



## **Origin of Metazoa**

### **[Academic Script]**

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# **Academic Script**

## **1.Introduction**

On a rough estimate, life began on Earth about 3.7 billion years ago. First cell to appear was a prokaryote cell without a definite nucleus. Later, the eukaryote cell developed having a well-organized nucleus. The earlier unicellular or non-multicellular organisms were neither plant (Protophyta) nor animal (Protozoa) in nature. Ernst Haeckel (1866) called them protista which may be defined as organisms, usually of small size, consisting of a nuclear apparatus (no definite nucleus, one nucleus or many nuclei) in a cytoplasmic body which is not divided into cells.

With an increase in complexity of life, multicellularity developed in plants and animals. As mentioned earlier, the term Metaphyta is used for multicellular plants and Metazoa for multicellular animals.

## **Premetazoan Ancestors**

There is no direct proof about the ancestors of Metazoa. But all Zoologists agree that the metazoans have evolved from some unicellular or acellular organisms, such as Protozoa. This is strongly evident by the facts of embryonic development in which each metazoan passes from an acellular (zygote) to a cellular condition (morula, blastula, gastrula, etc.).

A unicellular protistan individual performs all the functions of the living. From such a functionally complex

single-celled protistan arose the multicellular animals. But, how single-celled protozoa, which is evolved possibly 2,000 million years ago, gave rise to the fundamental mysteries of evolution. It is difficult to solve it because the earliest metazoans, like most invertebrates, were soft-body and left no fossils.

## **2.Theory**

### **Theories of Origin of Metazoa**

Different views have been expressed by many prominent scientists from time to time to explain the evolution of Metazoa from different groups of Protozoa. All these views can be generalized into three principal view:

- (1) The ancestral metazoan originated from a colonial flagellate through increasing cellular specialization and interdependence (Colonial theory).
- (2) The ancestral metazoan arose from a multinucleate syncytial ciliate which became compartmented or cellularized by the appearance of cell boundaries (Syncytial theory).
- (3) The metazoans had a polyphyletic origin from different unicellular groups (Polyphyletic theory).

#### **A. COLONIAL THEORY**

The Colonial or Flagellate theory is the classic and most frequently repeated theory of the origin of multicellular

animals. It maintains that hollow colonial flagellates, like *Volvox*, were probable ancestor of the metazoans. This idea was first conceived by Butschli, Lankester and Haeckel (1874), later modified by Metschnikoff (1886) and recently revived by Hyman (1940).

Colonial theory holds that multicellular animals came about through association of many one-celled flagellate individual forming a colony. With increase in the number of individual cells, they became more and more specialized in structure and functions. Soon, individuality in the cells was lost and the whole colony itself became a single multicellular individual or a metazoan.

The Colonial theory has been greatly accepted, since it conforms best with the facts of embryonic development. The belief in the flagellate ancestry of Metazoa is also supported by several facts.

The flagellates are a highly plastic group, which is capable of great changes. In all probability, the entire plant kingdom, and all other protozoan classes have originated from them.

The flagellates show a great tendency of forming compact colonies, and these clearly resemble various stages in the embryonic development of Metazoa.

The metazoan tailed sperm cell very closely resembles a modified flagellate. Therefore, the occurrence of flagellate or

tailed spermatozoa throughout the Metazoa is a clear indication of descent of Metazoa from the flagellata.

Flagellated body cells are common among the lower metazoans. Like sponges and coelenterates. Sponges produce flagellated larvae and also possess flagellated cells or choanocytes that closely resemble a choanoflagellate. In coelenterates, the endoderm cells have a tendency to give out flagella.

According to the Colonial theory, the metazoan ancestors were like existing fresh water volvocid phytoflagellates. But these are plants like organisms having cellulose cell walls, chlorophyll and autotrophic nutrition and undergo reduction division following fertilization. The theory does not explain how these plants like characteristics were lost during the course of evolution of the metazoan ancestors. However, this objection is met with by holding that probably metazoans arose from some group of existing zooflagellates having colonial organization similar to the volvocid phytoflagellates.

The flagellate protozoan colonies are of several types such as linear, tree-like, plate-like, spherical and solid as well as hollow. Of these, which type gave rise to the ancestral Metazoa, has been a subject of great speculation among scientists. Now, let see the some of the noteworthy views by different scientists.

**(I) Lankester's theory.** According to Lankester, the ancestral metazoan was a morula like solid colony, such as

synura or pandorina. Food taken by outer surface of the external flagellated cells (ectoderm) was passed into their inner ends, a process still seen in living sponges and coelenterates. Later, the inner ends of cells got separated forming an internal digestive layer or endoderm. Lankester named this hypothetical ancestor as planula. This was a solid organism. Later on, it developed mouth and digestive cavity.

**Lankester's theory found no acceptance because:**

- (1) Endoderm formation by primary delamination is very rare in the Metazoa.
- (2) Formation of internal digestive tube or endoderm will be of no use without a mouth for taking in food.

**(II) Butschli's theory:**

The plate like form such as Gonium was favoured by Butschli as the ancestral metazoan type. He postulated that first this became two layered by cutting off a lower plate of cells and later curved into a sphere. But this idea gets no support from the embryonic development of metazoans.

**3.Theory**

**(III) Haeckel's theory of blastaea and gastraea:**

The Colonial theory is based mainly on E.H.Haeckel's theory of Metazoan ancestry, presented in 1874.

According to Haeckel, the metazoans evolved by aggregation of single protistan cells into a little hollow, spherical, flagellate colony, similar to Volvox. It possessed a distinct antero posterior axis and swam about with one pole directed forward. This hypothetical organism was named blastaea by Haeckel and considered similar to the blastula or coeloblastula stage in the embryogeny of living metazoans. Blastaea showed early differentiations between somatic cells and reproductive cells. Somatic cells were meant for perception, food capture and locomotion by the action of flagella. But, certain cells were specialized to become sex cells, a process already seen in Volvox. The embryonic archaeocytes of sponges and interstitial cells of coelenterates, which later become reproductive cells, are reminiscent of the same phenomenon.

The blastaea invaginated at the posterior pole to become a double walled sac termed gastraea by Haeckel. The inner endodermal sac thus formed was termed primitive intestine or archenteron and its single opening to the exterior primitive mouth, protostoma or blastopore. The endodermal cells lining the digestive cavity were relieved from perceptive and locomotory functions and became specialized for engulfing and digesting food for the whole colony. According to the famous Gastraea theory of Haeckel.

- (1) A two-walled hollow gastraea was the hypothetical common ancestor of all the Metazoa.
- (2) It is represented in the embryonic development of Metazoa by the two-layered gastrula stage.

- (3) The two layers of gastraea are retained through out Metazoa as ectoderm and endoderm.
- (4) Endoderm is fundamentally produced by invagination, all other methods being secondary modification of invagination.

Haeckel's Gastraea theory about ancestry of the Metazoa is mainly based on the embryological evidences.

- (1) According to Haeckel's recapitulation theory, the blastula and gastrula stages in the embryonic development of higher metazoan represent repetition of the adult stages of the original metazoan ancestors that is blastaea and gastraea.
- (2) In the 19<sup>th</sup> century, Cnidaria (Coelenterate) were regarded to be the first or most primitive metazoan phylum because of their radial symmetry. Haeckel also compared close structural similarity between the ancestral gastraea and lower metazoans like hydrozoan coelenterates and certain sponges. Like gastraea, they are also radially symmetrical, double walled and with a single opening (mouth or osculum) leading into a sac-like digestive cavity.

Gastraea theory by Haeckel was widely accepted as it simplifies the embryologic and phylogenetic history of animals and gives a convincing explanation of the stages by which complex metazoan structure might have been achieved. However, it had to face some objections.

- (1) Chief objection is that in metazoan embryology, endoderm is not always formed by invagination. Even in the Coelenterata, which are structurally nearest to the hypothetical gastraea, endoderm is formed by the inwandering of ectodermal cells (multipolar ingression), and the larva is a parenchymal or planula rather than a gastrula. Invagination is an unusual method of gastrulation which in most cases take place by immigration or delamination. It is probable that invagination is a derived rather than original method and represents one of the short cuts common in embryology.
- (2) According to Haeckel, possession of radial symmetry was regarded as primitive character of cnidarians (Coelenterates). But, in echinoderms and some chordates (tunicates) it is a secondary condition derived through metamorphosis of a bilaterally symmetrical larva. Thus, radial symmetrical may be an adaptation due to a sedentary or sessile mode of life rather than a phylogenetically primitive condition, so that there is no compulsion to consider the ancestral metazoan to be a radially symmetrical, two-layered and hollow sac-like organism.
- (3) Haeckelian recapitulation theory has been largely discarded now due to its many discrepancies.

#### **(IV) Metschnikoff's theory:**

Haeckel's Gastraea theory was later modified by Metschnikoff (1866). Metschnikoff noted that the primitive

mode of gastrulation in coelenterates is by ingression, and not by invagination, producing a solid gastrula. He also discovered that digestion is intracellular and phagocytic in lower Metazoa. According to him, certain ectodermal cells of blastaea became phagocytic and wandered (multipolar ingression) into the inner blastocoel which became filled up with amoeboid cells embedded in a gelatinous material. Therefore, he argued that the diploblastic ancestral gastraea was a solid rather than a hollow organism, and he named it parenchymula. It would not have required a digestive sac or mouth because of phagocytic intracellular digestion. Formation of archenteron and blastopore were regarded as later, secondary processes.

According to Metschnikoff, his theory of solid gastraea was strongly supported by the discovery of Proterospongia by Saville Kent in 1880. It is a choanoflagellate colony embedded in a gelatinous matrix. Some outer collared cells frequently lose their collars and flagella and move into the jelly as amoeboid cells, indicative of ingression.

Facts of embryonic development also support Metschnikoff's theory rather than Haeckel's because gastrulation by inwandering of cells or multipolar ingression is far more common than invagination.

#### **(V) Modern view by Hyman:**

Modern supporters of Colonial theory, such as Hyman (1940), also derive Metazoa from an axiate hollow spherical

flagellated colony, similar to blastaea of haeckel. It showed an early differentiation into somatic and reproductive or germ cells. The somatic cells also became differentiated into locomotor-perceptive and nutritive types. Through the migration or wandering of nutritive cells inside (multipolar ingression), the originally hollow sphere became converted into a solid, ovoid and radially symmetrical Parenchymula or sterogastrula. It had no mouth and no digestive cavity. Food was caught, as in Protozoa, by the outer flagellated locomotor-perceptive cells and passed to the inner amoeboid nutritive and reproductive cells, for intra-cellular digestion.

The anterior pole probably bore special sensory cells or a tuft of sensory cilia. This hypothetical organism has been called the Planuloid ancestor because of its close similarity with the planula larva of coelenterates. According to this view, the radial symmetry of coelenterates is primitive and derived directly from this hypothetical planuloid ancestor.

#### **4.Theory**

#### **B. SYNCYTIAL THEORY BY HADZI**

Resemblance between multinucleate ciliates and acoelous flatworms led Hanson (1958) and Hadzi (1963) to propose a ciliate origin for metazoans. Their theory may be called the Syncytial theory. Syncytial refers to the multinucleate condition in which cell membranes are absent between adjacent nuclei. The theory was first proposed by Sedgwick many years ago but was ignored. Later, jovan Hadzi (1963), a

Yugoslavian, studied it for about 50 years and gave many logical reasons in its support.

Hadzi's theory states that Metazoa did not evolve by aggregation of uni-nucleate protistans, but by cellularization of a primitive multinucleate syncytial ciliate, thus producing a typical multicellular condition. The main tenets of Hadzi's theory:

- (1) The ancestral metazoan was at first syncytial in structure and bilaterally symmetrical. It gave rise to acoel, flatworms (Turbellaria) by process of cellularization. Acoel turbellaria are, therefore, regarded to be the most primitive living metazoans and their bilateral symmetry is considered to be primitive.
- (2) Cnidaria, especially the Anthozoa, were derived from the rhabdocoel turbellarians. Anthozoa became radially symmetrical externally by adopting a sessile mode of life. However, internally they still retain some of their ancestral bilateral symmetry as shown by stomodaeum, mesenteries and muscle bands. Accordingly, the radially symmetrical Hydrozoa are not primitive but advanced than Anthozoa, and their structural simplicity is a secondary development.
- (3) Ctenophores and the Muller's larva of polyclad turbellarians are both planktonic, exhibit octoradial symmetry, and their embryology is also similar in several important details (Lang and MacBride). Therefore, Hadzi held that ctenophores evolved from polyclads by the

neotenus retention of several structural features of Muller's larva.

- (4) Theory of germ layers is rejected by Hadzi's theory. According to Blastaea-Gastraea theory of Haeckel, ectoderm and endoderm were formed with the evolution of two-layered gastrula, while mesoderm appeared later on. But, in the development of Acoela, 3 regions are formed in situ without any formation of germ layers. Thus, Hadzi presumes that the 3 germ layers were formed contemporaneously in the ancestral ciliate following cellularization.
- (5) It is assumed that conjugation in ciliates is a form of sexual reproduction equivalent to copulation in Metazoa.

Hadzi compared an acoelous turbellarian, such as *Convoluta*, with certain multinucleate ciliates. Both are in the same size range, have an antero-posterior axis, are ciliated and distinctly bilaterally symmetrical. Both tend to be syncytial and lack a digestive cavity. Multinucleate ciliates practice asexual conjugation show a differentiation into inner, middle and outer material and organelles, and possess trichocysts which are similar to turbellarian sagittocysts and Cnidarian nematocysts. Central parenchymula of Acoela looks syncytial due to imperfect cellularization. Hadzi considered these similarities as evidence in support of the primitive position of acoelous turbellarians.

According to Hadzi, all that is needed to convert such a Protist to an acoelous turbellarian, which has neither gut nor

complete cellularization and a primitive nerve net. A hollow gut comes later.

A number of objections have been raised against the Syncytial or Turbellarian theory of Hadzi. It disregards the evidence of embryology, while pays too much importance to adult structural similarity.

- (1) Recent electron microscopic studies have revealed that epidermis of Acoela is cellular and not syncytial as claimed by the supporters of ciliate origin of Metazoa. Parenchyma of Acoela may also prove to be cellular on closer examination.
- (2) Syncytial theory considers Biradial Anthozoa to be primitive and radial Hydrozoa to be most specialized. This is based on the presumption that bilaterally symmetrical acoelous turbellarians are the most primitive living metazoans. But evidence show radial symmetry of Coelenterates to be primary and not secondary evolved form a bilateral ancestor.
- (3) Body plan of primitive groups (or phyla) is generally more variable or less fixed. Naturally, Hydrozoa being more variable should be considered more primitive and low in evolutionary line than Anthozoa.
- (4) Anthozoa, with few exceptions, are not hermaphroditic, although most sessile animals are. Thus, Anthozoa seem improbable descendants of hermaphroditic turbellarians, as claimed by Hadzi's theory.
- (5) Flagellated sperms occur in Metazoa but not in ciliates. Therefore, it is difficult to explain a de novo origin of

motile sperm in the ciliate metazoan ancestor. Hadzi's theory holds that in some ciliates, the male nucleus is already cellularized, that is, flagellated like a metazoan sperm. Thus, during conversion from ciliata to Metazoa, cellularization of female gamete must not involve great difficulty.

- (6) A macronucleus is present in ciliate but absent in acoels. It is assumed that macronucleus was absent in the multinucleate metazoan ancestor. It probably developed later in the evolutionary line leading to higher ciliates.

### **C. POLYPHYLETIC THEORY**

More recently, Greenberg (1959) and Preston (1967) held that probably all Metazoa have not originated from any single ancestor. They have suggested a polyphyletic origin for the metazoans. It is fairly certain that sponges developed by way of colonial flagellates (e.g. Proterospongia), whereas other multicellular groups originated from the cellularization of Syncytial protociliates or perhaps the mesozoans.

### **5.Summary:**

In this lecture we have covered the origin of Metazoa as well as views expressed by many prominent scientists to explain the evolution of Metazoa from different groups of protozoa. Different theories proposed by various scientists such as Colonial theory, Syncytial theory and Polyphyletic theory were also discussed.