NETAJI SUBHAS OPEN UNIVERSITY

# STUDY MATERIAL

# POST GRADUATE ZOOLOGY

## PAPER - 1
## GROUP : A

Structure and Function
of Chordates &
Non-chordates

# PREFACE

In the curricular structure introduced by this University for students of Post-Graduate degree programme, the opportunity to pursue Post-Graduate course in Subjects introduced by this University is equally available to all learners. Instead of being guided by any presumption about ability level, it would perhaps stand to reason if receptivity of a learner is judged in the course of the learning process. That would be entirely in keeping with the objectives of open education which does not believe in artificial differentiation.

Keeping this in view, study materials of the Post-Graduate level in different subjects are being prepared on the basis of a well laid-out syllabus. The course structure combines the best elements in the approved syllabi of Central and State Universities in respective subjects. It has been so designed as to be upgradable with the addition of new information as well as results of fresh thinking and analyses.

The accepted methodology of distance education has been followed in the preparation of these study materials. Co-operation in every form of experienced scholars is indispensable for a work of this kind. We, therefore, owe an enormous debt of gratitude to everyone whose tireless efforts went into the writing, editing and devising of a proper lay-out of the materials. Practically speaking, their role amounts to an involvement in invisible teaching. For, whoever makes use of these study materials would virtually derive the benefit of learning under their collective care without each being seen by the other.

The more a learner would seriously pursue these study materials the easier it will be for him or her to reach out to larger horizons of a subject. Care has also been taken to make the language lucid and presentation attractive so that may be rated as quality self-learning materials. If anything remains still obscure or difficult to follow, arrangements are there to come to terms with them through the counselling sessions regularly available at the network of study centres set up by the University.

Needless to add, a great part of these efforts is still experimental—in fact, pioneering in certain areas. Naturally, there is every possibility of some lapse or deficiency here and there. However, these do admit of rectification and further improvement in due course. On the whole, therefore, these study materials are expected to evoke wider appreciation the more they receive serious attention of all concerned.

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Vice-Chancellor

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# POST GRADUATE : ZOOLOGY
# [M.Sc.]

## PAPER : GROUPS
## PGZO-1 : A(I) & A(II)

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# PGZO - 1
# Structure and Function of Chordates & Non-chordates

## Group–A (I)

## Group-A (II)

# Group–A (I)

## Structure and Function of Chordates

# Unit 1 ❐ Origin of Chordata

*Structure*

## 1.1 Origin of chordates

### 1.1.1 Introduction

The origin of chordates, and consequently of the vertebrates, is really shrouded in mystery. It was and is still a genuine paradox to the systematists as to what evolutronary changes in the general organization of the animal body led to the emergence of chordates. This leads us to the realm of earlier chordates or lower chordates represented at present by the three very interesting animal forms such as, *Balanoglossus, Ascidia* and *Branehiostoma*. Of these the last two are now unmistakably held as primitive true chordates, while the first one is possibly a hemichordate or a half-chordate, originating from the same ancestral stock some 500 or 550 million years ago from which the last two groups may or may not have arisen. Due to closer affinities amonget themselves and to the ancestors of the chordates they are frequently designated as the **'protochordates'**.

**19th Century concept** : Geoffray St. Hilaire (1818) was one of the earliest exponents to explain the origin of chordates. Later Dohrn (1875), Semper (1875-76), Owen (1883), Patten (1891-92), Gaskell (1896, 1898-1906) and others suggested that the chordates originated from some form of jointed invertebrates.

However, the present-day zoologists have eliminated most of the invertebrate phyla (except phylum Echinodermata) from the long list of possible ancestors of chordates.

**Diagnostic chordate characters** : Besides the three very unique and diagnostic chordate characters such as, the presence of a **notochord** (a pliant, rod-like structure-composed of a peculiar kind of connective tissue) sometime during life, a **hollow tubular dorsal nerve cord** lying just above the notochord and present sometime during life and the **pharyngeal gill slits,** also present sometime during life, there are a number of other fundamental characters of the chordates common to the members of some other phyla as well. These characters are bilateral symmetry of the body, a true body cavity lined with mesoderm, triploblastic condition and metamerism of the body, cephalization and concentration of the nerve tissue and sense organs toward the head and a ventrally located heart.

The hemichordates represent a problem. Though they possess the pharyngeal gill slits, the adult lacks a notochord and a hollow, dorsal. tubular never cord of a true chordate (although the nerve sheet is rolled up to form a sort of nerve cord in both the collar and the trunk).

### 1.1.2 Search for the ancestry of chordates : different views

Since later part of the nineteenth century various conflicting views have been proposed to explain the origin of chordates. Although most of these earlier views tracing the origin of chordates from a number of invertebrate phyla have been discarded now-a-days, yet among the major invertebrate phyla the annelid and arachnid theories claiming possible source of chordate ancestry, also discarded now, have been briefly mentioned here. Only the echinoderm theory having an utmost relevance with and holding key to chordate ancestry has been discussed here at length.

1. **Annelid theory :** Semper (1875-76), Dohrn (1875), Minot (1897) and many others suggested that the annelids were the possible ancestors of chordates and vertebrates, based on segmentation, muscles, nerves, bilateral symmetry, etc. The theory explains that by reversing the body of an annelid, the chordate stage may be derived.

   But the fact that the annelid worms lacking a notochord and the gill slits and showing developmental processes and the larva entirely different from those of the chordates, have been left out as the possible source of chordate ancestry.

Young (1981) comments that it is exceedingly unlikely that such animals have given rise to chordates.

2. **Arachnid theory** : Some authors like Gaskell (1908) and patten (1912) postulated the arachnid theory of the origin of vertebrates. Patten had drawn some similarities between the armoured eurypterids and the armoured earlier vertebrates like the ostracoderms. According to Patten, the living *Limulus* is the neareat living survivor of the invertebrate ancestor of vertebrates. Gaskell (1908) described 'ammococte—Limulus' theory. Both Gaskell and Patten cited a number of palaeontologial evidences in favour of their arachnid theory. A pair of median eyes of eurypterids and their ancestors have been linked up with the single median eye of ammocoets larva of the cyclostomes and a pair of median eyes of ostracoderms.

   However, the basic design of the two phyla are so different that mere correspondences between particular parts can not be accepted as phylogenetic relationship.

   Hence the arachnid theory has also been discarded.

3. **Echinoderm theory** : Among the major phyla of non-chordates, the echinoderms present the most striking evidence of chordate ancestry. The formation of mesoderm in Amphioxus and in the echinoderms, the presence of three body segments, the form of **tornaria larva** of *Balanoglossus* and. the **auricularia larva** of echinoderms and the larval bilateral symmetry present strong resemblances between the two groups. Some authors consider that this is not possible without genetic affinity.

   Larval forms usually represent past ancestral forms. Larval evidence strongly suggests that the prechordates evolved as small, bilaterally symmetrical animals possessing many of the features of larval echinoderms, or the hemichordates but lacking specializations of either the fully formed chordates (or vertebrates) or the echinoderms. With the assumption of radial symmetry and sessile mode, these forms gave rise to the echinoderms, but some of them retained the original bitateral symmetry and by developing gill stits, better musculature and notochord gave rise to the chordates.

   Biochemistry also provides strong evidence for a relationship between the echinoderms and the chordates. The similarity of blood serum, muscle chemistry and the presence of phosphocreatinine and phosphoarginine as suppliers of energy to muscles in both echinoderms and chordates claims much closer relationship between the two groups. These two compounds are not present together in other invertebrate phyla.

4. **W. Garstang's (1894, 1928) neotenous larva theory :** Garstang (1894) proposes that the ancestry of chordates and of the vertebrates is to be searched in the larval stages of the invertebrates rather than in their adults. According to him, as also pointed out by **de Beer,** 'if the ciliated bands on the auricularia larva of a sea-cucumber were to become accentuated and rise up as ridges leaving a groove between them, and if these ridges were to fuse, converting a groove into a tube, a structure would be produced which has all the relations of a nervous system'. Garstang's theory further asserts that if the larval forms of such animals persisted and became sexually mature, they would provide exactly the necessary material for the evolution of the chordates.

   Towards the close of nineteenth century, Garstang's theory was no doubt sensational, but throughout the twentieth century, several other views by different authors, based on critical appreciation of the subject, assessed and accepted Garstang's theory in a modified form and not in the manner in which Garstang assumed the origin of chordates to have taken place.

5. Some authors regard that the similarity between the larval forms may be produced by similar ecological factors. H.B. Fell (1965), working on echinoderm phylogeny, concludes that the similarity of the free-swimming larvae of certain echinoderms and *Balanoglossus* supplies no trustworthy evidence of common ancestry. Gregory (1951) states that *Balanoglossus* may not be a chordate at all and that its baglike ciliated swimming larva is merely a parallel adaptation for securing suitable location for their sessile adults.

6. N. J. Berrill (1955) suggests the following larval sequence : **Echinoderm—auricularia → hemichordate-tornaria → protochordate-ascidian tadpole → permanently free-swimming chordate.**

   This view agrees with Garstang's theory but not in the manner in which Garstang assumes the changes to have taken place. However, Berrill's view places the ascidians is the main line of the origin of chordates, at least as larvae.

7. Weichert and Presch (1977) suggests that we must look for the origin of chordates and vertebrates not among free-living active groups but among small, sessile filter-feeding forms.

   The most generally accepted view is that the protochordates represent specialized off shoot stages along the main line of evolution of the vertebrates from a shared ancestor with echinoderms. Hence, according to weichert and Presch (1977), the earliest sessile filter-feeding forms represents today by the hemichordates gave rise to a mobile larval condition represented today by the urochordates and to a group which left the sessile adult condition through neotenic development, representing the ancestral form from which two groups, the cephalochordates and the earliest vertebrates arose.

8. Hyman (1959) and others also believe that the pterobranchs (Hemichordate) may be similar to the common ancestor of both the echinoderms and the hemichoidates.

9. Jefferies' (1975) view that the ancestry of chordates is to be found among the carpoid fossils (subphylum–Homalozoa; phylum–Echinodermata) which have an echinoderm-like skeleton of calcite has been known as 'calcichordate theory'

   **Jefferies' (1975) calcichordate theory :** Jefferies has argued that two of the carpoid orders, the "Cornuta' and 'Mitrata' should be placed in a separate subphylum 'Calcichordata' which while showing, echinoderm affinities are actually more closely related 'to the early chordates. Jefferies states that a cephalodiscus-like hemichordate gave rise to two lines in evolution, one by losing the gill-slits and elaborating the tentacles towards the echinoderms and the other by losing the tentacles and elaborating the left gill slits toward the early chordates whose earliest representatives was the carpoid comuta.

10. Barrington (1979) states—'The view that larval biology contains the key to chordate ancestry is highly speculative, although it does not lack biological plausibility. It is not the only way of looking at the problem'. Barrington has also discussed about Jefferies' view.

11. Young (1981) states that the Bateson (1886)—Garstang (1894) theory of the origin of chordates is correct. The chordates are related to the sessile lophophore-feeders which in course of time acquired the pharyngeal gill slits and their larva to have muscles, a notochord and a nerve tube. Then by

paedomorphosis the sessile stage disappeared and the free chordates began their course of evolution.

12. Pough, Heiser and McFarland (1990) comment—The phylogenetic affinities of chordates and invertebrates remain uncertain. Although the weight of evidence

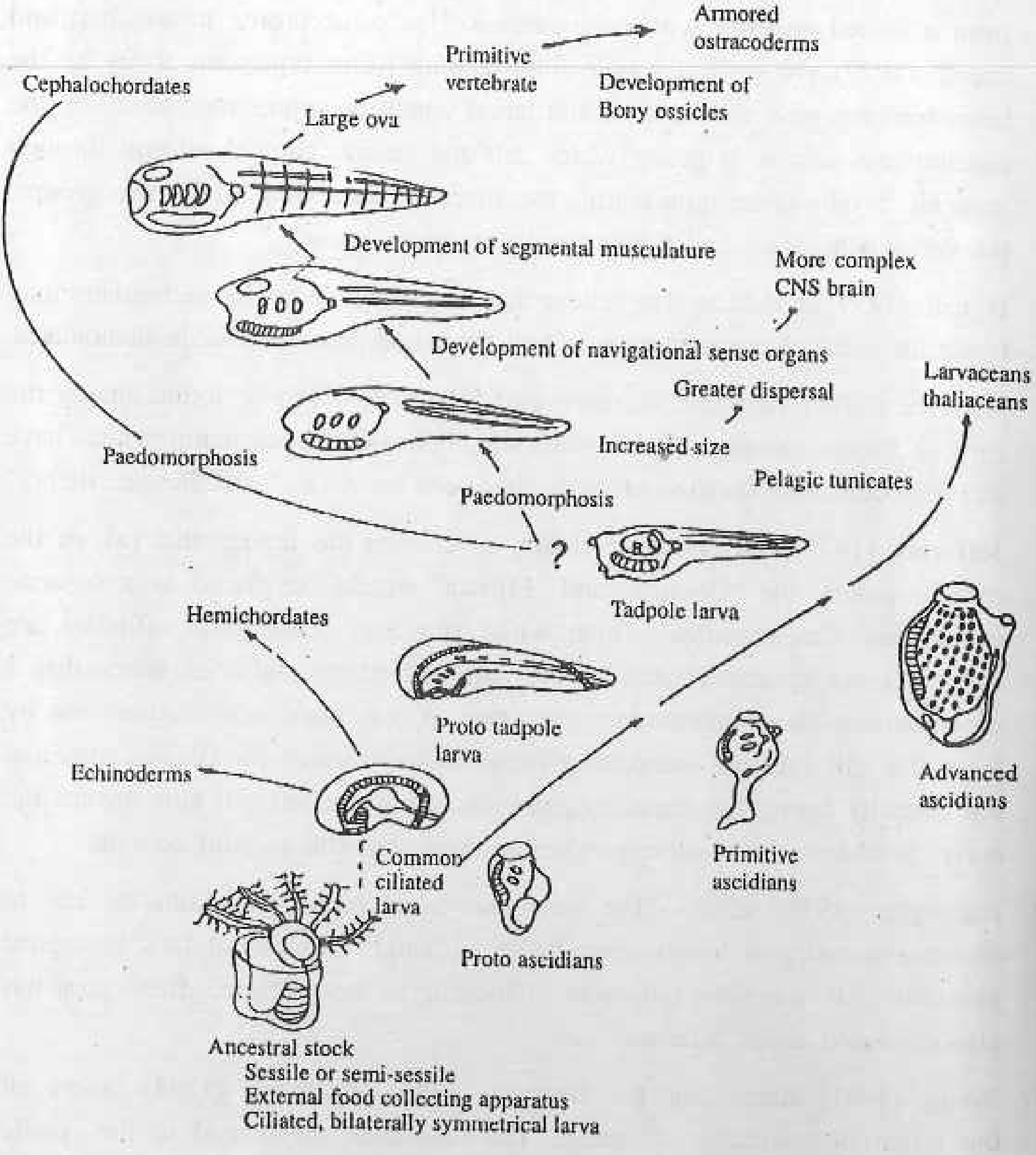

**Fig 1.1** : Garstang's hypothesis of the origin of vertebrates by paedomorphosis from an ancestral lophophorate (Based on Pough, Heiser and McFarland, 1990)

fovours deuterostomes as the group from which chordates arose, no living adult or larval deuterostomes can yet be identified as their closest living relatives.

### 1.1.3 Concluding remarks

We have travelled long to explore the source for the origin of chordates. Different authors have put forward their different view points. Young (1981) partly supports Jovan Hadzi's (1963) proposition for the classification of the animal kingdom and clearly states that the Bateson-Garstang theory of the origin of chordates is correct. Romer (1965, 1970) points out that the cordates have arisen from some sort of echinoderm-like ancestor. His ancestral prototype is a sessile filter-feeder which acquired pharyngeal gill-slits and their larval forms possessed muscles, notochord and nerve tube. Then by paedomorphosis the sessile stage disappeared and the free chordates started their evolution.

Inspite of this generally agreed proposition, an element of uncertainty still remains due to lack of adequate concrete evidences.

## 1.2 Concept of protochordata

Phylum chordata is comprised of four subphyla : subphylum Hemichordata, subphylum Urochordata (= Tunicate), subphylum Cephalochordata and Subphylum Vertebrata (= Craniata). Of these the first three subphyla are usually designated as 'Protochordates', although due to doubtful phylogeny of the hemichordates, many authors disagree to consider the group in the main line of the evolution of protochordates. Even then they agree that the study of the hemichordates is relevant in understanding the evolution of. protochordates, particularly the tomaria larva of Balanoglossus and the Pterobranchs. Hence, the **true protochordates are represented by the tunicates and the cephalochordates.**

The salient features of each group of the protochordata are described below with comments on their phylogeny and systematic position.

I. **Subphylum–Hemiclordata :**

This group comprises two classes :

**Class 1. Enteropneusta** (acorn worms)

e.g., *Balanoglossus* sp.

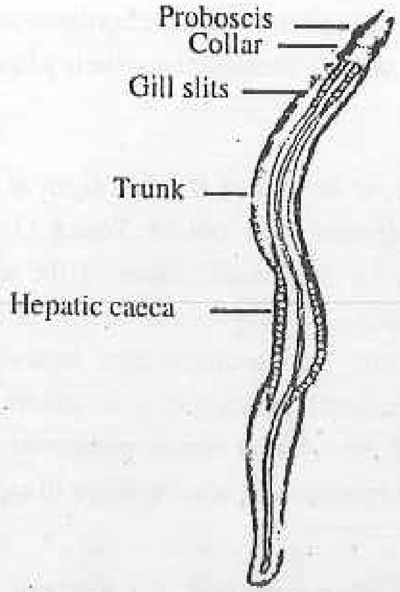

Fig 1.2 : *Balanoglossus* sp. (entire acorn worm)

**Class 2. Pterobranchia** (Feather gills)

e.g., *Cephalodiscus* sp.

**Note** : The name *Balanboglossus* was first introduced by Delle Chiaje in 1829. Larval affinities between Echinodermata and *Balanoglossus* was first observed by Johannes Muller in 1846. Metschinikoff (1870), Huxley and Bateson (1885) assigned it to the chordate rank.

Dawydoff (1948) introduced the term **'stomochordata'** for this group.

### A. Anatomical Peculiarities

The anatomical peculiarities of *Balanoglossus* as a popular example of the class enteropneusta are enumerated below :

**External Characters :**

1. worm-like ciliated body divisible into proboscis, collar and trunk.
2. numerous paired gill slits on the dorsal surface of the trunk.
3. a pair of genital ridges behind the branchial region.
4. two prominences of hepatic caeca occur behind the branchial region.

**Internal Characters :**

5. **Alimentary canal and associated structures :**

   (i) mouth ventral and lies in a groove at the base of the proboscis and collar.

   (ii) straight alimentary canal with terminal anus.

   (iii) pygochord may be present as an epithelial outgrowth from the intestine.

   (iv) gastrocutaneous pores connect alimentary canal with the surface; skin profusely ciliated all over the body.

   (v) anterior part of the trunk contains a wide pharynx which possesses a series of U-shaped gill slits; the gill slits either open into an atrium formed by lateral folds that turn upward, leaving a long middorsal opening or in many cases the stits open into gill pouches (except in *Ptychodera)* and through them to the exterior.

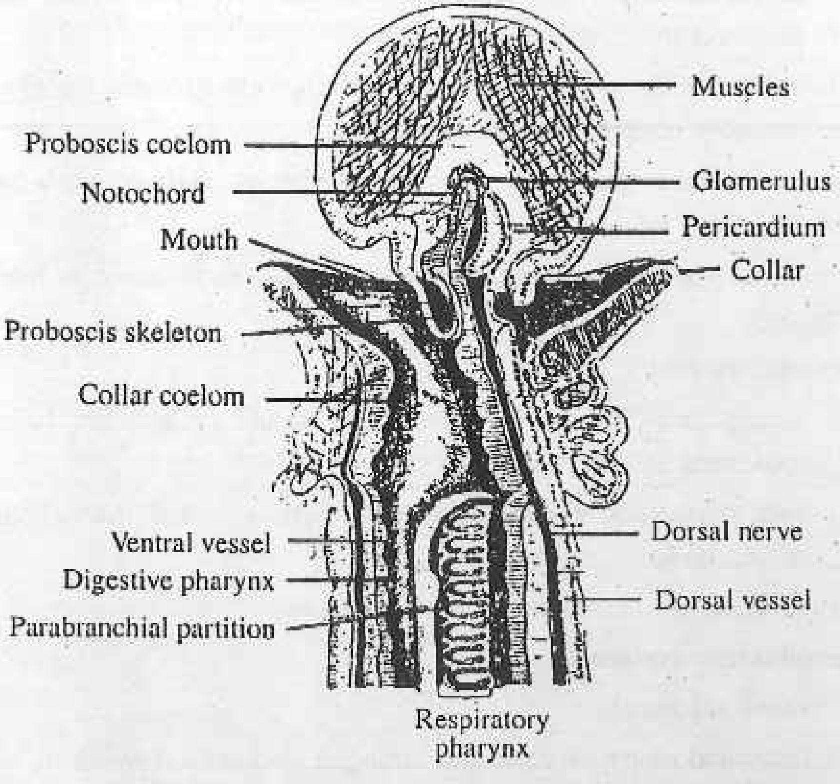

Fig 1.3 : Sectional view of the anterior end of *Balanoglossus* sp.

(vi) two limbs of the U-shaped slips are separated by tongue bars that are supported by skeletal rods—forked median and unforked lateral, connected by transverse rods, the synapticulae.

(vii) gills absent, the whole branchial apparatus serving as food collecting chamber : filtering out excess water.

6. **Stomochord :**

   (i) dorsal wall of a part of the pharynx projects forward into the proboscis after giving off a short ventral branch; the diverticulum contains a narrow lumen and its walls are made up of vacuolated cells. This structure has been homologized by many authors as the notochord; on ventral surface of the diverticulum lies the proboscis skeleton that bifurcates behind into flattened bars on either side or the buccal carity.

7. **Blood vascular system :**

   (i) presence of dorsal and ventral longitudinal vessels.

   (ii) dorsal sinus or heart situated at the posterior part of the proboscis, enclosed by a sac.

   (iii) in front of the sinus, a number of vessels form a plexus, the glomerulus, probably exerctory in function.

8. Absence of endostylar organ, but ventral part of pharynx partly separated from the rest.

9. Numerous **hepatic caeca** in the anterior part of the intestine as folds of the body wall.

10. **Nervous system :**

    (i) echinoderm-like sheet of nerve fibres and cells occur beneath the epidermis all over the body.

    (ii) both dorsal and ventral nerve strands may extend throughout length of the body.

    (iii) absence of the organs of special sense.

11. **Reproductive system :**

    (i) sexes separate.

    (ii) testis and ovary saccular and arranged in double rows along branahial region and they open by pores to the exterior.

(iii) larva is a **'yornaria'.**

(iv) development similar to that of echinoderms; cleavage holoblastic like that of amphioxus and ascidians; gastrulation by invagination; coelom enterocoelic, later tripartite into proboscis, collar and trunk coeloms.

(v) *Balanoglossus* may replace lost parts of the trunk through regeneration.

**B. Ciliary mode of feeding**

Food particles are driven to mouth by cilia of proboscis. Respiratory current produced by cilia of gill slits drive water from the gill slits to the exterior through gill pouches. Food particles, sand, mud, etc. are entrapped by proboscis and drawn in the postero-ventral surface of proboscis where there is a ciliary organ with sensory cells. A sample of particles pass over this organ. The sand or mud is taken into the gut and pass out through anus as casting.

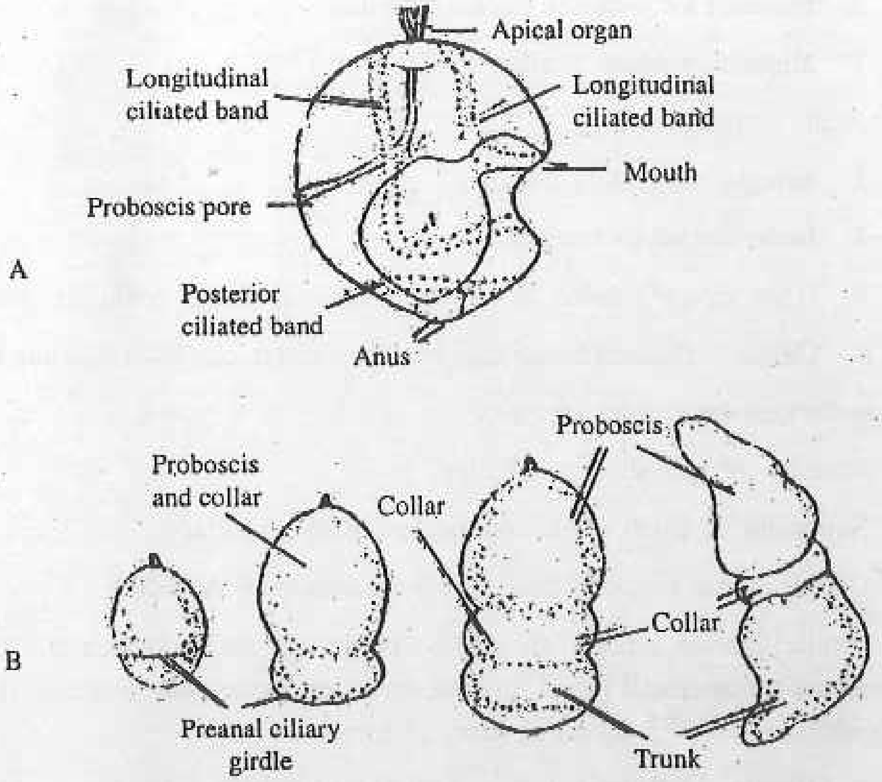

Fig 1.4 : A. Young tornaria lerva of *Balanoglossus* (Lateral view); B. Metamorphosis of the tornaria larva (Based on S.N. Prasad, 1972)

## C. Affinities of Balanoglossus

*Balansoglossus* and the other hemichordates show their affinities with so may non-chordate phyla that their systematic position as a chordate still remains controversial. To assign them the rank of a chordate or a protochordate based both on their larval and adult stages is not universally agreed, rather the subject has remained open to criticism since long back in the face of strong arguments and counte-arguments.

Some of their affinities with non-chordates as well as chordates are mentioned below :

### I. With Annelida :

A. Larval similarities (between Tornaria and Trochophore) :

1. presence of anteriorly placed apical plate.
2. presence of postoral circlet of cilia.
3. alimentary canal similar.

B Adult similarities :

1. straight alimentary canal.
2. Heart dorsal to the gut.
3. Body cavity formed from segmentally arranged coelomic pouches.
4. Collar of *Balausglossus* may be compared to clitellum of some annelids.

Dissimilarities (adult and larva) :

1. Absence of gill slits in annelids.
2. Nephridia of trochophore unrepresented in tornaria.
3. Double nerve cords of *Balanoglossus* absent in Annelida.

The similarities are superficial, as the two groups are fundamentally different. Trochophore is the ancestral larval form of the invertebrates, and hence, it may have some connection will the ancestral form of tornaria.

**Note** : Affinities of **Balanoglossus** with **Graphtolithina** (Hydrozoa, Cnidaria), **Nemertina** (Entoprocta) and **Phoronida** (Ectoprocta) as advocated by a few authors in the past have not been mentioned here due to lack of justifiable reasons.

**II. With Echinodermata :** The affinities of the lower Chordates with this group have been mentioned in the discussion of the origin of chordates. Striking similarities have been drawn between the tornaria larva of *Balanoglossus* and the auricularia and bipinnaria larvae of the echinoderms.

Similarities have been drawn chiefly on the basis of ciliated bands, enterocoelous coelomic sacs in three divisions, nervous system and glomerulus of enteropneusta with axial glands of Echinodermata, etc.

However, resemblances in the external appearance and ciliated bands have been considered superficial and appearance and the apical tuft of cilia and heart of tornaria have no corresponding structures either in auricularia or bipinnaria.

It has been stated by many authors that some of the larval similarities alone do not necessarily establish a near connection between the two groups, but it suggests that tornaria is nearest to echinoderm larvae. It is probable that both the echinoderms and hemichordates arose from a common ancestor. *Cephalodiscus* which is possibly the earliest of the hemichordates has been suggested by Grobben (1923) and later Jefferies (1971, 1975, 1979) as the common ancestor.

**III. With Chordata :** The chordate affinities of *Balansglossus,* first suggested by sedgwick and later supported by Bateson (1885), are based on three fundamental chordate characters which in their opinion are shared by *Balansglossus.* But later studies reveal that except the possession of gill slits (and that too is not in conformity as in the true chordates), the presence of other two characters such as, the notochord and the dorsal tubular nerve cord in *Balansglossus* is largely speculative.

**Notochord :** The solid, rod-like buccal or the pharyngeal diverticulum composed of vacuolated cells and present only in the proboscis has been designated by most authors as the stomochord and by a few others as the remains of a notochord. The argument in favour of notochord and skeletal plate in the collar being restricted to the proboscis only is based on the logic that a highly contractile animal like *Balanoglossus* has dispensed with a notochord of full length as it would have been disadvantageous to the animal.

However, most zoologists seriously question if this structure is really homologons with the true notochord. Nevertheless the hemichordate affinities to both non-chordates and chordates are necessary to understand the paradox in the course of evolution.

**Dorsal nerve cord** : It has already been mentioned that a dorsomedian insinking of the dorsal epidermis in the form of a dorsal nerve cord in the collar region has been compared to the hollow, dorsal tubular nerve cord of the chordates.

However, the nerve cord is tubular in the collar region only, open at both the ends, and there is also a ventral nerve cord which is not the characteristic of a chordate.

**IV. With Urochordata** : *Balanoglossus* shows similarities with the tunicates in the presence of notochord, respiratory pharynx, enterocoelic origin of coelom and dorsal nerve cord. However, the notochord in tunicates is present only in the larva and there is no retrogressive metamorphosis in *Balanoglossus.*

**V. With Cephalochordata** : *Balanoglossus* shows similarities with Amphioxus in the possession of segmentation of eggs, notochord, respiratory pharynx, enterococelic coelom and series of paired gonads.

Differences between the two groups are also plenty, particularly in the structure and position of the gill slits.

**D. Discussion on the systematic position of Balanoglossus and the hemichordates :** *Balanoglossus* and the hemichordates in general reflect characters which do not fully confirm to the three fundamental chordate characters. They are rather on the midway in the evolutionary history of chordates through protochordates with which the hemichordata claims to be as much an associate as with the echinoderms and certain lophophorate groups.

Around middle of the twentieth century several authors like komai (1951), Newell (1952), Rudall (1955), Newman (1955), Hyman (1959) and others strongly argued that the buccal diverticulum in *Balanoglossus* without the sheath and supporting function is not to be considered as the notochord of a chordate. Similar objections have also been raised against the occurrence of pharyngeal gill slits and the dorsal nerve cord in *Balanoglossus* as representatives of a true chordate. Present day zoologists agree that Garstang's (1894) theory of the origin of chordates and vertebrates is to be commonly accepted, although not unmistakably confirmed.

Hence the systematic position of the hemichordata has been retained as the earliest protochordata group (with incomplete chordate characters) that diverged possibly from an echinoderm-like lopohophorate ancestor, earlier than the emergence of the true protochordates like the urochordates and cephalochordata.

The undermentioned schematic representations by different authors will help understanding the origin and cause of evolution of hemichordates, echinoderms, urochordata and cephalochordates.

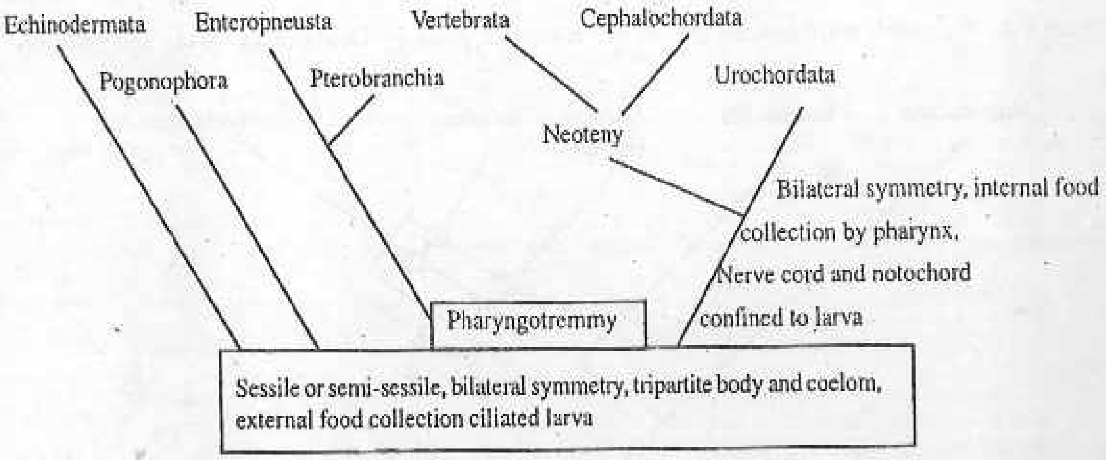

**Chart 1.1** : Evolution of Echinodermata and Hemichordata.

This interpretation suggests that the hemichordata and echinodermata were derived from sessile or semi sessile ancestor that were bilaterally symmetrical, with a tripartite body and coelom. They would have been microphagous and would have collected their food externally.

Nevertheless, the hemichordates have developed an important new character, **pharyngotremmy.** In course of time, it led to the development of internal food collection through specialized pharynx in a group which was the common origin of vertebrates, cephalochordates and urochordates. The larvae of this group perhaps derived from a ciliated larva of earlier form became pelagic and neotenic to give rise to the swimming adult from which the vertebrates and cephalochordates evolved.

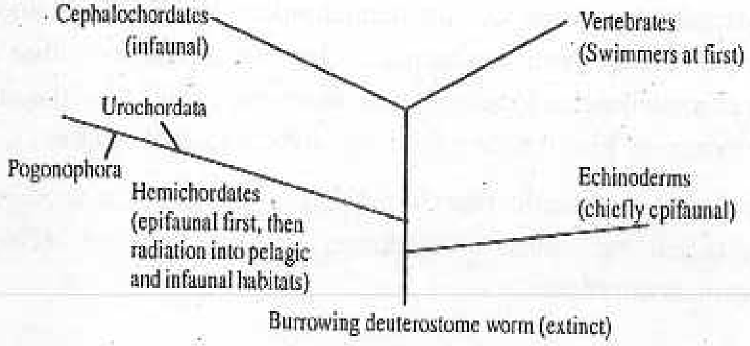

**Chart 1.2** : A possible phylogenetic tree of deuterostomia given by Dobzhansky, Ayala and Stebbins

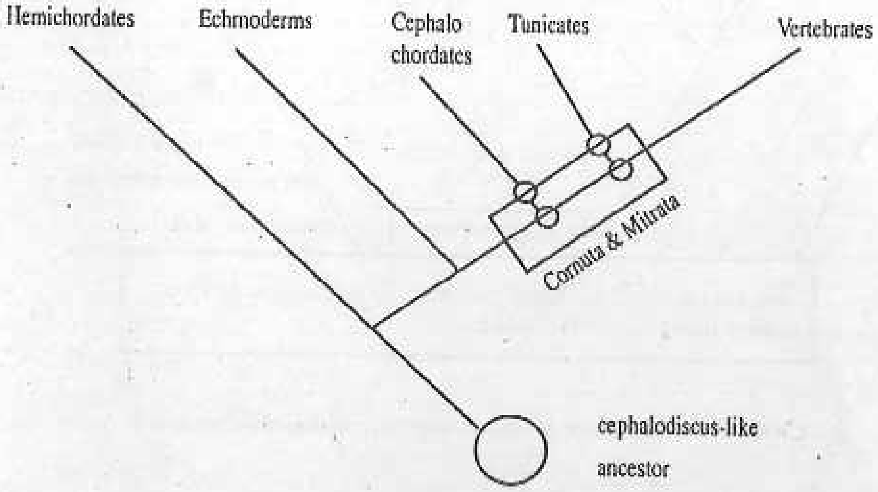

**Chart 1.3** : Proposed origin of hemichordates, chordates, echinoderms and vertebrates (Jefferies, 1971, 1975, 1979).

From the cepholodiscus-like ancestor, the hemichordates took their origin in the late pre-cambrian or possibly earliest cambrian times. A cephalodiscus-like hemichordate began to crawl on the sea floor on the right side—a condition known as 'dexicothetica'. It gave rise to calcichordata which is divided into two groups, namely, Cornuta and Mitrata.

## II. Subphylum-Urochordate (= Tunicata) :

This group comprises three classes :

### Class 1. Ascidiacea

e.g., *Ciona, Clavelina; Ascidia*

**Class 2. Thaliacea**

e.g., *Salpa; Doliolum*

**Class 3. Larvacea**

e.g., *Oikopleura*

This subphylum includes animals commonly known as sea-squirts which inhabit the sea bottom as sessile filter feeders. This group offers a variety of forms living in diverse habits and habitats. The members of this group may live separately or in colonies and their tadpole larva only depicts the fundamental characteristics of chordates.

### A. Anatomical peculiarities

Some of the salient features of the group are enumerated below :

(i) The entire external surface of the body is invested by a test or tunic; hence the name Tunicates.

(ii) The adults are mostly sessile, the free end bearing two pores, the mouth and atriopore, both carried on siphons.

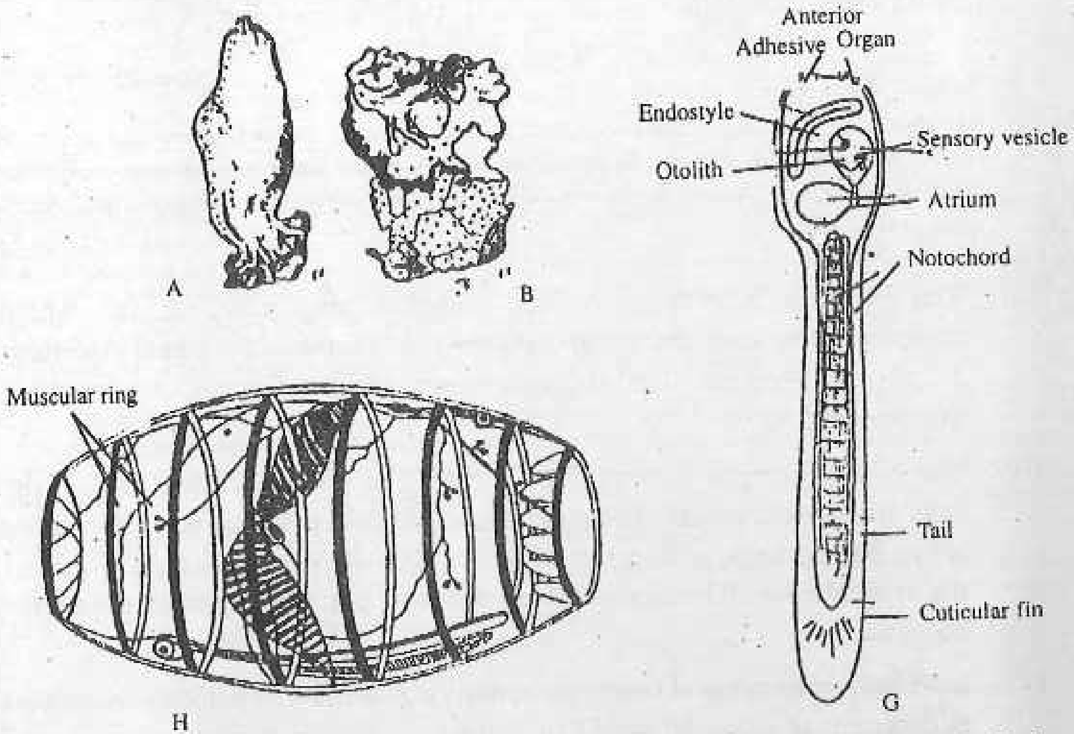

**Fig 1.5** : Urochordata : A, Ascidia (entire); B, Hardmania (entire); G, An ascidian tadpole larva; H, Doliolum (entire).

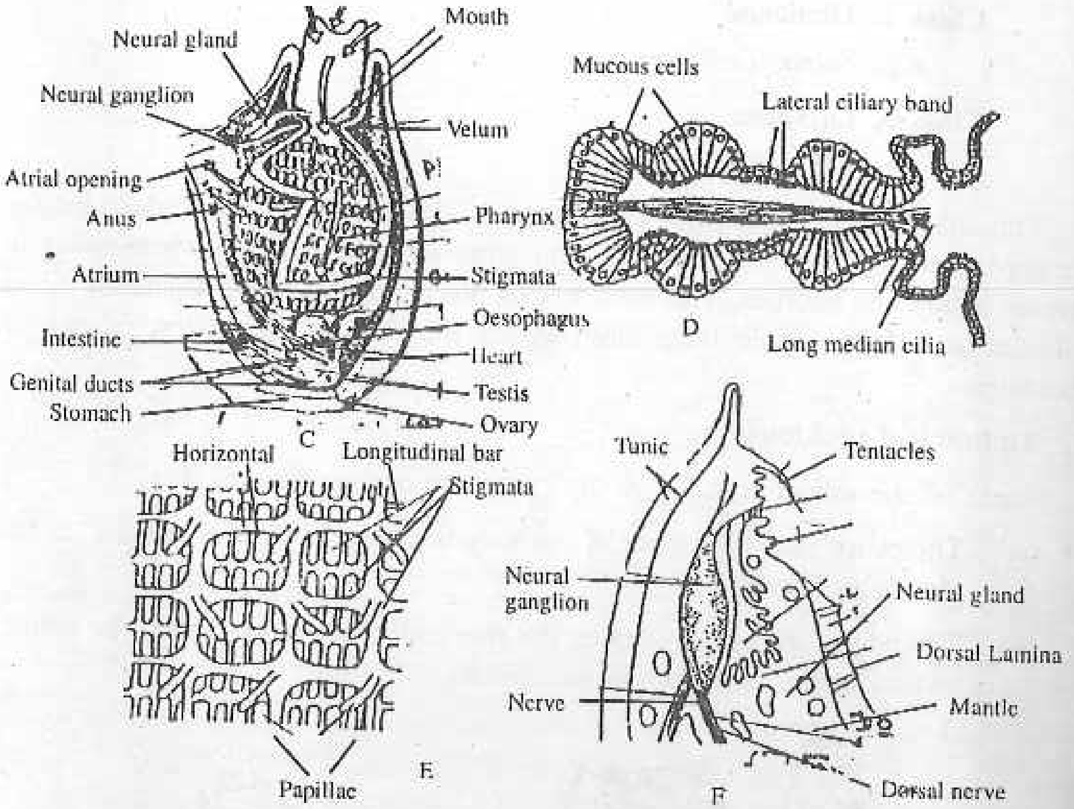

**Fig 1.5** : Urochordata : C, Longitudmial section of Ascidia showing various organs and course of water current through pharynx; D, Magnified view of endostyle; E, An enlarged view of the pharyngeal wall; F, Antero-dorsal view of an ascidian showing neural gland and neural ganglion.

(iii) The pharynx is a huge saclike chamber, the branchial sac which communicates with the atrial cavity by a number of vertical apertures called the stigmata. The stigmata bears series of papillae containing muscles and cilia.

(iv) The roof of the sac is formed by a ridge the **dorsal lamina** and on the floor lies the **endostyle.** There are about 10,000 square areas, each bearing about 20 **stigmata**, giving rise to about 200,000 stigmata on each side of the branchial sac. The stigmata bear series of **papillae** containing muscles and cilia.

(v) In the **hypopharyngeal tract**, the endostyle is formed as a highly developed mid-ventral pharyngeal band that extends from near the oesophagus upto the oral siphon.

The **endostyle** is glandular having two rows of mucous cells separated by rows of ciliated cells. The cilia of the median row of cells along the floor of the endostyle are extremely long appearing as tufts of flagella.

(vi) The dorsal lamina is the middorsal corrugated ridge of the inner wall of the pharynx. Its free edge may be armed with tentacle-like processes called the **dorsal languets.** The dorsal lamina and the endostyle are joined by the peripharyngeal ciliary bands.

(vii) In adult tunicates, the notochord completely degenerates but well represented in the tadpole larva, extending from the tip of the tail up to the pharyngeal region.

(viii) The tadpole larva is bilaterally symmetrical, but not the adult stage.

(ix) The adult tunicate is non metameric, its mesoderm remains unsegmented. The only indication of metamerism is observed in the repetition of gill slits, which Gregory (1951) states as a case of **'secondary polyisomerism'**.

(x) The coelom in tunicates is either completely absent or greatly reduced.

(xi) The digestive system is well represented; from the pharynx the short oesophagus leads to a large saclike stomach, a short intestine and rectum that opens near the atriopore.

(xii) The blood vascular system needs special mention. The heart is saclike and lies below the pharynx.

The blood spaces have no true endothelial lining, and are without capillaries and valves.

Another interesting feature is the periodic reversal in the direction of blood flow.

(xiii) The nervous system is. simple with a single, elongated nerve ganglion lying between the oral and atrial siphons. Ventral to this ganglion, there is a neural gland which spans by a duct into the pharynx.

The dorsal nerve cord, absent in the adult, is well represented in the ascidian tadpole larva.

(xiv) The sea squirts are hermaphrodite, the saclike ovary and testis open by their ducts close to the atriopore. Fertilization is external in solitary forms, internal in the colonial forms. Cleavage and gastrulation are in general similar to those of amphioxus. The developmental process only can strongly establish the true chordate characters of a tunicate.

(xv) **Ascidian tadpole larva and retrogressive metamorphosis :** 'In **Ascidia,** the larva that develops within the follicle hatches out as a fish-like **ascidian tadpole larva.** The larva has an oval head and a long tail supported by the notochord (that runs all throughout the length of the tail), a hollow dorsal nerve cord and the pharynx perforated by gill slits. The larval head is provided with three adhesive papillae, one middorsal and two ventrolateral.

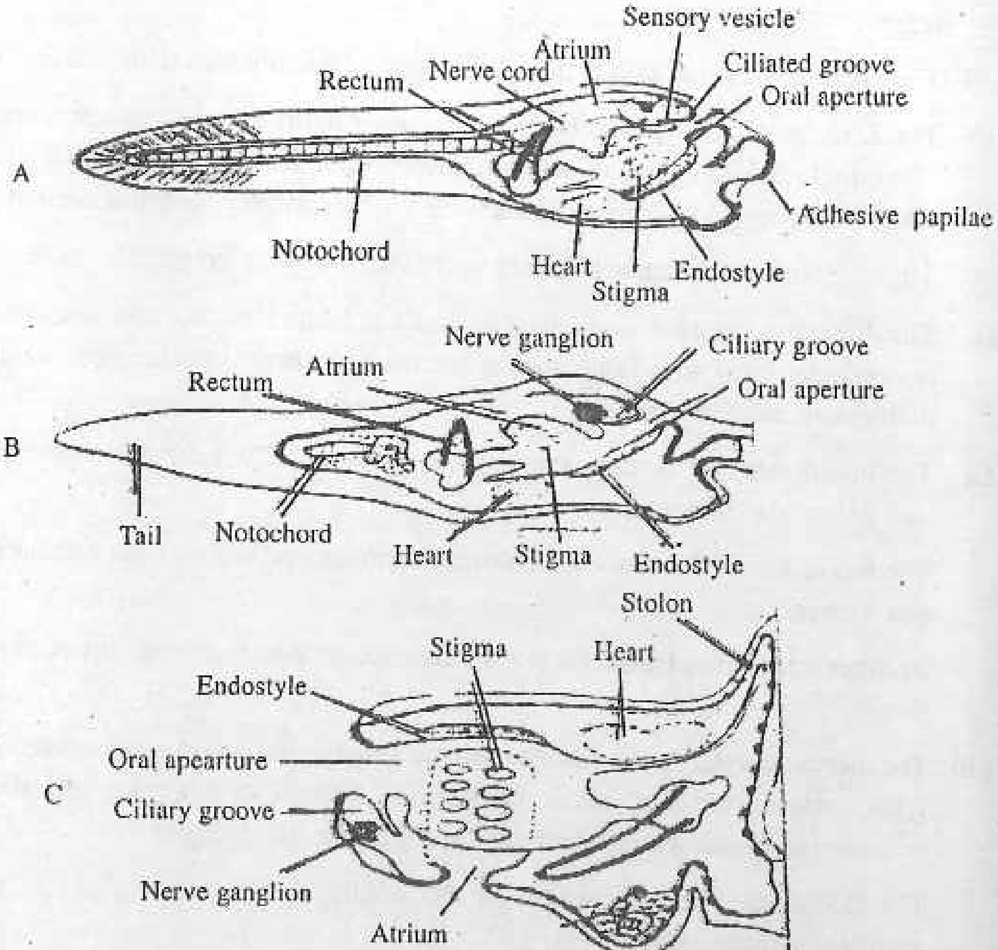

**Fig 1.6 :** The free-swimming tadpole metamorphoses into the sessile adult (from Parker and Haswell, after Seelinger) : Based on S. N. Prasad, 1972.

The caudal half of the tail is provided with a dorsoventrally continuous caudal fin. The nervous system is represented by a hollow, dorsal nerve cord running dorsal to the notochord up to the tail and in front enlarged to form the **cerebral vesicle** within which lie the lens cells, visual cells and single statocyst with an otolith.

The notochord is ensheathed and on either side of the notochord there are three rows of muscle cells derived form the mesodermis. The epicardium, heart, mesenchyme cells lie caudal to the endostyle. The larva does not take any food and its alimentary canal is poorly developed. The pharynx has a single pair of gill slits opening into the atrium.

The larval development proceeds for a short period of only one or two days after which the larva sinks to the bottom and finds a suitable surface for attachment with the help of the adhesive papillae.

The metamorphosis of the larva into adult occurs very fast. The long tail of the larva is first reduced and then totally lost. The notochord becomes reduced and first restricted to the trunk region and later completely disappears. The muscle bands degenerate and the dorsal nerve cord is reduced to a neural ganglion. The trunk becomes broader and it accommodates a spacious, large pharynx.

The metamorphosis is now complete for the sessile life of an ascidian. The loss of diagnostic chordate features in the adult ascidian has been occasionally mentioned as retrogressive but such changes may be interpreted as a survival strategy of the animal, as its short larval stage with chordate characters ensures distribution in search of a suitable locality for the adult. Besides this aspect, certain progressive changes also occur during metamorphosis such as enlargement of the pharynx with numerous stigmata, elaboration of the alimentary organs and of the atrium, development of the gonads and gonoducts from mesoderm, etc.

The significance of the tadpole larva in the life-history of an urochordate is enormous, as it reflects the origin of an ancestral chordate on its evolutionary pathway towards vertebrates.

Besides sexual reproduction, the tunicates also possess the power of regeneration. Often, they are found to multiply by budding in which case the tissue of the bud may be outer epicardial, mesenchymal, pharyngeal or atrial.

## B. Salient characters of the classes

### 1. Class–Ascidiacea :

(i) typically bottom-living sessile forms found in all the seas, mostly in the littoral zone (except ascidians that live in deeper water).

(ii) may be solitary (Ascidiae simplices) or colonial (Ascidiac composite); colonies formed by budding may include a number of neighbouring individuals *(Clavelina)* or embedded in a common gelatinous test *(Botryllus).*

(iii) Free-swimming tadpole larva metamorphoses into a sessile adult in which the tail, notochord and nerve cord are completely lost, only the pharynx becomes greatly enlarged with numerous stigmata.

e.g., *Aseidia; Clavelina*

### 2. Class–Thaliacea :

(i) free-swimming pelagic tunicates living in warm and temperate seas.

(ii) notochord and tail are absent in the adult.

(iii) test thin, transparent and traversed by complete *(Doliolum)* or incomplete *(Salpa)* muscle bands, the contraction of which helps the animals to shoot through water.

(iv) atriopore located posteriorly, opposite the mouth.

e.g.; *Doliolem; Salpa*

### 3. Class–Larvacea :

(i) very small, planktonic, neotenous animals that feed by filtering non-planktonic organisms.

(ii) instead of the test, each animal builds a 'house' secreted by the 'oikoplastic epithelium' of the skin.

(iii) broad tail is supported by notochord and muscle cells.

(iv) nerve cord is persistent.

(v) pharynx has two stigmata, directly opening to the exterior.

(vi) atrium is lacking.

*e.g., Oikopleura*

## C. Evolutionary position of tunicates

It has already been mentioned in the discussion on the origin of chordates that the tunicates establish two very important aspects in their life history such as, branchial feeding replacing tentacle feeding in the sessile adult and their characteristic tadpole larva assuming a fishlike chordate form with fundamental characters of a chordate. Garstang's (1928) neotenous larva theory provides, plausible explanation how the adult tunicate organization may be derived from that of a sessile lophophore-feeding animal and its larva taking origin from an echinoderm-like larva. If the larval form persists and becomes sexually mature (neoteny), it becomes the potential source for the origin of chordates and vertebrates and in the course of evolution the sessile adult stage is eliminated from the life-history.

## III. Subphylum—Cephalochordata :

The cephalochordates e.g., *Branchiostoma* (Amphioxus) represent an ideal protochordate group whose adult members are provided with all the fundamental characters of a chordate. For this reason, amphioxus is considered for the 'Type' study of a generalized chordate, and it is described as a simplified chordate animal. Although both urochordates and cephalochordates are truly protochordates, the latter is unmistakably the nearest ally or a close relative to the ancestor of Craniata.

Since lower Ordovician time about 500 million years ago, amphioxus has relatively changed very little :

A short description of the anatomy and life history of Amphioxus is given below :

### A. Anatomical peculiarities of Amphioxus :

1. The adult Amphioxus has a lanceolate body, tapering at both the ends; hence the name, *Branchiostoma lanceolatus.*
2. The adult lives a semisessile life in coastal sandy bottom of the sea; it keeps rostral part of the body above the sandy bed allowing passage of the incurrent water carrying food particles through the mouth.
3. Adult *Branchiostoma* measures about 5 cm in length, fish-like laterally compressed and almost transparent.
4. Series of muscle blocks are known as **myotomes** which can be seen externally as the skin is devoid of pigment cells.

5. Pharynx is provided with numerous gill slits which lie covered by the two **metapleural folds**, one running along either side of the body and joining ventrally to form a spacious cavity, the **atrium**. The atrium opens externally as the **atriopore** where the two metapleural folds join posteriorly.
6. Body divisible into trunk and tail; head prolonged anteriorly as **snout** or **rostrum**.
7. Ventral to the snout and surrounding the mouth dorsally and laterally lies an **oral hood**.
8. About twenty **oral tentacles** or **buccal cirri** arise from margin of the oral hood; the cup-shaped cavity of the oral hood is called **vestibule**.
9. The **dorsal fin** running all along dorsally covers round the caudal end of the body and continues ventrally as the **ventral fin** up to the atriopore; a portion of the dorsal fin forms the narrow **caudal fin** around end of the tail. Ventrally the caudal fin extends up to the anus.
10. The dorsal and ventral fin folds are protected respectively by one row and two rows of serially arranged **fin-ray boxes** formed of connective tissue.
11. The outermost body wall is the epidermis formed of a single layer of columnar epithelial cells.
12. The muscle layer is present just beneath the subcutis in the form of serially arranged muscle blocks.
13. During locomotion or swimming, the muscle fibres of the myotomes do not contract all at a time.

    The alternate arrangement of the muscle blocks and longitudinal contraction of the muscle fibres bring about a curvature and transverse motion of the body. This becomes possible due to the presence of an elastic, rod-shaped notochord which prevents shortening of the body during contraction of the longitudial muscles.
14. The skeletal system in Amphioxus is formed of the following organs : **notochord and its sheath; sheetlike densely fibrous connective tissue; fin-ray box; oral hood skeleton** formed of gelatine; **pharyngeal skeleton**.

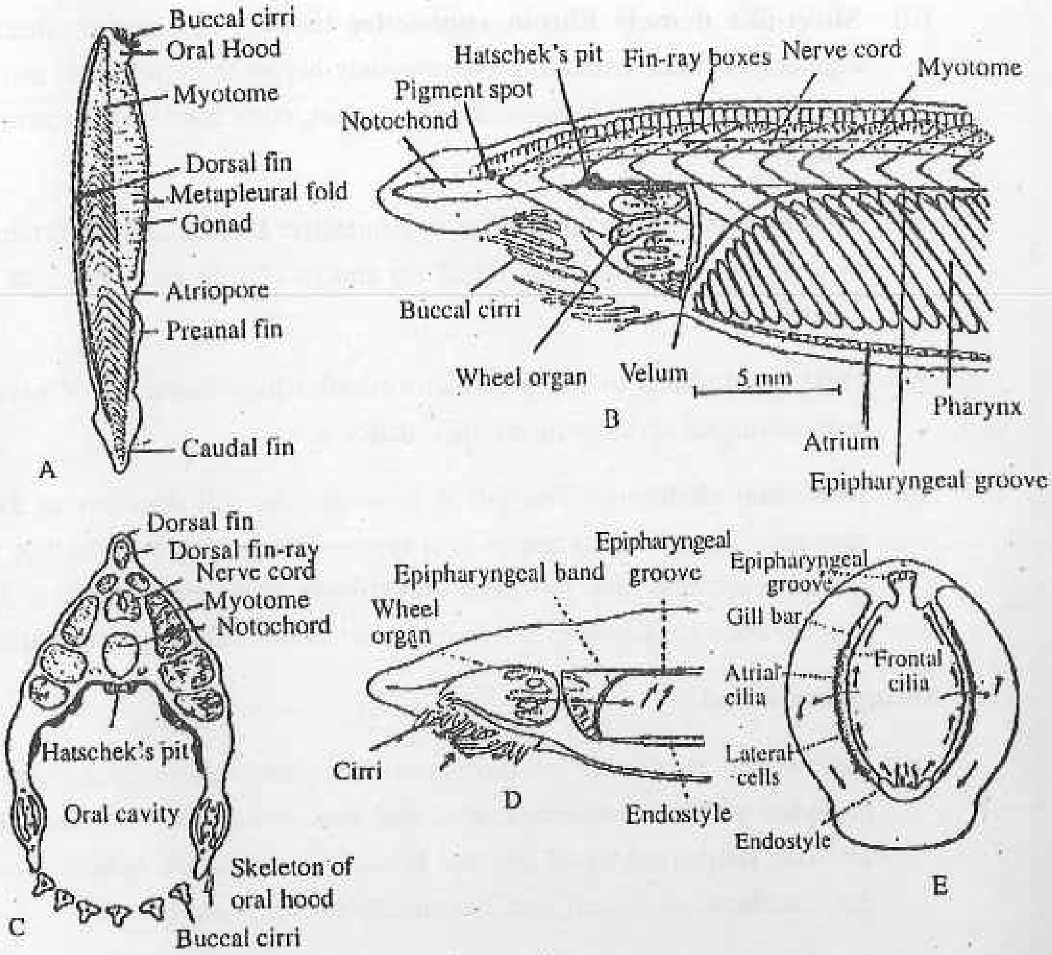

**Fig 1.7 :** *Branchiostoma* : A, External morphology; B, Lateral view of anterior end of *Branchiostoma;* C. Transverse section through the anterior end; D, Anterior end showing direction of food-current; E, Diagrammatic transverse section showing direction of food-currents by arrows.

(i) **Notochord and its sheath :** It is the most characteristic organ in the skeletal system; it extends as a rod-shaped structure from the end of the tail to the front end of the snout, lying just ventral to the dorsal nerve cord. The notochord is formed of transversely arranged plates, each constituted of vacuolated cells. Externally the notochord is enveloped by a notochordal sheath. The **turgor pressure** of the notochordal cells acting against the sheath renders elasticity as well as rigidity to the notochord.

(ii) **Sheet-like densely fibrous connective tissue :** A compact sheet of connective tissue extending continuously below the epidermis and the somatic peritoneum encloses the myotomes, notochord and the nervous system.

(iii) **Fin-ray box** : These are formed of connective tissues and are arranged in a single row below the dorsal fin and in double rows inner to the ventral fin.

(iv) **Oral hood skeleton** : A gelatinous circular loop made up of several rods arranged serially forms this skeleton.

(v) **Branchial skeleton** : The gill rods within the gill bars act as axial skeleton. The gill rods are of two types—the **primary rods** that are forked ventrally and the **secondary rods** that are unforked. The primary rods are joined by transverse connections called **'synapticulae'**.

15. **Alimentary canal** :

(i) Just ventral to the tip of the snout, the membranous oral hood is provided with about twenty buccal cirri containing many sensory cells. The cup shaped cavity of the oral hood is the vestibule behind which the membranous velum and the mouth opening are present.

(ii) The inner wall of the oral hood forms a complex organ, the **'wheel organ'** developing from a number of ciliated ridges. A whirlpool of water current is formed in this region and hence the name wheel organ.

(iii) **Hatschek's groove or pit** is a glandular pit that is located on the roof of the oral hood and between the ciliated folds of the wheel organ. The Hatschek's pit secretes mucous that spreads over the wheel organ.

(iv) **Pharynx** : The pharynx is wide, spacious, cylindrical and somewhat laterally compressed. The lateral walls of the pharynx are perforated by about two hundred obliquely arranged gill slits which increase in number with advancing age of the animal.

The gill slits do not open directly to the exterior but they connect the pharyngeal cavity with the atrial cavity.

Both primary and secondary gill bars are ectodermal on the outer face and endodermal on the inner face. Each primary or the secondary gill bar has a dense tuft of **frontal cilia** uniformly dense **lateral cilia** and a thin layer of **atrial cilia**.

(v) **Endostyle** : Besides the cilia of wheel organ, velar tentacles and gill bars, the inner wall of the pharynx also contains several ciliated areas of which endostyle is the most important organ. It lies on the floor of the pharynx and contains columns of ciliated cells alternating with several groups of mucous-secreting gland cells. The longer median cilia form the most prominent bundle.

It is believed (Barrington, 1965, 1979; Young, 1981) that the endostyle is the forerunner of the thyroid gland in vertebrates. They serve to produce iodinated mucoproteins which are then absorbed farther down the gut. Amphioxus containing mono- and di-iodotyrosine, as well as, tri-iodothyronine ($T_3$) and thyroxine ($T_4$). Unlike higher vertebrates, $T_3$ is more abundant in Amphioxus than $T_4$. However, the iodine compounds have no endocrine action in the animal itself.

Food particles are entangled in the sticky threads of mucous secreted by the endostyle and then various currents drive the sticky material toward the midgut. The peripharyngeal ciliated tracts and the epipharyngeal groove assist in the conduction of the food-containing sticky thread.

(vi) **Peripharyngeal band and epipharyngeal groove :** A longitudinal ciliated groove called the **epipharyngeal groove** lies along the dorso-median pharyngeal cavity, opposite the endostyle. This groove is extended caudally up to the oesophageal opening. Two more ciliated grooves, each running along either side of the pharyngeal cavity have connected the endostyle with the epipharyngeal groove. These are known as **peripharyngeal bands**.

(vii) **Other parts of the alimentary canal :** The pharynx opens behind into a narrow ciliated oesophagus which in turn opens into a broader midgut. A large sac-like midgut diverticulum arises from the right side of the pharynx and extends into the atrium. This organ appears to produce digestive enzymes. An ileo-colon ring is present behind the wide midgut. The ileo-colon ring passes backward to join a straight, narrow intestine or hindgut that opens out through the anus.

(viii) **Feeding mechanism in Amphioxus** : The characteristic feeding mechanism in Amphioxus is remarkable and quite complex. While collecting food particles, the water current carrying food enters into the mouth and leaves the body through the atriapore.

The course of water current is shown below :

Oral hood → Mouth → Pharynx → Gill slits
↓
Atrium
↓
Atriopore
↓
Out of the body.

The water current is chiefly produced by the movements of the lateral cilia. The microscopic plants and animals and other organic particles (e.g., protozoa, algae, diatom, etc.) are collected with the help of mucous. This type of food collection is known as **mucous ciliary mode of feeding** or simply **ciliary mode of feeding.**

The buccal cirri weed out the undesirable particles and allow access of only appropriate food particles through the mouth and oral hood. Due to velar reflex the **velar tentacles** come close and form another strainer.

The water current is mainly formed by the movements of the **lateral cilia of the gill bars.** Within the pharynx the frontal cilia of the gill bars move in such a manner that an upward current flows from medioventral to mediodorsal aspect of the pharynx and the mucous-containing water current from the endostyle reaches the **epipharyrgeal groove** and thence towards opening of the oesophagus.

Due to movements of the lateral cilia the water current from the pharynx reaches the atrium through the gill slits and the movements of the atrial cilia expels this water to the exterior through the atriopore.

The food collection process of Amphioxus is not continuous; it stops at times to facilitate the process of digestion (Bone, 1960).

Van Weel (1937), Bone (1958), Barrington (1965,1979), Young (1981) are of the opinion that the movements of the lateral citia are under the control of the nervous system.

In the ciliary mode of feeding in Amphioxus, the following two characteristics are specially noteworthy :

1. **The water current is produced entirely by the movements of the cilia.**
2. **In Amphioxus the water current is primarily food current; its role in respiration remains doubtful.**

**Digestion** : From the epipharyngeal groove, the food-chord, due to ciliary movement, reaches the midgut through the oesophagus. From the midnight the food-chord reaches the ileo-colon ring and begins to revolve there anti-clockwise due to movements of cilia in the ileo-colon ring. On the wall of the midgnt diverticulum or the caecum zymogen cells are present. Some of these cells are protein secretor and some secrete rough endoplasmic reticulum and secretory granules. Other cells are rich in glycogen and lipids and comparable to liver cells. The epithelium of the caecum secretes adequate digestive enzymes which get mixed up with the food particles. The food particles break down into finer particles due to rotational movements of food chord and the finest particles only enter into the caecum.

Both extracellular and intracellular digestion occur in Amphioxus. The extracellular digestion mainly takes place in the midgut and partly in the caecum.

The intracellular digestion through phagocytosis is rare among chordates, and hence, it is quite significant in Amphioxus.

16. **Respiration** : Haemoglobin is lacking in the blood of Amphioxus. Activities in their life processes are so minimum that whatever oxygen is absorbed in blood and transported to different tissues in the body is sufficient to meet the required energy for the animal.

Opinions by recent authors state that the $O_2$—$CO_2$ exchange takes place in the lacunae underneath the skin, particularly in the lacunae attached to the metapleural folds (Carter, 1967; Young, 1981).

17. **Blood vascular system** : Although the general scheme of the blood vascular system of Amphioxus and vertebrates has cartain common features, yet Amphioxus has got the following peculiarities of its own :

(i) Blood flows through blood vessels which do not form capillaries or network. Body tissues are directly bathed by blood.

(ii) Blood is colourless and there is no respiratory pigment in it.

(iii) Heart is absent; regional contraction of blood vessels keeps the blood flowing.

(iv) As the blood is not pumped out, by the heart and oxygen is not absorbed in the gill bars, the separation of arteries and veins in Amphioxus is doubtful. However, the naming of arteries and veins has been followed as in other vertebrates.

A pair of lateral dorsal aortae, one running on either side of the pharynx join in the posterior pharynx and continues caudally as a single dorsal aorta. The paired, aortae collect blood from the primary and secondary gill bars in the pharynx. Blood from the ventral aorta is brought to the gillbars through afferent branchial vessels and the efferent branchial vessels from the gill bars join the paired dorsal aortae.

18. **Exeretory system** : Unlike in other chordates the exeretory organs in Amphioxus comprise 80-100 pairs of nephridia. Besides these the Hatschek's nephridium, a pair of brown funnels, atrial papillae and gonad help in the process of excretion.

80-100 pairs of nephridia, lying on the dorsal surface of the secondary gill bars in the pharynx open into the atrium or peribranchial space. Each nephridium appears like a curved sac and has a vertical anterior and a horizontal posterior end. The nephridia are of ectodermal origin and are of the nature of protonephridia. Number of branches arise from the lateral wall of each nephridium, each branch is connected to a bundle of solenocytys (Kardong, 1998). Each solenocyte has a swollen part formed of cytoplasmic projections (pedicels) and a rod-shaped stand containing a long flagellum inside. Each swollen part is connected to its nearest glomerulus.

The solenocytes attached to glomerular blood vessels and pedicels are comparable to the podocytes and foot processes in vertebrates.

19. **Nervous system** : Among the protochordaters, the nervous system in *Branchiostoma* shows certain similarities comparable to that in vertebrates. As in vertebrates; a hollow dorsal spinal cord lies above the notochord. The hollow dorsal nerve cord becomes dilated anteriorly to form a cavity called **cerebral vesicle.** Its wall is thin as it is covered with a single layer of epithelial cells. The cerebral vesicle or the so called 'brain' is divisible into four parts. The dorsal nerve supplies a pair of nerves to each segment. On the floor of the third part of the vesicle lies a bundle of ciliated columnar cells known as **infundibular organs**. This part is comparable to the Infundibulum of vertebrates, as proved by Gomori test.

    In front of the cerebral vesicle some photoreceptive cells are present; these are known as **'pigment spot or macula'.**

20. **Sense organs** : In Amphioxus, various types of sensory cells are present. These serve as the sensory organs. These organs are the **pigment** or **macula, pigmented eyes, infundibular organ, Kolliker's pit and sensory receptors of skin.**

21. **Atrium** : Unlike in other vertebrates, the gill slits in Amphioxus open into a spacious chamber, the atrium. Atrium extends between the booywall and the pharynx. The atrium is elosed anteriorly and opens behind through the atriogore.

**Functions :**

(I) Atrium surrounds the soft pharynx and thus protects it. It also protects the body from friction while entering through a sandy hole.

(II) The excess water being filtered out of food particles is expelled through the atriopore.

(III) At the time of reproduction the gonads rupture and the gametic cells are thrown in the atrium and then find their exit through the atriopore.

(IV) The excretory materials collected by nephridia are thrown in the atrium to be expelled out through the atriopore.

22. **Coelom :** Besides atrium, coelom is the other body cavity which is covered by mesoderm. This cavity is quite spacious in the region of the midgut and hindgut behind the pharynx.

23. **Reproductive system :** Amphioxus is unisexual, but sexual dimorphism between male and female is not observed. The gonads (either ovary or testis) are located within the atrium at the ventrolateral wall of the pharynx as swollen sacs arranged serially. A pair of such reproductive sacs are present in each segment beginning from 31 to 51 segment. The reproductive sacs are mesodermal, while the gametic cells develop from the wall of the gonad, either testis or ovary. There are no reproductive ducts.

    Fertilization is external, taking place in sea water.

24. **Transverse section of the body of Amphioxus :** Transverse sections through the pharyngeal and intestinal regions of Amphioxus reveal certain common characters in both the regions and a number of dissimilarities. .

    **Similarities :** The following characters are common in both the pharyngeal and intestinal regions in Amphioxus :

    (I) The outermost covering of the body is formed of a single layer of columnar epithelial cells.

    (II) Beneath the epidermis lie successively the fibrous **cutis** and a thicker **subcutis.**

    (III) Underneath the subcutis lie a number of muscle segments or myotomes formed of striated fibres and separated from one another by myoseptum.

(IV) A dorsal fin along mid-dorsal line remains protected by a single row of fin-ray boxes.

(V) Dorsal to gut lies the notochord enclosed by notochordal sheath and the nerve cord lies dorsal to notochord.

**Dissimilarities :**

| Characteristics | Pharyngeal region | Intestinal region |
|---|---|---|
| 1. Shape | almost triangular | oval |
| 2. Metapleural fold | a pair of metapleural folds are<br>containing lymph spaces. | absence of metapleural folds.<br>present, one on either side, |
| 3. Ventral fin | absent; epipleura is formed ventrally. | a mid-ventral fin is present; the ventral fin is protected by two rows of fin-ray boxes. |
| 4. Coelom | not spacious | spacious |
| 5. Atrium | wide and spacious | narrow, present only on the right side |
| 6. Dorsal aorta | two; located dorsolaterally. | one, located dorsal to the intestine |
| 7. Alimentary canal | on both sides of the lateral wall of the large pharynx many gill bars and gill slits are seen; dorsally in the pharynx and on the pharyngeal floor, the epipharyngeal groove and the endostyle are present respectively. | intestine is rounded or oval. |
| 8. Caecum or midgut diverticulum | caecum seen on the right side of the pharynx. | caecum absent |
| 9. Reproductive organs | seen on the lateral walls of atrium | absent |
| 10. Brown funnel | two brown funnels are present in the dorsal coelomic cavity | absent |
| 11. Nephridium | present in the coelomic cavities of the primary gill bars | nephridia absent |

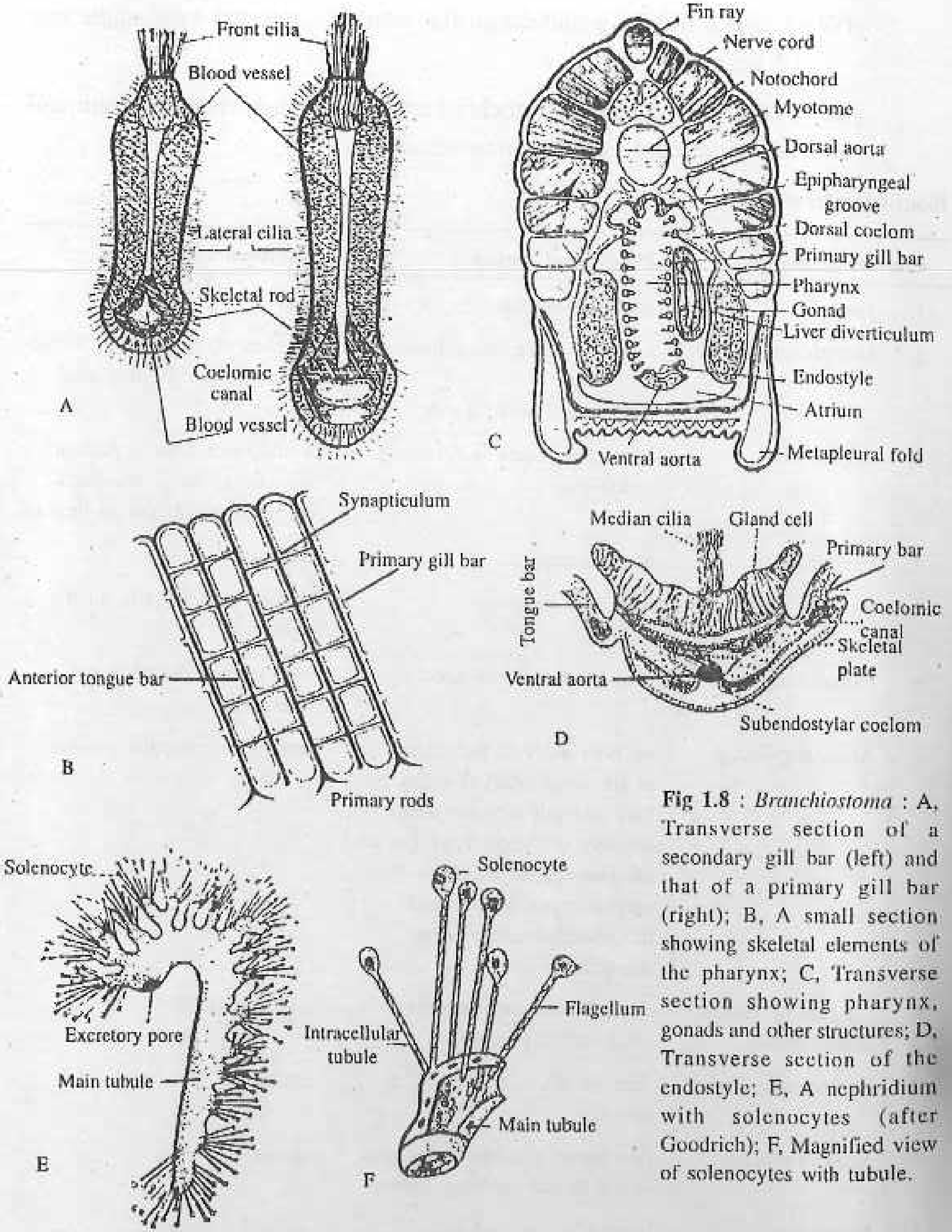

**Fig 1.8** : *Branchiostoma* : A, Transverse section of a secondary gill bar (left) and that of a primary gill bar (right); B, A small section showing skeletal elements of the pharynx; C, Transverse section showing pharynx, gonads and other structures; D, Transverse section of the endostyle; E, A nephridium with solenocytes (after Goodrich); F, Magnified view of solenocytes with tubule.

## B. Development and life history of Amphioxus

In Amphioxus development takes place in sea water outside the body.

The fertilized egg after quick and successive mitotic divisions forms the zygote that undergoes **holoblastic cleavage** but **unequal.** The cells resulting from cleavage are called blastomeres and the cellular ball is called blastula. Due to unequal rate of division, the cells produced are also unequal in size so that the smaller cells or **micromeres** occupy the animal pole and **macromeres** or the larger cells occupy the vegetal pole.

In 64-stage cellular ball, a cavity is formed centrally. It is called **blastocoel** which is filled up with a kind of jelly-like substance.

At the initiation of **gastrulation** the larger cells of **blastoderm** at the vegetal pole begin to turn inward, thus forming a two-layered cup which has its opening at the vegetal pole. The outer layer is now destined to form the epidermis and the nervous system derived form the ectoderm. The inner wall mainly forms the endoderm. The **presumptive notochordal** and **mesodermal cells** lying first at the rim of the cup soon migrate inward and occupy their usual locations. The opening at the vegetal pole through which the cells migrate inward is called blastopore and this type of inward movement of cells is called **invagination** and the central cavity is now known as the primitive gut or **archenteron.** The rims of blastopore form the **dorsal, ventral** and **lateral lips.** The mesodermal horns converge dorsally and come to lie around the presumptive notochord. Gradually within the embryo, the notochordal, mesodermal and endodermal layers become separated from one another. From dorsolateral wall of the archenteron two mesodermal pouches bulge out (by **enterocoelic method)** and then cut off from the archenteron, enclosing a cavity inside called the **coelom.** The mesoderm segments later unite forming a large coelomic cavity which is thus bounded by the outer **somatic layer and inner visceral layer of mesoderm.**

The **neural plate** developing from the ectoderm becomes folded to form the **neural tube.** The central canal of the neural tube remains connected to the **neuropore** and to the gut, and hence, known as the **neurenteric canal.** At this stage the embryos elongates and the larva comes out breaking through the egg membrane and actively swims with the help of long cilia. This larva is called **'Neurula'.**

Extreme asymmetry of the body is one of the main characteristics of this stage. The month appears anteriorly on the left side, while the single gill slit first appears on the right side. The food canal elongates anteriorly and forms two closed sacs, one on either side. The sac on the right side forms the head coelom, while that of the left forms the preoral pit. Later, the Hatschek's pit and the wheel organ develop from this preoral pit. At this time, the right side of the pharyngal wall becomes thickened with cilia and gland cells in the form of a 'v'-shaped structure called the **endostyle** which functions as the main site for the secretion of mucous. The gill

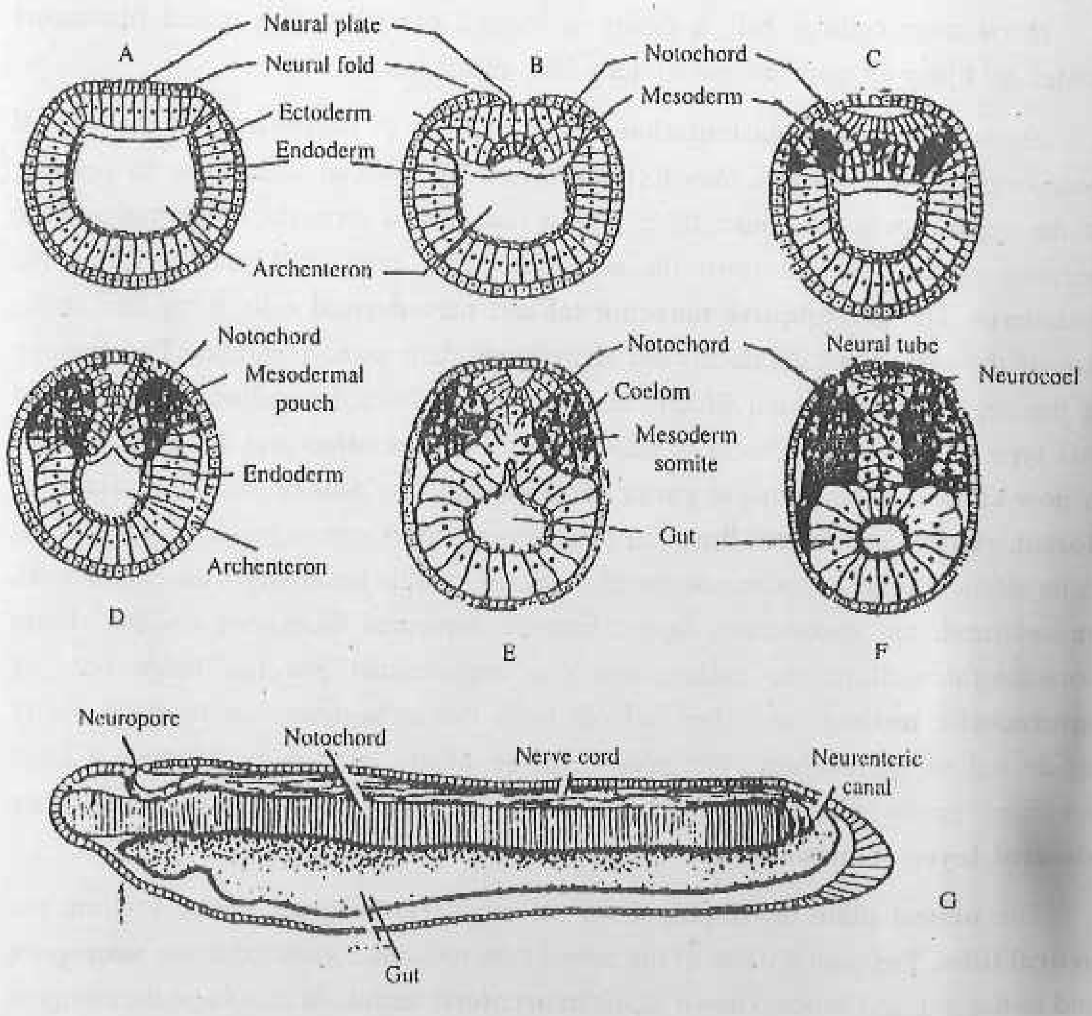

**Fig 1.9** : Developmental stages in *Branchiostoma.* A - F, Later stages of development; G, Neurula larva of *Branchiostoma.*

slits appear; serially in two rows, both (primary and secondary) occupying the right side. The pharyngeal wall widens and the gill slits become further divided by the tongue bars.

Like the adult animal, the larva also does not allow the undesirable particles to enter into the mouth with the help of free nerve endings and receptor cells occurring in this region.

Like the adult, the larva also may stop feeding temporarily to facilitate digestion. Many authors are of the opinion that the forward extension of the notochord results in asymmetry of the larva. But according to Van Wijhe (1925), Garstang (1928) and Bone (1958b), the location of different organs, particularly of the mouth and the mode of food collection by the larva are the main causes for larval asymmetry.

Wickstead and Bone (1959) have proved that during daytime the larvae live on the bottom surface and after sunset they come up to the upper surface. This migration is not for collection of food. Wickstead (1964) proposes that the contact of the larva with the sea-bottom induces metamorphosis. The gill slits are reorganized, the atrium becomes fully developed and the atripore opens to the exterior. The gill slits also gradually increase in number; the mouth becomes ventral and the fold around the mouth becomes the oral hood. The reproductive organs appear and the larva attains adulthood.

## 1.3 Terminal questions

1. Discuss echinoderm theory and modern concept on the origin of chordates with illustrations.
2. Discuss Jefferies' calcichordate theory and Garstang's neotenous larva theory on the origin of chordates.
3. What are protochordatres? Why are they named so? Mention the three essential chordate characters.
4. Describe affinities of *Balanoglossus* and discuss validity of including *Balanoglossus* among the protochordates.
5. Make a neat labelled sketch of the structures revealed in a median longitudinal section of *Balanoglossus* and comment on its chordate characteristics?

6. Describe Tomaria larva of *Balanoglossus* and elucidate its echinoderm affinities.

7. Is Urochordates a true protochordate? Why? Mention chordate characteristics of an ascidian.

8. Draw, label and describe structures of an adult ascidian.

9. Draw, label and describe the structure of an ascidian pharynx.

10. Draw, label and describe detailed structural organization of an ascidian tadpole larva.

11. Justify if the metamorphosis of an ascidian tadpole larva can be called retrogressive?

12. Draw, label and describe the digestive system and the mechanism of feeding of an ascidian.

13. What do you understand by ciliary mode of feeding? Describe the role of endostyle in *Ascidia.*

14. Mention the habit, habitat and external mosophology of *Amphioxus.*

15. Draw, label and describe the structures present at the anterior end of *Branchiostoma.*

16. Describe the ciliary mode of feeding in *Amphioxus,* illustrating movements of the food-current.

17. Describe the pharynx of *Branchiostoma* with special reference to its skeletal frame work.

18. Give an account of the development of mesoderm and coelom in *Branchiostoma.*

19. Describe affinities of *Amphioxus.*

20. Compare the excretory organs of *Branchiostoma* and *Ascidia.*

21. Draw, label and describe the structures revealed in the transverse section of an *Amphioxus* through the branchio-genital region.

22. Describe structures and functions of the following in *Branchiostoma* : oral hood; wheel organ; velum; Primary and secondary gill bars; synapticulae; epipharyngeal groove; endostyle; buccal diverticulum; hepatic caeca.

23. Give an account of the development of *Branchiostoma,* pointing out its larval asymmetry.

24. From the life-history of *Amphioxus,* enumerate the following :

    (a) 3 essutial chordate characters

    (b) Primitive chordate characters

    (c) Some specialized characters.

25. Compare pharynx of *Balanoglossus, Ascidia* and *Branchiostoma.*

# Unit 2 □ The Nature of Vertebrae Morphology

*Structure*

**2.0 The nature of vertebrate morphology**
**2.1 Definition and scope**
**2.2 Importance of the study of vertebrate morphology**
**2.3 Terminal questions**

## 2.0 The nature of vertebrate morphology

We have seen in the earlier chapter in the description and discussion of protochordates that both the groups—the tunicates and the cephalochordates started showing many signs of evolution towards vertebrates. Since about 500 millions of years ago, from the Ordovician period primitive ostracoderms and the jawless vertebrates began to appear with diverse habits, habitats and behaviour. Alongaide, the earth's surgace also changed dramatically with the submergence and upheaval of landmasses, recession of vast water bodies from low lands; confluence of rivers and birth of the mountains and large lakes, deserts, as well as, amazing diversity in the surviving floral and faunal populations living in distinct biomes.

The nature of vertebrate morphology has to be understood and studied in the context of the above-mentioned changing parameters on the earth's surface. Even in recent times when many of the problems, controversies and opinions of scientists working in the fields of functional morphology, evolutionary biology, palaeontology, physiology, ecology, etc. are being assessed through molecular genetics, DNA hybridization techniques and other more and more recent technologies, the role of morphological, or rather, functional morphological studies still holds the key to its interrelations with other disciplines of biology.

## 2.1 Definition and scope

Subphylum Vertebrata or Craniata includes animals known as fishes, amphibians, reptiles, birds and mammals, as they are distinctly characterized by the presence of a cranium and a vertebral column, a complex brain, a heart of two, three or four persistent chambers and blood containing RBC.

This definition applies to true vertebrates that are gnathostomes or with jaws. But the subphylum also includes agnathans or jawless vertebrates represented by the cyclostome-like forms lacking cranium and with a persistent notochord.

Vertebrate morphology may be defined as that branch of zoology that deals with the external and internal structural organization of the body (organ and organ-systems) of a vertebrate, taking into consideration the biological role (structure + function) of that structure. The description of the form-function complex in totality provides databases to systematics and evolutionary biology and to other branches like comparative anatomy, palaeontology, ecology (and a comparatively recent subdivision, ecomorphology), physiology, endocrinology, embryology, etc. The impact of vertebrate morphology lies in the fact that an evohtiongy biologist or a systematist has to examine the functional morphological observations of the structures before he gives any analytical explanation or evolutionary position of the structures under study. This leads the scientist to probe into other branches as well for a confirmation of his study.

## 2.2 Importance of the study of vertebrate morphology

The importance in the study of vertebrate morphology therefore lies in the basic concept of the diversity of vertebrates, which provides ground materials for cladistic evolution and phylogenetic systematics. There is a tendency in recent times to minimize the importance of an elaborate morphological description of animals and their parts for the purpose of assigning their systematic position. But it must be remembered that descriptive morphology of the gross structure and function of a vertebrate gives us first-hand information of the animal to enable us to compare it with those of another animal, both of which may be closely or distantly related.

Without comparative morphological description how could we distinguish between the wing of a butterfly and that of a bird or between the scale of a fish and that of a lizard? The distinction between homology and analogy could hardly be ascertained without morphological description at the beginning and then testing it in the light of embryology, palaeontology and other disciplines.

The biological role of a structure is determined by its function. And the form-function complex of an organ or organ system is in turn interrelated to or it influences other disciplines such as, ecology or the sum total of environmental factors shaping habit or habitat of the vertebrate organism, behavioral adaptations, embryology, heredity, past history of the organism and the like.

The modern diversification of zoology into more than two dozens of specialized branches has established vertebrate morphology as an important subdivision of zoology dealing with the structure and function of vertebrates and then analysing evolutionary significance of these structures. Obviously such analyses will require the knowledge of other disciplines.

In the vast domain of vertebrates, the knowledge of vertebrate morphology reveals that within very different life and habitats of vertebrates (spanning from the deep sea to high altitudinous mountains and distributed all over the world except in poloar ice caps) there is a general plan of conformity among the animals With respect to their bodily structures, not found among the non-chordates where even within a single class of a major phylum such as, class hydrozra, class crustacea, class arachnida, class gastropoda, etc., the variations in characters are much more pronounced.

In recognition of the importance in the study of vertebrate morphology as any other specialized branch of zoology, International Congress in Vertebrate Morphology is held after every four years to assess the progress in research and interactions of the subject with other disciplines.

## 2.3 Terminal questions

1. Define Vertebrate morphology. State the scope of studying vertebrate morphology in the light of interdisciplinary parameters.
2. State the importance of studying vertebrate morphology and functional morphology.
3. 'The study of functional morphology provides data bases to evolutionary biology and systematics'—explain.

# Unit 3 ❐ Origin and Classification of Vertebrates

*Structure*

## 3.0 Introduction

Vertebrate animal is characterized by the presence of a vertebral column made up of cartilage or bone and divided into segments called vertebrae. Hence the vertebrate is essentially a chordate with an axial endoskeleton, either cartilaginous or bony, and divisible into a vertebral column containing a central canal through which passes the nerve cord (spinal cord) and an anterior cranium which houses the brain and the sense organs. These are the two unique features of vertebrates, not possessed by any other chordate.

## 3.1 Origin of vertebrates

### 3.1.1 Introduction

It is also relevant to mention here that besides the two above mentioned outstanding characters of vertebrates they also possess the three fundamental characters of chordates such as, the notochord, the pharyngeal gill slits and the hollow dorsal nerve cord at certain stage of their life history. To these three essential chordate characters may also be added the post-anal tail. Of these chordate characters only the dorsal nerve cord is retained in the adult vertebrate, the rest appearing at some stages of their development.

According to Pough, Heiser and McFarland (1990), the notochord is a primitive character state for vertebrates because all chordates share this trait. The notochord is a shared derived character that separates chordates from other deuterostomes, such as the echinoderms which do not possess a notochord. In evolutionary relationships between organisms, the word 'primitive' implies an ancestral condition, not a condition of inferior quality.

### 3.1.2 The basic vertebrate body plan

The basic vertebrate body plan has been illustrated in Fig. 3.1. Although a wide range of variation exists in the evolutionary process through which different vertebrates evolved differently, yet the general plan of an ancestral vertebrate depicts bilateral symmetry with a distinct head and tail ends and the internal organization ensures an inner body tube represented by the alimentay canal and its derivatives and the outer tube represented by body wall. The space lying between the two tubes is called the body cavity or coelom. The coelom is lined, entirely with mesoderm and forms the future peritoneal, pericardial and pleural cavities in vertebrates. Pough *et al* (1990) comment that in those respects the ancestral vertebrate is not unlike many higher invertebrate animals which also possess these general body features—mollucs, annelids and arthropods.

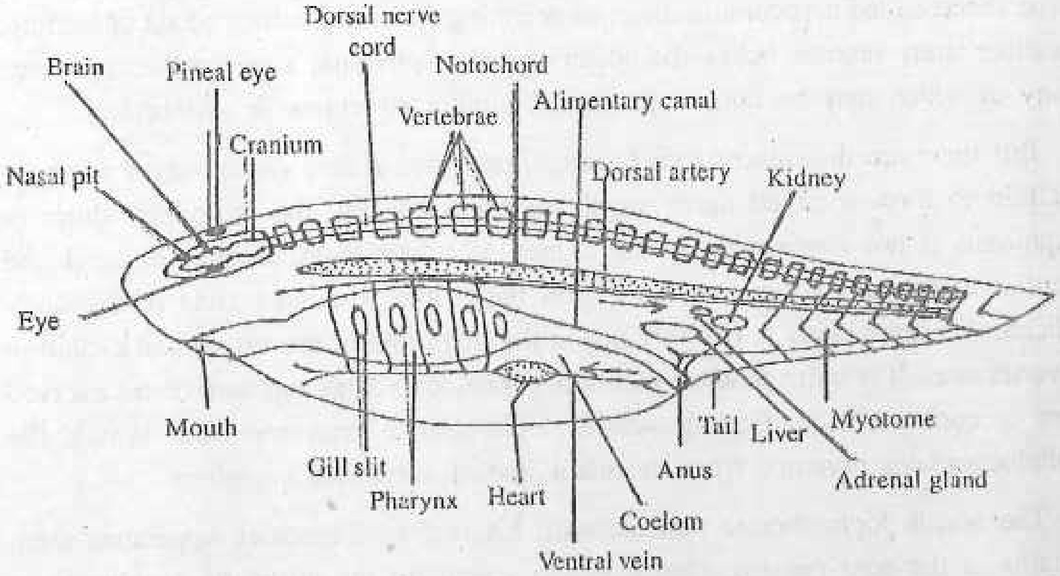

Fig 3.1 : Diagrammatic body plan of an early vertebrate

However, in addition to the poosession of the above-mentioned features of an ancestral vertebrate, a vertebrate becoming more and more advanced with the activity of fife not found in its predecessor must necessarily possess, for proper functioning and reproduction, several other organs and organ-system in the body. These are basic vertebrate systems such as, integumentary, skeletal, muscular, digestive, circulatory, respiratory, excretory, reproductive, endocrine and nervous systems.

### 3.1.3 Theories and explanations on the origin of vertebrates

To explore the origin of vertebrates, one practical difficulty with which the biologists are confronted with is that there is practically no fossil evidence earlier than that of ostracoderms. So, to a large extent we have to depend upon indirect evidences gathered from the knowledge of comparative anatomy and embryology by using the principle of homology. This leads us to the realm of protochordates—the urochordates and the cephalochordates. These two groups with their essential chordate characters may well fit in as prospective ancestral groups from either of which the vertebrates might have taken their origin.

Pough *et al.* (1990) have described *amphioxus* as the model prevertebrate having possessed a larva similar to that of the ammocoete larva of lampreys, fishlike movements resulting from the contraction of myotomes separated by connective tissue sheets called myocommas,mucous-seercting endostyle, ciliary mode of feeding, a saclike sinus venosus below the posterior end of pharynx, a cerebral vesicle, etc., many of which may be homologized with similar structures in vertebrates.

But there are differences too. In *amphioxus,* dorsal and ventral nerve roots do not join to form a mixed nerve supplying each segment, the protonephridium in amphioxus is not comparable to the kidney of a vertebrate, absence of head and peculiar extension of the notochord from the rostral to caudal ends of the body indicate that amphioxus is possibly not in the main line of the origin and evolution of vertebrates. It is quite possible that both cephalochordates and vertebrates evolved from a common filter-feeding sessile lophophorate ancestor from which the cephalochordates diverged from the main line of vertebrate evolution.

The sessile lophophorate tunicate with external food-catching apparatus, then, remains as the next possible choice in the search for the origin of vertebrates.

The adult tunicate as found today is so different in its bodily organization that it can hardly be considered as the ancestor of vertebrates. Its free-swimming tadpole larva, however, possesses all the qualities of a prevertebrate. The larva has a notochord, pharyngeal gill slits and a dorsal tubular nerve cord. In addition, it possesses a muscular tail with the help of which swimming and muscular contractions as in fishes are possible. The tunicate tadpole stage is very short, but Garstang's (1928) neotenous larval theory suggests that paedomorphosis (i.e., retention of the larval stage with sexual maturity) of the larval tunicate is a satisfactory answer to the problem. However, most authors use the term paedomorphosis and not neoteny as the latter has an implication of a different meamng.

Garstang proposes that the ciliated larva from some sort of a sessile or semisessile lophophorate tunicate-like ancestral stock gave rise to the echinoderms and hemichordates on one hand and to a free-swimming tadpole larva with all the characters of a prevertebrate on the other. The tadpole larva then by the process of paedomorphosis gave rise to the prevertebrates and vertebrates.

In the discussion on the origin of chordates, it has been stated that many vertebrate evolutionists accept Garstang's view with some modifications till concrete evidences are available in favour or against the view. Northcutt and Gans (1983), accepting Garstang's view suggest that from tunicate-like larvae to organisms similar to *amphioxus* or to larvae of lampreys and to full-fledged vertebrates with cranium and vertebral column is possible. However, most authors agree that the origin of bone is a later acquisition, as it can not be homologized with hard part found among the invertebrates.

The other theories by Berril (1955), Barrington (1965) and Jeffries (1975) have already been discussed in the earlier chapter. Jeffries' recent book on the ancestry of the vertebrates proposes that the vertebrates and other living deuterostomes each originated from the calcichordates in the Palaeozoic era. In Jeffries' scheme, tunicates are the sister group of verteotates, not the cephalochordates (Pough *et al.*, 1990).

Lovtrup (1977) proposes the phylogeny based on physiological, chemical and histological characters, as he considers them more stable in evolution than the morphological charactyrs. Jeffries (1979, 1986), Northcutt and Gans (1983) and Schaeffer (1987) do not accept that the origin of vertebrates took place through paedomorphosis. But these authors were not mutually agreeable to any alternative proposal.

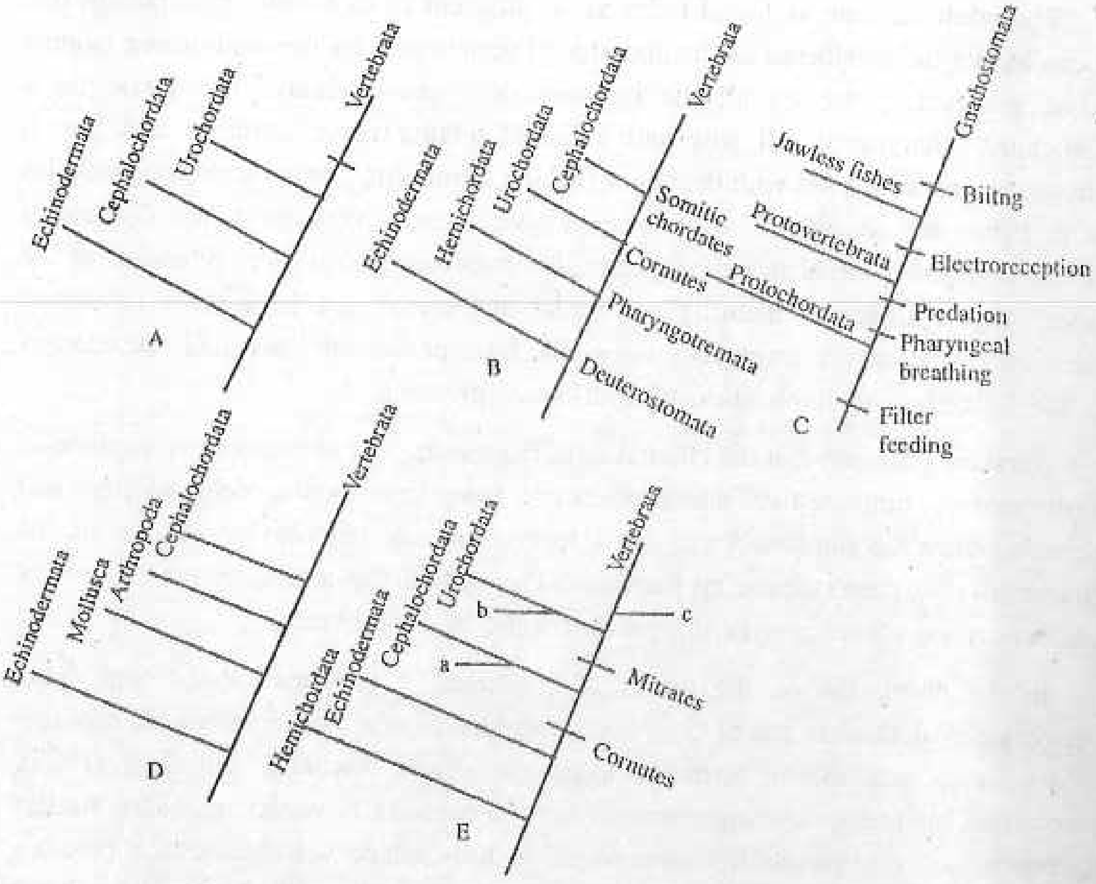

**Chart 3.1** : Suggested phylogenetic relationship of vertebrates to other taxa : A. Garstang's theory on the origin of vertebrates by paedomorphosis; B. Schaeffer's hypothesis relates chordates as the sister group of vertebrates; C. Northcutt and Gans' proposal is based on some important functional chatracteristics of vertebrates; D. Lovtrup's hypothesis is based on physiological, chemical and histological characters; E. Jeffries' calcichordate theory (Based on Pongh *et al.*, 1990).

Smith (1953), Romer (1967) and Romer and Parson (1986) advocated fresh water origin of the first vertebrates. Romer's (1967) proposal of the fresh water origin was based on palaeontological evidences.

Repetski (1978) observes that all recently discovered fragmentary fossils of ostracoderms reveal that the first vertebrates originated from the marine environment. In fact all protochordates and deuterostome invertebrate phyla are exclusively or primitively marine forms. It has also been found that like the. hagfishes (Myxinoidea), tunicates. and other deuterostomes as well as the first vertebrates were all in osmotic equilibrium with sea water. Fossil evidences accumulating more and more in recent years point towards marine origin of vertebrates.

To sum up the early history of vertebrates we arrive for the time being at such a conclusion which may not stand the test of time, but from the evidences gathered so far and from critical analyses by different authors it may be stated that the early vertebrates appeared in the late Cambrian or early Ordovician periods in marine habitat. The invertebrate ancestral stock of vertebrates is still based on speculation. Garstang's theory of the origin of vertebrates from a tunicate-like larval stage which attains sexual maturity through paedomorphosis is acceptable to most authors. In course of evolution, the sessile adult stage may have been abandoned.

## 3.2 Classification of vertebrates

In contrast to the overwhelming number of species of non-chordates, the chordates occupy a rather smaller area in the vast circle of animals. Yet the classification of nearly 50,000 vertebrate species (with ten times the number now extinct) is not an easy task, as systematists very often differ in their opinions, to locate exact position of the species from evolutionary standpoint.

It has already been mentioned in the earlier chapter that Phylum Chordata is divided into four subphyla of which the first one, Subphylum Hemichordata has been half heartedly included in the Phylum Chordata. Romer and Parson (1986) have placed the hemichordates in a separate Phylum. They have classified the subphylum Vertebrata into Superclass Pisces and superclass Tetrapoda. Under the Pisces have been included the classes Agnatha, Elasmobranchiomorphi and Osteichthyes. **In Romer and Parson's classification there is no mention about the superclass Gnathostomata.**

However, in this chapter, the classification of subphylum vertebrata has been mainly followed as that adopted by J. Z. Young (1981). The classification has been followed here up to living orders except in Fishes and Birds where the classification has been given mainly upto subclasses and only the names of orders have been maintained to-acquaint the students with the volume of the subject.

**Subphylum—Vertebrata (= Craniata) :** Some of the salient morphological. characters :

- (i) Bilaterally symmetrical; triploblastic and with distinct head and tail.
- (ii) Dorsal nerve cord swells in the head to form a brain and the nerve cord continues behind as the spinal cord up to the tail end.
- (iii) Endoskeleton may be cartilaginous or bony or may be formed by both, the endoskeleton forms the cranium and the vertebral column.
- (iv) Usually two paits of jointed appendages which my be variously modified.
- (v) Epidermis and dermis give rise to scales, feathers, hairs and various kinds of skin glands.
- (vi) In the head region, paired eyes, ears and nasal organs occur as sensory organs.
- (vii) Livers and pancreas are important digestive glands.
- (viii) Heart ventral; closed circulatory system connected to middorsal aorta and other aortae; portal system present.
- (ix) Respiaration through gills, lungs, skin capillaries and mucous membranes of buccopharynx.
- (x) From the brain arise 10 or 12 pairs of cranial nerves.

**A. Superclass—Agnatha**

- (i) These are jawless vertebrates.

Divided into several extinct classes and orders of which the Cyclostomata is the only living order or class.

**Order—cyclostomata (or class Cyclostomata)**

- (i) Eel-like elongated body, sucker-like round-mouth and known as lampreys.
- (ii) No scales or paired fins—dorsal, ventral and caudal fins are unpaired.
- (iii) Notochord unchanged in the adult; skull and vertebral column cartilagineous.
- (iv) 6–14 gill pores on either side opening into gill pouch for respiration.

(v) Heart with one auricle and one ventricle; renal portal system absent.

(vi) Lampreys have ammocoetes larval stage which is absent in hagfishes (Myxinoidea)

e.g., *Petromyzon; Myxine.*

## B. Superclass-Gnathostomata

(i) Mouth bounded by two well developed jaws; paired appendages present.

(ii) Gnathostomes comprise all fishes, amphibians, reptiles, birds and mammals.

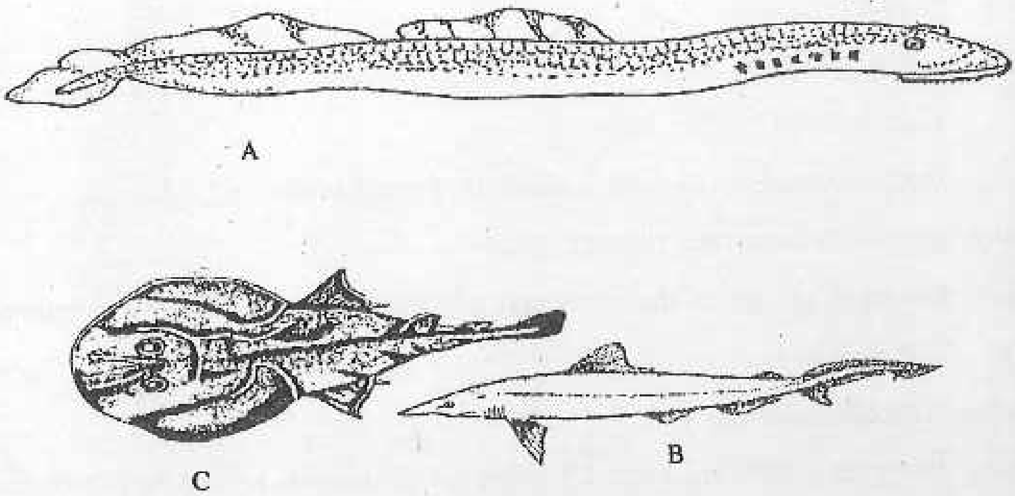

**Fig 3.2** : A, *Petromyzon* (Lamprey); B, *Scoliodon* (Dogfish); C, *Narcine* (Torpedo ray).

(iii) Skull and vertebral column bony.

## I. Class-Chondrichthyes

(i) Almost all species are marine and carnivorous.

(ii) Body covered by minute placoid scales.

(iii) Endoskeleton cartilaginous.

(iv) No operculum.

**Sub-class 1. Elasmobranchii :**

(i) Jaws and muscles strong; brain-and sense organs well developed.

(ii) Tail heterocercal (i.e., longer dorsal segment and shorter ventral segment).

(iii) Pelvic fin in males forms a clasper.

(iv) Spiral valve in the intestine.

e.g., *Scoliodon; Torpedo.*

**Sub-class 2. Holocephali (or Brachyodonti) :**

(i) Mouth smaller, covered by jaws and lips.

(ii) Teeth plate like; upper jaw strongly ankylosed to skull (Holostylic).

e.g., *Chimaera*

**II. Class—Osteichthyes :**

(i) Endoskeleton mainly bony.

(ii) Body covered by cycloid, ctenoid or ganoid scales.

(iii) Skin with numerous mucous glands.

(iv) Mouth at the tip of the snout and gill slits covered by bony operculum.

(v) Tail mainly homocercal.

**Sub-class 1. Actinopterygii :**

V. G. Jhin gran (1991) has listed 22 orders under this subclass. Berg (1940) has introduced 'formes' at the end of each order. This subclass contain 3 Infraclasses :

1. **Infraclass—Chondrostei :**

(i) Endoskeleton mainly cartilaginous; notochord persists in between the vertebrae.

(ii) Tail fin heterocerecal.

e.g., *Polypterus; Acipenser*

2. **Infraclass—Holostei :**

(i) Except two freshwater species, most of the species are extinct.

e.g., *Lepidosteus, Amia.*

3. **Infraclass—Teleostei :**

(i) Endoskeleten fully ossified.

(ii) Body covered by dermal scales which my be ganoid, cycloid or ctenoid.

e.g., *Polynemus, clarias, Anabas, Notopterus, Hilsa, Labeo*

**Sub-class 2. Sarcopterygii :**

Most extinct, but the living species are very characteristic.

(i) Each paired fin has a median fleshy outgrowth.

(ii) Body covered with cosmoid scales.

(iii) Air bladder transformed into lungs.

e.g., *Coelacanths; Protopterus* (Africa); *Lepidosiren; Neoceratodus* (Australia; South America).

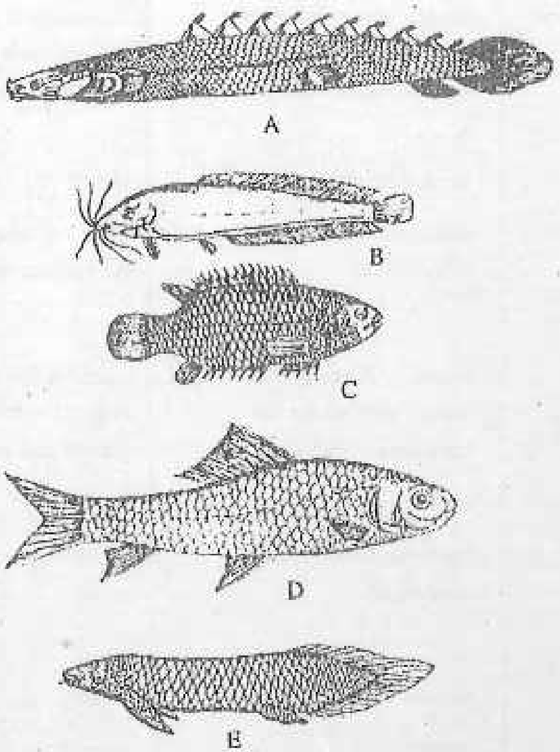

**Fig. 3.3** : Bony fishes : A, *Polypterus;* B, *Clarias;* C, *Anabas;* D, *Labeo rohita;* E, *Neoceratodus* (Australian lung fish)

**Distinction between cartilaginous and bony fishes** : In the number of species and in the diversity of structure, the fishes claim distinction from other classes, of vertebrates. Different scientists have classified fishes differently, but all of them agree that all the fishes may be divided into two major groups; the cartilaginous fishes or chondrichthyes and bony fishes or Osteichthyes.

The salient features of distinction between the two are mentioned below in a tabular form :

| **Morphological haracters** | **Chondrichthyes** | **Osteichthyes** |
|---|---|---|
| **Habitat** | usually marine and carnivorous. | marine, brackish or fresh water. |
| **External morphology** | | |
| (i) Body shape, scales, mouth | cylindrical placoid scales; mouth ventral | usually bilaterally compressed; cycloid, ctenoid or ganoid scales; mouth terminal or sub terminal. |
| (ii) Gill slits and operculum | usually five pairs of gill slits opening directly outside; operculum absent. | four pairs of gill slits lodged in gill; chamber and covered by operculum and caved by operculum |
| (iii) Clasper | present in males | absent |
| (iv) Paired fins and tail fin | fins cartilaginous; tail fin heterocercal | bony fin rays support the fins; tail fin homocercal |
| **Skeletal system** | | |
| (v) Exoskeleton | primarily covered with placoid scales; such scales are transformed into teeth. | except a few species, body usually covered with cycloid, ctenoid, ganoid and cosmoid scales. |
| (vi) Endoskeleton | cartilaginous | bony |
| (vii) Jaw suspension | hyostylic, autostylicc or amphistylic. | hyostylic |
| **Digestive system** | | |
| (ix) Spiral valve | present within the intestine | absent |
| (x) Cloaca | present | absent |
| (xi) Pancreas | well developed | absent |
| (xii) Pyloric cacca | absent | present |

| Morphological haracters | Chondrichthyes | Osteichthyes |
|---|---|---|
| **Blood circulating System** | | |
| (xiii)Conus arteriosus | muscular, contractile and with several rows of valves; acts like accessory chamber of the heart. | Conus gradually disappears; bulbus arteriosus-formed at the base of ventral aorta. |
| (xiv) Afferent branchial arteries | 5 pairs | 4 pairs |
| **Respiratory system** | | |
| (xv) Gills | leaflike gills lodged in gill chamber | comblike gills bourne on gill arches |
| (xvi) Air bladder | absent | present |
| **Exeretoy system** | | |
| (xvii) Exeretory organ | Opisthonephric; in males kidney and testis are closely related | Opisthonephric, kidney and testis are not related. |
| **Reproductive system** | | |
| (xviii) Oviduct | not directly connected to ovary; ova released in coelom through an ostium. | ova released by ovary into the oviduct |
| (xix) Fertilization | Internal | External |
| **Endocrine glands** | | |
| (xx) Thyroidgland | Unpaired | Paired |

## III. Class—Amphibia

The emergence of Amphibia from some prospective line of evolution of the lung fishes is a remarkable phenomenon. Scientists are of the opinion that towards end of the Devonian period an Osteolepid fish, *Eusthenopteron* might have given rise to early amphibians. In Permian period a small crocodile-like *Eryops* and *Cacops* possessed land adaptations like tetrapods. Acquisition of pentadactyl limbs is one such milestone in land adaptation.

Class Amphibia contains more than 2000 species and excepting a few species, all the animals included in this class have to return to aquatic life at some period in their life history.

Hans Gadow (1901), Sedgwick (1905), G. K. Noble (1954), Parker and Haswell (1962), Romer (1966), J. Z. Young (1981), Romer and Parson (1986) and Duellman and Trueb, 1986) have classified Amphibia with some differences in their schemes.

Here in this text, classification given by J. Z. Young (1981) has been followed.

**Salient characters :**

(i) Bilaterally symmetrical; skin without scales (except in Gymnophiona); plenty of skin glands.

(ii) Body divided into head and trunk; neck absent; cold blooded animals.

(iii) Two pairs of limbs—forelimbs with four and hindlimbs with five digits.

(iv) Respiration in adult through lungs, skin and mucous membrane of the buccal cavity.

(v) Heart with two auricles and one ventricle; accessory chambers—one sinus venosus and one conus arteriosus.

***Subclass 1. Labyrinthodontia**

Animals included in all the orders of this subclass are extinct.

e.g., *Ichthyostega; Eryops; Seymouria*

***Subclass 2. Lepospondyli**

Extnict; e.g., *Diplocaulus*

**Subclass 3. Lissamphibia:**

(i) Scaleless (except order Apoda); skin smooth; All living amphibians are included in this subclass.

**Order 1. Anura (= Salientia;** tailless)

The toads and frogs included in this order have a wide distribution throughout the world for their successful land adaptation.

(i) Tailless, with four well developed feet; hindlegs longer than the forelegs.

(ii) Body short, without neck and abdomen laterally broad.

(iii) Vertebral column short and with a specific number (8-10) of procoelous vertebrae.

(iv) Adult animal respires through lungs; true gills or gill slits are absent.

(v) Posterior end of tongue remains free and can be ejected while preying on insects.

(vi) Life-history with metamorphosis

e.g., *Bufo, Rana, Hyla, Rhacophorus.*

**Order 2. Urodela (= Caudata)**

Tailed amphipians; adult of some species live in water *(Necturus)* or land *(Salamandra maculosa).* A few aquatic species retain larval stage which attains sexual maturits. This phenomenon is called *neoteny* or *paedogenesis.*

(i) Elongated, lizard-like body divided in to head, trunk and tail.

(ii) Vertebral column long and usually with many opisthocoelous vertebrae; some; species have amphicoelous vertebrae.

(iii) Tympaum absent; skull without jugal and quadrato jugal.

e.g., *Necturus, Salamander, Ambystoma*

**Order 3. Apoda (= Gymnophiona or Coecilia)**

All animals included in this order are living.

(i) Snakelike elongated body, limbless and living in burrows.

(ii) Very minute scales arranged within transverse furrows of the body.

(iii) Eyes without eyelids, inactive and covered wholly or partly by skin.

(iv) Tympanum absent.

(v) Right lung very large, the left one small and vestigial.

(vi) Vertebrae, amphicoelous

e.g., *Ichthyophis; Uraeotyphlus.*

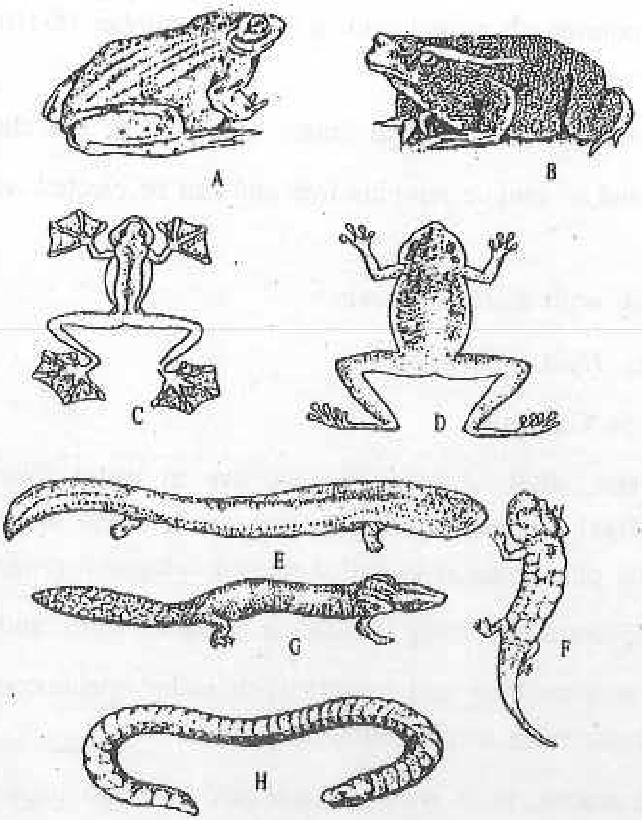

**Fig 3.4 :** Amphibia : A, *Rana* sp. (Frog); B, *Bufo* sp. (Toad); C, *Rhacophorus* sp. (Tree frog); D, *Hyla* sp. (Tree frog); E, *Megalobatrachus* sp., F, *Salamandra* sp. (Salamander); G, Necturus sp., H, *Ichthyophis* sp.

**Discussion on the classification of Amphibia :** The classification of Amphibia followed at present has undergone several modifications based 011 Romer's (1945) older classification followed by Romer and Parson's (1986) modified version. In 1966, Romer comments that there was no strong evidence in favour of the presence of apsidospondylous vertebrae in Anura. Accordingly, he holds the view that Labyrinthodontia, Lepospondyli and Lissamphibia are of the same rank. Later Young (1981) also supported this view.

However, different opinious have been held by different authors. Of these G.K. Noble's (1954) scheme is given below :

Class—Amphibia

Order—*Labyrinthodontia

Order—*Phyllospondyli

Order—*Lepospondyli

Order—Gymnophiona

Order—Caudata

Order—Salientia

* Extinct

Later, Romer and watson (1962) propose a revised version of the classification of Amphibia. They have divided the class into two main subclasses based on phylogeny such as, Apsidospondyli and Lepospondyli. In both the subclasses extinct as well as living orders pave been included.

In Romer and Watson's (1962) scheme, there is no mention about the subclass Lissamphibia. Young (1981), Kent (1983), Romer and Parson (1986) and Kardong (1998) have included all the living orders of Amphibia under the subclass Lissamphibia. Kardong's cladogram of Amphibia is almost similar to that of Young.

Duellman and Trueb (1986) comment that the argument in favour of the monophyletic origin of the living orders of Amphibia may not be fully acceptable, but the evidences gathered so far point towards the monophyletic origin. In the recent past, Trueb and Cloutier (1987) and Pough *et al* (1990) comment that Lissamphibia originated from branchiosaur temnospondyl group and is a **monophyletic sister clad.**

## IV. Class—Reptilia

About 350 million years ago, tetrapod evolution progressed through two main lines—one limites to batrachomorph animals and the other to reptiliomorph group that marked the beginning of Amniota. Within the reptiliomorpha were included Anthracosauria, Seymouriamorph and diadectomorph animals.

Towards the end of carboniferous, the amphibians diverged into two lines : Temnospondyli and Anthracosauria which were abundantly distributed on land. Carron (1964, 1969) claims that the oldest amniote evolved even in mid-carboniferous.

The contemporary fossils of animals named *Romeriscus, Solenodonsaurus, Seymouria, Diadectes and Captorhinus* formed an assemblage which came to be known as cotylosaur or stem reptiles.

Romer (1945, 1966) proposed a scheme of classification of the reptiles, based on skull arcades. From a somewhat different viewpoints, the classification of reptiles has been proposed by Parker and Haswell (1962), Romer (1966), Carl Gans (1969-79), Bellairs and Attridge (1975), Young (1981), Kent (1983), Romer and Parson (1986) and J3enton (1997).

In this text, the classification has been mainly followed after Young (1981).

The reptiles may be defined as poikilothermous animals which possess dry cornified skin containing scales covering the body, a single occipital cordyle, lungs for respiration, two right and left separate aortic arches and embryonic membranes called amnion, chorion and allantois.

**Salient characters :**

(i) Body covered with dry, cornified skin containing epidermal scales or scutes; skin glands scanty.

(ii) Body bilaterally symmetrical and divided into head, neck, trunk and the post-anal tail.

(iii) Two pairs of pentadactyle limbs; each with five clawed digits, feet variously modified for movements both in water and on land.

(iv) Anus usually transverse (exception Chelonia and Crocodilia)

(v) Skeleton fully ossified and skull with a single occipital condyle.

(vi) Heart with a sinus venosus, two auricles, an incompletely divided ventricle; absence of conus arteriosus; ductus caroticus connecting *3rd* and *4th* aortic arches may be present.

(vii) Respiration through lungs.

(viii) 12 pairs of cranial nerves.

(ix) Fertilization internal, no metamorphosis.

**Subclass 1. Anapsida**

(i) Dorsal surface of skull without any temporal cavity ('Apse' = arch)

Order 1. *Cotylosauria (stem reptiles); all extinct.

e.g., *Romeriscus; captorhinus*

Order 2. *Mesosauria

All extinct

e.g., *Mesosaurus*

**Order-Chelonia** (Turtles and Tortoises)

(i) Living fossils surviving through 170 to 200 million years from the end of Permian period; commonly tortoises are land living, terrapins live in freshwater and turtles are marine.

(ii) Body somewhat round and dorsoventrally flat.

(iii) Body covered by a hard exoskeleton formed of a dorsal convex carapace and a ventral flat plastron; thoraeic vertebrae and ribs are connected to carapace; part of pectoral girdle is connected to plastron.

(iv) Head, neck feet and tail may be withdrawn within the shell.

(v) Digits of feet are clawed for land species and in aquatic forms, feet transformed into paddles for swimming.

(vi) Jaws without teeth and covered with horny plates.

(vii) Skull withouttemporal vacuity; quadrate immobile; cloacal aperture longitudinal.

e.g., *Chelone; Testudo; Dermochelys; Trionyx,*

***Subclass 2. Synaptosauria (= Euryapsida)**

All animals extinct.

These animals have a single temporal cavity high up in the skull—a condition called **'Parapsid'.**

Order 1. Pratarosauria

e.g., *Araeoscelis*

Order 2. Sauropterygia

e.g., *Larios Clurus*

Order 3. Placadantia

e.g., *Placodus*

**Subclass 3. Ichthyopterygia**

Marine animals of Triassic and Jurassic periods; all extinct

Order 1. Ichthyosauridae

e.g., *Ichthyosaurus.*

**Subclass 4. Lepidosauria**

They are papularly knawn as 'Diapsid' reptiles due ta the presence of two temparal vacuities in the skull. In recent classification the diapsid group has been divided inta two subclasses—Lepidasauria and Archasauria both of which are believed by many recent warkers (Gauthier, 1986; Cracraft, 1986; Sanz *et al.*, 1995; Zweers *et al.*, 1997) to have arisen separately from the cotylasaur stem reptiles.

**Order 1.* Eosuchia** (= Dawn reptiles)

Extinct

(i) Lizard-like dawn reptiles having palate and jaws bearing teeth.

e.g., *Youngina*

**Order 2. Rhynchocephalia** (= Beak-headed)

*Sphenodon* or Tuatara of New Zealand are alsa called 'living fassils', as their cantemporary animals have all been extinct long ago, but *Sphenodon* is still surviving under care and conservatian by the Government.

(i) Lizard-like, carnivorous, nocturnal and burrowing animal which may grow up to 60 cm in length.

(ii) Body covered by granular scales; with pentadactyl limbs and a long tail.

(iii) A row of middorsal spine-like **frill.**

(iv) Vertebrae amphicoelous; atlas with a small proatlas in front; tail vertebrae divided and tail capable of regeration.

(v) Single-headed rib and a few with cartilaginous uncinate process.

(vi) Two temporal vacuities in skull; pineal and parietal eyes present.

(vii) Quadrate immobile; jaws connected by ligaments; abdominal ribs present.

(viii) Anal aperture transverse.

e.g., *Sphenodon punctatum* (only living species)

### Order 3. Squamata :

This order includes more than 6000 species of different types of lizards and snakes.

(i) Body covered with epidermal scales

(ii) Skull diapsid type, but only superior temporal fossa present.

(iii) Quadrate movable; maxilla, palatine and pterygoid immovably joined to skull.

(iv) Vertebrae procoelous; teeth acrodont or pleurodont.

(v) Paired organs of Jacobson present.

This order comprises three suborders : Suborder—Lacertilia, Suborder—Ophidia and Suborder—Amphisbaenia. Lacertilia includes different kinds oflizards; Ophidia, the snakes and Amphisbaenia the worm-like tropical reptiles which can move both forward and backward.

### Suborder—Lacertilia :

(i) Body elongates; usually pentadactyl four-footed animals.

(ii) Pectoral girdle, sternum, pelvic girdle present.

(iii) Tympanum present, vertebral column divided into cervical, thoracic, lumbar, sacral and caudal regions;

(iv) Occipital condyle single and undivided; mandibular symphysis rigid.

(v) 12 pairs of cranial nerves.

e.g., *Calotes; Gecko; Mabuia; Chamaeleon; Hemidactylus; Varanus*

**Suborder—Ophidia :**

(i) Body cyhidrical; No legs except in Boa and Python where traces of hindlegs are present.

(ii) Pectoral girdle and sternum absent; pelvic girdle and hindlegs absent in most cases.

(iii) Tympanun absent; Vertebrae divided into precaudal and caudal regions.

(iv) Occipital condyle single and tripartite; mandilular joint ligamentous and hence larger gape of the mouth is possible.

(v) 10 pairs of cranial nerves.

**Non-poisonous snakes :**

e.g., *Natrix; Crysopelea; Python; Boa*

**Poisonous snakes :**

*Naja naja naja* (Coummon Indian Cobra)

Ophiophagus hannah (King Cobra) : Longest among all living poisonons snakes; may reach up to 5.5 meters.

*Vipera russelli* (Russel's viper)

*Bungarus fasciatus* (Banded Krait)

*Crotalus* sp. (Rattle snake)

**Note** : Of more than 3000 species of snakes in the world, most are non-poisonous. In India there are about 300 species of poisonous snakes.

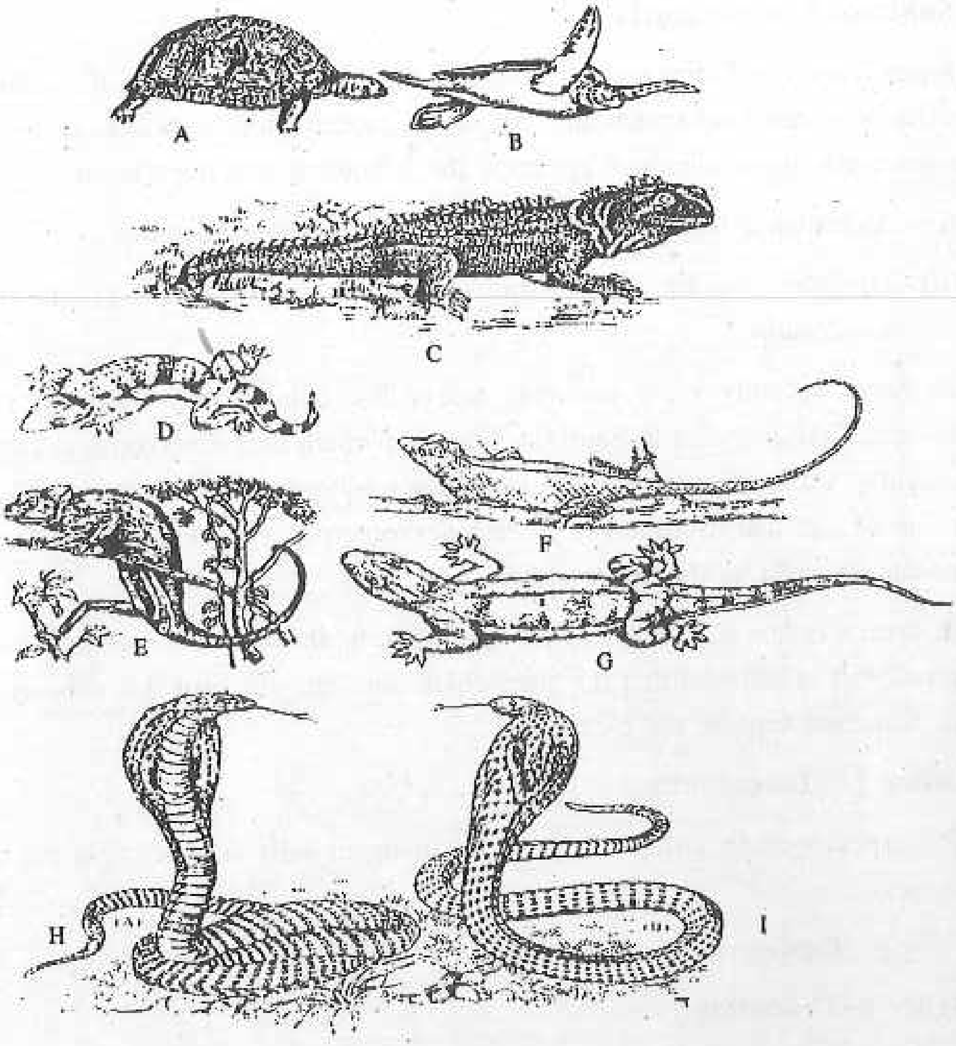

**Fig 3.5 :** Reptilia : A, *Testudo;* B, *Chelone;* C, *Sphenodon;* D, *Gecko;* E, *Chamaeleon;* F, *Calotes;* G, *Hemidactylus;* H, *Naja naja* showing ventral scales; I, *Naja naja* : dorsal surface of hood showing binocellate spot.

### Suborder—Amphisbaenia :

(i) Legless snakes mostly of tropical countries.

(ii) Specially adapted to live in burrows.

(iii) Scales are arranged circularly around the body; tail very short; may move forward as well as backward.

e.g., *Amphisbaena*

### Subclass 5. Archosauria :

From Triassic to Cretaceous—throughout the entire Mesozoic era, the archosauria were the dominant land vertebrates. Inspite of contradictory views about the origin of archosauria, most scientists agree on the following two hypotheses :

(i) Archosauria has directly arisen from any cotylosaur group

(ii) Eosuchia of the Lepidosaurian stock might have given rise to archosauria.

However, recently most scientists are of the opinion that the stem reptiles cotylosauria first gave rise to Sauria or Diapsida which then diverged into two lines of descent—Archosauromorpha and Lepidosauromorpha. Archosauria arose as the main line of reptilian evolution from archosauromotpha and Lepidosauria from the Lepidosauromorpha as the sister group.

Of several orders under the subclass Archosauria, the order Crocodilia is the only living order. It is believed that the saurischian dinosaur group of this subclass gave rise to feathered bipeds, the birds.

### Order 1. *Thecodontia :

The pseudosuchian group of this order living in early triassic were the oldest archosaur.

e.g., *Euparkeria, Saltoposuchus*

### Order 2. Crocodilia :

These are the largest among living reptiles; Late Triassic, having similarities with *Protosuchus* and *Pseudosuchus.*

(i) Head large and elongated; jaws very strong and rigid; nostrils situated at the tip of snout.

(ii) Maxilla, palatine and pterygoid join to form a secondary palate.

(iii) A specially modified scaly flap guards the tympanum; sense of hearing and vision yery well developed.

(iv) Stomach with a highly muscular gizzard; thecodont dentition.

(v) Forelimbs with five clawed digits and webbed; hindhimbs with four clawed digits and without web.

(vi) Tail laterally compressed, long and very powerful.

(vii) Osteoderm present below dorsal and ventral scales.

(viii) Heart distinctly partitioned into four chambers—two auricles and two ventricles.

(ix) **Foraman of Panizzae** at the joining of pulmonary arch.

9 genera and 25 species of living crocodieles are present. They are divided into three main groups; Alligators and Caimans; Crocodiles and Gavials.

e.g., *Alligator;* North America and China; fresh water species

*Crocodylus;* South America, Africa, Asia, Malayasia; live in marine habitat.

*Gavialis;* India; large river mouth and lagoons.

**Order 3*. Sourischia :**

All extinct; divided into two suborders: Theropoda (biped and carnivorous) and Sauropoda (large quadruped and vegetarian).

e.g., Theropoda : *Compsognathus; Ornitholestes;*

*Struthiomimus; Deinonychus.*

e.g., Sauropoda : *Diplodocus, Brontosaurus*

**Order 4*. Ornithischia**

All extinct; Vegetarian dinosaurs.

e.g., *Iguanodon; Stegosaurus.*

**The dinosaurs are comprised of both the orders, Saurishia and Ornithischia.**

**Order 5*. Pterosauria** (lizard-like winged reptiles)

e.g., *Pterodactylus; Rhamphorhynchus.*

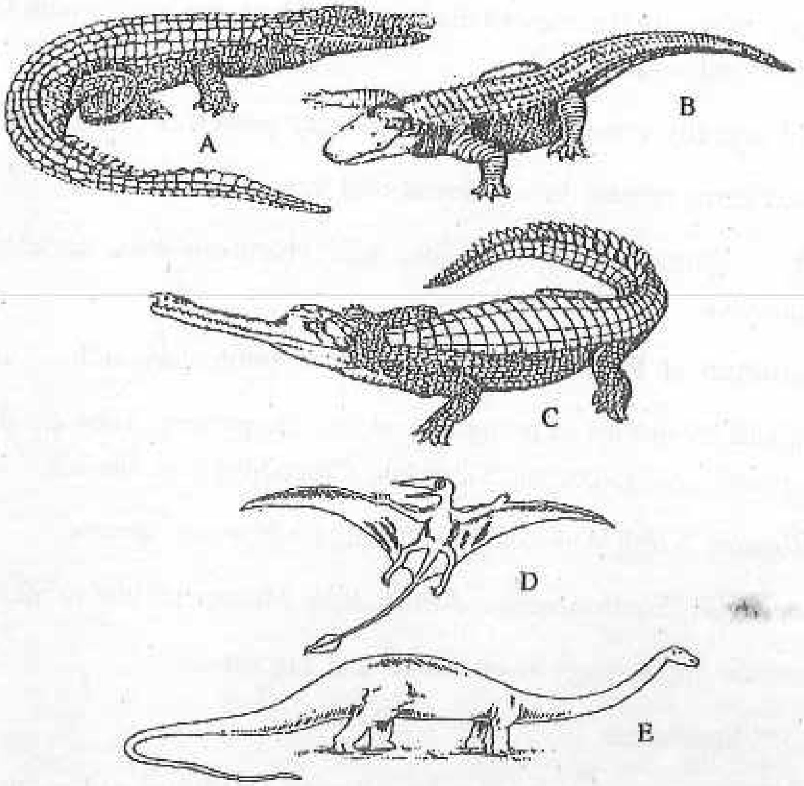

**Fig 3.6** : Reptilia (contd.) : A, *Crocodylus;* B, *Alligator;* C, *Gavialis;* D, *Rhamphorhynchus;* E, *Diplodocus.*

**Subclass 6*. Synapsida** (= Jointed arches)

All extinct. The therapsid theriodonts of this subclass gave rise to the mammals. They had a wide distribution throughont the world.

**Order 1*. Pelycosauria**

All extinct; oldest among synapsids.

e.g., *Varanosaurus*

**Order 2. Therapsida**

All extnict; the Theriodontia of this order is believed to have given rise to the mammals.

e.g., *Dicynodon; Cynognathus.*

### Discussion on the classification of Reptilia :

With the emergence and evolution of tetrapods, the reptiles because the true land vertebrates, but initially there was a tendency to go back to water (e.g., turtles and tortoises, Ichthyosaur, Plesiosour, Phytosaur, Crocodiles and a few dinosaurs). Having originated from the same basal stock, several branches of reptiles proceeded through parallel evolution, yet retained their individuality and distinction.

Romer (1945, 1966) classified Reptilia on the basis of temporal vacuities in the skull. Thus he recognized four principal types such as;

(i) **Anapsida** : without any vacuity in the skull.

(ii) **Synapsida** : single temporal vacuity situated low in the skull.

(iii) **Parapsida** : single temporal vacuity situated high in the skull.

(iv) **Diapsida** : two temporal vacuities joining in the middle of postorbital and squamosal.

However, this system of classification of the reptiles based on skull arcades is not in use at present.

Present system of classification of the reptiles recognizes five or six subclasses (colbert, 1969; kent, 1983; Romer and Parson, 1986). Romer and Parson (1986) have referred to subclass Euryapsida and subclass Parapsida as the same subclass, but colbert (1969) classified them separately.

The classification of reptiles followed here is based on that by Young (1981).

### V. Class-Aves

The origin and evolution of birds from some dinosaurian reptile is a milestone in the history and evolution of the vertebrates.

The birds are warm-blooded (homoiothermal) feathered biped having the jaws elongated as beaks or the bill, forelimbs modified as wings for sustained flight and having almost all the structures in the body, both external and internal modified to suit their volant adaptation. The appearance of feathers replacing scales of reptiles is a unique feature in birds.

Palaeontological studies made by Ostrom (1969–1991) and his earlier or contemporery authors and both palaeontological and molecular studies made by later workers (de Beer, 1956; Bock, 1964; Young, 1981; king and McLelland, 1984; Olson, 1985; Gauthier, 1986; Cracraft, 1986; Sibley and Ahlquist, 1990; Sariz et al. 1995; Feduccia, 1996; Beuton, 1997; Copper and Penny, 1997; Zweers et al, 1997/98) help us to reach a summary of different opinions that from some maniraptoran reptilian stock the coelurosaur represented by the deinonychosaur repliles evolved. Two such deinonychosaur representatives, *compsognathus longipes* and recently discovered *confuciusornis sanctus* were probable ancestors of Pre-archaeopteryx stage through which the remarkable lizord-bird, *Archaeopteryx* has evolved. In this context, *Euparkeria* as mentined by Romer (1966) and Colbert (1969) and Saltoposuchus as mentioned by Young (1981) might have evolved from the biped pseudosuchian reptile of the early triassic and then through coelurosaur and several pre-Archaeopteryx stages could evolve as *Archaeopteryx.*

The appearance of *Archaeopteryx* may be traeed back to 150-170 m. years toward the end of Jurassic period (according to some authors mid-Jurassic or end of Triassic).

## A short history on the classification of birds :

More than 100 years of history in the classification of birds has recorded several checklists, addition, alteration, revision and contradictions in the past. Till recently J. L. Peter's (1931-51) 'cheeklist of Birds of the World' was the main guideline. Mayr and Amadon's (1951) classification of birds was a revised scheme, but that too has been revised now. The conventional classification of recognizing 7 ratite orders (5 living and 2 extinct) and 27 flying orders was being followed for quite a long time.

K. H. Voous (1980), based on Molecular systematics founded by Sibley and Ahlquist (1972-1992) and on biochemistry, immunology and other findings classified birds with only two ratite porders such as struthioniformes and Tinamiformes and all earinate birds under 23 orders. In Voous classification, 4 families such as, Phoenicopteridae, Cathartidae, Accipitridae and Pteroclididae have been raised to the status of orders (Phoenicopteriformes, Cathartiformes, Accipitriformes and Pteroclidiformes). Voous has classified all carinate birds under 23 orders. Young (1981) has classified birds into 6 ratite orders and 22 carinate orders.

Monroe and Sibley's (1993) 'A Checklist of Birds of the World' is mainly based on Sibley and Ahlquist's (1972–1992) Molecular Systematics.

Considering all aspects, the system of classification followed here is mainly based on that given by King and Mclelland (1984; In : Form and Function in Brids). Because, in this system, a co-ordination has been attempted between the three systems of avian classification such as, **cladistic approach, molecular analysis of DNA characters and evolutionary analysis of fossils.**

As per syllabus, avian classification has to be limited here up to subclasses only. However, the names of orders have also been mentioned with one or two examples of each.

**General characters of the class Aves :**

(i) Birds are warmblooded biped vertebrate; body covered with feathers; small, rounded head; jaws prolonged anteriorly into upper and lower beaks; jaws without teeth.

(ii) Forelimbs modified as wings; hindlimbs act as feet, each with four clawed toes and variously modified for walking, perching, running, swimming, climbing, etc.

(iii) Body spindle-shaped with long neck; body devided into head, neck, trunk and tail.

(iv) Skin dry, loose and devoid of glands.

(v) Exoskeleton consists of beaks, claws, scales and feathers—all derived from epidermis.

(vi) Endoskeleton fully ossified; long bones light, hollower, pneumatized.

(vii) Single occipital condyle; heterocoelous vertebra; synsacrum in most birds.

(viii) Sternum with a vertical keel for attachment of large pectoral muscles.

(ix) Heart 4-chambered with complete partition between the right and left sides.

(xi) Lungs with air sacs; syrinx formed at the base of trachea is the sound-producing organ.

(xii) Stomach forms glandular proventriculus and a muscular gizzard.

(xiii) Absence of urinary bladder.

(xiv) 12 pairs of cranial nerves.

**Subclass 1. Archaeornithes :**

These are known as 'lizard birds.' After the discovery of the fossil of the Jurassic bird, *Archaeopteryx lithographica,* fossils of other primitive birds discovered in contemporary times were all grouped together into a single order, Archaeopterygiformes.

As the order represents characters of the subclass, a few characters of the order are given below :

**Order-Archaeopterygiformes :**

(i) Discovery of the fossil of *Archaeopteryx* by Andreas Wagoner in 1961 from the lithographic slate bed of solenhofen, Germany was followed by the discovery of four more specimens during contemporary times and all identified as *Archaeopteryx.* Another contemporary fossil of *Confudusornis,* later fossils of *Sinornis, Gobipteryx* and *Patagopteryx* have all been helpful in tracing the origin of birds.

(ii) Slightly larger then a crow, *Arehaeopteryx* has its body covered with feathers, forelimbs modified as wings and each wing proyided with 3-clawed digits.

(iii) Single occipital condyle; upper jaw with 13 teeth and the lower Jew with 3.

(iv) Number of vertebrae variable between 50 and 56; the tail alone bears 18-23 vertebrae; vertebrae amphicoelous type.

(v) Thoracic vertebrae without uncinate process.

e.g., *Archiopteryx, Confuciusornis*

**Subclass 2. Neornithes :**

Except a few extinct species, all species of this subclass are living.

(i) Carpal and metacarpal bones united; Second digit in the forelimb longest.

(ii) Number of caudal vertebrae 13-14; sternum keeled or keelless.

This subclass has been divided into 2 superorders :

**Superorder 1. Odontognathae :**

These are toothed birds living in marine habitat in cretaceous period.

The superorder contains 2 orders : Order Hesperornithiformes and order Ichthyornithiformes.

e.g., *Hesperornis, Ichthyornis*

*** Superorder 2. Neognathae :**

These are known as modern birds having Jaws without teeth, with well developed wings for flight and with a short tail. Except the first 5-6 orders which contain birds that lost flight, the rest of all birds possess sternum usually with a keel. These birds have been living since *Eocene* period.

The birds that lost flight have been grouped under 7 orders (5 living and 2 extinct) which have been placed by many authors under a separate Superorder Palaacognathae owing to their possession of a primitive type of palate and considering their time of origin and evolution, this Superorder has been placed prior to Neognathae.

Names and one example each of the orders of Palaeognathae and Neognathae are given below :

**Superorder 3. Palaeognathae**

Order 1. **Struthioniformes**

e.g., *Struthio camelus* (ostrich)

Order 2. **Rheiformes**

e.g., *Rhea Americana*

Order 3. **Casuariiformes**

e.g., *Casuarius casuarius* (Cassowary)

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* If the ratite birds are grouped under a separate superorder Palaeognathae, then this super order should be placed in No.2 and the Superorder Neognathae at No.3.

*Order 4. **Dinomithiformes**

e.g., *Dinornis* (Moa)

*Order 5. **Aepyomithiformes**

e.g., *Aepyornis* (Giant Elephant Bird)

Order 6. **Apterygiformes**

e.g., *Apteryx australis (Kiwi)*

Order 7. **Tinamiformes**

e.g., *Tinamous; Rhynchotus* (Tinamou)

**Superorder 4. Neognathae** (Modern birds)

Order 1. **Sphenisciformes**

e.g., *Aptenodytes forseri; Spheniscus humboldti* (Penguins)

Order 2. **Gaviiformes**

e.g., *Gavia immer* (Common Loon)

Order 3. **Podicipediformes**

e.g., *Podiceps cristatus* (Grebes)

Order 4. **Procellariiformes**

e.g., *Diomedea exulans* (Wandering Albatross)

Order 5. **Pelecaniformes**

e.g., *Pelicans onocrotalus*

*Phalacrocorax niger* (Little Cormorant)

Order 6. **Ciconiiformes**

e.g., *Ardea cinerea* (Grey Heron)

*Bubulcus ibis* (Cattle Egret)

Order 7. **Phoecopteriformes**

e.g., *Phoenicopterus roseus* (Flamings)

Order 8. **Anseriformes**

e.g., *Anas platyrhyncos* :

*Anas indicus*

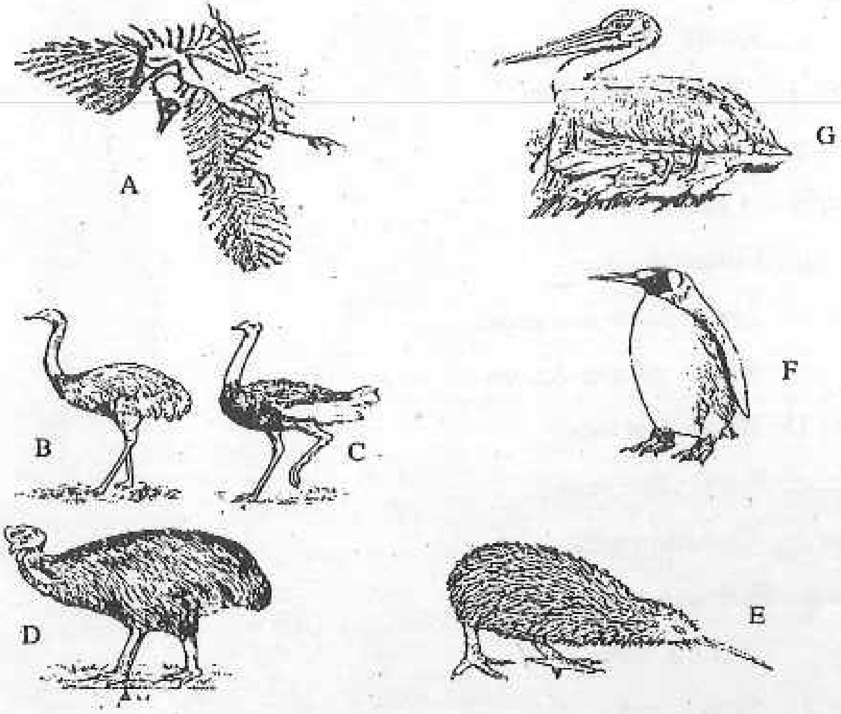


**Fig 3.7 :** Aves : A, Fossil of *Archaeopteryx* (inpression of skeleton and feathers; B - E (ratite birds); B, Rhea; C, Ostrich; D, *Casuarius;* E, *Apteryx* (kiwi); F, *Aptenodytes* (Penguin); G, Pelecanus (Pelican).

Order 9. **Falconiformes**

e.g., *Milvus migrans*

*Gyps bengalensis*

Order 10. **Galliformes**

e.g., *Gallus gallus*

*Pavo cristatus*

*Coturnix coturnix*

Order 11. **Gruiformes**

e.g., *Grus antigone*

Order 12. **Charadriiformes**

e.g., *Pluvialis* sp.
*Larus* sp.

Order 13. **Pterocliditormes**

e.g., *Pterocles* sp.

Order 14. **Columbiformes**

e.g., *Calumba livia*
*Streptopelia chinensis*
*Treron phoenicoptera*

Order I5. **Psittaciformes**

e.g., *Psittacula krameri*

Order 16. **Cuculiformes**

e.g., *Eudynamys scolopacea*
*calculus varius*

Order 17. **Strigiformes**

e.g., *Tyto alba*

Order 18. **Caprimulgiformes**

e.g., *Caprimulgus asiaticus*

Order 19. **Apodiformes**

e.g., *Apus affinis*
*Trochilus* sp.

Order 20. **Coliiformes**

e.g., *Colius* sp.

Order 21. **Trogoniformes**

e.g., *Harpactes* sp.

Order 22. **Coraciiformes**

e.g., *Halcyon smyrnensis*
*Merops orientalis*
*Upupa epops*

Order 23. **Piciformes**

e.g., *Megalaima asiatica*

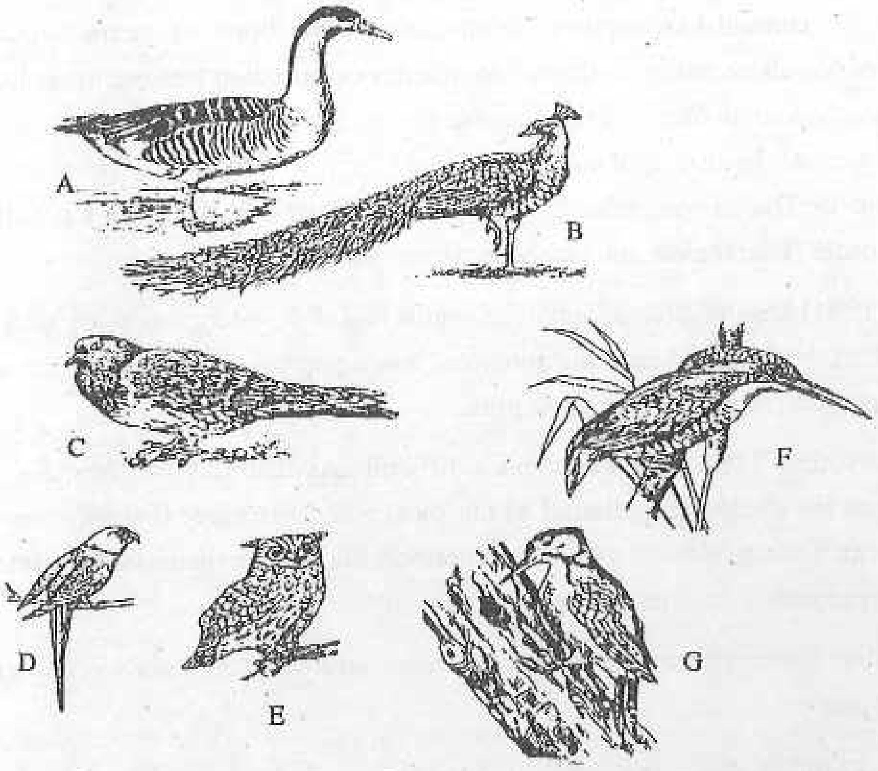


Fig 3.8 : Aves (contd.) : A, *Anser anser* (Greylag Goose); B, *Pavo cristatus* (Peacock); C, *Columba* sp. (Pigeon); D, *Psittacula* krameri (Roseringed Parakeet); E, *Bubosp.* (Brown fish owl); F, *Alcedo* sp. (common blue kingfisher); d, *Picoides* sp. (woodpeeker).

Order 24. **Passeriformes**

e.g., *Corvus splendens*
*Passer domesticus*

*Dicrurus adsimilis*
*Acridotheres tristis*
*Pycnonotus cafer*

## VI. Class-Mammalia

The line of evolution by which the synapid reptile, *Solenodonsaurus* originated from the stem reptile, Cotylosaur later during Permian—Triassic periods laid the foundation of mammal-like reptiles about 200-180 millions of years ago. Later discoveries of fossils showing evidences of distinct mammalian features revealed that the mammals appeared during mid-Jurassic period about 150 m. years ago. Even before that period, the origin of mammals could be traced back to *cyrwgnathus* of early Triassic or *Diarthrognathus* of late Triassic, both belonging to the subclass Synapsida, order Therapsida and suborder Theriodontia.

Young (1981) has defined mammals as warm blooded vertebrates with hairy skin in most species, with large brain and inner ear having spiral cochlea, with left aortic arch only and nourished by mother's milk

To classify class Mammalia is no less a difficult task than that for the class Aves. However, from the evidences gathered so far, most scientists agree that the mammals arose the order Therapsida and suborder Theriodontia whose mammal-like features were well represented in *Cynognathus* or *Diarthrognathus.*

Among the living mammals the monotremes and the marsupials retain many reptilian features.

**General characters of the class Mammalia :**

(i) Body covered with hairs and presence of mammary glands secreting milk; these are the two unique features of the class Mammalia.

(ii) External ear with pinna; Sweat glands and sebaceous glands in skin.

(iii) A muscular diaphragm separates the thoracic and abdominal cavities.

(iv) Lower jaw formed of a large dentary which articulates directly with the squamosal; teeth thecodont, heterodont and diphyodont.

(v) Two occipital condyles; usually 7 cervical vertebrae; vertebrae acoelous or amphiplatyan.

(vi) Only left systemic arch present; RBC circular, without nucleus.

(vii) Corpus callosum connects the two cerebral hemispheres; 4 optic lobes.

(viii) Usually separate urinary and reproductive apertures; No cloaca (except in Monotremata)

(ix) 12 pairs of cranial nerves; placenta present (except in monotremes).

Detailed classification of the class Mammalia is a lengthy chapter. As such, characters of orders have been omitted in most cases; only names of orders with examples have been mentioned.

**Subclass I. Prototheria :**

(i) Mammae without nipples.

(ii) Cloaca present; both urinary and reproductive apertures open in the cloaca.

(iii) Females lay eggs; testis abdominal.

*Order 1. **Docodonta**

Triassic—Jurassic; Extinct

e.g., *Morganucodon.*

*Order 2. **Triconodonta**

Triassic—Jurassic; Extinct.

e.g., *Triconodon*

Order 3. **Multituberculata**

Jurassic—Eocene; Extinct

e.g., *Plagiaulax*

Order 4. **Monotremata**

Pleistocene—Recent

(i) Geographical distribution—Australia, Tasmania and New Zealand; reflect many reptilian features.

(ii) Body covered with hairs which on dorsal surface are transformed into spines.

(iii) Lips transformed into beaks; digits with sharp claws; webbed foot present.

(iv) Platypus with teeth; spiny anteater without teeth.

(v) Skull bones without sutures.

(vi) Cervical vertebrae with ribs; corpus callosum absent.

(vii) Young nourished in a special abdominal pouch outside the body.

e.g., *Ornithorhynchus* (Duck-billed Platypus) *Tachyglossus* (spiny Anteater)

**Subclass 2. Theria :**

(i) Pinna distinct; mammae with nipples.

(ii) Intrauterine development.

(iii) Ureter directly opens into urinary bladder.

(iv) Males discharge urine and sperms through a common duct (urethra); In females oviduct forms fallopian tube and uterus.

***Infraclass 1. Pantotheria**—Jurassic period; Extinct

*Order 1. Eupantotheria

e.g., *Amphitherium*

*Order 2. Symmetrodonta

e.g., *Spalacotherium*

**Infraclass 2. Metatheria** (Cretaceous—Recent)

(i) Young born immature and nourished in mother's special abdominal pouch called **'marsupium'**

(ii) Placenta absent.

**Order—Marsupialia :**

(i) Numbering about 250 species, they live in Australia, Tasmania, North, Central and South America and later in some parts of Europe.

(ii) Body covered with very soft hairs called 'fur'; tail very powerful;

(iii) Most females possess 'marsupium' (marsupial pouch);

(iv) Forelimb's much shorter than hind limbs.

(v) In most species, two uteri and two vaginae are present laterally; the two vaginae unite to form a common urinogenital sinus.

(vi) Placenta is usually absent.

e.g., *Didelphis* (Opossum)

*Macropus* (Kangaroo)

**Infraclass 3. Eutheria = Placentalia :**

(i) Face elongated.

(ii) Single vagina present; no marsupium; placenta present.

(iii) Cloaca absent; anal and reproductive apertures separate.

(iv) Ribs double-headed.

Simpson (1945, 1975) suggested bunching of several orders into what is called **'cohort'**. In Young's (1981) classification, out of 26 orders, 16 orders are living, 10 extinct; in Romer and Parson's (1986) classification, out of 28 orders, 15 orders are living, 13 extinct.

All the mammalian orders have been grouped into 4 larger 'cohorts' which system has also been followed in Young's (1981) classification.

**Cohort 1. Unguiculata :**

(i) Orders included in this cohort are comprised of such mammals which reveal many primitive characteristics of mammals.

(ii) These animals are with nails or claws.

This cohort includes the following orders, the animals of which appeared earliest among the eutherian mammals : Order **Insectivora** (e.g. *Tupaia, Sorex);* Order **Chiroptera** (e.g., *Pteropus, Desmodus);* Order **Dermoptera** (e.g., *Cynocephalus = Galeopithecus);* Order **Taeniodontia** (extinct) (e.g., *Stylinodon);* Order **Tillodontia** (extinct) (e.g., *Trogosus);* Order **Edentata** (e.g., *Dradypus);* Order **Pholidota** (e.g., *Manis);* Order **Primates** (e.g., *Loris, Lemur, Gorilla).*

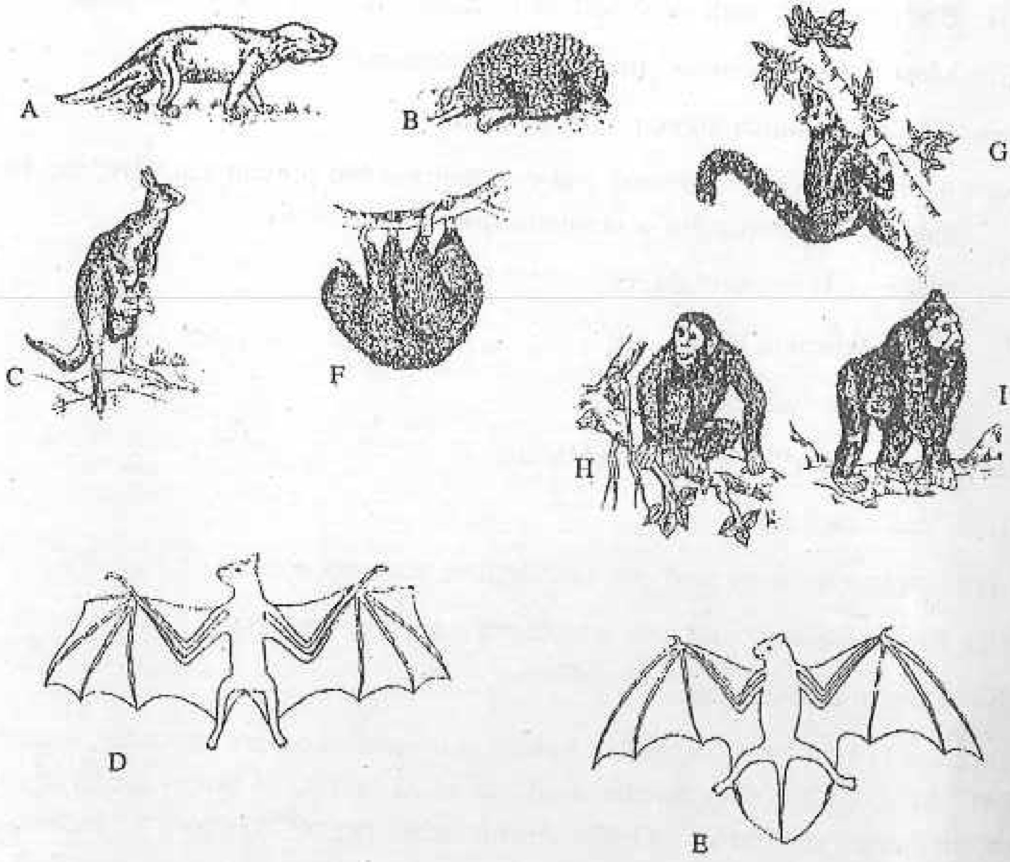


**Fig 3.9** : Mammalia : A, *Cynognathus* (Mammal-like reptile); B, *Tachyglostus* (spiny anteater); C, *Macropus* (Kangaroo); D, *Pteropus* sp. (Megachiroptera); E, *Vespertilio* sp. (Microchiroptera); F, *Bradypus* sp. (Stoth); G, *Lemur* sp.; H, *Pan* sp. (Chimpanzee); I, *Gorilla* sp.

### Cohort 2. Glires :

(i) Smaller in size, body covered with soft fur; vegetarian.

(ii) Distinct diastema present; forelimbs shorter than the hindlimbs.

This cohort includes the Orders **Rodentia** (e.g., *Cavia)* and Order **Lagomorpha** (= Duplicidentata) (e.g., *Lepus, Oryctolagus).*

### Cohort 3. Mutica :

(i) Aquatic and almost devoid of hairs; some species have sensory hairs on face.

(ii) Corimmnicate through sound vibrations.

This cohort includes only one Order : Order **Cetacea** (e.g., *Balaenoptera, Phocaena).*

**Cohort 4. Ferungulata :**

Largest assemblage of a very diverse group of mammals. Simpson (1945, 1951, 1953) proposed the name of the cohort Ferungulata on the ground that the oldest members of this group originated from condylarthra.of Palaeocene period.

This large cohort has been divided into 5 superorders and 15-16 orders, based on the diversity of habit, habitat, food, evolution of teeth, etc.

**Super order 1. Ferae :**

This is the central group of Ferungulata

This Super order contains the living Order **Carnivora** which is widely distributed and characterized by the presence of sharp and strong **'Carnassial teeth'** in the Jaws (e.g., *Canisjamiliaris; Felis domesticus; Felis tigris; Felis leo)* and one extinct Order **Creodonta** (e.g., *Oxyaena).*

**Superorder 2. Protoungulata :**

Primitive ungulates appearing by the end of cretaceous or early Palaeocene;

This Superorder contains 4 extinct and 1 living Orders : Order **Condylarthra** (e.g., *Arctocyon);* Order **Notoungulata** (e.g., *Palaeostylops);* Order **Litopterna** (e.g., *Thoatherium);* Order **Astrapotheria** (e.g., *Astrapotherium);* Order **Tubulidentata** (e.g., *Orycteropus).* **The first 4 orders are all extinct.**

**Super order 3. Paenungulata :**

The name of this group indicates that these animals are near ungulates. Except Hyrax, elephant and the aquatic Sirenia, most species were extinct in the Oligocene period.

This Superorder contains the following orders : Order **Hyracoidea** (e.g., *Procavia = Hyrax);* Order **Proboscidea** (e.g., *Elephas maximus; Loxodonta africana);* Order **Pantodonta** (extinct) (e.g., *Pantolambda);* Order **Dinocerata** (extinct; e.g., *Uintatherium);* Order **Pyrotheria** (extinct; e.g. *Pyrotherium);* Order **Embrithopoda** (extinct; e.g., *Arsinoitherium);* Order **Sirenia** (e.g., *Dugong = Halicore; Manatus).*

**Comment :** The cetacea and sirenia, though arising from different sources have many structural similarities due to their aquatic habitat. This is the result of convergent evolution.

**Superorder 4. Mesaxonia** (Le., middle axis) :

(i) axis of foot passes through the middle of the third digit.

This Superorder contains only one living Order : Order **Perissodactyla,** meaning uneven toes (e.g., *Equus; Phinoceros).*

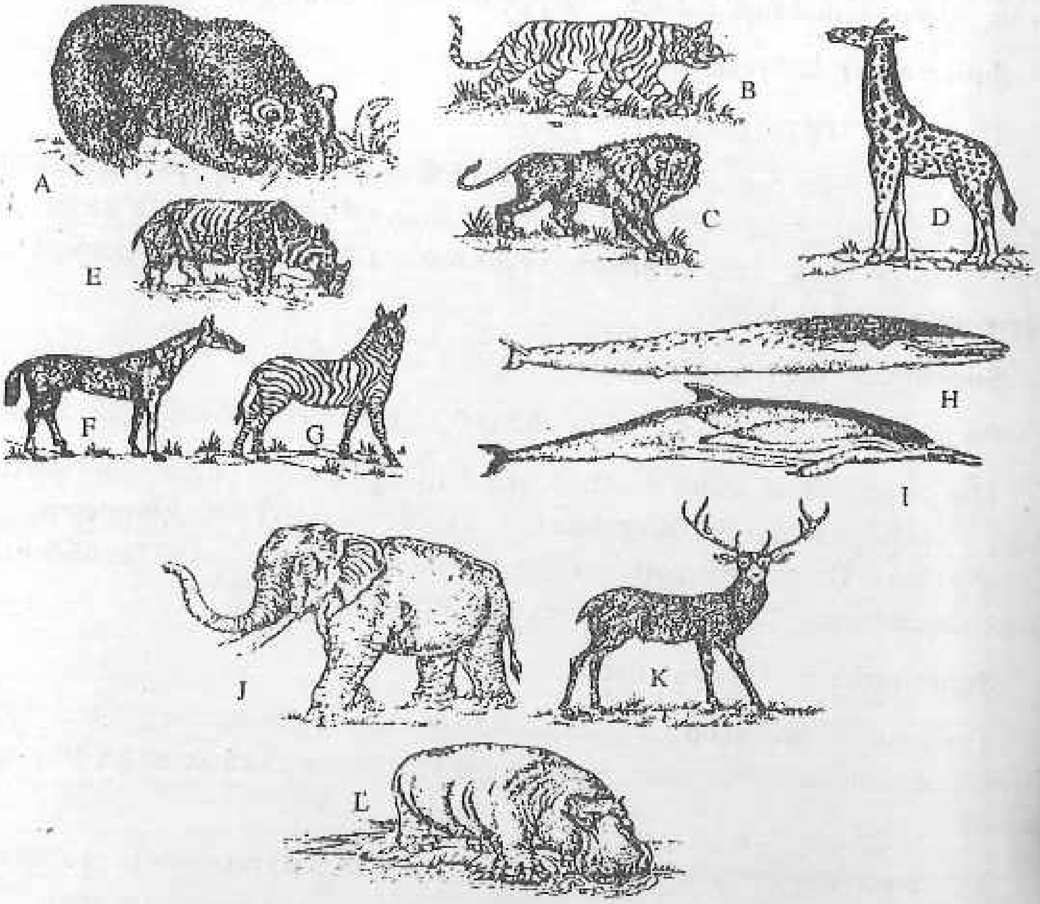


**Fig 3.10 :** Mammalia (contd.) : A, *Ursus* sp. (Grey Bear); B, *Felis tigris* (Tiger); C, *Felis leo* (Lion); D, *Giraffa* sp.; E, *Rhinoceros unicomis* (Indian rhindceros); F, *Equus* sp. (Horse); G, *Equus* sp. (zebra); H, *Balaenoptera* sp. (Blue Whale); I, *Delphinus* sp. (Dolphin); J, *Elephas* sp. (Asian elephant); K, *cervus* sp. (Deer); L, *Hippopotamus* sp.

**Superorder 5. Paraxonia :**

(i) axis of body passes through the third and fourth digits.

This Superorder contains only one living order : Order **Artiodactyla,** meaning even-toed (e.g., *Bos; Ovis; Giraffe; Camelus).*

**A brief discussion on the classification of mammals :**

With the divergence of the synapsid line form the Cotylosaurs in the Permian period towards evolution of the mammal-like reptiles and then step by step on to the early mammals a long history of adaptations of the animal types have been examined from the fossil evidences gathered up to the end of Jurassic period. But the history of modern mammals has been more convincingly assessed by the scientists from the Cretaceous period.

The older classification of the mammals by simpson (1945), followed by Young (1962, 1969) recognized only four subclasses namely, Eotheria, Prototheria, Allotheria and Theria. Later, based on the differences of opinions by different scientists on the classification of mammals, simpson (1975) revised his older, classification into two subclasses—Prototheria and Theria and the latter into three Infraclasses. Another characteristic feature of this classification is that the orders under Eutheria, based on certain common features, have been bunched into four **Cohorts.**

This scheme of classification was followed by Young (1981) and the same has been presented here.

It is relevant to mention here that recently Kardong (1998) has included Monotremata as ari Infraclass under the Subclass Prototheria and Multituberculata as an order under the subclass Allotheria (= Theria).

## 3.4 Terminal questions

1. Define a true vertebrate animal. Illustrate the basic body plan of a vertebrate.
2. Discuss different theories on the origin of vertebrates. Provide a few cladograms by different authors explaining possible evolutionary lineage of vertebrates.
3. Enumerate salient characters of the subphylum vertebrata.

4. Mention a few diagnostic features of the agnathans and Gnathostoma vertebrates with two examples of each.

5. Classify living amphibians up to Orders. with distinctive characters and examples (including Indian species).

6. Classify living reptiles up to Orders with distinctive characters and examples (including Indian species).

7. Classify class Aves up to subclasses with characters and examples.

8. Mention the Orders under Super order Palaeognathae with examples.

9. Mention a few characters of the Superorder Neognathae and names of two orders of aquatic and two orders of terrestrial birds with examples.

10. Mention names of Orders for the birds listed below (Provide scientific names of birds) :

    (i) Emperor Penguin
    (ii) Little Cormorant
    (iii) Flamingo
    (iv) Bareheaded Goose
    (v) White-backed or Bengal Vulture
    (vi) Red Junglefowe
    (vii) Sorus Crane
    (viii) Blue Rock Pigeon
    (ix) Roseringed Parakeet
    (x) Barn owl
    (xi) House Swift
    (xii) Hoopoe
    (xiii) Goldenbacked Woodpecker
    (xiv) Golden Oriole
    (xv) House Crow
    (xvi) Baya Weaver Bird

11. Classify class Mammalia up to Cohorts with distinctive characters and examples?

12. Mention two characters each of the following mammalian groups with examples :

    (i) Prototheria

    (ii) Eutheria

    (iii) Monotremata

    (iv) Marsupialia

    (v) Mutica.

13. Give a brief note of discussion on the classification of any one of the following :

    (a) Class Amphibia

    (b) Class Aves

    (c) Class Mammalia.

# Unit 4 ❐ Vertebrate Integument and its Derivatives

*Structure*

## 4.0 Introduction

In non-chordates, the outer body covering is formed of a single layer of epidermal cells and the outermost cuticle secreted by this layer. In vertebrates, the outer body covering or the skin or integument is formed of stratified epidermal cells with an underlying thick dermis. Thus the skin is a double-layered structure in vertebrate.

**Structural organization of integument :** Morphologically, the integumentary system may be defined as the outermost covering layer of the body—the skin which with its various derivatives not only protects the body from changes in the external environment, but also influences and coordinates some functions of the internal environment as well.

The integumentary system is formed of the skin and its various derivatives. The skin extends as a continuous layer with the mucous membrane of the buccal cavity, eyelids, nasal cavities, rectum and the urinogenital ducts. The skin being provided with different types, of receptor cells and nerve endings serves as an essential coordinator between the external and internal environments of the body. Although the integumentary system offers considerable diversity in different groups of vertebrates, yet in all the groups there are certain basic similarities.

The integumentary system contains both epidermal and dermal derivatives. The epidermal derivatives are the glands, scales, horns, claws, feathers, hairs, etc. The dermal derivative are the dermal scales, bony plates, etc.

## 4.1 Development, general structure and functions of skin and its derivatives

### 4.1.1. Development and structure of skin

In vertebrates, the skin is composed of an outer, comparatively thinner epidermis and an inner thicker dermis.

Embryonically, the epidermis develops from the germinal layer of ectoderm cells and dermis from the embryonic mesenchyme cells of the dermatome.

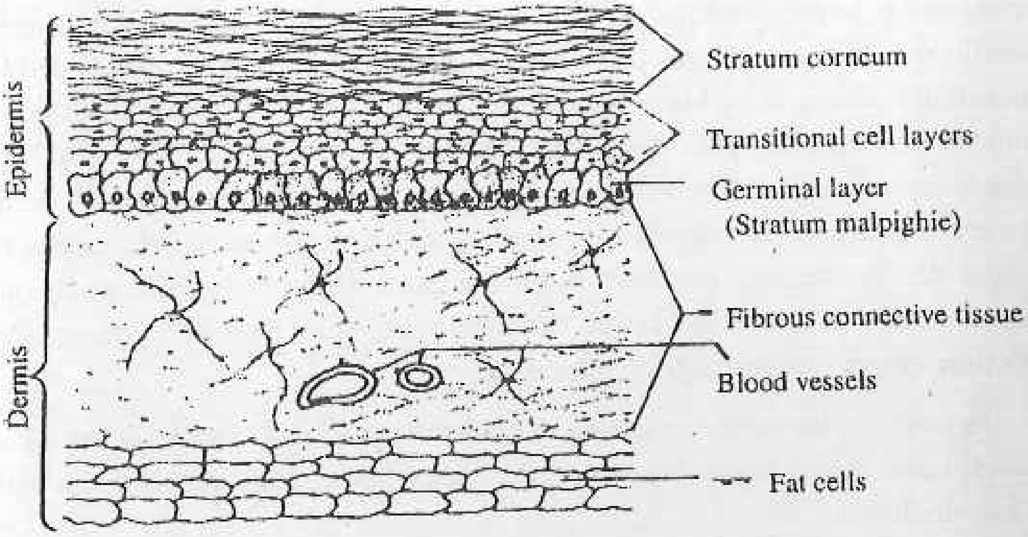


**Fig 4.1** : A generalized cross-sectional part of the skin of a tetrapod

A. **Structure of epidermis** : Of the two cell-layers epithelial cells, lying perpendicular to the underlying dermis, form the outermost covering of the body, the epidermis. Epidermis is mainly a thin cellular layer, while the dermis is a thick fibrous layer with much lesser number of cells. The epidermal cells being joined to one another through delicate intercellular connections form the continuous outer covering. The innermost living layer of columnar epidermal cells is called **'stratum germinativum'** or **malpighian layer**. This layer through exhaustive mitotic divisions produces several transitional cell layers outwardly. The cells of these layers being closely packed appear some what flat. In higher vertebrates, these transitional cell layers are arranged in three district layers. From below outward, these are called **stratum spinosum, stratum granulosum** and **stratum lucidum**. The outermost layer of epidermis is called **stratum corneum**. In this layer the cells are flat scalelike, anucleate and dead. This layer is formed of a horny substance called **keratin** which is a very hard proteinaceous layer insoluble in water. The cell layers moving outward become keratinized, the process being known as '**Keratinization**'.

In fish and aquatic amphibians, the entire epidermis is formed of a layer of living protoplasmic cells; keratin, if present, is very scanty. In fish and amphibians, the skin is mostly permeable and rich in blood capillaries; hence the skin takes an important role in respiration. In land animals, on the other hand, the structure of epidermis is largely modified and the other layers of cells become more and more keratinized. In the epidermis of fishes, the abundance of mucous glands and other unicellular glands is a characteristic feature. In semi-terrestrical adaptation the number of such gland cells diminishes. In fully adapted land animals, few mucous glands occur, unicellular glands are absent and a distinct stratum corneum becomes thicker and thicker. In amphibians, reptiles, birds and mammals, the keratin layer of the skin is variously modified in different parts of the body (e.g., **warts** on the dorsal surface of a toad and **callus** on its palm and sole; **footpad** in mammals and **friction ridges** on the palm of primates).

In amniotes the stratum corneum of epidermis gives rise to scales, scouts, crests, claws, nails, hoops, horns, baleen, rattle, rhamphotheca, feathers, hairs and various other structures.

**B. Structure of dermis** : Just beneath the epidermis, the inner thicker layer of the skin is called **dermis** or **corium**. In most vertebrates this layer is formed of a closely packed fibrous .connective tissues. These cells arise form the embryonic mesenchyme. In the dermis of vertebrates, usually collagen fibres are found most abundantly. With these, a smaller number of elastic fibres also occur. Besides the connective tissues, the dermis contains blood vessels, lymph vessels, muscle fibres, nerve fibres, ciuomatophores, fat cells, etc. The colour variations in the body of animals depend on different kinds of chromatophores which appear star-shaped due to their long branching processes. Usually these cells are of three types : (i) **melanophores** that are dark brown containing melanin; (ii) **lipophores** that contain carotinoid granules and appear yellow to red; and (iii) **iridocytes** or **guanophores** which do not contain colouring granules but contain crystals of an organic substance called guanine. Guanine, with the help of reflection of light may change usual functions of other chromatophores.

In vertebrates, the inner parts of epidermal hairs, sebaceous glands, sweat glands, etc. being embedded within the dermis, the living cells of epidermis may easily draw their nourishment from the dermis through blood vessels, lymph vessels, etc.

The presence of osteoderms or the bony plates in the dermis is very remarkable. The earlier view that the fibrous state of the dermis was more primitive than the bony plates, scales, etc. acquired secondarily has now been changed. It is now held that the primitive tetrapods which evolved from fishes possessed bony plates in their dermis as primitive character. In later periods, disappearance of the bony plates and acquisition of fibrous condition in the dermis is rather secondary (Kent, 1983; Romer and Parson, 1986).

### 4.1.2 Functions of the integument in vertebrates

The integumentary system i.e., the skin and its derivatives perform many essential functions in the body of a vertebrate. Of various functions of the integument, the following are very important.

(i) As the most external covering the skin protects the body from various mechanical injuries and prevents entry of harmful substances from the exterior to the interior of the body.

(ii) Maintains required **humidity** of the body through optimum conservation of water.

(iii) The skin being in direct contact with the external environment acts as an efficient **defensive organ** of the body. The structures involved are broad bony plates, both small and large epidermal and dermal scales, the latter forming a system of dermal skeleton (sometimes fused to endoskeleton), osteoderms, scales of modern fishes and reptiles, layers of fat, poison gland, spiny skin, beaks, claws, feathers and various other keratinized organs.

(iv) **Thermoregulation** ; The fishes amphibians and reptiles are called **poikilothermous** because their body temperature fluctuates with the temperature of the external environment and hence called exothermic (except a few primitive reptiles). Whereas, birds and mammals are **homoiothermous,** because they are able to maintain a stable body temperature irrespective of the changes in temperature of the external environment. In birds and mammals, the skin and its derivatives play a significant role in the conservation and regulation of temperature.

(v) In a number of aquatic mammals like whales and seals, thick layers of fat deposits in the skin form **'blubber'** which serves for both food storage and heat conservation.

(vi) The skin also acts as an organ of secretion. In different vertebrates, mucous gland, poison gland, uropygial gland, sebaceous gland, sweat gland, mammary glands, etc. act as secretory organs.

(vii) Ecdysis is a phenomenon by which certain excretory materials deposited in the skin are expelled. In mammals, a portion of exeretory materials is expelled through sweat secreted by the sweat glands.

(viii) In amphibians, the thin moist skin rich in blood supply acts as a respiratory organ.

(ix) The fins in fishes and the webs in amphibians assist in locomotion of the animals. The so-called 'wings' in flying lizard, squirrel, bat, pterodactyl, etc. are actually memboueous extensions of the skin.

(x) The abundant supply of tactile receptor cells in the skin help the animal in sensing touch, temperature, pressure, pain, etc.

The functions of skin derivatives will be mentioned along with structures of the derivatives.

## 4.2 Glands, scales, horns, claws, nails, hoofs, feathers and hair

### 4.2.1 Introduction

Likewise the internal organs, the integument in vertebrates has been variously modified and give rise to various structures, both from the epidermis and the dermis.

These structures may be defensive, secretory, excretory or respiratory and may influence metabolism of the body. Comparatively, however, the epidermal modification have excelled than those of dermis in the vertebrates.

An account of the integumentary derivatives is briefly described below. Mention may be made here that except dermal scales in fishes and bony plates or osteoderms, the integumentary derivatives are epidermal in origin.

### 4.2.2 Epidermal derivatives

#### I. Glands :

The epidermal glands of the integument are of different shapes, sizes and function. These arise from the malpighian layer of the epidermis. Structurally, these glands are of three types : (i) **unicellular glands** (ii) **tubular glands** and (iii) **alveolar** or **saccular glands**.

(i) **Unicellular glands :** In the cellular layer of the epithelium, certain individual cells may be transformed into gland cells as observed in the larval stage of cyclostomes, fishes and amphibians. For example, the mucous cells, goblet cells, granular cells and beaker cells of cyclostomes are all unicellular gland cells. Most of them secrete mucin which keeps the body slippery and germ free.

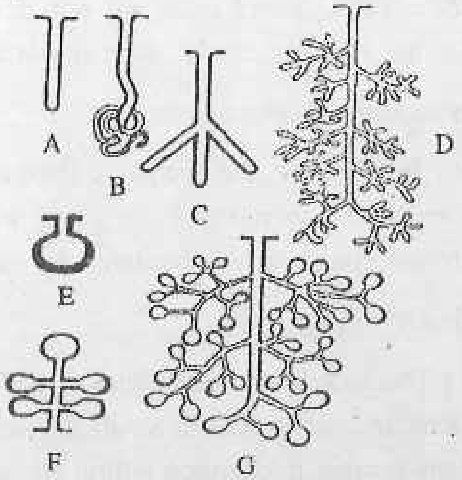


Fig 4.2 : Types of epidermal glands in vertebrates :A, Simple tubular gland; B, Simple coiled tubular gland; C, Simple branched tubular gland; D, Compound tubular gland; E, Simple alveolar (saccular) gland; F, Simple branched alveolar gland; G, Compound aloveolar gland. (Based on Weichert and Presch, 1977).

(ii) **Tubular glands :** These are multicellular tubular glands, the tubules being almost of the same diameter. Arising from the malpighian layer of epidermis, the tubule enters into dermis and forms the gland. These glands may be **simple tubular** (e.g., **glands of moll** in the corner of the eye of human beings), **simple coiled** (e.g., sweat glands in mammals), or **compound tubular glands** (e.g., digestive glands; mammary glands in monotremes, etc.).

(iii) **Alveolar or saccular glands :** These glands also arise from the malpighian layer of epidermis, enter into dermis and form tubular, multicellular funnel-shaped glands called alveolar or saccular glands. Such an alveolar gland may be simple, saclike or compound. The compound alveolar gland is formed of a number of branching lobules whose secretory tubules finally open into the main tubule. Each lobule appears as a swollen gland composed of many small, elongated secretory sacs. The mammary glands and salivary glands of metatherian and eutherian mammals one of this type.

**Merocrine, holocrine and apocrine glands :** Based on the nature of secretion, the epidermal glands may be divided into the following three types :

(a) **Merocrine glands :** These gland cells are not destroyed as a result of secretion; rather these cells are recharged with secretory materials.

e.g., mucous glands; salivary glands, etc.

(b) **Holocrine glands :** In this type, the secretory fluid accumulates within the cells and on death of the cells, the secretory fluid along with the dead cells are thrown out. The dead cells are continually substituted by new cells.

e.g., sebaceous glands of sign.

(c) **Apocrine glands :** The secretion accumulates outside the gland cells from which the secretion gets detached along with a small amount of cytoplasm. Most of the cytoplasm and nucleus remain unchanged within the gland cells. This cycle is repeated after an interval of time.

e.g., mammary glands and sweat glands are of this type.

**Different types of epidermal glands in vertebrates :** In vertebrates, from fishes to mammals, different types of epidermal glands and their modifications are observed. A few examples are cited below :

(i) In the epidermis of fishes, the **goblet cells, granular gland cells** and **beaker cells** are present, but along with these, simple saccular and multicellular mucous glands are also present.

In some elasmobranch (e.g., sting ray) and teleost fishes (e.g., some common catfishes), the epidermal glands are transformed into multicellular poison glands. In *Heteropneustes fossils,* the duct of the poison gland opens at the base of the spine of the pectoral fin.

In certain elasmobranch and teleost fishes living in deep sea, some epidermal cells in the ventral region of the body are transformed in a row to form gland called phosphorescent organ or photophore that emits light.

(ii) In toads, the insert **warts** on the dorsal surface of the body and the parotid gland near the tympanum on either side are actually formed of an integration of a number of epidermal poison glands.

(iii) Skin glands are practically absent in the reptiles. The femoral glands in the ventral region of the thigh of a male lizard, musk glands in crocodiles and in a few turtles and tortoises are to be considered as exceptions.

(iv) In birds the only **uropygial gland (preen gland; oil gland)** at the base of the uropygium is an important integumentary gland. This gland is a simple, branching saccular gland, divided into two by a septum. This marks the bilateral, paired origin of the gland.

(v) In mammals, the abundance and diversity of skin glands are remarkable. Two basic types of skin glands in mammals—the **sebaceous gland** and the **sweat** or **sudorific gland** have been modified and have given rise to different types of glands in different parts of the body.

## II. Epidermal scales :

In a number of vertebrate classes the animals have their body covered with scales. These scales are of two types : epidermal and dermal, both performing mainly protective function of the body, but their origin is different.

The epidermal scales arise from the cornified epithelium produced by the malpighian layer of epidermis. Along with tetrapod evolution the epidermal scales have been modified in different vertebrates suited to their diversified adaptations.

In fishes, there are no epidermal scales. In modern amphibians in general, the skin is smooth, scaleless and moist with glandular secretion. In a few anurans (toads and frogs), however, the hind-legs and the digits of hand contain epidermal scales. Similarly, the scales are also found in a few species of the burrowing caecilians.

It is in the class Reptilia that for the first time highly developed epidermal scales appear with significant diversification throughout the class. In reptiles, the scales are chiefly of two types, one in the lizards and snakes and the other in the turtles, tortoises and crocodiles. In both the cases the scales arise from the keratin layer of epidermis, although the nature of their origin is slightly different. In lizards and snakes, the scales are arranged in an overlapping fashion i.e., the caudal end of each scale overlaps rostral part of the next scale behind.

During development of scales, the malpighian layer of epidermis along with dermis push the keratin layer upward and the cells with alpha and beta keratin form a number of swollen papillae. A pit-like follicle develops between the two papillae. Thus the scales at their bases from a continuous layer.

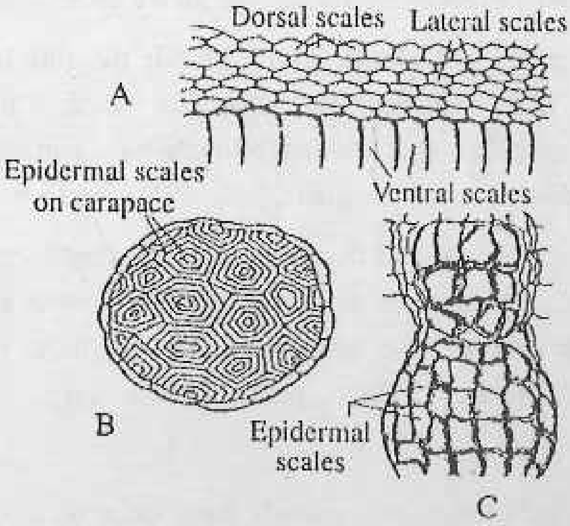


Fig 4.3 : Epidermal scales in reptiles: A, Dorsal, lateral and ventralscales of a snake: B, Epidermal scales on the carapace of a tortoise; C, Dorsal epidermal scales of a crocodile.

In lizards and snakes, after periodic intervals, the old corneal layer containing the scales is cast off the body and replaced by a new layer which is already in the process of growth beneath the old one. This phenomenon of casting off the old skin is called **'ecdysis'**. The broad tape-like transversely arranged ventral scales in .snakes help them in their locomotion.

In a few lizards and snakes, the epidermal scales are diversely modified. In the Horned Lizard, *Phrynosoma,* the middorsal scales are transformed into a row of spines and two large horns at the back of the head. In Gekko lizards *(Gecko* sp.), the scales are modified to form **digital lamellae** for the purpose of climbing steep wall. At the tail-end of a rattk snake *(Crotalus* sp.), the rattle producing warning sound is formed by a few (4-6) old scales, dried and loosely arranged.

In turtles and tortoises, the dorsal carapace and the ventral plastron covering the body are formed by modified scales. These scales are not of the same size as that of the plates underneath. Here each scale is formed anew. The malpighian layer of epidermis lying below extends outwardly and forms a new scale below the old one. As a result the old scales are arranged outwardly like rings. In some species, however, (e.g., Painted turtle) the old scales are thrown outside. In soft leathery tortoise, the epidermal scales with underlying long dermal plates are absent.

In crocodiles, the large epidermal scales completely cover the body. A pit is formed in each scale at the lateral and ventral sides, as well as, in the tail of the body. A small receptor membrane lies within the pit. In crocodiles, the old scales are not thrown out by ecdysis. New scales develop when the old scales degenerate and are worn out.

In birds, the epidermal scales are limited to only tarsometatarsal region and to base of the bill.

In some species of gallinaceous birds, (e.g., Jungle fowl), a bony projection called **'Spur'** develops on one side of the tarsometatarsus. A modified epidermal structure in the form of a keratinized scale covers the bony spur alround. The whole structure becomes very rigid and sharp.

In swans, ducks and may aquatic birds, the scales in the webs are epidermal.

As in birds, the epidermis in mammals too has been variously diversified. In **scaly anteaters**, the whole body except the ventral region is covered with large overlapping arrangement of hard keratinized scales. At the time of ecdysis, the scales are cast off the body singly. **In armadillo,** large and broad epidermal plates are united to form plates which like broad, ringlike bands encircle midregion of the body (except midventral region). Even the head, shoulder and caudal part of the body are covered with these scaly plates. In the gap between these plates scanty distribution of hairs are observed. In other mammals, reptilian type of epidermal scales are usually limited to the tail, hand and sole of feet (e.g., small and large rats, cat, beaver, etc.). However, hairs emerge outward from below the scales.

### III. Horns :

True horns develop in mammals in a variety of ways and generally function as their offensive and defensive organs. In herbivorous mammals like cow, sheep, goat, rhinoceros, antelope, etc., the horn arises as a dermal bony projection from the skull. This bony core is then covered allover by a hollow, keratinized epidermal cone.

Based on the differences in origin, the horns may be classified into four, types (Weichert and Presch 1977) : Keratin fibre horn, hollow horn, pronghorn, antler.

(i) **Keratin fibre horn :** This horn is found in rhinoceros only. This horn arises as a long cone-shaped dermal papilla that remains covered by a hard, keratinized epidermal cells with fibres. The cells between the papillae act like cement, binding the fibres.

There is only one such median horn in Indian rhinoceros *(Rhinoceros unicornis)* and two bilateral in African rhinoceros *(Rhinoceros bicornis).*

(ii) **Hollow horns :** This type of horn grows in cow, sheep, goat, buffalo, etc. In some species, only males possess the horns. The keratiniged epidermis surrounding a projection form the frontal bone of the skull forms this type of horn. The inner cavity of the horn extends up to the frontal sinus.

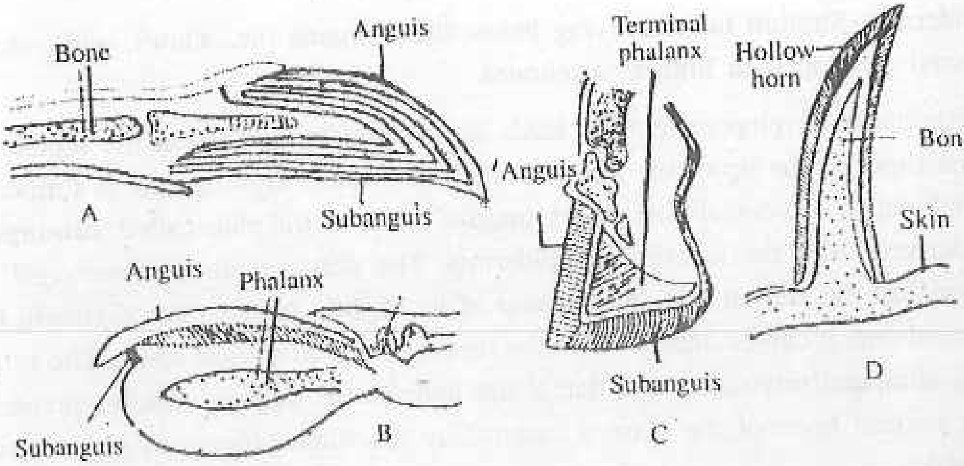


**Fig 4.4** : Development of various epidermal structures : A, Claw of a reptile; B, Nail of a mammal; C, Hoof in the foot of a horse; D, A hollow horn.

(iii) **Prong-horns :** This characteristic horn is possessed only by the North American Antelopes *(Antilocapra* sp.). Here also the keratin layer of the epidermis surrounds a bony projection from the frontal bone. This horn appears as a prong i.e., the horn divides into two branches like two arms of a forcep. The keratinized covering of the horn is cast off annually and a new covering is formed in its place.

(iv) **Antlers :** Usually in the males of the species of deer, the branched horns called antlers develops as projections of the frontal bone of the skull. Exceptions are observed in Rein Deer, Giraffe and Caribou where both the males and females possess antlers. While growing in young males, the bony projection on either side remains covered by soft hairy epidermis. This covering is called **'Velvet'**. When growth of the antler is completed, the epidermal velvet is cast off by the animal; what remains now is the branching antler which is a bony structure of mesodermal origin.

In Giraffe, the antler is small unbranched and remains covered by the velvet permanently.

## IV. Claws :

In vertebrates, the claws, nails and hoofs are considered as homogenous structures, because all these three organs develop in the same manner from the keratin layer of epidermis. Stratum lucidum lying below these organs (i.e., claws, nails, etc.) is very well developed in higher vertebrates.

True claws develop in reptiles, birds and mammals, and so, in the reptiles for the first time. At the tip of the terminal phalanx of each digit, a claw is formed by the combination of a dorsal plate called **'unguis'** and a ventral plate called **'subunguis'**, both derived from the keratinized epidermis. The dorsal plate is more rigid and stronger than the ventral one and because of its slightly higher rate of growth than the ventral one, it curves downward in the form of a sharp, conical spine. The ventral plate is comparatively softer and flat; it lies beneath the unguis, closely apposed to it. The corneal layer of the claw is cast off by the same process of ecdysis as in the reptiles.

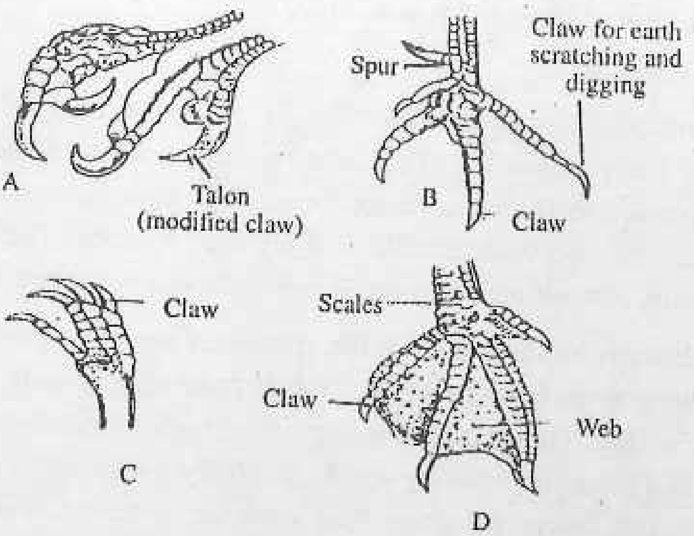


**Fig 4.5 :** Different types of claws in birds : A, Sharp, curved talon in an osprey (Falconiformes); B, Claw in Jumgle fowl for digging and scratching earth; C, Claws in a swift for climbing vertical wall; D, Web of a duck for swimming.

In birds, the structure and development of the claw are the same as in the reptiles. But in some birds the claws in the digits of feet have become highly curved, strong and sharp in response to particular feeding adaptation (e.g., sharp talons in the feet of osprey and vulture). Here the corneal layers are not thrown out as in ecdysis, but a new claw develops in phases below the old one and when it is fully formed, it replaces the old one.

Usually claws are present in the feet of birds only, but in newly hatched Hoatzin *(Opistho comas cristatus)*, the first two fingers of the wing bear claws.

In mammals, the subunguis becomes much reduced arid it merges with the **'torus'** or pad lying ventral to the tip of the digit. In Lemurs and Tarsiers (order Primates) some of the digits of the foot bear claws and some nails.

### V. Nails :

In the arboreal primates, nail in formed at the upper surface of the digital tips of both hands and feet. In fact the nails are the flat and broad replica of the claws. At the base and inner surface of the nail, the germ layer called the '**nail bed**' gives rise to the nail.

### VI. Hoofs :

In the bovine species (Ungulates; class-Mammalia), the number of digits become reduced and the animals have to walk or run on the tips of remaining digits. Here the claw becomes short and wide and the hardened corneal layer of epidermis forms a sub-cylindrical covering on the tips of the digits. Due to increased growth of the unguis, it assumes the shape of a curved V-shaped structure. The body weight of the animal rests on the distal tips of the V-shaped hoofs. The subunguis forms inner pad between the arms of the hoof.

### VII. Feathers :

Although a discussion on the beaks or bill of birds has not been included in the present syllabus, it is considered relevant to mention that the contour of the beaks has been rendered suitable for diverse feeding adaptations in birds due to thick; hard and keratinized epidermal covering around the beaks. The thick, hard, keratinized covering of the beaks is called **rhamphotheca** and the sharp edges of the beaks formed by rhamphotheca is called **tonia** (Sing. **tomium**).

The appearance of feathers in birds is unique. The entire class comprising birds may be isolated from the rest of the vertebrates by this single character. Of all the epidermal derivatives, the appearance of feathers is the most significant, because without feathers it would not have been possible for the birds to conquer air.

Evidences print out that the reptilian scales have been strangely modified into feathers. The stratum corneum of epidermis has reached the peak of its. 'development in birds.

**Development of feathers :** Observation on the development of a small down feather reveals that the process of development of a feather is similar to that of a scale. The outpushing **feather papilla** of epidermis forms a pit-or the **feather follicle** through which the **feather bud**, produced as a result of continued division of the malpighian layer of epidermis, pushes ahead of the skin in the form of a feather shaft containing **barbs**. In a contour feather the barbs produced by division of the feather bud are arranged horizontally or some what obliquely on either side of a midrib or the **rachis**. The outermost, temporary cornified sheath of epidermis that surrounds the growing feather is called **periderm**. In fact the barbs of a down feather penetrate this periderm to come out. The barbs gradually start separating out—at the base of the feather.

In the development of a contour feather, the basic method of development is the same but the detailed process of development is more complex. The scales in reptiles and feathers in birds both are from the beta carotin layer of epidermis.

**Pterylosis :** The arrangement of feathers on the skin of a bird is called **pterylosis**. On the body of a bird, the feathers grow in definite tracts and in specific arrangement that defeats from species to species. These tracts from which the feathers grow are called pterylae. Between the **pterylae** the featherless tracts are called **apteria**. Both pterylae and apteria on a bird's body have been given names according to their location on the body (e.g., spinal pteryla, femoral pteryla, lateral apterium, etc.).

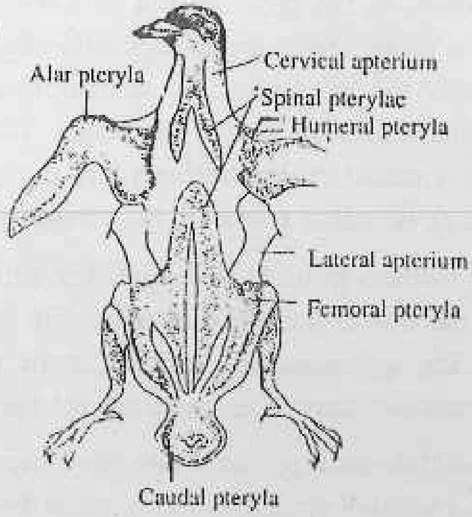


Fig 4.6 : Pterylosis in a bird.

**Colour of feathers :** One of the enchaniting quality of birds is their colour of feathers which may be black, white, blue, green, yellow, pink, red, grey, brown, etc. The colour may be bright in some birds, dull in others and may occur in a variety of combinations. Usually there are two types of pigments in feathers : (1) **melanin type** which produces black, yellow, red and brown colpurs and (ii) **lipochrome type** (Xanthophil and carotenoids) which produces yellow, orange and red colours. However, colour diversity may occur due to structural variations in feathers. Some reflected or iridescent colours result from structural variations in feathers.

**Moulting of feathers :** Based on the presence or absence of feathers in hatchlings, all the species of birds have been divided into two categories; (i) Nidifugous (Precocial) and (ii) Nidicolous (altricial), the former with already a coat of down feathers at the time of hatching and the latter hatches out almost with the bare skin and the feathers grow on the body of the nestlings while they are nourished by their parents at the nest. The precocial species are able to fly out of their nest, either being guided by their parents or on their own, after a few days (sometimes after a day or two).

In both the cases, periodic moulting of feathers in birds is an usual phenomenon. In most species of birds, moulting occurs twice in a year—before the breeding season and after. The winter moulting of feathers remains incomplete, because their flight at this time compels them not to go for moulting of their wing and tail feathers.

Of several causes initiating moulting the secretion of endocrine glands is of great significance.

**Classification of feathers :** Different scientists have classified feathers differently. According to Weichert and Presch (1977), the feathers are mainly of three types : **filoplumes, plumulae** or **down feathers** and **plumae** or **contour feathers.** According to them, all the other types of feathers are modifications of these three main types. Bologna (1995) has classified feathers into four types : contour feathers, down feathers, semiplume and filoplume. He has described bristles as modification of filoplume.

However, the classification followed here has been adopted from that given by Stettenheim (1972) and Pough, Heiser and MeParland (1990). They have divided the feathers into five types : 1. **Contour feathers**; 2. **Filoplume**; 3. **Down feathers**; 4. **Semiplume** and 5. **Bristles.**

**1. Contour feathers :** These are large feathers covering general surface of the body of a bird and giving characteristic shape and contour of the body in different birds. The larger flight feathers i.e., the wing and tail feathers are also modified contour feathers. Each leaflike feather has a mid-rib-like central axis divided into two parts : the thicker, hollow basal one third of the axis without barbs is called **'Quill** or **Calamus'** and the distal two-third of the solid axis up to the tip of the feather is called **'Rachis'**. At the base of the calamus, there is a small aperture called **inferior umbilicus** by which the calamus remains embedded in the skin and through which the feather draws its nourishment during development. At the junction of the calamus and rachis, ventral to the calamus, there is another small aperture, the **superior umbilicus** which remains covered by a fine, delicate bundle of feathers called **aftershaft**. In an adult feather which is nonliving, both the inferior and superior umbilici become inactive and closed due to retraction of the dermal papilla.

In pigeons, doves and many other species the after shaft or the hyporachis appears as a bundle of soft, hairlike down feather with bards and barbules.

In **Emu, Cassowary** and in the extinct *Dinornis* (Ratite birds), the after shaft is very well developed and is almost of the same length as of the main feather.

The median longitudinal groove that runs throughout the solid rachis from the superior umbilicus up to distal tip of the feather is called **umbilical groove**. On both sides of the rachis the leaf like extended portion of the feather is called **Vane or Vexillum.** The rachis usually divides the vane into two unequal halves. Both the rachis and the vane become gradually narrower from the calamus towards distal tip of the feather. The central part of the rachis is filled with dense **pith cells**. On both sides of the rachis, the lifelike expanded blade of the feather is formed of numerous threadlike barbs that arise from the rachis and run outward, somewhat obliquely parallel. The barbs also become shorter distally. From either side of the barbs arise large number of still finer bronchus called **barbules** which are distinctly of two types : **distal barbules** directed outwardly and provided with many minute **hooklets** or **hamuli** (also called **barbicels**). And the **proximal barbules** directed inwardly and provided with **flanges** and **grooves** in their curly anterior two-third. Due to oblique position of the barbs the hooklets of the distal barbules rigidly anchor against the flanges and grooves of the proximal barbules. As a result the entire vane of the feather remains interwoven with its barbs, barbules and barbicels in such a manner that the feather becomes broad, flexible, yet rigid and flat leaflike structure most suitable for flight.

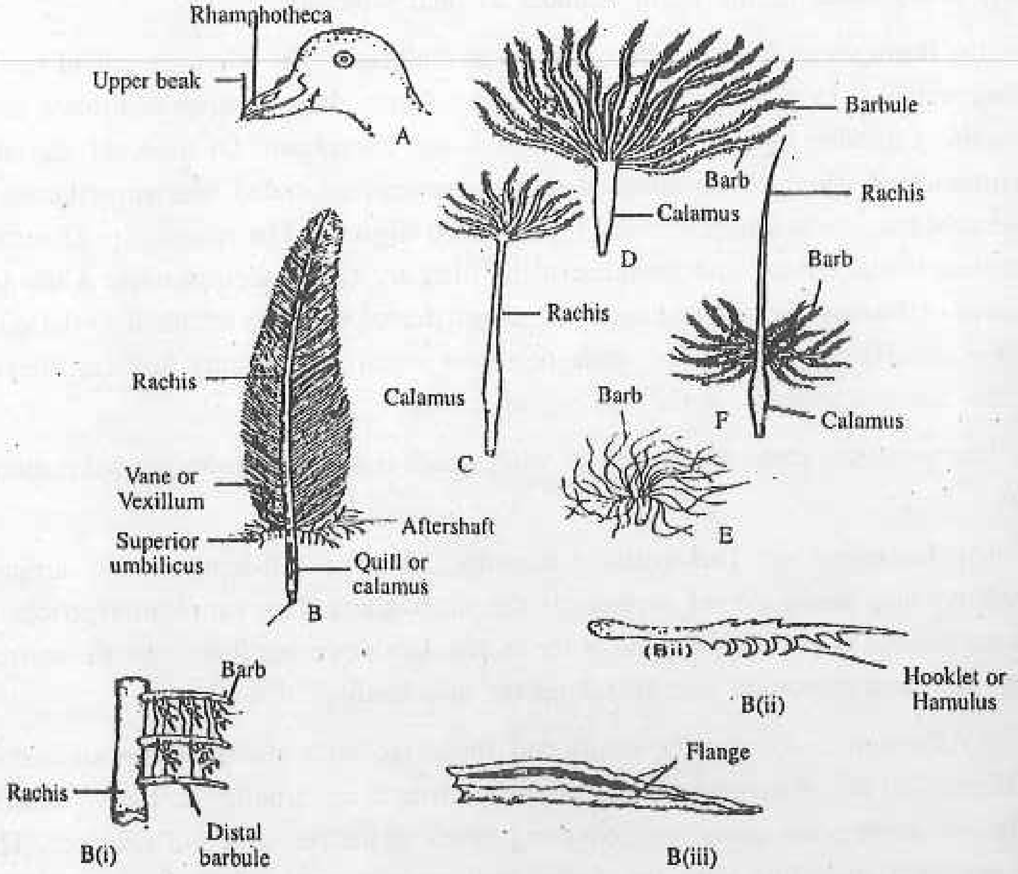


**Fig 4.7 :** A, Rhamphotheea on the upper beak of a pigeon; B-F, Different parts of a generalized feather; B, A eontaur feather; C, A filoplume; D, A down feather; E, A powder down; F, A bristle.

The proximal portion of the vane is **plumulaceous** i.e., soft, loose and fluffy. This character provides **thermal insulation** to the feather whereas, the distal portion of the vane is **pennaceous** i.e., like a thin sheet but hard, rigid and compact. Thus the distal portion acts as an **airfoil** that helps in the flight of birds, protects the inner layer of down feathers, helps shaking off water from the body and either reflects or absorbs solar radiation. The barbules help maintain the thin but rigid pennaceons aerofil of the vane.

**Flight feathers and coverts :** The large feathers of the wing and tail directly taking part in the flight of a bird are more or less species specific in number. **These are specialized contour featners.** The coverts are arranged in two, three or more rows along bases of the flight feathers as their covering.

(a) **Remiges or Wing-quills :** The large feathers of the wing are called remiges (Sing. remex). In pigeons and in many other birds, their number is limited to 23. In quite a number of species, however, there are exceptions. Of these 11 are called **primaries** of which 7 are attached to the metacarpals called metacarpallaries and 4 attached to the second and third digits called **digitals**. The remaining 12 feathers attached to the tendon and muscles of the ulna are called **secondaries. Alula (Ala spuria** or **Bastard wing)** is a small bundle of feathers that is attached to the pollex in the metacarpal region. The alula regulates small air currents and considerably assists the tail feathers in the landing of a bird.

The posterior part of the vane in wing quills is much broader than the anterior part.

(b) **Rectrices or Tail-quills :** Usually 12 long tail-feathers are arranged semicircularly along dorsal surface of the uropygium. The vanes in rectrices are almost of equal size on either side of the rachis. Besides other functions, the rectrices play the most important part in taking off and landing of a bird.

(c) **Coverts :** As already mentioned these are also modifications of contour feathers with all of their complements. The coverts are smaller feathers occurring in two or more rows across and covering bases of the remiges and rectrices. They are arranged in a line with the flight feathers whose slots (between two flight feathers) at the bases are closed by them from both the sunaces i.e., from above and below. Thus the coverts act as effective covering that strengthens the bases of the light feathers and ensures smooth flight in air.

2. **Filoplumes :** These are also known as hair-feathers or pin feathers, as their long, narrow whiplike rachis, devoid for the most part of barbs and barbules, resemble a hair or a pin. Its quill is very short and the long rachis bears at its apex a bundle of weak barbs and bartules. There are no barbicels or hooklets. The filoplumes are seen after removal of contour feathers from the body surface.

Recent investigations about the functions of filoplumes have revealed that abundant free nerve endings are present in the follicle walls of filoplumes.

These nerves being connected to the vibration and pressure receptors around the follicles of feathers transfer movements of the contour feathers to these receptors. This sensory system possibly help the' contour feathers to remain at their proper places and has a role in the rearrangement of the contour feathers during flight.

The filoplumes in peacock is unusually long.

3. **Down feathers :** The immediate outer coating of the skin formed by the numerous small, soft wooly bunches of feathers are called **down feathers**. Each down feather has a short, distinct calamus but there is no rachis. From the apex of the calamus a bundle of long, flexible and delicate barbs arise. The barbs are provided with finer and more delicate barbules but there are no hooklets.

In a hatchling just hatching out of the egg or for a few days thereafter, the very fine, delicate, soft wodly coat of down feathers that cover the body are called **natal down** or **nestling down**. In a newly hatched bird, the nestling down feathers provide a very effective **thermal insulation** to the body. These feathers are the first to appear in the body before the appearance of the contour feathers and filoplumes. The definitive down feathers, however, develop along with other feathers in the body. The down feathers associated with the uropygial gland help transferring the oily substance to the beaks of birds.

**Powder feathers :** These are also known as **'powder down'.** Structurally, these feathers are much smaller but similar to down feathers, has a short calamus but there is no rachis. Unlike down feathers, the apex of a powder down feather does not reach beyond the size of a nestling down. The apex of the feather continuously breaks down and produces a powder-like substance. In many birds, these feathers appear yellowish like the yellow tinge of the skin (e.g., egrets, parrdts, barbets, etc.). These feathers break down and produce white powder-like substance which forms a water-resisting insulation over the contour feathers.

4. **Semiplumes :** Young (1981) comments that the semiplumes are down feathers of an adult bird and being located below the contour feathers these maintain heat and shape of the body. However, Pough *et al.* (1990) comment that the semiplumes

are feathers intermediate between the contour and down feathers. Completely plumulaceous (i.e., soft and tuffy) vane and a long rachis are the characteristics of semiplumes. Unlike in down feathers, they have a rachis that is much longer than the longest barbs.

5. **Bristles :** Many scientists believe them to have arisen from the filoplumes. These specialized feathers occur in the rictal region (rictus = Junction of the upper and lower beaks) or around eyes of certain insectivorous birds like flycatchers (Muscicapidae), nightjars (caprimulgidae), etc. Each bristle has a short calamus and a long rigid rachis. Some barbs and barbules are present at the base of the rachis near the junction of the calamus and rachis. The rest of the long rachis is without barbs and the rachis becomes gradually narrower towards its apex.

The bristles help catching insects in air and prevent unwanted particles to enter into the eyes. The bristles also act as organs of touch.

**Functions of feathers :** The feathers in birds not only function as the chief organs of flight but various other functions of which some important functions are mentioned below :

(i) The covering of feathers render distinct shape and size to the body of a bird. The feathered coat is light, rigid, flexible and dry.

(ii) In all flying birds, the wing and tail feathers are specially adapted for flight.

(iii) Thermoregulation is a very important function of feathers which maintain equilibrium between heat loss and heat gain. The feathers act as suitable insulator in the process of heat loss.

The down, semiphemes and contour feathers act as insulator in the process of conductive heat transfer by holding dead air. This insulation of the plumage protects the smaller birds in cold countries or in arctic climate.

(iv) **Colour diversity, self-protection, exhibitionism, courtship, etc.** The colour diversity in feathers plays significant role in social contact, self protection from the predators, hunters, etc. and heat exchange in radiation. The shape, size and colour of feathers are changed in such a manner that these act as visual signals or exhibitionism. Besides size differences, the diversity in the colour of feathers is an important factor in sexual dimorphism. The feather colours are thus used in courtship, mate choice and in identification of the male and female birds (e.g., Speculum on the secondary feathers of Drake ducks, tail feathers in Birds of Paradise and Peacock).

(v) **Waterproof coat of feathers** is rendered water resistant due to frequent preening of feathers by the bird with oily substance from the preen gland.

(vi) **Sound production :** Doves, ducks, humming birds and many other birds may produce a sort of whistling sopnd by changing slightly the size or the curvature of the feathers. This sound is meant for **territorial advertisement** or used as a signal when they fly in a flock during night or in a dense fog. Sound production by feathers is also used in courtship or for the defence of an individual or the party (e.g., Woodcock, go.atsuckers, owls, doves, etc.).

(vii) Feathers are used in **nest building** by birds, for decorating human habitation or worn by warriors in their headgear or helmet.

## VIII. Hairs :

Just as feathers are the unique character of a bird, the hairs are the same to a mammal, although some aquatic mammals are almost devoid of hairs (e.g., a few coarse hairs are present at the snout of a whale). The delicate, soft, patchy covering of hairs found during embryonic development of a mammal is called **'Lanugo'**. Before the birth of the animal, these hairs are replaced by a new coating of hairs.

**Structure, development and growth of hair :** Compared to the development of a feather, it may be stated that the hair is fully epidermal in origin. Because, (i) hair is not a modification of scales present in the reptiles and (ii) unlike in feathers, the dermal papilla does not enter into the hair follicle.

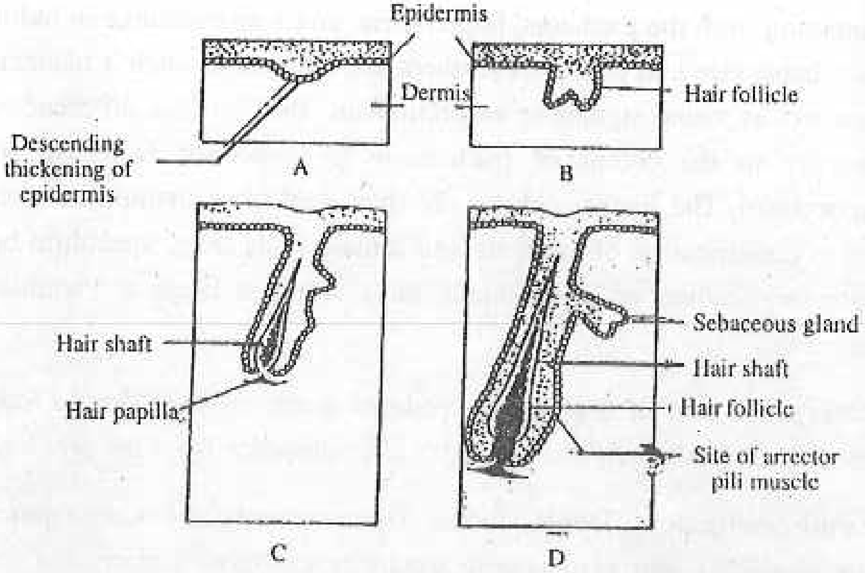


**Fig 4.8** : Stages in the development of a hair.

An ideal hair is formed of two parts : a narrow, rod-shaped **hair shaft** that is projected slight obliquely from the skin outward and the **hair root** embedded in the dermis. At the time of development, the germinal cells of epidermis form the **hair follicle** that reaches deep into the dermis a bit angularly and the germinal cells form a **bulb of hair follicle** that surrounds the hair root. The hair arises from the hair root, travels through the hair follicle and projects outside the epidermis. Except at the base of the hair root, the entire hair shaft is dead, as formed by keratinized cells. The **dermal papilla** below the hair root being supplied with blood vessels and connective tissues adds nutrition to the bulb and follicle cells.

In the longitudial section of a hair, three layers can be marked distictly. The hair shaft is formed entirely of epidermal cells. The outermost layer of the shaft is called the **cuticle**. Just beneath the cuticle i.e., outer to the shaft lies the **cortex** which is rich inkeratin and with some pigment cells and air cavities. The central layer of the shaft is called **medulla** which is composed of comparatively thin, curly irregular cells and large air gaps. The hair follicle and the hair root are enclosed by a double-layered **hair sheath** whose inner layer is called **Huxley's layer** and the outer layer is called **Henle's layer**. These two layers do not reach beyond the follicle. Two swollen bulbs are formed on the outer lateral surface of the follicle. The distal bud is the site for the epidermal sebaceous gland which opens by its very fine canal into the follicle. The other proximal bud of the follicle at its inner lateral wall is the site for the attachment of the arrector pili muscle. The contraction of this muscle, controlled by the autonomic nervous system, results in erection of the hair.

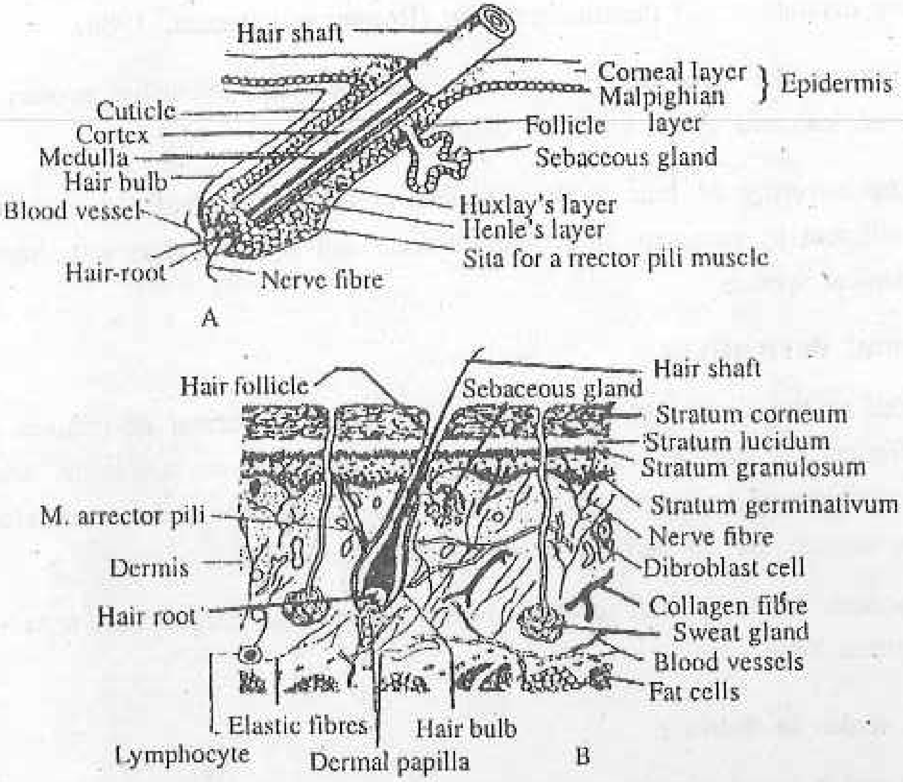


Fig 4.9 : A. Internal structure of a hair with folhicle and gland; B, Sectinal view of the skin of a mammal showing hair, gland and other internal structures.

The structure, shape and size, colour, brightness of hair, etc. depend on the nature of pigment cells of the cortex. Such characteristics of hair are variable in different species. Hairs are not permanent structure in the body; they fall off and are replaced by new growth of hairs.

**Functions of hairs :**

(i) Hairs perform various functions in the body of a mammal, either as a complete covering or having special functions in different parts of the body.

Such special functions may be cited as the presence of touch-perceiving special hairs called **'vibrissae'** on the snout of many mammals and the bundle of long hairs or **'mane'** along the middorsal neck of lion and male horse.

(ii) Besides several special functions performed by hairs, the main functions. are insulation and thermoregulation (Romer and Parson, 1986).

(iii) Hairs in the nasal organs and ears, eyebrows and eyelashes protect the nose, ear and eye from entry of dust particles.

(iv) The covering of hair is the heaviest in arctic mammals, moderate or sufficient in mammals of temperate zone and is rather thin and short in tropical species.

### 4.2.3 Dermal derivatives

Compared to the variety of epidermal derivatives, the dermal derivatives are fewer in number. The dermal scales in fishes, both cartilaginous and bony, scales in certain amphibians and mammals, the bony plates or osteoderms in the osteacoderm fishes and mammals are all derived from the mesoderm cells.

The structures of the dermal scales in fishes as the main dermal derivative are briefly described here.

**I. Dermal scales in fishes :**

In fishes and in many other vertebrates, the scales derived from the dermis form the dermal skeletal system. In primitive bony fishes, two separate lines in the origin and evolution of scales are observed such as, cosmoid scales and ganoid scales. These two types of scales are considered to have given rise to other types of scales in modern fishes.

(a) **Cosmoid scales :** In the primitive ostracoderm fishes, the dermal plates were very large and massive. In the later placoderm and sarcopterygian fishes, these large plates became reduced and evolved as the characteristic cosmoid scales which are present in *Latimeria,* the only living representative of a primitive group of fishes. The other fishes possessing cosmoid scales are all extinct. Each scale is rhomboidal in shape, thick and pitted and on the bony layers of the scale are deposited distinct but complex layers of cosmine. According to Thomson (1975), the cosmine layers possess both hard and soft tissues and a system of fine canaliculi. This scale was present in some extinct agnatha, dipnoi and rhipidistia.

Each cosmoid scale has four distinct layers : (i) the lowermost layer is called **isopedine** or **dentine** which is compact like a bony layer; (ii) the layer just above this is like spongy bone and is supplied with blood vessels; this layer also contains **pulp cavity** and **odontoblast cells**; (iii) the third layer from below upward is the **cosmine layer** which is hard, compact and with complex tissues; (iv) the fourth or the upper most extemallayer is a hard **vitreodentine** layer containing **enamel**.

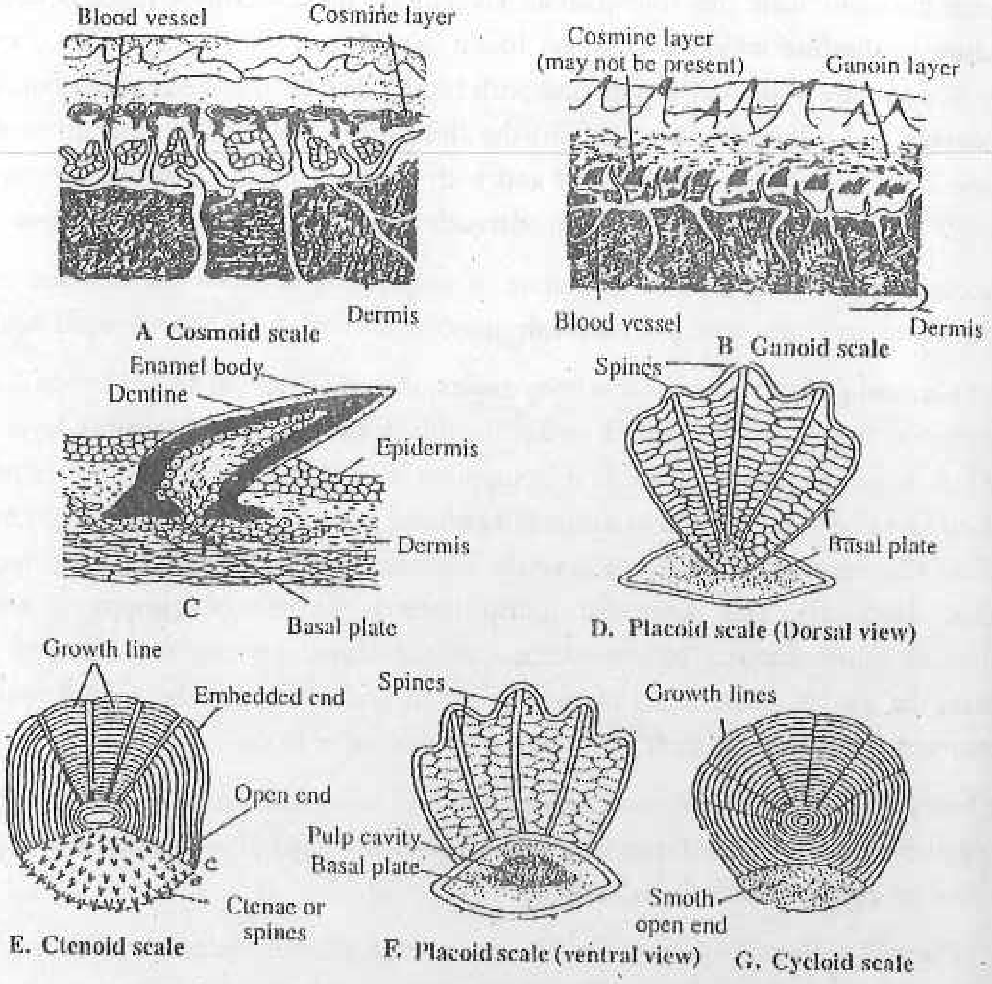
According to Young (1981), the nature of pulp cavity between the cosmoid and placoid scales indicates that placoid scale may be derived from the cosmoid scale.

(b) **Ganoid scales :** In primitive bony fishes, the other type of scale that evolved in a different line is called **ganoid scales.** In this scale also the innermost layer is formed of isopedine, the layer above it is supplied with blood vessels and capillaries. The third layer outward may have a thin and reduced cosmine. layer.(e.g., *Polypterus;* Infraclass Chondrostei) or may not have the cosmine layer at all (e.g., *Lepidosteus;* Infraclass Holostei). The outermost fourth layer is formed of **ganoin**, a hard, transluscent shiny material of mesodermal origin. Based on slight differences in structure, the ganoid scale exists in two forms. In both the types the ganoid scales are arranged obliquely by their ends like the tiles on a floor.

It has already been mentioned that the cosmoid and ganoid are the two separate lines of evolution in scales. From the former arises the placoid scales and the latter gives rise to ctenoid and cycloid scales.

(c) **Placoid scales :** With very few exceptions, the placoid scales are present only in the elasmobranch fishes (class **Chondrichthyes**). Each placoid scale has a bony diamond shaped **basal plate** embedded in the dermis and a spine projected from the basal plate outwardly and backwardly. The fully formed spine appears as a wavy trident spine. Both basal plate and the spine are mesodermal in origin and both are formed of **dentine.** To the former is added calcium and the latter is enclosed by a hard **vitrodentine** layer. No enamel layer is present in the fully formed spine. The **dermal pulp** formed of connective tissues and blood vessels enter into the **pulp cairty** of the spine through an aperture located at the centre of the basal plate.

(d) **Ctenoid Scale :** This scale is found in greater numbers in most teleostean fishes. Ctenoid scale may be compared to a ganoid scale (minus ganoin layer) in many respect.



A Cosmoid scale

B Ganoid scale

D. Placoid scale (Dorsal view)

E. Ctenoid scale

F. Placoid scale (ventral view)

G. Cycloid scale

**Fig 4.10 :** Development and structure of scales in different types of fishes : A, cosmoid scale; B, Ganoid scale; C, Development of placoid scale; D, Placoid scale (dorsal view); E, ctenoid scale; F, Placoid scale (ventral view); G, Cycloid scale.

Each ctenoid scale is embedded in the shallow pit of the dermis. The scales are obliquely arranged such that the posterior end of each scale covers much of the anterior margins of the scale behind. Ctenoid scale has a number of similarities with the cycloid scale also found in many teleosts except that the free distal end of the ctenoid scale bears along its margins several rows of spines or **ctena** (from which the name of the scale is derived). Proximally, the scale bears several small concentric lines of growth in the middle and longer wavy concentric lines on the sides.

(e) **Cycloid Scale :** The cycloid scales are also abundantly found in many teleost fishes, These scales appear somewhat circularly elongated and embedded in the dermis. This scale is thicker centrally and thinner marginally. The inner layer of this scale is formed of fibrous connective tissue and its upper layer is made up of isopedine. The isopedine layer is further modified outwardly to form dentine. These scales are also placed obliquely in an overlapping arrangement. The free margins of the scale are smooth and the concentric lines of growth are larger and wavy.

In may fishes the scales just above the lateral line have pores through which the minute canaliculi of the lateral line open outside. In a number of fishes both ctenoid and cycloid scales are present (e.g., flat fish; *Lates,* etc.). In such fishes, the ctenoid scale may be present on the dorsal surface, while the cycloid on the ventral surface. In the group of catfishes (e.g., *Heteropneustes; Clarias; Mystus,* etc.), scales are absent. In the Eelfish, very minute granular scales may be present deep in the dermis.

## 4.3 Terminal questions

1. Give an account of the generalized structure of the skin of a vertebrate.
2. What are the functions of integument in vertebrates.
3. What are the different types of epidermal glands found in vertebrates? Illus trate with examples.
4. Distinguish between merocrine, holocrine and apocrine glands with examples.
5. Describe various types of epidermal scales found in vertebrates. Provide sketches.
6. Draw and describe various types of horns found in mammals.
7. Draw and describe various types of claws and hoofs found in mammals.
8. Why feathers in birds are called a unique character? Classify different types of feathers found in different birds. Draw, label and describe structure of a contour feather.

9. What are flight feathers? Draw, label and describe different types of feathers found in a pigeon.
10. Draw and describe development of feathers, pterylosis and moulting of feathers.
11. What are the various functions of feathers?
12. Draw, label and describe development and structure of hair in a mammal.
13. State functions of hairs in a mammal.
14. What are dermal derivatives in vertebrates? Draw and describe different types of dermal scales in fishes.

# Unit 5 ☐ General Plan of Circulation in Various Groups of Vertebrates

*Structure*

## 5.0. General plan of circulation

Along with the complexity in various systems in different vertebrates, the necessity for the transportation of fluids and nutrients to and from all the cells and tissues in the body become imperative. The increasing demand for the transportation of such essential materials to every part of the body of complexly evolving vertebrates could only be met by a **'closed' type of blood vascular system** containing blood as the circulating fluid. The blood besides containing the nutrients, water, ions, oxygen etc. also contains the respiratory pigment, **haemoglobin.** Haemoglobin is an iron-containing protein that combines with oxygen to form a loose chemical compound, **oxyhaemoglobin** from which oxygen is supplied to the cells and tissues. However, neither blood nor any part of the blood vascular system is in direct contact with the cells and tissues. The role of intermediary is taken up by **tissue fluid** or **interstitial fluid** in which the cells and tissues are bathed.

Thus the blood vascular system is comprised of a system of well defined blood vessels named **arteries, veins** and their branches and subbranches, the **arterioles, venules** and the **capillaries**. These vessels contain blood, a form of liquid connective tissue that is circulated throughout the body to supply all the organs, cells and tissues by the action of a contractile pumping organ, the **heart**, situated ventrally in the anterior thorax. There is another system of blood vessels, the **lymphatic system** which carries **lymph**, the other circulatory fluid distinguished from blood by the absence of red blood corpuscles (RBC). The lymph vessels carry fluid away from the cells and tissues and drain the lymph into larger veins on their way to the heart.

Thus the blood vascular system is a closed system of tubes and channels that are closely connected with the lymphatic system and the two systems play a complementary role in the circulation of blood and lymph towards and away form the cells and tissues in the body of a vertebrate respectively.

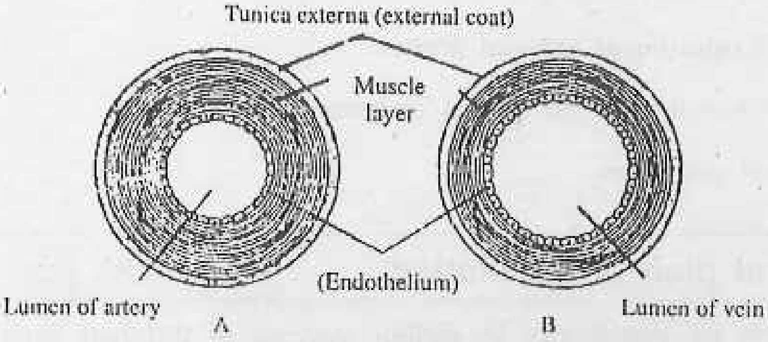


**Fig 5.1** : Cross-sectional view of an artery and a vein of *Bufo* sp., A, artery; E, Vein.

The blood vessels are mesodermal derivatives, arising from the mesenchyme cells in embryonic development. In certain parts of the embryo, **blood islands** first appear in the from of small gathering of cells which soon form an endothelium enclosing a narrow, fluid-filled cavity. The fluid, secreted by the cells of the blood islands, is called **blood plasma** within which certain loose blood cells float about. These form the blood corpuscles. The blood islands later join together to form a network of small blood vessels. More and more blood vessels are formed by further division and expansion of the original endothelium. Each blood vessel formed, including the heart, is provided with an endothelial lining. In later stages, the mesenchyme surrounding the endothelium provides differentiating layers in the heart and other blood vessels like arteries, veins, etc.

Both arteries and veins have their wall composed of three layers such as, the innermost **tunica interna (= intima)** formed of an **endothelium** and an **internal elastic membrane,** a middle thick **tunica media** formed of smooth muscle cells with a **network of elastic fibres** and an outer layer, the **tunica externa (= adventitia)** formed of connective tissues. The elastic and muscular layers in arteries are specially well developed. The arterioles with thick muscular wall and narrower lumen maintain much higher rate of blood pressure than in veins. In veins, the intermediate layer is thinner as the muscular and elastic layers are poorly developed. In birds and mammals, paired semilunar valves occur in the endothelium of large and medium-sized veins. The capillaries are extremely thin-walled being formed of endothelium only, because the capillaries are the terminal vessels for the exchange of nutrient and other fluids. However, in certain parts of the body, there may be a direct connection between an artery and a vein in which case it is called **arteriovenous anastomosis** (e.g., toes in birds; terminal phalanges of fingers and toes in man). Sinusoid is another type of larger anastomosis between an artery and a vein where the endothelium is not continuous. Sinusoids are formed in the liver, pancreas, bone marrow, etc.

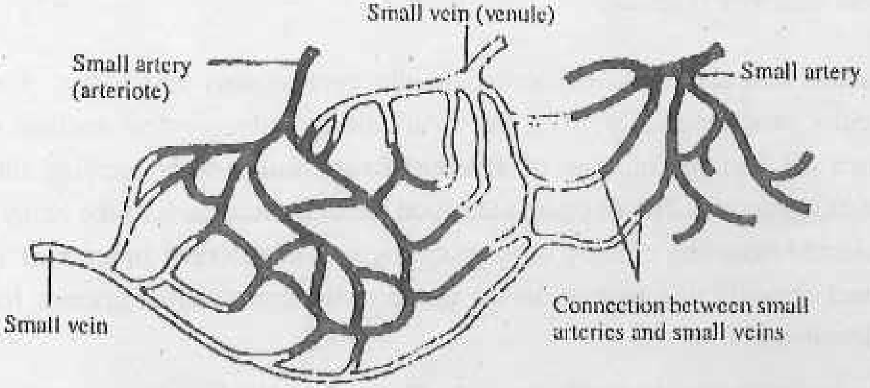


**Fig 5.2 :** Diagrammatic view showing connections between arterioles and veinules.

**Nature of circulation in different groups of Vertebrates** : In the closed type of blood vessels that established connection with the central pumping organ, the heart, circulation became more and more complex with the switch over in the life of vertebrates from aquatic habitat to the terrestrial one. Tremendous adaptational changes also brought about distinctive modifications in the circulatory system in vertebrates. The two-chambered heart (one auricle and one ventricle) in cyclostomes and fishes (except Dipnoi) having gill breathing possess a scheme of blood circulation that is referred to as **'Single circuit circulation'**. With the evolution of land vertebrates where lung breathing fully or partly replaced gill breathing, a **'double-circuit circulation'** commenced from the amphibians and reached perfection in the birds and mammals.

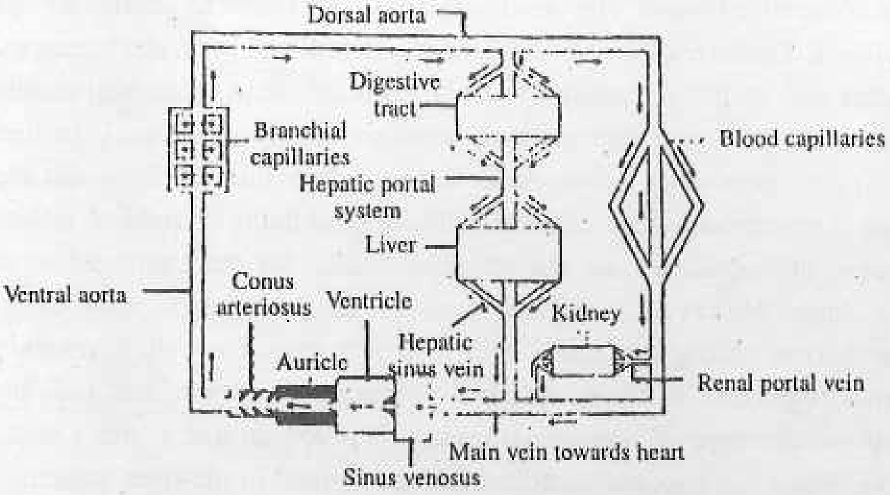


**Fig 5.3** : Schematic diagram showing single-circuit pathway of blood circulation in cyclostomes and fishes (except in dipnoans).

In branchial circulation as evidenced in the cyclostomes and fishes, a ventral aorta that runs ventromedially from the heart along outer ventral surface of the pharynx gives off variable number of **afferent branchial vessels** carrying blood to the gills for oxygenation. The oxygenated blood never comes back to the heart again, but it is collected from the gills by corresponding sets of **efferent branchial vessels** which connect dorsally to a pair of dorsal aortae or the epibranchial arteries forming the main dorsal aorta.

In cyclostomes each set of afferent and efferent branchial arteries numbers eight on either side, in cartilaginous fishes such numbers in most cases are five and four whereas, in bony fishes, in keeping with the number of gill pouches, the number of afferent and efferent branchial arteries are four on either side.

The venous system in cyclostomes is more primitive than in fishes but more or less built on the same plan except that in cyclostomes there are extensive sinuses and contractile venous heart in many places. Also there is a single ductus cuvieri and a distinct hepatic portal vein.

In the elasmobranch and lung fishes well developed branchial circulation is established. Unlike in the lung fishes, each efferent branchial artery divides into two branches around the gill. As in the bony fishes, ductus cuvieri are present on both sides and both hepatic and renal portal systems are well developed.

In the elasmobranch fishes, the lymphatic system is absent, but it is well developed in the bony fishes.

In Dcpnoi, there are certain changes in the afferent and efferent branchial vessels; the ventral aorta is shortened to a muscular bulbus cordis and the pulmonary artery arises from the dorsal aorta. There is an inferior vena cava as in the amphibians.

The nature of blood circulation had a remarkable switch-over from the fishes to the first land vertebrates, the amphibians. With the development of lungs for pulmonary respiration the course of blood circulation becomes largely modified with the introduction of a double-circuit heart and necessary reduction in the number of aortic arches. The gill breathing in this class has been retained only in the larval

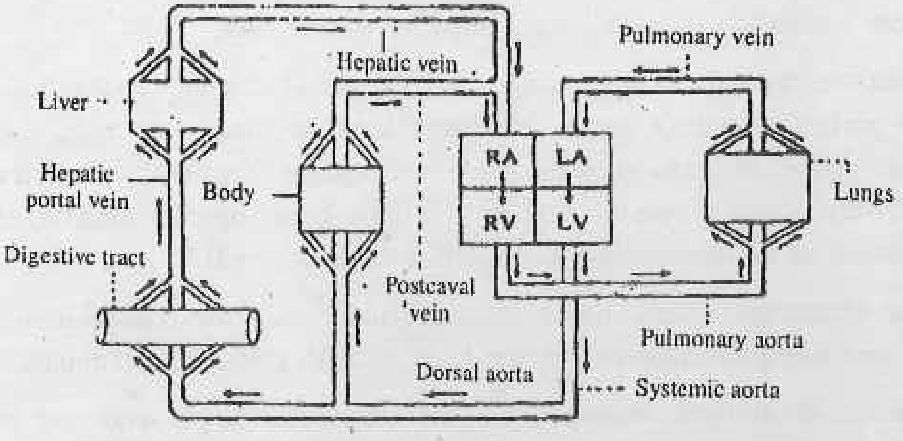


**Fig 5.4** : Schematic diagram showing double-circuit pathway of blood circulation in *Columba* sp.

stage and in most adults, two courses of blood circulation i.e., pulmonary and systemic become well established. The sinus venosus and the auricle are pushed ahead of the ventricle and the sinus venosus comes to lie dorsal to the auricle. As against the venous heart in fishes where the heart has to tackle with venous blood only, the structure of the amphibian heart ensures **'double circulation'** in the sense that both arterial and venous blood are distributed and collected by the heart.

In the reptiles that are truly land vertebrates and the first amniotes, the double course of circulation becomes better established as the left and right systemic aortae and the pulmonary aorta arise independently from the ventricle. Although the possibility of the admixture of oxygenated and less oxygenated blood is still there due to incomplete separation of the ventricle, it is less so than in the amphibians. In crocodiles, however, the ventricular partition is complete but even then the minimum possibility of the mixing of blood still remains through the **Foramen of Panizza** at the point of crossing of the left and right systems arches.

In birds and mammals the double course of blood circulation has reached perfection where the arterial blood remains completely separated from the venous blood. The high rate of metabolism and constant high temperature in birds ensure rapid circulation and speedy supply of oxygen to all the cells and tissues in the body. In both birds and mammals, both the **hepatic portal** and **renal portal** systems are well developed. Advancement in the circulatory system of birds compared to reptiles has been achieved in may ways. The basic metabolic rate (BMR) and a constant higher temperature in birds (38°C—42°C or even higher in some cases) have in many cases excelled the mammals. The circulatory mechanisms in birds has also ensured complete respiration through lungs, aided by the air sacs.

With the diversity in mammalian life, the blood vascular system has reached greater perfection with a single left aortic arch (in birds only right aortic arch persists), greater elaboration of the heart with variety of valves, and with complex arterial, venous and lymphatic systems that have been superbly tuned to the usual homeostasis of the mammalian body, either large or small.

The circulatory system has a great contribution in the conservation of heat, energy and overall metabolism of the body in both birds and mammals.

The blood in birds, however, has the corpuscles large, oval and nucleated whereas, in mammals, they are small, spherical and anucleated.

## 5.1 Blood

### 5.1.1 Components of blood

In vertebrates, blood is a translucent liquid connective tissue which as a carrier in the circulatory system supplies essential nutrients and hormones to all the organs, cells and tissues in the body and also return from them the materials required for expulsion from the body. Two essential components of blood are the **plasma** and the **corpuscles** or **blood cells**. The liquid, slightly yellowish matrix of blood is the plasma in which float the corpuscles or blood cells of different size and colour and are transported to various organs in the body.

A description of the plasma and corpuscles is given here briefly.

(i) **Plasma :** It is the liquid matrix that approximately amounts to about 55 percent of the total composition of blood and the rest 45 percent is formed of corpuscles. The plasma contains about 91 percent water containing inorganic salts in true solution and 7 percent proteins in colloidal solution. The total salts present amount to only about 1 percent by weight of the plasma. The salts of the plasma usually contain ions of sodium, Potassium, chloride, bicarbonate, sulphate, phosphate, etc. in solution. Of the blood proteins, alobumin and globulin chiefly function as antibodies while prothrombin and fibrinogen are concerned with clotting of blood. The chemical composition of plasma is slightly alkaline, (pH 7.3), and the proteins and bicarbonates of plasma maintain the above pH through mutual reactions. The plasma also contains glucose, amino acids, fats and fatty acids from the dissolved nutrients of food, urea and uric acid from the exeretory organs, as also, dissolved gases, hormones and vitamins for transportation to their terminal sites.

(ii) **Blood corpuscles :** The blood corpuscles are also derived from the connective tissue and are transported through blood vessels to different parts of the body. The blood corpuscles are of three types : (a) Red Blood Corpuscles (RBC or Erythrocytes), (b) White Blood Corpuscles (WBC or Leukocytes) and (c) Thrombocytes or Blood platelets.

(a) **Red Blood cells (RBC or Erythrocytes) :** Of different cellular components of blood, the RBC are the largest in number. The red blood cells are red due to the presence of **haemoglobin**, an iron-containing protein in the cells. Haemoglobin contains four protein molecules each of which combines with an oxygen ion to form an oxyhemoglobin compound from which oxygen is released in the vicinity of the cells and tissues in all the parts of the body. Haemoglobin is a complex protein composed of 95% of a colorless protein called **'globin'** and 5% of a red iron compound called **'hematein'**. Haemoglobin is present in the red cells of all vertebrates except in some deep sea fishes.

In cyclostomes the RBC are large, nucleated and spherical. The red cells are smaller in bony fishes than in elasmobranchs. Some bony fishes have blood count higher than in man, and in the antarctic ice-fish, *Chaenocephalus,* there is no haemoglobin at all (Young, 1981).

In frogs and toads, and in the amphibians in general, the red blood cells are flat, oval and nucleated. While the red cells are in a group, they appear red, but when scattered, a single cell appears greenish-yellow. In reptiles and birds too, these cells are oval and nucleated (in birds larger than in the reptiles) and in the mammals, the RBC are circular biconcave and without nucleus. In the anurans, reptiles, birds and in the adult mammals, the RBC are formed in the bone marrow less so in the spleen and lymphoid nodules. In other vertebrates the RBC are usually formed in the livers, spleen and lymphoid tissue discretely present in the body. In mammals their life is short, which may be due to absence of nucleus. They are destroyed in blood by phagocytosis and replaced by new ones.

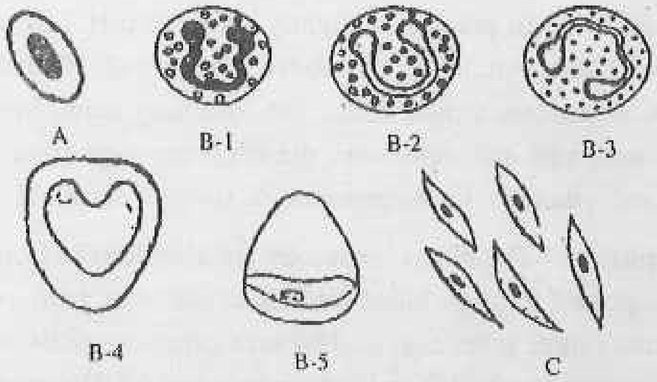


Fig 5.5 : Different types of blood corpuscles; A, Erthrocyte (RBC); B-1—B-5, Leucocytes; B1, Basophil; B2, Eosinophil; B3, Neutrophil; B4, Monocyte; BS, Lymphocyte; C, Thrombocytes.

(b) **White Blood cells (WBC or Leukocytes) :** Among the cellular components of blood, the white blood cells are larger in size and are of different shapes, compared to RBC. But the number of WBC is much less in comparison to that of RBC. Their cytoplasm contains a distinct nucleus but because of the absence of haemoglobin these cells are called white Blood Cells. The WBC are chiefly divided into two classes, **granular** and **agranular leucocytes**, based on the structure of nucleus and on the smooth or granular state of the cytoplasm.

In the cytoplasm of the **granular WBC** there are large numbers of grains and the nucleus of each cell may be divided into two or three segments by constrictions. These cells are usually spherical and by their amoeboid movement may come out through the endothelial cells of the capillary network or may re-enter into them.

Based on staining methods, these cells may be of the following three types :

(i) **Basophil :** These cells may be stained with basic dyes such as, Methylene Blue or Haematoxylene. Each cell has large-sized grains and the nucleus divided by constrictions into two or three segments.

(ii) **Eosinsphil :** These are also known as **acidophilic cells** and may be stained with acid dyes such as, eosin. The nucleus of each cell is divided into two segments that are connected by a narrow threadlike part.

(iii) **Neutrophil :** These are much greater in number than the above two types of cells and may be stained with neutral dye. The cytoplasm of each cell has numerous fine grains and the nucleus is divided into three or more segments that are connected by narrow threadless part. Because of the greater number of nuclear segments, the neutrophil cells are referred to as **polymorphonuclear leucocytes.**

In the cytoplasm of **agranular leucocyte**, there may be a few fine grains of neutral nature or commonly the grains are totally absent. But the nucleus is never divided into segments.

These cells may be of the following two types :

(i) **Lymphocyte :** These are large cells, usually spherical and the large nucleus may be slightly grooved at one side. The cell is with lesser amount of cytoplasm that surrounds the nucleus.

(ii) **Monocyte :** These are also large cells, each having a large nucleus on one side, slightly cleft or curved in the middle. The amount of cytoplasm is more than in the lymphocyte.

Neutrophil and sometimes monocytes have a phagocytic role, feeding on bacteria and other harmful cells. In fact, the main function of leucocytes is to combat infection of the body by germs and bacteria and thus act as defence mechanism.

In man the normal range of leucocytes is about 8000 per cmm of blood. The amoeboid movement by which the leucocytes come out of the endothelial cells or re-enter is called **'diapedesis'**.

(c) **Thrombocytes and Platelets :** Besides the above-mentioned types of blood cells, blood in all vertebrates, except in mammals, contains another type of spindle-shaped cells with narrow elongated nucleus called **thrombocytes**; the corresponding circular platelike cells in mammalian blood is known as **platelets**. Each thrombocyte has an oval or spherical nucleus and clear cytoplasm. The platelets are, however, without nucleus. Their origin is also from a different source. These are not considered as cells by some authors.

However, both thrombocytes and platelets have active role in the **clotting** of blood. In the process of clotting a pre-catalyst **prothrombin** present in blood is converted to the catalyst **thrombin** in presence of **thromboplastin** and **calcium ions**. Thrombin is not present in active form in blood. Thrombin then reacts with a blood protein called **fibrinogen** to precipitate a delicate threadlike protein called **fibrin**. The delicate network of fibrin causes clotting of blood.

$$\begin{array}{ccc} \text{Prothrombin} & \xrightarrow{\text{Thromboplastin} + \text{Ca}^{++}} & \text{Thrombin} \\ & & + \\ & & \text{Fibrinogen} \\ & & \downarrow \\ & & \text{Fibrin} \end{array}$$

### 5.1.2 Blood-forming tissues (Hemopoietic tissues)

The cells and tissues that form different kinds of blood cells are called **hemopoietic tissue**. Different types of blood cells arise chiefly from two sources : (i) in the lower vertebrates the blood cells arise from various structures like the livers, spleen, lymphoid tissue, mesenchyme, etc. (ii) from the anuran group of the amphibians and in the reptiles birds and mammals, all types of blood cells are formed in the bone marrow.

In the mammals, however, the bone marrow is concerned with the production of erythrocytes and platelets as also some granular WBC; the granular and other kinds of WBC are produced by the lymphoid tissue and other structures mentioned above.

The **red bone marrow** which also has hemopoietic function is present only in the embryonic condition of mammals and in their newborn offsprings.

Estrogens inhibit the production of erythrocytes. Just as erythropoietin (a hormone possibly from the kidneys) stimulates it (Weichert and Presch, 1977).

### 5.1.3 Functions of blood

(i) Blood is the most important component of the blood vascular system as it transports the essential nutrients to all the organs, cells and tissues (through tissue fluid) and returns the wastes to appropriate organs for their expulsion outside the body.

(ii) The haemoglobin contained in the RBC of blood supplies oxygen to all the cells and tissues in the body and together with plasma returns $CO_2$ from the cells and tissues to appropriate respiratory organs.

(iii) The urea and uric acid contained in the plasma as excretory metabolites first reach the livers and are then expelled through the kidney.

(iv) The blood plasma also transports the hormones that are secretions of the endocrine glands to distant organ-sites for controlling various functions.

(v) Blood plays essential roles in the regulation of body temperature and conservation of heat as well as in controlling water content of the body cells.

(vi) The White Blood Cells combat and destroy the germs and bacteria,—thus resisting any infection in the body.

(vii) The thrombocytes and platelets (in mammals) present in blood plasma take active role in the clotting of blood.

## 5.2 Evolution of heart

It will be evident from the earlier description of the blood vascular system that the most vital organ for the maintenance of flow of blood throughout the body is the heart that lies antero-ventrally (unlike in non-chordates) as the central pulsating organ for receiving and pumping out blood.

To understand the evolution of heart in different vertebrates, its origin and development, adaptational changes due to change from aquatic to terrestrial mode of life (i.e., switching over from gill breathing to lung breathing) and structural changes in the heart as demanded by the circulatory mechanism in higher vertebrates are to be taken into account

### 5.2.1 Development of heart

In the embryonic development in vertebrates, ventral to the archenteron, some mesenchyme cells from the splanchnic mesoderm layer become modified to form the **heart forming cells** or **endocardial cells.** These cells rearrange themselves to form two endocardial tubes (or endothelial tubes) that are closely adjacent Subsequently, ventral to the pharynx, these two tubes unite to form a single **endocardial tube** that lays the foundation of the heart. Although the heart appears as the modification of a single endocardial tube, its origin is bilateral. The external membrane or the **epicardium** of this tube is formed by the coelomic peritoneum. The thick, muscular middle layer called **mesocardium** or **myocardium** is formed by the mesenchyme cells and the innermost layer of the tube called **endocardium** is formed by **endothelial** cells. The dorsal and ventral mesocardia disappear. As a result, a single **pericardial cavity** now encloses the cardiae tube behind which a **transverse septum** separates the pericardial cavity from the general body cavity. The increase in length of the cardiac tube in the mid-region renders it into a S-shaped structure which becomes twisted, constricted and distended to form two spacious chambers, the **atrium** (or the **auricle**) in front and the **ventricle** behind. A **conus arteriosus** is formed in front of the atrium and at the entrance of the cardinal veins into the heart behind the ventricle, another chamber called **sinus venosus** is formed. Valves present at the entrance of the chambers prevent backflow of blood. At this stage the alignment of chambers is like that of the cyclostomes and fishes. From this simple arrangement of the fish-heart, more and more complex types of heart have arisen in the ascending vertebrate series..

The sinus venosus and the conus arteriosus are not permanently represented throughout the vertebrate series; so most authors agree that the auricles and ventricles are the **persistent chambers** and the sinus venosus and conus arteriosus (or bulbus arteriors) are accessory **chambers** of the heart.

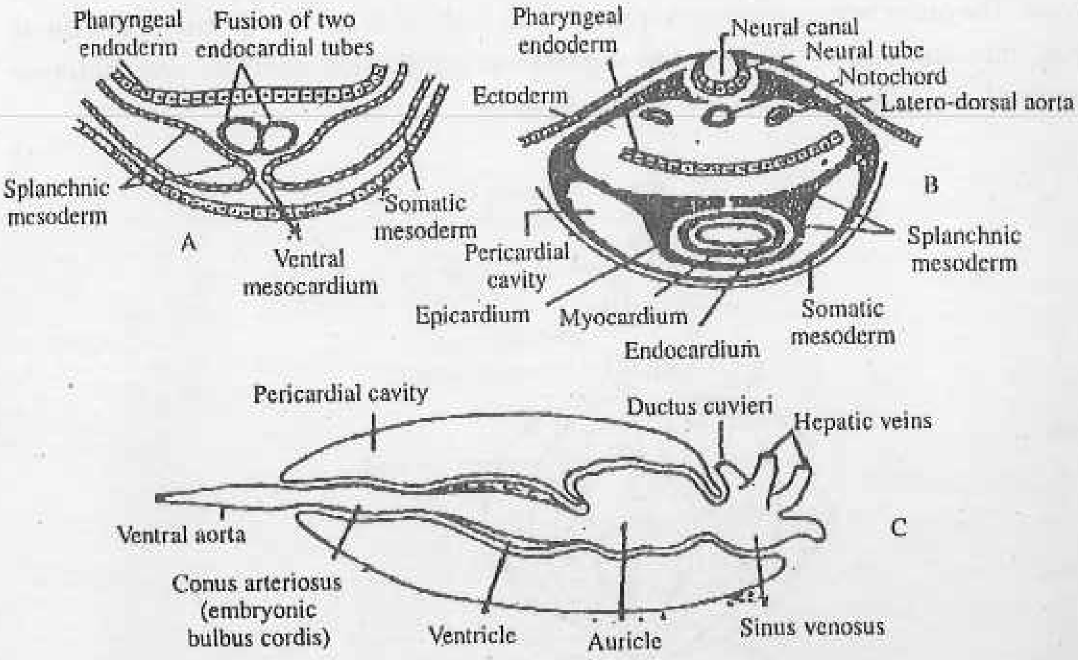


**Fig 5.6 :** Development of heart in a vertabrate; A, Fusion of two endocardial tubes developed from the heart-forming cells; B, Three layers of the heart developed from splanchnic mesoderm; C, Ventral aorta and location of primitive chambers of the heart.

## 5.2.2 Anatomy of the heart in different classes of vertebrates :

**1. Class–Cyclostomata** (e.g., *Petromyzon)* : The structure of the heart has similarities with that of the fish in general except that in cyclostomes, the conus is poorly developed with only two sets of valves and the heart is situated in the body cavity with other visceral organs.

**2. Class–Chondrichthres** (e.g., *Scoliodon)* : Here also the pericardial cavity is not completely separated from the body cavity. As a result, these two cavities are connected by a narrow pericardio-peritoneal canal. In cartilaginous fish, the posterionnost chamber, the sinus venosus lies horizontal to the other three chambers.

The larger atrium lies dorsally and ventral to the atrium lies the comparatively thick-walled ventricle and in front of the ventricle, the well developed conus arteriosus has the shape of a swollen tube. The narrow ventral aorta lying mid-ventrally along the pharyngeal wall is connected to the conus. Inside the conus usually two rows of three semilunar values are arranged longitudinally. These prevent backflow of blood. The sinus venosus appears narrower on both sides where the **cuvierian ducts** open into the sinus. The **Ductus cuvieri** on either side receives one **anterior cardinal** and one **posterior cardinal** smuses.

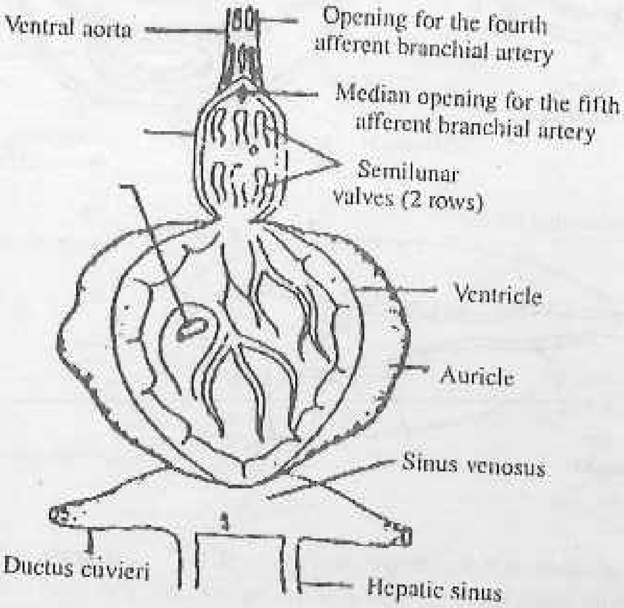


**Fig 5.7** : Heart of a cartilagenous fish.

**3. Class–Osteichthyes** (e.g., *Labeo* sp.) : In the bony fishes, the alignment in the chambers of the heart is the some as in the cartilagineous fishes. The sinus venosus is slightly reduced and the conus becomes gradually reduced in the earlier osteichthyes, its place being taken over by a thin-walled **bulbus arteriosus**; the conus becomes restricted as a reduced structure at the base of the ventral aorta (e.g., *Amia;* Holostei). In teleostean fishes the conus arteriosus totally disappears but a small, thin -walled bulbus arteriosus persists at the base of the ventral aorta. Unlike conus arteriosus which is a part of the heart, the bulbus is only a dilated structure at the base of the ventral aorta.

Corresponding to the five gill pouches in elasmobranch fishes, five afferent branchial arteries arise from the ventral aorta to supply them, whereas, four afferent bronchioles supply four gill pouches in bony fishes.

Except in the dipnoans (Lung fishes); in both elasmobranch and bony fishes, the heart is a **single-circuit heart** or the **venous heart** as it is called, because through this type of heart only unoxygenated venous blood collected from all over the body flows unidirectionally into the ventral aorta and therefrom to the gills for oxygenation. The bulbus arteriosus contains only one set of two valves.

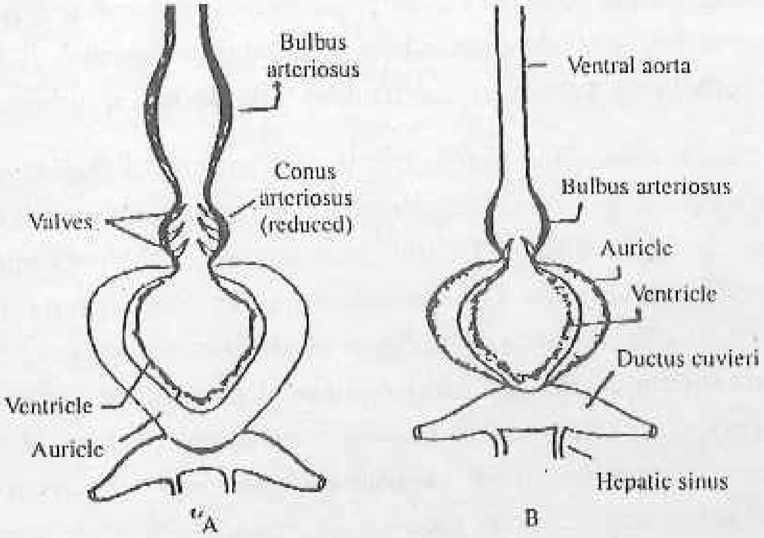


**Fig 5.8** : Heart in bony fishes; A, Reduced conus arteriosus in *Amia* (Holostei); B, Heart in a teleostean fish.

An important evolutionary change in the structure of the heart is first observed in the order Dipnoi (Lung fishes) where the auricle is partially separated into a right and left auricle by an incomplete **interarticular septum.** It has been observed in the lungfish *Protopterus* that the unoxygenated blood from the sinus venosus and the oxygenated blood from the lung (i.e., modified swim bladder) enter into the right and left auricles respectively. The saclike cavities in the inner wall of the ventricle, as well as the fibres and muscular tissues of the ventricle possibly prevent, though poorly, a complete mixture of the blood corping from the right and left auricles. So, in ventricular contraction less oxygenated blood goes to the posterior gill and the lungs and more oxygenated blood towards the dorsal aorta.

In the dipnoan fishes for the first time some sort of a **double circuit heart** appears, although it is an intermediate stage.

4. **Class–Amphibia** (e.g., *Bufo* sp.) : With the emergence of land vertebrates some notable changes occur in the evolution of the heart. With further twisting of the cardiac tube the sinus venosus and the auricle are shifted forward ahead of the ventricle and the sinus is placed dorsal to the auricle as a triangular structure. The apex of the triangle receives the postcaval vein, while the base of the triangle receives two precaval veins, one on either side. A wide, tubular **conus arteriosus** lies ventral to the right auricle. As the conus in the amphibians is considered as a modification of the bulbus arteriosus, it is also known here as the **'bulbus cordis'.** It divides into two branches, each being known as the **truncus arteriosus** on either side.

The wide tubular part of the conus contains a somewhat S-shaped spiral valve inside. The conus is capable of contraction and dilatation as its inner wall is provided with cardiac muscles. The conus is divisible into two parts : the proximal part near the ventricle is called **pylangium** while the distal part is called **synangium.** The S-shaped spiral valve divides the cavity of the conus longitudinally into two compartments **cavum pulmocutaneum** on the left and **cavum aorticum** on the right. According to Romer and Parson (1986), from the ventricle less oxygenated blood enters into the cavum pulmocutaneum and more oxygenated blood into the cavum aorticum. Thus the spiral value may separate the two qualities of blood to some extent. Anteriorly, each truncus is formed of three arterial arches bound together in the form of a bundle, the upper carotid arch, the middle systemic. arch and the lower pulmocutaneous arch.

The introduction of the double circuit of blood through the heart of the dipnoans has reached some stability in the amphibians with greater complexity of heart. Thus in the amphibians, two circuits are in action : the pulmonary circuit that transports the unoxygenated blood collected from all over the body to the lungs for oxygenation and the carotid-systemic circuit which supplies oxygenated blood received from the lungs to different organs, cells and tissues of the body.

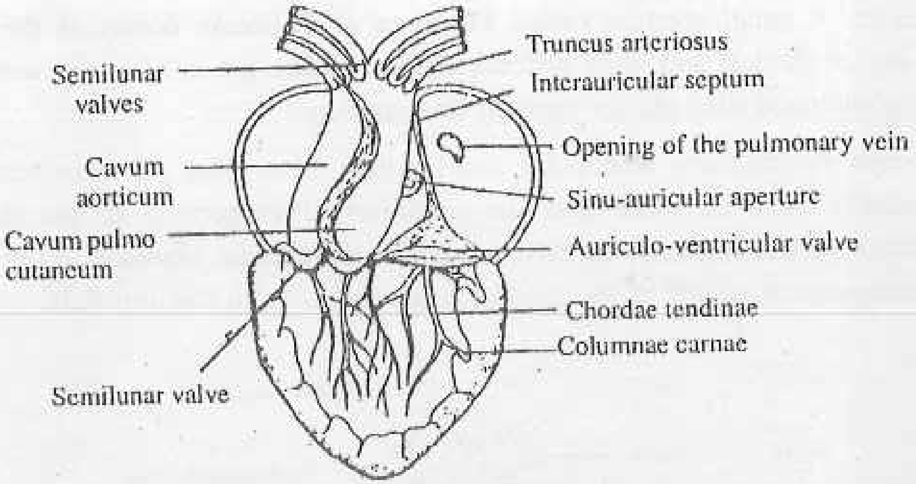


**Fig 5.9** : Internal structures of the heart of an amphibian.

The rhythmic heartbeat is controlled by the action of the central nervous system that excites the sinoauricular node lying on the inner wall of the sinus venosus. The excitation brings about muscular contraction of the heart called **'systole'** following **'relaxation'** (diastole) at specific intervals.

In anurans, there is a coronary circulation of the heart itself, but in many other amphibians, coronary circulation is absent.

5. **Class-Reptilia** (e.g., *Calotes; Crocodylus)* : Being the first terrestrial amniote vertebrate, lungs are the main respiratory organs in the reptiles.

In all the reptiles (except in the order crocodilia) the heart consists of two auricles and one incompletely separated ventricle. The interventricular septum completely divides the ventricle into two chambers in the Order crocodilia. The septum divides the ventricle obliquely into a right **'cavum ventrale'** and a left **'cavum dorsale'**. The latter is further divided by traberculae into a right-sided **cavum venosum** and a left-sided **cavum aorticum**. The sinus venosus being mostly absorbed by the right auricle appears extremely reduced, Conus arteriosus as such is absent but it splits longitudinally to form the three aortic arches such as, (i) the pulmonary aorta arising from the extreme right of the ventricle; (ii) the left systemic arch that arises independently from the cavum venosum of the ventricle and then turns to the left side of the heart and (iii) the right systemic arch that arises from the cavum arteriosus on the left of the ventricle and then turns to the right side of the heart. A small aperture called **Foramen of Panizzae** occurs at the point of crossing of the left and right systemic arches. Hence not only in the ventricle but mixing of blood also occurs through this aperture.

From evolutionary standpoint the reptilian heart may be considered to be structurally more advanced than the amphibian heart because of the incomplete separation of the ventricle, better musculature and chordae tendinae in the ventricle and independent origin of the three arterial arches from the ventricle.

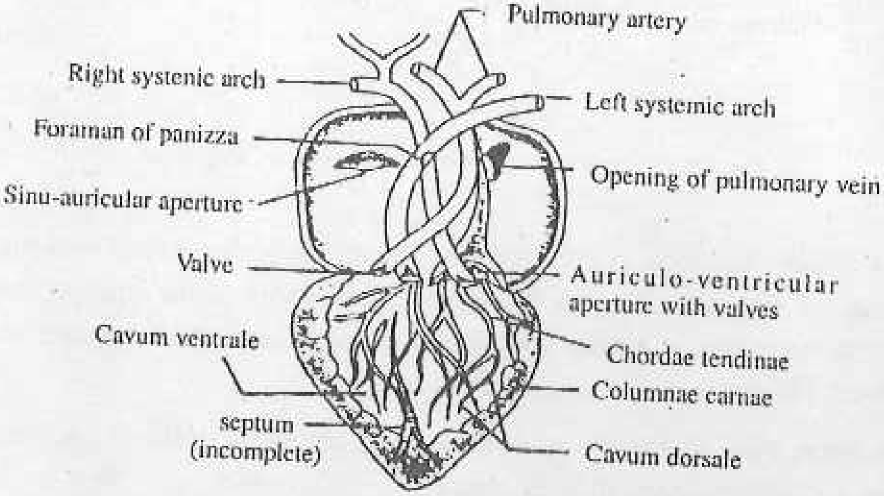


**Fig 5.10** : Internal structures of the heart of a reptile *(Calotes)*.

In the Order crocodilia, the interventricular septum completely divides the ventricle into two chambers so that in adult crocodiles the heart is four-chambered, and the separation of unoxygenated and oxygenated blood is nearly complete except at the Foramen of Panizzae and at the junction of the right and left systemic arches where they form the dorsal aorta.

6. **Class-Aves** (e.g., Pigeon) : It is in this class of animals in which a true double circuit heart operates without any possibility of the admixture of the unoxygenated and oxygenated blood.

Compared to body size, the size of the heart in birds is larger with more compact musculature and thicker and wider aortae than in the reptiles. The heart is enclosed by a double walled pericardial membrane. The heart is distinctly divided into four chambers. The sinus venosus and conus arteriosus completely disappear in birds. The two precavals and a single postcaval vein directly open into the right auricle whose cavity is larger than that of the left auricle. The presence of a single-cusped muscular valve guarding the right auriculo-ventricular aperture is a characteristic feature in birds. The left auriculo-ventricular value is however a bicuspid valve (also known as **mitral valve**) as in the mammals. Along inner wall of the ventricles, the thick, muscular **columnae carnae** project as slender papillary muscles (**musculi papillares**) in greater numbers within the cavity of the left ventricle, less so within the right ventricle. The thread-like, muscular chordae tendinae attached to the auriculo-ventricular valves at one end and the papillary muscles at the other end help proper alignment of these structures.

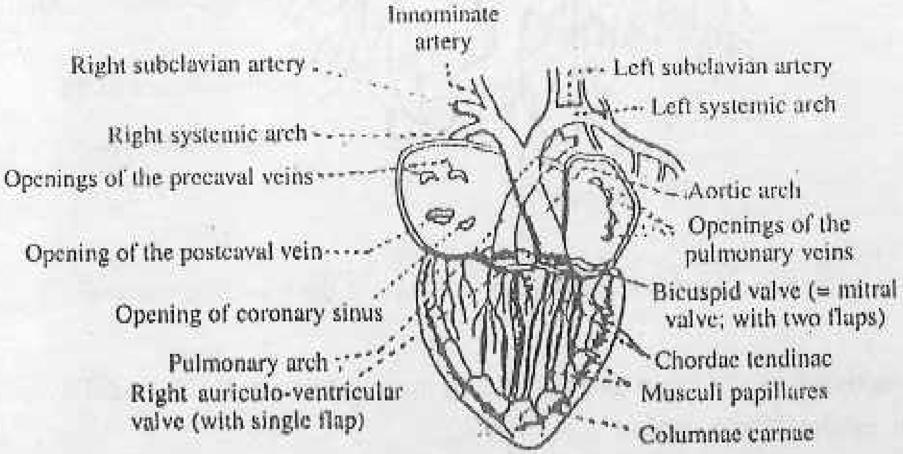


**Fig 5.11** : Class Aves : Internal structures of the heart of a pigeon.

In the evolution of the heart, it is evident that in the higher amniotes represented by the birds and mammals, a complete double circulation has been established. The structure of an avian heart is so well accomplished to meet the demands of volant adaptation that greater quantity of venous blood is received by the heart through large veins and the same is transported to the lungs for full oxygenation. The oxygenated blood is quickly disposed through the arteries by the left ventricular systole to reach the muscles, cells and tissues in no time to ensure their full oxygenation. The efficiency of blood circulation has become obligatory due to higher basic metabolic rate and energy expenditure in the body.

Furthermore it is to the noted that the **special junctional tissues of the heart** i.e., the **nodal system** comprising the SA node, the A V node, the internodal tracts, the Bundle of His, the Bundle Branches, Purkinje fibres, etc. are very well developed in birds and mammals.

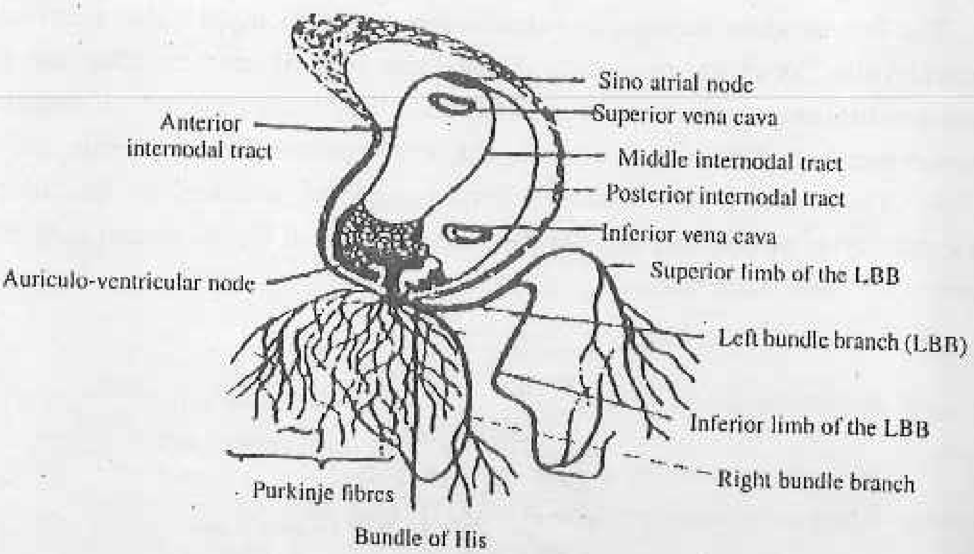


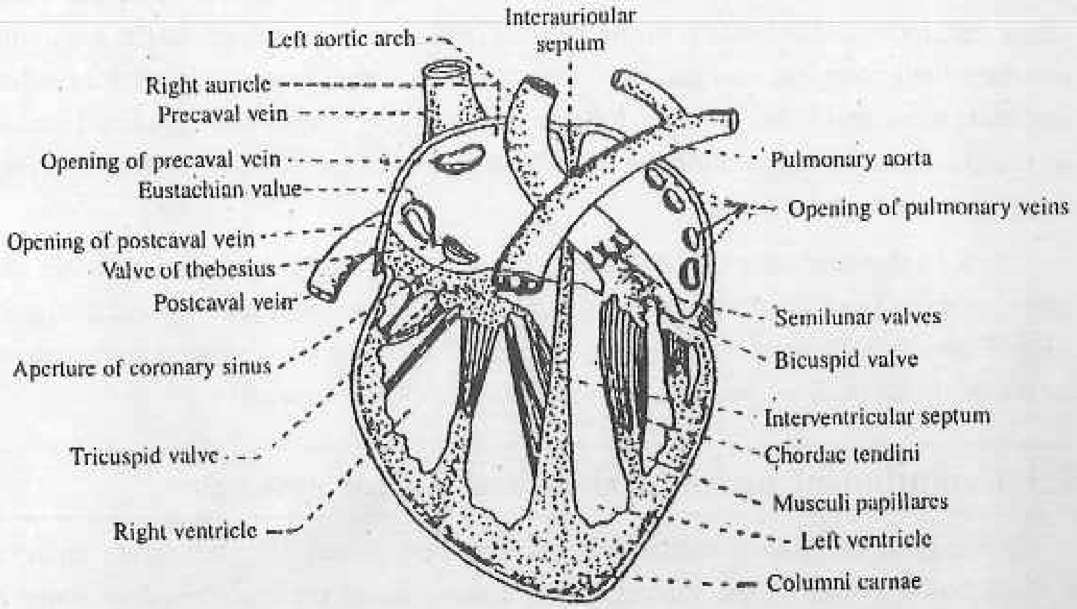
**Fig 5.12** : Special junctional tissues (Pacemaker) in the heart of a mammal.

As the activity of the heart is Initiated by nervous control, the nodal system is also known as the **'Pace maker'**.

The coronary circulation is also well developed in birds and mammals.

7. **Class-Mammalia** (e.g., *Cavia* sp.) : The mammalian heart is much the same in structure as that of an avian heart. A four-chambered heart with complete double circulation is maintained by the unoxygenated and oxygenated blood throughout the body. The heart is located in the space between the two lungs called **mediastinum**. A double-walled pericardial membrane having pericardial fluid in between encloses the heart. An oval depression, the **fossa ovails** present on the interauricular septum has a ringlike ridge around the fossa called **annulus ovails**. In relaxation, when the two auricles rest on the two ventricles, the outer edge of the auricle hang over the ventricle on either side somewhat angularly as an appendage called **auricular appendage**. The appendage is striated by comblike muscles inside called **'musculi**

**pectinati'**. The openings of the postcaval vein and the coronary sinus are guarded by the **eustachian valve** and the **value of thebesius** respectively. The oxygenated blood reaches the left auricle by one or two pairs 'of pulmonary veins. The **tricuspid valve** guarding the right auriculo-ventricular aperture is characteristic of the mammalian heart. The left auriculo-ventricular value is a bicuspid valve as in birds. Only in the monotremes this valve is tricuspid.



**5.13** : Sectional view showing internal structures of the heart of a generalized mammal

### 5.2.3 Evolution of heart in vertebrates

Many notable changes are observed in the evolution of the heart throughout vertebrate series. Such changes resulted from the aquatic life of vertebrates to their terrestrial mode of life—first amphibious and then fully terrestrial.

In the cyclostomes and in the cartilagineous and bony fishes, the persistent chambers of the heart, the single auricle and the single ventricle as well as the accessory chambers the sinus venosus and the conus arteriosus—all lie in a linear arrangement with the ventral aorta located midventrally along the ventral pharyngeal wall. From the ventral aorta, afferent branchial vessels carry venous blood to the gills for oxygenation. The gills return the oxygenated blood through efferent branchial vessels dorsally. These vessels are connected to the arterial system in the body. Hence, the heart functions as the venous heart only, and in the cyclostomes and fishes (except in the lung fishes) the heart is referred to as a **single circuit heart**. In the dipnoans and in the amphibians, with the beginning of lung respiration (in adult dipnoans both gill respiration and lung respiration are functional) many changes occur in the structure of the heart and in the course of blood circulation such as, gradual reduction and then complete absence of the sinus venosus and the conus arteriosus, incomplete division of the cavities of auricle and ventricle at the beginning and later their complete division into four chambers, increase in the number of valves and their more and more efficient functioning in higher vertebrates, gradual increase in the thickness of the ventricular musculature and acquisition of a double-circuit heart in course of evolution.

Thus in the evolution of vertebrates, from simpler early agnathans to more and more complex Gnathostomes, the structural design of the heart and of the circulatory system as a whole have been notably modified in relation to other organ-systems in the body as well as increased metabolic rate of the animal.

## 5.3 Evolution of aortic arches and portal systems

It has been mentioned earlier that during development of a vertebrate embryo, a stout blood vessel called ventral aorta running along the midfrontal pharyngeal floor gets connected posteriorly to the conus arteriosus of the heart. Further rostrally the ventral aorta divides into two branches forming the **external carotid arteries**. Each branch of the ventral aorta on either side gives off the first aortic arch, the **mandibular arch** which on reaching top of the pharynx curves round dorsally and continues posteriority on either side of the pharynx as the **lateral dorsal aorta** or **radix aorta** (pl. **Radices aortae**). The two lateral dorsal aortae unite dorsally behind the heart to form the main **dorsal aorta** of the arterial system. Just behind the mandibular arch, the ventral aorta gives off the second aortic arch, the **hyoid aortic arch**. The third, fourth, fifth and sixth aortic arches arise serially from the ventral aorta to supply blood to the gills, and hence these are known as **branchial arches**. The forward extension of the lateral dorsal aorta forms the **internal carotid artery** on either side. The first, second and third aortic arches join the lateral dorsal aorta with an upward curvature whereas, the fourth, fifth and sixth aortic arches do so with a downward curvature. A pair of **vitelline arteries** supply blood to the embryos with yolk sac. In the, embryo of an amniote animal, a pair of **umbilical** or **allantoic arteries** arise from the dorsal aorta and supply the **allantois**. In the adult amniotes, the two vitelline' arteries unite to form the main **mesenteric artery** whereas, greater part of the allantoic arteries degenerate, but the remaining forms the hypogastric or the **internal iliac arteries**.

### 5.3.1 Modifications of aortic arches in different classes of vertebrates

The six pairs of aortic arches that arise in the primitive vertebrates are largely modified, reduced or abortive in the ascending scale of evolution of the vertebrates. However, the basic design in the organ and evolution of the arterial arches remains uncharged in all the classes of vertebrates.

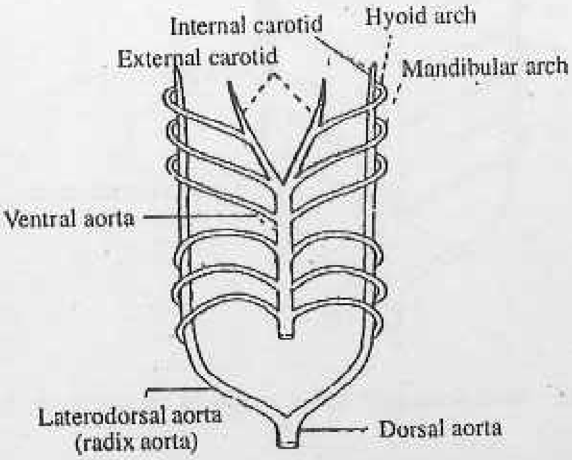


**Fig 5.14** : Primitive aortic arches in a vertebrate embryo

The following is an account of the modifications of aortic arches in different classes of vertebrates :

1. **Class—Cyclostomata : In Petromyzon** of this class, there are seven gill pouches. The ventral aorta on reaching near the fourth gill pouch splits into two branches. From each branch four afferent branchial arteries and from the proximal unbranched ventral aorta four afferent branchial arteries arise on either side to supply blood to the gill pouches. Of the eight afferent branchial arteries on either side, the first and the last supply the heniibranchs as unbranched vessels; the remaining six afferent branchials divide each into two branches to supply each gill pouch.

2. **Class—Chondrichthyes :** In both cartilaginous and bony fishes, a gradual reduction in the number of arterial arches is observed. In some primitive sharks, much greater number of arterial arches may be present in relation to the number of gill pouches. The six pairs of aortic arches present in the embryo of most cartilaginous fishes represent the primitive number of aortic arches present in the embryo of higher vertebrates.

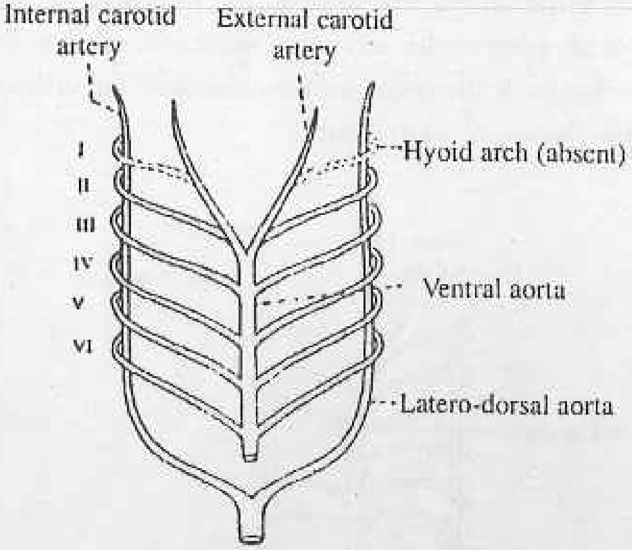


**Fig 5.15** : Modification of aortic arches in cartilagenous fishes

The two lateral dorsal aorae extend anteriorly as the internal carotid arteries to supply blood to the brain. The afferent branchial arteries are distributed through the **interbranchial septa** of the gills.

In adult dogfishes (e.g., *Scoliodon* sp.) and most other cartilagineous fishes, there are five pairs of afferent branchial arteries and four pairs of efferent branchial arteries.

3. **Class—Osteichthyes :** In the teleostean and other bony fishes, the first and second aortic arches disappear, so that in these fishes, the third, fourth, fifth and sixth aortic arches persist. In *Polypterus* (order chandrostei) and in the lung fishes (order Dipnoi), either the sixth aortic arch or the dorsal aorta gives off a branch to supply the air bladder.

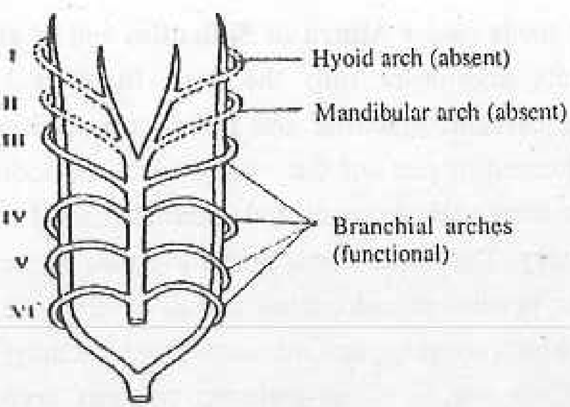


Fig 5.16 : Modification of aortic arches in bony fishes

4. **Class—Amphibia :** With the emergence of land vertebrates as represented by the adult amphibians, and from them upward in the ascending series of vertebrates, the first and second aortic arches completely disappear.

In the salamanders (order Urodela or Caudata) external gills are present, in addition to lungs. Hence, third to sixth—all the four aortic arches are present here, although the fifth aortic arch is much reduced. Here the aortic arches do not form the afferent and efferent arteries, but the fourth, fifth and sixth aortic arches form blood capillaries within the gills for respiratory exchange. In this group, the portion of radix aorta between the third and fourth aortic arches persists as a connection between these two arches. The sixth aortic arch form the pulmonary arch directing towards the lungs. A portion of the sixth aortic arch remains as the **ductus arteriosus** (**ductus botalli**) between the pulmonary arch and the radix aorta which has now been modified as the systemic arch.

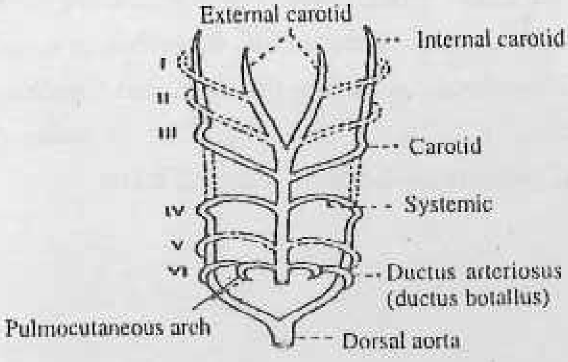


Fig 5.17 : Modification of aortic arches in Urodela (class Amphibia)

In the frogs and toads (order **Anura** or **Salientia**) and in all amniotes, the fifth aortic arch completely disappears; only the third, fourth and sixth aortic arches persist and form the **carotid**, **systemic** and **pulmocutaneous arches** respectively. The carotid arch is formed of parts of the ventral aorta and radix aorta. The portion of ventral aorta that forms the external and internal carotid arteries is called the **common carotid artery**. The fourth aortic arch surrounds the heart from either side, taking in most of the portion of radix aorta and is modified to form the right and left systemic arches which converge towards each other dorsally, and form the single **dorsal aorta**. The sixth arch is called **pulmocutarieous arch**, because this arch divides into two branches to supply blood to the lungs and skin. In adult anurans both **ductus caroticus and ductus arteriosus** disappear.

5. **Class—Reptilia :** As in the amphibians, the third, fourth and sixth aortic arches only persist in the adults of reptiles. Because of the incomplete division of the ventricle, the distal part of the conus arteriosus and a part of the ventral aorta (i.e., **truncus arteriosus**) are longitudinally split into three blood vessels. The fourth aortic arch on the left is separately connected to the right side of the partially divided ventricle. This arch curves around left side of the heart and by joining the radix aorta forms the left systemic arch. From the extreme right of the ventricle arises the pulmonary aorta which is the modified sixth aortic arch. The pulmonary aorta divides into two branches, each entering into the respective lung of that side. The fourth aortic arch of the right side arises from extreme left of the ventricle, curves round right side of the heart, and forms the **right systemic arch**. Both the left and right systemic arches unite dorsally to form the dorsal aorta. The third aortic arch forms **a common carotid artery** on either side. Each common carotid divides into on external and an internal carotid arteries. The **ductus caroticus** is usually lost, but in some snakes and lizards, it persists connecting the third and fourth aortic arches. Ductus arteriosus is also absent in most of the reptiles but in ***Sphenodon*** and in some turtles and tortoises, it persists in a much reduced form.

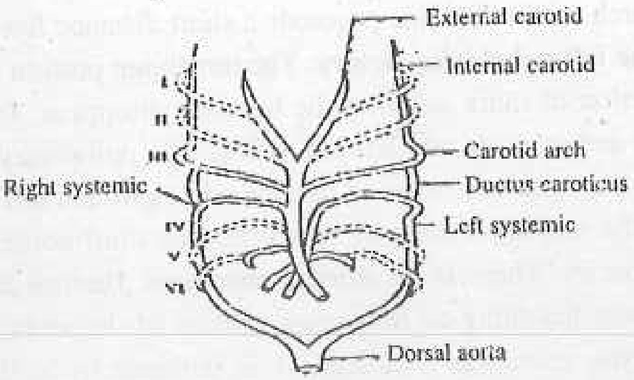


Fig 5.18 : Modification of aortic arches in *Calotes* sp. (class Reptilia)

6. **Class—Aves :** In reptiles, birds and mammals, the third, fourth and sixth aortic arches persists, but there are certain evolutionary changes in the three groups. In birds, as in the crocodiles of the class Reptilia, the ventricle becomes completely divided into two so that there is a complete separation of the venous and arterial blood in the right and left side of the heart respectively. The ventral aorta having split into two parts gives rise to two main aortae : the **systemic aorta** from the left ventricle and the **pulmonary aorta** from the right ventricle. The fourth aortic arch curves round right side of the heart and by joining the radix aorta reaches dorsally to form the **dorsal aorta**.

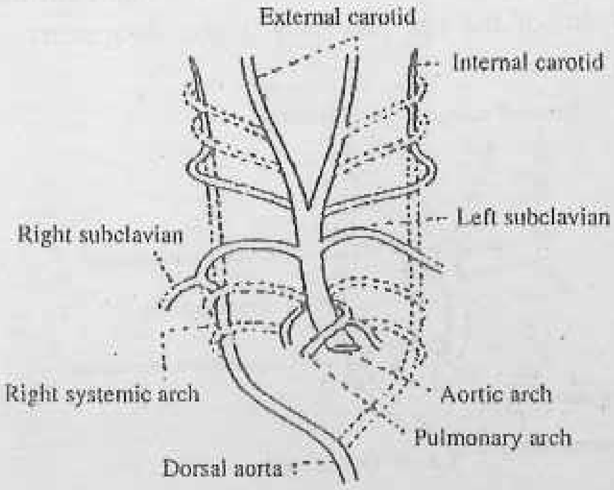


Fig. 5.19 : Modification of aortic arches in *Columba* sp. (class Aves)

The fourth aortic arch on the left side proceeds a short distance from the ventral aorta and then forms the **left subclavian artery**. The remaining portion of the fourth aortic arch and the portion of radix aorta on the left side disappear. Thus in birds, only the right systemic arch persists, the left one is lost. The pulmonary aorta (sixth aortic arch) arises from the right ventricle and divides into **right** and **left pulmonary arteries** to enter into the respective lung of that side. The third aortic arch forms the common carotid arteries. There is no **ductus caroticus. Ductus arteriosus** is present only in the young hatchling as remaining portion of the sixth aortic arch; in adult birds, the ductus arteriosus is absent. It is replaced by a 'Ligamentum arteriosum' formed of fibrous connective tissues.

7. **Class—Mammalia :** The modifications of aortic arches in mammals are the same as in birds, except that in mammals, the fourth aortic arch joins the radix aorta of the left side form the left systemic aorta only, the right systemic aorta being absent (a situation, apposite to that in birds). A portion of the fourth aortic arch and of the radix aorta form the **right subclavian artery**, the remaining portion of the fourth aortic arch and of the radix aorta disappears. The third aortic arch is modified to form the **right and left common carotid arteries** which unite at the base of the right subclavian and form a distinct **brachiocephalic artery** (also known as **innominate artery**). The common carotid and the subclavian arteries arise from the brachiocephalic artery at the top of the arch of aorta. The ductus arteriosus is present on both sides in the mammalian embryo but within a short period the one on the right side disappears; the one on the left side remains as the **ligamentum arteriosum** till the hatchling comes out of the egg and later it also disappears.

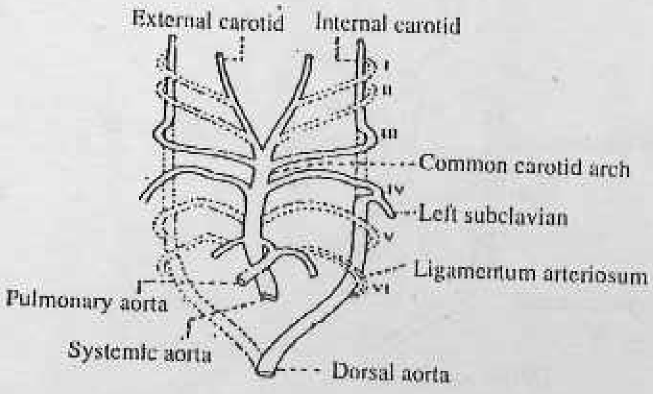


**Fig 5.20** : Modification of aortic arches in *Cavia* sp. (class Mammalia)

### 5.3.2 Evolution of arterial arches in vertebrates

In the evolution of arterial arches from the class Cyclostomata to the class Mammalia it is evident that the greater number of arterial arches (6, 7 or even more) present in the primitive vertebrates shows gradual reduction in the higher classes of vertebrates.

In the aquatic cyclostomes and fishes, greater number of gill pouches are supplied by many more aortic arches. In the primitive elasmobranchs (e.g., dogfishes, sharks and allies) and in the embryos of vertebrates, the six pairs of arterial arches that supply blood to the gills are reduced in number along with the beginning of lung respiration from the dipnoans, the lung respiration becoming more pronounced in the amphibians and the gill respiration completely replaced by the lung respiration in the next higher groups of vertebrates. From the class Amphibia, the first and second aortic arches (hyoid and mandibular arches) are lost and the fifth aortic arch is present in a much reduced form in some or completely lost in others. So practically from the class Amphibia, the third, fourth and sixth aortic arches become operative and through suitable changes in the structure of the heart a well developed arterial system is formed throughout the body. The venous system is also modified in relation to the structure and disposition of the heart and lungs.

Jolie (1957) has cited the example of ***Branchiostoma*** and states that the large number of arterial arches in *Branchiostoma* are used for food collection. Hence, it appears that the arterial arches are primarily meant for food collection; their role in blood circulation is a secondary one.

However, it is quite logical to assume that the evolution and modification of the arterial arches in vertebrates are the outcome of several factors of which the change from aquatic life to semiterrestrial and then fully teuestrial mode of life is the main. And even in the biggest form of vertebrates, the appearance of primitive aortic arches in their embryo is of great phylogenetic significance.

### 5.3.3 Evolution of the portal systems

The portal system of veins carry blood (on its way to the heart) from, one organ to the other or from a system of organs to the other, but a portal vein never carries blood directly to the heart or to the main venous trunk. This system of veins start with capillaries and end in capillaries.

Three types of portal systems are functional in different groups of vertebrates : (i) the **hepatic portal system** which is more extensive and represented in all the groups of vertebrates as also in *Branchiostoma;* (ii) the **renal portal system** bringing blood from the caudal region of the body to the kidneys are well represented in the amniotes but much reduced in reptiles and birds and completely absent in the mammals; (ii) a third system called **hypophysio-portal circulation** which transports blood from some branches of the internal carotid artery to the anterior lobe of the pituitary gland via the median eminence of the hypothalamus and the hypophysial stalk.

### 5.3.3.1 The hepatic portal system

This system has its origin from the vitelline-subintestinal group of veins in vertebrate embryo. In a vertebrate embryo, the liver bud is formed as an outgrowth of the gut. In embryonic circulation, the pair of vitelline veins are very important in the yolk-sac embryos. In vertebrate embryos without yolk sac a pair of **subintestinal veins** replace the vitelline veins. As the liver grows out larger, the right vitelline vein gradually disappears; the left one becomes the functional **hepatic portal vein** which breaks up into capillaries forming sinusoids within the liver. At the other end, this vein is formed by capillaries and small venules collecting blood from all the gut elements as well as the spleen. The earlier connections of the paired vitelline veins from the liver to the heart now become the **hepatic veins.** The subintestinal veins behind the anus is continued posteriorly as a single **caudal vein.**

In **cyclostomes**, the subintestinal vein becomes the hepatic portal vein. A contractile 'portal heart' is also present in the hepatic portal vein of cyclostomes.

**Fishes** in general possess a well developed hepatic portal vein which is derived from the left vitelline vein and branches from the subintestinal vein.

In the **amphibians,** a single, mid ventral **anterior abdominal vein** which first appears in the lung fish, *Epiceratodus,* joins the hepatic portal vein so that the renal portal and the hepatic portal veins are in close association. In this arrangement, blood on its way to the heart must pass through one or the other.

In the **reptiles** too, there is little change in the venous system from that of the amphibians. The anterior abdominal vein collecting blood from the posterior region joins the hepatic Portal vein anteriorly and breaks up into capillaries within the liver. The capillaries reunite to form the hepatic veins which return blood to the postcaval on way to the heart.

In **birds,** as the sinus venosus disappears, the two precavals and the single post caval veins return blood directly to the right auricle. The original post cardinal connections do not exist.

The hepatic portal system in birds is well developed. It is characterized by joining with the **inferior mesenteric** or **coccygeomesenteric** vein that establishes connection with the reduced caudal vein and the posterior parr of the hepatic portal vein. The connection of the coccygeomesenteric vein with the caudal vein also means a connection with the renal portal veins and because of this connection with two portal veins, some authors consider the coccygeomesenteric vein homologous with the anterior abdominal vein of the amphibians and reptiles; others consider the **epigastric vein** in birds homologous with the anterior abdominal vein. The hepatic veins in birds join the postcaval vein near the heart.

In mammals, as in birds, the two precaval veins (one in some) and the single postcaval vein enter into the heart directly as the sinus venosus has been absorbed by the right atrium.

The hepatic portal vein and the hepatic veins have their usual structural configuration as in the amphibians and reptiles.

### 5.3.3.2 Renal portal vein

Wherever the renal portal system is present it collects blood through capillaries from the legs and posterior part of the body and breaks up into capillaries on reaching the kidneys. The sets of renal veins then transport blood from the kidneys to the postcaval vein.

There is no renal portal system in the cyclostomes.

In fishes, some changes occur in the course of the posterior cardinal veins and in the development of a **subcardinal vein** and a **renal portal vein**. With the posterior elongation of an opishonephric kidney in fishes, the post cardinal now running along inner border of the kidney is known as the subcardinal vein. The bifurcated caudal vein (as the continuity of the post cardinal and the caudal veins is broken) now runs along inter border of the kidney on either side and this vein is now known as the

**renal portal vein.** It breaks up into capillaries within the kidney and the capillaries reunite to gain the subcardinal veins that finally transport blood through the postcardinal veins to the heart.

The lateral abdominal veins present in the elasmobranch fishes as described above are not present in the teleosts. In the lungfish. ***Epiceratodus***, the lateral abdominal veins fuse to form a single midventral **anterior abdominal vein** as found in the amphibians.

In the amphibians, the renal portal system is well developed and formed by the union of sciatic and femoral veins bringing, blood from the legs and posterior part of the body. In fact, blood from the hindlinbs and posterior region of the body is returned to the heart by either of the two routes : renal portal—kidney post caval route and pelvic—anterior abdominal—hepatic portal—postcaval route. In the lungfishes the position is different, as the anterior abdominal vein returns blood directly to the heart. In the amphibians, the postcaval vein remains the main pathway for returning blood from the posterior part of the body to the heart.

In the reptiles, the situation is almost similar to that in the amphibians. The renal portal vein is reduced in the reptiles and in some species, there may be direct connections between the renal portal and the postcaval veins. In both the amphibians and the reptiles, the postcaval vein has its origin partly from the subcardinals and partly from the vitelline veins.

In birds, both the hepatic portal and renal portal system are well developed, although the renal portal vein directly passes through the kidney and joins the iliac vein on either side. The two iliac veins unite—to form the thick and wide post caval vein. The renal portal passes directly through the kidneys without breaking up into capillaries. The renal portal veins represent the old posterior cardinal veins.

In the adult *mammals,* the renal portal system is completely absent. Blood from the posterior region of the body is collected by branches of the postcaval vein. The anterior abdominal vein also disappears in mammals (except in the monotreme, *Echidna).*

### 5.3.3.3 Hypophysio-portal circulation

A reference has already been made earlier that the branches of carotid arteries supply blood to the pituitary gland. While some of the branches supply the gland directly, some break up into capillaries within the median eminence of the hypothalamus and the hypophysial stalk. A different set of capillaries reunite to form hypophysis-portal venules which return blood to the sinusoids of the anterior lobe of the pituitary. This constitutes the hypophysial-portal circulation carrying hormones or neurosecretions from the hypothalamic regions to the pituitary gland and thus control or influence the total output of the pituitary gland.

## 5.4 Terminal questions

1. What are the various structures in the blood vascular system? Explain with the aid of a sketch the mechanism by which the nutrients reach the cells and tissues in a vertebrate.
2. Draw, label and distinguish between an artery and a vein.
3. What do you understand by a 'single-circuit heart'? Where is it found? Give a schematic diagram of a single-circuit circulation.
4. What is a 'double-circuit heart'? Explain it with the help of a schematic diagram.
5. Elucidate the distinguishing features between anamoniote and amniote blood circulation.
6. Describe composition of blood.
7. Draw, label and describe different types of blood corpuscles. Are the platelets in mammalian blood to be regarded as cells?
8. What are hemopoietic tissues? Where are they formed?
9. Mention different functions of blood.
10. Define heart. Draw, label and describe the development of heart in a vertebrate.
11. Draw, label and describe the structure of an amphibian heart. How does it differ from the heart of cartilaginous and bony fishes?
12. Draw, label and describe the structure of the heart of an amniote. How does it differ from the heart of an anaminote?

13. Draw, label and describe the structure of a mammalian heart. Describe structures involved in the pacemaker of a mammalian heart.

14. Draw, label and describe the embryonic aortic arches in a vertebrate.

15. Draw, label and describe the aortic arches in a cartilagineous and a teleostean fish.

16. Trace the evolution of aortic arches in the amphibians and reptiles.

17. Draw, label and describe the modifications of aortic arches in reptiles, birds and mammals.

18. Discuss trend of the evolution of aortic arches in vertebrates.

19. Write short / explanatory notes on :
    - (a) Persistent and accessory chambers of the heart
    - (b) Bulbus cordis
    - (c) Conus arteriosus
    - (d) Ductus caroticus
    - (e) Ductus arteriosus
    - (f) Tricuspid and Bicuspid valves
    - (g) Musculi papillares
    - (h) Auricular appendage
    - (i) Eustachian valve
    - (j) Anterior abdominal vein
    - (k) Ligamentum arteriosum
    - (l) Hepatic veins
    - (m) Vitelline vein and subintestinal vein

20. Draw, label and describe the hepatic portal system in an amphibian. How does it differ from that of a bird?

21. Draw, label and describe the renal portal vein in *Bufo* sp. How is this vein modified in reptiles and birds?

# NOTE

Most of the sketches in this text are based on or modified from either of the following books :

1. 'Pranividya' (in Bengali); Vol. 2; 2001, 2003-2004; Ray et al.
2. A Text Book of Vertebrate Zoology; 11th ed., 1972; S.N. Prasad.
3. The Vertebrate Body; 6th ed., 1986; Romer and Parson.
4. Comparative anatomy of vertebrates; 1983; George C. Kent
5. Vertebrate diversity, function and evolution; 1990; Pough, Heiser and McFarland.
6. Elements of chordate anatomy; 1977; Weichert and Presch.
7. The life of vertebrates; 3rd ed., 1981; J. Z. Young.

# Unit 6 ☐ Respiratory system

## Structure

## 6.1 Introduction

The principal function of the respiratory system is to supply the body's living cells with oxygen, and remove carbon dioxide. The process of respiration involves four distinct steps:

- Pulmonary Ventilation–the action of breathing moves air into and out of the lungs in a continuous flow.
- External Respiration–gas exchange between the blood and the gas-filled chambers of the lungs.
- Transport of Respiratory Gases-between the site of gas exchange in the lungs and the respiring tissues of the body. This transport is achieved by the blood flowing through the cardiovascular system.
- Internal Respiration–gas exchange between the blood and the respiring tissues.

The close coupling of the respiratory system with the cardiovascular system is essential for efficient and effective gas exchange. Because the respiratory system is involved in generating air flow, it also plays a role in speech and the sense of smell. The respiratory system can be divided into two functional portions, the conducting zone and the respiratory zone. The conducting zone is composed of all the passageways which provide a route for air to pass between the external environment and the respiratory zone, and the latter is the site of gas exchange in the lungs.

## 6.2 Characters of respiratory tissue

A respiratory organ consists of a surface across which gas exchange by diffusion can occur between blood and either water or air. The characteristics of respiratory surface must be :

(i) Moist enough to allow the cells to live.

(ii) Large enough to permit sufficient gas exchange.

(iii) Thin enough to permit rapid diffusion.

In respiration:

- blood entering the respiratory organ must be high in $CO_2$ and low in $O_2$ content
- both gases must move into and out of the body tissues through diffusion
- requires a functional connection between the respiratory and circulatory systems
- the external air/water medium must be frequently replenished

The primary respiratory organs of vertebrates are gills and lungs, although the skin is sometimes used.

**6.2.1 External cutaneous respiration** is the ancestral form of respiration found in most protochordates. During external respiration—

- gas exchange occurs at the level of the skin and oxygen and carbon dioxide are passed into and out of tissues.
- the process still occurs in small vertebrates as long as they have low activity levels and live in cool flowing water or in damp air - frogs meet about half of their needs for gas exchange through their skin.

Because most vertebrates are too large for each cell to interact directly with the environment, many organisms have evolved specialized organ systems to undertake the process of diffusion. Generally, fishes use gills and tetrapods use lungs, although the distinction is not absolute. Through ventilation of the organs of the respiratory system, gaseous exchange can occur. Ventilation of respiratory structures depends on :

**6.2.2 Ram ventilation** : forward momentum contributes to flow of water across the gill membranes. It is the production of respiratory flow in some fish in which the mouth is opened during swimming, such that water flows through the mouth and across the gills. In fish which have a reduced or no ability to pump water through buccal chamber, such as mackerel and sharks, perpetual swimming is required to maintain ventilation.

**6.2.3 Dual pump** : buccal and opercular action operating in tandem drives water in a nearly continuous unidirectional flow across the gill curtain between them. the **suction phase** begins with compressed buccal and opercular cavities and closed valves.

- as the buccal cavity expands, the internal oral valves open and water moves into the buccal cavity and across the gill curtain.
- during the **force phase**, the oral valve closes and water is forced out through the opercular valve.

**6.2.4 Pulse pump** : the dual pump is modified into an inhalation/exhalation phase.

- the **exhalation phase** begins with transfer of spent air from the lungs into the buccal cavity.
- the exhalation phase concludes with expulsion of air from the buccal cavity to the outside either through the mouth or under the operculum.
- the **inhalation phase** begins with the organism taking fresh air into the mouth.
- the inhalation phase concludes with transfer of air from the buccal cavity into the lungs

**6.2.5 Aspiration pump** : air is sucked in, or aspirated, by low pressure created around the lungs

- the lungs are located within the pump so that the force required to ventilate them is applied directly.
- a moveable diaphragm and rib cage cause pressure changes rather than the action of the buccal cavity.

Gills usually consist of thin filaments of tissue, branches, or slender tufted processes which have a highly folded surface to increase surface area. A high surface area is crucial to the gas exchange of aquatic organisms as water contains only 1/20 parts dissolved oxygen compared to air. With the exception of some aquatic insects, the filaments and lamellae (folds), contain blood or coelomic fluid, from which gases are exchanged through the thin walls. Oxygen is carried by the blood to other parts of the body. Carbon dioxide passes from the blood through the thin gill tissue into the water. Fish has specialised structures called the gills to carry out exchange of gases in water, the medium in which they live. The region between the buccal cavity (mouth) and the oesophagus is called the pharynx. In the pharyngeal region, the wall on either side shows slits which open to the exterior. These slits are called the gill slits. The gill slits are separated by a tissue called the gill arch or the branchial arch. There are four pairs of gill arches separating five pairs of gill slits. However, the number of gill arches and gill slits varies in different fishes.

## 6.3 Internal and external respiration

Respiration is the physiological process by which organisms supply oxygen to their cells and the cells use that oxygen to produce high energy molecules. Respiration occurs in all types of organisms including animals. In higher animals, respiration is often separated into three separate components: (a) external respiration, the exchange of oxygen and carbon dioxide between the environment and the organism; (b) internal respiration, the exchange of oxygen and carbon dioxide between the internal body fluids, such as blood, and individual cells; and (c) cellular respiration, the biochemical oxidation of glucose and consequent synthesis of ATP (adenosine triphosphate). External respiration, commonly known as breathing, is the exchange of oxygen and carbon dioxide between an animal and its environment. Most animals use specialized organs or organ systems, such as lungs, trachea, or gills, for external respiration.

In all cases, exchange of gases between the environment and an animal occurs by diffusion through a wet surface on the animal which is permeable to oxygen and carbon dioxide. Diffusion is the random movement of molecules and causes a net movement of molecules from a region of high concentration to a region of low concentration. Thus, oxygen moves into an organism because its concentration is lower inside than in the environment (air or water); carbon dioxide moves out of an organism because its concentration is higher inside than in the environment. Different organisms have different mechanisms for extracting oxygen from their environments.

1. **Diffusion into blood :** Amphibians use this method. In this method, oxygen diffuses through a moist layer of epidermal cells on the body surface and from there through capillary walls and into the blood stream. Once oxygen is in the blood, it moves throughout the body to different tissues and cells. While this method does not rely upon respiratory organs and is thus quite primitive, it is somewhat more advanced than direct diffusion.

2. **Gills :** Fish and other aquatic animals use this method. Gills are specialized tissues with many infoldings, each covered by a thin layer of cells and impregnated with blood capillaries. They take up oxygen dissolved in water and expel carbon dioxide dissolved in blood. Gills work by a mechanism called countercurrent exchange, in which blood and water flow in discrete pathways and opposite directions. This allows gills to extract oxygen more efficiently from water and expel carbondioxide into the water. Certain details of gill anatomy differ among different species.

3. **Lungs :** Terrestrial vertebrates use this method. Lungs are special organs in the body cavity that are composed of many small chambers impregnated with blood capillaries. After air enters the lungs, oxygen diffuses into the blood stream through

the walls of these capillaries. It then moves from the lung capillaries to the different muscles and organs of the body. Humans and other mammals have lungs in which air moves in and out through the same pathway. In contrast, birds have more specialized lungs which use a mechanism called cross-current exchange. Like the countercurrent exchange mechanism of gills, air flows through the crosscurrent exchange system of avian lungs in one direction only, making for more efficient oxygen exchange.

Breathing occurs to provide oxygen to the alveoli and remove carbon dioxide and water from the body. The purpose of respiration is to provide oxygen to cells for the process of cellular respiration. Cellular respiration occurs in the mitochondria of cells and produces ATP energy for cellular processes. During cellular respiration, glucose and oxygen (nutrients) are converted to carbon dioxide and water (wastes). Respiration also removes these waste products with the help of the circulatory system.

Blood transports oxygen, carbon dioxide, and water between the lungs and body cells. Oxygen is carried by hemoglobin molecules (Hb - actually called deoxyhemoglobin when no oxygen gas is attached) inside red blood cells forming oxyhemoglobin ($HbO_2$). Carbon dioxide is transported mainly in blood plasma in the form of bicarbonate ion with some carbon dioxide molecules attached to hemoglobin as carbaminohemoglobin ($HbCO_2$). Hydrogen ions attach to hemoglobin forming reduced hemoglobin (HHb).

External respiration occurs at the alveoli. The reactions that occur in the lungs are aided by the lower temperature and higher pH found there. The reactions are summarized in the image below.

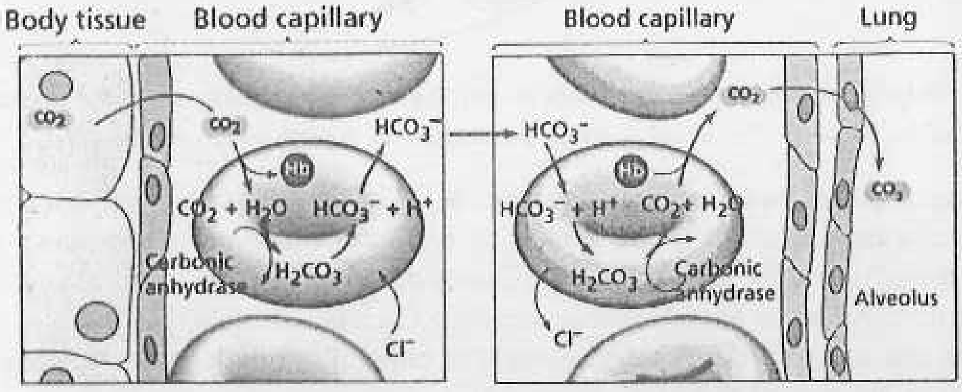
Blood with low oxygen gas content picks up oxygen which diffuses from the alveoli (where it is in high concentration) into the blood capillaries where it is in low concentration. Hydrogen ions are released from reduced hemoglobin and combine with bicarbonate ions to form carbonic acid. An enzyme, called carbonic anhydrase, helps convert the carbonic acid into carbon dioxide and water which diffuse into the alveoli. The small amount of carbon dioxide found as carbaminohemoglobin diffuses into the alveoli as well.

Internal respiration occurs in the capillary beds of the tissues. The reactions that occur in the tissues are aided by the higher temperature and lower pH found there. The reactions are summarized in the image below.

Blood high in oxygen gas releases oxygen gas which diffuses into the tissues. Water and carbon dioxide diffuse into the blood where they form carbonic acid. In the blood, carbonic acid is converted into bicarbonate ions and hydrogen ions by the enzyme *carbonic anhydrase*. Bicarbonate ions are transported in plasma back to the lungs and hydrogen ions combine with hemoglobin to form reduced hemoglobin in red blood cells. A small amount of the carbon dioxide combines with hemoglobin to form carbaminohemoglobin in red blood cells and is returned to the lungs in this form.

## Gas exchange in fish

The gas exchange organs of fish are called gills. Fish possess several gills located between their mouth cavity (buccal cavity) and a chamber at the sides of their mouth called the operculum. Figure 6.1 shows the main elements that are involved in gas exchange in fish.



(a) (b)

**Fig. 6.1 (a, b) :** Showing the process of gas exchange in fish.

### *Gill filaments*

From each gill arch arise two rows of filaments, which are arranged in a V-shaped manner. The gill arch along with the filaments is called a gill.

### *Gill lamellae*

Each filament is made up of plate-like structures called lamellae, which have a rich supply of blood capillaries. Thus the barrier between the blood capillaries and the water is only few cells thick. The lamellae also serve to increase the surface area greatly. Along the gill arch run the blood vessels which give off branches into the filaments and the lamellae. The whole arrangement on either side is covered by a movable cover called the operculum (refer to the first diagram in this section). It consists of muscles and thin layers of bone. The thousands of fine branches on each filament expose a large surface area to the water. Blood circulates in the filament branches and is separated from the water by a thin epithelium so that oxygen and carbon dioxide diffuse through easily.

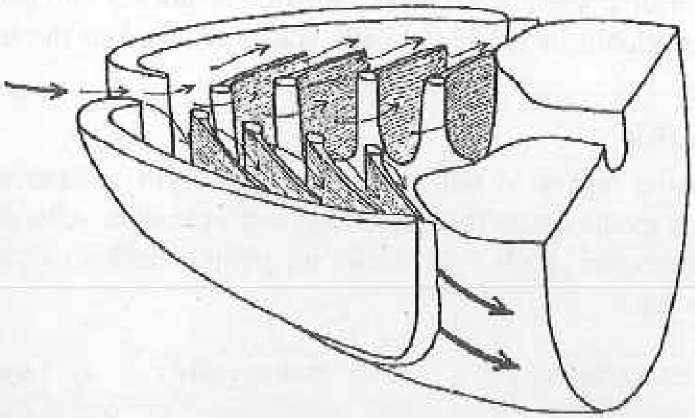


**Fig. 6.2 :** Diagram showing the arrangement of the gill filaments on a gill arch, and of the secondary lamellae on the filaments. The arrows indicate the direction of flow of water over the gills.

Oxygen passes from the water into the blood at the gills. Removal of carbon dioxide also occurs, as the blood containing high concentrations of the waste gas goes to the gills, and the carbon dioxide diffuses out into the water down a diffusion gradient (external water has lower concentrations of carbon dioxide than levels in the blood, so this sets up a diffusion gradient). The blood flows through the lamellae in the opposite direction to that of the water. This is a counter current system. It ensures that the maximum exchange possible occurs.

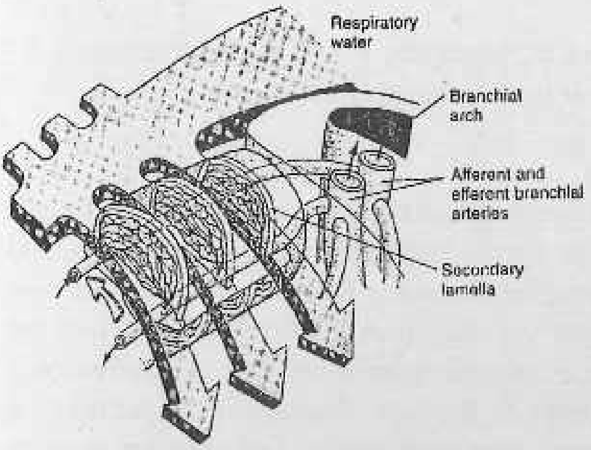


**Fig. 6.3 :** Gill ventilation in teleost. Water flow is directed across the secondary lamellae opposite to that of blood flowing within each secondary lamella, establishing a counter current exchange between them.

Gills are made efficient in a number of ways—

(1) A large surface area for gaseous exchange means that more oxygen can enter the bloodstream over a given period of time. A single gill of a bony fish consists of a

curved gill arch bearing a V-shaped double row of gill filaments. Each filament has many minute folds in its surface, giving it a sort of fuzzy appearance and increasing the amount of surface area along a given length of filament. Consequently, the surface area of the gills is commonly 10 to 60 times more than that of the whole body surface.

(2) A short diffusion, or travel distance for the oxygen increases the rate of oxygen entry into the blood. The blood travelling in the folds of the filaments is very close to the oxygen-containing water, being separated from it by a very thin membrane usually 1 to 3 microns (4/100,000 to 1/10,000 in) thick, and possibly less.

(3) By using counter current circulation in the gill, the blood in the filament folds travels forward, in the opposite direction to the water flow, so that a constant imbalance is maintained between the lower amount of oxygen in the blood and the higher amount in the water, ensuring passage of oxygen to the blood. If the blood were to flow in the same direction as the water, oxygenated blood at the rear of the gills would be traveling with deoxygenated water and not only could it fail to extract oxygen from the water but would even lose oxygen to it.

(4) Gills have little physiological dead space. The folds of the filament are close enough together so that most of the water passing between them is involved in the gas-exchange process.

(5) Water flows continuously in only one direction over the gills, as contrasted with the interrupted, two-way flow of air in and out of lungs of mammals.

## 6.4 Comparative account of respiratory organs

### 6.4.1 Internal gills

- developd from the pharynx as evaginations called pharyngeal pouches.
- visceral grooves opposite to the pharyngeal pouches are separated from the pharyngeal pouches by a thin layer of tissue called the closing plate - the closing plates rupture in the embryo to establish the communication between the gill chamber and the surrounding medium - tetrapods retain the first closing plate, which becomes the eardrum (tympanic membrane), while the remaining ones disappear.
- the pouches are also separated by the visceral arches, which combine to form the parabranchial gill chambers.
- the first visceral arch becomes the spiracle.

**The general structure of a mature gill is composed of several parts**

- gill rakers are cartilagenous or bony parts on the pharyngeal margin of the gill and function in preventing food particles from entering the gill chambers.

- gill rays are found within the interbranchial septa and provide support for the gill.
- gill filaments are the feather-like projections of the gills across which diffusion of gases occurs.
- gill filaments also possess gill lamellae, which are small crevices through which water passes for diffusion.
  - lamellae are oriented parallel to the stream of water through the gills to maximize efficiency of diffusion.
  - the blood flow through the gills opposes the flow of water through the lamellae (countercurrent flow) and maximizes the efficiency of diffusion - this is important because water has about 1/30th the oxygen concentration of air.

Three primary types of gill morphology are found in fishes:

***Holobranch*** : gill bar with anterior and posterior rows of gill filaments (jawed fishes).

***Hemibranch*** : gill bar with gill filaments found on either the posterior or anterior side (sharks).

***Pseudobranch*** : gill bar with posterior filaments modified to serve a nonrespiratory function such as sensory or salt balance.

- spiracular pseudobranch in rays and skates with much reduced hemibranch providing unobstructed flow of water for gill irrigation.

Gills can also be used in excretion of nitrogenous wastes (in the form of ammonia) and regulation of salts in the body.

There are three general variations in gills found in fishes:

***Pouched gills. Example*** : Agnatha

- have external and internal pores rather than gill slits
- water is drawn into the gill chambers through the mouth and then passed over the gills

***Septal gills. Example*** : Elasmobranchs

- have gill slits rather than pores and gill septa that help support gill filaments
- inspiration occurs through the mouth and expiration occurs through the gills
- the exception is when the shark is feeding; when water moves into the pharynx through the spiracle

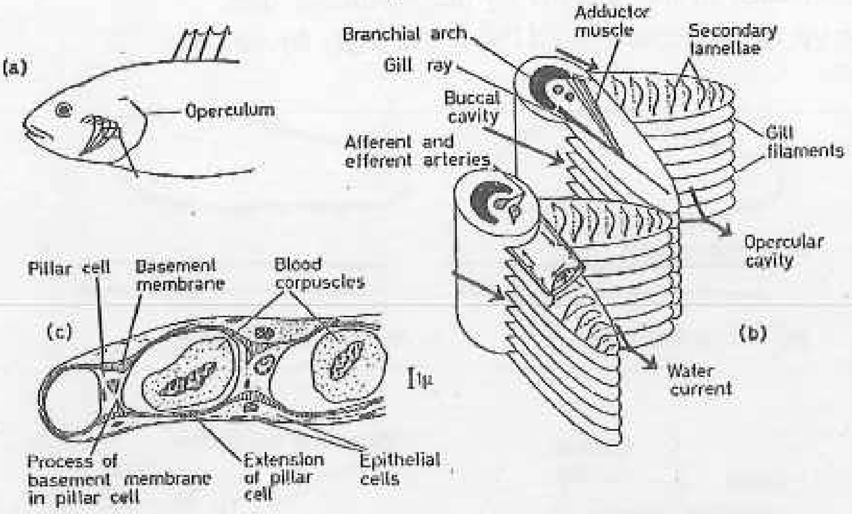


**Fig. 6.4 :** The gills of teleost fishes. (a) View from left side to show the position of four gill arches beneath the operculum. (b) Filaments and associated structures attached to two neighbouring branchial arches. (c) Section through a secondary lamella, based upon electron micrographs.

***Opercular gills. Example*** : bony fishes

- have no septa (aseptal) but gill bars anchor gill filaments
- the operculum protects the filaments and expiration occurs through a single gill slit

### 6.4.2 External gills

- develop from the skin ectoderm of the branchial area but are not directly related to the visceral skeleton or branchial chambers
- are found most often in larval or paedomorphic amphibians.

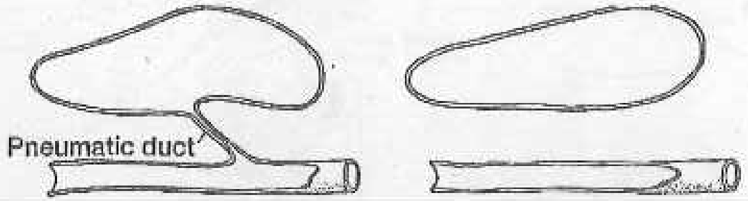
### 6.4.3 Swim bladders and the origin of lungs

Lungs are found among fishes found in warm or stagnant water, as well as in primitive fishes, and allow for the fish to gulp air and undergo diffusion in an environment with relatively low dissolved oxygen. Such fishes undergo long periods of breath-holding (**apnea**) alternated with short periods of lung ventilation.

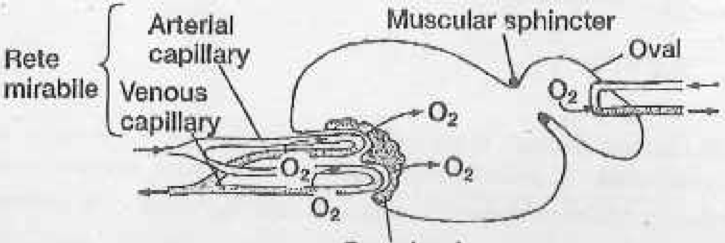
#### Swim bladders

Swim bladders are similar to lungs, but are found in fishes that live in more oxygen-rich environments - thus, the air-filled spaces serve less of a purpose in respiration and function more as a hydrostatic organ.

- are connected to the pharynx by the pneumatic duct.
- make up approximately 4 - 11% of the body by volume.



(a) Physostomous (b) Physocleistous



(c) Swim bladder

**Fig. 6.5 :** Swim bladders. (a) Physostomous (pneumatic duct present), and (b) physocleistous (pneumatic duct has been lost). (c) The rete mirabile is a knot of capillaries. As blood leaves the gas gland of the swim bladder via the venous capillaries of the rete, lactic acid is added. This reduces haemoglobin's affinity for oxygen. Oxygen, therefore, tends to diffuse out and enter adjacent arterial capillaries passing blood to the rete. Consequently, the oxygen concentration builds in the arterial blood as it approaches the gas gland so that the partial pressure of oxygen in the arterial capillaries of the rete is high when it reaches the gas gland. This encourages oxygen release into the swim bladder.

- counters the increased density and sinking tendency from an ossified skeleton.
- gas is secreted into the swim bladder from blood by action of the gas glands or may be connected directly to the digestive tract via the pneumatic duct in primitive teleosts.
- air is added to the swim bladder to maintain its volume as fish dive and removed as the fish surfaces.
- gas glands may be associated with a countercurrent rete mirabile, which affects partial pressure and flow of oxygen into and out of the bladde.

Following is the gas gland of two teleost fishes.

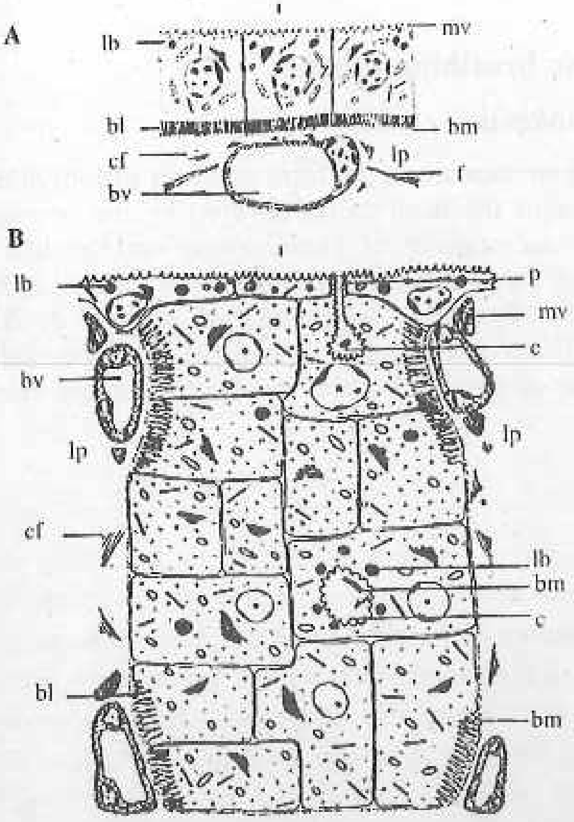


**Fig. 6.6 : (A)**. Swim bladder of the European eel where gas gland cells form a monolayer over the secretory part of the swim bladder epithelium. The gas gland cells show a clear polarity with a remarkable basal labyrinth (bl) and lamellar bodies (lb). At the apical membrane, the cells form small microvilli (mv). Below the gas gland cells a thin *lamina propria* (lp) containing collagen fibres (cf), fibroblasts (f), and blood vessels (bv) is present. **(B)** Swim bladder of the perch, where the gas gland cells form a distinct gas gland. Flattened epithelial cells are facing the lumen. These cells contain a large number of lamellar bodies (lb). The gas gland cells are located in several layers between the lamina propria (lp), where blood capillaries and nerves (nv) are found. The cells show a well-developed basal labyrinth (bl) when they are lying near blood vessels (bv). In some cells, a canal is present with small microvilli and tubular myelin. Lamellar bodies are present in the cytoplasm near the canal. bm, basement membrane.

### 6.4.4 Accessory respiratory organ

A system of air chambers formed by outgrowths from the mouth or gill region of those fish that occasionally leave the water. The uptake of oxygen from the air is facilitated by a dense network of tiny blood vessels in the skin lining these air chambers, and their possession enables such fish as labyrinth fish (*Anabantidae*), snakeheads (*Channidae*), or air-breathing catfish (*Clariidae*) to survive outside water for some considerable time. The *swim-bladder* also may serve as an accessory respiratory organ.

## Structure of the air breathing organs

### 1. *Monopterus (=Amphipnus) cuchia*

In *M. cuchia,* the air sacs are in the form of a pair of lung-like structure situated along the lateral sides of the head partly covered by the operculum. The mucosa lining the respiratory sac consists of vascular and non-vascular regions. Vascular areas are composed of small and large respiratory islets studded with hundreds of vascular rosettes; each of which is comprised of a group of 20-30 papillae. The vascular papillae are the terminal bulb-like ends of sub-epithelial blood capillaries. The air/blood pathway is extremely thin, the total thickness being 0.435ìm in *M. cuchia.*

### 2. *Channa punctatus*

In *C. punctatus* and *C. striata* the main air breathing organ is a pair of suprabranchial chambers which develop dorsal to the gill arches above the pharynx. The suprabranchial chamber is connected with the pharynx through inhalant apertures. The exhalent aperture of the suprabranchial chambers of each side is modified dorsal region of the first gill slit. The structure of the respiratory mucosa consists of vascular and non-vascular areas. Vascular areas contain respiratory islets. The thickness of the air-blood barrier in *C. striata* is about 2ìm to 0.5 ìm. The non-vascular part of the respiratory membrane is formed of stratified, columnar and polyhedral cells.

### 3. *Clarias magur*

The suprabranchial chambers of each side comprises two recesses – a small dorsal and a more extensive ventro-posterior chamber. The primary gill lamellae belonging to 1st, 2nd, 3rd, and 4th gill arches move away from the branchial arches and migrate on to the surface of the suprabranchial chambers where respiratory islets are formed. The air/blood barrier comprises a singe epithelial layer (0.38ìm), a very thin basement membrane (0.024ìm) and a thin lining of pillar cell flanges (0.146ìm).

### 4. *Heteropneustes fossilis*

The suprabranchial chambers extend backward into the trunk region in the form of sacs deeply embedded in the trunk myotomes. Air first enters the suprabranchial chamber through the inhalant slit and then into the posterior tubule. The respiratory mucosa of the air sacs is thrown into folds and ridges. Each ridge is covered by respiratory epithelia. The vascular epithelium comprises small and large secondary

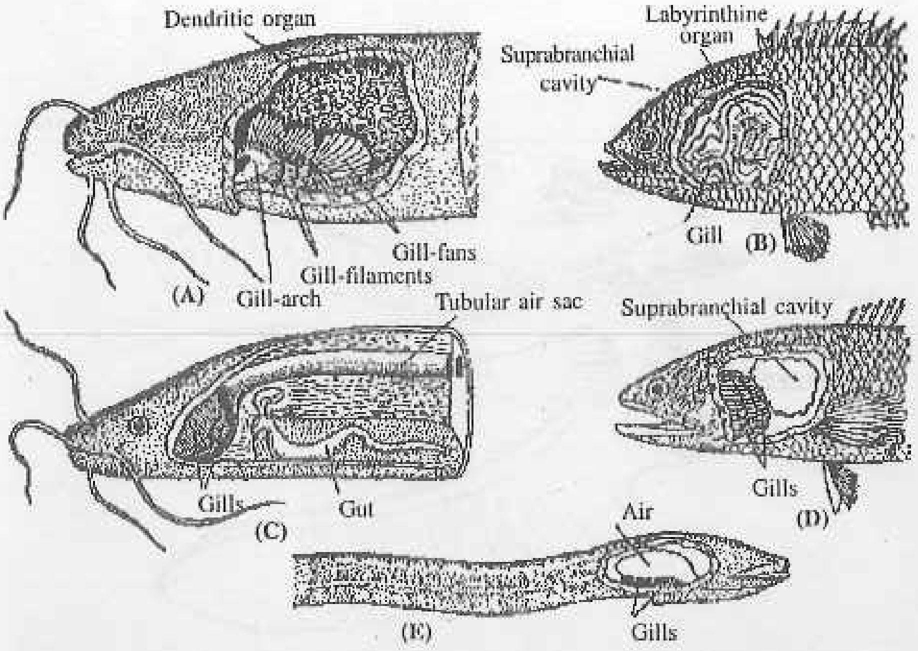


Fig. 6.7 : Accessory respiratory organ of different fishes. (A) *Clarias batracus*; (B) *Anabas testudineus;* (C) *Heteropneustes fossilis* (D) *Channa punctatus*; (E) *Monopterus cuchia*

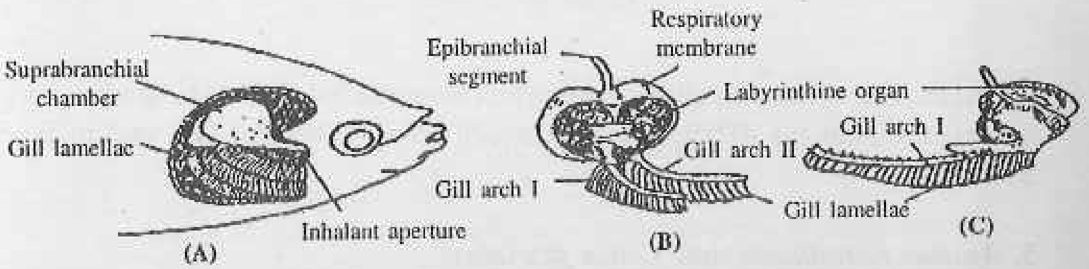


Fig. 6.8 (A-C) : Detail of the suprabranchial chamber and respiratory membrane of a jeol fish

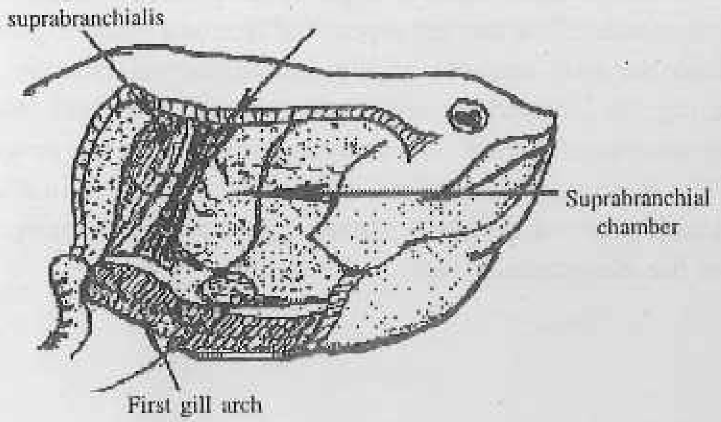


Fig. 6.9 : Lateral view of the head of *Channa punctatus* to show the relation of the supra branchial chamber with the constrictor suprabranchialis, the first levator arcus branchialis

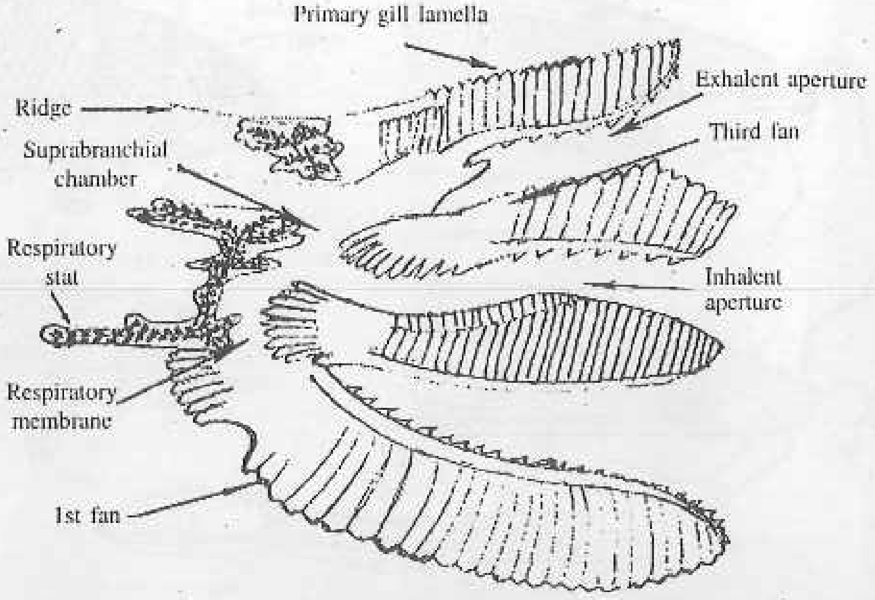


**Fig. 6.10 :** The respiratory sac opened out by means of mid-ventral incision to show the relation between the 'fans', the inhalant aperture, exhalent aperture, the gill arches, the supra-branchial chamber and the respiratory sac

lamellae. The air/blood pathway comprises an epithelial lining (1.36ìm), a very thin basement membrane (0.05ìm) and pillar cell lining (0.020ìm).The total thickness is about 1.6ìm.

### 5. *Anabas testudineus* and *Colisa fasciatus*

While in *Anabas* the labyrinthine organs are of complex nature, in *Colisa fasciatus* they are of simple type. The labyrinthine organ in *C. fasciatus* possesses two leaf-like expansions situated on either side of the median septa. The free and broad expansions of this organ project into the two recesses of the suprabranchial chamber. The respiratory mucosa covering the labyrinthine organ and the suprabranchial chamber contain both vascular and non-vascular areas. The respiratory membrane has developed many respiratory islets. The structure of respiratory islets is more complex in *Anabas.* Each islet consists of double rows of parallel channels. Specialized chemoreceptor cells have been found in the non-vascular part of the lining.

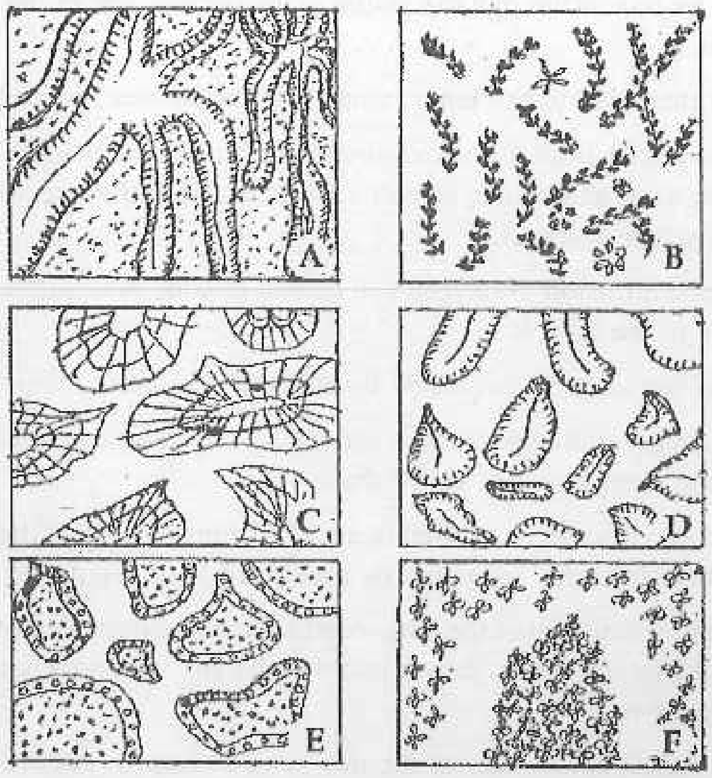


**Fig. 6.11 :** Respiratory islets of A. *Clarias batrachus;* B. *Heteropneustes fossilis;* C. *Anabas testudineus;* D. *Colisa fasciatus;* E. *Amphipnus cuchia;* F. *Channa punctatus.*

### 6.4.5 Lungs and their ducts

Tetrapod lungs are paired organs surrounded by pleura and contained in the pleural cavity—

- they have a higher surface to area volume ratio than the gills
- are joined to the ventral side of the gut tube by the trachea
- in general, any increase in overall body size leads to an increased amount of compartmentalization of the lungs.

**During respiration**

- air enters through the mouth, or into the external nares to the choanae, and then passes into the pharynx.

- from there, air travels through the glottis to the trachea, and in the trachea splits into bronchi.
- the bronchi then lead to the lungs, which are themselves highly lobed.
- branching continues from the bronchi into bronchioles with penulfimate branches then alveolar sacs, and end in alveoli - small sac-like structure within the lung where gas exchange occurs.

  As in gills, the diffusion of oxygen and carbon dioxide is facilitated by counter-current flow in the alveoli.
- the lining of the lungs is lubricated by surfactant, a tension depressant
- surfactants are generally lipoproteins and reduce the resistance to lung expansion as well as the energy needed to fill the lungs.

  In the evolution of lungs from amphibians to mammals, several modifications to the respiratory structures are primarily associated with ventilation of the lungs.
- In amphibians, ventilation of the lungs occurs through external nares and choanae rather than the mouth - air is drawn into the pharynx by muscle contraction that lowers the pharynx floor.
- In reptiles, muscle action against the ribs helps to change internal air pressure, causing inspiration - the action is assisted by contraction of the diaphragmatic muscle, which is not the same thing as the diaphragm.
- In birds, the lungs are half the size of the lungs of a similarly-sized mammal.

  - however, the lungs connect to a system of air sacs in the bones and abdominal cavity, which increases the capacity to 2 - 3 times that of a similarly-sized mammal.

  - the result is to decrease overall body mass, but still maintain respiratorefficiency.

  - conducting passages continue to subdivide into parabronchi and air capillaries with one-way airflow through the lungs.
- The primary mammal modification is the formation of the diaphragm dividing the thoracic and abdominal cavity - movement of air into the lungs is facilitated by contraction of the diaphragm to change the pressure in the chest cavity.

## Amphibian lungs

The lungs of most frogs and other amphibians are simple balloon-like structures, with gas exchange limited to the outer surface area of the lung. This is not a very efficient arrangement, but amphibians have low metabolic demands and also frequently supplement their oxygen supply by diffusion across the moist outer skin of their bodies. Unlike mammals, which use a breathing system driven by negative pressure, amphibians employ positive pressure. The majority of salamander species are lungless salamanders which conduct respiration through their skin and the tissues lining their mouth. The only other known lungless tetrapods are also amphibians — the Bornean Flat-headed Frog (*Barbourula kalimantanensis*) and *Atretochoana eiselti*, a caecilian

## Reptilian lungs

Reptilian lungs are typically ventilated by a combination of expansion and contraction of the ribs via axial muscles and buccal pumping. Crocodilians also rely on the hepatic piston method, in which the liver is pulled back by a muscle anchored to the pubic bone (part of the pelvis), which in turn pulls the bottom of the lungs backward, expanding them.

## Avian lungs

Avian lungs do not have alveoli as mammalian lungs do. They contain millions of tiny passages known as para bronchi, connected at both ends by the dorsobronchi. The airflow through the avian lung always travels in the same direction - posterior to anterior. This is in contrast to the mammalian system, in which the direction of airflow in the lung is tidal, reversing between inhalation and exhalation. By utilizing a unidirectional flow of air, avian lungs are able to extract a greater concentration of oxygen from inhaled air. Birds are thus equipped to fly at altitudes at which mammals would succumb to hypoxia. This also allows them to sustain a higher metabolic rate than an equivalent weight mammal. Because of the complexity of the system, misunderstanding is common and it is incorrectly believed that that it takes two breathing cycles for air to pass entirely through a bird's respiratory system. A bird's lungs do not store air in either of the sacs between respiration cycles, air moves continuously from the posterior to anterior air sacs throughout respiration. This type of lung construction is called circulatory lungs as distinct from the bellows lung possessed by most other animals.

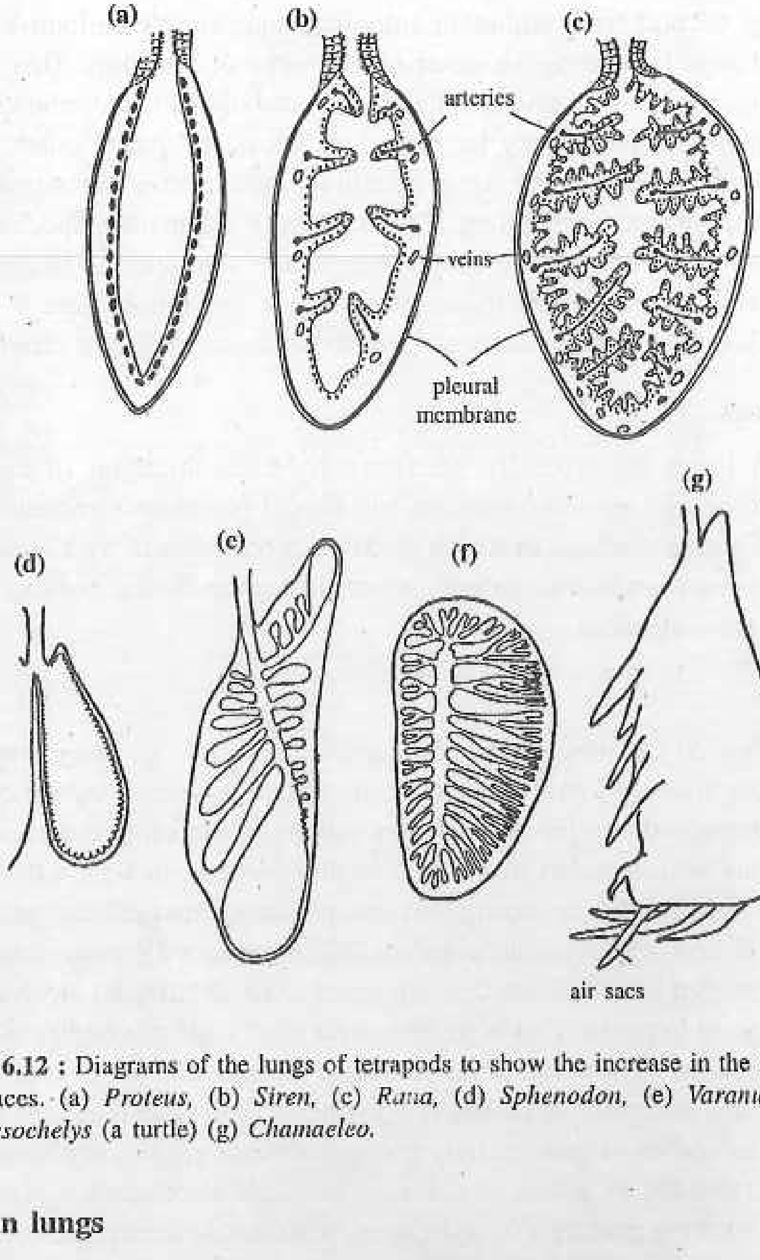


**Fig. 6.12 :** Diagrams of the lungs of tetrapods to show the increase in the infolding of their surfaces. (a) *Proteus,* (b) *Siren,* (c) *Rana,* (d) *Sphenodon,* (e) *Varanus* (a lizard), (f) *Thassochelys* (a turtle) (g) *Chamaeleo.*

## Mammalian lungs

The lungs of mammals have a spongy texture and are honeycombed with epithelium, having a much larger surface area in total than the outer surface area of the lung itself. The lungs of humans are a typical example of this type of lung.

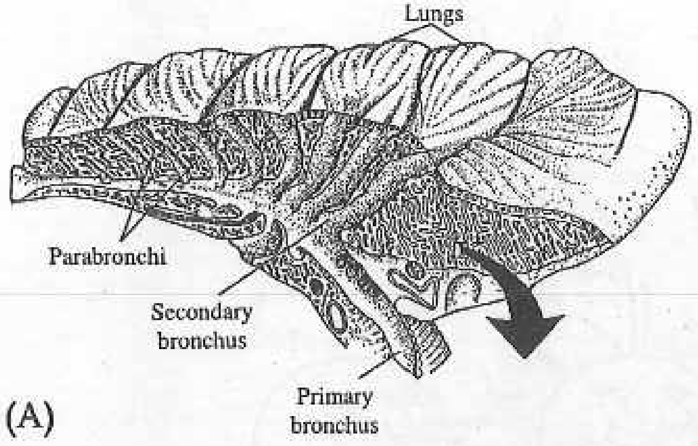
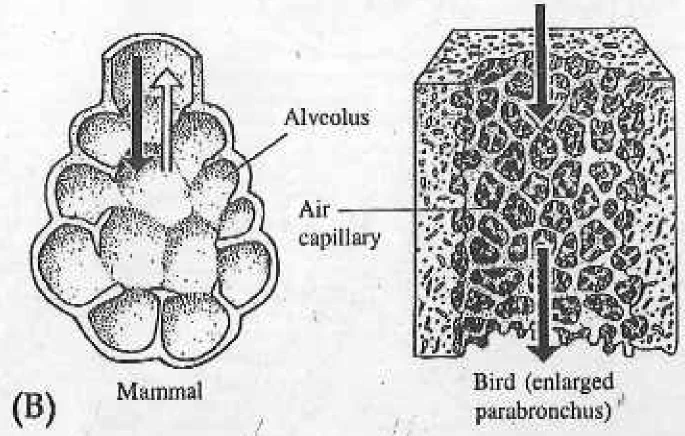
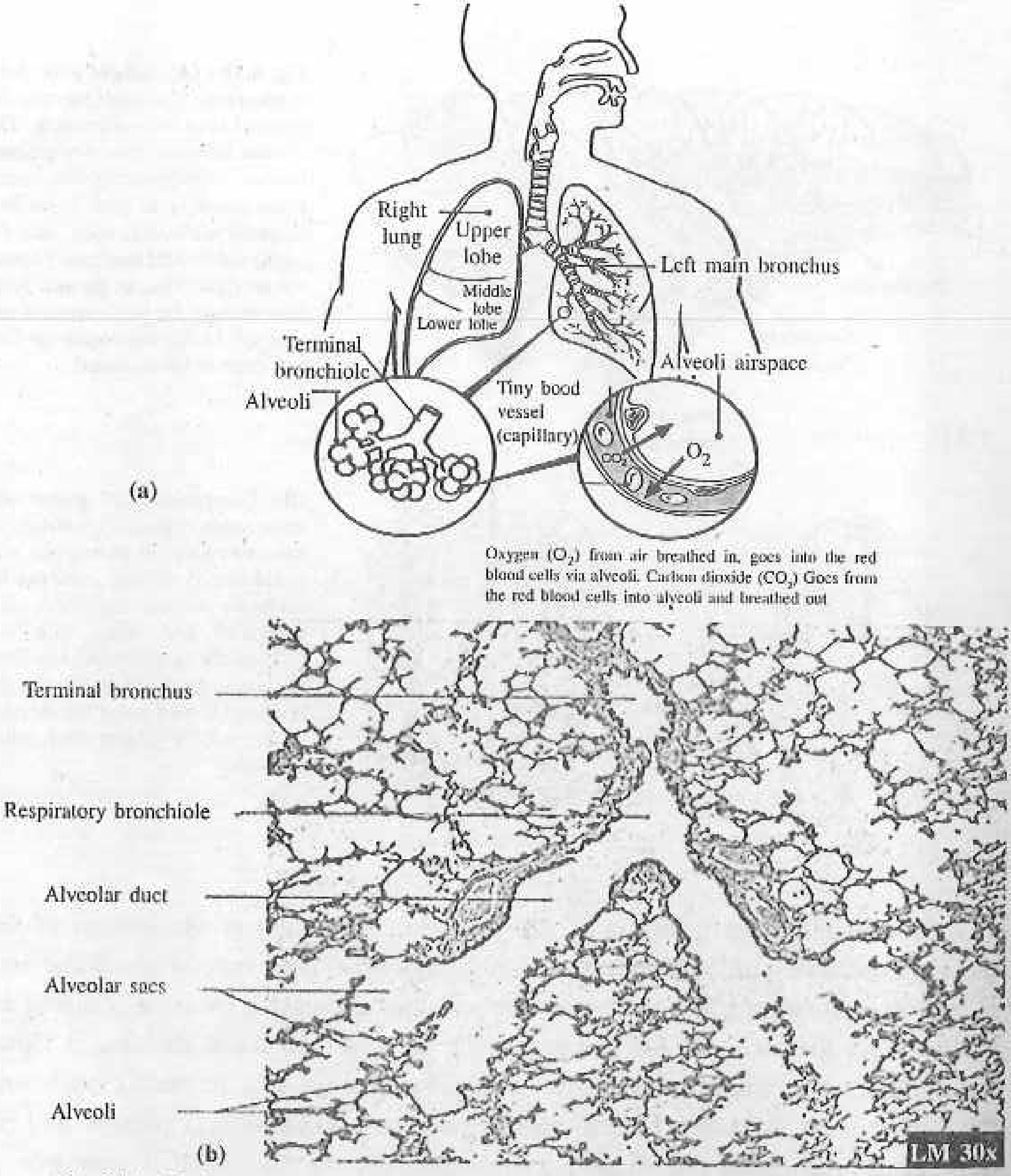


**Fig. 6.13 : (A)** Isolated avian lung is sectioned. The small pores in the exposed lung are parabronchi. The trachea branches into two primary bronchi (mesobronchi) that extend to the posterior air sacs. These lead to parabronchi that open into the highly subdivided respiratory tissue, the air capillaries. In the bird lung, flow through the parabronchi is one way, unlike the mammalian airflow that ends in blind alveoli.



**(B)** Comparison of avian and mammalian respiratory surfaces. In the avian lung air passes one way (solid arrow) through parabronchi, replacing the air capillaries that surround and open into the parabronchi. In the mammalian lung, the alveoli are blind-ended. For gas exchange to take place, the air must move tidally (open and solid arrows).

Breathing is largely driven by the muscular diaphragm at the bottom of the thorax. Contraction of the diaphragm pulls the bottom of the cavity in which the lung is enclosed downward, increasing volume and thus decreasing pressure, causing air to flow into the airways. Air enters through the oral and nasal cavities; it flows through the larynx and into the trachea, which branches out into the main bronchi and then subsequent divisions. During normal breathing, expiration is passive and no muscles are contracted (the diaphragm relaxes). The rib cage itself is also able to expand and contract to some degree, through the action of other respiratory and accessory respiratory muscles. As a result, air is sucked into or expelled out of the lungs. This type of lung is known as a bellows lung as it resembles a blacksmith's bellows.



Oxygen ($O_2$) from air breathed in, goes into the red blood cells via alveoli. Carbon dioxide ($CO_2$) Goes from the red blood cells into alveoli and breathed out

**Fig. 6.14 :** The lung contains millions of tiny alveoli (a) Lung showing the position of alveoli; (b) Microscopic structure of alveoli.

### 6.4.6 Vocalization in relation to respiration

The larynx is the primary organ that functions in producing sounds

- supported caudally by the cricoid cartilage, dorsally by the arytenoid cartilage, and by the addition of the thyroid cartilage in mammals.

- all support cartilages are derived from the visceral arches.

The vocal cords themselves are flaps of epithelium supported by cartilage - produce bursts of air that can be modified by the pharynx, lips and tongue to produce speech.

In birds, the syrinx is located at the distal end of the trachea and contains tympanic membranes to assist in sound production

- consists of one or more tympanic-like membranes lying between cartilaginous rings in its wall
- membranes are vibrated by air moving across them and changed into meaningful sounds by changes in tension on the tympani, by the configuration of the trachea and buccopharyngeal cavity, and by tongue movements
- can be quite elaborate in some birds (such as cranes) and may be incorporated into the sternal keel.

## 6.5 Some definitions

**Alveolus** - a small sac-like structure within the lung where gas exchange occurs (plural alveoli).

**Closing plate** - thin layer of tissue separating the pharyngeal pouch from the external environment.

**Gill filament** - feather-like projection of the gill across which diffusion of gases occurs.

**Gill raker** - bony part on the pharyngeal margin of the gill which functions in preventing food particles from entering the gill chamber.

**Gill rays** - found within the gill filaments, and provides support for the gill.

**Hemibranch** - gill bar with gill filaments found on either posterior or anterior side (sharks).

**Holobranch** - gill bar with anterior and posterior rows of gill filaments (jawed fishes).

**Operculum** - bony gill covering in teleost that protects the gill filaments.

**Pseudobranch** - gill bar with posterior filaments modified to serve a non-respiratory function, such as sensory or salt balance. Found in the first gill bar of teleost.

**Rete mirabile** - a network of small arteries or capillaries associated with the gas glands.

**Spiracle** - the reduced first gill pouch of some fishes through which water may enter the pharynx; also, the opening from the gill chamber of frog- tadpoles.

**Surfactant** - tension depressant found on the lining of the lungs.

**Syrinx** - the voice box of birds, located at the distal end of the trachea.

## 6.6 Suggested questions

1. What is Ram ventilation?
2. Describe the structure of gill of a teleost fish.
3. Compare avian lung with that of mammalian lung.
4. What are the characteristic features of an amphibian lung and reptilian lung?
5. What is counter current mechanism in fish respiration?
6. Describe the structure of gas gland of a swim bladder.
7. What are accessory respiratory organs in fish? Describe the structure of accessory respiratory organ of any fish you have studied.
8. What is respiratory islet? Draw and describe one respiratory islet.
9. What are dual pump and pulse pump?
10. Mention the characteristic feature of respiratory tissue.
11. Explain internal respiration with suitable diagram.
12. Explain air flow through avian lung.
13. Draw and label the structure revealed in the section of mammalian lung and explain the mechanism of $O_2$ - $CO_2$ exchange.
14. Explain vocalisation in relation to respiration?

# Unit 7 ☐ Skeletal system

## Structure

## 7.1 Introduction

One of the processes that becomes increasingly important in vertebrate phylogeny is that of endochondral ossification. In this ontogenic process a cartilaginous model of the adult structure develops and is subsequently invaded by blood vessels and bone-forming cells. The cartilage is eroded and replaced by bone. Ultimately, the entire structure, which retains the general shape of the original cartilage, is ossified. This process is quite different from the formation of dermal bone or intramembranous ossification. Although these processes are distinct and appear to have separate phylogenetic histories, finally the bony tissue of the dermal or endochondral skeleton is identical.

## 7.2 Form, function, body size and skeletal elements of the body

Bone is a connective tissue unique to vertebrates. It serves several purposes:

- a reservoir for chemicals used in metabolic processes,
- provides structural support for soft tissues,
- acts as armor to shield vulnerable body parts,
- a framework upon which muscles can exert forces to facilitate movement.

In addition to being biologically important in the day to day lives of animals, bone is useful to paleontologists because it is readily preserved as fossils. Most of the information we use to reconstruct the evolutionary relationships between fossil vertebrates comes from their bones and teeth. Because of this, we must have at least a basic knowledge of the bones of the vertebrate skeleton. We should also be able to identify these elements from figures or on specimens.

## Terms of orientation

The terms "dorsal", "lateral", "medial" and "ventral" are used to describe the relative relationships in space between anatomical features.

**Anterior**: towards the front, or head.

**Posterior**: towards the rear, or behind.

**Dorsal**: towards the back side.

**Ventral**: towards the belly side.

**Medial**: towards the middle, or midline.

**Lateral**: towards the side, or outside.

**Proximal**: relatively closer to the body's center of mass .

**Distal**: relatively further away from the body's center of mass.

The **postcranium** (everything **posterior** to the **cranium**), composed of:

The **axial** skeleton (spine, ribs, and related features of the neck, trunk, and tail)

The **appendicular** skeleton (forelimb, hindlimb, and their **girdles**)

## The axial and appendicular skeleton

The vertebrate skeleton is easily divided into two distinct parts. These are the axial, and the appendicular, skeletons. The axial skeleton includes the skull, vertebral column, ribs, and sternum. The appendicular skeleton includes the bones of the limbs and the limb girdles that attach the limbs to the rest of the body.

## A. Axial skeleton

### I. Skull

The skull, or cranium, is an important and complex piece of vertebrate anatomy. It is a complex structure that performs a variety of tasks. These include :

- Housing and protecting the delicate brain and sensory organs,

- Housing feeding structures such as the jaws and teeth,

- Providing attachment points and space for the powerful muscles that close and open the jaw.

## Openings and their relative positions in skull

***Foramen Magnum*** : the opening in the rear of the skull through which the spinal cord passes to reach the brain.

***Naris (pl. nares)*** : the bony external opening for the nostril. Air or water enters the nasal cavity through the naris. In water-breathing vertebrates, water enters and exits the naris the same way. In air-breathing vertebrates, air passes through the naris, down the nasal passages, and enters the mouth or pharynx through the choanae.

***Choana (pl. choanae)*** : bony openings in the roof of the mouth (or pharynx in mammals and crocodilians) that communicate with the nares.

***Orbit (pl. orbits)*** : The bony socket that houses the eyeball.

***Antorbital fenestra (pl. antorbital fenestrae)*** : "Fenestra" means "window". This particular fenestra is found only in archosaurs (crocodilians, dinosaurs and a few other extinct groups). It is located between the orbit and the naris, on the side of the snout. These fenestrae are found in most dinosaurs (including birds), primitive crocodilians (modern crocs have closed these openings), pterosaurs, and many other extinct archosaurs. Several hypotheses have been put forth to explain the function of these fenestrae. The most popular hypothesis now is that the antorbital fenestra houses a large pneumatic sinus in the side of the face.

***Openings for jaw muscles*** : The temporal region of the skull, behind the orbit, is the attachment zone for numerous jaw muscles. Primitively, the braincase lies deep below the outer bones and jaw muscles of the temporal region. As a muscle contracts, it gets shorter, but the volume remains constant. This means that as muscles shorten they also get wider. The jaw muscles of vertebrates originate on the inside of the temporal bones of the skull, between them and the braincase. This means that when a primitive vertebrate flexes its jaw muscles (e.g. during biting) the muscles bulge, putting strain on the bones of the skull and braincase. The earliest vertebrates and tetrapods had a skull that was fully enclosed in bone. This meant that these animals had to keep their jaw muscles small to keep from seriously damaging their skull or brain, or they had to find a way to make more room for muscles. Many tetrapods chose the latter strategy, with different groups evolving fenestrae in the temporal region to allow large muscles to bulge. Keep in mind that lineages can secondarily (after it already evolved) lose a feature, and close over these openings.

***Postemporal fenestrae (sing. fenestra)*** : The earliest terrestrial vertebrates have this pair of openings, located on the rear of the skull. Among reptiles these are especially large in turtles, exposing most of the braincase.

***Infratemporal fenestrae (sing. fenestra)*** : paired openings in the lower, temporal region. They have evolved independently between reptiles more derived than turtles and in the lineage leading to mammals. In lizards and snakes the lower border of the infratemporal fenestra is lost, exposing the side of the braincase.

***Supratemporal fenestrae (sing. fenestra)*** : paired openings in the upper part of the temporal region, above the infratemporal fenestrae. Among living animals these openings are present in the tuatara, lizards, snakes (where they are secondarily lost), crocodilians, and birds.

***Mandibular fenestrae (sing. fenestra)*** : Many ancient animals, as well as modern birds and crocodilians, allow their jaw muscles to invade the space within the lower jaw. The mandibular fenestrae allow these muscles to expand, in much the same manner the temporal fenestrae do around the cranium.

In the past, terrestrial vertebrates were divided into three groups based upon their arrangement of temporal fenestrae. The **anapsid** skull type possesses no lateral (side) temporal fenestrae, but did possess postemporal fenestrae (e.g. turtles). The **synapsid** skull condition exhibits only an infratemporal fenestra on each side of the skull (e.g. mammals and their extinct relatives). The **diapsid** skull type possesses an infratemporal and a supratemporal fenestra on each side of the skull (e.g. lizards, snakes, crocodiles, birds).

## II. Vertebrae

The vulnerable spinal cord of vertebrates is protected by a series of spool-shaped bones meeting end to end, called **vertebrae** (sing. **vertebra**). Together the series makes up the vertebral column. In terrestrial vertebrates, the vertebral column also braces and supports the weight of the body. The column is divided into four basic sections.

**(a)** ***Cervical vertebrae*** : the vertebrae of the neck.

**(b)** ***Dorsal vertebrae*** : the vertebrae of the back, extending from the last cervical vertebra to the vertebrae to which the pelvis attaches.

(c) ***Sacral vertebrae*** : the vertebrae to which the pelvic bones, specifically the ilium, attach. They are often modified and strongly built to withstand the forces of bearing the weight of the animal. There may be as few as one or over a dozen in a given species.

**(d)** ***Caudal vertebrae*** : The vertebrae of the tail.

Other components of the axial skeleton include:

### III. Ribs

Ribs are associated with and connect to most types of vertebrae. Depending upon their location along the column, and with which vertebrae they articulate, they are called **cervical, dorsal, sacral,** or **caudal ribs**.

### IV. Haemal arches

Caudal vertebrae are often equipped with these downwardly projecting bones that articulate in the spaces below and between adjacent vertebrae. Viewed from the front or behind, a haemal arch has a vaguely "Y" shaped profile. In life, blood vessels and nerves run along the underside of the caudal vertebrae, in the notch formed by the two branches of the "Y".

### V. Sternum

The breastbone. This single element is located along the ventral side (belly side) of the chest cavity. The tips of many of the dorsal ribs directly or indirectly connect to it via cartilage. It also serves as an attachment site for the pectoral (chest) muscles. The sternum of flying birds is greatly modified to support the huge pectoral muscles needed for powered flight.

## B. Appendicular skeleton

### I. Pectoral girdle

The bones of the pectoral girdle evolved to provide a firm foundation for the forelimbs and their muscles, while maintaining a loose muscular connection to the axial skeleton.

***Scapula*** : the shoulder blade. This is the largest bone of the pectoral girdle. It generally extends upward (dorsally) from the articulation of the forelimb.

***Coracoid*** : This bone abuts the bottom end of the scapula and extends towards the body's midline. In mammals the coracoid is very strongly reduced.

***Glenoid fossa*** : not a bone, but rather the shoulder socket itself. The humerus articulates with it. The glenoid fossa is made up of both scapula and coracoid in most vertebrates.

***Clavicle*** : the collar bone. It forms a bony articulation between the appendicular skeleton of the pectoral girdle and the midline of the axial skeleton.

## II. Pelvic girdle

The bones of the pelvic girdle evolved to provide a solid connection between the hind limbs and the axial skeleton. The solid connection ensures that as much power as possible is transmitted from the hind legs to the body of the animal. Primitively in terrestrial vertebrates the pelvic girdle consists of three bones.

***Acetabulum (pl. acetabula)*** : This is not a bone, but rather is the hip socket itself. It lies near the center of the pelvic girdle. In primitive tetrapods and mammals, the acetabulum is a solid socket. In dinosaurs it is open, or perforated.

***Ilium (pl. ilia)*** : The ilium is the one bone of the pelvic girdle that attaches to the sacral vertebrae, and usually the largest bone of the girdle. It forms the upper third of the acetabulum.

***Pubis (pl. pubes)*** **:** The pubis forms the lower, front portion of the acetabulum. It extends forward and downward from the socket.

***Ischium (pl. ischia)*** **:** The ischium forms the lower, rear portion of the acetabulum. It projects downward and rearward from the socket.

## III. Fore and hind limbs

Tetrapod limbs are modifications of crossopterygian fins. Tetrapod limb skeletons consist of three segments: propodium, epipodium, and autopodium. In the forelimb, these correspond to the bones of the upper arm, forearm, and manus, or hand. The skeleton within homologous segments in the various tetrapods is remarkably similar despite outward appearances; it is the orientation of the bones, the relative mobility of the joints, and the complexity of the appendicular muscles as much as the skeleton *per se* that makes possible the variety of locomotor activities of the tetrapods.

The humerus is the bone of upper arm. The radius and ulna are bones of the forearm. The wrist, palm, and digits constitute a functional unit – the hand (manus). Wrist composed of carpus, radiale, and ulnare. Metacarpals are the bones of the palm. Each digit consists of phalanges. Modifications of the manus with few exceptions involve reduction in the number of bones by evolutionary loss or fusion. The most striking modifications of the manus are in flying tetrapods (birds and bats), in water adapted amniotes, and in ungulates.

**Table** : Homologous components of the anterior and posterior limbs

| | **Name of segment** | | **Skeleton** |
|---|---|---|---|
| Anterior limb | 1. Upper arm (brachium) | | Humerus |
| | 2. Forearm (antebrachium) | | Radius and ulna |
| | 3. Wrist (carpus) | Manus | Carpals |
| | 4. Palm (metacarpals) | | Metacarpals |
| | 5. Digits | | Phalanges |
| Posterior limb | 1. Thigh (femur) | | Femur |
| | 2. Shank (crus) | | Tibia and fibula |
| | 3. Ankle (tarsus) | Pes | Tarsals |
| | 4. Instep (metatarsus) | | Metatarsals |
| | 5. Digits | | Phalanges |

The femur is the bone of the thigh, and the tibia and fibula are bones of the lower leg. Digits have been reduced to four or fewer in modern amphibians, three in birds, and as few as one in some ungulates. Loss of digits is accompanied by loss or reduction of associated carpals and metacarpals or tarsals and metatarsals. Mammalian stances are plantigrade, digitigrade, or unguligrade. Ungulate feet are hoofed and mesaxonic (perissodactyles) or paraxonic (artiodactyls). A reduces number of ankle bones in birds have fused with the tibia and metatarsals to add an additional elongated segment to the hind limbs. An intratarsal joint adds to the flexibility of the pes.

## 7.3 Comparative account of jaw suspensorium and vertebral column

### 7.3.1 Jaw suspensions

***Craniostyly***: entire upper jaw incorporated into skull; lower jaw suspended from squamosal bone.

***Metautostyly***: jaw attached to skull via quadrate (the posterior palatoquadrate); hyomandibular becomes the *stapes* involved in hearing (amphibians, birds, reptiles).

***Hyostyly***: entire mandibular arch connected to skull by hyomandibular (bony fishes); emergence of *symplectic bone.*

***Paleostyly*** : none of arches attach directly to skull (agnathans).

***Euautostyly*** : mandibular arch suspended from skull w/o help from hyoid arch (placoderms).

***Amphistyly*** : two articulations of mandibular arch with skull - ligament connecting palatoquadrate to skull and hyomandibular articulating posterior portion (sharks, some other fish).

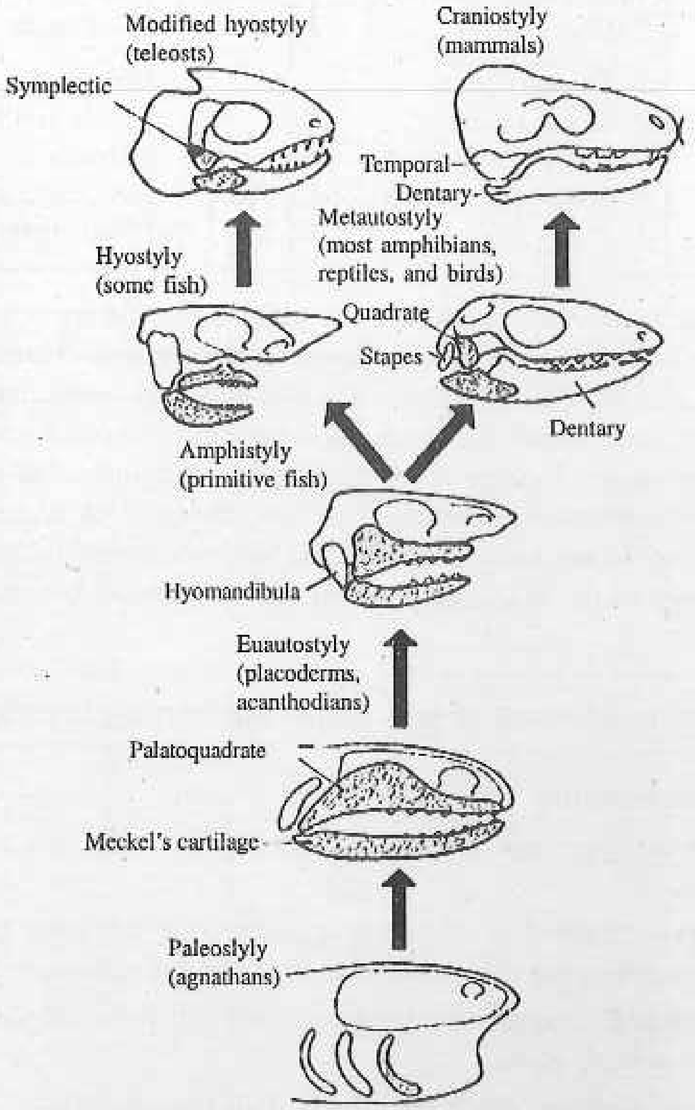


**Fig. 7. 1** Schematic representation of the origin of jaw suspension

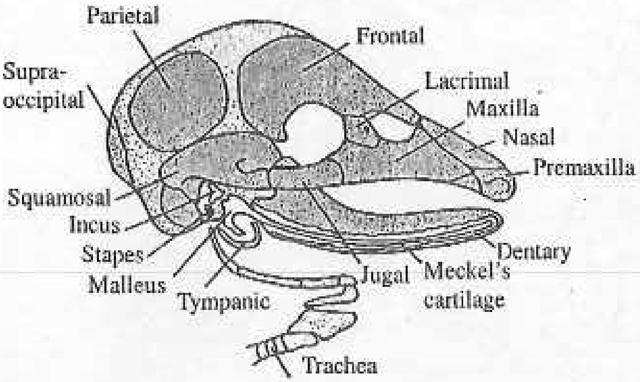


**Fig. 7.2 :** Mammalian jaw

### Mammalian Jaws (Craniostyly)

- Lower jaw consists of dentary bone
- Palatoquadrate becomes *incus*
- Meckel's cartilage becomes *malleus*
- Splanchnocranium (SC) not associated with jaws or suspension
- SC provides foundation for dentary, and middle ear bones

### Cranial Kinesis

Movement between upper jaw and braincase via joints

**Present in**: fishes, early amphibians, reptiles, birds, therapsids

**Absent in**: modern amphibians, turtles, crocodiles, mammals

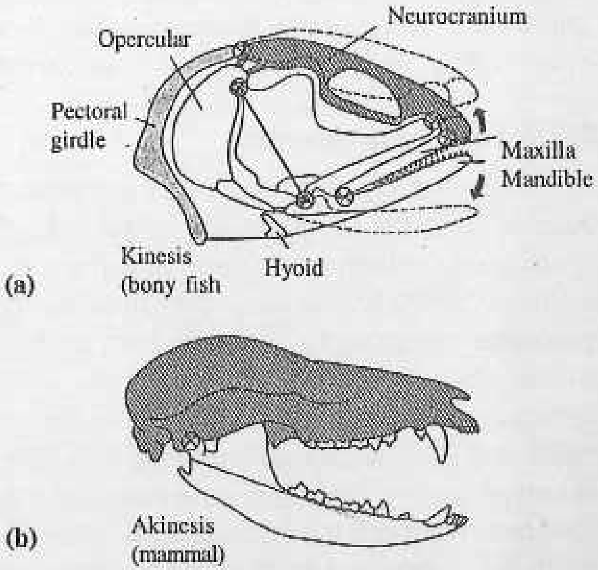


**Fig. 7.3 :** Cranial kinesis; (a) Kinesis (bony fish); (b) Akinesis (mammal).

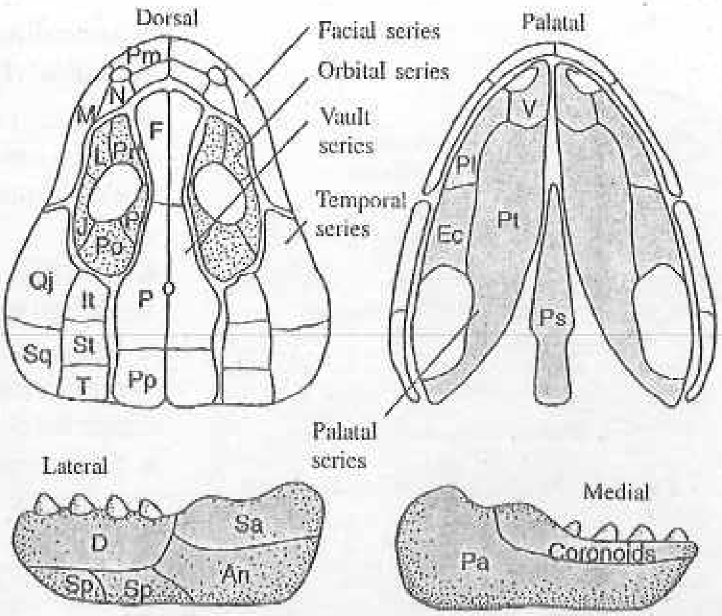


**Fig. 7.4 :** Dermatocranium morphology ; Facial series: Premaxilla (Pm); Maxilla (M); Nasals (N); Orbital series: Lacrimal (L); Prefrontal (Prf); Postfrontal (Pf); Postorbital (Po); Jugal (J); Temporal series: Intertemporal (It); Supratemporal (St); Tabular (T); Quadratojugal (Qj); Squamosal (Sq); Vault series: Frontal (F); Parietal (P); Postparietal (Pp); Parietal foramen (pineal); Palatal series: Pterygoid (Pt); Vomer (V); Palatine (Pl); Ectopterygoid (Ec); Parasphenoid (Ps); Mandibular series: Dentary (D); Splenials (Sp); Angular (An); Surangular (Sa); Prearticular (Pa).

### 7.3.2 Vertebral column

The vertebral column encases and protects the spinal cord, which runs from the base of the cranium down the dorsal side of the animal until reaching the pelvis. From there, vertebrae continue into the tail. Individual vertebra is composed of a centrum (body), arches protruding from the top of bottom of the centrum, and various processes projecting from the centrum and/or arches. An arch extending from the top of the centrum is called a neural arch, while the hemal arch or chevron is found underneath the centrum in the caudal (tail) vertebrae of fish, most reptiles, some birds, and some mammals with long tails. The vertebral processes can either give the structure rigidity, help them articulate with ribs, or serve as muscle attachment points. Common types are tranverse process, diapophyses, parapophyses, and zygapophyses (both the cranial zygapophyses and the caudal zygapophyses).

*Amphicelous* refers to a centrum that is concave at both ends, similar to those found in most fish. *Opisthocoelous* centra are convex in the front and concave in the back, similar to those of most salamanders. In contrast, *procelous* centra are concave in the front and convex in the back, as found in most frogs and modern reptiles.

Centra with flat ends are *acelous*, like those in mammals. Birds have *heterocelous* centra, shaped like saddles at both ends.

A typical vertebra consists of two essential parts: an anterior (front) segment, which is the vertebral body; and a posterior part – the vertebral (neural) arch – which encloses the vertebral foramen. The vertebral arch is formed by a pair of pedicles and a pair of laminae, and supports seven processes, four articular, two transverse, and one spinous, the latter also being known as the neural spine.

When the vertebrae are articulated with each other, the bodies form a strong pillar for the support of the head and trunk, and the vertebral foramina constitute a canal for the protection of the *medulla spinalis* (spinal cord). In between every pair of vertebrae are two apertures, the intervertebral foramina, one on either side, for the transmission of the spinal nerves and vessels.

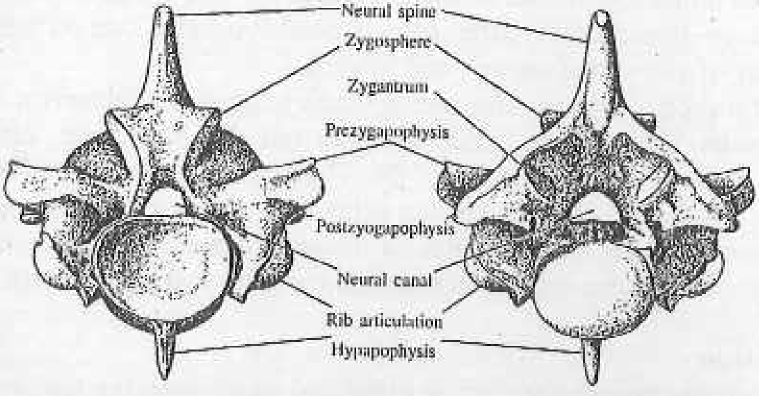
Two transverse process and one spinous process are posterior to (behind) the vertebral body. The spinous process comes out the back, one transverse process comes out the left, and one on the right. The spinous processes of the cervical and lumbar regions can be felt through the skin. Superior and inferior articular facets on each vertebra act to restrict the range of movement possible. These facets are joined by a thin portion of the neural arch called the *pars interarticularis*.

## Classification

The centra of the vertebra can be classified based upon the fusion of its elements. In aspidospondyly, bones such as the neural spine, the pleurocentrum and the intercentrum are separate ossifications. Fused elements however, classify a vertebra as having holospondyly.

A vertebra can also be described in terms of the shape of the ends of the centra. Humans are said to be acoelous, or with flat ends. These flat ends of the centra are especially good at supporting and distributing compressive forces. Amphicoelus vertebra is represented by both ends of the centra being concave. This shape is common.in fish, where most motion is limited. Amphicoelus centra often are integrated with a full notochord. Procoelus vertebra are anteriorly concave, and posteriorly convex. An opisthocoelus vertebra however, possess anterior convexity, and posterior concavity. Heterocoelous vertebrae are saddle shaped at each end of the centra. This type of configuration is seen in turtles that retract their necks, and birds, because it permits extensive lateral and vertical flexion motion without stretching the nerve cord too extensively or wringing it about its long axi

Each vertebra is composed of a *body* anteriorly and a neural arch posteriorly. The arch encloses an opening, the *vertebral foramen*, which helps to form a canal in which the spinal cord is housed. Protruding from the posterior extreme of each neural arch is a *spinous process* and extending from the lateral edges of each arch are *transverse processes*. These bony elements serve as important sites of attachment of deep back muscles. The neural arch of each vertebra is divided into component parts by these processes. The parts of the neural arch between the spinous and transverse processes are known as the *laminae* and the parts of the arch between the transverse processes and the body are the *pedicles.* At the point where the laminae and pedicles meet, each vertebra contains two *superior articular facets* and two *inferior articular facets.* The former pair of facets form articulations, which are synovial joints, with the two inferior articular facets of the vertebra immediately above (or the skull, in the case of the first cervical vertebra). The pedicle of each vertebra is notched at its superior and inferior edges. Together the notches from two contiguous vertebrae form an opening, the *intervertebral foramen,* through which spinal nerves pass.



(a) (b)

**Fig. 7.5 :** Vertebrae (a) Anterior view; (b) Posterior view

A **typical vertebra** consists of two essential parts—viz., an anterior segment, the **body**, and a posterior part, the vertebral or **neural arch**; these enclose a **foramen**, the **vertebral foramen**. The **vertebral arch** consists of a pair of **pedicles** and a pair of laminae, and supports seven processes—viz., four articular, two transverse, and one spinous.

When the vertebrae are articulated with each other the bodies form a strong pillar for the support of the head and trunk, and the vertebral foramina constitute a canal for the protection of the medulla spinalis (spinal cord), while between every pair of vertebrae are two apertures, the intervertebral foramina, one on either side, for the transmission of the spinal nerves and vessels.

**Body (corpus vertebrae) :** The body is the largest part of a vertebra, and is more or less cylindrical in shape. Its upper and lower surfaces are flattened and rough, and give attachment to the intervertebral fibrocartilages, and each presents a rim around its circumference. In front, the body is convex from side to side and concave from above downward. Behind, it is flat from above downward and slightly concave from side to side. Its anterior surface presents a few small apertures, for the passage of nutrient vessels; on the posterior surface is a single large, irregular aperture, or occasionally more than one, for the exit of the basi-vertebral veins from the body of the vertebra.

**Pedicles (radices arci vertebrae) :** The pedicles are two short, thick processes, which project backward, one on either side, from the upper part of the body, at the junction of its posterior and lateral surfaces. The concavities above and below the pedicles are named the vertebral notches; and when the vertebrae are articulated, the notches of each contiguous pair of bones form the intervertebral foramina, already referred to.

**Laminae** : The laminae are two broad plates directed backward and medialward from the pedicles. They fuse in the middle line posteriorly, and so complete the posterior boundary of the vertebral foramen. Their upper borders and the lower parts of their anterior surfaces are rough for the attachment of the ligamenta flava.

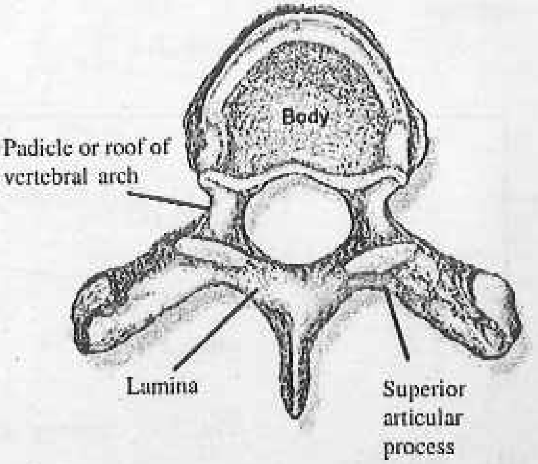


Fig. 7.6 : A tyical thoracic vertebra, viewed from above.

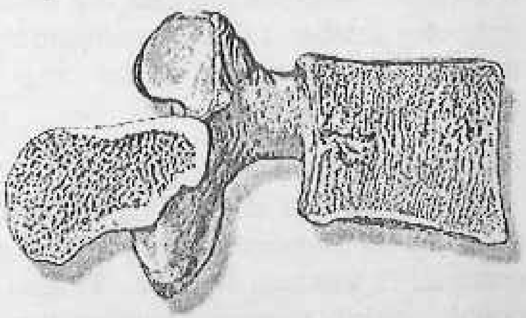


Fig. 7.7 : Sagittal section of a lumbar vertebra

## Processes

**Spinous Process (processus spinosus)** : The spinous process is directed backward and downward from the junction of the laminae, and serves for the attachment of muscles and ligaments.

**Articular Processes** : The articular processes, two superior and two inferior, spring from the junctions of the pedicles and laminae. The superior project upward, and their articular surfaces are directed more or less backward; the inferior project downward, and their surfaces look more or less forward. The articular surfaces are coated with hyaline cartilage.

**Transverse Processes (processus transversi)** : The transverse processes, two in number, project one at either side from the point where the lamina joins the pedicle, between the superior and inferior articular processes. They serve for the attachment of muscles and ligaments.

## (A) Fish

Two vertebral regions only, trunk, and caudal (tail); trunk vertebrae with ribs, neural arches and spines, caudal vertebrae with neural and hemal arches. In Agnathan (jawless) fish like Ostracoderms and Cyclostomes, the notochord is prominent with small cartilaginous vertebral elements. This condition can also be seen in the sturgeon where the cartilage has been replaced by bone. In sharks and bony fish, the notochord has been reduced to a small thread through the centrum but fills the concavities between vertebrae. Examine the **caudal** region of the bowfin, ***Amia*** and notice that there are two centra per body segment (hypo and pleuro centra). This is the **Dispondylous** or the **Diplospondylous** condition. The neural arches, in this caudal region, are borne only on alternate centra. Other fishes display the Diplospondylous condition, but duplicate the neural arches only; still others duplicate both arches and centra.

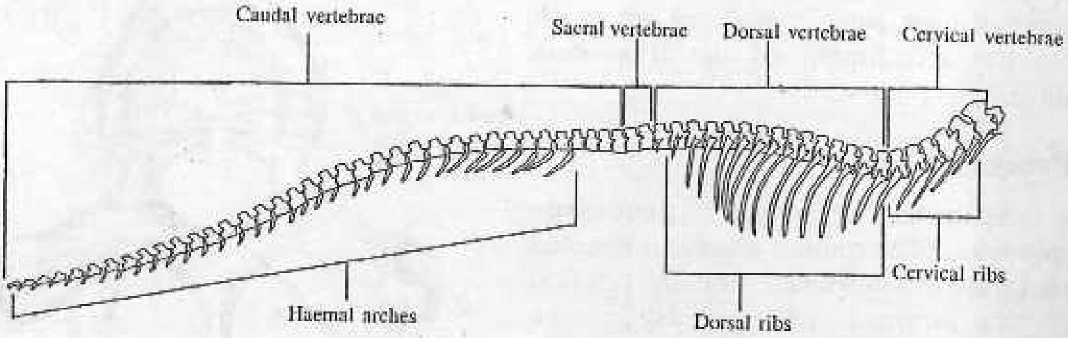


**Fig. 7.8 :** Showing different vertebrae and ribs

## (B) Amphibia

There are four vertebral regions, **cervical, trunk, sacral** and **caudal.** The Anurans (tail-less Amphibia) lack the caudal region. If we compare the frog and salamander *(Necturus)* skeletons, we find that both cervical and sacral regions each consist of only one vertebra. Likewise compare the ribs in frog and *Necturus.* They are **fused** to the vertebral column in the frogs (pleurapophyses), and are **double-headed articulating ribs** in *Necturus.*

## (C) Reptiles

There are five vertebral regions, **cervical, thoracic, lumbar, sacral** and **caudal.** Compare the vertebral columns of Alligator, Snake and Turtle. The **Alligator** has 8 cervical, 11 thoracic, 5 lumbar, 2 sacral (fused) and 40 caudal vertebrae. Moveable, double-headed, ribs are borne on the thoracic vertebrae. Ribs, if present on the lumbar vertebrae are fused. **Snakes** may have as many as 500 vertebrae. Both thoracic and lumbar regions bear ribs. The **Turtle** vertebral column has 8 cervical, 10 trunk, 2 sacral and 16 to 30 caudal vertebrae. The first caudal as well as all the sacral and trunk vertebrae are fused with dermal bone to form the carapace. The ribs are expanded and fused to the inner surface of the costal plates of the carapace. The ribs are single headed. Note that in the Reptiles the two anterior cervical vertebrae are specialized. The first cervical vertebra, the **Atlas,** is ring-like and lacks a centrum, and articulates with the occipital condyles of the skull. The second cervical vertebra, or **Axis,** has an anteriorly projecting process, the **odontoid** process, which fits into the cavity of the Atlas, acting as a pivot in turning the head.

### (D) Birds

Rigidity of the vertebral column is achieved by the fusion of many vertebrae. The cervical vertebrae number 13 to as many as 25, and have great flexibility, due to the heterocoelous centra. There are 5 thoracic vertebrae, but the last one is fused into the synsacrum, and the first four are fused together. The last thoracic, all the lumbar, the 2 sacral and several caudal vertebra all fuse to form one bone, the **Synsacrum.** This in turn is fused to the pelvic girdle. There are several free caudal vertebrae then the tail ends in an enlarged **Pygostyle,** which represents several fused vertebrae. The ribs bear posteriorly projecting **Uncinate** processes, each being ankylosed to the next posterior rib, the distal region of the ribs are joined to the sternum via sternal processes.

### (E) Mammals

There are five vertebral regions - cervical, thoracic, lumbar, sacral and caudal. In the cat there are 7 cervical, 13 thoracic, 7 lumbar, 3 sacral and 4 to 26 caudal vertebrae. Only the thoracic vertebrae bear ribs. The ribs are double headed. The three sacral vertebrae fuse to form one bone, the **sacrum,** with which the pelvic girdle articulates. Between the vertebrae are intervertebral cartilages (disks), which are composed of fibers and notochord remnants.

## 7.4 Limbs and girdles

The pectoral and pelvic girdles and the skeleton of fins and limbs constitute the appendicular skeleton. Girdles brace fins and limbs against the counterforces that appendages transmit from the water or from a substrate. The girdles, in turn, are braced against one or more components of the axial skeleton, thereby achieving stability. The forces transmitted to the girdles from the appendages are generally greatest in terrestrial amniotes because their limbs elevate the body above the ground.

The limb girdles form the foundation for the movement for the limbs. The pectoral girdle is connected to the forelimbs (e.g. our scapula and clavicle). The pelvic girdle attaches to the hind limbs (e.g. our pelvis). Together with our limbs the girdles form the appendicular skeleton.

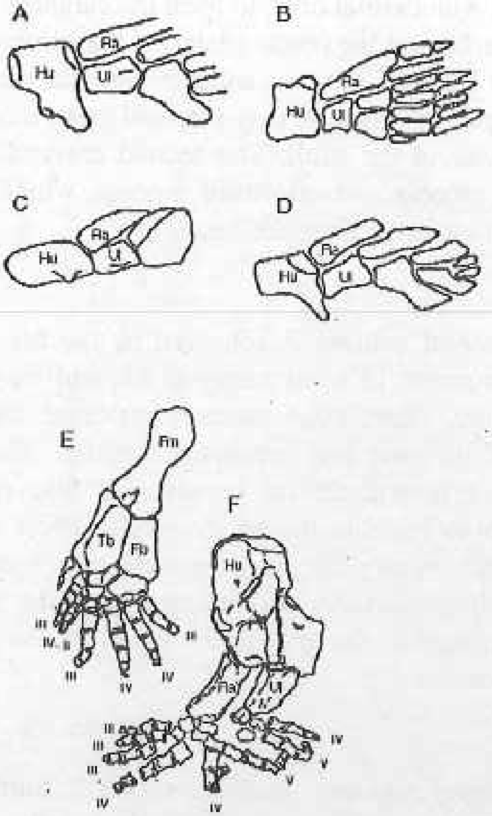


**Fig. 7.8 :** Comparison of paired anterior fins of lobe finned fishes (A-D) and limbs of early tetrapods (E, F) A. Sterropterygion, B. Sauripterus, C. Panderichthys, D. Eusthenopteron, E. Ichthyostega, F. Acanthostega. Fm, femur; Fb, fibula; Hu, humerus; Ra, radius; Tb, tibia, Ul, ulna

### 7.4.1 Pectoral girdle and fore limb

The pectoral girdle is a skeletal complex in the body wall immediately behind the head that articulates with the anterior fins or limbs. A pectoral girdle consisted of three pairs of replacement bones that were part of the endoskeleton, and at least four pairs of investing bones were derived from dermal armor.

Each of the two pectoral (shoulder) girdles consists of two bones: the S-shaped clavicle and the flat, triangular scapula. The clavicle articulates with the sternum and the scapula. In turn, the scapula articulates with the humerus of the arm. The upper limb, which consists of the arm, forearm, and hand, is made up of 30 bones.

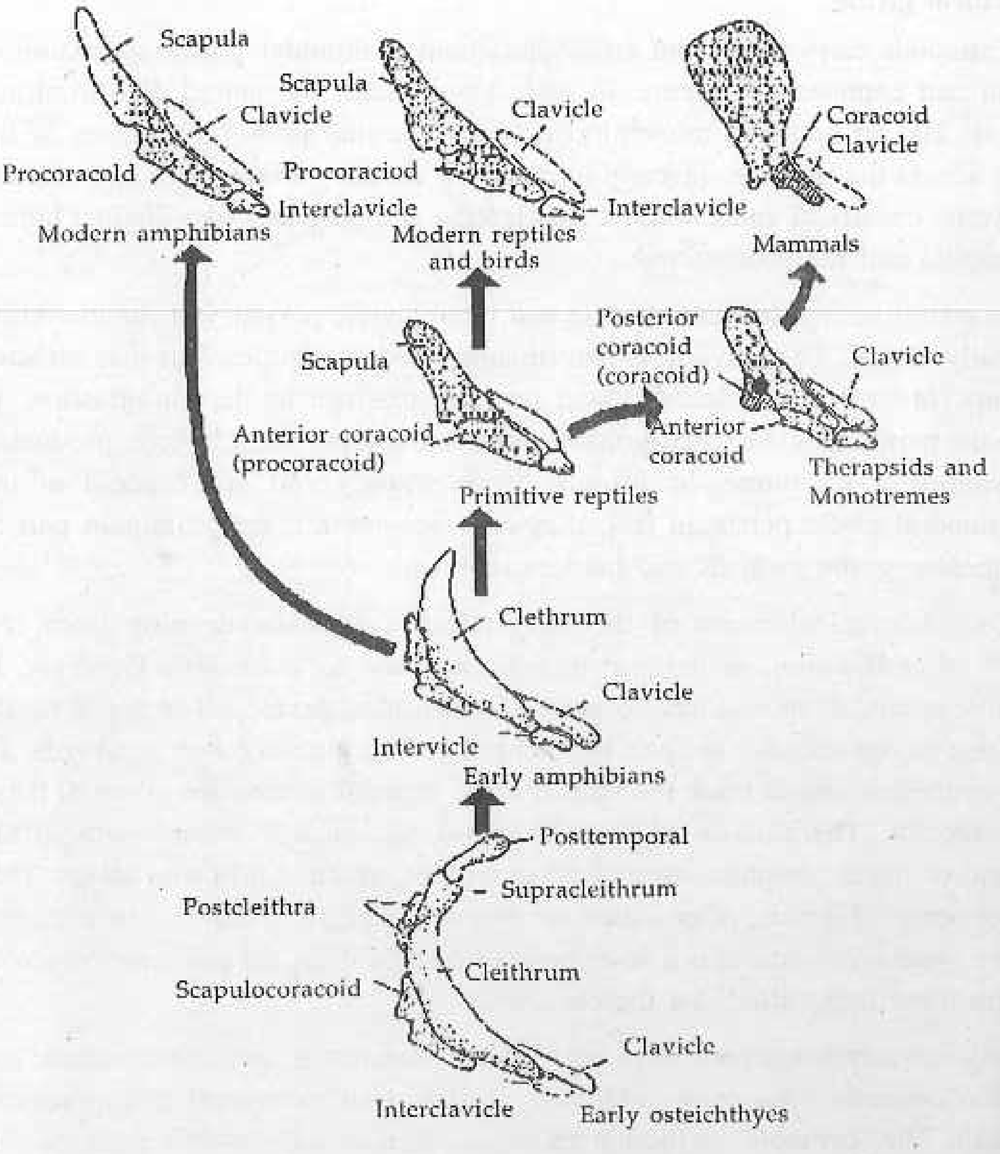


**Fig. 7.10 :** Summary of pectoral girdle evolution. The dermal elements (no shading) of the girdle tend to be lost and endochondral elements (shaded) tend to assume a greater role. In primitive therapsids, a third endochondral bone appears—the posterior coracoid, to join with the phylogenetically older scapula and anterior coracoid bones. The three persist in the primitive mammals. In marsupials and placental mammals, only the scapula and posterior coracoid (called just coracoid) persist. In modern reptiles and birds, the scapula and anterior coracoid (or procoracoid) persist.

## I. Pectoral girdle

Tetrapods carry over from crossopterygians a shoulder girdle consisting of dermal and endoskeletal events. In early amphibians, the paired cleithrum and clavicle, and an unpaired midventral interclavicle that joins both halves of the girdle across the midline. In early tetrapods it actually arises from two distinct embryonic centers of endochondral ossification and produces two distinct bones, the scapula and the procoracoid.

In primitive reptiles, the clavicle and interclavicle persist, but the cleithrum is usually absent. The clavicle is lost in some modern reptiles, but it is retained in many. In turtles it is incorporated into the plastron as the entoplastron. In birds, the paired clavicle usually fuses with the unpaired interclavicle, producing the composite wishbone, or furcula. Both scapula and procoracoid of the endochondral girdle persist.in fact, they now become a more prominent part of the shoulder girdle in birds and modern reptiles.

Endochondral elements of the early tetrapod shoulder develop from two centers of ossification, giving rise to a scapula and a "coracoid". However, in primitive synapsid reptiles, three centers of ossification develop. The dorsal center gives rise to the scapula, and the two ventral centers produce two coracoids. To avoid confusion and to track the fate of each, separate names are given to these two coracoids. The anterior of these synapsid coracoids is homologous to the coracoid of fishes, amphibians, and other reptiles we have followed so far. This anterior coracoid is more often called the procoracoid (precoracoid). The posterior of these synapsid coracoids is a new center of osscification, the posterior coracoid; or more often it is called just the coracoid.

Both coracoids are present in pelycosaurs, therapsids, and monotremes, but only the coracoid (posterior coracoid) persists into marsupial and placental mammals. The "coracoid" in therian mammals, then, is really a different coracoid from that found in other amniotes. Thus the coracoid element in birds, reptiles, amphibians, and fishes (where applicable) should be called procoracoid. The term coracoid should be reserved for the new coracoid element in synapsids and therian mammals.

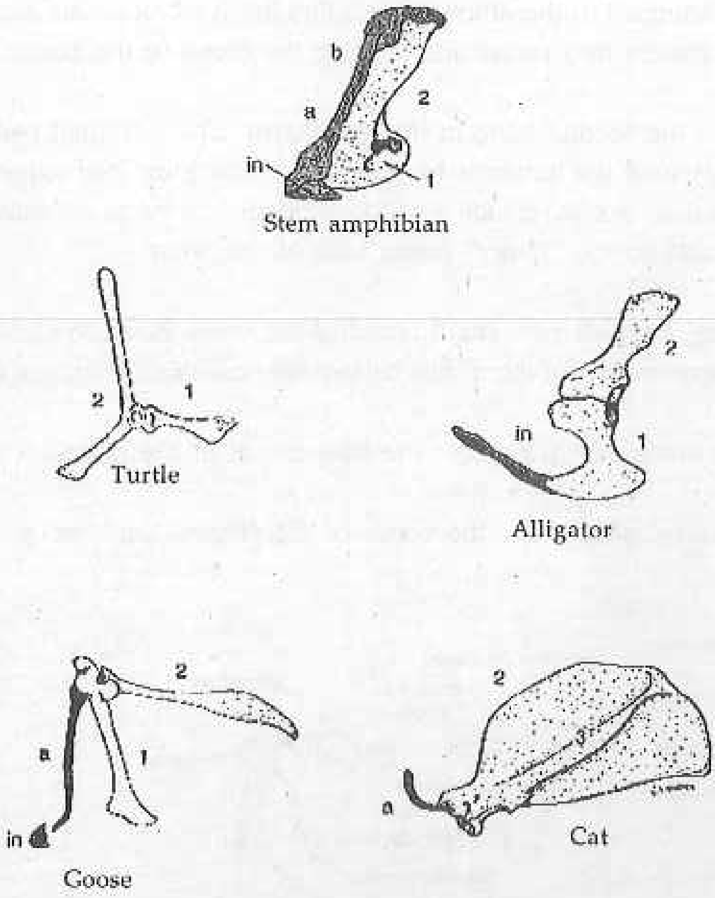


**Fig. 7.11 :** Left half of the pelvic girdles of some tetrapods, lateral views. Dermal bone are *black*. 1. coracoid or procoracoid; 2. scapula; 3. scapular spine; a. clavicle; b. cleithrum; in. interclavicle. In turtles the clavicle and interclavicle are fused with the shell. The cat's clavicle is almost vestigial.

## II. Fore Limb

Although they can be highly modified to perform different tasks and functions, the bones of the forelimb remain remarkably consistent in number and arrangement.

***Humerus (pl. humeri)*** : the single, large bone of the upper arm. It articulates with the glenoid fossa to make the shoulder joint.

***Radius (pl. radii)*** : one of the two bones of the lower arm. The distal (far) end of the radius always articulates on the thumb side of the wrist. In tetrapods that can flip the hand over (such as humans and other primates), the proximal (near) end of the radius is loosely attached to the elbow joint, allowing it to rotate on its axis. The far end of the bone travels in a radial arc, lending the name to the bone.

***Ulna (pl. ulnae)*** : the second bone in the lower arm. The proximal end of the ulna articulates strongly with the humerus to make the elbow joint (the radius also makes up the elbow, but does not have such a solid connection in some animals). The distal end always connects to the "pinky" finger side of the wrist.

**Carpals (sing. carpal)** : the small bones of the wrist. Each one has a name, but you are not responsible for them. Just collectively call these elements the "carpals".

***Metacarpals (sing. metacarpal)*** : the long bones of the palm of the hand.

***Phalanges (sing. phalanx)*** : the bones of the fingers (and toes).

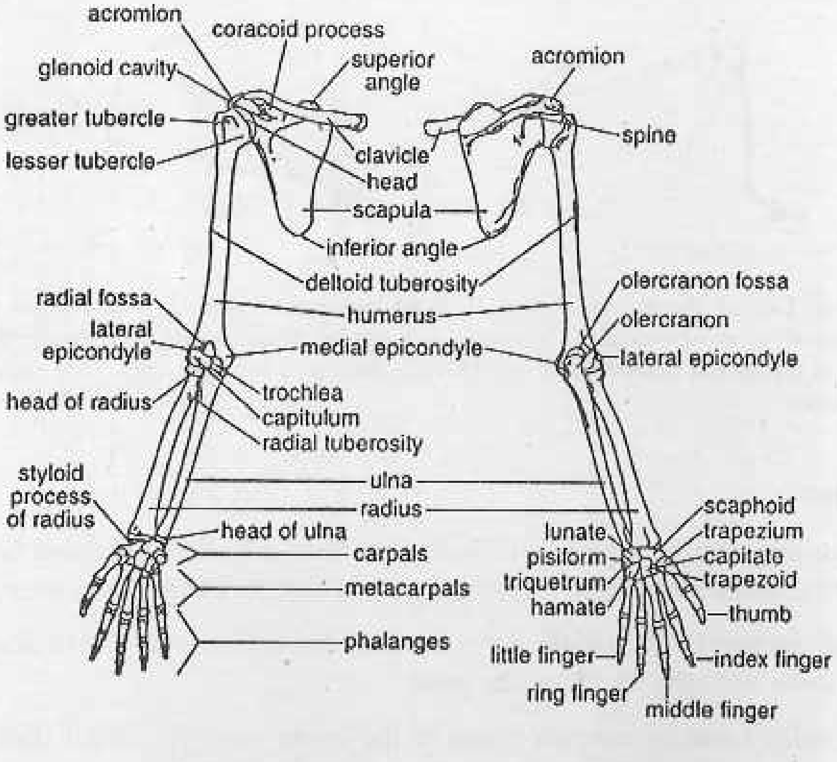


**Fig. 7.12 :** The pectoral girdle and the fore limb

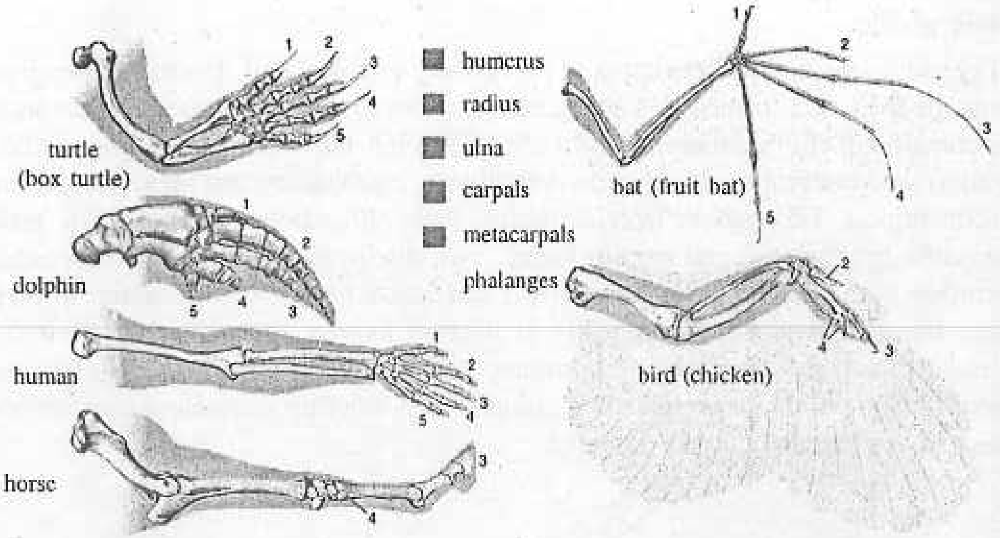


**Fig. 7.13 :** Homologies of the forelimb among vertebrates, giving evidence for evolution. The bones correspond, although they are adapted to the specific mode of life of the animal.

## 7.4.2 Pelvic girdle and hind Limb

Pelvic girdles in most fishes consist of a pair of simple cartilaginous or bony pelvic (ischiopubic) plates that meet in midventral pelvic symphysis and provide a brace for the pelvic fins. Tetrapod embryos also develop cartilaginous pelvic plates. Each plate ossifies at two centers to form a pubis (pubic bone) and a more posterior ischium.

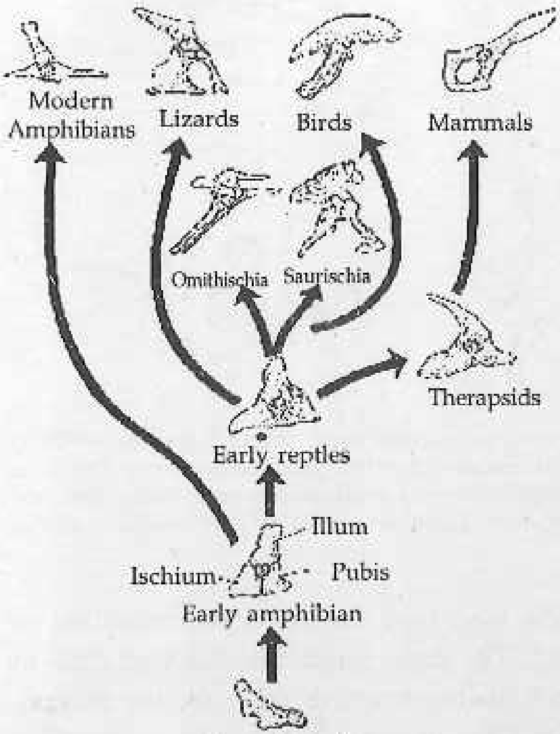


**Fig. 7.14 :** Summary of pelvic girdle evolution. Three endochondral elements – ilium, ischium and pubis – characterize the pelvic girdle in early tetrapods. This basic pattern persists into later tetrapods.

## I. Pelvic girdle

The pelvic girdle in placoderms is exclusively endoskeletal. In crossopterygians, as in most fishes, it is formed of a single element, but in tetrapods, three endochondral bones contribute: ilium, ischium, and pubis. Through the ilium, the pelvic girdle is attached to the vertebral column first in amphibians, establishing and therefore defining the sacral region. Throughout later amniotes, these three bones of the pelvic girdle persist, although their general pattern varies. Two distinctive patterns, the saurischian and ornithischian pelvic girdles, define two respective groups of dinosaurs. In birds, all three bones appear embryologically as distinct centers of ossification, but then they fuse to form the composite innominate bone, usually with no trace of sutures between the composite innominate and composite synsacrum introduces considerable firmness in the posterior avian skeleton.

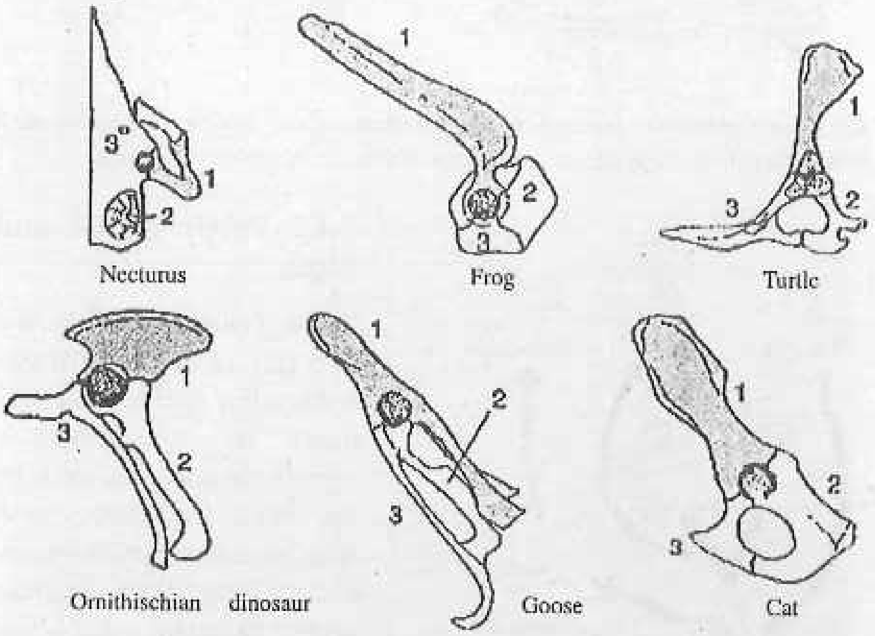


**Fig. 7.15 :** Left halves of pelvic girdles of some tetrapods, lateral view, except *Necturus*, which is ventral view. 1. ilium (shaded); 2. ischium ; 3. pubis (unossified pelvic plate in *Necturus*). *Stipple* is acetabulum. In *Necturus* the ischium is an ossification centre in a cartilaginous ischiopubic plate and a sacral rib is seen attached to the dorsal end of the ilium. There are no dermal bone in pelvic girdle.

## II. Hind limb

As with the forelimb, the bones of the hind limb can be highly modified to perform a wide range of tasks and functions. The main purpose of the hind limb in most terrestrial vertebrates is to provide the main propulsive force for the animal. Obviously this is not the case with vertebrates that have greatly reduced or lost their limbs.

***Femur (pl. femora)*** : the thighbone. It articulates with the acetabulum.

***Tibia (pl. tibiae)*** : the shinbone. The tibia is the larger of the two bones in the lower leg, and forms the medial (inner) side of the ankle joint.

***Fibula (pl. fibulae)*** : the smaller, lateral (outside) bone in the lower leg.

***Tarsals (sing. tarsal)*** : These are the small, individually named bones that make up the ankle joint. They are collectively called as "tarsals".

***Metatarsals (sing. metatarsal)*** : the long bones of the sole of the foot.

***Phalanges (sing. phalanx)*** : the bones of the toes (and fingers).

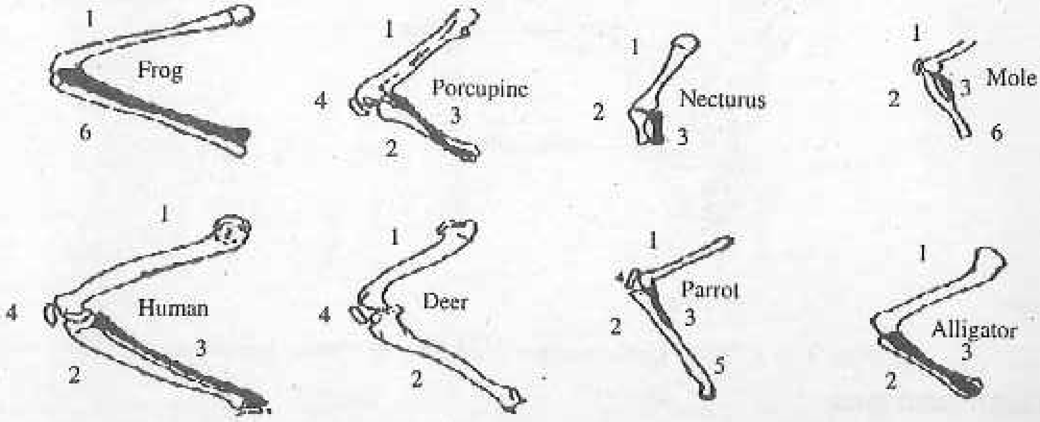


**Fig. 7.16 :** Left thigh and shank bones of representatives of tetrapods, lateral views. 1, femur; 2, tibia; 3, fibula; 4, patella; 5, tibiotarsus; 6, tibiofibula, fibular component in black.

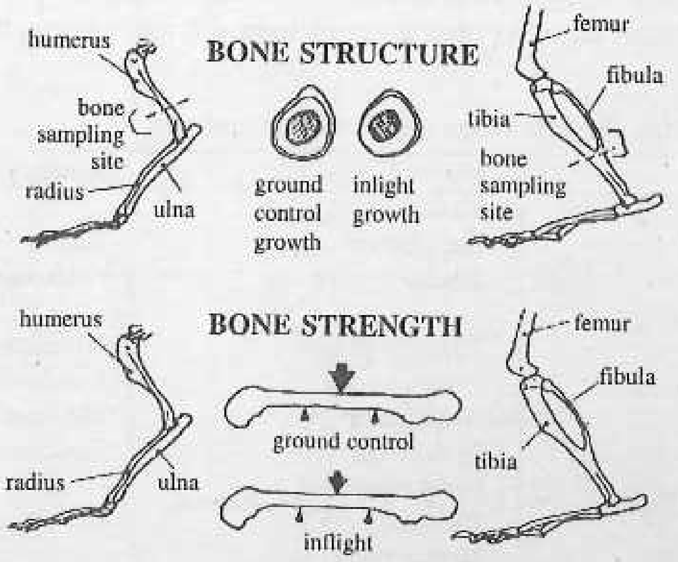


**Fig. 7.17 :** During space flight, changes in structure and strength have been noted in both the fore limbs and hind limbs

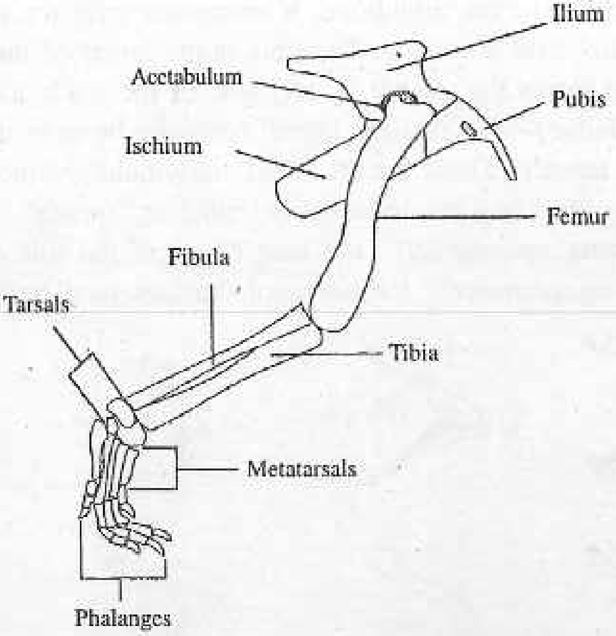


**Fig. 7.18 :** Pelvic girdle and the hind limb of typical vertebrate.

## Manus and pes

Bones elongate postnatally by endochondral ossification as cells of the cartilaginous growth plate undergo a differentiation cascade of proliferation, cellular hypertrophy and matrix synthesis. Interspecific comparisons of homologous bones elongating at different rates has been a useful approach for studying the dynamics of this process.

**Table :** Comparable skeletal elements of manus and pes

| **Manus** | **Pes** | **Synonyms in humans** |
|---|---|---|
| Radiate | Tibiale | |
| Intermedium | Intermedium | Talus or astragalus* |
| Ulnare | Fibulae | Calcaneus |
| Pisiform (sesamoid) | | |
| Centralia (0 to 4) | Centralia (0 to 4) | Navicular |
| Distal carpal 1 | Distal carpal 1 | Entocuneiform |
| Distal carpal 2 | Distal carpal 2 | Mesocuneiform |
| Distal carpal 3 | Distal carpal 3 | Ectocuneiform |
| Distal carpal 4 } Hamate | Distal carpal 4 } Hamate | Cuboid |
| Distal carpal 5 | Distal carpal 5 | |
| Metacarpals (1 to 5) | Metacarpals (1 to 5) | |
| Digits (I to V) | Digits (I to V) | |

* incorporates the intermedium and a centrale.

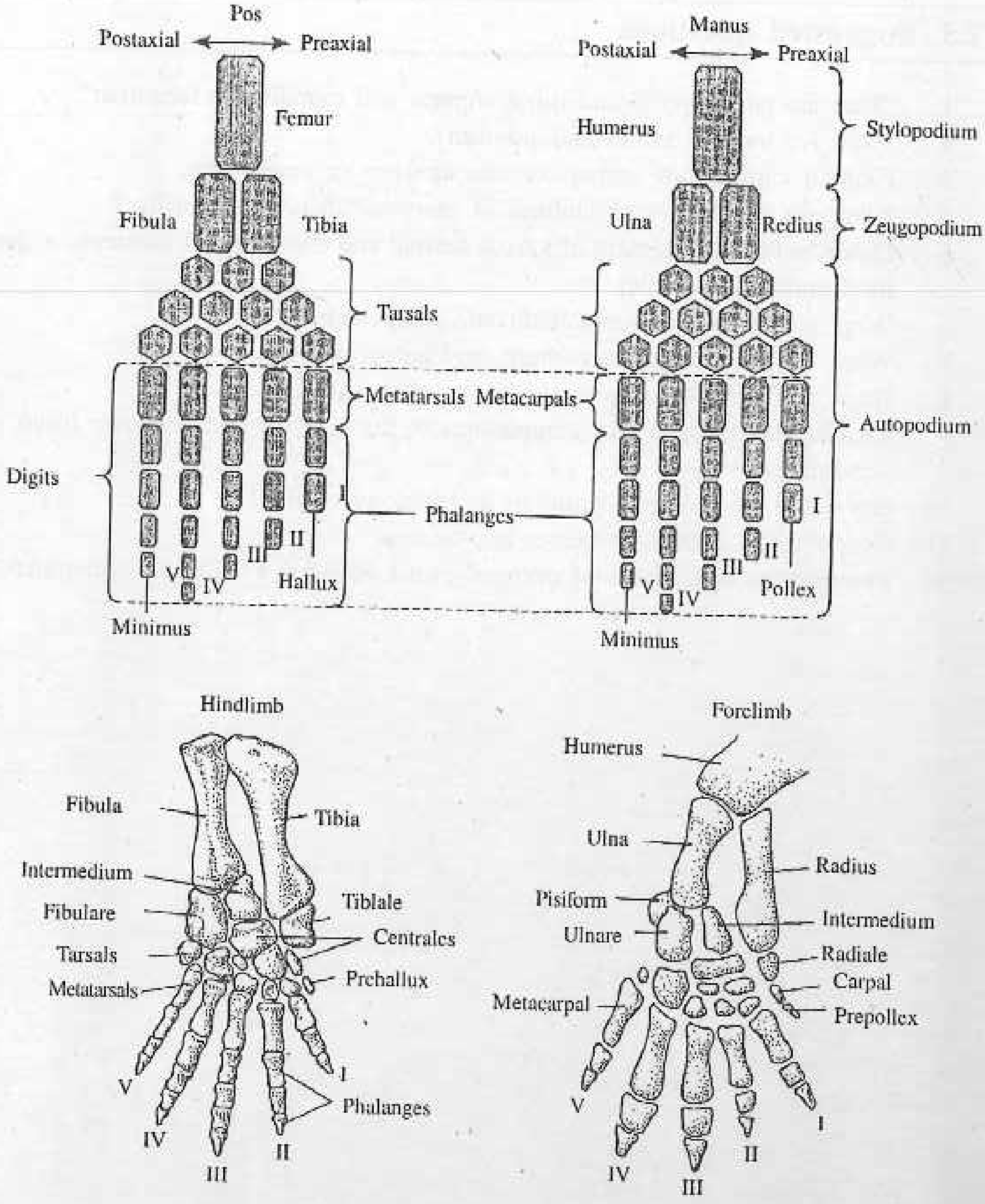


**Fig. 7.19 :** Basic organization of fore- and hind limbs. (a) Manus and pes have five digits; each digit includes its metacarpal or metatarsal and chain of phalanges. These digits in turn articulate with various wtist and ankle bones. (b) Fore- and hind limbs of primitive tetrapods.

## 7.5 Suggested questions

1. What are postemporal and infratemporal and mandibualr fenestrae?
2. What are haemal arches and sternum?
3. Explain various jaw suspension mechanisms in vertebrates.
4. What are characteristics features of mammalian jaw suspension?
5. Describe the involvement of versus dermal and endoskeletal elements in pectoral and pelvic girdles.
6. What are cleithrum, supracleithrum, and postcleithra?
7. What are propodium, epipodium, and autopodium?
8. Draw and describe a cervical vertebra of mammal.
9. Tabulate the homologous components of the anterior and posterior limbs of vertebrates.
10. Draw and label dermatocranium morphology of skull.
11. Describe the various processes of vertebra.
12. Mention the differences of pectoral girdle between a bird and a mammal.

# Unit 8 □ Evolution of urinogenital system in vertebrate series

## Structure

## 8.1 Introduction

In anatomy, the **genitourinary system** or **urogenital system** is the organ system of the reproductive organs and the urinary system. These are grouped together because of their proximity to each other, their common embryological origin and the use of common pathways, like the male urethra.

The urinary and reproductive organs are developed from the intermediate mesoderm. The permanent organs of the adult are preceded by a set of structures which are purely embryonic, and which with the exception of the ducts disappear almost entirely before the end of fetal life. These embryonic structures are on either side; the pronephros, the mesonephros and the metanephros of the kidney, and the Wolffian and Müllerian ducts of the sex organ. The pronephros disappears very early; the structural elements of the mesonephros mostly degenerate, but the gonad is developed in their place, with which the Wolffian duct remains as the duct in males, and the Müllerian as that of the female. Some of the tubules of the mesonephros form part of the permanent kidney.

## 8.2 Basic pattern of the archinephros

Vertebrate kidneys are built in accordance with a basic architectural pattern consisting of glomeruli, renal tubules, and a pair of longitudinal excretory ducts. Variations in details from fishes to humans are principally in the number and arrangement of glomeruli and in the relative complexity of the tubules.

The most primitive glomeruli are suspended in the coelom surrounded by peritoneum. They discharge their filtrate into the coelomic fluid, which is then swept into a peritoneal funnel, or nephrostome, leading to a tubule. These are external glomeruli. In todays vertebrates, external glomeruli are confined to embros and larvae. Glomeruli in adults are embedded within the dorsal body wall (hence said to be retroperitoneal) and are ensheathed by Bowman's capsule,a delicate double walled outgrowth from a kedney tubule. Its inner wall adheres to the surfaces of the vascular loops. The capsular cavity collects the glomerular filtrate,which then passes into a renal tubule. These are internal glomeruli. A glomerulus and the surrounding capsule constitute a renal corpuscle. A renal tubule, and the associated peritubular capillaries constitute a nephron, the functional unt of a gnathostome kidney.

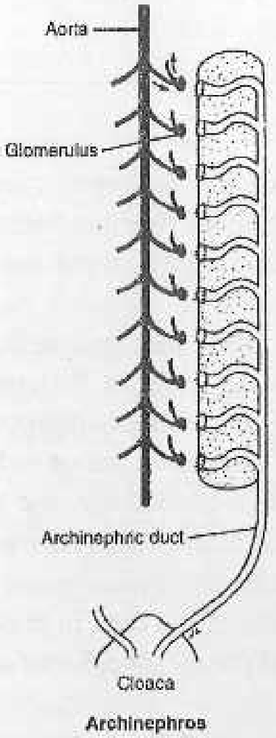


**Fig. 8.1 :** Hypothetical archinephros with one external glomerulus, nephrostome and tubule per body segment

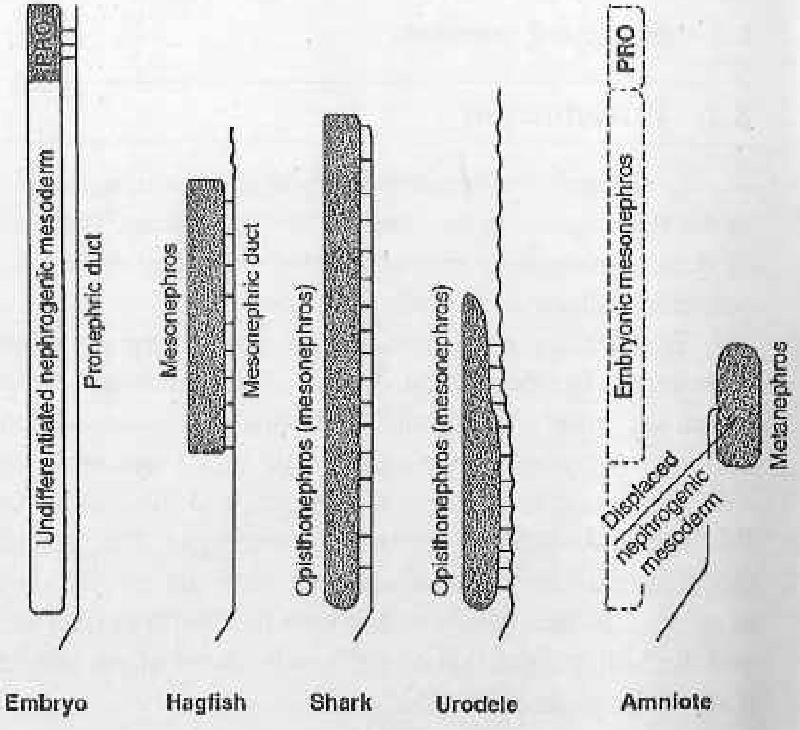


**Fig. 8.2 :** Fate of the nephrogenic mesoderm (shaded) in representative vertebrates. The pronephric duct persists in adult anamniots to drain the adult kidney.

Several of the most anterior kidney tubules of some adult fishes and many tetrapod embryos and larvae have nephrostomes and vestigial nephrostomes lacking a lumen are often found in avian and mammalian embryos. Nephrostomes may be vestiges of the kidneys of a postulated ancestral protochordate in which there may have been one external glomerulus, one nephrostome, and one unconvoluted tubule in each body segment along the entire length of the coelom. This hypothetical ancestral kidney has been termed an archinephros. The nearest approach to such a kidney in living vertebrates is seen in larval hagfishes, in which a transient series of segmental external glomeruli, nephrostomes, and tubules is formed throughout much of the extent of the nephrogenic mesoderm. However, at this stage of body elongation the kidney is still elongated. Segmental tubules with closed nephrostomes and renal corpuscles develop farther caudad. This transient larval hagfish kidney has been termed a holonephros. The adult hagfish kidney is a mesonephros.

### 8.2.1 Pronephros

It is the most basic of the three excretory organs that develop in vertebrates, corresponding to the first stage of kidney development. It is succeeded by the mesonephros, which in fish and amphibians remains as the adult kidney. In amniotes the mesonephros is the embryonic kidney and a more complex metanephros acts as the adult kidney. Once a more advanced kidney forms, the previous version typically degenerates by apoptosis or becomes part of the male reproductive system.

The pronephros develops from the intermediate mesoderm, as do the later kidneys. It is a paired organ, consisting of a single giant nephron that processes blood filtrate produced from glomeruli or glomera- large embryonic glomeruli. The filtrate is deposited into the coelom. It then passes through thin ciliated tubules into the pronephric nephron where it is processed for solute recovery.

The organ is active in adult forms of some primitive fish, like lampreys or hagfish. It is present at the embryo of more advanced fish and at the larval stage of amphibians where it plays an essential role in osmoregulation. In human beings, it is rudimentary, appears at the end of the third week (day 20) and replaced by mesonephros after 3.5 weeks. Despite this transient appearance in mammals, the pronephros is essential for the development of the adult kidneys. The duct of the pronephros forms the Wolffian duct and ureter of the adult kidney. The embryonic kidney and its derivatives also produce the inductive signals that trigger formation of the adult kidney.

### 8.2.2 Mesonephros

The **mesonephros** (Greek for "middle kidney") is one of three excretory organs that develop in vertebrates. It serves as the main excretory organ of aquatic vertebrates and as a temporary kidney in higher vertebrates. The mesonephros is included in the **Wolffian body** named after Caspar Friedrich Wolff who described it in 1759. (The Wolffian body is composed of : mesonephros + paramesonephrotic blastema).

The mesonephros is composed of the mesonephric duct (also called the Wolffian duct), mesonephric tubules, and associated capillary tufts. A single tubule and its associated capillary tuft is called a *mesonephric excretory unit*; these units are similar in structure and function to nephrons of the adult kidney. The mesonephros is derived from intermediate mesoderm in the vertebrate embryo.

### 8.2.3 Metanephros

The metanephros, the adult kidney of amniotes, organizes from the caudal end of the nephrogenic mesoderm, which becomes dosplaced cephalad and laterad during development. This is the same mesoderm that gives rise to the caudalmost part of the adult kedney of fishes and amphibians; differentiation of the metabephric kidney commences when a hollow metanephric bud sprouts from the caudal end of the mesonephric duct. Surrounding the dud is nephrogenic mesoderm. The bud grows cephalad, carrying the metanephric blastema along with it. Eventually, the basic components of a metanephric kidney organize in the displaced nephrogenic mesoderm, which continues to enlarge. The hollow stalk connecting the metabephros with the embryonic mesonephric duct becomes the ureter, and the end of the stalk surrounded by the developing blastema geves rise to the urinary channels witin the kidney up to and including the common cpollecting tubules. Meanwhile s-shaped renal tubules are organizintg within the bloastema. One end of each renal tubule grows toward and acquires and opening into, a common collecting tubule. Failure to establish this connection may result in a fluid filled renal cyst. In mammalian kidneys, a renal pelves with funnel shaped extensions(calyces) collects urine from the common collecting tubules.

The third and final excretory organ develops in a vertebrate embryo. In birds, reptiles, and mammals it replaces the mesonephros as the functional excretory organ and develops into the adult kidney.

The **metanephros** develops from **three intermediate mesoderm structures** of the sacral region:

- Ureter anlage
- Metanephric vesicle
- Glomerular capillary network

## 8.3 Testes and male genital ducts

Vertebrate testes are essentially the same with few exceptions. Germinal epithelium lines the seminiferous tubules where sperm are formed. Mature sperm are microscopic and abundant. They separate from the lining of the tubules and, propelled by flagellum-like, tails, swim the length of the tubule to reach the vasa efferentia, which leads to the sperm duct. In mammals, sperm are first collected in a network of fine channels, the rete testis, before entering the vasa efferentia. Vasa efferentia are mesonephric tubules that invade the developing testis instead of becoming associated with glomeruli. The vasa efferentia (usually called efferent ductules in mammals) conduct sperm to the spermatic duct. Efferent ductules number a dozen, more or less, in humans. In most vertebrates with mesonephric kidneys the mesonephric ducts carry both urine and sperm.

In some fishes and urodeles, there has been a tendency to form a new sperm duct to replace the mesomephric duct as a carrier of sperm. In teleosts this has culminated in a mesonephric duct that carries no sperm whatsoever. In all other fishes and amphibians, and from reptiles to humans, the embryonic mesonephric duct remains in sdult males to carry sperm. A duct that carries only sperm is termed a vas deferens (ductus deferens)

Spermatic ducts generally empty into the cloaca or a derivative thereof in vertebreates below placental mammals. In placental mammals, they empty into the urethra at the prostate gland. This development is a result of the complete separation of the embryonic cloaca into urinogenital sunus and, rectum.

As a result of caudal migration of the testes in mammals during late fetal life, the spermatic ducts become "hung up" on the ureters, so that therafter they loop over the latter en route to the urethra.

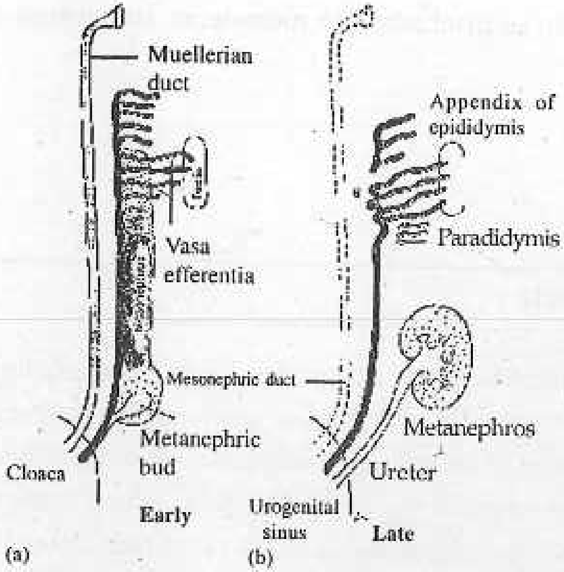


**Fig. 8.3 :** Developmental changes in the urogenital system of male mammals. In the early bisexual stage there is a rudimentary female duct (Mullerian duct) and a mesonephros. Some of the mesonephric tubules had invaded the genital ridge (testis) to become vas efferentia. Later (right), the Mullerian duct has regressed (broken lines), the mesonephros has regressed except for remnants (appendix of epididymis, paradidymis), and the mesonephric duct remains to carry sperm. e, epididymal portion of mesonephric duct.

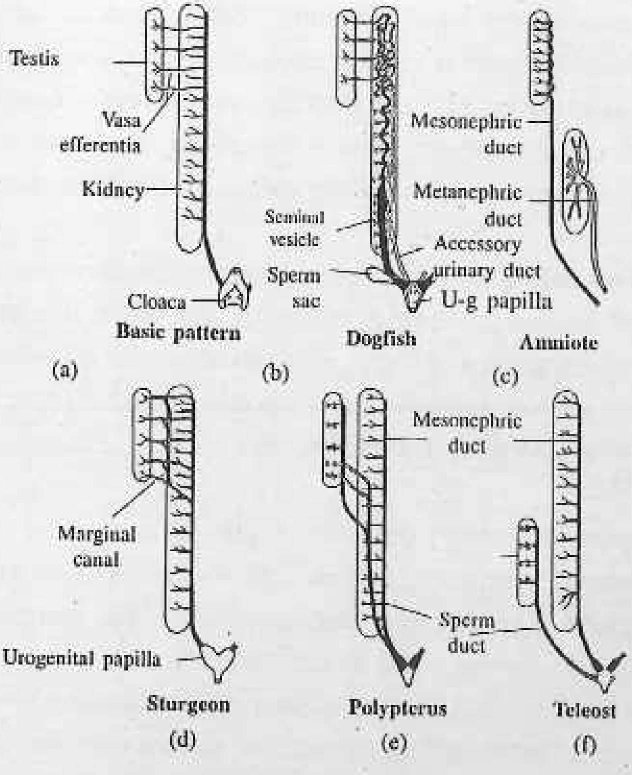


**Fig. 8.4 :** The mesonephric duct (black) as a carrier of sperm and urine. (a) carrying both sperm and urine. (b) carrying urine from the anterior part of the kidney only; chiefly a spermatic duct. (c) carrying sperm only. (d) to (f) trend toward a separate sperm duct. In fishes, the mesonephric duct ultimately carrying only urine. The reverse is found in amniotes (c).

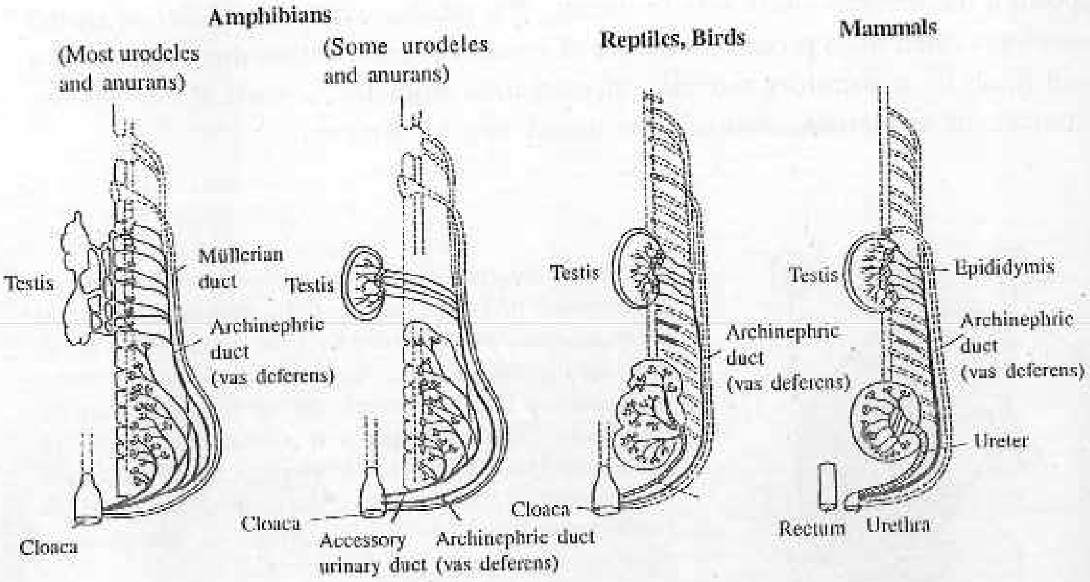


Fig. 8.5 : Urogenital ducts of tetrapod males

## 8.4. Ovary and female genital ducts

**Fish :** in female bony fishes, like most other anamniote females, the archinephric ducts serve the kidneys and the paired oviducts (müllerian ducts) serve the paired ovaries. In some teleosts, such as salmonids, eggs released from the ovaries fill the body cavity. Eventually they reach short funnel like remnants of the oviducts situated at the posterior part of the coelom. However, in many teleosts, the oviducts regress entirely, leaving egg transport to new ovarian ducts. These ovarian ducts are not homologous to the oviducts (müllerian ducts) of other vertebrates. Instead, they are derived from peritoneal folds that embrace each ovary and have grown posteriorly to form new ducts.

**Tetrapod :** Amphibian ovaries are paired, hollow structures that usually show a prominent cortex covered by germinal epthelium. The genital ducts of female amphibians are usually sinple and consistent. The archinephric ducts serve the opisthonephric kidneys, the oviducts (müllerian ducts) serve the ovaries.

In amniotes, remnants of the mesonephros may persist in larval stages, but adults have metanephric kidneys drained exclusively by new paired ducts, the ureters (metanephric ducts). In females, the archinephric ducts are rudimentary. The oviducts (müllerian ducts) persist in their roles of transporting ova from the ovaries and supporting the embryo while it is in transit. The tubular oviducts (müllerian ducts) of amniotes often have prominent sheets of smooth muscle within their walls and a lumen lined by a secretory mucosa. In oviparous amniotes, a shell gland may be prominent; in viviparous amniotes, the uterus may be distinct.

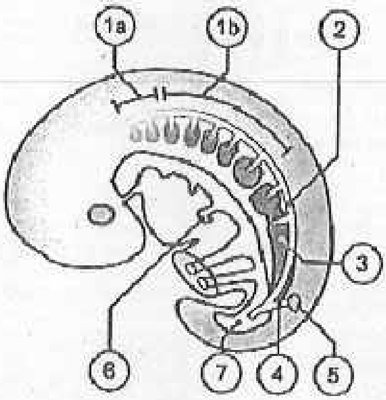
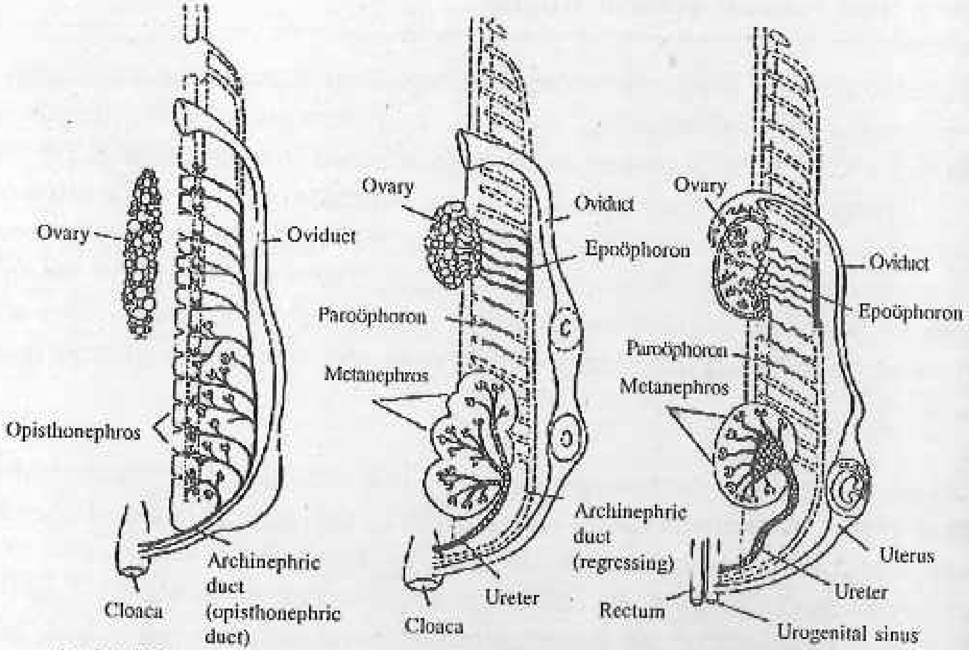


**Fig. 8.6 :** Sagittal section of a 5-week-old embryo - development of the metanephros. In the caudal region of the nephrogenic cord one observes the development of the metanephrogenic blastema that is in contact with the ureter anlage. In this stage the pronephros has disappeared almost completely. The mesonephros is also in the process of atrophying. (**1a.** Pronephros (atrophying), **1b.** Mesonephros (atrophying), **2.** Mesonephric duct (Wolffian duct), **3.** Nephrogenic cord, **4**  Ureter anlage, **5.** Metanephric blastema, **6.**  Liver anlage, **7.** Cloaca)



(a) Amphibians (b) Reptiles, Birds (c) Mammals

**Fig. 8.7 :** Urogenital anatomy of tetrapod females

The ureter anlage is an epithelial diverticulum from the caudal part of the mesonephric duct (Wolffian duct) in the area of the first sacral vertebra (S1). The anlage intrudes into the metanephric vesicle and forms the extra- and intrarenal excretory passages.The metanephric blastema corresponds to the sacral part of the nephrogenic cord below L3. It is mesenchymal tissue out of which the metanephric vesicles arise. From these originate the nephrons (= functional units of the kidneys). At present it is still not clear whether the glomerular capillary network develops through vasculogenesis (direct development of vessels from the metanephric vesicles) or through angiogenesis (development from existing vessels of the metanephros).

## 8.5 Kidney phylogeny

**Fishes:** The most primitive vertebrate kidneys are found among cyclostomes. In the hagfish *Bdellostoma*, pronephric tubules arise in the anterior (cranial) part of the nephric ridge during embryonic development. These tubules unite successively with one another, forming the urinary or pronephric duct. Anterior tubules lack glomeruli but open to the coelom via peritoneal funnels, whereas posterior tubules are associated with glomeruli but lack connection to the coelom. In the adult, anterior aglomerular tubules together with several persisting posterior glomerular tubules become the compact pronephros. Although the adult pronephros may contribute to formation of coelomic fluid, the mesonephros is considered to be the functional adult kidney in hagfishes. Each paired mesonephros consists of 30 to 35 large glomerular tubles arranged segmentally along the excretory duct(pronephric duct) and connected to it by short tubules.

In larval fishes, the pronephros usually develops and may for a time become functional, but it is usually supplemented by a mesonephros. In few teleost species, the pronephros persists as the fucttional adult kidney; however, in most fishes, the pronephros degenerates and tubules are added caudal to the mesonephros to for a functional opisthonephric kidney in the adult.

**Tetrapod:** Among amphibians having active, free living larvae, a pronephros may develop and become functional for a time. One or two pronephric tubules may contribute to the adult kidney as well. In caecilians, as many as a dozen pronephric tubules have been reported in the adult kidney. However, the early embryonic pronephros is usually succeeded by the larval mesonephros, which upon metamorphosis is replaced by an opisthonephros in most amphibians. Nephrons within the opisthonephros tend to differentiate into proximal and distal regions before joining the urinary ducts. In amphibians, as in many sharks and teleosts with opsthonephric kiidneys, the anterior kedney tubules transport sperm, illustrating again the dual use of ducts that serve both genital and urinary systems.

In amniotes, the anterior end of the nephric ridge rarely produces pronephric tubules. When present, these are few in number and without excretory function. The predominant embryonic kidney is a mesonephros, but in all amniotes, it is supplemented in late development and completely replaced in the adult by the metanephros drained by a new urinary duct, the ureter. Metanephric tubules tend to be long with well differentiated proximal, intermediate, and distal regions. In mammals, in particular, the intermediate section of the tubules is especially elongated, constituting the major patt of the loop of Henle. This term refers to both a positional and structural feature of the nephron. Positionally, the loop includes the part of the nephron that departs from the cortex and dips into the medulla(the descending limb), makes a sharp turn, and returns to the cortex (the ascending limb). Structurally, three regions contribute: the straight portion of the distal tubule. Notice that the terms descending and ascending limbs refer to the loop that are departing or entering the cortex, respectively. The terms thick and thin refer to the height of the epithelial cells forming the loop. Cuboidal cells are thick, and squamous cells are thin.

In few species of birds, the kidneys contain some nephrons with short, distinct loop segments. Although analogous to the loops of Henle in mammals, these short avian loops evolved independently. These avian kidneys exhibit a modest ability to produce concentrated urine. Their product is about 2 to 4 times more concentrated than their blood. However, the nephrons of most birds do not have loops. In the absence of a loop, the avian nephron is similar to the nephron of reptiles.

## 8.6 Suggested questions

1. Explain pronephros organisation of kidney and its evolutionary significance.
2. Explain with diagram the relationship between mesophric and metanephric kidney.
3. Describe with diagram a tetrapod kidney.
4. Explain the kidney phylogeny in vertebrate.
5. Explain with diagram the relationship between testes and urinary system.
6. Describe how ovary and its genital ducts are associated urinary system in eutheria.
7. Compare the urogenital sytem of an a mphibia and a reptile.
8. Explain the fate of nephrogenic mesoderm in vertebrates.
9. Describe hypothetical archinephros.
10. Mention with diagram the developmental changes in the urogenital system of male mammal.

# Unit 9 ❐ Sense organs

**Structure**

## 9.1 Simple receptors

Vertebrates evolved with an array of essential sense organs and the necessary central nervous system pathways for processing the information. These include somatic receptors (exteroceptors, propriceptors), visceral receptors (enteroceptors), and intermediary nonnervous receptor cells.

In a sensory system, a **sensory receptor** is a sensory nerve ending that recognizes a stimulus in the internal or external environment of an organism. In response to stimuli the sensory receptor initiates sensory transduction by creating graded potentials or action potentials in the same cell or in an adjacent one.

The Sensory receptors involved in taste and smell contain receptor molecules that bind to specific chemicals. Odor receptors in olfactory receptor neurons, for example, are activated by interacting with molecular structures on the odor molecule. Similarly, taste receptors (gustatory receptors) in taste buds interact with chemicals in food to produce an action potential.

Other receptors such as mechanoreceptors and photoreceptors respond to physical stimuli. For example, photoreceptor cells contain specialized proteins such as rhodopsin to transduce the physical energy in light into electrical signals. Some types of mechanoreceptors fire action potentials when their membranes are physically stretched. The sensory receptor functions as the first component in a sensory system.

Sensory receptors respond to specific stimulus modalities. The stimulus modality to which a sensory receptor responds is determined by the sensory receptor's adequate stimulus. The sensory receptor responds to its stimulus modality by initiating sensory transduction. This may be accomplished by a net shift in the initial states of a receptor(see a picture of these putative states with the biophysical description – link.

Receptors are the peripheral (distal) endings of sensory neurons. They are used by animals to obtain information about the environment. Receptors are specific for the type of stimulus that they can detect. For example, photoreceptors can only detect light, heat receptors can only detect heat, pressure receptors can only detect pressure, etc. Receptors function by depolarizing neurons and producing action potentials.

### Types of receptors

***Chemoreceptors:*** detect ions or molecules. Smell (olfaction) and taste rely on chemoreceptors.

***Mechanoreceptors:*** detect changes in pressure, position, or acceleration; include receptors for touch, stretch, hearing, and equilibrium.

***Electromagnetic receptors:*** are specialized for infrared radiation, visible light, or magnetic fields.

***Thermoreceptors:*** detect hot or cold temperatures.

***Pain receptors:*** detect severe heat and pressure and chemicals released by inflamed tissue.

## 9.2 Organs of olfaction and taste

Olfaction, taste and trigeminal receptors together contribute to flavor. The human tongue can distinguish only among five distinct qualities of taste, while the nose can distinguish among hundreds of substances, even in minute quantities.

### 9.2.1 Olfaction

Olfaction (also known as olfactics or smell) refers to the sense of smell. This sense is mediated by specialized sensory cells of the nasal cavity of vertebrates, and, by analogy, sensory cells of the antennae of invertebrates. For air-breathing animals, the olfactory system detects volatile or, in the case of the accessory olfactory system, fluid-phase chemicals. For water-dwelling organisms, e.g., fish or crustaceans, the chemicals are present in the surrounding aqueous medium. Olfaction, along with taste, is a form of chemoreception. The chemicals themselves which activate the olfactory system, generally at very low concentrations, are called odors.

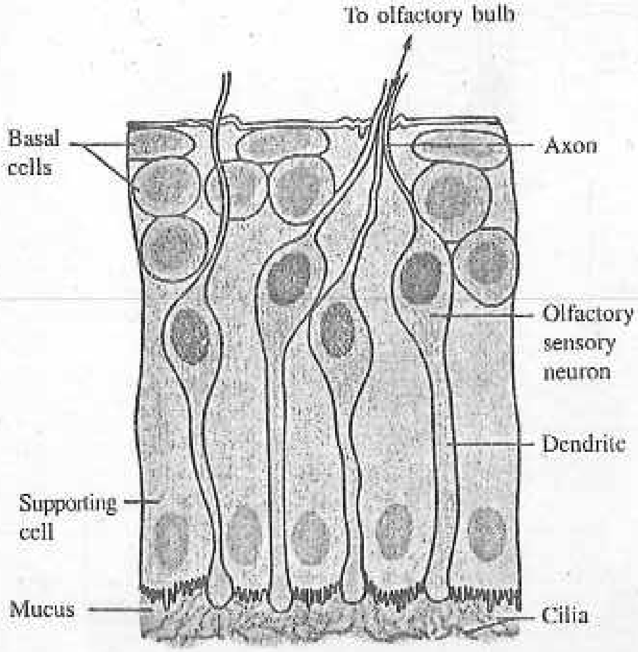


**Fig. 9.1 :** Four olfactory sensory neurons are shown with their cilia projecting into the mucus.

Things that we smell are varied. Attempts to reduce the number of smelled qualities to a few categories have been largely unsuccessful (in providing only a few categories). All things smelled are aerosolizable and water soluble because they must reach and dissolve in the mucus that covers the olfactory receptors. Unlike the hair cell receptors, the olfactory receptors are themselves sensory neurons. They have cilia that project into the mucus surrounding the olfactory epithelium as shown in Fig. 9.1. It is on these cilia that the odorant receptors are thought to be located. Each olfactory neuron expresses only one type of odorant receptor. Binding of the odorants to receptors activates a G protein, which in turn activates adenlyl cyclase to produce cAMP. It is cAMP that activates a cyclic nucleotide-gated cationic channel. When the channel is opened, sodium and calcium enter the cell, hypopolarizing it. The location of the receptors and second messenger cascades and the sequence of events in channel opening are shown schematically.

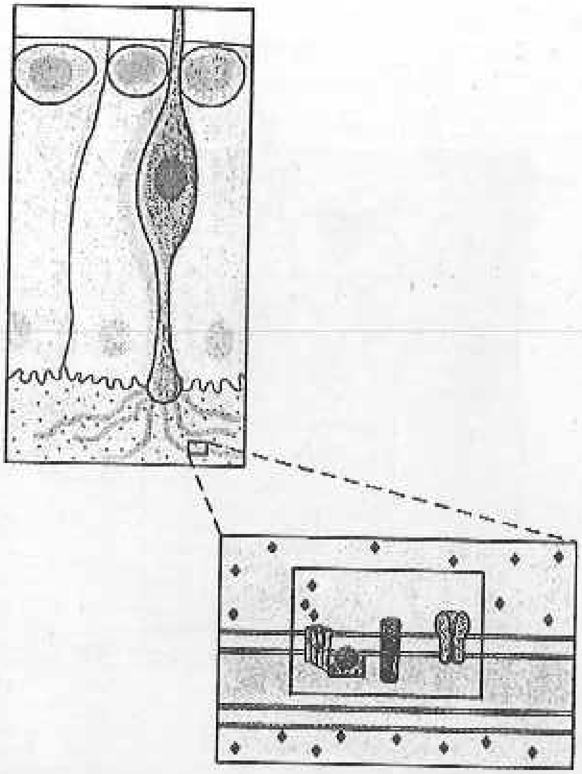


Fig. 9.2 : Inset shows an enlargement of a portion of the membrane of a cilium showing the location of the receptor and the G protein system.

### 9.2.1 Taste

The sense of perceiving different flavors in soluble substances that contact the tongue and trigger nerve impulses to special taste centers in the cortex and thalamus of the brain. The four basic traditional tastes are sweet, salty, sour, and bitter. The front of the tongue is most sensitive to salty and sweet substances; the sides of the tongue are most sensitive to sour substances; and the back of the tongue is most sensitive to bitter substances. The middle of the tongue produces virtually no taste sensation. Chemoreceptor cells in the taste buds of the tongue detect different substances. Adults have about 9000 taste buds, most of them situated on the upper surface of the tongue. The sense of taste is intricately linked with the sense of smell, and taste discrimination is very complex. Many experts believe the capacity to perceive different tastes involves a synthesis of chemoreactive nerve impulses and coordinating brain processes that are still not completely understood. The peculiar sensation caused by the contact of soluble substances with the tongue; the sense effected by the tongue, the gustatory and other nerves, and the gustatory centre.

There are four basic tastes: sweet, salt, sour and bitter. Sometimes alkaline and metallic are also included as basic tastes. All other tastes are combinations of these. The taste buds are specialized, and each responds only to the kind of basic taste that is its specialty. The location of and the number of taste buds varies between animal species.

Other senses, including smell and touch, also play an important role in tasting.

**Taste bud, taste organ**

The organ of taste; spherical nests of cells embedded in the mucosa of the mouth and tongue are composed of supporting and gustatory cells. The gustatory cells have a delicate, hair like process which protrudes from the peripheral surface of the cell. Substances must be in solution to be tasted, solids must be chewed and mixed with saliva.

**Conditioned taste aversion**

Animals have been shown to develop aversions to foods associated with illness or other adverse experiences.

**Conditioned taste preference**

Theoretically, the reverse of conditioned taste aversion, which is a naturally occurring phenomenon; it is not widely accepted that animals will associate recovery from illness with a specific taste or food.

**Taste pore**

Opening from the exterior to a taste bud.

**Taste receptor**

One of the three types of cell in a taste bud; called also gustatory cells.

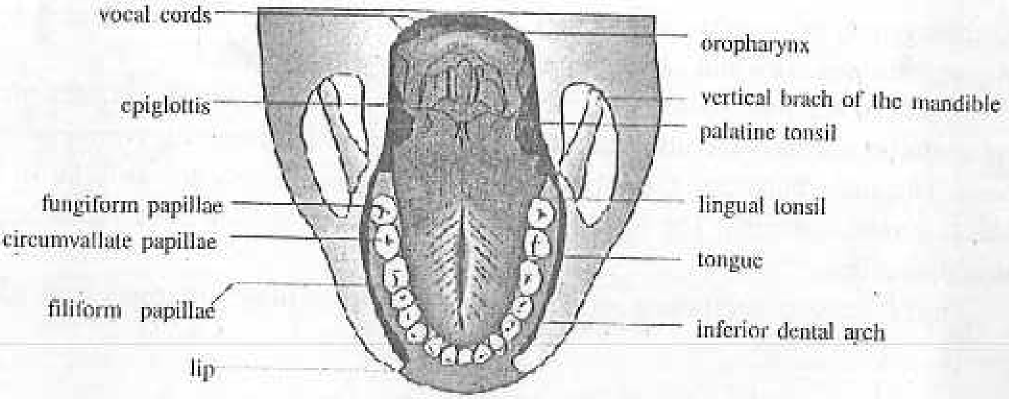


**Fig. 9.3 :** Showing different taste organs

### 9.2.3 Types of papillae

The majority of taste buds on the tongue sit on raised protrusions of the tongue surface called *papillae*. There are four types of papillae present in the human tongue:

- Fungiform papillae - as the name suggests, these are slightly mushroom-shaped if looked at in longitudinal section. These are present mostly at the apex (tip) of the tongue, as well as at the sides. Innervated by facial nerve.

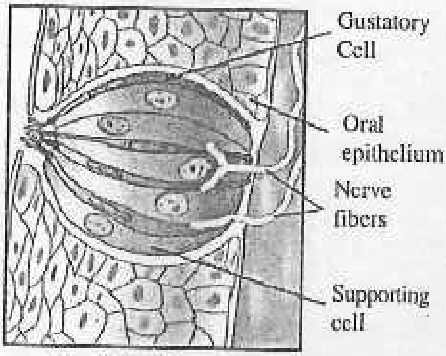


**Fig. 9.4 :** Taste bud

- Filiform papillae - these are thin, long papillae "V"-shaped cones that don't contain taste buds but are the most numerous. These papillae are mechanical and not involved in gustation. Characterized increased keratinization.
- Foliate papillae - these are ridges and grooves towards the posterior part of the tongue found on lateral margins. Innervated by facial nerve (anterior papillae) and glossopharyngeal nerve (posterior papillae).
- Circumvallate papillae - there are only about 3-14 of these papillae on most people, and they are present at the back of the oral part of the tongue. They are arranged in a circular-shaped row just in front of the sulcus terminalis of the tongue. They are associated with ducts of Von Ebner's glands. Innervated by the glossopharyngeal nerve.

Taste buds are small structures on the upper surface of the tongue, soft palate, upper esophagus and epiglottis that provide information about the taste of food being eaten. These structures are involved in detecting the five elements of taste perception: salty, sour, bitter, sweet, and umami (or savory). Via small openings in the tongue epithelium, called taste pores, parts of the food dissolved in saliva come into contact with the taste receptors. These are located on top of the taste receptor cells that constitute the taste buds. The taste receptor cells send information detected by clusters of various receptors and ion channels to the gustatory areas of the brain via the seventh, ninth and tenth cranial nerves.

A taste bud has taste cells of all 5 tastes. Every taste cell has receptors on its surface. The receptors consist of transmembrane proteins that help them to attach to free molecules to produce the taste sensations. It is possible that only one taste sensory receptor is active in the cell when compared to other sensory receptors. Since bitter and sweet are extreme tastes, both these tastes are not found active in a single cell on normal conditions.

A synapse connects the receptor cell to the sensors related neurons to the brain. A sensor related neuron can connect many taste cells in different more taste buds. As in the case of all senses, taste sensation lies in the brain.

Sweet and bitter tastes activate gustuducin that results in a electrochemical transmission between receptors and basal cells and the information is relayed to the gustatory cortex in the brain which says 'this is sweet'. In the case of salt and sour tastes, sodium and potassium ions with increased positive charge buildup generated a small electric current that gets transformed to the brain as something salty or sour is being eaten.

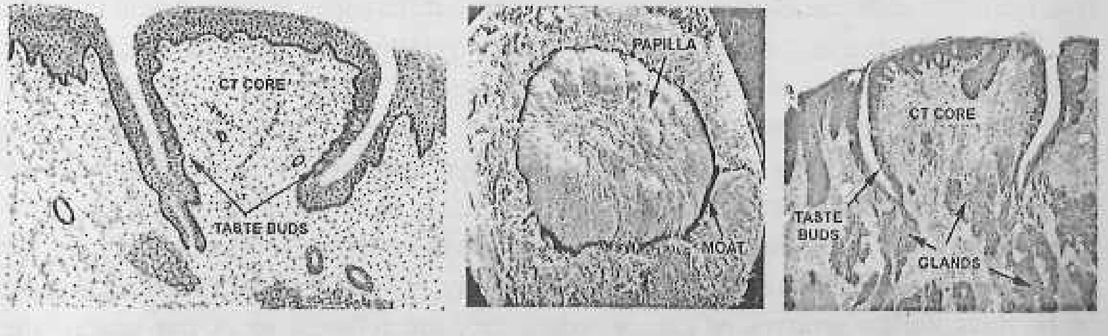


**Fig. 9.5 :** Three views of a circumvallate papilla : Schematic, Scanning E.M., and low-power light microscope (SEM image courtesy of Dr. Suraj Kum)

**Table :** Examples of some human thresholds are furnished as follows—

| Taste | Substance | Threshold for tasting |
|---|---|---|
| Salty | NaCl | 0.01 M |
| Sour | HCl | 0.0009 M |
| Sweet | Sucrose | 0.01 M |
| Bitter | Quinine | 0.000008 M |
| Umami | Glutamate | 0.0007 M |

**Taste receptor**

The pleasant tastes (sweet and umami) are mediated by a family of three T1R receptors that assemble in pairs. Diverse molecules that lead to a sensation of sweet bind to a receptor formed from T1R2 and T1R3 subunits. Cats have a deletion in the gene for T1R2, explaining their non-responsiveness to sweet tastes. Also, mice engineered to express the human T1R2 protein have a human-like response to different sweet tastes. The receptor formed as a complex of T1R1 and T1R3 binds L-glutamate and L-amino acids, resulting the umami taste.

The bitter taste results from binding of diverse molecules to a family of about 30 T2R receptors. Sour tasting itself involves activation of a type of TRP (transient receptor potential) channel. Surprisingly, the molecular mechanisms of salt taste reception are poorly characterized relative to the other tastes.

## 9.3 lateral line system

The lateral line system, found in many fishes and in some aquatic amphibians, is sensitive to differences in water pressure. These differences may be due to changes in depth or to the current like waves caused by approaching objects. The basic sensory unit of the lateral line system is the neuromast, which is a bundle of sensory and supporting cells whose projecting hairs are encased in a gelatinous cap. The nueromasts continuously send out trains of nerve impulses. When pressure waves cause the gelatinous caps of the neuromasts to move, bending the enclosed hairs, the frequency of the nerve impulses is either increased or decreased, depending on the direction of bending. Neuromasts may occur singly, in small groups called pit organs, or in rows within grooves or canals, when they are referred to as the lateral line system. The lateral line system runs along the sides of the body onto the head, where it divides into three branches, two to the snout and one to the lower jaw.

A swimming fish sets up a pressure wave in the water that is detectable by the lateral line systems of other fishes. It also sets up a bow wave in front of itself, the pressure of which is higher than that of the wave flow along its sides. These near-field differences are registered by its own lateral line system. As the fish approaches an object, such as a rock or the glass wall of an aquarium, the pressure waves around its body are distorted, and these changes are quickly detected by the lateral line system, enabling the fish to swerve or to take other suitable action. Because sound waves are waves of pressure, the lateral line system is also able to detect very low-frequency sounds of 100 Hz or less.

### Anatomy

The receptors in the lateral line are **neuromasts**, each of which is composed of a group of hair cells. The hairs are surrounded by a protruding jelly-like **cupula**, typically 1/10 to 1/5 mm long. The hair cells and cupolas of the neuromasts are usually at the bottom of a visible pit or groove in the fish. The hair cells in the lateral line are similar to the hair cells inside the vertebrate inner ear, indicating that the lateral line and the inner ear share a common origin.

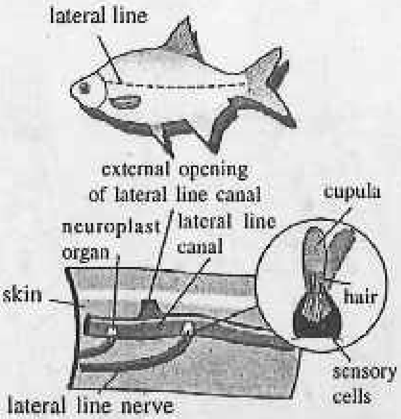


**Fig. 9.6 :** Position of the lateral line sense organ in fish

Teleosts and elasmobranchs usually have **lateral-line canals**, in which the neuromasts are not directly exposed to the environment, but communicate with it via **canal pores**. Additional neuromasts may appear individually at various locations on the body surface.

There are receptors in the line, called neuromasts, each consist of a group of hair cells, and these cell hairs are surrounded by a protruding cupula (an organ that gives an animal a sense of balance). Neuromasts may occur singly, in small groups called pit organs, or in rows within grooves or canals, when they are referred to as the lateral line system. The lateral line system runs along the sides of the body onto the head, where it divides into three branches, two to the snout and one to the lower jaw. These neuromasts are usually at the bottom of a pit or groove in the fish, which is large enough to be visible.

Skates, rays and sharks usually have lateral-line canals, in which the neuromasts are not directly exposed to the environment, but communicate with it via canal pores. The hair cells in the lateral line are similar to the hair cells inside the others vertebrates

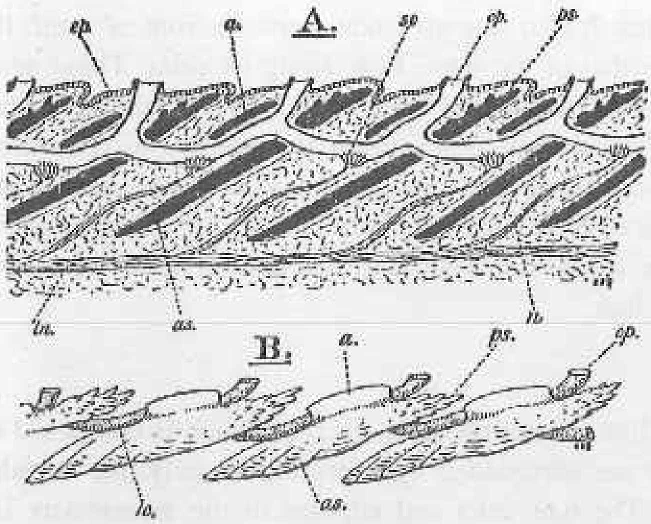
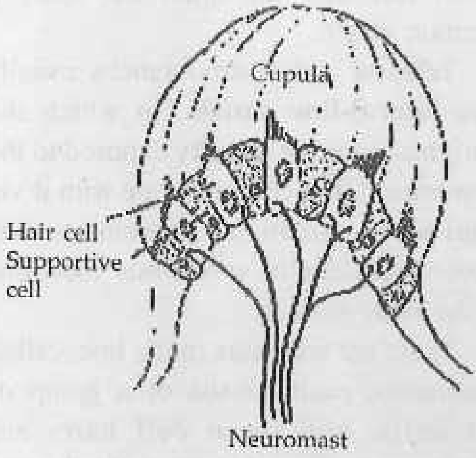


Fig. 9.7 : The relation of the lateral line canal to the scales. A. longitudinal section, B. scales and canal seen in side view. *a.* bridge of scale covering the canal, as. anterior region of scale; *ep.* Epidermis; *lc.* Lateral line canal; *ln.* lateral line nerve; *n.* nerve to sense organ; *op.* external opening of the canal; *ps.* Posterior edge of scale; *so.* Sense organ in canal.



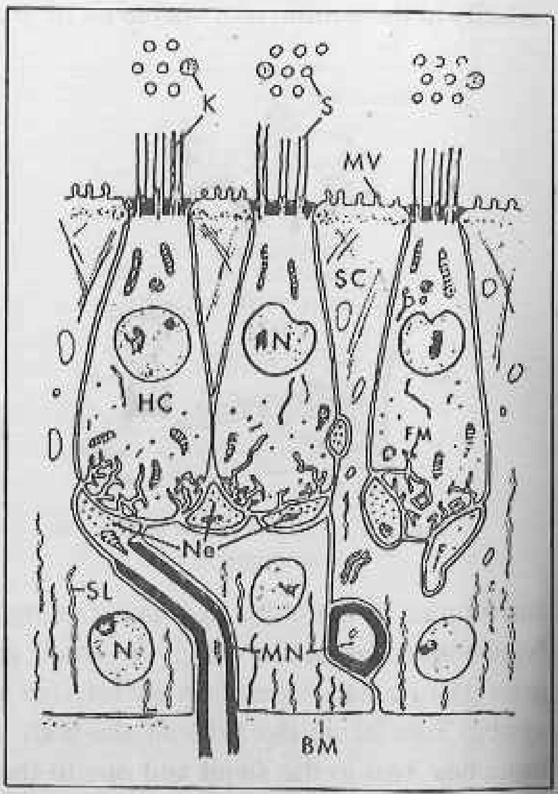


**Fig. 9.8 :** Highly schematic drawing of the sensory epithelium of the lateral line canal organ. *HC* = hair cell, *SC* = supporting cell, *MN* = myelinated nerve fiber, Ne = nerve ending, K = kinocilia, *S* = stereocilia, *MV* = microvilli, N = nucleus, *FM* = folding membrane system, *SL* = supporting lamellae, *BM* = basal membrane.

inner ear (such as the cupula in humans where hair cells within the cupula sense rotational acceleration), indicating that the lateral line and the inner ear share a common origin. Some active fish that are constantly swimming tend to have more neuromasts in canals than on the surface, and the lateral line will be further away from pectoral fins, to reduce the noise generated by fin motion.

The lateral line system, found in many fishes, is sensitive to differences in water pressure. These differences are thought to be due to changes in depth or to the current like waves caused by approaching objects.

An adaptation of the pressure-sensitive systems is seen in the modified groups of neuromasts called the ampullae of Lorenzini (special sensing organs, forming a network of jelly-filled canals), which are found in sharks, rays and a few bony fishes. The ampullae of Lorenzini are able to detect electrical charges, or fields, in the water. Most animals, including humans, emit a DC (Direct Current) field when in seawater. This is thought to be caused by electrical potential differences between body fluids and seawater and between different parts of the body. An AC field is also set up by muscular contractions. A wound, even a scratch, can alter these electrical fields.

## 9.4 Electroreception

Electroreception simply means the ability to detect electrical currents. Electroreceptors are present in the skin of fish, amphibia and lower mammals, e.g. platypus. Animals use these receptors for detecting weak electric and magnetic fields. Electroreceptors of fish and amphibia belong to the secondary receptors in which the primary transduction is carried out by neuroepithelial hair cells that transmit synaptically to the afferent nerve fibres.

### Electroreceptor system

The electroreceptor system is an array of many primary sensory neurons in small, widely dispersed sense organs sending afferent axons to the brain via the lateral line nerves. Two broad classes are: (i) "ampullary" receptors which act as low-pass filters, insensitive to stimulus components above about 20 Hz. Some groups of fish are excited by one polarity, for example, current entering the skin and inhibited by the other polarity. Other groups of fish are the opposite: (ii) "tuberous" receptors are high-pass filters, sensitive in the range of hundreds of Hz but not below about 30 Hz, Some of these respond by increasing the probability of firing nerve impulses as the stimulus is increased in amplitude ("probability coders or P units"). Others respond by shortening the response time of the single nerve impulse that follows each brief stimulus ("phase coders or T units"). Each fish typically has all three kinds of receptors – ampullary, T, and P units, sometimes answering to only one kind of stimulus – social, passive, extraneous, or active distortion of its own EOD by an object of higher or lower conductance than the surroundings. Under artificial respiration of fish the electroreceptor fibres were fairly rhythmically active (10–25 imp./sec). Under the natural respiration of fish the burst of impulses appeared in some fibres in time with respiration, while in the others the activity was suppressed. The thresholds for electric stimulation were in the range $10^{-9}$-$10^{-11}$ A/mm$^2$. The fibers showed phasic-tonic responses to the pulse. An adaptation of receptors to long-lasting current with intensity up to $10^{-7}$ A/mm$^2$ was found.

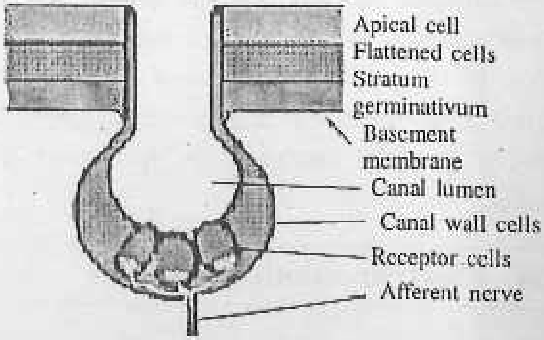


Fig. 9.9 : Electroreceptor system

Electroreception is the alternative source of sensory perception used by electric fish. There are two basic types of cell which can perceive electrical frequencies, both derived from the lateral line detectors, cells found in fish for the detection of movement in water. Ampullary receptors are found in species of fish outside of the "electric" fish category, such as sharks. These receptors pick up frequencies from 0.2 to 20 Hz. Tuberous receptors pick up much higher frequencies in the range of 30 to 1500 Hz. Right is an ampullary receptor, which detects the surrounding waters' charge by a neuro-signal, sent to the brain when a potential difference between the cell and the water is present. The afferent nerve is the motor neuron responsible for the signal. The latter cell type is subdivided into two further groups, Pulse makers and Burst duration receptors. Pulse makers emit one action potential and code for frequency perception, whereas burst duration receptors emit bursts of action potentials and code for amplitude. Both

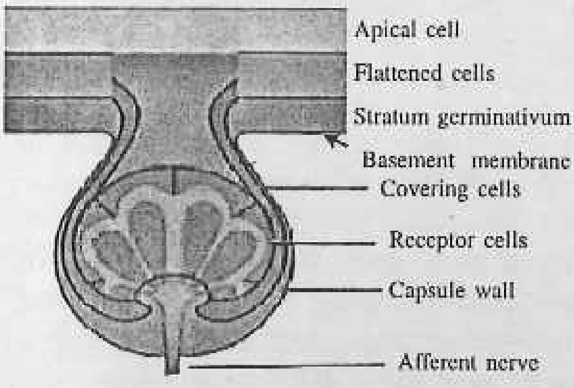
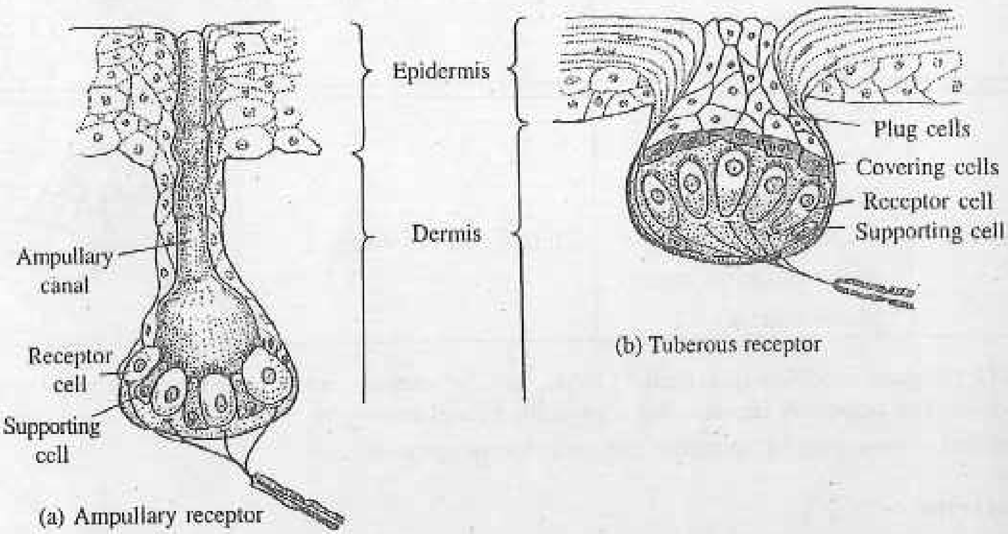


**Fig. 9.10** : Tuberous receptor

cell types are triggered by electric signals in the surrounding water and result in a neuro-transmitted response, (electric organ discharge, movement etc) just like any other sensory feature such as taste or smell.

Figure 9.10 shows a tuberous receptor, both types of receptor cell are found in the skin of the eel. Electric fields from other fish are generated regardless of whether or not they are electrogenic. The use of any muscle creates an electric field, so the contractions of a heart could be detected in another fish. The eels can locate objects accurately by measuring frequencies and amplitudes on different parts of the body as well as static electricity, caused by flow of water against the bottom of the river.



(a) Ampullary receptor

(b) Tuberous receptor

**Fig. 9.11** : Receptors; (a) ampullary; (b) tuberous

By using its own electric organ discharge (EOD) and sensing differences in the current around itself, the eel is able to deduce the conductivity of any surrounding objects, another way of navigation and obstacle detection. In addition, the EOD from other electrogenic fish can be used for communication. When swimming, the eel minimizes undulating movement by use of its long anal fin, so as to avoid disturbance of its own EOD. It also has the ability to swim backwards.....if scanning potential prey, it will start scanning tail end first and finish with its head at the "right end" of the prey, it will then stun the prey.

**Table :** Different type of electroreceptors, location, sensitivity and structure are furnished in the following figure

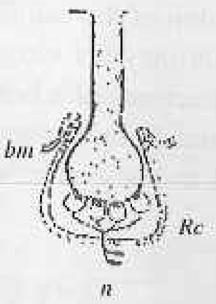
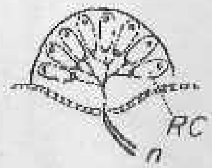
| Type | Where Found | Sensitivity | Structure |
|---|---|---|---|
| Ampullary | Sharks and Rays;<br>Non-teleost fishes (except holosteans);<br>Certain teleosts (mormyrids, certain Notopterus, gymnotiforms, catfish);<br>Amphibians (except frogs and toads). | 0.01 microvolt per cm in marine species, 0.01 millivolt/cm in freshwater; sensitive to DC fields or to frequencies less than 50 Hz |  |
| Tuberous | Mormyrid fish (Knollenorgans. Mormyromasts);<br>Gymnotiform fish (burst-duration coders, phase coders) | 0.1 mV to 10 mV/cm. |  |

**Fig. 9.12 :** Figures modified from Szabo (1965). R.C. = receptor cell; b.m. = basement membrane; n = nerve. The ampullary receptor has a jelly-filled canal leading to the skin surface; the tuberous receptor has a loose plug of epithelial cells over the receptor organ.

## Monotreme

Monotremes are the most prevalent mammals that use electroception. Among these, the platypus has the most acute sense. The platypus appears to use electroreception along with pressure sensors to determine the distance to prey from the delay between the arrival of electrical signals and pressure changes in the water. The bill sense of the platypus exhibit a sophisticated combination of electroreception and mechanoreception that coordinates information about aquatic prey provided from the bill skin mechanoreceptors and electro-receptors, and provide an evolutionary account of electroreception in the three extant species of monotreme (and what can be inferred of their ancestors). Three different kinds of receptor have been identified in the bill skin of monotremes, all of which have an easily distinguishable surface morphology that makes it possible to determine their density distribution.

**Comparison of electroreception in electric fish and in monotremes**

1. Multiple evolutions of similar strategies with different hardware. Monotreme electroreception clearly evolved independently of the same system in fish, just as mormyrids (in the Palaeotropics) have evolved electroreception independently of gymnotiforms (in the neotropics). This is apparent in the different sensory placodes involved, the different sensory transduction mechanisms and the different supporting roles played by mechanoreception.
2. The threshold in the whole animal is much lower than in individual receptors as a result of signal processing of many electro-receptive afferents.
3. The electroreceptor is excited by cathodal current and responds to very low stimulus frequencies.
4. The receptor is protected at the base of the epithelial pore (gland duct in monotremes; ampulla in fish).

## 9.5. Suggested questions

1. Name the types of receptors cells found in vertebrates.
2. Describe with a labeled diagram the olfactory epithelium in fish.
3. Draw and describe taste papillae of a mammal.
4. How many types of electroreceptor are found in fishes? Describe with a neat diagram one of the receptors.
5. Describe with diagram tuberous receptor or ampullary receptor. Mention their function.
6. Describe the lateral line sense organ of fish.
7. Describe with a labeled diagram the neuromast cell and mention its function.
8. Compare the electroreception in a fish and a monotreme.
9. Briefly describe the electroreception in monotreme.
10. What do you mean by electroreception?
11. Draw and describe I the sensory epithelium of the lateral line canal organ.

# Unit 10 ☐ Nervous system

**Structure**

## 10.1 Introduction

The nervous system consists of two main divisions: the central nervous system, which is made up of the brain and the spinal cord, and the peripheral nervous system. The peripheral nervous system consists of the nerves that bring information from the outside world via the sensory systems, and the nerves that carry information from the body's interior to the spinal cord and brain. These nerves also convey commands from the brain and spinal cord to the external muscles that move the skeleton, as well as to various internal organs and glands.

## 10.2 Comparative anatomy of the brain in relation to the function

The brain is the center of the nervous system in all vertebrate animals. In vertebrates, the brain is located in the head, protected by the skull and close to the primary sensory apparatus of vision, hearing, balance, taste, and smell.

The brain forms embryologically from the neural tube anterior to the spinal cord. It includes three anatomical regions. The most posterior region is the hindbrain which includes the medulla oblongata, pons, and cerebellum. Next is the midbrain, which includes a sensory tectum and a motor tegmentum. The brain stem includes all regions of the hindbrain and midbrain except for the cerebellum. The most anterior region of the brain, the forebrain, includes the telencephalon, or cerebrum, and the diencephalon, which is the source of the thalamus.

The brain is divided into a forebrain, a midbrain, and a hindbrain. Phylogenetically, there is a tendency for the forebrain to enlarge during vertebrate evolution. This accompanies increasingly complex behaviors and muscle control.

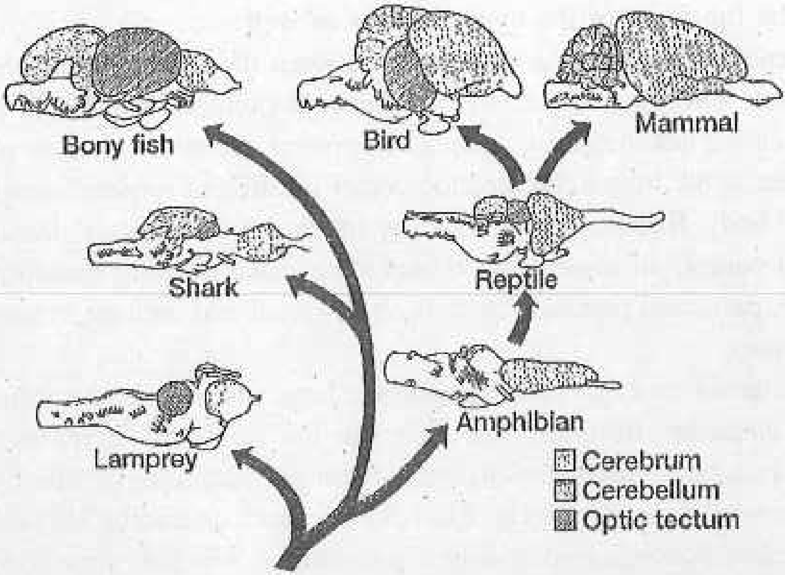


**Fig. 10.1 :** Evolution of the vertebrate brain. Phylogenetic enlargement of the cerebrum is prominent.

## 10.2 Forebrain

The forebrain is a very complex region that consists of the thalamus, the hypothalamus, the epithalamus, and the cerebrum or telencephalon. The diencephalon includes four regions: epithalamus, hypothalamus, ventral thalamus, and dorsal thalamus. The roof of the diencephalons produces the epithalamus, which includes the pineal gland and the habenular nucleus at its base. The function of the habenular nucleus is uncertain. In lower vertebrates, the pineal gland affects skin pigmentation by acting on melanocytes, and it may be important in regulating photoperiod as well. In higher vertebrates, the pineal plays a role in regulating biological rhythms.

The floor of the diencephalons produces the hypothalamus, and the mammillary bodies, which contain nuclei that function in olfaction. The hypothalamus houses a collection of nuclei that regulate homeostatis to maintain the body's internal physiological balance. Homeostatic mechanism adjusted by these nuclei pertain to temperature, water balance, appetite, metabolism, blood pressure, sexual behavior, alertness, and some aspects of emotional behavior. The hypothalamus stimulates the pituitary gland situated beneath it to regulate many homeostatic functions. In addition, the forebrain contains the limbic system, which has components in all regions of the forebrain as well as continuing into the midbrain. The limbic and reticular systems influence the functions of the hypothalamus as well.

The ventral thalamus is a small area between the midbrain and the rest of the diencephalon. The largest part of the diencephalons is the dorsal thalamus, or sometimes called just thalamus, an area comprising nuclei that receive sensory input. The thalamus is the major coordination center of afferent sensory impulses from all parts of the body. Except for the olfactory tracts, which transmit stimuli directly to the cerebral cortex, all sensory tracts including those relaying sensations of touch, temperature, pain, and pressure, as well as all visual and auditory fibers are located in the thalamus.

The thalamus processes and regulates a large quantity of the information that enters and emanates from the forebrain. As the cerebrum increases in size and complexity in land animals, the thalamus increases accordingly. The hypothalamus regulates autonomic functions as well as behaviors such as feeding, drinking, courtship and reproduction, parental, territoriality, and emotional, which it controls in conjunction with the limbic system. The hypothalamus also regulates the endocrine system. The size and complexity of the hypothalamus, relative to the rest of the brain, is greatest in fishes and sharks; it declines considerably in proportion to the rest of the brain in land animals. The epithalamus contains the pineal gland, which is involved in various biological rhythms that depend on daylight, including seasonal changes. In some animals, such as certain reptiles, the pineal takes on the form of an eye, located on the top of the head and known as the parietal eye. This eye has a lens and a primitive retina that captures light and transmits information, such as the amount of daylight, to the hypothalamus. The epithalamus, like the hypothalamus, is relatively smaller in the brains of land animals.

The telencephalon, or cerebrum, is a pair of expanded lobes known as cerebral hemispheres. The outer wall of these hemispheres forms the cerebral cortex, or cortical region. The sub-cortical region comprises the remaining cerebral tissue. The hemispheres appear embryologically at the most anterior end of the neural tube. In actinopterygian fishes, the embryonic telencephalon proliferates outward to form the everted adult cerebrum. In all other fishes and tetrapods, the embryonic telencephalon forms lateral swellings, which give rise to the cerebral hemispheres of adults. The greatest evolutionary expansion of the forebrain is seen in the cerebrum.

**Table 1 :** Comparison of recent and former terms designating the telencephalon. Former terms

| Morphological | Descriptive | Recent terms |
|---|---|---|
| | **Roof of telencephalon** | |
| Pallium | | Pallium |
| Archipallium | Hippocampus | Medial pallium<br>Dorsal pallium<br>Dorsomedial cortex (cingulate) |
| Neopallium<br>(Neocortex)<br>(Isocortex) | Cerebral cortex | Dorsolateral cortex<br>Lateral pallium<br>Dorsal Ventricular ridge |
| Paleopallium | Piriform lobe | Lateral cortex |
| | **Floor of telencephalon** | |
| Corpus striatum | Basal nuclei | Subpallium |
| Paleostriatum | Globus pallidus | |
| Neostriatum | Caudate nucleus, putamen | Striatum |
| Archistriatum | Amygdala | |
| Septum | Septal area | Septum |

Reception of olfactory information is a major function of the telencephalon. In reptiles and especially in birds and mammals, the cerebral region enlarges five to twenty fold compared with most anamniotes of similar body size. This phylogenetic enlargement occurs, in part, because the cerebrum mist process more sensory information from the thalamus. This is accompanied by and increased number of association centers within the cerebrum. Among chondrichthyan fishes, primitive sharks and rays possess cerebrums comparable in size with those of amphibians, but in advanced sharks and skates, the relative size of the cerebral hemispheres approaches that of birds and mammals.

In many mammals, the cerebral cortex is folded in a complicated fashion to accommodate its increased volume. The rounded folds are gyri, and the intervening grooves are called sulci. The term fissure is often used to note a deep sulcus that separates major surface regions of the cerebrum. Not all mammals show such folding. In the duckbill platypus, opossum, and many rodents, the cerebral cortex is smooth. In the echidna, kangaroos, and most primates, the degree of folding is variable.

The cerebrum has two regions, a dorsal pallium and a ventral subpallium. The pallium possesses medial, dorsal, and lateral divisions. The subpallium consists of a striatum and a septum. All vertebrates have a cerebrum based on this basic plan. Major phylogenetic changes in the cerebrum center on loss, fusion, or enlargement of one or more of these regions. *Pallium* the medial pallium receives secondary olfactory information. The dorsal and lateral pallia receive ascending input, including visual information relayed from the thalamus.

The elasmobranch pallium includes lateral, dorsal, and medial divisions; the lateral pallium receives the main olfactory input via the lateral olfactory tract. Parts of the dorsal pallium receive visual, lateral line, thalamic, and possibly auditory of information between hemispheres is likely because they fuse across the midline.

In living amphibians, the pallium consists of above three regions, which receive olfactory input as well as sensory input from the thalamus. The amygdala is another region of the amphibian pallium that is primarily concerned with receiving accessory olfactory information from the vomeronasal organ.

The dorsal pallium is enlarged in mammals. In the course of this enlargement, the dorsal pallium thickens and differentiates into layers. The resulting mammalian cerebral cortex is an extensive area celled the isocortex. In primates, approximately 70% of the neurons in the central nervous system are found in the cerebral cortex. The isocortex is devoted to deciphering auditory, visual, and somatosensory information as well as to controlling the function of the brain stem and spinal cord. All sensory areas are channeled or relayed to the cerebral cortex, bringing together sensory and recall information.

The mammalian medial pallium (hippocampus) receives sensory information and seems to initiate inquisitive or investigative behaviors. It is also concerned with memory of recent events. Olfactory information is shunted to the mammalian lateral pallium (piriform).

The subpallium is divided into two regions: a medial septum and a more extensive latero-ventral striatum. The septum receives information from the medial pallium and is connected to the hypothalamus of the forebrain as well as to the tegmentum of the midbrain. The striatum or basal ganglia controls the sequence of actions involved in complex movements. In receives sensory input from the pallium and input from a nucleus called the substantia nigra, located in the midbrain tegmentum. In reptiles and birds, the striatum receives information from the DVR (dorsal ventricular ridge) and transmits it first to the brain stem and avian striatum is often organized into layers or bands. Expansion of the DVR and the isocortex (mammals) is accompanied by a corresponding expansion of the striatum.

### Limbic system

This system is a functional association of brain centers that include nuclei of the thalamus, hypothalamus, amygdale, medial pallium, cingulated gyrus, and septum. The fornix is a two way fiber system that connects al nuclei of the limbic system. The limbic system receives stimuli from the isocortex and returns to the isocortex and to the autonomic nervous system. The hypothalamus contains nuclei that affect heart rate, respiration, and general visceral activity through the autonomic nervous system. Changes in these usually accompany strong emotion. The amygdale is active in the production of aggressive behavior and fear. The hippocampus (medial pallium) lies adjacent to the amygdale. Damage to it causes loss if recent memory. The cingulate gyrus and septum are other routes of input to this system.

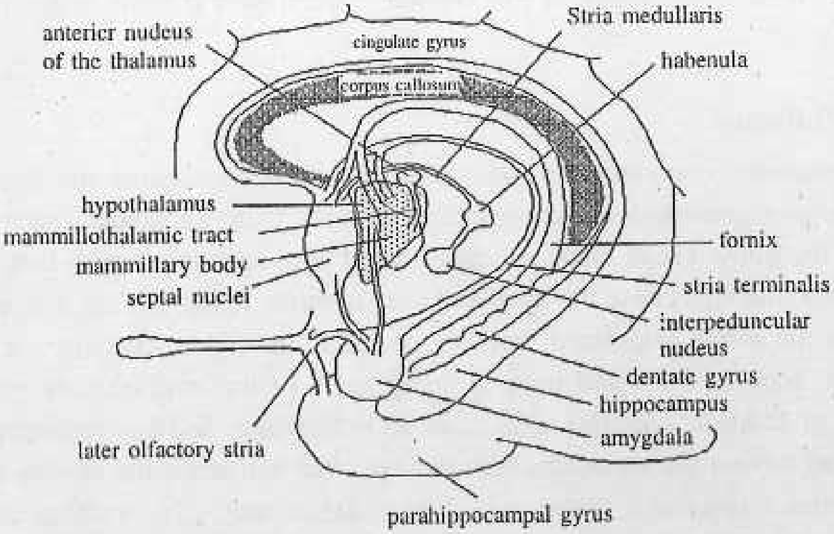


**Fig. 10.2 :** Showing the limbic system

## Functions

The limbic system is involved in two functions: first function is that it regulates the expression of emotions. Experimental or accidental removal of parts of the limbic system leads to emotional passiveness. This function is important to survival. To sustain itself, an animal must actively seek food, be alert to danger, and respond appropriately when threatened. The limbic system has been called the "visceral brain' because of its substantial influence ion visceral functions through the autonomic nervous system.

The second function of the limbic system involves memory. The medial pallium seems to be essential to sustain recent memory. Damage to the hippocampus does not destroy the memory of events prior to the injury, but subsequent events are recalled only with great difficulty or not at all. Memory is probably resident in the isocortex rather than in the limbic system, but the limbic system is involved in temporarily retaining the memory of a recent experience until the experience becomes established as long term memory in the isocortex.

The cerebrum is relatively small in animals with laminar brains and larger in those with complex brains. Scientists have only begun to catalog the many complicated behavioral functions of the cerebrum. Among them appear to be memory, thinking and reasoning, and planning. With the advent of life on the land, the cerebrum underwent an extreme degree of elaboration in reptiles and birds and especially in mammals.

### 10.2.2 Midbrain

The midbrain contains the motor cranial nerves that move the eyes. It also contains neuron groups that are organized to form maps of visual space, auditory space, and the body. These maps are coordinated with each other such that a sudden, unexpected sound will cause the head and eyes to move to the precise region of space from which the sound originated. In those animals that make extensive use of sound localization, such as owls and bats, the map areas of the midbrain are very highly developed. In addition, certain snakes, such as rattlesnakes and boa constrictors, have infrared detectors on the snout or under the eyes that can sense the minute heat from a small animal's body at a distance of 1 m (3 ft) or more. The midbrains of these animals also have infrared maps that are in register with the auditory, visual, and body maps to permit the animal to correlate all the necessary information to make a successful strike on prey in virtually total darkness.

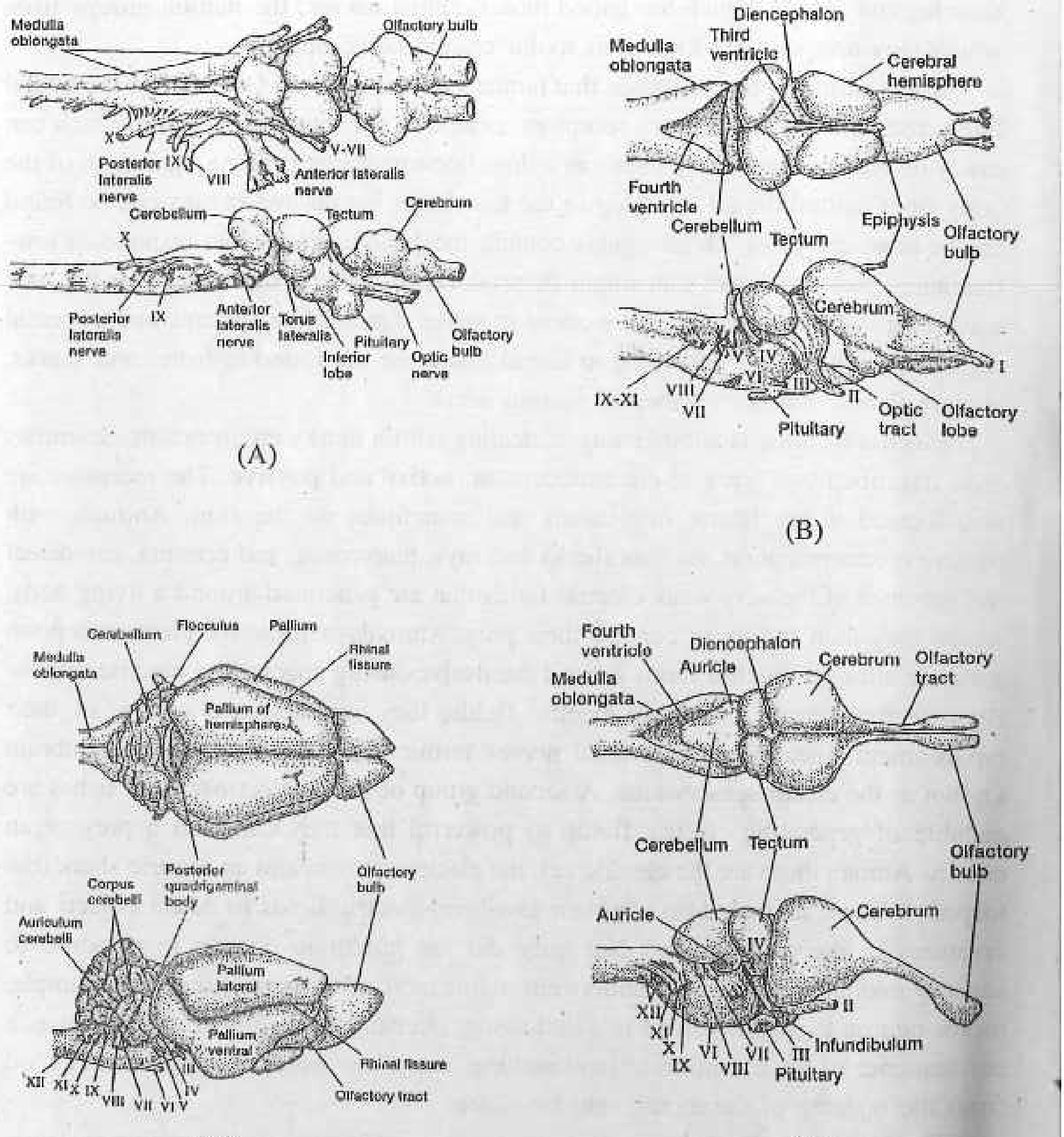
### 10.2.3 Hindbrain

The hindbrain is a region that contains nerve endings that receive information from the outside world and from the body interior; these are known as sensory cranial nerves. The neuron groups upon which they terminate are known as sensory cranial nuclei. Also found in the hindbrain are motor nerves that control internal and skeletal muscles and glands, which are called motor cranial nerves; the neuron groups from which they originate are known as motor cranial nerve nuclei.

Many animals possess senses that humans do not possess. One such is the lateral line sense, which derives from receptors located in the lateral line organ which can easily be seen on most bony fishes as a thin, horizontal line running the length of the body from behind the gill opening to the tail. Other lateral line organs can be found on the head and jaws. These organs contain mechanoreceptors that respond to low-frequency pressure waves that might be produced by other fishes nearby or the bow wave of a fast-swimming predator about to strike. Lateral line systems and a special region of the hindbrain dedicated to lateral line sense are found in fishes and sharks, jawless fishes, and bony fishes of various sorts.

Electroreception is another way of dealing with a murky environment. Scientists have described two types of electroreception: **active** and **passive**. The receptors are also located in the lateral line canals and sometimes on the skin. Animals with passive electroreception, such as sharks and rays, platypuses, and echidna, can detect the presence of the very weak electric fields that are generated around a living body, which they then follow to capture their prey. Animals with active electroreception generate stronger electric fields around themselves using specialized electric organs. By detecting changes in these electric fields, they can derive a picture of their environment. Electrosensory cranial nerves terminate in a region of the hindbrain known as the electrosensory area. A second group of active electrosensory fishes are capable of generating electric fields so powerful that they can stun a prey or an enemy. Among these are the electric eel, the electric catfish, and an electric shark (the torpedo). These animals also use their low-level electric fields to detect objects and creatures in the environment. Not only did the hindbrain change in response to sensory evolution, but it also underwent major motor transformations; for example, motor-neuron groups involved in swallowing, chewing, and salivating evolved as a consequence of the transition to land and the loss of the water column to carry food from the opening of the mouth into the throat.

The hindbrain also contains two important coordinating or integrating systems: the **cerebellum** and the **reticular formation**. The functions of the cerebellum are varied; they include the integration of a sense of balance with aspects of movement and motor learning and motor memory, as well as playing an important role in electrosensory reception.



(A)

(B)

(C)

(D)

*Fig. contd.*

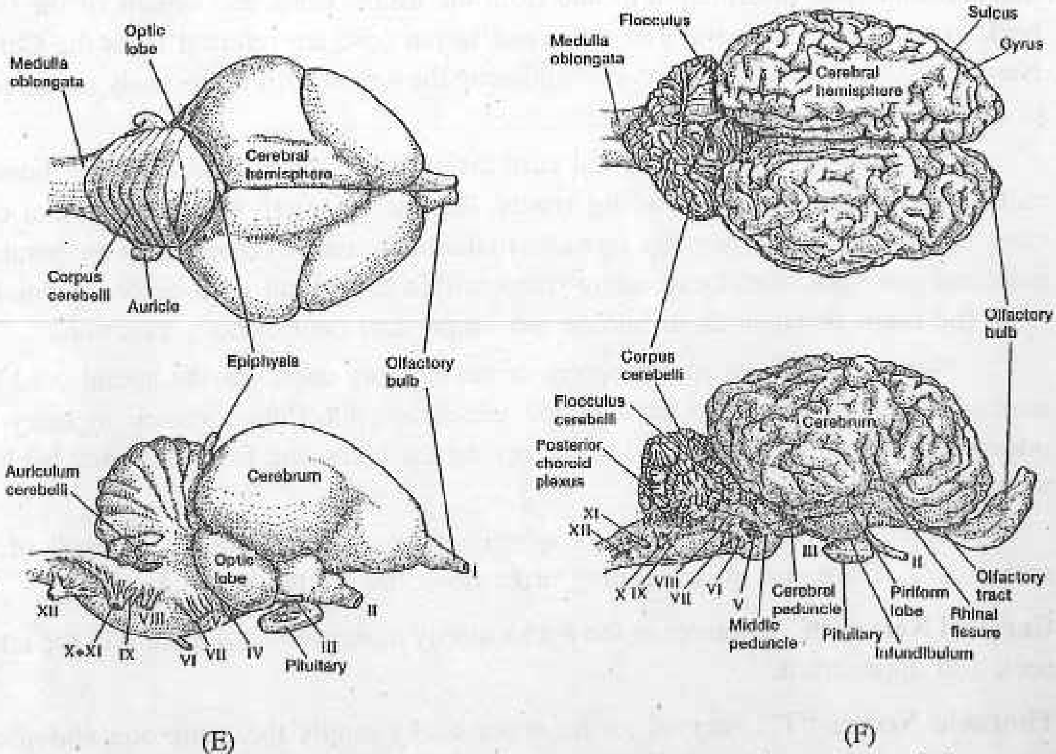


**Fig. 10.3 :** Vertebrate brains. Dorsal views are shown above, lateral views below. (A) *Amia* (B) *Rana* (C) *Gymnura* (D) *Alligator* (E) *Anser* (F) *Equus*

The reticular formation coordinates the functions of various muscle groups. For example, the actions of the jaws and tongue must be coordinated so that an animal does not eat its own tongue while eating its meal. It also coordinates the motor-neuron groups that control the air column that enters and leaves the mouth and throat, which produces the various vocalizations of land animals, including speech. The reticular formation also is involved in sleep, wakefulness, and attention.

## 10.3 Comparative anatomy of spinal cord

The Spinal Cord is connected to the brain and is about the diameter of a human finger. From the brain the spinal cord descends down the middle of the back and is surrounded and protected by the bony vertebral column. The spinal cord is surrounded by a clear fluid called Cerebral Spinal Fluid (CSF), that acts as a cushion to protect the delicate nerve tissues against damage from banging against the inside of the vertebrae.

The anatomy of the spinal cord itself consists of millions of nerve fibers which transmit electrical information to and from the limbs, trunk and organs of the body, back to and from the brain. The brain and spinal cord are referred to as the Central Nervous System, whilst the nerves connecting the spinal cord to the body are referred to as the Peripheral Nervous System.

The nerves within the spinal cord are grouped together in different bundles called **Ascending** and **Descending tracts.** Ascending tracts within the spinal cord carry information from the body, upwards to the brain, such as touch, skin temperature, pain and joint position. Descending tracts within the spinal cord carry information from the brain downwards to initiate movement and control body functions.

Nerves called the spinal nerves or nerve roots come off the spinal cord and pass out through a hole in each of the vertebrae called the foramen to carry the information from the spinal cord to the rest of the body, and from the body back up to the brain

There are four main groups of spinal nerves which exit different levels of the spinal cord. These are in descending order down the vertebral column:

**Cervical Nerves "C":** (nerves in the neck) supply movement and feeling to the arms, neck and upper trunk.

**Thoracic Nerves "T":** (nerves in the upper back) supply the trunk and abdomen.

**Lumbar Nerves "L" and Sacral Nerves "S":** (nerves in the lower back) supply the legs, the bladder, bowel and sexual organs.

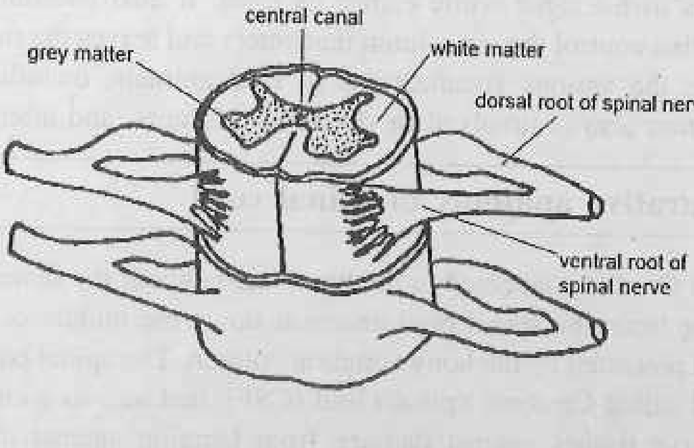


**Fig. 10.4 :** Diagram showing the relationship between spinal nerve roots and vertebrae

## 10.4 Nerves – cranial, peripheral and autonomous nervous systems

### 10.4.1 Cranial nerves

The cranial nerves (CNs) are major nerves that run into the brain from the brainstem or originate in the brain itself. This is differentiated from the peripheral nerves that originate from the spinal cord. The cranial nerves are numbered with Roman numerals I through XII; there are twelve recognized cranial nerve pairs serving the face and running directly into the respective sensory areas of the cerebrum for the senses, some overlapping in function and location. Disruption of these transmission pathways, such as the oxygen deprivation and damage from a stroke, can cause facial and sensory disturbances.

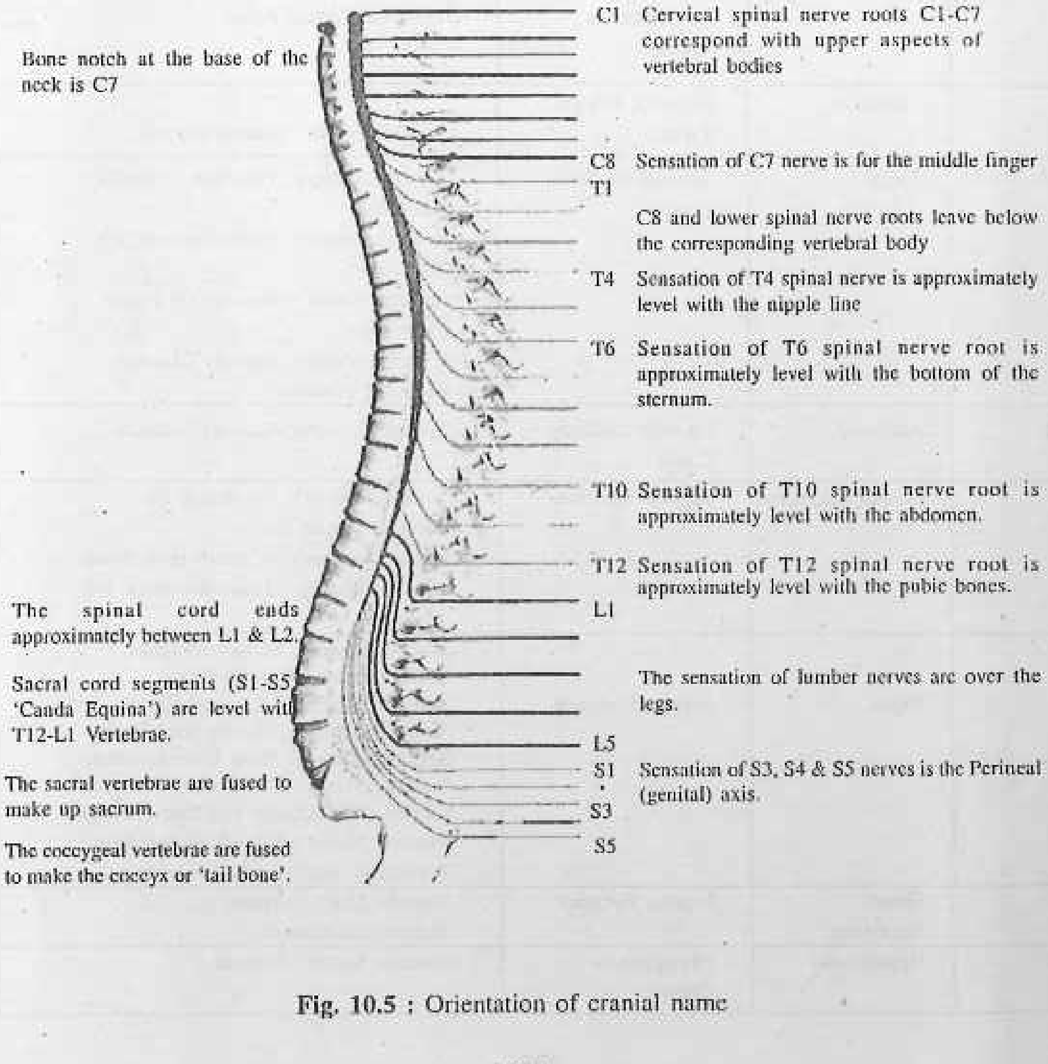


**Fig. 10.5 :** Orientation of cranial name

## Cranial nerve summary

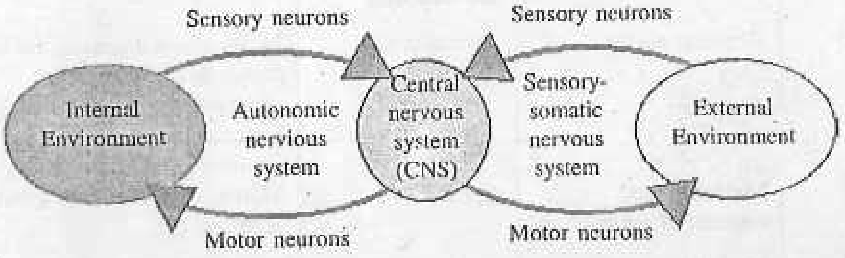
| Cranial nerves number | Name | Foramen | Function |
|---|---|---|---|
| I | Olfactory | Cribiform Plate | Special Sensory: Smell |
| II | Optic | Optic Canal | Special Sensory: Sight |
| III | Oculomotor | Superior Orbital Fissure | Somatic Motor: Superior, Medial, Inferior Rectus, Inferior Oblique<br>Visceral Motor: Sphincter Pupillae |
| IV | Trochlear | Superior Orbital Fissure | Somatic Motor: Superior Oblique |
| V | Trigeminal | V1: Sup Orb Fissure<br>V2: Foramen Rotundum<br>V3: Foramen Ovale | Somatic Sensory: Face<br>Somatic Motor: Mastication, Tensor Tympani, Tensor Palati |
| VI | Abducens | Superior Orbital Fissure | Somatic Motor : Lateral Rectus |
| VII | Facial | Internal Auditory Canal | Somatic sensory: Posterior External Ear Canal<br>Special Sensory: Taste (Anterior 2/3 Tongue)<br>Somatic Motor : Muscles Of Facial Expression<br>Visceral Motor : Salivary Glands, Lacrimal Glands |
| VIII | Auditory | Internal Auditory Canal | Special Sensory: Auditory/Balance |
| IX | Glossopharyngeal | Jugular Foramen | Somatic Sensory : Posterior 1/3 Tongue, Middle Ear<br>Visceral Sensory : Carotid Body/Sinus<br>Special Sensory : Taste (Posterior 1/3 Tongue) |
| X | Vagus | Jugular Foramen | Somatic Motor : Stylopharyngeus<br>Visceral Motor: Parotid Gland<br>Somatic Sensory : External Ear<br>Visceral Sensory : Aortic Arch/Body<br>Special sensory : Taste Over Epiglottis<br>Somatic Motor : Soft Palate, Pharynx, Larynx (Vocalization and Swallowing)<br>Visceral Motor : Bronchoconstriction, Peristalsis, Bradycardia, Vomiting |
| XI | Spinal Accessory | Jugular Foramen | Somatic Motor : Trapezius, Sternocleidomastoid |
| XII | Hypoglossal | Hypoglossal Canal | Somatic Motor : Tongue |

### 10.4.2 Peripheral nervous system

The peripheral nervous system (PNS) resides or extends outside the central nervous system (CNS), which consists of the brain and spinal cord. The main function of the PNS is to connect the CNS to the limbs and organs. Unlike the central nervous system, the PNS is not protected by bone or by the blood-brain barrier, leaving it exposed to toxins and mechanical injuries.

The peripheral nervous system is subdivided into the

- **sensory-somatic nervous system** and the
- **autonomic nervous system**



By function, the peripheral nervous system is divided into the somatic nervous system, autonomic nervous system and the enteric nervous system. The somatic nervous system is responsible for coordinating the body movements, and also for receiving external stimuli. It is the system that regulates activities that are under conscious control. The autonomic nervous system is then split into the sympathetic division, **parasympathetic division**, and **enteric division**. The *sympathetic nervous system* responds to impending danger or stress, and is responsible for the increase of one's heartbeat and blood pressure, among other physiological changes, along with the sense of excitement one feels due to the increase of adrenaline in the system. The *parasympathetic nervous system*, on the other hand, is evident when a person is resting and feels relaxed, and is responsible for such things as the constriction of the pupil, the slowing of the heart, the dilation of the blood vessels, and the stimulation of the digestive and genitourinary systems. The role of the enteric nervous system is to manage every aspect of digestion, from the esophagus to the stomach, small intestine and colon.

There are two types of cells in the peripheral nervous system. These cells carry information to (sensory nervous cells) and from (motor nervous cells) the central nervous system (CNS). Cells of the sensory nervous system send information to the CNS from internal organs or from external stimuli.

Motor nervous system cells carry information from the CNS to organs, muscles, and glands. The motor nervous system is divided into the somatic nervous system and the autonomic nervous system. The **somatic nervous system** controls skeletal muscle as well as external sensory organs such as the skin. This system is said to be voluntary because the responses can be controlled consciously. Reflex reactions of skeletal muscle however are an exception. These are involuntary reactions to external stimuli.

**Table:** Location and functions of descending and ascending nerve tracts of the spinal cord.

| Tract | Source | Destination | Function |
|---|---|---|---|
| | | **Descending** | |
| Lateral and ventral corticospinal tract | Cerebral cortex | Spinal cord | Motor connections direct from cortex to primary motor neurons of arms and legs (places motor neurons under direct voluntary cortical control) |
| Rubrospinal tract | Midbrain (red nucleus of tegmentum) | Spinal cord | Motor connections in spinal cord |
| Lateral and ventral reticulospinal tract | Medulla reticular formation | Spinal cord (dorsal horn) | Postural reflexes |
| Tectospinal tract | Midbrain (colliculus, roof) | Spinal cord | Visual and auditory stimuli to limbs and trunk |
| Vestibulospinal tract | Medulla (vestibular nucleus) | Spinal cord | Postural reflexes accomplished by axial and limb musculature |
| | | **Ascending** | |
| Fasciculus gracilis and fasciculus cuneatus | Spinal cord | Medulla | Sensations of posture and spatial judgments about positions of limbs and body |
| Dorsal and ventral spinocerebellar tract | Spinal cord | Cerebellum via peduncle | Proprioceptive information from muscles to cerebellum |
| Lateral spinothalamic tract | Spinal cord | Thalamus | Pain and temperature sensations to thalamus |
| Ventral spinothalamic tract | Spinal cord | Thalamus | Tactile sensations to thalamus |
| Spinotectal tract | Spinal cord | Midbrain (tectum) | Proprioceptive information from neck and shoulders |
| Spinoreticular tract | Spinal cord | Medulla (reticular formation) | Pain and sensations from internal organs |

### 10.4.3 Autonomic nervous system

The autonomic nervous system (ANS or visceral nervous system) is the part of the peripheral nervous system that acts as a control system functioning largely below the level of consciousness, and controls visceral functions. The ANS affects heart rate, digestion, respiration rate, salivation, perspiration, diameter of the pupils, micturition (urination), and sexual arousal. Whereas most of its actions are involuntary, some, such as breathing, work in tandem with the conscious mind. The autonomic nervous system (ANS) is a regulatory branch of the central nervous system that helps people adapt to changes in their environment. It adjusts or modifies some functions in response to stress. The ANS helps regulate :

- blood vessels' size and blood pressure
- the heart's electrical activity and ability to contract
- the bronchium's diameter (and thus air flow) in the lungs

The ANS also regulates the movement and work of the stomach, intestine and salivary glands, the secretion of insulin and the urinary and sexual functions. The ANS acts through a balance of its two components, the sympathetic nervous system and parasympathetic nervous system.

It can be divided by subsystems into the parasympathetic nervous system and sympathetic nervous system. It can also be divided functionally, into its sensory and motor systems. The enteric nervous system is sometimes considered part of the autonomic nervous system, and sometimes considered an independent system. The reflex arcs of the ANS comprise a sensory (afferent) arm, and a motor (efferent or effector) arm. Only the latter is shown in the illustration.

### 10.4.4 Sensory neurons

The sensory arm is made of "primary visceral sensory neurons" found in the peripheral nervous system (PNS), in "cranial sensory ganglia": the geniculate, petrosal and nodose ganglia, appended respectively to cranial nerves VII, IX and X. These sensory neurons monitor the levels of carbon dioxide, oxygen and sugar in the blood, arterial pressure and the chemical composition of the stomach and gut content. (They also convey the sense of taste, a conscious perception). Blood oxygen and carbon dioxide are in fact directly sensed by the carotid body, a small collection of chemosensors at the bifurcation of the carotid artery, innervated by the petrosal (IXth) ganglion.

Primary sensory neurons project (synapse) onto "second order" or relay visceral sensory neurons located in the medulla oblongata, forming the nucleus of the solitary tract (nTS), that integrates all visceral information. The nTS also receives input from a nearby chemosensory center, the area postrema, that detects toxins in the blood and the cerebrospinal fluid and is essential for chemically induced vomiting or conditional taste aversion (the memory that ensures that an animal which has been poisoned by a food never touches it again). All these visceral sensory informations constantly and unconsciously modulate the activity of the motor neurons of the ANS.

### 10.4.5 Motor neurons

Motor neurons of the ANS are also located in ganglia of the PNS, called "**autonomic ganglia**". They belong to three categories with different effects on their target organs: **sympathetic, parasympathetic and enteric.**

Sympathetic ganglia are located in two sympathetic chains close to the spinal cord: the prevertebral and pre-aortic chains. Parasympathetic ganglia, in contrast, are located in close proximity to the target organ: the submandibular ganglion close to salivatory glands, paracardiac ganglia close to the heart etc. Enteric ganglia, which as their name implies innervate the digestive tube, are located inside its walls and collectively contain as many neurons as the entire spinal cord, including local sensory neurons, motor neurons and interneurons. It is the only truly autonomous part of the ANS and the digestive tube can function surprisingly well even in isolation. For that reason the enteric nervous system has been called "the second brain".

The activity of autonomic ganglionic neurons is modulated by "preganglionic neurons" (also called improperly but classically "visceral motoneurons") located in the central nervous system. Preganglionic sympathetic neurons are in the spinal cord, at thoraco-lumbar levels. Preganglionic parasympathetic neurons are in the medulla oblongata {forming visceral motor nuclei: the dorsal motor nucleus of the vagus nerve (dmnX), the nucleus ambiguus, and salivatory nuclei} and in the sacral spinal cord. Enteric neurons are also modulated by input from the CNS, from preganglionic neurons located, like parasympathetic ones, in the medulla oblongata (in the dmnX).

The feedback from the sensory to the motor arm of visceral reflex pathways is provided by direct or indirect connections between the nucleus of the solitary tract and visceral motoneurons.

**Function**

Sympathetic and parasympathetic divisions typically function in opposition to each other. But this opposition is better termed complementary in nature rather than antagonistic. For an analogy, one may think of the sympathetic division as the accelerator and the parasympathetic division as the brake. The sympathetic division typically functions in actions requiring quick responses. The parasympathetic division functions with actions that do not require immediate reaction. Consider sympathetic as "fight or flight" and parasympathetic as "rest and digest". However, many instances of sympathetic and parasympathetic activity cannot be ascribed to "fight" or "rest" situations. For example, standing up from a reclining or sitting position would entail an unsustainable drop in blood pressure if not for a compensatory increase in the arterial sympathetic tonus. Another example is the constant, second to second modulation of heart rate by sympathetic and parasympathetic influences, as a function of the respiratory cycles. More generally, these two systems should be seen as permanently modulating vital functions, in usually antagonistic fashion, to achieve homeostasis. Some typical actions of the sympathetic and parasympathetic systems are listed below.

### 10.4.6 Sympathetic nervous system

Promotes a "fight or flight" response, corresponds with arousal and energy generation, and inhibits digestion.

- Diverts blood flow away from the gastro-intestinal (GI) tract and skin via vasoconstriction.
- Blood flow to skeletal muscles and the lungs is not only maintained, but enhanced (by as much as 1200% in the case of skeletal muscles).
- Dilates bronchioles of the lung, which allows for greater alveolar oxygen exchange.
- Increases heart rate and the contractility of cardiac cells (myocytes), thereby providing a mechanism for the enhanced blood flow to skeletal muscles.
- Dilates pupils and relaxes the lens, allowing more light to enter the eye.
- Provides vasodilation for the coronary vessels of the heart.
- Inhibits peristalsis.

### 10.4.7 Parasympathetic nervous system

Promotes a "rest and digest" response, promotes calming of the nerves to return to regular function, and enhances digestion.

- Dilates blood vessels leading to the GI tract, increasing blood flow. This is important following the consumption of food, due to the greater metabolic demands placed on the body by the gut.
- The parasympathetic nervous system can also constrict the bronchiolar diameter when the need for oxygen has diminished.
- Dedicated cardiac branches of the vagus and thoracic spinal accessory nerves impart parasympathetic control of the heart or myocardium.
- During accommodation, the parasympathetic nervous system causes constriction of the pupil and lens.

- The parasympathetic nervous system stimulates salivary gland secretion, and accelerates peristalsis, so, in keeping with the rest and digest functions, appropriate PNS activity mediates digestion of food and indirectly, the absorption of nutrients.
- Is also involved in erection of genitals, via the pelvic splanchnic nerves 2–4.

## 10.5 Suggested questions

1. Describe the components of fore brain of a vertebrate.
2. Mention the changes found in fore brain between a reptile and a mammal.
3. Give a comparative account of fore brain in vertebrate series.
4. Describe with the help of diagram the fate of cerebrum, cerebellum, and optic tectum in vertebrate brain.
5. Draw and describe the brain of an amphibia.
6. What is limbic system? Mention its function.
7. Mention the anatomical components of limbic system in diagram and show the flow of information.
8. What are recent terminology of hippocampus, paleopallium and corpus striatum?
9. Mention the functions of ascending / descending spinal nerves.
10. Explain the subdivisions and functional relationship of peripheral nervous system with the help of schematic diagram.
11. What is cribiform plate?
12. How motor and sensory neurons work together?
13. Mention the functions of parasympathetic / sympathetic nervous system.
14. Mention the functions of motor neurons.
15. Explain with a diagram the relationship between spinal nerve roots and vertebrae.

# Group–A(II)

## Structure and Function of Non-chordates

# Unit 1 ☐ Organization of Coelom

*Structure*

1.1 Introduction

1.2 Acoelomates

1.3 Pseudocoelomates

1.4 Coelomates

1.5 Protostomes and Deuterostomes

## 1.1 Introduction

The coelom is a cavity lined by an epithelium of cells derived from embryonic mesoderm. Animals having coelom are known as coelomates. Animals that rely on simple diffusion for internal transport do not have a coelom (or blood system) are said to be acoelomate organisms. The space between the gut and the body wall is filled with mesenchyme. Pseudocoelomates are those animals in which the body cavity is not a true coelom or lined by mesoderm. Leaving aside unicellular animals, the sponges, where multicellularity evolved, the body has a cellular grade of organization. Before epithelia evolved in metazoans, steadystate regulation (homeostasis) was more or less limited to regulation within separate cells as in sponges. Although cnidarians are the first to evolve a cavity, coelenteron, for extracellular digestion and absorption, it can not direct its circulatory, hydrostatic, excretory and reproductive functions. This divestiture occurred in larger bilateral animals as the multi functional coelenteron lining was replaced by two new epithelia which delineate a total of three new compartments—(a) gut—the cavity and its specialized lining for digestion and absorption, (b) the coelom—for hydrostatic support, circulation, reproduction and excretion and (c) the blood vascular systems, for blood circulation.

Mesozoa is a minor group of multicellular animals, constructed by two solid cell layers but these two layers do not correspond to the ectoderm and endoderm of the metazoa because the inner layer is reproductive and not digestive.

The metazoans (except sponges; very unlike most metazoans) arising from the colonial protists are characterized by the presence of three germ layers during development. Some members of this group constitute the Radiata, because they have radial symmetry. The Radiata includes the cnidarians and the ctenophores. In these animals, the mesoderm is rudimentary, consisting of sparsely scattered cells in a gelatinous matrix. Most metazoans, however, have bilateral symmetry and thus constitute, the **Bilateria**. These bilateral phyla are classified as either flatworms, protostomes or deuterostomes. All bilateria are thought to have descended from a primitive type of flatworms. These flatworms were the first to have a true mesoderm although it was not hollowed out to form a body cavity. While the flatworms are acoelomate, the round worms (and rotifers) have a body cavity distinctive from all other animals since it is not lined by mesoderm.

The majority of the phyla are coelomate, that is, they possess a mesodermlined body cavity. There may be two types of coelom formation—(a) cavities are formed by hollowing out a solid mesodermal block; this is **schizocoelous** formation of the body cavity, (b) cavities are formed from mesodermal pouches extending from gut; this is **enterocoelous** formation of body cavity.

## 1.2 Acoelomates

Acoelomates are the animals which are devoid of coelom. These groups have a solid body construction in which the space between the digestive tract and the body wall is filled with mesenchyme. The acoelomate body plan is primary and ancestral with coelomate plan. The acoelomate flatworms are the stem group in the evolution of bilateral animals. As these animals do not have coelom, the functions of coelom are to be performed by other means. As coelom is one of the transport systems for the mass flow of internal fluids, these animals have to rely on simple diffusion for internal transport (Fig. 1.1).

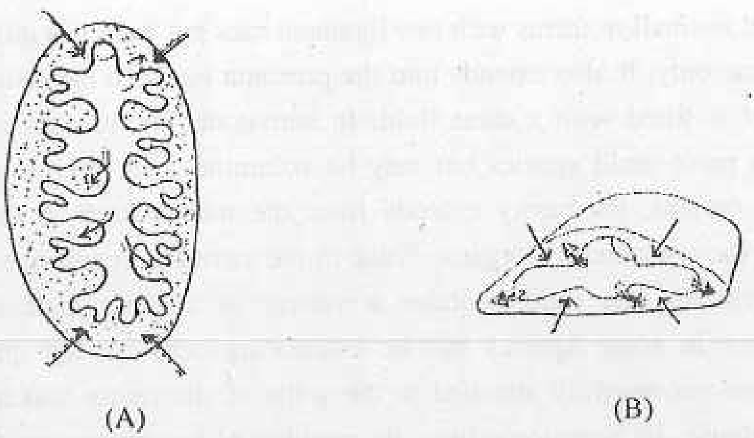


**Fig. 1.1** : In small or flat animals (A, B) gases diffuse across the body wall and nutrients diffuse from the gut to the consuming tissues, because diffusion distances are very short.

In special cases of very wide acoelomates, where the distance from a central tubular gut to the body margins often exceeds the range of simple diffusion, the gut develops branches that transport nutrients within periphery. Such transport is fundamentally similar to gastrovascular transport in cnidarians and ctenophores. Acoelomete phyla includes Gnathostomulida, Platyhelminthes and Mesozoans.

## 1.3 Pseudocoelomates

Pseudocoelomates are animals where a fluid-filled body cavity occupies the space between the body wall and gut called pseudocoel. Like a blood space, a pseudocoellacks an epithelial lining. Pseudocoel is the blastocoel or the primary body cavity which persists in the adult as a spacious cavity.

Pseudocoelomates are included under phyla Rotifera, Acanthocephala, Gastrotricha, Kinorhyncha, Nematoda, Nematomorpha, Loricifera and Entoprocta. However, Parker and Haswell (1972) have included the groups Nematoda, Nematomorpha, Rotifera, Gastrotricha and Kinorhyncha as separate classes under the phylum Aschelminthes and the rest as separate phyla.

In Rotifers, a more or less spacious fluid filled pseudocoel lies beneath the body wall and surrounds the gut and others internal organs. In Acanthocephala the pseudocoel is small in forms with two ligament sacs but becomes quite large in those with one sac only. It also extends into the presoma between the muscle bands. Here pseudocoel is filled with a clear fluid. In nematodes pseudocoel is small or non-existent in most small species but may be voluminous in large forms like *Ascaris* sp. When present, the cavity extends from the musculature to the gut wall and surrounds the reproductive organs. Fluid in the cavity is pressurized and functions as a hydrostate. The fluid contains a variety of organic metabolites including haemoglobin in some species but no circulating cells. A few phagocytic cells, however, are permanently attached to the walls of the cavity and are important in internal defense. In Nematomorpha, the pseudocoel has connective tissue partitions formed by loose cells in a fibrous collagenous matrix. In Entoprocta, the pseudocoelom is found within the tentacles, and the space between the digestive tract and the body wall. It is filled with gelatinous material containing mesenchyme cells. The gelatinous materials renders the tentacle rigid. The pseudocoel is spacious in the kinorhyncha and filled with a fluid containing numerous active amoeboeytes.

## 1.4 Coelomates

In coelomates, coelom is present and in all the cases, coelom is lined by an epithelium of cells, derived from embryonic mesoderm. This living epithelium separates and presumably regulates the composition of the coelomic cavity independent of adjacent connective tissue and gut compartments. The epithelial lining of the vertebrate coelom is a thin, non-contractile layer called peritoneum which separates the coelomic fluid from the underlying (retroperitoneal) muscle and connective tissue. A few invertebrate coelomates actually have a vertebrate like peritoneum. A part from the major invertebrate phyla, a few minor invertebrate phyla also have coelom. They are Priapulida, Sipunculida, Onychophoran Pentastomida, Tardigrada, Phoronida, Brachiopoda, Bryozoa and Chaetognatha. The major phyla are Annelida, Arthropoda, Mollusca, Echinodermata, Hemichordata and Chordata.

Some bilaterians (Fig. 1.2A) have unpartitioned coelom that is continuous throughout the body. In these, the coelomic fluid reaches all tissues and is the sole circulatory system. In most bilaterians, however, the coelom is divided by septa and mesenteries (Fig. 1.2B) and because of them, the coelomic fluid can only circulate locally. For whole body transport these animals have evolved a blood-vascular system or haemal system, which consists of fluid-filled channels comprised of connective tissue.

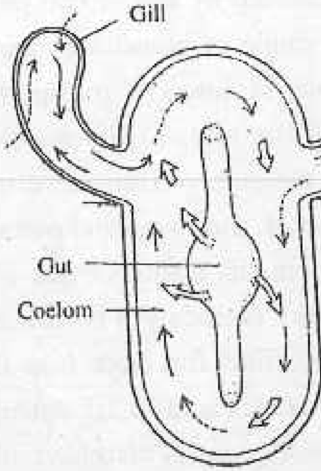


**Fig. 1.2A** : Unpartitioned coelom. Coelomic fluid reaches all tissues and is the sole circulatory system

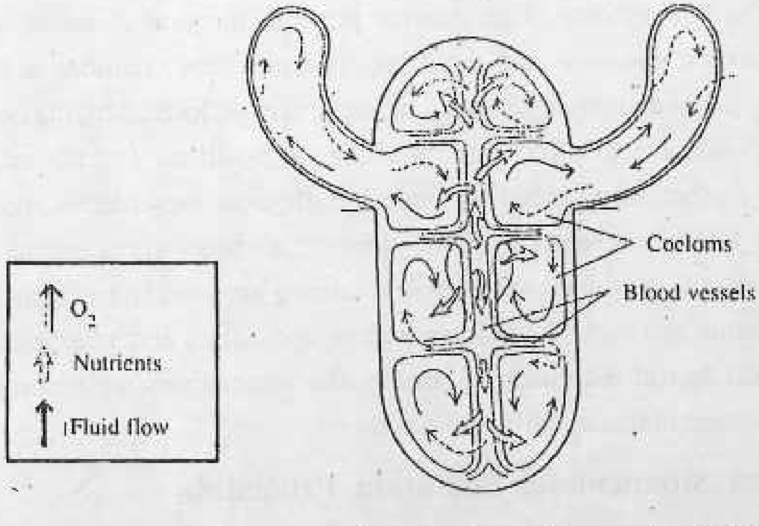


Fig. 1.2B : Coelom is divided by septa and mesenteries and thus, coelomic fluid can only circulate locally

The minor phyla Bryozoa, Brachiopoda and Phoronida are called lophophorate phyla because they have a structure called lophophore, which is nothing but a circular or horse shoe-shaped fold of the body-wall surrounding the mouth and bears numerous ciliated tentacles. In Bryozoa, the coelom is divided by an incomplete septum, into (a) an anterior ring that occupies the base of the lophophore and extends into each tentacle as a part of the mesocoel and (b) a larger posterior or trunk coelom (metacoel). The two divisions are connected by one or two pores. The trunk coelom is crossed by muscle fibers and by a single or branching tube of mesothelial tissue, forming funnicules and plays a role in nutrient transport between zooids. In Brachiopoda, the coelom extends into the folds of the mantle. It is divided into a right and left half by a dorsoventral mesentery. Transverse mesentery also occurs. Here, the coelom is divided into **protocoel, mesocoel** and **metacoel** by two imperfect transverse septa. The coelomic fluid contains coelomocytes of several sorts, one of which contains hemerythrin (a respiratory pigment) in burrowing forms. $O_2$ transport is probably provided by the coelomic fluid for there is a definite circulation of coelomic fluid through the mantle channels and $O_2$ is carried at least in part by hemoerythrin in the coelomocytes. These animals also have blood vascular system. In phoronids, body cavity is a coelom and filled with a fluid containing colourless corpuscles. The coelom is divided into two unequal chambers by a transverse septum at the level of the lophophores. The anterior portion, the oral chamber is smaller and continues into the epistome and tentacles. The posterior chamber is larger and houses alimentary canal and other viscera. The septum is perforated by the oesophagus but not by the rectum because the anus is aboral in position. The aboral chamber of the coelom is further sub-divided by three longitudinal mesenteries, one median ventral and two lateral mesenteries, into three chambers—(i) a rectal chamber between right and left lateral mesenteries containing rectum, (ii) a right chamber between the medium and right lateral mesentery and (iii) a left chamber between the median and left lateral mesentery. Aborally, the mesenteries are incomplete and so the chambers communicate with one another.

## 1.4.1 Coelom in Sipunculida, Echiutida Priapalida

In non-segmented coelomate worms of phyla Sipunculida, Echiutida and Priapulida, the following characteristics are notable :

**Sipuncula** has two coelomic cavities—(i) tentacular coelom, forming a ring at the base of the tentacle and extending in each tentacle, and (ii) trunk coelom, spacious, separated from the tentacular coelom by septum. Coelomic fluid in both the cavities is kept in circulation by cilia on some of the peritoneal cells.

Hemoerythrocytes are the most common and conspicuous of the numerous coelomocytes. Similar type of coelom is found in Echiutida. Coelomic fluid is circulated by muscular contraction. Trunk coelomic gland contains erythrocytes, amoebocytes and germ cells. There is a controversy about the coelom in Priapulida. It is possible that its body cavity is a coelom with a primitive grade of organization. In Pogonophora also, the coelom is divided into compartments and extended into the tentacles. Sometimes coelomic fluid of some coelomic spaces may contain respiratory pigment, haemoglobin. In Onychophora coelom is reduced to gonadal cavity and to small sacs associated with the nephridia.

### 1.4.2 Coelom in Mollusca

Coelom in Mollusca is small and in most of them the coelom comprises a pericardial coelom around the heart, a gonadal coelom and paired coelomic ducts, which together with the pericardial wall, serve as excretory organs.

### 1.4.3 Coelom in Annelida

In Annelida, the primary segmental structures are the coelomic compartments created by partitioning of the coelom with transverse septa (Fig. 1.3A). Each septum is composed of two layer of peritoneum, one derived from the segment in front and one from the segment behind and a layer of connective tissue sandwiched in between coeloms are usually paired and arranged in a longitudinal series; for example, one pair in each of the many segments of an earthworm. The left part is separated from

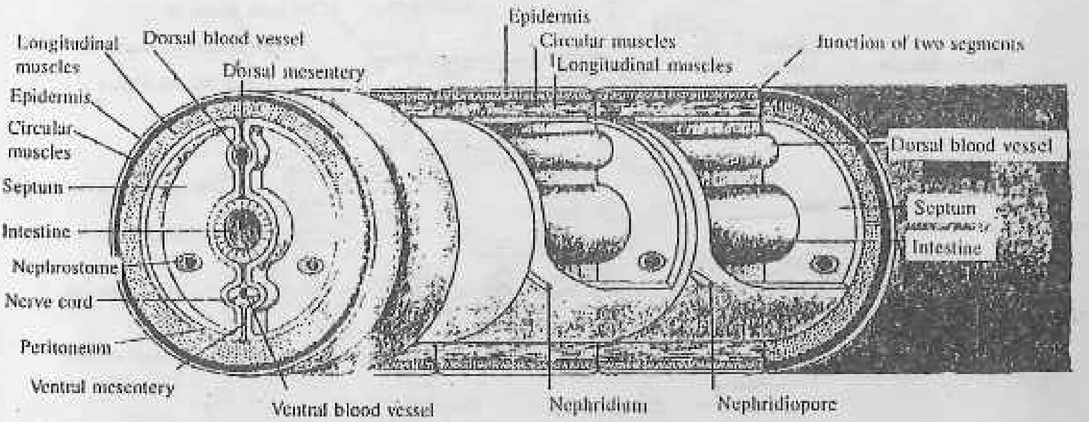


Fig. 1.3A : Annelid segments and anatomy

the right where their wall about above and below the gut. Together, they form a partition in the sagittal plane, called a mesentery. The mesentery is composed of a double fold of peritoneum of coelomic epithelium. The mesenteries and the septa divide the coelom into two separate fluid-filled compartments. As an accommodation to serve the primary segmentation of the coelom, the lateral nerves of the body wall musculature, blood-vessels and excretory organs are also segmentally arranged with the development of a visceral musculature from the associated mesoderm, and mesentery; thus movement of the digestive tract becomes easy (See Figs. 1.3B, C).

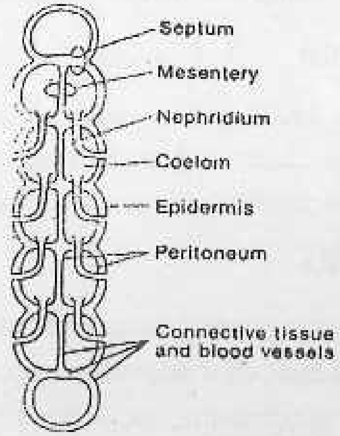


**Fig. 1.3B** : Dorsal view showing septa and coelom

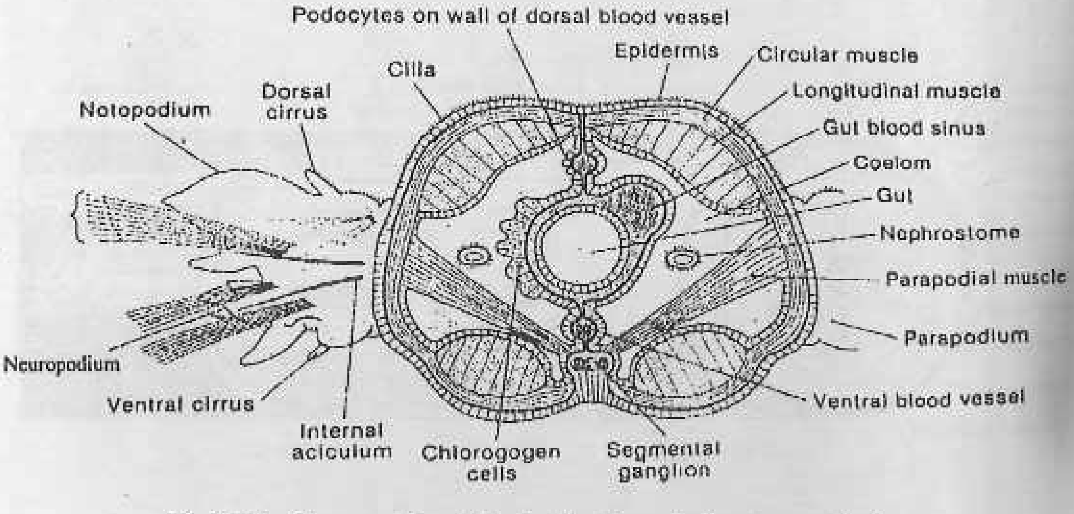


**Fig 1.3C** : Cross section of trunk showing polychaete organization

The coelomic fluid serves as a medium of transport. The excretory organs, whether nephridia or coelomoducts, open into the body cavity and extract dissolved nitrogenous waste from it. The coelomic fluid also has an important role in osmoregulation. The coelom is also important in reproduction because the gonads arise from the coelomic epithelium, the germ cells mature in it and are eventually discharged through the coelomoducts. These ducts are probably genital in their initial function and only later become concerned with the excretion and osmoregulation. Coelomic fluid functions as a hydraulic skeleton against which the muscles act to change the body shape. Contraction of the longitudinal muscles causes the coelomic fluid to exert a laterally directed force and the body widens. Contraction of the circular muscle causes the coelomic fluid to exert an anteriorly and posteriorly directed force and the body elongates.

There is a functional significance of transverse septa. At any instant, the peristaltic waves of both warms, without septa and with septa, are identical in appearance but the musculature of the non-segmented worm is more active than that of the segmented worm and requires more energy to maintain the proper body shape. Along the body of the non-segmented worm, where circular and longitudinal muscles are contracted maximally, the pressure of the coelomic fluid is at a maximum. As the coelom is unpartitioned, the elevated fluid pressure is transmitted throughout the coelom and must be antagonized by the action of the body wall muscles to prevent aneurism and other deviations from proper peristaltic, wave shape. Segmented animals, on the other hand, isolate changes in fluid pressure to individual segments or groups of segments. As a result, body regions between contracted segments do not experience high fluid pressures and need not contract fully or at all to maintain the preferred shape of the body.

### 1.4.4 Coelom in Arthropoda

The well-developed segmented coelom of annelids has undergone drastic reduction in Arthropoda, and is represented by only the cavity of the gonads and in certain arthropods by the excretory organs. In the early development, segmental blocks of mesoderm (future coelomic cavities) are conspicuous, where as the connective tissue compartment is relatively inconspicuous. Later, the connective tissue compartments enlarge greatly to form a haemocoel and the mesodermal somites become restricted to the cavities of the gonads and excretory organs.

## 1.4.5 Coelom in Chaetognatha and Hemichordata

Coelom so far discussed is quite different from the coelom which will now be discussed as regards its embryogenesis.

Coelom in chaetognaths is compartmented and lined by a mesothelium and a thin non-contractile peritoneum. The head contains a single coelomic space that is separated by a septum from the paired trunk coelomic spaces. Another septum separates the trunk from the one or two coelomic compartments that occupy the tail. The chaetognaths are tricoelomate in organization.

Hemichordates, were once classified as chordates along with vertebrates. When homology of the chordate notochord and a similar structure in hemichordates was thrown into doubt, the hemichordates were removed from the chordates and was given the status of a separate phylum. But the biology of hemichordates continues to be a source of information as regards chordate evolution. Hemichordates are tricoelomates like most lophophorates, chaetognaths and echinoderms. A Single unpaired protocoel occupies the proboscis, a pair of mesocoels are found in the collar and a pair of metacoels are found in the trunk. Protocoel opens to the exterior on the proboscis stalk via small opening. Each mesocoel has a duct that leads to the

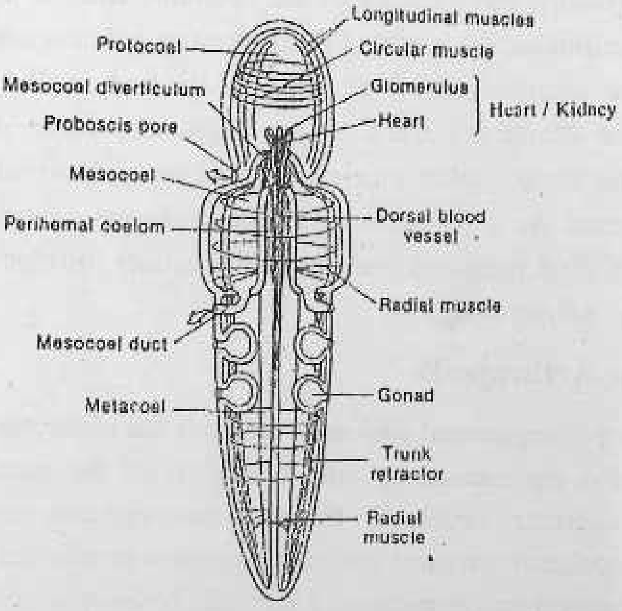


**Fig. 1.4 :** Musculature, blood-vascular and coelomic organization of enteropneusts, dorsal view. Note that a single unpaired protocoel occupies the proboscis, a pair of mesocoels in the collar and a pair of mesocoels in the trunk.

exterior by way of the first gill pore. Metacoel lacks coelomic ducts. Diverticula may develop from one coelomic region and project into another.

### 1.4.6 Coelom in Echinodermata

During development in echinoderms, a pair of lateral pockets or pouches separate from the archenteron. These cavities or pouches represent the future coelomic cavity and the cells comprising the pouch wall become the mesoderm. The two original pouches, one on each side, give rise by sub-divisions, to coelomic vesicles, arranged one behind the other and called respectively, the **axocoel**, the **hydrocoel** and the **somatocoel**. These coelomic vesicles correspond to the **protocoel, mesocoel** and **metacoel** of hemichordates. The two somatocoels meet above and below the gut to form gut mesenteries. The left axocoel opens dorsally through a pore called the hydropore.

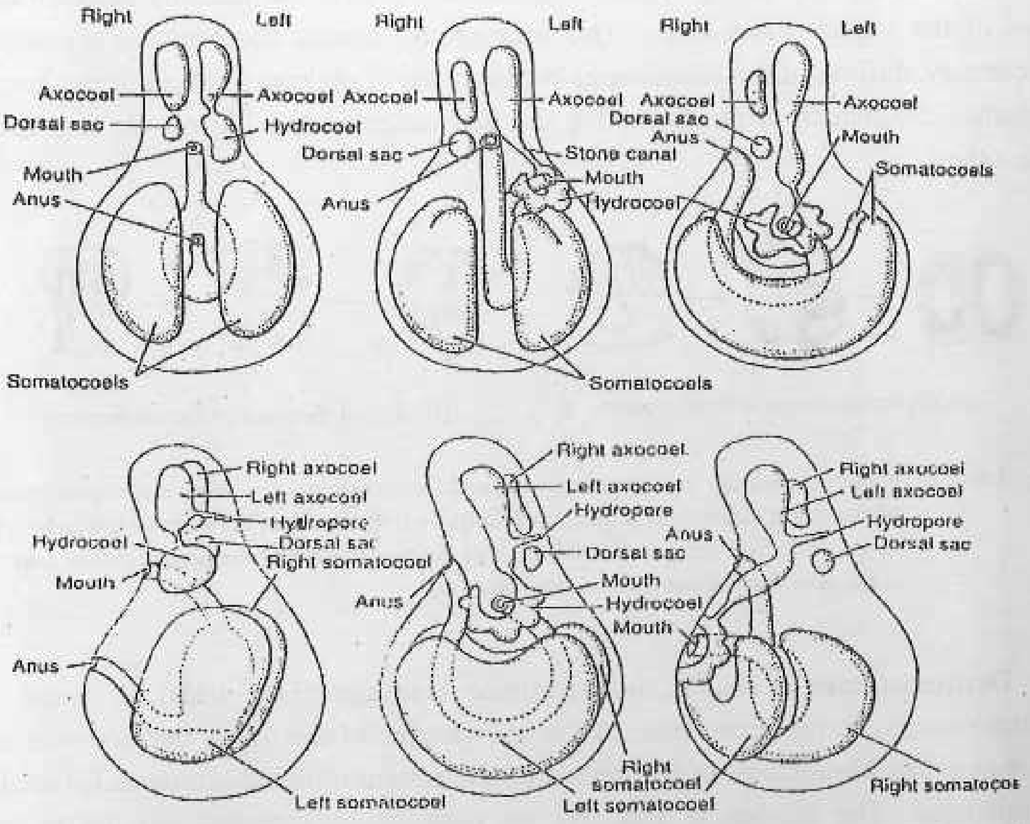


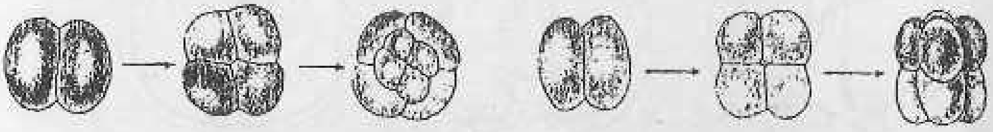
**Fig. 1.5 :** Generalized echinoderm metamorphosis showing development of coelom from the pouches or pockets separated from the archenteron. Enterocoelous development of the coelom as in other deuterostomes.

## 1.5 Protostomes and Deuterostomes

Protostomes and deuterostomes are the two coelomate divisions of the Bilateria. Protostomes include Molluses, Arthropods, Annalids and some other minor phyla. The other great division of bilateria is the deuterostomes lineage. Phyla in this division include Chaetognatha, Echinodermata, Hemichordata and Chordata. These two groups differ from each other in the following aspects.

### 1.5.1 Nature of cleavage

**Protostomes** : Spiral and determinate cleavage (Fig. 1.6A) are found in protostomes. In spiral cleavage, the planes of cell division are diagpnal to the vertical axis of the embryo. As seen in the eight-cell stage resulting from spiral cleavage, small cells lie in the grooves between larger underlying cells. So they come to lie not over the corresponding vegetal blastomeres but over the junction between each two of the vegetal blastomeres. This arrangement comes about not as a result of secondary shifting of the blastomeres but becomes of oblique position of the mitotic spindles. So that from the beginning the two daughter cells do not lie one above the other.


(A) Spiral cleavage in Protostomes

(B) Radial cleavage in Deuterostomes

**Fig. 1.6A, B** : Nature of cleavage in Protostomes (A) and Deuterostomes (B). Note that in protostomes where spiral cleavage is found, small cells lie in the grooves between larger underlying cells; while in deuterostomes (B) each of the blastomeres of the upper tier lies over the corresponding blastomeres of the lower tier.

**Deuterostomes** : Radial, indeterminate cleavage (Fig. 1.6B) is found in deuterostomes. In this case, each of the blastomeres of the upper tier lies over the corresponding blastometes of the lower tier, the pattern of the blastomeres is radially symmetrical. The furrous in this type of cleavage are oriented parallel to and perpendicular to the animal-vegetal axis of the egg. In deuterostome, indeterminate cleavage is found. Here, each cell produced by early cleavage division retains the capacity to develop into a complete embryo. If the cell of a sea urchin embryo, for example, is separated of the four-cell-shage, each will go on to form a normal larva.

### 1.5.2 Fate of blastopore

Another difference lies within fate of blastopore in protostome and deuterostome. In gastrulation, the rudimentary gut of an embryo forms as a blind pouch (the archenteron) which has a single opening to the outside known as the blastopore. In Protostome, this opening (blastopore) forms the mouth and a second opening, formed as the opposite end of the archenteron forms the anus. In deuterostomes, the blastopore forms the alms and the mouth is divided from a secondary opening.

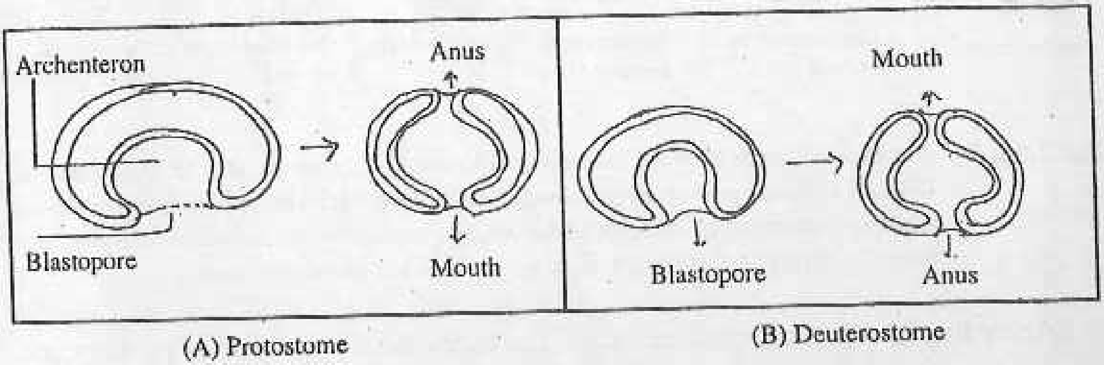


**Fig. 1.7 :** Fate of blastopore in Protostome (A) and Deuterostome (B). In (A) blastopore form the mouth and a second opening at the opposite side from the anus. In (B) blastopore forms the anus and the mouth is derived from a secondary opening.

### 1.5.3 Development of coelom

A third fundamental difference between protostomes and deuterostomes is the development of the coelom. In protostome, schizocoelous development occurs. As

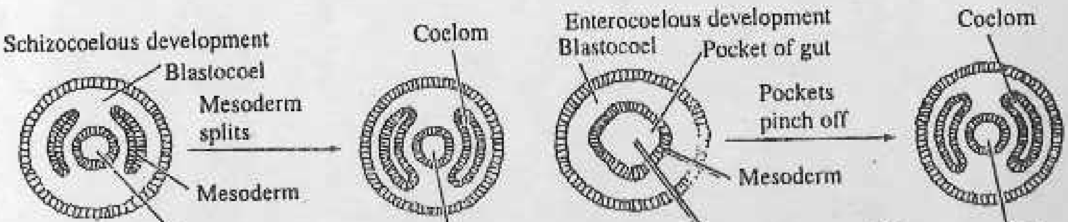


**Fig. 1.8A, B :** Development of coelom in Protostomes (A) and deuterostomes (B). Note the difference in schizocoelous and enterocoelous type of coelom development.

the archenteron develops, solid masses of mesoderm split to form the coelom. In deuterostomes, the mesoderm buds off from the wall of the archenteron and hollows to become the coelomic cavities. This type of development of the coelom is called enterocoelous development.

## 1.5.4 Evolutionary aspects

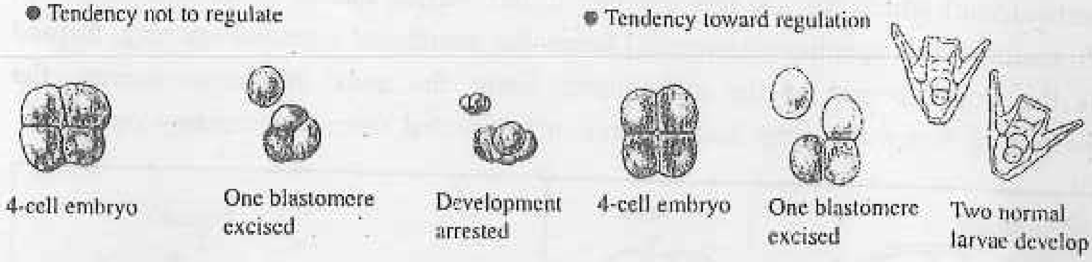


**Fig. 1.9A, B** : Another difference between Protostome (A) and Deuterostome (B). In Deuterostome (B) each cell produced by early cleavage retains the capacity to develop into a complete embryo (indeterminate cleavage) whereas, in Protostome the individual cell does not have the ability to form a complete embryo (determinate cleavage).

According to the schizocoelous theory, the acoelomate body plan is primary and ancestral to the coelomate plan. The acoelomate flatworms are the stem group in the evolution of bilateral animals. The enterocoel theory proposes that all bilateral animals are basically coelomate and that acoelomate forms, such as the flatworms, are secondarily derived from coelomate ancestors by loss of the cavity. However, the enterocoel theory has never gained much acceptance because it is difficult to postulate functional steps that would have led to a change in both design from coelomate to acoelomate and symmetry from bilateral to radial.

# Unit 2 ❒ Locomotion

***Structure***

**2.1 Flagella and ciliary movement in Protozoa**

**2.2 Hydrostatic movement in Cnidarians, Annelids and Echinoderms**

## 2.1 Flagella and ciliary movement in protozoa

The protozoan locomotor organelles may be flagella, cilia or flowing extensions of the body called pseudopodia. Flagella and cilia are hair like structures but are effective organelles and occur repeatedly throughout the higher animal phyla.

### 2.1.1 Structural aspect

On a functional level, it is relatively easy to distinguish between flagella and cilia. But the distinction is not sharp and their ultrastructure is identical. Flagella and cilia arise from a basal body (or kinetosome) located in the ectoplasm adjacent to the plasma membrane. There is also evidence that basal bodies contain DNA and perhaps have some powers of self replication. A highly organized bundle of microtubules originates from the basal body and projects outward to form the central axis of the flagellum or cilium. The microtubular bundle, or axoneme, consists of two central tubules encircled by nine double tubules (Fig 2.1). The axoneme is surrounded by a plasma membrane continuous with that of the entire organism. Microtubules are composed of protein sub-units that are rather similar, even though they are found in variety of cell types. The term **tubulin**, used for the principal protein of cilia and flagella, is also used for the protein of cytoplasmic microtubules. Tubulin is a dimer of 110,000 to 120,000 daltons. The monomers of similar size are believed to be composed of 4 nm × 6 nm subunits. It has been shown that two different monomers—tubulin A and tubulin B are present in flagella. In most cases, tubulin is a heterodimer having two monomers of different kinds although they are quite similar in molecular weight.

The paired peripheral microtubules have an ellipsoidal profile where as the central ones are circular. The peripheral doublets are skewed at about 10 degrees, so that one tubule, termed as subfibre A like closer to the axis than the other (subfiber B). The microtubule of subfibre A is smaller, but complete, where as their of subfibre B is larger and incomplete since it lacks the wall adjacent to A. In fact, while A has 13 tubulin subunits, B has only 11. Furthermore, subfibre A has processes the so called **dynein arms**—that are oriented in the same direction in all the microtubules. The orientation is clockwise when the axoneme is viewed from base to tip.

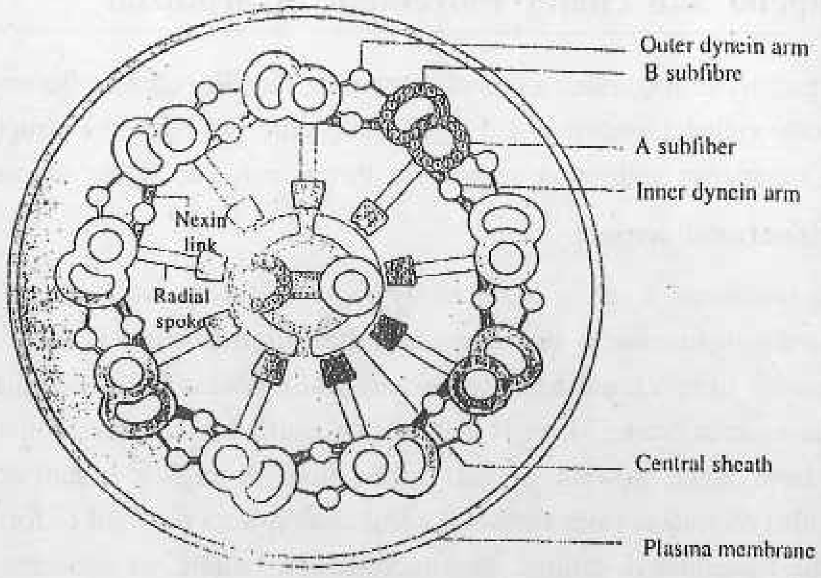


**Fig. 2.1** : Diagram of a cilium or flagellum seen in cross section. Note that the micro tubular bundle or axoneme consists of two central tubules encircled by nine double tubules and that subfibre B is larger than subfibre A. Subfibre A is complete whereas B is incomplete. Subfibre A has inner and outer dynein arms. Radial spokes can be seen between central sheath and subfibre A. The doublets are connected by nexin.

The arms of subfibre A are generally called dynein arms because they contain dynein, a higher molecular weight ATP-ase. The interaction between tubulin and dynein is thought to underlie the basic mechanism of ciliary and flagellar motion.

The peripheral doublets are linked by interdoublet or nexin links. This is a separate protein component isolated from these links. The function of these links is unknown but they many serve as stimulators that maintain the geometric integrity of the axomeme during the sliding motion. There occur some links or radial bridges between subfibre A and the sheath containing the central microtubules. These spokes terminate in a dense knob or head, which may have a fork like structure. The observations that the spokes are attached perpendicularly with ciliary axis where it is straight and that they are relatively detached in bent or tilted regions or the axis have led to the hypothesis that they may be active in the conversion of active shading between the outer doublets into local axial bending.

The basal body forms the template in which developing axonemes are organized. Basal bodies, in fact, have an ultrastructure like that of an axoneme except that the central singlets are absent and the nine fibrils in the outer circle are triplets, two of the three being continuous with the doublets of the flagellum (Fig. 2.2). Dynein arms are absent on the triplets. A basal body (and its cilium or flagellum) are usually

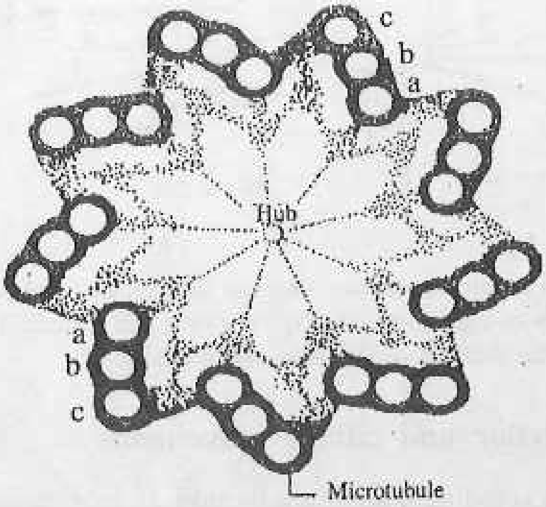


**Fig. 2.2** : Diagram of the basal body (also centriole) seen in cross section. Note that the central singlets are absent. Dynein arms are absent. Nine fibrils in the outer circle are in triplets. Strands of materials extend inward from each tubule and join at the central hub.

anchored in the cell, often to the nucleus and cell membrane, by one or more root structures. The proteinaceous rooflet fibres are contractile and can, on contraction, pull the flagellum into a shallow pocket or alter its orientations. Cilia and flagella originate from basal bodies (Fig. 2.3). The ultrastructure of a flagellum or cilium is shown in Fig. 2.3.

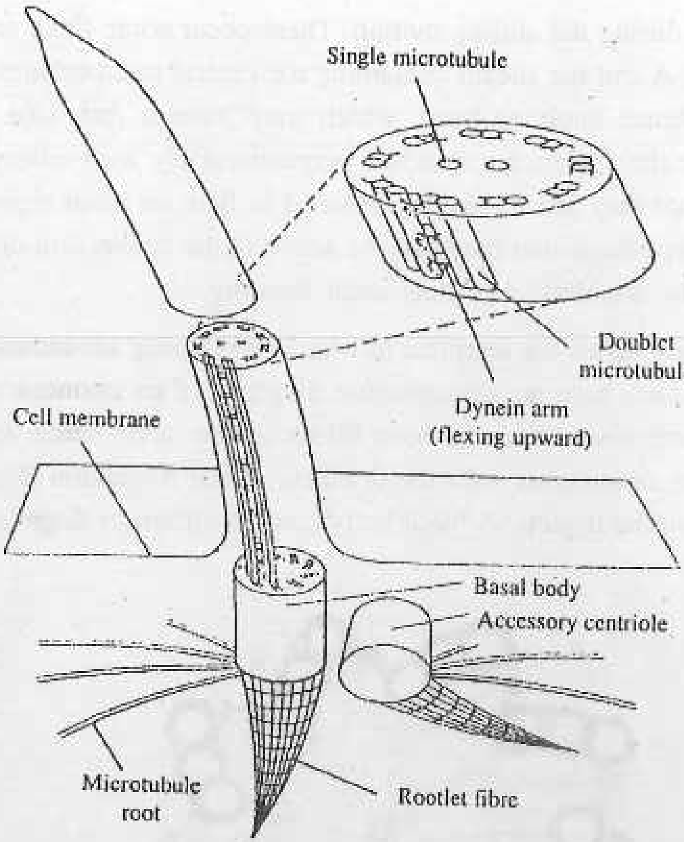


**Fig. 2.3 :** Ultrastructure of a flagellum or cilium. Diagram showing the basal body and its connection with the flagellum or cilium immediately below the cell surface. Two of the triplets are continuous with the doublets of the flagellum or cilium.

## 2.1.2 Nature of flagellar and ciliary movements

Flagella bend with a standing undulating motion. In most cases, waves originate from the flagellar base and pass outward along the shaft; oppositely directed impulses are rare but do occur (Fig. 2.4A). The entire undulation either is confined to a single plane or it describes a helix. Flagellar action exerts forces on the surrounding medium in the direction of wave propagation (Fig. 2AC). Mastigonemes, tiny lateral projection along the shaft, increase the surface area of the organelle and thus improve its capacity to push against the environment. Mastigonemes influence the direction of water flow along the flagellum and thereby steer the organism.

Bending of the flagellum is caused by active gliding of adjacent doublets past each other. The dynein side arms are in doublets provide the gliding force. In the presence of adenosine triphosphate (ATP), the arm on one doublet attaches to an adjacent doublet and flexes, causing the doublets to glide past each other by one increment. Successive attachments and flexes cause the doublets to slide smoothly passed one another over a distance sufficient to bend the flagellum (Fig. 2.6).

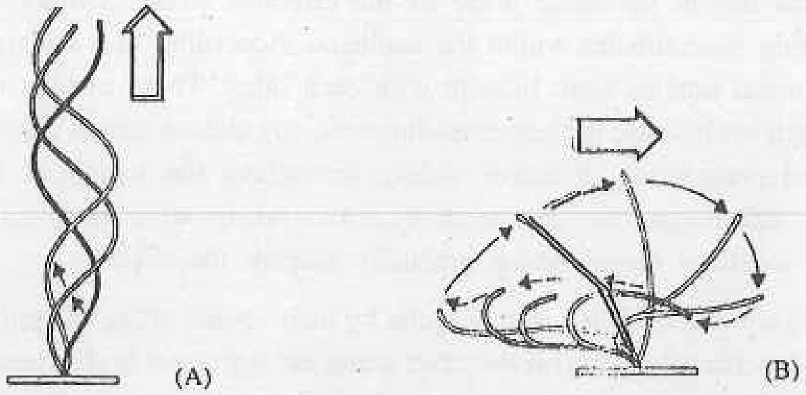


**Fig. 2.4A, B** : Two typical patterns of flagellar and ciliary motion. (A) Flagella bend with a standing undulatory motion. In most cases waves originate from the flagellar base and pass outward along the shaft. (B) The power stroke ofa cilium is similar to the action of an oar in a row boat; the recovery stroke (in dotted lines) may not take place in the same plane as the power stroke. The large arrows show the direction of movement of the surrounding liquid.

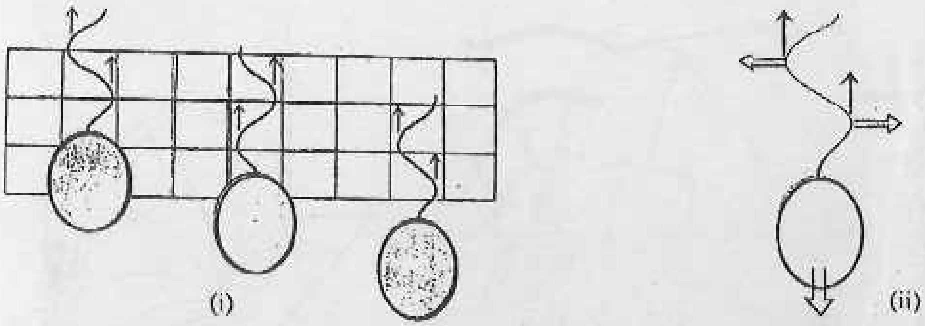


**Fig.2.4C** : Flagellar propulsion. Flagellar action exerts forces on the surrounding medium. (i) Base to-tip wave propagation. (ii) Forces generated by base-to-tip wave propagation. Lateral forces (outlined arrows) cancel each other longitudinal forces (solid arrows) combine to produce forward thrust in the opposite direction.

In contrast to flagellar undulations ciliary movements are of a stroking nature. Cilia are often compared to the oars of a rowboat (Fig. 2AB). The shaft stiffens through a quick, effective storke and then bends as a slower recovery stroke brings the organelle to its original position. The recovery stroke is typically is counter clockwise and nor in the same plane as the effective stroke. Ciliary movement involves sliding microtubules within the axoneme. According to a widely accepted theory, peripheral tubules form linkage with each other. These tubules maintain a constant length but because of their cross-linkages, any sliding causes cilium to bend. An organized programme of active sliding throughout the length of the cilium produces the effective stroke. The recovery stroke occurs when reversed sliding is limited to a localized region which gradually ascends the shaft.

Cilia also are distinguished from flagella by their coordination. Flagella are quite independent functionally. Cilia on the other hand, are organized both structurally and functionally and their coordinated strokes produce faster and more precisely controlled locomotor patterns. Cilia do not beat simultaneously but rather sequentially in each longitudinal row. The sequential activation of cilia over the surface of the cell is seen as waves, called metachronal waves. (Fig. 2.5). In this beat each cilium performs an effective and a recovery stroke. During the effective stroke, the cilium is outstretched stiffly and moves, like an oar, from a forward to a backward, position in a plane

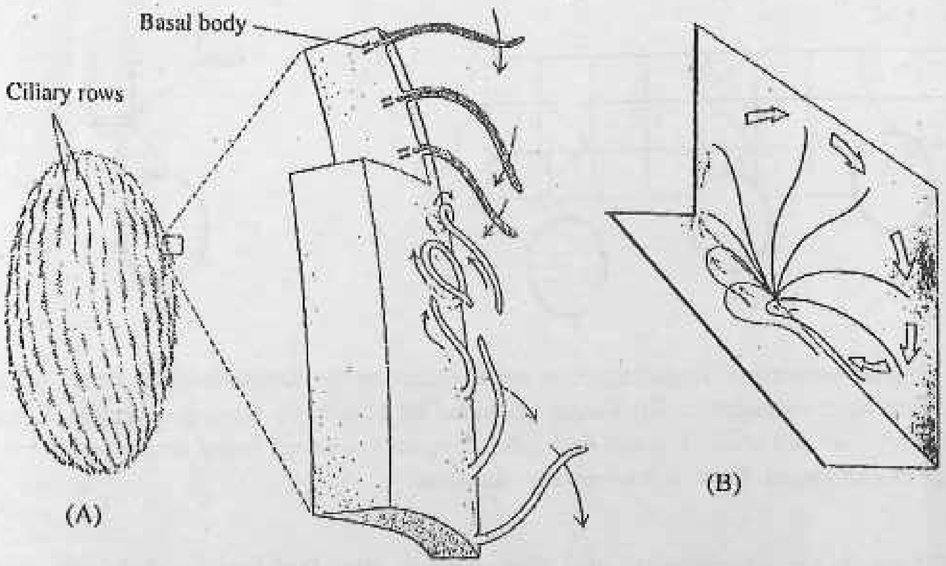


**Fig. 2.5A :** Metachronal wave of ciliary beating. Along the length of a row, the cilia are in a sequential stages of the beat cycle over the surface of the cell.

B : The effective forces (outlined arrows) are recovery (solid arrows) strokes in the beat cycle of a single cilium.

perpendicular to the body surface. In the recovery stroke in cilium flexes and sweeps forward, snakelike, close to and in a plane parallel to the body surface. Effective strokes are directed in a slightly diagonally posterior direction. Such an arrangement causes a ciliate to rotate as it moves along a spiral path. Although the search for intracellular control systems continues, there is only limited evidence that the infraciliature or the cytoplasm plays a major role in ciliary coordination. Most probable is the theory that cilia beat in organized patterns simply because the cilia are stimulated simultaneously and / or because the cilia themselves stimulate each other mechanically, and a so-called hydrodynamic linkage occurs between adjacent cilia.

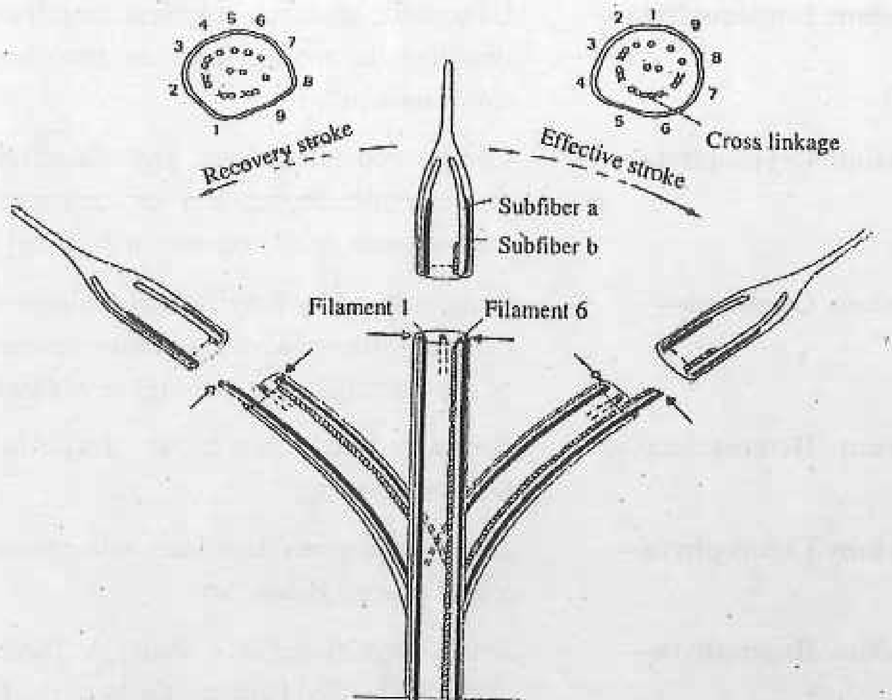


Fig. 2.6 : The sliding filament hypothesis of ciliary motility. The nature of two double filaments (1 and 6) is illustrated when a cilium is bent to either side of a straight position.

### 2.1.3 Flagellated and Ciliated protozoa

**(A) Flagellated Protozoa :** All flagellated protozoans are included in either of the fallowing phyla.

| | |
|---|---|
| (i) **Phylum Dinophyta**— | Dinoflagellates. Phytoflagellates with an equatorial and a posterior longitudinal flagellum located in grooves. e.g. ***Noctiluca*** sp. |
| (ii) **Phylum Parabasalia**— | Zooflagellates with forms fewer to many flagella. e.g. ***Trichonympha*** sp. |
| (iii) **Phylum Metamonada**— | Multiflagellates, Zooflagellates. e.g. ***Trichomonas*** sp, ***Giardia*** sp. |
| (iv) **Phylum Kinetoplastida**— | One or two flagella emerging from a pit. e.g. *Trypanosoma* sp, *Leishmania* sp. |
| (v) **Phylum Eugleuophyta**— | Elongated, green or colorless flagellates with two flagella arising from an anterior recess. e.g. ***Euglena*** sp. |
| (vi) **Phylum Cryptophyta**— | Compressed biflagellate, phytoflagellate, with an anterior depression or reservoir. e.g. ***Chilomonus*** sp. (Common in polluted water). |
| (vii) **Phylum Opalinata**— | Body covered by longitudinal, oblique rows of cilia (not true cilia, infrastructure characteristic of the true ciliates is lacking). e.g. ***Opaline*** sp. |
| (viii) **Phylum Heterokonta**— | Having two dissimilar flagella. e.g. ***Ochromonas*** sp. |
| (ix) **Phylum Chlorophyta**— | Autotrophic green flagellates with chloroprhylls a and b. e.g. ***Volvox*** sp. |
| (x) **Phylum Haptophyta**— | Small phytoflagellates living a flagella-like organella located between the two true flagella. e.g. ***Coccolithus*** sp (marine). |
| (xi) **Phylum Choanoflagellide**— | Zooflagllate, with a single flagellum surrounded by a collar of microvilli e.g. ***Proterospongia*** sp. |

Locomotion in flagellates is done by flagella and most species possess two flagella. They may be of equal or unequal length, and one may be leading and one trailaing as in dinoflagellates. Flagellar propulsion follows essentially the same principle as that of a propeller, the flagellum undergoes undulations that either push or pull. The undulatory waves pass from base to tip and drive the organism in the opposite direction, or more rarely, the undulations pass from tip to base and pull the organision. Hydrodynamic effect of flagella with mastigonemes causes the flagellum to pull rather them push even though the flagellar waves are passing from base to tip.

(B) **Ciliated protozoa :** The phylum ciliophora is the largest and most homogeneous phylum in which all ciliated protozoa are included. All evidences indicates that its members share a common evolutionary ancestry. All possess cilia or compound ciliary structures as locomotor or food-capturing organelles at same time in the life cycle. Also present is an infraciliary system, composed of ciliary basal bodies or kinetosomes, below the level of the cell surface and associated with fibrilss that run in various directions. Ciliates are the fastest moving protozoa. Hydrodynamic forces impose a coordination on the cilia. The beat of individual cilia, rather than being random or synchronous, is part of the metachromal waves that sweep along the length of the body. There is no evidence that the infra ciliature functions as a conducting system in coordination. It may serve primarily in ciliary anchorage and controlling cell shape.

In ***Paramoecium*** sp., the direction of the effective ciliary stroke is oblique to the long axis of the body. This causes the ciliate to swim in a spiral course and at the same time to rotate on its longitudinal axis. If the organism wants to avoid reaction it can do so by reversed ciliary beating. The backward movement is for a short distance and then it terns slightly clockwise or anticlockwise and moves forward again. External stimuli are probably detected through the cell membrane. The direction and intensity of the beat are controlled by changing levels of $Ca^{2+}$ and $K^+$ ions.

In highly specialized hypotrichs, like ***Euplotes*** sp., ***Urostyle*** sp. body cilia are modified. The body has become differentiated into distinct dorsal and ventral surfaces and cilia have largely disappeared except on certain areas of the ventral surface. Here cilia occur as a number of tufts, called **cirri**. The cilia of cirrus beat together and coordination is believed to result from viscous forces between the closely associated cilia.

## 2.2 Hydrostatic movement in Cnidarians, Annelids and Echinoderms

Invertebrates commonly use a hydrostatic skeleton for hydrostatic movement. An organism unit uses water contained in a body compartment for support and for transmission of muscular forces is said to have a hydrostatic skeleton. Hydrostatic skeletons are enclosed by the body wall and are, by necessity, endoskeletons. This hydrostatic skeleton features a contained body of fluid. Hydrostatic skeletons exploit in fact that water easily adapts to various container shapes, but cannot be compressed in volume. In invertebrates with hydrostatic skeletons, fluid is contained within a closed, usually tube-shaped cavity surrounded by two or more layers of muscles arranged at right angles to one another, commonly in longitudinal and circular patterns Fig. 2.7. Contraction of the circular muscles causes the contaminated fluid to exert pressure against the end walls of the cavity, elongating the cavity and stretching the longitudinal muscles in the process. Longitudinal contractions have the opposite effect and result in a shorter wider cavity and stretched circular muscles. By alternately contracting these muscles layer, invertebrates with hydrostatic skeletons manage general body movements, including creeping, crawling and swimming.

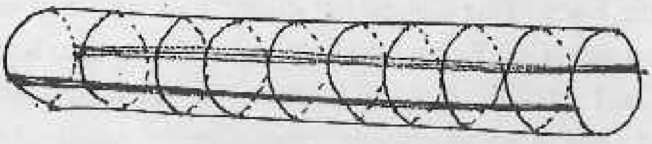


**Fig. 2.7 :** A hydrostatic skleleton features an enclosed volume of fluid with surrounding circular and longitudinal muscle autogtnisos. Contraction of circular muscles produces a thinning and lengthening of the body while contraction of the antagonistic longitudinal muscles produces a thickening and shortening of the body.

### 2.2.1 Hydrostatic movement in coelenterata

A coelenterata can react to its environment as a whole organism, responding in a neuromusclliarly coordinated manner to environmental stimuli. The coelenteron at polypoid forms performs excellently as a hydrostatic skeleton. Filled with water and punched shut by oral sphincter muscles, it becomes a shift tube manipulated by body wall muscles. Accordingly, polyps can lean, squat, twist and now from side to side.

Solitary polyps may creep slowly along the substratum by graded contractions of circular muscles in the pedal disk. Others paddle with their muscular tentacles perform same results. Such active behaviour, rare among polyps, is typical of medusoid coelenterates. Contraction of strong circular muscles of its subumbrella rapidly expels water from the lower skits of the medusa, jetting the airmail away. These muscles are stretched by the elasticity of the thick mesoglea layer. Medusae exercise limited directional control over their water jet. Controlled movements are confined largely to the vertical plane, and horizontal travel is dominated by sea currents.

In sea anemone, ciliated channels, called **siphonoglyphs** are located at one or both ends of the mouth These continue on to the pharynx and pumps water into the bag like coelenteron. Continuous beating of the cilia pumps sufficient water into the anemone to inflate the column and the hollow tentacles that are continuous with the coelenteron. The mouth closes and the cilia continue to beat to maintain a positive pressure within the coelenteron and provide sea water as the fluid for the hydrostatic skeleton. Muscle fibers in the column wall are organized in a circular configuration around the circumference of the column. Contraction of these muscles causes the column to decrease the diameter. As the column decreases in diameter, the water trapped in the coelentenon, since it is not compressible, forces the column to elongate. Elongation of the column causes the muscle fibers of the mesenteries, which are arranged parallel to the long axis of the column, to be stretched. When these longitudinal muscles contract the column shortens, the circular muscles in the column wall are stretched; and the diameter of the column increases. In response to vigorous stimule, the longitudinal muscle contracts and the mouth opens, forcing the water out of the coelenteron and flattening the sea anemone against the bottom. Compression ression of the enclosed fluid, be it sea water, body fluid or blood, by the contraction of one set of the antagonistic muscles causes the stretching of the other set of the antagonistic pair. This, the hydrostatic thing allows the animal's body to achieve a degree of rigidity sufficient to allow the muscles toward against one another and is identical as a hydrotatic skeleton. In the sea anemone movement is achieved even through it stands in one plan. The anemone is able to extend its column and tentacles, carry captured food to its mouth, put in its tentacles and flatten itself when in danger (Fig. 2.8 & 2.9).

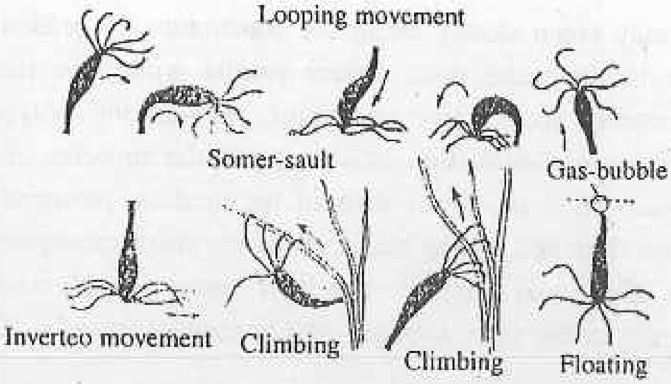


**Fig. 2.8 :** Different types of movement in Hydra. Normally the Hydra moves by a Soemr salting or looping type of movement

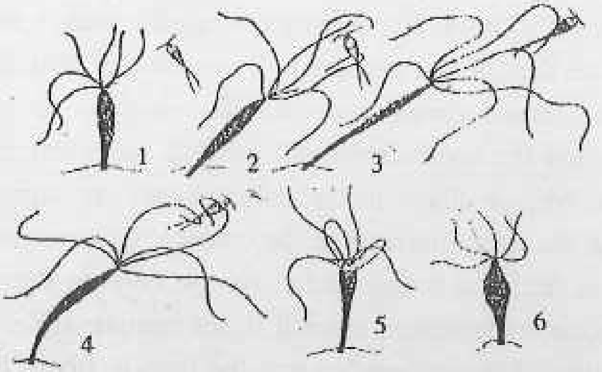


**Fig. 2.9 :** Movement of Hydra while capturing food. Movements are brought about by hydrostatic activities.

## 2.2.2 Hydrostatic movement in annelida

The movement of most annelids worms are controlled by hydrostatic skeleton. Polychaetes have a wide variety of locomotory adaptations depending on their lifestyle and body design. Some have well developed parapodia, and setae. Some use reversible pharynx to pinch and anchor in the sediment and then, upon retraction, to pull themselves forward. Some produce rapid lateral undulations of the body and laterally swim through loosely consolidated sand. Some show peristaltic movement specially burrowing as they have elongated bodies, reduced parapodia and head appendages. But these movements are the result of combined action of parapodia (appendages), musculature and to some extent the hydrostatic action of the fluid-filled coelom.

Oligochaetes move by peristaltic contraction. Movement in earthwarm has been studied in details by many authorities. Circular muscle contraction and the consequent elongation of segments are most important in crawling and these always generate a coelomic fluid pressure pulse. In a earthworm the body cavity of each segment of the trunk is separated from that of the next by a partition, so that the segmented body possesses a series of more or less isolated coelomic fluid-filled spaces of fixed volume. The body wall contains circular and longitudinal muscles and some minor muscles. As a worm crawls or burrows, a group of segments shorten and widen, their total volume remaining the same; contact with the ground is maintained by setae. Groups of short, wide segments are formed at intervals along the body; the segments between these groups are longer, narrower, and not in contact with the ground. As the worm crawls, the thickened zones appear to travel backward along the body because the segments just behind each zone thicken and widen and thing to the ground, while the segments at the front and of each wide zone free themselves from the ground and become longer and narrower. Thus, the head end of the body intermittently progresses forward over the ground or enter a crevice as the longitudinally extending segments are continuously being lengthened a outward from the front end of each thickened zone. It is therefore, only the long narrow segments that are moving forward. This mechanism of crawling by the alternate and antagonistic action of the longitudinal and circular muscles is made possible by the hydrostatic action of the incompressible coelomic spaces (Fig. 2.10).

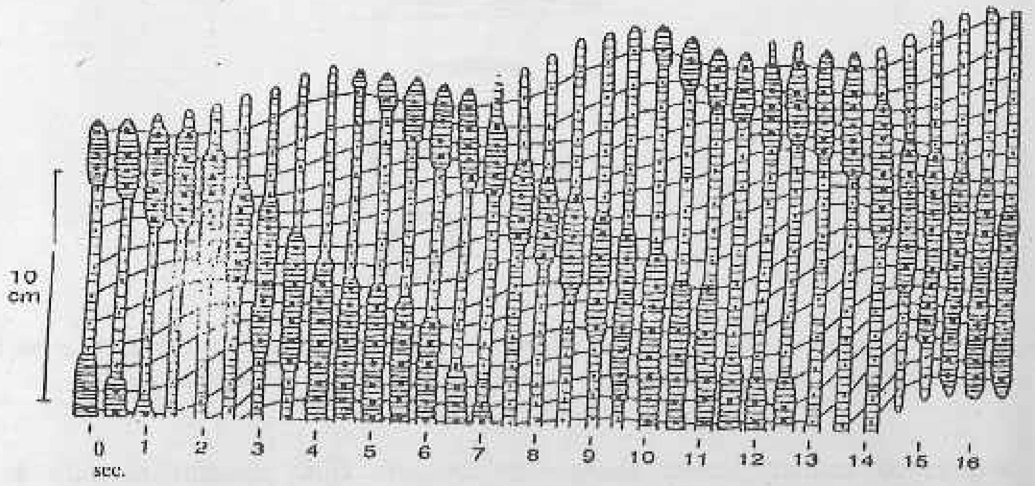


**Fig. 2.10** : Diagram showing mode of locomotion of an earthworm. Segments undergoing longitudinal muscle contraction (marked with larger black dots) are wider than those undergoing circular muscle contraction (marked with small dots). The forward progression of a segment during the course of several waves of circular muscle contraction is indicated by the horizontal lines connecting the same segments.

In Hirudinea, the body-wall consists of a typical annelidan cuticle and epidermis but unlike polychaetes and most oligochaetes, the fibrous connective tissue beheath the epidermis is very thick and it occupies much of the iriterior of the body. In leeches, septa have disappeared and the coelom has become reduced and specialized into a circulatory system composed of interconnected sinuses and channels. Movement of leeches is a crawling movement or swimming; the body is lenghtened or shortened. The diagonal muscles may also enable leeches to twist their raised bodies. They can. flatten the body during swimming by contraction of the dorsoventral musculature. Leeches do not show peristaltic movement. So the movement in leeches is brought about by different types of muscles and the hydrostatic actions of the circulatory system composed of interconnected sinuses and channels (Fig. 2.11).

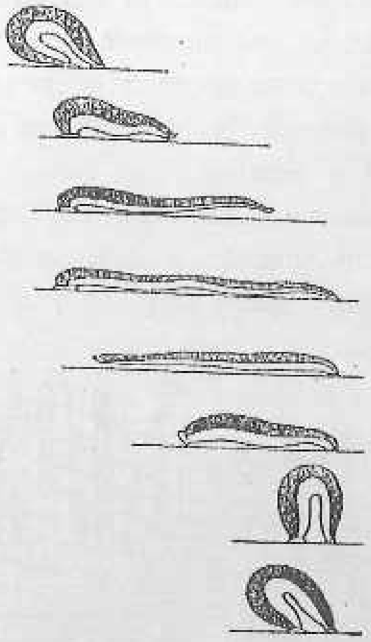


**Fig. 2.11 :** Locomotion in Leech. The body is lengthened and shortened. This is brought about by hydrostatic actions of circulatory system and actions of different muscles.

Segmented animals isolate changes in coelomic fluid pressure to individual segments or groups of segments. As a result, body regions between contracted segments do not experience high fluid pressures and need not contract fully, or at all, to maintain the preferred shape of the body. Along the body of the non-segmented worm, where circular or longitudinal muscles are contracted maximally (regions of minimum and maximum body diameter), the pressure of the coelomic fluid is at a maximum. Because the coelom is unpartitioned, the elevated fluid pressure is transmitted throughout the coelom and must be antagonized by the action of body wall muscles to prevent aneurisms and other deviations from the proper, peristaltic, wave shape (Fig. 2.12).

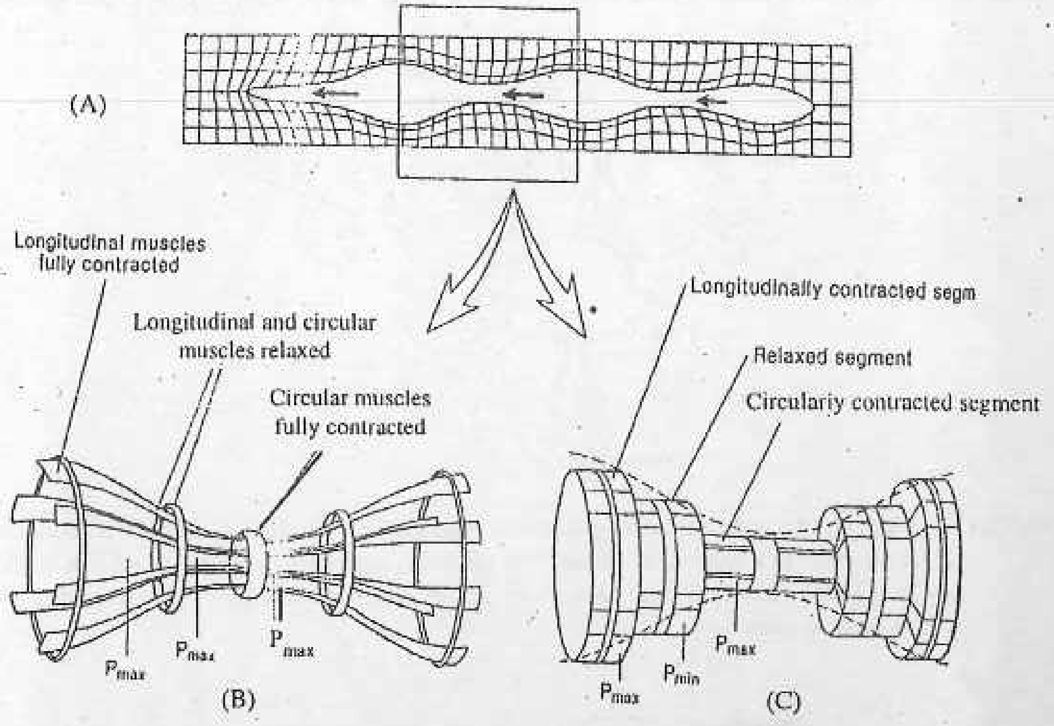


**Fig. 2.12 A** : Peristaltic burrowing.

B : In worms without segmentation. Muscular involvement is much more in nonsegmented worms.

C : In segmented worms muscular involvement is less and fluid pressure maxima are localized to a few segments.

$P_{min}$—maximal pressure in hydrostat

$P_{min}$—mininal pressure in hydrostat.

## 2.2.3 Hydrostatic movement in echinodermata

A unique characteristic feature of echinodermata is the **water vascular system**. This system of canals are derived from the coelom and the canals are lined by ciliated epithetium. This water vascular system is well developed in asteroids and functions as a means of locomotion. The entire water vascular system is filled with fluid that is similar to sea water except that it contains coelomocytes, a little protein and a high potassium ion content. The system operates during locomotion as a hydraulic system. The most characteristic effector organ is the **podium** or the **tube feet**, an ambulacral appendage which operates by an antagonistic musculature and a contained volume of watery fluid. The podium and its proximal bulb, the ampulla, are separated from the lateral ambulacral cannal by a valve (Fig. 2.13, 2,14). The closing of this

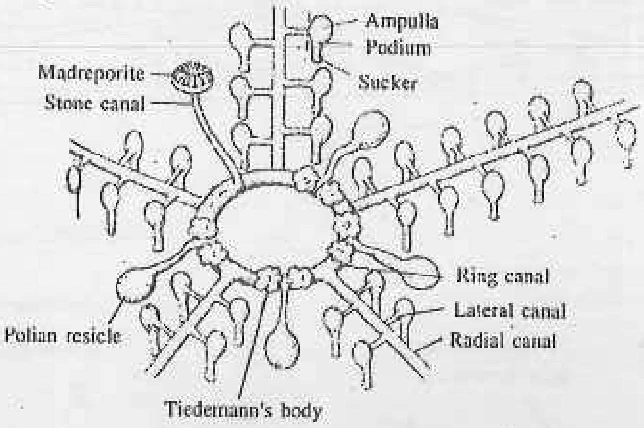


**Fig. 2.13A** Diagram of a water vascular system in asteroids, which functions as a means of locomotion. It operates as a hydraulic system. The effector organ is the podium or tube feet, shown in the picture. The picture also shows the disposition of different canals of they water vascular system.

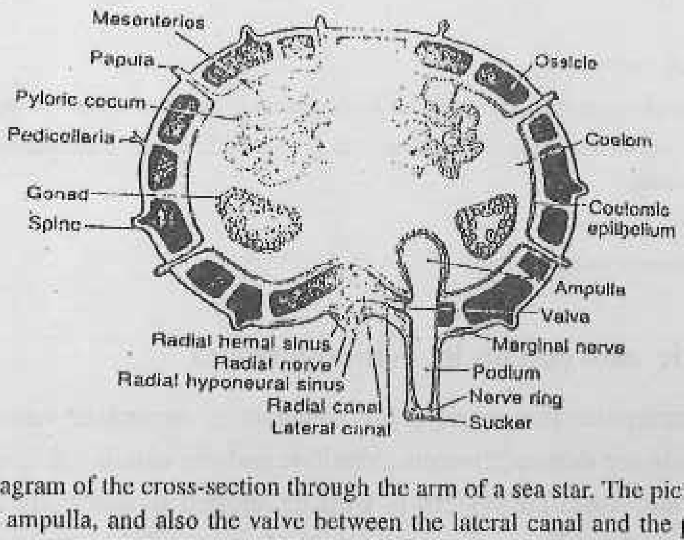


**Fig. 2.13B** Diagram of the cross-section through the arm of a sea star. The picture shows the podium, its ampulla, and also the valve between the lateral canal and the podium which regulate the flow of water in the tube-feet.

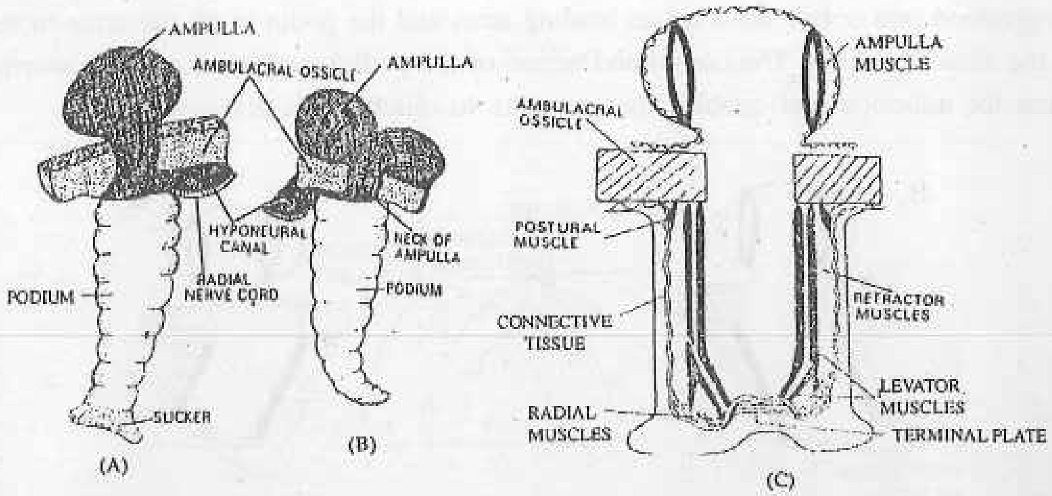


**Fig. 2.14** Diagrammatic view of tube-feet. A : a scheme of ampulla and attached podium with a sucker in *Asterias rubens.* B : The same in *Astropection* sp. with podium without a sucker. C : Arrangement of chief muscles in a longitudinal section through a foot and ampulla.

valve isolates a volume of fluid within the podium. The contraction by circular muscle in the walls of the ampulla forces the fluid into the tube foot proper. The tough dermal walls of the podium prevent radial expansion, so the organ elongates. Longitudinal muscles in the podium contract to shorten the foot, forcing water back into the ampulla and thus stretching the latter's circular fibers. Differntial contraction of longitudinal muscles on opposite sides of the foot causes bending movements, while muscle on the terminal disc may produce suction. The tube feet may pull the echinoderm along by alternate contractions of their circular, terminal and longitudinal muscles or the podia may step forward when longitudinal muscles alternately contract along an extended foot (Fig. 2.15). It has been generally thought that other parts of the water vascular system—the **madriporite**, the **stone canal,** the **ring cannal**, the muscular **pollan vesicles** and the **radial cannel**—perhaps functions in maintaining the proper water volume necessary for the operation of the ampulla and podia, because there is some leakage across the podial wall during fluid pressure elevation. During movement each podium performs a sort of slepping motion. The podium swings forward, grips the substratum and then moves backward. In a particular section of an arm most of the tube feet are performing the same step and the animals moves forward. The action of the polia is highly coordinated. During progression one or two arms act as leading arms and the podia in all the arms move in the same direction. The combimed action of the podial suckers exerts a powerful force for adhesion and enables the sea stars to climb vertically over rocks.

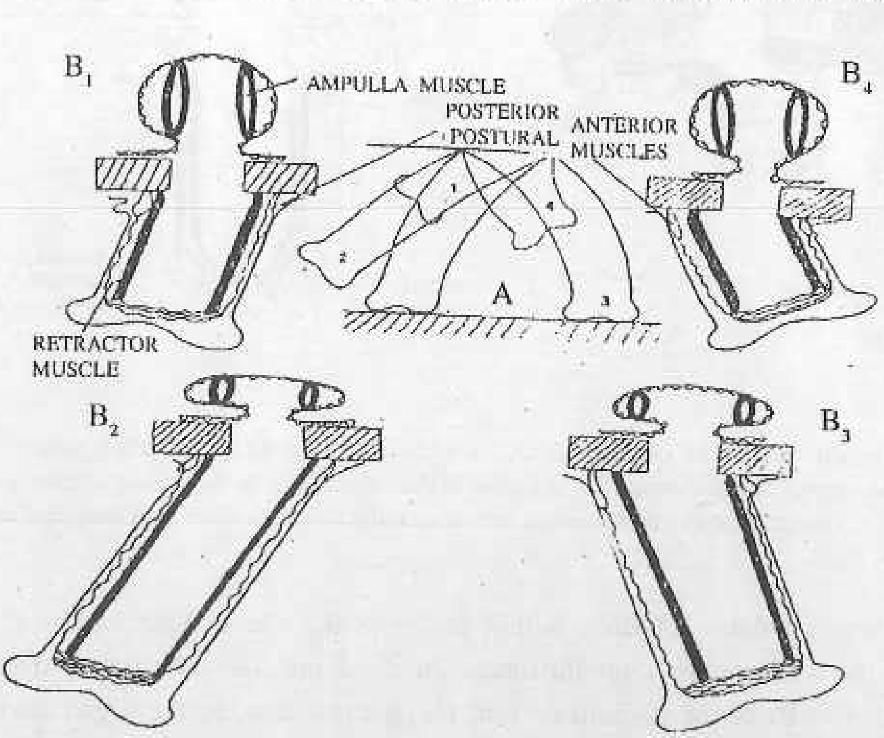


Fig. 2.15 Movement of tubes-feet (Asterias rubens) A—1—4, the successive phases of the ambulatory step $B_1$—$B_4$—conditions of contraction and relaxation of the muscles of tool during successive stages of the static posture of the 'ideal' step. Locomotion is brought about by means of a kind of hydraulic pressure mechamsm.

The ophiurods are the most mobile echinqderms. During movement the disc is held above the substratum, with one or two arms extended forward and one or two arms trailing behind. The remaining two lateral arms perform a rapid rowing movement against the spbstratum that propels the animal forward in leaps or jerks. Brittle stars can move in any direction. In climbing over rocks or in sea weeds and hydroid colonies, the ends of the arms after coil around the objects.

The water vascular system in ophiuroidea is somewhat different form the other echinoderms. The water ring bears four polian vesicles and also gives rise to a pair of lateral canals, which lead to the podia. The paired lateral canals of ophuiroids contrast with the slaggered arrangement of other echinoderms. Ampullae are absent, probably correlated with the reduction of the arm coelom, but a valve is present between the podium and the lateral canals. Fluid pressure for production is generated by a dialated, ampulla-like section of the podial canal and in some forms by localized contraction of the radial water canal.

Echinoids or sea urchains are able to move on both hard and soft bottoms and spines and podia are used in movement. Sea urchins can move in any direction. The water vascular system of echinoids is essentially like that of the sea stars. The lateral canals of the side of the radial canal alternate with those of the other side. The canals connecting the ampulla and podia, unlike those in other echinoderms, penetrate the ambulacral ossicles rather than pass between them. The canals are also peculiar in being doubled; that is from each ampulla two canals pierce the ambulacral plate and became confluent on the outer surface to enter a single podium. The suckers of the podia are highly developed and have a system of muscles and supporting ossicles.

Holothuroids or sea cucumbers are relatively sluggish animals and live on the botton surface or burrow in sand. Species with podia on the hole, function with the podia functioning as in asteroids. Some are so sedentary that the podia are used more for attachment than for locomotion. The water vascular system of holothuroids is basically like that of other echinoderms, the madreporite in most species has lost its connection with the body surface and is not attached in the coelom. Perivisceral coelomic fluid rather than sea water, enters the system. The wall of the cloaca is perforated by short ciliated ducts in many and these connect the coelom with the exterior. Coelomic fluid is lost through these ducts when the body contracts strongly and sea waters may enter via ciliary action when the channel relaxes. The ring cannel encircles the base of the pharynx and gives rise to polian vesicles. These vesicles may function as expansion chambers in maintaining pressure within the water vascular system or as pumps to aid in circulation of third in the water vascular system.

Class crinoidea has sessile sea lilies which show bending movements of the stalk and flexion and extension of the arms. The stalkless comatulids, however, are free-moving and are capable of both swimming and crawling. In the ten-arm sealily, every other arm sweeps downword which the alternate set moves upward. In species more than ten arms, the arms still move in sets of five but sequahtially.

Feather stars swim and crawal only for short distances and swimming is largely an escape response. In crinoids, a single madreporite is absent. Instead, numerous surface pores and pore canals perforate the tegmen and open into the coelom near the sone canals, .which open into the perivisceral coelom. The ring canal encircles the mouth and at each interradius gives off a large number of stone canals. At each radius of the ring canal a radial canal extends into each arm just beneath the ambulacral groove and forks into all branches and into the pinnules. From the radial canals extend lateral canals supplying the podia. There are no ampullae and one lateral canal supplies the cluster of three podia except in the buccal region. Hydraulic pressure for extension of the podia is generated by contraction of the radial water canal which is provided with muscle fibres that span the canal.

# Unit 3 ❐ Nutrition and Digestion

*Structure*

3.1 **Patterns of feeding and digestion in lower Metazoa**

3.2 **Filter feeding in Polychaete, Mollusca and Echiodermata**

## 3.1 Patterns of feeding and digestion in lower Metazoa

Metazoans are multicellular, motile, hetromorphic organisms that pass through a blastula stage in the course of their early embryonic development. Sponges, which constitute the phylum porifera, are the most primitive multicellular animals. They have a cellular grade of organization as compared to other metazoans which have tissue-grade of organization. Sponge cells show a high degree of independence and the sponge body resembles a protozoan colony in some respects. So these animals are somewhat intermediate between metazoans and colonial protozoans. To emphasize this intermediate condition, some biologist classify the phylum in a distinct subdivision of the Metazoa, the Patozoa.

### 3.1.1 In Sponges

Sponges eat and digest small planktonic organisms and organic detritus trapped by the fibrous meshwork of the choanocyte collar and transferred to the cell body. Digestion, which is completely intracellular may begin with the choanocytes, but nutrients are rapidly transferred to amebocyte. Within food vacuoles in these wandering cells, the common acid-to-alkaline transition takes place. The products of digestion are distributed throughout the sponge body by amebocytes and indigestible materials are existed into the canal system and eventually expelled through the osculum (Fig. 3.1).

### 3.1.2 In Cnidarians

Cnidarian are generally carnivorous and feed mainly on small crustaceans. The tentacles contain nematocysts which have toxic substances that paralyze the prey. The tentacles then pull the paralyzed prey towards the mouth which open to receive it. All of these feeding responses are initiated by various amino acids and peptides

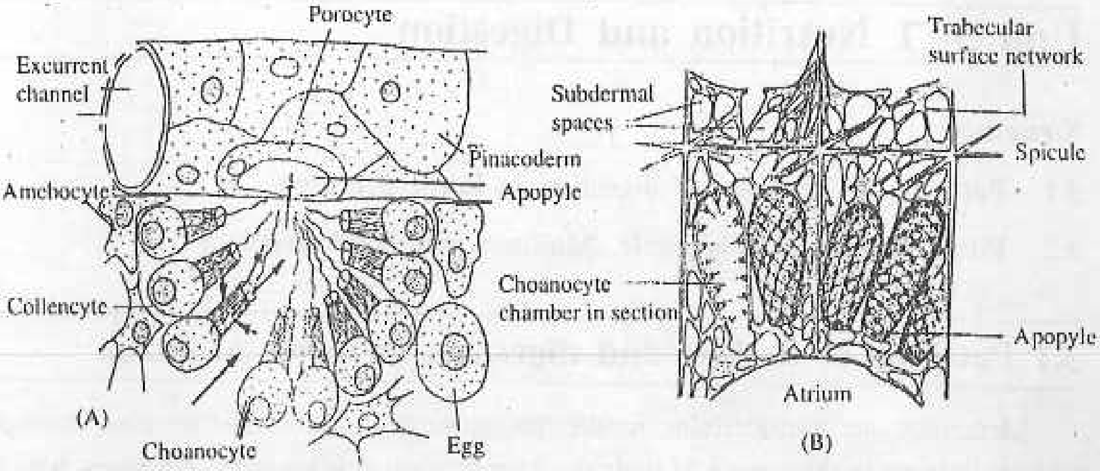


**Fig. 3.1A, B** A—Section through flagellated chamber of freshwater sponge. Arrows indicate direction of water currents. Food is trapped by the fibrous network of choanocyte collar and transferred to cell body. B—Choanocyte chambers within the body wall of the hexactinellid sponge.

liberated from the prey, presumably through nematocyst puncture wound. Mucous secretions aid in swallowing and the mouth can be greatly distended. Eventually, the prey is pushed into the gastrovascular cavity, and enzymatic-gland cells discharge proteolytic enzymes, gradually reducing the prey tissues to a soupy broth. After the extracellular digestion, intracellular digestion continues. The nutritive muscular cells of the gastrodermis engulf small fragments of tissue. Further digestion of proteins and fats occur within food vacuoles in the nutritive-muscular cells (Fig. 3.2) and

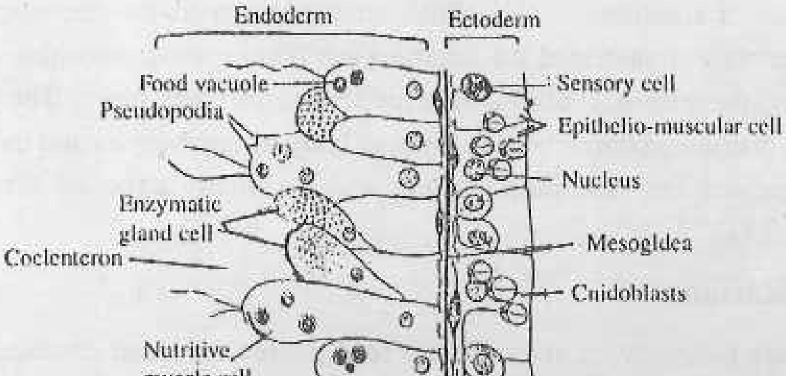


**Fig. 3.2** Diagrammatic view of the histological structure of a portion of ectoderm and endoderm showing different types of cells. Note the presence of gland cells (enzyme secreting cells) and nutritive muscular cells where intracellular digestion takes place.

the food vacuoles undergo the acid and alkaline phases characteristic of protozoan. Products of digestion are disconnected by diffusion. Indigestible materials are ejected from the mouth when the body contracts. In colonial forms of hydrozoa gastrozooids collect food and extracellular digestion takes place in the gastrozooid itself, after which the partially digested broth passes into the common gastrovasuclar cavity of the colony where intracellular digestion occurs. Distribution is probably facilitated by rhythmic pulsation and contraction waves.

The plan of the scyphozoan gastrovascular system is somewhat different from that seen in hydromedlisae. In a hydromedusa, the mouth opens as the end of a tube like extension called the **manubrium** which hangs from the centre of the subumbrella and corresponds to the hypostome of the polyp. Mouth leads to a central stomach from which typically extends radial canals linked with gastrodermies. The radial canals join with a ring canal running the around margin of the umbrella. However, in a scyphomedusa, four gastric pouches extend from the central stomach. Between the pouches are septa, each of which contains an opening to help circulate water. Thus all from pouches are in lateral communication with each other. The manubrium of many species is drawn out into, four to eight oral arms containing **cnidoblasts** and aid in capturing and ingestion of prey. Ciliated grooves of the oral arms carry the food to the mouth and stomach. The margin of the septa between the gastric pouches bears a number of gastric filament which contain cindoblasts and gland cells. A ring canal may or may not be present. The gastric filaments are the source of extracellular enzymes, and cindoblasts are probably used to quell prey that is still active. The digestion is essentially same as in hydrozoans.

### 3.1.3 In Ctenophora

The ctenophores are carnivouous. Tentaculate ctenophores catch their preys with the tentacles which contain **colloblasts,** the adhesive cells. The lobate ctenophores, use both the tentacles and the mucus—covered oral surfaces of the lobes to capture prey, especially small crustaceans. The cylindrical *Beroe* sp., which lack tentacles, feeds on other ctenophores. Contact of the large mouth with the prey causes an inward gulp, and the prey is swallowed. One ctenophore feeds on jelly fish and conserves the nematocysts, which are then transported by gastrodermal cells with tentacles and utilized by the ctenophore instead of colloblasts. Digestion is both extracellular and intracellular and indigestible wastes are passed out through the anal pore and mouth (Fig. 3.3).

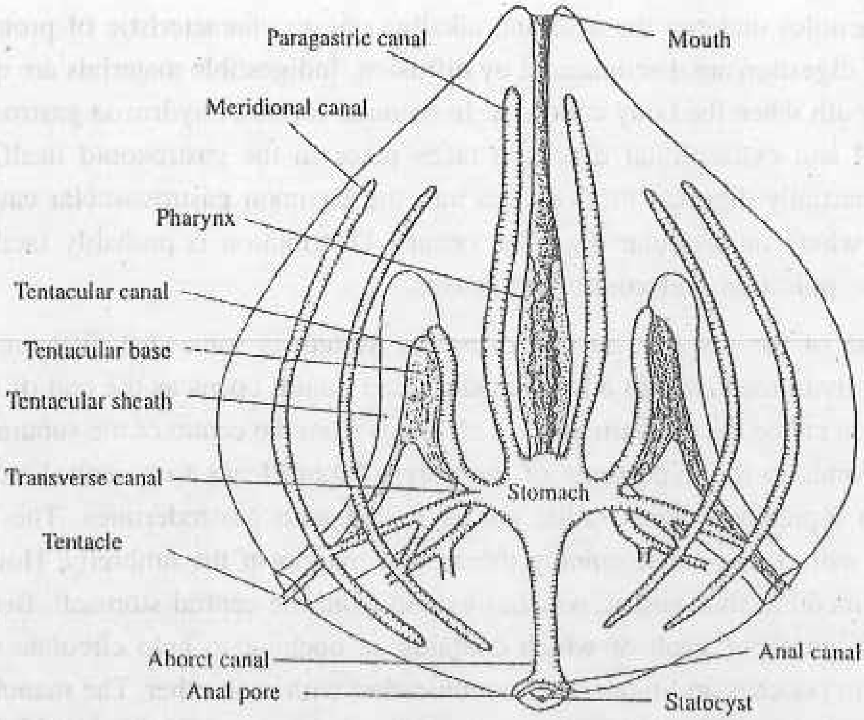


**Fig. 3.3** Digestive system of a cydippid ctenophore showing branching of the alimentary system

### 3.1.4 In Platyhelminthes

Phylum platyhelminthes, is rather diverse, it has free living fonns, included under class turbellaria and parasitic form belonging to the classes trematoda and cestoda. The digestive cavity or gut of Turbellaria is typically a blind sac and mouth is used for both ingestion a egestion (Fig. 3.4). In a very few long worms and worms with highly branched gut on anus or multiple anuses are present because the normal return of undigested wastes to the mouth is apparently complicated by the extreme length or complex branching of the gut. The gut is single layered and have phagocytic cells and gland cells. Larger turbellarians have guts that have lateral diverticula which increases the surface area for digestion and absorption and compensate for the absence of an internal nutrient transport system. The mouth is commonly located on the midventral surface but may be situated anteriorly, posteriorly or anywhere along the midventral line. Pharynx may or may not be present. Where present, it may be a complex inactive organ. The pharynx may be folded or plicate as found in polyclads and triclads. In rhabdococla the pharynx is bulbous. Feeding behaviour is elicided at least in some species by substances emitted from the potential foods source. Protozoa, rotifers, insect larvae, small crustaceans, snails and small annelid worms are common preys. Several species harbour green zoochlorellae or golden zooxanthellae or diatoms in their parenchyma and these species rely on them and these platyhelminthes do not ingest food as long as the algal symbionts are present.

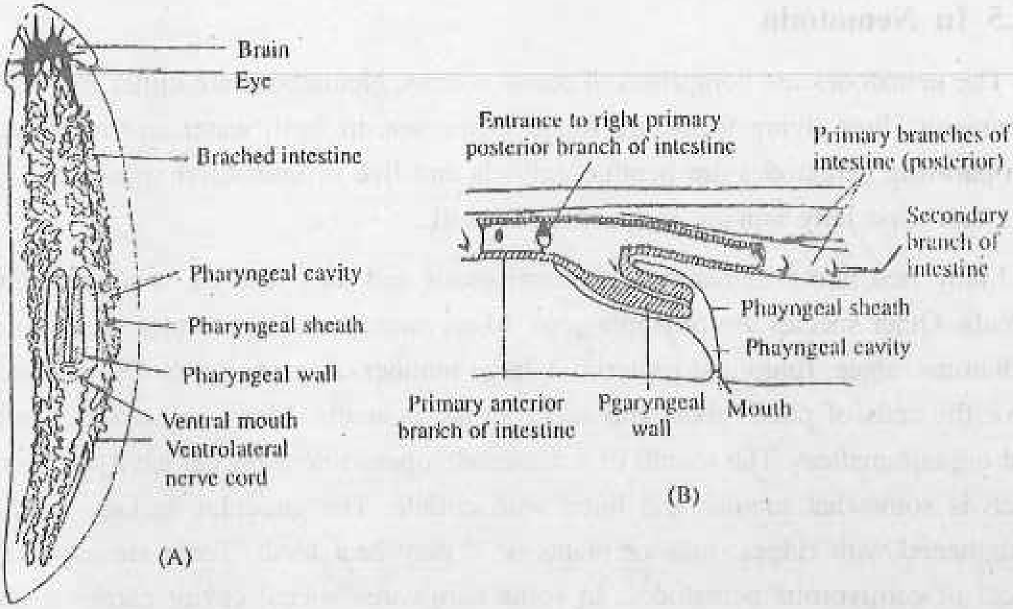


**Fig. 3.4A, B** A : Dorsal view of digestive system (a portion of nervous system is also fund). Note the highly branched intestine.

B : Cross section of the body at the level of the pharynx and gut showing.

Prey is swallowed whole by those turbellarians with a simple pharynx, by those with a protrusible bulbous pharynx and even by the polyclads, which have a plicate pharynx. The exoskeleton of crustacean is penetrated at thin points and ingestion of body tissues of the prey are aided by proteolytic enzymes produced by pharyngeal glands that open on to the tip of the pharynx. The partially digested and liquefied contents are then pumped into the gut by peristaltic movement. Digestion is first extracellular and additional endopeptidase is supplied by gland cells of the intestine. The resulting food fragments are then engulfed by the phagocytic cells, where digestion by endopeptidases continues in an acid medium. About 8 to 12h following ingestion the phagocytic vacuoles become alkaline which marks the appearance of exopeptidases, lipases and carbohydrate splitting enemies to complete digestion.

During the course of intracellular digestion, the vacoule sinks more deeply into the phagocytic cell and eventually disappears.

Freshwater planarians are able to withstand prolonged periods of starvation experimentally. Although parasitism in flatworms is usually associated with trematodes and cestodes, there are a number of commensal and parasitic turbellarians.

### 3.1.5 In Nematoda

The nematodes are comprised of round worms. Nematodes are either free living or parasitic. Free living forms are found in the sea, in fresh water and in the soil. Non-parasitic nematodes are benthic animals and live in interstitial spaces of algal mats and especially aquatic sediments and soil.

Many free living nematodes are carnivorous and they feed on small metazoan animals. Other species are phytophagous. Many marine and freshwater species feed on diatoms, algae, fungi and bacteria. A large number of terrestrial (soil) nematodes pierce the cells of plants roots and suck out the contents. Many nematodes live on dead organic matters. The mouth of a nematode opens into a buccal cavity or stoma which is somewhat tubular and lined with cuticle. The cuticular surface is often strengthened with ridges, rods or plates or it may bear teeth. Teeth are especially typical of carnivorous nematodes. In some carnivores buccal cavity carries a long hollow or solid, circular stylet which can protrude from the mouth. Stylets are used to puncture the prey and the hollow stylet may act as a tube through which the contents of the victim are pumped out by the pharynx.

Species with stylet secrete pharyngeal enzymes that initiate digestion of the prey or plant cell contents and that may even aid on the penetration of the plant cell wall. The buccal cavity leads to a tubular pharynx; this pharynx is also referred to as the oesophagous by nematologists. The pharyngeal lumen is triradiate in cross-section and lined with cuticle. The wall is composed of myoepithelial and gland cells. Frequently, the pharynx contains more than one muscular swelling or bulb. The pharynx or pharyngeal bulbs act as pumps and bring food from the mouth into the intestine. From the pharynx the long tubular intestine composed of a single layer of epithelial cells extends the length of the body. These cells many have cilia or mircoville, these may be absent in some cases also. A short cuticle—lined rectum connects the intestine with the anus. Digestive enzymes are produced by the pharyngeal glands and the intestinal epithelium. Digestion begins extra-cellularly within the intestinal lumen but is completed intracellularly. The intestine is also an important organ of nutrient storage and yolk synthesis for developing oocytes.

In parasitic nematodes, the mid gut is syncytial, lacks a lumen and does not function in digestion. Instead, nutrients that are absorbed through the body wall are stored in the gut syncytium which thus functions as a liver.

### 3.1.6 In Mesozoa

In the animal kingdom there are other lower metazoa and same minor coelamate and acoelomate groups. Some of them are parasites and some are free living. Some of them have certain specialized structure which help them capture preys and ingest food. Among these groups we find **mesozoa** which is regarded as an intermediate form between protozoa and metazoa.

### 3.1.7 In Rhynchocoela

**Nemertinea** or **Rhynchocoela** are ribbon worms. The characteristic feature of this phylum is the proboscis apparatus. In most of the species, the digestive system is completely separate from the proboscis apparature. The mouth is ventral and located at the anterior end of the body near the level of the brain. It opens into a foregut which is often subdivided into a buccal cavity, an oesophagus and glandular stomach. The foregut opens into a long intestine which his lateral diverticula. One intestine opens at the anus located at the tip of the tail. In some mouth has disappeared another proboscis opens into the anterior part of the gut.

Nemertines are entirely carnivores and feed primarily an annelids and crustaceans. Proboscis helps in capturing the prey. It coils around the prey and sticky toxic secretions form the anterior region of the proboscis and in holding and immobilizing the prey. The immobilized prey is either swallowed whole or its tissues are simply sucked into the mouth. Digestion takes place in the intestine; initially digestion is extracellular but ultimately intracellular digestion takes place in phagocytic cells.

### 3.1.8 In Rotifera

**Rotifers** are mainly fresh water forms but some (few) are marine and some species line in mosses with protozoans and small crustaceans, dominate the freshwater planktons and are important in nutrient recycling in aquatic systems.

The mouth of the rotifers is ventral. The mouth may open directly into the pharynx or a situated buccal tube may be situated between the mouth and the pharynx, Pharynx or **mastax** is an efficient chewing apparatus characteristics of this group. It is provided internally with hard chitinous jaws used to grasp, cut and grind the food. The mastax is used both in capturing and in triturating food and its structure therefore, varies considerably, depending on the type of feeding behaviour. Most rotifers are either suspension or raptorial feeders, although the latter group is rather omnivorous. Suspension feeders (Bdelloids) feed on minute organic particles that are brought to the mouth in the water current produced by the coronal cilia. The food particles brought in by the water current are swept by both preoral and postoral cilia into a food groove that lies between them. The mastax of suspension feeders is adopted to grinding. Here the mastax also acts as a pump, sucking in the particles that have collected at the mouth. Food intake can be regulates in various ways. In ***Brachionus*** sp., for example, the ciliated buccal field can be screened or uncovered by certain large coronal, cirri, the buccal field's ciliary bent can be reversed, or the mastax can reject particles. The carnivorous species which feed an protozoa and other small metazoan animals, capture their prey by trapping or suction. The forceps-like troptn of suction feeders are used to hold or manipulate prey once it is in the mastax cavity. After the prey is broken up, the indigestible parts are discarded. The captured organisms are sucked into the foregut by the mastax, which functions as a pump and it is called the **proventriculus**. A number of epizoic and parasitic rotifers live primarily on small crustaceans, particularly the gills. Endoparasitic species inhabit snail egg, heliozoans, the interior of volvox and coelom of earthwarms and fresh water oligochaetes and shrimp.

Salivary glands are present in the mastax walls of most rotifers. These are enzymatic glandular bodies which open through ducts just in front after mastax proper. A tubular aesophagus comments the pharynx with the stomach. As the junction of the oesophagus and stomach is a pair of enzyme-secreting gastric glands, each of which opens by a pore into each side of the digestive tract. The digestive and absorptive stomach is a large sac or tube that passes into a short intestine. The excretory organs and the oviduct also open into the terminal end of the intestine, which functions as a cloaca. The anus opens dorsally near the posterior end of the trunk. An intestine and anus are absent in large predatory species. In some sessile tube dwelling species the anus has shifted anteriorly to allow egestion of wastes over the tip of the tube.

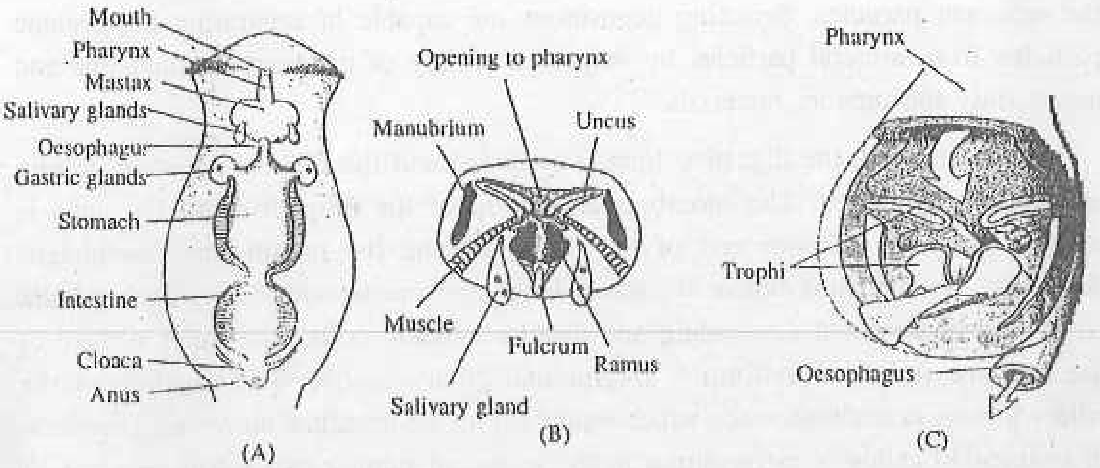


**Fig. 3.5A, B, C** A—Anatomy of digestive system in dorsal view. B—Enlargement of a mastax. C—Diagrammatic picture, showing relative position of pharynx, mastax and oesophagus arrows indicate the route of food through the alimentary canal

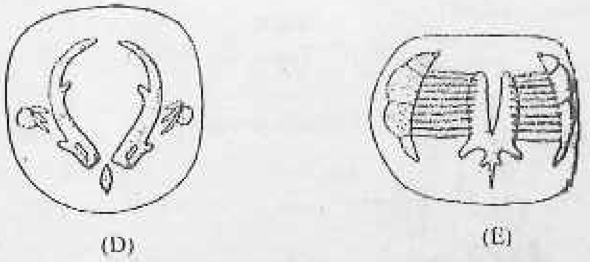


**Fig. 3.5D, E** Trophi in mastax; D—Incudilte trophi for seizing prey; E—Malleoramate trophi for grinding

## 3.1.9 In Sipunculida, Echiurida and Priapulida

Among non segmented coelomate worms, the animals under these smalls phyla are deposit feeders. Small organic particles derived from decomposing algae, aquatic plants & animals, the faecal pellets of many different animals settle at the between of the marine a freshwater environment. All of these deposited materials, which become mixed with mineral particles on the bottom, is an important source of food for deposit feeding animals. Deposit feeders may be selective or non-selective. Non-selective deposit feeders ingest both organic and mineral particles and then digest some of the organic materials, especially bacteria that here colonized the surface of the sediment particles. Selecting depositions are capable of separating the organic particles from mineral particles by way of a variety of different mechanisms and ingest only the organic materials.

In Sipunculida, the digestive tract is J-shaped and the tubular intestine is long and complexly coiled. The mouth is as the tip of the introvert, and the anus is middorsal on the anterior end of the trunk. Behind the mouth, the oesophagus descends into the trunk where it joins a long intestine wound into a double helix consisting of proximal descending and distal ascending coils. The inner surface of the intestine is folded to form a longitudinal ciliary groove. The function of the ciliary groove is to shunt water, which would dilute the intestinal enzymes. Digestion in sipunculan callus is extracellular in the intestinal lumbar two tuftlike groups of rectal glands may occur close to the anal opening. Epithelial gland cells are present in the descending arm of intestine which probably series for digestion and absorption. The ascending intestine probably serves for faecal formation (Fig. 3.6).

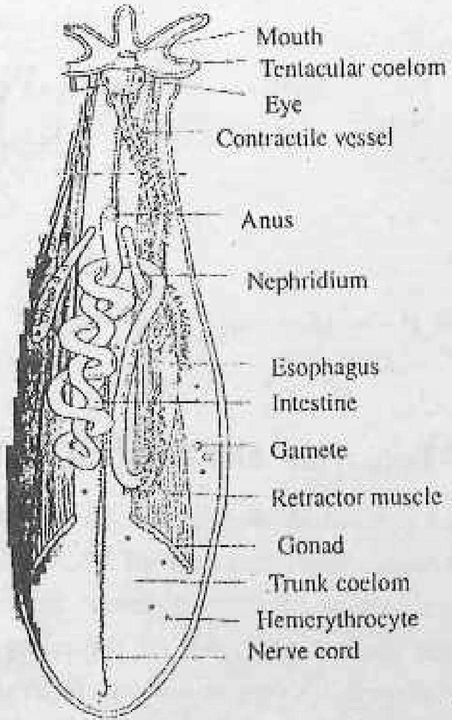


Fig. 3.6 Organization of a generalized sipunculan showing the digestive system

In Priapulida, the alimentary canal is not coiled. Mouth lead to muscular pharynx lined by a cuticle beset with cutaneous spines or teeth. The intestine or midgut is a straight or slights curved, thin-walled tube, the epithelial living of which remains conspicuously tolded. A construction separates the mid gut from the rectum. Which is lined with cuticle, that leads to the anus, located at the posterior end of the trunk. Large priapulids are thought to be carnivorous and others are deposit feeders. The carnivores feed an soft-bodies, slow-moving invertebrates, particularly polychaete worms. The mouth and the pharyngeal regions can be everted owing feeding. The straight tubular intestine lacks cuticle and cilia but is lined with a brush border of absorptive microvilli. A combination of extracellular and intracellular digestion occurs in the midgut.

Most **echiurans** are deposit feeder and at least one is a filter feeder like polychaetes. The echiurnas casts a mucous net from a glandular girdle an its anterior trunk to its burrow wall and then pumps water through it virtuality all particles including plankton. When loaded with food, the net is detached from the body seized by the prostomium and swallowed. The digestive tract is extremely long and coiled and loosely suspended in the coelom. The mouth is situated ventrally at the base of the prostomium and the anus opens on the posterior end of the trunk. Intestine is the silt of digestion. An accessary gut, the siphon originates from the anterior intestine, runs parallel to the intestine and rejoins it posteriorly where the intestine joins the hind gut. The siphon is an intestinal bypass that probably transports water ingested with food around the digestive region of the gut. It is this functionally similar to the intestinal ciliary groove of sipunculas. The hindgut widens into a cloaca which receives the excretory tubules before opening to the anterior through the anus.

### 3.1.10 In Lophophorate phyla

Phylum **Phoronida,** phylum **Brachiopoda** and phylum **Broazyoa** are all included in a single group, the Lophophorate. They all have lophophores. One lophoprohe is a circular or horse-shoe shaped fold of the body wall that encircles the mouth and bears numerous ciliated tentacles. The ciliary tracts on the tentacles, drive a current of water through the lophophore and suspended food is collected in the process. Lophophorates are generally filter-feeders.

In **Phoronida,** the tentacular cilia beat downward creating a water current from which plankton and suspended detritus are collected and entangle in mucus on contact with the tentacles. Cilia with groove between the two ridges of the lophophore convey the food particles under the epistome and into the mouth. The digestive tract is U-shaped and digestion causes extracellularly within the oesophagus and stomach; intracellular digestion probably takes place in the stomach.

In the **Phylum Brachiopoda** the mouth lies at the center of the base of the lophophore in a transversely directed food groove. It is a narrow, transversely elongated or crescentic and slit-like aperture, bounded dorsally by the brachial fold or lip and ventrally by the tentacular fringe of the lophophore. The alimentary canal is usually V-shaped and lined with ciliated epithelium. Mouth leads to oesophagus that extends dorsally and joins a dialated stomach. The stomach is surrounded by a digestive gland that opens through the stomach wall by means of one to three ducts on each side. Digestion is mainly intracellular within the digestive gland. In the class **Articulata** the intestine is short and it terminates blindly, there is no anus. In the class **Inarticulata**, the intestine is long and coiled and it opens by an anus.

**Bryozoans** are sessile colonies composed of zooids, often polymorphic, but typically the body of each consists of a stationary trunk and an reversible introvert, which bears the lophophores. The mouth at the centre of the lophophore opens into a U-shaped digestive tract. The anus opens through the dorsal side of the introvert and is situated outside the lophophore (Fig. 3.7). During feeding the lophophore is pushed outward through the atrial and origin, causing the tentacular gnash to ever. The tentacles then expand, forming a bell-shaped tunnel. Small phytoplanktonic organisms are probably the principal food of bryozoans. These are driven into the funnel with the water current, trapped on the tentacles and delivered to the mouth by the tentacular cilia. Two ideas have been advanced to understand the mechanism by which food particles are filtered from the water. The **ciliary reversal theory** suggests that when suspended particles touch the lateral cilia, they cause a local reversal of beat, which kicks the particle back into the upstream, toward frontal side of the tentacle for transport to the mouth. The **impingement theory**, on the other hand, proposes that particles are removed from the water streams as they strike the frontal surface of each tentacle. However, the particles are cleared from the water, the general mode of feeding may be classified as an **upstream ciliary collecting system.**

Tentacle flicking is a common accessory feeding mechanism in many species. A particle is batted toward the mouth by a rapid inward flick of one tentacle. ***Bugula*** sp. captures zooplankton by closing the tips of the tentacles to form a cage around the prey. Many species scan the particles by rotating or bending the lophophore. Food particles accumulate beneath the epistome.

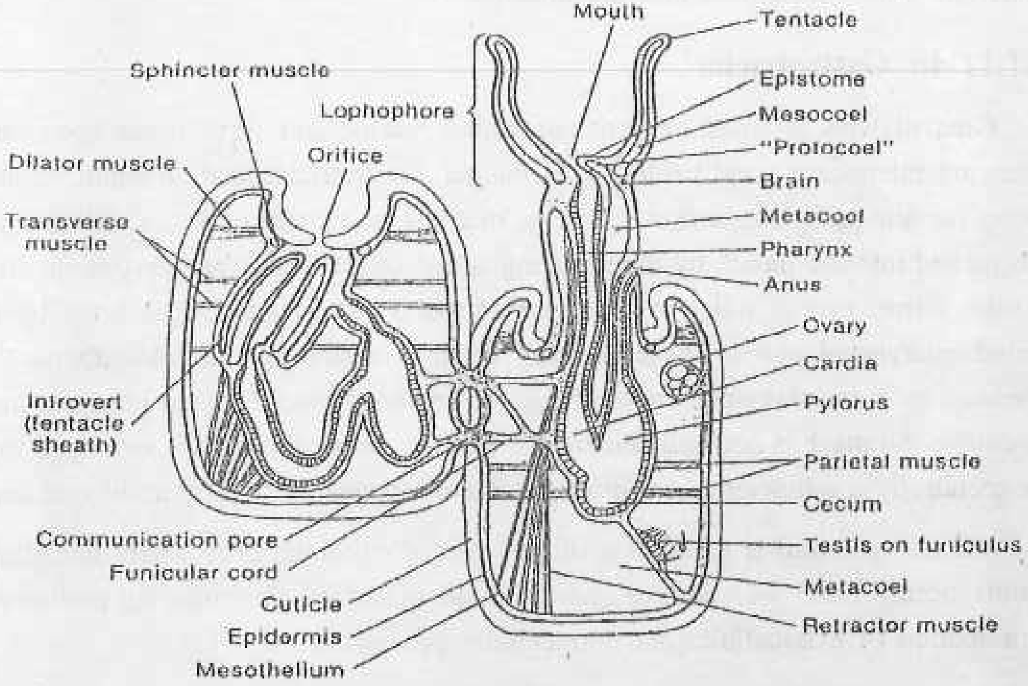


**Fig. 3.7** Organization of two generalized ed bryozoan zooid, showing alimentary system. The right zooid is with an eversible introvert, bearing the lophophore.

When the bugulas reaches a certain size, the muscular sucking pharynx dilates rapidly and together with oesophagus pumps the food into the stomach. Particles may be rejected by mouth closure, tentacle flicking, funnel closure, or simply being passed between the tentacles. The stomach occupies much of the U-shaped gut. The dilated anterior tentacular part of the stomach, called cardia, is separated from the oesophagous by a valve. The posterior region of the stomach is separated from the intestine and rectum by a valve-like construction. A large caecum projects backward from the central part of the stomach. In some bryozoans the anterior part or cardia is modified into **gizzard**. The gizzard has a well developed, circular muscle layer and the lining or the epithelial cells bear chitinous teeth.

Digestion is both extracellular and intracellular within the stomach, with the caecum being the principal site for intracellular digestion. Food passes through the stomach by peristaltic contraction but the pylorus rotates and compacts waste materials which then pass into the intestine.

### 3.1.11 In Gastrotricha

**Gastrotricha** is small phylum containing marine and fresh water specimens. They are microscopic and benthonic in habitat. Gastrotricha feed an small, dead or living organic particles, such as, bacteria, diatoms, and small protozoa, all of which are sucked into the mouth by the pumping action of the muscular pharynx. In some marine forms, excess water ingested with food is released from the body by the paired pharyngeal pores. The alimentary canal is a straight tube. Mouth may be bordered by numerous small curved hooks or bristles. Mouth leads to pharynx, lined by cuticle. Stomach is not well demarcated from intestine. Intestine is separated from the rectum by a sphincter or constriction. Rectum opens outside by middorsal anus.

The mid-gut wall is made of a single layer of epithelial cells where unicellular glands occur. Their secretions digest the food materials. Digestion is probably a combination of extracellular and intracellular processes.

### 3.1.12 In kinorhyncha

The **Kinorhyncha** includes species which are exclusively marine. They are benthonic in habitat living in the slime, mud or sand at the sea bottom in both shallow and deep waters. They feed on diatoms or ingest fine detritus and other fine organic materials. The alimentary canal is a straight tube similar to that of gastrotrichas. The mouth is placed on the mouth cone and is surrounded by styles. The foregut is lined by cuticle and consists of a filtering buccal cavity, a sucking pharynx and a short oesophagus, which joins the midgut. Midgut leads to hindgut and opens to the exterior via a terminal anus. Presence of salivary and other glands have been reported by some workers but the physiology of digestion is unknown.

### 3.1.13 In Entoprocta

Phylum **Entoprocta** or **Calyssozoa** is a small group of sessile aquatic animals in which the body cavity is believed to be a pseudocoel by some zoologists. The entoprocts are ciliary feeders and their food consists of diatoms, protozoans and organic debris in the water. The frontal cilia of tentacles enters the suspended food particles and pass them on to the ciliated vestibular grooves leading to the mouth. Mouth leads to a small funnel-shaped buccal cavity, a narrow intestine and a terminal rectum opening by the anus. The anal opening often lieson an elevation called the **anal cone.** Stomach glands are believed to secrete enzymes for extracellular digestion.

### 3.1.14 In Acanthocephala

Another group of worm-like pseudocoelomate animals belongs to the phylum **Acanthocephala.** These animals, known as spriny or thorny headed worms, are endoparasitic forms. So mouth and alimentary canal are absent. Food is absorbed directly by the body wall from the host. Body cavity contains nutritive cells.

### 3.1.15 In Nematomorpha

The **Nematomorpha** superficially resembles the Nematoda. This group is comprised of long worm known as hair worms or horsehair worms. The adult worms are free-living and short-lived and the larvae are parasites of arthropods mainly and are the dominate stage in the life cycle. Larvae actively penetrate or are ingested by arthropod hosts, mainly living in water. Their nutrition as parasites is apparently accomplished by direct absorption of food materials through the body wall. Larvva develop by moulting and attain the form of adult. They come out of the host body when the host is in the water or near the water. The adults are short lived. In post reproduction adults, however, the body cavity is an open fluid filled pseudocoel. The digestive tract is vestigial and adults do not feed and die after the eggs are laid and fertilized.

### 3.1.16 In Pogonophora

Pogonophorans are exclusively marine animals; they are sessile, living in secreted tubes that are composed of a mixture of protein and chitin. A remarkable feature of adult pogonophore is the absence of mouth and normal digestive tract. In the absence of digestive tract the mode of nutrition in these animals was puzzling. In the trunk of these animals is a central mass of tissue, called the **trophosome** that is packed with symbiotic bacteria. The bacteria oxidise sulfur-containing compounds and use the resultant energy to fix carbon. The pogonophoran host obtains its nutrition from the production of excess organic compounds by the bacteria and by lysis and subsequent absorption of bacterial components.

### 3.1.17 In Chaetognatha

The **Chaetognatha** are a small group of pelagic organisms commonly known as the arrow worms. Phylum chaetognatha means "bristle-jawed". The alimentary canal is a simple straight tube running from mouth to anus. Mouth leads to a short muscular oesophagus or pharynx. The pharyngeal wall contains glandular vacuolated cells. A true stomach is lacking. The pharynx widens posteriority to from the intestine which is a straight tube extending through the trunk and it opens by the ventral anus at the junction of the trunk and tail. The anterior part of the intestine gives out a pair of lateral diverticula. The intestine is lined by cuboidal or columnar epithelial cells of glandular and absorptive nature. Digestion is probably entirely extracellular.

## 3.2 Filter feeding in polychaeta, Mollusca and echionodermata

Filter feeding is a type of suspension feeding in which particles (plankton and detritus) are removed from a water current by a filter. Filter feeding is a means by which many relatively passive invertebrates obtain food. Filter feeding is limited to aquatic and particularly to marine forms. Tentacles, mucous glands and ciliary tracts are common structures of filter feeders.

### 3.2.1 Filter feeding in Polychaeta

Many of the sedentary burrowers and tuberclous polychaetes are filter feeders. The head is usually equipped with special feeding processes that collect detritus and plankton from the surrounding water. The particles adhere to the surface of the feeding structures and are then converged to the mouth along ciliated· tracts.

**Structures associated with filter feeding & mechanisms** : (a) The crown-like, bipinnate radioles of serpulid, sabellid and spirobid worms form a funnel of one or two spirals when expanded outside the end of the tube (Fig. 3.8). Beating of the

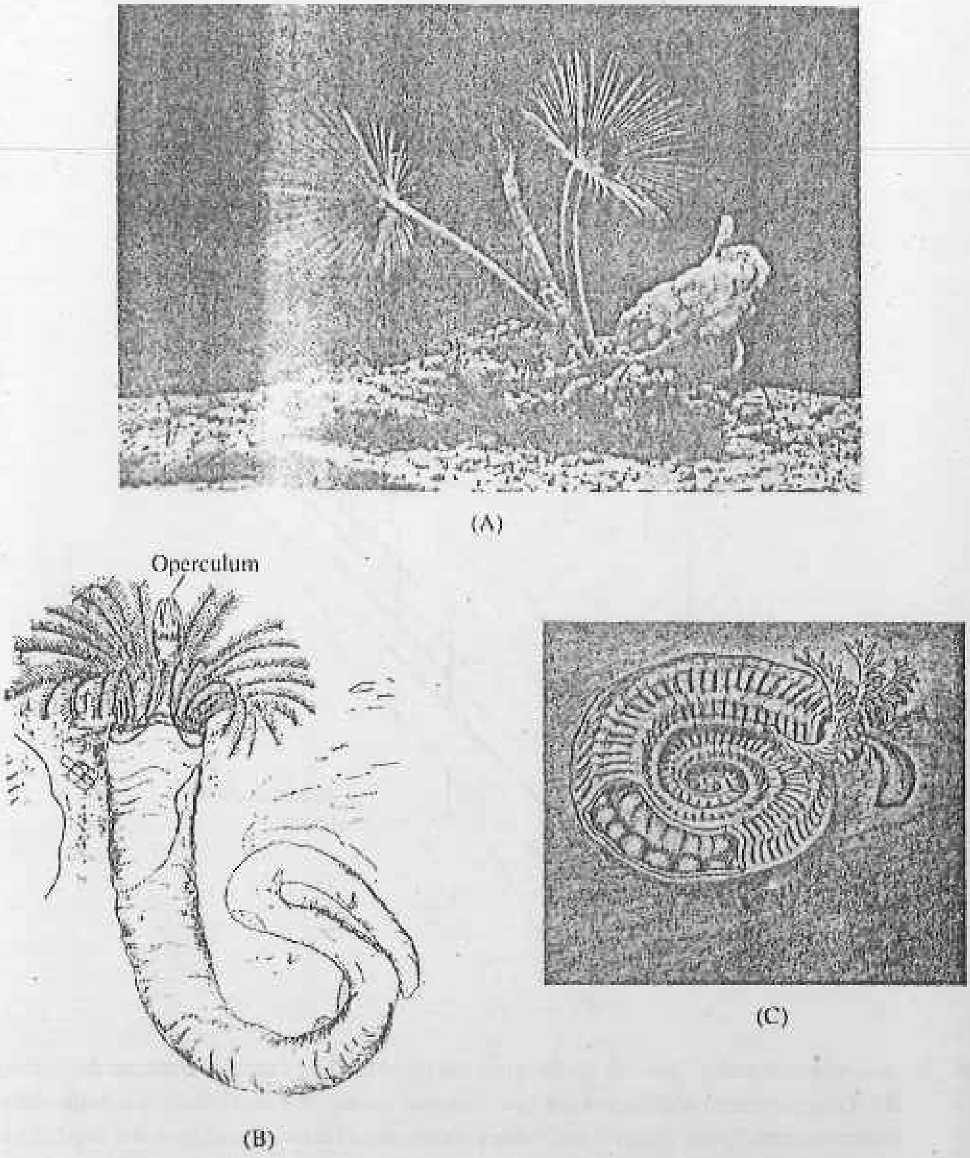


**Fig. 3.8** Filter-feeding polychaetes. A. The sabellid, *Sabella paronina*, showing the expanded radioles projecting from the apertures of the tubes. B. The serpulid, *Hydroides* sp. with radioles and operculum extended from the end of the calcareous tube attached to a rock. C. A common spirobid, *Spirobis* sp. with a snail-like tube found attached to a substrata.

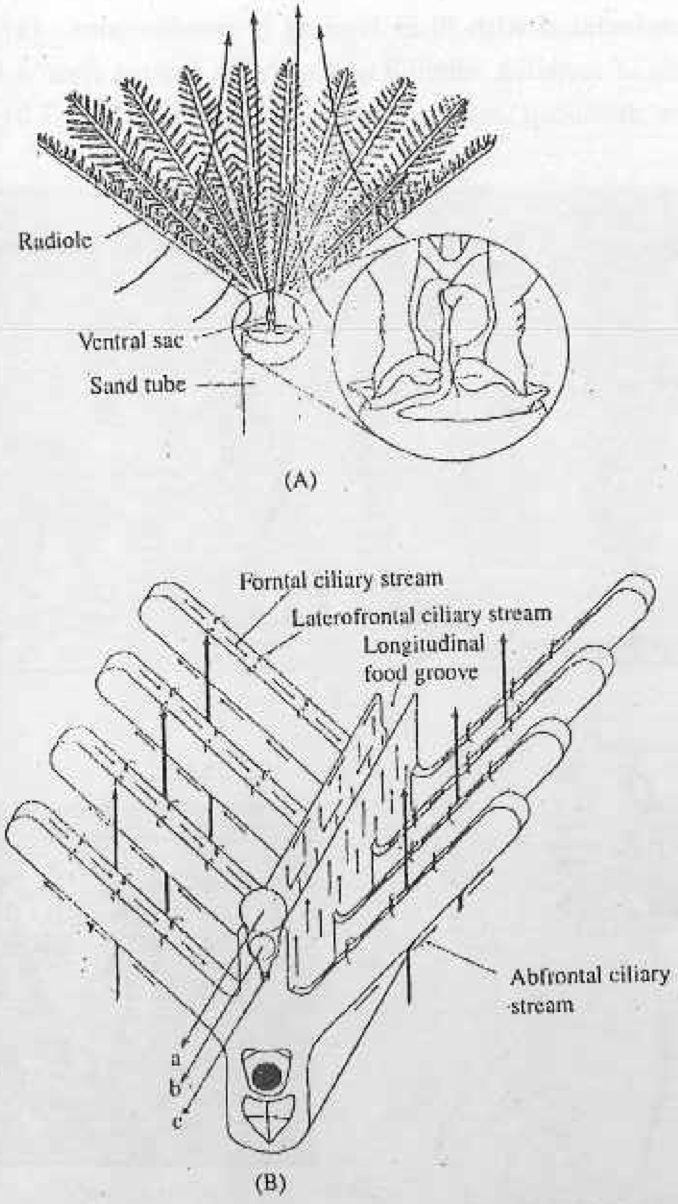


**Fig. 3.9A, B** A—Anterior end of *Sabella* sp showing the filter feeding currents (indicated by arrows). B—Diagrammatic representation (an enlarged view) of a section of a radiole showing water currents (large arrows) and ciliary tracts (small arrows) and how the food particles of different size (a, b, c) are trapped and are driven by the cilia into agroove, running the length of each radiole.

cilia situated on the pinnules produces a current of water that flows through the radioles into the funnel and then flows upward and out. Particles are trapped on the pinnules and are driven by the cilia into a groove running the length of each radiole. The particles ate carried along the groove down to the base of the radiole, where a rather complex sorting process takes place. The largest particles are rejected and fine materials are carried by ciliated tracts into the mouth. Many sabellids sort particles into three grades and store the medium grade for the use in tube construction (Fig. 3.9).

(b) The feeding mechanism in chaetopterus differs from others. Chaetopterus has a highly modified body structure. It lives in U-shaped tube. The notopodia on the twelvth segment are extremely long and wing-like. Its epithelium is ciliated and richly supplied with mucous glands. The notopod of 14th & 16th segments are modified and fused, forming semicircular fans that project like piston rings against the cylindrical wall of the tube. The beating of the fans produces a current of water that enters the chimney or the U-shaped tube near the anterior and of the worm, flows through the tube and then flows out of the opposite chimney.

The paired, wing-like notopodia are stretched out around the walls of the tube and a sheet of mucous is secreted between them. The mucous film is continuously secreted from each endopodite and so the sheet assumes the shape of a bag. Water brought into the tube by the rhythmic beating of the fan—parapodia passes through the mucous bag, which strains suspended detritus and plankton. Large objects brought into the tube by the water current are detected by peristomial cilia; the wing-like notopodia then are pulled back to let the large objects pass by. The food-laden mucous bag is continuously being rolled up into a ball by the dorsal cupule. When the ball reaches a certain side, the bag is cut loose from the notopodia and rolled up with the ball. The cupule then projects forward and deposits the mucous food ball on to middorsal groove, which extends anteriorty and the ball is carried to the mouth. A specimen (*chaetopterus*) of 18-20 cm long may produce mucous film for the bag at the rate of approximately 1 mm/s, with food balls averaging 3 mm in diameter.

(c) The other members of chaetopteridae build straight, vertical tubes but utilize mucous bags for filter feeding. The number of mucous bags and the site of their formation vary as many as 13 are formed at one time is ***Spiochaetopterus***. In several genera the water current is activated by cilia rather than by pumping.

**Digistive system and digestion :** In polychaetes alimentairy canal is a straight tube extending from the mouth at the anterior end of the worm to the anus. The digestive tube is differentiated into pharynx, (in some forms where pharynx is not present, buccal cavity is found), short oesophagus, stomach (in sedentary species), intestine and rectum. The stomach or anterior intestine elaborates enzymes for extracellular digestion. The intestine is the site of absorption and sometimes the walls are folded, increasing the intestinal surface area. In *Nereis* two large, glandular caeca open into the oesophagus. They along with the anterior end of the intestine, secrete digestive enzymes.

The egested wastes from a worm living in a tube with double openings, are readily removed by water currents. Such flushing is less efficient when the tube is deeply buried in mud and sand or is secreted with only one opening, as in serpulid fan worms and sabellariids. Some species produce fecal pellets or strings, which reduce the risk of fouling. A fan worm has a ciliated groove, which carries fecal pallets from the anus anteriorly out of the tube.

### 3.2.2 Filter feeding in Mollusca

In no other molluscan class does the shell so dominate external morphology as in the bivalvia. The hinged two part shell completely encloses these annuls. In many bivalves, apertures remain only for incurrent and excurrent water flow and for extension of the blade like fuot. The gills dominate the mantle cavity in most bivalves. Subclass Lamellibranchia displays the largest and most complex of all molluscan gills. These gills filter plankton and other small edibles from waters of the mantle cavity. Before the rise of the lamellibranchia ctenidial cilia and mucous alrealy served molluscs as means for cleaning particulate matter from the gills. Lamellibranchs, however, are adapted to use such particles for food. The gills become elongated and developed complex folds which increased the filtering area. An explosive evolution followed this development and the filter feeders, lamellibranch, came to dominate the bivalve fauna. In some group of early protobranch bivalve, filter feeding evolved. The gills and ventilating current of protobranchs preadapted them for filter feeding. As the lamellibranchs evolved, detrital practicles and microarganism in the ventilating current came to be utilized as a source of food, the gills became filters and the gill cilia that originally served to keep the gills clean became adapted for the transport of particles trapped in mucous from the filter to the labial palps and mouth (Fig. 3.10).

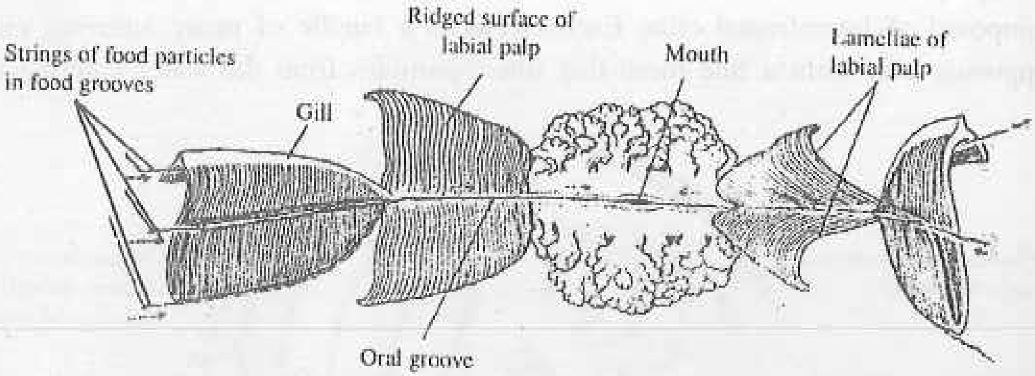


**Fig. 3.10** Diagram of labial palps each with its two lamellae turned back, showing relationship to the gills and mouth. The mouth is surrounded by bushy folds. Gill cilia that originally served to keep the gills clean became adapted for the transport of particles trapped in mucous from the filter to the labial palp and mouth.

**Modification of the gills for filter feeding and the mechanism :** The principal modification of the gills for filtering was the lengthening and folding of the gill filaments, which greatly increased their surface area. Many filaments were added to the gills so that they extended anteriorly, reaching the palps. Each gill filament on each side at the axis became folded or U-shaped. The arm of the 'U' that is attached to the axis of the gill is called the **descending limb,** and the arm next to the mantle or visceral mass, the **ascending limb.** The net result of the filaments on both sides of the axis becoming folded has been to transform each the original single gill into what appears to be a pair of gills, or demibrandies; the original outer filaments form one member of the pair and the original inner filaments forms the other (Fig. 3.11). The lengthened, folded filaments and their attachments to one another give the gill a sheet like form, hence, the name of these bivalves, lamellibranchs, meaning **"sheet gill"**. Four large, broad, filtering surfaces (lamellae) are present, two on each demibranch. At the angle of flexure, the frontal surface of each filament has developed an indentation, or notch, which, when lined up with the notches of adjacent filament, form a food groove that extends the length of the underside of the gill. These modifications in gill structure have necessitated a change in ciliation. The frontal cilia carry food particles trapped on the gill surface vertically to the food grooves (Fig. 3.12 and 3.13). The abfrontal cilia, now inside, are usually host from most filaments. Lateral cilia still produce the water current through the gills. On each side of the filament, between the internal and the frontal cilia, is a new ciliary tract composed of laterofrontal cilia. Each **cirrus** is a bundle of many adhering cilia. Opposing cirri form a fine mesh that filters particles from the water entering the

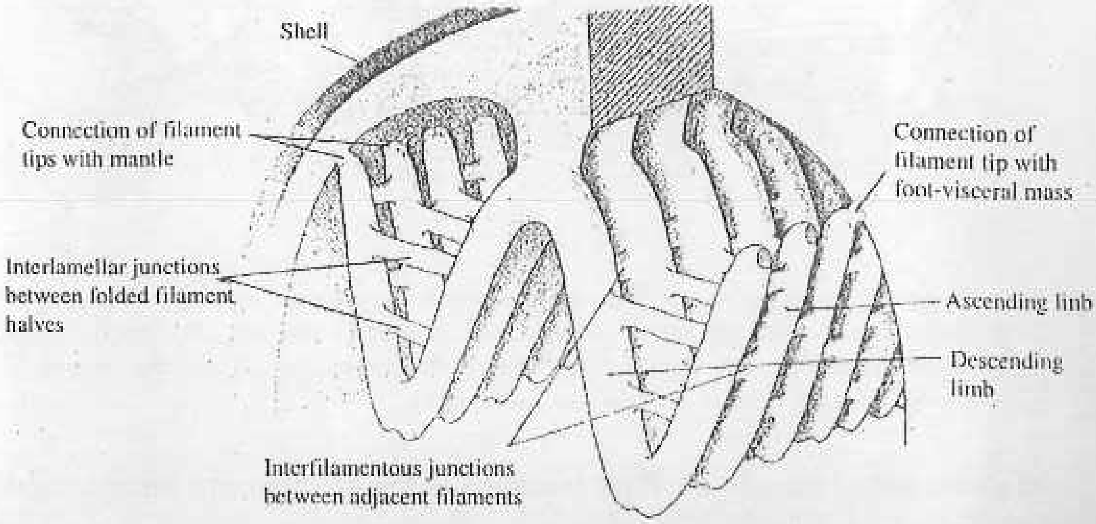


**Fig. 3.11** Diagram showing modification of gills for filtering. Lengthening and folding of the gill filaments increased the surface area. Note the tissue connections that provide support for the folded lamellibtanch filaments.

gill, the cirri then move the particles onto the frontal cilia. The pressure of the water stream generated by the lateral cilia is more than sufficient to overcome the resistance offered by the cirri. The inhalant, feeding or ventilating current enters the lower part

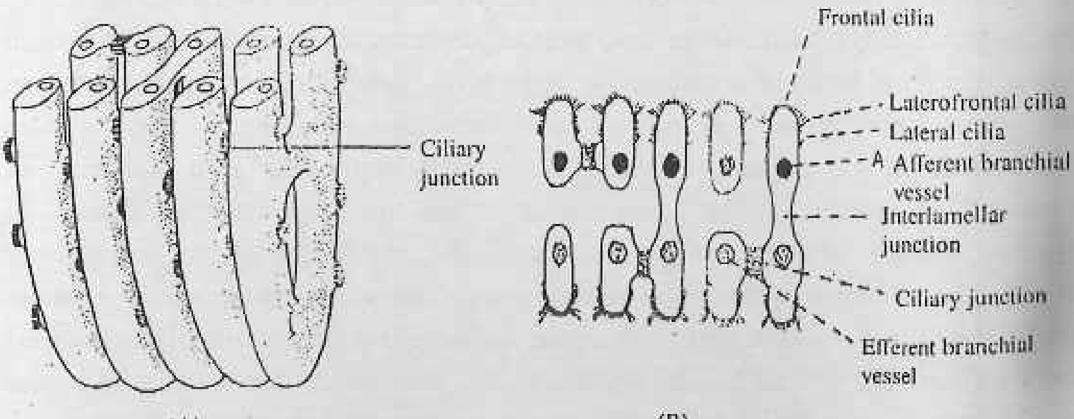


**Fig. 3.12A, B** A—Diagram showing five adjacent filaments (3D view). B—Frontal section.

of the mantle cavity or the infrabranchial chamber as the posterior end of the animal, flows between the filaments, and then moves up between the two lamellae. From the interlamellar spaces, the water passes into the exhalant or suprabranchial chamber and finally flows out through the posterior exhalant opening.

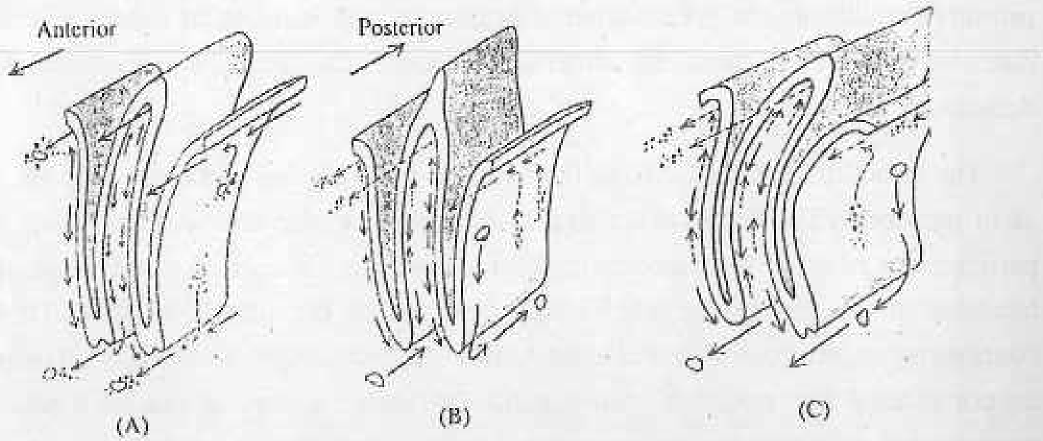


**Fig. 3.13** A—Transverse section of different lamellibranch gills, showing direction of frontal cilia beat and position of anteriorly moving food tracts. In B and C broken arrows indicate the fine frontal cilia carrying food particles, upward; solid arrows indicate the coarse frontal cilia carrying particles ventrally.

A—Mytilidae and Pinnidae; B—Arcidae and Anomiidae and C—Ostreidae and Pectinidae.

Support for the long, folded filaments is provided by three kinds of new tissue connections at various points within the gill : (1) cross connections, called inter lamellar junctions, between, the folded filament halves or lamellae; (2) connections, called interfilamentaous junctions, between adjacent filaments; (3) connections between the tips of the filaments and the mantle or foot. The extent of these connections varies in different groups of lamellibranchs and accounts for several types of lamellibranch gills (Fig. 3.11).

**Feeding and Digestion :** Most lamellibranchs feed on fine planktons and suspended detritus. Food particles, in some cases as small as 1 mm are removed from the water currents passing between filaments or entering the ostia. The particles are then passed into the frontal cilia, where they are entangled in mucous and moved up or down the margin of the filament to a food groove.

The primitive lamellibranch has five food grooves transporting particles anteriorly to the palps. Three of the grooves are located at the top of the gills between and outside the demibranchs; the other two are located ventrally, one along the margin of each demibranch. The frontal cilia are divided into separate tracts of coarse and fine cilia, one carrying particles upward and one downward. Such a two way vertical tract system with five food grooves is found in oysters and scallops. From such a primitive condition, the great variation in number and location of food grooves and direction of vertical tracts encountered in other lamellibranchs is believed to be derived by deletion.

The lamellibranch palpal lamellae have the same sorting and conveying function as in protobranchia. Particles are said to be sorted by size and weight. Small, light particles are retained for ingestion and large particles are carried to the edge of the lamellae in the grooves between ridges and fall to the mantle or foot. There is controversy regarding the selection of particles by the crests of the ridges. The palps do not receive free particles from the gills but rather a cord of particles bound in mucous that travels in the oral grooves at the junction between the palpal lamellae. The rejected materials, called pseudofeces, (from the palps and the gills) leave the mantle cavity most commonly by the inhalant aperture. When the valves are closed, water is forced out of the inhalant opening periodically, taking out the accumulated wastes with it.

The animal can regulate water flow by changing the size of the apertures into the mantle cavity and by gill contraction or expansion, which permits less or more water to pass between the filaments.

In carnivorous septibranchs, gills have been modified to from a pair of perforated muscular septa, separating the suprabranchial (exhalant) chamber from the intrabranchial (inhalant) one. By muscular action the septum moves up and down, forcing water into the inhalant chamber and out of the exhalant chamber. The pumping action, thus produced, is sufficient to bring small worms and crustaceans to the mantle cavity. These preys are then seized and carried to the mouth.

Digestion is extracellular in the stomach and absorption occurs in the digestive glands. The use of finer particles as food in the filter feeding forms is reflected in

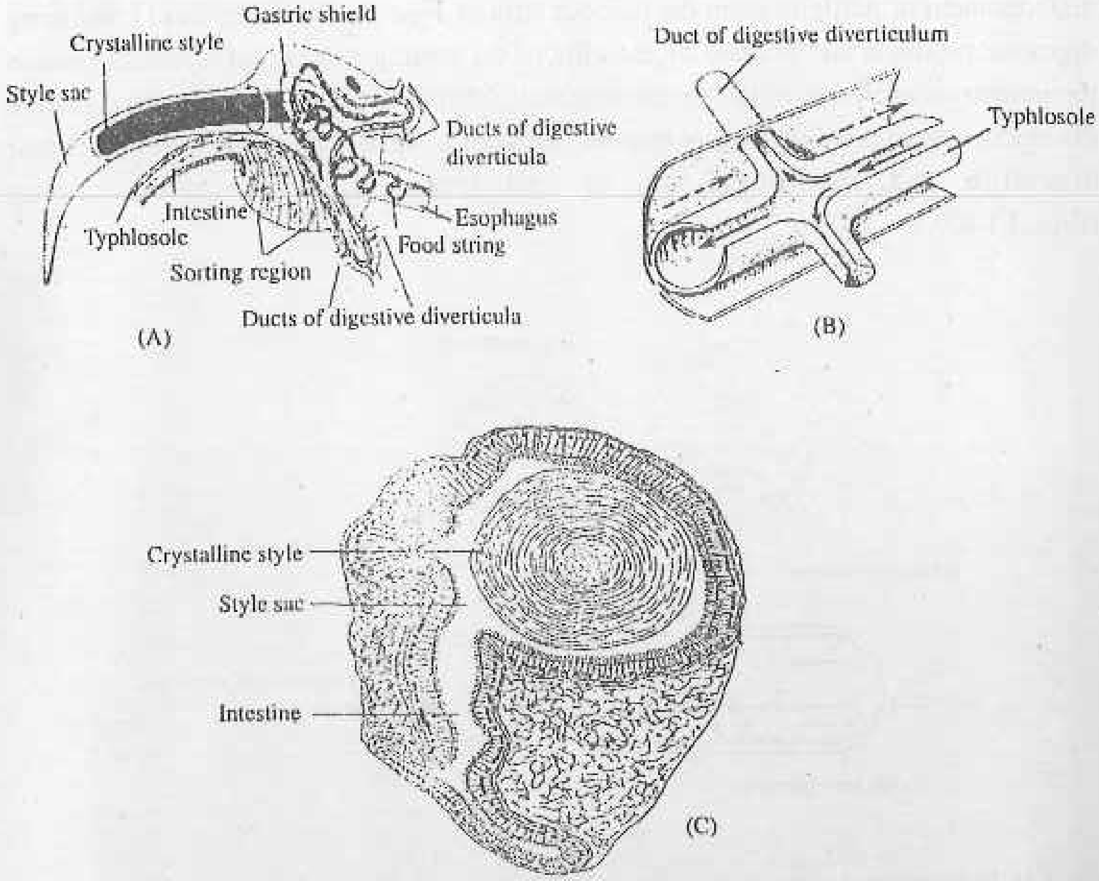
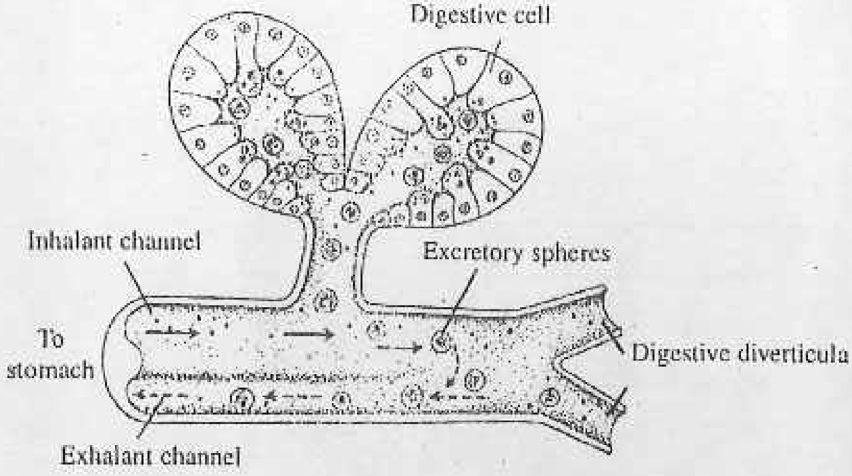


**Fig. 3.14** A—Stomach showing rotation of crystalline style and winding of mucous food string in a lamellibranch. Arrows indictate the ciliary pathways. B—Style sac and intestine of the freshwater clam. C—Typhlosole within the caecum of the stomach showing extensions into the ducts of the digestive diverticula. Solid arrows indicate inhalant ciliary currents; dashed arrows indicate exhalant currents.

a number of stomach modifications. A style sac is present; the mucous becomes consolidated into a very compact and often long rod, the **crystalline style**. The style is rotated against the plate like gastric shield by cilia in the style sac (Fig. 3.14A,C). In this process the style end is dissolved, releasing various carbohydrate splicing enzymes. Similar enzymes are released from the stomach wall. Thus, carbohydrates and lipids are digested at least in part extracellularly. Most protein digestion occurs intracellularly within the gastric gland. The rotation of the style also aids in mixing the enzymes with the stomach contents and acts to pull food-laden mucous strings from the oesophagus into the stomach. The lower pH of the stomach facilitates the dislodgement of particles from the mucous strings. Fine particles and fluid containing digestive products are retained by the cilia of the sorting ridges and directed towards the numerous apertures of the digestive glands. Within the main ducts of the digestive diverticula there is a continuous two-way flow of materials entering for intracellular digestion and absorption and of cell fragments and wastes leaving (Fig. 3.14D).



(D)

**Fig. 3.14 D** Diagram of a section of digestive diverticulum showing the absorption and intracellular digestion of material passed inward from the stomach, extension (solid arrows), and the outward passage of wastes (dashed arrows)

## 2.3.3 Filter feeding in Echinoderms

Echinodermata constitutes the only major group of deuterostome invertebrates. This phylum is exclusively marine and are largely bottom dwellers.

Among different classes of echinoderms some members of the class ophiuroid are filter feeders. Ophiuroids are carnivores, scavengers, deposit-feeders, filter feeders or suspense-feeders. Most use several feeding modes, but one is generally predominant (Fig. 3.15).

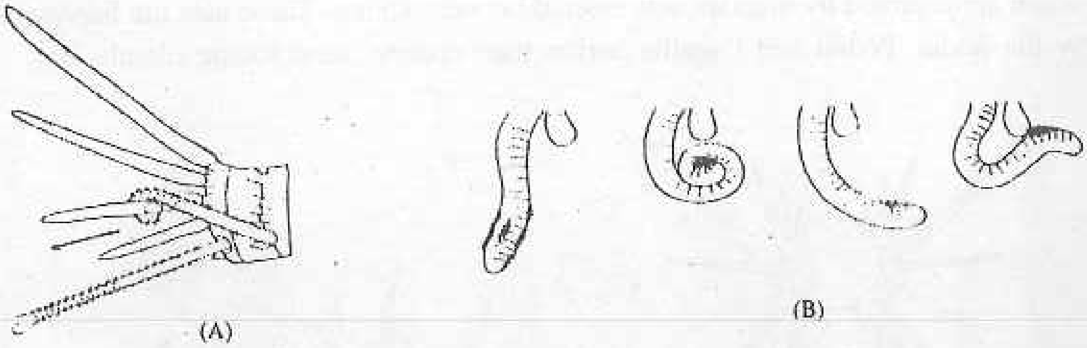


**Fig. 3.15** Feeding activity of podia in brittle stars. A—Spine wiping, podium of one side wipes the spines on the opposite side of the arm. B—Particle consolidation and transfer in the suspense-feeding brittle star.

**Filter feeding :** In filter feeding, the arms (*ophiocomina* sp) are lifted from the bottom and waved about in the water. Planktons and detritus adhere to mucous strands string between the adjacent arm spines. The trapped particles may be swept downward toward the tentacular scale by ciliary currents or collected from the spines by the tube feet, which extend upward for the purpose. A tentacular scale is a reduced spine. The tube feet are then scraped across the tentacular scales, depositing collected particles in front of the scale. This is also where the ciliary tracts deposit their material. On each side the food particles are picked up by adjacent podia, compacted into a bolus and passed along the mid dorsal line of the arm, where movement toward the mouth is facilitated by cilia (Fig. 3.16).

In *Ophiothria fragilis* papillate podia are used for filter feeding. The feeding arms are elevated and twisted so that the oral surface is directed toward the current. The podia are extended well beyond the spines, forming comblike filtering series on either side of the arm. Collected particles are periodically removed and transported as a growing bolus by a wave action of the podia that travels down the arm towards the mouth.

Such mechanisms of filter feeding have the advantage of permitting the animal to extend only two or three feeding arms from its protective retreat as well as to utilize a variety of food sources.

**Digestion :** Ophiuroids augment their basic diet of bottom material with occasional larger prey detritus and protozoans of the marine floor are staple items, which are captured by mucous nets erected between spines. These nets are harvested by the podia. Podial and flagellar action then conveys food to the mouth.

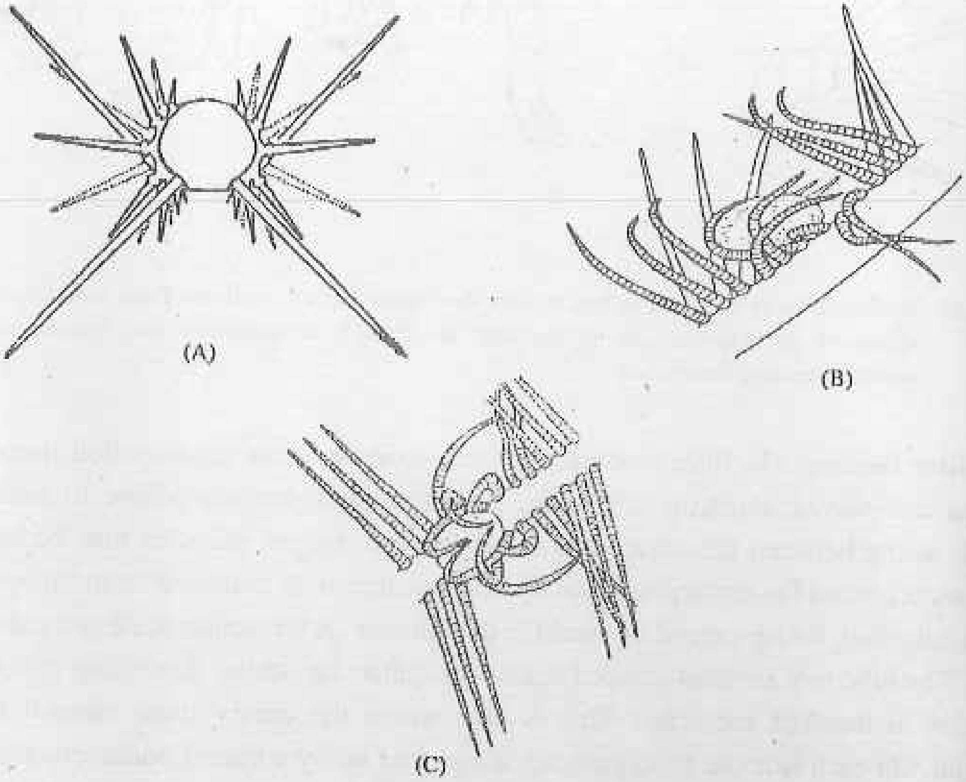


**Fig. 3.16** Filter feeding in ophiuroids. A—End view of arm section of the brittle star showing spines and position of tube feet. Alternate tube feet are directed orally and aborally. Tube feet may also be extended laterally, forming a single filtering series on either side of the arm. B—C, particle collection and transport seen in side view (B) and orally (C). Particles are added to a bolus which is about 1 mm in diameter on reaching the month.

The digestive system is simple. The ophiuroid digestive system consists of a prebuccal cavity lying behind the joints, a peristomial membrane surrounds the mouth and a short oesophagus leads to the stomach. The ophiuroid stomach is suspended by aboral mesenteries. Extending from the stomach margins, 10-pouches alternate in position with bursae and gonads. They have no intestine or anus. Both extracellular and intracellular digestion and absorption take place within the stomach. Undigested materials come out through mouth.

# Unit 4 ❐ Respiration

*Structure*

4.1 Organs of respiration : Gills, Lungs and Trachea

4.2 Respiratory pigments

4.3 Mechanism of respiration

## 4.1 Organs of respiration : gills, lungs and trachea

### 4.1.1 Introduction

Respiration in its widest meaning is sometimes defined as the gaseous exchange between an organism and its environment. Respiration has two distinct phases. Firstly, there is an exchange of gases, namely, oxygen and carbon dioxide between the organism and the external environment; this phase is known as the **external respiration** and .the second phase is called the **internal respiration** in which the complex reactions take place within the cells that results in the release of energy by oxidation of food materials. For these purposes, the respiratory surfaces, and the other structures that are involved in conveying the oxygen to the metabolizing tissue and carrying back carbon dioxide to the respiratory surfaces, constitute organs of respiration. Among non-chordates, the important organs of respiration, other than integument, are the gills, lungs and trachea.

**Gills** are the typical respiratory organ of aquatic animals like polychaetes, crustaceans, molluscs and echinoderms.

**Lungs** are vascularized air sacs. These are found in several terrestrial invertebrate groups, viz., pulmonale snails, scorpions, spiders, chilopods, decapods etc. Basically these lungs are diffusion-lungs. Ventilation lungs are characteristics of terrestrial vertebrates.

The **tracheal system** found in terrestrial and flying insects is a highly efficient system. The air tubes branch are give rise to a network of fine tubes in the intercellular space that bring air very close to the cells and close to mitochondria where oxidation of food stuff takes place.

### 4.1.2 Gills

(A) **In Polychaetes :** Gills are common in polychaetes but they vary greatly in both structure and location, indicating that they have arisen independently within the class a number of times. Many species that possess gills are already protected, since they live in tubes and burrows. Polychaetes that are very small or have thread like bodies do not have gills. Most commonly gills in annelids are associated with parapodia, the locomotory organ. In nereis notopodium may possess a flattened branchial lobe, acting as a gill. Commonly, the gills arise from the base of the dorsal cirrus. In many sedentary species gills are not associated with parapodium but they are situated on the dorsal surface of the anterior segments, as found in terebellids (Fig. 4.1).

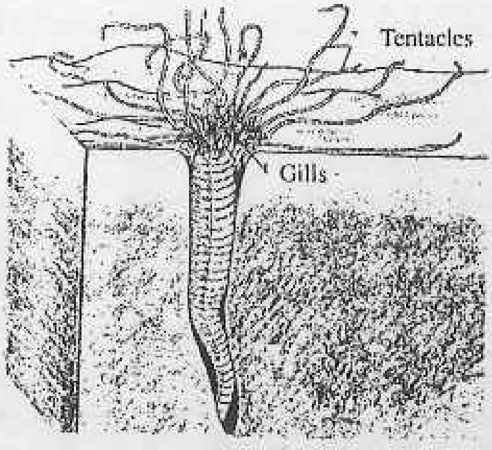


**Fig. 4.1** Diagrammatic view of a polychaete showing the gills and outstretched tentacles over the substratum.

(B) **In Crustacea :** In crustaceans, gills are the usual organs for gaseous exchange. They are typically associated with the appendages. But gills vary greatly in form, location and derivation. In *Palaemon,* the gills are enclosed within a special chamber, the gill chamber, lying on each side of the cephalothorax. There are eight gills; gills are crescent-shaped and their size increases gradually anteroposteriorly. Each gill has a slender axis on which double rows of rhomboidal leaf-like gill-plates are arranged like the pages of a book. This type of gills are called **phyllobranch.** According to the position of origin, the gills are of there types : (i) Podobranch, (ii) Arthobranch,and (iii) Pleurobranch. Podobranch is the first gill from the anterior side, which remains attached with the coxa of the second maxilliped. Arthrobranch is attached with the arthrodial membrane of the third maxilliped. Second and eighth gills are arthrobranch. Pleurobranch is attached with the outer border of the thorax and over the articulating surface of the walking legs (Fig. 4.2A). Third to seventh gills are pleurobranchs. The gills are highly vascular. Two lateral and one median longitudinal blood channels pass throughout the length of gill base. The lateral channels are interconnected by numerous transverse channels. In malacostraca there are four gills in primitive forms, in penaeid shrimps there are 24 gills on each side in *Homarus* sp. There are 20 gills on each side of the body.

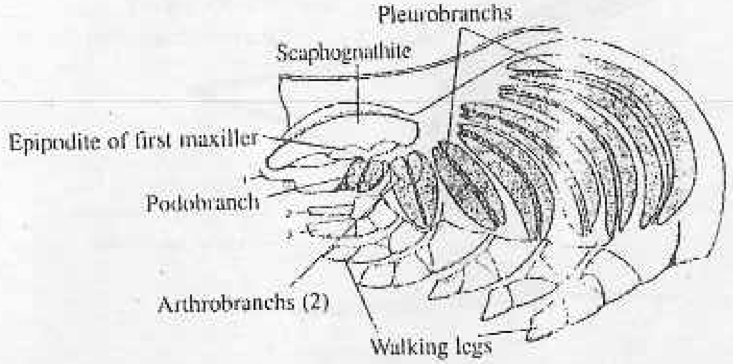


**Fig. 4.2A** Diagrammatic view of the gill-chamber of prawn exposed to show the arrangement of gills. Gills are pleurobranchs.

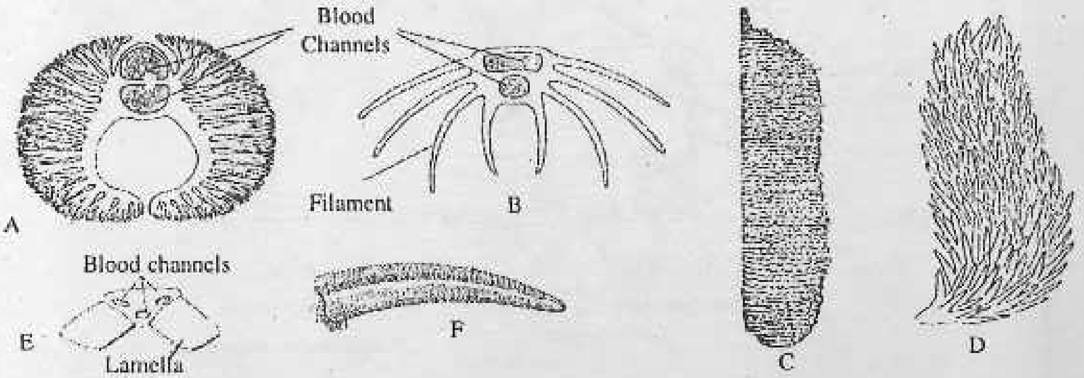


**Fig. 4.2B** Diagrammatic representation of decapod gills. A and C, dendrobranchiate gill of penaeid shrimp. The gill branches are subdivided. A—transverse section; C—Lateral view of the entire gill. B and D—filamentous or trichobranchiate gill of lobster, crayfishy and some other groups. The gill branches are not subbranched. B—transverse section; D—Lateral view of the entire gill. E and F—lamellar or phylobranchiate, gill of brachyuran crabs, most anomurans and shrimps. E—transverse section, F—Lateral view of the entire gill.

The structure of gill branches varies among decapods (Fig. 4.2A & 4.3). In cirrepedia gills are lacking and the mantle and cirri are probably the principal sites for gas exchange (Fig 4.4).

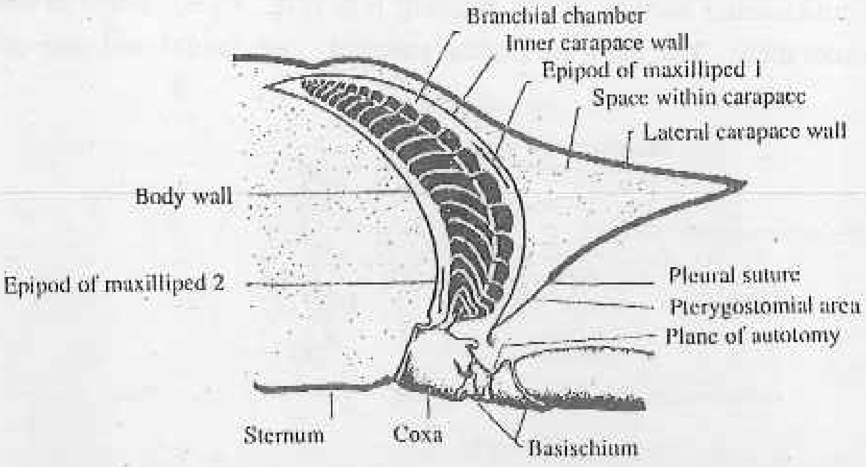


**Fig. 4.3** Diagrammatic view of cross section through the gill chamber of a crab.

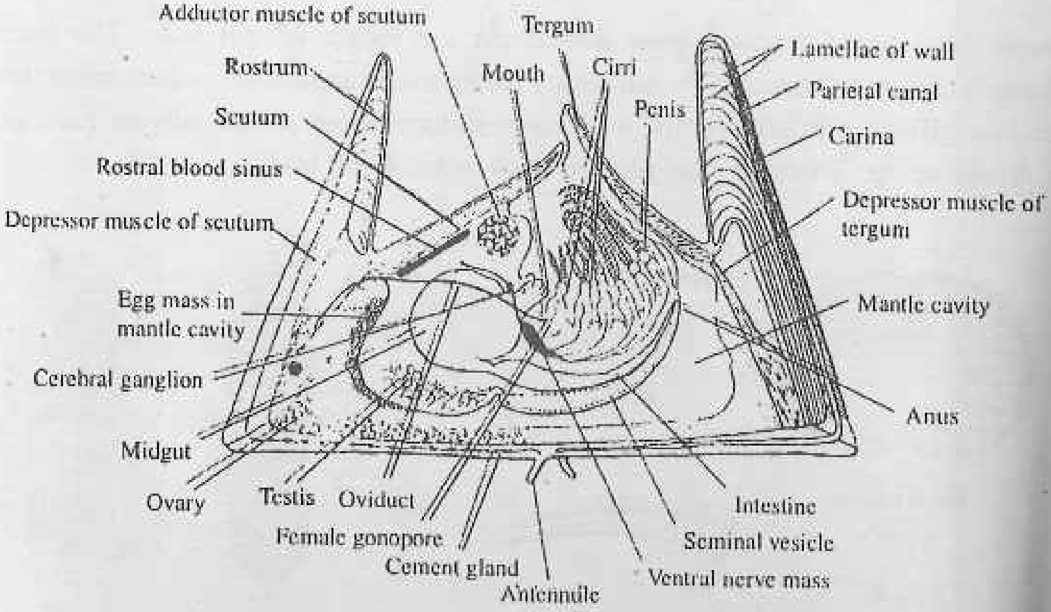


**Fig. 4.4** Diagrammatic view of the vertical section of *Balanus* sp. showing the visceral. Note six pairs of long, biramous cirri, probably the principal sites for gas exchange.

(C) **In Xiphosura :** Subclass Xiphosura is under the class Merostomata of the phylum Arthropoda and the class includes some fossil forms and saine living ones.

The living ones are included in this subclass. They are characterized by five or six pairs of abdominal appendages modified as gills. The first pair farms the genital aperculum bearing two genital pores on the underside. Posterior to the genital aperculum are five pairs of flap like, membranous appendages modified as gills. The under surface of each flap is formed into many leaf like folds called lamellae, which provide the actual surface for gas exchange. This arrangement af leaf like lamellae has caused the appendage to be called book gills. The movement of the gills maintains a constant circulation of water over the lamellae and the gills also help in swimming as they move during swimming (Fig. 4.5).

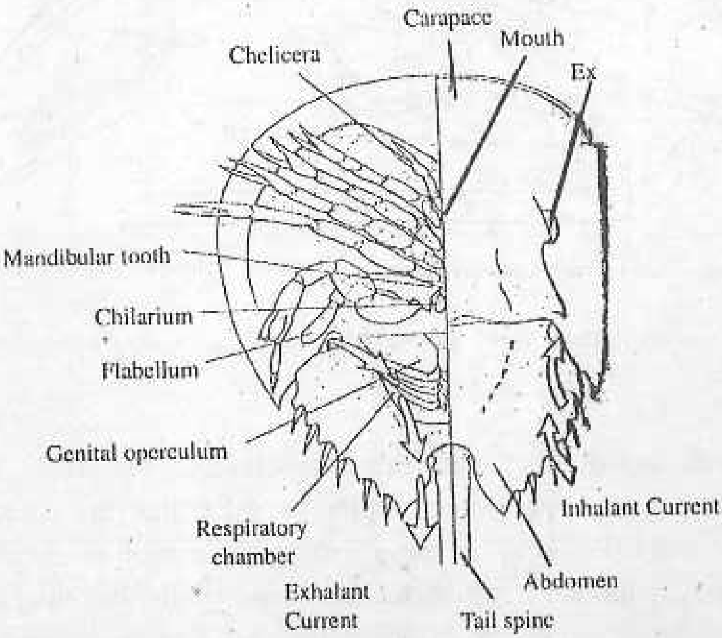


**Fig. 4.5** A horse shoe crab (left half-ventral; right half-dorsal). Ventral side shows book gills containing lamellae on the under surface of each flap which provides actual surface for gas exchange.

(D) **Mollusca** : Within the mantle cavity of the mollusca pairs of gills are farmed (Fig. 4.6). Each gill or ctenidium consists of a long, flattened axis projecting from the anterior wall of the mantle cavity and contains blood vessels, muscles and nerves.

To each side of the broad surface of the axis are attached flattened, triangular filaments that alternate in pasitian with those filaments an the opposite side of the axis. Such a gill is said to be **bipectinate**. Many living molluscs, however, have **monopectinate** gills in which the filaments occur on only one side of the axis, like teeth on a comb. The gills are located on opposite sides of the mantle cavity and are held in position by a ventral and a dorsal membrane. Propulsion of water through the mantle cavity is largely effected by the beating of a powerful band of lateral cilia located on the gills. Two blood vessels run through the gill axis.

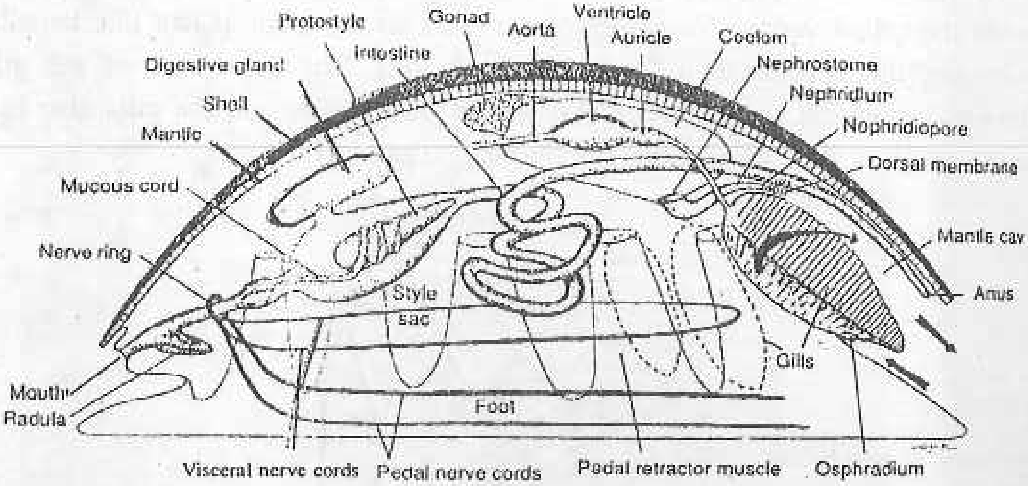


**Fig. 4.6** Generalized mollusc (lateral view). Arrows indicate path of water current through mantle cavity.

The **gastropods** ate divided into three subclasses. The first, known as prosobranchia, includes gastropods that respire by gills, that are located at the anterior part of the body (Fig. 4.7). In these gastropods, torsion is clearly evident. The second sub-class, pulmonata, which includes land snails, has no gills. In the third subclass opisthobranchia, due to detorsion the shell and the mantle cavity are usually either reduced in size or absent. So original gills have disappeared. But in same sea slugs secondary gills are arranged in a circle around the posterior arms (Fig. 4.8A, B).

In some group of early protobranch bivalves, filter feeding evolved. The filter feeders, called lamellibranchs, came to dominate the bivalve fauna. The gills and ventilating current of protobranchs preadapted them for filter feeding. The principal modification of the gills for filtering was the lengthening and folding of the gill filaments, which greatly increased their surface area. The most specialized lamellibranch gill is known as a eulamellibranch gill in which the union of filaments has developed further so that the lamellae actually consist of solid sheets of tissue.

Furthermore, the interlamellar junctions have increased in number and extend the length of the lamellae (dorsoventrally). Thus, the inter-lamellar space is partitioned

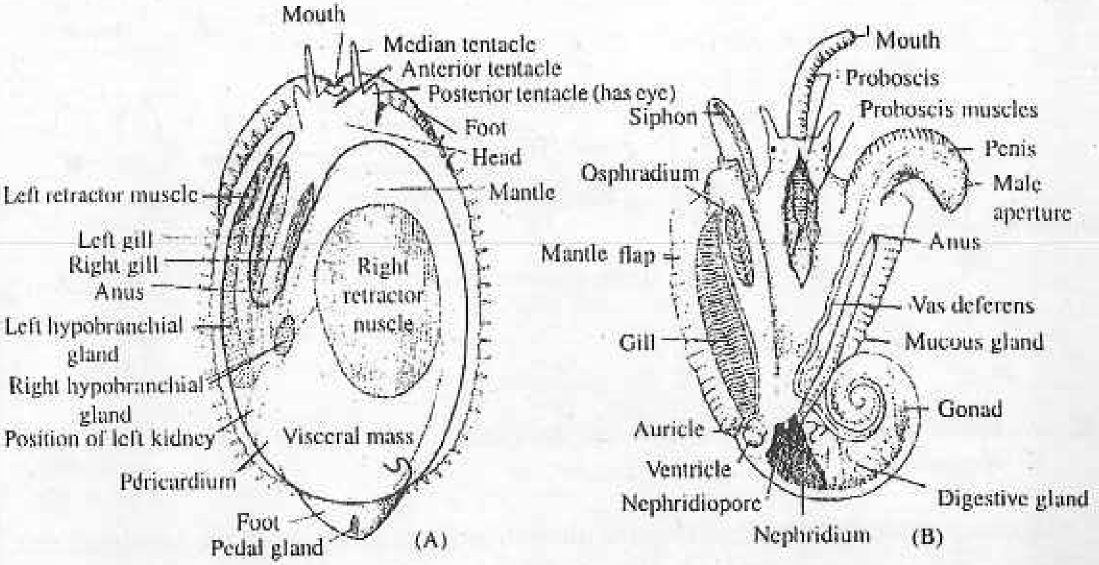


**Fig. 4.7** Dorsal view of (A) *Haliotis* sp (prosobranch) with the shell removed and the mantle cavity exposed, showing the anterior position of the gill. (B) *Buccinum undatum* (prosobranch); dorsal view with shell removed & mantle cavity exposed.

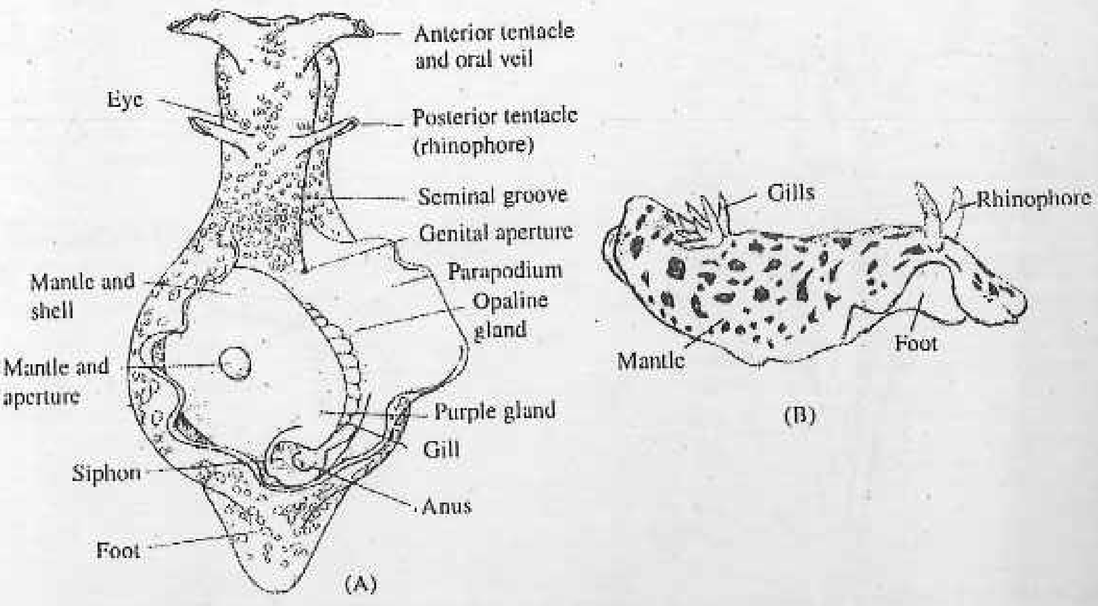


**Fig. 4.8 A, B** (A) Opisthobranch, a sea hare, an anaspidean, here gill is present. (B) *Glossodoris* sp. with secondary anal gills.

into vertical water tubes. Oxygenation of the blood takes place or the water moves over the surface of the gill and dorsally in the water tubes (Fig. 4.9).

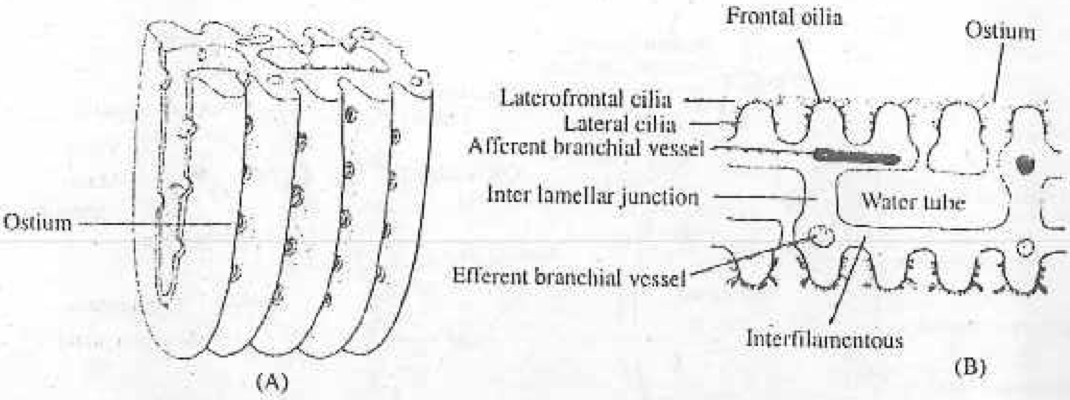


**Fig. 4.9** Eulamellibranch gill. A : Five fused, adjacent filaments; B : Frontal section. (Diagrammatic representation).

In many **cephalopods** that swim with webbed' arms, the gills are vestigial and gas exchange takes place through the general body surface. However, the nautiloids have four gills but coleoids have only two. The circulation of water through the mantle provides oxygen for the gills (Fig. 4.10).

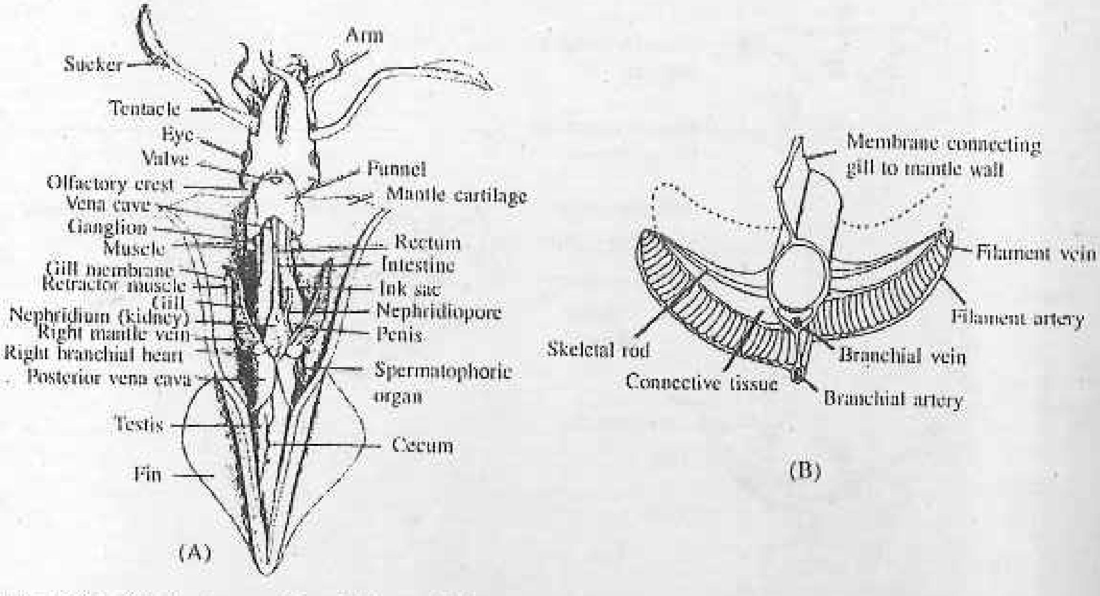


**Fig. 4.10** (A) Anatomy of squid (ventral view) with mantle cut, revealing organs. Note the position of the gills: (B) Section of the gill axis, showing two filaments on either side; only the outlines of the posterior two are shown.

(E) **Echinoderms :** In Echinoderms, gas exchange structures vary from one group to another and appear to have arisen independently within different classes. In echinoids five pairs of bushy projections are found on the oral hemisphere. These are the gills. In regular echinoids five pairs of peritonial gills are important centers of gas exchange (Fig. 4.11). Each gill is a highly branched outpocketing of the body wall and is therefore lined within and outside by a ciliated epithelium. Coelomic fluid from the lantern coelom is pumped into and out of the gills by a system of muscles and ossicles. There are no peristomial gills in the heart of urchins and sand dwellars. Gas exchange in most holothuroids is accomplished by a remarkable system of tubules called **respiratory trees,** which are located in the coelom on either side of the digestive tract.

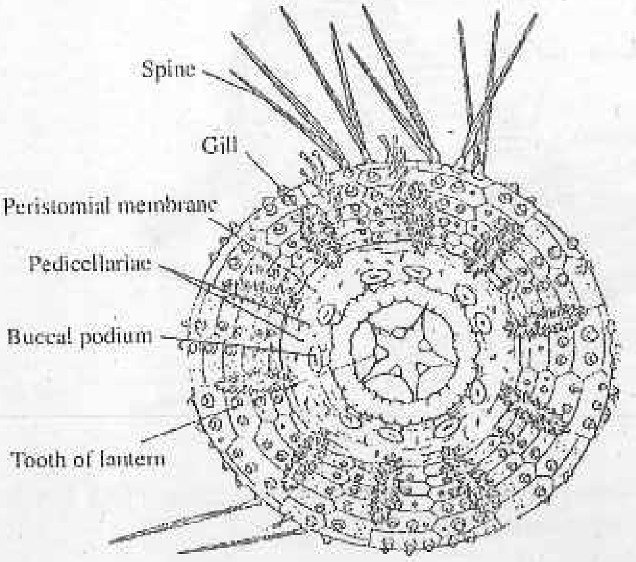


**Fig. 4.11** In regular sea urchin (echinoid) five pairs of peristomial gills are important centers of gas-exchange.

## 4.1.3 Lungs

(A) **In Pulmonates (Gastropoda; Mollusca) :** This subclass of Gastropoda contains land snails as well as many fresh water forms. The distinctive feature from which the group gets its name is the conversion of the mantle cavity into a lung. The edges of the mantle cavity have became sealed to the back of the animal except for a small opening on the right side called **pneumostome**. The gill has disappeared and the roof of the mantle cavity has become highly vascularized. Ventilation is done by the arching and flattening of the mantle cavity floor. Gas exchange by diffusion through the pneumostome is important in most pulmonates.

(B) **In Arachnids (Arthropoda) :** Arachnids possess book lungs or tracheae or both. Book lungs which are always paired, are more primitive and are probably a modification of book gills. Each book lung consists of a sclerotized pocket that represents an invagination of the ventral abdominal wall. The wall on one side of the pocket is folded into leaf like lamellae, which are held apart by the bars that enable the air to circulate freely. The non-folded side of the pocket forms an air chamber (atrium) that is continuous with the interlamellar spaces and opens to the outside through a slit-like opening called **spiracle** (Fig. 4.12 & 4.13).

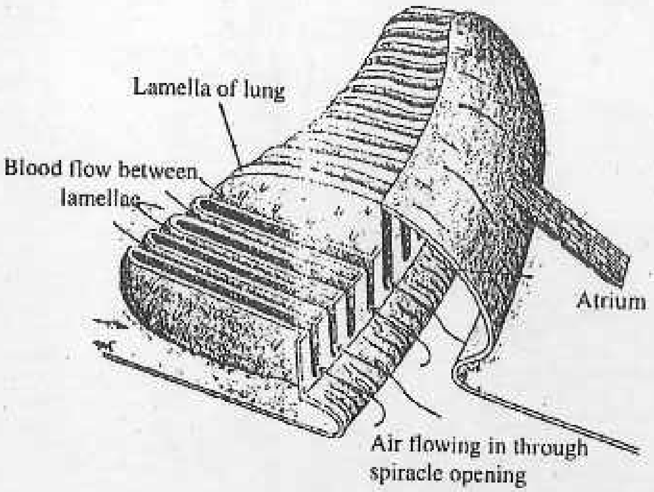


**Fig. 4.12** Diagrammatic section through a book lung. Arrows indicate blood flow (on the-left) and air flow (on the right) through spiracles.

(C) **Class—Chilopoda :** The members of the class chilopoda known as centepedes; are perhaps the most familiar of the myriapodan arthropods. In the order scutigeromorpha, the tracheal system is lung like and probably evolved independently from that of the other centepedes. The spriacles are located middorsally near the posterior margin of the targal plates covering the leg bearing segments. Each spiracle opens into an atrium from which extend two large fans of short tracheal tubes. The tracheae are bathed with blood of the pericardial cavity. The blood of scutigeromorphs contains **haemocyanin**.

(D) **Order—Decapoda (Class—Malacostraca) :** Though gills are the primary organs for respiration, there is also a tendency for a branchial chamber to become rather like a lung, with some surface (other than gills) given over to gas exchange. The gill continues to provide for ventilation, but it moves air rather than water.

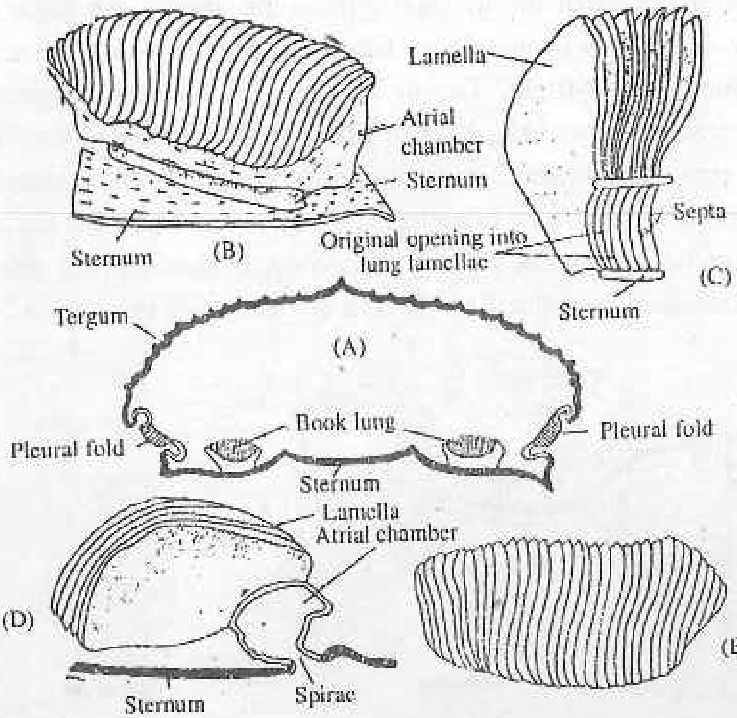


**Fig. 4.13** Structure of the book-lung of scorpion. A : Cross section of the body of Scorpion showing the position of the book lung. B : Dorso-posterior view of the right book lung. C : A few lamellae in natural position. D : Vertical section of a book lung, E : Dorsal view of book-lung.

### 4.1.4 Trachea

(A) **In Insects :** Respiration in insects takes place through tracheae. A pair of spiracles is usually located above the second and third pairs of legs or only above last pair. The first seven or eight abdominal segments possess a spiracle on each lateral surface. So there is a maximum of ten pair of spiracles. Tracheal spiracles are simple holes in the integument as in some apterygota. In most insects, however, the spiracles open into a pit or atrium from which the tracheae arise. The spiracle is generally provided with a closing mechanism and in many terrestrial insects, the atrium contains filtering devices. The closing mechanism of the spiracle reduces water loss and the filtering structures prevent the entrance of dust and parasites. The pattern of internal tracheal system is variable but a pair of longitudinal trunks with cross connections form the ground plan of most species.

The tracheal tubes are supported by thickened spiral rings of cuticle, the **taenidia**. The rings resist or prevent collapse of the tubes and also permit stretching of the tube. The diameter of the tracheal tube is not always the same in the body; sometimes they widen in various places forming air sacs. These air sacs are found in insects capable of rapid flight. The air sacs provide for both oxygen storage and ventilation. The tracheal tubes branch out and the smallest subdivisions, the **tracheoles** are less than 1 mm in diameter. These fine tubes are given off in clusters from the larger tubes and their still finer branches form network over the tissue cells. The cuticle of the tracheae (but not of the tracheoles) is shed during moulting. After moulting new tracheae are joined to the old tracheoles (Fig. 4.14 A, B).

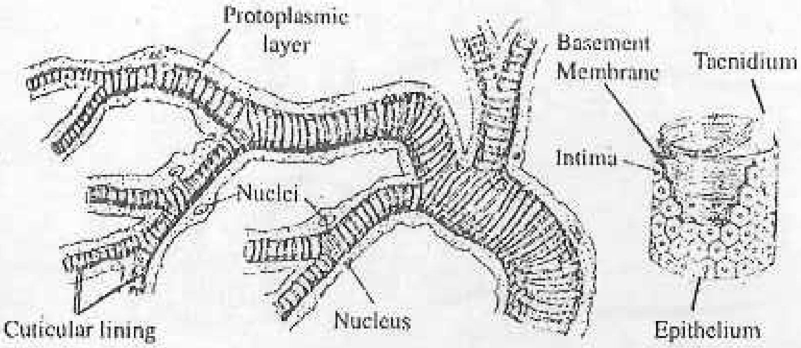


**Fig. 4.14A** Diagrammatic view of a portion of trachea (enlarged view)

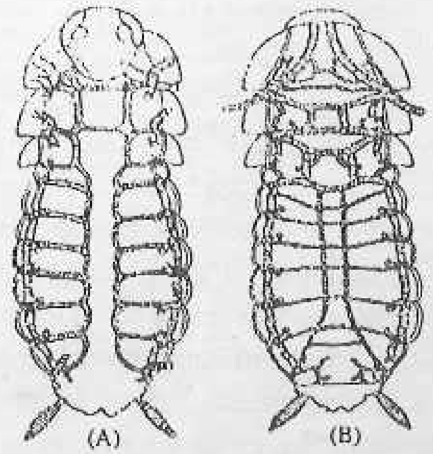


**Fig. 4.14B** Tracheal system of *Periplaneta* sp.

(A)—With the ventral integument and viscera removed showing dorsal tracheae.

(B)—With dorsal integument and viscera removed showing ventral tracheae.

(B) **In Myriapods (Arthropoda) :** In these arthropods, except scutigeromorphs, the spiracles of the tracheal system lie in the membranous pleural region above and just behind the coxae. There is basically one pair of spiracles per segment, but some segments lack them and the pattern of distribution varies in different groups. The unclosable spiracles opens into an atrium liped with cuticular hairs (trichomes) which may reduce drying or prevent the entrance of dust particles. The tracheal tubes open at the base of the atrium. Depending on the order the tracheal system may contain longitudinal trunks, a network of tubes or unconnected tubes.

(C) **Phylum—Onychophora :** The respiratory organs are trachea. The spiracles are minute openings and are present in large numbers all over the surface, of the body between bands of tubercles. Each spiracle opens into a very short atrium, at the end of which arises a tuft of minute tracheae. Each trachea is a simple, straight tube extending directly to the tissue that it is supplying.

## 4.2 Respiratony pigments

### 4.2.1 Introduction

Respiratory pigments are substances which can combine with $O_2$ at high pressures of gas and release it where oxygen tension is lower in the tissues. So they are oxygen carriers. Respiratory pigments may be present in the blood plasma or corpuscles or in both. Because they chemically bind oxygen, respiratory pigments increase the capacity of blood, coelomic fluid or tissue to transport or store oxygen. An enhancement of oxygen transport is important in situations in which metabolic oxygen demand is not met by a supply of oxygen via simple diffusion or transport in physical solution. Animals that have higher oxygen demand or that occupy oxygen-poor habitats usually have a respiratory pigment. Functionally, different forms of the same respiratory pigment may occur in different body compartments of the same animal. For example, there may be one haemoglobin in the tissues, one in the coelom and one in the blood-vascular system, each with a different porien component (globin) that determines the affinity of the haemoglobin for oxygen. The oxygen affinity of the pigment increases from the blood compartment near the environmental source to an inner compartment, such as muscle tissue, containing the metabolic sink. This stepwise arrangement of affinities from low to high as one moves from outsite to inside the animal, creates a cascade down which oxygen is transferred from blood to coelom to tissues.

### 4.2.2 Important respiratory pigments

The pigments commonly met within the animals, are (i) **haemoglobin,** (ii) **haemocyanin,** (iii) **haemoerythrin** and (iv) **chlorocruorin.** Of these, the first two are widely distributed among protostomes. In addition to these, there are certain other pigments which are found in some animals. These are **puniaglobin, echinochrome, vanadium** and **molpadin.** It is interesting to note that haemocyanin and chloracruorin are found in plasma of the blood, while, haemoglobin and haemoerythrin occur in the corpuscles or in plasma.

### 4.2.3 Outline chemical nature

(i) A haemoglobin molecule consists of two parts, a **porphyrin ring** with an iron atom at its centre, called **heme**; and a protein part, called **globin.** So it is a conjugated protein with 'heme' as the prosthetic group. An important function of globin is to prevent oxygen from binding too tightly to heme; when globin is present, oxygen binds reversibly to heme and can be released to the tissues. The extracellular haemoglobins are typically large molecules of high molecular weight compared with the relatively small size of intracellular haemoglobins. The extracellular occurrence of few large molecules rather than many small ones may be necessary to keep the osmotic concentrations of the blood within reasonable limits, perhaps to prevent loss of the molecules during ultrafiltration. In the respiratory organs haemoglobin combines with $O_2$ at the normal temperature and pressure so as to form **oxyhaemoglobin.** At the level of tissues where the $O_2$ pressure is very low it readily liberates $O_2$ and its effect is reduced to haemoglobin.

(ii) **Haemocyanin** by its distribution ranks next in importance to haemoglobin. This is a copper-containing protein occurring in crustaceans, a few arachnids such as scorpion and Ring crab and in cephalopodes such as ***Sepia, Loligo, Octopus*** and in gastropods. It occurs in two forms, oxidized and reduced and the crystals of the latter forms are prism-shaped or needle-shaped which are soluble in water. Haemocyanin binds a molecule of oxygen between a pair of copper atoms. The many pairs of copper atoms are bound directly to the protein part of the molecule and a heme is absent. Haemocyanins always remain dissolved in the plasma. The molecular weight is very high, varying from 4,00,000 daltons in some crustaceans to 13,00,00,000 daltons is some gastropods. Haemocyanin only occurs as large extracellular molecules and is never found in cells. The number of subunits vary from a few to many in haemocyanin. The pigment gets saturated with oxygen at different concentrations in different species. In oxygenated state haemocyanin is bluish while it is colourless in deoxygenated form. The oxygen transporting capacity of haemocyanin is less than that of haemoglobin.

(iii) **Chlorocruorin** is a green coloured metallo-protein found in the plasma of same polychaetes. It also exists in oxygenated and reduced fomes. The metal which is found here is also iron ($Fe^{++}$); the metalloporphyrin is similar to heme of haemoglobin except that one vinyl group ($CH = CH_2$) is replaced by formyl group ($O = CH$) in chlorocruorin. This porphyrin is called **chlorocruorin**.

(iv) **Haemerythrin,** like haemoglobin, uses atoms to bind oxygen, but unlike haemoglobin, the two iron atoms are bound directly to the protein and not to the heme. It is pink or violet when oxygenated and colourless when deoxygenated. Haemoerythrin is always found in cells and never free in plasma or coelomic fluid. This metallo-protein is found in Sipunculida, Priapulida, Brachiopoda and also in a few polychaetes.

(v) Among other less common pigments are **Pinnaglobin, Echinochrome, Molpanis** etc. Pinnaglobin is browncoloured. It contains manganese as the prosthetic group. The pigment is present in the plasma of Lamellibranch.

**Respiratory pigments in invertebrate**

| **Pigment** | **Colour** | **Site** | **Metallic group** | **Distribution in non-chordates** |
|---|---|---|---|---|
| Haemoglobin | Red | Plasma | Iron | Annelids & Moluscs |
| Haemocyanin | Blue | Plasma | Copper | Molluscs (gastropods Cephalopods), Crustaceans |
| Chlorocruorin | Green | Plasma | Iron | Annelids |
| Haemoerythrins | Red | Corpuscles | Iron | Sipunculids & Brachiopods |
| Pinuaglobin | Brown | Plasma | Manganese | Lamellibranchs |

## 4.3 Mechamism of respiration

Same invertebrates can obtain energy from their food stuffs without oxygen, but these animals constitute a minority. Anaerobic metabolisin is always less efficient than its aerobic counterpart and leaves organic acids as waste products. Aerobic metabolism has advantages; not only does it release energy more efficiently, but its waste product, carbon dioxide, is more easily disposable. Accordingly, the respiration of most animals involves the uptake of oxygen and the removal of carbon dioxide.

In aquatic organisms oxygen is always absorbed in a dissolved state. Difficulties may occur, however, concerning its availability water seldom contains even 1% dissoved oxygen and increased temperature and salinity rapidly reduce its gas-holding capacity. Fresh water is particularly vulnerable in this respect. In freezing temperature, surface ice may isolate a freshwater body from atmospheric oxygen. Moreover, the limited size of freshwater system allows them to heat rapidly thus, diminishing their oxygen supply.

Terrestrial invertebrates have a different oxygen problem. The oxygen supply is plentiful on land, as air consistently contains 21% oxygen, but there the difficulty lies in absorbing the gas in dissolved form. A moist respiratory surface is required but such a surface is threatened continuously by desiccation. If its respiratory surface is not secluded in a cavity or tube with limited outside exposure, an animal is forced to minimize its direct contact with the air. Among invertebrates only insects, a few other arthropods and some terrestrial snails possess a well protected respiratory oxygen. Other terrestrial invertebrates are confined to moist soils or other shaded, humid regions, where the threat of desiccation is minimal.

**Lower organism**

In lower organisms where there is no particular organ for respiration, exchange of gases takes place by the cell surface and cellular respiration follows. There may be some anaerobic forms also. Facultative anaerobiosis is common among fresh-water protozoans, whose environment can be depleted in oxygen. The obligate anaerobes of this phylam are mostly endoparasitic forms. Large volume of water passes through the canal system in sponges and cells take up oxygen and carry out aerobic respiration. Endoparasites are mostly anaerobes. In case of other lower metazoans where no specific respiratory organ is present, respiration takes place in the same way. Gas exchange in these animals usually involves simple diffusion.

(A) **Annelids** : Some annelids rely essentially on oxygen uptake aaoss the general epidermal surface. This reliance necessiates the continual lubrication of that surface, specially in terrestrial and burrowing forms. However, Such gerieral epidermal exchange can never be as efficient as gas exchange within well structured internal gills, lungs or similar respiratory pockets.

In some annelids, where gills are present, ventilation may be provided by gill cilia or by gill contractions but many burrowing and tube-dwelling polychaetes drive water through their burrowrs or tubes by undulating or peristaltic contractions of the body. Worms that ventilate by muscular activity typically exhibit a spontaneous ventilating rhythm in which a period of ventilation alternates with a period of rest. In most polychaetes a well-developed blood -vascular system is present and blood is enclosed within vessels. The gills are usually provided with afferent and efferent vascular loops premitting a two-way flow. In small polychaetes blood is colourless but in large species respiratory pigments are found in blood which is dissolved in the plasma. In fact, in these worms (polychaetes) three or four respiratory pigments are found. Among them haemoglobin is the most common pigments. Other pigments are chlorocruorin, a kind of haemoglobin and haemoerythin when present in polychaetes respiratory pigments are typically small molecules in corpuscles in the coelom and large extracellular molecules in the blood plasma. The extracellular molecules in the blood plasma carry orygen. The respiratory pigments function in oxygen transport. Oxygen is delivered to the target tissue where cellular respiration takes place. In same polychaetes, (*Glycera*), the haemoglobin may also store oxygen during the resting periods between ventilation on at low tide, when oxygen tension of the water in the burrow and surrounding area is considerably decreased. $CO_2$ is similarly transported by the respiratory pigments to the respiratory surface for giving out. The gas exchange depends on the difference in the partial pressure of the gases.

(B) **Arthropods :** Diffusion of gases accross the general body surface as found in same annelids, is not suitable for arthropods owing to their impermeable exoskeleton.

Arthopords have different kind of more efficient respiratory systems. Arthropods were confronted with these respiratory problems very early in the evolutionary history and divergent evolution of the phylum has resulted in a variety of novel respiratory adaptations.

**Tracheal respiration** : Most terrestrial arthpropods have the tracheal system, formed of chitin-lined tubes which ramify deep within the body. External openings are controlled by valves; the internal branches of the system terminate beside or within the cells with which respiratory gasses are exchanged.

Exchange through the trachea has been thought to occur primarily by diffusion; however, the spiracles are closed most of the time and exchange is probably a result of both diffusion and venfilation. Recent studies have demonstrated that the spiracles open very briefly and not all at once in response to a localized reduction in hemocoelomic pressure. The spiracle is literally sucked open and a "gulp" of air is taken in. The pressure drop is due to intersegmental muscle contraction and is under the control of the nervous system, which in turn may be regulated by the oxygen / carbon dioxide tension of the blood. More spiracles are therefore open during flight than when the insect is at rest. Because an insect must balance oxygen need against the danger of water loss, the number and duration of open spiracles are generally held to the lowest possible level. Ventilating pressure gradients results from body movements, largely abdominal, which bring about compression of the air sacs and the longitudinal extension and contraction of trachea. Ventilation is facilitate by the sequence in which certain spiracles are opened and closed.

At the tissue / tracheole level gases are exchanged by diffusion down a concentration gradient. Tracheoles are permeable to liquids and in most insects their tips are filled with liquids. This fluid is believed to be involved in the final transport of gases. As tissue gas exchange is handled fluid directly by the tracheal system, the blood plays a very minor role in gas transport. Blood in insects is usually colourless.

The tracheal system in arachnids is similar to that of insects. In one tracheal system here, the spiracle opens into an atrial or tube like chamber from which arises a great bundle of tracheae, which terminaes in the hemocoel rather than in muscle or other tissues as in insects.

**Gill respiration** : In crustacea gills are the usual gas exchange organs. They are typically associated with the appendages. The water current for ventilation is generally provided by the beating of certain appendages within the blood or hemolymph, oxygen is transported either in simple solution or bound to plasma haemoglobin or hemocyanin. Hemocyanin is found in the large species, but both the pigments have a sporadic distribution.

In malacostracan the structure of the gill branches varies among decapods. In the axis of each gill runs on afferent and an efferent branchial channel. Blood flows from afferent channel into each filament or lamella and then back into the efferent channel. The blood of decapods contains hemocyanin dissolved in the blood plasma and in large, active forms, such as the swimming crabs, hemocyanin transports about 90% of the blood's oxygen. the ventilating current is produced by the beating of a paddle-like scaphogmithite or gill bailer, a projection of the second maxilla. Water is pulled forward and the exhalant cutrent flows out anteriorly in front of the head. In shrimps, the ventral margins of the carapace fit loosely against the sides of the body, the water can enter the branchial chamber at any point along the posterior and ventral edges of the carapace (Fig. 4.15). In other decapods, the carapace fits somewhat more tightly and the entrance of water is limited to the posterior carapace margins and around the bases of the legs. The points of entrance of the ventilating stream is most restricted in the brachyuran crabs in which the inhalant opening is located around the bases of the chelipeds. The forward position of the inhalant

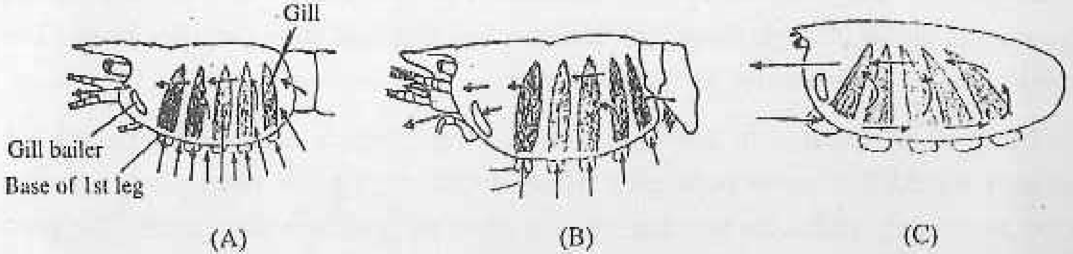


**Fig. 4.15A, B, C** Paths of water circulation through the gill chamber of three decapods, showing progressive restriction of openings into the chamber.
A—Shrimp; water enters along entire ventral and posterior margin of the carapace.
B—Crayfish; water enters at the bases of the legs and at the posterior carapace margin.
C—Crab; water enters only at the base of the cheliped.

openings in the brachyurans results in water taking a U-shaped course through the gill chambers. On entering the inhalant opening, the water passes posteriorly into the hypobranchial part of the chamber and then moves dorsally, passing between the gill lamellae. The exhalent current flows anteriorly in the upper part of the gill chamber and tissues from paired openings in the upper lateral comers of the buccal frames. As majority of decapods are bottom dwellers and includes many burrowers, a variety of mechanisms have evolved to prevent changing of the gills with silt and debris.

In subclass **xiphosura** of class merostomata the abdomen bears six pairs of appendages. The fused first pair forms the genital operculum bearing the two genital pores on the underside. Posterior to the genital operculum are five pairs of flap like, membranous appendages modified as gills. The undersurface of each flap is formed into many leaf like folds called lamellae, which provide the actual surface for gas exchange. This arrangement of leaf like lamellae has caused the appendages to be called **book gills**. The movement of the gills maintains a constant circulation of water over the lamellae and the gills also function as paddles during swimming. Water can enter the gap between cephalothorax and abdomen, the gap acting as anincurrent siphon. The water stream is then directed backward by the flagellum. The movement of the gills not only causes water to circulate over the outside of the lamellae but also pumps blood through these structures so that gas exchange can take place. The blood contains hemocyanin as oxygen carrier.

**Lung respiration** : In arachnids, book lungs, which are always paired are probably a modification of book gills. Here, diffusion of gases takes place between blood circulating within the lamellae and the air in the interlamellar spaces. The non-folded side of the pocket forms an air chamber (atrium) that is continuous with the inter / lamellar spaces and opens to the outside through a slitlike spiracle. Some ventilation results from the contraction of a muscle attached to the dorsal side of the air chamber. This contraction dilates the chamber and opens the spiracle but most gas movement is by diffusion. Blood is still the intermediate gastransporting agent in these animals and many arachnids contains hemocyanin as respiratory pigment.

(C) **Mollusca**

**Gill respiration :** The generalized molluscs possesses a special respiratory gill. This gill, is usually called a **ctenidium**. A respiratory current is drawn through the ctenidium by the beating of lateral cilia on the thin, wedge-shaped filaments. The current enters venterolaterally, passes over the vascularized surfaces of the gills and exits dorsolaterally or posteriorly from the mantle cavity. Other ctenidial cilia may remove excess particulate matter from the gill and thus prevent its folding by dirty water. These clearing cilia are located on the front and rear margins of the filaments.The so-called frontal cilia are the first to contact incurrent waters; they remove particles from the water and transport them upward over the filament to the abfrontal cilia of the rear margin. The direction of blood flow through the ctenidium is opposite to that of the water flow. Blood enters the molluscan gill through an afferent vessel located near the abfrontal margin of the central axis. As the blood percolates across the broad surface of each filament, it absorbs oxygen from mantle cavity waters. Oxygenated blood drains into an efferent vessel near the frontal margin of the central axis and then flows back to the heart. The opposing directions of blood and water flow allow well oxygented water to contact well-oxygenated vascular surfaces, while water with less oxygen meets ctenidial areas also low in oxygen. Such a counter flow system maximizes gas exchange. Oxygen uptake and transport are facilitated by respiratory pigments. Same molluscs have hemoglobin but the most common blood pigment in molluscs is hemocyanin dissolved in the blood plasma.

Cephalopods, however, lack the counter flow relationship exploited by other molluscs. Despite the loss of the counter flow relationship, respiratory efficiency remains quite high because of the rapid water flow through the mantle cavity and the closed nature of the ciraulatory system. Cephalopod blood contains hemocyanin and it is dissolved in the blood plasma.

**Lung respiration :** Terrestrial gastropods lost their gills entirely. The mantle cavity is converted into an air-breathing lung, which has a highly vascularized roof and a very small, adjustable opening called the **pneumostome.**

(D) **Echinodermata :** In echinoderms gas exchange occurs wherever internal body fluids are brought near the surrounding sea water, in areas such as body wall evaginators, sunken pouches and respiratory tubes. The most common respiratory surface is the podium. The evagination of the ambulacral system probably did not evolve primarily as a respiratory organ, but its thin wall and fluid-filled lumen are exploited in gas exchange by all echinoderms. Podia represent the major respiratory surface and handle upto 50% of the gas exchange in sea-stars. They also possess numerous papulae. The thin-walled peristomial gills of sea urchins are ventilated by flagellar action or by the pumping of the oral musculature. In holothuroids, animals pump water through paired branching tubules, the respiratory trees which ramify throughout the body. These tubules are associated with hemal system. The hemal fluid contains **hemocytes**, specialized hemoglobin containing coelomocytes which transport oxygen. Most echinoderms demonstrate a rather passive respiratory attitude.

# Unit 5 ❐ Excretion

***Structure***

## 5.0 Introduction

Excretion is the process by which the removal of the waste products of metabolism, which comprise the carbon dioxide and water that are releaed by the oxidation of energy rich compounds, and the nitrogenous waste that results from the metabolism of proteins and nucleic acids, take place. However, the removal of carbon dioxide is part of the respiratory process, and because of this, there is more than one route for the passage of water, excretion has commonly been thought of as the removal of nitrogenous wastes. The process of excretion is closely bound up with the regulation of the flux of water and certain electrolytes between the organisms and external environment.

## 5.1 Organs of excretion

In the major animal groups we fina a variety of different excretory organs, each sufficient to meet the needs of a species in its natural habitat. Among invertebrates, Protozoa, Porifera, Cnidaria and Echinodermata do not possess excretory system in a well organized form; rather the general body surface removes various excretory products.

Goodrich (1895) first clearly formulated the fundamental principal that the animal body is primitively connected with the external environment by two distinct sets of tubular structures, the **nephridia** and the **coelomoducts** with cilia or flagella providing their motive power.

Goodrich defined nephridium as on organ that is developed centripetally, and quite independently of the coelom, being probably derived from the ectoderm. Its lumen is formed by the hollowing out of the nephridial cells, and is consequently intracellular. Primarily this lumen is closed internally, in which case the organ is called a **protonephridium.** Frequently, however, it secondarily acquires an opening into the coelom, this opening being the **nephridial funnel** or **nephrostome.** The organ is then called a **metanephridium.**

In complete contrast to a nephridium, a **coelomoduct** is developed centrifugally as a mesoblastic structure, formed as an outgrowth of the gonad or of the wall of the coelomic cavity. Its lumen, which is an extension of that cavity in coelomate animals, is not intracellular, but is bounded by a layer of epithelial cells; it opens into the coelom by ciliated funnel, the **coelomostome.**

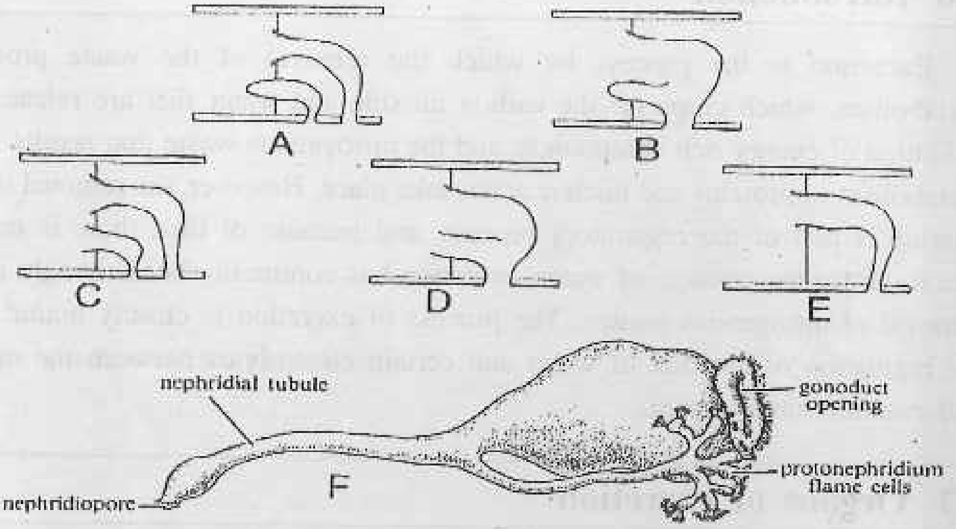


**Fig. 5.1** Annelid nephridia. A, B, C, D, E. Variations in union of gonoduct and nephridium. A. Primitive condition, with separate protonephridium and gonoduct with ciliated funnel, as in **Vanadis,** B. Protonephridium united with gonoduct, as in **Phyllodoce,** C. completely separate metanephridium and gonaduct, as in Notamastus. D. united metanephridium and gonoduct, as in **Hesione.** E. completely united nephridium and gonoduct, as in **Arenicola.** F. Nephridium of Alciopa (After Goodrich).

Ultrastuctural studies have shown that there are at least three main categories of **protonephridia.**

In one of these the inner blind end of the protonephridium is formed of a terminal organ, which is actually, a compound structure composed of two cells which interdigitate by means of finger-shaped processes. One of these cells is a **flame cell,** bearing a bunch of motile flagella forming the flame. The other is a tubule cell, tubule of which is formed by the wrapping of cytoplasm around an extra cellular space, the two edges of the cytoplasm being bound together by a desmosome. Protonephridia of this type are especially characteristic of the platyhelminths, nemertines and entoproctans.

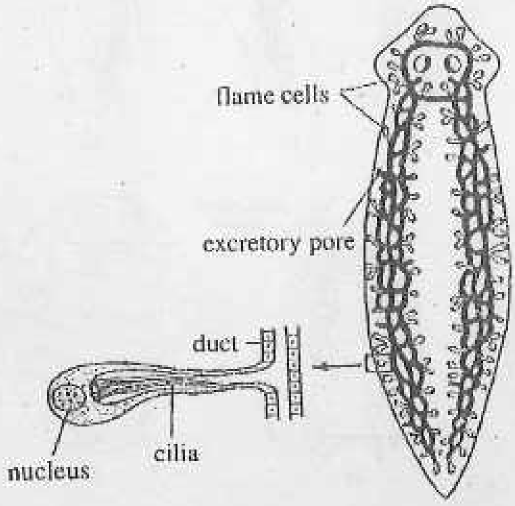


**Fig. 5.2** Excretory system & nephridium of *planaria*

The second category of protonephridium, characteristic of rotifers, has a terminal structure called a **flame bulb,** formed of a single cell. A flame of flagella arises from the apical cytoplasm of the flame bulb, the latter being connected with the nephridial tubule by a complex of cytoplasmic channels, columns, pillars, and microfilaments, which presumably serve to anchor the flame.

The third category has a terminal structure formed of elongated tubular cells called **solenocytes,** with a nucleus in the apical cap and with a single flagellum. These cells are found in *Priapulus,* in the gastrotrich *Chaetonotus,* in the archiannelid *Dinophilus,* in certain polychaetes (*Glycera),* and in the protochoradate *Branchiostoma.* It has been suggested that the protonephridial terminal structures may have evolved from a choanatoflagellate type of cell.

Wilmer Year is properly cautions in suggesting that genetic information for such cell structure might have been retained in suppressed form in many groups, and have become activated independently when conditions favoured this.

Playthelminthes may be thought of as having a pair of protonephridia, their canals being much branched and bearing flame cells at the ends of the branches. These cells, therefore, are scattered throughtout the parenchyma.

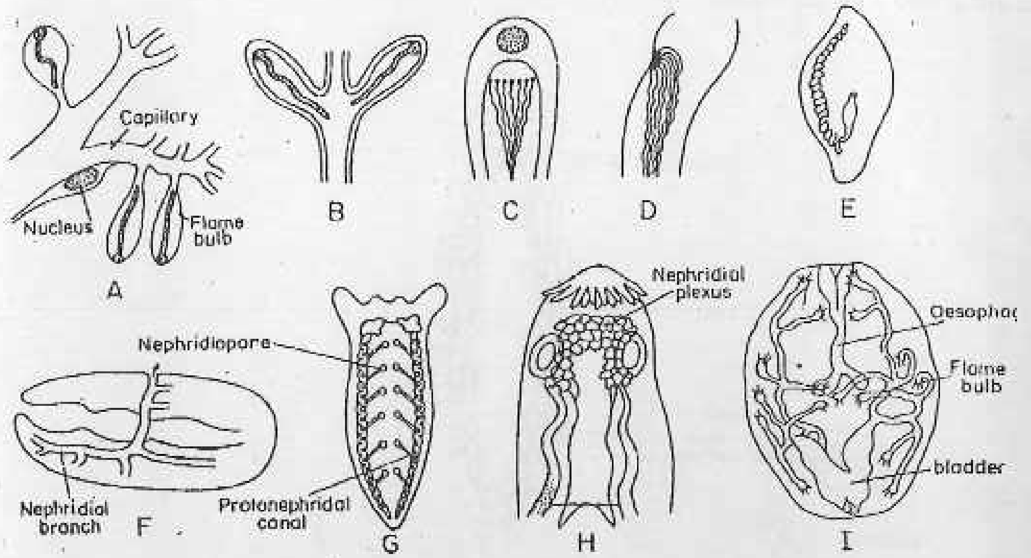


**Fig. 5.3** Showing the excretory organs in different platyhelminathes (A). A part of nephridia showing flame bulb derived fro a single cell. (B) Flame bulb showing the tip of flame. (c) Typical flame cell (C) A typical flame cell. Nephridium of *Rhabdoceelcs.* (E) *Alloeocoeles.* (F) *Triclad.* (G—H) Nephridial plexus of *Taenia.* (I) Excretory organs of *Microphallus.*

Similar protonephridia are found in the nemertines, sometimes as a single pair situated far forwards. Sometimes they may be extended into longitudinal collecting canals, into which open smaller effercent canals that lead from the scattered flame cells. In *Geonemertes,* the system consists of many hundreds of separate protonephridia, each discharging through its own efferent canal.

In annelids, each typical segment primitively possesses a pair of the organs, opening independently of each other at segmental nephridiopores. The nephridia themselves are intersegmental in position, their inner end penetrating the anterior septum of the segment in which the main body of the organ lies.

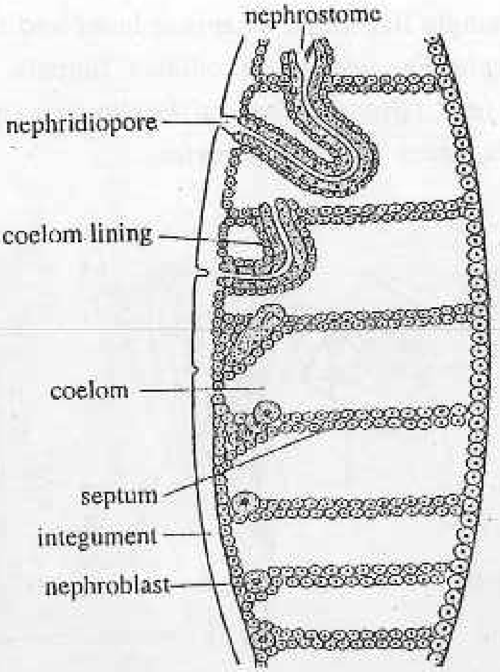


Fig. 5.4 Relationship of coelomoducts & nephridia in primitive annelids.

The particular complication in the polychaetes is that their nephridia frequently bears ciliated funnels, they are then termed **metanephridia.**

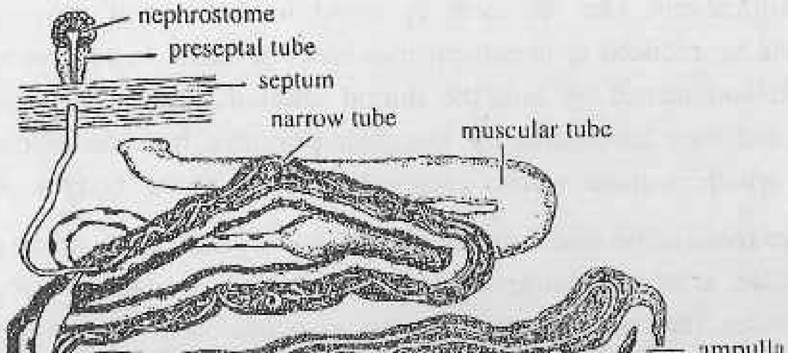


Fig. 5.5 Nephridia in *Lumbricus* sp.

The trochophore larva of certain polychetes (*Nereis, Pamatoceros*) possesses a pair of simple and typical protonephridia, the so-called head kidney. These structures, each with a flame cell bearing a single flagellum, disappear latter and the nephridia of the adult worms are metanephridia, with open ciliated funnels. Sometimes, however, even adult polycheates (e.g. *Glycera, Nephtys, Phyllodoce.*) possess only protonephridia, which in these instances have **solenocytes.**

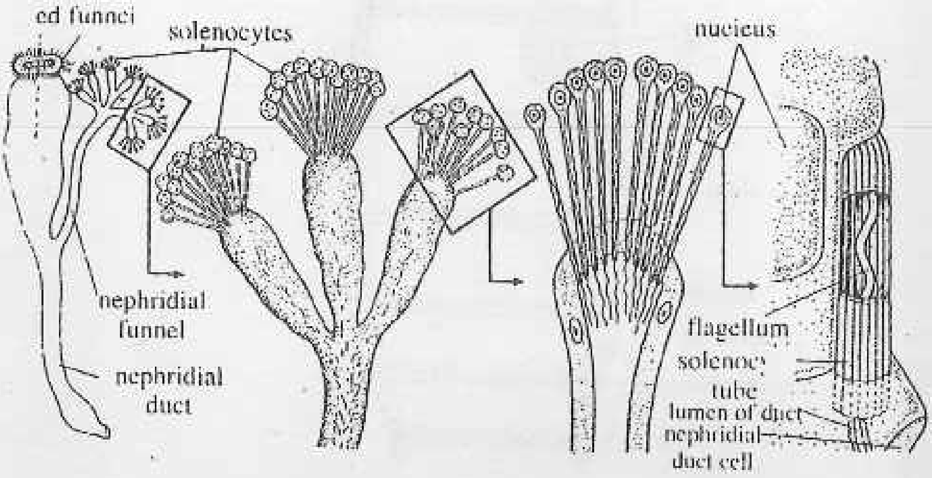


**Fig. 5.6** Structure of excretory apparatus in Annelida

**Coelomoducts** are also typically present in polycheates, not necessarily in every segment, but at least in those in which germ cells develop. They give rise, however, to two modifications. One of these is found in the Nereid worms, where the coelomoducts are reduced to in conspicuous areas of ciliated epithelium, discovered by Goodrich and named by him the **dorsal ciliated organ.** These are passively phagocytic, but they have certainly lost their primitive function of conveying the germ cells, which in these worms escape by rupture of the body wall.

The other remarkable modification is found in only one family of the polychaetes, the Capitellidae, in which coelomoducts and nephridia are separate from each other. In other families, the two structures become associated to form a compound organ called a **nephromixium,** in which the nephridial tube bears a ciliated mesodermal funnel. The nephridial component of nephromizium may be of two types—

(i) **Protonephrimixium** types are found in Phyllodicidae, where the nephridial component is a protonephridium and the developing coelomoducts grow backwards alongside the protonephridial canal, an open communication between the two arising at sexual maturity.

(ii) Alternatively, and more commonly, the nephridial component of the nephromixium is a metanephridium, and the resulting organ being calle a **metanephromixium** or a **mixonephridium,** according to the way in which the junction is formed.

For example in Arenicola, there are usually six pairs of these organs, conspicuous with their rich vascularization, frilled funnel tip, and attached gonad, serve both for the passage of germ cells and presumably, for the regulatory functions.

*Nematodes have an unusual excretory system, develop from the renette cells and are not protonephridial in origin. It consists of a single gland like cell that has a short duct opening to the exterior thourgh an excretory pore. In fresh water forms, the duct is lined with a thin impermeable cuticle. They have also a series of lateral tubules.*

The important groups in which there are no sign of nephridia are the Nematoda, the Echinodermata and Hemichordata.

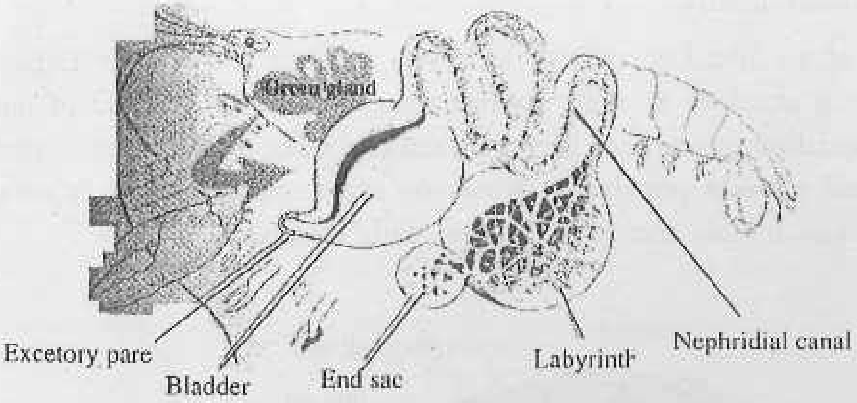


**Fig. 5.7** Excretory system of Cry fish

The excretory system of **arthropods** is no less complex than other aspects of the organization of this group. In *Peripatus,* coxal glands are present in pair in almost every one of its segments. Hollow coelomic follicles or somites appear in each segment, in trunk segment it is subdivided into dorsal, lateral and ventral portion. The cavity of the ventral portion persists to form end sac, which opens by a ciliated canal, regarded as coelomostome, in to a coiled excretory canal and a terminal enlarged vesicle or bladder. The derivation of the coxal glands from coelomoducts is perfectly clear. Coxal glands of similar structure are also in the Arachnida and Crustacea, but are greatly reduced in number.

In those arthropods that have become fully adapted to terrestrial life there is an important development in the organization of the excretory system: the appearance of **malpighian tubules.**

Malpighian tubules are formed in Myriopoda, Insecta and Arachnida. These are long, thin, blindly ending tubules arising from the gut near the junction of midgut and hindgut and lying freely in the body cavity. In some Coleoptera, the tubules clearly arise·from the midgut. While in caterpillars, they arise from the anterior hindgut. They may open independently into the gut or may join in groups at an ampulla or a more tubular ureter, which then enters the gut. In *Carausius* (Phasmida), there are three distinct groups of malpighian tubules : superior and inferior tubes arising at the junction of midgut and hindgut, and lateral tubules opening into the midgut. The different tubules show some histological differentiation and the inferior tubules are dilated distally.

The wall of the tubule is one cell thick with one or a few cells encircling the lumen. The cells stand on a tough basement membrane with a strand of muscle forming wie spiral (Orthoptera) or having no muscles other than a series of circular and longitudinal muscles proximally (Rhodnius and Lepidoptera and Diptera) or have a continuous muscle sheath (Coleoptera and Neuroptera).

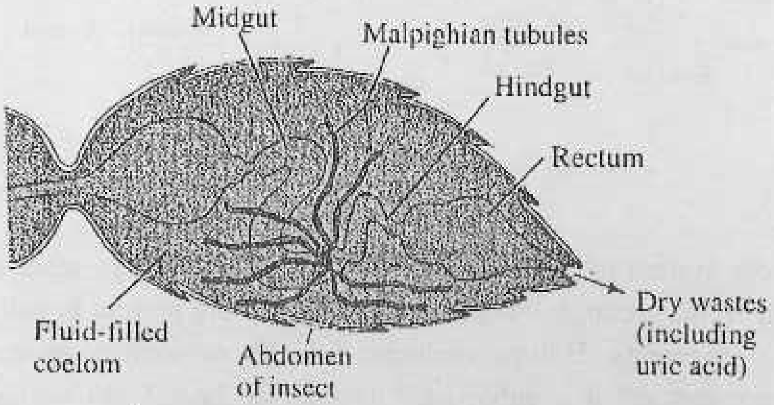


**Fig. 5.8** Malpighian tubules in Insect

The principal cell types in the wall of the tubule have microvilli at their free margin, forming honeycomb. The plasma membrane of the basal regions of the cell is deeply invaginated. These are probably the secretory cells of the tubule.

Different types of cell occur proximally in tubules of some insects (e.g., *Rhodnius).* This has more widely dispersed microvilli, forming a brush border, and varying in length at different times. The in folding of the basal membrane are less complex. They are mostly concerned with reabsoption of some solutes from the fluid secreted into the tubule.

Small number of another cell type sometime occurs scattered irregularly between the commonly occurring cells. They appear to secrete acid mucopolysaccharide, but may also have other functions.

In many Coleoptera and larval Lepidoptera, the distal parts of the amlpighian tubules are closely associated with the secretion, forming a convoluted layer over its surface (Ramsay, 1964; Saini, 1964). This is known as a cryptonephridial arrangement of tubules.

In **molluscs,** the tubular excretory system open at both ends, forming metanephridia, drained from the embryonic mesoderm.

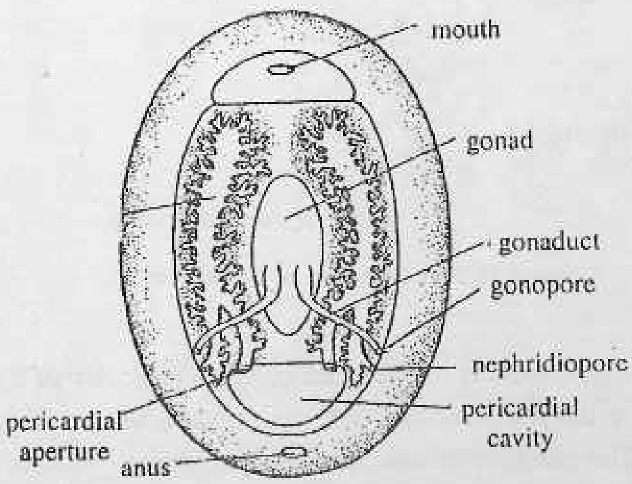


**Fig. 5.9** Excretory system of *Chiton*

Tubular opening into the coelom is funnel shaped and fimbriated with ciliary bands. The waste products, collected from the coelom by ciliary movements, are captured by funnel and are passed directly into the nephridial tubules through a ciliated nephrostome. Each nephridium may open outside by separate nephridial pore or collectively inside a bladder where excretory products are stored temporarily before their subsequent eliminatin.

In **annelids,** the body is divided into a series of similar segments separated by walls (septa). Each segment is equipped with a pair of metanephridia, one on each side of the body. The inner opening nephrostome lies near the posterior end of a segment, from there, the metanephridium run through the septum into the next rearward segment. In the rearward segment, it coil around extensively and is in initimate contact with blood vessels (capillaries) that wrap about it. The metanephridium ends in a nephridiopore, through which urine drains to the outside.

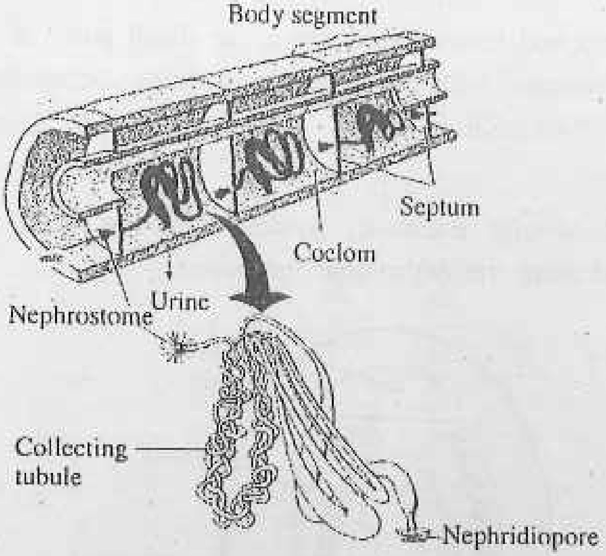


**Fig. 5.10** Metanephridia in Earthworm

In **molluscs,** the coelomoducts of the adult consists typically of a pair of tubular structures, leading from the coelomic cavity to the outside, and primitively consisting of the genital ducts. The paired coelomic cavities met dorsally to enclose the heart, the walls of which proliferated the germ cells. This metanephridial type of organization of excretory system in molluscs is usually called kidneys. The simple arrangement of paired cavities gave rise by further differentiation to an anterior region, the gonad; a central region, the pericardial coelom; and a posterior region, the gonoduct. Although a typical kidney tubule has one end connected to the outside through a nephridiopore, in most mollusks the connection with the pericardial cavity (renopericardial canal) and the nephridiopores are at the same end of the nephridium.

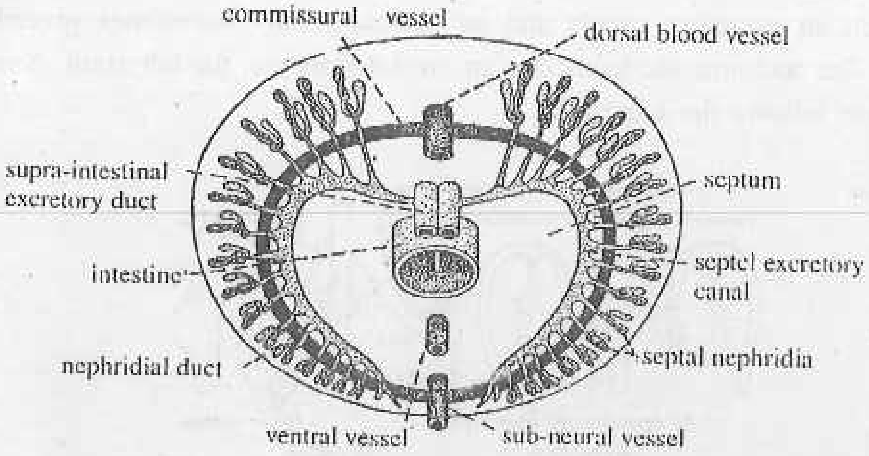


**Fig. 5.11** Relative position of septal nephridia and intestine in Earthworm

The nephridium is thus a blind sac (protobranches). In pulmonates, the nephridiopore opens at the back of the mantle cavity.

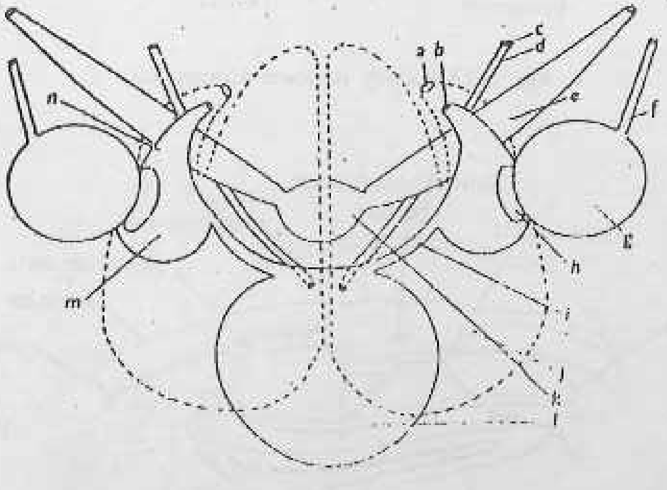
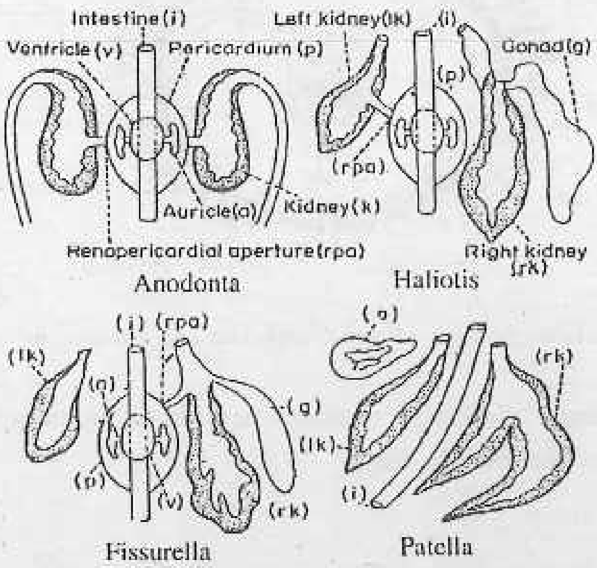


**Fig. 5.12** Diagram showing the relationships between the excretory system, circulatory system and derivatives of the coelom in the octopus, a. Urinary pore; b. renopericardial canal opening into the renal sac; c. gonopore; d. gonoduct; e. auricle; f. afterent branchial vein; g. branchial heart; h. branchial heart appendages; i. aquiferous canall; j. renal sac; k. ventricle; l. gonidial coelom, m. pericaldial carity; n. reno-pericardial canal.

The modification of a primitive segmental metanephridial system is found in crustacean excretory organs, which consist of a pair of antennary glands (green glands), located in the head region. Generally, a gland consists of a coelomic sac (end sac), an excretory tubule and an excretory duct sometimes preceded by a bladder. The coelomic sac leads into an involuted tubule, the labyrinth. A nephridial canal then follows the labyrinth.



Anodonta

Haliotis

Fissurella

Patella

**Fig. 5.13** Kidney in some Grastropods

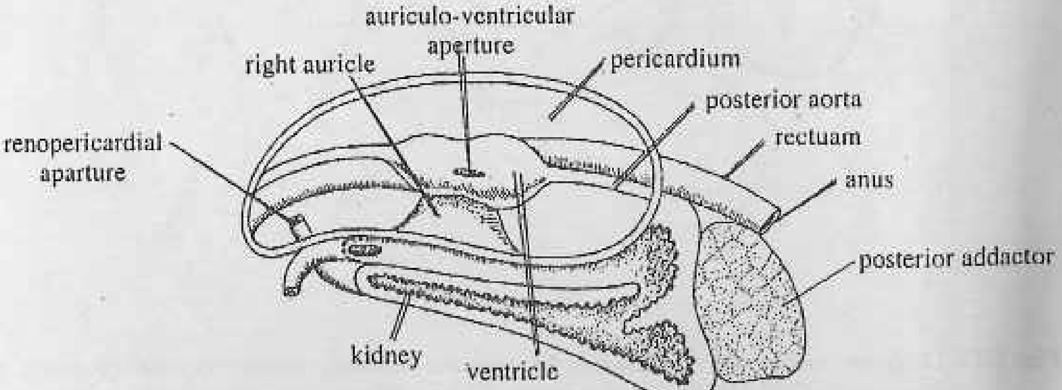


**Fig. 5.14** Relative position of heart, rectum and kidney of *Unio* sp.

Electron Microscopic studies showed that in the region of the coelomic sac podocyte like cells are present in cray fish. They possess a brush border that increases the effective surface area for the exchange of materials.

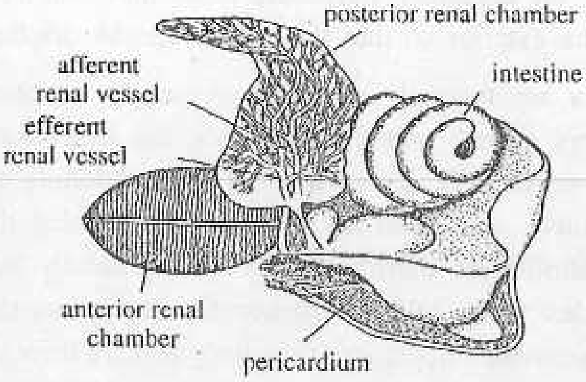


Fig. 5.15 Kidney of *Pila* sp.

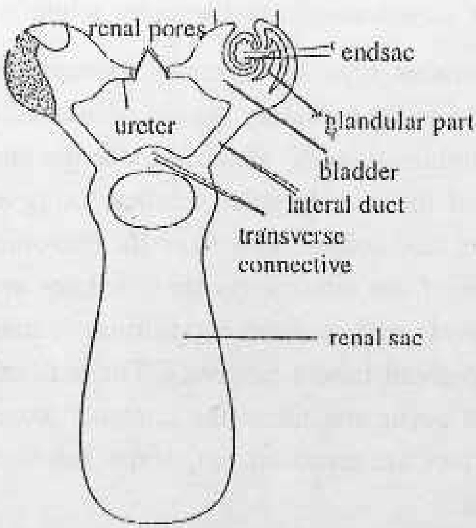


Fig. 5.16 Excretory system of *Palaemon*

## 5.2 Mechanism of excretion

With the appearance of the coelom, improtant new potential rises among organisms. Organisms use the coelom and its fluid as a primary transport system.

It is common for the coelomic lining bearing cilia or flagella that help to circulate the coelomic fluid and facilitate its use in picking up waste and delivering food materials. With wastes accumulating in the coelom, it is necessary to get them out again. Therefore, for excretory purposes, it is important for the coelom to the connected with the exterior so that the wastes can be discharged.

Protonephridia are typically excretory organs in annelids that lack a high-pressure circulatory system and therefore lack the hydrostatic forces needed for ultrafiltration. However, little is known about the functioning of these organs. These are usually extremely small, and no methods of collecting their fluids have been devised. Protonephridia are narrow ducts that end blindly in two types of motin creating cells, either flame cells or solenocytes. It appears that fluids pass into a protonephridium from the remainder of the body and are driven to the excretory pore on the surface by the beating of cilia or a flagellum. Along the way, it is likely that the reabsorption of salts and some other materials through the wall of the tubules change the composition of the fluid. The net effect of the action of protonephridia is to remove some substances from the body while retaining others.

A somewhat similar type of excretory system is found in insects and other terrestrial arthropods. In the excretory system of insects we find a tuft of multicellular, blind tubules (malpighian tubules) attached to the gut and floating into the fluid filled coelom. The cells of these malpighian tubules, using active transport, take up uric acid, potassium ions, and sodium ions from the coelomic fluid and secrete them into the internal channel of the tubules. As these solutes are added to the tubular fluid, water follows passively and osmotic equilibrium is maintained. Some other solutes also enter the Malpighian tubule passively. The wall of the tubule is muscularized, so that contractions occur and move the contents towards and evenly into the gut. Finally, before excreta are removed out, some substances are selectively absorbed in the rectal region.

In annelids, the coelomic fluid enters the metanephridium by way of the nephrostome and is slowly swept along by cilia that line the inside of the tubule. During the lengthy passage thorugh the metanephridium, this tubular fluid gradually changes composition. The overall process may be described as nonspecific loss of fluid from a body segment (at the nephrostome) followed by the selective reabsorption of needed materials in the segment posterior to it (along the tabule) and, finally, excretion from the body by the way of nephridiopores. Because of selective removal of salts, the tubular fluid ultimately becomes hypotonic to the blood, and copious, dilute urine is released. Thus the worm is able to cope with a tremendous rate of osmotic water uptake without simultaneously discarding all its needed solutes.

In crustaceans the antennary glands (green glands) located in the head region and representing modification of a primitive segmental metanephridial system. A key feature of this type of excretory system is that fluid is driven into the end sac by the hgh pressure within the coelom. Although proteins and other large molecules are unable to pass through the cell membranes, water, ions and small molecules are squeezed through as an ultra filtrate. During passage of ultra filtrtc from end sac to the exit duct, potassium, sodium, calcium, chloride ions, glucose, water and other materials are reabsorbed whereas excess of magnesium and sulphate ions are excreted.

There is an interesting structural and functional difference between the excretory systems of marine and freshwater crayfish. Freshwater crayfish must excrete large amount of unite but, at the same time, must retain salts. The retentions of salts is accomplished by means of a nephridial canal or slat-absorption tubule between the end sac and bladder. In this tubule, potassium and sodium ions are actively reabsorbed, whereas other materials may be secreted to be expelled from the body. In marine crayfish, salt retention is not a major problem, and the nephridial canal is accordingly absent or much reduced. These systems of ultra filtration followed by selective reabsorption and secretion wil be seen to follow the same principle as that used in the vertebrate kidney.

In lamellibranch molluscs, the circulatory system is intimately related to the excretory system at the heart itself. Ultrafiltration of the blood occurs through the walls of the heart in to the pericardium and then the filtrate (or urine) is passed through a pair of excretory ducts.

Some species have a pair of such organs, others only a single one. In *Anodonta*, the blood filtrate passes through the kidney, where salt is reabsorbed and nitrogenous wastes are secreted in to the urine. Different experimental studies have indicated that the two kidneys (left and right) differ in their activities with respect to ionic regulation and excretion of waste products.

In the Octopus, urine is formed at a different location. A pericardial cavity surrounds an appendage of each branchial heart instead of the main heart. The site of formation of urine is not known for terrestrial gastropods because no fluid can be obtained from the pericardial cavity of any snail so far examined.

## 5.3 Excretion and osmoregulation

Osmoregulation implies the maintenance of an internal osmotic concentration different from that of the external medium. The field of osmoregulatory studies is a large and complex one. It includes studies of the overall mechanisms used to regulate internal water and solute content; the organs used for excretion, which are, in most cases, as important as ionic or water regulatory systems; the cellular activities that are basic to their regulatory mechanisms; and the molecular basis for these mechanism. Osmoregulatory studies are also concerned with the adaptive significance of these regulatory processes as they relate to the type of environment in which the animal lives and the mechanisms that some organism used to adapt to changes in this environment.

Protonephridia are usually extremely small in structure, and no methods of collecting their fluids have been devised. So little is known about their functioning for excretion and osmoregulation. It has been suggested that the activity of the cilia or flagellum given rise to negative pressures inside the lumen of the protonephridia. If this were the case, urine could be formed because of a higher external hydrostatic pressure, driving water and solutes into the tubule. However, it is difficult to imagine how such ciliary activity could give rise to the needed pressure differential. There is no definite proof that protonephridia function is osmoregulation. Suggestive evidence for osmoregulation function is found in the rotifer, *Asplanchia,* where the rhythm of the flame bulb activity, of contractile bladder movements, and the volume of fluid flow, all can be altered by changing the osmotic gradient between the animal and its environment.

Kromhand (1943) compared the protonephiridial system of marine, brackish, and freshwater forms of one turbellarian, *Gyratrix,* and found that differences in habitat were associated with major modifications in the nephridial system. In fresh water forms, copious urine could be formed and modified so that salt is conserved and water removed. In fresh water forms, the protonephridia are becoming complex structure enveloped with paranephrocytes and tubules with pulsatile ampulla.

In the brackish-water form, the ampulla and paranephrocytes are absent, living only an undifferentiated tubule. The animal in this environemnt has less of an osmotic problem and presumably requires a less specialized osmoregulatory system.

In the marine form, the entire system is missing. The organism is nearly isosmotic with seawater; there is little demand for an osmoregulatory organ. Thus, the development of nephridial system appears to be correlated with the osmotic environment in which the animal lives.

In marine and fresh water nematodes, the excretory system becomes specialized by the presence of renette cells, and excretory tubules. The system is considered to play a role in osmoregulation because the discharge rate increases with increasing hypotonicity of the external medium.

In Annelida, coelomic fluid enters the nephrostome of open metanephridia and is processed as it passes through the tubule, eventually becoming urine. Differences between coelomic fluid and urine reveal something of what goes on in the tubule. Depending on the conditions to which the animal is adapted, the main changes of the fluid are :

1. Changes in the water content as urine becomes either hypotonic or hypertonic to the coelomic fluid, depending on whether water must be excreted or retained to preserve the osomotic balance;
2. Changes in the salt concentration, as salts are excreted or retained;
3. Changes in the concentration of the nitrogenous eastes; and
4. Changes in the sugar content or concentrations of other organic compounds that may be useful to the organism.

Water regulation is less critical in marine than in fresh water and terrestrial species. Littoral marine species, however, may encounter considerable dilution of seawater in estuaries, and their distribution may be partly determined by their ability to cope with a more dilute medium.

Some annelids are osmotic conformers, adjusting their salt content to that of the environment. *Arenicola,* for example, has blood with a freezing point identical to that of the surrounding water in a range of –0.29 to –1.72°C. It evidently has a high tolerance for the dilution of its body fluids.

Polychaete worm, like *Perinereis cultrifera,* is an osmotic conformer. Its saclike nephridia provide little surface. The body fluid of *Nereis diversicolor* becomes some what diluted, but remains hypertonic in diluted seawater. Its nephridia are long and convoluted that excrete water by forming urine more dilute than its body fluid, either by reabsorbing salts at the nephridial surface or by actively discharging water. The ability of nephridia to regulate the osmotic properties of the urine probably depends in part on the length of the tubule, whether water or salts are being reabsorbed.

In the earthworm *Lumbricus terrestris,* the coelomic fluid is always hypertonic to the blood. These concentratiin difference, produced by an unknown mechanism, may serve to withdraw water from the blood. The earthworm excrete a urine that is strongly hypotonic to body fluids except when placed in very concentrated media, in which case the unite become isotonic to the blood. This is a situation similar to that found in the vertebrate distal tubule. Absorption of salts takes place along most of the nephridial tubule. *Lumbricus* excretes both ammonia and urea in approximately equal amount through the nephridia.

Crustacea occur in a wide range of aquatic habitats and markedly in the detains of water and salt regulatory mechanisms. Some of the marine crustacea have very little control over water intake. Most of the marine crabs, lobstars and barnacles are osmotic conformer and secrete isotonic urine in larger or smaller quantities, as the situation demands.

Shore and estuarine crabs are usually osmoconformers in more saline habitats and become hypertonic in brakish water. The body surface and gills are less permeable to water than in marine forms. *Artemia,* the brine shrimp, which lives in high-salinity waters can produce a hypertonic urine but depends on other mechanisms as well for osmoregulation.

In insects, uric acid is the most important waste, but small amounts of ammonia, urea, and alantoin are also excreted. Malpighian tubules are the principle excretory organs in insects. In genera, water loss is limited by the production of hypertonic urine and elimination of nitrogenous wastes as uric acid. In the rectum of the insects water reabsorption takes place that causes the drying of the wastes. Water reabsorbed in the rectum is returned to the blood. The recycling of water makes the most of the modest water resources of the insect body.

When some marine gastropods are placed in dilute seawater, they promptly swell, showing very little control over water intake. Water regulation by means of salt excretion is far from perfect. The blood concentration of fresh water snails and clams is distinctly lower than in marine species. Land snails have considerably more salts in their blood than do freshwater snails, but have poor mechanisms for controlling the concentration. A heavy rain may reduce the salt concentration of the blood by over half water loss resulting from excretion if held to a minimum by excretion of uric acid and by a few adaptations that reduce evaporation at the body surface. Thus, changes in the excretory pattern, i.e., from ureotelism to urecotelism in accordance with the state of the body has solved the problem of osmoregulation. Hibernating or aestivating snails, secrete a partition over the shell aperture, thus reducing water loss during inactivity.

The asmatic exchanges taking place between animal and its environment can be froadly divided into two categories : (1) *Obligatory exchanges* in response to physical factors over which the animal has very little or no physiological control; and (2) *regulated exchanges* having physiological control that servies to maintain internal homeostasis.

Factors influencing the obligatory exchanges include : (a) Gradients between the extracellutar compartment and the environment; (b) surface volume ratio; (c) Permeability of the integument; (d) feeding; (e) Temperature, exercise and respiration, and (f) metabolic factors.

The regulatory exchanges performed by various groups of invertebrates that are either osmoregulaters or osmoconformers in fresh water, marine or terrestrial environments have already been discussed above. Some aquatic invertebrates are *stict osmoregulators,* some are *limited osmoregulators* and some *strict osmoconformers.* With changes in the osmolarity of the environment, the osmolarity of a strict osmoconformer also changes by an equal amount. On the other hand, a strict osmoregulator maintains a constant internal osmerlarits over a large range of external osmolaerities. Limited osmoregulators regulate over a limited range of osmolarities.

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# Unit 6 ❐ Nervous System

*Structure*

## 6.0 Introduction

During evolution, as the complexity of the body increased owing to trend of division of labour, the need to control, co-ordinate and integrate various body parts become equally important. This problem is solved by the evolution of nervous system which is present in one or other form in all the animals starting from protozoans up to mammals.

In general, the function of the nervous system is co-ordination—a process in which parts of a whole action are combined into a harmonious relationship and integration—the process in which parts are put together to form a whole action. This is achieved with the help of a complex system of reception and response.

The nervous system is an organized collection of nervous tissue specialized for the repreated conduction of an exited state from receptor sites to effectors. Commonly this includes passage through a central nervous system, which interconnected different pathways, but this is not an essential feature of neural organization; there are primitive types of nervous system without a differentiated central nervous system.

## 6.1 Nervous system in invertebrates

Specialization of cells for the functions of information receptor, transmission, co-ordination and integration evolved in the early development of animal phyla. In cellular organisms although well organized nervous system as such is not evident, its protoplasm exhibits all the responses characteristic of nervous system. In the remaining phyla of invertebrates the nervous tissue is generally organized in many degrees of structural complexity.

## 6.2 Primitive nervous system

### 6.2.1 In Cnidaria

Phylogenetically, the most primitive type of nervous system appears for the first time in the phylum Cnidaria. They have a system consisting of bipolar or tripolar occasionally multipolar nerve cells, arranged in a continuous layer to form an irregular nerve net or plexus.

Most cnidarian-neurons are through-conducting i.e., they conduct impulses without any attenuation of the signal. The predominance of bipolar and multipolar neurons in Cnidarians means that impulses spread in all directions from their origin; and because impulses are not attenuated, generalized responses can result from local stimuli.

Conduction tends to be slower than in most other animals, but giant, fast conducting neurons do occur, particularly in medusae. The neurons lie among the bases of the epitheliomuscular cells and form synapses with sensory cells, muscle fibres and other effectors, particularly cnidocytes and battery cells.

The simplest known nervous systems are those of polyps, particularly hydrozoan polyps. In these animals the nervous system consists of two networks of neurons, one of the epidermis and one in the gastrodermis. These networks are not connected across the mesoglea.

Madusae have more elaborate nervous systems, associated with the control of swimming.

### 6.2.2 In Ctenophora

There is a diffuse subepidermal nerve net, which is more concentrated under the comb rows and around the mouth, and a sparse subgastrodermal net. They are also nerve cells in the mesoglea, including large strands in the tentacles. These synapse with the mesogleal muscle fibres and control muscular movement.

### 6.2.3 In Echinodermata

The nervous system is structurally a relatively simple system, much of it relating to a primitive position and in close relationship with the epidermis.

Echinoderms lack a centralized nervous system, and their behaviour appears to be controlled by a series of local reflexes. A nerve plexus is located at the base of the epidermis and is condensed in places to form distinct nerves. The tube feet, ampullae, tentacles are supplied with nerves that originate from the oral nerve ring.

The nervous system includes an extensive ectoneural (sensory and motor) system, mostly associated with the surface, and a more localized hyponeural (motor) nervous system which supplies the muscles. The nerve cords usually contain both ecotoneural and hyponeural elements.

The juxtaligamental cells involved in connective tissue mutability are associated with the nerve cords, as individual cells or in distinct ganglia.

The echinoderms nervous system becomes specialized by having the small size of neurons (less than 1.0 µm in diameter). An exception is the Ophiuroid radial nerve cord, which are 'giant' (20 µm in diameter) by echinoderm standards.

Surface epithelium of echinoderms is sensory, with ciliated cells that bear microvilli. Below the epithelium which is sensitive to touch, light and chemical stimulation are the cell bodies of multipolar neurons; there are no ganglia.

There is also the evidence of neural control during locomotion in starfish.

## 6.3 Advance nervous system

As we trace out the history of invertebrate life we see animals developing increasingly complex behaviour patterns, which enable them to exploit their environment with ever-improving efficiency and with an endless variety of means. The nervous system play a key role in this history. The primitive nerve net rapidly diminishes in importance, and becomes very difficult. In its palce there is established a system of nerves, formed of tracts of fibres that convey impulses into and out of a central nervous system.

The particular importance of the central nervous system is that cell bodies, apart from those of the receptor cells, become largely localized within it. Many of these cells are connecting cells. These form links in the reflex pathways and junctions that are the structural basis of advances in integration.

Another important feature of the central nervous system, is the formation of systems of giant fibres. These carry further another tendency toward formation of through conduction pathways that imporve the efficiency of reactions by increasing the speed of propagation of nerve impulses.

Finally, the modification leads to an increasing dimination of the cephalic end of the central nervous system over the remainder of the organism, and thus to the appearance of that morphologically and physiologically complex structure called the brain.

### 6.2.1 In Annelida

The metameric nervous system of annelids is based upon a ground plan which is discernible in arthropods. This plan comprises a pair of nerves in each segment; anteriorly, the cords continue as circumoseophageal connectives which end dorsally in the cerebral ganglia (brain). Bipolar receptor cells lie peripherally, while within the nerve cords are found the motor neurons and the interneurones. These neurons are concentrated in the ganglia.

Motor neurons tend to innervate only the muscles of their own segments, so that it is possible for segments to act independently. It has been suggested that in the polychaetes the motor innervations may be multiterminal, and aosl polyneural.

The original paired separate ganglia in each segment of more primitive annelids are found to have moved medially and finally united in higher annelids. Although the nerve cords may unite and may be covered by a single sheath, they often each retain a separate histological form with two neuropiles. In higher annelids the brain tends to assume a more posterior postition than in lower species, in which the brain occupies the first segment (the prostomium). In earthworms, the brain is usually fund in the third segment, whereas in leeches it is the fourth of fifth segment.

In most advanced polychaete brains it is possible to identify many cell masses and fibre tracts. Some of these cells are neurosecretory ones; the functions of other can be deducted from their peripheral connections. Some of the cell masses are thought to be motor or sensory centres others probably have integration functions.

Annelids, posses a fast conducting system of giant fibres that function primarily as a rapid escape mechanism. Most earthworms have five giant fibres : a large middorsal fibre, a pair of dorsolateral fibres, and a pair of smaller ventral fibres.

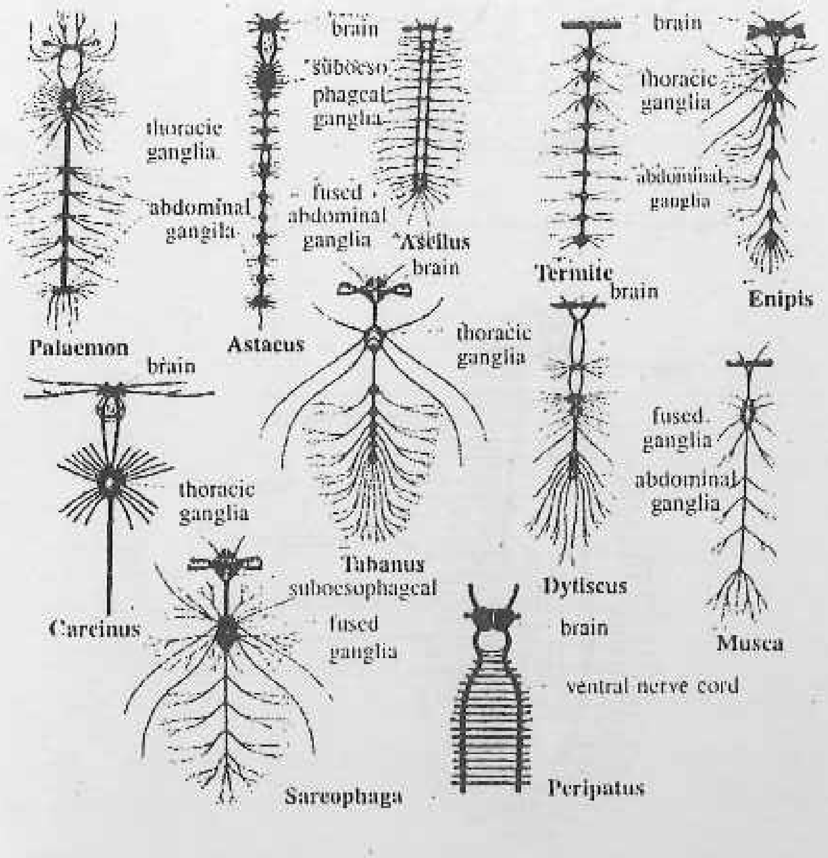


**Fig. 6.1** Nervous System of different animals

According to J. E. Smith Nereid bipolar sensory cells are well developed, being particularly numerous on the parapodia (especially on cirri) and in the ventral body wall. Information from these receptors is conveyed into the central nervous system by afferent fibres running in the segmental nerves, four pairs of which arise from each of the segmental ganglia.

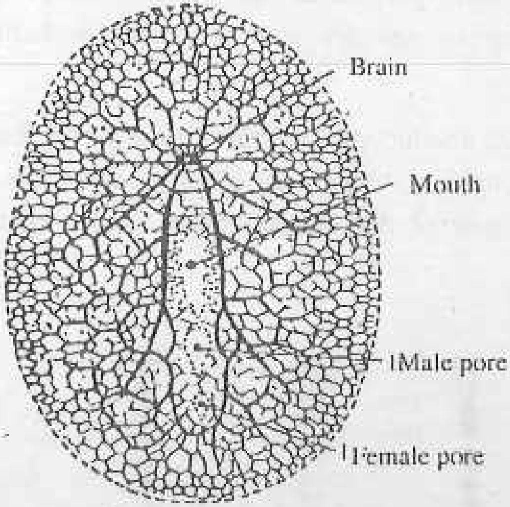


**Fig. 6.2** Nervous system of *Plamocera graffii*

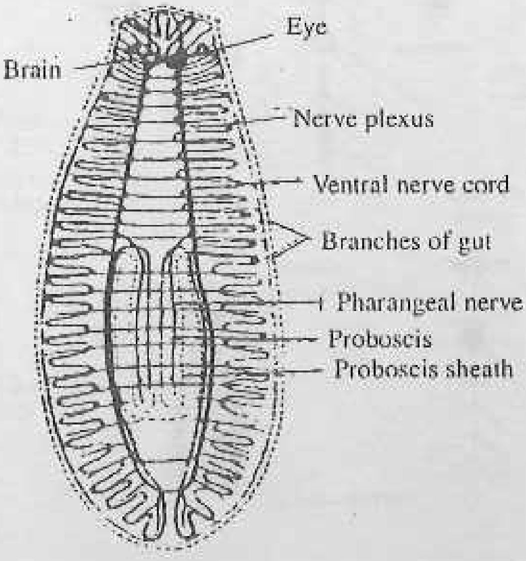


**Fig. 6.3** Nervous system of *Procerodes Segmentata*

The annelid movement involves a delicately programmed interaction of the muscles of the body wall with the hydrostatic skeleton, and with the segmental musculture of the parapodia and the chaetae. The execution of these programmes must depend upon the integrative action of the nervous sytem. In the earthworm, a rhythmic activity can be detected in the central nervous system during normal peristaltic movement, the rhythm being identical in frequency with that of the muscular contractions. Suboesophageal ganglion exerts some excitatory influence on the endogenous rhythms in the segmental ganglia which play an important part in locomotion.

### 6.3.2 In Arthropoda

The nervous system is more complex than that of annelids, but its structure and functional properties reveals the same interaction of centrally driven rhythms, sensory excitation and cephalic modulation for a more wide ranging exploitation of the environment.

Generally the arthropodan nervous system consists of a brain joined to a ventral nerve cord via circumoesophageal connectives. The nerve cord is composed of ganglia joined by longitudinal connectives and transversely by commissures. There is a tendency toward the fusion of ganglia in the adult, especially toward the anterior end. The higher insects and crustaceans fusion of ganglia is generally complete.

In many arthropods, a stomadeal system is found that innervates the anterior part of the digestive tract.

Here the cephalic dominance has become still advanced. The brain is the major anterior or superior ganglionic mass and innervates sensory organs and musculature in the head region. In insects and crustaceans, the brain is somewhat more complex with three main regionations protocerebrum, deuterocerebrum and tritocerebrum. Protocerebrum is mainly a visual centre and receives optic nerves from the eyes.

The deutocerebrum usually lies ventroanteriorly and many contain large antenual centres as well as olfactory lobes.

The tritocerebrum lies behind and receives nerves from the mouthparts and stomatogastric nerves.

The subesophageal ganglion is the first ganglion of the ventral nerve cord and functions as a co-ordination centre for chewing movement as well as source of tonic excitation necessary for the partially autonomous activity of more posterior ganglia.

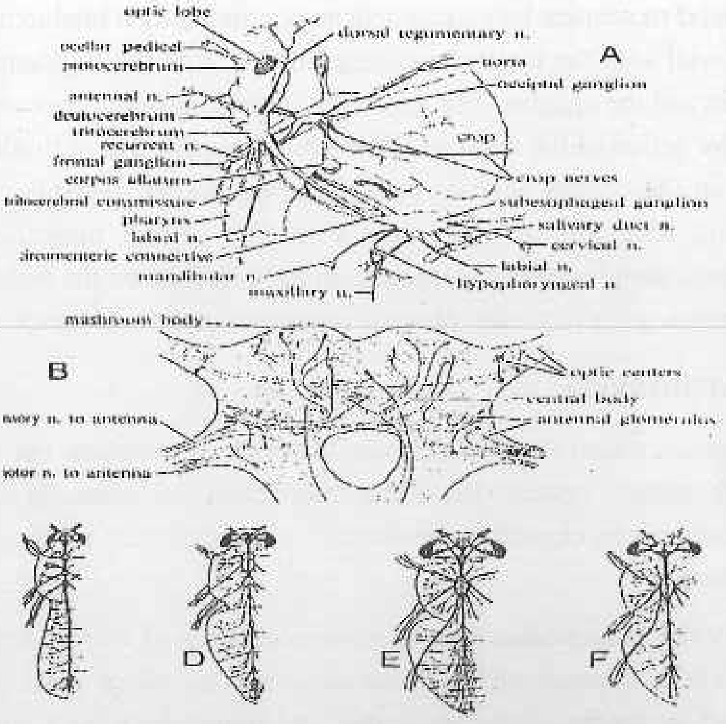


**Fig. 6.4** Nervous system. A. Side view of brain and head nerves in grasshopper. B. Chief nuclei and tracts in the brain of the cockroach. C.D.E.F. Evolutionary trends in central nervous system of Diptera with concentration of nervous system by union of ganglia and predominance of more anterior centrers. (A. after Snodgrass; B. after Hanstrom; C, D, E, F. after Brandt, from Folson and wardle).

## Nervous system in Crustacea

In the generalized condition, paired ventral nerve cords fun the length of the body, with a ganglion in each trunk segement. The anterior ganglia of the head (protocerebrum, deutocerebrum and tritocerebrum) are fused to form a brain and those of the mouthpart segments are united as a suboesophageal ganglion.

In many malocostracans, the anterior thoracic ganglia are also fused. This trend searches an extreme in crab, where all the thoracic ganglia are fused into a single massive ganglion and the abdominal ganglia are reduced and fused. The brain receives major sensory input from the anterior concentration of sensory organs, notably the eyes, antennae and statocysts, and also acts in motor control of the anterior head appendages. The segmental ganglia receive sensory input from the segments they serve and provide motor nerves to the associated appendages.

### Nervous system in Insects

In insects the central nervous system centres on a dorsal brain connected to a double nerve cord by a circumenteric ring. Segmental ganglia occur on the nerve cord. They are actually double, although in many cased they appear single to the naked eye. Commissures connect the ganglionic pairs and segmentally arranged lateral nerves issue from each ganglion to the sense organs and muscles of the somite.

The union of the ventral nerve cord leads to further centralization of the nervous system. However, this has not progressed very far in any myriapod. The ganglia of first three trunk somites of millipedes are close together and sometimes have partly fused.

The brain is highly differentiated into three regions (i.e., protocerebrum, deutocerebrum and tritocerebrum). The protocerebrum is composed of the large protocerebral lobes, an intercerebral region, and some times accessory lobes.

The deuterocerebrum contains the antennual relay centres, connected by a commissural tract. The tritocerebrum is small in insects, as there is no appendage in the somite to which it belongs.

Suboesophageal ganglion is a compound ganglion and innervates all three of the somites associated with the mouthparts, the salivary glands and some of the neck muscles.

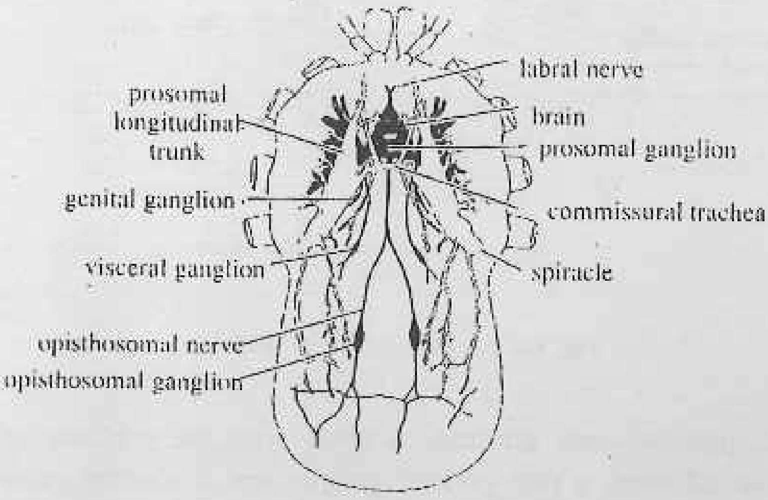


**Fig. 6.5** Nervous system of spider

The stomodeal nervous system corresponds functionally to the autonomic nervous system of vertebrates. It centers in the frontal ganglion and recurrent nerve, which passes along the floor of the brain and extends to the stomodeal region. It serves in feedback mechanisms that affect the physiological functioning of the viscera.

### 6.3.3 In Mollusca

Due the absence of metameric segmentation in mollusca the neural organization differ from those of annelids and arthropods, but apart from this there is a very similar trend in the establishment of a ganglionic system controlling local reflexes.

The primitive form of molluscan nervous system found in Chiton, is very similar to that of platyhelminthes, where there is very little concentration of nerve cells, but no cerebral ganglia. Longitudinal nerve cords are linked by transverse commissures to form ladder like system with pedal cords running along the foot and pallial cords lying more laterally. These cords connect with a ring of nervous tissue encircling the oesophagous, but the only ganglia present are a pair of buccal ganglia.

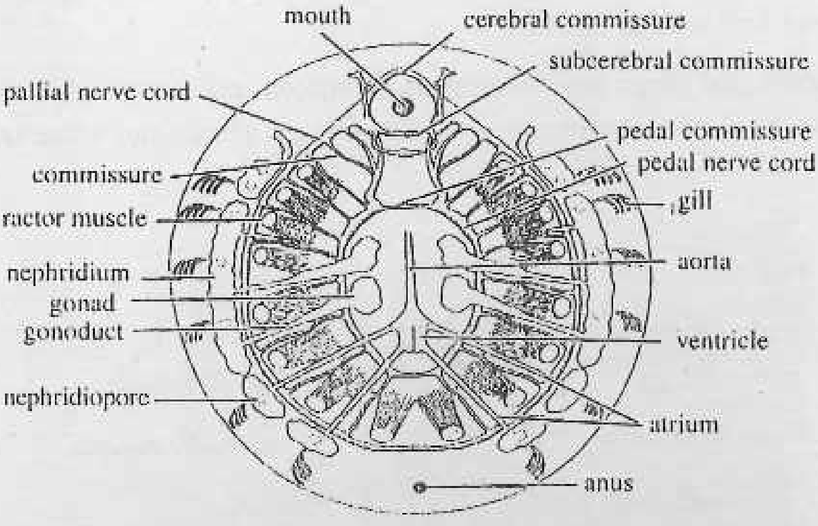
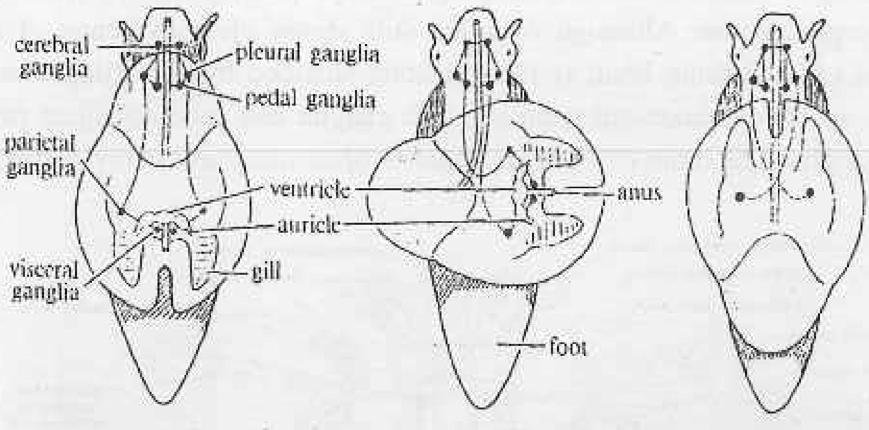


**Fig. 6.6** Nervous system of spider

Gastropods possess some primitive features with the presence of a pleural ganglion, a visceral loop, a pair parietal ganglia and a visceral ganglion. Later developments involve further concentration of the nerve cells, with a pair of ganglia appearing in the nerve-ring, and a pair of pedal ganglia at the anterior end of the pedal cords; these cords then disappear. The torsion of gastropods leads to a twisting of the visceral loop, the original left and right parietal ganglia now forming respectively the sub-intestinal and supra-intestinal ganglia.



Before During After

**Fig. 6.7** Effect of torsion on nervous system in gastropoda

In bivalves, having no head, the nervous system is of a very simple character. The localized actions of the ganglia innervate anterior structures, including the palps,

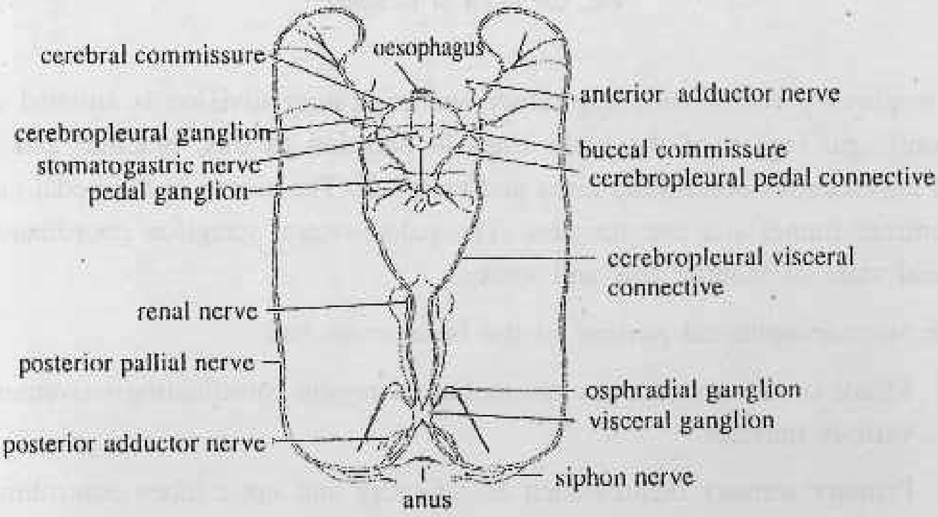


**Fig. 6.9** Nervous system of rarer clam tagalua

otocyst, osphradia and the anterior adductor muscle. The visceral ganglion innervates the gills, siphons, pallial sense organ, munch of the mantle, and also the posterior adductor muscle.

Cephalopoda among the molluscs represents a group attaining climax in the trend of cephalization. Although *Nautilus* still shows clear evidence of unfused ganglia, in other definite brain is recognizable, shielded by a cartilaginous casing and made up of a supraoesophageal cerebral ganglia and subesophageal pedal and brachial ganglia. The brain of *Octopus* consists of as many as twenty distinct lobes.

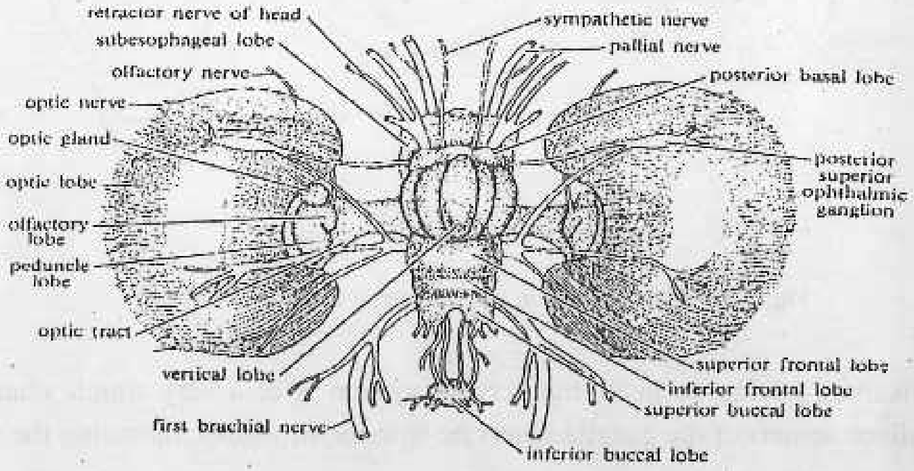


**Fig. 6.9** Brain of *Octopus*

A respiratory centre with inspiratory and expiratory division is situated in the suboesophageal region of the brain ring. In addition to this, brachial and pedal ganglia have centres controlling arms and tentacles. The centre in the pedal ganglia also controls funnel and eye muscles. The paleovisceral ganglion coordinates the functional state of mantle, fins and viscera.

The supraoesophageal portion of the brain mass has :

1. Motor centres in the circumoesophageal region coordinating movements of various muscles.
2. Primary sensory centres such as olfactory and optic lobes controlling the chromatophores and mantle and fin movements.

3. The dorsal visceralis complex comprising of three lobes represents an area analogous to associational cerebral complex of mammals and no function has been attributed to it.

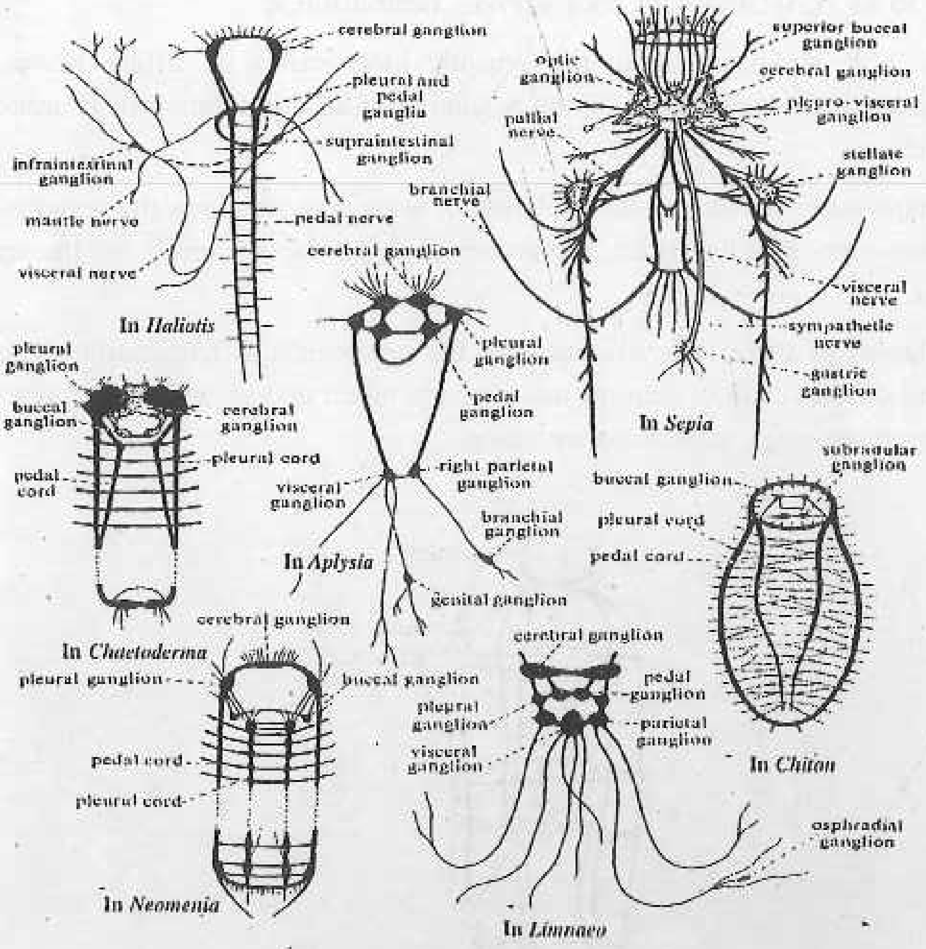


**Fig. 6.10** Nervous system of different molluscs

## 6.4 Trends in neural evolution

The fossil record is not at all adequate to understand the evolution of nervous system, because the soft neural tissues leave little trace.

At the cellular level of function, the nervous system appears to have undergone less modification during the course of evolution than the other tissues. Chemical and electrical properties of vertebrate and invertebrate nerve cells are very similar.

Anatomically the most simple type of nervous system occur in Cnidarians, without a well organized central nervous system, fine nerve fibers criss-cross to form network, and having no preference in direction of conduction. Radial symmetry appears to be correlated with poor nervous centralization.

Very little is known about the synaptic mechanisms in diffuse nerve nets. Cnidarians and Ctenophores show the beginning of an organization of neurons into reflex arcs.

A major early advance in the evolution of nervous system was the organizations of neurons into ganglia which are common in all higher levels of the animal kingdom.

In flatworms there were evidences of the cytological differentiation of axons, functional differentiatin of neurons into sensory, motor and associational types. This is an important stage in nervous evolution.

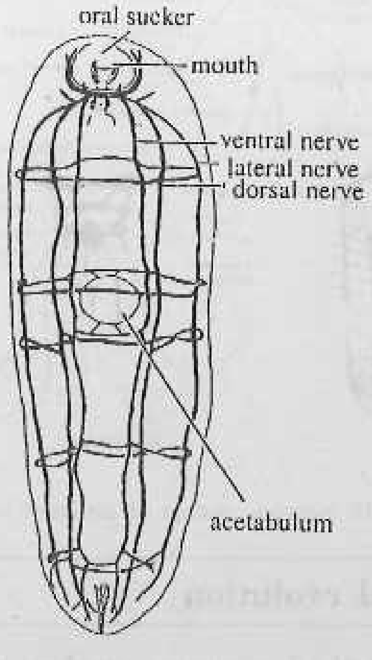


**Fig. 6.11** Nervous system of digoricam parasite

In segmental invertebrates, each body segment is equipped with a ganglion, usually serving the reflex functions of the segment, it occupies, and also one or more adjacent body segments.

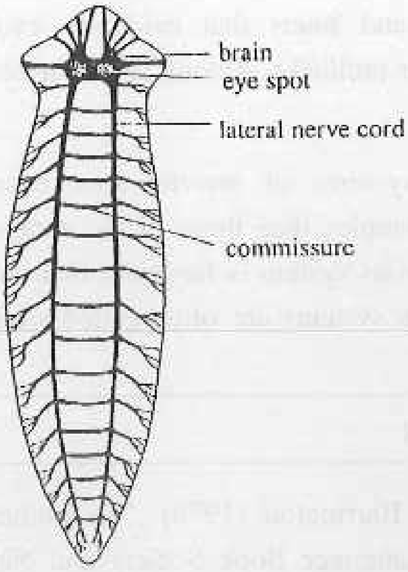


Fig. 6.12 Nervous system of *planeria*

An important development in the evolution of complex behaviour was the trend toward the fusion of several of more anterior ganglia into supraganglia or brain.

The outstanding developments of nervous system in insects are :

1. Continued progressive specialization of the brain, with the formation and development of specific nuclei and relay centres;
2. Centralization of the nervous system by anterior migration and coalescence of ganglia on the ventral nerve chain; and
3. The lengthening of the peripheral nerves to compensate for the position of ganglia.

The mollusks have nonsegmented nervous system with several dissimilar ganglia connected by long nerve trunks. The absence of metameric segmentation is a point of obvious difference from the neural organization of the annelids and arthropods, but apart from this there is a very similar trend in the establishment of a ganglionic system controlling local reflex.

The most complex nervous system of all the invertebrates belongs to *Octopus*. The brain alone contains about $10^8$ neurons. These are arranged in a series of highly specialized lobes and tracts that evidently evolved from the more dispersed ganglia of the lower mollusks. Among invertebrates, the *Octopus* is quite intelligent indeed.

The nervous systems of invertebrates, especially below the Octopus are significantly less complex than those of the vertebrates. The number of neurons in an invertebrate nervous system is far lower than that of a vertebrate one, for which invertebrate nervous systems are often called simple.

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# Unit 7 ❐Invertebrate Larvae

*Structure*

## 7.0 Introduction

Development is a process of progressive change by which and organism takes on the forms characteristic of the sexual stages of its life circle. Development is not just the changes that occur during the growth of the embryo; rather, it continues until the death of the animal. The differences between direct and indirect development is a familiar feature of life histories. In the former, the adult stage is attained by progressive growth and differentiation, whereas in the latter there is a larval stage, differing both in its structure and in its habit from the adult, and acquiring adult form through radical and sometimes sudden metamorphosis. Therefore, larva can be defined as an immature form of a animal, feeding independently and differing in appearance from the adult of the same species. Many kinds of animals go through a larval stage in development. The adaptive significance of an adaptive larval stage varies among groups.

Primarily three main types of larvae can be distinguished. There is firstly the **lecithotrophic larva** that feeds exclusively upon the yolk originally laid down in the egg and does not, therefore, take many foods from external sources. Nevertheless, such larvae may have a long period of life in the planktons being carried along largely by currents that can distributed them over areas. They haver a better chance of reaching metamorphosis. A far commoner type of larva is the **planktotrophic larva** that feeds on plankton, well adapted for prolonged movement and swim actively for 2-4 weeks in summer and perhaps 3 months during winter.

Finally, there are other **planktotrophic larvae** with only a short period of free-swimming life. Their chief functions are to spread the larval stock and to find suitable substrata.

## 7.1 Larval forms of free living invertebrates

**1. Planula larva :** In the ontogenic development of cnidarians, a larva is found, called planula.

1. A solid gastrula, consisting of an outer ciliated ectoderm and an inner mass of endodermal cells, accompanied by yolk.
2. Planulae are elongated (less than 100μm to about 5 mm long) and with a mouthless broad anterior end.
3. They use cilia to swim or creep on the subtratum. Many species have an apical sensory organ with a tuft of cilia.
4. They may depend upon yolk stores or feed on microplankton.
5. The fate of planula larva is quite varied. It may attach and form a polyp, as in hydroidans and anthozoans.

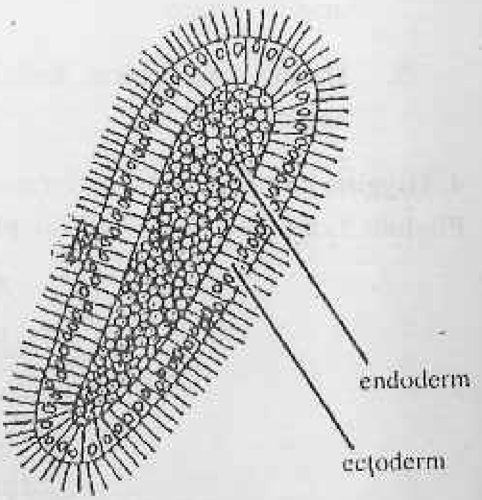

Fig. 7.1 Planula larva

6. In semaeostomes, the planula forms a polypoid larva, the scyphistoma, which later strobilates, and asexually divides to form ephyrae.
7. In most hydrozoans, planula an actinula larva that transforms into a medusa.

**2. Cydippid larva :** It is the characteristic larval type found in all orders in Ctenophora, except in Beroids. The transformation from cydippid to adult form is gradual.

**3. Müller's larva :** Some polyclades pass through free-swimming larval stage, known as Müller's larva, which is supposed to foreshadow the Trochophore.

1. It is oval in shape and bears eight prominent arms which are beset with long cilia forming one continuous band.
2. General body surface is covered by small cilia.
3. Mouth aperture is located in the midventral line.
4. Three eyes exist in the anterior part of the dorsal surface.
5. During development, the ciliated arms are absorbed.

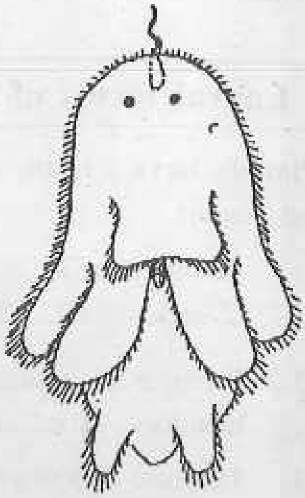

**Fig. 7.2** Muller's larva

**4. Higgins larva :** This larval form is found in the development stages of loriciferans. Phylum Loricifera is the newest phylum, described in 1983.

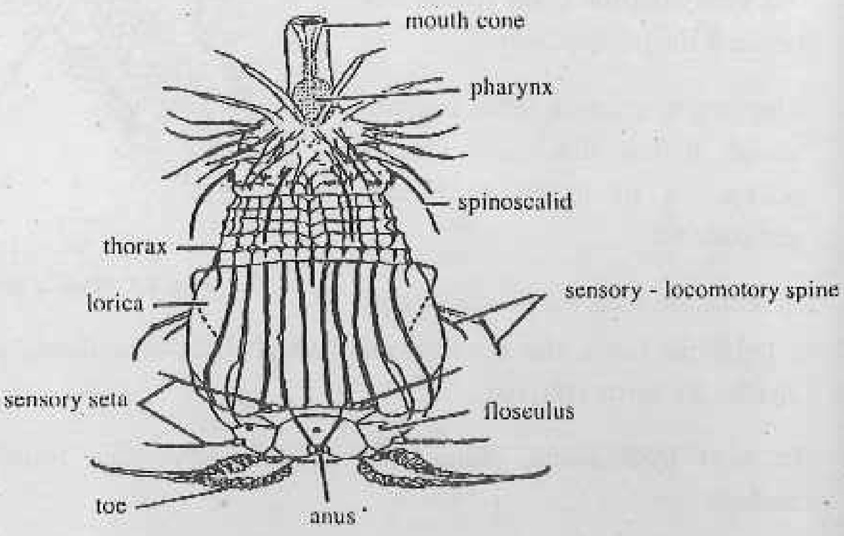

**Fig. 7.3** Higgins larva

1. The head of the larva is armed with scalids, and the neck is covered with five rows of plates. These plates prevent the neck from being completely retracted into the lorica.
2. The anterior edge of the abdomen is equipped with pairs of three locomotory spines.
3. The most prominent features of this larva is a pair of caudal appendages or toes that either leaf like or blade like and are able to move in all directions. The leaf like toes serve to assist the larva in swimming.
4. There are glandular adhesive organs at the base whose scertions allow the animals to attach and release from a substrate.

**5. Priapulus Larva :** The marine pseudocoelomates, under the phylum Priapulida, possess a larval stage, Priapulus larva at their development process.

1. Priapulus larva has a lorica, composed of dorsal, ventral and three pairs of lateral circular plates.
2. A terminal foot is present at the posterior end of the priapulus larva.

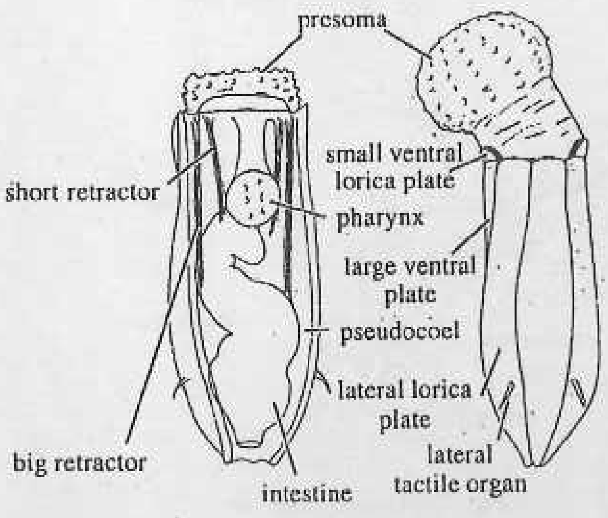

Fig. 7.4 Priapulus larva

3. Larvae live as juveniles for some times, eventually shed the lorica by molting and therefore gradually acqure adult characteristic through a series of molts.

**6. Trochophore larva :** The larval types called trochophore occurs in annelids and several other marine invertebrate groups, including sipunculids, echiurids and molluscs.

It was first discovered by Swidish naturalist Loven in 1840 and was known as **Loven's larva.** In 1877 Ray Lankester termed it as trochosphaera. In 1878 Hatschek named it as trochophore.

In annelids, it appears especially in the class Polycheta. In gastropoda, the occurrence of trochophore sage is observed particularly in the archaegastropods (e.g. *Patella*) and in the Bivalvia; it is found in the development of *Chiton* (Amphinera) and *Dentalium* (Scaphopoda).

**Structure**

1. A typical trochophore larva is biconical with a tuft of cilia at the apical end.
2. A conspicuous girdle of cilia, prototroch, rings the body about $^{1}/_{3}$ to $^{1}/_{2}$ of the distance from the apical tuft, extending around the equator.

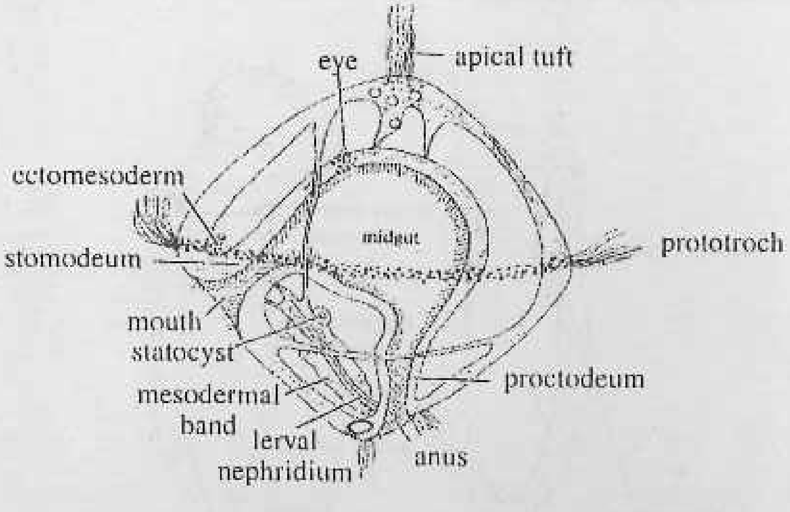

**Fig. 7.5** Trochophore larva

3. A second ciliary band, metatroch develops below the mouth.
4. A third girdle of cilia, the telotroch forms just before the anus at the posterior end.

5. The gut is a complete tube and the mouth opens just the prototroch, near the mid ventral line of the body.
6. Mouth leads into a short ectodemal stomodaeum or oesophagus, followed by an expanded stomach or midgut, endodermal in origin, and a short intestine opens outside via anus at the narrow end of the body. The whole digestive tract is ciliated (suspension feeder).
7. The alimentary canal lies within the body cavity, which is a blastocoel.
8. The cavity contains also a pair of mesoderm bands, developed from the teloblosts, and a pair of protonephridia together with muscle fibers and mesenchyme cells, which represent the ectomesoderm.
9. At the apical pole is an area of thickened ectoderm, the apical plate, which bears a tuft of sensory cilia.
10. Beneath the plate is a ganglion, the primordium of cerebral ganglion, from which extend radial nerves.
11. These radial nerves are united by one or more delicate nerve rings, the chief on being associated with the prototroch.
12. Statocysts and eyespots are often present towards the apical pole, while other parts of the ectoderm may well be sensory.

**7. Glochidium Larva :** A larval stage of fresh water mussels.

1. Two valves enclose the larva.
2. Each edge of the valve may bear a hook (*Anodonta*).
3. The shell valves cover a larval mantle, which bears cluster of sensory bristles.
4. There is neither mouth nor anus, and the digestive tract is rather poorly developed.

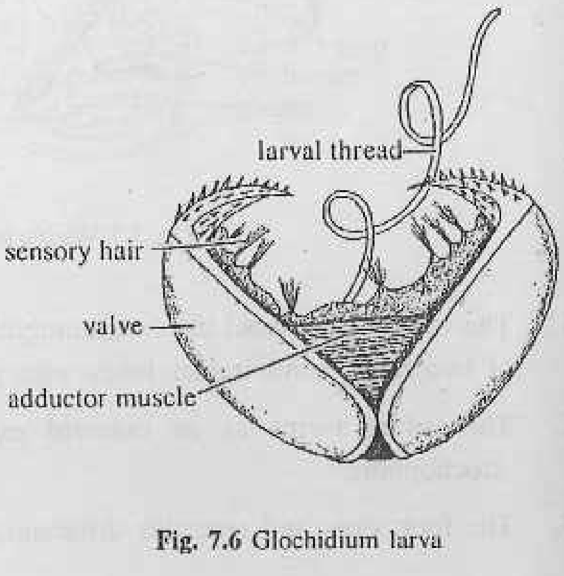

**Fig. 7.6** Glochidium larva

5. A rudimentary foot is present, to which is attached a long adhesive thread.
6. When mature, the glochidium ranges in size from 0.5 mm to 5 mm depending on species.
7. The way the glochidia are released is related to the habits of the host. In *Unio* and *Anodonta,* the glochidia leave the gills through the suprabranchial cavity and exhalent aperture.
8. Further development of the larvae requires a period of parasitism on an appropriate fish.

**8. Veliger Larva :** The development process in marine Gastropod is characterized by possessing a free-swimming larval stage, the **veliger larva.**

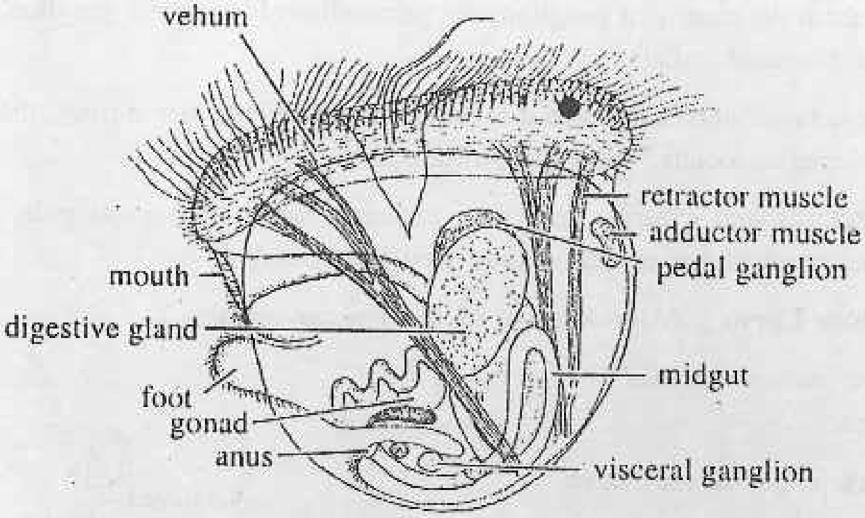

**Fig. 7.7** Veliger larva

1. The veliger has funnel like swimming organ, called a velum, which consists of two large, semicircular lobes with prominently ciliated margins.
2. The velum forms as an outward extension of the prototroch of the trochophore.
3. The foot, eyes and tentacles differentiate from the body of the embryo.

4. A Shell gland appears on the posterodorsal surface and starts to secrete the larval shell.
5. Some gastropods have feeding (planktotrophic) veligers with a larval life that may last as long as three months, others have short lived, yolk laden, and non-feeding (lecithotrophic) veligers.
6. The long cilia of the velum function not only in locomotion but also in suspension feeding.
7. The beating of long velar cilia brings fine plankton in contact with the shorter cilia of subvelar food groove.
8. Within the food groove, particles become entangled in mucous and are conducted to the mouth.
9. At this stage torsion occurs and the shell and visceral mass twist 180 degrees in relation to the head and foot.
10. As development proceeds the veliger swims by means of the velum, and also foot is sufficiently formed for creeping.
11. Ultimately setling and metampphosis occur.

**9. Nauplius Larva :** One of the most interesting features of he Crustacea is the occurrence in all the chief groups, a larva with certain constant characters, the **nauplius**.

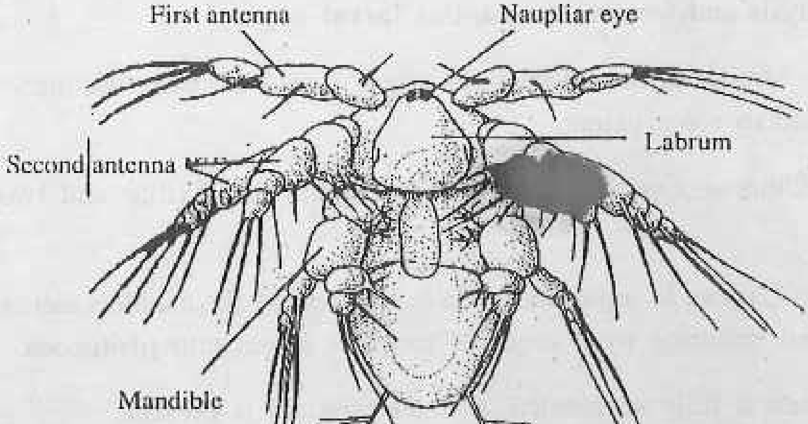

Fig. 7.8 Nauplius larva

1. The body is oval in shape, anterior part of the body is wider than the posterior and no trace of external segmentation.
2. Dorsal shield is usually absent.
3. A pair of setae projects on either side of the posterior end.
4. It has three pairs of appendages.
5. The anterior first antennae are uniamous and placed in front of the mouth.
6. The middle second pair of antennae are biramous.
7. Posterior mandibles are biramous and postoral in position.
8. The second antennae carry a masticatory endite directed inwards and acting as a jaw.
9. A large upper lip projected in front of the mouth and the alimentary canal presents a division into oesophagus, mid-and hind gut, anus is not always open on hatching.
10. The median eye is the characteristic of nauplius and is often referred to as the nauplius eye. The median eye may degenerate or persist in adult crustacean.

**10. Metanauplius Larva :** The nauplius larva of Copepoda metamorphosed by a series of ecdysis and form **metanauplius larval** stage.

It is very similar to that of nauplius stage, except the body becomes elongated and segmented to some extent.

Some additional appen[illegible]ise as two pairs of maxillae and two pairs of maxillipeds

**11. Protozoea Larva :** In some Decapoda (e.g. *Penaeus*), the nauplius metamorphoses by growth and moulting by a series of nauplius stages into **protozoea**.

1. Thorax is fully segmented, a small carapace is present.
2. The appendages comprise antennules, antennae and mouthparts and 1st and 2nd maxillipeds.

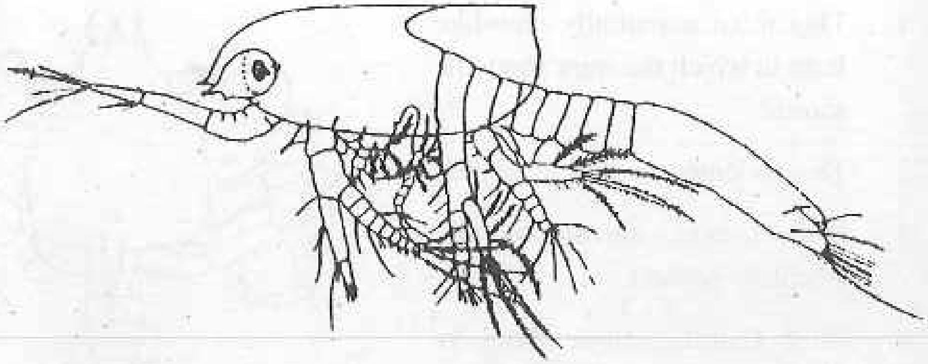

Fig. 7.9 Protozoea larva

3. It still lacks compound eyes.
4. Telson forked.

**12. Zoea Larva :** Protozoea larva metamorphoses into **zoea larval** stage in certain decapod crustaceans.

1. The larval body is divisible into a broad cephalothorax and an abdomen.
2. The carapace bears two long spines : a median rostral one, extending forwards, and a median dorsal one.
3. Cephalothorax bears eyes and seven pairs of biramous appendages.
4. Abdomen is six segmented and have a forked telson.

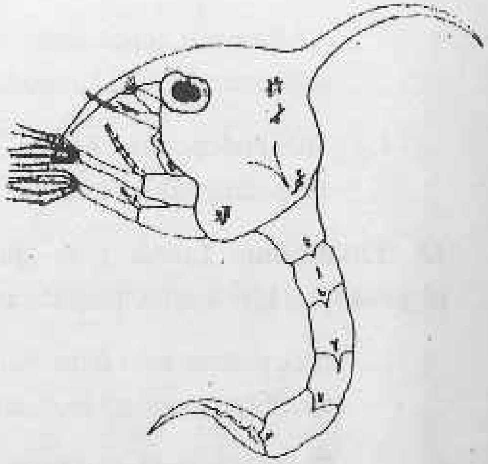

Fig. 7.10 Zoea larva

**13. Megalopa Larva :** Certain decapods like cabs have short life cycle. It hatches as zoea larva, which becomes transformed into another clearly defined stage, the **megalopa**.

1. This is an essentially crab-like form in which the spines become shorter.
2. The abdomen is still extended.
3. Stalked eyes, antennules and antennae present.
4. First thoracic appendage is chelate.
5. Abdomen bears biramous pleopods.

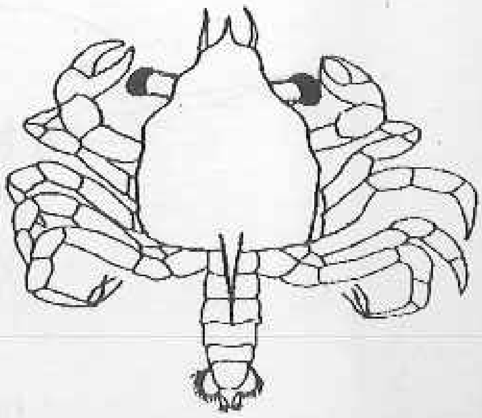

Fig. 7.11 Megalopa larva

**14. Schizopod Larva :** The larvae of lobsters (*Astacura*) illustrate another abbreviation of life cycle.

1. All the thoracic appendages are present, with well-developed exopodites.
2. The first three pairs of legs chelate.
3. Abdominal appendages are absent or rudimentaryin stage 1 larvae, but swimmierets and uropods appear in subsequent moults.
4. The endopodites of the thoracic appendages lengthen markedly, but the exopodites show only a small increase in size.

**15. Phyllosoma Larva :** In spiny lobster *Palinurus*, the larva hatches as the **phyllosoma larva** which is a modified schizopod larva.

1. It possesses two large pairs of maxillaipeds and three pairs of legs. Fourth and fifth pairs of legs are small buds.
2. Flattened thorax and glossy transparent.
3. A large carapace covers the head and the first two thoracic segemetns.
4. Presence of compound stalked eyes.
5. Thorax bears six pairs of appendages. 1st thoracic or maxilleped are rudimentary, 2nd are uniramous, 3rd well formed biramous, remaining three pairs are large and biramous.

6. Abdomen segmented but without appendages.

**16. Cypris Larva :** In some Cirripedia (*Lepas, Sacculina*) the nauplius larva after several moults develops into **cypris** stage.

1. It is enclosed into a bivalved shell.
2. In addition to median eye, a pair of compound eyes are present.
3. Anterior antennae and six pairs of biramous thoracic appendages are present.

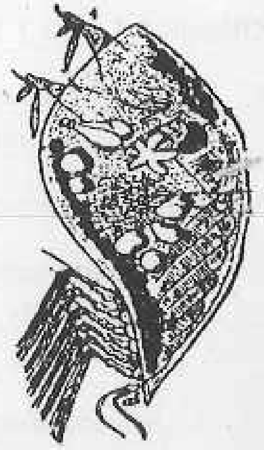

**Fig. 7.12** Cypris larva

**17. Alima Larva :** In some Malacostraca (*Squilla*), egg directly hatches into a young stage the **alima larva.**

1. Transparent, slender body with short and broad carapace.
2. In addition to all cephalic appendages, only 1st two thoracic appendages are found.
3. Abdomen has six segments with four or five pairs of pleopods.

**18. Erichthus Larva :** Found in some Stomatopoda.

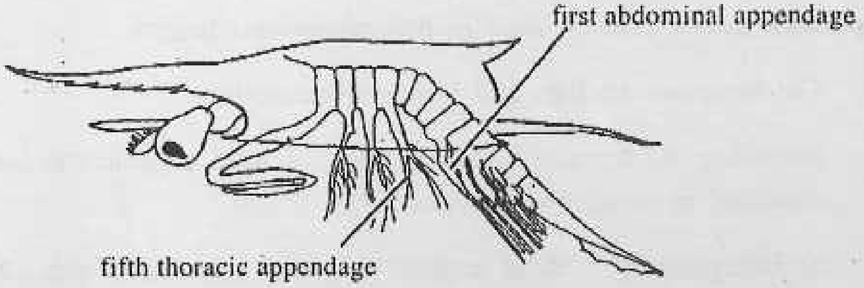

**Fig. 7.13** Erichthus larva

1. Larva possesses a median and two lateral well developed eyes.

2. Five biramous swimming thoracic appendages, the 2nd are is largest.

3. Presence of large caudal plate, the telson terminates the body.

**19. Oligopod Larva :** Found in holometabolous insects.

1. The oligopod larva is a hexapadous form with well-developed head capsule; mouthparts similar to that of adult, but no compound eye.

2. Oligopod larvae occur in two forms :

   (a) Combidiform larva, which is well sclerotised, dorsoventrally flattened and usually a longlegged predator with a prognathous head, (e.g., Neuroptera, Trichoptera, Strepsiptera and some Coleptera)

   (b) Scarabaeiform larva, which is a fat with a poorly sclerotised thorax and abdomen, which is usually short legged and inactive, burrowing in wood or soilfound (e.g. Scarabacoidea and other Coleptera).

**20. Polypod Larva :** Occurs in holometabolus insects.

1. In addition to the thoracic legs, has abdominal prolegs.

2. Prolegs are poorly sclerotised and is a relatively inactive form living with its food.

3. The larvae of Lepidoptera, Mecoptera and Tenthredinidae are of polypod type.

**21. Apodous Larva :** Also found in holometabolous insects.

1. The larva has no legs and is poorly sclerotised.

2. According to degree of sclerotisation of head capsule the larvae can be classified in to following types :

   (a) Eucephalous : Head capsule is well sclerotised e.g., Nematocera, Buprestidae Cerambycidae and Aculeata.

   (b) Hemicephalous : Head capsule reduced in size and can be retracted within the thorax, e.g. Tipulidae and Brachycera.

   (c) Acephalous : Head capsule absent, e.g. Cyclorrhapha.

**22. Hemimetabolous Larva :** They are some times called nymph, occur in all hemimetabolus insects.

1. The larvae essentially resemble the adults.
2. The wings are developed as external buds, which become larger at each moult, finally enlarging to form the adult wings.

**23. Bipinnaria Larva :** The characteristic larva of Asteroidea is the Bippinaria.

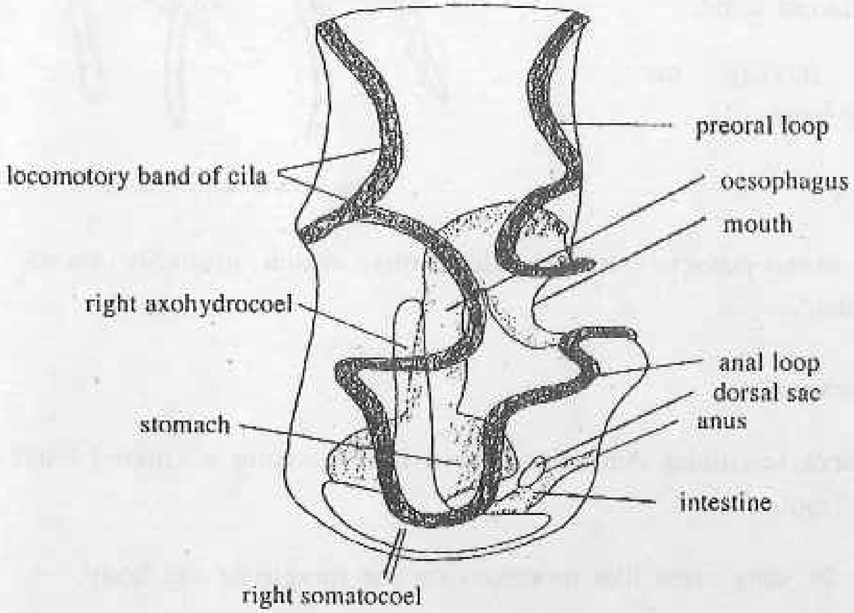

**Fig. 7.14** Bipinnaria larva

1. Pre-oral surface of the ventral surface along with the part of ciliated band becomes isolated.
2. The ciliated bands are separated into two parts-the aboral and adoral bands, the latter being longer.
3. By budding and outgrowth the principal parts of the larva arises longer and shorter processes, which are bordered with ciliated bands.
4. As the larva grows, the peripheral parts differentiate into a series of arms.

**24. Brachiolaria Larva :**

1. This larva arises from Bipinnaria as a subsequent stage of the formation of three additional process at the base of the preoral region, the so-called brachidarian arms.
2. Arms having no ciliated bands.

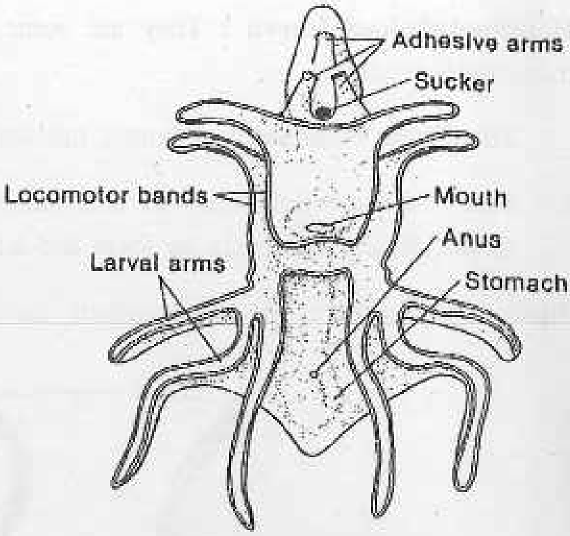

Fig. 7.15 Brachiolaria larva

3. These arms posses wart-like elevations, which probably serves for attachment.

**25. Pluteus Larva :**

1. This larva resembles Auricularia larva in possessing a ciliated band but differs from it :

   (a) by the long arms like processes on the margin of the body,

   (b) by the small size of the lobe,

   (c) Calcareous rods support the arms.

2. Calcareous rods support the arms.

In Echinoidea and Ophiuroidea this larval forms are called **echinopluteus** and **ophiopluteus.**

**(a) Echinopluteus :**

(1) The posterolateral arms when present are directed backward.

(2) Preoral arms are present.

(3) Calcareous skeletons arise form 5 to centres.

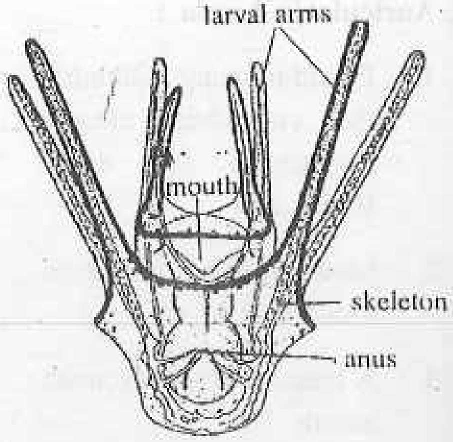

**Fig. 7.16** Echinopluteus larva

**(b) Ophiopluteus :**

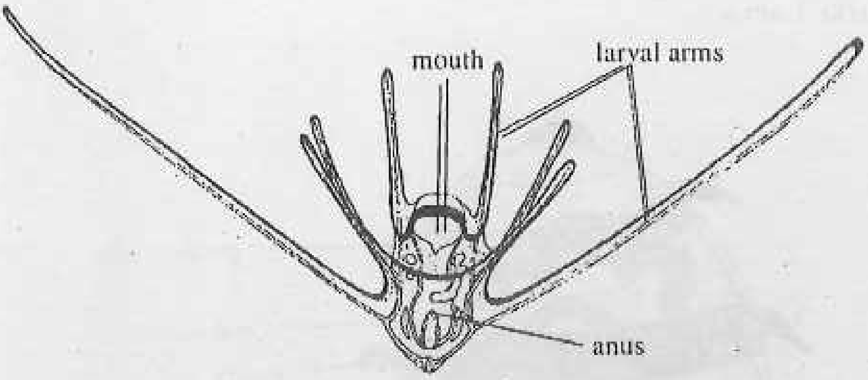

**Fig. 7.17** *Ophiopluteus* larva of *Ophiomaza* (oral view)

(1) Posterolateral arms are the longest and are directed forward.

(2) Preoral and anterodorsal arms are absent.

(3) Calcareous skeletons are on two halves, each half proceeding from the calcification centre.

## 26. Auricularia Larva :

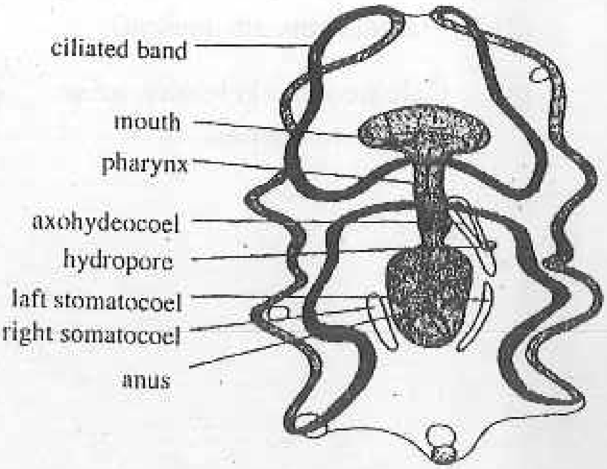

Fig. 7.18 Auricularia larva

1. Found in many holothuria (sea cucumber), closely resembles the early Bipinnaria.
2. Mouth opening lies within a depression.
3. A band of cilia surrounds mouth.
4. Infront of the mouth, pre-oral loop and infront of anus, anal loop is present.
5. The anus present near the pole of the larva.

## 27. Doliolaria Larva :

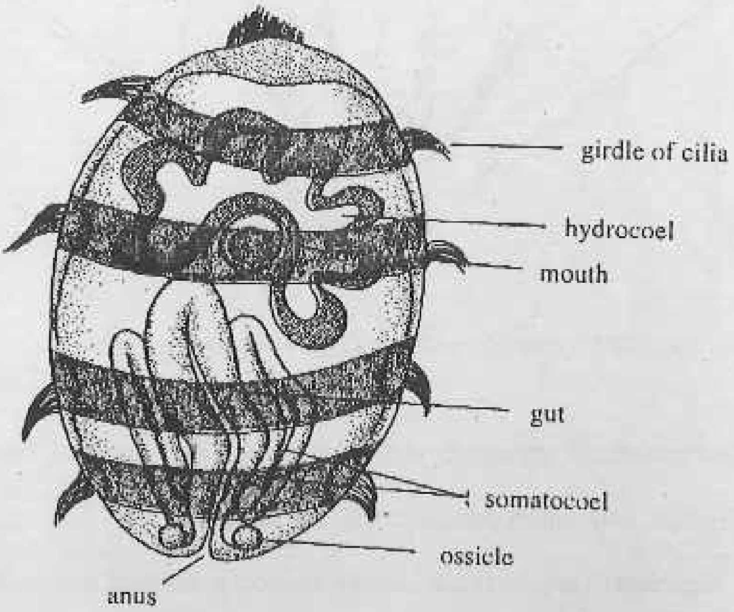

Fig. 7.19 Doliolaria larva

1. The Auriclaria larva of Holothuroidea results in a Doliolaria larva, which is also an initial larval stage of Crinoids.
2. Simple barrel shaped body with five ciliated rings encircle the body transversely.
3. Presence of a tuft of long cilia at the anterior end.
4. Mouth lies at the ventral side interiorly between the 2nd and 3rd ciliated ring.
5. A small adhesive pit on the ventral surface near anterior end serves as attaching organ.

**28. Vitellaria Larva :**

1. There are many species of holothuroids and crinoids and also few ophiruoids possess this larval form.
2. They possess a non-feeding barrel shaped form with four to five ciliated bands.
3. Apical end possesses and apical sensory plate with a tuft of cilia.

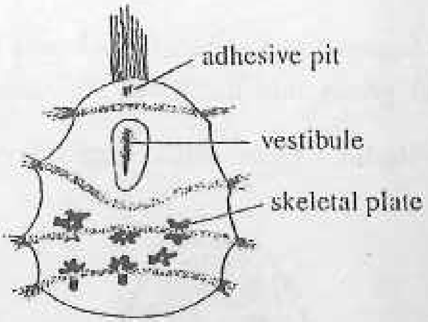

**Fig. 7.20** Vitellaria larva

## 7.2 Larval forms of parasites

There are many invertebrates, which are parasitic on or in other animals, and their life histories involve free-living or parasitic stages, essentially for despersal to new host. Son important larval forms of parasitic inverterbrates are described here.

**1. Digenean Larvae :**

In digeneans, the typical newly hatched larva is a **miracidium;** Special features are :

1. locomotory cilia and eye spots that assists in host finding.
2. anteriorly placed penetration organ, used for securing admission into the internal organs of the mollusc host.

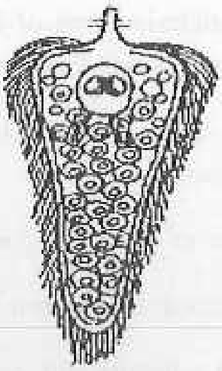

Fig. 7.21 Miracidium larva of *Fasciola hepatica*

The free-swimming miracidium does not feed but it perishes within hours of hatching if it does not find a suitable host.

**2. Sporocyst :** Miracidium losses its ciliated epidermis on entry in to the mollusk and grows into a hollow, and some times branched sac, the sporocyst.

**3. Redia :** Germ balls in sporocyst may give rise to Rediae.

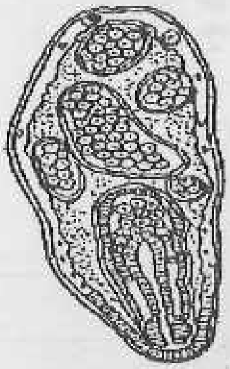

Fig. 7.22 Sporocyst larva of *Fasciola hepatica*

1. It has a pharynx and a simple intestine.
2. It lacs external cilia and has no genitalia.
3. Special features are a birth pore to permit the escape of new larval form in the hollow interior.
4. A muscular collar around the anterior region of the body.
5. A pair of backwardly projecting process near the posterior end of the body which helps in movement.

**4. Cercaria :** It is essentially a tailed distributive and infective larva after emerging from redia.

It already has some adult organs like the oral sucker, pharynx, intertine and ventral sucker and often the rudiment of genitalia.

It also possesses some larval features like;

1. a tail for swimming
2. either penetration glands of cystforming glands or both.

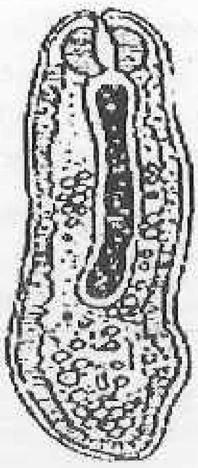

**Fig. 7.23** Radae larva of *Fasciola hepatica*

It either actively invades the vertebrate host or encysts as **metacercaria.**

**5. Monogenean Larvae :**

The larvae of monogeneans is an **oncomiracidium.** It has a posterior haptor baring hooks, and also has a gut; It has no penetration organ.

In *Polystoma,* the oncomiracidium invades the external gills of tadpole, develops into neotenic individual and takes three years to reach maturity.

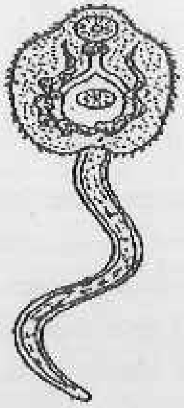

**Fig. 7.24** Cercaria larva of *Fasciola hepatica*

**6. Cestode Larvae :**

In the 'primitive' cestodes (having uterine openings), the newly hatched larvae, **coracidium** is ciliated and without a gut, and bears six posterior hooks, some times free-swimming.

In the 'advanced' cestodes, which have blind uterine sacs, have a larval stages, the **hexacanth embryo** or **oncosphere.** It is enveloped by a protective ciliated layer, the embryophore. In the free-swimming hexacanth the anterior end grows, leaving the posterior end undeveloped as a hook-bearing 'tail' or cercomere. In the more 'primitive' cestodes such as a larva is called a **procercoid.** This procercoid larva further develops into a relatively large, unsegmented **plerocercoid larval** stage in the body cavity of the definitive or second intermediate host. Plerocercoid is equipped with the definitive scolex.

In cyclophyllideans, the developing scolex of hexacanth embryo is accommodated within the hallow bladder like body of the larva; if the scolex is merely retracted into the body the larva is called a **cysticercoid,** but if the scolex is invaginated into the body, the larva is called a **cysticercus.** At this stage multiplication by budding may take place, as in *Echinococcus,* by the proliferation of scolices from the wall of the parent bladderworm, and the so-formed larva is named **hydatid cyst.**

## 7. Nematode Larvae :

The growth or development to the adult stage in Nematode is characterized by one or two or a series of three or four moults of larvae or juveniles. The larval nematodes are differentiated according to the character of their oesophagus. When the length of the oesophagus is short compared to the length of the larva and its posterior end is bulbous, it is called **rhabditiform** larva and its posterior end is not dilated into bulbs, it is called a **filariform larva.**

## 8. Rhabditiform Larva :

This larval stage is the first developmental form, which is hatched out from egg. They have a short mouth and double-bulb (*Strongyloides*) or 'rhabditic' i.e., three sectioned (*Anchylostoma*) oesophagus. The rudiment of genital organs are large and clearly visible. These rhabditiform larvae give rise either directly or indirectly to filariform larvae which constitute the infective stage.

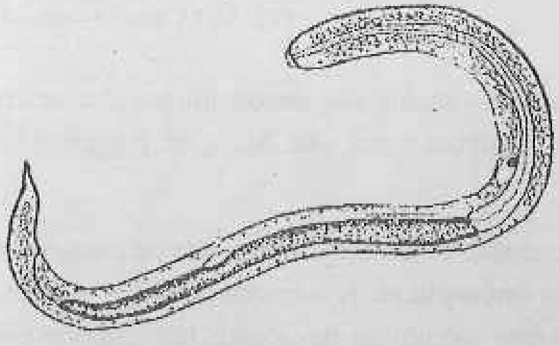

**Fig. 7.25** Rhabditiform larva (2nd stage) of *Ascaris lumbricoides*

**9. Filariform Larva :**

The filariform larvae are longer and more slender than the rhabditiform larvae. The have a well-formed short mouth and elongated and cylindrical oesophagus. They do not take any food, hence the digestive tracts are thin and their lumen almost obliterated, The may be sheathe and unsheathed. The filiform larvae show several forms of 'tropisms' such as geotropism, hygrotropism, thermotropism, thigmotropism and histotropism. These are the biological adaptations of parasites, which may be ragarded as means of self-preservation of the species.

The microfilariae larvae show a characteristic habit of periodicity as in *Microfilaria bancrofti,* which have a nocturnal periodicity.

**10. Crustacea :**

**Kentrogen Larva :** Found in case of *Sacculina,* followed by the cypris stage.

1. Bivalve shell absent.
2. The whole thorax with its muscles and appendages are thrown off and a new cuticle is formed under the old one.
3. The larva is provided with a spike like organ to be introduced into the tissues of the host.

**11. Insecta :**

**Hymenoptera :** Metamorphosis between larva and adult is extreme, requiring a pupalstage. Larvae are usually leglers with a well developed head. Many parasitic forms are either carnivorous or omnivorons; some species herbiorous.

**Arachinda :**

**Ticks :** In favourable conditions the six legged larvae, often called 'seed ticks' hatch from the eggs must find a host and live feeding on blood. After moulting, the larvae become nymphs, which have eight legs, but no genital opening. Nymphs moult after feeding and become adults.

**Mites :** The larvae of itch and mange mites have six legs, frequently produce lateral tunnels in cutaneous burrows of their host species (dogs, pigs, horses, cattle) six legged larvae (chiggers) of the families Trombidiidae and Trombiculidae are parasite on soil arthropods and many kinds of vertebrates (especially mammals) respectively. The cause an intense, intolerable itch on the skin of man and animals.

## 7.3 Strategies and evolutionary significance of larval forms

Larva is a developmental stage in the life cycle of many invertebrates and also in some vertebrates that leads an existence. It differs from both in its structure and its habit from the adult. Whole edifices of invertebrate relationships have been erected on the basis of larval similarities, and complex transformation sequences between dissimilar larvae and between similar larval and adult forms have been devised.

The three major fundamentally important aspects of the development of larval stage in the evolutionary histories of invertebrates are :

1. the need for the delicate young organism to grow in conditions which satisfy its special requirements, and which avoid unnecessary competition with the adult.
2. there is the need to provide for dispersal of the species, and thus to avoid overcrowding,
3. the need to select a habitat that is suited to the requirements of the adult.

Because of these varied functions they often become very highly specialized, and all of them undergo some degree of metamorphosis as we have seen in the Planula larva of Coelenterata. In Hydroidans planula transforms into a polyp, whereas in Anthozoans it metamorphoses into a polypoid larva, the Schyphitosoma, which asexually form Ephyrae. But in most hydrozonas, the planula larva metaborphoses into an actinula larva.

Muller's larva of polyclads is correlated to the trochophore larva of annelids by their locomotor mechanism. Mullar's larva consists of a ciliated band lying above the mouth, and corresponding to its position to the prototroch. The characteristic feature of the larva is that its band is situated on the edge of eight posteriorly directed lobes. These disappear after a few days, when a flattening of the body converts the larva is essentially an early development stage of the flat worm, adapted for pelagic life its specialized ciliation.

The Pilidium larva of heteronemartines, possesses a helmet-shaped body, with an apical plate and tuft (but with sign of nervous structure), and a mouth that leads into a blind alimentary tract, the organisation in this latter respect being platyhelminth-like. It shows similarity with Muller's larva, as its locomotion depends upon a lobed ciliated girdle on the edges of a pair of oral lobes.

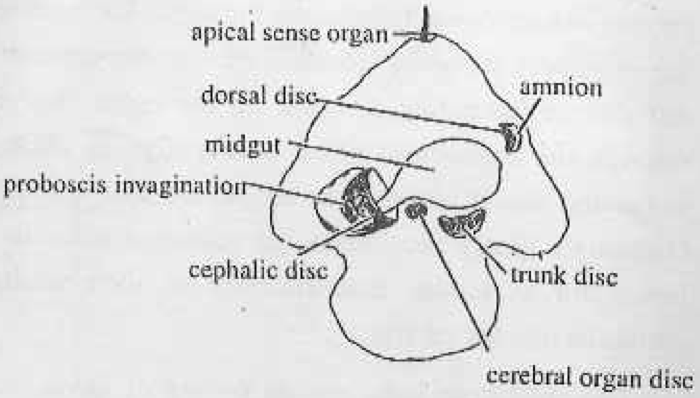

Fig. 7.26 Pilidium larva

The trochophore larva with varying degree of modifications occurs in annelids and several other marine invetebrate groups, including sipundulids, echurids and molluscs. It is also somewhat similar to adult form in the ctenophores, and in particular in rotifers, both sometimes thought to be neotenous derivation from it. These facts led Hatsckek as far back as the midninteenth century to propose that it repesented a remote common ancestor of all of the Protostomia, including acoelomate and pseudocoelomate groups.

Salvini-Plawen L (1973-1980) believes that annelids and echiurans are closely related by their larval stage where as flatworms, nemerteans and entoproct larvae are unrelated.

Close relationship with the annelids is seen in the occurance of trochophore stage in many forms, particularly in the archeogastropods (e.g. *Patella*), and in the Bivalvia; it is found also in the development of Chitons (Amphineura) and Dentalium (Scaphopoda). This larva is rapidly transformed into more complex stage, the veliger larva, which is particularly characteristic of the gastropods and bivalves.

In veliger larva the prototroch is drawn out into a pair of ciliated lobes, and arrangement that considerably increases the support given to the larva and makes for a more vigorous and controlled locomotion. This development is explained by the advanced stage of differentiation reached by the veliger. It has something of the form of a mollusk, with a shell, a mantle cavity, and the beginnings of a foot, the latter sometimes bearing an operclum that can close the opening of the shell. Clearly the improved ciliation is necessary for the support and movement of this heavier and more complex body.

In the early larval life of gastropods there is another complication, i.e., the torsion, which twists the viscera through 180° relative to the rest of the body, brings the originally posterior mantle cavity to the anterior end, and leaves the originally left side of the pallial complex on the right. This transformation is brought about through the contraction of an asymmetrically arranged retractor muscle. Garstang suggested that it arose as an adaptation that was carried over into the adult stage. Garstang's theory recognizes the immense potential importance of the capacity of larvae for evolution, independently of their adults, in adaptation to their own particular modes of life.

The crustacean have a wide variety of larvae, but these are entirely crustacean in form, and show no relationship at all with the ciliated larvae of annelids.

In fact, almost complete loss of cilia by the phylum extends to their larval stages; these like the adults, rely upon their limbs for locomotion. The larvae hatch in a relatively advanced stage of development, with at least a few functional appendages present and with the accompanying metameric segemntation.

The simplest crustacean larva is the nauplius, a three-segmented organism with three pairs of limbs.

In the brachipods the further development of the nauplius involves continuous growth, interrupted by periodical moults; the adult form is thus achieved without drastic metamorphosis. This simple type of life history in brachipods was the primitive mode of development in crustacea. In other groups with free larvae, however, including the Copepoda, Ostracoda, Cirripedia, and Decapoda, we find one or more stage which include a sharply defined metamorphosis.

How the adult mode of line influences larval development is well seen in the Cirripedia. They have free-swimming phase as a nauplius, characterized by a distinct pair of anterior lateral horns, and by a posterior forked spine. This larva undergoes a series of moults, and then passes at a single moult into the cypris stage.

In the Decapods, with more complex life histories, the hatching is usually at a later stage, the nauplius being no longer recognizable.

*Penaeus,* hatches as a nauplius which through a series of stages transforms into protozoea.

Gurney has emphasized that the organization of the main development stages of the higher Crustacea is primarily determined by their mode of locomotion. The nauplius depends upon the antennal propulsion, and so, in general, does the protozoea. The apperance of thoracic propulsion depends upon the maxillipedes which is initiated by the transformaiton of the protozoea into the zoea larva.

The megalopa, often referred to as a larva, can alternatively by ragarded as a first post larval stage, which marks, with its abdominal propulsion, the transition to the specialized form of the adult crab.

The schizopod larvae of lobsters illustrate another abbreviation of the life cycle. Analysis of the swimming mechanism of this larva amply justifies Gurney's argument that larval form is determined by mode of locomotion.

The Phyllosoma larva is an extreme example of planktonic adaptationl; it is not easily comparable with any other crustacean larva, and illustrates very well the possibilities of independent larval evolution.

The course of evolution of insect life histories can only be guessed at, and there is more than one opinion regarding the relationship between the heterometabolan and holometabolan type of development. There is a divergence between two views : one that the larva is a specialized nymph, and the other that it is new development inserted into the life cycle in advance of the nymph as result of earlier hatching.

On the former view the pupa is a specialized last-stage nymph, whereas in the latter view it represents a fusion of nymphal stage, the larva being essentially an elaboration of an embryonic phase. Whatever the truth may be, the origin of these life histories is rooted in coenogenetic changes. These have brought about alternation in the relative rates of development of juvenile and adult characters, with conswquent divergence of the youthful and adult stage.

The fundamental characteristics of deuterostome larvae are to be seen in the array of larval forms produced by the phylum Echinodermata. Considering the larval development, it is suggested that there are some general similarities in the embryonic development of Echinodermata. These similarities have led to the conception of common ancestral form, the diplurula (hypothetical).

This larval foams have the following echinoderm features :

(i) Bilaterally symmetrical elongated or oval body,

(ii) Ventrally placed mouth and anus,

(iii) Digestive canal differentiates into an oesphagus, stomach and intestine,

(iv) The general surface ciliation becomes reduced to a ciliary band,

(v) The pre-oral lobe, anterior to mouth, bears apical sensory plate and tuft of cilia.

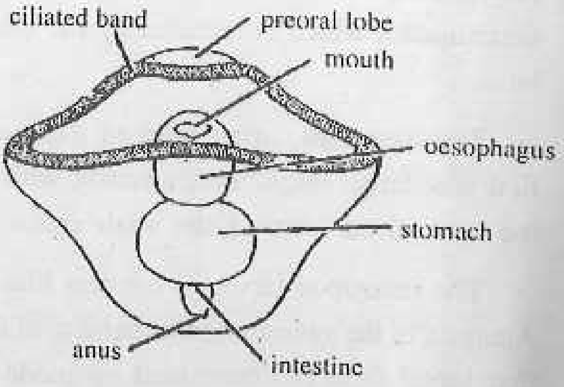

Fig. 7.27 Diplurula larva

The diplurule larva is distinguished from the trochophore larva by the circumoral course of the ciliary band, the parired coelomic enterocoelic sacs and by the absence of rpotonephridia.

Mortensen (1921) regarded these larvae as highly specialized adaptation of the original pelagic ancestral form.

Fell (1945) suggested that they have arisen in response to the need for a temporary food gathering stage.

In the Echinodea and the Ophiuroidea the diplurula stage develops into the pluteurs larva, the organization and further development of which provides for improvement of locomotion and of suspension in the water.

The characteristic larva of the Asteroidea is the Bipinnaria, where the ciliated band of the diplurula stage extends into an anterior and a posterior folds and then subdivides to form two ventral loops. The asteroid larva metamorphoses by developing three brachiolar arms, lying anterior to pre-oral loop, and the larva is now known as a Brachiolaria.

The larva closely resembling the early Bipinnaria is found in many Holothuria, hatching as an Auricularia larva which metamorphoses into Doliolaria larva with three to five transverse ciliated bands

Abbreviation of the larval life history, and even direct development, are not uncommon in Echinoderms. For example, the ophiuroid *Ophioderma brevispina* lacks a plutenus stage, having instead a vitellaria larva with four ciliated bands. Reduction of the larval stage may be associated with brood protection, viviparity and embryonic attachments to the parents, which, however, are not necessarily nutrivite.

Convergence and divergence are marked features of Echinoderm life history. There has clearly been an independent evolution of cylindrical larvae with cililated rings (Vitellaria larva) from the yolky eggs of holothuroids, crinoids and ophiuroids, but there are also more specific cases of close resemblances between unrelated species.

Fell has urgued that this remarkable plasticity in echinoderm development makes it impossible to attach pylogenetic significance to their larvae. Certainly one cannot possible justify interpreting them as a strict recapitulation, in the Haeckelian sense, of phylogetic history. Larvae undergo independent adaptation to their particular modes of life, and to their primary function of ensuring development and dispersal of the species.

In spite of these, it is possible to see in many echinoderm larvae certain common features of organization, including bilateral symmetry, an apical plate and tuft, an antero-ventral mouth, a posterior anus derived from blastopore, a tripartite and paired enterocoles, and a ciliated band curving to run round the mouth and in front of the anus. These we may regard as primary features, part of the foundation of the concept of the Deuterostomia.

The drastic character of echinoderm metamorphosis must surely reflect a time in their history when a bilateral symmetry and free-living stage settled and in due course developed pentamerous symmetry.

Viewing the metamorphic events of all of the echinoderm groups as a whole, we may reasonably infer that the settling of the ancestral stock took place by the anterior end; this became a stalk of fixation, with the left side of the organism becoming the oral surface and the right side the aboral one. This was presumably followed by the development of radial symmetry, by the rotation of the oral surface upwards and the aboral one downwards, and the consequent asymmetrical development of the coelomes of the two sides.

Garstang (1928) considered a progressive larval evolution by neoteny. The sequence is : Auricularia of Echinoderm – Tornaria of Hemichordata – Tadpole of Ascidia – Neoteny – Present free-swimming Chordate.

Berril (1955) was in agreement with the main theory of Garstang but differs on the origin of tadpole larva. Bone (1979) and Young (1981) supported the neotenous larval theory of Garstang.

The tornaria larva of hemichordate is strikingly similar to the larva of echinoderms. But this larva, in its mode of origin and in its organization, differs from echinodem larvaem notably in presence of a posterior telotroch.

So it will be logical to conclude that chordates originated from non-chordate group and echinoderm larvae hold the key position. According to Barnes (1974) the evidences of phylogenetic relation ship between hemichordates, echinoderms and chordates are very convincing at the early development stages.

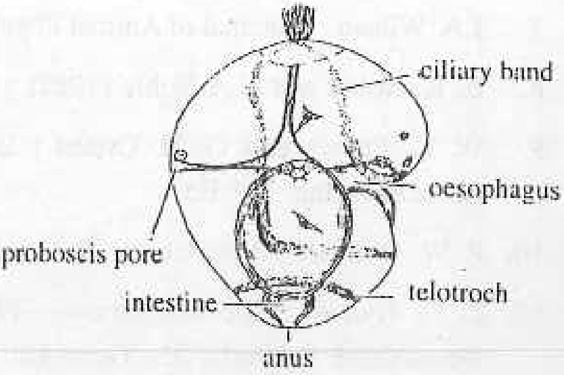

**Fig. 7.28** Tornaria larva

Strickberger (2000) analyzed the concept of common ancestry showed by echinoderms and vertebrates. According to him 'the echonoderms are of the pluteus-types or variation of it, such as the auriculara lavae in holothurians (sea cucumbers). By contrast, the annelid superphylum produces trochophore larvae. Since the acron worm, *Balangolosus,* has an auticularia-type larva (called tornaria) and biologists generally believe this animal to be a chordate, although primitive, it seems to follow that echinodems and vertebrates are closely related.

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