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ZOOLOGISKA BIDRAG FRÅN UPPSALA, BAND 30

ON THE EARLY
PHYLOGENY OF THE METAZOA

THE BILATEROGASTRAEA THEORY

BY

GÖSTA JÄGERSTEN

UPPSALA 1955
ALMQVIST & WIKSELLS BOKTRYCKERI AB

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With 8 figures in the text

Contents

I. Introduction	321
II. Origin and Evolution of the Metazoa up to and including the "Bilaterogastraea"	322
III. Phylogeny of the Coelenterata	330
1. Cnidaria	330
2. Ctenophora	335
3. Porifera	337
4. Planuloidea	341
IV. Origin of Mouth and Anus in the Coelomata	342
V. "Protocoeloma", its Origin and Organization	346
VI. Summary	351
VII. References	353

I. Introduction

During the latter half of the last century a number of phylogenetic as well as other zoological theories saw the light of day. They were based on the accumulation of important facts, which were rapidly established at that time. From then on the amount of facts increased incessantly; theorizing, on the other hand, decreased. Phylogenetic investigations even fell to a certain extent into disrepute, partly justified on account of many unreflecting and uncritical argumentations.

Nobody can, however, get away from the value of trying to arrange scattered facts under unitary points of view. Even the discussion to which a theory can give rise is of value through the ensuing ventilation and expression of the problem. Fortunate to say, also the main features in the phylogeny and taxonomy of the animal kingdom have lately once more become the subject of discussion. Names such as SNODGRASS, HADŽI, REMANE, BOETTGER, and HYMAN can be mentioned in this connection.

In the present paper I have taken up an examination of the earlier phylogeny of the *Metazoa* from new angles. It is included as a link in investigations on the phylogeny of all the large groups of the animal kingdom. This is natural with regard to the fact that in investigations of this type the only possible approach is to start from the facts in the recent groups, i.e., from the tops of the "phylogenetic tree" (paleontology unfortunately contributing nothing in this matter), and "conclude backwards" in time. Yet the early phylogeny of the *Metazoa* constitutes to a certain extent a separate section, concerning in the first place the evolution of the so-called coelenterates, which warrants a special publication.

II. Origin and Evolution of the Metazoa up to and including the "Bilaterogastreae"

When the derivation of *Metazoa* is concerned, HAECKEL is considered an authority. Starting from his biogenetic rule he believed their origin to be found among the *Protozoa*. Within these some form is supposed to have become colonial and thereby have given rise to a blastula-like being, "*Blastaea*", which became the ancestor of all *Metazoa*.

An indication as to the correctness of this opinion was seen, amongst other things, in the existence of the plant genus *Volvox*. Mainly owing to the strikingness of this train of thought but also due to HAECKEL's authority, this conception of the origin of the *Metazoa* was and still is dominant.

Other possibilities have, however, also been put forward. Thus FRANZ (1924 and other papers) considers it improbable that the *Protozoa* should be phylogenetically older than the *Metazoa*. The unicellular organisms should be a polyphyletic group, originating partly from multicellular algae, partly from fungi. FRANZ cites the following in support of this theory, here summarized in short statements.

- 1) Nothing postulates a diminutive size of the really primitive organisms.
- 2) The supposition that the *Protozoa* are more original than the *Metazoa*, is connected with the long-prevailing belief in spontaneous generation.
- 3) It is far from true that the simple is always more primitive than the more complicated. There are numerous cases of secondary simplification in the organisms.
- 4) The circumstance that the *Protozoa* seem to constitute a connecting link between plants and animals, ought also to have contributed to the prevailing opinion. In reality no definite dividing-line can be drawn between unicellular and multicellular plants, nor between unicellular plants and unicellular animals. On the other hand one finds no taxonomic relationships between the latter and multicellular animals.

5) The amoebae, previously considered as the most primitive of all animals, are now regarded, as is the case with the other protozoan groups, as descendants of phytoflagellates of different kinds.

FRANZ thus being of the opinion that *Protozoa* originated from multicellular plants, he finds it improbable with regard to DOLLO's law that they should then have returned to multicellular condition. He therefore believes that the multicellular animals (like the multicellular plants) cannot originate from unicellular organisms. The ancestral form for the *Metazoa* was instead a multinucleate organism, not necessarily very small, which after the formation of partition walls in the cytoplasm between the nuclei evolved into a multicellular "*Archicytologus*". This later gave rise on the one hand to the plant kingdom (including *Protozoa*) and, on the other, to *Metazoa*. *Archicytologus* should have been a plant, which in all essential characteristics closely agreed with *Fucus*. The similarity between this genus of brown alga and the *Metazoa* as regards nucleate and reproductive conditions FRANZ does not thus consider to be a convergence phenomenon but a phyletically grounded one. (FRANZ wants to reverse completely the idea of the phylogeny of the algae.) *Blastaea* should have evolved in some way, of which no details are given, from *Archicytologus*.

I have touched upon FRANZ' opinions here, as on the whole they have not received sufficient attention in literature. It has mostly been considered self-evident that *Protozoa* are more primitive than all the multicellular organisms. I, for my part, cannot come to any other conclusion than that FRANZ has touched on a sore spot in our conception of the protists. His idea should be taken into consideration in phylogenetic investigations of them.

On the other hand, FRANZ' derivation of *Blastaea* from a form resembling *Fucus* is not very convincing. The changes implied appear hardly probable. Yet even if FRANZ' conception of the *Protozoa* should be accepted, it is fully imaginable that some flagellate once more returned to colony formation. When such a relatively uncomplicated process is concerned, we can well visualize an exception from DOLLO's law. Finally, in my opinion the possibility is not excluded that *Blastaea* can have evolved from some "protist" of far more ancient date than those now in existence. In any case, as FRANZ does not question *Blastaea* to have existed but only derives it in a way different from HAECKEL, I shall not deal any further with FRANZ' highly imaginative and no doubt interesting ideas.

A scientist, who takes a stand in direct opposition to the theory of *Blastaea* (and even *Gastraea*) is HADŽI (1944 and later papers). He derives the *Metazoa* instead via acoelous turbellarians from some solitary ciliate. Here is not the right place to enter into a detailed treatment of this bold speculation; this must be done in conjunction with a discussion of the *Turbellaria*, to which

I shall return in another connection. I only want to point out that I hardly believe that a derivation of this kind will gain many followers.

According to HAECKEL, as is well known, the pelagic *Blastaea* has changed into a "*Gastra*" through invagination of the wall in the posterior pole. This opinion was, however, not universally accepted in the beginning. Several other hypotheses regarding evolution from *Blastaea* were put forward, and eagerly discussed during the last decades of the 19th century.¹ HAECKEL's idea was, however, victorious.

One of these competitive hypotheses, viz. METSCHNIKOFF's (1886 and other papers) has in recent years acquired an eager advocate in HYMAN (1940, 1942). Since this writer through her excellent handbook has gained considerable authority, which can conceivably contribute to an acceptance of her ideas — DODSON (1952), for example, has uncritically agreed with them — I shall here touch upon METSCHNIKOFF's theory and HYMAN's points of view in some detail.

METSCHNIKOFF emphasizes the circumstance that the entoderm in many forms of animals arises otherwise than by invagination, and that this is particularly the case in *Cnidaria*, which is specially significant, as just this group is considered to stand closest to the hypothetical ancestral form. According to METSCHNIKOFF's conception *Blastaea* should have become two-layered through scattered inwandering of cells to the interior from the surface layer. It should, in other words, have changed into a planula-like creature, a "planuloid".² Contrary to HAECKEL's opinion entoderm formation by invagination should be a secondary process, constituting "one of those short cuts common in embryology" (HYMAN). On the basis of his important discovery of phagocytosis METSCHNIKOFF considers that the planuloid with its surface cells ingested food particles, which were then carried to the central digestive cell mass. HYMAN emphasizes this conception and thinks that the early metazoan creature did not need to have a mouth, whereby an important argument in HAECKEL's theory should disappear. For HAECKEL assumes that there would have been an advantage in ingestion via a concavity, i.e., the primitive intestine ("Urdarm"), in which the food could be stored.

Yet to speculate on what is necessary, or what is advantageous or not, is extremely difficult on account of the impossibility of realizing all situations and conditions, and can therefore hardly lead to any certain result. On the other hand, one may well agree that it is hard to understand the advantage in ingestion being moved to the posterior pole in a pelagic creature such as

¹ Regarding these, see for example KORSCHOLT & HEIDER, *Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere*. Allg. Teil (1909) or HYMAN (1942).

² It is HYMAN who uses this term. METSCHNIKOFF first employs the name "*Parenchymella*", later "*Phagocytella*".

Blastaea. Personally I can also admit that the evolution of a planuloid ancestor in itself is very well conceivable. The difficulty lies instead primarily in its acceptance leading to improbable consequences.¹ Furthermore it is obvious that HYMAN bases her idea on incorrect assumptions when claiming (1940, p. 252) that "the chief objection to the gastraea theory is that in metazoan embryology the entoderm is more frequently formed by other methods than it is by invagination". HYMAN also claims "that the inwandering of cells into the interior to form a solid mass is the most common method of formation of the entoderm among the sponges and coelenterates" (1942, p. 36).

This latter statement is entirely correct. Polar or multipolar inwandering is probably predominant in *Cnidaria* from a purely statistical point of view; in any case this type of gastrulation is entirely dominant in *Hydrozoa* (invagination being unknown here). But this is not essential, the essential point is instead the fact that invagination also occurs in *Cnidaria* (both in *Anthozoa* and *Scyphozoa*).

Of the greatest significance in this connection is, further, the way in which gastrulation occurs in the other large groups ("phyla") of the animal kingdom. And there it is without doubt invagination which dominates. It is also important to note that the process is found in such widely separated groups as, for example, *Cnidaria*, *Annelida*, *Chaetognatha*, and *Acrania*. If inwandering were the original process, change to invagination would have occurred during the phylogeny of the animal kingdom parallel in several separate lines of evolution. One then asks oneself: why precisely a change to invagination everywhere, when there are so many other possibilities? Is it not far more probable that there exists a historical reason for invagination, i.e., that this is the original form of gastrulation, which later on, independently within separate lines, was changed secondarily in different ways? This has certainly happened in those cases, where the quantity of yolk in the egg is so great as to make invagination mechanically impossible. We then get epiboly or intermediate forms between this type and invagination.

We thus come to the result that everything indicates that invagination, common as it is to *Cnidaria*, *Porifera*, and to the majority of groups of the *Coelomata*, already occurred at that point in the "phylogenetic tree", where the lines to these complexes divided. In other words, *the common ancestor possessed invagination, i.e., was simply a Gastraea*.

This important result we thus arrive at with the usual phylogenetic method, i.e., without referring to the biogenetic rule. This is, of course, a strong point, especially with regard to the hypothesis occasionally put

¹ I shall deal with these consequences more closely in another connection. Here need only be mentioned that they mainly consist of the intestine lumen and mouth in the *Metazoa* having arisen parallel in several different lines of evolution.

forward that the gastrula is not a phyletically but only a mechanically determined stage. If this should be correct, we have every reason to suppose that the same condition prevailed during the earliest periods of the phylogeny as well. The objection has thus no convincing force. Neither are there, in my opinion, any reasons for such a hypothesis either (it being a fact that even animals with small quantities of yolk can lack invagination gastrula), and therefore *it ought to be permissible to invoke the biogenetic rule, too*.

As a third argument, the organization in the adult forms of the recent groups, especially the *Cnidaria*, can finally be added. *Gastraea* is, in other words, the type of organization from which all *Metazoa* most simply and without serious consequences can be derived.

Concerning the occurrence of the different forms of gastrulation within the *Cnidaria*, it is of special interest that *Hydrozoa* present the most diversified picture. Here the original form of gastrulation has apparently been changed in several different directions. (This agrees very well with *Hydrozoa* even in other respects being, in my opinion, the most modified of the three cnidarian groups, see section III: 1). It is unnecessary in this connection to speculate how these changes have taken place in detail. I shall only emphasize that I do not find it impossible for a course of evolution, as imagined by METSCHNIKOFF (1886), to have taken place, although in the opposite direction, i.e., from invagination via polar inwarding to multipolar and delamination.

It may be emphasized that it is hardly the embryological conditions, which in the first place caused HYMAN to try the resuscitation of METSCHNIKOFF's theory. Therein she was probably prompted rather by her belief in the primitive character of the acoelous turbellarians. This opinion (already raised by v. GRAFF 1882) does not, of course, harmonize with the *Gastraea* theory. I shall return to the *Acoela* in another connection. Here need only be mentioned that I cannot share the opinion of their primitiveness, in any case not as far as regards the intestine.

It results from the analysis carried out above that the *Gastraea* theory must still be upheld, in spite of HYMAN's attempt to replace it with the "planuloid" theory.

Is HAECKEL's idea quite unassailable then? It is not, and it must, in my opinion, be modified in one important respect. In the following I shall expose my view on this problem.

In its earlier period of evolution *Blastaea* was a polarized, globular or perhaps rather egg-shaped, hollow creature with a one-layered wall. It lived a pelagic life near the surface of the sea and was no doubt a plant whose autotrophic nutrition was supplemented, possibly already at that period, by phagocytic intake. The entire outer surface was flagellated, and when moving forwards the body rotated round the longitudinal axis. Reproduction

was entirely or partly sexual with anisogametes. *Blastaea*, in short, probably closely agreed with *Volvox* except as regards the circumstance that it was very likely diploid. The similarity to *Volvox* is probably not due to any closer relationship.

Regarding the earlier evolution of *Blastaea*, I thus agree on all essential points with the prevailing opinion. It is concerning the further evolution that I must disagree, the reason for this being amongst other things the organization in the *Anthozoa*.

HAECKEL and his followers believe that the change to *Gastraea* occurred during the pelagic life, and with retention of the radial symmetry. First as fully established the *Gastraea* should descend to the bottom, attach itself, and give rise amongst other groups to the recent *Cnidaria*. HAECKEL imagines that ingestion in a concave surface would be advantageous, on which account the invagination in the posterior pole came into being. If such a concavity really should be an advantage in a pelagic organism, then, in my opinion, it must be a still greater advantage in a bottom-dweller, which takes its food from the substratum.

I must therefore suppose that the *Blastaea*, on account of more favourable food supply, turned to living near the bottom, finally becoming a bottom-dweller gliding forwards over the substratum with the aid of its flagellae. In connection with this change, rotation round the axis ceased, one and the same side being permanently turned towards the bottom, and herewith the conditions for a primitive bilateral creature were given.

This blastaeian being, modified in connection with benthonic habits, "*Bilateroblastaea*", probably was shaped roughly as shown in Fig. 1a: flattened ventral side; arched dorsal side, which can have lost its flagellae; a group of simple sensory cells in the front end and a few scattered among the flagellated cells on the ventral side. The very beginning of a nervous system probably existed, consisting of an extremely simple plexus, which connected the sensory cells. The interior can have been empty as previously, i.e., without cell tissue, but probably a small quantity of cells had already wandered in. The sexual cells at least were probably situated inside, although in close connection with the cell layer of the ventral side. The body cavity is unlikely to have been entirely filled with "mesoderm".

At the change to benthonic life in darkness the autotrophy was entirely lost, and the now exclusively prevailing *phagocytosis was limited to the cells on the ventral side*, where it became instead all the more active.

The food consisted during the first period of benthonic life of the small organic particles, which the animal happened to glide over when moving. When some larger dead organisms were encountered, the animal probably, approximately as Fig. 1b shows, arched its ventral side over the food, and in this position waited for its decomposition. Gradually this occasional

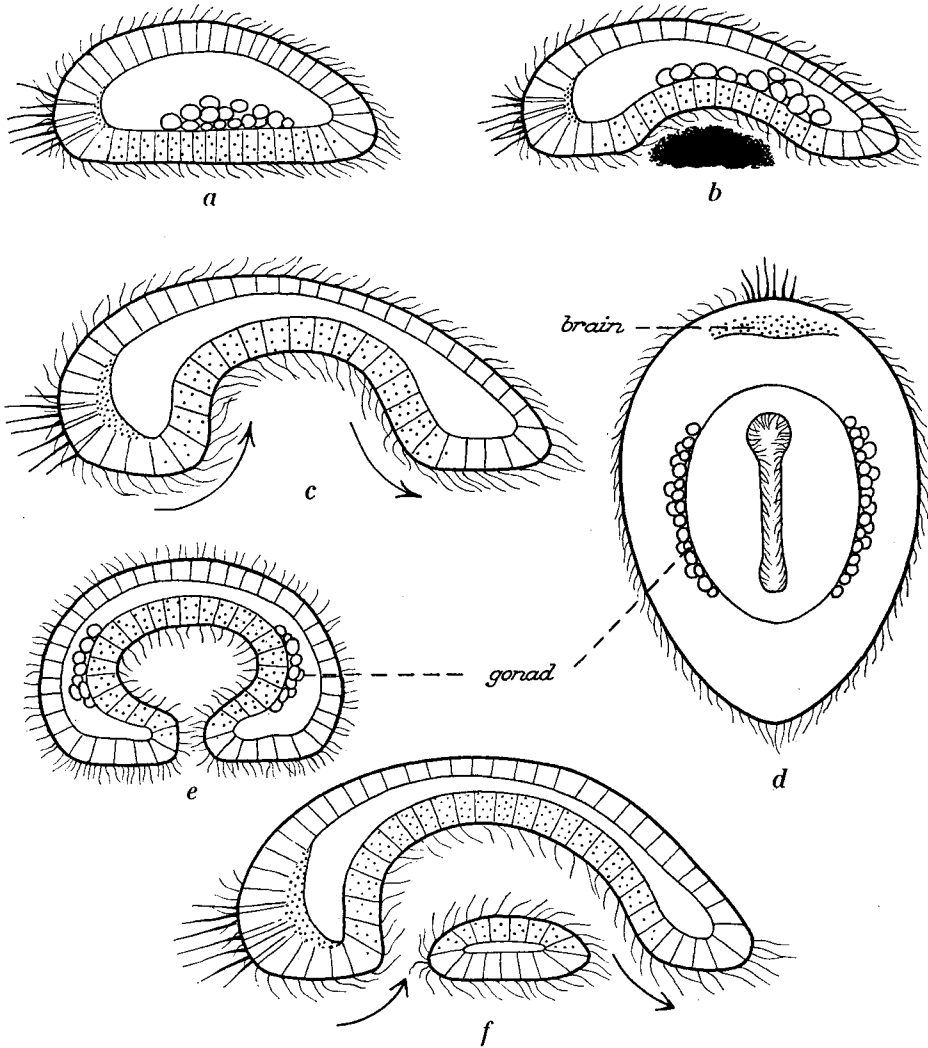


Fig. 1. *a*, "*Bilateroblastaea*"; *b*, the same at a somewhat later stage with temporary intestine curved over a larger food particle; *c-e*, "*Bilaterogastraea*" (still without gastric pockets): *c*, longitudinal section, *d*, seen from ventral side, *e*, cross section; *f*, stage after the margins of the primitive mouth have fused in the middle part ("*Protocoeloma*").

concavity, the first beginning of an intestine, began to hasten decomposition and facilitate ingestion by secreting ferments from differentiated glandular cells. In a "short time" the concavity became permanent and increasingly marked: the gastraeal stage in the evolution of the *Metazoa* was reached (Fig. 1*c*). In order to distinguish this *Gastraea* from HAECKEL's we can use the name "*Bilaterogastraea*".

It seems probable that the primitive intestine retained the cilia, and that

ingestion of food particles occurred by means of cilia activity. It is likely, however, that the animal had epitheliomuscular cells, for which reason the primitive mouth can have widened when ingesting any larger food particle (or evacuating any larger excrement) and then narrowed, or perhaps even closed entirely. The intake of smallish particles undoubtedly occurred at the front end only, while smallish excrements were discharged at the posterior one (Fig. 1c and 1d).

Otherwise the organization was on the whole probably like that of the *Blastaea*. Nevertheless, the nervous system may have been somewhat more complicated, presumably as a diffuse nerve plexus with a faint centralization ("brain") in the front end (under the sensory cells to be found here), and perhaps also as a concentration on either side of the elongated mouth.

A course of evolution like that now described with bilateral *Blastaea* and *Gastraea* forms ought on account of the gradual changes both as regards morphology and feeding-biology to be as near the truth as phylogenetic constructions of this kind can at all be. Nevertheless this is not the first and foremost reason which has prompted me to modify HAECKEL's theory. I have, as already said, in reality been forced to accept an evolution of that kind, amongst other things on account of the conditions within the *Anthozoa*. The inner bilateral symmetry prevailing here is, in my opinion, incompatible with the current opinion that *Cnidaria* are primarily a radially symmetrical group. If — as HAECKEL thinks — it was a pelagic, radially symmetrical *Gastraea* which gave rise to the *Cnidaria*, then the organization of the *Anthozoa* is quite incomprehensible (see more on this matter in section III: 1).

We should also have great difficulty in deriving *Coelomata* in a natural way, and without troublesome consequences. The derivation must then be made from a radially symmetrical "coelenterate", whereat it is not possible to develop definite conceptions regarding the changes both from morphological and functional points of view in the same natural way as above. The many different theories regarding radial ancestors which have been put forward during the course of times, and of which none have gained any more general acceptance, should be considered against the background of these difficulties.

An opinion regarding the earliest phylogeny of the *Metazoa*, which to a certain extent resembles my theory presented above, and which I therefore shall not omit to mention, is NAEF's (1931). He considers that upon the pelagic *Blastaea* should follow a "*Progastraea*", which partly should lead a mobile life on the bottom, and in accordance with this have a flattened, food-absorbing underside, which temporarily could be made concave. When the concavity became permanent, a "*Metagastraea*" existed. It is very surprising that NAEF is so dependent on the embryological conditions that he attributes a regular radial symmetry to the common ancestor of *Coelenterata* and *Coelomata*. In this way the good idea is wasted.

III. Phylogeny of the Coelenterata

After the presentation of the theory of the *Bilaterogastraea* the phylogeny of the so-called coelenterates shall now be discussed. In this connection it is first of all necessary to investigate to what extent the theory can find support in the conditions within these groups. I shall start with the cnidarians on account of their importance in this connection.

1. *Cnidaria*

It is a generally prevailing opinion that the *Cnidaria*, in spite of their numerous different forms, are a homogeneous and well limited group. The general organization and the occurrence of such a special phenomenon as the nettle cells differentiate these animals very markedly from other metazoans. No objections can very well be raised to this.

It is also a general opinion that the group is primarily radially symmetrical, and that of the subgroups the *Hydrozoa* are the most primitive, the *Anthozoa* the "highest" developed. This view was also shared by HAECKEL, who derived *Cnidaria* from his radially symmetrical, pelagic *Gastraea*. The most primitive genus of the *Hydrozoa*, according to HAECKEL, is *Hydra*.

HYMAN (1940) disagrees in part with this opinion. Although she cannot get away from the primitiveness of the *Hydrozoa*, she will not begin with *Hydra* but with a primitive trachyline medusa.

In reality it is extremely remarkable that the opinion of the primitiveness of *Hydrozoa* has been able to dominate phylogeneticists for such a long time. The reason has probably primarily been HAECKEL's authority. It is otherwise difficult to understand how such a remarkable phenomenon as the bilateral inner organization in *Anthozoa* could be disregarded. Such an organization in a sessile group with an origin like that supposed is a biological absurdity. *Only one thing can lead out of the difficulty, namely to change the opinion regarding the phylogeny of Cnidaria. We must derive them from some bilaterosymmetrical ancestor!* It is, amongst other things, for this reason that I have considered myself called upon to set forth the theory of a benthonic, mobile, and in connection therewith bilateral gastraea (see previous section). An important consequence of this will be that we must altogether reverse the sequence *Hydrozoa* → *Scyphozoa* → *Anthozoa*. It is the first-mentioned group that should stand last in the series. In other words, *Anthozoa* show in their organization the most primitive features, *Hydrozoa* are the most modified group.

The bilateral symmetry in *Anthozoa* is indeed such a well-known phenomenon that I can express myself very summarily. It is most marked in

Octocorallia, where it is caused by the arrangement of the muscles in the septa, the single siphonoglyph, and the divergent character of the "dorsal" directives. A distinct bilaterality also exists in *Ceriantharia*, *Antipatharia*, *Zoanthiniaria*, and many *Hexactiniaria* as regards stomodaeum and septa. Even the fossil *Tetracorallia* are clearly bilateral both in their inner structure and their eccentric attachment to the substratum. It may finally be noted that many anthozoan larvae, in spite of their pelagic life, are more or less definitely bilateral. This latter fact is not the least remarkable.

Bilateral symmetry thus occurs in all the large anthozoan groups. Some scientists have considered the reason to be that the solitary primitive anthozoan sat eccentrically attached, roughly like the tetracorallians. Such a condition is, however, not an explanation but, on the contrary, is in need of one. The eccentric attachment was simply part of the bilateral symmetry.

Other cnidarologists have considered it necessary to presume that the anthozoans once crept about free, but they have not dared to go the whole length, and attribute such a mode of living to the ancestor of the entire cnidarian group. The consequence of this supposition is that the evolution in the anthozoan stem should have begun with sedentary life and radial symmetry. After this a period of mobile life with accompanying bilaterality should have occurred, whereupon followed once more sedentary life and return to an increasingly marked radial symmetry. Such a course of evolution is not probable and nothing speaks in its favour.

A few examples of freely moving anthozoans (with movement in axial direction) are certainly to be found nowadays (*Ceriantharia*, some *Actiniaria*), but in these cases it seems to be only a question of occasional and forced divergences from sedentary life (K.-G. NYHOLM, verbal information), and in any way it is undoubtedly a question of secondary changes, which have occurred parallel in different lines. This very modest mobility has not had any influence on conditions of symmetry. (During motion the animals do not assume any particular orientation either in relation to the substratum.)

It is an interesting fact that the bilateral symmetry ("monosymmetry") in *Cnidaria* does not directly change to radial symmetry ("polysymmetry"), but first to bisymmetry (disymmetry, biradial symmetry). We have fine examples of this in *Hexactiniaria*. Here forms are to be found, which still show original features, such as a single siphonoglyph (e.g., *Edwardsia*, *Peachia*),¹ or when two are to be found, one of them (sulculus) is smaller. The sulculus is obviously a new formation, as (quite apart from the derivation of the cnidarians) is indicated partly by its instability even in one and the same species (it is to be found in specimens arisen sexually, and is

¹ It is possible that this bilateral organization in actinarians is due in certain cases to a secondary return to primitiveness. Such a possibility, however, has no effect on the line of thought followed here.

lacking in those formed by laceration), partly by the fact that there often appear specimens possessing a large number of siphonoglyphs (e.g. *Metridium*). Only in connection with strong reductions of the septal muscles and loss of the siphonoglyphs has bisymmetry changed into radial symmetry, as is the case in the *Madreporaria*, where it is, however, still possible to demonstrate traces of the original bilaterality.

There is, in my opinion, no objection to the usual conception that the *Madreporaria* are derived from ancestors of actiniarian type. Hence it is also obvious that it cannot well be claimed, although it has sometimes been done, that the general bilaterality has its reason in colony formation. (For certain particular details the place of the individual in the colony can, of course, play an inconsiderable role.) Nor is there anything to indicate that *Actiniaria* or *Ceriantharia* previously were colonial.

The direction of evolution *Actiniaria* → *Madreporaria* also speaks against the possibility occasionally put forward, that the bilaterality should depend on the elongation of the mouth into a slit, which in its turn should have its reason in the need for a better flow through the gastric cavity for the sake of respiration in conjunction with increasing body size. This possibility which in itself is not entirely improbable, hardly explains, however, the bilateral arrangement of the muscles. Moreover, it is not in the large actinarians, that bilaterality is most widely realized (here, as previously stated, bisymmetry is dominant).

Summing up we can say that the attempts hitherto made at an explanation of bilaterality in *Anthozoa* have not been convincing, and none of them has met with more success than any of the others. In this situation the derivation of the *Cnidaria* from a *Bilaterogastraea* seems to be preferable. It removes with one stroke all difficulties connected with the conditions of symmetry.

But apart from this, the derivation also explains the total lack of medusae in *Anthozoa* in the simplest possible way: *no medusoid generation has ever existed!* The derivation is furthermore in accordance with the circumstance that the original type of gastrulation in the animal kingdom, i.e., invagination (see p. 325), in several cases is established in *Anthozoa* (and *Scyphozoa*), but not in *Hydrozoa*. Finally this derivation is in complete harmony with the fact that the cnidae are most differentiated and complicated in *Hydrozoa*, simplest and most uniform in *Anthozoa*.

In this connection it may also be emphasized that it ought by no means to be more difficult to derive *Scyphozoa* and *Hydrozoa* from the anthozoan type than the contrary. The phylogeny within the *Cnidaria* is, however, a problem, which does not fall within the scope of this paper, but would deserve a closer investigation starting from the points of view presented here. I shall content myself with emphasizing that the usual opinion regard-

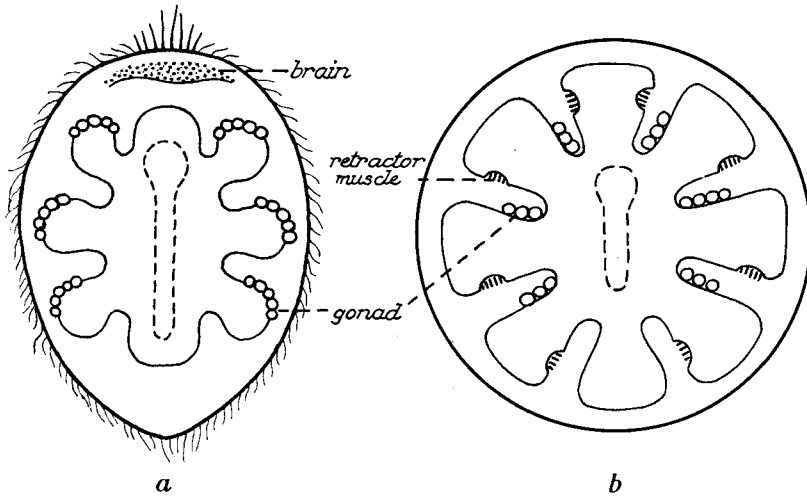


Fig. 2. a, "*Bilaterogastraea*" with three pairs of gastric diverticula provided with gonads; b, the organization in *Octocorallia*. The oral slit is dotted.

ing the *Cnidaria* must be considered incorrect. The evolution of the group instead constitutes a very interesting parallel to that of the *Echinodermata*. In both cases the ancestor was a mobile bilateral form, which after attachment changed to a marked radial symmetry, which however was not entirely able to suppress the original organization. Within the *Cnidaria* this was, however, achieved in *Hydrozoa* and *Scyphozoa*, owing to the uncomplicated organization in the ancestral form, mainly the primary lack of a separate anus.

Not before the above was written has it come to my knowledge that the yugoslav cnidarologist HADŽI had claimed, as early as in 1944, that the *Cnidaria* could not possibly be primarily radial. HADŽI therefore finds himself compelled to reject HAECKEL's theory and to present a new one, according to which the *Cnidaria* should be derived from rhabdocoeloid *Turbellaria*. (These should have attached themselves with the posterior end and developed a crown of tentacles round their mouth.) HADŽI then completes this astonishing idea by trying to revive the old hypothesis that the *Turbellaria* are descendents of *Ciliata* (JEHRING and others), which already METSCHNIKOFF (1886) had found to be completely impossible.

However, HADŽI's opinion—probably as a result of the remarkableness of the basic idea—has received in some quarters (for example PAX 1954 and DE BEER 1954) a favourable, indeed almost enthusiastic reception. Yet I find it unnecessary to criticize it more closely here. The bilaterality in *Cnidaria* can be explained without such breakneck hypotheses. The above-presented modification of HAECKEL's theory is quite sufficient. The *Cnidaria*

are undoubtedly to be derived from free-living bilateral forms, though not from any coelomate group, either living or extinct.

In the previous section we have followed the evolution from *Blastaea* to *Gastraea*. It now remains to investigate how the latter was organized at the point where the branch to *Cnidaria* issued from the main stem (point 8 in the diagram on p. 352).

The most interesting feature in the organization is without doubt the intestine. What, then, was the shape of this organ? In answering the question regard must be had partly to the intestine in the original type of the *Anthozoa*, partly to its derivatives in the ancestor of the *Coelomata*. Doing this, we arrive at the result that the intestine at that actual point must have had gastric pockets, more exactly three pairs, each of which was provided with gonads (Fig. 2a).

This assumption is primarily based on the fact that in primitive groups of *Deuterostomia* three pairs of coelomic sacs are to be found, and that these arise as enterocoels (see further details in section V).

It now appears that such a *Bilaterogastraea* provided with three gastric pockets could very well be thought to constitute the ancestral form of *Octocorallia*, and thereby also of all cnidarians. The gonads situated at first in the outer wall of the pockets were displaced forward while at the same time the lumina widened, and the foremost and hindmost parts of the central "stomach" were likewise set off as pockets. In connection with the rounding off of the body, these two unpaired pockets gradually assumed a great similarity with the paired ones. Through the widening of the pockets and the stretching of the body in height the parts between the pockets were successively modified into increasingly typical septa. Under their front surface a marked dorsoventral band of muscle fibres developed. The forward displacement of the gonads resulted in the hindmost pair of septa (the "dorsal" directives) becoming sterile. Finally the ectoderm in the mouth margin was pushed in and formed the stomodaeum. The relative insignificance in principle of these changes is evident from the fact that (see Fig. 2) it is unnecessary even to draw an intermediate form. On comparing *a* and *b* the course of events is immediately understood.

These inner changes occurred hand in hand with the outer ones:— The previously free-creeping animal attached itself by its front, after which through unequal growth, perhaps in combination with tipping over (resulting in the body finally being attached by the original back) the mouth came uppermost. During this inversion a crown of tentacles developed round the mouth. The organization characteristic of *Cnidaria* was thus attained.

This derivation signifies that the foremost part of the gastraeian mouth, where the ingestion of food particles took place (see Fig. 1 c), became included in the siphonoglyph of the coral polyp. This is in accordance with the

physiological conditions still prevailing in the octocorallians, with inflow in the siphonoglyph and outflow at the opposite end. Even the circumstance that the current in the middle part of the stomodaeum varies in direction, is in agreement with what has been supposed above (p. 329) regarding the function of the oral slit in *Bilaterogastraea*. The theory is thus not contradicted by any changes as regards feeding biology.

After this derivation the question presents itself whether the *Octocorallia* really are the most primitive group. Some scientists believe that *Antipatharia* are more primitive. It should be noted, however, that *Antipatharia* are considerably more variable in several respects (some even having an organization which closely resembles that of *Octocorallia*!), while *Octocorallia* are a very homogeneous and stable group. For this, as well as for other reasons it can be supposed that the primitive cnidarian was a smallish, solitary polyp without skeleton, with eight septa and eight tentacles, i.e., on the whole with an organization like that of recent octocorallians.

(No difficulties are involved, however, if the primitive cnidarian had possibly only six septa. We need in such a case only to assume that, for example, the middle pair of pockets in the gastraeal progenitor was reduced at or already before the change to the primitive cnidarian.)

Finally it might be pointed out that as a consequence of the derivation from a *Bilaterogastraea* the terms "ventral" and "dorsal" hitherto used in *Anthozoa* instead of being meaningless have now become positively unsuitable. They should be replaced by "anterior" and "posterior" respectively.

2. *Ctenophora*

The most varied opinions have been advanced about the phylogeny of the *Ctenophora*. Several scientists have in different ways associated them with *Polycladida* and then usually regarded the group *Platyctenea* as the connecting link. The *Polycladida* have at times been considered as being descendants of *Ctenophora* (LANG and others), at times as the ancestral group (LAMEERE and others). Since the *Platyctenea* have, however, proved incontrovertibly to be typical ctenophores apart from their secondary specialization for benthonic life (notice the free-swimming *Cydippe*-stage of *Tjalfiella*), these opinions can be definitely ignored. The same can be done with HADŽIĆ'S (1923) view that the *Ctenophora* should have evolved from neotenic polyclad larvae, and on the whole with every association with the *Coelomata*. None of these hypotheses has won any permanent approval in literature either.

Other scientists have in different ways connected *Ctenophora* with *Cnidaria*. Primarily through their well-developed stomodaeum have they thus been closely compared with *Anthozoa*, and several authors have derived them from these latter. FRANZ (1924) goes even so far as to include them

in *Cnidaria*. Others have referred to similarities with hydroid medusae. This has been done by HAECKEL in several papers, and of modern authors HYMAN, for example, believes to see a relationship to "the trachyline stem form, which is here considered ancestral to the *Cnidaria*" (1940, p. 693).

I shall not go further into these and other opinions, which are often and in detail referred to in handbooks and textbooks. I want only to point out one thing, which has not been clearly observed. If one derives *Ctenophora* from any of the three branches of *Cnidaria*, the consequence will be either that *Ctenophora* or their evolutionary line have had nettle cells, or that these formations have developed parallel in at least two different instances in *Cnidaria*. This latter possibility is hardly probable with regard to the particular, complicated nature of the nettle cells, neither is any support to be found for the first alternative.¹ If there is a common origin for the adhesive cells of the *Ctenophora* and the nettle cells (and thereby also for *Ctenophora* and *Cnidaria*), it should probably lie below the first branching off within the cnidarian complex. In other words: it seems to me that there are no reasons at present to associate *Ctenophora* and *Cnidaria* more closely than to let them have a short common stem (as is shown in the diagram on p. 352).

Perhaps even this association is too intimate. The differences with regard to embryology are indeed considerable. As, in addition, the organization in these groups is very primitive—*Cnidaria* as well as *Ctenophora* are in reality only somewhat specialized gastraeans—and as original characteristics do not say anything about phylogenetic relationship, the *Ctenophora* can very well have arisen without any connection whatsoever with the cnidarian branch, i.e., from some *Bilaterogastraea* in the main stem (somewhere between 5 and 8 or even somewhat above 8 in the diagram). As, however, this gastraeans form ought not to diverge in any essentials from the one that gave rise to the *Cnidaria*—it should, like the latter, have had or in any case "in a short time" have got gastric pockets—it is in reality relatively unimportant exactly where we let the *Ctenophora* branch off. The standpoint taken has no consequences for the formation of the "phylogenetic tree" in other respects. For this reason I follow the usual opinion and associate the two groups, although, as already said, only far down, in the neighbourhood of the main stem leading to the *Coelomata*.

It is important, however, in this connection, to know whether the placing of the ctenophoran group is in accordance with the idea which I presented above concerning that *Gastraea*, from which I derived the *Anthozoa* (and thereby the other *Cnidaria* as well). If this should not be the case, the placing

¹ It may be emphasized that KOMAI (1942) maintains to have established nettle-capsules in *Ctenophora*. HADZI (1951) claims, however, apparently convincingly, that it is here a question of ingested capsules ("cleptocnidae").

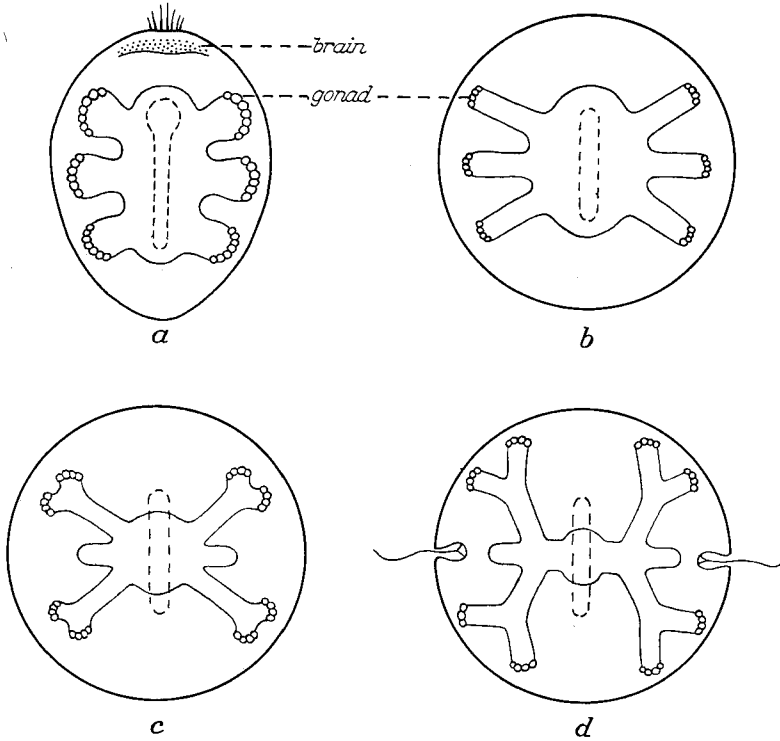


Fig. 3. Diagrams showing the imagined evolution in *Ctenophora*. *a*, "*Bilaterogastraea*" with three pairs of gastric pockets; *d*, typical ctenophore; *b* and *c*, intermediary forms. The oral slit is dotted.

attempted is not possible, and this might then supply an indirect indication that the *Ctenophora* had their origin higher up in the cnidarian complex, viz. from a radially symmetrical type. According to my opinion it is, however, not only possible to derive the *Ctenophora* from a *Bilaterogastraea*, but there is even one point which indicates such an ancestor rather than a radial one, viz. the bisymmetry, which suggests a comparison with the conditions in *Hexactinaria*. Here, as has been found above (p. 331), the evolution went from bilaterality to bisymmetry, and further towards radial symmetry. As a pelagic life, like a sessile one, leads to more or less marked radial symmetry, it seems that the parallel drawn could be justified.

It must, however, also be examined if a derivation of the *Ctenophora* from a gastraea with three pairs of gastric pockets is possible. On this point I can be very brief by referring to Fig. 3, which demonstrates the following possible evolution:— In connection with a rounding off of the formerly somewhat elongated body (*a*) the central intestine was shortened, and the pockets were pushed together, so that they obtained a common basis (*b*). The middle pocket on either side lost its gonads and decreased in size (*c*).

It became the tentacular canal of the *Ctenophora*. The remaining pockets, on the other hand, were each divided up into two diverticula (*d*), from whose blind ends the meridional canals later developed. In connection with this transformation of the intestine, the bilaterality concerning the other parts of the body, too, changed into marked bisymmetry.

It is obvious that the possibility of constructing in this way a transition from one type to another does not by any means constitute a proof. So much should be clear, however, that the *Ctenophora* fit very well with the basic idea in this paper, built on facts from other coelenterate groups. In any case, they do not contradict it.

3. *Porifera*

The sponges have caused the phylogeneticists quite particular difficulties. Owing to the radical differences in several respects between them and the other coelenterates they have even been considered as having no connection at all with other multicellular animals but as being evolved parallel with these from some group of flagellates. In this connection the choanoflagellates have been put forward on account of their similarity with the collar cells of the sponges (BÜTSCHLI). Taxonomically this opinion has led to the sponges, as *Parazoa*, being put on an equal footing with all other multicellular animals, the *Eumetazoa*.

The weight of this hypothesis must be tested by further detailed investigations, amongst other things of both choanoflagellates and choanocytes. For the time being I find the counter-argument brought forward, viz. that the flagellated cells of the larvae are quite unlike choanoflagellates, not entirely without justification. It must furthermore be added that cells resembling choanocytes are reported also in other groups of animals (*Mollusca*, *Echinodermata* and others, acc. to HEIDER 1914, p. 463), that the sexual cells in *Porifera* in all essential respects agree with those of other multicellular groups,¹ and that invagination processes have been demonstrated during ontogeny. I find it, therefore, best not to take such a radical step as to remove the *Porifera* from the stem of the other multicellular animals. As I shall attempt to show in the following, there exists also a possibility of explaining the differences, and of deriving the group from an ancestor, common with other metazoans, viz. the above-described *Bilaterogastrea*.

Comparison is rendered particularly difficult by the considerable variation as regards the larvae and the earlier ontogeny of the sponges. Conditions are to be found, however, in *Calcarea* which more or less agree with those in the other metazoans. This makes it possible to suppose that the *Calcarea*

¹ Thus in *Porifera* the same primitive spermatozoan type (with a circle of mitochondrian globules at the base of the barely changed nucleus) is to be found, which occurs in so many and in so widely separated phyla as, e.g., *Cnidaria*, *Annelida*, and *Acrania*.

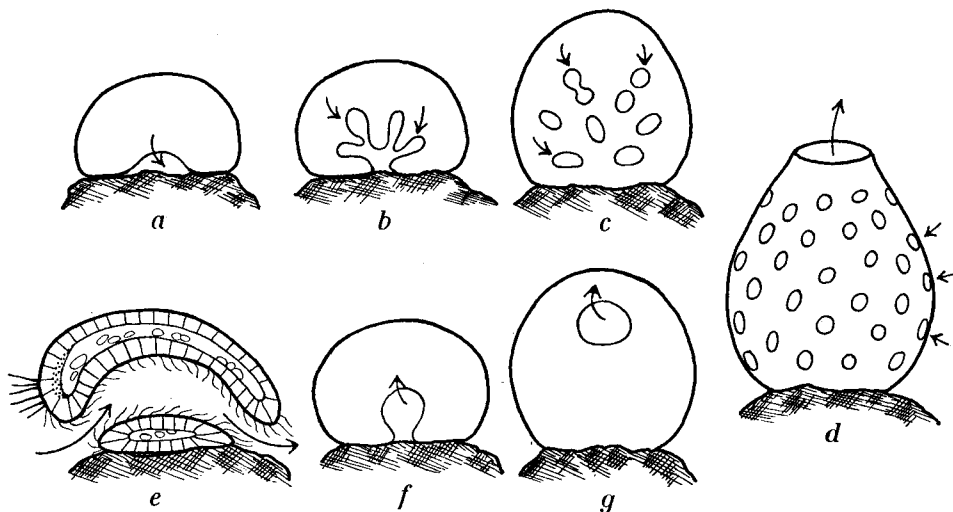


Fig. 4. Diagrams illustrating the supposed phylogeny in *Porifera*. *a-c* (anterior view) show the origin of the incurrent pores out of the front part of the primitive mouth (raised above the substratum); *f-g-d* show evolution of the osculum from the hindmost part of the primitive mouth and moving up to apex (*d*, *Ascon* type); *e*, approx. same stage as *a* in median longitudinal section (a number of cells have immigrated into the blastocoel). (Further explanation in text on this page.)

are the most primitive even in regard to ontogeny. The invagination, which in *Sycon*, and others, occurs at the front pole immediately after the larva is attached, has, indeed, quite generally been interpreted as a gastrulation. If this is correct—at present we have no sufficient reasons for doubt—we can imagine the phylogeny in the following way (see Fig. 4).

The creeping *Bilaterogastraea* became sessile by attaching itself with the margin of the middle part of the elongated primitive mouth. As no fixation to the substratum thus took place in front and behind, where an uplifting occurred instead, the alimentary current through the intestine could continue unhampered as before, i.e., with intake at the anterior end and outlet at the hindmost one (*e*). These two openings were not affected by the increase in size of the surface of attachment by the fusion of the lateral margins of the primitive mouth.

Then the following changes occurred in connection with an everincreasing size of body. The incurrent opening grew larger and more complicated through the formation of indentations in the margin (*b*). These indentations were cut off through fusions, so that a number of pores were formed (*c*). After multiplying copiously by division and displacement, these incurrent pores were finally distributed over the entire surface of the body. The excurrent opening, on the other hand, remained undivided. It was only displaced upwards, and took up an apical situation. Through these changes a form thus arose, agreeing with the recent *Ascon* type (*d*).

A course of evolution of this kind seems to me to be probable on account of the gradual changes in form, which at no point demand an improbable alteration of the feeding biology. It has the whole time been a question of ingestion of food particles following with the water current, and no change in the direction of flow has to be assumed.

To consider the pores as phylogenetically new formations (which has usually been done because the blastopore closes after attachment) is a biological absurdity. They are new acquisitions only ontogenetically speaking, i.e., it is the ontogeny that is changed, a conclusion well in accord with the great variation regarding the larvae in the group.

It may be mentioned that also NAEF (1931), although without motivation, claims a successive origin of incurrent pores out of the primitive mouth. On the other hand, he considers, strange to say, that the osculum can be a new formation. REMANE (1954) agrees with this opinion. I, for my part, find it difficult to imagine such a possibility.

Finally, to return to the larvae once more, it has often been pointed out as a peculiarity that they attach themselves with the pole of the primitive mouth, or, more correctly speaking, that the primitive mouth develops in the front. If *Porifera* and *Cnidaria* have their origin in one and the same gastraeal type, then, as the larvae in the latter group have their mouth at the posterior end, a displacement must have occurred in one of the groups, or perhaps even in both. As the sponge larvae are so variable, it might seem most probable that it is these that have changed. I admit that this can very well have been the case, but I want at the same time to draw attention to the change, to which the orientation of the body has obviously been subjected in the cnidarian line during the evolution from gastraea (see p. 334). The change in position of the primitive mouth derivatives has, in any case, been very considerable in both groups, and it is therefore really impossible to give preference to any of the possibilities. With regard to the fact that even in numerous other groups great changes in the orientation of the body and position of the mouth and other openings happen during ontogeny, and have happened during phylogeny, I cannot see in the above-mentioned difference any decisive obstacle to a phylogenetic connection between the larvae of *Porifera* and *Cnidaria*.

On the basis of the above attempt to reconstruct the phylogeny of the *Porifera* it is, therefore, not impossible to let the group emanate from the same side-branch as *Cnidaria* and *Ctenophora*. That is to say, these three groups could all have a common origin from some gastraeal form in the stem which later leads to *Coelomata*.

On the other hand, can both the peculiarity that *Porifera* however show, as well as a certain other reason, motivate an earlier, direct branching off from a still more primitive gastraeal ancestor in the main stem (see diagram,

p. 352). This other reason is that the gastraea, from which both *Cnidaria* and *Coelomata* evolved, had reached a certain complication as regards the intestine, inasmuch as this had diverticula (see p. 334). As there is no reason at all to suppose such an intestine organization in the ancestor of *Porifera* as well, I have adhered to this earlier branching off of the sponges.

Whichever branching we accept, we must nevertheless start from a *Bilaterogastraea*, as only a being of this kind is able to explain satisfactorily the organization and the course of the food current in the sponges.

It may be emphasized that this opinion has the consequence that even the *Porifera* — in spite of their undoubted primitiveness — must be considered to a certain extent as a regressive group. It seems to me a priori hardly probable that the sessile mode of living and the special food-intake should not at all have brought about reductions. The lack of sensory cells, of a nervous system, and of muscles should be seen against this background (compare the organization in *Bilaterogastraea*, p. 329).

4. *Planuloidea*

This mysterious group cannot be entirely ignored in this discussion on account of its being as a rule included among or near to the "coelenterates". LEUCKART's supposition, that they should be descendents of trematodes, greatly changed and simplified through parasitism, has not received any support, and there is therefore really no alternative, unless we are prepared to consider the group as being directly derived from *Protozoa*, via a stem which has nothing to do with that of the other multicellular animals. On this account I include the *Planuloidea* in my phylogenetic diagram (p. 352), even if I do so with some hesitation. The attempt at interpreting the phylogeny, illustrated here, is in accordance with the opinion expressed by HYMAN (1940), amongst others, that the group can be placed "in an isolated position between *Protozoa* and *Porifera*".

The place for the branching off in the diagram is primarily conditioned by the fact that the organization of the *Planuloidea* exhibits no sign of the group having passed beyond the blastaeal stage. The cells situated inside the "somatoderm" are all concerned with reproduction only, and nothing indicates that they have ever had anything to do with nutrition. We can, therefore, not speak of an entoderm. Conditions here evidently agree in principle closest with those in *Volvox*.

It is of special interest in this connection, that the *Planuloidea* display certain features of bilateral symmetry. This applies both to the arrangement of the cells in the anterior end of the body in the agamogenetic individuals of certain species, and to the entire organisation of the category that HARTMANN considers to be males.

We can thus make this important statement, that the organization in the *Planuloidea* by no means contradicts the basic idea of this paper. It has on the contrary strengthened the derivation of the group from a *Bilateroblastaea* as attempted in the evolution diagram.

IV. Origin of Mouth and Anus in the Coelomata

As is well known, the *Coelomata* are divided according to HATSCHEK into two great taxonomic categories, which nowadays are generally designated by the names of *Protostomia* and *Deuterostomia*. With these expressions GROBBEN emphasized the difference between the complexes as regards the connection of the blastopore with the mouth and anus respectively. This was thought to constitute a profound difference, which not only concerned embryology but also phylogeny. In agreement with GROBBEN (1908) it has also been rather universally supposed that *Protostomia* and *Deuterostomia* have a common root, i.e., that the *Coelomata* should have a monophyletic origin from "*Coelenterata*". As these latter have only a single gastric orifice, the opinion has more or less clearly been pronounced that this orifice of the ancestor gave rise to the mouth in the one case (*Protostomia*), and to the anus in the other (*Deuterostomia*). The matter can also be expressed by saying that the mouth in *Protostomia* should be homologous with the anus in *Deuterostomia*, while the anus in the former and the mouth in the latter should be new formations without any phyletic connection, which have arisen secondarily in two different regions of the body.

This opinion has hardly been presented anywhere in such a direct and unambiguous way, but even in several later authors (e.g., FRANZ 1924 and v. D. HORST 1939) it is quite obvious that this is the innermost intention. Nor should such great weight have been laid on a purely embryological condition, if it was not supposed to recapitulate the phylogenetic changes.

According to GOETTE's opinion (Lehrbuch der Zoologie, 1902), to which, amongst others, FRANZ gives his close support, the large primitive mouth in the earliest protostomian ancestor should have been closed from behind and forward, so that only a smallish opening was left in the front, which there assumed the exclusive function of mouth, while an anus was newly developed in the posterior end. In the deuterostomian ancestral form, on the other hand, the gastrula-like body should have lengthened in its main axis and laid itself on one side, a mouth at the same time being newly formed in what thus became the anterior end (originally the apical pole). On account of these dissimilarities in the evolution the front end of the *Protostomia* should thus correspond to one of the long sides (the ventral one?) of the *Deuterostomia*, and the ventral side of the *Protostomia* should be identified with the posterior end of the *Deuterostomia*. In accordance

herewith GOETTE maintains that *Protostomia* and *Deuterostomia* "können daher nicht auf eine gemeinsame ursprüngliche Bilateralform zurückgeführt, sondern müssen als getrennte Stammreihen aufgefasst werden, mögen sie gelegentlich und im einzelnen einander noch so ähnlich erscheinen" (1902, p. 125). These are far-reaching conclusions from the embryological conditions!

A somewhat different opinion has recently been advanced by BOETTGER (1952). He supposes that a primitive ancestral form of coelenterate type "lay down" in conjunction with its body being lengthened longitudinally, and then became bilateral. In the original aboral pole an opening was newly formed, whereupon the wormlike body thus had an orifice at each end, one being original, the other secondary. At that stage the food current could pass the body alternately in both directions! When division into *Protostomia* and *Deuterostomia* occurred, conditions were stabilized inasmuch as in the former line the original opening became exclusively an intake opening (mouth), the secondary exclusively an outlet pore (anus). In the deuterostomian line, on the other hand, the food current took the opposite direction. In other words, the anterior end in *Deuterostomia* corresponds, according to BOETTGER, to the posterior end in *Protostomia*.

This attempt at interpretation has the advantage over the older opinion mentioned above that a new formation of a gastric orifice need be assumed only once.

Are we then really justified in such an assumption that a mouth and an anus can be newly formed? This is a very important phylogenetic question, which must not be overlooked. When so far a new formation has rather generally been considered possible, this thought was probably, even where this is not directly avowed (and inasmuch as premisses and consequences were at all given due consideration), based upon the fact that there occur, particularly in cnidarians, several secondary pores. These have been newly formed, and the same might also have happened with a mouth.

For my part I consider this to be a happy-go-lucky reasoning. The origin of a mouth in the way supposed implies not only that the intestine connects itself with the outer world, but also a radical change in function and morphology in numerous points: musculature, nervous system, sensory organs, cilia activity, etc. Indeed it probably affects the entire organization of the body. The changes in this respect are not completed at the moment of, or shortly after, the formation of the opening itself, and even if one imagines that the opening, to begin with, had a different function or perhaps no function at all, and first gradually began to be used as a mouth, I have great difficulty in agreeing to this reasoning. The circumstance that the animal kingdom displays many morphological phenomena which are hard to explain, gives us no right in phylogenetic argumentations to draw any sort of improbable conclusion.

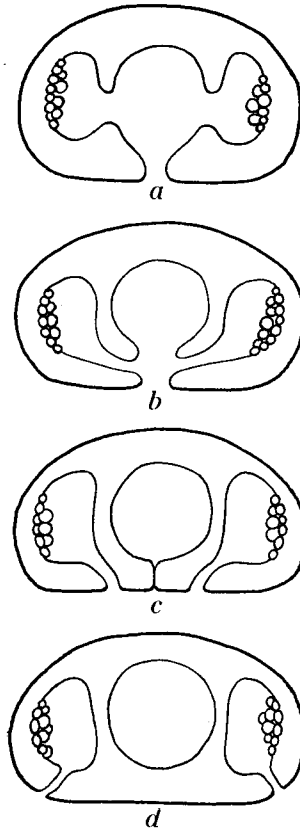


Fig. 5. Diagrams showing the changing of the gastric pockets into coelomic sacs and the downward wandering of the orifices from the intestine. Cross section of body. *a*, "*Bilatero-gastraea*"; *d*, "*Protocoeloma*"; *b* and *c*, intermediary forms.

One doubtless asks oneself in this connection, why the food-transport into the intestine (respectively the conveyance of the excrements out from it) after the new formation of a gastric pore should take quite a different way than before. Since, as has been said, a change in any case cannot have occurred quickly, one must presume that the animals during a period of evolution had two mouths. We have no example of such a strange morphological state, and it is, at least in a creeping bilateral animal, very unlikely.

Now, what has given rise to this improbable doctrine about new formation of mouth and anus? Well, as has already been hinted, it is the way for the embryological development of these openings that is the cause and the *only* cause! The doctrine arose during an epoch when embryological facts often were over-estimated in phylogenetic investigations. The understanding of caenogenetic embryonic stages was limited. Apart from this the difference

between *Proto-* and *Deuterostomia* as regards the embryological formation of mouth and anus was overemphasized. As is well known, we have in both the categories examples of the blastopore being completely closed, and thus not being retained in either of the openings. There exist, in addition, reports that the blastopore also in *Protostomia* can give rise to the anus (e.g., *Paludina*). If we moreover consider that it also occurs that both mouth and anus arise from a longish blastopore (*Peripatus*), and further that the mouth is formed in front of, and the anus behind a shrunken remainder of the blastopore (the nemertine genus *Drepanophorus*), we realize on what shaky ground the doctrine mentioned is based.

If, in return, the above-described "*Bilaterogastraea*" is taken as the starting point in the derivation of mouth and anus in *Coelomata*, no difficulties are encountered.

It has been presumed above that this creature had an elongated ventral gastric opening, of which the front part served as a mouth, the hind part as an anus. The middle part, on the other hand, was of subordinate importance from a functional point of view. No difficulty is therefore met in assuming that the margins gradually approached one another in the median plane, and finally fused (Fig. 5c and d). Mouth and anus as they exist in *Coelomata* had thereby been formed in principle (Fig. 1 f).

In this connection no changes as regards the course of the food current have had to be assumed.¹ Nor does this way of thinking lead to any improbable consequences in a comparison between *Proto-* and *Deuterostomia* as far as the orientation of the body is concerned. Both these great categories can be derived without difficulty from a primitive coelomate ancestor (see further details in next section).

Such a fusion of free margins as has been assumed here, is not by any means a unique occurrence. Numerous similar cases are well known, e.g., as regards the funnel of the cephalopods, and the mantle-border of the mussels. A still more interesting parallel we find in *Anthozoa*, where in certain sea anemones the siphonoglyphs have been entirely separated from the middle part of the stomodaeum through fusions in the mouth margin, so that three openings have been formed. Mention may also be made of *Tjalfiella*, in which the margins of the middle part of the mouth are fused in essentially the same way as has been assumed above.

As is well known, the theory presented here regarding the origin of mouth and anus is by no means new. It has been maintained by both older and more recent (REMANE 1950) supporters of the cyclomerism theory, and also by phylogeneticists, who derive the *Coelomata* from a radial gastraea (e.g.,

¹ I consider it very important that the food current can be assumed as being unaltered. On this point I disagree with NAEF (1931), who considers that mouth and anus originally had the same function.

NAEF 1931, SNODGRASS 1938). When in spite of this I have here discussed the problem in some detail, it is primarily on account of the new points of view which have arisen in connection with my theory of *Bilaterogastraea*, but also because of the obstinacy with which the improbable conception of new formation of the mouth still lingers on, and which recently appeared in a new variation in BOETTGER's above-mentioned account.

It may finally be pointed out that no doubt is thrown, by what has been said above, on the general opinion as to the division of the coelomates into *Protostomia* and *Deuterostomia*. The distinction of these great taxonomic categories is still sufficiently warranted, even if the differences with regard to the origin of mouth and anus are eliminated from the phylogeny.

V. "Protoceoloma", its Origin and Organization

Above I have arrived at the result that the *Bilaterogastraea* in the main stem, which gave rise to the *Cnidaria*, had three pairs of gastric pockets containing the gonads. As this gastraea is also the ancestor of the *Coelomata*, its organization is deduced from the conditions in the primitive forms in both the complexes. I have, in other words and briefly expressed, homologized the three pairs of coelomic sacs in, in this feature, primitive deuterostomians with the paired gastric pockets in *Octocorallia* (see above, p. 334).

I admit that originally this was not my opinion but that I derived the *Cnidaria* from a gastraea with a simple intestine. The position taken in the question has not any influence either on the construction of the phylogenetic diagram (p. 352). However, it is necessary in any case to suppose that gastric pockets developed in the main stem "fairly soon" after the branching to the *Cnidaria*. For this reason, and since nothing seems to prevent the above-mentioned homologization, it can be justifiable to presume the existence of gastric pockets already in the common ancestor of *Cnidaria* and *Coelomata* (at point 8 in the phylogenetic diagram). This conclusion is obtained more or less as a by-product (although an important one) when analysing the diagram. When, as I showed above, the organization in *Anthozoa* can very well be thought to date back to the conditions in a *Bilaterogastraea* provided with three pairs of gastric pockets, the whole seems to work out very well.

The following must be emphasized regarding the gastric pockets and their change into coelomic sacs. The supposition that they contained the gonads in their wall can be considered justified with regard to the conditions in both *Cnidaria* and *Coelomata*. (The fact that the gonads in *Hydrozoa* lie in or close to the ectoderm is in accordance with this group being modified also in other respects.) The sexual products in *Bilaterogastraea* thus were discharged from the mouth. There is reason to suppose that the mode of

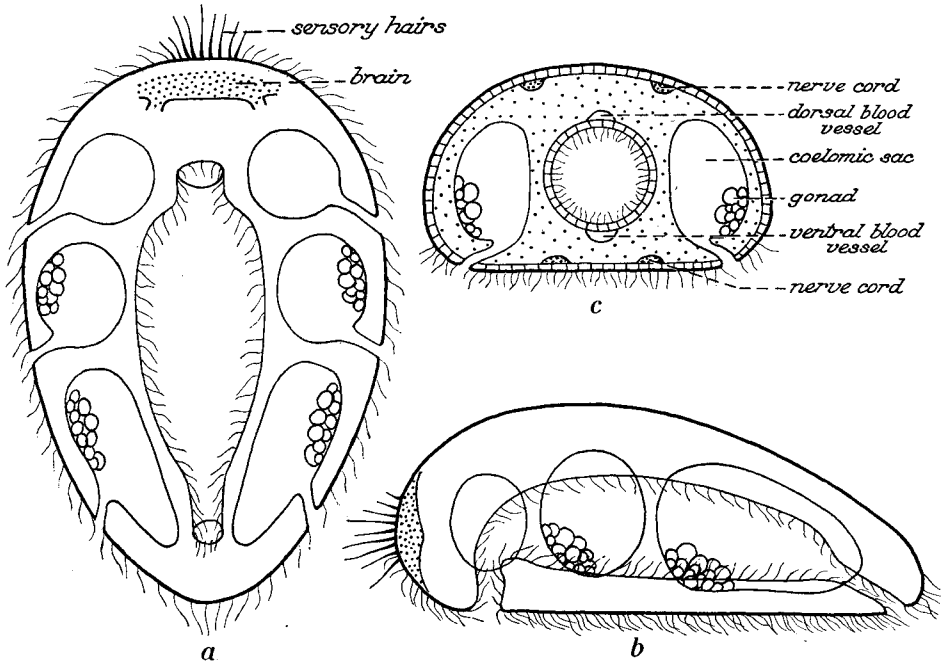


Fig. 6. Diagrams showing "Protocoeloma": a, seen from ventral side; b, longitudinal section (coelomic sacs are projected in the median plane); c, cross section.

discharge was not subjected to any speedy change. A possibility like the forcing of the sexual products directly through the integument along newly-formed passages, once the gastric pockets had been cut off from the central intestine, appears to me improbable. We must instead presume a more "natural", successive change, consisting of the openings of the pockets in the central stomach being shifted more and more in a ventral direction, so that finally they came to lie in the ectoderm outside the oral slit. Fig. 5 illustrates some steps in this displacement of the coelomic pores. First after the downward displacement the fusion occurred between the lateral margins of the oral slit, as described in the previous section.

Herewith the ancestor of the *Coelomata* was established in principle; *Bilaterogastraea* had evolved into a "Protocoeloma". Its most important features in this connection were mouth and anus as well as three pairs of coelomic sacs, containing the gonads, and provided with a direct outlet each. It is possible that the foremost pair of sacs had lost the gonads (Fig. 6).

Regarding the organization in other respects the following can be said. The shape of the body probably did not differ essentially from that of *Bilaterogastraea*: flat ventral, and somewhat arched dorsal side, and at least ventrally a covering of cilia serving locomotion, thus on the whole resembling

a turbellarian externally. The size was undoubtedly inconsiderable, one or a few millimetres.

The nervous system retained its organization from the gastraea with a primitive brain at the base of the sensory cells in the front end as well as a diffuse nerve plexus, but to this might have come at least two pairs of longitudinal nerve cords, one dorsal and one ventral, differentiated from the plexus and communicating with the brain. The nervous system was certainly still epidermal.

Special excretory organs were probably lacking. Excretion can be assumed as being located in the coelomic sacs, and the excretory products were ejected through the coelomic ducts. (The supposition of the urogenital function of the coelom and the coelomic ducts is based on well-known conditions in *Coelomata*. It is not only the discharge of the sexual cells but also the removal of the excretory products, which necessitate the supposition of a successive displacement of the openings of the coelomic ducts.)

The blastocoel was probably for the greater part encroached upon by the capacious intestine and the coelomic sacs. Between these organs and the epidermis a scanty connective tissue and insignificant muscles were to be found, the latter partly in the form of a weak subepidermal musculature. This mesenchymal mesoderm was probably for the major part of an entomesodermal nature. It is doubtful if any circulatory system was differentiated. (In Fig. 6c, however, the possibly existing longitudinal vessels have been indicated.)

The ontogeny in *Protocoeloma* took place as in the gastraeal being with cleavage of the radial type and with coeloblastula and invagination gastrula. At the formation of the mouth, anus, coelom, etc. the phylogeny was recapitulated. A pelagic stage (larva) is to be assumed.

With a derivation as undertaken here I have, although by a different way, arrived at the same result as the cyclomerism theory, which likewise claims that the coelomic sacs are homologous with the gastric pockets in *Anthozoa*. The cyclomerism theory in its original form (SEDGWICK 1884) differs, however, from my derivation in two important respects, viz. in that it assumes the ancestor to have been an anthozoan type, and that the annelid type should have arisen directly from this.

More in agreement with *Protocoeloma* is the primitive coelomate animal, which REMANE (1950) has arrived at in his modification of the cyclomerism theory: It should have had a tripartite coelom (axo-, hydro- and somatocoel). Its ancestor should have been a tetramerous, radial coelenterate, and hereby REMANE shows that his opinion is based on HAECKEL's idea regarding a radial gastraea. REMANE's derivation has, however, according to my opinion not only an improbable foundation; it also leads to a serious consequence, viz. that both the first and the third coelom section in primitive coelomate

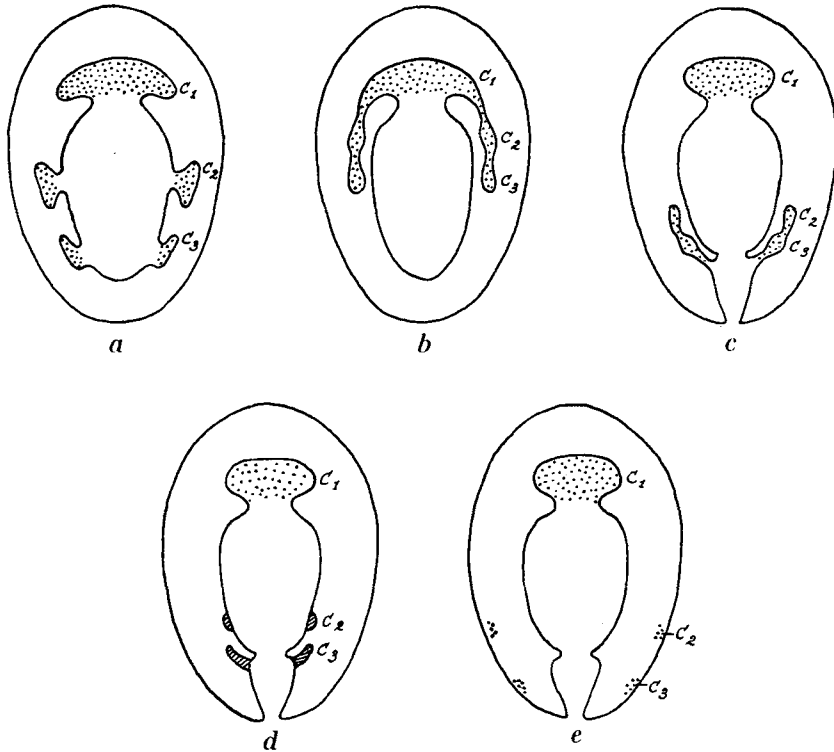


Fig. 7. Diagrams showing different ways for coelom formation in helminthomorphous *Enteropneusta*. a, *Dolichoglossus kowalevskyi*; b, *Dolichoglossus pusillus*; c-e, different Tornaria larvae. (From KORSCHULT & HEIDER 1936.)

animals must be considered as primarily unpaired. It is apparent from REMANE's discussion that he has here got into a quandary. He admits that much speaks in favour of the "axocoel" being originally paired, and his arguments for primary unpairedness are also scarcely convincing. (This opinion was retained, however, also in a paper published quite recently, 1954.) REMANE emphasizes first the uncertainty in the often presented opinion that the pericardial sac in the *Enteropneusta* should be a counterpart to the big proboscis cavity. He then bases his views on the usual opinion that in *Cnidaria* the tetramerous character is more primitive than the hexamerous, as well as on certain embryological conditions in *Coelomata*, which should indicate that the "somatocoel" both in *Enteropneusta* and in the fundamental type of the annelids should have an unpaired origin.

Concerning, first, the opinion about the primitiveness of the tetramerous character in *Cnidaria*, we need only point out that this is incompatible with the basic idea in the present paper. Besides, if we accept the *Bilaterogastraea* as an ancestor of *Coelomata* as well, the symmetry conditions in *Cnidaria* are entirely without importance in this connection.

Concerning the pericardium of the *Enteropneusta* opinions are admittedly divided, but the nature of the organ is not of decisive importance. The proboscis coelom can very well have originally been paired, even if it should prove that the pericardial cavity is not a modified coelomic sac.

Neither does the unpaired ontogenetic origin of the proboscis coelom seem to me to be decisive, as it is obvious that the *Enteropneusta* show numerous secondary modifications as regards the ontogeny of the coelom (see Fig. 7).

REMANE's attempt at obtaining support for the view that the third coelomic section should have been changed secondarily to paired condition seems to me to be hardly convincing, quite apart from the difficulty of using, in this case, ontogeny as a basis for conclusions. REMANE makes use of a drawing in BATESON (1884) showing the development of the coelomic sacs in *Dolichoglossus kowalevskyi*. BATESON intends to show that the "somatocoel" (like the "hydrocoel") arises as a paired formation. REMANE, however, thinks that the entire posterior portion of the entoderm can be regarded as a single unpaired enterocoel formation, and alters BATESON's drawing accordingly.

This interpretation of REMANE's seems to me to be rather arbitrary. Moreover it should be noted that the helminthomorphous *Enteropneusta* display several other variations as regards the development of the enterocoel; even in the genus *Dolichoglossus* very great differences are to be found (see Fig. 7). If, in spite of this, one should attach importance to the embryological conditions in the group, then it is not in any case possible to discover any hints that the third section of the coelom is primarily unpaired. The embryology indicates instead that this section, similarly to the middle one, has a paired origin.

In addition to what has now been said the following facts, at least, are of importance in this connection:

- 1) Both in *Helminthomorpha* and *Pterobranchia* the occurrence of two pores leading out from the proboscis cavity has been established. These are of the same nature as, and apparently homodynamic with, the pores of the collar coelom.

- 2) In the echinoderm larvae three pairs of sacs appear during the course of development and the two sacs in the foremost pair (the axocoel) have at times a pore each.

- 3) All three coelomic sections are paired in the *Chaetognatha*.

These facts do not agree very well with REMANE's theory about a radial ancestor with four gastric pockets but they perfectly agree with my opinion that also the *Coelomata* originated from a *Bilaterogastraea* with three pairs of gastric pockets, via a *Proto-coeloma* with three pairs of coelomic sacs, each of which opened outwards directly through a pore or short duct. When it is a question of choosing between a bilateral ancestor or a radial

one for bilateral groups of animals, the arguments for the latter must be considerably stronger than those presented by REMANE. It should be noted, however, that no acceptable alternative to a radial ancestor had really existed until the presentation of the theory of the *Bilaterogastraea*. This theory fills in reality a need, also when the understanding of the original organization of the *Coelomata* is concerned.

In expounding above my opinion of the evolution from *Bilaterogastraea* to *Protocoeloma*, attention has been paid to the origin of the coelomic ducts. REMANE, on the other hand, does not touch on this question, nor on the history of the gonads.

A derivation of the coelom from gastric pockets containing gonads in a gastraeal ancestor has also been attempted by NAEF (1931), yet he does not assume more than one pair of pockets, respectively one pair of coelomic sacs in the hypothetical "helminthoid". The reason for this is that NAEF connects his idea directly with the corm theory and thus lets the primitive coelomate via asexual reproduction become metameric. It should be noted that also HEIDER (1914) provides his "sphenula" with only one pair of enterocoel sacs. The reason is that HEIDER follows HATSCHKE's trochophore theory and therefore constructs the sphenula in such a way that it fits in this connection. (Ultimately HEIDER derives the *Coelomata* from the ctenophore type and thinks that the bilaterality arose in spite of the pelagic way of living! As is well known, also GROBBEN has imagined such an origin.)

When I claim here that the coelom is derived from gastric pockets, I am partly standing on the same ground as the above-mentioned and other supporters of the enterocoel theory, i.e., I attach in this case importance to the ontogenetic facts too.

Still more important, however, are the comparative morphological arguments. The enterocoel theory can be regarded as one of the more well-founded morphological theories, and it might also be considered as generally accepted at the present time. It may, however, be emphasized that I, similarly to HEIDER and NAEF and others, give a *special content to the enterocoel theory: it becomes a "gono-enterocoel" theory*. This view stands on firm ground owing to the conditions in the coelenterates and ought to be applicable as a sustaining principle in the explanation of the highly variable organization in the *Coelomata*. (I hope to be able to revert to this in another connection.)

VI. Summary

Since an explanation of the adjoining evolution diagram (Fig. 8) constitutes, to a certain extent, a summary of the main results of the present investigation, I shall conclude this paper by such an explanation.

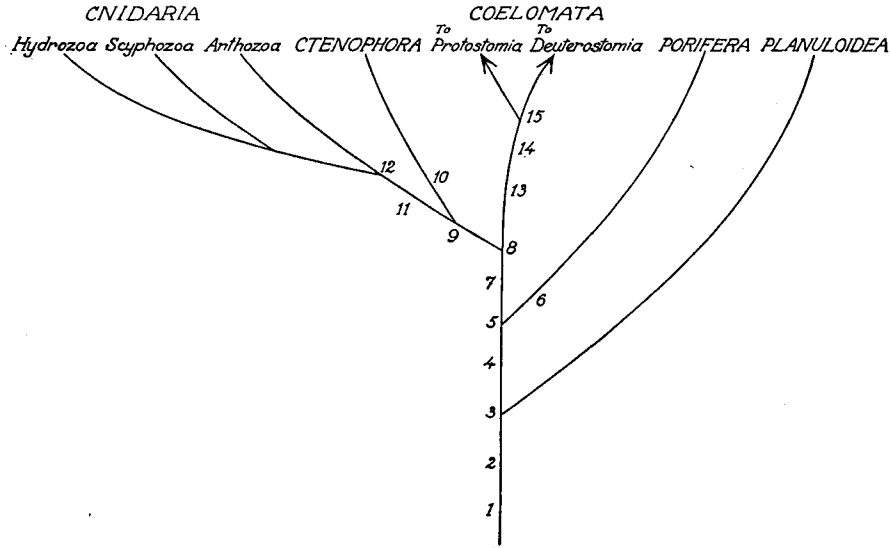


Fig. 8. Explanation in text below.

The diagram illustrates only the lower part of the "phylogenetic tree" of the *Metazoa*, up to the very beginning of the differentiation of the *Coelomata* into two main branches; a branching off to the numerous present-day phyla had not as yet occurred. Regarding the four so-called coelenterate groups it may, on the other hand, possibly be assumed that, at the time in question, they had already reached in principle the organization which they have retained up to the present day. (It might be conceivable that the *Planuloidea* had not yet changed to parasitism.)

The figures in the diagram mark the places where specially important conditions were present or occurred. These places are:

1. Pelagic, spherical "*Blastaea*".
2. Change to benthonic life.
3. Benthonic, creeping "*Bilateroblastaea*" (Fig. 1a).
4. Formation of primitive intestine through invagination of the ventral side.
5. "*Bilaterogastraea*" with simple intestine (Fig. 1c-e).
6. Attachment and subsequent change to *Ascon* type (Fig. 4).
7. Formation of three pairs of gastric pockets.
8. "*Bilaterogastraea*" with three pairs of gastric pockets, containing the gonads (Fig. 2a).
9. On the whole resembling 8.
10. Change to pelagic life and then successive transformation towards the ctenophore type (Fig. 3).

11. "*Bilaterogastraea*" with three pairs of gastric pockets attaches itself and subsequently changes successively towards the primitive cnidarian type (Fig. 2).

12. The ancestor of the *Cnidaria*, most closely resembling a small, solitary octocorallian polyp, without skeleton.

13. "*Bilaterogastraea*" with gastric pockets changing into coelomic sacs.

14. Type between 13 and 15 with the coelomic ducts opening outside the oral slit, which now begins to fuse in the middle part (Fig. 5c).

15. "*Protocoeloma*" with three pairs of coelomic sacs (of which the foremost probably had lost the gonads) as well as mouth and anus (Fig. 6).

The presented "*Bilaterogastraea*" theory implies, in addition to what has been said in the explanation of the diagram, inter alia the following conclusions:

a) In all animal groups with an alimentary current through an intestine this current has its origin in the locomotory movement (due to cilia action) of the common blastaeon ancestor,

b) Invagination is, in spite of other attempts at interpretation, to be considered as the original mode of gastrulation,

c) No multicellular animal group is to be considered as primarily radially symmetrical,

d) The incurrent pores as well as the osculum in *Porifera* are derivatives of the primitive mouth of the gastraeon ancestor,

e) The *Anthozoa* are the most primitive of the three cnidarian groups. Their lack of a medusoid generation is an original feature,

f) Mouth and anus, respectively, in *Protostomia* are, in spite of other attempts at interpretation, to be considered as homologous to the orifices with the same function in *Deuterostomia*,

g) The coelomic sacs in *Coelomata* are homologous to the paired gastric pockets in *Octocorallia*,

h) The gonads lay primarily close to the intestine (entoderm) and were separated from it in connection with the origin of the coelomic sacs. The enterocoel theory is to be given a special content, i.e., must become a "gono-enterocoel" theory.

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