On the Origin and Phylogeny of the Coelenterates[1]

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IN the last few years an intriguing argument has developed concerning the origin and phylogeny of the coelenterates, or more properly, the Cnidaria. The argument, in its simplest form, consists of two quite opposite views which hold that on the one hand the Hydrozoa are the more ancient class of the phylum while the other argues for the Anthozoa as the more ancient. This latter view stems from the work of Hadzi (1944, 1953), while the opposing view is an older one and is discussed, championed, and extended by Hyman (1940, 1959). The more traditional viewpoint, that of Hyman, holds that the ancestral cnidarian was a primitive medusa which developed from a planula to an actinula. The actinula at some time evolved the habit of budding other actinulae before its own metamorphosis to the medusa. This habit of budding established the hydroid phase as we know it today. In this theory the pre-cnidarian is held to have been a gastraea type of organism, polarized and free-swimming. Hyman (1940, p. 634) further suggests that the gastrea went on to a hypothetical stage which she pictures as being ". . . a small rounded bottom-feeding organism with a ciliated surface, mouth, archenteron, and aboral sense organ. There were probably some mesenchyme cells of ectodermal origin between ectoderm and entoderm, and the archenteron may have had lateral pockets in which the sex cells ripened. Such a hypothetical organism has been named by Naef a metagastraea."

This theory may be called the *medusa theory* and accepts the radial symmetry of the cnidarians as a basic and primitive character.

The opposing point of view to the medusa theory is the *turbellarian theory* as developed by Hadzi. He holds that the primitive cnidarian was an anthozoan polyp, derived ancestrally from a rhabdocoel turbellarian. This derivation assumes that a flatworm became sessile and developed the features of the anthozoan polyp. Thus the bilaterality seen in anthozoan polyps would be a primitive and basic cnidarian feature. Radiality would be a secondarily developed character derived as a by-product of the sessile habit. Jägersten (1955) and Marcus (1958) both accept the Anthozoa as the most primitive of the Cnidaria, although neither adds new factual material to the general theory.

It is the purpose of this paper to assess these two contrasting theories to see if a marshalling of the data can lead us to a conclusion that one or the other can better be accepted. It is not my intention to delve into the question of the origin of the Metazoa nor to assess in detail all of the phylogenetic speculations set forth by any of the afore-mentioned authors. Our question is, "*Is radiality or bilaterality the more primitive symmetry of the Cnidaria and, as a corollary, is the tetramerous medusa or a bilateral polyp the more ancestral body form?*" Like Carter (1954, p. 163) I hope that it will be ". . . on a *balance* of all the evidence, whether old or new, that we should [will] found our conclusions."

With this brief introduction it is time now to examine our theories in detail.

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[1] Dr. Hand was unable to be present in person. Dr. M. J. Greenberg of the zoology department of the University of Illinois kindly consented to read his paper.

There is one interesting similarity between them, namely the general agreement that the pre-cnidarian was planula-like. Beyond this the theories diverge completely. That the planula as a larva is basic to the Cnidaria is readily acceptable and that a planuloid organism may have been ancestral to both flatworms and cnidarians seems reasonable. These conclusions unfortunately do not tell us which came first, the Cnidaria or Platyhelminthes, however, and so do not help us solve the problem at hand.

The question, which seems most in need of resolution, is what was the original or primitive symmetry of the Cnidaria. If we could answer this we could take some stand on the phylogeny of the group. Actually part of what we are trying to answer is more fundamental than our immediate question. What we are seeking an answer to is whether the Radiata (Cnidaria and Ctenophora) is a valid evolutionary concept; that is, is radial symmetry more ancient of itself than bilateral symmetry?

Radial symmetry is clearly referable to a sessile way of life. The radiality of echinoderms or of acorn barnacles seems best explained in this way. We could also point to the radial arrangement of the tentacles of such sessile groups as entoprocts, ectoprocts, some polychaetes, and phoronids as further evidence that our generalization is valid. Using these groups as evidence the contention that the radial symmetry of the Cnidaria could be derived from sessility is admissible. This, of course, is an important part of the turbellarian theory. However, the admission of the association of radial symmetry and a sessile way of life does not necessarily prove that the Cnidaria have been derived from sessile ancestors. I think the possibility must still be admitted that radial symmetry can have other origins as I will now try to show.

The early development of many organisms takes place in an aqueous environment. Sometimes eggs are spawned freely into the surrounding water and sometimes each egg or a few eggs are confined in a capsule or a gelatinous envelope. The point is that cleavage and early development in many organisms takes place in an environment that impinges on all sides. For many marine organisms the environment is that of open waters and the developing individual is in fact planktonic. This particular habitat may well be the ancestral one of Metazoa, and the radial symmetry exemplified by most cleaving embryos through the time of their gastrulation may be related to their planktonic development. I think there is no argument that in general the stages of embryos up to the gastrula are radial, and that it is only in the later stages that this radial symmetry is lost. Therefore I hope we can agree that it is possible that radial symmetry could be primitive in the evolution of the Metazoa and that it could come from sources other than adaptations to a sessile existence.

In the foregoing I stressed the planktonic way of life as being a factor in the development of radial symmetry. Let us explore this further. The Protozoa as a non-metazoan group may be worth looking at critically. Body form in this group must be susceptible to the same evolutionary changes and selective forces as in the Metazoa, but we do not have to be concerned about differences between their embryonic and adult symmetries. Thinking only of the non-parasitic species we can identify spherically, radially, and bilaterally symmetrical forms. As in the Metazoa, many sessile forms are radial. Among the completely free-floating, non-motile forms we find the spherically or radially symmetrical Radiolaria. Some flagellates, foraminiferans, and ciliates are radially symmetrical too. Bilateral symmetry is closely approximated in many creeping ciliates. It is my contention that the radial symmetry seen in the free-floating and weakly swimming forms is the expression of selective forces which tend to lead to radial symmetry in these organ-

isms, just as a creeping existence seems to lead to bilaterality. So far I hope I have established that radial symmetry may be primitive on purely embryological grounds, and that, as well as being related to a sessile existence, it may also result from a free-floating or very feebly swimming way of life.

The only satisfactory examples of radially symmetrical and planktonic metazoans which we can readily cite are to be found among the Cnidaria and Ctenophora. Superficially some rotifers, some trochophores, and other larvae also fit our requirements. Why, one asks, if a planktonic existence is conducive to evolution toward radiality, are not radially symmetrical plankters more common? I believe the answer is that all planktonic organisms at evolutionary levels higher than the coelenterates are derived from bilateral ancestors. This, plus their stronger swimming powers, has made the retention of bilaterality of greater advantage than a secondary change to radiality. I think, too, that the absence of change of body form of such radially symmetrical plankters as the planktonic sea cucumber *Pelagothuria,* the sea anemone *Minyas,* the colonial hydroid *Velella* or *Porpita,* or the colony form of many of the floating siphonophores argues for radiality as being an acceptable and useful body in that habitat. If what I have developed so far is acceptable, both credit and doubt must be equally bestowed on the polyp and medusa as the ancestral body form of the Cnidaria. The radial symmetry of the phylum could be an ancestral inheritance from the origins of the Metazoa, from evolution as planktonic organisms, or from sessility.

Embryology has contributed a great deal to our knowledge of phylogeny and some discussion of what evidence is available here seems well worthwhile. The turbellarian theory requires a flatworm as ancestral to the Cnidaria, and, interestingly, the free-living flatworms at least seem to have settled upon a very precise cleavage pattern known as spiral cleavage.

This same cleavage pattern is typical not only of flatworms, but of nemerteans, annelids, mollusks, and certain additional minor groups. These seems to be little doubt that these great and successful groups, including the flatworms, represent a closely related series of phyla. Hence, one cannot but wonder why the Cnidaria, if they are derived from flatworms, show no signs of spiral cleavage in their embryology. Not only is there no spiral cleavage, but there is no single pattern of cleavage which is descriptive of the Cnidaria in general. This group instead shows a wide variety of cleavage patterns which suggests to me that they represent a very old group, in fact a group so old that cleavage patterns were still being experimented with as this group evolved. I do not believe that one can find a parallel anywhere in the animal kingdom to the one which the turbellarian theory asks us to accept. That is, it asks us to believe that the determinate spiral cleavage which runs through so many successful animal phyla was discarded along with the free-living mode of life, and in its place a whole new series of embryologies has been invented.

One additional and perhaps very significant feature of the embryology of the Cnidaria should be mentioned here. This is that the embryological axis is maintained as the adult axis by this phylum, as indeed it is by the Ctenophora. In all metazoans higher than these two groups, the animal–vegetal axis of the cleaving embryo is soon disguised as the organism assumes its adult form. Blastulae and more particularly gastrulae of many phyla have a simple radial symmetry around the animal–vegetal axis, but in flatworms and all higher groups this symmetry disappears and is replaced with bilateral symmetry. Our two hypotheses about the origins of the Cnidaria look upon these data in very different fashions. The medusa theory accepts the symmetry of the phylum as radial and the radiality is cited as evidence of the primitive nature of the group. The turbellarian theory assumes

the radiality to be secondary and cites the bilaterality of the Anthozoa as evidence. To my mind the maintenance of the embryological axes, as well as the fact that radial symmetry precedes bilateral symmetry in development, is evidence that the primitive symmetry of this phylum is in fact radial. The bilaterality of the Anthozoa will be discussed shortly.

The two theories before us contrast sharply in that one calls the Anthozoa the primitive class of the phylum while the other bestows this position on the Hydrozoa. In general I believe we can show that primitive groups are more variable and less fixed in body plan than are the less primitive or more highly evolved. As examples we could cite the Crustacea as more variable than insects, the polychaetes as more variable than oligochaetes or leeches, the gastropods as more variable than lamellibranchs or cephalopods, and the turbellarians as more variable than flukes or cestodes. If this principle is accepted I think we can also say the Hydrozoa are more variable than Anthozoa or Scyphozoa, and by this suggest that the Hydrozoa are the more primitive. I think one has only to look at the diversity shown among such hydrozoans as the tentacleless *Protohydra,* a hydromedusan, a siphonophore, a hydrocoral, and the pteromedusan *Tetraplatia* to see that this is greater than that exhibited by the other classes. In fact, the Anthozoa exhibit only two body forms, that of the alcyonarian and the zoantharian polyp. These two, while clearly separable, are none-the-less much more uniform between themselves than are the medusoid phases of the nine hydrozoan orders with medusae. We will add here, too, that the nematocysts of the Hydrozoa are more variable than in any other order, a matter we shall mention again. This seems further evidence of the primitive nature of this group. This evidence seems therefore to suggest that the Hydrozoa may be more primitive than the Anthozoa.

Although I do not believe any facts presented so far prove conclusively that the Hydrozoa are the ancestral group of the Cnidaria, we might in any event look at that class to see whether we might be able to make a decision as to whether the polyp or medusa is the primitive adult form there. Throughout the class we find that the medusa is the sexual adult and in most instances where the polyp is the possessor of gonads, we can show that these are borne on structures which are clearly medusoid in origin. Rees (1957) in what should become a classic article on evolution in capitate hydroids has concluded, as have many others, that the medusa is the original body form in this class and that the polyp is of secondary origin. This conclusion seems inescapable and as a corollary the life history of the trachyline medusae which involves no sessile polyps seems to be a logical example of what the primitive hydrozoan life history may have been like.

Earlier in this paper we noted the general agreement between modern theorists that the cnidarian ancestor was planuloid in body form. This planuloid organism must have been ciliated and most likely swept food into a more or less posterior mouth with the help of cilia just as do some ciliates. These planuloid organisms may have lived on the bottom or somewhere above it. We can well imagine a sensory tuft of cilia evolving as a useful anterior structure. Our planuloid may also have possessed structures similar to trichocysts, rhabdoids, or nematocysts. This particular feature seems to me a most critical point and needs careful consideration. Trichocysts as seen in various protozoans may be cnidotrichocysts, *with eversible structures like a nematocyst,* or typical trichocysts, of solid construction. These structures have several functions apparently, such as protection against predators, food capture, and attachment to the substrate. Rhabdoids, a turbellarian feature, have many varieties, *none nematocyst-like,* and are used for protection and temporary attachment. It is of interest that many of the apparently most primitive turbellaria do not possess rhabdoids.

The nematocysts of the Cnidaria come in many varieties, and they function, like trichocysts, in food capture, protection, and attachment to foreign objects. From this brief discussion of trichocysts, rhabdoids, and nematocysts we could well conclude from the modern distribution and function of these structures that our planuloid was more closely derived from the ciliates than from the Turbellaria. We can add here that nematocyst-like structures also occur in the cnidosporidians and the dinoflagellates. This reinforces our general point of the moment that the planuloid may have been closer to the Protozoa than the Platyhelminths.

How now might our planuloid have evolved? In the development of coelenterates the planula must grow tentacles, either as it becomes an actinula or medusa, or as it settles and attaches to become a polyp. Also, both the medusa and turbellarian theory suggest that the development of tentacles is intimately concerned in the evolution of the Cnidaria. That tentacles arise early in development and that they are characters of the Cnidaria is a matter of fact. Now, can we derive some conclusion about the early cnidarian from this information? Tentacles are used by cnidarians primarily as aids in the capture of active food organisms. We can now imagine our planuloid developing tentacles armed with intracellular nematocysts. As this little organism's arms contact small prey, the prey is stung and carried to the mouth. This newly tentacled animal fits our concept of the actinuloid, but where did it live? If it had been a creeping bottom dweller one wonders if tentacles spread out to the sides or trailing behind would have been practical. I would think these structures would have soon found themselves tangled with minute debris and difficult to work with for a creeping organism. It seems better, then, to imagine our actinuloid with a planktonic way of life, using its tentacles to capture other little plankters.

Another possibility must be discussed at this point. The turbellarian theory requires that sessility develop as a first step in the evolution of the Cnidaria. If we look at the many other sessile groups of animals we note that nearly all utilize ciliated surfaces in food gathering. This is a most successful way of life as is shown by the following list of sessile forms which feed this way: sponges, entoprocts, ectoprocts, most rotifers, phoronids, brachiopods, mollusks, sipunculids, echiuroids, polychaetes, ophiuroids, hemichordates, and urochordates. The only exceptions are the cnidarians, some ctenophores, the barnacles which capture their food with setous nets, and a few rotifers which have developed special traps. The Turbellaria, with their ciliated surfaces, would seem well preadapted to ciliary feeding if they became sessile. However, ciliary feeding is restricted among the Cnidaria to a few anemones and corals. Even in these forms, nematocysts capable of capturing prey are present, and these animals are seldom solely dependent on cilia for food gathering. The ciliary feeding here is best interpreted as a recent innovation. None of these facts seems to support a flatworm as an ancestral cnidarian. I find Hadzi's contention that a well organized flatworm gave rise to an anthozoan polyp unacceptable on this account alone, since by analogy the ancestral flatform should have evolved as a small particle feeder, not as a predator of the cnidarian type. The strength of our argument would seem to be that nowhere in the flatworms can we find an acceptable prenematocyst structure, but this can be reasonably presumed to have been present in our ancestral actinuloid. This suggests a very early, pre-flatworm stage, separating the two groups of organisms. Moreover, the development of tentacles by the cnidarian ancestor would seem best interpreted as related to a developed or developing predacious way of life in which nematocysts were playing an important role. These tentacles in turn would have handicapped a creeping organism and would seem to have been more effective

and meaningful to a free-swimming form rather than a sessile one.

Now to go a step further with our imaginative story of the evolution of the Cnidaria it would seem to be logical enough if our tentacled-actinuloid by simple and a slight change in form became a recognizable medusa. This would leave us with a hydrozoan medusa, probably of the general group of trachylines, as the ancestral cnidarian.

One would like some additional evidence for the scheme just presented and some indication of the primitive and basic nature of the actinula within the class Hydrozoa is available to us. Totton (1954) has pointed out that the actinula larva is widespread among the Hydrozoa, and Rees (1957) has noted that it is only among the more primitive families of the gymnoblastic hydroids that this larval form is found. From these facts plus our earlier conclusion that the medusa, not the polyp, is the primitive form of the Hydrozoa, we must conclude that the early Hydrozoa did indeed have an actinula larva. Thus, it does not seem unreasonable to imagine that the actinula was a free-floating planktonic organism and was ancestral to the primitive hydrozoan medusa. These conclusions do not tell us whether the Hydrozoa or the Anthozoa may better be considered the more primitive group, however, so let us turn our attention to that matter.

At the undated time at which cnidarians first made their appearance as a discrete phylogenetic entity, they must have had as their companions myriads of other *small* marine organisms. These other small organisms must have served as the food of our ancestral cnidarians, and it seems logical to invoke the use of nematocysts as intimately associated with food gathering. If this is accepted it now is logical to argue that the full grown adult cnidarians were themselves still quite small and that they most logically would have had simple guts. Complexly organized and divided guts such as are seen in the Scyphozoa or Anthozoa seem better

interpreted as adaptations for handling large food, such as probably did not exist at the time of origin of the Cnidaria. I think too that the characteristic presence of nematocysts in the endodermal tissues of these two classes is a sign of their evolution in relation to large and active prey which, even after swallowing, still needed a coup de grâce. This line of thought leads, like others used earlier, to the Hydrozoa, with their simple guts free of nematocysts, as the primitive cnidarian.

Another matter relative to nematocysts can also be developed to support the medusa theory. Many Hydrozoa, although not the simplest groups such as the trachylines, possess a remarkable variety of nematocysts. In the class there occur all the major categories, rhopalonemes, desmonemes, haplonemes, and heteronemes whereas neither of the first two types occur in the Scyphozoa or Anthozoa. The rhopalonemes and desmonemes can be described functionally as being for adhesion and entwining respectively. These nematocysts are effective in holding minute, weakly-swimming prey, but they seem of doubtful utility in capturing large or active prey. On the other hand, the occurrence of only haplonemes and heteronemes, types specialized primarily for penetrating and poisoning prey, in the Anthozoa and Scyphozoa is evidence that these groups evolved later, along with larger and more active food organisms. We should note here too that nematocysts as independent effectors suggest an origin of these structures at a time before the evolution of nervous systems. Thus, the nematocyst might better stem from a protozoan ancestry than from a group as complex as the flatworms.

Another argument, related to feeding habits, can be developed to support our thesis. Loomis (1955) discovered that the omnipresent substance, glutathione, induced the feeding response in *Hydra,* even though no food substances were present. H. A. Schneiderman and H. W. Lenhoff (personal communication) have further shown that this response is widespread in

the Hydrozoa. They could not demonstrate its presence in scyphozoan scyphistomae or such anthozoans as sea anemones. Again in examining the feeding habits of the Hydrozoa we note that they typically feed upon very small metazoans and larvae. The contact of these small food items initiates an immediate nematocyst response, which when the organism is penetrated releases glutathione. This in turn apparently triggers the mouth-opening response. This is an exceedingly valuable bit of behavior since many organisms eaten by hydrozoans are such feeble swimmers and of such low specific gravity that there must be little in the way of mechanical stimuli related to their contact with the hydrozoan. The Anthozoa do not have this response system, and this I would correlate with their evolution as feeders upon larger, more active, and highly evolved metazoans. It must, of course, be admitted that many Scyphozoa and Anthozoa do feed on minute organisms and even detritus, but these forms possess either haplonemes or heteronemes or both; that is, they also possess nematocysts adapted to the capture of large and active prey. This evidence seems to argue that these organisms have only secondarily turned to small particle feeding and supports our contention that the Scyphozoa and Anthozoa evolved in the presence of larger food items than were available to the early Hydrozoa; that is, the Anthozoa presumably are more recent in origin than the Hydrozoa.

One feature of the coelenterates which might, if we could understand it completely, yield some important information is the position of the mouth. As the mouth develops in a planula it clearly is terminal in position, that is it occupies the center of the posterior end of the body as far as locomotion is concerned. The mouth of an adult cnidarian, polyp or medusa, also occupies a central position. Among the free-living flatworms the mouth occupies a ventral position and may be close to the posterior end of the animal, but as far as

can be determined is never terminal. In the embryology of both the flatworms and cnidarians the blastopore develops at the vegetal pole. It remains there in the Cnidaria but among the flatworms it soon occupies a ventral position as a result of differential growth of the larva. Among all of the Cnidaria the mouth or blastopore develops and remains terminal. In view of its generally ventral position in the flatworms, it seems curious that there is no sign of this in such organisms as the creeping planulae of many anthozoans, had they descended from flatworms. I interpret the radial symmetry of the Cnidaria as embryos, as larvae, and as adults to be a truly primitive feature. It clearly is a feature of the embryo and of the planula and only as the planula of the Anthozoa develops its pharynx, siphonoglyph, and mesenteries do the signs of bilaterality occur. These last are adult features and are secondary. The terminal month of the Cnidaria then can be interpreted as a truly primitive feature. Only in the Cnidaria and Ctenophora is this true. Since terminal months seem to be lacking in small creeping animals such as ciliates and flatworms, I interpret the terminal mouth of the Cnidaria as having developed in the pelagic realm. This evidence favors the medusa theory.

A curious feature of the Cnidaria is that the planula attaches by its anterior end if it is to become a polyp. The polyp retains the same axes as the planula, but no "anterior" is identifiable in the attached stage. In all other sessile organisms, and the once sessile echinoderms, the mouth is accepted as an anterior structure. No matter what changes sessility brings on, this landmark seems to retain its anterior location. From these facts I conclude there are basic and profound differences between the Cnidaria and the remaining animal phyla. It is intriguing that, like the planula, the sponge amphiblastula attaches by its anterior end. Also intriguing is the posterior mouth of the Ctenophora. These facts reaffirm my contentions that

the medusa, a pelagic organism, is the primitive form of the Cnidaria.

The relationship of the anterior point of attachment and the posterior mouth in the Cnidaria is also of interest if we look to the flatworms for indications of its origin. Many types of adhesive organs occur in the Turbellaria, some of them at the anterior margin. These anterior structures seem to be used to hold food or in fact to capture it, while more posteriorly located attachment structures may be used to grip the substrate while the worm struggles with some food organism. The only example of a turbellarian flatworm which spends much of its life attached to the substrate which I can find is that of the Temnocephala. These animals attach by a posterior sucker, however, and have an anterior mouth. There may also be a small and anteriorly located adhesive area in certain temnocephalans, but the primary adhesion appears to be the result of posteriorly located structures. In the monogenetic trematodes too, the primary adhesive organ is posteriorly located, and in the rest of the Trematoda the primary adhesive organ is at least posterior to the mouth. The location of the primary attachment structures of the cestodes is not so clear, but if our interpretation of the attachment hooks in the procercoid larva of some pseudophyllidian tapeworms as posterior is correct, then their attachment, too, may at least primitively have been at the posterior end. Granted that there are devices for attachment at the anterior end of some flatworms, none-the-less this group today seems to have settled upon posteriorly located adhesive structures in those forms which spend any considerable portion of their lives as sedentary or attached organisms. From this, as from other arguments, I find it difficult to believe that some archaic flatworm attached at its anterior end and became a cnidarian.

Another discordant feature of the turbellarian theory concerns the fact that, while many sessile animals are hermaphroditic, the sessile Anthozoa usually are not. Quite typically such sessile groups as sponges, barnacles, tunicates, lamellibranchs, and bryozoans are hermaphroditic. Why, one wonders when there seem to be selective forces leading to an association of hermaphroditism and sessility, would the Anthozoa not also show this pattern? This seems all the more curious when we note that the Turbellaria are nearly universally hermaphroditic themselves. Thus we have the picture of a free-living hermaphroditic group giving rise to a dioecious sessile group. This is contradictory indeed. Also contradictory are the hermaphroditic but free-living ctenophores. While I cannot resolve all the contradictions here, I do feel that the dioecious but sessile Anthozoa seem unlikely descendents of hermaphroditic flatworms.

The turbellarian theory also asks us to accept other curious changes. For example as the evolution of the group progressed from flatworms to proper anthozoans the cellular mesenchyme gave way to the much less cellular mesoglea. Complex reproductive organs were replaced by simple epithelial gonads, and all signs of the protonephridial excretory system of the flatworms were lost. The only portion of the nervous system which was retained was the epithelial nerve net. Mesodermally derived muscles also disappeared and striking changes in embryology must have occurred; determinate spiral cleavage gave way to a curious assemblage of patterns of indeterminate cleavage. The derivation of the mesodermal layer largely from endoderm was replaced with a derivation nearly exclusively from ectoderm. While I readily recognize that sessility is accompanied by many changes as compared to related free-living forms, I do not see why the changes outlined above should have occurred. Valuable structures, even to a sessile organism, would need to have been lost and substitutes, no better than the original, had to be invented. This does not seem to me to be the way evolution operates, particularly as judged by other sessile groups. With sessility we see the loss of sensory and

locomotory structures and a nearly universal adoption of small particle or filter feeding as a way of life. We do not, however, see changes in such basic features as their embryology, origin of mesoderm, and organ systems. The degenerative changes suggested by the turbellarian theory are far greater than any parallel, other than the adoption of parasitism, demonstrates to us, and from this it seems impossible to accept the turbellarian theory.

A number of the difficulties I find in accepting the turbellarian theory are associated with differences in the mesoderm of cnidarians and flatworms. If now we examine the medusa theory we see what I believe is the primitive role of the third body layer as it is expressed in the Cnidaria. In planulae, actinulae, and small polyps, there is little need for a third layer. These organisms closely approximate the two-layered condition of a hypothetical gastraea and with their small size and few epithelio-muscular cells need little more than the cementing layer to hold them together. Their body form is maintained by cell turgor. What I am arguing for here is that two cell layers as seen in these larval cnidarians is a truly primitive condition. I find it entirely unacceptable to believe that the evolution of the Metazoa involved an evolution of three cell layers before two and that the Cnidaria have lost that third layer. In view of the tremendous success which animals with a readily recognized mesoderm have had, whether sessile or free-living, the idea that a phylum could afford effectively to discard the mesoderm is difficult to accept and indeed there seem to be no examples available. To go on beyond the primitive condition seen in planulae, the development of the medusoid form required the development of a very special structure, the mesoglea. Perhaps as an elaboration of the cementing layer, or perhaps as a new invention, the development of an elastic filler between the two body layers was necessary before the medusa could have evolved as a pulsating, swimming animal. In general function the mesoglea of the medusa increases buoyancy, gives form, provides a solid substance for the attachment of cells and is pliable and elastic. With increasing size, as seen in the Scyphozoa, more cells become involved in the development and maintenance of the massive mesoglea and even in the scyphozoan polyp there is a well developed mesoglea. The polyp of the Scyphozoa, however, foreshadowing the need for a large gut of its adult form, has become partly dependent on an aqueous skeleton. Water is driven into its coelenteron by cilia and the maintenance of an expanded state is dependent upon the maintenance of a slight pressure of water inside. The septation of the gut of the adult is also foreshadowed in the polyp here, and, as larval features, retractor muscles are developing along the four mesenteries. In the Anthozoa, as in the scyphozoan polyp, the mesoglea plays but a very minor role in the support of the body, but does provide much strength from its tough but pliable nature. Masses of fibers and scattered cells characterize this very tough mesoglea. Thus the mesoglea seems to have developed first in the Hydrozoa as an elastic skeleton against which muscles could operate and then been modified as a tough fibrous support for muscles in polyps. These suggestions give to the mesoglea the character of an early solution to increasing size and an acceptable functional role. They do not demand a change in role as would be necessitated if flatworm mesenchyme were the antecedent of mesoglea. To what extent mesoglea is a homologue of mesoderm is difficult to answer, but that mesoglea is a kind of mesoderm seems obvious.

I mentioned above the septation of the gut of the Scyphozoa. In all classes of the Cnidaria there are examples of guts which are more or less subdivided. Some trachyline medusae show pouched stomachs and the radial canals can be interpreted as a sort of division of the digestive system. These canals, however, are probably better thought of as devices to speed up the movement of nutritive materials to such marginal structures as tentacles. The

the medusa, a pelagic organism, is the primitive form of the Cnidaria.

The relationship of the anterior point of attachment and the posterior mouth in the Cnidaria is also of interest if we look to the flatworms for indications of its origin. Many types of adhesive organs occur in the Turbellaria, some of them at the anterior margin. These anterior structures seem to be used to hold food or in fact to capture it, while more posteriorly located attachment structures may be used to grip the substrate while the worm struggles with some food organism. The only example of a turbellarian flatworm which spends much of its life attached to the substrate which I can find is that of the Temnocephala. These animals attach by a posterior sucker, however, and have an anterior mouth. There may also be a small and anteriorly located adhesive area in certain temnocephalans, but the primary adhesion appears to be the result of posteriorly located structures. In the monogenetic trematodes too, the primary adhesive organ is posteriorly located, and in the rest of the Trematoda the primary adhesive organ is at least posterior to the mouth. The location of the primary attachment structures of the cestodes is not so clear, but if our interpretation of the attachment hooks in the procercoid larva of some pseudophyllidian tapeworms as posterior is correct, then their attachment, too, may at least primitively have been at the posterior end. Granted that there are devices for attachment at the anterior end of some flatworms, none-the-less this group today seems to have settled upon posteriorly located adhesive structures in those forms which spend any considerable portion of their lives as sedentary or attached organisms. From this, as from other arguments, I find it difficult to believe that some archaic flatworm attached at its anterior end and became a cnidarian.

Another discordant feature of the turbellarian theory concerns the fact that, while many sessile animals are hermaphroditic, the sessile Anthozoa usually are not. Quite typically such sessile groups as sponges, barnacles, tunicates, lamellibranchs, and bryozoans are hermaphroditic. Why, one wonders when there seem to be selective forces leading to an association of hermaphroditism and sessility, would the Anthozoa not also show this pattern? This seems all the more curious when we note that the Turbellaria are nearly universally hermaphroditic themselves. Thus we have the picture of a free-living hermaphroditic group giving rise to a dioecious sessile group. This is contradictory indeed. Also contradictory are the hermaphroditic but free-living ctenophores. While I cannot resolve all the contradictions here, I do feel that the dioecious but sessile Anthozoa seem unlikely descendents of hermaphroditic flatworms.

The turbellarian theory also asks us to accept other curious changes. For example as the evolution of the group progressed from flatworms to proper anthozoans the cellular mesenchyme gave way to the much less cellular mesoglea. Complex reproductive organs were replaced by simple epithelial gonads, and all signs of the protonephridial excretory system of the flatworms were lost. The only portion of the nervous system which was retained was the epithelial nerve net. Mesodermally derived muscles also disappeared and striking changes in embryology must have occurred; determinate spiral cleavage gave way to a curious assemblage of patterns of indeterminate cleavage. The derivation of the mesodermal layer largely from endoderm was replaced with a derivation nearly exclusively from ectoderm. While I readily recognize that sessility is accompanied by many changes as compared to related free-living forms, I do not see why the changes outlined above should have occurred. Valuable structures, even to a sessile organism, would need to have been lost and substitutes, no better than the original, had to be invented. This does not seem to me to be the way evolution operates, particularly as judged by other sessile groups. With sessility we see the loss of sensory and

pouching of the gut is of course very obvious in the Scyphozoa and Anthozoa. The turbellarian theory requires these gut pouches to be interpreted as homologues of the pouches of turbellarian guts. If this is so we see some very interesting differences. The subdivisions of cnidarian guts occur by the ingrowth of mesenteries or septal sheets of tissue from the body wall, not as outgrowths of an endodermal sac as in the Turbellaria. These mesenteries also are radially distributed around the long axis of the polyp, not laterally as seen in the flatworms. Also, the pouches of the gut represent the great bulk of anthozoans and extend orally along the pharynx as well as to the very aboral extremity of the body. This is most unflatwormlike since the pouches should be well removed from the pharynx and should be distributed along the gut. The musculature which characterizes the faces of the mesenteries of anthozoan polyps has to be homologized with the muscles of the gut of the Turbellaria. It would indeed be remarkable if in the transition from worm to polyp, these intestinal muscles were transformed into the primary longitudinal muscles of the body. According to the turbellarian theory, the stomodaeum and bilaterality are the best preserved flatworm characters. The stomodaeum is necessary to a polyp as a muscular, food-handling structure and makes possible the separation of incoming and outgoing water currents. It is necessary if a siphonoglyph is to exist. The bilateral development of couples of mesenteries seems more readily referable to the organization of the anthozoan polyp around the functionally very crucial structure, the siphonoglyph, than to any ancestral reminiscence of a bilateral ancestor. In anthozoans having a strongly developed retractor on one face of the mesentery, this organization seems necessary since the opposite face is occupied by radial muscles and a mixture of the two sets would be a very unlikely organization. The bilaterality of the Anthozoa, therefore, is a superficial one, imposed on an ancestrally radial animal as a by-product of its own specialization in developing a highly efficient aqueous skeleton. There seems to be no anlage or homologue of a siphonoglyph or of the mesenteries of anthozoans in the Turbellaria and to point to these or the bilaterality of an anthozoan as a flatworm derivative is unacceptable. The presence of a stomodaeum in both groups seems in part referable to the solution of how to pass food on to an open gut, but solves for the cnidarian the problem of water transport too.

Before I close this paper and by way of summary, I think we might briefly note some points. My contention that the Hydrozoa are the most ancient of the Cnidaria and that the medusoid body form is primitive leads to the conclusion that the Cnidaria are a phylum of radial organisms. The radiality here is a by-product of evolution in the realm of open waters, not a by-product of sessility. Bilaterality as seen in the polyps of the Anthozoa must have evolved as a result of increasing size and the necessity to provide an aqueous skeleton against which the body musculature could operate. Thus the development of the siphonoglyph, the primary incurrent water structure, imposed on the ancestral radiality a superficial bilaterality. This bilaterality is, however, fundamentally different from bilaterality as seen in flatworms where dorso-ventral, left-right, and antero-posterior axes are present. Only the anterior-posterior axis is present in the Cnidaria with the interesting exception perhaps of the zoanthella larva of some zoanthideans. Here we find a recognizable ventral surface with long cilia. Some coral planulae may also show a similar differentiation. However, this phenomenon seems better referable to the creeping activities of these planulae than to their ancestry from any flatworm. The locomotory anterior ends of some planulae also show specialized sensory tufts of cilia similar perhaps to those found in flatworm and other larvae, but no such structures seem to occur in even the simplest adult flatworms. I believe we can better

conclude that the bilaterality suggested in some of the structures of planulae are purely larval inventions, not ancestral reminiscences.

We can also conclude from our earlier discussions that nematocysts may have played a crucial role in the differentiation of the Cnidaria from their forebears. These structures seem most readily derivable from protozoan structures such as cnido-trichocysts. Their occurrence as independent effectors strengthens this argument, and the specialization in the Hydrozoa of nematocysts and behavioral responses for the capture of minute prey argues for an early origin of this group.

The muscular system of cnidarians bears some intriguing similarities to parts of the musculature of turbellarians. Epithelio-muscular cells are known to exist in some of the lower Turbellaria, and Hyman (1951) has suggested that the subepidermal musculature of these organisms is homologous with the muscle cylinder of coelenterates. However, in the simplest turbellarian there is also a complex parenchymal (mesodermal) musculature, while the largest and most complex of the coelenterates, say a large sea anemone, possesses only epidermal musculature. Also, the gut of some turbellarians, if it has a musculature of its own, is sheathed in muscles of mesodermal origin, not with epithelio-muscular cells. If the Cnidaria had been derived from the Turbellaria, it seems curious that all of the mesodermal musculature would have been abandoned and that epithelio-muscular cells of endodermal origin would have been invented to replace the mesodermal muscles there. I would prefer instead to continue to believe that the cnidarian muscles are truly primitive, and that the mesodermal muscles of flatworms represent an evolutionary advance of that group over the Cnidaria.

The general absence of hermaphroditism in the phylum Cnidaria seems also to argue against the flatworms as ancestors and against the Anthozoa as ancestral even more so. Some Anthozoans are her-maphroditic, but this is a truly rare phenomenon in the class. Why more Anthozoa are not hermaphroditic in view of their sessile nature seems a riddle with no good answer.

The presence of two well organized tissue layers in the Hydrozoa can now be taken as a primitive feature, although the mesoglea certainly is indicative of a third tissue layer. The more abundant cells of the mesoglea of Scyphozoa and Anthozoa clearly mark these animals as triploblastic, but the pattern of derivation of this third layer from the endoderm has not yet set in. The nervous system of cnidarians must also be regarded as quite primitive. Its unpolarized and diffuse nature seem much more fitting as an early attempt at an integrated system rather than as a degraded system.

The embryology of the Cnidaria is a curious assemblage of different modes of cleavage and subsequent embryological activities. Essentially all of the phyla higher than the Cnidaria can be characterized by some specific embryological pattern. The cnidarian multivalence here, I think, must point to the origin of the group at a time so ancient that the Metazoa, in their newness, were still experimenting with varying modes of development. Whether this be a good interpretation or not, the fact that the Turbellaria and several higher and major groups of organisms have settled upon spiral cleavage as their way, and the absence of any sign of spiral cleavage in the Cnidaria, must weigh heavily against a flatworm ancestor for the Cnidaria.

Having reviewed the evidence available to me and having used what I hope are slightly new lines of reasoning, I have, for myself, answered the question posed in the introduction of this paper. That is, I conclude that the medusa was the body form of the ancestral cnidarian and that radiality is the primitive symmetry of the phylum. This conclusion accepts the medusa theory and rejects the turbellarian theory. As concomitants to my conclusions, I believe the flatworms as a phylum

must also stem from a "planuloid" but from a line well removed from the Radiata. The Ctenophora have been only lightly touched on in my discussion, but if we accept the recent evidence that this group may possess intrinsic nematocysts, along with other points noted, they must be placed close to the Cnidaria, if not re-established as members of the Coelenterata. The Porifera remain safely ensconced on the phylogenetic tree, one branch below the Cnidaria. I must admit here that some of my arguments can be questioned by the simple device of turning them around, however, this is true only of *some* of them. The *balance of all the evidence* indicates that the Cnidaria occupy the position that the phylogenetic principle, *simple before complex,* dictates; that is, they are pre- not post-turbellarian in origin.

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