Subject: Zoology

Class: 2nd Semester

Comparative Anatomy and Developmental Biology of Vertebrates

UNIT: 1

3.1. Skin Structure

Skin or integument covers body, nasal sacs, openings (gut and urinogenital openings). It has outer thin epidermis and inner thick dermis. Epidermis is ectodermal in origin and dermis is mesodermal.

1. ***Epidermis****:* It is a stratified epithelium, made up of many layers inner most layer called stratum germinativum or Malpighian layer outermost layer called stratum corneum or horny layer.

Innermost layer is made of tall, undifferentiated, actively dividing cells. outermost layer is made of flat, horny cells and is sloughed off in small pieces or as a whole and replaced by cells produced from Malphighian layer.

2. ***Dermis****:* It is formed of connective tissue containing blood, lymph vessels, nerve fibre, receptors, smoothmuscle fibers. It is distinguished into two regions: outer region stratum laxum or spongiosum having loosely arranged connective tissues. Bears branched pigment cells (chromatophores).

Inner region stratum compactum have packed connective tissue.

Comparative Anatomy

1. Cyclostomes and fishes: Slimy Skin, outer layers of epidermis show little flattening and keratinization consequently stratum cornea is lacking. It bears similar cells all through its thickness. In epidermis are present abundant unicellular mucous glands. Dermis gives rise to dermal scales is fishes. It bears chromatophores.

Cyclostomes can change skin color to some extent.

2. Amphiba: Thin, Slimy, naked skin. Stratum corneum is heavily keratinized in toads, moderately in others. Dermis bears chromatophores, vertical and horizontal collagen fibre, large multicellular mucous and poison glands (more in toads than in frogs), scent glands (certain tailed forms). Dermis forms minute dermal scales in limbless amphibians.

Change of skin color is common.

3. Reptiles: Thick, dry skin. Stratum corneum heavily keratinized. Forms scales all over and claws over digit tips. Epidermal scaly exoskeleton is shed periodically as a whole in snakes

and as fragments in others. Glands are lacking altogether.Dermis contains abundant chromatophores; forms dermal bony plates in some cases (Tortoise, turtles, crocodiles).

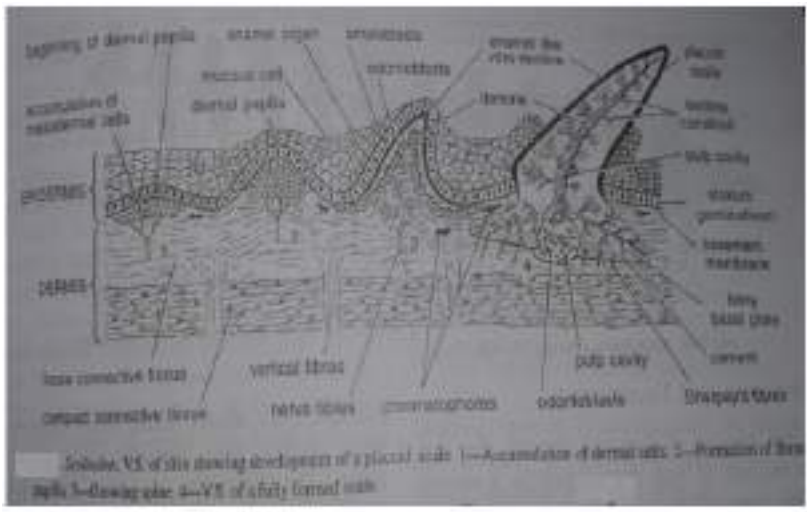
Skin color changes occur in chamaeleons and blood suckers.

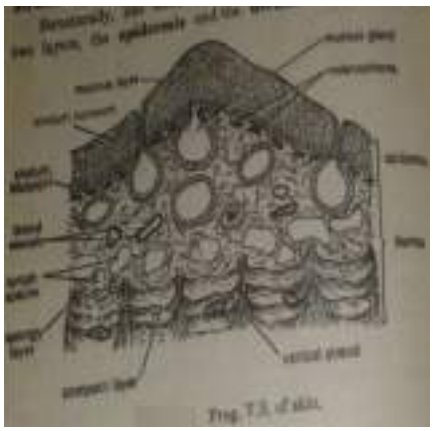
4. Birds: thin, dry skin. Stratum corneum is keratinized. It forms feathers, scales and claws on feet, horny sheath on jaws to form beak.

Glands lacking except oil gland on tail. Pigment confine to feathers. Dermis has abundant receptors.

5. Mammals: Thick, glandular skin.Stratumcorneum is keratinized. Forms hair, fur, claws, nails, hoofs at digit tips. Scales in Pangolin, Armadillo and Rat; spines in Hedgehog and spinny ant eater besides hair, horns in ungulates. Epidermis contains melanophores.

Dermis is rich in receptors and various glands (sweat, sebaciousetc). skincolor not changed.





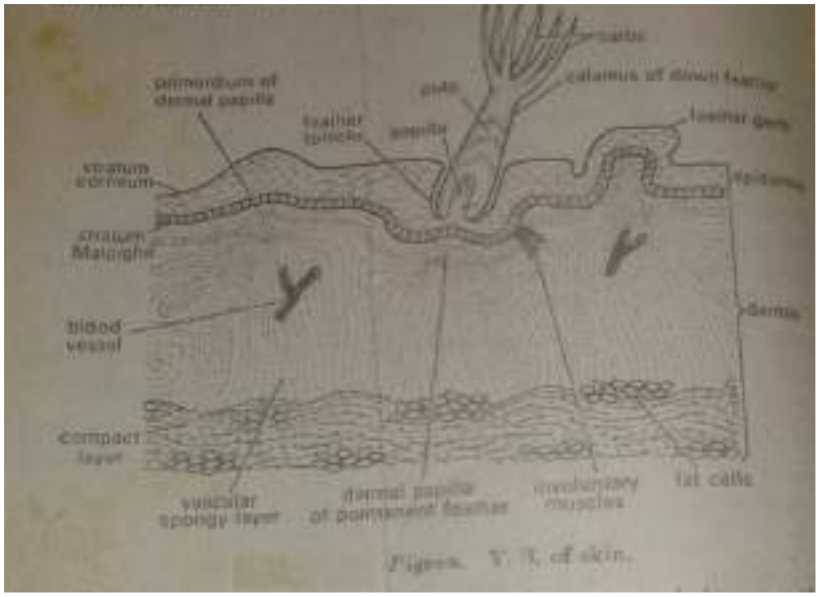
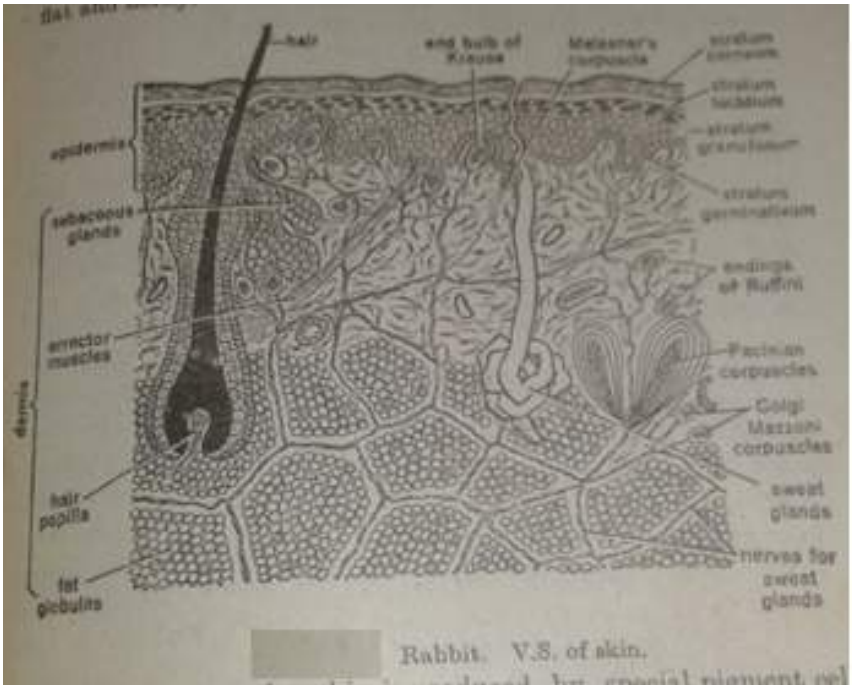


Figure. V. S. of skin.



Rabbit. V.S. of skin.

INTEGUMENTARY DERIVATIVES

Integumentary derivatives are

Epidermal derivatives

Glands

Exoskeltal structures

i) Scales (Reptiles, few mammals, bird feet)

ii) Feathers – Birds

iii) Hair – Mammals.

Digital tips

iv) Claws – (Reptiles, Birds, Mammals)

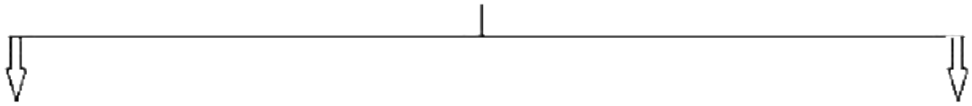
v) Nails – (Primates among mammals)

vi) Hoofs- (Ungulate Mammals)

vii) Horns – (Mammals)

viii) Beak – Birds.

ii) Dermal derivatives:

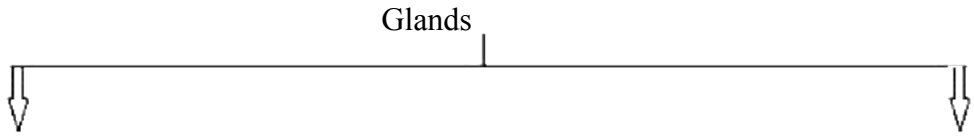


Exoskeltal structures

i) Scales (in fishes)

Endoskeletal structure

e.g: Membrane bones in skull of vertebrates framed in dermis sink down and become Incorporated into endoskelton



Unicellular

Modified epidermal cells

e.g.mucous glands in cyclostomes, larval amphibians secreting mucus having a protein substance mucin.

Multicellular

Formed by ingrowth of stratum germinaitivum into dermis.

Tubular Sacular

or

Tube like with alveolar acinous

Uniform diameters expansion at the

ends

Simple Compound Simple

Compound

1) Tubular:

a) Simple

i) Straight (Glands in nuptial pads of frog)

ii) coiled (sweat glands in skin of mammals)

iii) Branched tubular (large sweat glands of certain regions like arm pits; Sudorific or sweat gland)

b) Compound (mammary glands of monotremes or egg laying mammals)

2) Sacculer

a) **Simple** (Branched or unbranched)

i) Simple unbranched (cutaneous glands of frog)

ii) Branched (Meibomian glands of eye lids –sebaceous or oil glands in mammals)

b) **Compound (mammary glands of placental and marsupial mammals)**

Distribution of glands in various groups

1) Cyclostomes + Fishes+Larval amphibian:

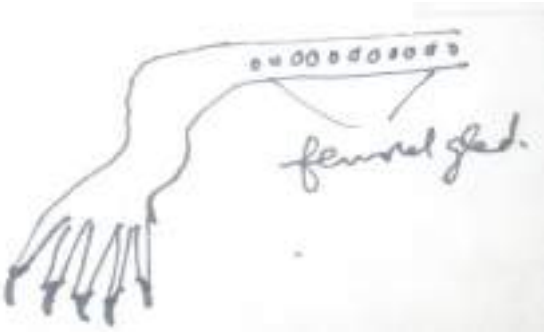
Unicellular modified epidermal glands called mucous glands secrete mucin protein which combines with water to form mucous lubricating surface.

In some deep sea fishes ventral side of body are present longitudinal rows of luminescent organs or photophores. Each photphore is a group of epidermal cells lying in dermis. It has glandular cell in lower layer below which is reflecting pigment; upper layer forms lens. Glandular cells produce light helping to attract prey in deep sea regions.

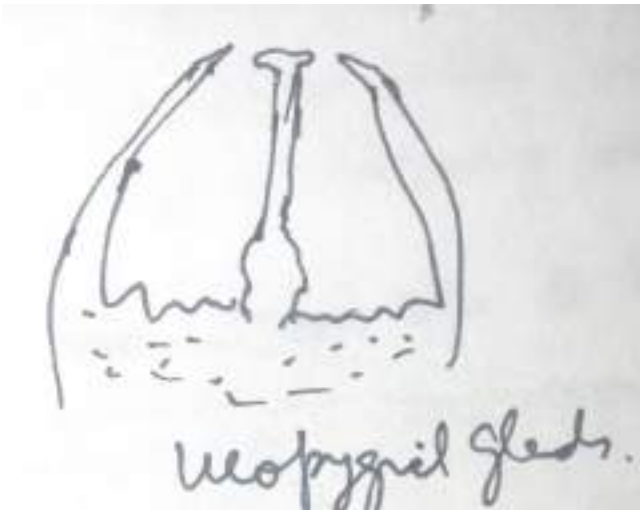
2) Amphibians: These have multi cellular cutaneous glands which secrete mucus keeping skin moist to aid in respiration. They also have poison glands. In toads masses of poison glands

form parotid glands behind head. Secretion of poison glands has burning taste and is used as defence. Apods have giant poison gland.

3) Reptiles: Femoral glands in male lizards below the thighs in a row from knee to cloaca, secrete sticky substance which hardens into short spines, used for holding female during copulation.



4) Birds: Glands in birds , best developed in aquatic bird. Branched alveolar. Present on dorsal side of tail or uropygium . Secrete an oil (odoriferous) during sexual activity. Oil contains pomatum which is picked up with beak and used for preening and water proofing feathers.



5) Mammals: i) Sweat glands. (Sudorific glands) – removing wastes in the form of sweat. cool down body during high temperatures.

Distributed differently.

In ruminants on muzzle, in hippopotamus on pinnea

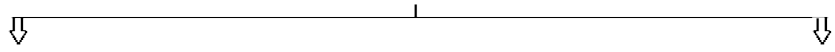
In rabbit on lips , in cats, rates on soles of feet

In man more on soles, palms, arm pits

Absent in Tachyglossus, Sirenie and cetacea.

Sweat is red colored in hippopotamus, and giant kangaroo (Macropesrufus)

Sweat glands are modified into



Glands are moll in region of human eye in connection with eye lashes

Ceruminous glands in external ear passagesecreting waxy substance (ear wax) catching dust.

2. **Sebaceous glands** :- Found in hair follicles. Secrete oil (Sebum) to lubricate hair. Absent in Pangolin (Mammal) Sirenia, cetacea.

   Modified sebacious glands are:

   (a)Meibomian glands in eye lids secreting tears to keep eye moist

   (b) Scent Glands located in deer family on head near eyes, shunks. In carnivores around arms and in pigs and goats between toes. Secretion allures opposite sex

3. **Mammary Glands:-** Produce milk

   In monotremes, both sexes secrete milk (Gynaecomastism). Mammary glands are without nipples, open on the surface of skin and young ones get milk by licking tufts of hairs. In others nipples or teats open to outside. Number of mammae is 2-25 (25 in Oppossum).

According to modes of secretion, skin glands are of three types:

1. **Merocrine glands**: Cells are not injured or destroyed during secretion. A cycle of formation, discharge and reformation continues e.g., Unicellular glands.
2. **Holocrine glands**: Secretion collects in cell, which dies and shed with their contained secretion. Cells replaced with new cells e.g. Sebaceous glands.
3. **Apocrine glands**: Secretion collects in free ends of cells and only this part of cell is cut off. Greater part of cells is left behind with nuclei to repeat the process after repair. e.g, Mammary glands

Integumentary Derivatives in fishes

In fishes skin derivatives are scales, which are derived from dermis. Hence called Dermal scales (Mesodermal in origin).

In earliest vertebrates (Ostracoderms) was present armour of large bony plates which in placoderms became smaller and gave rise to cosmoid scales. Cosmoid scales are not found in any living form today (Except in Latimeria). Besides in earliest primitive bony fishes were present Ganoid scales which are still present in most.

Cosmoid scales has four distinct layers:-

1. Lowest isopedine (Dentine) resembling compact bone.
2. Next layer with vascular spaces having pulp cavities and odontoblasts resembling spongy bone.
3. Third layer called cosmine which is hard compact with cannaliculi.
4. Outer most layer thin but hard –vitrodentine (Enamel like)

A ganoid scale has;

1. Basal isopedine
2. Reduced Cosmine (Polypterus) or no cosmine (Lepisostus)
3. Uppermost layer with hard , translucent substance called Ganoin.

Evolution:

Cosmoid scales by losing its lower three layers, only 4th enamel like dentine was retained and gave rise to Placoid scales

Ganoid scales by loss of its upper layer of ganoin gave rise to thinner Laptoid scale having two types (Cycliod and Ctenoid).

Thus in present fishes there are four types of scales:

Placoid, Ganoid, Cycloid, Ctenoid.

1. **Placoidscales** are present in Cartilaginous fishes only. In sharks they are small and rough but in Skates they are large.

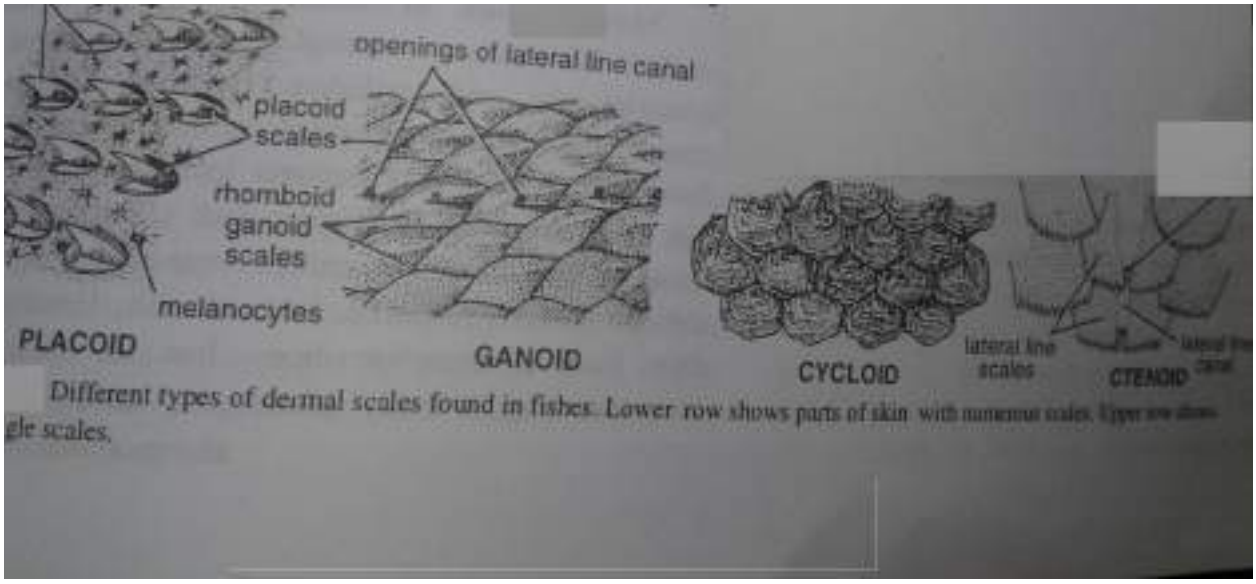
   A placoid scale has basal plate in dermis- made of calcified dentine. Spine projecting above epidermis and points backwards. It has pulp cavity, connective tissue, blood vesseles, odontoblast cells. It is made up of dentine covered by layer of modified dentine called vitrodentine and not enamel. Enamel is present in teeth of vertebrates (ectodermal in origin), while as basal plate and spine of placoid scale is mesodermal in origin.

   Tanned skin of sharks containing placoid scales is called Shagreen. It is used for polishing and handle covers.
2. **Ganoidscales**: They are diamond shaped and closely arranged in diagonal rows like tiles in a floor. They are found in Polypterus and Lepidosteus.

3. **Cycloidscales** are round, thick in centre and thin towards margins. They show concentric lines of growth indicating age of fish. Scales lie diagonally overlapping each other; posterior part of each overlaps anterior part of scale behind, thus covering the body with double layer of scales. Posterior part has a smooth edge while concealed part wavy margin. Found in many bony fishes.
4. **Ctenoidscales** resemble cycloid scales. But have small teeth on free posterior part; anterior concealed part has notched or scalloped margin. Found in many bonny fishes.

   Cycloid or ctenoid scales covering lateral line are perforated with openings on the surface.

   In sea horses, scales form a continuous armour covering the body.



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

Integumentary derivatives in reptiles

In reptiles Integumentary derivative are of the following types:

1. Scales-epidermal in origin
2. Claws- Epidermal in origin
3. Bonny plates or osteoderms or dermal scales- dermal in origin.
4. Femoral Glands

1. Scales are highly keratinized stratum corneum, well adapted to terrestrial life. They overlap each other (Lizards and snakes) or arranged end to end (Tortoise and crocodiles)

Parts of skin including epidermis and dermis, bulge out at places as papillae which then grow but forming overlapping plates. Later dermis and stratum germinativum from

plates: cells of plates undergo keratinisation and form thin, flat, non living scales. Adjacent scales are continuous at the base.

The scaly covering is periodically cast off as one piece turned inside in snakes and as fragments in lizards. A new covering of scales is formed beneath old one, before old one is shed.

Scales on ventral side of snakes differ from others and transversely arranged and help in locomotion.

In Turtles and crocodiles, scales don't overlap. They don't shed periodically but are gradually worn off and replaced.

Large epidermal scales (on shell of turtles and on head of snakes) are called Scutes. They are not shed but worned out and replaced.

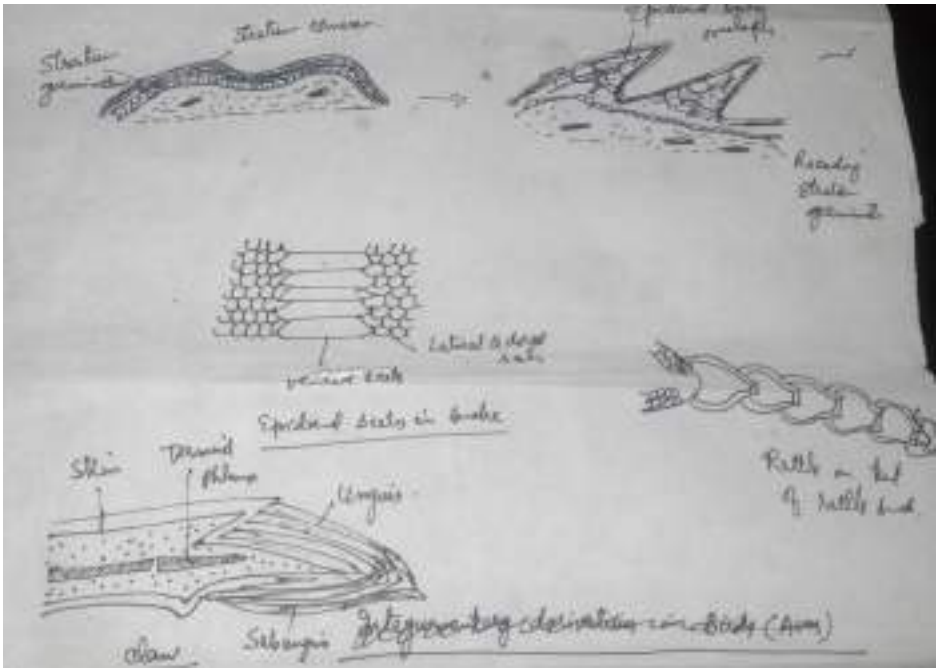
Modification of scales:

1. Horn on snout of male horned lizard ceratophore is modified scale.
2. In rattle snake; during ecdysis, scale at tip of tail is not shed but forms a ring. After several ecdyses a series of ring (8 to 12) form rattle which consists of old moulted scales. Each new ring of rattle is large than the previous rattle may wear off and break at tip

Dermal scales:

Two ancient groups of reptiles (Turtles and crocodiles) have retained bony dermal scales. Turtles have continuous osteoderms below epidermal scales of Carapace and Plastron. These osteoderms have rigid dermal skeleton which becomes connected with endoskeleton.

In crocodiles, the osteoderms are only below epidermal scales on back and throat.



3 Claws:

Claws made their appearance first in the reptiles. A claw is made up of two keratin plates: Upper large Unguis and Lower smaller subunguis or sole horn.

In reptilian claws, unguis is arched longitudinally as well as transversely and encloses the subunguis between its lower edges.

Claws are derived from horny layer of epidermis. They differ from other epidermal derivatives but they grow parallel to surface of skin. A claw covers the terminal part of the last phlanax. At the base of claw, epidermis isinvaginated to form claw root which provides new keratin layers for growth of claw.

Outer layers of reptilian claws are cast off and replaced periodically.

Integumentary derivatives in Aves (Birds)

In birds integumentary derivatives are :-

1. Feathers
2. Beak
3. Scales (Epidermal)
4. Claws
5. Glands

A. Feathers are present in Birds only. They are modified reptilian scales formed from epidermis in which *stratum corneum* is highly specialized. Thus *stratum corneum* has attained a height of specialization.

Feathers are light, strong, water proof show many colours due to pigments and structural arrangement. They form protective covering, regulate body temperature and support body in flight.

Various types of feathers in birds are:-

1. Contour feathers or Pennae , which occur all over body. They are of two types:

a) Flight feathers or Quills

b) Coverts

2. Down Feathers

3. Filoplumes

Quills are large feathers found in wings and tail. Those on wings are called Remiges and those on tail are called Rectrices. A quill feather has long stiff central axis called Shaft. Small proximal part of shaft is hollow and translucent and cylindrical called Calamus. Long distil part of shaft is solid, opaque and tapers called Rachis. An umbilical groove extends all along ventral side of Rachis. Proximal end of calamus has a small hole, inferior umbilicus. Another hole called superior umbilicus is at the junction of calamus and rachis on ventral side.

A small conical projection of skin fits into the inferior umbilicus.

Rachis has on either side vexillum or vane composed of a series of slender parallel filaments, the barbs. Each barb has a long either border Barbules.

Distal barbules of each barb has minute hooklets (barbicels or hamuli) which fit into grooves or flanges of proximal barbules on the next adjacent barb. Thus all barbs are fastened together firmly and form a single continuous surface to offer resistance to air.

A small tuft of separated barbs with barbules (hamuli) occur near and cover superior umblicus. It is called after shaft or Hyporachis. In birds like (Emu, Cassowary) after shaft is as long as main shaft.

Each feather has its own basal muscles in skin to erect in flight, cold weather and emotional excitement.

In pigeon there are 23 remiges in each wing and 12 rectrices arranged in semicircle around tail. Number is constant in each species of birds. Number of other feathers is not constant varying with seasons.

2) **Coverts:**

Small feathers and cover the body. Their hamuli are poorly developed. They cover body, wings, legs and tail.

Resemble quills, except they are small in size and with short calamus

3) **Down feathers:**

Cover newly hatched called as nestling downs. Each has short calamus, thin reduced rachis bearing long, flexible barbs with barbules.

They are also present beneath contours called as permanent or powder downs. Each has short calamus bearing at its tip long, flexible barbs with barbules without interlocking hooklets.

Down feathers of elder duck are used for stuffing pillows and have commercial value.

III) **Filoplumes**

Occur beneath contour feathers. Extremely small in size. Each has a long, slender shaft bearing at tip a few weak free barbs with barbules.

It is seen in plucked bird only .

In fly catcher birds Filoplumes are near mouth helping them to catch insects called rictal bristles. Peacocks have very long longFiloplumes. First digit of four limbs (wings) bears tuft of small feathers called alaspuria or bastard wing.

Arrangement of feathers (Pterylosis)

Contours occur in definite feather tracts, Pterylae separated by featherless tracts, apteria.

Filoplumes are present in Apteria.

Penguins, Ostrichs, touchauns are without Apteria

Colouration:

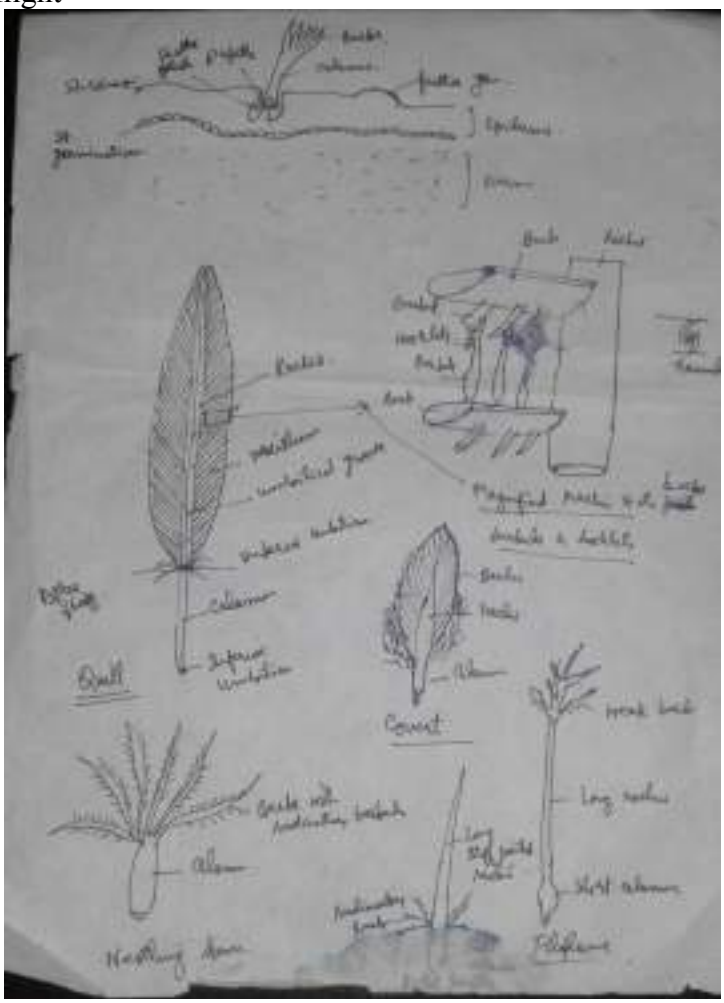
Pigments in feathers give coloration. Pigment deposition is under hormonal influence. This is chemical coloration.

Coloration is due to refraction, interference of light rays as they are reflected from surfaces of feathers. This is physical or structural coloration. White color is produced not by white pigment but by reflection of light without absorption of any of its component rays.

First set of feathers developed by a young bird consist of down feathers only. These feathers are called neossoptiles .Growing bird develops one are more sets of juvenile feathers called messoptlies. Feathers of adult bird are called as teleoptiles. Feathers are shed (moulted) periodically.

Functions:

1. Contours form insulating covering to prevent loss of heat.
   Reduce loss of water from body surface by reducing air circulation.
   Prevent water from reaching skin.
2. Wing quills (Remings) are part of organs of flight
3. Rectrices (Tail quills) form braking and steering device.
4. Give colour to body
5. Assist in warming eggs during incubation.



Origin:

Feathers evolved from horny epidermal scales of ancestral reptiles (archosaurs).

Both bird feathers; in surface of archosaurian scales contain ß- keratin. Feathers originally developed for insulation but later became organs for flight.

B. **Beaks**:-

Each jaw bone of birds is covered with a modified epidermal scale to form a hard beak or bill. Horny sheath of each jaw is called Rhamphotheca. In relation to mode of feeding,

beak of birds shows a great variation. It is short and stout in seed eating birds, long and narrow in insect eating birds, strong and hooked in birds of prey.

C. Scales:-

Birds have epidermal scales of reptilian type on feet. They generally overlap. Webs on feet of aquatic birds (ducks, geese, swans) also develop epidermal scales on them.Spur on foot on some male birds (Fowl) is covered by a sharp pointed sheath, which is a modified horny epidermal scale. Spur is used in fighting. Certain birds have spur on wings.There are no dermal scales in birds except for membrane bones on skull.

D.**Claws**:-

Bird claws resemble those of reptiles but occur only on toes. They grow and wear away almost at an equal rate.Young hoatzin bears claws on first two fingers of wing. These are used for climbing. As bird grows older, they disappear. Extinct bird Archeopteryx had three claw- bearing digits on each wing.

E.**Uropygial glands**:-Already discussed

INTEGUMENTARY DERIVATIVES IN MAMMALS

These include:

Hair, Scales, Digital tips (Claws, Hoofs, Nails), horns, Baleen and glands.

Hair occurs in mammals only. Cover entire skin in some and in others like whales few coarse hairs are on the snout. In embryonic period, all mammals are covered with a coating of fine hair called Lanugo, which is shed after birth. Hair is entirely epidermal and are not modified scales but new outgrowths of epidermis.

A thickening of epidermis pushes into dermis and becomes cup shaped at lower end. Dermis extends into cup forming hair pappilae, having blood vessels which supply nourishment. Epidermal down growth which at first is a solid cord of cells now splits to form a central shaft of keratinized cells and a space around it: the epidermal cells around the space form the hair follicle. Lower part of hair follicle becomes large and is called Bulb. Cells of follicle thickens and bud off a sebaceous gland. Central shaft grows in length and emerges outside skin. Development of hair differs from feather. Hair is entirely formed from solid column of epidermis. In feathers there is mesodermal (dermal) feather pulp extending into the hallow quill.

Shaft of hair is made of dead cornified cells. It has external cuticle of transparent overlapping cells which have lost their nuclei. Inside cuticle is cortex and a central core or medulla. Cortex has pigment and some air spaces in its cornified cells. Medulla has shrunken

cornified cells and large air spaces. In the follicle, Root is surrounded by outer and inner sheaths which donot extend beyond follicle.

Sebacious gland opens into follicle to oil the hair. In danger, hair is caused to stand, by erector pili muscles. It projects not vertically but at an acute angle from skin. This condition in man is called cutis anserina or goose flesh.

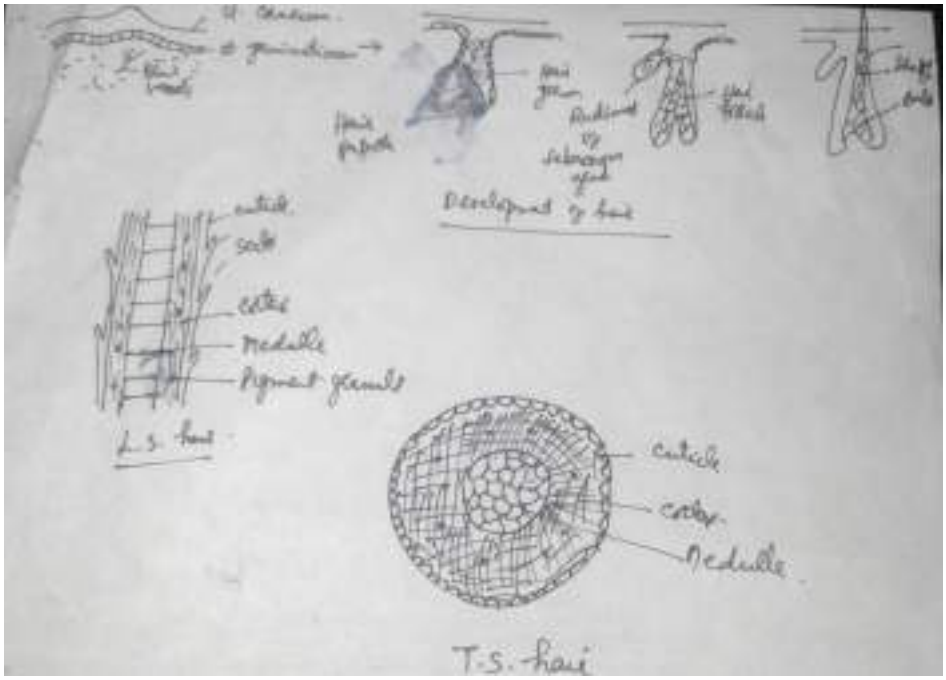
Hair in rabbits is short, soft, called as Fur. In duck bill fur seal and mink there is soft underfur (short, close-set hair for insulating) and long coarse guard fur scattered over surface for protection against wear. Hair in sheep have rough scaly surface, scales or adjacent hair interlock and form wool, used for preparing cloth.

In human embryo, lanugo is shed before birth or shortly after except on head, eyelid margins and eyebrows. Later these hairs are also shed and replaced by coarse hair. New hair grow over most of the rest of body as a fine downy coat called Vellus. There are humans with no hair (Atrichosis); Scanty hair (Hypotrichosis) and abnormally excessive hair- a condition known as Hypertrichosis.

Hair colour is due to amount of pigment in cortex, nature of hair surface, amount of air in intercellular spaces of medulla.Pigment deposition stops in later part of life. In some it is seasonal. In winter, brown pelage-hair coat is replaced by white coat for camouflage.

White colour is due to lack of pigment and reflection of light in all directions from air spaces in medulla. Grey hair in human result from reduction in pigment and reflection from increased number of air spaces.

In spinny ant eater, Hedgehog, Porcupine, hair over upper surface are modified into defensive spines or quills. Hair in nostrils and auditory canal checks entry of foreign substances. Eyelashes have some protective role. In carnivore vibrissae or whiskers on snout are tactile in function. Beared in man, Mane in lion, crests and tufts in some regions are secondary sexual characters, hairs on tail are used to drive away insects, hairs form an insulating coat which provide colour to body and prevent water from penetration into skin, pubic and axillary hair lessens friction between limbs and body during locomotion.



Scales:-

Certain mammals have epidermal scales and some bonny dermal scales also.

a) **Epidermal** scales-present on tail of rats, mouse, muskrat, beaver. These scales are not molted and hair project beneath them.

In scaly Ant eater or Pangolin, body is covered with large, thick, overlapping scales called Corneoscutes except on undersurface. They are periodically molted singly.

Armadillo has horny epidermal scales overlying dermal bonny plates on the body except undersurface around tail and on outer surface of limbs. Some hair project between scales. Scales are not shed, but gradually worn off and replaced from beneath.

In most under surface of hands and feet bear relics of scales. Fraction ridges on human hands and feet represent scale rudiments. These ridges are used in making fingerprints.

Some mammals-rat, bear friction ridges on Raised Pads called Tori present on undersurface of feet.

b) **Dermal Scales**-Mammals mostly lack dermal scales but for membrane bones of skull. Armadillo has dermal bonny plates under the horny epidermal scale. Certain whales may have bonny plates on the back and in the dorsal fin.

4. **Digital tips**:

a) **Claws**;-In mammalian claws, subunguis is reduced and is continuous with a fleshy pad or torus , present on under side of digit. Torus bears friction ridgesCat, lion, tiger have retractile claws. These when not in use are withdrawn into a sheath so that they remain sharp. Lemur and tarsier have claws on some digits and nails on others

b). **Nails**- are present in primates among mammals. Unguis is broad and flat. Subunguis is greatly reduced. Dermis underlying unguis is very vascular called nail bed, imparting pinkish colour at the base of the nail. At the base of nail epidermis is invaginated and called Nail root. It produced Keratin for growth of nail. It lies in a groove called Sulcus Unguis or Nail Groove.

Crescent shaped, whitish area of the base of thumb nail is called Lunule. Thin skin adherent to nail at the base is called Eponychium or cuticle.

c) **Hoofs**-occur in ungulates. Unguis is thick and curved all around the end of the digit and it enclose the subunguis which fills unguis. Behind the hoof is pad called Frog. Digit doesnot touch the ground and animal walks on unguis. Unguis is very hard and wears off quite slowly. Horse and Ox are shod with steal horse shoes to check rapid wearing away of unguis.

Nails and hoofs of mammals are modified claws.

4) **Horns**-found in ungulate mammals only. Five types of horns are

1)

Simple hollow horn-Found in cows, buffaloes, sheep, goat usually in both sexes. They have permanent bonny dermal core arising from frontal toes. This is covered by, hollow sheath of keratinized layers of epidermis. They are unbranched; grow throughout life, though growth slows down with age. They are not shed. They may be arched, Conical, coiled, twisted, smooth. A new born calf has two loose button like bones(Oscornua) under the skin over frontal bones. They grow with calf and ultimately fuse with frontal bones. Skin covering them secretes keratin which grows into horn. If Oscornua is destroyed or removed, horns don't develop.

2) **Prong-horn**: occur only in antelope. Resemble simple horn in structure consisting of keratin sheath over bonny core of frontal bone. However, sheath gives off a branch or prong and horny sheath is shed annually. Epidermis that persists on bonny core then produces a new horny sheath

3) **Branched Horn** or Antlers-occur in Deer, Elk and Caribou.

They are solid and consist of bone without any covering of skin or keratin. They are thus mesodermal in nature and not horns in real sense.

Antlers are branched. They are shed each year in spring and regain during summer, becoming complete before the mating season in autumn.

When growing, they are covered with Velvety fur which is lost in full grown antlers.

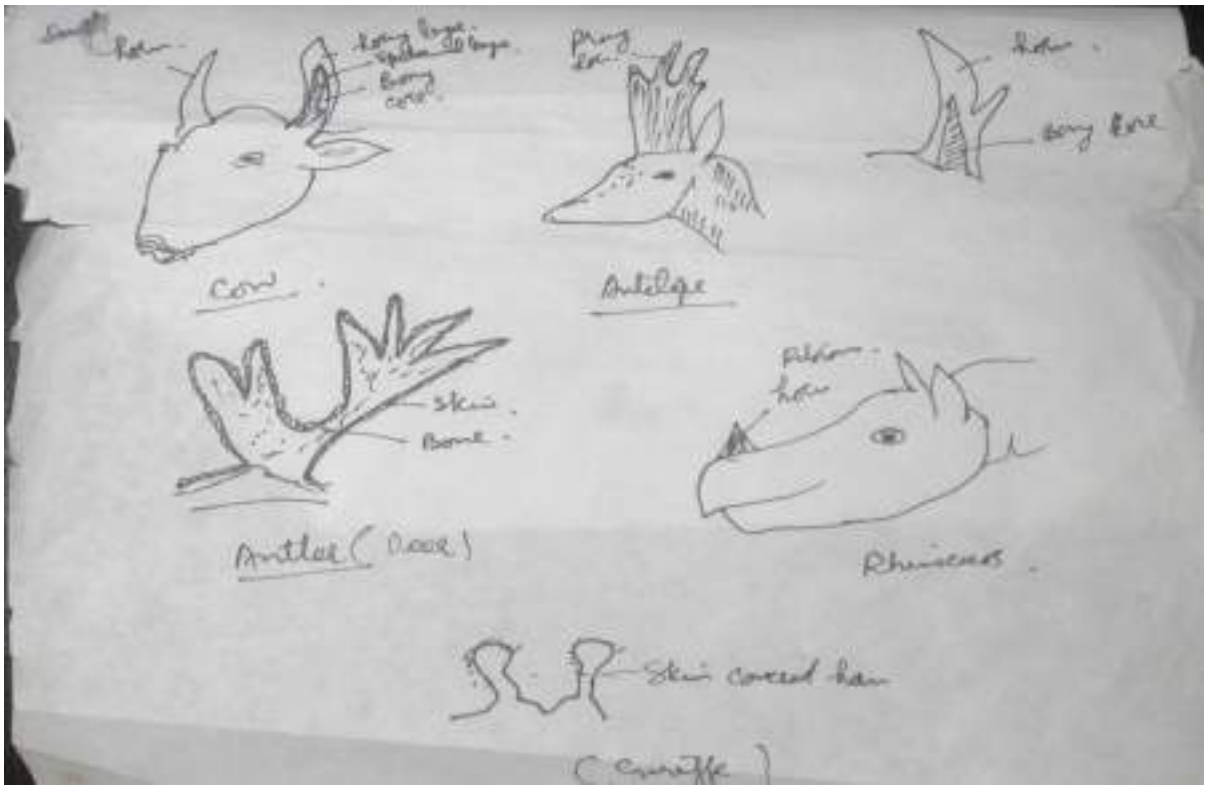
Antlers occur in males except Rein Deer and Caribou.

Growth of antlers is regulated by hormones from testis and anterior pituitary

4). **Fibrous horn**-occur in Rhinoceros. They are conical structures without any bonny core, composed of keratin fibre resembling very thick hair. Unbranched grow from epidermis in median line or snout. If broken, grow again. There is one horn in Indian Rhinoceros and two horns in African rhinoceros.

5) **Skin covered horns**-occur in Giraffes. Consist of bonny core covered with skin which is never shed. They are short, unbranched, permanent and present in both sexes.

All types of horns are used for defense.



Baleen (Whale bone)-:-It occurs in tooth less whales. It has large horny plates derived from oral epithelium which hang from palate and the edges of upper jaw. Their lower ends are fringed.

It is used for straining microscopic organisms from water which form chief food of these huge animals.

3.2 COMPARATIVE ACCOUNT OF ALIMENTARY CANAL OF VERTEBRATES

In primitive invertebrates (protozoa, porifera) digestion is intracellular. With the evolution of multicellularity, intracellular digestion has been replaced by extracellular digestion.

Traces of gut are found in coelenterates, where coelentron has a single opening for ingestion and egestion. Digestion in the canal is both extra and intracellular.

Gut is completely like coelenterates in turbellarians and trematodes (platyhelmenthis). Intestines are branched to distribute food as there is no coelom.

Due to development of pseudocoloem in Nematyhelmenthis, gut has become complete with two openings mouth and anus and is a straight tube.

With diverse feeding habits (carnivores, herbivores, omnivores, scavengers, sangvivores, deposit feeding, parasites) various animals have undergone modification.

Basically gut is divisible into 3 regions in chordates:

i) Stomodaeum or Foregut: Derived from ectoderm, outermost region.

ii)Mesentron: Derived from and lined with endoderm.

iii) Proctodeum: Derived from ectoderm

There is no clear demarcation between 3 regions.

There is no proctoderm in cyclostomes. Entire intestine develops from endoderm.

Typically alimentary canal (gut) has; buccal cavity, pharynx, oesophagus, stomach, small intestine, large intestine, anus (cyclostomes, boney fishes and mammals) or cloaca (cartilaginous fishes, amphibia reptiles and birds).

1) Mouth: In cyclostomes, it is without jaws and is permanently open. In Gnathostomes, it is provided with upper and lower jaws and is closed. It is ventral in(cartilage fishes),terminal or sub-terminal. Slit is bordered by lips (immovable in all vertebrates except mammals in which it is movable). Birds lack lips; bear beaks acting as foreceps in picking up things. Prehensile tongue of diverse animals- toads, ant eaters and cattle is effective substitute for a grasping hand.

Some snakes,with no-means of killing their prey have backwardly directing teeth.They swallow food(frogs) alive by propalinal motion of jaws.

Trunk of elephant (drawn out nose and upper lip combined) is a unique device for reaching food without necessity of lowering the heavy head.

2) Buccal cavity: Immediately within mouth aperture is buccal cavity. Roof is called palate. In fishes and amphibians, plate is primary, formed by base of skull.

In most reptiles and birds, platal folds grow towards median line but donot meet, leaving a cleft between them.

In crocodiles and mammals, platal folds meet in median line forming secondary palate (secondary roof).

Internal nares open into buccal cavity in forms with primary or incomplete secondary plate.

Internal nares open into pharynx in forms with complete secondary plate.

Buccal cavity has variety of mucous glands; tongue; teeth.

3) Pharaynx: It serves merely a passage for food to oesophagus, no digestion occurs in it.

Its walls contain muscles that intiate swallowing movements. It plays role in respiration also. Gills of fishes and lungs of tetrapods are derived from pharyngeal wall.

In cyclostomes, it underlies the oesophagus, ends blindly and is only respiratory in function.

In mammals, epiglottis acts as trap door device to guard entrance of trachea, so that food should not go wrong way.

4) Oesophagus: It serves merely as a passage for food to stomach. No digestion occurs here.

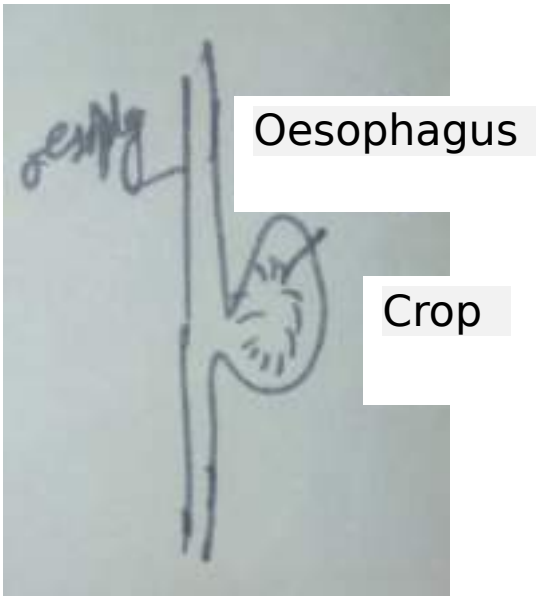
Its length depends upon presence or absence of neck. In fishes, frogs and toads, neck is reduced to minimum, so that food (fly in frogs) entering mouth finds itself almost immediately landed in stomach. It is long in reptiles, very long in birds and mammals. In bony fishes, pneumatic duct leads from roof of oesophagus to air bladder.

In birds, oesophagus has lateral enlargement crop; for temporary storage of food hastily secured in presence of enemies or competitors. Pigeons produce pigeon milk from lining of crop to feed to nestlings by regurgitation.

Of all vertebrates, birds and ruminants are exceptions which have voluntary muscle fibres in whole length of oesophagus and are able to regurgitate food at will. Milk in birds is fed to young ones. Ruminants regurgitate their hastily swallowed food for prolonged chewing.

In snakes violent peristalsis is necessary in swallowing a comparatively large morsel of food (frog). Swallowing in supplemented by muscles of body wall.

Inner lining of oesophagus of Marine turtles is beset with backwardly projecting horny papillae, which enable them to swallow the slippery seaweeds upon which they habitually feed.

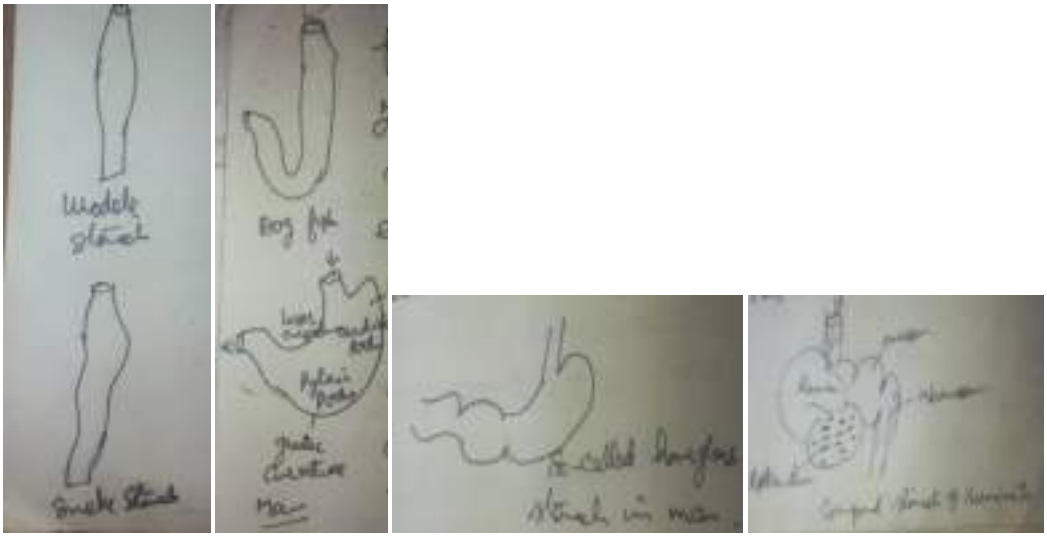


5) Stomach: No stomach in cyclostomes, here oesophagus directly leads into intestine.

Originally (as in some fishes and Salamanders); it is spindle shaped and arranged to conform with general contour of an elongated body. But in higher vertebrates, it becomes sac like in shape to assume transverse position in body cavity. Between these two extremes are found many gradations of form and position.

Stomach of dog fish (insteado f spindle shaped) is doubled back in the form of a J-Shaped tube. In some fishes Perch, herring, loop becomes fused along its inner bend in such a way that bag shaped pouch (or fundus) is formed with entrance and exit brought together at one side.

This type of stomach, when shifted into a transverse position is much like that of man(lesser curvature on upper side between entrance and exit and greater curvatures around outer margin of stomach).



Exit from stomach is closed by pyloris or pyloric valves. There is tendency for stomach to become differentiated into 2 or more regions. In J- shaped stomach of dog fish, one speaks of a cardiac limb and a pyloric limb; while in certain mammals (e.g mouse), a constriction in the middle part of stomach marks off a cardiac chamber from a pyloric chamber. Such a stomach is called a hourglass stomach. Medical references indicate that occasionally man has hourglass stomach similar to 2-chambered stomach of mice. Certain monkeys (Hylobasts and Semnopithecus) show some features. Whether such unusual structures in human stomach are pathological or ancestral is uncertain.

Extreme sub-division of stomach is reached by ruminants having compound stomach with 4 chambers.

Rumen, Reticulum, Omasum, abomasums. Rumen receives and stores hurriedly swallowed, partly masticated food. From here, food is regurgitated at leisure(cud) either directly or by way of reticulum and chewed thoroughly and reswallowed. It now passes into omasum for mechanical breaking and then to abomasum for chemical digestion. Micro-organisms (bacteria and Protozoa) in rumen and reticulum help in digestion of cellulose; also synthesizes vit. B complex and proteins.

In whales and hippotami, stomach is divided into many compartments.

Vampire bat (Desmodus) exhibits peculiar adaptations with reference to its blood-sucking habits, fundus of stomach being drawn down into a deep elastic pouch. When vampire fastens on a victim, it can fill this reservoir (spacious) with blood until the entire body is swollen in consequence.

Cardiac and pyloric regions of stomach in birds have become separated into chambers, cardiac chamber or proventriculus, which opens into ventriculus or gizzard. Proventriculus is glandular, where preliminary maceration and chemical digestion occurs. Gizzard has thick muscular wall. It is lined with a hard secreted layer. In this muscular mill food is ground up; by gizzard stones. Highest differentiation of gizzard is reached in seed- eating birds and least in birds of prey.

3- general functions are performed by vertebrate stomach

1) Storage- By periodic voluntary filling of storage chamber, opportunity is left for other activities.

2) Mechanical digestion- Muscular walls of stomach knead food mass around and around by peristalisis until it has been reduced to a suitable consistency.

3) Chemical digestion- Depends upon presence of glands in lining of stomach. In fundus region, gastric glands are numerous secreting enzymes for digestion of proteins. Vertebrate pepsin always functions in acidic medium. Hcl in dogs enables them to dissolve bones which they crunch and swallow.

6) Small intestine: It is meant for final digestion and absorption of digested food. Cyclostomes have short, straight has absorbing surface increased by typlosole(making few spiral turns in whole intestine).

Elasmobranches have typlosole with numerous spiral turns. It is much longer than intestine, with the result, it becomes twisted into a spiral valve. This makes an enlarged surface within a very compact space for diversion of food, since intestine is no longer than J-shaped and is not bend.

Teleost fishes have given up spiral valve idea and developed sac like diverticula or tuft of tubules.- pyloric caecae- occupying considerable space within constricted body cavity. No. varies from 1-200.

Amphibians mark beginning in vertebrate series, where there is distinction between small and large intestine. Inner surface of small intestine posseses villi, which reach greatest differentiation in mammals.

Sluggish reptiles have large intestine marked off from small intestine. At the junction, colic caecum (new diverticulum appears).

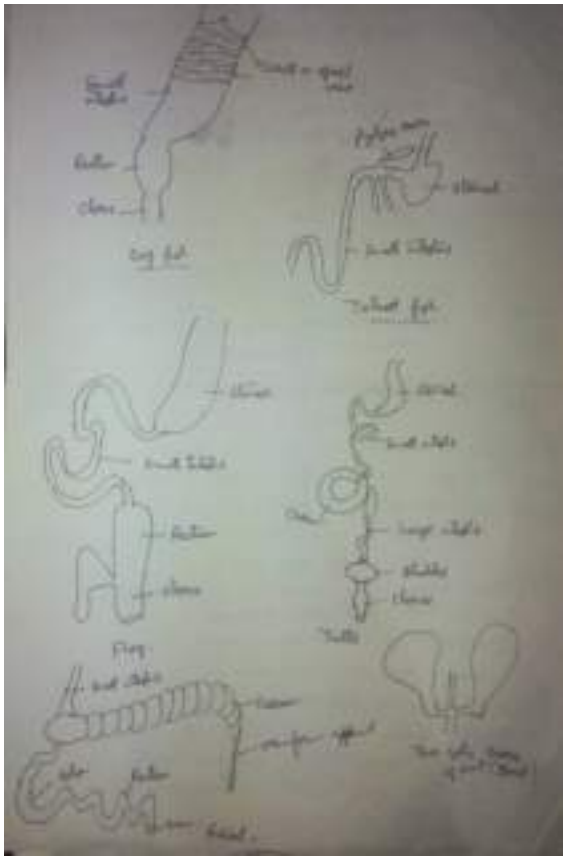
Colic-caecum of turtle is hardly more than a slight enlargement but higher up among rabbits and some rodents. It becomes enlarged tube with internal capacity equal to that of rest of digestive canal to which it is attached.

Birds have much coiled small intestine, two colic-caecae, a large intestine. In ostriches, single colic-caecum is capacious and has spiral valve inside.

Mammals have small intestine easily distinguishable from large intestine.

Colic-caecum single (except edentates, hyrax having 2 colic caecae).Monotremes, carnivore marsupials, bats, carnivores; toothed whales either lack or have only one colic caecum. But in herbivores, it is so large that it may even exceed body in length.

Herbivores also have a longer small intestine than carnivores.



Degenerate free end of colic caecum forms vermiform appendix in man and bears.

Small intestine is divided into duodenum, jejunum and ileum (distinction first made out in man, applies to most other mammals).

Part next to stomach is short duodenum receiving bile and pancreatic ducts. It is followed by jejunum and post ileum. Jejunum is richer in blood vessels and has thicker wall and wider lumen than ileum.

Characteristic modification of lining of mammalian small intestine is presence of innumerable thick projections villi, increasing absorptive surfaces. Each villus has capillary loop and lacteal absorbing digested products of carbohydrates and proteins (through capillary loop) and lipids (through lacteal).

Along mucous membrane of small intestine are oval, white lymphoid patches called peyer'spatches . In typhoid fever, chief lesions occur in these areas.

7) Large intestine: Through this residue of food mass is forwarded for expulsion. Except in embryo, it is without villi.

In man it is 5 feet long, differentiated in colon (ascending, transverse and descending) and finally rectum, ending at anal opening. Only rectum of mammals is homologous with large intestine of lower vertebrates (I,e it is medium sized there).

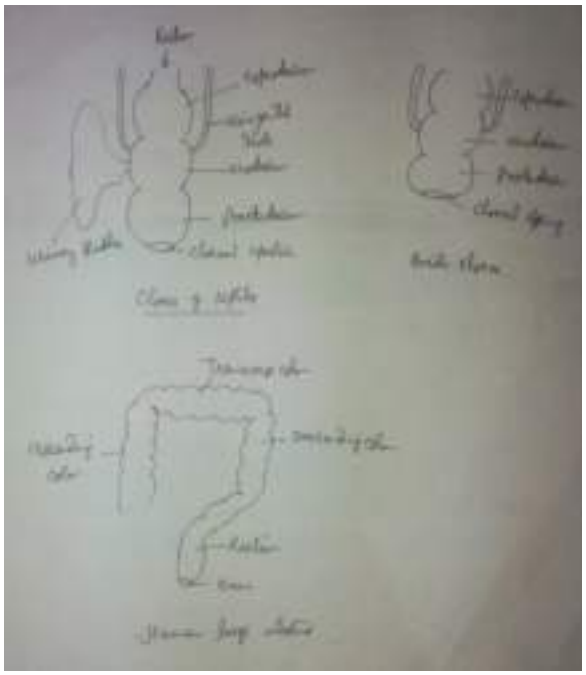
In birds rectal region is reduced. It is a disadvantage for them because it will increase weight and disturb flight of these aerial creatures. Hence as soon excreta is formed, it is rapidly disposed-off.

In many, like reptiles, birds, monotremes(among mammals) urinary, genital ducts enter post part of large intestine which also receives faeces. Thus it is common exit for 3 products (faeces,genitalproducts,urine).it is called cloaca. It is simple chamber in elasmobranches and amphibians.In reptiles and birds, it is divisible into coprodaem(receiving rectum), urodaeum(receiving urinogenital ducts) and proctodaeum(leading to exterior by cloacal aperture).

Aperture is longititudinal in sharks,crocodiles and tortoises.

Aperture is transverse in lizards, snakes, birds

Aperture is circular in frogs, toad and limbless amphibians.



Increase in digestive surface

So long animal's body remains small, a straight digestive tube has an adequate internal surface to meet all alimentary demands. As animal grows, straight unmodified digestive tube becomes inadequate to take care of accompanying mass.

There are 4 general ways in which need for increase of digestive surface has been met in various animals. These are:-

1) Increase in diameter:

It is not extensively employed, because of limitations of space in body cavity. If inner tube increases in diameter; outer tube of body will must also enlarge, which tends to defect the object to be gained.

Certain regions(stomach and large intestine) are nevertheless of greater diameter than remainder of tube.

2(Increase in length:

It is universal device for adding to available digestive surface among vertebrates; since body cavity provides possible space for coiling and looping of the tube.

Body cavity not only makes place for an intestine longer than the body itself, but also frees intestinal tube from muscular control of surrounding tissues, permitting its freedom to exercise peristaltic movements of its own.

Characteristics swollen shape of a tadepole, is due to enormously lengthened digestive tube, coiled many times, packing body cavity fully just before metamorphosis. It may measure 8-10cms in length; when tade pole is adapted for plant food. After metamorphosis, when young frog switches over to insect food, requiring less digestive surface, tube shortens to 3-4 cms in length, although body itself is now considerably longer than before.

In man, entire digestive tube is 25-30 ft long, although entrance and exit are only about 2 ft. apart.

3) Internal folds: Increases both in diameter and length of digestive tube make demands that soon encroach upon limits of possible space within body cavity.

Internal folds within food tube itself avoid this difficulty by adding to the expanse of surface to which food is exposed without adding to external size of tube.

Typhlosole in cyclostomes; spiral valve in Dipnoii, elasmobranches and ganiod fishes are examples of internal folds. Plicate circulares(transverse folds) to inner surface of anterior part of human intestine, villi in higher vertebrate intestines are other examples.

4) Supplementary diverticula:

These are abundant in fishes at junction of stomach with small intestine,(Pyloric caecae), numbering 1-200.

Colic caeca at junction of small and large intestines in amniotes. Large colic caecum of rabbit, birds have typically 2 colic caeca.

Large intestine of man, and of several mammals is pushed out into enlargements called haustra. Rectal glands of elasmobranches, urinary bladder of amphibians, bursa of Fabricius in birds; anal gland in certain mammals; serve different uses, although not necessarily connected with process of digestion.

TEETH

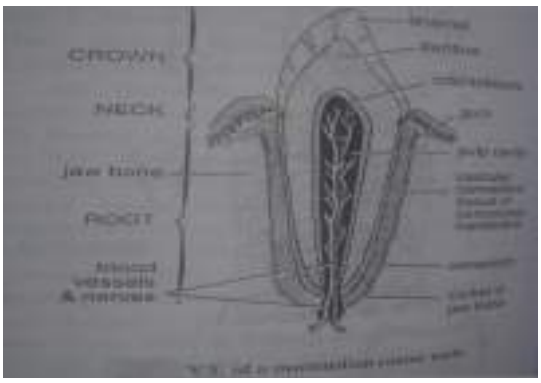
Teeth have purpose of grasping, cutting or grinding. In some they help in prehension of food, defence, offence. Even they help in locomotion (e.g. Walrus, using its tusks in dragging its slippery body out of arctic water on to ice).

1) Structure of typical tooth:

A tooth has central cavity-pulp cavity filled with pulp, connective tissue, blood vessels, nerves. Pulp cavity is surrounded by cement like dentine which in turn is covered by shining enamel. Dentine (Mesodermal in origin);enamel (ectodedrmal in origin).Teeth of Armadillo & sloths lack enamel. Enamel is much harder than dentine.

In mammals (bone-like material-cementum) covers proximal half of dentine, fusing tooth in cavity of jaw bone. (Cement also mesodermal).

In mammals, a tooth has root, neck & crown. Root is in bony socket; neck in gum, crown exposed part showing cusps.



2) Number:

Lower vertebrates have indefinite number of teeth, but in mammals number becomes definite & limited. Reduction in number is a mark of evolutionary advancement associated with terrestrial life, less food, more chewing, shorter jaws, strong muscles of mastication.

Increase in number of teeth (secondarily occurring in Dolphins & toothed wheels) may be regarded as reversion to ancestral conditions in connection with aquatic life, more abundant food, less mastication.

There are some toothless species representing every class of vertebrates. Toothless ones are:-

Fishes [Sturgeon-Acipenser; sea horses & pipe fishes, coregonuswartmani- is toothless member of large family of toothed fishes---(salmonidee)].

Amphibians---toads; siren (among urodels) are toothless. Frogs lack teeth in lower jaw.

Reptiles --- Entire order of Chelonia (Turtles & tortoises) are toothless. Some fossil reptiles possessed beaks instead of teeth.

Aves --- All modern birds are toothless .However fossil form Archaeopteryx showed teeth in its beak.

Mammals --- Monotremes (-prototherians-pletypus& spiny ant eater) teeth present only in young. In adult they are absent, adult have horny beak.

In Edentata (Armadillo, sloth) teeth may be absent or present .If present, incisors & canines are always absent. Their teeth also lack enamel.

Teeth are absent in pholidota—Manis—(scaly ant eater--pangolin) & large whales(Mystacoceti).

A curious instance of hereditary toothlessness in man is reported by Thadani. (from Hyderabad, Sind in India),where an inbred community called "Bhudas" or toothless in which males never have any teeth. This abnormality is accompanied by baldness & extreme sensitivity to heat.

These toothless mammals furnish embryonic evidence that they are degenerate descendants of ancestors with teeth.

3) **Succession:**

Polyphyodont: Animalsthat have a continuous succession of teeth throughout life (lower vertebrates- sharks and Dog fishes).

Diphyodont: Animals have replacement of temporary milk teeth by permanent teeth. Milk teeth in young allows to chew food at a time, when jaws are small and cannot accommodate permanent teeth (most mammals).

Monophyodont: Animals retaining all their milk teeth. e.g., Marsupials, moles, toothed cetaceans (Odontocoeti), some rodents, reptile Sphenodon.

4) **Situation:**

Teeth in fishes and other aquatic animals occurs attached to various skeletal foundations within mouth cavity; such as vomer (vomerian teeth in frog); Palantine ;Pterygoid, Parasphenoind.

In Labeo, teeth occur on pharyngeal floor and bite against a hard horny part on base of skull. In some they occur on tongue, on hyoid and gill arches.

Teeth in reptiles and mammals are usually confined to jaws, although in some snakes and in Sphenodon, they occur on roof of mouth on vomer and palatine bones.

5) **Attachment:**

Acrodont: Teeth without roots, that are held to the edge of jaws or other skeletal foundation either by fibrous membrane or ankylosed directly to bone in shallow pits. They are broken off easily. They are generally polyphyodont.

In some they are hinged on by a ligamentous base and may be folded down when not in use as in pike and hake (fishes) in many snakes.

Fishes and amphibians are generally acrodont.

Pleurodont: Here not only base but one side of tooth is involved in attachment to a shelf like ledge along inner margins of jaw e.g, certain Urodela(Necturus) and Lizards (Reptiles).

Thecodont: Highest and most efficient tooth, here roots are present in long sockets in jaw. Capillaries and nerve enter pulp cavity through open tips of hollow roots (some fishes, some reptiles i.e. alligators and crocodiles); fossil birds and all mammals.

6) **Differentiation:**

Homodont: Teeth similar. Present in primitive water dwelling species, which do not chew . they are adopted for prehension e.g., Amphibia, fishes reptiles , mammals (whales, dolphins, porpoises).

Heterodont: Due to variety of foods and occasion for chewing, teeth are of various types like incisors, canines premolars ,molars . e.g., Therapsid reptiles and mammals:

Incisors: Chisel shaped, monocuspid, help in seizing, cutting , cropping bitting and gnawing. Totally absent in Sloth; absent in upper jaw of ox. Modification are :

Gnawing (Rodents and Lagomorphs)

Incisors in Beaver(Castor) are deeply set in sockets and can cut down large trees with such teeth.

Combing – Lemures

Tusks – In elephants upper incisors modified as tusks

Canines : Pointed, monocuspid, helps in piercing and tearing food as well as for defense. In males they are large sized.

They are called tearing teeth in carnivores.

Absent in rodents, lagomorphs , some ungulates.

Premolars (Cheek teeth) and Molars :premolars are two rooted, dicuspid.

Molers :3 or 4 rooted polycuspid. Help in crushing, chewing and gridding.

In carnivores, upper last premolar and lower first molar are specialized acting like scissors and are called carnassial teeth or sectorial teeth or shearing teeth for cracking bones. In man, last molars are called wisdom teeth.

In case of rodents, lagomorphs, some ungulates due to absence of canines, a large gap is found between incisors and premolars called as diastema that occurs in upper jaw in ox.

Depending upon the shape of cusps in crowns of premolars and molars, they are of various types

I. Bunodont: With small separate rounded cusps for grinding (man, monkey, pig etc.)
II. Lophodont: Cusps join to formridges called lophs, used for grinding plants (Elephant).
III. Sclenodont: crescent shaped cusps found in herbivores grazing mammals (Horse, cattle, squirrel). If teeth have high crowns and short roots- they are called hypsodont (Horse and Cattle). If teeth have low crowns they are called brachyodont (Ground Squirrel)
IV. Secodont: Pointed cusps for tearing and cutting flash (carnivore mammals).

7) Dental formula

In species with heterodontteeth , it is useful to express their diversity in some convenient and compact form , which is accomplished by dental formula

Man (permanent teeth) = 2123 = 32
2123

Sheep, Goat, Cow = 0033 = 32
3133

Cat = 3131 = 30
3121

Rabbit = 2033 = 28
1023

Squirrel =1023= 22
1013

Kangaroo = 3124 =34
1024

Bat= 2132 = 34
2133

Dog =3142 = 42
3143

Rat = 1003 = 16
1003

Elephant= 1003 = 14
0003

8) Specialized teeth (Unusual teeth):

Tusks are either incisors or canines, tusks are found in both sexes of elephants and Walrus.Tusks of extinct mammoth (Archidiskodon) weighs 250 pounds, 16 feet long. Wild boar tusks are modified canines.

3.3 Respiratory System in Vertebrates:-

Gill Respiration:-

Paired endodermal outgrowths of pharynx (Visceral or Pharyngeal pouches) fuse with invaginations of surface ectoderm (visceral furrows), to form branchial or gill pouches or gill clefts. The opening of gill cleft into pharynx is known as internal gill slit and that to exterior as external gill slit. Inside gill clefts are gills. The gill clefs are separated from each other by mesodermal interbranchial septum. Covering epithelium of septum is endodermal and raised on each surface into a number of plate like process (gill lamellae), or rod like process (gill filaments), which are richly supplied with blood capillaries. Gills formed of lamellae are described as lamelliform, those composed of filaments are said to be filiform or pectinate. Gill lamellae may be borne on one or both sides of interbranchial septum. Lamellae on one side of septum form half gill or hemibranch or demibranch. Two hemibranches with their intervening septum constitute a complete gill or holobranch. Within each interbranchial septum is a supporting visceral arch which is cartilaginous or bony bar.

Inner end of interbranchial septum encloses epibranchial cartilage and adductor muscle. Epibranchial cartilage constitutes gill bar. Remaining part of interbranchial septum encloses fibromusculartissue , nerve endings , blood vessels and supported by gill ray or

branchial ray arising from gill bar. Gill rakes arise from dorsal side of each gill bar and extend into cavity of pharynx.

In all vertebrate embryos, floor and side of pharynx supported by 7 pairs of visceral arches known as:

1st or Mandibular

2nd or Hyoid

3rd or 1stbranchial

4th or 2ndbranchial

5th or 3rdbranchial

6th or 4thbranchial

7th or 5thbranchial

Cyclostomes have 6-14 and fishes 5-7 pairs of gill pouches bearing gills. Amphibians & reptiles develop 5 pairs, birds have 5 pairs, mammals have 4 pairs of gill pouches in embryonic stage. These have no gills & disappear except 1st which forms Eustachian tube & middle ear on each side. In some amphibians, however, 2nd-4th pairs of pouches bear gills & persist in the adult.

1. In Protochordates& Amphioxus, pharynx is highly developed & its wall perforated by series of slits called gill-clefts communicating pharynx with exterior. These have developed as feeding apparatus, but served respiratory function as well as seen in larva of petromyzon.
2. In lampreys, there are 7 pairs of gill pouches. These are 6 holobranchs& 2 hemibranchs.

   Hag fishes have 6 pairs of gill pouches, opening to external by common branchial duct, however hag fish Eptatretus has 6-14 pairs of pouches, each opening individually to exterior.
3. In fishes 1st gill pouches lies between mandibular & hyoid. It is either reduced to narrow passage called spiracle or closed altogether. Spiracle has redumentary gill lamellae called as pseudobranch (may be organ of special sense). First functional gill occur in gill pouches between hyoid arch & 1stbranchial arch.

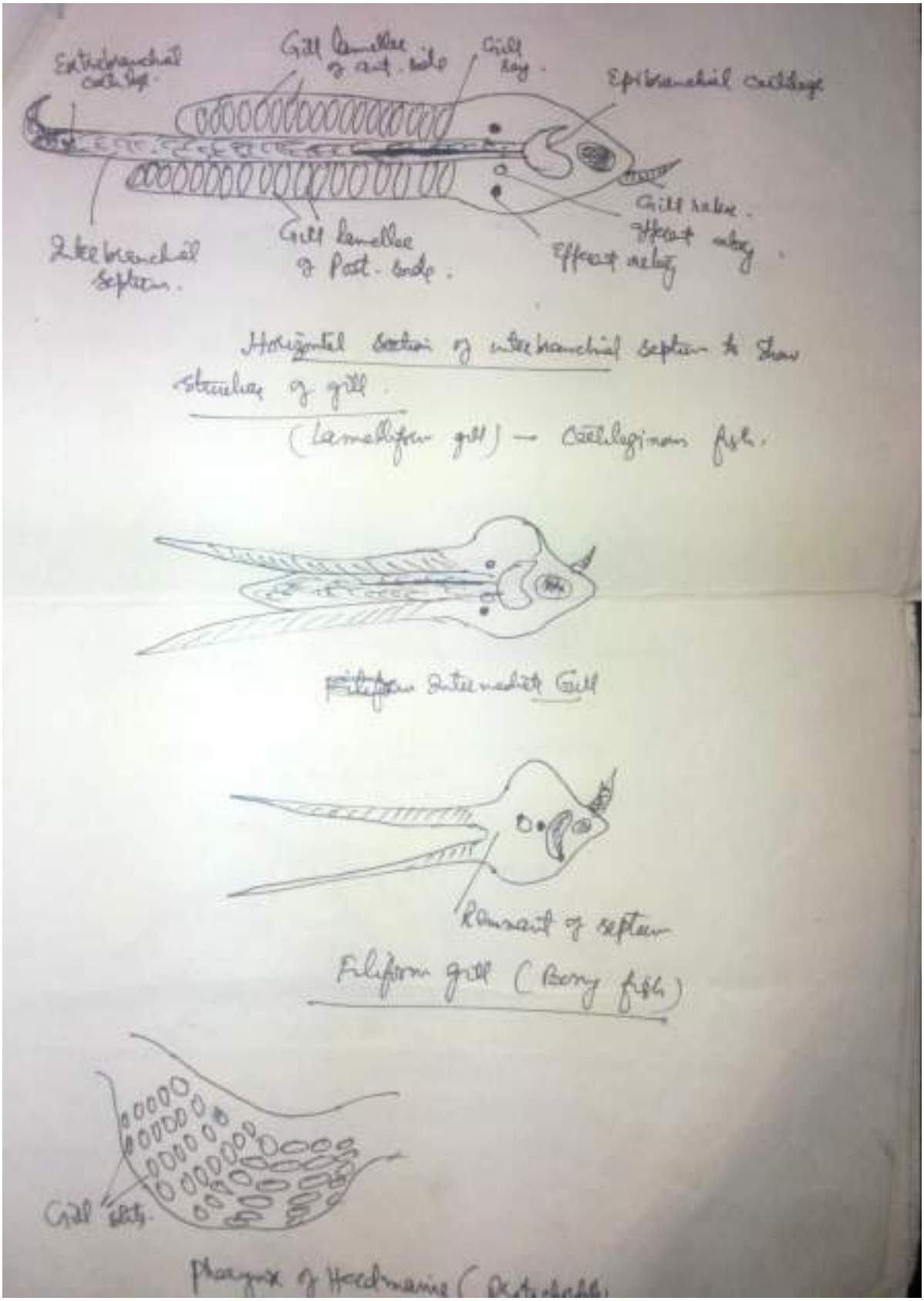
   In cartilaginous fishes, gills are lamelliform, external gill slits uncovered. Interbranchial septum well developed reaching to surface, where it slightly bends backwards to guard external gill slits. Generally there are 5 pairs of gill pouches, (one pair of hemibranch& 4 pairs of holobranchs on 1st, 2nd, 3rd& 4thbranchial arch and 5thbranchial arch is abranch). Hexanchus&Heptanchus have 6 & 7 pairs of gill pouches. Chimaera has only 4 pairs. In Pleurotremata gill slits open laterally, spiracles are closed with pseudobranch. In Hypotremata, gill slits open ventrally, spiracles serve to draw a respiratory current.

In bony fishes, gills are filiform, external gill slits are covered by a flap, operculum. Operculum grows backwards from hyoid arch. It encloses between itself & body wall an extrabranchial chamber, opening out by a single branchial aperture behind. Interbranchial septum reduced &gill freely hang out into extrabranchial chamber. Generally there are 5 pairs of gill pouches (4 pairs of holobranches on 1^{st}, 2^{nd}, 3^{rd}, 4^{th}branchial arch. Hyoid & 5^{th}branchial arch are abranch). Spiracle closed externally except in Acipenser&polypterus. Many have opercular gill or pseudobranch on posterior side of hyoid arch, which is believed to be spiracularpseudobranch shifted to hyoid arch due to closure of spiracle. In Lepsosteus, hyoid arch bears both opercular gill & true hemibranch. In Hippocampus &Syngnathus, gill has pecular tufted process instead of filaments and are called Lophobranchs.

Lung fishes have 5 pairs of gill slits except Lepidoserin having only 4 pairs. In Protopterus(Hyoid, 1^{st}& 2^{nd}branchials – abranch, 3^{rd}& 4^{th}branchails – holobranch, 5^{th}branchails – hemibranch on anterior side).

External Gills:

Present in few larval fishes (Polypterus), all larval amphibians & few adult tailed amphibians (Necturus, Proteus & Siren). These are extensions of internal gills (endodermal) in fishes & derived from skin (ectodermal) in Amphibians. There are branching filaments arising from 3^{rd}, 4^{th}, 5^{th}branchail arches & hang freely on sides of head. These are in direct contact with water & exchange gases between blood &environment without any effort of animal. Larvae of frogs & toads develop internal gills also. External gills fall off, when internal gills become functional. Gill slits covered by opercula enclosing branchial chamber opening out by a common aperture, spiracle. Internal gills & opercula disappear during metamorphosis.



Lung Respiration (PulmonarySystem)

Entrance to pulmonary system is usually through nasal chamber, lined with mucous membrane, beneath which is tissue richly supplied with capillaries. This provides moisture & warmth to incoming air. From nasal cavity air passes through nasopharynx& enters trachea through glottis.

Trachea is very short (frogs & toads, where lungs are far anterior in body cavity). It is longer in urodela. In lizards shorter than other reptiles. In turtles & crocodiles so long that it becomes convoluted or even spiral in form. Birds with long necks have long trachea. In swans, it forms loops. Long trachea makes it possible to stretch neck without pulling out lungs "by the roots". Trachea is kept distended by encircling rings of cartilage to prevent it from collapsing. In tailed & limbless amphibians, reptiles, mammals there are incomplete cartilage rings. In birds there are long bony rings complete with bronchi and incomplete cartilage rings. Frogs & toads lack neck, they have trachea incorporated into larynx forming laryngeo-tracheal chamber.

In birds & mammals, bronchi formed by bifurcations of trachea are called primarybronchi. They divide into secondary, tertiary bronchi &give off fine bronchioles inside lungs. Bronchioles send alveolar ducts to air sacs in mammals.

Lungs in amphibians & reptiles are simple, thin walled elastic sacs having on inner surface low ridges, the septa, which enclose shallow depressions (the alveoli). Septa & alveoli increase inner surface of lungs. Wall in frog lungs has outer peritoneum, middle connective tissue & inner epithelium. Peritoneum is protective, connective tissue, supportive & provides elasticity. Epithelium has mucus cells keeping inner surface moist for absorption of O_2 . In chamaeleons, posterior halves of lungs give off a number of thin walled diverticula, which enable them to swell up, a device used perhaps to frighten their enemies. Inflated lungs of sea turtle, on the other hand serve as floats in maintaining a position at the surface of water. In limbless lizards & snakes, left lung is reduced.

Lungs in birds are relatively small, nearly solid, little distensible and in contact with dorsal muscle, having peritoneum only on ventral side. Lungs are highly modified due to presence of supplementary **air sacs, cellulaeaereae**, which facilitate circulation of air through lungs, but **air sacs** are not directly respiratory in function, as shown by paucity (decreasing or less no.) of capillaries over their surfaces.Bronchioles open in to reservoir like air sacs .air tubules are surrounded by capillaries serving as actual respiratory surfaces.Air is drawn back and forth through air tubules of lungs with gaseous exchange taken place both on the way through the lungs to the air sacs as well on the return.**Air sacs** sprout out from lungs at various points and extend into body cavity ,occupy spaces between viscera,beneath skin

(pelicans), between muscles,supporting and connective tissue,between and around joints of cervical vertebrae,and penetrating even into pneumatic,cavities of hallow bones.Although**air sacs** of bird lungs are not supplied to greater extent with capillary network and are not directly respiratory in function,yet they have several different functions .**Air sacs** act as bellows enabling air to be forced back and forth through lung proper (because lungs elasticity is hampered by being attached to dorsal wall of thoracic basket).**Air sacs** act as balloons, reducing specific gravity by retaining heated air. **Airsacs** act as ballast maintaining Centre of gravity for balanced flight by shifting air content of sacs from one part of body to other. **Air sacs** act as friction pads between muscles lessening friction ,giving flexibility and grace to aerial moment of birds. As they are filled with moist warm air, they maintain and regulate body temperature. **Air sacs** act as internal reservoir. **Air sacs** are resonance aids to voice. In pigeon there are 9 air sacs, paired abdominal, paired posterior thoracic, paired anterior thoracic, paired cervical, unpaired interclavicular air sac.

Lungs in mammals are characterized in 2 ways:-

1. Being subdivided externally into lobes.
2. Showing some degree of asymmetry in accommodation to surrounding organs. When asymmetrical, lobes are more numerous on right than on left side. In man, right lung is 3 lobed, left is 2 lobed. Upper most odd lobe of right lung lies behind the right pulmonary artery, while absence of a corresponding lobe on left side permits presence of large left aortic arch. Rabbit has 4 lobes on right and 2 on left side. Rat has 4 lobes on right and entire left lung.

Lungs lie in air tight compartments formed by visceral and parietal pleura. Exchange of gases takes place in the air sacs.

Lungs of whales are hydrostatic as well as respiratory. They imprison air in capacious nasal chamber occupying major part of whales head. The apertures leading from nasal passage to lungs can be shut off by 2 plugs of tissue which function like the stopper in a bathtub. As air becomes stale, plugs open to exchange stale air with pure air in nasal reservoir. When whale comes to surface, reservoir is emptied with violence.

Pleural envelops:-

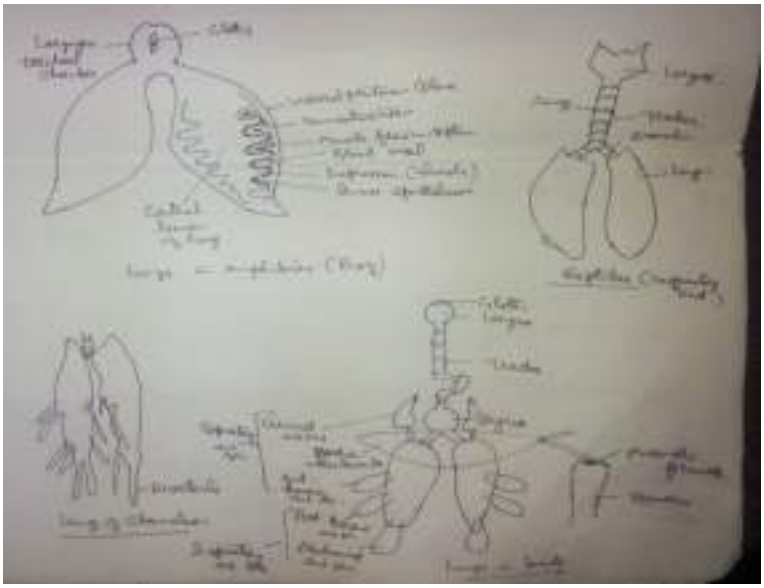
Primitive lungs of amphibians push down into general body cavity having thin covering of serosa continuous with peritoneum lining common cavity. There is no formation of pleural chambers.

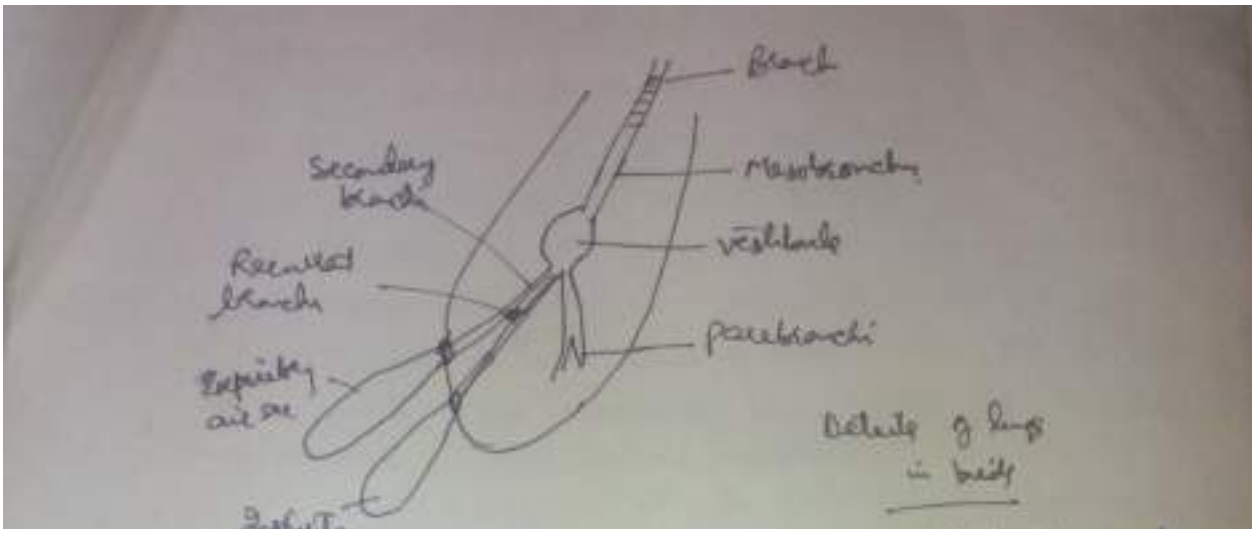
In reptiles, formation of transverse septum by peritoneal folds and privacy for heart by partitioning of a pericardial chamber, led to development of a second envelop (derived

from peritoneal serosa) around lungs. It constituted outer or parietal wall of pleural cavity. Inner or visceral wall is original derivative of peritoneum. This intimately invests lungs like a tight fitting garment.

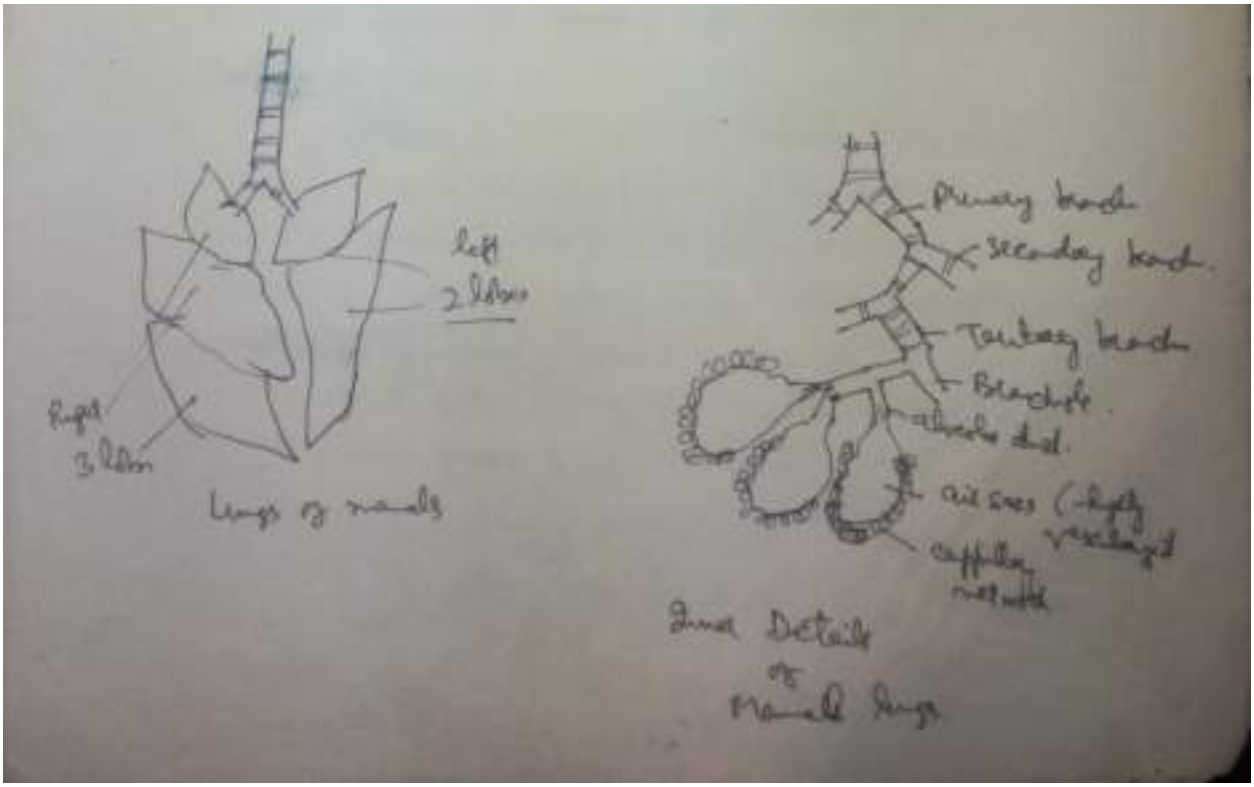
Space between two is pleural cavity filled with pleural fluid allowing freedom of movement & lubricating them.

Pleural cavities are developed in higher vertebrates, where lungs enclosed in them are separated from abdominal cavity which is storehouse of most internal organs.





Inspiratory air sacs are filled first during inspiration. Air from them move to rest of the air sacs through recurrent bronchi and from them to lungs, then to outside. On account of which they are called expiratory air sacs. Due to interconnection of air sacs, there is no dead pause i.e, air sacs are never empty.

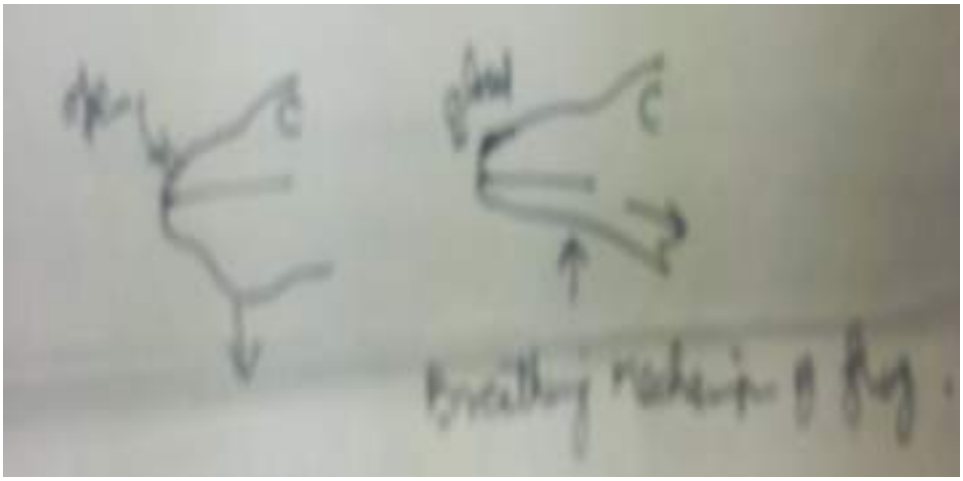


Mechanism of Terrestrial Respiration

Amphibians:-They never breath through open mouth but instead inspire air through nostril (external nares) & internal nares (choanae) as newly established passage ways into the mouth cavity. They do not resort emergency breathing through mouth as mammals do.

Intake of air in frog is accomplished by combination of pump like throat muscles and nostril valves. When nostril valves open and throat muscles draw down, oral cavity is enlarged and air is necessarily inhaled (aspiration). With closure of nostril valves, and contraction of throat muscles, lungs automatically become filled by the mouthful of air that is forced backward (inspiration).

Expiration of air alternates with inhalation and is accomplished by means of contraction of body muscles, lungs, lowering of throat (creating partial vacuum).



Reptiles:- Here it is much like that of amphibians, however, some improvement is seen, since ribs and rib muscles (intercostal muscles) furnish a mechanical means for admitting air, which is not present in ribless amphibians.

Contraction of outer intercostal muscles pulls ribs outwards, causing lungs to expand, reducing pressure in them. Fresh air at high pressure rushes in (inspiration). Exchange of gases occurs in depressions between septa (alveoli) and air becomes foul. Contraction of internal intercostal muscles pushes ribs inwards to their original position. Lungs due to their elasticity and pressure by ribs causes pressure of air to rise and it passes out through tracts.

This improvement is ineffective in turtles whose ribs form rigid box – like armor. They resort to amphibian method of utilizing throat muscles and nostril valves, swallowing air. No doubt, in & out movement of turtles head and neck help in pumping air into lungs, while pectoral muscles (inside ribs instead of outside as in other vertebrates) are helped by abdominal muscles in bringing about expulsion of air from lungs.

Usefulness of rib muscles is very apparent in panting snakes, lizards and alligators.

Birds:-

When bird is not in flight, it breaths by means of its rib muscls on the typical reptilian pattern. Lowering and raising of sternum enlarges and reduces body cavity respectively helping in inspiration and expiration. Intercostal and abdominal muscles raise and lower sternum.

During flight, inactive rib muscles remain temporarily fixed and rigid. Powerful pectoral muscles are anchored up on rigid thoracic basket making sternum immovable.

According to J. Z. Yong, movement or pressure of wings and slight movement of posterior end of body helps in breathing.

According to Walter and Sayles (Biology of vertebrates) bellows-like air sacs are filled and emptied by action of flying muscles rather than rib muscles which provide means of irrigation of lungs by air of a flying bird. More rapid the flight, greater automatic supply of air occurs through lungs.

Violent action in mammals interferes with respiration, but in birds it increases it. It is why fast flying birds do not "get out of breath" or suffer from" mountain sickness" in high altitudes because necessary increased wing stroke bring in a compensatory supply of rarefied air.The frigate bird, Fregata, (maintaining a rate of 100 miles/hour) has about best development of air sacs to be found in any bird.

Mammals:-

In mammals both nasal and oral breathing is possible by backward migration of glottis to a position in posterior region of throat.

In reptiles, secondary plate starts its formation, partly separating nasal passage from buccopharyngeal cavity. In crocodiles and mammals, secondary plate has become complete with the result internal nares open far back into pharynx near the opening of trachea. Nasal breathing, however, with greater facilities thus provided for warming and moistening inhaled air and added advantage of testing its quality by passing it over sensitive olfactory surfaces. Nasal breathing is better and more favored method among mammals generally.

Outstanding advance in breathing mechanism is provided by muscular diaphragm. Diaphragm when relaxed becomes arched. When contracts becomes flat, increasing space within thoracic cavity.Consequently atmospheric pressure from outside, forces air into lungs. Abdominal viscera within body cavity are crowded down bulging out the abdominal wall. Muscular opponents of diaphragm are strong walls of abdomen.

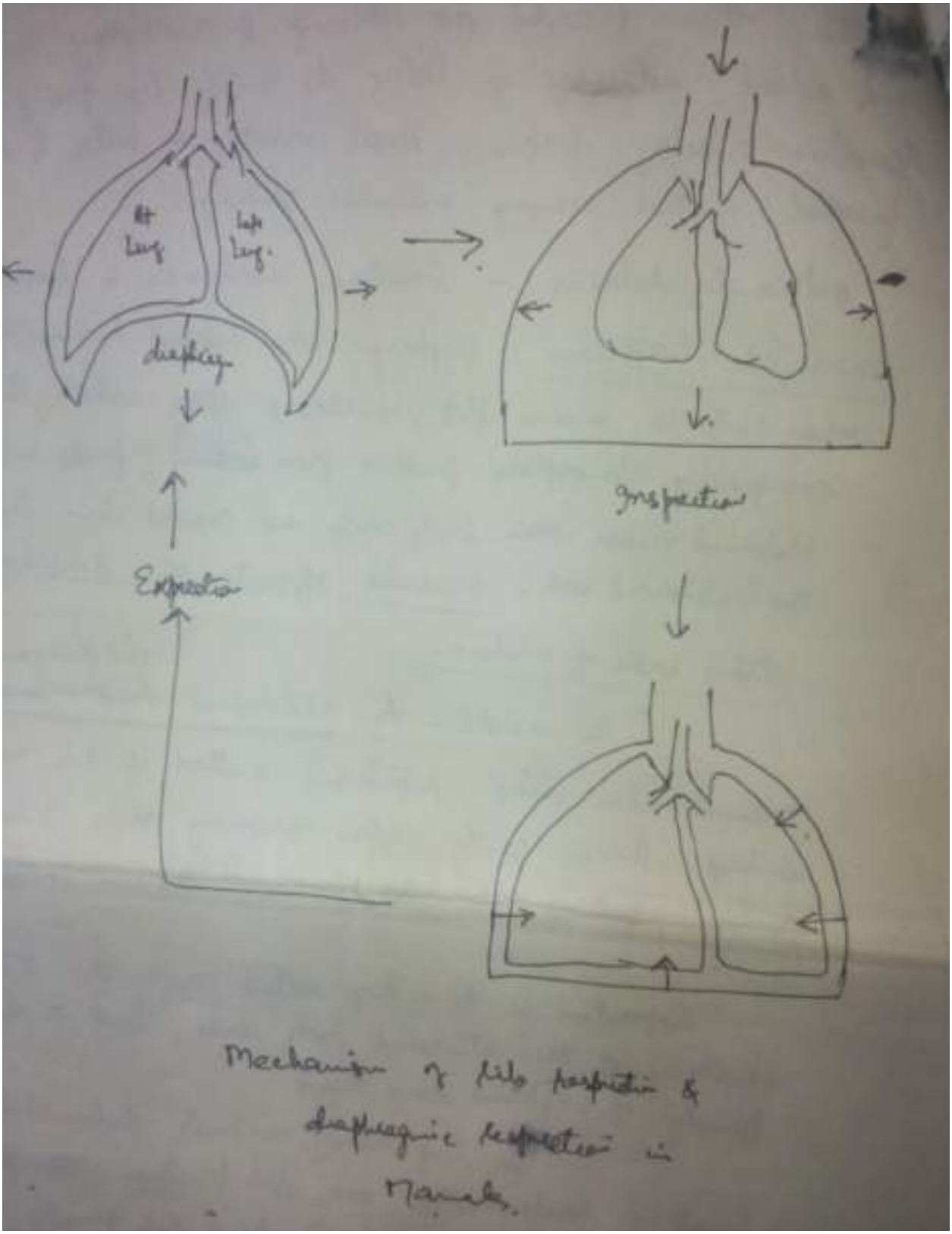
In addition to abdominal diaphragmic breathing, mammals also utilize reptilian method of rib muscles to enlarge thoracic cavity when inspiring air.Intercostal muscles contract, pulling out ribs, increasing spaces of thoracic cavity bringing in air.

Expiration is to a large extent automatic through the elasticity of the stretched body walls, taut ends of bent ribs tensity of expanded lung tissue.

In big heavy animals, abdominal or diaphragmic breathing predominates over rib breathing. Jumping animals (like kangaroos & monkeys) utilize rib muscles rather more than the diaphragm in respiration.

Breathing by ribs is more pronounced in human females than in males in whom abdominal breathing predominates. Reason for difference may be an evolutionary adaptation

brought about in connection with pregnancy, during which period presence of growing fetus interferes with freedom of movement of diaphragm.



Mechanism of Rib respiration & diaphragmic respiration in Mammals.

Mechanism of respiration in aquatic vertebrates:-

Cartilaginous Fishes:-

For breathing, external gill slits are closed, mouth is opened and buccopharyngeal floor is lowered. Because of reduced pressure, in buccopharyngeal cavity, water rushes in through the mouth.

Now mouth is closed, external gill slits are opened and buccopharyngeal floor is raised. This increases internal pressure, forces water through internal gill slits into gill pouches and thence to exterior via external gill slits.

During this process, oesophagus is kept closed to check entry of water into it.

Gill pouches themselves also help in maintaining a respiratory current by alternate contraction and relaxation of their intrinsic muscles in rhythm with buccopharyngeal movements. When passing through gill pouches, water washes the gills, bringing about exchange of gases.

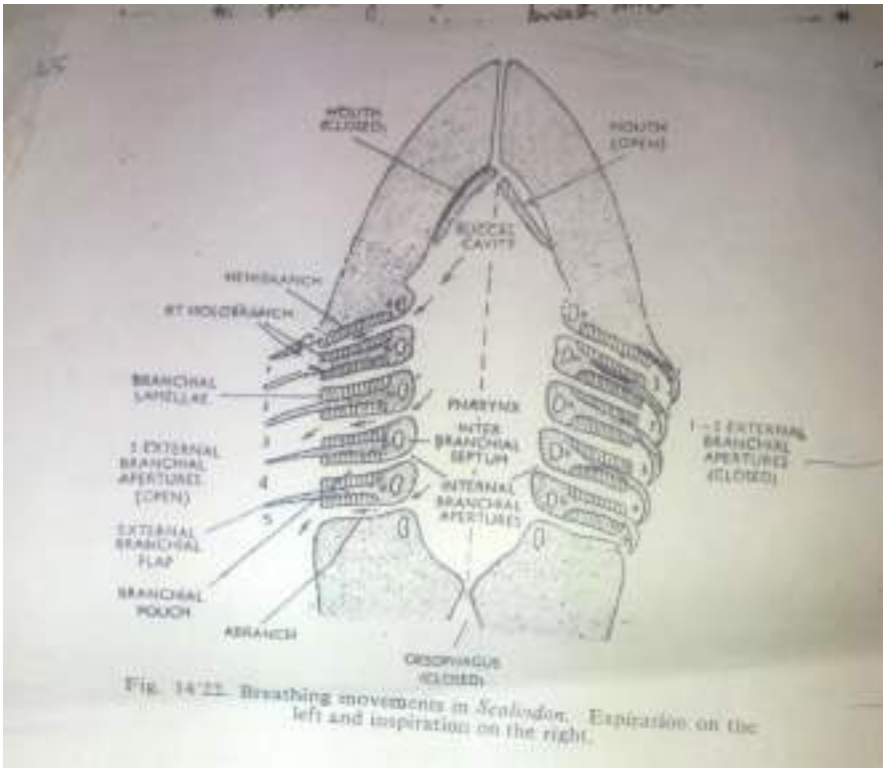


Fig. 14·22. Breathing movements in *Scoliodon*. Expiration on the left and inspiration on the right.

Bony fishes:-

Water enters mouth or spiracles & passes through gill slits. It is forwarded & directed not only by muscular movements which alternately expand and contract the walls of orobranchial chamber, but by a system of valves that prevent water from going the wrong way.

Anterior set of valves are along inner edge of mouth opening, those of upper edge (maxillary) and of lower edge (mandibular). Posterior set of valves, (branchiostegal) are membranes along free margins of opercular flaps.

Anterior set of valves lie flat, mouth opens & posterior set of valves close. Walls of orobranchial chamber spread apart by muscular action, pulling water into mouth to occupy increased space . Then valves reverse, anterior ones close and posterior ones open, chamber cavity squeezes forcing water over gills and out of opercular openings.

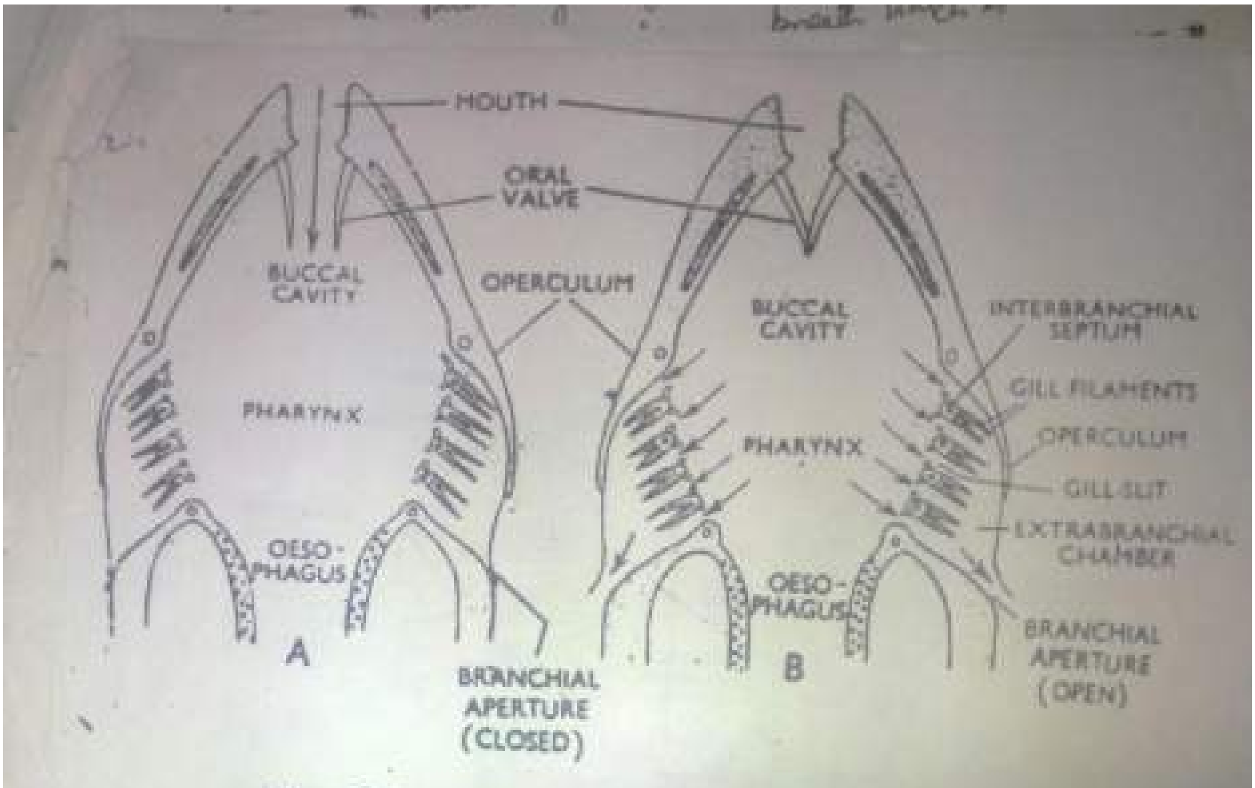


Fig. . Respiratory mechanism in a bony fish.

Aquatic Amphibians:-

Necturus and other urodels have external gills hanging freely. They are in direct contact with water and exchange of gases occurs in them without any effort on the part of animal.

Necturus& other perennibranchateurodels sometimes come to surface of water and gulp air through mouth, which soon escapes through gill slits in the form of bubbles, although it is doubtful whether much of it reaches the lungs. This occasional air – gulping behavior does not furnish fresh air for external gills having outside gill slits. Since they are waved back and forth by muscles to obtain supply of dissolved O2 in water.

Aquatic Reptiles:-

Alligators have elongated nasal passage – way with velum, that closes off the internal nares from mouth cavity . This device helps alligator to breath with mouth open under water while holding the drowning prey between the cavernous jaws, only the tip of the snout with the opening of the external nares being above water line.

Aquatic Mammals:-

Lungs of whales are located rather posteriorly. They are hydrostatic as well as respiratory. They have unique breathing apparatus. They imprison air in the capacious nasal chamber, which occupies major part of whales head and is capable of storing a generous supply of air (which would otherwise be forced out by lungs by enormous pressure of water).

Apertures leading from nasal passage to lung can be shut off by 2 plugs of tissue which function like stopper. As air in lungs becomes stale, plugs open long enough to exchange stale air with pure air in nasal reservoir. When whale comes to surface, reservoir is emptied with considerable violence accompanied by condensation into a thick cloud with coller air outside. Cloud ascends to height of 365 cm and can be seen from a long distance. This phenomenon is called blowing or spouting.

Unit 2

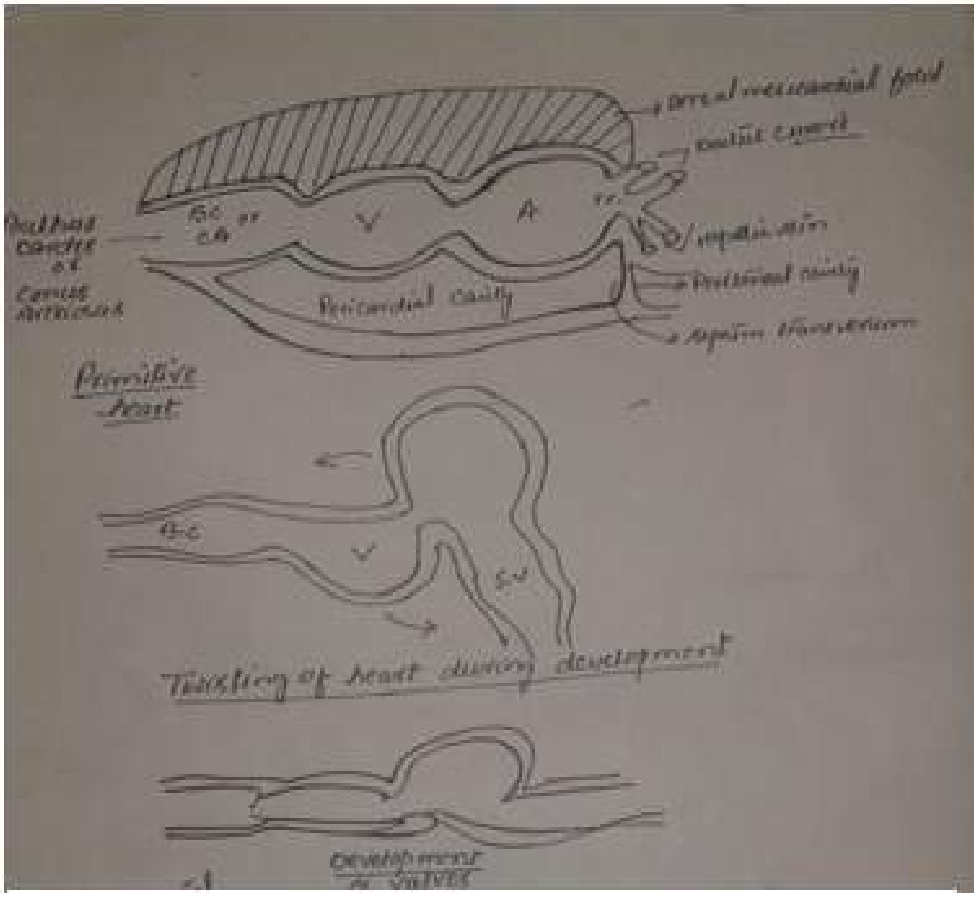
Heart

Heart of chordates differ from those of lower phyla in their ventral location.

The heart lies in the pericardial cavity a subdivision of coelom anterior to septum transversum and lies suspended in the cavity by dorsal mesocardial fold which disappears later on.

Heart is really a modified blood vessel, like other blood vessels. It is lined with an endothelium – endocardium. This is surrounded by a muscular layer, myocardium- composed of peculiar cardic muscle tissue. Outside the myocardium lies epicardium or visceral pericardium.

Heart when first formed in embryo is a simple tube. The appearance of constrictions, folds and partitions of one kind or another results in the formation of 2, 3,4 – chambered hearts, as the case may be.



Comparative anatomy

In Amphioxus, heart is absent but a ventral blood vessel extending between liver diverticulum and gills is contractile enough to pump blood into various body organs. First step towards differentiation of heart is seen in ammocoete larva of Peteromyzon. Ventral aorta lying between liver and gills is somewhat enlarged, thickened and constricted. It consists of an atrium and a ventricle. Conusarteriosus is absent

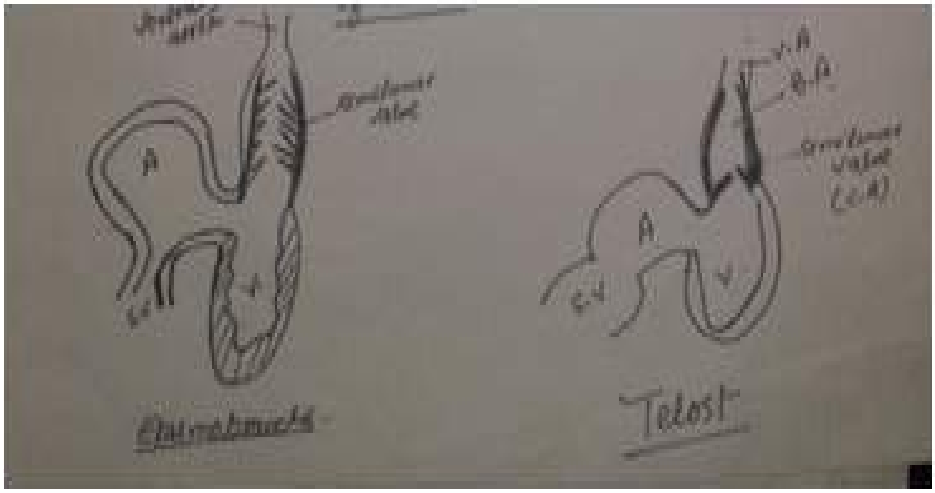
Fishes:

Heart is relatively small consisting a series of four compartments, sinus- venosus, atrium, ventricle and conusarteriosus (Bulbuscordis in embryo). First two are receiving parts having thin and elastic walls. Ventricle is a pumping structure having thick and muscular walls conusarteriosus has moderately thick walls and its elasticity regulates backward flow into ventricle. Deoxygenated blood received from body by heart is pumped into gills for aeration.- thus blood passing only once through heart – Single circuit or Brachial heart.

In elasmobranches semi lunar valves in C. arteriosus (which prevent backflow of blood into heart) are numerous arranged in three longitudinal rows, several in each row. However, there is reduction in number of valves.

In Teleostsconus has a single row of semi lunar valves.Ventral aorta here is drawn into pericardial cavity. It develops thick muscular walls and is without valves – known as Bulbosus- arteriosus (B. arteriosus).

In lung fishes, inter auricular septum divides atrium into right and left auricle. It is incomplete because auricles are intercommunicated by an aperture, Foramanovale. Ventricle is also partly divided. This heart is called transitional heart. Due to incomplete partition mixing of blood is not avoided.



Amphibia

Two streams of blood (oxygenated and deoxygenated) enter heart –double circuit heart .Here sinus venosus also occupies dorsal position receives ducts-cuvieri (precavels) from upper side and post Vena cava from behind.

Inter- auricular septum complete and foramanovale is absent. Ventricle is not partioned but its lining is thrown into many pockets by muscular bands, which to some extent prevent mixing of blood. From the ventricle arises a tubular Truncusarteriosus(T. arteriosus). The opening of which is guarded by three semi lunar valves.

T. arteriosus is formed of basal thick C. arteriosus and distal thin Walled ventral aorta . Its C. arteriosus part which is next ventricle is Pylangium and distal ventral part is Synangium. Distal end of Pylangium is provided with a row of semi lunar valves. One of these is modified to form spirally twisted spiral valve dividing cavity of C. arteriosus into two passage- Dorsal and left cavumpulmocutaneum and ventral right cavumaorticum , both of which communicate with ventral aorta. At its anterior end, Synangium divides into two trunks each having a Carotid arch, systemic arch and pulmonary arch.

Reptiles

Sinus venosushas been reduced and incorporated within the wall of right atrium. Ventricle is partially divided by incomplete inter ventricular septum. In crocodiles it is complete.

Conus no longer exists as such and has splitted at its base into three main trunks , each of which has a single row of semi- lunar valves at its base.

Three trunks are – Pulmonary Aorta going to lungs leaving right side ventricle.

Two systemics right and left arising from left and right.

A small aperture of Foramanof Panizzae is present at a point where two systemics cross each other. Here some admixture of arterial and venous blood occurs. It is also present in crocodiles.

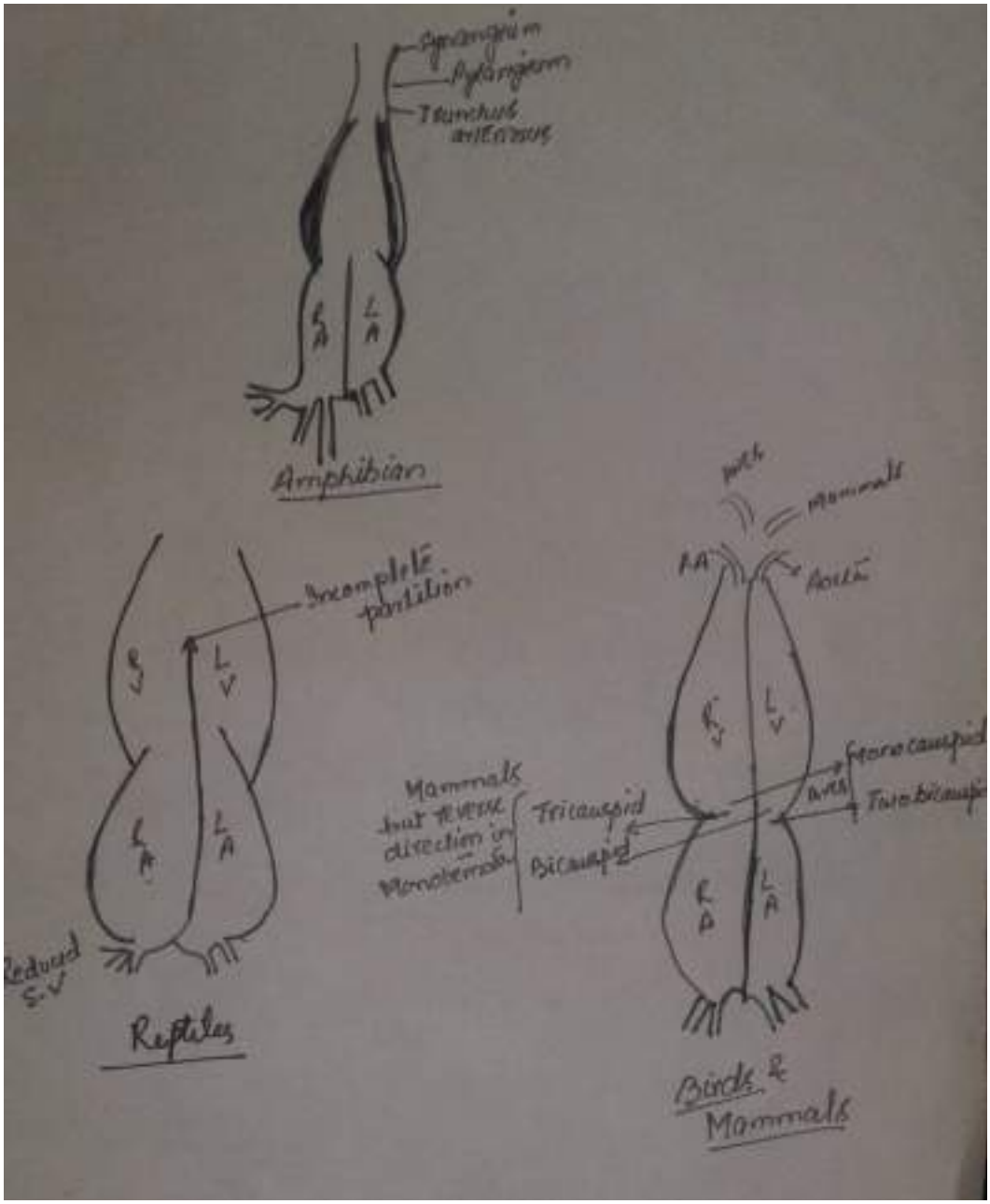
Aves and Mammals: Complete Double Circulation:

Sinus venosus is completely absorbed in right auricle, hence precavels and post cavels directly open into right auricles and their openings are guarded by valves.

Ventricles are completely separated, muscular wall of left being heavier than that of right. A single valve (monocuspid) separates right atrium from right ventricle and two (bi cuspid or mittral valve) present at the left atrio-ventricular aperture inaves. In mammals right aperture is guarded by tricuspid valve, while left one is guarded by bicuspid valve, but in monotremes tricuspid valve is on left side and bicuspid on right side.

Systemic aorta arises from left ventricle in both groups. In aves it goes on right side forming right systemic, while in mammals it goes on left side forming left systemic.

In mammals venous coronary blood is returned through several vessels which enter the right auricle through coronary sinus guarded by valve of Thebesius. Coronary sinus is situated between openings of post caval and atrio-ventricular opening. Other small openings foramina of Thebesius bring blood to right atrium directly from heart muscle.



Conclusions:

Thus, we see that in the development of heart, there is progressive separation of oxygenated and deoxygenated blood with the introduction of lungs to share in respiratory processes; heart begins to divide into arterial and venous halves. Hence main evolutionary trend has been that the heart of vertebrates has passed through a series of changes form a single circuit heart of fishes to a complete double circuit of mammals.

Aortic Arches

From the heart runs forward a blood vessel i.e. Ventral aorta from which arises a number of blood vessels – Aortic arches. The blood vessels run upwards to lateral to pharynx

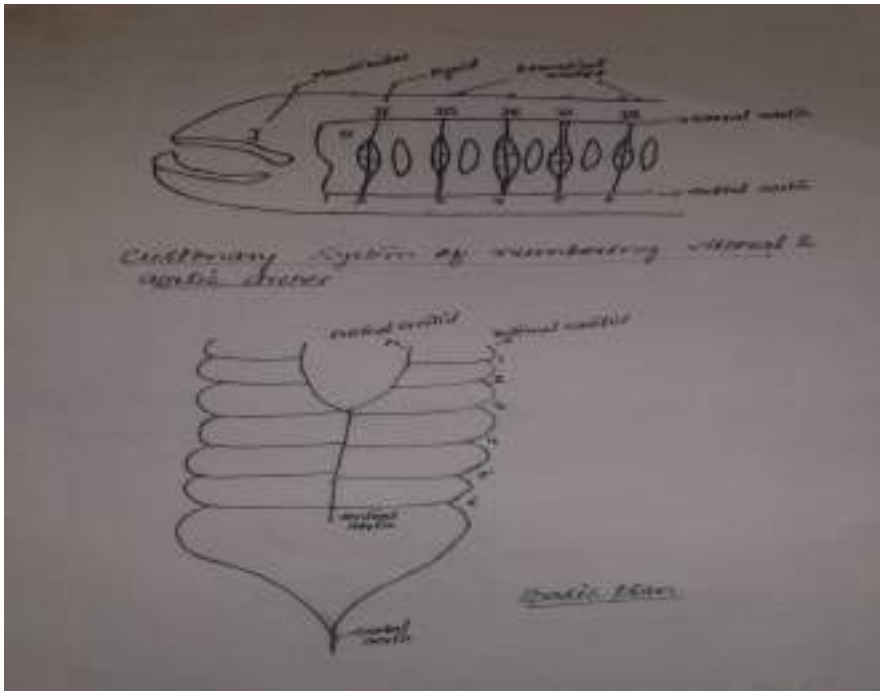
and finally open into a blood vessel on their side- radix aorta. There are two radices aortae dorso-lateral to pharynx and runs backwards and after the pharyngeal region they join to form dorsal aorta.

Origin of theses aortic arches can be traced back to cephalochordates like Branchiostoma where number of aortic arches is 60 pairs. In Cyclostomes like Bdellostomastouti number of aortic arches is 15 pairs .

In majority of vertebrates during their embroyonic stage there are 6 pairs of aortic arches called as first pair or mandibular, 2nd or hyoid, 3rd,4th ,5th and 6th pairs of aortic arches as Ist, 2nd 3rd,4th branchial arches respectively. This is only hypothetical stage because in no adult vertebrate there are six pairs of aortic arches as their number gets reduced. Diversity is mainly due to two factors

(1) Change in respiratory organs from gills to lungs

(2) Increase in complexity in heart from two to four chambered condition



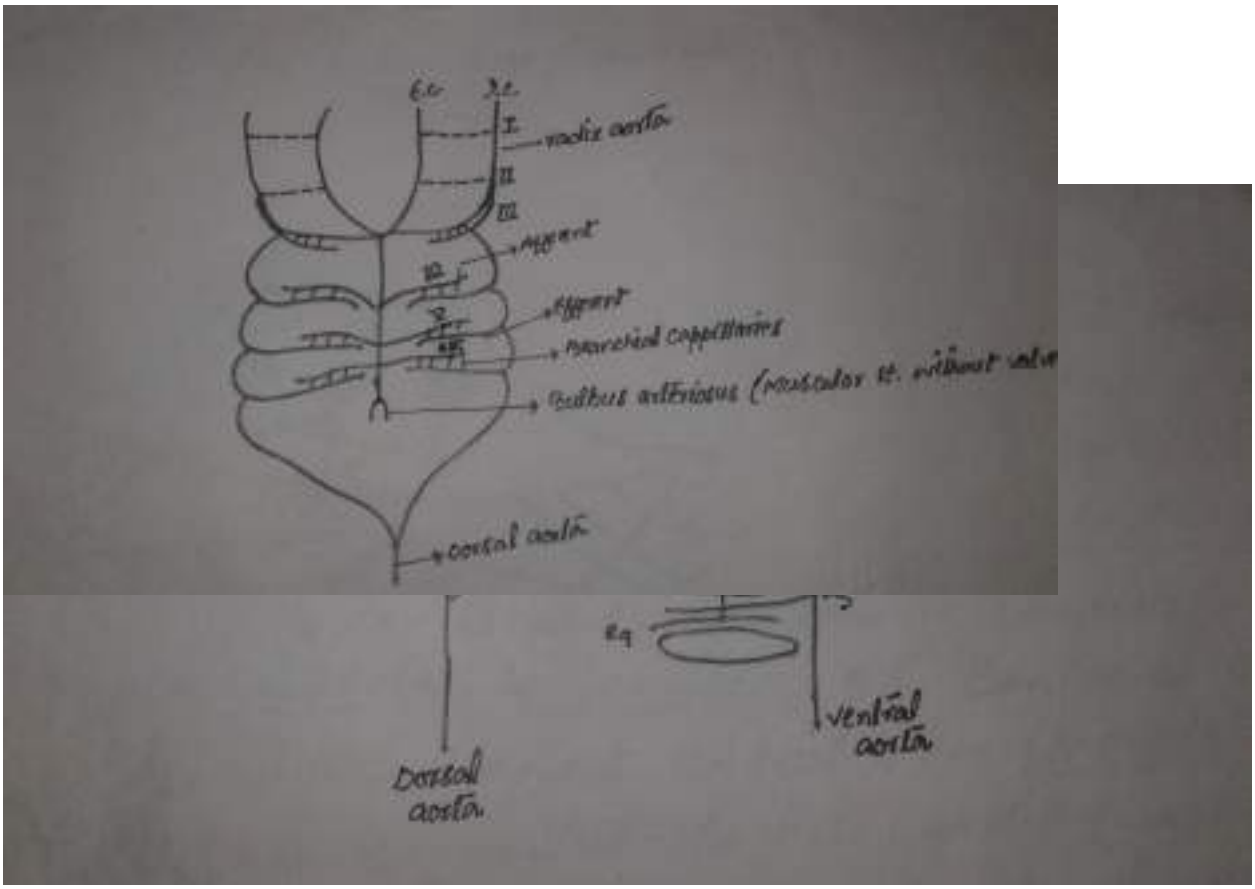
Pisces

Here each aortic arch gets differentiated into 2 pairs i.e. afferent and efferent branchials. Afferent carries deoxygenated blood from ventral aorta to gills. Efferent collects oxygenated blood from gills. Anterior prolongation of ventral aorta acts as exterior carotid which bifurcates , similarly ant. prolongation of radix aorta acts as internal carotid.

Elasmobranches:

In primitive sharks (Heptanchus-7 gilled shark) 7 pairs of aortic arches are in adult. Six pairs are found in adult Sclachians (Hexanchus&chlamydoselachus).

In most cases Ist aortic arch is lost, rest 5 include 5 afferent brachials and 4 loops of efferent branchials.



Teleostomes:

Ist and 2nd pair lost. Size of ventral aorta gets reduced.

Dipnoi:

Similar pattern to teleosts except last aortic arch (6th) bears pulmonary artery supplying to swim bladder.

Amphibia:

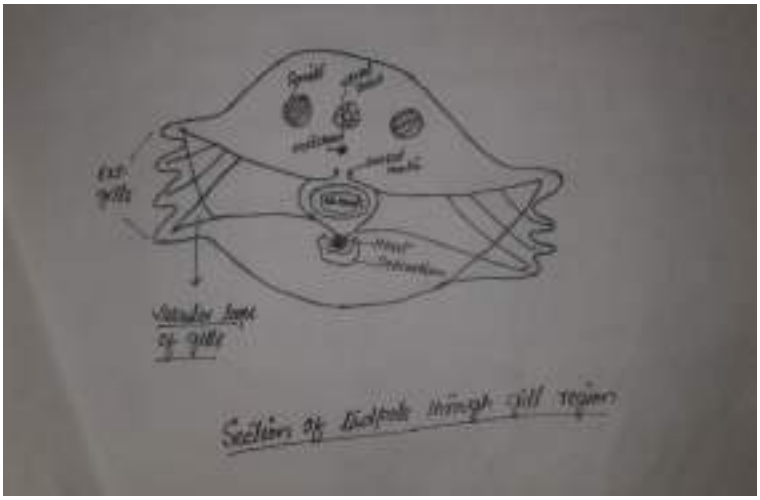
Majority of amphibians respire by gills in larval life, while by lung in adult stage. But Urodela retain gills in addition to lungs.

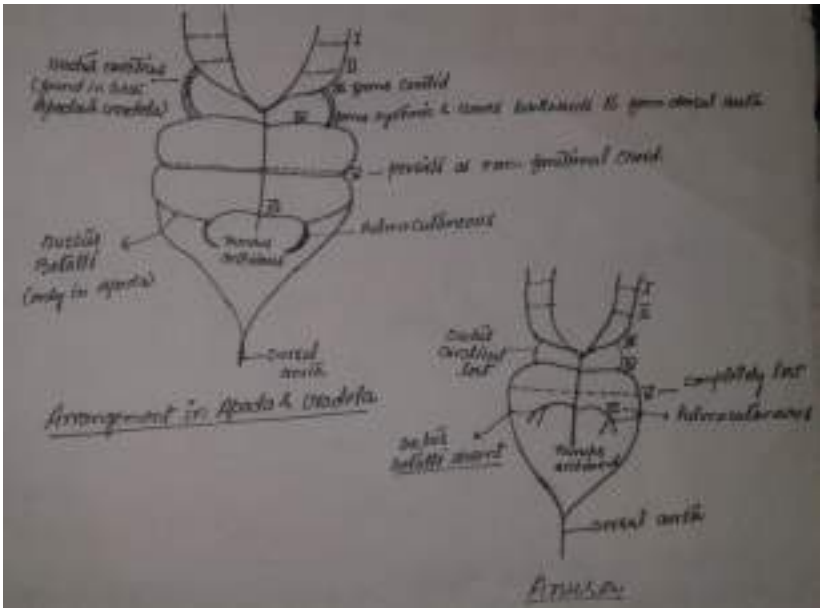
Ventral aorta is absent. However, truncusarteriosus can be said to represent a reduced ventral aorta.

In all amphibians Ist, 2nd pairs lost 3rd pair on its side differentiates into ext. and int. carotid. 4th acts as systemic curves backwards to form dorsal aorta, while 6th acts as pulmocutaneous arches.

In Anura, 5th pair is completely lost, while in Apoda and Urodela , 5th contracts and persists as non functional chord. In Urodela and Apoda 4th is connected to int. carotid (part of 3rd) of

its side by a small blood vessel- ductuscaroticus. In Apoda in addition to ductuscaroticus 6th is connected to 4th of its side by a small vessel – Ductusarteriosus/botalli.





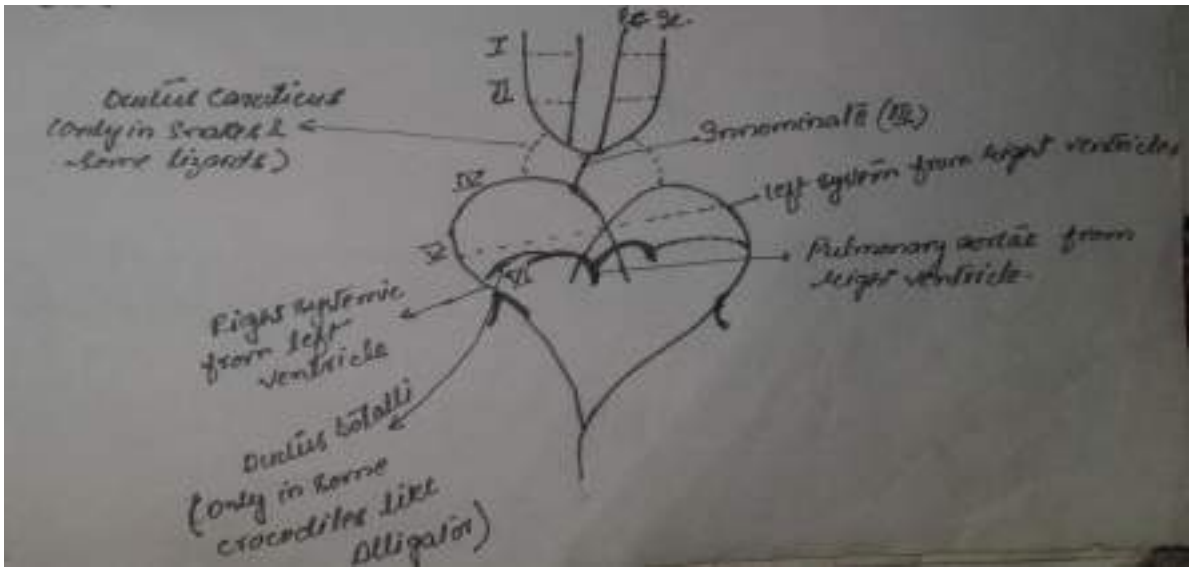
Reptilia

Respire by lungs, ventral aorta is totally lost. Aortic arches directly arises from heart. Ist, 2nd, 5th are completely lost .

3rd pair arises from right systemic from a common base cardio-primaria/innominate. Each carotid divided into ext. and int. carotoid on its side. 4th pair acts as systemic and they arise independently. At their crossing there are connected by a pore-foramen of panizzae, while posteriorly systemics join to form dorsal aorta. 6th acts as pulmonary.

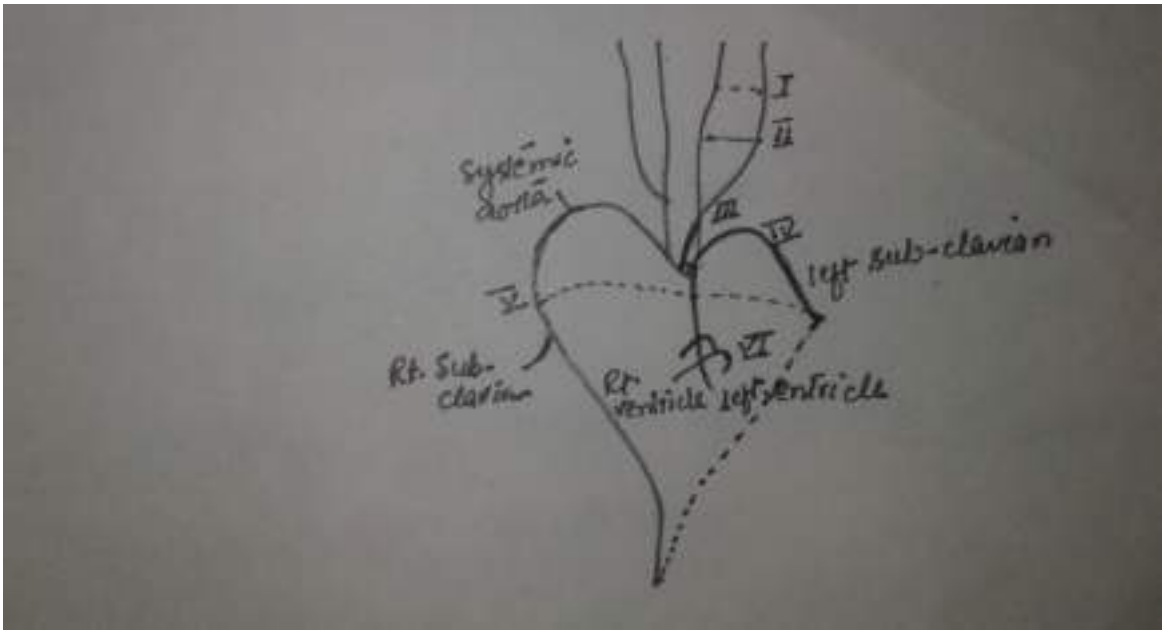
Ductuscaroticus disappears but persists in snakes and some lizards.

In some crocodiles like alligator there is present ductusarteriosus (ductusbotalli).



Aves

Ist, 2nd , 5th lost. 3rd forms carotids. 4th of right side forms systemic aorta, part of 4th of left side form left sub- clavian rest along with its lateral dorsal aorta disappears .6th forms pulmonary aorta.

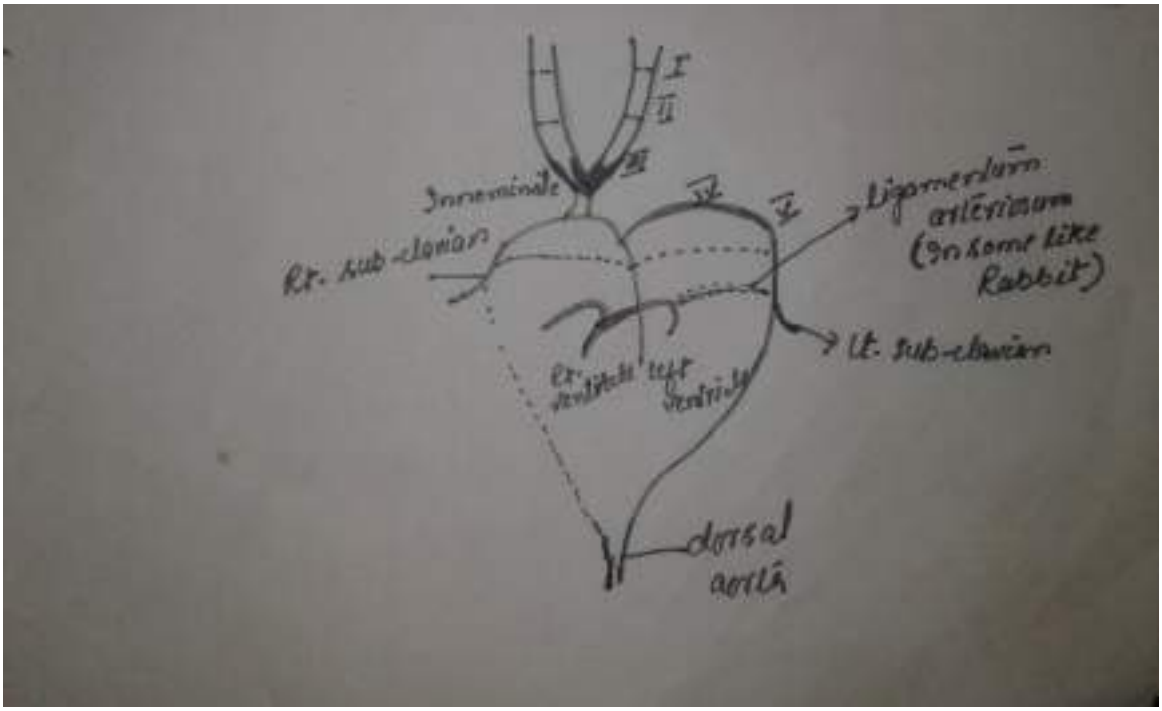


Mammals :

1st, 2nd , 5th lost. 3rd forms carotids

4th of left side arising from L. ventricle acts as systemic which forms dorsal aorta while on right side its proximal portion forms innominate and right sub-clavin, rest along with its lateral dorsal aorta disappears. 6th forms pulmonary aorta.

In some mammals (rabbit) 6th is connected to left systemic by ductusarteriosus which on the time of birth gets closed but persists as a chord- ligamentumarteriosum.



Conclusions:

We conclude that there is a progressive reduction of aortic arches in vertebrates. The original six pairs become variously modified, modification correspond with change in:

1. Respiratory habitat: brought about by transition from aquatic to terrestrial habitat.
2. Transition of heart from 2 chambered condition to 4 chambered condition.

UNIT 2

Comparative Anatomy

2.1

Evolution of Heart in Vertebrates: The heart is an unpaired organ but its origin is bilateral. In an embryo the mesenchyme forms a group of endocardial cells below the pharynx. These cells become arranged to form a pair of thin endothelial tubes. The two endothelial tubes soon fuse to form a single endocardial tube lying longitudinally below the pharynx. The splanchnic mesoderm lying below the endoderm gets folded longitudinally around the endocardial tube. This two-layered tube will form the heart in which the splanchnic mesoderm thickens to form a myocardium or muscular wall of the heart and an outer thin epicardium or visceral pericardium. The endocardial tube becomes the lining of the heart known as endocardium. Folds of splanchnic mesoderm meet above to form a dorsal mesocardium which suspends the heart in the coelom. Soon a transverse septum is formed behind the heart which divides the coelom into two chambers, an anterior pericardial cavity enclosing the heart and a posterior abdominal cavity. The heart is a straight tube but it increases in length and becomes S-shaped because its ends are fixed. Appearance of valves, constriction, partitions in the heart, and differential thickenings of its walls form three or four chambers in the heart. 1. Single-Chambered Heart: In Amphioxus (primitive chordate), a true heart is not found. A part of ventral aorta beneath the pharynx is muscular and contractile and acts as heart.

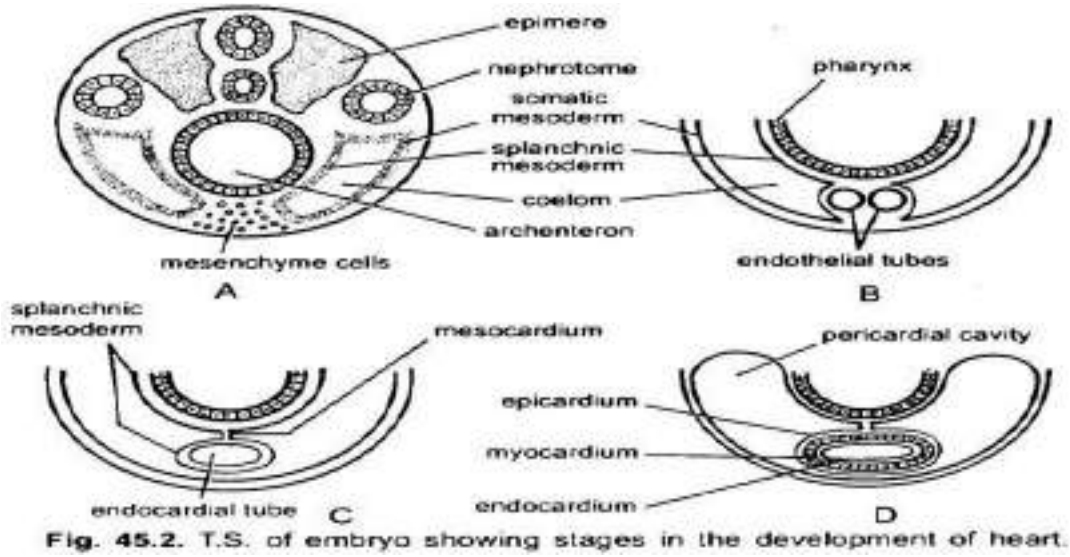


Fig. 45.2. T.S. of embryo showing stages in the development of heart.

2. Two-Chambered Heart: In cyclostomes, there are four chambers arranged in a linear order- a thin-walled sinus venosus, a slightly muscular atrium (auricle), a muscular ventricle and a muscular conus arteriosus or bulbus cordis. It lies in the body cavity in which other visceral organs are also present. Out of four chambers, only atrium and ventricle correspond to the four chambers (paired atria and paired ventricles) of the higher vertebrates. In the evolution of heart many changes have taken place. Elasmobranchs: Except Dipnoi, the circulatory system in fishes from cyclostomes to teleosts, only unoxygenated blood goes to the heart, from there it is pumped to the gills, aerated and then distributed to the body. The heart of cartilaginous dogfish is muscular and dorsoventrally bent S-shaped tube with four compartments in a linear series. They are sinus venosus and atrium for receiving venous blood, and a ventricle and conus arteriosus for pumping this blood. The heart is a branchial venous heart. The sinus venosus and conus arteriosus are accessory chambers. Atrium and ventricle are true chambers, thus, it is a 2-chambered heart. The sinus venosus opens anteriorly into atrium through sinu-atrial aperture guarded by a pair of valves. Atrium lies dorsal to ventricle and opens ventrally into ventricle through an atrio-ventricular aperture guarded by a pair of valves. The thick-walled, muscular ventricle opens into a narrow conus arteriosus containing valves in two series.

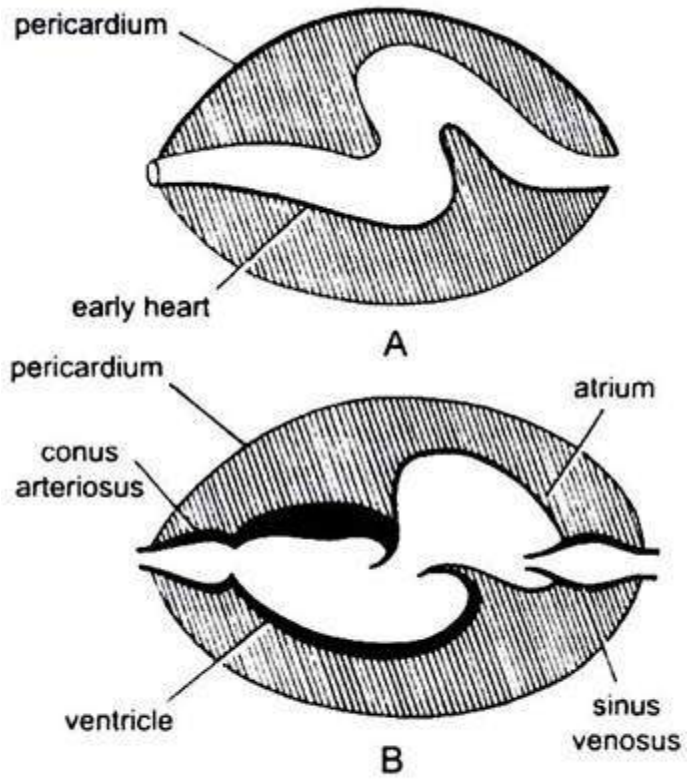


Fig. 45.3. Stages in the formation of heart.

The heart is enclosed within pericardial cavity separated from body cavity by a transverse septum. Conus pierces the pericardium and becomes continuous with the ventral aorta. Pericardial cavity communicates with the body cavity through two perforations in the transverse septum. Teleosts: Their heart resembles to that of clasmobranchs. In teleosts, the conus is reduced and has a single pair of valves. The proximal part of ventral aorta close to conus becomes greatly enlarged and thick-walled, called bulbus arteriosus. It is elastic and dilates at the time of ventricular contraction. The heart is, thus, 2-chambered with a single circulation of blood. 3. Three-Chambered Heart: c: In diphoans a septum divides the atrium into a right and left chamber. This is correlated with the use of the swim-bladder as an organ of respiration and represents the first step toward the development of the double-type circulatory system whereby both oxygenated and unoxygenated blood enter the heart and are kept separate. Blood from right auricle of the lungfish passes into the right ventricle and is then pumped into the primitive lung-like gas bladder by pulmonary arteries which branch off

from the sixth pair of aortic arches. The oxygenated blood returns to the left atrium by way of pulmonary veins like amphibians.

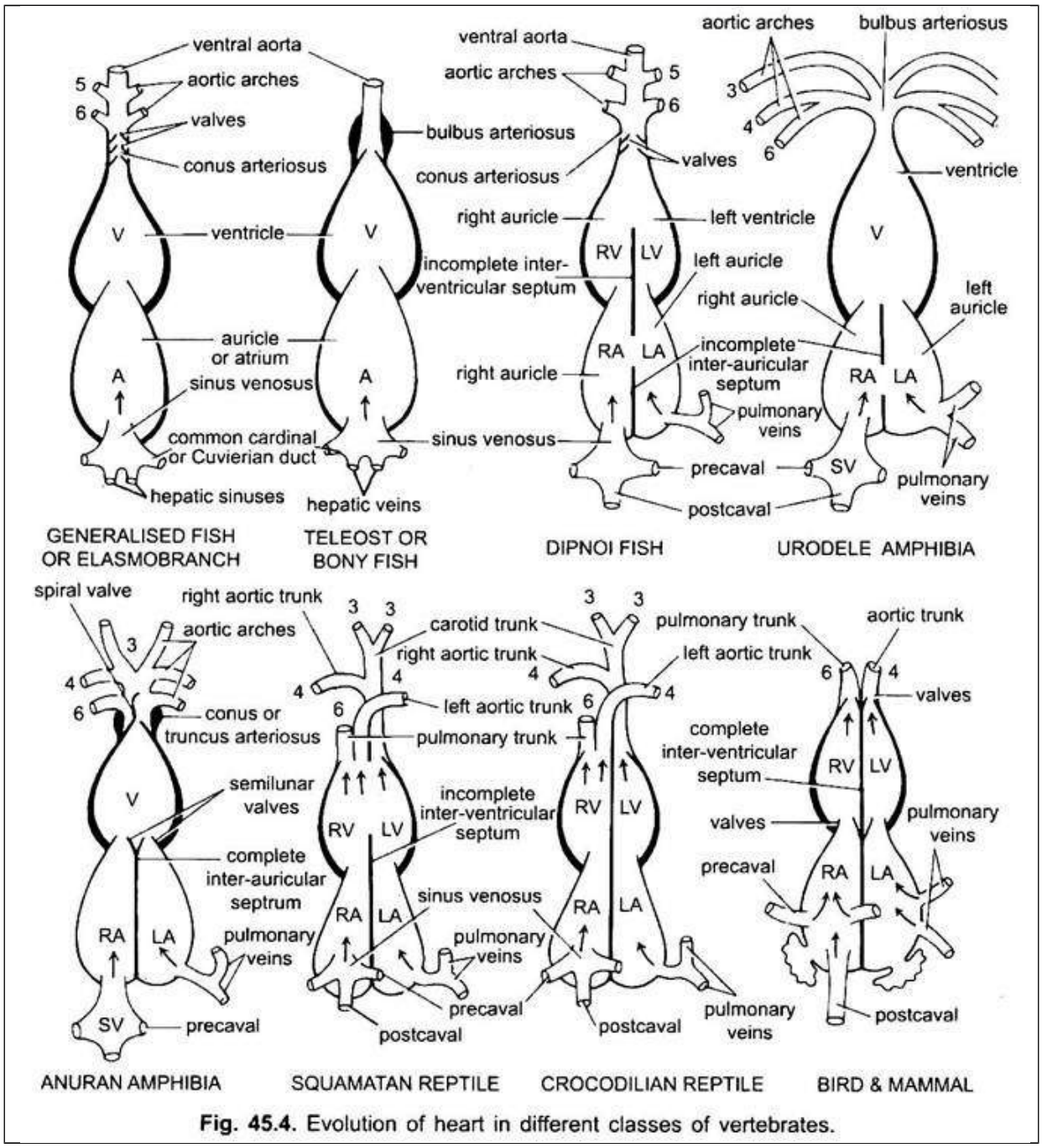


Fig. 45.4. Evolution of heart in different classes of vertebrates.

Amphibia: In amphibians, the dorsal atrium shifts anterior to ventricle. The sinus venosus opens into right atrium dorsally and not posteriorly. The atrium is completely divided into right and left chambers and has no foramen ovale in the inter-auricular septum, which remains open in dipnoans. Deep pockets develop in the ventricular cavity. The conus arteriosus divides into systemic and pulmonary vessels by a spiral valve. In lung less

salamanders, the interatrial septum is incomplete and pulmonary veins are absent. Reptilia: In reptiles, the heart is further advanced. The atrium is always completely separated into a right and left chamber, and in many forms the sinus venosus is incorporated into the wall of the right atrium. The ventricle is also partly divided by a septum in most reptiles, and in the alligators and crocodiles is completely two-chambered. This means that oxygenated blood coming from the lungs to the left side of the heart is essentially separated from the non-oxygenated blood from the body to the right side. Thus, in crocodilians, the two types of blood is completely separated, and nearly complete in other reptiles, but some mixing does occur in other parts of the circulatory system. The embryonic conus arteriosus splits into three instead of two vessels: (i) Pulmonary arch carrying blood to the lungs from right side of the ventricle. (ii) Right systemic aorta carrying blood from left side of the ventricle to the body by way of right fourth aortic arch. (iii) Left systemic comes from the right ventricle to the left fourth aortic arch. At the point of contact with the systemic aorta from the left ventricle, even in crocodilians, an opening between the two is present, called the foramen of Panizzae where there may be some mixing of the two types of blood. Thus, reptilian heart represents the transitional heart against amphibian heart-2 complete auricles and 2 incomplete ventricles with a little mixing of blood in right and left systemic. 4. Four-Chambered Heart: Aves and Mammalia: In birds, the ventricle is completely divided into two, so that the heart is four chambered (2 auricles and 2 ventricles). There is complete separation of venous and arterial blood. The systemic aorta leaves the left ventricle and carries blood to the head and body. While the pulmonary artery leaves the right ventricle and carries blood to the lungs for oxygenation. Thus, there is double circulation in which there is no mixing of blood at any place. The sinus venosus is completely incorporated into right auricle, which receives two precavals and a postcaval. The left auricle receives oxygenated blood through pulmonary veins, conus arteriosus is absent, the pulmonary aorta arises from the right ventricle, and single systemic aorta arises from the left ventricle, and both have valves at their bases.

Aortic Arches in Various Vertebrates

Modification in Fishes:

Branches from ventral aorta produce aortic arches, which divide into capillary beds within the gills. The part of the aortic arches delivering blood to the gills is called afferent branchial artery. From the dorsal end of the capillary bed arises another artery, called efferent branchial artery, which joins the dorsal aorta.

The capillary beds partially or completely encircle the gills and empty first into the collecting loop that joins the efferent artery. The first afferent artery, which is expected to supply first

pharyngeal slit, goes to a vascular sprout adjacent to the first pharyngeal slit. This vessel constitutes the afferent spiracular artery. The dorsal section of the first arch forms the efferent spiracular artery. The remaining aortic arches (II – VI) complete the circle. The external carotid artery arises embryo-logically from the anterior end of the ventral aorta and becomes associated with the collecting loop, to carry oxygenated blood to the lower jaw. The internal carotid artery supplying the brain, receives oxygenated blood from the first fully functional collecting loop (pharyngeal slit II) via the efferent branchial artery (II) (Fig. 2.44B).

Aortic Arches of Anamniotes and Some Derivatives

Modifications in Amphibians:

In amphibians, the first two aortic arches (I and II) disappear early in the development. The distribution pattern of other arches differs between larvae and metamorphosed adults. In most larval salamanders, the IIIrd to Vth aortic arches carry blood to the external gills, and the last aortic arch (VI) sprouts the pulmonary artery to the developing lung .During metamorphosis, the external gills are lost, but the aortic arches are retained as major systemic vessels.

The short section of dorsal aorta between aortic arches III and IV, termed the carotid duct, usually closes at metamorphosis. The section of neutral aorta between arches III and IV becomes the common carotid artery, which supplies the external and internal carotids.

The carotid body is an enlarged portion of the carotid artery that usually forms near the point at which the common carotids branch. Carotid body plays a role in sensing the gas content or pressure of the blood and may have some endocrine functions. The IV and Vth aortic arches constitute major systemic vessels that join the dorsal aorta. The Vlth aortic arch also joins the dorsal aorta, its last short section forming the ductus arteriosus. Shortly before joining the dorsal aorta, it gives off the pulmonary artery, which again divides into small branches to the floor of the mouth, pharynx, and oesophagus before actually entering the lungs.

In frogs, the larva has internal gills that reside on the last four aortic arches (III-VI), and the embryonic pulmonary artery comes out from Vlth arch. During metamorphosis internal gills are lost together with the carotid duct and all of arch V. The III, IV and VI arotic arches persist and expand to supply blood to the head, body and pulmonary circuits, respectively. The IIIrd arch becomes internal carotid. The anterior extension of ventral aorta becomes external carotid. The Vlth arch loses its connection to the dorsal aorta because the ductus arteriosus closes and becomes the pulmocutaneous artery.

Modifications in Reptiles:

The symmetrical nature of aortic arches of the embryo tends to become asymmetrical in adult. This feature appears first in reptiles and then birds and mammals. The III, IV and VI aortic arches persist in reptiles. Maximum modification occurs in arch IV.

During embryonic development, the ventral aorta splits to form the bases of three separate arteries leaving the heart — the left aortic arch, the right aortic arch and the pulmonary trunk. The left aortic arch (IV) and the curved section of the left dorsal aorta constitute the left systemic arch. The right systemic arch includes the same components of the right side of the body. The two systemic arches unite behind the heart to form the common dorsal aorta. The right systemic arch gives rise to many additional vessels than left systemic arch.

Aortic Arches of Amniotes

Modifications in Birds:

Only right systemic arch develops in birds. The bases of the right aortic arch (IV) and the adjoining section of the right dorsal aorta form the right systemic arch during embryonic development. The right aortic arch III and parts of the neutral and dorsal aortae contribute to form the carotids.

Modifications in Mammals:

Only three embryonic aortic arches persist in the adult mammals — the carotid, pulmonary and systemic arch Carotid and pulmonary arteries develop from same components as in case of reptiles.

The systemic arch arises embryo logically from the left IV aortic arch and left member of the paired dorsal aorta and therefore, is a left systemic arch in mammals. Development of subclavian arteries is peculiar — the left subclavian departs from the left systemic arch, while the right subclavian includes the right aortic arch (IV), part of the adjoining right dorsal aorta.

Portal system in vertebrates:

Portal system is the part of the venous system. A portal vein has its origin in capillaries and it ends in capillaries. The blood from the portal vein returns to heart through an intermediate organ. There are two types of portal systems in vertebrates – hepatic portal system and renal portal system. In hepatic portal system, capillaries from the gut unite to form hepatic portal veins, which again breaks up into capillaries in liver.

In case of renal portal system, the capillaries from the posterior part of the body unite to form renal portal veins, which, in turn, break-up into capillaries in the kidneys on their way

to heart. The renal portal system is present in all classes of vertebrates except mammals. Mammals have only hepatic portal system.

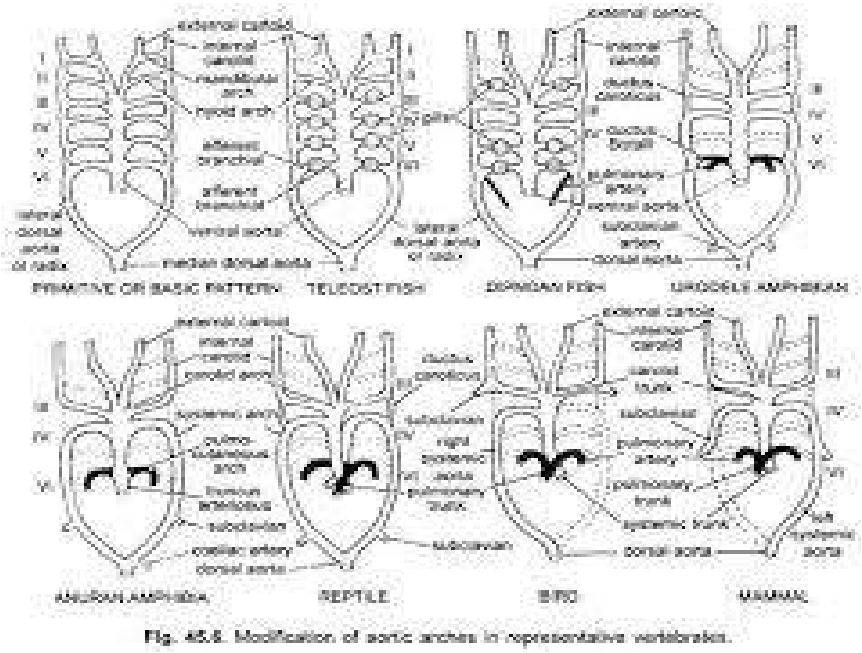


Fig. 45.6. Modification of aortic arches in representative vertebrates.

4.1. Comparative Account of Brain in Vertebrates:

Brain of all vertebrates, from fish to man, is built in accordance with the same architectural plan. However form of brain differs in different vertebrates in accordance with the habits and behaviour of the animals.

4.1.1. Cephalochordates:

In amphioxus, brain does not consist of forebrain, midbrain and hindbrain. Instead, the so-called brain is made of anterior prosencephalon or cerebral vesicle with a single enlarged ventricle. It is lined with cilia and long filamentous processes of ependymal cells as revealed by electron microscope. Anterior extension of notochord may suggest absence of a forebrain.

4.1.2. Cyclostomes:

Brain is very primitive. Subdivisions are not well marked. Two olfactory lobes are prominent, but cerebral hemispheres are quite small. Cavities of cerebral hemispheres or lateral ventricles are rudimentary. Pineal apparatus and parapineal body are very well

developed in Petromyzon, though they are vestigial in Eptatretus and absent in Myxine. Connected to pineal apparatus is epithalamus made of two habinulae ganglia. The two optic lobes are imperfectly differentiated. Medulla oblongata is very well developed while cerebellum is a small transverse dorsal band. A well defined infundibulum from hypothalamus of diencephalon bears a hypophysis or pituitary body.

4.1.3. Fishes:

Brain of fishes is more advanced than that of cyclostomes. However, subdivisions of brain are seen in their primitive relations.

4.1.3.1. Elasmobranchs:

In elasmobranches fishes (shark or dogfish), olfactory organs are enormous so that olfactory lobes of brain are correspondingly large, attached to cerebrum by short but stout olfactory tracts or peduncles. Optic lobes and pallium are relatively moderate in size. Midbrain cavity is quite large and extends into optic lobes. A thin walled sensory organ, called saccusvasculosus, is attached to pituitary and connected by fibre tracts with cerebellum. Pineal apparatus is well developed. Topographical features of hindbrain are least pronounced. Cerebellum is especially large due to active swimming habit. To assist cerebellum in the maintenance of equilibrium, ruffle like restiform bodies are present at the anterio-lateral angles of medulla.

4.1.3.2. Osteichthyes:

In bony fishes, brain is more specialized than in elasmobranches. In perch, olfactory lobes, cerebral hemispheres and diencephalon are smaller while optic lobes and cerebellum larger than in a shark. Some bony fishes have restiform bodies. In bottom-feeders, having scattered taste buds on body surface, the anterio-lateral sides of medulla show unusual bulging or vagal lobes. Parapineal body is absent in modern teleosts.

4.1.4. Amphibians:

Brain of frog shows many contrasts from that of dogfish. Smaller olfactory lobes and larger optic lobes indicate a greater reliance on sight rather than smell. Corpus striatum or paleostriatum (floor of cerebrum) receives greater number of sensory fibres projected forward from thalamus than in fishes. Two cerebral hemispheres show greater development in accordance with more complex activities of locomotion, hibernation, breeding etc. However, optic lobes are probably the dominant coordinating centres in amphibian brain. The walls of mid brain are thickened and reduce the lumen into a narrow passage called, aqueduct. Poor development of cerebellum, a mere transverse band, shows

relative decrease in muscular activity. Medulla is also small. A small pineal body is present in all the modern amphibians.

4.1.5. Reptilians:

Reptilians brain shows advancement in size and proportions over that of amphibians that of amphibians because of complete terrestrial mode of life. Telencephalon increases to become the largest region of brain. Two long olfactory lobes are connected to cerebral hemispheres which are larger than in amphibians because of greater thickness and enlargement of corpora striata. A fine vomeronasal nerve from the organ of Jacobson goes to the olfactory bulbs. Parapineal body, more often called the parietal eye, is still found in sphenodon and some modern lizards, but is vestigial or absent in other reptiles. A pair of auditory lobes is found posterior to optic lobes which are not hollow. The III ventricle is reduced to a narrow cerebral aqueduct. Cerebellum is somewhat pear shaped and larger than in amphibians.

4.1.6. Birds:

Avian brain is proportionately larger than that of reptile, and is short and broad. Olfactory lobes are small due to poor sense of smell. Two cerebral hemispheres are larger, smooth and project posteriorly over the diencephalon to meet the cerebellum. Pallium is thin but corpus striatum is greatly enlarged making lateral ventricle small and vertical. Third ventricle is also narrow due great development of thalami. Optic lobes on mid-brain are conspicuously developed in correlation with keen sight, but they are somewhat laterally displaced. The cerebellum is greatly enlarged with several superficial folds due to many activities involving muscular coordination and equilibrium such as flight and perching.

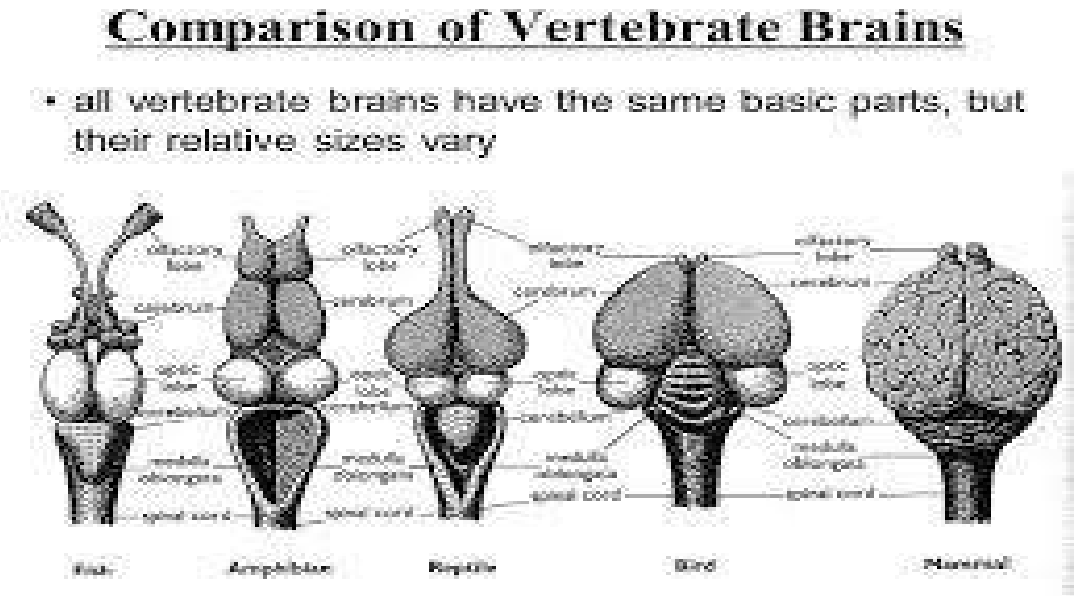
4.1.7. Mammals:

Parts of vertebrates brain in linear arrangement become progressively enlarged from fishes onwards until they reach their peak in mammals. Brain is proportionately larger than in other vertebrates. Cerebral hemispheres of prototheria are smaller and smooth, like those of reptiles. They are larger but smooth in metatheria. In higher mammals (Eutheria), cerebral hemisphere become greatly enlarged and divided into lobes, with thick cerebral cortex of gray matter. In mammals such as rabbit, the surface of cerebral hemispheres is relatively smooth with few fissures. In others, such as man and sheep, surface is immensely convoluted with a number of elevations (gyri) separated by furrows (sulci). This folding increases the surface cortex or gray matter containing nerve cells, resulting in greater intelligence without adding to the size of brain. The two hemispheres are joined internally by

a transverse band of fibres, the corpus callosum, not found in other vertebrates or even in Prototheria and Metatheria.

Olfactory lobes are relatively small but clearly defined and covered by the hemispheres. Diencephalon and midbrain are also completely covered by the cerebral hemispheres. Characteristic of mammals are 4 almost solid optic lobes, called corpora quadrigemina, on the roof of midbrain. The third ventricle or iter of mid brain is a laterally compressed vertical passage, called cerebral aqueduct.

Cerebellum is also large, conspicuously folded and may overlie both midbrain and medulla. Usual folds are a median vermis, two lateral flocculi and their mushroom like projections, the paraflocculi. The other chief topographical features of mammalian hindbrain include the pyramids carrying voluntary motor impulses from higher centres , the pons varoli with crossing or decussating fibres connecting opposite sides of cerebrum and cerebellum, and the trapezoid body of transverse fibres relaying impulses for sound. Hindbrain contains centres for the regulation of digestion, respiration and circulation.



2.2 Comparative Account of Kidneys and their ducts in Vertebrates:

Basic structure and origin:

Vertebrate kidneys are a pair of compact organs, lying dorsal to coelom in trunk region, one on either side of dorsal aorta. They are all built in accordance with a basic pattern. Each kidney is composed of a large number of units called uriniferous tubules or nephrons. Their number complexity and arrangement differ in different groups of vertebrates.

Kidney tubules arise in the embryo in a linear series from a special part of mesoderm called mesomere or nephrotome. It is the ribbon like intermediate mesoderm, running between segmental mesoderm (epimere) and lateral plate mesoderm (hypomere) on either side along the entire trunk from heart to cloaca. A uriniferous tubule is differentiated into three parts: peritoneal funnel, tubule and malpighian body.

Peritoneal funnel:

Near the free end of a uriniferous tubule is a funnel like ciliated structure called peritoneal funnel. It opens into coelom (splanchnocoel) by a wide aperture, the coelostome or nephrostome, for draining wastes from coelomic fluid. Nephrostomes are usually confined to embryos and larvae and considered vestiges of a hypothetical primitive kidney.

Malpighian body:

A tubule begins as a blind, cup-like, hollow, double walled Bowman's capsule. It encloses a tuft of blood capillaries, called glomerulus. It supplies blood by a branch of renal artery called afferent glomerular arteriole. An efferent glomerular arteriole emerges out of a glomerulus to join the capillary network surrounding the tubule.

Bowman's capsule and enclosed glomerulus together form a renal capsule or malpigh ıich are common. Those e called external glomeru omerular, such as found ı

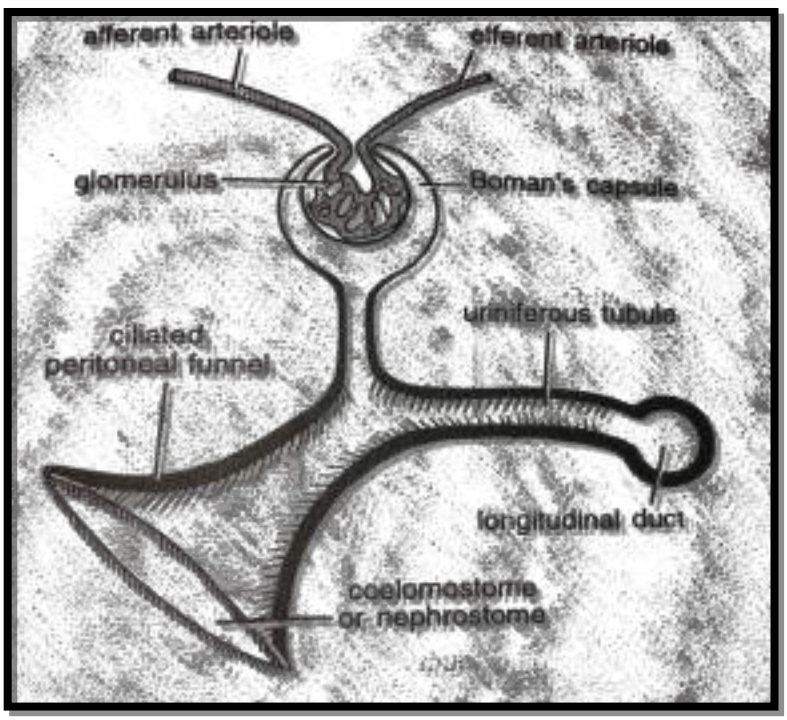


Fig. 1. Structure of an embryonic kidney tubule

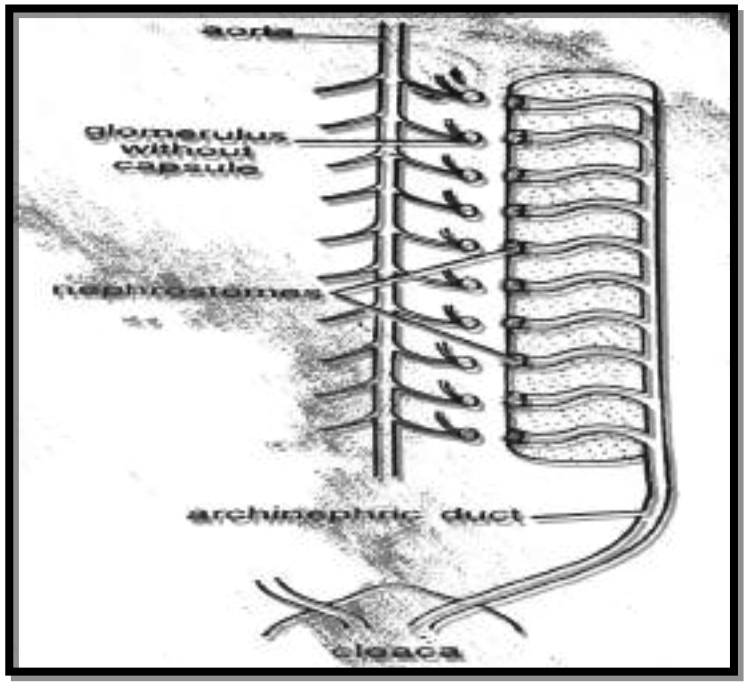


Fig. 2. Hypothetical primitive ancestral vertebrate kidney (Archinephros)

Tubule:

Malpighian bodies filter water, salts and other substances from blood. During passage through tubules more substances are secreted into filtrate, while some are reabsorbed. All the tubules of embryonic kidney are convoluted ductules that conduct the final filtrate to a longitudinal duct which opens behind into embryonic cloaca.

Archinephros:

Archinephros is the name given to the hypothetical primitive kidney of ancestral vertebrates (Fig. 2). It may be regarded as a complete kidney or holonephros as it extended the entire length of coelom.Itstubuleswere segmentally arranged , one nephrons for

each body segement. Each tubule opened by a peritoneal funnel, or nephrostome into coelom. Near each nephrostome was suspended in coelom an external glomerulus (without capsule). All the tubules were drained by a common longitudinal wolffian or archinephric duct opened behind into cloaca.

Such a hypothetical archinephros is found today in the larvae of certain cyclostomes (Myxine), but not in any adult vertebrate. It is supposed to have given rise to all the kidneys of later vertebrates during the course of evolution. Modern vertebrates exhibit three different types of adult kidneys: Pronephros, Mesonephros and Metanephros. It is supposed that these represent the sequence or three successive stages of developement of the ancestral archinephros, and all the three are never functional at the same time.

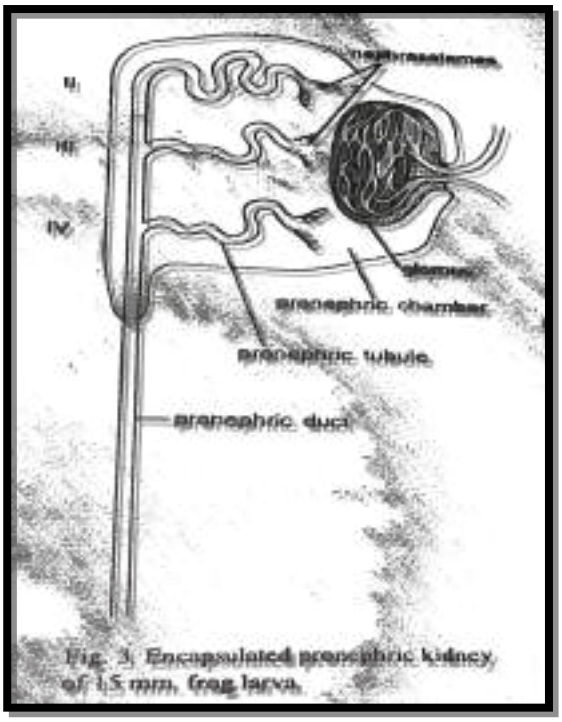


Fig. 3. Encapsulated pronephric kidney of 1.5 mm. frog larva.

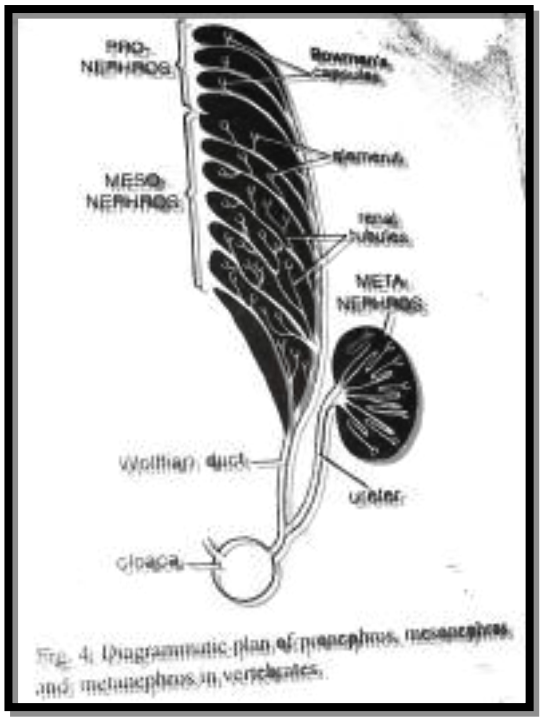


Fig. 4. Diagrammatic plan of pronephros, mesonephros and metanephros in vertebrates.

4.2 ant the call (Fig. 3). Pronephros is also termed head kidney due to the anterior position immediately behind the head. A pronephros consists of 3 to 15 tubules segmentally arranged, one opposite each of the anterior mesodermal somites. There are only 3 pronephric tubules in frog embryo, 7 in human embryo and about a dozen in chick embryo. Each tubule opens into coelom by a funnel or nephrostome. Also projecting into coelom near each tubule and not connected with it is an external or naked glomerulus without capsule. In some cases, glomeruli unite to form a single compound glomerulus, called glomus. Glomus and tubules become surrounded by a large pronephric chamber derived from pericardial or pleuroperitoneal cavity. Originally each tubule has its individual external aperture, but secondarily all tubules of a pronephros open into a common pronephric duct, leading posteriorly into the embryonic cloaca.

Pronephros is functional, if at all, only in embryonic or larval stage. It is mostly transitory and soon replaced by the next stage or mesonephros. However, a pronephros is retained throughout life in adult cyclostomes and a few teleost fishes, but it is non urinary and mostly lymphoidal in function.

Mesonephros:

In the embryo, a mesonephros develops from the middle part of intermediate mesoderm, posterior to each pronephros soon after its degeneration (Fig. 4). At first, the new mesonephric tubules join the existing pronephric duct and segmentally disposed. Later on the tubules multiply by budding so that their segmental arrangement is disturbed due to increased number of tubules per segment. Tubules of pronephros and mesonephros develop similarly and are homologous. However, mesonephros is functionally better than pronephros because mesonephric tubules are more numerous, longer and develop internal glomeruli enclosed in capsule forming Malpighian bodies. Thus, they remove liquid wastes directly from glomerular blood rather than indirectly from coelomic fluid as in case of a pronephros. The mesonephros is also termed Wolffian body. With disappearance of pronephros the old pronephric duct becomes the Wolffian or mesonephric duct.

In amniotes (reptiles, birds and mammals), mesonephros is functional only in the embryos, replaced by metanephros in the adults. In fishes and amphibians, mesonephros is functional both in embryos as well as adults. In sharks and caecilians, tubules extend posteriorly throughout the length of coelom. Such a kidney is sometimes called a posterior kidney or opisthonephros. Whereas in adult anurans, urodeles and embryonic amniotes, the mesonephros does not extend posteriorly. Mesonephric kidney is not metameric, but in myxinoids it is segmental and sometimes called holonephros. Nephrostomes are generally lacking in mesonephros of embryonic amniotes.

Metanephros:

The functional kidney of higher vertebrates or amniotes is a metanephros. It is formed from the posterior end of the nephrogenic mesoderm which is displaced anteriorly and laterally. When metanephric tubules develop all the mesonephric tubules disappear except those associated with the testis in male and forming vas efferentia. The adult kidney (metanephros) of amniotes differs from that anamniotes (mesonephros or opisthonephros) chiefly in:

- Its origin from only caudal end of nephrogenic mesoderm.

- In greater multiplication and posterior concentration of nephrons or tubules. They are particularly very large in number and highly convoluted in birds and mammals, hence the large size of kidney. It is estimated that each kidney of man is composed of about 1 million nephrons. The high rate of metabolism yields a large amount of wastes to be excreted.
- In developing a new urinary duct, called metanephric duct or ureter. It is budded off from the base of the wolffian duct (mesonephric duct). It grows anteriorly and dorsally, and eventually the metanephric tubules open into it. Its dilated distal tip forms pelvis which forks several times to become the collecting tubules. Its proximal portion becomes the metanephric duct or ureter that empties into cloaca or urinary bladder in mammals.
- The mammalian metanephrons shows greatest organization of all, with several additional features. A thin, U-shaped loop of henle forms between proximal and distal convolutions of metanephric tubule. Such loops are absent in reptiles and rudimentary in birds. Kidney shows an outer cortex with concentration of renal corpuscles, and an inner medulla having collecting tubules and loop of henle, which are aggregated into one or several pyramids tapering into pelvis. Mammalian kidneys do not receive afferent venous blood supply as there is no renal portal system.

Most vertebrates have a urinary bladder to store urine before it is discharged. However, it is lacking in cyclostomes, elasmobranches, some lizards, snakes, crocodilians and most birds. In most fishes it is simply a terminal enlargement of mesonephric ducts and called tubule bladder. In Dipnoi, it evaginates from dorsal wall of cloaca and is probably homologous to the rectal gland of elasmobranches. In tetrapods, it evaginates from the ventral wall of cloaca. In amniotes, the adult bladder is derived from the proximal part of embryonic allantois, hence called an allantoic bladder.

Kidney ducts or ureters generally open dorsally into cloaca. But in mammals, except monotremes, the ureter lead directly into the urinary bladder which opens to outside through a short tube, the urethra. Mammals lack a cloaca as the dorsal part of embryonic cloaca forms the rectum and ventral part becomes the urethra.

Comparative Account of gonads and their ducts in Vertebrates:

Reproduction is sexual in vertebrates, and the sexes are separate (dioecious) with the exception of hagfishes and a few bony fishes having a hermaphrodite gonad. Reproductive glands or gonads of males are called testis which produce the male gametes called sperm. Female gonads are called ovaries which produce ova. In the embryo, gonads originate as pair of thick elevated folds or genital ridges of coelomic epithelium from the roof

of coelom, one on either side of the dorsal mesentery. Genital ridges are much longer than the functional adult gonads, suggesting that in the ancestral vertebrates the gonads extended the whole length of the pleuroperitoneal cavity. The functional adult gonad is derived from the middle or gonal part of genital ridge, while its anterior progonal and posterior epigonal parts remain sterile. Gonads remain suspended in coelom from dorsal body wall by a fold of dorsal mesentery, called mesorchium in males and mesovarium in females. Generally, one pair of gonads is present. But, some vertebrates have a single gonad only because of either fusion of both embryonic genital ridges (most cyclostomes, perch and some other fishes), or degeneration of one juvenile gonad (hagfishes, some elasmobranches and lizards, alligators and most birds). Associated with the gonads are special gonoducts or genital ducts, vasa deferentia in males and oviducts in females, to transport gametes to cloaca or outside body. However, cyclostomes and a few elasmobranches lack genital ducts. Their eggs and sperm escape body cavity via abdominal pores.

Testis and male genital ducts:

Testis of vertebrates are paired organs of moderate size, usually found attached to kidneys. Each testis is a compact gland, covered by coelomic epithelium and composed of numerous highly coiled somniferous tubules embedded in connective tissue. Tubules are lined by germinal epithelium which gives rise to billions of sperms. On maturity the sperm are set free in the lumen of tubules and move towards the genital ducts.

Some cyclostomes have a single median testis without a genital duct. Sperms are released in the coelom from where they pass through abdominal pore, located at posterior part of coelom. In dogfish, the two testis are elongated bodies. In most anamniotes, the opisthonephros (or mesonephros) is differentiated into anterior genital and posterior renal portions. In the anterior genital portion in males, some uriniferous tubules lose excretory function, form slender vasa efferentia, and become continuous with seminiferous tubules of the adjacent testis. They serve to convey sperm of testis to the mesonephric duct of kidney. Thus, in male anamniotes, mesonephric or wolffian duct forms a urinogenital duct, serving both as a vas deferens for sperm as well as a ureter for urine. However, in many elasmobranches (e.g. dogfish), accessory urinary ducts drain urine from kidney to cloaca so that the mesonephric duct serves entirely or mainly as a vas deferens. The anterior genital part of kidney along with the part of mesonephric duct forms an epididymis.

In the embryos of Anura, each testis is made of two portions. In male frog, the anterior portion disappears and the posterior portion becomes the adult functional testis. In

adult male toad, the anterior portion also persists to the Bidder's organ, containing large cells similar to immature ova.

In male amniotes, a metanephros develops as the adult functional kidney with its own urinary duct or ureter to transport urine. Thus, mesonephric or wolffian duct becomes solely a genital duct or vas deferens. The remnants of embryonic mesonephros and a coiled portion of mesonephric duct become the epididymis of the adult kidney. From each testis sperms pass first through epididymis, then through vas deferens to reach urethra.

In most mammals testis descend permanently into extra abdominal skin bags called scrotal sacs. In rabbits, bats and rodents, they are lowered into sacs and retracted at will. Passage between abdominal cavity and scrotal sac, through which testis descends is called inguinal canal. However some mammals such as monotremes, insectivores, elephants, whales etc., lack scrotal sacs so that heir testis remain permanently intr-abdominal like ovaries.

Copulatory organs:

Copulatory organs are absent in anamniotes, since they have usually external fertilization. But, amniotes, fertilization is internal and preceded by copulation or mating. Male amniotes usually develop intromittant or Copulatory organs for transferring sperm into the genital tract of females, during copulation. They are particularly characteristic of reptiles and mammals.

In elasmobranches (e.g. dogfish), bases of pelvic fins are modified as intromittant organs called claspers. These are grooved, cylindrical structures that are inserted into the female cloaca to inject sperm. In dog fishes and allied forms there is a blind muscular sac called siphon, located at the base of claspers. This sac gets filled with sea water which is used to force the spermatic fluid into the cloaca of female. In several teleosts, the anal fin is modified as a gonopodium for sperm transport. It is modification of anal fin. Snakes and lizards have a pair of retractile, grooved and sac-like hemipenes which can be everted through cloaca. Their retraction is controlled by modified body wall musculature. Turtles, crocodilians, some birds (drakes, ganders, ostriches) and prototherian mammals have an unpaired, grooved and erectile penis formed as a thickening of cloaca floor. Only higher mammals have a true external, erectile penis with a tubular groove continuous with a spongy urethra. A series of accessory sex glands associated with penis secrete a fluid in which sperm are carried.

Ovaries and female genital ducts:

In female anamniotes, ovaries are large, occupying much of the body cavity and produce thousands of eggs as fertilization is external. In amniotes, ovaries produce fewer eggs because fertilization is internal. Ovaries of reptiles and birds are still large and the eggs produced contain much yolk. However, mammalian eggs contain very little yolk so that their ovaries also remain quite small.

Ovaries are generally paired structures, but only a single median ovary occurs in cyclostomes, as also in some teleosts (e.g. perch). They are not attached to kidney like testis in the males. Only the right ovary is functional in many elasmobranches, whereas only the left ovary becomes mature in birds and some primitive mammals (e.g. ornithorhynchus).

Histologically, an ovary is a mass of connective tissue with an outer layer of germinal epithelium showing ova in various stages of development. Ovaries are hollow and saccular in fishes and amphibians but compact in amniotes, especially in mammals, in which each ovum is surrounded by a follicle. Mature eggs are released either internally into the central ovarian cavity (teleosts) which is continuous with the lumen of the oviduct or extruded externally into the surrounding coelom or body cavity (tetrapoda). This process is termed ovulation.

In all vertebrate embryos, except cyclostomes, the coelomic epithelium on the outside of mesonephric duct develops a groove which becomes closed to form a tube called Mullerian duct. In adult males, Mullerian duct becomes vestigial and functionless. In adult females, it grows larger and becomes the female genital duct or oviduct. It opens anteriorly into coelom, in the region of degenerating pronephros, by a coelomic funnel or ostium, and terminates posteriorly into cloaca. In female elasmobranches, the mullerian duct is formed differently by the longitudinal splitting of the pronephric duct. Thus, in adult female anamniotes, both the mullerian duct (oviduct) and the Wolffian duct (mesonephric or urinary duct) are present. But, in adult female amniotes, with the development of adult metanephros and its metanephric duct or ureter, mesonephros and its duct degenerate leaving only vestiges known as provarium.

In viviparous mammals posterior ends of both the Mullerian ducts become fused and are modified into a uterus in which the embryos develop and a vagina which receives the male intromittant organ during copulation. The remaining anterior parts or oviducts are relatively short, narrow and convoluted and called the fallopian tubes. Condition of uteri varies in different mammals. When uteri remain double without fusion, it is called duplex uterus (marsupials). When uteri partially fuse so as to form two horns and two separate lumen inside, it is called bipartite uterus (hamster, rabbit). When there are two horns

but a single internal cavity it is termed bicornuate uterus (ungulates). When uterine horns are absent and both uteri fuse completely with a single internal cavity, it is termed simplex uterus (Primates, some bats, armadillos).

EARLY EMBRYONIC DEVELOPMENT

3.1. Gametogenesis

Gametogenesis is a biological process by which diploid or haploid precursor cells undergo cell division and differentiation to form mature haploid gametes. Depending on the biological life cycle of the organism, gametogenesis occurs by meiotic division of diploid gametocytes into various gametes, or by mitotic division of haploid gametogenous cells. For example, plants produce gametes through mitosis in gametophytes. The gametophytes grow from haploid spores after sporic meiosis. The existence of a multicellular, haploid phase in the life cycle between meiosis and gametogenesis is also referred to as alternation of generations.

Animals produce gametes directly through meiosis in organs called gonads (testicles in males and ovaries in females). Males and females of a species that reproduces sexually have different forms of gametogenesis

- **spermatogenesis** (male)

- **oogenesis** (female)

Spermatogenesis

Spermatogenesis is the process in which spermatozoa are produced from male primordial germ cells by way of mitosis and meiosis. The initial cells in this pathway are called spermatogonia, which yield primary spermatocytes by mitosis. The primary spermatocyte divides meiotically (Meiosis I) into two secondary spermatocytes; each secondary spermatocyte divides into twospermatids by Meiosis II. These develop into mature spermatozoa, also known as sperm cells. Thus, the primary spermatocyte gives rise to two cells, the secondary spermatocytes, and the two secondary spermatocytes by their subdivision produce four spermatozoa.

Spermatozoa are the mature male gametes in many sexually reproducing organisms. Thus, spermatogenesis is the male version of gametogenesis, of which the female equivalent is oogenesis. In mammals it occurs in theseminiferous tubules of the male testes in a stepwise fashion. Spermatogenesis is highly dependent upon optimal conditions for the process to occur correctly, and is essential for sexual reproduction. DNA methylation and histone modification have been implicated in the regulation of this process.It starts atpuberty and usually continues uninterrupted until death, although a slight decrease can be discerned in the quantity of produced sperm with increase in age

Purpose

Spermatogenesis produces mature male gametes, commonly called *sperm* but specifically known as *spermatozoa*, which are able to fertilize the counterpart female gamete, the oocyte, during conception to produce a single-celled individual known as a zygote. This is the cornerstone of sexual reproduction and involves the two gametes both contributing half the normal set ofchromosomes (haploid) to result in a chromosomally normal (diploid) zygote.

To preserve the number of chromosomes in the offspring – which differs between species – each gamete must have half the usual number of chromosomes present in other body cells. Otherwise, the offspring will have twice the normal number of chromosomes, and serious abnormalities may result. In humans, chromosomal abnormalities arising from incorrect spermatogenesis results in congenital defects and abnormal birth defects (Down Syndrome, Klinefelter's Syndrome) and in most cases, spontaneous abortion of the developing fetus.

Location

Spermatogenesis takes place within several structures of the male reproductive system. The initial stages occur within the testes and progress to the epididymis where the developing gametes mature and are stored until ejaculation. Theseminiferous tubules of the testes are the starting point for the process, where stem cells adjacent to the inner tubule wall divide in a centripetal direction—beginning at the walls and proceeding into the innermost part, or *lumen*—to produce immature sperm. Maturation occurs in the epididymis. The location [Testes/Scrotum] is specifically important as the process of spermatogenesis requires a lower temperature to produce viable sperm, specifically 1°-8 °C lower than normal body temperature of 37 °C (98.6 °F). Clinically, small fluctuations in temperature such as from an athletic support strap, causes no impairment in sperm viability or count.

Duration

For humans, the entire process of spermatogenesis is variously estimated as taking 74 days (according to tritium-labelled biopsies) and approximately 120 days (according to DNA clock measurements). Including the transport on ductal system, it takes 3 months. Testes produce 200 to 300 million spermatozoa daily. However, only about half or 100 million of these become viable sperm.

Stages

The entire process of spermatogenesis can be broken up into several distinct stages, each corresponding to a particular type of cell in human. In the following table, ploidy, copy number and chromosome/chromatid counts are for one cell, generally*prior to DNA synthesis and division* (in G_1 if applicable). The primary spermatocyte is arrested after DNA synthesis and prior to division.

Spermatocytogenesis

Spermatocytogenesis is the male form ofgametocytogenesis and results in the formation of spermatocytes possessing half the normal complement of genetic material. In spermatocytogenesis, a diploid spermatogonium, which resides in the basal compartment of the seminiferous tubules, divides mitotically, producing two diploid intermediate cells called primary spermatocytes. Each primary spermatocyte then moves into the adluminal compartment of the seminiferous tubules and duplicates its DNA and subsequently undergoes*meiosis I* to produce two haploidsecondary spermatocytes, which will later divide once more into haploidspermatids. This division implicates sources of genetic variation, such as random inclusion of either parental chromosomes, and chromosomal crossover, to increase the genetic variability of the gamete.

Each cell division from a spermatogonium to a spermatid is incomplete; the cells remain connected to one another by bridges of cytoplasm to allow synchronous development. It should also be noted that not all spermatogonia divide to produce spermatocytes; otherwise, the supply of spermatogonia would run out. Instead, certain types of spermatogonia divide mitotically to produce copies of themselves, ensuring a constant supply of spermatogonia to fuel spermatogenesis.

Spermatidogenesis

Spermatidogenesis is the creation of spermatids from secondary spermatocytes. Secondary spermatocytes produced earlier rapidly enter meiosis II and divide to produce haploid spermatids. The brevity of this stage means that secondary spermatocytes are rarely seen in histological studies.

Spermiogenesis

During spermiogenesis, the spermatids begin to form a tail by growing microtubules on one of the centrioles, which turns into basal body. These microtubules form an axoneme. The anterior part of the tail (called midpiece) thickens because mitochondria are arranged around the axoneme to ensure energy supply. Spermatid DNA also undergoes packaging, becoming highly condensed. The DNA is packaged firstly with specific nuclear basic proteins, which are subsequently replaced with protamines during spermatid elongation. The resultant tightly packed chromatin is transcriptionally inactive. TheGolgi apparatus surrounds the now condensed nucleus, becoming the acrosome.

Maturation then takes place under the influence of testosterone, which removes the remaining unnecessary cytoplasm andorganelles. The excess cytoplasm, known as *residual bodies*, is phagocytosed by surrounding Sertoli cells in the testes. The resulting spermatozoa are now mature but lack motility, rendering them sterile. The mature spermatozoa are released from the protective Sertoli cells into the lumen of the seminiferous tubule in a process called *spermiation*.

The non-motile spermatozoa are transported to the epididymis in *testicular fluid* secreted by the Sertoli cells with the aid ofperistaltic contraction. While in the epididymis the spermatozoa gain motility and become capable of fertilization. However, transport of the mature spermatozoa through the remainder of the male reproductive system is achieved via muscle contraction rather than the spermatozoon's recently acquired motility.

Role of Sertoli cells

At all stages of differentiation, the spermatogenic cells are in close contact with Sertoli cells which are thought to provide structural and metabolic support to the developing

sperm cells. A single Sertoli cell extends from the basement membrane to the lumen of the seminiferous tubule, although the cytoplasmic processes are difficult to distinguish at the light microscopic level.

Sertoli cells serve a number of functions during spermatogenesis, they support the developing gametes in the following ways:

Maintain the environment necessary for development and maturation, via theblood-testis barrier

Secrete substances initiating meiosis

Secrete supporting testicular fluid

Secrete androgen-binding protein (ABP), which concentrates testosterone in close proximity to the developing gametes

Testosterone is needed in very high quantities for maintenance of the reproductive tract, and ABP allows a much higher level of fertility

Secrete hormones affecting pituitary gland control of spermatogenesis, particularly the polypeptide hormone, inhibin

Phagocytose residual cytoplasm left over from spermiogenesis

Secretion of anti-Müllerian hormone causes deterioration of the Müllerian duct

Protect spermatids from the immune system of the male, via the blood-testis barrier

The intercellular adhesion molecules ICAM-1 and soluble ICAM-1 have antagonistic effects on the tight junctions forming the blood-testis barrier. ICAM-2 molecules regulate spermatid adhesion on the apical side of the barrier (towards thelumen).

Influencing factors

The process of spermatogenesis is highly sensitive to fluctuations in the environment, particularly hormones and temperature. Testosterone is required in large local concentrations to maintain the process, which is achieved via the binding of testosterone by androgen binding protein present in the seminiferous tubules. Testosterone is produced by interstitial cells, also known as Leydig cells, which reside adjacent to the seminiferous tubules.

Seminiferous epithelium is sensitive to elevated temperature in humans and some other species, and will be adversely affected by temperatures as high as normal body temperature. Consequently, the testes are located outside the body in a sack of skin called the scrotum. The optimal temperature is maintained at 2 °C (man)–8 °C (mouse) below body temperature. This is achieved by regulation of blood flow[13] and positioning towards and away from the heat of the body by thecremasteric muscle and the dartos smooth muscle in the scrotum.

Dietary deficiencies (such as vitamins B, E and A), anabolic steroids, metals (cadmium and lead), x-ray exposure, dioxin, alcohol, and infectious diseases will also adversely affect the rate of spermatogenesis. In addition, the male germ line is susceptible to DNA damage caused by oxidative stress, and this damage likely has a significant impact on fertilization and pregnancy. Exposure to pesticides also affects spermatogenesis.

Hormonal control

Hormonal control of spermatogenesis varies among species. In humans the mechanism is not completely understood; however it is known that initiation of spermatogenesis occurs at puberty due to the interaction of the hypothalamus, pituitary gland and Leydig cells. If the pituitary gland is removed, spermatogenesis can still be initiated by follicle stimulating hormone(FSH) and testosterone. In contrast to FSH, LH appears to have little role in spermatogenesis outside of inducing gonadal testosterone production.

FSH stimulates both the production of androgen binding protein (ABP) by Sertoli cells, and the formation of the blood-testis barrier. ABP is essential to concentrating testosterone in levels high enough to initiate and maintain spermatogenesis. Intratesticular testosterone levels are 20–100 or 50–200 times higher than the concentration found in blood, although there is variation over a 5- to 10-fold range amongst healthy men. FSH may initiate the sequestering of testosterone in the testes, but once developed only testosterone is required to maintain spermatogenesis. However, increasing the levels of FSH will increase the production of spermatozoa by preventing the apoptosis of *type A spermatogonia*. The hormone inhibinacts to decrease the levels of FSH. Studies from rodent models suggest that gonadotropins (both LH and FSH) support the process of spermatogenesis by suppressing the proapoptotic signals and therefore promote spermatogenic cell survival.

The Sertoli cells themselves mediate parts of spermatogenesis through hormone production. They are capable of producing the hormones estradiol and inhibin. The Leydig cells are also capable of producing estradiol in addition to their main product testosterone. Estrogen has been found to be essential for spermatogenesis in animals. However, a man with estrogen insensitivity syndrome (a defective ERα) was found produce sperm with a normal sperm count, albeit abnormally low sperm viability; whether he was sterile or not is unclear. Levels of estrogen that are too high can be detrimental to spermatogenesis due to suppression of gonadotropin secretion and by extension intratesticular testosterone production. Prolactin also appears to be important for spermatogenesis.

Oogenesis

Oogenesis, **ovogenesis**, or **oögenesis** is the creation of anovum (egg cell). It is the female form of gametogenesis; the male equivalent isspermatogenesis. It involves the development of the various stages of theimmature ovum.

Oogenesis in mammals

In mammals, the first part of oogenesis starts in the germinal epithelium, which gives rise to the development of ovarian follicles, the functional unit of theovary.

Oogenesis consists of several sub-processes: oocytogenesis, ootidogenesis, and finally maturation to form an ovum (oogenesis proper). Folliculogenesis is a separate sub-process that accompanies and supports all three oogenetic sub-processes.

Oogonium —(Oocytogenesis)—> Primary Oocyte —(Meiosis I)—> First Polar Body (Discarded afterward) + Secondary oocyte —(Meiosis II)—> Second Polar Body (Discarded afterward) + Ovum

It should be noted that oocyte meiosis, important to all animal life cycles yet unlike all other instances of animal cell division, occurs completely without the aid of spindle-coordinating centrosomes.

The creation of oogonia

The creation of oogonia traditionally doesn't belong to oogenesis proper, but, instead, to the common process of gametogenesis, which, in the female human, begins with the processes of folliculogenesis, oocytogenesis, andootidogenesis.

Human oogenesis

Oocytogenesis

Oogenesis starts with the process of developing oogonia, which occurs via the transformation of primordial follicles into primary oocytes, a process called oocytogenesis. Oocytogenesis is complete either before or shortly after birth.

Number of primary oocytes

It is commonly believed that, when oocytogenesis is complete, no additional primary oocytes are created, in contrast to the male process of spermatogenesis, where gametocytes are continuously created. In other words, primary oocytes reach their maximum development at ~20 weeks of gestational age, when approximately seven million primary oocytes have been

created; however, at birth, this number has already been reduced to approximately 1-2 million.

Recently, however, two publications have challenged the belief that a finite number of oocytes are set around the time of birth. The renewal of ovarian follicles from germline stem cells (originating from bone marrow and peripheral blood) has been reported in the postnatal mouse ovary. In contrast, DNA clock measurements do not indicate ongoing oogenesis during human females' lifetimes. Thus, further experiments are required to determine the true dynamics of small follicle formation.

Ootidogenesis

The succeeding phase of ootidogenesis occurs when the primary oocyte develops into an ootid. This is achieved by the process of meiosis. In fact, a primary oocyte is, by its biological definition, a cell whose primary function is to divide by the process of meiosis.

However, although this process begins at prenatal age, it stops at prophase I. In late fetal life, all oocytes, still primary oocytes, have halted at this stage of development, called the dictyate. After menarche, these cells then continue to develop, although only a few do so every menstrual cycle.

Meiosis I

Meiosis I of ootidogenesis begins during embryonic development, but halts in the diplotene stage of prophase I until puberty. The mouse oocyte in the dictyate (prolonged diplotene) stage actively repairs DNA damage, whereas DNA repair is not detectable in the pre-dictyate (leptotene, zygotene and pachytene) stages of meiosis. For those primary oocytes that continue to develop in each menstrual cycle, however, synapsis occurs and tetrads form, enabling chromosomal crossover to occur. As a result of meiosis I, the primary oocyte has now developed into the secondary oocyte and the first polar body.

Meiosis II

Immediately after meiosis I, the haploid secondary oocyte initiates meiosis II. However, this process is also halted at themetaphase II stage until fertilization, if such should ever occur. When meiosis II has completed, an ootid and another polar body have now been created.

Folliculogenesis

Synchronously with ootidogenesis, the ovarian follicle surrounding the ootid has developed from a primordial follicle to a preovulatory one.

Maturation into ovum

All 3 polar bodies disintegrate at the end of Meiosis II, leaving only the ootid, which then eventually undergoes maturation into a mature ovum.

The function of forming polar bodies is to discard the extra haploid sets of chromosomes that have resulted as a consequence of meiosis.

In vitro maturation

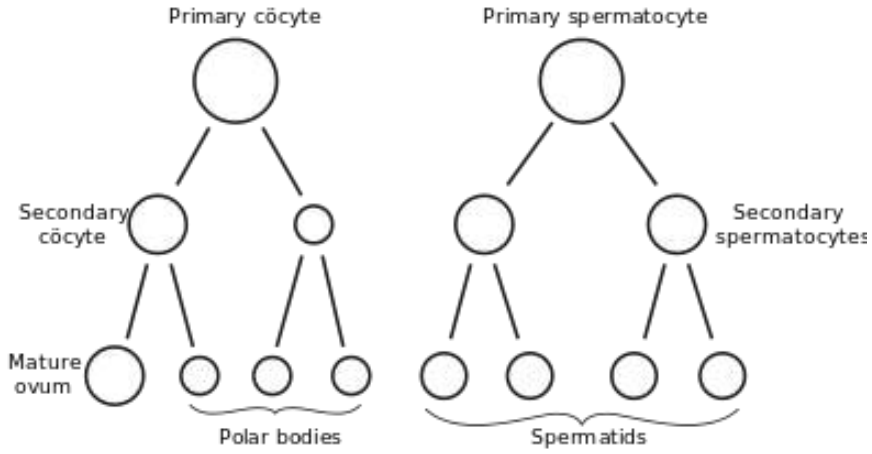
In vitro maturation (*IVM*) is the technique of letting ovarian follicles mature in vitro. It can potentially be performed before anIVF. In such cases, ovarian hyperstimulation isn't essential. Rather, oocytes can mature outside the body prior to IVF. Hence, no (or at least a lower dose of) gonadotropins have to be injected in the body. However, there still isn't enough evidence to prove the effectiveness and security of the technique.

Oogenesis in non-mammals

Some algae and the oomycetes produce eggs in oogonia. In the brown alga *Fucus*, all four egg cells survive oogenesis, which is an exception to the rule that generally only one product of female meiosis survives to maturity.

In plants, oogenesis occurs inside the female gametophyte via mitosis. In many plants such as bryophytes, ferns, andgymnosperms, egg cells are formed in archegonia. In flowering plants, the female gametophyte has been reduced to an eight-celled embryo sac within the ovule inside the ovary of the flower. Oogenesis occurs within the embryo sac and leads to the formation of a single egg cell per ovule.

In *ascaris*, the oocyte does not even begin meiosis until the sperm touches it, in contrast to mammals, where meiosis is completed in the estrus cycle.



Fertilization in Animals: The Process of Fertilization in Animals

The union of the cytoplasm and pronuclei of the male females gametes to form a diploid zygote is known as the fertilization.

External and Internal Fertilization:

Fertilization necessitates discharge of ova and sperms in close proximity. This may be accomplished in water in aquatic animals, or in special cavities of the female, more commonly in land animals.

In most aquatic animals, such as echinoderms, many fish and amphibians (frogs) both ova and sperms are laid directly into water where they fertilize. This is called external fertilization taking place outside the body of the organism. In other aquatic animals (e.g., cephalopods) and in most terrestrial animals, the male deposits sperms, during copulation, either into the oviduct of the female (as in vertebrates) or into special receptacles called spermathecae (e.g., insects, spiders), so that fertilization takes place inside the body of the organism. This is called **internal fertilization**.

Site of fertilization:

In human being, fertilization takes place mostly in the ampullary-isthmic junction of the oviduct (Fallopian tube).

Arrival of sperms:

Male discharges semen into the female's vagina close to the cervix during coitus (copulation). This is called insemination. A single ejaculation of semen may contain 300 million sperms.

Movement of sperms:

From the vagina the sperms travel up the uterus but only a few thousand find their way into the openings of the fallopian tubes. Primarily, contractions of the uterus and fallopian tubes assist in sperm movement but later on they move by their own motility. Sperms swim in the fluid medium at the rate of 1.5 to 3 mm per minute to reach the site. The leucocytes of the vaginal epithelium engulf millions of sperms.

Arrival of secondary oocyte:

In human being, the secondary oocyte is released from the mature Graafian follicle of an ovary (ovulation). The oocyte is received by the nearby Fallopian funnel and sent into the Fallopian tube by movements of fimbriae and their cilia. The secondary oocyte can be fertilized only within 24 hours after its release from the ovary.

The secondary oocyte is surrounded by numerous sperms but only one sperm succeeds in fertilizing the oocyte. Since the second meiotic division is in progress, so the sperm enters the secondary oocyte. Second meiotic division is completed by the entry of the sperm into the secondary oocyte. After this secondary oocyte is called ovum (egg).

Capacitation of sperms:

The sperms in the female's genital tract are made capable of fertilizing the egg by secretions of the female genital tract. These secretions of the female genital tract remove coating substances deposited on the surface of the sperms particularly those on the acrosome. Thus, the receptor sites on the acrosome are exposed and sperm becomes active to penetrate the egg. This phenomenon of sperm activation in mammals is known as capacitation. It takes about 5 to 6 hours for capacitation.

The secretions of seminal vesicles, prostate gland and bulbourethral glands (Cowper's glands) in the semen contain nutrients which activate the sperms. The secretions of these glands also neutralise the acidity in the vagina. Alkaline medium makes the sperms more active.

Physical and Chemical Events of Fertilization:

These events include the following processes:

(i) Acrosomal reaction:

After ovulation, the secondary oocyte reaches the Fallopian tube (oviduct). The capacitated sperms undergo acrosomal reaction and release various chemicals contained in the acrosome. These chemicals are collectively called sperm lysins. Important sperm lysins are:

(i) hyaluronidase that acts on the ground substances of follicle cells,

(ii) corona penetrating enzyme that dissolves corona radiata and (iii) zona lysine or acrosin that helps to digest the zona pellucida.

Optimum pH, Ca^{++}, Mg^{++} ions concentration and temperature are essential for acrosomal reaction. Ca^{++}plays major role in acrosomal reaction. In the absence of Ca^{++}, fertilization does not occur.

Due to acrosomal reaction, plasma membrane of the sperm fuses with the plasma membrane of the secondary oocyte so that the sperm contents enter the oocyte. Binding of the sperm to the secondary oocyte induces depolarization of the oocyte plasma membrane. Depolarization

prevents polyspermy (entry of more than one sperm into the oocyte). It ensures monospermy (entry of one sperm into the oocyte).

(ii) Cortical reaction:

Just after the fusion of sperm and plasma membranes of oocyte, the secondary oocyte shows a cortical reaction. The cortical granules are present beneath the plasma membrane of the secondary oocyte. These granules fuse with the plasma membrane of the oocyte and release their contents including enzymes between the plasma membrane and the zona pellucida. These enzymes harden the zona pellucida which also prevents entry of additional sperms (polyspermy).

(iii) Sperm entry:

At the point of contact with the sperms, the secondary oocyte forms a projection termed the cone of reception or fertilization cone which receives the sperm. The distal centriole of the sperm divides and forms two centrioles to generate the mitotic spindle formation for cell division. The mammalian secondary oocyte (egg) does not have centrioles of its own.

(iv) Karyogamy (Amphimixis):

Sperm entry stimulates the secondary oocyte to complete the suspended second meiotic division. This produces a haploid mature ovum and a second polar body. The head of the sperm which contains the nucleus separates from the middle piece and the tail and becomes the male pronucleus. The second polar body and the sperm tail degenerate.

The nucleus of the ovum is now called, the female pronucleus. The male and female pronuclei move towards each other. Their nuclear membranes disintegrate mixing up of the chromosomes of a sperm and an ovum is known as karyogamy or amphimixis. The fertilized ovum (egg) is now called zygote (Gr. zygon- yolk, zygosis- a joining). The zygote is diploid unicellular cell that has 46 chromosomes in humans. The mother is now said to be pregnant.

(v) Activation of egg:

Sperm entry stimulates metabolism in the zygote. As a result, the rates of cellular respiration and protein synthesis increase greatly.

Process of fertilization:

The process of fertilization includes the following steps which are as follows:

(a) Activation of the egg:

It is completed in the following stages:

(i) Movement of the sperm towards the egg:

Encounter between the sperm and ovum is purely accidental, because the movements of spermatozoa are entirely at random. But in some species the sperms are guided towards the

ovum by chemical substances. The fertilizins and antiferlilizins become active after the chance collision of the sperms with the ova.

Egg secretes a chemical substance known as fertilizin (composed of glycoprotein). Sperm has on its surface layer a protein substance called antifertilizin (composed of acidic amino acids). The fertilizin of an egg interacts with the antifertilizin of a sperm of the same species. This interaction makes the sperms stick to the egg surface. Adhesion of spermatozoa to the surface of the egg is brought about by linking of fertilizin molecules which establish an initial bond.

(ii) Activation of the sperm:

The peripheral portion of the acrosome of sperm breaks and releases its contents, the sperm lysins. The central portion of the acrosome elongates and forms a thin, long tube known as the acrosomal filament.

When the sperm possesses such an acrosomal filament protruding out from the sperm head it is said to be activated for the penetration in the unfertilized egg. The released enzyme hyaluronidase (sperm lysin) by the acrosome dissolves the corona radiata, zona pellucida and vitelline membrane, enabling the sperm to penetrate these coverings.

(iii) The activation of egg insemination:

At the point of contact with the sperm, the egg forms a projection, termed the cone of reception or fertilization cone which receives the sperm. The penetration of the sperm in the egg is known as the insemination. Just after the entry of the sperm into the egg, a fertilization membrane is formed in the egg to prevent the entry of other sperms.

(b) Amphimixis:

During the insemination the entire sperm may enter in the egg as in mammals or the sperm leaves its tail outside the egg or sheds it shortly after entering the egg's cytoplasm. The ovum completes the second meiotic division and extrudes the second polar body. The head of the sperm swells to form the male pronucleus and the nucleus of the ovum becomes the female pronucleus. The fusion of the haploid male pronucleus with the haploid female pronucleus forms the nucleus of the fertilized egg or zygote.

3.2. TYPES AND PATTERN OF CLEAVAGE

Cleavage

In embryology, **cleavage** is the division of cells in the early embryo. The zygotes of many species undergo rapid cell cycleswith no significant growth, producing a cluster of cells the

same size as the original zygote. The different cells derived from cleavage are called blastomeres and form a compact mass called the morula. Cleavage ends with the formation of theblastula.

Depending mostly on the amount of yolk in the egg, the cleavage can be **holoblastic** (total or entire cleavage) or **meroblastic** (partial cleavage). The pole of the egg with the highest concentration of yolk is referred to as the vegetal polewhile the opposite is referred to as the animal pole.

Cleavage differs from other forms of cell division in that it increases the number of cells without increasing the mass. This means that with each successive subdivision, the ratio of nuclear to cytoplasmic material increases

Mechanism

The rapid cell cycles are facilitated by maintaining high levels of proteins that control cell cycle progression such as thecyclins and their associated cyclin-dependent kinases (cdk). The complex Cyclin B/CDK1 a.k.a. MPF (maturation promoting factor) promotes entry into mitosis.

The processes of karyokinesis (mitosis) and cytokinesis work together to result in cleavage. The mitotic apparatus is made up of a central spindle and polar asters made up of polymers of tubulin protein called microtubules. The asters are nucleated by centrosomes and the centrosomes are organized by centrioles brought into the egg by the sperm as basal bodies. Cytokinesis is mediated by the contractile ring made up of polymers of actin protein called microfilaments. Karyokinesis and cytokinesis are independent but spatially and temporally coordinated processes. While mitosis can occur in the absence of cytokinesis, cytokinesis requires the mitotic apparatus.

The end of cleavage coincides with the beginning of zygotic transcription. This point is referred to as the midblastula transition and appears to be controlled by the nuclear:cytoplasmic ratio

Types of cleavage

Determinate

Determinate cleavage (also called mosaic cleavage) is in most protostomes. It results in the developmental fate of the cellsbeing set early in the embryo development. Each blastomere

produced by early embryonic cleavage does not have the capacity to develop into a complete embryo.

Indeterminate

A cell can only be indeterminate (also called regulative) if it has a complete set of undisturbed animal/vegetal cytoarchitectural features. It is characteristic of deuterostomes – when the original cell in a deuterostome embryo divides, the two resulting cells can be separated, and each one can individually develop into a whole organism.

Holoblastic

In the absence of a large concentration of yolk, four major cleavage types can be observed in isolecithal cells (cells with a small even distribution of yolk) or in mesolecithal cells (moderate amount of yolk in a gradient) – **bilateral** holoblastic, **radial**holoblastic, **rotational** holoblastic, and **spiral** holoblastic, cleavage. These holoblastic cleavage planes pass all the way through isolecithal zygotes during the process of cytokinesis. Coeloblastula is the next stage of development for eggs that undergo these radial cleavaging. In holoblastic eggs, the first cleavage always occurs along the vegetal-animal axis of the egg, the second cleavage is perpendicular to the first. From here, the spatial arrangement of blastomeres can follow various patterns, due to different planes of cleavage, in various organisms.

- Bilateral

  The first cleavage results in bisection of the zygote into left and right halves. The following cleavage planes are centered on this axis and result in the two halves being mirror images of one another. In bilateral holoblastic cleavage, the divisions of the blastomeres are complete and separate; compared with bilateral meroblastic cleavage, in which the blastomeres stay partially connected.

- Radial

  Radial cleavage is characteristic of the deuterostomes, which include some vertebrates and echinoderms, in which the spindle axes are parallel or at right angles to the polar axis of the oocyte.

Rotational

Mammals display rotational cleavage, and an isolecithal distribution of yolk (sparsely and evenly distributed). Because the cells have only a small amount of yolk, they require immediate implantation onto the uterine wall in order to receive nutrients.

Rotational cleavage involves a normal first division along the meridional axis, giving rise to two daughter cells. The way in which this cleavage differs is that one of the daughter cells divides meridionally, whilst the other divides equatorially.

Spiral

Spiral cleavage is conserved between many members of the lophotrochozoan taxa, referred to as Spiralia.[3] Most spiralians undergo equal spiral cleavage, although some undergo unequal cleavage (see below).[4] This group includesannelids, molluscs, and sipuncula. Spiral cleavage can vary between species, but generally the first two cell divisions result in four macromeres, also called blastomeres, (A, B, C, D) each representing one quadrant of the embryo. These first two cleavages are oriented in planes that occur at right angles parallel to the animal-vegetal axis of the zygote At the 4-cell stage, the A and C macromeres meet at the animal pole, creating the animal cross-furrow, while the B and D macromeres meet at the vegetal pole, creating the vegetal cross-furrow.[5] With each successive cleavage cycle, the macromeres give rise to quartets of smaller micromeres at the animal pole .The divisions that produce these quartets occur at an oblique angle, an angle that is not a multiple of 90°, to the animal-vegetal axis. Each quartet of micromeres is rotated relative to their parent macromere, and the chirality of this rotation differs between odd and even numbered quartets, meaning that there is alternating symmetry between the odd and even quartets In other words, the orientation of divisions that produces each quartet alternates between being clockwise and counterclockwise with respect to the animal pole. The alternating cleavage pattern that occurs as the quartets are generated produces quartets of micromeres that reside in the cleavage furrows of the four macromeres.When viewed from the animal pole, this arrangement of cells displays a spiral pattern.

Specification of the D macromere and is an important aspect of spiralian development. Although the primary axis, animal-vegetal, is determined duringoogenesis, the secondary axis, dorsal-ventral, is determined by the specification of the D quadrant. The D macromere facilitates cell divisions that differ from those produced by the other three macromeres. Cells of the D quadrant give rise to dorsal and posterior structures of the

spiralian. Two known mechanisms exist to specify the D quadrant. These mechanisms include equal cleavage and unequal cleavage.

In equal cleavage, the first two cell divisions produce four macromeres that are indistinguishable from one another. Each macromere has the potential of becoming the D macromere.[6] After the formation of the third quartet, one of the macromeres initiates maximum contact with the overlying micromeres in the animal pole of the embryo. This contact is required to distinguish one macromere as the official D quadrant blastomere. In equally cleaving spiral embryos, the D quadrant is not specified until after the formation of the third quartet, when contact with the micromeres dictates one cell to become the future D blastomere. Once specified, the D blastomere signals to surrounding micromeres to lay out their cell fates

In unequal cleavage, the first two cell divisions are unequal producing four cells in which one cell is bigger than the other three. This larger cell is specified as the D macromere. Unlike equally cleaving spiralians, the D macromere is specified at the four-cell stage during unequal cleavage. Unequal cleavage can occur in two ways. One method involves asymmetric positioning of the cleavage spindle. This occurs when the aster at one pole attaches to the cell membrane, causing it to be much smaller than the aster at the other pole. This results in an unequal cytokinesis, in which both macromeres inherit part of the animal region of the egg, but only the bigger macromere inherits the vegetal region. The second mechanism of unequal cleavage involves the production of an enucleate, membrane bound, cytoplasmic protrusion, called a polar lobe. This polar lobe forms at the vegetal pole during cleavage, and then gets shunted to the D blastomere. The polar lobe contains vegetal cytoplasm, which becomes inherited by the future D macromere.

Meroblastic

In the presence of a large amount of yolk in the fertilized egg cell, the cell can undergo partial, or meroblastic, cleavage. Two major types of meroblastic cleavage are **discoidal** and **superficial**.[8]

Discoidal

In discoidal cleavage, the cleavage furrows do not penetrate the yolk. The embryo forms a disc of cells, called a blastodisc, on top of the yolk. Discoidal cleavage is

commonly found in monotremes, birds, reptiles, and fish that havetelolecithal egg cells (egg cells with the yolk concentrated at one end).

Superficial

In superficial cleavage, mitosis occurs but not cytokinesis, resulting in a polynuclear cell. With the yolk positioned in the center of the egg cell, the nuclei migrate to the periphery of the egg, and the plasma membrane grows inward, partitioning the nuclei into individual cells. Superficial cleavage occurs in arthropods that have centrolecithal egg cells (egg cells with the yolk located in the center of the cell).

Summary of the main patterns of cleavage and yolk accumulation

I. Holoblastic (complete) cleavage	**II. Meroblastic (incomplete) cleavage**
A. Isolecithal (sparse, evenly distributed yolk) • 1. Radial cleavage (echinoderms,hemichordates, amphioxus) • 2. Spiral cleavage (annelids, most mollusks,flatworms) • 3. Bilateral cleavage (tunicates) • 4. Rotational cleavage (placental mammals,nematodes, marsupials [?]) B. Mesolecithal (moderate vegetal yolk disposition) • Displaced radial cleavage (amphibians, some fish [the lampreys, gars and bowfins)	A. Telolecithal (dense yolk throughout most of cell) • 1. Bilateral cleavage (cephalopod molluscs) • 2. Discoidal cleavage (some fish [the hagfishes, chondrichthyans and mostteleosts], sauropsids [reptiles and birds], monotremes) B. Centrolecithal (yolk in center of egg) • Superficial cleavage (most insects)

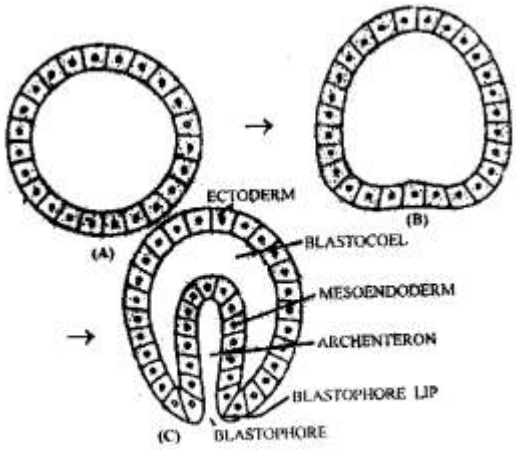
3.3 BLASTULATION AND GASTRULATION

Blastulation and its Types

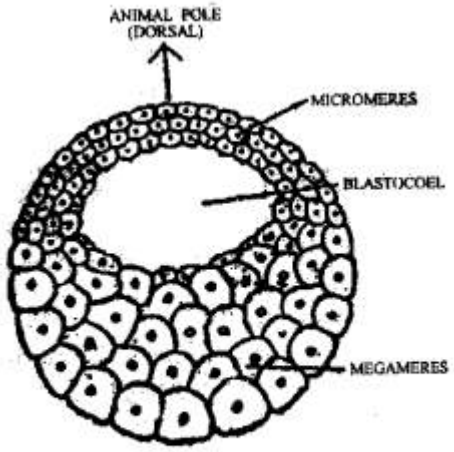
The formation of a segmentation cavity or blastocoele within a mass of cleaving blastomeres and rearrangement of blastomeres around this cavity in such a way as to form the type of definitive blastula characteristic of each species. The blastocoele originates as an intercellular space which sometimes arises as early as the four- or eight-cell stage. Thus blastulation is initiated during early cleavage stages, and formation of the definitive blastula is thought to terminate cleavage and to initiate gastrulation. Accordingly, cleavage and blastulation are simultaneous events which follow activation of the egg and precede the next major step in development, namely, gastrulation. Initially the diameter of the blastula is no greater than that of the activated egg; subsequently it increases.

TYPES OF BLASTULA -

Blastulas are of following type -



(Blstulation in isolecithal Eggs)



(Blastula of Telolecithal frog Eggs)

1. STEREOBLASTULA -

The blastocoel is very small. It's blastomere are less in number but large in size.

It is formed as a result of spiral cleavage. eg. Neries and some molluscs.

2. COELOBLASTULA -

The blastula of echinoderm and amphioxis is called coeloblastula.

It is formed through complete holoblastic cleavage. The blastoderm is formed of a single layer of cells.

Its blastocoel is filled wiht mucopolysaccaharide. In microlecithal egg blastocoel is centric.

In megalecithal egg blastocoel is excentric, eg. Some animal of echinodermes and amphioxis.

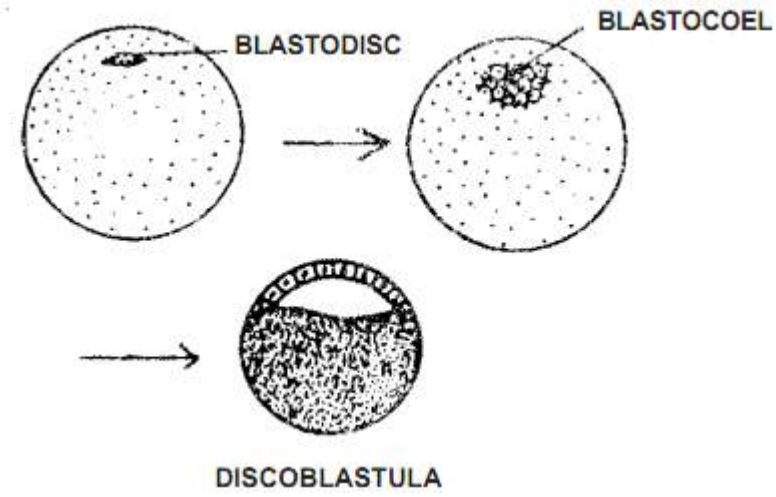
3. PERIBLASTULA OR SUPERFICIAL BLASTULA -

It is formed as a result of superficial cleavage. The blastocoel is absent.

There is a single layer of blastomeres around the uncleaved yolky part, eg. Insect.

4. DISCOBLASTULA -

It is formed as a result of discoidal cleavage. The blastocoel is small & it is called as subgerminal space. It is situated below the blastoderm, eg. Boney fishes, reptile, birds & prototherian mammals.



5. AMPHIBLASTULA -

It is formed of two types of structurally different blastomeres.

Example, in sycon the anterior half fo blastula is formed of flagellated cells while the posterior half is formed of large rounded granular cells on in amphibians where the two types of cells are micromeres and macromeres.

eg. Amphibians.

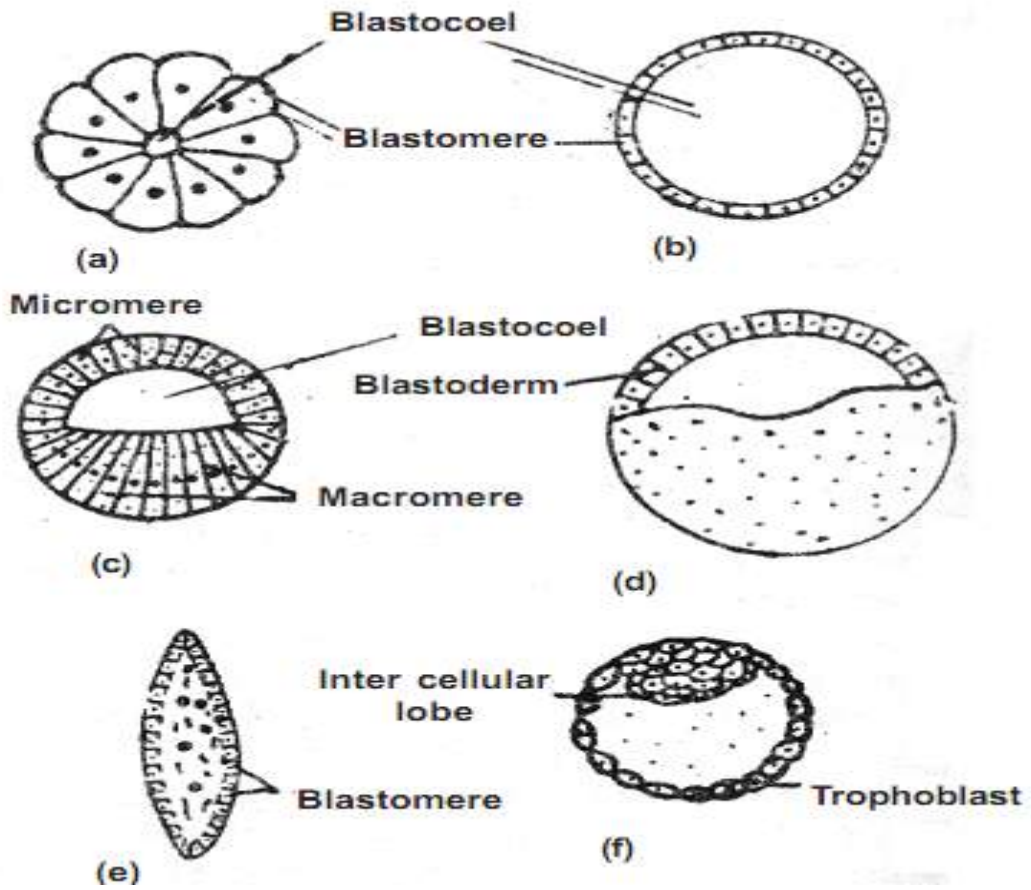
6. BLASTOCYST -

It is formed in mammals as a result of holoblastic cleavage.

Outer cells are called as trophoblasts or cells of Rauber. They form a trophoderm. This layer get attached to the uterine wall.

Inner cells form the embryo & are called as inner cell mass.

eg. Human beings.



Gastrulation:

It is a process by which blastocyst is changed into a gastrula larva with three primary germ layers. It starts immediately after implantation. In this, cells of blastodermic vesicle visibly move in small masses to their final and pre-determined positions.

These movements are interdependent and are called morphogenetic movements. These movements change a hollow spherical blastula into a complex gastrula with three primary germ layers i.e., ectoderm, mesoderm and endoderm.

The developmental fate of cells of each of these primary germ layers is determined to develop specific organs and organ-systems of the individual and that fate is same in all the triploblastic animals.

Formation of gastrula from the monoblastic blastula is called gastrulation. Gastrulation is that phase of embryonic development during which the cells of blastula (in frogs) / blastodermic vesicle (in mammals) move in small masses or as a sheet of cells to attain the final location.

Such movements of cells are called morphogenetic movement. It is differentiated into two types.

1. Epiboly:

The term epiboly is derived from Greek language, meaning 'throwing on' or 'extending upon'. Epiboly means overgrowth of the ectoderm – forming regions around the endoderm forming region. It occurs in frog where the micromeres divide rapidly in the animal half and spread over the megameres over the vegetal half.

2. Emboly:

The term emboly is also derived from Greek language meaning "throw in" or "thrust in". Migration of prospective endodermal and mesodermal cells from the surface into the interior of the embryo is called emboly. It includes invagination, involution, ingression and delamination.

(i) Invagination:

It is the process of infolding or inpushing of the vegetal pole of the embryo (blastula) into its cavity (blastocoel), forming a double-walled structure. It is just like the pushing in one side of a rubber ball with a thumb. Invagination occurs in the blastula of frog.

(ii) Involution:

The term involution means a 'turning in' or 'rolling under'. Involution is the process of rolling or turning in of the surface cells into the interior of the embryo. It occurs in frog's blastula.

(iii) Ingression:

The term ingression means "inward migration". In ingression the blastomeres form new cells from their surface. New cells migrate into the blastocoel of the blastula to form a solid gastrula. It means, it forms solid gastrula or sterogastrula without archenteron (primitive cavity). Archenteron is formed later by splitting the internal cell mass. Ingression is of two kinds.

(a) Unipolar Ingression:

Inward migration of cells is restricted to the vegetal pole only. It is seen in Obelia.

(b) Apolar Ingression:

Inward migration of cells occurs from ail sides of the blastoderm (wall of blastula). It occurs in Hydra.

(iv) Delamination:

The term delamination means 'splitting off'. Delamination is a process in which the separation of a layer of cells occurs from the original layer of the blastula. It occurs during gastrulation of chick and rabbit.

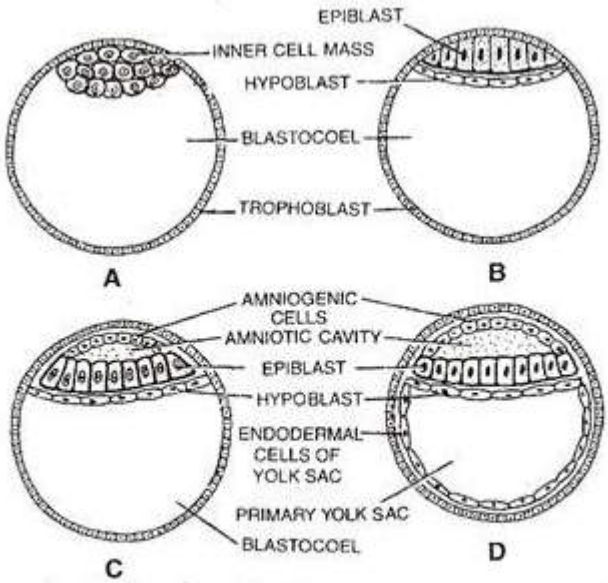
In all the triploblastic animals, three germs layers namely ectoderm, mesoderm and endoderm, are formed by the morphogenetic movements.

Process:

In human, the germ lavers are formed so quickly that it is difficult to determine the exact sequence of events.

Formation of Embryonic Disc:

We have seen that early blastocyst consists of inner cell mass and trophoblast. The inner cell mass contains cells called stem cells which have the potency to give rise to all tissues and organs. The cells of the inner cell mass differentiate into two layers around 8 days after fertilization, a hypoblast and epiblast. The hypoblast (primitive endoderm) is a layer of columnar cells and epiblast (primitive ectoderm) is a layer of cuboidal cells. The cells of the hypoblast and epiblast together form a two layered embryonic disc.



Diagrams showing formation of epiblast, hypoblast, amniotic cavity and yolk sac.

Formation of Amniotic Cavity:

A space appears between epiblast and trophoblast, called amniotic cavity filled with amniotic fluid. The roof of this cavity is formed by amniogenic cells derived from the trophoblast, while its floor is formed by the epiblast.

Formation of Extra-embryonic Coelom:

The cells of the trophoblast give rise to the mass of cells called the extra-embryonic mesoderm. This mesoderm is called extraembryonic because it lies outside the embryonic disc. It does not give rise to any tissue of the embryo itself. The extraembryonic mesoderm is differentiated into outer somatopleuric extra-embryonic mesoderm and inner splanchnopleuric extraembryonic mesoderm. Both these layers enclose the extraembryonic coelom.

Formation of Chorion and Amnion:

At this stage, two very important embryonic membranes, the chorion and amnion, are formed. The chorion is formed by the somatopleuric extra-embryonic mesoderm inside and the trophoblast outside. The amnion is formed by the amniogenic cells inside and splanchnopleuric extraembryonic mesoderm outside.

As mentioned earlier the amniogenic cells are derived from the trophoblast. Later on chorion becomes the main embryonic part of the placenta. The chorion also produces human chorionic gonadotropin (hCG) an important hormone of pregnancy.

Amnion surrounds the embryo creating the amniotic cavity that is filled with amniotic fluid. The amniotic fluid serves as a shock absorber for the foetus, regulates foetal body temperature and prevents desiccation.

Formation of Yolk Sac:

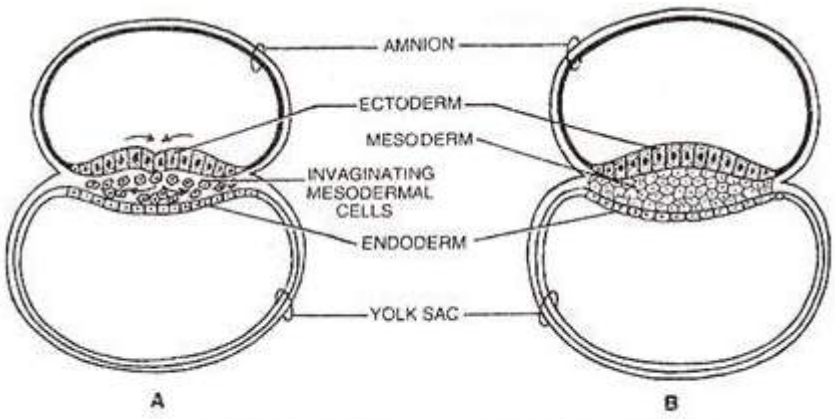
Flattened cells arising from the hypoblast spread and line inside the blastocoel. These are endodermal cells lining the primary yolk sac. With the appearance of the extraembryonic mesoderm and later of the extraembryonic coelom, the yolk sac (embryonic membrane) becomes much smaller than before and is now called the secondary yolk sac.

This change in size is due to change in the nature of the lining cells. These cells are no longer flattened but become cubical. The secondary yolk sac consists of outer splanchnopleuric extra embryonic mesoderm and inner endodermal cells.

The yolk sac is a source of blood cells. It also functions as a shock absorber and helps prevent desiccation of the embryo.

Formation of Primitive Streak:

Gastrulation involves the rearrangement and migration of cells from the epiblast. A primitive streak which is a faint groove on the dorsal surface of the epiblast is formed. It elongates from the posterior to the entire part of the embryo. The primitive streak clearly establishes the head and the tail ends of the embryo as well as its right and left sides.



Formation of primitive streak and three germ layers.

Formation of Embryonic Layers:

After the formation of the primitive streak, cells of the epiblast move inward below the primitive streak and detach from the epiblast. This inverting movement is called invagination. Once the cells have invaginated, some of them displace the hypoblast forming the endoderm. Other cells remain between the epiblast and newly formed endoderm forms the mesoderm. Cells remaining in the epiblast form ectoderm.

Thus three germ layers, namely endoderm, mesoderm and ectoderm are formed which give rise to all the tissues and organs of the body.

Organogenesis:

The primitive germ layers formed during gastrulation spilt into groups of cells called as primary organ rudiments and the process of formation of organs from the three germ layers is known as organogenies. The primary organ rudiments further subdivide into secondary organ rudiments which are the initial stages in the formation of organs and their parts. A this stage the embryo acquires resemblances with the adult or a larva.

Mechanism:

Gastrulation includes the formation of following structures:

1. Formation of endoderm

The blastodermic vesicle enlarges and cells present on the lower surface of the embryonal knob detach by delamination from the embryonal knob. The detached cells become flat, divide, increase in number and form the endoderm inside the trophoblast of the blastodermic vesicle.

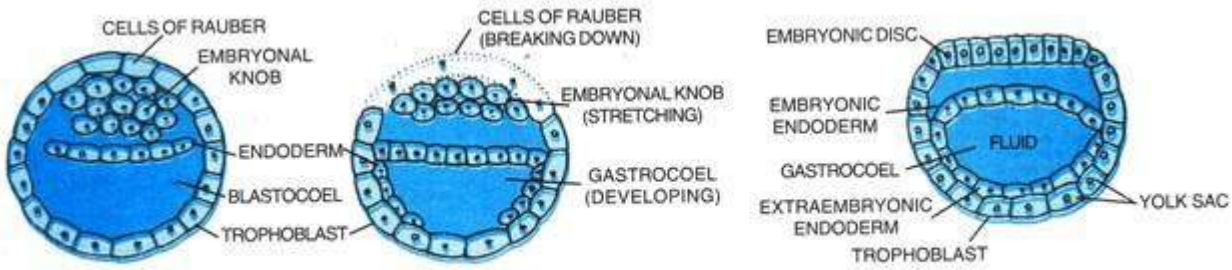


Fig. 3.27. Formation of Endoderm and Embryonic disc.

The embryo at this stage is tubular and encloses a hollow tube (called primitive gut or archenteron) lined by endoderm. The part of endoderm located under the embryonal knob is called embryonic endoderm which later forms embryonic gut, while the remaining part of endoderm along with trophoblast forms the yolk sac.

Fate of endoderm:

The endoderm is pre-determined to form mid-gut or archenteron {archi=priinitive; enteron = gut) from pharynx to colon; middle ear; gastric and intestinal glands ; tongue; urinary bladder; respiratory tract; liver; pancreas; thyroid; parathyroids; anterior lobe of pituitary gland; thymus gland and primordial germ cells.

2. Formation of Embryonic disc

Meanwhile, the blastocyst continues to grow due to absorption of more and more uterine milk. The embryonal knob stretches and cells of Rauber start breaking off and dispersing. So the cells of embryonal knob form a regular layer called embryonic disc which becomes continuous with the trophoblast. Embryonic disc is differentiated into cephalic, embryonic and caudal regions.

3. Formation of embryonic mesoderm

It starts at the caudal region of the embryonic disc where cells undergo rapid proliferation and form a localized thickening of the embryonic disc. The proliferated cells later get detached from the embryonic disc and form the mesodermal layer between ectoderm and endoderm.

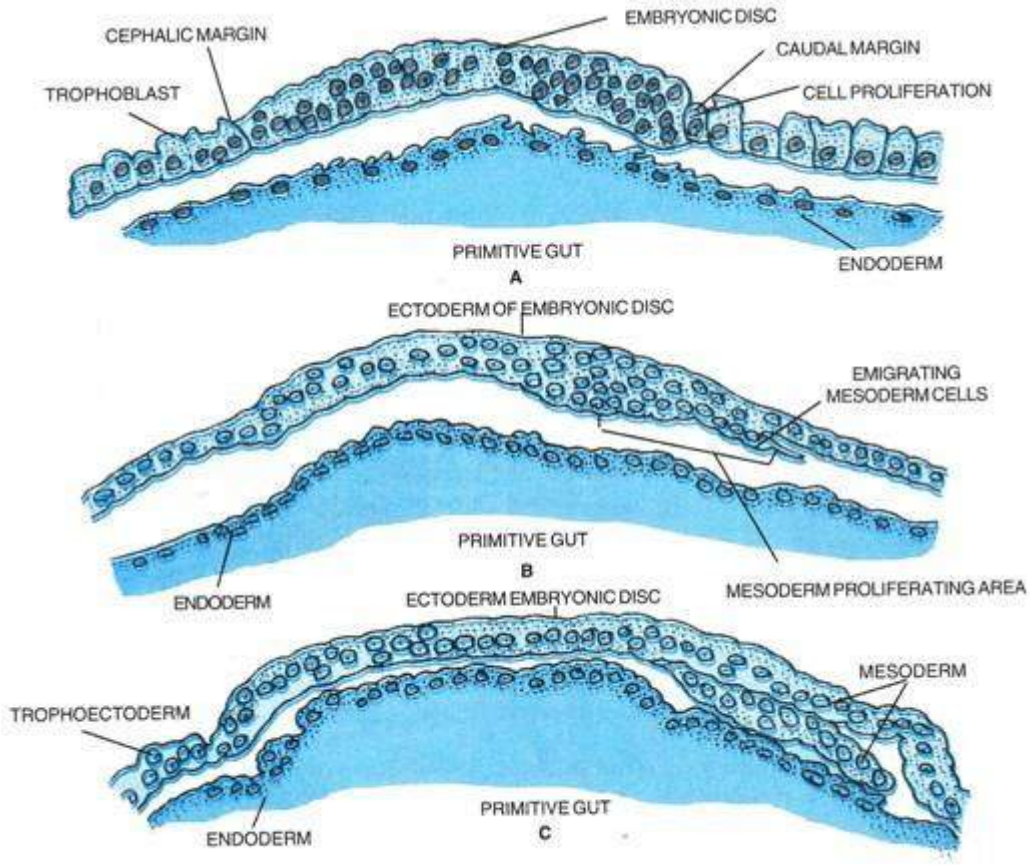


Fig. 3.28. Formation of Mesoderm.

Fate of mesoderm:

It is determined to form most of muscles; connective tissues; dermis of skin; peritoneum; skeleton (bones and cartilages); circulatory system (heart, blood vessels, blood, lymphatic system); excretory system except urinary bladder; adrenal cortex and most of the reproductive system.

4. Formation of ectoderm:

The remaining cells of blastodisc become columnar and form ectoderm.

Fate of Ectoderm:

It is predetermined to form the epidermis; epidermal glands; fore and hind gut; pigment cells; brain; spinal cord; sense-organs like eyes (retina, conjunctiva, cornea, lens); internal ear; nasal chamber; middle and posterior lobes of pituitary gland; adrenal medulla and pineal.

5. Formation of amniotic cavity:

A space appears between the ectoderm and the trophoblast and is called amniotic cavity which gets filled with a watery fluid called amniotic fluid. It provides protection to embryo from mechanical shocks by acting as a shock absorber and from dryneses. At the floor of

amniotic cavity there lie ectodermal cells, while at the roof of it there lie amniogenic cells derived from the trophoblast.

Main structures formed from Ectoderm, Mesoderm and Endoderm of gastrula larva.

Germ layer	Structures formed
Ectoderm	Epidermis, epidermal glands, hair, conjunctiva, lens, retina, internal ear, foregut, hindgut, CNS, middle and posterior pituitary, adrenal medulla, pineal gland.
Mesoderm	Muscles, connective tissue, dermis of skin, bones and cartilages, peritoneal layers, coelom, circulatory system (heart, blood vessels, blood, lymphatic system), kidneys and ureters, gonads, adrenal cortex.
Endoderm	Midgut, bladder, lungs, liver, pancreas, thyroid, parathyroid, thymus, anterior pituitary, primary germ cells.

Significance of Gastrulation:

(a) Three primary germ layers are formed.

(b) It marks the beginning of morphogenesis and differentiation.

(c) Metabolic activities of the cells are increased due to great morphogenetic activities of the blastomeres.

(d) Blastocoel is obliterated and archenteron is formed**.**

3.4. ROLE OF PRIMARY ORGANIZER

Primary Organizer and its role

The term “organizer,” or “primary organizer,” was introduced by the Germanembryologist an d 1935 Nobel laureate H. Spemann to designate the material of thedorsal lip of the blastopore —the prospective chordamesoderm—in the amphibiangastrula (GASTRULA). When transpl anted to a remote site, for example, theventral side of the embryo or the blastocoel, the materi al of the dorsal

lip not onlydifferentiates into organs that would normally arise had the transplant not takenpla ce but also induces the development of neural and other structures in areasadjacent to the tran splant site; this is an example of primary embryonal induction(NDUCTION). As a result of th e action of the organizer, a new, more complexembryo forms in which the organs are situated roughly according to their futuredistribution.

Two organizers are distinguished. The cephalic organizer consists of the anteriorsection of the notochord and the material of the prechordal plate and inducesformation of the anterior sectio ns of the brain. The trunk organizer, consisting of theremaining material of the notochord and the somites, induces formation of theposterior sections of the brain and the trunk and tail stru ctures. Organizersanalogous to amphibian organizers have been found in all classes of chorda tes;these include Hensen's node in birds and the posterior section of the embryonaldisc in tele osts.

The term "organizer" is also applied to other embryonic organ rudiments that exertan inductiv e effect on adjacent areas; these are the secondary and tertiaryorganizers, as distinct from the chordamesoderm, which is called the primaryorganizer. Thus, the rudiment of the eye that ori ginates as a result of primaryembryonal induction is a secondary organizer; it induces formati on of the iens in theectoderm. The lens, in turn, is a tertiary organizer that induces formation of thecornea.

The term "organizer" stresses the concept that it is the rudiments of organs of livingembryos t hat act as inductors and not substances excreted from the tissues ofembryos or adults.

What is an organizer?

The effect of embryonic interaction or organizer is a morphogenetic effect by which one organic tissue transmits a chemical substance that influences other embryonic part to produce a structure that otherwise could not come into existence. The embryonic tissue which exerts such an influence is called an inductor and the chemical substance secreted by an inductor is known as evocators. The tissue on which evocator works and the tissue responses is known as responsive tissue. The action of the indicator through evocator is known as induction action or organizer action. This process of induction influences greatly the protein synthesis mechanism of responsive tissues as a result of which definite structure forming cells become very active.

Origin of the concept of the organizer

Spemann's experiment (1924): A German embryologist Hans Spemann and his student Hilde Mangold (1924) performed transplantation experiment on a newt *Triturus cristatus*, an Urodela of class Amphibia. Spemann grafted a piece taken from the dorsal lip of early gastrula of *Rana*sp. to the lateral lip region of the early gastrula of *Triturus cristatus*. The embryo of *Rana* sp. is donor and the embryo of *Triturus* is the host. They observed that the cells of the grafted piece enter into the gastrula and form notochord and somites. In this

embryo its own dorsal lip of blastopore forms neural groove, notochord, mesoderm etc. Similarly the grafted tissue influences to form notochord, neural groove and mesoderm. That is in the same embryo double set of notochord, nerve cord and mesoderm are produced. In this case donor tissue has secreted some chemical substances which has induced to form neural groove, notochord etc. in the host embryo. The donor tissue had pigments and the induced neural groove has also coloured pigments. After the completion of the gastrulation they observed that a larva has developed with two heads. One head is due to normal development and the other head production has been induced by donor tissue.

They examined the larva under the microscope and found that notochord, renal tubules, gut etc. have been formed by the tissue of the host embryo as a secondary set. If the donor tissue would not have been grafted such secondary structures wound not develop. From this experiment they concluded that dorsal lip of the donor had influenced greatly the tissue and thus has brought about change in the host tissue development. If it is not the fact then how a head had developed in the abdomen of the host. This secondary head formation is due to induction effect of donor tissue. This process of influencing other tissue was termed as induction by Spemann and the tissue that induced the tissue was known as the inductor or organizer.

Primary organizer:

Spemann continued his grafting experiments taking tissues from different zones of the gastrula and observed that except dorsal lip of the early gastrula other zone of tissue can not create any induction effect but when dorsal lip is grafted a complete embryo is formed. He named the dorsal lip as organizer as this dorsal lip organizes the developmental process of the embryo. According to him this dorsal lip induces to form neural tube and the neural tube then induces to form the eyes. The dorsal lip is composed of chorda-mesoderm and as it primarily acts as inducer so he named the dorsal lip or chordamesoderm as primary organizers.

Secondary, tertirary and quaternary organizers:

As the gastrulation proceeds due to primary organizer's induction primary organs begin to form and the early stages of organ development are known as organ rudiments. These organ rudiments themselves may act as organizer and then they are known as secondary organizer. Tissues formed by the action of secondary organizer may in turn induce further development. Then they are known as tertiary organizer. These successive stages of organizer activities start from the primary organizer.

How these organizers act in succession can clearly be understood from the examples of the development of eye in amphibian, chick etc. First of all due to induction effect of the primary

organizer forebrain and within the forebrain eye forming cells are produced. These cells push out as a vesicle outside the forebrain. These vesicles are known as optic vesicle. This vesicle grows through the lateral mesenchyme and reaches the epidermis.

As soon as the vesicle comes in contact with the epidermis the outer layer of the vesicle invaginates to form a double layered optic cup. The inner layer of the optic cup is formed of sensory cells and the outer layer is formed of pigmented cells. They two together form the retina. The chemical substances secreted by the optic cup induce to form the lens between the optic cup and the epidermis. The peculiar thing is that if the optic vesicle is prevented from coming in contact with the epidermis there will be no lens formation. So the optic cup acts as secondary organizer. Similarly lens and retina together induce to form cornea so lens and retina together act as tertiary organizer and so on.

Classification of induction:

Lovtrup (1974) classified induction into two principal classes.

1. Endogenous induction: Shapes and sizes of some of the embryonic cells changes after secreting inducting substances and this induction brings about differentiation of cells. As for example small cells of the dorsal lip carrying yolk granules act as endogenous induction.

2. Exogenous induction: When either by external influence or by contact any cell or tissue induces nearby tissue to differentiate, then it is known as exogenous induction. Exogenous induction may again be of two types. -

1. Homotypic: When the contact induction induces to form same types of cells, it is known as homotypic.

2. Heterotypic: When the contact induction induces different types of cell differentiation, it is known as heterotypic induction.

Embryonic induction in vertebrates:

Spemann observing the induction effect of dorsal lip named it as primary organizer but Ebert and Sussex (1974) said the formation of secondary embryo is due to cell differentiation of both the donor as well as of the host. They preferred to call the primary organizer of Spemann as embryonic inductor. As the primary organizer induces the epidermis for the formation of neural tube so now a days the primary organizer has been renamed as primary inductor or neural inductor.

Morphology of Neural inductor:

Vogt (1924) has shown by vital staining technique that cells of the dorsal lip of blastopore of a newt's gastrula, move interior and form the roof of the archenteron. If a block of tissue from archenteron roof is transplanted to the abdomen of another gastrula then from the abdomen created by the host gastrula tissue, a secondary larva is formed. All parts of the dorsal lip can not induce such induction. If only endodermal cells are grafted it will give rise to a partial embryo. If the anterior part is grafted it will induce to form the mouth, sensory organs head with the brain of the partial embryo. If the middle part is grafted it will give rise to eye and nasal cavities, lateral side induces to form posterior part of the head and if the posterior part is grafted then it will induce to form spinal cord, trunk and tail mesenchyme. From these experiments it can be concluded that the dorsal lip possess the regionality of its induction activity

Types of inductors:

On the basis of various experimental evidences Lehmon (1945) said that specific regionality of induction effects present in the dorsal lip of the blastopore. He further said that the roof of the archenteron definitely possess specific induction activities for the differentiation of head and trunk regions. On the basis of the regional specificity he classified the inductors into three groups. They are:

Archenocephalic inductor: Due to induction effect of this inductor partial head, fore-brain, eye, nasal cavities are formed.

1. **Deuterencephalic inductor:** By its induction effect posterior portion of the head, ear cavities etc. are formed.

As arechenocephalic and deuterencephalic inductors induce the formation of different parts in the head region so they together are known as cephalic or head inductors.

1. **c) Spino-caudal inductor:** Their inductive influence leads to the formation of spinal cord and different structures of the tail region.

Development of Eye in Chick

The first sign of the development of the eyes is a bulging at the lateral sides of the prosencephalon. These are the rudiments of the optic vesicles which lie beneath the head ectoderm. Meanwhile, the distal part of each optic vesicle (the future sensory layer) invaginates and presses against the proximal part (the future pigment layer of the retina, iris and ciliary body). This results in the formation of the optic cup, the elimination of the original lumen of the optic vesicle and the formation of a new lumen, the future vitreous chamber.

The lens is formed from the lens placode, a thickening of the ectoderm formed in response to an inductive signal from the optic cup. The lens sinks beneath the surface of the ectoderm, the latter becoming the cornea.

As the lens continues to grow, the cells in the thickened region lose their ability to divide and become converted into fibres that will become the core of the adult lens. New fibres are formed from the cells at the periphery of the lens which divide rapidly and become arranged in concentric circles around the original core. By the time of hatching there are three concentric layers of fibres, the core, the intermediate layer of irregularly arranged fibres, and the radial layers which continue to grow after hatching. The lens capsule, which is an extracellular material with a high collagenous component, starts to form about day 7. The ciliary body develops close to the lens, its role being to secrete the fluid of the vitreous chamber.

As the lens loses contact with the ectoderm a space is formed, the anterior chamber of the eye. The corneal epithelium develops from the ectoderm covering the anterior chamber, whilst the corneal stroma forms from the mesenchyme and becomes visible on day 4 as a thin layer beneath the epithelium. It becomes thicker as mesenchyme cells migrate into it during day 7.

The iris arises from cells at the margin of the anterior chamber at about day 7. Removal of the lens results in disorganization of the components of the anterior chamber.

The retina is formed from the optic cup. Its inner layer becomes the neural retina and its outer layer the pigmented retina.

The choroid and sclera differentiate from the mesenchyme around the optic cup, forming the inner pigmented vascular layer, and the outer, fibrous layer, respectively. The melanophores of the choroids are derived from cells of the neural crest that reach the eye during day 2 and develop pigment on day 7. Cartilage starts to form in the sclera on day 8.

The eyelids start to form at about 7 days from a circular fold of skin surrounding the eye.

The choroid fissure usually begins lo close in the region near the lens about day 4. At this time a ridge of mesoderm, carrying with it a blood vessel, migrates along the choroid fissure into the posterior chamber of the eye and enlarges during day 5 to form the pectin. The pigment cells of the pecten are derived from the pigmented retina. The pecten is a structure characteristic of birds, and it is thought that it acts not only by bringing oxygen and nutritive materials to the eye but that it may also play a role in vision. The vitreous humour is secreted by the cells of the optic cup.

UNIT IV LATE EMBRYONIC DEVELOPMENT AND CONTROL

4.1 EXTRA EMBRYONIC MEMBRANES

These membranes are formed by Trophoblast cell & three germ layers. They perform specific function. The embryos of reptiles, birds, and mammals produce 4 extraembryonic membranes, the

- amnion
- yolk sac
- chorion, and
- allantois

In birds and most reptiles, the embryo with its extraembryonic membranes develops within a shelled egg.

- The **amnion** protects the embryo in a sac filled with **amniotic fluid**.
- The **yolk sac** contains yolk — the sole source of food until hatching. Yolk is a mixture of proteins and lipoproteins.
- The **chorion** lines the inner surface of the shell (which is permeable to gases) and participates in the exchange of O_2 and CO_2between the embryo and the outside air.
- The **allantois** stores metabolic wastes (chiefly uric acid) of the embryo and, as it grows larger, also participates in gas exchange.

With these four membranes, the developing embryo is able to carry on essential metabolism while sealed within the egg. Surrounded by amniotic fluid, the embryo is kept as moist as a fish embryo in a pond.

Although (most) mammals do not make a shelled egg, they do also enclose their embryo in an amnion. For this reason, the reptiles, birds, and mammals are collectively referred to as the **amniota**.

Mammals fall into three groups that differ in the way they use the amniotic egg.

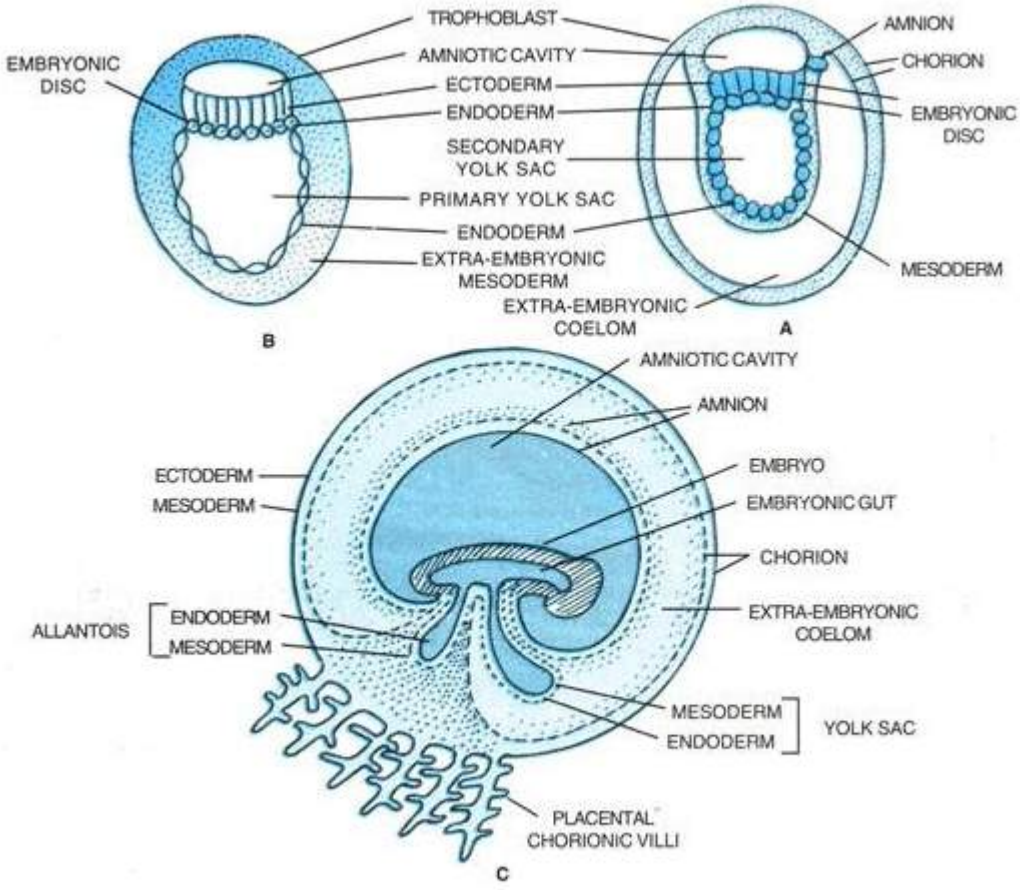
4. Types of Extra Embryonic

Some of the important types of extra embryonic membranes are:

1. Yolk sac
2. Amnion
3. Allantois and
4. Chorion

These membranes are formed outside the embryo from the trophoblast only in amniotes (reptiles, birds and mammals) and perform specific functions.

These are of four types



Formation of extra embryonic membranes.

1. Yolk sac:

It is formed of splanchnopleur (inner endoderm and outer mesoderm) and is well developed in reptiles, birds and prototherians having poly lecithal egg. It is mainly digestive in function so acts as extra embryonic gut. It also absorbs the dissolved yolk and passes it to developing embryo. In human beings, it is vestigial.

2. Amnion:

It is innermost fold of somatopleur (inner ectoderm and outer mesoderm) above the embryo. Between the amnion and embryo, there is amniotic cavity filled with amniotic fluid secreted by both embryo and amnion. Amnion protects the embryo while amniotic fluid acts as shock absorber and also prevents dessication of embryo.

3. Allantois:

It is a fold of splanchnopleur developed from the hind gut of the embryo. It is well developed in amniotes with polylecithal egg (e.g., reptiles, birds and prototherians) and stores the nitrogenous wastes of the embryo so acts as extra embryonic kidney. In most of eutherian, it combines with chorion to form allantochorion which takes part in placenta formation (Allantoic placenta). It is reduced in human beings.

4. Chorion:

It is outermost fold of somatopleur and surrounds the embryo. In reptiles, birds and prototherians, allantochorion acts as extra embryonic lung and helps in exchange of gases. But in primates including human beings, only chorion forms the placenta (chorionic placenta) while in other eutherian, allantochorion forms allantoic placenta.

4.2. TYPES OF PLACENTA

The **placenta** (also known as **afterbirth**) is an organ that connects the developing fetus to the uterine wall to allow nutrient uptake, provide thermo-regulation to the fetus, waste elimination, and gas exchange via the mother's blood supply, fight against internal infection and produce hormones to support pregnancy. The placenta provides oxygen and nutrients to growing babies and removes waste products from the baby's blood. The placenta attaches to the wall of the uterus, and the baby's umbilical cord develops from the placenta. The umbilical cord is what connects the mother and the baby. Placentas are a defining characteristic of placental mammals, but are also found in some non-mammals with varying levels of development

The placentas of all eutherian (placental) mammals provide common structural and functional features, but there are striking differences among species in gross and

microscopic structure of the placenta. Two characteristics are particularly divergent and form bases for classification of placental types:

1. The gross shape of the placenta and the distribution of contact sites between fetal membranes and endometrium.

2. The number of layers of tissue between maternal and fetal vascular systems.

Differences in these two properties allow classification of placentas into several fundamental types.

Classification Based on Placental Shape and Contact Points

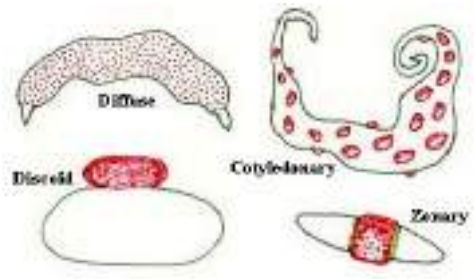
Examination of placentae from different species reveals striking differences in their shape and the area of contact between fetal and maternal tissue:

- **Diffuse**: Almost the entire surface of the allantochorion is involved in formation of the placenta. Seen in horses and pigs.

- **Cotyledonary**: Multiple, discrete areas of attachment called cotyledons are formed by interaction of patches of allantochorion with endometrium. The fetal portions of this type of placenta are called cotyledons, the maternal contact sites (caruncles), and the cotyledon-caruncle complex a placentome. This type of placentation is observed in ruminants.

- **Zonary**: The placenta takes the form of a complete or incomplete band of tissue surrounding the fetus. Seen in carnivores like dogs and cats, seals, bears, and elephants.

- **Discoid**: A single placenta is formed and is discoid in shape. Seen in primates and rodents.



Classification Based on Layers Between Fetal and Maternal Blood

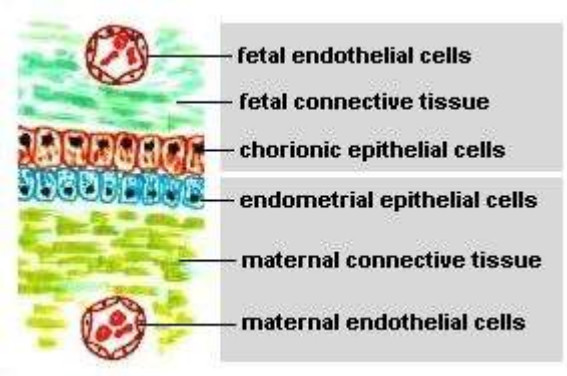
Just prior to formation of the placenta, there are a total of six layers of tissue separating

maternal and fetal blood. There are three layers of fetal extraembryonic membranes in the chorioallantoic placenta of all mammals, all of which are components of the mature placenta:

1. Endothelium lining allantoic capillaries
2. Connective tissue in the form of chorioallantoic mesoderm
3. Chorionic epithelium, the outermost layer of fetal membranes derived from trophoblast

There are also three layers on the maternal side, but the number of these layers which are retained - that is, not destroyed in the process of placentation - varies greatly among species. The three potential maternal layers in a placenta are:

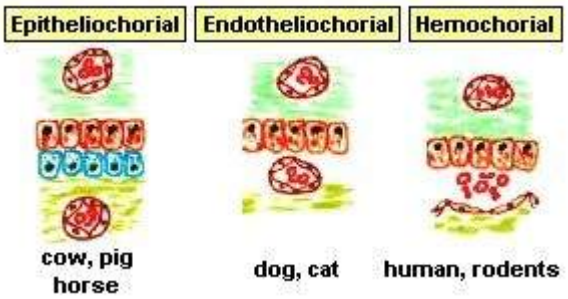
1. Endothelium lining endometrial blood vessels
2. Connective tissue of the endometrium
3. Endometrial epithelial cells



One classification scheme for placentas is based on which maternal layers are retained in the placenta, which of course is the same as stating which maternal tissue is in contact with chorionic epithelium of the fetus. Each of the possibilities is observed in some group of mammals.

Type of Placenta	Maternal Layers Retained			Examples
	Endometrial Epithelium	Connective Tissue	Uterine Endothelium	
Epitheliochorial	+	+	+	Horses, swine, ruminants

Endotheliochorial	-	-	+	Dogs, cats
Hemochorial	-	-	-	Humans, rodents



In humans, fetal chorionic epithelium is bathed in maternal blood because chorionic villi have eroded through maternal endothelium. In contrast, the chorionic epithelium of horse and pig fetuses remains separated from maternal blood by 3 layers of tissue. One might thus be tempted to consider that exchange across the equine placenta is much less efficient that across the human placenta. In a sense this is true, but other features of placental structure make up for the extra layers in the diffusion barrier; it has been well stated that "*The newborn foal provides a strong testimonial to the efficiency of the epitheliochorial placenta.*"

Summary of Species Differences in Placental Architecture

The placental mammals have evolved a variety of placental types which can be broadly classified using the nomenclature described above. Not all combinations of those classification schemes are seen or are likely to ever be seen - for instance, no mammal is known to have a diffuse, endotheliochorial, or a hemoendothelial placenta. Placental types for "familiar" mammals are summarized below, with supplemental information provided for a variety of "non-familiar" species.

Type of Placenta	Common Examples
Diffuse, epitheliochorial	Horses and pigs
Cotyledonary, epitheliochorial	Ruminants (cattle, sheep, goats, deer)
Zonary, endotheliochorial	Carnivores (dog, cat, ferret)
Discoid, hemochorial	Humans, apes, monkeys and rodents

Placentation in mammals

In placental mammals, the placenta forms after the embryo implants into the wall of the uterus. The developing fetus is connected to it via an umbilical cord. Animal placentas are

classified based on the number of tissues separating the maternal from the fetal blood. The placentation types found in animals are:

- **endotheliochorial placentation**

In this type of placentation, the chorionic villi are in contact with the endothelium of maternal blood vessels. (e.g. in most carnivores like cats and dogs)

- **epitheliochorial placentation**

Chorionic villi, growing into the apertures of uterine glands (epithelium). (e.g. in ruminants, horses, whales, lower primates)

- **hemochorial placentation** (e.g. in higher order primates, including humans, and also in rabbits, guinea pigs, mice, and rats)[]

In hemochorial placentation maternal blood comes in direct contact with the fetal chorion, which it does not in the other two types.[]It may avail for more efficient transfer of nutrients etc., but is also more challenging for the systems of gestational immune tolerance to avoid rejection of the fetus.

During pregnancy, placentation is the formation and growth of the placenta inside the uterus. It occurs after the implantation of the embryo into the uterine wall and involves the remodeling of blood vessels in order to supply the needed amount of blood. In humans, placentation takes place 7–8 days after fertilization.

In humans, the placenta develops in the following manner. Chorionic villi (from the embryo) on the embryonic pole grow, forming chorion frondosum. Villi on the opposite side (abembryonic pole) degenerate and form the chorion laeve (or chorionic laevae), a smooth surface. The endometrium (from the mother) over the chorion frondosum (this part of the endometrium is called the decidua basalis) forms the decidual plate. The decidual plate is tightly attached to the chorion frondosum and goes on to form the actual placenta. Endometrium on the opposite side to the decidua basalis is the decidua parietalis. This fuses with the chorion laevae, thus filling up the uterine cavity[]

In the case of twins, **dichorionic placentation** refers to the presence of two placentas (in all dizygotic and some monozygotic twins). **Monochorionic placentation** occurs when monozygotic twins develop with only one placenta and bears a higher risk of complications during pregnancy. Abnormal placentation can lead to an early termination of pregnancy, for example in pre-eclampsia

4.3. BASIC PROCESSES IN DEVELOPMENT

Determination

Determination is the commitment of a particular cell in the embryo to form particular cell type in the developing embryo. The cells giving rise to various organs with different forms and functions arise from a single celled zygote. Thus, zygote is said to be totipotent as it gives rise to whole organism. As development proceeds the number and kinds of cells arising from the zygote become restricted. Such cells are pluripotent because these cells have the ability to develop into any other type of cell in the animal body.e.g., kidney cells, heart cells, liver cells, nerve cells etc. Finally in the developing embryo, they are destined to become a single cell type hence called unipotent.e.g., stem cells. A cell which has the potential to generate different cell types loses its potential (potency) during development and become restricted in making one or a few cell types. This process by which cells become progressively restricted in their potency is referred to as determination. Thus, a cell is said to be determined once it has been instructed/programmed or has somehow decided itself to become a specific cell type at some advanced stage of developmental process.

Mechanism of Determination

There are three ways by which cell commitment can take place. The first mechanism of commitment involves the cytoplasmic segregation of determinative molecules during embryonic cleavage, wherein the cleavage planes separate qualitatively different regions of the zygote cytoplasm into different daughter cells. Each cell becomes specified by the type of cytoplasm it acquires during cleavage and cell fate is thereby determined without any reference to neighbouring cells. This mechanism of committing cell fate is called autonomous specification because the cells are specified by their own internal cytoplasmic components.

A second way of committing cell fate involves interactions with neighbouring cells. Here the cells originally have the ability to follow more than one path of differentiation, and the interaction of these cells with other cells or tissues restricts the fate of one or both of the participants. This type of cell fate determination is sometimes called conditional specification because the fate of a cell depends upon the conditions in which it finds itself. All organisms use both autonomous and conditional means to specify different cell types.

Many insects utilize a third means to determine cell fate. Here, interactions between maternal components within the syncytial blastoderm occur before the cell membranes separating nuclei have formed. In syncytial specification, major cell fate decisions are made even before cells have formed.

Embryonic induction

During embryogenesis of multicellular organisms, some cells are induced to differentiate into specific organs or tissues by the presence of other tissues. This process of inducement by cells is called embryonic induction or dependent differentiation. The embryonic induction is a morphogenetic effect in which one embryonic tissue transmits a chemical stimulus that influences other embryonic part to produce a structure that otherwise would not come into existence. The cells/embryonic tissue that induce or control the developmental fate of the neighbouring cells/embryonic tissue in an embryo are/is called inducers or organizers. The chemical substances which the inducers release to guide the fate of adjacent cells are called evocators or inductors. The cells/tissue that respond to the stimulus is called responsive tissue or competent.

Primary Organizer/Neural Inductor

Fertilization involves the fusion of haploid male and female gametes to form diploid zygote. This zygote then undergoes rapid mitotic divisions to form blastomeres. These blastomeres adhere to each other and arrange themselves into unilayered epithelium called blastoderm. Then a fluid filled cavity called blastocoel appears in the centre of blastoderm. This hollow, spherical and uniepithelial thick embryonic stage is called blastula/blastocyst. The blastomeres of blastula are totipotent (that is having the ability to differentiate into whole organism) except one region of blastula called blastoporal lip. The blastoporal lip which is later on called chordamesoderm (Notochord + mesoderm) develops from grey crescent region of developing embryo. This blastoporal lip in normal course of development induces neighbouring blastomeres to develop into neural tube, hence called neural inductor. Since blastoporal lip is able to organize the whole embryo it is also called primary organizer. Because of this inducing capacity, blastoporal lip is also known organizing centre and the whole phenomenon is called as organizer phenomenon or induction.

Along with gastrulation growth, various organ systems of the embryo begin to differentiate and acquire the power of inducing the differentiation of later formed structures or organs such as eyes, ears, limbs and lungs. These organs develop organizing property and become the source of induction. Therefore, this series of organizers can be called as secondary, tertiary and quaternary organizers. One embryonic tissue interacts with the adjacent one and induces it to develop and this process continues in sequence.

Parts of organizer

During gastrulation, cellular movements occur that produce germinal layers. Endoderm is formed first as a single layer around blastocoels. It forms primitive gut or archenteron. In the

course of gastrulation, then ectoderm and mesoderm are formed. In the post gastrular stage (Neurulation and Organogenesis) organizer is located in the roof of archenteron and is distinguished into two parts:

(i) Anterior head organizer including: Archencephalic organizer, inducing development of fore brain, eye, nasal-pit and Dueterencephalic organizer, inducing development of hind brain, ear vesicle.

(ii) Posterior trunk organizer (spinocaudal inductor), inducing the development of spinal cord and its associated organs.

Mechanism of Neural Induction

During gastrula stage the roof of archenteron contains the primary organizer and it causes the overlying ectoderm to develop into neural tube through the following two mechanisms:

One mechanism suggests that, the contact of two cellular layers at archenteron-ectoderm interface may provide a device that produces changes in the geometry and behaviour in the cells of overlying ectoderm that determines it to develop into neural plate, which acts as a primodium of nervous system.

The other mechanism supports the chemical mediation of the inductive effect. It suggests that chemical substances are produced and released by inducing chordamesoderm cells (primary organizer of later stage) at the archenteron-ectoderm interface may act upon, or enter the ectodermal cells to initiate cellular activities leading to neural development

4.4. BASIC PROCESSES IN EMBRYONIC DEVELOPMENT

Cell Differentiation

All cells of the body in an organism develop from a single cell called zygote. The formation of a variety of cells from a single cell is called differentiation. Cellular differentiation is the process by which a less specialized cell becomes a more specialized cell.

Characteristics of differentiation

1. Differentiation usually involves changes in cell shape, the appearance of new subcellular organelles or rearrangement of old ones, synthesis of specific products in the cytoplasm (e.g., haemoglobin in RBCs) and in some cases their release through the plasma membrane (e.g., extracellular matrix in cartilage).

2. Differentiation involves the events by which cells and other parts become different form one another and also different from what they were originally. Thus during embryogenesis there arise different organs and systems of organs, each made up of tissues in various combinations and arrangements. And each of these tissues comprises certain kind of cells that

are clearly recognizable as different from other kinds: the cells of skeletal muscle are quite different from liver cells.

3. Differentiated cells are able to perform special functions. For example, nerve cells are capable of conducting nerve impulses to great distances, liver cell secretes bile and so on.

Types of Differentiation

1. Morphological differentiation: During the course of multiplication, individual cells and groups of cells become structurally different from other cells and groups of cells. For example, from a common starting point in generalized ectoderm, nerve cells and epidermal cells acquire distinguishing features of size, shape and internal structure. Morphological differentiation occurs in various ways: (i) cell migration (ii) cell aggregation (iii) localized growth (iv) enlargement (v) constriction (vi) fusion (vii) splitting (viii) folding (ix) evagination (x) invagination etc.

2. Physiological or histological differentiation: In physiological differentiation, the individual cells and groups of cells acquire the ability to perform their special functions.

Every cell is capable of performing the process of metabolism. These functions are found in undifferentiated as well as in differentiated cells. Differentiated cells, however, are able to perform special functions. For example, nerve cells are capable of conducting nerve impulses to great distances at a high speed, liver cell secretes bile, melanophores produce pigment in their cytoplasm. These are special functions of nerve cells, hepatic cells and melanophores.

3. Chemical differentiation: In chemical differentiation, the individual cells and groups of cells become biochemically different from one another. For example, epidermal cells become keratinized, RBCs contain haemoglobin etc.

Mechanism of Differentiation

There are many ways by which cell differentiation can take place.

Cytoplasmic control: The eggs have certain substances called determinants of development in the cytoplasm. As development advances, these cytoplasmic determinants become unequally distributed in the cytoplasm of each cell at the time of cleavage such that each cell contain specific determinant to form particular cell type during the process of differentiation.

Environmental control: Cell interactions are very important in differentiation. At the stage of gastrulation, extensive cell movements and migrations occur and different types of cells interact with each other to act a embryonic inducers. This is known as embryonic induction.

Nuclelar control: As specialized cells from different tissues contain the same kind and number of genes, therefore, differences between specialized cells must be due to differential gene expression (changes in gene expression) i.e., due to repression of certain genes and activation of other genes in different cell types. It is established that increase in number of copies of one kind of gene (selective gene) occurs during differentiation through the mechanism of gene amplification. For example, immature RBCs are involved in the synthesis of only one kind of protein i.e., haemoglobin. There could be the possibility that gene amplification might give rise to increased amounts of mRNA, necessary for the synthesis of globin protein of haemoglobin.

Cell Death

Cell death, is a central mechanism controlling multicellular development, leads to deletion of entire structures (e.g., the tail in developing human embryos), sculpts specific tissues by ablating fields of cells (e.g., tissue between developing digits), and regulates the number of neurons in the nervous system. In the mammalian nervous system, for instance, the majority of cells generated during development also die during development.

Cellular interactions regulate cell death in two fundamentally different ways. Most, if not all, cells in multicellular organisms require signals to stay alive. In the absence of such survival signals, frequently referred to as trophic factors, cells activate a "suicide" program. In some developmental contexts, including the immune system, specific signals induce a "murder" program that kills cells. Whether cells commit suicide for lack of survival signals or are murdered by killing signals from other cells, recent studies suggest that death is mediated by a common molecular pathway. In this final section, we first distinguish programmed cell death from death due to tissue injury, then consider the role of trophic factors in neuronal development, and finally describe the evolutionarily conserved effector pathway that leads to cell suicide or murder.

Programmed Cell Death Occurs through Apoptosis

The demise of cells by programmed cell death is marked by a well-defined sequence of morphological changes, collectively referred to as apoptosis, a Greek word that means "dropping off" or "falling off" as in leaves from a tree. Dying cells shrink and condense and then fragment, releasing small membrane-bound apoptotic bodies, which generally are phagocytosed by other cells (Figure 23-45). Importantly, the intracellular constituents are not released into the extracellular milieu where they might have deleterious effects on neighboring cells. The highly stereotyped changes accompanying apoptosis suggested to early workers that this type of cell death was under the control of a strict cellular program.

Ultrastructural features of cell death by apoptosis. (a) Schematic drawings illustrating the progression of morphologic changes observed in apoptotic cells. Early in apoptosis, dense chromosome condensation occurs along the nuclear periphery. The cell

In contrast, cells that die in response to tissue damage exhibit very different morphological changes. Typically, cells that undergo this process, called necrosis, swell and burst, releasing their intracellular contents, which can damage surrounding cells and frequently cause inflammation.

Different kinds of cell death have been observed and were originally classified based on distinct morphological features: (1) type I programmed cell death (PCD) or apoptosis is recognized by cell rounding, DNA fragmentation, externalization of phosphatidyl serine, caspase activation and the absence of inflammatory reaction, (2) type II PCD or autophagy is characterized by the presence of large vacuoles and the fact that cells can recover until very late in the process and (3) necrosis is associated with an uncontrolled release of the intracellular content after cell swelling and rupture of the membrane, which commonly induces an inflammatory response. In this review, we will focus exclusively on developmental cell death by apoptosis and its role in tissue remodeling.Facts

Apoptosis has a crucial role in a variety of morphogenetic events.

Apoptosis can either shape an organ by the simple elimination of cells that are no longer required, without inducing tissue remodeling (e.g. digit individualization), or participate in morphogenesis by inducing cellular reorganization in the surrounding tissue (e.g. dorsal closure or genitalia rotation).

In normal conditions, apoptotic cells induce the formation of an actomyosin ring in their neighbors for their extrusion. In stress conditions, apoptotic cells can also produce mitotic signals to induce compensatory proliferation. Depending on the context, apoptosis can either generate a pulling force or act as a biological scissor to release the neighboring tissue.

The term ‘apoptosis’ was introduced by Kerr *et al.* to describe naturally occurring cell death in mammalian tissues. Since then, work in various model organisms has been instrumental in gaining insights into the mechanism and regulation of apoptosis, and in identifying the diverse biological roles of this process. The apoptotic pathway was first characterized in *C. elegans* where somatic cell death occurs in an invariant, cell lineage-directed pattern. In this organism, programmed cell death allows a single-cell lineage program to operate in each sex or in different parts of the animal, with only minor modifications. In other organisms, including insects and mammals, apoptosis is epigenetically regulated and is also important

for the removal of potentially harmful cells. In addition, apoptosis can function in a variety of morphogenetic events, such as, digits individualization.

Cells undergoing apoptosis show a series of well-characterized physical changes such as plasma membrane blebbing, permeabilization of the mitochondrial outer membrane, DNA fragmentation, nucleus disintegration and eventually cell disintegration into apoptotic bodies that are then engulfed and degraded by phagocytes. These steps involve a conserved molecular program that leads to the activation of caspases, a family of cysteine proteases that proteolyses numerous substrates in dying cells to facilitate cell clearance.

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