ON THE ORIGIN OF MOLLUSCS, THE COELOM, AND COELOMIC SEGMENTATION

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Abstract

Molluscs had a common origin with the annelids, as shown by remarkable ontogenetic similarities. Their common ancestors were non-segmented (non-eumetameric), acoelomate animals. Molluscs developed from the common stock through incorporation of the distinguishing molluscan characters such as the shell, mantle, mantle cavity, radula and ctenidium and annelids by the adoption of coelomic segmentation and of changes accompanying it. The assertion that molluscs hand ancestors with coelomic segmentation is contradicted by ontogenetic and anatomical facts as well as by theoretical considerations. The common molluscan-annelid stock most likely originated from ancestral flatworms; this is indicated by the developmental, and to a lesser extent, structural similarities between the flatworms, molluscs and annelids, and by the lower level of organization of the flatworms.

The coelom is a phylogenetically new structure in the molluscs and annelids, and was acquired independently in the two phyla. Coelomic segmentation also is a phylogenetically new acquisition of the annelids; it came about through developmental changes affecting the growth of the mesoderm bands. These views are the corollaries of ontogenetic considerations.

A widely held hypothesis concerning the origin of molluscs is the so-called annelid theory. According to Hyman (1951:4), the "annelid theory" states that ". . . annelids, arthropods, and chordates are closely related and [that] lower bilateral groups may have arisen from annelids by degeneration." In the present paper the term is restricted, referring to the theory that annelids gave rise to molluscs. Early proponents of this theory (Pelseneer, 1899; Heider, 1914; Söderström, 1925; Naef, 1926) believed that the serial repetition of certain organs in some molluscs represented vestigial segmentation, and claimed on this basis that molluscs descended from the segmented worms, annelids. They also believed that the far-reaching similarities in cleavage and early development were further indications of this relationship. More recent investigators added other viewpoints to these arguments. Thus, Garstang (1928) theorized that molluscs evolved from the trochophore larvae of the annelids by neoteny. Johansson (1952) aimed at giving a functional explanation to the annelid theory, when he proposed that the molluscs had lost the segmentation of their annelid ancestors in turning to living on hard, rocky surfaces of the intertidal zone, and assuming a creeping, crawling mode of locomotion. And finally, Lemche (1957) reported the discovery of a "living fossil," a primitive, segmented mollusc, *Neopilina galatheae* Lemche, 1957. Soon two more species of *Neopilina* were found, *N. ewingi* Clarke and Menzies, 1959, and *N. veleronis* Menzies and Layton, 1963. These discoveries were accepted by many as evidence for the segmented origin of molluscs (Lemche, 1959a, 1959b, 1960; Lemche and Wingstrand, 1959b; Portman, 1960; Fretter and Graham, 1962). Lemche went so far as to postulate that molluscs are more closely related to the arthropods than to the annelids, and that the latter arose independently of the former two groups. Fretter and Graham supported this argument by claiming that the coelom is primarily small in the arthropods as well as in the molluscs.

Opponents of the annelid theory have repeatedly pointed out the weaknesses of it. Thus, Nierstrasz (1922), Hammersten and Runnström (1925), Ivanov (1928, 1944), Beklemishev (1958a, 1958b), Boettger (1959), Steinböck (1962) and Hunter and Brown (1965) argued that molluscs cannot be considered as annelids with reduced segmentation, because of fundamental anatomical and developmental differences in segmentation. Odhner (1961) pointed out that molluscs attained segmentation independently of the annelids. Beklemishev (1958b), Boettger (1959), Steinböck (1962) and Hunter and Brown (1965) have argued convincingly that *Neopilina* cannot be considered proof for the annelid origin of molluscs, because of differences in the segmentations, because *Neopilina* is not at the root of the molluscan phylogeny, and for various other reasons. Yochelson (1963) reached a similar conclusion from paleontological studies; he maintained that the monoplacophoran molluscs (to which *Neopilina* belongs) do not constitute *the* basic molluscan stock; rather, they are a primitive group of the more advanced molluscs. The results of Schmidt's microscopic and crystallographic studies (1959) on the shell of *Neopilina* are neatly consistent with this conclusion. Further objections, not expounded in the literature, also can be brought up against the annelid theory. The theory does not explain why we must consider molluscan segmentation secondary and reduced, or why we must accept the ontogenetical similarities between molluscs and annelids as a proof of the annelid theory, when alternative assumptions also are possible. Weaknesses in Garstang's and Johansson's theory also are found, as I will show in a later section.

To supplant the annelid theory, Lang (1896), Nierstrasz (1922), and Graham (1955) proposed that molluscs evolved from flatworms or ancestors to the flatworms, completely independently of the annelids. Hammarsten and Runnström (1925), Boettger (1959 and Beklemishev (1963, on the other hand, argued that molluscs and annelids evolved together but separated from each other before the annelids acquired coelomic segmentations. Whereas, however, Hammarsten and Runnström believed that the common molluscan-annelid stock originated from the ancestors of the flatworms, Boettger thought that the common stock evolved from a group near the root of the aschelminths, and Beklemishev thought it evolved from "larval" coelenterates.

The claims of Lang, Nierstrasz and Graham that molluscs originated independently of the annelids overemphasize the similarities between the molluscs and flatworms and underemphasize those between the molluscs and annelids. Also, it is not certain whether some of the molluscan-flatworm similarities are due to close relationships or to parallel evolution. For these reasons, I reject these claims. It also seems doubtful that the construction by Beklemishev of hypothetical larval forms satisfying superficial morphological requirements is of any help. The ideas expressed by Hammarsten and Runnström and Boettger (that the ancestors of aschelminths came from ancestors of the flatworms), on the other hand, account both for the molluscan-flatworm and the molluscan-annelid similarities, and avoid making unwarranted and unnecessary assumptions. Therefore, they appear to represent "the truth," according to our present knowledge.

Thus, it seems that the problem of the origin of molluscs already has been solved. Many zoologists, however, perhaps even the majority, are either unaware of, or unwilling to accept, this answer. The present paper has been written with the purpose of summing up the arguments, elaborating upon those that were not explicit or expounded in due detail, adding some new arguments, and thereby presenting a unified and hopefully convincing argument for the case.

Discussion

It seems profitable to arrange the argument around the three main points of the theory followed here. These are: 1) molluscs and annelids had evolved together; 2) the molluscs separated from the annelids before they acquired the distinguishing molluscan criteria such as shell, mantle, mantle cavity, radula and ctenidium (Yonge, 1960; Morton and Yonge, 1964), and the annelids acquired coelomic segmentation; 3) the most likely ancestors of the common molluscan-annelid stock were the forms ancestral to the present-day flatworms.

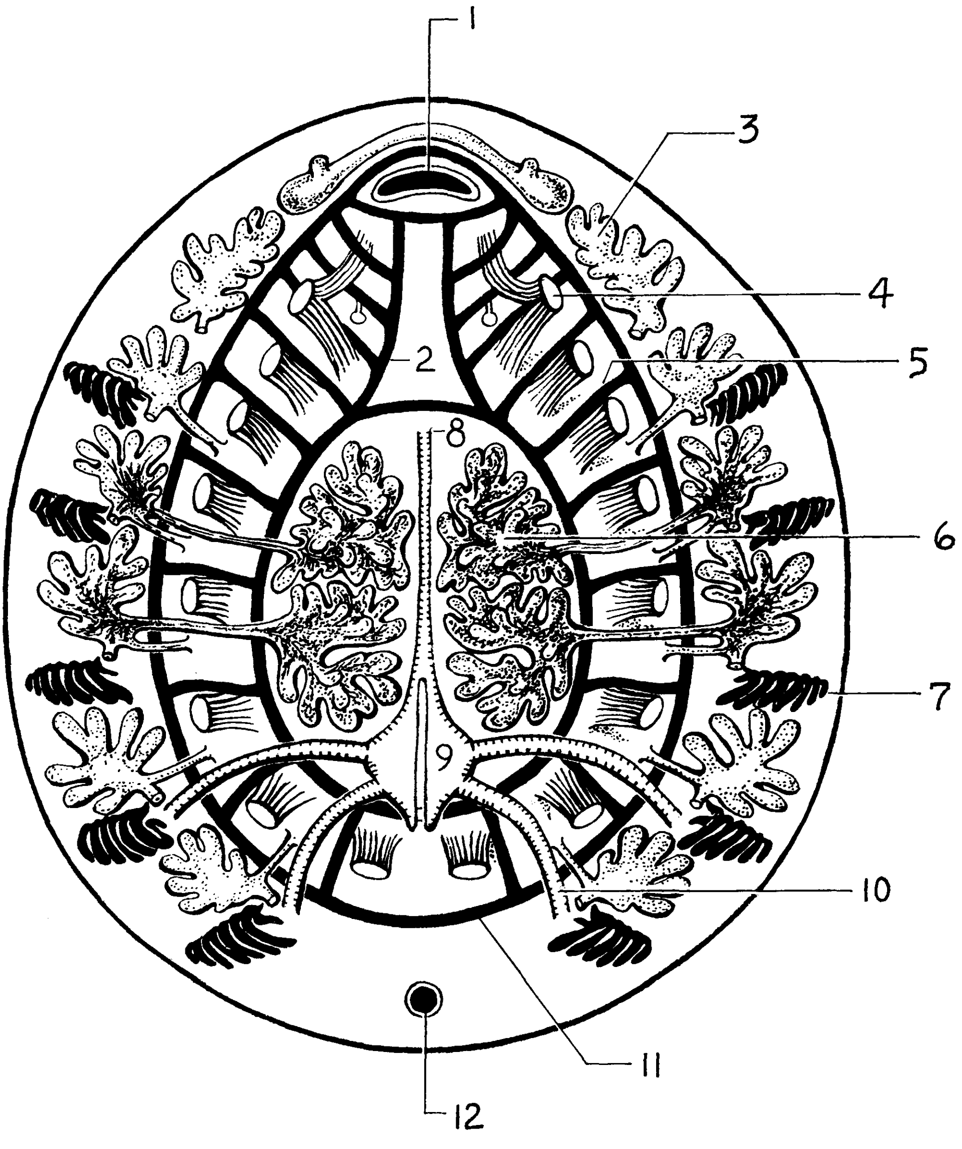

FIG. 1. Segmentation (pseudometamery) of the monoplacophoran mollusc *Neopilina galatheae*; diagrammatic. Notice that the various segmented organs occur in different numbers, and that there is only partial harmony in their arrangement. The coelomic cavity is represented by the pericardial (not shown) and nephridial cavities. (From Lemche and Wingstrand, 1959b, Galathea Rep. 3:9–71, with permission of the editor.) 1, mouth; 2, pedal nerve cord; 3, nephridium; 4, pedal retractor muscle; 5, commissure; 6, gonad; 7, gill; 8, aorta; 9, ventricle; 10, auricle; 11, lateral nerve cord; 12, anus.

The common origin of molluscs and annelids.—This contention is based upon the similarities between the molluscs and annelids in cleavage, embryonic development, and early larval stage. Both the molluscs and the annelids have spiral cleavage; the fate of certain cells is, with some exception, the same in the two groups; mesoderm bands arise from cell *4d* in both groups; and the early larval stage, the trochophore, is nearly identical. These similarities are accepted as indications of a genuine and close relationship by practically all zoologists (Hyman, 1951; Barnes, 1963). A consensus, admittedly, does not constitute a proof; it does give, however, the best support to the above view.

The developmental similarities in question were interpreted by some followers of the annelid theory (Naef, 1926) as supporting the contention that the molluscs evolved from the annelids. It is quite clear, however, that this claim is unwarranted. Similarities in the ontogeny only "prove" that the groups in question are closely related, but they do not "prove" the direction of evolution. On the basis of the developmental similarities alone, the direction could equally well be from molluscs to annelids, from annelids to molluscs, and from a common ancestor toward both. Only *differences* in the ontogeny could indicate direction; a primitive condition in one group, and a more advanced in the other, would indicate that evolution proceeded from the former to the latter.

There are two obvious, although slight, differences between the molluscan and annelid ontogenies. One is the formation of the crosses, the other that of the coelomic cavities. The cells forming the major part of the equatorial ciliary band of the trochophore larva are arranged, at an early stage, in the shape of a cross centered on the animal pole; the arms of the cross are radial in molluscs, interradial in annelids, and they are derived from cells $1a^{12}$–$1d^{12}$ in molluscs, from $1a^{112}$–$1d^{112}$ in annelids (Nierstrasz, 1922). Now, if we could ascertain which type of cross formation were the more primitive, we could possibly draw some conclusion as to the direction of evolution; but, unfortunately, nothing is known on this subject. In the formation of the coelom (p. 158), the direction seems to have been from molluscs to annelids. Thus, summing up, the developmental similarities indicate close relationship between the molluscs and annelids, they suggest that in some respects molluscs are more primitive than annelids, but they do not support the claim that molluscs developed from annelids.

The separation of molluscs and annelids.—The separation of molluscs and annelids must have happened at or before the time molluscs and annelids acquired their distinguishing features (Hammarsten and Runnström, 1925; Boettger, 1959), but not after. There is no evidence whatsoever for the assumption that annelids had ancestors with characteristic molluscan features, or that molluscs had ancestors with characteristic annelid feature. Therefore we have to assume that each line acquired its own characteristic features after the separation of the two lines.

Most zoologists would agree with the first part of this conclusion, that annelids did not come from molluscs; but many would also maintain that molluscs did have segmented ancestors. They argue that a) primitive molluscs are segmented, and that b) this must mean that molluscs descended from ancestors with a more complete segmentation.

The decision whether the primitive molluscs, or the molluscs in general, are or are not segmented depends upon one's definition of segmentation. Adherents of the annelid theory consider segmentation to be any repetition of organs along the main axis of the body. Thus, they say that the molluscs are segmented. Evidently, these workers consider the segmentation of molluscs of the same kind as that of the annelids. Many others, however, consider the serial repetition of certain organs, without corresponding coelomic subdivisions and without the developmental characteristics of the annelid segmentation (see below) merely regularization metamery or pseudometamery; and these others distinguish between this and the mesodermal or coelomic or true segmentation, referred to henceforth as eumetamery, of the annelids (Ivanov, 1928, 1944; Beklemishev, 1958a, 1958b; Steinböck, 1962; Clark, 1964; Hunter and Brown, 1965). In this view, then, the molluscs lack true segmentation or eumetamery and have only pseudometamery.

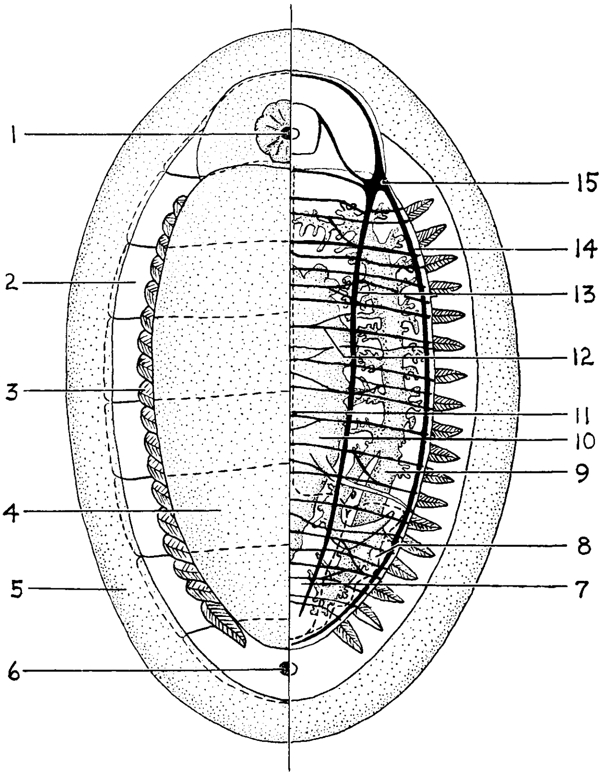

FIG. 2. Segmentation (pseudometamery) of a polyplacophoran mollusc (chiton); diagrammatic. Notice that the number and arrangement of the various segmented organs, as in *Neopilina*, is not matching. The coelom is represented by the pericardial (not shown) and nephridial cavities. (Redrawn from Barnes, R., 1963, Invertebrate zoology, after Haller, Lang and Yonge, with permission of the author and the publisher.) 1, mouth; 2, shell plate; 3, gill; 4, foot; 5, girdle; 6, anus; 7, ventricle; 8, auricle; 9, kidney; 10, gonad; 11, aorta; 12, commissure; 13, pedal nerve cord; 14, lateral nerve cord; 15, brain.

The differences between the pseudometamery of molluscs and the eumetamery of annelids are anatomical, ontogenetical and phylogenetical. There are three main anatomical differences (Beklemishev, 1958a; Boettger, 1959; Steinböck, 1962). First, the molluscan coelom is not segmented (figs. 1 and 2; also see p. 158 about the nephrocoel), whereas in annelids, there is typically a pair of coelomic sacs in each segment (Fig. 3). The molluscan coelom is not even fully homologous with the annelid coelom; this topic may be discussed more profitably later, after the ontogeny has been described. Second, in molluscs the various segmented organs may occur in different numbers. Thus, the monoplacophoran mollusc *Neopilina galatheae* has two pairs of atria, five pairs of gills, two pairs of gonads, six pairs of nephridia, eight pairs of pedal retractor muscles and ten pairs of nerve commissures; these numbers may slightly be different in *N. ewingi* and *N. veleronis*. Chitons have eight shell plates with attached muscles, and a varying, sometimes very great, number of gills and nerve commissures. Furthermore, the gills of chitons are not even paired, strictly speaking; their number may be different on the right and left sides in as many as 48% of the specimens in some species (Hunter and Brown, 1965). In contrast to this, the segmented organs of the annelids, the parapodia, ganglia, commissures, circular blood vessels, nephridia, coelomoducts and coelomic sacs occur in identical numbers (or multiples), and are strictly paired. Third, the arrangement of the various segmented organs is less regular in the molluscs than in the annelids. It is true that *Neopilina* exhibits an almost completely orderly arrangement; but in chitons the gills are unevenly distributed between the body segments, as determined by the shell plates, and the commissures are arranged discordantly from both the gills and the shell plates. Thus, we have to maintain that molluscs as a group have a less orderly arrangement than do annelids.

The ontogenetic differences between molluscan and annelid segmentation are as follows. In molluscs, specifically in the chiton *Acanthochiton discrepans* Brown (Hammarsten and Runnström, 1925; Raven, 1958), coelomic cavities do not develop inside the mesodermal bands, and the latter do not become metamerized; instead, they differentiate into various organs, among them the pericardial-nephridial complex. It is true that Naef (1926), following earlier authors, speaks of coelomic cavities in the mesodermal bands, but Hammarsten and Runnström categorically deny the existence of these when they write: "*. . . die von Kowalewsky beschriebenen Cölomsacke nicht existieren . . .*" (1925:277). These authors assume that Kowalewky mistook the nerve strands, the liver anlage, etc., for the mesodermal bands. Raven, in his comprehensive work on molluscan development (1958), follows Hammarsten and Runnström. According to these authors, a single coelomic cavity appears in chitons, in the anlage of the pericardial-nephridial complex. This cavity has, at the beginning, a single pair of ducts, which will become the nephridia; the genital ducts appear only later, and primarily from ectodermal sources, not from the mesoderm which makes up the pericardial-nephridial complex. The coelomic cavity may become partially subdivided into pericardial and nephridial cavities, but it is the only cavity to appear. In the annelids, on the other hand, a series of coelomic cavities appear in the mesodermal bands. Therefore, the molluscan coelom is not entirely homologous with the annelid coelom. It qualifies as a coelom since it is surrounded by mesodermal tissue, but this is the extent of its homology with the annelid coelom.

We turn now to the development of other segmented organs. The shell plates first appear in the early larva; they originate by the simultaneous subdivision of the originally undivided shell gland into six plates. Later, one more plate will be added anteriorly and another posteriorly, and thereby the definitive number of eight will be established (Beklemishev, 1958a; Hunter and Brown, 1965). The gills appear weeks later, after thirty days of life; first the posterior gills appear, and, as the animal grows, more gills are added anteriorly (Hunter and Brown, 1965). The nerve commissures originate in a different manner again (Hammarsten and Runnström, 1925; Raven, 1958). Isolated cells from the cerebral ganglia migrate posteriorly, dividing mitotically as they go, and form thereby the lateral and pedal connectives and the ganglia thereupon. From the connectives, the commissures grow out presumably by this same method. Hammarsten and Runnström mention, however, that in other molluscs the ganglia in the body and the foot arise from local ectodermal thickenings, and the connection between them is established secondarily (1925:311). They presume, however, that the manner of growth observed in chitons is the primary, primitive method. We may conclude this section saying that the development of the various segmented organs is not coordinated in molluscs; the segmented organs develop from different rudiments, at different times and different rates.

The ontogeny of the annelid segmentation is completely different (Ivanov, 1928, 1944; Beklemishev, 1958a; Dales, 1963). We will consider the presumably primitive mode of development, found in the oligochaetes and some polychaetes; but it must be pointed out that the other polychaetes also follow a basically similar course of development, the differences being inconsequential from the point of view of the present argument. In this primitive ontogeny of segmentation, the mesoderm of the early embryo, derived from *4d*, becomes metamerically subdivided into a small number of segments, depending upon the number of the ectodermal metameric organs. The subdivision of the mesoderm of the early larva is a simultaneous process. Not so the segmentation of the mesoderm of the metatrochophore stage. This mesoderm also is derived from the cell *4d* (in oligochaetes and some polychaetes); it forms two bands, one on each side of the body. Inside the mesodermal bands, a series of cavities appear, in an anterior-to-posterior order. Each pair of cavities plus the surrounding tissues develop into a segment; thus, each segment arises as a unit. The cavities become the coelomic sacs, while their lining differentiates into the peritoneum, the musculature of the gut and the body wall, the blood vessels and the coelomoducts; from the ectoderm of each segment, the epidermis, the ganglia, the nerve strands and the chaetae develop. At the posterior end of the mesodermal bands, cell division continues and new coelomic cavities appear, and thereby new segments are continuously produced. Clearly, molluscs do not have this kind of segmentation.

The presumed phylogenetic differences between the molluscan and annelid segmentation are as follows. The molluscan segmentation (pseudometamery) was probably achieved in two stages. These can be sharply distinguished for didactic purposes but could have been concomitant in reality. In the first stage, there was an increase in the number of certain organs; this may have come about by actual multiplication of an organ, or by the breaking up of one large organ into several smaller ones (the nephridia of *Neopilina* may exemplify this). The increase was not necessarily equal; certain organs were multiplied to a greater extent than others. In the second stage, there was a regularization of the multiplied organs in number and position, so that they became arranged according to a unified plan. The second stage is now often incomplete. The annelid segmentation (eumetamery), on the other hand, came about in

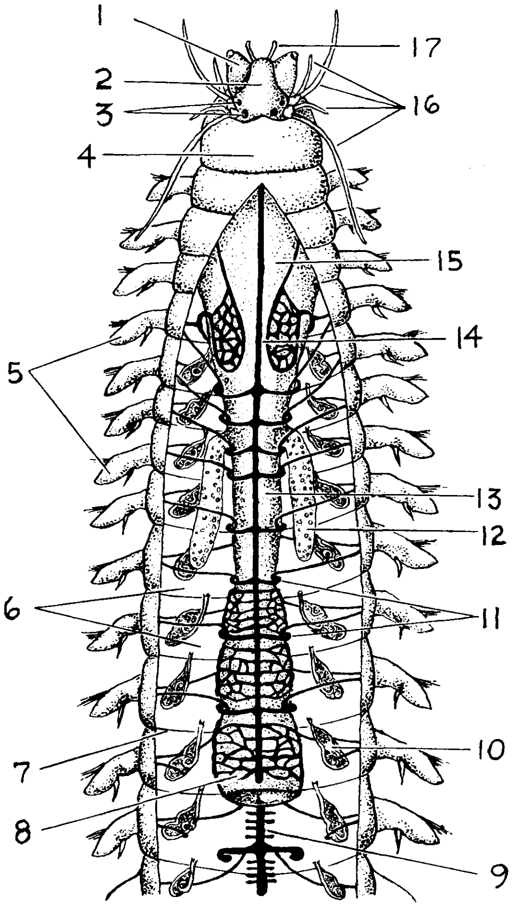

FIG. 3. Segmentation (eumetamery) of the polychaete annelid, *Nereis virens*. Only the anterior region is shown; the total number of segments may reach 200. The dorsal body wall has been partially removed; the ventral nervous system is not shown. Notice that the number and arrangement of the various segmented organs are matching, and that there is a pair of coelomic sacs in each segment. (From Brown, F. A. [ed.], 1950, Selected invertebrate types, with permission of the publisher.) 1, palp; 2, prostomium; 3, eyespots; 4, peristomium; 5, parapodia; 6, coelomic sacs; 7, septum, separating coelomic sacs; 8, stomach; 9, ventral blood vessel; 10, nephridium; 11, lateral blood vessel; 12, esophageal coecum; 13, esophagus; 14, dorsal blood vessel; 15, pharynx; 16, cirri; 17, tentacle.

one stage, by the production of identical sets of organs in great numbers; thereby the number and arrangement of the various segmented organs immediately exhibit a unified, segmented pattern (Beklemishev, 1958a).

The above presumptions are supported by ontogenetic considerations. As ontogeny shows, the segmented organs of the annelids develop in sets, each set differentiating out from an ectodermal and mesodermal block of cells. The segmented organs of the molluscs, on the other hand, develop from different rudiments, at different times and different rates from one another. Furthermore, in the various molluscan groups that exhibit segmentation (monoplacophorans, polyplacophorans, some gastropods and cephalopods), different organs may be multiplied, and the regularization may be on quite different levels. Thus, the monoplacophoran mollusc *Neopilina galatheae* has six organs in multiple numbers (Fig. 1), which are quite harmoniously arranged; chitons have their shell plates, musculature, gills and commissures multiplied, but only the shell plates and the muscles are harmoniously arranged; some prosobranch snails have but one structure, the commissures, multiplied; tetrabranch cephalopods have their gills and atria multiplied, which are in complete harmony. Had the molluscan segmentation evolved in the same manner as the annelid segmentation, this chaotic pattern would make no sense.

Most of the differences between molluscan and annelid segmentation were known by the adherents of the annelid theory. Thus, Naef wrote (1926:41): "*Man muss nun zugeben, dass ein solcher Prozess* [segmentation of the mesoderm bands] *bei Mollusken nicht in typisch unverkennbarer Form beobachtet ist . . . . Weiter ist zuzugeben, dass von einer Segmentierung des Cöloms in zahlreiche und regelmässige Abschnitte und weiter von einem Cölom vom funktionellen Character dessen wohlausgebildeter Anneliden bei Mollusken keine Rede sein kann.*" But, in spite of these admissions, he equated the segmentation of the molluscs and the annelids, and tried to derive the former from the latter. And, similarly, Lemche and Wingstrand wrote (1959b:66): "We do not know whether the dorsal coelom is metamerically subdivided or not, but the metameric tendency is present in the gonads which may be regarded as part of the coelomic system." And (p. 67): "The complete organization and the presence of a heart in the last segment makes it [the last segment] very different from an arthropod or annelid telson, indicating that the metameres in *Neopilina* are not formed by a rhythmic activity of a terminal growth centre. The more probable explanation is that the mesoderm in the body region of *Neopilina* is simultaneously subdivided in the manner characteristic of the most anterior segments in annelids and arthropods [i.e., those formed in the early larva]." But, nevertheless, they conclude (p. 66): "The metamerism of *Neopilina* is so regular and is present in so many organ systems that there is no reason to regard it as different from that of annelids and arthropods." Portman (1960) repeats this argument almost word for word. Extending this argument, one could maintain that there is no reason to regard the segmentation of the cestodes or the vertebrates as "different" from that of the annelids and arthropods, because all are very regular.

We may conclude this section saying that the molluscan segmentation differs from the annelid segmentation in anatomy, ontogeny and phylogeny; the molluscan segmentation is pseudometamery, the annelid eumetamery.

The second assumption of the annelid theory is that molluscan segmentation developed through reduction from a previous fuller segmentation. Generally this is interpreted as meaning that the molluscs developed from annelids that lost their segmentation. This assumption is not only hypothetical (Hammarsten and Runnström, 1925) but also erroneous. First of all, the segmentation of molluscs is different in kind from that of the annelids, and thus irreducible from the latter. A second considera-

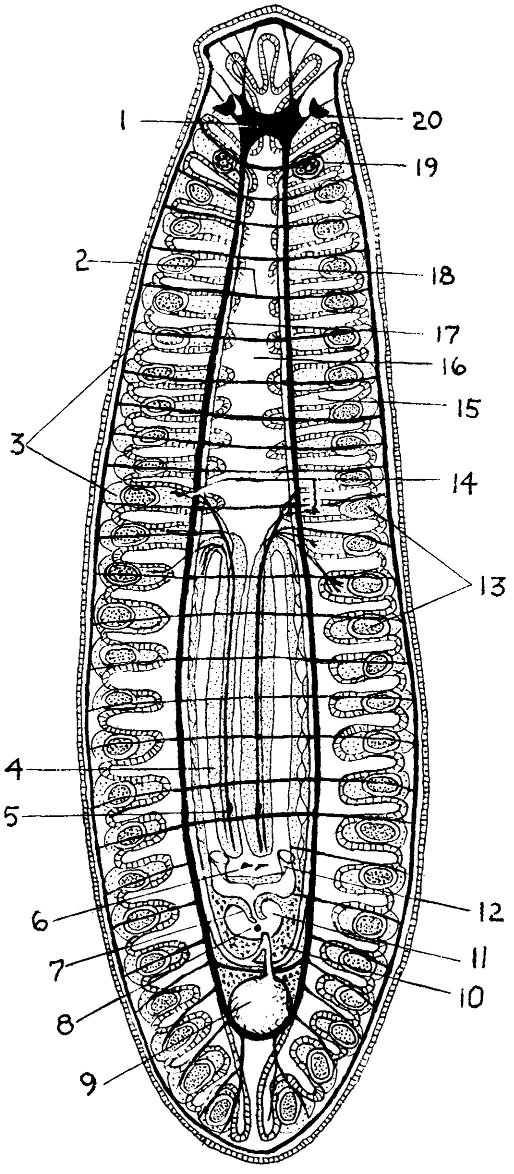

FIG. 4. Segmentation (pseudometamery) of the triclad flatworm *Procerodes lobata*. Excretory system omitted. Notice that the number and arrangement of the commissures does not match that of the other segmented organs, and that there is no coelom at all. The segmentation of flatworms is of the same kind as that of the molluscs. (From Lang, A., 1881, Mittheil. Zool. Stat. Neapel 3:187–251, with permission of the publisher.) 1, brain; 2, commissure; 3, yolk gland; 4, proboscis; 5, circular nerve of proboscis; 6, mouth; 7, penis; 8, genital opening; 9, albumen gland; 10, uterus; 11, genital atrium; 12, sperm duct; 13, testes; 14, salivary glands; 15, intestinal diverticulum; 16, intestine; 17, oviduct; 18, nerve cord; 19, ovary; 20, eye.

tion is as follows. An atypical or incomplete segmentation such as that of the molluscs may be interpreted in two different ways: either as primarily incomplete or as secondarily reduced. The former is the simpler interpretation, the latter the more complicated. On the principle of parsimony we should accept the simpler interpretation as valid unless some evidence compels us to do otherwise. No such evidence has been brought forth by the annelid theory. Therefore, we should consider valid the simpler interpretation, that the molluscan segmentation is primary.

In Johansson's opinion however, this is not so. He maintains that the segmented coelom of the presumed ancestors of molluscs was reduced when the latter became ". . . adapted to hard bottoms in the surf region and has developed a foot and a shell . . . . In this connection the segmented coelom, being no longer of importance for locomotion, was reduced to form a single cavity with one or two pairs of ducts" (1952: 290). He considers the constancy in the number of the shell plates of chitons as the proof ". . . of a formerly complete true metamery as in the Arthropoda" (p. 287). He fails to explain why the constant number of the shell plates has such significance. He did not explain either why he disregarded the facts that, during ontogeny, the segmentation and the subsequent reduction of the coelom can be followed step-by-step in the arthropods, not at all in the molluscs, or why life on the rock bottom in the surf zone had to lead to the reduction of segmentation. The truth is that coelomic segmentation is fully compatible with life in such habitats, as shown by the fact that ". . . polychaetes are extremely numerous in the rocky regions along the shore . . ." (McGinitie and McGinitie, 1949:194).

Contrary to Johansson's opinion, a comparison of the locomotory mechanisms of the molluscs and annelids makes it appear unlikely that the molluscs ever had coelomic segmentation. The argument is as follows. The locomotion of the lower molluscs, such as the polyplacophorans and primitive snails, is rather primitive in kind; these animals slide over the substrate on a sheet of slime deposited by the mucous glands of the foot, by ciliary action or by locomotory waves executed primarily by the longitudinal muscles of the sole (Elves, 1961; Clark, 1964). The annelids have a more efficient locomotory mechanism, namely, a form of peristaltic motion. These animals have two muscle layers beneath the epidermis: an outer layer of circular muscles and an inner longitudinal layer. By contracting the circular muscles in a certain segment or segments, pressure is exerted against the hydraulic skeleton (coelomic fluid), and this in turn stretches the relaxed longitudinal muscles, leading to the elongation of the segment or segments in question. Conversely, the contraction of the longitudinal muscles and the resulting stretching of the circular muscles will cause the shortening and thickening of the particular bodily region. By stretching out a certain region, anchoring it, and then pulling up the remainder of the body, the animal will be able to move. It should be emphasized that peristaltic motion could be carried out with a single, unsegmented coelomic cavity, or even without one (simply by using the tissues of the body as a hydraulic skeleton, as in nemertines); but the division of the coelomic cavity into many, at least partially isolated, compartments makes the system more controllable, maneuverable, and thus more economical (Clark, 1964).

The loss of such an efficient system is understandable in arthropods, which acquired exoskeleton, some endoskeleton, skeletal muscles, and, most of all, jointed appendages, availing themselves of a locomotory mechanism superior to peristalsis. But it is difficult to see why the primitive molluscs should have abandoned peristaltic locomotion and regressed to the more primitive ciliary-mucous-muscular locomotory mechanism that they still own today.

Actually, evolution of the molluscs proceeded not toward but away from this primitive mechanism. Cephalopods developed a very advanced jet-propulsion system, and the bivalves evolved a mechanism which, similarly to that of the annelids, utilizes the the body fluids as hydraulic skeleton. The latter will be considered more closely. The foot in the bivalve molluscs contains a large, blood-filled cavity, the contents of which, when put under pressure by the contraction of the powerful adductor muscles, cause the dilation of the stretched-out foot; the latter is thereby anchored in the sand, and the rest of the body can be pulled to it (Trueman, 1960). Thus, bivalves developed a way of digging, burrowing in the sand, which is superficially similar to that of the annelids. The differences are that, whereas the cavity being utilized is coelomic in nature in the annelids, it is haemocoelic in the molluscs; the cavity is segmented in the annelids, unsegmented in the molluscs; and the antagonistic muscles are located differently. The two animal groups thus have evolved, in response to similar environmental demands, superficially similar locomotory mechanisms; they represent a case of convergent evolution, rather than regression.

According to Morton (1958:26, and *in litt.*, 1966) Garstang in prose and verse (1928, 1962) and conversation adumbrated the idea that the molluscs developed from the annelids through neoteny; that is to say, molluscs are annelid larvae which became sexually mature. According to Morton this can explain why the segmentation (eumetamery) of the presumed annelid ancestors is not observable in molluscs: because the post-trochophoral stage, in which eumetamery ensues, is omitted from the life cycle. Garstang's article (1928) indeed implies that the molluscs developed from the larvae of the annelids when he says (p. 88): ". . . the Veliger [a post-trochoporal larval stage, characteristic of the molluscs] . . . is a trochosphere [trochophore] transformed by the incorporation of Molluscan characters . . ." (p. 88). It is also true, however, that this is far from proposing a theory on the origin of molluscs. But whether Garstang elaborated upon it or not, I doubt that neoteny could be the means by which the molluscs developed from the annelids. First, because molluscs have, in their life cycle, a genuine and sexually immature trochophore stage; one who assumes that the adult stage corresponds to a sexually mature trochophore, has to explain the presence in the life cycle of this "supernumerary" trochophore. Second, to claim neoteny, one ought to have a good agreement between the larva of a certain group and the adult of another, to which the former supposedly gave rise. In some more widely accepted cases of neoteny this is actually the case; thus, the coelenterates' planula larva is remarkably similar to the flatworm adult, and the diplopod larva to the insect adult (Hyman, 1951; Hand, 1963; de Beer, 1946). In the annelid trochophore and the molluscan adult, however, the similarity could not be less. Thus it seems safe to say that molluscs are not neotenic annelids.

We may conclude this section saying that evidence is lacking for the assumption that the segmentation of molluscs (pseudometamery) arose from the segmentation of the annelids (eumetamery) through reduction. The two kinds of segmentation are fundamentally different, one cannot be reduced from the other. The explanations that the reduction and loss of segmentation in molluscs was due to functional reasons or neoteny are groundless.

The origin of the molluscan-annelid stock.—The third topic to be discussed is: where did the common molluscan-annelid stock originate? One possible answer is, from the flatworms, or, more accurately, from the ancestors of flatworms (Hammersten and Runnström, 1925; Boettger, 1959). The evidence for this view comes from the similarity in cleavage between the flatworms, molluscs and annelids, and from the fact that flatworms are on a lower level of organization than are the other two groups.

The similarities in cleavage are widely acknowledged (Nierstrasz, 1922; Naef, 1926; Hyman, 1951); typically, flatworms are said to conform to the spiral cleavage pattern, found in molluscs and annelids. Deviations from this pattern occur—e.g., having two blastomeres instead of four—but these are regarded as secondary modifications (Ax, 1963; Steinböck, 1963). Further similarities between the flatworms and the molluscs also have been noted; thus, the structure of the nervous system, the organzation of the musculature, body wall and the manner of locomotion based thereupon, and the mode of digestion (primarily intracellular) are remarkably similar in the two groups (Nierstrasz, 1922; Graham, 1955).* As Hartman (1963) emphasized, however, similarities in lower levels of organization can easily owe to analogous solutions of the same problems by unrelated groups. Thus, the manner of locomotion, or the prevalence of intracellular digestion are not unequivocal proofs of relationship. The structure of the nervous system may be a better indicator of the assumed relationships (figs. 1, 2, and 4).

The flatworms are said to be on a lower level of organization than molluscs and annelids: they lack a coelom, anus, circulatory system, and have a very simple nervous system and primitive locomotory mechanisms. The molluscs, and particularly the annelids, are definitely on a higher level in most or all of these features. Some authors argue, though, that the simplicity of the flatworms is secondary, the result of regression from coelomate animals (Ax, 1963; Remane, 1963); but their theories are emphatically rejected by many (e.g., Beklemishev, 1963). Thus, we may conclude that evolution proceeded from the flatworms toward the molluscs and annelids.

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* The fact that the annelids do not share these similarities does not contradict the flatworm origin of the molluscan–annelid stock; the annelids, with the "invention" of coelomic segmentation, have radically departed from the flatworm–molluscan type of organzation, in structural and functional aspects.

The common ancestors of the molluscs and annelids may be reconstructed from the features common to, or typical of, the primitive molluscs and annelids, as follows. They were small, probably pseudometameric, animals without a coelom (p. 156); with a ciliated body, a one-way alimentary canal and a primarily intracellular digestion; probably with no circulatory system; with sexes separate, cleavage spiral, and trochophore larva; living in marine, benthic habitats.

A different origin for the molluscan-annelid stock was proposed by Beklemishev (1963). He began from a comparison of the planula stage of the coelenterates with the adult stage of the flatworms (turbellarians) and the protrochophore stage of the annelids (the latter he took as representatives of the trochophoric animals or Trochozoa, to which annelids, molluscs, etc., belong). The first two structures are so well known that they need not be described here. The protrochophore, according to Beklemishev (p. 240), ". . . is a protaxial larva with an aboral sense organ and a primary mouth opening on the oral pole . . . . [it] has a nervous system of the orthogon type, situated radially around the main axis of the body. . . . [In] all these respects . . . [it is] similar to the Turbellaria and, on purely promorphological grounds, to the planula of the Coelenterata . . . . Whereas the mouth in the Turbellaria is a small opening, . . . the primary mouth opening or blastopore of the protrochophore forms a narrow slit . . . . When the blastopore closes, the definitive mouth and anus are formed at its ends and the physiologically ventral side is formed along the whole blastopore. The circumblastoporal nervous plexus gives rise to the ventral nervous stems of the Trochozoa . . . . The Turbellaria do not possess anything homologous to the blastoporal side of the body or to the longitudinal nervous stems of trochophoric animals."

From the above findings, Beklemishev concluded (*loc. cit.*) that the ". . . trochophoric animals, independently of the Turbellaria, have developed from the larvae of the Coelenterata . . . . [which had] a slit-shaped mouth, an intestine with an epithelial lining, and a pair of aboral tentacles . . . . by means of 'progressive' neoteny."

I believe that Beklemishev has insufficient ground to claim an independent origin for the flatworms and the Trochozoa. First, as he himself emphasized, the protrochophore is, in various respects, similar to the turbellarians (adult stage), not only different from them. Second, he had to create a hypothetical larval form to accommodate his theories; this larva, a coelenterate with an intestine, seems quite unrealistic to me. Third, there is a huge difference between a coelenterate larva with a slit-shaped mouth, and a trochozoan adult in which the gut was formed by the closure of the middle portion of the blastopore; it seems that Beklemishev too easily bridged this gap. We have to add that the cleavage pattern of the turbellarians is sufficiently similar to that of the molluscs and annelids for most zoologists to consider them as having a common origin (Hyman, 1951), and that, were Beklemishev's theory true, we would have to accept a dual origin for bilateral symmetry and cephalization, which is possible but not proven. On all these grounds it seems simpler to assume that the flatworms and the molluscs and annelids did not evolve independently, as Beklemishev suggested, but had a common origin, and that the differences Beklemishev emphasized arose after the trochozoan line branched off from the flatworms; possibly the changes in promorphology themselves played a role in the separation of the two lines.

With this, we conclude the discussion of the origin of molluscs. Two other problems seem pertinent to the subject. One is the origin of coelomic segmentation (eumetamery), and the other that of the coelom. These are the two major "innovations" acquired about the time when the divergence of the molluscan and annelid lines took place.

The origin of the coelom and coelomic segmentation in molluscs and annelids.—

Several theories have been put forth to explain the origin of the coelom and coelomic segmentation. Since they have been discussed by recent authors (Hartman, 1963; Hyman, 1951; Clark, 1963, 1964; Remane, 1963), I will consider them very briefly. The gonocoel theory suggests that the coelom arose from the expansion of the cavity of the gonads; the enterocoel theory says that it arose from the cavities of digestive diverticula, and the nephrocoel theory that it came about by the expansion of the flame bulbs of protonephridia. The first two theories assume that the organs giving rise to the coelom were serially arranged (pseudometameric), and thus their transformation produced not one single coelomic cavity, but a series. In other words, these theories propose to solve the problem of the origin of segmentation (eumetameric) together with that of the coelom. This may appear as an advantage, but in actuality it is one of the most serious objections to these theories. Because, having once accepted them, one also must assume that animals with unsegmented coelom, such as molluscs, phoronids, ectoprocts, etc., all had to descend from ancestors with segmented coelom, which is not certain at all. Another serious objection to all of the above theories is that they consider the coelom homologous throughout the animal kingdom, which seems absurd in the case of independent phyletic lines such as the protostomes and the deuterostomes. Further objections can be found in the papers cited. The conclusion is that none of these theories is acceptable.

The coelom in the molluscs and annelids seems to be a "new" structure, not only in the sense of appearing for the first time, but also in being additional to any one of the already existing structures, not homologous to them. This mode of origin of the coelom was suggested by the schizocoel theory, upheld by Hartman (1963). Ontogenetic data support this contention, roughly as follows: In molluscs and annelids the coelom is formed in different manners; in molluscs it develops inside the pericardial-nephridial complex and in annelids inside the mesoderm bands. Neither the gonocoel, the enterocoel or the nephrocoel theories have enough flexibility to explain these differences with ease. It is simpler to believe that both groups acquired the coelom independently and anew, and by their own methods (this also means that their common ancestors did not have a coelom at all, p. 156).

Several theories have been proposed to explain the origin of coelomic segmentation (Hyman, 1951; Clark, 1964). The gonocoel and enterocoel theories, as mentioned above, combine the origin of segmentation with that of the coelom. The theory of cyclomerism, which says that segmentation arose by the bilateral, serial rearrangement of originally radially situated gastric pouches, is another form of the enterocoel theory. Criticism of these theories was given previously. The fission or corm theory, which says that segmented animals arose from incomplete fission, i.e., fission without subsequent separation of the products of fission, has also been understandably rejected by Hyman. She finds that the origin of segmentation can best be explained by a combination of the theories of pseudometamerism and locomotory mechanisms. According to the first, the ancestors of the segmented animals were pseudometameric, with a series of gonads in the body (note similarity to the gonocoel theory). The swelling of the gonads during sexual maturity made the bending of the body difficult except at the sites between the gonads, and this supposedly led to the serial constriction—segmentation—of the body. The second theory also presupposes a long and pseudometameric body, but it emphasizes the impact of locomotion on the musculature; it was, according to the theory, serpentine swimming motions that led to breaking up of the musculature into segments. I doubt that either of these explanations is valid. First, both are decisively Lamarckian. Second, and mainly, because segmentation is primarily a developmental process, it needs a developmental explanation.

Such an explanation has come forth from Berrill, concerning the origin of the segmentation of the chordate musculature. He wrote (1955:171): "Segmentation . . . is primarily a phenomenon of development and growth and requires analysis in terms of growth activity before we can consider how it may have arisen during the course of evolution." And (p. 173): "Segmentation . . . is not something that can be gradually attained—it appeared suddenly as the result of a critical modification of a developmental process and could well have appeared as a single mutant type, as readily as almost any other kind of innovation or mutation. The magnitude of the structural, functional, and evolutionary consequences is somewhat beside the point. Admittedly it would be a form of macro-evolution, but as the developmental outcome of just as small an initial change as most others." Except for one reservation to be mentioned below, I agree with this theory and believe that the coelomic segmentation of the annelids has had a similar origin. This conclusion is derived from a comparison of the molluscan and annelid ontogenies as follows.

In molluscs, the growth of the mesoderm bands is short, differentiation sets in soon, and the mesoderm bands will give rise to various mesodermal organs. Rhythmicity in growth is not evident. This condition is taken as primitive, and the following one, found in the annelids, as advanced and derived. The latter arose presumably through two changes from the former. First, the differentiation of the teloblasts, which by mitotic divisions produce the mesoderm bands, is postponed; the teloblasts retain their capacity to divide, usually throughout life (Berrill, 1961:312). Second, the rate of growth, or the rhythm of the differentiation of the products of growth, has changed from non-rhythmic to rhythmic. It seems that both kinds of changes can easily be explained by mutations. It is neither necessary nor profitable to assume that the two kinds of changes were achieved in a single mutation, or that they occurred simultaneously. I believe that these aspects of Berrill's theory do not apply to the origin of annelid segmentation.

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