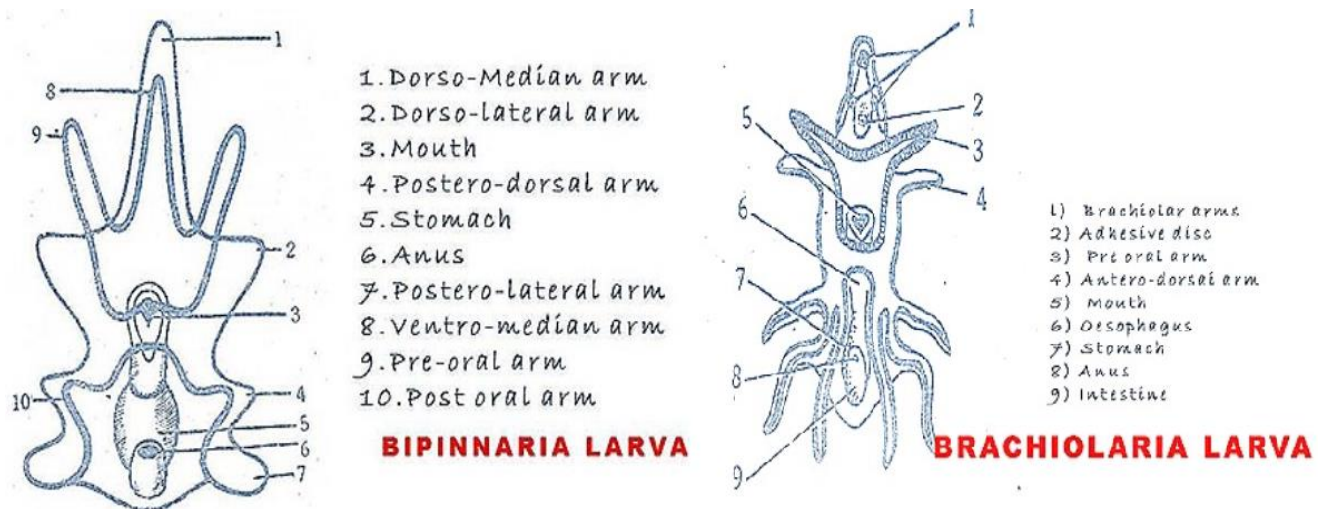


LARVAL FORMS IN ECHINODERMATA

In echinoderms eggs and sperms are released in water and fertilization takes place in water forming zygote. Echinoderms are deuterostomes and hence cleavage is radial, holoblastic and indeterminate. The larvae hatch in water and feed and grow through successive larval stages to become adults. The larvae of echinoderms are bilaterally symmetrical but lose symmetry during metamorphosis. Different classes of echinoderms show structurally different larval stages and their comparisons can reveal their evolutionary ancestry.

LARVAE OF ASTEROIDEA

There are three larval stages in Asterozoa in the course of their development to adult stage. **Early bipinnaria** appears like hypothetical **dipleurula**. It has oval body without arms and ciliary bands for locomotion. It has well developed alimentary canal for feeding and grows to become bipinnaria.



Bipinnaria larva possesses 5 pairs of ciliated arms which do not have any skeletal support inside. These arms are used for swimming in water while feeding on planktons. Preoral and postoral ciliary bands are also present. This larva resembles auricularia larva of Holothuroidea in general appearance.

Brachiolaria larva is formed after 6-7 weeks of life and growth of bipinnaria. This larva is sedentary and remains attached to a hard substratum for which it possesses three brachiolarian arms having adhesive discs at the tip. Ciliated arms get reduced and become thin and functionless, while mouth, anus and gut are well developed. It has axocoel, hydocoel and somatocoel that later on give rise to water vascular system. Development of starfish takes place inside the sedentary brachiolaria which ruptures and releases tiny starfish into water.

LARVAE OF HOLOTHUROIDEA

Class Holothuroidea demonstrate two larval stages, namely, auricularia and doliolaria larvae.

Auricularia larva has striking resemblance with bipinnaria of Asterozoa as it also possesses 4 or 5 pairs of ciliated arms for swimming and has a well-developed mouth, gut and anus.

Doliolaria larva is the next stage after auricularia. It has barrel like body with 5 ciliated bands surrounding it. Mouth or vestibule is on the ventral side for feeding. There is neural sensory plate on the anterior side and an apical tuft of cilia for balancing while swimming. Doliolaria transforms into adult but in some holothurians doliolaria stage may be absent.

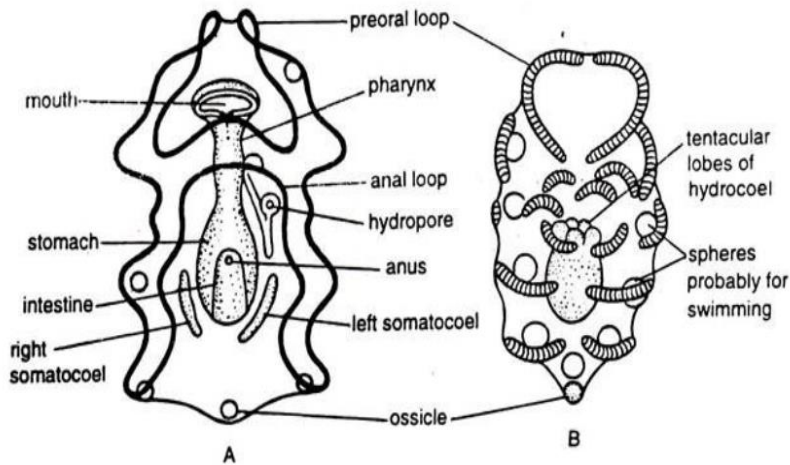


Fig. 27.12. A. Auricularia larva B. Transitional stage from Auricularia to Doliolaria larva

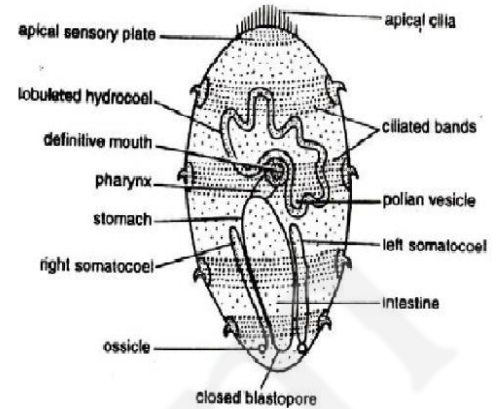


Fig. 27.13. *Leptosynapta inkaerens*. A mature Doliolaria larva

LARVAE OF ECHINOIDEA

There is a single larval stage in echinoidea called **Echinopluteus** which is bilaterally symmetrical. The larva has oval body and long paired ciliated arms that are supported by calcareous skeletal rods. **Preoral arm** is present but posterolateral arm is absent. The other three arms are anterolateral, postoral and posterodorsal arms. Mouth, anus and gut are well developed.

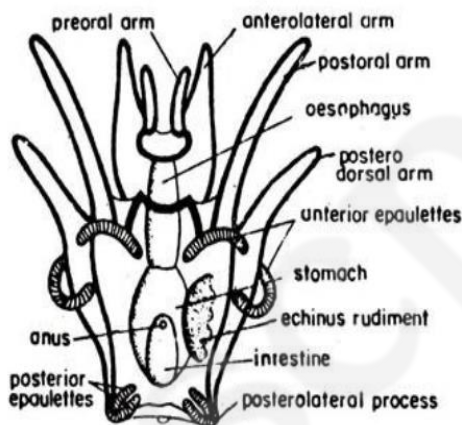
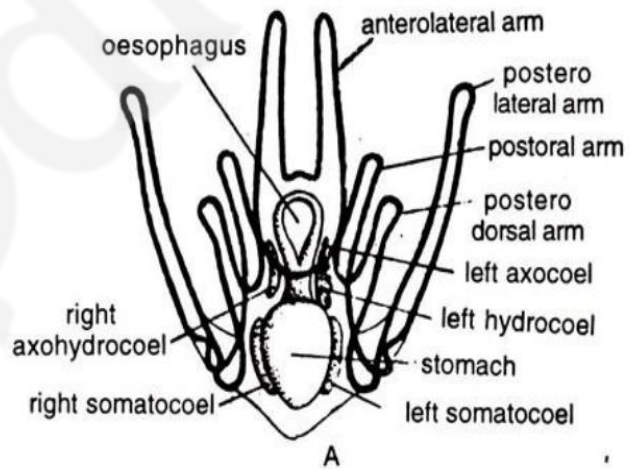


Fig. 27.11. Echinopluteus larva



LARVAE OF OPHIUROIDEA

Ophiopluteus is the only larva of Ophiuroidea that resembles echinopluteus larva of Echinoidea in general features. Anterolateral, postoral and posterodorsal arms are present but preoral arm is absent. Instead, it has very long posterolateral arms. All arms are supported by calcareous skeletal rods. This larva metamorphoses to become adult.

LARVAE OF CRINOIDEA

Pentactula is the basic larval stage of Crinoidea but it passes inside the egg. There is one or two larval stages in sea lilies. **Doliolaria** larva, which is also called Vitellaria larva, is found in some sea lilies. It resembles doliolaria of holothuroids but has an **adhesive pit** on the ventral side with which it attaches to substratum and becomes sedentary. This larval resemblance demonstrates close evolutionary relationship between Crinoidea and Holothuroidea.

Pentacrinoid larva is sedentary and attaches to substratum with an attachment plate. Body is supported by a stalk. There are 10 cilia bearing tentacles which are used for capturing food. Both mouth and anus are on the same side of the disc.

The affinities among larval stages of echinoderms demonstrate evolutionary relationships among different classes. However, the same relationship cannot be shown in the cladistics classification of echinoderms, which is based on adult characteristics. Adults are highly modified organisms in echinoderms.

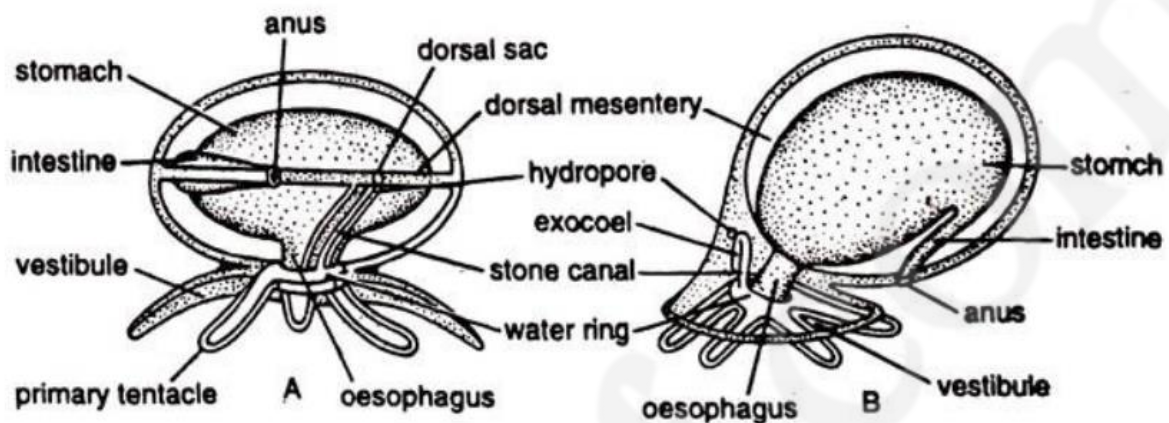


Fig. 27.15. Pentactula (ancestor larva) A. Bilateral form. B. Radial condition after torsion

ORIGIN OF CHORDATES

Chordates evolved sometime during Cambrian period, 500 million years ago during Cambrian explosion, almost at the same time when invertebrates were beginning to evolve. They may have evolved from some freshwater forms, as Chamberlain (1900) pointed out that all modern chordates possess glomerular kidneys that are designed to remove excess water from body. However, early fossils of chordates have all been recovered from marine sediments and even modern protochordates are all marine forms. Also glomerular kidneys are also found in some marine forms such as myxinoidea and sharks. That makes the marine origin of chordates more plausible.

Chordates evolved from some deuterostome ancestor (echinoderms, hemichordates, pogonophorans etc.) as they have similarities in embryonic development, type of coelom and larval stages. Fossils of the earliest vertebrates are known from the Silurian-Devonian period, about 400 million years ago. The following theories have been given to explain the origin of chordates:

1. Echinoderm Origin:

The theory was given by Johannes Muller (1860) and is based on the comparative studies of larval stages of echinoderms and hemichordates. Tornaria larva of hemichordates resembles echinoderm larvae such as Bipinnaria, Auricularia, Dipleurula and Doliolaria, which all possess ciliary bands and apical tuft of cilia. Johannes Muller, W. Garstang and DeBeers proposed that echinoderm larvae gave rise to chordates by neoteny. Also like chordates, echinoderms are also deuterostomes and possess mesodermal skeletal elements.

The discovery of fossil echinoderms called **Calcichordata** from Ordovician period (450 mya) further confirms echinoderm ancestry of chordates. Calcichordates were asymmetrical animals which demonstrate affinities with both echinoderms and chordates but their skeleton is made of CaCO_3 whereas in vertebrates the bones are made of hydrated Ca and phosphate. They had large

pharynx with a series of gill slits, each covered with flaps for filter feeding, a small segmented body and a post-anal tail. A perforated pharynx for filter feeding appears to have evolved in diverse groups of animals during Cambrian-Orodovician periods when planktons were abundant in water.

2. Hemichordate Origin:

Romer (1959) suggested that ancestral deuterostomes were sedentary tentacle feeders whose mucous-laden ciliated tentacles served to trap planktons as they were waved in water as do the modern lophophorates and pterobranch hemichordates, *Cephalodiscus* and *Rhabdopleura*. By some mutation pharyngeal gill slits evolved in these ancestors, which made the pharynx sieve-like to trap planktons as the water current passed through it. Extant pterobranchs possess both ciliated arms and pharyngeal gill slits. Tornaria larva of hemichordates shows phylogenetic relationship with echinoderm larvae and hemichordates also show affinities with chordates.

3. Urochordate Origin:

W. Garstang (1928) and N.J. Berrill (1955) gave importance to the tadpole-like larva of urochordates which carries typical chordate characters, namely, a notochord in tail along with segmented myotomes, dorsal hollow nerve cord, sense organs and pharyngeal gill slits. Garstang (1928) suggested that chordates evolved from some sessile filter feeding urochordate by the larval stage evolving into adult by neoteny and by losing the sedentary adult stage.

4. Cephalochordate Origin:

Chamberlain (1900) studied the primitive and advanced characters of cephalochordates and proposed that while extant cephalochordates possess all chordate characters in typical state, they also show some primitive features of non-chordates, such as, absence of heart, head, sense organs, respiratory pigment, filter-feeding mode of food capture and excretion by solenocytes. Fossils of 60 specimens from mid-Cambrian of the earliest chordate, *Pikaia gracilens* have been discovered from Burgess Shale in British Columbia, Canada. The Amphioxus-like fossils show streamlined, ribbon-shaped, 5 cm long body having notochord in the posterior two-third of body and myomeres. It has a small head with two tentacles and gill slits in the neck region. Other chordate-like fossils are: *Cathaymyrus* from early Cambrian sediments in China and *Palaeobranchiostomata* from early Permian from South Africa that appears to be more similar to Amphioxus.

5. Combined theory:

E.J.W. Barrington (1965) combined all the above theories and proposed that the common ancestor of echinoderms and chordates was a sessile ciliary arm feeder that lived in the plankton-rich environment of the Cambrian. Modern Crinoidea (Echinodermata), Pogonophora and Pterobranch hemichordates evolved from a similar ancestor by retaining the original mode of feeding, perhaps because they continued to inhabit the same environment as occurred in ancestral days. However, pharyngotomy (perforation of pharynx with gill slits) must have evolved in a large number of groups at that time, which must have been much more superior method of food gathering by filtering water through pharynx as compared to ciliated arm feeding. Hence, the sedentary Protoascidians of that time lost ciliated arm feeding and adopted pharyngeal filter feeding as the only method of food gathering. Sometime later, when the plankton population in water declined, free-swimming tailed larva of these urochordates did not metamorphose and became a neotenic adult, since free-swimming mode was superior in food searching at a time of food scarcity. Cephalochordate-like ancestors evolved by perfection and expansion of chordate characters that were already present in the ascidian

tadpole larva. We already have fossils of such primitive chordates, e.g. *Pikaia gracilens* from mid-Cambrian.

RESPIRATION IN FISHES

Gills of bony fishes

In bony fishes gills are covered with an operculum that is made of flattened skeletal plates and there is no spiracle as in elasmobranchs. There are 4 pairs of gill pouches, each containing two demibranchs, making the total number of demibranchs in bony fishes as 8 pairs or four pairs of complete gills or holobranchs.

Teleosts always breathe with their mouth open and eject expiratory water by opening operculum. Gills in Chondrostei, Holostei and the lungfish *Neoceratodus* exhibit partial reduction in their interbranchial septa, which happens to be somewhat intermediate condition between elasmobranchs and teleosts.

EXTERNAL GILLS

External gills develop from the outer wall of pharynx or from the exposed portion of branchial arch. They occur in larval lampreys, few larval fishes, *Polypterus*, lungfishes, some larval teleosts and all larvae and some adults of amphibians. There is a single pair of larval gill in the chondrosteian bony fish, *Polypterus*, which has a long axis carrying gill lamellae.

The African and South American lung fishes possess 4 pairs of feathery external gills. The larval forms of some amphibians and some adult urodeles possess external gills which arise simply as folds of skin on the surface of the III, IV and V branchial arches but weakly supported by the skeletal system. **Perennibranch** amphibians as *Necturus* and *Proteus* retain external gills throughout life along with 2 or 3 pairs of gill slits, which are functionless as the water does not pass through pharynx.

Instead, gills are waved in water by means of muscles attached at the base of gill axis for respiration. The larvae of limbless amphibian, *Caecilia*, have a pair of exceptionally large leaf-like gills with profuse blood supply. Salamanders that inhabit hill streams, e.g. *Eurycea* and *Salamandrina*, which belong to family Plethodontidae have neither gills nor lungs for respiration and survive only on cutaneous respiration.

AIR BLADDER

Barring agnathans, cartilaginous fishes and few bottom dwelling teleosts, all fishes carry a gas-filled air bladder on the dorsal side of the gut, which serves as hydrostatic organ. On the ventral side of the bladder there occurs a highly vascularised area called **red gland** that is supplied by intestinal artery and portal vein and which has unique capability of extracting free oxygen from the blood and release it into the air bladder in order to make it inflate.

A small pouch-like diverticulum called **oval** that can be closed or opened by sphincter muscles is the site of reabsorption of gases. Secretion and absorption of gases in swim bladder occurs under the control of autonomic nervous system, based on the depth at which a fish is swimming.

In Cypriniformes (Teleostei), a series of four small bones (**tripus**, **intercalarium**, **scaphium** and **claustrum**), derived from the first three vertebrae and called **Weberian Ossicles**, connect the anterior end of air bladder with the sinus impar of membranous labyrinth. Sound vibrations received by air bladder from the surrounding water are conveyed to the internal ear through this unique apparatus to bestow some hearing ability to these fishes.

In some fishes as for example ganoids, carps and catfishes, a pneumatic duct connects the air bladder with oesophagus. Such condition is called **physostomous** (Gr. *physo*=bag; *stoma*=opening). Fishes which do not have such a pneumatic duct connecting the air bladder are called **physoclistous** (Gr. *physo*=bag; *clista*=closed).

The comparative study of air bladders in different groups of fishes and striking similarity between the swim bladder and lung suggest a phylogenetic relationship between the two. The conventional belief is that lungs evolved from the air bladder of fishes. However, recent evidences point to the contrary that lungs evolved first in fishes for supplementing oxygen from air and then they got transformed into swim bladder as the oxygen concentration in water increased.

Accessory Respiratory Organs in Fishes

Many species of fishes developed breathing organs other than gills for supplementing deficiency of oxygen in water. These are as follows:

Dendritic Organs: They are also called arborescent organs as they are highly vascularised tree-like, branched structures produced by the second and fourth gill arches and located in the suprabranchial chamber, posterior to the gills. Paired gill fans at the opening of branchial chamber force air over the dendritic organs as the fishes gulp air. Dendritic organs are found in catfishes such as *Clarias*.

Labyrinthine Organs: These are rosette-like concentric plates of tissue present in the suprabranchial chamber of climbing perch (*Anabas*), *Trichogaster*, *Osphromanus* and *Polycanthus*. Respiration takes place when these fishes gulp air. Perches can migrate from one pond to another by breathing air through labyrinthine organs and using pectoral fin spines to walk on land.

Pneumatic Sac: It is a tube like extrabranchial diverticulum that extends up to tail in some cat fishes such as *Heteropneustes*, which can survive out of water for considerable time using these organs for air breathing.

Air Chamber: Air chamber is a small, highly vascularised sac located behind the gills of some fishes, e.g. *Ophiocephalus*, *Macropodus* and cuchia eel (*Amphipnous*). These fishes can gulp air and use it as air breathing organ.

Buccopharyngeal epithelium: Mud skippers (*Periophthalmus*, *Balaeophthalmus*) possess vascularised buccopharyngeal epithelium and also a respiratory tail. They skip around in swamy areas, breathing air by buccopharyngeal epithelium or keep their tail in water for aquatic respiration.

Integument: Eels (*Anguilla*) breathe through skin while migrating from the American and European rivers to Sargasso Sea in Bermuda. As much as 60% exchange of gases takes place through the highly vascularised skin.

Gut epithelium: Fishes such as *Callichthys*, *Hypostomus*, *Doras*, *Misgurnus*, *Cobitis* can suck and release water through anus and exchange of gases can take place in the rectal lining. In giant loach (*Cobitis*) and *Misgurus* lining of stomach and intestine is used as respiratory organ.

LUNGS

Lungs of *Polypterus* and the ganoid fish *Calamoichthys* are asymmetrical and connected by pneumatic duct on the ventral side of pharynx. The blood is supplied to lung by pulmonary artery that emerges off the 6th aortic arch, but unlike in lungfishes venous blood returns to hepatic vein.

Lungs of Dipnoi (Choanichthys) are bilobed or paired as in *Protopterus* (African lung fish) and *Lepidosiren* (South American Lung fish) and are connected to oesophagus via a pneumatic duct. But the Australian lung fish (*Neoceraodus*) has a single lung that is used as hydrostatic organ.

In tetrapods, embryonic lungs arise from pharyngeal wall as a hollow mid-ventral evagination that subsequently bifurcates to form two lungs that carry an envelope of peritoneum.

SWIMMING IN FISHES

Swimming is the most economical form of animal locomotion because the body of aquatic animals is supported by water and hence the animals do not have to spend energy to counter gravity. While a squirrel spends 5.43 kcal for walking and a gull spends 1.45 kcal for flying, a salmon spends only 0.39 kcal for swimming one kilometer distance. Almost neutral buoyancy is achieved by the air bladder of bony fishes and by the fatty liver in sharks. Streamlined body of fishes provides least resistance while moving through viscous water. Locomotion in fishes was studied by Breder (1926) and Gray (1933).

Based on energy costs, swimming can be classified into 3 groups (Hoar & Randall, 1978), namely, sustained, prolonged and burst swimming.

1. Sustained swimming

Swimming speed is slow, almost 6-7 body lengths per second and is maintained for long periods. Energy required by muscles is provided by aerobic respiration and since the speed is slow, oxygen debt is not built up as fatigue comes very slowly. This type of locomotion is used for foraging over large areas or for long distance migrations.

2. Burst swimming

This type of locomotion is used for escaping predators, chasing a prey or for swimming against currents of water. High speeds of up to 20 body lengths/second are achieved but can be sustained only for short periods. Power is generated by anaerobic respiration in which creatinine phosphate and muscle glycogen are used up. Fatigue comes very rapidly and therefore burst swimming can be sustained for short periods.

3. Prolonged swimming

This type of swimming is intermediate between the above two types in speed and energy. Energy is supplied by both aerobic and anaerobic respiration. Prolonged swimming can last up to 3 hours and longer bouts can end up in fatigue. This type of locomotion is used occasionally as the situation demands.

FISH HYDRODYNAMICS

Fishes live in viscous medium where they face two types of drags that must be overcome in order to move forward in water. Fishes are able to move through water causing almost no turbulence.

1. Viscous drag. As the fish moves forward viscous drag is created due to friction between the fish body surface and water. Thin and small body faces high viscous drag owing to larger surface area as compared to bulky body. Therefore, larval fishes having larger surface area, experience viscous drag as a major force against them. Hence these tiny creatures must always actively swim since they are unable to glide forward without actively swimming. Mucous coated streamlined body of fishes reduces viscous drag.

2. Pressure drag or inertial drag. Displacement of water by fish body creates pressure drag. It is the pressure of water from all sides on fish body. Bulky fishes face high inertial drag as they replace more water as compared to smaller fishes. Pressure drag increases with speed as well as depth. Streamlining reduces pressure drag and fishes keep their body in straight line in order to minimize drag.

Aspect ratio of caudal fin. Aspect ratio is the dorsal to ventral width of caudal fin divided by anterior to posterior length. High aspect ratio gives efficient forward motion as in sharks. Caudal fins of trouts, minnows and perches are flexible and can change aspect ratio according to the needs.

Fishes swim by metachronal contraction of myomeres alternately on either side of axis. Lateral push of the caudal fin on water produces a reactive force on the opposite side at right angle to the axis of body. Reactive force has two components—forward thrust and lateral force. Thrust propels the body forward and overcomes drag while lateral force makes the head yaw from side to side. Push force of the caudal fin is always stronger than any other force.

Yawing is side to side movement of head created by the lateral reaction force generated by the sideways lashing of the tail fin. Yawing is countered by the use of pectoral fin so that fish can move in straight line.

Pitching is up and down movement of the head produced by uneven drag on the body or by heterocercal or hypocercal tail fin. Pitching is countered by pectoral fins.

Rolling is spinning of the body on its anterior-posterior axis. Rolling must be controlled while turning right or left and it is done by the dorsal fin. Bony fishes have foldable dorsal fin that is supported by fin rays, so that rolling can be controlled at will.

There are three types of locomotions in fishes depending on the shape of body.

Anguilliform locomotion

Eels (*Anguilla*) and cyclostomes having serpentine body swim by lateral undulation of the entire body that is caused by metachronal rhythm in the contraction of myotomes. This type of swimming is quite efficient at low speeds but consumes a lot of energy since the whole of the body is involved in locomotion.

Carangiform locomotion

In majority of fishes lateral undulation of body is restricted to the posterior one-third of body. Tail is lashed from side to side in such a way that it always has a backwardly facing component of push and caudal fin increases the area and the force of backward push of tail.

Ostraciform locomotion

This type of locomotion is found in box fishes and trunk fishes (family Ostraciidae) in which body is not flexible and hence cannot undergo lateral undulation. Therefore, only tail fin propels the body forward.

LOCOMOTION IN SHARKS AND DOGFISHES (PLEUROTREMATA)

Sharks and dogfishes have long, streamlined body with a heterocercal tail fin. Pectoral fins are located in front of the centre of gravity that lies just below the dorsal fin. Larger upper lobe of the caudal fin produces lift force on tail due to which head pitches downward. Pitching force is countered by the pectoral fins which also function as elevators. Heterocercal tail fin helps elasmobranchs to swim near the bottom of sea as most of the elasmobranchs are natural bottom dwellers.

Dorsal fins are antirolling devices and they stop rolling of the body while the fishes turn right and left. Pelvic fins in cartilaginous fishes do not contribute to swimming or balancing.

LOCOMOTION IN SKATES AND RAYS (HYPOTREMATA)

Like other elasmobranchs, rays also have heterocercal tail fin and two dorsal fins on the tail. But they have a dorsoventrally flattened body and enlarged pectoral fins are fused on the lateral margins of body. Pectoral fins can produce metachronal contractions and propel the body forward. Rays being dorsoventrally flattened have no problem of rolling and hence dorsal fins are reduced.

LOCOMOTION IN BONY FISHES

Majority of bony fishes possess homocercal or diphyercal tail fin that produces a straight forward push on the body to counter viscous as well as pressure drag. Dorsal fin is foldable and can be stretched whenever required. Pectoral fins are placed high and are used as brakes and for turning right and left. Anteriorly placed pelvic fins stop the upward lift of head while braking. Bony fishes also use operculum to eject water to help in quick turning. Swim bladder maintains the fish steady at a given depth.

LOCOMOTION IN FLYING FISH

Flying fishes, owing to their enlarged pectoral fins can glide in air for considerable distances. Caudal fin is hypocercal with enlarged lower lobe that helps to pull the tail down and keep head upwards while swimming so that they can swim upward rapidly and jump out of water to glide. Even pelvic fin is enlarged to give upward lift to the body.

LOCOMOTION IN SEA HORSE AND PIPE FISH

Sea horse and pipe fish have no fins except the single dorsal fin and hence this fin is used to push the body forward in a vertical position. Tail is prehensile to hold on to the sea weeds and corals where these creatures remain camouflaged and prey upon planktons.

Some bony fishes such as *Amia* have very long dorsal fin extending to almost the entire length of the back. This fin is capable of undulation to propel the body forward while swimming at slow speed. Similarly, *Notopterus* and *Wallago* have very long anal fin which almost continues up to the tail fin and is used to push the body forward.

Trigger fish that can produce fast bursts of speed at short distances, have very high caudal fin to increase the surface area. Dorsal fin and anal fins are also broad and placed posteriorly near the caudal fin to increase the aspect ratio of the posterior region so that a powerful push can be created to propel the body forward.

MIGRATION IN FISHES

Migration is the movement of large number of animals from one place to another for feeding, reproduction or to escape weather extremes. When large numbers of fishes come together and move socially it is called **shoaling**. But sometimes migrating fishes exhibit high degree of coordination in their movements and carry out synchronized manoeuvres to produce different types of shapes. This is called **schooling**, as seen in tunas and sardines.

Feeding or alimental migration takes place in fishes for feeding. In high populations fishes exhaust food resources in an area quickly and therefore must migrate constantly in search of new feeding resources. Salmons, cods and sword fish constantly migrate for food from one place to another in the sea.

Spawning migration takes place in breeding season in those fishes which have spawning grounds far away from feeding places. Migratory fishes such as eels and salmons and a large number of riverine fishes spawn in tributaries of river in hills and migrate in large number for laying eggs in these oxygen rich waters.

Juvenile migration involves larval stages of fishes which hatch in spawning grounds and must migrate long distances in order to reach the feeding habitats of their parents.

Recruitment migration takes place when large number of larvae moves from nursery habitat to the habitat of adults which may sometimes be distinctly different. Adults of eels live in rivers in Europe and America but their larval stages live and grown in sea and migrate to reach rivers which may take one to two years.

Seasonal migration takes place in fishes that inhabit arctic areas where in summer climate is conducive and food abundant but as winter approaches temperatures fall below zero and food becomes scarce. Hence fishes must migrate towards subtropical and tropical areas to escape extremes of weather conditions.

TYPES OF MIGRATION IN FISHES

Fishes live in two different types of aquatic habitats, namely, freshwater and marine habitats, which pose different osmotic problems because of which it is difficult to migrate from one type of habitat to another. Nevertheless, some fishes do migrate.

POTAMODROMOUS MIGRATION

When fishes migrate from one freshwater habitat to another in search of food or for spawning, it is called potamodromous migration. There are about 8,000 known species that migrate within lakes and rivers, generally for food on daily basis as the availability of food differs from place to place and from season to season. Fishes also must migrate to lay their eggs in places where oxygen concentration in water is more and where there is abundance of food for juveniles when they hatch from eggs.

OCEANODROMOUS MIGRATION

This migration is from sea water to sea water. There are no barriers within the sea and fishes have learned to migrate in order to take advantage of favourable conditions wherever they occur. Thus there are about 12,000 marine species that regularly migrate within sea water. Herrings, sardines, mackerels, cods, roaches and tunas migrate in large numbers in search of food by way of **shoaling** (migrating together socially but without much coordination) or **schooling** (swimming with high degree of coordination and synchronized manoeuvres).

DIADROMOUS MIGRATION

When fishes can migrate from fresh water to sea or from sea to fresh water, it is called diadromous migration. There are about 120 species of fishes that are capable of overcoming osmotic barriers and migrate in these two different types of habitats. This migration is of three types.

Catadromous migration

This type of migration involves movement of large number of individuals from fresh water to sea water, generally for spawning as happens in the case of eels (*Anguilla*) inhabiting European and North American rivers.

Both European eel (*Anguilla anguilla* or *Anguilla vulgaris*) and the American eel (*Anguilla rostrata*) migrate from the continental rivers to Sargasso Sea off Bermuda in south Atlantic for spawning, crossing Atlantic Ocean during the journey and covering a distance of about 5,600 km. The adult eels that inhabit rivers are about a metre long, yellow in colour and spend 8-15 years feeding and growing. Before migration the following changes take place in their bodies:

- They deposit large amount of fat in their bodies which serves as reserve food during the long journey to Sargasso Sea.
- Colour changes from yellow to metallic silvery grey.
- Digestive tract shrinks and feeding stops.
- Eyes are enlarged and vision sharpens. Other sensory organs also become sensitive.
- Skin becomes respiratory.
- Gonads get matured and enlarged.
- They become restless and develop strong urge to migrate in groups.

They migrate through the rivers and reach coastal areas of the sea where they are joined by the males and then together they swim in large numbers, reaching Sargasso Sea in about two months. They spawn and die. Each female lays about 20 million eggs which are soon fertilized by males.

First clue about life cycle of eels was given by two Italian scientists Grassi & Calandruccio in 1896. Details of migration and life cycle were later studied by Johann Schmidt (1905). Eggs hatch into leaf-like, semitransparent, larvae having small head called **Leptocephalus**. Leptocephali of American eels take about 10 months to fully grow while those of European eels take about 18 months. Upon reaching coastal waters leptocephali metamorphose into another larval stage called **Elver** or Glass eel. Female elvers ascend to the rivers and metamorphose into yellow-coloured adults, while males stay back in the river mouth and wait for the females to return for spawning journey.

Anadromous migration

Adults of anadromous fishes live and feed in ocean waters but their spawning grounds lie in the tributaries of rivers. Salmons, sturgeons, Hilsa and lampreys are some of the marine fishes that undertake anadromous migration to spawn in rivers.

Atlantic salmon (*Salmo salar*) migrates to the North American rivers for spawning while six species of Pacific salmon (*Onchorhynchus*) migrate to various rivers of Asian countries.

Salmons living in sea are metallic silvery grey in colour but before migration they turn reddish-brown in colour. During fall, they enter rivers and swim energetically against water currents (**contranantent**), clearing all obstacles, including waterfalls and reach tributaries in hilly areas where they make a saucer-like pit in which female lays eggs and male releases smelt over them. Eggs take 2-3 months to hatch in the following spring, when the juvenile stage called **Alvin** emerges out but remains within the nest, obtaining its nourishment from the yolk sac attached to its belly. Alvin then transforms into **Fry** which feed on planktons. Fries are **denatant** (they swim along with water current) and feed and grow into fingerlings which take the shape of adult fish. They change into **Smolt** which congregate at the river mouth in large numbers and then enter sea water in to metamorphose into adult salmons.

Problem of navigation

How fishes find their way in huge expanses of sea and reach their destinations which lie thousands of kilometres away has been a mystery. It is believed that they orient by the positions of stars and moon in the night sky and sun in daytime to find the direction of swimming. However, it has been experimentally proven by A.S. Hasler that salmon are guided by the odour of their parent stream during return journey. Eels can also migrate to Sargasso Sea using similar odour maps but how leptocephali find their way back to the river mouths, crossing vast stretches of Atlantic Sea is a mystery.

Anadromous migration in lampreys

Adult lampreys are parasitic on other fishes and live in sea for 3-4 years and grow to become 30 cm long. For breeding, they stop feeding and migrate in rivers hundreds of miles upstream. Males make nest in sand and gravel in which female lays eggs and male fertilizes them. In about 3 weeks time, eggs hatch into 7 cm long, yellowish-brown ammocoete larva that lies buried in sand and feeds on detritus by filter feeding method. Larva lives in river for 3-7 years and grows from half centimetre to 17 centimetres long. Then these fully grown larvae start their downstream journey and enter the sea to metamorphose into adults.

ORIGIN OF TETRAPODS

The first tetrapods were amphibians that evolved from the Devonian crossopterygian fishes which lived in shallow marshy locations and already possessed lungs for respiration and lobed fins to support their bodies on muddy banks of ponds, rivers and marshland. The anatomical changes that took place during transformation from fishes to amphibia were as follows:

- A tetrapod limb evolved to support the body out of water as on land the entire body weight fell on the four limbs, whereas in fishes body weight is supported by water and fins have to just propel it forward.
- Gills were lost in the adult stage as lungs became more and more efficient air breathing organs and air contained more oxygen as compared to water.
- The hyomandibular bone of the second visceral arch transformed into columella to transmit sound vibrations from air to the inner ear.
- Loss of scales permitted cutaneous respiration which evolved as an alternative method of respiration in the absence of gills while the animal lived and swam in water.
- The skull developed two occipital condyles that fitted in an atlas vertebra so that skull could move upward and downward for locomotion as well as for better visibility.
- In terrestrial environment vertebral column must be strong to support the body weight and hence centra of vertebrae transformed from amphicoelous to procoelous type.
- The lateral line system that was not useful in terrestrial environment simply disappeared.
- Adipose tissue that stores fat and provides insulation developed under the skin to stop loss of water by evaporation on land.

FOSSIL ANCESTORS OF TETRAPODS

Labyrinthodonts were ancestors of all tetrapods and they had evolved from crossopterygian fishes. These ancestors had large teeth with labyrinthine folds on enamel that traversed deep into dentine.

They still carried dermal scales on body and functional lateral line system. They had strong girdles and limbs. They diversified from Devonian to Permian periods and were dominant predators on land.

Osteolepis. It was a lobed-finned fish belonging to Crossopterygii that lived about 375 million years ago and breathed with gills as well as lungs. Fins had bony elements homologous to humerus, radius, ulna and digits of tetrapod limbs.

Eusthanopteron. This was another crossopterygian fish of Devonian period with lobed fins having bones arranged in the pattern of a tetrapod limb, even though the fish was completely aquatic.

Tiktaalik roseae (Order Ichthyostegalia). The fossils of this labyrinthodont from Devonian (375 million years) were discovered from the river delta on Ellesmere Islands in Arctic Canada by Edward Daeschler of the Academy of Natural Sciences and Neil Shubin of the University of Chicago in 2006, who nicknamed it as “fishapod”.

It had 2.75 m long, scaly body with broad, 20 cm long skull and a flexible neck. Snout was long and flat with nostrils located near the base that suggests that it breathed air by sticking its head out of water and probably also caught terrestrial prey by hauling itself onto land. It had a big interlocking rib-cage to protect lungs while it dragged its body on muddy shores. Limb bones had typical tetrapod arrangement with 5 digits and primitive wrist bones. But the limb bones were wrapped in a fish-like fin which enabled it to swim and walk in shallow waters but incapable to confer locomotion on land.

Acanthostega (Order Ichthyostegalia). It is more aquatic and better known animal than *Ichthyostega* and anatomically intermediate between fish and tetrapods. Fore limbs were more paddle-like with 8 digits, and hind limbs had 6 digits but the elbow and knee joints did not bend and could not support animal's body on land and definitely were not capable of carrying out an effective terrestrial locomotion. Vertebrae were less ossified and ribs were short and straight and not overlapping and incapable to prevent collapse of the chest cavity out of water.

Ichthyostega (Order Ichthyostegalia). The earliest fossils were discovered in 1932 from Greenland from the late Devonian (360 mya) deposits. Skull was flat and fish-like. Teeth had labyrinthine folds around dentine. Body was covered with dermal scales and lateral line system was present. Although tail carried fin rays, there is no indication of the presence of gills and respiration was carried entirely through lungs. Limbs were paddle-like, suggesting aquatic mode of life and were probably also used to drag the body on land. Digits were 5 or 6 in the hind limb but in fore limb the hand part is missing in fossil.

Eryops, Cacops & Amphibamus (Suborder Rhachitomi). They are also called stem animals that evolved from stegocephalians, developed terrestrial adaptations, grew to become giants and became dominant terrestrial carnivores of Carboniferous and Permian. They had massive bodies and some reached a length of five feet and had strong limbs with four digits in the front leg and five in the hind leg. Tail was massive that contained a chevron bone in vertebrae and perhaps assisted in locomotion on land. Body was covered with dermal scales for protection.

Buettneria (Suborder Stereospondyli). They were aquatic animals having secondarily simplified vertebral column in which intercentra expanded and became ring-like. They were the largest amphibians of their time that attained a length of up to 6 feet and were perhaps aquatic as suggested by the flattened tail and came on land briefly to feed or escape from predators.

Eogyrinus (Suborder Embolomeri). They were small lizard-like, pentadactyle labyrinthodonts that had 5 digits in each limb. Each vertebra had two disc-shaped centra. They were ancestors of Anthracosauria which later evolved into reptiles.

Microbrachis & Sauropleura (Subclass **Lepospondyli**). They were ancestral to limbless caecilians and lived from Carboniferous to Permian periods. Vertebrae were ossified around the notochord and neural arch was continuous with centrum.

Branchiosaurus (Subclass **Phyllospndyli**). They were small amphibians with large flat head and short tail and are believed to be ancestors of urodeles and anurans. The transverse process of the vertebrae and ribs were stout. Pectoral girdle was made of coracoid, scapula, cleithrum and clavicle. Limbs had four fingers and five toes.

ORIGIN OF AMPHIBIANS

Amphibians evolved in specialized situations during Devonian period, just after the Devonian mass extinction when climate became warm and humid, and huge swamps and marshlands appeared on land. By Carboniferous period there were dense gymnosperm forests all over the land areas. Advancement of forests on land attracted insects, worms and molluscs that had already achieved the capability to inhabit terrestrial forests and which were part of fish and amphibian diet.

Swamps of Devonian period were inhabited by highly specialized lobe-finned fishes that were already equipped with lungs to obtain oxygen from air as the marshland water was low in oxygen content. These fishes also had lobed fins with strong bony elements to support the body in muddy water or on submerged vegetation.

Perfection of these two anatomical features, that is, lungs and lobed fins transforming into tetrapod limbs must have taken place in marshy conditions, which later proved to be important adaptations to conquer land, as seen in labyrinthodonts, such as *Tiktaalik*, *Acanthostega* and *Ichthyostega*.

As forests started invading land, followed by invertebrates, these primitive labyrinthodonts also tried to venture on land in pursuit of abundant prey or to escape predators. They soon mastered terrestrial living and became the dominant predators on land in Carboniferous and Permian periods, e.g. *Cacops*, *Eryops* and *Buettneria*. Large amphibians were wiped out by the Permian mass extinction, when over 70% of tetrapod families and almost 90% of species vanished.

PARENTAL CARE IN AMPHIBIA

Parental care means care of the eggs or juveniles till they reach the reproductive age. Parental care evolved to reduce the energy expenditure on reproduction, as in the absence of it animals must produce millions of eggs so that few could survive to replace the parents to ensure existence of the species. Lower animals produce excessively large number of eggs and do not exhibit parental care but higher animals such as vertebrates, show varied degree of parental care in order to reduce the energy expenditure in reproduction. Terrestrial environment being much harsher than the aquatic one, amphibians were the first vertebrates to have evolved different kinds of parental care to protect their young ones as given in the following description.

APODA (=GYMNOPHIONA)

Caecilians or apoda are long, worm-like legless amphibians having about 165 species in 33 genera. Little is known about these animals, most of which are tropical or subtropical, and occur in Central and South America, Africa, and south and Southeast Asia.

Caecilians exhibit parental care. The female coils around the egg clutch and periodically rotates it, till the eggs hatch. The mother caecilian does not take any food during the parental care period. The Beddome's Caecilian, *Ichthyophisbeddomei*, found in Kerala (India) is known to have 25 to 38 eggs in

an egg clutch. Egg size ranges from 6 mm at the time of laying to 12 mm at the time of hatching. Eggs generally hatch in 60 to 90 days. A newly hatched larva possesses 3 pairs of external pinnate gills.

Mothers of the Kenyan caecilian, *Boulengerulataitanus* provide their own cast skin as a food source to their offspring. *Boulengerula taitanus* is a direct-developing oviparous caecilian, the skin of which is transformed in brooding females to provide a rich supply of nutrients for the developing larvae, which are equipped with a specialized dentition, which they use to peel and eat the outer layer of their mother's modified skin.

Dermophismexicanus is a Central American salamander, whose embryos are 2 mm in diameter and feed on the egg yolk supply for only about three months of gestation before the yolk supply is exhausted. After that the mother produces a nutritious secretion from the internal oviductal glands. Foetal caecilians move around within the oviduct and have specialized dentition with which they scrape the oviduct skin in order to stimulate and ingest the mother's nutritive secretion. The dentition is shed at birth and a different adult dentition is rapidly acquired within a few days. Foetuses also have elaborate tri-branchiate gills for respiration (Wake 2003).

Viviparity is reported in *Gegeneophisseshachari* in which the oviducts are highly vascularized and contain patches of thickened, layered tissues, similar to foetal gut contents. It resembles other viviparous caecilians in having foetuses that ingest thickened oviduct lining using specialized deciduous teeth. *Gegeneophis* is the only caecilian genus known to include oviparous and viviparous species, and *G. seshachari* is the smallest known viviparous caecilian. Phylogenetic analysis of mitochondrial DNA sequences supports the assignment of *G. seshachari* to a monophyletic genus *Gegeneophis*.

In general, it is hypothesized that maternal care should be found in taxa with internal fertilization, and paternal care should be found in taxa with external fertilization.

URODELA (=CAUDATA)

Hynobius retardatus is a slender, chocolate brown salamander having length of 18 cm. The distribution is limited to the Northern Japanese island Hokkaido. Each female attaches an egg sac on the robust branches that run horizontally touching the water surface. Sato (1990) reports that in nature the egg sacs are mainly set off about 3 cm under the water surface. Each egg sac contained between 44 & 102 eggs.

The Paghman mountain salamander (*Paradactylodon mustersi*) is entirely water-dwelling and is restricted to three tributaries of the Paghman stream drainage system in Afghanistan. The stream is fed by glaciers and this species seems to prefer cold, fast-flowing water below 14°C. Fertilisation of eggs in paired egg sacs is external, and these sacs are attached to the underside of rocks and are guarded by the males.

The Gorgan mountain salamander (*Paradactylodon gorganensis*) is restricted to a single cave and stream in the mountains of northern Iran. It lives almost entirely in water, feeding on invertebrates and breeding in a long, narrow pool within the Shir-Abad cave. During mating, the female produces paired arc-shaped, gelatinous egg sacs, each containing 35-70 eggs. The male grasps these and fertilises them externally.

Cryptobranchids are generally found living in depressions under stones in streams and rivers. *Andrias* occurs in central China and Japan, whereas *Cryptobranchus* lives in eastern North America, where mating occurs in late summer or early fall. Males prepare nests below large,

submerged stones or logs. Females lay long, paired strings of several hundred eggs which are fertilized externally by the male. Males guard the eggs until they hatch in 2-3 months after egg-laying.

ANURA (=SALIENTIA)

Some frogs carry the eggs and tadpoles on their hind legs or back (e.g. the midwife toads, *Alytes* spp.). Some frogs even protect their offspring inside their own bodies. The male Australian Pouched Frog (*Assa darlingtoni*) has pouches along the side of body in which the tadpoles reside until metamorphosis. The female Gastric-brooding Frogs, *Rheobatrachus*, from Australia, swallow its tadpoles, which then develop in the stomach. To do this, the Gastric-brooding Frog must stop secreting stomach acid and suppress peristalsis. Darwin's Frog (*Rhinoderma darwinii*) from Chile puts the tadpoles in its vocal sac for development.

The strawberry poison-dart frog (*Oophaga pumilio*) is a species of poison dart frog found in Central America. Strawberry Poison Dart Frogs avoid laying eggs in ponds and streams. Instead, the eggs develop on land until the tadpoles are ready to hatch. Then the mother carries the tadpoles on her back to water-filled bromeliads (epiphytic plants) on the trees. The tadpoles complete their development in these tiny, predator-free pools, and the mother feeds them with unfertilized eggs. The males defend and water the nests and the females feed the oophagous tadpoles with their unfertilized eggs. *O. pumilio* tadpoles are considered obligate egg feeders as they are unable to accept any other form of nutrition. After mating, the female will lay an average of three to five eggs on a leaf or bromeliad axil. The male will then ensure that the eggs are kept hydrated by transporting water in his cloaca. After about ten days, the eggs hatch and the female transports the tadpoles on her back to some water body.

Care about the young reaches the highest degree in the case of two species of Australian toads — Southern gastric-brooding frog (*Rheobatrachus silus*) and Northern gastric-brooding frog (*Rheobatrachus vitellinus*). These species are the only ones which carry about 20 young in the stomach, during which they do not feed. The female swallows the eggs after the male fertilizes them. Seven or eight weeks afterward, fully formed froglets come out of the stomach to the mouth of the mother, sit on its tongues, and jump out from it to the water. It was found that tadpoles secrete special chemical substance — prostaglandin E₂, which suppresses secretion of the acid by the mother's stomach.

Jamaican endemic frogs exhibit some amount of parental care. All the Eleutherodactyls have direct development from heavily yolked eggs to small froglets, bypassing the tadpole stage, presumably as an adaptation to scarcity of water. But *Eleutherodactylus cundalli*, which breeds in the Windsor Great Cave, where the humidity is 100%, guards the egg clutch until the young hatch as tiny froglets, which then climb onto the back of the mother to be carried out of the cave.

Jamaica's hylid frogs breed in the water-filled leaf-axils and have adapted to the harsh environments of bromeliads (i.e., low oxygen levels and limited food reserves), by producing rapidly developing eggs and by laying further eggs which are eaten by the first-born larvae. Remarkably, the eggs laid during the first few days are fertilised and later the unfertilized eggs are laid, which the larvae consume rapidly.

Mountain Chicken Frog (*Leptodactylus fallax*) is highly endangered and limited to Dominica, St. Kitts, Martinique and a few neighbouring islands, lays eggs in foam nests underground, and the tadpoles develop without ever seeing water. The startling footage taken by some researchers shows tadpoles feeding on unfertilized eggs produced by their mother. Subsequent research has revealed that the mother uses her rear legs to re-distribute the unusual food, and perhaps to give all of her progeny a

chance to feed and survive. The 25-50 tadpoles that she rears require 10,000 to 25,000 unfertilized eggs to see them through metamorphosis to adult stage.

There are some species of poisonous frogs in South America where the males transport tadpoles. The males crouch down in the leaf litter next to the hatching eggs and the tadpoles wriggle up onto the father's back and he transports them to water. Mothers of the Jamaican cave frog species—*Eleutherodactyluscundalli*—carry their froglets from the cave into the rain forest. It is the only known example of females transporting froglets.

Dendrobates auratus female lays up to six eggs in a small pool of water. The eggs are encased in a gelatinous substance for protection. The mating season occurs throughout the rainy season, from mid-July to mid-September. During the two week development period, the male returns to the eggs periodically to check on them. Once the tadpoles hatch, they climb onto the males back and he carries them to a place suitable for further development, such as a lake or a stream. For the duration of this trip, the tadpoles are attached to the males back by a mucus secretion, which is soluble only in water so that there is no chance of them accidentally falling off. Once they are at their final destination, the tadpoles are on their own. They take an additional six weeks to develop into adult frogs.

Males of *Rhinodermadarwinii*, Darwin's Frog, brood their developing young in their vocal sacs until they metamorphose. The Darwin's frog males have a very unusual behaviour in the amphibian community. After the male and female mate, the female lays her eggs in moist leaf litter on the forest floor. She then hops off, leaving the male to attend to them. Dutifully he guards the eggs until a few days later when they begin to transform into tiny tadpoles, but still encased in the egg sac. The movement inside the eggs stimulates the father frog to swallow them into the modified vocal sac called **gular pouch**. There they remain until transformed into miniature adults, upon which he opens his throat and allows them to leave and live on their own.

The commonly named Moustache frog, *Vibrissaphora ailaonica* undergoes quite a transformation just before the breeding season. The males begin growing long, hair-like skin extensions from one end of their mouth to the other. They also choose a large boulder near a stream and begin building a nest underneath it. From here they will call incessantly for females, and then guard the eggs of any and all females who come and mate with them. The eggs typically take a month to hatch and tadpoles slip into the waters below. Metamorphosis will not fully occur until two years later. The microhylids, *Anodonthyla*, *Platypelis* and *Plethodontohyla*, which are all natives of Madagascar, deposit their eggs in the rain filled axils of plants. Male frogs then stay nearby the eggs for anywhere from 26 to 35 days; the time it takes for the different species to hatch.

The genus *Alytes* contains the midwife toads, such as *A.cisternasii* and *A. obstetricans* . Both species attach the fertilized eggs to their hind legs. This starts by the male wrapping them first around his ankles. Sometimes they mate up to four times, carrying up to 200 eggs upon their bodies. The father frogs then keep the eggs moist by settling into shallow puddles and pools, allowing the eggs to double in size. Midwife toads sense when their eggs are ready to hatch, and will then wade into shallow waters to allow the young tadpoles to escape into water.

Male Leptodactylid, *Thoropa petropolitana* also cares for the eggs in a similar way. The microhylid males *Breviceps adpersus* and *Synapturanus salseri* also do the same.

DIRECT DEVELOPMENT

The frog genus *Pristimantis* lays eggs on land, which develop directly into miniature adults with no tadpole stage. These are the most widespread and commonly occurring frogs in the New World

tropics. In Africa the genus **Arthroleptis**, known as “squeakers”, are all direct developers. There are also many other direct developing frogs on Madagascar and in Southeast Asia. Among salamanders most species of the largest family, the Plethodontidae, are direct developers.

A few species of frogs give birth to living young. Members of the African genus **Nectophrynoides** retain eggs in the oviduct and some nourish the young as they grow. These are born as miniature adult. One Puerto Rican species of the genus **Eleutherodactylus**, now thought to be extinct (**E. jasperii**), also retained eggs in the oviduct to give live births. **Salamandrasalamandra**, **S. atra** and some related species either give birth to larvae or to completely metamorphosed juveniles.

PAEDOMORPHOSIS

The term **neoteny** is derived from Latin *neotenia*; *neo* + Greek *teinein* = to extend, meaning when larval life is extended. **Neoteny** also called **juvenilization**, is the retention, by adults in a species, of traits previously seen only in juveniles. Neoteny has two forms depending upon capability of individuals to breed.

Pedomorphosis was first proposed by **Walter Garstang** in 1922. The underlying mechanisms for this include **heterochrony** (change in features during development). Pedomorphosis is common in many animal species domesticated by humans, including dogs, chickens, pigs and cattle. It is believed to be a side-effect of the selective pressure of human-directed breeding for juvenile behavioral characteristics such as docility and cuteness. Pedomorphosis also occurs in termites and several species of cockroach. Humans are considered by some scientists to be pedomorphic, due to their flattened face, short jaw, and bulbous forehead compared to other adult primates.

Paedogenesis is the act of reproduction by an organism that has not achieved physical maturity. In other words paedogenesis is the production of offspring by an organism in its larval or juvenile form and elimination of the adult phase of the life cycle. It is associated with **progenesis**, where sexual maturity is achieved in the juvenile form and further physical maturity is not achieved. Paedogenesis is found in insects in which the larval stage reproduces without achieving maturity. It occurs in the females of certain beetles, Strepsiptera, bagworms, scale insects and gall midges.

EXAMPLES OF NEOTENY

Flightless birds

Flightless birds such as ostriches, emus, cassowaries and kiwis are believed to have evolved by retaining characters of chicks and losing ability to fly. Physical proportions of these birds resemble those of the chicks of flighted birds.

Humans

With human traits such as sparse body hairs and enlarged heads are thought to be reminiscent of baby primates. Lactose tolerance in adults is a form of neoteny now considered normal in certain populations that traditionally consume milk while most other humans are lactose intolerant as adults. Although females mature at an earlier age, women do not go on to acquire the toughened skin, coarse body hair, thyroid cartilage, bony eye ridges, or deepened voices which are the common inheritance of most adult hominoids and other primates. Pedomorphic characteristics in women are widely acknowledged as desirable by men. For instance, vellus hair is a juvenile characteristic. However, while men develop longer, coarser, thicker, and darker terminal hair through sexual differentiation, women do not, leaving their vellus hair visible.

Stephen Jay Gould was an advocate of the view that humans are a neotenus species of chimpanzee. The argument is that juvenile chimpanzees have an almost-identical bone structure to humans, and that the chimpanzee's ability to learn seems to be cut off upon reaching maturity.

Another theory suggests that humans' neotenus characteristics were an evolutionary strategy that enabled Cro-Magnons to gain predominance over neanderthals (and possibly *H. erectus* and *H. heidelbergensis*) by appealing to these species' nurturing instincts through pedomorphic cuteness and to avoid territorial aggression.

Bolk (1926) provided an abbreviated list of human neotenic characters:

- Our "flat faced" orthognathy.
- Reduction or lack of body hair.
- Loss of pigmentation in skin, eyes, and hair.
- The form of the external ear.
- The central position of the foramen magnum (it migrates backward during the ontogeny of primates).
- High relative brain weight.
- Persistence of the cranial sutures to an advanced age.
- The labia majora of women.
- The structure of the hand and foot.
- The form of the pelvis.
- The ventrally directed position of the sexual canal in women.
- Small teeth and variations of the tooth row and cranial sutures. Late eruption of teeth.
- Absence of eye brow ridges.
- Absence of cranial crests.
- Thinness of skull bones.
- Position of orbits under cranial cavity.
- No rotation of the big toe.
- Prolonged period of infantile dependency and prolonged period of growth.
- Long life span.
- Crying is among the child-like behaviors. Certainly human facial anatomy and physiology are intricately engineered for both the discharge of tears and the facial and vocal expressions that accompany them to draw attention and sympathy.

Origin of chordates

It is possible that **chordates** originated by neoteny. Molecular evidence suggests that the nearest relatives of the chordates are the tunicates, marine filter feeders. Although sessile in their adult,

sexually mature form, tunicates have a motile larval dispersal form, which has a notochord similar to that found in chordates. At some point, the motile larvae of the tunicate became sexually mature before metamorphosis and gave rise to free swimming chordates.

Neoteny in amphibia

Natural pedomorphosis occurs in many species of amphibians, especially ambystomatid and protean salamanders. In amphibians it can be obligate or facultative. For example, some salamanders retain their gills during adulthood, unlike most other amphibians.

Most neotenic populations belong to the Tiger Salamander complex – *Ambystoma tigrinum*, *Ambystoma velasci*, *Ambystoma mavortium*, and their close relatives. Wholly neotenic *Ambystoma* species include the *Axolotl*, *Ambystoma taylori*, *Ambystoma andersoni*, and *Ambystoma dumerilii*. Neotenes retain ability to regenerate limbs, tails, and nearly every organ in their body. Neoteny, sometimes called pedomorphism, is apparent in Urodela, except Rhyacotritonidae.

There are three types of neoteny, **obligate**, **inducible obligate**, and **facultative**.

Obligate neoteny

All members of the families Amphiumidae, Sirenidae, Cryptobranchidae, and Proteidae are obligate neotenes, meaning they never fully metamorphose, and retain larval characteristics in varying degrees into adulthood. Most of these species are insensitive to thyroid hormone doses.

Inducible obligate neoteny

Inducible obligate neotenes of the family Ambystomatidae, and some species of the family Plethodontidae are unique in that metamorphosis can be induced by manipulating the thyroid function in the laboratory. The most famous inducible obligate neotene is perhaps *Ambystoma mexicanum* (Ambystomatidae).

Facultative neoteny

Facultative neoteny is observed in Salamandridae, Dicamptodontidae, Ambystomatidae, Hynobiidae, and Plethodontidae. Facultative neoteny occurs in individuals or entire populations as a result of environmental factors. For example, in extremely cold temperatures, where a terrestrial existence would be inhospitable, individuals or populations may remain aquatic, retaining larval characteristics into adulthood.

The Axolotl larva and Neoteny

A sexually mature axolotl, at age 18–24 months, ranges in length from 15–45 centimetres. Axolotls possess features typical of salamander larvae, including external gills and a caudal fin extending from behind the head to the vent. Their heads are wide, and their eyes are lidless. Their limbs are underdeveloped and possess long, thin digits. Males are identified by their swollen cloaca lined with papillae, while females are noticeable for their wider bodies full of eggs. Axolotls have barely visible vestigial teeth which would have developed during metamorphosis. Three pairs of external gills are used for respiration, although buccal pumping (gulping air from the surface) may also be used in order to provide oxygen to their lungs.

Factors affecting neoteny

In the axolotl, metamorphic failure is caused by a lack of **thyroid stimulating hormone**, which is used to induce the thyroid to produce **thyroxine** in transforming salamanders. Axolotls can be induced to

metamorphose by an injection of **iodine** (used in the production of thyroid hormones) or by shots of **thyroxine** hormone.

Another method for inducing metamorphosis is to keep them in shallow water tanks. They will then, over a period of weeks, slowly metamorphose into adult salamanders. However, most attempts at inducing metamorphosis lead to death. This is likely due to the strong genetic basis for neoteny in pet axolotls. Artificial metamorphosis also dramatically shortens the axolotl's lifespan, if they survive the process.

Research indicates that neoteny occurs because the **hypothalamus** of the brain fails to produce the hormone that causes the pituitary to stimulate the thyroid gland to produce growth hormones that trigger metamorphosis. Some scientists think that neoteny may have evolved as a response to the hazards of life on land.

ORIGIN OF REPTILES

Reptiles evolved from amphibians of Carboniferous period, which depended on water bodies for laying eggs and development of larval stages and hence could not exploit arid habitats far away from water bodies. They invented a large yolk-laden shelled egg that could be laid on land and in which an amniotic sac contained fluid in which embryo could develop to an advanced stage, capable of fending for itself when hatched. The following anatomical changes transformed the ancestral amphibians into land adapted reptiles:

- Body developed a covering of epidermal scales to prevent loss of body moisture, and skin glands were lost.
- Skull became monocondylic for better movement and flexibility. Atlas and axis vertebrae together permitted skull movement in all directions.
- Limb bones and girdles became stronger but limbs were attached on the sides of body, and belly touched the ground during creeping mode of locomotion.
- Sacral region involved two strong and fused vertebrae to support the body weight on hind legs.
- Pentadactyle limbs developed claws that helped in climbing on rocks and trees.
- Lung respiration became more efficient.
- As a water conservation strategy, metanephros kidneys excreted uric acid which did not require water for excretion.
- Reptiles continued to be ectothermal since ventricle was not completely partitioned by a septum and blood mixed in heart.
- Internal fertilization evolved as a large cleioid shelled egg was laid on land.
- Embryonic membranes amnion, allantois and yolk sac evolved to enable embryonic development in arid conditions.

ANCESTORS OF REPTILES

THE COTYLOSAURS

They were the most primitive stem reptiles that evolved from the labyrinthodont amphibians (Embolomeri) in Carboniferous period.

Seymoriamorphs were a lizard-like animal, with pentadactyle limbs and a short tail. It had homodont labyrinthine teeth on the jaw bones as well as on vomer and palatine bones. Presence of lateral line indicates its amphibious habits. Skull was monocondylic for better movement of head. *Seymoriamorphs* indicates gradual transition from labyrinthodont amphibians to reptiles. Another 5 foot long cotylosaur fossil, *Limnoscelus* was found in Mexico that had large premaxillary teeth and long tail.

THE PARAPSIDS

They possessed superior temporal vacuity in the skull and were adapted for aquatic mode of life.

Plesiosaurus was marine long-necked, fish-eating animal with 15 metre long fusiform body, short tail and paddle-like limbs modified for swimming. The skull was euryapsid type with a superior temporal vacuity. The fossils are from lower Jurassic (about 180 million years) and they are believed to have become extinct in end-Cretaceous mass extinction.

Ichthyosaurus had fish-like body with fore limbs modified into paddle-like fins and hind limbs disappeared. There was a fleshy dorsal fin too. Caudal fin was large and bilobed. Jaws projected into an elongated snout and teeth were homodont, an adaptation for fish-catching. Skull was parapsid type with additional postfrontal and supratemporal bones behind the eye orbit. Vertebral column became secondarily simplified with amphicoelous vertebrae.

THE SYNAPSIDS

Synapsids split off from the primitive reptilian stock very early in evolution, perhaps in the middle carboniferous period. Synapsids had started developing mammalian characteristics that enabled them to be fleet-footed and active predators. Their legs commenced to move under the body. Heterodont dentition and false palate started developing in pelycosaurs and had been completely formed in therapsids. Two types of synapsids occurred from carboniferous to Permian, namely, the primitive Pelycosaurs and advanced therapsids.

Pelycosaurs are represented by *Dimetrodon* whose fossils were discovered from North America and Russia from the late Carboniferous to Permian periods. They were primitive reptile-like animals in which limbs had moved under the body but not completely and each limb had 5 digits with claws. Neural spines on the back were excessively long stretching highly vascularized skin between them that formed a fin-like or sail-like structure. They had heterodont dentition with incisors, canines and molars clearly defined but the false palate had not been completely formed.

Therapsids were more advanced and active synapsids which were perhaps endothermic animals with high rate of metabolism. Heterodont dentition with false palate allowed these animals to chew and grind food for quick digestion in the gut so that high metabolic demand of the body could be fulfilled. Jaw muscles were attached to zygomatic arch to make chewing effective. Carnivore therapsids were called Cynodonts (ex. *Cynognathus*) and herbivores were Dicyodonts.

THE THECODONTS

They evolved from the sauropsid Archosauria, a group of insignificant lizard-like reptiles that survived the Triassic mass extinction. They evolved into bipedal and highly agile predators.

Euperkeria and **Ornithosuchus** fossils were unearthed from South Africa and Europe. They were about 2 ft long bipedal lizard-like animals with small head but very long tail for balancing while they chased flying insects by rapid running. Endothermy must have evolved in thecodonts to meet the extraordinary energy demands of their predatory life style.

THE SAURISCHIANS

They were dinosaurs with lizard-like pelvic girdle in which ischium and pubis bones radiated away from each other. They were both bipedal and quadrupedal and carnivores as well as herbivores.

THE ORNITHISCHIANS

They were dinosaurs with bird-like pelvic girdle in which ischium and pubis bones were directed towards posterior as found in modern birds. These were also highly diversified carnivores as well as herbivores and both bipedal and quadrupedal.

THE PTEROSAURIA

They were flying or gliding dinosaurs of Mesozoic that varied in size from sparrow-sized to some species, like *Pteranodon*, having a wing span of 8 meters. They had pneumatic bones. Last digit of the fore limb was extraordinarily long and served to attach the membranous patagium between fore limb, hind limb and the body. Hind limbs were used for clinging on to the rocks and cliffs and 3 digits of fore limbs also had curved claws, an adaptation for clinging. Their jaws were modified into beak that possessed homodont dentition but *Pteranodon* did not have teeth.

SKULL TYPES IN REPTILES

Reptiles are ectothermic animals whose body is covered by epidermal scales. They possess monocondylic skull that rests on a long neck made of atlas, axis and other cervical vertebrae. They have two sacral vertebrae, which are fused together to transfer the weight of body onto the hind limbs. Pentadactyle limbs bear sharp claws which help the animal in creeping and climbing. Reptiles were the first vertebrates that laid a large, shelled, cleoid egg that could develop on land. The egg has three membranes, amnion, allantois and yolk sac which help in the development of the embryo on land in dry conditions. Generally in reptiles with big jaws and large head, the skull becomes too heavy for the neck to support it. Therefore vacuities or fossae developed in reptiles to lighten the skull and also to provide space for accommodating powerful jaw muscles.

The skull names come from the word “**apse**,” which means “**arch**.” The number and types of arches, or enclosed fenestrae or windows, give the skull types their names. These openings actually give the skull extra space for the attachment of jaw muscles, allowing animals to snap their jaws more forcefully.

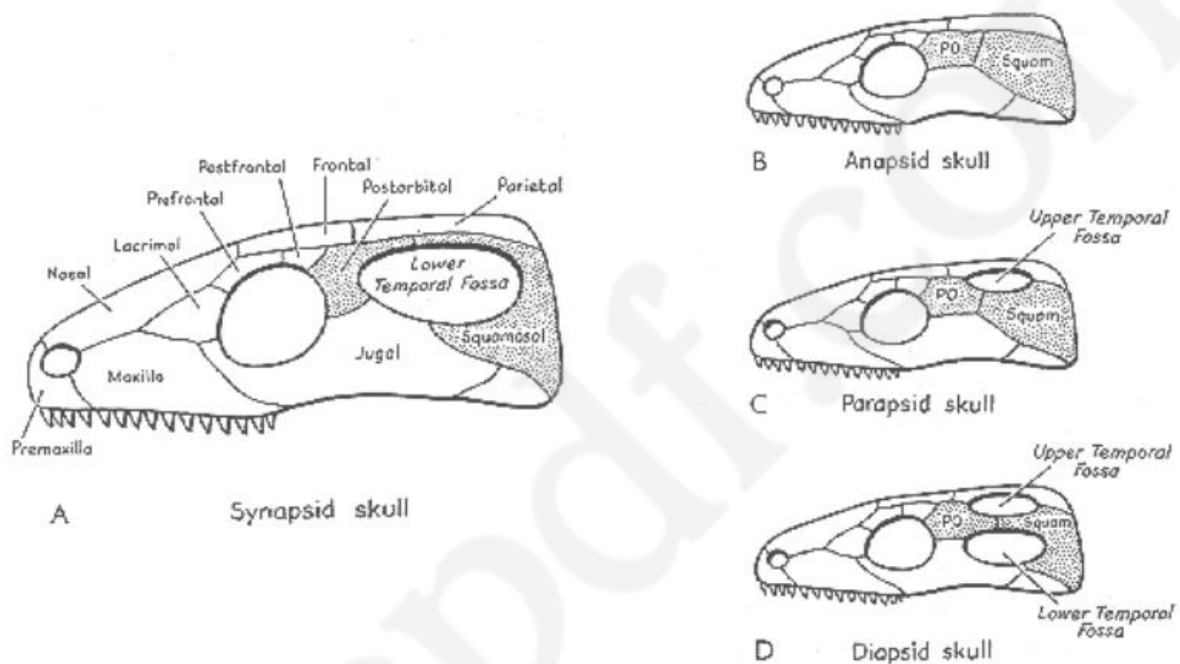
Temporal fenestrae have been used to classify amniotes by Osborn, 1903. Taxa such as **Anapsida**, **Diapsida**, **Euryapsida**, and **Synapsida** were named after their type of temporal fenestration. Temporal fenestrae are large holes on the sides of the skull. The function of these holes has long been debated (Case, 1924). Many believe that they allow muscles to expand and lengthen, resulting in greater bulk of jaw musculature. The longer muscle fibres allow an increase in the gape of the jaw to handle larger prey (Pirlot, 1969).

ANAPSID SKULL (found in Cotylosauria and Chelonia)

This is the most primitive type of skull of reptiles that occurred in primitive labyrinthodont amphibians and then in primitive reptiles like *Seymoria*. The anapsids were the first reptiles to appear in the

Carboniferous Period (345 to 280 million years ago). “**Anapsid**” means “**without arch**”, meaning that they have no fenestrae in their skulls. The anapsids were first represented by small, herbivorous Procolophonids, and the much larger, herbivorous Pareiasaurs.

Chelonia that today includes tortoises and turtles, still possess this type of skull, which has complete skull roofing, without temporal vacuities or fossa. As the skull is completely covered by bones, this type of skull is heavy but strong. Turtles have small head and jaws without teeth and hence the weight of the skull can be borne by the neck, but other reptile that evolved massive jaws and head, must evolve lighter skulls so that it could be supported by the neck and also larger and stronger jaw musculature. This is achieved by developing vacuities or empty spaces in the temporal area of the skull and sometimes before the eye orbit.



EURYAPSID SKULL (found in *Plesiosaurus*)

Euryapsid means “**wide arch**”. They have one fenestra high on both sides of the skull. The euryapsids are represented by the marine reptiles such as the ichthyosaurs, plesiosaurs, and placodonts, which are all completely extinct groups. The euryapsids arose from the diapsids which had two fenestrae, but sealed one of the openings to strengthen their skulls for life under water.

Plesiosaurus was aquatic giant reptile with a long neck, small skull and fish-eating jaws. Its limbs were modified into paddles for swimming and there was no tail fin but a small tail. Skull had a single pair of temporal vacuities bordered by parietal, postorbital and squamosal bones. Maxilla and premaxilla had sharp teeth for fish catching.

PARAPSID SKULL (found in *Ichthyosaurus*)

This type of skull evolved in *Ichthyosaurus*, which included dolphin-like aquatic reptiles that preyed upon fishes or other aquatic animals. This skull also had only one pair of temporal vacuities on the upper side, guarded by two additional bones, namely, postfrontal and supratemporal, which push the postorbital and squamosal bones towards the lower side. The vacuities are guarded by parietal bones above. The condition found in *ichthyosaurs* is distinguished from the euryapsid condition because their temporal fenestrae are only bordered by the parietal, postfrontal, and supratemporal (Pirlot,

1969). This condition has been called parapsid, but it only represents a minor variation from the euryapsid pattern.

DIAPSID SKULL (found in *Sphenodon*, snakes, lizards, crocodiles and dinosaurs)

This type of skull has two temporal vacuities on either side of the skull. The superior temporal vacuity is surrounded by parietal above and postorbital and squamosal below. The inferior temporal vacuity is guarded by the postorbital and squamosal above and jugal and quadratojugal below. This type of skull is lighter and has more space for the attachment of jaw muscles. It is found in a large number of living reptiles and also in extinct dinosaurs. Dinosaurs and crocodiles also have a pair of preorbital vacuities anterior to the eye orbits.

SYNAPSID SKULL (found in Pelycosauria and Therapsida)

This type of skull was found in *Dimetrodon* (Pelycosauria) and the mammal-like therapsid reptiles (*Cynognathus*), in which there was only one inferior temporal vacuity on each side of the skull but it was guarded by postorbital and squamosal bones above and jugal and quadratojugal below. "Synapsid" means "together arch." The synapsids were the dominant land vertebrates from the Late Carboniferous Period (280 to 230 million years ago) to the end of Triassic Period (230 to 195 million years ago). Although the synapsids were reptiles, they later gave rise to mammals.

STATUS OF SPHENODON

Rhynchocephalia, an Order of Class – Reptilia is considered as an aberrant group of reptiles which appeared first in Triassic and passed smoothly through the Mesozoic. It is a true diapsid reptile now represented today by one very conservative living species *Sphenodon punctata*. It is called by the natives of New Zealand as 'tuatara' (tua = back, tara = spine).

It is a lizard like reptile which grows to about 2 feet long and has well developed pentadactyle limbs adapted for walking. Gadow refers it as "the last living witness of the by-gone ages". This primitive reptile is called the "living fossil". It is a very lazy creature. It lives in the holes on the slopes of the sand hills of the shore with the petrels on amicable returns. This animal is rigidly protected by law. It emits a soft frog like croak. It feeds on insects, crustaceans and worms.

Distribution

Sphenodon was formerly known on the main islands of New Zealand, but is now restricted to some small islands in the Bay of Plenty and appears to be on the verge of extinction.

General anatomical features

- The lizard like body of *Sphenodon* is about 2 feet long and the tail measures about 1/3 of the whole length of the body- The animal is nocturnal.
- The body and tail are laterally compressed and a series of spines are dorsally present (along the middle line).
- Limbs are pentadactyle, legs are short and primitive in nature. Sometimes 10-11 carpels are present.
- Hind limbs are typically plantigrade.
- The upper surface of the body is covered with small granular scales and the lower surface is covered with transverse rows of large squarish scales.
- The head is large and there is prominent ridge over the eye.
- There is a foramen above the outer and one above the inner condyle of the humerus.

- There are eleven carpal elements in all, four in the proximal row, two centrals and five in the distal row.
- In the tarsus the tibial and fibular elements are quite distinct, though firmly united. The intermedium and the centrale are firmly fixed to the tibiale. There are three tarsal bones.
- Teeth are pleurodont and homodont like reptiles but they are monophyodont. The teeth are pointed, triangular, laterally compressed and arranged in two parallel rows, one along the maxilla, and the other along the palatine. The teeth of the lower jaw bite in between the two upper rows, all the rows becoming worn down in such a way as to form continuous ridges. Each premaxilla bears a prominent, chisel-shaped incisor, represented in the young animal by two pointed teeth. In the young *Sphenodont* a tooth has been found on each vomer — a condition unusual among reptiles.
- The pubes are united in a Symphysis, in front of which is a cartilaginous epipubis. A large oval foramen intervenes between the ischium, and the pubis. A cartilaginous hypischium is attached to the ischia behind.
- In the skull, there is a complete lower temporal arch. The quadrate is immovably fixed, wedged in by the quadrate-jugal, squamosal, and pterygoid. The premaxilla are not fused together but separated by a suture. There is a broad palate, formed by the plate-like vomer, palatine and pterygoids. The pterygoids meet in the middle line and extend forwards to the vomers. There is an epipterygoid extending from the parietal to the pterygoid and quadrate.
- *Sphenodon* retains the large parietal foramen, in which, is the non-functional median pineal eye.
- There is no antorbital foramen.
- The anal opening of *Sphenodon* is transverse.
- There is no copulatory organ (Penis) in the male.
- The vertebrae are amphicoelous and fully ossified and intercentra are present.
- The ribs are single headed and have uncinat processes. There is a sternum and abdominal ribs.
- Chevron bones occur in the caudal region of the vertebrae.
- There is a median bone, the Pro-atlas, intercalated between the atlas and the occipital region of the skull.
- Caudal ribs become fused with the vertebrae.
- The lateral temporal fossa is bounded below, by an inferior temporal arch composed of jugal and quadrato-jugal (Palato-quadrato).
- Jacobson's organ is present in a rather primitive form.
- A urinary bladder is present.
- There is a T-shaped interclavicle.
- Coracoid is without fenestra.
- It lays 10-13, leathery shelled eggs which are buried few inches below the surface of the soil. The young ones are hatched 13 months later.

Causes of its long survival

There are three important causes of its long survival. These are —

- a) It was free from its enemies because the placentals and other large terrestrial animals were introduced in New- Zealand quite lately.
- b) Slow rate of metabolism and conservation of sufficient energy.

c) Lethargic habit and long period of incubation of the fertilized eggs.

Why called a living fossil

The living fossil is an animal that has survived beyond its era. It is the one species or such a group of species that has continued existence when the other closely related contemporary species have become extinct. *Sphenodon* is the sole survival of the order Rhynchocephalia. Its anatomical features indicate several primitive characters such as —

- The skull bones are shaped and disposed in the manner of extinct group of reptiles.
- Teeth are fused to the jaw bones.
- Presence of pineal foramen.
- There are several characters (discussed in affinities) which resemble that of Dinosaurs and other extinct reptiles.
- It resembles with the ancient Homaeosaurs in several features except the presence of uncinat process of the ribs in *Sphenodon*.

Thus, the term 'living fossil' is justified for *Sphenodon*. This animal which has been called the "Voice of the Past" has been given absolute protection by law in New Zealand.

Affinities

Sphenodon (Order – Rhynchocephalia) possesses several characters which are present in different groups of animals. So, actual position of *Sphenodon* in the animal kingdom was somewhat controversial for some time. Its affinities with different groups have been discussed below:

Affinities with amphibia

The circulatory system of *Sphenodon* has some resemblances with Caudata or Urodela. These resemblances are —

- Aortic arches arise from a short common stalk which is comparable to conus arteriosus of the amphibians.
- Presence of ductus arteriosus and ductus caroticus
- The pattern of distribution of blood vessels almost similar but, these resemblances are mainly because of the reason that *Sphenodon* is an animal of primitive nature. Because of the presence of several reptilian features which have been discussed below, amphibians affinities can not be accepted.

Affinities with Dinosaurs

There are some resemblances with the dinosaurs. These are—

- Diapsid condition of the skull i.e. the skull has two vacuities (fossae).
- Fixed quadrate bone
- Abdominal ribs.
- Uncinate process of the ribs.

But, there are some differences also — e.g.

- In Dinosaurs, double headed ribs are present – not single headed like *Sphenodon*.
- Dentition is thecodont in dinosaurs
- Absence of clavicle and interclavicle

- Absence of Parietal foramen
- Absence of third eye elements

So, *Sphenodon* can not be linked with the dinosaurs, however, its reptilian ancestry is evident.

Chelonian affinities

The following are the important resemblances with the chelonians:

- Fixed quadrate bone
- Ribs of caudal region fused with the vertebrae
- Pecten not present in the eye
- Urinary bladder present

The differences with chelonians include the following —

- *Sphenodon* is terrestrial but chelonians are aquatic.
- Teeth absent in the chelonians, only horny beaks present
- Parietal foramen in chelonians
- Unpaired vomer
- No sternum in chelonia
- Cloacal opening longitudinal in chelonia but transverse in *Sphenodon*
- Males have penis in chelonia
- Opening of oviduct on ventral side

Affinities with Crocodilia

The following are the important resemblances.

Crocodilia—

- Diapsid condition of the skull
- Fixed quadrate
- Presence of Pro-atlas
- Presence of abdominal ribs
- Fusion of caudal ribs with vertebrae
- Uncinate process of ribs
- Presence of chevron bones
- Cochlear process tubular

The differences between the two are:

- Thecodont dentition in crocodiles
- Single nostril in Crocodile but double in *Sphenodon*
- Procoelous vertebrae in Crocodile and amphicoelous in *Sphenodon*
- Clavicles not present in Crocodilia.
- Pecten present in Crocodiles
- Penis present in male Crocodile

Affinities with Lacertilia

The important resemblances are the following —

- The body plan is similar
- Pro-atlas present
- Ampluocoelous vertebrae in certain geckos
- Single headed ribs
- Chevron bone present in both
- Structure of the respiratory organs
- Parietal organ common
- Cloacal glands present

However, there are some differences also, which are —

- Quadrate fixed in *Sphenodon*
- Most lizards have procoelous vertebrae
- Rami of the jaw united by symphysis in lizards
- Erect ilium in *Sphenodon*
- Clavicles and interclavicles present in *Sphenodon*
- Absence of conus arteriosus in Lacertilia
- Presence of Pecten
- Uncinate process of tire ribs absent in Lacertilia
- Copulatory organs present in Lacertilia
- Presence of lower temporal arch

Conclusion

Thus, we see that Rhynchocephalia retains many primitive characters and resembles chelonians, crocodilia and dinosaurs in many features. But it is convincing that *Sphenodon* is more closely allied to the lacertilia than any other group discussed above.

Because of the occurrence of certain peculiar features it seems justified that the Rhynchocephalia should be placed as a separate order of class-Reptilia as suggested by Romer.

FLIGHT ADAPTATION IN BIRDS

Flying is a balance between two sets of forces, lift and weight, and thrust and drag. Weight is the result of gravity and Lift is generated by the flow of air over the wings.

Bird wings are not flat but are concave below and convex above. The air that passes over the top of the wing has more distance to travel and thus it speeds up, causing the pressure to drop because the same amount of air is exerting its pressure over a greater area above the wing than below the wing. This effectively sucks the wing up. Meanwhile the air going below the wing has the opposite effect.

It slows down, generates more pressure and effectively pushes the wing up. Hence a bird with air moving over its wings is pulled up from above and pushed up from below. The low pressure of air on top of the wings represents a sink that the high pressure air under the wing tries to fill.

This happens most along the thin trailing edges of the wing and causes a spiralling vortex of disturbance at the wing tip, which increase drag. Therefore, the most efficient wings are those which provide lift but reduce drag, such as the crescent shaped wings of swallows and swifts.

Aerodynamic properties are measured by **aspect ratio**, which is the ratio of wing length divided by wing breadth. Long wings are better for gliding but harder to flap quickly and are therefore not much

good at quick acceleration. **Wing loading** is the relationship between total body-mass measured in grams versus total wing area measured in square centimetres.

Non-flapping Flight or Gliding

Many soaring or gliding birds like vultures hang in the air and gain height without moving the wings. Essentially this means that their wings generate a lot of lift without producing much drag. Large birds have evolved to be gliders partly because gliding becomes easier with larger wings and the mechanical flapping flight become harder with larger wings.

With the exception of Hummingbirds, all birds glide to some extent when flying. As a rule, the smaller the bird, the shorter the distance it can glide and the faster it sinks. Gliding can be observed in game birds. A pheasant ascends from the ground like a rocket with fast wing beats and then glides for some distance down to the nearby woods.

Flapping Flight

Flapping flight is a more complicated process in which bird's wing changes shape and angle of attack during both the up and down stroke. Flapping flight is basically rowing in the air with the added effort to generate lift as well. If a Blue Tit stops flapping its wings it better be about to land on a branch or it will fall to the ground. Flapping flight consists of two distinct movements: the **power stroke** and the **back stroke**. In the power stroke, the wings move forward and down; the back stroke returns the wings to the position from which the next power stroke will commence.

Soaring flight

Soaring differs from gliding flight in that the bird does not lose altitude and sometimes even climbs up in air. When soaring, a bird uses no energy of its own; instead it depends on external forces called thermal currents, which are rising masses of air that form over areas where the ground warms up rapidly. Obstruction currents are produced when wind currents are deflected by mountains, cliffs, or tall buildings. The resulting upward rise of air lifts birds to high altitudes, providing a base for further gliding. Soaring birds always have large and broad wings, and the ratio of their body weight to the size of the airfoils is low.

Hovering Flight

In hovering flight, a bird generates its own lift by means of rapid wing beats. Holding its body nearly vertical, with its wings firmly flexed at the elbow joint, a hovering bird moves its wing surfaces forward and back in a horizontal plane; each of the two phases of the stroke generates lift. Hummingbirds' wings are made in such a way that when in motion they act like lifting rotors. Their pointed wings do not flap and glide as other bird wings do, but propel them through the air by moving up and down, at a rate of 70 times a second.

After feeding at a flower they can fly backward, climb vertically, turn at lightning speed, and come to a sudden standstill in midair. Hummingbirds have been known to fly up to speeds of 60 miles an hour and no bird of prey can ever catch a hummingbird in flight.

ANATOMICAL ADAPTATIONS

BODY SHAPE

Birds have short, light and compact body as compared to other animals.

Most organs and large muscles are located near the center of gravity, which is slightly below and behind the wings to provide better balance during flight.

FEATHERS

Contour feathers cover the body and make it streamlined and decrease drag. Down feathers are soft and meant for insulation. Primary feathers are on the wings and are also called remiges, which help in flight and also provide wing shape. Tail feathers are called rectrices which stretch sideways so that tail can be used like a rudder for turning and balancing.

SKELETON

The evolution of flight has endowed birds with many physical features in addition to wings and feathers. One way to reduce weight in birds is by the fusion and elimination of some unnecessary bones and the “pneumatization” of the remaining ones. Not only are some bones of birds hollow but many of the larger ones are connected to the air sacs of the respiratory system.

To keep the cylindrical walls of a bird’s major wing bones from buckling, the bones have internal strut-like reinforcements. Fusion of bones in birds makes the skeleton light as well as strong. Coracoid, furcula, and scapula form a sturdy tripod for supporting the wings and broad surfaces for the attachment of large flight muscles.

One key adaptation is the fusing of caudal bones into single **pygostyle** which supports the tail feathers. Birds also lack teeth or even a true jaw, instead having evolved a beak, which is far more lightweight.

Birds have uncinat processes on the ribs. These are hooked extensions of bone which help to strengthen the rib cage by overlapping with the rib behind them.

Skull is composed of thin, hollow bones, which is extremely light in proportion to the rest of the body due to elimination of a heavy jaw, jaw muscles, and teeth. The job of chewing has largely replaced by the gizzard. The skull usually represents less than 1 percent of a bird’s total body weight.

LIMBS

Forelimbs (wings) are attached closer to center of gravity and farther from head than in other animals. The natural motion of wings is up and down, rather than back and forth. Forelimbs fold into a Z-shape and closer to the body. Hand bones are small, fused, flattened and specialized to manipulate the flight feathers. Aerodynamic shape of forelimb provides lift and propulsive force.

MUSCLES

There are about 175 different muscles in the bird. They mainly control the wings, the tail, neck and the legs. The largest muscles in the bird are the muscles that control the wings. They are called the pectorals or the breast muscles, and make up about 15 – 25% of a bird’s full body weight. They make the birds’ wing stroke very powerful so that they can fly, and provide most of the movements the bird needs for its down stroke.

The muscle below the pectorals is the supracoracoideus. It raises the wing when a bird is flying. The supracoracoideus and the pectorals together make up about 25 – 35% of the birds’ full body weight. Leg muscles are massive for bipedal locomotion but are tight and close to the body. Legs are tucked next to body in flight to reduce drag. Flight muscles are enormous as they have to generate thrust and vigorous movement of wings during flight.

DIGESTIVE SYSTEM

Birds consume high-energy foods such as insects, seeds, fruits, meat, and nectar. The digestive system is extremely efficient in absorbing energy from small amounts of food at a rapid rate. Birds possess a gizzard that is composed of four muscular bands that act to rotate and crush food by shifting the food from one area to the next within the gizzard.

Depending on the species, the gizzard may contain small pieces of grit or stone that the bird has swallowed to aid in the grinding process. Many birds possess a muscular pouch along the esophagus called a **crop**. The crop functions to both soften food and regulate its flow through the system by storing it temporarily.

RESPIRATORY SYSTEM

The respiratory system of birds is adapted to the energy demands of flight. A bird's respiratory system is proportionately larger and much more efficient than in other animals, since flight is a more demanding activity than walking or running.

An average bird's respiratory system occupies about one-fifth of its body volume, while in an average mammal it is only about one-twentieth. Lungs of birds are less flexible, and relatively small, but they are interconnected with a system of large, thin-walled air sacs in the front and in the posterior portions of body. These, in turn, are connected with the air spaces in the bones.

Inhaled air passes first into the posterior air sacs and then, on exhalation into the lungs. When a second breath is inhaled into the posterior sacs, the air from the first breath moves from lungs into the anterior air sacs. When the second exhalation occurs, the air from the first breath moves from the anterior air sacs out of the lungs, while the inhaled air moves into the lungs.

The air thus moves in one direction through the lungs. All birds have this one-way air flow system and many also have two-way flow system which may make up as much as 20 percent of the lung volume. In both systems, the air is funneled down into air capillaries carrying oxygen-poor venous blood. At the beginning of the tubules the oxygen-rich air is in close contact with that oxygen-hungry blood, while in distal tubules the oxygen content of air and blood are in equilibrium. Birds' respiration creates a "crosscurrent circulation" of air and blood, which provides greater capacity for the exchange of oxygen and carbon dioxide across the permeable respiratory membrane.

Oxygen exchange occurs during both inhalation and exhalation. The posterior and anterior air sacs expand during inhalation. Air enters lungs via trachea. Half of the inhaled air enters the posterior air sacs, while the other half passes through the lungs and into the anterior air sacs. The sacs contract during exhalation. The anterior air sacs empty directly into the trachea, the posterior air sacs empty via the lungs into the trachea and to outside.

Since during inhalation and exhalation fresh air flows through the lungs in only one direction, there is no mixing of oxygen rich air and carbon dioxide rich air within the lungs as happens in mammals. Thus the partial pressure of oxygen in a bird's lungs is the same as in the environment.

Avian lungs do not have alveoli, as mammalian lungs do, but instead contain millions of tiny passages known as parabronchi, connected to air capillaries, where oxygen and carbon dioxide are exchanged with cross-flowing blood capillaries by diffusion. A diaphragm is absent in birds and instead the entire body cavity and air sacs act as bellows to move air through the lungs.

HEART

Bird's heart is large, powerful, four-chambered and of the same basic design as that of a mammal. The segregation of the two kinds of blood makes a bird's circulatory system, like its respiratory system, well equipped to handle the rigors of flight.

The flight muscles of most birds are red in color because of the presence of myoglobin and cytochrome. They are also richly supplied with blood and are designed for sustained flight. Light-colored muscles are found in pheasants, grouse, quail, and other galliformes birds. These are also well supplied with blood, are apparently capable of carrying a heavy work load for a short time, but fatigue more rapidly.

A Ruby-throated Hummingbird's heart beats up to a rate of 1200 beats per minute (about 20 beats per second). The human heart weight amounts to 0.42 percent of body weight and the pulse rate at rest averages 72 beats per minute. The House Sparrow's heart constitutes 1.68 percent of the body weight and the pulse rate at rest averages 460 beats per minute. In the Ruby-throated Hummingbird these figures rise to 2.37 percent and a pulse rate of 615.

BLOOD

Blood of birds has high blood pressure and high blood sugar, almost twice that of mammalian glucose levels). Fast flying and migratory birds have smaller red blood cells with greater surface-to-volume ratios for greater oxygen-absorbing capability.

BRAIN

Brain is large with enormous cerebral hemispheres but the surface is white and without grey matter. Olfactory lobes are greatly reduced but optic lobes are excessively enlarged. Cerebellum is well developed with a median lobe, vermis and later lobes flocculi for coordination of muscular activity and balance.

EYES

Eyes are large, with wide field of view and binocular vision. Nictitating membrane is transparent or translucent and covers the eye ball during flight. Sclerotic ring of bony plates protects the eye ball and increases the distance between the lens and retina for sharp distant vision. Birds have acute eyesight, with raptors having vision eight times sharper than humans.

This is because of high density of photoreceptor cells retina (up to 1,000,000 per square mm in *Buteos*, against 200,000 in humans). An indented fovea on retina magnifies the central part of the visual field. Many species, including hummingbirds and albatrosses, have two foveas in each eye, and the ability to detect polarized light is also common in birds.

METABOLISM

Birds have high metabolism and endothermy for quick generation of power and for maintenance of high body temperature. Birds require large amounts of energy for flight, and need efficient oxygen circulation in high altitudes. The highest flight recorded for a bird was 11,274 m (37,000 ft.) when a Ruppell's griffon vulture collided into a commercial airline over western Africa (Martin, 1987).

Birds normally maintain a body temperature of 38.0C to 42.0C (100.40F-107.60F) (Brooke and Birkhead, 1991).

REPRODUCTIVE SYSTEM

Ovaries and testes are reduced in size except in the breeding season. Usually only one functional ovary is present in most of the birds and second ovary is greatly reduced to decrease the weight of body. Female liver is displaced to the right to compensate for weight difference. But in the case of birds of prey generally both ovaries and oviducts are present. This is because during hunting these birds have to pounce on the prey with great force and struggling prey can kick and break the eggs in reproductive system. Eggs developing in two ovaries can compensate for this loss.

MIGRATION IN BIRDS

The primary aim of migration is to take advantage of the longer days of the northern summer for breeding and to feed their young and to avoid harsh winters. The extended daylight hours allow diurnal birds to produce larger clutches of eggs than those of non-migratory species that remain in the tropics all the year round. As the days shorten in autumn, the birds return to warmer regions where the available food supply is more. During northern winters there is little food and cold temperatures, whereas in south, there is more food and less cold.

Between 1500 and 4000 species of birds are known to migrate. In India and South Asia, out of over 2000 species and sub-species, about 350 are migrants. It is estimated that over 100 species of migratory birds fly into India, either in search of food or to escape severe winter of their native habitat. In the Indian subcontinent the majority of migratory birds are winter migrants.

The first naturalist to write about migration was Aristotle, who studied pelicans, turtle doves, swallows, quail, swans and geese as migrants and observed that all migrating birds fatten themselves up before migrating. Every year, during autumn and early winter, birds travel from their breeding grounds in the northern regions of Asia, Europe and America to the southern lands of Asia, Africa and South America. They make the return journey again during spring and early summer.

Birds of prey, Swallows and Crows migrate in daytime, whereas thrushes, warblers, cuckoos, woodpeckers and most songbirds migrate by night. Large birds fly faster than small birds. Ducks and geese maintain an average speed of 64-80 km/h, while hawks and ravens fly at 35-45 km/h. Most birds migrate at an altitude of 3,000 feet or less but cranes and geese migrate at altitudes of 15,000-21,000 feet.

Before migration birds eat more food and store it as fat for their long journey. Some migrants almost double their body weights by storing fat before migration. The ruby-throated hummingbird weighs only 4.8 grams and can use stored fat to fuel a non-stop, 24-hour flight across a 600 mile stretch of open sea from the U.S. Gulf coast to the Yucatan Peninsula of Mexico.

The Arctic Tern (*Sterna paradisaea*) is a sea bird that breeds in Arctic and sub-Arctic regions of Europe, Asia, and North America in marshes, tundra lakes and shorelines. The species is strongly migratory, seeing two summers each year as it migrates from its northern breeding grounds to the oceans around Antarctica and back, covering a distance of about 38,000 km each year that take 90 days each side. This is the longest regular migration by any known animal.

The arctic tern flies as well as glides through the air, performing almost all of its tasks in the air. Arctic Terns are mainly grey, with red beak and feet, white forehead, a black-nape and crown and white cheeks. It is one of the most aggressive birds that fiercely defend its nests and young. Arctic terns leave the Arctic Circle and head eastwards across the Atlantic Ocean, flying down the west coasts of Europe and Africa.

In spring they fly north back to the Arctic, following the east coasts of South and North America. Considering an Arctic tern lives up to 30 years, a single bird may travel more than 650,000 miles in its

lifetime. The young stay in the southern hemisphere until they are about two years old and will then migrate back to their birthplace. One Arctic Tern, ringed as a chick on the Farne Islands off the British east coast, reached Melbourne, Australia in just three months from fledging, a sea journey of over 22,000 km. The arctic tern may hold the record for longest migration distance since it flies about 35,000 km each year travelling between its arctic breeding ground and non-breeding area in the Antarctic.

Pied Crested Cuckoo (*Clamator jacobinus*) migrates to large areas in northern India in monsoon and has often been called the harbinger of monsoon or “rain visitor” from Africa. They move across the Arabian Sea and Indian Ocean to reach India in May or June. Some believe that the bird uses monsoon winds to assist its flight during this migration. It breeds during June-August and leaves the subcontinent in September/October for Africa.

The Common Cuckoo (*Cuculus canorus*) is a widespread summer migrant to Europe and Asia, and winters in Africa. It is a brood parasite, which lays its eggs in the nests of other bird species, such as meadow pipits and reed warblers.

The American Golden-Plover (*Pluvialis dominica*) breeds in Arctic Tundra and has a long, circular migration route. In the fall it flies offshore from the East Coast of North America non-stop to South America. It leaves the breeding grounds in early summer, but juveniles usually linger until late summer or fall. Some adults arrive on the wintering grounds in southern South America before the last juveniles have left the Arctic.

On the return journey in the spring it passes primarily through the middle of North America to reach its arctic breeding grounds. The bird has one of the longest known migratory routes of over 25,000 miles, of which 2,400 miles is over ocean where it cannot stop to feed or drink.

Manx shearwater (*Puffinus puffinus*) nests in a small number of island colonies from the Western Islands, Iceland, in the Faroes, in northern and western Britain and Ireland, Brittany, to the Azores, Madeira and the Canaries.

They nest in burrows, laying one white egg which is only visited at night to avoid predation by large gulls. They form life-long monogamous pair-bonds. Young Manx Shearwaters go to sea at night, without their parents, and immediately head for the winter quarters off the coast of southern Brazil and Argentina. Ringing studies in Stockholm show that some of the young make this 6000–7000 mile journey in less than a fortnight.

Manx Shearwaters migrate over 11,000 km to South America in winter, using waters off southern Brazil and Argentina, so this bird has covered a minimum of 1,000,000 km on migration alone in its lifetime. Another bird ringed in 1957 and breeding on Bardsey Island off Wales was calculated by ornithologist Chris Mead to have flown over 8 million km during its life.

Penguins. After breeding most penguin species moult, relying on fat reserves to sustain them for a period of 2-5 weeks without food. After moulting, penguins can enter water to find food and migrate. All penguins, except six species that are adapted to inshore life, migrate over long distances and return to land only for the breeding season.

Satellite telemetry of Adelie penguin migration shows that these birds travel a path along the coastline of the Antarctic continent to a winter feeding ground in an area north-west of the Balleny Islands, off the Ross Ice Shelf, a distance of 5,500 km. Tracking of Humboldt penguins revealed that most stayed within a 90 km radius of the island on which they breed. Migration is also the time when penguins are

most vulnerable, with annual survival estimates ranging from 75% for the Little Penguin to 95% for the Emperor penguin.

Bar-tailed Godwit (*Limosa lapponica*) is a large wader in the family Scolopacidae, which breeds on Arctic coasts and tundra mainly in the Old World, and winters on coasts in temperate and tropical regions of the Old World. It makes the longest known non-stop flight of any bird and also the longest journey without pausing to feed, 11,680 kilometres along a route from Alaska to New Zealand.

It was shown in 2007 to undertake the longest non-stop flight by any bird. Birds in New Zealand were tagged and tracked by satellite to the Yellow Sea in China. According to Dr. Clive Minton, the distance between these two locations is 9,575 kilometres but the actual track flown by the bird was 11,026 kilometres. This is the longest known non-stop flight of any bird. The flight took approximately 9 days. At least three other Bar-tailed Godwits also appear to have reached the Yellow Sea after non-stop flights from New Zealand.

Albatrosses. Albatrosses are roaming seabirds that live up to 60 years, spending many continuous years at sea before returning to land to breed. Young birds leave New Zealand waters and fly circumpolar through the Pacific, Indian and Atlantic Oceans before returning to New Zealand waters to breed as adults when 6-10 years old. Satellite transmitters have been put on wandering albatross and have shown that birds can travel an incredible 700 kilometres a day.

Unfortunately, they also reveal huge losses to long line fishing. The Wandering Albatross, Snowy Albatross, or White-winged Albatross, *Diomedea exulans*, is a large seabird, which has a circumpolar range in the Southern Ocean. Based on tracking the precise movements of 22 birds, reveals that males are most likely to circumnavigate the world, with the fastest managing a distance of 14,000 miles in 46 days – the equivalent of a steady 13mph. More than half then made amazing round-the-world journeys – the fastest in just 46 days.

As the loggers only provide two positions per day, an accurate estimate of the distance is impossible but it is likely to have been at least 14,000 miles. Using satellite telemetry scientists have learned that some parent birds fly as much as 1000 kilometres per day, covering anywhere from 2900 kilometres to an astonishing 15,000 kilometres in a single foraging flight.

Siberian Crane (*Grus leucogeranus*). The Siberian Cranes nest in Yakutia and western Siberia of Russia and migrate to India. The migration route stretches for 4000 miles. Their resting place at the time of migration is the Lake Ab-i-Estada in Afghanistan.

The Kaladeo Ghana National Park or the Bharatpur National Park has been declared a world heritage site because the Siberian Crane traverses nearly half of the globe to reach it. The eastern population winters on the Yangtze River and Lake Poyang in China, the central population at Keoladeo National Park, India (the last Siberian Crane in this population was observed in 2002), and the western population in Fereydoon Kenar in Iran. It breeds and winters in wetlands, where it feeds on the shoots, roots and tubers of aquatic plants.

Ducks, shovellers, teals and geese. Some duck species, mainly those breeding in the temperate and Arctic Northern Hemisphere, are migratory; those in the tropics, however, are generally not. Some ducks, particularly in Australia where rainfall is patchy and erratic, are nomadic, seeking out the temporary lakes and pools that form after localised heavy rain.

Black-headed bunting (*Emberiza melanocephala*). The males are quite gorgeous with their black heads, brilliant yellow underparts and rich reddish-brown upperparts. The females are much duller although they often show at least a hint of yellow, especially on the undertail coverts and the head is

usually distinctly darker than the throat, creating a hooded effect which mimics the pattern of the male. Migratory, wintering in western and central India. Arrives in the breeding areas in late April or May and departs in July or early August.

Black poll warbler (*Dendroica striata*) is a New World warbler. These birds breed in northern North America, from Alaska, Canada, and up to New England and winter in north-western South America. Part of their fall migratory route is over the Atlantic Ocean from the north-eastern United States to Puerto Rico, the Lesser Antilles, or northern South America. This route averages 1,864 miles over water, requiring a potentially non-stop flight of up to 88 hours. To accomplish this flight, they nearly double their body mass and take advantage of a shift in prevailing wind direction.

Humming birds. Most hummingbirds of the U.S. and Canada migrate south in fall to spend the winter in northern Mexico or Central America. Ruby-throated hummingbird flies 600 miles across the Gulf of Mexico in 25 hours non-stop. A few southern South American species also move to the tropics in the southern winter. A few species are year-round residents in the warmer coastal and interior desert regions.

Migratory Birds Coming to India in Winter Season

Siberian Cranes, Greater Flamingo, Ruff, Black winged Stilt, Common Teal, Common Greenshank, Northern Pintail, Yellow Wagtail, White Wagtail, Northern Shoveler, Rosy Pelican, Gadwall, Wood Sandpiper, Spotted Sandpiper, Eurasian Wigeon, Black tailed Godwit, Spotted Redshank, Starling, Bluethroat, Long billed Pipit.

Migratory Birds Coming to India in Summer Season

Asian Koel, Black crowned Night Heron, Eurasian Golden Oriole, Comb Duck, Blue-cheeked Bee Eater, Blue-tailed Bee-Eater, Cuckoos.

BIRD NAVIGATION

Birds use a number of methods to find their way during migration. Many use celestial navigation, a method of orienting the body to the arc of the sun, to the phases of the moon, or to the pattern of the stars in a particular season, which is called **menotaxis**. Others, such as hummingbirds and pigeons, are able to determine the position of the sun even on overcast days because they can detect the ultraviolet radiation it emits.

Experiments in planetarium on night migrant birds, such as white throated warblers and indigo buntings reveal that they orient themselves by the position of stars in the night sky.

Some birds are sensitive to coriolis force that arises by deflection of winds in the northern hemisphere by earth's rotation.

Some diurnal birds use topographical landmarks such as mountains, river valleys, and forests to orient themselves on the migration route. Some are able to detect infrasound or low-frequency sounds that are produced by pounding of the ocean surf that travel long distances and are detected by birds. Many birds, particularly seabirds, identify their destinations by characteristic odours.

Many birds possess instinct or some kind of internal compass or biological clock that guide them to the route of migration. Young birds follow the migration route accurately without previous training or experience.

Some birds such as oil birds of South America possess echolocation and can be guided by it.

The classic experiment proving the internal-clock theory was done by German **Gustav Kramer** during the early 1950's. He placed caged Starlings wanting to migrate so they could see the sun. The birds would sit looking in the direction toward which they wanted to fly. Significantly, if the Starlings couldn't see the sun, they didn't face in any particular direction.

Also during the 1950's, the German **Franz Sauer** did a similar experiment with birds that could and could not see the night stars. The results were the same: Certain species can orient themselves according to the sky's major stars. In fact, an experiment with Mallard Ducks found that if the moon is so bright that important stars are hidden by glare, released ducks can't orient themselves as well as on darker, moonless nights.

Some birds, such as pigeons, are sensitive to changes in the earth's magnetic field and to gravity because of **magnetite** they possess in their head and neck muscles. During the early 1970's, **W.T. Keeton** did a series of elegant experiments to get the answer. He glued small, non-magnetic brass bars on the backs of pigeons and on the backs of a similar group he glued miniature magnets which, he thought, might disrupt the Earth's magnetic field in the vicinity of the pigeons. When released at locations the birds had never seen before, the pigeons with non-magnetic brass bars found their ways home much better than those with magnets on their backs.

In a 2007 article in the German journal *Naturwissenschaften* scientists announced that they'd found tiny **iron oxide** crystals in the skin lining of the upper beak of homing pigeons, laid out in a 3-dimensional pattern in a way that the birds might be able to sense the Earth's magnetic field independent of their motion and posture, and thus identify their geographical position.

The researchers discovered molecules called **cryptochromes**, which change their chemistry in the presence of a magnetic field, in the retinas of migratory birds' eyes. When light hits these molecules, their chemistry changes and magnetism can influence them. The molecules might then affect light-sensing cells in the retina to create images, which would help the brain navigate during flight.

Infrasound travels much farther than ordinary sound and it comes from many different natural sources, including ocean waves, surf, winds, storms, earthquakes and other geologic events. If you can hear infrasound, you can listen to the whole world.

ORIGIN & EVOLUTION OF MAMMALS

Mammals originated from reptiles but the fossils show that the reptiles that gave rise to mammals were Synapsids that diverged from the main reptilian stock almost at the base of phylogeny during Permian period. Hence, mammalian relationship with the extant reptiles is remote. Sailbacks or Pelycosaurs from North America and Russia were primitive synapsids, without a false palate and heterodont dentition. The large sail on their back was perhaps a thermoregulatory device.

Synapsids were heavy-bodied, large-headed, stumpy-legged creatures, adapted to various types of habitats and food. Some were rodent-like seed-eaters, some insectivores. Cynodonts were dog-sized carnivorous therapsids known from all over Gondwanaland and dominant predators.

Mammalian characters in Therapsids

Increased feeding and respiratory rate due to the presence of heterodont dentition and diaphragm indicates high metabolism and endothermy in therapsids. They had developed many mammalian characteristics due to which they became dominant predators as well as herbivores of Permian period.

Majority of therapsids died out in the Triassic mass extinction. Those survived were small insectivores, the size of a small cat that thrived in hidden habitats away from the reach of the mighty dinosaurs and

gradually evolved into archaic mammals. This mode of life developed acute sense of smell, sight and hearing in early mammals and consequently brain too enlarged to refine their wits that was so necessary to escape dinosaur predators of that time.

MAMMALS OF THE MESOZOIC

Mesozoic mammals were small rabbit-sized insectivores, herbivores or seed eaters, partially arboreal and active animals that were not allowed to proliferate due to the presence of ubiquitous dinosaurs. Cretaceous mass extinction eliminated most of them, leaving only small insectivorous pantotherians which found all ecological niches vacant after the extinction of dinosaurs. That led to the unusually rapid evolution in Palaeocene epoch when 7 distinct mammalian groups were differentiated, namely, insectivores, carnivores, primates, ungulates, rodents, edentates and cetaceans. By Pleistocene, mammals had become giant rulers of the earth, when another mass extinction eliminated the largest of them. Today mammals are on the decline. The mesozoic mammals were the following:

Triconodonts. They were the size of cat and had three sharp cusps on the grinding teeth. Ex. *Priacodon*.

Symmetrodonts. Cusps were three but were symmetrically placed in a triangle. Ex. *Spalacotherium*.

Pantotheres. Upper molars triangular with two cusps and lower molars with three cusps. Ex. *Amphitherium*.

Docodonts. Molars were nearly squarish having 4 cusps for grinding grasses. Ex. *Disacus*.

Multituberculates. Rodent-like herbivores with chisel-like incisors and broad molars with rows of grinding cusps. Diastema was present and canines were absent. Ex. *Plagiaulax*.

THE COENOZOIC PLACENTALS

Early branching of marsupials, placentals and perhaps monotremes had been accomplished before the end of cretaceous period. During early coenozoic period at least 7 mammalian groups had already been differentiated, namely, insectivores, carnivores, primates, ungulates, rodents, edentates and whales.

- 1. Insectivores.** Shrew-like insectivores lived in hidden situations. Ex. hedgehogs, shrews etc.
- 2. Carnivores.** They probably evolved from insectivores and continued with their ancestral carnivorous habit. Creodonts were archaic carnivores that rapidly diverged from earlier insectivores. Ex. cats, dogs, tiger, lion
- 3. Primates.** Their evolutionary process can be traced through tree shrews, lemurs, tarsiers, monkeys.
- 4. Ungulates.** Condylarths were primitive ungulates of Palaeocene and Eocene epochs that gave rise to all modern ungulates. Ex. Perissodactyla such as horse and Artiodactyla such as cow, buffalaw, deers, goat, sheep etc.
- 5. Rodents.** Their fossils are known from the late Palaeocene strata that possessed chisel-like incisors. They are related to Lagomorpha. Ex. Rats, mice, guinea pigs etc.
- 6. Edentates.** Evolutionary origin of armadillos and South American anteaters is not known.
- 7. Whales.** Earliest known whales of the middle Eocene were completely aquatic with fore limbs modified as flippers but whales evolved from mesonychids in Palaeocene.

8. Proboscideans. They evolved from some marsh-dwelling ancestor that was forced to migrate to land due to arrival of dry conditions. Sirenia and Hyracoidea are related orders that evolved from a common ancestor. Ex. Elephants.

MONOTREMES (The Egg-laying Mammals)

Monotremata is derived from the Greek term, *monos* = single and *trema* = hole, referring to the single excretory opening cloaca in these animals. They lay eggs instead of giving birth young ones.

The ECHIDNA (*Tachyglossus* and *Zaglossus*)

Echidna is sometimes referred to as a Spiny Anteater since it has sharp spines on their backs. The Echidna is found all over Australia in different temperatures and habitats. Echidnas live in forests, woodlands, deserts and mountains.

They are generally crepuscular and nocturnal. Its body is covered with 2 different types of hair: short coarse hair to keep them warm and long sharp spines, which are modified hairs. Echidnas are dark brown with lighter coloured spines. They have long jaw bones, which form a snout that has no teeth. They have ear holes and good hearing power.

The short-beaked echidna (*Tachyglossus aculeatus*) is found throughout Australia and southern New Guinea. The males grows to a length of about 30-45 cm and weighs up to 7 kg and the females are slightly smaller. Echidnas can live for up to 45 years.

They have a long sticky tongue, which is about 18 cm long and can be moved in and out 100 times per minute. It is perfect for catching ants, termites and insect larvae. The tongue and the roof of the mouth are covered with spines to grind up insect skeletons, making it easier for the animal to digest its food. They find ants and other insects using their sense of smell and powerful digging claws.

Echidnas are solitary animals, only coming together during the mating season, which lasts from two to three weeks in July to August. During this time, the female is followed by males from which she chooses one to mate. The female usually gives birth to only one leathery egg. The egg is placed into a 'pouch' made by folds of skin, where it hatches after ten days.

The foetus has an egg tooth, like reptiles and birds, which it uses to break open the leathery eggshell. The young feeds by licking milk from the milk tisse patches on the mother's skin. It is carried in the pouch until its spines begin to grow when the mother places it in a nursery burrow hollowed in the ground. She returns frequently to feed the young echidna, which becomes independent in a year. When in danger the echidna curls up to protect its body by erect spines. If on soft ground it digs into soil, projecting sharp spines.

The PLATYPUS (*Ornithorhynchus anatinus*)

The platypus which is the only animal in the world to have a beak, fur and webbed feet, is found in lakes, creeks, rivers and streams along the eastern side of Australia, from Cooktown in north Queensland to Hobart.

Body is exceptionally well stream-lined for aquatic life. The fur is waterproof, with an outer layer of long flat-bladed guard hairs and an inner layer of fine hairs, which trap air and maintain body temperature.

The female platypus grows to about 44.5 cm long and weighs 1.2 kg and does not have a pouch to carry her young. She lays eggs in her special nesting chamber and feeds her young on milk. The egg

shells are soft. The male platypus grows to about 50 cm in length and weighs 1.6 kg. and has a hollow poisonous spur behind each of his hind legs.

The webbed feet of platypus are modified for swimming and digging. When it feeds above water level, it shakes its head from side to side so that the nerves in its bill can sense food. Their diet includes shrimps, larvae, horsehair worms, fish eggs and plants.

Platypus can live for 10 years or more. They dig burrows and build nests for laying eggs and rearing young which feed on milk that they suck from the tuft of hair located above the mother's mammary glands. When the offspring are born they have a spur on each hind-leg which the males retain for life but the females lose within a year. The spur, which is connected to a venom gland, is about 1.5 cm long and can inflict a very serious wound and the venom is strong enough to kill a large dog.

Platypuses feed on insect larvae, fresh water shrimps, bivalve mollusks, frogs and fish eggs. They have an exceptionally sensitive bill to detect electric signals generated by the muscle activity of small prey. When foraging they dive repeatedly, capturing food and storing it in cheek pouches. The young possess teeth but they are lost as the animals mature. Adults have horny buccal pads for grinding their food.

TEETH

Teeth are hard bony structures in the oral cavity that are variously modified to capture, tear, cut or grind food material before it is swallowed. Epidermal teeth are hard cornified epidermal structures of rare occurrence, as in the buccal funnel of cyclostomes and on the edges of tadpole jaws. Dermal teeth are found in mosts of the vertebrates.

TYPES OF TEETH

Polyphyodont dentition involves replacement of teeth from time to time several times in lifetime so that jaws are never left without teeth. Lower vertebrates having loose attachment of teeth lose teeth while feeding and capturing prey and hence teeth must grow again to replace the lost ones.

Diphyodont dentition is a characteristic of mammals in which milk teeth appear in the young ones but as they grow and jaw becomes larger, milk teeth are replaced by larger permanent ones to fit in the larger jaw bone.

Monophyodont teeth appear only once in lifetime and if they fall they are never again replaced by the new ones. Toothless animals have this kind of teeth and marsupials retain their milk teeth.

Based on the type of attachment of teeth on the jaw bone the following three types are found in vertebrates:

Acrodont teeth are attached on the top surface of the jaw bone as in fish and amphibians. This type of attachment is not very strong and teeth are lost easily and are replaced by new ones.

Pleurodont teeth are attached on the inner side and upper side of the jawbone that brings larger surface area of tooth in contact with jawbone and hence attachment is stronger, as in lizards and urodeles. But this attachment is also not as strong as thecodont.

Thecodont dentition is found in mammals in which root of the tooth is firmly fixed in a socket of the jawbone, making the attachment strongest in vertebrates. This is a peg and socket attachment with the help of cementum that surrounds the root portion of the tooth.

Based on the kinds of teeth found there are two types of dentition:

Homodont dentition is found in the majority of vertebrates such as fish, amphibia and reptiles in which all teeth are functionally and anatomically of the same type, although their size may be variable depending on the location. Sometimes functionally some teeth may be specialized as fangs of snakes.

Heterodont dentition occurs in mammals in which there are 4 functionally different types of teeth, namely, flat incisors for cutting, long and pointed canines for tearing flesh and large and broad premolars and molars with flat grinding surface. Molars have no counterparts in the milk teeth.

There are also some other type of teeth as follows:

Secodont teeth have sharp cutting edges that function like scissors to cut flesh as in some primates and in carnivores.

Bunodont teeth are small with smaller cusps or tubercles on the surface for handling soft diet as in man, monkeys, rodents etc.

Brachyodont teeth are smaller and low crowned suitable for feeding on soft diet.

Hypsodont teeth possess larger crown that can resist wear and tear of feeding on tough and fibrous diet as in ungulates.

Selenodont teeth are found in horses and other ungulates in which silica deposits around cusps and in the depressions of the grinding surface. This makes the grinding surface of teeth harder to prevent wearing.

Lophodont teeth are found in elephants which feed on the roughest diet that any mammal can feed on. The ridges on the grinding surface are in the shape of rounded lophs and the depressions are filled with silica.

DEVELOPMENT OF TOOTH

Teeth develop over the jaw bone where certain malpighian cells start actively multiplying forming a mass of cells called dental lamina or enamel organ. A dental papilla made of group of dermal cells appears below the dental lamina that supplies nourishment to the growing mass of cells. Cells of the outer layer of dermal papilla arrange themselves in a row and get differentiated into **odontoblast cells**. Epidermal cells of the dental lamina that cover the growing dentine are called **ameloblasts**.

The tooth gradually grows outwards and eventually gets exposed by penetrating through the skin covering the jaw bone. The dental papilla inside the pulp cavity remains active along with its blood supply and nerve intact. This development of tooth is identical to the development of dermal scales in fishes. Hence shark teeth are also called modified placoid scales.

COMPARATIVE ACCOUNT OF DENTITION

Cyclostomes have only epidermal teeth. Some fishes are toothless such as sturgeons, sea horse and pipe fish and others like lung fishes and *Chimaera* have teeth modified into crushing plates. Majority of fishes possess Polyphyodont, Acrodont and homodont dentition suitable for seizing prey.

In amphibians teeth are located on jaw bones, palatine and vomer bones and are Polyphyodont. Tadpoles lack true teeth and their jaws have horny epidermal ridges which are used to scrape algae on which they feed.

Among reptiles, turtles lack teeth and have horny beak. In others, teeth are generally confined to jaw bones but in snakes and lizards may occur on palatine and pterygoid bones. Fangs of snakes are modified upper maxillary teeth and in *Heloderma* they are lower maxillary or mandibular.

Modern birds lack teeth but *Archaeopteryx* had thecodont dentition and so were the toothed birds *Ichthyornis* and *Hesperornis*.

DENTITION IN MAMMALS

Mammals as a rule possess heterodont, diphyodont and thecodont dentition. However, some mammals lack teeth as given below in detail.

Among monotremes, the spiny anteater or echidna (*Tachyglossus* and *Zaglossus*) lacks teeth.

Edentates, as the name suggests are toothless such as the giant anteater of South America.

Among the aquatic Cetacea baleen whales have no teeth, such as the blue whale, *Balaenoptera musculus* and, the whalebone whale.

Among humans, and astonishingly, males in “Bhudas” tribe of Hyderabad Sindh in Pakistan are genetically so predisposed that they never grow teeth all their lives.

The Dental Formula

Mammals have heterodont dentition having four types of teeth meant for different function in handling food in the oral cavity. Incisors in front are flat teeth designed for cutting food into pieces and the canines next to them are generally long and pointed spike-like used for tearing flesh by carnivore animals. Premolars and molars are located on the posterior side of the jaw, have flat surface with tubercles called cusps and are used for grinding food of plant origin. They are therefore well developed in herbivore animals. Number and arrangement of teeth in mammals is specific in different groups of animals so much so that mammalian orders can be identified by their teeth and dental formula, which is written for one half of the upper and lower jaw as follows:

$3 - 1 - 4 - 3 \times 2 = 44$. This dental formula belongs to horse and pig.

$3 - 1 - 4 - 3$

PRIMATES. Primates are basically arboreal animals whose ancestors were insectivores and some of them still continue with their original diet. Generally they possess larger pointed canines and flat molars.

UNGULATES. Ungulates belong to two orders, the even-toed Artiodactyla and the odd-toed Perissodactyla that includes horses and rhinoceroses. They are all herbivores and fleet footed grazers and browsers, with teeth adapted for grinding tough vegetation. **Musk deer** also has large upper canines hanging on either side of the jaws. **Hippopotamus** has large canines too with sharp edges meant for defense against the lurking crocodiles in their amphibious habitat.

Pigs and horses have full set of 44 teeth as depicted in the dental formula given above. Premolars and molars are similar in shape and size, have flat grinding surface, with silica deposits between cusps. Such grinders are called selenodont and are designed to grind tough grasses. Wild boars have large canines for digging roots of plants and also for defence.

INSECTIVORES. In insectivores such as shrews, hedgehogs and moles, all teeth are pointed and grinding teeth possess peg-like cusps for crushing hard exoskeleton of insects on which they feed. In the mole genera *Scalopus* and *Condylura* milk teeth are retained throughout life.

CHIROPTERA. In bats milk teeth are shed before birth and they are born with permanent teeth. Insectivorous bats have conical cusps on the grinding teeth for crushing insects.

RODENTIA. Rodents include rats, mice, squirrels and guinea pigs which possess chisel-shaped front incisors for gnawing nuts and hard objects. These teeth grow throughout life due to the wide opening of the pulp cavity but they are worn out equally fast. Premolars and molars have flat grinding surface.

LAGOMORPHA. In rabbits also the upper incisors are chisel shaped adapted for gnawing, canines are absent and cheek teeth are modified for grinding. As in other herbivores, a big **diastema** is present between incisors and premolars.

PROBOSCIDA. The order includes elephants which have upper incisors modified as long tusks which are used for digging roots of plants, for removing barks from trees or for offence and defense. Premolars and molars are alike in appearance and they have broad and lophodont surface, in which cusps unite to form circular lophes of ridges with silica deposits in the depressions. Tusks of African elephant can reach a length of two metres and may weigh as much as 100 kg each.

CARNIVORES. Carnivores include cats, tigers, lions, dogs, wolves, jackals and bears and the aquatic seals, sea lions and walruses. Their canines are long and pointed, dagger like for tearing flesh of the prey. Canines of walruses are modified into long **tusks**. Carnassial teeth are enlarged teeth with pointed cusps. These teeth also have sharp cutting edges and are called secodont teeth used for shearing flesh.

CETACEA. There are no teeth in Mysticeti or baleen whales which possess baleen plates hanging from the palate that are suitable for straining planktons from sea water. In Odontoceti or toothed whales, teeth are homodont and monophodont which are used to seize fish or other prey.

MARSUPIALS. Generally marsupials retain milk teeth except the last premolars that are replaced. Herbivores have a diastema and premolars and molars modified for grinding.