ZOOLOGY (H) : SEMESTER III

ZOOACOR05T

Unit 3: Origin of Chordata

Dipleurula concept and the Echinoderm theory of origin of chordates

Evolution of chordate was one of the most important event in the history of chordate as it was the beginning of evolution of more advanced chordates like bird and mammals. It is the story of origin from a primitive invertebrate like creatures to early chordates. Though first fossil of the first vertebrate the ostrachoderm was discovered from the Ordovician period but it might have originated in late Cambrian period. As early chordates were soft bodied, their fossil records are not preserved. Hence, to trace their ancestry, we have to find out the similarity among different deuterostomes to trace the origin of chordates. Some structural features shared by them such as bilateral symmetry, antero-posterior body axis, triploblastic coelomate condition, etc., may he because of their common ancestry.

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The Phylum Chordata encompasses a vast group of diverse animals ranging from ascidians to man. A few characteristics like Notochord, Dorsal hollow tubular nerve cord and Pharyngeal gill-slits unite these diverse animals under a common phylum. They differ from the non-chordates significantly by the position of nerve cord. The non-chordates possess a ventral solid nerve cord below the alimentary canal, while a dorsal hollow nerve cord above the gut is the diagnostic character of the chordates.

- **Time of Origin**: Chordates evolved sometime during **late Cambrian period, 500 million years ago during Cambrian explosion**, almost at the same time when invertebrates were beginning to evolve.
- **Place of Origin: Fresh water -** Chamberlain (1900) pointed out that all modern chordates possess glomerular kidneys that are designed to remove excess water from body so they have evolved from freshwater forms. Modern sherks, myxinoidea as well as primitive protochordates posses glomerular kidney making it plausible for chordate origin.
- 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.
- **DIVISION OF BILATERIA:** The Bilateria is divided into two major divisions (1) Protostomia and (2) Deuterostornia. This division is based on the differences in embryonic and larval developments. Protostomia includes from Annelida to Arthropoda while deuterostomia includes Echinodermata, Pogonophora and Chordate.
- **DEUTEROSTOME LINE OF CHORDATE EVOLUTION** Following common features of all Deuterostomes suggests strong evidence of a closer evolutionary relationship between the three principal deuterostome phyla – Echinodermata, Hemichordata and Chordata. i) Early cleavage of zygote is indeterminate ii) Blastopore of gastrula develops into anus. iii) Coelom (enterocoelous except vertebrates) is formed by the fusion of pockets developed from the endoderm of developing archenteron of the embryo iv) Pelagic larvae of echinoderms and hemichordates have a close resemblance. Vertebrate does not have a floating larva. v) Deuterostomes use creatine as phosphagen whereas invertebrates use arginine. Some hemichordates as well as echinoids use both.
- The members of the Phylum Chordata possess many features in common.
- **The most important features are:**

(a) The notochord,

(b) The dorsal tubular nerve cord,

(c) The pharyngeal gill-slits and

(d) A post-anal tail.

These four characteristics are unique to the phylum. Existence of such common structures is interpreted as a result of inheritance from a common ancestry. Besides these four basic structures, there are a few other characteristics which have less diagnostic value.

Chordate Features Shared by the Non-Chordates:

Besides the four unique features of the chordates, there are many characteristics which are also present in many higher invertebrate chordates. The significance of the structural similarities is very difficult to interpret from the phylogenetic point of view. However, it may be suggested that the chordates as a group evolved from some higher groups of non-chordates and, hence, the structural resemblances are due to remote common ancestry.

Bilateral Symmetry: Both the chordates and most of the non-chordates like annelids, arthropods, etc. exhibit distinct bilateral symmetry.

Axiate Organization: All the chordates have a distinct polar axis. The anterior end is marked by the presence of head and the posterior end is characterised in most cases by the tail. The axis extending from the head to the tail end is regarded as the anteroposterior axis.

The anteroposterior axis of the chordates corresponds to that of most of the higher non-chordates. The axiate organization is not strictly homologous, because many fundamental differences exist between the two groups.

Triploblastic Condition: All animals above the rank of cindarian coelenterates have a third germ layer besides ectoderm and endoderm. This third layer is known as mesoderm. Although the embryonic formation of the mesoderm is different in non-chordates, its formation is similar in chordates, echinoderms, brachiopods, chaetognaths and in some other enterocoelous forms. The triploblastic condition has added more weight to the phylogenetic relationship of the chordates with the non-chordates.

Metamerism: Segmental organisation is characteristic of most of the non-chordates and the chordates. In annelids and arthropods, segmentation is well-marked both internally as well as externally but in chordates the external segmentation is not seen. The segmental arrangement of the body wall musculature is prominent in chordates.

Coelom: The eucoelom or true coelom is the secondary body cavity of triploblastic animals, situated between the gut and body wall. The space of body cavity is lined by coelomic epithelium and contains coelomic body fluid.The mode of origin of coelom is different among the different groups of invertebrates and chordates. In annelids, arthropods and molluscs the coelom formation is of schizocoelic type, because the coelom develops by the splitting of the embryonic mesoderm layer.In echinoderms, hemichordates and in other chordates the coelom formation is of enterocoelic type, or the coelom is called enterocoel, because the coelom develops from the embryonic archenteron or enteron. Here mesoderm arises in the embryo as paired lateral pouches growing out from the endoderm.These pouches gradually lose continuity with the endoderm and grow downwards and inwards until they meet and fuse. The inner splanchnic part remains against the wall of developing gut and outer somatic part of the mesoderm becomes applied against the developing body wall.

Embryonic Development: Protostome and deuterostome are the two groups of animals which differ in the embryonic origin of the mouth. Among protostomes, the mouth is formed from the blastopore, hence protostome means 'first mouth'. Among the deuterostomes, the mouth does not form from blastopore. Instead it may give rise to anus.

In this group the mouth is the second opening, hence called deuterostome. The differences on the basis of embryological development have strongly supported by analysis of phosphate-containing storage molecules that are found in muscles and are used in the synthesis of ATP.

Protostomes (e.g., Annelids, arthropods and molluscs) contain arginine phosphate and deuterostomes (e.g., echinoderms and chordates) contain creatine phosphate.

These features are present in some parts of the life cycle. Other features are :

i) **Heart situated ventrally** — no specialized heart in cephalochordates; a median ventral aorta which is contractile, and drives the blood forwards.

ii) **Blood flow pattern** — dorsally backwards and ventrally forwards.

iii) **Endostyle** — the iodine secreting tissue in protochordates (Urochordates and Cephalochordates) and regarded as the precursor of the thyroid gland of higher vertebrates.

iv) **Cephalization** — a condition of concentration of principal sense organs in a head and brain.

Table 2 : Characteristic features of the adult deuterostomes

i)	Absence of chitin
ii)	Tripartite body
iii)	Mesodermal skeleton
iv)	Intra epidermal nervous system

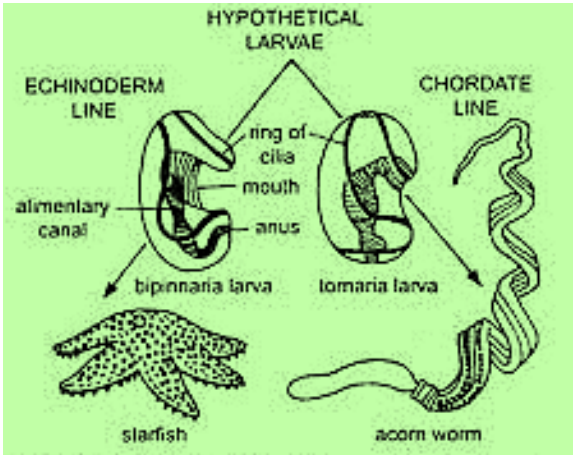

Fig. 9.4. Similarity of larval forms of echinoderms and hemichordates has supported the idea that both came from a common ancestor.

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Concept of Dipleurula larva : The term dipleura or dipleurula was coined by Semon (1888) but the proper illustration of this hypothetical form was given by Bather in 1900, which was accepted by most of the zoologists. Majority of echinoderms have indirect development with free swimming and bilaterally symmetrical larval stages. These echinoderms have small eggs and the fertilized eggs develop in seawater. The cleavage is holoblastic, nearly equal, radial and intermediate to form a hollow one layered ciliated blastula. The blastula transforms into a gastrula by invagination. The cilia of the gastrula are restricted to (i)a large pre oral band present around the mouth on the ventral side and (ii)a small adoral band lining the mouth or stomodeum. This larval stage is called Dipleurula larva. This dipleura larval form is regarded as the hypothetical ancestral form of echinoderms as this larva is universally present in all echinoderms and from it all the larvae of echinoderms have been derived. All well known forms of larvae of echinodermata are derived from the hypothetical dipleurula. Among them fall the Bipinnaria and the Brachiolaria of the sea stars, the Auricularia of the sea rollers and the plutei of the sea hedgehog etc.

- **Echinoderm theory : It was given by Johannes Muller(1860)** and is based on the comparative studies of larval stages of echinoderms and hemichordates. **Garstang and DeBeers proposed the echinoderm larvae gave rise to chordates by neoteny**.
- The theory was given by Muller 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.
- **Fossil evidence :** 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 postanal 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.
- It is believed that chordates have originated from invertebrates. It is difficult to determine from which invertebrates group the Chordates developed. Chordate ancestors were soft bodied animals. Hence they were not preserved as fossils. There are several theories have been put forwarded to explain the origin of chordates. These are directly from some invertebrate group or through the intervention of some Protochordates. Almost every invertebrate phylum- Coelenterates, Nemertean, Phoronida, Annelida, Arthropods and Echinoderms has been suggested. But these theories are far from being satisfactory and convincing and have been only historical value. Only Echinoderm Theory has received some acceptance.

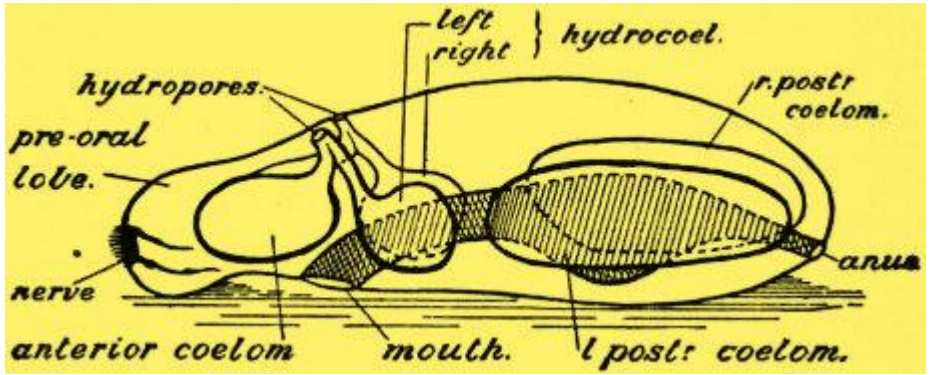

Figure : Hypothetical Dipleurula larva

Proposition: The hemichordate larva (tornaria) is strictly similar to the larva (bipinnaria or dipleurula) of echinoderms. Both are small, transparent, free swimming, bilaterally symmetrical. Both have similar ciliated band in loops, a dorsal pore, sensory cilia at the anterior end and a complete digestive system of ventral mouth and posterior anus. This striking larval resemblance Johannes Muller and Bateson to suggest a common ancestry for the echinoderms and the hemichordates.

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Note : Fossilization of soft bodied animals is very rare occasion. If a soft bodied animal is to fossilized, it must go through the very process without being decomposed. It means the animal either buried alive and also escape decomposition by fast fossilization in mud volcano conditions, thus a rapid death caused by devoid of oxygen. The fast fossilization needs very low amount of oxygen and proper burying substratum, under all of this circumstances soft animal can be fossilized.

Supporting Evidence: This theory infers origin of chordates, hemichordates and echinoderms from a common ancestors. This theory is based on the following evidence:

- **A) Embryological Evidence:** Both echinoderms and Chordates have enterocoelic coelome, mesoderm and deuterostomous mouth. There is resemblances between the bipinnaria larva of echinoderms and the tornaria larva of hemichordates.
- **B) Serological Evidence**: A close similarity between the proteins of the body fluid of chordata and echinoderms. Hence the chordates are more related to echinoderms.

The radial symmetry of adult echinoderms will disapproved the relationship with the bilaterally symmetrical chordates. The bilateria is divided into two major divisions- Prostomia and Deuterostomia. The division is based on the differences in embryonic and larval development. Prostomia includes from Annelida to Arthropoda while Deuterostomia includes Echinodermata,Pogonophora and Chordates.

- **C) Deuterostome line of Chordate Evolution:** Following common features of Deuterostome suggests strong evidence of a closer evolutionary relationship between the three principal Deuterostome phyla- Echinodermata, Hemichordata and Chordata.

(i) Early cleavage of zygote is indeterminate.

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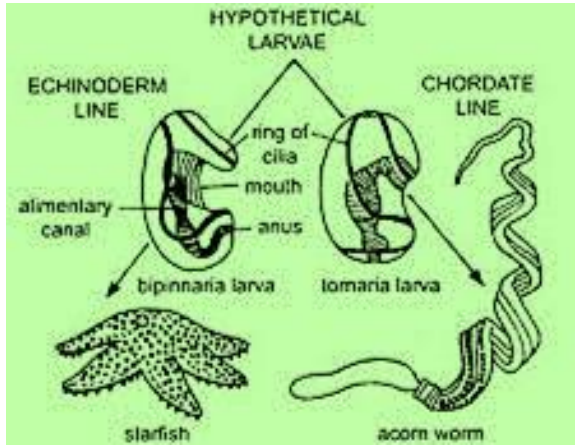
(iv) Pelagic larva of Echinoderms and Hemichordates have a close resemblance vertebrate does not have a floating larva.

(v) Deuterostomes use creatinine as phosphogen whereas invertebrates use arginine. Some Hemichordates as well as echinoids use both.



Dissimilarity and Doubts:

- Presence of apical plate with eyespots in tornaria larva builds doubts the common ancestry of echinoderms and hemichordates. Garstang and DeBeers proposed the Neotenous larva theory suggesting that probably the Auricularia larva of echinoderms became sexually mature and later this neotenic larva gave rise to chordates. Cambrian and Ordovician fossil records of carapoid echinoderm lead Torsten and Gisten to assume that carapoid echinoderms might have evolved from tornaria like creatures which have began to settle down to lead sedentary life. The water vascular system might have developed out of ciliated grooves of these creatures. Besides this, it was also claimed that in the lower Silurian period, one carapoid echinoderm had the calyx perforated by a series of 16 small apertures. These apertures can be compared with the gill slits of Branchiostoma. Some isolated biochemical studies (Needham,1932 and Whelmi,1942) put some weight on the concept of the diversion of Chordates from echinodermates. Most of the non chordates use arginine phosphate for the transfer of energy but Ophiuronoids, Cephalochordates, ascidian and vertebrates use creatinine phosphate. On the other hand, Hemichordata and Echinoderms use both arginine and creatinine phosphate as phosphate carrier. The descent of chordata from echinodermates by the direct transformation of any echinoderms or its neotenous larva into a chordate is no longer accepted now-a days. Instead they had a common an immediate ancestor.

Other theories: The geological records established beyond doubt that the chordates originated prior to Cambrian period because the relics of some lower chordate forms have been discovered in Cambrian strata. There are various theories regarding the origin of the chordates from the non-chordate groups. Most of the theories suffer from serious defects.

Of all the theories regarding the ancestry of chordates from some non-chordates, Garstang's suggestion that the chordates have evolved from some free-swimming echinoderm larvae (possibly auricularian larvae) by means of paedomorphosis has been accepted by many workers.

The role of paedogenesis (reproduction in pre-adult stage) in evolutionary dynamics is emphasised by many workers on this line. But in recent years the ancestry of the chordates from the echinoderm source is not accepted.

Recent workers regard the differences between the vertebrates and the non-chordates (invertebrates) to be artificial in nature. Inclusion of the echinoderms, pogonophores and chordates under deuterostomia (animals where the anus develops from the blastopore and the mouth is formed anew) is accepted nowadays. The protochordates (urochordates and cephalochordates) are the members of the Phylum Chordata.

The protochordates provide connecting link between the vertebrates with other deuterostomes. The deutorostomes are highly specialised groups and it will be improper to regard them in the direct line of vertebrate descent.

The phylogenetic status of the hemichordates is a subject of great controversy. But the chordate nature of the urochordates and the cephalochordates is well-established though their relationships with the vertebrates and with each other are difficult to ascertain.

Barrington (1965) suggested that the deuterostomes have evolved from sessile/semi-sessile ancestors having bilaterally symmetrical and tripartite body and coelom. The echinoderms have departed a long way from the ancestors, while the hemichordates remained closer.

The hemichordates have developed pharyngotremy (i.e., existence of openings in the pharyngeal wall) which is associated with its ciliary mode of feeding. In course of time a group with internal food collection mechanism by elaborate and complicated pharynx gave rise to the urochordates, cephalochordates and vertebrates.

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