Fossorial (digging) mammals such as moles and aardvarks share convergent skeletal adaptations including: (1) stout, shortened forearms containing enlarged attachment sites for powerful digging muscles; (2) modified manus with enlarged claws or specialized digits; (3) reinforced articulations between forelimb elements that resist forces generated during digging; and (4) frequently enlarged processes on the humeri which furnish mechanical advantage for digging muscles.

#### **UNIT 13**

#### Comparative account of urinogenital system in vertebrates

#### **Definition and Function of the Urogenital System**

Comprising a pair of functionally distinct yet anatomically integrated systemsthe urinary and genital systems-the urogenital system is one of the most intriguing examples of evolutionary adaptation among vertebrate lineages. This interrelationship is neither incidental nor superficial, but rather a consequence of the deep developmental, physiological and anatomical associations that have been preserved and modified during the evolution of vertebrates. The urinary system, whose adult functions center on the removal of nitrogenous wastes and the regulation of fluid balance in the body, is also closely related developmentally and functionally to the genital system whose essential role is the generation, fertilization, and in some species the early development of gametes. Just the basic functions of the urogenital system are much more than the removal of toxins from the body and reproduction. It serves as a key player in osmoregulation-regulating saline and water homeostasis-especially important for vertebrates that moved from aquatic to terrestrial habitats. Through selective retention or excretion of hydrogen ions and bicarbonate, this system plays a critical role in acid-base homeostasis. The kidneys, the principal organs of the renal system, are responsible for filtering blood, as well as excreting metabolic byproducts, and reabsorbing molecules that the body needs. On the other hand, reproductive parts of vertebrates ensure that each species continues to exist through gametes, which have internal or external fertilization, embryonic development, and parental care adaptions. The development of the urogenital system in embryo shows their prime unity. Both systems originate from the intermediate mesoderm, the progenitor of three successive forms of kidney during vertebrate development: the pronephros, mesonephros and metanephros. This developmental and functional association



of the two systems is further exemplified by the use of modified components of the excretory system in the reproductive ducts. This is especially clear in looking at the male reproductive tract, where sperm moves through ducts that originally had an excretory function.

#### Vertebrate Kidney Types

The adaptive nature of kidney morphology in relation to secular changes in the environment is one of the most striking examples in vertebrates. The vertebrate kidney has evolved through three successive stages of development, each demonstrating distinct stages of function: pronephros, mesonephros, and metanephros. The two kinds of kidneys are also different in terms of structural organization, efficiency of filtration, conservation, and the degree to which they dominate in development and life in different groups of vertebrates. The pronephros is the most basic form of kidney, developed only transiently in the embryo of all vertebrates and only seen as the fully functional adult kidney in the most primitive vertebrates, namely the cyclostomes (hagfish and lamprey). The pronephros is composed of very few nephrons arranged simply, and usually with nephrostomes (ciliated funnels) that communicate directly with the coelom. This arrangement permits the filtration of coelomic fluid, rather than blood, and thus results in a relatively inefficient filtration system. The pronephros typically spans the anterior segment of the trunk region and empties into the pronephric duct ending in the cloaca. The its development importance of it your first organ but this will primarily embryonic in vertebrates most it establishes consecutive rights forms kidneys. The mesonephros was a step forward evolutionarily in terms of kidney structure, as the number and intricacy of nephrons increased. The mesonephros differs from the pronephros in that its nephrons usually have complex, tufted masses of capillaries (i.e; glomeruli) to augment filters. The mesonephros contains nephron units consisting of a glomerulus surrounded by Bowman's capsule, a proximal convoluted tubule for reabsorption and distal tubule. It is the functional adult kidney in fishes and amphibians, but in amniotes (reptiles, birds, and mammals), it is responsible for embryo function and is replaced mainly by the metanephros. In males, portions of the mesonephros persist and are remodeled into elements of the reproductive tract, such as the epididymis and vas deferens, providing further evidence of the close developmental connection between urinary and reproductive systems.

Of these, the metanephros is the most advanced kidney type and is found only in amniotes (reptiles, birds, and mammals). Its evolution is associated with the move to land, where retaining water would have been at a premium. Metanephros functions with higher filtration efficiency and reabsorption ability than its evolutionary predecessors. The kidney has a cortex filled with glomeruli and convoluted tubules as well as a medulla containing the loops of Henle and collecting ducts. This anatomical arrangement facilitates the countercurrent multiplication mechanism, which is essential for producing hypertonic urine and conserving water, both adaptations that are critically important for a terrestrial existence. The metanephros opens through the ureter, which is a separate duct that arises independently of the pronephric and mesonephric ducts, directly into the urinary bladder in mammals or the cloaca and reptiles and birds. These two kinds of kidneys are not just different in evolutionary sense; they are actually significant adaptations to environmental conditions and physiological demands. In contrast, in aquatic vertebrates such as fish, the mesonephros typically does not have a loop of Henle and secretes hypotonic or isotonic urine, adapting to the water-rich environment. In contrast, the mammalian metanephros, characterized by a functional set of nephrons featuring extensive loops of Henle, has the ability to concentrate urine—a vital adaptation for conserving water in dry terrestrial habitats.

### Different Types of Excretion: Ammoniotelic, Ureotelic and Uricotelic Animals

In this respect, the excretion of nitrogenous waste in vertebrates represents a remarkable study of adaptive physiology, reflecting the pressures endured as organisms adapted to their environments and how it contributed to the fundamental metabolic processes we see. Among vertebrates, there are 3 main

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strategies to eliminate nitrogen: ammonotelism, ureotelism, and uricotelism, each reflecting a different approach to the challenges of ridding the body of toxic nitrogen and managing water. The most primitive form of nitrogen excretion is ammonotelism in which the animal excretes nitrogen as ammonia (NHf) directly. This strategy is mainly applied in aquatic vertebrates such as the majority of teleost fishes, aquatic invertebrates, and larval amphibians. Ammonia is an ideal excretory product but comes with huge limitations as well. It is energetically cheap to produce, being a straight-off product of protein catabolism and not requiring any copy of itself to undergo additional metabolic processing. Ammonia is highly toxic and very water soluble so it requires a quick dilution and removal. The high solubility and toxicity of ammonia enable it only in environments with ample water, where after excretion the toxic compound will get rapidly diluted. Most teleost fish excrete ammonium through the gills (60-90%) rather than via the kidneys, utilizing the counterflow arrangement of blood and water across gill epithelia, which maintains a favorable diffusion gradient. In these species, the kidneys are a secondary route for ammonia disposal.

Ureotelism is an evolutionary upgrade, especially advantageous for the waterreistant tetrapods who must rid their bodies of nitrogenous substances. Ureotelic animals: Animals such as mammals, most adult amphibians, some turtles, and tortoises that convert the highly toxic ammonia into urea (CO(NH, ), ) through the ornithine-urea cycle in the liver. The conversion is energy consuming, with around 4 ATP molecules used for each urea molecule made. But this exuberant investment is worthwhile: urea is far less toxic than ammonia and can be stored temporarily in the bloodstream and tissues of the body without causing immediate damage. Urea is also soluble, but its required elimination volume is much lower than that of ammonia. In particular, the emergence of ureotelism was adaptive to amphibians that had to address nitrogen waste while in both aquatic and terrestrial stages of their life cycles. Ureotelism provides mammals with an energy efficient solution to water conservation, which is ideal for animals that can reliably access water, but still require more water conservation than strictly aquatic beings. Uricotelism the least water-polluting method of expelling nitrogen and is mainly
found in birds, reptiles (apart from aquatic turtles), insects and land snails. These animals excrete nitrogenous wastes mainly as uric acid (C... H., N., Of), which is nearly insoluble in water. Conversion is energetically costly, needing roughly 6 ATP per uric-acid molecule synthesized" a heavy price when weighed against other excretory strategies. But this energy-intensive cost results in exceptional water conservation savings. Uric acid can be excreted as a viscous semi-solid or pastelike substance with little formal water loss, making uricotelic animals highly adapted to life in dry habitats where desiccation is the major threat. Such changes were vital for the successful colonization of land by reptiles, which later evolved into birds. For birds, uricotelism provides the added benefit of lighter nitrogenous waste to carry in flight. In addition, this embryonic development is facilitated in birds and reptiles, where they hatch from amniotic eggs; again, uricoceles has been shown to be beneficial in this casealso by allowing storage of non-soluble uric acid in the allantois without fear of toxicity to the embryo.

The presence of these renal strategies within the vertebrate clades shows strong association with habitat and evolutionary history. Ammonotelism is mostly performed by aquatic vertebrates, who have access to plenty of water in the environment for dilution of potential ammonia toxicity. Amphibians possess exceptional physiological adaptability; they are often ammonotelic during the larval stage and may subsequently become ureotelic depending on the environment. Other amphibians increase urea cycle enzyme activity in response to dehydration or estivation, which speaks to the adaptive significance of metabolic plasticity. When it comes to excretion, mammals, which have to balance the retention of water with the energetic costs of converting wastes to urine, have all evolved to be ureotelic. Birds and reptiles, the taxa experiencing the most extreme water limitations, depend on uricotelism despite its high energetic cost, highlighting the fact that in arid environments, conservation of water can impose greater selective pressure than energetic characteristics.

#### Diversity of the Male and Female Reproductive Systems in vertebrates

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Reproductive structures have changed across vertebrate lineages more than almost any aspect of structure at all, which makes them one of the great comparative anatomical success stories in terms of understanding how selective pressures have reshaped reproductive methods yet created a variety of instances of fundamental homology. Despite wide variation in the structures and functions of vertebrate reproductive systems, the processes that lead to the formation of gonadal tissues and associated structures required for reproduction are conserved and highlight the evolutionary relationship among vertebrate species. The male vertebrate gonads, which are the principal reproductive organs-the testesdisplay a remarkable conservation of basic architecture across the majority of taxonomic groups. The basic functions of all vertebrate testes are spermatogenesis in the seminiferous tubules and steroidogenesis by interstitial (Leydig) cells. However, testes differ significantly in the position: cyclostomes and most fish retain permanently abdominal testes, while mammals (monotremes, elephants and sirenians being notable exceptions) have descended testes which take place in a specialized scrotal sac. This descent, driven by the sperm-production temperature requirements of mammals, is a unique adaptation that required the evolution of the inguinal canal and related structures. In humans and most other primates, testicular descent happens as part of embryogenesis, but in rodents it occurs perinatally and in some marsupials postnatally. Thus, sperm are released directly into the coelom in cyclostomes and then exit through abdominal pores without specialized ducts. In teleost fish, sperm prepare more specialized passage, moving from testicular lobules through a reticulum of efferent ductules that merge into sperm ducts then connecting to the urogenital sinus or cloaca at the far end. The repurposing of mesonephric (Wolffian) ducts for sperm transport illustrates the relationship between the excretory system and reproduction in tetrapods. In amniotes, this modification produces a convoluted sequence of structures through which sperm migrates from the testes via the efferent ductules, to the epididymis (derived from the anterior mesonephric tubules), and eventually through the vas deferens (derived from the mesonephric duct) to the urethra. Birds and reptiles maintain a cloaca as a common outlet for reproductive, urinary and digestive

systems, but most mammals (excluding monotremes) have diverged to separate openings for the digestive and urogenital systems.

Male vertebrates exhibit an extraordinary diversity of accessory sex glands. Amphibians have primitive prostate-like glands, and reptiles have more complex prostatic tissue. Bird species do not have specialized accessory glands, with the exception of the reproductive secretions being produced by a series of specialized zones in the reproductive tract. The diversity and specialization of the accessory glands is greatest in mammals, including prostate, seminal vesicles, bulbourethral glands, and in some species, ampullary and coagulating glands. In mammals, these evolved functions include seminal fluid that are sperm-survival boosting, nutrition providing, capacitation-inducing, and in some cases even copulatory plugs that can affect sperm competition and paternity assurance. Female reproductive structures have gone through equally driven evolutionary diversification. While the fundamental role of the ovaries as sites of oogenesis and steroidogenesis is relatively constant, morphology and organization are radically different. Fish generally have sac like ovaries that cannot store their eggs and empty from an oviduct, while tetrapods have more coalesced and solid ovaries, from which ova are spilled into the coelom and caught by the oviducts. Traditionally, mammalian ovaries have a cortical-medullary organization, followed by the development of the follicles in the cortex. Ovulation mechanisms also differ a lot: For example, fish typically will have cyclic ovulation for numerous eggs while mammals ovulate fewer eggs in a species-specific cyclicity pattern. The evolutionary diversification of the female reproductive tract is even more striking than that of the male reproductive tract. Eggs are excreted directly to the coelom and excrete through abdominal pores in cyclostomes. In the majority of teleost females, the ovarian cavity is continued as an oviduct that opens into the genital pore or cloaca. In tetrapods, the Müllerian ducts develop into oviducts independent of the excretory system as compared with the male reproductive tract co-opting excretory structures. The latter has paired oviducts, which transport eggs — and secrete the protective yolk and shell coverings — to the cloaca. Birds exhibit an impressive asymmetry, as they develop only the left

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oviduct during development, whereas the right one undergoes regression. In mammals, the ducts undergo the most prominent changes, giving rise to the fallopian tubes, uterus, and vagina, all formed from the two pairs of Müllerian ducts. The uterine morphology varies dramatically among mammals, from the duplex uterus (completely paired) in monotremes and most marsupials, to the bipartite and bicornuate forms in many ungulates and carnivores, to the simplex uterus (completely fused) in humans and higher primates.

The emergence of viviparity is one of the most significant reproductive transitions in vertebrates, having arisen independently many times in vertebrate lineages. Most fish, amphibians, and reptiles are oviparous (egg-laying), but viviparity has independently evolved in a number of fish lineages (including some sharks, sea horses, and guppies), some amphibians (certain salamanders and caecilians), and several reptile lineages (including many snakes and lizards). At the far end of the gradient, mammalian viviparity has been increasingly specialized to provide both in utero and postnatal nourishment in the case of marsupials that undergo short intrauterine development and extended postnatal lactation, and eutherian mammals which have extended intrauterine development coupled with a placenta that derives from the embryo but acts as a functional interface between the mother and the fetus, allowing for intimate maternal-fetal communication. The placenta itself is masterpiece of structure/function diversity across mammalian input; fetal and maternal blood are separated by six tissue layers in ungulates (the epitheliochorial type), and in humans and anthropoid primates maternal blood directly bathes fetal chorionic villi in the hemochorial type.

### Urogenital System in Other Groups of Vertebrates

**Cyclostomes (Hagfish & Lampreys):** However, only cyclostomes have evolved with this ancestral position reflected in their urogenital system and such additional evolutionary advantages. In adult cyclostomes the excretory system consists of either a functioning pronephros or a transitional stage between pronephros and mesonephros, depending on the species. Unlike hagfish, lampreys upgrade their pronephros to a more complex kidney, which in some systems is considered an

archinephros or primitive mesonephros. Nephrons of cyclostome kidneys are simple, potentially persisting nephrostomes (ciliated funnels to coelom), and most lack tubular differentiation (see more below) of higher vertebrates. In terms of structure, the reproductive system of cyclostomes is quite simple. Hagfish and lampreys both have ambilateral gonads attached by a mesentery to the dorsal body wall of the body. There is minimal sexual dimorphism; male and female gonads are similar in appearance until maturing. Cyclostomes do not possess separate reproductive ducts as do most vertebrates. Rather, mature gametes are released directly into the coelom and leave the body via genital pores (in hagfish) or a urogenital papilla (in lampreys). In a departure from the common shared-duct arrangements seen in many higher vertebrates, these two sets of waste materials use different efferent channels in Chondrichthyes. Heteronchus: fertilisation is entirely external, and there are no copulatory organs. The majority of cyclostomes are semelparous (reproduce only once before death) with the exception of the hagfish, which may be iteroparous (reproducing in multiple cycles).

**Cartilaginous Fish (Chondrichthyes):** The urogenital system of the cartilaginous fishes is a notable evolutionary step forward relative to the cyclostome condition. The kidney in adult fishes such as sharks, rays and chimaeras is also an opisthonephros, being essentially a posterior extension of the mesonephros. This kidney is typically elongated and located dorsal to the peritoneal cavity along the vertebral column. Functionally, the opisthonephros has excretory as well as osmoregulatory functions, which is especially important for keeping osmotic balance in marine elasmobranchs where urea and TMAO are retained to match osmotic levels with seawater. The reproductive system in these chondrichthyans displays abundant sexual dimorphism and specialization. [This unique feature is also found in montremes] Males have testis pairs that empty through efferent ductules into the adjacent kidney. The anterior part of the opisthonephros and its mesonephric duct become modified for reproductive roles such that the former develops into the epididymis and the latter the vas deferens. The male of these chondrichthyan

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species have evolved claspers from their modified pelvic fins that allow for internal fertilization. Females have two ovaries but only one is active (the right). Oviducts (Müllerian ducts), which are not part of the excretory system, contain specialized sections (shell gland, or nidamental gland) that secrete protective coverings on egg cases in oviparous species, or build temporary egg cases in viviparous forms. In some chondrichthyans, reproduction can be either oviparous (egg laying) or viviparous; some chondrichthyans retain their eggs until hatching, while other species develop a more complex relationship between the mother and the unborn embryo, with some even exhibiting a yolk-sac placenta. This diversity of reproductive modes is one of the earliest vertebrate experiments with viviparity, occurring long before any mammalian adaptations for live birth.

Bony Fish (Osteichthyes): Although this diversity would fit neatly into the persistent pattern of vertebrate evolution, the urogenital system of bony fishes represents an undeniable evolutionary mess, according to some aquatic biologists that study these animals. Like in chondrichthyans, the kidney in adult teleosts is usually an opisthonephros, but with substantial morphological and functional adaptations to their diverse habitats. In freshwater teleosts, the kidney is responsible for producing dilute urine to mitigate passive water influx, whereas in marine teleosts the kidney produces minimal and isotonic urine due to the emphasis on water conservation. Others, such as teleosts, have specialized renal portals that increase filtration efficiency. The bony fishes exhibit fascinating reproductive diversity. While the majority of teleosts possess paired gonads, the relationship between the gonads and their ducts varies widely among taxa. In less derived bony fishes (example being sturgeons), the gametes are released into the coelom and are collected by gonoducts or abdominal pores, similar to the cyclostome condition. In contrast, most teleosts have continuous gonoducts, which in females are oviducts (extensions of the ovarian cavity) rather than Müllerian ducts, and in males are sperm ducts derived from the mesonephric system. This arrangement is a unique teleost adaptation distinct from both more basal and more derived vertebrates. Bony fishes display a remarkable array of reproductive strategies. The majority of species are oviparous bud

external fertilization, with thousands or millions of eggs which may be produced by a reproductive season. Many lineages have independently evolved internal fertilization, using a variety of adaptations, such as anal fin modifications (gonopodium) in poeciliids, pelvic fin modifications in some blennies, and even specialized intromittent organs homologous to modified scales in some characins. Although viviparity evolved independently multiple times in teleost lineages, and its mechanisms span a spectrum from simple egg retention with no transfer of maternal-embryonic nutrients (ovoviviparity) in seahorses and pipefishes, through true viviparity with placenta-like structures in some surfperches and rockfishes.

Amphibians: The urogenital system of amphibia exhibits their intermediate status because they are amphibious animals. Adult amphibians possess an opisthonephros, like fishes, but adapted for life on land. The posterior kidney of anurans (frogs and toads) is compact and that of urodeles (salamanders) and caecilians is more elongated. Loops of Henle are generally absent from amphibian nephrons and thus their ability to concentrate urine is limited in comparison to other vertebrate classes, which correlates well with their predominantly moist environments and relatively large skin surface area that prohibits much water conservation. Amphibians have a reproductive system that is a mix of primitive and advanced features. Male have two testes that drain kidney via efferent duct: The mesonephric (Wolffian) duct is a urogenital duct draining both urine and sperm to the cloaca. Most male amphibians do not possess copulatory organs, though exceptions to this rule include certain caecilians that have an eversible phallodeum. Females have paired ovaries that release egg cells into the coelom, where they are swept into the ciliated ostia of the oviducts (Müllerian ducts). These oviducts carry the eggs to the cloaca while secretions coat them with protective jelly coats. Amphibians exhibit a remarkable diversity of reproductive strategies, which reflect adaptations to a variety of aquatic and terrestrial niches. External fertilization is common and eggs are deposited in water or moist surroundings. Yet internal fertilization evolved independently in many lineages, including all salamanders,

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even when few have intromittent organs (sperm is transferred via spermatophores). Most amphibians are oviparous, but some salamanders and caecilians have independently evolved viviparity resulting in stunning cases of convergent evolution with viviparous reptiles and mammals.

**Reptiles:** The reptilian urogenital system is of particular interest as it constitutes the most complex adaptations associated with the amniote's transition to life on land. Adult reptiles have a metanephros, the most complex type of kidney, the excretory duct draining to the ureter not the mesonephric duct. The metanephric kidney contains substantial adaptations for conserving water, especially in desertdwelling species. Certain reptiles have a renal portal system that improves filtration efficiency. Interestingly few reptiles have a urinary bladder, except some turtles and lizards. Reptiles have adaptations for terrestrial reproduction evident in their reproductive system. The paired testes are connected to the epididymis through efferent ductules in Males. The vas deferens (from the mesonephric duct) carries sperm to the cloaca, or to a pair of hemipenes in the squamates (lizards and snakes), or to a single median penis in crocodilians and some turtles. These intromittent organs allow for internal fertilization that is critical for terrestrial reproduction. Females are equipped with paired ovaries and oviducts (Müllerian ducts) that transport to the cloaca while secreting albumen, shell membranes, and often calcified shells surrounding the eggs. The amniotic egg, a key reproductive adaptation to land, opening the way for the evolution of terrestrial (non-aquatic) reproductive modes complete with the avoidance of an aquatic larval stage. Connective tissue called mesoderm (mes-, "middle") is formed between ectoderm and endoderm, and these more complex structures — the extraembryonic membranes (amnion, chorion, allantois, and yolk sac) - fulfill the need of the embryo to have access to a self-contained aquatic environment while also facilitating gas exchange and waste storage. Although the overwhelming majority of reptiles are oviparous, viviparity (live birth) has evolved independently in many squamate lineages-with varying degrees of placentation-marking one of the largest examples of convergent evolution in vertebrate reproductive modes.

Birds: The avian urogenital system shows both reptile characteristics and specific adaptations which are connected to flight. In birds, the kidney is also a metanephros (as in reptiles), although it is characterized by distinct lobulation and functional adaptations. Due to the presence of both reptilian-type nephrons (without loops of Henle) and mammalian-type nephrons (with loops of Henle), avian kidneys are capable of flexible filtration and water conservation. And, unlike many other animals, birds have evolved to convert nitrogenous waste first into uric acid to conserve water even further by excreting semi-solid urates rather than liquid urine. Avian reproductive anatomy is characterized by considerable asymmetry and specialization. Males have two pairs of testes that often change size dramatically with seasons; they can swell to 500 times the size in breeding season. The sperm transport system is made up of an epididymis and a vas deferens that can form a vesicle-like expansion for sperm storage. The majority of birds have no external genitalia and sperm transfer occurs by cloacal contact (the "cloacal kiss"), with notable exceptions among ratites (ostriches, emus) and some waterfowl that have a phallus or intromittent organ. For female birds, embryonic development normally results in the remainder of the right ovary and the right oviduct regressing (though a few raptors do develop both). The oviduct is highly specialized with separate regions with specific functions including albumen secretion, shell membrane secretion, and calcification. All birds are oviparous, meaning they reproduce using eggs; no bird species are viviparous. The avian egg is the advanced reproductive stage of the vertebrate amniotic egg and possess numerous structural and compositional features that respectively favour the metabolic demands of avian embryos without compromising gas exchange and/or fluid conservation. The emergence of parental care (egg incubation behavior and post-hatching provisioning) is another evolutionary strategy to increase offspring survival in a terrestrial environment, which developed in parallel with viviparity in some lineages.

**Mammals:** The mammalian urogenital system is the most complex and specialized of the vertebrates. In mammals, the kidney takes the form of a

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metanephros with separate cortical and medullary areas. In this regard, mammals have a well-developed loop of Henle that extends deep into the medulla, generating a concentration gradient in the renal pyramids for dehydration of urine-to conserve water in terrestrial conditions. Mammalian kidneys link with a urinary bladder through ureters, and urine excretes through a urethra that in males is additionally a reproductive passage. Extreme sexual dimorphism and specialization of the reproductive system is seen in female mammals. Males have paired testes that descend into a scrotum in most therian mammals, a thermoregulatory adaptation that ensures testicular temperature is below core body temperature for optimal spermatogenesis. This male reproductive tract comprises an elaborate epididymis for sperm maturation, a vas deferens for sperm transport, and several accessory glands (the prostate, seminal vesicles, and bulbourethral glands) that assist in semen production. All male mammals have a penis, but its morphology and developmental origin vary between the three lineages: monotremes, marsupials, and placentals. And there are sperm-competitive adaptations on the female side as well. The ovaries produce relatively little oocytes compared to other vertebrates: one or few oocytes per cycle. For example, the female reproductive tract varies from the duplex uterus (entirely paired) of monotremes and many marsupials to the simplex uterus (entirely fused) in higher primates, with many intermediate types (bicornuate, bipartite) in other groups. In therian mammals, the vagina is both reproductive canal and birth canal. Reproduction is typically through viviparity (with exceptions in monotremes) with prolonged internal development. Therian evolution of the placenta is seen as a key revolution that enables the intimate maternal-fetal interaction while restricting immunological interactions between genetically polyclonal maternal immune system and its genetically distinct offspring. Placental morphology varies dramatically among the mammalian orders, ranging from the epitheliochorial placenta (six tissue layers separating maternal and fetal blood) in ungulates, to the hemochorial placenta (direct contact between maternal blood and fetal chorion) in the primates and rodents. Lactation, the key trait in defining mammals, is an extra round of maternal investment beyond birth, rendering nutrients and immunization to young as they undergo a vulnerable growth stage.

# Themes and Adaptations in the Evolution of the Vertebrate Urogenital System

**Urogenital system:** The vertebrate urogenital system has undergone immense evolutionary changes that reflected the adaptation of environmental conditions and reproductive strategies. The change from the simply added pronephros to the intricately diagenetic metanephros shows an improvement in the ability to conserve water that is vital to terrestrial living, so as the excretory system goes, possibly so too goes the reevaluation of its specialization in the vertebrate lineage. Likewise, the shift from ammonotelism to ureotelism and uricotelism signifies adaptations for nitrogenous waste removal with a progressively lower need for water, again correlated to the aquatic-to-terrestrial transition. The evolutionary trends seen in the reproductive system are (1) increased internalization of fertilization, from external fertilization in most fish and amphibians to obligate internal fertilization in amniotes; (2) increased embryonic protection and provisioning, from simple eggs with minimal yolk in primitive vertebrates to complex amniotic egg in reptiles and birds, and finally to extended viviparity in therian mammals; (3) reduced reproductive output and increased parental investment, from millions of eggs without parental care in most fish to single offspring with extended gestation and postnatal care in many mammals. These trends are consistent with fundamental trade-offs between reproductive quantity and quality, and many lineages have independently evolved such K-strategies, which involve fewer but better offspring with a higher chance of survival, particularly pronounced among the vertebrate classes. Notably, viviparity has originated over 100 times independently in vertebrates (mostly among squamate reptiles), reflecting the evolutionary advantage of prolonged fetal protection in a variety of ecobiological contexts.

The coalescence of urinary & reproductive systems in vertebrates is more than anatomical expediency; it's a developmental & functional convergence that has COMPARATIVE ANATOMY IICOMPARATIVE ANATOMY II

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enabled major evolutionary transitions. These two structures in male tetrapods are examples of how developmental constraints can be exploited for new adaptations, as excretory ducts used for drainage of bodily waste are repurposed for reproductive functions. Likewise, the amnion, chorion, and allantois membranes for waste storage, gas exchange, and embryonic fluid environment, respectively — are examples of how innovations in waste management have played an integral role in allowing vertebrates to conquer the land. By comparative examination of the urogenital system between vertebrate classes, we not only understand the specific adaptations present in each grouping, but also the wider principles guiding evolutionary change, namely the tension between conservation and innovation, the significance of developmental constraint, and the repeated convergent evolution of similar adaptations to common environmental pressures.

### SELFASSESSMENT QUESTIONS

Multiple Choice Questions (MCQs):

1. Which of the following is NOT a function of the vertebrate digestive system?

a) Digestion

b)Absorption

c) Hormone secretion

d) Respiration

2. Which organ is primarily responsible for gas exchange in fish?

a) Lungs

b) Gills

c) Skin

d) Trachea

3.	Which vertebrate group has a cloaca for excretion and reproduction?		
a) Mammals			
b) Birds			
c)Amphibians			
d) Both B and C			
4.	Which type of skeletal system do vertebrates primarily possess?		
a) Exoskeleton			
b) Endoskeleton			
c) Hydrostatic skeleton			
d) None of the above			
5.	What is the main function of the urinary system in vertebrates?		
a) Excretion of nitrogenous waste			
b) Digestion of food			
c) Production of red blood cells			
d) Gas exchange			
6.	Which of the following is an adaptation for aerial respiration in birds?		
a) Tracheal system			
b) Air sacs			
c) Book lungs			
d) \$	d) Spiracles		

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7. T	The bony skeleton first appeared in which group of
v a)An	nphibians
b) Re	ptiles
c) Fis	hes
d) Ma	ammals
8. V iı	Vhich organ is involved in the excretion of nitrogenous waste n birds?
a) Lu	ngs
b) Sk	in
c) Ki	dneys
d) Liv	ver
9. V li	Vhich vertebrate group has both gills and lungs at different ife stages?
a) Fis	hes
b)An	nphibians
c)Re	ptiles
d) Bir	rds
10. V	Vhat type of excretory product do reptiles mainly produce?
a)An	nmonia
b) Ur	rea

- c) Uric acid
- d) None of the above

#### **Short Questions:**

- 1. What are the main functions of the digestive system in vertebrates?
- 2. How does the respiratory system in birds differ from that of mammals?
- 3. Explain the role of the cloaca in amphibians and birds.
- 4. What are the different types of kidneys found in vertebrates?
- 5. Define gills and their function in aquatic vertebrates.
- 6. What is the difference between an open and closed circulatory system?
- 7. How does the skeletal system help in movement?
- 8. What are the major differences between excretion in fish and mammals?
- 9. What are the adaptations of the skeletal system in flight birds?
- 10. Explain the role of the liver in digestion and excretion.

#### Long Questions:

- 1. Discuss the comparative anatomy of the digestive system in vertebrates with examples.
- 2. Explain the evolution of respiratory organs from fish to mammals.
- 3. Compare and contrast the structure and function of different types of kidneys in vertebrates.
- 4. Describe the modifications in the skeletal system in relation to locomotion in various vertebrates.
- 5. Discuss the differences in nitrogenous waste excretion in fish, amphibians, reptiles, birds, and mammals.
- 6. Explain the evolution of lungs and their role in gas exchange.

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- 7. Describe the adaptations of the bird respiratory system for efficient oxygen exchange.
- 8. Compare the structure of the vertebrate skeletal system across different groups.
- 9. Discuss the role of the vertebrate urinary system in osmoregulation.
  - 10. Explain the relationship between respiration and metabolism in vertebrates.

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## **MODULE 5**

### **COMPARATIVE ANATOMY III**

#### 5.0 Objective

- To study the structure and function of vertebrate sense organs.
- To compare the anatomy of the nervous system across different vertebrate groups.
- To analyze the adaptations of the brain, spinal cord, and peripheral nervous system.

#### **UNIT 14**

#### Sense organs

The sense organs are specialized structures that allow organism to collect data from the environment and transmit it as neural signals to the brain for processing. These extraordinary biological systems enable the interaction between an organism and its environment by detecting light, sound, chemicals, pressure, and electric fields. The Evolution of Sense OrgansOne of the most important adaptations in animal life was the evolution of sense organs that expand the range of environmental challenges that these creatures can deal with-to find food, escape from danger, find mates, and communicate with conspecifics. The sense organ's specialized sensory receptor cells form the basic functional units of the sensory organ that responds to some particular type of environmental stimulus. These receptor cells contain specialized molecular mechanisms that allow for the transduction of physical or chemical energy into electrical signals readable by the nervous system. The process by which environmental stimuli are converted to neural activity is called sensory transduction, and it is the foundation of all sensory perception. From simple organisms that can only differentiate between light and dark to higher-order a wide range of stimuli, the animal kingdom exhibits vast complexity and specificity when it comes to sense organs — and for good reason, an organism's mode of perceiving the world depends highly on their ecological niche. These diverse sense organs have evolved since the first simple, photoreceptive proteins in unicellular organisms to the complex, camera-like eyes of vertebrates, adapted to the sensors' sensory needs. 'Some are extremes of specialization, and they can perceive stimuli to which we are completely blind or deaf, from ultraviolet light and infrasound to electrical fields.

Embryogenesis of sense organs: the role of genes and cell-cell interactions The ectoderm, the outermost of the three germ layers during embryo development, is the source of many sense organ specifics. Example: Development of the vertebrate eye involves evagination of the optic vesicle from the diencephalon, followed by induction of the lens from surface ectoderm. The otic placode gives rise to the inner ear, whereas the olfactory placode becomes olfactory epithelium. Sense organs can only work properly when integrated into the central nervous system. Afferent neural pathways transmit sensory information from receptor cells to regions in the brain for processing and interpretation. This means that sensory processing goes way beyond passively receiving information from the world around us. Our conscious perception of the world relies on the brain's ability to interpret and make meaning of the overwhelming amount of sensory input it receives. Sensory organs play a vital role in how organisms respond to changes in their environment, fostering sensory organ dysfunction, which can severely hinder an organism's ability to perceive its surroundings and trigger numerous sensory disorders. In humans, one can experience blindness, deafness, anosmia (smell loss), or hypogeusia (diminished taste sensitivity) due to genetic mutations, accidents, infections, or degenerate processes in the respective organ of sense. The study of the structure and function of sense organs is thus important not only from the perspective of basic biology but also in designing interventions for sensory impairments.

#### **Overview of Sensory Modes**

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Vision: "The sense of vision is the ability to sense (detect and interpret) light stimuli from the environment. It is the most complex and information-dense sensory modality available to most organisms, and it offers detailed information about the surroundings, such as the shape, color, distance, and motion of objects in the environment. The eye, the most important organ of vision, has evolved separately at various times in various animal lineages and adapted unique structures suited to their ecological niches. The vertebrate eye is a complex optical device made of many parts that work in combination to gather and direct rays of light to a layer of neurons called a retina (layer of neurons) that transduce the energy of light into a neural encoding of that light. The eye of a vertebrate has a cornea and lens for focusing light as well as an iris that controls the amount of light entering, giving rise to an inverted retina with photoreceptive cells (rods and cones). Rods are more sensitive to light but do not allow for color vision, making them important in low-light scenarios. Unlike rods, cones are less sensitive but allow color discrimination by responding differently to different wavelengths of light. The range of visual systems in invertebrates is exceptionally diverse. In contrast, arthropods have compound eyes made up of thousands of independent visual units called ommatidia, each with its own lens and photoreceptor cells. This configuration offers broad fields of view and good motion sensing but poor spatial resolution; i.e., pixel-level demographics in the climbed-down images at best. Cephalopods (like octopuses and squids) have evolved camera-type eyes closely resembling those of vertebrates — an impressive case of convergent evolution. Neural processing of visual information starts in the retina itself, where complex networks of horizontal, bipolar, and ganglion cells carry out initial processing of the visual signals. This processed information is then sent through the optic nerve to different parts of the brain including the lateral geniculate nucleus of the thalamus and eventually to the primary visual cortex in mammals where it is further processed to extract features like edges, motion and eventually shape up to complex object recognition However, the number

of features that can probably be extracted directly from the raw input is too few to recognize a pattern and only very simple patterns would be detectable.

Hearing: Hearing, or audition, is the perception of sound waves traveling through air or water. Sound is a crucial source of information from the environment, providing information about potential predators or prey, communication with conspecifics, and navigation in complex habitats. The vertebrate ear is the specialized organ that transduces sound pressure waves into neural signals. Mammalian ear consists of three main parts; the outer ear, collecting sound waves and funneling them to the eardrum; the middle ear, containing three ossicles bones, which are amplifiers to the vibrations from the eardrum and transmitting to the inner ear; and the inner ear consisting of the cochlea, where mechanical vibrations are transduced into electrical signals, via mechanosensory hair cells, relayed by the auditory nerve to the brain. Within the cochlea is the organ of Corti — a specialized sensory epithelium that includes rows of hair cells, both inner and outer. As sound vibrations occur, fluid movements cause the stereocilia (modified microvilli) of these hair cells to bend. This bending opens ion channels that cause the cell to depolarize and release neurotransmitters that excite the auditory nerve fibers. Anatomy of the auditory pathwayThe cochlea is tonotopically organized so that different sound frequencies functioning hair cells are located at different position along the length of the cochlea; thus, it provides a frequency map that is maintained through the auditory pathway towards the brain. The organisation of the auditory system is significantly different in nonmammalian vertebrates. Birds have no outer ear and only one middle ear ossicle, the columella. The fish have no outer and middle ear but can sense sound through their inner ear, and many species also sense sound through connections with the swim bladder, which amplifies sound waves. Many invertebrates have evolved various modes of sound or vibration detection. Many insects have tympanal organs, which are membrane-covered air sacs linked to sensory neurons that respond to the vibration of the membrane when sound waves hit it. Other invertebrates use specialized hairs or setae on their body surface for the air or water movements that are associated with sound.

**Smell (Olfaction):** The sense of smell (olfaction) is mediated by the presence of a chemical molecule in the environment. This sensory modality is critical for

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many behaviors, including foraging for food, predator avoidance, mate choice and social communication. The olfactory system is extremely sensitive: Some odors can be detected at very low concentrations, and it can discriminate between thousands of different odorant molecules. The olfactory epithelium in the nasal cavity is the main olfactory organ in vertebrates. This specialized epithelium is composed of olfactory receptor neurons (ORNs), supporting cells, and basal cells. They are bipolar neurons, with dendrites extending to the surface of the epithelium where they form olfactory cilia bearing odorant receptors. These receptors bind specific odorant molecules and trigger a signal transduction cascade that ultimately results in action potentials that are sent to the brain. The axons of ORNs together constitute the olfactory nerve (cranial nerve I) that projects to the olfactory bulb within the brain. In the olfactory bulb, axons from ORNs come together to form spherical structures known as glomeruli in which they synapse with second-order neurons known as mitral and tufted cells. This convergence is structured in a way that ORNs that express the same odorant receptor coalesce into the same glomeruli, forming an ordered representation of what the odor is. After being processed by the olfactory bulb, information is transferred to several other regions of the brain, including the piriform cortex, amygdala, and hippocampus, which are responsible for odor perception, emotional responses to smells, and the fixation of memories. In addition to the main olfactory system, many vertebrates have an auxiliary olfactory system, the vomeronasal organ (VNO), specialized for the detection of pheromones and other chemicals relevant to social interactions. In mammals, the VNO lies at the base of the nasal septum and contains receptor neurons that project to the accessory olfactory bulb, a distinct structure from the main olfactory bulb. Olfactory systems are diverse even among invertebrates. Insects, for instance, sense smells mainly with sensilla on their antennae. The sensilla are housing olfactory receptor neurons that express odorant receptors and project towards the antennal lobe, the functional equivalence of the vertebrate olfactory bulb. That information is then sent to higher brain centers — the mushroom bodies, involved in learning and memory, for example.

Taste (Gustation): Taste, or gustation, is a chemosensory modality, allowing organisms to assess the chemical properties of food before consumption. This sense is key to deciding food preferences, avoiding toxic substances, and controlling nutrient intake. Although the number of distinct stimuli that can be perceived by taste is much smaller than that of olfaction, taste is nevertheless the essential chemosensory modality for detecting the nutritional and toxic potential of ingested foods. In vertebrates, taste is perceived primarily via taste buds on the tongue but also on the palate, pharynx, and upper esophagus. A taste bud consists of approximately 50–100 epithelial cells, including taste receptor cells, supporting cells, and basal cells. Taste receptor cells project microvilli, or taste hairs, into the taste pore that interact with taste molecules suspended in saliva. Humans have five traditional taste qualities: sweet, sour, salty, bitter, and umami (savory). Different types of taste receptor cells that express different sets of taste receptors detect each of these taste qualities. Sweet, umami, and bitter tastes are sensed by G protein-coupled receptors (GPCRs), while salty and sour are mediated by ion channels. These taste molecules activate their relevant intracellular signaling pathways, activating gustosensory nerve pathways (synapsing with gustatory nerves) that result in neurotransmitter release and action potential generation. Three cranial nerves convey taste information to the brain: the facial nerve (VII), the glossopharyngeal nerve (IX), and the vagus nerve (X). These nerves project to the nucleus of the solitary tract in the medulla oblongata, and the information is relayed from there to the thalamus and finally to the gustatory cortex in the insula and frontal operculum. In invertebrates, taste systems diverge dramatically. For instance, insects have gustatory sensilla on their proboscis, legs and wing margins. These sensilla have gustatory receptor neurons that express gustatory receptors that can detect diverse tastants, including sugars, bitter compounds, and salts.

**Touch (Somatosensation):** Touch/somatosensation refers to signals of mechanical stimuli acting upon one's body such as pressure, vibration, stretching, or tension. This modality conveys important cues about an organism's physical

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engagement with its environment, supporting behaviors such as manipulating objects, moving through space, and avoiding damaging stimuli. Somatosensation is mediated by a variety of mechanoreceptors that provide the body to differentiate between mechanical stimuli and to respond with an appropriate motor command. Mammalian skin has a variety of mechanoreceptors as well, including Meissner's corpuscles (rapid-adapting receptors for light touch and vibration), Pacinian corpuscles (rapid-adapting receptors for harsh, highfrequency vibration), Merkel's discs (slow-adapting receptors for touch and texture), and Ruffini endings (slow-adapting receptors for skin stretch). There are also proprioceptors that give signals from the muscles, tendons, and joints for body position and movement, along with nociceptors that respond to damaging stimulus (pain). Mechanoreceptors are sensory neurons (mechanosensory neurons) or specialized epithelial cells that translate mechanical deformation into electrical signals, utilizing mechanically gated ion channels. Mechanical forces activate these channels to permit the influx or efflux of ions along their chemical gradient across the cell membrane, resulting in the generation of receptor potentials that can trigger action potentials in downstream connected sensory neurons.

Somatosensory information is relayed to the central nervous system through the dorsal root ganglia (for the body) or trigeminal ganglia (for the face). These signals travel up to the brain along the dorsal column-medial lemniscus pathway (for discriminative touch and proprioception) or the anterolateral system (for pain and temperature). All of this information finally arrives at the primary somatosensory cortex in an area in the parietal lobe known as the postcentral gyrus and is processed to give us our conscious perception of tactile sensation. In invertebrates, mechanosensation is mediated by diverse specialised structures. For example, insects possess mechanosensory bristles and campaniform sensilla on their body surface that sense mechanical deformation. Many aquatic invertebrates have special mechanoreceptive organs, such as the statocysts in crustaceans, acting as gravity and balance receptors.

Electroreception: Electroreception is the perception of electrical fields in the environment and this sense has evolved in multiple clades of aquatic animals. This intercircuitry is the only such sensory modality allowing organisms to sense other organisms in their environment by either detecting the weak bioelectric fields they emit (an electroreception capacity) or by perceiving their surroundings through the active generation of electric fields (an electrocommunication capacity). Electroreception is generally divided into passive and active forms. Passive electroreception is the sensing of naturally produced bioelectric fields emitted by other organisms. These fields are produced by the ionic currents moving across cellular membranes in typical physiological processes. Ampullae of Lorenzini, sensory organs used to detect weak electric fields (down to 5 nanovolts per centimeter), are found in sharks, rays and some bony fish species. These organs are gel-filled canals that open at the skin surface, with clusters of electroreceptor cells at their inner ends. In contrast, active electroreception is the generation of an electric field by the organism itself and the detection of disturbances in that field caused by an object in the environment. Weakly electric fish, on the other hand, use this form of electroreception; they have specialized electric organs from muscle tissue that generate weak continuous discharges. These fish also possess electroreceptors that are spread over their body surface and sense distortions in the self-created electric field allowing them to take a detailed electrical "picture" of their surroundings, which they can do under visualization-constrained conditions such as dirty water or during the night.

There are specialized pathways that process electroreceptive information in the brain. Specifically, in sharks and rays, electroreceptive signals are relayed through the anterior lateral line nerve to the dorsal octavolateral nucleus of the medulla, and subsequently to higher-order brain centers. In weakly electric fish, the electrosensory lateral line lobe, a specialized region of the hindbrain, processes electroreceptive information. Electroreception is a fascinating example of how sensorial systems adapt to particular environmental exigencies. It enables some marine organisms to locate prey, orient themselves, and communicate in spaces where other modalities may be less effective. That electroreception

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originated independently in several lineages (i.e. convergently) highlights the importance of this sensory modality for survival in the aquatic habitat.

### **Organs of Olfaction and Taste**

# Structure and Function of the Olfactory System

The olfactory system is an incredibly powerful sensory device that allows organisms to smell and differentiate thousands of different airborne chemical subclasses collectively referred to as odorants. This ability to sense chemicals is critical for survival, affecting behaviors including feeding, predator avoidance, mating and social behaviors. This organization of the vertebrate olfactory system is highly conserved across species, with notable differences that correspond to divergent ecological requirements. The olfactory epithelium is a specialized pseudo-stratified epithelium in the nasal cavity, which is the primary olfactory organ in vertebrates. In humans, only about 2-4cm<sup>2</sup> of the roof of the nasal cavity is covered with olfactory epithelium, whereas in macrosmatic animals (animals with a well developed sense of smell such as dogs and rodents) the olfactory epithelium covers a proportionally larger surface area. The olfactory epithelium is mainly composed of three types of cells: olfactory receptor neurons (ORNs), supporting cells, and basal cells. Olfactory receptor neurons are bipolar neurons, each with one dendrite that extends to the epithelial surface and one axon that projects into the brain. The dendrite ends in a knob at the epithelial surface from which many cilia project into the mucus covering the epithelium. These cilia hold the olfactory receptors, which are G protein-coupled receptors (GPCRs) that bind the odorant molecules. [This is supported by the fact that the human genome encodes about 400 functional olfactory receptor genes, compared to rats and mice, which have around 1,000, making them smell 4x better than humans. When an odorant molecule docks onto its matching receptor, it activates a G protein (Golf) that in turn activates adenylyl cyclase III to generate cyclic adenosine monophosphate (cAMP). The cAMP then binds to and opens cyclic nucleotide-gated (CNG) channels, resulting in a flux of calcium and

sodium ions into the cell, depolarizing the cell membrane. This is sufficient, if depolarization is sufficient to generate action potentials that propagate along the ORN axon to the brain.

Hitherto, supportive cells also known as sustentacular cells have a number of roles such as providing structural and metabolic support for ORNs, detoxifying toxins, and regulating ion composition of the mucus layer. Basal cells are the stem cell population within the olfactory epithelium that can divide and give rise to new ORNs (olfactory sensory neurons) throughout life. This regenerative potential is particularly important because ORNs are short-lived (on the order of 30–60 d in mammals) and need to be replaced regularly. The olfactory epithelium is associated with mucus layer that is crucial for its function in olfaction. Mucous droplets are secreted by Bownam glands in the lamina propria beneath the epithelium and contain odorant-binding proteins that assist with transporting hydrophobic odorant molecules to receptors, and enzymes that can metabolize odorants to terminate signaling and limit receptor adaptation. ORNs extend their axons, which aggregate to form the olfactory nerve (cranial nerve I), laterally through the cribriform plate of the ethmoid bone into the olfactory bulb of the brain. One remarkable feature of the olfactory system is that odorant receptor neurons (ORNs) expressing the same olfactory receptor, despite being distributed throughout the epithelium, project the axons of their axons to the same glomeruli in the olfactory bulb. The integration of these inputs leads to an outward spatial map of odor quality in the olfactory bulb because each glomerulus corresponds to a specific type of olfactory receptor. The axons of ORNs synapse with second-order neurons (mitral and tufted cells) within the glomeruli in the olfactory bulb. These secondary-order neurons then extend to different centers in the brain, such as the piriform cortex (the main olfactory cortex), the amygdala, and the entorhinal cortex. In fact, unlike other sensory systems olfactory information can bypass the thalamus before transmitting to the cerebral cortex, illustrating the

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evolutionary antiquity and importance of the olfactory system. Most vertebrates also have a secondary olfactory system, the vomeronasal system, that is specialized for sensing pheromones and other socially relevant chemicals. The vomeronasal organ (VNO) is a paired tubular structure situated at the base of the nasal septum. It is composed of vomeronasal sensory neurons that express a distinct family of receptors (V1R and V2R) than the main olfactory epithelium. These neurons send projections to the accessory olfactory bulb, from which information ascends to defined targets in the amygdala and hypothalamus, nuclei linked to reproductive and social behaviors. The function of the VNO is speciesdependent; while it is fully functional in rodents and many other mammals, it is vestigial or completely absent in adult humans and some primates.

#### Structure and Function of the Gustatory System

The gustatory system — the sense of taste — enables organisms to assess the molecular composition of potential food sources, guiding feeding and food transition behaviors. The human gustatory system can discriminate between thousands of different taste qualities, but it is commonly used for the classification of tastants into five basic taste modalities: sweet, sour, salty, bitter and umami (savory). Each of these taste qualities has a specific biological role: Sweetness warns of the presence of carbohydrates, an energy-rich macronutrient; umami indicates protein content; saltiness aids electrolyte balance; sourness may signal unripe fruits or spoiled foods; and bitterness frequently indicates potentially toxic compounds. The main gustatory organs are taste buds which are primarily located on the dorsal surface of the tongue, but are also found on the palate, pharynx, larynx, and upper esophagus. Humans have around 2000-5000 taste buds, most of which sit on the tongue. In contrast to an old idea called the "tongue map," receive all taste qualities all over the tongue, though sensitivity to some tastes is a little greater in some regions than in others. Taste buds are barrel-shaped structures inserted into the epithelium, with a small projection, the taste pore that exposes tastant molecules in solutions of saliva to receptor cells. Each taste bud in the tongue consists of 50-100 cells that can be classified into three major types: taste receptor cells (TRCs), supporting cells, and basal cells. TRCs are specialized epithelial cells with microvillar projections (taste hairs) that project into the taste pore. In contrast to olfactory receptor neurons, TRCs are not neurons and are neuroepithelial cells that synapse on to sensory nerve fibers. There are different classes of TRC, each tuned to diverse qualities of taste. The observed Type I cells are likely supporting cells with glial-like functions. Type II cells have G protein coupled receptors (GPCRs) for sweet, bitter, and umami taste. Type III cells are activated by sour tastes and form classical synapses with afferent nerve fibers. The salty taste receptors are not fully characterized yet, but likely include epithelial sodium channels (ENaCs) in a cohort of TRCs.

Specific signaling cascades are activated when tastant molecules bind to their receptors. Sweet, bitter and umami tastes bind to GPCRs and activate phospholipase C â2 (PLCâ2), generating inositol trisphosphate (IP3), which causes calcium to be released from intracellular stores. Calcium is then raised and causes activation of the TRPM5 channel, membrane depolarization, and release of ATP through pannexin-1 channels. ATP is a neurotransmitter that excites purinergic receptors on sensory nerve fibers and nearby cells. Hydrogen ions enter ionotropic type III cells via channels such as PKD2L1 (polycystic kidney disease 2-like 1 protein), leading to membrane depolarization and activation of neurotransmitter release to convey sour taste. Salty taste is mediated mainly by the direct influx of sodium ions through ENaCs which causes cell depolarization. Taste information is relayed to the brain by three cranial nerves: the facial nerve (VII), which innervates the anterior two-thirds of the tongue; the glossopharyngeal nerve (IX), which innervates the posterior third of the tongue; and the vagus nerve (X), which innervates taste buds found in the pharynx and larynx. These nerves send taste signals to the nucleus of the solitary tract (NST) of the medulla oblongata, which represents the primary gustatory nucleus in the brainstem. From the NST, tastant information is relayed to the ventral posteromedial nucleus of the thalamus and subsequently to the primary gustatory cortex, situated in the insular cortex and frontal operculum. Apparently, the gustatory cortex is responsible for taste discrimination and identification. Taste perception also transmits information to other regions of the brain responsible for the emotional,

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motivational, and hedonic (pleasure-based) aspects of taste processing, such as the amygdala, hypothalamus, and orbitofrontal cortex. In contrast to olfactory receptor neurons, TRCs have a relatively short lifespan (around 10-14 days) but are constantly replenished by newly-differentiating cells from basal cells within the taste buds, preserving the structure of taste buds during the entire lifespan. Although the ability of our taste buds to regenerate is reduced by ageing, certain medications, radiation treatment and zinc deficiency, disorders of taste can occur. The gustatory system displays a high degree of plasticity, and tastes preferences and sensitivities can be affected by genetics, early taste experiences, cultural upbringing, and even disease state. For example, consistent exposure to certain foods can change preferences for tastes, and states like pregnancy or particular diseases can change sensitivity to tastes. Such plasticity underscores the pivotal role of taste in directing dietary selections, be it meeting the requirements for key nutrients or avoiding harmful substances.

# Comparative Studies on Anatomy and Evolution of Chemosensory Systems

Chemosensation, the capacity to perceive chemical stimuli, stands as one of the earliest established sensory modalities in the animal kingdom, its evolutionary lineage tracing back to primordial multicellular life. The systems of chemosensation across the taxonomic divide share astonishing conservation in their underlying mechanisms but also staggering diversification at the level of their structure and function, mirroring the diverse ecological niches and challenges faced by different lineages. Molecularly, chemoreception typically operates by specific receptor proteins that bind chemical ligands with the resulting initiation of signal transduction cascades that give rise to ultimately neural signals (Classen et al., 2010). Although there are many different types of chemosensory organs within most animal phyla, the proteins that function as receptors for odors and pheromones are frequently derived from several closely related families of proteins, most notably in the form of G protein-coupled receptors (GPCRs) and ion channels. This indicates that these systems might have evolved from shared ancestral solutions.

Chemosensory systems are highly diverse in invertebrates. C. elegans, a much simpler organism, encodes for 1200 putative chemoreceptors (mostly GPCRs), which corresponds to 7% of the genome. The investment in this genetic machinery reflects the crucial role played by chemosensation in the life of this organism. C. elegans is able to detect chemicals in its environment using amphid sensilla in the head and phasmid sensilla in the tail containing the ciliated endings of chemosensory neurons. Insects, in particular, have evolved highly advanced chemosensory systems. The olfactory and gustatory systems of insects are made up of two specialized chemosensory organs: the antennae for olfaction and gustatory sensilla that are located in different parts of the insect body, including the proboscis, tarsi, and wing margins. Insects use two main families of chemoreceptors in neuron olfactory receptors, the Or43a160 (ORs) and the ionotropic receptors (IRs), the latter an evolutionarily older receptor family thought to originate from ionotropic glutamatergic receptors. Insects ORs operate as heteromeric combinations with the co-receptor Orco, where they generate ligand-gated ion channels, a framework that differs from vertebrate chemical senses where receptors belong to metabotropic GPCRs.

Evolution of chemosensory systems has been considerably adapted to different environments during vertebrate evolution. Fish have well-developed sense of smell, with paired olfactory rosettes containing sensory epithelium. Many fish, in addition to their oral cavities, have taste buds scattered over their body surface and fins, so they can "taste" their environment. Certain fish species, such as the catfish, possess an astonishing number of external taste buds, allowing them to detect potential prey in murky waters where sight may be impaired. The switch from aquatic to terrestrial habitats posed major challenges for chemosensory systems. In aquatic environments, chemical stimuli are soluble in water, thus directly available to receptor cells. In terrestrial habitats, volatile chemicals are extracted from the air and combined with mucus before activating receptors. Amphibians, encompassing both aquatic and terrestrial lifestyles, often bear two olfactory systems working in tandem: a "water nose" (the principal cavity) for water-soluble odorants and an "air nose" (the middle cavity) that responds to airborne odorants.

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In reptiles, the adaptations become even more pronounced; for example, many of them have a well-developed vomeronasal system. Tongue-flicking behavior is used by snakes and lizards to sample chemical cues from the environment and subsequently transfer them to an accessory olfactory structure, the vomeronasal organ, and this behavior is thought to be critical for prey detection and mate recognition. This behaviour is nuanced, especially when it comes to snakes, which have a forked tongue that allows them to sample chemical cues from their environment in a directional manner. The mammalian chemosensory system is a central processing apex of complexity. Mammals demonstrate wide variation in olfactory capacity, as evidenced by the number of functional olfactory receptor genes present in their genome. Rodents, dogs, and most ungulates are macrosmatic mammals, possessing large olfactory epithelial areas, large olfactory bulbs, and many active olfactory receptor genes. Conversely, most primates, particularly humans, cetaceans, and certain marine mammals are microsmatic mammals that possess diminished olfactory systems.

Within some lineages, including primates, olfactory capabilities have evolved to be reduced, often in conjunction with heightened reliance on other sensory modalities (including vision). This change in species has reduced the share of olfactory genes to about 60% of the olfactory receptor gene repertoire as pseudogenes (inactive genes) in humans. Nonetheless this number has been adjusted downwards and even then the human olfactory system is still incredibly sensitive (it can detect thousands of different odours). The vomeronasal system shows even wilder evolutionary variability. The vomeronasal organ is well developed in many mammals, notably rodents, but it may vestigial or absent in adult catarrhine primates (including humans), cetaceans and some bats. This variation is explained, in part, by lineage-specific retention and loss of vomeronasal receptor genes. In contrast to the olfactory system, the gustatory system appears to be relatively conserved among vertebrates, and most vertebrate lineages appear to have retained family members from each of the three main classes of taste receptor (bitter, sweet, and umami). Notably, however, cats and other obligate carnivores have functional sweet taste receptors

that have decayed completely, a reflection of their strictly carnivorous diet, where there is little positive selective pressure for the ability to detect carbohydrates. Likewise, a few marine mammals have lost several divisions of taste receptorsperhaps to adapt to their aquatic life and their specific feeding strategies. Chemosensation is a dynamic process that has been shaped by gene duplication, gene loss, and sequence diversification at the molecular level. This coupled with evolutionary shifts in the perceptual environment has resulted in the expansion of chemoreceptor repertoires in certain lineages to detect novel chemical cues that are ecologically relevant to a particular niche, and contraction in others, in instances where certain chemosensory abilities are no longer advantageous for survival. By employing comparative approaches and integrated methods, we are able to characterize the evolutionary significance of chemosensory modalities and explore the selective pressures behind their variation in the animal world. Furthermore, this comparative framework of interpretation led us to discover the functional organization of the human chemosensory systems, from olfaction to taste, and to understand their role in human behavior and cognition.

#### Lateral Line System and Electroreception

#### The Lateral Line System: Structure and Function

The lateral line system is a unique sensory system possessed by aquatic vertebrates such as fish and amphibians that allows them to sense water movements, pressure gradients, and low-frequency vibrations in the surrounding water environment. This highly developed mechanosensory system enables the animals to exhibit an array of behaviors related to survival including schooling, detection of prey, evasion of predators, navigation around obstacles, and communication under low-light or visually impaired conditions. Structurally, the lateral line system is made up of a series of mechanoreceptive organs known as neuromasts, distributed over the body surface in characteristic arrangements. Neuromasts may reside on the skin surface (superficial neuromasts) or in fluid-filled canals (canal neuromasts), which communicate with the environment through a series of pores. Structure and function of neuromasts vary greatly among species, correlating to their specific environmental

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needs. A neuromast consists of a cluster of specialized hair cells, the mechanoreceptors that serve as the functional unit of the lateral line system. These hair cells are similar to those found in the inner ear of vertebrates, suggesting an evolutionary relationship between these sensory systems. On its apical surface, each hair cell has one kinocilium (true cilium) and numerous stereocilia (modified microvilli) arranged into a staircase pattern. This stereocilia and kinocilium bundle is surrounded by a gelatinous cupula, which extends into adjacent water. Deformation of the cupula due to water movements or pressure waves leads to the bending of the stereocilia bundle, allowing the opening or closing of mechanically gated ion channels depending on the direction of the bending. Bending towards the kinocilium results in depolarization of the hair cell (excitation), whereas bending away from the kinocilium the hair cell hyperpolarizes (inhibition). Because they are more sensitive to movement from certain directions than others, neuromasts can detect the direction of the water movement in addition to its presence.

The sensory hair cells synapse with afferent sensory neurons of the lateral line nerve, a branch of the acousticolateralis system innervated by cranial nerve VII (facial), IX (glossopharyngeal), and X (vagus). Depolarization of hair cells causes the release of neurotransmitter which inhibits the associated afferent fibers, generating action potentials that are sent to the brain. The obligatory relay from the lateral line nerve synapses on the octavolateral nucleus in the medulla oblongata, which is the principal processing center of the lateral line information. These lateral line functional classes are complemented by the tumid superficial and canal neuromasts. Superficial neuromasts are directly exposed to the external environment andare particularly sensitive to water velocity, and are important for detecting steady-flowing situations such as swimming or currents. These neuromasts are mainly responsible for rheotaxis (orientation in water currents), as well as stabilizing swimming speeds and body postures. For comparison, canal neuromasts are found in subdermal canals, which are filled with a mucopolysaccharide-rich fluid that resembles endolymph. A series of pores connect these canals to the outside environment. This canal system serves as a filter, adequately protecting the neuromasts from the effects of water flowing over the body surface while making it very sensitive to different pressures at neighbouring canal pores. This structure should render canal neuromasts highly effective in sensing the acceleration of water flow and gradient-based pressure changes caused by a localized moving object in the vicinity (e.g., predators, prey, conspecifics). The lateral line system is extremely sensitive and capable of sensing water displacements on the order of a few nanometers. They use this exquisite sensitivity to detect the minuscule water movements caused by prey organisms or nearby predators even in the complete absence of light (complete darkness) or highly turbid waters. In addition, the system possesses a wide operational frequency bandwidth (<"1 Hz to several hundred Hz), where epidermal neuromasts are typically sensitive to lower-frequency sounds and canal neuromasts receive signals when higher-frequency inputs are stimulated.

### **UNIT 15**

#### Nervous system

#### **Comparative Account of the Brain in Relation to Its Function**

The brain is the central command center of the nervous system throughout vertebrate animals, but its structure and complexity differ markedly throughout evolutionary history. True brain is absent in the most basic chordates like amphioxus; unlike the framework of evolutionary brainy study called the vertebrate brain this simply comes in the form of a slight expansion to the anterior neural tube. And there you have it — it is not an innovative architecture with clear separation of concerns, but it does the necessary sensory integration and motor coordination required for the organism to survive. The vertebrate brain has evolved through a process of increasing complexity and specialization. In cyclostomes such as lampreys and hagfish, the earliest example of a true brain is present with three embryonically derived divisions: forebrain, midbrain, and hindbrain. Although this organization is somewhat a simplification, it provides the basic archetype on which all vertebrate brains

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are built. The forebrain is largely concerned with the processing of olfactory information, the midbrain with the processing of visual information, and the hindbrain with that of motor responses and equilibrium, and there is evidence of functional regionalization of the brain early in its development, even when it is still relatively simple in its anatomy. Fishes are a major step with a more identifiable brain structure. Olfaction dominates the telencephalon and a cerebellar structure appears in the hindbrain, evidencing complex motor coordination for 3D aquatic locomotion. In the midbrain, for example, the optic tectum is prominent, with great development particularly in predatory groups where visual processing is critical for prey detection. But, even at this high level of evolution, the fish brain is arranged linearly compared to its modern sophisticated vertebrate counterparts, the cerebral hemispheres arise as evaginations of the forebrain but lack the elaboration of a well-defined cortex.

Amphibians represent an intermediate stage in brain evolution, one that links aquatic and terrestrial organisms. Much of the brain remains fish-like, though changes have occurred which are consisitent with adaptations to life on land. The cerebral hemispheres grow a bit bigger to process more sophisticated behavior patterns necessary to survive in two habitats. In terrestrial environments, where airborne chemicals become essential environmental signals, the olfactory bulbs are much larger, reflecting this newly forged olfactory connection. The amphibian cerebral cortex has a simple three layer structure and is chiefly involved in olfactory processing rather than higher cognitive activity. Brain of the reptilian brain(the first one) has considerable evolutionary sophistication compared to the mammal era of the brain they have a far more enlarged cerebral hemispheres, and the first appearance of the dorsal ventricular ridge; both the structures help in the processing of complex sensory information and the major precursor of mammalian neocortex. In species with complex motor skills the cerebellum becomes increasingly complex during series of evolution. All these developments notwithstanding, however, the reptilian brain is still ruled by instinctual behavior patterns and low behavioral flexibility (the control of stereotyped behavior
patterns due to the relatively large basal ganglia). Despite a divergent brain organization, birds evolved out of theropod dinosaurs, and birds achieved impressive feats of similar intelligent traits and behaviours, and possess with admirable brain specializations. With a telencephalon that is largely composed of a striatum as opposed to a six-layered neocortex, birds have nevertheless evolved complex cognitive abilities through the expansion of the hyperpallium and nidopallium—brain structures functionally comparable to those in the mammalian cortex. These neural adaptations enable elaborate behaviors such as advanced vocalization, social learning, tool use, and extraordinary navigation skills. The avian cerebellum is particularly well-developed, capable of fine-grained motor control critical for flight, and the optic tectum efficiently processes the high-resolution visual input needed for aerial navigation.

The mammalian brain is a unique evolutionary innovation, surpassing in complexity and functional capacity previous brain structures with the most striking advancement being the emergence of the neocortex, a cortical column consisting of six layers that provides sensory processing, motor control, and associative function. Brain organization is strikingly consistent, given the vast size and specialization differences among mammals. The cerebral cortex expand massively, and evolved specialized regions for primary sensory processing and higher-order processing or integration of information. Neocortical expansion is exaggerated among anthropoid primates that also show considerable mediocortex growth in the prefrontal cortex region involved in executive functions, planning and social cognition. In primates, the visual cortex becomes highly elaborated, presumably to facilitate the use of vision in arboreal habitats. This trend culminates in humans, with the cerebral cortex making up about 80% of brain volume, with particularly remarkable expansion of prefronto-parietal-temporal association areas providing the neural bases for language, abstract reasoning, and consciousness. The direction of evolution in the human brain shows adaptation to the ecological niche and selective pressures, not a progressive march toward "higher" forms. Each group of verterbrates has specialized adaptations for their lifestyle. For example, cetaceans (the group of whales and dolphins) have exceptionally large brains with highly folded cortices

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that give rise to complex social systems and elaborate echolocation processing. Of note, elephants are also analogous for impressive levels of encephalization with specialized neuroadaptations to support their social memory and communication. Even "primitive" vertebrates such as electric fish have evolved specialized neural circuits that generate and process electrical signals used for navigation and communication.

Body size relative to brain size, or encephalization quotient (EQ), differs widely between vertebrates and correlates broadly with behavioral complexity. Humans have the highest EQ of any vertebrate, at a rough estimate seven times that predicted for a mammal of similar size. But overall brain size does matter for some building block capacities — the reason that animals with big brains, such as elephants and whales, show cognitive performance at times superior to smaller-brain species with greater EQs. Brain function, however, emerges not only from structural organization, but also neurochemistry and connectivity patterns. Neurotransmitter systems have conserved an extraordinary evolutionary track record with core systems such as the cholinergic, dopaminergic, serotonergic, and GABAergic pathways recurring among vertebrates while mammal systems have exhibited an expanding complexity and regionalization. These systems oversee everything from rudimentary arousal and feeling to sophisticated reward learning and executive command. Evolution has led to an increased complexity of connectivity patterns within the brain, and the generation of elaborate cortico-cortical connections in mammals for distributed information processing. Expansion of association cortices and their interconnections is a key innovation facilitating higher cognitive functions. These afferent connections can be short-range intracortical circuits but also long-range white matter tracts integrating distant brain regions. The corpus callosum, a large fiber tract linking the cerebral hemispheres, is a unique feature of eutherian mammals that enables interhemispheric coordination.

There are also layers of evolution across brain development and plasticity. Developmental plasticity is much less in lower vertebrates; however, they have a great deal of regenerative ability throughout life. By contrast, mammals have substantial developmental plasticity - through critical periods early in life but more limited regenerative capabilities. The human brain requires extended development time, particularly the prefrontal cortex, which is one of the last areas to develop-consistent with the prolonged effort needed during development to learn complex cultural information and social skills. Functional lateralization-the specialization of each of the cerebral hemispheres for certain functions-seems most pronounced in humans, but is found to a lessor or greater extent in all vertebrates. In humans, language is generally left lateralized, whereas spatial processing and emotional regulation are frequently right lateralized. This lateralization could be an efficient strategy for organizing neural information, reducing computational redundancy and enabling parallel processing of diverse types of information. In their evolution, glial cells have evolved alongside neuronal complexity from mere supportive cells. Additional processes in mammalian brain astrocytes are more extensive/complex compared to those in other vertebrates, and mammalian brain astrocytes play their active role in synaptic transmission, provision of metabolic support and information processing. The proportion of glia relative to neurons increases with mammalian brain size, implying the differential roles such cells play in meeting the cerebral metabolic demand and computational demands of complex brains. The history of brain evolution shows an intriguing mix of conservation and novelty. Fundamental components and mechanisms of brain development are conserved in all vertebrates (including processes such as the formation of the neural tube or specification of specific progenitor pools), however so-called differentiating regions are expanded in relation to the evolutionary needs offering higher-order cognitive and behavioral capabilities. This comparative point of view highlights that vertebrate brains have been iteratively remodeled and have expanded throughout evolution to facilitate varying lifestyles and cognitive features, resulting in the high computational capacity and behavioral adaptability in our human brains.

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### Spinal Cord Comparative Anatomy



While the spinal cord has been exceptionally well conserved throughout evolution in its basic structure, vertebrate taxa can show considerable adaptive modifications in organization within the central nervous system (CNS), including all classes of fish and tetrapods. This long, tubular neural structure continues from the brain stem, namely, from the medulla oblongata, and is the main channel for information relaying between the brain and peripheral tissues, and kilometers of circuits that coordinate the indirect response of the reflex kind, as well as locomotion, independent of higher brain operations. In the simplest forms of chordates, like amphioxus (lancelet), there is a true spinal cord, a tubular structure that is hollow and runs along the dorsal length of the organism. This simple construct, despite its simplicity relative to that of a vertebrate, sets up the primitive dorsal-ventral axis that governs all chordate nervous systems, with sensory neurons entering dorsally and motor neurons exiting ventrally-a ground plan that persists through vertebrate evolution. In lampreys and hagfish (cyclostomes), the spinal cord is more vertebrate-like, being characterized by a central canal with surrounding gray matter containing neuronal cell bodies and peripheral white matter made of myelinated and unmyelinated axons. This general anatomical pattern is maintained through all classes of vertebrates with changes that reflect functional adaptation. As a result, fishes exhibit a spinal cord with a more uniform diameter along most of its length, indicating that swimming is an integrated activity widely engaging the full body axis. In cross-section, it has a butterfly- or H-like arrangement, with dorsal horns of gray matter receiving sensory input and ventral horns containing Lmn that innervate segmentally arranged myomeres. One prominent aspect of many fishes is the existence of Mauthner cells, enormous neurons whose explosive activation simultaneously sets in motion trunk musculature on the side opposite an intimidating stimulus for speedy escape. The C-start escape response produced by this specialized neural circuit is a defining characteristic across many fish species, which demonstrates how tailored adaptations in the spinal cord can allow for essential survival behaviors.

Amphibians represent an intermediate phase in the evolution of the spinal cord, due to their partly aquatic and terrestrial computing needs. Notable adaptations occur in the regions related to limb control: the spinal cord has cervical and lumbar enlargements housing an increased number of motor neurons that innervate fore and hind limbs respectively. This marks a major innovation linked to tetrapod movement. The lumbar enlargement is especially exaggerated in anurans (frogs and toads) that built a strong musculature in their hind limbs for jumping; urodeles (salamanders) have more modest enlargements relating to less specialized limb use. Amphibians adapt central pattern generators (neural circuits that generate rhythmic output to produce motor patterns) to modulate the timing, extent and integration of the extensive muscles that control their swimming and terrestrial activities. In line with the jatmonates that prefer the spasm or flex, an intermediate stage between that of the amphibia and reptiles with expanded cervical and lumbar enlargements, with adapted morphology for such species as are capable of high activity. The gray matter becomes increasingly more elaborate, and the more pronounced lamination of the dorsal horn indicates a more complex level of sensory processing. In secondarily limbless snakes, the spinal cord is strikingly uniform along its length, with no cervical or lumbar enlargement, but specialized circuitry does exist to orchestrate the laterally alternating arrangements of the undulatory sequences that these species use for locomotion (Ni et al., 2010). The white matter increases in a relatively linear manner, reflecting increased descending control from higher centers in the brain, as well as an increased number of propriospinal connections-axons that project between different spinal segments to coordinate more complex behaviors by integrating multiple regions of the body.

There are some avian spinal cords that display dramatic adaptations for flight. The cervical enlargement is very well developed as it needs to innervate the motor control of the wings, while lumbosacral alliances support very powerful muscles for the legs used to perch, land and navigate on land. A specialized structure found in birds is the glycogen body, a glial aggregate that appears to be located in the lumbosacral region and contains glial cells rich in glycogen,

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but a clear and accepted function of this structure in bird behavior is yet to be determined. Another bird novel structure in the general region large lumbosacral nerve roots passed through known as sinus rhomboidalis has a unique expansion of the central canal and is filled with cerebrospinal fluid, probably with mechanical function. Birds, like all vertebrates, have well-developed white matter, especially in long descending tracts from the brain that control flight. Whereas in mammals, the spinal cord attaches further down from the base of the skull, in birds the cord ends earlier and the tailmost segments are concentrated to form a region known as the cauda equina, a collection of nerve roots that tosckExtend away from the spinal column to supply muscles in the back end. The spinal cords of mammals are the most complex and regionally diverse in vertebrates. Especially in animals with highly dexterous forelimbs or manipulatory adaptations, the cervical and lumbosacral enlargements become considerably more pronounced. The gray matter displays a clear laminar organization with the Rexed laminae serving as relatively stable descriptor of the functional organization of sensory and motor processing. The dorsal horn is a complex structure that performs regionalized sensory processing, with several specialized laminae for separate modalities processing at different stages. The ventral horn comprises alpha motor neurons, organized in topologically and functionally defined pools, with muscle targets following a common developmental path that allows highly controlled, fractionated movements-the ability to move individual muscle groups independently, which reached its peak in primates.

Mammalian spinal cords become filled with white matter, indicative of connections to higher brain centers. The major descending pathways are the corticospinal tract, allowing for direct cortical control of voluntary movement, and the most developed pathway in primates, especially humans, where lateral corticospinal projections allowed for fine manipulative abilities. Additional motor control pathways are made available by rubrospinal, vestibulospinal and reticulospinal tracts that show differing importance among the mammals. Much of the ascending pathways, including the dorsal column-medial lemniscus system and spinothalamic tracts, relay sensory information to "higher" centers, with specialized representation

of tactile input seen in tactile specialists such as primates and cetaceans. With respect to the development of the corresponding vertebral column, the mammalian spinal cord becomes proportionately shorter; the nerve roots of the more posterior segments course some distance along the vertebral canal prior to exiting through the intervertebral foramina. A prominent feature of humans and many other longlegged mammals is the emergence of the cauda equina, as the actual spinal cord ends at the L1-L2 vertebral level. In addition to the gross anatomical differences, these classes exhibit pronounced differences in spinal cord neurochemistry and cellular composition when compared with each other. Neurotransmitters and neuromodulators are conserved during evolution but often have specialized roles. Presently the excitatory transmitters at all vertebrate motor synapses are acetylcholine and glutamate, whereas glycine and GABA are the inhibitory transmitters. The distribution of monoaminergic modulatory systems (serotonergic, dopaminergic, and noradrenergic projections) however is highly variable and is in accordance with differences in the requirements for locomotor control and sensory processing.

The development of myelin, the insulating sheath around axons that drastically increases conduction speed, varies across vertebrate taxa. Myelin is absent in agnathans (lampreys and hagfish), restricting conduction speeds. Myelin should be considered present in cartilaginous and bony fishes in which it is not as pronounced as in terrestrial vertebrates in which the rapid transmission of signals becomes the most critical to the coordination of movement and reflexive response. Myelination is most prominent in mammals with extensive myelination seen in descending motor pathways where high-speed transmission is critical for movement speed and precision. In other words, evolutionary complexity has a general trend of correlating inversely with regenerative capacity. Fishes and amphibians retain considerable capacity to regenerate spinal cord tissue after injury and often recover functional locomotor capacity. This regenerative capacity slowly decreases going from reptiles to birds and mammals, where spinal cord injuries generally give rise to irreversible functional deficits. This disparity likely

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reflects an evolutionary compromise between regenerative potential and the intricacy of neural circuitry, as the mammalian spinal cord, highly specialized for specific functions, displays little in terms of plasticity, yet provides high specificity. The spinal cord structure reveals a real drama in the evolutionary process between specialization and flexibility. The spinal cord, which originated from a simple neural tube in primitive chordates at the dawn of evolutionary history, retains key organizational properties while acquiring unique specializations that support diverse locomotor strategies and sensory processing mechanisms of vertebrate taxa. This framework allows for a more comprehensive understanding of both the aspects of neural organization that have been conserved and those that have evolved in response to new constraints, as vertebrates came to embark on cold-blooded omnivorous lifestyles and occupy nearly every ecological niche on the planet, all within the span of 150 million years.

#### Nerves: Cranial, Peripheral & Autonomic Nervous System

Through an extremely complex network of specialized, axon bundles called nerves, the nervous system exerts its power across the entire body. The neural infrastructure consists of cranial nerves that depart from the brain, peripheral nerves that emerge from the spinal cord, and the autonomic system that governs internal organ function. We find remarkable conservation and adaptation patterns across vertebrate taxa for each. Cranial nerves are a vertebrate anatomy hallmark, arising directly from the brain to innervate mainly head and neck structures. Let us first establish that the general organization of cranial nerves is highly conserved across vertebrates, with major differences reflecting adaptations to a variety of ecological needs (including sensory specialisations) during evolutionary time. In the most primitive of the vertebrates, the cyclostomes (lampreys and hagfish), ten pairs of cranial nerves are established, delineating the basic ground from which more derived types arise. In vertebrate evolution, we eventually reach the more stable configuration which is twelve pairs present in gnathostome (jawed vertebrate) vertebrates, although a few authorities consider the inclusion of additional nerves in some taxa. Fascinatingly, both the olfactory (I) and optic (II) nerves show evolutionary patterns. Technically these

are not peripheral nerves but brain tracts since they are direct extension of the central nervous system. The olfactory nerve exhibits striking variation in development that aligns with the ecological relevance of olfaction. In macrosmatic animals with an acute sense of smell, like canids, rodent animals, the olfactory nerve contains millions of small unmyelinated axons from olfactory receptor neurons. In contrast, humans and other microsmatic species have diminished olfactory systems. In cetaceans, the olfactory nerve has regressed extensively, becoming vestigial or entirely lacking in many species as an adaptation to an aquatic lifestyle in which airborne odorants are not especially relevant.

The optic nerve also varies according to visual specialization. Many birds of prey have extremely large optic nerves related to their acute vision, while some fossorial mammals display regressed optic nerves due to their decreased use of vision in their burrows. The evolution and derivative specialization of these sensory nerves are a direct reflection of underlying ecological type and sensory hierarchy. The oculomotor (III), trochlear (IV), and abducens (VI) nerves, which control eye movements, however, are highly conserved across vertebrates, even if relative dominance can vary by visual specialization. These nerves consistently innervate the extraocular muscles in a pattern, highlighting the essential role of coordinated ocular movements. The trochlear nerve is unique among the cranial nerves in exiting the brain dorsally and crossing to innervate contralateral musculature in all vertebrates; an idiosyncratic evolutionary arrangement that has persisted in widely divergent taxa. The most diverse of all cranial nerves, the trigeminal nerve (V), exhibits remarkable adaptive radiation in vertebrates. The nerve has three divisions ophthalmic, maxillary, and mandibular which will provide sensory supply to the face and motor supply to the muscles of mastication. The trigeminal also has some of the most striking adaptations in species with specialized facial morphology. For example, starnosed moles have unparalleled sensory innervation to their specialized nasal appendages, and crocodilians have special receptors in their jaws to detect their prey movements. Remarkably profound changes are seen in duck-billed

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platypuses, which innervate electroreceptors are responsive to the fine electrical fields produced by prey organisms.

The facial nerve (VII) is highly modified in divergences of vertebrates. In fishes, it is crucial for lateral line system innervation, which detects disturbances in water. As vertebrates adapted to land, the nerve's duties evolved to include taste sensation and facial muscle control. In mammals, especially in primates, the facial nerve elaborates quite substantially in correlation with complex facial musculature development used for expression and communication. This trait culminates in humans, where extensive facial nerve interconnections allow subtlety in facial movement required for nuanced expression in a species with a powerful capacity for nonverbal communication. Anatomy of the vestibulocochlear nerve (VIII) across vertebrates highlights some unusual evolutionary adaptations. Initially related only to vestibular function (balance) in basal vertebrates, this nerve became more cochlear (auditory) in nature as hearing grew more complex. In echolocating bats and cetaceans, this cochlear part is greatly expanded to accommodate their high-performing hearing. 2. In contrast, within fossorial reptiles, reduction of the cochlear component is manifested but there is uniform presence of vestibular innervation, indicative of the importance of both sensory modalities in their ecological niche. The glossopharyngeal (IX), vagus (X), and accessory (XI) nerves comprise a complex that innervates derivatives of the embryonic pharyngeal arches. The vagus nerve has especially broad functions among vertebrates, innervating the heart, lungs and most of the digestive tract. In fish the vagus includes branchial branches that innervate the gills, which undergo evolutionary modification in terrestrial vertebrates to innervate pharyngeal and laryngeal structures. The surprising long course of the recurrent laryngeal nerve in giraffes, which descends and loops all the way around the aorta to reach the larynx, provides an extreme case of how anatomical constraints in development shape a neural anatomy outcome across evolution.

The hypoglossal nerve (XII), which controls tongue movements, is the only cranial nerve, besides HMNs, to appear as a separate structure in tetrapods.

As in mammals, the analogous innervation in fish originates from the anterior spinal nerves, which is grounded in the ontogenesis and evolution of the hypobranchial musculature that translocated from the trunk area to the head area. In mammals, the nerve is modified to a significant degree, most notably in species with manipulative tongues for intricate feeding behaviors or vocalizations, with human hyoglossus innervation the most advanced of all, adapting tongue movements to speech rather than simple feeding functions. Among vertebrates, the peripheral nervous system of the spinal cord has an intrinsic segmental plan, but undergoes extensive modification in various lineages. In its most primitive form as observed in amphioxus and to some extent in the cyclostomes, a wellstructured arrangement of dorsal sensory and ventral motor roots radiate from each segment with minimal intermingling of these functional elements. These roots unite in gnathostomes to create mixed spinal nerves with both sensory and motor neurons (dorsal horns with sensory neurons and ventral horns with motor neurons), which then bifurcate ventrally and dorsally to innervate the dorsal and ventral body region, respectively. The structure of the body along the body axis-primarily the repeating segments-is significantly altered in tetrapods with limb evolution. In the territories of limb innervation, adjacent spinal nerves generate complex plexuses-networks where fibers reorganize before targeting peripherally. The brachial plexus supplying the forelimb and the lumbosacral plexus to the hindlimb are basic tetrapod traits, but their morphology and segmental contributions differ widely between taxa. By permitting bundles of motor neurons across segments to project onto these functionally related pairs of muscles rather than being limited to strictly segmental innervation, these plexuses allow for the coordinated control of multi-jointed limbs. The anatomy of cranial and spinal nerves diverges substantially between vertebrates, mirroring functional requirements and evolutionary trajectory. An essential feature of the peripheral nervous system in aquatic vertebrates is lateral line nerves, which are specialized for sensing the motion and pressure of water. These nerves tend to regress as animals adapted to land life, but they have retained in aquatic amphibians. Peripheral nerves innervating flight muscles become dramatically

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expanded in flying vertebrates, including birds and bats, with distinctive fastconducting properties that enable the fine motor control necessary for aerial locomotion.

Spinal nerve composition differs sharply among vertebrate clades. In cyclostomes, unmyelinated fibers dominate and conduction velocities are limited. In gnathostomes, the advent of myelin enabled very high potential conduction speeds, considerably increased in birds and mammals (that needs to be very stable for quick and exact movements). Functional demands also influence distributions of fiber diameters within nerves. Nerves governing fine movements (such as in primate hands) contain relative higher proportions of small-diameter axons allowing for fine spatial resolution; nerves that govern larger muscle groups contain relative higher proportions of large-diameter, fast-conducting fibers. Interestingly, the autonomic nervous system, responsible for the control of visceral functions such as heart rate, the contraction of smooth muscle, and the secretion of glands, exhibits both conservation and specialization throughout vertebrate evolution. Much of this system functions underneath our conscious awareness, keeping homeostasis in check with balanced activation of its main sympathetic and parasympathetic divisions-referred to as the body's "fight-or-flight" and "rest-and-digest" systems, respectively. Although the basic organizational layout of two-neuron circuits - with central nervous system-derived preganglionic neurons synapsing on peripheral ganglionic postganglionic neurons — is maintained among jawed vertebrates, extensive variations in ganglionic organization and target innervation patterns exist. The sympathetic nervous system is originally developed from thoracolumbar spinal segments, displaying a relatively conserved organization throughout vertebrates. Sympathetic ganglia usually form paravertebral chains alongside the vertebral column, although the extent of segmental organization is variable. In fish and amphibians, sympathetic ganglia preserve segmental correspondence with spinal nerves, whereas in amniotes, and especially mammals, considerable fusion occurs resulting in more complex ganglionic organization. The uparers in that previous schema thus are irrelevant in this primary intimate contact of sympathetic nerve with adrenal medulla, which occurs in the metallic labyrinth of that organ, without the interposition of post. The response is about the rapid; because in the stress responses the protective and fended state shine bright, e.g. catecholamines which losses systemic barcos are in this form characteristic of mammal.

In contrast, the parasympathetic system demonstrates a higher degree of evolutionary variability, functioning with contributions from both cranial and sacral spinal regions. The cranial parasympathetic outflow runs mainly in the oculomotor, facial, glossopharyngeal and vagus nerves. The vagus nerve is the major parasympathetic pathway in all vertebrates, but its relative importance varies. In fish, the primary targets of vagal parasympathetic fibers are the heart and proximal digestive organs. As the digestive tract lengthened throughout vertebrate evolution, vagus innervation remained to the proximal gut, whereas distal gut became more and more reliant on sacral parasympathetic outflow in tetrapods. Such paired innervation is further exaggerated in mammals, with vagal fibers predominantly innervating the proximal colon and sacral fibers projecting to more distal territories. Parasympathetic ganglia exhibit considerable evolutionary variation in their organization. Parasympathetic ganglia are located in close proximity to or within target organs in lower vertebrates. In mammals, more complex arrangements form which include separate cranial parasympathetic ganglia such as the ciliary, pterygopalatine, submandibular, and otic ganglia, which receive information from specific cranial nerves and project to particular target structures. In mammals, this arrangement allows for finer control of specific paradigms of the parasympathetic subsystem compared to the more diffuse distribution found in other vertebrates. The enteric nervous system, often referred to as a second brain in the gut, is a relatively recent evolution of the autonomic system that can function on its own without centralized communication or control. This complex neural network embedded in the gut wall modulates motility, secretion and blood flow through several complex local reflexes. The enteric system has an ancient origin in all vertebrates but displays considerable structural elaboration during evolution, with the mammalian enteric

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plexuses being the largest and most complex, containing up to several million neurons arranged into functional circuits that govern specialized digestive functions.

Yet, during the emergence of new vertebrate taxa, evolutionary novelty manifests in the evolution of new autonomic components. Additionally different from mammals, birds have a unique adrenergic system in the lung that is not involved in bronchoconstriction but instead modulates pulmonary blood flow to maximize gas exchange capability during flight. Teleost fish possess a subtype of cholinergic innervation of chromatophores, specialized for rapid color changes used in both camouflage and communication. It allows some reptiles to autonomously regulate blood flow with extreme precision to help maintain a more constant body temperature through behavioral thermoregulation, despite their ectothermic physiology. There is conservation and innovation in neurochemical evolution in the autonomic system. From jawed vertebrates onward the main neurotransmitters are the same-acetylcholine at all preganglionic synapses and at parasympathetic postganglionic synapses, with norepinephrine being the predominant one at sympathetic postganglionic synapses. Co-transmitters range widely, including neuropeptides that can modulate the effects of the synapse. The distributions of multiple neuropeptides such as vasoactive intestinal peptide, neuropeptide Y, and substance P in autonomic circuits demonstrate a significant degree of interspecies variability that mirrors an adaptive specialization to specific physiological requirements. It is in a comparative framework, where the design of nerves — cranial, peripheral, and autonomic — is compared across opposing vertebrate taxa that we find extraordinary evolutionary trends. The core organizational principles of embryogenesis established early on in vertebrate evolution remain in place across widely divergent vertebrate lineages, with subsequent adaptations reflecting broader diversification pressures defined by specialized Ecological niches and behavioral specializations. This evolutionary perspective elucidates not only the ancestral basis of neural organization but also the astounding flexibility that has allowed the vertebrate nervous system to



accommodate different functional demands over vastly different body plans and lifestyles.

## SELFASSESSMENT QUESTIONS

### Multiple Choice Questions (MCQs):

1. Which of the following vertebrates possesses a lateral line system?

a) Mammals

b) Birds

c) Fishes

d)Amphibians

#### 2. The olfactory organ is responsible for detecting which type of stimuli?

a) Sound

b) Light

c) Chemical

d) Mechanical

#### 3. Which structure is responsible for electroreception in sharks?

- a) Lateral line
- b)Ampullae of Lorenzini
- c) Cochlea
- d) Nictitating membrane

## 4. Which part of the brain is responsible for balance and coordination?

a) Cerebrum

b) Cerebellum

c) Medulla oblongata

d) Hypothalamus



- 5. The autonomic nervous system controls which type of functions?
- a) Voluntary movements
- b) Involuntary functions
- c) Reflex actions only
- d) None of the above
- 6. Which sensory organ is most highly developed in nocturnal birds?
- a) Olfactory organs
- b)Auditory system
- c) Visual system
- d) Gustatory organs
- 7. Which type of nerve is responsible for transmitting signals from the spinal cord to the muscles?
- a) Sensory nerve
- b) Motor nerve
- c) Cranial nerve
- d) None of the above
- 8. Which vertebrate group has the most developed cerebral cortex?
- a)Amphibians
- b) Reptiles
- c) Birds

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d) Mammals

# 9. Which sensory structure is responsible for detecting water vibrations in fish?

- a) Tympanic membrane
- b) Semicircular canals
- c) Lateral line system
- d) Jacobson's organ

#### 10. Which structure protects the eye in reptiles and birds?

a) Retina

b) Cornea

c) Nictitating membrane

d) Optic nerve

#### **Short Questions:**

- 1. What are the five major sense organs in vertebrates?
- 2. Explain the function of the lateral line system in aquatic vertebrates.
- 3. What is electroreception, and in which vertebrates is it found?
- 4. What is the difference between olfactory and gustatory organs?
- 5. Explain the role of the cerebellum in vertebrate movement.
- 6. What is the difference between the central and peripheral nervous system?
- 7. What is the function of the cranial nerves in vertebrates?
- 8. Define autonomic nervous system and its functions.

### COMPARATIVE

#### **ANATOMY III**

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CHORDATE AND COMPARATIVE ANATOMY	



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