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.

Professor (Dr.) Manimala Das
Vice-Chancellor

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	Writer	Editor
	GROUP : A (I)	
Units 1 - 5	**Prof. B. N. Bhattacharya**	**Prof. B. N. Bhattacharya**
Units 6 - 10	**Dr. Kamales Kumar Misra and Dr. Korak Kanti Chaki**	**Prof. B. N. Bhattacharya**
	GROUP : A (II)	
Units 1 - 4	**Dr. Runu Bhattacharya**	**Prof. B. N. Bhattacharya**
Units 5 - 7	**Dr. Rupa Mukhopadhyay (Bose)**	**Prof. B. N. Bhattacharya**

Netaji Subhas
Open University

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 'ammocoete—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

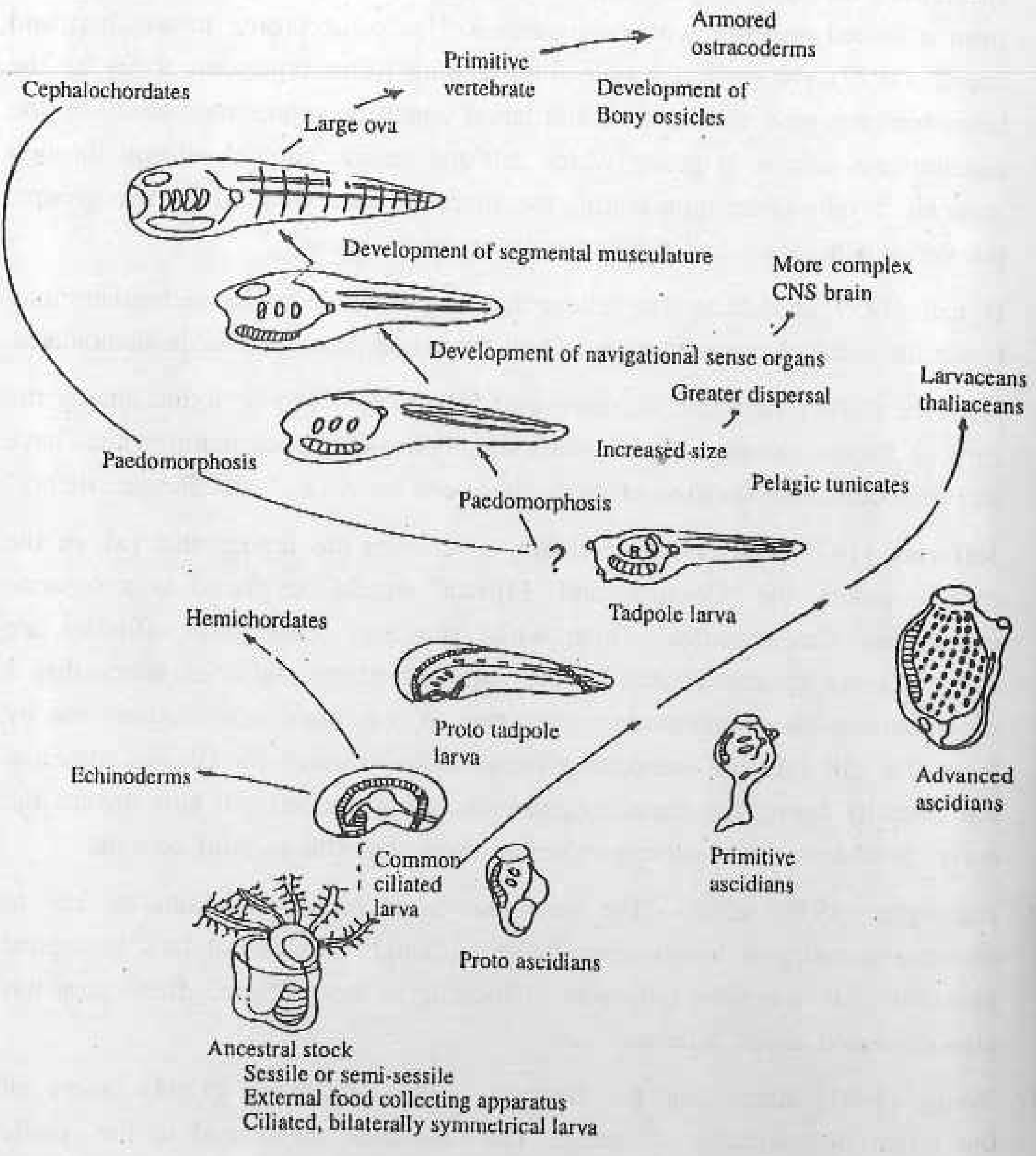


Fig 1.1 : Garstang's hypothesis of the origin of vertebrates by paedomorphosis from an ancestral lophophorate (Based on Pough, Heiser and McFarland, 1990)

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.

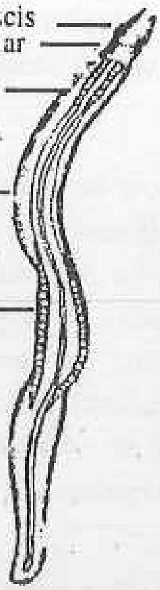


Fig 1.2 : *Balanoglossus* sp. (entire acorn worm)

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.

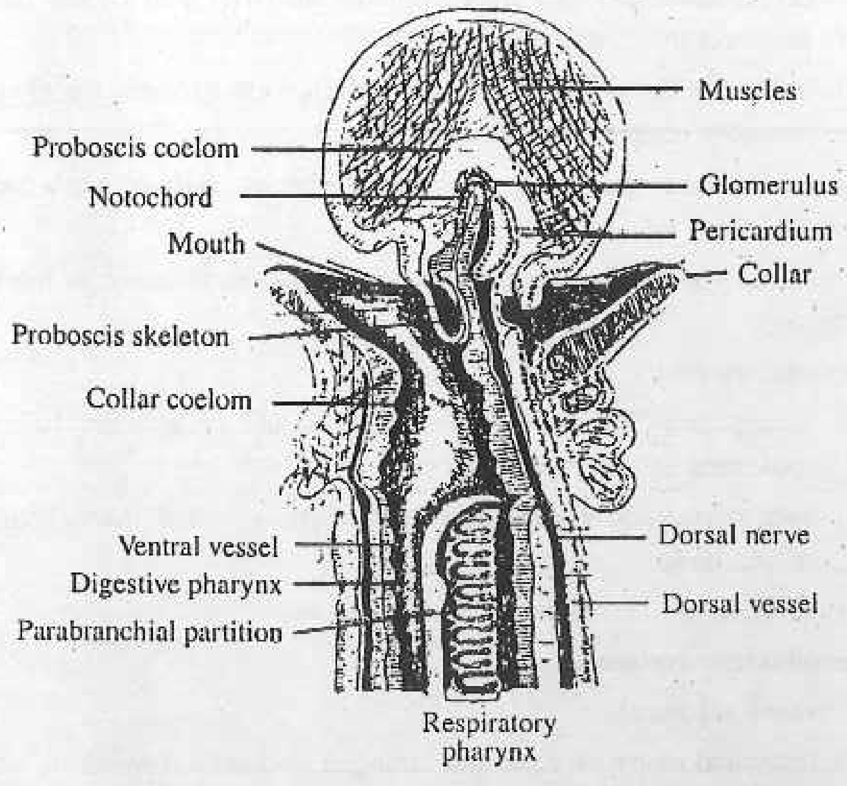


Fig 1.3 : Sectional view of the anterior end of *Balanoglossus* sp.

(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.

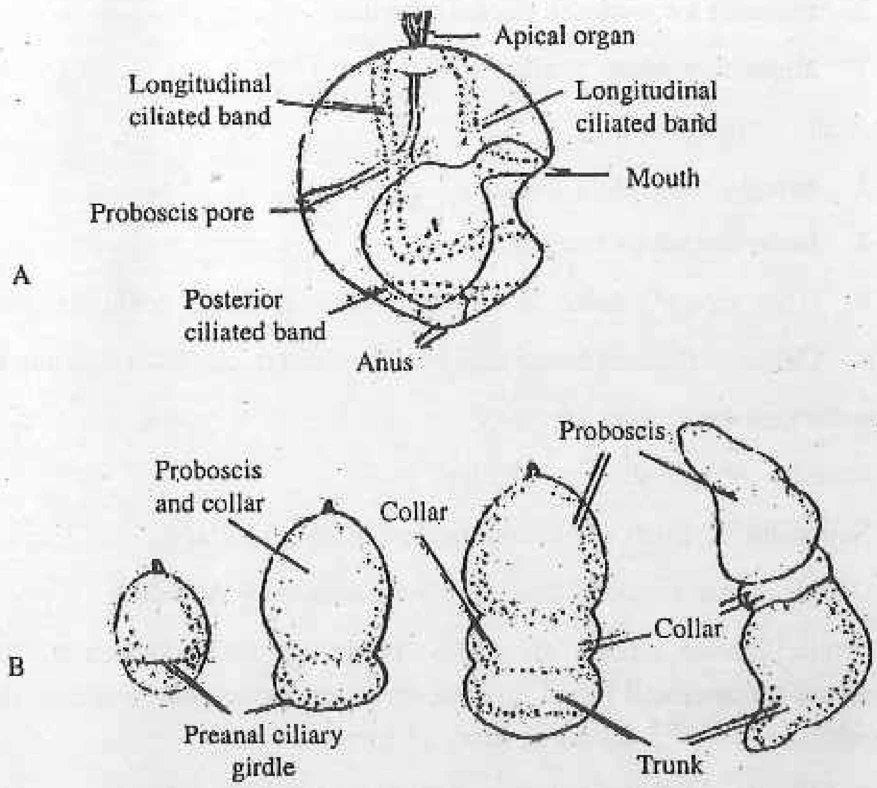


Fig 1.4 : A. Young tornaria lerva of *Balanoglossus* (Lateral view); B. Metamorphosis of the tornaria larva (Based on S.N. Prasad, 1972)

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 éxternal 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.

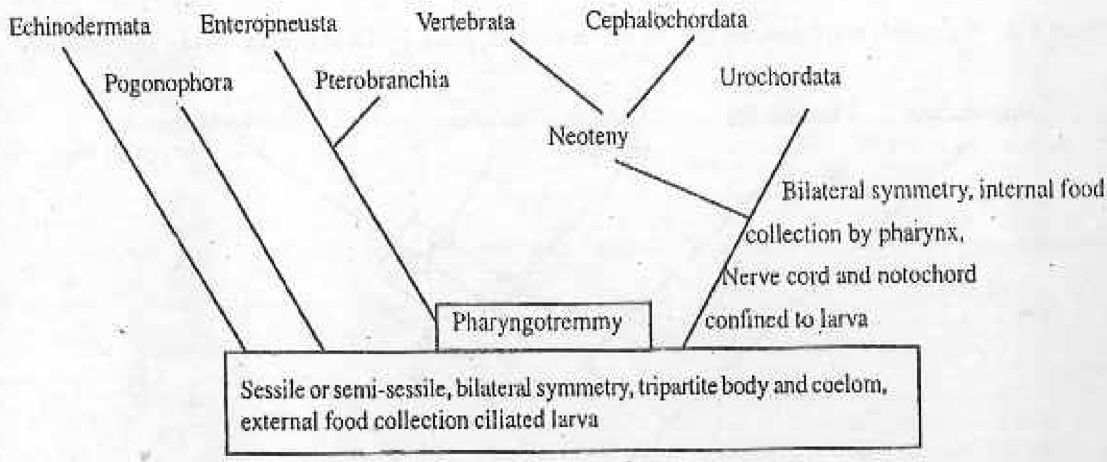


Chart 1.1 : Evolution of Echinodermata and Hemichordata.

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.

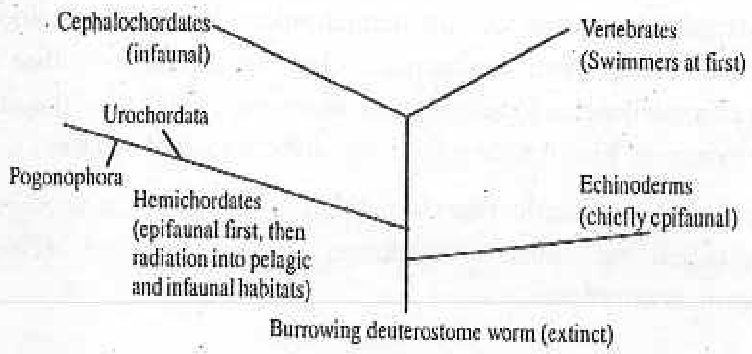


Chart 1.2 : A possible phylogenetic tree of deuterostomia given by Dobzhansky, Ayala and Stebbins

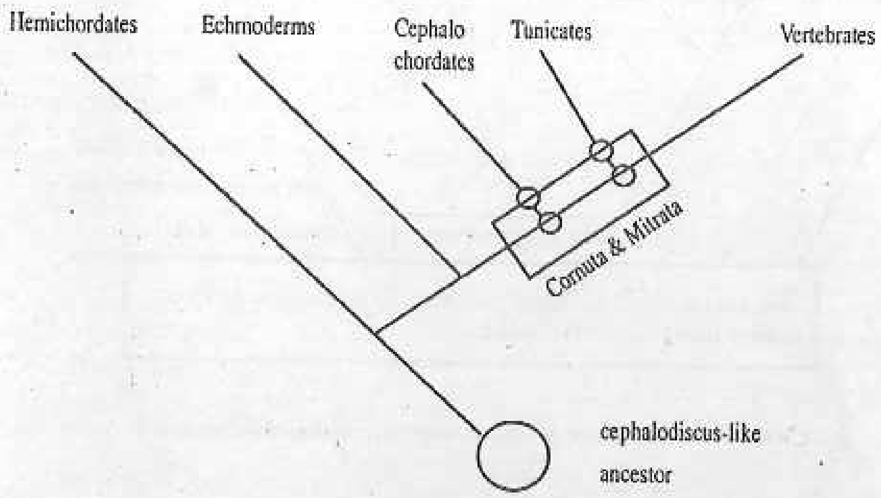


Chart 1.3 : Proposed origin of hemichordates, chordates, echinoderms and vertebrates (Jefferies, 1971, 1975, 1979).

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.

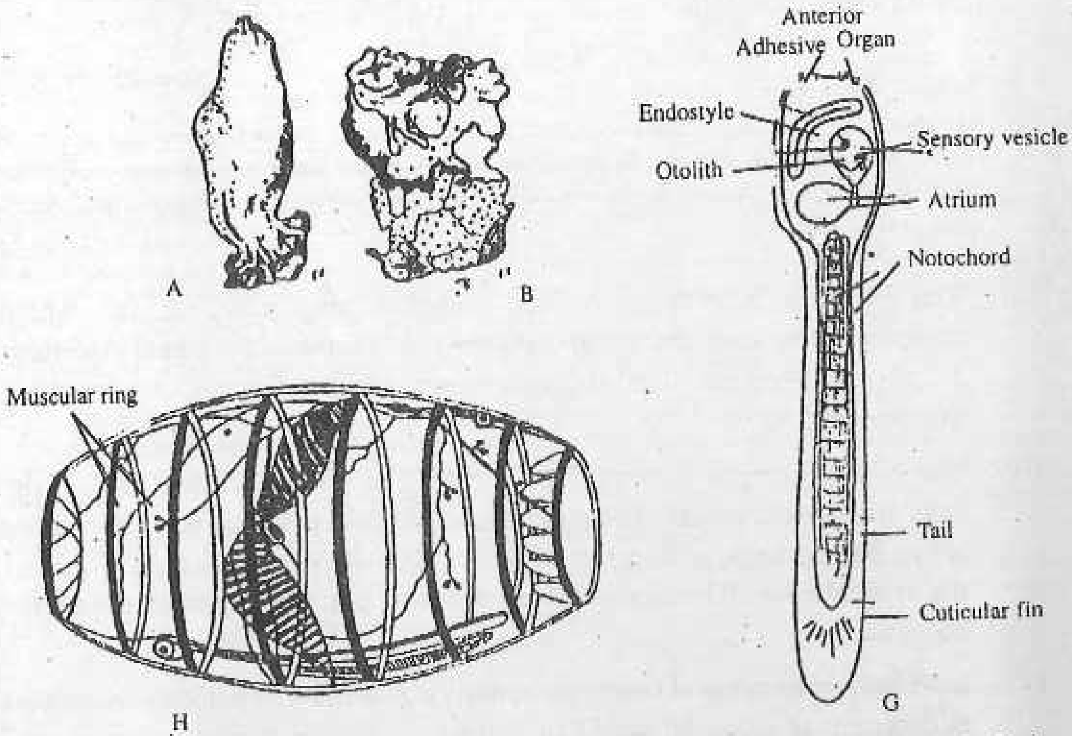


Fig 1.5 : Urochordata : A, Ascidia (entire); B, Hardmania (entire); G, An ascidian tadpole larva; H, Doliolum (entire).

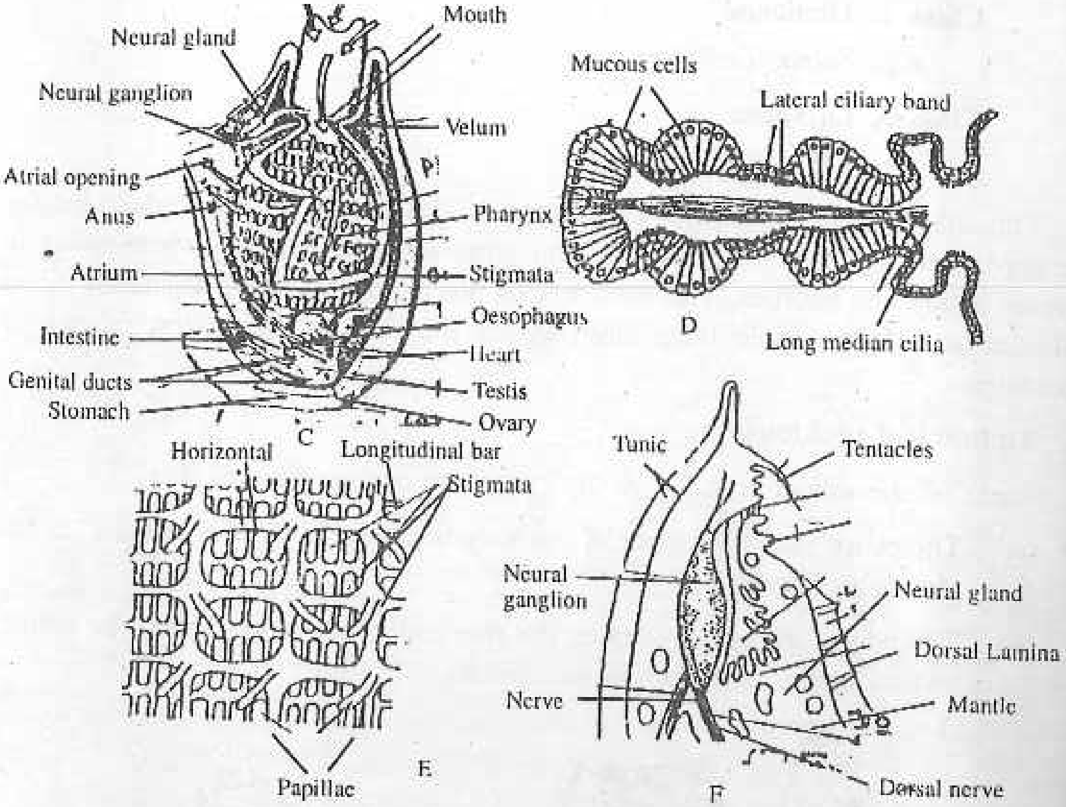


Fig 1.5 : Urochordata : C, Longitudmial section of Ascidia showing various organs and course of water current through pharynx; D, Magnified view of endostyle; E, An enlarged view of the pharyngeal wall; F, Antero-dorsal view of an ascidian showing neural gland and neural ganglion.

(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.

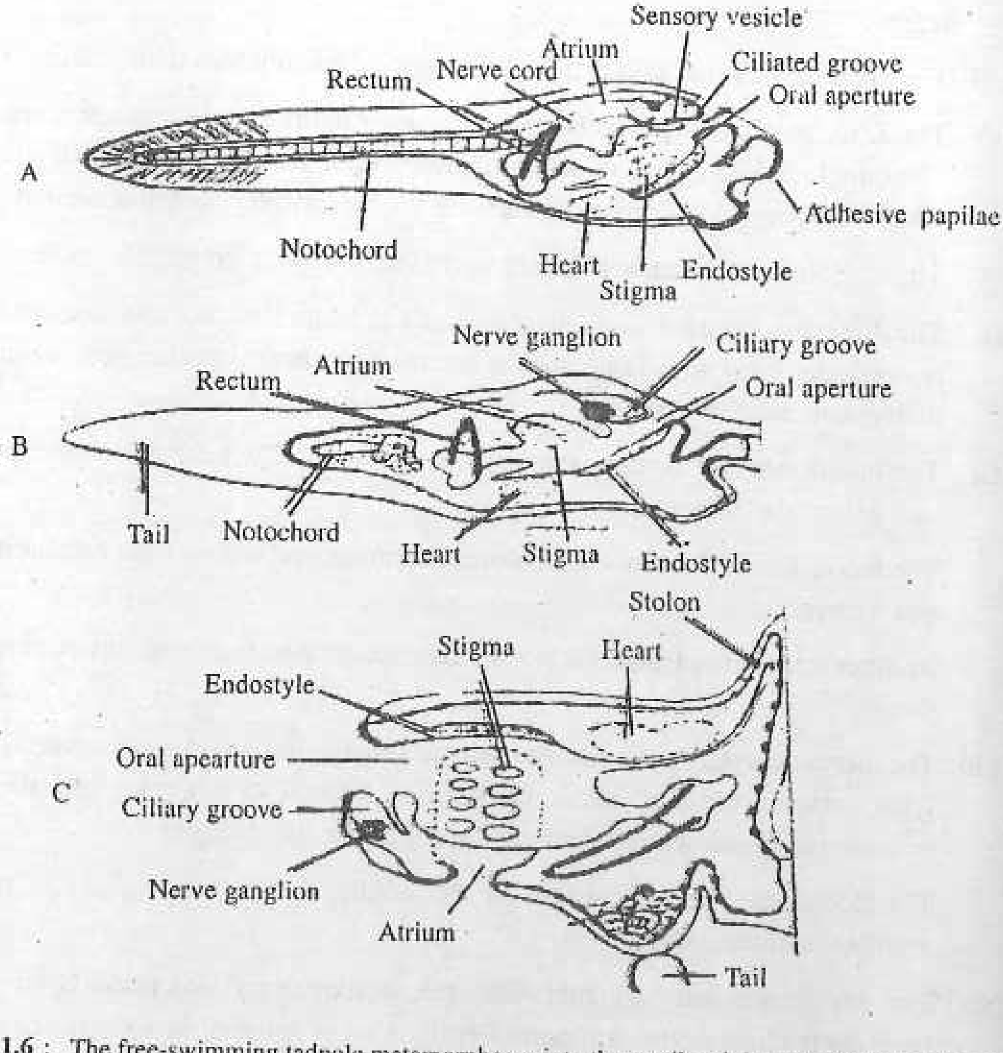


Fig 1.6 : The free-swimming tadpole metamorphoses into the sessile adult (from Parker and Haswell, after Seelinger) : Based on S. N. Prasad, 1972.

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**.

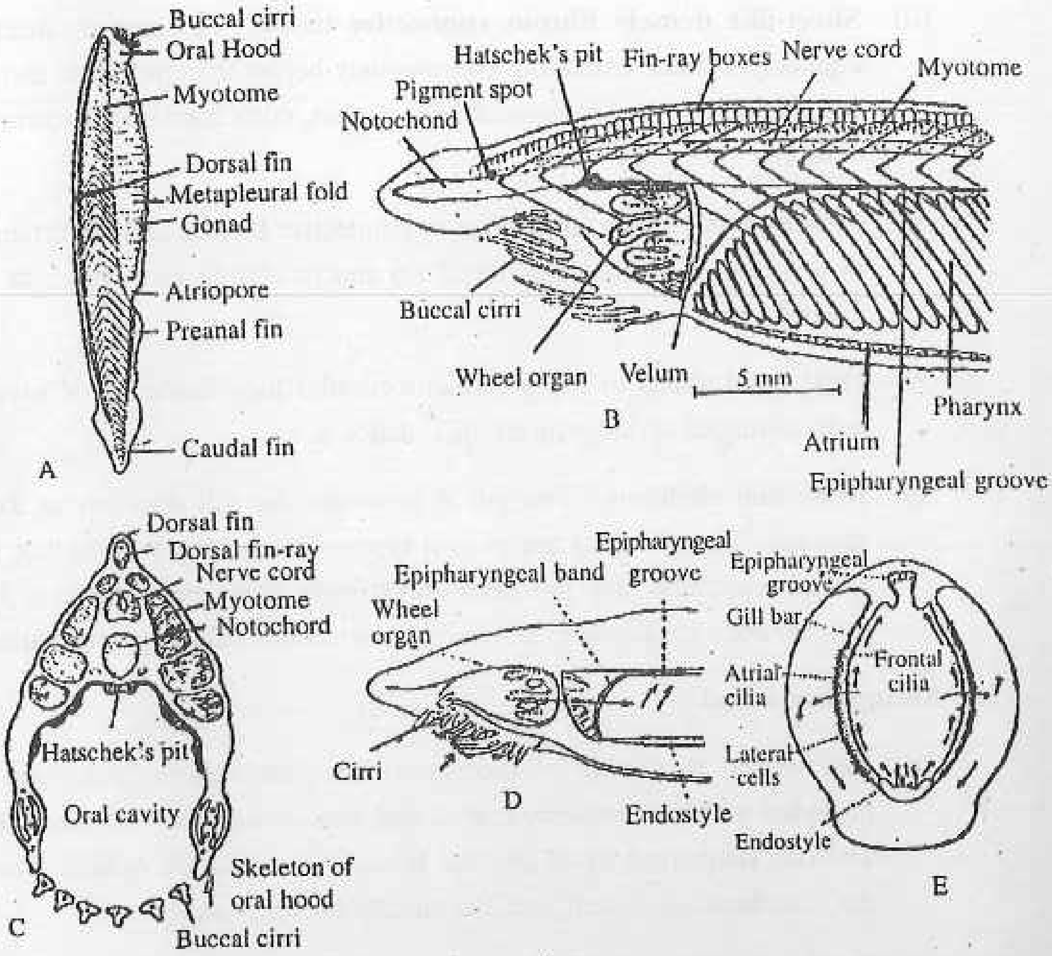


Fig 1.7 : *Branchiostoma* : A, External morphology; B, Lateral view of anterior end of *Branchiostoma;* C. Transverse section through the anterior end; D, Anterior end showing direction of food-current; E, Diagrammatic transverse section showing direction of food-currents by arrows.

(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 scerctes 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.**

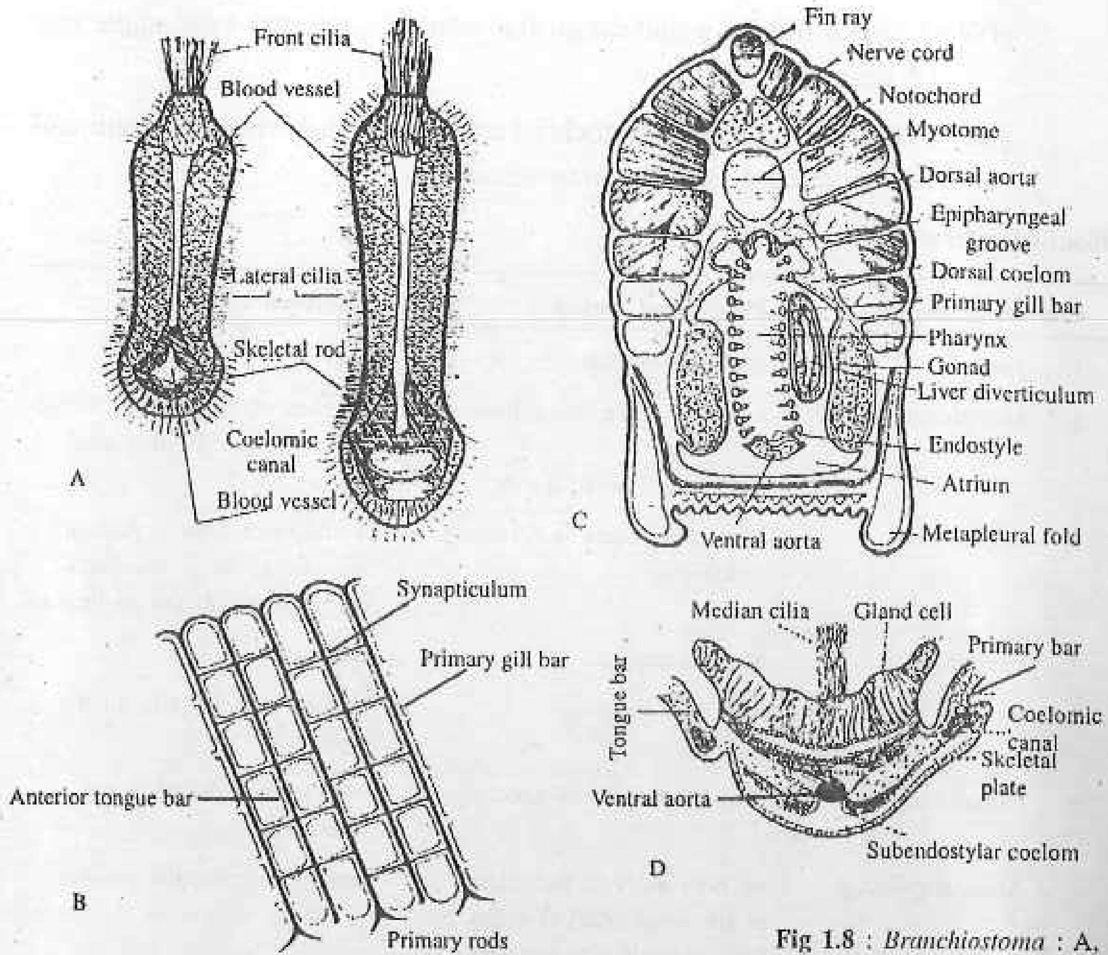
    (III) Underneath the subcutis lie a number of muscle segments or myotomes formed of striated fibres and separated from one another by myoseptum.

(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 containing lymph spaces.	absence of metapleural folds. 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



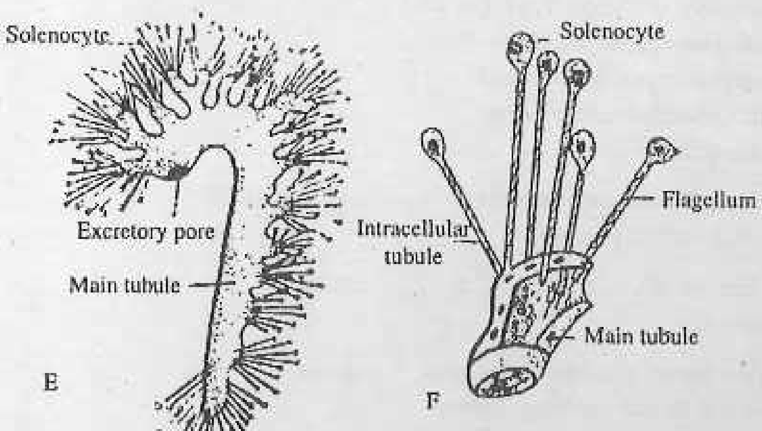


Fig 1.8 : *Branchiostoma* : A, Transverse section of a secondary gill bar (left) and that of a primary gill bar (right); B, A small section showing skeletal elements of the pharynx; C, Transverse section showing pharynx, gonads and other structures; D, Transverse section of the endostyle; E, A nephridium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

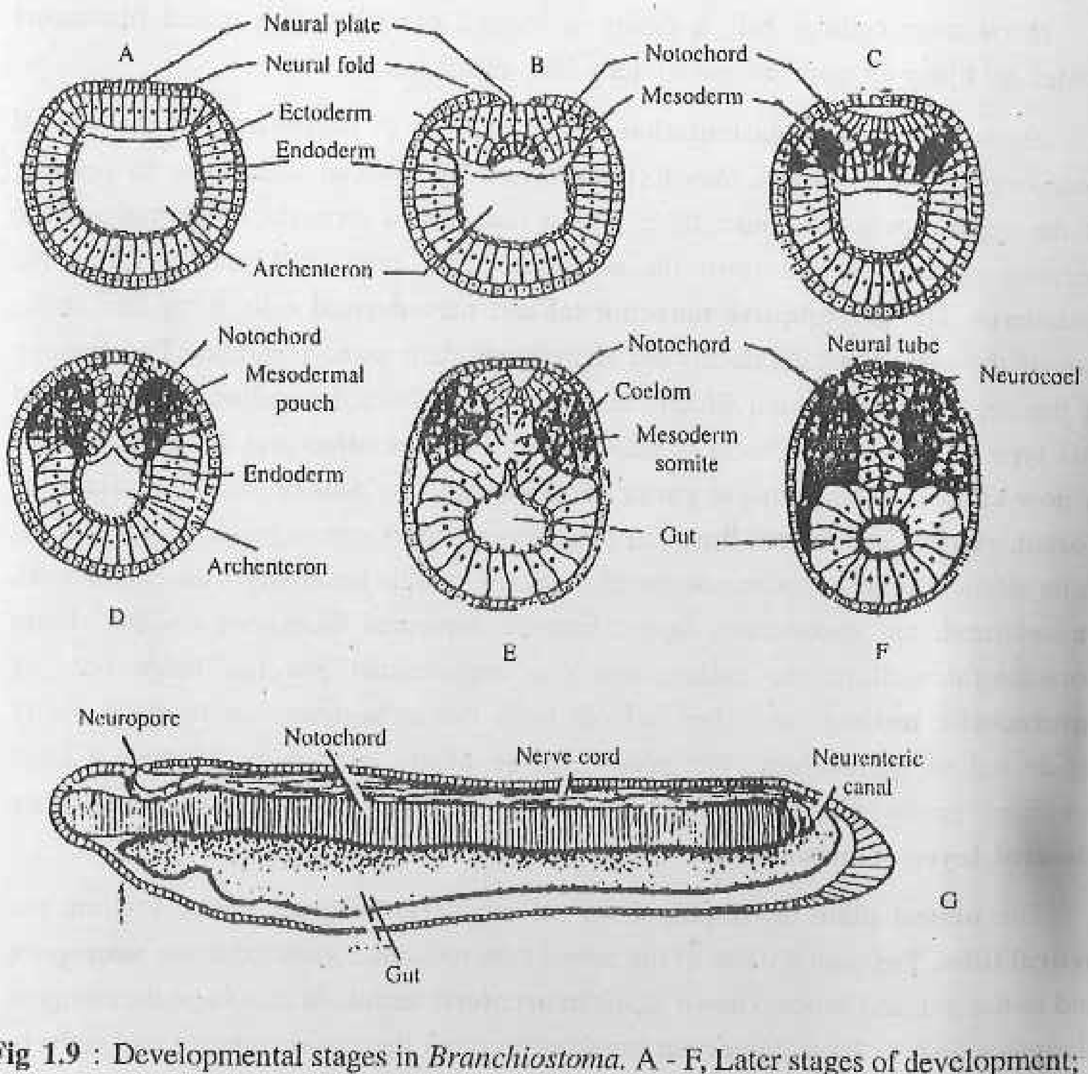


Fig 1.9 : Developmental stages in *Branchiostoma.* A - F, Later stages of development; G, Neurula larva of *Branchiostoma.*

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

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 landlllasses, 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.

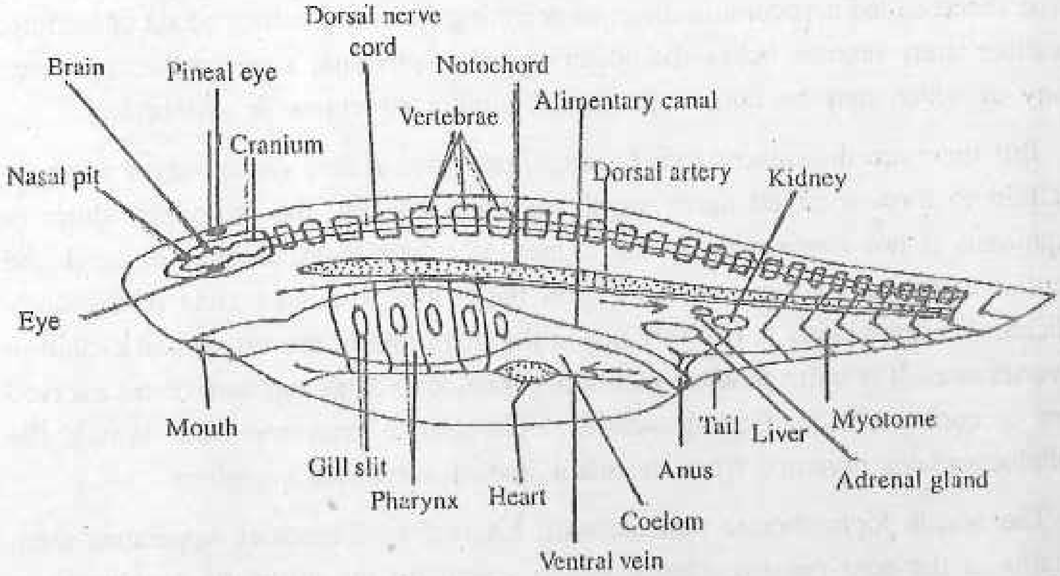


Fig 3.1 : Diagrammatic body plan of an early vertebrate

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.

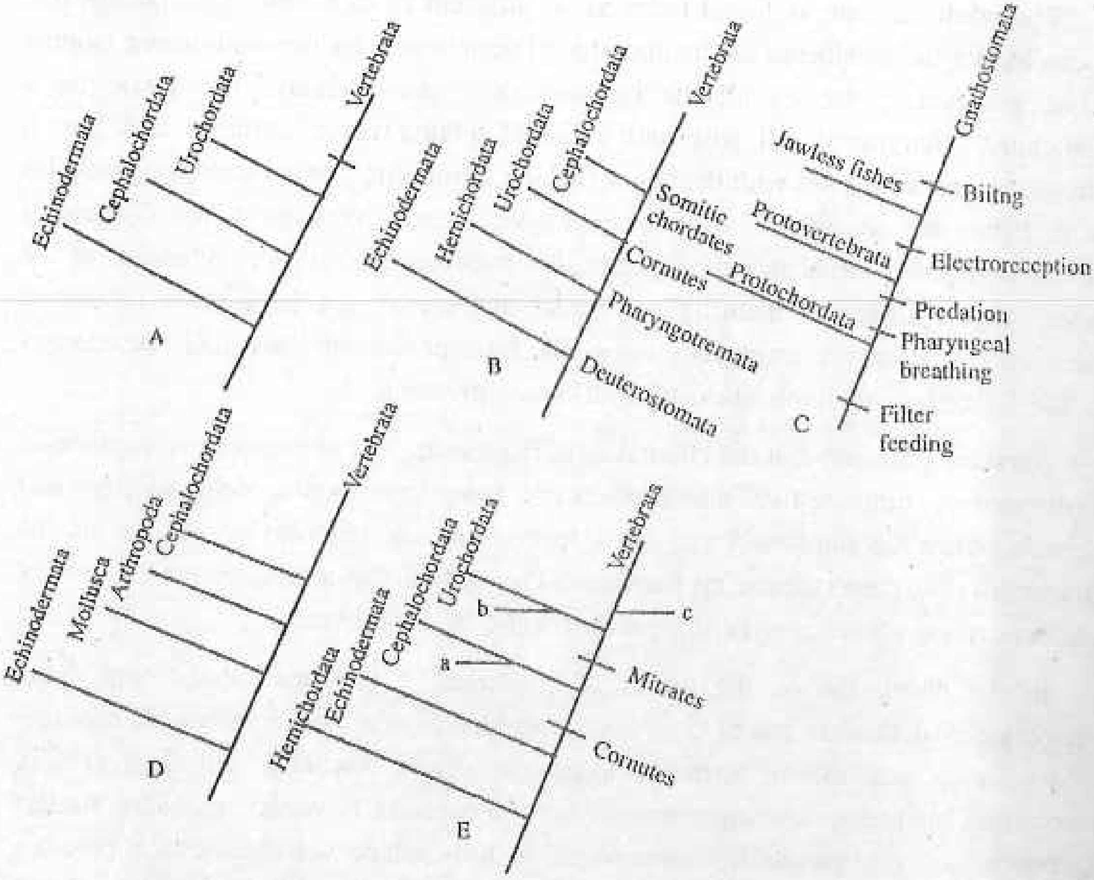


Chart 3.1 : Suggested phylogenetic relationship of vertebrates to other taxa : A. Garstang's theory on the origin of vertebrates by paedomorphosis; B. Schaeffer's hypothesis relates chordates as the sister group of vertebrates; C. Northcutt and Gans' proposal is based on some important functional chatracteristics 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, Etasmobranchiomorphi 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.

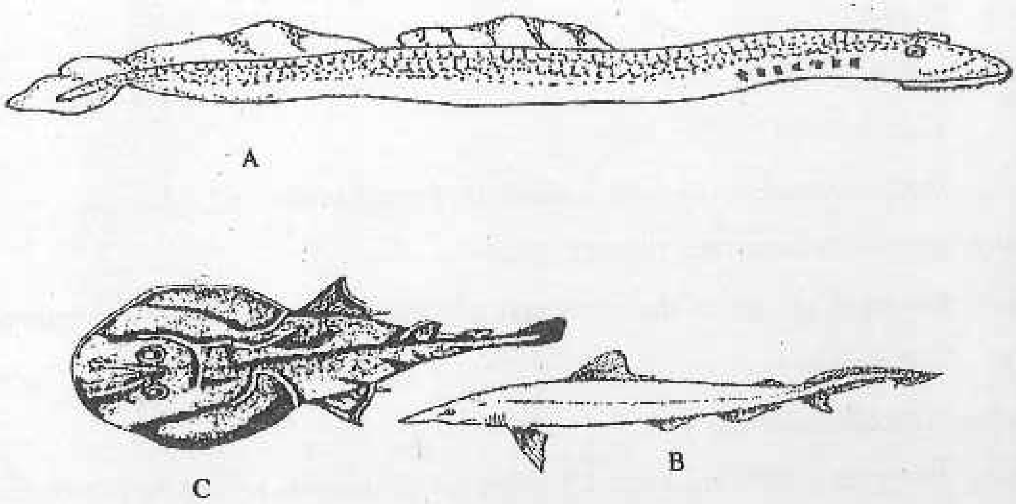


Fig 3.2 : A, *Petromyzon* (Lamprey); B, *Scoliodon* (Dogfish); C, *Narcine* (Torpedo ray).

(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).

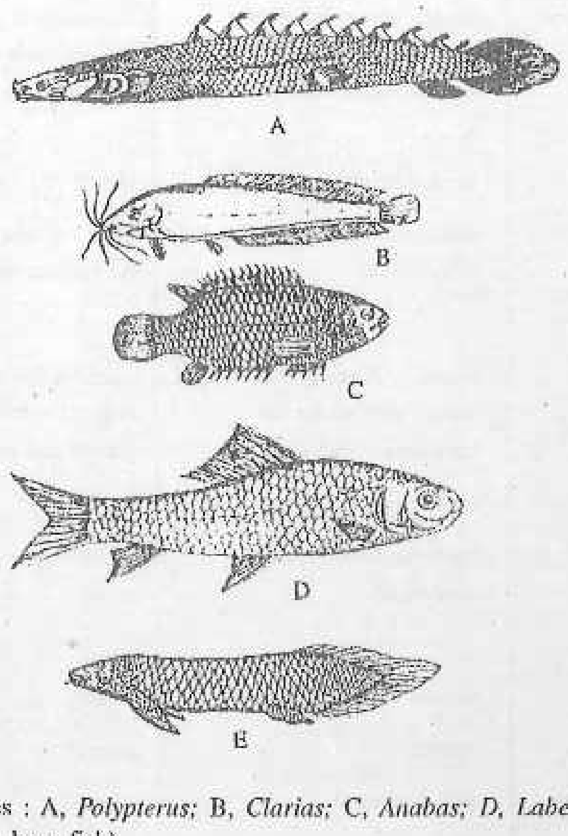


Fig. 3.3 : Bony fishes : A, *Polypterus;* B, *Clarias;* C, *Anabas;* D, *Labeo rohita;* E, *Neoceratodus* (Australian lung fish)

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 caeca	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.*

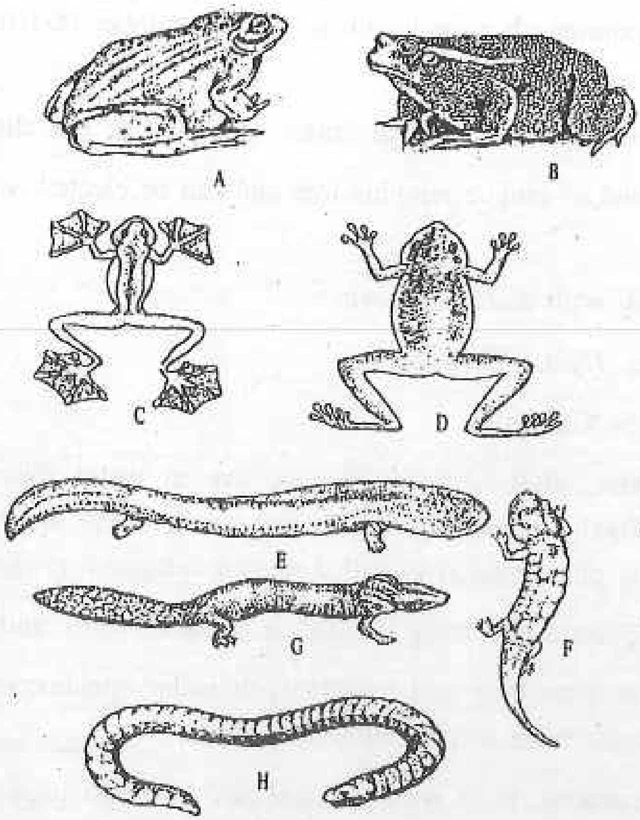


Fig 3.4 : Amphibia : A, *Rana* sp. (Frog); B, *Bufo* sp. (Toad); C, *Rhacophorus* sp. (Tree frog); D, *Hyla* sp. (Tree frog); E, *Megalobatrachus* sp., F, *Salamandra* sp. (Salamander); G, Necturus sp., H, *Ichthyophis* sp.

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.

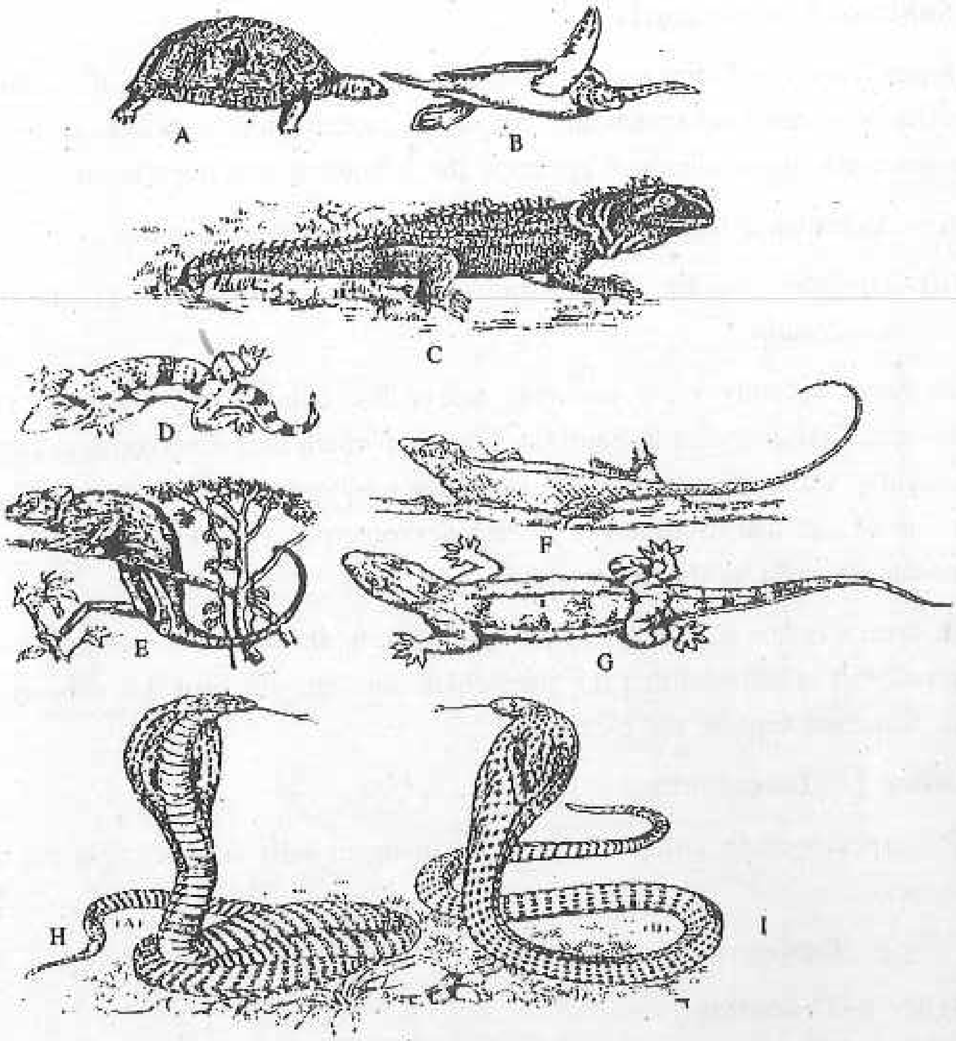


Fig 3.5 : Reptilia : A, *Testudo;* B, *Chelone;* C, *Sphenodon;* D, *Gecko;* E, *Chamaeleon;* F, *Calotes;* G, *Hemidactylus;* H, *Naja naja* showing ventral scales; I, *Naja naja* : dorsal surface of hood showing binocellate spot.

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.*

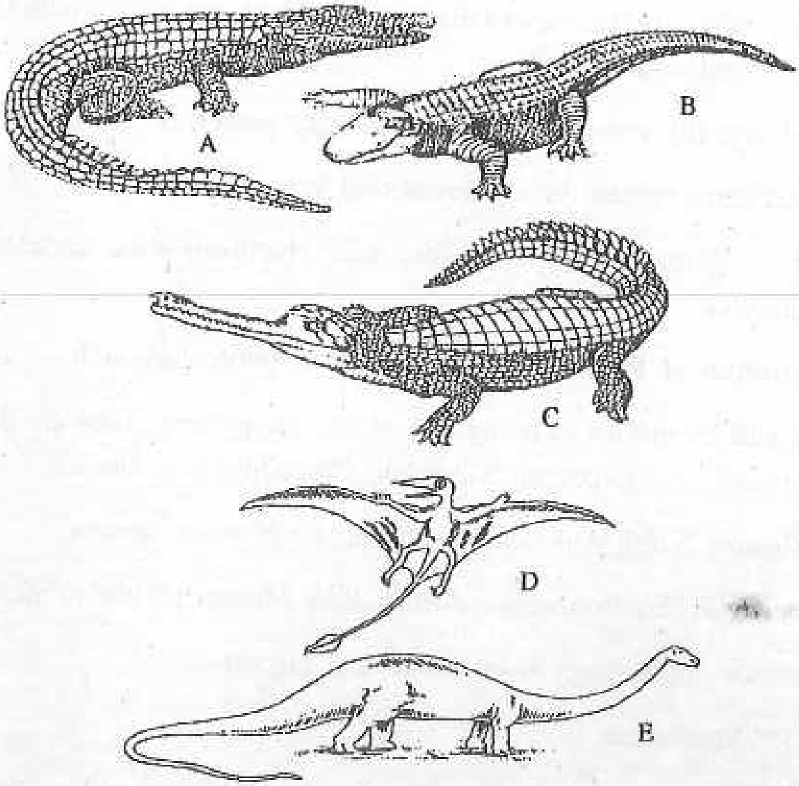


Fig 3.6 : Reptilia (contd.) : A, *Crocodylus;* B, *Alligator;* C, *Gavialis;* D, *Rhamphorhynchus;* E, *Diplodocus.*

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

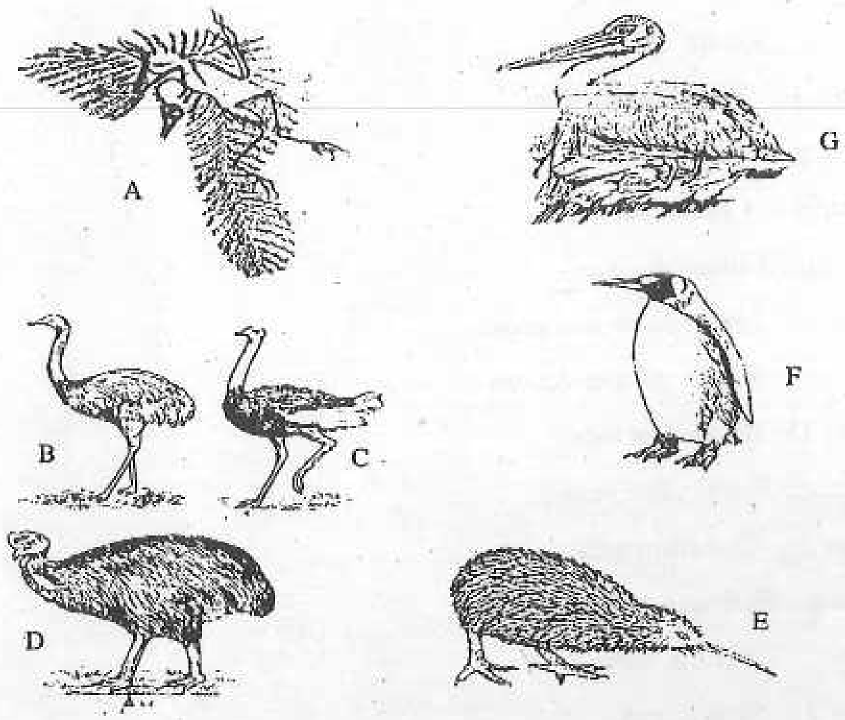


Fig 3.7 : Aves : A, Fossil of *Archaeopteryx* (inpression of skeleton and feathers; B - E (ratite birds); B, Rhea; C, Ostrich; D, *Casuarius;* E, *Apteryx* (kiwi); F, *Aptenodytes* (Penguin); G, Pelecanus (Pelican).

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. **Pteroclidiformes**

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*

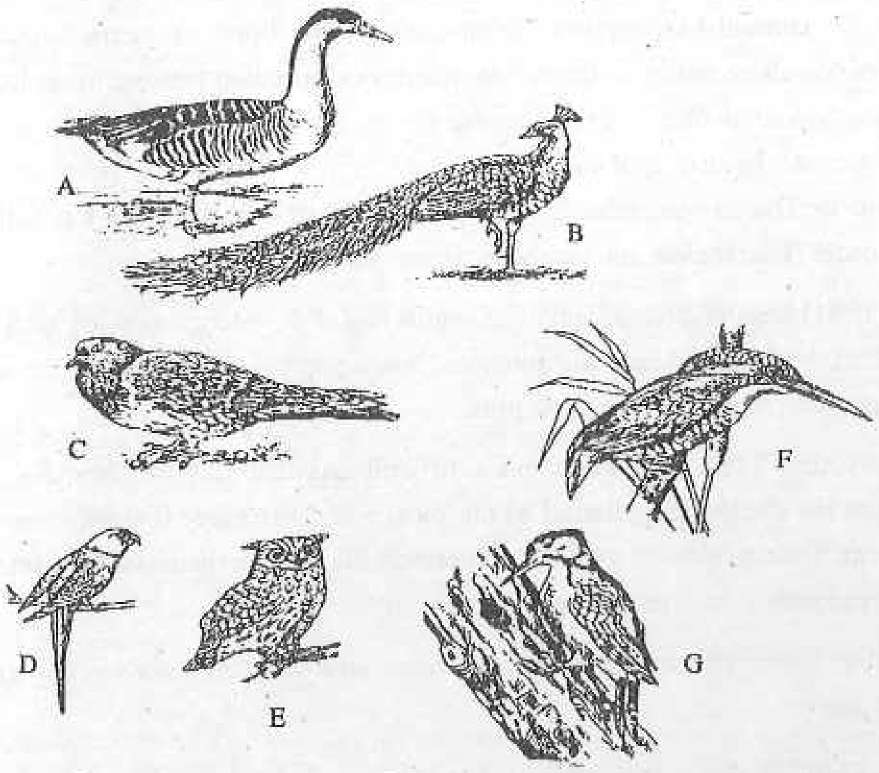


Fig 3.8 : Aves (contd.) : A, *Anser anser* (Greylag Goose); B, *Pavo cristatus* (Peacock); C, *Columba* sp. (Pigeon); D, *Psittacula* krameri (Roseringed Parakeet); E, *Bubosp.* (Brown fish owl); F, *Alcedo* sp. (common blue kingfisher); d, *Picoides* sp. (woodpeeker).

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).*

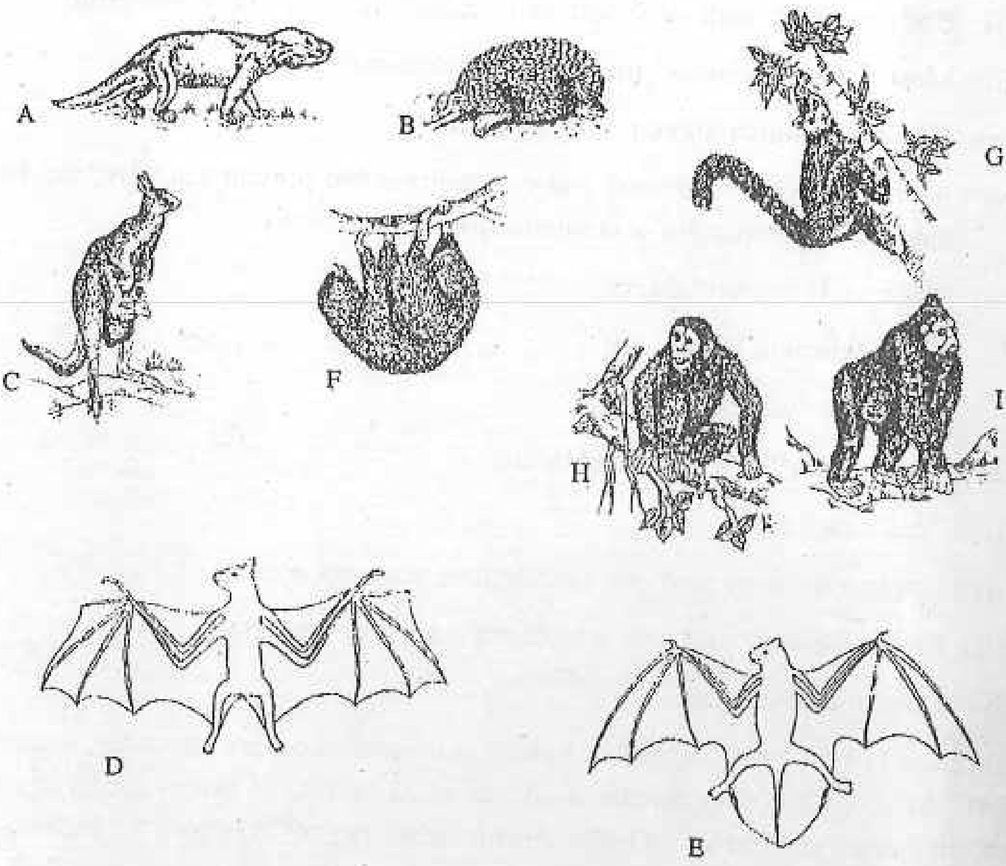


Fig 3.9 : Mammalia : A, *Cynognathus* (Mammal-like reptile); B, *Tachyglostus* (spiny anteater); C, *Macropus* (Kangaroo); D, *Pteropus* sp. (Megachiroptera); E, *Vespertilio* sp. (Microchiroptera); F, *Bradypus* sp. (Sloth); G, *Lemur* sp.; H, *Pan* sp. (Chimpanzee); I, *Gorilla* sp.

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 (I.e., 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).*

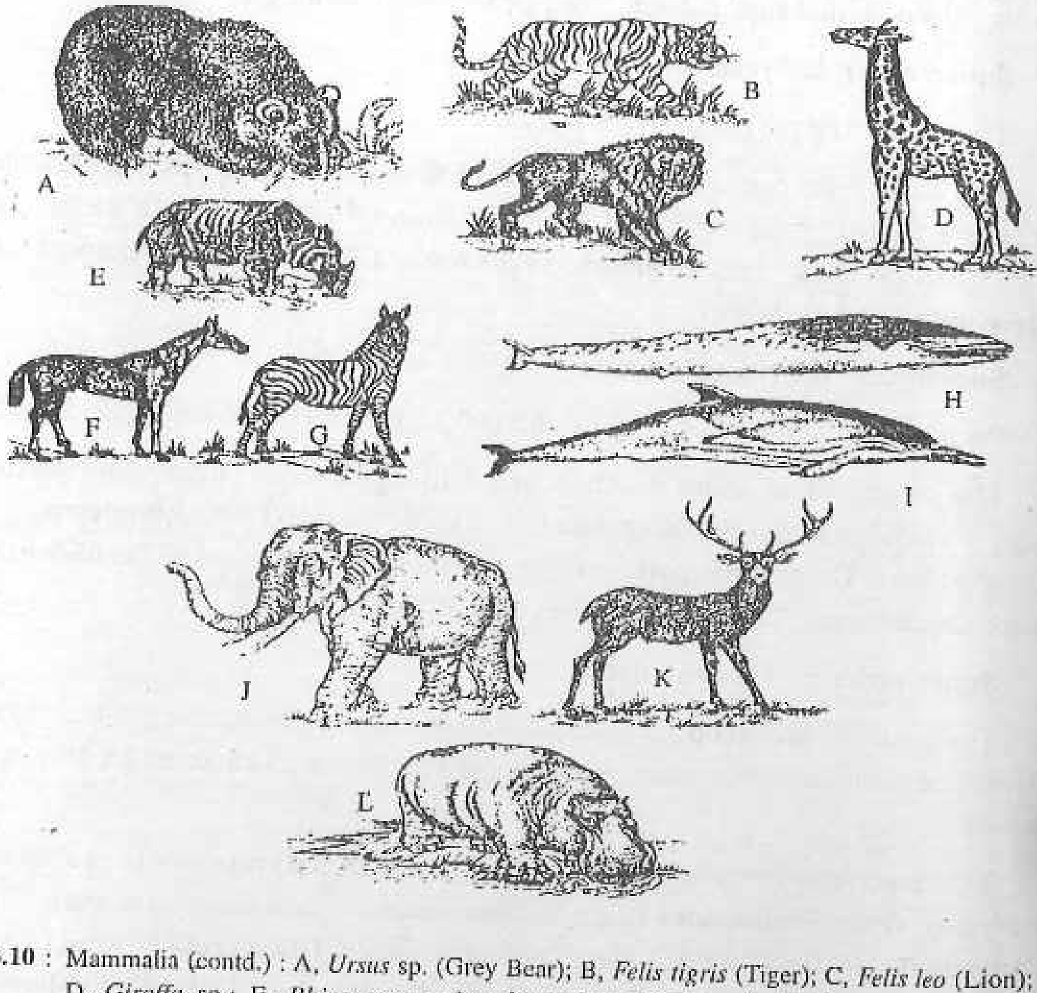


Fig 3.10 : Mammalia (contd.) : A, *Ursus* sp. (Grey Bear); B, *Felis tigris* (Tiger); C, *Felis leo* (Lion); D, *Giraffa* sp.; E, *Rhinoceros unicornis* (Indian rhinderos); F, *Equus* sp. (Horse); G, *Equus* sp. (zebra); H, *Balaenoptera* sp. (Blue Whale); I, *Delphinus* sp. (Dolphin); J, *Elephas* sp. (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.

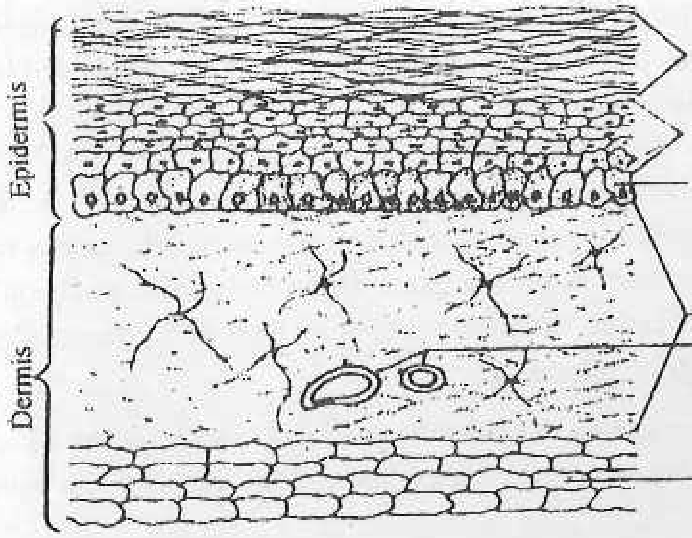


Fig 4.1 : A generalized cross-sectional part of the skin of a tetrapod

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.

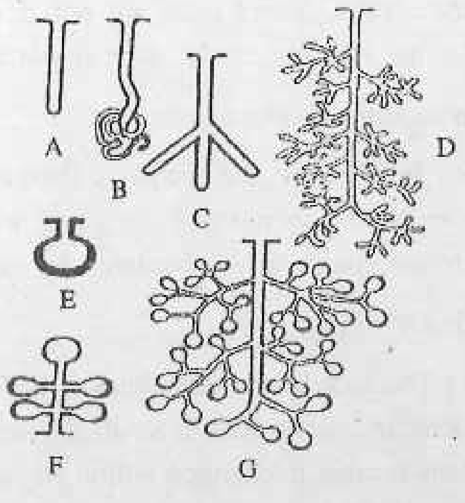


Fig 4.2 : Types of epidermal glands in vertebrates :A, Simple tubular gland; B, Simple coiled tubular gland; C, Simple branched tubular gland; D, Compound tubular gland; E, Simple alveolar (saccular) gland; F, Simple branched alveolar gland; G, Compound aloveolar gland. (Based on Weichert and Presch,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

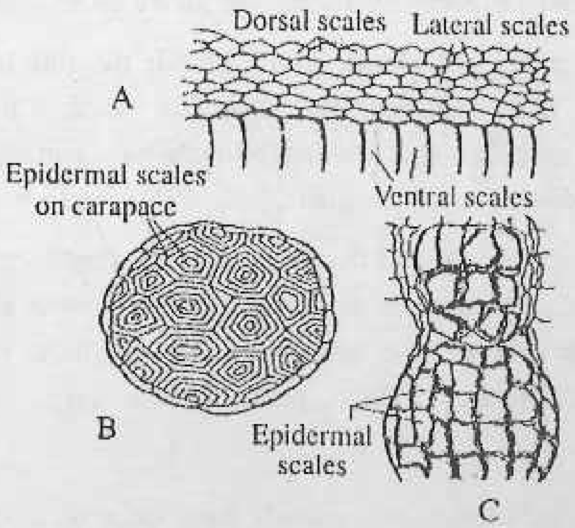


Fig 4.3 : Epidermal scales in reptiles: A, Dorsal, lateral and ventralscales of a snake: B, Epidermal scales on the carapace of a tortoise; C, Dorsal epidermal scales of a crocodile.

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.

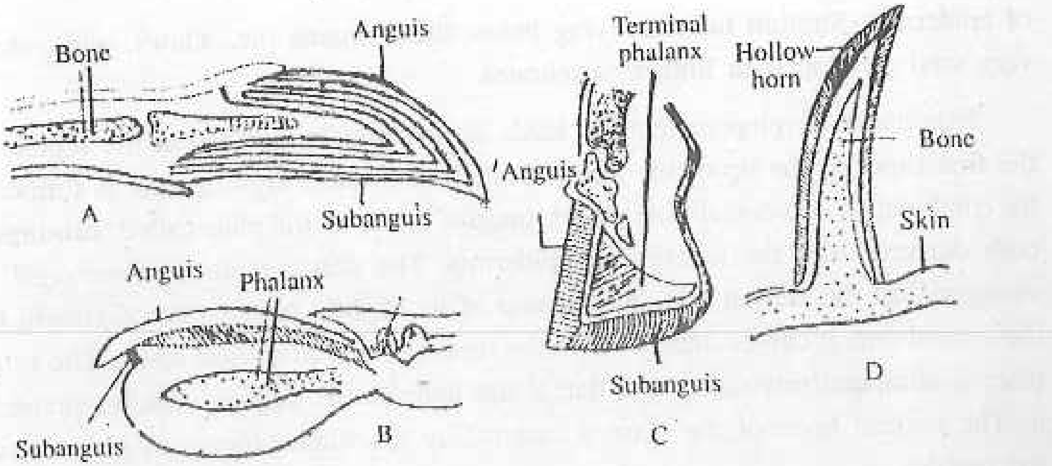


Fig 4.4 : Development of various epidennal structures : A, Claw of a reptile; B, Nail of a mammal; C, Hoof in the foot of a horse; D, A hollow horn.

(iii) **Prong-horns :** This characteristic horn is possessed only by the North American Antelopes *(Antilocapra* sp.). Here also the keratiu 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.

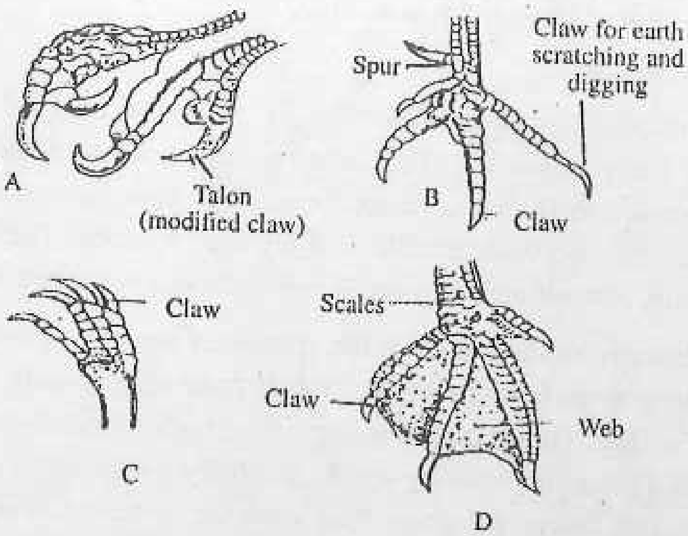


Fig 4.5 : Different types of claws in birds : A, Sharp, curved talon in an osprey (Falconiformes); B, Claw in Jumgle fowl for digging and scratching earth; C, Claws in a swift for climbing vertical wall; D, Web of a duck for swimming.

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.).

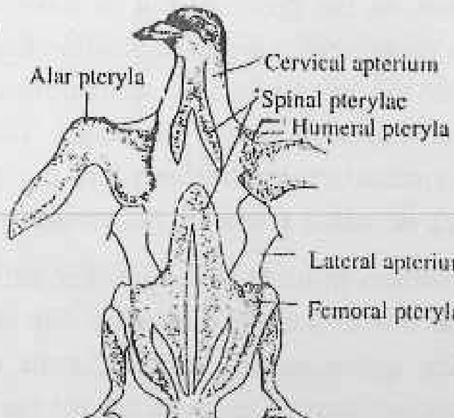


Fig 4.6 : Pterylosis in a bird.

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.

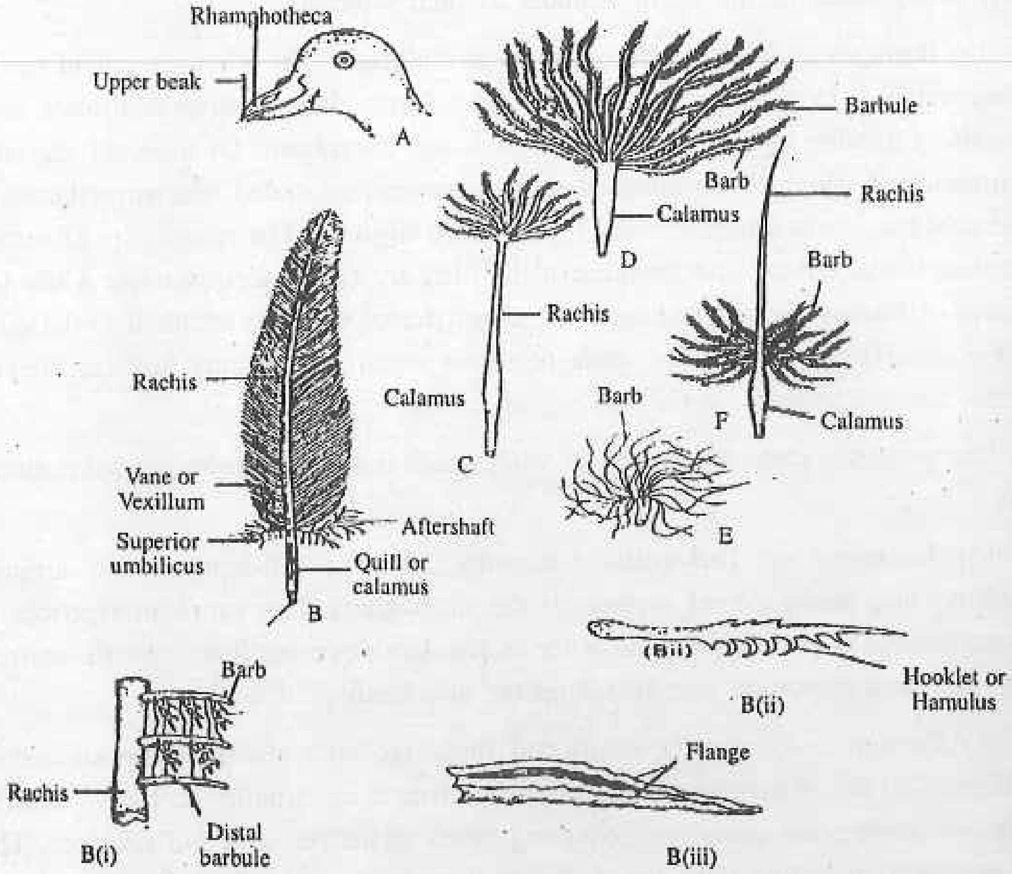


Fig 4.7 : A, Rhamphotheca on the upper beak of a pigeon; B-F, Different parts of a generalized feather; B, A contaur feather; C, A filoplume; D, A down feather; E, A powder down; F, A bristle.

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.

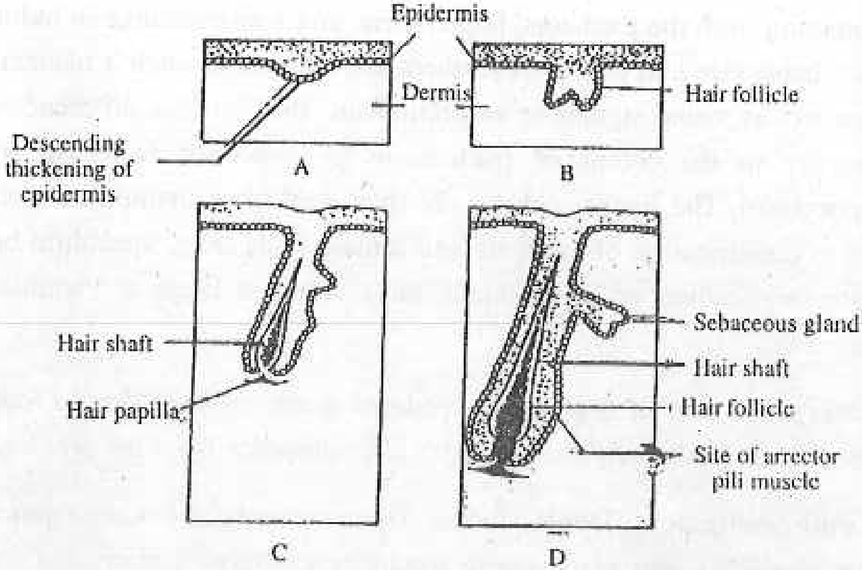


Fig 4.8 : Stages in the development of a hair.

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.

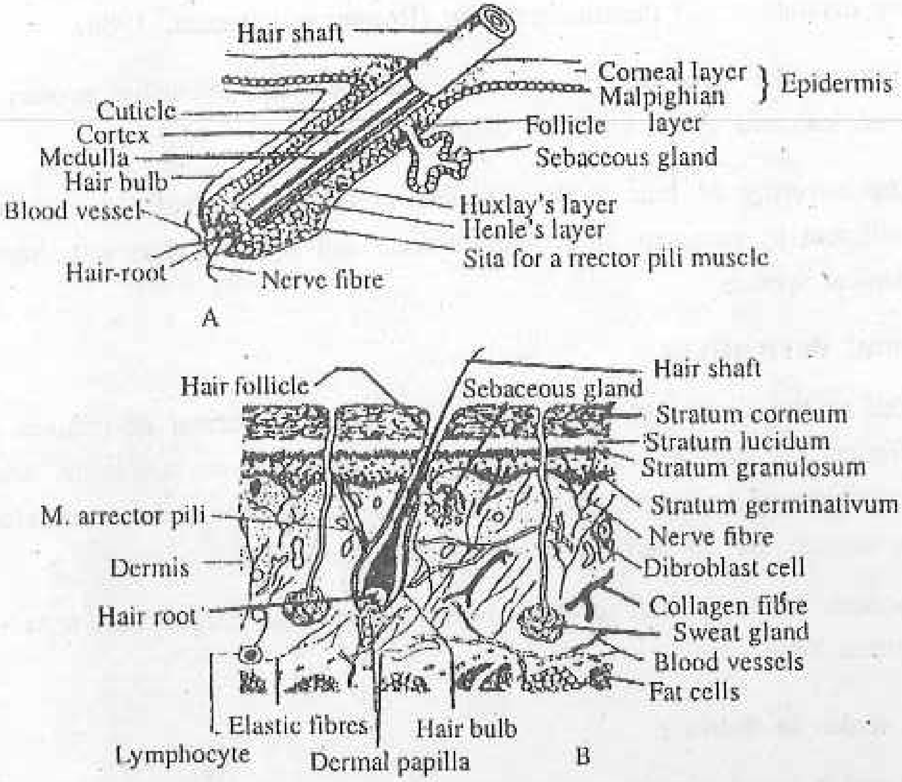


Fig 4.9 : A. Internal structure of a hair with folhicle and gland; B, Sectinal view of the skin of a mammal showing hair, gland and other internal structures.

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.

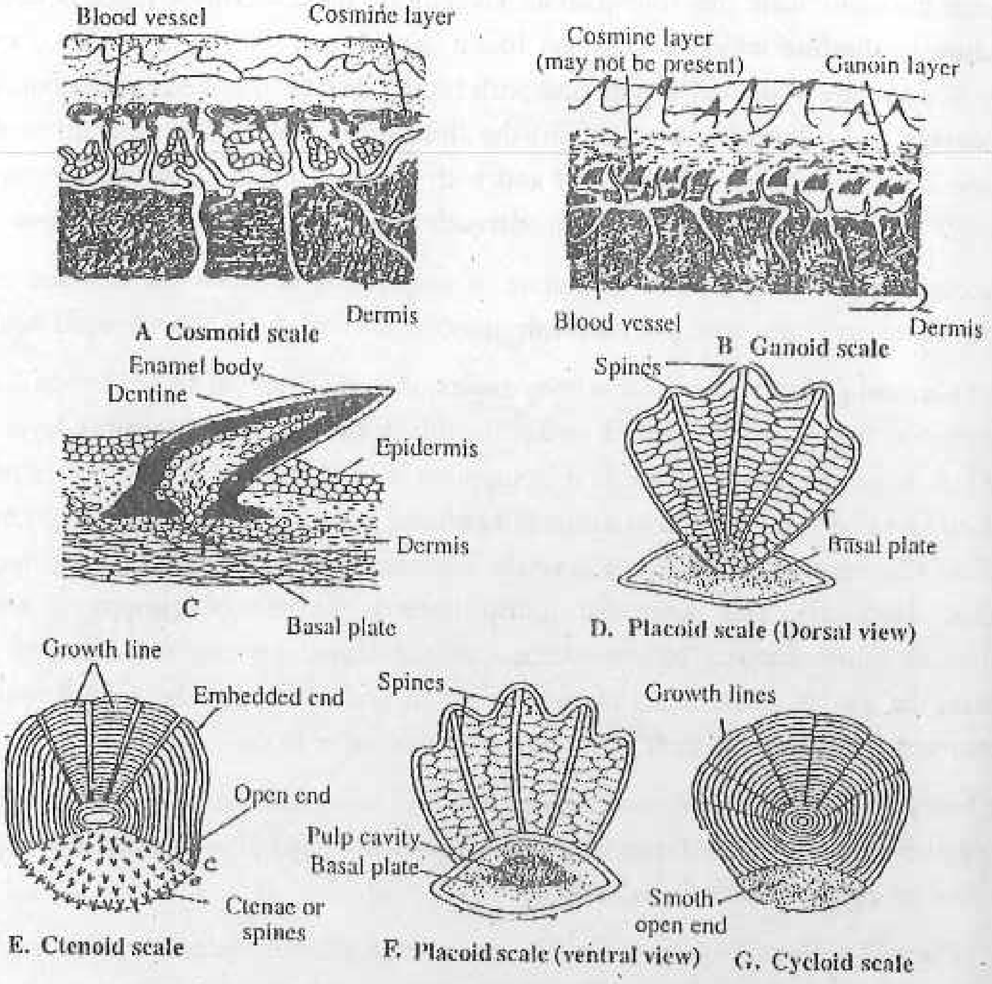


Fig 4.10 : Development and structure of scales in different types of fishes : A, cosmoid scale; B, Ganoid scale; C, Development of placoid scale; D, Placoid scale (dorsal view); E, ctenoid scale; F, Placoid scale (ventral view); G, Cycloid scale.

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.

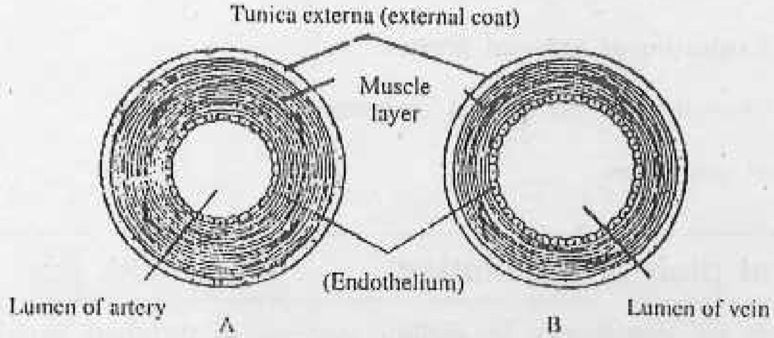


Fig 5.1 : Cross-sectional view of an artery and a vein of *Bufo* sp., A, artery; E, Vein.

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.

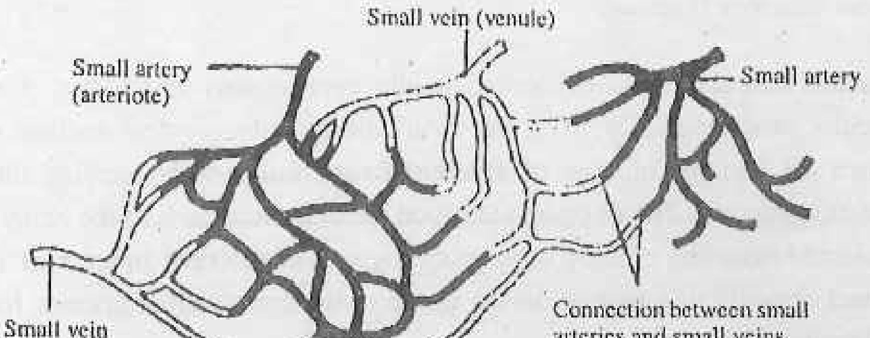


Fig 5.2 : Diagrammatic view showing connections between arterioles and veinules.

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.

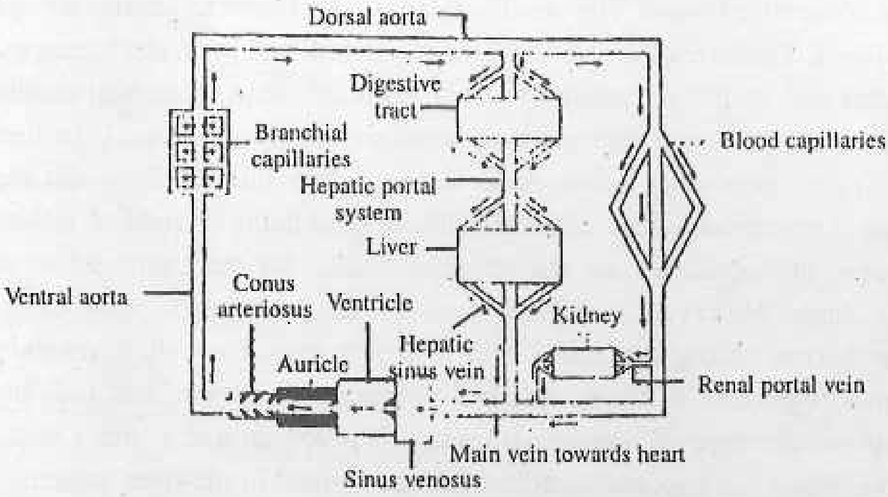


Fig 5.3 : Schematic diagram showing single-circuit pathway of blood circulation in cyclostomes and fishes (except in dipnoans).

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

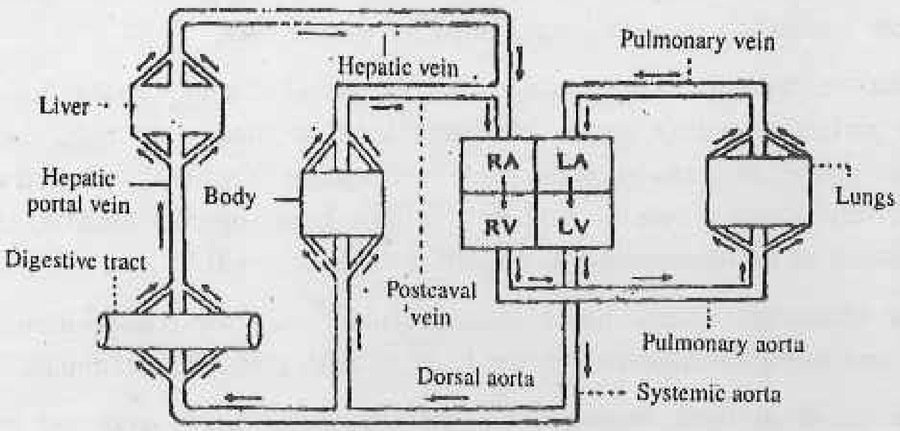


Fig 5.4 : Schematic diagram showing double-circuit pathway of blood circulation in *Columba* sp.

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.

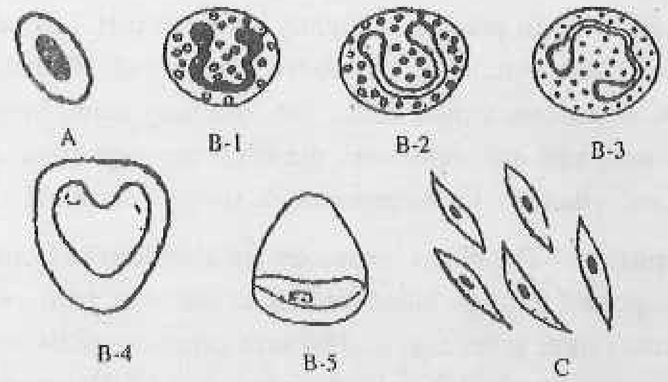


Fig 5.5 : Different types of blood corpuscles; A, Erthrocyte (RBC); B-1—B-5, Leucocytes; B1, Basophil; B2, Eosinophil; B3, Neutrophil; B4, Monocyte; BS, Lymphocyte; C, Thrombocytes.

(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.

$$\text{Prothrombin} \xrightarrow{\text{Thromboplastin} + Ca^{++}} \text{Thrombin}$$

$$+$$

$$\text{Fibrinogen}$$

$$\downarrow$$

$$\text{Fibrin}$$

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.

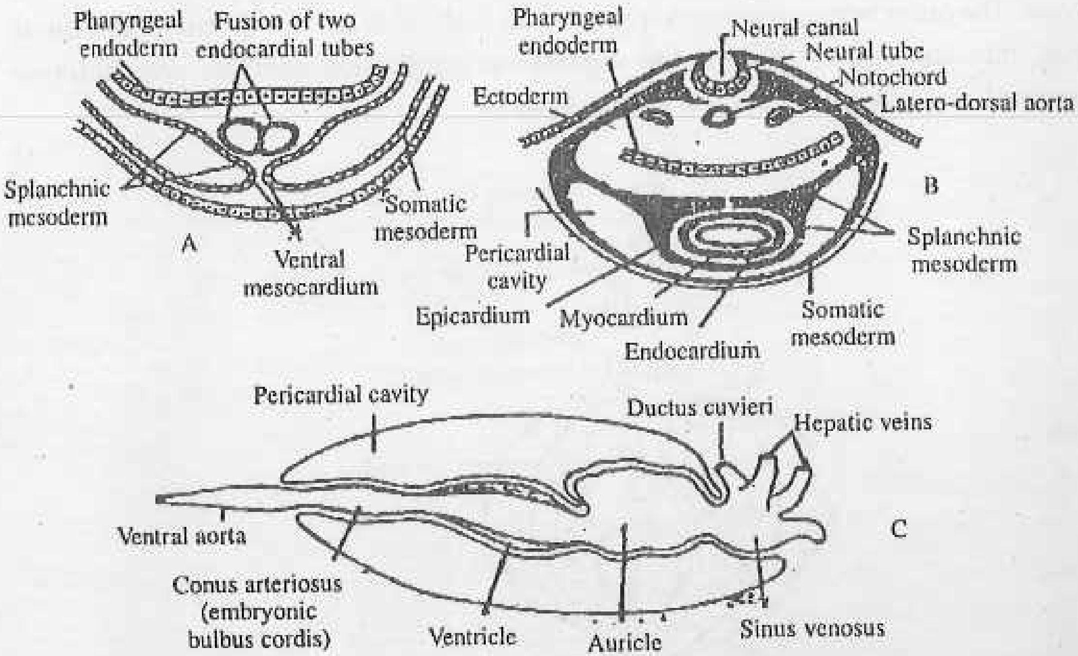


Fig 5.6 : Development of heart in a vertabrate; A, Fusion of two endocardial tubes developed from the heart-forming cells; B, Three layers of the heart developed from splanchnic mesoderm; C, Ventral aorta and location of primitive chambers of the heart.

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.

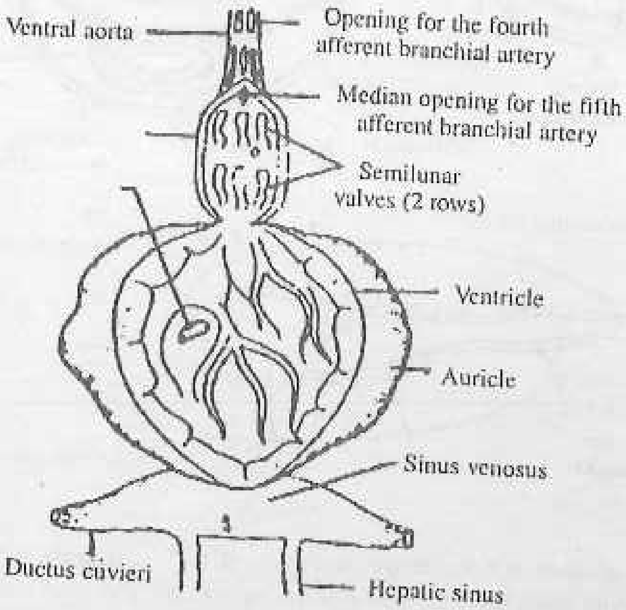


Fig 5.7 : Heart of a cartilagenous fish.

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.

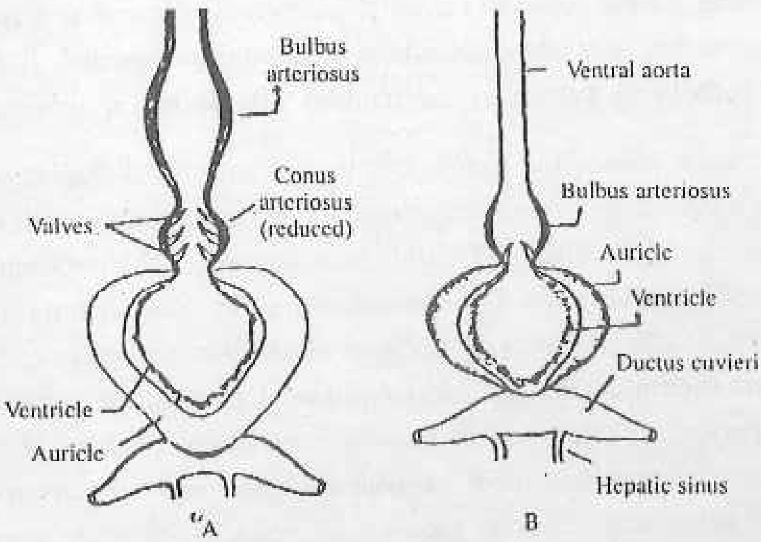


Fig 5.8 : Heart in bony fishes; A, Reduced conus arteriosus in *Amia* (Holostei); B, Heart in a teleostean fish.

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.

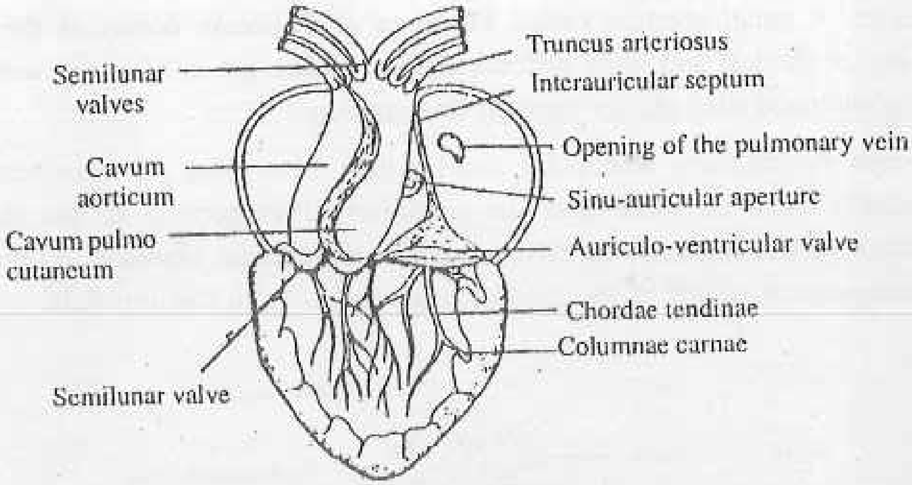


Fig 5.9 : Internal structures of the heart of an amphibian.

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.

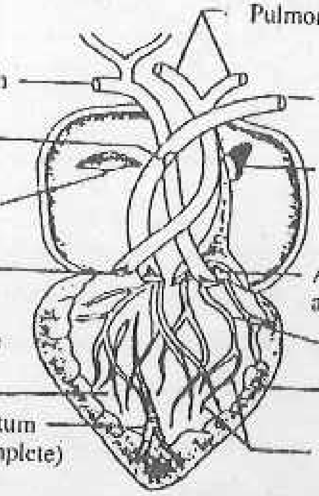


Fig 5.10 : Internal structures of the heart of a reptile *(Calotes)*.

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.

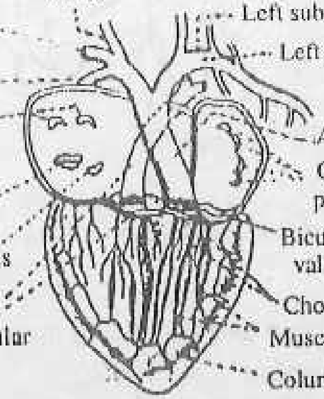


Fig 5.11 : Class Aves : Internal structures of the heart of a pigeon.

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.

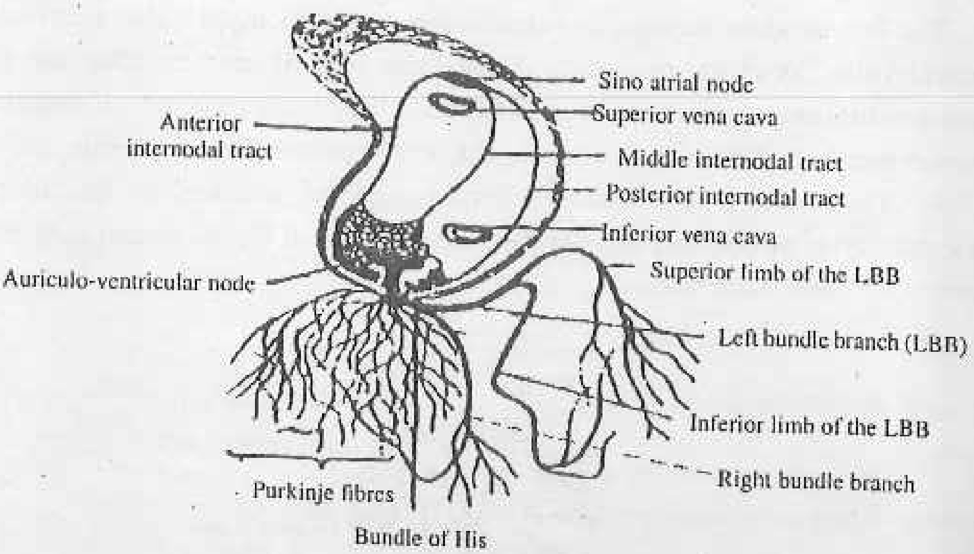


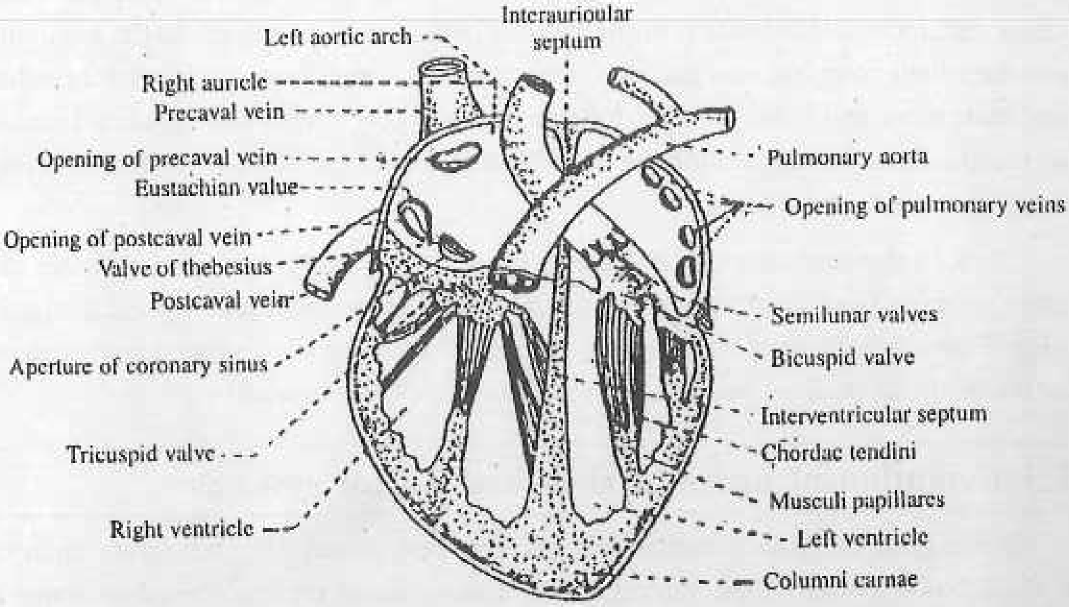
Fig 5.12 : Special junctional tissues (Pacemaker) in the heart of a mammal.

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.

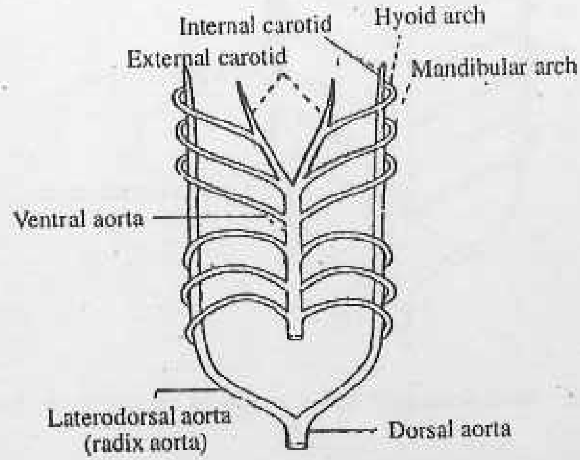


Fig 5.14 : Primitive aortic arches in a vertebrate embryo

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.

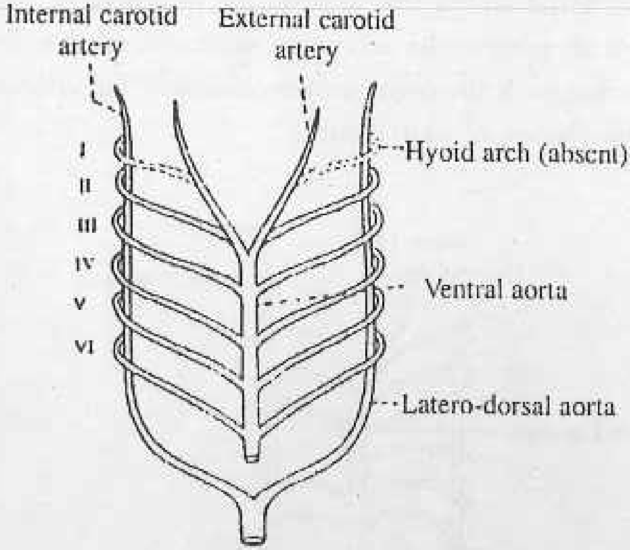


Fig 5.15 : Modification of aortic arches in cartilagenous fishes

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.

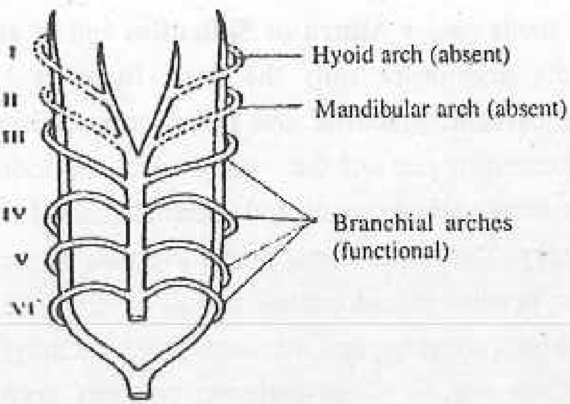


Fig 5.16 : Modification of aortic arches in bony fishes

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.

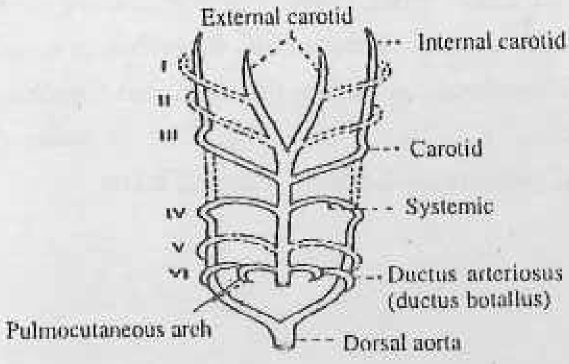


Fig 5.17 : Modification of aortic arches in Urodela (class Amphibia)

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.

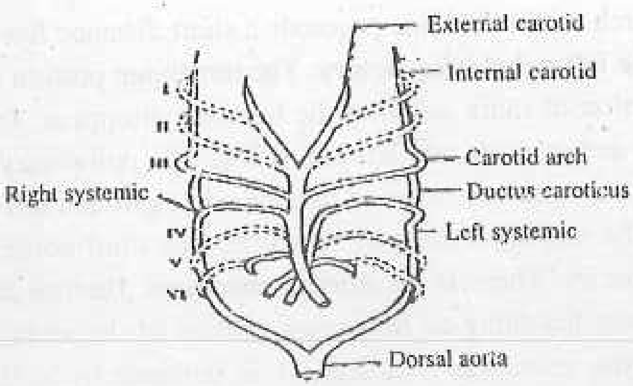


Fig 5.18 : Modification of aortic arches in *Calotes* sp. (class Reptilia)

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**.

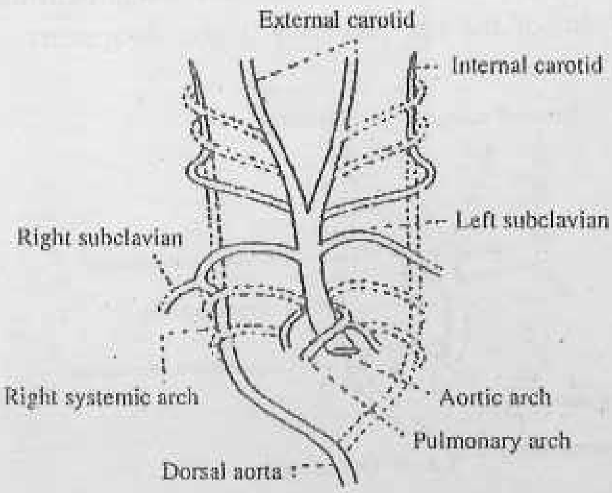


Fig. 5.19 : Modification of aortic arches in *Columba* sp. (class Aves)

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.

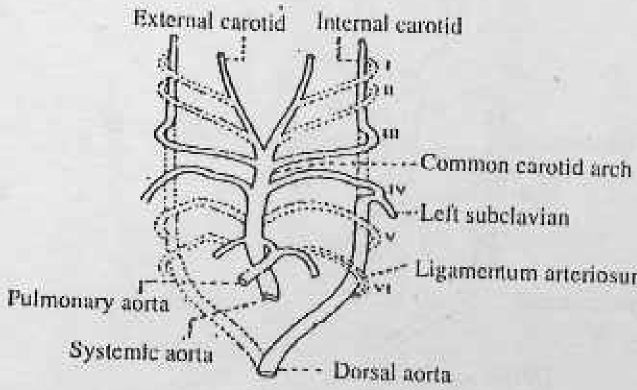


Fig 5.20 : Modification of aortic arches in *Cavia* sp. (class Mammalia)

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.

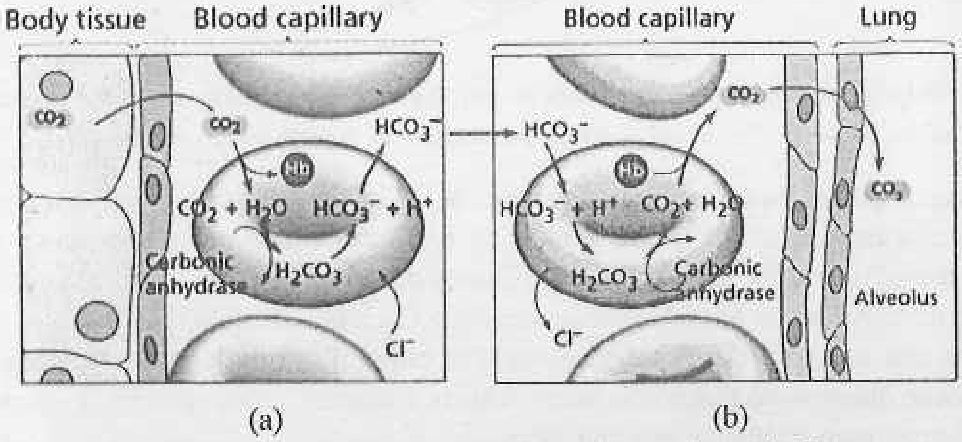


Fig. 6.1 (a, b) : Showing the process of gas exchange in fish.

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.

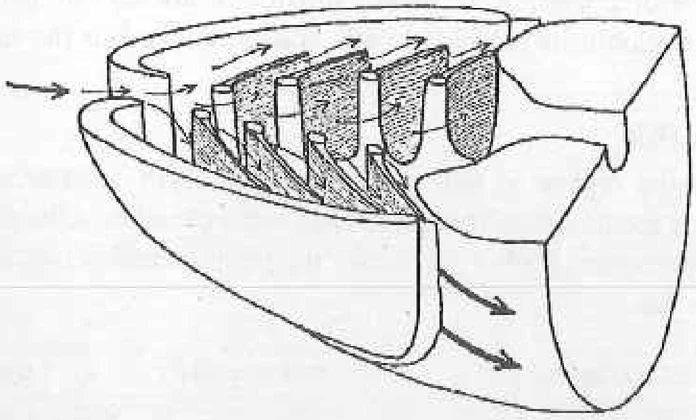


Fig. 6.2 : Diagram showing the arrangement of the gill filaments on a gill arch, and of the secondary lamellae on the filaments. The arrows indicate the direction of flow of water over the gills.

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.

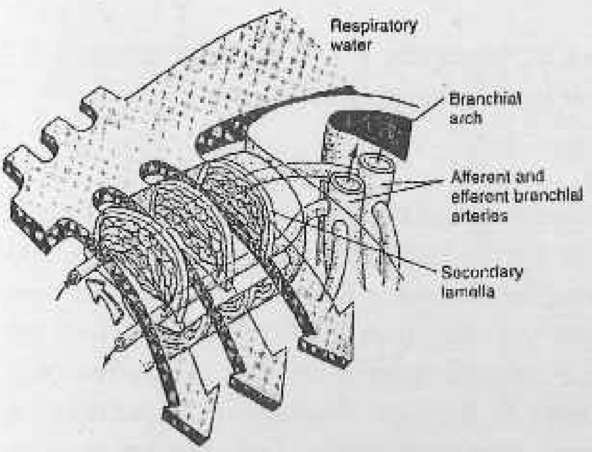


Fig. 6.3 : Gill ventilation in teleost. Water flow is directed across the secondary lamellae opposite to that of blood flowing within each secondary lamella, establishing a counter current exchange between them.

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

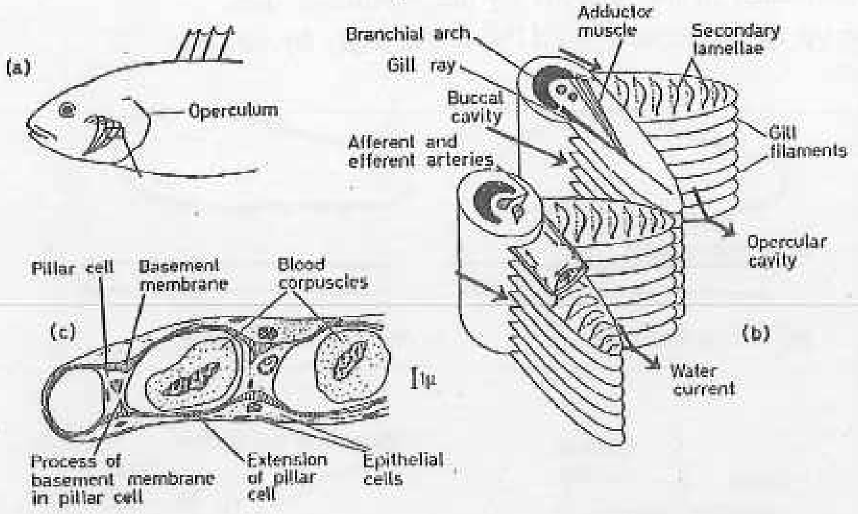


Fig. 6.4 : The gills of teleost fishes. (a) View from left side to show the position of four gill arches beneath the operculum. (b) Filaments and associated structures attached to two neighbouring branchial arches. (c) Section through a secondary lamella, based upon electron micrographs.

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.

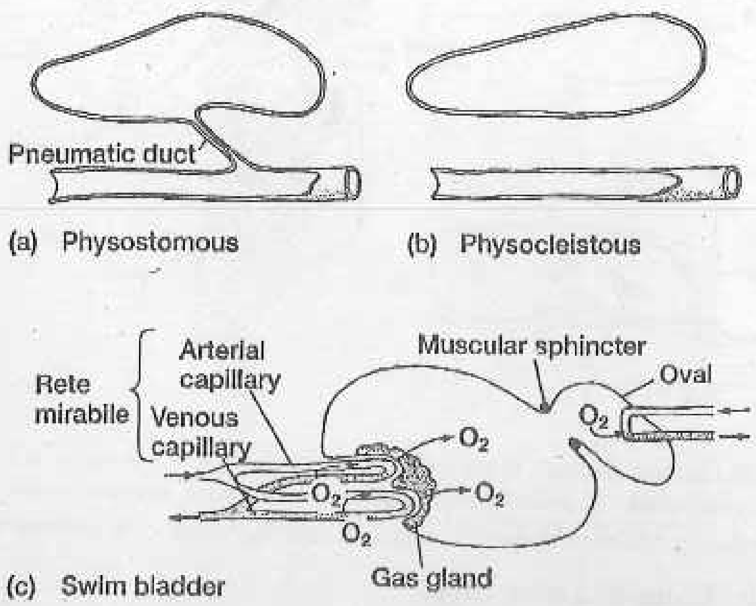


Fig. 6.5 : Swim bladders. (a) Physostomous (pneumatic duct present), and (b) physocleistous (pneumatic duct has been lost). (c) The rete mirabile is a knot of capillaries. As blood leaves the gas gland of the swim bladder via the venous capillaries of the rete, lactic acid is added. This reduces haemoglobin's 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.

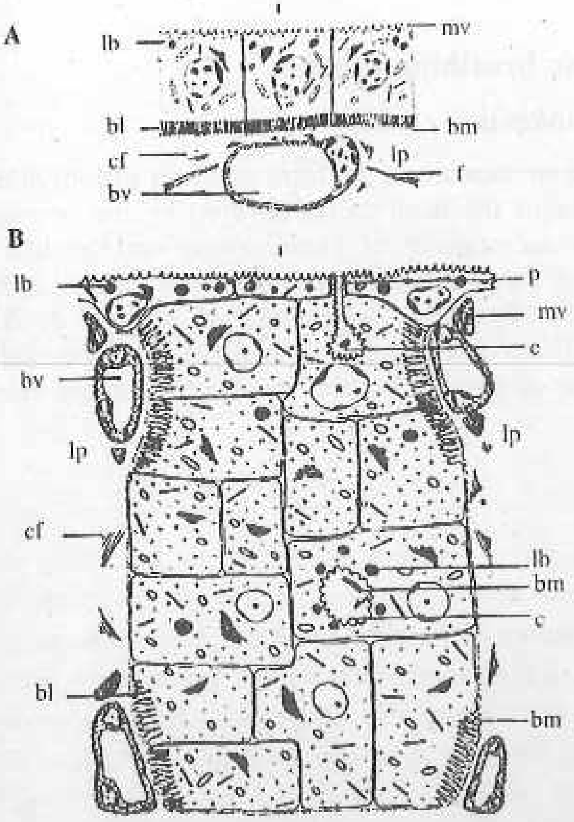


Fig. 6.6 : (A). Swim bladder of the European eel where gas gland cells form a monolayer over the secretory part of the swim bladder epithelium. The gas gland cells show a clear polarity with a remarkable basal labyrinth (bl) and lamellar bodies (lb). At the apical membrane, the cells form small microvilli (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 1^{st}, 2^{nd}, 3^{rd}, and 4^{th} 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

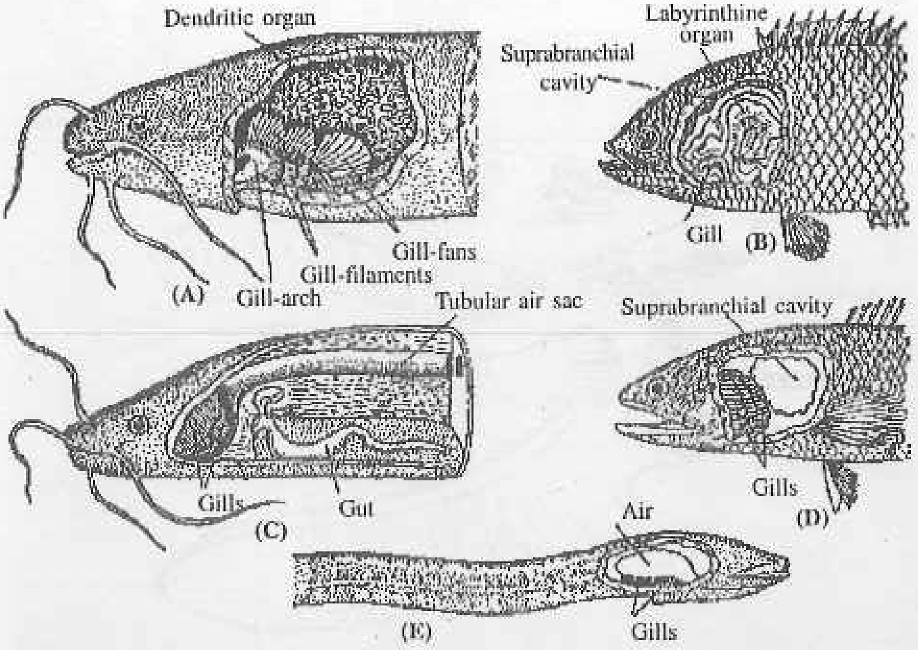


Fig. 6.7 : Accessory respiratory organ of different fishes. (A) *Clarias batracus*; (B) *Anabas testudineus*; (C) *Heteropneustes fossilis* (D) *Channa punctatus*; (E) *Monopterus cuchia*

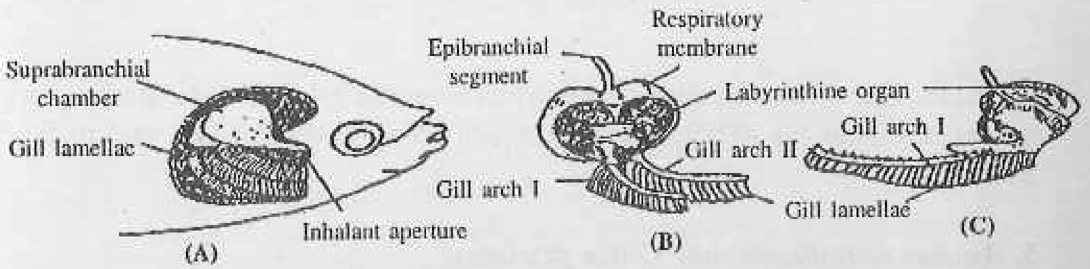


Fig. 6.8 (A-C) : Detail of the suprabranchial chamber and respiratory membrane of a jeol fish

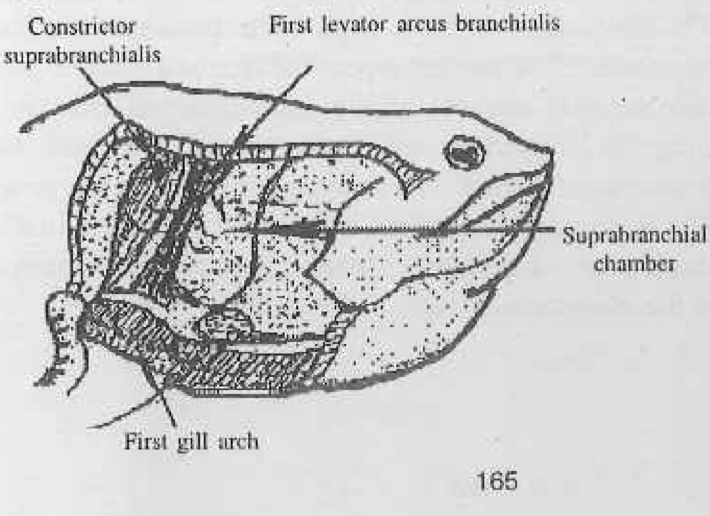


Fig. 6.9 : Lateral view of the head of *Channa punctatus* to show the relation of the supra branchial chamber with the constrictor suprabranchialis, the first levator arcus branchialis

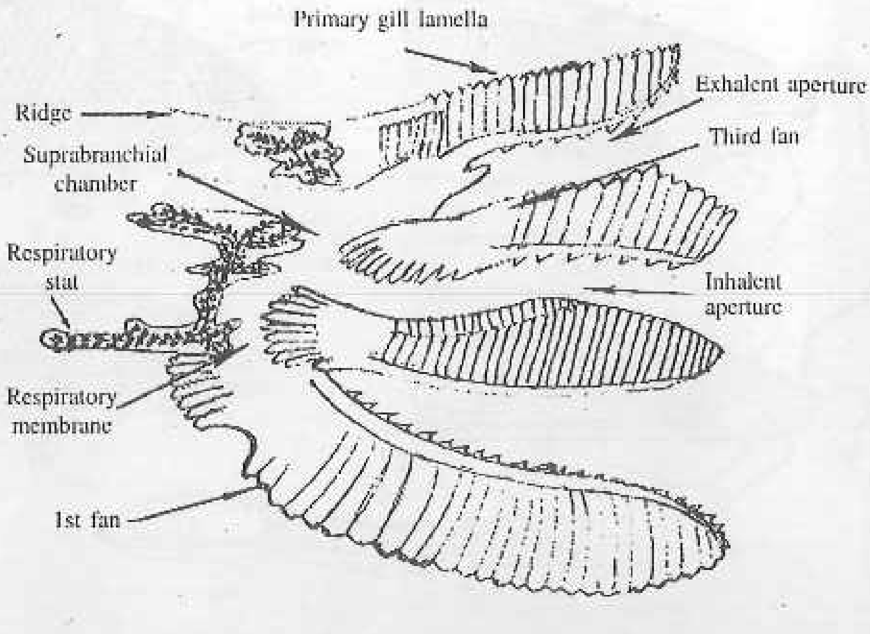


Fig. 6.10 : The respiratory sac opened out by means of mid-ventral incision to show the relation between the 'fans', the inhalant aperture, exhalent aperture, the gill arches, the supra-branchial chamber and the respiratory sac

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.

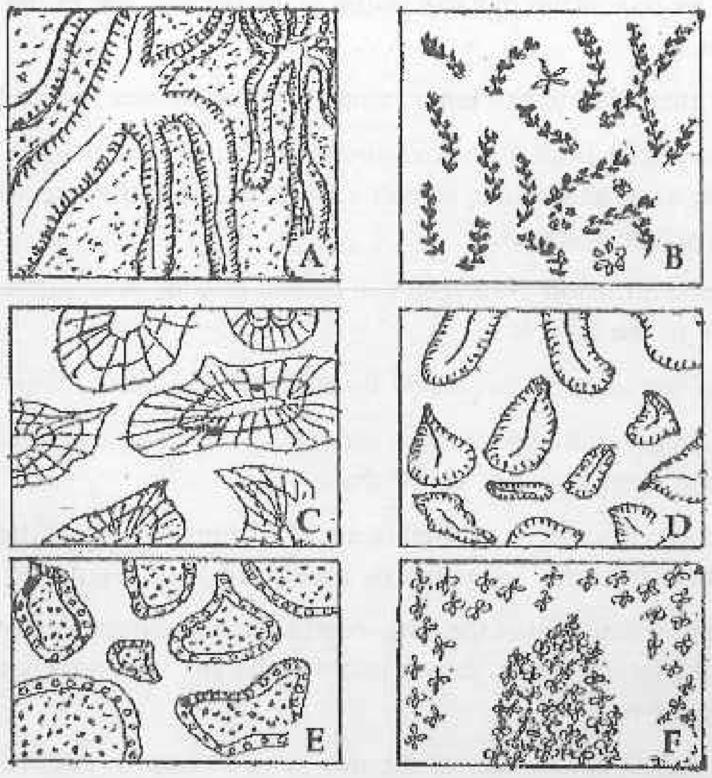


Fig. 6.11 : Respiratory islets of A. *Clarias batrachus;* B. *Heteropneustes fossilis;* C. *Anabas testudineus;* D. *Colisa fasciatus;* E. *Amphipnus cuchia;* F. *Channa punctatus.*

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 wifh 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.

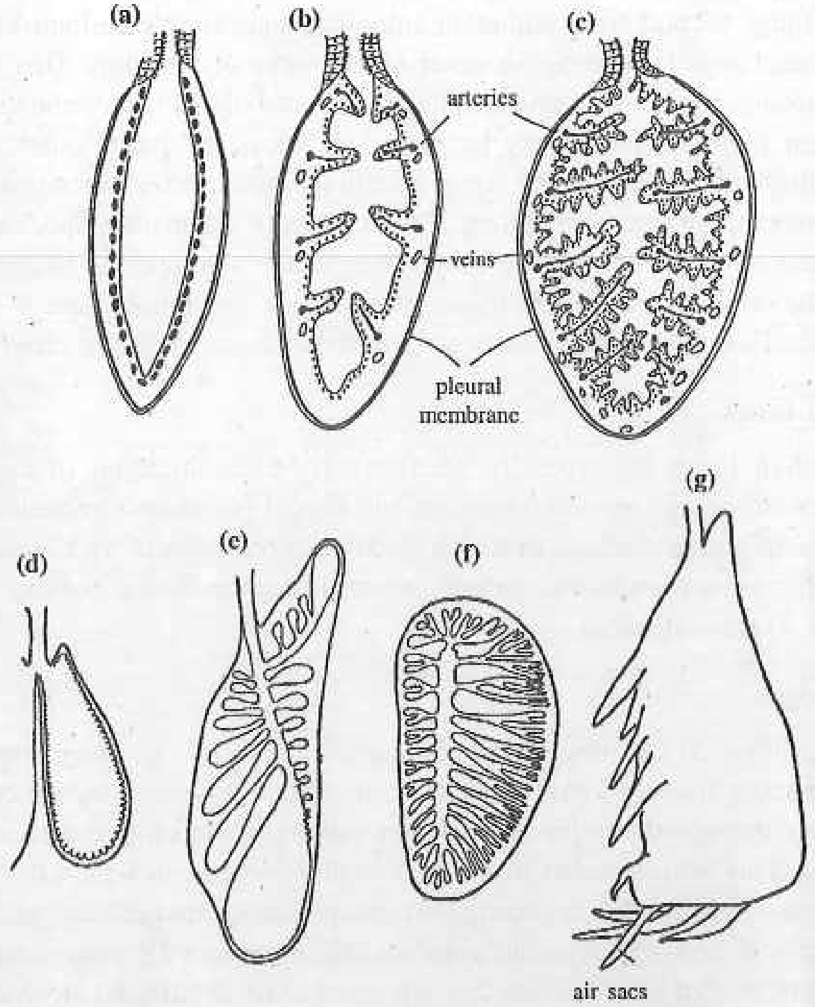


Fig. 6.12 : Diagrams of the lungs of tetrapods to show the increase in the infolding of their surfaces. (a) *Proteus,* (b) *Siren,* (c) *Rana,* (d) *Sphenodon,* (e) *Varanus* (a lizard), (f) *Thassochelys* (a turtle) (g) *Chamaeleo.*

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.

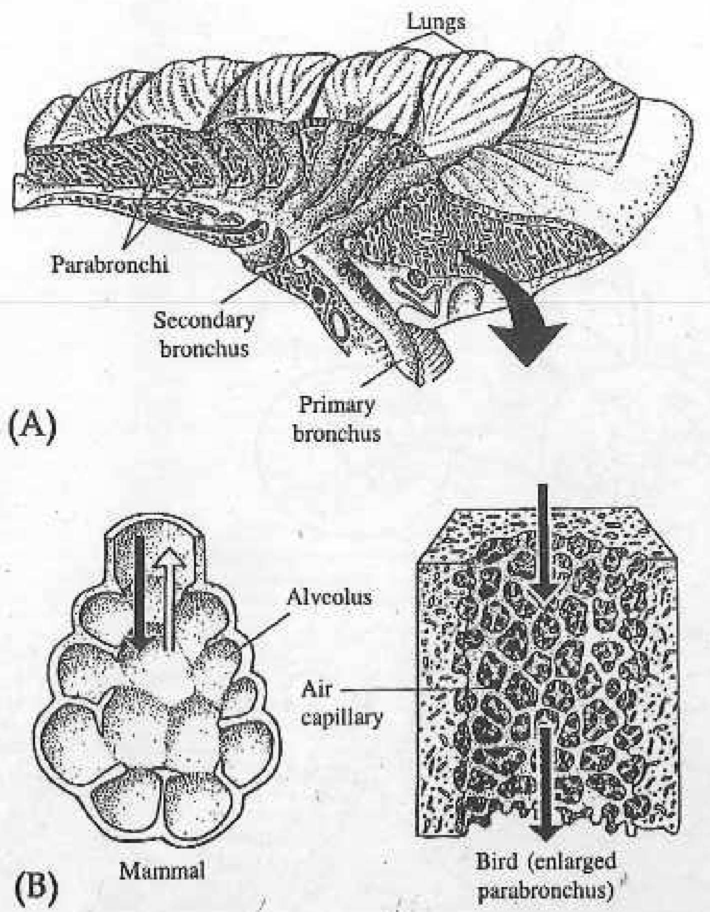


Fig. 6.13 : (A) Isolated avian lung is sectioned. The small pores in the exposed lung are parabronchi. The trachea branches into two primary bronchi (mesobronchi) that extend to the posterior air sacs. These lead to parabronchi that open into the highly subdivided respiratory tissue, the air capillaries. 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.

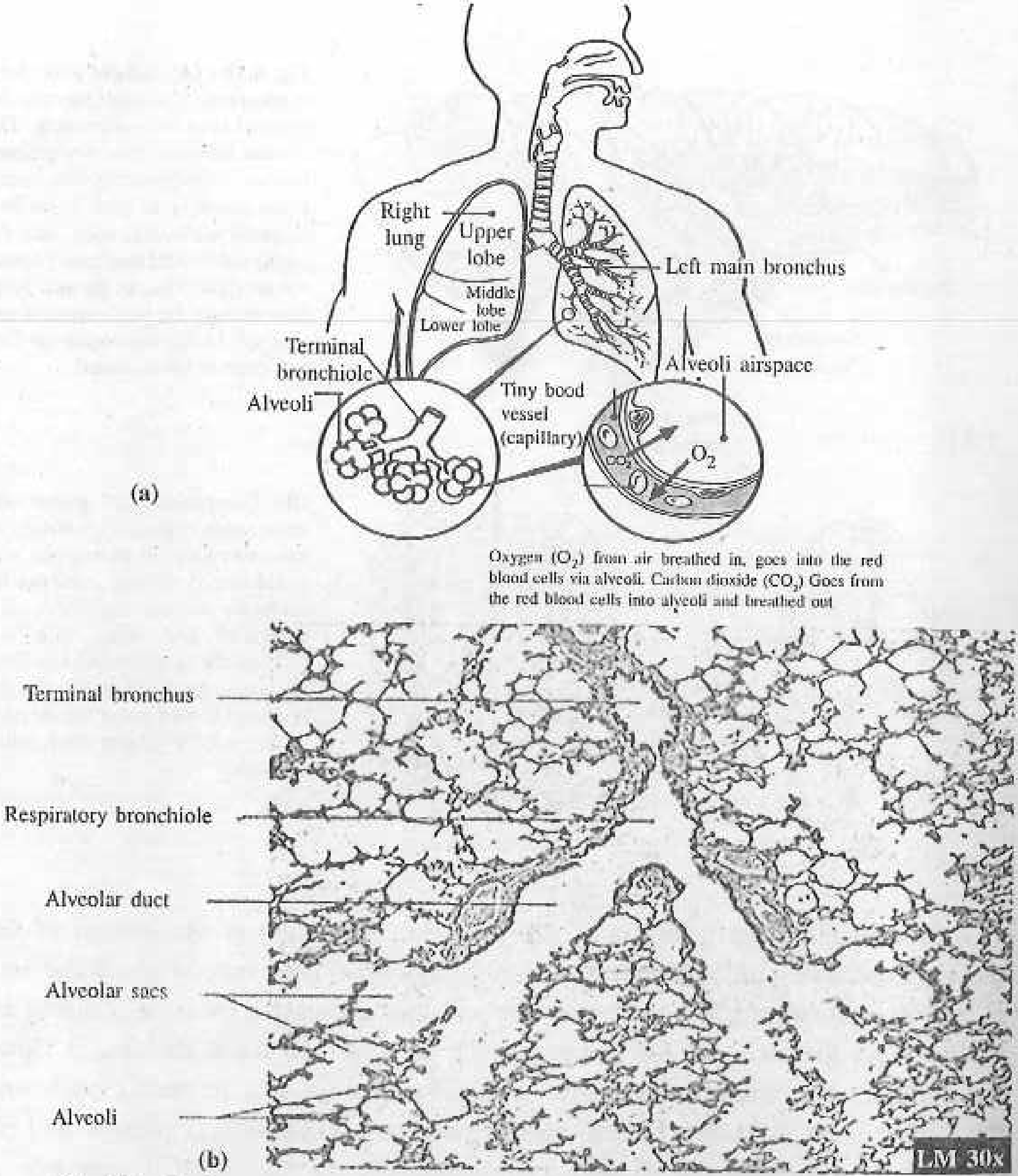


Fig. 6.14 : The lung contains millions of tiny alveoli (a) Lung showing the position of alveoli; (b) Microscopic structure of alveoli.

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).

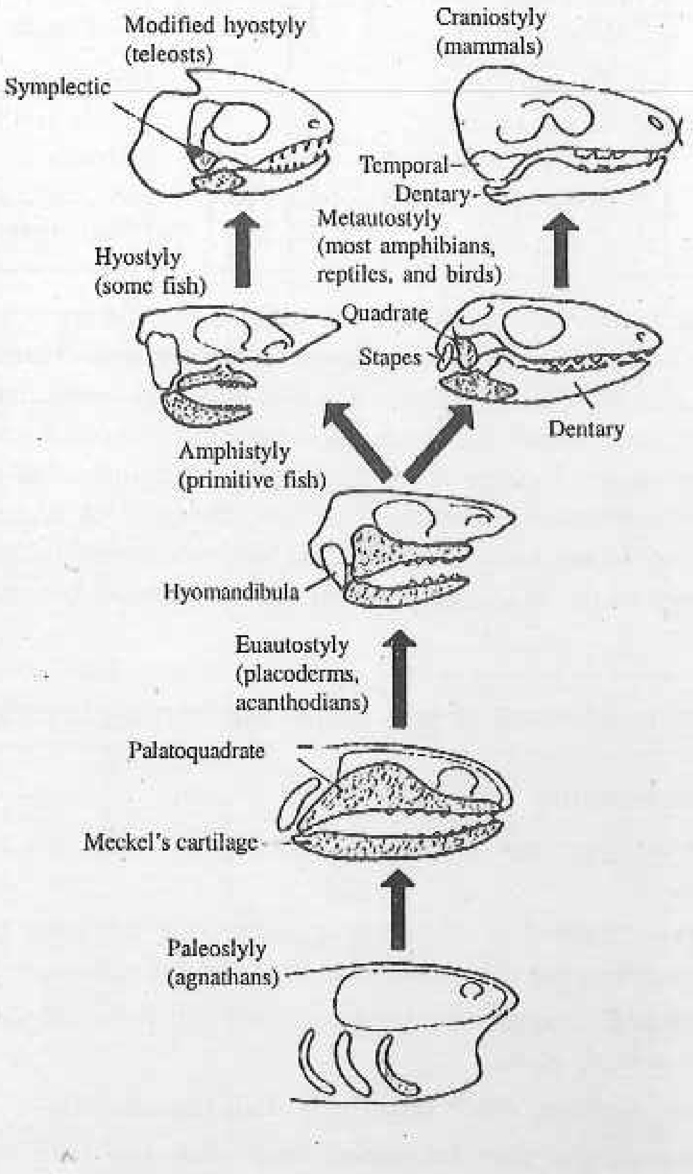


Fig. 7. 1 Schematic representation of the origin of jaw suspension

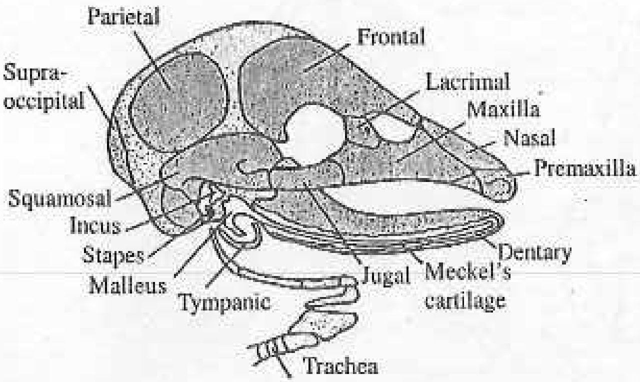


Fig. 7.2 : Mammalian jaw

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

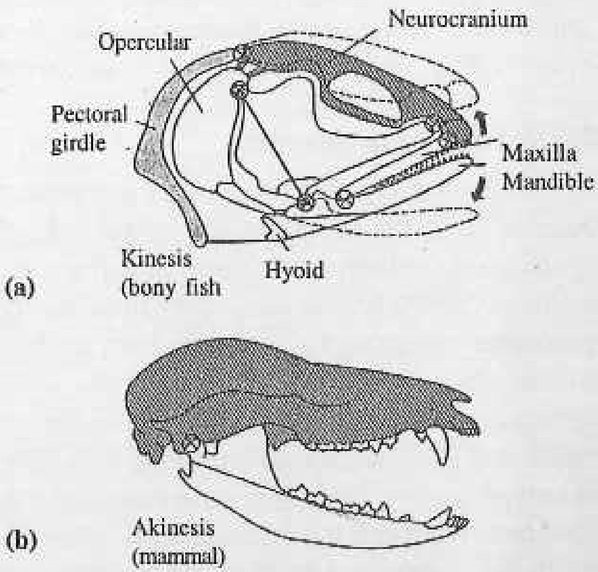


Fig. 7.3 : Cranial kinesis; (a) Kinesis (bony fish); (b) Akinesis (mammal).

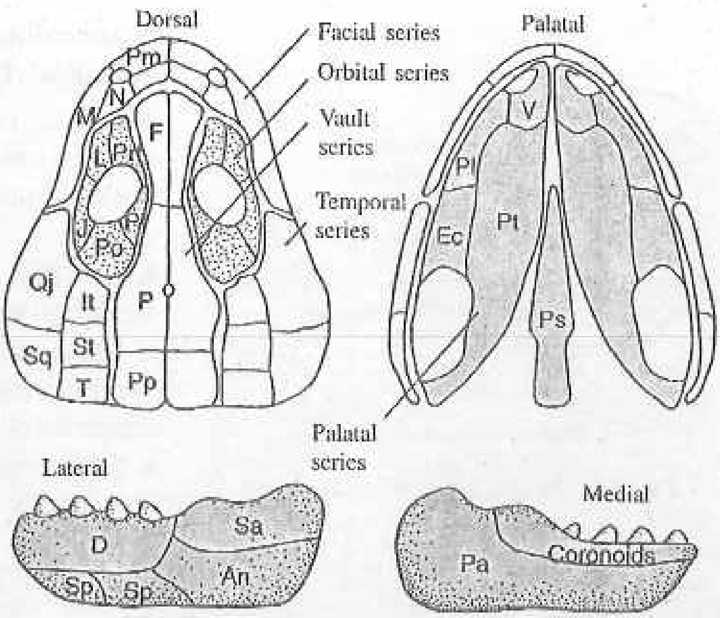


Fig. 7.4 : Dermatocranium morphology ; Facial series: Premaxilla (Pm); Maxilla (M); Nasals (N); Orbital series: Lacrimal (L); Prefrontal (Prf); Postfrontal (Pf); Postorbital (Po); Jugal (J); Temporal series: Intertemporal (It); Supratemporal (St); Tabular (T); Quadratojugal (Qj); Squamosal (Sq); Vault 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.

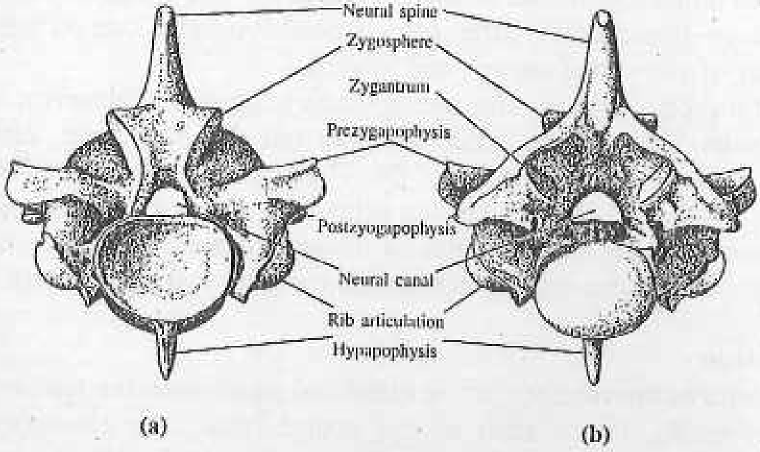


Fig. 7.5 : Vertebrae (a) Anterior view; (b) Posterior view

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.

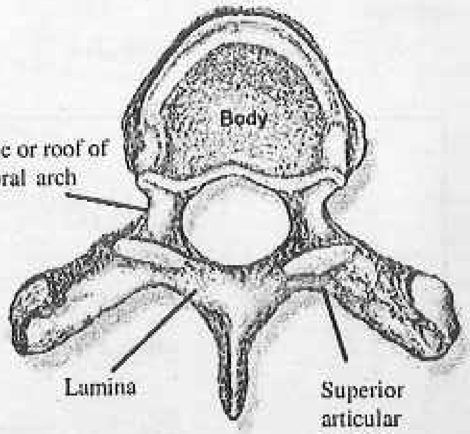


Fig. 7.6 : A tyical thoracic vertebra, viewed from above.

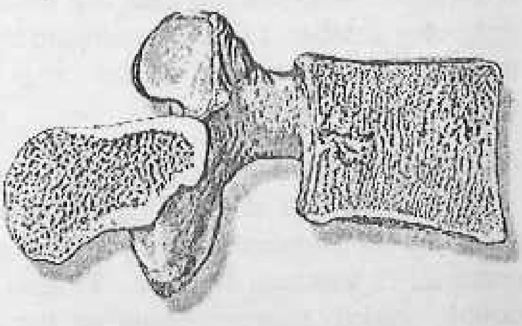


Fig. 7.7 : Sagittal section of a lumbar vertebra

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.

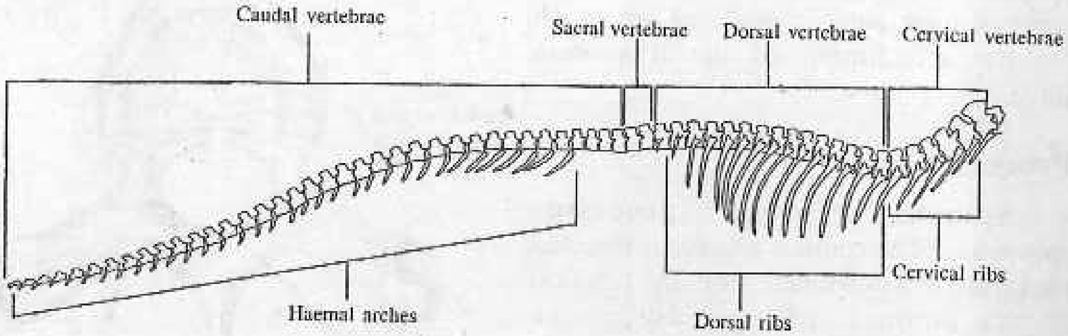


Fig. 7.8 : Showing different vertebrae and ribs

(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.

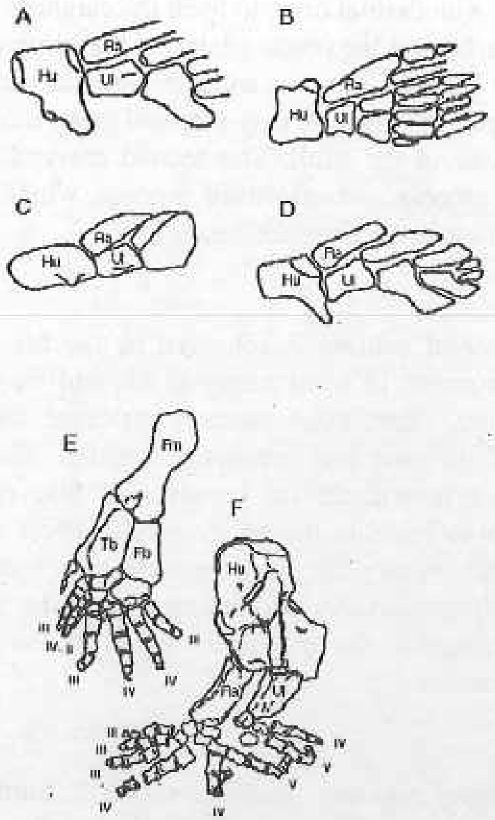


Fig. 7.8 : Comparison of paired anterior fins of lobe finned fishes (A-D) and limbs of early tetrapods (E, F) A. Sterropterygion, B. Sauripterus, C. Panderichthys, D. Eusthenopteron, E. Ichthyostega, F. Acanthostega. Fm, femur; Fb, fibula; Hu, humerus; Ra, radius; Tb, tibia, Ul, ulna

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.

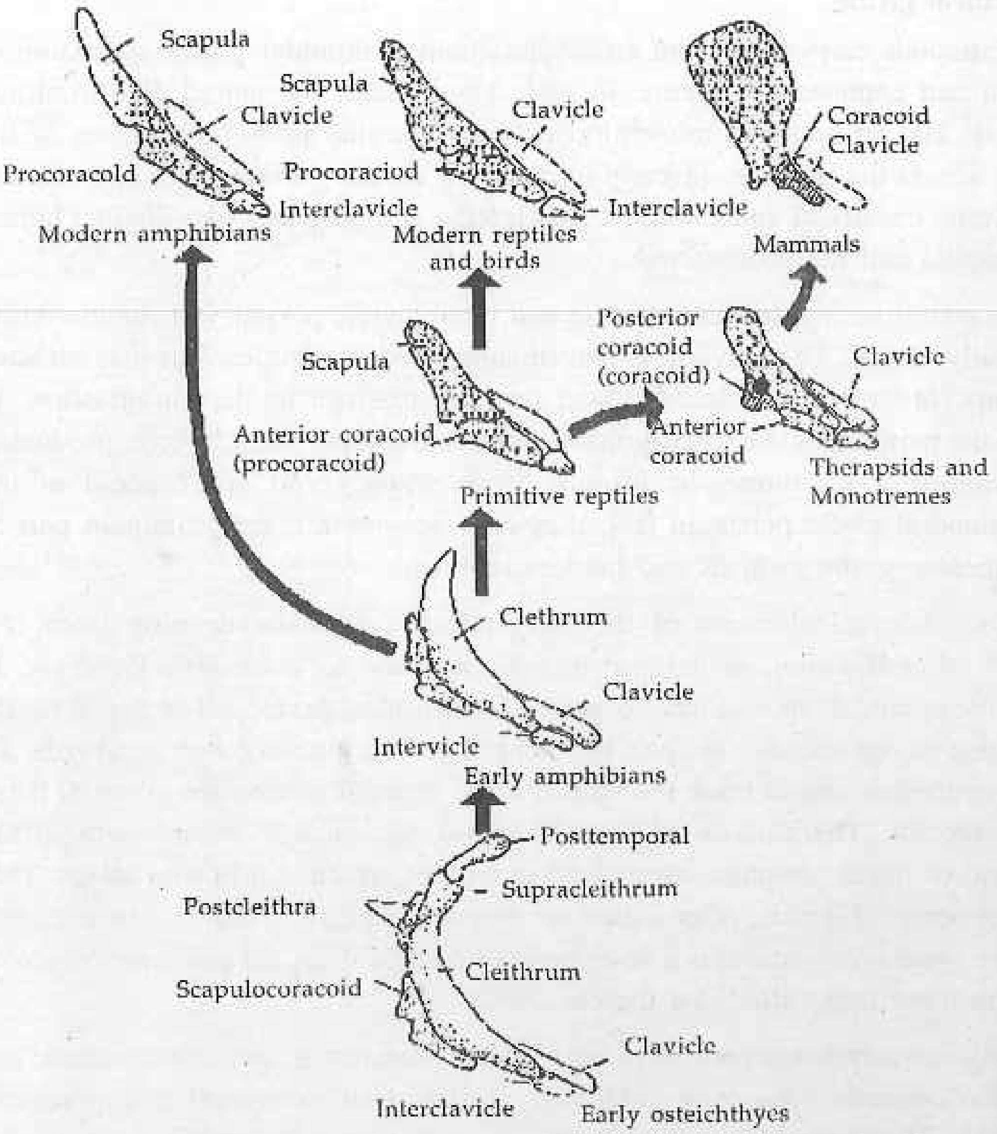


Fig. 7.10 : Summary of pectoral girdle evolution. The dermal elements (no shading) of the girdle tend to be lost and endochondral elements (shaded) tend to assume a greater role. In primitive therapsids, a third endochondral bone appears—the posterior coracoid, to join with the phylogenetically older 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.

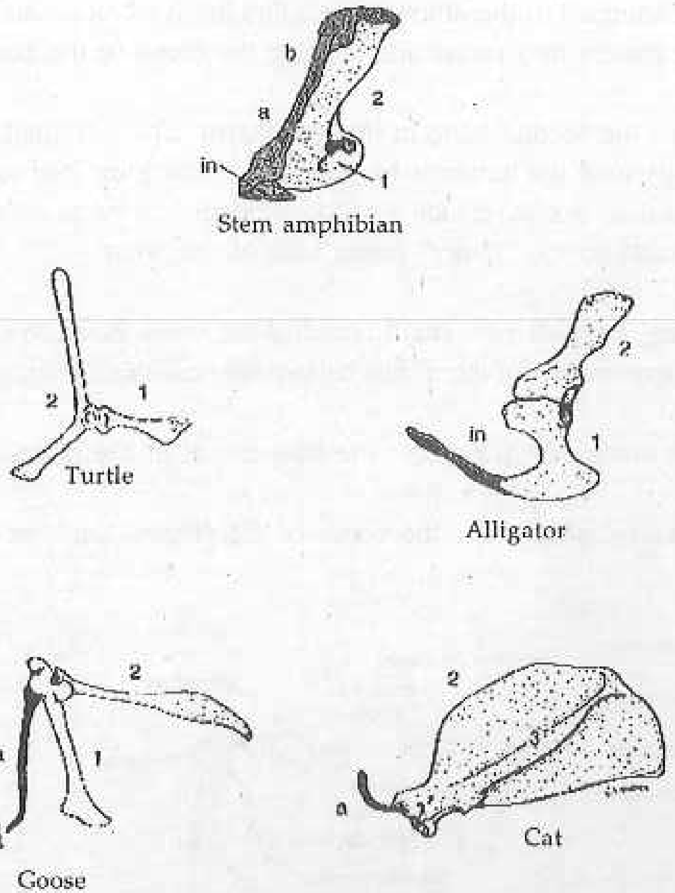


Fig. 7.11 : Left half of the pelvic girdles of some tetrapods, lateral views. Dermal bone are *black*. 1. coracoid or procoracoid; 2. scapula; 3. scapular spine; a. clavicle; b. cleithrum; in. interclavicle. In turtles the clavicle and interclavicle are fused with the shell. The cat's clavicle is almost 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).

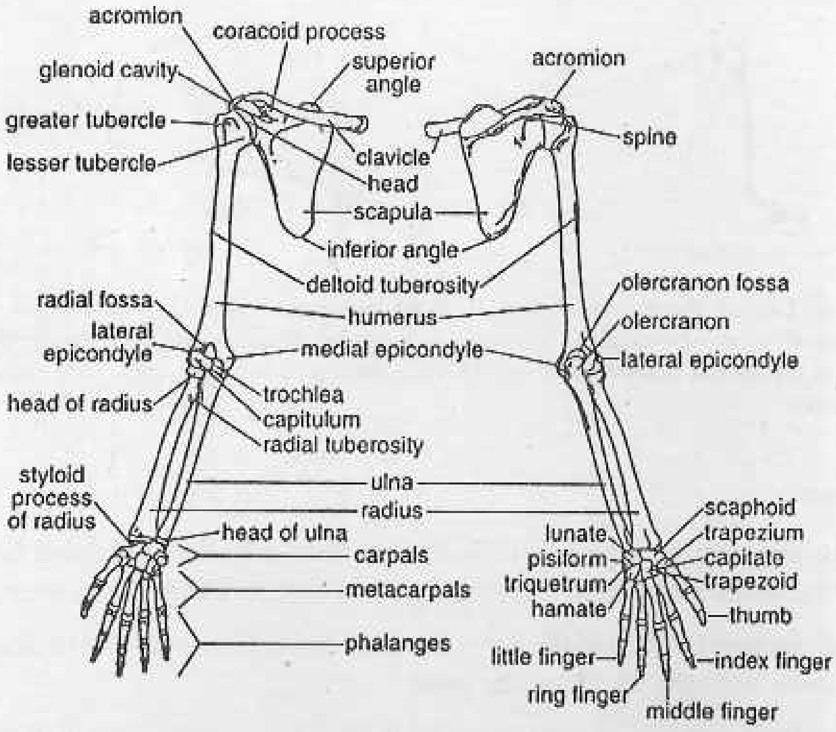


Fig. 7.12 : The pectoral girdle and the fore limb

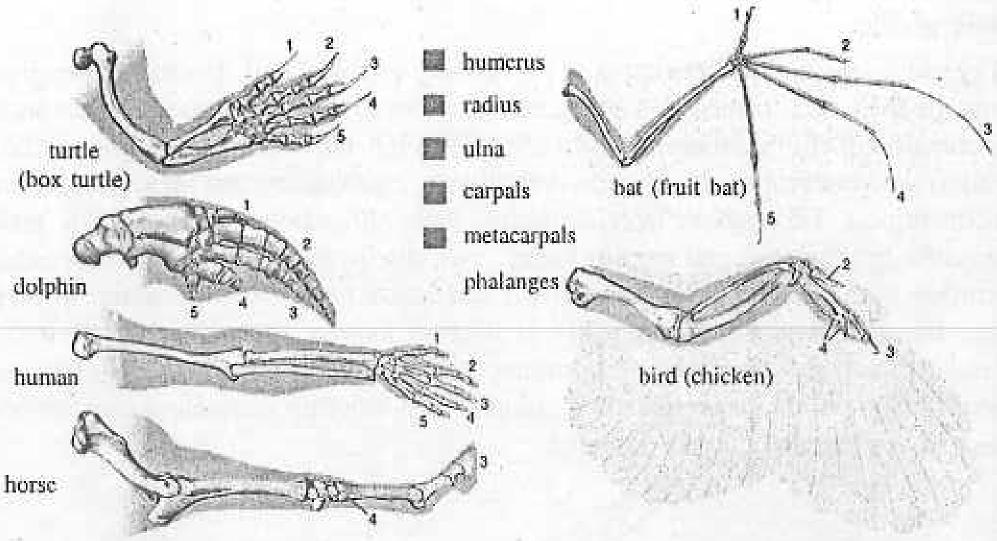


Fig. 7.13 : Homologies of the forelimb among vertebrates, giving evidence for evolution. The bones correspond, although they are adapted to the specific mode of life of the animal.

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.

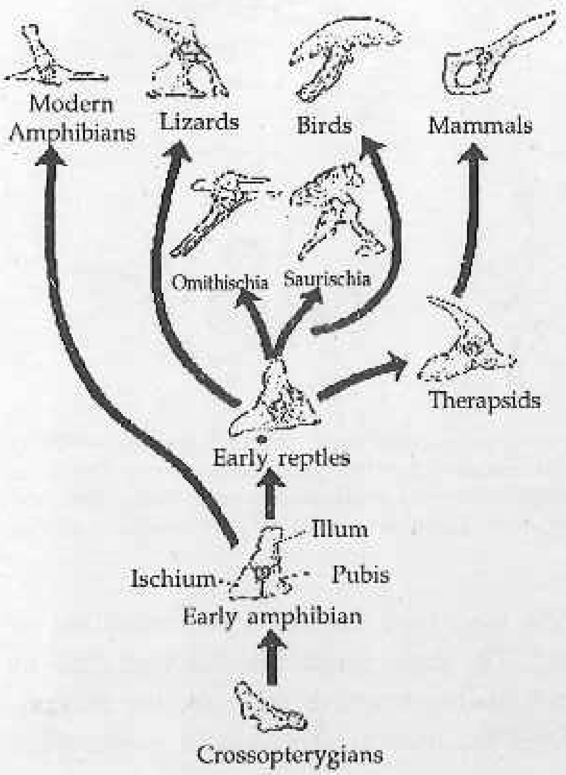


Fig. 7.14 : Summary of pelvic girdle evolution. Three endochondral elements – ilium, ischium and pubis – characterize the pelvic girdle in early tetrapods. This basic pattern persists into later tetrapods.

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.

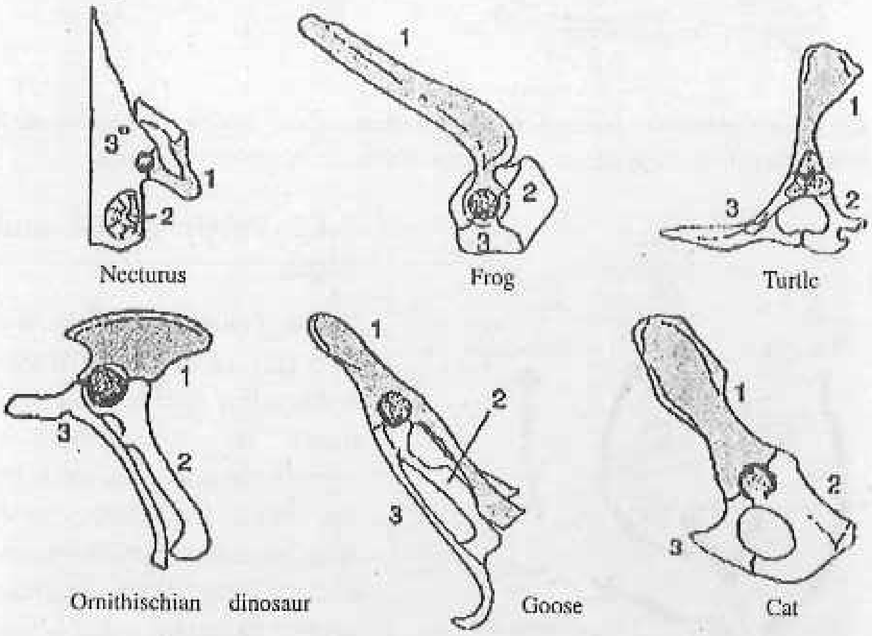


Fig. 7.15 : Left halves of pelvic girdles of some tetrapods, lateral view, except *Necturus*, which is ventral view. 1. ilium (shaded); 2. ischium ; 3. pubis (unossified pelvic plate in *Necturus*). *Stipple* is acetabulum. In *Necturus* the ischium is an ossification centre in a cartilaginous ischiopubic 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).

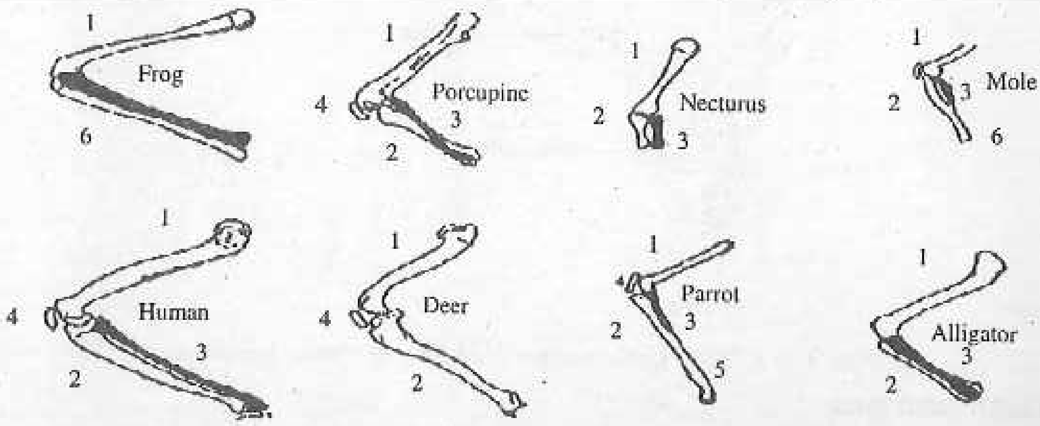


Fig. 7.16 : Left thigh and shank bones of representatives of tetrapods, lateral views. 1, femur; 2, tibia; 3, fibula; 4, patella; 5, tibiotarsus; 6, tibiofibula, fibular component in black.

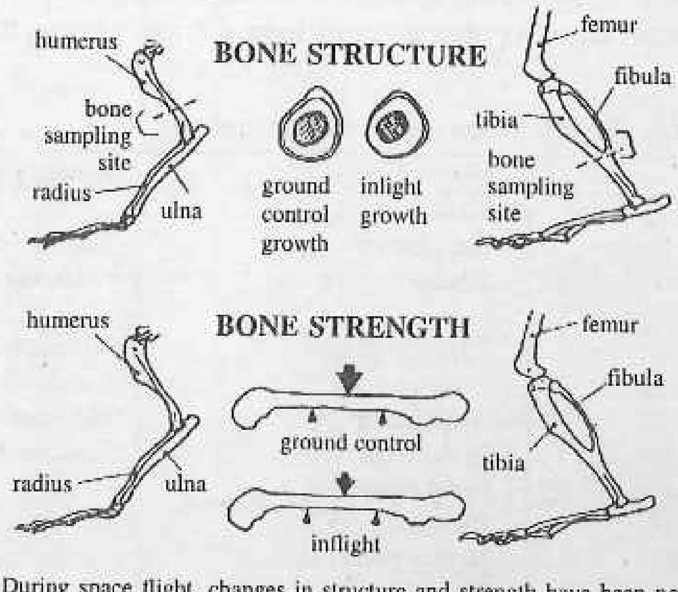


Fig. 7.17 : During space flight, changes in structure and strength have been noted in both the fore limbs and hind limbs

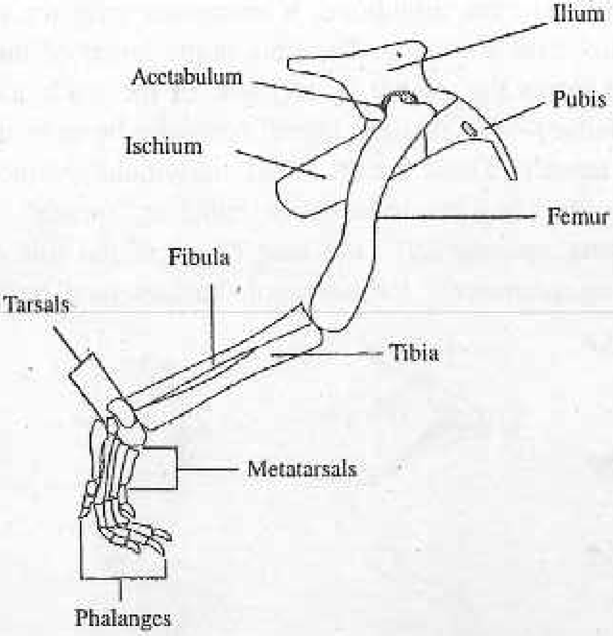


Fig. 7.18 : Pelvic girdle and the hind limb of typical vertebrate.

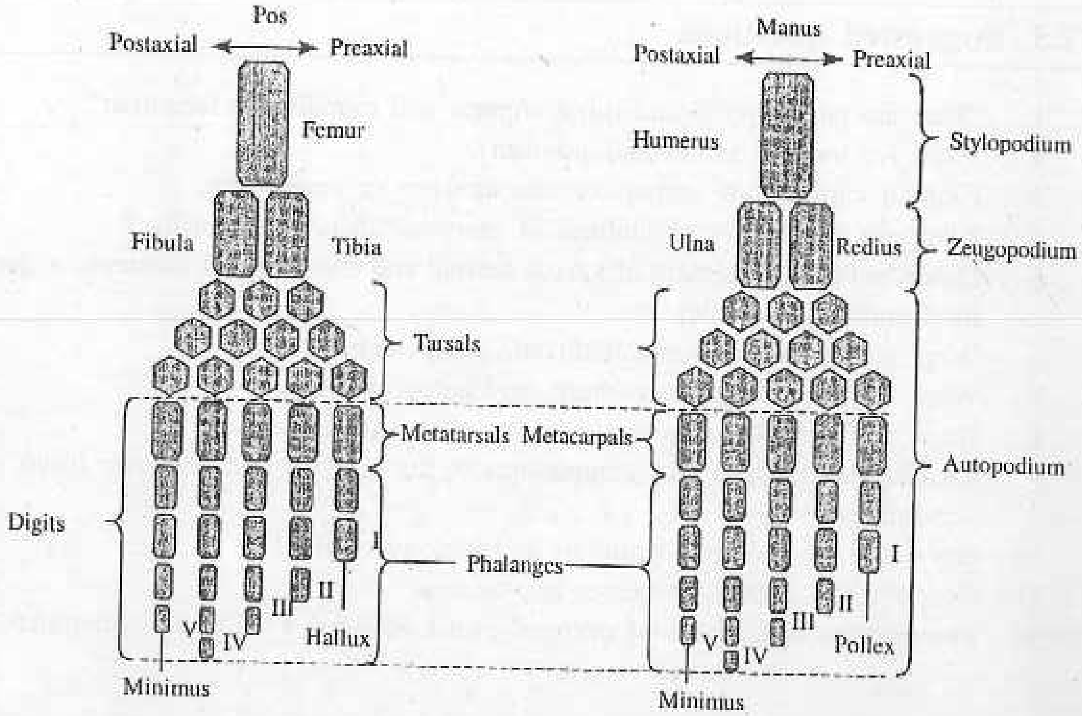
Manus and pes

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	
Distal carpal 5 }	Distal carpal 5 }	Cuboid
Metacarpals (1 to 5)	Metacarpals (1 to 5)	
Digits (I to V)	Digits (I to V)	

* incorporates the intermedium and a centrale.



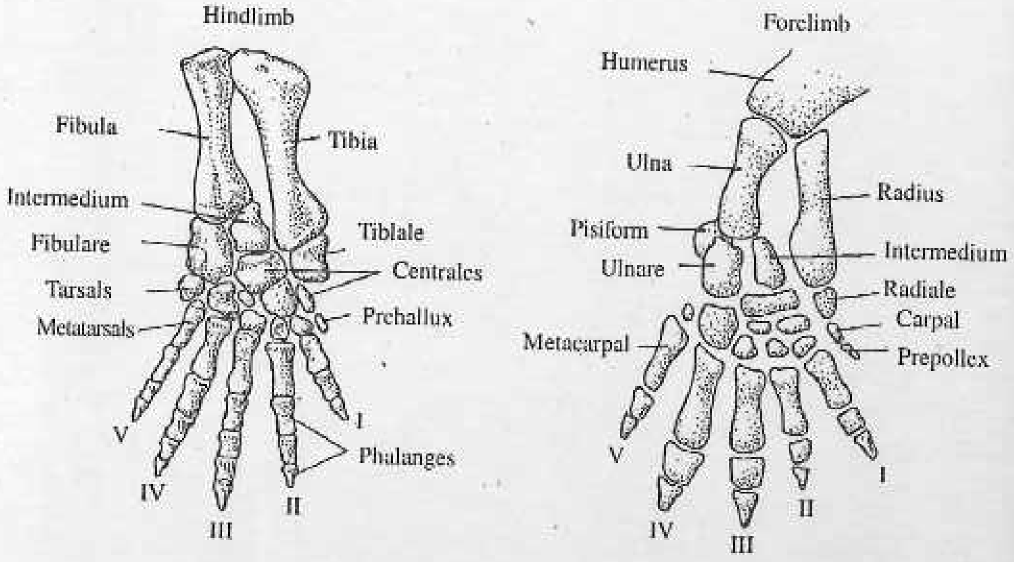


Fig. 7.19 : Basic organization of fore- and hind limbs. (a) Manus and pes have five digits; each digit includes its metacarpal or metatarsal and chain of phalanges. These digits in turn articulate with various wtist and ankle bones. (b) Fore- and hind limbs of primitive tetrapods.

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.

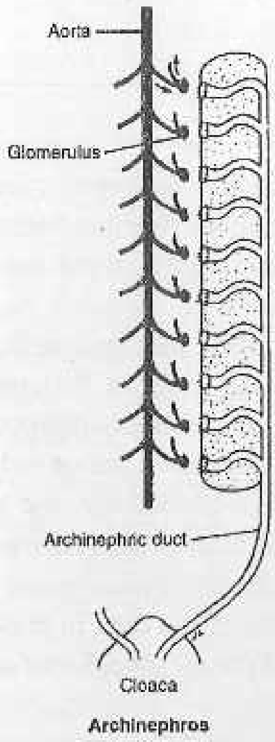


Fig. 8.1 : Hypothetical archinephros with one external glomerulus, nephrostome and tubule per body segment

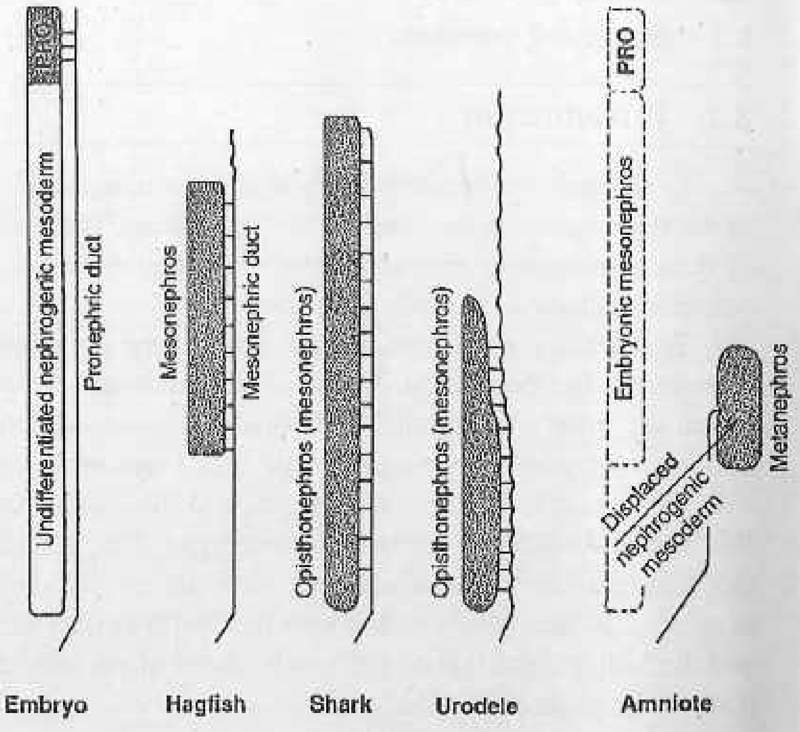


Fig. 8.2 : Fate of the nephrogenic mesoderm (shaded) in representative vertebrates. The pronephric duct persists in adult anamniots to drain the adult kidney.

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.

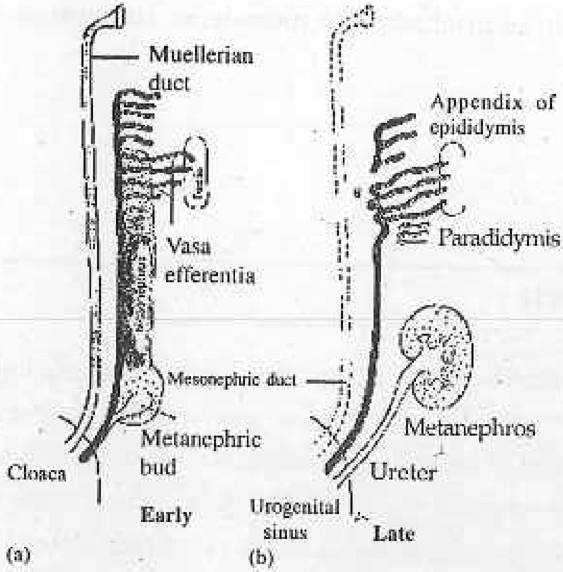


Fig. 8.3 : Developmental changes in the urogenital system of male mammals. In the early bisexual stage there is a rudimentary female duct (Mullerian duct) and a mesonephros. Some of the mesonephric tubules had invaded the genital ridge (testis) to become vas efferentia. Later (right), the Mullerian duct 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.

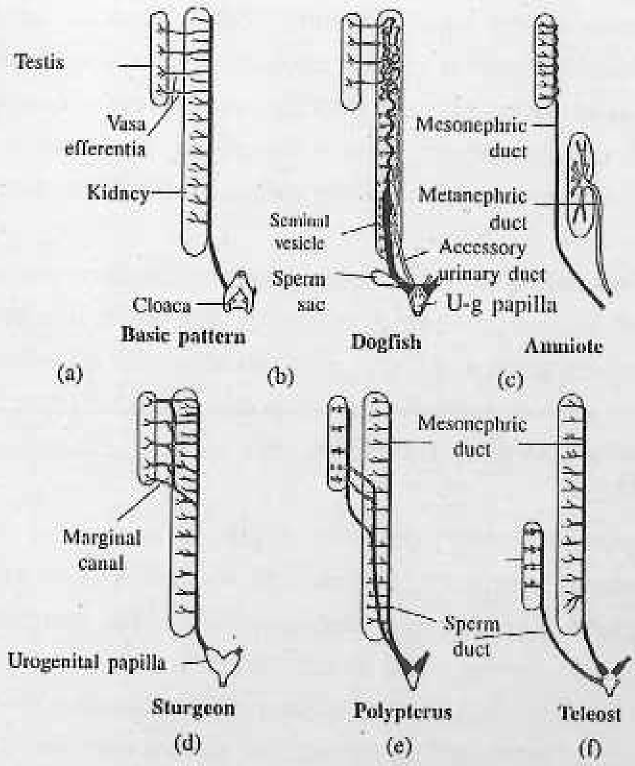


Fig. 8.4 : The mesonephric duct (black) as a carrier of sperm and urine. (a) carrying both sperm and urine. (b) carrying urine from the anterior part of the kidney only; chiefly a spermatic duct. (c) carrying sperm only. (d) to (f) trend toward a separate sperm duct. In fishes, the mesonephric duct ultimately carrying only urine. The reverse is found in amniotes (c).

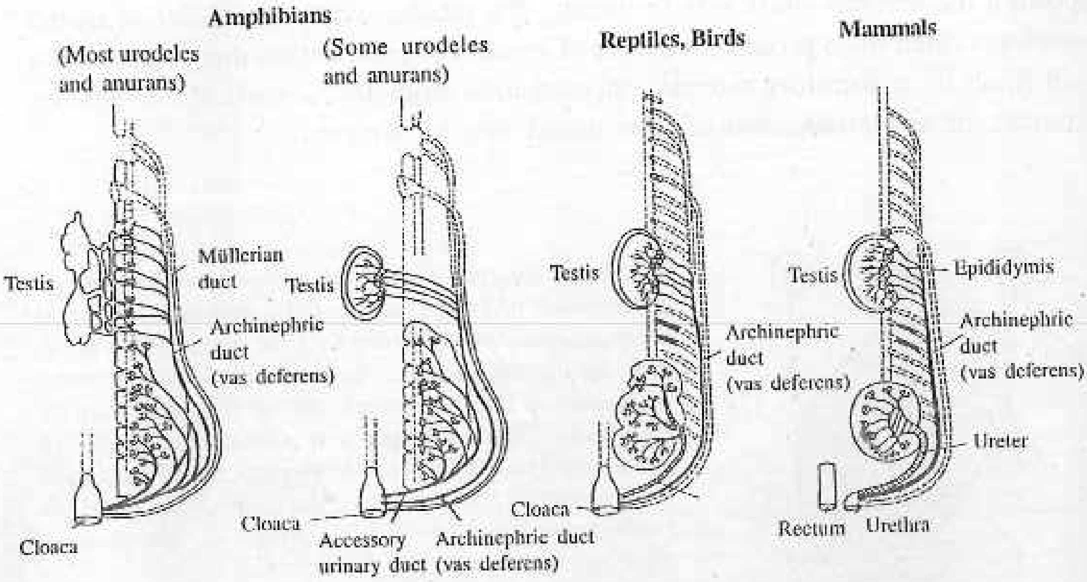


Fig. 8.5 : Urogenital ducts of tetrapod males

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.

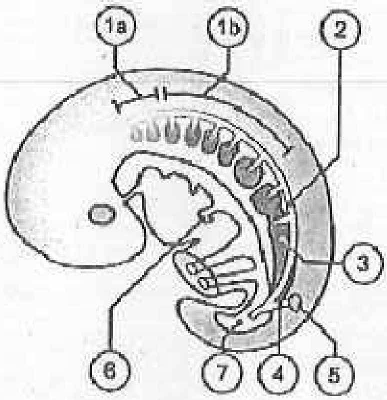


Fig. 8.6 : Sagittal section of a 5-week-old embryo - development of the metanephros. In the caudal region of the nephrogenic cord one observes the development of the metanephrogenic blastema that is in contact with the ureter anlage. In this stage the pronephros has disappeared almost completely. The 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)

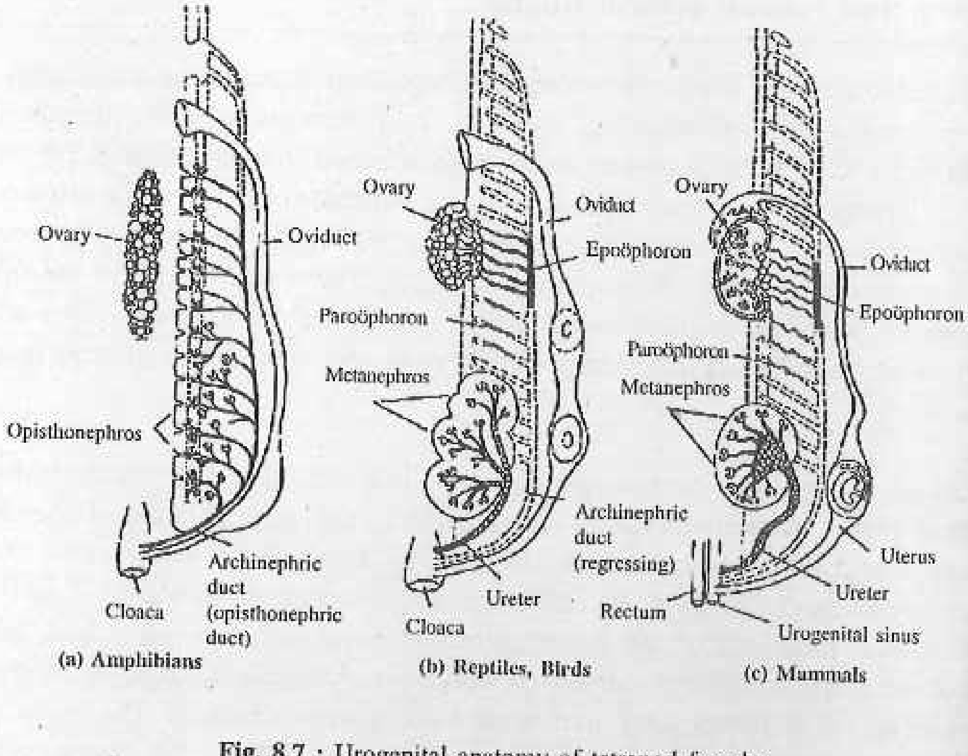


Fig. 8.7 : Urogenital anatomy of tetrapod females

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.

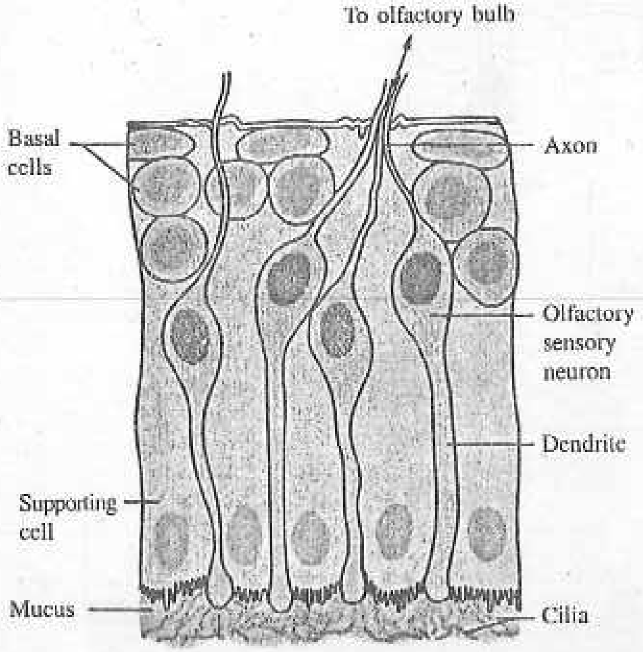


Fig. 9.1 : Four olfactory sensory neurons are shown with their cilia projecting into the mucus.

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.

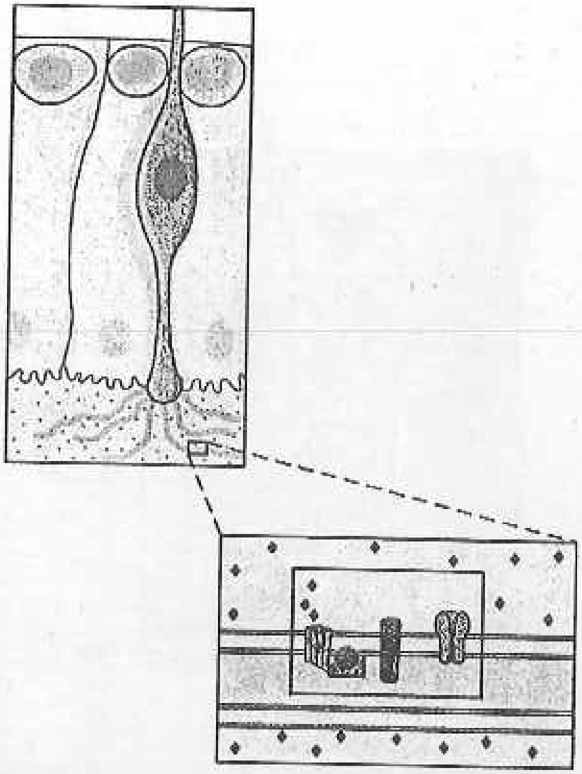


Fig. 9.2 : Inset shows an enlargement of a portion of the membrane of a cilium showing the location of the receptor and the G protein system.

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.

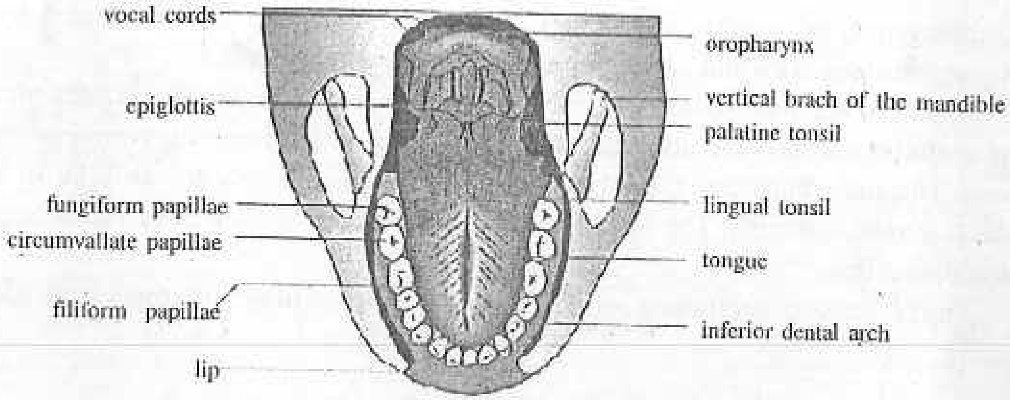


Fig. 9.3 : Showing different taste organs

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.

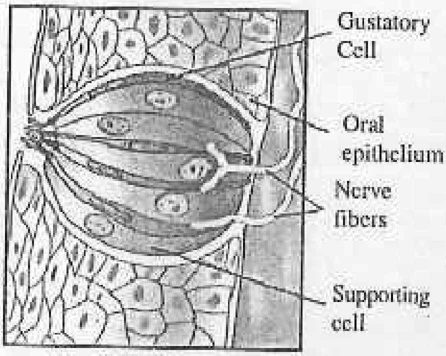


Fig. 9.4 : Taste bud

- 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.

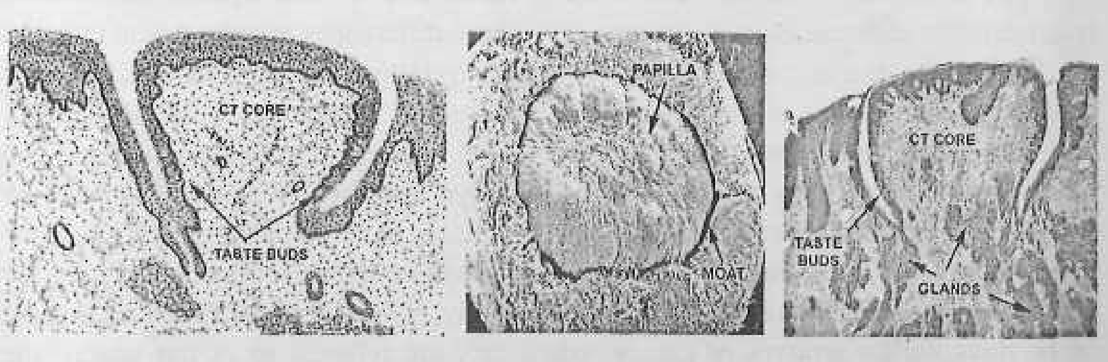


Fig. 9.5 : Three views of a circumvallate papilla : Schematic, Scanning E.M., and low-power light microscope (SEM image courtesy of Dr. Suraj Kum)

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.

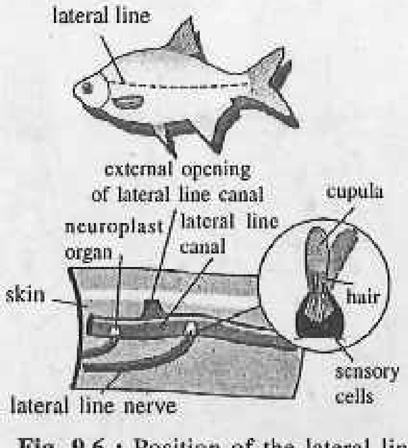


Fig. 9.6 : Position of the lateral line sense organ in fish

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

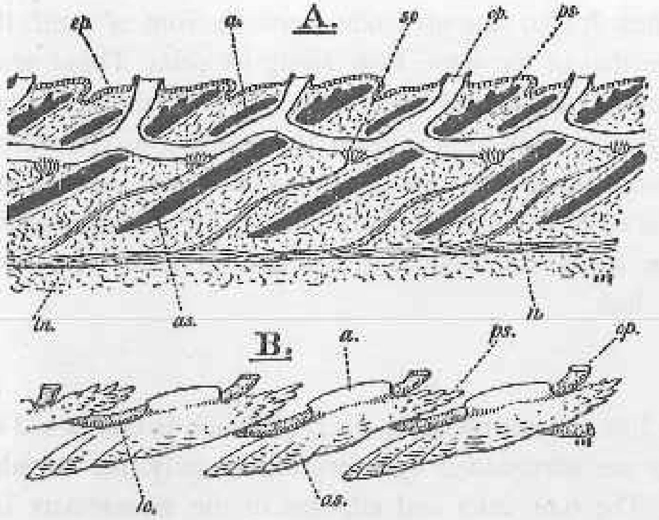
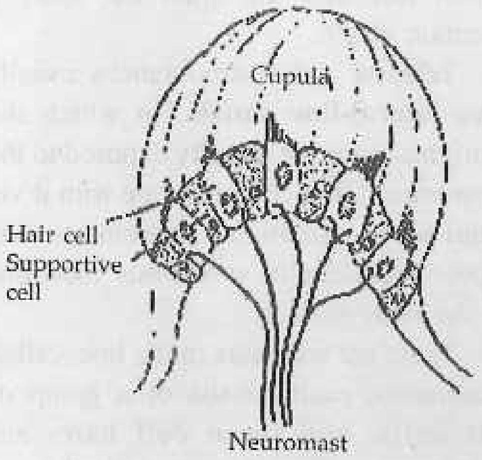


Fig. 9.7 : The relation of the lateral line canal to the scales. A. longitudinal section, B. scales and canal seen in side view. *a.* bridge of scale covering the canal, as. anterior region of scale; *ep.* Epidermis; *lc.* Lateral line canal; *ln.* lateral line nerve; *n.* nerve to sense organ; *op.* external opening of the canal; *ps.* Posterior edge of scale; *so.* Sense organ in canal.



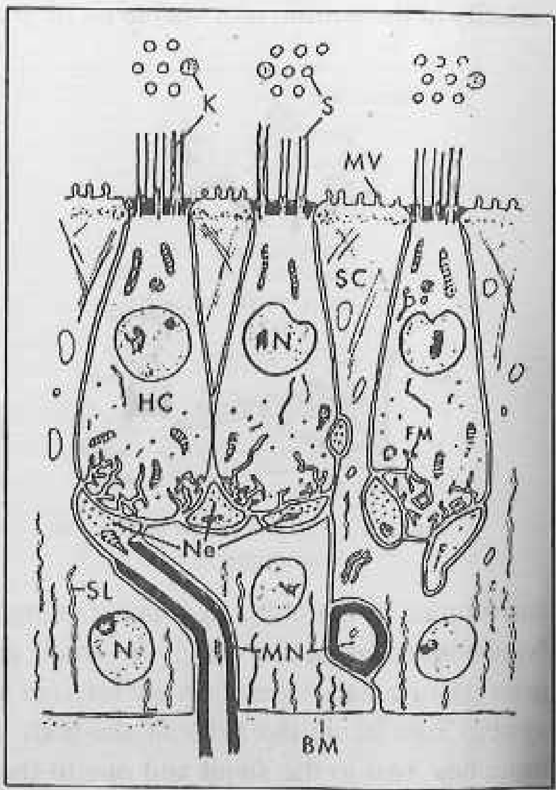


Fig. 9.8 : Highly schematic drawing of the sensory epithelium of the lateral line canal organ. *HC* = hair cell, *SC* = supporting cell, *MN* = myelinated nerve fiber, Ne = nerve ending, K = kinocilia, *S* = stereocilia, *MV* = microvilli, N = nucleus, *FM* = folding membrane system, *SL* = supporting 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.

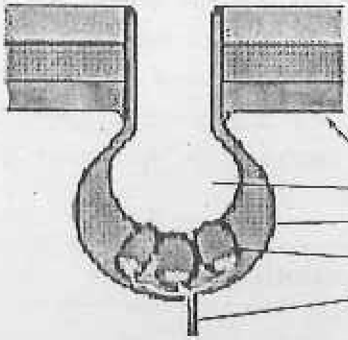


Fig. 9.9 : Electroreceptor system

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

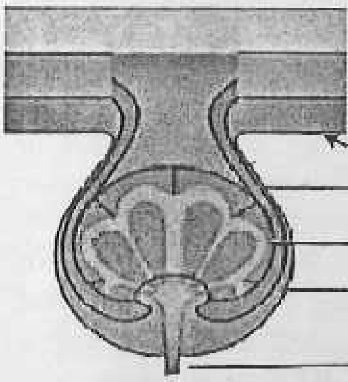


Fig. 9.10 : Tuberous receptor

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.

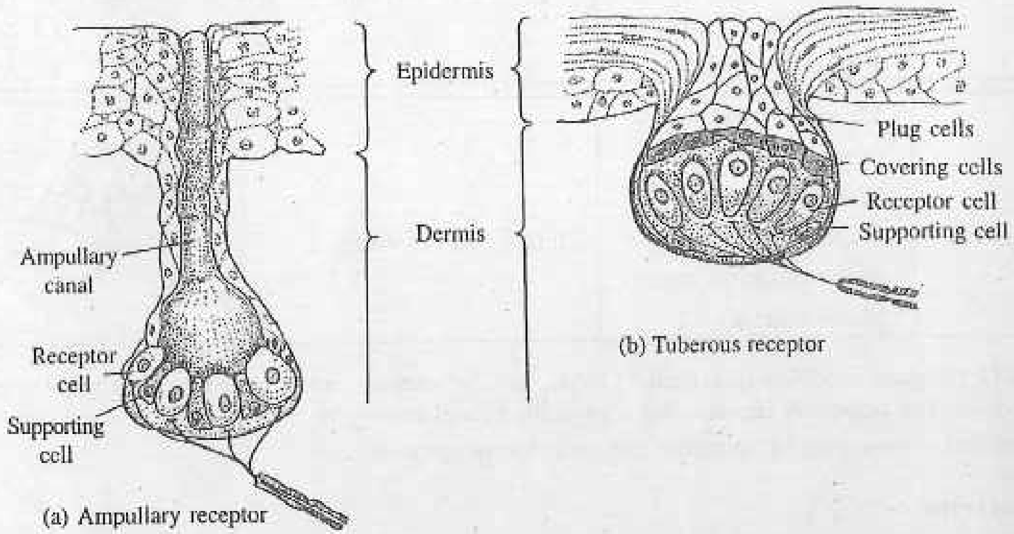


Fig. 9.11 : Receptors; (a) ampullary; (b) tuberous

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

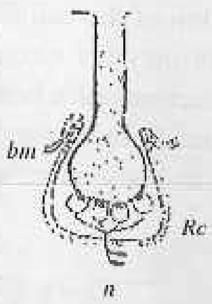
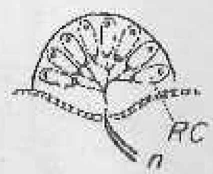
Type	Where Found	Sensitivity	Structure
Ampullary	Sharks and Rays; Non-teleost fishes (except holosteans); Certain teleosts (mormyrids, certain Notopterus, gymnotiforms, catfish); Amphibians (except frogs and toads).	0.01 microvolt per cm in marine species, 0.01 millivolt/cm in freshwater; sensitive to DC fields or to frequencies less than 50 Hz	
Tuberous	Mormyrid fish (Knollenorgans. Mormyromasts); 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.

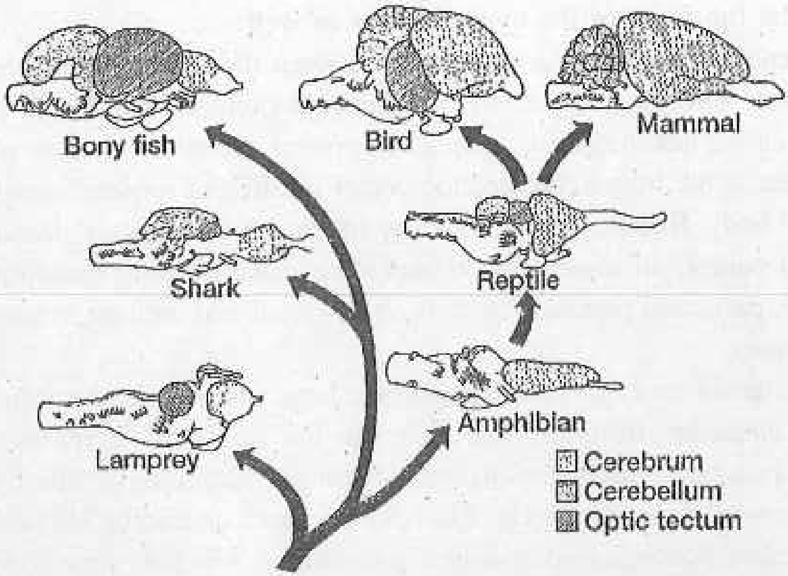


Fig. 10.1 : Evolution of the vertebrate brain. Phylogenetic enlargement of the cerebrum is prominent.

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
		Dorsal pallium
		Dorsomedial cortex (cingulate)
Neopallium (Neocortex) (Isocortex)	Cerebral cortex	Dorsolateral cortex
		Lateral pallium
		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.

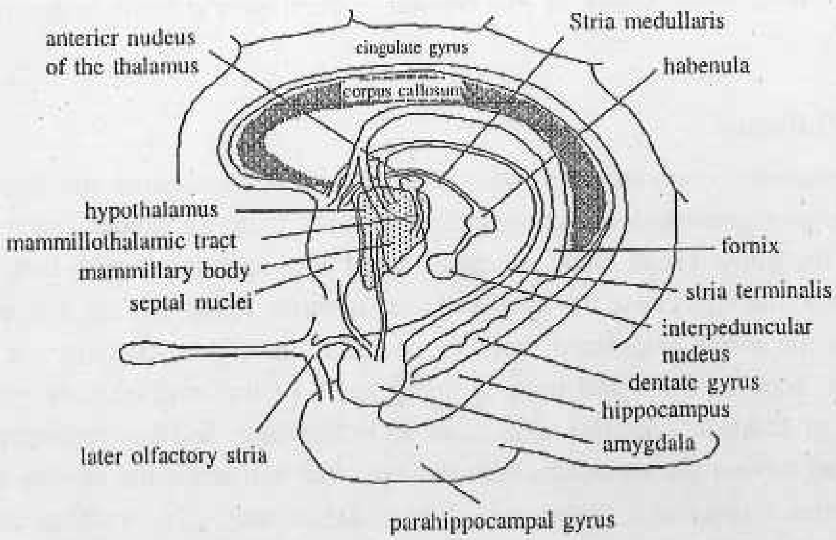


Fig. 10.2 : Showing the limbic system

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.

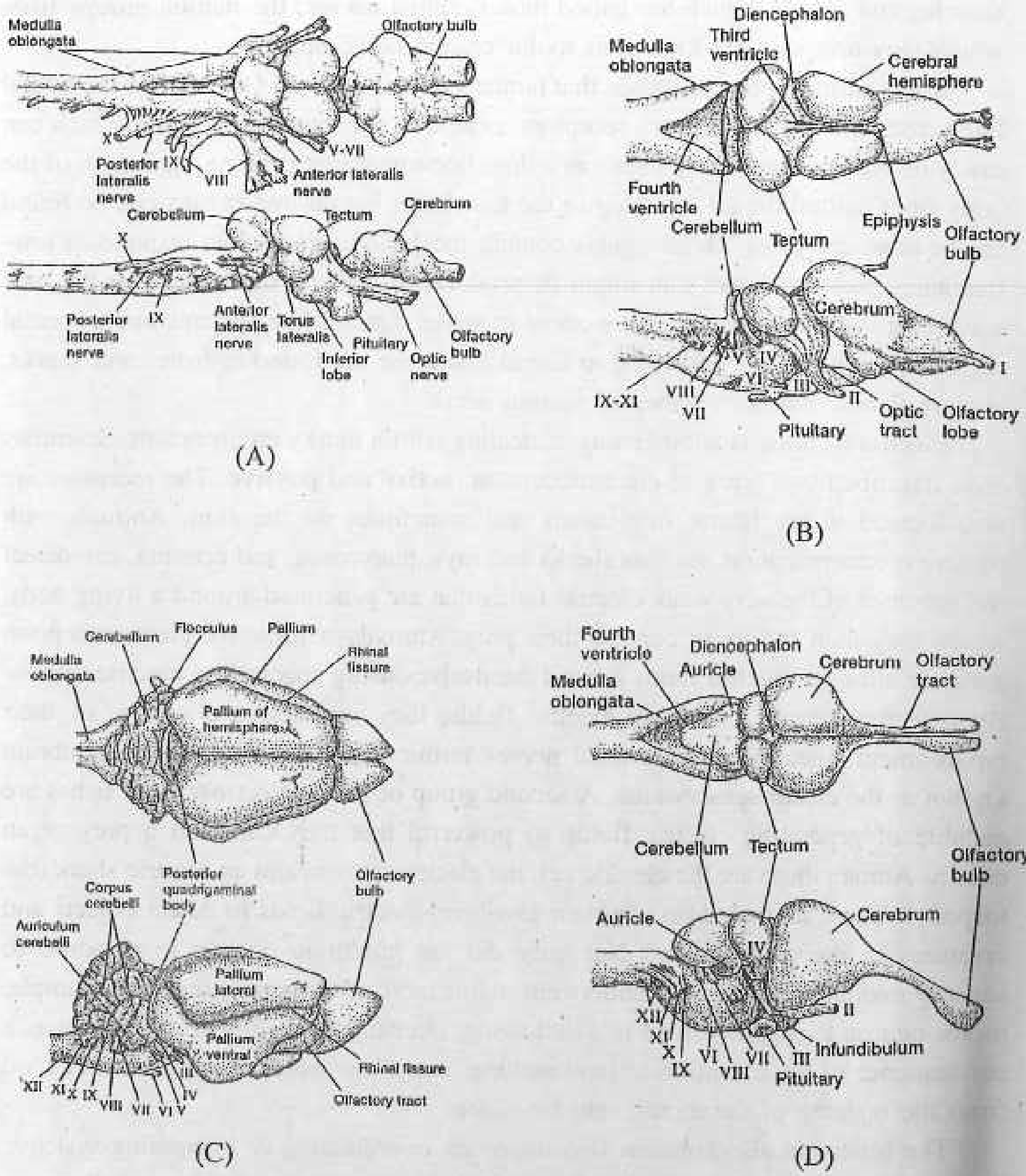
10.2.3 Hindbrain

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.



Medulla oblongata
Olfactory bulb
X
Posterior lateralis nerve
IX
VIII
V-VII
Anterior lateralis nerve
Cerebellum
Tectum
Cerebrum
X
IX
Posterior lateralis nerve
Anterior lateralis nerve
Torus lateralis
Pituitary
Inferior lobe
Optic nerve
Olfactory bulb
(A)
Diencephalon
Third ventricle
Medulla oblongata
Cerebral hemisphere
Fourth ventricle
Cerebellum
Tectum
Epiphysis
Olfactory bulb
Cerebrum
IX-XI
VIII
VII
V
IV
VI
III
II
I
Pituitary
Optic tract
Olfactory lobe
(B)
Cerebellum
Flocculus
Pallium
Medulla oblongata
Rhinal fissure
Pallium of hemisphere
Posterior quadrigeminal body
Corpus cerebelli
Auriculum cerebelli
Olfactory bulb
Pallium lateral
Pallium ventral
Rhinal fissure
Olfactory tract
XII
XI
X
IX
VIII
VII
VI
V
IV
III
(C)
Fourth ventricle
Diencephalon
Auricle
Cerebrum
Olfactory tract
Medulla oblongata
Cerebellum
Tectum
Olfactory bulb
Auricle
Cerebrum
IV
II
XII
XI
X
IX
VI
VIII
VII
III
Infundibulum
Pituitary
(D)

Fig. contd.

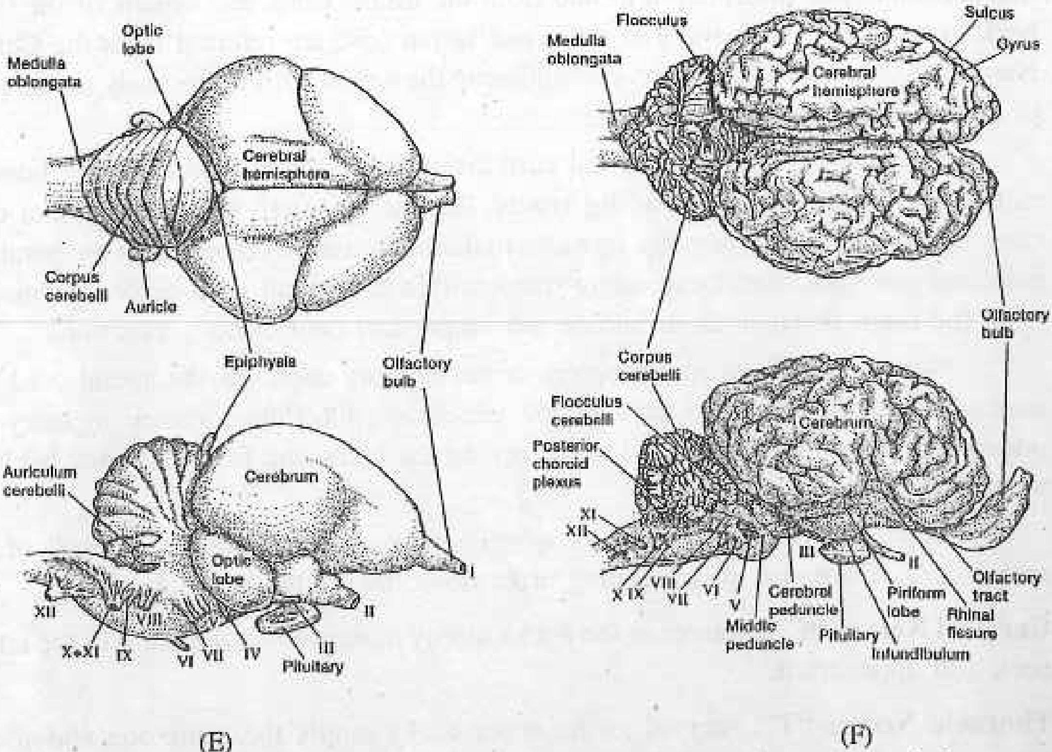


Fig. 10.3 : Vertebrate brains. Dorsal views are shown above, lateral views below. (A) *Amia* (B) *Rana* (C) *Gymnura* (D) *Alligator* (E) *Anser* (F) *Equus*

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.

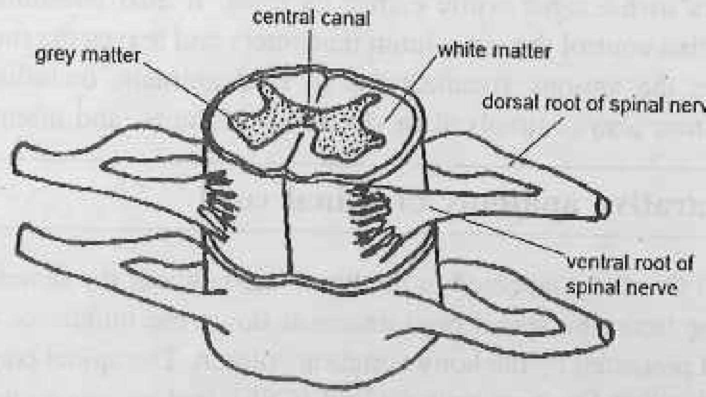


Fig. 10.4 : Diagram showing the relationship between spinal nerve roots and vertebrae

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.

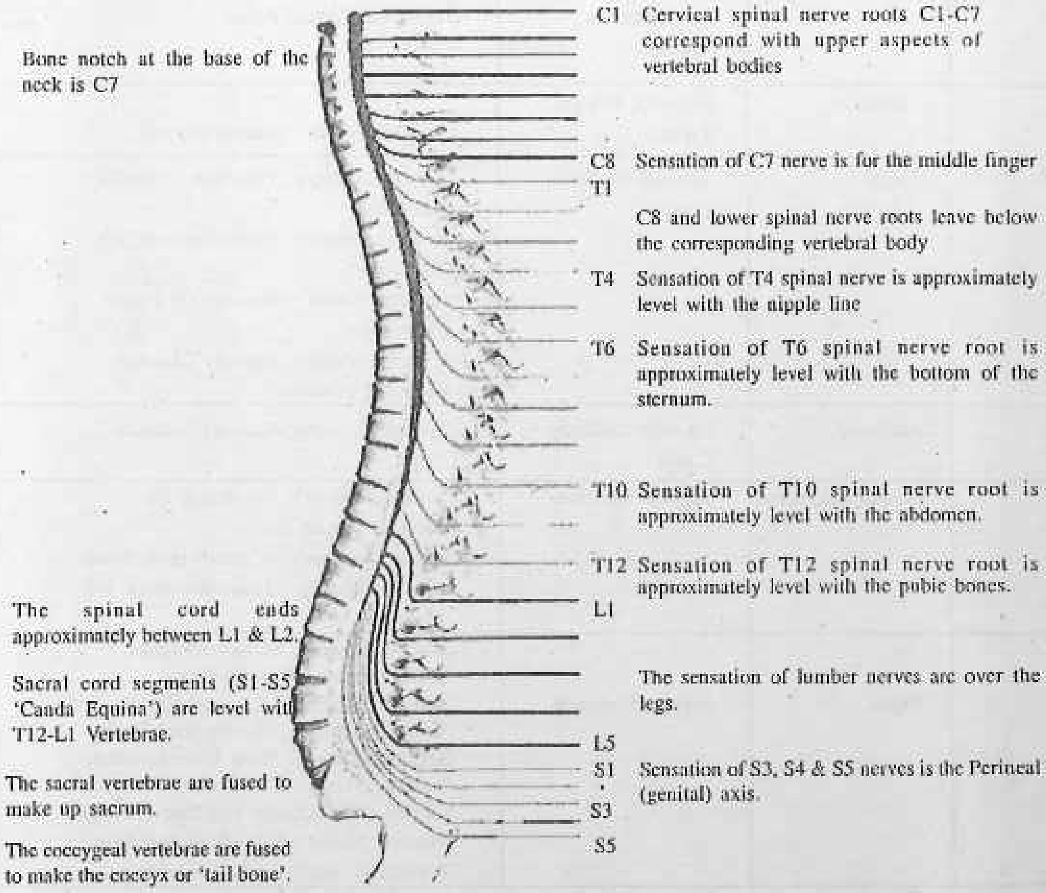


Fig. 10.5 : Orientation of cranial name

Cranial nerve summary

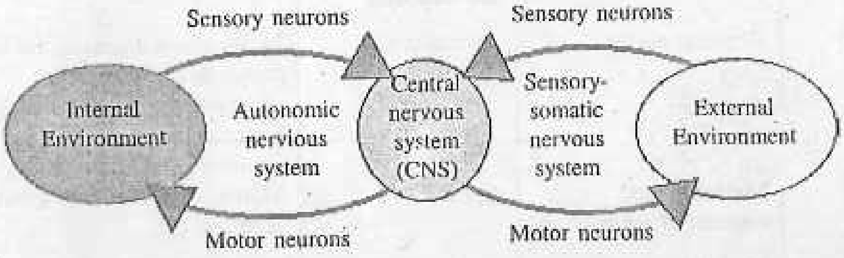
Cranial nerves number	Name	Foramen	Function
I	Olfactory	Cribiform Plate	Special Sensory: Smell
II	Optic	Optic Canal	Special Sensory: Sight
III	Oculomotor	Superior Orbital Fissure	Somatic Motor: Superior, Medial, Inferior Rectus, Inferior Oblique Visceral Motor: Sphincter Pupillae
IV	Trochlear	Superior Orbital Fissure	Somatic Motor: Superior Oblique
V	Trigeminal	V1: Sup Orb Fissure V2: Foramen Rotundum V3: Foramen Ovale	Somatic Sensory: Face 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 Special Sensory: Taste (Anterior 2/3 Tongue) Somatic Motor : Muscles Of Facial Expression 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 Visceral Sensory ; Carotid Body/Sinus Special Sensory : Taste (Posterior 1/3 Tongue) Somatic Motor : Stylopharyngeus Visceral Motor: Parotid Gland
X	Vagus	Jugular Foramen	Somatic Sensory : External Ear Visceral Sensory : Aortic Arch/Body Special sensory ; Taste Over Epiglottis Somatic Motor : Soft Palate, Pharynx, Larynx (Vocalization and Swallowing) 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

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.

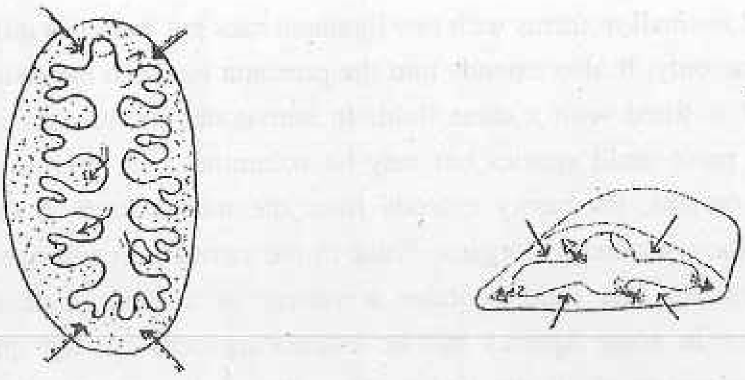
Mesozoa is a minor group of multicellular animals, constructed by two solid cell layers but these two layers do not correspond to the ectoderm and endoderm of the metazoa because the inner layer is reproductive and not digestive.

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).



(A) (B)

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.

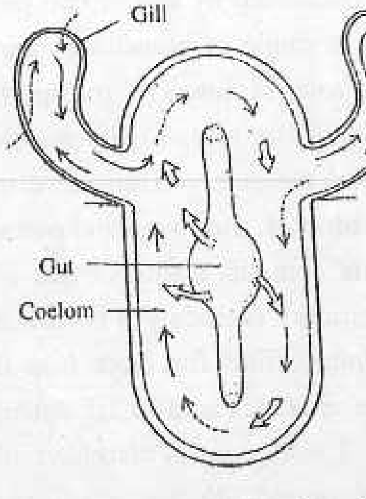


Fig. 1.2A : Unpartitioned coelom. Coelomic fluid reaches all tissues and is the sole circulatory system

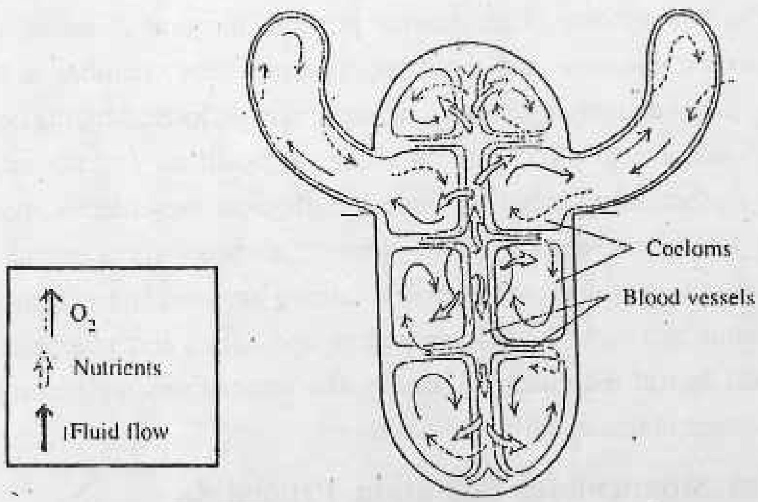


Fig. 1.2B : Coelom is divided by septa and mesenteries and thus, coelomic fluid can only circulate locally

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

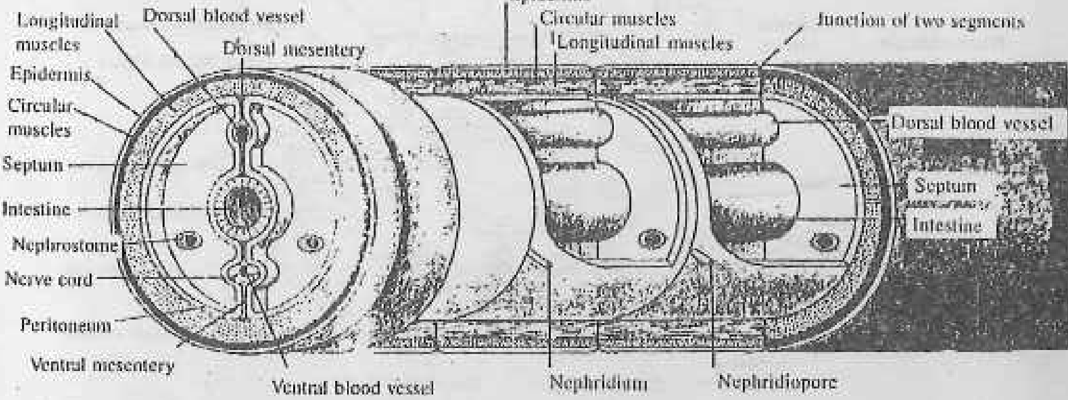


Fig. 1.3A : Annelid segments and anatomy

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).

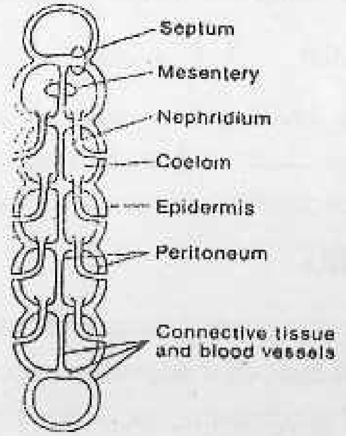


Fig. 1.3B : Dorsal view showing septa and coelom

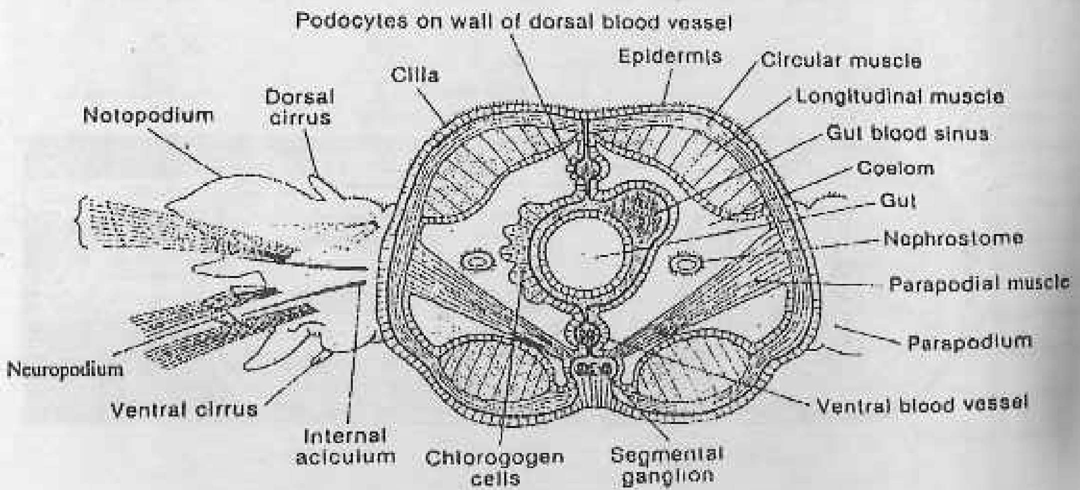


Fig 1.3C : Cross section of trunk showing polychaete organization

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 Hemicnordata

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

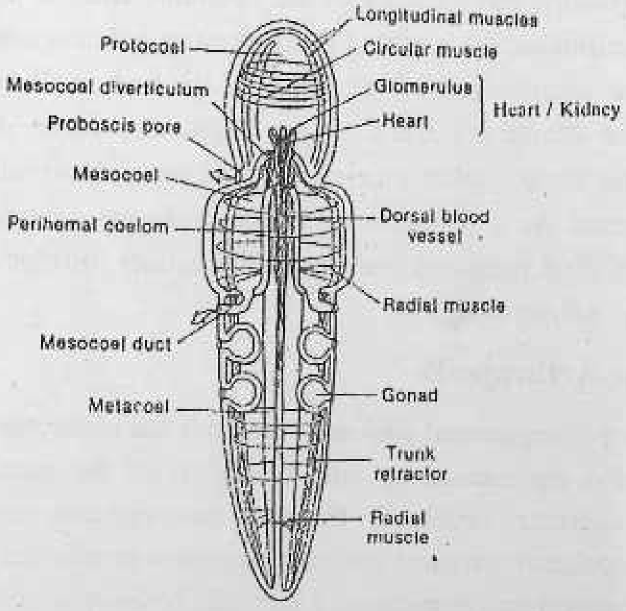


Fig. 1.4 : Musculature, blood-vascular and coelomic organization of enteropneusts, dorsal view. Note that a single unpaired protocoel occupies the proboscis, a pair of mesocoels in the collar and a pair of mesocoels in the trunk.

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.

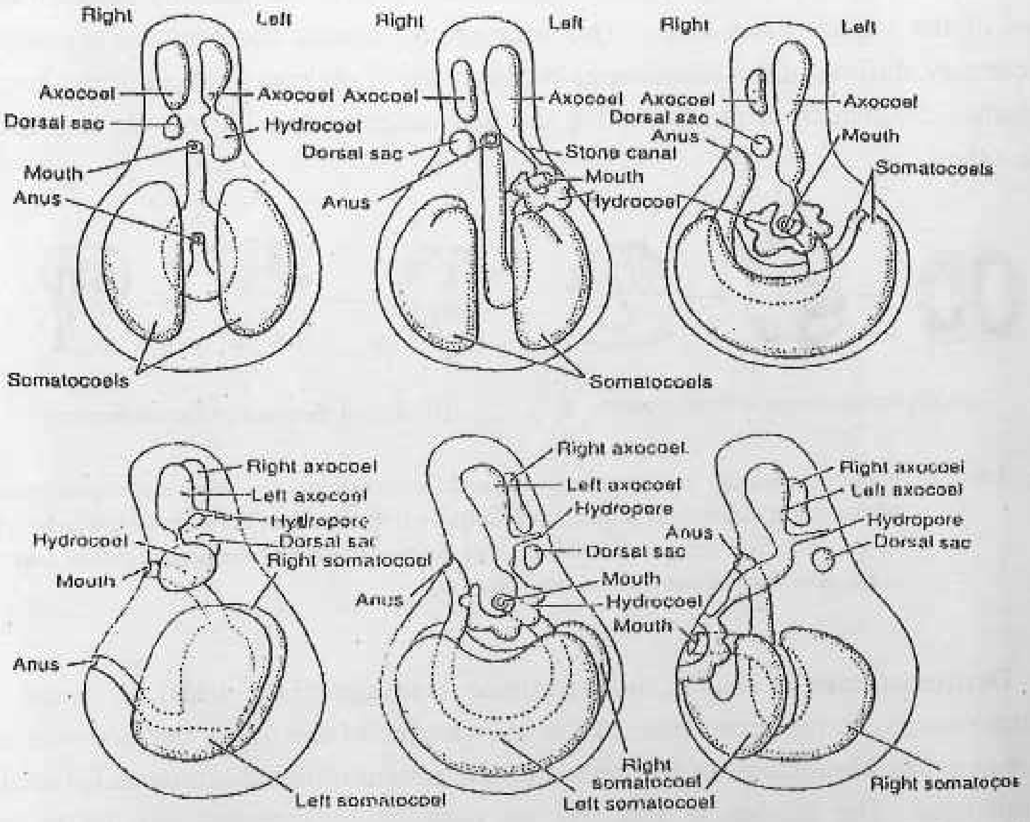


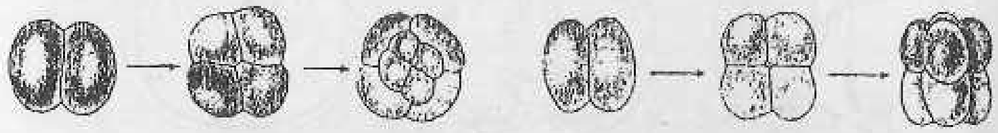
Fig. 1.5 : Generalized echinoderm metamorphosis showing development of coelom from the pouches or pockets separated from the archenteron. Enterocoelous development of the coelom as in other deuterostomes.

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.



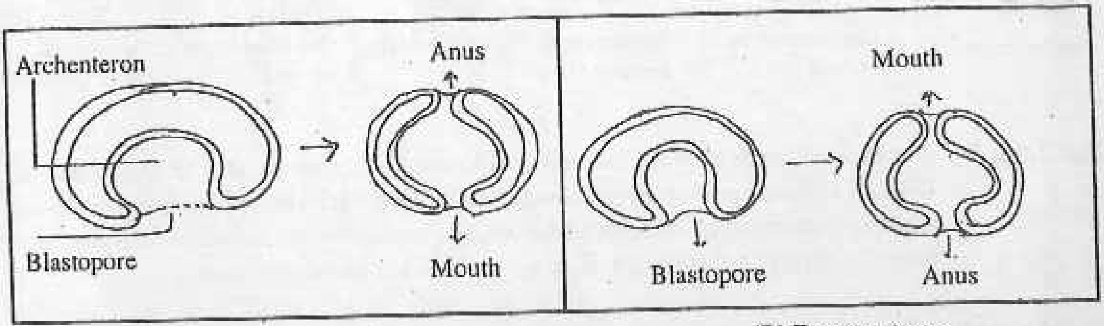
(A) Spiral cleavage in Protostomes (B) Radial cleavage in Deuterostomes

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.



(A) Protostome (B) Deuterostome

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

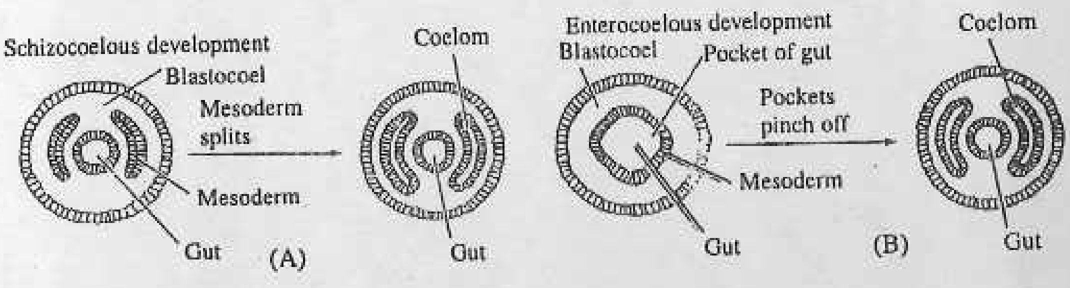


Fig. 1.8A, B : Development of coelom in Protostomes (A) and deuterostomes (B). Note the difference in schizocoelous and enterocoelous type of coelom development.

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

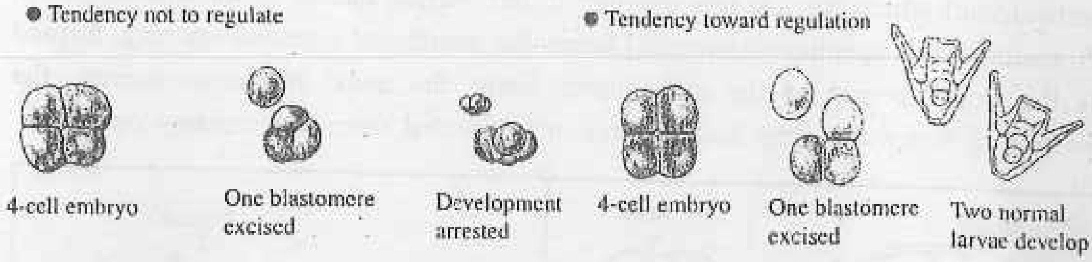


Fig. 1.9A, B : Another difference between Protostome (A) and Deuterostome (B). In Deuterostome (B) each cell produced by early cleavage retains the capacity to develop into a complete embryo (indeterminate cleavage) whereas, in Protostome the individual cell does not have the ability to form a complete embryo (determinate cleavage).

According to the schizocoelous theory, the acoelomate body plan is primary and ancestral to the coelomate plan. The acdelomate 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.

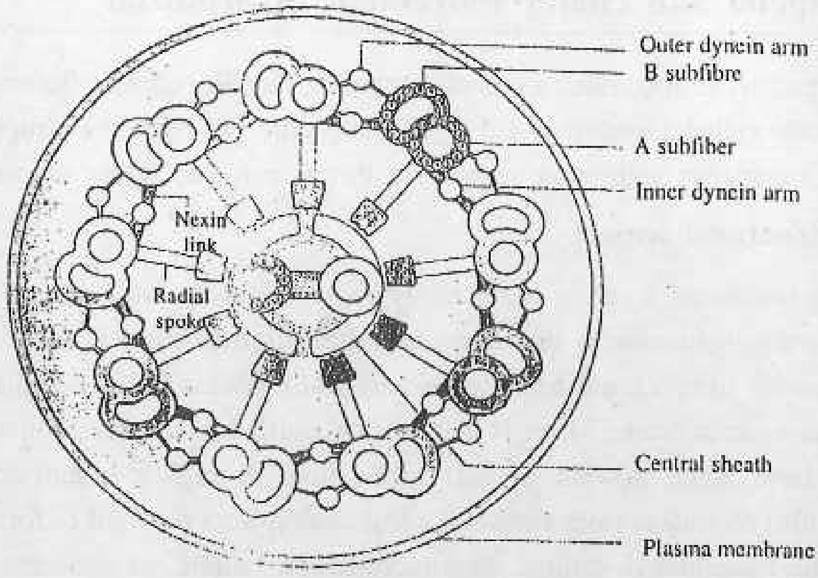


Fig. 2.1 : Diagram of a cilium or flagellum seen in cross section. Note that the micro tubular bundle or axoneme consists of two central tubules encircled by nine double tubules and that subfibre B is larger than subfibre A. Subfibre A is complete whereas B is incomplete. Subfibre A has inner and outer 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

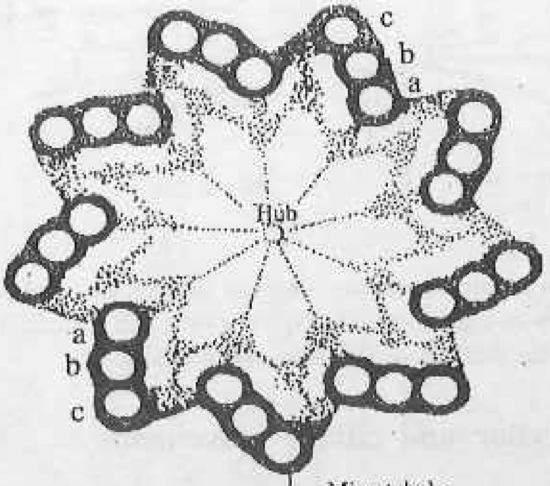


Fig. 2.2 : Diagram of the basal body (also centriole) seen in cross section. Note that the central singlets are absent. Dynein arms are absent. Nine fibrils in the outer circle are in triplets. Strands of materials extend inward from each tubule and join at the central hub.

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.

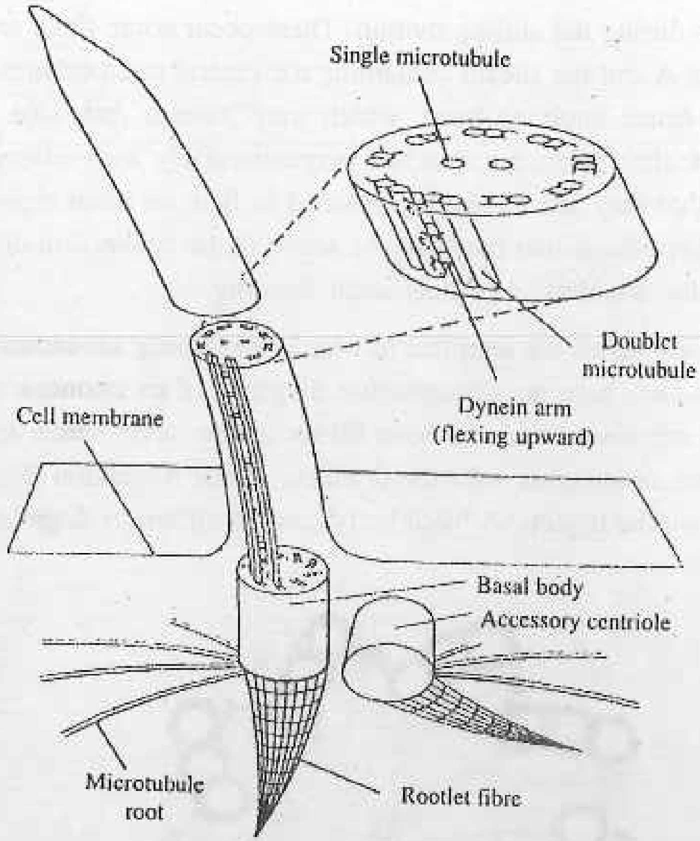


Fig. 2.3 : Ultrastructure of a flagellum or cilium. Diagram showing the basal body and its connection with the flagellum or cilium immediately below the cell surface. Two of the triplets are continuous with the doublets of the flagellum or cilium.

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

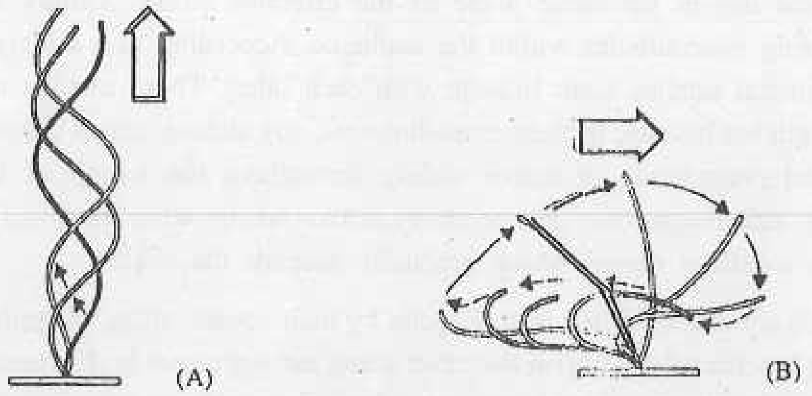


Fig. 2.4A, B : Two typical patterns of flagellar and ciliary motion. (A) Flagella bend with a standing undulatory motion. In most cases waves originate from the flagellar base and pass outward along the shaft. (B) The power stroke ofa cilium is similar to the action of an oar in a row boat; the recovery 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.

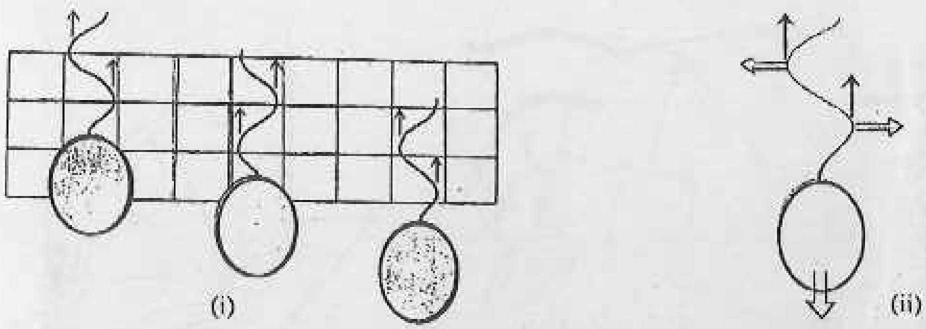


Fig.2.4C : Flagellar propulsion. Flagellar action exerts forces on the surrounding medium. (i) Base to-tip wave propagation. (ii) Forces generated by base-to-tip wave propagation. Lateral forces (outlined arrows) cancel each other longitudinal forces (solid arrows) combine to produce forward thrust in the opposite direction.

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).

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

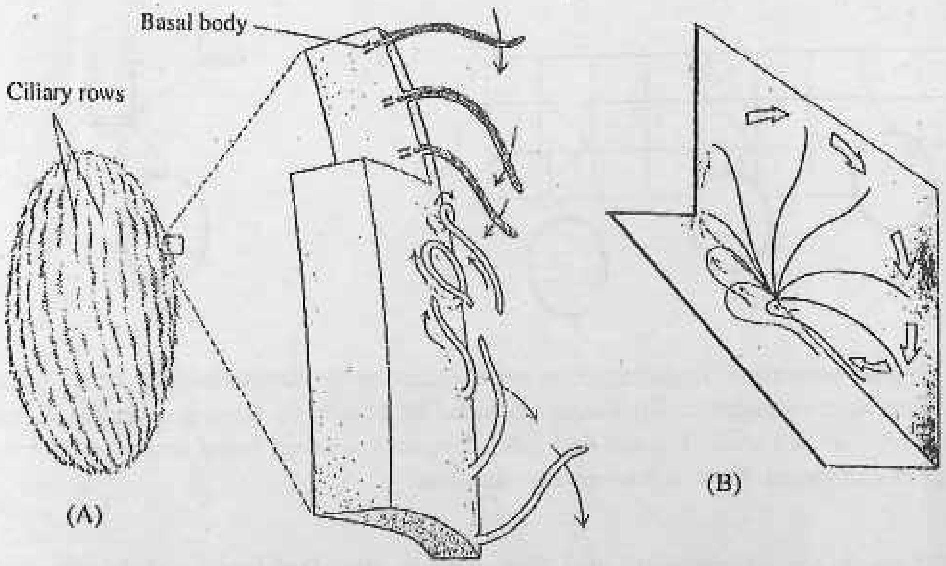


Fig. 2.5A : Metachronal wave of ciliary beating. Along the length of a row, the cilia are in a sequential stages of the beat cycle over the surface of the cell.

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.

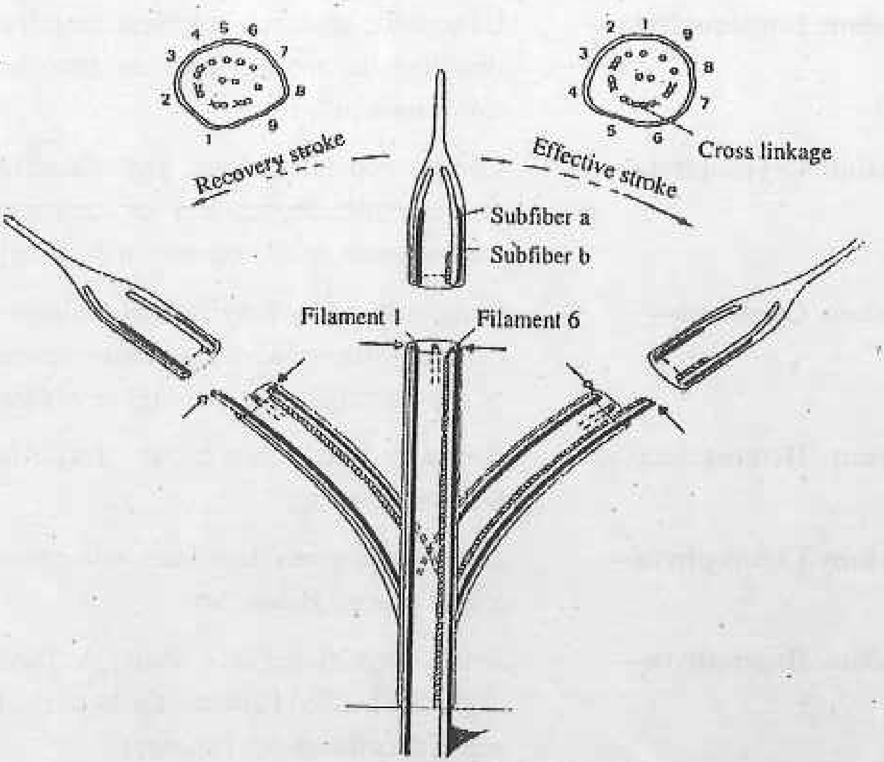


Fig. 2.6 : The sliding filament hypothesis of ciliary motility. The nature of two double filaments (1 and 6) is illustrated when a cilium is bent to either side of a straight position.

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.

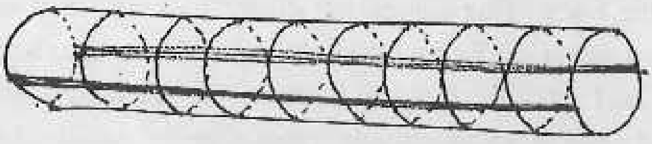


Fig. 2.7 : A hydrostatic skleleton features an enclosed volume of fluid with surrounding circular and longitudinal muscle autogtnisos. Contraction of circular muscles produces a thinning and lengthening of the body while contraction of the antagonistic longitudinal muscles produces a thickening and shortening 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).

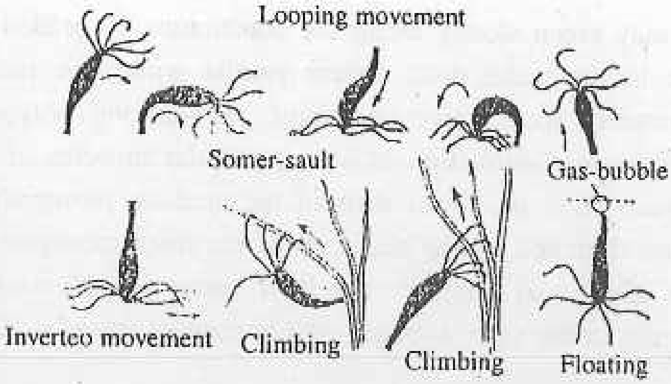


Fig. 2.8 : Different types of movement in Hydra. Normally the Hydra moves by a Soemr salting or looping type of movement

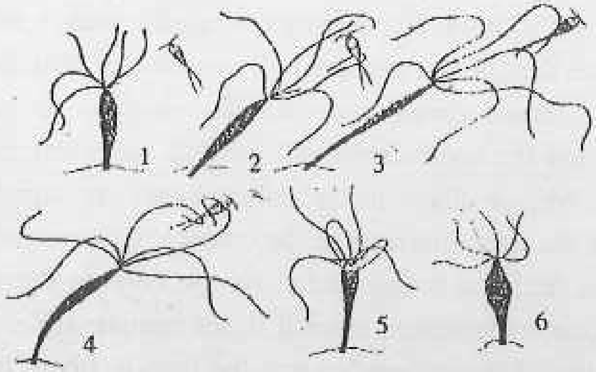


Fig. 2.9 : Movement of Hydra while capturing food. Movements are brought about by hydrostatic activities.

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).

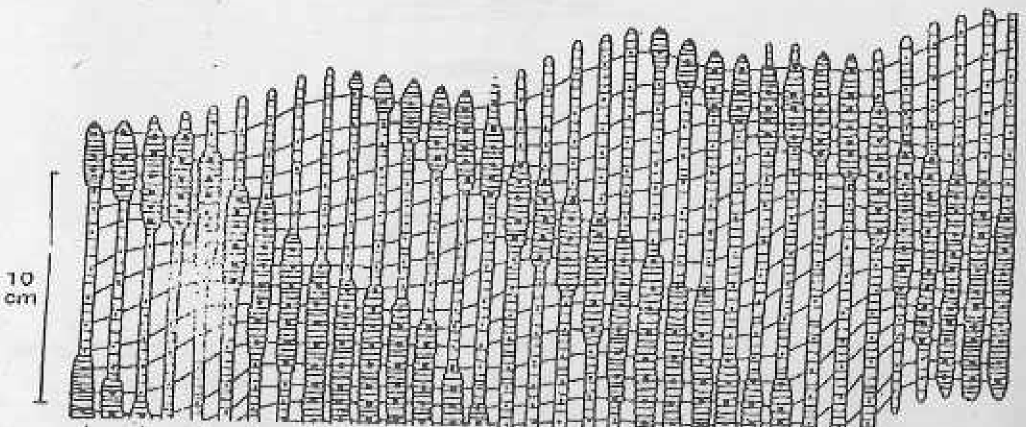


Fig. 2.10 : Diagram showing mode of locomotion of an earthworm. Segments undergoing longitudinal muscle contraction (marked with larger black dots) are wider than those undergoing circular muscle contraction (marked with small dots). The forward progression of a segment during the course of several waves 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).

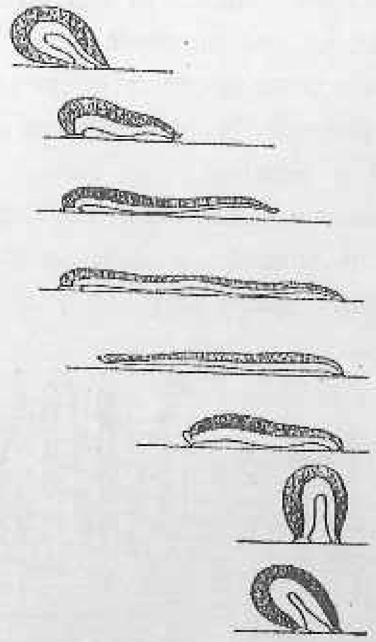


Fig. 2.11 : Locomotion in Leech. The body is lengthened and shortened. This is brought about by hydrostatic actions of circulatory system and actions of different muscles.

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).

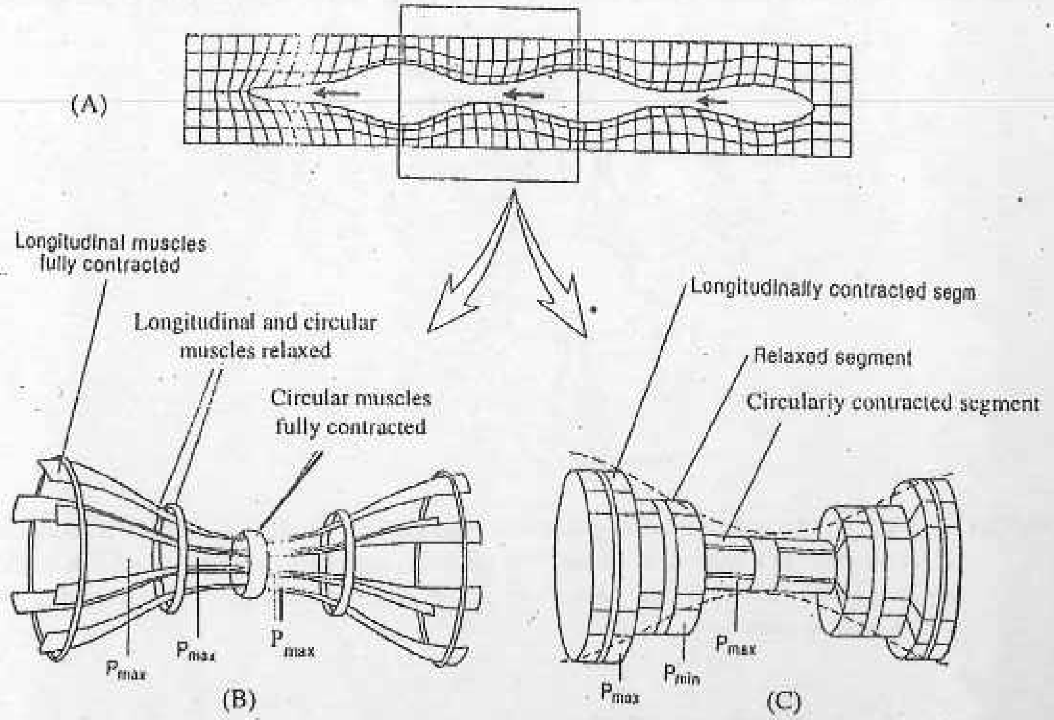


Fig. 2.12 A : Peristaltic burrowing.

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

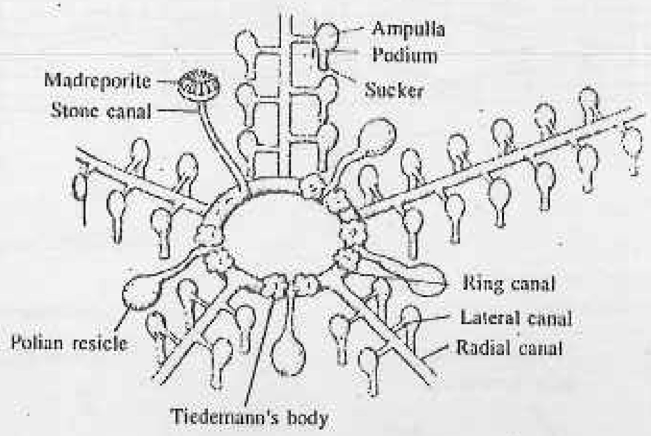


Fig. 2.13A Diagram of a water vascular system in asteroids, which functions as a means of locomotion. It operates as a hydraulic system. The effector organ is the podium or tube feet, shown in the picture. The picture also shows the disposition of different canals of they water vascular system.

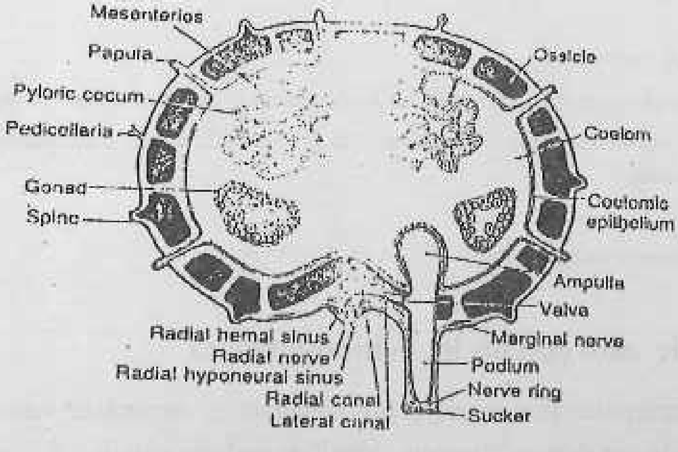


Fig. 2.13B Diagram of the cross-section through the arm of a sea star. The picture shows the podium, its ampulla, and also the valve between the lateral canal and the podium which regulate the flow of water in the tube-feet.

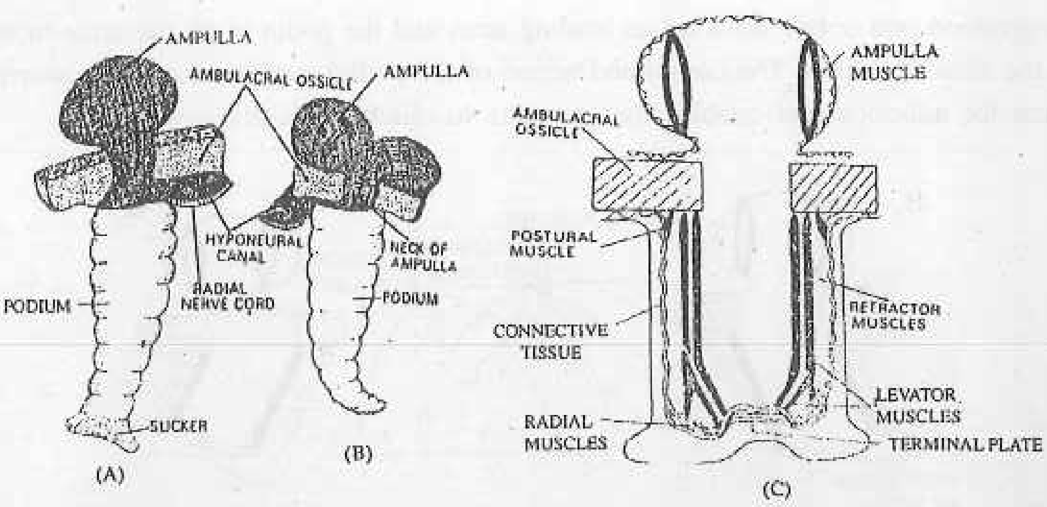


Fig. 2.14 Diagrammatic view of tube-feet. A : a scheme of ampulla and attached podium with a sucker in *Asterias rubens*. B : The same in *Astropection* sp. with podium without a sucker. C : Arrangement of chief muscles in a longitudinal section through a foot and ampulla.

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.

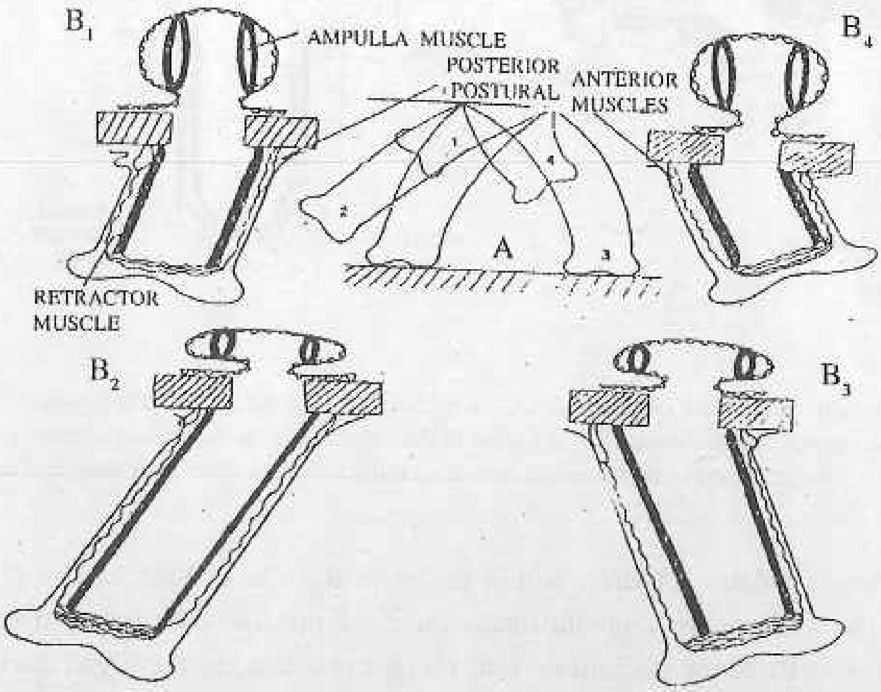


Fig. 2.15 Movement of tubes-feet (Asterias rubens) A—1—4, the successive phases of the ambulatory step B_1—B_4—conditions of contraction and relaxation of the muscles of tool during successive stages of the static posture of the 'ideal' step. Locomotion is brought about by means of a kind of hydraulic 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

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

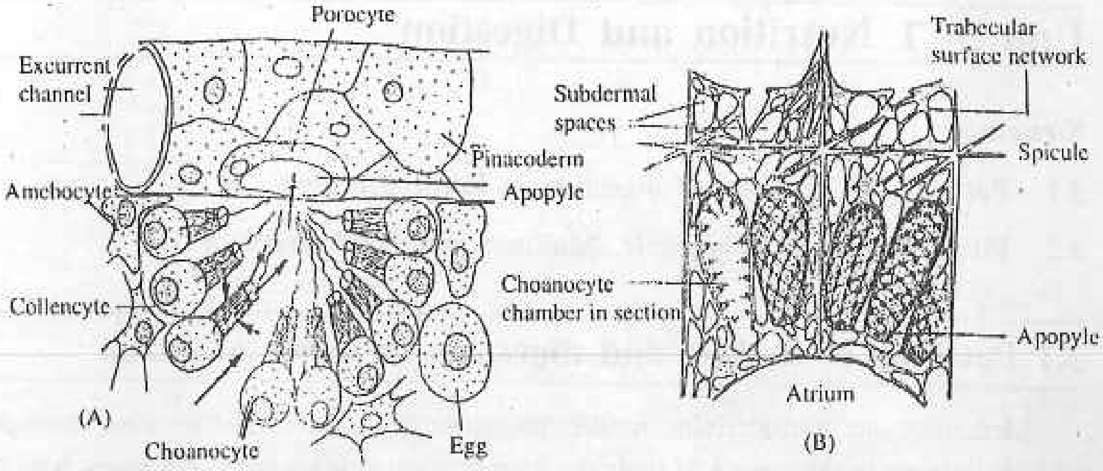


Fig. 3.1A, B A—Section through flagellated chamber of freshwater sponge. Arrows indicate direction of water currents. Food is trapped by the fibrous network of choanocyte collar and transferred to cell body. B—Choanocyte chambers within the body wall of the hexactinellid sponge.

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

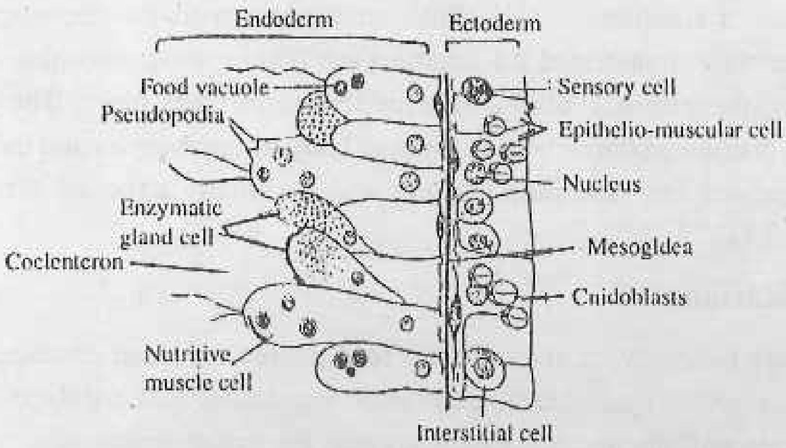


Fig. 3.2 Diagrammatic view of the histological structure of a portion of ectoderm and endoderm showing different types of cells. Note the presence of gland cells (enzyme secreting cells) and nutritive muscular cells where intracellular digestion takes place.

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).

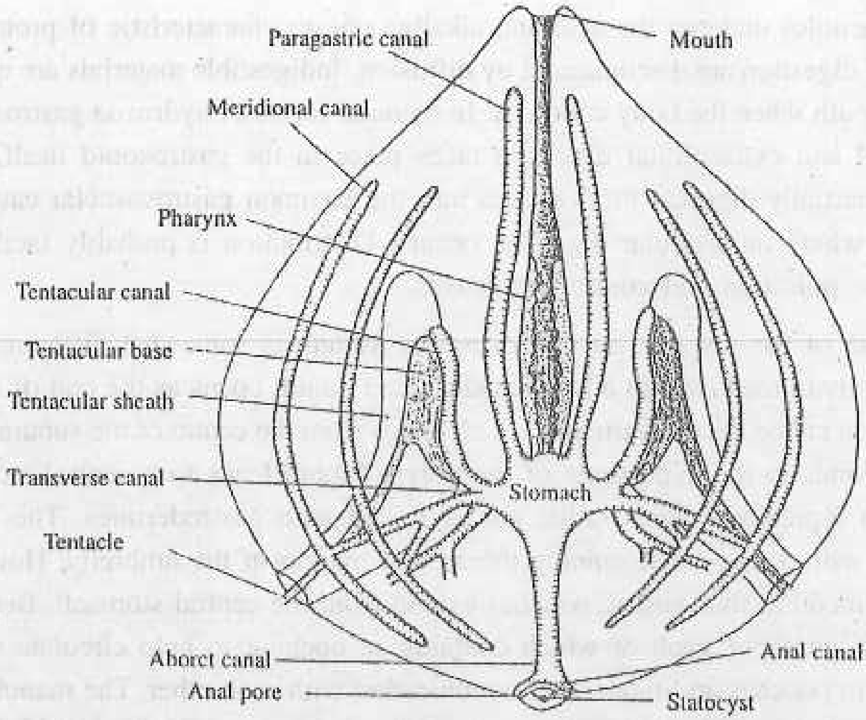


Fig. 3.3 Digestive system of a cydippid ctenophore showing branching of the alimentary system

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.

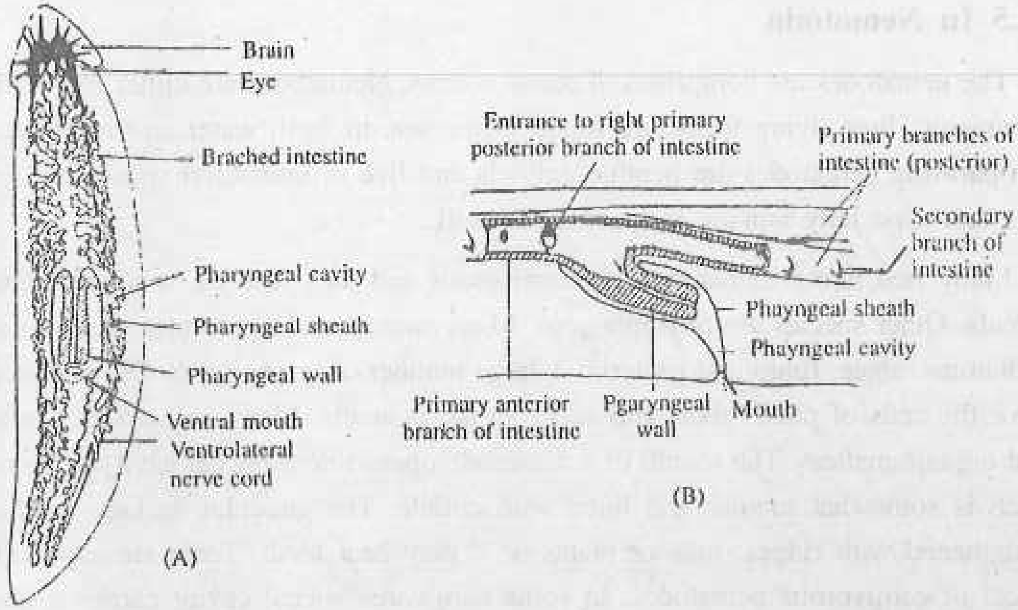


Fig. 3.4A, B A : Dorsal view of digestive system (a portion of nervous system is also fund). Note the highly branched intestine.
B : Cross section of the body at the level of the pharynx and gut showing.

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.

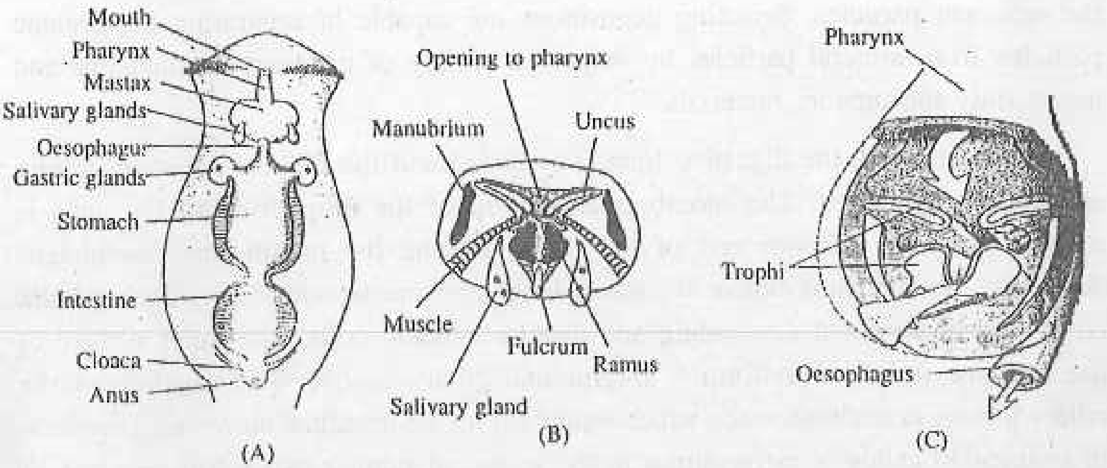


Fig. 3.5A, B, C A—Anatomy of digestive system in dorsal view. B—Enlargement of a mastax. C—Diagrammatic picture, showing relative position of pharynx, mastax and oesophagus arrows indicate the route of food through the alimentary canal

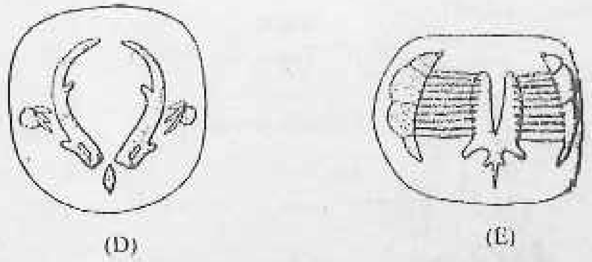


Fig. 3.5D, E Trophi in mastax; D—Incudilte trophi for seizing prey; E—Malleoramate trophi for grinding

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).

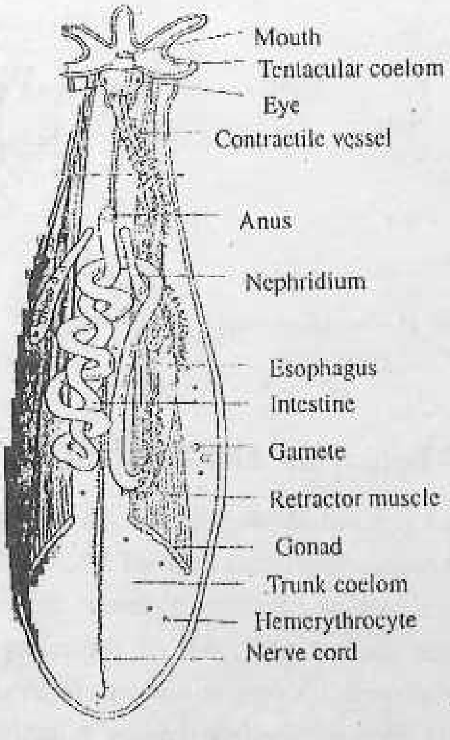


Fig. 3.6 Organization of a generalized sipunculan showing the digestive system

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.

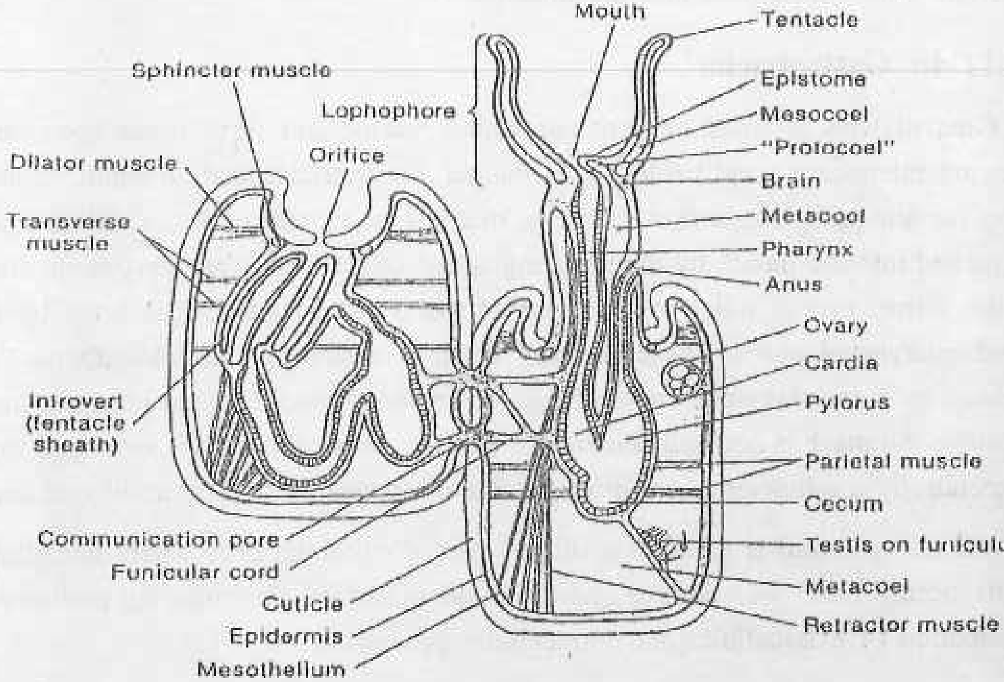


Fig. 3.7 Organization of two generalized ed bryozoan zooid, showing alimentary system. The right zooid is with an eversible introvert, bearing the lophophore.

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

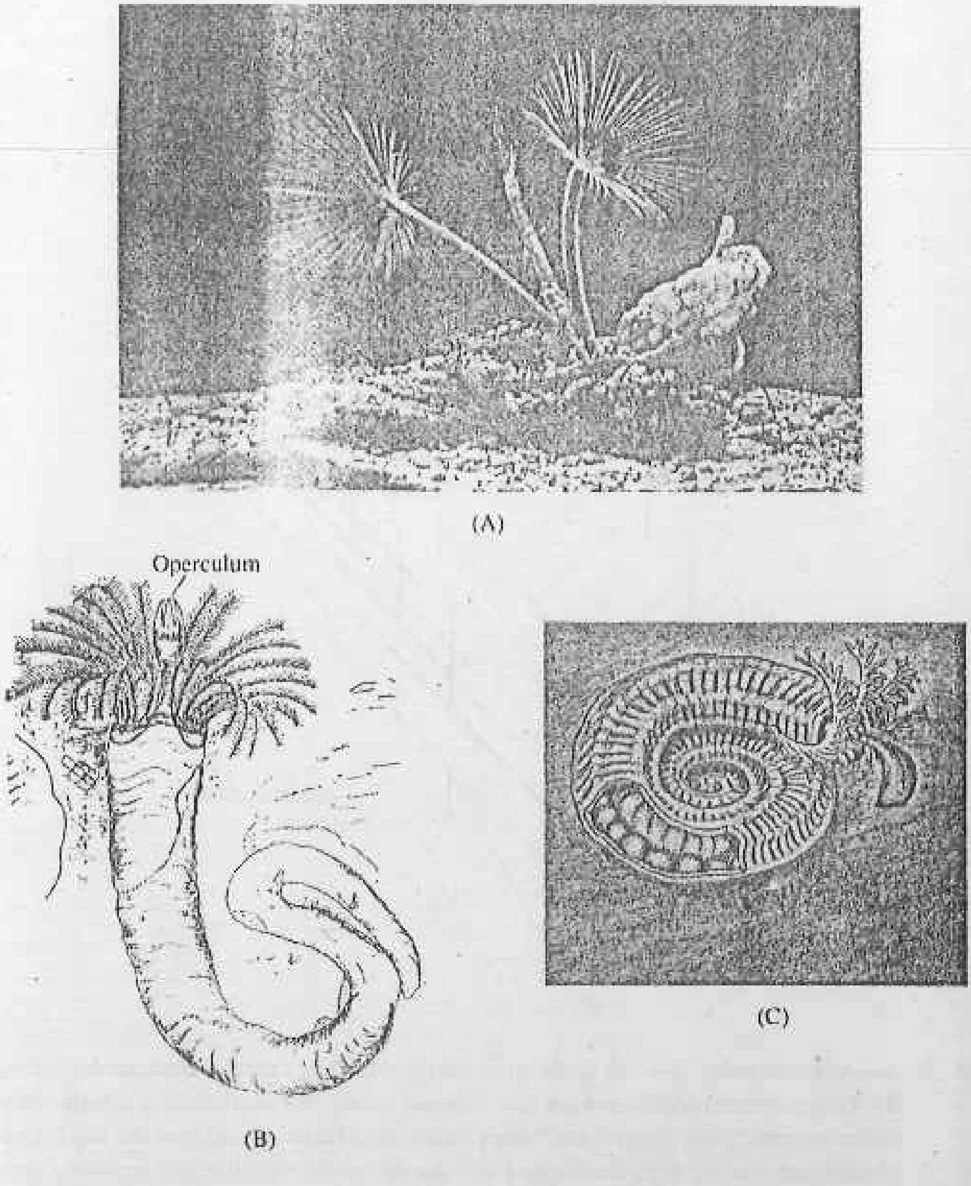


Fig. 3.8 Filter-feeding polychaetes. A. The sabellid, *Sabella paronina*, showing the expanded radioles projecting from the apertures of the tubes. B. The serpulid, *Hydroides* sp. with radioles and operculum extended from the end of the calcareous tube attached to a rock. C. A common spirobid, *Spirobis* sp. with a snail-like tube found attached to a substrata.

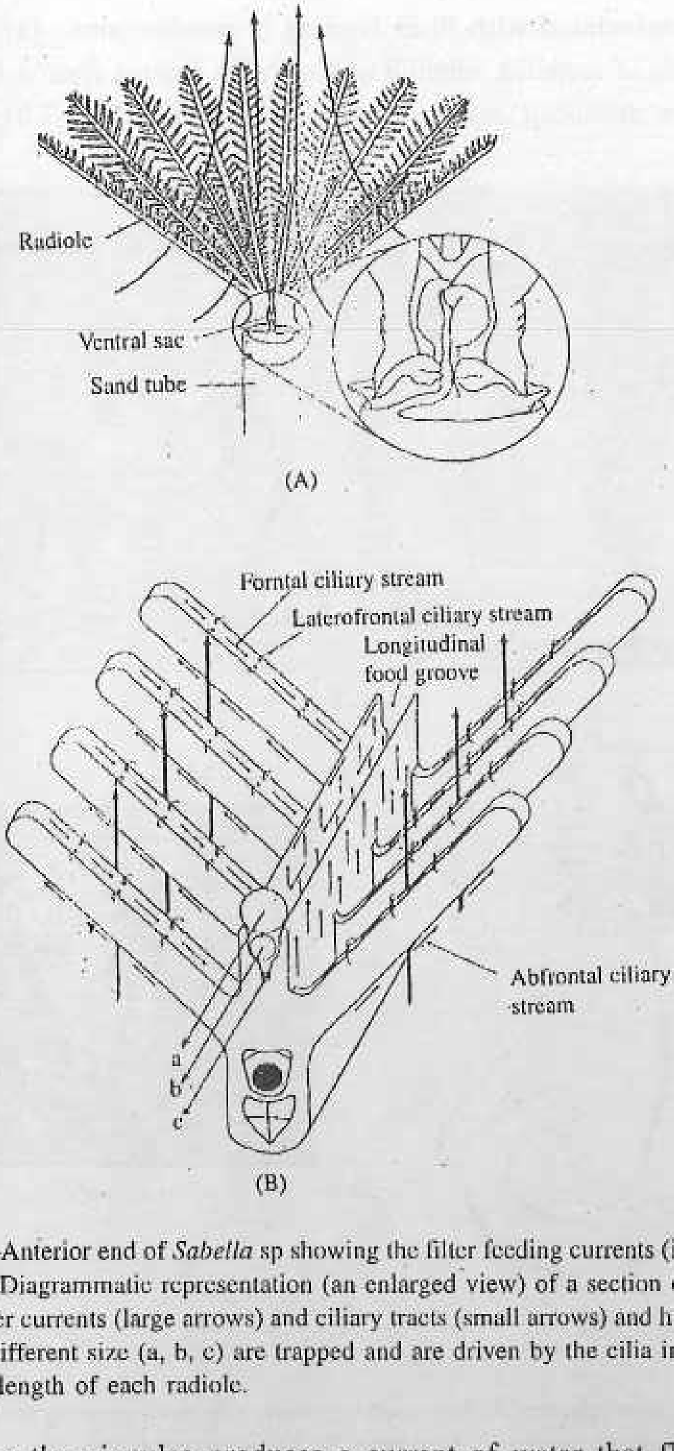


Fig. 3.9A, B A—Anterior end of *Sabella* sp showing the filter feeding currents (indicated by arrows). B—Diagrammatic representation (an enlarged view) of a section of a radiole showing water currents (large arrows) and ciliary tracts (small arrows) and how the food particles of different size (a, b, 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).

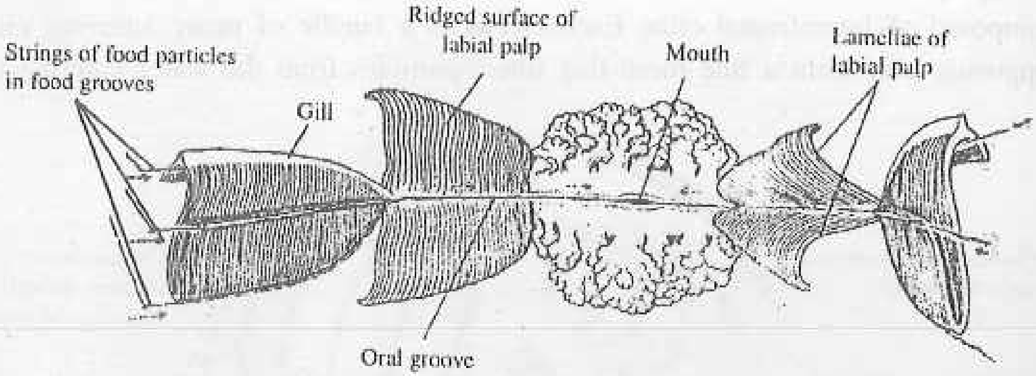


Fig. 3.10 Diagram of labial palps each with its two lamellae turned back, showing relationship to the gills and mouth. The mouth is surrounded by bushy folds. Gill cilia that originally served to keep the gills clean became adapted for the transport of particles trapped in mucous from the filter to the 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

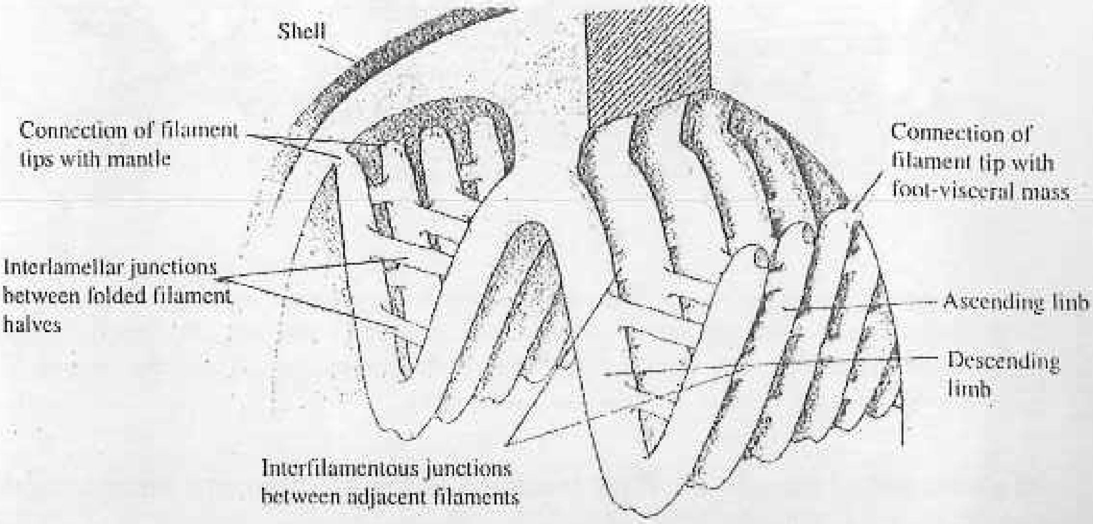


Fig. 3.11 Diagram showing modification of gills for filtering. Lengthening and folding of the gill filaments increased the surface area. Note the tissue connections that provide support for the folded lamellibtanch filaments.

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

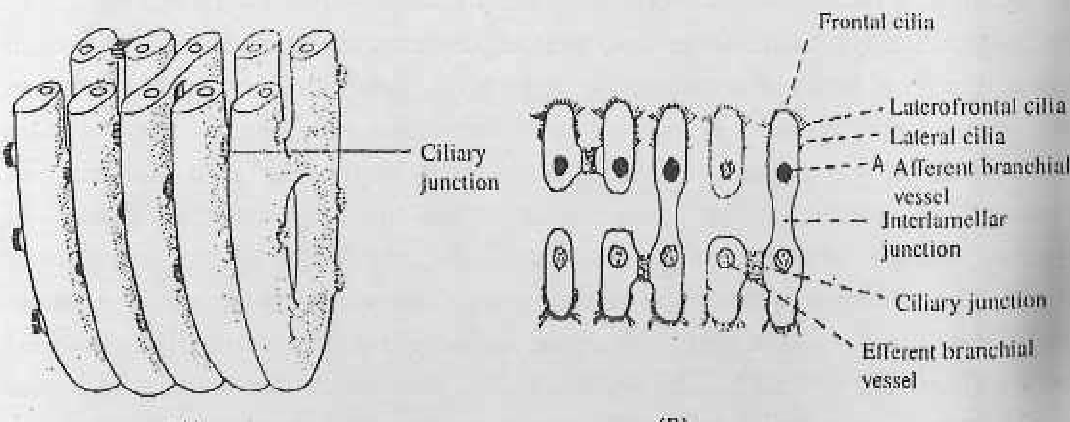


Fig. 3.12A, B A—Diagram showing five adjacent filaments (3D view). B—Frontal section.

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.

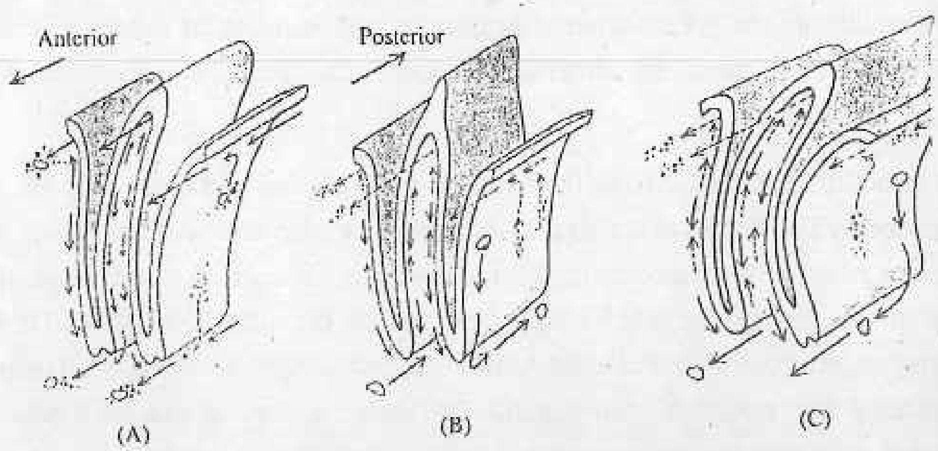


Fig. 3.13 A—Transverse section of different lamellibranch gills, showing direction of frontal cilia beat and position of anteriorly moving food tracts. In B and C broken arrows indicate the fine frontal cilia carrying food particles, upward; solid arrows indicate the coarse frontal cilia carrying particles 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

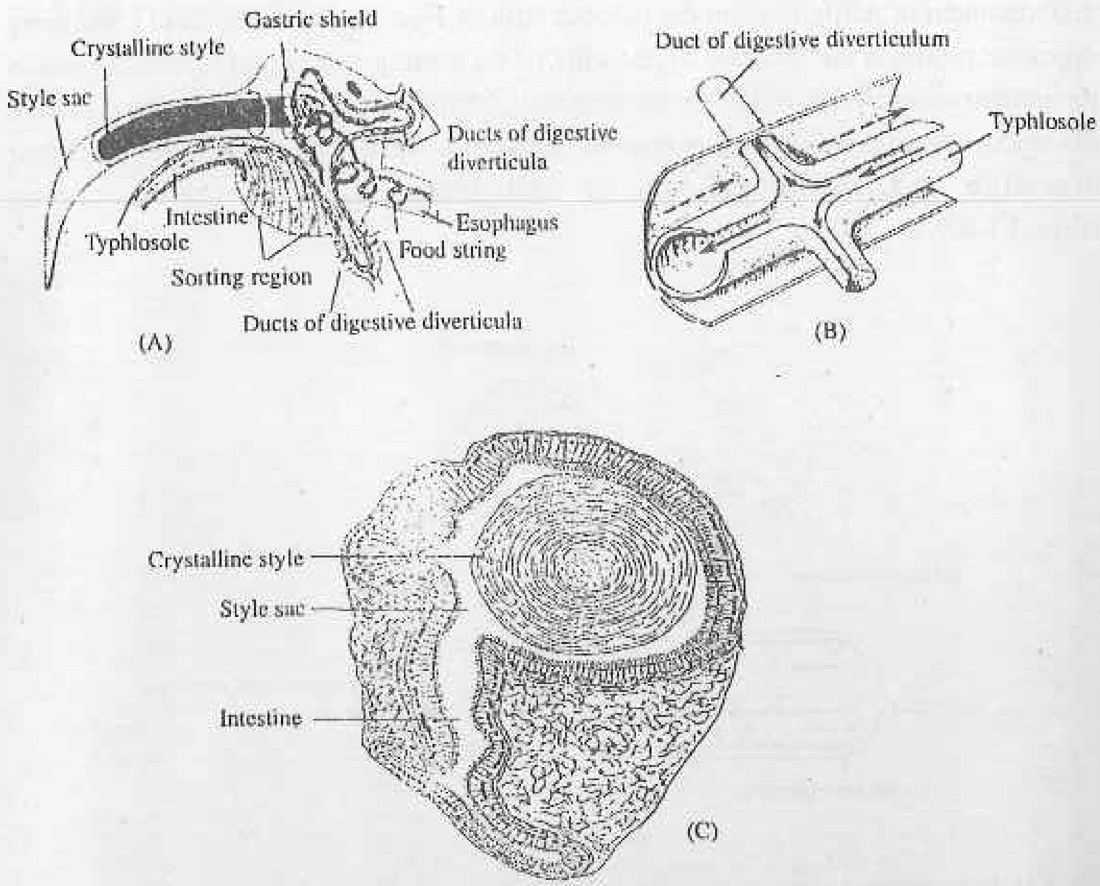
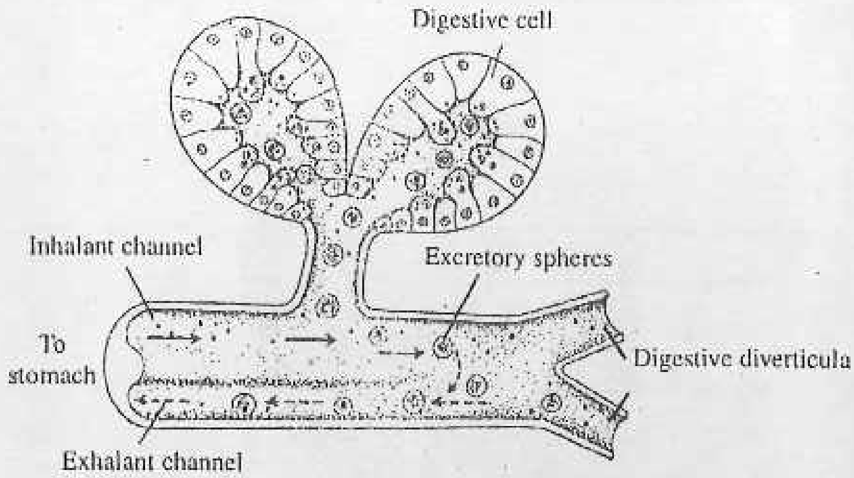


Fig. 3.14 A—Stomach showing rotation of crystalline style and winding of mucous food string in a lamellibranch. Arrows indictate the ciliary pathways. B—Style sac and intestine of the freshwater clam. C—Typhlosole within the caecum of the stomach showing extensions into the ducts of the digestive diverticula. 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).

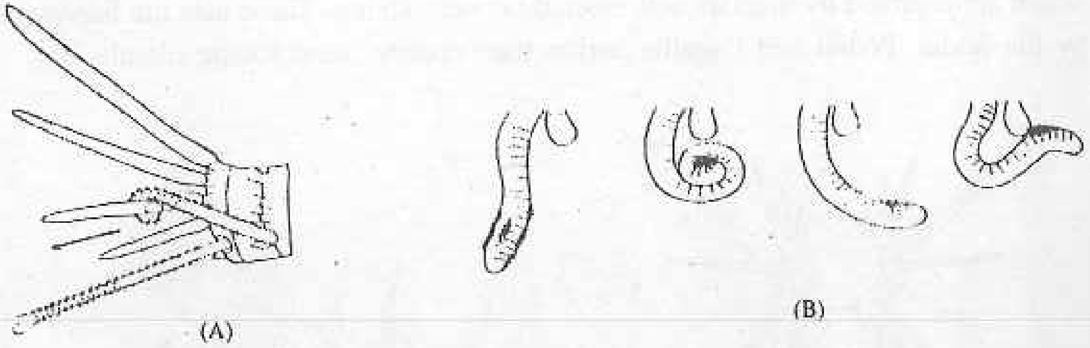


Fig. 3.15 Feeding activity of podia in brittle stars. A—Spine wiping, podium of one side wipes the spines on the opposite side of the arm. B—Particle consolidation and transfer in the suspense-feeding brittle star.

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.

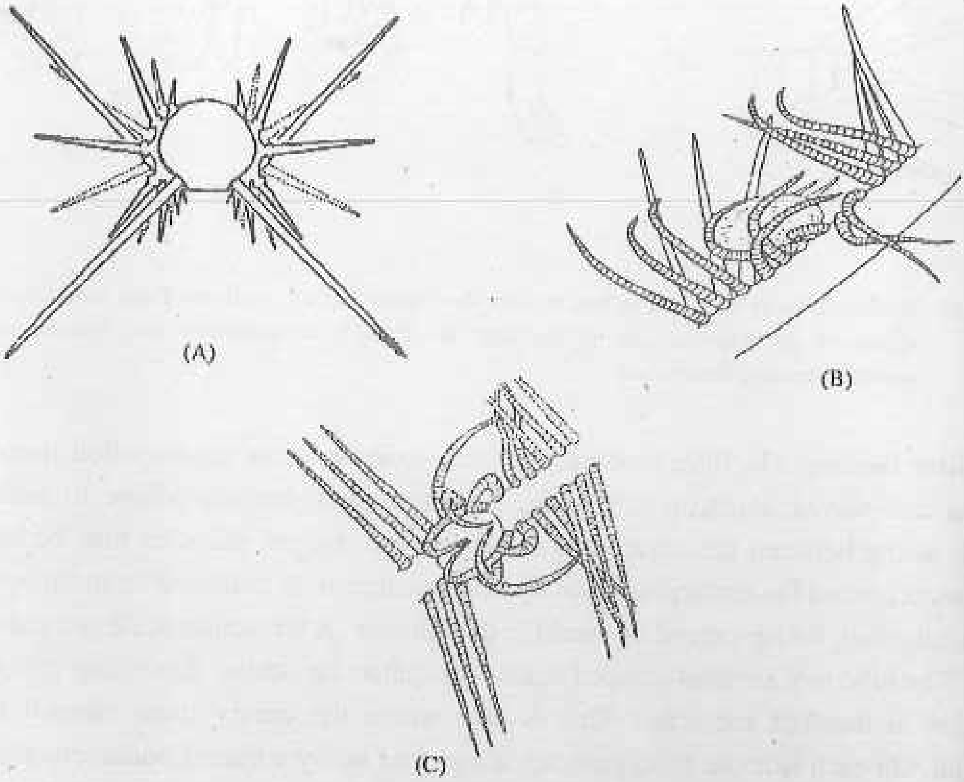


Fig. 3.16 Filter feeding in ophiuroids. A—End view of arm section of the brittle star showing spines and position of tube feet. Alternate tube feet are directed orally and aborally. Tube feet may also be extended laterally, forming a single filtering series on either side of the arm. B—C, particle collection 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).

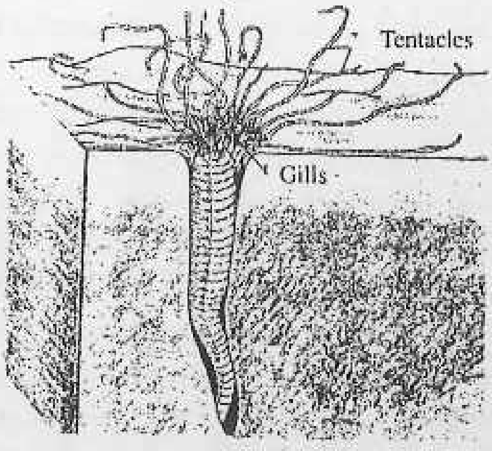


Fig. 4.1 Diagrammatic view of a polychaete showing the gills and outstretched tentacles over the substratum.

(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

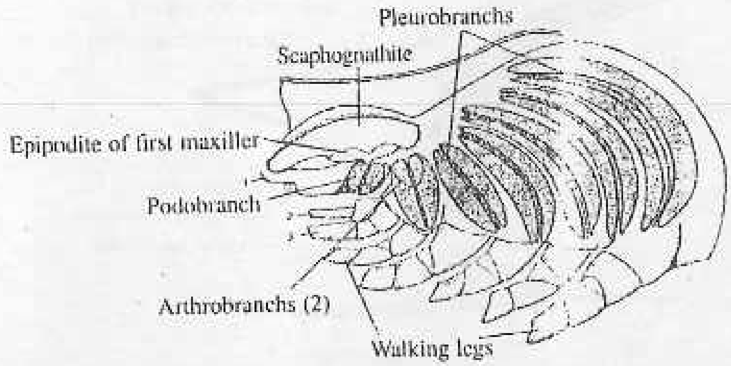


Fig. 4.2A Diagrammatic view of the gill-chamber of prawn exposed to show the arrangement of gills. Gills are pleurobranchs.

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.

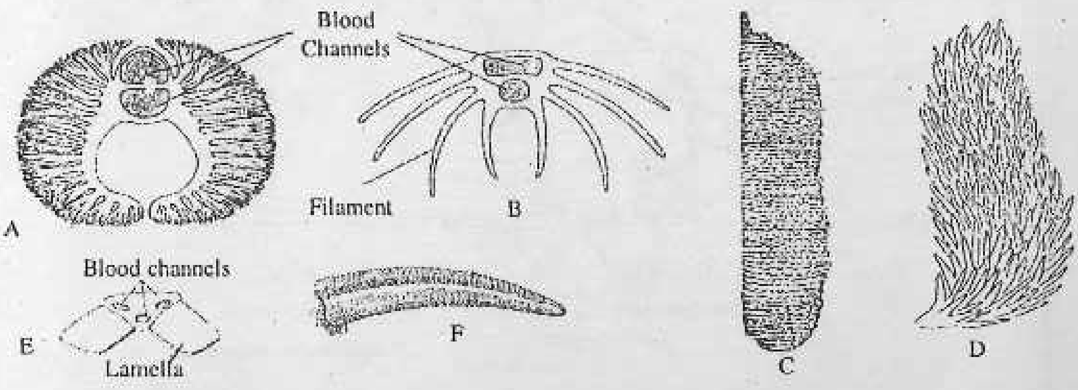


Fig. 4.2B Diagrammatic representation of decapod gills. A and C, dendrobranchiate gill of penaeid shrimp. The gill branches are subdivided. A—transverse section; C—Lateral view of the entire gill. B and D—filamentous or trichobranchiate gill of lobster, crayfishy and some other groups. The gill branches 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).

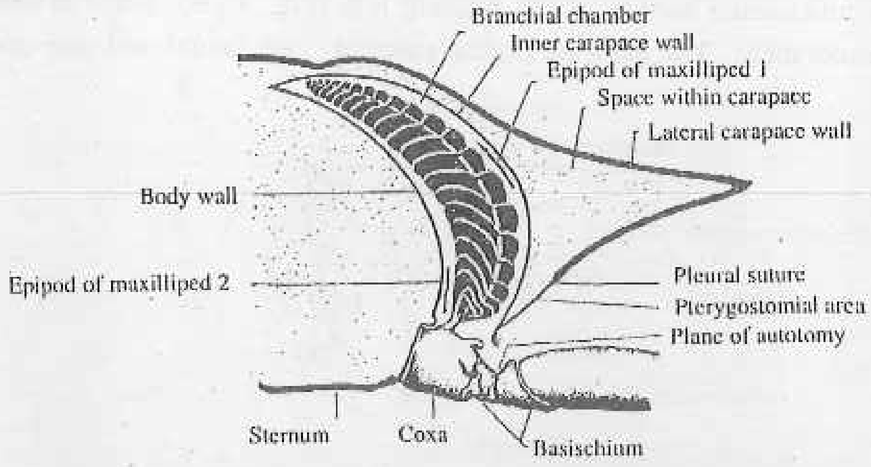


Fig. 4.3 Diagrammatic view of cross section through the gill chamber of a crab.

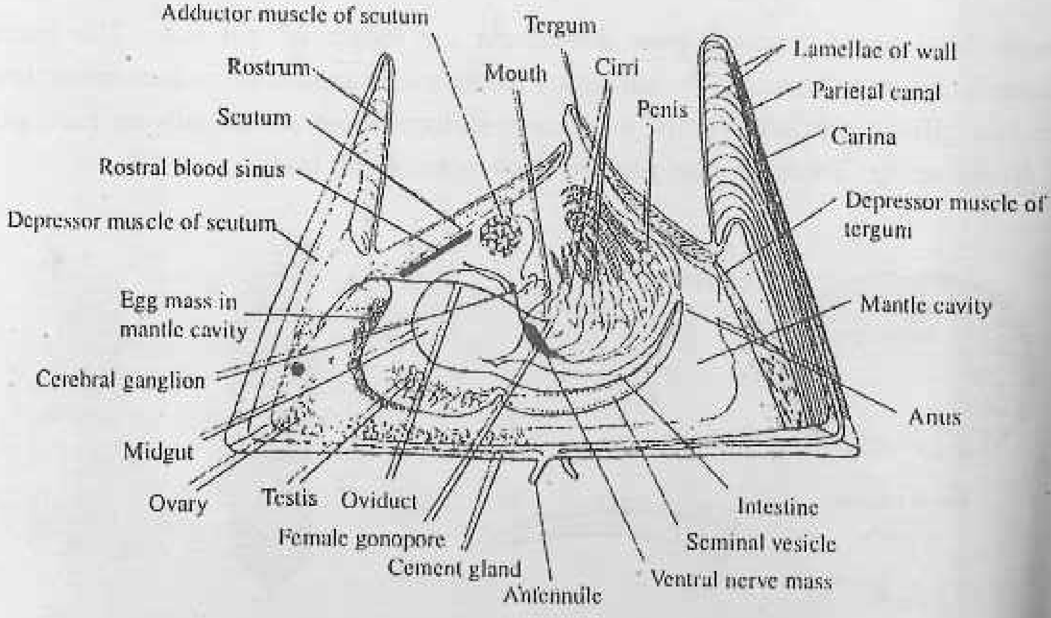


Fig. 4.4 Diagrammatic view of the vertical section of *Balanus* sp. showing the visceral. Note six pairs of long, biramous cirri, probably the principal sites for gas exchange.

(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).

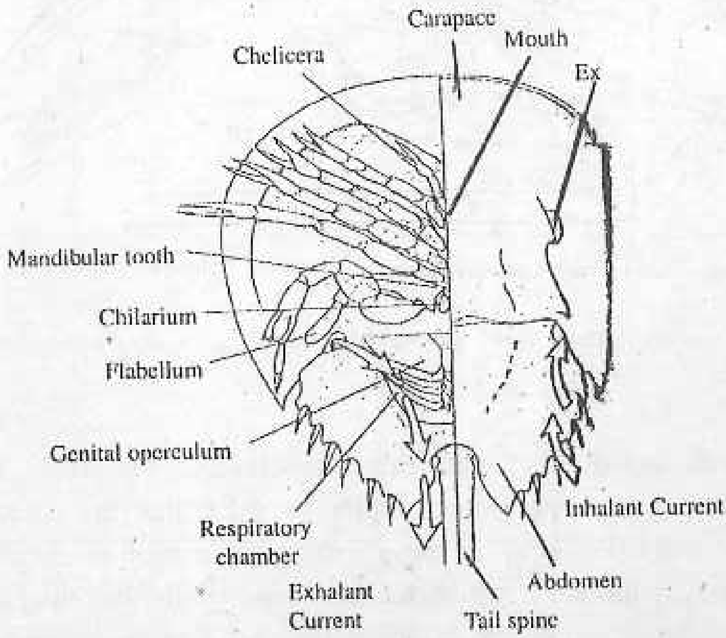


Fig. 4.5 A horse shoe crab (left half-ventral; right half-dorsal). Ventral side shows book gills containing lamellae on the under surface of each flap which provides actual surface for gas exchange.

(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.

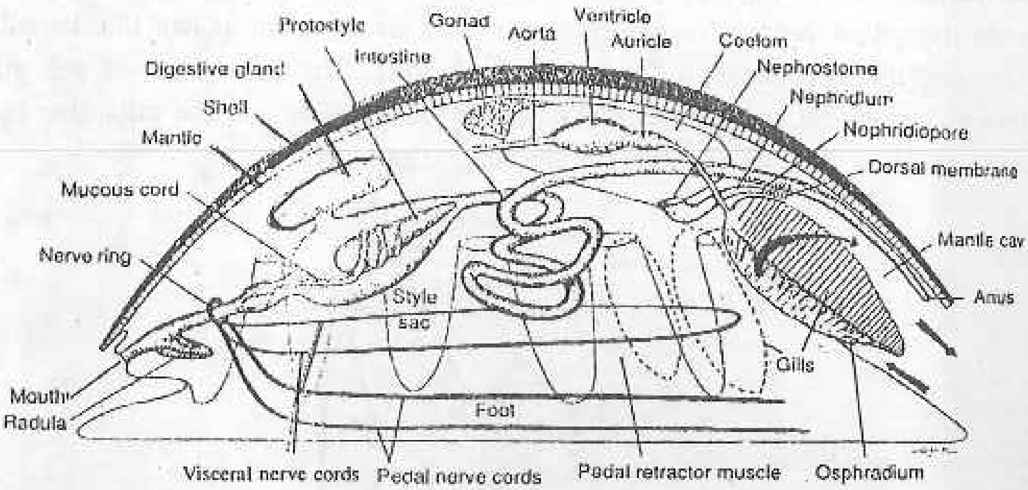


Fig. 4.6 Generalized mollusc (lateral view). Arrows indicate path of water current through mantle cavity.

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 culamellibranch 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

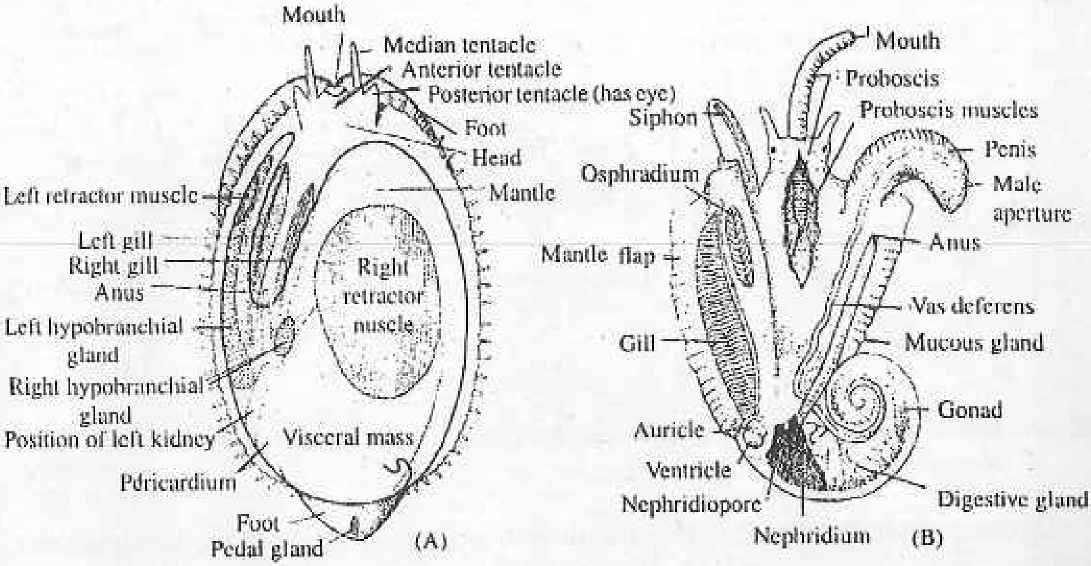


Fig. 4.7 Dorsal view of (A) *Haliotis* sp (prosobranch) with the shell removed and the mantle cavity exposed, showing the anterior position of the gill. (B) *Buccinum undatum* (prosobranch); dorsal view with shell removed & mantle cavity exposed.

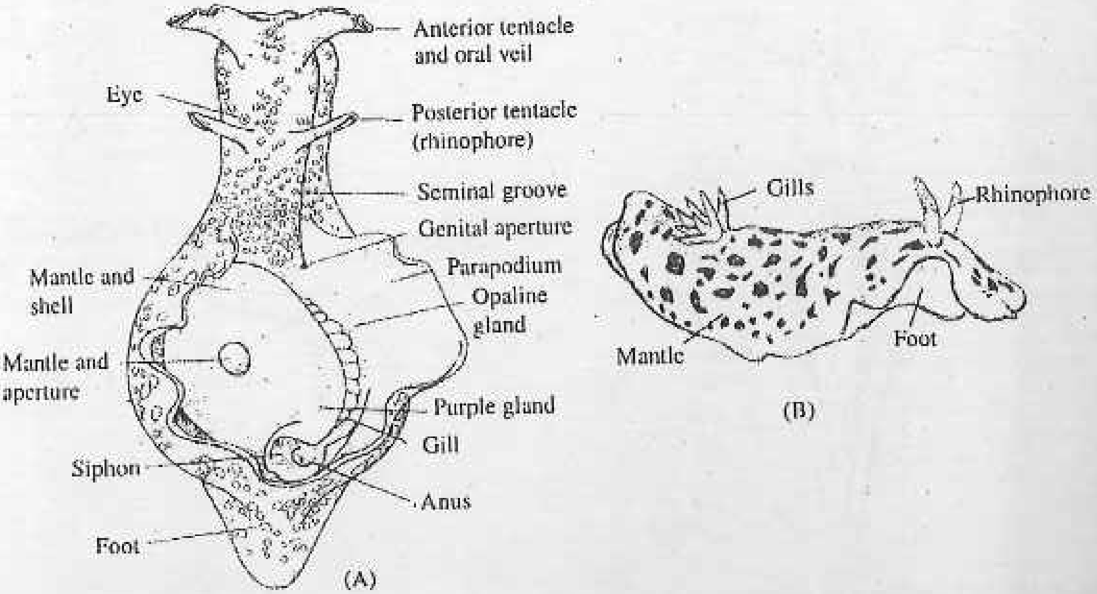


Fig. 4.8 A, B (A) Opisthobranch, a sea hare, an anaspidean, here gill is present. (B) *Glossodoris* sp. with secondary anal gills.

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).

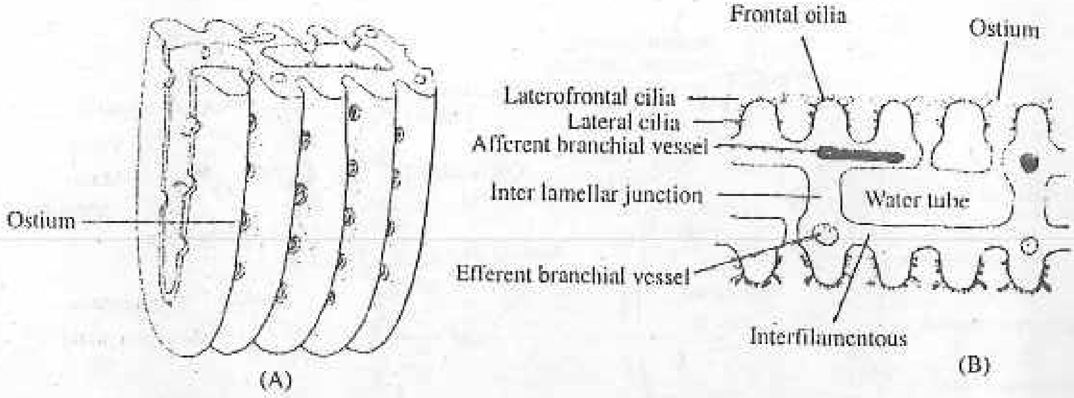


Fig. 4.9 Eulamellibranch gill. A : Five fused, adjacent filaments; B : Frontal section. (Diagrammatic representation).

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).

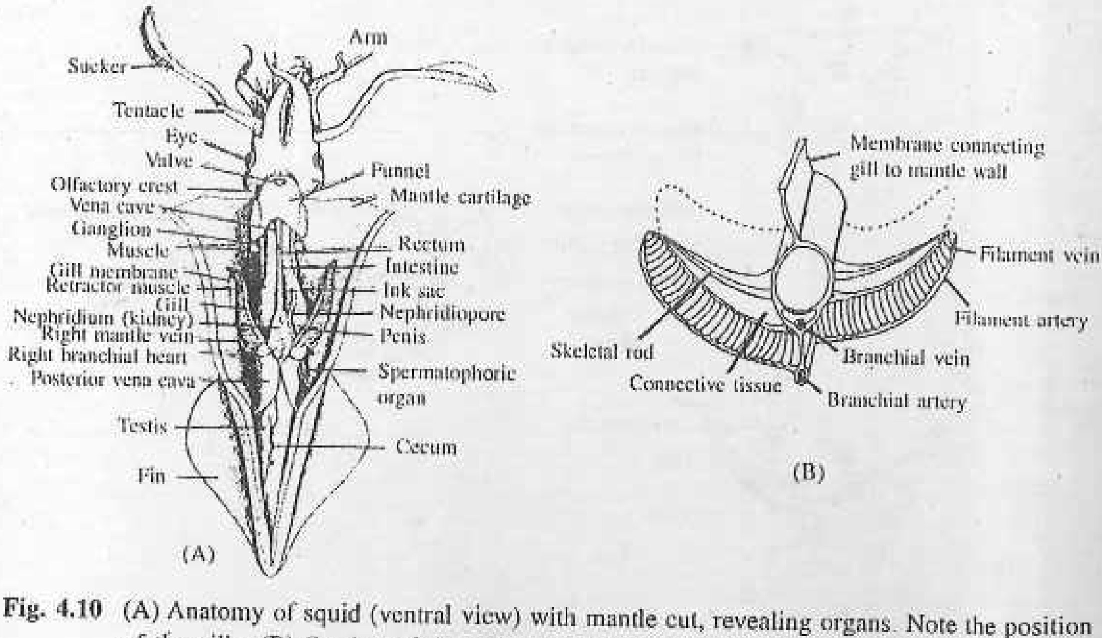


Fig. 4.10 (A) Anatomy of squid (ventral view) with mantle cut, revealing organs. Note the position of the gills: (B) Section of the gill axis, showing two filaments on either side; only the outlines of the posterior two are shown.

(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.

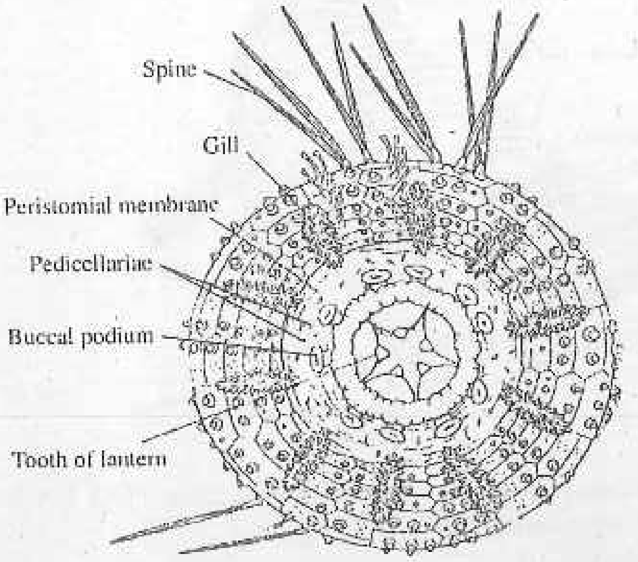


Fig. 4.11 In regular sea urchin (echinoid) five pairs of peristomial gills are important centers of gas-exchange.

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).

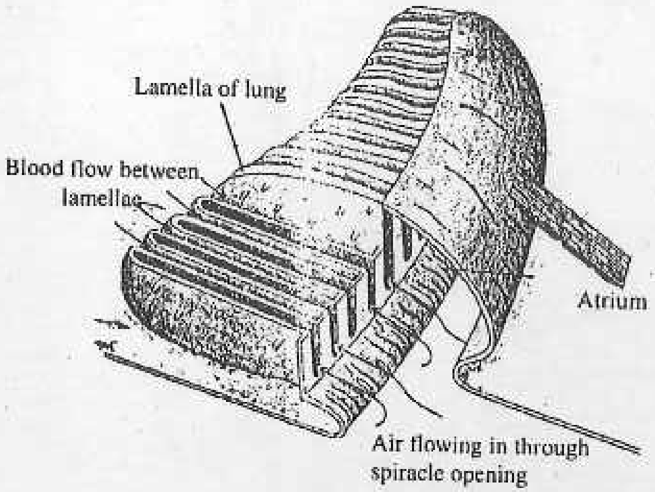


Fig. 4.12 Diagrammatic section through a book lung. Arrows indicate blood flow (on the-left) and air flow (on the right) through spiracles.

(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.

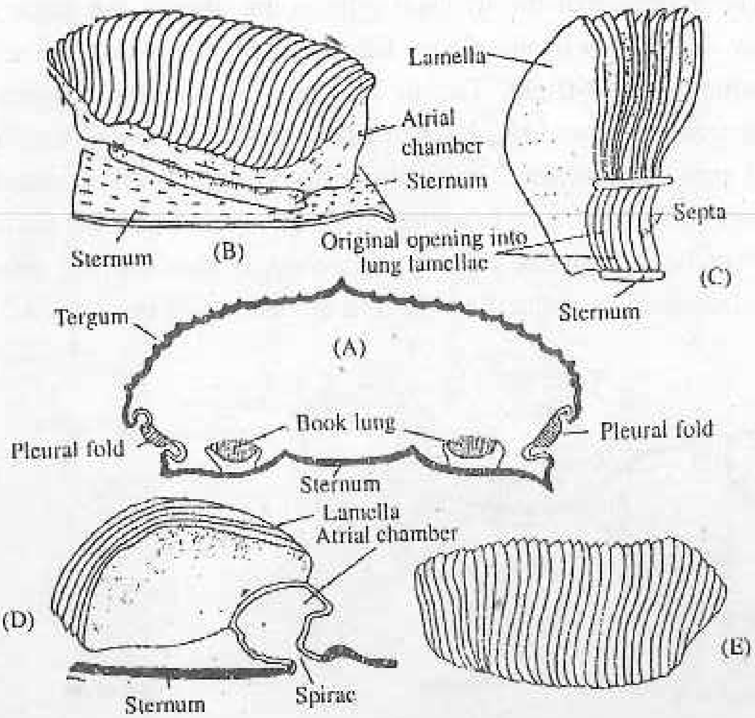


Fig. 4.13 Structure of the book-lung of scorpion. A : Cross section of the body of Scorpion showing the position of the book lung. B : Dorso-posterior view of the right book lung. C : A few lamellae in natural position. D : Vertical section of a book lung, E : Dorsal view of book-lung.

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).

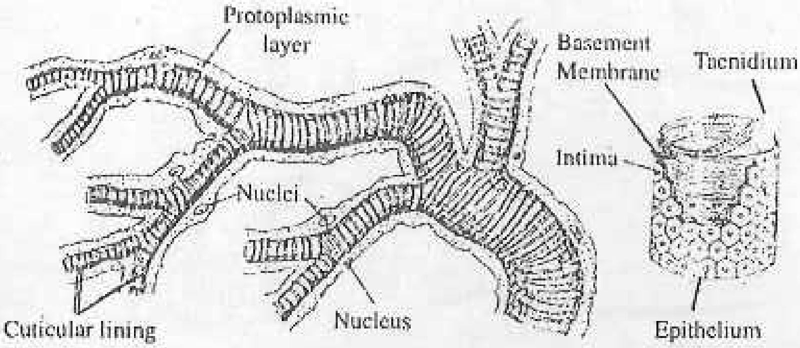


Fig. 4.14A Diagrammatic view of a portion of trachea (enlarged view)

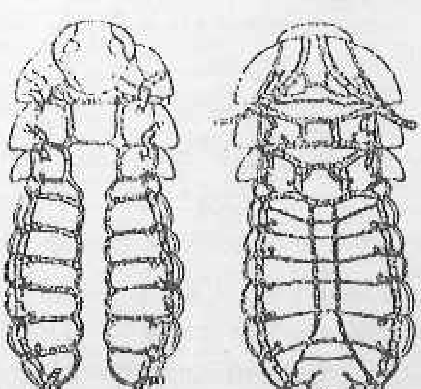


Fig. 4.14B Tracheal system of *Periplaneta* sp.

(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 hemococlomic 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

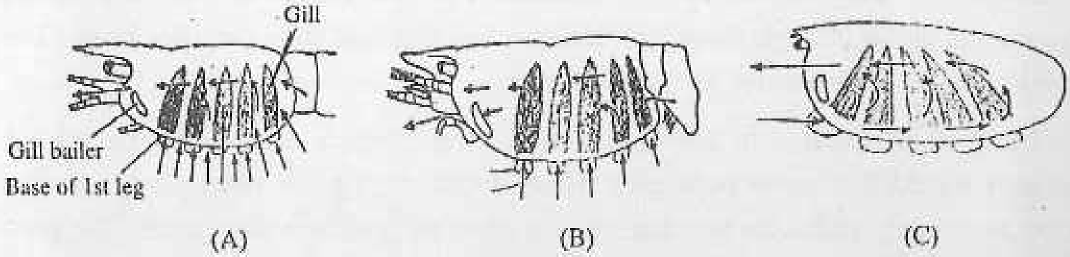


Fig. 4.15A, B, C Paths of water circulation through the gill chamber of three decapods, showing progressive restriction of openings into the chamber.
A—Shrimp; water enters along entire ventral and posterior margin of the carapace.
B—Crayfish; water enters at the bases of the legs and at the posterior carapace margin.
C—Crab; water enters only at the base of the cheliped.

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 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 etenidial 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.**

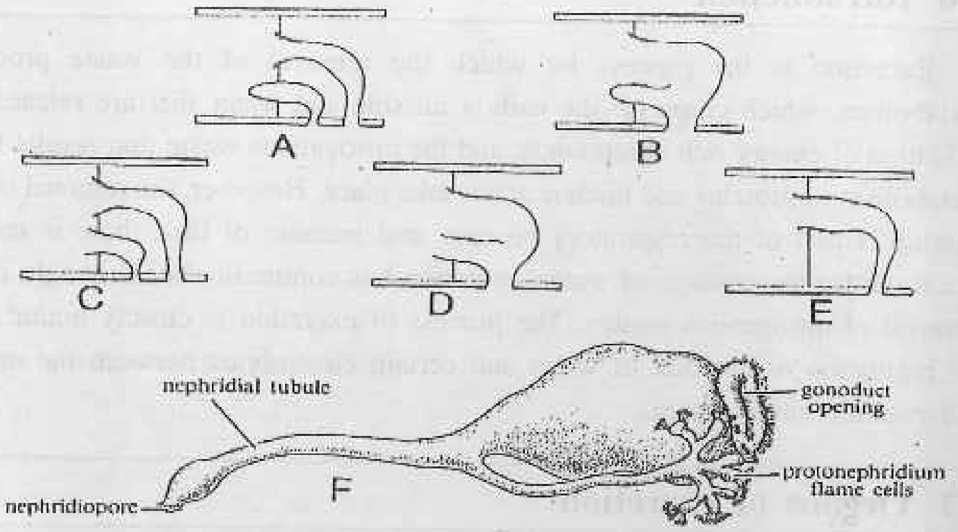


Fig. 5.1 Annelid nephridia. A, B, C, D, E. Variations in union of gonoduct and nephridium. A. Primitive condition, with separate protonephridium and gonoduct with ciliated funnel, as in **Vanadis,** B. Protonephridium united with gonoduct, as in **Phyllodoce,** C. completely separate metanephridium and 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.

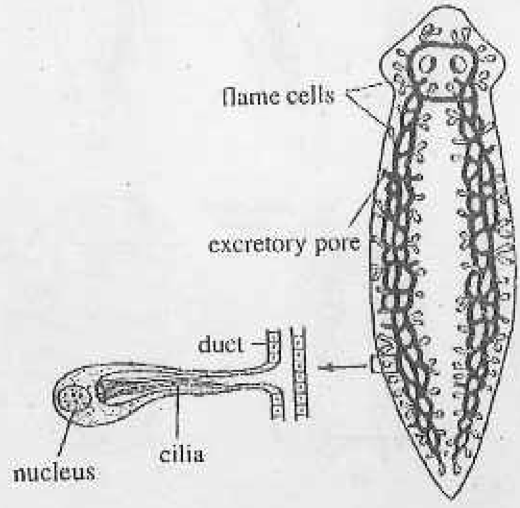


Fig. 5.2 Excretory system & nephridium of *planaria*

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.

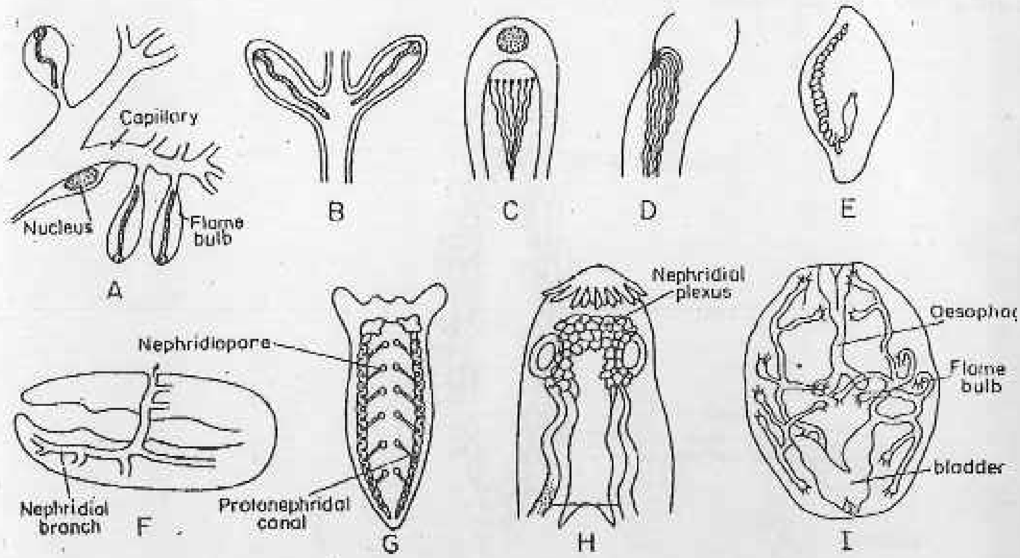


Fig. 5.3 Showing the excretory organs in different platyhelminathes (A). A part of nephridia showing flame bulb derived fro a single cell. (B) Flame bulb showing the tip of flame. (c) Typical flame cell (C) A typical flame cell. Nephridium of *Rhabdoceelcs.* (E) *Alloeocoeles.* (F) *Triclad.* (G—H) Nephridial 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.

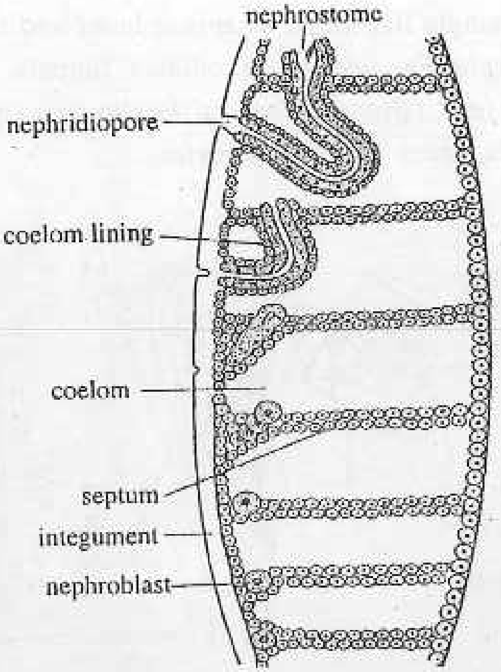


Fig. 5.4 Relationship of coelomoducts & nephridia in primitive annelids.

The particular complication in the polychaetes is that their nephridia frequently bears ciliated funnels, they are then termed **metanephridia.**

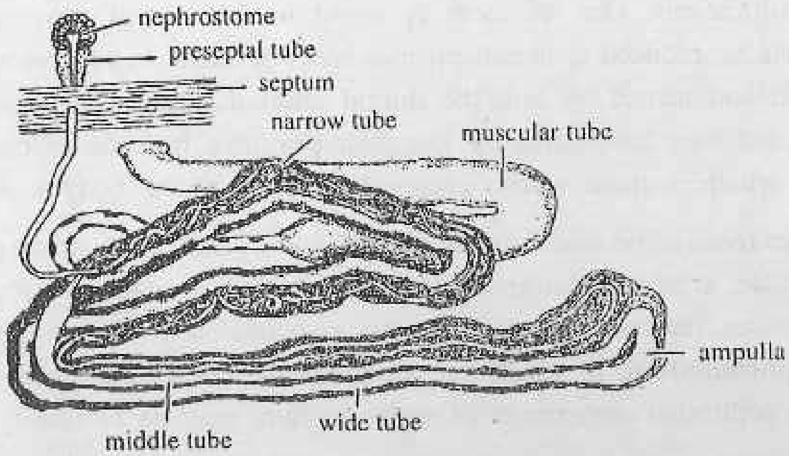


Fig. 5.5 Nephridia in *Lumbricus* sp.

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.**

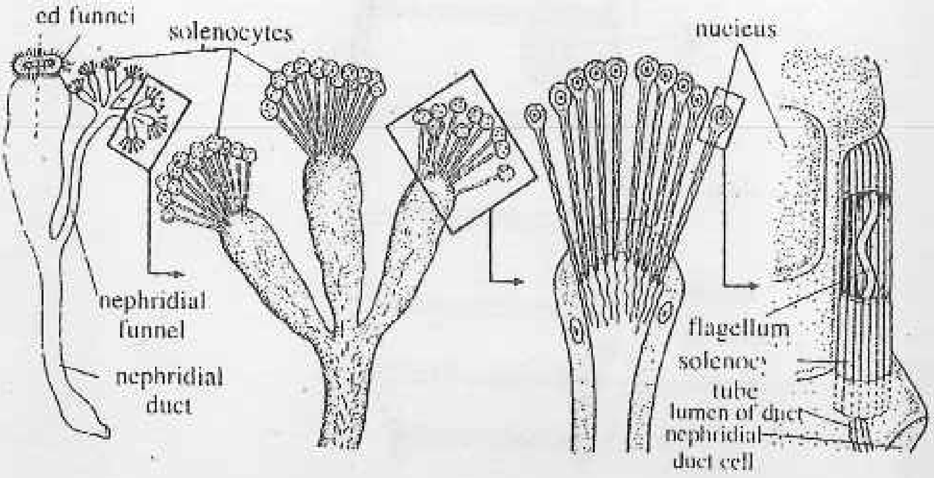


Fig. 5.6 Structure of excretory apparatus in Annelida

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.

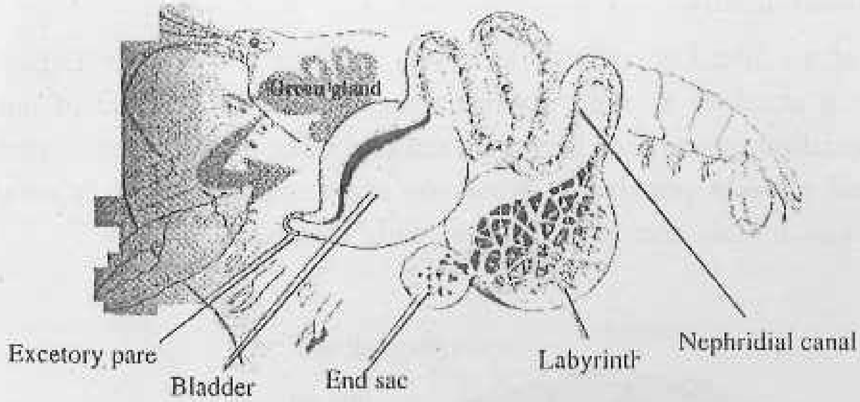


Fig. 5.7 Excretory system of Cry fish

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).

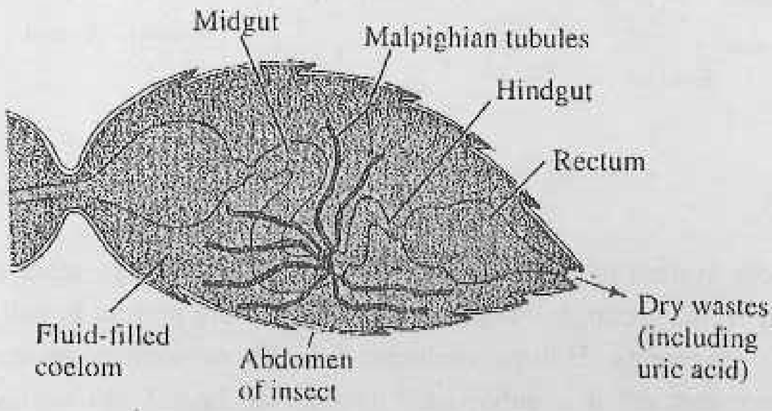


Fig. 5.8 Malpighian tubules in Insect

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.

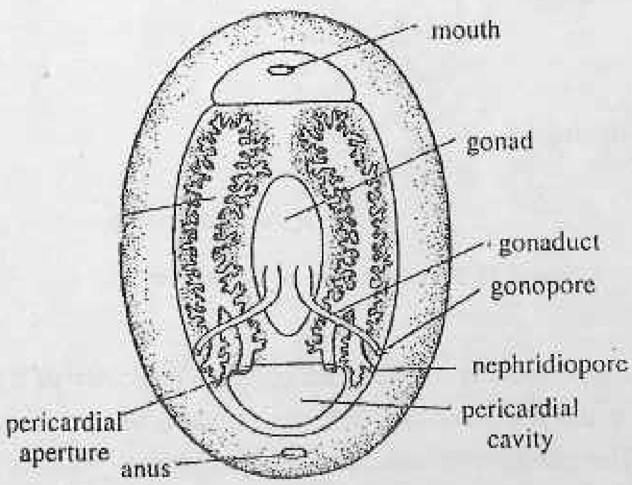


Fig. 5.9 Excretory system of *Chiton*

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.

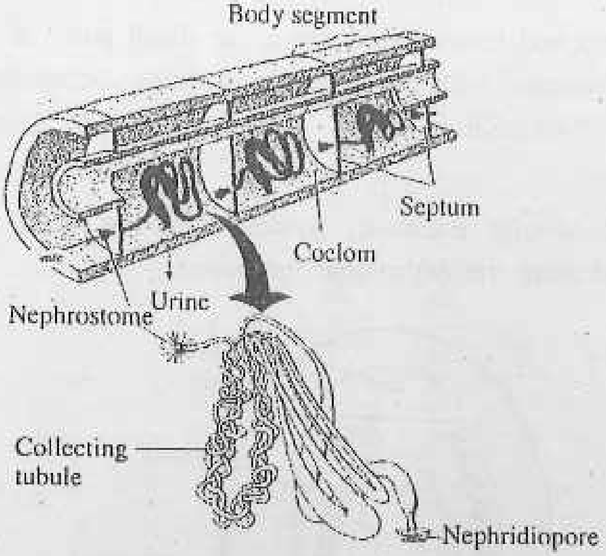


Fig. 5.10 Metanephridia in Earthworm

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.

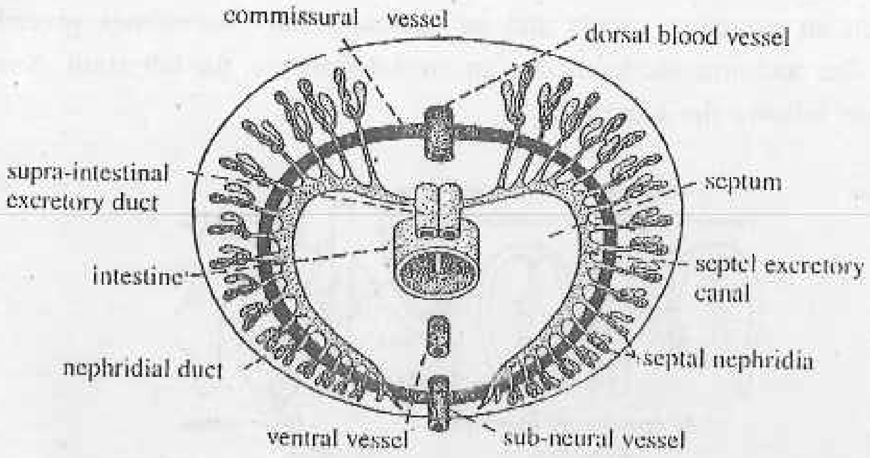


Fig. 5.11 Relative position of septal nephridia and intestine in Earthworm

The nephridium is thus a blind sac (protobranches). In pulmonates, the nephridiopore opens at the back of the mantle cavity.

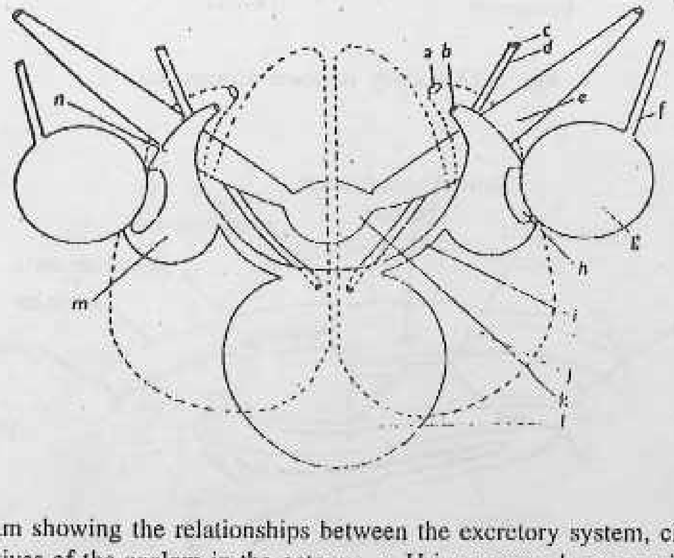


Fig. 5.12 Diagram showing the relationships between the excretory system, circulatory system and derivatives of the coelom in the octopus, a. Urinary pore; b. renopericardial canal opening into the renal sae; c. gonopore; d. gonoduct; e. auricle; f. afterent branchial vein; g. branchial heart; h. branchial 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.

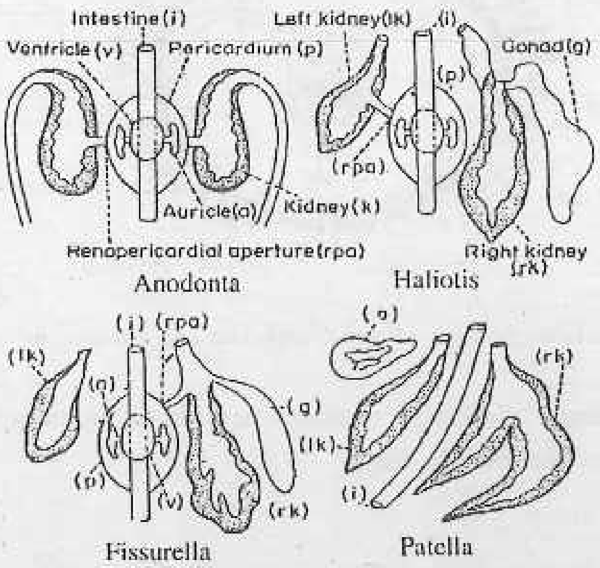


Fig. 5.13 Kidney in some Grastropods

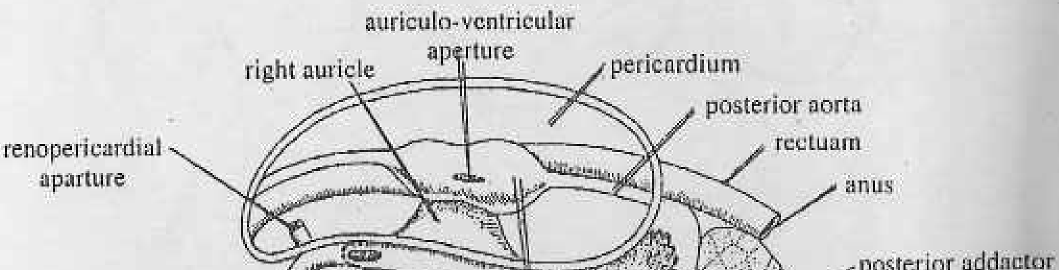


Fig. 5.14 Relative position of heart, rectum and kidney of *Unio* sp.

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.

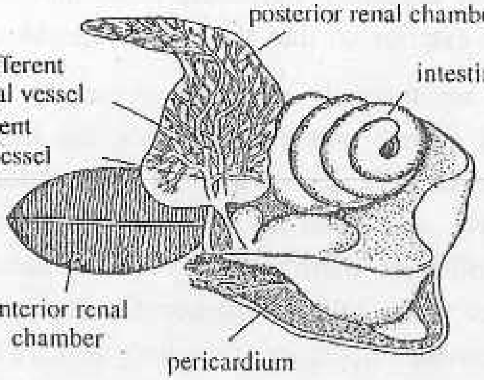


Fig. 5.15 Kidney of *Pila* sp.

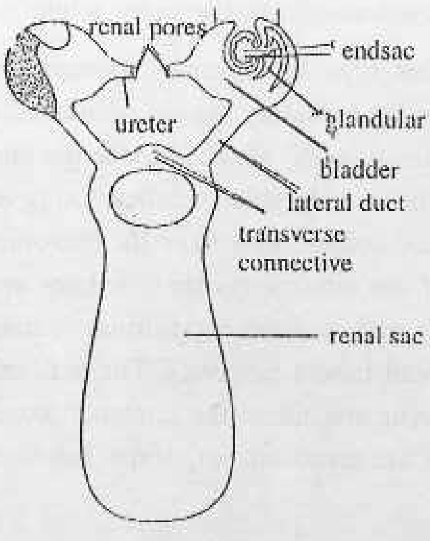


Fig. 5.16 Excretory system of *Palaemon*

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 filtrte 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 details 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 urcocotelism 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.

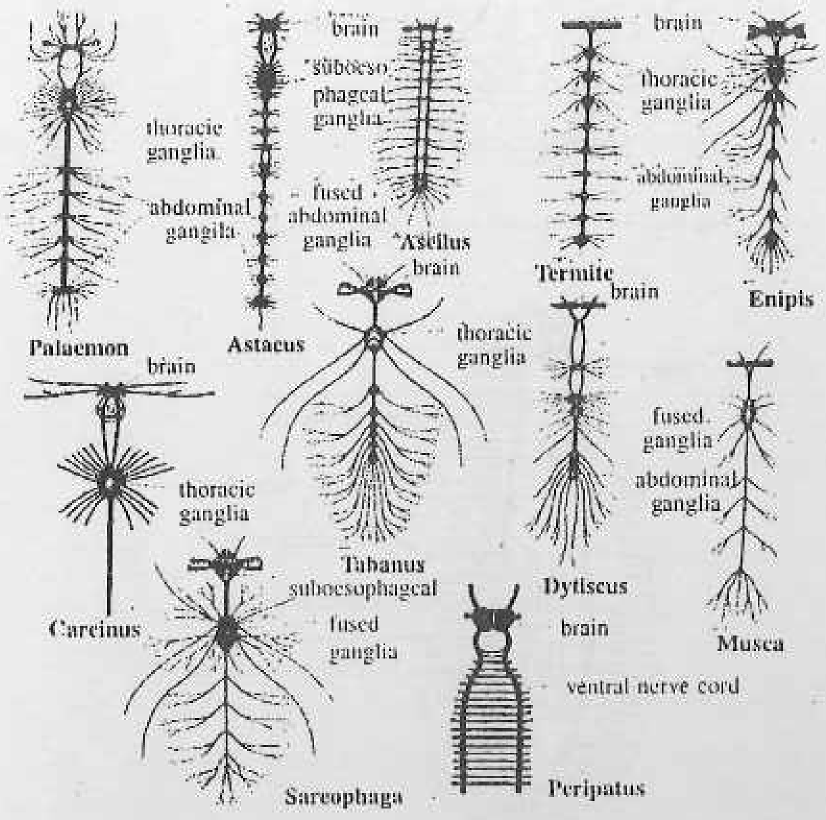

Fig. 6.1 Nervous System of different animals

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.

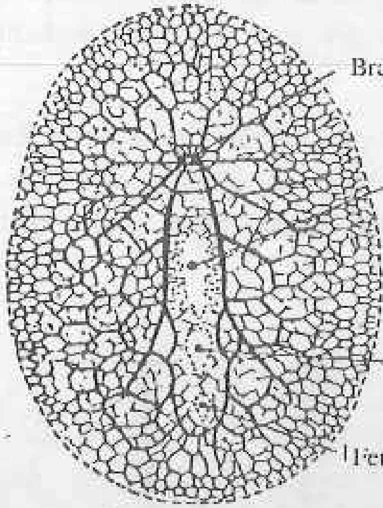

Fig. 6.2 Nervous system of *Plamocera graffii*

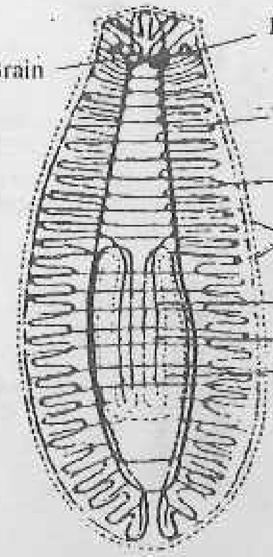

Fig. 6.3 Nervous system of *Procerodes Segmentata*

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.

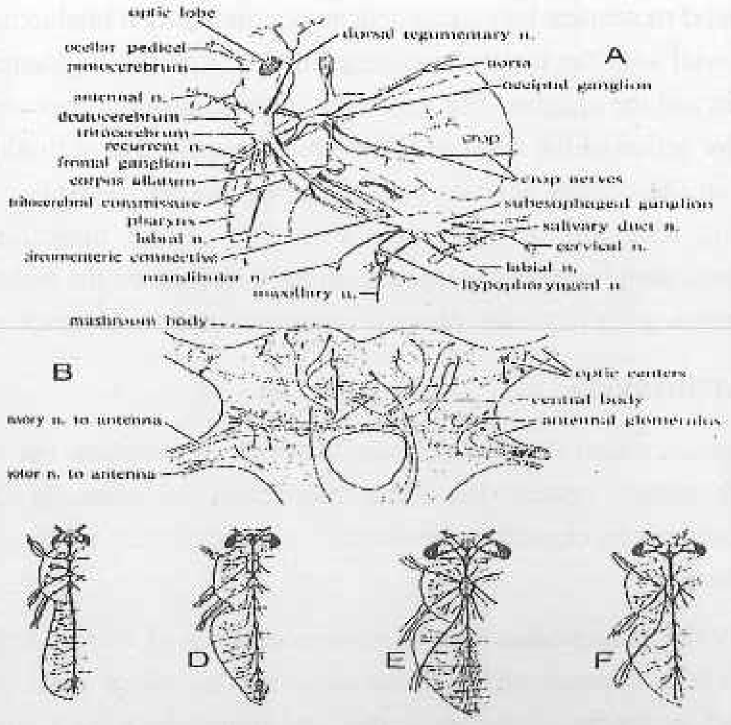

Fig. 6.4 Nervous system. A. Side view of brain and head nerves in grasshopper. B. Chief nuclei and tracts in the brain of the cockroach. C.D.E.F. Evolutionary trends in central nervous system of Diptera with concentration of nervous system by union of ganglia and predominance of more anterior centrers. (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.

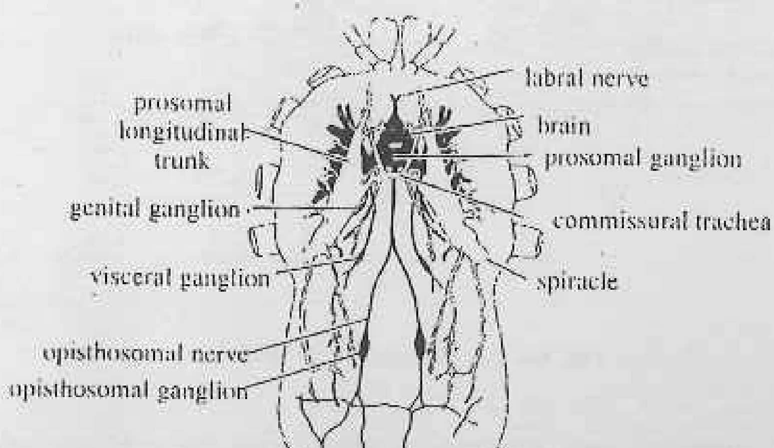

Fig. 6.5 Nervous system of spider

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.

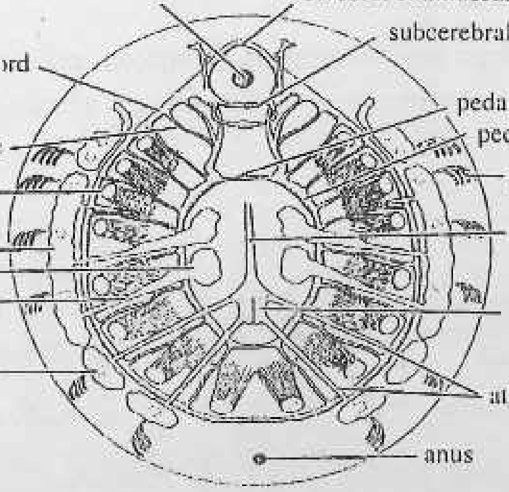

Fig. 6.6 Nervous system of spider

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.

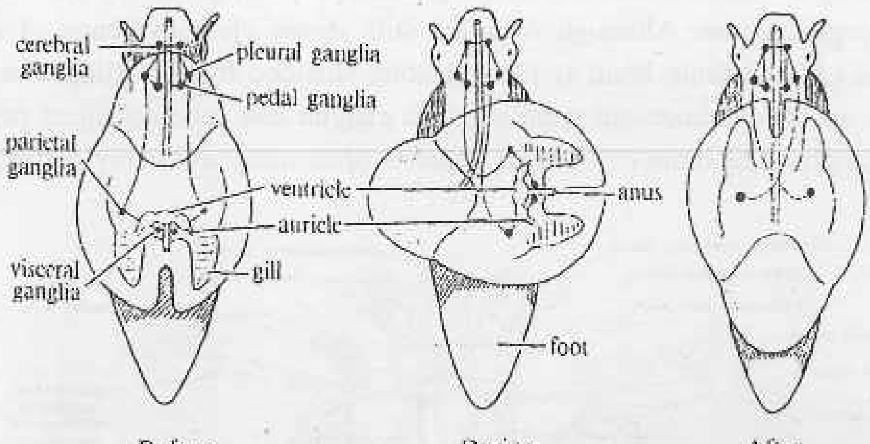

Fig. 6.7 Effect of torsion on nervous system in gastropoda

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,

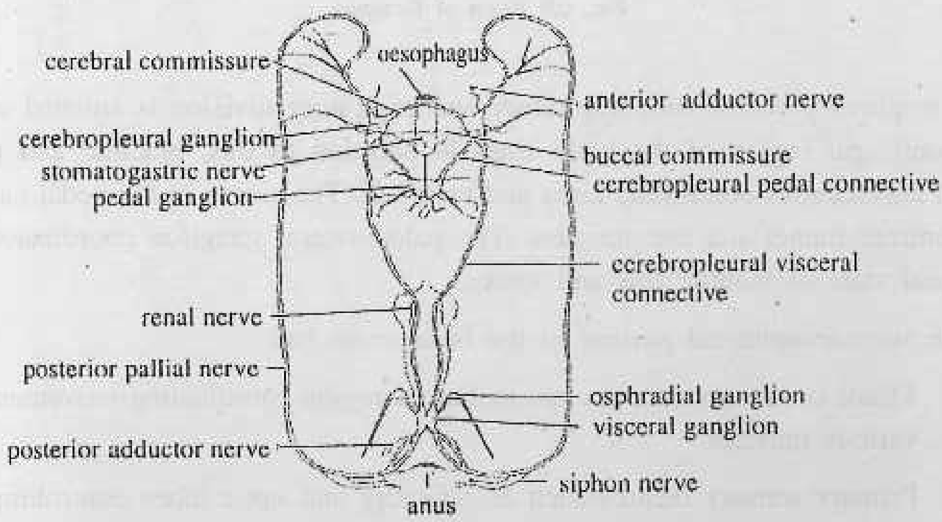

Fig. 6.9 Nervous system of rarer clam tagalua

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.

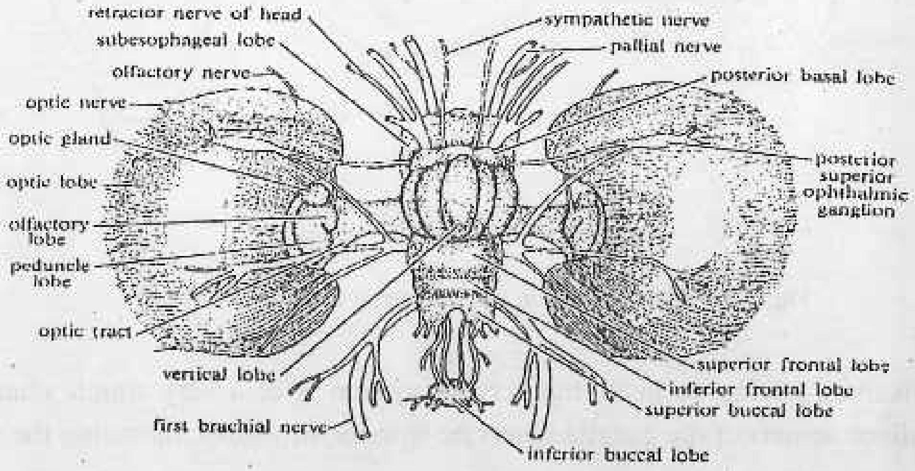

Fig. 6.9 Brain of *Octopus*

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.

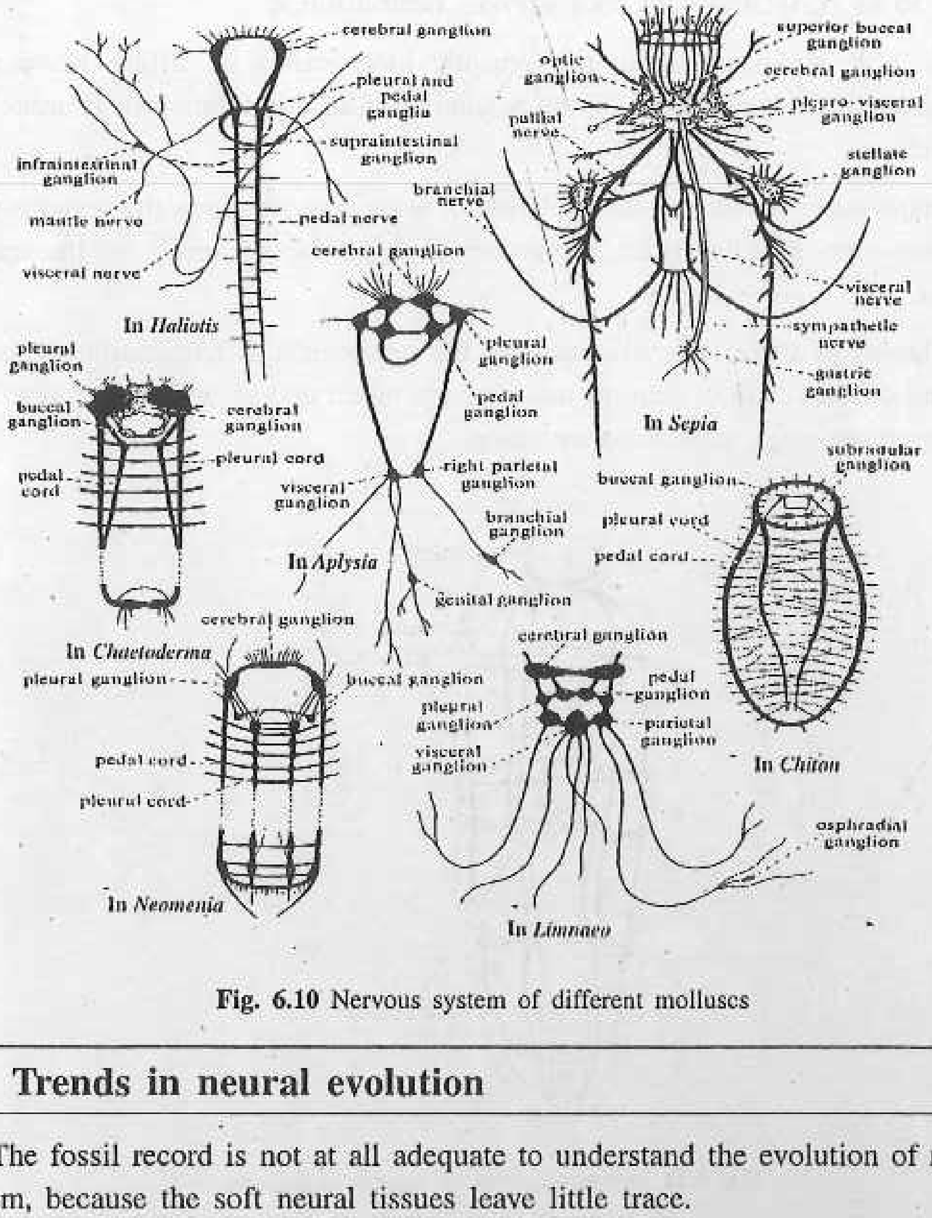

Fig. 6.10 Nervous system of different molluscs

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.

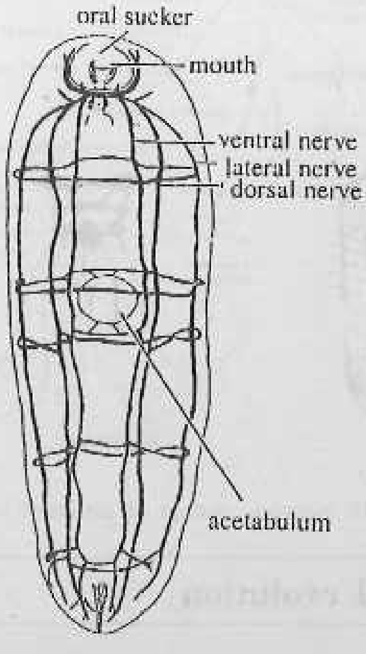

Fig. 6.11 Nervous system of digoricam parasite

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.

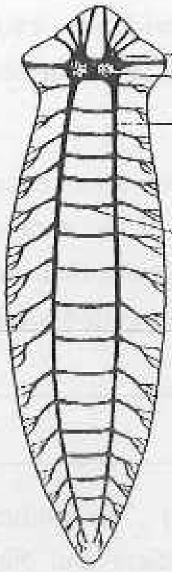

Fig. 6.12 Nervous system of *planeria*

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.
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.

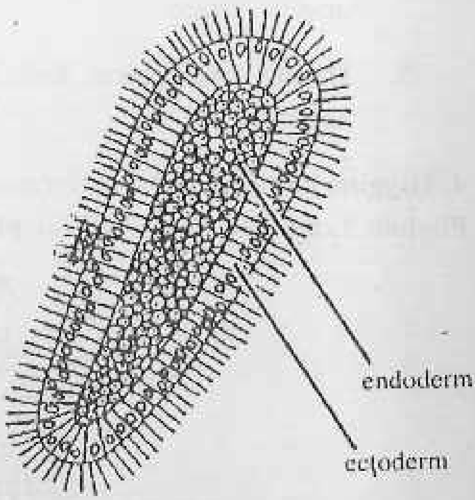

Fig. 7.1 Planula larva

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.

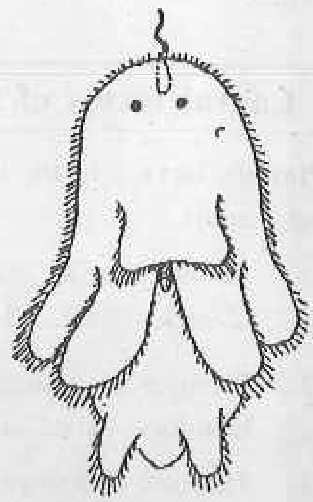

Fig. 7.2 Muller's larva

4. Higgins larva : This larval form is found in the development stages of loriciferans. Phylum Loricifera is the newest phylum, described in 1983.

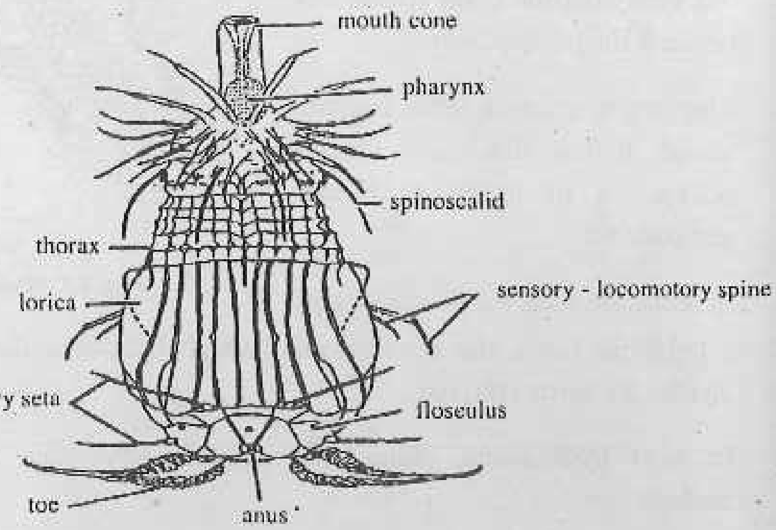

Fig. 7.3 Higgins larva

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 secrtions 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.

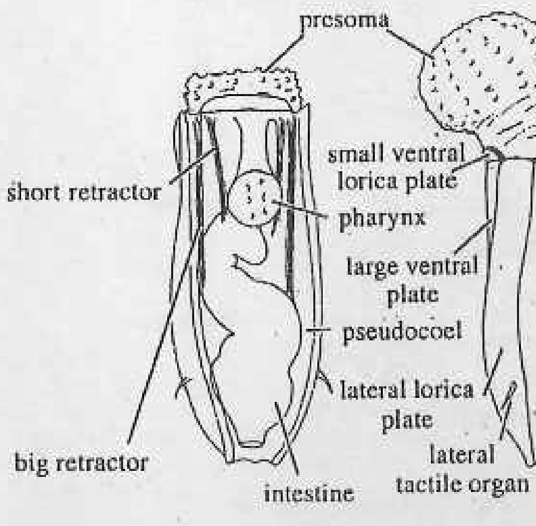

Fig. 7.4 Priapulus larva

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.

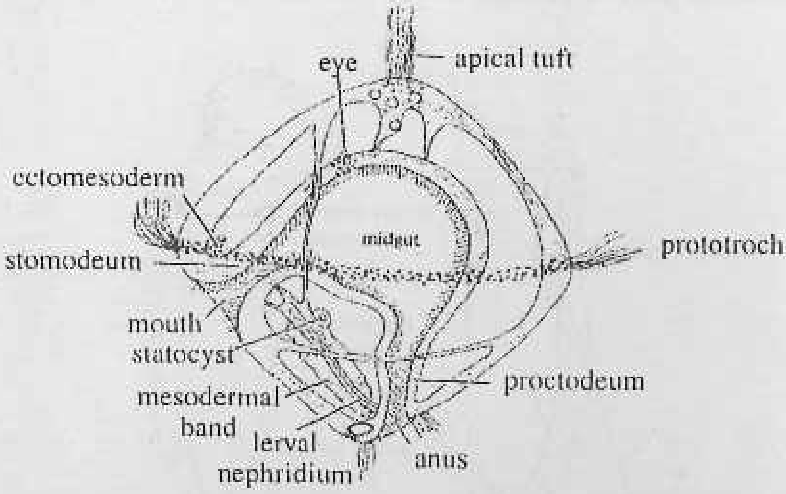

Fig. 7.5 Trochophore larva

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.

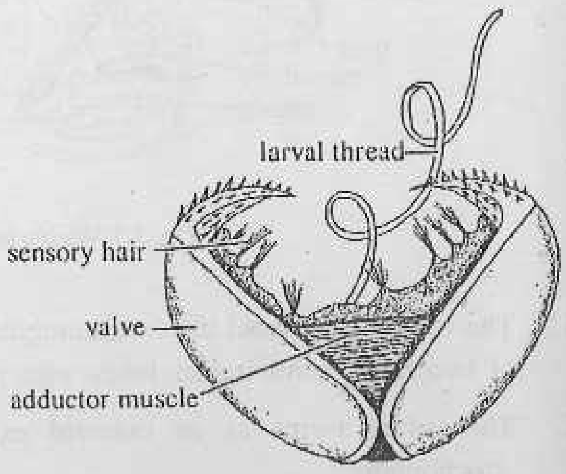

Fig. 7.6 Glochidium larva

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.**

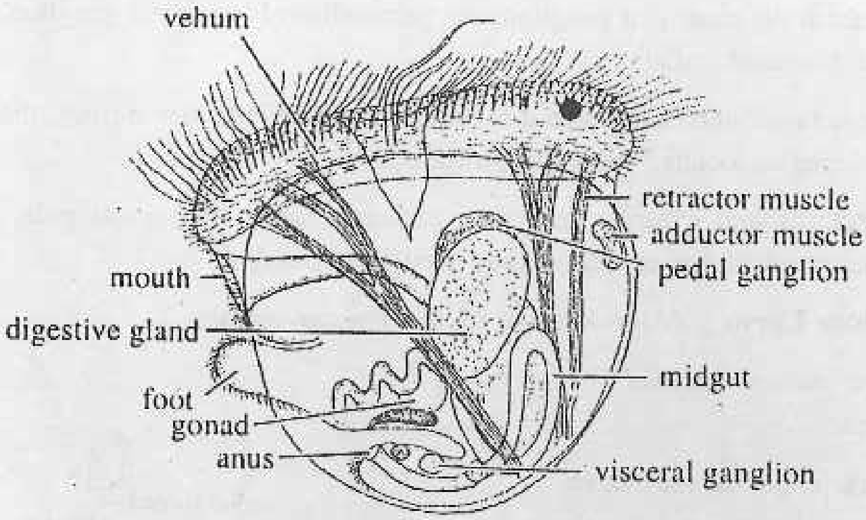

Fig. 7.7 Veliger larva

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**.

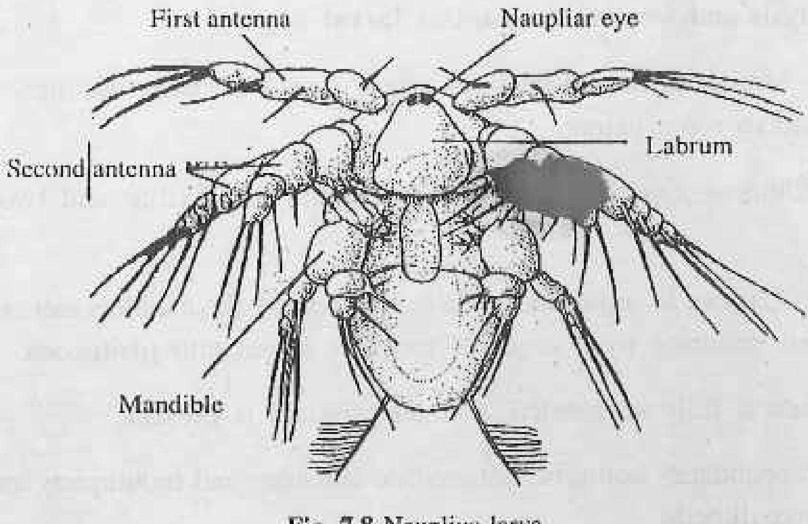

Fig. 7.8 Nauplius larva

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]se 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.

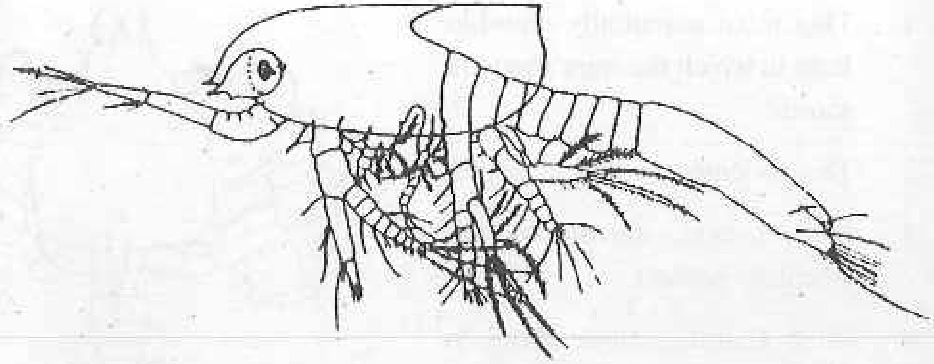

Fig. 7.9 Protozoea larva

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.

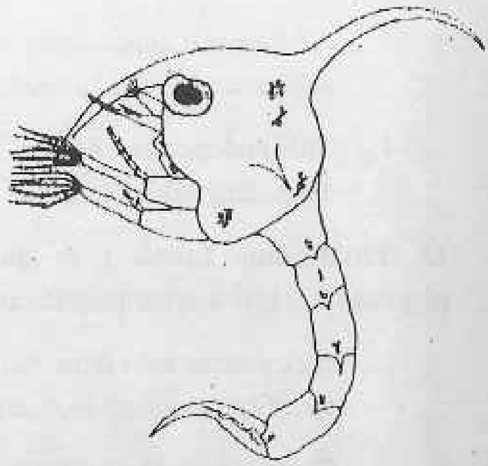

Fig. 7.10 Zoea larva

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**.

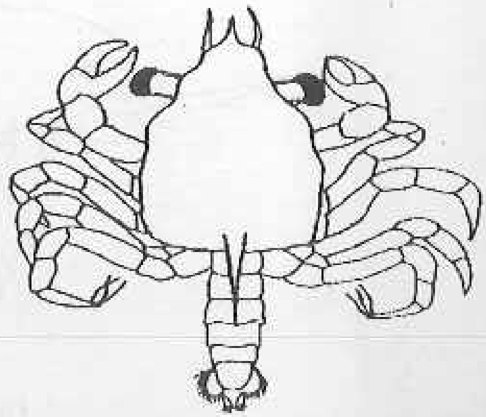

Fig. 7.11 Megalopa larva

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.

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 maxillepeds 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.

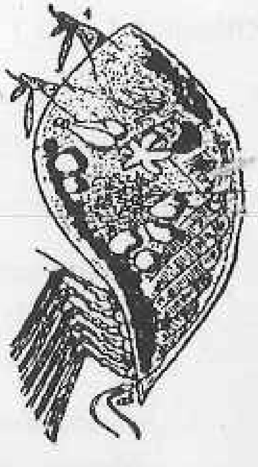

Fig. 7.12 Cypris larva

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.

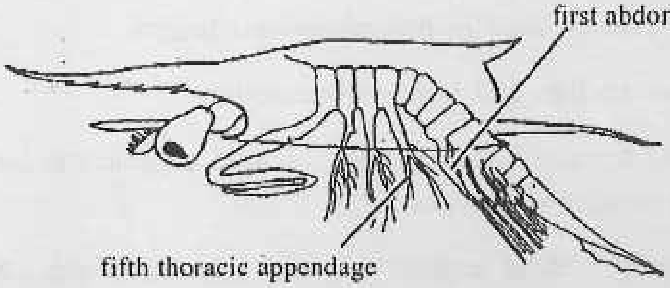

Fig. 7.13 Erichthus larva

1. Larva possesses a median and two lateral well developed eyes.

2. Five biramous swimming thoracic appendages, the 2^{nd} 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.

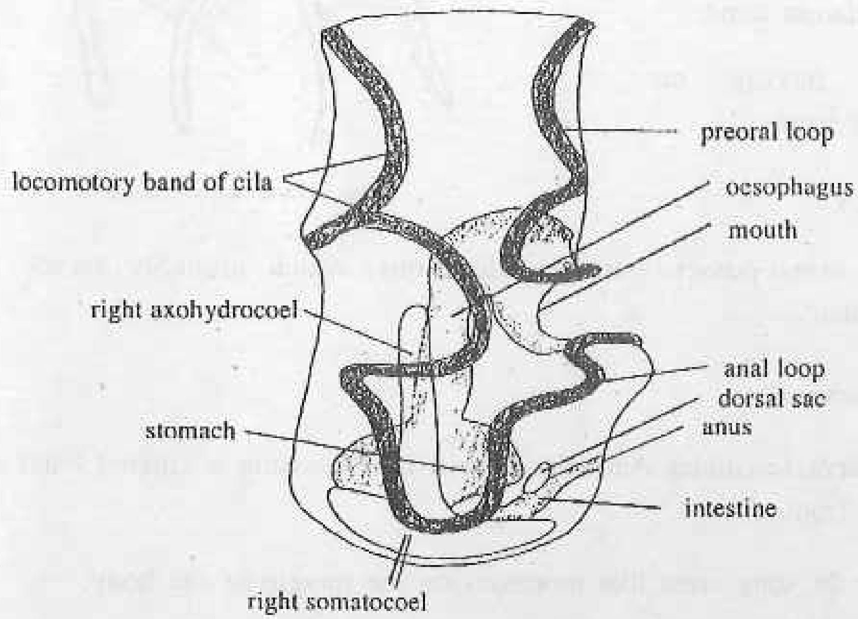

Fig. 7.14 Bipinnaria larva

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.

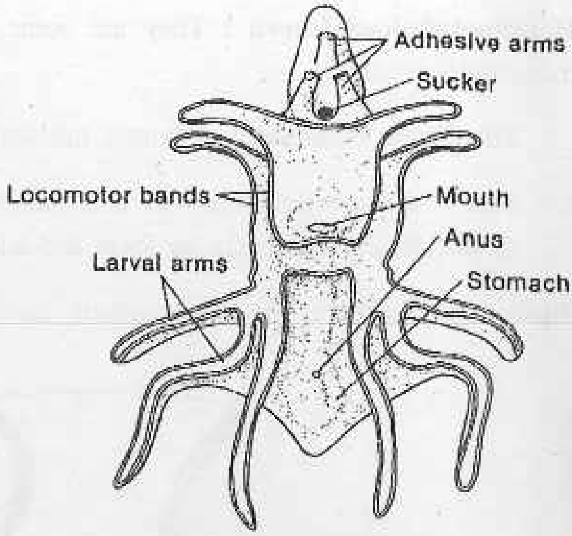

Fig. 7.15 Brachiolaria larva

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.

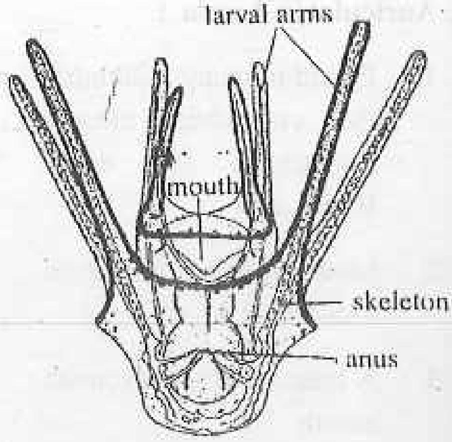

Fig. 7.16 Echinopluteus larva

(b) **Ophiopluteus :**

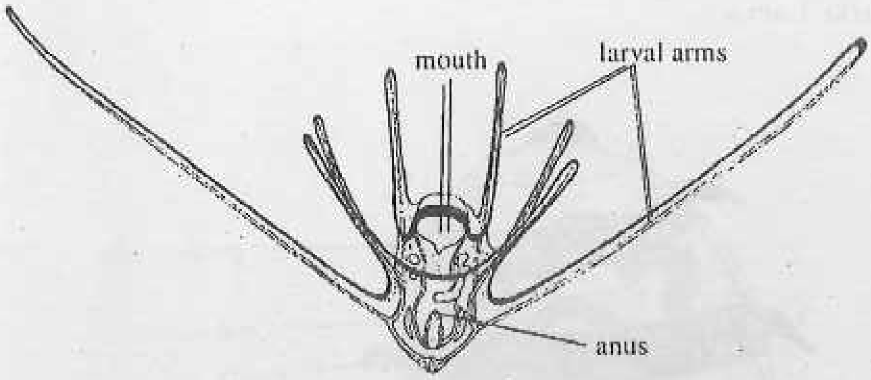

Fig. 7.17 *Ophiopluteus* larva of *Ophiomaza* (oral view)

(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 :

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.

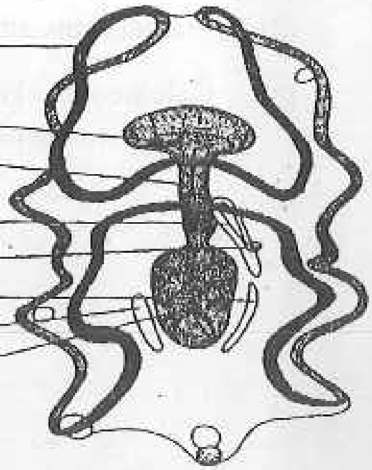

Fig. 7.18 Auricularia larva

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.

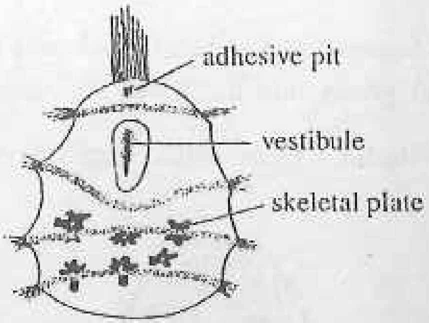

Fig. 7.20 Vitellaria larva

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.

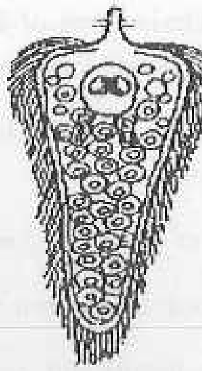

Fig. 7.21 Miracidium larva of *Fasciola hepatica*

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.

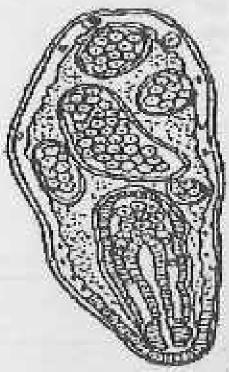

Fig. 7.22 Sporocyst larva of *Fasciola hepatica*

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.

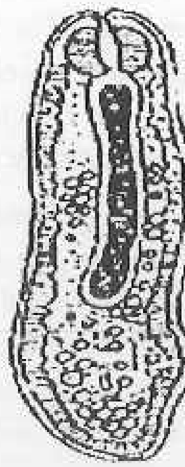

Fig. 7.23 Radae larva of *Fasciola hepatica*

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.

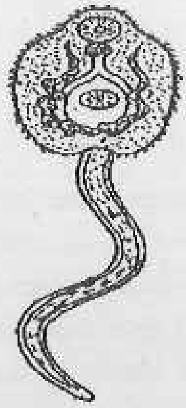

Fig. 7.24 Cercaria larva of *Fasciola hepatica*

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.

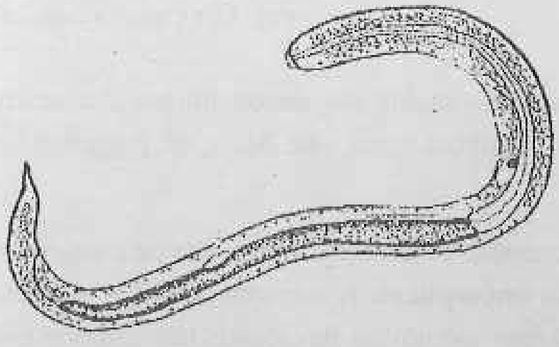

Fig. 7.25 Rhabditiform larva (2nd stage) of *Ascaris lumbricoides*

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.

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.

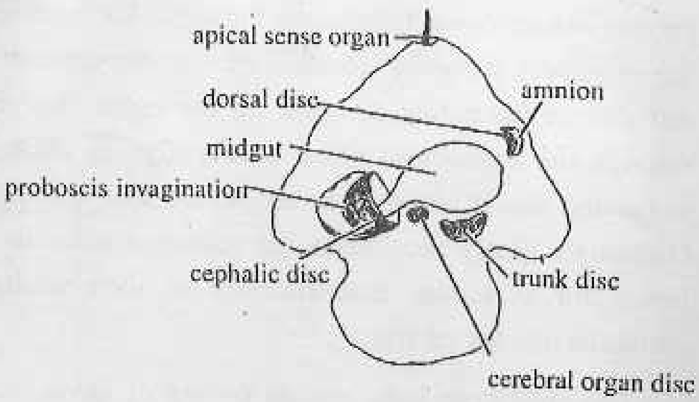

Fig. 7.26 Pilidium larva

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,

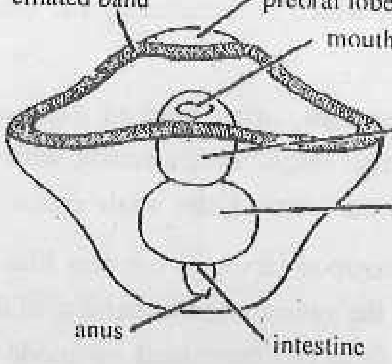

Fig. 7.27 Diplurula larva

(v) The pre-oral lobe, anterior to mouth, bears apical sensory plate and tuft of cilia.

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.

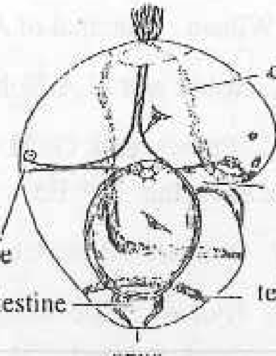

Fig. 7.28 Tornaria larva

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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মানুষের জ্ঞান ও ভাবকে বইয়ের মধ্যে সঞ্চিত করিবার যে একটা প্রচুর সুবিধা আছে, সে কথা কেহই অস্বীকার করিতে পারে না। কিন্তু সেই সুবিধার দ্বারা মনের স্বাভাবিক শক্তিকে একেবারে আচ্ছন্ন করিয়া ফেলিলে বুদ্ধিকে বাবু করিয়া তোলা হয়।

— *রবীন্দ্রনাথ ঠাকুর*

ভারতের একটা mission আছে, একটা গৌরবময় ভবিষ্যৎ আছে, সেই ভবিষ্যৎ ভারতের উত্তরাধিকারী আমরাই। নূতন ভারতের মুক্তির ইতিহাস আমরাই রচনা করছি এবং করব। এই বিশ্বাস আছে বলেই আমরা সব দুঃখ কষ্ট সহ্য করতে পারি, অন্ধকারময় বর্তমানকে অগ্রাহ্য করতে পারি, বাস্তবের নিষ্ঠুর সত্যগুলি আদর্শের কঠিন আঘাতে ধূলিসাৎ করতে পারি।

— *সুভাষচন্দ্র বসু*

Any system of education which ignores Indian conditions, requirements, history and sociology is too unscientific to commend itself to any rational support.

— *Subhas Chandra Bose*

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NETAJI SUBHAS OPEN UNIVERSITY

STUDY MATERIAL

POST GRADUATE ZOOLOGY

PAPER - 1

GROUP : B

Taxonomy, Biodiversity and Conservation

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 analysis.

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 it 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.

Professor (Dr.) Subha Sankar Sarkar

Vice-Chancellor

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POST GRADUATE : ZOOLOGY

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Paper	**: Group**
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	Writer	**Editor**
Part–I		
Units 1–3	Dr. Tushar Mukherjee	
Unit 4	Prof. Sujit Kr. Dasgupta	Prof. Sujit Kr. Dasgupta
Part–II		
Units 5–10	Dr. Sumit Homechaudhuri	
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NETAJI SUBHAS OPEN UNIVERSITY

PGZO – 1
Taxonomy, Biodiversity and Conservation

Group B

Part – I : TAXONOMY

Part – II : BIODIVERSITY AND CONSERVATION

UNIT 1 ❑ Definition and Basic Concepts of Biosystematics and Taxonomy

Structure

1.0 Introduction

1.1 Historical resume of systematics

1.2 Importance and applications of biosystematics

1.3 Material basis of biosystematics-different attributes

1.0 Introduction

Study of taxonomy in undergraduate and postgraduate courses was not strictly taken into consideration in many of our institutions probably till 1980. The correct meaning of many terms and sentences remained obscure to many students and teachers. The lack of interest in this very basic science therefore created no further impact in the student society. Still to day only few get involved in taxonomic work. It is true that taxonomic work in its current meaning is really the hardest pursuit even for a single species. Moreover people in planning are more interested in instant productivity in terms of money from research and forget the very need of any basic work life sciences.

The results of numerous biological researches may be proved to be faulty if they really face erroneous nomenclature of the zoological object worked upon. Thus the accuracy in naming or identification of organism needs utmost care. There are recognized organizations and institutes working upon various groups, which constitute only a fragment of the entire animal world, and hence many workers depend on foreign institutes for clarifications and identification. It is therefore an attempts to present this very basic chapter of biology in lucid and easier way as well as in a more acceptable manner to students.

Although there are many books and journals of taxonomy there are still some deficiency to clarify the principles, objectives and procedures in taxonomy. There should be more examples and data pertaining to real taxonomic characters to clarify the various principles and methods. Anyone can find various terms, old and new, which needs to be clarified in details. Many texts do not often clearly explain relevant points or some steps in mathematical explanations. Only repeated reading and keen study can make one understand these.

Taxonomy is the basic and the ultimate part of biology. Any work must start with the help of some sort of classification and can be completed after proper incorporation of data from all possible fields of research. So the declining popularity in taxonomy is now reversed and there is increasing effort by scientists to find out possible links in understanding the biodiversity. In fact, if properly understood, taxonomy will open up new vision about the diversity, relationship and evolution of animal kingdom.

Definition of taxonomy, systematics and biosystematics

Taxonomy

The study of animal diversity is unknowingly or broadly referred as taxonomy or systematics. Very often they are treated synonymously. Although they are very much related and interdependent there is a basic difference between these terms.

The pioneer plant taxonomist, de Candole (1813), coined the term *taxonomy*. As we know, *taxis* means 'arrangement' and *nomos* means 'law'. Therefore taxonomy clearly means arranging of organisms on the basis of some laws. To understand those laws and procedures of arrangement one should know the theory and then apply them. Hence taxonomy has been defined as "theory and practice of classifying organisms". This classification involves the identification, description, naming (to assign a binomial nomenclature) and finally to ascertain its classification status. In this way taxonomy is highly intermingled with both systematics and biosystematics. This popular definition may be expanded in today's thinking as to prepare a classification on the basis of data obtained from the study of variations- their causes and consequences.

Classification is a logical system that consists of several *categories* or *ranks* each of which contains some number of organisms such that by the name of a category we can immediately imagine about the structure and other aspects of those organisms. That the organisms are to be placed under a specific category requires the study of their relationships. The term relationship is vital and means phylogenetic and all biological relationships. Relationships emerge out of extensive study of species in question. That will show how they are related to each other and how they differ from others. This again will show the path of origin and evolution of the group. Hence *Zoological classification* "is the ordering of animals in to groups (or sets) on the basis of their relationship" (Simpson, 1961). Here ordering means arranging the animals into groups. Here a little more should be cleared about the term classification. It is the result of taxonomic studies. Because the taxonomist "classify" organisms based on certain principles and the end result is the classification.

Again classification is not *identification*. One identifies organisms or individuals and place them in a previously established *taxon*, which may even, be based on a single character. Therefore the process is purely deductive. But classification is quite different because in classification population of organisms is ordered at all levels by inductive procedures. It deals with and evaluates a multitude of characters to interpret their relationships on the basis of which a classification is done. Example is the identification of a fish or an insect on the basis of characters and to place them in a specified taxon. But if we say classificaton of birds or fishes the meaning becomes clear at once.

Systematics

Systematics was originally used to describe the system of classification prescribed by early scholars like Linnaeus (1735). This was later defined by Simpson (1961) as "the scientific study of kinds and diversity of organisms and of any and all relationships among them". The other simple definition by Mayr (1969) is "systematics is the science of diversity of organisms". Therefore study on systematics include quite a broader areas of research which include not only morphology and anatomy, but also genetics, behavioural aspects and population study (including population genetics, ecology and evolutionary biology). The unique properties of each species, common characters of certain taxa and the variation within taxa are the products of systematics that ultimately help to construct a phylogeny. Mayr's definition of diversity includes all theses aspects and reflects the 'all relationships' of Simpson's definition. Evolution and classification can only be achieved through variation. There may be genetically, developmental and environmentally induced variations.

For a better understanding of it may be recalled that systematics starts with taxonomic works and as a result of the taxonomic works, the information obtained about a group of organisms are analysed critically to understand the causes and the evolutionary pathway leading to the formation of those organisms. Therefore the study of inter relationships is of much importance and the various types of these relationships among different taxa reflect the degree of relationship of the species having a common ancestor, various forms of relationships are morphological, anatomical cytological, geographic distribution and ecological relationships (concerned with nutrient dependence, competition and many others).

Biosystematics

Biosystematics is basically said to be synonymous with systematics. The term was originally applied at species level to solve criticical cases with the help of data from cytogenetics and population biology and thereby to produce a system of classification. It is the assessment of taxonomic relationships based on the cytogenetical or biochemical data within an evolutionary framework.

Therefore many authors agree to clearly differentiate biosystematics and classical taxonomy. Biosystematics has also been given the name 'experimental taxonomy' while classical taxonomy is said to be 'orthodox taxonomy'. In biosystematics population and not individual are considered and their evolutionary characters are studied. In this sense it is *genecology*- the study that is concerned with the variations of genotype and phenotype of individuals in a population in relation to the ecosystem.

Therefore the various terms are somehow much interrelated and overlap with each other to an extent. Sometimes another term **neotaxonomy** is used to describe modern procedure adopted in taxonomy and thus previously described morphological species are now called biological species. Although most emphasis are given on morphological data which are easily recognized, some organisms need further analysis with the help of modern techniques and thus expanse of taxonomy of 19th century has been extended to biosystematics. The recognition of common ancestor is based on similarity or differences and these are not merely morphological but also cytological, embryological behavioural and many others. Use of electron and scanning electron microscopy opened up a new horizon in morphotaxonomy. However, biosystematics is definitely an extension of age-old taxonomy where scientists are more interested and more keen to pour further information of organisms from various experiments. From information of genetical studies inferences can be made about the ancestral history of a species and thus speculate speciation. This also indicates the growing interest in taxonomy and a better understanding of interrelationships and evolutionary mechanism. The word "experimental taxonomy" is used to separate earlier taxonomy (orthodox taxonomy) when most species were described and their interrelationships were analysed on the basis of morphological features. But the trend has changed in the last 50 years and emphasis is already given on all aspects, which are now the key words in the definition of biosystematics. It is a new word in true sense separate from morphotaxonomy and more related to "systematics" as defined earlier. The definition of systematics clearly indicated far greater span and biosystematics is a part of it.

Some of the many closely related terms used are *chemical taxonomy*- deals with taxonomic characters obtained from chemical analysis; *systematic anatomy*- to find out data from anatomical studies and *cytotaxonomy*- similarly the data obtainable from cytological studies. These all are part of one term- the biosystematics and the collective results of this study will help systematics of a group of organism (= population) and their evolutionary relationships.

1.1 Historical resume of systematics

Taxonomy started its journey from the onset of human endeavour to know the curious nature of the living beings. It is the basic and oldest biological science and is probably the most controversial one. It is still facing the dramatic attack and counter-attack by taxonomists who are trying to solve the great puzzle of origin and evolution of living things on the earth. Again the contributions of many naturalists and thereafter the taxonomist have provided fresh impetus to the newer generation scientists, particularly so after 1960s.

The typical taxonomy has changed over the past century and now has been enriched by the addition of newer information from many fields of research. The nature of taxonomy may change with the passage of time and development of newer fields of investigation. Particularly during the last three decades there was enormous input in the explanatory field of theories of taxonomy. There is still incessant effort to find out a most acceptable procedure to find out true line of descent and the lines leading to related groups. The newer lines of investigations are pouring down valuable data about organism and the ultimate aim of these numerous research is to unify them to concrete information about a population and their interspecific relations. Although little work has been done but gradually tendency towards this is growing fast. These can be explained only through the principles of taxonomy. So the new taxonomy is looked upon differently and newer nomenclatures are adopted. In this way systematics contributed to the explanation of diversity, evolutionary theory, population biology and population genetics.

In the absence of a scientific classification, however, ignorant natives were well versed about the nature of local population of animals and plants. Many authors provided the trend in the development of systematics. Simpson (1961) and Mayr (1982a) gave excellent history of the taxonomic development. Mayr named it as history of theories of classification and Mayr and Ashlock (1991) as history of taxonomy and the same reflects the concept and trend in systematics. The various phases are briefly mentioned below following Mayr (1969).

Phase I : Studies done by natives or tribals

As mentioned, local people can identify many living organisms and give their name. This trend has the origin from the beginning of mankind. Still today many tribal natives are better to identify as they are associated to that ecosystem and know the nature guided by their parents. They are often apt to identify the beneficial and harmful plants and animals better than many scientists. Even rudimentary classification probably existed long before. Some tribes of Asia and America used two parts in the naming of organisms. Therefore some sort of binominal nomenclature started prior to Linnaeus.

Hippocrates (460-370 B.C.) gave many names of animals but not classified them. Aristotle (384-322 B.C.), the father of biological classification, studied the fauna of Lesbos

Island and clearly proposed that the characters of a species depends upon the habit, habitat and structural organization. Many of his contributions are still in text books. According to his *Scala Naturae* animals should be classified on the basis of their 'perfection' into 'lower' and 'higher' groups which is now explained in terms of evolution.

Phase II : Contribution by Linnaeus

Aristotle's thought was the sunrise in the study of systematics. The inspiration is seen in the establishment of a higher classification by John Ray (1627-1705). Information on many aspects of the unthinkable number of animals came as a result of worldwide voyages and explorations. The Swedish naturalist Carolus Linnaeus (1707-1778) was most influential of this and later periods for his extensive works. In the 10th edition of *Systema Natuare* (1758) he introduced the binominal nomenclature and strongly favoured Aristotlian principle in classification. The thought of systematics still was far away because animals were thought to be created by God and the classification was the presentation of the creator. Actually classification was based on any character and through dichotomous key, which resulted in '*artificial classification*'. This was very soon realized by many workers later on. However, Linnaeus felt the need to create hierarchy and some of his classification were more natural, particularly insects.

Phase III : A century of slow me amorphosis

This period extends from publication of *Systema Naturae to Origin of Species* by Darwin. Lamarck (1744-1829) added some practical approaches in classification of invertebrates. Although Cuvier (1769-1832) made some progress in systematics, still depended on '*priory weighting*' of characters. There was a gradual decline in the popularity of Aristotlian principle of essentialism (to depend on fewer characters). Thus priory weighting metamorphosed into '*posteriory weighting*' by the trend to classify on the basis of totality of characters (an empirical approach).

Phase IV : The era of Darwinism

The contribution of Darwin actually revealed the meaning of systematics and also helped in the establishment of a natural classification. His theory of evolution saved taxonomists from *creating* taxa and inspired them to *discover* taxa through intellectual justification. He pointed that separation of taxa depends on branching and these taxa should be ranked on the basis of their different degrees of modifications. He also explained the importance of posteriory weighting and methods to identify them.

The other events of this period were describing endless species, classify them and also to search the synonyms. Later in 1920s genetics and population biology started to develop and compete with typical taxonomy of this period.

Phase V : Rise of population systematics

Taxonomy started to be reshaped in the light of population biology when species collected from different geographical and ecological niches exhibited small or large variation. A new term '*population systematics*' was applied to the study of infraspecific population. Another term was '*New Systematics*' by J. S. Huxley (1940) attached to the new explanation of species concept and more biological sense in taxonomic research. Later population genetics was added to this to make population systematics healthier. However, population systematics should be regarded as an extension of classical taxonomy (Mayr).

Phase VI : Cladistics and Phenetics-two new schools

Hennig's (1950. 1966) theory of classification (Cladism) and Phenetic method of classification of Sokal and Sneath (1963) were published almost simultaneously and they created a wave of rethinking of the theories of classification and phylogeny. Both have merits and demerits and very soon Phenetic method became less reputed for more of demerits. Cladism today, however, refined by the contribution of followers still is under experimental stage. It seems true that a blend of several approaches should be there without sticking to a particular method or theory.

1.2 Importance and applications of biosystematics

Taxonomic study has put much importance beyond morphology. Its extension is seen in field observation and critical laboratory analysis. All these studies depend on the availability of often sufficient number of live specimens and sophisticated instruments. It may be unusually awesome for rare groups. Some specimens can be handled for a short time in the year or they may take several years to complete a generation. Therefore we still find more interest on typical taxonomy and, if done religiously, may not be 'bad' enough.

In spite of all such difficulties, genetics, population biology and biochemical data have been proved worthwhile for numerous taxa. Some taxa or their characters sometimes give trouble (due to *homoplasy,* convergent evolution or parallelism) and biosystematics becomes quite helpful if not the only procedure. Evolution of species characters always follow a very well defined sequence of events of minor or major changes in nucleotide composition or changes in protein structure. It is true that numerous changes in the above have, however, proved to exert very negligible effect of the survival of tile extant form. But these changes are very useful to decide its evolutionary history of line of descent. Again, highly variable characters are normally of low weight and are unreliable as are the retrogressive characters.

Experimental taxonomy on genetical studies is mainly based on the assumption of a common gene pool for a taxon and this is sufficiently different from nearer taxon. The differences lying in the chromosome number, nucleotide content and sequence not only prevents natural hybridization but the same show some near ratio to its nearer taxon from which it has recently been separated. The same holds true for other data pertaining to biochemical research. Added to these are the various forms of chromosomal changes, which are unique event in evolution.

The kind of most of the macromolecules and metabolic pathways of many prokaryotes and highest evolved animals are strikingly similar. This is due to common descent of the pathway of their evolution and function. However all these show specificity at every taxon and scientists have proved those specificity as a key character to a taxon. For example the immunological data have been widely used now to determine kin from non-kin (Williams, 1964; Leone, 1964). Another method is blood-group genes (" immunogenetics") in the study of pigeon (Irwin, 1947) and primates.

Various types of electrophoresis are now every-day schedule to compare amino acids and many other macromolecules of related species and the data clearly provide valuable information on relatedness and probable line of descent. Most recent in this trend is the DNA matching. As all organ or system has its own rate of evolutionary changes, the same is obviously exhibited by these tests.

Behavioural features are so exciting and so much specific that a naturalist can immediately identify a species from the structure of nest or its call. The call of specific bird during specific urge are now analyzed and matched with previously identified wavelengths to understand the nature of the call. This is proved to be highly species specific and is significant to study their behaviour. New sibling species of frogs were discovered from the study of their sounds. Ecologists are depending on biosystematics to explain their research results.

All these discussions remind what Simpson (1945:1) stated "..(taxonomy is) the most elementary and most inclusive part of zoology, most elementary because animals cannot be discussed or treated in a scientific way until some taxonomy has been achieved, and most inclusive because [systematics] in its various branches gathers together, utilizes, summarizes, and implements everything that is known.

After the loss of typological concept of species and emergence of biosystematics, samples obtained from different geographical area found to contain various degrees of dissimilarities. This led to formulate *polytypic species* concept. Such studies gained importance and reached maximum height in 1930-1940. Now taxon is a population and a species is defined in more biological sense. They are treated as samples of natural populations. This in turn led to the development of population genetics. Therefore evolution at species level was explained in a new way and the outcome was the great synthesis in evolutionary biology.

Since all sciences are inter-disciplinary, we see that stratigraphic distribution of oil need the knowledge of Foraminifera. Therefore micropaleontology became important. Biological, chemical or other forms of insect control plannings need proper guidance from biosystematics. The great field of marine biology depends on the biosystematics for most of its activities. The comparative biochemistry and molecular information of so many organisms are finally shaped through biosystematics.

1.3 Material basis of biosystematics-different attributes

To find out the true nature of an animal both its taxonomy and systematics studies are undertaken to find out the following types of characters :

- **Morphological :** These are the external features related to anatomy, embryology, karyotype and various external characters including the structure of genitalia.
- **Physiological :** These are metabolic, serological, biochemical, various secretions and some of the sterility factors.
- **Ecological :** These are food, host, season and effects due to parasitism.
- **Ethological :** These are behaviour related to territoriality, courtship, mating and others aspects of life.
- **Geographical :** These are the characteristics of distribution related to geography and its inter-relationship.
- **Embryological :** Provides information of ancestral characters, some intermediary features or characters not existing in adult but are taxonomically valuable. These show many plesiomorphic characters which may or may be expressed in adult.

It is really tough to find all the above characters of a taxon. However, a diagnostic feature of a taxon not only differentiates a taxon but it also becomes a strong character at lower category. It also shows relationship, which is a key factor in systematics assessment. The morphological characters are the first available features to identify any animal and these dates back to humanity. Added to this is the study of genitalia and later on, the internal organization and their correlation to functional aspects.

Today biosystematics depends on the recording of as many possible characters as possible of live as well as long dead remains of animals. However specific tests are made according to the nature of material. Its expanse of study starts from submicroscopic level. Since many experiments are time consuming and expensive, morphological studies by naked eye, by stereomicroscope and such instruments still occupy major role in taxonomy. Added to this is the scanning and transmission microscopy to peep deep into structural details. The high magnification and resolution helped to understand more about finer details of structures, which were impossible by light microscopy.

Use of SEM and TEM

The numerical taxonomy depends on characters as well as character states. The development of a character is governed by a definite set of nucleotides. Therefore a change in a character must be due to certain change in that locus. Such changes may be in different directions and different phenotypic or biochemical or other form of changes can be determined by experiments. These various changes of a character are the states of that character. Determination of phylogeny requires all possible data or such characters of each taxon. The data are obtained from adults as well as immature stages (embryological etc.) including eggs. Retrogressive modifications and other evolutionary factors may obscure adult's true nature.

Genetical changes are important for study

With the advent of biochemical researches, there was more and more need for pure identification of animals. This has immense applied and economy oriented value. These activities helped a lot to add to the score of 'characters' of a species and thereby help in rising of biosystematics. Numerous techniques and sophisticated instruments are developed for quicker and accurate study of the constituent bio-molecules (enzymes, hormones and such others).

Study of bio-molecules is an important tool in the study of biosystematics

Embryological studies on various stages of an organism proved to be a success many times and avoided confusions over so called new species. Many forms are so long lived like any natural organisms (during their developmental period) that many renowned scientists treated them as new taxa. Therefore study of embryonic details is well known facet in animal science. An example is the study of egg structure helped to solve the true sibling species under *Anopheles maculipennis* complex (Table-1). Similarly many identification procedures for sponges depend on embryological studies. Experimental embryology is also a quite old and interesting study that provides much information on the specificity of organism and thereby

Embryological features show gradation of characters including ancestral traits providing stable feature. The latter are used as the basis to draw conclusions on biosystematics and phylogeny.

Table-1

Sibling species of *Anopheles maculipennis* complex divided on the basis of ecological data

Species	Habitat	Hibernating	Non-hibernating
(a) *maculipennis*	Cool running fresh water	+	—
(b) *messeae*	Cool stagnant fresh water	+	—
(c) *melanoon*	Fresh water of rice field	—	+
(d) *atroparrus*	Cool brackish water	—	+
(e) *saccharovl*	Mostly stagnant brackish water	—	+
(f) *labranchiae*	Mostly warm brackish water	—	+

Earlier naturalists depended on ecological data to classify and identify organisms. Plato, Aristotle and their followers consistently stressed on this. This has gained importance to day specially to segregate sibling species. Very often ecology acts as yardstick for first hand postulation or instant identification and this often proved to be accurate. Same species inhabiting differing habitats may or may not show speciation in future although develops special structures. Similarly closely related species differing in many traits and inhabiting diverse habitats may have similar ecological characters. Therefore ecological characteristics may often put enough selection pressure of importance and they, thus, have good taxonomic value in judging a species. Briefly the changes in abiotic and biotic factors of the habitat from a habitat of its origin stimulate deviations from parental food habit, behaviour, reproduction and others. This is again conceived in the sibling species of *Anopheles maculipennis* complex which is clearly divisible on the basis of ecological data. Here the habitat is clearly governing the pattern of hibernation of the eggs (Table-1).

Ecological data help to segregate hidden species and may act as hand-book to identify species

Ethology is not new but the use of ethological data in biosystematics is a bit recent. However local people or naturalists have already recognized many such features that are much specific to an organism. Such behaviours are many, for example, production of pheromones, sound production (for many purposes), aggressive or submissisive behaviour, nest building, territoriality, mate selection, courtship and such others. The evolution of such activities is again imprinted in their genome and thus important taxonomically. Recording of

Ethology determines the instinct and learned behaviour of an organism

sound wave produced by a single species at different situations are now analyzed and they serve as perfect indicator of specific behaviour.

Proper survey of any species over a large geographical area always conforms with a definite pattern. All realms, although specified, have no sharp boundaries. The distribution pattern remarkably shows the route of dispersal, similarities in ecological conditions and gradation of climate, soil and other biotic and abiotic factors. On the other side, species distribution itself can predict the ecosystem to which they belong.

Geographical distribution pattern of species clearly indicates the nature of a species and predicts some facts about its ancestors

Species belonging to a geographical area also reflect the nature of their ancestors which also inhabited similar conditions. Thus ancestral-descendant relationships are related to geographical distribution. A rodent (hystricomorph) of South America seemed to be close to African porcupine. Later it was proved to have originated from separate ancestor (Woods, 1950). Much confusion in taxonomy was only solved through geographical analysis:

Effect of geography is exhibited by local variations in a species and hence they are important in the study of true nature of a species. Hence study of sympatric and allopatric populations becomes necessary to understand homoplassy, new developments or character gradients.

Physiological parameters, such as regulation of morphological changes in different stages of development and in life style of adult, i.e., the biochemical factors determining the adult activities are species specific. All these depend upon enzyme system and are ultimately controlled by genetic constitution.

However, such studies can only be done in living species excepting some specific and expensive tests on fossils. But these are not always permissible and there are many other obstacles.

Physiological activities depend upon coordinated activities of biochemical parameters

Physiological activities depend upon coordinated activities of biochemical parameters and, hence study of latter may reflect the type of physiology of a species.

Many important and common biochemical pathways in almost all organisms show similarities. This is due to common descent during organic evolution. However there are lots of parameters by which each species differs from its nearest kin and show specificity in organization and behaviour of bimolecules. Among many techniques to identify them possibly the most and widely studied is the immunological analysis. But this process is not free from demerits and newer techniques are coming up to solve them. The biochemical assay and their roles in taxonomy are discussed in chapter two.

UNIT 2 ❑ Trends in Biosystematics—Concepts of Different Conventional and Newer Aspects

Structure

2.0 Introduction

As already discussed, biosystematics has its own array of working principles and procedures. Numerical taxonomy paved the way of high popularity of biosystematics as the former needs numerous characters of an organisms and uses computer to assess the phyletic position of an organism. There are many contributions by morphotaxonomy but there are limitations. Any character is known to be governed by the specific combination of nucleotides and their final expression depends upon a series of complicated non-genetic factors (endogenous and exogenous).

Therefore there was increasing demand on the availability of information related to structure and modifications of chromosomes, the nature and positions of genes and effects due to their changes. The effects of above changes were seen in their biochemical profile. Therefore correlation of these two aspects (or three) was necessary to study an organism properly. Now these features are expected to be very much specific for a species since these evolved through a long process of evolution and natural selection.

Trends in modern morphotaxonomy

However, it is also well known that morphotaxonomy has made a progress in the study of finer surface texture (external or internal) with the help of scanning electron microscope (SEM). Similarly the addition of transmission electron microscope (TEM) and fluorescence microscope have provided detailed features of various protozoan, pathogens, other prokaryotes and such organisms, different types of cells and their changes, tissue sections prepared through special procedures and such cases where light can pass through the material. Thus innumerable data on characteristic parts are available. This study is particularly important for the characters subjected to selection pressure such as bristles on head and wings in many insects and thus are useful in taxonomy.

Scanning electron microscope

SEM helps to identify the actual structural details, which, by light microscope, appeared different. This helps to vividly recognize the many types of fine structures particularly on the body of arthropods, which are of immense taxonomic value. For example, the *Argas* (tick) was re-characterized and a dichotomous key was prepared from the study by SEM. The world of invertebrate has been much benefited with the invention of SEM. SEM has a magnification from 50 to 10,000 times and a depth of focus of more than 300 times than light microscopes (Figure 1 and 2).

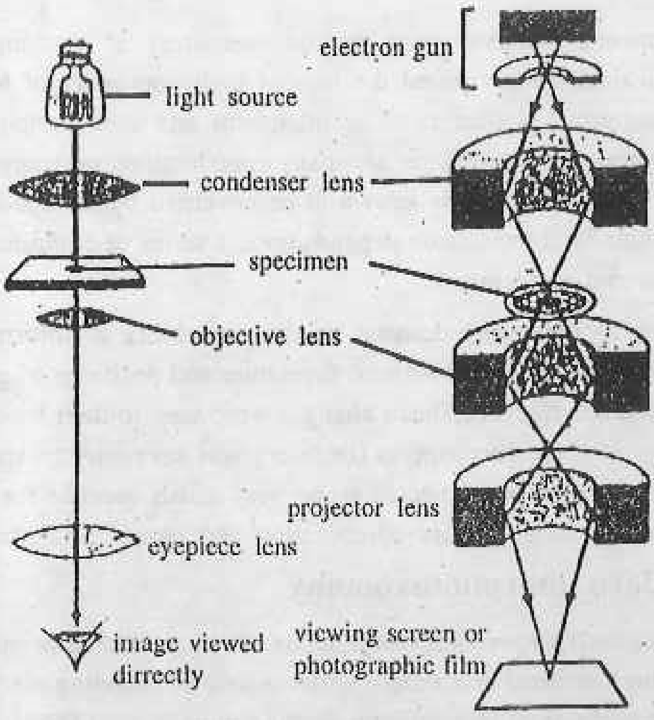

Figure 1. Different parts and pathway of light in light microscope (left) and transmission electron microscope (right)

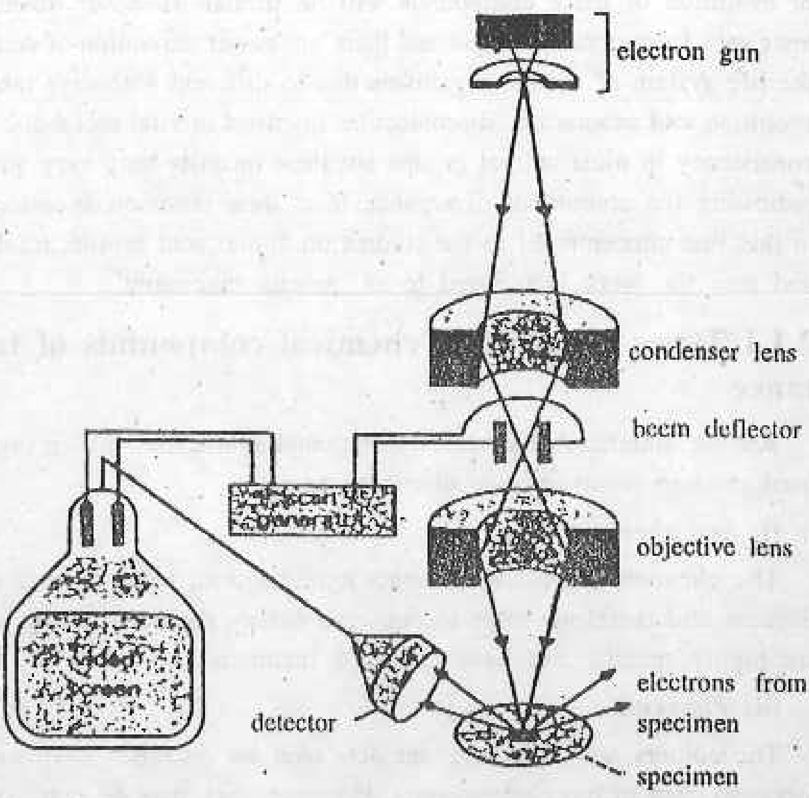

Figure 2. Different parts and pathway of light in scanning electron microscope

Transmission electron microscope

It has even higher magnification than SEM and is used to study further details of thin sections of tissues or organs. It helped in the identification *Amoeba* and *Thecamoeba*, some turbellaria, the egg-shell structure of certain Diptera (fruit flies). In comparison, SEM is more used in taxonomy than TEM.

2.1 Chemotaxonomy

Biochemical relationships among organisms reflect the relatedness and also help to determine the distance between the taxa. It has become very important to determine the chemical nature of constituents of organisms to differentiate very closely related species. In the absence of suitability of many other approaches, many taxonomists were compelled to search the biochemical differences. Both similarities and differences of some compounds are analyzed. It is true that many similar compounds will occur in many organisms as they have descended from some common ancestor at some time and the basic pattern of evolution of these compounds will be similar. However quantitative and qualitative tests vary from organ to organ and there are newer derivation of some compound to match the life system of certain organisms due to different pathways taken up by them during evolution and adaptation. Biomolecules involved in vital metabolic activities show nearly consistency in most animal groups but their quantity may vary widely in some relatives indicating the amount of divergence from their common ancestors. Most of the works in this line concentrated to the studies on amino acid profile, total protein, peptides etc. and thus the work is referred to as 'protein taxonomy'.

2.1.1 Types of common chemical compounds of taxonomic importance

Among innumerable chemical compound synthesized by an organism, the commonly used ones in taxonomy are discussed here.

(i) ***Sex pheromones*** :

The chemical signalling prevents hybridization, helps to find mate, indicates receptiveness and therefore helps to conserve energy during breeding season. Sex attractants are highly specific and have has good taxonomic value.

(ii) ***Pigments*** :

The colours and their arrangements over an organism have many purposes and are foremost data in morphotaxonomy. However, they may be confusing in mimetic forms. Sometimes they are temporary or change with age. The colour pattern helps mate identification or selection in sympatric species. The compounds necessary for colour production are attractive bio-molecules in taxonomic research. The notable colours of butterflies more easily identify them. The white and yellow pigments in Pieridae (Lepidoptera) are due to the presence of pterins. But mimicking unrelated forms develop similar colour by white flavones.

(iii) ***Animal toxins*** :

Animals produce toxins for self-defense, attack and to capture prey. These are subjected to vigorous research for medicine and thereby helped a lot in taxonomy. The works are in two ways, - to find the chemical nature and their effects on animal system. The chemicals are varied in nature and show convergent adaptations in many unrelated forms. For example, a mimetic chemical (argiotoxin) is found in orb web-weaving araneid spider and the other similar chemical (δ-philantha toxin) seen in bee wolf. Both the chemicals target the same receptor molecule in prey's neuromuscular junction.

(iv) *Neurotransmitter* :

Little work has been done on the phylogenetic distribution of neuroexcitatory chemicals in animals excepting those of Walker and Holden-Dye (1989). Beside acetylcholin as principal compound, many other specific chemicals are known to work in tandem on muscle activity. One important finding with no further explanation to its significance so far is the occurrence of L-glutamic acid as principal excitatory peripheral neurotransmitter in Chelicerata, Crustacea and Uniramia. It seems therefore that L-glutamic acid is an apomorphous compound with respect to acetylcholin showing monophyletic origin of those arthropods.

(v) *Lipids and hydrocarbons* :

The role of cuticle is many and some are prevention of water loss, gender recognition and identification of members of a colony. Those inhabiting in the nest of unrelated animals as symbionts or such are found to synthesize similar compounds. These compounds are easily extracted and identified chromatographically and show much similarity in related species. This compounds helped in separating cryptic species in some instances.

(vi) *Secondary plant metabolites* :

Plant taxonomists put much stress on seasonal or non-seasonal production of secondary plant metabolites. These compounds have many roles such as deter leaf eaters, as anti-fungal, anti-bacterial and others. Many plants shed leaves that contain waste substances. Among such many chemicals, the most important are the flavonoids, terpenes, diterpenes and alkaloids. The seasonal production of some compounds are due to seasonal gene expression and latter is governed by environmental factors. Many such compounds have economic value and thus took the attention of scientists who purified and analysed them. These studies again contributed to plant taxonomy and many names of categories are after these compounds.

(vii) *Pyrolysis product* :

Degradation of organic compounds in inert environment at high temperature is called pyrolysis. The volatile compounds can be separated by gas chromatography. The results are computerized and can be used in taxonomic matching with unknown samples. The data can also be used to measure taxonomic distance between species. This procedure is mostly used in identification of strains in microbiology.

Discussion

Presence of a set of chemicals in a species changes with age, sex, climate and many other factors. So taxonomic study with these data can only be suggestive and not deterministic. Chemical mimicry is an obstacle to confirmation of specificity. Many compounds take to different routes of synthesis. So construction of phylogeny of such compounds becomes a serious problem. Moreover a compound formed by a single or few gene expression cannot have much taxonomic weight than one morphological character because latter is the result of multiple gene expression.

2.1.2 Immunotaxonomy

With the immense progress in immunology, immunotaxonomy became a separate subject in taxonomy. From the days of Pasteur, immunology is developing day by day particularly in medicine as a principal tool in identifying antigens in many organisms. Molecules or mixture of molecules of an organism can initiate immunological reaction in a recipient. Such molecules (antigens) may be carbohydrate, lipid, protein, glycoprotein or such other compounds. The serum of recipient produces some specific proteins (antibodies) which binds specifically to the antigens to denature its activities. The quantity and stability of the antibodies produced in response to general immunoglobins (IgGs) depends upon the nature of the latter (antigens).

Antigen-antibody reaction produces an insoluble complex called *precipitin* and the latter is analyse both quantitatively and qualitatively. These data can be used in identifying relations between species (immunological distance).

Principles and techniques in immunotaxonomy

(i) ***Precipitin reaction***

A second antibody capable of precipitating the first antibody can precipitate a protein-antibody complex which is not completely insoluble or by addition of Protein A from *Staphyloccocus aureus* which has the property of cross linking IgG molecules can precipitate that protein.

Precipitin can only be produced when the quantity of antigen and antibody is in the ratio of 1:1.5; otherwise the complex remains in soluble state. Nuttall and co-workers (1904) obtained different kinds of serum proteins and glycoproteins by using whole blood serum as antigenic mixture. The quantity and quality of these compounds were studied and used as specific value for that particular organism. Similar such tests can be carried out in related or unrelated organisms and the values can be utilised in taxonomy as direct data of immunological distance. More similarity with data represents more similarity in their amino acid sequence. Differences in value or its wider difference means degree of separation of taxa and this also shows amount of amino acid replacement or loss.

Human serum → Rabbit → Anti-human serum

	Human Serum	Chimpanzee serum	Baboon serum	Dog serum
Anti-human serum	Maximum precipitation	Nearly Maximum precipitation	Nearly half amount of precipitation	No precipitation

Checker board shows relatedness among some mammals on the basis of quantity of precipitation. Higher the amount of precipitation more closer the two taxa are.

(ii) *Immunodiffusion*

When soluble antigens diffuse from a homogeneous solution into an agar gel, there is a continuous fall of its concentration from starting edge to final end to a value of zero. Somewhere along this concentration gradient is the concentration of antigen that gives equivalent concentration of the antibody.

In double diffusion technique (Ouchterlony, 1953), an antiserum is raised in an animal in response to an antigen or antigenic mixture. In a suitable gel medium, a central well and several other test wells are placed concentrically at a distance of few millimeter from

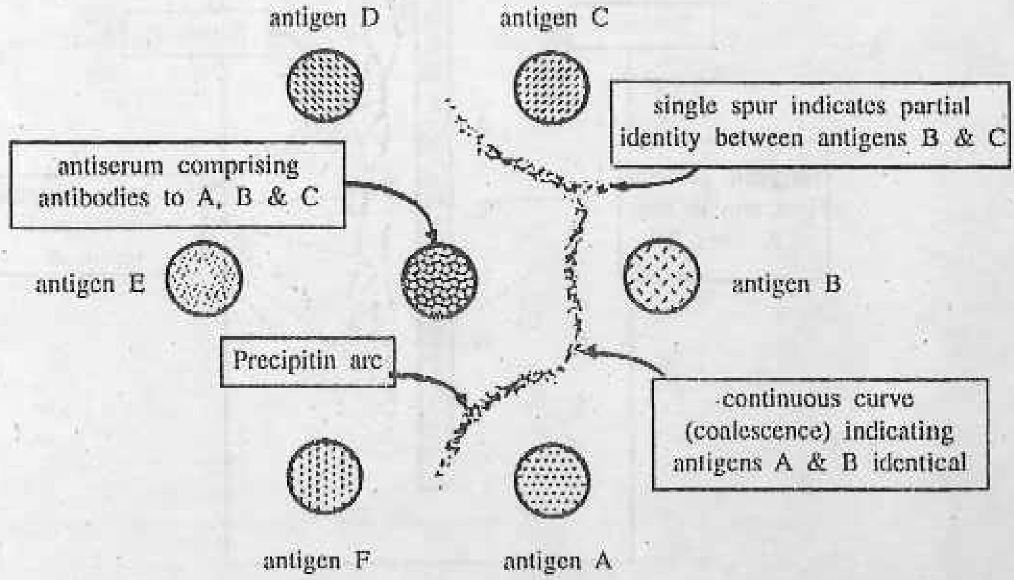

Figure 3. Immunodiffusion: arcs of precipitin showing degree of identity among antigens

each other and also from central well. Now antisera containing antibodies to test antigens is taken in central well while test antigens in peripheral wells. The antigens and antibodies diffuse into gel and depending on molecular sizes, will move up to a certain distance from their wells where precipitation will be formed (samples A-C). If there is no precipitation, then there will be no curved lines indicating mismatch between antigens and antibodies (samples D-F). Today patterns are cut in agar layers on microscope slides with stainless steel cutters. This process uses very small quantities of antigen and antisera and results are obtainable in a few days (Figure 3).

(iii) ***Immunoelectrophoresis***

This process has finer resolution in identifying complex mixture of antigens. Here antigens are first separated on the basis of their net electric charges and then visualized by precipitation reaction.

After electrophoretic separation, the median longitudinal well is filled with antiserum raised against one of the antigen samples. Both antigens and antibodies diffuse till they meet to form precipitation arcs. Since there are antigens of varying molecular weight,

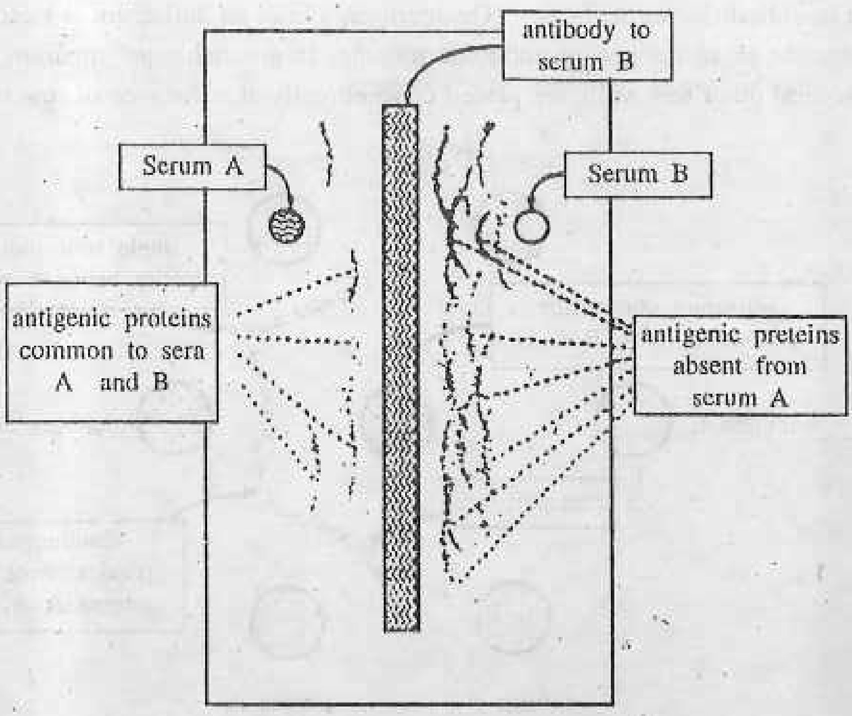

Figure 4. Immunoelectrophoresis to compare antigens of two taxa A and B.

there will be different mobility and these will create separation arcs separated longitudinally and also in width. The number of arcs on two sides clearly demonstrate the relatedness or distances and the difference of total arcs on two sides is the immunological distance between the two taxa. This technique detects the purity and the particular antigens in sera, culture filtrates, tissue or cell extract (Figure 4).

(iv) ***Immunofluorescence***

Fluorochromes (dyes) exposed to ultraviolet, violet or blue light become fluorescence or emit visible light. These dyes (examples rhodamine B or fluorescein isothiocyanate) can be fixed to antigen or antibody.

In direct immunofluorescence, microorganisms or cells (containing antigen) is fixed on a slide and then treated with fluorescence labelled antibodies. When viewed under fluorescent microscope, the pattern of fluorescence reveal the location of antigens in that cell. This is used in microbiology to identify surface antigens.

Indirect immtunoflurescence is done on serum of an organism infected by microorganisms. A known antigen is fixed on a slide and allowed to react (if occurs at all) with test antisera to form fixed antibody. Now fluorescein labelled antiimmunoglobin reacts with fixed antibody. The presence of test antigen is observed if there is any fluorescence.

(v) *Radioimmunoassay*

This highly sensitive modern technique requires only picogram quantity of antigen of test organism. A soluble and purified antigen labelled with radio-isotope and test antigen is allowed to compete for the binding sites of an antibody. At equilibrium in the presence of an antigen excess there will be both free and labelled antigens. Therefore, if concentration of test antigen is high, it will bind more with antibody and there will be less amount of bound activity. Here some of the exposed sites of the antibody will be taken up by labeled antigen during complex formation.

$$\boxed{TA} + \boxed{SA} + \boxed{AB} \rightarrow \boxed{TA \mid AB \mid SA}$$

[Test antigen (TA) at higher concentration than SA (labelled antigen) will show fewer radioactivities in antigen-antibody-antigen complex]

Radioimmunoassay is the only best choice where very limited amount of antigen is available for study as in case of fossil (Westbroek et al., 1979). In general radioactive iodine (^{125}I) is used which means cost and risk in such experiment. The major advantages of this techniques are that it detects any pure antigenic compound; it is highly sensitive and specific and it requires minimum handling and data processing. The disadvantages are that it is costly, requires some chemicals that have limited half-life, radioacitivity problems and takes days to complete assay.

(vi) *Microcomplement fixation (MC'F)*

This method helps to identify the amount of sequence divergence in the particular antigenic protein. The concept of this procedure is that a given protein has few separate antigenic sites (20 or more). Such a protein is purified and a polyclonal antibody is raised in a suitable organism. Any antibody of this will definitely recognize antigenic sites of that protein.

Complement or complement system is composed of at least 17 complement protein and they act in a cascade. They are activated after antigen-antibody complex has formed. And this serial phenomenon of complement binding with antigen-antibody complex is called complement fixation. A fixed amount of complement is added to antigen-antibody complex and only that amount of former will be used up which binds with the complex (that is proportional to the number of antigenic determinants). Actually after reaction, the amount of free complement is measured. This is done by allowing it to lyse sheep R.B.C. that are previously coated with anti-sheep R.B.C. antibody.

During divergence of taxa that protein also show deviation and has lost some or all antigenic sites and this will be shown by the divergence of amino acid sequences. Therefore antibodies in the mixture (polyclonal) will show some to bind to their specific antigenic determinants, which still persist in that protein of those taxa. A change or replacement of even one amino acid will affect antigenic determinant and thereby prevent antibody attachment (Maxson and Maxson, 1990).

MC'F procedure requires purification of antigenic protein from two or more species, raising of respective polyclonal antibody, preparation of standard complement fixation curve and similar curves between same antibody but different antigens. Differences in the amount of complement fixation are the measure of dissimilarity between two antigens (= two taxa).

Maxson and Maxson (1990) obtained different ID values proportional to amino acid replacement. The immunological distance (ID) is equal to 100 $\text{Log}_{10\,x}$ (heterologous antibody titer/homologous antibody titer).

(vii) ***Hybridomass-Production of monoclonal antibody***

Gearges Kohler and Cesar Milstein (1975) developed hybridomass which is obtained by membrane fusion (with the help of polyethylene glycol) between spleen cells and myeloma cell. A rat is injected by a specific antigen so that B cells of rat produce antibody. Then the spleen cells are fused with myeloma cells (cancerous cells not able to produce immunoglobulin). These cells are now called hybridomass, which is tested for the production of desired antibody. The cells are uniform, specific and can be readily produced in large quantity.

Monoclonal antibody, unlike polyclonal antibody from hybridomass detects specific antigenic site on protein, if present, from different taxa and can be used in parsimony analysis. But this process requires commercial production of more monoclonal antibodies and this is costly and time consuming (Greenstone et al., 1991)

Remarks

Many other immunological methods are employed in research particularly in medicine. Some of these are Enzyme Linked Immunosorbent Assay (ELISA), Immunization and Transplantation Rejection. There are also some types of spectroscopic analysis such as Spectroscopy, Nuclear Magnetic Resonance Spectroscopy (NMR), Optical Rotatory Dispersion (ORD), Infra Red Spectrometry (IRS), Atomic Absorption and Flow Cytometer. These are now commonly used as modern techniques to identify macromolecules and the data can even be used as specific characters of taxa and thereby can be used to calculate similarities or dissimilarities among taxa. ELISA is relatively cheap to operate, lacks radioacitivity hazards and suitable for small laboratory. Raman spectroscopy is helpful to determine intermediate sized molecules such as small peptides, pollutants, metabolic intermediates and substrates.

2.1.3 Applications of chromatography

(i) *Ion Exchange Chromatography*

This process separates amino acids and proteins by their presence of negative or positive charges when passed through a column of ion-exchanger (compounds like polystyrene) in presence of specific pH. Generally anionic buffers like Acetate, Barbiturate and cationic buffers like Tris, Pyridine etc. are used in this experiment.

(ii) *Affinity Chromatograohy*

Purification and separation of any macromolecule such as protein, enzyme, mRNA can be done by passing through a column containing substance that binds with the sample compound. For enzyme a ligand and for protein antibody is selected for this purpose.This method helps better purification within a short period.

(iii) *Partition, Adsorption and Gas Chromatography*

A substance is shaken in two immiscible liquid phases in a separating funnel. The substance, upon shaking forms two phases; if one phase is allowed to move, the substance will also move on the basis of its partition coefficient. The movement will be rapid if the sample prefers mobile phase or will be slower if it takes stationary phase. The rate of movement depends upon the intensity of characteristics of adsorption. Silica gel, aluminium oxide, cellulose etc, are used as adsorbent.

In gas chromatography, a gas acts as mobile phase. A non-volatile liquid acts as stationary phase and is the coat of the matrix substance of the column.. The principle of separation is the differences in partition coefficient of the volatilized compound between gas and liquid phases. Both qualitative and quantitative analysis of many compounds is done by this method.

2.2 Cytotaxonomy

The study of chromosomal complement of a cell or organism (Karyotype) is recognized as a taxonomic character for a long time. But the study so far yielded little information in taxonomy in spite of its wealth of data. Cytotaxonomy in broader sense includes major chromosomal changes and also those changes of few nucleotides. Both of these changes essentially change the genome, either the number of chromosome is altered or sequence of nucleotide is altered. Addition or subtraction of whole chromosome is frequent in plants while it is rare in animals. The chromosomal rearrangement that took place during natural hybridization between different karyotypes has contributed to the evolution of many organisms with the present day genome. Many other innumerable combinations must have taken place and later deleted by natural selection.

(i) ***Karyotype analysis***

The haploid chromosome number in animal may be even 1 in *Myrmecia* (ant) up to 250 in some fern. The chromosome number usually does not vary much in related species. While in Lepidoptera and many organisms the number shows consistency, in *Myrmecia* this is found to vary widely from 1 to 42 (Imai and Taylor, 1983). This number varies from 2n= 4 (*Haplopappus gracilis*) to 2n= 530 (*Poa litterosa*). In some closely related plant species, the number increased in multiple of a haploid number. For example, this number is 7 and the species were found to have chromosome numbers as 2n= 14, 28, 42, 56, 70 etc. This doubling, tripling onwards of basic number is called polyploidy. Opposite to this, in some plants, there may be loss of one or more number of chromosomes (aneuploidy). It is observed that the karyotype of members of same species remains fairly constant. This is most chosen tool in cytotaxonomy and also used in phylogenetic reconstruction.

However, sometimes one or few parts of a chromosome or even a whole chromosome may be lost or doubled showing enormous changes in the offspring. Many processes may bring about changes in chromosome number. These are chromosomal deletion, duplication, inversion, fusion and fission. Among these, overlapping inversion is widely used to detect phylogeny. By suitable staining method, chromosomal rearrangements can be detected and these data are used as characters for a species. A cross between species with normal chromosomes and another with major change in its chromosomal arrangement will show reduced fertility due to unbalanced genome. But in many *Drosophila* and Grasshopper, unrelated species with enough differences in morphology of chromosomes show little or no reduction in fertility. White (1982) explained these as exceptions and no further explanation is so far available.

Any form of chromosomal rearrangement in an offspring will produce ephemeral population if that particular arrangement is disadvantageous. Sometimes, however, such disadvantageous heterozygotes may produce stable population under condition of enough time to undergo inbreeding. Chromosomes may break at certain points along the length and afterwards join at any point. So there may be many combinations of chromosomal rearrangements. A reversal, ie., back to parental configuration is an unlikely event in evolution of a species. In practice, identification of similar but non-identical inversions is not an easy task although that may be associated with other evidences. Farris (1978) suggested that polymorphism in a population can occur for that inversion which may or may not be selected by nature.

(ii) *Chromosome banding*

At finer level, individual chromosomes and their homologous are thoroughly studied in several species for their morphological and biochemical properties. These characters are found to be fairly consistent indicating specificity. Excepting few results, this part is still at research level in cytotaxonomy. The study involves identification of banding pattern, differences in densities of chromatin and heterochromatin, ratio of A-T and G-C content and total number of chromosomes with regard to position of centromere (i.e. number of metacentric or acrocentric or telocentric chromosomes).

Banding pattern identification solved separation of cryptic species and indicated their phylogeny in Simulidae (Diptera) that contains many important vectors of tropical diseases (Dunbar, 1966). However, the easiness in the study of Diptera (also in Collembola and Protista) by the presence of polytene chromosomes is not available in most other organisms. Special techniques, such as C-, G- and Q- banding methods are employed in cases with polytene chromosomes and revealed translocation and other chromosomal changes and homologies with related species. All these data were incorporated to cladogram preparation.

(iii) *Chiasma frequency*

This frequency is very much specific for a species and hence used in taxonomy. The chiasma is genetically controlled and seen in diplotene stage of meiosis when genetic exchange occurs. It depends basically upon the extent of homologies of sister chomatids. Therefore normal number of chiasma will be found in con-specific members only.

(iv) *DNA hybridization*

Since all expressed characters are due to the sequential arrangement of nucleotides within expressed genes, any change in their position will alter those characters partly or wholly. Few to many nucleotide may change or lost to affect a character. The differences between two species can be measured by the amount of genetic differences between them. This is actually the amount of nucleotide difference, that is, the unpaired portions of

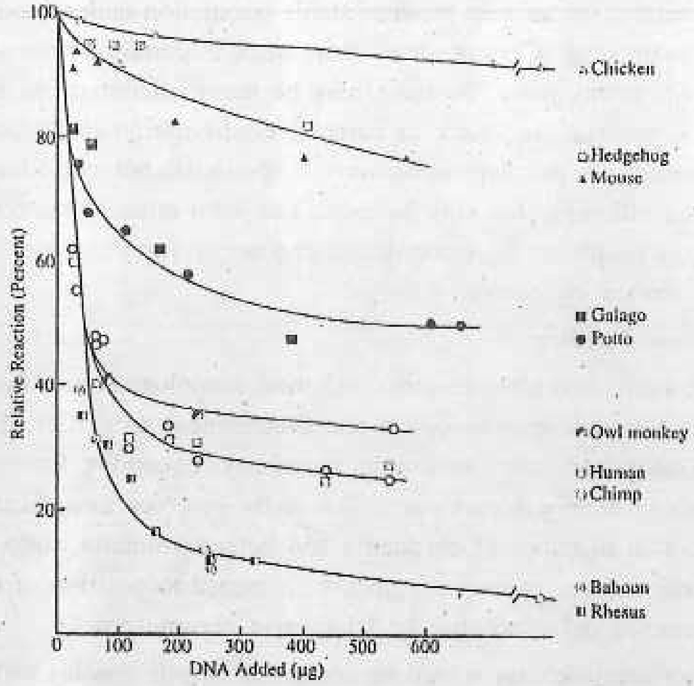

Figure 5. Relative similarities in DNA sequences in some animals

nucleotide when allowed to hybridize. This can be measured in two ways: one is the amount of DNA of two species that actually hybridize and the other is the amount of complementary DNA in the hybrid molecule. Such experiment shows the relatedness in mammals clearly (Hoyer and Roberts, 1967) (Figure 5).

One of the various methods of DNA hybridization is to allow two types of single stranded DNA to hybridize. The duplex is then denatured at increasing temperature at 1° C at every few minutes. The resultant single strand DNA is collected at every new temperature and the proportion is plotted against respective temperature. Now the dissociation curve of hybrid DNA and control DNA is compared. The thermal stability (TS) is that temperature at which 50% of the duplex DNA has dissociated. The difference

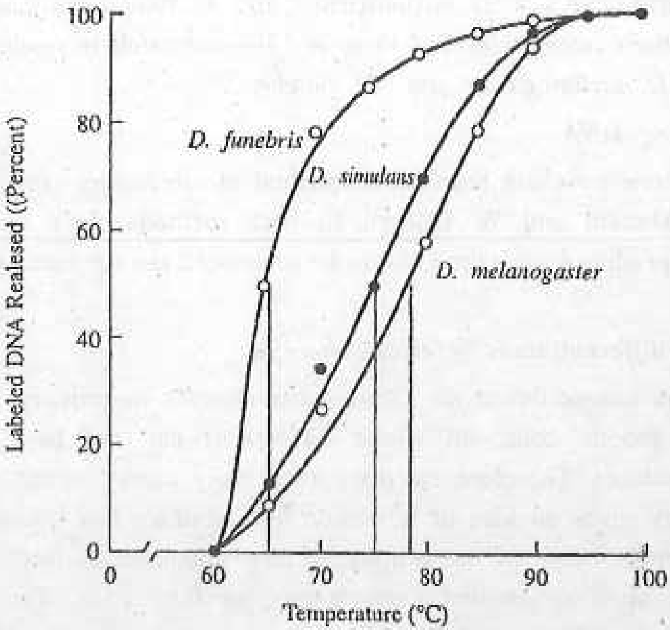

Figure 6. Comparison of thermal stability of DNA among three species of *Drosophila.*

(ΔTS) between hybrid and control is directly proportional to the amount of unpaired nucleotide in the hybrid DNA. It was found that for 1° C, the ΔTS is equal to 1.5% mismatched nucleotide pairs (Laired, McConaughy, and McCarthy, 1969) and the more presumed value is probably for 1° C, the ΔTS = 1% (Figure 6).

(v) ***DNA phylogeny***

Hybrid DNA always tends to dissociate at a temperature lower than their parents. This is constant for that hybrid molecule and is called *thermal stability* profile, which indicates rates of nucleotide changes per unit time. Therefore this is an important tool in diagnosing degree of differences between two species under study. 3H- labeled DNA of *Drosophila melanogaster* and DNA of other species were hybridized and their thermal stability was measured and the values were:

Drosophila melanogaster (Homologous duplex) TS = 78°C

D. melanogaster + *D. simulans* (Heterologous duplex) TS = 75°C

ΔTS = 3°C

D. melanogaster + *D. funebris* (Heterologous duplex) TS = 65°C

ΔTS = 13°C

Therefore hybrid DNA's of *D. melanogaster* and *D. simulans* are noncomplementary in about 3% of their nucleotides and there is 13% mismatch in nucleotides in case of hybrid DNA of *D. melanogaster* and *D. funebris.*

(vi) *Sequencing DNA*

This can be done by chain termination method of F. Sanger or chemical cleavage method of A. Maxam and W. Gilbert. In both methods, four sets of radioactive oligonucleotides produced from the DNA to be sequenced are subjected to high resolution electrophoresis.

(vii) *Genetic differentiation by electrophoresis*

Electrophoresis cannot detect all amino acids changes in primary structure. Due to peculiarities of genetic code, all allelic differences can not be detected by their corresponding proteins. Therefore electrophoresis truly cannot detect genetic variation perfectly and only gives an idea of it. Hence few arbitrary loci are selected for study which act as representative of the genome of that organism. A few such homologous loci in different taxa are studied through proteins they code. The average genetic differentiation observed in the samples will represent the genome. Thus the differentiation over a number of loci is approximately proportional to the time since their last common ancestor and this view help to construct the phylogeny. The data will also show *Genetic Identity* (I) and *Mean Genetic Distance* (D) as follows:

$$I_1 = \Sigma(a_i \times b_i) / (\Sigma\sqrt{a_i^2} \times \Sigma b_i^2)$$

I_1 is the genetic identity of a locus I; a_1 and b_1 are the frequencies of i-*th* allele in population A and B. $I_1 = 1$, if two populations have same alleles in identical frequencies and $I_1 = 0$, if they have no alleie in common.

Mean Genetic Identity (I) = $[J_{AB}]/[\sqrt{(J_A} \times J_B)]$

J_{AB}, J_A and J_B are the arithmetic means, over all gene loci studied, of $\Sigma(a_i \times b_i)$, Σa_i^2 and Σb_i^2 respectively. Here I = 1 (complete genetic identity) or may be I = 0 (complete genetic differentiation).

$D = -\log_e I$ (D = 0 – infinite; 0 means no genetic differences.)

It is believed that nucleotide substitution occurs independently and this follows Poisson distribution, then D is equal to average number of electriphoretically detectable nucleotide substituion accumulated in that taxa since it has separated from common ancestor. The *willistoni* group of *Drosophila* consists of six closely related and morphologically alike species and these has been separated by electrophoresis at 36 loci.

(viii) *Pulsed Field Gel Electrophoresis (PFGE)*

Here at first, Gel electrophoresis of DNA cut with restriction enzymes followed by specific hybridization is done and the fragment sizes are measured. The method can separate DNA with 50 kb size. But when direction of electric field is periodically (pulse) changed, the power of DNA separation increases (Schwartz and Cantor, 1985).

(ix) *Spectrophotometric technique*

Most compounds absorb light in visible wavelength or ultraviolet region. Each compound shows different absorption at different wavelengths of light. This values constitute the absorption spectrum for that compound. Its value for nucleic acid is 260nm and proteins 280nm. The difference is due to the presence of more unsaturated rings in nucleic acids.

2.3 Molecular taxonomy

Comparative taxonomic analysis of various bio-molecules can be done by various methods as described earlier. Molecular taxonomy deals with identification, sequencing, analyses and importance of proteins and nucleic acids along with some related and specific techniques.

Due to common descent, similar compounds will occur in many organisms and these are dealt as conservative molecules. Still some chemicals show gradual or rapid changes during evolution and these rates are important in phylogenetic research. Again quantitative and qualitative tests of biomoelcules which are expected to deviate from ancestors by the differences in physiological activities can be made to measure the extent of divergence. Recently much attention has been given to sequencing of protein, nucleotide, and correlation between the two.

The analysis is usually done in two ways, viz. quantitative and qualitative studies of biomolecules. The amount and kinds of different protein, the constituent amount and kinds of amino acids of these proteins are identified and the values are compared among related taxa. The resultant values are then numerically arranged into data matrix and the phenogram or cladogram is prepared. This type of analysis was done to construct the phyletic lines of some groups or animals. For example, a study on the location of synthetic activity and amount of L-ascorbic acid in birds shows that it was synthesized in kidney only in most birds. Later, in a few advanced groups, liver also took responsibility for its synthesis and it is absent in modern Passeriformes (Figure 7).

Ratio of similar and dissimilar amino acids is studied for many proteins. A study in this line was done on fibrinopeptides of 34 mammalian species. Out of three chains (α, β and γ) of fibrinogen, the α and β chains (called fibrinopeptide A and fibrinopeptide B) were sequenced for amino acid positions. The data obtained used in phylogeny and that

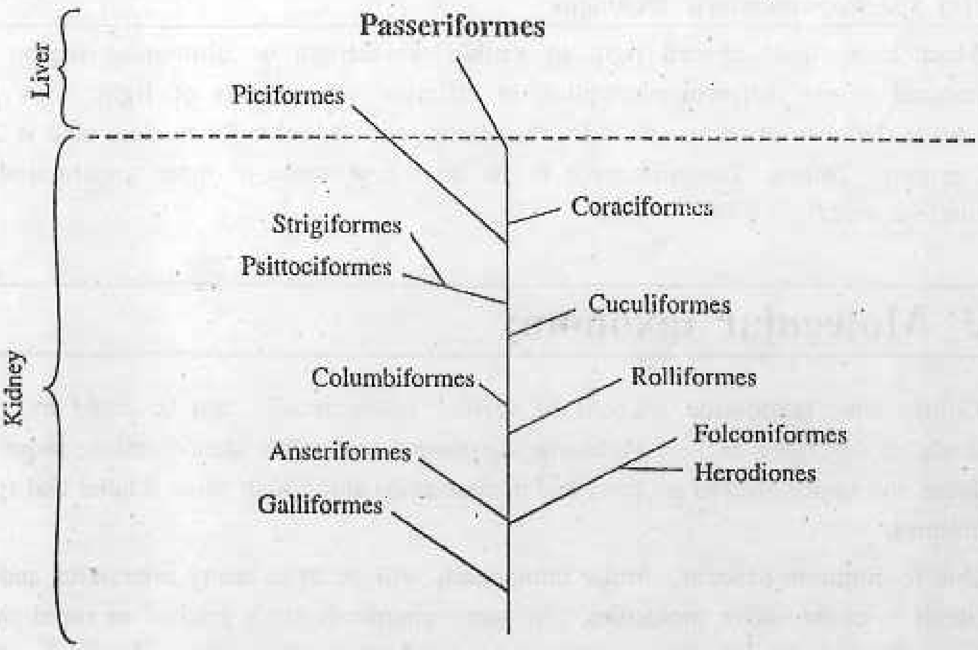

Figure 7. Phylogeny of birds on the basis of sites of synthesis of L-ascorbic acid

has supported the existing phylogeny for those species. There is distinct divergence of canines and bovids from human, monkeys and rabbits.. Similar study on cytochrome C (containing 110 amino acids) has been done on many species and the results perfectly match with established classification.

The essence of chemotaxonomy lies in that every organism synthesizes numerous chemicals on demand of physiological activities. The molecules are product of complex gene action and are ultimately controlled by specificity of genome of a species. The most observable changes are the coloration and communication. Many taxonomists, however, argue to the relative importance of chemotaxonomy than morphotaxonomy

The nucleotide sequence of structural genes determines the sequence of amino acids in a protein. So protein taxonomy is a good tool in species identification. The commonly employed technique is electrophoresis which is not hundred percent accurate and this is discussed latter. Lewontin (1975) pointed that out of 1/3 of all amino acid replacements are detectable by gel electrophoresis..

Gel electrophoresis has contributed valuable data in taxonomy to measure genetic differences among related species and thus helpful in phylogenetic study.

2.3.1 Principles and techniques in electrophoresis

Because proteins have net electric charge, isoelectric point (discussed later) and specific molecular weight, they can be separated from a sample through their differential rates of migration over a gel. Some commonly employed methods are discussed here.

(i) *SDS polyacrylamide electrophoresis*

This methods depends upon the fact that proteins binds the same amount of SDS per gram and binding occurs predominantly at hydrophobic regions. It requires some reference proteins, very little material and is simple. If coupled with silver staining method, it can be used in submicrogram level. SDS or sodium dodecyl sulphate is negatively charged ionic detergent, which binds with protein chain at regular intervals and also denatures it. This unfolds globular proteins (excepting regions with disulphide bonds). The net charge of SDS-protein complex depends upon the length of original protein chain and does not depend on the amino acid sequence. Migration of SDS-protein complex reflects the molecular weight of test protein.

(ii) *Gradient gel electrophoresis*

Proteins differ in their molecular weight and sizes. A suitable gel medium is prepared which allow a gradient of strength that changes from one end of gel to other. This allows initial protein sample at low strength (ie. having large pore size) and their rate of progression is retarded and then arrested. In this way proteins having varying shapes are isolated.

(iii) *Isoelectric focusing (IEF)*

Some amino acid replacement may not alter net charge of a protein (e.g. when amino acid Lysine is replaced by Arginine: both having amino group in side chain). Such amino acids and proteins having both carboxylic and amino acids as side groups (zwitterions) show changes in ionization states of its side groups in response to pH changes. For example, at high pH, only carboxylic and at low pH only amino groups are found to be ionosed.. By trial a pH value can be obtained at which there will be ionization of equal numbers of both positively and negatively charged groups and hence there will not be any net charge. This pH value is isoelectric point for that protein. This is a highly specific and sensitive value of a protein and any minor change in amino acid composition will be detected easily.

This procedure is expensive and is usually combined with other methods. The combinations are standard electrophoresis followed by IEF or SDS, IEF followed by SDS or standard electrophoresis followed by gradient electrophoresis.

(iv) ***Two Dimensional Electrophoresis***

This technique is much used in gene technology, detection of many diseases and also contributed to human chromosome mapping by sequencing DNA and protein. The requisites of this method are IEF, a pH gradient (increasing gradually from anode to cathode) and a special buffer called carrier ampholytes. First proteins are separated in a tube gel of polyacrylamide gel followed by electrophoresis perpendicular in a second dimension in a slab gel.

2.3.2 Allozymes and isozymes in taxonomy

These are those different enzymes produced from a single locus. Isozymes (isoenzymes) are enzymes produced by genes at different loci. In practice enzymes of Kreb's cycle and glycolysis are studied and these are stained after electrophoresis. Monomeric allozymes (single protein chain) normally, but not always; gives single band in zymogram. If it is

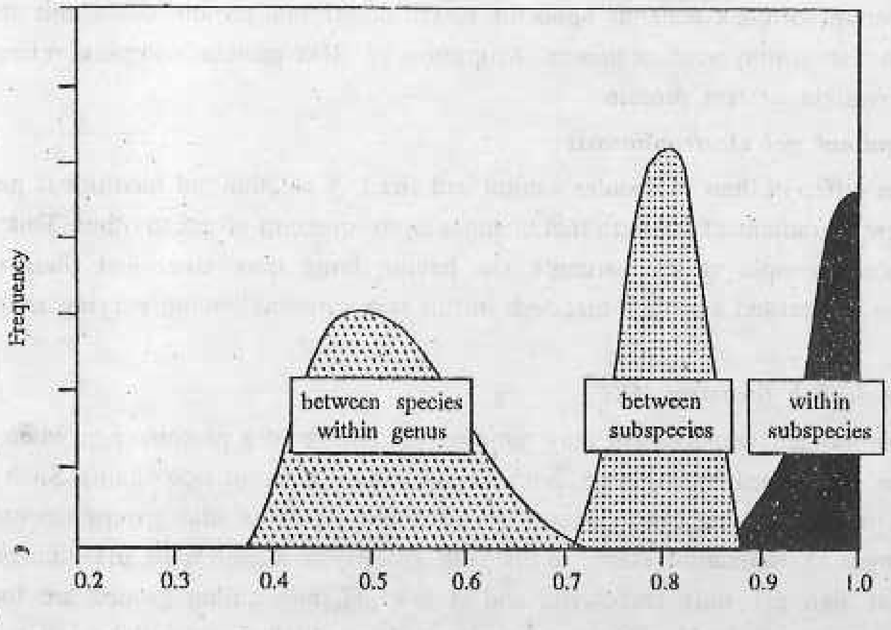

Figure 8. Genetic similarity index based on allozymes at subspecies, species and genus levels

oligomeric, say a dimmer (consisting of two separate protein molecules coded by same gene), then homozygotes give single band and heterozygotes will give three bands (one for two fast moving, one for two slow moving and the third one comprising one of each).

Allozyme study has profound effect on population genetics and taxonomy. Keeping in mind that there are other sources of variations in allozyme mobility, its banding pattern generally correspond to the genotype. The frequencies of different alleles of a polymorphic gene, under stable natural condition, follow Hardy-Weinberg equilibrium. If the samples show different frequencies, we may predict that they belong to separate populations.

Avise (1974) stressed the importance of isozyme studies in systematics and found very high degree of genetic similarity within species and the value is quite low among congeneric species with virtually no overlap between two sets of results (Figure 8).

2.3.3 Protein sequencing

(i) *Selective cutting of protein chains*

Endopeptidases cut protein chain where a particular amino acid or groups of amino acids occur. For example *Staphylococcus aureus* V8 cuts at carboxyl side of glutamyl or glutamyl and aspartyl residues. Some chemicals such as cyanogens bromide cuts proteins at carboxyl side of methionine residues and produces large sub-units of that protein. Trypsin cuts proteins at arginine and lysine residues. Thereafter electrophoresis becomes easier for such smaller digests.

(ii) *Sequencing amino acids and triplet codon*

Since there are twenty different amino acids, therefore each amino acid position can be dealt as a character. Thus there are twenty-one different possible combinations (including one chance for an amino acid to be lost). A change for methionine to tyrosine or opposite requires a change at all three positions in the triplet codon (AUG → UAU). Similarly to change an aspargine to lysine requires only one change at 3rd position in the codon (AAU → AAA). Based on these observation Fitch and Margoliash (1967) proposed that a transition in amino acid sequence should be thought in the light of base changes in triplet codon and calculation to be done on their probability which actually shows the sequence in separation and direction of divergence of taxa.

Nucleotide replacement data are used in taxonomy in two ways: distance based analyses and parsimony analysis. In former a distance matrix is prepared by summing up the total number of nucleotide replacement between a pair of taxa. In parsimony analysis, as shown before, twenty-one different alternatives are treated as character states.. The amino acid serine, however, is treated as two separate characters because its codons are variable.

Remarks : There are some difficulties in the application of data on amino acid sequence in taxonomy. Although the parsimony analysis based on protein sequence done by Penny and Hendy (1985) shows good correlation between tree length and different proteins, the shortest tree was not shortest for all five proteins individually. Thus this method is an approximation to true phylogeny.

An interesting observation by Grahthan et al., 1986 is that for a particular amino acid, organism shows preference for a particular codon (although an amino acid can be coded by any of six combinations). There is so far no explanation to this and probably related to unavailability of specific tRNA. This prefernce may alter to some extent one amino acid to another. However this biasness is not uniform and is quite different in different taxa.

Fitch (1984) advocated that merits of parsimony analysis yields better results done on amino acid replacement data than that of nucleotide replacement data as later increases the number of characters for analysis.

2.3.4 DNA-types, sequencing, principles, use in taxonomy

DNA technology is progressing at a high rate and lots of data on nucleotide sequencing are now available for taxonomic purpose. The various types of DNAs and RNAs studied so far show both potentiality and problems in their use in sequencing.

(i) ***Functional and non-functional nuclear DNA***

The length of eukaryote DNA may be about 100Mbp (megabase pairs, as in Horse-chestnut tree and a nematode) and up to 100,000Mbp in some organisms. The average value ranges from 1000 to 10000 Mbp. However the number of functional genes along with their associated sequences account for only 100Mbp and rest are, therefore, non-functional. It is observed that their haploid genome contains one or few copies of these functional genes. Their number, however, increase by gene duplication.

(ii) ***Repetitive DNA***

Besides functional genes, eukaryote genome contains 25% to 80% of nonsense sequences. Some highly repetitive sequences form satellite DNA. By specific endonuclease, such DNA can be cut and separated elctrophoretically. This method was applied to the phylogeny of whalebone and toothed group and has proved the monophyletic origin of the Order Cetacea.

(iii) ***Mitochondrial DNA (mtDNA)***

Excepting four phyla of Protista and few fungi, all organisms have mitochondria. Again, the mtDNA is circular excepting some alga and species of *Paramecium* where this is probably linear. This DNA may contain 16 to 100 or even 240 kilobasepairs in some higher plants. The rate of mutation of mtDNA is five to ten times more than nuclear DNA(exceptions are echinoderms where both the rates are similar). Thus either mtDNA is showing higher rate of evolution than nuclear DNA or opposite to this. Therefore high rate of change in sequence means the population will be polymorphic for particular nucleotide substitution in the absence of proper time for selection. This fact is useful to draw intraspecific as well as interspecific relationships. Study on nucleotide sequences of mitochondrial rRNA shows that this is far more similar in prokaryotes than eukaryotes.

(iv) *Chloroplast DNA (cpDNA)*

This DNA is circular, about 135000 to 160000bp long and unlike mtDNA is more conservative and is inherited through 'mother'. These features are compared with nuclear DNA and results are utilized to predict their history, such as past hybridization or introgression. This has proved multiple origin of a hybrid *Aegilops triucalis* which contains two distinct types of cpDNA.

(v) *Ribosomal RNA and ribosomal genes*

Ribosomes evolved quite early in organic evolution. It is present in large number in each cell and very much similar in all organisms. It has been proved that there are differences in average rates of nucleotide substitution in different domains of rRNA. Thus each subunit of ribosomes contains some information of divergence in relation to changes in sequence. Some sequences show very little changes so far and these can act as primer (called universal primers) for other organisms to detect changes in rest of the sequences.

(vi) *Transfer RNA*

Transfer RNAs (tRNAs) are universal occurrence in living system and are highly conservative in nature. There are nearly 60 tRNA genes in prokaryotes and up to 8000 in eukaryotes and latter may be due to large tRNA turn over for the demand by cellular activities. The genetic code is almost uniform in living organisms. But this is not the rule for some protistan ciliates. The codes used by mtDNA and cpDNA also varies from nuclear DNA. This aspect probably is helpful in future phylogeny analysis.

(vii) *Prokaryote and viral genome*

Viral genome may be a DNA or RNA and show enormous variation. Whether they had single or multiple origins is yet to be decided. In prokaryotes, the main or nuclear DNA is a closed loop, without histone. The DNA other than this nuclear DNA is called plasmids. The plasmids do not regulate major metabolic activities but one involved in sex has role in antibiotic activities.

(viii) *G+C and A+T ratio*

This ratio varies widely even in major groups of organisms. In prokaryotes the range of variation is 25% to 75% with very little variation in relatives (10% to 15%). This data reflects the constitution of entire genomeand therefore can be used as yardstick in measuring phylogenetic distance between taxa. The principle of this method of measuring the G+C and A+T content is that G+C is more heat stable (by the presence of three hydrogen bonds, A+T has two such bonds). So DNA separation is related to increased absorbance of UV light at 260nm.

(ix) *Restriction site analysis*

Restriction enzymes (endonucleases, such as Bam HI, Hind III etc.) can recognize and cut DNA at specific sites depending upon length and purity of DNA. The sites are fixed for members of a species population and different in unrelated groups.

There are different probes that recognize different sequences and they can be used for each restriction enzyme. Thus a range of combinations of these two will determine presence or absence of restriction sites. This data is used in phylogenetic analysis. In case of large nuclear genome, there is large number of restriction fragments which will show their length polymorphism (Restriction Fragment Length polymorphism, RFLP). In case of RFLP, the observed variants are not due to deletion or insertions but simply due to gain or loss of restriction sites (Shields and Helm-Bychowski, 1988).

The importance of restriction site analyses is manifold. For example, restriction fragment analysis of nuclear rRNA genes provides evidence of events over far greater time scale than similar study of mtDNA. Latter provides evidence of events during recent past including intraspecific events (such as origin of human race). The procedure is often cost effective (Hillis and Moritz, 1990).

(x) *DNA fingerprinting*

This technique, so far developed, is used in forensic medicine to detect close relation between organisms(human). This involves detection of the length of 'minisatellite DNA' sequences present in genome. Such DNA consists of various lengths of uniformly repetitive DNA in many separate loci. Each such repeat unit has a highly conserved core sequence of about 30bp. A single restriction enzyme with radio-labelled core sequence probe will produce restriction fragments that may contain many minisatellite loci.

(xi) *Rates of transition and transversion*

Through mutation a transition will occur when a purine or pyrimidine base is replaced by the other purine or pyrimidine base.. A tranversion mutation is the replacement of a pyrimidine by a purine base or vice versa. The rate of transition is far more than transversion although there is double chances of transversion mutation than transition mutation. Depending on time scale, it is expected that closely related taxa will show more transition and transversion. Distantly related taxa (with enough time to deviate and evolve through mutation) are expected to show a ratio approximately equal to 1:1 (transition: transversion) (Figure 9).

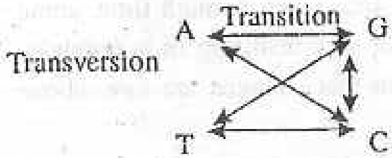

Figure 9. Possible routes to transition and tranversion

(xii) ***Insertion and deletion***

The differences in two DNA sequences may be by a single base pair or multiple base pairs. In former case, the single base pair difference may be due to addition or deletion during the course of evolution. This event can be treated as single character state and is not a problem in parsimony analysis. But in case of multiple base pairs where the difference is high, there are many events of addition or deletion or both during evolution and they have created divergence in the taxa.

(xiii) ***Secondary structures of DNA and RNA***

Secondary structures of DNA and RNA show that some parts are complementarily double helical in nature while some regions are single (unpaired). The complementary nucleotides do not easily mutate showing their conservativeness while unpaired sequences are prone to alteration. Their mutation rate is high and this may be related to their less functional significance. Therefore these unpaired sequences have less detectable expressions and fail to yield valuable taxonomic data.

(xiv) ***Dealing with fossil DNA***

Available DNA content of fossils is very low than originally it had in living state. This is due to denaturation and oxidation of bases particularly the pyrimidines. Still, the minute quantity that is available can be easily amplified many times and, with the help of suitable probe, their base sequences can be determined. The nature of the preservative in the fossil is an important factor in DNA preservation. For example, Cano et al. (1992) analyzed nearly 1000bp from the DNA of amber preserved Cretaceous stingless honeybee (55 mya*). Similarly Golenberg et al. (1990) successfully analyzed many sequences of magnolia leaves (17 mya). Other studies were on ground sloth (13 000 ya), quagga (relative of horse and ass). However attempts to decipher the sequence of mammoth failed.

Discussion

The achievements on DNA technology are outstanding. Still many aspects are unsolved. Some are summarized here.

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* mya-millions of years ago

(a) Each nucleotide sequence has four possible variants and, given enough time, some positions in homologous chromosomes may alter in a similar way resulting in homoplasy. Therefore parsimony analysis which is based on assumption that changes are rare, above phenomena create problems.

(b) Reversal can well be a problem in parsimony analysis.

(c) If there is more than 75% divergence in two sequences, the information content in the sequences cannot be utilized or assessed. In this case tranversions can be studied as a rare event.

(d) Proportion of transitions decrease as the two taxa are diverging.

(e) DNA of some organisms show strong bias in thir base composition and if such DNA is very rich in A-T content, then more transversions are likely to occur and A to G or T to C transitions will be rare. In such case, transitions will be more reliable and informative for parsimony analysis.

(f) Amino acids are more subjected to selection pressure thereby increasing problem in the analysis of protein coding sequences. So we choose to analysis of third position in the codon. But this third position changes at higher rate.

(g) At present stage, complete sequencing of DNA of any fossil specimen seems impossible particularly due to oxidation and denaturation. This is more true for older fossils.

UNIT 3 ❑ Dimensions of Speciation and Taxonomic Characters

Structure

3.1 Dimensions of speciation-types of lineage changes, production of additional lineage

3.2 Mechanism of speciation in panmictic and apomictic species

3.3 Species concepts-species category, different species concepts, sub-species and other infra-specific categories

3.4 Theories of biological classification, hierarchy of categories

3.5 Taxonomic characters-different kinds, origin of reproductive isolation-biological mechanism of genetic incompatibilities

3.1 Dimensions of speciation

Each member of a deme (a local population) has an equal chance of mating with a partner of opposite sex and this follows Mendelian laws and hence also called Mendelian population by Wright. The gene frequency (or allele frequency) and the gene pool are the two aspects of importance in consideration to evolution of this population. According to Hardy and Weinberg principle the result of random mating (panmixia) among the members will preserve the gene frequency although the genotype frequency may change in the first generation provided that no external influence will act on this population. However, after the first generation, the genotype frequencies will also remain stable, that is at equilibrium.

3.1.1 Factors influencing gene frequency

1. However, Hardy and Weinberg principle is unfit for the population with inbreeding or non-random mating (extreme cases are self fertilization). But ***inbreeding does not alter gene frequencies***. It expresses rare recessive genes (allele) due to increased homozygosity. There is also inbreeding depression when the expressions are deleterious.

2. ***Mutation changes the gene frequency*** of a population through the production of changes in the nucleotides. However Fisher calculated that the chance of losing of the newly mutated gene in just by one generation is 33%. The only alternative way to change the gene frequencies is the frequency of mutation. This rate is, however, not constant.

The approach to mutational equilibrium is very slow and is hardly ever reached. Thus this is not a good cause to change gene frequency.

3. Gene frequency can be altered by the ***differential viability and fertility of the genotypes***. Some are more viable than others and thus selection works on the various genotypes. The number of fertile offspring produced is an index of fitness of a genotype. This selection works at haploid (gametic) or diploid (zygotic) stage when the gene expression affects the survival. A selection in haploids will show no difference between dominant and recessive genes since they show phenotypic expression. The deleterious recessive alleles are expressed and are eliminated in one generation. Thus the selection effect is more rapid and direct on haploids.

4. In cases of reversal of selection a ***recessive allele may be favoured over the dominant***. If the dominant one is lethal, its frequency falls to zero. Therefore the degree of heterozygote expression of deleterious genes determines the effectiveness of selection.

5. Heterosis (or hybrid vigor) is the superiority of heterozygote by way of reproductive fitness over the homozygotes. This condition is called ***overdominance***.

6. Superior heterozygotes with different genotypes show ***polymorphism***. The example is the *HbA/HbS* (sickle cell gene) in men can protect them from malaria than men with *HbS/HbS* or *HbA/HbA*. Industrial melanism is an example of differential selection coefficients in different environments of a widespread population. With change of situation (reduction in pollution) there was reverse evolution, the melanic forms showed reduction in population.

7. Batesian mimicry, Mullerian mimicry and self-sterility in plants are examples of ***frequency dependent selection***.

8. A selection usually tends to be stable and most phenotypes cluster around the optimal phenotype. A selection may be ***directional*** (used by animal and plant breeder to produce better yield) and in evolution extreme phenotypes show adaptation to a changed environment. But in discontinuous environment these selections are ***disruptive*** or ***centrifugal***. According to Red Queen hypothesis, each species faces environmental changes and hence newer selective challenges and fitness. Thus attainment of equilibrium frequency of a mutant gene both mutation frequency and selection coefficients are vital.

9. The presence of ***modifier genes reduces the effects of deleterious genes*** at other loci.

10. Since different populations have different gene frequencies, ***migration will cause receipt of gene flow***. The effect of migration depends on differences in gene frequencies of the two populations and amount of genes taken into by the population. However, migration affects the local evolutionary changes.

11. ***Genetic drift alters the gene frequency,*** particularly if the size of the population is small. Random genetic drift is a non-directional force.

Thus it is evident that there are three directional forces - mutation, selection and migration. The one non-directional is genetic drift. There are some other unnatural events when the gene frequency may change. These are sudden change in environment, rare hybridization event, and unusually favourable mutation. These rare events change the course of evolution to a situation, which is not easily explainable.

Genetic variation and evolution

Drawin was aware of heritable variations but could not explain the underlying mechanism. He even concluded that some variations were better than others, and natural selection favoured former and helped the progeny with better reproductive fitness. Thus useful variations spread while less useful variations Were gradually eliminated from the population.

R. A. Fisher (1930) stated in the Fundamental Theorem of Natural Selection "the rate of increase in fitness of a population at any time is equal to its genetic variance in fitness at that time." Similarly Ayala (1965a, 1968a) working on *Drosophila* has experimentally shown that there is a positive correlation between the rate of evolutionary change and amount of genetic variation. His observation was based on 25 generations under conditions of increased genetic variation. The rate of adaptation to the experimental condition of increased and stiffer natural selection, where the fly had to compete for food and space, was found to be significantly greater.

Genetic variation in loci

H.G.Muller and his students proposed the so called *Classical* hypothesis to state that a typical individual having wild type allele at every loci is said to bear the 'normal', ideal genotype. The individual is heterozygous for a small proportion of the entire genotype by the presence of mutant allele. The mutation pressure introduces the mutant allele in the population and, being deleterious, is later on rejected by the natural selection. However, any mutation that increases reproductive fitness will be preserved by natural selection and will increase its frequency and replaces the original wild type.

The *balanced* hypothesis was proposed by Dobzhansky and his students (1970) as well as E.B.Ford(1971) of Great Britain, They disapprove any 'wild' or 'normal' type and the gene pool is heterozygous at most of the loci. Only a little portion of the genotype is homozygous. That means allelic polymorphism and fitness of an individual depends on the presence of the different allele at different loci and the impact of the environment. Gradually there is a change in frequency of this allele and in kinds of allele at many loci. The deleterious allele rarely appears in homozygous state and these are kept at low frequency by natural selection.

The balanced model has proved its superiority over classical and during last decade allelic variation has been extensively studied. Some of the studies include polymorphism in snails, butterflies, grasshoppers, ladybird beetle and birds. By artificial selection of specific genetic variation has provided us a lot of commercially desired traits in plants and animals.

Rates of mutation and evolution

Considering the total amount of genetic variability present in a natural population, the vast variants arising in each generation will represent only a small fraction of the entire population. Molecular techniques have shown that in sexually reproducing population 50% of the loci are polymorphic and an individual is heterozygous at 5%-20% loci only. The number of variants produced, hence, would be 25%-10% total structural genes. Therefore mutation rate and evolutionary rate are not likely to be closely correlated.

Genetic variability and production of lineage

The genetic variability in a gene pool are acted upon by natural selection and finally produce or accumulate useful and heritable varieties of changes in the population. The paleontological method to classify evolutionary rates into those commonly found (horotely) into slower rate (bradytely) and faster rate (tachytely). Such heritable changes may be minute (*microevolution*) or large and distinctly visible (*macroevolution*).

The three factors responsible for different rates of evolution are :

(a) The size, genetic variability and pattern of distribution of a population. The fragmented populations show faster evolution than a homogeneous and interconnected population (Wright).

(b) Developmental constraints can limit or dictate the structures and functions organism can achieve. Evolution never stops by presence of constraints, only latter open up newer paths.

(c) The direction and intensity of selection were different during different major geological events in the past.

3.1.2 Theories on differential rates of evolution

(a) Punctuated equilibrium theory :

Punctuated equilibrium theory by Gould and Stanley is based on the studies of fossils. It is proposed that fossils show rapid macroevolutionary events after long intervals of microevolutionary stasis or equilibrium, punctuated by rapid macroevolutionary periods during which new taxa arise through entirely new causes and mechanisms.

(b) theory of macromutational events :

The theory of macromutational events was proposed by Goldschmidt (1930s, 1940s). According to this view, each macroevolutionary change is a macromutational event. Such mutation was enough to produce large developmental effects in organisms, which entered new adaptive zones.

But any such serious mutation that is able to produce a new species would probably be non-viable. Hence proponents of punctuated equilibrium have partly rejected the idea that i) significant developmental effects can be produced by regulatory mutations and ii) there may be occurrence of "founding accidents" or "bottle neck"; these two are sources of macroevolutionary mechanisms.

Microevolution

Studies on invertebrate fossils by Rowe and Fenton provided examples, which show slowly, and gradually a species evolved from existing species with very little changes in intermediate forms (or variants). These minute changes accumulated and ultimately produced 'living fossils' like *Latimeria* and *Neopilina*.

The examples of microevolution by Rowe distinguished several lines of descent in *Micraster*, a sea urchin. The changes that took place in a static environment have forced the transformation of *Micraster corbovis* to *Micraster coranguinum*. The brachiopod *Spirifer* found in the Devonian strata suffered rhythmic fluctuation of environment. But the evolutionary changes found in these organisms were not correlated with the environmental changes.

Microevolution takes quite longer time and the process is very slow. Successive forms are represented in successive strata in a paleontological series. Hence this is also named as 'successional evolution'. A parent population may break up into two or more subpopulation and each division undergoes its own history of evolution. The interbreeding population will spread its acquired genetic mutation and this subpopulation is tested by natural selection.

Microevolution is a gradual change in an interbreeding population through gene mutation. These mutations are either spontaneous or result from environmental pressure. Goldschmidt identified macroevolution for the origin of subspecies and race while macroevolution for the origin of species and genus.

Macroevolution

The parent population splits into several species population in a shorter period due to some urgent situations prevailing in nature and is also explained as *adaptive radiation*. Simpson gave the name *quantum evolution* to this process. It involves allometric changes with increase in size and weight in response to environmental situation among members of different populations. The examples are in the evolution of horse, elephant and others. According to Savage (1969) the reptiles also show macroevolution. The drastic and diverse conditions in nature help in divergence of a population and the time required is mostly short. Therefore the rate of changes in environment is the determining factor whether an evolution should be micro-or macro-in nature. The fossil records suggest that during the Silurian period no major taxa underwent rapid evolutionary changes because it was a period of almost uniform conditions. But most modern phyla evolved during the Cambrian. Similarly many groups radiated in the Devonian. Both plants and animals again radiated in the Jurassic and Cretaceous. Above changes are correlated with the six mass extinctions.

Our recent time is again a period of mass extinction, which is caused by the extensive modification of habitat by human species. The destruction of tropical rain forest, which harbours more species than any other habitat, is most threatening. Biologists predict that one million species are going to be lost within the next century and it means that the present rate of extinction will be unparallel in the history of life on the earth. Another important aspect of present extinction is that it will not see any new adaptive radiation by the interference of human itself.

Mechanism of macroevolution

The pattern of evolution of various groups show that there was far rapid evolution in some groups than other groups with slower rates. The causes so far known are natural selection and unknown unique historical phenomena. Adaptive radiations in many groups were due to changes in geo-climate and related newer ecology. Many structures were remodelled and newly developed to adjust with newer environment. The result is also decline or even extinction of many groups that failed in their speed of acquisition of structures or adjustment needed to survive. The time was important criterion to solve their problems within short span in relation to geological events. Dispersal played an important role where new comers to a new zone responded quickly to adjust with the newer habitat.

The development of trunk in modern elephants is another example of adaptive radiation. The evidences show that the ancestral fossil Mastodon, *Gomphotherium* of mid-Miocene of North America had short tusks and trunk. Gradually there were reductions in the size of lower tusks and lower jaw with a consequent elongation of trunk. This was helpful for this large grazer who requires more food and hold more amount of vegetation at one time. The second line of radiation for the same purpose was the increase in the width of mouth instead of development of trunk was going on in white rhinoceros.

Isolation by physical means is a great example of macroevolution by radiation. South America lost its continuity with the North America and mammals on either continents evolved separately. Thereafter (about two to three million years before), the continents were connected by a narrow land bridge, the Panamanian land bridge, and massive interchanges started. Now the separated oceanic forms evolved in their own way and presently there are three hundred and ten pairs of species on either side of the bridge, which undoubtedly evolved from the one ancestral species. South America experienced radiation of monkeys and histricomorph rodents (guineapigs and related forms). Both of these groups came from north or from the nearer continent (Africa). There was also radiation and consequent diversity in marsupial fauna in South America.

Paleontologists believe that macroevolution resulted from continental drift and this is also an important cause of mass extinction and adaptive radiation. It is easy to understand that the single mass of land (Pangea) of late Paleozoic was the source of origin of most of the land animals. Later fragmentation and separation of the land masses acted as a barrier and forced separate evolution. Through dispersal newer forms entered the changed habitats.

The phylogeny of the different taxa reveals that, soon after appearance of any major phylum it undergoes evolution of various classes and the latter underwent modifications to produce various families. This divergence may be at different rates along different lines.

The incomplete fossil record provide little clue to how the new phyla appear suddenly. One explanation seems to be speciation at peripheral zones where members are subjected to a situation different from the core area of the parental species. The core forms gradually become rare and restricted as local forms. Another explanation is that the sudden and changing environment after mass extinction forced development of newer characters among members of parental species and they undergo new stiffer pressure of natural selection. Only few survive those quick changes while most face extinction. Thus evolution goes on along any undetermined ways and is 'opportunistic in nature'.

Evolutionary lineages

Animal classification today is based on critical analysis of evolution; still many places in animal hierarchy are controversial or unsolved. Taxonomists usually group together taxa with common evolutionary history. The work is toughest one and sometimes opinions differ in this regard so that different phylogenetic schemes are not uncommon.

The members of *monophyletic* taxa are descended from one common ancestor. If the members of a taxon originate from more than one ancestor, they will be called *polyphyletic*. According to different views the monophyly can be achieved in three ways.

(i) The members are said to be *strictly monophyletic* if they descend from single parent or at least from same species or population (Fig. 2a and 2b).

(ii) The ancestor belonged to a different taxon but later on undergone much changes and radiation and ultimately produced several lineages all of which belong to taxa different from ancestral taxon.

(iii) The ancestor and its monophyletically evolved taxa belonged to a single higher taxon (Figure 10).

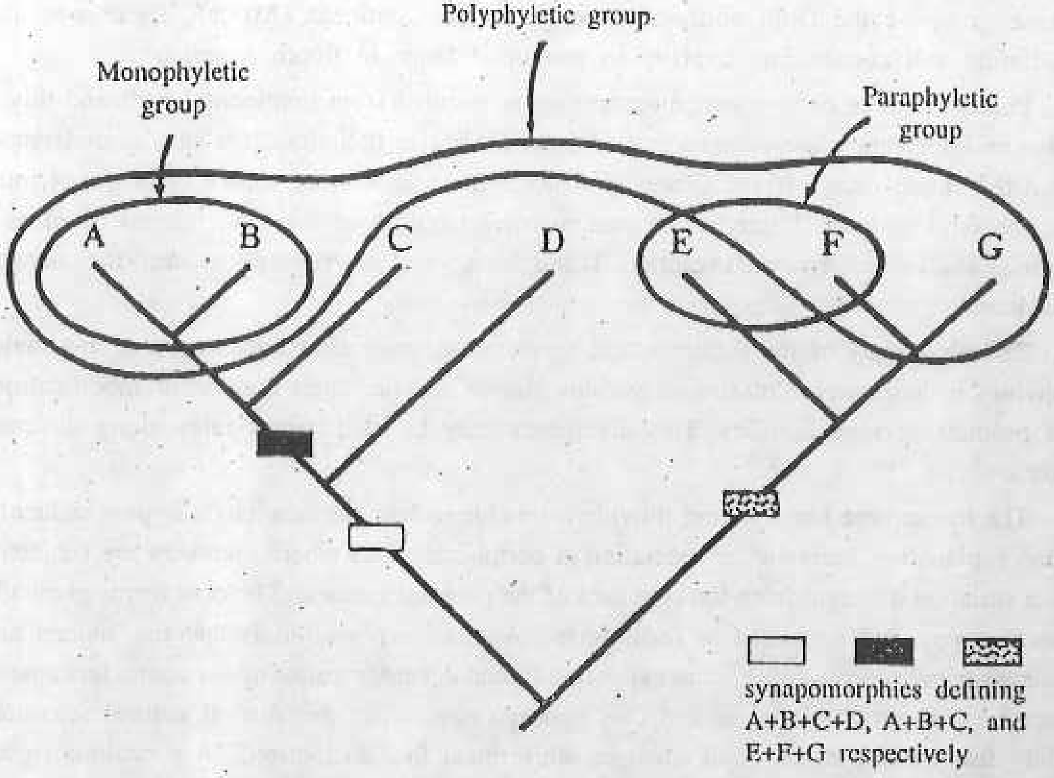


Figure 10. Diagrammatic representation of monophyletic, paraphyletic and polyphyletic groups

Simpson defined monophyly as the derivation of a taxon through one or more lineages from one immediately ancestral taxon of the same or lower rank. For example the derivation of several genera from one immediate ancestral genus or species.

Relationship between evolutionary changes, additional lineage and persistence

A lineage shows character changes upon passage of time as also branching to produce daughter lineages. Hence Rensch (1954) proposed two terms to explain this phenomenon:

Anagenesis : It is any kind of evolutionary change (advance type or not). The changes produce some novel characters than that of their ancestor and taxa with such characters are grouped together to a new *grade*. This grade may be monophyletic or polyphyletic (example is the independent origin of warm-blooded nature in birds and mammals).

Cladogenesis : It is the splitting or branching of a lineage. Here clades are the branches of a lineage that has undergone splitting and in broader sense, are monophyletic.

Stasigenesis : It is the phenomena in which a lineage does not split or undergo so much of changes in course of time hence preserve parental characters (Huxley) (Figure 11).

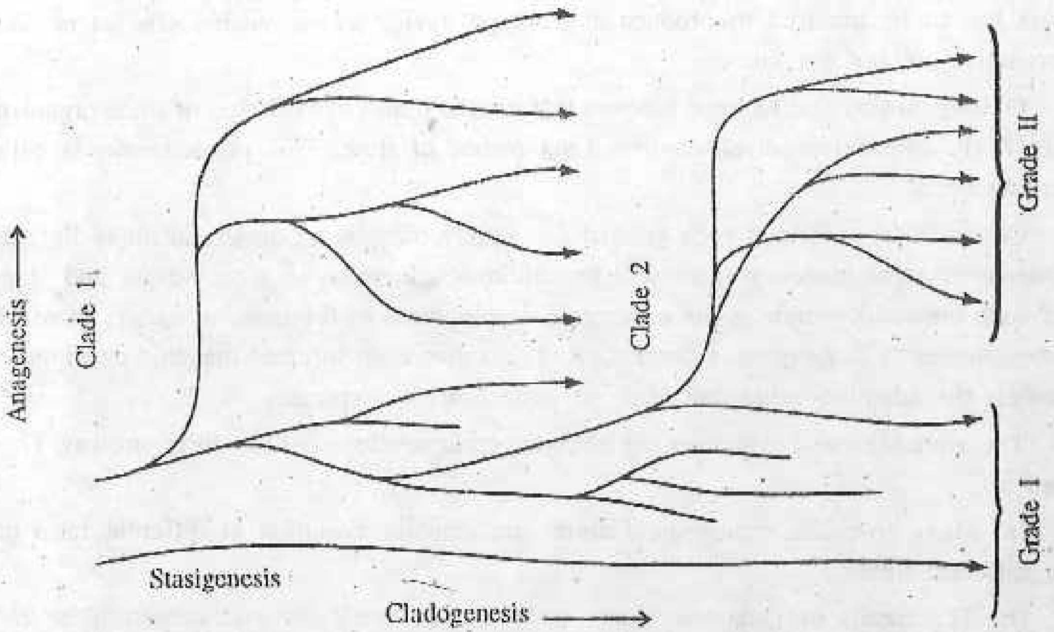


Figure 11. Different lineages showing anagenesis, cladogenesis and stasigenesis

3.1.3 Theories on the production of discontinuous lineages

A search for the ancestor of any two phyla reveals that the branches or lineages that lead to those phyla are well separated when they first appeared in fossils.

The co-adapted characters, according to Darwin, are those characters, which are grouped together into one and, like lineage group, move as a whole group. However, evolution of numerous harmoniously coadapted characters is probably impossible.

A. Saltation concept :

The set of co-adapted characters is unique for a group and if it splits into two or more lineages, then each will develop its own set of novel co-adapted characters at a single jump (***saltation***). This means that there will be no intermediates. Schindewolf (1950) explained the sudden appearance of many new lineages as fossils based on this concept.

Milvart (1871) supported saltation concept and refused natural selection. Through the emergence of Mendalian theory of heredity, the mutation was believed to be the cause of the sudden appearance of new characters and this again believed to support saltation concept.

Goldschmidt supported the large mutations are the causes of appearances of monstrosities which have wide phenotypic differences from ancestral forms. But nearly cent percent loss has to be incurred to produce a genotype having newer visible characters. Such examples are not yet known.

Orthogenesis : Due to some inherent features the trends of evolution of some organisms are fairly constant in direction over long period of time. This phenomenon is called orthogenesis.

Cope (1896) explained such gradual and steady increase in organs in many lineages. Due to inherent tendency there will be continuous increase in size, weight and length of such organs. Example is the orthogenic development of the massive antlers of extinct *Megaloceros* (a large corvine deer). Lull (1922), however, inferred that this development lowers the adaptive value and leads to extinction of a species.

The available fossil evidences explain orthogenic development in a different way. These are :

(a) Many so-called orthogenic features are actually evolution at different rates and at different times.

(b) The trends are adaptive; large body evaded predators and helped more food collection. The antlers were probably used not in fighting and had a role in courtship displays and thus were a better selection and reproductive fitness.

(c) Many lineages exhibited long term trends and increase in body size was normal.

(d) Gould (1973) showed that increase in body size and antler had a positive allometric relation.

B. Concept of adaptive peaks :

Saltation concept was proved to be quite unfit to explain the above trend. The present concept is that adaptive characters are favoured and push better adaptive species to further expansion through fitness. Such adaptive characters are novel and hence have higher adaptive value since their appearance in a population and their gradual refinement up to final stage to be established as a characteristic feature for a higher taxon. This was the essence of the concept of 'adaptive peaks' of Sewall Wright and explains how a population shows transformation of some members without intermediates. Simpson (1944, 1953) explained that members of a population enters completely different ecosystem through dispersal, barrier and other factors. These isolated areas are so much separated and so much different from the home of the parental population that each set requires different sorts of adaptations. The vastness of differences put pressure or adaptive threshold and is the prime driving force for the development of newer characters. Each such new zone may have more than one sub-zones. Simpson termed this as 'adaptive zone', which consists of a taxon together with its environmental characteristics.

Mayr mentioned that due to peculiar environment at periphery the members inhabiting such zones undergo peculiar specializations and evolutionary adjustments (= post adaptation) and gradually evolve into separate lineages. Many of their adaptations are beneficial to the neighbouring zone. These pre-adaptations help the new lineages to flourish in the new zone through better utilization. The new community may suffer huge loss since the new environment possesses unknown threats. Such a population of reducing size may undergo genetic drift and acquire new genotype to overcome the low frequency that might happened through natural selection. However extinction is not uncommon among these forwarding lineages during the episode. The new habitat was unoccupied by same species and there will be no intraspecific competition for the food such new phenomena lead to anagenesis followed by post adaptations and then extensive cladogenesis.

Examples of adaptive radiation and production of additional lineages are well studied in cases like Darwin's finches, Hawaiian honeycreepers, snails along coast of Southern California and others.

Amadon (1950) studied the generic evolution in Hawaiian honeycreepers. The islands provided isolation and subsequent occasional inter-island migration and thus initial allopatry and later sympatry many times for several species. In this family of birds (Drepanididae), the structure of bill and feeding mechanism were important factors determining their radiation; there were food preferences among the members or exploitation of available food types. Bock (1970) explained that initial geographic isolation and obligatory reproductive isolation were responsible for the differences with parental population. This was followed by character displacement which occurred after migration and becoming sympatric. The character displacement is the measurable phenotypic differences in relation to resource partitioning. In Galapagos finches the species coexisting same island show greater differences in size of bill than where these species occur on separate islands.

The Drepanididae has two subfamilies, the Drepanidinae and Psittirostrinae. Latter evolved from former and are far rich in species diversity. The most primitive genus of

Psittirostrinae is *Loxops*, which probably evolved from some early Drepanidinae and radiated into five species. The four of these remained congeneric while the fifth, with many distinctive features, became a new genus *Hemignathus*. The *Hemignathus* radiated into three species with which it forms a rather distinctive adaptive group. *H. lucidus* gave rise to a fourth species so distinct so as to form a separate monotypic genus, the *Pseudonestor xanthrophrys*. Latter radiated to give rise to six living species forming a compact group of their own under generic name *Psittirostra*.

Types of lineage production in short, therefore, are:

a. It is known that numerous aspects of biospace act on a population and force the production of lineages. It may so happen that the functional biospace may undergo division, generally two, or more sub-zones, each with some characteristic adaptive threshold. During anagenesis, a lineage may cross or overcome new adaptive challenges and enter different sub-zones or biospaces. The novel characters that develop in these advancing lineages are peculiar to this group and flow in its descendents.

b. A second pattern may not involve biospace partitioning. Here morphologically distinctive groups may arise due to inherited qualities present in the stem lineage. The stem lineages are quite different from their sister lineages.

c. Cluster of species may show morphological distinctiveness due to extinction of intermediate forms. Thus pattern of extinction may be used as yardstick to develop taxonomic classification.

d. The origin of a new family may be similar to that of the origin of genera. But the differences lie in the degree of variation achieved. This is possible when anagenesis goes on for for a longer period to establish those large differences.

e. Any new evolutionary pathway will follow a new adaptive mode and are sufficiently successful to produce offsprings, which are better adapted through selection. These, of course, create competition among sister lineages and result in extinction of some lineages. The successful ones may acquire fitness through preadaption whose required genetic endowments come from ancestral species.

3.2 Mechanism of speciation in panmictic and apomictic species

The definition of species given by several authors in different times show a change according to the new thoughts and critical examinations through experiments and analysis.

The basic criteria of a species are that it has its own gene pool shared by its members and adjusted to a given environment. The other attributes are the reproductive and ecological separation from any other species and it has own isolating mechanisms.

Earlier in history, Darwin considered a species, as permanent and distinctive variety and each species earlier existed as variety. The term variety was not well explained then and, although races and subspecies are taken as 'incipient species', not all of them will finally become a true species. Only few of these incipient species will show divergence in their genetic combination from parent population and will go on further speciation.

The ultimate production of a species therefore requires genetic differences. This may arise gradually through transformation of geography of distribution and this is also known as *allopatric speciation*. Some authors believe that geographic isolation is not a must for speciation.

The members of a population belonging to one geographical area may face territorial differences (sub-zones). The biotic and abiotic differences of these sub-zones produce initially minor variations. The result is the production of many incipient species within the parent population and selection pushes a few to the status of a new species.

A.R.Wallace (1889) believed that due to differential adaptability among hybrids, the natural selection would favour those that show better adaptations to the prevailing conditions. This separation of the weaker from better forms will create a sort of reproductive barrier. This is a selection for sexual isolation that results from strong adaptations to specific environment by most races and species. Dobzhansky and some other authors supported this view. However a cross between two similarly strongly adapted populations will produce a genotype which i) will be totally different from parent population; ii) obviously will not match the parental environment and hence bound to be disadvantageous. Such hybrids are naturally rejected through selection.

3.2.1 Some experiments and inferences

1. Wasserman and Koepfer showed that allopatric species show no mating barrier on *Drosophila arizonensis* and *D. majavensis*. The sympatric species mated rarely (14/377) while allopatric species mated more frequently (119/473). However the F_1 hybrids were all sterile in both cases.

2. John A. Moore found 29 separate allopatric populations of leopard frog extending from North America (Quebec) to Mexico. They are distinctive populations but produce normal offsprings by cross breeding among adjacent populations. The rate of production of viable offsprings decreases with increase in distance between the populations.

3. Sexual selection is strong in sympatric population. Phelan and Baker observed that there is more scent emitting glands in male of sympatric species inhabiting same host plant than species on different host plants (allopatric).

3.2.2 Different types of speciation in panmictic species

Panmictic or sexually reproducing organisms produce zygotes with diverse genotypic combinations obtained during meiosis and gamete production. If there is heterozygosity for n number of genes, a single parent will produce $2n$ genetically different zygotes. So two such parents heterozygous for n number of different genes will produce $4n$ genetically different zygotes. Hence Wright proposed that there is unimaginable potentiality in sexually reproducing organisms and what we observe is actually a very small fraction of the same.

In panmictic species, speciation may occur in three ways.

A. Allopatric or geographic speciation

This is the most widely accepted mode of speciation and is almost exclusive for animals. It is a gradual and slow process by which some form of barrier develops to separate a population.

Among many examples, the historical one is a Darwin's finch on Galapagos Islands, which probably originated from a single South American mainland stem species. The fourteen species today are totally distinct from each other. This would have not been possible if all the island masses were a single one. That is what happened to Cocos Island and a single species inhabits there still today without any speciation.

Some of the important factors in allopatric speciation are the type of species, time necessary for speciation, inability to cross a barrier and the size of the geographical area concerned. What is a barrier to a fresh water inhabitant or a terrestrial form may not be the same for some other forms of animals. This is depicted in the figure 12.

Similarly the population in mountain lakes is isolated and shows regional diversity. In this way a single population undergoes fragmentation. *Rana pipiens*, through this process, produced several species today.

Geographic or ecological isolation by some barrier separates the parent population. Now given enough time, the two populations will grow separately and in the long run, there will be much genetic divergence between them. If there is a partial merger in ecosystem (i.e. partial barrier breakdown), the two separate populations will quickly adapt and evolve mechanisms for reproductive isolation. When this isolation is complete, there will be no gene flow between them and a firm species is evolved in this way.

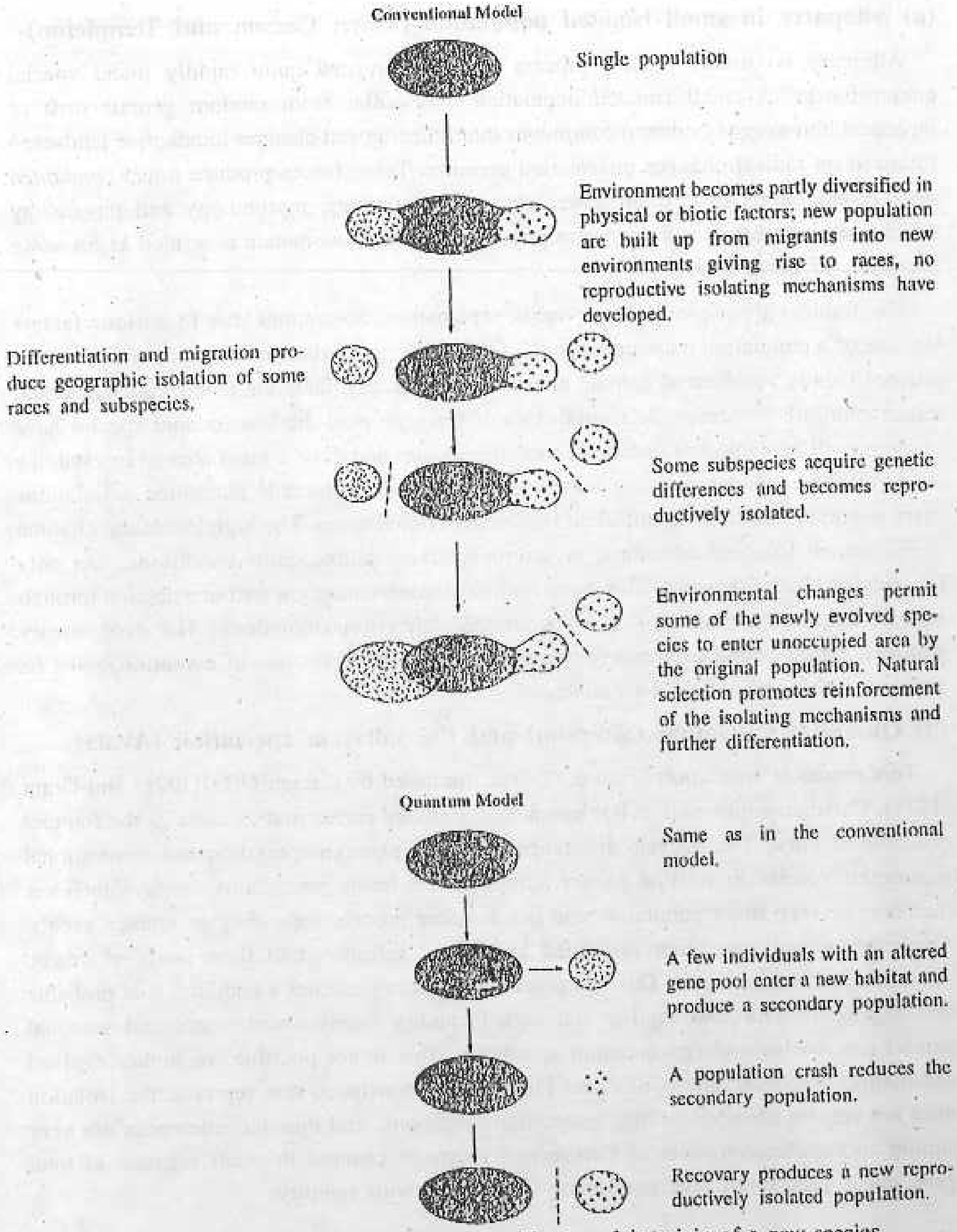


Figure 12. Conventional and quantum models to explain origin of a new species

(a) Allopatry in small isolated population (Mayr, Carson and Templeton)

Allopatry is usually a slow process but may proceed quite rapidly under special circumstances. A small isolated population may suffer from random genetic drift or increased homozygosity due to continuous interbreeding and changes in adaptive landscape followed by radical changes in selection pressure. These forces produce novel *coadapted gene combinations* to develop newer changes in ethology, morphology and physiology which are quite different from parent population. This phenomenon is termed as *founding accidents* or *bottlenecks*.

The founder principle of Mayr needs explanation. Sometimes due to various factors the size of a population may remain small for several generations even this may sometimes reduce. This is an effect of genetic drift and consequent effects on gene frequencies (and thus evolution). Whatever the combination of the gene pool the few founder species have in them, will be subjected to test by natural selection and have a good chance to establish As a result of founder event (= bottleneck effects). It is probable that some populations carry genotypes sufficiently different from parent populations. The high incidence of some genes, which have no advantage in heterozygous or homozygous conditions, can only be explained by bottlenecks. This event nullifies the advantages of earlier selection through loss of favourable mutations and encourages deleterious mutations. The evolutionary pathway, hence bound to change in new direction, which, by law of evolution, must be adaptive, otherwise would be extinct.

(b) Quantum speciation (Simpson) and the saltation speciation (Ayala)

This model of speciation (Figure 12) was discussed by Carson (1973,1975) and Grant (1971). Carson mentioned it as bottlenecks as discussed earlier and its same as the founder principle of Mayr. The relevant differences between quantum speciation and conventional geographic speciation are that former is rapid, takes fewer generations, starts with fewer members or very small population and is a budding process depending on chance events. The conventional speciation is guided by natural selection and there may be drastic reduction in the population. This is a process of splitting and not a budding. It is probable that organisms with low vagility and high fecundity (many invertebrates and seasonal plants) are able to undergo quantum speciation. This is not possible for higher evolved organisms. The observations of Ayala (1975a) also concluded that reproductive isolation does not require changes in large proportion of genome and thus the inferences are very similar to the closed system of Carson that indicated changes in small segment of total gene pool. This small part may easily reorganize with rapidity.

Carson explained that gene pool of each species has two systems- open and closed types. In open system, the genes undergo free recombination during meiosis and resultant offspring are subjected to natural selection. Therefore there are different gene frequencies and offspring face different environments to produce races or subspecies.

In closed system, the 'super genes' or blocks of gene loci of a species are transferred as a block to offspring. So any change (mutation) or substitution of a new allele will reduce the fitness of the offspring drastically. Carson, therefore, explained that in such a closed system, there is an accidental 'genetic revolution' by which population outbreak takes place followed by a crash. The survivors of this crash have sufficient genetic difference from parent population and slowly increase in number. Carson applied this concept in the speciation of *Drosophila* on Hawaiian Islands. The few founder species (5 in number) from the oldest island (age about 5.6 million years) moved to Oahu Island, which at present has 29 species. There was an interchange of species between Oahu and Maui. The Maui complex became significantly rich in species diversity, which contributed to speciation in Hawaii Island (with present 26 species). Inter-island migration of very few species was also observed and such species have developed formidable reproductive isolation among parental population. The tectonic plate moved the islands formed at hot spot (Hawaii) in a northwest direction until they fragmented and submerged.

In opposition to the concept of bottlenecks, Barton and Charlesworth suggested that speciation caused by single founder event couldn't produce immediately significant change in an isolated population. This is because gene frequency will be altered by genetic drift through many generations. Moreover, the effect of isolation, environmental differences and continuous changes in genotype- are all associated with impact of population bottlenecks. Bryant *et al.* observed increase, instead of any decrease, in phenotypic variation.

Rice and Hostert claim that during genetic differences between populations divergent selection takes place. When such populations undergo dispersal, reproductive barrier develops as a secondary attribute.

(c) Species-specific mutation concept (Goldschmidt for animals and Lamprecht and others for plants).

This concept has not gained support because there was no experimental explanation. The semi-fertile interspecific hybrids of *Drosophila pseudoobscure* and *persimilis* (Dobzhansky (1941) and *Phaseolus mutiflorus* and *vulgaris* (Walls and York, 1957) are reproductively isolated due to presence of genetic differences in several gene loci and no 'species specific mutation' was recognized.

It appears that speciation may occur in different ways, some with rapidity while some at a slower rate. Results of barrier breakdown are the production of viable and fertile hybrids which are particularly common in plants than in animals. This is termed as *zone of hybridization* or *hybrid swarms* and the population has a genotype and phenotype different form the parental population.

When such hybrids are intermediate to a different species, they help to adapt the forthcoming species to its ecological range. Such phenomenon is called *introgressive hybridization* (Anderson)

Hybrid sterility acts as a common barrier in animals but not in plants. In plants polyploidy in a normally vegetative propagated plant ensures production of fertile gametes. Studies shown that half of all angiosperms and most of pterydophytes are polyploid of one or another type and allopolyploid are most common event.

B. Parapatric (Bush, 1975) or stasispatric (White, 1973) speciation

In parapatric model of speciation, there is no geographic barrier and the members belong to a continuous population. It is a rapid process like quantum speciation involving fewer members. But, unlike quantum speciation, the reproductive isolation takes place entirely by natural selection.

Murray (1972) provided evidence in support of this model in the origin of land snails *Partula* on Moorea Island near Tahiti. The total eleven species of *Partula* fall into two functional groups; species of one group while behave as distinct species in one locality, they, however, interbreed freely at other locality only 200 meter away. No geographical difference is observed in these two localities.

White (1968, 1978) observed differences in chromosome configuration in morabine (sedentary wingless) grasshoppers of Australia and suggested this shift in chromosomal arrangement initiated the task of reproductive isolation. The process spread to form a narrow zone of hybrid. But a genetic drift in a small population becomes necessary to increase the lowered fertility gained through chromosomal mutation.

Both of the above evidences lack proper genetic data and it is not clear how these evidences differ from quantum speciation. Thus parapatric speciation is an obsolete concept.

C. Sympatric speciation (Mayr)

Mayr proposed that a population undergoes dispersal and acquire reproductive isolation. Various authors supported this concept for many years. The term *disruptive selection* or *centrifugal selection* was applied to this concept. In a disruptive selection there are members with phenotypic differences at two extremes of expression while intermediate forms are abolished and both belonged to same population. It happens when members of a population are subjected to divergent or oscillating changes of environment and the various genotypes of its members are most suited to such changing situations. Such events may establish genetic differences in a population. Bush accepted that this type of selection might be possible for few specific kinds of organisms (parasites). A female parasite upon entering a new host may undergo sequential events to speciate to acquire new adaptations to establish in the host. There is, therefore, every chance to decline in population as well as the female is producing acquired genetic variations to offspring. Migration followed by natural selection and final equilibrium between the environments of host and the parasite are essential phenomena for the parasite. These and some other unexplained areas put questions on distinction between quantum and sympatric speciation in parasites.

Bush and others proposed that within single geographical habitat different groups of insects undergo speciation by adapting to different kinds of host plants as food source.

According to Mather and Thoday disruptive selection and increase in genetic variability leads to polymorphism and this has been shown in *Biston betularia* and polymorphism and mimicry in *Papilio dardanus*. But Mayr (1963) questioned whether it is possible to maintain divergent condition in a single locality for a long period necessary for speciation.

In plants, sympatric speciation is commonly achieved by polyploidy within a single geographic locality. Close interbreeding is unusual among animals (with few exception as parasitic hymenoptera). In this insect brother and sister emerging from same host mate and Askew (1968) suggested this type of mating is responsible for high species diversity in this group. However reproductive isolation between closely related species cannot be achieved by genetic difference at a single locus, rather several loci need to be changed. Therefore there must be strengthening of barrier between gene flow and the process is stepwise, not rapid.

3.2.3 Speciation in apomictic species

Most of the apomictic plants originated initially and hybrids and thereafter became stabilized. These, by definition of species, are difficult to classify and are not recognized by taxonomists. These plants fall into two categories. In the first category the descendents of the sexually reproducing plants secondarily lost their sexuality including formation of gametes or zygotes. In course of time their polyploid nature is stabilized and no further increase or decrease in chromosomal number takes place excepting rare mutations to produce variants. New apomictic plants are further produced from sexual species. Those of the second category (e.g. *Rubens, Poa* etc.) also cannot produce variants. These are facultative apomictic producing seeds both asexually and sexually. They cannot show new adaptive characters but exist indefinitely. This conclusion is drawn from their distribution and being very common in nature.

Apomixis or parthenogenesis in higher plants is an adaptation to avoid hybrid sterility. Such plants form a complex of many sexual forms, which are quite different from each other, and species recognition among them is unwanted.

In animals, thelytoky (production of eggs without fertilization) is not uncommon in some animals belonging to different phyla. Crustacea (*Artemia*), Coleoptera (weevil), Lepidoptera (moths) even in fish (Schultz 1969, Uzzell 1970), lizard (Darevsky 1966). Complete sexuality or obligate apomixis is characteristic in these forms. But facultative apomixes is not known in animals. There is a tendency for any species to reach an *evolutionary dead end* and probably the number is one out of every 1000 species group. And apomixis in animals appears to be recent in origin.

Lower organisms like bacteria, blue-green algae and others continue genetic recombination by non-sexual methods, such as transduction (transfer of one or some genes by infective non-lethal virus from one bacterium to another. Transduction is easier in closely related strains. However transduction in distantly related strains is not uncommon. Hence it seems that evolution in the prokaryotes took place through diversifying selection and less stress on reproductive isolation. Similar is the situation in fungi imperfecti, many ciliates and sarcodines. Thus the difference between transduction and sexual reproduction is that in former, there is no participation of two full sets of genome obtained from different parents. The new generation of bacteria, after transduction, will not express expected characters of both parents, excepting those few contained in genes came into them. Such events may occur between wide taxonomically distant prokaryotes so that resultant form cannot be placed into any perfect category. That is why Mandel (1969) defined it, as "a bacterial species is a type culture and those cultures resembling it". This definition is far easier and perhaps better.

The evolution of apomictic species of plants is well illustrated by Babcock and Stebbins (1938) in figure 13.

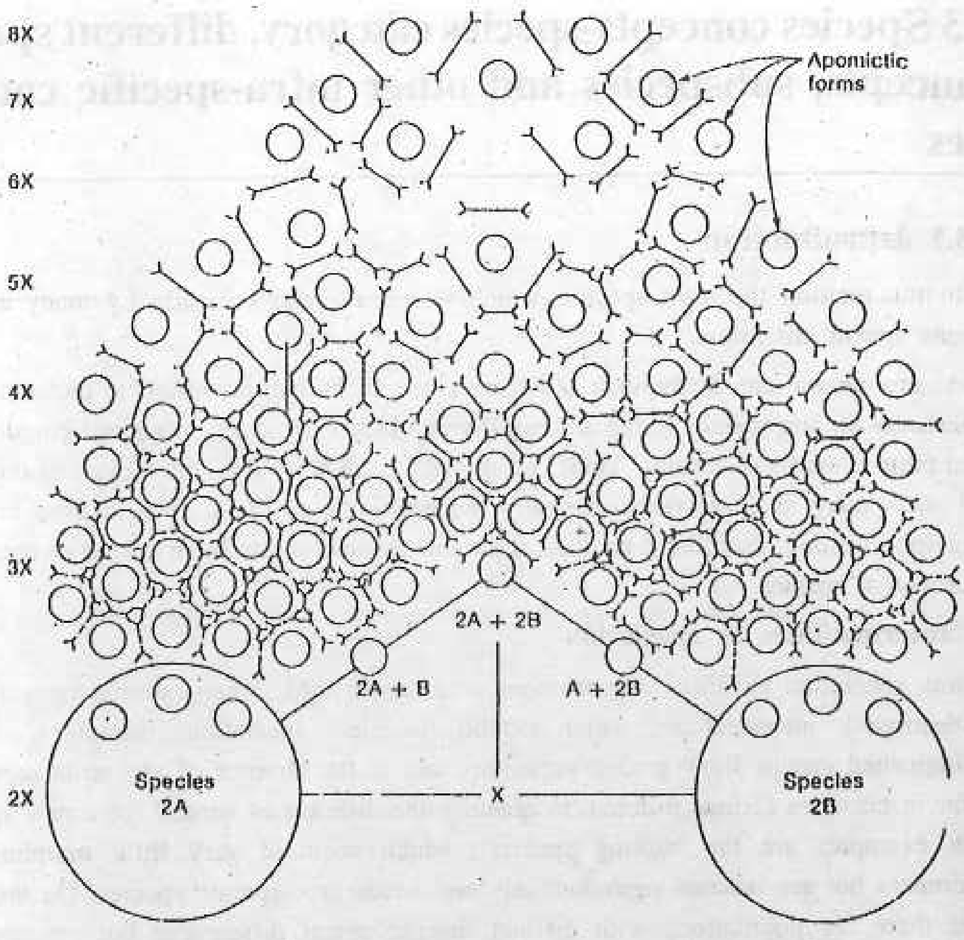


Figure 13. Chromosomal arrangements in an apomictic complex

Explanation to figure 13 :

There are three sets of offspring obtained from two different sexually reproducing organisms. Since these all are sexually infertile, no genetic exchange is possible, which is shown by heavy border I——I. Facultative sexuality may occur among some individuals there the barriers are broken (I——I) thereby producing offspring with higher chromosome number (products of gametes with unreduced chromosome number). In this way higher levels of polyploidy is produced and these agamic complexes have vast array of recombination of characters, but they cannot produce distinctively new characters.

3.3 Species concepts-species category, different species concepts, subspecies and other infra-specific categories

3.3.1 Introduction

In this section the term species, which was dealt with critically by many authors, needs special attention.

As any animal can distinguish self from non-self, human also tried to understand the differences among various living and non-living objects. However in animal kingdom any local fauna consists of several "kinds" of animals. Each such kind, upon close examination will show many features which are very much specific to them, such as their breeding behaviour, nesting, food habit ecological parameters and so on. Such a kind of organisms is termed a species.

(a) Intermediates in speciation

Any speciation produces a continuous or discontinuous (when intermediates are lost or destroyed) intermediates, which exhibit 'incipient speciation'. Members of such distinguished groups show graded variations, and in the absence of any strict regulation so far, it becomes serious problem to quantify the differences needed for a new species. Such examples are the 'sibling species', which acquired very little morphological differences but are isolated reproductively and hence are separate species. On the other hand there are populations with distinct morphological differences but are normally interbreeding. These are considered as same species.

(b) Hybrid breakdown

Occasional hybrids are produced by temporary or permanent loss of barriers thus bringing two once separated close species together. The resultant population is usually sterile with low adaptive fitness. Therefore they do not survive and do not create problem to taxonomists. If the barrier is completely lost in a local population, an extensive hybrid swarm is produced and introgression may occur. These are not formally recognized as species.

Taxonomists have assigned species status to many hybrids unknowingly and those were later rejected after thorough observation in nature (populations) when their hybrid nature became established.

Exceptionally two parental species fuse completely and give rise to a single new species. Such event is yet to be established and this will create problem in fixing their species status.

(c) Allospecies and semispecies

Earlier many taxonomists used the term semispecis to designate intermediates below species and subspecies. This may be due to less survey or the intermediates being lost from nature. Occasionally, due to presence of lots of differences from nearest species, groups of likely species is kept as allospecies. The taxonomists feel that they have attained species level differences but for further studies (collection and observation in nature) they keep them as member of superspecies.

(d) Sympatric and allopatric populations

Biological species concept cannot be tested for their gene flow in allopatric species. When two sympatric populations are brought closer artificially, there is normal fertilization and produces a progeny of reduced fitness.

Since the subject taxonomy is quite old, naturalists coined various terms and they were often misleading for their inherent meaning. Moreover some terms were used in different sense by few later authors. All these together made the explanation of the term species and many others quite perplexing. The meaning and definitions also need to be re-explained in the light of advancing science. To day many terms are well clear and the unusual fear in the study of taxonomy is gone. Rather it is now a most interesting subject in the days of molecular biology.

In the grammar of taxonomy, however, the terms, which are posing some problem with 'species', are phenon, taxon and category.

Taxon : Simpson defined taxon as 'a group of real organisms recognized as a formal unit at any level of hierarchic classification'. Mayr defined it as 'a taxonomic group of any rank that is sufficiently distinct to be worthy of being assigned to a definite category'. Some examples can make things understand better. If we say red crab, crow, sparrow, bony fish, reptile, king cobra etc. they will definitely mean some groups of concrete objects and any such group of population is called a taxon. This taxon (or the population) should have sufficient distinctness so that it can be ranked (categorized) in a hierarchy. A taxonomist will judge the worthy of placing such a taxon with other taxa of a category or to a different category. Thus the taxon name is a common word (not a scientific or taxonomic name). The words 'fish' and 'Pisces' both refer to a group of vertebrates; however the latter is the rank (category) in a hierarchy classification while the former is not. The former is a common English word (hence non- scientific). Similarly species, class, order are not taxon but category. Again *Bufo melanostictus* is a species and not a taxon while the name toad is a taxon of species rank. Thus the lowest taxon is a species. There are higher taxa such as birds or amphibians.

Phenon : The term was used by Camp and Gilly (1943) and assigned to 'a sample of phenotypically homogeneous organisms at species level'. In taxonomy, phenotypically reasonably uniform samples help in making more correct statement about a group of organisms (frequently a species). Although there is no generally accepted term to such 'uniformly phenotypically similar group' the term phenon is more appropriate to assign for this. The term 'morphospecies' should not be confused with phenon; former is a typological species recognized merely on the basis of morphological differences while phenon is a sample of phenotypically similar specimens. In the phenetic classification of Sokal and Sneath (1963), however, the term has a different meaning. The word phenon means individual variants and any species has many variants or phena. Phenon of one species may well resemble other species.

3.3.2 The Species Category

A *taxonomic category* is a level or rank in a hierarchic classification. A category contains members and all those taxa belonging to and assigned a given rank. In simpler way, a category consists of many taxa and these taxa have same level in a hierarchic classification. Thus genus, family, order etc. are categories and each of these contains one or more subordinate taxa (as a family contains one or more genera, a genus with one or more species). But a *species category* contains those members who belong to those species taxa.

, Over the past century, there were debates and controversies in the understanding of the term species. In fact, the species definition depends upon the requirements; it may be defined on the basis of attributes of the organisms constituting a species. The other way to define a species may be based on the process that gives rise to a species. Both definitions have merits and demerits. There are definitions, which have the attributes as well as the process of the origin of the species. However taxonomists prefer a definition based on attributes.

The lots of species definitions in the past are based or are outcome of several concepts-the species concept. Among the five species concepts, first two are considered more historical; still have some important facts in the understanding a species. The rest three are have much of the merits.

A. Typological species concept

According to the great philosopher Plato there are some 'universals' or 'types' on the earth the members of which are actually inhabiting on this planet and the diversity of nature which one finds is actually due to 'variations' of those few universals. This concept was continually accepted beyond post-Linnaean period. The approach to the meaning of species by this concept is based on the assumption that a species is constant in time, has a limit of possible variation and thus separated from other species by distinctiveness and finally members of a species share same attributes.

Thus the concept has some basic positive values but could not be accepted for the following facts:

a. Conspecific individuals may be morphologically distinctly different.

b. Sibling species are alike but belong to different species status.

c. Age differences, sexual dimorphism, polymorphism are some phenomena by which same species develop striking differences.

A taxonomist preliminarily may separate individuals into some species taxa merely based on outward appearance. These separated 'species' need to be verified through biological and other necessary studies.

B. Nominalistic species concept

Occam, the proponent of this concept and his followers (Buffon, Bessey, Robinet and Lamarck) believed that there is no need to express or designate anything as 'species'. They did not consider the presence of any 'real' universals, rather only organisms are present on the earth because they are the product of nature. Therefore such mental concept (ie. species) of man has no value. Bessey (1908), however, modified the concept and explained that 'species' has been invented so that species collectively refer to great number of individuals.

Such a concept was popular in France in 18th century and still today there are few adherents to this concept. Presently this is a historical one without any practical value. Because anyone knows man cannot create a species and only nature can create it. Species is different from any inanimate object created by man.

Nominalists, like any native, can group individuals on the basis of similarities. Thus they deny or did not acknowledge the evolutionary mechanisms (speciation, adaptation and others).

The similarities among members of a species population are due to common heritage and they are dissimilar from such members of another species population because of different ancestry. This hidden truth was absolutely ignored by nominalists.

C. Biological species concept

This entirely new concept of species emerges in 1750 due to continuous pressure from naturalists. The incompleteness of the earlier concepts lies in the proper understanding of true nature of a species. This concept is based on a philosophy that is different from that in inanimate world.

According to this concept, the widely used species definition of Mayr is as follows. "A species is a group of interbreeding natural population that is reproductively isolated from other such groups". Mayr explained that a species has three following properties.

(a) Reproductive community-which means that the members seek potential mates from among the members of this community and many factors or devices play important role fro successful intraspecific mating.

(b) Ecological unit-the members differ from each other for many features but all members together form a unit, which interacts with other such units in any ecosystem.

(c) Genetic unit-the members freely interbreed and whatever the diversity the individuals possess, these all variations together form a gene pool and all variants are part of this pool. Thus species has its own gene pool that is actually shared by its members.

This species definition is based upon biological parameters and that is why it is called biological species concept. There cannot be any comparison of a species with anything inanimate.

Gradually it became clear that species has independent reality and separated from other by its own population parameters. The essence of typological concept is that species has independent reality and of the nominalistic concept is that species are product of nature by the fact that members of a species population are different from other such by the presence of its own sets of attributes. However the biological species concept differs from previous two by the presence of genetic unity (because all species share a common gene pool) and its reality lies in the genetic combination that is an outcome of evolution and has been tested by natural selection.

This concept explains discreteness of the local species at a given time. The differences, according to Linnaeus (and typological concept), are due to differences in their 'types' (=species status) and in this way the evolutionary process has been ignored by typological concept. According to biological species concept a species is always plastic; it has the potentiality to undergo modifications required by the evolution.

The biological species concept is important to understand the functioning of a species as a genetic, ecological and ethological unit. These studies, when compared with other related species would clearly give an idea about how a species actually works in nature.

The above species definition, although widely accepted by evolutionists, is not free from criticisms. Its shortcomings were attacked by systematists (Sokal and Crovello, 1970; Cracraft, 1983; Donoghue, 1985). However a single definition for a dynamic object 'species' can hardly be achieved. The conflict between evolutionist and systematist lie in the fact that species should be considered as evolutionary unit (evolutionist) or as reproductive unit (systematist). Although the currently accepted basic unit of taxonomic differences is a population, many taxonomists are forced to rely differences among individuals or subspecies or local species. In nature we cannot judge reproductive isolation in allopatric population, which is a major bombshell to population concept..

Difficulties in the use of biological species concept

Apomictic population

Biological species concept is difficult to apply to apomictic or asexual groups that show uniparental reproduction by hermaphroditism, apomixis, parthenogenesis, budding and gynogenesis. Most of such apomictic groups show facultative sexuality depending on endogenous or exogenous factors thereby making things more complicated. A thorough knowledge of all sexual and asexual forms can only unfold the true nature of the organism.

Uniparental reproduction is observed in lower invertebrates (including insects) and lower vertebrates (even in reptiles). Such lineages are termed *agamospecies*, *binoms* (Grant, 1957) or *paraspecies* (Mayr, 1987). In the definition of population, it will not be much contradictory to include all asexuals with sexuals. But for taxonomists it is difficult to assign a status to a strain, stocks, pure lines, biotypes of an organism. Mayr (1963) clearly stated that these are not any sub-division of biological species. According to Ghiselin (1987) as well as Mayr (1988) the application of the word 'species' is not justified to such uniparental population.

The above situations are solved separately depending on the reproductive behaviour of apomictic organisms as follows.

(a) Permanently uniparental population :

Numerous studies on similar asexual groups of individuals revealed that some have attained so much perfection towards this line of evolution that they became permanently asexual groups. Once originated from sexual ancestors, they have deviated so much in time that their genetic combinations are different among different asexual populations and by no means they can perform genetic exchanges. Thus they are reproductively isolated. They are also morphologically well differentiated with a distinct gap from the near relatives. This discontinuity has been favoured by natural selection. Such well-separated uniparental populations are regarded as separate species (= *microspecies* of Mayr) than conventional use of the term '*race*'.

(b) Thelytoky :

This is a form of parthenogenesis in which males are non-functional or do not exist at all. White (1978) observed that in a population of similar organisms, there are two distinct sub-populations depending on the behaviour of chromosomes during meiosis; one shows tendency towards homozygosity and the other towards heterozygosity. Nature selects heterozygosity over homozygosity and the latter is rarely seen in fewer groups. There is even coexistence of thelytoky alongside bisexuality. White mentioned that, as a measure of survival, the interspecific hybrids took the route of parthenogenesis (thelytoky) and they are producing heterozygosity. This event seems to be recent in origin *e.g. Cnemidophorus*, a lizard of South-Western United States and Mexico). Thelytoky in some salamanders, fishes and in one grasshopper evolved to get rid of difficulties arose by hybridization.

(c) Mixed population of both sexuals and asexuals

Aphids, *Daphnia*, rotifers and digenic trematoda are known to produce in both procedures. Species status is not given to temporary clones produced asexually. Sometimes in aphids asexuals are known to be permanent and never regain sexuality and they are morphologically and ecologically quite different from sexuals. Whether they have sufficient genotypic variation for a separate species status is debatable.

Biological species concept is similarly not applicable to Protista or Prokaryotes where genetic exchange does not occur. However there are evidences of conjugation among bacteria and this led to the concept of '*genospecies*' (a group of bacteria able to exchange genetic material).

(d) Allotetraploids

These are obtained by chromosomal doubling of the sterile hybrids and become fertile and produce cross- fertilizing allotetraploid progeny. The new progeny has sufficiently distinct characters and are given species status although the route of their origin may be known.

D. Evolutionary species concept

This concept was proposed by Simpson (1961) and has undergone many modifications. The concept is as follows: "An evolutionary species is a lineage (an ancestral -descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies". This definition is concerned more with phyletic lineage. Simpson attempted to solve the species definition by adding to it the time dimension, which was deficient in biological species concept. Wiley (1981) provided a revised definition as follows " a species is a single lineage of ancestral descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate".

Here 'maintains its identity' refers to reproductive isolation. This definition is that of species taxon, not of the species category (Mayr and Ashlock, 1991).

Wiley explained that an evolutionary species is a branch or part of branch in an evolutionary tree and due to its own 'evolutionary tendencies' the branch may produce smaller branches and all (the branch and its smaller branches) will show historical fate. Here the relationships of the descendant populations of that single branch are not clearly understood. While Simpson separated every lineage on the basis of reproductive isolation, Wiley believes that 'no presumed separate, single evolutionary lineage may be subdivided into a series of, ancestral-descendant species'. Therefore the disadvantage of Wiley's explanation is that one cannot predict or know the fate of an extant lineage. Many such lineages have produced descendants in evolution. If we strict to only one lineage (for the sake of definition) we cannot proceed from one species to a future descendant species.

According to this concept the evolutionary role of cryptic species is not possible to estimate because of the similarity in their evolution. Another problem is that the natural hybridization of agamospecies (for example plants) produces lineages for their survival, which are quite different than those normally produced in biparental species. These progeny survive in nature successfully. Thus evolutionary concept has not explained their evolution.

E. Phylogenetic species concept

To avoid the strictness of breeding potentiality of biological species concept, Cracraft (1983) proposed this concept and put stress on genetic and behavioural criteria of organisms. Subsequent authors also modified the present concept later and the widely discussed version is: 'a species is the smallest possible group of sexually reproducing organisms that possesses at least one diagnostic character, which is present in all group members but is absent from all close relatives.

Biological species concept depends on biological characteristics but this concept is more based on diagnostic characters acquired through evolution (Donoghue, 1985; Baum, 1992). Such a group of species population must be sexually reproducing; it has acquired fixed genetic diagnostic features through evolution which are absent in all close relatives.

The basic drawback of this concept is that any species may be paraphyletic considering the plesiomorphic characters. This was avoided in modified definition by adding requirements for monophyly (Mishler, 1985; De Queiroz and Donoghue, 1988, 1990). Another deficit is that distinct populations of many species would be raised to species rank by considering 'smallest possible group' (Mayr, 1992). Wheeler, 1990 pointed that in that case the estimate of the number of species on the earth would be far greater than it is by the more traditional biological species concept.

F. Species recognition concept

Paterson (1985) and Lambert *et al.* (1987) proposed this concept to overcome some demerits of biological species concept and also claimed its superiority. The definition is: "a species is a population of biparental organisms, the members of which share a common fertilization system". Here fertilization system includes all biological parameters of the organism, which act together and ultimately enable fertilization to increase in number. The organism actively (by courtship etc.) or passively (gamete movement, either positive or negative gamete recognition) recognizes its partner.

Post-fertilization barriers are not considered in this concept and this may produce unsuccessful progeny. Butlin (1987), Coyne, Orr, Futuyma (1988) and Mayr (1988b) suggested that this concept has more problems and is based on misinterpretation of biological species concept. This concept gained no popularity and is invalid.

Discussion

Mayr (1957) has pointed out that morphological distinction is secondary attribute of a species and the primary and most vital aspect is the biological distinctiveness. The former may be changed or acquired secondarily.

Christoffersen (1995) proposed his *'ontological (theoretical) species concept* in which interbreeding nature of a species has been stressed. The definition of species given is 'a species is a single lineage of ancestral-descendant sexual populations genetically integrated by historically contingent events of interbreeding'. This concept is almost similar to the revised evolutionary species concept of Wiley (1981).

The *'operational (epistomological) concept of species* proposed by Christoffersen is actually a modification of the concept of Cracraft (1983, 1987), Davis and Nixon (1992) and Wheeler and Nixon (1990). According to this concept the species is 'an irreducible cluster of sexual organisms within which there is a parental pattern of ancestry and descent and that has diagnosable distinctiveness from other such clusters by a unique combination of fixed characters.

Thus the former concept of Christoffersen is transformational (dynamic) where a species is formed at a node of a phylogenetic tree and the latter concept is static, where a species is the smallest recognizable population produced as an outcome of former process.

The definition given by Florkin (1964) is that 'a species is a group of organisms with more or less similar combinations of sequences of purine and pyrimidine bases in their macromolecules of DNA and with a system of operators and repressors leading to the biosynthesis of similar amino acid sequences'.

Emerson (1941) suggested that a species is 'which has evolved or evolving, reproductively isolated and genetically distinct groups of natural population'.

Most of the concepts discussed above overlap each other and one can find one is suitable for a group of organisms while another for another group. So no one concept can fulfil all the requirements demanded by a species definition. Hence Mishler and Donoghue (1982) suggested that since no single concept can cover all the taxa, systematists have to adopt on all concepts together and there should not be any biasness for any specific concept.

After the development of numerical systematics and cladistics in 1960s, lots of exercises were done to arrive to the definition of a species (Butlin, 1987; Christoffersen (1995); Coyne, Orr, Futuyma, 1988; Cracraft, 1983, 1987; Davis and Nixon (1992); De Queiroz and Donoghue, 1988, 1990; Emerson, 1941; Mayr, 1988b; Lambert et al., 1987; Mishler, 1985; Nixon, 1992; Paterson, 1985; Wheeler and Nixon, 1990; and Wiley, 1981).

The essence of the different species concepts may be summarized as follow.

1. Species is a group of interbreeding population.

2. Species has its own gene pool highly protected from other pools by various isolating mechanisms. When the mechanism fails and hybrids are produced, they take a path of evolution different from parent.

3. A species must be sufficiently distinct from its nearest relative by the presence of distinctiveness from other such clusters by a unique combination of fixed characters.

4. Species has its own role in evolution mate finding, migration, adaptation and other forces of the nature produce subpopulations with different gene frequencies. These will show distinctiveness and separation sufficient to attain a new species status.

5. Caution should be taken for those populations, which have intermediate or transitional habitat or environment where different organisms show different degrees of interbreeding potentialities.

6. Agamospecies, unisexual or hermaphrodite species mostly develop mechanisms enabling cross-fertilization to revive own gene pool that has undergone wear by homozygosity. However presently we find many asexual species that flourished in present environment. It is difficult to say whether these represent intermediate stages in evolution of these species or they are more permanent towards a new trend in evolution is uncertain. It is more probable a route to extinction than any further evolution but are favoured by

natural selection in relation to present day environment. Any sudden change in the environment will alter their gene frequency when they may take active role in speciation.

7. Since the various experimental results depend upon true identification of the species worked upon, any experienced taxonomists should remember the definition of a species. Often it is said that 'a species is that which a competent taxonomist says a species'. This simple phrase hides many factors to determine a species.

3.3.3 Infra-species category

In taxonomy, there is strict use of infraspecific category. Only subspecies category is used with certain cautions. But still many scientists use following infraspecific terms, which are not taxonomically recognized.

Subspecies

Linnaeus coined the term 'subspecies' to describe any deviation from the type of the species. Early taxonomist indiscriminately used to designate variety to any variation because there were no clear-cut rule to decide how far differences may be taken for a variety. Thus many earlier 'variety' were mere expressions of a species population. This term is obsolete today.

In nineteenth century the term subspecies replaced variety. Ornithologist Schlegel (1844) coined the new term 'variety'. Subspecies is actually a category below species and is different from latter. Kant (1775) advised to separate species from subspecies or variety.

Introduction of subspecies and its recognition by International Rules of Zoological Nomenclature provided the trinomial nomenclature. In fact Darwin's "Origin of Species" (1859) provided examples of variations. It was an impetus to later taxonomists to use the term. But too many names of a same species became not only an unwanted heap in zoological nomenclature but also confusing to taxonomists. Hence Inger (1961), Wilson and Brown (1953) proposed the withdrawal of subspecies category. Subspecies is a "pseudotaxa" which cannot be classified (Blackwelder, 1967).

Mayr defined subspecies as "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species differing taxonomically from the other population of the species". A trinomen is used to designate a subspecies.

The various populations over different geographical areas face differences in ecosystem. Genetic differences accumulate due to continued exposure to those different environmental features over a long period. In spite of overall similarities, these subpopulations become different from one another both in genotype and phenotype. Their differences in biochemical, morphological or genetic parameters are tested for statistical differences and thus must reach a taxonomic level sufficient to designate them as subspecies. It may not be true that each geographical sub-population be a subspecies. Again individuals at the zone of intermingle of two geographical areas show intermediate features of two subspecies. Species or subspecies do not overlap rather their extensions of occurrence meet at a place. In this way subspecies is a collective category.

With the introduction of polytypic concept (Beckner, 1959), it is widely accepted that genotypic variation within allopatric species exists. This concept, in turn, gave rise to population taxonomy which reduced the excess burden of naming many 'different' species. This also simplified animal classification. Not all species are polytypic and there are many monotypic ones. This concept clearly gave the solution to the fact that many previously recognized morphospecies were not reproductively isolated and hence not separate species; they are now treated as subspecies (not as a taxonomic category).

The recognition of subspecies is difficult and only experience and sufficient data can solve the status. Generally speaking it is an interbreeding group with various forms of differences (*e.g.* morphological, geographical, ecological, physiological and such others) which give it species like distinctness (Grant, 1960). The amount of differences is always debatable and the matter is left with experienced taxonomists who actually deal with a lot of materials from various localities.

Rothanaler (1954) advised that two subspecies must be separated completely over a long period. The barrier must influence to create differences among the separated populations according to the need of modified environment.

The other feature of a subspecies is that it is an isolated gene pool and may behave as incipient species. The subspecies category provides possible phylogenetic trend of a polytypic species (Grant, 1960).

Benefits of the use of subspecies category are strongly felt by Goldschmidt (1940), Simpson (1961), and Mayr (1969). They suggest its rank different and below a species category. While subspecies are very similar and not reproductively isolated, the species are different from each other through isolation mechanism.

Starting with a species we can trace the origin of subspecies that evolved through breakup of the original population by barriers and dispersal. These isolated populations, through ages, attain sufficient genetic and morphological differences to become finally reproductively isolated. Thus a new species can be formed very near to the original species.

Various authors used the term subspecies to specify their species features and those, according to Edwards (1955) are as follows.

(a) *Geographical subspecies* is formed by separation of members of a species population during reproduction or migration into different geographical areas where they adjust to new environment and gradually acquire differences except for reproductive isolation.

(b) *Temporal subspecies* are those different fossils of different ages. These, however, may be contemporary and geographically separated and hence may belong to same species. Sometimes geographical races replace each other owing to climatic changes and are discovered in succeeding strata. Fossils help to understand relationship and also the evolutionary trend. However subspecies is always a classificatory device.

Populations of a species active in different era in past geological periods may have been totally separated and thus were not synchronic. Their reproductive isolation may be assumed complete. Their differences in genetic combination are directly proportional to the time elapsed, except the periods of mass extinction when there was rapid speciation. Their genetic distances can be calculated by modern technique (DNA fingerprinting) and there should be significant taxonomic differences to call one a subspecies.

Mayr (1969) advised that geographical and temporal subspecies should not be used as separate terminology. It is not possible to determine whether these separate subspecies are precisely contemporary or not. Even if any sequence of subspecies is found from same locality they may not be purely temporal

If an infra-specific population becomes isolated temporarily during mating but nevertheless crossbreed freely under sympatric condition with the members of any subpopulation, then these are often regarded as temporal subspecies. This type of definition may create confusion with fossil subspecies (temporal subspecies of Mayr, 1969).

(c) *Seasonal subspecies* are the members of two distinct sympatric populations of a given species that show sexual maturity at different periods of a year. Thus the two populations are kept isolated and no genetic interchange takes place. Therefore, if they never meet together and there is no genetic exchange, they should not be considered as subspecies but as true species. Often this has been known as *Annual subspecies.*

(d) *Ecological subspecies* are micro-geographically isolated but are freely and naturally interbreeding under sympatric condition; these occur in different biotopes or populations of biotopes. These are indicated on topographic map or faunal maps which show their micro-geographic habitats.

(e) *Polytopic subspecies* is a geographically heterogeneous subspecies. Several unrelated and more or les widely separated populations may show convergent adaptation of very similar phenotype although they vary widely in their genotypes. Such different subspecies are combined into one subspecies taxon called polytopic subspecies. Due to disadvantage (since they belong to different species category) polytopic subspecies concept is usually not used in taxonomy except to refer to heterogeneity in a collection of subspecies quite superficially.

Difficulties in the application of subspecies category

The use of subspecies category helps a lot to understand the polytypic species. However, this has been used differently by different authors without restricting to its definition or by misunderstanding or has misused this category. Hence Wilson and Brown (1953) pointed the following disadvantages:

(a) There is no uniform opinion to determine the degree of differences or amount of distinctiveness.

(b) Even within an established subspecies there may be several microgeographic variations.

(c) Phenotypically inseparable allopatric populations may develop independent to each other and such populations cannot be recognized as subspecies although they should be by definition.

(d) Many characters show their own independent trends of geographic variation.

In spite of usefulness to taxonomists, the three criteria remained unsolved and there are the nature of distinctiveness, interbreeding nature (in allopatric population) and weightage of characters used to differentiate. If the populations are separated naturally there may not be genetic exchange under normal condition and their potentiality to reproduce normally cannot be tested. It may be true that they breed normally if brought closer. Time is an important factor and separated subpopulations, in future, may exhibit reproductive isolation. It should be remembered that members of all subspecies populations belong to same species and they are convenient device for intraspecific classification. Variation in population is a natural phenomenon and the degree of such differences is used to recognize subspecies. Only this much is the utility of subspecies. The different subspecies are similar for most of the characters and they differ in fewer characters (genotypically and phenotypically). These characters are mostly adaptive in nature and probably have no role in evolution.

3.3.4 Other infraspecific categories in relation to subpopulations of a species

Variety

As discussed earlier, this term was commonly used in Linnaean period. Any such designation (variety) after 1960 is not recognized by zoological commission. There were no distinct criteria to differentiate a subpopulation as variety.

Race

It has been used in different sense among scientists. Taxonomists working on insects, birds and mammals used geographical race and subspecies synonymously. In general, race is a local population within subspecies.

Subpopulations of a species inhabiting different ecosystems are called ecological race and thus every subspecies becomes an ecological race, since the different localities differ in ecological parameters. But often no significant taxonomic differences are available although they differ in their ecological needs. Parasites and plant feeders may become isolated by living in or on hosts and gradually becomes separated from original group. Moreover there is a tendency to evolve according to the nature of the host's resistances (such as host-parasite interaction and insect-plant co-evolution etc.). These separated progeny with drastic reduction in gene flow will be equivalent to geographic race.

Strickberger (1996) defined race as 'a population or groups of population in a species that share a geographically and/ or ecologically identifiable origin and have unique gene frequencies and phenotypic characters that distinguish them from other races.'

The sharp differences between race and subspecies may need clarification. On closer examination, following characters of a race may be observed.

1. Race is not taxonomically recognized but subspecies is.

2. Expected rate of more fertile progeny is higher in races than in subspecies. Because in subspecies the gene frequency is altered to greater extent.

3. Race is a vague and controversial term and used indiscriminately. It is frequently used to describe any form of minor phenotypic changes within a subspecies.

Cline

Huxley (1939) used this term to describe a character gradient or gradual changes of a character which is usually observed in contiguous population. Variation in any character is clinal and this is usually gradual (smooth) or rarely sudden (step clinal). Population showing smooth cline should not be regarded as subspecies. However two subspecies are found at two extremes of a cline where changes are taxonomically significant.

Isophene is the stretch along which all members show much similarities and this line, hence, perpendicular to the cline.

Morphotype

This is a very superficial and non-taxonomic term applied to a sample within a subpopulation. It is a 'distinguishable sympatric and synchronic interbreeding populations of a single species' (Edwards, 1955).

Rassenkreis, formenkreis and artenkreis

Rassenkreis (Rensch, 1929) and formenkreis (Kleinschmidt, 1926) are synonymous and they refer to the polytypic subspecies (Mayr, 1969). Both are not accepted by Zoological Commission. Kleinschmidt defined formenkreis as 'a collective category of allopatric subspecies or species' and in paleontology it is 'a group of related species or variants'. However it is established that a species is quite different and belongs to a higher category; it encompasses all sorts of geographical variations of its members. Rassenkreis was given to a genetic species with a series of intergrading but local populations and only those at extreme ends show wide gap in gene frequencies and fail to interbreed (isolation is complete). Rensch later redefined formenkreis and proposed the term artenkreis. This was described as a genetical species, which is a local undivided geographic race and does not exchange its gene pool with adjacent subpopulation.

Infrasubspecific and superspecific terms

Deme

Mayr described *'deme'* as only one subspecific category and it is not taxonomically recognized. Zoologists consider deme as evolutionary unit inhabiting a small local ecosystem.

In earlier days, taxonomists proposed and used several other terms to designate variations among subspecies. With the rise of population biology, such subdivisions were proved to be useless. Mayr also advised not to recognize formally every local population showing some differences. This is because there is always a tendency in individual variation or variation in subpopulations inhabiting only few miles apart.

Superspecies

The literal meaning of the term artenkreis is 'circle of species' and to avoid confusion, Mayr replaced it by an international term superspecies. It is defined as a 'monophyletic' group of closely related and largely or entirely allopatric species'. Mayr described it as polytypic species, the members all descendant from a common ancestor. They include, in broader sense, both allopatric and those in areas of geographical contact (*parapatry*) still maintaining reproductive isolation. According to Simpson (1961), a superspecies is 'groups of populations that seem on other groups (morphology, ecology etc.) to have passed beyond the point of potential interbreeding and to have acquired separate evolutionary roles, but that are not demonstrated to have done so by the more conclusive evidence of remaining separate when sympatric. It is to be presumed that they are still near the critical point of speciation, that of definite isolation, and it cannot be quite certain whether they are really past that point and are not just below it. They are nascent species, when survive, shall collectively form a subgenus or eventually a genus but have hardly yet reached that degree of divergence and expansion'.

Superspecies has a unique gene pool and it is not interchanged with its close one. There is usual gradation of ancestral characters and it acquires gene frequency different from relatives. The number of the members of such a species is very low initially and it dynamically struggles to increase in number. Characters of higher weight are developed anew or through modification of some characters. Thus it occupies a higher category (subgenus or genus).

In spite of this meaningful event in speciation, taxonomists do not feel to insert a new category above species. There is also a problem of explaining the sharp difference between a species and superspecies.

Superspecies is not taxonomically recognized although it was used in many earlier monographs and other publications. Superspecies is a transitional event, not a final form on which a category may be established. Some authors, however, felt the usefulness of the term to study zoogeography and speciation events.

3.4. Theories of biological classification, hierarchy of categories

Man and animal study anything around themselves by self or by learning. He needs to classify insect, plant, water, land, poisonous and non-poisonous objects and such others for future reference or to communicate to others. In the absence of any classification, simply knowing and understanding the multitude of objects would leave everything beyond control. From the period of early philosophers till recent, classification of living and non-living objects is continuously modified according to the availability of further knowledge.

So far there are one and half million described species, more than twelve thousand fossil species and there is a continuous downpour of newer species description. A classification, hence, is dynamically accommodating all these species according to their relationships. A good classification is a system of enormous amount of information about organisms which are readily and conveniently available to a scientist. Information means the characters some of which are exclusive for a group. Selection of character is a vital matter in classification.

Mayr defined zoological classification as 'the ordering of animals into groups on the basis of similarity and relationship'. According to Mayr and Ashlock (1991), 'a biological classification is the ordered grouping of organisms according to their similarities and consistent with their inferred descent'. Such a definition makes classification natural because it reflects the evolutionary pathway of the organisms.

3.4.1. Differences between classification and identification

Classification	*Identification*
1. It is the delimitation, ordering and ranking of taxa.	1. It is the determination of the taxonomic identity of an individual.
2. It deals with population or groups of populations and is based on maximum available characters.	2. It deals with individuals and is based on fewer characters, ideally single.
3. It is based on inductive reasoning.	3. It is based on deductive reasoning.
4. It is the ordering of the vast diversity of nature or any part of it into sets or groups.	4. An unidentified object is fitted into a given set of taxa.
5. Quality of classification depends upon the theory on which it is based.	5. Quality of identification depends on the quality of classification on which it is based.

According to the traditional definition, classification is 'the grouping of objects into classes owing to their shared possession of attributes'. Such a definition clears the meaning of classification and identification.

3.4.2. Properties of good classification

1. Classification should be natural, *i.e.,* instead of being based on arbitrary characters, it should reflect descent. This was what Darwin realized.

2. An ideal and acceptable classification will rank all animals according to their characters

3. Classification is based on a theory by which one can easily understand the relationships between a close or distant taxon.

4. It will store information on the structures of the taxa and the analysis of that information will help to trace the phylogeny of the taxa.

5. Since classification is based on relationships, therefore similar organisms (hence organisms having similar genotype) will be grouped together. If genotype of an unknown organism is known, then one can predict about the characters of that organism. However such predictions are not always correct, because taxa may be polythetic or undergo specialization.

6. An advanced (*i.e.* recent) organism will have more complex genotype. Because such organism will have more characters and will be categorized in higher rank.

7. Classification is alterable; like othe science, classification will be revised or modified on the basis of newer findings.

8. Classification contains information about many structures the functions which are unexplainable in the recent context. These are present as a continuum from the ancestor. These characters help to identify homologous structures.

9. Classification constructs the most homogeneous groups; they are descendant of the nearest common ancestor.

3.4.3 Comparison of artificial and natural classification

Artificial classification	Natural classification
1. Proposed during early stages of the development of taxonomy and the proponents were Aristotle (384-322 B.C.), Lamarck (1707-78), Cuvier (1769-1832) and others.	1. Proposed later (post-Darwinism) and proponents were Simpson (1959, 61), Cain (1959a) and others.
2. It is useful in classifying inanimate objects.	2. It is useful for organisms, which essentially shows evolution.
3. It is based on priory weighting of taxonomic characters.	3. It is based on posteriori weighting of taxonomic characters.
4. It is based on convenient and diagnostic characters with no stress on relationships.	4. It is based on diagnostic or hidden characters with stress on relationships.
5. This classification usually based on fewer, even single character (like "identification").	5. This classification is not based on fewer characters; here evaluation of the totality of characters is done.
6. No emphasis is given on the presence of constant characters.	6. Emphasis is given on the presence of constant characters (*i.e.* correlated or aggregated characters).
7. It is a downward classification based on logical divisions (by dichotomy). This system dominated up to end of 18th century.	7. It is an upward classification based on assembling species (by inspection) into groups of related species and forming a hierarchy of higher taxa by again grouping similar taxa of the next lower rank. This system evolved by middle of 18th century.

Artificial classification	Natural classification
8. Since it depends on any unwisely selected characters, this can never depict any relationship of organisms and therefore cannot help to find out the phylogeny.	8. It reflects most closely the actual relationship of the included taxa. Therefore it clearly helps to find out the phylogeny.
9. It ignores the fact that groups of organisms are related by descent and possesses a unity by the shared portion of their DNA heritage.	9. It signifies and explains why and how groups of organisms related by descent because they possess a unity by the shared portion of their DNA heritage.
10. This classification never thought of and even hindered the search for missing link and common ancestors.	10. This classification put scientists to work in field, search their ancestral types, missing links, to study comparative aspects like embryology, systematics, anatomy etc., and thus widening the array of taxonomic research and clearly explained the theory of evolution.

3.4.4 Upward and downward classification

Downward classification

The principle of downward classification dominated up to the middle of eighteenth century. Essentialists (Plato, Aristotle and later Linnaeus) believed species as unchanging types (essence). Based on this concept, they proposed the logical subdivision of animal kingdom by dichotomous branching. This is on the presence or absence of certain characters; such as presence of hair or absence of hair, presence of shell or its absence and similar dichotomy. They, therefore, included many unrelated groups together and produced an artificial classification and that was an identification scheme started at kingdom down to species.

Linnaeus made significant contribution to his familiar group (Insect) most of which is still in use. But for chordates this was poor.

Upward classification

The shortcoming of downward classification was soon understood and after middle of eighteenth century, it was converted to upward classification. Buffon (1749) said 'it would seem to me that the only way to design an instructive and natural method is to group together things that resemble each other and to separate things that differ from each other'.

In this method, species were assembled into groups of similar or related species and forming a hierarchy of higher taxa by again grouping similar taxa of the next lower rank. Taxa were delimited by evaluation of numerous characters and *posteriori weighting* (weighting is a method of inferring the phyletic information content of a character. A character of high information content appears to be a product of a major and deeply integrated portion of genotype. Examples are the complex character, joint possession of derived character, consistency and constancy).

3.4.5 Theories of classification

Mayr (1969) recognized five theories and among these, first three are pre-Darwin. These are *Essentialism, Nominalism, Empiricism, Cladism* and *Evolutionary classification*. Two more theories are mentioned elsewhere are *Natural classification* and *Omnispective classification*. Mayr and Ashlock (1991) recognized three schools of macrotaxonomy-*Phenetics, Cladistics* and *Evolutionary classification*.

Recent books do not mention the pre-Darwinian theories. It appears that brief knowledge about those historical theories will give an idea of the evolution of the later theories. The current three are the theory of *Evolutionary Classification, Numerical Phenetics* and *Cladism*.

(a) ***Essentialism (Aristotle's natural sytem)***

According to Aristotle (384-322 B.C.), all members of a taxon reflect the same essential nature, *i.e.*, they conform to the same type; the number of the basic types is fixed (= constant) and the variation is considered to be irrelevant. All essentialists agreed with Plato that by pure knowledge, the hidden nature or form or essence of things are to be discovered.

Aristotle is called the father of biological classification. The principle was so profound that their method of classification continually practiced for next two thousand years. Many of the term they applied are in use to day. However, the classification was not orderly and consistent. The demerits are: (i) there is no principle to discover and identify the essential characters; (ii) species is a descendant of an ancestor and they are related to each other; (iii) variation is an innate property of a species; (iv) no species is fixed in nature; (v) many species of some higher taxa may not exhibit those essential characters and (vi) 'characters in common' are not rigidly taken into account. These are the wrong ideas of this theory.

-(b) ***Nominalism***

According to this concept there is no such things as species, type, groups, class or universal and believed that only individuals exist. These terms are artifacts of human mind. Classification of plants, animals and inanimate objects are based on the same principle of reasoning of sense data. But we know that the descent of organisms shows a relation due to the presence of shared attributes. This principle was not adopted by this school and also misinterpreted this basic nature of organisms.

But we know that animals are natural groups and not a product of human mind. Similarity among related groups is due to the possession of shared attributes and they evolve from common ancestor. The classification of biological object depends upon biological criteria and thus it is different from inanimate objects.

(c) *Empiricism*

Linnaean classification continued for about one hundred years till the publication of Darwin's *Origin of species*. Scientists felt that a classification must be based on totality of characters, not just few or even one. Renowned scientist of this period is Lamarck but Cuvier's contribution was more practical although the latter was a mixture of previous concept and some very sound practical taxonomy.

Empiricism, however, ignores any principle for classification; rather intellectual evaluation of as many characters as possible will produce a natural classification. The consistent disagreement to any principle made this theory untenable.

(d) *Evolutionary classification*

Darwin's publication first gave the world the basic foundation of evolutionary mechanism and the meaning of the 'naturalness' of animals. Soon the basis of classification got the proper guideline and a new dimension. The theoretical basis for classification given by Darwin was 'groups within groups' and explained that separation of taxa must be based on branching and ranking of taxa depends on degrees of modifications they have undergone in time. Darwin also proposed the concept of constant presence of some characters in related forms (*posteriori weighting*) and constant association of several characters. The last two principles opened up the best guideline for a natural classification.

Thus evolutionary classification is based on Darwin's principles: one is genealogy (common descent) and degrees of difference or modifications. According to this theory, natural groups of organisms (*i.e.* taxa) exist in nature. Darwin explained that mere similarities are not enough criteria; rather reasons for such similarities are to be explained by a natural classification. Thus scientists have to 'discover' the taxa and not have to 'create' them. Characters are the evidences, not that characters are classified. The evolutionary classification combines phylogenetic branching with the degree of evolutionary divergence among different taxa, which is the best combination, required by a natural classification.

The methodology of this *classical or evolutionary classification* has been explained by Cain and Harrison (1960), Simpson (1961), Mayr (1969), Bock (1977), Wiley (1981) and Farris (1977). Mayr and Simpson developed the principles fully in their papers and the evolutionary school is also called Simpson-Mayr school.

A difficult approach in evolutionary classification is to combine 'similarity' and 'descent' and to prepare a classification on the basis of both. Evolutionary taxonomists construct a provisional classification based on overall similarity and thus show all taxa in a classification. Thereafter such taxa are interpreted for monophyly, *i.e.*, for their origin from nearest common ancestor. However, the last part can be done by cladistic method.

(e) ***Natural classification***

According to Blackwelder (1967) animals are placed into as many groups or subgroups as are the similarities. Here groups are recognized on the basis of maximum common attributes and such groups are limited (*i.e.*, separated from others) by discontinuities in the diversity and by judgment, deductions about the correlation of other features will come up. Smith (1965) and others explained the natural classification as a phylogenetic one, which shows evolutionary relationship of the groups.

The above statement is not different from the first part of the principle of evolutionary classification (phylogenetic approach or ancestral-descendant relationship). Discontinuities in diversity may be due to various reasons and these will not always give correct deductions. The second part of the evolutionary classification i.e., the degree of divergence in time is not explained by this theory.

(f) ***Omnispective classification***

Blackwelder (1967) modified the concept of natural classification and proposed this omnispective classification. According to this concept, an experienced classifier initially works upon all available characters to classify the organisms into groups. Thereafter only few vital characters are selected for grouping and separation of groups.

Such a practice may help the taxonomists but there is possibility to produce an incorrect classification. Because without considering the weightage of characters, the classification tends to be artificial. The importance of ancestral characters for grouping and characters responsible for monophyly (*i.e.*, branching) are expected to be used in a natural classification.

(g) ***Phenetic classification***

Principles of Numerical Taxonomy (Sokal and Sneath, 1963), which is later known as *Numerical Phenetics* (because cladists also uses numerical methods) and more commonly as *Phenetics* is the first to provide a technique to draw phyletic lineage on the basis of similarities and differences. They adopted Darwin's principle of similarity due to common descent and claim that 'overall similarity' can be obtained from the recording of similarities and differences in large number (>60).

In 1973, Sokal and Senath published the second and the revised edition of this theory. They defined the theory as: 'Numerical Phenetics is the methodology of assembling individuals into taxa on the basis of an estimate of unweighted overall similarity'.

Pheneticists explained the merits of their theory as follows :

1. There is no requirement of knowledge of the taxa to be studied; the person should have the ability to find out as many characters as possible and to quantify them. So trained technicians will collect data from specimens and all question of systematics will be answered (Ehrlich 1964).

2. Computer programmer can fit the observed similarities and differences.

3. Gilmour (1940, 1961) said that in phenetics, the number of characters used is far more than traditional system and this eventually would produce a more natural classification.

Pheneticists believe that theory-free inductive approach of their theory would create correct classification. They adopted Bridgman's (1945) philosophy of 'operationalism', whose 'clear and possible (operational) instructions, replaced biological theories. and explanations. Pheneticist's operational method denied reference to species and thus they, in principle, adopted the nominalistic philosophy. They are giving equal weightage to all characters and such a classification may become artificial. They replaced species by the concept of '*operational taxonomic unit*' (OTU) and an OTU may be individual or population. Phenotypically different individuals are sorted out into different OTU. Thus pheneticist faced the crisis of explaining the individual variations and sexual dimorphism.

A phenogram is obtained as end product of clustering process. There are several methods to convert a phenogram into a classification (Rohlf and Sokal 1981; Mc Neil 1979).

Merits of phenetics

1. Phenetics opened the window to classify above species level and removed the dissatisfaction of traditional approach.

2. Introduction of computer in taxonomy is their credit and this proved to be efficient in making quick and error free comparison of data matrix for similarity and differences among taxa and inspired to search more differentiating characters.

3. Phenetic approach is more suitable for closely related taxa originated from common ancestor and thus with similar evolutionary roles and hence, abundant homoplasy.

Therefore, for each apomorphic character a separate assemblage of species can be recognized. Daly and Balling (1978) used this method to classify African and European honeybees and their hybrids.

4. Although phenetic method was not accepted by later systematists in animal classification, this has been consistently applied in plant taxonomy and molecular biology.

Demerits of phenetics

1. The method is laborious and time consuming because it has to score more number of characters than traditional method.

2. There is no scope to pay attention to the weightage of characters.

3. Not all animal taxa provide enough characters and there phenetic method faces trouble.

4. Addition of new character requires fresh calculation and may reject earlier decision.

5. OTU lost biological sense and phenetic concept goes back to pre-Darwin age.

6. Variation of organisms is not accepted as natural phenomenon of members of a given taxon.

7. Lack of theoretical base in the choice among clustering method, selection of character, arbitrary assignment of values and choice of clustering method; all depend on personal choice. Hence Sokal (1985) felt that 'different clustering methods yield different fits by cophenetic correlation coefficients to the same resemblance matrix'.

8. The choice of different algorithms (computational methods) yields different phenograms (Minkoff 1965); Felsenstein 1983; Presch 1979).

9. Unweighted similarity method will force pheneticists to fit sibling species in a single OTU.

10. Parallel, convergent and reversed characters are equally treated without paying attention to the cause of their origin. This leads to wrong clustering.

11. Numerical values of phena in different taxa cannot be compared to each other. This value will change when compared to another set of taxa. Thus no universal scale can be established. 'Phenetic technique will not reach perfect congruence of classification when these are based on different sets of characters (Sokal)'. Ghiselin (1966) pointed out that some conspicuous characters develop due to specialization and these have less taxonomic value; such characters when taken in phenetic clustering would leave the phenogram far from true phylogeny.

12. Phenetic method fail to take mosaic evolution into account. Because every character has its own evolutionary role. Therefore different similarity estimates will be obtained

when one type of character or the other is used. Phenotypic expression reveals only a very small or often highly biased portion of genotype and there is varying correlation between the two (Rohlf 1963, 1964).

13. Pheneticists do not depend upon plesiomorphic and apomorphic characters. They cannot distinguish a primitive group from an advance group.

(h) *Cladistic Classifiaction*

This theory was proposed by German Entomologist Willi Hennig (1950, 1957) and was initially published in german language. It was not much circulated among scientists till its English translation and revisions (Hennig 1965, 1966, 1975). This was immediately accepted as a standard method of inferring phylogeny. Now there began fall of numerical phenetics.

This concept is based on :

1. Taxa should exclusively be based on synapomorphic characters while ancestral (plesiomorphic) characters are ignored.

2. Every taxon should be monophyletic (= holophyletic) consisting of stem species and all its descendants including all 'ex-groups'.

3. All sister groups should be accorded the same categorical rank.

The worthiness of cladism lies in that it does not rely solely on similarity and it separates apomorphic character from plesiomorphic character.

There is no doubt and any systematist will agree that the revolution in macrotaxonomy was actually initiated by Hennig. His simply structured methodology was immediately exercised on the vast pending field of systematics, which was lying unattended due to many difficulties. Examples are the previously believed unnatural groups, such as turbellarians, many groups of insects, fishes and turtles. After Darwinism, there was a continuous effort to produce a natural classification and perfect theories were proposed (the evolutionary theory of classification). But in practice there was no guideline to determine the genealogy. Cladism provided and explained this procedure from an analysis of the characters of the living forms and this does not depend on availability fossils. Mayr and Ashlock (1991) pointed out that the most important merits of cladism are as follows:

5. Cladism reemphasized that taxa are product of evolution and this is kept in mind during delimitation of taxa.

6. The methodology adopted in cladism is based on careful evaluation of taxon characters and the entire process shows evolutionary history of species.

7. Cladism is first to show how characters could be weighted and separated into plesiomorphic and apomorphic ones. Many previously developed and well-established categories were ascertained by inspection and experiences.

8. Cladistic analysis helps to unmask convergent polyphyly (taxa obtained from different ancestor that undergone convergence and became so similar that they form a separate polyphyletic taxon).

For the above reasons, cladisrn at once gained overall appreciation and it is now practiced by most systematists. According to this theory, the categorical status depends on the position of the branching point on the phylogenetic tree.

It is to be cleared that some authors have mixed. up cladism with phylogenetic classification. Mayr (1969) mentioned that 'Hennig. ...and others have designated themselves misleadingly as the phylogenetic school. .. .' and also stressed that' .... splitting of the branches is only one of several phylogenetic processes .... warned to look out for misleading use of the term phylogeny by cladisrs. Cladism has also been designated as genealogical approach (Gisin 1964)'. Cladists claim to show relationship between members of a group of taxa and they call it '*Cladistics*' or '*Evolutionary systematics*'. In some places even, cladism has been referred to as "*Phylogenetic systematics*". Thus so many names have been applied to the cladism. It should be remembered that original concept has been revised many times in the light of phylogeny and evolution.

Christoffersen (1995) mentioned the differences between cladistics and phylogenetic classification as follows: phylogeny is predominantly bifurcating, asymmetrical and truncate dendrogram whose height increases with passage (increase) of time. But a cladogram is a non-truncate dendrogram with no defined vertical or horizontal axes in relation to time. Cladogram is a graphical model showing speciation points (=branching) and thus an ancestral-descendant sequence but without any explanation of the length of the line or distance between any two line at any given height (angular divergence). Both cladistic and phylogenetic dedrograms show sister group relationship. Horizontal separation, as we know, shows the amount of differences acquired by two taxa.

Deficiencies of cladism

Gradually some aspects of this theory proved to be insufficient and some other needs further research.

1. *Deficiencies in their principle are :*

(i) The categorical rank of a taxon is to be determined by its genealogical age.

(ii) When a species splits, one of the two daughter species tends to deviate more strongly than the other from the common stem species (Hennig 1966).

(iii) Each species in terminated by a split into two daughter species: i.e., all branching points are dichotomous.

(iv) A species begins at a branching point and ends at the next branching point in the cladogram.

Cladists have rejected the first one and the rest three are accepted by some or rejected by others. Farris quantified the contribution of apomorphic characters and thus studied on anagenesis; the results made subsequent modification in cladism (Camin and Sokal 1965), Cladists used some of the traditional terms (e.g. phylogeny, monophyletic, polyphyletic, paraphyletic etc.) in modified sense (Mayr and Ashlock 1991) although this was defended by Wiley (1981).

2. *Homoplasy can put unrelated taxa together.*

Due to convergence, parallelism or reversal of a character may show homoplasy. Such characters confuse the true status of the taxa under study.

3. *Different sets of characters may produce different cladograms.*

Rosen *et al.*, (1981) and Holmes (1985) obtained such different cladograms on origin and sister groups analysis of amphibia. By cladistics and using sets of character different from traditional ones. Gardiner (1982) came to conclusion that birds and mammals are sister group taxa.

4. *A branching point not necessarily is dichotomous always.*

Orthodox cladists believe that an ancestral species breaks up into two daughter species. This phenomenon is rare. Mostly parental species remains little changed while it gives rise to one or many lineages in different situations. In case of such simultaneous speciation, a cladogram becomes trichotomous or polytomous. This has been acknowledged by modern cladists (Wiley 1981).

(i) *Variability of a higher taxon cannot be judged if only fewer taxa are analyzed which may not have expressed apomorphy.*

(ii) *Cladism better can compare sister groups, not ancestor-descendant group.*

This is because a species of a holophyletic taxon is more closely related to any other species of that taxon than to any species of an ancestral or sister taxon.

5. *Cladists recognize a holophyletic taxon as a separate taxon and that consists of stem species and all as descendants; its member species share one or more synapomorphic characters.*

But a holophyletic taxon may be very heterogeneous where 'in a lengthy phyletic lineage, the early stem groups are very different from later ones and particularly from the ultimately crown group or because some relatively undifferentiated stem groups give rise to a highly divergent ex-group (e.g. family of turbellarians that gave rise to the parasitic trematodes and cestodes) (Mayr and Ashlock 1991).

6. *Wrong assumption of equal rates of evolution in all phyletic lines.*

The stem species may remain static while the neospecies may show quick changes. Thus there are unequal rates of changes in different phyletic lines which is ignored by cladist.

7. *Wrong theory of ranking.*

According to Hennig's rule for ranking, the product of dichotomy is given the next lower rank from parental taxon and both sister taxa are to be given same rank. This rule will produce far large number of categorical levels than by traditional classification.

8. *Restriction to synapomorphy lead to misuse of information content of many vital characters.*

Traditional classification makes fullest use of most of the characters. Cladists concentrate on only few *synapomorphic* characters and in this way they are ignoring the importance of many vital characters including plesiomorphics, which are part of evolution. 'Systematics in general consists of the search for defining characters of groups' (Nelson and Platnick 1981)'.

9. *Neglect of autatomorphic characters.*

Autaomorphic characters (characters that evolve in only one of the two sister groups) help to analyze the amount of anagenesis and Hennigians thus neglected the anagentic information in the construction of a cladogram.

10. *Cladists excluded fossils from their classification or at best list them as 'plesions'.*

11. *The cladogram may become instable by the introduction of new taxa.*

Such an inclusion makes the holophyletic taxon a paraphyletic. Minor disagreement among the cladists can make a taxon holophyletic by some or paraphyletic by others. This has been found in the classification of agnatha (Halstead 1982) and in Psocoptera, Mallophaga and Anoplura (Boudreaux 1979).

Discussion

In the last several decades some schools emerged to solve the difficulties in the theory and practice of classification which differ in their philosophy. Some deviated from Hennig's rule to varying degree (Hull 1988). Pattern cladists deviated most (Platnick 1979); some retained most of Hennig's principles while Wiley (1981) and others based more on evolutionary taxonomy. Felsenstein (1988) pointed out two major splits: one remained adhered to Hennig's 'phylogenetic systematics' and the other group engaged themselves to computer-based numerical analysis. Edwards, Cavalli-Sforza and Camin and Sokal were developing algorithm based on parsimony and they, along with pheneticists, formed the second group. It is to be noted that some systematists of the second group are not supporter of the cladism although their attempts are based essentially on cladistic techniques.

3.4.6 Comparison of cladistic and evolutionary classification

Cladistic classification	*Evolutionary classification*
A. Synapomorphic characters are used to recognize branching point.	A. Synapomorphic characters are used to discover and reject polyphyly.
B. Parsimony helps to determine best cladogram.	B. Parsimony helps to test homoplasy.
C. A cladogram is constructed.	C. A phylogram is constructed.
D. Taxa are determined by holophyly.	D. Monophyly and maximum number of shared characters determine taxa.
E. As low as single synapomorphic character is needed.	E. Maximum number of shared characters is needed.
F. Sister groups assigned same categorical rank.	F. Sister groups assigned different categorical rank if they differ by sufficient autatomorphy.
G. Ranking depends on diagnostic synapomorphic character.	G. Ranking depends on homologous and ancestral characters.
H. Classification is based on branching of lineage.	H. Classification is based on branching and divergence of lineage.
I. Categorical ranking is arbitrary.	I. Categorical ranking is based on degree of difference.
J. Autapomorphic characters are usually ignored.	J. Autapomorphic characters used in ranking.
K. Stem group is always with crown group.	K. Stem group sometimes with sister group.

Summary

(i) A best classification should be a natural classification.

(ii) Pheneticists believe that 'most similar' organisms are product of evolution and thus show relationship with ancestors.

(iii) Cladists claim to reflect accurately the branching pattern.

(iv) Evolutionary taxonomists claim to adhere to principles of classification and genealogy.

3.4.7 Hierarchy of categories

In a hierarchic classification, each rank (or level) is a category. Categories are designated by such terms as species, genus, family, order etc. Each such category contains one or more taxa and these taxa belong to a given rank. Each such rank is a category.

Category is defined as 'a class whose members are all the taxa that are assigned a given rank'. Thus a genus category contains one or more genera; a species category contains one or more species.

3.4.7.1 Differences between a taxon and category

A taxon refers to concrete zoological objects i.e., groups of organisms, such as sponges, annelids, reptiles, birds etc. Taxon is defined as *'a group of real organisms recognized as a formal unit at any level of a hierarchic classification* (Simpson 1961)'. The definition given by Mayr (1969) is *'a taxon is a named taxonomic group of any rank that is considered sufficiently distinct by taxonomists to be formally recognized and assigned to a definite category'.*

The species name is not a taxon, but the organisms that constitute the species belong to a taxon. A genus name is not a taxon but the organisms that are the members of that genus together given a higher taxon name. A taxon name is usually a common word, not a scientific abstract term to describe a particular group of animals. When we say insect (a taxon), we know what is an insect and also know that there are many orders and families of insects; when we say butterfly we at once recognize a butterfly (a taxon of lower rank than insect). In these examples, the insect belongs to class Insecta (a higher category) and the butterfly belongs to order Lepidoptera (a lower category in respect to class category, but a higher category in respect to genus or other categories below order rank). We can define a species or a genus. But we cannot define, say a butterfly, but can describe the butterfly. So taxon is a thing (zoological object) that can be described and not defined.

'A higher taxon is an aggregate of related species separated from others by a discontinuity' (Mayr 1969). The lowest taxon is at the species level and all taxa above species rank are higher taxa. This definition is not suitable for monotypic taxa whose members are all alike; e.g., if members belong to one species or if members belong to one genus. Such a monotypic higher taxon is separated from the next one higher taxon by all lot of differences.

Higher categories

A category is an abstract term, the name of a class. Higher categories are not perfectly delimited. Specialists have often ranked a taxon higher which other scientist ranked lower. For this arbitrariness, higher category differs from the species category.

3.4.7.2 Hierarchy

Aristotle's *Scala Naturae* predominated for over two thousand years and his theory profoundly made scientists to believe that all animals are arranged from 'most primitive' to 'most perfect'. Thus animals were thought to undergo a continuous change and at any time, all animals are members of same class (types). Linnaeus was a follower of Aristotle; he framed higher categories but could not explain the significance of a hierarchy in the light of *Scala Naturae*. Their explanation was that a higher category splits into lower categories. This was just reverse to what emerged in post-Darwin era.

Darwin saw the organic diversity as a result of speciation; the gradual evolution of higher and higher taxa separated by gaps was by chance and adaptive processes and these were the cause for divergent evolution. Therefore speciation, adaptive divergence and extinction are reflected in a best hierarchy. He clearly explained the fundamental principles as: 'the natural system is genealogical in its arrangement, like a pedigree; but the degrees of modification which the different groups have undergone have to be expressed by ranking them under different so called genera, subfamilies, families, sections, orders, classes'. Thus higher categories evolve through evolution; not that higher categories subdivide to produce lower orders.

Species has no subordinate category and thus it is the lowest category. As a genus consists of one or more species, a family consists of one or more genera. Here genus and family both are higher categories. In this way all organisms are placed or ranked according to their comprehensiveness, in a hierarchy of categories, which is commonly known as *Linnaean hierarchy*.

Linnaeus recognized five categories and these are *classis, ordo, genus, species* and *varietas*. The variety (= *varietas*) was used to designate infraspecific variations when present i.e., it was optional. This was discarded or replaced by the category subspecies. Two more categories soon developed, the family (Butschli 1790) and phylum (Haekel 1886). With the addition of kingdom, there became seven categories and any organism belongs to these seven categories. Hence these seven categories are known as obligatory categories (variety is excluded, as it is optional). These are kingdom, phylum, class, order, family, genus and species. All living organisms belong to five kingdoms, protista, monera, fungi, plantae and animalia. Linnaean hierarchy consists of a nested set of taxa of different categorical ranks. A number of taxa of any rank are closely related because of their common ancestor. However degree of differences increases among the members with the higher rank. More similarity is observed among members of taxa of very lower rank. Because the common ancestor in the previous case is far (*i.e.*, more separated in time and with greater variation in genotypes); in latter case, the common ancestor is very recent.

Merit of Linnaean hierarchy

The merit of Linnaean hierarchy is its flexibility. More and more newer categories can be included as more organisms are dealt in future. It is thus provisional, allowing taxonomists to store greatest information by splitting or lumping of categories and thereby presenting best hierarchy. It was once proposed to assign specific numerical values for categories. This was rejected for two reasons: one, assignment of value need far greater knowledge about their relationship based on 'all species on earth' and two, assignment of value will freeze the number of categories and the hierarch will loose its flexibility.

Based on the scrutiny of the classifications done by taxonomists, Mayr (1969) found that they recognize taxa on the relative merits of five considerations:

1. Distinctness (size of gap).
2. Evolutionary role (uniqueness of the adaptive zones).
3. Degree of differences.
4. Size of the taxon.
5. Equivalence of ranking in related taxa.

3.4.7.3 Additional categories

Since Darwin's publication, there began active search for newer species throughout the globe and scientists were more interested to draw relationship and evolutionary mechanism. The result was the growing uneasiness to rank known species into those fixed seven categories. In other words, due to immense pressure to rank them all and due to the presence of so many distinctive groups that the number of existing categories were increased by splitting them. The additional categories were mostly designated by adding prefixes as " super"(above an existing category) and "sub" (below that category). Thus we have superfamily, subfamily and others. However there are no categories as superphylum, supergenus or superspecies.

Two more category names were added to the hierarchy. These are "tribe"(below subfamily) in entomology and "cohort"(below subclass) in vertebrate paleontology.

Categories from superfamily to tribe are formed by adding suffixes: "-oidea" for superfamily, "-idae" for family, "-inae" for subfamily and "-ini" for tribe. Such standardized term are not available for categories above the family rank. An example is given below:

Superorder Blattopteroidea, Order Mantodea, Family Mantidae, Subfamily Mantinae and Tribe Mantini.

3.5 Taxonomic characters-different kinds, origin of reproductive isolation-biological mechanism of genetic incompatibilities

3.5.1 Taxonomic characters-different kinds

Mayr defined taxonomic character as '.. any attribute of a member of a taxon by which it differs or may differ from a member of a different taxon". Taxonomic characters are the characters of a population and not the individual differences in age, sex and such others. When two populations differ by presence or absence of a character, then that becomes a taxonomic character. Thus the character must show potential or diagnostic feature of a taxon. Therefore the taxonomic character of a taxon reveals relationship between itself and other taxa and those characters help in the study of higher taxa. The diagnostic features are strong at the level of lower categories by which the taxa is specified.

Out of many taxonomic characters, some are chosen for comparative study. These characters, as an experienced taxonomist feels, have more information content and reveal relationship in a better way. A taxonomic character may not be a phenotypic expression. Any such expression is ultimate product of complex gene interaction. Till to day, genotype of most taxon remained unsolved and not all genotypic variations are good taxonomic character. Again not all phenotypes exhibit real information all the time. Adaptation to one environment by unrelated taxa will produce lots of characters, which are redundant for the phylogenetic study.

So long potential characters are not identified, a taxonomist searches for all available characters and thus gives equal weight to all characters, he or she will be misled. Because this procedure will conceal the effects of convergent or parallel evolution.

An unreliable character has low weight and examples are those characters which vary quite frequently. For example the branching of the arteries varies in the members of a species population. While wing venation is an important taxonomic character in some group of insects, it varies widely in some others thereby looses its taxonomic importance.

Some characters show gradual decline in its shape, size or function. Examples are the shortening of wing, loss of eye etc. These regressive characters have low weight.

Both identification and classification depends on analysis of characters. Some characters are used in both the cases, but very few and selective characters are required in identification works. Identification at species level depends on easily available (chiefly morphological) characters and such identification can even be done on specimens long preserved in museums and are always available to future scientists. Such specimens will not be useful in any further biochemical, physiological and such other works that demand live one. Although we know that any experimental analysis related results are useful for systematic work, these are not much useful in identification or other methods to be undertaken are complex.

Significance of characters :

Besides temporary characters (such as seasonal, sexual or those which are variable characters), all organisms evolve certain configurations or characters, which is therefore, outcome of long history of manipulations under various thresholds of environmental influences. Added to this are the natural mutations, hybridization and intrinsic phenomena, which drive those changes. We should not forget that instant, temporary or seasonal characters have a past history and they serve good purpose in species identification.

Field study of organisms clearly shows many diagnostic features of an organism. Actually the ecosystem moulds an organism inhabiting to its specific nature. Such as darkness makes all organisms uniformly colourless or animals in the arctic region becomes white to match the surrounding. Tropical organisms are variously coloured. Organisms show development of similar characters due to convergence, but the organs are analogous. Related sympatric species develop stronger morphological differences to get rid of accidental hybridization and competitive exclusion. This process was termed as Character displacement by Brown and Wilson (1956).

Taxonomists looked upon speciation by isolation as a curious phenomenon to which the definition of species is related. At a given time the separation of two taxa is based on their separation so as to prevent hybridization. This is accompanied with development of contrasting characters observed in their reproduction strategies.. They have passed through many generations and natural selection to achieve this goal. It is not certain that all the present species on the earth are those best selected form. Rather all organisms are still changing or evolving along with the nature and many today will be proved to be less fit in future or in the present situation of the ecosystem. Natural hybrids are formed in genotypically closely related species and some of them may show better fitness to at least in present scenario.

The entire above situation expressed in the form of characters are valuable in taxonomic study. Stable characters are conservative and are of high weight. These are important in tracing of ancestral history of a species and in the construction of phylogeny.

Taxonomists may often ignore many, perhaps minute characters. This is because having sufficient characters at hand and probably completed a systematic work; he or she may willfully avoid those characters as unwanted. This will create lot of problems in future study and surely lead to a wrong conclusion about the lineage. Any character, whether minute or big, is the outcome of functional genes. All characters interact with the environment and we are ignorant about each such phenomenon. A study of members of a species over a wide range show how the characters are associated or adapted to their respective ecosystem.

Morphological characters are the product of a part of the genome and not of the entire genome. So genetic relationship is not fully expressed by these characters. Therefore, taxonomist now deal with many other types of characters including the studies of biomolecules (proteins, nucleic acids) and correlation of these biomolecules with the phenotypic expressions. This wider range of viewing a species is the essence of *New Systematics*. This vision has solved many confusing problems in typical morphotaxonomy. Although this approach is still very young, it has actually strengthened the evolutionary classification that was actually established on the basis of classical approach.

Kinds of taxonomic characters :

Mayr (1969) has categorized these characters under five heads, each with their further subdivisions as follows.

1. Morphological characters :

The external features and often anatomy of living or museum specimens provide most of the important taxonomic characters of a species. There are many internationally famous museums and research institutes, which preserves the history of organic evolution. They also periodically publish the status of their materials, new additions, condition of them and such related events. Research articles on these materials are also available from their library. For microscopic organisms, external characters include anything visible under microscopes of different kind up to any resolution as needed. Surface texture or surface structures or derivatives e.g. test, shell, theca, warts, epidermal structures such as scales, feathers, hair and variation of all these and other prominent features are studied in cases of larger animals. Morphology of sperm has received attention in identification of a species as a key to species isolation. Study of specialized cells (by histology, histochemistry, TEM) is routine work in understanding the functional aspects of an organ.

Colour pattern is nearly specific and easily available morphological character. But there are many colours which are seasonal or develop temporarily in response to environment (including prey-predator relationship, courtship etc.). Some colours are specific and permanent as those of many insects, birds, and many other organisms. They serve to identify them easily. Colour is lost in long preserved museum specimens and later does not match with originally published account. Polymorphism or gradation of character (colour) is common in a population of some species. Variable colour should be examined and judged carefully.

Much attention has been paid to the structure of genitalia for interspecific distinction and sometimes this character has been used in separation of higher taxa. By definition of a species, this will differ in closely related species. Problem arises in cases of similar (but not identical) structure of genitalia as to whether they belong to same species. Actually the amount of difference needed for separation of a species is not available. This is the reason why some natural hybrids are found in nature. In the absence of proper mate of own species or similarity in mating behaviour often brings about such event. Reproductive isolation in nature can not be proved so easily in such case. Many cases of gradation of variation in genitalic complex is known in insects and other groups. However the genitalia morphology is very strong tool to distinguish morphologically alike unrelated species in most cases. Genitalia are carefully dissected out, preserved in proper medium for future reference.

Task of obtaining characters are now easier by innovation of instruments and techniques. The results is the accumulation of heaps of raw data. Unfortunately little of these have been summarized to be utilized in the study of the evolution of the group. However stray works on some groups are available and until all of a family or higher taxon is done, the systematic work will remain pending.

Usually vertebrates being highly evolved have developed characters, which show more constancy, conservativeness and are less fluctuating. These are easy to handle because they are more distinct and highly dependable. Measurements of whole organism or parts, dissection of formaline preserved material for anatomical studies on the comparison of soft parts or organs, or bones are important in understanding the line of descent and modifications. A vital part like a skull with jaws and teeth can tell many taxonomic characters.

2. Developmental characters :

Characters shown by developmental stages and their adults have been used as good taxonomic characters in some groups. Embryological features are used in the taxonomy of sponges where adults are very similar (Le´vi, 1956). For example. Sibling species of

Anopheles maculipennis are classified on the basis of egg morphology and in white flies (Aleyrodidae) identification is principally based on pupal differences. It was noticed that many taxonomic characters are distorted due to adaptation at any stage of life. As in digger wasp (Sphecidae) Evans (1964) has shown that certain adult structures were paid high weightage and that has improved taxonomy of the group based on larval characters. In frogs, studies were made on the larvae and their characters were judged with that of adults for perfect analysis (Orton, 1957; Igner, 1967).

3. Chromosomal characters :

Karyotype study is easier in groups like Diptera and Orthoptera where the chromosomes are bigger and fewer in number. In most organisms this is just the reverse and therefore, difficult to analyse in Lepidoptera and birds. Characteristics of chromosomes usually differ in related species and a complete data of a group help in phylogenetic analysis of a group. Intersetingly the changes in the characteristics of a chromosome is not always reflected in phenotypes and this one reason that many sibling species identification is based on karyotype studies. On the othet hand, related species show considerable rearrangement while some species are polymorphic due to chromosomal rearrangements.

From phylogenetic angle, any form of chromosomal change being a permanent event is seen in descendants and is used as a marker in identifying a phyletic line. Polyploidy (a rare event in animals), aneuploidy or structural changes in chromosomes (such as deletion, duplication, insertion etc.) are all important taxonomic characters and, now-a-days, specialized techniques help to identify them. Innumerable data are now available in this subject.

Chromosomal matching percentage between two taxa is long used as a measure their taxonomic distance. But there is no specific value to this because the percentage differ widely in different groups. In spite of many exceptions, rate of production of viable and fertile offspring obtained by hybridization of interspecific (or sometimes intergeneric) is a good measure of taxonomic relatedness between two taxa. Because post-zygotic isolation acts at many stages as a result of mismatch in protein syntehesis by deformed functional genes. Duck shows wide range of interspecific or even intergeneric fertility although there are examples of exception to this (hybrids of *Aix sponsa* and *A. galericulata* is sterile). Evolutionary significance is not clear why some groups of birds show fertility while some insects show sterility in related interspecific hybridization. For this reason Blair(1963) studied this comptibility in hybridization in *Bufo* and rearranged the species.

4. Physiological characters :

Probably all physiological characters are only studied in living animals. Taxonomists who rely on museum specimens (for comparative studies) can not get physiological data, such as effect of abiotic factors, enzyme system and others. Lots of work have been done to understand physiological variation among taxa to reflect correlation with the environment. These data between species show certain differences and can be treated as characters of a species. Plants and animals continually or discontinuously produce certain metabolites to the exterior and these are specific for an organism. Genic sterility is a physiological phenomenon but this is more discussed as chromosomal event.

5. Biochemical characters :

Major biochemical pathways are nearly uniform in all the evolved taxa. Still there are very much specificity in many biochemical reactions in all organisms. Such specificity even exists within the members of a species population (e.g. blood transfusion in human). Taxonomists widely used immunology as efficient method to determine closeness between species although there are many shortcomings of these methods. Identification of proteins, nucleic acids and their sequencing are going on some taxa to identify closeness of taxa, which are again not totally free from various technical difficulties. But such studies at finer level create critical situations. Gross analysis of vital protein, enzymes or DNA hybridization are easier to handle and are frequently used in taxonomy. One such widely studied is the hemoglobin of primates and man show that African Apes (*Pan*) and man (*Homo*) show very little changes in hemoglobin and serum since their separation from common ancestor although their adaptive zones are very widely different.

6. Ecological character :

Every species has its own specific niche in an environment and thus displays good taxonomic character for separation of very close relatives. These factors are period of activity, habitat, food selection, breeding period and others. These are so vital that morphologically alike so-called same species living on different plants were proved to be different species. Host differences do not always mean separate species. Mayr (1969) has shown that peripheral population of a species shows differences in ecology as a local population. And thus subspecies shows distinctions. Among many examples of ecological separation that of Galapagos finches and *Anopheles maculipennis* complex are well illustrated examples.

7. Parasitism as a character :

Host parasitic interaction is a result of co-evolution and often shows characteristic pattern that help in species identification. Although parasites normally invade any unexplored host, but they mostly show constancy in host selection. Probably they fail to survive in unlikely host and sometimes a parasite shows closer affinity to related taxa. Parasites with wider adaptation can be found in unrelated taxa (e.g. bird lice, Mallophaga on geese). Many intestinal protozoans are useful indicator of relationship among termites

(Kirby, 1950b). Intracellular symbionts are absent in primitive tribes of coccids but they are present in some descendants (Buchner, 1966a). So under careful studies, many such observations can halp to indicate phylogeny of an organism.

8. Ethological characters :

Similar to niche separation, every species shows distinct behaviour (except mimicry and such adaptations). Besides morphotaxonomy and cytotaxonomy, ethology is an interesting and widely investigated area in biology. It provides lots of highly informative characters which are genetically imprinted in any species. These are diverse such as mate selection, courtship, nest building, predation or prey capture, mating call or songs of different meanings. Classification of many insects, fishes, amphibians, birds and others were refined on the basis of ethological data.. Among many data, some are those of digger wasp (Evans, 1957, 1966), sweet bees (Sakagami and Michener, 1962), gulls (Tinbergen, 1959 and Moynihan, 1959), North-American crickets (Walker, 1964). Sibling species of frogs and toads were clearly identified from their different calls (Littlejohn, Main, Mecham and others). Many bird calls have been recorded and the copies are available to match with a given a specimen in nature for easy identification.

9. Geographical character :

It is expected that all descendants of an ancestor will inhabit same broad geographical area. A perfect classification shows a relationship with the distribution (habitat) of an organism. Any variation in the organization will also be related to the changes in the of pattern distribution. This is true as a descendant with some vital modification or acquisition of characters to suit that environment occupies the new adaptive zones. Each geographical area has its history of development (geological history) and this is meaningfully associated with its own animal evolution. Therefore the adaptive characters of an organism tell many features of its habitat and its distribution shows the range of habitat. The range is usually distinct although may be inhabited by many related or unrelated taxa in the same area are not uncommon.

3.5.2 Origin of reproductive isolation

Natural species are kept as true species in nature by means of diverse mechanisms that isolates them from other species. Although some amount of hybridization occurs in nature they are supposed to face many hindrances to become successful species. Still some exceptions are there and they will be discussed.

New species are formed from an existing species when some factors isolate some members of the parental stock in such a way that in the long run, they fail to interbreed with the parental members. Wagner and Darwin emphasized its importance in the evolution of animals. Later on Mendelian genetics confirmed this route of evolution. Newman suggested that evolution couldn't be explained without the role of isolation.

The isolating mechanisms are of various nature and strength. Chiefly they are ethological, ecological and hybrid sterility. These are important in maintaining the genotypic identity of a species.

The origin of the reproductive isolation, according to one view is an accidental by-product of genetic divergence. Different populations, in course of time, become more and more dissimilar in their genetic identities. The other proposition by Wallace and supported by many modern evolutionists is that reproductive isolation is a gift of natural selection. Since the hybrids are less fit and have less adaptive capacities, they will be gradually eliminated. While the true species, which are already adapted to ecosystem will produce more successful generations.

3.5.2.1 Theories on the origin of reproductive isolation

Two theories were proposed to explain the origin of reproductive isolation.

1. The theory of Muller states that the members of a parent species may inhabit various geographical regions and gradually become adapted to newer ecosystem. Dispersal of species is a common affair and due to various reasons the dispersed groups occupy newer niches. This separation over a long period causes accumulation of genetic differences from parental stock to such a degree that there is origin of subspecies and species in those allopatric populations. Therefore reproductive isolation is an incidental by-product of genetic divergence.

2. The second theory proposed by Wallace (1889) and later supported and explained by Dobzhansky states that reproductive isolation is an outcome of natural selection. This theory is based on prevention of hybridization in nature. In other words, the natural selection has formed a barrier between species and prevents unwanted mating. This type of reproductive isolation operates after accidental hybridization. The hybrids are generally non-viable and are gradually eliminated from environment and reduce wastes of gametes.

3.5.2.2 Evolutionary origin of reproductive isolation or Genetic basis of origin of reproductive isolation

In nature, the hybrids formed show various degrees of success. However the progeny does not proceed further and is eliminated by natural selection. Species 'a' species 'b' cannot be considered as distinct species only if they produce sterile hybrids. This is because, as explained earlier, hybridization may occur in nature and shows various degrees of success. Many species frequently hybridize in artificial conditions.

The importance of prevention of hybridization is that each species has its own gene pool, which has been tested by natural selection and exclusively matches the environment. It has many deleterious genes, which are rare in expression. But a hybrid or break up of barriers between other two or more gene pools will expose innumerable genes, which will be of very low in success or highly or partially lethal to offspring. There lies the need for separation of gene pool.

According to Mayr (1942) and Sibley (1957), some species-specific characters functions to prevent unwanted reproduction. These characters are favoured more and more by natural selection and become exceedingly conspicuous. The species of birds without pair formation is an example of such character development.

The production of new genotypes is actually exploration by the species and may or may not found an unoccupied adaptive niches. The result may be a success with varying degrees or may be a total loss. Thus newer combination is simply a luck try. This results in huge loss of progeny, which even can cost to extinction of the species. However the parental gene pool, which is firmly adapted to present environment, continues at normal rate. Only few successful newer variants may pave the way to revolution through hazards of natural selection.

Recombination of genotypes of distinct species sometimes presents offspring, which are equally, or more fit to the environment of the parental stock. Such variants emerge out of introgresive hybridization, allopolyploidy and recombination and all these have effective role in evolution. However there are occasional hybrid breakdown in nature.

The three most important factors in evolution are isolation, adaptation and variation. Mutation helps in evolution but is not considered as a basic factor. Isolation is achieved when any external or internal factor prevents interbreeding. Isolation is the phenomenon of separating a population into two or more sub-populations through prevention of interbreeding.

The male and female gametes unite to give rise to a new offspring. These gametes may come from a male and a female partner or from same individual (hermaphrodite). There are a variety of mechanisms in unicellular forms including bacteria. However many unisexuals prevent self-fertilization through different mechanisms; in others the self-fertilization is the only means of propagation of the race.

The zygote receives a recombination of parental chromosomes. Enormous gene combinations are possible through meiosis and recombination. Therefore the new generation offspring with newer genotypes are now subjected to natural selection. The prevalent environmental conditions may be favorable or unfavorable to them. Even some genotypes may be proved to be better preadapted to a future condition. Some new genotypes may try to establish to the present situation at the cost of huge loss of offspring. They may achieve success and some may endanger the perpetuation of the species during the loss of excessive number of offspring in the battle for survival.

3.5.3 Biological mechanisms of genetic incompatibilities

According to Mayr, sympatric species maintain its identity of gene pool by the following types of isolating mechanisms:

(a) Prevention of mating by potential mates by restricting random dispersal.

(b) Prevention of mating by some ethological, structural or other mechanisms by which potential mates are not allowed to meet.

(c) Hybrid sterility and reduction of fertility.

According to Dobzhanśky the isolation of sympatric species is achieved by geographical or permanent separation.

3.5.3.1 Prezygotic and postmating (zygotic) isolation

Species is defined as a Mendelian population between which there is no or very little genetic exchange is possible. The isolating mechanisms which operate among species may be premating (prezygotic) or postmating (zygotic).

Premating (prezygotic) isolation ways

1. Habitat isolation : This isolation is an outcome of continued adaptation of a population to its biotic and abiotic nature of the environment. Thus it is governed by soil profile and geography, climate and all those exert direct and indirect effects on vegetation and population. Within an apparently homogeneous environment, there are many minor differences in its biotic environment (such as differences in salinity, light, pH, oxygen, nutrient etc.). These are, therefore, act as barrier to smaller animals.

It should be noted that in areas of hybridization of two subspecies, the hybrids show characters of both subspecies. Since all the members of the subspecies and the hybrids are actually the members of one species population, we should not use the term 'overlap' of the subspecies. The term subspecies has been used and defined differently by many authors and created lots of trouble. If used in proper sense, the category subspecies has much usefulness to population taxonomists.

Distance becomes a barrier to many invertebrates and several vertebrates. Therefore dispersed and isolated population may not be able to return to home stock and will eventually evolve separately. Newer areas exert newer adaptations which changes gene frequency in those forwarding group. Mammals radiated from 'Holarctica' (Northern Asia, Northern Europe and North America) and undergone spatial isolation to give rise to many new taxa even in the absence of distinct barrier.

The partial barriers those permit migration and interbreeding give rise to progeny with almost homogeneous basic features. But the members show minute differences and continue to adapt to partially differentiated habitats. Such incompleteness of barriers produces diversity in species population. Such a situation continues till the formation of a perfect barrier, which actually isolates the populations on either side of that barrier. By this time the populations have accumulated newer alleles and therefore gene combination becomes different from the parental population.

Different species may inhabit same area but different ecological habitats and hence ecologically isolated. The *Anopheles maculipennis* group consisting of six species is a good example of sibling species. They are morphologically similar but genetically and reproductively isolated good species and occur in different geographical areas. The species show distinct differences in the selection of breeding sites, courtship, transmission of pathogen, egg-float characters and many others.

2. Seasonal or temporal isolation : Different species exhibit sexual maturity or become competent to mate or reproduce at different time and thus seasonally or temporally isolated. This is very common in plants. An interesting study (Blair, 1941; Cory and Manion, 1955) on *Bufo americanas and Bufo fowleri* shows that the two species become sexually mature at different periods of the year and reproduce at those specific seasons of the year. However, since a particular period overlaps between their separate reproductive seasons, some amount of hybrid offspring are also produced in some man made artificial habitats. Pulmonates are hermaphrodite and are known to mate for mutual insemination. There are different phases in a successful fertilization and production of viable offspring. These are search for suitable mate, courtship and transfer of gametes. Each of the steps play crucial role in a species and are highly species specific which all are to prevent hybridization in nature. Experimental keeping of females of *Drosophila pseudoobscura* and *D. persimilis* in same container along with the only the males of *D. persimilis* produced 79.2% of *D. persimilis* and 22.5% of *D. pseudoobscura*. The cue to such species selection may lie in their various tactile senses and pheromones. Littlejohn (1965) have demonstrated that auditory signals of frogs and toads are species-specific.

3. Mechanical isolation : This is due to different shapes or structures of genitalia of different species. This is, hence, a good taxonomic character. Entomologist Dufour (1844) proposed lock-and-key theory of selection of species, which is based on structure of genitalia. However it is true that many different species with structural variation in genitalia mate well to produce successful progeny. However there are instances of injury and death in such attempts.

4. Chemical isolation : The structure and or chemical nature of surface of gametes of many species are so different that they only attract and unite with conspecific ones.

5. Ethological isolation : The different species inhabiting very close to each other do not mate because they do not have any attraction to opposite sex of a different species and thus an ethological isolation works.

6. Gametic mortality : It was observed by Patterson in case of *Drosophila* where the sperms were unable to withstand the physiological conditions (pH, temperature, salinity and others) in the female tract and the wall of the latter swelled and finally the sperms die.

Post-zygotic isolation

These mechanisms are classified into three broad categories- hybrid inviability, hybrid sterility and hybrid breakdown.

(a) Hybrid inviability

This happens from the starting point of the zygote formation upto various stages in the life of the hybrid. It is better for a species to avoid anything that will decrease its fitness. If any hybrid in nature becomes unsuccessful it is better not to produce them to avoid loss by fitness. The best way to avoid this is prezygotic isolation. However, in nature, occasional hybrids are produced having varying degrees of success. There are different stages where the life of the hybrid is culminated. Mostly the embryos do not proceed beyond the two to three cell division stages. The reasons may be the dissimilarities in the genetical, biochemical or physiological properties of the embryo or the environment associated with its development. Sonneborn observed the phenomenon in *Paramoecium aurelia* group where the embryos continue development for some stage and then die away. Embryos that cross above stage of development suffer from malformation and eventual death.

Moore observed differential inviability in 12 species of *Rana* and confirmed that in some cleavage stopped, in some no gastrulation occurred while in others later stages did not flourished. Hybrids of *Ranunculus millanii* and *R. dissoctifolius* (this two belong to different soil and climate conditions) do survive only in intermediate habitat caused by man. In plants Clausen 1951, Stebbins 1950 and others observed similar situation. The hybrids obtained by interspecific crosses of *Datura* cannot proceed beyond eight-cell stage.

(b) Hybrid sterility

The hybrids may be partially or completely sterile. The sterility arises due to chromosomal or genic dissimilarities. The sex organs of such hybrids normally continue the process of production of gametes up to premeiotic stage but suffer unsuccessful pairing of parental sets of chromosomes at meiosis. Grant (1981) observed that chromosomes of such hybrids suffered multiple translocation; many gametes are aneuploid (deficiency in proper number chromosomes) or deficient of portions of specific chromosomes). Karpechenko (1927) found that sterile the hybrid obtained from *Raphanus* and *Brassica* produce gametes bearing 6-12 varying number of chromosomes and hence no viable pollen or ovule is formed. However, the allotetraploid (*Raphanobrassica* with 18+18 chomosome number) obtained from unreduced gametes produce viable pollen and ovule. Clearly this sterility is due to difference in partner chromosomes that could not be matched. This mismatch was rectified in allotetraploid. Similar observation was found in *Primula verticillata* and *P. floribunda*.

Hybrids obtained from *D. Pseudoobscura* and *D. persimilis* show abnormal cell division producing some bivalents with full numbers of chromosomes (in primary spermatocyte) or some chromosomes may remain unpaired. But some female hybrids can successfully be backcrossed to male of any parental species. The reason of such genic sterility lies in abnormiality during development by uncoordinated behaviour of gene complements during germ cell (but not somatic cell) formation.

Genic sterility is more common in animals than in plants. While chromosomal sterility exerts its effect at or after meiosis, the genic sterility act as isolating factor before, after or at any stage of meiosis. Some hybrid sterility proved to be due to combined effect of both gene and chromosomal abnormality.

Sterile hybrids sometimes show vigorous somatic growth and mule (hybrid of donkey and female horse, each with 33 chromosomes) is the best example. This is due to dissatisfied pairing of genes or cytoplasm of different sources.

(c) Hybrid breakdown

Hybrids very often fail to perpetuate because they fail to exchange gene with any species population. Occasionally they fail to reproduce after second generation or during backcross with a parent. In both cases the progeny contain genotypes of low fitness and are weak; many are sterile. Artificial insemination of female cattle by semen of sterile hybrid buffalo (obtained by crossing American bison and beef cattle) was done. This backcrossed hybrid was fertile and this buffalo propagated themselves.

D. *persimilis* and *D. pseudoobscura* show habitat difference. The former is active in the morning period and latter is active in the evening of the day although the range of their distribution overlaps in large part of the Western United States. Thus it is more probable that both hybrid breakdown and differences in ethology act to isolate the two species.

Hybrid breakdown was also observed in plants (*Gossipium baradense, G. tomentosum* and *G. hirsutum*, (Stephens 1950).

3.5.4 Discussion

3.5.4.1 Isolation, inbreeding and selection

Isolation of animals is related to habitat isolation achieved by various natural phenomena. Among many such events some are submergence or rising of land mass, desertification, permanent snow fall, change of course of water body and tectonic movement. Change of vegetation is often correlated to these events. However, newly developing land mass gradually acquire both vegetation by various natural passive or active methods.

So far best studied isolation is those on oceanic islands although the pattern of speciation may differ from that in mainland. The fauna and flora on Galapagos and Hawaiian Islands are probably the best studied speciation in isolation. Studies reveal that taxa present on continents or on islands once connected to those continents, are absent on oceanic islands which were never part of the continents. Rather some taxa are quite diverse in later islands. The reason might be that the species accidentally reached the islands and enjoyed previously unoccupied niches. Usually absence of competetor, predator and unlimited resource enable a founder species to flourish at a rate higher than that possible on mainland. The descendants of an ancestral species probably from nearby continent migrated or were carried accidentally to such oceanic island and undergone speciation at a quicker pace. In that case, the number of species will be more on such island than on continent. This was the probable cause of the occurrence of fourteen species of Darwin's finches in comparison to only six species of all other passerine and single species of cuckoo are now present on Galapagos. The finches arrived first and enjoyed time and space for diversification. Similarly the hundreds of species of *Drosophila* in Hawaiian Island Archipelago are descendants of one or two ancestral species.

In almost all cases, speciation on oceanic island is very rapid and diverse. The founder species takes a small fraction of ancestral gene pool of a nearby continent in most probability. Since in a new niche, there is no immediate occasion of genetic variability, there will be inbreeding for many generations. Any isolated group with fewer members will continue to increase in number by inbreeding. This small gene pool will gradually develop more homozygosity and express lethal and deleterious genes. The result is a severe loss of fitness. It happens that high rate of production allows high rate of recombination of ancestral gene pool and each offspring gets equal chance of survival in a homogeneous environment free from all fear of competition or predation. Many of these are very similar and few develop certain new combinations that are bit advanced in the new environment of this island. There are obviously many differences in flora of such island from a continent. So the newer progeny may find it suitable or unsuitable. Those able to adjust will radiate better than others and those others seek other habitat in that geographical area. Each generation multiplies probably geometrically to occupy more resource resulting to varied adaptations through dispersal. The new population shows rapid change in its initial genetic combination, which adds to species formation.

Besides the chance of recombination at higher rate, genetic drift is a very important mechanism of speciation. Mutations that increase reproductive fitness will be preserved by natural selection and will increase in frequency thus changing the genetic combination of the founder group. Natural selection keeps the frequency of deletrious allele at lower frequency by elimination.

Formation of separate geographical locality by isolation of a landmass from a continent the population in a different way. The separated population takes a higher amount of ancestral gene pool and has better chance of recombination. But due to the existence of all features of parental habitat, the changes in gene frequency is almost as normal as that of the ancestral home. Therefore, speciation is not rapid if there is no exceptional change in climate. Tectonic movement produces change in the climate of a land mass and hence the populations are subjected to a gradually changing environment. Since the phenomenon is slow, the speciation will be slower. Once separated, the organisms will thereafter evolve separately chiefly due to differences in climate along with changes in flora. Such an isolated mass may act as filter-bridge or other form so that this may be inaccessible to most while accessible to few forms. Therefore diversity in such island depends upon its own history.

3.5.4.2 Introgressive hybridization

According to Anderson, 'introgressive hybridization' is the phenomenon of backcross between a new hybrid and parental species whereby some parental genes will 'introgress' or included in genotype of the hybrid. Anderson opined that introgressive hybridization is useful for hybrid survival. The necessesity lies in the fact that any hybrid, due to the presence of combined genotype in them, will prefer a habitat intermediate to the different parents. This means almost something like 'hybridization of habitat' and such habitat dose not occur naturally. We find that man has created many unnatural habitat and these can easily be taken up by such hybrids formed through easy exchange of genes between related populations.

However, not much work on introgressive hybridization has been done with animals. Studies of Anderson and Heiser on plants proved that such events take place in nature in enough number. Backcrossed individuals were found to be so much effective that they produce 'hybrid swarms'. An example cited by Heiser on sunflower revealed that *Helianthus annuus* and *H. bolanderi* are believed to be originally inhabitant of eastern and western coast of United States and thus ecologically well separated. Their natural hybrids are found in many disturbed ecosystems and actually produced hybrids swarms. Such a hybrid swarm develop by segregation of hybrids in first, second or later generations. Such segregated populations are in the meantime may be mixed up with the backcrossed progeny. The total result is the production of numerous gene combinations along with varying degrees of fertility and viability excepting only backcrossed progeny.

3.5.4.3 Failure of isolating mechanism

Often due to natural or unnatural reasons, the barriers responsible for isolation and speciation may be withdrawn or removed or lost. In some cases indirect barriers to isolation may be lost. The result is mixing of previously allopatric species to become sympatric. Such new population shows different features in course of time.

Studies on birds of Central Europe by Mayr show the origin of sympatric species of birds. During Pleistocene glaciation Scandinavian and Alpine ice caps approached each other in central Europe, which separated the originally inhabiting temperate fauna and flora into Southern France and Spain in one hand, and Balkans at the other, i.e. at the opposite ends of Mediterranean Sea. Again, with the recession of the ice cap, the two segments, now already well speciated came to occupy the parental habitat. The result of such previously isolated and now co-existing populations are many.

(a) The two populations may accumulate such genetic differences that they remained as a good separate species in the sympatric population.

(b) There is rare hybridization of two once separated populations; the example is those of hedgehogs, *Erinaceus europaeus* and *E. roumanicus*.

(c) The hybrids of two stable species of crow *Corvus corone* and *C. cornix* are observed in the transitional areas between eastern and western habitats. This are the examples of polytypic species (also earlier termed as rassenkreis (Rensch) and formenkreis (Lorenz, Kleinschmidt)

3.5.4.4 Some remark on isolation

Experiments on the number of gene differences to produce hybrid inviability shows that a single gene in plant *Crepis tectorium* is lethal enough to produce the effect. This gene, however, has no visible effect in that species. It is assumed that at least two genes are required for reproductive isolation and instead of acting as post-mating barrier, may be eliminated by natural selection; thus enhancing the chances of occasional hybrids in nature.

The effects of natural selection become greater and greater on species that acquired post-mating isolation. This helps to reduce the loss of fitness from inter-specific mating. Another effect is the feedback enhancement of pre-mating isolation.

Observation by Littlejohn (1965) proved that phenotypic or behavioural similarities exist among different species, which are allopatric. The same species will show differences of characters where they are sympatric. Example is the similar mating calls of *Hyla ewingi* and *H. verreauxi* when they are allopatric but dissimilar when they are sympatric.

Isolated groups of sister population undergoing natural selection will loss some of parental characteristics while adopt newer ones. Thus it is expected that either parental genes undergo modifications or new genes are accumulated in the gene pool. In course of time, this event makes the population sufficiently different from the parental group.

3.5.4.5 Chromosomal characters in hybrids

How much genetic differences should there be to consider a species distinct from nearest species. This is an unsolved part. The opinion of de Vries is that a single mutation can give rise to a different species. It is possible if there is allopolyploidy which produces new species in the next generation. Morgan correctly interpreted that several mutations accumulate to give rise to a different species. Morgan termed the various intermediate forms in different progeny as *variants*. Morgan, however, did not established however the number of genes required to be mutated for a new species.

Regarding chromosome number, it appears that many related or non-related species have similar numbers. Therefore chromosome number cannot distinguish species differences.

However, the various sources of chromosomal abnormalities (such as deficiency, duplication, translocation and inversion) were studied for chromosomal polymorphism as well as chromosomal differences among species. The latter technique helped to discover that some minimum number of breakage of chromosome of *Drosophila pseudoobscura* can give rise to *Drosophila Miranda* and this was nearly 100 in number.

Differences in gene arrangement might be regarded as a cue to the evolution of several species of *Drosophila*. It has been observed that 25 inversions of blocks of genes is a difference between *Drosophila flavomontana* and *Drosophila virilis*. But studies on 96 species of *Drosophila* by Carson and his collaborators proved that pairs or groups of related species were homosequential. Therefore gene differences alone cannot be accounted for species differences.

3.5.4.6 Allozyme studies in different species

From 1966, allozyme studies geared up in quest for cues to species differences. Enzymes of different populations studied by gel electrophoresis reveal differences, which is due to different gene expressions. The object of this study is the estimation of genetic differences and similarities between species. However the estimates, i.e. the genetic differences and similarities are not constant for all species. The reasons are many; the process of species formation is gradual, some require more time to accumulate more gene differences. Others evolved from some races. Thus the pathways to species formation are different for different species.

The problem of this study is that alleles code for different allozmes with similar mobility and are said to be identical and the amount of these identical genes is about 80% in different subspecies or semispecies. This in *Drosophila* is about 56% in sibling species, 35% in morphologically distinguishable species under same subgenus.

The studies also indicated that average genetic distance is same between subspecies and semispecies. Still semispecies of *Drosophila willistoni* group acquired some amount of reproductive isolation and they exist as sympatric population.

The genetic distance between man and chimpanzee (King and Wilson 1975) is 0.62 and genetic identity is 0.54. These values match for sibling species of *Drosophila*. But sibling species, by definition, are indistinguishable externally. Thus comparing values and phenotypes of *Drosophila* and those for man and chimpanzee, we can conclude that in latter case, the divergence of regulatory genes far exceeds the divergence of structural genes coding for allozymes. The electrophoresis hardly can detect the divergence of regulatory genes.

Unit 4 ❑ Procedure keys in Taxonomy

Structure

4.0 Introduction

4.1 Taxonomic procedures

4.2 Taxonomic keys

4.3 Systematic publications

4.4 Process of typification and different zoological types

4.5 International code of zoological nomenclature

4.0 Introduction

This part of the **Taxonomy** syllabus consists of the following topics :

4.1 Taxonomic procedures-taxonomic collections, preservation, curating and process of identification.

4.2 Taxnomic keys-different kinds of taxnomic keys, their merits and demerits.

4.3 Systematic Publications-different kinds of Publications.

4.4 Process of typifications and different zoological types.

4.5 International Code of Zoological Nomenclature (ICZN)—its operative principles, interpretation and application of important rules, zoological nomenclature; formation of scientific names of various taxa.

The topics with their respective break up in fact cover up the essential aspects of the working practices of the science of animal taxonomy and systematics. An introductory review of all those items may be presented as follows :

(1) The first item of taxonomic procedures of collection, preservation and curating processes of identification are three basic items in a taxonomic study. **Collections of specimens** or samplings are mainly outdoor exercises in easy to hazardous terrain covering all natural **niches** including high altitude realms to underwater sites in deep oceans having at the same time laboratory facilities for extracting live forms from supporting substrates or by breeding and rearing target samples by appropriate techniques. By studying the intricacies and modalities involved in such complex procedures, we are able to understand that the collection of animal samples for a scientific study needs suitable planning and instrumentation. A collector must be familiar with various gadgets used for his success.

Just as there are various kinds of instrument based for procedures for collection there are gadgets for rapidly sorting out similar forms from a bulk collection as well.

(2) **The process of preservation** following collection in cases where live forms are not required as in most cases of animal taxonomy is also important. Preservation in liquid preservatives or in dry state after adequate processing of target samples needs a careful and appropriate handling. A wide range of techniques is in use for different groups of animals. Parts of specimens are also preserved as imprints of animals, their left out material, their recorded behaviour patterns etc., may also be of critical help in taxonomy. Preservation by curating samples, specimen by specimen, is a hightech subject that needs trained personnel. Photographs and illustrations are most often useful and for critical analysis, computerized data processing and electron microscopy together with biochemical and cytological studies become necessary. Thus, present-day collection for identification of animals is not merely based on any or more samples of the same but includes their behaviour, habits and habitats, their biochemistry and high-blown structure analysis etc., overriding the barrier of light microscopy.

(3) **The process of identification** is the most complex one and needs utmost care and integrity. A gross identification upto ordinal level or to family level can be done by one having either the speciality or the tenacity besides having a generalized theoretical knowledge. But for identification down to species or infra-species, the subject needs to be dealt by an expert after samples as per requirement have been submitted to him. Identification keys to genera and species where available are used, illustrations and key-characters are compared. In difficult cases, attempts are made to establish correct matching between the sample in question and the type form of the species to which it is theorised to belong. Free exchange of relevant specimens are made from one to another centre of study. Adequate processing and packaging are done for safe transactions. Housing and storage for indefinite period of taxonomic collections specially of type forms and reference samples are essential and are done conforming to universal standard by trained and experienced personnel in establishments made specially for such purpose in different countries.

(4) **Taxonomic keys** are ready-reckoning devices mostly on the principle of dichotomous descriptive contrasts of salient features and those are devised for segregating different species of a genus, different genera of a family and so on. Various kinds are in use and for use by amateurs of natural history studies, there are branching type keys or pictorial keys which are easy to use.

(5) **In the item, Systematics (or Taxonomic) publications,** the specialities of the papers, monographs, books and all relevant literature which bring to light through passage of time all kinds of information and appraisal at gross/critical level about the diversity

of the animal life (and other life for us) are discussed as the core matter includes description of characteristics of life forms at different taxon level with illustrations.

(6) **The process of typification** is an important aspect of taxonomic work in establishing any new taxon or filling up the gap in this respect of any known taxon. Here the models for the taxon is fixed either at the time of describing the taxon or while filling up this gap for a described taxon. These models need to be preserved as long possible and are taken and consulted as reference specimens/items for the taxa concerned. These models are called as types of which there are several important ones such as holotype, allotype, paratype, neotype, lectotype etc.

(7) **The last item of the present section, The ICZN–The International Code of Zoological Nomenclature,** is perhaps the most important one as it forms the internationally accepted theoretical basis on which the science of taxonomy of animals rests and is worked out. Framing scientific names for various taxa and classifying them in the most correct manner along with all necessary requirements to important items of the present section (4.1-4.3) are more or less governed by the rules and regulations put in the ICZN from time to time. Anyone practising/working in animal systematics must be conversant with the ICZN, and must abide by the rules and their implications of the same.

Thus through our perusal of the present section we become aware of the following :

- ways and means of collection of animals, their preservation and curating and processing for correct identification and taxonomic study of collected animals.
- consulting/preparing taxonomic keys of different kinds for identification of animals at different taxon level.
- speciality and differences of literature/publications on systematics and taxonomic work on animals compared to those on other aspects of animal science.
- obligatory rules and means of the process of typification of animals to determine and consult various types.
- rules and regulations of the ICZN (International Code of Zoological Nomenclature) which govern the activities of taxonomy and systematics of animals both in theory and practice.

We may now describe and discuss the different section of our present study in subsequent pages.

4.1 Taxonomic Procedures-Taxonomic collection, preservation curating,process of identification

(A) Taxonomic collection : Collections of animals of different groups form an essential part of surveillance and sampling, necessary to assess and understand activity of the animals concerned whether beneficial, harmful or innocuous. Briefly speaking, this helps us to detect species, known or new, and comprehend population density, dispersion and dynamics having bearings on pest and parasite management (PPM), plant protection and Quarantine programmes (PPQ), conservation programmes and many other biological information. Surveys for all these purposes and importance are classified as qualitative and quantitative, the first one helping us to know the relative diversity while the second one is to know the numerical abundance of an animal population in time and space.

Usually, collection's of target samples are made by worker himself or at his initiation by employing standard techniques or method/s he may formulate suiting local conditions in nature that formed his study area. Broad-based efforts are better and collected samples that are outside his target may be profitably dealt with by other workers/organisations as exchange materials. Study-material may be procured direct or by raising them in laboratory: Repositories like national-museums or research centres have variable stocks of collected materials some of them from remote or "lost" areas and often lying unattended. Procuring such collected samples may also be a suitable way to amass and enrich collections for taxnomic studies.

(a) Value of collections : Good collections implying abundance and zero damage (intact samples) are always laudable. These help us to be comprehensive in our knowledge on evolutionary diversitv and distributional overlaps and extent. A comprehensive study on faunistics, speciation and other useful aspect can be attempted if the study can be based on good collections which act as reference tools both during and after the study. Imperfect and insufficient number of samples cannot as a rule be the adequate basis.

Biological classifications now consist of ordering population. In view of great variability of most natural population rich stocks of collected samples are necessary. Museum collection are thus invaluable both in providing unstudied stocks as well as labelled types and materials for reference consultation. With increased urbanization, emphasis is now placed on exhaustive collections in such areas so that extant formal diversity of these areas cannot be missed even if species cease to exist with intensified urban activities with time.

(b) Types of Collections : Different stages of life-cycle of whole samples are collected as a rule. Since taxonomic characters of an animal from all its aspects are considered at present, collections of live specimens are also studied in nature or in laboratory. Modern taxonomists seek to have not only morphoanatomical characters but also such characters which may be (i) ecological characters, (ii) ethological characters, (iii) cytological characters, (iv) biochemical characters, (v) geographical characters etc. For this, collection must be supplemented by material/parts of animals to enable us study as many aspect as necessary. Films of animals' courtship and other behavioural aspects, recordings of their vocalization degrees (as tapes, sound spectrograms etc.,), photographs or casts of animals activities (nests, galls, webs, tracs etc.) should also be collected. Access to a host of infrastructure facilities for biochemical analyses and electron microscopic study, of aquarium, aviary and insectarium etc., is essential for better results for which specialised centres must be consulted as necessary.

(c) Methods of Collections : This varies from such a simple means of catching/picking/trapping a single specimen by hand without a device or with very simple device from place visited by such one to using elaborate system of equipments and trained personnel for the purpose specially when sampling aims at covering easy to difficult sites.

The method of collection of sample animals either individually or **in mass** form a subject by itself with continuous innovations for the same. Different means are used for different groups which may vary even from species to species level, the keyword of success in all these being the maximum catch at minimum investment. While collection of microscopic forms is based on gathering the substrates that harbour them, the macroscopic forms are collected directly from nature. Caging, netting, trapping and baiting are the standard ways to collect larger forms from fishes to mammals. Smaller forms like various invertab rates are collected by these and other specific techniques suited to their size, habit and habitat. In all cases, enough care is taken to avoid damage to the collected material.

Standard methods usually practised for collecting animals are now briefly discussed as follows-

(1) **Knock down technique :** here, samples are removed from habitat by jarring, by chemicals or by heating, jarring (= shaking) being the most common one for disloging samples from plants. A tray or cloth-piece or other receptacle is placed on the ground below the overhanging target branch of plant which after jarring is gently beaten repeatedly with a stick.

In chemical treatment for dislodgement, substances like methyl isobutyl ketone or turpentine vapour is used. Plant parts treated thus on being shaken are freed from animal, specially the insects in no time which accumulated in the underlying tray/receptacle/cloth-piece or even in a hand net.

For a whole plant, polyethylene envelope with pyrethrum vapour is useful.

2. Plain hand-catching : A resting specimen can be caught off- guard and put into a receptacle with or without a liquid to immobilise or kill it, the whole operation completed by bare hands of the collector. Hand-picking from nesting or resting or feeding sites of samples may also he done. A careful collector may collect impressive number of samples in this no-cost system though in most cases to a limited extent at considerable spending of time. One advantage is that here, the collector needs no preparation and can try it at any point of time at any place.

3. By hand net : One wooden rod (3'–5'long) with a wire-ring fitted to its narrower end (ring diameter 12"–15") and a conical bag of muslin cloth or of fine nylon net or organdy stitched by its broad, open rim to the ring-covering cloth border. There are two kinds of such a hand-net, butterfly net and sweep net (differing in mesh nature of the clothing), both being quite common tools for field collection of insects by amateurs and specialists.

Extracting the insects after trapping them by sweeping across the target surface (s) by the handnets needs deft handling aided by the use of on-the-spot anaesthetizing chemicals.

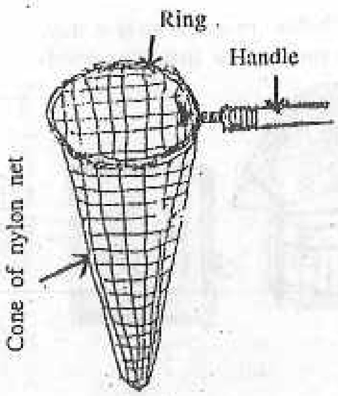
Aquatic insects are collected by **Pond nets**, same as the handnets, except that the mouth of pond nets is semicircular.

More sophisticated net, the **Vacuum net** (trade name D-Vac), consisting of a plastic cone with a removable net attached inside and connected to an engine powered fan by a flexible hose for sucking in target animals, effective for forms not too large as the efficiency of this net varies inversely with the body-size and clining ability of the target forms.

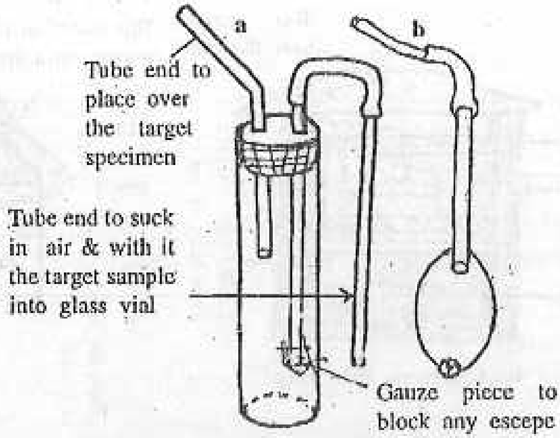
Aerial nets to capture insects on flight are the **Rotary net** (of one or more nets fixed to the ends of beams kept at variable heights from soil level, with nets rotated by a motor-driven shaft).

4. By Aspirator : One simple suction apparatus is used for collecting small insects and arachnids individually while resting or feeding. Suction is generated in bulb aspirator by pumping the bulb vigorously.

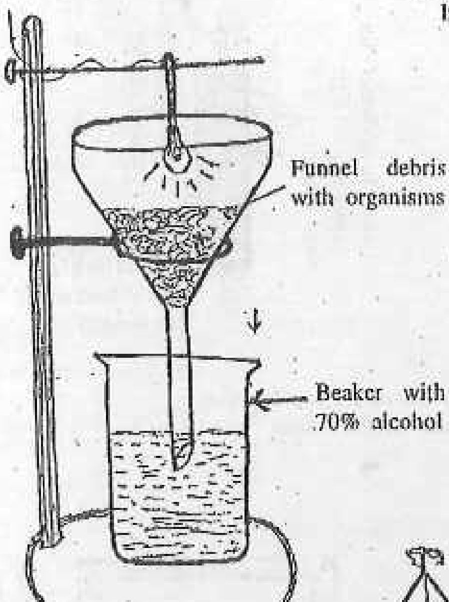
5. By Berlese Funnel : Also called the teslgen funnel, it is quite useful in extracting insects and other small arthropods from organic soils and leaf litter or from loose bark, rotting wood, fungi, mosses, flowers, stored food products, manure etc. The apparatus here consists of a metal or plastic funnel with one wire–mesh inside to hold the sample. The narrow end of the funnel goes inside one underlying beaker having in it some 70% alcohol mixed with a few drops of glycerine. The mouth of the funnel is covered by



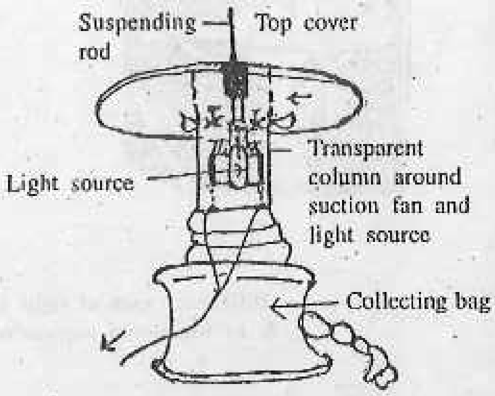
1. Butterfly net



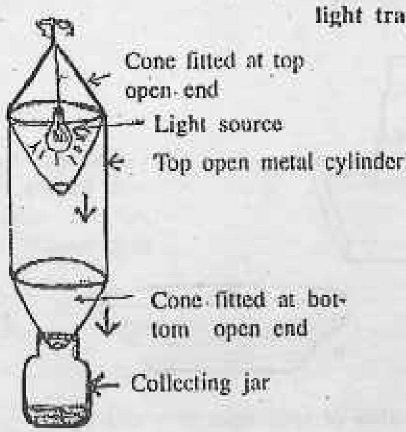
2. Aspirator (a-simple type full view; b-bulb aspirator in part view).



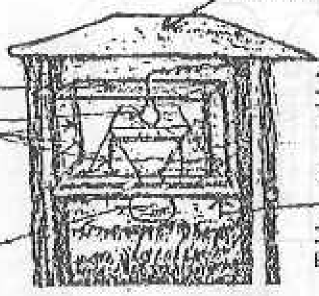
3. Berlese Funnel



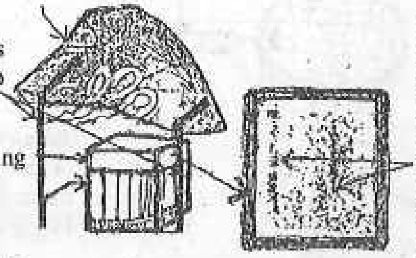
4a. CDC-Miniature suction light trap



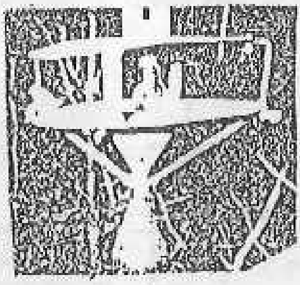
4b. Both end open cylinder light trap



4c. Chinsura light trap



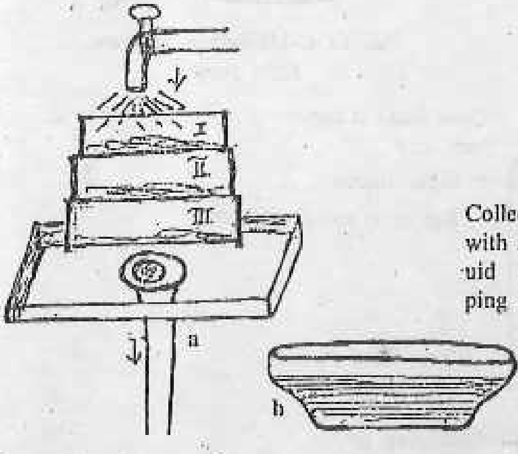
4d.



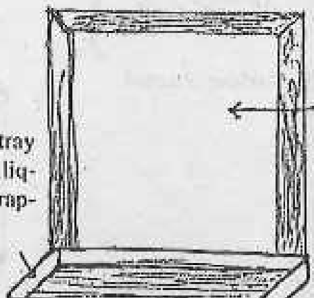
4e.

4f.

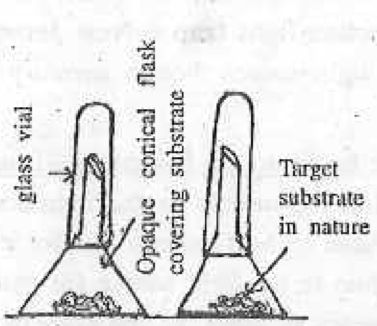
4a-f : Different types of light traps (b, d, e-f local make & in functional suspended state in the open)



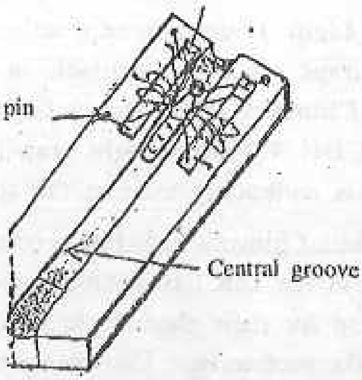
5a-b : set up for extraction of specimens from soil by floating process (I-III in a are the sieves, b = bowl)



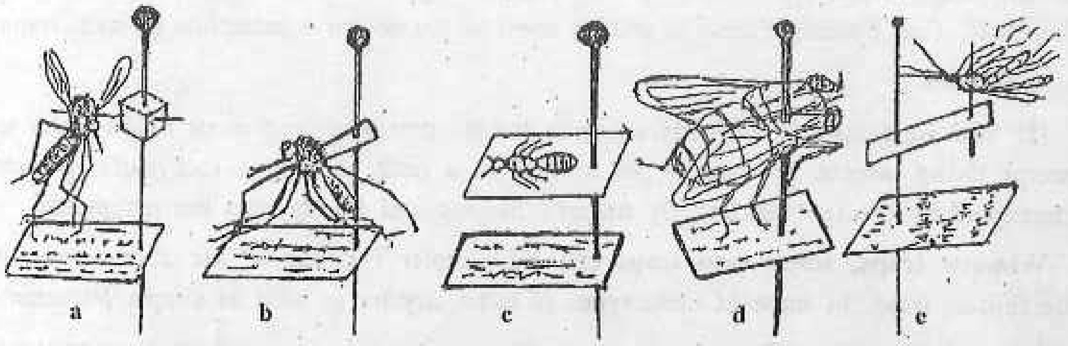
6. window trap



7. Emergence traps



8. Thermocol/soft pasteboard piece with central groove having an insect spread & fixed by paper pieces & pins for fixed-posture-drying.



9. a-e : Dry preservation of insects, pinned/glued variously, for storage and study (taxonomic).

a lid at the middle of which rests one electric bulb of low wattage. As the light is switched on (at a stretch for nights together), the organisms inside sample move away from light (being – vely phototropic and thermotropic) to fall ultimately into the collecting beaker.

6. By flotation method : Used for collecting immature forms and adults of insect and other arthropods from soil or matted vegetation; such substrates collected from open nature is broken up in a basin filled up with magnesium sulphate solution in water (1:3). The content is gently stirred for a while and then left; organisms of the substrate soon float in the liquid surface whence they are collected by a small sieve/filter paper/pipette. This is essentially a mechanical process of differential sieving. Dry sieving, without use of any liquid, is also useful.

7. **By Trappings :**

a. Light Traps : Insects active at night and positively phototropic are collected by light traps which are available in simple, local forms or as technically modified form as in **Chinsura light trap** or the most effective **Suction light trap** (=**New Jersey light trap/CDC Miniature light trap** using ultraviolet light source though mercury vapour lamp is commonly used as the source).

While Chinsura light trap a country-made device based on the Rothamstead light trap (used in the U.K.) is a simple collective device drawing insects to the light-source of the trap for their phototropic habit and entrapped due to heat-exhaustion factor of the trap, the suction light trap uses a small fan in addition to the light source for generating a suction force leading to the trap for which no-escape factor of the trap increases. Underwater light traps are used to entrap aquatic insects and other arthropods.

b. Sticky traps : Here, adhesive surfaces of various designs (usually cylindrical) at various height level above ground are used to trap insects on flight from different directions. Tree banding greese is usually used as the adhesive materials in such traps.

c. Others :

(I) Malaise trap : Is basically an open fronted tent made cotton or nylon mesh to incerpt flying insects. Its root slopes upward to a peak heaving a receptacle. Insects intercepted by the tent tend to fly towards the top and finally into the receptacle.

Window traps, water pan traps etc. are simpler versions of the above type of intercepting traps. In some of these types of traps, dry ice is used as simple attractant.

(II) Pitfall traps and Emergence traps : These are simple devices for collecting some kinds of arthropods, the first one a simple receptacular device with a reactive fluid inside placed in a tunnel for letting surface crawlers in advertent entrapped while moving a cross the pit, the second one being simple, conical receptacle with a collecting tube at top and placed on substrate surface in nature that harbours immatures of the target samples and easily entrap the emerging adults in the collecting tube which has transparent surface and hence is the place of choice for emerging adults, phototropic by nature.

(III) Various kinds of nets : Preferably of nylon thread are used for collecting larger forms by mechanical means. **Mist nets** are useful for entrapping birds.

(IV) Bishop fly trap : Made of a screen cone under a vertical cage and baited with carrion or faeces or **Lard can trap** (made of a horizontal cylinder with screen entry cones at each open end with a bait or lure such as dry ice, a live host, or carrion placed on the floor of the cylinder) are useful for entrapping different kinds of flies.

(B) Preservation : Modes to preserve collected materials vary from group to group. Intricacies of these may briefly be stated basing on uses and nature of collected material. There are two levels of preservation.

1. Field level Temporary preservation : Here, materials are enclosed neatly between two layers of cotton wool or cellulose sheets with relevant date written on a card and wrapped in an envelope of old newspaper. Bits of Carbon tetrachloride/Naphthalene/ paradichlorobenzene are added to cellucotton to keep out predators. Many such packets can be stored in a wooden box temporarily for a few years.

Papering consists of enclosing the sample (preferably a soft-trodied insect large wings and/or legs, moth-butterfly-cranefly etc.) in a triangular envelope prepared thus–a paper - piece sized into a rectangle with sides in ratio of 3:5, and then folded such as to form an isoccles triangle.

2. Permanent Preservation : Methods for this are broadly of three kinds:

(a) Preserving sample specimen dry.

(b) Preserving sample specimen in a liquid.

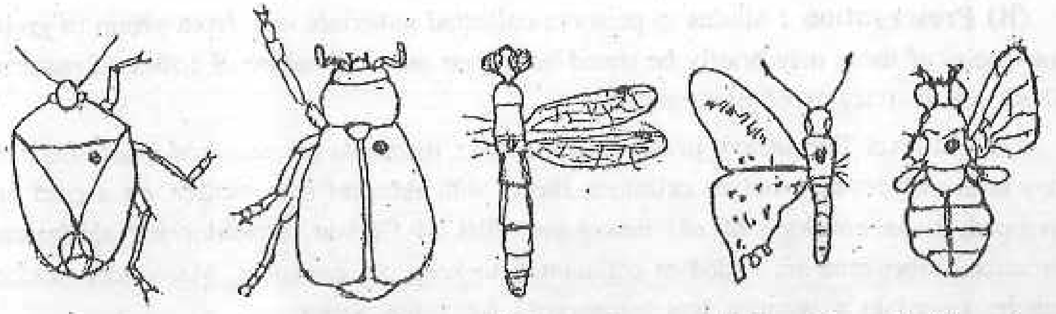
(c) Mounting sample specimen in full or part in microslide for microscopic study.

a. Dry Preservation : By drying and Pinning; insect samples are preserved thus a dead/killed sample (in killing bottle) is 'spread for pinning state' and a rustles entomological pin passes through thorax; such samples kept in drying chamber for a few days after which those are transferred to glass-top storage box with due labelling attached to every pinned sample, some special treatment in these respects being noteworthy:

(i) Direct Pinning : By long, thin and sharp pin (entomological/continental pin) passing through a body – point of the sample with a label of rectangular card beneath the sample. Different body – points are suitable in different insect groups for a pin to pass through and broadly speaking, this is as follows:—

- large bugs (Hemiptera) pinned at mesoscutellum near its anterior margin just right of midline.
- large beetles (Coleoptera) at inner edge of right elytron.
- dragonflies and damselflies (Odonata) at thorax between two hind wings.
- moths and butterflies (Lepidoptera) through middle of thorax.
- dipterous insects specially flies through right of midline in thorax at the level of midlegs.

In all such cases, the pin must pass through dorso-ventral axis of the body.



(a) Bug (b) Beetle (c) Dragonfly (d) Butterfly (e) Housefly

Outline figures of whole insects showing differences in thoracic pinning for their dry-state curation [point of dorsal aspect of thorax through which the pin is inserted is shown by a thick dot-mark (●). Note that pin passes slightly asymmetrically in samples a, b, & e, but exactly through midline of thorax in samples c & d].

(ii) Micro-pinning or Staging or Double Mounting : This technique is quite useful for small insects. An insect in this system is first pinned on a support or stage (Polyporous pith, cork strip or balsa wood strip) using headless, very small steel pin which passes through the free end of the pith/strip and also through the appropriate body – point of the sample, through basal end of that pith/strip.

(iii) Carding and Pointing : Carding is for insects of larger size while **Pointing** i.,e., **triangle carding** is for very small, dry samples. In both cases, the sample is glued to the surface of a strip of Bristol Board Card or the like (best gluing material is clear **cellulose acetate cement**), card strip is rectangular (5 × 8 mm or 5 × 12 mm) for Carding with the sample glued near tip in front while for pointing, it is triangular with the sample glued to pointed tip of the card.

(iv) Relaxing and spreading (or Setting) : Samples after a few days since collection become hard and brittle as they do not survive for long. Pinning of such samples causes fracture in them, so these need to be softened and relaxed which is done by keeping them in a humid atmosphere. Tin can or wide mouthed jar is first filled at its bottom with sand/saw-dust and the same moistened with water and a few drops of phenol or ethyl acetate added to prevent fungal growth. The whole is covered with a piece of blotting paper so that the moisture from bottom cannot directly touch the sample put inside the jar for relaxation. Three/four day exposure softens and relaxes the sample.

Setting/spreading an insect to be preserved dry means to spread body in a straight line with wings and legs stretched horizontally and this is achieved as follows : Place the sample's body antero-posteriorly stretched in the 'medial' groove of a setting/board (locally made from a thermocol sheet or cork sheet) with wings and legs outstretched properly. A long entomological pin is passed through the right point of insertion and slim paper-strips are placed on different positions firmly pressing the outstretched parts of the sample. The strips are kept in place by small pins fixed in inclined manner to those parts. The gut content of the abdomen of the sample thus pinned should be taken out before starting the process to avoid shrinkage of abdomen, specially in case of large, soft-bodied samples. Thus processed and set, sample should be left undisturbed for a few weeks in a full-proof way from predators (by treating storage boxes with naphthalene, Camphor of Paradichloro benzene).

b. Liquid Preservation : Insects and other animals are best preserved in spirit solution (75%-85% ethyl alcohol). Formalin though used as the cheaper liquid preservative for many others, it is not recommended for insects for it hardens them easily. A few drops of glycerine is added in any case, if preservation in liquid is for a long time, to avoid stiffening of samples. Regular checking for liquid preservation to ensure that the liquid has not dried up totally is necessary. Labels written by Indian Ink should be put also inside the tube/jar containing the preserved samples.

c. Preservation by mounting samples in suitable mounting medium on microslides : Small samples are best kept in this manner as those can be put to high power microscopic study without which they can't be studied. Maceration by caustic potash treatment for highly sclerotizel samples is the first step. The samples are then cleared by a dip in clove oil, cedar wood oil or phenol (treated thereafter with xylol in first two cases) and mounted on a microslide in mounting medium like canda balsam solution, or 'Deepex' mountant or Euparol or phenol-balsam mixture (1:1). A cover slip is put over the sample in the mountant and the whole is made bone – dry after keeping for sometime in a constant temperature chamber at 50° Celsius. The dried slides are 'ringed' around their coverslip edges with a varnish to save the sample in the mountant from harmful polluted atmosphere.

(C) **Curating :** After stocks of specimens and their collections are obtained by a custodian Institute or organization of the same for taxonomic preservation and use, the important basic step is to ensure their safe-keeping, cataloguing etc. *i.e.,* curating of the deposited specimens amongst which there are types; additional and voucher specimens or their body-parts (for higher animals), of photographs, films and recordings of or relating to those animals (tape-recordings of or relating to those animals). All are the properties of global science and must be treated on that basis complying with the internationally accepted guidelines as available from time to time in the relevant journal **Curator, Museum Journal** (London), the ASC **Newsletter** (Association of Systematic Collections) etc., besides data on exchange basis. The personnel in a museum engaged in curating must be professional curators having a clear understanding of the functions of collections always attending to the need of updating keeping in mind the groups of animals which needs procurement, areas urgently to be surveyed and various policies about the collections in his Institute. His success depends on his ability to preserve the collections, to gain both in more specimens and infrastructure and maintain readily referrable data about his stock.

A brief review of the essential, activities relating to curating animal specimens in a museum or the like-Institutes/places are as follows :

a. Housing and Storage: Collections of animals or their parts or photographs, films and other preparations for study and research should he preserved in a proper manner and stored in air conditioned, fire-proof buildings. Exposure to fluctuating temperature and humidity is harmful. Storage-cases for specimens must be dust-proof and insect-proof. Steel cases built now–a–days as containers are better. National level museums have all such facilities as well as experts and specialised technicians to handle the collections of diverse groups as required. So it is desirable that collections made and studied at other centres be ultimately deposited to such larger depositories which act as reference centres for scholars of the present and the future. Some well-known museums in different parts of the world are – Zoological Survey of India's principal office and select centres and some select branches (India), British Museum of Natural History in London (Great Britain), Bishop Museum in Honolulu (Hawaii), U.S. National Museum and many such centres in other countries.

b. Arrangement and Preparation of Material : Essential aspects of arrangement are :

(i) Collections kept in museum in the same sequence as of an animal parade from lowest to highest classificatory taxa.

(ii) Sequence of orders and families should he maintained in arranging material whether identified of not with exception in cases where serially arranged samples are disproportionately unequal in size (*e.g.*, fish group) as very large samples may need to be arranged separately.

(iii) Contents of trays and cases in any arranged gallery must clearly be indicated outside.

Essential steps for preparation of material are : (i) Bird and mammalian skins are studied as sent from the field by the collector, skulls need to be cleaned.

(ii) Liquid/dry preserved material may be studied as those exist. In many cases, study of parts under microscope is necessary (e.g., insect genitalia) and permanent microslide mount of such parts must be made without delay.

(iii) For Protozoans, special techniques are needed for preservation as study -worthy material.

c. Cataloguing : Cataloguing of specimens or other samples preserved in a museum in a most easily referrable procedure must be kept updated as a compulsory house-keeping step.

The old practice of giving every specimen preserved a separate catalogue number specially for vertebrates where specimens are limited in number is replaced by the system of putting areawise collection of all kinds in one catalogue facilitating easy data retrieval and faunistic analysis.

For insect collections, where addition to the museum every year is sometimes of about a hundred thousand specimens, it is the practice to catalogue their accessions by lots with each lot consisting of a set of specimens from a given locality or region. Minimum data entered in cataloguing are : consecutive museum number (lot number), original field number, scientific name (at least generic name), sex, exact locality, date of collection and collector's name, remarks etc.

Type specimens in many, museums are catalogued together usually in a bound book serially from lower to higher taxa. In such cases, curators often have rather elaborate card-filling systems. With time, as collections in museums increased in size and quantity, the elaborate card-filling systems have been replaced by Electronic data Processing (EDP) comprised of several ways of employing computers in cataloguing.

d. Other aspects : Three things are noteworthy in these cases :

(i) Material Exchange : When definitely ascertained that a museum has enough of a species or subspecies samples, it is advisable to donate a part of the same to other repositories trying to procure similar excess stuff, in exchange, but of such taxa which are necessary.

(ii) Discarding useless material : improperly preserved or definitively labelled specimens are valueless. Curator must ensure such items in his stocks and get rid of them for better use of his infra-structure.

(iii) Loans : Researchers are in need of comparing labelled samples of a museum with their material of the same group under study and are often granted loans of museum specimens. Sometimes, specialists are sent unstudied material of a museum for their study, identification and status determination of those material on loan basis.

In every case of such loaning, terms and conditions should be made clear to both the parties and those should be honoured affecting the safety of the materials. It must be noted that the borrowing of museum samples by outside researcher or specialist is a need of the science of taxonomy, so there should not be any stringency except that necessary for the safety of the samples in point.

(D) Process of identification : Identification means to determine the kind of organism or given sample/specimen is and the process involves a group of special activities for correct appraisal. An identification scheme permits placement of an undertermined specimen in one of the taxa which together form a classification. One uses a few characters for identification (ideally a single diagnostic character) lining up the specimen along this or that track of identification. The process of identification is based on deductive reasoning.

Following are the main aspects in any identification process of stray/mass collection of animal samples/specimens :

(a) Sorting of collections : materials collected in study-trips and expeditions are first sorted and tentatively recognised by the broad groups (order and family level) they belong to. This is a sort of broad-level categorisation and is necessary for proper preservation on a long term basis with the prime compliance of cataloguing.

(b) Methods of identification : Museum personnel including the curator may take up their respective group of animals collected according to the specialization. The important methods used in identification process are :

(i) by comparing relevant data on descriptions and illustrations available in literature available as stray papers to monographic work on extensive revisionary basis.

(ii) by running through the identification keys available from literature or as handouts of the specialist of the subject.

(iii) by direct comparisons of material now under study with identified parallels of the same group loaned from outside and

(iv) by combining all the above-said methods for better result.

Concluding Remarks

The topics discussed and reviewed in this section are the practical work aspects of the science of taxonomy in the sense that the material for taxonomic studies composed of samples of animals in their different aspects of morpho-anatomy, behaviour, habit and habitat types, their biochemical structures and processes, their cytological and embryological make-up, this immature stages and life-cycles need to be preserved, processed and conserved as reference material for parallel futuristic studies in such authorised public centres which are meant exclusively for the same having both the physical and manpower compliments as required. What was originally a line-up arrangement and maintenance of dried samples of animals in series of wooden containers together with such additional samples in containers in liquid preservatives or processed and mounted permanently in microslides when very small in size or in isolated container or fitted in open space of the room, if of large size, became with time a more intricate and complex job as newer dimensions are being added to these aspects of taxonomy. Two relevant features are emphasized and briefly now as examples :

(a) Living culture collections : Collections of living cultures of microorganisms such as protozoan animals and animals of such other kinds in which morphology provides little clue to identify. Continuous maintenance of such cultures is highly expensive and needs specially skilled personnel for the purpose.

Cultures, however, are not regarded as type specimens.

(b) Collection of voucher specimens etc. : These are scores of 'additional' specimens which are consulted as supportive or furnishing as the base of research in other aspects of the tax on concerned. They seem to be 'left overs' of study but their conservation and availability for further study remain undeniable and hence well-funded repositories of animal collections try to obtain and maintain them with almost equal care.

The above two and the need to accommodate infrastructure for materials of Molecular Taxonomy besides replacing old methods by newer instrumentations and appliances including switch over to electronic data processing systems make the subject increasingly dependent on more skilled personnel and costlier infrastructure.

4.2 Taxonomic keys-different kinds of taxonomic keys, their merits and demerits.

Taxonomic keys are interlinked, condensed versions of select characters/features distinctive of included taxonomic units arranged such in continuation from start to end-point of a key with scientific names of those taxa at appropriate level of the key so that by using a key to a group of taxonomic units, those units may be neatly identified in a reasonably correct manner by locating the listed features as those exist in concerned units of neutral samples.

Taxonomic keys thus represent an important aspect of taxonomic activity and of taxonomic/systematic publications, Their references as synoptic tables which contain summarised version of many features are inappropriate.

Determination of zoological status (position) of any animal at all hierarchical levels of Zootaxonomy (from Phylum down to infra species level) is a basic exercise preliminary to any methodical interest or investigation centring the animal. This means identifyirg or establishing the identity of the animal as per scientific, norms which may be done by any or due combination of such **three** methods as (i) comparison of the animal/s (*i.e.* identifiable sample/s) with already identified specimens (done by experts) and preserved in Natural History Museums or other recognised repositories (at Zoological Survey of India, in India: U.S. National Museum, in the U.S.A.: British Museum of Natural History, London the U.K. etc.) – Direct Comparison Method, (ii) comparison by consulting published keys to identification and taxonomic descriptions including other available data relevant to the concerned animals, and (iii) taking help of the concerned experts for correct identification of the three above said methods, immediate and **approximately** correct identification may be made by the second method, specially by careful use of a good taxonomic key aided by supportive illustrations. By comparing a sample, feature by feature, with the key-couplets, all the non-agreeing ones can be eliminated and the only one with which it agrees can be arrived.

(I) Purpose, Properties and features : More important aspects here are –

(1) A taxonomic key is essentially a printed information retrieval system into which one puts information regarding a specimen to whatever level the key is designed to reach. It is a systematic frame-work for zoological classification with a sequence of classes at each level. Its construction is based on a thorough analysis of the stable and best possible taxonomic characters.

(2) The purpose of a key is to facilitate easy identification, almost as ready-reckoner for diagnosing identity by presenting contrastable characteristics in a series of alternative choices. A well constructed key also focusses on the natural relationships of the taxon units it covers.

(3) A taxonomic key must use minimum essential characters worded telegraphically but in nature easily comprehensible. Simple, line drawing illustrations for lucid presentation of critical features may add to the value of the keys.

(4) A good key for identification of animals is strictly dichotomous in nature, not having more than two alternatives at any point of differentiation in the key. Ideally, such alternatives are precise and sufficiently definite to identify a sample without a reference to other species. Each of these alternatives is called a segment or a 'lead' or a 'leg' and two 'segments' form a couplet. A dichotomous key is thus composed of couplets of contrasted characters *i.e.,* a two-way choice key and from start to end point, each of the two segments of a couplet leads to the next couplet in the key, either to just next or to subsequent couplet/s (all couplets in the key numbered from start). A segment in a couplet ends either in the name of the identified taxon or in the number of the couplet to which it may lead.

(5) If a segment of a couplet contains more than one characters, the same are stated in order of their relative importance. The most important character is stated first and

this forms the **primary character**, subsequent ones are the **secondary, tertiary characters** etc. Presence of additional contrasting characters in the couplets in a key makes it useful also for samples which may have part/s damaged with one or two characters missing. With only one character in a segment, the key is **monothtic** while with more than one character per segment, the key is a **polythetic key**.

(6) A monothetic, dichotomous key may be written for example as follows (*Dacus* is a genus of fruit fly insects, the key below included its species in India – example below shown in part to economise space) :

1. Wings opaque 2
–. Wings transparent 4
2. Antenna serrate 3
–. Antenna filiform .... *Dacus minuta*

N.B. First segment of the first couplet ends in a number meaning that this particular character exists not in a single species but in a cluster of more than one species, as is the case with the other segment, Number 2 couplet (leading from first segment of first couplet) is then analysed and it is found that while its second segment leads to one single species, its first segment leads to a cluster of species which is numbered 3 and analysed in full to species in couplet no. 3 (a segment taken up subsequently for analysis thus put under a couplet no. in the key). The key then continues with second segment which ends in number 4 and becomes couplet no. 4 for further analyse. Use of a dash and dot (–.) prefix to second segment, is a style with some while some prefer to leave the concerned space blank, unmarked).

(7) In many old time keys including some in recent times, one may come across 3 or 4 segments forming a couplet in an otherwise dichotomous key. This is specially the case while a principal contrasting character in the taxa mass of the key shows differences in more than two ways. Instead of braking this by using extra couplets, some prefer to lump it into one couplet as follows :

Sensu lato* dichotomous** (key to Indian species of genus ***Culicoides biting midge insects, based on female samples only)

1. Functional spematheca one only 2
–. Functional spermatheca two only 4
–. Functional spermatheca three in number 40
2. – (further analysis not shown here) 3
–. ________________ .... species A

The *sensu stricto* dichotomous arrangement of the above is as follows:-

1. Functional spermatheca one only 2

_. Functional spermatheca more than one in number.4

2. ______________________________..............3

_. ______________________________..............Species A

3. ______________________________..............Species B

_. ______________________________..............Species C

4. Functional spermatheca two only 5

_. Functional spermatheca three in number................40

(further analysis not shown; Long dash mark stands for the character of the segment, unstated here for convenience)

(8) A type of Tabular key which involves simultaneous appraisal of a small set of characters at each level is also in point. Though not strictly dichotomous this type is useful for 'incomplete' specimens (damaged/mutilated when some characters may be missing). An example is as follows (Part key to species of a genus of Calcutta ants) :

3x	1x	2x
3x	1x	2y
3x	1y	4x
3x	1y	4y
3y		

[Explanation of indices in the table (1x, 1y, 2x, 2y, 3x, 3y, 4x, & 4y are used in lieu of species names) :

1x = specimen with stout, conical mandibles

1y = ... with long, linear & slender mandibles

2x = ... with 2- segmented maxillary palp

2y = ... with 3- segmented maxillary palp

3x = ... with antenna of 10 or lesser no of segments

3y = ... with antenna of 11 or more no of segments

4x = ... with pectinate claws in legs

4y = ... with simple claws in legs]

(9) As opposed to dichotomous type keys, are the **Multiple-Entry Keys** or the **Polyclades** whose recent versions are in the form of punch card Indexing. A card with name and character of a taxon bears a hole at a particular point of the card. Dissimilar taxa have cards with dissimilar features and holes at dissimilar points. While similar cards tie up together, one that is dissimilar can not be tied to it thus showing its difference.

(II) Type of Keys : More important taxonomic keys are—(1) Indented Key, (2) Non-Bracketed Key, (3) Bracketed Key, (4) Spider Key, (5) Grouped-type Key, (6) Combination Key, (7) Pictorial Key, (8) Branching type Key, (9) Circular Key and (10) Box-Type Key. An another view of these keys is as follows :

(I) Indented Key : Couplets are indented from left-hand margin of the page in such a way as to show their relative importance at a glance. Thus, two or more members of primary couplets, are nearmost to left-hand margin, the secondary couplet is indented after leaving 4 or 5 species, the tertiary with equal number of species beyond the secondary and so on.

An Indented key has the advantage that the relationship of the various divisions is apparent to the eye from the key itself. It has the disadvantage as the alternatives are widely separated so that it may be used for short keys, Keys to higher taxa or comparative keys. *e.g.* (by a sketchy key) :

A. Wings mostly hyaline

  B. Costa swollen at tip

    C. Scutellar bristles 1 pair ..... *D. cucurbitae*

    CC. Scutellar bristles 2 pair ..... *D. tau*

  BB. Costa not swollen at tip

    C. ....

    CC. ....

AA. Wings mostly opaque

  B. ....

    C. ....

    CC. ....

  BB. ....

    C. ....

    CC. ....

N.B. Features for B to CC under A or under AA to CC being same hence not repeated for AA to CC), Key to 8 species (last six indicated by a short line and not named to **avoid burden for a learner)**

(2) Non-Bracketed Key : Typically dichotomous in nature with alternative features side by side in a couplet for ready comparison, such a key is more economical in space because it is not indented. Specimens to be identified can run through this key forward easily though a backward run across this type of key is slightly inconvenient. Another disadvan-tage is-relationship of the divisions not apparent. *e.g.,*

1. Wings mostly hayaline 2
_. Wings mostly opaque 5
2. costa swollen at tip 3
_. Costa not swollen or tip 3
3. Scutellar bristbes 1 pair ....*D. cucurbitac*
_. Scutellar bristbes 2 pari ....*D. tau*
4. Thorax with median yellow stripe ....*D. diversus*
_. Thorox without median stripe................................*D. dorsalis*
5. ....
_. ....

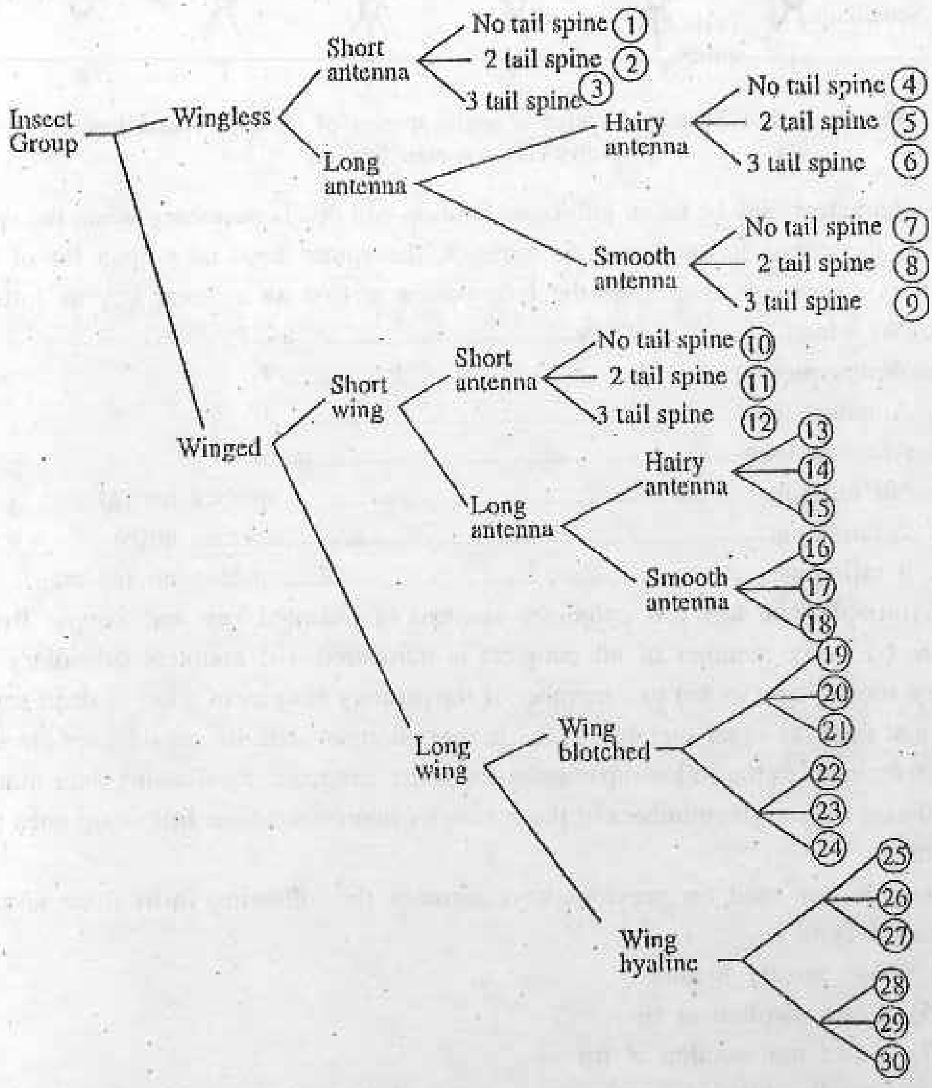
(3) Bracketed Key : Similar to the simple, non bracket key expect that a couplet's continuation is shown here distinctly in the key by inserting the number of the couplet whence the said couplet originates in parentheses just after its own number. One can move both forward and backward through such a key which is said to be the best of all and most used by modern taxonomists, specially when a key is very long covering many units.

Thus, it is to be noted, if a certain couplet no., in parentheses, it is a simple bracket key; if not, it is a non-bracket key. Example of bracket key is as follows :

1. wings mostly hyaline 2
_. Wings mostly opaque..5
2. (1). Costa swollen at tip 3
_. Costa not swollen at tip...4
3. (2). Scutellum bristles 1 pair .... *D. cucurbitae*
_. Scutellum bristles 2 pair .... *D. tau,* etc..........

(4) Spider Key : For gross grouping of species etc., and as a precursor to the preparation of the dichotomous bracket keys, the taxonomists often prepare such basic keys one example of which in brief is stated now—

The, 'Insert group' referred to as in the key represents a hypothetical genus and thirty-end points on right–hand side of the key represents thirty species of that genus, the sorting from genus to species being done on basis of 6 morphological features as—(i) Presence or absence of wings, (ii) Wing short or long (iii) Wing blotched or hyaline, (iv) Antenna short or long, (v) Antenna smooth or hairy, and (vi) Tail spine absent or present (2-3 per individual); a sketchy pictorial presentation of these features is as follows :



N.B. encircled figures in the key stand for species (not named to avoid burden for a learner but marked by numbers, 1 to 8 illustrated in fig 4, as a-h).

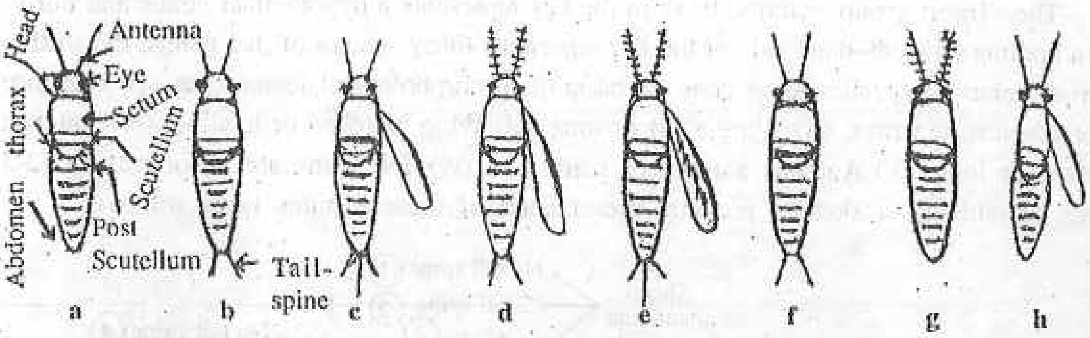


Figure 4a-h : Sketchy pictures of eight species of closely related insects (hypothetical) for classification.

More characters may be taken into consideration and this is necessary when the species number in the genus is too large. As a result, the spider keys take up a lot of room and so it is customary to arrange the information at first as a linear key as follows :

1a. No wings 2
1b. Wings present 7
2a. Antenna short... 3
2b. Antenna long 4
3a. No tail-spine .... species no (a)
3b. 2 tail-spine .... species no(b)
3c. 3 tail-spine .... species no (c) etc.

(5) Grouped-Type key : It combines element of indented key and Simple Bracket key; Here (i) every member of all couplets is numbered, (ii) couplets subsidiary (i.e., secondary, tertiary and so on) to a member of the primary couplet of a key is dealt serially under it and then the other member of the primary couplet with its subsidiaries are dealt, and (iii) references to the follow-up couplet-members are made by showing their numbers in parentheses next to the numbers of those couplet-members whose follow-up ones those happen to be.

The sample key used for previous keys assumes the following form when arranged as a grouped-Type key :

1. (8) Wings mostly hyaline
2. (4,5). Costa swollen at tip
3. (6,7). Costa not swollen at tip
4. —— Scutellar bristles 1 pair .... *D. Cucurbitae*
5. ____ Scutellar bristles 2 pairs .... *D. Tau*

etc.,...

8. (9). Wings mostly opaque

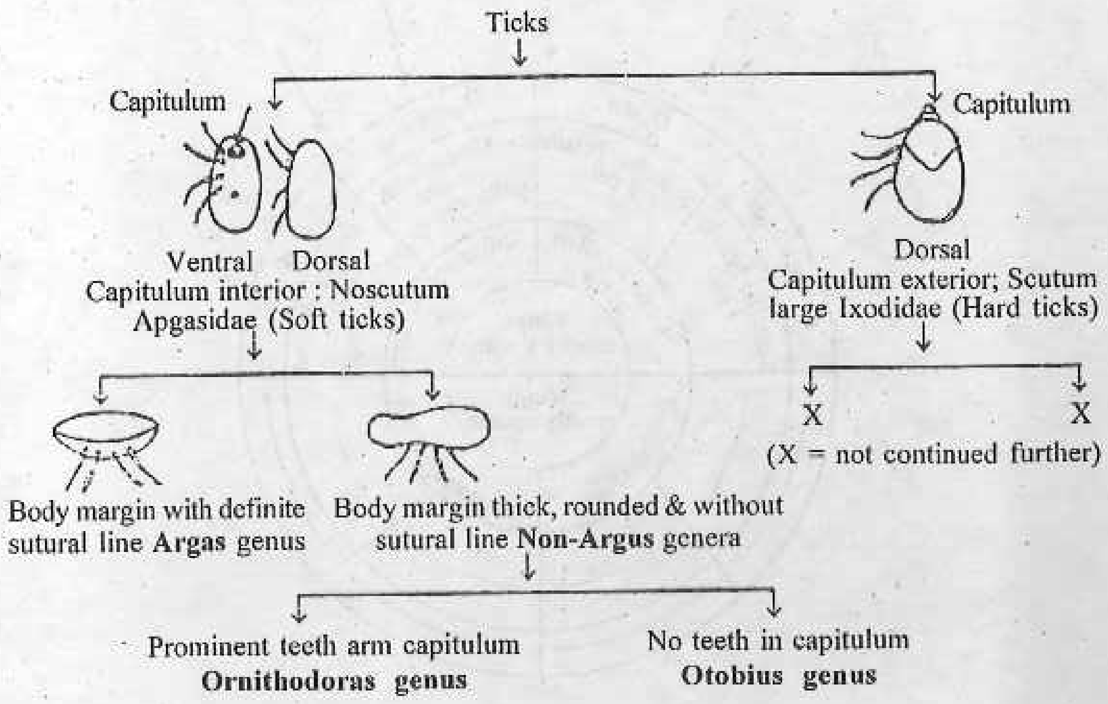
9. (11,12) Wings with stripes
10. (13,14) Wings reticulate
etc., ...

(6) Combination Key : This is prepared basing on good features of Indented Key, Simple Non-Bracket key and Grouped-Type key. *e.g.* :

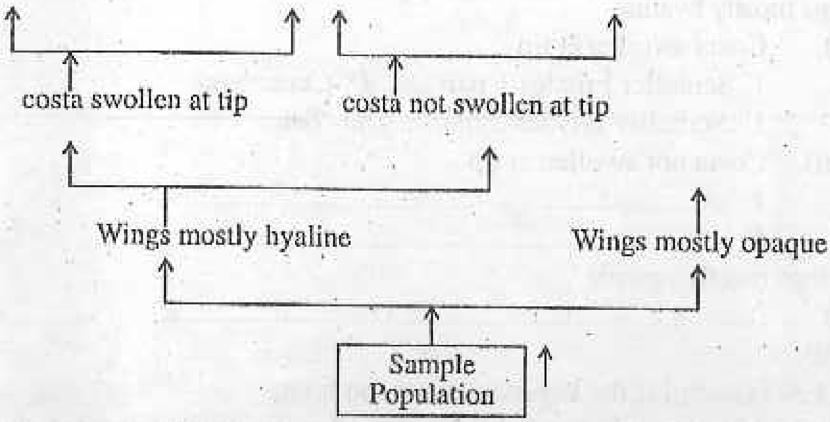
A. Wings mostly byaline
  B. Costa swollen at tip
    1. Scuteller bristles 1 pair ...... *D. Cucurbitae*
    1'. Scuteller bristles 2 pair ...... *D. Tau*
  BB. Costa not swollen at tip
    1. ....
    1'. ....
AA. Wings mostly opaque
  B. ....
  BB. ....

Such a key is useful if the key-size as not too long.

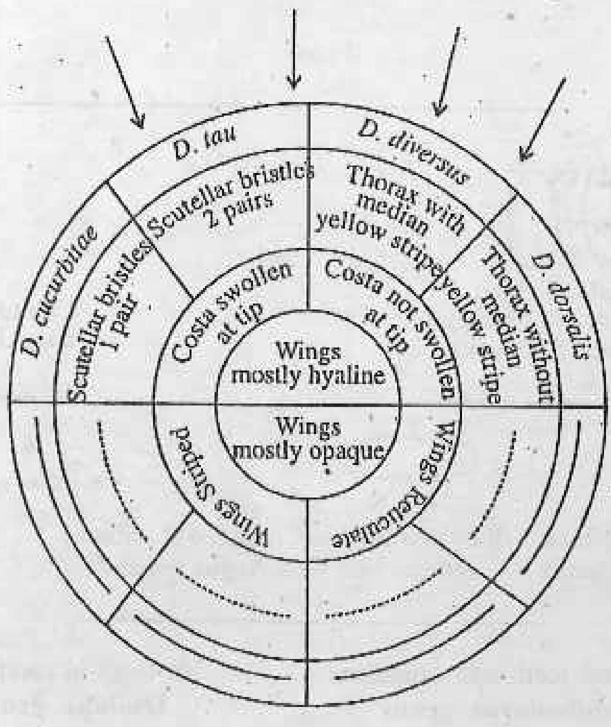
(7) Pictorial Key : This key helps in easy identification of species showing their comparative features (not number) by illustrations in dichotomous plan. It is especially meant for field-workers and non-taxonomists, and medical importance being widely used for pests of agro-veterinary and medical importance. eg. (with ticks)



(8) **Branching Type Key :** Though on dichotomous plan, features are not numbered here. It is an unorthodox type, easy to use for field workers as pictorial key. It is usable with small-size groups—



(9) **Circular Key :** This is also suitable for field workers to cover up works on small-sized samples. *e.g.* (cited below)



(10) Box type key : It has a semblance with the branching-Type key and is quite useful for field workers, *e.g.*,

		D. cucurbitae	*D. tau*				
Thorax with median stripe	Thorax without median stripe	1 pair scutellar bristles	2 pairs scutellar bristles	Scutellum with 5 black spots	Scutellum with 4 black spots	3 hyaline spots in wing's posterior margin	5 hyaline spots in wing's posterior margin
Costa not swollen at tip		Costa swollen at tip		Wings with stripes		Wings reticulate	
Wings mostly hyaline				Wings mostly opaque			
SAMPLE POPULATION							

(III) Computerized key Constructs

(1) Construction of good keys needs shuffling of many character to achieve appropriate combination for separating the taxal unit in a cluster of the same. With accumulation of too many characters and taxal units through newer techniques and letter perecption and instrumentation, manual manipulation for working out clearer taxonomic pictures in respect of sample identification and classification is time-consuming and potentially error-prone. Computerized exercises in these aspects offer a much-sought better method specially for the case with which even an outsized taxonomic construct can be prepared and correction or change of the same later on may be made as required.

(2) Computerization of key-construct at its simplest is composed of **taxon × character data matrix,** its improved version being the **DELTA (Description Language for Taxonomy)** system used in all recent key packages for taxonomic identification.

(3) All key-construct programmes in computerised study programmes are done by scanning all relevant characters at every decision level and determining which one fits best the programmes' prescribed sectional algorithms. In the simplest such a case, the selection parameter (s) is solely ascertained by the equation of the taxan-units that would be forked using that parameter which in turn would reduce key-length ($s=n_1 n_2$; n_1, n_2=taxon-units) due to split caused by that parameter.

(4) Recent modification is in the Interactive Computerized Programme (ICP) which involves offering computer's choice of best character at every stage of key-construction with operator's ability to accept or override the same by something different based on his expertise.

(5) Numerous computer-based key-construction packages have been developed with more on the way. For dichotomous key, packages like **KEY, GENKEY** and for polyclades packages like **CABIKEY, CDKEY** are more recent ones.

(IV) Methods in construction of keys

(1) Construction of keys is a painstaking arduous and time-consuming task even for an expert with effective infrastructures as the work involves judicious selection of most useful and most clearly diagnostic characters either from his own study of material or from data available in literature of others' work which he may have means to directly verify or not. In any case, he can be more sure of his collection and selection of character of material covering which he is constructing the key, if he is able to examine the 'types' or the authentic samples of the material in point. He needs to give extra effort and time for those samples.

(2) The constructor of a key must try hard to select such character for his key which will apply similarly to all individuals of a population avoiding age or gender related ones as far as possible. Ideal characters are also **absolute** (two versus one or so; located at top or bottom etc.), **external** (thus directly visible and constant. Sharply contrasts characters with perceptible gradations are also useful but here, one must be careful to use them in the key without the scope of ambiginity (**e.g.** smaller or larger in size, **darker** or lighter) and **overlapping** features (using length 10 to 18 mm versus wing 16 to 22 mm etc.)

(3) In case of taxonomic keys, sorting out right, stable characters with 'meaningful' difference within the populations representing the taxon level to be keyed is the first step. These characters covering different structures and aspects must then by arranged taxon-unit wise (say, species-wise or genuswise etc. and included in the key to be prepared) in a tabular form as follows in part :—

(a) **Example 1 :**

Key to important Indian species (♀ ♀) **Culicoides** genus (Diptera), haematophagous in females only in parr :—

Name of species	Characters from structures and others aspects averaged from species samples			
	Wing surface	Scutal shade	Hind tibial comb	functional spermathecae
1. anophelis	marked by pale and dark areas, apex narroly pale; II radial cell (= r.c.) broadly large	yellowish brown with dark streaks	of 4 spenes; II from spur longest	3; ovoid-subspherical; just unequal in size
2. *brevitarsis*	interconnected pale areas in smoky surface; II r.c. small	pruinose gray with two sublateral dark spots	of 5 spines; I from spur longest	2; ovoid, unequal
3. *innoxius*	circular pale spots in smoky surface; II r.c. narrowly large	dark reddish brown	of 6 spines; II from spur longest	-do-
4. *macfiei*	similar to pale-smoky shading of *palpifer*, apex here narrowly pale; II r.c. broadly large	dark brown	of 4 spines; II from spur longest	3; oval to ovoidal; unequal as in palpifer
5. *oxystoma*	pale spots mostly circular even those at anterior margin & the one at apical angle bilobed characteristically; radial cells absent	bright gray pruinose with brown punctures arrnged in 3 vertical bands	of 4 spines; I from spur longest	2; pyriform, subequal

6. *palpifer*	2 pale spots at anterior margin other pale spots mostly interconnected; apex very broadly pale; II r.c. broadly large	pale yellow	of 4 spines; II from spur longest	3; middle one very large, subrectangular; other two small, ovoid, subequal
7. *peregrinus*	pale spots below upper branch of radius small, circular, that at apical angle bilobed & one preceding it large, conical covering most of small II r.c.	dark brown with two lateral darker bands & two such subcaudal spots	of 6 spines; II from spur longest	2; elongate oval; just unequal
8. *raripalpis*	same as in *palpifer* except that apex not pale; II r.c. broadly large	dark brown	of 4 spines; II from spur longest	3; ovoidal unequal as in *palpifer*

Such tables can include more species and more characters if the relevant key is prepared to cover more species. For preparing a key only to adult males or only to adult females of the species tables as above should than be constructed with characters common in both the sexes others applicable wither to males or to females. Differences in 6 important characters (first five common to both males and females, last one only to females) may be used in more than way to prepare a non-bracket type simple, dichotomous key to the eight species concerned one of which is as follows : —

1. Hind tibial comb of 4 spines 2
   Hind tibial comb of 5 or more spines 6

2. First spine from spur in hind tibial comb longest. Radius unbrached, ... *C. oxystoma*

–. Second spine from spur in hind tibial comb longest. Second radial cell, broadly large 3

3. Scutum dark brown 4

–. scutum shaded otherwise – pale yellow to yellowish brown......... 5

4. Wing apex clearly pale though narrowly .... ***C. macfiei***

–. Wing apex not pale, smoky .... ***C. raripalpis***

5. Scutum shaded pale yellow. Wing apex Very broadly pale .... ***C. palpifer***

–. Scutum shaded yellowish brown with dark streaks. Wing apex narrowly pale...***C. anophelis***

6. Hind tibial comb of 5 spines...........................***C. brevitarsis***

–. Hind tibial comb of 6 spines 7

7. Pale spot at apical angle of wing circular, never touching wing margin. Dark reddish brown scutum .... ***C. innoxious***

–. Pale spot at apicla angle of wing bilobed and broadly touches wing margin, Sentum dark brown with two lateral darker bands and two such subcaudal spots .... ***C. peregrinus***

Since in such keys, emphasis is given on characters which are better contrasted, the selection obviously is some what random in nature. This results after in grouping or clustering of less related species (or taxon-units together and the resultant key though of a much utility value fails to reflect on the photogenic aspects correctly. In the sample key furnished above, species with three functional sparmathecal are evolutionar primitive than those with two. The species ***C. oxystoma*** is clustered in first segment of complete no. 1 with primitive species like ***anophelis, macfiei, palpifer*** and ***raripalpis*** as ***C. oxystoma*** agrees with these four in having four spines in hind tibial comb in contrast to five or six spines in the same of other advanced species like ***brevitarsis, innoxius*** and ***peregrinus***.

(b) Example 2 : Key to seven common ants (worker caste only, ♀) covering species to subfamily taxon each belongs to in bracket type dichotomous mode for practice-identification work,

Serial/Sample no.	Subfamily status	Genus-species status (Author's name)
1	Formicinae	*Oecophylla smaragdina* Fabricius (Fig.6)
2	Formicinae	*Camponotus compressus* Fabricius (Fig.4)

3	Formicinae	*Camponotus confudi* Forel (Fig.5)
4	Ponerinae	*Diacamma vegans* Smith (Fig.3)
5	Myrmecinae	*Solenopsis geminata* Fabricius (Fig.2)
6	Myrmeciinae	*Solenopsis mtens* Bingham (Fig.1)
7	Pseudomyrmecinae	*Tetraponera rufonigra* Jerd. (Fig.7)

The proposed key to the above-listed species may now be presented as follows ((X) in the key in all cases means the cluster not further pursued because of no necessity now) :-

1. Pedicel of one lobe/node/segment 2

–. Pedicel of two lobes 10

2(1). First gastral segment demarcated from the second gastral sement by a constriction; sting developed, exserted. First gastral segment with all its surface striation marks in concentric arches and with two spines thick at base and directed backwards in its posterior aspect .... **Subfamily Ponerinae** (3)

–. No constriction between first two gastral segments; sting vestigial .... **Subfamily Formicinae** (5)

3(2). Antennal carinae cover antennal bases at least in part. Pedicel free with flexible joints; claws simple; mandibles articulated wide apart at lateral angles. Posterior margin of clypeus defined by a suture. Pronotum with out teeth or spines. Node of pedicel bispinous posteriorly. Claws simple .... Genus *Diacamma* (4)

–. Above-said features structured otherwise .... (X)

4(3). Pronotum with transversely arched surface striae arranged more or less in anteriorly concentric manner. First gastral segment striate and with all its striations in concentric arches. Two spines at posterior end of pedicel thick at base and directed backwards .... *Diacamma vegans*

–. Above-said features structured otherwise .... (X)

5(2). Mandibles long, linear, cylindrical and bent at right angles being dentate at apex but denticulate on inner margin .... (X)

–. Mandibles otherwise, not as above 6

6(5). Antenna 11-segmented; metanotum and node of pedicel bi-spinose or bidentate .... (X)

–. Antenna 12-segmented; metanotum and node of pedicel neither bi-spinose nor bidentate .... 8 .

7(6). Maxillary palp 5-segmented. Mandible long with very broad masticatory margin, the apical tooth acute; curved; thorax, thorax, pedicel and Legs are all elongate but abdomen short, oval; body colour rusty red to yellowish red .... Genus *Oecophylta*: and sample (no. 1) is .... *O. smaragdina*

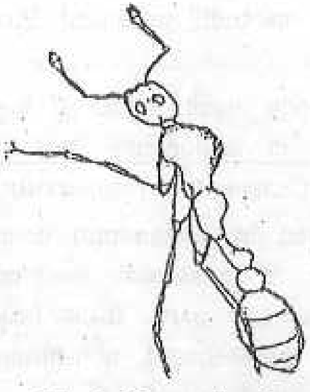


Fig. 1 Solenopsis nitens

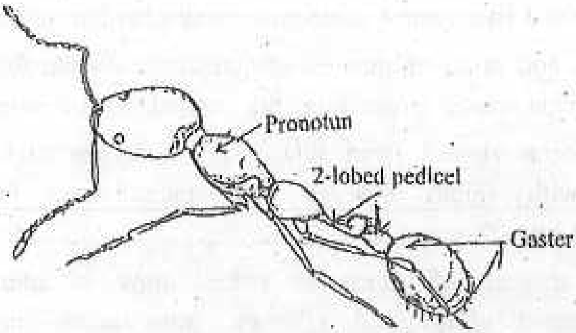


Fig. 2 Solenopsiis geminato

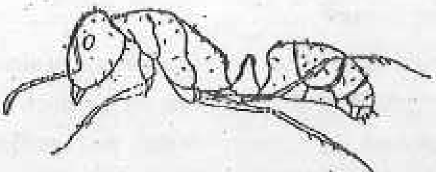


Fig. 4 Camponotus compressus

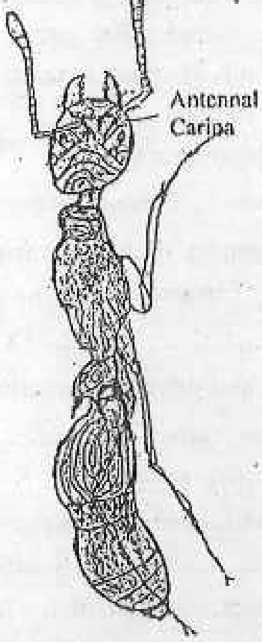


Fig. 3 : Diacamma vagans

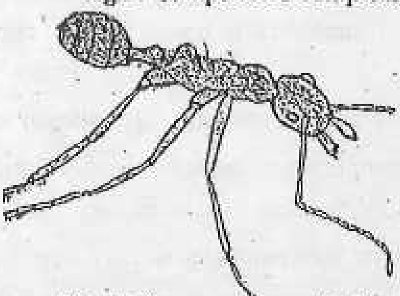


Fig. 5 Camponotus confucii

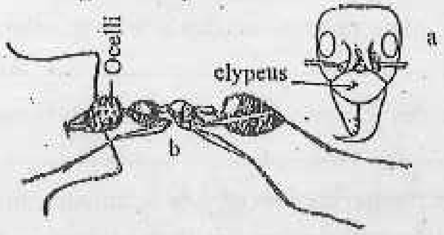


Fig. 6 Oecophylla smaragdina

Fig. 7 Tetraponera rufonigra

Fig. 1-7 : Outline drawing (free hand) of seven species of ants most common in West Bengal (caste).

-. Maxillary Palp 6-segmented; other features not as above (of the first segment of this couplet ..... (X)

-. Maxillary palp 6-segmented. Other featuers not as above 8

8(6). Thorax and node of pedicel smooth, never dentate/spinous/with angles markedly produced. Basal two gastral segments equal/subequal in length ... Genus *Camponotus* (9)

-. Thorx and node of pedicel spinous/dentate/with angles markedly produced. First gastral segment much larger than the second gastral segment .... (X)

9(8). Thorax viewed from side forms a regular arch. Body black; tibiae of legs prismatic with spines beneath and sparse erect hairs in abdomen's surface; body-length over 9 mm. .... *Camponotus compressus*

-. Regular arch of thorax as stated above is interrupted by metanotum being raised, rounded above and gibbose. Anter-lateral angles of pronotum rounded, not dentate; soft-body grayish black with antennae, legs and parts from head to pedicel all long but abdomen rather small, condensed; quick-footed, non-biting; body length under 9 mm .... *Camponotus confudi*

10(1). Head with visible ocelli; clypeus not projecting between bases of antennae each of which is 12-segmented. Second lobe of pedicel and gaster black, legs orange red and rest of body brick-red iin colour; thorax and pedicel long, slender but gaster elongate oval. Tibial spurs of mid- and hind-legs pectinate *i.e.,* comb-like; no longish mass of hairs (= psammophore) underneath head-capsule; claws toothed .... Genus *Tetraponera* (11)

-. Above-said features are structurally opposite in nature ... Genus *Solenopsis* (12)

11(10). Ocelli *i.e.,* simple eyes present in mid-dorsal aspect of head-capsule .... *Tetraponera rufonigra*

Ocelli totally absent in head-capsule... (X)

12(10). Body-length over 3 mm.; body smooth, polished and of pale to reddish yellow in colour while abdomen is blackish brown. Antennae rather long .... *Solenopsis gemlnata*

-. Body-length under 2 mm.; body dark reddish brown with head and thorax smoorth, highy polished .... *Solenopsis nitens*

(4) With rapid computerization of key – construction packages and their continuous improvement, question arises as to the dependence on printed – type keys used so long everywhere unilaterally. For laboratory – based situations such as identifying micro organizations, computerized key – packages are more useful than printed key – works as the former permit wider searching in a short time with less effort. But for vast majority of cases of identifying macroorganisms, printed key works are still found more useful

than their packages. Till all round computerized keys using high density storage media like computer disease are available more widely and in user – friendly application modes printed key – works will continue to dominate though it is not difficult to guess that they will be replaced by their computerized form with time totally and universally covering even on the spot identification in field situation. A significant effort in this respect is to computerize all specimens in a museum or a collection or even all museums and all collections through boarding of specimens for electronic storage of their complete data an dissemination of the same for wider use and application via satellite communication system.

(V) Merits and Demerits—Concluding Remarks :

(A) Merits :—

(1) Devising key to species, genus or other taxon level populations is one of the pressing needs to scientifically handle the task of identification in a more or less easier and correct way than by laborious matching devices either with the volume of descriptive data or with the labelled, preserved samples. As new spe ies, genius an infraspecies taxa come to light from time to time, the need for key–ba ed facilit, occupied the centre -stage of taxonomic activity.

(2) For most groups of animals, the most popular and effective means of identification an respect of systematic position has been through the use of taxonomic keys, specially the dichotomous keys, containing the series of essential characters that permit easy separation as one works through them which are in fact point by point verifiable systems having title or no opinion factor and operable even by a nontechnical person with little practice.

(3) Keys form an essential part of taxonomic proc lures as they represent the concise and precise presentation of taxonomic findings.

(4) Good keys consulted by the experts can yield correct diagnosis while a non-expert can organise his non-taxonomic study of his target animals identify them basing on same and can have confirmation later on of his identifications from an expert. Taxonomic keys have thus a very wide application in the act of identifying the animal samples from nature being reliable tools both for the experts and non-experts. For rapid recognition of field samples *in situ*, some types of keys (pictorial keys, circulars, keys, spider keys etc.) are indeed very useful facilitating any emergency decision about pestiferous animals for control programmes etc.

(B) Demerits :—

(1) Taxonomic keys, however concise and precise are highly technical having respective terminologies and stylizations differing widely from group to group. Some efforts and

basic studies are necessary to understand and use the language of the taxonomic keys of a group by a non-expert worker.

Authoritative identification can always be obtained if it is done by the concerned expert of considerable experience and repute. A non-expert with some strains can certainly achieve at least a first - hand identification of his samples working through a relevant taxonomic key even down to species in some cases. For confirmation, he should refer his material and inferences to the expert conversant with the taxonomy of his materials.

(2) Taxonomic keys though an important item in animal identification which again is the prime prerequisite for any scientific investigation with the animals have not been attended upon so substantially specially in respect of invertebrates barring some stray groups of high economic importance as those along with comprehensive studies of related taxonomic aspects deserve. To simplify the point in view, it may be said that to be an expert of the systematics of single family of insects of any area, of a country or of a realism, one need lifetime association and study with adequate infrastructure facility at his disposal. Any deficiency here means, less precise keys whose abundance specially from developing countries add to the complication of key-based analysis. Revisions of past works and attention to move critical aspects are lacking causing further difficulty.

(3) With maximum emphasis on utilarian subjects in recent times, much-needed attention on such basic subjects as taxonomy of animals is neglected it is undesirable that updated and move comprehensive knowledge specially of fauna of developing countries are essential for proper appraisal of the final; biodiversity. Thus the drawbacks of the taxonomic keys of animals, available or not, continue to be treated as unsatisfactory and deficient barring a limited number of thoroughly worked out and updated keys published by the reputed scholars and experts mainly from the developed countries.

(4) Taxonomic, keys which are carefully prepared are indeed of good use so far determination of identity of the taxa involved are concerned.

But such keys are essentially built upon a process of segregation in whatever combination of characters the process brings out the differences of the segregated units most prominently. Thus, these keys are utilarian and not necessarily truly reflective of correct phylogenetic closeness and relationship of the units.

A comparison in the relative efficacy of different types of taxonomic keys merits a reference. All contrived keys are basically dichotomous in nature and each one is indeed effective in identifying the target samples. However, a qualitative difference in them can be made out as follows :

(a) Keys of unlimited character range : Indented keys, bracket and non-bracket type keys, and grouped type and combination type of dichotomous keys, characters from all aspects of target animals are used here which often become too extended. These are effectively usable with basic expertise in the subject.

(b) Keys of limited characters range : Spider keys, pictorial keys, branching type keys, circular keys and box type keys, these involve limited tax on units in a key and very limited type characters are used to prepare them. These are simple, easy to follow a very useful for on the spot identification in field conditions even by laymen.

(C) Concluding remarks :—

(1) Taxonomic keys are devised with core data on salient characters of target groups of animals. Such a key covers different units of a particular taxon level (family level to subspecies level) of a country or of a zone in view, with selected characters interwoven such as to form a running series of couplets, each of two segments of contrasting characters and each segment leading either to one single unit of animals (i.e., a single species etc.,) or to one cluster of such units (shown by a number) which is put into subsequent series of the key till one single unit by a follow-up segment is reached.

(2) To arrive at correct identification basing on taxonomic keys, it must be ensured that the user is conversant with the terms used in the key consulted and also that the key is a 'good' one being prepared in clear format and worded such as leaving no scope for ambiguity. A 'bad' key may cause defective identification but a good; key cannot be held responsible for the same.

(3) In view of remarkable progress in culling characters from different aspects of animal groups aided by complex technical applications, there is hardly any dearth of 'worthy' characters being used in the keys. But it is obvious that lesser the use of characters called through complex technical processes, the use of key is easier. Therefore, the stress on 'gross' features which are easily cullable should not be replaced by complex 'fine' features though none should be minimised. Keys prepared for a group of animals by using morphotaxonomic, cytotaxonomic, biochemical and molecular taxonomic features etc. are not mutually antagonistic but are, in fact, complementary simpler ones should be used as far as possible for routine purposes leaving the complex ones for intricate cases.

(4) Computer application in preparation of keys and identification of target samples are being increasingly attended upon with time. Handling of vast amount of data and their processing for prompt retrieval and searching yielding correct results in shortest possible time show a great potential for a rapid identification work of a sample by using this modern marvel of instruments. There is perhaps no doubt that with more development of computer applications in the field of animal taxonomy, the printed formats which we consult now for identification work may be replaced in full by the computerized discs of key packages. However, the principles of segregation and marking of animals at different

taxon levels, perfected so far since Linnaeus' time, will continue to be the basis of concerned exercises till the science of animal classification rests on existing concepts of speciation.

4.3 Systematic Publication—Different Kinds of Publications

Publication form an essential tool for taxonomy—The science of classification of animals and other organisers, as for other branches of human knowledge. They make possible the wider circulation of knowledge created by individual/collective effort in any place at any point of time which then may be used for any purpose and may provide direction for further efforts in future. People capable of creating knowledge have an obligation "to bring to light their results" through publications.

Taxonomic publications may be of several kinds, ranging from a short description of a new taxon to lengthey monography or handbooks of several volumes covering identification manuals as well as revisionary works and new classifications. Some stress on nomenclatural aspects, other an life history, distribution or illustration. Many different titles are used sing such **key-words** as, **synopsis, review, revision, catalogue, monograph, atlas, fauna, manual, hand book, field guide** etc. major ones may be briefly explained as follows :

(A) Kinds of Publications :

(a) **Description of new taxa :** There are ordinary description papers of new species, subspecies, gensla etc. Such stray publication are obviously not very comprehensive and do not serve much purpose/unless the taxon units treated in them were of well-known groups or needed an identity due to relevance to economic importance or any biological work.

(b) **Synopses and Reviews :** Consist of brief summaries of current toxonomic knowledge of a group. Newe taxa are not included in these. Such works actually provide in one cover all scattered information to considerable advantage of a working toxanomist. e.g. a paper titled or "Synopses of Nearitic Ephydridae", published in pp. 151-227 of the journal, **Trans. American Ent. Soc., 1954.**

(c) **Taxonomic Revisions :** Such works consist of a mix up study of all previous knowledge and those discovered as new during the study undertaken generally covering a perticular germs; somewhat monograph type in nature.

e.g., Revision of the oriented species of *Stilobezzia* kieffer (Diptera : Ceratopagonidae), of 148 pages in the U.S. National Museum Belletin no. 283 published by Smithsomian Just. Press, 1968.

(d) Monographs : These are the most complete systematic publications involving full systematic treatment of all species and subspecies etc., plus a through treatment of comperative structure and biology with data on life-history, immature stages, distribution etc. e.g. paper titled, "Monograph of Cimicidae (Hemiptera : Heteroptera)", of 585 pages, 1966; Thomas Say Foundation publication. No. 7.

(e) Faunal Studies : These are detailed studies of the fauna of a single region, being restricted to a single group of animals, by a specialist of long standing of that group. e.g. Fauna of British India—printed in many volumes covering different groups of animals of Indian subcontinent since 1888, and published by the Zoological Survey of India which continue to update those pesides covering unstudied animal groups in changed titles.

(f) Atlases : These furnish comparative characterd of animals in picture form which are semi-diagrammatic drawings or photographic plates. *e.g.* "Mosquito Atlas", of 44 pages, published by American Entorological Society, 1943.

(g) Catalogues and Check-lists : A Catalogue is essentially an index to published taxa arranged such as to provide a complete series of references for both zoological and nomenclateral purposes.

A catalogue contains the following :-

(i) Original description reference,

(ii) Later references,

(iii) Synonyms with references,

(iv) Range, type-lotality (also its repository),

(v) Type of the genus,

(vi) Miscellaneous pertinent data (like biology, hosts, if any, zoogeography etc.)

Taxa are usually listed alphabetically in a catalogue which is compilation work by an experienced specialist having comprehensive data-base and infrastructure at his disposal. e.g., "Catalogue of the Diptera of the Oriental Region, vol. 1-II.....",—published by the University of Hawai Press, Honolule, U.S.A.

A check-list provides a convenient source of reference for the correct names of specimens and the arrangement of collections. A list of names is a check-list if a careful distinction is made within it between valid names and synonymd and a critically made check-list forms a primary zoological literature."

Check-list are more usefull in better known groups of animals like birds mammals, butterflies etc.

e.g., Check-list of the Lepidoptera of Canada and the United States of America, part I-II, of 177 pages.

(h) Miscellaneous :

(i) Field guides : These are literature made simple for easy use by non-taxonomists to identify the common animals in the field. Some are specially designed in the forms of pamphlets for periodical check of the pests in an area.

(ii) Manuals : Like field-guides, these are also published in simple form including key characters for common species of animals for use of students or layman. Manuals differ as assorted animal forms are included in then [e.g. A manual of the common invertebrats animals (exclusive of insects) by H.S. Pratt 1951 of 854 pp. McGraw Hill Company, N.Y. publication].

(iii) Handbooks : The term 'Handbook' is used for field guides, manuals and the likes (e.g. Handbook of Salmaners of 555 pages, cornell Univ. Pres publication, 1949).

A 'Handbook' is also called sometimes as a 'Treatise'.

(B) Major Features of Taxonomic Publications (Preparation of taxonomic publication) :

Most taxonomic publications contain a set of major components which deserve thorough discussion. It is only in taxonomy that oldest works even remain valuable of consulted universally. Names of descriptions known since Linnaeus (1758) are still of same value components and their formats of taxon publications are as follows :

(a) **Description :** It is the main body of all published works. Its main aim to is to aid in the subsequent recognition of taxon involved. Mainly there are two kinds of description—those of essential characters forming **Diagnosis**, and those of general characters forming **General Description.**

Diagnosis : It consists of brief listing of the most important characters or character combinations peculiar to the given taxon and by which it may be differentiated from other similar or closely related ones (= Differential Diagnosis).

General Desctiption : More or less a complete account of all the characters of the taxon providing also information of interest to othre besides taxonomists. Description published while proposing a new taxon (species, genus etc.) is called the **original description.** It is most important in relation to that taxon as it has two primary functions—(i) to facilitate subsequent recognition and identification and (ii) make available the new name as per ICZN. A good describer must have (i) a through knowledge of the group, (ii) throughness of structure of terminology (iii) ability to assess differences and similarities (iv) ability to emphasize the significant features neglecting irrelevant ones, (v) a full understanding often nomeneclatural technicalities, and (v) concern for future works.

Several important aspects of a **description** are—

(i) Style : For a taxonomic description, language used to describe is always concise and telegraphic. e.g. 'The head is one-third longer then it is wide, the antennae are shorter than the body, and the outer antennal segments are serrate', is written in a taxonomic publication as : 'Head one-third longer than wide; antennae shorter than body; outer segments serrate.'

(ii) Sequence of Characters : Arrangement of characters for diagnosis is different from that for description, characters arranged for diagnosis in sequence of most to least important while for description, characters are arranged from anterior to posterior end of the organism.

e.g., For description of an insect, characters are arranged under such headings in sequence as—head, thorax, abdomen etc.

Comparison of colouration of different parts lend easy but definite identification, but in absence of the practice of describing this aspect in terms of colour names in a standardized literature. This aspects often fails to be of value, use of measuring devices (spectrophotometers) provides good comparison.

Use of numerical data is another important aspect where also accuracy and care involving good number of samples are necessary.

(iii) Illustrations : These are extremely important part of taxonomic descriptions. It is almost mandatory now to furnish illustrations of whole or noted parts of organisms at least in the form of **camera luida** drawings or photographes to complete a texonomic description. Graphs charts etc., should also be added where necessary.

(iv) Keys : To identification of taxonomic units involved, key/s add to the value of a publication and attempt should be made to frame them in the paper having scope for such addition.

(v) Other aspects : Are the bibliography, nomenclatural accuracy and synonyms involved. These pertinent to a paper must be throughly worked out and placed in it.

(C) Format of a Taxonomic Treatment :

Full description of a paper on species which forms of the following items :

(i) Title (ii) Name of the author and with address(es) (iii) Abstract (iv) Introduction (v) Text [Description of species, one or more etc. and such—

Scientific name of species, its Author(s); References of species if any; its type and type locality; synonym and, if any

Description account of one/both sexes as possible with illustration of diagnosing structural parts :

Distribution;

Miscellaneous data, discussion]

(vi) Acknowledgement (vii) References.

An abridged copy of a published paper presented below may explain the highlight features :

"**Pacific Insects 12 (4) : 875-882** **30 January 1971**

A NEW GENUS OF SPHAEROMIINI

(Diptera : Ceratopogonidae) FROM THE ORIENTAL REGION[1]

By **Sujit Kumar Das Gupta[2]** and **Willis W. Wirth[3]**

Abstract : Neosphaeromias new genus is described from the Oriental Region, with type-species *gibbus n.* sp. from Laos and Thailand. three additional species are included : *caesius* (Macfie) from Sumatra, *magnus* n. sp. from Vietnam, and *niger* n. sp. from Ceylon.

This paper is the third in a series of revisions of Oriental Ceratopogonidae, with previous studies by Wirth & Delfmado (1964) on *Alluaudomyia* Kieffer, and Das Gupta & Wirth (1968) on *Stilobezzia* Kieffer. The ceratopogonid material which has been sorted and mounted on slides from extensive light trap collections brought to the U. S. National Museum for the study by Wirth & Hubert (in preparation) on the *Culicoides* of Southeast Asia provides a source which we hope will facilitate much needed revisions of other genera of biting midges.

We are especially indebted to the following persons for collection and sending us the material presently reported : M. E. Griffith, D. R. Johnson, and Manop Rattanarithitul, formerly of the U. S. Agency for International Development in Thailand, and J. L. Gressitt, L. W. Quate, and C. Yoshimoto of the B. P. Bishop Museum in Honolulu, Hawaii. Types of our new species are deposited in the U. S. National Museum in Washington, D. C., and the Bishop Museum. Paratypes, when available, will also be deposited in the British

1. Partial results of field supported by grant AI-017223 from the U.S. National Institutes of Health to Bishop Museum.
2. Department of Zoology, Government College, Darjeeling, India.
3. Systematic Entomology Laboratory, Agr. Res. Serv., USDA. Mail address : c/o U.S. National Museum, Washinton, D.C. 20560."

Museum (Natural History) in London; the Zoological Survey in India, Calcutta; School of Public Health, University of Sydney, Australia; and the Applied Scientific and Research Corporation of Thailand in Bangkok.

Neosphaeromias Das Gupta and Wirth, new genus

Type-species : *Neosphaeromias gibbus* Das Gupta and Wirth, new species.

Diagnosis : Species of moderate to large size; body coloration brownish black to black; strong erect spine present on anteromedian margin of scutum; fore femur swollen with 10-30 stout ventral spines; fore tibia arcuate; tarsal claws each with small, external, toothlike process usually present, in ♀ also with a lamellate internal barb.

Head : Eyes bare, their inner margins (fig. 1a) tending to meet in frontal part of frontover-tex. Antenna long and slender, in female (fig. 1b) with segments 3-10 short, oval to barely-cylindrical; 11-15 strongly cylindrical with slightly uneven contour. Maxillary palpus (fig. 1c) in both sexes with last 2 segments pale, the first 3 dark; 3rd segment slender, without sensory

....

"shading. *Abdomen*; Color intensely blackish; terga with scattered small setae and some long marginal bristles. Female with internal sclerotized gland rods absent; 8th segment without hair tufts or sclerotization. Spermatheca (fig. 11) one, strongly sclerotized, suboval to subsphe-rical, with prominent slender neck. Male genitalia (fig. 1n) with 9th sternum narrow; 9th tergum prominent with shallow to deep caudomedian notch and a pair of setose apicolateral lobes; basistyle with well developed mediangular process; diststyle slender with pointed, hooked tip; aedeagus (fig. 10) with slender basal arms, main body broad; parameres separate, long and lamellate, with rounded tips.

Discussion. The sessile media, absence of macrotrichia on the wing, ventral batonnets of ♀ 5th tarsomere, and absence of internal sclerotized gland rods in the ♀ abdomen are characters placing *Neosphaeromias* in the tribe Sphaeromiini. The stout body, ventral black spines of fore femur, 8th abdominal segment of ♀ without tufts or sclerotization, and presence of 2 radial cells are similar to *Sphaeromias* Curtis, but the short costa and presence of a strong external tooth on the ♀ claws are quite different from that genus. The combination of the strong external tooth and the internal lamellate process on the ♀ claws of 2 of the species is unique in the tribe Sphaeromiini. In Wirth's (1962) key to the genera of Sphaeromiini and related tribes, *Neosphaeromias* was keyed out in couplet 16 as "New Genus (S. E. Asia)" near *Mallochohelea* Wirth and *Nilobezzia* Kieffer.

KEY TO THE SPECIES OF NEOSPHAEKOMIAS

1. Small species, ♀ wing less than 2.0 mm long; wing with brownish streak from middle of anal vein small and vague; tarsomeres 1-4 entirely pale, only 5th dark brown

... **gibbus** n. sp. Large species, ♀ wing more than 2.0 mm long; wing with brownish streak from middle of anal vein prominent and almost reaching posterior wing margin; at least 3 distal tarsomeres partly or entirely dark brown 2

2. Dorsal surface of scutum with patches of silvery pruinescence .... **caesius** (Macfie)

Dorsal surface of scutum dull black or with vittae of dull grayish tomentum 3

3. Tarsomeres 1-5 partly or entirely dark brown, none totally pale; 5th tarsomere of female with batonnets covering only proximal half of tarsomere .... **magnus** n. sp.

Tarsomeres 1-2 entirely pale, 3-5 each partly or entirely dark brown; 5th tarsomere of female with batonnets covering entire length of tarsomere .... **niger** n. sp.

Neosphaeromias gibbus Das Gupta and Wirth, new species Fig.1

♀. Small blackish species; wing length 1.75 (1,69-1.79, n = 15)mm; breadth 0.63 (0.61-0.64, n = 15)mm.

Head : Dark brown. Eyes large, broadly separated on their inner margins ; vertex small,"

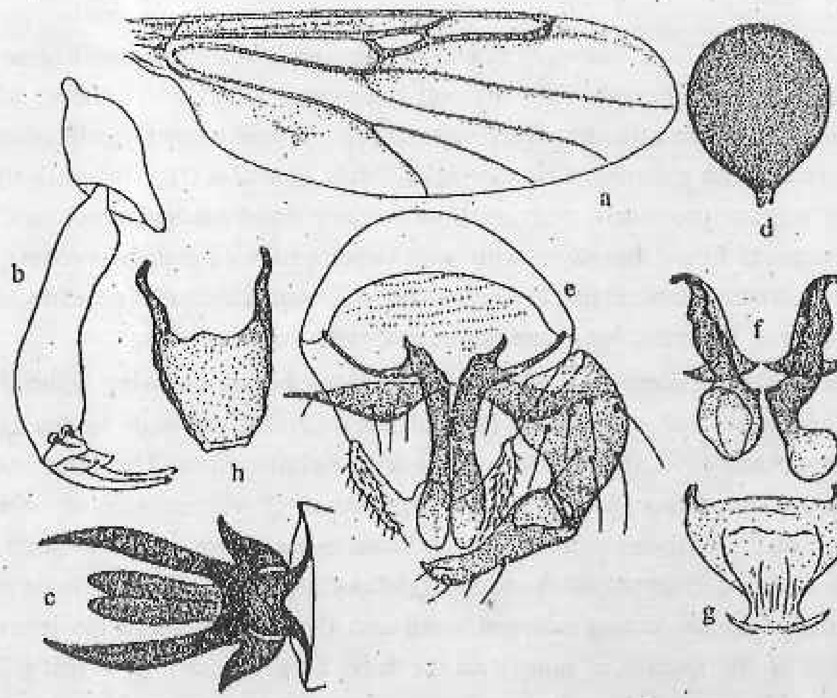


Fig. 1 *Neosphaeromias gibbus,* ♀ (a-h) : Line sketches (*camera lucida aided*) of several stuctural parts : a-wing, b-last two tarsemeres and claws, c-details of pair of clas, d-spermdtheca, and e-h : ♂ genitalia (external).

....

with "feebly spiculate; 9th tergum subtriangular, its caudal end tapering with caudal margin mesally notched, a pair of slender, setose, apicolateral lobes present. Basistyle stout at base, mediangular process large; dististyle stout at base, narrowed abruptly past middle, its tip bluntly hooked. *Aedeagus* (fig. 1o) a broad, lightly sclerotized plate; basal arms slender and slightly crooked; main body broad, the caudal margin blunt with tip sometimes flattened, caplike (fig- 1q). Parameres separate, strongly sclerotized, each with slender anterolateral process and shorter anterior process; main portion long and clavate, with rounded caudal tip; in one slide (fig. 1p) foreshortening produces the appearance of a strongly capitate tip.

DISTRIBUTION. Laos, Thailand.

Holotype ♀, allotype ♂, Loei Prov., Thailand, June 1959, Manop-R., light trap (Type no. 70655, USNM). Paratypes, 3 ♂♂, 52 ♀♀. LAOS : Muong Sing, 7.VI.1960, L. and S. Quate, 1 ♀. THAILAND : Same data as types, 3 ♂♂, 42 ♀♀. Khon Kaen Prov., Ban Pai and Choom Pae Dists., V.1959, Manop-R., 8 ♀♀. Udonthani Prov., Nong Han Dist., VI.1959, Manop-R., 1 ♀.

Discussion. Neosphaeromias gibbus is apparently abundant in Thailand, as evidenced by the relatively large number of specimens taken in light traps. Some differences appear in the ♂ genitalia, according to orientation of the slide mounts, and an extreme is figured in which the parameres (fig. 1p) and aedeagus (fig. 1q) are foreshortened due to nearly perpendicular orientation on the slide."

....

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Concluding Remarks : Taxonomic papers are different in style, content and overall treatment from papers in other branches of human knowledge. Maintenance of correct niceties are essential; so, preparation of a taxonomic paper and proof-reading of a manuscript must be done with extreme care, copies of a published paper should have wide circulation and inclustion in such referral volumes of International Standing as— The **Zöological Record** (published from the U.K.*) and the **Biological Abstracts** (published from the U.S.A).

Thes copies are often called as :

(i) Author's extras : pages removed unchanged from extra copies of the publication and so often contain parts of other papers.

(ii) Separators : These are copies printed from the same type as the original minus the extraneous matter; almost similar to original.

(iii) Reprints : These are copies rearranged to fit most satisfactorily the presentation often paper in a printed from retaining all the traits of the original (through pages may be renumbered and somewhat rearranged and so not the exact copy of the original).

The Zoological Records provide in a series of annual volumes, a bibliography of essential data of taxonomic literature and other basic zoological literature published throughout the world since 1864. It was a British Enterprise (C/o Zoological Society of Landon British Muesume History and Commonwealth Institute of Entomology) but from 1980, collaboration of Biosciences Information Service, U.S.A. is being also utilized now, however, its publication is 4-5 years behind schedule.

The taxonomy part of Biological Abstracts have undergone a change. Since 1970, references on Insects, mites and arachnids of Biological Abstracts are being published separately as **Abstracts of Entomology**.

4.4 Process of Typification and Different Zoological Types

In all works related to binomial nomenclature of zoological systematics, the basic features (= Characters) are taken from specimens (= samples) collected in nature. Various 'type'/forms are selected from them and these 'types' are the standard of reference for them pertain to their taxonomic data. In other words, a 'type' is a zoological object on which the original published description of a name if based. **Typification is the fixation or determination of the type material for a zoological name at different taxon level at the time of first published description of that name by a concerned taxonomist or in absence of types by loss or damage or non-fixation at the time of their first description, their types, by a revising or subsequent expert who selects types from duly preserved samples of the first describer of a zoological name or from his own**

collection of samples preferably from the first describer's locality of collection of concerned samples. The process must conform to the norms and stipulations laid down by the International Commission on Zoological Nomenclature (I.C.Z.N).

(I) Essential Features : (1) A 'Zoological type' is the objective basis with which a certain 'Zoological name' is linked permenently and designated 'type' cannot be changed unless very necessary.

(2) The 'type' of a nominal species is **a natural specimen** (= **Type-specimen** of that species), that of a nomial genus is **a species** (= Tycp-species of that genus), and that of a family is a genus (= **Type-genus** of that family). Depending on their relative importance to the expert determining the types or on the criteria of their determination, types are variously labelled and categorised dispelling any arbitrariness in their relative quality. This process of categorisation is the main task of typificetion which at a taxon level, say species level, say species level, for a species means in fact the act of labelling the specimens of that species used in preparing its taxonomic description for the first time or its any subsequent description after the **appropriate type names.** In short, **typification** is the act of **specimen labelling, species labelling** and **genus labelling** so that the labellings using appropriate names could be the material reference for any subsequent work involving them in respect of concerned samples collected from nature from time to time.

(3) The type concept (= Type Method) to establish a zoological taxon by name actually matured in last 70 years. Previously, taxonomists used to guided by the Aristotlian concept of types. The idea was rather vague and it was held that there were as many types as there were typical specimens of a species whose taxonomic description is based not merely on types but as average of many of that species. Types are not meant to be exclusive basis or even the tertiary basis of the description whose salient features should, however, prevail in the types increasingly from peripheral to the centric one. A species consists or variable populations. No single species can essentially project this variability; type cannot be typical of a species. But a type remains the standard "name bearer" of the taxon it represents.

(4) At the onset of the present form of toxonomy dating from the Linnaeus' time, typification practised somewhat casually. Linnaeus himself never designated any specimen as the type and had the habit of replacing his old 'type' by the better new ones! This continued until the taxonomists started labelling one specimen as the 'type' and the others as 'cotype' (= paratypeof recent taxonomists). With time, many more kinds of types difined from different aspects were in use a study (of 1940) listed ove a hundred of such type names grouped into three categories (seven categories, as per one study in 1967).

Some of the type-and group-names, mentioned above, are out of use now while a good number have found a wide acceptance by the practising taxonomists.

(5) Simpson (1940) coined the term **Hypodigm** as the name of the whole lot of specimens available to a taxomomist at any point of time and recognised by him as members of one taxon i.e., species (= conspecific). This term is widely used by the Palaeontologists though many zootaxonomists are reluctant to accept it as, in their view, the term is essentially a synonym of 'material', a term used by them usually to refer to their animal samples under study.

(II) Important terms for specimen typification : This in other word is the act of determination of category of types out of specimens of a species for its taxonomic reference.

Some 12 catogories of types are commonly used under two broad divisions as follows (explained mainly) in respect of specimen typication in a species.)—

A. Primary Types (= Proterotypes) :

These are fixed at the time of description of the taxon (species etc.) by the author of the taxon out of specimen/s of the taxon at his disposal, The more important Primary Types of specimens are as follows :

1. Holotype : One specimen of any sex selected by the author as the 'model' sample of his species; a true type, this is the most important all types. When a species is described on basis of a single specimen, the same unavoidably is marked by the author as the holotype of his said species.

The holotype is the key to the name of the species and settles questions in connection with the name of the species itself. However, it need not be the type of the species and settles questions in connection with the name of the species itself. However, it need not be the type of the species, nor even necessarily a typical individual of the species; it is the type of the same.

2. Allotype : A specimen of the same species as the holotype but being the sexual opposite of the holotype, i.e., if the holotype of a species is female, a male sample of the species will have to be fixed as the allotype of the species. It can be designated subsequently.

The zoological code does not favour the use of allotype which is viewed as a mere paratype. Its use, however, is of advantage in adding sexual characters ofthe opposite sex of the holotype.

3. Paratype : While describing a species on basis of a good number of specimens, its author selects several specimens for basing his description of the species. He marks one of these as the holotype and a sexual opposite of the holotype as the allotype. He then labels the remaining specimens as paratypes (i.e., specimens of paratype status).

The early practice of labelling 'type-seires' specimens as 'types', 'co-types', 'syntypes' etc., does not facilitate an author to treat his specimens of a species differentially in spite of presence of natural variations in those specimens. All these specimens are given 'equal' importance which obviously is not the correct feature. Typing them as holotype, allotype and paratype, their differential importance is duly pointed out.

(4) Chirotype : This is the type specimen upon which a species name in manuscript is based, i.e., type in pre-published account of a new species (or of a genus etc.).

(5) Metatype : A specimen compared by the author of a new species with the type and determined by him both as conspecific.

B. Secondary Types :

These typicfications are mostly done not by the original author of a species but by a revising author. More important secondary types are as follows—

(6) Homotype (= Homoeotype/Homeotype) : A specimen compared with the type by a person other than the describer and determined by the said person as conspecific with the type. This is generally done when original type is damaged or lost. A homotype is important as a type.

(7) Lectotype : If it is seen that the original author of a species has life his concerned specimens of a species duly preserved and named (i.e., identified but labelled as of scientific value or without any typification at all and the said species thus no individual type labelled anywhere, a revising author/-researcher then selelct one specimen out of those syntypes and typify it as of holotype status for the said species. Such a holotype, recognised by its type-status not during the original description of the species but titled so sub sequently is called the lectotype of the species, with the remaining scientific specimens of the species called the paralectotypes. The deficiency of the holotype individual of the species is thus compensated by the 'creation' of the lectotype individual.

Selection of a lectotype must be done very carefully and by a specialist of the subject concerned having considerable expericne as such a work needs consideration of the following :

(i) If syntypes of the concerned species are preserved at more than one place, it must be checked if all can be accessed upon for consideration. If not, the slection then should be made from amongst the pool of maximum number of available syntypes;

(ii) If any of the preserved syntypes of a species was based upon for description or illustration of both, of the said species, by its original author and the same mentioned or indicated in his original text in point. With other things being equal between such a 'mentioned or indicated' scientific specimen and other scientific speciments (i.e., their quality as a preserved lot is the same the determining choice becomes limited to the "mentioned or indicated" scientific specimen for the obvious fact that only the said specimen was used as a sort of 'holotype' for the species by its original author and though holotype-labelling was not made, the concerned specimen only enjoyed that status to the original describer of the species concerned.

(iii) If syntype specimens, marked out so by the original author of the species concerned, are from different localities but the type-locality for the said species is marked out clearly by the concerned original author or by a reviser of the original work, syntypes only of the said marked-out locality will be considered for fixing up the lectotype.

(8) Neotype : If due to loss, destruction and damage or due to other reasons, specimens of type value and correctly so labelled do not exist or are untraceable and believed tobe permanently out of access, a revising worker of that species may select a specimen (collected by him and identified by him as ofthe said species) labelling it as of holotypic value for the species. Such a type is called the neotype of that species. Neotype stands for the species in absence of its holotypic, lectotypic or syntypic specimens.

Nomenclatural code does not support and furnish any typificational provision for the creation of a neotype for any and every species merely lacking in its regular types (holotype, lectotype etc.).

Neotype creation is recommended only '... when a neotype is necessary in the interest of the stability of momenclature'. In such a case of creation of type of allotypic value and of paratypic value is also recommended for that species if its suitable samples are obtained by the reviser, two such created types being called as **neoallotype** and **neoparatype** respectively.

(9) Plastotype : A plastercast of a type of a species forms the plastotype of that species. If is extensively used in palaeozoology.

(10) Topotype : It is a specimen of a species which is earmarked as 'collected from type-locality' of the species by a reviser or a subsequent worker who may collect and identify the sample himself. It is quite a valuable type specially when original type gets lost or becomes inaccessible.

The type-and topotype-locality of a species are the one and the same and the populations of the said species the said locality are known as the topotype populations.

(III) Important terms for species typification : The typification of species essentially is the task of selecting a species of genus, both being validly described either before or at the time of selection. The species is called the **type-species of the genus it belongs to** and it is taken more or less as the bearer of the typical characters of its genus. The position of a type-species is quite important and previously it used to be called as the **genotype species.** To avoid any confusion involving this term Genotype species with its counterpart term used in the science of genetics (where **Genotype** means hereditary) and genetic constitution of an individual), the use of the term genotype in taxonomy is forbidden by a zoological code of 1961.

The selection of type-species of a genus, *i.e.*, species typification, for a genus, may be any of the two following kinds :

(i) *Type-species, by original designation, i.e.*, a type-species determined at the time of establishment of the genus it belongs to,

(ii) *Type-species, by monotypy, i.e.*, a type-species of such a genus which was established with only that species under it, there being no other species known in that genus at that time though subsequently, more than one species belonging to that genus may be described.

A third kind, *i.e.*, **Type-species, by tautonymy** may be made. Here, the type-species selected is such that its generic name and specific name are *one and the same, egs., Bison bison, Gorilla gorilla* etc.

In some cases, even the subspeices part of the name may be also the same as the species and the genus part of the complete name of the subspecies of a species (*e.g., Apus apus apus* the three parts respectively being the genus, species and the subspecies name.

(IV) Special kind of typification : In some cases, specially in Prokaryotes, bacterial forms etc., biochemical features are essential for identification and for this, those forms need to be maintained in laboratory in live states for idefinite period. Thus their cultures are to be maintained. Whenever particularly such a culture is referred to, it is called as the **Type Culture,** as it forms the basis of species description. If such a culture is lost or destroyed for unavoidable reasons, a new one is started and maintained as its substitute and this substitute new one is called as **Neoculture** or **Neotype culture.**

In case of Protozoa, samples which form the basis of description of a species are all preserved mounting them permanently on a microslide in appropriate-mounting medium after due processing including staining of the specimens as required. A single specimen of such a slide has no special value. Any of these specimens thus preserved in a slide is called as **Hapnotype** a special type in the realm of typification, and the microslide containing them is called as the **type-slide** of the concerned species.

(V) Data on types, type labels and type deposition : All collected specimens should be properly sorted, processed, identified and labelled as necessary. Essential data should be indeliably written or printed in a durable piece of label for every type specimen to which the label must remain tagged permanently. Those data for a label are :

(i) taxonomic identity of the type (its scientific name with author's name and family it belongs to,

(ii) sex of the type,

(iii) locality name of its colletion,

(iv) date of collection,

(v) mode of collection,

(vi) Name of collector(s),

(vii) Other data (behavioural peculiarity, breeding habit, habitats etc., as observed during collection).

For a quick recognition of the various 'types' in the study material of specimens of a taxonomist describing his new species, it is the couvention to use labels coloured differingly for the holotypes, the allotypes and the paratypes and as follows :

Red or Pink coloured label for holotype;

Green coloured label for allotype;

Yellow coloured label for paratype.

The secondary equivalents of these three primary types are neotype, neoallotype and neoparatype and these three secondary types, the labels coloured as for respective primary counterpart may be used. Otherwise, white coloured labels should be used for these three secondary types.

Custody of types, their deposition : All types are properties of science and are irreplaceable and indespensible as reference-material. An 'individual worker or an established researcher may retain his types during his period of study but must ensure that the types of his published species etc., are deposited as early as possible to any authorised custodial concern of national importance concern in out country for custody of animal types.

It is desirable that in case a worker has several paratypes and additional specimens of his new species, he distributes these as duplicates to other custodial centres including such reputed ones abroad as the British Museum of Natural History, the U.S. National Museum, Bernice P. Bishop Museum (Hawaii), Australian National Insect Collection (Conberra) etc.

(VI) Merits and Demerits of Type Concept and Typification : The subject and its working, in point, have rationalised the handling of specimens of a working taxonomist for a better understanding of the spicies in relation to one another. The Type concept is a sound scientific concept that projects the naturally occurring speciation system from taxonomisc view point in a cogently illustrated manner.

The onset of typification in taxonomic work has made it obligatory for a taxonomist to leave behind the basis of his observations and inferences for any future comparison and evaluation directly and in a stark manner. The system's value is understood while confirming any case of taxonomist identification. If populations of a species, of considerable variation, abundance and wide distribution range become unavoidably divisible into more than one species on critical studies by revisers and other experts, the existing species with its category of populations is 'represented' by the type specimen of that species already to recognised. For newer species having respective section(s) of specimens of the original species (species *in lato*), respective types are determined afresh and in reference to the type specimen already in existence *i.e.,* the holotype of the original species.

The only **demerit** of the subject of type concept and typification is perhaps the intense fabrication of the number of credited types that grew up at one stage during last 70 years' tenure of the subject. Of course, many of those have been subsequently abolished simplifying the whole thing as an easily workable system.

The other drawback which some point out is the expensive procedure in preservation and continued maintenance for extended duration. Dry state preservation of insects like butterflies, beetles and dipterous ones are to be preserved in constant temperature, pollution free sterilized rooms in equally sophisticated containers which also involves quite a number of technical persons. Even then, quality of material deteriorate and a preserved specimen becomes unfit for any study. As type samples attain such state, they need to be sorted out and replaced by appropriate duplicates in the form of secondary or tertiary types. This limitation forces a custody centre to limit its stock of types etc. The need for 'everlasting' preservation and availability of a type is always there but technically that is not feasible. Moreover, the quality of a material deteriorates though very slowly with time. Reliable duplicates to occupy the place of work out types cannot be made in all cases keeping the lacuna of typification to that extent at least yet a matter of fact for the subject.

(VII) Concluding observation : (i) Typification, (the type concept of animal classification in action and actual practice) while describing new species or any infra or supra-species taxon out of samples of collections or in a revisionary work gives us the properly labelled type specimens etc., which are invaluable and essential as reference material being the properties science. Type material plays a role in taxonomy fixing the meaning of a specific name and are invaluable additions for a museum which preserve them as long as possible and later on arranges replacements as the need arises [The British Museum of Natural History, London, has a gross total of 22 million specimens of which a total of 2,50,000 are the **primary types.**]

(ii) The Type concept and Typification made out of that concept is a basic step in taxonomic thought, the action being an important feature of the code of Nomenclature. Type status given to select samples must be followed with care and in determining and establishing types, the following features must be covered —

(a) full description of types, their illustrations and results on observation and experimentation with them must be published.

(b) full data on types regarding their collection, processing, place of preservation etc. must be published also along with the details outlined above (a).

(c) preservation of types must be made with recognised depositories and such whence those may be obtained by future workers for their consultation.

(d) while describing types, they must be compared with comparable samples of other species and relationship must be clearly stated alongwith reasons for establishing new species by the describer.

(e) The worker establishing a new species or other new taxon status must follow the rules of ICZN, and if necessary will contact the Commission on ICNZ.

Deviation from any of the above dishonours the concept of type status much to the detriment of the quality of Taxonomy as a subject for establling its progress.

4.5 International code of zoological nomenclature (ICNZ)—Its operative principles, interpretation and application of important rules, zoological nomenclature, formation of scientific names of various taxa

From a perusal of this section we may known how a system for classifying animals and naming the various units from highest to lowest level and perfected through decades of thinking and contributions along scientific lines and how the system administered by an International body was made universally acceptable for all working to ascertain the systematic position and scientific name/s of animal/s of their concern.

The International boidy in point are like (i) International Zoological congress which elects a judicial body named (ii) International Commission on Zoological Nomenclature

Classificatory or naming problems must be referred to the Commission for a finalisation. The ICZN (= International Code on Zoological Nomenclature) formulated by the commission gives the regulatory guidelines for working and understanding animal taxonomy and all these are discussed in pages to follow under such break—ups and framework as outlined below :—

- Introduction
- Definition and Basic Features of ICZN
- Brief History of ICZN
- Operative Principles and other Features of ICZN (Interpretation and Application of rules, Formation of scientific names/Zoological Nomenclature).

(A) **Introduction :** Nomenclature (names=name; calare = to call, L.,) literally means, to call by name(s). Critically it means, allocation of names of to the biological taxa as per nocus of the concerned International Code (here, Zoological code), the purpose being to provide a designation that will mean the same thing to all people of all nations through all foreseeable time. A correct and fixed nomenclature is an imperative to all truly scientific investigation and discussion. Even the most primitive natives knew living beings of their surroundings by names. But such names and local names in different languages in different countries lack clearly in having (i) any classificatory value and (ii) international communicability, in spite of their having a limited advantage as a means of ready reference. The science of zoological nomenclature tries to avoid ambiguity and inconsistence providing suitable **lables** to the organisms at all classificatoty **lavels** ensuring an error-free, unique and stable means to comminicate correctly and internationally abnout them for all time to come. As such, zoological names are unimportant; they gain importance because they are useful and scientific reference to such "name—bearers" is not possible without using those names.

(B) Definition and basic features : Zoological Nomenclature is mainly the Bionomial System of Nomenclature, as applied to a species of animals for the first time, by Linnaeus (Karlvon Linne, the Swedish Naturalist of 17th century). A species is designated by a combination of its specific and generic names thus having the need of two names to be called in a scientific names which as thus a binomial system.

In the lenth edition of this teratise, **systema natural**, of Linnaeus, and following this, the first date of January 1758 was accepted both as the date of publication and the starting point of the binomial naming system for animals (**only exception** : nomenclature of spiders that starts from 1757 A.D.)

In strict sense, the term **binomial** is not valid though it replaced the original term **binary** during the past-Linnaean era. Since 1961, the term **bionomial** has been replaced by the term binomial (originating from the latin term **binomen**) and hence, in spite of the erroneous usage still persisting, the Linnaeus' binomial nomenclature should be correctly referred to as **binominal nomenclature**.

The International Code of Zoological Nomenclature (i.e. The ICZN) applies both to the living and the extinct animals, including the animal-like Protista (Protozoa). It regulates the names from family level down to subspecies level; names above family level are not yet within its formal ambit. The baisc principles of the code are to ensure that (i) any given taxonomic grouping of a given rank can have only the correct name, and (ii) stability in the naming and classification of organisms.

The ICZN consists of three main parts : (i) The code Proper, (ii) The Appendices, and (iii) The Glossary. The Code proper includes a preamble followed by 87 articles which are composed of mandatory rules devoid of any explanation and told in starkly concise words. There are recommendations in some cases but those are not mandatory. The appendices, like the recommendations, need not be strictly followed. The Glossary contains the pointed definition of the terms used in the code.

(C) Brief History of ICZN : The early naturalists used scientific names according to their personal preferences. Some tried to use the names devised by others. Some worked without any library facility or paid scant attention to what others did or were doing. Some accepted the authority of leading naturalists and rejected others totally. As a result, many species and genera were given different names by different workers to entirely different animals. Linnaeus himself was the 'Father' of a set of rules of nomenclature published in his **Critica Botanica** (1737) and **Phisophica Botanica** (1751). His authority waned in nineteenth century and was replaced by various loval rules causing confustion. To stop it, Zoologists of the western countries drafted formal rules and principles of nomenclature. Those were adopted as an International code at the Fifteenth Zoological Gongress held in Berlin in 1901. As a code, however, the subject was formulla issued after the sixth Congress. The code countinued to be rectified with each congress till at the Fifteenth Congress held in London in 1958, a new version of the code was adopted and issued. That formed the guiding reference till now with additions or alterations of a minor nature from time to time being officially operative with effect from the sixth day of November, 1961 (the Code's updated version, however, was made available only in 1964).

The International Zoological Congresses are the legislative bodies so for the codes of Nomenclature are concerned. They elect the International Commission on Zooligical Nomenclature, a judicial body on a permanent basis, to interprete or suspend the provisions of the code in individual cases and to submit to the Congress the recommendations for the classification or modification of the code. The Division of Zoological Sciences, or the General Assembly of the International Union of Biological Sciences are the recognised equivalents of the International Congress of Zoology.

For nomenclatural problmes on animals, nay Zoologist may submit cases to the Commission but he/she must not use, his/her contentions till the Commission judged those and got those approved by the Congress or its counterparts. The commossion maintains the official lists of family, genus and species names in Zoology, the official indices of rejected and invalid names etc. anyone can have access to these documents of Commission on suitable notification to it.

(D) Operative Principles and other features of ICZN :

(1) Framing a name (Uni., Bi-, Tri-nominalism etc.) : Naming of a species taxon is done by two words (binomen) of any taxon above species i.e., for any macrotaxonomic unit, is by one word (uninomen). To write a zoological (= scientific) name down to subspecies, one has to use three words (trinomen) and if a subgenus name is included, the name becomes a 4-word name (quadrinomen).

Full citation of a sc. name in any critical writing consists of all parts of the above as available and always the surnames of the author of the species (i) though in routine citation, the same is excluded (ii-iii) as shown below :

Name/Status	Genus	Subgenus	Species	Subspecies	Author
(i) *Firstly*	*Dacus*	(*Afrodacus*)	*aberrans*	*nigritus*	Hardy
(ii) Indian tiget	*Panthera*		*tigries*	*tigris*	—
(iii) Modern man	*Homo*		*sapiens*	*sapiens*	—

Workers in taxonomy prefer also to write the year when the species is established by its author Hardy (done as : "... Hardy, 1934").

No punctuation mark is used from one to other end of the name, but if any worker's name other than that of the author (the first describer of the species) needs to be mentioned in any particular case, the same may be written by putting punctuation mark (; / :) after the species name. Similarly, no diacritic mark (ü), apostrophe (s') hypen (-) etc., should be used in a sc. name [müllcri is written as mülleri, d'urviellei as durvielled]. Use of number in sc. name is also not approved (10-lineate) written as decimlineate).

Abbreviated use of author's name (Linn./L.–for Linnaeus) is not couated as a good practice as per code. Genus to subspecies part of a scientific name is italicised or underlined, if not italicised.

In a two-word/two-part structure of a sc. nane for which it is called as Binomial System of Nomenclature, the first word/part denotes genus name ans second word/part denotes species name. First alphabet of genus name is always in capital/block letters while the other alphabets of genus name and all of species name are in small letters (for a species name made after a country/locality i.e., for a geographical sc. name the first alphabet of species part may also be written in capital letter e.g. *Culicoides Calcuttensis*), instead of the usual small letter.

(2) Basic language of scientific names : Latin or latinished form of words or other languages if used (Latin was the **lingua franca** of the educated people of western countries when animal taxonomy in present sc. from developed, and once started as the medium for sc. names, the same cannot be altered).

All taxonomic names are unique, i.e., same name not applicable more than once under a taxonomic state (species/genus etc.). Species names ordinarily are based on any of its characteristic features, morphological or otherwise. /any such name must be adjective form in nominative singular agreeing in gender with genus name. which is in noun form; examples—

Ending-in species name	in genus name	** Name in full to exemplify
feminine ending (–a/–e)	(–a/–e)	*Dasyhelea setigera***
neuter ending (–um/–us etc.)	(–um/–us etc.)	*Plasmodium falciparum*
masculine ending (–i)	(–i/–us/–es)	*Anopheles stephensi***
(generally for patronyms)		

(** all are blood-sucking dipterous insects)

The compatibility/suitability factor involving genus and species parts of a scientific name is, however, inoperative once a name is framed and published (a butterfly species having long tails if published as **brevicauda** or the vice-versa, then it cannot be changed.).

Similarly, a geographic name is framedto indicate that the species either is dominant in its name-locality or restricted to that only; if subsequent studies prove its distribution otherwise, the name in use being published already cannot be changed though it now contradicts its factual prosition in nature.

(3) In all codes, some provisions exist for regulating naming of suprageneric taxa Zoological Code only deals with taxa from superfamily to tribe andtherulesandthe practices in this respect lay down that the endings of such names should be framed conforming to following (Macrotaxonomic names, taxa above family, lie outside code's provisions as a rule, in deposits) :

Taxon Level (T.L.) Ending of the name :—

Superfamily ... *oidea*

Family ... *idae*

Subfamily ... *inae*

Tribe ... *ini*

Subtrive ... *ina*

(4) Rules on Priority/Law of Priority : A search through taxonomic literature specially through the species or the genus catalogues of different animals of different zoogeographical areas may reveal the following anomalous instances :

(a) Cases of Synonymy : It so happens sometimes that the different species names are applied to such sets of animal populations that are actually conspecific. This is due to the fact that the concerned taxonomists fail/s to appreciate correctly the status of the animal populations involved in his/their studies and take/s them as new to science ignoring the conspecificity of the species with the known, related ones. The case of synonymy however persists and subsequent, revising worker/s correct/s the situation by holding the synonymous species, described earliest of all such species, as the **Senior Synonym** and the Valid Species while sinking down the remaining species as the **Junior synonyms** and the **Invalid Species.** No change of authorship of the species name is permitted in any case or homonymous revision and correction. Another provision is that the various synonyms are replaced by the senior synonym i.e., the name in synonym-cluster published first provided the junior synonym has not been in use for more than 50 years. Judged from other viewpoints, the synonymy may also be divided into following two types :

(i) Subjective Synonymy (also called, Taxonomic Synonymy, or Heterotypic Synonymy) : These are based upon different types and they remain synonyms only as long as their respective types belong the the same taxon. The synonymy in such cases is not absolute and hence it is indicated by the mathematical sigh of equality (=)

(ii) Objective Synonymy (also called **Nomenclatural Synonymy,** or **Obligate Synonymy,** or **Homotypic Synonymy**) **:** These are based upon same type and hence, these are always absolute, such a synonymy is indicated by the mathematical sign of congruence ($\equiv$).

The synonyms of any kind, however, pose great problems for the taxonomists. A great significance follows them since they provide considerable information. It is not easy to establish them as the work needs high level thoroughness and expertise.

[*egs.* (a). Some 251 species of **Anodonta** (Fresh-water Mussel) from France, were subsequently found by the experts to be the mere habitat-variants (the Junior Synonyms) of 2 valid species of the genus.

(b) The instances involving the blood-sucking biting midge insect ***Culicoides schultzei*** (Enderlein) illustrate the cases of subjective *synonymy* more aptly. This variable and widely abundant species was first described from Africa. Subsequently, over years, its existence was recorded from different parts of Asia covering such diverse countries as Iran, Iraq, Israel, India, Pakistan, Sri Lanka to China and the Asian parts of the U.S.S.R. its amazing array of morphotaxonomic variability led the working taxonomists indifferent countries to call the populations concerned in their area by different scientific names trating each as a distinct species. Critical studies covering all such species later on concluded the following —

Culicoides schultzei (Enderlein), 1908, is the Senior Synonym and hence the valid speices; the following are conspecific to it and hence sunk as its Junior Synonyms :

(i) ***C. kingi*** Austen, 1912 ... described from Africa

(ii) ***C. mesopotamiensis*** Patton, 1920 ... described from Africa

(iii) ***C. oxystoma*** Kieffer, 1920 described from India

(iv) ***C. kiefferi*** Patton, 1913 1920 described from India

(v) C. **alatus** Dasgupta & Ghosh, 1956 described from India

(vi) ***C. housei*** Causey, 1938 described from Thailand

(vii) ***C. punctigerus*** Tokunaga, 1950 described from Indonesia

A more recent study treats the above complex divisible into two distinct species—the African ***C. schultzei*** (other African spp. being its junior synonyms) and the Australo-Asian *C. oxystoma* (other Asian spp., being its junior synonyms).]

(b) Case of Homonymy : It may be detected by a reviser that a particular species name has been used by a describer to describe his new species in a genus being unaware, through mistake or insufficiencieson his part, that the said species name was already used by some previous worker to describe the worker's newly found species of that very genus, i.e., the species name in the genus was preocupied. This forms the case of homonymy and it requires correction as two different species of a genus cannot be called by the same name though their authors are different. Thus, *the homonyms are the scientific names of animals which are spelt in a similar manner (i.e., those names have identity in spelling) or in a way so similar as to be treated identical as per the Zoological Code though the taxon levels of the animals are based on different types.*

The reviser dealing a case of homonymy corrects the anomaly by retaining the case described earliest (the Senior Homonym) as it is but he alters the species name of the other concerned (The Junior Homonym/s) in his own free way and the authorship of the species whose name is thus altered (= newly named species, i.e., species nomen novum, or, sp.n.n.) now belonged to the reviser. Sen and Dasgupta (1958) detected a case of homonymy involving two species of biting midge insects of the genus *Culicoides* as follows :

(i) *C. orientalis* Macfie, 1932, the Senior Homonym, described on samples collected from different parts of Southeast Asia, including India:

(ii) *C. orientalis* Gutsevich, 1956, the Junior Homonym, described on samples collected from the Asiatic parts of the former Soviet Union.

The taxonomic separateness of the populations of macfie's species from those of Gutsevich's species was clear and the situation was corrected by Sen and Dasgupta (1958) by renaming the latter's species (the Junior Synonym) in honour of him, the patronym thus framed being *C. gutsevichi* Sen and Dasgupta, *nomen novum, i.e.*, new name, for *C. orientalis* Gutsevich.

(c) Primary Homonyms and Secondary Homonyms : In the example of a homonymy involving biting midges, cited above, the homonym cluster of the two identical species names belonged to the same nominal genus. Such cases form the Primary Homonym Cluster or simply, the Primary Homonyms as these involve a single genus i.e., the genus taxon is common to the homonymous species from beginning. Another example of the Primary Homonym Cluster is :

(i) *Rana tigrina* Linnaeus,, 1758—the Senior Homonym;

(ii) *Rana tigrina* Fabricius, 1795—the Junior Homonym.

The Junior homonym *tigrina* Fabricius is invalid and it is replaced by a new name.

Now, if in a homonym cluster, any one of the names originally is in a different genus but shares the common genus creating the problem of homonymy due to its subsequent shift from its original genus to the common genus, the cluster in view forms the Secondary Homonym Cluster or simply, the Secondary Homonyms.

[egs. (i) A case involving earwigs, the insects of the order dermaptera, is as follows : *Forficula riparia* Dufour, 1805, is reassessed by Bolivar (1897) who finds that the species actually belongs to the genus *Labidura*. He therefore enacts the the generic shift due and the species henceforth is 'correctly' written as *Labidura riparia* (Dufour). But a problem of homonymy arises as there already existed a valid earwig species named *Labidura riparia* Pallas, 1790. It was obvious that the case was one of Secondary Homonym Cluster, and *L. riparia* Pallas was the Senior Homonym while *L-riparia* (Dufour) was the Junior Homonym. The correction was instantly made by Bolivar (op.cit.) who changed the name of the Junior hononym as *L. indians* Boliver.]

(ii) In determining the junior/senior status in a case of Secondary Homonymy, the year of original description of the species counts, Notwithstanding if its status is correct from the beginning. A speçics described earlier in a wrong genus and corrected genuswise at a data to that of the description of the species with which it forms the homonym cluster is taken as the senior homonym. It needs no change in its species part, but the other species being the Junior homonym undergoes change of name in its specific part.

Caratopogon falcatus Meunier, 1904, was corrected by Szadziawski (1988) as *Stilobezzia falcate* (Meunier), new combination, while earlier, Chaudhuri *et al.* (1974) described a new Indian species as, *S. falcata*. As per rules governing Secondary Homonomy, *S. falcate* (Mouriar) is the senior Homonym and after its creatinby intergeneric shuffling, Choudhuri *et al.* changed their species patronymically and as : *S. szadziewskii* Choudhuri *et al.* 1990).

(d) Merits and Demerits : The Law of Priority in Zoological Nomenclature is also used to tackle problems as explained above at super-species and higher levels.Though its application may generate controversy among the taxonomists, it is a basic law of International Code to promote stability. Whenever a case showing two or more names of the same taxon is detected or it is seen that the case is the other way round, the problem of validity of one is settled by this law. Its only drawback, however, is that under cover of this law, even the names poorly and incompletely described originally become valid because those are oldest. In other faculties of science, there is no such provision for valuing any work that is not preciseor complete, and those are simply ignored. Of course, the requirements and peculiarities of different faculties need not be the same. Thus, Priority Rules form a somewhat controversial part though essential of the zoological code. A zoological name must be "available" in the first instance being published as per the relevant clauses of the code. The name of a taxon is "valid if it is the oldest available name applied to ..." the taxon. Date of publication of a name is thus very important.

Priority means Priority of Publication, not priority of usage.

Law of Priority in Zoological Nomenclature applies only to the categorical levels of species (and subspecies), genus and family but not to higher categories.

(5) Rule of New Combination : If a described species is found placed in a wrong genus either through an initial error of generic misidentification or through any subsequent shift in the generic conception, an intergeneric transfer of the species becomes necessary. The name of the original author of the species that forms a part of the scientific name ofthe species is now kept in parentheses (a set of first brackets) in the corrected from of the name, with the name of the original author in parentheses, is called the *new combination name*. The year of the original author first describing the species may also be cited as also the name of the reviser who affected the New Combination, together with the year of his doing so. Some commonplace examples of writing the New Combinatin names, showing part or full details, are as follows :

(i) Indian lion, correctly written as,

Panthera leo (Linnaeus), New Combination,

(ii) Flatworm *Taenia dminuta* Rudolphi, after the required intergeneric correction, is written as,

Hymenolepis diminuta (Rudolphi), New Combination

(iii) Fruitfly species *bipars* Walker, 1862, after correction, is written as, *Hemilea bipars.* (Walker, 1862), Hardy, 1959, New Combination.

It is obvious that in all three cases as above and in similar cases, every species historically has double names—one, the original scientific name given by the first describer (egs. *Sophira bipars* Walker, for fruit fly, *Taenia diminuta* Rudolphi, for the flatworm etc.) and this original name of the species is called as its *Basionym*; the other name of the species is the corrected scientific name (eg. *Hemilea bipars*) (Walker), for the fruit fly in point), the *New Combination name* of the species.

Patronyms : The scientific name whose species part is framed by latinising a geographic location name (after which the species is named) or the surname part of the name of a person (after whom it is named)is a patronym. Such a dedicational name after a localityis assigned to indicate that the species so named is endomic or common to that locality, while after a person, to recognise the fame/contribution/involvement of the intended person direct or indirect, with the subject of study of the framer of the name, or sometimes simply to prtpetusto the memory or a person whom the framer ofthe name may hold in personal effection or storm. As a rule, the surname part (modern family name) of the whole name of a person in view is used. It is suitably latinised by just adding the alphabet 'i' at its end if the person is male and adding the alphabet 'ae' at its and if the person is female.

Examples : *Culicoides wirthi* is the name given to a Nearctic species of *Culicoides* insects, dedicating th species part after the surname of the famed American Dipterist Dr. W. W. Wirth, for his monumental contrinution on those insects. Earlier, Dr. Wirth dedicated a new species of genus Stilbezzia biting midyes from Virginia, USA; in remembrance of untiring help of his wife Mrs. Austin Syble Wirth, he named it after her as *Stilobezzia* (*Stilobezzia*) *sybleae.*

(6) Other provisions

(a) Use of Square Bracket : The citation of the name of the author of a species in square brackets, [...], means that the said author's name has been taken from any indirect source because of the original anonymity.

The square breakets are also used to include statement of misidentification.

(b) Names given to hybrids : Hybrids are normally individuals, not populations,and hence are not taxa.·A name given to an animal which later onis found to be a hybrid is a *nomal hybridum*, available for a limited use only—it is not applicable to either of the parental species, not applicable for purpose of synonymy as well; it is usable only for purpose of homonymy.

(c) Protection of well-established names : A valid sc.name if not inuse forover 50 years at a stretch in literature but is referred to by any of itsjunior synonyms consistantly, then as per a provision of the Code, the unused valid and senior name becomes a nomen oblitum (i.e., obliterated name) and its junior name in maximum use becomes the official name for the cluster involved.

(d) Miscellaneous : A genus name is uninominal; so are the names of of taxa above genus rank being however in plural (expressions thatwe commonly do such as, The Culicidae is the dipterous family that includes all mosquitoes, is not correct; we are to say, The culicidae are the ...

A family name should be based on the valid type-genus name.

New species are to be indicated in the first or original description by writing, sp. n., or sp.nov., or spec. nov. (in each case being the abbreviation for species *nouvelle* i.e., new species) after the full name of such a species or by writing full species name followed by the surname/s of author/s of that speices and than putting the words n.sp./ new species (meaning just new species) after a coma-punctuation (,)., or not. examples are :

(i) *Culicoides oxystoma* n.sp.

(ii) *Culicoides oxystoma* Kieffer, sp.n.

(iii) *Culicoides oxystoma* Kieffer,

(iv) *Culicoides oxystoma* sp. nov.

(v) *Culicoides oxystoma* Kieffer, new species

(vi) *Culicoides oxystoma* Kieffer, n.sp.

(vii) *Culicoides oxystoma* spec. nov. ... etc.

Similar provisions also exist for describing other taxon units (gen. nov. for genus etc.)

(e) General remarks : The Linnean System of Binomial Nomeclature is a compromise of the Aristotlian logic and a simple informaiton retrieval system.

The principles perfected so far for this system have helped us to refer to animal populations as per the ways of science. But diversities in the animal groups are so many that quite often, the different groups cannot be tackled satisfactorily. Then, there exists the eternal confusion amongst the various taxonomic school—the conflict of the 'Lumpers' and the 'Splitters', extended lists of the animal taxa reduced to smaller ones by the yardsticks of the former which the latter category of workers are unable to support!

The simplification of the principles guiding to frame the binomial names is also in point. A generic name no longer tells us much about the organism concerned. The worst aspect is the extreme instability of the system itself. The original Linnaean way was generic name + *differentia, i.e.,* species name given in several words explaining in brief the characters of the species, and it was inherent that a change at one point in the system sets in a number of changes as a whole. This is a serious drawback as genera are split or lumped and the species are frequently shifted from one genus to the other. Such changes reduce the practical efficiency of the binomial system, as a reference system, and suggestions are made from time to replace it as follows :

(i) addition of prefixes and suffixes to generic names to indicate class, order etc. Eg. **Papilio** (a butterfly genus) recommended to be written as **YIP apila,** where Y = Insecta, I = Lepidoptera, and a = Invertebrata!

(ii) Michener (1964) favours replacement of binominalism by uninominalism or mononominalism. He proposes freezing of original scientific name of a new species for all times by connecting generic and specific name with a hyphen, Eg. *Homo sapiens*, recommended to be made uninomen and written as, *Homo-sapiens*. This has superficial advantages as problems of homonymy willendings to agree with the gender of the genus-name. But, this may create confusion when transfer of one species from one genus to another becomes unavoidable (e.g. bee species **jenseni** first placed in genus **nomia** in the family Halictidae, but now it is placed in genus **Leioproctus** in the family Colletidae). Such a change cannot be adjusted as per Michener's proposal.

(iii) According to Griffiths (1976), the binomial nomenclature is there to stay since species are far too numerous for uninominal specific nomenclature to be practicable. He suggests that the first (the Generic) name in *Binomina* be called the forename (latin : Praenomen), to avoid the essentialist connotations of the term generic, and fresh conventions for choosing forenames be established.

(iv) The adoption of a numerical scheme for the hierarchy in classification, replacing the *binomen* system by a running identification number, is advocated by Hall (1966), Bullis and Roe (1967) and their followers. The numbering is to be done in a Central International Office.

As per this formulation of Numerical Taxonomy, all species described in 1968 will be called as (from the very first species described as new in that year irrespective of the animal group on a global basis) : 968-I, 968-2, 968-3 etc.

(v) Henning (1969) advocates a scheme of unclassified hierarchy for fossil insects by appending a numerical indication of the subordination sequence. Analysing the phylogeny of 6 fossil species of Mecoptera insects, the names of those soecies are given as : a (1-3), b (2-3), c (3.4), d (4-5) and f (5-7), in numerical sequence.

With a rising need for easy information retrieval and easy programming for computers, there is little doubt that the taxonomists may need to adopt some other system sooner or later. The old binomial system will stay side by side with this system for sometime and may finally get totally replaced. However, of what have been suggested so for, the binomial system is found to be the most satisfactory one since all the numerical systems contrived fail to cope fully with the subtlities produced by the continuous discovery of new taxa in different parts of the world and the resultant shifts in classification. The binomial system reflects classification of the species taxon in its proper perspective. It shows that one taxon is a member of a next higher taxon. When the classification of a group is well advanced and the genera are trully the natural units, the binomial system can form excellent basis for prediction of phylogenetic, evolutionary and zoogeographical speculation, other systems have hardly such in-built scopes and provisions.

UNIT 5 ☐ The Meanings of Biodiversity

Structure

5.1 Introduction

5.2 Levels of biodiversity

5.3 The regional / historical perspective on species richness

5.4 Local and regional components of diversity

5.5 Ecosystem diversity

5.1 Introduction

Biodiversity is the variety and variability of plant and animal species on our planet. There is a distinction between biological resources and biological diversity. The part of the biological diversity, which are used, or potentially to be used by human civilization is considered as biological resource.

In 1735, Carolus Linnaeus, published a book on the classification of plant and animal species. He proposed a hierarchy of classification, from species through genus, family, order, class, phylum and kingdoms, into which all plant and animal species would fall. The first edition was only 142 pages long but the sixteenth edition was over 2300 pages, as Linnaeus was flooded with information from all over the world. The Linnaean system has come to form a basic tool of biological science. We have, of course, made great progress in understanding the biology of the world in the last two centuries. Concern over the rate of loss of the plant and animal species on our planet has been growing for some years.

Extinction has always been a fact of life. But the intervention of humans has injected a novel thrust into its causes. A large array of impacts has been brought to bear, including over-exploitation, habitat destruction, introduction of exotic pest species and current spurt in various forms of pollution. Therefore, the loss of Biodiversity should be of concern to every one for at least three reasons : First, we have a moral responsibility to protect what are our only known living companions in the universe. Second, humanity has already obtained enormous benefits from biodiversity in the form of foods, medicines, and industrial productions and has the potential to gain many more benefits. Thirdly biodiversity provides essential ecological services to mankind by maintaining the stability of its environment. Not surprising conservation of the world's remaining species has come to assume great importance in the present times.

Biodiversity is the variety of life. The concept of biodiversity includes the entire biological hierarchy from molecules to ecosystems, or the entire taxonomic hierarchy from alleles to kingdoms, all the logical classes in between (individuals, genotypes, population, species etc.), and all of the different members of all those classes. It also includes the diversity of living interactions and processes at all these levels of organization. This is such a wide-ranging description that it has kept the definition of the term "biodiversity" vague and ensured that its measurement remains difficult. For practical purposes we need a much more precise definition. This context is the one in which short term human needs and desires led to broad scale destruction of the biological inheritance of the plant, and in turn gave rise to a movement aimed at protecting that inheritance. This movement has the implicit goal of protecting the variety of life, which is a different goal from the equally legitimate one of preserving particular species. The term "biodiversity" was coined by Walter G Rosen during the organization of the 21-24 September 1986 "National Forum on Bio Diversity" held in Washington DC, under the auspices of the US national academy of science and the Smithsonian Institution (Takacs 1996). The term "biodiversity" found wide use immediately following its coining.

The biological realm-patterns and processes are marked by variability and complexity at every level of organization. It is useful at this stage to distinguish between biological diversity and what has come to be called biological integrity. Integrity refers to the persistence of ecosystem processes such as the generation of biomass or the flow of nutrients and energy within specific bounds. The conservation of biodiversity is presumably related in some way to the maintenance of biological integrity. At one time it was widely believed that complexity of process pathways led to the stability of ecosystems (Mac Arthur 1955; Elton 1958). Since increased diversity at almost any level of biological organization leads to increased complexity and stability presumably implies integrity, such a complexity stability relationship implies a biodiversity integrity relationship. However, there remains little uncontroversial theoretical rationale (May 1973) or empirical results (Pimm 1984, 1991; Shrader-Frechette and Mc Cay 1993) supporting the diversity stability relationship. Nevertheless, it is at last likely that the maintenance of ecosystem processes will contribute to the conservation of biodiversity since it may ensure that all important biological processes persist (Karr 1991; Angermeier and Karr 1994; Margules and pressey 2000).

5.2 Levels of biodiversity

It has become a widespread practice to define biodiversity in terms of genes, species and ecosystems, corresponding to three fundamental and hierarchically - related levels of biological organisation.

Genetic diversity : This represents the heritable variation within and between populations of organisms. Ultimately, this resides in variations in the sequence of the four base pairs which as components of nucleic acids, constitute the genetic code. New genetic variation arises in individuals by gene and chromosome mutations, and in organisms with sexual reproduction can be spread through the population by recombination. Other kinds of genetic diversity can be identified at all levels of organization, including the amount of DNA per cell, and chromosome structure and number.

This pool of genetic variation present within an interbreeding population is acted upon by selection. Differential survival results in changes of the frequency of genes within this pool, and this is equivalent to population evolution. The significance of genetic variation is thus clear that it enables both natural evolutionary change and artificial selective breeding to occur. Only a small fraction (often less than 1%) of the genetic material of higher organisms is outwardly expressed in the form and function of the organism; the purpose of the remaining DNA and the significance of any variation within it is unclear.

Each of the estimated 10' different genes distributed across the world's biota does not make an identical contribution to overall genetic diversity. In particular, those genes which control fundamental biochemical processes are strongly conserved across different taxa and generally show little variation, although such variation that does exist may exert a strong effect on the viability of the organism; the converse is true of other genes.

Species diversity : Because the living world is most widely considered in terms of species, biodiversity is very commonly used as a synonym, of species diversity, in particular of species richness, which is the number of species in a site or habitat. Discussion of global biodiversity is typically presented in terms of global numbers of species in different taxonomic groups. The species level is generally regarded as the most natural one at which to consider whole organism diversity. Species are the primary locus of evolutionary mechanisms, and the origination and extinction of species are the principal agents in governing biological diversity in most senses in which the latter can be defined. On the other hand, species cannot be recognised and enumerated by systematists with total precision, and the concept of what a species is differs considerably between groups of organisms.

Further, a straight forward count of the number of species only provides a partial indication of biological diversity.Organisms which differ widely from each other in some respect by definition contribute more to overall diversity than those which are very similar. A site with many different higher taxa present can be said to possess more taxonomic diversity than another with fewer higher taxa but many more species. Marine habitats frequently have more different phyla but fewer species than terrestrial habitats, *i.e.*, higher taxonomic diversity but lower species diversity. The ecological importance of a species can have a direct effect on community structure, and thus on overall biological diversity.

Between habitat and within habitat diversity : Small uniform habitats must be shared, but relatively large patches of land may be partitioned among species. Mac Arthur (1965) introduced convenient terminology to described these two conditions : "within - habitat diversity" and "between habitat diversity." Earlier Whittaker (1960) had pointed out the same essential dichotomy, calling the two conditions "alpha diversity" and "beta diversity". If animals colonize a large empty habitat with considerable resource plasticity, they will share all parts of the habitat, resulting in an initial within habitat diversity (Alpha diversity). But if more colonizing animals arrive, the greater crowding might will cause the habitat to be divided into subhabitats by species keeping themselves apart. Between habitat diversity (ß diversity) has now been added to the original within habitat diversity.

Cody (1975) extended the classification for bird species diversity to allow comparison among whole geographic regions. "Point diversity" describes the complete overlap of bird ranges over very small areas. "Gamma diversity" describes the species replacements that occur over very large geographic regions. Adding these two concepts results in the following scheme : -

Within habitat	Point diversity	=	Found together in very small samples
	Alpha diversity	=	Found together in small homogeneous habitats
Between habitat	Beta diversity	=	Diversity across a diversity of habitats
	Gamma diversity	=	Regional diversity including geographical replacement.

Contemporary thinking about community organization reconciles the regional historical and local /deterministic views of regulation of diversity :—

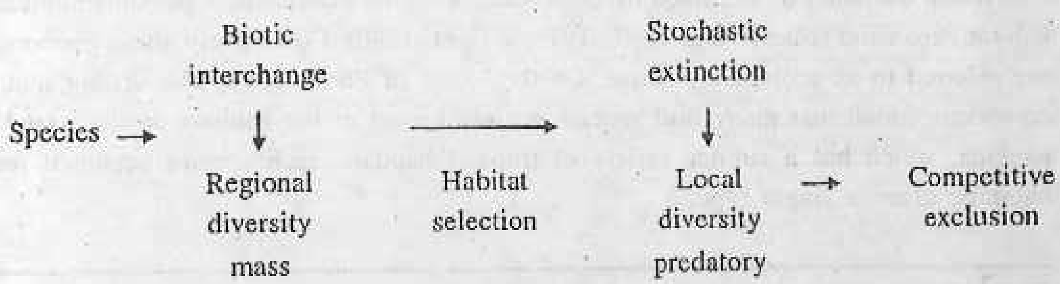
Until the late 1950s, ecologists viewed species diversity as a regional phenomenon representing the outcome of historical events. We shall refer to this view as the regional / historical view of species richness. Subsequently, ecologists began to ask questions about how population interactions such as predation and competition affect species diversity. Fundamental to this local/deterministic view is the idea that local interactions, which tend to reduce diversity through competitive exclusion and extinction, somehow balance regional processes that increase diversity through specialisation and migration, maintaining a kind of equilibrium. Let us examine the local/deterministic and regional /historical views in more detail.

5.3 The regional/historical perspective on species richness

While emphasizing the importance of local population interaction in determining local diversity, ecologists were still faced with the reality of regional processes. Local interections, taking place within a milieu of local conditions, determine the number of the species that can coexist in the local community. This number is the saturation point, beyond which no new species can be added to the community. Regional processes, such as species production, migration, and historical accidents of geographic location, determine regional diversity. The difference between the two is accommodated by difference in the degree of habitat specialization, or beta diversity which is adjusted to maintain the number of species locally in accordance with local conditions while the number of species in the region may vary.

5.4 Local and regional components of diversity

Local and regional factors are expressed in different components of species diversity, two of which are alpha (or local) diversity and gamma (or regional) diversity (Whittaker 1972). Local diversity is the number of species in a small area of more or less uniform habitat clearly.



Local diversity is sensitive to definition of habitat, area, and intensity of sampling effort. Regional diversity is the total number of species observed in all habitats within a region. By region, ecologists generally mean a geographic area that includes no significant barriers to dispersal of organisms. Thus, the boundaries of a region depend on which organisms we consider. The important point is that within a region, distributions of species should reflect their selection of suitable habitats rather than their inability to disperse to a particular locality.

When each species occurs in all habitats within a region, local and regional diversities are the same. When each habitat has a unique flora and fauna, regional diversity equals the average local diversity times the number of habitats in the region . Ecologists refer to the difference, in species from one habitat to the next as beta diversity. The greater the difference, or turnover, of species between habitats, the greater the beta diversity. There are many different ways of quantifying beta diversity, but a useful one is the number of unique habitats recognized by species within a region. When all species are habitat generalists, there is effectively only a single habitat within the region, and beta diversity is equal to 1. As habitat specialization increases, more habitats are recognized. Accordingly, gamma diversity equals alpha diversity X beta diversity. It is not practical to measure beta diversity directly because the habitat distributions of species overlap. But we can calculate the number of unique habitats recognized by species within a region from the relationship, beta diversity = gamma diversity/alpha diversity.

Where many species coexist within a region, each occurs in relatively few kinds of habitats (Mac Arthur *et al.*, 1966). Changes in gamma diversity generally result from parallel changes in both alpha and beta diversity. This relationship has been most carefully noted in comparisons of islands and mainland regions, in which one may examine a range of species diversity resulting from different degrees of geographic isolation within similar ranges of physical conditions. Islands usually have fewer species than comparable mainland areas. Island species often attain greater densities than their mainland counterparts, a phenomenon called density compensation (Crowell, 1962). Also they expand into habitats that would normally be occupied by other species on the mainlands, a phenomenon called habitat expansion (Mac Arthur *et al.*, 1972, Wright ,1980). Collectively, these phenomena are referred to as ecological release. On the island of Puerto Rico, Mac Arthur and his coworkers found that many bird species occupied most of the habitats on the island. In panama, which has a similar variety of tropical habitats, each species occupied fewer habitats, often a single type.

5.5 Ecosystem diversity

It is possible to define what is in principle meant by genetic and species diversity, and to produce various measures thereof, there is no unique definition and classification of ecosystems at the global level, and it is thus difficult in practice to assess ecosystem diversity other than on a local or regional basis and then only largely in terms of vegetation. Ecosystems further differ from genes and species in that they explicitly include abiotic components, being partly determined by soil parent material and climate. Ecosystem diversity is often evaluated through measures of the diversity of the component species. This may involve assessment of the relative abundance of different species as well as consideration of the types of species. In the first instance, the more equally abundant different species are, then in general the more diverse that area or habitat is considered to be. Weight is also given to the numbers of species in different size classes, at different tropic levels, or in different taxonomic groups. Thus, a hypothetical ecosystem, which consisted only of several species of plants, would be less diverse than one with the same number of species but which included animals herbivores and predators.

UNIT 6 □ The Value of Biodiversity

The value of biodiversity is difficult to define, and is often impossible to estimate. Although biodiversity rarely has a money price in local or international markets, its economic value is wide-ranging and significant. Economists recognize two main types of value : use values and non-use values. Use values refer to the current or future utilitarian value of biodiversity to humankind, and can in turn be sub-divided into direct, indirect, and option values. Examples include the use of wild genes in crop breeding, the tourism value of game reserve, or the ecosystem services of a unique wetland habitat. Non use values refer to the intrinsic, vicarious values attached by individuals to, for example, the continued existence of a particularly "charismatic" species such as the African elephant. These various types of value are shown in table 1 below.

The direct use value of biodiversity can be further sub divided into three categories consumptive, productive and non-consumptive. The main difference between consumptive and productive value is that the former is consumed directly without being traded. This makes valuation more difficult, and may involve a wider range of goods, but is not otherwise of major significance.

Biodiversity confers direct use value in at least three areas : agriculture, medicine and industry. The benefits of biodiversity in agriculture include new crops, diverse traditional farming systems, and improved varieties of existing crops and new pesticides. The introduction of new crops has a massive economic impact in the past (98% of US crop production is based on species originating outside its borders). New products such as the Kiwi fruit from China, continue to be important. It is nevertheless instructive to note that less than, 20 species of the thousands of edible plants known to exist produce most of the worlds food. Three species-wheat, maize and rice-account for 54% of the calorific consumption in developing countries. This demonstrates the important point that economic growth in agriculture is best served by concentrating on a reduced range of species (and a reduced range of varieties). Recent claims that multi-species extractive forest systems give higher financial returns than timber and agriculture need to be assessed critically in this light. The main reasons why diverse extractive systems and subsistence agricultural systems are replaced by more specialized agro-ecosystems is because they are inherently less productive. The important qualification to this is that even specialized agro-ecosystems benefit from local habitat diversity (wild pollinators, natural predators etc.) and from management which maintains diversity, such as crop rotation.

While the exploitation of a diverse range of species may have long run economic cost, genetic diversity is more clearly beneficial. Whether bred into advanced agrosystems, or inherent in transitional one, genetic diversity has considerable economic value. In uncontrolled environments and with low technology levels, genetically diverse traditional agricultural systems exhibit greater stability in the face of climatic, pest and disease risks. Production in any one year might be higher if a smaller range of species and genes was utilized, but the long run average production and/or the minimum production in a particularly bad year, is higher if a wider range is utilized. Traditional technologies are more stable and sustainable than, for example, genetically narrow green revolution technologies, but are also considerably less productive, 1987). Few seriously question the value of replacing local varieties with high yielding varieties.

Genetic diversity will remain extremely important in the future because of the increasing genetic uniformity, and therefore vulnerability, of improved varieties. These have a finite life, and require periodic infusions of new genetic material if pest and disease resistance is to be maintained. New biotechnological techniques can be expected to increase the use of wild germplasm in breeding programmes. The threat presented by global climatic change also requires that the maximum biodiversity be retained, and also that access to important genetic resources in the transition zones is protected. Maintaining the flexibility to respond to climatic change will be an important benefit. With developing country agriculture increasingly vulnerable, the conservation of local lands and wild relatives of economic crops and livestock is of overriding importance.

In addition to the 20 or so major food crops, between 5,000 and 10,000 plant species provide an important source of food and materials. Examples include timber and fuelwood; root crops; beverage crops; spices; fruits, and fibres. Many of these may currently be only of local importance, but have wider potential. Much less is known about the diversity of these species compared with the major food crops, and very little is being done to conserve them, either *ex situ or in situ*. The value of plant germplasm derived by "genepoor" developed countries from "gene-rich" developing countries has led to demands for free access to all plant resources (including elite breeders' lines) and/or financial compensation. The fact that south-south germplasm flows are probably more important than south north flows has not been fully appreciated.

The consumptive and productive value of medicines directly or indirectly derived from wild species is often cited as one measure of the current, and particularly the future, value of biodiversity. In developing countries up to 80% of the people rely on traditional medicine for their primary health care, most of which involves the use of plant extracts. Around 20,000 plant species are believed to be used medicinally in the third world. Some plant-derived drugs have also proved to be extremely valuable for advanced health care.

One quarter of all prescriptions in developed countries is based on plants, including 21 indispensable mainstream drugs. In addition to current drugs, plants contain complex chemical structures which may never be synthesized in the laboratory, and which might provide important clues for new medicines. One of the more remarkable examples are the so-called vinca alkaloids used in the treatment of childhood leukaemia and Hodgkin's disease. These were developed from an extract of the Madagascar periwinkle (*Catharanthus roseus*) and had a market value to the Drug Company concerned of US$ 100 million in 1985.

The value of medicinal diversity *per se* is less easy to determine. There are real costs, which would follow from the reduction in the diversity of accessible medicinal plants. These would either be the costs of subsequent untreated disease, and/or the additional costs of commercial alternatives. These costs have not been estimated. However, the low current value of patented or unpatented novel chemical compounds—measured in terms of commercial companies' willingness to pay - is indicative of a low market value. Few naturally occurring compounds are marketable without an enormous input of costly research and testing. This accounts for most of the value added in drug development. Undeveloped and untested novel chemical compounds are readily available and very cheap for this reason. This indicates that the value attached by the market to biodiversity at source is low, even though the potential economic value to society may be considerably higher. Similar considerations will apply in the case of traded industrial raw materials. The market value of biodiversity for a developing country is not the total export value of natural products. It is the difference between the discounted present value of the export earnings of diverse export portfolio over time, and the export earnings of a less diverse portfolio. This calculation is not easy to do. As in the case of agriculture, it is likely that the trend towards specialization in line with comparative advantage means that the long —term export value of biodiversity is limited. Diverse habitats and species can also have non-consumptive use-value, such as tourism and scientific research. Tourist revenues are clearly affected by the diversity of species that can be seen, and the range of habitats that can be visited. Species diversity, and particularly the presence of charismatic big game species, is a selling point. However, it is doubtful whether much tourism value can be attached to the vast majority of species, such as the 1 million species of invertebrates, except as part of special ecosystems. No overall valuation of wildlife diversity has ever been attempted. Indirect use values of biodiversity include ecosystem processes only to the extent that these are dependent on species diversity. While the total loss of a unique habitat involves the loss of the ecological processes dependent upon it, the precise effect of a partial reduction in species diversity will vary from site to site. There is, for example, no clear evidence of what effect, if any, the removal of a large percentage of the populations of large whales has had on oceanic ecosystems. Nevertheless, valuable ecological services are provided by certain ecosystems, and attempts have been made to value these services in particular situations. An overall estimation of the value of ecosystem services attributable to biodiversity has never been attempted for obvious reasons Other types of indirect use value - such as the welfare gain from television and other media coverage of aspects of biodiversity - could conceivably be estimated.

The potential value of biodiversity in the future provides one of the main justifications for conservation. Given the immense uncertainly about future values, the option value represents the willingness to pay to retain the option of preserving access to a diverse range of habitats/species/genes. A quasi-option value is the economic value of choosing not to take irreversible steps if new information about alternative outcomes will become available in future. There will certainly be a need for new genetic material to offset new disease or past threats to major food crops. Conservationists also point to the current value of a few naturally occurring compounds, and to the fact that only a fractions of the number of existing species have been assessed for their value to science, agriculture, medicine and industry. Most plant - derived drugs, for example, are obtained from less than 100 of the 250-750,000 species of higher plants in existence. However, the costs of accessing and realizing this genetic potential are immense, and may be prohibitive. Only a small fraction of the number of species existing have ever been screened, and there is evidence that gene banks are already too large and poorly documented to be effectively used.

The final category of value is existence value. These are intrinsic values, unassociated with actual or potential use, which reflect the ability that people receive from simply knowing something exists.The fact that hundreds of thousands of people in developed countries are willing to pay conservation organization to campaign on behalf of endangered species and habitats indicates that people do attach economic value to the existence of some species. There are reasons for thinking that the existence values attached to charismatic species such as whales, elephants and rhinos may not be indicative of existence value more generally. On the other hand, high existence values are attached to habitats even when most of the constituent species are neither known nor valued individually.

UNIT 7 ☐ Threats to Global Biodiversity

Structure

7.1 Introduction

Extinction is a natural event and, from a geological perspective, routine. We now know that most species that have ever lived have gone extinct. The average rate over the past 200 million years is 1-2 species per year, and 3-4 families per million year. The average duration of a species is 2-10 million years. There have also been occasional episodes of mass extinction, when many taxa representing a wide array of life forms have gone extinct in the same blink of geological time.

In the modern era, due to human actions, species and ecosystems are threatened with destruction to an extent rarely seen in earth history. Probably only during the handful of mass extinction events have so many species been threatened, in so short a time.

What are these human actions? There are many ways to conceive of these - let's consider two.

First we can attribute the loss of species and ecosystems to the accelerating transforming of the earth by a growing human population. As the human population passes the six billion marks, we have transformed, degraded or destroyed roughly half of the word's forests. We appropriate roughly half of the world's net primary productivity for human use. We appropriate most available fresh water, and we harvest virtually all of the available productivity of the oceans. It is little wonder that species are disappearing and ecosystems are being destroyed.

Second, we can examine following types of human actions that threaten species and ecosystems :

7.2 Causes of the extinction of biodiversity

Over-hunting : Over hunting has been a significant cause of the extinction of hundreds of species and the endangerment of many more, such as whales and many African large mammals. Most extinctions over past several hundred years are mainly due to over-harvesting for food, fashion and profit. Commercial hunting, both legal and illegal, is the principal threat. Snowy egret, passenger pigeon, heath hen are USA examples. At $16,000 per pound and $40,000 to $100,000 per horn, it is little wonder that some rhino species are down to only a few thousand individuals, with only a slim hope of survival in the wild. The pet and decorative plant trade falls within this commercial hunting category, and includes a mix of legal and illegal activities. The annual trade is estimated to be at least $5 billion, with perhaps1/4 to 1/3 of it illegal.

Sport or recreational hunting causes no endangerment of species where it is well regulated, and may help to bring back a species from the edge of extinction. Many wildlife managers view sport hunting as the principal basis for protection of wildlife.

While over-hunting, particularly illegal poaching, remains a serious threat to certain species, for the future, it is less important than other factors mentioned next.

Habitat loss/degradation/fragmentation : Habit loss/degradation/fragmentation is an important cause of known extinction. As deforestation proceeds in tropical forests, this promises to become the cause of mass extinction caused by human activity.

Habitat damage, especially the conversion of forested land to agriculture, has a long human history. It began in China about 4,000 years ago, was largely completed in Europe by about 400 years ago, and swept across USA over the past 200 years or so. In the new world tropics, lowland, seasonal, deciduous forest began to disappear after 1500 with Spanish and Portuguese colonization of the New world. These were the forested regions most easily converted to agriculture, and with a more welcoming climate. The more forbidding, tropical humid forests came under attack mainly in 20th century, under the combined influences of population growth, inequitable land and income distribution, and development policies that targeted rain forests as the new frontier to colonize.

Tropical forests are so important because they harbor at least 50%, and perhaps more, of world's biodiversity. Direct observations, reinforced by satellite data, documents that these forests are declining. The original extent of tropical rain forests was 15 million km^2. Now there remains about 7.5-8 million km2, so half is gone. The current rate of loss is estimated at near 2% annually. While there is uncertainty regarding the rate of loss, and what it will be in future, the likelihood is that tropical forests will be reduced to 10-25% of their original extent by late. 21st century.

Habitat fragmentation is a further aspect of habitat loss that often goes unrecognized. The forest, meadow, or other habitat that remains generally is in small, isolated bits rather than in large, intact units. Each is a tiny island that can at best maintain a very small population. Environmental fluctuations, disease, and other chance factors make such small isolates highly vulnerable to extinction. Any species that requires a large home range, such as a grizzly bear, will not survive if the area is too small. Finally, we know that small land units are strongly affected by their surroundings in terms of climate, dispersing species, etc. As a consequence, the ecology of a small isolate may differ from that of a similar ecosystem on a large scale.

For the future, habitat loss, degradation, and fragmentation combined is the single most important factor in the projected extinction crisis.

Invasion of non-native species : Invation of non-native species is an important and often-overlooked cause of extinction. The African Great Lakes - Victoria, Malawi and Tanganyika are famous for their great diversity of endemic species, termed "species flocks", of cichlid fishes. In Lake Victoria, a single, exotic species, the Nile perch, has become established and may cause the extinction of most of the native species, by simply eating them all. It was a purposeful introduction for subsistence and sports fishing, and a great disaster.

Of all documented extinction since 1600, introduced species appear to have played a role in al least half. The clue is the disproportionate number of species lost from island : some 93% of 30 documented extinction of species and sub-species of amphibians and reptiles, 93% of 176 species and sub-species of land and freshwater birds, but only 27% of 114 species and sub-species of mammals. Why are island species so vulnerable, and why is this evidence of the role of non-indigenous species?

Islands are laboratories for evolution that effects the entire biological system. Effects are especially likely when two or more species are highly inter-dependent, or when the affected species is a "keystone" species, meaning that it has strong connections to many other species.

The seeds of the tree Calvaria major, now found exclusively on the island of Mouritius, must pass through the abrasive gut of a large animal in order to germinate. Their tough seed coats are protection against digestion, but also a kind of living coffin, for the seed can not germinate unless abraded. None of the animals currently on Mouritius have that ability. The dodo, hunted to extinction in the late 17th century probably was the key to recruitment in this species. Some seeds, abraded, roughened, and excreted by dodos, germinated and grew. Today, no seeds germinate, and only a few very old trees now survive. The blackfooted ferret was once very abundant in the western prairies. It preyed upon prairie dogs and used their burrows to nest in poisoning of prairie dogs has greatly reduced their abundance, and the blackfooted ferret is now the rarest mammal in North America.

Pollution : Pollution from chemical contamination certainly poses a further threat to species and ecosystems. While not commonly a cause of extinction, it likely can be for species whose range is extremely small, and threatened by contamination. Several species of desert pupfish, occurring in small isolated pools in the US southwest, are examples.

Climate change : A changing global climate threatens species and ecosystem. The distribution of species is largely determined by climate, as is the distribution of ecosystems and plant vegetation zones. Climate change may simply shift these distributions but, for a number of reasons, plants and animals may not be able to adjust. The pace of climate change almost certainly will be more rapid than most plants are able to migrate.

Presence of roads, cities, and other barriers associated with human presence may provide no opportunity for distributional shifts. Parks and nature reserves are fixed locations. For these reasons, some species and ecosystems are likely to be eliminated by climate change. Agricultural production likely will show regional variation in gains and losses, depending upon crop and climate.

As a consequence of these multiple forces, many scientists fear that by end of next century, perhaps 25% of existing species will be lost. Estimates of current and future extinction rates are based on well-documented relationships between the number of species in a region and habitat area, and on reasonable well-known rates of habitat loss. We must also employ some ratio to approximate the total number of species, from the number of described species. The relationship between species (S) and area (A) is described by the equation : S = CAz, where z is the slope of the log-linear relationship, and C is a constant which described the height of the line. Based on censuses of species on islands, the number of species found on an island increases log-linearly with island area. Conversely, as island is reduced, so is the number of species that will be found there. The slope (z) usually varies between 0.15 to 0.35. When combined with current rates of loss of tropical forest, these values of the slope translate into species extinction rates of roughly 0.5% annually. Extrapolated to the year 2020, roughly 20% of remaining species will disappear. Simply using the most conservative values of the slope, and assuming the true biodiversity to tropical forests is roughly 10 million species, the projected rate of loss of species is 27,000 per year, and three during this hour.

UNIT 8 ☐ Approaches Determining Conservation Priorities

Structure

8.1 Introduction

8.2 The regional approach

8.3 The national approach

8.1 Introduction

Some ecosystems within a nation have more species than others, so do some nations have more species than others (usually because they contain more ecological diversity). It seems worthwhile to identify which parts of the world contain the greatest diversity. This problem can be approached on at least three different levels : the region, the nation, and the site.

8.2 The regional approach

8.2.1 The regional approach : Critical areas in tropical forests and temperate areas

It is generally accepted that the greatest threat of species loss is in the tropical forests, which are thought to contain at least half the world's species on just 7 percent of the world's land surface (Wilson, 1988a). But within this richest of the world's biomes, a relatively small number of particularly rich areas harbor an inordinately large share of the earth's biodiversity, featuring exceptional concentrations of species with exceptional levels of endemism.

The committee on Research Priorities in Tropical Biology (NAS, 1980) identified 11 areas in the tropics that, because of their great biological diversity, high levels of endemism, and the rate with which their forests are being converted to other purposes, seem to demand special attention. These are :

- Coastal forests of Ecuador,
- The " Cocoa region" of Brazil,

- Eastern and southern Brazilian Amazon,
- Cameroon,
- Mountains of Tanzania,
- Madagascar,
- Sri Lanka
- Borneo,
- Sulawesi,
- New Caledonia, and
- Hawaii.

Myers (1988c) developed the approach to critical areas identifying 10 tropical forest "hotspots, " (Plus 2 in the developed world -Hawaii and Queensland) totaling about 3.5 percent of the primary remain tropical forest (and only 0,2 percent of the land surface of the planet) but containing at least 27 percent of the higher plant species found in the tropics, no less than 13.8 percent of the world's plants are found only in these hotspots.

The focus on tropical countries, however, can lead to insufficient attention being given to extremely important temperate areas. For example, of the 23,200 species of plants estimated to occur in Southern Africa (South Africa, Lesotho, Swaziland, Namibia and Botswana), 18,560 (i.e., 80 percent) are endemic to the region. This gives the area the highest species richness (calculated as species/area ratio) in the world, 1.7 times greater than that of Brazil. Of these, 2,373 have been reported as threatened,

8.2.2 The regional approach : diversity in the seas

While the tropical forests are thought to still contain millions of undescribed species, the world's oceans are also poorly known and regularly yield major new discoveries. A totally new phylum, Loricifera, was described only in 1986; a shark over 5 meters long (known as "the megamouth shark") has been discovered in the past decade a species of mussel living near hydrocarbon seeps in the Gulf of Mexico was found to be feeding on methane. Deep-sea communities have been found to be far richer than suspected, with seafloor sediments at depths of 1,500 to 2,500 meters off the coast of New Jersey found to contain 898 species in more than a hundred families and a dozen phyla (Grassle, 1989). Entirely new habitats - hydrothermal ocean vents have been discovered in the past decade to consist of at least 16 previously unknown families of invertebrates. At the higher taxonomic level of phylum, marine ecosystems are actually more diverse than either terrestrial or fresh water biomes, with more phyla and endemic phyla.

The oceans are a great new frontier whose productivity is just beginning to be harnessed by humans. Far greater efforts are required to ensure that the exploitation is based on a more complete knowledge of how marine ecosystems function, how marine biodiversity contributes to productivity, and what management activities are required to ensure that the characteristic diversity of the seas is maintained.

8.3 The National Approach : "Megadiversity Countries"

As developed by Mittermeier,1988, Mittermeier and Warmer, 1989, the megadiversity country concept recognizes that :

- Basic scientific information on biodiversity and endangered ecosystems should be our first step in assessing international conservation priorities and conservation programmes are to be developed with and by the governments of sovereign national.
- Biodiversity is by no means evenly distributed among the world's 168 countries; and that a very small number of countries, lying partly or entirely within the tropics, accounts for a very high percentage of the world's biodiversity (including marine, freshwater and terrestrial diversity), and that these countries require very special international conservation attention.

The megadiversity concept integrates biological information of many different kinds, but the two main criteria for inclusion in this category are total species numbers and levels of endemism both as the species level and at higher taxonomic categories (e.g., genus, family).

Although data are still being gathered on this topic, preliminary indications are that about a dozen countries belong to the megadiversity list, including Brazil, Colombia, Ecuador, Peru, Mexico, Zaire, Madagascar, Australia, China, India, Indonesia and Malaysia. These countries by themselves account for 60 to 70 percent (and perhaps even more) of all the world's biodiversity. Of these, Brazil, Colombia, Indonesia and Mexico are especially rich in species numbers (and often have high endemism as well) for most groups of organisms on which information is available. Madagascar and Australia, though usually not as high in total species numbers (but see Box 19 for reptile diversity in Australia), belong to the megadiversity list because of their very high degrees of endemism, both at the species level and also at higher taxonomic categories like the genus and family. Although the megadiversity countries (e.g., Brazil, China) are among the world's largest and would be expected to have high diversity simply because of their size, their diversity for exceeds that of other countries of similar size (e.g., Canada, U.S.A, Russia). Furthermore, several of megadiversity countries are quite small (e.g. Ecuador, Madagascar, Malaysia), with the diversity being due more to topography, climate and/or long isolation than to surface area. In any case, large, small or medium - sized, these countries have great strategic importance in conservation of biological diversity worldwide. They themselves have a great responsibility to the world to conserve their biological wealth, and the international community has a special responsibility to them to provide any assistance that might be required to achieve their conservation goals.

The biological resources of each and every country are of critical importance, at least to their own survival and well being (even not particularly important in the global picture), and therefore worthy of national and international attention for the reason alone. Rather, the megadiversity approach is aimed at focusing attention on these highly diverse, strategically critical megadiversity countries roughly in proportion to the biological wealth that they harbor and regardless of how difficult it might be to achieve conservation within them. Furthermore, it recognizes that if we do not pay sufficient attention to these megadiversity countries, we will loss a major percentage of the world's biodiversity regardless of how successful we are in the other less diverse countries.

UNIT 9 ☐ Biodiversity Distribution of the World

Structure

9.1 A profile of biodiversity distribution

Globally, about 1.7 million organisms have been indentified and designated. About 6% of the identified species life in boreal or polar latitudes, 59% in the temperate zones, and the remaining 35% in the temperate zones, and the remaining 35% in the tropics (See Table below).

Table : The estimated number of species in three major climatic zones

Zones	Number of identified species (x 106)	Estimated total number of species	
		Assume 5 × 106	Assume 10x 106
Boreal	0.1	0.1	0.1
Temperate	1.0	1.2	1.3
Tropical	0.6	3.7	8.6
Total	1.7	5.0	10.0

Clearly, tropical and subtropical biotas are much more species rich than those of temperature higher-latitude regions. Invertebrates comprise the largest proportion of described species, with insects making up the bulk of that total, and beetles (Coleoptera) comprising the greater fraction of the insects.

Table : Estimated number of species in various classes of organisms

	Number of identified species	Estimated total number of species
Nonvascular plants	150.000	200.000
Vascular plants	250.000	280.000
Invertebrates	1,300.000	4,400.000b
Fishes	21.000	23.000
Amphibians	3123	3500
Reptiles	5115	6000
Birds	8715	9000
Mammals	4170	4300
Total	1,742.000	4,926.000

Furthermore, it is believed that there is a tremendous richness of undescribed insects in the tropics, possibly as many as another 30 million species, again mostly beetles.

These estimates of enormous numbers of underscribed species of tropical insects have been challenged as being unrealistically large (*e.g.*, Gaston, 1991). In some respects, however, the actual numbers of insect species are less important than the fact that so many of them are becoming extinct through loss of their tropical forest habitats.

Although it is often downplayed in conservation programmes that tend to focus on large, charismatic vertebrates or on particularly noteworthy plants, the species richness of insects and other invertelrates is ecologically important in its own right. Acording to Janzen (1987), these animals "are more than just decorations on the plants, rather they are the building blocks and glue for much of the habitat." These conclusions were based on a number of observations, including the following : (I) insects are the primary foods of most of the small, vertebrates carnivores of tropical forest; (2) insects are important predators of seeds and they thereby influence the plant species composition of the forest, and (3) insects are important pollinators, often in obligate, species specific relationship with particular plant species. These and other observations indicate that insects have a strong influence on the structure and functioning of tropical ecosystems.

These tropical forests are much more species rich than temperate forests, which typically have fewer than 12-15 tree species. The great smokes of the United States harbur some of the richest temperate forests in the world, and they typically contain 30-35 species (Leigh, 1982).

Note, however, that not all tropical forests are rich is species. In Sumatra, for example, mangrove forests only have about six species of tree, while some lowland stands dominated by ironwood (Ensider oxylon zwageri) are virtually monospecific, with as many as 96% of trees being this valuable species, prsent in all size and age categories (Whiten et al., 1987).

A few systematic studies have been made of the richness of avian species in plots of moist tropical forest. Ferborgh et al. (1990) found 245 resident and another 74 transient species in a a7-ha plot of Amazonian floodplain forest in peru. Thiollay (1992) recorded 239 species of birds in a primary Amazonian rainforest in Franch Guiana, Whitten et al. (1987) reported 151 species in a 15-ha plot of lowland forest in Sumatra. These species richness are substantially greater than what is found in typical, temperate forests in North America. For example, during a 15 year monitoring period, the number of bird species breeding in a 10-ha plot of hardwood forest at Hubbard Brook, New Hampshire, ranged from 17 to 28 (Holmes *et al.* 1986).

There have been few systematic studies of all biota of particular tropical ecosystems. In one case, a savannah like, dry tropical forest in Costa Rica was studied for several years (Janzen, 1987). It was estimated that a particular 108 - km2 reserve had about 700 plant species, 400 vertebrate species, and a remarkable 13 thousand species of insects, including 3140 species of moths and butterflies.

9.2 Biodiversity profile of India

Geography and Major Biomes

India is the seventh largest country in the world and Asia's second largest nation with an area of 3,287,263 square km. The Indian mainland stretches from 8 4' to 37 6' N latitude and from 68 7' to 97 25' E longitude (Figure 1). It has a land frontier of some 15,200 kms and a coastline of 7,516 km. India's northern frontiers are with Zizang (Tibet) in the Peoples Republic of China, Nepal and Bhutan. In the north-west, India borders on Pakistan; in the north-east, Bangladesh and China and Myanmar; and in the east, Myanmar The southern peninsula extends into the tropical waters of Indian Ocean with the Bay of Bengal lying to the south-east and the Arabian Sea to the south-west.

Physically the massive country is divided into four relatively well defined regions - the Himalayan mountains, the Gangetic river plains, the southern (Deccan) plateau, and the islands of Lakshadweep, Andaman and Nicobar. The Himalayas in the far north include some of the highest peaks in the world. The highest mountain in the Indian Himalayas is Khangchenjunga (8586 m), which is located in Sikkim on the border with Nepal. To the south of the main Himalayan mass lie the Lesser Himalaya, rising to 3,600-4,600 m, and represented by the Pir Panjal in Kashmir and Dhaula dhar in Himachal Pradesh. Further south, flanking the Indo-Gangetic Plain, are the Siwaliks, which rise to 900-1,500 m.

The northern plains of India stretch from Assam in the east to the Punjab in the west (a distance of 2,400 km), extending south to terminate in the saline swamplands of the Rann of Kachchh (Kutch), in the state of Gujarat. Some of the largest rivers in India including the Ganga (Ganges), Ghrghara, Brahmaputra, and the Yamuna flow across this region. The delta area of these rivers is located at the head of the Bay of Bengal, partly in the Indian state of west Bengal but mostly in Bangladesh. The plains are remarkably homogeneous topographically : for hundreds of kilometres the only perceptible relief is formed by floodplain bluffs, minor natural levees and hollows known as 'spill patterns', and the belts of ravines formed by gully erosion along some of the larger rivers. In this zone, variation in relief does not exceed 300 m (FAO/UNEP, 1981) but the uniform flatness conceals a great deal of pedological variety. The agriculturally productive alluvial silts and clays of the Ganga-Brahmaputra delta in north-eastern India, for example, contrast strongly with the comparatively sterile sands of the Thar Desert which is located at the western extremity of the Indian part of the plains in the state of Rajasthan.

The climate of India is dominated by the Asiatic monsoon, most importantly by rains from the southwest between June and October, and drier winds from the north between December and February. From March to May the climate is dry and hot.

Wetlands

India has a rich variety of wetland habitats. The total area of wetlands (excluding rivers) in India is 58,286,000ha, or 18.4% of the country, 70% of which comprises areas under paddy cultivation. A total of 1,193 wetlands, covering an area of about 3,904,543 ha, was recorded in a preliminary inventory coordinated by the Department of Science and Technology, of which 572 were natural (Scott, 1989). Two sites - Chilka Lake (Orissa) and Keoladeo National Park (Bharatpur) - have been designated under the Convention of Wetlands of International Importance (Ramsar Convention) as being especially significant waterfowl habitats. The country's wetlands are generally differentiated by region into eight categories (Scott, 1989) : the reservoirs of the Decan Plateau in the south, together with the lagoons and the other wetlands of the southern west coast; the vast saline expanses of Rajasthan, Gujarat and the gulf of Kachchh; freshwater lakes and reservoirs from Gujarat eastwards through Rajasthan (Kacoladeo Ghana National park) and Madhya Pradesh, the delta wetlands and lagoons of India's east coast (Chilka Lake); the freshwater marshes of the Gangetic Plain; the floodplain of the Brahmaputra; the marshes and swamps in the hills of north-east India and the Himalayan foothills; the lakes and rivers of the montane region of Kashmir and Ladakh; and the mangroves and other wetlands of the island arcs of the Andamans and Nicobars.

Forests

India possesses a distinct identity, not only because of its geography, history and culture but also because of the great diversity of its natural ecosystems. The panorama of Indian forests ranges from evergreen tropical rain forests in the Andaman and Nicobar Islands, the Western Ghats, and the north-eastern states, to dry alpine scrub high in the Himalaya to the north. Between the two extremes, the country has semi-evergreen rain forests, deciduous monsoon forests, thorn forests, subtropical pine forests in the lower montane zone and temperate montane forests (Lal, 1989).

One of the most important tropical forests' classifications was developed for Greater India (Champion, 1936) and later republished for present-day India (Champion and Seth, 1968). This approach has proved to have wide appliation outside India. In it, 16 major forests types are recognised, subdivided into 221 minor types. Structure, physiognomy and floristics are all used as characters to define the types.

The main areas of tropical forest are found in the Andaman and Nicobar Islands; the Western Ghats, which fringe the Arabian Sea coastline of peninsular India; and the greater Assam region in the north east. Small remnants of rain forest are found in Orissa state. Semi-evergreen rain forest is more extensive than the evergreen formation partly because evergreen forests tend to degrade to semi-evergreen with human interference. There are substantial differences in both the flora and fauna between the three major rain forest regions (IUCN, 1986; Rodges and Panwar, 1988).

The Western Ghats Monsoon forests occur both on the western (coastal) margins of the ghats and on the eastern side where there is less rainfall. Figure 4 shows the distribution of forest in Kerala State, which contains part of the Western Ghats range. These forests contain several tree species of great commercial significance (*e.g.* Indian rosewood *Dalbergia latifolia*, Malabar Kino *Pterocarpus marsupium*, teak and *Terminalia crenulata*), but they have now been cleared from many areas. In the rain forests there is an enormous number of tree species. At least 60 percent of the trees of the upper canopy are of species which individually contribute not more than one percent of the total number. Clumps of bamboo occur along streams or in poorly drained hollows throuout the evergreen and semi-evergreen forests of south-west India, probably in areas once cleared for shifting agriculture.

The tropical vegetation of north-east India (which includes the states of Assam, Nagaland, Manipur, Mizoram, Tripura and Meghalaya as well as the plain regions of Arunachal Pradesh) typically occurs at elevations up to 900 m. It embraces evergreen and semi-evergreen rain forests which are found in the Assam Valley, the foothills of the eastern Himalayas and the lower parts of the Naga Hills, Meghalaya, Mizoram, and Manipur where the rain fall exceeds 2300 mm per annum. In the Assam Valley the giant *Dipterocarpus macrocarpus* and *Shorea assamica* occur singly, occasionally attaining a girth of up to 7 m and a height of up to 50 m. The monsoon forests are mainly moist sal *Shorea robusta* forests, which occur widely in this region (IUCN, 1991).

The Andamans and Nicobar islands have tropical evergreen rain forests and tropical semi-evergreen rainforests as well as tropical monsoon/moist monsoon forests (IUCN, 1986). The tropical evergreen rain forest is only slightly less grand in stature and rich in species than on the mainland. The dominant species is *Dipterocarpus grandiflorus* in hilly areas, while *Dipterocarpus kerrii* is dominant on some islands in the southern parts of the archipelago. The monsoon forests of the Andamans are dominated by *Pterocarpus dalbergioides* and *Terminalia* spp.

Marine Environment

The nearshore coastal waters of India are extremely rich fishing grounds. The total commercial marine catch for India has stabilised over the last ten years at between 1.4 and 1.6 million tonnes, with fishes from the clupeoid group (e.g. sardines *Sardinella* sp., Indian shad *Hilsa* sp. And whitebait *Stolephorus* sp.) accounting for approximately 30% of all landings. In 1981 it was estimated that there were approximately 180,000 non-mechanised boats (about 90% of India's fishing fleet) carrying out small scale, subsistence fishing activities in these waters. At the same time there were about 20,000 mechanishtra, Kerala, Gujarat, Tamil Nadu and Karnataka.

Coral reefs occur along only a few sections of the mainland, principally the Gulf of Kutch, off the southern mainland coast, and around a number of islands opposite Sri Lanka. This general absence is due largely to the prsence of major river systems and the sedimentary regime on the continental shelf. Elsewhere, corals are also found in Andaman, Nicobar (**Figure 5**), and Lakshadweep island groups although their diversity is reported to be lower than in south-east India (UNEP/IUCN, 1988).

Indian coral reefs have a wide range of resources which are of commercial value, Exploitation of corals, coral debris and coral sands is widespread on the Gulf of Mannar and Gulf of Kutch reefs, while ornamental shells, chanks and pearl oysters are the basis of an important reef industry in the south of India. Sea fans and seawees are exported for decorative purposes, and there is a spiny lobster fishing industry along the south-east coast, notably at Tuticorin, Madras and Mandapam Commercial exploitation of aquarium fishes from Indian coral reefs has gained importance only recently and as yet no organized effort has been made to exploit these resources. Reef fisheries are generally at the subsistence level and yields are unrecorded.

Other notable marine areas are seagrass beds, which although not directly exploited are valuable as habitats for commercially harvested species, particularly prawns, and mangrove stands. In the Gulf of Mannar the green tiger prawn *Penaeus semisulcatus* is extensively harvested for the export market. Seagrass beds are also important feeding areas for the dugong *Dugong dugon*, plus several species of marine turtle.

Five species of marine turtle occur in Indian waters; Green turtle *Chelonia mydas*, Loggerhead *Caretta caretta*, Olive Ridley *Lepidochelys olivacea*, Hawksbill *Eretmochelys imbricata* and Leatherback *Dermochelys coriacea*. Most of the marine turtle populations found in the Indian region are in decline. The principal reason for the decrease in numbers is deliberate human predation. Turtles are netted and speared along the entire Indian coast. In south-east India the annual catch is estimated at 4,000-5,000 animals, with *C. mydas* accounting for about 70% of the harvest. *C. caretta* and *L. olivacea* are the most widely consumed species (Salm, 1981). *E. imbricata* is occasionally eaten but it has caused deaths and so is usually caught for its shell alone. *D. coriacea* is boiled for its oil which is used for caulking boarts and as protection from marine borers. Incidental netting is widespread. In the Gulf of Mannar turtles are still reasonably common near seagrass beds wehre shrips trawlers operate, but off the coast of Bengal the growing number of mechanized fishing boats has had the effect of increasing incidental catch rates (Kar and Bhaskar, 1981).

9.3 Biodiversity

Species diversity

India contains a great wealth of biological diversity in its forests, its wetlands and in its marine areas. This richness is shown in absolute numbers of species and the proportion they represent of the world total.

Table. Comparison between the Number of Species in India and the World.

Group	Number of species in India (SI)	Number of species in the world (SW)	SI / SW (%)
Mammals	350(1)	4,629(7)	7.6
Birds	1224(2)	9,702(8)	12.6
Reptiles	408(3)	6,550(9)	6.2
Amphibians	197(4)	4,522(10)	4.4
Fishes	2546(5)	21,730(11)	11.7
Flowering Plants	15,000(6)	250,000(12)	6.0

India has a great many scientific institutes and university departments interested in various aspects of biodiversity. A large number of scientists and technicians have been engaged in inventory, research, and monitoring. The general state of knowledge about the distribution and richness of the country's biological resources is therefore fairly good.

Inventories of birds, mammals, trees, fish and reptiles are moderately complete Knowledge of special interest groups such as primates, pheasants, endemic birds, orchids, and so on, is steadily improving through collaboration of domestic scientists with those from overseas.

Endemic species

India has many endemic plant and vertebrate species. Among plants, species endemism is estimated at 33% with 140 endemic genera but no endemic families (Botanical Survey of India, 1983). Areas rich in endemism are north-east India, the Western Ghats and the north-western and eastern Himalayas. A small pocket of local endemism also occurs in the Eastern Ghats. The Gangetic plains are generally poor in endemics, while the Andaman and Nicobar Islands contribute at least 220 species to the endemic flora of India (Botanical Survey of India, 1983).

WCMC's Threatened Plants Unit (TPU) is in the preliminary stages of cataloguing the world's centres of plant diversity; approximately 150 botanical sites worldwide are so far recognized as important for conservation action, but others are constantly being identified (IUCN, 1987). Five locations have so far been issued for India : the Agastyamalai Hills, Silent Valley and New Amarambalam Reserve and Periyar National Park (all in the Western Ghats), and the Eastern and Western Himalaya. Endemism among mammals and birds is relatively low. Only 44 species of Indian mammal have a range that is confined entirely to within Indian territorial limits. Four endemic species of conservation significance occur in the Western Ghats. They are the Lion-tailed macaque *Macaca silenus*, Nilgiri leaf monkey *Trachypithecus johni* (locally better known as Nilgiri langur *Presbytis johnii*), Brown palm civet *Paradoxurus jerdoni* and Nilgiri tahr *Hemitragus hylocrius*.

Only 55 bird species are endemic to India, with distributions concentrated in areas of high rainfall. These areas, mapped by BirdLife International (formerly the International Council for Bird Preservation) are shown in Figure 7. They are located mainly in eastern India along the mountain chains where the monsoon shadow occurs, south-west India (the Western Ghats), and the Nicobar and Andaman Islands (ICBP, 1992). In contrast, endemism in the Indian reptilian and amphibian fauna is high. There are around 187 endemic reptiles, and 110 endemic amphibian species. Eight amphibian genera are not found outside India. They include, among the caecilians, *Indotyphlus*, *Gegeneophis* and the frogs *Ranixalus*, *Nannobatrachus* and *Nyctibatrachus*. Perhaps most notable among the endemic amphibian genera is the monotypic *Melanobatachus* which has a single species known only from a few specimens collected in the Anaimalai Hills in the 1870s (Groombridge, 1983). It is possibly most closely related to two relict general found in the mountains of eastern Tanzania.

Threatened species

India contains 172 species of animal considered globally threatened by IUCN, or 2.9% of the world's total number of threatened species (Groombridge, 1993). These include 53 species of mammal, 69 birds, 23 reptiles and 3 amphibians. India contains globally important populations of some of Asia's rarest animals, such as the Bengal Fox, Asiatic Cheetah, Marbled Cat, Asiatic Lion, Indian Elephant, Asiatic Wild Ass, Indian Rhinoceros, Markhor, Gaur, Wild Asiatic Water Buffalo etc.. The number of species in various taxa that are listed under the different categories of endangerment is shown below in the **Table.**

Table : Globally Threatened Animals Occuring in India by Status Category.

Group		1994 IUCN	Red List	Threat Category	
	Endangered	Vulnerable	Rare	Indeterminate	Insufficiently Known
Mammals	13		20	5	13
Birds	6	20	25	13	5

Group		1994 IUCN	Red List	Threat Category	
	Endangered	Vulnerable	Rare	Indeterminate	Insufficiently Known
Reptiles	6	6	4	5	2
Amphibians	0	0	0	3	0
Fishes	0	0	2	0	0
Invertebrates	1	3	12	2	4
TOTAL	26	49	45	2	24

Source : Groombridge, B. (ed). 1993. The *1994 IUCN Red List of Threatened Animals.* IUCN, Gland, Switzerland and Cambridge, UK, lvi+286 pp.

A workshop held in 1982 indicated that as many as 3,000-4,000 higher plants may be under a degree of threat in India. Since then, the Project on Study, Survey and Conservation of Endangered species of Flora (POSSCEP) has partially documented these plants, and published its findings in Red Data Books (Nayar and Sastry, 1987).

UNIT 10 ❑ Theories on Biodiversity

The following are the different theories relating to biodiversity.

1. The Time hypothesis : In 1878, the English naturalist Alfred Russel Wallace suggested that diversity in the tropics was greater than in temperate regions because tropical conditions appeared on the earth's surface earlier than more polar environments. Furthermore, temperate regions have been subjected to more frequent and widespresd disturbance - for example, glaciation - than tropical regions during the history of the earth. Thus, tropical regions have enjoyed longer periods of stability and, thus, have had more time for species differentiation. This idea is now sometimes referred to as the time hypothesis of species diversity.

A number of types of evidence may be used to examine the time hypothesis.

Evidence from the fossil record that diversity has increased over time would lend support to the time hypothesis. The fossil record is so fragmentary that this test can be applied to only a few taxa and is restricted to certain types of habitats, particularly marine habitats.

2. Species diversity increases with primary production : Primary production sets a limit on the amount of energy available for use by species within a community. Thus, we might expect that species richness would be limited by the productivity of the environment. Some authors suggested that species richness should be greatest in relatively stable environments having high rates of productivity. This idea, which was first proposed by Whittaker and Niering and given theoretical grounding by Tilman, is called the productivity - stability hypothesis of species diversity. On a regional scale - that is, over areas of about 106 km^2 - species diversity has been found to be positively related to productivity in some cases. However, it is unclear how strong the relationship between productivity and species richness is, or what the possible mechanisms for such a relationship might be. Tilman and Pacala suggest that diversity does not increase monotonically with productivity for any group of species, but that species richness varies depending on what environmental factor is used as a measure of productivity and which species are being considered. Currie found that bird, mammal, amphibian, and reptile species richness increased with increasing potential evapotranspiration. For amphibians and reptiles, the increase was monotonic; for birds and mammals, there was a slight but insignificant decrease in richness at the higher PET levels.

Rosenzweig and Abramsky have recently evaluated other ideas regarding the relationship between productivity and species richness. One possibility is that productivity is simply correlated with species richness, rather than a determinant of it. That is to say, some other factor, such as disturbance, the spatial distribution of habitats, or some other as yet unidentified variable that is correlated with productivity may be at play. For example, some have suggested that predator - prey ratios increase as productivity increases, and thus, at high productivity levels, predators consume a disproportionate share of the available production, thereby causing a reduction in community diversity.

3. Intertaxon competition hypothesis : Rosenzweig and Abramsky have suggested that two hypotheses are most worthy of further consideration. The first is what they call the intertaxon competition hypothesis. This idea holds that the peaks of species diversity for different multispecies taxa should occur in areas having different productivity levels. For example, they point out that among small mammals in the south - western deserts of the low productivity west of the El paso River, whereas carnivore species richness is highest in East Texas in areas of much higher productivity. Rosenzweig and Abramsky suggest that, as a whole, a taxon will compete better at a certain productivity level than at others. Consequently, where that productivity level exists, that taxon will have an advantage over another taxon whose richness peaks at another productivity level, thereby reducing overall species richness through intertaxon competition. Rosenzweig and Abramsky hasten to point out that this idea is virtually untested.

4. Habitat heterogeneity : Another hypothesis worthy of consideration is that of Tilman and others, who have suggested that habitat heterogeneity increases with productivity to a certain point, after which it decreases.

5. Lottery hypothesis : Colonization by lottery, which produces random variation in time, reduces competitive exclusion to chance extinction and may contribute to the coexistence of large numbers of fish species in tropical reef communities. But the lottery model cannot explain the high diversity of larval fish in the plankton from which coral residents come. Nor can it explain the difference in fish diversity between tropical and temperate oceans.

6. Pest pressure hypothesis : Naturalists have thought that both selective and nonselective herbivory may influence the diversity of plant species. In particular, several authors have suggested that herbivory could promote the high diversity of tropical forests. It is argued that herbivores feed upon the buds, seeds, and seedlings of abundant species so efficiently that their densities are reduced. This allows other, less common species to grow. The key to this idea is that abundance *per se*, rather than the intrinsic quality of individuals as food items, makes a species vulnerable to consumers. Consumers locate abundant species easily, and their own populations grow to high levels. This idea became known as the pest pressure hypothesis.

7. Intermediate disturbance hypothesis : A number of mechanisms have been proposed to explain the effects of disturbance on species diversity. Consideration of tropical rain forests and coral reefs led scientists to relate high diversity to intermediate levels of disturbance, an idea referred to as the intermediate disturbance hypothesis. Disturbances caused by physical conditions, predators, or other factors open space for colonization and initiate a cycle of succession by species adapted to colonize disturbed sites. With a moderate level of disturbance, the community becomes a mosaic of patches of habitat at different stages of regeneration; together these patches contain the full variety of species characteristic of the successional sere. For this hypothesis to account satisfactorily for differences in diversity between regions, especially on the magnitude of the latitudinal difference in tree species diversity, there must be comparable differences in levels of disturbance. Rates of turnover of individual forest trees do not differ systematically between temperate and tropical areas. Nor is it likely that major disturbances such as storms and fires are more frequent in the Tropics. Thus, while distirbance may promote diversity, it seems unlikely to account for much of the observed variation in diversity among forests or, indeed, other types of communities.

UNIT 11 ❑ Introductory Note on Conservation

Structure

11.1 Wild life

Wildlife commonly refers to all wild undomesticated animals in their natural habitats. Philosophically, it should include all the biotic elements that evolved and flourished as a consequence of evolution. From ecological point of view, it includes every form of life-flora and fauna in their natural habitats.

Wildlife embraces all living creatures and implies their conservation (E. P. Gee, 1964).

According to wildlife society, wildlife includes all wild vertebrates and larger invertebrates important from aesthetic, sporting, utilitarian and nuisance standpoint.

According to Wildlife (Protection) Act, it includes any animal, bees, butterflies, crustacean, fish and moths and aquatic and land vegetation which forms part of any habitat.

The term 'wildlife' is appropriate while dealing with the management control and conservation of wild animal population as a whole as distinct from the purely game animals.

11.2 Wildlife wealth of India

India is very rich in biodiversity. India is one of the twelve megadiversity country and has three hot spots region (Western Ghats, Khasi- Manipur and Eastern Himalayas) out of twenty five.

It is estimated that 18% of the Indian plants are endemic to the country and found nowhere else in the world. Among amphibians found in India, 62% are unique to this country. Among lizards, of the 153 species recorded, 50% are endemic. High endemism has also been recorded for various groups of insects, marine worms, centipedes, mayflies and freshwater sponges.

	India's world ranking	Number of species in India
Mammals	8th	350
Birds	8th	1200
Reptiles	5th	453
Amphibians	15th	182
Angiosperms	15th- 20th	14500

But unfortunately there are constant depletion of wildlife in India.

11.3 Causes of wildlife depletion

1. Due to natural calamities like floods, droughts, fire, epidemics, super cyclone and absence of cover or shelter to wild animals.

2. Sometimes distribution range and degree of specialization of their own leads toward extinction.

3. Unlimited and over exploitation of natural resources for our best possible life

4. Tremendous explosion of human population and as a result it demands development and further need for more food and urbanisation.

5. Encroachment of forst for agricultural extension, industry and mining operation.

6. Reckless deforestation for urbanisation, cultivation, road construction, railway routes, dam and hydroelectric projects resulting in reduction of free movement area and reduction in reproductive potentiality of most wild animals.

7. Hunting,poaching and trading of wild animals for food, recreation, skin, tusk, fur, horn, pharmaceuticals, perfume industries etc. is one of the major cause of loss of wildlife.

8. Pollution like noise and water adversely affect animal life.

9. Last but not the least is the lack of enforcement of existing laws.

11.4 Wildlife : present status

Of all vertebrate species world-wide, 6.69% are considered threatened and, of all invertebrate species, only 0.16% are considered threatened.

Estimated number of described species (2002)

Taxonomic Group	Number of species		% in India
	World	India	
Protista Protozoa	31250	2577	8.24
Total (Protista)	31250	2577	8.24
ANIMALIA			
Mesozoa	71	10	14.08
Porifera	4562	48	10.65
Cnidaria	991	842	8.49
Ctenophora	100	12	12.00
Platyhelminthes	17500	1622	9.27
Nemertinea	600	-	-
Rotifera	2500	330	13.20
Gastrotricha	3000	100	3.33
Kinorhyncha	100	10	10.00
Nematoda	30000	2850	9.50
Nematomorpha	250	-	-
Acanthocephala	800	229	28.62
Sipuncula	145	35	24.14
Mollusca	66535	5070	7.62
Echiura	127	43	33.86
Annelida	12700	840	6.61
Onychophora	100	1	1.00
Arthropoda	987949	68389	6.90
Crustacea	35534	2934	8.26
Insecta	867391	59353	6.83
Arachnida	73440	5818	7.90
Pycnogonida	600	16	2.67

Pauropoda	360	-	-
Chilopoda	3000	100	3.33
Diplopoda	7500	162	2.16
Symphyla	120	4	3.33
Merostomata	4	2	50.00
Phoronida	11	3	27.27
Bryozoa (Ectoprocta)	4000	200	5.00
Entroprocta	60	10	16.66
Brachiopoda	300	3	1.00
Pogonophora	80	-	-
Priapulida	8	-	-
Pentastomida	70	-	-
Chaetognatha	111	30	27.02
Tardigrada	514	30	5.83
Echinodermata	6223	765	12.29
Hemichordata	120	12	10.00
Chordata	48451	4952	10.22
Protochordata (cephalochordata + Urochordata)	2106	119	5.65
Pisces	21723	2546	11.72
Amphibia	5150	209	4.06
Reptilia	5817	456	7.84
Aves	9026	1232	13.66
Mammalia	4629	390	8.42
Total (Animalia)	1196903	86874	7.25
Grand total (Protista + Animalia)	1228153	89451	7.28

Estimated number/percentage of endemic species in India (2004)

Taxon	Number of species		Percentage
	Total	Endemic	(%)
Protozoa :			
Free living	1247	90	7.21
Parasitic	1330	550	41.33
Mesozoa	10	10	100.00
Porifera :			
Freshwater	31	13	41.93
Cnidaria	842	10	-
Platyhelminthes	1622	1160	71.88
Rotifera	330	23	7.00
Gastrotricha	100	64	64.00
Kinorhyncha	10	7	70.00
Nematoda	2850	400	-
Acanthocephala	229	203	88.64
Mollusca :			
Terrestrial	1487	498	33.50
Freshwater	183	77	41.80
Echiura Annelida	43	12	28.00
Oligochaeta	473	368	77.80
Hirudinea	59	25	'2.37
Arthropoda :			
Crustacea	2934	501	17.70
Insecta	59353	20717	34.90
Arachnida	5818	2623	45.08
Phoronida	11	1	1.00
Bryozoa	4000	12	-
Entoprocta	10	1	1.00
Chaetognatha	111	3	2.70

Chordata :			
Pisces	2546	223	8.75
Amphibia	209	128	61.24
Reptilia	456	214	47.00
Aves	1232	176	14028
Mammalia	390	36	9.23

Floral wealth of India and world number of species in different groups of plants in India and the world

Groups	Number of species			% of
	India		World	World flora
Angiosperms	17500	(5725)	250000	7.0
Gymnosperms	48	(10)	650	7.4
Pterydophytes	1200	(193)	10000	12.0
Bryophytes	2850	(938)	14500	19.7
Lichens	2021	(466)	13500	15.0
Fungi	14500	(3500)	70000	20.7
Algae	6500	(1924)	40000	16.25
Virus/ Bacteria	850		8050	10.6
Total	45469	(12756)	406700	11.18

UNIT 12 □ Biomes & Wild Life : Characterisation, Faunal make up & Adaptation

Structure

12.0 Boimes

12.1 Terrestrial biomes

12.2 Tropical rainforests

12.3 Desert biome

12.4 Marine enviornments

12.0 Biomes

Within these Bio-geographical realms regional climate interacts with regional biota and substrate to produce large easily recognizable community units called **Biomes**-characterized by the kinds of animals and plants present. The definition of biome not only includes the climax community of a region but also the several intermediate stages as well dominated by other life forms. Ecologists have identified the following biomes.

12.1 Terrestrial biomes :

Temperate climates are characterized by average annual temperatures in the range of 5°-50°C at low elevations. Such climates are distributed between approximately 30°N and 45°N in North America and between 40°N and 60°N in Europe, which is warmed by the Gulf Stream current. Frost is an important factor throughout the temperate zone. Seven terrestrial biomes of the temperate zone are listed below -

Deciduous Forest Biome : found in North America principally in the eastern part of the United States and Southern Canada, but also occurs widely in Europe and Eastern Asia. It is poorly developed in the Southern Hemisphere (New Zealand and Southern Chile) because of the milder winter temperatures at moderate latitudes. The vegetation is dominated by deciduous trees, predominantly oak, maple, beech, birch and hickory, often with a subcanopy layer of small trees and shrubs. Herbaceous plants complete their growth and flower early in spring, before the trees have fully leaved out.

Temperate Needle-leaved Biome : dominated by pines and exists under conditions of water and nutrient stress, often on sandy soils. The most important of these formations in North America are the pine forests of the coastal plains of the Atlantic and Gulf States, the jack pine forests of the northern parts of the Great Lakes states and central Canada, and the montane pine forests of the American West. Because soils tend to be dry, fires are frequent, and most species are able to resist fire damage.

Temperate Rain Forest Biome : occurs near the Pacific coast in the northwestern United States and British Colombia, and also in southern Chile, New Zealand and Tasmania. Mild winters, heavy winter rains and summer fog create conditions that support extremely tall evergreen forests. Trees are typically 60-70 meters high and may grow to over 100 meters. In contrast to rain forests in Tropics, the species diversity of temperate rain forests typically is very low.

Temperate Grassland Biome : develops where rainfall is between 30 and 85 cm per year, depending on the average temperature. Summers are hot and wet; winters are cold. North American grassland biomes are often called Prairies. Extensive grassland is also found in central Asia, where they are called Steppes. Because annual precipitation is low, organic detritus does not decompose rapidly, and the soils are rich in organic matter. The vegetations are dominated by grasses, which grow to over 2 meters in the moisture parts of the grassland biome and less than 0.2 meters in more arid regions. There are also nongrass herbaceous species, which are called forbs. Fire has a dominant influence in the grassland, particularly where the habitat dries out during the late summer. Most grassland species have fire-resistant underground stems or rhizomes or have fire-resistant seeds.

Temperate Shrub-land Biome : here precipitation ranges between 25 and 50 cm per year, and the winters are cold and the summers are hot. The shrub-land biome covers most of the Great Basin of the western United States. In these shrublands, potential evapo-transpiration exceeds precipitation during most of the year, and so soils are dry and little water percolates through them to form streams and rivers. Fire occurs infrequently because the habitat produces little fuel.

Mediterranean Woodland Biome : distributed at 30°-40°latitude north and south of the Equator - somehow higher in Europe-on the western sides of continental landmass. Representatives of this biome include southern Europe and southern California in the Northern Hemisphere, and central Chile, the Cape region of South Africa, and southwestern Australia in the Southern Hemisphere. Mediterranean climates are characterized by mild temperature, winter rain and summer drought which support thick, evergreen, shrubby vegetation 1-3 meters in height, with deep roots and drought-resistant foliage.

Subtropical Desert Biome : develops at latitude of 20°-30° north and south of the Equator in areas with very sparse rainfall (less than 25 cm per year) and generally long growing seasons. Because of low rainfall, the soils of subtropical deserts are shallow, virtually devoid of organic matter and neutral in pH. Wetter sites support a profusion of succulent cacti, shrubs and small trees. Most subtropical deserts receive summer rainfall, during which many herbaceous plants sprout from dormant seeds and quickly grow and reproduce before the soils dry out again. Species diversity is much higher than it is in temperate lands.

Boreal and Polar Biomes : Three biomes are characteristic of the high latitudes of the Northern Hemisphere and of areas of high elevation in temperate and tropical regions.

Boreal Forest Biome or Taiga : stretches in a broad belt centered at about 50°N in North America and about 60°N in Europe and Asia. The average annual temperature is below 5°C and winters are severe (temperature may reach -60°C). Precipitation is in the range of 40-100 cm, and because evaporation is low, soils are moist throughout most of the growing season. The vegetation consists of vast, dense stands of evergreen needle-leaved trees, mostly spruce and fir, which grow to be 10-20 meters high. Because of the low temperature the leaf litter decomposes very slowly and accumulates at the soil surface. Species diversity is very low.

Tundra Biome : lies north of the boreal forest in the polar climate zone. It is treeless expanse underlain by permanently frozen soil or permafrost. The soils thaw to a depth of 0.5-1 meter during the brief summer growing season. Soils tend to be acid because of their high organic matter content, and they are very low in nutrients. Most plants are dwarfs, prostrate, woody shrubs.

Alpine Tundra Biome : these areas occur above the treeline, most broadly in Rocky Mountains in North America and especially in the Tibetan Plateau of central Asia. Alpine tundra generally have warmer and longer growing seasons, higher precipitation, less severe winters, greater productivity, better-drained soils and higher species diversity than the arctic tundra.

Equatorial and Tropical Biomes : In the regions of the world within 20°north and south of the equator, temperature vary more throughout the day than average monthly temperature s vary through the year. Average temperatures at sea level generally exceed 20°C. Environments of tropical latitudes are distinguished by the seasonal course of rainfall, which creates a continuous gradient of vegetation from wet, seasonal rain forests, to seasonal forests, to scrub, savanna and desert. Frost is not a factor in tropical biomes. Three biomes are typically distinguished within these equatorial and tropical climate zones.

Tropical Rain Forest Biome : develops in climates that are always warm and that receive at least 200 cm of precipitation throughout the year, with not less than 10 cm during any one month. These conditions exists in three important regions within the Tropics: the Amazon and Orinoco Basins of South America, with additional areas in Central America and along the Atlantic coast of Brazil, constitute the American rain forests; the area from southernmost West Africa and extending eastward to the Congo River basin constitute the African rain forests; and the Indo-Malayan rain forests cover parts of Southeast Asia, the islands between Asia and Australia and the Queensland coast of Australia.

Rain forest soils are typically old and deeply weathered. Because they are relatively devoid of humus and clay, they take on the reddish colour of aluminium and iron oxides and have poor ability to retain nutrients. In spite of the low nutrient status of the soils, rain forest vegetation is dominated by a continuous canopy of tall evergreen trees rising to 30-40 meters, with occasional emergent trees rising above the canopy to heights of 55 meters. The productivity of the rain forest biome is greater than that of any other terrestrial biome. Species richness is extremely high.

Tropical Seasonal Forest Biome : develops within the Tropics beyond 10° north and south of the equator. These climates often exhibit a pronounced dry season, corresponding to winter at higher latitudes. Seasonal forests in the Tropics have a preponderance of deciduous trees that shed their leaves during the season of water stress.

Tropical Savanna Biome : may be defined as grassland with scattered trees and it typifies large areas of the dry Tropics, especially in Africa. The tropical savanna biome has an average rainfall of 90-150 cm per year, but the driest three or four months receive less than 5 cm each. Fire and grazing play an important role in maintaining the character of the biome, particularly in wetter regions, as grasses can persist better than other forms of vegetation under these influences.

Note : The biome concept was developed for terrestrial ecosystems, and biomes are principally distinguished by the growth form of their dominant vegetation. As a consequence, "aquatic biomes" do not exist in the sense in which the term is applied to terrestrial ecosystems. Indeed, employing a vegetation concept would be impossible in aquatic systems because the primary producers in many aquatic systems are single-celled algae, which do not form "vegetation" with a characteristic structure. As a result, classifications of aquatic systems have been based primarily on physical characteristics : salinity, water movement, depth and so on. The major kinds of aquatic environments are streams, lakes, estuaries and oceans.

12.2 Tropical rainforests

1. Characteristics :

(I) **Location** : Located in a band around the Equator, between the Tropic of Cancer (23.5° N Latitude) and the Tropic of Capricorn (23.5° S Latitude) which forms a 4800 km wide band called 'Tropics'. Tropical rain forests are found in South America (the Amazon and Orinoco basins), West Africa (Congo, Niger & Zambezi basins), Australia, South-East Asia and India (Assam, Meghalaya, and Western Ghats).

(II) **Physical Enviornment** :

a. Very dense, warm, wet forest.

b. Temperature is high, but even and minimal seasonal changesare recorded (in summer : 13°C to 43°C and in winter : 10°C to 32°C).

c. Rainfall abundant (250 - 400 cm).

d. Temperature and relative humidity are comparatively high and remains constant throughout the day.

e. Due to high temperature evaporation is fast.

f. Days and nights are of uniform in length.

g. Soil which is exceedingly thick is red latosols. Leaching of minerals very fast-makes it unfit for agricultural practices.

h. Speedy nutrient cycling makes the soil very fertile.

i. Community is most diverse- heaven for both plants and animals.

j. **Nutrient cycling** : Tropical rain forests are found on soils which are nutrient poor. However, high productivity does not require soils to contain large nutrient reserves. What seems to happen in undisturbed tropical rain forests is that any organic matter that falls on the ground is rapidly decomposed. The nutrients thus released into the soil are then rapidly taken up by the surface roots of trees and other plants or occasionally leached from the soil.

Tropical trees produce a large number of biomass which is concentrated near the surface. These roots seem to be very effective in absorbing nutrients. Another feature of tropical trees which favour nutrient retention is that, their leaves are often long lived, tough and resistant to insect attacks.

(III) **Zonations** : Based on living environment rain forests may be divided into I :

a. Emergents : Giant trees (200 ft) much higher than average canopy height. Emergent dwelling animals are birds and insects.

b. Canopy (80-100 ft.) : Uppermost part of trees, leafy environment and full of insects, reptiles, birds, mammals.

c. Understory : A dark cool environment under the leaves over the ground.

d. Forest floor : Teeming with animal life, specially insects and large mammals.

2. Faunal make-up :

a. Rich in density as well as in varieties.

b. Animal communities are stratified vertically.

c. Mostly arboreal forms (Sloths, lemurs, *Dendrologous* sp, bats etc.), some ground dwellers (*Panthera tigris, Elephas maximus, Bos gaurus; Axis axis* - from peninsular India) and few amphibians.

d. Majority of the animals are nocturnal in habit.

e. Symbiosis between animals and epiphytes very common.

f. Invertebrate density and abundance very high- worms, snails, centipedes, millipedes, isopods, spiders, scorpions, leeches and insects (heteroptera, orthoptera, mantids, Phasmids, butterflies, bees, ants, termites.)

g. Vertebrates mostly arboreal :

Amphibians : *Hyla, Rachophora.*

Reptiles : Iguanas, Geckos, Chameleons, snakes.

Birds : Parakeets, Hornbills (frugivorous), humming birds (necter feeding), woodpeckers etc. are common.

Mammals : Insectivores, leopards, jungle cat, flying squirrels, monkey, Sloths, deers etc.

3. Adaptations :

Each species has evolved with its own sets of unique adaptations so as to survive. Every animal has the ability to protect itself from being the next meal. In rainforest there are twigs that walk, leaves that leap bark that flies, and masses of thorns that explode into fragments when touched. Insects frogs, lizards, snakes, birds, cats find refuge by blending into pattern and textures of the rain forest.

Protective mimicry/colorations :

Organisms mimic either some other organism or object in form colour or behaviour to protect themselves from predators. This could be obtained by concealment or warning

1. Geometrid moths mimic the pattern of dead leaves.

2. Lichen Katydid lives surrounded by the lichen on which they feed and has evolved an appearance of spiny processes and wing venation that that duplicates lichen's appearance

3. In glass wing butterfly *Cithaerias sp.*- a false eye spot located on the edge of the hind wing which prevent attack by bird.

4. The tent bat *Ectophylla alba* chew the leaf veins of heliconias on the either side of midrib causing the leaf to fold down thus creating shelter from sun and rain and reducing exposure to predators.

5. The flat footed bugs produces noxious; malodorous secretions when disturbed and their specialized colourful hind legs makes it easy for predators to avoid them.

6. The bold pattern of freshly emerged passion vine butterfly is a form of warning coloration that advertises unpalatibility.

7. The palatable viceroy butterfly *Lementis sp.* can easily be preyed upon, thus it mimics the non palatable monarch butterfly.

Adaptations for prey capture :

1. The green palm viper (*Bothrops sp*) and the golden eye lash viper (*B. schlegelii*)are able to hunt at night using the large loreal pits located ahead of their eyes. These organs are effective in targeting small mammals while tree snake (*Imantodes sp*) instead relies on its huge eyes to locate prey at night.

2. The blunt headed tree snake (*Imantodes cenchoa*) has a uniquely constructed backbone that enables it to reach across wide spaces without support - an adaptation useful for preying upon sleeping lizards.

3. The eyelash viper has a molted skin pattern that makes it difficult to see - an excellent strategy of camouflage for life as a sit and wait predator that feeds on small rodents, frogs, lizards.

4. Vine snakes (*Oxybelis sp*) possess an extremely thin elongate green brown body, a combination that provides while they hunt through tangled vegetation in search of food.

5. The huge eyes of many rainforest frogs (eg. *Agalychnis sp*) enable them to hunt at night. Some others like transparent glass frog (*Centrolenella sp*) avoids bright tropical sun and are active on wet warm nights.

6. The male strawberry poison tart frogs wrestle on the forest floor for control over territory their bold colors advertise their toxicity to their would be predators.

Adaptations for arboreal mode of life :

1. In the porcupine (*Coendou mexicans*) prehensile tail helps to support its full weight. The spine free underside of the tail enables it to grasp branches securely when feeding at the edge of tree crown.

2. In highly mobile spider monkeys (*Ateles sp*) the dexterous tails act as fifth limb enabling the monkeys to dangle at the very tip of branches where flowers and fruits are located.

3. One of the most common arboreal mammals the Kingkajou (*Potas flavus*) is among the few carnivorous that have specialized in fruit diet. The prehensile tail allows it to make greater use of its fore limbs for plucking and handling fruits.

4. Sloths are superbly engineered for a life time of suspension hanging upside down high above the forest floor. The adaptive elegance of sloths have been an almost catatonic accident of nature. Their various anatomical adaptations are :

(a) Small animal, light weight.

(b) Strongly built chest ribs and limb girdles.

(c) Thorax subcircular and ribs more curved.

(d) Number of ribs increased to give support to the viscera during inverted position.

(e) Lumber vertebrae elongated and number has increased.

(f) pectoral girdles strongly built, as for limb support the body weight while hanging.

(g) The clavicle and scapula are prominent to withstand the strain of contraction of powerful breast muscles.

5. Syndactily found in Koala, where the2nd and 3rd toes are syndactylus.

6. In Chameleon the digits are arranged into opposable bundles of 2 or 3 digits in both fore and hind limbs to hold branches (grasping type).

7. Long, curved claws are common in bats, squirrels, lizards but modified into powerful hooks in sloths.

Different Types of Arboreal Animals are :

Branch Runner : Progression on the upper surface of the trees by both the pairs of the limbs, e.g. - Squirrels, Lemurs, Chameleon.

Suspended form : hang head down from the branches, unable to walk on the branches. Move while suspended upside down. Clinging on the branches with claws, e.g. - Bat, Sloth etc.

Branchiator : Move from branch to branch swinging forelimbs with great speed and accuracy, e.g. - Apes, monkeys.

12.3 Desert biome

Desert is the arid region of the earth surface, where rainfall and moisture are insufficient to support normal life. In these regions average rainfall never exceeds 10-15 inches per year. Depending upon rains deserts can be categorized into :- (a) low rainfall deserts e.g. -Atacama, (b) cold deserts such as Alps and Scandinavian mountains, (c) hot deserts of equatorial regions, (d) low nutrient deserts such as North American deserts (e) high salt deserts found in Chile, S. America and Australia.

1. Characteristics :

- Scarcity of water : This is due to rainfall and absence of natural sources of water.
- Extremes of Temp : The temperature in the day time is very high and relative humidity is very low. During night the temperature goes down tremendously because of the radiation of heat into space.
- Dust storms : Lack of moisture and extreme of temperature cause an increase in the air movement and dust storms in every evening..
- Lack of vegetation : Due to scarcity of water , plants are unable to grow. The vegetation is also modified for this mode of life being succulent and thorny, which prevents excessive evaporation of water.

2. Faunal Makeup :

- Under the harsh and shimmering sun the arid backed sand of the desert may appear to be devoid of animal life, but surprisingly large numbers of animal species thrive there. These are either drought evaders or drought resistors.
- They make their appearance only when rain sets in, for the rest of the day they remain dormant either in egg or pupal stage.
- Insects like crickets, grasshoppers, ants, bees, wasps, butterflies, moth and beetles swarm in the desert, when rain arrives and plants flourish.
- Tiny shrimps appear in temporary ponds.
- Lizards and snakes are also very common.
- Birds are few and live in places which have surface water for drinking within their flying range.
- Small rodents like kangaroo rats, pocket mice, desert mongoose, desert fox, desert hedgehog, kit-fox, jack rabbit and the camel, deers, antelopes, and asses are the mammalian forms found in the desert.

3. Adaptations :

The fauna of desert is peculiarly adapted to these drastic conditions and the modifications are mostly associated with the conservation and availability of water, protection against extreme heat and cold and obtaining food.

(A) Adaptations for obtaining water :

- Higher animals cannot live long without drinking water and need water at frequent intervals. Therefore, desert animals try to utilize water from every available source.

• A few animals absorb dewdrops along with plant food.

• Certain desert animals such as desert rabbit, turtles and wood rat do not drink water even it is available to them. These suffice their need by eating succulent plants.

• The most specialized group of animals (ant and rats- Jerboas and kangaroo rat) depends entirely upon metabolic water produced in their body during the oxidation of foodstuffs.

• Carnivorous animals get needful water from the body of their prey.

• Skin like certain animals like *Moloch* is hygroscopic and absorbs water like a blotting paper.

(B) **Adaptation for Conservation of Water :**

Terrestrial animals may lose water from their body in three ways :-

a. By evaporation, through the body surface.

b. By exhaling moisture during respiration, and

c. By expelling water or liquid urine during excretion.

a. To avoid evaporation through the body surface- Desert animals have developed several protective measures, such as -

• Development of thick hides which water loss by perspiration.

• Number of sweat glands in the skin of desert mammals is very much reduced or in some cases they are totally absent.

• Scorpions and reptiles have developed almost impermeable outer covering. Sometimes, scales and spines are developed in the exposed surfaces, e.g. - sand lizard (*Moloch*) and horned toad (*Phrynosoma*).

• Some desert animals produce epiphragms and secretions to prevent loss of water. Desert insects are wax-proof.

• Camels have developed more tolerance to heat. Their body temperature fluctuates more with the atmosphere and thus reduced the amount of moisture loss through sweating and panting.

b. To avoid loss of moisture during respiration- many desert mammals cool the exhaled air in their noses, before it is expelled out through nostrils. As a result moisture condenses in the nose and is not lost as water vapours along the exhaled air.

c. To avoid loss of water during excretion- this is brought about by excreting concentrated urine or urine in semisolid state. Desert rats and kangaroo rats excrete urine which contains 24% urea, whereas in man urine contains just 6% urea. Even reptiles, insects and birds pass their body wastes in such concentrated state as uric acid that little or no moisture is lost in the process.

(C) Protection against heat/cold :

• Desert animals have thick hide or have protective armour of scales, spines or dermal scutes.

• Desert animals have long legs, which no doubt help in jumping and swift running, but also lift the body above the ground and thus avoid direct contact of the body with burning sand, e.g. - kangaroo rat, Jerboa etc.

• The desert animals hide themselves in the burrows during day time and come out only late in the evening and at night or early in the morning when temperature is low and relative humidity is high in the air.

• The other animals that can not remain in the burrows hide themselves under some suitable shelter and avoid the scorching sunrays of the noon.

(D) Protection against sand storms :

• Nostrils in majority of desert animals are either reduced to small pinholes or they are protected complicated valves. For example in Camel, the nostrils can be closed in the same way as eyes are closed by the eyelids.

• Eyelids exhibit various modifications and are capable of closing the eyes without hindering the vision. In Camel the eyes are high on the head and are protected by long and thick eye lashes.

• Ears are often protected with fringes of scales or hairs. In *Phrynosoma* the ear apertures are absent. Nocturnal animals need a sharp sense of hearing. Jack rabbits, hare have large ears.

(E) Swift running or speed :

• Since desert animals have to move far in search of food and water, majority of them have great speed. Also the limbs are specialized and adapted to walk on sand.

• In leaf hopper and kangaroo rat the limbs are long.

• Desert cat has wide soles thickly covered with fur which enables it to walk comfortably even on hot sand.

• Legs of ostrich are padded with heavy callosities.

• The undersurface of camel's feet also padded.

(F) Colour :

The colouration in desert animals is dull and is found to match with the sand-dunes. The body hues vary from grey, brown to red and are less heavily pigmented. This type of colouration helps the animals in camouflaging. Warning colouration is exhibited by poisonous animals like lizards, Heloderma, rattle snake, spiders and red ants.

(G) Spinescence :

The spine studded body is characteristics features of many desert animals like *Moloch horridus* (flat. spiny lizard), *Phrynosoma* (horned lizard) etc.

(H) Venom :

Possession of venom is another attribute to desert animals. Rattle snakes, trap door spider and Tarantula are poisonous *creatures of the desert.*

(I) Sense Organ :

Organs of sights, smell and hearing are specially developed.

12.4 Marine environments

The sea covers about 70% of the earth's surface and is great reservoir of life. Among the three major habitats of the biosphere marine realms provide the largest inhabitable space for living organisms.

1. Characteristics :

Temperature :

Ocean is the largest store house of the sun's heat and it occupies much space. The extremes of temperature ranges from 3°C to 40°C, while in the Indian seas the temperature ranges between 18°C to 25°C at the surface. The density of the sea water and solubility of oxygen increases with decrease in temperature.

Salinity :

The salinity of the open ocean at about 300 meters depth is about 3.5%. There is slight variation in salinity in some seas, such as- in Mediterranean Sea it is 3.95% and in Red Sea it is 4.6%. The sea water is weekly alkaline (pH 8 to 8.3) and strongly buffered. The salinity of the sea is due to two elements - Sodium and Chlorine which account of the 86% salts of the sea. An increase or decrease in the salinity brings about changes in specific gravity of the sea water.

Light :

On the basis of the penetration of the light the ocean is divisible into two zones :-

The lighted or littoral zone : The littoral zone extends upto the outer edge of continental shelf (around the continents below sea level a small portion of the ocean bottom forms a shallow platform, called continental shelf) and roughly upto the depth of 200 meters. The littoral zone of the sea is broadly divided into supralittoral, intertidal or eulittoral and subtidal or sublittoral zones. The supralittoral zone is the uppermost of the all littoral habitat and in the beach down to the edge of the sea. Below this zone is the eulittoral zone which is represented by the intertidal zone (zone between high tide and low tide) of the continental shelf. Below the intertidal zone is the sublittoral zone which extends from low water tide mark to about 200 meters.

The deep sea system : Comprises of three main zones - bathyal, abyssal and hadal zones respectively. The bathyal zone extends onto the continental shelf where the ocean descends rapidly from 200 meters to about 4000 meters. From 4000 meters to 6000 meters is the abyssal zone covering the entire ocean floor. In the trenches of the ocean, the sea is as deep as 10000 meters. This region is called as hadal zone.

Pressure :

Pressure affects marine animals in various ways. The deposition of calcium is difficult at heavy pressure. Carbon dioxide accumulates in high pressure and makes calcium carbonate more soluble.

Waves :

The waves have their maximum effect in the intertidal zones. The maximum height that is normally reached by the waves in the ocean is 17 meters. When the waves strike, the impact is very heavy and can even turn huge stones. The force of impact of the waves is roughly about 1.5 kg per sq. Cm.

Tides :

The tides are caused by the gravitational pool of the moon and sun on the waters of the ocean. The tides may appear once in 24 hours or once in twelve and half hours.

Currents :

The sea is in continuous circulation. Air temperature differences between poles and equator set up strong winds which create definite currents in the ocean. Because of the circulation oxygen depletion is so common in freshwater lakes and very rare in oceans.

2. Faunal Makeup :

Fauna of the Littoral Zone :

The eulittoral zone is the most favourable of all the habitats afforded by sea. Due to abundance of light, water, oxygen, carbon dioxide and less salinity of water, the tidal zone is characterized by dense growth of vegetation which provides shelter and food for animals. Animals of every phylum of animal kingdom are represented in the region and are mostly sedentary and sessile.

The rocky shores are inhabited by a large number of sessile animals. Many sponges and coelenterates abound here. Among the molluscs *Chiton, Patella, Nerita, Oysters, Mytilus* etc. are very common. Also here is predominance of boring invertebrates like *Pholas, Teredo* and *Lithodomus.* Echinoderms, especially sea urchins and star fishes are sometimes found here.

The sandy shores usually have a lot of sea weeds and form an ideal place for many animals to live and hide in between them. The fauna includes protozoans, turbellarians, nematodes and copepods. Certain fishes bearing rostrum such as *Hemiramphus, Belone* etc. plough the sand in search of prey. Protochordates like *Balanoglossus* and *Amphioxus* are major sand dwellers.

In the muddy shore there is abundant supply of food due to plenty of dead organic material along with bacterial populations are inhabited by a large number of protozoans, nematodes, small Crustacea, amphipods, isopods and ostracods. Many molluscs bury themselves inside the mud while soft bodied nudibranchs move over the surface. Among the fishes Boleopthalmus and Periopthalmus are common.

The bottom fauna of sublittoral zone consists of several types of foraminiferans, sponges (*Clione*), segmented worms, coelenterates (sea-pen, sea-fan etc.), sipunculids, crustaceans, star fishes, brittle stars, sea urchin and sea cucumbers, stone crabs, spider crabs, hermit crabs and rock lobsters are also found. The most characteristic feature of sublittoral zone is the presence of coral reefs.

Fauna of Deep Sea :

In spite of the hostility of the deep sea atmosphere, almost all the phyla (except air breathing arthropods and land vertebrates are represented in deep sea.

Protozoa : Radiolarians and Foraminiferans occur abundantly in archibenthic and abyssal benthic zones respectively.

Porifera : Glass sponges of class Hexactinellida occur almost exclusively in deep sea being fixed to the sediments by long root spicules.

Coelenterate : Stony corals, few soft corals like sea-pens, sea-anemones and gorgonids are found in deep sea.

Annelida : Annelids are mostly littoral but tube dwelling polychaetes like *Chaetopterus, Sabella, Serpula* etc. often found.

Arthropoda : A few of the arthropod groups such as barnacles, isopods and amphipods are found at the sea bottom. Crabs, lobsters and shrimps are very common in the abyssal water. *Limulus* (king crab) is the only arachnid found in deep sea habitat.

Mollusca : Almost all the classes of Mollusca are represented in the deep sea. Chitons, bivalved and single valved molluscs i.e. Lamellibranchs and gastropods all occur abundantly.

Echinodermata : Echinoderms are most numerous in deep sea habitat. Stalked crinoids are exclusively deep sea animals.

Fishes : *Chimera* and *Hariotta* are from deep sea. Teleosts fishes like *Photostomias, Idiacanthus, Gastrostomus, Cryptoceras, Bassogigas, Bathypterois, Lesiognathus, Malacostus, and Gigantactis* etc. are from deep sea. All the flat fishes belonging to order Heterostomata are exclusively deep sea fishes found at the bottom.

3. Adaptations :

Adaptations found in Littoral Zone animals :

The animals of rocky shore have developed following adaptations for attachment and protection from desiccation of feeding :-

1. Mostly these animals are sessile because rocks provide them secure places for attachment.

2. Because of sedentary mode of life several morphological changes have taken place in these animals-

- Loss of locomotory organs, e.g. - Mytilus and *Ostrea*.
- Mouth and anus at the same level, e.g. - Ascidians and Polyzoans.
- Development of efficient sense organ as in tube dwelling polychaetes.
- Development of thick test as *Balanus*, Bivalves and Ascidians.
- Development of ciliary mode of feeding.
- Power of reproducing by budding thereby, forming large colonies, e.g. - *Botryllus*.

3. To conserve water and to avoid desiccation, sedentary animals have developed tube dwelling habit which also help them in escaping from the impact of waves and from predators.

4. The animals living in the exposed rocks have developed various defensive mechanisms such as spicules in sponges and stinging cells in coelenterates. Many snails possess spiny shells.

5. To reduce friction, many rocky shore animals have flattened body such as *Oscarella*, leaf-like Turbellarians, Tunicates (*Botryllus*) and certain crabs.

6. Some rock inhabitants have developed protective resemblance. *Octopus* which is found in crevices among stones often resembles the colour of the stone.

Most of the marine sand-dwelling forms are burrowing in nature. They show following adaptations for successful living in the sandy sea shore.

1. To escape from the action of waves, evil effects of desiccation, lower salinity and extremes of temperature most of the sandy shore animals lead a burrowing mode of life.

2. Due to burrowing mode of life these organisms have developed certain devices such as digging organs, ciliary mode of feeding and certain respiratory devices.

3. Burrowing molluscs have developed long siphons.

4. The fishes *Trachinus* and *Uronoscopus* which bury in the sand do not have air bladders.

5. Burrowing annelids have lost their parapodia.

6. Fishes that feed on the sandy shore fauna have elongated jaws which are used to plough the sand.

Muddy-shore animals show following adaptations for successful living -

1. The colouration of mud-dwellers are yellowish grey or white.

2. All mud-dwellers are soft bodied and the body musculature is generally weak. If they possess shells, then they are very thin.

3. In the case of molluscs the siphons are very long.

4. Sense organs like eyes are degenerated or absent and the nervous system is poorly developed.

5. The foot of animals like *Aplysia* is very broad and prevents sinking while moving over sand.

6. Mud animals possess special structures to provide respiratory currents and also have specialized organs for digging purposes.

Deep Sea Adaptations :

1. Size : In general, deep sea organisms are relatively smaller than their relatives on the surface. *Chimera* (Holocephali) and *Scapanorhyuchus* (shark) are two exceptions to this rule. Scarcity of food explains for their small size.

2. Form : Body of deep sea animals is observed to be delicate and slender, because the struggle for existence is absent and the water at sea bottom is perfectly calm with no movement. Some deep sea fishes are so much laterally flattened that the eye of one side comes to lie on the other side and body becomes band or ribbon like.

3. Skeleton : Skeleton of deep sea forms is soft and noncalcareous, because they are unable to synthesize Calcium at low temperature. For this reason calcareous sponges are completely absent from deep sea. The protozoans and corals have exoskeleton of silica. Deep sea molluscs have fragile shells and fishes have either sparsely calcified or totally uncalcified (*Chimera*) endoskeleton.

4. Colour : due to complete absence of light the deep sea forms exhibit uniform colour pattern. These may be red, brown, black, violet and blue etc. but red colour predominates.

5. Food & Feeding : vegetation is absent in the sea bottom. Therefore deep sea animals have three alternative source of food :

- Prey upon one another.
- Depend on the falling excreta of the surface animals.
- Depend upon surface plants and animals which sink to the bottom.

Most of the deep sea animals are predatory. The predaceous animals possess powerful jaws and strong, sharp teeth. The stomach is much distensible that sometimes it contains prey even larger than the size of animal.

The vegetarian animals of deep sea have elongated alimentary canal and a reduced radula. In addition they are characterized by the possession of an elongated excretory tube which carries the excreta away from feeding place of the animals so that it is maintained clean.

6. Bioluminescence : The phenomenon of production of light is most widespread in deep sea forms. It is very common among fishes, Crustaceans, Cephalopods, many Coelenterates, some star fishes and few annelids. Bioluminescence can be useful to deep sea forms in recognition of sex and attracting the prey.

7. Eyes : Mesopelagic animals of the deep sea have large eyes like that of the terrestrial twilight animals like Geckos, owls and the Loris. The deep sea fishes have more rods while cones are either reduced or absent. The eyes are completely absent in *Pecten* and *Eulemia*.

8. Sensory Organs : In deep sea crustaceans the loss of sight is compensated by the development of long feelers or antennae. Even those animals which have well developed sight the antennae are of unusual length. In deep sea fishes the fin rays are considerably elongated (e.g. - *Bathypterois*, one fin ray of the pectoral fin is produced in a sensory filament). These structures are sensory to touch and perceive slightest disturbance in the surrounding water.

9. Lateral-line System : In the deep sea fishes the lateral-line system is very well developed to compensate for the sight.

10. Mucous secreting glands are presenting all deep sea fishes.

11. Low Metabolic rate : The deep sea animals usually have very low metabolic rate due to the prevailing low temperatures.

12. Sexual Adaptations : Deep sea population is very thin and it is difficult to find mates. In Angler fishes the males are small and are attached to the females during breeding season. In *Edriolychnus* the tissue of both the sexes are fused and the blood stream is also connected. The barnacle *Scapellum* has complementary males.

UNIT 13 ❑ Wildlife Conservation

Structure

13.0 Indroduction

Conservation is the management of natural resources both living and non-living in such a way so as to yield the greatest sustainable benefit to the future needs and aspirations of the mankind. It is also referrred as an insurance policy for the future.

13.1 Necessity and objective of wild life conservation

13.1.1 Necessity for Conservation :

Balance of Nature :

Each biotic components by virtue of its position in the food chain maintain the delicate balance of an ecosystem. If a species is lost, it may upset the balance of Nature - makes the system vulnarable. The destruction of carnivores will help the increase the herbivores which in turn will affect the forest vegetation. Once the forest vegetation is reduced, herbivores will invade cultivated lands. The reduction in the extent of the forest will affects rains and thereby affects the economy of our land. Sometimes if tiger turns man eaters and hyenas become child lifters, it is because man has interfered with their natural food.

Economic value :

The animal products like hides, horns, ivory, fur etc. are good source of income for our country. Much revenue is realized by way of fees for the license to shoot and also as duty imposed for the import of arms and ammunition. The collection and supply of live and dead specimen to the zoos and museums also bring in lot revenue.

The wildlife wealth can be used as a source for increasing our earnings on tourism.

Scientific Value :

From time immemorial, animals and birds have provided example and incentives to man for gaining mastery over his environment. The efficiency of new medicines or any new surgical method is often tested on animals, for example, the common Rhesus monkey has been subjected to such many tests. The preservation of wildlife will help many naturalists to study the animals in close quarters.

Game Value :

The wildlife of our country is a source of sport and enjoyment. It gives healthy recreation to people of all walks of life. Bird watching is a very popular pastime among many foreigners. A visit to the Sanctuaries and National Parks can become a regular schedule for school children and college students. It is a thrilling experience to see these animals in close quarters and especially in their natural surroundings.

Cultural Value :

The wildlife of India has got interwined with our culture. The early Indus civilization shows the use of animal symbols in their seals. Our mythology and literature are full of accounts of these animals.

Religious Attachment :

An important place of honour has been given to animals in the galaxy of Hindu gods and their associates.

To Protect our Civilization :

One of the causes attributed by Historians for the culmination of the Mohenja-daro civilization was the absence of protection to wildlife. The people of that era were good hunters who waged a relentless war against the carnivores which resulted in the increase of herbivores. The enormous number of herbivores that were present reduced the forests and grasslands causing the advance of deserts and the end of an enviable civilization.

Genetic Resources :

It is require for advantageous characters like disease resistance, higher production or other desired characters.

Aesthetic Value :

For natural activities of colourful and melodious birds and mammals, thick forest belt become a source of pleasure and happiness.

13.1.2 Objectives of the Conseravation :

Conservation is chiefly concerned with the protection, preservation, preparation and judicious control of populations for rare species of plants and animals in their natural habitats. Intelligent exploitation of nature with all its biological and physical components in its original form as far as practicible. Actually conservation of wild life is equated with the proper management of nature. Conservation require for the folowing purposes-

1. To protect and preserve the rare species of plants and animals from extinction.
2. To preserve the breeding stock.
3. To prevent deforestation
4. To study the relation of plants and animals in their natural habitat.
5. To maintain the balance of nature.

For the above purpose several strategies have been employed like :-

Conservation through laws : To stop illegal hunting, poaching, trade, over exploitation of nature several laws are introduced such as Indian Wildlife (Protection) Act, 1972 which was amended in 1983, 1986 and 1991 respectively; Madras Wildlife Act, 1873; All India Elephant Preservation Act, 1879; The Wild Birds and Animal Protection Act, 1972 etc.

Establishment of more amenity areas : There are a chain of 93 National parks, 500 Sanctuary, 14 Biosphere Reserve and 28 Tiger Reserve in India for conservation of different animals.

Species Presevation Scheme : Special conservation programme for some threatened animals were granted. Such as Tiger Project, Operation Rhino, Gir Lion Project etc are running.

To Prevent Deforestation : afforestation schemes were introduced.

Habitat improvement : It can be done through-

- Improving structure of food chain.
- Nourishing fodder grasses and food plants.
- Providing more water holes, salt licks in the wild.
- Research on ecological requirements of wild animals and their documentation.

Periodic Census : periodic census of different wild animals are necessary to understand the trend in population - decreasing or increasing.

Preservation of Breeding Stock : It is done by artificial stocking of wild population in captive areas (by developing Captive Breeding programmes). This process is very difficult and expensive too.

People's participation :

For achieving success in conservation programmes it is very necessary to make aware the common people. It can be done by—

● Educating common people with the consequence of wild life loss.

● "Wildlife conservation and its benefit to the Society" be included in school/ college curricula.

13.2 Categories of enderngered animals and red data book

13.2.1 Categories Of Threatened Animals (IUCN) :

To highlight the legal status of threatened species for purpose of conservation, the International Union for Conservation of Nature and Natural Resources (IUCN) (1984, 1988) has established the following five main conservation categories.

Extinct : species that are no longer known to exist in the wild. Searches of localities where they were once found and of other possible sites have failed to detect the species.

Mountain Quail (*Ophrysia superciliosa*)

Asiatic Cheetah (*Acinonyx jubatus)*

Critical : Facing an extremely high probability of extinction in the wild in immediate future.

e.g. - Yak (*Bos mutus*)

Sangai (*Cervus eldi*)

Black necked Crane (*Grus nigricollis*)

Endangered : species that have a high likelihood of going extinct in the near future.

e.g. - Himalayan Newts (*Tylototriton ver*rucosus)

Lion-tailed Macaque *(Macaca silenus)*

Hoolock Gibbon (*Hylopetes hoolock*)

Adjutant Stork (*Leptotilos dubius)*

Vulnerable : species that may become endangered in the near future because populations of the species are decreasing in size throughout its range.

e.g. - Slender Loris *(Loris tardigradus*)

Langur (*Presbytis* spp.)

Whistiling Teal (*Dendrocygna bicolor)*

Rare : species that have small total number of individuals often due to limited geographical ranges or low population densities.

e.g. - Giant Heron (Ardea *goliath)*

Insufficiently Known : species that probably belong to one of the conservation categories but are not sufficiently well known to be assigned to a specific category.

e.g. - Andaman Wild Pig (Susscrofa *andamanesis*)

Tibatan antelope (*Pantholops hodgsoni)*

13.2.2 Red Data Book :

International Union for Conservation of Nature and Natural Resources (IUCN), also known as World Conservation Union, with Headquarters at Gland, Switzerland, has established the six main conservation categories. Using the IUCN categories, the World Conservation Monitoring Centre (WCMC) has evaluated and described threats to about 60000 plant and 2000 animal species in its series of Red Data Books. The great majority of the species on these lists of Red Data Books are plants. However, there are also species of fish, amphibians, reptiles, invertebrates, birds and mammals. The IUCN system has been applied to specific geographical areas as a way to highlight conservation priorities.

To help focus attention on the threatened species most in need of immediate conservation efforts, IUCN has begun to issue lists of the world's most threatened plants and animals. These lists include species of unique conservation value. On a global basis, the IUCN have estimated that about 10% of the world's vascular plant species totaling of about 20000-25000 species are under varying degrees of threat. IUCN published the "IUCN Red List of Threatened Animals" for the first time in 1988 and "IUCN Plant Red Data Book" in 1978.

In India, the problem of threatened plants was first discussed in the 11th Technical Meeting of the IUCN in 1969. In 1980, the Botanical Survey of India (BSI) published a small booklet entitled "Threatened Plants of India - A State-Of-The Art Report". The first volume of Red Data Books on Indian Plants was published by Botanical Survey of India in 1987; it includes 235 vascular plant species of Indian flora.

13.3 Wildlife census

13.3.1 Objective, Comprehensive knowledge on direct and indirect census techniques

Objective of Census

- An estimation of the total number of a particular animal population present in a particular area in a particular time. It is not absolute, but relative one.

- To determine trends in population - whether increasing, decrescasing or stable.
- It indicate the change of population with time.
- To draw comparison between areas, seasons or treatments.
- To compare the situation before and after mangement intervention.
- Comprehensive Knowledge on Techniques

1. Selection of a appropriate technique : It depends upon the following points.

- Area to be surveyed
- Species to be censused
- In which season the animal will be censused?
- Direct or indirect census technique will be adopted.

2. Which species is to be censused?

For management purpose it is obviously impossible to census all species in the area concerned. Therefore it has to make a choice such as one the following :

- Species which require management intervention (over grazing, competition)
- The species should be nationally or internationally endangered.
- The species should have either economic importance or is a important prey species.
- The species should have tourist attractions.

3. Selection of proper timing : It depends upon the following criteria

- Type of census.
- The reason for which the census operation is being conducted.
- Visibility of habitat varies with season.
- In case of water- hole census- dry season is best.
- Period of disturbance such as tourist season, fire, timber working etc. must be avoided.

4. Types of Census : There are two types of census :

Direct census technique : It is applicable to those animals which have relatively high densities and can be seen directly. Generally medium to large sized ungulates rhino, elephant are censused through this technique.

Indirect census technique : It is applicable to those species which have very low densities, difficult to see because of poor habitat visibility or cryptic behaviour. It is appilicable to carnivores, small, nocturnal mammals and also large mammals in dense habitat. Generally dung, pellet, nests, burrows, pugmark count comes under this category. Indirect census technique rarely yields a good estimate of actual population.

13.3.2 Sample count, line transect method, pug marking

TOTAL COUNT

For total count the entire area under consideration is searched. Major disadvantages of total counts are that maximum manpower is needed and one can not account for unavoidable errors. It is very difficult to treat the data statistically. Area size species, terrain, cover and available resources decide when a total count becomes prohibitively expensive or simply impossible.

SAMPLE COUNT

Here only a part of the area is counted (sampling unit). The cumulative area covered by these sample counts is a known (calculated) proportion of the total area, hence, the total [population size can be estimated by extrapolating the outcome of the sample count to the entire area. This population estimate can be subjected to statistical treatment, as the data are based on an independent count. By this way, there will be a maximum and minimum range within which the actual population size will fall. Sample counts are more efficient than total counts and can be repeated, which is the basis of monitoring.

A number of techniques have been suggested for estimation of population density of wild species which are varied and diverse, but none is so elastic to embrace all groups and all habitats.

LINE-TRANSECT METHOD

Line transect is one of the well known distance methods for sampling biological populations. This method has been used since early 1930's (Burnham et al 1980) for estimating the abundance of wildlife populations. It is not only practical and efficient but is relatively inexpensive too. It is based on the theory of walking along a predetermined route (at regular interval) to record the objects on or near the line.

Study Design :

Site Selection : Either random (stratified random) or systematic manner (stratified design) based on research goal and objective of the study.

Type of Habitat : Transects are well suited for open habitats and flat areas, but they have also been successfully tested in hilly areas both in India and other countries.

Placements of Transect : The marked transects is more or less straight so that there is no error in estimation of perpendicular distances and sighting of objects. Transects should also be well spaced out, distances between two parallel transects should be not less than 200m.Transects can be placed in random, stratified (acc. to habitat) and in piece wise_linear fashion in hilly and more rugged terrain.

Permanent Vs Temporary : If the aim is to monitor transects in different seasons and for successive years the transect line should be marked using boulders /stones or permanent posts such as trees.

Transect Length : Transects of up to 800m have been found to be adequate. Uniformity and extent of the vegetation type and topography can also influence the Transect length.

Travel Speed : While monitoring Transect one has to walk at a standard pace covering about 8-10m/min.Ideally a 1-1.5km long Transect should be covered in about 1-2hrs.All census operations should be conducted in the morning, which is the period of peak bird activity.

Time of the Day : At early morning, 10- 15 minutes after sunrise and for 2- 3 hours.

Weather Condition : Fair weather necessary and cloudy, windy and rainy days must be avoided.

Periodicity : Fortnightly or weekly monitoring of Transects is a standard practice. For long term monthly monitoring can be adopted.

Replicates and Number of Monitoring : Two replicates for a Transect are ideal in most cases, as often during analysis.

Data Collection :

Direct sightings or calls :

For each monitoring of Transects, perpendicular distances (PD), sighting angles (SA) and sighting distances (SD) can be recorded. In addition, other ancillary data for instance sex, age and group size can also be recorded for every bird detected.

Calls can also be recorded for density estimation. But based on the studies in Dudwa (SJ), we would like to caution the potential users of line Transects that there are chances of grater error in estimating densities from calls. The reason is that in field it becomes difficult to fix the call and hence cause the first error in estimating the perpendicular distance. Secondly, with call intensity and prevailing wind condition, one can easily ascribe call coming from different habitats to the habitat being sampled. And, lastly taking call cues for density estimates requires tremendous knowledge of the birds and their calls, not to forget that there are good imitators in the forest e.g. Redheaded Thrush and Racket-Tailed Drongo.

Variables to be recorded :

1. Perpendicular distance/sighting angle. At every detection, perpendicular distance of the object from the Transect line is recorded.

2. Bird species and their number.

3. Perch height or vertical distance.

4. Sighting angle.

5. Primary activity.

Biases :

Observer bias- employ same observer.

Habitat bias.

Bird/ animal behaviour.

Weather.

Advantages of Line-Transect :

Based on its versatility, easy monitoring, we list the following advantages associated with line Transect sampling :

More economical.

Greater species turnover.

Larger area is covered in relatively shorter time.

Applicable throughout the year.

Permanent Transects can be monitored for longer period of time.

Can be used in most of the habitat types.

With little care can also be used for hilly terrain.

Disadvantages of Line- Transect :

The line Transect method of sampling has certain disadvantages, which are not a great handicap if one looks at ease, usefulness and applicability of this method across a wide range of habitat and terrain types. Some of the disadvantages are :

Distances are not correctly measured.

Movement of observer may disturb the birds.

Chances of missing skulking, cryptic and shy birds are high.

Precautions :

For better results keep line as straight as possible.

Perpendicular distance should be measured correctly.

Transect should be representative of the habitats.

Observer must be trained, competent and interested.

PUG MARKING

There is no scope to enumerate Tiger by direct count. We all know that Tiger-sighting is heavily dependent upon "luck", and that, before we see a Tiger once, the Tiger would have seen us a hundred times. Yet, we know of signs that speak about the presence of Tiger. Some of the main evidences include kills, scat, pugmarks, ground-scratches, tree-scratches etc. Among all the field evidences, pugmarks are the most common, most revealing and easiest to use, verify and interpret to produce reliable information on minimum numbers of Tigers.

"Project Tiger" was launched in 1972 at the Dhikala Forest Rest House in Corbett National Park. The first all India Census of Tigers was conducted in summer 1972 using Chaudhury's method of Cooperation Tiger Census with the Tiger Tracer. The method has been in use since then but not without national and international doubts about the figures which was achieved for the Tiger population.

In the 1990s, a fresh spate of doubt arose about the number of Tigers in India. In the process, the technique of Pugmark Tracking was attacked in the media.

(I) Requirements for pugmark tracer :

1. 1 pane of colourless glass with holes drilled at the corners.
2. Metal screws with nuts and washers to fit (these are legs of tracer).
3. Thin paper to transfer the tracing from glass to paper.
4. Rubber band, felt pen, measuring tape.

(II) Selection of track for tracing :

1. A well formed impression of the rear pug from a series of tracks should be selected.
2. If no perfect impression is available a composite tracing should be made using 2 or 3 pugmarks of the same animal.
3. Left and right pugs should be identical mirror images.
4. Front pug is larger than the rear pug. Middle toes in front pugs come to same level.
5. Decision should be made earlier whether left rear or right rear pugmark is to be traced.

(III) Tracing the track :

(A) The procedure :

The tracer should be placed directly above the clear track. The legs of the tracer is pushed inside the soil until the glass pane is above the track surface. If the ground is hard the glass pane should be lowered by adjusting the wing nuts. With both the knees on the ground, left and right of the tracer and by looking straight down tracing should be started. Parallax should be avoided to get an accurate tracing.

Next the tracing paper is attached to the glass by means of rubber bands and by holding it against light the outline of the pugmark is transferred from glass to tracing paper by avoiding parallax. Other information to record :

Name of researcher.

Date and time of tracking.

Direction of movement.

Location eg. section of road.

(B) Measurements :

1. Lines are drawn on all sides of the pugmark touching the edges, thus forming a quadrangle.

2. The lines are at right angles to each other.

3. The center of toes and pad are marked.

4. The vertical distance i.e. Pad to toe length is called Pugmark Length (PML).

5. The horizontal distance i.e. Toe to toe length is called Pugmark Breadth (PMB).

6. Distance between center points of toes are measured. It is called Toe to Toe Breadth (TTB).

7. Distance between center points of toes and the center point of pad is called Pad to toe length.

(C) Step and stride :

Step is that particular distance covered by two consecutive legs (left and right) during walking. Stride is the distance between same-sided legs during walking.

(IV) Timing of survey :

1. If an estimate of population size and structure is the only purpose, survey should be done for several weeks when tiger tracks can be conveniently located.

2. In order to locate home range and habitat utilization within a given area the survey should be extended through a full season.

3. The pugmarks records obtained are compared every day and individual locations are entered in a map. In a few weeks these will lead to identification of all individuals using the area.

(V) Interpretation of track data :

Distinguishing characters

Male tiger	Female tiger.
The quadrangle is a square or almost a square. PMB=PML. The PML > 12 cm.	The quadrangle is a rectangle. PML>PMB. PML is 9.5-12 cm.

Pugmarks of cat family Impression of pad and toes present	Pugmarks of dog family Impression of claw along with that of pad and toe present.

Pugmarks of :	Adult male tiger	Adult female tiger	Tiger cub	Leopard	Leopard cub
Pugmark length :	>12 cm	9.5-12 cm.	Upto 9.5 to 10 cm.	5 -9.5 cm.	Upto 5cm.

Pugmarks of tiger cub	Pugmarks of leopard
PML 9.5-10 cm and found with pugmarks of adult female in the vicinity because cubs are associated with the mother	Only one type of pugmark of 5-9.5 cm PML is found without any other type of pugmarks. Leopard cubs are still smaller accompanied by their mother.

Once the pugmark of an animal is positively identified it should be given a number so that it can be remembered and referred to. The number can be pinned to a map to indicate locations where its track has been located. This will show the general whereabouts of the animal during the survey.

(VI) Precautions :

1. Pre-caution should be taken for multiple tracks.

2. Proper decision should be made to discriminate a tiger and a leopard track - it is difficult to discriminate the tracks of young tigers (six months or less) from those of leopard tracks, however tiger cubs of that age are always accompanied by their mothers.

(VII) Subjects of main criticism :

1. **Population growth rate presented in the initial years and its agreement with natality/mortality figure for tigers** : After about ten years of Project Tiger estimates indicated that the Tiger population had increased in almost in all habitats. This situation was varied with suspicion, and it was argued that the population estimates were not correct.

However, now it is agreed that it is indeed possible to estimate whatever the population growth rate has been.

2. The claim that by using pugmark technique we are identifying individual tigers : It has often been claimed that we always identify all individual Tigers from pugmarks. This claim is a little premature and needs to be properly explained. In fact, such identification of individuals is necessary only in a limited number of instances. It is necessary to establish the identification of two Tigers if they have pugmarks of equal size and obtained from two adjoining census units. Where separate identity is not distinct, it is always safe to state the two evidences belonging to one Tiger. Moreover, we are aiming to arrive at the minimum size of the Tiger population.

3. Pugmarks varying on different ground condition : Pugmark impressions vary in depth, size and clarity depending on ground conditions. Therefore, soil-conditions have to be taken into account and the actual tracing of the pugmark has to be determined. Pug Impression Pads (PIPs) with about 1cm layer of fine dust of soil provide a very stable and uniform ground condition.

4. Tracing varying from person to person : Field staffs of Forest Department do Tiger tracking and pugmarks tracings. The staffs are often knowledgeable about wildlife but are not always good at tracings.

5. Interpretation varying from person to person : The most commonly cited criticism is about an experiment where a selected few individuals were asked to determine the number of Tigers from a particular number of plaster casts. It is said that different individuals gave different results. The above situation arose because field data and analysis were incomplete. It is always necessary that information about field conditions and movement of Tiger have to be there to aid in analysis. These aspects have been taken care of in a prescribed format.

6. Underestimation of the number of cubs : By this technique we can identify one, rarely upto to three cubs. Therefore, the number of tiger cubs is underestimated.

7. Distinction of male and female : Male and female Tigers are distinguished on the basis of the quadrangle into which their hind pugmarks may fit. The contention had been that, if the pugmarks fits into a square it is male, otherwise it is female. Since it is rare event to have a perfect biological square, there have been arguments about sex-interpretation.

8. Distinction of tracks of tiger cub and leopard adult : The size of the pugmark of Tiger cubs and adult Leopard is almost the same but they differ in proportionate size of the toes and their arrangement. But distinguishing this requires experience.

9. Inadequate experience about the significance attached to population figures : This situation, if it is there, has definitely changed due to criticisms in the media, better standardization of the technique, and introduction to staff at all levels.

(VIII) Improvements made :

A number of aspects of the pugmark technique have been improved since 1990. Broadly, these aspects relate to the following :

A. Clarity and transparency has been introduced through non-official participation.

B. Simplification of the procedure has been made to make it intelligible to all field-level staff.

C. There is now adequate verifiability through lying of PIP (Pug Impression Pad).

(i) Season/unit/route/PIP

(ii) Data collection procedure

(iii) Training need

(iv) Analysis procedure

(v) Data presentation

D. The entire procedure is available in print in English and Hindi

E. Illustrated Pocket Books are being made available to field level workers.

F. A beginning has also been made to make available the procedure in local languages.

G. An experimental approach has been made to develop a video film in local language for use during training.

H. Printed materials have been produced in various forms like Trainer's Reference Sheets, Tracking guidelines and a Pictorial Field Guide for Forest Guards.

(IX) Significance :

If practiced well, the Pugmark technique can lead us to :

- Identify species.
- Identify sex.
- Identify major age classes (population composition).
- Link male-female/mother-cub.
- Develop map showing territorial distribution and areas of movement.

UNIT 14 ☐ Special Projects for Endangered Species

Structure

14.1 Himalayan Musk Deer

14.2 Manipuri Brow Antlered Deer (Sangai)

14.1 Himalayan Musk Deer *(Moschus chrysogaster)*

Taxonomic position :

Order - Artiodactyla

Family - Cervidae

Intraspecific Varieties :

Taxonomy rather disputed - due to wide ecological variations.

Moschus maschiferus - only one species with several subspecies.

Flerov (1928) suggested three species -

Moschus maschiferus (Siberian)

Moschus chrysogaster (Himalayan)

Moschus berezovaskii (Chinese)

Groves (1975) recognized two species from India -

Moschus chrysogaster (Alpine)

Moschus sifanicus (Forest belt)

Distinctive features :

1. Small deer without antlers.
2. Head-body length 80-100 cm, height 50-70 cm and weight 13-18 kg.
3. In males upper canine long and extends below upper lip.
4. Ear large and rounded.
5. Rump higher than shoulders.
6. Hind legs are long and muscular, fore legs are short and weak.
7. Hairs long, coarse and bristle. Age related changes in hair coats and colorings are observed.

New born with short, dark brown, soft hairs and densely covered with yellowish or white spots. In winter the spots become less defined or absent.

8. Tail short and completely buried in the long hairs of the anal region.

9. Male deer possesses musk gland, present anteriorly to male genitalia.

10. Can be recognized by distinctive jumping movement- like kangaroo.

Distribution :

Musk deer has been recorded in at least 13 countries of Asia and Russian forest. In Asia it is found in the Southern slopes of Himalayas - India (Jammu and Kashmir, Himachal Pradesh, Uttar Pradesh, Uttaranchal, Sikkim, Andhra Pradesh), Pakistan, Nepal, China, Bhutan, Tibet, Burma, Korea, Russia, Vietnam.

Habitat preference :

Musk deer prefers rugged terrain between 2200-4000 m. altitudes and occupies both alpine and forest belt. Sections with rock outcrops is their favourite habitat which provide shelter from predator.

Food habit :

Feeds mainly on grasses, herbs, mosses, ferns, arboreal lichens (130 types). In winter generally takes arboreal lichens, terrestrial bushy lichens (70%); also eat young shoots, coniferous needles, leaves, buds and bark. In summer feeds upon herbaceous plants.

Breeding Habit :

Female deer attain sexual maturity within 16-17 months and males after 2-3 years. Estrus occurs during December-January and lasts for 3-4 weeks. Gestation period inbetween 185-195 days. Generally fawns one, rarely two at selected places - beneath dense shrubs, under low branches of fir, around fallen trees in between April-June.

Behavior :

They are shy and secretive animal and active at twilight or at night. Normally moves solitary - highly territorial or in groups of 2-3. Vision and hearing are keen but sense of smell is poor. The musk pouches releases a scent which attracts mate. Also shows migratory behaviour from Steep Mountain to grassy meadows near river valley.

Economic importance :

1. Musk deer are hunted for centuries for their musk. Musks are highly priced in Traditional Medicine (90%) and are used in more than 400 preparations for heart and nervous disorders. Remaining 10% are used in perfume industry.

2. One kg musk costs about 1,00,000 DM ($ 40,000- 50,000) i.e. Five times more than the price of gold.

3. For extracting 1 kg of musk it needs 40 males (approximately 160 specimens) on an average of 25 mg musk per male.

4. During the years 1857-58 Japan imported 1 lac sacs in a single year

5. In 1995-97, 1.5 tonnes of musk exported from Russia to Korea.

Present status :

1. Their timid nature and remote habitat makes a constrain for population to estimate; once a widespread species now become restricted to isolated pockets, assuming a global population of 4-8 lac.

Regional population about 30,000 and shows a declining trend at suspected reduction rate 20% per year. Russian population has reduced to half of its size in the last ten years.

2. National Status (1994) - Vulnerable (RDB), Critically Endangered (1997).

3. International Status (1996) - Lower Risk group.

4. CITES - Appendix I.

5. IWPA (1991) - Schedule I, Part- I.

Threats to survival :

1. Due to indiscriminate persecution throughout its range.

2. Destruction of habitat and livestock grazing inhibits natural regeration.

3. Predated by leopard, marten, wolf, lynx and remains in 43% in lynx's feces.

4. Because of small size, musks are easy to hide and transport thus making smuggling easier.

Conservation strategy :

1. Captive population kept in

- Himachal Pradesh Musk deer farm (Kufri)
- Dachigram Sanctuary (Kashmir)
- Padmaja Naidu Himalayan Zoological Park in Darjeeling.

2. One breeding enclosure is present at Kedarnath sanctuary; breeding and extraction done at Kufri (1975).

3. Enlisted in IWPA (I) & CITES (Appendix I) - thereby fully protected from killing and trade.

4. Sanctuaries and National parks on its distribution range will help to restore habitat.

5. Introduction of synthetic product allied to musk will reduce the demand for natural product.

6. International trade must be prohibited by increasing vigilance on smuggling.

7. In situ conservation should be encouraged.

8. Education and research on this dwindling species should be promoted.

14.2 Manipuri Brow Antlered Deer (SANGAI) *(Cervus eldi eldi)*

Taxonomic Position :

Order : Artiodactyla.

Family : Cervidae.

Distinctive features :

1. Sangai is a beautiful deer having height at shoulder 105-120 cm. and weight- 170 kg.
2. The male deer has a dark brown winter coat which turns to fawn in summer; the female is fawn all year round. The young are spotted.
3. Sangai has splayed hooves and long dewclaws.
4. Hind pasterns greatly developed and applied to the ground while walking.
5. Keen eyesight and speed allow it to be an open ground deer.

Distribution :

Sangai is Endemic to India and confined to Manipur (Loktak Lake) in Keibul Lamjao National Park which is less than 10 sq km area. The number of mature individuals is less than 100 (Gee, 1960) while the captive population consists of 94 individuals in 14 zoos.

Habitat preferences :

Sangai prefers open scrub jungle, flat or undulating lands between hills and river range (floating swamps called Phumids) and also marshy lands.

Food Habit :

Sangai is terrestrial in nature and lives in small herds and feeds mainly in the morning and evening mainly on grass.

Breeding habit : very little is known about its breeding behaviour.

Behaviour : This deer walks on hind surface of its pasterns, which are thus horny and not hairy. It moves with mincing hops over floating foliage and is also called 'Dancing Deer'. It is known to raid crops at night. A sharp grunt indicates alarm, while rutting calls are longer and louder.

Present Status :

It is declared Critically Endangered in the IUCN Red List.

It lives in a single population only in one location.

Globally - data deficient.

CITES - Appendix I ; Schedule - I; Part - I.

Threats to Survival :

1. Endemic to India, a single population present only in one location which is extremely regional.

2. Gradual decline in area of occupancy due to human settlement, interference, cattle grazing, damming, fishing, hunting and cultivation. Loss of habitat by siltation, burning of grass are also responsible.

3. Trade, diseases, genetic problems are among the other reasons of their declination.

Conservation strategy :

1. No reliable census has been done (Aerial Census only Desai, 1986 ; Forest Department data '94-'97)

2. No genuine Stud Book has been prepared.

3. Proper monitoring limiting factors should be done.

4. Habitat and genetic management are necessary.

5. Enhanced allocation of fund and stuff.

6. Captive breeding and reintroduction programmes are necessary to maintain the wild population.

UNIT 15 ❑ Wildlife Habitat Management with Special Reference to Sundarban

Structure

15.1 Wildlife habitat management in sundarban

Area :

The Sunderbans is the largest prograding deltaic region of the world. It extends through India to Bangladesh, covering a total area of about 26000 square kilometers - the largest single stretch of mangrove vegetation. About two-third of the total Sunderbans falls in Bangladesh. The Indian Sunderban measures 9630 square kilometers, out of which the Reserve Forest occupies around 4263 sq. km and the South 24 Parganas Forest Division Area occupies 1660 square kilometers. The administrative boundary is spread over two districts : South 24 Parganas and North 24 Parganas.

Latitude : 21°32 minutes and 22°40 minutes north.

Longitude : 88°30 minutes and 89° east.

Status :

At the launch of **"Project Tiger"** in the year 1973, the Sunderbans was among the nine Wildlife Reserves declared as **'Tiger Reserves'** (a total area of 2585 square kilometers). Within Sunderban Tiger Reserve, an area of 1330.12 square kilometers is designated the 'Core Area' which in the year 1984 was declared the **'Sunderban National Park'**. The rest of the area is the 'Buffer Area', part of which in the year 1976 was declared the **'Saznekhali Wildlife Sanctuary'**. In the year 1987 due to "high biodiversity" and "ongoing geological processes" Sunderbans National Park was declared a **'World Heritage Site'** by IUCN. The Sunderbans also achieved a milestone in 1989 when UNESCO declared it a **'Biosphere Reserve'**. The process of declaring it a **'Ramsar Site'** for being an outstanding wetland is in an advanced stage.

Climate :

Average annual temperature is 25°C.

Summer : middle of March to middle of June; maximum average temperature 29°C.

Winter : December to February; maximum average temperature 20°C.

Rainfall : average annual rainfall is about 192 cm. The rivers become calm between December and February.

Principal Rivers :

River Hooghly along with its tributaries and distributaries like Matla, Icchamati, Raimongol, Bidyadhari, Kalindi, Guasabha, Saptamukhani, Thakuran and innumerable crisscrossing channels and creeks forms the unique riverine system of this area.

The rivers of the Indian Sunderban carry much less silt and sweet water in comparison to those of the Bangladesh Sunderbans. Consequently they drew more seawater inside. Moreover, due to bulk drainage of water from the Hooghly river system to the Padma River in Bangladesh, the freshwater rivers like Matla and Bidyadhari do not get much fresh water and have become almost tidal rivers. Due to influx of sea water the salinity is intense and it has a threatening impact on the mangrove community.

Flora :

The mouth of the tidal creeks and rivers, where salt and fresh water mix in ideal proportions, show the greatest concentration of mangroves in the Indian Sunderbans. A total of 84 species of flora have been recognized in the mangrove forests of the Indian Sunderbans of which 34 are true mangroves. The other varieties are mangrove associated and back mangrove species. Another fact adds to the unique richness of this mangrove delta - it is home to 70% of all the species of mangrove in the world. As they are mostly restricted to inter-tidal belts at the land-sea interface, the mangroves here are exposed to high and low tides twice in 24 hours.

The mangroves have the ability to maintain a suitable water balance in spite of the salinity of water. It is believed that some even excrete salts from their leaves. The anchoring mechanism of the trees baffles even the most expert navigators. The roots are modified so that they can stand firmly in the mud. They spread horizontally as prop roots just below the surface of the mud and provide the necessary anchorage (e.g. - Garjan). This helps the trees in withstanding cyclonic weather and soil erosion. Since the aeration of the clayey soil is very poor, some trees have evolved special aerial roots whose tips protrude out of the mud upwards like spikes called 'pneumatophores' or commonly called respiratory roots (e.g. - Keora). They ensure sufficient supply of oxygen to the deeper roots. But accumulation of silt raises the mud banks continually thereby increasing the anaerobic zone. The growth of these pneumatophores has to keep pace with the raised water level. For the same reason, some roots of trees arching here and there above the surface of mud like knees (e.g. - Kankra).

The mangroves are extremely skillful in colonizing newly created mud banks. The future roots of the plant extend upto a length of 30 cm or more before they get detached from the parent plant. Eventually, when they fall, they are driven like stakes in the mud below the parent tree. Sometimes they are carried away by the water and strike root elsewhere. This is scientifically known as 'viviparous germination' (e.g. - Kankra).

The mangroves play an important role in the delta :

- They produce economically significant product like timber, firewood, honey, wax, tannin and other medicines.
- They produce leaf litter and debris which fulfill the nutritional requirements of the young prawns, adult shrimps, mollusks and fish of high economic value.
- They act as the breeding and feeding ground of shell fishes and fin fishes.
- They also protect the coastal land from storms, surges, tropical cyclones, high winds etc.
- The Sunderbans mangrove swamp is home to the single largest tiger population of the country.
- It protects the human settlements and even metropolitan Kolkata from the frequent gales originating in the Bay of Bengal.

SOME COMMON PLANT SPECIES

Common Name	Scientific Name	Family
Bakul	*Bruguiera cylindrical (L) Blume*	Rhizophoraceae
Sundari	*Heritiera fomes Buch-Ham*	Sterculiaceae
Bhola	*Hibiscus tilliaceous L*	Malvaceae
Golpata	*Nypa fruticans Wurmb*	Palmae
Hental	*Phoneix paludosa Roxb*	Palmae
Keya	*Pandanus tectorius soland*	Pandanaceae
Garjan	*Rhizophora apiculata Blume*	Rhizophoraceae
Keora	*Sonneratia apetala Buch-Han*	Lythraceae
Harguja	*Acanthus ilicofolius L*	Acanthaceae
Kankra	*Bruguiera gymnorhiza (L) Lam*	Rhizophoraceae
Nona jhau	*Tamarix troupii Hole*	Tamaricaceae
Hodo	*Acrostichum aureum L*	Pteridaceae

Fauna :

Marine Invertebrates :

The best season to observe marine life in the Sunderbans is from November to April, when the salinity of the water rises. The diversity of marine life is best explored at low tide, when the mudflats of the mangrove swamp or sandy beaches of Ganga Sagar and Bakkhali are exposed.

During the months of January-February the most exhilarating sight is of the migration of the thousands of jelly-fish swooping into the green waters of the rivers of the Sunderbans. Animals found on the rocky shores are Acorn barnacles, Sea anemones, Oysters, Periwinkles etc. The sandy shores of Sagar or Bakkhali seem barren at first sight as the inhabitant here mostly live beneath the surface. However, the evidence of their presence is seen in the typically designed sand or mud palates at the mouth of the animals' hole. Hermit crabs are abundant. Also sea-pen, polychaetes, ribbon worms, Telescopium, Wedge clams are common on the beach.

The Sunderbans has an immense diversity of crabs. Some of them are colourful, others dull. Sandy beaches of the far south are full of Ghost crabs which are deep red in colour. Red and yellow fiddler crabs are also very bright and colourful creatures. Among the edible varieties, Mud crabs are tasty and have good international market. The other important variety is the Horse-shoe crab which is a highly endangered species.

Fishes :

The rivers of the Sunderbans harbour hundreds of species of fish. Most of them are edible. A large number of people living on the edge of the forests are dependent on fishing for their livelihood. Some of the fishes are of high commercial value, such as Hilsa, Bhetki, Pomfret, Topse and Parse. Other tasty fish include Kanmagur, Paira Chanda, Gangdhara, and Bombay duck. Among many species of shell fishes, prawn (Bagda) and shrimps (Chapra) are the most important commercial varietie

COMMON ELASMOBRANCHS	
Common name	**Scientific name**
Bamboo shark	*Chiloscyllium sp.*
Tiger shark	*Stegostomata sp.*
Whale shark	*Rhinchodon sp.*
Hammer-headed shark	*Sphyrna sp.*
Pointed saw fish	*Pristis cuspidates*
Sting ray	*Dasyatis sp.*

MAJOR TELEOSTS FISHES	
Common name	**Scientific name**
Khaira	*Sardinella sp.*
Hilsa	*Hilsa ilisha*
Bombay duck	*Harpodon nehereus*
Kanmagur	*Plotosus canis*
Parse	*Mugil parsia*
Bhangan	*Mugil tade*
Topse	*Polynemus padiseus*
Bhetki	*Lates calcarifer*
Paira Chanda	*Scatophagus argus*
White Pomfret	*Chondropites chinensis*
Ban	*Mastocembelus armetus*
Moray eel	*Gymnothorax favagineus*
Bele	*Sillago sihama*
Chanda	*Pama pama*

Birds :

The unique ecosystem of the Sunderbans is very rich in avian or bird life. Over 200 species of birds have been recorded so far. The species vary from forested areas to villages, from mangrove swamp to estuaries and all canopies to mudflats.

The highest canopies of the forests are occupied predominantly by Osprey, Brahminy kite and White-bellied sea eagle which are raptors or bird of prey. The middle tier of tall trees is the nesting, perching and feeding place of birds like Rose-ringed parakeets, small bird like flycatchers, warblers, Small minivets, bee-eaters and tree creepers like Golden-backed woodpeckers and the wryneck. Other birds include orioles and barbets. In the lowest tier there is predominance of kingfishers. The Sunderbans harbours seven species of kingfishers, namely - White-breasted, Pied, Common blue, Black-capped, Collared, Brown-winged and Ruddy kingfishers.

The mudflats are full of waders, during the low tide. Waders include the Common sandpipers, Terek sandpipers, Redshank, Greenshank, White-breasted waterhen and others. The most typical birds of the muddy riverbanks are the curlew and whimbrel. Lesser adjutant storks are the largest storks of the Sunderbans. Open-billed storks are found near cultivation. Large egrets add beauty to the serene landscape of the Sunderbans. The Pond herons are most common of al herons. Grey and Purple herons are also seen but they are rare. The rarest of all herons is the Goliath heron.

Ducks come in thousands into the Sunderbans every winter. Gadwalls, Pintails and Shovellers are common. But Wigon and Common pochards are not rare. Brown-headed and Black-headed gulls are found throughout the year. In recent times, rare birds like the Spoon-billed sandpipers, Mangrove pitta and Rosy pelican have been recorded.

Reptiles :

The estuarine crocodile is the largest reptile of the Sunderbans. Ornamental and vine snakes are common non-venomous snakes of the region. But in the villages of the Sunderban most deaths take place due to bite of common krait. The Indian cobra and Russell's viper are among the other most poisonous snakes of the region. The coastal sandy beaches of Mechua, Chaimari, Kalash and Bijeara are the nesting grounds of the Olive Ridley turtles. Among fresh water species, one of the most endangered turtles, *Batagur baska*, is found in the Sunderbans.

TURTLES, TORTOISES, TERRAPINS

Common name	Scientific name
River Terrapin	*Batagur baska*
Green Turtle	*Chelonia mydas*
Olive Ridley Turtle	*Lepidochelys olivacea*

SNAKES

Common name	Scientific name
Common Checkered Keel back	*Xenochrophis piscator*
Rat Snake	*Ptyas mucosa*
Common Krait	*Bungarus caeruleus*
Banded Krait	*Bungarus fasciatus*
Indian Cobra	*Naja naja*
Russell's Viper	*Daboia russelli*
Ornamental Snake	*Chrysopelea ornate*
Sea Snake	*Hydrophis nigrocinctus*
Green whip Snake	*Ahaetulla nasuta*
Wolf Snake	*Lycodon aulicus*

LIZARDS & CROCODILES	
Common name	**Scientific name**
Tokay	*Gekko gecko*
Garden Lizard	*Calotes versicolor*
Chameleon	*Chameleon zeylanicus*
Water Monitor	*Varanus salvator*
Monitor Lizard	*Varanus flavescens*
Estuarine Crocodile	*Crocodylus porosus*

Mammals :

There is not much diversity in the mammalian species found in the Sunderbans. But, it can boast about its Royal Bengal Tigers. Due to hostile ecological and riverine conditions, these tigers have evolved different habits from the tigers of other forests of India. They are good swimmers, drink saline water, are more hardy and agile and eat anything from fish to human beings. The major preys of the Sunderban tigers are wild boars and chital deer. The Sunderban is rich in aquatic mammals.

MAJOR MAMMALS OF THE SUNDERBANS	
Common name	**Scientific name**
Royal Bengal Tiger	*Panthera tigris tigris*
Fishing Cat	*Felis viverrina*
Rhesus Macaque	*Macaca mulatta*
Axis Deer or Chital	*Axis axis*
Indian Wild Boar	*Sus scrofa*
Finless Porpoise	*Neophocaena phocaenoides*
Gangetic Dolphin	*Platanista gangetica*
Smooth Indian Otter	*Lutra perspicillata*
Irawaddy Dolphin	*Orcaella brevirostris*
MAMMALS WHICH HAVE BECOME EXTINCT	
Common name	**Scientific name**
Javan Rhinoceros	*Rhinoceros sondaicus*
Swamp Deer	*Cervus duvauceli*
Wild Buffalo	*Bubalus bubalis*
Barking Deer or Muntjac	*Muntiacus muntjak*

People :

At present out of 108 islands, 54 are inhabited. The population is about 4.1 million (2001 census). A unique religious harmony among Hindus and Muslims is observed here. Monocropping, agriculture, fishing, prawn seed collection and manual labour are the major occupation.

15.2 Threats to mangrove ecosystem :

There are a number of causes that threaten the Mangrove ecosystems.

Increased Salinity: Due to a shift in the freshwater flow from the Hooghly River system into the Padma River, major freshwater rivers like Matla and Bidyadhari were cut off from their freshwater sources. Embankments have been constructed in the coastal zone to protect human settlement in some areas. As a result of this, the salinity of water has increased to an intense level, leading to a change in the mangrove pattern of the region. Saline banks have formed on the islands. The 'Sundari' tree has become endangered due to this excess of salinity in the water, whereas it flourishes in low salinity areas of the eastern part of the Bangladesh Sunderbans.

Sewage Pollution : Part of the sewage from the city of Kolkata, Howrah and Haldia Complex gets released continuously into the river water, polluting it. Moreover, release of oil and grease from adjacent land, fishing vessels, trawlers etc. also contribute to such pollution of the mangrove ecosystem. It has a long standing effect on the flora and fauna of the Sunderbans.

Cyclonic Destruction : During April-May and October the area is exposed to repeated cyclonic storms and depressions that destroy the flora among the coast. Besides every year the sea encroaches on a large portion of the mudbanks. The continuous destruction and re-formation of land has created instability in the natural vegetation pattern.

Prawn culture : Collecting shrimps and prawn seeds by the crude method of netting is a popular and profitable activity carried out by peoples of almost all age groups. These prawn seeds (larvae of *Peneus monodon*) are supplied to the commercial prawn culture firms. During this operation the juveniles of a large variety of fin-fish and shell-fish are also caught in the nets. After scrutiny they are simply thrown away and wasted. An investigation reveals some startling facts - juveniles of about 50 species of fin-fish and 28 species of shell-fish are wasted per net per day. This unsustainable activity has already placed a strain on the fishery of the state. The dragging of nets along the coast uproots the mangrove seedlings, leading to soil erosion in the coastal zone. Expansion of aquaculture, prawn farming, drying of sea-fish etc. thus create a direct threat to the existing mangrove forests.

Endangered Species : Many species like the tiger, fishing cat, Gangetic dolphin, adjutant stork, estuarine crocodile, Olive Ridley turtle etc. have already acquired the endangered status, due to habitat destruction, poaching, increased salinity, anthropogenic stress and illegal trade. The Horse-shoe crab - a living fossil - is killed and sold in the markets of Kolkata with a misplaced belief that it can cure arthritis.

Man-Animal Conflict : Extremely high human density (over four million) on the forests fringes results in extremely high biotic pressure such as fishing, illicit felling and prawn seed collection. Straying of tigers into villages along the western boundary of the Sunderbans Tiger Reserve and north-western fringes of 24 Parganas (South) forest division causes acute man-animal conflict which poses a direct threat to conservation effort.

15.3 Current management practices :

Protection :

Establishments of camps, watch towers covering all the remote areas.

Supply of improved fire arms to field staff, providing patrolling vessels and mobile patrolling camps.

Afforestation :

Afforestation of mudflats and outer slopes of embankments with pure mangrove species for bank protection and soil conservation.

Afforestation of inner slopes with fast growing and endangered species.

Distribution of seedlings for planting on private lands.

Habitat Development Activities :

Development of water holes.

Opening up canopy though construction of observation lines. Such measures also help the growth of herbivores.

Reduction of Man-Animal Conflict :

Straying of tigers from the Reserve Forests into the habitat areas along the Northern and Western fringes of Sundarban Forest causes occasional death of cattle or human as well as tiger. Illegal entry of fishermen into core areas, as well as entry of honey bee collectors into the forest also leads to death of a number of people. To prevent straying of tigers into village's nylon net, fencing, tranquilization and capture of straying animal and their subsequent release into the forest is practiced.

Eco-Development Measures :

Community development projects : Construction of irrigation canals, sweet water ponds, village brick paths, jetties, tube wells, embankments, organization of regular medical camps.

Individual beneficiaries oriented schemes : Apiary, mushroom cultivation, Piggery, vocational training for cottage industries etc.

Census :

Biennials census of tiger is carried out in December. The last census has been done from 7-14 Dec, 2001.

Monitoring :

Geographical Information System (GIS) cell has been developed under Sundarban Biosphere reserve has updated forests/vegetation and topography map of Sundarban as on March, 2001, using satellite imageries from IRS-1D. GIS based information and maps have been used for updating the management Plan of Sundarban Tiger Reserve.

Management of Sundarbans forests involves an integrated approach towards management of all the above aspects with a goal to conserve the fragile mangrove ecosystem for prosperity.

Further Research :

Facilitating research, monitoring, education and training to perpetuate the progress made by the management. For this the total area of the Biosphere Reserve has been divided into :

- Core zone covering approx 1700 sq km.
- Buffer zone
- Transition zone.
- Project Tiger :

The Sunderbans can, no doubt, boast about its tigers. It is home to the largest number of tigers in India and perhaps in the world. This has put the Sunderbans on the international tourism maps.

The Sunderbans was declared a Tiger Project in 1973, covering an area of 2585 square kilometers, of which 1330 square kilometers is the core zone and 1225 square kilometers is the buffer zone. The total land area of the Sunderban Tiger Reserves is more or less 1580 square kilometers and the total water surface is about 1005 square kilometers.

The Project Tiger is headed by the Field Director who is a conservator. His team includes a Deputy Field Director who is one of the ranks of a Divisional Forest Officer, an Assistant Field Director who is the rank of Additional Divisional Forest Officer and 12 Range Officers.

CENSUS									
YEAR	24 Parganas (South) Division				Sunderban Tiger Reserve				Total Estimated Tigers
	Male	Female	Cub	Total	Male	Female	Cub	Total	
1997	13	16	06	35	99	137	27	263	298
1999	09	16	05	30	96	131	27	254	284
2001	07	13	06	26	93	129	23	245	271
2004	07	14	04	25	83	133	33	249	274

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মানুষের জ্ঞান ও ভাবকে বইয়ের মধ্যে সঞ্চিত করিবার যে একটা প্রচুর সুবিধা আছে, সে কথা কেহই অস্বীকার করিতে পারে না। কিন্তু সেই সুবিধার দ্বারা মনের স্বাভাবিক শক্তিকে একেবারে আচ্ছন্ন করিয়া ফেলিলে বুদ্ধিকে বাবু করিয়া তোলা হয়।

— রবীন্দ্রনাথ ঠাকুর

ভারতের একটা mission আছে, একটা গৌরবময় ভবিষ্যৎ আছে, সেই ভবিষ্যৎ ভারতের উত্তরাধিকারী আমরাই। নূতন ভারতের মুক্তির ইতিহাস আমরাই রচনা করছি এবং করব। এই বিশ্বাস আছে বলেই আমরা সব দুঃখ কষ্ট সহ্য করতে পারি, অন্ধকারময় বর্তমানকে অগ্রাহ্য করতে পারি, বাস্তবের নিষ্ঠুর সত্যগুলি আদর্শের কঠিন আঘাতে ধূলিসাৎ করতে পারি।

— সুভাষচন্দ্র বসু

Any system of education which ignores Indian conditions, requirements, history and sociology is too unscientific to commend itself to any rational support.

— Subhas Chandra Bose

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