UNIT 1

INTEGUMENTARY SYSTEM

Structure

1.1 INTRODUCTION

The integument is the outermost covering of an animal. It is a composite organ that includes the skin and everything derived from or contained in it, forming an essential and dynamic integumentary system. The surface is the **epidermis,** below it is the **dermis** and between them lies the **basement membrane.**

The integument is the largest organ of the human body. In humans it makes up some 15 per cent of the weight. Epidermis and dermis together form some of the most varied structures found within vertebrates. The epidermis produces hair, feather, baleen, claws, nails, horns, beak and some types of scales. The dermis gives rise to dermal bones and osteoderms of reptiles. Collectively epidermis and dermis form teeth as well as denticles and skin of fish.

As the critical border between the organism and its environment, the integument has a variety of specialized functions. It forms part of the exoskeleton and thickens to resist mechanical injury. The integument helps hold the shape of the animal. Osmotic regulation and movement of gases and ions to and from the circulation are aided by the integument in conjunction with other systems. Skin gathers needed heat or radiates the excess and houses sensory receptors. Skin pigments block some of the sunlight, hence protect the body from harmful UV radiation.

Objectives

After studying this unit, you should be able to:

- ❖ describe the components that make up the structure of integument,
- ❖ explain the basic functions of the integument,
- ❖ compare the integument of fishes and tetrapods, and
- ❖ discuss the specialized derivatives of integument.

1.2 EMBRYONIC ORIGIN

Neurulation is a stage in the development of vertebrates during which nervous tissue is separated from the ectoderm which separates the skin tissue.

Let us begin by examining the embryonic origin and development of skin.

By the end of neurulation in the embryo, most skin precursors are delineated. The single layered surface ectoderm proliferates to give rise to the multilayered epidermis. The deep layer of the epidermis, the **stratum basale** rests upon the basement membrane. Through active cell division, the basement membrane replenishes the single layer of outer cells called the **periderm** (Fig. 1.1a).

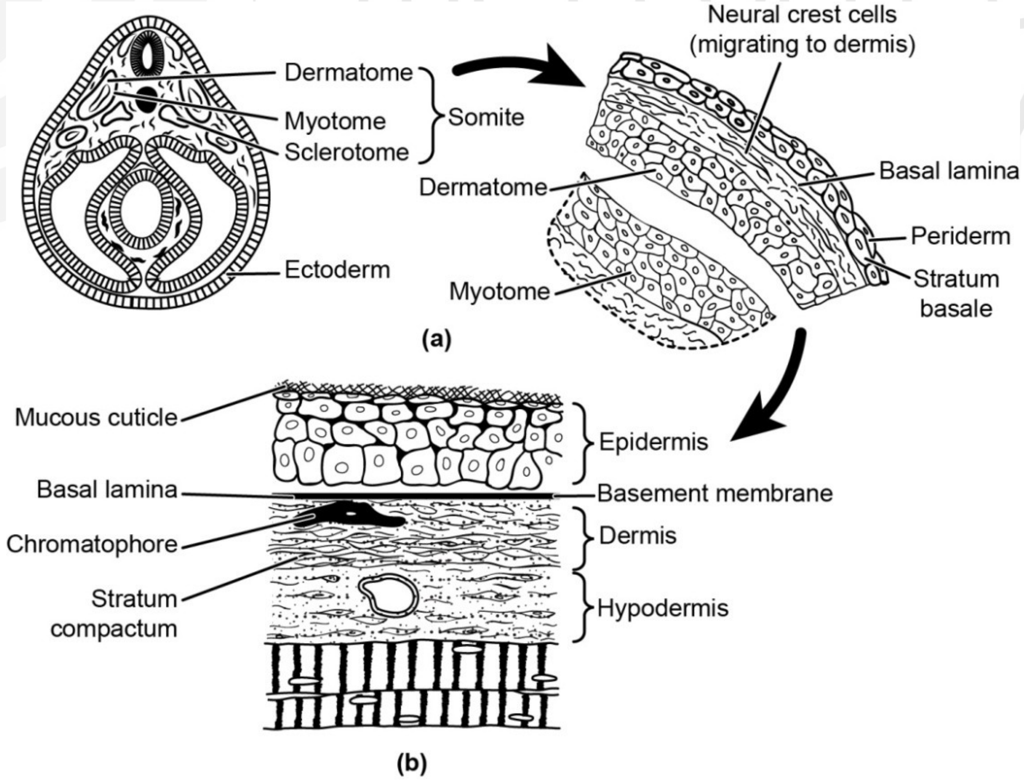


Fig. 1.1: Embryonic development of the skin. (a) Cross section of a representative vertebrate embryo. (b) The epidermis differentiates into a stratified layer that has cuticle on the surface.

The dermis arises from several sources, principally from the dermatome. Fundamentally, the integument is composed of two layers, epidermis and dermis, separated by the basement membrane. Vascularization and innervations are added, along with contributions from the neural crest. Interaction between epidermis and dermis stimulates specializations such as teeth, feathers, hair and scales of several varieties (Fig. 1.2).

A dermatome is the area of the skin of the human anatomy that is mainly supplied by branches of a single spinal sensory nerve root.

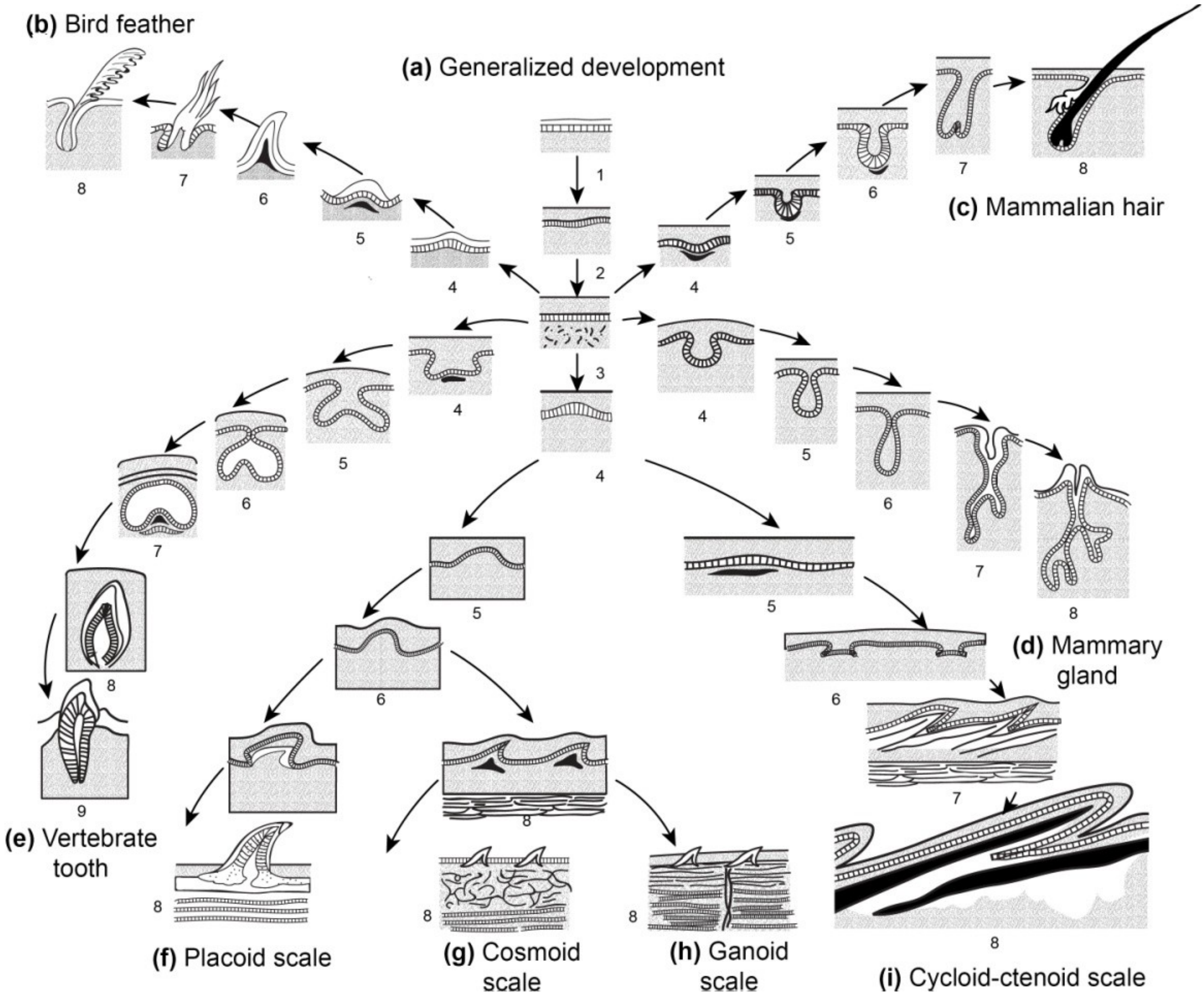


Fig. 1.2: Skin derivatives. (a) Out of the simple arrangement of epidermis and dermis, with a basement membrane, a great variety of vertebrate integuments develop. (b) Interaction of epidermis and dermis gives rise to feathers in birds. (c & d) Hair and mammary glands in mammals. (e) teeth in vertebrates. (f) Placoid scales in chondrichthyans and (g, h and i) Cosmoid, ganoid and ctenoid scales in bony fishes.

1.3 GENERAL FEATURES OF THE INTEGUMENT

Although we do not think of the integument in a vertebrate as an organ, it is made up of cells and tissue that work together as a single structure to perform very important functions in the body. The integument is made up of several layers of cells and can be divided as the outer layer of epithelial tissue forming the epidermis, below which is the region of tissue called the dermis and a third region below the dermis called the hypodermis which separates the skin from deeper tissue.

1.3.1 Epidermis

The epidermis in most animals is multilayered but thin. In many vertebrates it produces mucus to moisten the surface of the skin. In fishes, mucus seems to afford some protection from bacterial infection and helps ensure the laminar flow of water across the body surface. In amphibians, mucus probably serves similar roles and additionally keeps the skin from drying during the animal's sorties onto land.

In terrestrial vertebrates the epidermis covering the body often forms an outer **keratinized** or **cornified** layer, the **stratum corneum**. This layer is composed of mostly differentiated dead cells. New epidermal cells are formed by mitotic division, primarily in the deep epidermal layer **stratum basale.** These cells push more superficial ones towards the surface, where they tend to self destruct in an orderly fashion. During this process, various protein products accumulate and collectively form **keratin** (a water insoluble protein) in a process called **keratinization.** Keratin helps the skin to maintain a barrier against bacteria and gives some protection against injury.

Keratinisation and formation of **stratum corneum** also occur when friction or direct mechanical abrasion insult the epithelium. The stratum corneum may be differentiated into hair, hooves, horn sheaths or other specialized confined structures. Other epidermal cells may produce glands or they may be isolated glandular cells.

Scales form within the integument of many aquatic and terrestrial vertebrates. Scales are basically folds in the integument. If dermal contributions predominate, the fold is called a **dermal scale.** An epidermal fold produces an **epidermal scale.**

1.3.2 Dermis

The most conspicuous component of dermis is the fibrous connective tissue composed mostly of collagen fibres. The upper layer lies directly below the basal membrane that separates it from epidermis. It is composed of loosely packed cells. The layer below it has more tightly packed cells and is called stratum compactum. The dermis attaches the skin to the musculature lying below. It also includes nerves, blood vessels and pigment cells, bases of feathers, hair and its erector muscles and other associated structures. The dermis of many vertebrates produces plates of bone directly through intramembranous ossification. Because of their embryonic source and initial position within the dermis, these bones are called **dermal bones.** They are prominent in ostracoderm fishes but appear secondarily even in derived groups, such as in some species of mammals.

1.3.3 Functions of Integument

The integument is the first surface of the organism that comes in contact with the environment:

- It protects the internal soft tissue and organs from damage, microbes and abrasions. It is the first defence in the immune system against infections for instance, in our skin there are tiny oil glands that enhance the barrier function. It also protects against UV radiations.

- It receives and conducts external stimuli like touch, chemicals and temperature to the nervous system.
- Regulates the temperature of the body in most vertebrates. For instance the skin regulates the internal body temperature in most mammals by sweating.
- Protects against dehydration and water loss in terrestrial vertebrates.
- It helps in respiration in many aquatic vertebrates, may be the only respiratory organ in some aquatic vertebrates.
- Imparts colour which may be protective or for camouflage.

Let us now learn about the different forms of integument seen in the various groups of vertebrates. Though the fundamental pattern is the same, the skin is modified according to the environment in which they live.

1.4 PHYLOGENY

1.4.1 Integument of Fishes

With few exceptions, the skin of most living fishes is non-keratinized and covered instead by mucus. Exceptions include keratinized specializations in a few groups. The "teeth" lining the oral disc of lampreys, the jaw coverings of some herbivorous minnows, and the friction surface on belly skin of some semi terrestrial fish are all keratinized derivatives. However, in most living fishes, the epidermis is alive and active on the body surface, and there is no prominent superficial layer of dead, keratinized cells.

Two types of cells occur within the epidermis of fishes: epidermal cells and specialized unicellular glands. In living fishes, including cyclostomes, prevalent epidermal cells make up the stratified epidermis. Epidermal cells are tightly connected through cell junctions and contain numerous secretary vesicles that are released to the surface where they contribute to the mucous cuticle.

Unicellular glands are single, specialized and interspersed among the epidermal cell population. There are several types of unicellular glands. The club cell is an elongate, sometimes binucleate unicellular gland (Fig. 1.3).

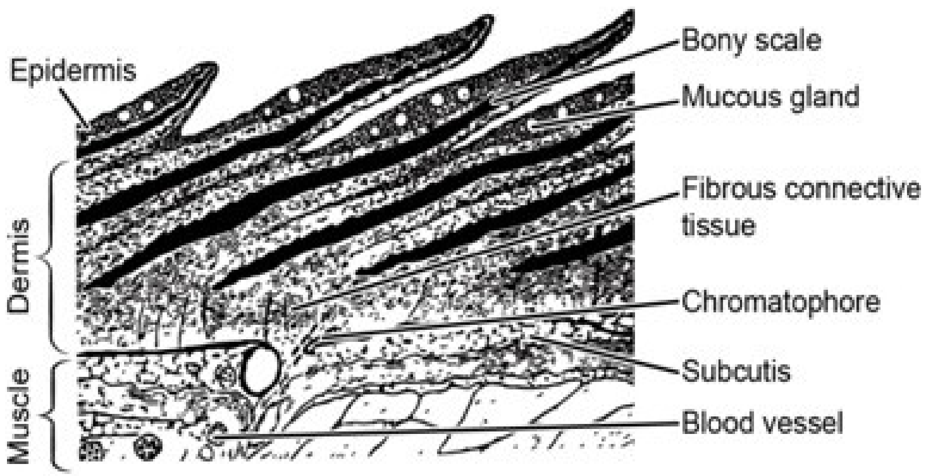


Fig. 1.3: Section of fish skin.

Collagen within the stratum compactum is regularly organized into plies that spiral around the body of the fish, allowing the skin to bend without wrinkling. In some fishes, the dermis has elastic properties. When a swimming fish bends its body, the skin on the stretched side stores energy that helps unbent the body. The fish dermis often gives rise to dermal bone, and dermal bone gives rise to dermal scales. In addition, the surface of fish scales is sometimes coated with a hard, acellular enamel of epidermal origin and a deeper dentinelayer of dermal origin.

Primitive Fishes

In ostracoderms and placoderms, the integument produced prominent body plates of dermal armor that encased their bodies in an exoskeleton. Dermal bones of the cranial region were large, forming the head shields, but more posterierly along the body, the dermal bones tended to be broken up into smaller pieces, the dermal scales. The surface of these scales was often ornamented with tiny, mushroom shaped tubercles. These tubercles consisted of a surface layer of enamel or an enamel like substance over an inner layer of dentine.

Agnatha

The skin of living hagfishes and lampreys departs considerably from that of primitive fossil fishes. Dermal bone is lost, and the skin surface is smooth and without scales (Fig. 1.4). The epidermis is composed of stacked layers of numerous living epidermal cells throughout. Interspersed among them are unicellular glands, namely, the large granular cells and elongate club cells. In addition, the skin of hagfishes includes **thread cells** that discharge thick cords of mucus to the skin surface when the fish is irritated. The dermis is highly organized into regular layers of fibrous connective tissue. Hagfishes also possess multicellular slime **glands** that release their products through ducts to the surface.

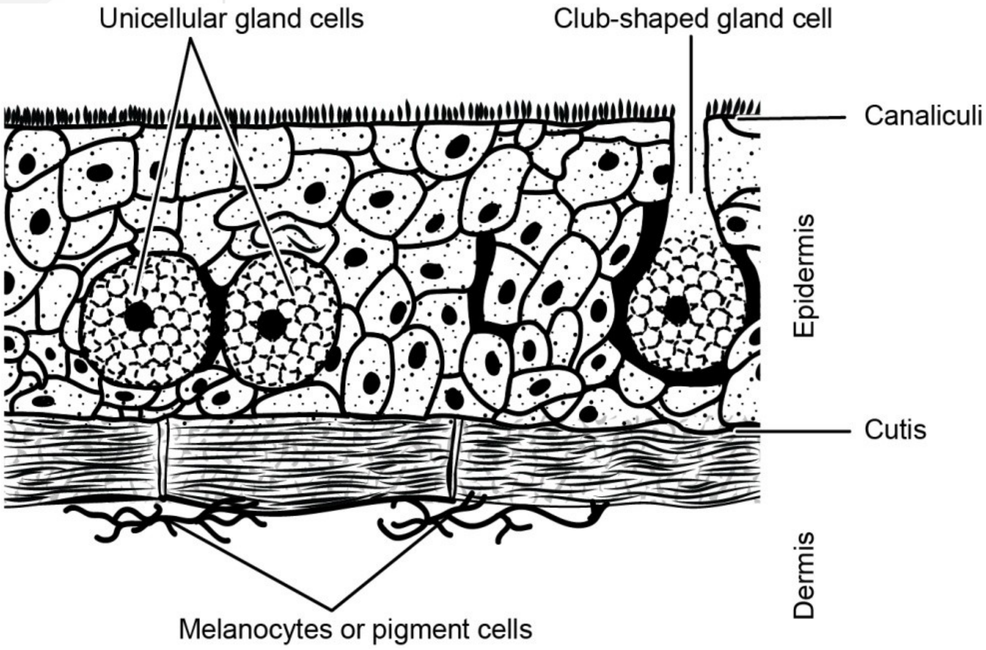


Fig. 1.4: Skin of larval cyclostomes in V.S.

Chondrichthyes

In cartilagenous fishes, dermal bone is absent, but surface denticles, termed **placoid scales**, persist. These scales give the rough feel to the surface of the skin (Fig. 1.5 a).

Recent evidence suggests that these tiny placoid scales favourably affect the water flowing across the skin as the fish swim forward to reduce friction drag. Numerous secondary cells are present in the epidermis as well as stratified epidermal cells. The dermis is composed of fibrous connective tissue, especially elastic and collagen fibres, whose regular arrangement forms a fabric like warp and weft in the dermis. This gives the skin strength and prevents wrinkling during swimming.

The placoid scale develops in the dermis but projects through the epidermis to reach the surface. A cap of enamel forms the tip, dentine lies beneath and pulp cavity resides within (Fig. 1.5 a, b).

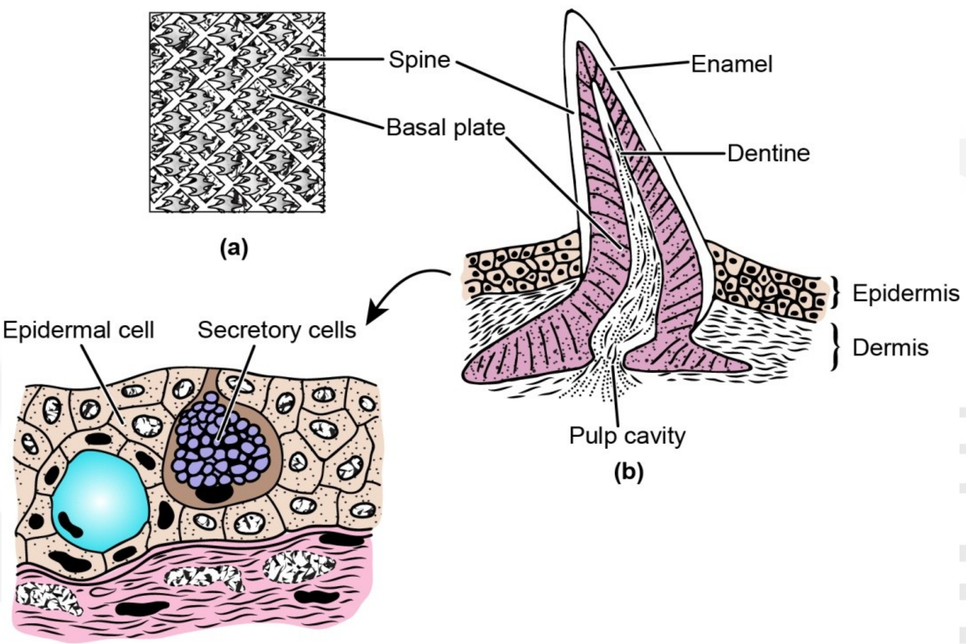


Fig. 1.5: Shark skin. (a) Surface view of the skin showing regular arrangement of projecting placoid scales. (b) Section through a placoid scale of shark.

Bony Fishes

The dermis of bony fish is subdivided into a superficial layer of loose connective tissue and a deeper layer of dense fibrous connective tissue Chromatophores are found within the dermis. The most important structural product of the dermis is the scale. In bony fishes, dermal scales do not actually pierce the epidermis, but they are so close to the surface they give the impression that the skin is hard (Fig. 1.6 a, b). These scales grow at the margins and over the lower surface which are lines of growth and represent the number of seasons the fish have lived. The dermis is vascular and permeable and in some small fish participates in gas exchange. The epidermis (Fig.1.6 b) contains many mucous glands; mucous helped reduce friction and prevent bacterial and fungal infections. Some fishes have poison glands, or granular glands that secrete poisonous/ irritating alkaloids. Some bony fishes have photophores and most have chromatophores that help in attracting prey or defence.

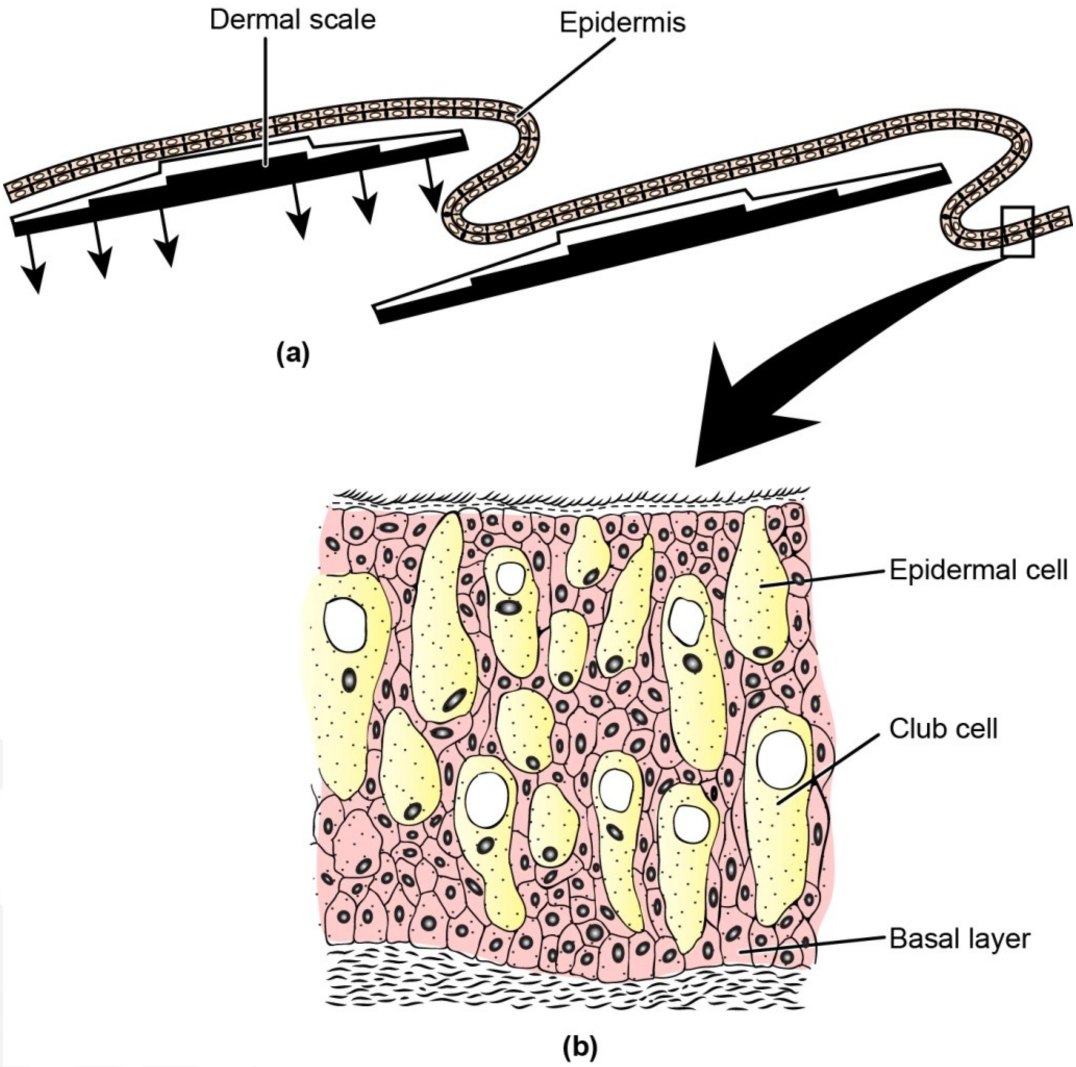


Fig. 1.6: Bony fish skin. (a) Arrangement of dermal scales within the skin of teleost fish. (b) Enlargement of epidermis.

On the basis of their appearance, several types of scales are recognized among bony fishes. The **cosmoid** scale, seen in primitive sarcopterygians resides upon a double layer of bone, one layer of which is vascular and the other lamellar. On the outer surface of this bone is a layer that is now recognized as dentine and spread superficially on the dentine is a layer now recognized as enamel.

The **ganoid** scale is characterized by the prevalence of a thick surface coat of enamel, without an underlying layer of dentine. Dermal bone forms the foundation of the ganoid scale, appearing as a double layer of vascular and lamellar bone or single layer of lamellar bone. Ganoid scales are shiny, overlapping and interlocking.

The **teleost scale** lacks enamel; dentine and vascular bone layer. Only lamellar bone remains, which is acellular and mostly non-calcified. Two kinds of teleost scales are recognized. One is **cycloid scale,** composed of **circuli.** The other is **ctenoid scale** with a fringe of projections along the posterior margin (Fig. 1.7).

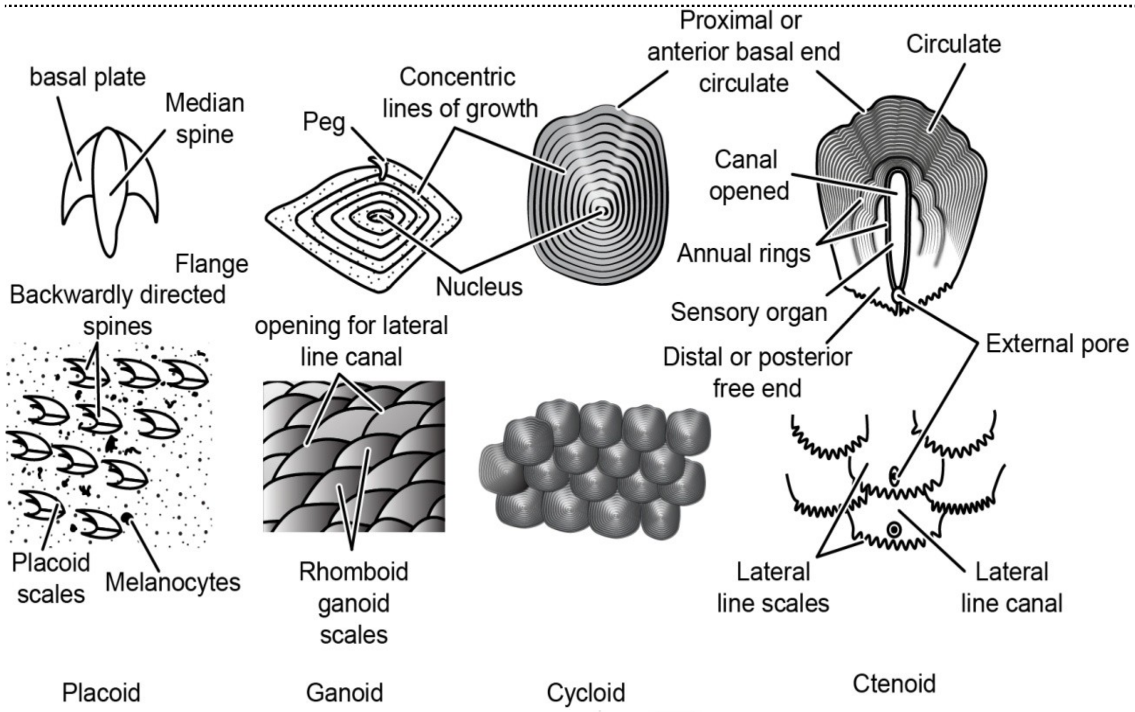


Fig. 1.7: Different types of dermal scales found in fishes. Lower row shows parts of skin with numerous scales. Upper row shows single scales.

SAQ 1

a) Which type of scales are present in cartilaginous fishes?

b) Bony fishes are characterised by which type of scales?

1.4.2 Integument of Tetrapods

Keratinization is a major feature of integument among terrestrial vertebrates. Extensive keratinization produces a prominent outer cornified layer, the stratum corneum, that resists mechanical abrasion. Lipids are often added during the process of keratinization or spread across the surface from specialized glands. The cornified layer along with these lipids increases the resistance of the tetrapod skin to desiccation. Multicellular glands are more common in the skin of tetrapods than in the skin of fishes. In fishes, the mucous cuticle and secretion of the unicellular gland at or near the surface of the skin. In contrast, among tetrapods, multicellular glands usually reside in the dermis and reach the surface through common ducts that pierce the cornified layer.

Amphibians

Amphibians are of special interest because during their lives they usually metamorphose from an aquatic form to a terrestrial form. Phylogenetically, amphibians are also transitional between aquatic and terrestrial vertebrates. The epidermis is composed of several layers of cells and amphibians are the first among the vertebrates to have a dead layer of cells, the stratum corneum. This layer is best developed in amphibians that spend most of their time on land. The dermis is thin, composed of two layers, the outer is loose stratum spongiosum and the inner more compact stratum compactum. Blood vessels, nerves and glands are located in the stratum compactum. In most modern amphibians, the skin is also specialized as a respiratory surface across which gas exchange occurs with the capillary beds in the lower epidermis and deeper dermis. In fact, some salamanders lack lungs and depend entirely on **cutaneous respiration** to meet their metabolic needs.

The most primitive amphibians had scales like the fishes from which they arose. Dermal scales are present only as vestiges in some species of tropical caecilians. Frogs and salmanders lack all traces of dermal scales (Fig. 1.8 a). In salamanders, the skin of the aquatic larvae includes a dermis of fibrous connective tissue. Scattered throughout are large Leydig cells to secrete substances that resist entry of bacteria or viruses. In terrestrial adults, the dermis is similarly composed of fibrous connective tissue. During the breeding season **nuptial pads** may form on digits of limbs of male salamanders or frogs. Nuptial pads are raised calluses of cornified epidermis that help the male hold the female during mating.

Generally, the skin of frogs and salamanders includes two types of multicellular glands, **mucus** and **poison glands** (Fig. 1.8 b). Chromatophores may occasionally be found in amphibian epidermis but most reside in the dermis.

Box 1.1: Poison Arrows and Poison Frogs

The skin of most amphibians contains glands that secrete products that are distasteful or even toxic to predators. In tropical region of the New World live a group of frogs, the poison arrow frogs, with especially toxic secretions. Native people of the region will often gather these frogs, hold them on sticks over a fire to stimulate release of these secretions and then collect the secretions on the tips of their arrows. Game shot with these toxin-laced arrows are quickly tranquilized or killed.

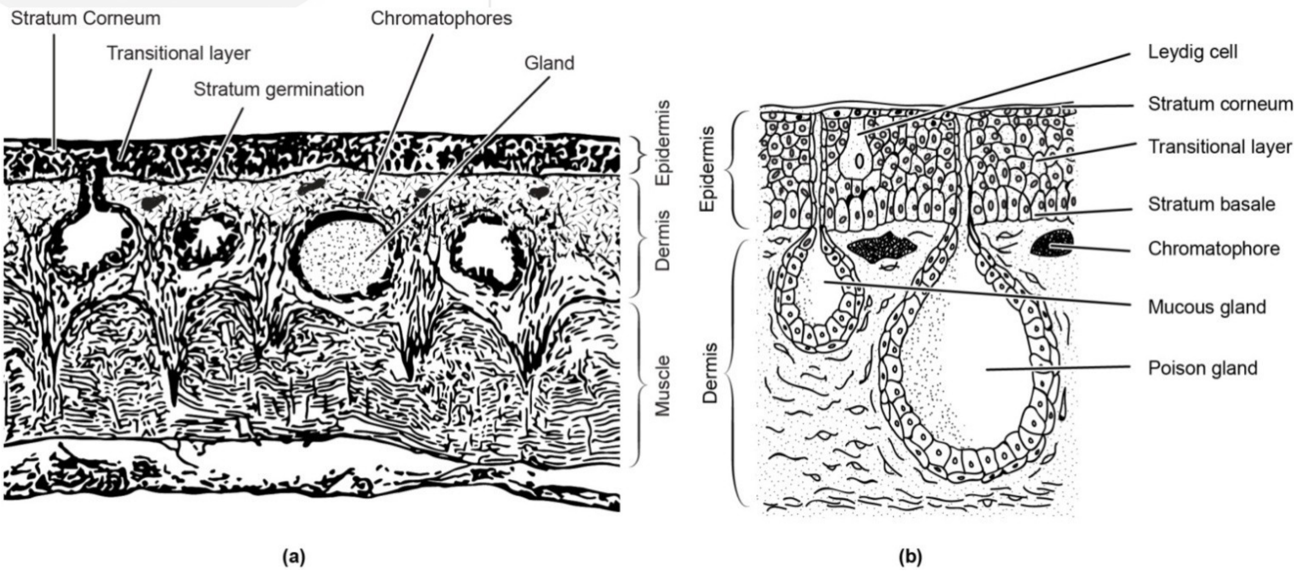


Fig. 1.8: Amphibian skin. a) Section through an adult frog skin. A basal stratum basale and a thin, stratum corneum are present. b) Diagrammatic view of amphibian skin showing mucous and poison glands that empty their secretions through short ducts to the surface of the epidermis.

Reptiles

The skin of reptiles reflects their greater commitment to a terrestrial existence. The epidermis has a well developed stratum corneum. Keratinization is much more extensive, with very few skin glands which is an adaptation to prevent loss of moisture. Horny scales are present, but these are fundamentally different from the dermal scales of fishes, which are built around bone of dermal origin. The reptilian scale usually lacks the bony undersupport or any significant structural contribution from the dermis. Instead it is a fold in the stratum corneum, hence it is an epidermal scale (Fig. 1. 9 a). If the epidermal scale is large and platelike, it is termed **scute**. Additionally, epidermal scales may be modified into crests, spines or hornlike processes.

Dermal bone is present in many reptiles. Where dermal bones support the epidermis, they are called **osteoderms;** plates of dermal bone located under the epidermal scales. Osteoderms are found in crocodilians, and some lizards. The dermis of reptilian skin is composed of fibrous connective tissue. In turtles and crocodiles, sloughing of skin is modest, in comparison to birds and mammals, in whom small flakes fall off at irregular intervals. But in lizards and in snakes, shedding of cornified layer, termed molting or **ecdysis** results in removal of extensive sections of epidermis (Fig. 1.9 b).

Integumental glands of reptiles are restricted to certain areas of the body. Many lizards possess rows of femoral glands along the underside of the hind limb in the thigh region. Crocodiles and turtles have scent glands. Most integumental glands of reptiles play a role in reproductive behavior.

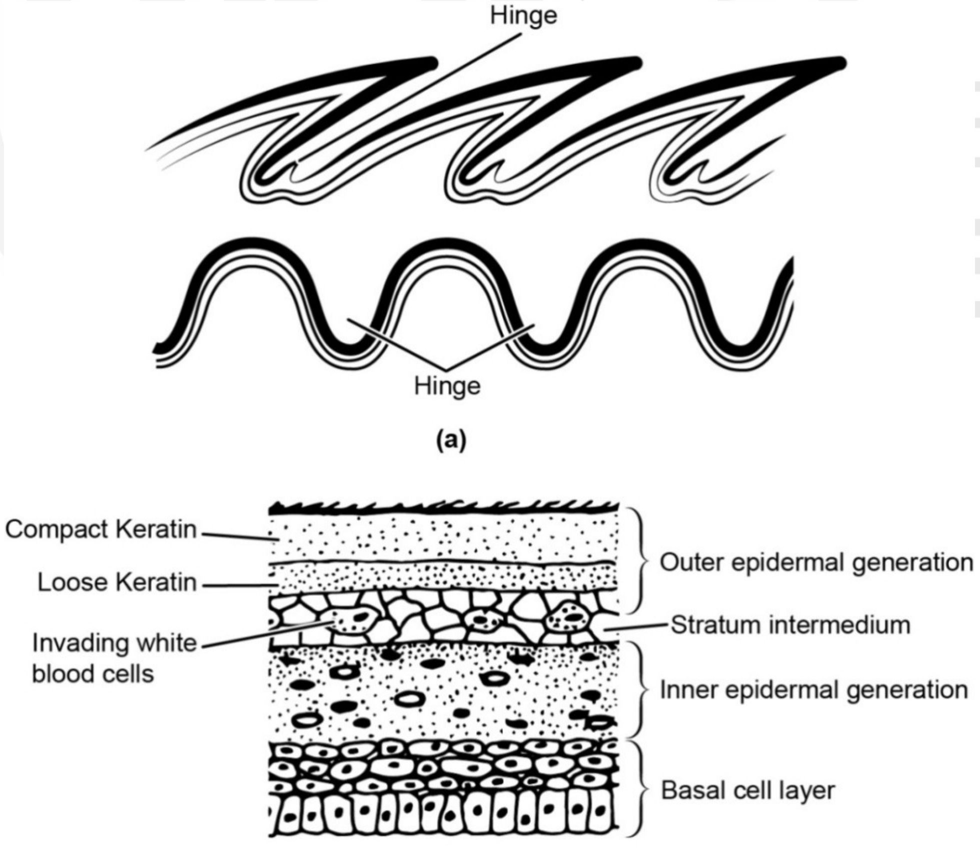


Fig. 1.9: Reptile skin. a) Epidermal skin scales. Extent of projection and overlap of epidermal scales varies among reptiles and even along the body of same individual. b) Section through epidermis of reptilian skin showing ecdysis.

Birds

The feathers of birds have been referred to as 'nothing more than reptilian scales'. This oversimplifies the homology, but probably not much. The dermis of bird skin, especially near the feather follicles, is richly supplied with blood vessels and sensory nerve endings. During brooding the dermis in the breast of some birds becomes vascularized, forming a **brood patch** in which warm blood can come in close association with incubating eggs.

The epidermis comprises the stratum basale and stratum corneum. Between them is the transitional layer of cells that gets transformed into the keratinized surface of stratum corneum (Fig. 1.10 a, b).

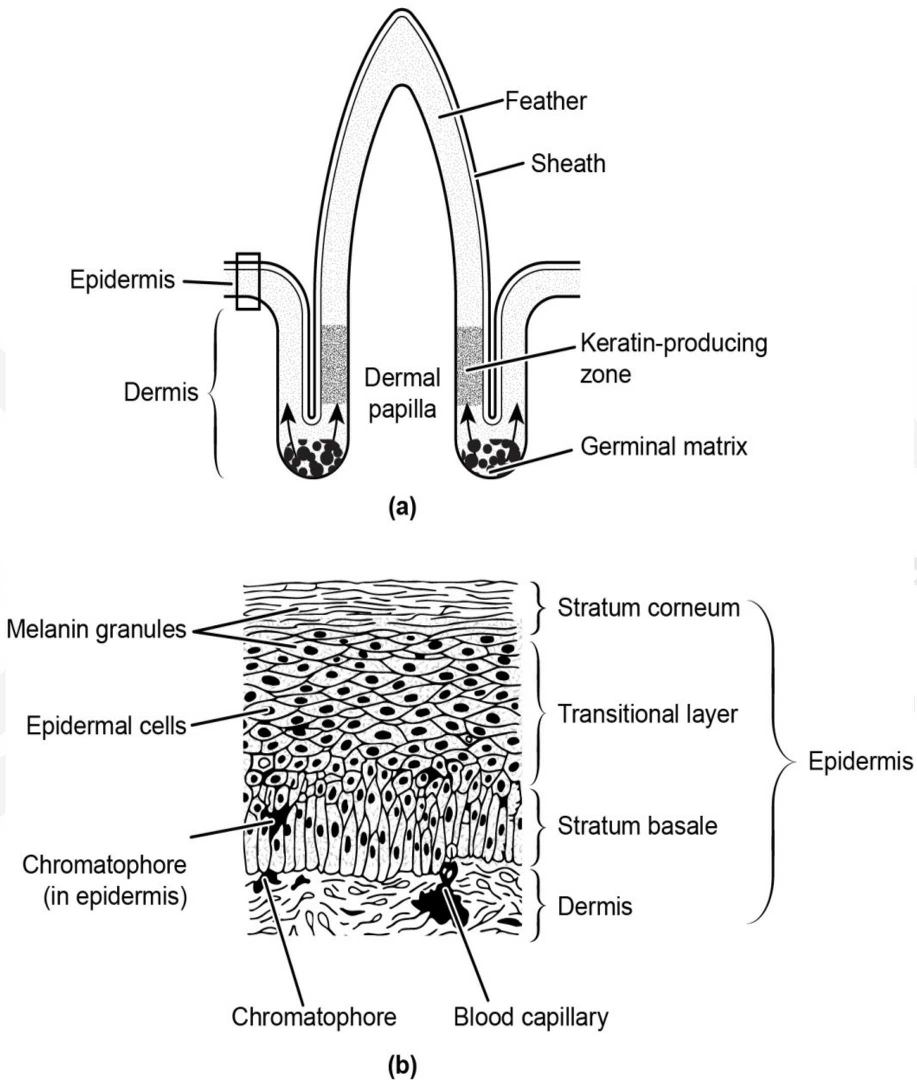


Fig. 1.10: Bird skin. (a) Growth of a feather follicle. The feather forms within a sheath, that is a keratinised derivative of epidermis. (b) Section of skin showing the stratum basale and keratinized surface layer, stratum corneum.

At least one bird has feathers and skin lightly coated with a toxin thought to deter predators. The brightly coloured bird, called a **hooded pitohui**, lives in New Guinea and is about the size of a blue jay. The poison works by repelling snakes, hawks, or other predators tasting one of the feathers. The bright plumage of the pitohui may represent a warning colouration to predators.

Bird skin is devoid of glands except the **uropygial gland,** located at the base of the tail (Fig. 1.11 b) secretes a lipid and protein product that birds collect on the sides of their beak and then smear on their feathers. The other gland located on the head of some birds, **salt gland,** is well developed in marine birds. Salt glands eject excess salt obtained when these birds ingest marine foods and sea water.

Feathers distinguish birds from all other vertebrates. Feathers can be structurally elaborate and come in a variety of forms. Yet feathers are nonvascular and non-nervous products of the skin, principally of the epidermis and the keratinizing system. They are laid out along distinctive tracts, termed pterylae, on the surface of the body (Fig. 1.11 b). Feathers develop embryologically from *feather follicles,* invaginations of the epidermis that dip into the underlying dermis.

The feather itself grows outward in the sheathed case. Within the sheath, the central axis is divided into a distal *rachis* that bears barbs with interlocking connections, termed barbules and a proximal *calamus* that attaches to the body.

There are several types of feathers (Fig. 1.11 b). *Contour feathers* lie close to skin as thermal insulation. *Filopumes* are often specialized for display and *flight feathers* constitute the major aerodynamic surface.

Flight feathers are characterised by a long *rachis* and *prominent vane* (Fig. 1.11 c). Their primary function is locomotion. Most feathers receive sensory stimuli and carry colours for display during courtship. Chromatophores are absent in birds, instead they have only one kind of pigment cells the melanocytes, just like mammals. These occur within the epidermis, and their pigments are carried into the feathers to give them colour.

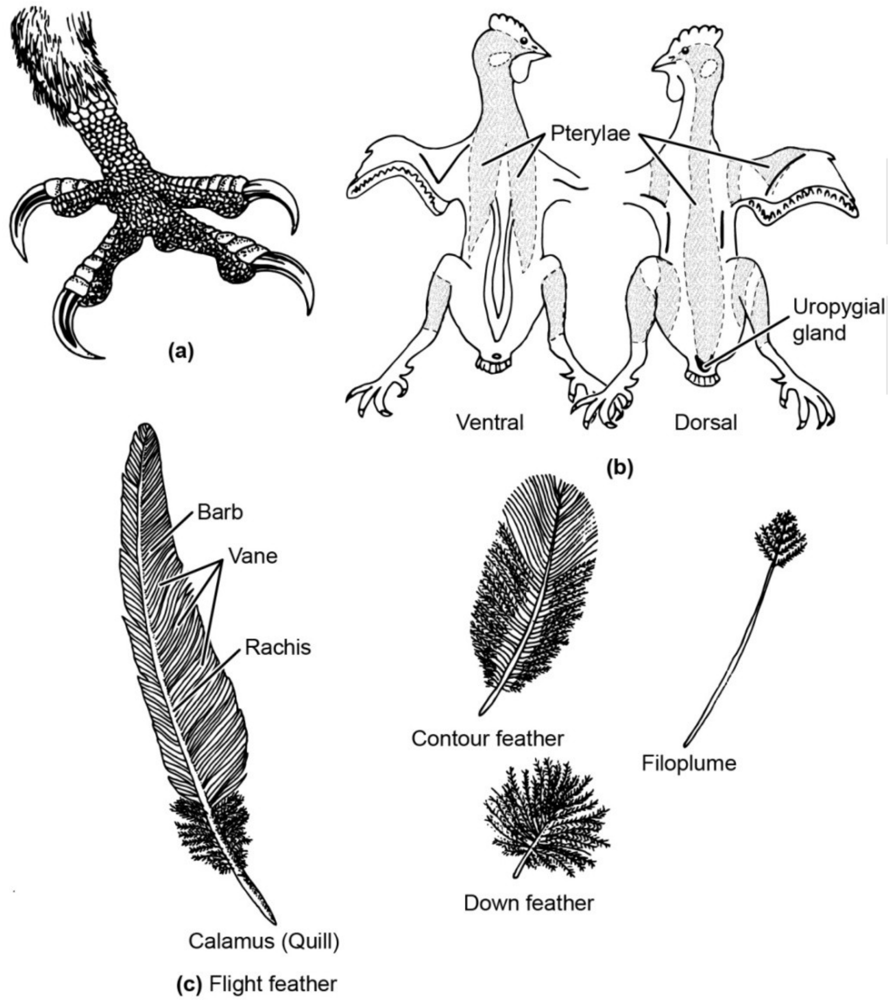


Fig. 1.11: Epidermal derivatives in the bird. (a) Epidermal scales are present on the feet and leg on birds. (b) Feathers arise along specific pteiylae tracts. (c) Feature types.

Mammals

As in other vertebrates, the two main layers of mammalian skin are epidermis and dermis which join and interface through the basement membrane. Beneath the dermis lies the hypodermis, composed of *connective tissue* and fat.

Epidermis

The epidermis may be locally specialized as hair, nails or glands. It is made up of stratified squamous epithelial tissue and has no blood vessels. Normal 'thin skin' has 4-5 layers of epithelial cells. From deep to superficial the layers are: *stratum basale* (also known as stratum germinativum) *stratum spinosum*, *stratum granulosum* and *stratum corneum* (Fig. 1.12). Epithelial cells of the epidermis are keratinocytes except the cells of stratum basale and belong to the keratinizing system that forms the dead superficial cornified layer of the skin. The surface kerantinized cells are replaced by cells arising primarily from the stratum basale cells. Cells within the basale divide mitotically. As they are displaced to higher levels, they pass through keratinization stages.

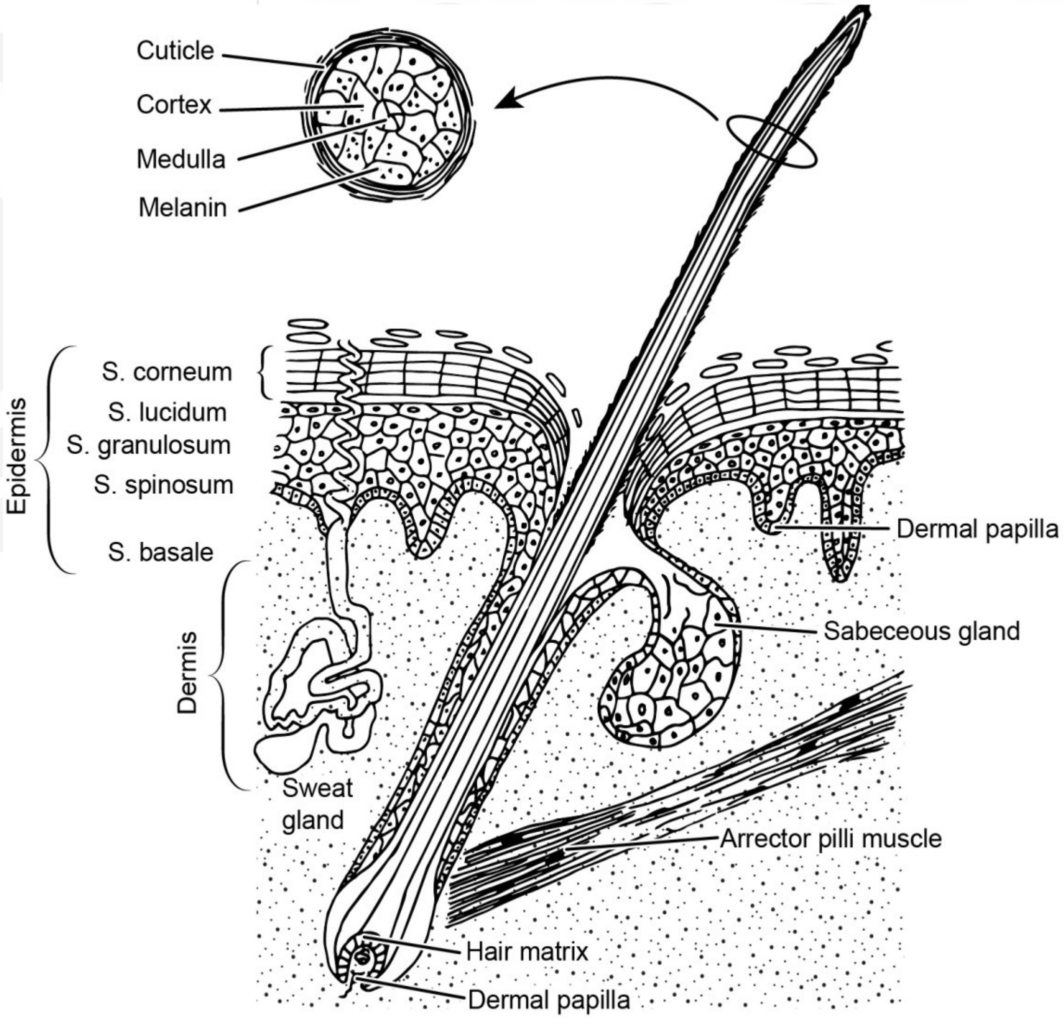


Fig. 1.12: Mammalian skin. The epidermis is differentiated into distinct layers. As in all other vertebrates, the deepest is stratum basale. The dermis pokes up dermal papillae that give the overlying epidermis an undulating appearance. Sweat glands, hair follicles and sensory receptors lie within the dermis.

The process of keratinization is most distinct in the regions of the body where the skin is thickest: as in the soles of the feet and palms. Elsewhere, these layers may be less apparent. Stratum corneum protects the delicate underlying cells of the epidermis from microbes, abrasions and water loss.

Though keratinocytes are the most prominent cell types of the epidermis, other cells are recognised although their functions are less clearly known. The *Langerhans Cells* are stellate cells dispersed throughout the upper part of stratum spinosum. These cells play a role in cell mediated action of immune system. The *Merkel cells*, originating from neural crest and associated with nearby sensory nerves, respond to stimulation that the brain perceives as touch. Merkel cells are more abundant in hands and feet. *Melanocytes* arise from embryonic neural crest cells. These secrete granules of the pigment *melanin,* which are passed directly to epithelial cells. Melanin imparts hair and skin its colour (Skin colour arises from a combination of yellow *stratum corneum,* the red underlying blood vessels and dark pigment granules secreted by melanocytes).

Dermis

The mammalian dermis is double layered. The outer *papillary layer* pushes finger like projections, called *dermal papillae* into the overlying epidermis. Dermal papillae increase the strength of the epidermis-dermis connection they also contain blood vessels, receptors, some adipocytes and phagocytes. The deeper *reticular* layer includes irregularly arranged fibres, connective tissue, blood vessels; nerves and smooth muscles occupy the dermis but do not reach the epidermis. The mammalian dermis produces dermal bones, but these contribute to the skull and pectoral girdle and rarely form dermal scales in the skin.

Hair follicles and glands project inward from the epidermis (Fig. 1. 12). The dermis is usually composed of irregularly arranged fibrous connective tissue that is often impregnated with elastic fibres to give it some stretch but return it to its original shape. As a person ages, this elasticity is lost and the skin sags.

Hypodermis

Mammalian skin has another layer below the dermis; the hypodermis. It is made up of loose connective tissue, adipose tissue and skeletal muscles. The adipose tissue stores fat which gives a cushion for the internal organs. The skeletal muscles move the skin to some extent.

Hair

Hair are slender, keratinous filaments. The base of a hair is the root. Its remaining length, constitutes the *shaft*. The outer surface of the shaft often forms a *cuticle.* Beneath this is the *hair cortex* and at its core is the *hair medulla* (Fig. 1.12).

The hair shaft projects above the surface of the skin but it is produced within an epidermal hair follicle rooted in the dermis.

At its expanded base the follicle receives a small tuft of the dermis, *hair papilla.* Melanocytes in the follicle contribute pigment granules to the hair shaft to give it further colour. The *arrector pili* muscle, a thin band of smooth muscle anchored in the dermis, is attached to the follicle and makes the hair stand erect in response to cold, fear or anger.

Some hair are specialized. Sensitive nerves are associated with the roots of *vibrissae* or *whiskers* around the snouts of many mammals. These are common in nocturnal mammals and in mammals that live in burrows with limited light. The quills of porcupines are stiff, coarse hairs specialized for defense.

Glands

Principally, there are two main types of glands in mammals, *sebaceous* and *sweat* glands. Derived from them are *scent* and *mammary glands.*

The *sebaceous glands* are present all over the body and produce an oily secretion *sebum,* that is released on the skin and mostly into hair follicles in order to condition and help waterproof fur. Sebaceous glands are absent from the palms of hands and soles of feet, but they are present without associated hair, at the angle of the mouth, on the penis, near vagina and next to mammary nipples The *wax glands* of outer ear canal, which secrete ear wax and *Meibomian glands* of the eye lid, which secrete on oily film over the surface of the eye ball are modified sebaceous glands.

The *sweat glands* produce a watery product called perspiration or *sweat.* Two types are usually recognized by the viscosity of their secretion (viscous or thin), by their association (with or without hair follicles) and by their functional onset (at puberty or before). One type called eccrine sweat gland produces thin sweat, and is found all over the body and more abundant on the palms, feet and forehead. It is not associated with hair follicles. It is a coiled gland present deep in the dermis and its mouth opens on the surface of epidermis. Its products are mostly water with some salt, antibodies, antimicrobial peptides and traces of metabolic waste; function in regulation of body temperature. The other apocrine sweat gland produces viscous sweat, is associated with hair follicles, and begins functioning at puberty. Apart from water and salt it secretes organic compounds that are decomposed by bacteria and this is responsible for body odor.

Sweat glands are not found in all mammals, and their distribution varies. Chimpanzees and human have the greatest number of sweat glands, including some on the palms and soles. In the duckbill platypus, sweat glands are limited to the snout. In deer, they are present at the base of tail. In elephants, sweat and sebaceous glands are absent entirely.

The *scent glands* are derived from sweat glands and produce secretions that play a part in social communication. Secretions of these glands are used to mark territory, identify the individual and communicate during courtship.

The *mammary glands* are also thought to be derived from sweat glands or perhaps from sebaceous glands. Functional only in the female, they produce milk and watery mixture of fats, carbohydrates and proteins that nourish the young. The number of mammary glands varies among species. Release of milk to suckling is *lactation.* Mammary glands consist of numerous lobules. Each lobule is a cluster of secretary alveoli in which milk is produced. The alveoli open into a common duct that, in turn, opens to the surface through a raised epidermal papilla or *nipple*. The nipple is surrounded by circular pigmented area of skin called *aerola.* Alveolar ducts open into a common chamber or cistern within a long collar of epidermis called *teat* (1.13 a, c). Adipose tissue can build up beneath the mammary glands to produce *breasts*.

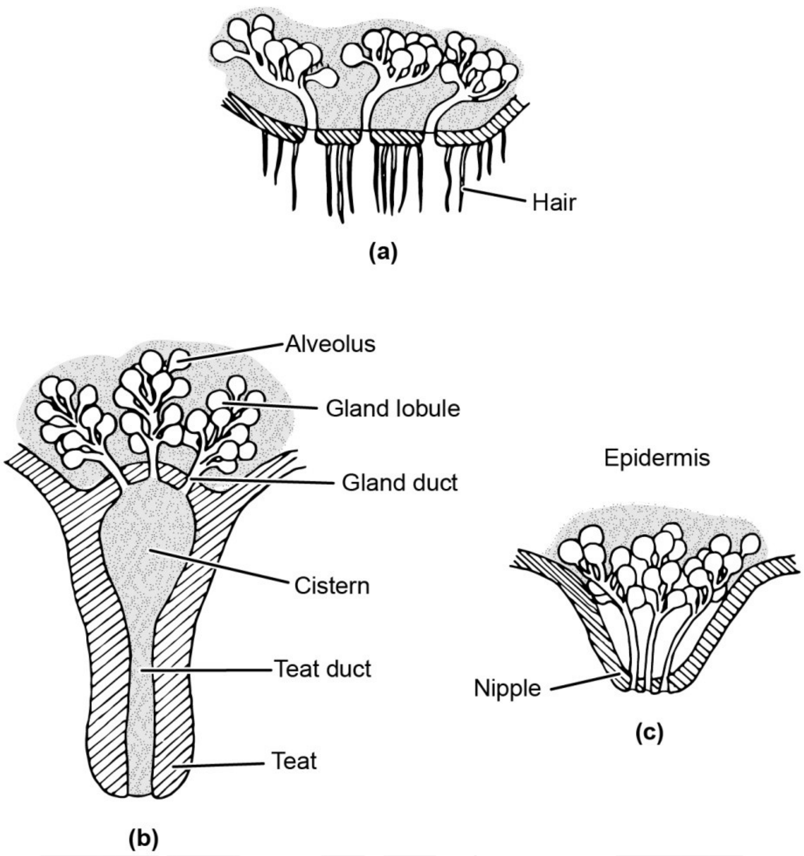


Fig. 1.13: Mammary glands. a) In monotremes, the mammary glands open to the unspecialized skin surface, and the young press their snout to skin where these glands open. b) In some marsupials, the mammary ducts open through specializations of the integument, c) The nipple is a raised epidermal papilla around which the supple lips of the infant fit to drink the milk.

In *monotremes, nipples* and *teats* are absent and breasts do not form. Milk is released from ducts into the flattened milk patch or aerola on the surface of the skin (Fig. 1.14 a). The point of infant's snout is shaped to fit the surface, permitting vigorous sucking. At sexual maturity adipose tissue builds up under the mammary glands to produce breast from which milk is released. In common language, this is termed *let down*.

SAQ 2

Fill in the blanks.

a) Dermal bones are most prominent in ……………….. .

b) In fishes and aquatic vertebrates, collagen fibres of the dermis are arranged to form ……………….. layer of the integument.

c) In terrestrial vertebrates, the epidermis covering the body often forms a keratinized layer called as ………………… .

d) Epidermal fold, in the form of thickened keratinized layer produces …………………… .

e) *Stratum basale,* the deepest layer of epidermis rests upon……………… .

SAQ 3

Match the following:

i)	Femoral glands	a)	Birds
ii)	Uropygial glands	b)	Crocodiles
iii)	Scent glands	c)	Lizards
iv)	Mammary glands	d)	Eye lids of mammals
v)	Meibomian glands	e)	Female mammals
vi)	Sebaceous glands	f)	Mammals

SAQ 4

Answer the following in one or two words:

a) Two types of cells present within the epidermis of fishes.

b) Surface denticles present in chondrichthyes.

c) Scales, characterized by prevalence of thick enamel, present in bony fishes.

d) Skin is specialized as a respiratory surface in these tetrapods.

e) In these reptiles, osteoderms are found.

f) The presence of major structure which distinguishes birds from all other vertebrates.

SAQ 5

a) Which are the four successive layers present in the integument of mammals?

b) Which muscle is attached to the hair follicle of human beings and makes hair stand erect?

1.5 SPECIALISED DERIVATIVES OF THE INTEGUMENT

Up to now you have studied comparative account of vertebrate skin. Let us now look at the special derivatives of skin in different vertebrates.

1.5.1 Nails, Claws, Hooves

Nails are plates of tightly compacted, cornified epithelial cells on the surface of fingers and toes, thus, they are products of the keratinizing system of the skin. The nail matrix forms new nail at the nail base by pushing the existing nail forward to replace that worn or broken at the free edge. Nails protect the tips of digits from inadvertent mechanical injury. They also help stabilize the skin at the tips of the fingers and toes, so that on the opposite side the skin can establish a secure friction grip on objects grasped.

Only primates have nails (Fig. 1.14 a). In other vertebrates, the keratinizing system at the terminus of each digit produces claws or hooves (Fig. 1.14 b, c). *Claws* or *talons* are curved, laterally compressed keratinized projections from the tips of digits. They are seen in some amphibians and in most birds, reptiles and mammals. *Hooves* are large keratinized plates on the tips of the ungulate digits.

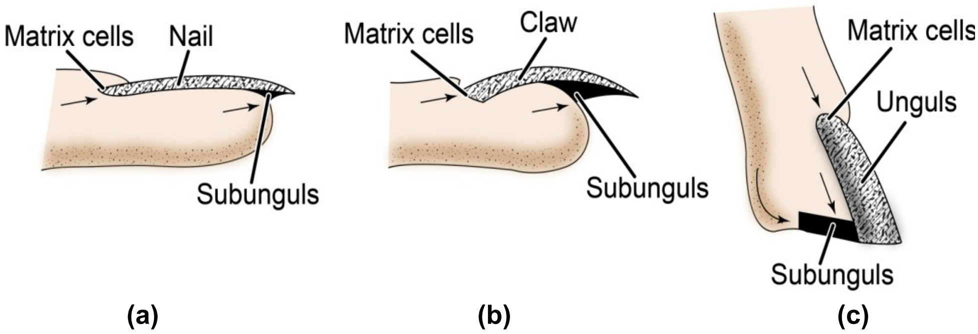


Fig. 1.14: Epidermal derivatives. (a) The nail is a plate of cornified epithelium growing outward (arrows) from proliferating matrix cells at its base and from subunguis. (b) Claw (c) Hoof.

1.5.2 Horns and Antlers

Horned lizards have processes extending from behind the head that look like horns but are specialized, pointed epidermal scales. Mammals are the only vertebrates with true horns or antlers.

The skin, together with the underlying bone contributes to both true horns and antlers. As these structures take shape, the underlying bone rises up, carrying the overlying integument with it. In horns, the associated integument produces a tough, cornified sheath that fits over the bony core (Fig. 1.15 a). In antlers, the overlying living skin (called 'velvet') apparently shapes and provides vascular supply to the growing bone. Eventually the velvet falls away to unsheathe the base bone, the actual material of the finished antlers (Fig. 1.15 b).

True antlers occur only in members of the *Cervidae* (e.g. deer, elk, moose). Typically, only males have antlers, which are branched and shed annually. There are notable exceptions. In deer, the antler usually consists of a main beam from which branch shorter points.

The annual cycle of antler growth and loss in the white-tail deer for example, is under hormonal control. In spring, increasing length of daylight stimulates the pituitary gland to release hormones that stimulate antlers to sprout from sites on the skull bones. By late spring, the growing antlers are covered by velvet. By fall, hormones produced by the testes inhibit the pituitary and the velvet dries.

Among mammals, true horns are found among members of the family Bovidae (e.g. cattle, antelope, sheep, goats, bison). Commonly horns occur both in males and females, are retained year round, and continue to grow throughout the life of the individual. The horn is unbranched and formed of a bony core and a keratinized sheath.

Unlike true horns of bovids, horns of the pronghorn, family Antilocapridae, are forked in adult males. The rhino horn does not include a bony core, so it is exclusively a product of the integument. It forms from compacted keratinous fibres.

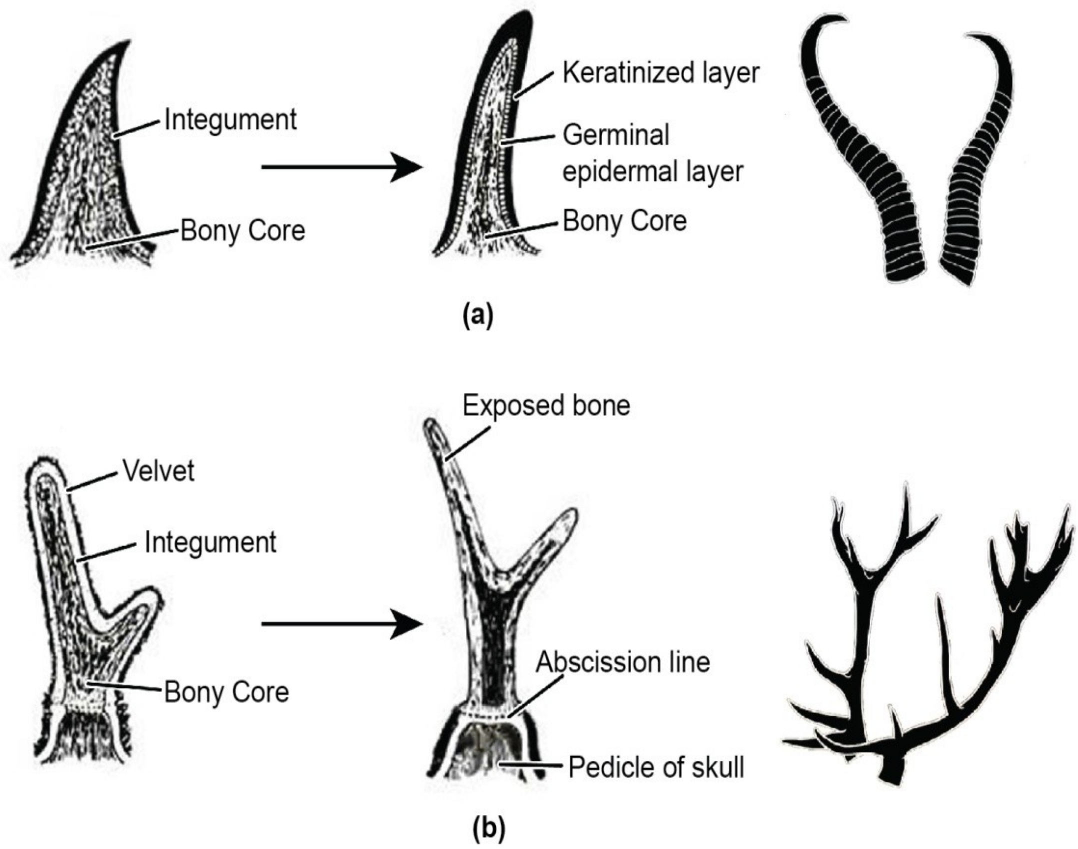


Fig. 1.15: Horns and Antlers. a) Horns appear as outgrowth of skull beneath the integument, which forms a keratinized sheath. b) Antlers also appeal as outgrowth of the skull beneath the overlying integument, which is referred to as 'velvet' because of its appearance.

1.5.3 Baleen

The integument within the mouths of Mysticete whales forms plates of *baleen* that act as strainers to extract krill from water gulped in the distended mouth. Although, it is sometimes referred to as "whalebone", baleen contains no bone. It is a series of keratinized plates that arise from the integument. During its formation, groups of dermal papillae extend and lengthen outward, carrying the overlying epidermis. The epidermis forms a cornified layer over the surface of these projecting papillae. Collectively, these papillae and their covering of epidermis constitute the plates of baleen (Fig. 1.16).

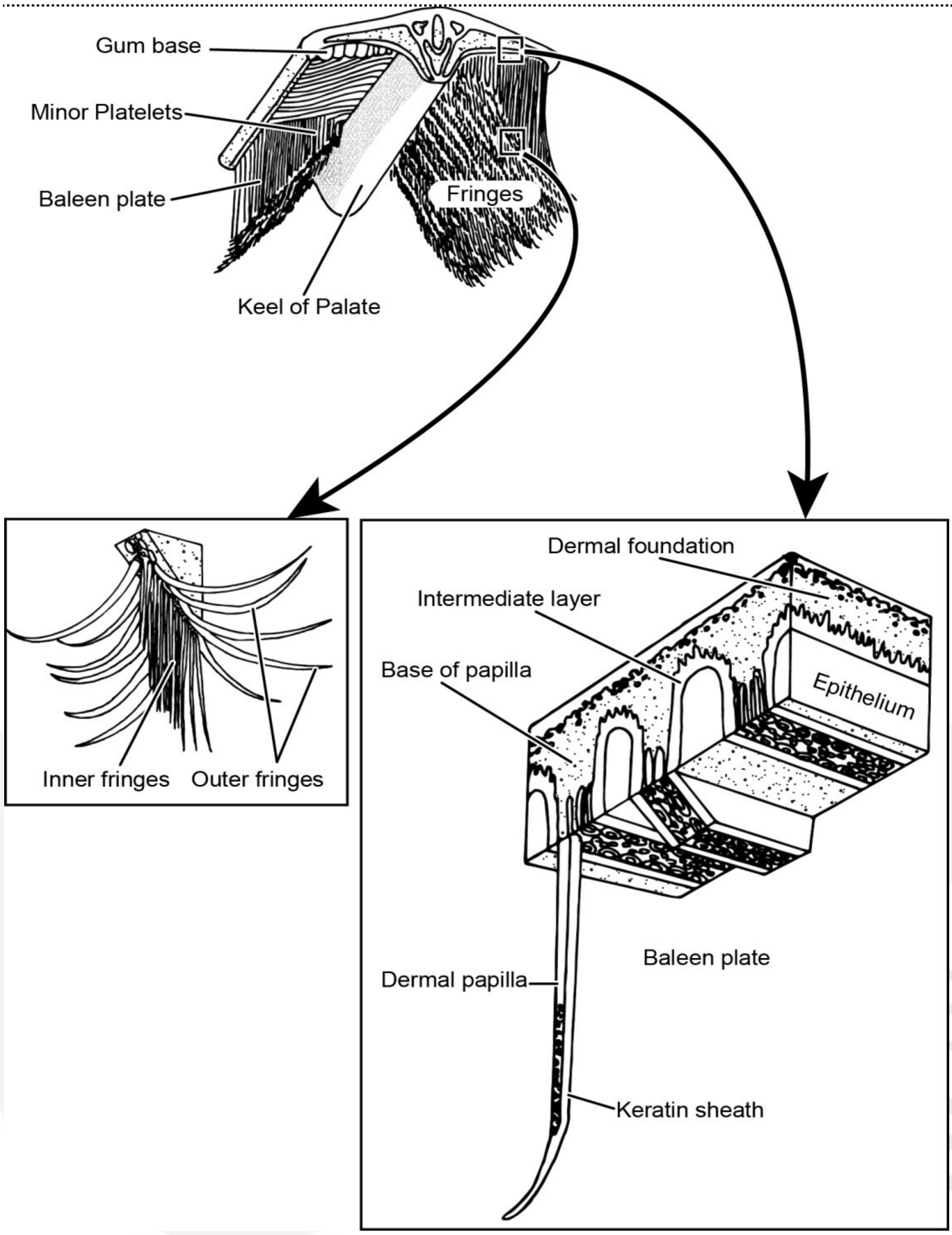


Fig. 1.16: Baleen from a whale. The lining to the mouth includes an epithelium with the ability to form keratinized structures. Groups of outgrowing epithelium become keratinized and frilly to form the baleen.

1.5.4 Scales

Scales have many functions. Both epidermal and dermal scales are hard, so when they receive mechanical insult and surface abrasion, they prevent damage to soft tissues beneath. The density of scales also makes them a barrier against invasion of foreign pathogens, and they retard water loss from the body. In sharks and fishes, scales dampen the boundary layer turbulence to increase swimming efficiency. Some reptiles regulate the amount of surface heat they absorb by turning their bodies forward or away from the sun.

1.5.5 Dermal Armor

Dermal bone forms the armor of ostracoderm and placoderm fishes. Being a product of the dermis, dermal bone has a great variety of structures. Dermal bone supports the scales of bony fishes but tends to be lost in tetrapods. It is absent in the skin of birds and most mammals. Exceptions have been noted earlier, namely, in the fossil mammal *Glyptodon* and in the skin of the living, armadillo. However, selected dermal bones take up residence in the fish skull and pectoral girdle.

The shell of turtles is a composite structure. The dorsal half of the shell is the *carapace* formed by fusion of dermal bone with expanded ribs and vertebrae. Ventrally the *plastron* represents fused dermal bones along the belly. On the surface of both carapace and plastron, keratinized plates of epidermis cover this underlying bone.

1.5.6 Mucus

Mucus produced by the skin serves several functions. In aquatic vertebrates, it inhibits entrance of pathogens and may even have slight antibacterial action. In terrestrial amphibians, mucus keeps the integument moist, allowing it to function in gas exchange. Although cutaneous respiration is prominent in amphibians, it occurs in many other vertebrates as well. For example, many turtles rely on cutaneous gas exchange as they hibernate submerged in ice-covered ponds during winter. Sea snakes may depend on cutaneous respiration for up to 30 per cent of their oxygen uptake. Similarly fishes such as the plaice, European eel and mudskipper may depend on some cutaneous gas exchange to meet their metabolic requirement.

Mucus is also involved in aquatic locomotion. As a surface coat, it smoothes the irregularities and rough surface features on the epidermis to reduce the friction met by a vertebrate swimming through relatively viscous water.

1.5.7 Colour

Skin colour results from complex interactions between physical, chemical and structural properties of the integument. Changes in blood supply can redden the skin, as in blushing in humans. The *differential scattering* of the light, referred to as *Tyndall scattering,* is the basis of much colour is nature. This is the phenomenon that makes the clear day sky appear blue. In birds, air-filled cavities within feather barbs take advantage of this scattering phenomenon to produce blue feathers of kingfishers, blue jays, and bluebirds. Many black, brown, red, orange and yellow colours result from pigments. Pigments produce colour by selective light reflection. Interference phenomena are responsible for iridescent colours.

Many of the pigments, producing colours by this variety of physical phenomena are synthesized by and held in specialized dermal cells termed chromatophores that arise from embryonic neural crest. They are responsible for generating skin and eye colour in ectotherms. On the basis of form, composition and function, four groups of chromatophores are currently recognized. The most well known of these is the melanophore that contains the pigment melanin which appears black or brown and is packaged in vesicles called melanosomes, these are distributed throughout the cell.

A second type of chromatophore is the *iridophore* which contains light reflecting, crystalline guanine plates. It is found in ectothermic vertebrates and in the iris of the eye of some birds. When illuminated by light the plates reflect the light producing iridescence. Two other types of chromatophores are the *xanthophores,* containing yellow pigments and the *erythrophore,* so called because of the red pigments. Sometimes both these pigments are found in the same cell and their ratio gives the overall colour.

Endotherms (birds and mammals) have only one class of pigment cells the melanocytes that are equivalent to the melanophores of ectotherms, to generate the skin and eye colour. You have read in the earlier sub section that melanocytes are present in the stratum basale of the epidermis and produce melanin that is built up in the keratinocytes giving the skin colour.

Sunlight can influence physiological changes in chromatophore activity. Increased exposure stimulates increased production of pigment granules, resulting in darker skin in humans over a period of days.

SAQ 6

a) Which pigment in human beings causes skin colouration?

b) Though misleadingly referred to as 'whale-bone', it contains no bone. What is it?

1.6 SUMMARY

- Integument is a composite organ. Fundamentally it is composed of epidermis, and dermis, separated by the basement membrane. It protects the animal from injury, microbes, water loss and regulates the body temperature.
- The epidermis is the outer layer of epithelial tissue and is several layers thick. The epidermis of terrestrial vertebrates forms keratinized layer, called as stratum corneum. The dermis is made up of connective tissue and in many vertebrates produces dermal bones, which is prominently seen in bony fishes.
- Living agnathans do not have scales but many mucous secreting glands in their skin while cartilaginous and bony fishes have protective scales derived from the integument.
- In cartiliginous fishes, placoid *scales* are present. Bony fishes are characterised by cosmoid *scales* and ganoid *scales.* Teleosts are characterised by two types of scales: cycloid scales and ctenoid scales.
- Skin of amphibians is specialized for respiration i.e. *cutaneous respiration. Mucous glands* and *poison glands in the dermis* are main characteristics of amphibians. Chromatophores may occasionally be found in the amphibian dermis.
- In reptiles keratinization is much more extensive. Integumental glands of reptiles are restricted to certain areas of the body. Many lizards possess *femoral glands* in the thighs. Crocodiles and turtles have *scent glands.*

- Feathers originating from dermis distinguish birds from all other vertebrates. Bird skin has no glands except *uropygial glands* at the base of tail and *salt gland* on the head.
- The epidermis of mammals is specialized as *hair, nails or glands.* Keratinocytes are the most prominent cell types of epidermis. Skin colour of mammals is due to pigment *melanin.* Principally there are two main types of glands in mammals i.e. *sebaceous* and *sweat glands.* Derived from them are *scent* and *mammary* glands.
- Baleen, claws, hooves, horns, antlers and dermal armor are specialized derivatives of the integument.

1.7 TERMINAL QUESTIONS

1. What is the difference between cycloid scale and ctenoid scale of teleosts?
2. Write two important differences between scales of reptiles and fishes.
3. What are the different types of feathers? What are their functions?
4. What is the function of sebaceous glands? Write the various types of sebaceous glands present in mammals.
5. Explain keratinization in terrestrial vertebrates.

1.8 ANSWERS

Self-Assessment Questions

1. a) Placoid scales

   b) Cosmoid and Ganoid scales.

2. a) ostracodem fishes

   b) *stratum compactum*

   c) *stratum corneum*

   d) epidermal scale

   e) basement membrane

3. i) c ii) a iii) b iv) e v) d vi) f.

4. a) epidermal cells and unicellular glands

   b) placoid scales

   c) ganoid scales

   d) amphibians

   e) crocodiles and some lizards

   f) feathers

5. a) i) *stratum spinosum*

   ii) *stratum granulosum*

   iii) *stratum lucidum*

   iv) *stratum corneum*

   b) Arrector pili.

6. a) Melanin, b) Baleen.

Terminal Questions

1. Cycloid scale is composed of concentric rings or **circuli** and ctenoid scale has a fringe of projections along its posterior margin.

2. The scales of fishes are of dermal origin. But reptilian scales lack bony undersupport or any significant structural contribution from the dermis. It is a fold in the surface epidermis.

3. There are four main types of feathers in birds: Contour feathers, down feathers, filoplumes and flight feathers. Contour feathers aerodynamically shape the surface of the bird. Down feathers lie close to the skin as thermal insulation. Filoplumes are often specialized for display and flight feathers constitute the major aerodynamic surface.

4. Sebaceous glands produce an oily secretion called sebum. The **wax glands** of outer ear canal, which secrete wax and **meibomian glands** of eyelid, which secrete an oily film on the surface of eyeball are derived from sebaceous glands.

5. Keratinocytes of epidermis form the dead, superficial cornified layer of the skin. The surface of keratinized cells are continually exfoliated and replaced by cells of stratum corneum.

Acknowledgement of Figures

Fig. 1.3: Source: General Biological Supply House

UNIT 2

Skeletal System

Structure

2.1 INTRODUCTION

In the previous unit you have studied about the integumentary system which forms the outer most protective covering of the body. In the present unit we shall discuss the skeletal system which provides strength and definite shape to the body of the vertebrates. You have already studied about soft-bodied animals in the core course BZYCT-131 (Animal Diversity). As you will recall the soft bodied animals can bend and twist their bodies as they like it. They can wriggle through burrows and crevices to avoid obstacles. At the beginning of evolution of life this ability appeared to be an advantage. But it is not always so. It puts a restriction on size because large soft bodies are difficult to manage. A large body needs support to prevent it from collapsing. The supporting structure needs to be hard, as only then can it provide a definite shape to the animal and also help protect the soft vital parts of the body. The supporting structure should also be helpful in locomotion. Locomotion as you know is brought about by the movement of the body due to contractions and expansions of muscles, the contractile tissue. Muscles need to be attached to hard surfaces to assist in contractions. In nonchordate animal as you will recall all these needs were fulfilled by the development of an external covering in the form of a chitinous hard structure as seen in arthropods or formation of a calcareous shell as in molluscs. In vertebrates, the bone or cartilage or both are present within the body in order to provide protection, support and locomotion to the body. Both the bone and cartilage are formed of connective tissue. This supporting structure of shell or chitin or cartilage or bone is called skeleton.

Generally there are two types of skeletons in animals; (a) the **exoskeleton** found on the outside of the body and (b) the **endoskeleton** found within the body of the animal. Vertebrates possess an endoskeleton which is formed of connective, living tissue that is mesodermal in origin and grows with the animal. It helps to hold the soft parts of the animal together and serves as a mechanical framework for the animal body giving it distinct shape and rigidity. It also provides a hard surface for the attachment of muscles and protects the vital internal organs of the body. In this unit we will study the composition and general structure of endoskeleton of vertebrates which in them is formed of connective tissue. We will also compare the skeleton of two vertebrates, an amphibian (an anamniote) and a mammal (amniote) which will help us understand the changes that have occurred in the skeleton of vertebrates during the course of evolution.

Objectives

After studying this unit, you should be able to:

- explain the advantages of endoskeleton of vertebrates,
- give the differences between the cartilage and the bone,
- describe the typical skeleton of a vertebrate, and
- describe the differences between the skeleton of frog and rabbit.

2.2 CARTILAGE AND BONE

The vertebrate endoskeleton is composed of two different types of supportive connective tissue, the **cartilage** and the **bone**. Cartilage is a relatively soft elastic connective tissue, whereas bone is a more ossified hard rigid connective tissue. Both the cartilage and the bone consist of non-living, ground substance, called matrix in which living cells are present.

Cartilage which is believed to have appearded first during embryonic development in vertebrates is later replaced by bone. However, in elasmobranch fishes and cyclostomes the complete skeleton is made only of cartilage, though the skeleton of a majority of vertebrates is bony. The matrix of cartilage contains elastic or tough white fibres. The protein found in cartilage is **chondrin** and the living cartilage cells are called **chondrioblasts.** There are no blood vessels or nerves in cartilage. Nutrients are diffused within the matrix and therefore, the cartilage is seldom thick (Fig. 2.1).

The matrix of the bones contains a protein called **collagen** that provides the surface on which the inorganic salts can adhere. These inorganic salts are formed when **calcium phosphate and calcium carbonates** combine to form **calcium hypoxyapatite** that gives the bone its hardness. The collagen on the other hand gives flexibility so that the bones are not brittle. Compact bone is composed of calcified bone matrix, arranged in concentric rings. The rings contain cavities (lacunae) filled with bone cells (**osteocytes**) which are interconnected by many minute passages called **canaliculi**. The **canaliculi** serve to distribute nutrients throughout the bone. This entire organisation of lacunae and canaliculi is arranged into an elongated cylinder called an **osteon** and also called the **Haversian system** (Fig. 2.2).

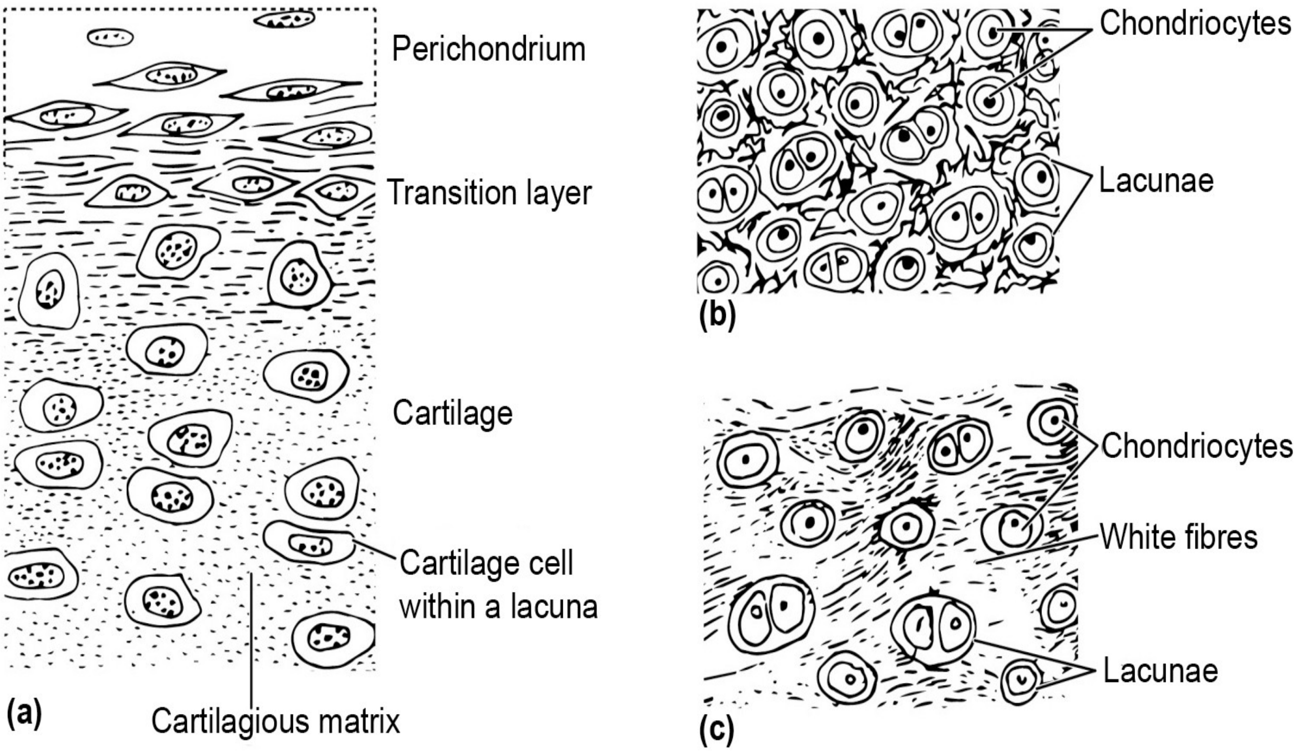


Fig. 2.1: (a) Section through a piece of hyaline cartilage, adjacent to the connective tissue perichondrium. Cartilage of this type would be found in joints and the rings of the trachea; (b) elastic cartilage; (c) Fibro cartilage which is found in the pubic symphysis.

The bone secreting cells are called **osteoblasts**. These do not divide but secrete collagen and calcium salts, and as the secreted matrix surrounds the cells, they get entrapped into it and the nature of the cells changes. They are then called **osteocytes** (see Fig. 2.2c).

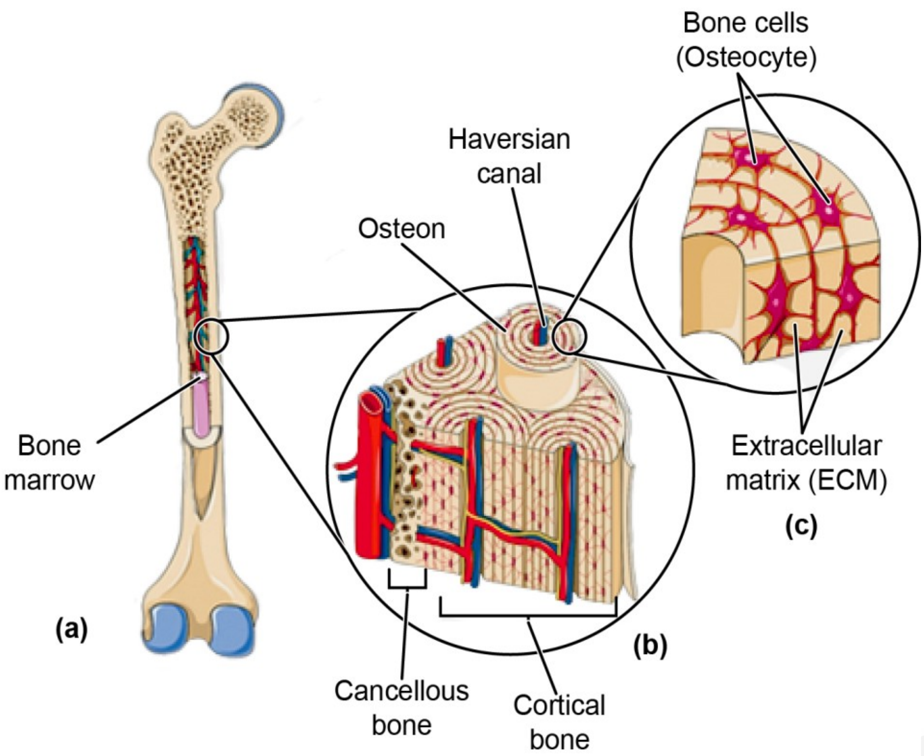


Fig. 2.2: Bone structure. (A) Adult long bone. (B) Enlarged section showing how bone cells and the dense calcified matrix are arranged in units called osteons.

There are two types of bones based on the manner of their formation during embryonic development. (i) Bones may be formed by ossification of the pre-existing cartilage which are then called **cartilage bones or replacment bones** because they replace the pre-existing cartilages. This type of ossification is known as **endochondral ossification** because the cartilage itself does not become a bone but serves as a template to be completely replaced by bone. The long bones (vertebrae, ribs and limb) and the bones at the base of the skull are formed by endochondral ossification. (ii) In the second type of formation of bones, the bones are formed afresh at places from membranes coverings. They are called **membrane bones** as they develop directly from sheets of mesenchymal tissue. They are also called **investing bones** because they form as an investment over the membranes. The flat bones of the face, most of the cranial bones and the collar bone (clavicle) are formed by this intramembranous ossification.

SAQ 1

Give one word answer for each:

i) Name the protein found in the matrix of the bone and in cartilage.

ii) Which type of cells do the osteoblasts cells change into when they are trapped in the bone matrix?

iii) What is the principal structure of compact bone known as?

iv) The long bones of the body are formed by which kind of ossification?

2.3 CLASSIFICATION OF SKELETON

The endoskeleton of vertebrates is divided into two main parts based on their position in the body.

a) **The Axial Skeleton:** is arranged along the anteroposterior axis of the body. It consists of the skull (head skeleton) and the vertebral column. The sternum, called the breast bone is also included in the axial skeleton.

b) **The Appendicular Skeleton:** is located on the sides of the body as appendages of the axial skeleton. It includes the skeleton of the limbs and the limb girdles.

2.3.1 Axial Skeleton

The skeletal elements of the axial skeleton consist of skull and the vertebral column. They surround and protect the structures of the central nervous system, the brain and the spinal cord. The skull is enlarged and specialised to enclose the brain and the sense organs present in the head. The vertebral column forms the longitudinal skeletal axis of the body behind the head. It encloses the spinal cord and blood vessels of the trunk and the tail that go through it.

The Skull

The skull also called cephalic skeleton or head skeleton forms the skeletal framework of the head of craniate vertebrates. Vertebrates are divided, on the basis of presence or absence of head skeleton into two sub-divisions. Those vertebrates in which head skeleton is absent are called **Acraniata** and those in which head skeleton is present are called as **Craniata**. Urochordates and cephalochordates belong to Acraniata and the rest of the vertebrates are grouped under **Craniata**.

The skull of craniate (with skull) vertebrates consists of different parts which enclose the brain, cranial nerves and other sense organs present in the head. The part of the skull, enclosing the brain is called the **cranium** and is composed of several bones. The parts of the skull enclosing the sense organs are called **sensory capsules**. Thus the **paired auditory capsules** enclose the hearing apparatus, the paired **olfactory capsules** enclose the apparatus of smell and the paired bony, cup-like structures the **orbits** contain the eye balls.

The cranium or the brain box is oriented anteroposteriorly. The olfactory capsules are present on the anterior end and the auditory capsules are present on the posterolateral sides of the cranium. The head skeleton provides passages for blood vessels serving various parts of the brain.

In living fishes of modern times gill slits are present on the pharyngeal wall and are supported by a skeletal structure called **visceral skeleton**. During the course of evolution of vertebrates, the visceral skeleton lost its importance when in terrestrial vertebrates gills were replaced by lungs. However, the structure which constituted visceral skeleton has been retained and has been incorporated in the formation of jaws, providing skeletal elements to the middle ear which have assumed the function of transmitting sound waves to the internal ear and forming the skeletal support for the floor of the buccal (mouth) cavity.

The skull of cyclostomes does not contain jaws and so they are jawless and are thus, included under the group **Agnatha** (meaning without jaws). The rest of the vertebrates have jaws and are included in the group **Gnathostomata** (meaning mouth bound by jaws).

In vertebrates, during the early stages of development of brain and sensory capsules, the brain and sensory capsules are surrounded by a tough membranous skull called the **membranocranium**. Later the membranous skull is strengthened by the development of cartilage. This cartilaginous skull is called the **chondrocranium**. The brain-case or chondrocranium of cartilage or its replacement bone, forms the anterior end of the axial skeletal system. Chondrocranium is modified in relation to the brain and specialised sense organs of the head appears as a stage in the development of head skeleton of various group of vertebrates. In most vertebrates, the brain case is fused with dermal and visceral skeletal materials to form a definitive and complex skull which is later replaced by a bony skull by ossification or by replacement of cartilages by bones and/or formation of fresh bones at places covered by membranes.

Visceral Arches

In addition to the cranium and the sensory capsules, the skull contains other structures which are derived from the visceral skeleton. The visceral skeleton when modified to form part of the cranium derived is referred to as **splanchocranium**. The visceral skeleton consists of a series of cartilaginous rods forming dermal support of the pharyngeal wall between gill slits in fishes. The number of **visceral arches** (Fig. 2.3) correspond to the number of gill slits which is assumed to be seven in the hypothetical vertebrate ancestor. These are modified in different groups of vertebrates depending on the presence or absence of gills and type of jaw suspension. The anterior most or the first visceral arch is called the **mandibular arch**. Each mandibular arch consists of a dorsal **palatoquadrate** (forms upper jaw) and a ventral **Meckel's cartilage** (forms lower jaw). It lies just behind the oral aperture (the mouth).The second arch is called the **hyoid arch and** consists of a **hyomandibular** and **ceratohyal cartilages**. Subsequent arches are called **branchial arches**. The skeleton of the branchial arches support gill slits in the aquatic vertebrates. Each visceral arch, consists of a series of cartilaginous rods encircling the pharynx forming paired half loops on the side wall. The left and the right bars of the corresponding arches are united on the floor of the pharynx by an unpaired midventral cartilage.

In cyclostomes there are innumerable number of gill slits and the visceral skeleton forms a structure called **branchial basket.** During the evolution of vertebrates there was a backward shift of the mouth thus establishing contact with the first gill slit. In the first jawed fishes the skeletal support of the first gill slit became the supporting structure of the mouth giving rise to jaws.

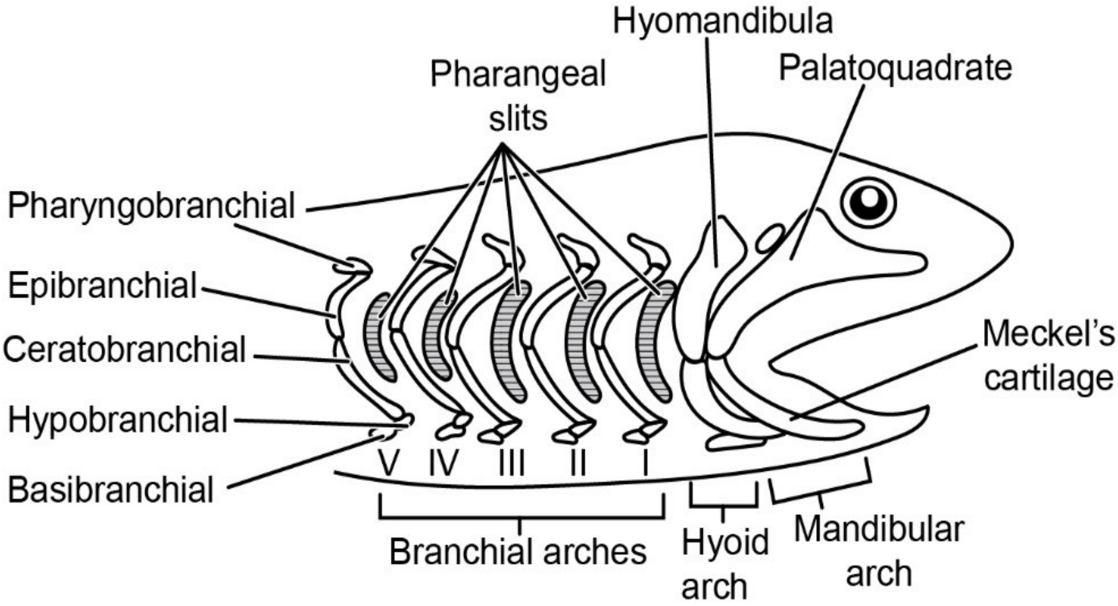


Fig. 2.3: The visceral skeleton showing the full complement of 7 visceral arches as seen in cartilaginous fish. The first arch is modified to form the jaws.

Jaw Suspensorium

The two palatoquadrates of the mandibular arch (dorsal part of first visceral) grow along the anterior or the upper margin of the mouth and unite with one another in the midline to form the upper jaw. Similarly the Meckel's cartilages of the mandibular arch (ventral part of first visceral) extend along the lower or posterior margin of the mouth and unite anteriorly in the midline to form the lower jaw. The quadrate portion of the palatoquadrate helps in the suspension of the jaws to the skull and so is called **suspensorium** (Fig. 2.4). In the earlier stages of evolution of gnathostomes, jaws were attached to the skull by means of ligaments. This condition is called **autodiastylic** type of suspensorium. In some sharks the upper jaw is braced against the skull and attached to the hyomandibula at the posterior end which is also braced against the cranium, this is known as **amphistylic** suspensorium (Fig. 2.4 a). In most living fishes the upper jaw is not directly attached to the anterior part of the cranium but by ligaments and the back portion is attached to the hyomandibula of the hyoid arch to which the lower jaw also attaches. This condition is called **hyostylic suspensorium** (Fig.2.4b). In tetrapods, chimeras and lungfishes the upper jaw is directly fused with the skull, the hyomandibula is not involved in the suspension of the jaws. This 'self bracing' condition is called **autostylic suspensorium** (Fig.2.4c). The elements of the hyoid arch are thus, released from participating in providing the suspensorium are incorporated into the middle ear as **ear ossicles**.

The branchial arches allow dilation and contraction of the pharynx in fishes. This enables, swallowing and expulsion of water during respiration. These elements of the branchial arches were lost in tetrapods with the loss of branchial respiration which was replaced by pulmonary respiration.

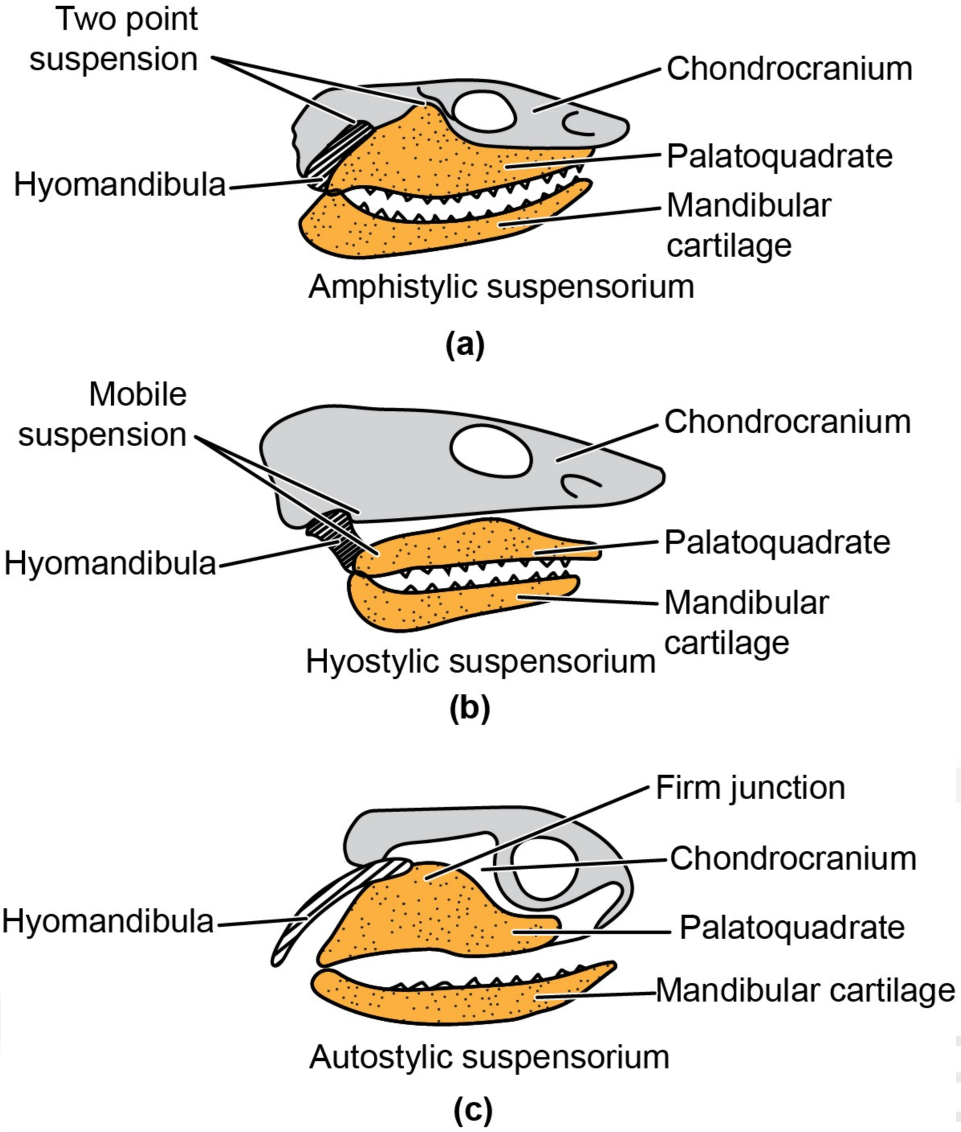


Fig. 2.4: Jaw suspensorium in vertebrates. a) Amphistylic Jaw Suspensorium (presumed primitive condition found in some sharks). b) Hyostylic Jaw Suspensorium (most modern cartilaginous and bony fishes). c) Autostylic Jaw Suspensorium (lung fishes, chimeras and tetrapods).

The Vertebral Column

The vertebral column is a chain of segmented structures called **vertebrae** (vertebra - singular). It begins anteriorly from behind the skull and extends posteriorly to the tip of the tail. It forms the longitudinal axis of the animal and provides both stability and mobility to the animal. Vertebrae have specific structures which allow them to be joined to each other firmly and also allow some amount of movement. Articulation of vertebrae is achieved by the presence of bulges (convexities) and depression (concavities) in the vertebrae (Fig. 2.5). The bulge present at one end of a vertebra fits into the depression present on the adjacent vertebra. Furthermore, additional structures are also present which strengthen the articulation between vertebrae and also keep the mobility in check to the required extent. This helps to prevent dissociation and dislocation of the vertebrae of the vertebral column. The series of vertebrae form a tube-like structure which is located dorsally in the body and encloses and protect the spinal cord. Similarly, the vertebrae of the tail region of some animals form a ventral tube to enclose blood vessels.

A typical vertebra consists of the following parts (see Fig. 2.5):

a) A central body in line with the notochord of early developmental stage, the **centrum**. The centrum bears depressions and bulges on its anterior and posterior ends for articulation with the vertebra in front of it and behind it.

b) A dorsal arch-like structure called the neural **arch** (Fig. 2.5) which encloses the spinal cord. The neural arches of all vertebrae together form the **neural** tube or the neural canal which encloses the spinal cord. Neural arches are formed by vertical neural plates that arise from the dorsolateral sides of the centrum. The two neural plates of either side meet above the spinal cord. There is usually a backwardly directed neural spine present dorsally, above the neural arch.

c) There is a pair of lateral processes known as the transverse processes. These extend outwards from the centrum. The transverse processes provide the attachment sites for muscles.

d) In fishes, salamanders, most reptiles and many long tailed mammals the caudal vertebrae usually have a **haemal arch** which is present ventrally. The **haemal arch** is formed by a pair of plates (**haemapophyses**) and contains a haemal canal which encloses the blood vessels. The **haemal arch** may also have a ventrally projected **haemal spine**.

e) The centrum bears a couple of plate-like projections both in front and behind (Fig. 2.5) which are called **prezygapophyses** and **postzygapophyses** respectively. These help in articulating the vertebrae firmly and the limit of movement between the vertebrae to the necessary amount.

f) In higher vertebrates a pair of lateral processes are also present which arise on each side, from the base of the neural arch. These are known as **diapophyses**. Usually there is another pair of processes that arise from the centrum and are known as **parapophyses**. These articulate with the ribs as the bifurcated heads of the ribs are attached to these processes on each side.

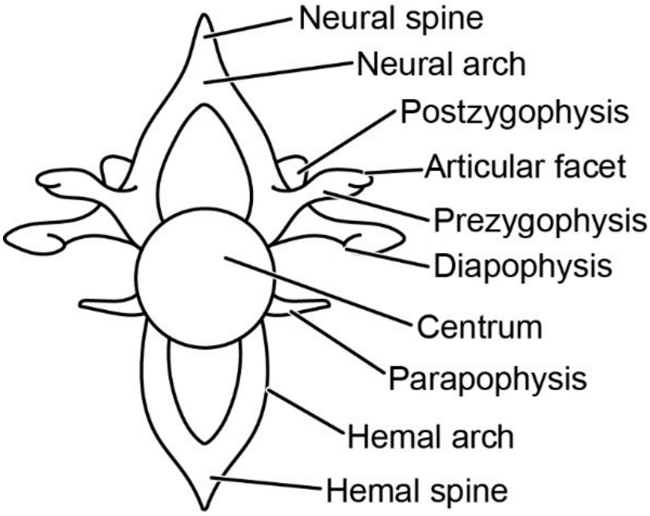


Fig. 2.5: Front view of a generalised vertebra.

Types of Vertebrae

The vertebrae are of different types depending on the structure of the centrum (see Fig. 2.6):

i) **Procoelous:** The centrum of the vertebra bears concavity in front (anterior) and a convexity behind (posterior) (Fig 2.6a). The convexity of the vertebra in front fits into the concavity of the vertebra behind, eg., typical vertebra of frog and lizards and other living reptiles

ii) **Opisthocoelous:** It is the opposite of procoelous vertebra as it has a convexity in front and a concavity behind (Fig 2.6b), as seen in most salamanders.

iii) **Amphicoelous:** The vertebral centrum has concavities both in front and behind (Fig 2.6c). The vertebra appears dumbbell shaped in lateral view and is found in most fishes, a few salamanders and caecilians.

iv) **Heterocoelous:** The centrum of this vertebra appears concave when seen from side to side and convex from above downwards and opisthocoelous in sagittal view. They are also described as saddle shaped. These saddle shaped vertebrae articulate together allowing extensive lateral and dorsoventral rotation and are characteristic of birds (Fig 2.6d).

v) **Acoelous or Amphiplatyan:** The centrum of this vertebra is usually flat on both sides,without any bulging or depressions (Fig 2.6e). These vertebrae are found in mammals.

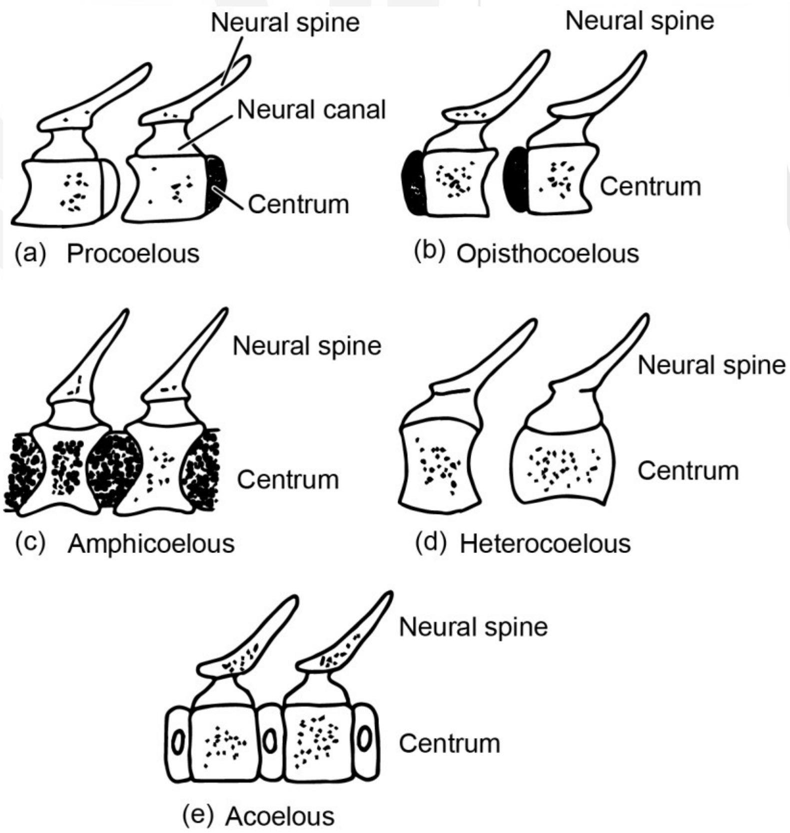


Fig. 2.6: Different types of vertebrae distinguished by their centra: (a) procoelous; (b) ophisthocoelous; (c) amphicoelous; (d) heterocoelous; (e) acoelous.

Vertebral column of vertebrates

The notochord is present in the embryonic stages of all vertebrates. Hagfish and lamprey retain the notochord, throughout their life which in other vertebrates is present only in the embryo. In cyclostomes (lampreys), the persistent notochord is supported by the lateral neural cartilages.

Teleost fishes have well ossified amphicoelous vertebrae. The vertebral column and vertebrae of teleosts can be divided on basis of their location in the body as the trunk vertebrae and the tail vertebrae. In tetrapods the vertebral column is divided into the following regions:1) the cervical region, 2) thoracic region, 3) lumbar region, 4) sacral region and 5) the caudal or tail region and shows regional specialisation. The number of vertebrae in each of these regions is variable depending on the animal group.

In tetrapods, such as amphibians only a single cervical vertebra is present amphibians which restrict their neck movement. Reptiles and most mammals as you have read earlier have 7 cervical vertebrae which give them increased flexibility. The first cervical vertebra in them is known as atlas and it articulates with the back of the skull which allows the head to move in all directions. The 2^{nd} vertebra is known as axis which has an anteriorly projecting process the **odontoid process** that fits into the cavity of the atlas vertebra and acts as a pivot for the movement of the head; the other 5 are similar cervical vertebrae (Figs.2.7 and 2.9). Birds however, have a variable number of cervical vertebrae depending on the length of the neck (swans have 25 cervical vertebrae).

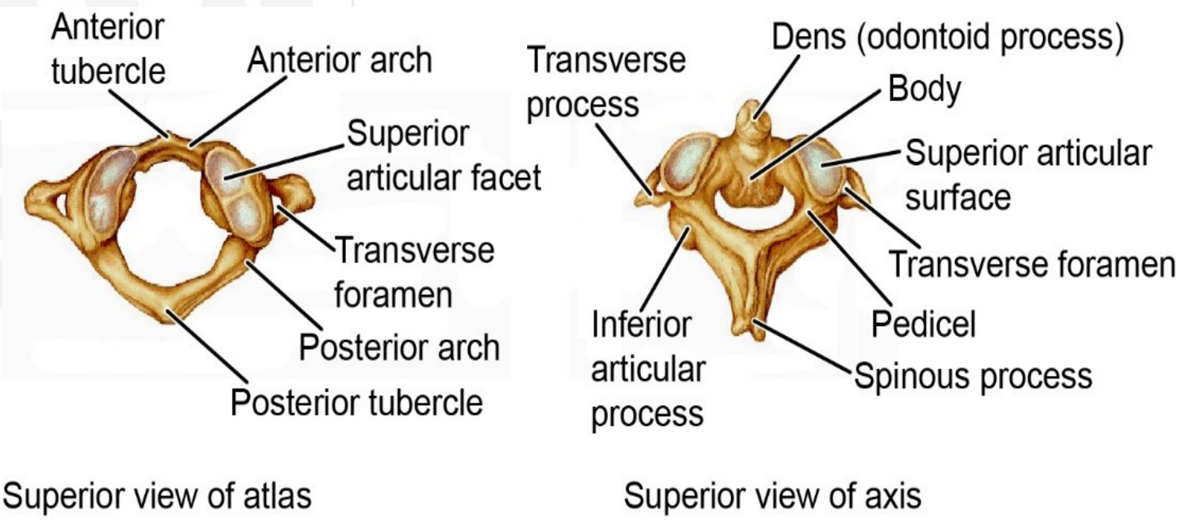


Fig. 2.7: First and second cervical vertebrae in mammals. Note the ring like centrum in atlas and the transverse foramen (TR) in both vertebrae that forms the passage for the blood vessels.

The thoracic region has the thoracic vertebrae. These articulate with the ribs. The lumbar vertebrae are present in the lumbar region and are more robust than the vertebrae of other regions. Sacral vertebrae are often fused to form a **sacrum** that is also fused with the pelvic girdle. In birds a structure known as **synsacrum** is present (Fig. 2.8) and is formed by the fusion of the last thoracic vertebrae and all lumber, sacral and a few caudal vertebrae. The synsacrum in turn is fused with the pelvic girdle in order to provide support for bipedal locomotion.

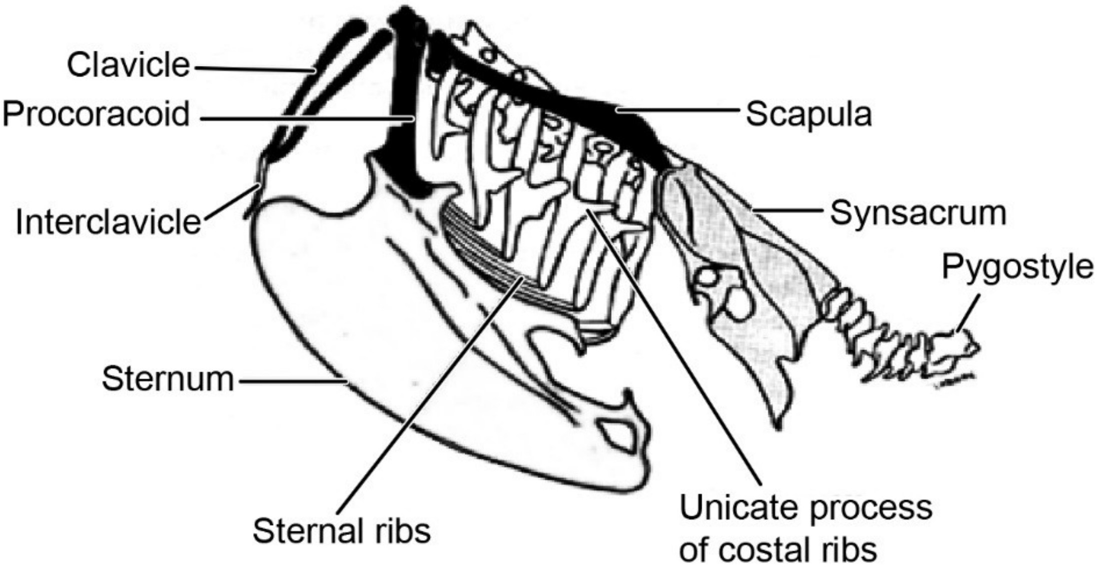


Fig. 2.8: Skeleton of bird showing the sternum, synsacrum, ribs, and free and fused vertebrae of the caudal region.

The caudal vertebrae form the tail region and may be fused in the tailless animals. The arches and spines of the vertebrae get progressively shorter in this region. In frogs and toads the terminal vertebrae form the **urostyle** and in birds the last 4-5 vertebrae fuse to form the **pygostyle** (see Fig. 2.8). In apes and humans the last 3-5 caudal vertebrae fuse to form the **coccygeal** or tail bone. The regions of the vertebral column and their specialised vertebrae in mammals, are shown in Figure 2.9. In the figure you can see the intervertebral cartilage disc made of fibrous tissue and remnants of notochord.

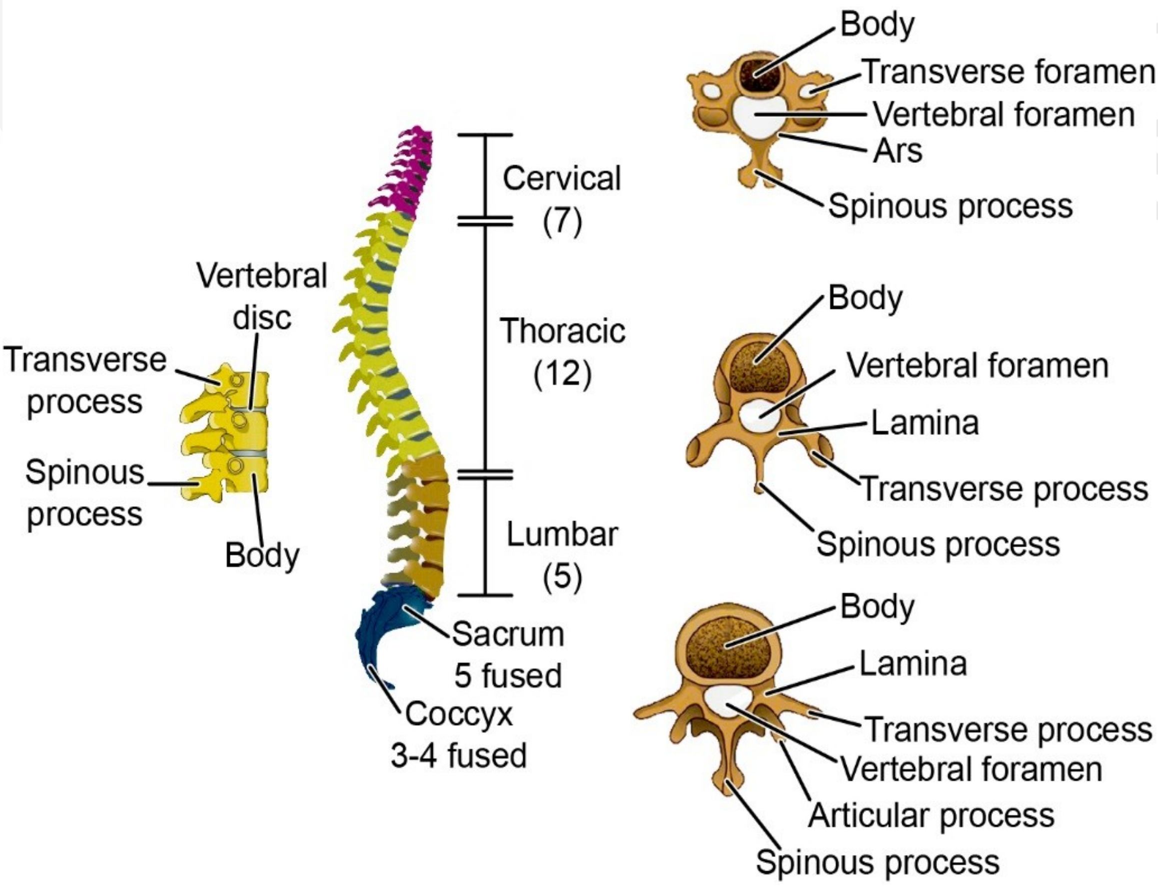


Fig. 2.9: Structure of the segments of vertebrae.

SAQ 2

A) Fill in the blanks:

i) Procoelous centrum of a vertebra bears a concavity in …………… and a convexity …………… .

ii) …………………… centra appear dumb bell shaped in the lateral view.

iii) …………………… centra are described as saddle shaped.

iv) Acoelous centra are usually ……………….. without any bulging or ………………... .

B) Choose the correct alternative:

i) The visceral skeleton is also referred to as (chondrocranium/ splanchocranium).

ii) Jaws arose from the (mandibular/hyoid) arch.

iii) The upper jaw is made up of the (palatoquadrate/meckel's cartilage).

iv) Branchial basket formed of the visceral arches is found in (teleosts/cyclostomes).

v) If the jaw is attached to the skull and not suspended by the hyomandibula, the suspensorium is (autodiastylic/autostylic).

2.3.2 Appendicular Skeleton

Most vertebrates have two pairs of appendages, an anterior (pectoral) and a posterior (pelvic) pair. Fishes have paired fins (pterygia) and other vertebrates with have jointed limbs (podia). During embryonic development the paired appendages of fishes appear as horizontal folds and the limbs of vertebrates appear as buds. The skeleton of paired appendages namely, forelimbs and hind limbs articulate and are supported by the anteriorly located pectoral girdle and the posteriorly located pelvic girdle respectively. Both the pectoral and pelvic girdles and skeleton of the forelimbs and hind limbs collectively constitute the **appendicular skeleton**.

The pectoral girdle is made up of both dermal and endochondral (replacement) bones. The pectoral girdle consists of two identical parts. In some vertebrate species each part of the pectoral girdle has three components which consist of the clavicle, scapula, and coracoid. In humans each part consists of the clavicle and scapula. Some mammalian species (such as the dog and the horse) have only the scapula. Each part of the pectoral girdle also has an **acetabular** cavity for the articulation of the head of the humerus bone of the forelimb.

The pelvic girdle is made up of 2 dermal bones, a dorsal **iliac** and a ventral **ischio-pubic** part. It is composed of two identical appendicular hip **bones.** Each part is formed of **ilium**, **ischium**, and **pubis**. The two parts are joined and oriented together to form a ring. Each part of the pelvic girdle contains a **glenoid** cavity which articulates with the head of the femur bone of the hind limb. The pelvic girdle also has the pelvic spine which consists of the sacrum and coccyx. The extremities of the vertebrate limbs are typically pentadactyl, being provided with five digits each. The vertebrate fore and hind limbs have similar joints and similar number of skeletal elements. The general pattern of the parts and skeleton can be listed as follows (Table2.1):

Table 2.1: Similarity of Plan between Anterior and Posterior Part of the Appendicular Skeleton.

1.	**Anterior part of the Appendicular Skeleton**	Shoulder Joint	1.	**Posterior part of the Appendicular Skeleton**	Hip joint
2.	**Point of attachment of the pectoral girdle with the fore limbs**	Head of the anterior bone (humerus) of the forelimb	2.	**Point of attachment of the pelvic girdle with the hind limbs**	Head of the anterior bone (femur) of the hind limb
3.	**Upper arm bone of forelimb**	Single bone: Humerus	3.	**Upper bone (thigh) of hind limb**	Femur
4.	**Lower bone(radio-ulna) of forelimb**	Two bones: Radius and Ulna	4.	**Lower bone (tibio-fibula) of hind limb**	Two bones: Tibia and Fibula
5.	**Point of attachment between the upper arm bone(humerus) and lower arm bone(radio- ulna)**	Elbow joint	5.	**Point of attachment of between the upper bone(femur) and the lower bone (shank/tibio-fibula) of the hind limb**	Knee joint
6.	**Wrist**	Carpal bones	6.	**Ankle**	Tarsals
7.	**Palm**	Metacarpal bones	7.	**Sole**	Metatarsal bones
8.	**Fingers**	Phalanges	8.	**Toes**	Phalanges

Ribs and Sternum

Ribs are found in the thoracic region of most vertebrates. They are sets of paired slender curved bones and are attached to vertebrae at one end and to the sternum (breast bone) at the other end. Ribs have a bony vertebral part and attach to the breast bone or sternum by a ventral cartilaginous or bony sternal portion (Fig. 2.10c).The ribs together with the vertebral column and the sternum form a skeletal cage that encloses and protects the organs of the thorax. During the course of vertebrate evolution ribs first appear in

Gnathostomes. There are two types of ribs (Fig. 2.10 a & b) : (1) the **dorsal** or **intramuscular ribs** and the (2) **ventral** or **haemal ribs**. The dorsal ribs grow as extensions of the vertebrae and extend into the horizontal septa. Dorsal ribs that occur in elasmobranchs and amphibians are short and incompletely developed. However, they are well developed in amniotes. The dorsal ribs establish contact with vertebral column and sternum and surround the body. A typical dorsal ribs has two heads (i) the **capitulum** which is the rib head that attaches at the centrum of the vertebrae and the (ii) the **tuberculum head** which attaches to the transverse processes of the vertebrae. The two heads of the ribs enclose a space between them known as the **vertebro-arterial or vertebrarterial canal** or foramen through which the vertebral artery passes. The ventral or haemal ribs seem to have arisen from the haemal arches. They also encircle the body but are located inside the peritoneal cavity. Ventral ribs are present in most teleost fishes, ganoid fishes and Dipnoi. Both dorsal and ventral ribs are found in most teleost fishes (Fig.2.10). In most reptiles, birds and mammals the ribs are attached by movable joints only to the thoracic vertebrae (snakes have ribs articulating with all the vertebrae). In birds the entire rib is ossified and firmly attached to the sternum, while in mammals the sternal part is cartilaginous. The ribs which are short and not directly attached to the sternum but to the other ribs are called **false ribs** (number 8 to 10 in humans). False ribs are also found in crocodiles. The ribs that are not attached to sternum but are free are known as floating ribs (numbers 11 and 12 in humans).

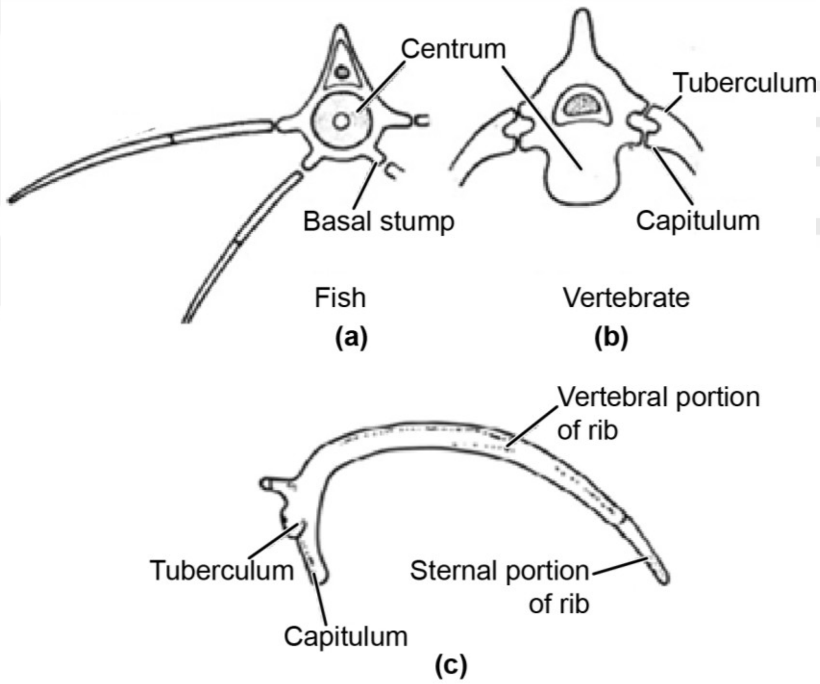


Fig. 2.10: Attachment of dorsal and ventral rib to the vertebrae in: (a) Fish and (b) Terrestrial vertebrates (c) Structure of a double headed rib of a vertebrate.

Sternum is a shield or rod shaped bone or group of bones found in the mid-ventral side of the thorax of vertebrates. Sternum is also commonly called the breast bone. In amniotes, the ventral ends of the ribs are attached to the sternum. The sternum of birds as you have read in the previous course is broad and develops a ventral keel-like projection and provides a surface for the attachment of wing muscles (see Fig. 2.8 again). Sternum is also usually present in vertebrates and is adapted according to the type of locomotion. Snakes which have lost limbs also have lost the sternum.

In the present section we have discussed the general features of the skeletal system in vertebrates. In the next two sections we will compare the salient features of the axial and appendicular skeletons of two vertebrate tetrapods namely, frog and rabbit. The frog shows the adaptations for terrestrial life while still maintaining a partly aquatic life, while rabbit a mammal, is fully terrestrial. The skeletons of both these vertebrates are suitably adapted to their life styles

SAQ 3

Match the statement given in column 'B' with the caption of the column 'A'.

A		B
a) Cartilage and bone	i)	The haemal arch contains the haemal canal which encloses the blood vessels.
b) The skull	ii)	The tetrapod limbs are typically pentadactyl being provided with five digits each.
c) The vertebral column	iii)	The matrix is composed mainly of mineral salts mostly of calcium combined with phosphates and carbonates.
d) Appendicular skeleton	iv)	The olfactory capsules are present on the anterior end and the auditory capsule are present on the posterolateral sides of the cranium.

2.4 AXIAL SKELETON OF FROG AND RABBIT

In the earlier section you studied the general features of the axial and appendicular skeletons of vertebrates. In this section we go into greater details of the axial skeleton of frog and rabbit by comparing the structures of their skull and vertebral column. Let us first examine the features of the skull.

2.4.1 Skull of Frog and Rabbit

The Skull of Frog

The skull of frog is interesting for several reasons. It is simple in structure with fewer number of bones and areas of ossification compared to other vertebrates. It is broad and flat, consisting of the cranium, sense capsules, large eye orbits, jaws, **hyoid apparatus** and cartilages of the larynx. Figure 2.11 shows the dorsal and ventral view of the frog's skull. Refer to both these figures while studying this subsection.

The **cranium** of frog is anterio-posteriorly elongated and is formed of just six bones. The posterior end of the cranium is called the occipital end and consists of a large aperture the **foramen magnum**. It is surrounded by a pair of bones the **exoccipitals** that bear two bulges, the **occipital condyles**, for articulation with the atlas, the cervical vertebra. The roof and sides of the cranium are covered by a pair of composite of bones called **frontoparietals.**

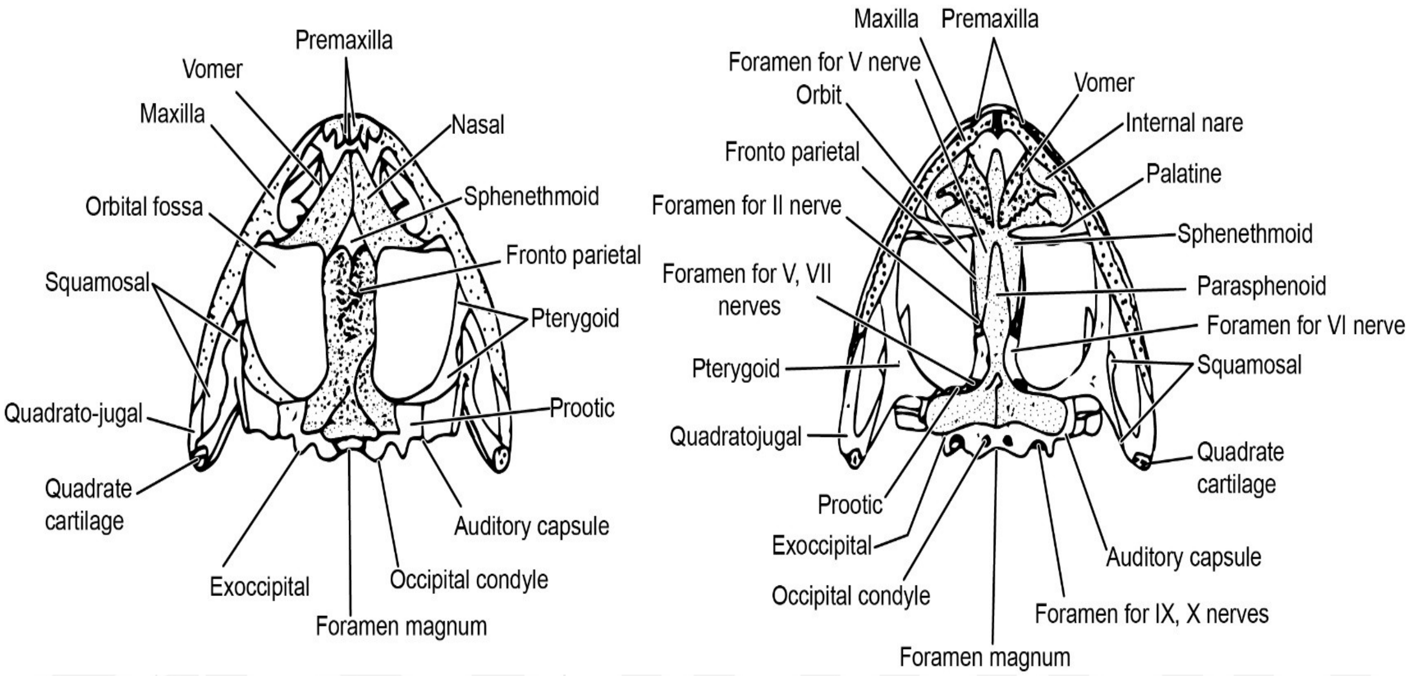


Fig. 2.11: Frog skull. a) Dorsal view; b) Ventral view.

At the front end of the skull, there is a single ring shaped bone, the **sphenethmoid** which almost covered on the dorsal side by the **nasal bones** and is only visible as a triangular bone on the dorsal side. On the ventral side the **sphenethmoid** bone is covered by the dagger- shaped **parasphenoid** bone, which forms the floor of the cranium.

Each of the paired auditory capsules of the frog skull is situated at the posterolateral side of the cranium. Each auditory capsule consists of only one bone, the **pro-otic bone**. The rest of the auditory capsule is covered by membranes. The middle ear has a cartilaginous extra stapes and a bony stapes that transmits the sound waves to the internal ear. The olfactory capsules are found anterior to the cranium. Each olfactory capsule is covered by the **nasal** bone above and a **vomer bone** below. The two bones are bound by membranes to the cranium and to each other. A space located anterolaterally on each sides, of the cranium forms the eye **orbit** which contains the eye ball. The eye socket is bound on the outer border by bones of the upper jaw, by bones of the olfactory capsule, the cranium on the inner margin and the bone of the auditory capsule behind. The floor is covered by tough membranes which bulge into the buccal cavity.

The upper jaw of frog is horse shoe shaped. It forms the outer margin of the skull anteriorly and laterally. The upper jaw is made up of two halves united in front and free behind. Each half of the upper jaw consists of an anterior **premaxilla**, a middle **maxilla** and a posterior **quadratojugal**. The two halves of the upper jaw are united at the premaxillar end. The upper jaw is immovably fixed to the skull on each side by means of three bones. These 3 bones consist of i) a bar-like **palatine** (Fig. 2.11) which connects the maxilla to

sphenethmoid of the cranium and ii) two other bones which are present at the posterior end on each side of the upper jaw and connect the auditory capsule of the respective side. A **'T' shaped squamosal bone** is present dorsally. The long limb of this bone is attached posteriorly to the quadratojugal. The inner tip of the horizontal limb of the **'T' shaped squamosal bone** is attached to the pro-otic and the other end is free. A tri-radiate bone, the **pterygoid** is present ventrally is on each side of the jaw. The three ends of this bone are attached to the maxilla anteriorly, the pro-otic on the mid posterior side and the quadratojugal posteriorly.

The lower jaw is complementary in shape to the upper jaw and so is also horse shoe shaped (Fig. 2.12). Each part of the lower jaw articulates posteriorly with the quadratojugal bone of the upper jaw and is free rest of the way. The two halves of the lower jaw are also united at the anterior end. Each half of the lower jaw consists of 3 bones: i) an anterior **mentomeckelian bone**; ii) the **dentary bone** behind the mentomeckelian bone and the; iii) posterior most **angulosplenial bone** present behind the dentary bone. The two mentomeckelian bones of the two halves of the lower jaw are united anteriorly. The angulosplenial bone of each side articulates with the quadratojugal bone of each side of the upper jaw. The quadratojugal bone of each side of the upper jaw, fits into a concavity present at the terminal end of each of the angulosplenial bone. A small ridge-like process is present in front of the concavity on the angulosplenial bone of each side which is called the **coronary process** (Fig. 2.12).

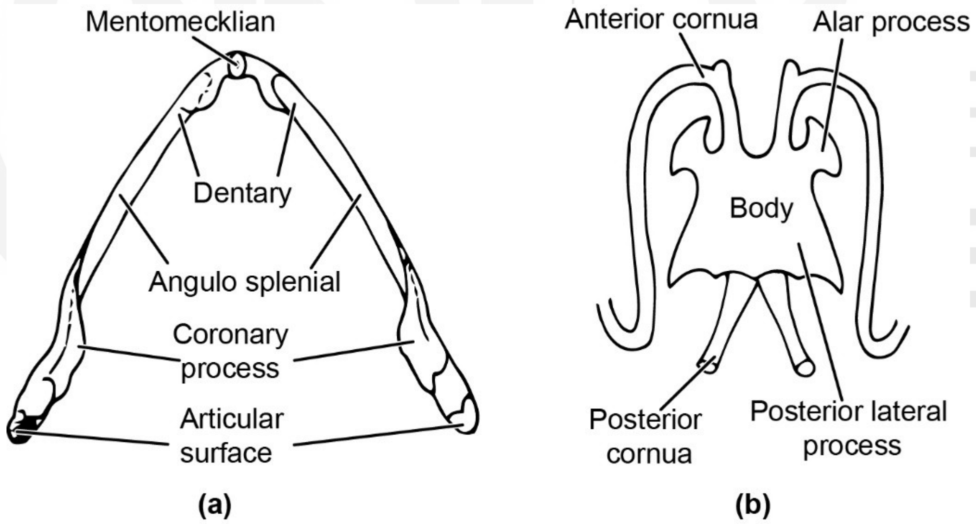


Fig. 2.12: a) Lower jaw of frog; b) hyoid bone of frog.

Teeth in frogs are found on the premaxilla and maxilla of the upper jaw and also on the vomers of the olfactory capsule (vomerine teeth). Teeth project into the buccal cavity. Teeth are curved, fused to the bones on which they are found and are arranged in a single row along the edges of the premaxilla and maxilla. They do not help in mastication but help to prevent the prey from escaping from the buccal cavity. A hyoid apparatus is present which forms the support for the floor of the buccal cavity, (Fig. 2.12 b). It is derived from the visceral skeleton and consists of a central plate-like body lying on the floor of the buccal cavity. The hyoid apparatus provides a surface for the attachment of the tongue. The central plate has two pairs of processes, one pair at the anterior end and another at the posterior end. They are called **anterior** and

posterior hyoid cornua respectively. The anterior hyoid cornua are long slender cartilaginous processes that curve back to extend into the auditory region of the skull where they are attached to the **collumella auris** of the middle ear. The posterior hyoid cornua are stout rod-like bones projecting backwards on either side of the glottis, which is the opening of the trachea on the floor of the buccal cavity.

The Skull of Rabbit

The skull of rabbit is thick and is elongated anteroposteriorly when compared to the skull of frog. The elongation of the skull is due to the prolongation of the jaws for forming a snout. The snout is required in order to provide more space for the attachment of the jaw muscles. The skull of rabbit (Fig. 2.13) can also be studied under the same divisions like that of the frog: i) the cranium enclosing the brain; ii) the sensory capsules enclosing the sense organs; iii) the two jaws and iv) the hyoid apparatus. The different parts of the skull of the rabbit in comparison to the frog are more complicated in structure due to addition of more bones either by ossification of pre-existing cartilages or by addition of a few investing bones where only membranes existed earlier. At present mammals represent the final stage of vertebrate evolution. The complexities of the mammalian skull and skeleton are due to adaptations in order to accommodate evolutionary features that have made survival on land possible.

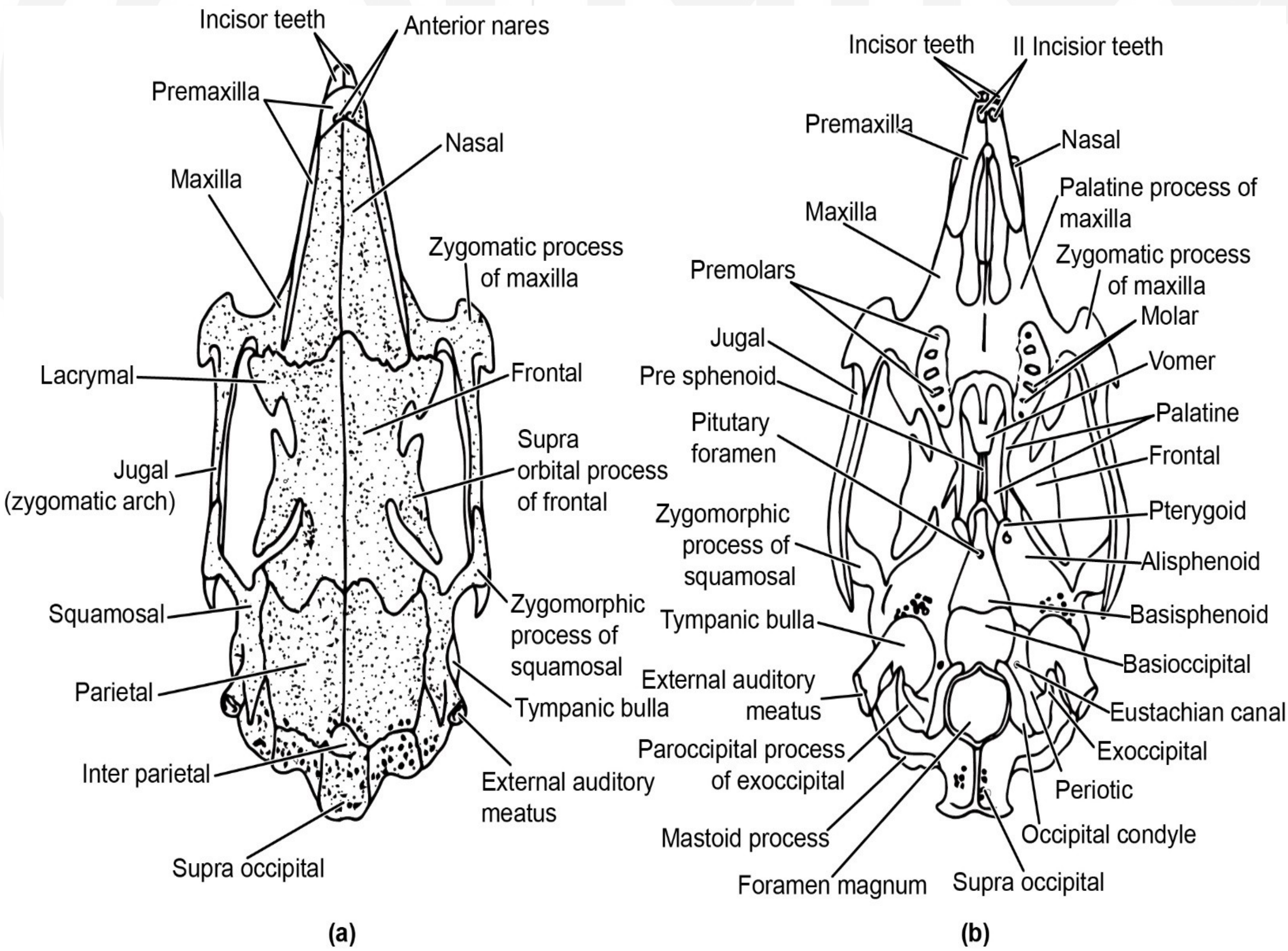


Fig. 2.13: a) Dorsal view of rabbit skull; b) ventral view of rabbit skull.

Cranium

The cranium is short compared to the length of the skull as a whole. The cranium is found behind the eye orbits. The cranium can be divided anteroposteriorly into three segments. The segments are in the form of rings which are placed one behind the other and they all collectively surround the brain. The posterior segment is the **occipital segment**. It consists of four bones as compared to only two bones in the frog. The four bones of the **occipital segment** surround the **foramen magnum** which is large and directed downwards and not backwards as in frog. The foramen magnum is surrounded at the top by the single **supraoccipital** bone, a pair of **exoccipital bones** on the lateral sides and a single plate-like **basioccipital** bone, on the lower side, (Fig. 2.13). The posterior end of the rabbit skull,similar to the frog skull rabbit has two **occipital** condyles for the articulation of the skull with the first vertebra. So the skulls of both frog and rabbit are **bicondylar**. The **occipital** condyles of rabbit project from the lower part of the exoccipitals. Both the exoccipitals and the basioccipitals contribute in the formation of condyles which are smooth and round, and articulate with the concavities on anterior face of the first vertebra (atlas).

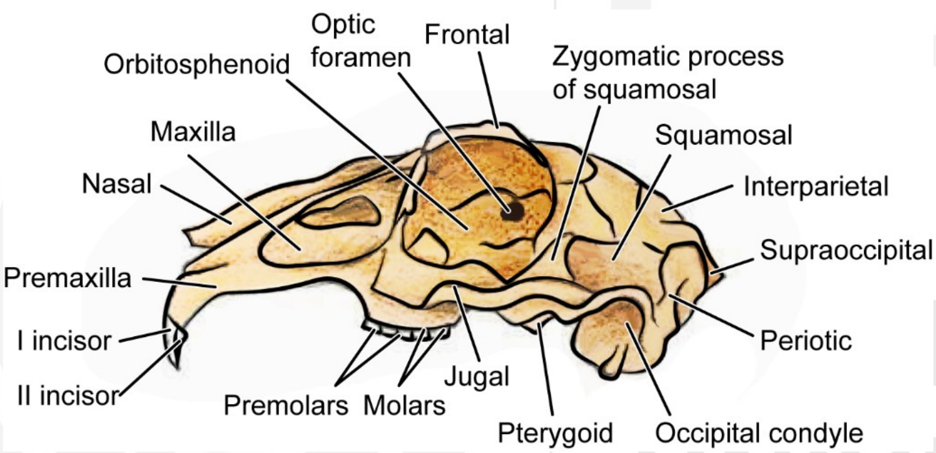


Fig. 2.14: Lateral view of rabbit skull showing its various bones.

The part of the cranium in front of the occipital region is the **parietal segment** and consists of six bones- i) A single, flat, triangular **basisphenoid** bone forms the floor in front of the basioccipital. A depression is present on the dorsal surface of basisphenoid in which the body of pituitary lodges (not visible in the figure). ii) A pair of **parietal** bones is present which, form the roof of the parietal segment. The two parietals bones are united in the mid-dorsal line. The sides of the **parietal** segment are formed by a pair of wing shaped **alisphenoid** bones that are present one on each side, (Fig. 2.13 b).The parietal bones are separated on each side from the alisphenoid bone by a rectangular bone known as **squamosal bone** which connects dorsally to the parietal and ventrally to basisphenoid. A projection from the squamosal called **zygomatic process** unites with the **jugal** bone on each side to form the **zygomatic arch.** Below the zygomatic process is a depression with which the lower jaw articulates. Dorsally between the two parietal bones and the supraoccipital bones located behind is a single wedge shaped bone called **interparietal bone**. The anterior part of the cranium is the **frontal segment**. The roof of the frontal segment is covered by a pair of **frontal bones** which have prominent ridges on each of them called **supraorbital** process. These processes project over the eye orbit on each side. There is a median **presphenoid** bone which forms the floor of the **frontal** segment. It is present in front of the basisphenoid. There is a pair of **orbitosphenoid bones**, which extend vertically on either side to form the inner boundary of the eye orbit. There is a vertical plate-like bone which forms the anterior boundary of the cranium called **cribriform plate**. This cribriform plate bears an aperture for the passage of the olfactory nerves.

1. Sensory Capsules

The auditory capsules are situated on the posterolateral sides of the cranium on each side, between the squamosal and exoccipital bones, (Fig. 2.14). Each auditory capsule in the adult, is represented by a complex of bones called the the **periotic**, which is made up by fusion of 3 embryonic bones **prootic**, **epiotic** and the **opisthotic**. In addition to this the auditory capsule consists of two other structures, the **tympanic bone** and the **auditory ossicles**. The periotic bone is divisible into two parts, the **petrous** which forms the internal ear and encloses the membranous labyrinth and the **mastoid process** which projects outside, between the periotic process and the exoccipital bone. The petrous bears two openings on its outer surface, the **fenestra ovalis** and the **fenestra rotundum**. The tympanic bone lies across the auditory meatus between the basisphenoid bone and the squamosal bone and is closely attached to the periodic bone on its outer surface. The tympanic bone is flask shaped (Fig. 2.14) consisting of an outer tubular part and a lower smaller part forming the **tympanic bulla** which contains the tympanic cavity enclosing the auditory ossicles. The tubular part encloses the auditory meatus. A tympanic membrane is stretched across the tympanic cavity at the inner end of the tube. The tympanic membrane separates the tympanic cavity from the tube of the tympanic bone. The auditory ossicles consist of three small bones the **malleus**, the **incus** and the **stapes**, (Fig. 2.15). They extend between the tympanic membrane and the periotic bone. An eustachian aperture is present anteriorly on the tympanic bone and opens into the eustachian canal which communicates with the pharynx.

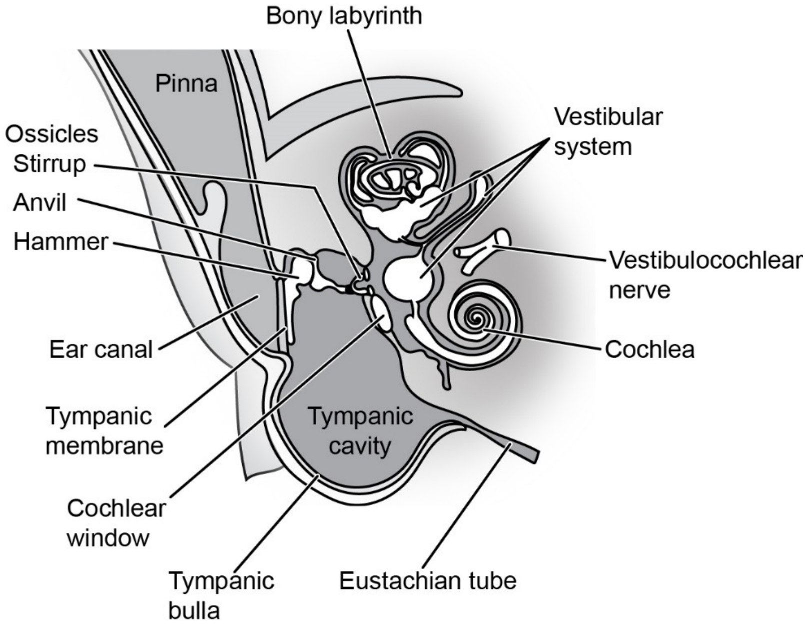


Fig. 2.15: Inside the rabbit ear.

The olfactory capsules are present in front of the cranium. They are roofed over by two flat nasal bones. These bones extend from the tip of the external **nasal** openings in front upto the frontal bones behind. The nasal cavity is separated into two separate cavities by a vertical plate-like **mesethmoid** bone, which lies in front of the cribriform plate. Each nasal cavity contains a scroll-like **turbinal** bone. The paired nasal cavity opens to the outside through the external nares and internally open into the buccal cavity far behind through the internal nares also called the posterior nares.

The paired eyes orbits are hollow spaces and each contains an eye balls. Each **eyes orbit is located** on the anterolateral sides of the cranium between the upper jaw and the olfactory capsule. A small **lachrymal** or lacrymal bone is present, on each side of the anterior wall of the orbit. It contains a lacrymal aperture, through which the **lachrymal glands (tear glands)** open into the orbit.

2. Jaws

The upper jaw of the rabbit consists of two halves that are united in front. Each half of the upper jaw consists of a **premaxilla (plural:** premaxillae**) bone**, anteriorly, and **a maxilla** bone behind (see Fig. 2.14 again). The two halves of the upper jaw are united in the front at the premaxillae end. The premaxillae are large bones and form anterior part of the snout. The premaxillae bones, bear incisor teeth on their ventral surface. The maxilla bone, which is present behind the premaxilla forms the major part of the upper jaw and bears premolar and molar teeth. A horizontal palatine process originates from the inner margin of each of the maxilla and both meet in the centre to form the anterior part of the palate. The anterior part of the palate forms the horizontal partition that separates the nasal cavity from the buccal cavity and also forms the roof of the buccal cavity. A zygomatic process projects outwards from the outer margin of each of the maxilla bone and forms the anterior border of the eye orbit. Each maxilla bone extends externally behind the nasal cavity. On each side of the upper jaw, between the palatine and the alisphenoid bones an irregular- shaped, **pterygoid** bone is present. A laterally compressed **jugal** bone with the zygomatic process and the squamosal bone is present on each side. The **jugal** bone, along with the squamosal and maxilla bones is involved in the formation of the zygomatic arch.

Each half of the lower jaw of the rabbit is similar to all mammal**,** instead of being composed of three bones as present in each half of the lower jaw of frogs, **is made up of a single bone known as dentary** (Fig. 2.16). The two dentaries are joined together in front in the midline by a symphysis. Each dentary consists of an anterior horizontal part which bears the incisors and premolars and molars. A **gap known** as the **diastema** is present in each half of the lower jaw, between the incisors and the rest of the teeth. The posterior ascending process of the dentary ends in a condyle at the upper tip. The condyle helps in articulating with the glenoid fossa on each side. The glenoid fossa is formed by the squamosal and the zygomatic process.

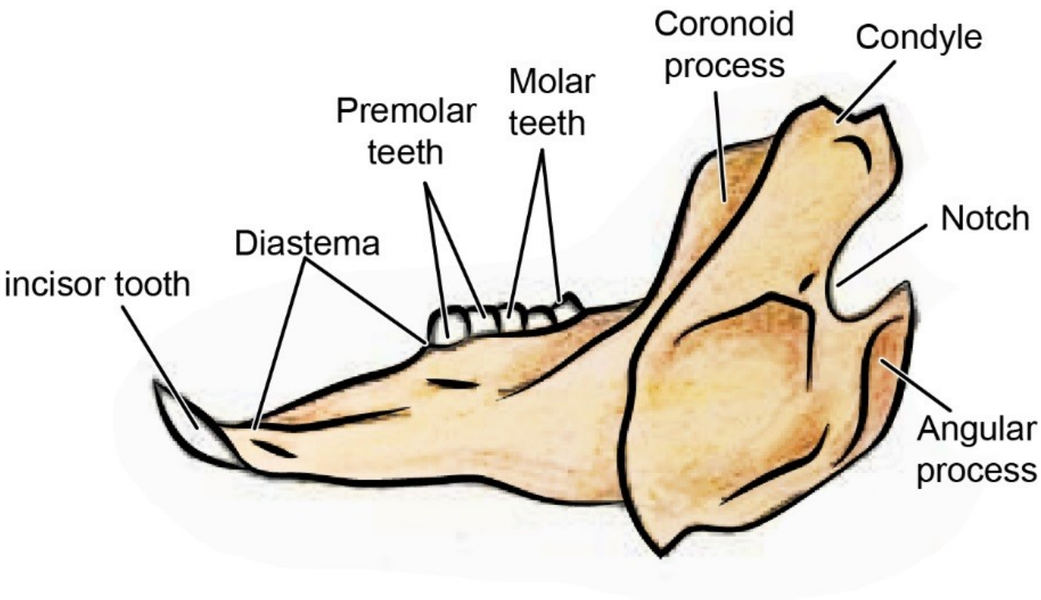


Fig. 2.16: Lower jaw (Mandible) of rabbit.

The hyoid apparatus is represented by a central plate, the **basihyal** (Fig. 2.17) which has two pairs of processes projecting backwards. The anterior cornua are connected to the periotic and consists of three bones. The posterior cornua are connected to the larynx.

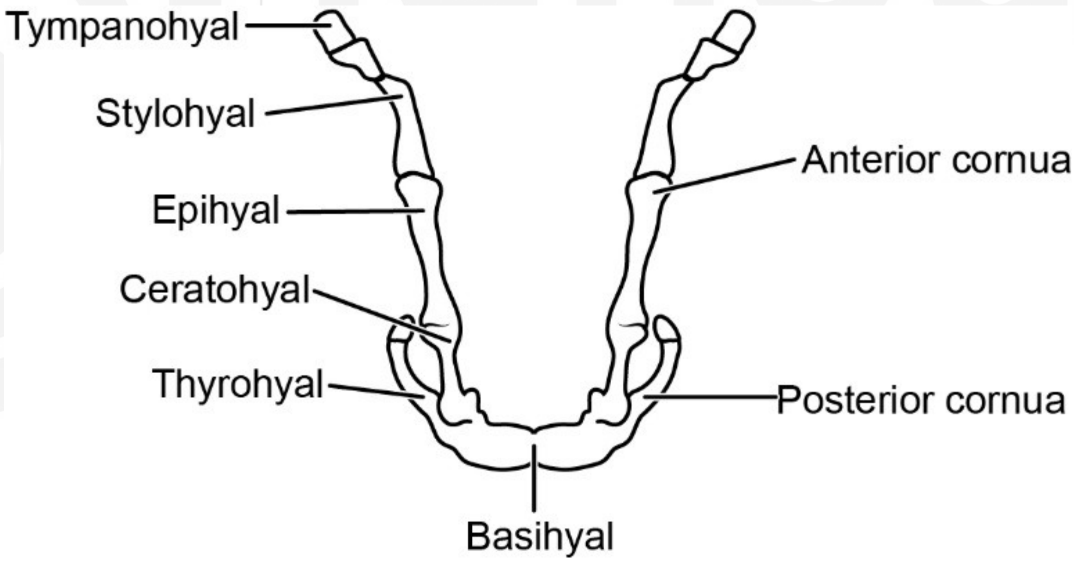


Fig. 2.17: Hyoid apparatus of rabbit.

Some of the key features of mammals as seen in the rabbit skull

- A true palate, which is only found in mammals is present. The true palate separates the respiratory passage from the buccal cavity.
- The bones of the skull are united or joined with each other by zig-zag lines called **sutures** which is characteristic of mammals.
- Teeth are accommodated in holes called sockets which are present on the jaw bones. The condition when teeth are present in sockets is called **thecodont** dentition. The teeth of most vertebrates including frog are all of the same type, and such a condition is known as **homodont** dentition.

In mammals however, teeth in each half of the jaw may be of different types -differing in shape and structure for performing different functions. The dentition in which the jaw has different types of teeth adapted for different functions as cutting, tearing and chewing food is called **heterodont** dentition. Mammals also have two sets of teeth during their life time. The dentition in which two sets of teeth are formed during the life term is termed as **diphyodont** type of dentition. In this condition one set of teeth appears early in life and such teeth are called **milk teeth.** Another set of relatively permanent teeth appears later in life which lasts for the rest of the adult life. This set is called **permanent set of teeth**.

SAQ 4

Match the following statements to the skulls of frog and rabbit by indicating **R** for **rabbit** and **F** for **frog**.

i) The foramen magnum is enclosed in 4 bones and directed downwards.

ii) The skull is flattened with few bones.

iii) The upper jaw has similar teeth

iv) A diastema is seen in the jaws

v) The true palate seperates the buccal cavity from the nasal cavity.

vi) Two occipital condyles articulate with the concavities on the atlas vertebra.

vii) The roof and sides are made up of 2 frontoparietal bones and the floor is made up of parasphenoid.

viii) The auditory capsule is made up of 2 bones periodic and tympanic.

ix) Middle ear has 3 ossicles malleus and incus and stapes

x) Each half of the upper jaw is made up of premaxilla, maxilla and quadratojugal bones.

2.4.2 Vertebral Column of Frog and Rabbit

Frog

The vertebral column of frog is simple and short (Fig. 2.18). It consists of a total of nine vertebrae with a rod-like urostyle at the posterior end. The first vertebra is called the **atlas** vertebra. It is ring shaped with a small centrum and two concavities on its front surface for articulation with two condyles of the skull. Transverse processes and the pre-zygapophyses are absent in atlas vertebra of frogs. The second vertebra in the vertebral column of frog is called the **axis** vertebra as in all other vertebrates.

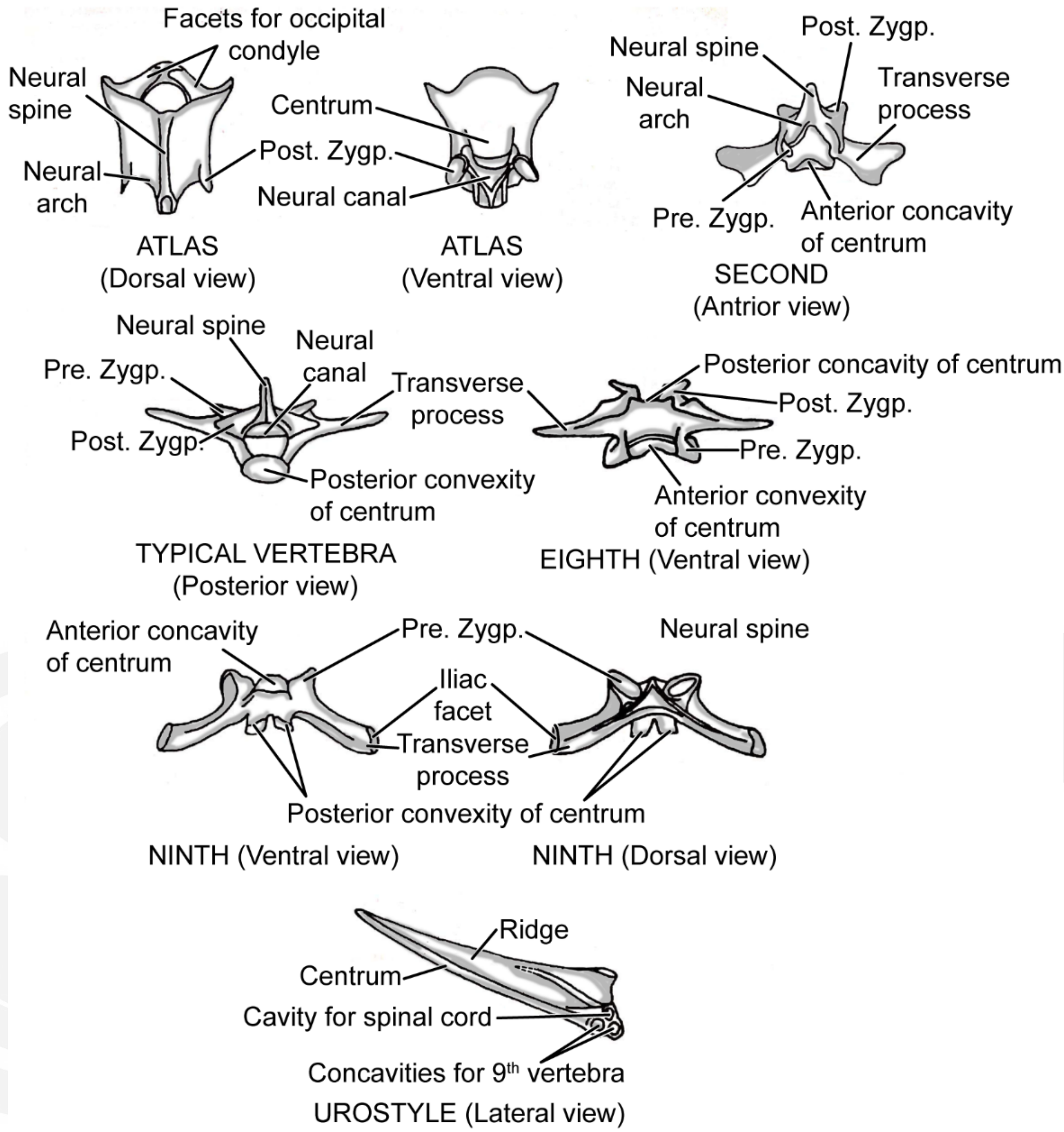


Fig. 2.18: Vertebrae of Frog.

The vertebrae from 3 to 7 of the vertebral column of frogs are typically procoelous. They possess a pair of transverse processes, a pair each of pre- and post- zygapophyses and a neural arch dorsally enclosing the neural canal.These vertebrae also have dorsally, a backwardly directed neural spine. The prezygapophyses of the vertebra lie behind the postzygapophyses which is present in front of the vertebra. The eighth vertebra is biconcave with concavities both in front and behind. The ninth vertebra has a convexity in front and two knob-like bulgings behind for articulation with the two depressions present on the anterior end of the urostyle. The ninth vertebra has transeverse processes which are directed backwards. However, the postzygapophyses are absent in the ninth vertebra.

The urostyle is a long, slender and rod-like in structure. In fact it is as long as the length of the whole vertebral column. The anterior end of the urostyle has two concavities in front for articulation with the two convexities present on the posterior end of the ninth vertebra. A longitudinal ridge is present along the dorsal surface of the urostyle and encloses the terminal part of the spinal cord. Urostyle is a composite structure which represents the fused caudal vertebrae of the tadpole, as a result of the loss of the tail of the tadpole during metamorphosis. In between the vertebrae, **paired apertures** called **intervertebral foramina** are present on either side for the passage of the spinal nerves. The vertebrae are also bound together by ligaments which permit limited movement.

Rabbit

The vertebral column of rabbit is long when compared to that of frog. The vertebral column of rabbit is divisible into five regions: i) the **cervical**, ii) the **thoracic**, iii) the **lumbar**, iv) the **sacral** and the v) **caudal** regions, (Fig. 2.19). There are a total of 45 vertebrae in the vertebral column of rabbits and include- 7 cervical vertebrae in the cervical region, 12 thoracic vertebrae in the thoracic region, 7 lumbar vertebrae in the lumbar region, 4 sacral vertebrae in the sacral region and 15 caudal vertebrae in the caudal region. The vertebrae are separated from each other by plates of fibrous cartilage known as **intervertebral discs**. The central part of the disc is known as nucleus pulpous which is a remnant of the notochord.

The number of vertebrae in the cervical region of mammals is constant irrespective of the neck being long as in giraffe (only the length of each cervical vertebra is larger) or short as in elephant. The exception in the number of seven cervical vertebrae are seen in mammals sloth and manatee about which you have read earlier in the theory course BZYCT-131. The centra of the cervical vertebra are short, the neural spine is small and the vertebral arterial foramina, through which the vertebral arteries come out are present at the base of the transverse processes of all cervical vertebrae except the 7th vertebra. The transverse processes of the cervical vertebrae are fused with the ribs to form a composite structure called the **cervical** rib.

The atlas, the first cervical vertebra has no distinct centrum. It is ring shaped. The neural spine is small and inconspicuous. Transverse processes are large, flattened and perforated. A pair of concavities is present on the anterior surface of the atlas vertebra for articulation with the two condyles of the skull. Small facets are on the posterior surface of the atlas vertebra for articulation with the second vertebra called the axis vertebra. The axis vertebra has a large neural arch which encloses a large neural canal which is divided into an upper part and a lower part by ligament. The spinal cord passes through the upper part and the lower part accommodates the anteriorly directed **odontoid** process of the axis vertebra.

The axis vertebra has a broad centrum which has an anteriorly directed plough-like process called the odontoid process that fits into the lower part of the neural canal of the atlas vertebra. The neural spine of the axis vertebra is long and compressed and the transverse processes are long. The anterior zygapophyses are absent in the axis vertebra

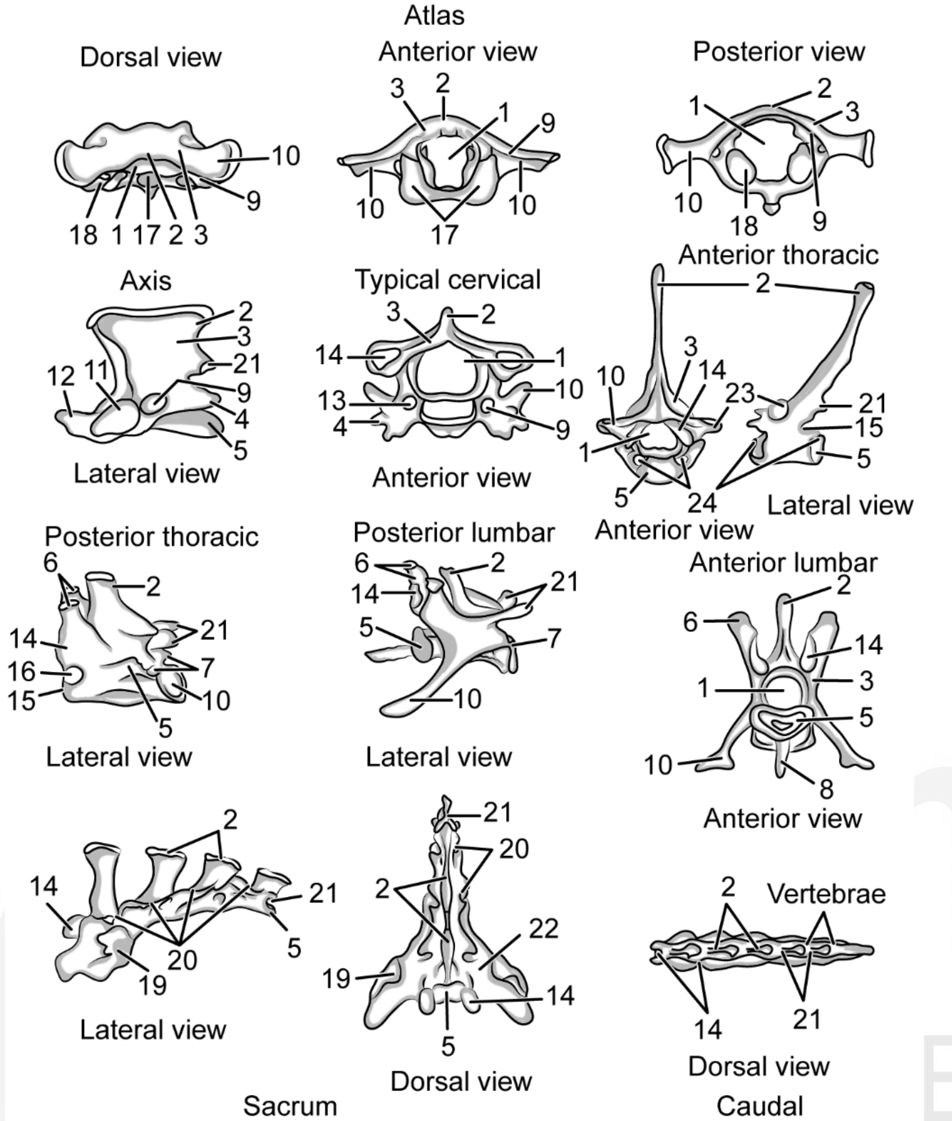
The cervical vertebrae from third to seventh are typical cervical vertebrae of the rabbit and are broad with a small flattened centrum. The typical cervical vertebra has a large neural arch but a small neural spine. A long neural spine is however, present in the 7^{th} vertebra. The transverse processes of all cervical vertebrae except the 7th are bifurcated into a dorsal and a ventral branch. The transverse processes are simple however, and do not possess the intervertebral foramen.

The thoracic vertebrae have a centrum, a neural arch with a backwardly directed neural spine, a pair of short and stout transverse processes, a pair each of the pre- and post-zygapophyses. The thoracic vertebrae are movably connected with ribs through their processes. In the 9th to 12th thoracic vertebrae a pair of **metapophyses** are present above the anterior **zygapophyses**.

The lumbar vertebrae also exhibit typical mammalian vertebrae structure. They are comparatively large with shorter neural spines and longer transverse processes. There is a median ventral process called **hypapophyses** in each of the first two lumbar vertebrae. **Metapophyses** and **anapophyses** are well developed. All the lumbar vertebrae bear short lumbar ribs at the tip of the transverse processes.

The sacral vertebrae are fused together to form a composite structure called sacrum which is wedged between the two halves of the pelvic girdle. The neural spines of the **sacral vertebrae** are large. Hypapophyses and anapophyses are absent in the sacral vertebrae while small metapophyses are present.

The anterior caudal vertebrae exhibit typical mammalian **vertebrae** structure. The **caudal vertebrae** gradually decrease in size posteriorly and the more posterior **caudal** vertebrae are represented only by centra.



1 - Neural canal	9 - Vertebraterial canal	17 - Facet for occipital condyle
2 - Neural spine	10 - Transverse process	18 - Facet for articular surface on axis
3 - Neural arch	11 - Articular surface for atlas	19 - Articular facet for ilium
4 - Cervical rib	12 - Odontoid process	20 - Intervertebral foramina
5 - Centrum	13 - Epiphysis on centrum	21 - Post zygapophyses
6 - Metaphyses	14 - Pre. Zygapophyses	22 - 1st sacral vertebra
7 - Anaphyses	15 - Intervertebral notch	23 - Facet for tuberculum of rib
8 - Hypophysis	16 - Facet for rib	24 - Demifacets for capitulum of ribs

Fig. 2.19: Mammalian vertebrae of rabbit.

2.4.3 Sternum and Ribs of Frog and Rabbit

The sternum is present in both in frogs and rabbits but the ribs are absent in frogs. Let us study in brief the main features of the sternum in frogs and the main features of the sternum and its attachment with the ribs in the rabbits.

Sternum of Frog

The sternum of frog is composed of cartilage and bone. It consists of four segments that are located in front and behind the epicoracoid of the pectoral girdle. Anteriorly the sternum has an omosternum which is connected to a cartilaginous episternum in front and to the epicoracoid of the pectoral girdle posteriorly. A mesosternum is present behind the epicoracoid and behind it a cartilaginous plate-like xiphisternum is present. The sternum of the frog is joined with the pectoral girdle on the midventral line where the two halves of the pectoral girdle are joined. Ribs are absent in frogs. This is present at end of the pectoral girdle of frog.

Sternum and Ribs of Rabbit

The sternum of rabbit is attached to the pectoral girdle only on the ventral side and is not attached to the short ribs. Twelve pairs of ribs in the thoracic region are associated with the vertebrae of the thoracic region. The first 7 pairs of ribs in the thoracic region are called **true ribs** and are connected with the sternum on the ventromedian side. The other 5 pairs of ribs, posterior to the true ribs are called **false ribs** or floating ribs and are not connected to the sternum. In rabbit the sternum is made up of many segmental bones, a feature found only in mammals. The sternum consists of the anterior most bone which is the longest and is called the **manubrium** sterna **or presternum** and has a keel (Fig. 2.20). The last segment of the sternum is called xiphisternum and is in the form of a rounded cartilaginous plate which ends in a rounded xiphoid cartilage. Between these two parts of the sternum are five elongated bony pieces called the sternebrae that make up the body of the sternum called the **mesosternum**. The ribs are attached to the sternebrae by their costal part which is cartilaginous. The other ends of the ribs as you have learned in the earlier section are connected to the thoracic vertebrae and form a ribcage.

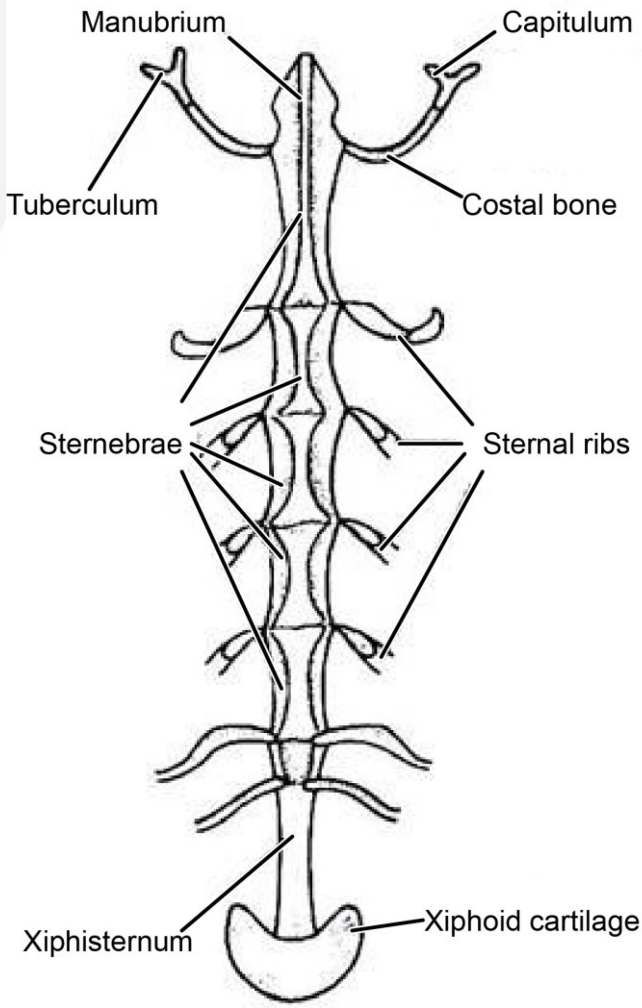


Fig. 2.20: Rabbit sternum.

SAQ 5

Identify the following statements as true or false. Write **T** for the correct statement and **F** for the wrong statement.

a) The first cervical vertebra of the rabbit, the atlas has a distinct centrum.

b) In both rabbit and frog the atlas articulates with the occipital condyles and axis.

c) All the vertebrae of rabbit are procoelous except the atlas.

d) Urostyle is typically found in frog not in rabbit.

e) The vertebral column in rabbit is divided into 5 regions in its entire length and vertebrae are separated from each other by intervertebral discs.

f) The cervical vertebrae in rabbit are connected to the ribs.

g) Lumbar vertebrae in rabbit have stout transverse processes and short spines.

h) The sacral vertebrae are loose and connected to the pelvic girdle in rabbit.

i) The caudal vertebrae decrease in size posteriorly in frog and rabbit.

j) The frog has only 9 vertebrae.

2.5 APPENDICULAR SKELETON OF FROG AND RABBIT

In this section, we will first compare the shoulder or pectoral girdle, of the frog and rabbit. After, which we will compare their pelvic girdle or hip. Finally, we will discuss the two sets of limbs attached to the girdles of the frog and rabbit.

2.5.1 Pectoral Girdle of Frog and Rabbit

The Pectoral Girdle is the anterior girdle found in the terrestrial vertebrates. The head of the humerus which is the anterior most bone of the upper arm of the forelimb articulates with the pectoral girdle of its side.

Frog

The pectoral girdle of the frog consists of two halves, which are united in the midventral line and are separate dorsally (Fig. 2.21 a).The outer ends of the two halves are bent upwards to form an arch-like structure for enclosing and protecting the organs of the thorax. The dorsally bent terminal parts of each half of the pectoral girdle, consists of a cartilaginous, triangular suprascapula, which is partially ossified. Attached to the inner end of the suprascapula on the ventral side, is a stout flat scapula bone. From each scapula two bones, i) the clavicle and the ii) coracoid, extend towards the midventral side. The clavicle of each side meet midventrally through a strip of cartilage called epicoracoid. Similarly, the coracoid of each side also meets the epicoracoid midventrally.

Each clavicle is a slender rod-like bone, located anterior to the coracoid of its side and separated from it by a wide space called coracoid fenestra. At the junction of the clavicle, the coracoid and scapula a depression called the glenoid cavity is present. The head of the humerus bone of the upper arm of the forelimb articulates with the glenoid cavity.

As discussed before, in subsection 2.4.3 the pectoral girdle of frog is joined with the sternum on the mid-ventral line where the two halves of the girdle are joined. We have already described the structure and details of the frog sternum in subsection 2.4.3.

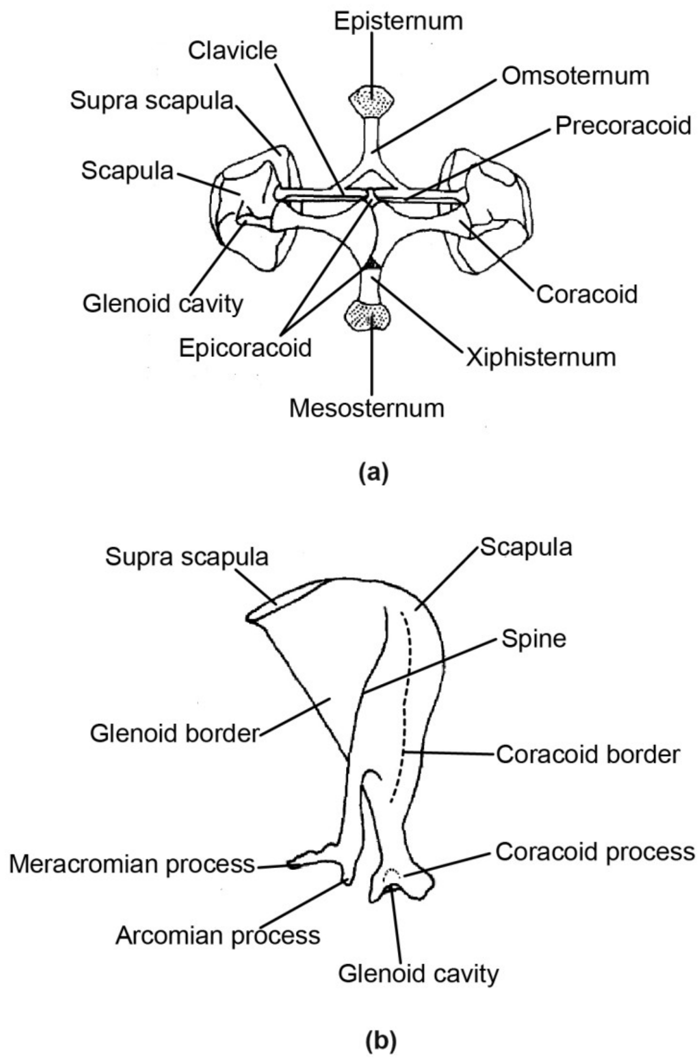


Fig. 2.21: Pectoral girdle a) frog and b) rabbit.

Rabbit

The pectoral girdle of rabbit consists of fewer bones when compared to frog (Fig.2.21 b). The pectoral girdle consists of a flat thin triangular **scapula** and the rod like **clavicle**. The glenoid cavity is present at the narrow end of the scapula where it articulates with the head of the humerus bone of the forelimb. The narrow end also articulates with the clavicle. In the pectoral girdle of rabbits, the coracoid is present as a small curved process called the **coracoids process** (instead of the prominent coracoid as seen in the pectoral girdle of the frogs) and is fused to the scapula at the narrow end in front of the glenoid cavity.

A thin strip-like **suprascapula is present** at the dorsal edge of scapula and a ridge called the **spine** is present on the outer surface of the scapula. The scapula on its free ventral end terminates in a process called the **acromian** process. The scapula also gives out posteriorly a branch like process called the **metacromian**. The clavicle lies obliquely between the presternum and scapula.

2.5.2 Pelvic Girdle of Frog and Rabbit

The pelvic girdle is the posterior girdle found in the terrestrial vertebrates. The head of the femur which is the anterior most bone of the upper leg or thigh of the hind limb articulates with the pelvic girdle of its side.

Frog

The pelvic girdle of the frog is simpler with fewer bones in comparison to its pectoral girdle. The pelvic girdle of frog, consists of two halves joined at one end and free at the other to form a V shaped structure (see Figure 2.22 a). Each half is made up of three bones the **ilium, ischium and pubis.** The ilium is elongated and its bar- like free end articulates with the transverse process of the 9th vertebra. The other end of the ilium together with the pubis and ischuim symphysis(the place where two bones pubis and ischuim in this case are closely joined, forming an immovable joint) forms a disc like structure with a cavity in the center known as **acetabulum.** The proximal head of the thigh bone femur articulates with the **acetabulum** (Fig. 2.22 b). The disc like structure of each side is fused together. The three bones of the pelvic girdle namely, **ilium, ischium and pubis** are distinct and separate during early developmental stages and become fused in the adult. The fusion is assisted by cartilage or bone and this is known as symphysis. In the pelvic girdle of frog there is both pubic and ischiatic symphysis.

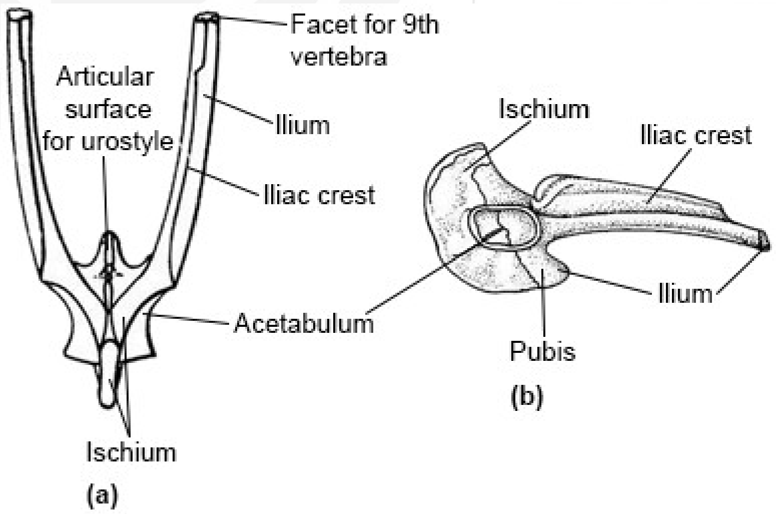


Fig. 2.22: Pelvic girdle of frog. a) dorsal view of the V shaped girdle that supports the hind limbs. b) Lateral view of one half of the girdle.

Rabbit

The pelvic girdle of rabbit also consists of two halves which are united together by symphysis. Each half is composed of the same three bones found in the pelvic girdle of frog, the **ischium**, the **pubis** and the **ilium**, (Fig. 2.23). Ischium and the pubis are united ventrally in the midline by symphysis. The acetabular cavity is found on the outside at the union of **ischium** and **ilium**. The three bones are separate in young animal but become completely fused into a single bone in the adult. This united structure is called **innominatum**. The **Ilium** is dorsal in position and is found in front of the **acetabulum**. It has a rough inner surface which is expanded and wing-like to which the transverse processes of the 1st sacral vertebra are articulated. Each Ischium lies posteriorly and dorsally and continues downwards to form the ischial tuberosity at the **ischiatic symphysis**. Pubis is the smallest of the three bones. It lies anteriorly and is directed downwards. It is separated from the ischium by a wide foramen called **obturator foramen**. The two pubis (plural: pubes) unite midventrally at the **pubic symphysis**. The acetabulum is bound by a small bone called **cotyloid bone.**

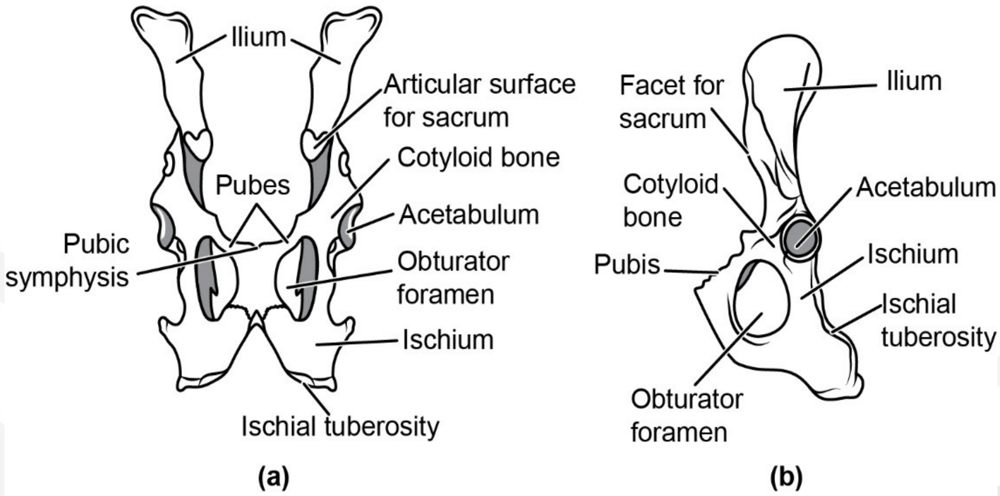


Fig 2.23: Pelvic girdle of frog. a) ventral view of the complete girdle; b) lateral view of left half.

2.5.3 Limbs of Frog and Rabbit

The pattern of the skeleton of the limbs is same in most vertebrates with very little variation. Thus, the pattern of the skeleton of the limbs in both frog and rabbit is similar. Recall the bones of the forelimbs and hindlimbs as given in Table 2.1.

Forelimb of Frog

A single bone called the **humerus** forms the upper arm of the forelimb of each side (Fig. 2.24). It is a stout, long and curved shaft- like bone, with swollen ends on each side. The head **of the humerus** at its proximal end fits into the glenoid cavity of the pectoral girdle. The distal end of the humerus is round with two projections side by side. A ridge known as the **deltoid ridge** extends from the proximal end of the **humerus** upto its middle on its inner side. **This is a characteristic of all vertebrates.** The humerus bone on its distal end articulates with the proximal end of the two bones radius and ulna of the lower arm of the forelimb. The radius and ulna bones are fused in the frog in order to form the **radio-ulna bone.**

The proximal end of the **radio-ulna bone** of the lower forelimb of each side contains a concavity. The distal rounded end of humerus articulate with this cavity to form the elbow joint. A backwardly directed process the **olecranon process** is present at the elbow joint. The distal end of radio-ulna is expanded into two articular surfaces that connect with the 3 proximal carpel bones of the wrist. The other 3 distal carpal bones are arranged below the three proximal carpal bone in order to form the complete wrist. The proximal carpals that articulate with the radius bones are called **radiale**.The proximal carpels present in the middle are called the **central** carpals while the proximal carpels that articulate with the ulna bones are called **ulnare.** The carpals of the distal row are fused and articulate with the metacarpals of the hand. The innermost metacarpal is reduced and the other 4 are long. These metacarpals articulate with the phalanges and provide them support. The thumb which corresponds to the first finger as seen in other tetrapod and bipedal vertebrates is absent in frog. Two phalanges are present in fingers 2 and 3 while there are 3 phalanges in fingers 4 and 5.

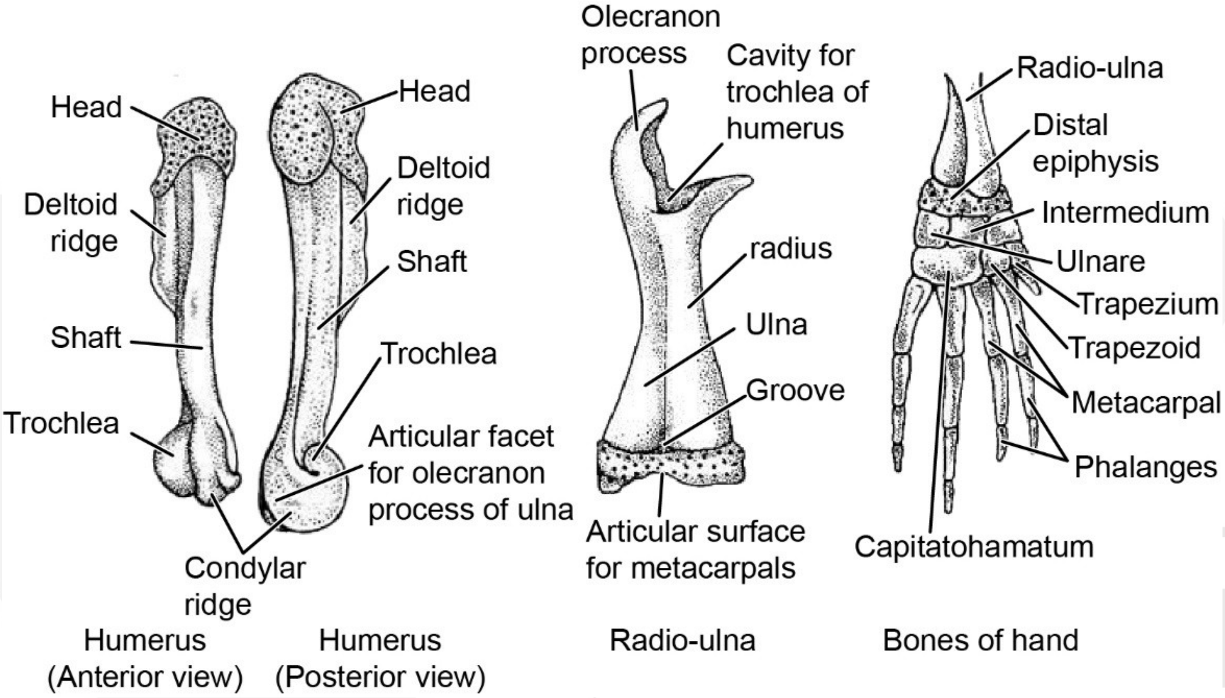


Fig. 2.24: Forelimb of frog.

Forelimb of Rabbit

The number and nature of bones in the rabbit are similar to the frog except for some differences. Look at figure 2.25.You will observe that the proximal end of humerus has two tuberosities at its outer border that provide attachment surface for the bicep muscles. The tendons of the muscles are inserted between the tuberosities in a **bicipital groove.** The deltoid ridge is present on the anterior surface of the proximal part of the shaft of the humerus. The distal end of the humerus also has two articular surfaces for articulation with the 2 bones radio-ulna of the lower arm of the forelimb. The part of the humerus bone that articulates with the ulna has a pulley like formation called **trochlea.** The part of the humerus called the **capitulum** articulates with the radius. Just above the trochlea are two fossae or depressions the anterior is coracoids and the posterior is the olecranon there is a **supratrochlear foramen** through these two depressions (see Fig 2.25 again). The bones of the lower arm, radius and ulna are connected to each other at the ends so that they do not move over. The ulna is the longer of the two and articulates with the olecranon fossa of the humerus by its **sigmoid notch.** The radius is the smaller bone and on the inner side of the arm. The radius and ulna are provided with epiphysis on the distal end that articulates with the wrist. The wrist has 9 bones arranged in 2 rows, the proximal row is made up of 3 bones-**radiale** below the radius, **ulnare** below the ulna and **intermedium** between them. The distal row is made up of **trapezium, trapezoid** situated below the radius; **magnum** and **centrale** situated below the intermedium and the **unciform** situated below the ulna. The metacarpals are narrow and long except the first which is shorter than the others and there are 5 fingers as opposed to the 4 found in frog. All of them have 3 phalanges except the first which has only 2. The distal phalanges have grooves for insertion of claws.

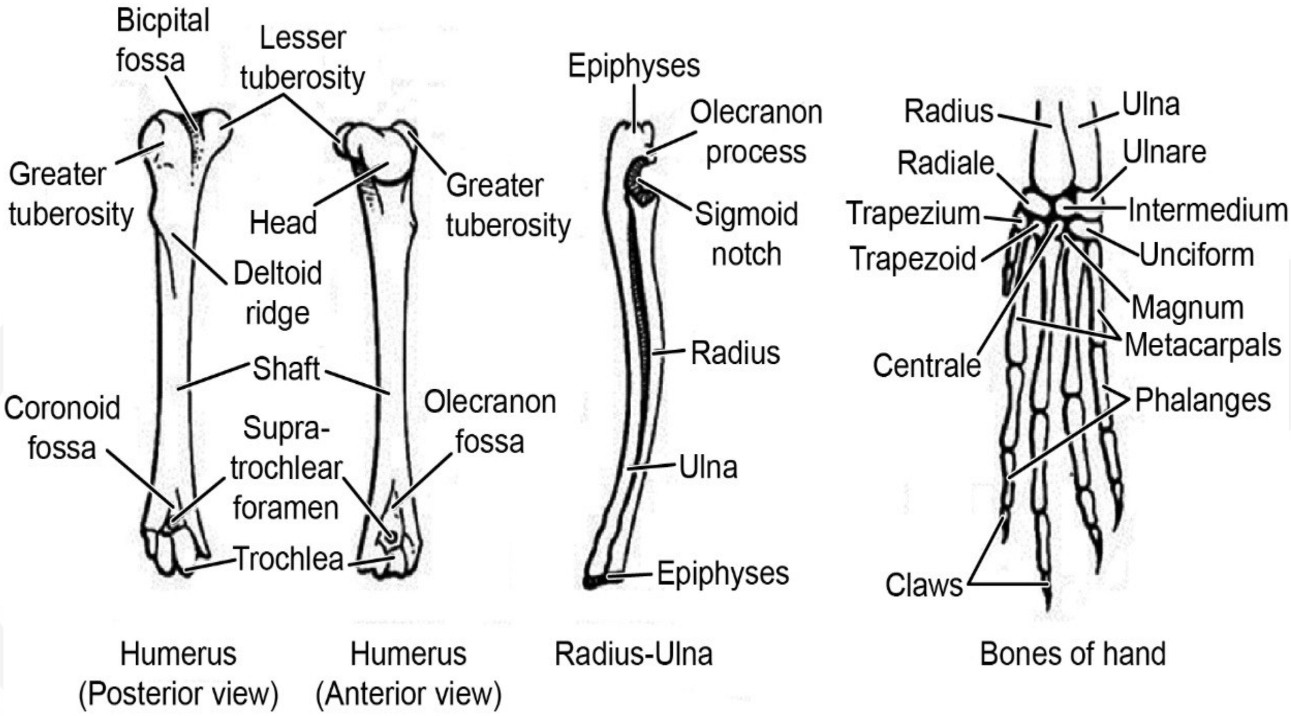


Fig. 2.25: Bones of the forelimb of rabbit.

Hindlimb of frog

As you can see, Figure 2.26, shows the single thigh bone called the femur which is long, slightly curved and swollen at both ends. The femur forms the upper bone of the hind limb and its proximal end fits into the acetabulum of the pelvic girdle. The distal end of the femur is flat and laterally expanded to articulate with the proximal end of the fused tibio-fibula bone (inner bone tibia and outer bone fibula) which forms the shank or lower bone of the hind limb. A median longitudinal groove is present in the tibio-fibula. Near the proximal end of the tibio-fibula a **tibial crest is present**. The distal end of the tibio-fibula bone articulates with the tarsal bones to form the ankle joint. The ankle consists of 4 tarsal bones that are arranged in two rows. The tarsals of the proximal row are longer and consists of two long bones the inner slender **tibale or astralagus** and the outer stout bone the **fibulare or calcaneum**. These two tarsals are united at their ends with a gap in between. These bones increase the length of the hind limbs and help in the jumping motion. The distal row of tarsals are small and fused with the metatarsals. There are 5 elongated metatarsals as the foot has 5 toes with 2 phalanges in the 1^{st} and 2^{nd} and 3 phalanges in the 3^{rd}, 4^{th} and 5^{th}. There is a supplementary 6^{th} toe in the form of a calcar formed of 2 short bones.

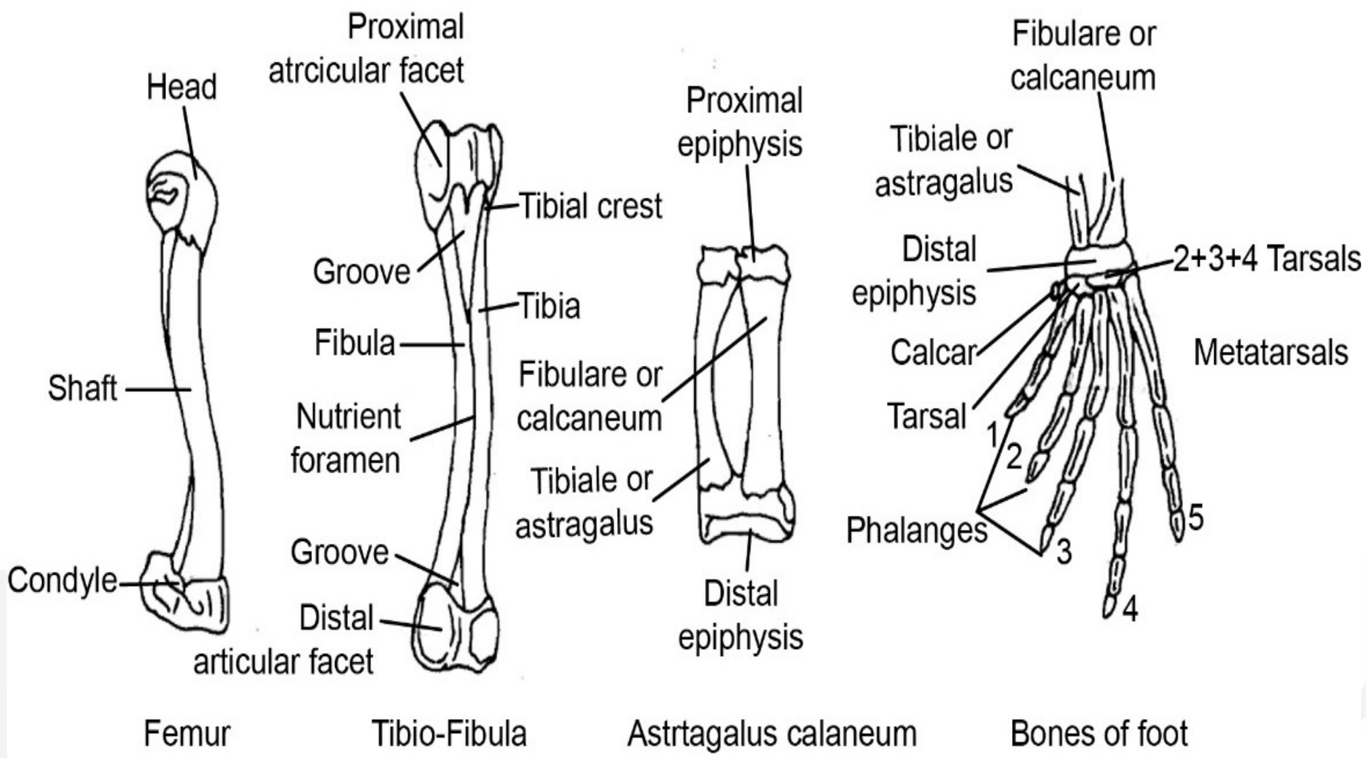


Fig. 2.26: Bones of hindlimb of frog.

Hindlimb of Rabbit

The femur of rabbit is long and stout with a prominent head at the proximal end for articulation with the acetabulum of the pelvic girdle. Three protuberances are present at the proximal head called of the femur which are termed as **greater trochanter, lesser trochanter** and **third trochanters** (Fig.2.27). The greater trochanter is situated above the head of the femur, the lesser trochanter is located below the head of the femur and the third trochanter is present below the greater trochanter. The shaft or main bone of the femur ends distally into a pair of expanded condyles enclosing the intercondylar groove for articulation with the proximal end of the tibia and fibula present below to form the knee joint. The tibia and fibula bones form the lower or shank bone of the hindlimb of the rabbit. The tibia and fibula bones are free above and fused below. The knee joint also has a large bone the patella or the knee cap. The fused distal end of the tibia and fibula articulate with the fused tarsal bones which are 6 in number as compared to 4 tarsal bones in frog. The tarsal bones are arranged in 2 rows with one tarsal in between. The astralagus and calcanium as you can see in Fig. 2.27 are larger than the rest and form the proximal row. The tarsals of the distal row are termed as the **mesocuneiform, ectocuneiform** and the **cuboid tarsals.** The bones of the sole of the foot are formed of 4 long metatarsal bones which articulate with 4 toes. Each toe has 3 phalanges.

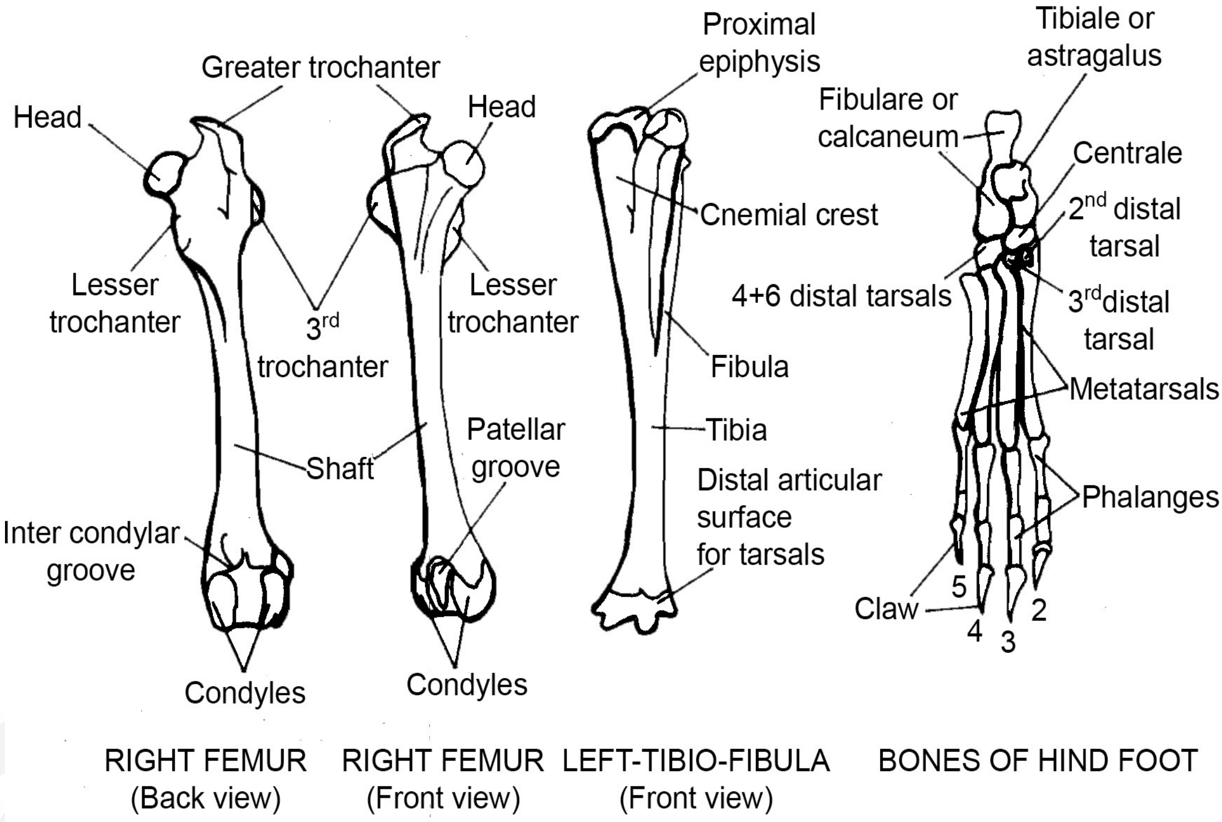


Fig. 2.27: Bones of hindlimb of rabbit.

SAQ 6

Which of the following descriptions relate to rabbit and which to Frog?

i) Tibiofibula or the shank bone has two distal articular facets.

ii) Calcaneum and Astralagus are two tarsals that are fused at the ends but separated in the middle.

iii) The pectoral girdle is made up of only two bones clavicle and scapula.

iv) There are 5 metatarsals in the foot each with 3 phalanges except the first which has 2.

v) The ankle bones or tarsals are fused and foot has 4 metatarsals.

vi) The tibia and fibula are free anteriorly while they are fused posteriorly.

vii) Humerus has anterior deltoid ridge and three tuberosities, distally it has pulley like trochlea and capitulum.

viii) The two bones radius and ulna are immovably articulated along their length.

ix) Six carpal bones in the wrist.

x) Wrist made up of 9 carpals arranged in two rows with 4 bones in each row and one between the two rows.

2.6 SUMMARY

Let us sum up what we have learnt in this unit:

- The vertebrate endoskeleton is made up of living tissue of mesodermal origin and grows with the growth of the animal. It supports and protects the internal organs and gives shape and rigidity to the animal form. The endoskeleton is made up of cartilage and bone both composed of living tissue and consisting of a nonliving matrix secreted by its living cells. Cartilage has a matrix of chondrin and bone has a matrix of collagen which entraps inorganic calcium salts. Bones are of two types the replacing (cartilage) bones and investing bones.

- The skeleton can be divided into axial and appendicular skeleton. The axial skeleton consists of the skull and vertebral column. The skull forms the skeletal frame work for the head of craniate vertebrates and consists of different parts enclosing brain, cranial nerves and other sense organs found in the head. In addition to the cranium and the sensory capsules the skull contains other structures which are derived from the visceral skeleton also refered to as **splanchocranium.**

- The visceral arches support the gills in fish and the mandibular arch gave rise to the jaws, jaw suspensorium and later have been modified in terrestrial vertebrates to form the ear ossicles.

- The vertebral column is a chain of segmented structures called **vertebrae** (vertebra - singular). It extends from behind the skull anteriorly to the tip of the tail posteriorly. It supports and protects the spinal cord. The vertebrae have similar basic structure consisting of a central body, neural arch, transverse processes. They are classified into different categories on the basis of their structure and specialised according to their location in the body.

- The appendicular skeleton consists of the anterior and posterior girdles to which the fins in fishes and paired limbs of tetrapod and bipedal vertebrates are attached. The extremities of the limbs of tetrapod and bipedal vertebrates are pentadactyl being provided with five digits each. The limbs of tetrapod and bipedal vertebrates have similar joints and similar number of skeletal elements.

- Sets of paired slender curved bones called ribs are found in the thoracic region of most vertebrates. They are attached to vertebrae at the dorsal end and to the sternum at (breast bone) at the ventral end, Together with the vertebral column and the sternum the ribs form a skeletal cage enclosing and protecting the organs of the thorax.

- The salient features of the axial and appendicular skeletons of two tetrapods: frog and rabbit are described in detail and compared. The frog shows the first adaptations for amphibious life among vertebrates while the rabbit a mammal, is fully terrestrial in its habitat. The skeletons of both these vertebrates are suitably adapted for their life styles.

2.6 TERMINAL QUESTIONS

1. Mention the two types of endoskeletal structures found in vertebrates. What is the difference between their ground matrix?

2. Fill in the blanks in the following sentences by selecting an appropriate word from those given in the parenthesis after each sentence:

   a) The skeleton of the head is known as ……………………. (vertebral column, pelvic girdle, skull)

   b) Cranium encloses and protects the ……………………… (eye, heart, brain)

   c) The brain within the cranium is in contact with the spinal cord through ………………………… an aperture found at the hind end of the cranium (fenestra ovalis, foramen magnum, external nares).

   d) The vertebra with concavity infront and convexity behind is called ………………….. type (amphicoelous, procoelous, opisthocoelous).

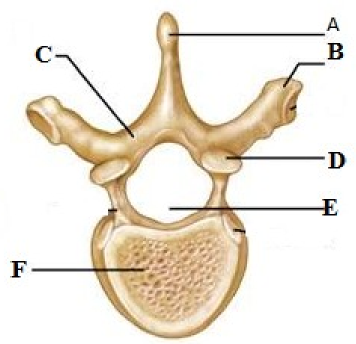
   e) The bone humerus of the upper arm articulates with the pectoral girdle at ……………………… cavity (glenoid, acetabulum, zygapophysis).

   f) Radio-ulna a composite bone is found in …….................. (rabbit, bat, frog).

3. Names of some bones are given in column A and the part of the skeleton in which these bones occur in column B. Match them.

Column A	Column B
a. Parietal	A. Pectoral girdle
b. Vomer	B. Cranium
c. Maxilla	C. Olfactory capsule
d. Dentary	D. Upper jaw
e. Clavicle	E. Pelvic girdle
f. Pubis	F. Lower jaw

4. Label the parts of the vertebra given below:



5. State whether the following sentences are true (T) or false (F).

   a. Cranium is a part of the vertebral column.

   b. Jaws are derived from the visceral skeleton.

   c. Axis is the name of the first vertebra.

   d. The bone in thigh segment of the hind limb is femur.

   e. Glenoid cavity is found in the pelvic girdle.

   f. Deltoid ridge is found on the humerus.

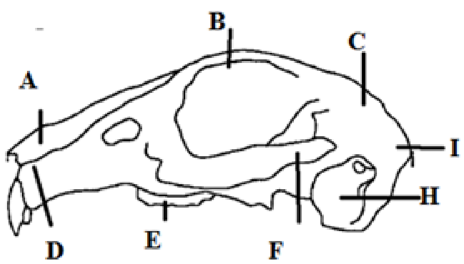
6. How many bones are found in the lower jaw of rabbit?

7. Mention the names of bones bearing teeth in the skull of frog.

8. Give five features that you can use to distinguish between the skulls of frog and rabbit.

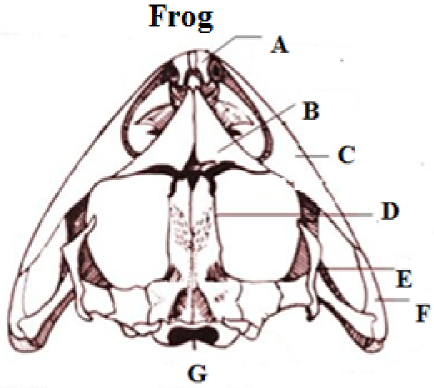
9. Label the given diagrams:

Rabbit



Skull lateral view

Frog



Skull dorsal view

2.7 ANSWERS

Self-Assessment Questions

1. i) Collagen in bone and chondrin in cartilage;

   ii) Osteocytes

   iii) Osteon

   iv) Endochondral ossification

2. (A). (i) front, behind; (ii) Amphicoelous; (iii) Heterocoelous;

   (iv) flat, depressions.

   (B) (i) Splachocranium; (ii) mandibular arch; (iii) Palatoquadrate;

   (iv) cyclostomes; (v) autostylic.

3. (a) iii (b) iv (c) i (d) ii.

4. i). R ii). F iii). F iv). R v). R vi). F & R vii). F viii). F ix). R x). F.

5. a) F b) T c) F d)T e) T f) F g) T h) F i) F j) T

6. (i) F (ii) F (iii) R (iv) F (v) R (vi) R (vii) R (viii) R (ix) F (x) R

Terminal Questions

1. Cartilaginous and bony; cartilage has a matrix of chondrin, bone has a matrix of collagen and mostly inorganic calcium phosphate

2. a. skull; b. brain; c. foramen magnum; d. procoelous; e. glenoid; f. frog

3. a & B; b & C; c & D; d & F; e & A; f & E.

4. A=neural spine; B=transverse process; C=neural arch; D=articular facet; E=neural canal; F=centrum.

5. a. false b. true c. false d. true e. false f. true

6. One.

7. Premaxilla, Maxilla and Vomer.

8. i). Foramen magnum in frog is directed backwards and encircled by 2 exoccipitals while in rabbit it is directed downwards and encircled by 4 bones 2 exoccipitals, supraoccipital and basioccipital

   ii). Frog skull is broads and flattened while rabbit skull has a domed cranium and elongated frontal end

   iii). Teeth in frog present only in the upper jaw and vomer and attached to them while in rabbit teeth are present in both upper jaw and lower jaw placed in individual sockets, they are heterodont.

   iv). Large orbits placed on top of head in frog while in rabbit the orbits are lateral and there is an interorbital bone.

   v). Lower jaw in frog is made up of three bones while in rabbit there is a single bone that makes the lower jaw

9. Rabbit skull: A=Nasal; B=orbit; C=parietal; D= premaxilla; E=Maxilla; F=zygomatic arch; H = Tympanic bulla; I =supraorbital.

   Frog Skull dorsal side: A=premaxilla; B = Nasal; C= maxilla; D=frontoparietal; E =squamosal; F= quadratojugal; G= foramen magnum

UNIT 3

DIGESTIVE SYSTEM

Structure

3.1 INTRODUCTION

In the previous unit you have studied about cartilage and bones of vertebrates. In this unit you will study that all vertebrates possess an alimentary canal as an organ for digestion and absorption of food materials. Digestion does not occur in a particular region of the alimentary canal but takes place in different regions so that digestion of food materials may be completed. All vertebrate alimentary canals have a common basic organization and similar major subdivisions. However, the differences seen in the anatomy in different animal groups is correlated to their different feeding habits. We shall discuss here the feeding mechanism in different groups of vertebrates such as fishes, amphibians, reptiles, birds and mammals and correlate with the adaptations seen in their alimentary canal.

We will start the unit with the study of structure and arrangement of teeth in vertebrates and see that they can be classified in different ways. Then we will discuss the feeding mechanisms and digestive systems of non-mammalian and mammalian vertebrates.

Objectives

After reading this unit you should be able to:

- describe the dentition pattern in vertebrates,
- describe the feeding adaptations in vertebrates,
- discuss the organisation of vertebrate alimentary canal in relation to their feeding habits, and
- discuss the specialisation of alimentary canal of mammalian herbivores, carnivores and omnivores.

3.2 COMPARATIVE DENTITION

Teeth are hard structure present in the oral cavity and are present in nearly all the vertebrates particularly in all mammals in some stage of their life with some exceptions. For example, among mammals, in some teeth are not present in adults eg. in Whalebone whales, while in *Ornithorhynchus* (platypus) and *Tachyglossus* (echidna) teeth are absent throughout life. In echidna teeth develop in foetus and are discarded in uterus resulting in adults being devoid of them.

In most other vertebrates teeth develop partly from the epidermis and partly from the underlying dermis. There is a covering of enamel with an underlying layer of dentine. Fishes, amphibians and reptiles have simple pointed teeth. Some fishes like the chimeras and lungfishes have plated teeth that have rough or serrated ridges separated by grooves. In mammals each tooth is lodged in a socket called alveolus in the jaw. The part of tooth developed from epidermis is **enamel.** The remainder of tooth - **dentine, cement** and **pulp** - is formed from the sub-adjacent **mesodermal** tissue (Fig.3.1). Amongst vertebrates the teeth of lampreys are quite different from all others as they are cornified epidermal structures that do not have either enamel or dentine.

In fact, the dentition is so distinctive in different groups that it often becomes the basis for identifying living animals and fossil species.

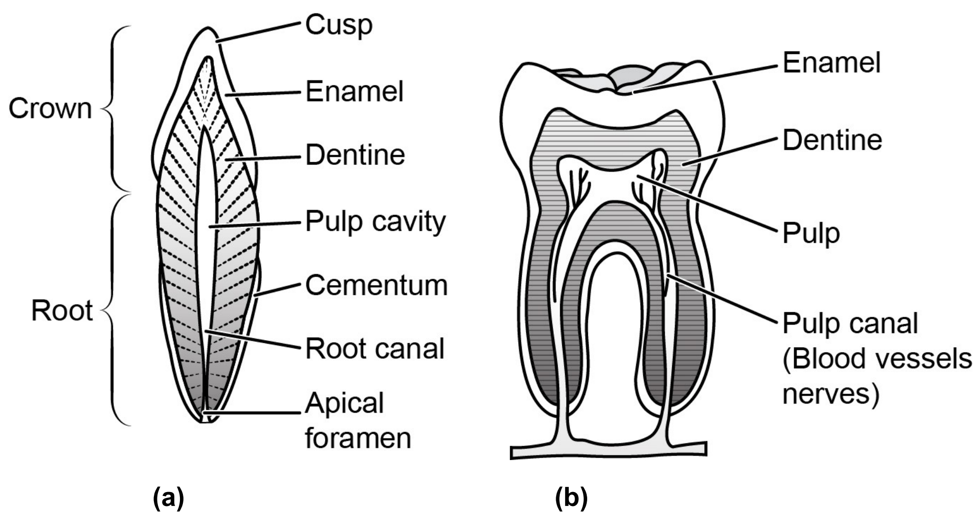


Fig. 3.1: Tooth structure (a) Tooth with single root, (b) Molar tooth with roots.

Teeth can be classified according to their attachment with the jaws (see Fig.3.2), appearance and nature of replacement as given in the Tables 3.1 and 3.2.

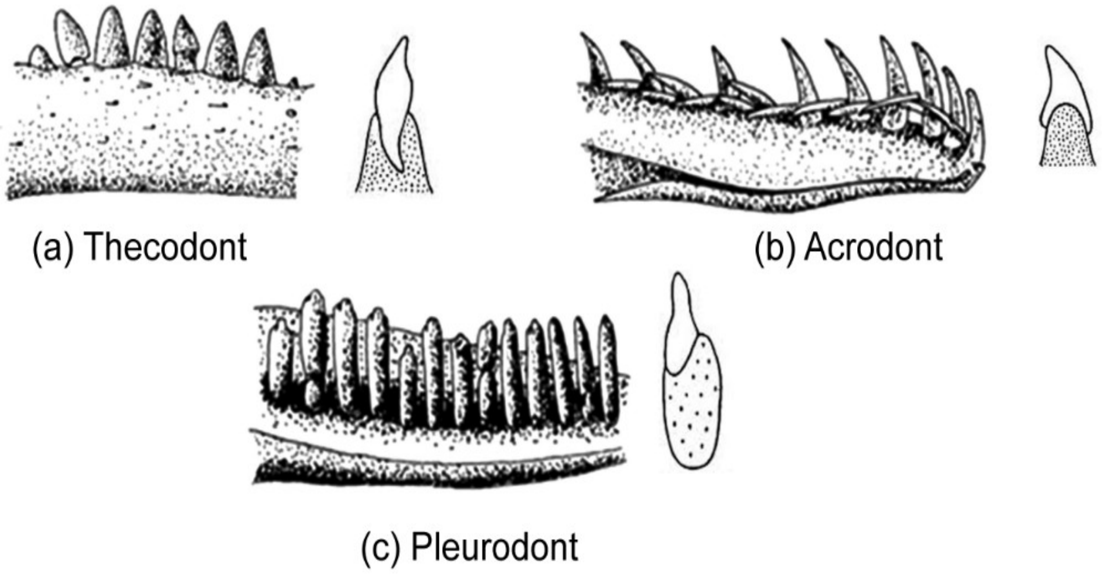


Fig. 3.2: Classification of teeth on the basis of attachment to the jaw bone. a) In thecodont type the teeth are set in sockets in the jaw bone as seen in mammals and alligators; b) In acrodont type the teeth are attached on the surface of the jaw bone as seen in most non-mammalian vertebrates; c) in pleurodont type the teeth are attached to the rim, on the inner side of the jaw bone as seen in modern amphibians and lizards.

Table 3.1: Types of teeth based on appearance.

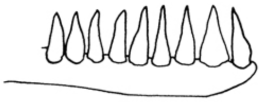
Types of teeth	Appearance	Example
 Homodont	Teeth are uniform in appearance	Most non-mammalian vertebrates; dolphins and porpoises
 Heterodont	Teeth differ in general appearance, (incisors, canines, premolars and molars)	Humans, other mammals

Table 3.2: Types of Dentition based on the nature of their replacement.

Types of dentition	Nature of replacement	Example
Monophyodont	Only one set of teeth are present throughout life. Milk teeth persist and do not get replaced by permanent teeth	Beluga whales, most of cetacean that also include porpoise, dolphins, narwal, some rodents, insectivorous moles and marsupials.

Types of dentition	Nature of replacement	Example
Diphyodont	With just two sets of teeth the first set the deciduous dentition, or milk teeth appears during early life. It consists of incisors, canines and premolars but no molars. As the mammal matures these teeth are shed and replaced by permanent dentition consisting of second set of incisors, canines, premolars and molars.	Most mammals, Humans and other Primates
Polyphyodont	Teeth are continuously replaced. This type of dentition ensures rejuvenation of teeth if wear or breakage diminishes their function	Most lower vertebrates, sharks, amphibians, reptiles.

Specialized Teeth in Mammals

The most specialized teeth among vertebrates are seen in mammals, the teeth are not only specialized to capture or clip food, but they are also specialized to chew it.

The heterodont dentition of mammals includes four types of teeth within the mouth - i.e. **incisor** at the front, **canine** next to them, **premolars** along the sides of the mouth, and **molars** at the back. Incisors are generally used at the front of the mouth for cutting or clipping; canines for puncturing and holding; premolars and molars for crushing or grinding food. It is often hard to distinguish premolars from molars visually. The collective term used for both is cheek or molariform teeth. Cheek teeth may be quite diverse, a reflection of their many specialized functions.

The number of each type differs among groups of mammals. The dental formula is shorthand expression of the number of each kind of tooth on one side of the jaw for a taxonomic group. For example, the dental formula of dog is:

$$I.\frac{3}{3}, C.\frac{1}{1}, Pm.\frac{4}{4}, M.\frac{2}{3}$$

This means that there are three upper and three lower incisors (I) one upper and one lower canine (C), four upper and four lower premolars (Pm), and two upper and three lower molar (M), 21 per side or 42 total (see Fig.3.3 also). Sometimes, the dental formula is written as 3-1-4-2/3-1-4-3, the first four numbers indicating the upper teeth and the second four numbers are the lower teeth. The dental formula for mouse is 1-0-0-3/1-0-0-3. You notice that the missing canines and premolars are indicated by zeros. Rodents do not have canines their incisors are used for gnawing, scraping and nibbling. The incisors are sharp and keep growing throughout life.

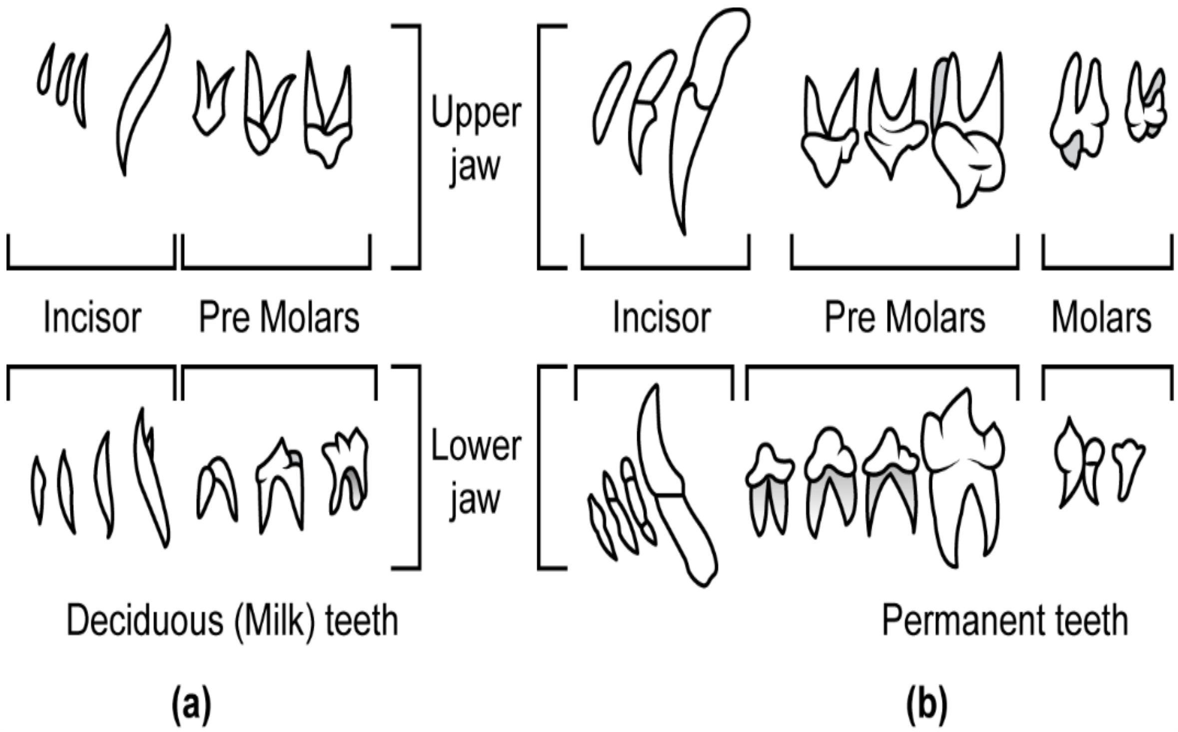
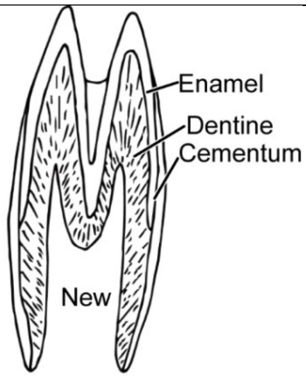
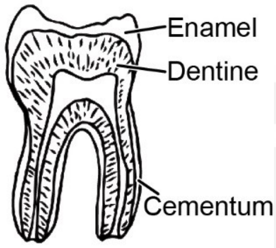
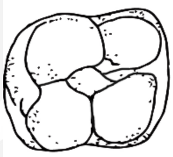
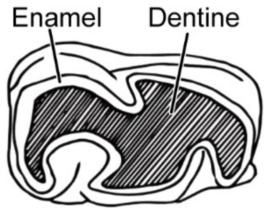
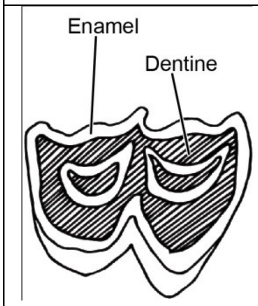


Fig. 3.3: a) Deciduous and b) Permanent dentition.

The teeth of mammals are modified according to their feeding habits and can be classified accordingly as given in Table 3.3. In herbivores the teeth are hypsodont that can grind plant material to break tough cell walls. Their cusp or occlusal surface is **worn** unevenly because the minerals which form the surface-enamel, dentine and cementum-differ in hardness. Occlusal surfaces are functionally important because they ensure that ridges and depressions persist throughout life, thereby maintaining a rough grinding surface which does not become smooth with continued use. The selenodont and lophodont teeth have folds of enamel running deep in between areas of dentine, as the teeth surfaces wear off the surface enamel is lost but the folds remain. The exposed dentine wears off so that ridges of enamel are separated by grooves of dentine thus forming good grinding surfaces.

Mammals possess a variety of specialized teeth. In some primates, cutting edges form on the upper canine and lower first premolar. These teeth are deployed in fights between individuals or in defense. In carnivores, the upper last premolar and lower first molar form **carnassials**, these specialized teeth slice against each other like a scissors to cut sinew and muscle. Tusks arise from different teeth in different species. In elephants, canines are absent but the tusks are elongated second pair of incisors in the upper jaw (Fig. 3.4) and in walruses, the paired tusks are upper canines that protrude downward (Fig. 3.4). In carnivorous mammals canine teeth together with powerful jaws are used to kill preys. Sometimes these teeth are used to puncture major blood vessels in the neck, of the prey causing the prey to bleed profusely and weakening it. Adult lion bites into the neck and collapses the trachea of the prey and suffocate. Some mammals such as anteaters and baleen whales lack teeth altogether (Fig. 3.4).

Table 3.3: Types of teeth on the basis of crown height and cusp pattern.

Types of tooth	**Position of the crown**	**Example**
 Hypsodont	Crowns are high	Horse
 Brachyodont	Crowns are low	Human and Pigs
States of cusp pattern		
 Bunodont	Cusps form peaks	Omnivores like human
 Lophodont	Cusps drawn out into ridges	Perissodactyls and Rodents Rhinoceros Zebra, Rabbits, rats, elephants.
 Selenodont	Crescent shaped cusps	Artiodactyls e.g., Hippopotamus and African buffalo

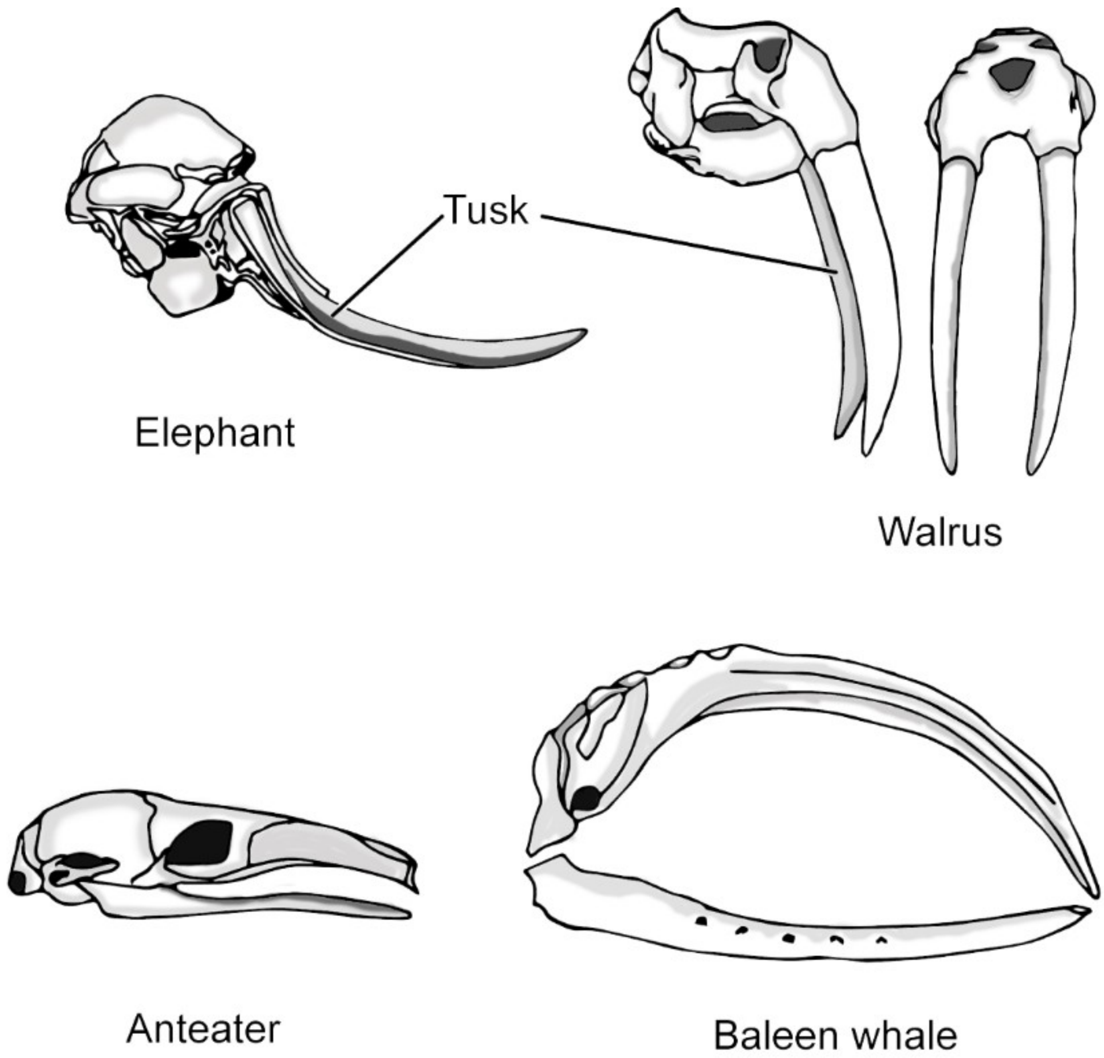


Fig. 3.4: Tusks arise from both upper incisors in the elephant, and from canines in walrus. The teeth are absent in adult anteaters, and baleen whales.

SAQ 1

In the following statements, put a tick mark (√) on the correct ones and a cross (×) mark on the incorrect ones in the given boxes.

i) The part of the tooth developed from the epidermis is the enamel. ( )

ii) Thecodont dention has teeth arising from sockets in the jaw bone. ( )

iii) Herbivores have specialized teeth known as carnassials. ( )

iv) Some mammals have indefinite number of teeth e.g. elephant and monkey. ( )

v) Elephants have extremely specialised teeth because they do not have canines and elongated pair of second incisors. ( )

vi) Bunodont teeth have almost flat cusps. ( )

3.3 FEEDING MECHANISMS

Obtaining nutritional essentials is clearly a key to the success of any animal/species. Much of the routine functioning of an animal is directed towards this purpose. For example, the complex and sophistication of the nervous system, evolved largely due to the selective pressure on obtaining of sufficient food and on avoidance of becoming someone else's meal. Animals use various strategies to feed. Some species search, stalk, pounce, capture, and kill. Sessile animals, unable to move about, resort to more subtle means, such as surface absorption, filter feeding or trapping. Vertebrate, have various feeding devices that are described here in a systematic evolutionary sequence. We will now discuss different devices employed by various groups of vertebrates.

3.3.1 Fishes

Cyclostomes, elasmobranchs, and teleosts, use a variety of feeding mechanisms. They have pointed teeth, mounted on jaws or palate, which aid in holding, tearing and/or swallowing prey. Most fishes are carnivores, they prey on a variety of animal food from zooplankton and insect larvae to large vertebrates. Some deep sea fishes are capable of eating prey nearly twice their own size. This is an adaptation for life in a world where meals are infrequent. Most advanced ray-finned fishes cannot masticate their food. Some such as the wolf eel have molar like teeth in the jaws for crushing their prey, that may include hard bodied crustaceans. Others grind their food using powerful pharyngeal teeth in the mouth to seize their prey. The incompressibility of water makes the task even easier for many large mouthed predators that use **suction feeding**. When the mouth is opened, a negative pressure is created which sweeps the prey inside. This method is mostly used by teleosts along with **ram feeding** in which the predator moves past the prey with its mouth open engulfing it along with the water.

One of the most important, successful and widely employed methods for feeding that evolved is filter feeding. Majority of filter feeders use ciliated surfaces to produce currents which can draw drifting food particles into their mouths. Free-swimming filter feeders like herring and basking shark have the advantage of being able to swim through their food and thus can be more selective in their feeding. The water flows out through the gills leaving the food behind (Fig. 3.5).

A second group of fishes are herbivores which eat flowering plants, algae and grasses. Although plant eaters are relatively few in number, they are crucial intermediates in the food chain especially in fresh water rivers, lakes, and ponds which contain very little plankton.

Another group of fishes are **omnivores** feeding on both plant and animal food. Finally there are **scavengers** which feed on organic debris and on the parasites that suck the body fluids of other fishes.

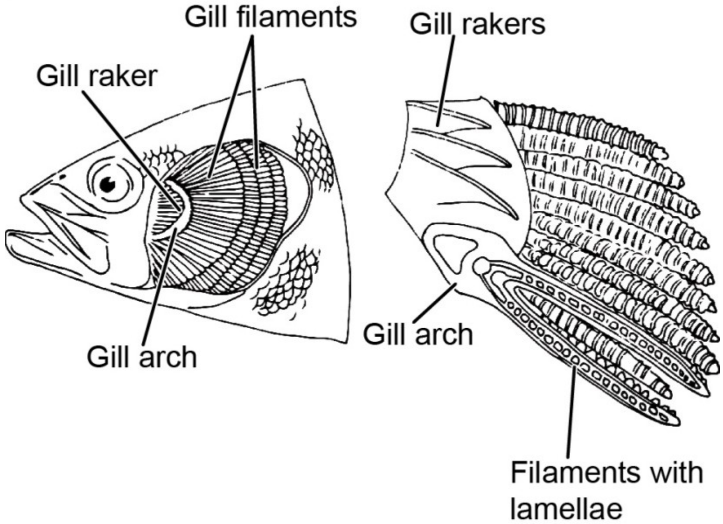


Fig. 3.5: Herring and other filter-feeding fishes use gill rakers, which project forward from the gill bars into the pharyngeal cavity to strain out planktons. Herring swim almost constantly, forcing water and suspended food into the mouth, food is strained out by gill rakers, and water passes out of the gill openings.

3.3.2 Amphibians

Adult amphibians consume a wide variety of food. Anurans and salamanders feed mostly on insects and other arthropods, while caecilians feed mostly on earthworms and other small bugs. Aquatic salamanders lunge at their prey with wide open mouths sucking it in with their expanded buccal cavity. Frogs are carnivores like most other adult amphibians. They feed on insects, spiders, worms, slugs, snails. millipedes or any thing else which moves and is small enough to be swallowed whole. They snap at moving prey with their protrusible tongue (Fig. 3.6) which is attached to the front of the mouth and is free behind. The free end of the tongue is highly glandular and produces a sticky secretion, that adheres to the prey. Teeth present on pre-maxillae, and vomers are used to prevent escape of prey but not for biting or chewing them. The larval stages of anurans (tadpoles) are herbivores, feeding on pond algae and other vegetable matter.

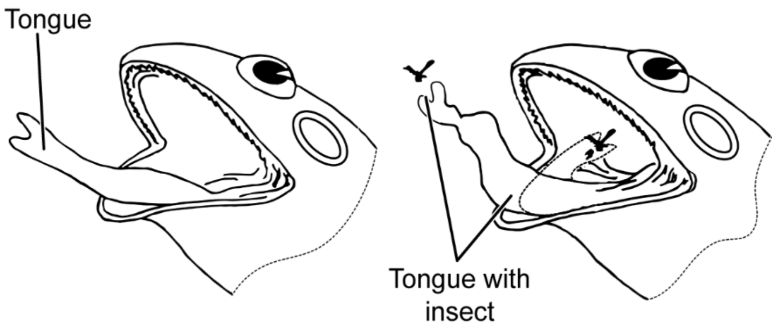


Fig. 3.6: Feeding in frog showing the position of tongue in catching an insect. The tongue in frog is highly mobile. It is attached to the front of the mouth permitting the sticky organ to be flicked far out with considerable speed and accuracy, the insect sticks at the end and the tongue returns back in the mouth. The prey is then crushed against a peculiar patch of teeth on the roof of the mouth and swallowed whole.

3.3.3 Reptiles

Reptiles are mostly carnivorous though some like the land turtles, tortoises are vegetarian feeding on grass and other vegetable matter. Green iguanas and *Uromastix* are also vegetarian while marine iguanas feed on sea weed. Reptiles like chameleon fling out their tongues to catch insects from a distance of several inches.

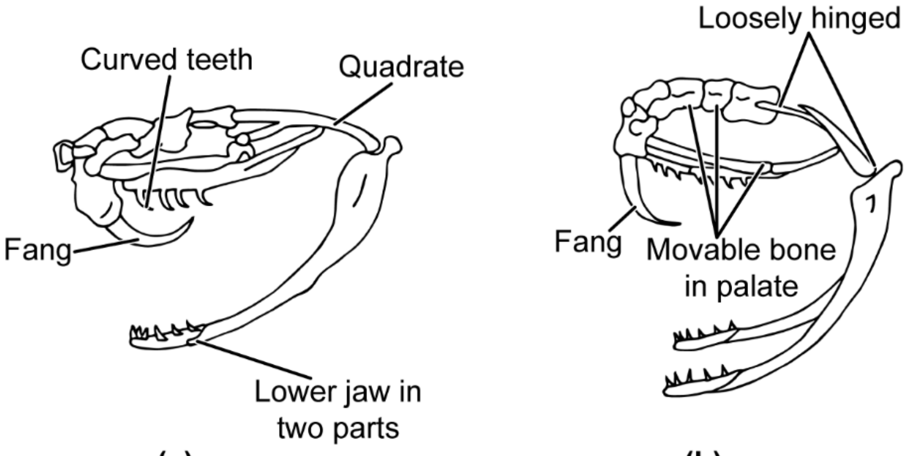


Fig. 3.7: Rattlesnake skull in a side view. (a) Partly open. (b) Open for striking. The fangs are tubular for delivery of toxin and are hinged to facilitate their storage between strikes.

Reptilian jaws or palate are provided with pointed teeth that help these animals in holding, tearing or swallowing their prey. Non-mammalian teeth are generally poorly differentiated from one another. One exception is found among the poisonous snakes, such as vipers, cobras and rattle snakes, which have modified teeth, called **fangs** which are used to inject venom (Fig. 3.7). These fangs are either equipped with a groove or are hollow, very much like a syringe needle to deliver venom at the site of bite. In rattle snakes, fangs fold back against the roof of the mouth, but extend perpendicularly when the mouth is opened to strike. Snakes cannot tear or chew their food. Captured prey is swallowed whole, a surprising feat since the prey is often larger than the snakes. The mouth is extremely flexible because of the arrangement of bones in the head and jaw. The lower jaw is loosely attached to the quadrate bone and can be disconnected while swallowing and even the bones of the palate are movable, all helping to draw the prey into the gaping mouth. The oesophagus and stomach can stretch considerably as can the body wall. There is no sternum, so the ribs can move freely as the prey passes through the gut. This enables a snake to swallow animals larger than the diameter of its head.

3.3.4 Birds

Birds have no teeth, but instead have horny beaks which exemplify adaptive radiation suited to a **gastronomic** (art of choosing, preparing and eating good food) life style.

Birds consume a variety of other animal foods such as seeds, fruit, insects, worms, molluscs, crustaceans, fish, frogs, reptiles, mammals as well as other birds. A very large group of birds feed on nectar. Some birds are **generalists** that is, omnivorous like crows and bluejays that eat whatever is seasonally abundant. Others are **specialists** called **stenophagous,** or “narrow range eating” species that focus on a specific type of food.

Beaks of birds are strongly adapted to their feeding strategies. Beaks may be generalised as strong, pointed beaks of crows, to grotesque, highly specialised ones in flamingoes, hornbills and toucans. Figure 3.8 shows some of the specialized type of beaks that suit the birds feeding habits. The beaks of small seed eaters are short, stout, pointed like that of a sparrow. The crossbill is a unique type of seed eater, its upper and lower beaks do not align and are crossed, it can use the beak to open pine cones. Seed eating birds eat their food as whole, but may subject it to grinding in a muscular gizzard which contains stones (gastroliths) pebbles which aid birds in the grinding process. Insect eaters have thin, short pointed beaks. A well known insect eater is the woodpecker which has a straight, hard, chisel like beak. Anchored to a tree trunk with its tail serving as a brace, the woodpecker delivers powerful, rapid blows (upto 20 times/sec) to build nests or expose the burrows of wood boring insects. It then uses its long, flexible, barbed tongue (three times longer than the bill) to seek out insects in their holes and tunnels. Woodpecker’s skull is especially thick and fitted close to the brain to absorb shock.

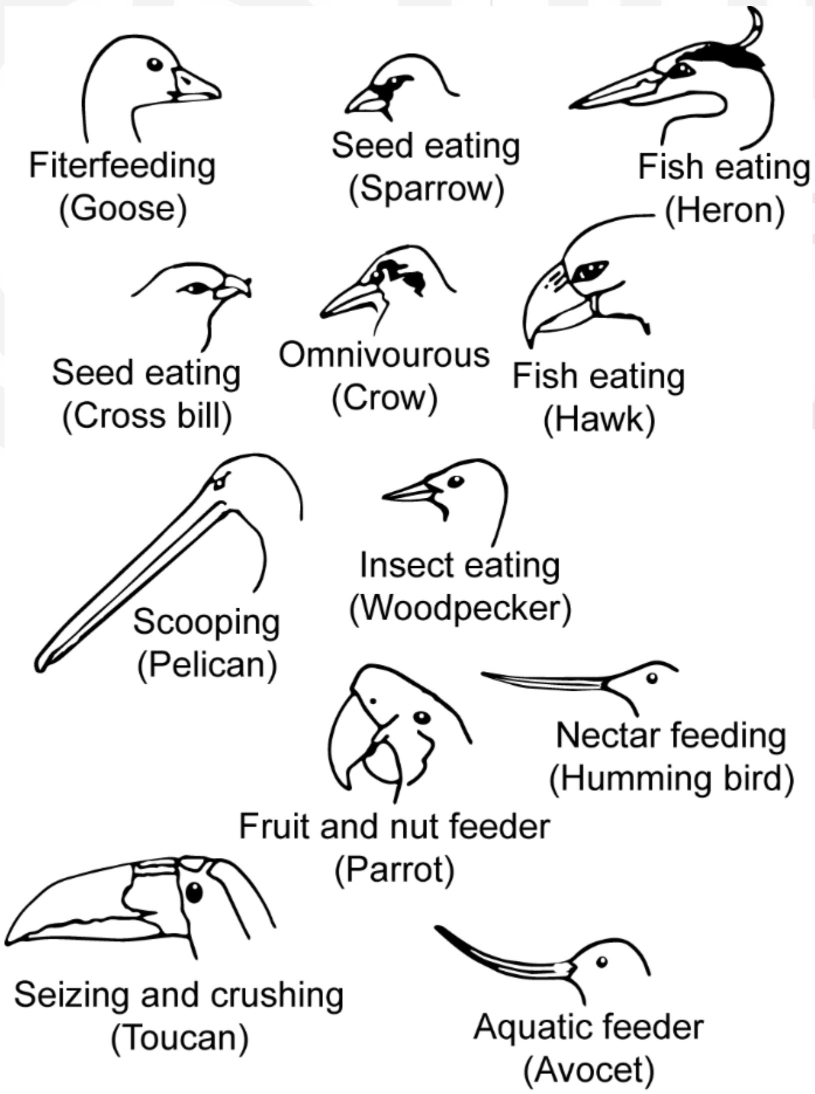


Fig. 3.8: Bird beaks adapted to different modes of feeding.

Water feeders like herons, egrets, kingfishers that eat fish have sharp pointed, spear like beaks. Though ducks and geese live near water, they don't eat fish and have long flat beaks that are used for straining water and mud from aquatic plants through comb like filters lining the beak edges.

Nectar eaters like the hummingbird has long, slender beak, that is a protective covering for its tongue. The tongue has two grooves that draw water by capillary action. They also supplement their diet by catching flying insects by widening the gape of the mouth as their mandible can be actively flexed downwards.

Birds of prey such as hawks, kites, owls, eagles etc., have interesting adaptations. In some cases, the feeding habits are reflected in the feet as well. Typically raptorial birds or birds of prey, have long, curved talons for grasping prey which they tear with their strong hooked beaks. Ground foraging species such as grouse and pheasants have heavy, strong feet for scratching the soil.

Fig. 3.9: Convergence in filter-feeding mechanisms in the flamingo. The fringe along the edge of the flamingo's bill acts as strainer

Flamingo uses a filter feeding apparatus (Fig. 3.9) to filter small organisms and other morsels it finds in the muddy bottoms of its fresh water habitat.

3.3.5 Mammals

Mammals feed on a wide variety of food sources. Some mammals require highly specialised diets, while others are opportunistic feeders which live on diverse diet. In all mammals food habits and physical structure are intimately linked. Specializations for finding, capturing, reducing, swallowing, and digesting food determine the shape and habit of a mammal, Teeth, more than any other single physical characteristic, reveal the life habit of a mammal (Fig. 3.10). All mammals have teeth, except certain whales, monotremes and anteaters and their modifications are correlated with what they eat.

As mammals evolved, major changes occurred in the teeth and jaws during the mesozoic era. Unlike the uniform homodont dentition of the reptiles. mammalian teeth became differentiated to perform specialized functions such as: cutting, seizing, gnawing, tearing, grinding or chewing (please refer to section 3.2 again). Teeth differentiated in this way are called heterodont. The primitive tooth formula, which represents the number of each tooth type in one half of the upper and lower jaw, was I,3/3, C 1/1, Pm 4/4, M 3/3. Members of the order Insectivora e.g., shrews, some omnivores and carnivores come closest to this primitive pattern (Fig.3.10). Unlike reptiles, mammals do not replace their teeth continuously throughout their lives. Most mammals grow just two sets of teeth, a temporary set called **deciduous** or **milk** teeth (set) which is replaced by a permanent set when skull has grown large enough to accommodate a full set. Only incisors, canines and premolars are deciduous; molars are never replaced and the single permanent set must last a life time.

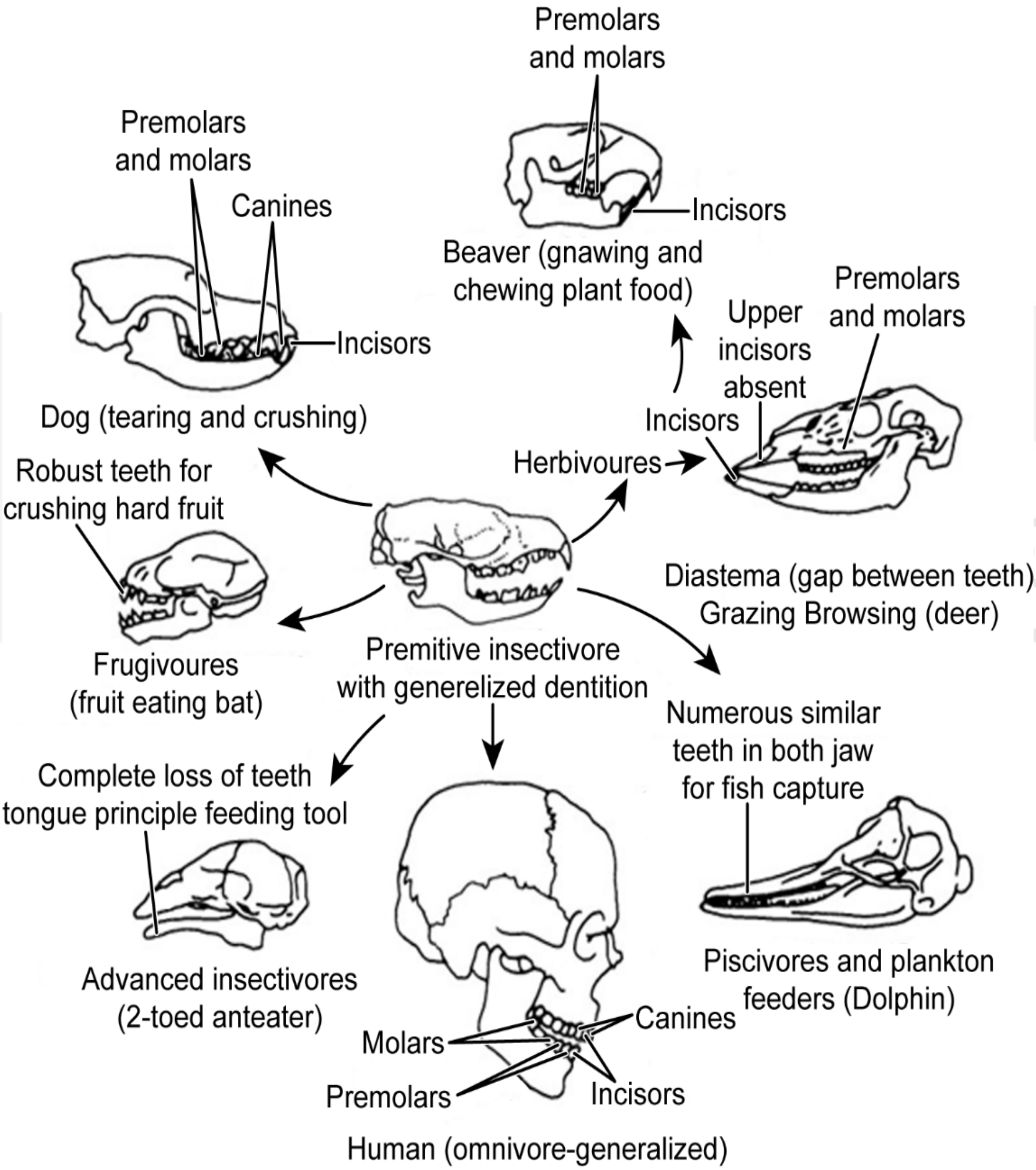


Fig. 3.10: Feeding specializations as shown by teeth of major trophic groups of eutherian mammals. The early eutherians were insectivores; all other types have evolved from them.

SAQ 2

Fill in the blank spaces with appropriate words from the text.

i) Majority of __________use ciliated surfaces to produce currents that can draw drifting food particles into their mouth.

ii) Fangs are either equipped with ____________which guides the __________or are hollow, very much like a ____________ needle.

iii) Raptorial birds capture prey with their ___________ or ___________.

iv) The tongue of frog flicks out to catch insects because it is attached in the ____________of the mouth.

3.4 DIGESTIVE SYSTEM IN NON-MAMMALIAN VERTEBRATES

The development of extracellular digestion in an alimentary canal was an important evolutionary innovation. It freed many animals from feeding continuously, for they could quickly ingest a few large chunks of food rather than slowly obtaining many particles small enough to enter cells and undergo intracellular digestion. The overall tubular organization of alimentary canal is efficient because it allows food to travel in one direction, passing through different regions of digestive specialization. Thus both acid and alkaline phases occur in the digestive tract of vertebrates, and both are active and at the same time providing different types of digestive action. In general, alimentary canals have four major divisions, the functions of which are (1) receiving food, (2) conducting and storing food, (3) digesting and absorbing nutrients and (4) absorbing water and defecating. Representative alimentary canals from different non-mammalian vertebrate classes are discussed in the following sub-sections.

3.4.1 Fishes

(a) Cartilaginous fishes

The digestive system of cartilaginous fishes comprises alimentary canal and glands of alimentary canal.

As you can see in fig. 3.11 the alimentary canal of *Scoliodon* consists of mouth, buccal cavity, pharynx, oesophagous, stomach, intestine and rectum. Mouth is a ventral crescentric opening which leads into a spacious dorso-ventrally compressed buccal cavity. The buccal cavity is lined with a thick mucous membrane raised ventrally into a thick fold to form the so called **tongue** which is non-muscular and non-glandular. The mucous membrane is rough due to the presence of dermal denticles. Teeth are oblique and have sharp more or less compressed cusps, the edges of which are smooth and non-serrated. Teeth are all alike in shape, **homodont**, and are borne in several parallel rows on the inner margin of the upper and lower jaws. Teeth are used to catch prey and prevent its escape but not to crush or masticate it.

Though there are several rows of teeth (polyphyodont) yet only one row functions at a time and the old row is replaced by a new one. There are no glands in the buccal cavity comparable to the salivary glands of higher vertebrates.

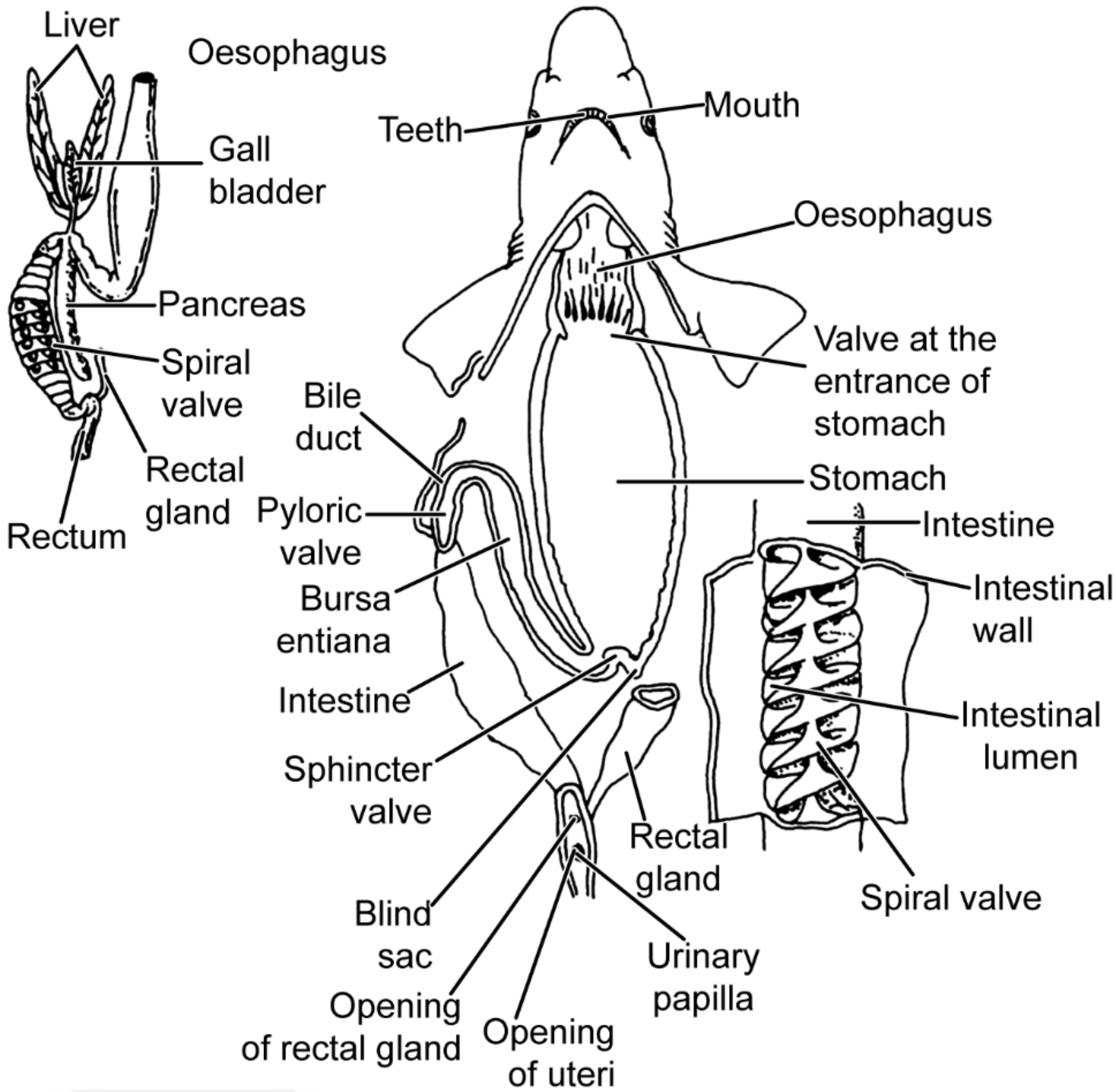


Fig. 3.11: *Scoliodon* alimentary canal.

The buccal cavity opens into pharynx on either side of which lie the internal openings of the spiracle and five gill-pouches. The cavity of pharynx is lined with mucous membrane containing numerous dermal denticles. The secretion of mucous glands in the pharynx has no digestive function but simply helps in lubricating the passage of food.

The pharynx narrows posteriorly to form the short oesophagus which has thick muscular walls with an internal lining of mucous membrane raised into longitudinal folds.

The oesophagus widens posteriorly to form a large muscular stomach. The stomach is bent on itself and forms a J-shaped organ, the long proximal limb called the **cardiac stomach** while the short distal limb is called the **pyloric stomach**. At the junction of cardiac and pyloric limbs there is a blind outgrowth, the **blind sac.** The inner mucous lining of the **cardiac stomach** is also thrown into prominent longitudinal folds that end in the depression of the **blind sac.** At the end of **pyloric** stomach there is a small muscular chamber called **bursa entiana.** The opening of pyloric stomach into the bursa entiana is guarded by a circular band of muscle fibres called the pyloric valve.

The bursa entiana continues into the intestine. The intestine is a wide tube running straight backward into the abdominal cavity and opens posteriorly into the rectum. The internal surface of the intestine is increased by a characteristic fold of the mucous membrane, the **spiral valve,** having one edge attached to the inner wall of the intestine and the other rolled up longitudinally on itself into a spiral, making an anti-clock wise spiral of about two and a half turns. In a transverse section the spiral valve looks like a watch spring. The spiral valve serves not only to increase the extent of the absorptive surface of the intestine but also prevents rapid flow of food through the intestine.

The rectum is the last part of the alimentary canal. The tubular rectal (caecal) gland opens dorsally into the rectum. The rectum leads into cloaca into which the alimentary canal as well as the urinogenital ducts open.

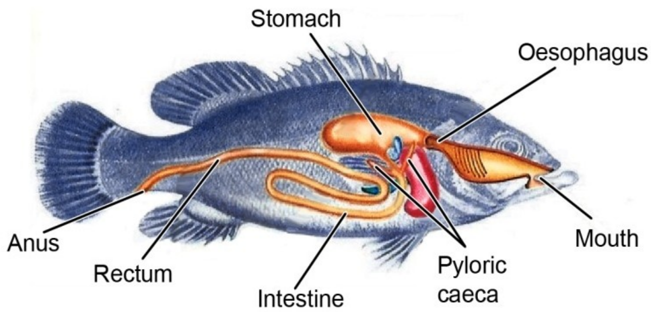
The glands of alimentary canal comprise a massive bilobed liver and a thin V shaped gall bladder. The bile duct opens in the anterior part of the intestine where the spiral valve starts. The pancreas is a pale compact irregular body lying between the fold of the stomach and intestine.

(b) Bony fishes

The digestive organs vary much in structure. The mouth, which is placed at, or near, the anterior end of the head, usually has the form of a transverse slit, and can sometimes be extended forward by means of the movable supporting bones of the upper and lower jaws. Some fishes are toothless but in most instances teeth are present, their succession is perpetual, i.e., injured or worn out teeth are replaced at all ages.

In a very large majority of teleost species the teeth are small, conical, and recurved, suitable for preventing the struggling prey from slipping out of the mouth, but quite unfitted for either tearing or crushing. In some bony fishes alimentary canal shows little differentiation into regions, but as a rule, gullet, stomach, duodenum, ileum and rectum are more or less clearly distinguishable histologically. The stomach is V-shaped but its cardiac region may be prolonged into a blind pouch (Fig. 3.12). This is often very distensible, allowing some of the deep-sea Teleostei to swallow fishes as large as themselves. In many genera of several families stomach is entirely absent.

Globe fishes can inflate the gullet with air or water, as a result of which they can float upside down. A spiral valve is very well developed in *Polypterus* and Sturgeons, vestigial in *Lepisoteus* and *Amia*, and absent or vestigial in all Teleostei, except possibly in Chirocentrus (Isospondyli). A trace occurs in the herring. Liver is usually large. Pancreas may be present as a compact gland, or may be widely diffused between layers of the mesentery, or in part surrounded by the liver. **Pyloric Caeca** are commonly present, and vary in number from a single one to two hundred. Anus is always distinct from, and in front of the urinogenital aperture.



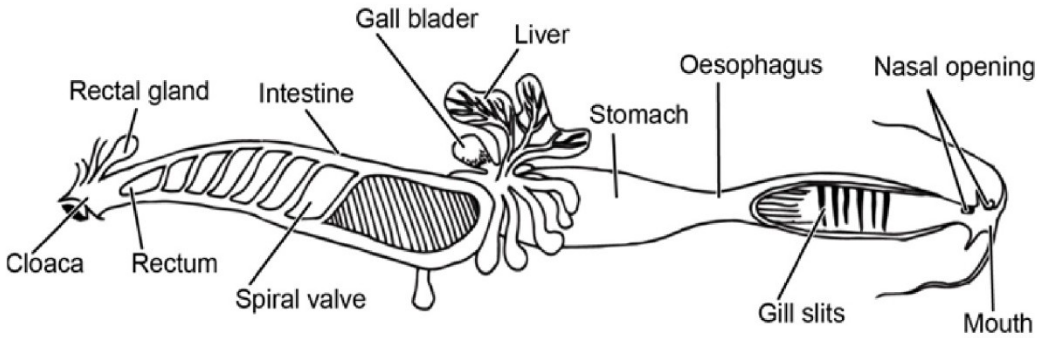


Fig. 3.12: Digestive tract of a Teleost fish (bass).

3.4.2 Amphibians

The mouth opening is a wide slit. Teeth, which are ankylosed to the bones, are present upon the premaxillae, maxillae and vomers, They are absent in *Pipa* and some toads. Tongue is immovable in Urodela, movable and free behind in Anura, in which it is used as a prehensile organ. Salivary glands are not present. In many oesophagus, stomach, small intestine and rectum are present.

We consider the frog as a typical example of amphibians. The alimentary canal of frog consists of buccal cavity, pharynx, oesophagus, stomach and intestine (Fig.3.13). Mouth leads into a wide and broad cavity called buccal cavity lying between the two jaws, the upper and the lower one. The buccal cavity in its roof near the vomerine teeth has two openings, the internal nares connecting with the nostrils through which respiratory gases pass to and from the buccal cavity during respiration.

The pharynx leads into a broad tubular part of the alimentary canal called oesophagus. This part of alimentary canal is very short due to the absence of neck. But the oesophagus is highly distensible as its inner lining is thrown into a large number of longitudinal folds that allow its expansion during the passage of the ingested food to the stomach. The stomach comprises two parts, the anterior expanded **cardiac part** and the posterior short narrow **pyloric part**. The stomach opens into long tubular part the intestine consisting of two parts the **small** and **large** intestine. The small intestine leads to a short, broad colon or large intestine called rectum. The hind end of the rectum is called the **cloaca** and possesses a median ventral appendage, the urinary bladder. The urinary and generative ducts open into cloaca. The cloaca opens to the exterior by the anus. The digestive glands such as liver and pancreas are present and the liver has a gall bladder.

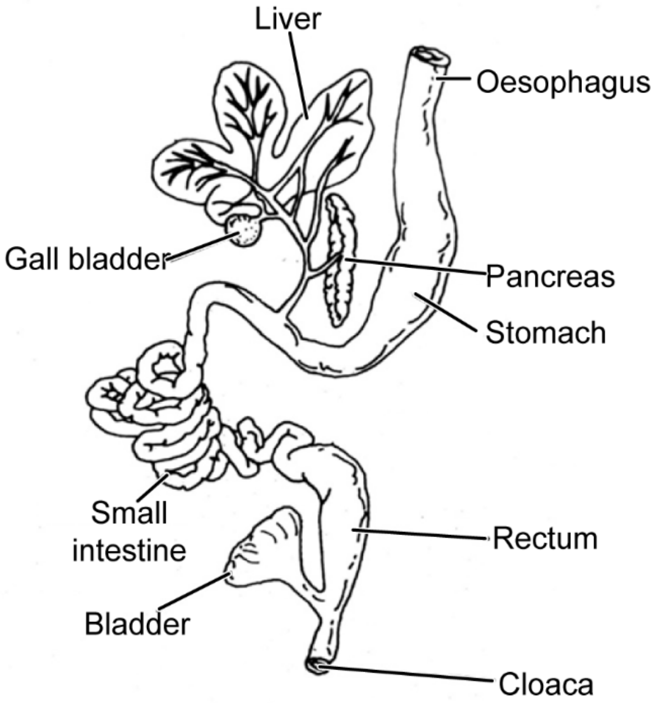


Fig. 3.13: Digestive tract of an amphibian (frog).

3.4.3 Reptiles

Teeth are usually present on the premaxillae, maxillae and dentary, and frequently on the palatine and pterygoid. They are continually replaced, and are pleurodont, acrodont, or thecodont. Teeth are conical or hooked and are adapted for prehension not for mastication except in some extinct forms. In Chelonia teeth are absent, being replaced by the horny epidermal beak-like covering of jaws.

In this section to make you understand the digestive system of reptiles we will describe the digestive system of a *Uromastix* lizard (Fig. 3.14). The alimentary canal is a long and convoluted tube. It can be divided into mouth, buccal cavity, pharynx, oesophagus, stomach, duodenum, ileum or small intestine, colon or large intestine, rectum and cloaca. The mouth opening is a wide gap bounded by the upper and lower immovable and muscular lips. The mouth opens into the buccal cavity which has a well developed muscular tongue on its floor. Tongue is attached to the floor of the buccal cavity along the median ventral line. The tongue is long, bifid and protrusible having voluntary muscles, taste buds and mucous glands. In the upper jaw, teeth are present on premaxillae and maxillae, whereas in the lower jaw the dentary bears teeth. The teeth of *Uromastix* are pleurodont which means teeth are attached to the outer border of the bones of jaw.

The pharynx lies posterior to the tongue. The lining of the pharynx is thrown into longitudinal folds. The pharynx leads posteriorly into the oesophagus. It is capable of great distension and it opens into long cylindrical sac like structure the stomach which is wider than the oesophagus. It has thick muscular walls and lies in the left half of the body and is curved having the appearance of U-shape. The stomach is differentiated into two parts; the anterior part is known as **cardiac stomach** which lies dorsal to the left lobe of the liver, and the posterior part is known as **pyloric stomach** lying slightly to the right side. The wall of the stomach is much thicker than that of the oesophagus and of the intestine. Numerous well developed longitudinal folds of mucous membrane are seen in the lumen of both cardiac and pyloric stomach. Stomach is the place where digestion occurs. The pyloric wall is in the form of a muscular ring lining of the inner wall of the posterier extremity of the pyloric stomach.

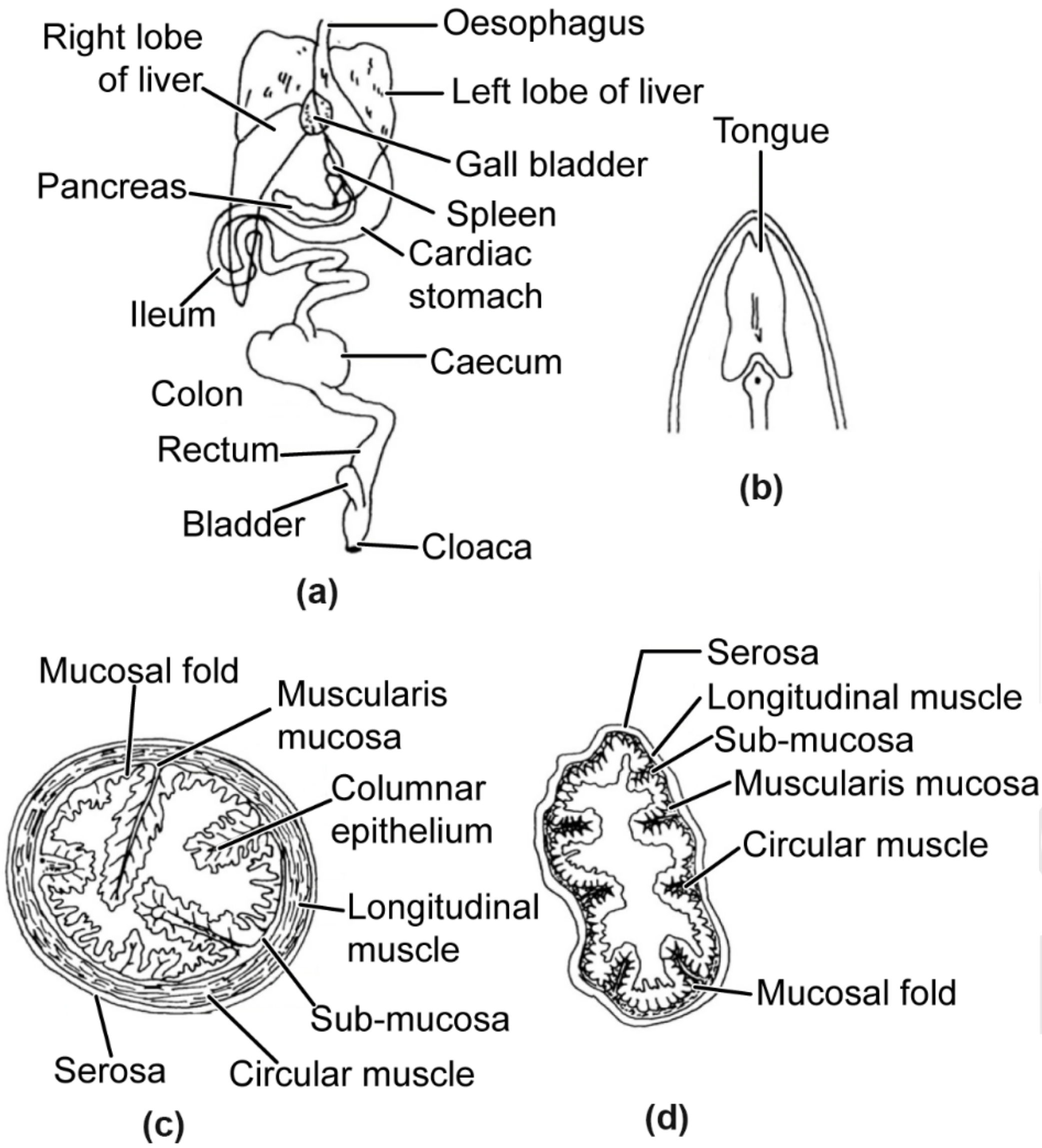


Fig. 3.14: *Uromastix;* a) Alimentary canal, b) Tongue, c) T.S. of cardiac stomach, d) T.S. of pyloric stomach.

The small intestine consists of an anterior duodenum and a posterior ileum. The duodenum is U-shaped and receives bile and pancreatic juices. Both duodenum and ileum show closely set wavy longitudinal folds of mucosa.

You can see from Fig. 3.14 a that ileum opens into a large intestine which comprises a proximal colon and distal rectum. The caecum pouch arises from the junction of ileum and colon. Rectum opens into cloaca that in turn opens to the exterior by the cloacal opening. The cloaca consists of three chambers, the coprodaeum, the urodaeum and the proctodaeum. Different chambers of cloaca serve for reabsorption of water both from faeces and urine. The digestive glands that are associated with the alimentary canal are gastric glands, liver, pancreas and intestinal glands.

The salivary glands are usually absent in all reptiles. There is a sub-lingual gland in *Chelonia*. Both upper and lower labial glands and palatal and lingual glands are always present. The poison glands of snakes are upper labial salivary glands.

3.4.4 Birds

Inspite of great differences in the mode of nourishment the avian digestive organs present a fairly uniform structure; their unusual structures in the digestive system are adaptations for flight. The jaws are covered by a hard horny sheath (rhamphotheca) and transformed into the beak. The rhamphotheca is often composed of several pieces (compound). True teeth are entirely absent, at least in living birds. While the upper beak is formed by the fused premaxillae, the maxillae and the nasal bones, the lower beak corresponds to the two rami of the lower jaw, the fused extremities of which are known as the **myxa** (Fig.3.15). The form and development of the beaks vary extremely according to the special mode of subsistence (see Fig. 3.8 again).

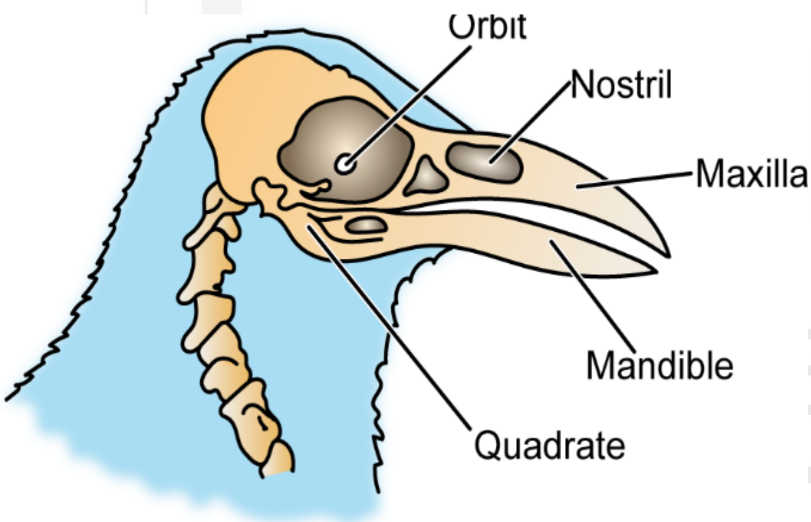


Fig. 3.15: Typical beak structure of birds.

Tongue which is always movable, lies on the floor of buccal cavity. It consists of horny or fleshy covering of two cartilages attached to the anterior end of the hyoidbone and serves for pushing the food back, and frequently for seizing food. Oesophagus is muscular, longitudinally folded and the length generally depends on the size of the neck. It frequently possesses a dilation known as crop especially in birds of prey, and also in granivorous birds, in which the food is stored and softened (Fig. 3.16a). In pigeons crop bears two small rounded accessory sacs.

The lower end of oesophagus is dilated into a glandular proventriculus, which is followed by wide muscular stomach called gizzard. While the proventriculus has, as a rule, an oval form and is smaller than the gizzard, the latter is provided with muscular walls, which are weak in birds of prey and strong in granivorous birds. In granivorous birds gizzard is well adapted for mechanical preparation of the softened food material by the possession of two solid plates, which form the horny internal wall and rub against one another (Fig. 3.16 b). It contains small stones which the bird swallows to aid in the grinding of the food. The first loop of small intestine which is corresponding to duodenum surrounds the elongated pancreas. The 3 ducts of pancreas and the usually double bile ducts, open in this region. A gall bladder is present. The beginning of the short, large intestine is marked by the presence of a circular valve, and by the origin of two caeca. There is no distinction between colon and rectum, and the large intestine passes into the cloaca, into which the urinogenital apparatus also opens. The entrance into the cloaca it marked by a sphincter-like circular fold. A peculiar glandular sac the bursa Fabricii-opens into the dorsal wall of the cloaca.

Cloaca usually presents three fairly well-marked divisions separated by folds (Fig. 3.16 c). The anterior of these, often called the **coprodaeum** is the dilated hind end of the rectum. The lining of coprodaeum is, however, different from that of the rectum from which it is often separated by a fold. The middle chamber is called the **urodaeum:** it is smaller than the other two chambers and receives the openings of the urinogenital duct. The posterior chamber which opens to the outside by the **vent**, may be termed the **vestibule;** it receives the bursa Fabricii dorsally.

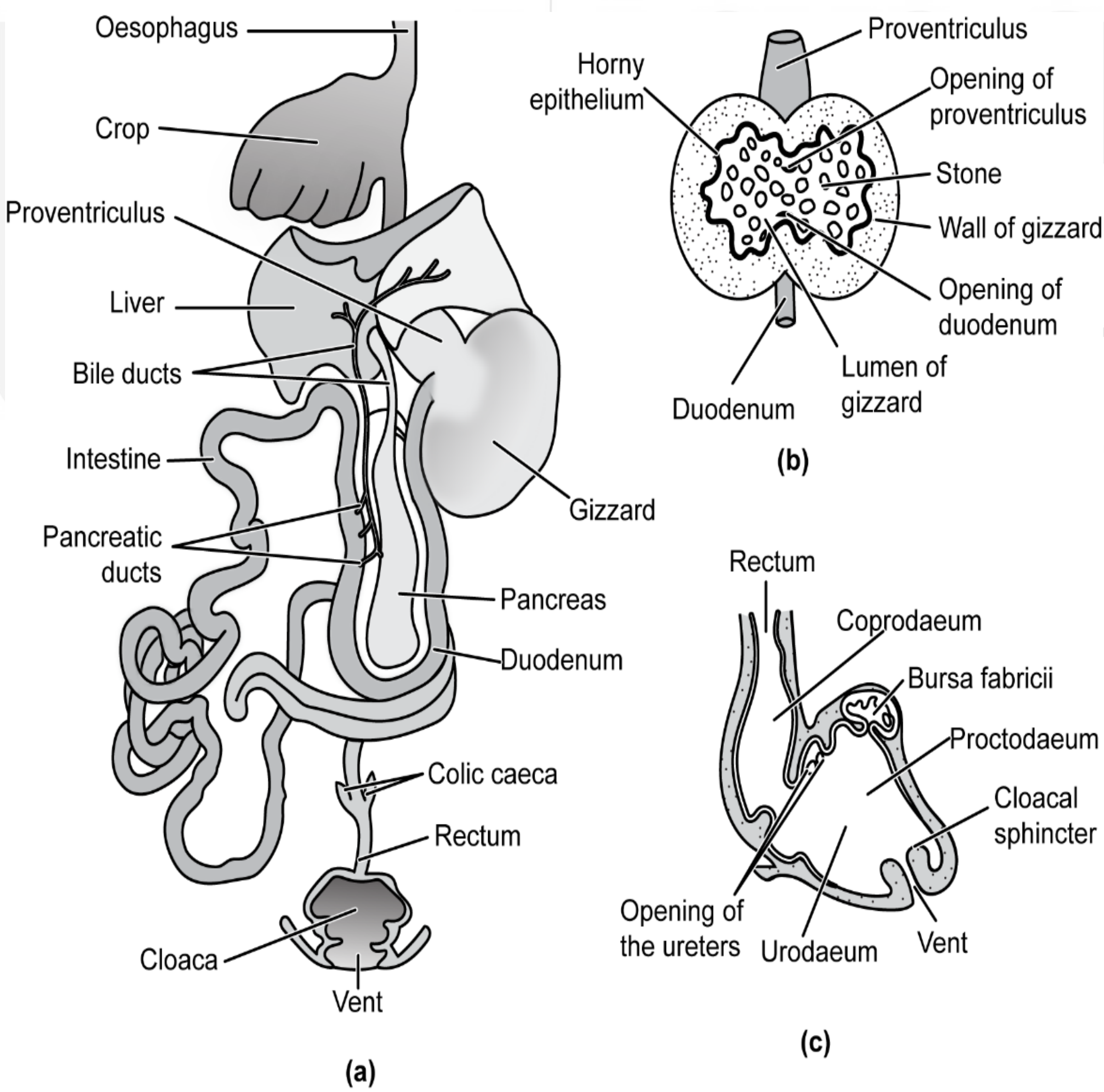


Fig. 3.16: Digestive tract of pigeon.

SAQ 3

Match the statement given in **column B** with the chordate group given in **column A**.

Column A	Column B	
Fish (cartilaginous and bony)	i)	A crop and gizzard is present
Amphibians	ii)	Salivary glands are absent but lingual glands are present.
Reptiles	iii)	In many genera of several families stomach is entirely absent.
Birds	iv)	True teeth are entirely absent.
	v)	Tongue like structure formed of ventrally raised mucous membrane.
	vi)	Teeth are polyphyodont but only one row functional at one time.
	vii)	Tongue is bifid has taste buds and glands.
	viii)	Intestine has spiral valve that increases the absorptive surface.
	ix)	Mouth is an anterior transverse slit that can be extended forward to catch prey.
	x)	Vomarine teeth present.

3.5 DIGESTIVE SYSTEM IN MAMMALS

The feeding or trophic, apparatus of a mammal includes the oral structures (teeth, jaws, tongue), alimentary canal, and accessory digestive glands (salivary glands, liver and pancreas). Accordingly their digestive tracts are adapted to their particular feeding habits. On the basis of food habits, mammals are divided among several trophic or nutritional groups (see Fig. 3.10 again).

3.5.1 Trophic Groups in Mammals

The three basic trophic groups in mammals are insectivores, carnivores and herbivores, and many feeding specializations have evolved in each groups.

Insectivores are small mammals, usually opportunistic feeders, that feed on a variety of small invertebrates, such as worms, grubs and insects. Examples are shrews, moles, anteaters, and most bats. Since insectivores eat little fibrous vegetable matter which requires prolonged fermentation, their intestinal tract tends to be short (Fig. 3.17). The insectivorous is not a sharply distinguished category since carnivores and omnivores often include insects in their diet. Even many rodents which are considered herbivores, may have a mixed diet of insect larvae, seeds and fruits.

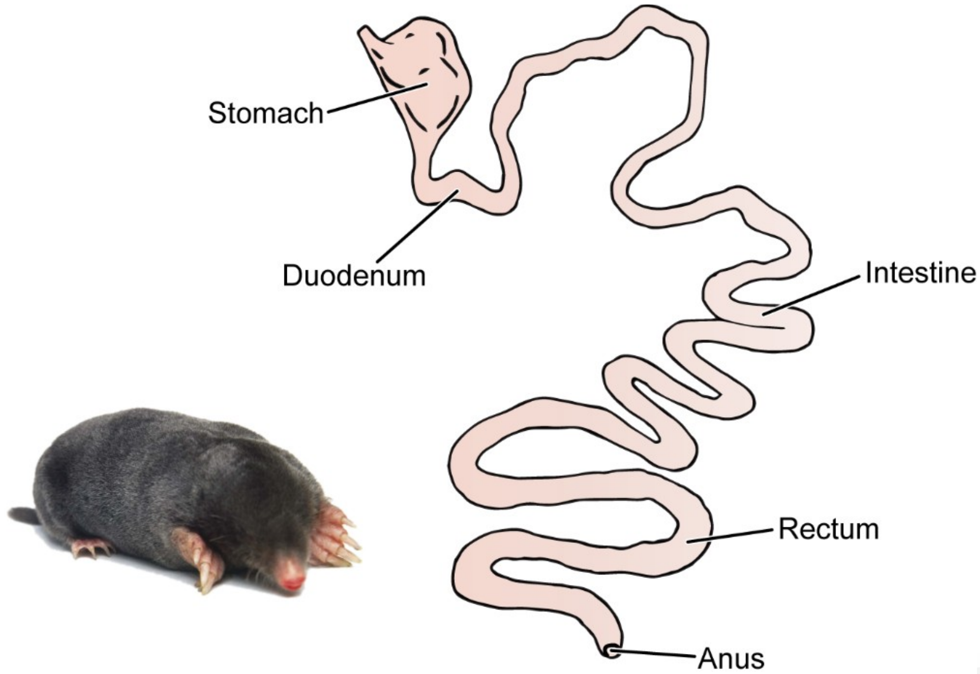


Fig. 3.17: Digestive System of an insectivore showing short intestine. Note there is no caecum.

Herbivorous mammals which feed on grasses and other vegetation form two main groups; the browsers and grazers, such as the ungulates, that are, hooved mammals including horses, deer, antelope, cattle, sheep and goats, and the gnawers such as the rodents which include rabbits and hares. In herbivores, the canines are either reduced in size or may be absent, while the molars that are adapted for grinding, are broad and usually high-crowned. Rodents have sharp chisel-shaped incisors which grow throughout life and must be worn away to keep pace with their continuous growth. If the incisors do not grow continuously, the cutting surface of the teeth will get eroded soon by its excessive use due to its continuous gnawing habit.

Herbivorous mammals have a number of interesting adaptations for dealing with their fibrous diet of plant food. **Cellulose,** the structural carbohydrate of plants, is potentially nutritious foodstuff, composed of long chains of glucose units. However, glucose molecules in cellulose are linked by a type of chemical bond that few enzymes can attack. No vertebrate synthesizes cellulose splitting enzymes. Instead, the herbivores harbour a microflora of anaerobic bacteria and protozoa in the gut. These bacteria and protozoa breakdown and metabolize cellulose, releasing a variety of fatty acids, sugars, and starches which the host can absorb and use.

In some of the herbivores like horses, zebras, rabbits, hares, deer, elephants and many rodents, gut has a spacious side pocket or diverticulum, called a **caecum** that serves as a fermentation chamber and absorptive area (Fig. 3.18 & 3.19). Hares, rabbits and some rodents often eat their faecal pellets **(coprophagy)** giving the food a second pass-through the fermentating action of the intestinal bacteria. Coprophagy also provides an opportunity for the animal to obtain vitamins produced by the bacteria lodged in the caecum.

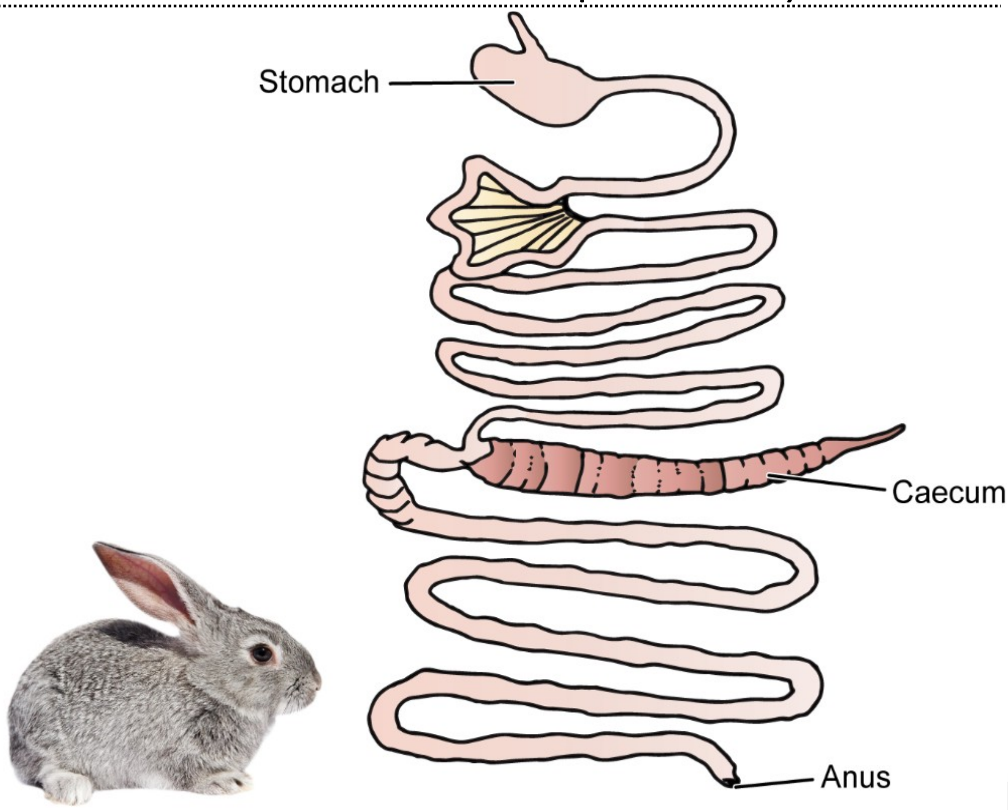


Fig. 3.18: Digestive System of a non-ruminant herbivore (rabbit) showing simple stomach and a large caecum.

Ruminants like cattle, bison, buffalo, goats, antelopes, sheep, deer, giraffes etc. have a huge four chambered stomach (Fig. 3.19). You will learn more about the specialized ruminant stomach a little later in this section.

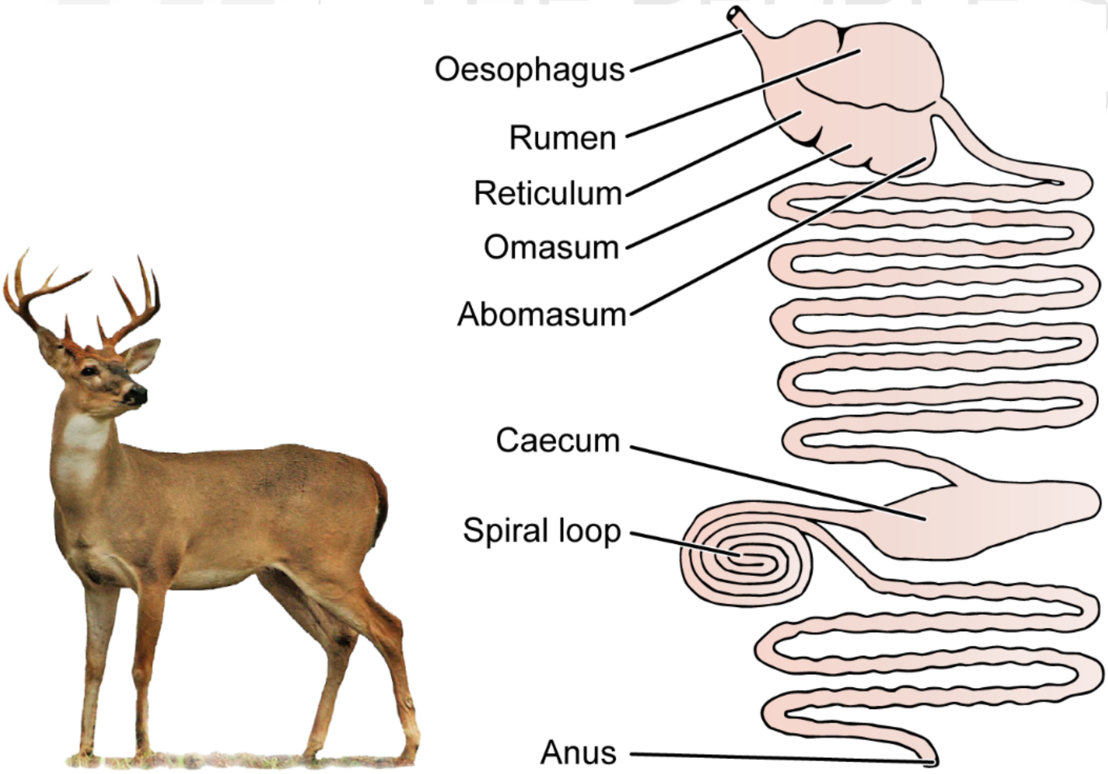


Fig. 3.19: Digestive System of a ruminant herbivore (deer) showing four-chambered stomach with Large rumen, and long sized small and large intestines.

Carnivorous mammals feed mainly on herbivores. This group includes foxes, dogs, weasels, wolverines, cats, lions, tigers etc. Carnivores are well equipped with biting and piercing teeth and powerful clawed limbs for killing the prey. Since their protein diet is easily digested in comparison to the woody food of herbivores, their digestive tract is shorter and the caecum is small or absent (Fig.3.20).

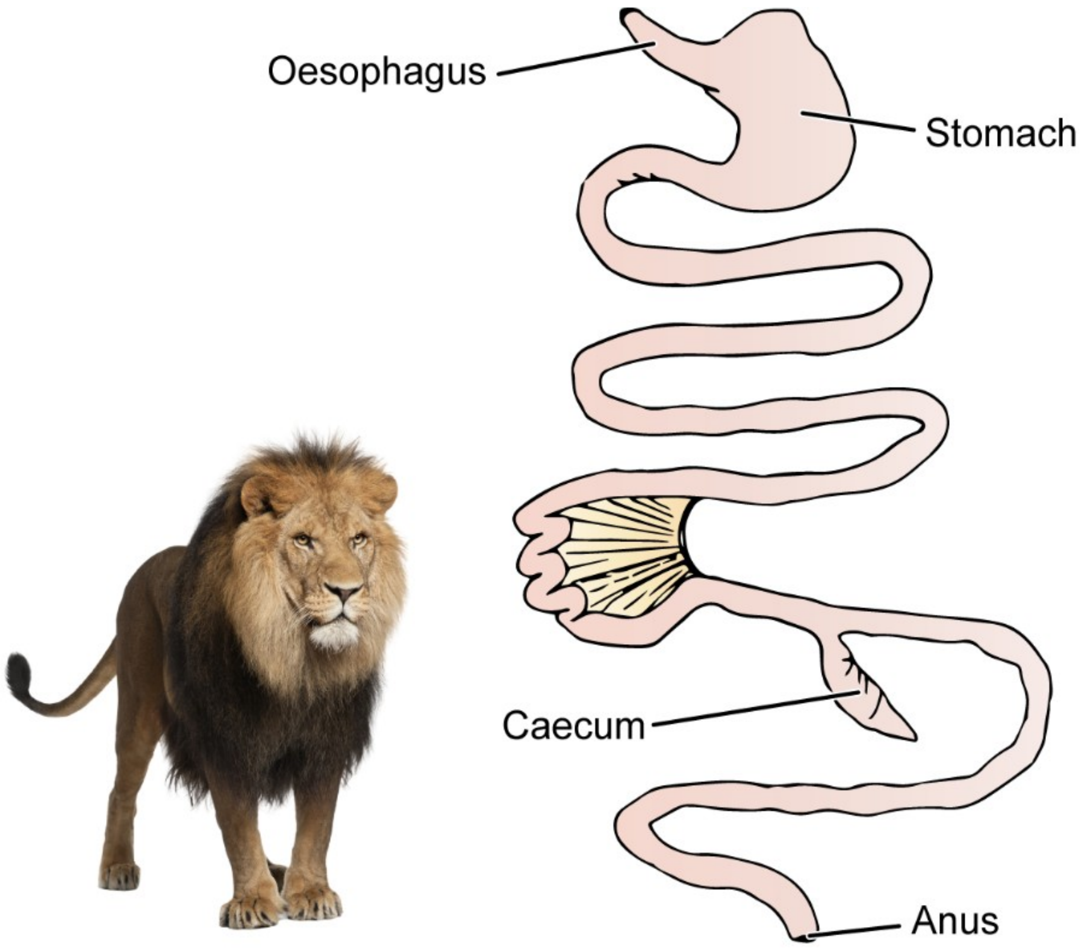


Fig. 3.20: Digestive system of a carnivore showing short intestine and colon, small ceacum.

Generally carnivores lead more active life than do the herbivores. Since a carnivore must find and catch its prey, there is a premium on speed and intelligence; many carnivores, such as cats are known for their stealth and cunningness in hunting prey. This has lead to a selection of herbivores capable either of defending themselves or of detecting and escaping carnivores. Thus for the herbivores, there has been a premium on keen senses and agility. Some herbivores, however, survive by virtue of their sheer size e.g. elephants or by defensive group behaviour for example North American musk oxen.

Omnivorous mammals live on both plants and animals for food. Examples are pigs, racoons, rats, bears and most primates including human beings. Many carnivore forms also eat fruits, berries and grasses when hard pressed. The fox which usually feeds on mice, small rodents and birds, eats frozen apples, beech nuts, and corn when its natural food is scarce. For most mammals, searching for food and eating occupy most of their active life. Some migrate to regions where food is in plenty, while others hibernate and sleep during the winter months. But there are many provident mammals which build up food stores during period of plenty. This habit is most pronounced in rodents such as squirrels, chipmunks, gophers and certain mice.

3.5.2 Digestive Tract

The mouth in mammals is bound by fleshy lips. On the floor of the mouth is situated a tongue which is usually well developed, but varies in size and shape in different orders of mammals. In some herbivorous animals it can be curled around grass and thus helps pull it into the mouth. Its surface is covered with papillae of different kinds. The papillae are sometimes horny, serving for either grinding of food, or for the dressing of the hairy coat. Thus the tongue and lip margins in many mammals are equipped with raised processes which can be moved up and down along the interspaces of the teeth (and on the surfaces of the teeth) in a cleansing action. In association with the papillae of the tongue there are special end organs of taste (**taste buds**) which are often arranged in zones. The sense of taste differs profoundly among various groups. The roof of the mouth is formed in front by the hard palate, consisting of the horizontal palatine plates of the maxillary and palatine bones covered with mucous membrane bearing palatal folds. Behind the hard palate there is a backward projection of the soft muscular fold of the soft palate which divides the cavity of the pharynx into an upper and a lower chamber. In some forms the soft palate also bears taste buds. In **Primates** a free-hanging **uvula** and soft palate are raised to close off the nasopharynx and prevent the entrance of food into it. In front of the opening, leading from the lower division of the pharynx into the larynx, is a cartilaginous plate called epiglottis a primitive form of which is found in certain lower vertebrates like frogs. The epiglottis, anatomically part of the larynx, assists the reflex swallowing mechanism by preventing food from entering trachea.

The oesophagus is a simple, straight tube in which food is propelled by peristaltic contractions of the muscular walls, which like the act of swallowing or deglutition, are reflex and involuntary. The opposite action, **retroperistalsis** enables ruminants to regurgitate stomach content for more leisurely mastication, and many other animals to expel injurious substances accidentally swallowed.

The stomach varies greatly in different mammalian orders. In majority of mammals including humans it is **monogastric** or single chambered (Fig. 3.21). When empty it is a rather small chamber but can stretch upto 20 times to accommodate food, a quality that is useful for animals that feed when food is available. It is the site of major protein digestion except in ruminants. But in certain groups it is complicated by the development of internal folds, and may be divided by constrictions into several functionally different chambers. Such complication reaches its extreme in the ruminants of order Artiodactyla. In a typical ruminant (see Fig. 3.22 (i)) such as sheep, deer or cow, stomach is divided into 4 chambers - the **rumen** (or punch), the **reticulum**, **omasum** and the **abomasums** (or rennet stomach). The epithelium of both rumen and reticulum is highly reminiscent of that of the oesophagus.

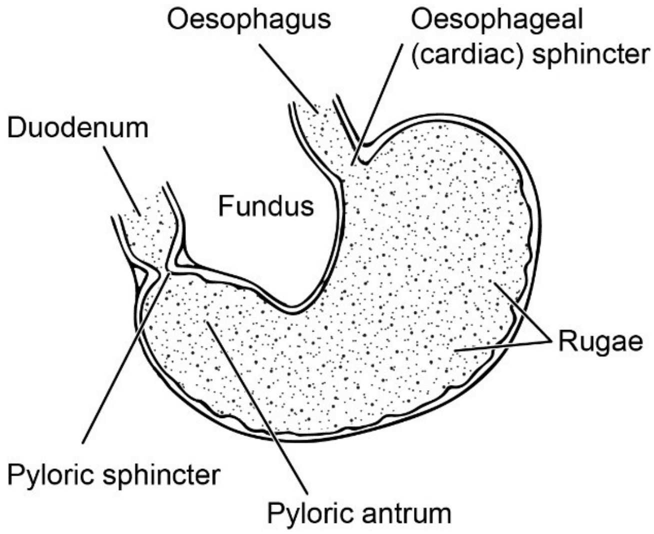
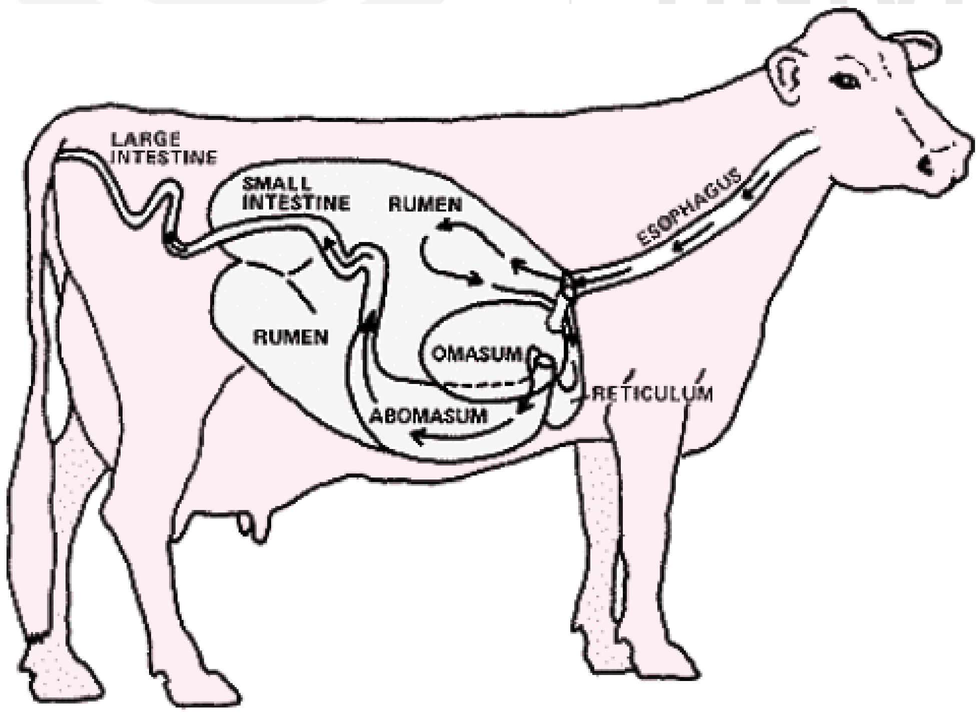
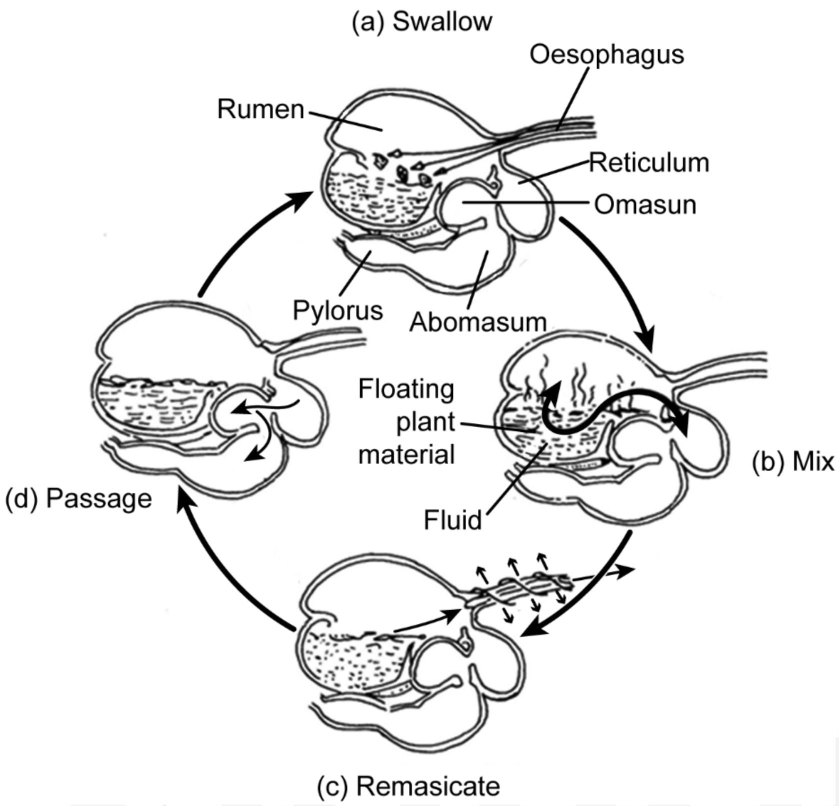


Fig. 3.21: Monogastric stomach showing major parts of the mammalian stomach.

When a ruminant feeds on grass, it is saturated by copious saliva passes down the oesophagus to the rumen, where it lies until the animal finishes eating. There the food is broken down by the rich microflora and then formed into small balls of cud. At its leisure the ruminant returns the cud to its mouth where the cud is deliberately chewed at length to crush the fiber. Swallowed again, food returns; to the rumen where it is digested by the cellulolytic bacteria (Fig. 3.22 (ii)).The pulp is then passed on to the **reticulum,** then to **omasum** and finally to the **abomasum** that is true acid stomach, where proteolytic enzymes are secreted and normal digestion takes place. In general herbivores having large, long digestive tracts must eat a considerable amount of plant food to survive. A large African elephant weighing 6 tons must consume 135 to 150 kg of rough fodder each day to obtain sufficient nourishment to survive.



(i)



(ii)

Fig. 3.22 : i) Digestive system of ruminants; ii) Foregut fermentation in the bovine stomach. (a) In ruminants, food is clipped, rolled into a bolus, mixed with saliva, and swallowed. (b) Contractions spread through rumen and reticulum in cycles that circulate and mix the bolus. Contents separate into fluid and particulate material. Floating, fibrous plant material and a pocket of gas forms during fermentation. (c) Poorly masticated bolus of plant material is regurgitated and re-chewed later to break down fibrous cell walls mechanically and expose further plant tissue to the enzymes cellulases. Respiratory inhalation, without opening the trachea, produces negative pressure around the oesophagus to draw some of this poorly masticated material into the oesophagus through the gastroesophageal sphincter. Peristaltic waves moving forward in the wall of the oesophagus rally the bolus into the mouth for rechewing. (d) The omasum transports reduced bolus from the reticulum to the abomasums in two phases. First, relaxation of omasal walls produces negative pressure that draws fine particulate material from the reticulum into its own lumen. Next, contraction of the osmasum forces these particulates into the abomasum, the stomach region rich in gastric glands. Thus, the abomasum is the first true part of the stomach.

The oesophagus opens into the rumen close to its junction with the reticulum. The rumen is much larger than the rest. Its mucous membrane is beset with numerous short villi. The reticulum, is much smaller than the rumen, has its mucous membrane raised up into a number of anastomosing ridges. These are capable of closing together in such a way as to convert the groove into a canal. The mucous membrane of omasum is raised up into numerous longitudinal leaf-like folds. The abomasum, smaller than the rumen but larger than the reticulum, has a smooth vascular and glandular mucous membrane.

In some ruminants omasum is absent. In the rumen and reticulum of deer, cattle, sheep etc., there exist a dense population of protozoa and bacteria that attack and break down cellulose which forms the major part of the diet. Fermentation produces acetic, butyric and propionic acids which are neutralized by sodium bicarbonate secreted in the saliva. As a result methane and CO_2 are produced and belched out.

Food residues, fluid and micro-organisms move down the alimentary canal. In the omasum fluid is absorbed. In the abomasum, the protozoa and probably the bacteria, are destroyed by secreted HCI. The abomasum also produces digestive enzymes. In camels stomach is not as complex as in the more typical ruminants. There is no distinct omasum, and the rumen is devoid of villi. Both rumen and reticulum have connected with them a number of pouch like diverticula, the openings of which are capable of being closed by sphincter muscles. In **Cetacea** stomach is also divided into compartments. In porpoises (sea animals like a dolphin or a small whale) oesophagus opens into a spacious rumen, the cardiac compartment of the stomach, which has a smooth, thick, mucous membrane. This is followed by a second median chamber of considerably smaller dimensions. This has a glandular mucous membrane, which is thrown into a number of complex folds. A long and narrow third or pyloric, compartment follows terminating in a constricted pyloric aperture. Beyond this beginning of the small intestine is dilated into a bulb.

Absorption of nutrients takes place in the small intestine which is the longest part of the alimentary canal in most vertebrates (see the figures of digestive tracts in the previous sub-section). The inner surface of the intestine is highly folded with finger like projections that increase the absorptive surface. In humans (see Fig. 3.23) the intestines are divided broadly in three regions: the **duodenum** which connects to the stomach, the **jejunum** where most of the carbohydrates and amino acids are absorbed and the third part is known as **ileum,** where vitamins and bile salts are absorbed into the blood stream.

A **caecum,** situated at the junction of large and small intestine is usually present, but varies greatly in extent in the different orders and families. In general, it is much larger in vegetarian than in carnivorous forms. Among herbivores it is those that have a simple stomach such as the rabbit, that have the largest caecum (Fig. 3.18). The caecum is simple in **monotremes,** absent in sloths, some **cetaceans** and in a few carnivores. It is relatively enormous (about 250 cm. long) in the marsupial Koala, *Phascolarctos* (which eats mostly eucalyptus leaves).In humans and a few other animals(civets, some rodents, monkeys) the distal end of the caecum has degenerated into an appendix vermiform is (Fig. 3.23). The proportion of vegetable material ingested is not, however, the only factor governing the size of the caecum. In ruminants caecum is relatively small. In ruminants the colon too, is comparatively unimportant: but in non-ruminant herbivores such as horses both caecum and colon are enormous. All material passing from ileum to colon enters caecum which in horses, may be some four feet long and holds as much as eight gallons. In horses caecum has fluid storing and digestive functions. The large colon in horses is principally absorptive in function although some bacterial but not enzymatic digestion occurs therein.

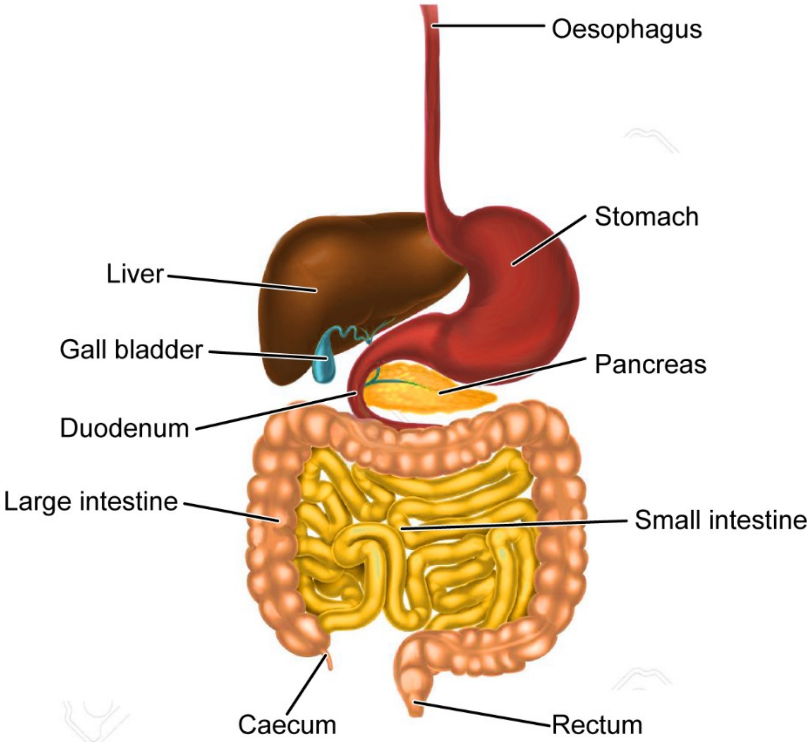


Fig. 3.23: Human digestive tract.

The rectum is the terminal part of the large intestine as seen in Fig.3.23. Its primary function is to store faeces until defecation through the anus. The Prototherians resemble reptiles, birds and Amphibia and differ from most mammals in the retention of a cloaca. Into this not only rectum but the urinary and the genital ducts open. In marsupials a common sphincter muscle surrounds both anal and urinogenital apertures. In female there is a definite cloaca. In nearly all eutherians the apertures are distinct, and separated from one another by a considerable space the **perinaeum.**

3.5.3 Digestive Glands of Mammals

The accessory glands of the mammalian digestive system are the three pairs of salivary glands, liver, its storage organ the gall bladder and the pancreas.

i) **Oral Glands :** The epithelium of buccal cavity contains a rich source of cells which secrete mucous and serous fluid. These secretary cells when clustered together and empty their secretion via common duct are called oral glands. Secretions from most of these glands, in addition to lubrication of food, may also help maintain healthy oral membranes, neutralize toxins carried by prey, and perhaps initiate the chemical stages of digestion.

The most common oral glands in mammals are the salivary glands. There are usually three primary pairs of salivary glands, named for their approximate positions: **mandibular** (submandibular or submaxillary), **sublingual,** and **parotid.** They form the **saliva,** which is added to food in the mouth. These three pairs of glands lie at the angle of the jaws, usually at about the juncture between the head and the neck, but they are positioned superficial to the neck musculature. Ducts from the mandibular and sublingual glands run anteriorly and release secretions into the floor of the buccal cavity. The duct from the parotid gland opens into the roof of the buccal cavity. In some species, additional salivary glands may be present. In dogs, cats, and some other carnivores, a **zygomatic** (orbital) gland is present, usually beneath the zygomaticarch (Fig. 3.24). Like most digestive secretions, saliva contains mucous, salts, proteins, and a few enzymes, most notably **amylase,** which initiates starch digestion. Saliva also aids swallowing by lubricating food.

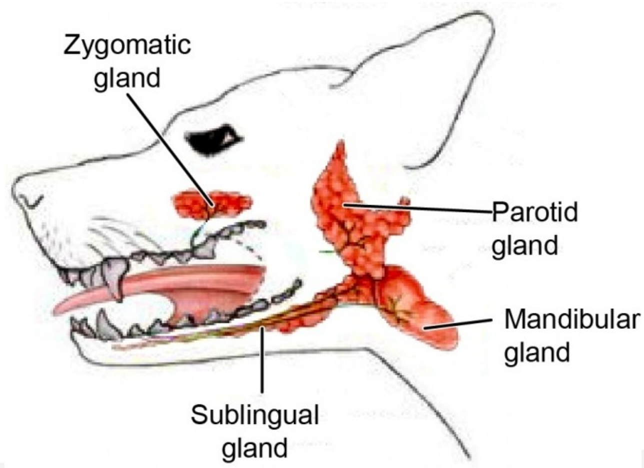


Fig. 3.24: Salivary glands of a mammal, dog. Note the locations of the main salivary glands (sublingual, mandibular, and parotid) along with their ducts leading to the buccal cavity. All mammals possess these three salivary glands. In dogs and cats, a zygomatic gland is also present.

ii) **Liver :** Like all vertebrates, mammals possess a liver. The liver is the second largest organ in the body only exceeded in size by the skin. It functions in a wide variety of roles. Early in foetal life, the liver is directly involved in the production of red blood cells, and later it is involved in the destruction of old blood cells. It consists of two parts or main divisions (i.e. right and left) completely separated from one another by a fissure termed the **umbilical,** owing to its marking the position of the foetal **umbilical** vein. Throughout life, liver detoxifies and removes toxic substance from the blood. Majority of mammals have a **gall-bladder**. When it is present, it is attached to or embedded in, the right central lobe of the liver. The gallbladder is absent in cyclostomes, most birds, and a few mammals, but otherwise is present throughout vertebrates. Gall bladder is absent in the Perissodactyla (horse, tapirs rhinoceros), the hyracoids and some rodents. Bile is manufactured by hepatocytes in the liver and collected in the bile ducts, stored in the gallbladder, and emptied into duodenum the via the common bile duct to **emulsify** fats, or break them up into smaller droplets.Carbohydrates, proteins, and fats are stored and metabolized in the liver. The liver is one of the most heavily vascularized organs of the body, being supplied with arterial blood via the hepatic artery. However, it is also supplied with venous blood via the hepatic portal vein which runs directly from the intestines and spleen to the liver, and deliversblood rich in nutrients absorbed products of digestion.

iii) **Pancreas :** In embryo the development of the pancreas is closely associated with liver development. The pancreas arises from two unpaired diverticula: the **dorsal pancreatic diverticulum,** a bud directly from the gut; and the **ventral pancreatic diverticulum,** a posterior bud of the hepatic diverticulum. These dorsal and ventral pancreatic rudiments may have independent ducts supplying pancreatic juices to the intestine.

Whether one or two, the ducts empty into the duodenal portion of the intestine and release an alkaline exocrine product, **pancreatic juice,** composed of the proteolytic enzyme trypsinogen, which is converted within the intestine to the active protease, **trypsin**. Amylases for carbohydrate digestion and lipases for fat digestion are also secreted. Embedded in the pancreas are small **pancreatic islets** (islets of Langerhans) that produce the hormones **insulin** and **glucagon,** both of which regulate the level of glucose in the blood. The pancreas is thus both an exocrine gland, producing pancreatic juice, and an endocrine, gland, producing insulin and glucagon.

SAQ 4

Tick out (√) the correct answer in the box.

(i) Which organ in herbivores serves a fermentation chamber and provides absorptive area?

(a) Liver ☐

(b) Gall bladder ☐

(c) Pancreas ☐

(d) Caecum ☐

(ii) In which mammals stomach is divided into 4 chambers?

(a) carnivores ☐

(b) ruminants ☐

(c) rodents ☐

(d) Insectivores ☐

(iii) In which mammal caecum has fluid storing and digestive functions?

(a) Kangaroo ☐

(b) Lion ☐

(c) Horse ☐

(d) Man ☐

(iv) In which mammals the cloaca is retained?

(a) Insectivores ☐

(b) Protherians ☐

(c) Carnivores ☐

(d) Cetacians ☐

3.6 SUMMARY

Let us sum up what we have learnt in this unit:

- Teeth are present in all vertebrates except birds at some stage in their lives. Teeth develop partly from the epidermis and partly from the underlying dermis. Teeth can be classified according to their way of placement in the jaw, nature of replacement and their appearance. Mammals have two distinct sets of teeth, the deciduous (milk) and the permanent dentition. The number of various categories of teeth in the jaws in mammals is conveniently expressed by a dental formula in which the kind of teeth such as incisor, canine, premolar and molar are indicated by the initial letters as i, c, pm, m.

- Animals use various strategies to feed. Some species search, stalk, pounce, capture, and kill. In lower vertebrates such as cyclostomes, elasmobranchs, teleosts, the most successful and widely used method for feeding is filter feeding. These filter feeders use ciliated surfaces to produce currents which draw drifting food particles into their mouths. Amphibians capture their food using their tongue, swallow their food whole, their teeth only help to hold the prey. In reptiles jaws or palate are provided with pointed teeth which help these animals in holding, tearing or swallowing their prey. Whereas birds have no teeth, but instead of that they have horny beaks which exemplify adaptive radiation suited to a gastronomic life style. Mammals make extensive use of their teeth for killing, cutting and grinding it up and accordingly teeth have evolved very different shapes for those purposes.

- The digestive organs very much in structure in different vertebrate groups which is correlated with the nature and abundance of their food. Overall the digestive system is a tabular organization of alimentary canal because it allows food to travel in one direction, passing through different regions of digestive specialization. In general alimentary canals in vertebrates have four major divisions, the functions of which are (1) receiving (2) conducting and storage, (3) digestive and absorbing nutrients and (4) absorbing water and defecating.

- The oral cavity receives the food and oesophagus conducts the food by peristaltic motion and connects to the stomach. In birds the oesophagus may have a diverticulum called crop to store grain. The stomach is amuscular chamber which is the site of storage and digestion. It shows increasing specialization from fishes to amphibians to reptiles. Birds have a proventriculus (glandular stomach)and ventriculus (muscular stomach or gizzard).

- In majority of mammals the stomach is relatively simple muscular sac like structure but in ruminants such as cattle, buffalo, goats, sheep, deer etc. it has four chambers. In ruminants food is swallowed, saturated by copious salivations and passes into the rumen and reticulum where it lies until, having finished feeding, the animal begins ruminating or chewing the cud.

- The small intestine is the longest part of the alimentary canal. It is the site of absorption of digested food. The colon is the large intestine and the site of absorption of water.

- The caecum is simple in monotremes, absent in sloths, some cetaceans and in a few carnivores. In humans and a few other animals like civets, some rodents, monkeys the distal end of caecum has degenerated into an appendix vermiformis. In some herbivores caecum is enormous.
- Associated with alimentary canal there are various digestive glands like oral glands in mammals, liver and pancreas found all vertebrates including mammals.

3.7 TERMINAL QUESTIONS

1. What is the difference between dentition of herbivores and carnivores ? Illustrate your answer with suitable examples.
2. Describe the various strategies used by fishes and amphibian to feed.
3. Explain the major differences between reptilian and avian digestive systems.
4. Describe the specializations found in ruminant stomachs.

3.8 ANSWERS

Self-Assessment Question

1. i) correct ii) correct
   iii) incorrect iv) incorrect
   v) correct vi) incorrect
2. (i) filter feeders
   (ii) groove, venom, syringe
   (iii) talons, beak
   (iv) front
3. Fishes: iii), vi), viii), ix)
   Amphibians: x)
   Reptiles: ii), vii)
   Birds: i), iv)
4. (i) d, (ii) b, (iii) c, (iv) b

Terminal Question

1. Refer to Section 3.2 of the unit.
2. Refer to Section 3.3 of the unit.
3. Refer to Sub Section 3.4.3 and 3.4.4 of the unit.
4. Refer to Sub Section 3.5 of the unit.

UNIT 4

RESPIRATORY SYSTEM

Structure

4.1 INTRODUCTION

In the previous unit you have learnt about the structure of various types of digestive systems that occur in vertebrates and their role in providing nutrients to the cells of the body. These nutrients are essential for fulfilling the energy requirements of the animal cells. The nutrients produce energy when they undergo oxidation during the process of respiratory metabolism. The end products generated by oxidation are energy, water, and carbon dioxide. Thus vertebrates consume oxygen for oxidation of nutrients present within the cells. This oxygen needs to be replenished and the waste byproducts like heat and carbon dioxide produced during oxidation metabolism must be removed in order to survive. The sequence of events that result in exchange of oxygen and carbon dioxide between an organism and its environment is known as **respiration**. This is done primarily by the respiratory system. The gas exchange between the environment and blood via the respiratory surface is referred to as **external respiration.** The utilization of oxygen for oxidation of nutrients within the cells and tissues may be termed as **internal respiration.** In this unit you will study the major respiratory structures *i.e.* gills, and lungs that facilitate respiration in both aquatic and terrestrial vertebrates.

Objectives

After studying this unit you should be able to:

- describe the structure and function of gills which form the respiratory system of aquatic vertebrates like fishes and amphibian larvae to breathe in water and air and explain how they are used;
- describe the structure and function of accessory respiratory organs in fishes; and
- describe the structure and function of respiratory organs in terrestrial vertebrates.

4.2 SALIENT FEATURES OF RESPIRATORY SYSTEM OF VERTEBRATES

Respiration is the sequence of events that result in exchange of oxygen and carbon dioxide between the environment and organism. External respiration refers to gas exchange between the environment and blood via a respiratory surface. Respiratory organs are of two types: (i) those that have respiratory surface turned out forming an evagination called **gills,** (ii)those that have respiratory surface turned in forming an invagination called **lungs**. Our own lungs are a good example of such invagination.

The organs of respiration in vertebrates (the gills or lungs and in some cases the skin) help in ventilation/breathing *i.e.* active movement of the respiratory medium (water or air) across the respiratory surface.

Ventilation may be

- non directional (water/air flows past the respiratory surface in an unpredictable pattern),
- unidirectional (water or air enters the respiratory surface at one point and exits at another), and
- tidal (water/air moves in and out from one point only)

For the respiratory organs to function efficiently they must have:

1. A provision for renewing the supply of oxygen-containing medium, namely, water or air that comes in contact with respiratory surface and provision for removing carbon dioxide that is released from the respiratory surface.
2. A large surface area which is provided with ample capillary network that has an access to the external environment;
3. A thin and moist membrane surface which facilitates passage of gases.

Let us now discuss the structure of gills as respiratory organs of aquatic vertebrates.

4.3 RESPIRATION BY GILLS

Gills are the main respiratory organs in fishes and some aquatic amphibians. They are composed of numerous gill filaments or gill lamellae, which are thin walled extensions of the epithelial surface. Each gill contains a vascular network. Blood is brought extremely close to the respiratory surface, thus facilitating ready exchange of gases.

4.3.1 General Gill Structure

Gills are enclosed in a gill cavity. This provides protection for the fragile organ and also permits the water to run over the gills in an efficient manner. Gills of fishes consist of several gill arches on either side (Fig.4.1a). The gill arches separate the opercular and the buccal cavities. From each gill arch extend two rows of gill filaments, Fig. 4.1b shows the arrangement of gill filaments in the arches. The tips of the filaments of adjacent arches meet forming a sieve like structure through which the water flows.

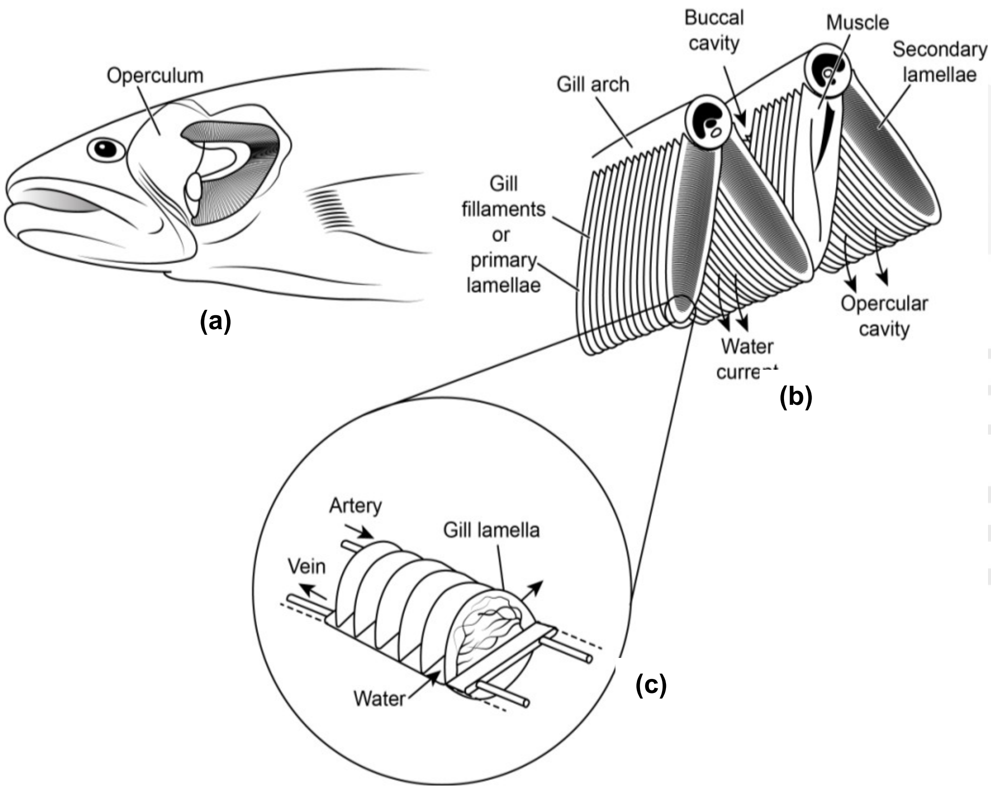


Fig. 4.1: a) Position of gill arches beneath the operculum on the left side of fish. The operculum has been lifted to show the arch; b) Part of two adjoining gill arches with their filaments. Note that the tips meet to form a sieve like arrangement for flow of water. The water moves through the mouth over the branched gills. Solid arrows show the flow of water; c) Part of a single filament showing the flat lamellae; the flow of water is opposite to the direction in which the blood moves.

Fish gills are covered by a thin epidermal membrane which folds repeatedly to form plate like lamellae that look like free flaps (Fig 4.1b). The structure of lamellae increases the surface area for respiration or exchange of gases. The flow of water is opposite to the direction in which the blood moves (Fig 4.1c). The area of gills present in different fishes varies depending on the activity of fishes. Fishes which are more active have larger gill areas. The rate of respiration in fishes is dependent on the amount of dissolved oxygen in water *e.g*. rate of respiration is more in fishes that live in waters with low oxygen content.

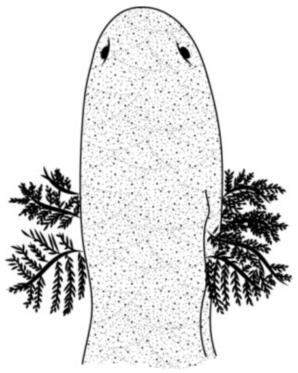


Fig.4.2: External gills of a salamander larva.

Gills are of two types : (i) external gills and (ii) internal gills.

(i) **External gills** (Fig.4.2) develop from the integument covering the outer surfaces of branchial/visceral arches and protrude into surrounding water. They are found in fish and larvae of many vertebrates including lung fishes, amphibians etc. They are usually branched; filamentous structures derived from ecotoderm. The functioning of external gills poses no problem since the gill filaments are in direct contact with water containing dissolved oxygen. The disadvantage of external gills is that they are easily damaged.

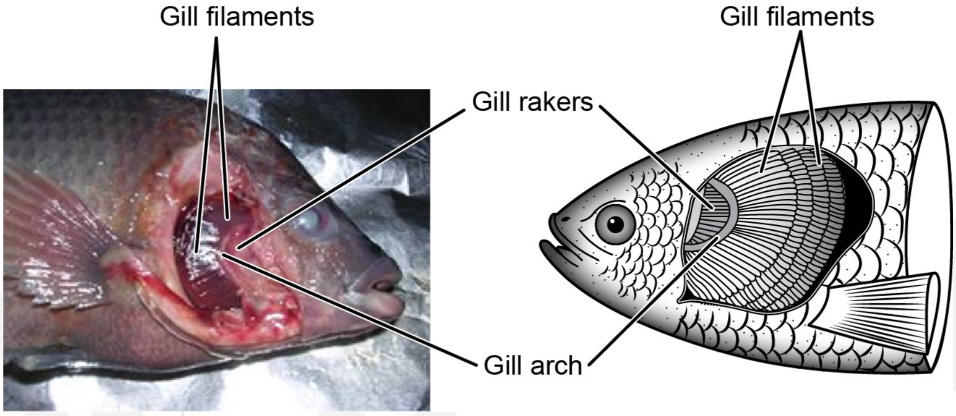


Fig. 4.3: Operculum of a bony fish removed to show internal gills.

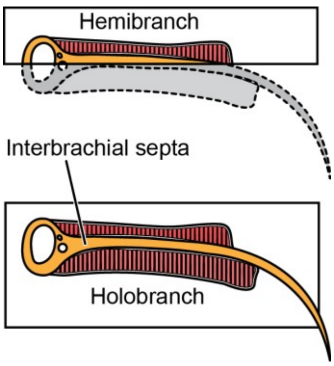


Fig.4.4: Hemibranch and holobranch.

(ii) **Internal gills** (Fig.4.3) are associated with pharyngeal slits (series of openings in the pharyngeal region between digestive tract and the outside of the body) and pouches (in some vertebrates, diverticula from the gut in the pharyngeal region that never break through to form open passageway to the outside; such diverticula are called pharyngeal pouches). Internal gills are composed of a series of parallel gill lamellae although in some forms they may be filamentous. They may be borne on both sides of the interbranchial septa but in some cases are present on only one side. A series of gill lamellae present only on one side of an interbranchial septum are termed as half-gill or **hemibranch**. Two hemibranchs join with interbranchial septum to form a complete gill or **holobranch** (Fig. 4.4).The gills are covered and protected laterally by soft skin folds such as interbrachial septum or by firm operculum. It is generally assumed that internal gills are derived from endoderm, although the exact origin is not clear.

There are **two main types of internal gills** in fishes. The first and more primitive types of internal gills are characteristic of elasmobranchs (cartiligenous fishes). In this group the interbranchial septa are exceptionally well developed and extend beyond the hemibranchs (Fig. 4.5a). The interbranchial septa, in addition to separating the gill clefts, serve to protect the gills themselves. The second type of internal gills is found in bony fishes. In these forms, the interbranchial septa are reduced to varying degrees

(Fig. 4.5b) from which hemibranchs protrude into a single branchial or extrabranchial chamber located on each side between the operculum and gills. The operculum, protects the gills in the branchial chamber which opens to the outside through a single gill aperture. Opening and closing of operculum bring about gill respiration in these fishes.

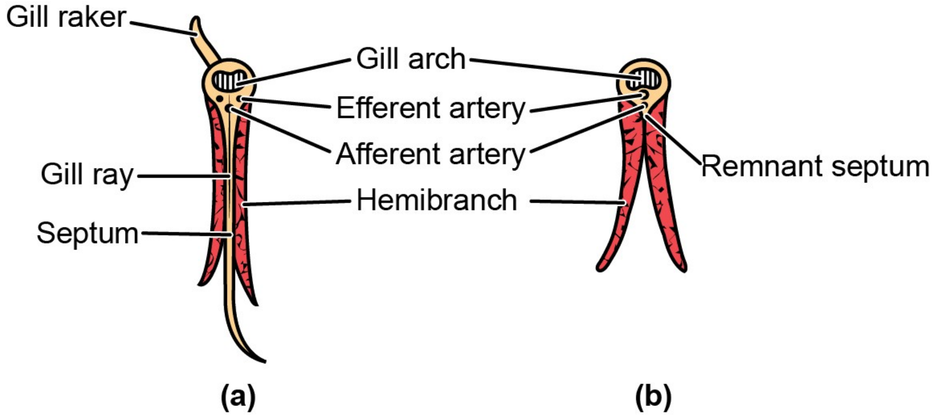


Fig. 4.5: Types of gill in fishes (a) elasmobranch; (b) teleost.

The gills are provided with dense capillary beds in the branchial region. Blood is carried very close to the respiratory surface, thus facilitating ready exchange of gases. In gills of most fishes ventilation or breathing is unidirectional. When internal gills are used in respiration, water containing dissolved oxygen enters through the mouth and passes through the internal gill slits into the gill clefts. As the water passes over the gill lamellae, oxygen is taken from the water and carbon dioxide is released. The water then passes through the external gills slits to the outside.

Let us now study respiratory systems of different vertebrates that use gills as their respiratory organs but before we do that try the SAQ given below.

SAQ 1

1. Indicate whether the following statements are true or false :

   (a) External respiration would mean utilization of oxygen for oxidation of nutrients in cells and tissues. T/F

   (b) One of the criteria for efficient functioning of the respiratory organs is that the respiratory surface should be thin and moist to facilitate exchange of gases. T/F

   (c) Internal gills develop from the integument covering the outer surface of branchial arches. T/F

   (d) Holobranch refers to a series of lamellae on one side of an interbranchial septum. T/F

4.3.2 Respiratory System of Cyclostomes

Cyclostomes are jawless vertebrates, and include the hagfishes (class:Myxini) and lampreys (class:Petromyzontida) (Fig.4.6). Among hagfishes the number of gill openings on each side vary (1 to 15) with the species. In lampreys, seven pairs of internal gill slits open from the pharynx into seven pairs of gill clefts, which are rather large and spherical in shape.

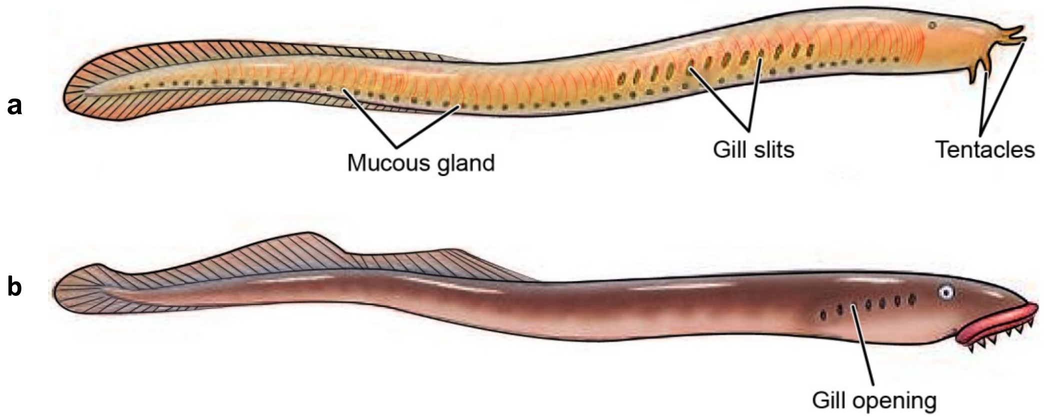


Fig. 4.6: Placement of gill slits (pharyngeal slits) in (a) hagfish and (b) lamprey.

Respiratory medium in hagfishes is water and its flow is unidirectional. The water enters through a single nasal opening, connecting to the pharynx via a broad tube called the nasopharyngeal tube, enters the gill pouches and exits through the numerous gill slits. In *Myxine* however there is only one gill opening on each side. In Figure 4.7 (a) you can see the external gill openings are located near the midventral line at some distance from the anterior end. The gill pouches connect to the pharynx internally by backwardly running channels that unite to form a single tube that opens on either side by a single external branchial opening (Fig. 4.7 b and c). In other species there may be 5 to 16 gill pouches, each opening externally through separate gill slits.

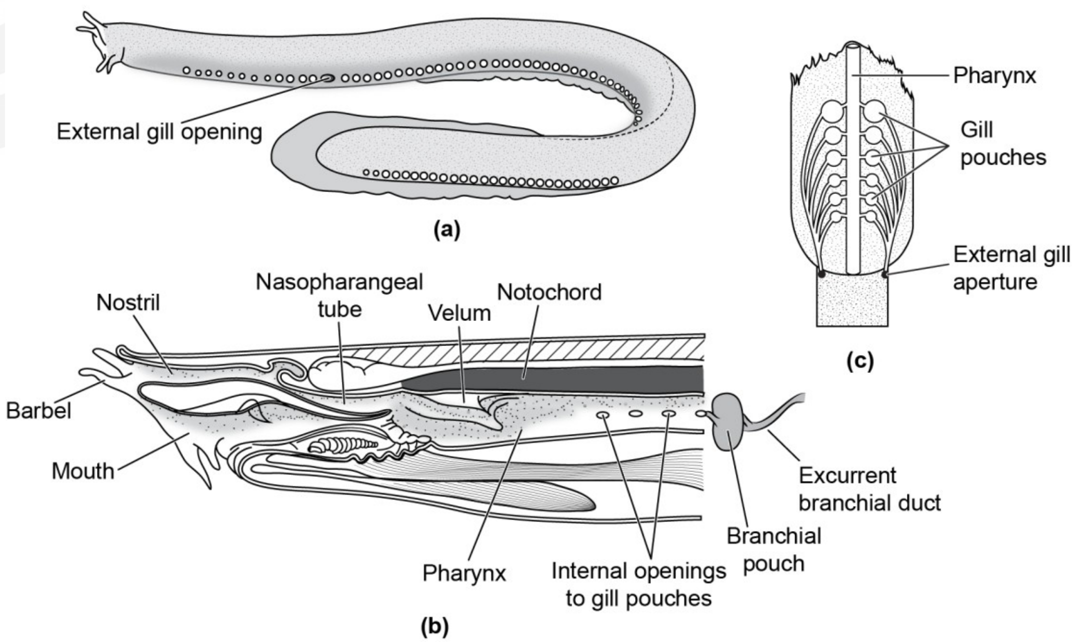


Fig. 4.7: (a) Lateral view of hagfish *Myxine* showing the external gill opening on one side; (b) sagittal section of head/anterior region showing respiratory structures of hagfish; c) Diagram, showing the relation of gill pouches to the pharynx and to the single pair of gill aperture in *Myxine*.

Breathing or ventilation in adult lamprey unlike hagfishes is tidal *i.e.* water enters and is expelled through the gill slits. However, in larvae lamprey ventilation is unidirectional as water is drawn into mouth and then pumped outside from the gills in a continuous flow.

Lampreys are only one of its kind amongst living vertebrates as they have a single nasal opening on their head which is connected to pituitary (hypophysis) with help of a duct and ends in a blind sac called the nasohypophysial pouch. Thus external nare does not connect to the pharynx but ends in a blind sac The pharynx is subdivided into a dorsal oesophagus and the ventral respiratory tube. This respiratory tube is separated from the mouth by a flap called the velum which prevents water from flowing out of the respiratory tube into the mouth while feeding (Fig. 4.8). Seven pairs of gill pouches are present between the respiratory tube and body wall which open just behind the head. The gill pouches have numerous gill lamellae developed on their inner surface that are separated from one another by wide membranous interbranchial septa. The gills pouches open internally by slits into the respiratory tube and they open separately to the exterior by external gill slits. Muscles surround gill pouches, and these together with elastic cartilages and appropriate valves pump the water tidally in and out of the external openings. In fact exhalation is the active movement and passive elastic recoiling of the branchial basket results in inhalation. Adult lampreys cannot ventilate the gills in a flow-through fashion as much of their time is spent with their sucker like mouth affixed to bodies of other fishes. Therefore, respiration is by tidal ventilation. However, in larval stages the water enters through the mouth and leaves through the external gill slits.

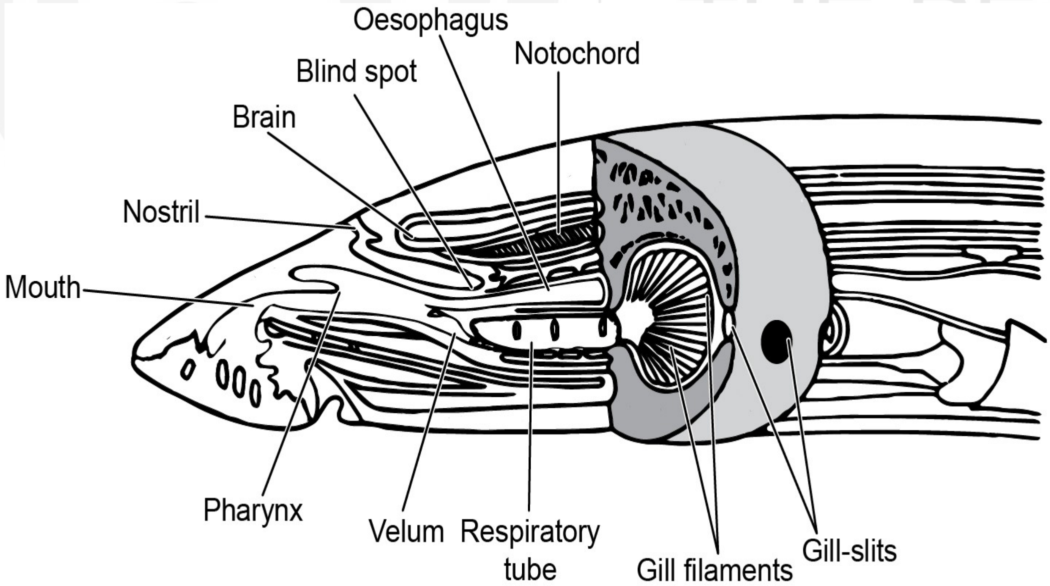


Fig.4.8: Longitudinal section of *Petromyzon* showing the internal structure. Note the division of the pharynx into a dorsal oesophagus and ventral respiratory tube and the gill pouches that connect to it and open externally through gill slits.

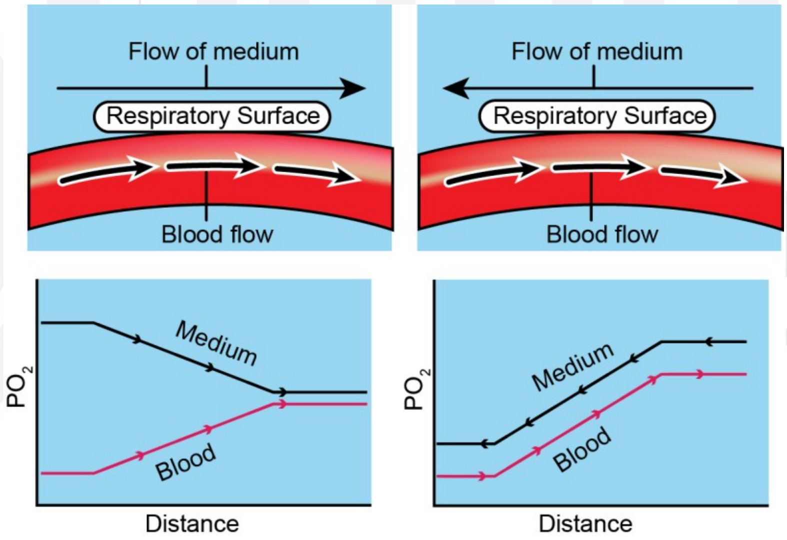
4.3.3 Respiratory System of Fishes

Ventilation or breathing in fishes is also unidirectional. Water enters the mouth and pharynx and is expelled through external gill slits in Elasmobranchii and through operculum in teleosts.

Counter current Exchange

pO_2 reflects the amount of oxygen gas dissolved in the blood. It primarily measures the effectiveness of the lungs in pulling oxygen into the blood stream from the atmosphere.

Gas exchange takes place in gill lamellae as water flows between them in one direction and blood within them in the other direction. This is called **countercurrent flow**. This type of flow has an important consequence. It permits the fish gills to have the highest possible oxygen levels. Figure 4.9 shows the advantage of countercurrent flow. Now let us suppose that the incoming blood in gills is devoid of all oxygen, and imagine the flow of water and blood is in the same direction i.e. it is concurrent (Fig. 4.9a) when the two streams come in contact oxygen is transferred from the water to blood at a high rate till an equilibrium is reached after which no transfer occurs. Now consider Fig. 4.9b which shows countercurrent flow. When blood which has zero pO_2 (Partial Pressure of Oxygen) comes in contact with water for the first time, the water also has low pO_2 (since it has been losing oxygen on its way to this point) but still sufficiently more than the pO_2 in blood for a pressure gradient to be maintained and O_2 flows from the water into the blood. As the blood moves on it meets with water richer in oxygen and the pO_2 of blood increases steadily. At all points along the capillary, pO_2 gradient is sufficiently high to permit transfer of oxygen from water to blood. The net effect is that blood leaving the gills in countercurrent exchange has extracted 80 per cent or more of the dissolved oxygen from water.



(a) Concurrent flow **(b)** Countercurrent flow

Fig 4.9: a) Concurrent flow: When blood and water move in the same direction, then no further exchange of O_2 takes place after equal concentration is reached. In this condition the pO_2 in blood reaches the pO_2 levels of the out flowing water; b) Countercurrent flow: favours better absorption of oxygen by blood. Blood enters with low pO_2 but leaves the lamellae with nearly the same pO_2 as water; Counter current flow also reduces the energy cost of pumping water over the gills.

Gills arches

A series of skeletogenous gills or visceral arches encircle the pharynx of fishes and of tetrapods. In fishes these arches primarily support the gills. They are located between the gill clefts, one behind the other at the bases of the interbranchial septa. The first arch is called mandibular arch and the second, hyoid arch. The remaining visceral arches are referred to by numbers (3, 4, 5, 6, etc.).

The first gill pouch or cleft lies between mandibular and hyoid arches and is often referred to as the hyomandibular cleft. In fishes it is either modified to form a spiracle or is closed altogether. The arrangement of gill arches and gills in elasmobranchs and bony fishes is shown in Fig 4.10.

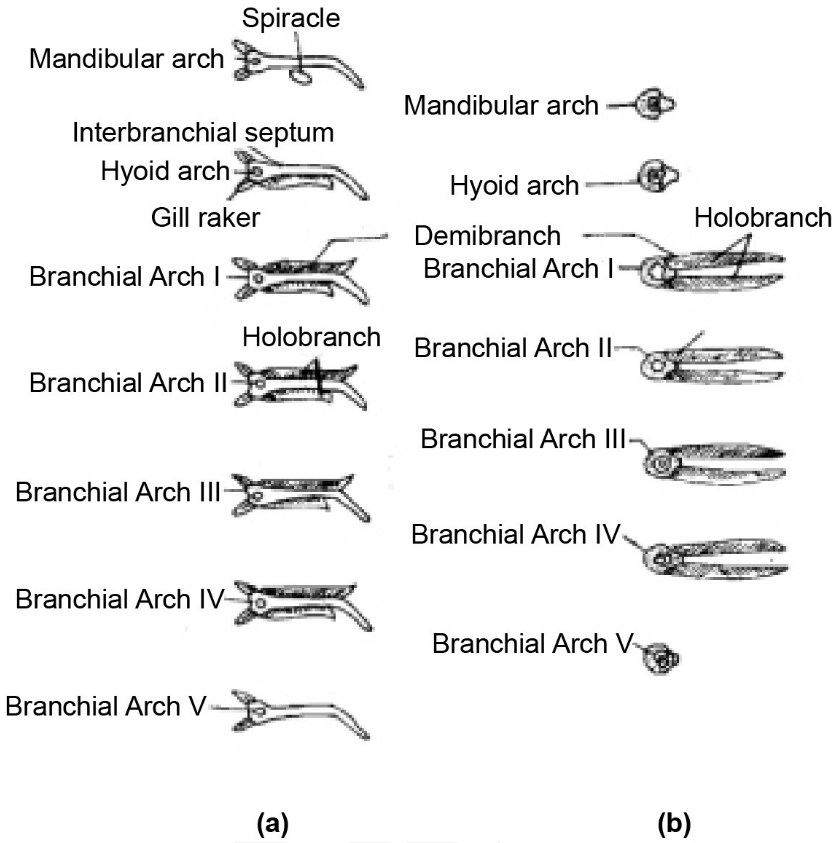


Fig. 4.10: Arrangement of gill arches and gills in (a) an elasmorbranch and (b) a teleost. Notice that bony fishes have a highly reduced interbranchial septum.

In *Acipenser*, *Polydon*, *Polypterus*, the first gill pouch has become modified and opens to the outside by means of a spiracle. Rudimentary gill lamellae may be located on the anterior wall of the spiracle. Since blood supply to these lamellae consists of oxygenated blood, they do not perform a respiratory function and the term false gill or **pseudobranch** is applied to them. The spiracles generally open on the top of the head and in some species they are provided with valves.

(I) RESPIRATION IN CARTILIGENOUS FISHES

Living cartiligenous fishes are placed in class **Chondricthyes** which includes mostly marine sharks, rays and skates **(Elasmobranchii)**; and elephant fishes, rat fishes and rabbit fishes (**Holocepahli)**. In Elasmobronchii five to seven gill arches and gill slits in separate clefts on either side along pharynx are present. Elasmobranchii lack operculum. Holocephali has 4 gill slits covered by cartilaginous operculum.

In Elasmobronchii breathing/ventilation occurs when large volume of water is sucked into the buccal cavity via the mouth and spiracles. The expansion of buccal cavity causes an increase in volume of water sucked in. The mouth and spiracle close and muscles around the buccal cavity contract forcing water past the gills and out from the external gill slits (Figure 4.11).

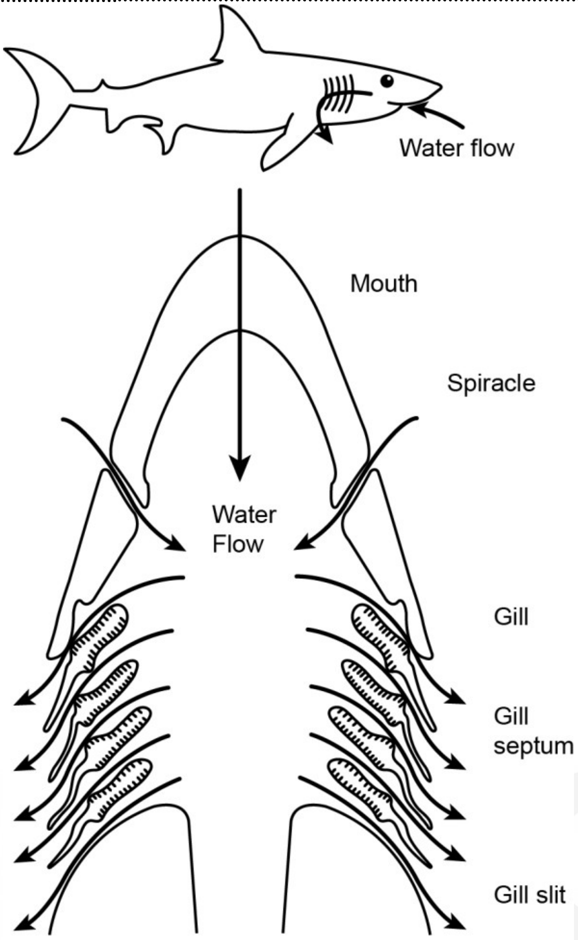


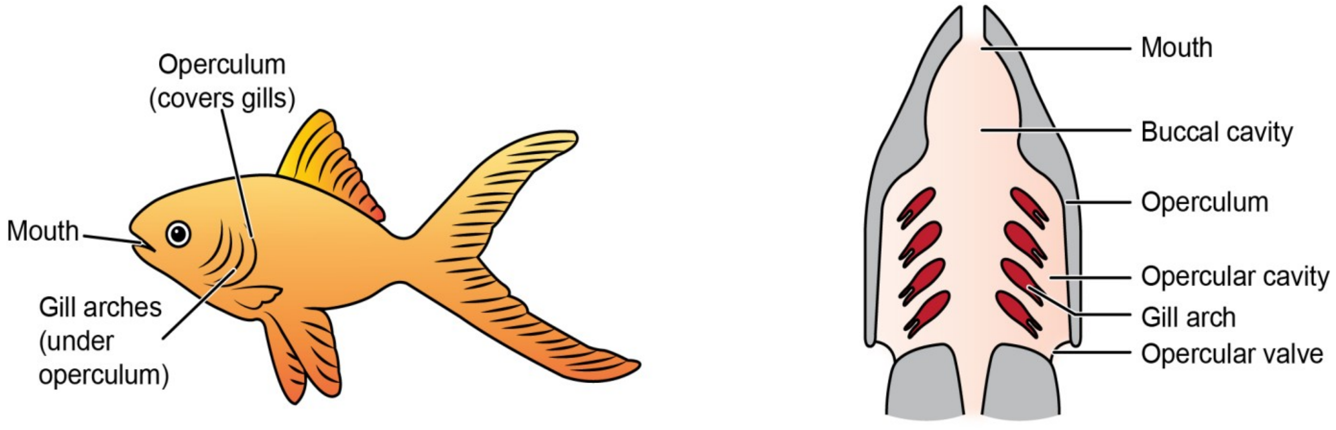
Fig. 4.11: Water ventilation in Elasmobronchii. Blood flow is countercurrent to the blood flow.

Most elasmobranchs are **pentachid** *i.e.* have five pairs of clefts in addition to the spiracles. Another form of shark, *Hexanchus*, has six and another *Heptanchus*has seven clefts. *Heptanchus* also has the largest number of gill clefts of any gnathostome (jawed vertebrates).

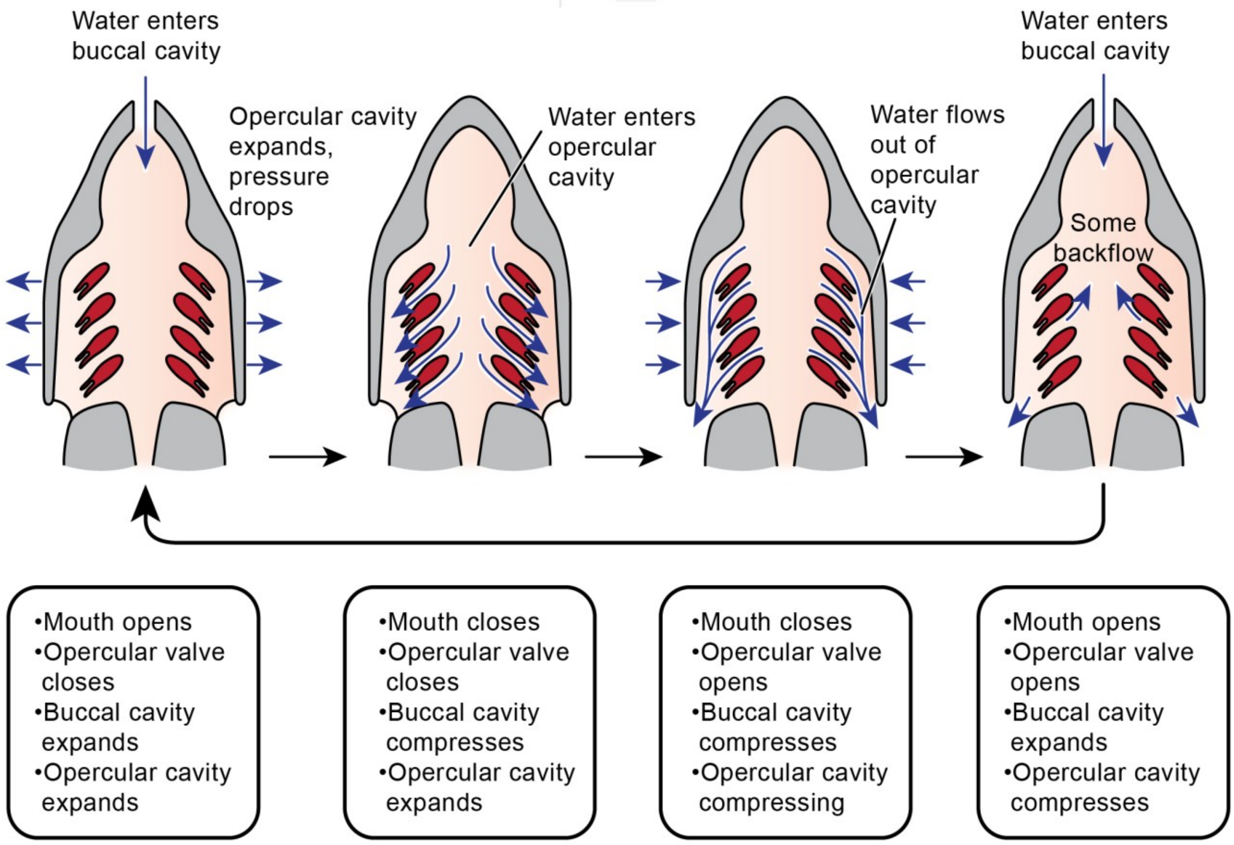
(II) RESPIRATION IN BONY FISHES

Recall from the previous course (BZYCT-131),that bony fishes includes the ray finned fishes placed in Class Actinopterygii which has subclasses **(i) Chondrostei** where spiracles are present; eg. *Polydon, Acipenser* (ii) **Neopterygii**: (gars, bowfins and teleosts); includes *Amia, Lepistoseus* and most of the world's bony fishes and **(iii) Cladistia** where spiracles and lungs are present eg., *Polypterus*. The other group of bony fishes includes the lobe-finned fishes placed in **Class Sarcopterygii.** These fishes are fishes with lungs.

The gill apparatus of bony fishes have five gill slits, a bony operculum which arise from the hyoid arch and moves backward over the gill chamber. Operculum provides a protective cover over the branchial arches and gills they support (Fig. 4.12a) . In bony fishes breathing or ventilation occurs when water enters buccal cavity through mouth over the gills as simultaneously the opercular cavity expands. Expansion of opercular cavity causes decrease in pressure so water enters opercular cavity. When opercular valve opens water flows out of the opercular cavity. Water is driven across the gills by two pumps; buccal pump and opercular suction. Opercular movement assists in the expulsion of water from gill chambers (Fig. 4.12b).



(a)



(b)

Fig.4.12: a) Teleost fish (lateral view and horizontal section) b) ventilation cycle in teleosts.

Most actinopterygian fishes have structures called swim bladder or air bladder between alimentary canal and vertebral column. The distended sac like air bladder varies in length and form in different fishes. It is essentially hydrostatic in function and aids in boyancy of fishes (see Box 4.1).

Box 4.1: SWIM BLADDER

All fishes are slightly heavier than water. This is because the skeleton and the tissue of fishes contain certain heavy elements that are present only in trace amounts in water. The bony fishes are aided in buoyancy in water by having a floatation device—a gas filled space—the swim bladder. Swim bladder is present in most pelagic fishes but is absent in fishes that live in abyssal waters and bottoms of the sea. The neutral buoyancy is achieved by adjusting the volume of the gas in swim bladder. Such an adjustment would enable the fish to remain suspended indefinitely at any depth with no muscular effort. Gas is added to the bladder when the fish descends to greater depth, and when it swims up, gas is removed from the bladder making the fish lighter. Swim bladders differ from lungs in three ways. First, swim bladders are usually situated dorsal to the digestive tract, whereas lungs are ventral. Second, swim bladders are single, whereas lungs are usually paired. Third, in swim bladders, returning blood drains to the general systemic circulation (cardinal veins) before entering the heart. In lungs, venous return enters the heart separately from the general systemic circulation

Lung fishes are air breathing forms and include; *Polypterus, Lepidosiren, Neocertodus and Protopterus*. The lungs fishes are characterised by either a bilobed lung as in most cases or just one lobe as in *Neoceratodus*. The presence of external gills is rare among lung fishes. In *Polypterus* a single pair of external integumentary gills is present in the region of the hyoid arch and a bilobed lung developed symmetrically and the duct opens ventrally into pharynx (Fig. 4.13).

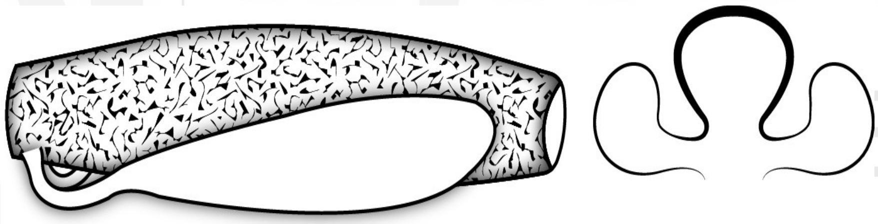


Fig. 4.13: The bilobed lung of *Polypterus*.

The epithelial lining of the lung is not smooth and there are a few furrows that increase the surface which is in contact with air. In *Polypterus*, lungs are supplied by pulmonary arteries off the sixth embryonic aortic arch, but the venous return is through the hepatic veins. *Neoceratodus* comes to the surface to breathe air but only when oxygen tension falls below 83 mm Hg and is known to survive foul waters that kills other fishes, though, the fish cannot live out of water. The other lungs fishes, *Protopterus* and *Lepidosiren*, have been shown to obtain nearly 98% of their oxygen requirements from air. The floor of the mouth is lowered and air drawn in through the mouth is forced back by a buccal pump, with the mouth being closed and the tongue pressed against the roof as a seal. The hyoid apparatus and the pectoral girdle help in the process of inspiration. Expiration is exclusively by the elasticity of the lungs, with ribs playing no role in the process. The gills in most lungfishes except *Neocerotodus* are atrophied and do not allow adequate air exchange

Most fishes die soon after being exposed to air, even though their gills are kept moist. Lack of water in the branchial chambers as well as the accumulation of mucus causes the gills to stick to each other. With the result the exposed respiratory surface is decreased and the exchange of gases is no longer adequate. Fresh-water fishes face the problem of their environment getting dried up and to overcome this problem, in addition to gills, they have evolved accessory organs for breathing air. In the following subsection you will briefly learn about the accessory respiratory structures of certain fresh water fishes.

Before you proceed to the next section attempt the given SAQ to test your understanding of what you have learnt about respiration in fishes.

SAQ 2

1. Fill in the blanks with suitable words.

   (a) The number of pairs of internal gill slits present in lampreys is ………………. .

   (b) In lampreys inhalation is a …………….. process and exhalation is an ……… process.

   (c) The first visceral arch of vertebrates is …………….. arch and the second is……………..

   (d) The system of water flow across the gills in fishes that ensures an 80% oxygen uptaken is knows as ………………. ……………. flow.

   (e) In elasmobranchs ………………….. ………………. are well developed and extend beyond hemibranchs.

2. Pick out the false statements and correct them.

   (a) Interbranchial septum support gill filaments in both bony and cartilaginous fishes.

   (b) Spiracles are present in all elasmobranchs.

   (c) All bony fish have only one external gill slit that opens to the exterior on each side.

   (d) All elasmobranchs lack opercula.

4.3.4 Accessory Respiratory Organs in Fishes

The accessory respiratory organs of fishes are the outgrowths either of the pharynx or the branchial chamber that are richly supplied with blood vessels. In most air-breathing fish, wide gill filament and secondary lamellar spacing prevents coherence and collapse. Air from outside is drawn into these chambers by mouth and retained there for aeration of the blood. Actinopterygians like *Anabas*, *Ophiocephalus*, *Amphipnous*, *Clarias*, and *Saccorbranchus* are some of the fishes provided with accessory respiratory organs.

Anabas, the climbing perch, migrates from pond to pond and during such times while it is on land, breathes air from the atmosphere. The two air chambers are the extensions of the branchial cavities and lie on each side of the head. The accessory organs, also known as **labyrinthine organs** (Fig. 4.14) are outgrowths of the upper part of the first branchial arch. Each organ consists of concentrically arranged wavy plates, covered by a vascular membrane. The air chamber communicates with pharynx by an opening situated between hyoid and the first branchial arch. Essentially air that is drawn by the mouth passes into the branchial chamber and exits through the branchial aperture. *Anabas* can remain outside water for nearly six to seven hours. It acquires about 54% of its oxygen requirement from air .

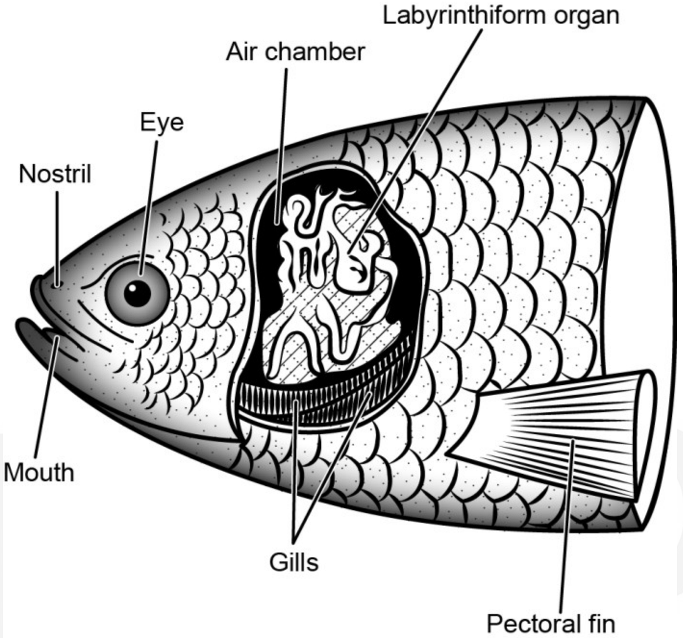


Fig. 4.14: The labyrinthine organ of *Anabas*.

Ophiocephalus, the murrel, also has a pair of air chambers one on each side of the head (Fig. 4.15). Each air chamber arises as an outgrowth of pharynx above the first gill arch and extends as far as the last gill cleft. Air enters into the chamber by the mouth and leaves through the opercular arch.

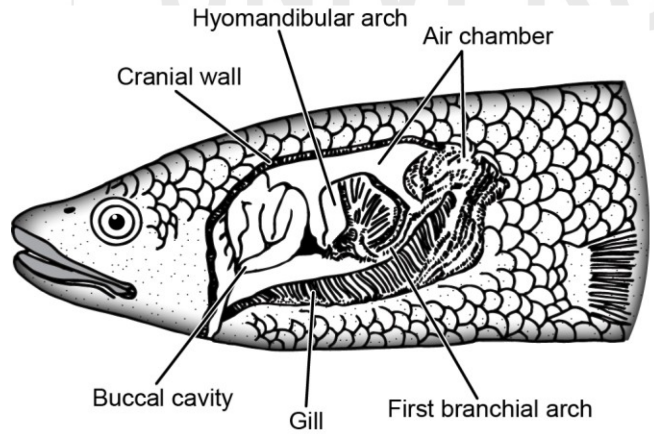


Fig. 4.15: The accessory respiratory organ of *Ophiocephalus*.

The Indian catfish *Clarias*, has the most complicated and highly branched vascularised paired accessory respiratory organs. These consist of a **suprabranchial chamber** with a highly vascularised membrane and branching **arboriform or dendriform organs** (Fig. 4.16) lying in suprabranchial chamber. These are more specifically derived from the upper parts of the second and fourth branchial arches. They are tree like supported by cartilaginous internal skeleton and the ends of each branch has a knob of cartilage core covered by a highly vascular membrane. There is a well developed inhalant and exhalent aperture in the suprabranchial chamber. The fish comes to the surface to take in gulps of air which goes in the suprabranchial chamber via the pharynx. The air is exhaled via the exhalent aperture by the contraction of the chamber.

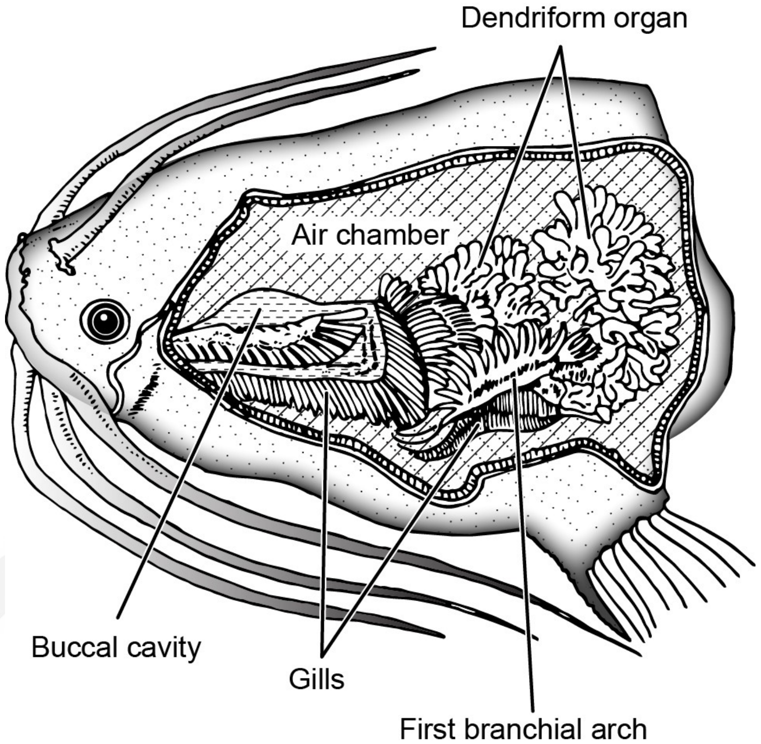


Fig. 4.16: The arboriform accessory respiratory organ of *Clarias*.

In *Amphinous* the air chambers (Fig. 4.17) arise as saccular outgrowths of dorsal wall of the pharynx extending as far as the third branchial arch. The walls of the sacs are folded and vascular. The sacs communicate with pharynx by an opening through which air is drawn in. The air exits through the gill slits and opercular opening. The gill filaments of the first gill arches are highly reduced.

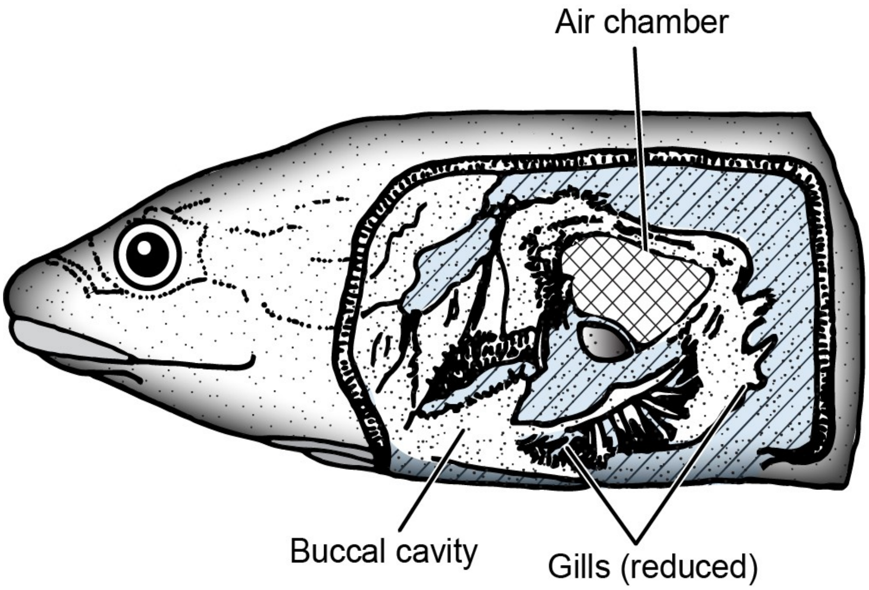


Fig. 4.17: The air chamber in *Amphipinous*.

In *Saccobranchus* there is a pair of tubular sacs that arise as outgrowths of gill chambers extending upto the middle of the tail region (Fig. 4.18). The folds in these tubes form a sort of air chamber that communicates with the buccal cavity by a slit. The air passes in an out of the chamber through the slit. The mudskipper *Periophthalmus* that lives in brackish waters has large opercular cavities that are filled with air drawn through the mouth. Mudskipper is so accustomed to life out of water; it dies of suffocation if prevented from living on land for a long period. A similar arrangement in which the opercular cavity functions as an aerial respiratory organ is noticed in the tropical rock skipper (*Andamia)*.

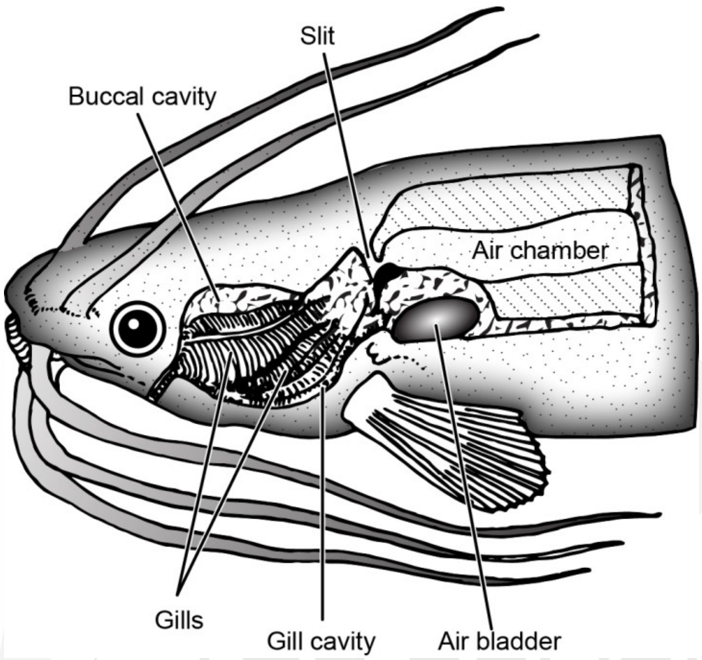


Fig. 4.18: The accessory respiratory organ of *Saccobranchus*.

4.3.5 Respiration in Amphibian Larvae using Gills

Most amphibians spend their larval life in water and, after metamorphosis into adults move to the land. During larval life, external gills are used as organs of gas exchange. In addition the moist and highly vascularised skin also serves as the respiratory organ. Skin and buccal cavity are the routes of oxygen entry for respiration. The amphibians respire through **skin, external gills, internal gills and the lungs.**

The three pairs of external gills that appear at the time of hatching are branched processes connected with the blood vessel from aortic arches. Subsequently folds from the posterior edges of the hyoid arches cover the gills as operculum. At a later stage the gills are resorbed.

The internal gills are formed with the establishment of mouth opening. The internal gills consisting of branchial filaments are formed ventral to the external gills on the branchial arches and project into the opercular cavity. The third, fourth and the fifth visceral arches possess two rows of filaments and the sixth arch has only one row on its anterior side. Blood vessels from aortic arches provide vascular connections. Water passes from mouth to pharynx and then through the gill slits into the opercular chamber. It finally leaves through the opercular aperture. The internal gills disappear at the time of metamorphosis.

In a few urodeles, gills are retained thoughout life, but in most urodeles and all the tailless amphibians, they disappear at the time of metamorphosis. Newly developed lungs then take over the function of respiration.

Structures analogous to gills may develop in reptiles, birds and mammals. In reptiles five pairs of pharyngeal pouches are formed during embryonic life and in birds and mammals only four develop. In the latter groups a fifth one may also develop, but it remains rudimentary and attached to the fourth pair. The pouches do not break through to the outside, but very occasionally, they may do so. If the pharyngeal pouches fail to disappear in the normal manner, they may lead to the formation of branchial cysts and fistulae.

SAQ 3

1. Match the type of accessory respiratory organ with the fish that possesses it.

(a)	Air Chamber	i.	*Amphipnous*
(b)	Tubular Chamber	ii.	*Anabas*
(c)	Arboriform organ	iii.	*Ophiocephalus*
(d)	Saccular Chamber	iv.	*Saccobranchus*
(e)	Labyrinthine organ	v.	*Clarias*

2. Choose the correct answer from the alternatives provided.

(a) The internal gills appear appear/disappear at the time of metamorphosis.

(b) In a few tailless amphibians/urodeles, gills persist throughout adult life.

(c) Gills develop/do not develop in association with the pharyngeal pouches of reptiles, birds and mammals.

(d) If the pharyngeal pouches fail to disappear/appear, they may lead to the formation of branchial cysts and fistulae.

4.4 RESPIRATION BY LUNGS

One of the most important changes in vertebrate evolution was the transition from water breathing to air breathing. In terrestrial animals the main respiratory organ is the lung. Vertebrate lungs are elastic bags designed for air breathing (Fig 4.19). The volume of lungs expands when air is inhaled and shrinks/contracts when air is exhaled. Embryologically, lungs develop from outpocketing of endoderm from the pharynx. The diverticulum divides into two halves, the lung buds, which are destined to give rise to the bronchi, and the lungs proper. The original unpaired duct, which connects the lungs to the pharynx, serves to carry air back and forth and is known, in most cases, as windpipe or trachea. Generally, the trachea branches into two bronchi, one to each lung. In some species, each bronchus branches into successively smaller bronchioles that eventually supply air to the respiratory surfaces within the lung. In snakes which have slender bodies one lung may be reduced in size; or may be absent.

The trachea and bronchi bring the air we breathe to the lungs. Each bronchus is shaped like a tree, with lots of smaller and smaller branches. They may branch to varying degrees, depending upon the species. The smallest branches are called bronchioles and at the end of these are air sacs (alveoli). They are about 600 million alveoli (large surface area provided with ample capillary network) in the lungs in humans. These are covered with capillaries, and here the exchange of gases takes place.

While evaginated gas exchangers like gills can be ventilated continuously and unidirectionally through buccopharyngeal pump or ram ventilation, the lungs developing as invaginated organs, and having a narrow entry/exit point to atmospheric air, can only be ventilated tidally, i.e. bidirectionally (= in-and-out). As a result, dead space is created in the major air-conducting passages. The trachea, bronchi, bronchioles and alveoli holds a significant volume of air. During exhalation most of the air from the lungs is expelled, however some air is left in the passageways. On inhalation, this air is again drawn into the lungs. This volume of air within the respiratory passageways is called the dead space. The total volume of air that is inhaled in a single breath/inspiration is known as the tidal volume. Normal tidal volume of humans at rest is approximately 500 ml. As the dead space is about 150 ml (30%), only 350 ml (500 ml—150 ml) of fresh air actually reaches the lungs. Lets us now see the structure of lungs and the respiratory system in different groups of vertebrates and how they have evolved/adapted to their environment.

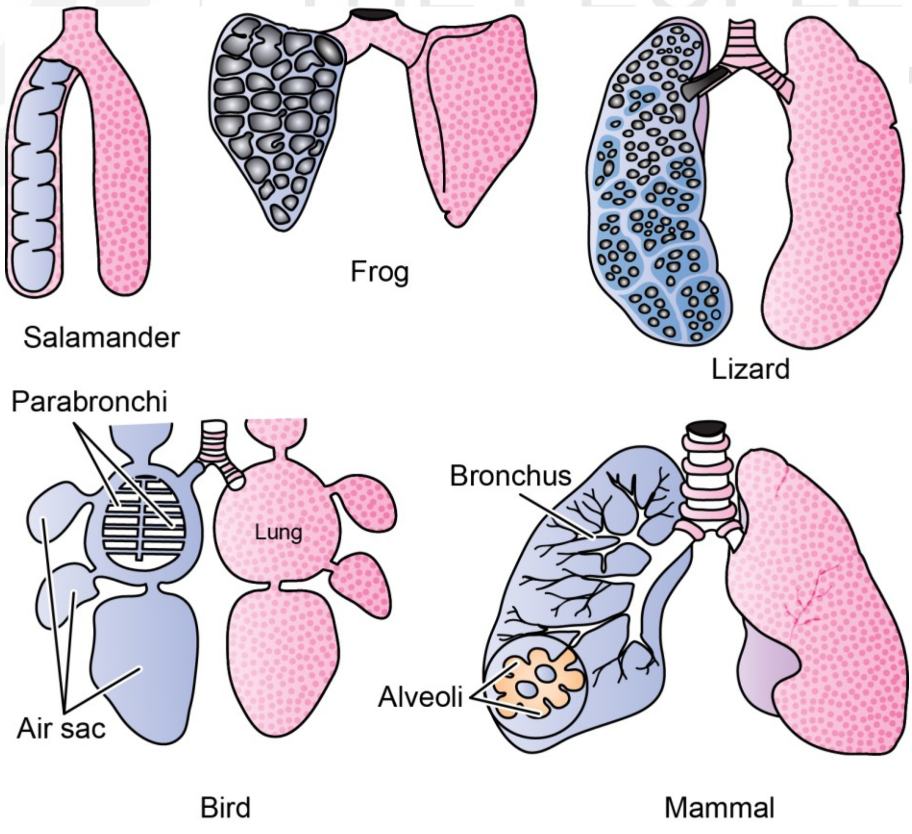


Fig 4.19: Lungs in terrestrial vertebrates.

4.4.1 Respiratory System in Amphibians

The amphibians are tetrapods with moist scaleless skins and include anurans (frogs), urodeles (salamanders) and caecilians. You have read in the earlier section how amphibians have transient internal and external gills in early stages of their life. Adult amphibians generally respire by lungs, bucco-pharyngeal cavity as well as by skin. Respiration by skin is known as the cutaneous respiration and by lungs is known as pulmonary respiration. The balance between cutaneous and pulmonary respiration varies among species and within a species it depends on body temperature and animal's rate of activity. Amphibians show more dependence on lungs (pulmonary) for oxygen uptake as temperature and activity increases.

A few urodeles do not develop a lung bud and lack both gills and lungs bud throughout life. A specially vascularised region of the pharyngeal and oesophageal lining is used as the respiratory membrane along with the skin. Salamanders inhabiting swift mountain streams may only have vestigial lungs which are few millimeters in length, as buoyancy would be a disadvantage in swiftly flowing currents.

(i) Cutaneous respiration

Amphibians depend on cutaneous respiration for a significant part of their gas exchange. When submerged in water they respire using the skin which is membranous containing large network of capillaries. The skin of the amphibians has mucus glands distributed over entire body surface which secrete glycopeptides and glycerol that keeps the skin moist. The skin is supplied with the capillaries of the cutaneous artery that carries the deoxygenated blood. The respiratory exchange of gases takes place between the atmospheric oxygen and the carbon dioxide carried in the blood. The oxygenated blood is returned to the heart by the cutaneous vein and thence to the general circulation.

(ii) Pulmonary respiration

The respiratory tract of frog includes the external nostrils, nasal chambers, internal nostrils, bucco-pharyngeal cavity, glottis, laryngo-tracheal chamber and a pair of bronchi. The median slit-like glottis on the floor of pharynx opens into larynx (laryngo-tracheal chamber). Lungs of amphibians appear as two simple sacs, elongated in urodeles and bulbous in anurans. They occupy the pleuriperitoneal cavity along with other viscera. The left lung is usually longer except in caecilians, in which it is rudimentary. The internal lining of the amphibian lung may be entirely smooth or have internal folds or septa that increase the inner surface to form many chambers that increase the surface are for respiration (Fig. 4.20).

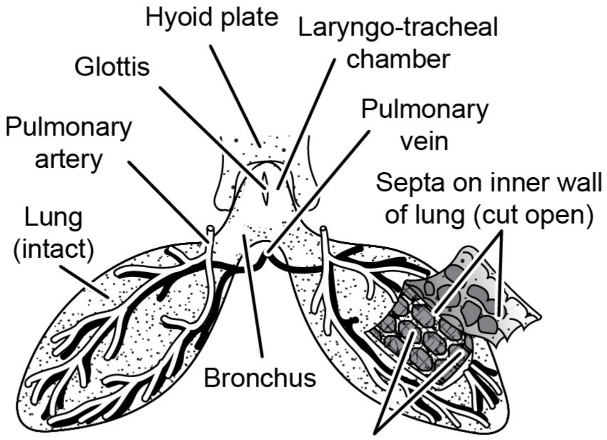


Fig. 4.20: The Respiratory organs of frog (dorsal view). Right lung partly cut to show inner partitions and alveoli.

There are two processes involved in pulmonary respiration. First is the drawing in of the air into lungs - the inspiration and second, the forcing out or air from lungs-the expiration. Since **ambhibians do not have ribs or diaphragm**, inspiration occurs in two stages (Fig.4.21). (i) Essentially in the first stage the air is drawn into the buccal cavity from outside. The lowering of the floor of the buccal cavity causes an increase in buccal space. This in turn leads to the rushing of air from outside into buccal space through external nostrils. The buccal cavity thus functions as a suction pump. It is believed that some gaseous exchange occurs in the buccal cavity (Buccopharyngeal respiration). This is followed by opening of glottis which causes release of air from the lungs into the buccal cavity. This released air mixes with the fresh inhaled air in the buccal cavity. (ii) In the second process, the nostrils as well as the mouth close. The floor of the buccal cavity is raised which causes an increase in pressure; but the pressure is insufficient to open the mouth. The air enters the laryngo-tracheal chamber through the glottis. The elastic wall of the lungs causes the dilation of lungs allowing the entry of air and exchange of gases takes place in the alveoli of the lungs. During expiration, the elastic wall of the lungs recoil expelling the air contained in them. The air arrives in the buccal cavity and from there moves outside through the nostrils.

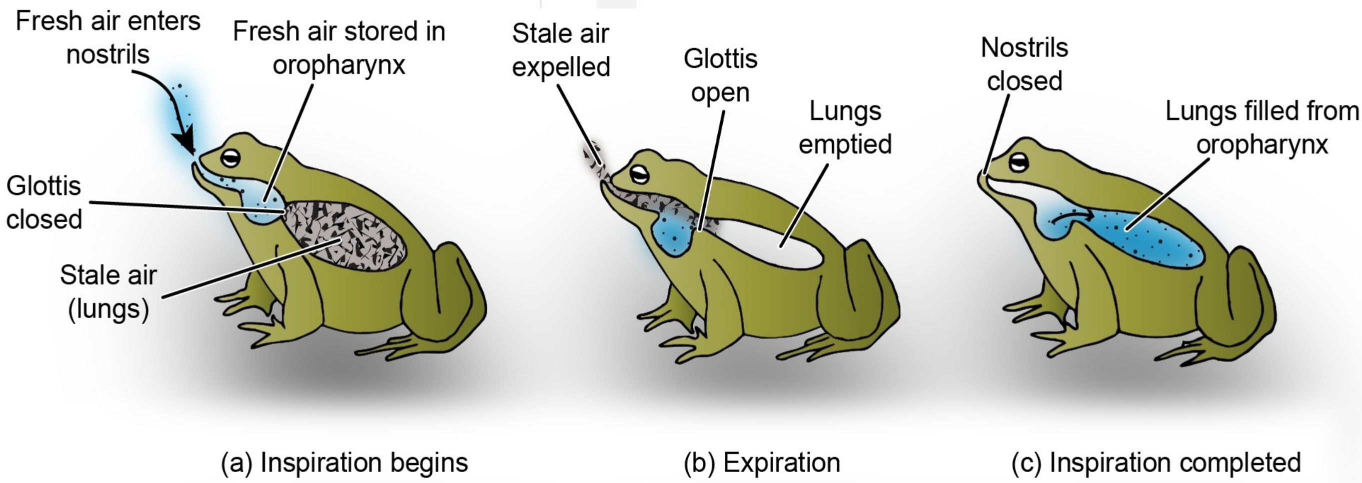


Fig. 4.21: Stages in inspiration of frog (a) first stage (b) expiration (c) second stage.

In Urodela (newts) where the animals are mostly aquatic, the lungs are poorly vascularised and internal surface is smooth while in metabolically active *Hyla* (tree frog) the lungs are more elaborate with many more blood capillary meshes per cm^2 than the aquatic newt. Thus we see that as animals became primarily terrestrial their respiratory surfaces also became more suitable for their life styles.

4.4.2 Respiratory System in Reptiles

Reptilians were the first vertebrates to adapt adequately to a completely terrestrial life. Their dry scaly skin reduces cutaneous respiration to a negligible level. As a result reptiles depend almost exclusively on lungs for gas exchange, supplemented in some of the aquatic turtles by pharyngeal membrane respiration. A larynx is present though vocal chords are absent. The respiratory passage is supported by cartilages. Lungs of most reptile unlike the simple sac like lungs of amphibians are composed of many small compartments and thus have a sponge like texture and a larger respiratory surface (See fig 4.19 again). This type of lung is needed because of the general increase in metabolic activity of reptiles. The lungs of many snakes and most lizards typically include a single central air chamber. The respiratory surface within the lungs is **septal** meaning that partitions form and subdivide to increase the surface area exposed to incoming air. The interconnecting septa divide the lumen into **faveoli** which are air compartments that open into a central chamber within each lung. Faveoli differ from alveoli of mammalian lungs as they are not found at the end of a highly branched tracheal system. The thin walls of faveoli have capillary beds and are subdivided into internal septa.

Lungs of reptiles are similar to those of mammals as they are aspiratory (drawing in air) *i.e.* air is sucked into lungs by changing the size and pressure muscle as in amphibians. Lungs change their shape and induce airflow in or out. The reptiles fill their lungs by expanding the rib cage. The expansion reduces the pressure in the lungs and air is drawn into lungs. Air is retained in lungs during a period of apnea (cessation of breathing) and is then forced out of the lungs by contraction of trunk muscles and elastic recoil of lungs.

The left lung in Amphisbaenas (limbless lizards) and in derived snakes (Colubridae,Viperidae, Elapidae) is **rudimentary or absent**. The more primitive snakes such as boas and pythons have both lungs. The elongated lungs of snakes and limbless lizards are divided functionally into two zones, the anterior vasculated zone and the posterior avascular, saccular zone which stores air. In marine reptiles lungs are multi-chambered. In higher lizards, crocodilians and turtles, the septa are so constructed that there are numerous large chambers, each with a multitude of individual sub-chambers.

Volume of lungs is relatively larger than in mammals but the surface area is sometimes 100 times smaller in proportion to body weight. In **puffing adder** an enormous diverticulum of the left lung extends into the neck region. Inflation of the diverticulum causes the neck to spread characteristically, and inflation of the lungs causes the body to swell. In the spotted king snake, the lung and its bronchus extend fully two-thirds the length of the body. The purpose of the large volume is to provide a reservoir of air, useful in diving species for holding breath. In aquatic forms lungs are often provided with smooth avascularised air sacs. They are also useful for maintaining buoyancy.

The oxygen requirement of reptiles is relatively low. Their standard metabolic rate is only 10 to 20 percent of that in homeotherms. Most reptiles are therefore incapable of sustained activity. Their movements are in short bursts during which their muscles contract anaerobically. However, reptiles can tolerate much greater changes in the circulatory components of the blood than in mammals. Such a property enables them to exist for a long period in low oxygen conditions. Lizards, snakes and crocodiles can survive for 30 minutes in pure nitrogen and turtles for several hours.

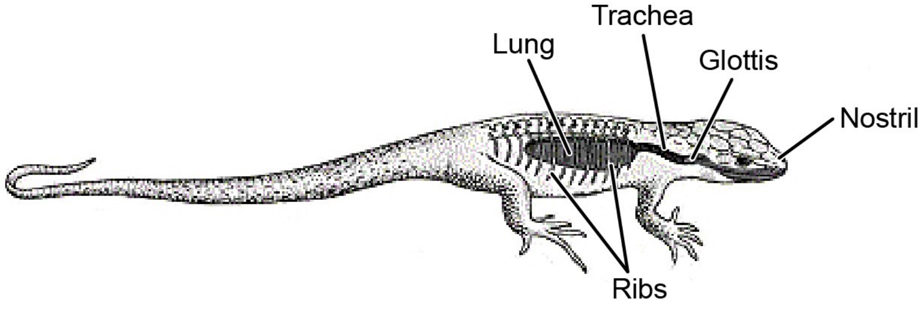


Fig. 4.22: The lungs of lizard.

Generally the respiratory system of lizards has the following features. The glottis leads into larynx, which is supported by cricoids and arytenoids cartilages. From the larynx the trachea passes backwards on the ventral side of the neck. Rings of cartilage support the long trachea. It bifurcates behind into two bronchi and each bronchus enters into a lung. The inner lining of the lung is raised into a network of delicate ridges so as to produce a spongy or honeycomb-like appearance. The ribs are pulled backwards and forwards by the muscles, which extend between them, thereby altering the size of the body cavity. When the body cavity is increased in size, air from outside passes through the nostrils into the lungs and dilates them, resulting in inspiration. The expiration is a passive act.

Crocodiles have a muscular diaphragm that pulls the pubis back (crocodiles have a mobile pubis bone) which pulls the liver down, thus creating space for the lungs to expand. This is known as the **hepatic piston** method of ventilation. They have a unidirectional flow of air during inspiration and expiration. Turtles have a rigid carapace that does not allow the type of expansion and contraction seen in other amniotes. They use their fore-limbs and pectoral girdle to force air in and out.

SAQ 4

1. Indicate weather of the following statements are true or false.

   (a) In terrestrial vertebrates, a diverticulum that grows out ventrally from the floor of the pharynx posteriorly to the last gill pouch develops into lungs T/F

   (b) In dipnoans lungs have only a hydrostatic function. T/F

   (c) *Protopterus* and *Lepidosiren*, the lung fishes can obtain nearly 98% of their oxygen from the air. T/F

   (d) In amphibians cutaneous artery carries deoxygenated blood and the cutaneous vein the oxygenated blood. T/F

   (e) During pulmornary respiration, the buccal cavity of frogs function as suction pump. T/F

   (f) Higher reptiles have voluminous lung but with a surface area that is 100 times smaller in proportion to body weight. T/F

   (g) In aquatic reptiles, lungs are provided with vascularised sacs that have hydrostatic function. T/F

   (h) Lizards, snakes and crocodiles have a higher standard metabolic rate and hence their oxygen requirements are quite high. T/F

4.4.3 Respiratory System in Birds

Though the respiration in birds, is pulmonary as it is in reptiles, the respiratory system of birds differs radically from that of reptiles and mammals and is marvelously adapted for meeting high metabolic requirements of flight. Fig. 4.23 shows the respiratory system of birds. The respiratory system of birds occupies as much as 20% of the volume of the body, as against only 5% in humans. In birds the lungs and the respiratory passages are highly modified. The highlights of such modification are: (i) the formation of extensive diverticula or air sacs in lungs that invade most parts of the body; (ii) the anastomosing of the air ducts within the lungs so that no passage terminates blindly within the lungs and (iii) isolation of lungs in pleural cavities. The air sacs are blind thin walled, distensible diverticula of the lungs that invade most parts of the body and store air.

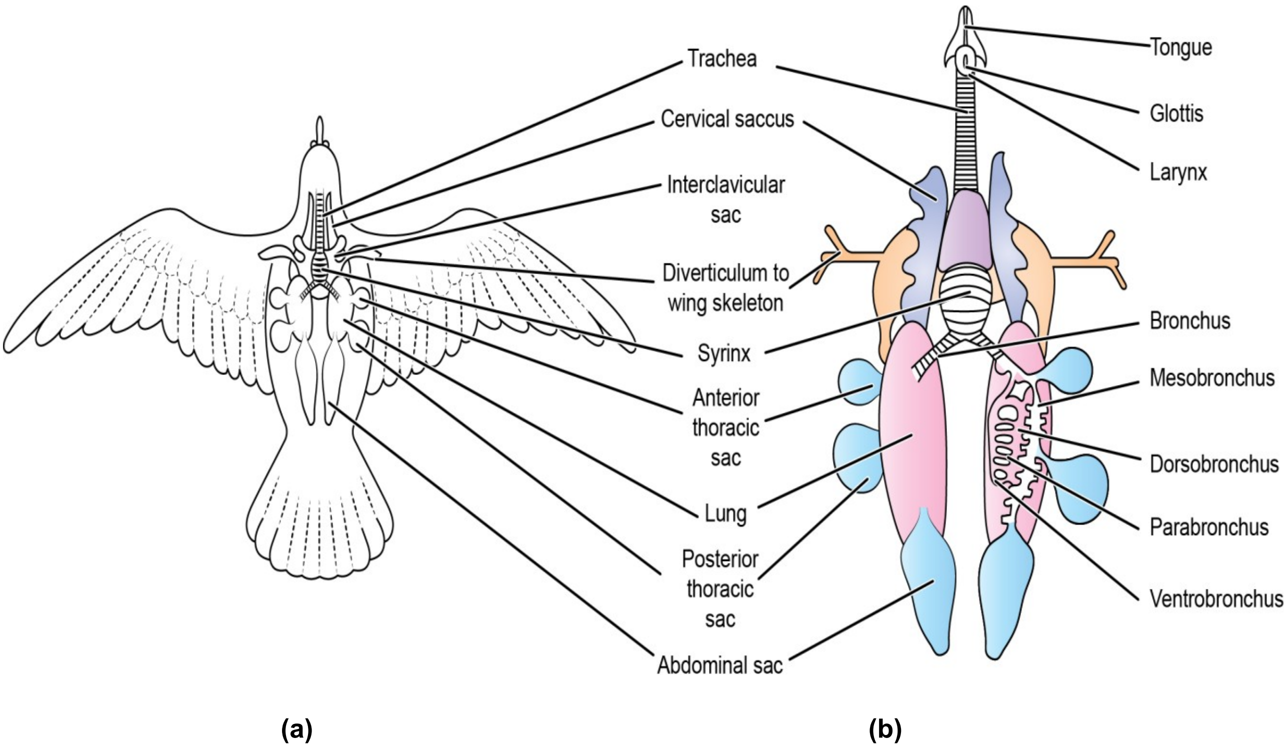


Fig. 4.23: The respiratory system of a bird showing: (a) location within the body; (b) its detailed structures

The paired nostrils of birds lead to internal nares above the mouth cavity. The slit like glottis in the floor of the pharynx opens into the long, flexible trachea. The trachea continues to the syrinx. The voice box of birds is called syrinx. From the syrinx primary bronchii enter the lungs and are then called mesobronchus. The lungs are small paired, spongy organs more rigid with little elasticity (Refer to Figs. 4.23 & 4.24).

Branching off from the mesobronchus are smaller tubes called dorsobronchus. The dorsobronchus, in turn, lead into the still smaller parabronchus. Unlike mammals where the tertiary branches end in sac like alveoli, the tertiary branches, in birds are tube like also known as air capillaries, through which air flows continuously. Gas exchange actually occurs in the air capillaries. A series of valves ensure that flow of air remains one way.

There are nine interconnected aspiratory air sacs (Fig. 4.23) which lie in various organs of the bird. The cervical, anterior thoracic, posterior thoracic, and abdominal sacs are paired and the interclavicular sac is unpaired. The cervical air sac lies at the base of the neck. The posterior thoracic air sac, is close to the side wall of the body. The anterior thoracic sac is just in front of posterior thoracic air sac. The unpaired intraclavicular sac gives off a diverticulum or axillary air sac.The abdominal air sacs lie one on each side of the body among the coils of the intestine. All these nine sacs extend into the bones, forming the pneumatic cavities and replacing a substantial amount of bone marrow in them. Some birds can thus respire through the humerus and other bones if they are fractured and exposed even if their trachea is blocked.

The lungs of birds are capable of little expansion, as they are attached to the ribs and thoracic vertebrae and are comparatively smaller than those of mammals. The lungs of birds are more efficient because air flows through them in one direction rather than back and forth (Fig. 4.24a). One way flow of air through the lungs leads to greater concentration of oxygen at the epithelial exchange surfaces than in other terrestrial vertebrates that ventilate their lungs bi-directionally. Birds can thus obtain enough oxygen even when flying at high altitude where partial pressure of oxygen is low.

Air in the bird respiratory system passes through in two breath cycles as explained below (Fig.4.24 a and b):

(i) During the process of respiration, air which is first inhaled by the bird passes through straight ducts namely, the bronchi and mesobronchi into the posterior air sacs.

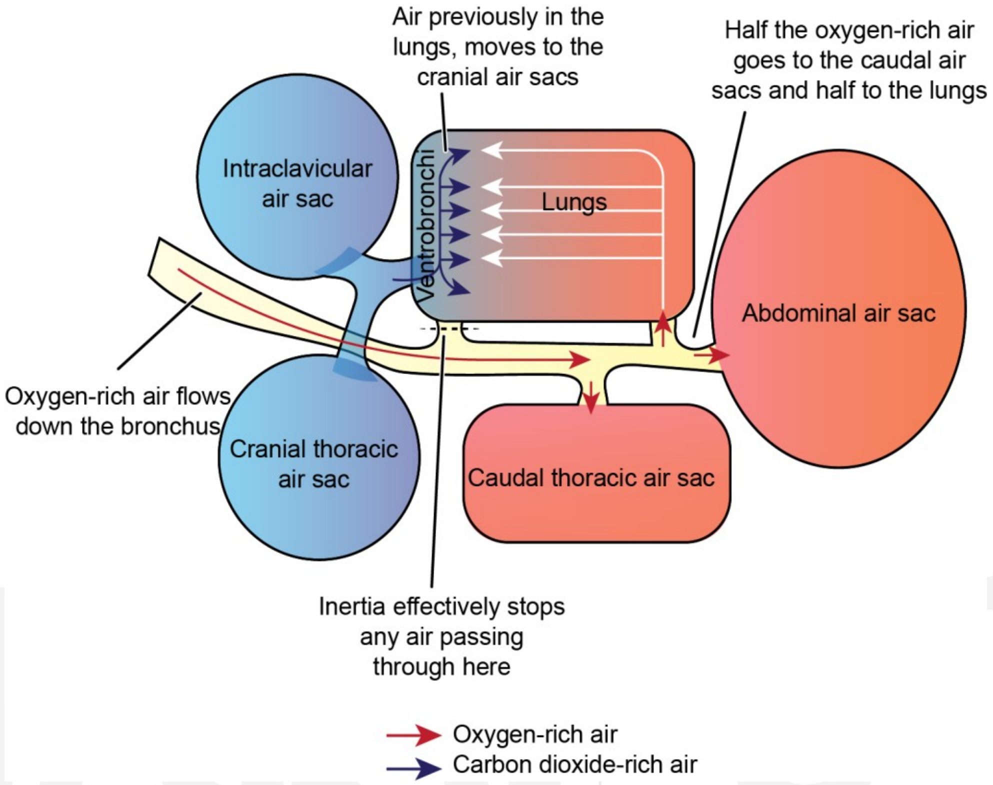
(ii) Inhalation of air is followed by exhalation which causes the previously inhaled air to move from the posterior air sacs into the parabronchi of the lungs.

(iii) The second inhalation moves this air which is present in the parabronchi of the lungs into the anterior air sacs. The second exhalation then passes the air through the bronchi and out of the system.

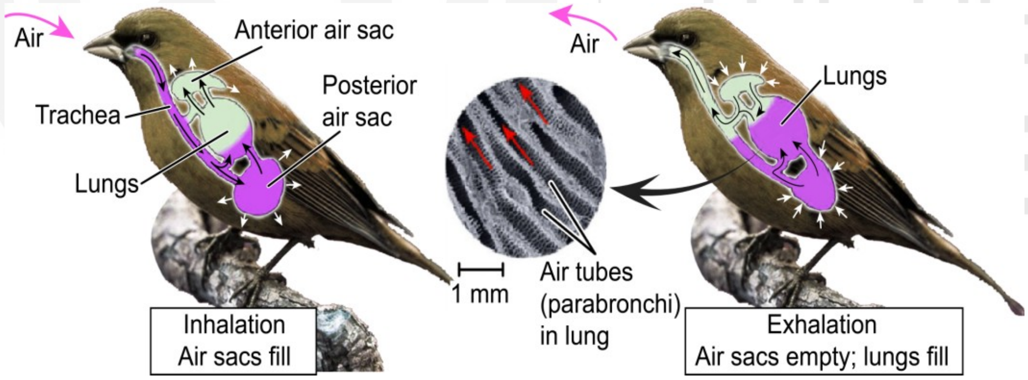
Oxygen exchange occurs both during inhalation and exhalation in this type of respiration. The posterior abdominal and the anterior air sacs expand during inhalation. All birds have this one-way air flow system and some may also have a two-way flow system which is not discussed in this unit.

The raising of the sternum when the animal is at rest and lowering of the backbone when the animal is in flight decreases the size of the body cavity, leading to the air being forced outside (exhalation). Thus expiration is an active process in birds. Inhalation is a process, brought about by the rebounding of the muscles to their original size, causing an increase in the size of the body cavity.

The lungs of small passerine birds that have a higher metabolic rate have more efficient lungs in comparison to gliding birds that use less energy during flight. Birds like fowls and the emu that do not fly much have a lower pulmonary blood diffusion capacity and Humboldt penguin has a much thicker blood-gas exchange barrier in the lungs which protects the lung from collapsing during diving due to hydrostatic pressure. Let us now see the adaptations in the respiratory system of mammalian vertebrates.



(a)



(b)

Fig. 4.24: a) Diagram showing the pathway of unidirectional flow of air in birds. b) Diagram showing the exhalation and inhalation in birds.

4.4.4 Respiratory System in Mammals

Mammals have a pair of lungs enclosed in a thoracic cavity. The bony framework of the thoracic cavity is formed of thoracic vertebrae, ribs and sternum. The lungs of the mammals are multi-chambered and usually divided into lobes. Usually the right side has more lobes than the left side. Humans have three right and two left lobes.

Figure 4.25 shows the respiratory organs of humans. The air from outside enters through the external nostrils and nasal passages into pharynx. From the pharynx it passes through the glottis into trachea. The trachea is a long tube that traverses the neck and lies ventral to gullet. The anterior part of the trachea is enlarged to form the voice box or larynx. The vocal chords are located inside the larynx and the vibrations of the vocal chords results in the production of the sound. The trachea bifurcates into two primary bronchi. Each primary bronchus enters into lungs and branches into secondary and tertiary bronchi, and finally into bronchioles. Terminal bronchioles lead into thin walled delicate alveolar ducts, the walls of which are evaginated to form clusters of alveoli. The lungs are protected and cushioned by the pleura. The pleura is made of two thin layers of tissue: a) the inner layer (visceral pleura) which wraps around the lungs and is stuck so tightly to the lungs that it cannot be peeled off, and; b) the outer layer (parietal pleura) which lines the inside of the chest wall. The pleura prevent the lungs from separating from the rib cage. The very thin space between the layers is called the pleural cavity. A liquid, called pleural fluid, lubricates the pleural cavity so that the two layers of pleural tissue can slide against each other as the lungs inflate and deflate during respiration.

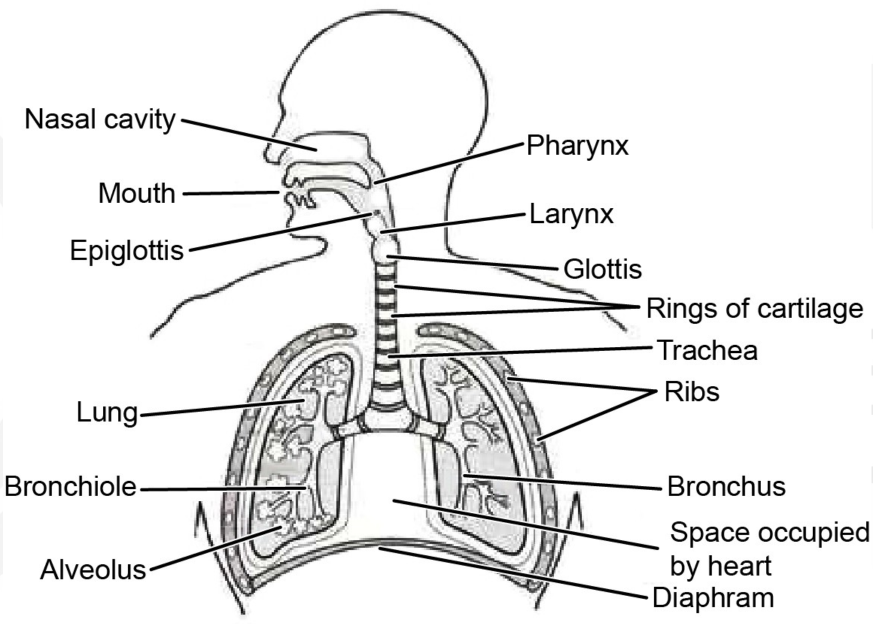


Fig. 4.25: The respiratory system of humans

In mammals buccal cavity plays no role in respiration, and the diaphragm and ribs play an important part. You can see in Figure 4.26, that during inhalation the rib muscles (external intercostal muscles extend between the ribs) and diaphragm contracts causing the raising of the ribs and flattening of the diaphragm increasing the size of the thoracic cavity. The pressure decreases and the air enters into lungs. The entire process constitutes inspiration. Expiration is a passive process, brought about by the relaxation of the intercostals muscles and the diaphragm. The thoracic cavity is brought to its normal size and as a result the air is forced out.

The alveoli are separated by thin wall vascularised, septa that measure 50μm in shrews and bats as they have a high metabolic rate and is as much as 1mm in sirenians (manatees and dugongs) that are more placid. The alveolar surface is covered by certain, Type I alveolar cells where gas exchange occurs and Type II alveolar cells that secrete the surfactant a substance that reduces the surface tension at the air-alveolar surface so that the alveoli can expand.

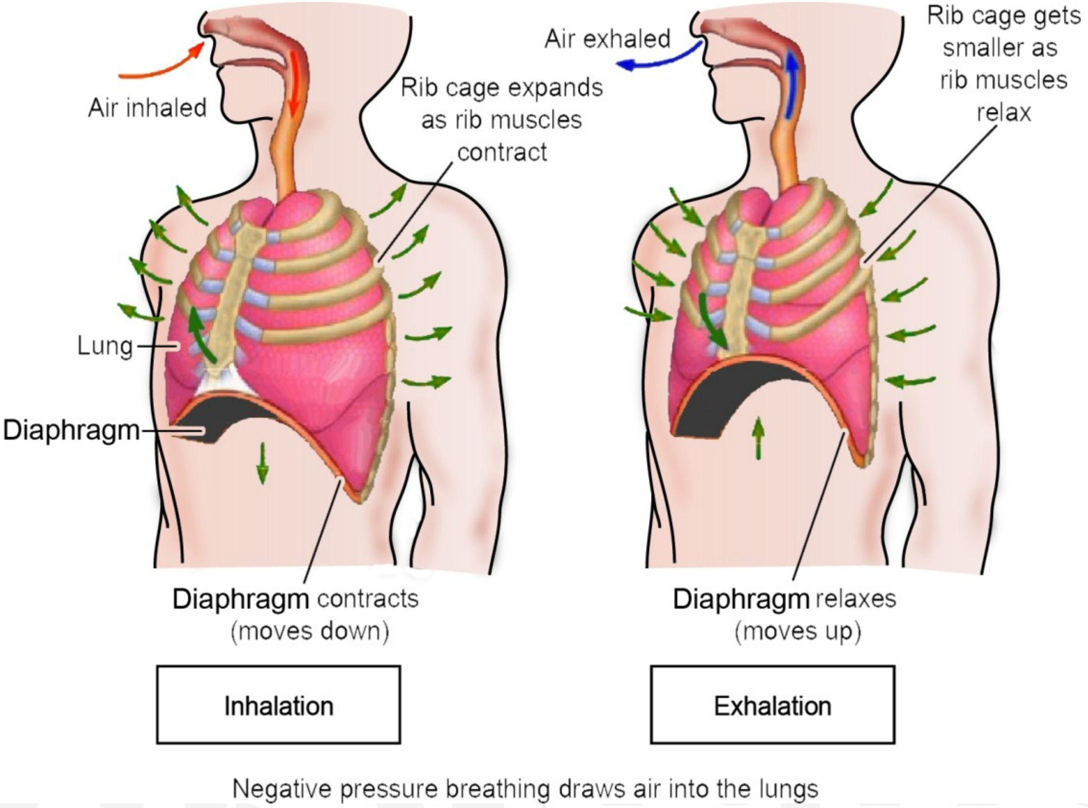


Fig. 4.26: Process of Inhalation and exhalation.

SAQ 5

1. Fill in the blanks with suitable words.

   (a) In human right lungs have …………………. lobes and the left lung has …………………. lobes.

   (b) Birds have …………………. number of air sacs.

   (c) In mammals inspiration is an …………… process and expiration is a ……………process.

   (d) Normal tidal volume of human at rest is approximately ………… ml.

   (e) The voice box of birds is called ………………….. .

4.5 SUMMARY

- The respiratory system is designed for exchange of oxygen and carbon dioxide between the organisms and the environment.
- In all chordate embryos a series of visceral pouches develop on either side of the pharynx. In fishes and larval amphibians perforations occur in the pouches, forming gill slits which connect the pharynx to the outside. The pouches are then called gill clefts. Gills are evaginations of the respiratory surface found in aquatic vertebrates. Internal gills, supported

by visceral arches, are vascular, lamellar or even filamentous extensions of the epithelial surface of the gill pouches. Internal gills are present in cyclostomes, fishes and some aquatic amphibians. Respiratory efficiency is increased by the countercurrent flow of blood and water in the gills.

- External gills, generally covered with ectoderm, may project from the outer surfaces of the visceral arches as filamentous outgrowths. They are found in larval amphibians, are usually confined to larval life and disappear at the time of metamorphosis. In a few urodeles, however gills occur throughout the adult life. Of the five pairs of pharyngeal pouches that develop during the embryonic life of amphibians, only the 2^{nd}, 3^{rd} and 4^{th} pairs are perforated and connected to the outside. Also during metamorphosis initially external gills appear which degenerate and a new set of internal gills develop from the tissue covering the same visceral arches.

- A few fresh water fishes have evolved accessory respiratory structures that are useful at times when there is an oxygen deficiency in the medium in which they live. The highly vascularised structures are essentially outgrowths of pharynx or the branchial chamber. *Anabas*, *Amphipnous*, *Clarias*, *Saccorbranchus* and *Ophiocephalus* are some of the actinopterygians, which posses, such organs.

- Lungs develop as a bilobed diverticulum from the floor of the pharynx posterior to the last gill pouch. They are invaginations of highly vascular respiratory surface. In higher forms the connection between lungs and pharynx lengthens and is called the trachea. The upper part of the trachea becomes modified as a larynx or voice box, the walls of which are supported by skeletal elements derived from the visceral arches.

- Lungs of lower vertebrate are rather simple, vascular sacs but in higher vertebrates the walls become subdivided into numerous pocket-like air spaces. Reptile lungs have vascular partitions known as faveoli. The divisions become more and more complex in the higher classes of vertebrates and reach the highest degree of branching in mammals where the ends of branches form extremely thin walled vasularised blind ends known as alveoli where the gas exchange actually occurs . The lungs of birds are complicated in that they are connected to air sacs, which penetrate among the viscera and even enter the hollow bones. Birds have a very efficient one-way -flow of air and they can exploit high altitudes during flight. Instead of alveoli or faveoli they have air tubes and air capillaries in the lungs where the gas exchange takes place.

- The mechanism employed for inflating and deflating lungs differ in different vertebrates. The most complex condition is encountered in mammals, in which the lungs lie in separate pleural cavities partitioned from the abdominal cavity by muscular diaphragm.

- In vertebrate the main voice producing apparatus are the larynx and syrinx. Larynx is present in most amphibians, reptiles and mammals but the syrinx is present only in birds.

4.6 TERMINAL QUESTION

1. Define external and internal respiration.
2. What are the peculiar features of respiratory system of agnathans?
3. Describe the structure of the respiratory system of cartilaginous fishes and state how does it differs from that of bony fishes.
4. Briefly discuss the mechanism of pulmonary respiration in frog. How is it different from reptilian mechanism of respiration?
5. How is the respiratory system of birds modified to meet their high oxygen requirement? How is it different from the respiratory system of mammals?

4.7 ANSWERS

Self-Assessment Questions

1. (a) F; (b) T; (c) F; (d) F.
2. i) (a) Seven, (b) passive, active; (c) mandibular, hyoid; (d) Counter current; (e) Interbranchial septum.

   ii) (a) False: only elasmobranch gills are supported by interbranchial septa bony fishes lack it; (b) True; (c) False: they don't have external gill slits but an operculum covering a common opening; (d) True.
3. i) (a) iii; (b) iv; (c) v; (d) i; (e) ii.

   ii) (a) disappear; (b) urodeles; (c) do not; (d) disappear.
4. (a) True; (b) False; (c) False; (d) True; (e) True; (f) True; (g) True; (h) False.
5. a) three, two; (b) nine; (c) active, passive; (d) approximately 500ml; (e) syrinx.

Terminal Questions

1. Refer to Introduction.
2. Refer to Subsection 4.3.2.
3. Refer to Subsection 4.3.3 and compare the two with reference to the gill structure and ventilation.
4. Refer to Subsections 4.4.1 and 4.4.2.
5. Refer to Subsections 4.4.3 and 4.4.4 and discuss the differences in terms of respiratory structure and method of ventilation.