TOPIC: INTRODUCTION TO PROTOCHORDATA AND GENERAL CHARATERISTICS AND CLASSIFICATION OF HEMICHORDATA

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PROTOCHORDATA

What Is Chordata?

In the scheme of classification, the Animal Kingdom is divided first into several major animal groups called *phyla* (singular, *phylum).* There are approximately 30 animal phyla currently recognised. The last major group of the Animal Kingdom is known as phylum *Chordata.* It was created by Balfour in 1880. The name of this phylum is derived from two Greek words, the "*chorde"* meaning a string or cord, and "*ata"* meaning bearing. The reference is to a common characteristic feature in the form of a stiff, supporting rod-like structure along the back, the which is found in all the members of the phylum at some stage of their lives. Thus, chordates are animals having a cord, i.e., notochord. The animals belonging to all other phyla of the Animal Kingdom are often termed 'the non-chordates' or 'the invertebrates since they have no notochord or backbone in their body structure.

Fundamental Characteristics of Chordates

All the chordates possess three outstanding unique characteristics at some stage in their life history.
These three fundamental morphological features includes :
(1) A dorsal hollow or tubular *nerve cord*

(2) A longitudinal supporting rod-like *notochord*
(3) A series of *pharyngeal gill slits*

1. Dorsal hollow nerve cord. The central nervous system of the chordates is present dorsally in the body. It is in the form of a longitudinal, hollow or tubular nerve cord lying just above the notochord and extending lengthwise in the body.
The nerve cord or *neural tube* is derived from the dorsal ectodermal *neural plate* of the embryo and encloses a cavity or canal called *neurocoel.* There are no distinct ganglionic enlargements. The nerve cord serves for the integration and coordination of the body activities. In vertebrates, the anterior region of nerve cord is specialized to form a *cerebral vesicle* or *brain* which is enclosed by a protective bony or cartilaginous cranium. The posterior part of nerve cord becomes the *spinal cord* and protected within the vertebral column.

2, **Notochord or chorda dorsalis.** The notochord is an elongated rod-like flexible structure extending the length of the body. It is present immediately beneath the nerve cord and just above the digestive canal. It originates from the endodermal roof of the embryonic archenteron. Structurally, it is composed of large vacuolated Protochordates have a typical notochord. In adult vertebrates, it is surrounded or replaced by the vertebral column.

3. **Pharyngeal gill slits.** In all the chordates, at some stage of their life history, a series of paired lateral *gill clefts* or *gill slits* perforate through the pharyngeal wall of the gut behind the mouth. These are variously termed as pharyngeal, branchial and visceral clefts or pouches. They serve primarily for the passage of water from the pharynx to outside, thus bathing the gills for respiration. The water current secondarily aids in filter feeding by retaining food particles in the pharynx. In protochordates (e.g. *Bronchia stoma)* and lower aquatic vertebrates, the gill slits are functional throughout life. But, in higher vertebrates, they disappear or become modified in the adult with the acquisition of pulmonary respiration.

The above three common features appear during early embryonic life of all the chordates.But all the three features rarely persist in the adult (e.g. *Brcmchiostoma).* Often they are modified or even lost in the adult stages of higher chordates. The notochord disappears during development in most vertebrates, while the nerve cord and the pharyngeal clefts or their derivatives remain in the adult. The three common chordate characters were probably characteristic of the ancestral chordates. They distinguish chordates from all other animals and appear to reveal their common ancestry.

Origin and Ancestry of Chordata

While a great deal is known about modern chordates, including the lower forms, their origin remains obscure. Scientists have not succeeded in determining which lower forms have given rise to them. Their early ancestors most likely were soft-bodied and left no definite fossil remains. They must have originated prior to Cambrian period as the oldest fossils of known vertebrates have been discovered in late Cambrian strata. Most scientists consider that the chordates have originated from invertebrates. Several theories attempt to explain the origin of chordates from non chordate groups, but they have serious drawbacks and are far from being satisfactory. One theory advocates the descent of Chordata from the Echinodermata as such. The remarkable similarities between the echinoderm (bipinnaria) and
hemichordate (tornaria) larvae is taken as good evidence for common ancestry. Garstang suggested that probably free-swimming auricularian larvae of some ancestral echinoderms evolved into chordates through paedogencsis, i.e., prolongation of larval life without undergoing metamorphosis and reproducing sexually.
Most zoologists (Romer, Berril, Barrington,etc.) now favour the deuterostome line of chordate evolution, according to which the phyla Echinodermata, Hemichordata and Chordata show common

ancestry on embryological and biochemical evidences. The protochordates provide the connecting link between early chordate ancestors and verebrates. The differentiation probably occurred much earlier than Cambrian period. The earliest traces of vertebrates have been found in the rocks of late Cambrian and Ordovician. A number of fishes followed in Silurian and became abundant in the Devonian. The subsequent periods show the evolution of amphibians, reptiles, birds and mammals.

Major Subdivisions of Phylum Chordata

Phylum Chordata is a rather heterogeneous assemblage of groups which differ widely from one another and show various degrees of relationships to each other. In a taxonomic outline classification of the phvluin, these groups are customarily arranged in larger functional divisions or subdivisions based on specific structures or features. These subdivisions or taxa havi been accorded different ranks under different systems of classification. The following terminology includes major subdivisions of phylum Chordata.

1. Subphyla and classes.

Phylum Chordata is first conveniently separated into 3 or 4 primary subdivisions, called *subphyla,* based on the character on notochord. These are :

Subphylum 1, Hemichordata (or Adelochordata)
Subphylum 2. Urochordata (or Tunicata)
Subphylum 3. Cephalochordata
Subphylum 4. Vertebrata

2. Protochordata and Euchordata.

The first two subphyla under phylum Chordata (i.e., Urochordata and Cephalochordata) are all marine, relatively small and without a vertebral column or backbone. They are often collectively referred as the *non vertebrate* or *invertebrate chordates or*

protochordates as they are regarded to be early, primitive, borderline or first chordates closely allied with the ancestral chordate stock.

3. Acrania and Craniata.

The protochordatesubphyla lack a head and a cranium, so that they are known as *Acrania* .On the other hand, the subphylum Vertebrata (subdivision Euchordata) has a distinct head and a cranium and is also called *Craniata.*

4. Agnatha and Gnathostomata.

The Vertebrata (or Craniata) are further subdivided in several ways. One possibility with universal agreement separates them into two unequal sections : Agnatha and Gnathostomata. *Agnatha* lack true jaws and paired appendages. Agnathans or agnathostomes include a small number of primitive but highly specialized fish-like forms, the extinct ostracoderms and the modern cyclostomes.

5. Pisces and Tetrapoda.

A basic division of **Gnathostomata** recognises two superclasses : Pisces and Tetrapoda. The superclass includes all the fishes which are strictly aquatic forms with paired fins. Sometimes, the fish-like agnathans are also embraced here. The superclass is formed by four-legged land vertebrates including amphibians, reptiles, birds and mammals.

6. Anamnia and Amniota.

Another method ofgrouping the vertebrates elicits an extremelyimportant advance in the pattern of embryological development. It is based on the presence of a special membrane, the *amnion,* that holds the developing embryo in a reservoir of fluid, and permits the laying of eggs on land. The animals that possess it belong to *Amniota* which includes the classes Reptilia, Aves and Mammalia. The animals without this membrane are *Anamniota* including cyclostomes, fishes and amphibians.Sometimes, the anamniotes are referred to as the

lower vertebrates, and the amniotes as *higher vertebrates.*

HEMICHORDATA

Meaning of Phylum Hemichordata:

The animals with notochord constitute the Phylum Chordata. It has a major subdivision, called the Vertebrata or Craniata for possession of vertebral column or cranium. The rest of chordates, namely Hemichordata, Urochordata and Cephalochordata are collectively called the Primitive Chordates or Protochordates.

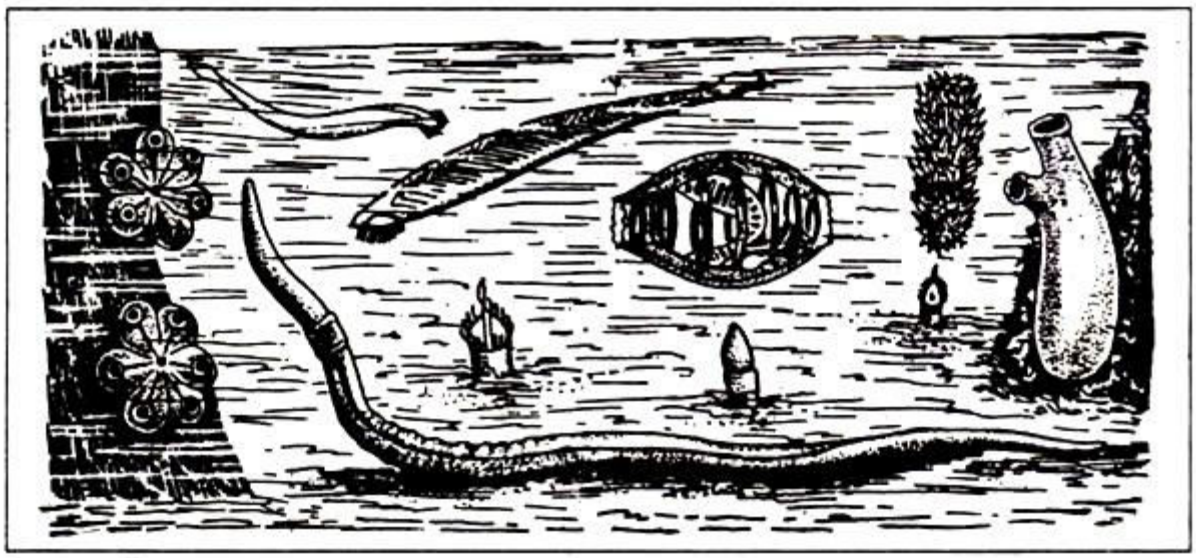

Fig. 2.1 : The invertebrate chordates are mostly sedentary animals and exploit the natural resources of their marine habitats.

But it is better to divide it into Invertebrate Chordates for Hemichordata, and Protochordata or lower chordates for Urochordata and Cephalochordata for the structural organisation of chordate features. The basic chordate features are present in Protochordata.

Hemichordata has long been considered as the lowest group of chordates for the construction of notochord, nerve cord and pharyngeal gill-slits, the main features of the Phylum Chordata. Recent workers claim that the notochord of hemichordates is not a true notochord, and the central nervous system containing a

longitudinal ventral nerve strand shows the characteristic of major invertebrate phyla.

The pharyngeal gill-slits or pharyngotremy is the only chief link between hemichordates and chordates. So the inclusion of Hemichordata in the Phylum Chordata remains a controversial issue and still remains of uncertain status (incerte sedis). Hemichordates are somewhat close to invertebrates in the body construction. So the term 'Invertebrate Chordates' for Hemichordata by some zoologists is partially justifiable.

The so-called protochordata including Hemichordata, Urochordata and Cephalochordata lead sedentary life in adult stage and perform ciliary mode of feeding to compensate the purpose of locomotion.

Phylum Hemichordata:
The phylum Hemichordata represents a group of lowest chordates having profound phylogenetic significance. The hemichordates furnish a clue to the link between the chordates in general and the non-chordates, specially the echinoderms in particular. The hemichordates have peculiar anatomical organisation and the free-swimming larva, tornaria, is strikingly similar to the larval stages of some echinoderms.

Classification of Phylum Hemichordata:

Historical Resume: The first member of the Hemichordata was recorded by Eschscholtz (1825). He named the animal Ptychodera and regarded it as a holothurian. Subsequently, Delle Chiaje (1829) added another member Balanoglossus clavigerus to the group.
Since then, many hemichordates have been put on record. All these hemichordates were included under the group Enteropneusti as proposed by Gegenbaur (1870).

Since then, this group was called Enteropneusta. Bateson (1885) studied the embryology of some enteropneusts and proposed the name Hemichordata to replace Enteropneusta. The tornaria larva was regarded as an echinoderm larva by Johannes Miller (1850), Krohn (1854), Agassiz (1864) and many others. Metchnikoff (1870) regarded tornaria as the larval stage of Enteropneusta.

The work of Kowalevsky needs special mentioning, because he gave the accurate description of Balanoglossus. The hemichordate possessing an exceptionally elongated proboscis was named Saccoglossus by Schimkewitsch (1892), but Spengel (1893), in his monograph, treated the same animal as subgenus Dolichoglossus under the genus Balanoglossus.

Van der Horst (1939) regarded Saccoglossus and Dolichoglossus as the synonyms of the same genus.

Sars (1867) and Allman (1869) recorded the strange colonial Rhabdopleura as a member of Bryozoa. Lankester (1877) introduced the term Pterobranchia for Rhabdopleura, but still retained it as a subdivision under Bryozoa.

Another similar animal, Cephalodiscus, was recognised by Mcintosh (1882) which was also regarded as a bryozoan. Hamer (1887) and Fowler (1892) removed Cephalodiscus and Rhabdopleura, respectively from the group Bryozoa and suggested their inclusion under Hemichordata. Another genus, Atubaria, was added to the group by Sato in 1936.

Willy (1899) divided the Hemichordata into two classes—Enteropneusta and Pterobranchia. But Harmer (1905) added another class Phoronida under Hemichordata. A peculiar pelagic larval form was discovered by Mortensen in 1910. Spengel (1932) named this larva Planctosphaera pelagica.

Important Features:

1. Hemichordates are bilaterally symmetrical deuterostome coelomates.

2. They are either solitary (enteropneusts) or colonial (pterobranchs).

3. The soft body is divided into 3 regions – Proboscis (Protosome), collar (mesosome) and trunk (metasome) – reflecting internally a tri-coelomate organization.

4. A preoral buccal diverticulum is considered as the stomochord rather than notochord.

5. The digestive tube is complete, straight or U-shaped.

6. The pharyngeal-slits are present or absent. When present, variable in number (one or more pairs), found in the trunk.

7. A heart and kidney occur in the proboscis (preoral lobe) and are supported by buccal diverticulum (stomochord).

8. The nervous system is intra-epidermal. The nervous system consists of a dorsal and ventral nerve cord extending to the whole length of the animal. In the collar region, the nerve is dorsal and hollow. This part represents the true chordate feature.

9. Sexes are separate (gonochoristic) but some species like Cephalodiscus nigrescens and C. hodgsoni are hermaphrodite.

10. Gonads are extra-coelomic.

11. Asexual budding also takes place in a few forms (Balanoglossus capensis, Rhabdopleura) and formation of buds occurs in the posterior end of the body.

12. Fertilization is external (enteropneusts) or internal (pterobranchs).

13. Cleavage holoblastic, radial (enteropneusts), but radial and bilateral in pterobranchs.

14. Planktonik, ciliated tornaria larva in some. Tornaria larvae are lecithotrophic (e.g., the larva is non-feeding and completes its developmental stages utilizing its stored reserved food of the egg). Six hypothetical developmental stages are recognised and these are named after renowned zoologists.

1st and 2nd stages are after the names of Muller and Heider. Other stages are Metschnikoff, Krohn, Spengel and Agassiz respectively.

Fossil Record:
Sufficient data have not been collected except Eocephalodiscus which has recovered from the Upper Cretaceous.

Geographical Distribution:
Hemichordates occur in all seas but may prefer warm and temperate waters. Majority of the species live in the intertidal zone and shallow waters but a few occur at great depths.

Habitat:
Members live in U-shaped burrows in sand, mud or amongst rocks and sea weeds.

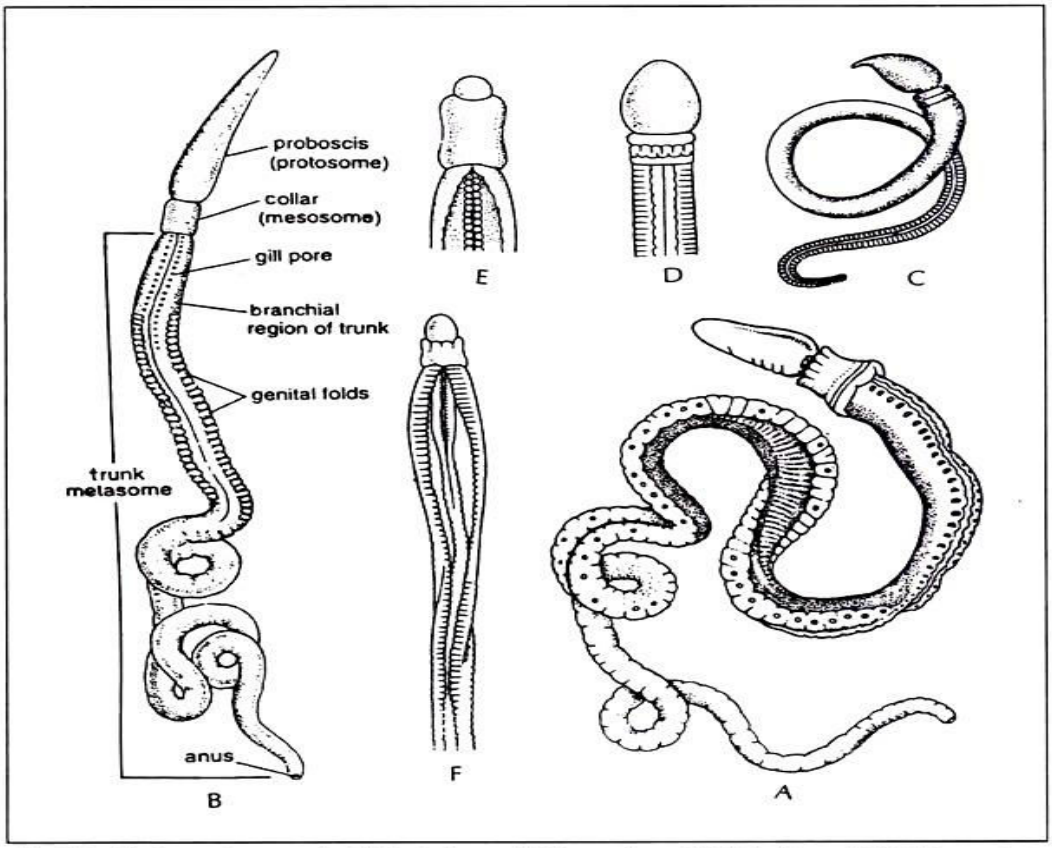

Fig. 2.15 : Various enteropneusts. A. *Protoglossus*, B. *Saccoglossus* (*Dolichoglossus*), C. *Schizocardium*, D. *Glandiceps*, E. *Balanoglossus numeensis*, F. *Ptychodera* (From Newman, 1939).

The Phylum Hemichordata includes two classes Enteropneusta Gegenbaur, 1870 and Pterobranchia Lankester, 1877. Authors like Marshall and Williams, 1964; Young, 1981; Romer and Parsons, 1986; Barnes, 1987; Ruppert and Barnes, 1994; Anderson, 1988; Pechemik, 2000; and Kardong, 1998, 2000 have mentioned only two classes in their books.

But Hyman (1959) and Barrington (1967, 79) include 3 classes – Enteropneusta, Pterobranchia and Planctosphaeroidea in their classification.