Anthozoa (e.g. anemones), and is best fitted for a floating life. Such symmetry has only 2 pairs of symmetrical sides. There are only 2 planes of symmetry, one through the longitudinal and sagittal axises, and the other through the longitudinal and transverse axises, which will divide the animal into equal halves.

4. **Bilateral symmetry.** In most higher animals, the longitudinal axis of body runs from the anterior end (head) to the posterior end (tail). There is a single plane, the *median longitudinal* or *sagittal* plane, through which the body can be divided into two similar right and left halves. This is called *bilateral symmetry*. Besides right and left sides, an upper or *dorsal* surface and a lower or *ventral* surface are also recognizable, which are unlike because they are exposed to different conditions.

Bilateral symmetry is characteristic of the most successful and higher animals, including the remaining invertebrates and all vertebrates. In most of them, the anterior end is differentiated into a *head.*

First phylum of animal kingdom to exhibit bilateral symmetry is the phylum Platyhelminthes. All bilaterally symmetrical metazoans were grouped together by Hatschek (1988-91) under the Division *Bilateria.* As already mentioned earlier, some Bilateria, such as echinoderms, display a radial symmetry which has been secondarily derived from bilateral ancestors due to assumption of an attached mode of life by adults.

Cephalization and Polarity

Bilateral symmetry is correlated with the locomotor movements brought about by these animals. One end of their body, usually containing the mouth, always moves forward in a particular direction. It is the first to come in contact with the environment, so that there is great concentration of nervous tissue and sense organs at this anterior end called *head.* The posterior or rear end is usually equipped with some locomotory organ. This modification of anterior or oral end of the animal into a definite head is called *cephalization* which is characteristic of most bilateral animals.

Cephalization is always accompanied by a differentiation along an antero-posterior or oral aboral axis. This condition is known as *polarity,* and it usually involves gradients which refers to ascending or descending activities between anterior and posterior ends.

Metamerism

[I] Meaning of metamerism

When the segmentation in bilateral animals, such as annelids, involves a longitudinal division of the body into a linear series of similar sections or parts, it is termed *metameric segmentation* or *metamerism.* Each section or part is called a *segment, somite* or *metamere* (Gr., *meta,* after; *meros,* part). Each metamere typically repeats some or all of the various organ units. The term metamerism is applied only when organs of mesodermal origin are so arranged. The primary segmental divisions are the body wall musculature and sometimes the coelom. This in turn imposed a corresponding metamerism on the associated supply systems (nerves, blood vessels and excretory organs). Longitudinal structures such as gut, principal blood vessels and nerves extend the entire length of body, passing through successive segments. While other structures, such as gonads, are repeated in each or few segments only.

Metamerism is always limited to the trunk region of the body. The *head* (or acorn) represented by the prostomium and bearing the brain and sense organs, and the *pygidium,* represented by the terminal part of the body which carries the anus, are not metameres. New segments arise just in front of the pygidium; thus the oldest segments lie just behind the head.

[II] Metameric animals

Metameric segmentation of the body, encountered for the first time in Annelida, is of considerable interest because the most successful groups of animal kingdom, i.e., Arthropoda and Vertebrata, also have their parts metamerically repeated. At least one group of Mollusca (Monoplacophora) also exhibits metamerism: Metameric segmentation seems to have evolved three times independently in animal kingdom (i) in the annelids-arthropods, (ii) in the chordates and in (iii) cestodes.

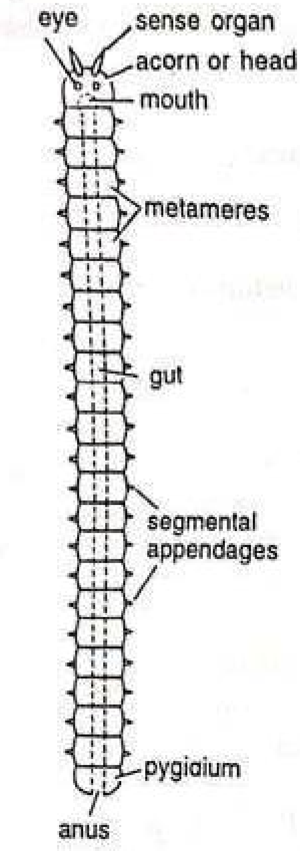


Fig. 2. A typical metameric animal, such as an annelid worm.

[III] External and internal metamerism

Metamerism is conspicuously visible in most annelids, both *externally* as well as *internally*. The common earthworm is a good illustration of both external and internal metamerism. Its body consists of a great number of similar segments and all the body organs, such as musculature, setae of locomotion, blood vessels, nerves, ganglia excretory organs and gonads, etc., are repeated segmentally. Even the coelom is divided into segmental compartments by the intersegmental transverse mesenteries, called *septa*. Only the digestive tract remains unaffected, but it also extends through every segment. In arthropods, metamerism is chiefly *external*, while man and other vertebrates show an *internal metamerism* of body muscles, nerves, certain blood vessels, vertebrae and ribs.

[IV] Complete and incomplete metamerism

In annelid worms, metamerism is *complete*, affecting practically all the systems. The metameres are essentially alike or *homonomous*, each having segmental blood vessels, nerves, nephridia and coelomoducts. This condition is called *homonomous metamerism*. On the other hand, higher animals such as arthropods and vertebrates, show *incomplete* metamerism. Because of division of labour, the segments or metameres of different regions of their body become greatly dissimilar. This is called *heteronomous metamerism*. However, incomplete metamerism should not be confused with the repetition of single organs such as shell plates or gills in certain unsegmented animals like molluscs.

In arthropods and vertebrates, metamerism is more complete and metameres are uniform and clear in the larval and embryonic stages. But, metamerism becomes obscure in the adut due to subsequent specialization or modification, so that the segments are no longer similar. It may result from simplification, by loss of metameres, by fusion of segments (cephalization), by differentiation between segments, by disappearance of organs, or by development of other structures, such as limbs. Heteronomous condition always appears first at the anterior end and progresses posteriorly. In segmented animals, varying degrees of specialization are met with some of which are extreme.

[V] Origin and evolution of metamerism (Theories)

How metamerism has been brought about is still doubtful. No satisfactory reason can be given for the origin of metamerism. Various hypothesis have been proposed to explain the origin of metamerism, but none is acceptable in the absence of convincing evidence. The main theories concerning the origin of metamerism emphasize primarily either repetition of organs or mesodermal segmentation and correlate i with the origin of coelom.

1. Pseudometamerism theory. This theory stresses that metamerism developed secondarily as a result of repetition of body parts, such a muscles, nerves, nephridia, coelom, blood vessels etc., in a single individual.

Such serial repetition of organs, such a testes, yolk glands and transverse connectives o two nerve cords, is seen in some elongat turbellarians and nemerteans. Later, a segmente condition was obtained by the formation

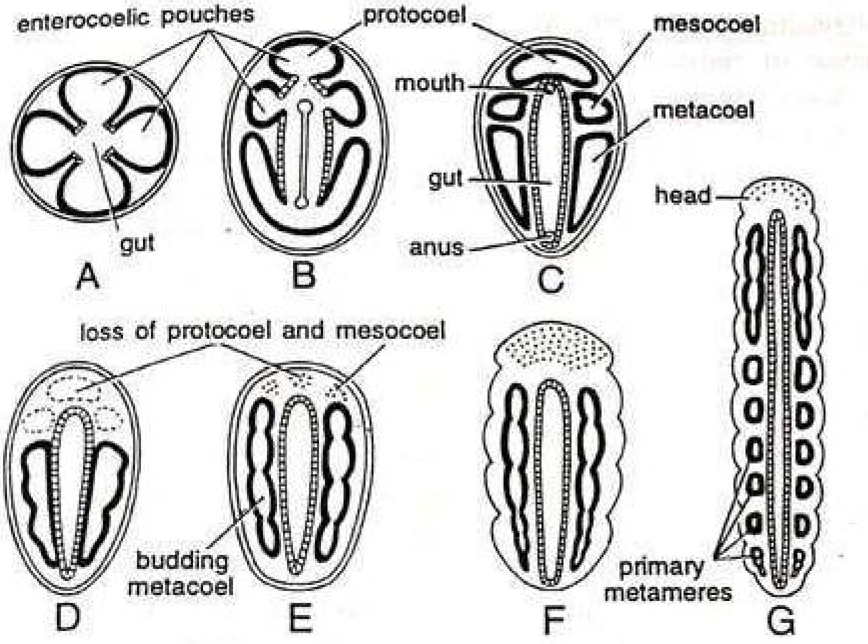


Fig. 3. Diagrams illustrating the Enterocoel-Cyclomerism theory of metamerism. A-C—Transformation of enterocoelic pouches of a radiate ancestor into coelomic pouches of a bilateral ancestor. D-E—Loss of protocoel and mesocoel. F-G—Subdivision of metacoel producing primary metameres.

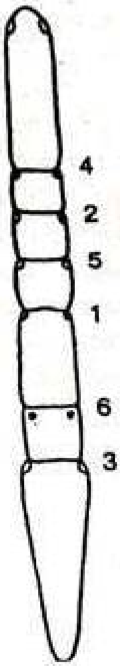


Fig. 4. Diagram showing development of a chain of zooids in rhabdocoel flatworm *Stenostomum*, according to Corm Theory. Numbers indicate sequences of fission planes.

cross-partitions in between them, so that each segment received a repeated part of each system. This process is witnessed even today in the formation of somites in larval and adult stages of some Annelida, in which cross-partitions develop after the basic segmentation is already laid down. Such segmentation was probably an adaptation for an undulatory mode of swimming. However, all ribbon-like animals swim in this vay, whether segmented or not. This theory is upported by Hyman (1951) and Goodrich.

2. Cyclomerism theory. Originally proposed y Sedgwick (1884) and greatly supported by Remane (1950, 1963), the cyclomerism theory is corollary of the enterocoelous theory for the rigin of mesoderm and coelom. This theory ssumes that coelom originated in some ancestral idiate actinozoan coelenterate, through the eparation of four gastric or enterocoelic pouches om the central digestive cavity or gut. Division two pouches resulted into three pairs of elomic cavities—the protocoel, mesocoel and etacoel, in the protocoelomate or ancestral elomate. Loss of protocoel and mesocoel led the unsegmented coelomates, such as molluscs d sipunculids. Later subdivision of metacoel produced primary segments, leading to the segmented annelids. The phylogenetic implication of this theory is that all bilateral metazoans were originally segmented and coelomate, and that the acoelomate unsegmented groups (flatworms, nemerteans) have lost these characters secondarily.

3. Corm or fission theory. According to this theory, metameric segmentation resulted when some non-segmented ancestor divided by transverse fission repeatedly or by asexual budding producing a chain of sub-individuals or zooids, united end to end due to their incomplete separation. This occurs in some Platyhelminthes and Annelida even today. Later, with the passage of time, these subindividuals or segments gradually became integrated morphologically as well as physiologically into one complex individuality. A segmented animal, according to this view, is a chain of completely coordinate subindividuals. This theory was supported largely during the 19th century and greatly elaborated by Perrier (1882). The chief objection to this theory is the lack of gradations of age in such a chain of zooids, which is true of segments in a metameric animal, such as an annelid. In platyhelminthes and scyphozoan strobilae the sequence of zooid formation is never serial, fission occurs always somewhere in the middle of the chain. In cestodes the proglottids are serially arranged but in a reversed order. Another objection is that reproduction by fission is usually confined to sessile animals, whereas the ancestors were probably free-swimming. Moreover, fission is a more extensive and disruptive division of body than is metamerism.

4. Embryological theory. It explains original metameric segmentation mainly as an embryological accident. It suggests that mechanical stresses in the mesoderm of the elongating embryo or larva resulted in its fragmentation leading to segmental repetition of mesodermal derivatives in the adult.

5. Locomotory theory. It is an amalgamation of pseudometamerism and embryological theories. It postulates that metamerism evolved as an adaptation to locomotion of different kinds. Annelid metamerism probably evolved as an adaptation for burrowing and chordate metamerism as an adaptation for undulatory, serpentine swimming movements.

R.B. Clark (1964) suggests that coelom evolved initially as a hydraulic skeleton to facilitate locomotion in response to the increasing body size. According to Clark, metamerism also evolved as an adaptation to burrowing in annelids. The ancestors of Annelida were in all probability elongate coelomate animals which burrowed in marine sand and mud. The evolution of compartmented coelom, due to development of septa and metameric segmentation, localized the function of the hydraulic skeleton. This allowed only part of the body to contract while other parts in the longitudinal axis relaxed. The locomotory movements can be more continuous and better controlled if the action of the bodywall muscles is localized, i.e., restricted to sections of the body. Metamerism permits such localization and accounts for the evolution of this condition in annelids. The localization enabled a strong peristaltic wave to propagate down the body, an efficient type of locomotion for worm-like burrowers. Thus, annelid metamerism is basically a modification of the coelom and the bodywall muscles. The initial segmentation of the coelom and bodywall muscles led to the subsequent segmental organization for the nervous, circulatory and excretory systems.

In chordates, metamerism evolved as an adaptation for undulating swimming movements. According to Berrill (1955), notochord evolved in the early chordates to provide support for the body, followed by metameric segmentation of bodywall musculature, so that alternate waves of contraction sweeping down the body could enable strong swimming. The initial muscle segmentation caused segmentation of the nervous and circulatory systems.

In cestodes, metamerism evolved as a response to reproduction. A reproductive package was formed which, once it had performed its function, was expendable. Proglottids are not additional to the body but are the body and so have to carry a complete series of organs.

Conclusion. Metameric segmentation met in one phylum is not necessarily similar to that in another. It probably arose independently in more than one line of evolution, each time in adaptation to a major advantage for the group in question. It probably evolved in response to burrowing in annelids, to swimming in chordates and to reproduction in cestodes. Therefore, we cannot device one explanation for all the cases of segmentation or think of a common ancestor of all sorts of segmented animals.

[VI] Significance of metamerism

It is not clear just how and why metameris evolved or how the primitive ancestors wer benefitted by it. Probably specialization metameres for particular functions showed a advancement.

It is possible that segmentation was initia in the musculature of an elongated swimmi worm. This breaking up of the body in metameres would facilitate swimming movemen Metamerism helps in locomotion in seve ways. The coordination of muscular action an fluid-filled coelomic compartments cause effici swimming and creeping which is advancement over the simple ciliary and creepi movement of lower invertebrates. Fluid-filled coelomic compartments also provide hydrostatic skeletons for burrowing. Precised movements can take place by differential turgor effected by flow of coelomic fluid from one part of the body to the other.

Another advantage of segmentation or metamerism is the opportunity for different segments to specialize for different functions, thus leading to a rapid evolution of high grade of organization. It is not clearly marked in annelids, but is well developed in arthropods. Metamerism has, therefore, contributed towards the greater complexity of animal bodies and rapid evolution of high organization in animals. Thus, some indication of primitiveness of an animal can be determined by the degree of segmentation it displays.

The fact that cestodes, annelids, arthropods and chordates have metamerism does not necessarily indicate a close relationship among them, for the metameric condition may have arisen independently by convergent evolution.

[VII] Pseudometamerism

True metamerism, as shown by annelids, must not be confused with the *pseudometamerism* or *strobilization* of the tapeworms. It refers to superficial segmentation and could be termed body annulation. True segments of annelids are laid down in the embryonic stage. Whereas proglottids of tapeworm are not true metameres but rather complete reproductive individuals produced by strobilization, a type of budding, with the buds remaining attached. *Table 1* shows the important differences between the two. However, the modern view now gaining favour is that cestodes are indeed metamerically segmented, although their metamerism is of a different type.

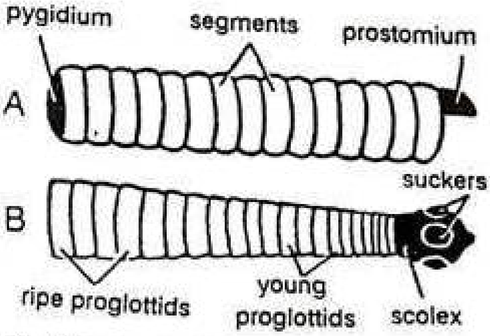


Fig. 5. Diagrams to illustrate differences between A – True metamerism of a generalized annelid. B – Strobilization of a generalized tapeworm.

Body Cavity or Coelom

[I] Definition

A body cavity can mean any internal space, or a series of spaces present inside body. Whereas coelom or true body cavity generally refers to a large fluid-filled space (cavity) lying between the outer bodywall and the inner digestive tube. It arises as a secondary cavity between two layers of embryonic mesoderm and contains most of the visceral organs.

Table 1. **Differences between True Metamerism and Pseudometamerism.**

True metamerism	Pseudometamerism
1. Number of segments is generally constant for each species; i.e., new segments are not added to the body after maturation except in asexual reproduction.	1. Number of segments or proglottids forming the body is not fixed as new segments are continually added throughout life.
2. Growth occurs due to simple elongation of pre-existing segments. The segments and ends of body have a fixed relationship to one another throughout life.	2. Growth occurs due to addition of new segments from a region of proliferation, just behind the scolex.
3. All segments are of the same age and at the same stage of development.	3. Proglottids differ from one another in age and in the degree of development.
4. Segments are functionally interdependent and integrated. Working in co-ordination, they preserve the individuality of body. For example, in a worm, during locomotion, muscles of each segment contract in a regular sequence so that rhythmical waves of contraction pass over the whole body which moves forward in an orderly manner.	4. Segments or *proglottids* are independent and self-containedunits, each having a full set of sex organs and a portion of excretory and nervous systems. They are productive units developed for detachment. A tapeworm represents a sort of colony or strobila made of a linear rows of incomplete individuals.

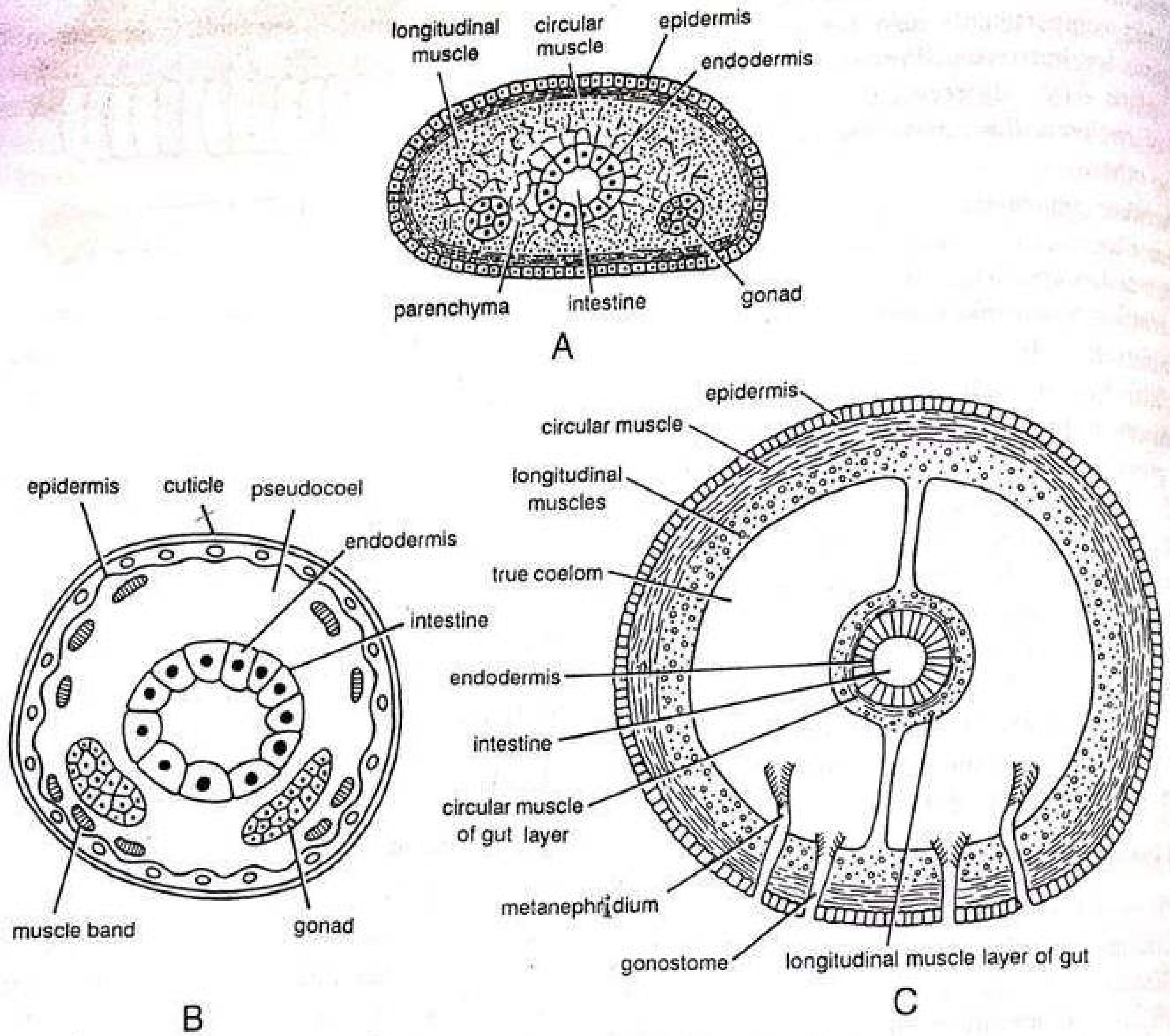
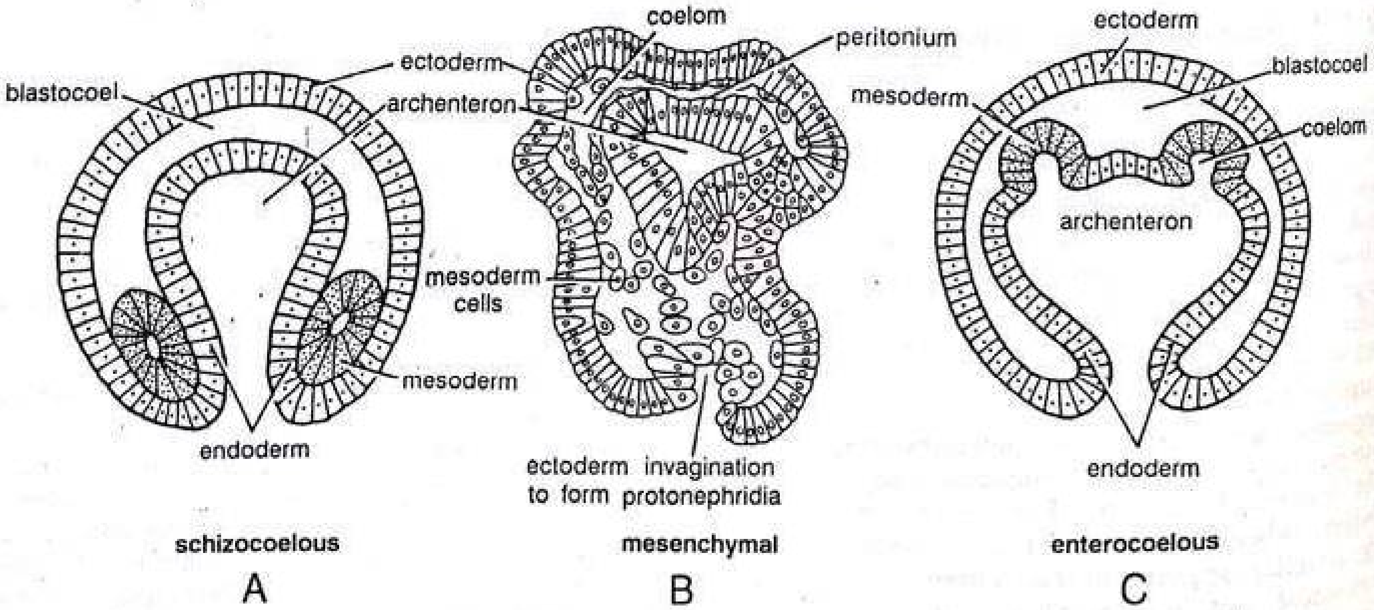


Fig. 6. Main types of body arrangements in Metazoa on the basis of coelom (In diagrammatic cross-sections). A—Acoelomate, with no body cavity. B—Pseudocoelomate, with body cavity not bounded by mesoderm. C—Coelomate or Eucoelomate with body cavity enclosed by mesoderm.



schizocoelous

A

mesenchymal

B

enterocoelous

C

Fig. 7. Three types of mesoderm and coelom formation. A—Schizocoelous. B—Mesenchymal. C—Enterocoelous.

Thus, a true coelom may be defined as a secondary body cavity, formed by the splitting of mesoderm during embryonic development and bounded on all sides by a definite coelomic epithelium or peritoneum. It contains a colourless coelomic fluid, the excretory organs open into it and the reproductive organs arise from its walls.

However, all animals do not possess a coelom, such as sponges, coelenterates, ctenophores, flatworms and proboscis worms. They are said to be *acoelomate.*

[II] Types of coelom

Two types of body cavities or coelom occur in Bilateria, *primary* and *secondary.*

1. Primary coelom. It is also called a false coelom or *pseudocoelom.* It is derived from the blastocoel of the embryo, rather it represents a persistent blastocoel ? Internal organs remain free in it since it is not bound by peritoneum or mesoderm. It is a space enclosed by ectoderm on the outside and endoderm (digestive tract) on the inside, and not by mesoderm on both sides. Such a pseudocoelom occurs in many worm-like animals including rotifers and roundworms, etc.

2. Secondary coelom. In more highly developed Bilateria, the blastocoel is gradually obliterated by the embryonic archenteron, without forming a primary coelom. Instead, a *secondary* or *true coelom* or *eucoelom* develops within the embryonic mesoderm and lined by a characteristic layer of flattened mesodermal epithelial cells, known as *peritoneum,* which also surrounds the internal organs of the body. A true coelom probably appeared for the first time in annelids.

[III] Coelomic division of Metazoa

On the basis of presence or absence of coelom, the Metazoa are divided into 3 major groups as follows :

1. Acoelomata. No body cavity or coelom is present. Embryonic mesoderm remains as a solid layer, space between endoderm (gutwall) and ectoderm (bodywall) is filled with mesenchyme and muscle fibres. Examples : Porifera, Coelenterata, Ctenophora, Platyhelminthes and Nemertinea.

2. Pseudocoelomata. Body space is a pseudocoelom or false coelom. It is a persistent blastocoel enclosed between outer ectoderm and inner endoderm, and not lined by mesoderm. Examples : Acanthocephala, Ectoprocta and Aschelminthes (Rotifera, Gastrotricha, Kinorhyncha, Nematoda, Nematomorpha).

3. Coelomata or eucoelomata. Body space is a true coelom, enclosed by mesoderm on both sides. Remaining phyla of Bilateria, from Annelida to Arthropoda, belong to Coelomata.

There are 3 different ways in which entomesoderm and coelom can arise during embryological development. Accordingly, Hyman (1951) further divides coelomate Bilateria in 3 groups as follows :

(a) Schizocoelomata. Coelom arises by a splitting of endomesodermal bands which originate from blastoporal region of larva and extend between ectoderm and mesoderm. It is a true coelom called a *schizocoel.* Examples : Most of the Protostomia (Annelida, Arthropoda, Mollusca, etc.).

(b) Mesenchymal coelomata. It is seen only in Phoronida in which mesenchymal cells rearrange to enclose a space or coelom, which is regarded an aberrant schizocoel.

(c) Enterocoelomata. Coelom arises in the form of mesodermal pouches from larval archenteron. After separation from endoderm, the pouches fuse and expand until they touch the gut and bodywall. Since the coelom arises from larval enteron, it is called an *enterocoel.* Example: Deuterostomia (Chaetognatha, Echinodermata, Hemichordata, and Chordata) and Brachiopoda.

[IV] Modifications of coelom

There are modifications of coelom in different animals. As already described, in a schelminths, it forms a *pseudocoelom* not lined with mesoderm. In arthropods, it is formed by scattered spaces, collectively known as *haemocoel,* in which blood circulates. In annelids, coelom is divided by *septa* into chambers corresponding to the somites. In mammals, coelom is divided by a muscular *diaphragm* into thoracic and abdominal cavities, with a separate *pericardial cavity* around heart.

[V] Significance of coelom

Evolution of coelom is of great significance in animals. It plays an important role in the progressive development of complexity of structure. It permits greater size and contributes directly to the development of excretory, reproductive and muscular systems of body. In a triploblastic animal (e.g. earthworm), the appearance of a perivisceral coelom between gut and bodywall leads to several advantages.

(1) It surrounds the internal organs like a water jacket and protects them from external shocks.

(2) It provides flexibility to the body. It provides space and gives the digestive tract and other internal organs freedom of movement and opportunity for enlargement, further differentiation and greater activity.

(3) The coelomic fluid often functions as a hydraulic skeleton and also serves as a circulatory medium for the transport and distribution of nutritive substances and gases.

(4) The excretory matter is collected into coelomic fluid and then passed out of the body through nephridia.

(5) The gonads arise from its coelomic epithelium and project into coelom. Ova and sperms are extruded through special gonoducts connecting the coelom with the exterior.

No doubt, the evolution of coelom made a major advance in the evolution of Metazoa. It is evident from the great increase in size and diversity in structure and ways of life met within coelomate phyla in comparison with acoelomate and pseudocoelomate phyla.

[VI] Evolution of coelom (Theories of Origin)

Origin of coelom in Metazoa is of great evolutionary significance. It has recently been extensively discussed by R.B. Clark (1964). There is no direct evidence of evolution of coelom available from palaeontology. There is only indirect evidence which is based mainly on the embryology of present day metazoans. This has been differently interpreted by different workers resulting in many conflicting theories about the origin and evolution of coelom. Out of these, there are 4 principal theories as follows :

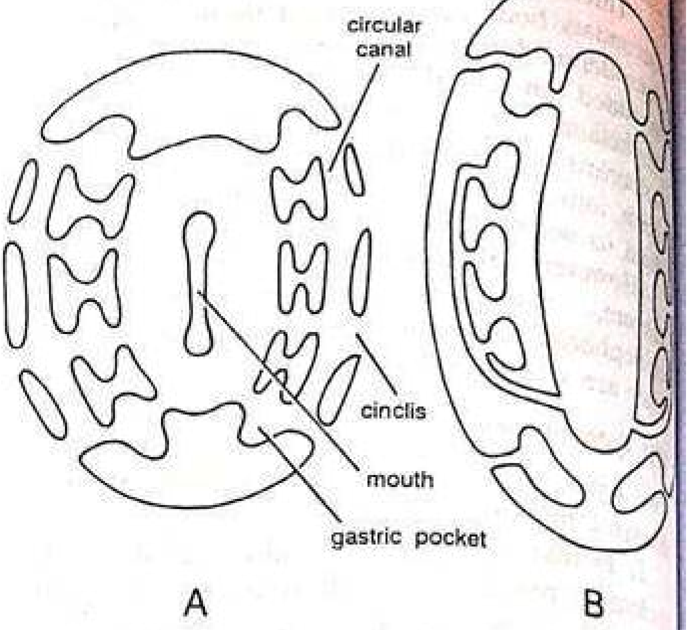


Fig. 8. Diagrammatic representation of coelom formation according to Enterocoel Theory. A—Formation of gastric pockets in an anthozoan. B—Gastric pockets become coelomic pouches.

1. Enterocoel theory. The theory holds tha the primitive mode of coelom formation wa enterocoelous. The idea was first proposed b Lankester (1875) and later modified by Sedgwic (1884) and till recently by Hartman (1963) and Ramne (1963). According to this theory, th bilateral metazoan ancestor of coelenterates ha gastric pockets which become separated from th central digestive cavity to form coelomic pouche (Fig. 8). However, the theory is mainly objecte on the following grounds :

(1) Gastric pouches occur in highly organize coelenterates, such as Scyphozoa an Anthozoa, which are not suitable for ancestra types.

(2) Sealing off of gastric pockets in the ancest would defeat the purpose for which they we formed, that is, for increasing the surfa area for digestion and absorption.

(3) Gastric pockets of coelenterates are n evaginations of gut endoderm, but form differently by ingrowth of bodywall-septa

2. Gonocoel theory. This is the most popu theory of origin of coelom. According to t theory, coelom represents a persistent expand gonadial cavity or gonocoel. The theory

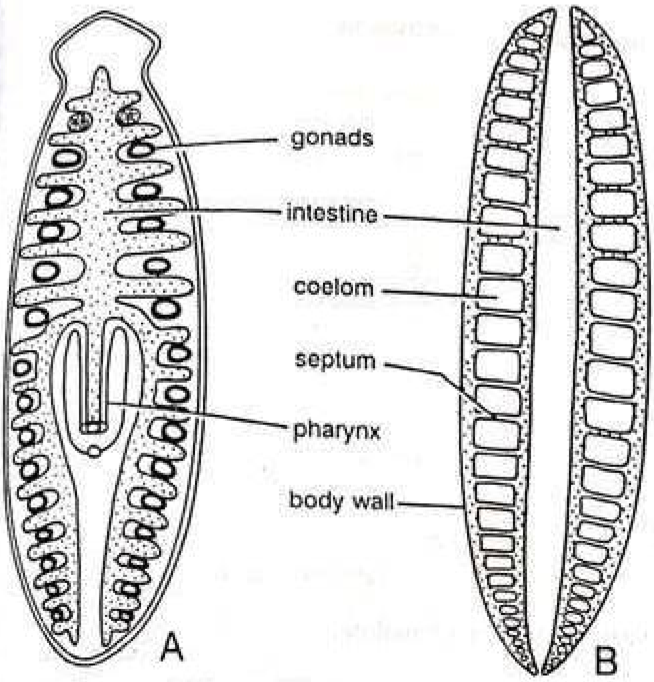


Fig. 9. Gonocoel Theory of coelom formation. A – Gonads alternating with intestinal branches in a triclad flatworm. B – Coelomic sacs or compartments in an annelid, formed by fusion of adjacent expanded gonads.

proposed in 1885 by Bergh, based on an idea earlier expressed in 1878 by Hatschek.

Meyer (1890) considered coelom initially unsegmented, arising from a single large pair of gonads. However Bergh and Lang (1903) believed that coelom initially arose in a segmented condition. In nemerteans and flatworms, especially in the triclad turbellarian *Procerodes lobata* (Fig. 9), they observed intestinal branches alternating with a linear series of gonads. If the intestinal branches withdraw and gonads enlarge with their walls meeting to become septa, they would resemble the row of coelomic compartments of an annelid. However, the chief defects of the Gonocoel theory are :

(1) It links the origin of coelom with that of metameric segmentation which is not acceptable phylogenetically.

(2) It is not supported by embryology because gonads do not arise before coelom.

(3) It does not account for unsegmented coelomate phyla, which are in majority, and there is no evidence that they have originated from segmented ancestors. Goodrich (1946) and Hyman (1951) have rejected the Gonocoel theory. They consider that metameric segmentation was preceded by a pseudometameric distribution of organs (such as gonads) in an elongated worm-like body.

3. Nephrocoel theory. According to this theory, proposed by Lankester in 1874, coelom originated as the expanded inner end of a nephridium. The theory is not seriously held because, (i) Protonephridia have been described in coelomates, and (ii) some coelomate groups, such as Echinodermata, do not have excretory organs.

4. Schizocoel theory. According to this theory, coelom has a mesenchymal origin and has no relation with nephridia and gonads of Lower Bilateria and endodermal pouches of Radiata.

Conclusion. None of the above theories satisfactorily explains the origin of coelom. Firstly, they do not explain the advantages of intermediate stages passed through during the course of evolution. Secondly, the connection between evolution of coelom and metameric segmentation together, has not been made clear. Thirdly, no exact nature of a coelom has been defined. Which cavities should be regarded coelomic and which not, has not been explained. Moreover, there is no evidence showing that secondary body cavity is homologous (with same origin) throughout the animal kingdom. Probably it is polyphyletic in origin. As Clark postulates, coelom might have arisen independently a number of times and in various ways in different animal groups– as a persistent blastocoel in pseudocoelomates, as an enterocoel in deuterostomes, as a schizocoel in protostomes, and as a gonocoel, etc.

Levels or Grades of Organization

All living plants and animals are made of cells. A cell is the unit of structure (histology) and function (physiology) of animals and plants, so that, differentiation of cells is always accompanied by physiological division of labour. Depending on the number and degree of complexity or specialization of cells present in individuals, we can divide animals into the following patterns, levels or grades of organization : (i) protoplasmic, (ii) cellular (iii) cell-tissue, (iv) tissue-organ, (v) and organ-system. These are approximately in the order in which they have evolved. Most animals fit